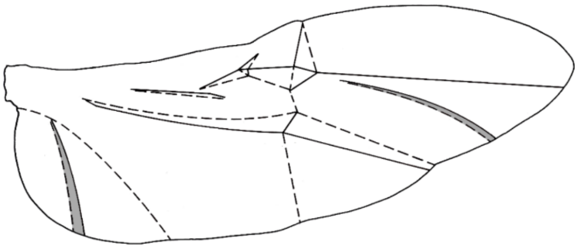
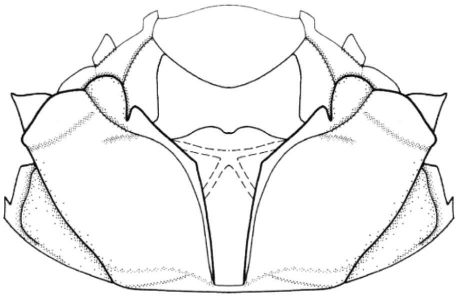
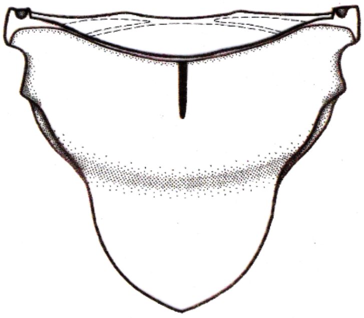
コウチュウ目コガネムシ上科における後翅折り畳み様式および胸部の比較形態学的研究

Comparative morphology of the hind wing folding patterns and thoracic structures (mesonotum and metanotum) in the Scarabaeoidea (Insecta: Coleoptera)







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第 1 章

緒言

コガネムシ上科 Scarabaeoidea は農林業害虫を多く含むコウチュウ目の巨大な一群であり，現在までに 13 科約 35,000 種が確認されている（Scholtz and Grebennikov 2016）．世界的に広く分布することから，様々な生息環境（市街地，森林，海岸，河川，荒野，島嶼部など）に適応し，多様な生態と形態を示すことが知られている（Hanski and Cambefort 1991, Scholtz and Grebennikov 2016, Kaneko and Shigetoh 2019a, b, Kaneko and Taru 2020）．また本グループに含まれる種は，多くの専門家および愛好家の手によって熱心に収集・保管されてきたため，科や亜科といった高次分類群の定義はよく確立されている．しかしその一方で，本グループの高次系統関係に関しては未だに不明確な部分が多く残された状態にあり，とりわけコガネムシ科 Scarabaeidae（コガネムシ上科における最大のグループ）の扱い方は研究者によってさまざまである．伝統的に、コガネムシ科は食糞群と食葉群の二つのグループに大別され，これらをまとめて一つの科として扱ってきた（Browne and Scholtz 1995, 1998, Ahrens and Vogler 2008, Gunter *et al.* 2016, Šípek *et al.* 2016, Mckenna *et al.* 2019）．しかし，近年頻繁に行われている，DNA などの分子データを基に構築された一部の分子系統仮説はこれを支持しておらず，現在のコガネムシ科はヒゲブトハナムグリ科 Glaphyridae やアツバコガネ科 Hybosoridae，アカマダラセンチコガネ科 Ochodaeidae を含む多系統の分類群であるとしている（Smith *et al.* 2006, Ahrens *et al.* 2014, Neita-Moreno *et al.* 2019）．この場合、食糞群と食葉群は異なる二つのクレードに分割され，食葉群はヒゲブトハナムグリ科やアツバコガネ科と近縁となる．分子系統学的手法が進歩し，革新的な系統仮説が多く提唱されてきている反面，それらの仮説を支持する形態学的証拠の探索に関する研究は減少傾向ある．より信憑性の高い系統仮説の構築には分子データと形態データの双方による考察と証明が必要不可欠であることから，新たな系統的に有用な形態形質の発見が求められている．また，詳細な形態情報の蓄積は系統関係の考察だけでなく，その種の生態や行動特性の解明へ向けた基盤研究ともなりえる．

コガネムシ上科を対象とした比較形態学研究は古くから多くの研究者の手によって，様々な部位を対象に検討が行われてきており，触角（Iablokoff-Khnzorian 1977, Meinecke 1975, Bohacz *et al.* 2020），複眼構造（Caveney 1986, Caveney and Scholtz 1993, Gokan *et al.* 1998, Gokan and Meyer-Rochow 2000），口器（Nel and Villiers 1988, Nel and Scholtz 1990），前胸後基節橋（Ritcher 1969a, Hlavac 1975），気門（Ritcher 1969a, b, Galbreath 1976），発音器官（Arrow 1904, Hirschberger 2001），翅脈（Forbes 1926a, Crowson 1967, Iablokoff-Khnzorian 1977, Kukalová-Peck and Lawrence 1993, Fedorenko 2009），翅基関節構造（Browne 1991a, b, 1993, Browne and Scholtz 1994, 1995, 1997, 1998），後胸内腹板（Crowson 1938, Iablokoff-Khnzorian 1977, Pretorius 1998, Pretorius and Scholtz 2001, Pretorius *et al.* 2001），雄交尾器（d’Hotman and Scholtz 1990a, b），雌交尾器（Tanner 1927, Holloway 1972, Lawrence and Newton 1982, López-Guerrero and Halffter 2000），卵巣小器官（Ritcher and Baker 1974），卵表面構造（Sreedevi *et al.* 2015），核型（Smith and Virkki 1978, Yadav and Pillai 1979, Yadav *et al.* 1979），幼虫形態（Böving 1929, Böving and Craighead 1931, Areekul 1957, Lotz 1962, Ritcher 1966, Hinton 1967, Costa *et al.* 1988）

などが挙げられる．これらの形質データは分類群間の類縁性を考察するうえで重要な情報となってきたが，口器形態などの昆虫の生態に直結する形質については，科や亜科レベルの高次系統関係を考察するためには不適であることが近年指摘され始めている（Frings *et al*. 2019）．そのため，新たな形態形質を探索するにあたっては，種の生態や生息環境の影響によって変異の起こりづらい形質を選定することが重要である．

そこで本研究では，コガネムシ科における主要グループ 11 科 132 属を対象に，3 つの新奇的形質（後翅折り畳み様式，中胸背板，後胸背板）の比較形態学的研究を行い，その基本構造を解明するとともに，各分類群を特徴づける形質情報を明らかにし，特徴的な形質状態の進化傾向の推定を行った（第 2 章）．次にこれら第 2 章で得られた成果と，既存の分子系統仮説（Ahrens *et al*. 2014 など）を比較・検証することで，その系統仮説の信憑性の検証ならびに新たな系統類縁関係の探索を行った（第 3 章）．系統的な制約を強く受ける新たな形質の発見は，既存の分子系統仮説の信憑性を証明する評価基準にできる可能性があり，本研究ではこうした形態情報の探索と蓄積を通して，更なる信頼性の高い系統仮説の構築へ貢献することを目指した．

第 2 章

比較形態学的研究

Chapter 2

Comparative morphology

2−1 Hind wing folding patterns

2−1−1

The relationship between body size and hind wing folding patterns in Rutelinae and Cetoniinae (Coleoptera, Scarabaeidae)

Introduction

Wing shape has been studied in various animals including birds, bats, and insects in relation to flight mechanics (e.g., Norberg and Rayner 1987, Dhawan 1991, Dudley 2000, Berwaerts *et al*. 2002, Sane 2003, Schunk *et al*. 2017). Among wing shape characteristics, there are two important indices (wing aspect ratio and wing loading) that affect aerodynamics and consequently may determine the flight performance of animals. Wing aspect ratio describes the ratio of the width (front to back) of the wing to its length, and wing loading is defined as the body weight supported by unit area of the wing. Fast flying species of insects tend to have high aspect ratio (long and narrow) wings, while slow and precise flying species tend to have low aspect ratio (short and broad) wings: this is particularly the case in butterflies (Betts and Wootton 1988, Berwaerts *et al*. 2002). Furthermore, high wing loading, indicating a small wing area relative to body mass, is associated with fast flying, while a low wing loading, representing a large wing area relative to body mass, is related to maneuverability (Betts and Wootton, 1988). These variations in wing shape may be affected by individual species traits and their habitats (Taylor and Merriam 1995, Johansson *et al*. 2009, Navarro *et al*. 2015, Suárez-Tovar and Sarmiento 2016). According to Tocco *et al*. (2019), the variations in hind wing shape are ascribed to differences in diel activity (i.e. diurnal, crepuscular, and nocturnal) between closely related genera in Scarabaeinae. On the other hand, Gibb *et al*. (2016) and Ospina-Garcés *et al*. (2018) note that the hind wing shape of some coleopteran species are little affected by habitat but are phylogenetically constrained. Thus, hind wing shapes are affected by various factors.

Hind wing folding patterns which are designated the combination of wing areas delimited by the folds are one of the important features of, and considered to be affected by variations in hind wing shape. Many functional and comparative morphological studies concerning hind wing folding patterns in Coleoptera have been conducted (Forbes 1926a, b, Haas and Beutel 2001, Fedorenko 2009, Saito *et al*. 2014, 2017, Kaneko and Kojima 2017, Shibuya *et al*. 2017). Kaneko and Kojima (2017) investigated hind wing folding patterns of the phytophagous scarabaeid beetles and suggested that they showed a specific structure within a subfamily or tribe. However, the scarabaeid species that they investigated did not have large differences in body size within a subfamily or tribe. Hence, it remains to be confirmed whether these specific folding patterns are independent of body size. However, the relationship between body size and folding patterns of hind wings has not been investigated in the scarabaeids as well as any other insect taxa.

This study examines whether body size affects folding patterns of hind wings in the scarabaeids. For this, two subfamilies (Rutelinae and Cetoniinae) were chosen because the species within these subfamilies vary in body size, have different flight behaviors (flight with elytra opened or closed), and are easily observed.

Materials and methods

In this study, I selected five species of Rutelinae and five species of Cetoniinae that are easily obtained in Japan and whose ecology is known to some extent. These species, their diel activities and habitats are as follows: Rutelinae —*Phyllopertha diversa* Waterhouse (diurnal, grassland), *Anomala schoenfeldti* Ohaus (nocturnal, sandy beach), *Mimela flavilabris* (Waterhouse) (diurnal, grassland), *Mimela costata* (Hope) (crepuscular, forest), and *Chrysophora chrysochlora* (Latreille) (diurnal, forest)— and Cetoniinae —*Gametis forticula* (Janson) (diurnal, grassland), *Anthracophora rusticola* Burmeister (diurnal, forest), *Protaetia orientalis submarmorea* (Burmeister) (diurnal, forest), *Rhomborhina polita* Waterhouse (nocturnal, forest), and *Mecynorhina torquata* (Drury) (diurnal, forest). Scientific names follow the recent catalogue of Bezděk *et al.* (2016) and Krajcik (2012). A total of ten specimens of each species involving five males and five females except for *P. diversa* (seven males and three females) were observed. Most of the examined specimens were collected by the first author, and some of specimens were provided from Tokyo University of Agriculture, Ehime University Museum and Research Institute of Evolutionary Biology in Japan.

All dissections were carried out on dried specimens. In order to relax them they were placed in 50% ethanol for a few minutes, after which the right hind wing was detached with fine forceps from the anterior and posterior notal wing process of the metanotum. Hind wing folding patterns were observed in 50% ethanol, and the folding patterns thus obtained were verified on a polypropylene sheet model replicating the hind wing of scarabaeid beetles (Fig. 1). The observed hind wing was unfolded on a slide glass and dried out. The dried hind wing was adhered to another slide glass using a water-based wood glue (Bondo®, Konishi, Japan) solution (wood glue : distilled water = 1:1).

Specific parts of the body and a hind wing were measured using the software ImageJ ver. 1.50i (Rasband, 1997−2012): 1) body length (Bl: from clypeal apex to pygidial apex) and width (Bw: width from shoulder to shoulder); 2) elytral length (El) and width (Ew); 3) hind wing length (Hl: from costa-subcostal base to hind wing apex) and width (Hw: from costa-subcostal base to edge of the folding line of the jugal area [J] and wedge area [Wd]); 4) length from costa-subcostal base to apical joint (Lba) and length from apical joint to wing apex (Laa); 5) hind wing area (Ha) (Fig. 2A–B).

To examine the relationship between body size and hind wing shape, correlations of hind wing aspect ratio and hind wing area to the body length were tested. For these tests, the mean values in males and females of each species were calculated. The correlation between the body length and hind wing aspect ratio was analyzed separately in males and females within subfamilies using these mean values by Spearman's rank correlation coefficient. The correlation between the body length and hind wing area was also analyzed in males and females by the linear regression analysis on the double-logarithmic scales. Then, the regression coefficients, i.e. the slopes of regression lines, were compared between sexes and between subfamilies by the analysis of covariance (ANCOVA). In addition, to compare the Hl/Bl and Lba/Laa ratios between sexes within a species and between species within a subfamily, Kruskal-Wallis tests were carried out. These statistical analyses were performed using the software JMP 9.0 (SAS Institute, 2010). The terminology of hind wing folding patterns mainly followed Fedorenko (2009), although the study of Kaneko and Kojima (2017) was also consulted (Fig. 2C). In this paper, another fold, which divides the main area into subareas (shown in gray in Fig. 2C), was added. Drawings were made with the aid of an Olympus SZX9 microscope and a Leica M165C digital microscope.

Results

Difference in aspect ratio of body size between species

Body size was quite different between species, some species being 2-fold body length of others (Table 1). The aspect ratios of body size (Bl/Bw) and elytra(El/Ew) varied independent of body size between species within the subfamilies (Table 2). These results show that the aspect ratio of the body and elytra, which determine an approximate body plan, are not much affected by variation in body size.

Difference in hind wing morphology between species

Hind wing morphology, especially the aspect ratio and hind wing area, seems to be affected by body size (Tables 1–2). Accordingly, the relationship between the body length and the hind wing aspect ratio or hind wing area was analyzed. The Spearman's rank correlation coefficients indicated that the hind wing aspect ratios became significantly smaller as the body length increased in males ($P = 0.0374$) and females ($P<0.0001$) of Cetoniinae (Fig. 3B), but the aspect ratios were not significantly correlated with the body length in both sexes ($P>0.5$) of Rutelinae (Fig. 3A). The linear regression analyses showed that the hind wing area was significantly correlated with the body length in both sexes in both subfamilies (Table 3). The regression coefficients were not significantly different between sexes (ANCOVA, Rutelinae: $t = 0.10$, $P>0.9$, Cetoniinae: $t = 1.26$, $P>0.2$) and between subfamilies ($t = 0.63$, $P>0.5$). Accordingly, the liner regression using the data of males and females in both subfamilies was calculated (Fig. 3C); the hind wing area became significantly larger as the body length increased ($r^2 = 0.986$, $P < 0.0001$).

Of ratios between body and wing parts, three ratios, i.e. Hl/Bl, El/Lba, and Lba/Laa, appeared to be similar between species within subfamilies (Table 2). However, most of these ratios were statistically different between species (Table 4). The ratios of El/Lba and Lba/Laa significantly differed between species in males and females within subfamilies. For the ratio of Hl/Bl, however, the results differed between the subfamilies; the Hl/Bl was significantly different between species in both sexes in Rutelinae, but it was not significantly different in Cetoniinae (Table 4).

Difference in hind wing folding patterns between species

Hind wing folding patterns of the five species within each subfamily were similar to each other independent of body size, although wing shape was affected by body size (Figs. 4A–J). The hind wing folding pattern of each subfamily was mainly characterized by the shape of the stigmatal (S), intercubital distal (Id), and Wd areas. Rutelinae exhibited a rectangular S area, triangle Id area and narrow Wd area, while Cetoniinae showed a S area expanded towards the tip, narrow rectangular Id area and wide Wd area. In Cetoniinae, some species had a small folding section (shown in gray in Fig. 4) at the jugal area (J), but the other species did not have this section. Presence or absence of this section did not depend on the body size. The medial (M) and principal (Pr) areas were larger in Rutelinae than in Cetoniinae, while the shapes of outer anal area (Oa) of two subfamilies were similar to each other.

Discussion

This study examined the hind wing morphology of scarabaeid species with different body sizes in two subfamilies (Rutelinae and Cetoniinae) and analyzed the relationships between body size and hind wing shape or folding patterns. The analyses showed that the aspect ratio of the hind wing was usually negatively correlated, and the hind wing area was positively correlated with body size, but hind wing folding patterns were not affected by body size and hind wing shape.

In larger species, to support heavier body mass during flight, larger hind wing areas should be required. To increase hind wing area, both length and width should be increased. However, increases in hind wing length is restricted because the hind wing needs to be foldable and tucked under the elytra. Indeed, the Lba was shorter than the elytra (El/Lba > 1) in all examined species (Table 2). Accordingly, it is predicted that the hind wing width increases at a larger rate than the hind wing length as the body length becomes larger. This is the case with Cetoniinae in which the hind wing aspect ratio (Hl/Hw) was negatively correlated with body length (Fig. 3B) and the ratio of hind wing length to body length (Hl/Bl) tended to be constant (Tables 2, 4). In Rutelinae, however, the hind wing aspect ratio was not significantly correlated with the body length (Fig. 3A). In Fig. 3A, the plots of *A. schoenfeldti* apparently deviated from a tendency in relationship between the body length and hind wing aspect ratio in other species. *A. schoenfeldti* showed a much lower hind wing aspect ratio for the body length compared with other Rutelinae species (Fig. 3A, Table 2). This lower aspect ratio may be associated with its specific biology. This species prefers sandy environments such as coast and lawn and occurs locally. Thus, this species inhabits a restricted area (Wada 2012). In such circumstances, *A. schoenfeldti* may not need fast flying ability, which leads to a low hind wing aspect ratio (Betts and Wootton 1988, Berwaerts *et al*. 2002).

The Lba/Laa ratio significantly differed between species within Rutelinae and Cetoniinae. In general, it has been considered that the wing shape is affected by environmental factors and behavioral traits of each species (Dempster 1991, Taylor and Merrian 1995, Johansson *et al*. 2009, Hassall 2015, Torres *et al*. 2015, Chazot *et al*. 2016, Suárez-Tovar and Sarmiento 2016). In Rutelinae and Cetoniinae, the variation in Lba/Laa might be also associated with differences in their habitats or behavioral traits. There are differences among these species in habitats (forest, grassland, and seaside), diel activities (diurnal, crepuscular, and nocturnal). These factors are likely to influence the hind wing shape of Rutelinae and Cetoniinae to some extent.

The hind wing folding patterns were similar within each subfamily although the wing shape differed between species (Fig. 4). The S, Id, Wd, Pr, and M areas showed stable shapes within each subfamily. This may indicate that these folding areas are likely to be important for identifying the subfamilies and analyzing the phylogenetic relationships between subfamilies or higher-level taxa in Scarabaeidae. In contrast, the shape of the J area was variable between species, as noted by Fedorenko (2009) and Kaneko and Kojima (2017). As an extreme example, the J area is completely lost in Valginae (Fedorenko 2009, Kaneko and Kojima 2017). In addition, the variations in the J area are associated with diel activity period (diurnal, crepuscular, or nocturnal) in dung beetles (Scarabaeinae; Tocco *et al*. 2019). Thus, the J area is variable and this variation is likely to be affected by various factors such as habitat, activity period, and body size. The additional folds appearing in J and Pr areas are inconsistent in subfamily, and Kaneko and Kojima (2017) mentions that these folds are unstable features between tribes. The J area and the additional folds are not significant for identifying phylogenetic relationships, but may be associated with behavioral functions.

Many researchers suggested that wing shape is closely related to environmental factors such as habitat vegetation and landscape, or behavioral traits of insects (e.g., butterflies and moths [Dempster 1991, Torres *et al*. 2015, Chazot *et al*. 2016)]; odonates [Taylor and Merrian 1995, Johansson *et al*. 2009, Hassall 2015, Suárez-Tovar and Sarmiento 2016]. The present study also suggests that the hind wing shape is affected by environmental factors. On the other hand, the folding patterns are similar within each of subfamilies Rutelinae and Cetoniinae. This result indicates that the folding patterns may be one of the phylogenetically steady traits. However, there is little evidence to support this hypothesis. Thus, it will be necessary to study more scarabaeid taxa including the coprophagous group in the future. If this hypothesis is true, hind wing folding patterns are one of important characteristic that can help determine phylogenetic relationships in higher-level taxa in Scarabaeidae.

Appendix

Specimens examined

Rutelinae

Mimela flavilabris **(Waterhouse, 1875)**

4♂1♀., Mt. Mikuniyama, Kanagawa Pref., Japan, 22. VII. 2012; 3♀., Tonemachi, Ohara, Numata-shi, Gunma Pref., Japan, 9. VI. 2016; 1♀., Tone-gun, Hotakabokujyôkyanpujyô, Gunma Pref., Japan, 26. VII. 2014.

Anomala schoenfeldti **Ohaus, 1915**

5♂5♀., Tsujidôkaihinkôen, Fujisawa-shi, Kanagawa Pref., Japan, 29. VI. 2014.

Chrysophora chrysochlora **(Latreille, 1811)**

3♂2♀., Macas (Oriente), Ecuador, III. 1963; 1 ♀., Tena, Ecuador, III. 2000; 1 ♂., San José de Alluriquín, Ecuador, VI. 2000; 1♂2♀., Puerto Misahuallí, Ecuador, VI. 2001.

Mimela costata **(Hope, 1839)**

3♂♂., Ichinose, Minobu-chô, Kyoma-gun, Yamanashi Pref., Japan, 6. VII. 2013; 2♂♂5♀♀., Mt. Maruyama, Yokose-chô, Chichibu-gun, Saitama Pref., Japan, 18. VIII. 2014.

Phyllopertha diversa **Waterhouse, 1875**

1♀., Kokuzô-san, Satoshô-cho, Asaguchi-gun, Okayama Pref., Japan, 11. V. 2006; 2♀♀., Tokyo University of Agriculture, Atsugi-shi, Kanagawa Pref., Japan, 4. VII. 2017; 7♂♂., Chūzenjiko, Chūgūshi, Nikkô-shi, Tochigi Pref., Japan, 17. VI. 2019.

Cetoniinae

Anthracophora rusticola **Burmeister, 1842**

3♂♂2♀♀., Hosaka-chô, Nirasaki-shi, Yamanashi Pref., Japan, 30. VIII. 1986; 1♀., Mt. Enkai-san, Isogo-ku, Kanagawa Pref., Japan, 28. VIII. 2007; 2♂1♀., Mt. Enkai-san, Isogo-ku, Kanagawa Pref., Japan, 8. IX. 2014; 1♂., Mt. Enkai-san, Isogo-ku, Kanagawa Pref., Japan, 8. IX. 2014; 1♀., Mt. Enkai-san, Isogo-ku, Kanagawa Pref., Japan, 14. VIII. 2015.

Gametis forticula **(Janson, 1881)**

5♂♂5♀♀., Mt. Kuburadake, Yonaguni-jima Is., Okinawa Pref., Japan, VI. 2014.

Mecynorhina torquata **(Drury, 1782)**

4♀4♂., Zaire, South Africa, V. 1977; 1♀., Northern Kivu, Zaire, South Africa, X. 1997; 1♂., Northern Kivu, Zaire, South Africa, IV. 2000.

Protaetia **(*Calopotosia*)** ***orientalis submarmorea*** **(Burmeister, 1842)**

1♀., Kokuzô-san, Satoshô-cho, Asaguchi-gun, Okayama Pref., Japan, 17. VIII. 2009; 2♀♀., Funako, Atsugi-shi, Kanagawa Pref., Japan, 23. VI. 2007; 3♂♂., Tokyo University of Agriculture, Atsugi-shi, Kanagawa Pref., Japan, 9. VII. 2012; 1♂., Heiwajima, Ota-ku, Tokyo, Japan, 16. VIII. 2015; 1♂., Heiwajima, Ota-ku, Tokyo, Japan, 21. VIII. 2015; 2♀♀., Heiwajima, Ota-ku, Tokyo, Japan, 21. VIII. 2012.

Rhomborhina polita **Waterhouse, 1875**

2♀., Mt. Terayama, Chichibu-shi, Saitama Pref., Japan, VII. 2012; 1♂., Funaka, Atsugi-shi, Kanagawa Pref., Japan, 20. VII. 2013; 2♀♀., Anayama-chô, Nirasaki-shi, Yamanashi Pref., Japan, 5. VIII. 2013; 1♀., Mt. Takao-san, Takaomachi, Hachiôji-shi, Tokyo, Japan, 14. VIII. 2013; 4♂., Mt. Enkai-san, Isogo-ku, Kanagawa Pref., Japan, 10. IX. 2014.

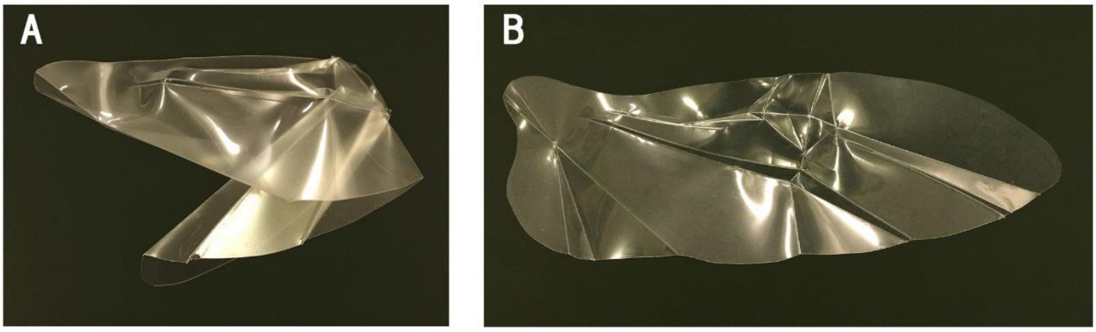


Figure 1. Polypropylene sheet model of the hind wing of *Mimela costata.*
A, folded state **B**, unfolded state.

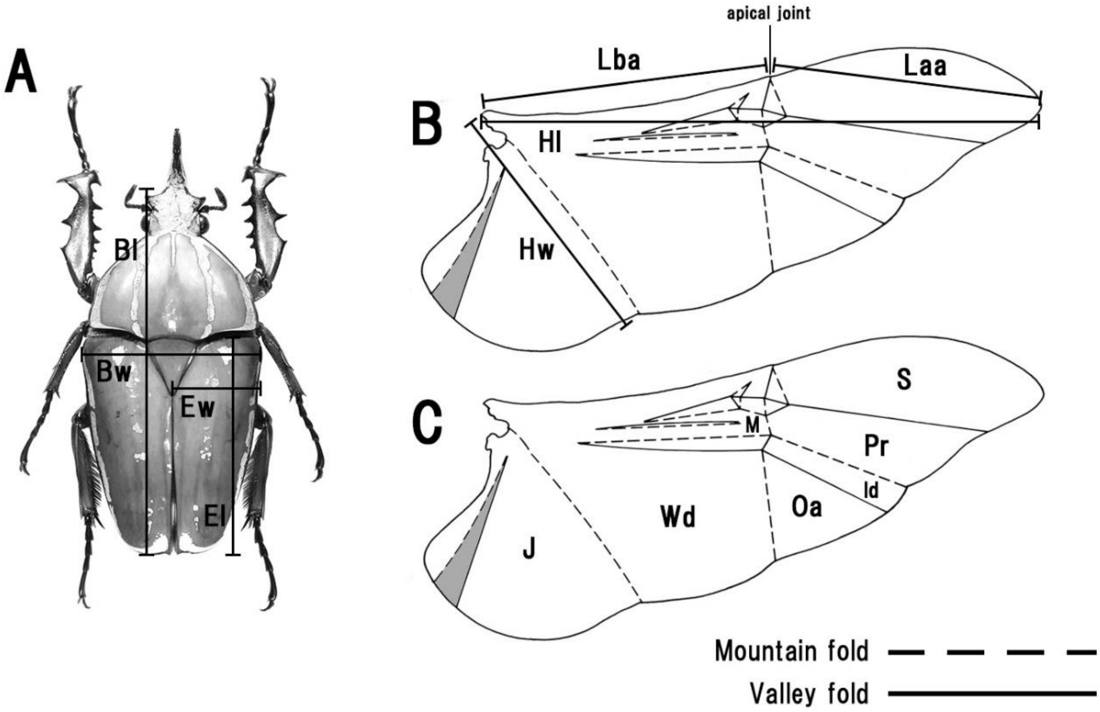


Figure 2. Measured parts and their abbreviations. **A** measured parts of the body and elytra, **B** measured parts of hind wing, **C** main regions of the hind wing folding area: Oa = Outer anal, J = Jugal, M = Medial, Id = Intercubital distal, Pr = Principal, S = Stigmatal, Wd = Wedge. Additional folds that subdivide the area are shown in gray.

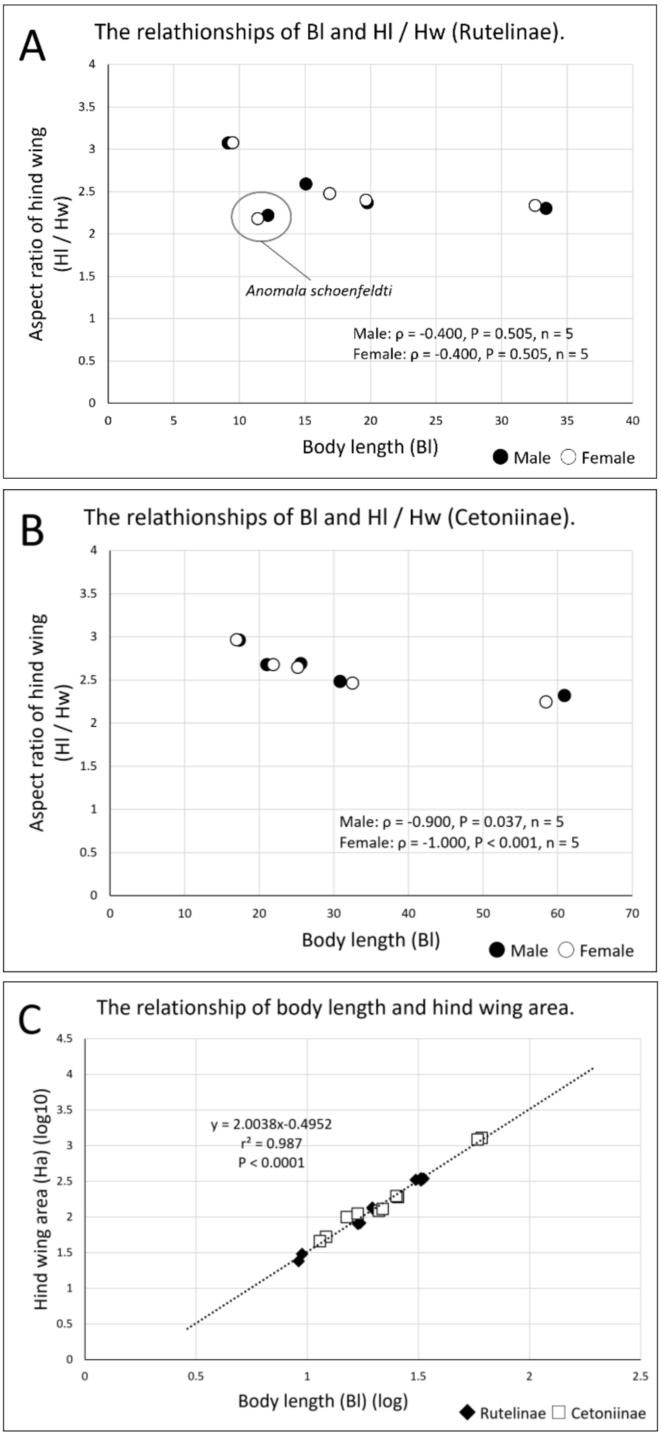


Figure 3. Results of statistical analyses. **A−B** the relationships between body length and hind wing aspect ratio tested by the Spearman's rank correlation coefficient for each subfamily, **C** the relationship between body length and hind wing area examined by the liner regression analysis including ten species of Rutelinae and Cetoniinae, and each plot represents the mean value of male or female in each species.

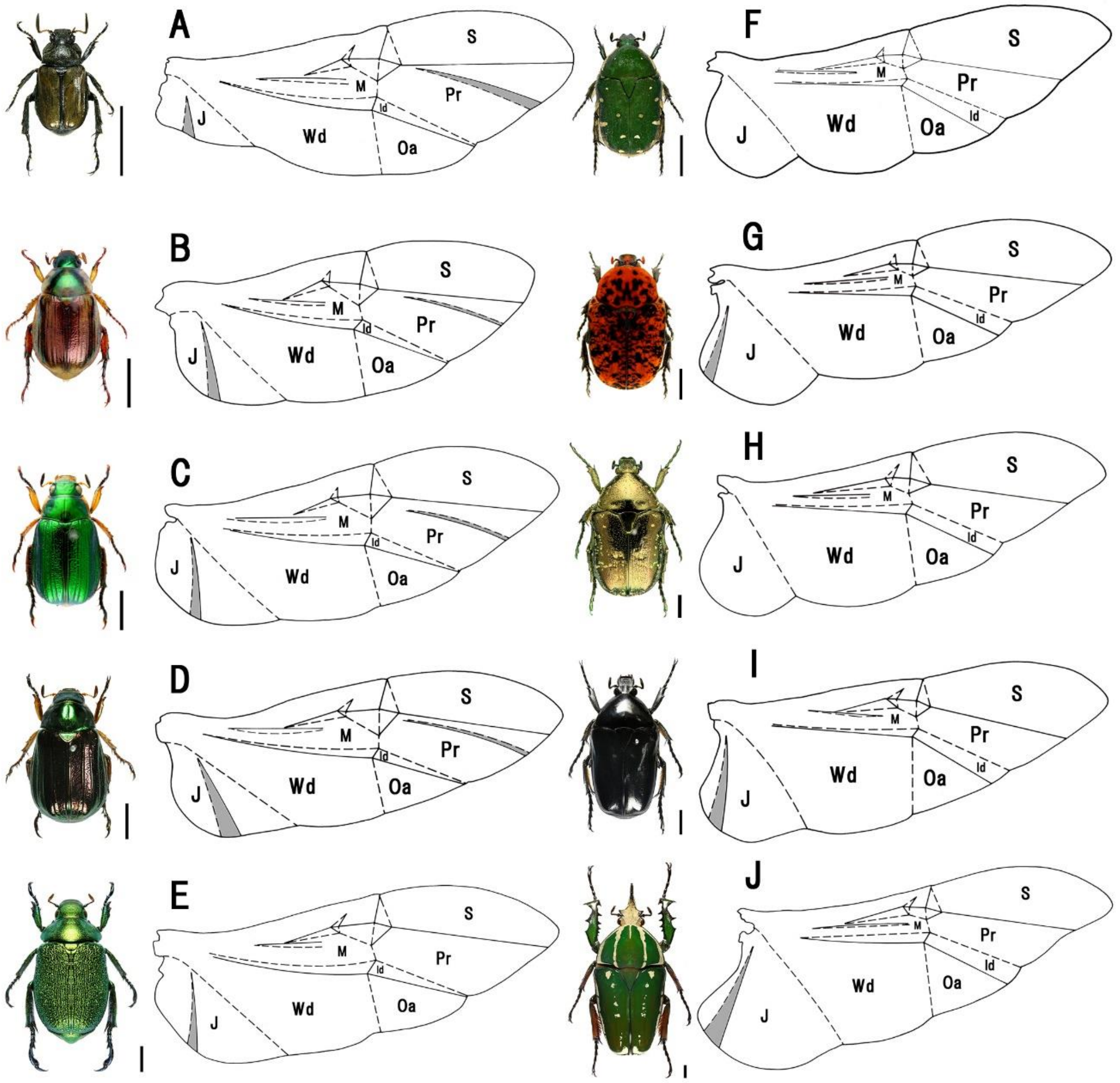


Figure 4. Hind wing folding patterns and habitus of six species of Rutelinae (**A–E**) and Cetoniinae (**F–J**).

A *Phyllopertha diversa* Waterhouse, **B** *Anomala schoenfeldti* Ohaus, **C** *Mimela flavilabris* (Waterhouse), **D** *Mimela costata* (Hope), **E** *Chrysophora chrysochlora* (Latreille), **F** *Gametis forticula* (Janson), **G** *Anthracophora rusticola* Burmeister, **H** *Protaetia orientalis submarmorea* (Burmeister), **I** *Rhomborhina polita* Waterhouse, **J** *Mecynorhina torquata* (Drury). Scale bars represent 5 mm. Additional folds that subdivide the area are shown in gray.

Table 1. Measurements (mean ± SE) of body and hind wings in ten species of Rutelinae and Cetoniinae. n = 10 for each species. For abbreviations, see text.

(n= 10)	species	Bl (mm)	Bw (mm)	El (mm)	Ew (mm)	Hl (mm)	Lba (mm)	Laa (mm)	Hw (mm)	Ha (mm^2)
Rutelinae	***Phyllopertha diversa***	9.24±0.12	4.28±0.12	5.33±0.12	2.15±0.06	9.75±0.11	5.32±0.12	4.43±0.22	3.17±0.08	26.03±1.20
	Anomala schoenfeldti	11.78±0.23	5.25±0.11	7.4±0.14	2.63±0.05	12.75±0.22	7.07±0.13	5.68±0.09	5.8±0.1	49.3±1.58
	Mimela flavilabris	15.97±0.37	6.52±0.12	10.36±0.17	3.26±0.06	18.86±0.14	10.07±0.1	8.79±0.23	7.46±0.17	105.62±2.67
	Mimela costata	19.71±0.25	8.92±0.2	12.58±0.18	4.46±0.1	21.84±0.16	11.94±0.08	9.9±0.21	9.17±0.08	132.96±3.09
	Chrysophora chrysochlora	32.98±0.55	15.45±0.24	20.79±0.35	7.72±0.12	34.85±0.52	19.20±0.29	15.65±0.24	15.03±0.29	348.26±11.89
Cetoniinae	***Gametis forticula***	17.13±0.26	8.97±0.14	10.53±0.15	4.48±0.07	17.27±0.21	8.78±0.11	8.50±0.11	5.83±0.09	81.46±2.2
	Anthracophora rusticola	21.44±0.32	11.44±0.19	12.86±0.18	5.75±0.11	20.79±0.35	10.7±0.16	10.09±0.19	7.77±0.14	125.94±4.18
	Protaetia orientalis	25.38±0.64	13.26±0.26	15.5±0.26	6.63±0.13	25.39±0.59	12.84±0.32	12.55±0.27	9.52±0.24	193.59±8.9
	Rhomborhina polita	31.66±0.52	15.25±0.24	19.94±0.24	7.62±0.12	32.82±0.19	17.16±0.18	15.66±0.35	13.26±0.16	328.01±6.42
	Mecynorhina torquata	59.68±1.45	29.30±0.78	34.86±0.79	14.64±0.4	61.89±0.66	32.22±0.59	29.67±1.23	27.11±0.49	1256.86±57.81

Table 2. Ratio of each measured body and wing part (mean ± SE) in ten species of Rutelinae and Cetoniinae. n = 10 for each species. For abbreviations, see text.

(n= 10)	species	Bl / Bw	El / Ew	Hl / Bl	Hl / El	El / Lba	Ha / Bl	Hl / Hw	Lba / Laa
Rutelinae	***Phyllopertha diversa***	2.17±0.04	2.49±0.03	1.05±0.02	1.83±0.03	1.00±0.02	2.81±0.11	3.07±0.03	1.20±0.01
	Anomala schoenfeldti	2.24±0.02	2.82±0.02	1.08±0.01	1.72±0.01	1.05±0.01	4.17±0.08	2.20±0.002	1.24±0.01
	Mimela flavilabris	2.45±0.02	3.18±0.02	1.18±0.01	1.82±0.01	1.03±0.01	6.62±0.06	2.53±0.03	1.15±0.01
	Mimela costata	2.22±0.05	2.83±0.04	1.11±0.02	1.74±0.01	1.05±0.01	6.75±0.16	2.38±0.01	1.21±0.01
	Chrysophora chrysochlora	2.14±0.04	2.69±0.04	1.06±0.01	1.68±0.01	1.08±0.01	10.48±0.24	2.32±0.01	1.23±0.01
Cetoniinae	***Gametis forticula***	1.91±0.02	2.35±0.01	1.01±0.01	1.64±0.01	1.20±0.01	4.75±0.09	2.96±0.02	1.03±0.01
	Anthracophora rusticola	1.87±0.01	2.24±0.02	0.97±0.01	1.62±0.01	1.20±0.01	5.87±0.16	2.68±0.02	1.06±0.01
	Protaetia orientalis	1.92±0.01	2.34±0.01	1.00±0.01	1.58±0.02	1.21±0.02	7.61±0.16	2.57±0.01	1.02±0.01
	Rhomborhina polita	2.08±0.02	2.62±0.03	1.04±0.02	1.65±0.02	1.16±0.01	10.38±0.25	2.48±0.01	1.1±0.01
	Mecynorhina torquata	2.04±0.02	2.38±0.02	1.04±0.01	1.78±0.02	1.08±0.01	21.00±0.6	2.28±0.02	1.09±0.01

Table 3. Results of the liner regression analysis of the hind wing area (log) on the body length (log).

Subfamily	Sex	*a*	*b*	r^2	*F*	*P*
Rutelinae	Male	-0.462	1.997	0.974	113.8	0.0018
	Female	-0.469	1.980	0.992	393.0	0.0003
Cetoniinae	Male	-0.805	2.201	0.997	859.4	<0.0001
	Female	-0.460	1.988	0.986	213.8	0.0007
Rutelinae and Cetoniinae	Male + Female	-0.490	2.002	0.986	1233.2	<0.0001

Table 4. The results of Kruskal-Wallis test of each ratio.

Ratios	Subfamily	Sex	χ^2	*df*	*n*	*P*
Hl / Bl	Rutelinae	Male	14.8	4	27	0.0051
		Female	13.1	4	23	0.0108
	Cetoniinae	Male	8.1	4	25	0.0868
		Female	8.8	4	25	0.672
El / Lba	Rutelinae	Male	11.0	4	27	0.0267
		Female	13.4	4	23	0.0096
	Cetoniinae	Male	18.0	4	25	0.0012
		Female	11.9	4	25	0.0182
Lba / Laa	Rutelinae	Male	15.2	4	27	0.0043
		Female	13.2	4	23	0.0104
	Cetoniinae	Male	21.6	4	25	0.0002
		Female	9.7	4	25	0.0453

2−1−2

Comparative morphology of the hind wing folding patterns in the Scarabaeoidea (Coleoptera)

Introduction

The coleopteran wing has long attracted the attention of numerous researchers. Several detailed studies on wing venation (Crowson 1967, Iablokoff-Khnzorian 1977, Kukalova-Peck and Lawrence 1993, Browne and Scholtz 1999, Fedorenko 2009, Lawrence *et al*. 2011), wing articulation (Kukalova-Peck and Lawrence 1993, Browne and Scholtz 1995, Browne and Scholtz 1999, Sugimoto *et al*. 2018), and functional morphology (Hass and Wootton 1996, Haas and Beutel 2001, Le *et al*. 2013, Truong *et al*. 2014, Saito *et al*. 2014, 2017, Shibuya *et al*. 2017) have been conducted. In the superfamily Scarabaeoidea, Browne and Scholtz (1994, 1995, 1997−1999) conducted detailed studies on wing characteristics, primarily useful for elucidating higher classification. In contrast, there have been relatively few comparative studies focusing on hind wing folding pattern, except in some researches as Forbes (1924, 1962a, b), Schneider (1978), Fedorenko (2009), and Kaneko and Kojima (2017). Forbes (1926a, b) and Fedorenko (2009) investigated several coleopteran species and suggested that the folding pattern characterizes higher taxa such as families and subfamilies, and is a valuable trait for considering the phylogenetic relationships between higher taxa. In addition, Kaneko and Kojima (2017), who focused on the phytophagous group of Scarabaeidae, suggested that the folding pattern in the Scarabaeidae is a useful trait demonstrating particular difference at the subfamily level, and revealed that it shows similar characteristics among closely related groups. Consequently, the hind wing folding pattern was also considered an important trait, significantly contributing to the elucidation of higher classification and phylogenetic relationships of Scarabaeoidea, similar to wing venations and articulations. However, the species used in the aforementioned studies are relatively few and the data are inadequate to characterize each group. Kaneko and Kojima (2017) conducted a comparative study based on the multiple phytophagous groups, but there were no observations regarding the coprophagous Scarabaeidae group and other families of Scarabaeoidea, rendering the study incomplete in some ways. In order to construct a more accurate phylogenetic hypothesis by comparison with phylogenetic analyses based on molecular data, which has been frequently performed in recent years, it is vital to find novel morphological traits to augment the data.

In this study, I examined in detail the hind wing folding pattern of 130 genera from 11 families within the superfamily Scarabaeoidea. Although the comparatively few representative species examined are inadequate and may thus not provide a completely reliable basis on which to discuss far-reaching phylogenetic and systematic implications, it has, nevertheless, been possible to identify similarities between the different families and subfamilies.

Material and methods

Preparation of specimens

All dissections were carried out on dried specimens. In order to relax them they were placed in 50% ethanol for a few minutes, after which the right hind wing was detached with fine forceps from the anterior and posterior notal wing process of the metanotum. Hind wing folding patterns were observed in 50% ethanol, and the folding patterns thus obtained were verified on a polypropylene sheet model replicating the hind wing of scarabaeid beetles. The observed hind wing was unfolded on a slide glass and dried out. The dried hind wing was adhered to another slide glass using a water-based wood glue (Bondo®, Konishi, Japan) solution (wood glue : distilled water = 1:1).

Terminology

The main morphological terminology for the hind wing folding patterns of Scarabaeoidea follows Fedorenko (2009) and Kaneko and Kojima (2017).

Hind wing folding patterns are designated as the combination of wing areas delimited by folds. The hindwing folding patterns in the superfamily Scarabaeoidea are usually composed of 17 or 19 main areas (Fig. 1). The areas are termed as follows: Aa = Antero-apical, An = Antero medial, Ce = Central, Cu = Cubital, Dp = Distal pivot, Fc = First costal, Oa = Outer anal, Im = Inside medial, J = Jugal, M = Medial, Wd = Wedge, Id = Intercubital distal, Pa = Postero-apical, Pp1 = Proximal pivot 1, Pp2 = Proximal pivot 2, Pr = Principal, S = Stigmatal, Sc = Second costal, Uf = Under first costal. Some of these areas may have an additional fold that divides the main area into subareas and some accessory or irregular folds. Of these, accessory or irregular folds are sometimes omitted as unnecessary details. The folding lines are indicated by solid and broken lines. The solid and broken lines indicate a valley and a mountain folds, respectively. Furthermore, all folding areas have two distinguishable regions [from the base to the apical joint (Fba) and from the apical joint to the apex (Faa)] divided by a continuous folding line between the Se-Dp, An-Ce, M-Pr, Cu-Id, and Wd-Oa extending from the apical joint. The apical joint is the cardinal point of folding to tuck the hind wing under the elytra.

Specimens studied

130 genera belonging to 11 families of superfamily Scarabaeoidea, which is Bolboceratidae, Geotrupidae, Glaresidae, Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Passalidae, Pleocomidae, Trogidae and Scarabaeidae, were examined in this study. Two species belonging to two genera of subfamily Bolboceratinae were selected in the family Bolboceratidae. Five species belonging to three genera of two subfamilies (Geotrupinae and Lethrinae) were selected in the family Geotrupidae. One species belonging to genus *Glaresis* Erichson, 1848 was selected in the family Glaresidae. Four species belonging to three genera were selected in the family Glaphyridae. Three species belonging to three genera of two subfamilies (Ceratocanthinae and Hybosorinae) were selected in the family Hybosoridae. 11 species belonging to 10 genera of four subfamilies (Aesalinae, Syndesinae, Lamprinae and Lucaninae) were selected in the family Lucanidae. Three species belonging to three genera were selected in the family Ochodaeidae. Three species belonging to three genera of two subfamilies (Aulacocyclinae and Macrolinae) were selected in the family Passalidae. One species belonging to genus *Pleocoma* LeConte, 1856 was selected in the family Pleocomidae. Three species belonging to three genera were selected in the family Trogidae. 134 species belonging to 101 genera of 14 subfamilies (Aegialiinae, Aphodiinae, Chironinae, Scarabaeinae, Aclopinae, Cetoniinae, Dynamopodinae, Dynastinae, Euchirinae, Melolonthinae, Orphninae, Rutelinae, Trichiinae and Valginae) were selected in the family Scarabaeidae (Table. 1).

Results

The hind wing folding pattern of the Scarabaeoidea is consists of up to 21 areas and is characterized by area's shape and development. Of the areas observed in the folding prototype presented in Fedorenko (2009), K (radial), N (intercubital proximal), F (anal), and W (oblong) tended to disappear in the species of Scarabaeoidea. These folding patterns can be formulated as the anterior part of the apical membrane being transformed into a stiffened lobe deflecting at the apical joint while remaining non-folded transversely, as a result, the wing folds like a jackknife.

Bolboceratidae (Figs. 2–3)

The hind wing folding patterns of the Bolboceratidae consist of 18 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp, An, Sc, Ce, Dp, Id, Pr, Pa, S, and Aa.

The ratio of Fba to Faa in the genera *Bolbocerosoma* and *Bolbochromus* is approximately 1.4:1 (Fig. 2), while the genus *Bolbelasmus* is about 1:1.1 (Fig. 3). J is mostly well-developed and is trapezoidal, but in the Bolbelasmus, J's development is weak and lobe-shaped. Wd is elongated trapezoidal and occupies approximately half the width of Fba. Oa has a narrow triangular shape. M occupies approximately one-fifth the width of the Fba. Usually, Pp is elongated and single triangular-shaped, but the genus *Bolbelasmus* presents two small triangular sectors Pp1 and Pp2. An is triangular, but in the genus *Bolbelasmus* (Fig. 3) this area is represented by a quadrangular shape. Dp is triangular shaped. Id is parallel-shaped, but in the *Bolbelasmus* (Fig. 3) this area is represented by a tapered shape. Pr is hexagonal shaped because of the presence of Pa and occupies approximately one-third of the area of Faa. S and Aa have a rectangular shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea. The Pp and An areas in the genus *Bolbocerosoma* and *Bolbochromus* show unique characteristics in Scarabaeoidea.

Geotrupidae (Fig. 4)

The hind wing folding patterns of the Geotrupidae is comprises 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.4–1.6:1. J is well-developed and is semicircular. Wd is elongated trapezoidal and occupies approximately half the width of Fba. Oa is triangular in shape. M occupies approximately one-fifth of the width of Fba. Pp consists of two small triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangular in shape. Id is parallel-shaped. Pr is pentagonal. S is rectangular.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea. In the subfamily Lethrinae, the hind wing was completely lost, so the hind wing folding patterns could not be observed.

Glaresidae (Fig. 5)

The hind wing folding patterns of the Glaresidae is consists of 21 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr (Pr1 and Pr2), S (S1 and S2), and Aa (Aa1 and Aa2).

The ratio of Fba to Faa is approximately 1:1. J is very narrow and elongated. Wd is trapezoidal with a deep notch, occupying approximately half the width of Fba. Oa is triangular and is divided into two sectors by an additional fold. M is wide and occupies approximately a quarter of the width of Fba. Pp consists of two small triangular sectors Pp1 and Pp2. An is pentagonal. Dp is quadrangular. Id is parallel shaped. Pr is pentagonal and occupies approximately one-third of Faa's area and consists of two areas Pr1 and Pr2. Pr2 originates from An and divides Pr1 into two sectors. S and Aa form a spatula shape, and each area is divided into two subareas S1 and S2, and Aa1 and Aa2, respectively. S2 has an additional fold, originating from Dp.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of the Scarabaeoidea.

Glaphyridae (Fig. 6)

The hind wing folding patterns of the Glaphyridae consists of 17 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.2−1.3:1. J is developed and is trapezoidal in shape. Wd is trapezoidal and occupies approximately half the width of Fba. Oa is triangular in shape. M occupies approximately one-fifth of the width of Fba. Pp consists of two small triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangular in shape. Id tapers toward the wing's posterior margin. Pr is pentagonal. S is spatula shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Hybosoridae (Fig. 7)

The hind wing folding patterns of the Hybosoridae consists of 19 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, S, Aa, and Pa.

The ratio of Fba to Faa is approximately 1.2:1. J is developed and is semicircular with an additional fold. Wd is trapezoidal and occupies approximately half the width of Fba. Oa is triangular in shape. M occupies approximately one-fifth of the width of Fba. Pp consists of two small triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangular in shape. Id tapers toward the wing's posterior margin. Pr becomes hexagonal due to the existence of the Pa, and occupies approximately one-third of Faa's area. S and Aa form a rectangle shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Lucanidae (Figs. 8−14)

The hind wing folding patterns of the Lucanidae consists of 18 or 20 areas, which are J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr (Pr1 and Pr2), Pa, S, and Aa.

The ratio of Fba to Faa is approximately 1.2:1 (*Dorcus*, *Figulus*, *Prismognathus*, and *Prosopocoilus*) (Fig. 8), but some genera show different ratios. For instance, *Lucanus*, *Ceruchus*, and *Aesalus* have a ratio of approximately 1.1:1 (Figs. 9, 10, 11), *Lamprima* and *Platycerus* have a ratio of approximately 1.3:1 (Figs. 12, 13), and *Nicagius* approximately 1.4:1 (Fig. 14). J is well-developed and is semicircular. Wd is trapezoidal and occupies approximately half the width of Fba. Oa is triangular in shape. M is wide and occupies approximately one-fifth the width of Fba. Pp consists of two small triangular sectors Pp1 and Pp2. An is pentagonal. Dp is triangular in shape. Id tapers toward the hind wing's posterior margin. In the genera *Dorcus*, *Lamprima*, *Nicagus*, *Prismognathus*, and *Prosopocoilus* (Figs. 8, 12, 14), Pr is pentagonal shaped, occupying about half the area of Faa and comprises two areas, Pr1 and Pr2. Pr2 originates from An and divides Pr1 into two sectors. In the genera *Aesalus*, *Ceruchus*, *Figulus*, and *Platycerus* (Figs. 10, 11, 13), Pr (Pr1 and Pr2) is hexagonally shaped due to the presence of Pa. S, or S and Aa usually taper towards the end, but in some species such as *Aesalus asiaticus* and *Platycerus acuticollis*, S and Aa form a rectangular shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Ochodaeidae (Fig. 15)

The hind wing folding patterns of the Ochodaeidae is usually consist of 20 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr (Pr1 and Pr2), Pa, S, and Aa.

The ratio of Fba to Faa is approximately 1:1.2−1.3. J is developed and is trapezoidal in shape. Wd is pentagonal due to has an additional fold and occupies approximately half of the width of Fba. Cu has an additional fold. Oa is quadrangular due to has an additional fold. M occupies approximately one-fifth of the width of Fba. Pp consists of two small triangular sectors Pp1 and Pp2. An is pentagonal in shape. Dp is triangularly shaped. Id tapers toward the wing's posterior margin. Usually, Pr is hexagonally shaped due to the presence of Pa, occupying about half the area of Faa and comprises two areas, Pr1 and Pr2. Pr1 has many irregularly additional folds. Pr2 originates from An and divides Pr1 into two sectors. In the genus *Notochodaeus*, Pr (Pr1 and Pr2) is pentagonal shaped, occupying approximately half area of Faa. S, or S and Aa usually taper towards the end.

The Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Passalidae (Fig. 16)

The hind wing folding patterns of the Passalidae comprises 16 areas: J, Wd, Oa, Cu, M, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 2:1. J is well-developed and is semicircular in shape. Wd is elongated trapezoidal and occupies approximately one-third the width of Fba. Oa is small triangularly shaped. M is narrow and occupies approximately one-sixth of the width of Fba. Im is completely lost. Pp consists of two small triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the wing's posterior margin. Pr is pentagonal, occupying about half the area of Faa. S is rectangular.

The Cu, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Pleocomidae (Fig. 17)

The hind wing folding patterns of the Pleocomidae consists of 17 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.3:1. J is well-developed and is semicircular in shape. Wd is trapezoidal and occupies approximately half the width of Fba. Oa is narrow triangularly shaped. M is very narrow and occupies approximately one-seventh of the width of Fba. Pp consists of two small triangular sectors Pp1 and Pp2. An is quadrangular in shaped. Dp is triangularly shaped. Id is parallel shaped. Pr is pentagonal, occupying approximately half area of Faa. S is tapering toward the end.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Trogidae (Fig. 18)

The hind wing folding patterns of the Trogidae consists of 20 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr (Pr1 and Pr2), S, Aa, and Pa.

The ratio of Fba to Faa in the genera *Glyptotrox* and *Trox* is approximately 1:1, while the genus *Omorgus* shows 1.2:1. J well-developed and is semicircular with an additional fold. Wd is trapezoidal with a shallow notch, occupying approximately half the width of Fba. Oa is triangular in shape. M occupies approximately one-fifth the width of Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is pentagonal and is adjacent to Uf. Dp is triangular. Id tapers towards the wing's posterior margin. Pr is hexagonally shaped due to the presence of Pa, occupying about half the area of Faa and comprises two areas, Pr1 and Pr2. Pr1 has an additional fold. Pr2 originates from the An and divides Pr1 into two sectors. S and Aa taper towards the end.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Scarabaeidae (Figs. 19−49)

The hind wing folding pattern in the Scarabaeidae is present in various states among subfamilies and tribes.

Aegialiinae (Fig. 19−20)

The hind wing folding patterns of the subfamily Aegialiinae consists of 20 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, S (S1 and S2), and Aa (Aa1 and Aa2).

The ratio of Fba to Faa is approximately 1:1. J is developed and is semicircular in shape. Wd is trapezoidal and occupies approximately one-third of the width of Fba, and this area has an additional fold. A small notch is observed at the posterior margin of the boundary line between J and Wd. Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of Fba. Pp comprises two triangular sectors, Pp1 and Pp2. An is quadrangular in shape. Dp is quadrangular in shape. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal and occupies approximately one-third of the width of Faa. S and Aa form a spatula shape, and each area is divided into two subareas S1 and S2, and Aa1 and Aa2, respectively. S2 has an additional fold, originating from Dp.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea. In the species *Aegialia nitida* (Fig. 20), the hind wing is remarkably reduced, so the hind wing folding patterns could not be observed.

These character states are similar to the subfamily Aphodiinae.

Aphodiinae (Figs. 21−23)

The hind wing folding patterns of the subfamily Aphodiinae comprises 20 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, S (S1 and S2), and Aa (Aa1 and Aa2).

The ratio of Fba to Faa is usually approximately 1:1−1.1, but some of tribes show different ratios, such as approximately 1:1.2 for Odochilini and Rhyparini. J is developed and is semicircular in shape. Wd is trapezoidal shaped and occupies about one-third of the width of Fba, and this area has an additional fold in the tribe Aphodiini. Usually, a small notch is observed at the posterior margin of the boundary line between J and Wd, but it is indistinguishable in the species *Aphodius quadratus*. Oa is triangularly shaped. M occupies approximately one-fifth of the width of Fba. Pp comprises wo triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is quadrangular in shape. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal and occupies approximately one-fourth of the width of Faa. S and Aa form a spatula shape, and each area is divided into two subareas S1 and S2, and Aa1 and Aa2, respectively. S2 has an additional fold, originating from Dp.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea. In the species *Psammodius kobayashii* (Fig. 22), the hind wing is remarkably reduced, so the hind wing folding patterns could not be observed.

The species in the tribe Rhyparini (Fig. 23) showed unique characteristics in the J and Wd areas. J is an elongated lobe. J and Wd have many additional complex folds.

Chironinae (Fig. 24)

The hind wing folding patterns of the subfamily Chironinae (genus *Chiron*) consists of 20 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, S (S1 and S2), and Aa (Aa1 and Aa2).

The ratio of Fba to Faa is approximately 1:1. J is developed and is semicircular in shape. Wd is trapezoidal and occupies approximately one-third of the width of Fba, and this area has an additional fold. Oa is triangularly shaped. M occupies approximately one-fifth of the width of Fba. Pp comprises two triangular sectors, Pp1 and Pp2. An is quadrangular in shape. Dp is quadrangular in shaped. Id tapers toward the posterior margin of the hind wing. Pr is elongated pentagonal and occupies approximately one-fifth of the width of Faa. S and Aa form a spatula shape, and each area is divided into two subareas S1 and S2, and Aa1 and Aa2, respectively. S2 has an additional fold, originating from Dp.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

These character states are similar to the subfamily Aphodiinae.

Scarabaeinae (Figs. 25−29)

The hind wing folding patterns of the subfamily Scarabaeinae consists of 20 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, S (S1 and S2), and Aa (Aa1 and Aa2).

The ratio of Fba to Faa is usually approximately 1:1.1−1.2, but some genera show different ratios, such as approximately 1.2:1 (*Paraphytus*) (Fig. 26), 1:1.3 (*Catharsius*), and 1:1.4 (*Heliocopris* and *Dichotomius*) (Fig. 27). J is developed and is triangular in shape. However, the genus *Paragymnopleurus* (Fig. 28) has two additional folds in the J area. Wd is trapezoidal and occupies approximately one-third of the width of Fba, and this area has an additional fold in the tribes Ateuchini, Coprini, Deltochilini, Dichotomini, Phanaeini, Sisyphini, and Scarabaeini (Figs. 25, 26, 27). Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An and Dp are quadrangular in shape. Id is weakly tapers towards the posterior margin of the hind wing. Pr is pentagonal and occupies approximately one-fourth of the width of Faa. S and Aa form a spatula shape, and each area is divided into two subareas S1 and S2, and Aa1 and Aa2, respectively. S2 has an additional fold, originating from Dp.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

The folding patterns of the tribe Onitini (Fig. 29) show different character states than the other scarabaeine species. The ratio of Fba to Faa is approximately 1:1. Dp is triangularly shaped. Id is parallel shaped. Pr is hexagonal shaped due to the presence of Pa. S and Aa form a spatula shape with no subdivisions. These character states may be similar to those of the subfamily Cetoniinae.

Aclopinae (Fig. 30)

The hind wing folding patterns of the subfamily Aclopinae (genus *Pachypus*) comprises 19 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, S, Aa, and Pa.

The ratio of Fba to Faa is approximately 1.1:1. J is developed and is semicircular in shape. Wd is trapezoidal and occupies approximately half the width of Fba. Oa is triangularly shaped. M is narrow and occupies approximately one-sixth of the width of Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr is hexagonally shaped due to the presence of Pa and occupies approximately one-third of the area of Faa. The Pr is divided into two sectors by an additional fold, originating from An. S and Aa forms rectangle shaped.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Cetoniinae (Figs. 31−32)

The hind wing folding patterns of the subfamily Cetoniinae consists of 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1:1. J is well-developed and is semicircular in shape, and in the tribes Diplognathini (*Anthracophora*) and Goliathini (Fig. 32) this area have an additional fold. Wd is trapezoidal and occupies approximately two-third of the width of Fba. Oa is triangularly shaped. M is very narrow and occupies approximately one-seventh of the width of the Fba. Pp comprises two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shaped. Pr is pentagonal and occupies approximately one-third of the area of the Faa. S is spatula shape.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Dynamopodinae (Fig. 33)

The hind wing folding patterns of the subfamily Dynamopodinae consists of 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.3:1. J is developed and is semicircular in shape. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangular shaped. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal, with an additional fold, occupying approximately one-third of the area of Faa. S is rectangular in shape.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Dynastinae (Fig. 34)

The hind wing folding patterns of the subfamily Dynastinae consists of 17 areas, which are: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.2:1. J well-developed and is trapezoidal with several irregularly additional folds. Wd is trapezoidal and occupies approximately half of the width of Fba. Oa is triangularly shaped. M occupies approximately one-fifth of the width of the Fba. Pp comprises two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal, with some additional irregular folds, occupying approximately half of the area of the Faa. S tapers towards the end.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Euchirinae (Fig. 35)

The hind wing folding patterns of the subfamily Dynastinae consists of 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1:1. J is largely well-developed and is trapezoidal with several irregular additional folds. Wd is trapezoidal and occupies approximately half of the width of Fba. Oa is triangularly shaped. M occupies approximately one-fifth of the width of the Fba. Pp comprises two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal, with some additional irregular folds, occupying approximately half of the area of Faa. S tapers towards the end. The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

These character states are similar to those of the subfamily Dynastinae.

Melolonthinae (Figs. 36−40)

The hind wing folding pattern in the subfamily Melolonthinae shows a unique character state between tribes.

Diplotaxini (Fig. 36)

The hind wing folding patterns of the tribe Hopliini consists of 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1:1. J is developed and is semicircular in shape. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of the Fba. Pp comprises two triangular sectors Pp1 and Pp2. An is quadrangular in shaped. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal and occupies approximately one-fourth of the width of the Faa, and this area is divided into two sectors by an additional fold originating An. S is spatula shape with a large additional fold.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Hopliini (Fig. 37)

The hind wing folding patterns of the tribe Hopliini comprises 19 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, Pa, S, and Aa.

The ratio of Fba to Faa is approximately 1:1.1−1.2. J is narrow and is semicircular in shape, but the genus *Pachycnema* present lobe shaped J. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shaped. Pr becomes hexagonal due to the existence of the Pa, and occupies approximately one-third of Faa's area. S and Aa form a rectangle shaped.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Melolonthini and Rhizotrogini (Fig. 38)

The hind wing folding patterns of the tribes Melolonthini and Rhizotrogini consists of 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.4:1. J is developed and is trapezoidal in shape. In the tribe Rhizotrogini, the J has an additional fold. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal and occupies approximately one-third of Faa's area, and this area has an additional fold. S is rectangular in shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Sericini (Fig. 39)

The hind wing folding patterns of the tribe Sericini consists of 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.3−1.4:1. J is developed and is semicircular in shape with an additional fold. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id is tapers toward the posterior margin of the hind wing. Pr is pentagonal and occupies approximately one-third of the width of the Faa. S is rectangular in shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

These character states are similar to the tribe Melolonthini, except in the characteristics of Pr additional fold.

Tanyproctini (Fig. 40)

The hind wing folding patterns of the tribe Tanyproctini comprises 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.4:1. J is narrowly elongated shape. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shaped. Pr is pentagonal and occupies approximately one-third of Faa's area, and this area has an additional fold. S is rectangular in shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

These character states are similar to the tribe Melolonthini, but the Id shows different characteristics.

Orphninae (Fig. 41)

The hind wing folding patterns of the subfamily Orphninae consists of 19 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, Pa, S, and Aa.

The ratio of Fba to Faa is typically approximately 1:1. J is well-developed and is semicircular in shape. Wd is trapezoidal and occupies approximately half of the width of the Fba. M occupies approximately one-fifth of the width of the Fba. Pp comprises two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of hind wing. Pr becomes hexagonal due to the existence of the Pa, and occupies approximately one-fourth of Faa's area. S and Aa form a rectangle shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Rutelinae (Figs. 42−45)

The hind wing folding pattern in the subfamily Rutelinae is observed four types.

Anatistini , Anomalini, Anoplognathini, and Rutelini (*Chrysophora*) (Fig. 42)

The hind wing folding patterns of the tribes Anatistini, Anomalini, Anoplognathini, and Rutelini (*Chrysophora*) comprise 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is typically approximately 1.2:1. J is developed and is semicircular with an additional fold. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M is wide and occupies approximately one-fourth of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal and occupies approximately one-third of Faa's area, and this area has an additional fold. S is rectangular shape.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

These character states are similar to the tribe Melolonthini, except for the ratio of Fba to Faa.

Popiliina (*Malaia*, *Popillia*, and *Spilopopillia*) (Fig. 43)

The hind wing folding patterns of the genera *Malaia*, *Popillia*, and *Spilopopillia* comprise 17 areas, which are J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S, whereas the genus *Malaia* and *Spilopopillia* are constituted to 19 areas, which are J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, Pa, S, and Aa.

The ratio of Fba to Faa is approximately 1:1.1−1.2. J is developed and is semicircular with an additional fold. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M occupies approximately one-fifth of the width of the Fba. Pp consist of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id parallel shaped. Pr in the genus *Popillia* is pentagonal and occupies approximately one-third of the area of the Faa. In the genera *Malaia* and *Spilopopillia*, the Pr becomes hexagonal due to the existence of the Pa. S, or S and Aa form wide spatula shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

These character states are similar to the tribes Triciini and Incaini.

Rutelini (*Dicaulocephalus*, *Kibakoganea*, *Parastasia*, and *Pelidnota*) (Fig. 44)

The hind wing folding patterns of the tribes Triciini and Incaini consist of 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.2:1. J is developed and is semicircular with an additional fold. Wd is trapezoidal and occupies approximately half of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of hind wing. Pr is pentagonal, with some additional irregular folds, occupying approximately half of the area of the Faa. S tapers toward the end.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of

Scarabaeoidea.

These character states are similar to the subfamily Dynastinae.

Adoretini (Fig. 45)

The hind wing folding patterns of the tribe Adoretini consists of 19 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, Pa, S, and Aa.

The ratio of Fba to Faa is approximately 1:1. J is developed and is semicircular with an additional fold. Wd is trapezoidal with an additional fold and occupies approximately half of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr becomes hexagonal due to the existence of the Pa, and occupies approximately one-thirds of Faa's area, and the Pr and Pa have some additional irregular folds. S and Aa form a rectangular shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Trichinae (Figs. 46−48)

The hind wing folding pattern in the subfamily Trichiinae has two known types.

Triciini and Incaini (Figs. 46−47)

The hind wing folding patterns of the tribes Triciini and Incaini comprise 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is typically approximately 1.1:1 (Fig. 46), but the genus *Lasiotrichius* present approximately 1:1.1 (Fig. 47). J is developed and trapezoidal with an additional fold. Wd is trapezoidal and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M occupies approximately one-fifth of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular shaped. Dp is triangularly shaped. Id is parallel shape. Pr is pentagonal and occupies approximately one-fifth of the area of the Faa. S is wide spatula shape.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

These character states are similar to the subfamily Cetoniinae.

Osmodermini (Fig. 48)

The hind wing folding patterns of the tribe Osmodermini comprise 17 areas: J, Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, and S.

The ratio of Fba to Faa is approximately 1.1:1. J is well-developed and is semicircular with an additional fold. Wd is trapezoidal and occupies approximately two-third of the width of the Fba. Oa is triangularly shaped. M is very narrow and occupies approximately one-seventh of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shape. Pr is pentagonal and occupies approximately one-third of the area of the Faa. S is spatula shape.

The Cu, Im, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

These character states are similar to the subfamily Cetoniinae, especially the tribe Goliathini and Diplognathini.

Valginae (Fig. 49)

The hind wing folding patterns of the subfamily Valginae consists of 18 areas, which are Wd, Oa, Cu, M, Im, Uf, Fc, Pp (Pp1 and Pp2), An, Sc, Ce, Dp, Id, Pr, Pa, S, and Aa.

The ratio of Fba to Faa is approximately 1:1.3-1.7. J is completely lost. Wd is triangularly and occupies approximately half of the width of the Fba. Oa is triangularly shaped. M is remarkably narrow and occupies approximately one-seventh of the width of the Fba. Pp consists of two triangular sectors Pp1 and Pp2. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shape. Pr becomes hexagonal due to the existence of the Pa, and occupies approximately one-fifth of Faa's area. S and Aa form a wide spatula shape.

The Cu, Im, Uf, Fc, Sc, and Ce are consistent with the general characteristics of Scarabaeoidea.

Discussion

Based on the examination of the hind wing folding patterns in Scarabaeoidea, the following inferences were made.

Types of the hind wing folding pattern in Scarabaeoidea

Generally, the shape of wings is considered to be significantly affected by body size, behavioral traits and environmental factors of insects (Taylor and Merriam 1995, Johansson *et al*. 2009, Navarro *et al*. 2015, Suárez-Tovar and Sarmiento 2016, Tocco *et al*. 2019). In the coleopteran species, the hind wing shape is restricted because they need to be foldable and tucked under the elytra. However, as seen in subchapter (2–1–1), the hind wing folding patterns are not affected by the aforementioned factors, and they have been suggested to represent a unique character state in each taxon (Kaneko and Kojima 2017, subchapter 2–1–1). In Fedorenko (2009), the scarabaeoid folding pattern is categorized as "staphyliniform type", characterized by some features such as the distal portion of the Oa and Oblong (absent in Scarabaeoidea species) involved in the Pr when folding, the Ce and Dp are subequally large and of similar shape, and the wing folds like a jackknife. Here, I suggest further dividing the hind folding patterns in Scarabaeoidea in to fifteen types as following: glareresine, lucanine, ochodaeine, geotrupine, pleocomine, glaphyrine, hybosorine, aphodiine, melolonthine, diplotaxine, hopliine, dynastine, adoretine, cetoniine, and valgine. The following features are essential in distinguishing each type: ratio of Fba to Faa, development of J, development of Wd, shape of An, shape of Dp, shape of Id, shape of Pr and presence of Pa, presence Pr2, shape of S and presence of Aa, and presence of some additional folds.

Glaresidae belongs to the glaresine-type (Fig. 5). The ratio of Fba to Faa is approximately 1:1. J is very narrow and elongated. Wd has a deep notch and occupies approximately half of the width of the Fba. An is pentagonal. Dp is quadrangular in shape. Id is parallel shaped. Pr is pentagonal shaped and consists of Pr1 and Pr2. Anterior region of the Faa is composed of S and Aa and has a spatula shape. S and Aa are divided into two subareas S1 and S2, and Aa1 and Aa2, respectively. Specific additional folds are present in Oa and S2. An additional fold of S2 originates from Dp.

Lucanidae and Trogidae belong to the lucanine-type (Figs. 8, 9, 10, 11, 12, 13, 14, 18). The ratio of Fba to Faa is typically approximately 1.2:1. J is semicircular or narrow elongated. Wd occupies approximately half of the width of the Fba, and the species in the Trogidae have a shallow notch. An is pentagonal. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal or hexagonal depending on the presence or absence of Pa, and consists of Pr1 and Pr2. Anterior region of the Faa is composed of only S, or S and Aa, and has tapering toward the end.

Ochodaeidae belongs to the ochodaeine-type (Fig. 15). This type is similar to the lucanine-type, but the ratio of Fba to Faa is represented to remarkably different proportion, which approximately 1:1.2–1.3. Moreover, specific additional folds are present in Cu, Wd, and Oa. These additional folds are continuous. Aa, Pa, and Pr1 have multiple additional irregular folds.

Bolboceratidae, Geotrupidae, and Passalidae belong to the geotrupine-type (Figs. 2, 4, 16). Fba is remarkably long and the ratio of Fba to Faa is approximately 1.5–2 : 1. J is semicircular. Wd is elongated and trapezoidal, and occupying approximately half the width of the Fba. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shaped, but in the species of Passalidae, it tapers toward the posterior margin of the hind wing. Pr is pentagonal or hexagonal, depending on the presence or absence of Pa. Faa’s anterior region consists only of S, or S and Aa, and is rectangular in shape.

Pleocomidae belongs to the pleocomine-type (Fig. 17). The ratio of Fba to Faa is approximately 1.3:1. J is semicircular. Wd occupies approximately half of the width of the Fba. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shaped. Pr is pentagonal. Faa’s anterior region consists only S, and tapers towards the end.

Glaphyridae belongs to the glaphyrine-type (Fig. 6). The ratio of Fba to Faa is approximately 1.3:1. J is trapezoidal. Wd occupies approximately half the width of the Fba. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr is pentagonal. Faa’s anterior region consists only S, and is spatula in shape.

Hybosoridae, Aclopinae, and Orphninae belong to the hybosorine-type (Figs. 7, 30, 41). The ratio of Fba to Faa is approximately 1−1.1:1. J is semicircular. Wd occupies approximately half of the width of the Fba. An is quadrangular in shape. Dp is triangularly shaped. Id tapers toward the posterior margin of the hind wing. Pr becomes hexagonal due to the existence of the Pa. Faa’s anterior region consists of S and Aa, and is rectangular in shape.

Aegialiinae, Aphodiinae, Chironinae, and Scarabaeinae belong to the aphodiine type (Figs. 19, 21, 23−28). The ratio of Fba to Faa is usually approximately 1:1.1–1.2. J is semicircular. Wd occupies approximately one-third of the width of the Fba, and in many cases this area has an additional fold. An is quadrangular in shape. Dp is quadrangular in shape. Id is weakly tapering toward the posterior margin of the hind wing. Pr is pentagonal. Anterior region of Faa is composed of S and Aa and has a spatula shape. S and Aa are divided into two subareas S1 and S2, and Aa1 and Aa2, respectively. Specific additional folds are present in S2, originating from Dp.

Dynamopodinae, Melolonthinae (tribes Melolonthini, Rhizotrogini, Tanyproctini, and Sericini), and most of Rutelinae belong to melolonthine-type (Figs. 33, 38−40, 42). The ratio of Fba to Faa is approximately 1.4:1 (Dynamopodinae, Melolonthini, Rhizotrogini, Tanyproctini, and Sericini) or 1.2 : 1 (most of Rutelinae). J is semicircular. Wd occupies approximately half of the width of Fba. An is quadrangular in shape. Dp is triangularly shaped. Id is tapering toward the posterior margin of the hind wing. Pr is pentagonal. Anterior region of Faa is composed of only S and has a rectangular shape. Specific additional fold is present in J.

Diplotaxini belongs to the diplotaxine-type (Fig. 36). The ratio of Fba to Faa is approximately 1:1. J is semicircular. Wd occupies approximately half of the width of Fba. An is quadrangular in shape. Dp is triangularly shaped. Id is tapering toward the posterior margin of the hind wing. Pr is pentagonal and is divided into two subareas by an additional fold originating from An. Anterior region of the Faa is composed of only S and has a spatula shape. Specific additional fold is present in S.

Hopliini belongs to the hopline-type (Fig. 37). The ratio of Fba to Faa is approximately 1:1.1. J is semicircular. Wd occupies approximately half of the width of Fba. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shape. Pr becomes hexagonal due to the existence of the Pa. Anterior region of Faa is composed of S and Aa and has a rectangular in shape.

Dynastinae, Euchirinae, and some groups of Rutelinae (genera *Dicaulocephalus*, *Kibakoganea*, *Parastasia*, and *Pelidnota*) belong to the dynastine-type (Figs. 34−35, 44). The ratio of Fba to Faa is approximately 1.1:1. J is semicircular and has some additional irregular folds. Wd occupies approximately half of the width of Fba. An is quadrangular in shape. Dp is triangularly shaped. Id is tapering toward the posterior margin of the hind wing. Pr is pentagonal and has some additional irregular folds. Anterior region of Faa is composed of only S and has a tapered shape.

Adoretini belongs to the adoretine-type (Fig. 45). The ratio of Fba to Faa is approximately 1:1. J is semicircular. Wd occupies approximately half of the width of Fba. An is quadrangular in shape. Dp is triangularly shaped. Id is tapering toward the posterior margin of the hind wing. Pr becomes hexagonal due to the existence of the Pa, and has some additional irregular folds. Anterior region of Faa is composed of S and Aa and has a rectangular shape.

Cetoniinae, Trichinae, and Rutelinae (genera *Popillia*, *Malaia*, and *Spilopopillia*) belong to the cetoniine type (Figs. 31−32, 43, 45−48). The ratio of Fba to Faa is approximately 1–1.1:1. J is semicircular shaped. J is semicircular or trapezoidal. Wd occupies approximately two-thirds of the width of Fba, but in the Trichinae (except in tribe Osmodermini) and Rutelinae (genera *Popillia*, *Malaia*, and *Spilopopillia*) it occupies approximately half of the width. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shape. Pr is pentagonal and the additional fold never existence in this area. Anterior region of Faa is composed of only S and has a spatula shape.

Valginae belongs to the valgine-type (Fig. 49). Faa is remarkably long and the ratio of Fba to Faa is approximately 1:1.3–1.7. J is completely lost. Wd occupies approximately half of the width of Fba. An is quadrangular in shape. Dp is triangularly shaped. Id is parallel shaped. Pr is hexagonal and the additional fold never existence in this area. Anterior region of Faa is composed of S and Aa and has a spatula shaped.

Evolution of the hind wing folding pattern and the most ancestral states in Scarabaeoidea

The hind folding pattern, or fold system, is a highly complex structure. However, Fedorenko (2009) suggested that the folding pattern typology is useful for estimating evolutionary tendencies and phylogenetic relationships. Moreover, the folding patterns can be ordered into a hierarchical system, more precise in reflecting evolutionary changes in the wing folding apparatus than wing venation characteristics. Fedorenko (2009) presented the prototype hypothesis of the hind wing folding patterns in Coleoptera, and he also considered that primitive folding patterns are highly complex. With regard to estimating evolutionary trends and phylogenetic relationships in the Scarabaeoidea, my observations indicated that the following characteristics are of particular importance: ratio of Fba to Faa, shape of An and the accompanying development of Pr2, shape of Dp and the accompanying difference in the S, and shape of Id.

The ratio of Fba to Faa was represented in various proportions, but these proportions were roughly distinguished into the following three types: Fba longer than Faa (Fba > Faa), Fba and Faa almost equal in length (Fba = Faa) which is approximately the ratio 1–1.1:1–1.1, and Faa longer than Fba (Fba < Faa) which approximately the ratio 1:1.2-1.3. Of these, the Fba > Faa could be further divided into two subtypes: Fba >> Faa (approximately 1.4–2:1) and Fba > Faa (approximately 1.2–1.3:1). In species of the Bolboceratidae, Geotrupidae, Passalidae, and Melolonthinae (tribes Melolonthini, Rhizotrogini, Sericini, and Tanyproctini), the ratio is approximately 1.4–2:1. In Glaphyridae, Lucanidae, Pleocomidae, Trogidae, Scarabaeinae (tribe Ateuchini), Dynamopodinae, and most Rutelinae, the ratio is approximately 1.2–1.3:1. In Glaresidae, Hybosoridae, Aegialiinae, Aphodiinae, Chironinae, Aclopinae, Cetoniinae, Dynastinae, Euchirinae, Melolonthinae (tribes Diplotaxini and Hopliini), Orphninae, Rutelinae (tribe Adoretini), and Trichinae, the ratio is approximately 1–1.1:1–1.1. In Ochodaeidae, Aphodiinae (tribes Odochilini and Rhyparini), Scarabaeinae, Rutelinae (genera *Malaia*, *Popillia*, and *Spilopopillia*), and Valginae species, the ratio is approximately 1:1.2–1.3. The Fba in the prototype hindwing folding pattern of Fedorenko (2009) presents very long ratios, and species in Scirtoidea, believed to be the most primitive group in Polyphaga (Friedrich and Beutel 2006, McKenna *et al*. 2019), also shows very long ratios Fba. Therefore, in the superfamily Scarabaeoidea, it is considered that the characteristics, Fba >> Faa or Fba > Faa, represent the most ancestral state, whereas Fba = Faa and Fba < Faa represent the derived state. Indeed, many taxa characterized by Fba >> Faa or Fba > Faa (Geotrupidae, Passalidae, Bolboceratidae, Glaphyridae, Hybosoridae, Lucanidae, Pleocomidae, and Trogidae) are generally treated as primitive groups in the superfamily

Scarabaeoidea (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990), and Fba = Faa and Fba < Faa are usually observed in the intermediate and derived taxa.

There are two types of shapes of Dp (triangle and quadrangle), and the number of areas that constitute S or S + Aa varies according to shape. Among the families Bolboceratidae, Geotrupidae, Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Passalidae, Pleocomidae, and Trogidae, and the phytophagous group of Scarabaeidae, the Dp is triangularly shaped, and the accompanying areas consist of one (S) or two areas (S and Aa). In the family Glaresidae and the coprophagous group of Scarabaeidae, the Dp is quadrangular in shape, and the accompanying areas are comprised of two (S1 and S2) or four areas (S1, S2, Aa1, and Aa2). Since the quadrangular shaped Dp is observed in the family Glaresidae which is generally treated as the most ancestral group of Scarabaeoidea (Scholtz *et al.* 1994, Browne and Scholtz 1999, Scholtz and Grebennikov 2005, Bai *et al.* 2013), the quadrangular shape appears to indicate a primitive character state. However, the prototype folding pattern of by Fedorenko (2009) and Staphylinoidea, treated as a sister group of Scarabaeoidea (McKenna *et al.* 2019), possess a triangular shaped Dp. Consequently, it can be concluded that the triangular shape represents a plesiomorphy, while the quadrangular shape represents an apomorphy. Although the Glaresidae and coprophagous groups of Scarabaeidae exhibit a quadrangular shape, it was concluded that the similarity of this characteristic is a homoplasy as both groups are systematically distant (Ahrens *et al.* 2014).

The shape of An was found to be of two types, quadrangle and pentagon. The pentagonal shaped An was accompanied by Pr2. Among the families Bolboceratidae, Geotrupidae, Glaphyridae, Hybosoridae, Passalidae, Pleocomidae, and Scarabaeidae, An has a quadrangular shape. In the families Glaresidae, Lucanidae, Ochodaeidae, and Trogidae, An is pentagonal. The evolutionary trend of An has been presented by Fedorenko (2009). A triangular shape characterizes the most primitive state of An, and the quadrangular shape is considered a secondary occurrence. From this reference, the pentagonal shaped An with Pr2 observed in the Glaresidae, Lucanidae, Ochodaeidae, and Trogidae is considered a relatively derived state. Furthermore, these characteristics may indicate close relationships among the families Glaresidae, Lucanidae, Ochodaeidae, and Trogidae.

The shape of Id was divided into tapered and parallel shapes. Among the members of the families Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Passalidae, Trogidae, and many scarabaeid subfamilies [Aegialiinae, Aphodiinae, Chironinae, Scarabaeinae (except tribe Onitini), Aclopinae, Dynamopodinae, Dynastinae, Euchirinae, Melolonthinae (tribes Diplotaxini, Sericini, Melolonthini, and Rhizotrogini), Orphninae, Rutelinae (except the genera *Malaia*, *Popillia*, and *Spilopopillia*)], Id is tapered. Among the members of the families Bolboceratidae, Geotrupidae, Glaresidae, Pleocomidae, and some scarabaeid subfamilies [Scarabaeinae (tribe Onitini), Cetoniinae, Melolonthinae (tribes Hopliini and Tanyproctini), Rutelinae (genera *Malaia*, *Popillia*, and *Spilopopillia*), Trichinae, and Valginae], Id has a parallel shape. The primitive state of Id is considered to be tapered based on Fedorenko (2009), and the parallel shaped Id is derived from the above state. However, the parallel shaped Id may not be useful in inferring the relationships between higher groups because many taxa characterized by parallel shapes tend to be positioned in different lineages in the recent phylogenetic analysis (Ahrens *et al*. 2014). The parallel shaped Id is considered to be a homoplasy acquired at multiple stages of evolution.

My observation indicates that the most ancestral scarabaeoid species have the following folding pattern characteristics: Fba is longer than Faa (Fba > Faa), Dp is triangular shaped, An is quadrangular shaped, and Id is tapered. The characteristics of the hind wing folding pattern have shown that the families Glaresidae and Lucanidae, traditionally considered as primitive taxa (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990, Scholtz *et al*. 1994, Browne and Scholtz 1999, Scholtz and Grebennikov 2005, Bai *et al*. 2013, Ahrens *et al*. 2014), have relatively derived states compared with other scarabaeoid families.

Phytophagous and coprophagous groups of Scarabaeidae

Although the primary hind wing folding pattern is similar in the coprophagous and phytophagous groups of the family Scarabaeidae, these groups can be clearly distinguished based on the characteristic shape of Dp. In this regard, a triangular shaped Dp is typical of the phytophagous group. Subfamilies of the coprophagous group are characterized by a quadrangular shaped Dp, and accompanying areas consist of two (S1 and S2) or four areas (S1, S2, Aa1, and Aa2). Traditionally, the coprophagous and phytophagous groups of Scarabaeidae have been treated as sister groups based on morphological observations (Browne and Scholtz 1995, 1998) and some molecular phylogeny (Ahrens and Volger 2008, Gunter *et al*. 2016, Šípek *et al*. 2016, McKenna *et al*. 2019). However, recent molecular phylogenetic analyses indicate that the coprophagous and phytophagous groups are not closely related, and that the phytophagous group is grouped within a clade that includes either Glaphyridae or Hybosoridae (Smith *et al*. 2006, Ahrens *et al*. 2014, Neita-Moreno *et al*. 2019). The characteristics of Dp may support this phylogenetic hypothesis.

Families Glaresidae, Lucanidae, Trogidae, and Ochodaeidae

Traditionally, the family Glaresidae has been considered as the most ancestral extant scarabaeoid taxon (Scholtz 1994) and is judged to be a sister group of the remaining Scarabaeoidea by some authors (Scholtz *et al*. 1994, Browne and Scholtz 1999, Scholtz and Grebennikov 2005, Bai *et al*. 2013). However, morphological studies based on the adult head structure (Anton and Beutel 2012) and some recent phylogenetic analyses (Smith *et al*. 2006, McKenna *et al*. 2019, Neita-Moren *et al*. 2019) have indicated that the families Glaresidae and Trogidae constitute a sister group. Among these, Smith *et al*. (2006) and McKenna *et al*. (2019) also indicated a close relationship between the Lucanidae and Glaresidae + Trogidae clades. On the other hand, the phylogenetic analysis in the Ahrens *et al*. (2014) proposed a close relationship between Glaresidae and Lucanidae, with Trogidae positioned in another lineage.

The members of families Glaresidae, Lucanidae, Trogidae, and Ochodaeidae are characterized by a pentagonal shaped An with Pr2 which is proposed as a derived character state. Since these characteristics are observed only in the above groups, the presence of pentagonal An and Pr2 is likely to indicate a close relationship between the above families.

Families Bolboceratidae, Geotrupidae, and Passalidae

The family Bolboceratidae had been treated as a subfamily of family Geotrupidae in early studies. However, since the study of Scholtz and Browne (1996), it has been regarded as an independent family. In other recent studies, the relationship between Bolboceratidae and Geotrupidae is not supported and molecular phylogenetic analyses conducted by Ahrens *et al*. (2014), and Neita-Moren *et al*. (2019) showed that Bolboceratidae is more closely related to Passalidae than Geotrupidae. However, the latter also showed that the Bolboceratidae + Passalidae and Lucanidae + Geotrupidae clades form a sister group.

The families Bolboceratidae, Geotrupidae, and Passalidae are characterized by remarkably long Fba and elongated Wd (geotrupine type). Since these characteristics are observed only in the above groups, this finding supports the close relationship between Bolboceratidae and Passalidae. Moreover, the relationship between Bolboceratidae and Geotrupidae has was also been proposed. These three taxa are closely related.

Relationships between the subfamilies Cetoniinae, Trichinae, and Valginae

The subfamilies Cetoniinae, Trichinae, and Valginae, are often treated as a single subfamily Cetoniinae (Ahrens *et al*. 2014, Bezděk 2016, Šípek *et al*. 2016). Indeed, the hind wing folding pattern in these subfamilies is characterized by some similar features, such as the spatula shaped S or S + Aa and parallel shaped Id. However, at the same time, Trichiinae (except tribe Osmodermini) and Valginae have different characteristics than Cetoniinae. Trichinae is characterized by Wd, which occupies half of the width of Fba, and a wide spatula shaped S. Valginae is characterized by a completely lost J, Wd occupying half of the width of Fba, and remarkably elongated S + Aa. Consequently, my observational results in the folding pattern surmise that Cetoniinae, Trichinae, and Valginae may be treated as independent subfamilies.

The tribe Osmodermini has been regarded as one of the tribes in Trichinae (Krikken 1984, Krajcik 2012). However, many recent phylogenetic studies have indicated a close relationship between the subfamily Cetoniinae (Micó *et al*. 2008, Šípek *et al*. 2009, Šípek *et al*. 2011, Šípek *et al*. 2016) since Browne and Scholtz (1998) suggested that the tribe Osmodermini is the sister group of Cetoniinae. The hind wing folding patterns were also similar to that of Cetoniinae.

Relationships between the subfamilies Aegialiinae, Aphodiinae, and Chironinae

The subfamilies Aegialiinae and Chironinae are closely related to Aphodiinae (Scholtz and Grebennikov 2016). Although the subfamilies Aegialiinae and Chironinae are often considered different families, Aegialiidae and Chironidae (Nel and Scholtz 1990, d'Hotman and Scholtz 1990a, Paulian and Baraud 1982, Carpaneto and Piattella 1995, Huchet 2000, 2002, 2003, 2004, 2019, Huchet and Lumaret 2002), I found that variations in hind wing folding patterns in these subfamilies are remarkably low and are characterized by a quadrangular shaped Dp. Based on a comparison of folding patterns among the Aphodiinae, Aegialiinae, and Chironinae, it was considered that Aegialiinae and Chironinae might be included in the subfamily Aphodiinae. In this regard, my findings are consistent with those of Browne and Scholtz (1998), Smith *et al*. (2006), and Ahrens *et al*. (2014), who showed that Aegialiinae and Chironinae are included in a clade with Aphodiinae, and also with the findings of Ritcher (1969a, 1974) and Stebnicka (1977), who, based on morphological data, concluded that Aegialiinae and Chironinae are close to Aphodiinae.

Subfamilies Rutelinae and Dynastinae

The close relationships between the subfamilies Rutelinae and Dynastinae have been suggested by morphological (Browne and Scholtz 1998) and molecular phylogenetic analyses (Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, Eberle *et al*. 2019). However, since the hind wing folding pattern in the Rutelinae and Dynastinae indicated quite different characteristics respectively, the closely relationship between both groups were not supported. In addition, some unique characteristics were observed in the following groups in the subfamily Rutelinae: tribes Adoretini, Anomalini (genera *Popillia*, *Malaia*, and *Spilopopillia*), and Rutelini (genera *Dicaulocephalus*, *Kibakoganea*, *Parastasia*, and *Pelidnota*).

In the tribe Adoretini, the folding pattern is typified by almost equal lengths of Fba and Faa and the presence of Aa, Pa, and some additional irregular folds. Traditionally, the tribe Adoretini is considered one of the tribes included in the subfamily Rutelinae (Smith 2006, Bouchard *et al*. 2011, Krajcik 2012, Bezděk *et al*. 2016, Scholtz and Grebennikov 2016). However, in recent phylogenetic analyses based on molecular data, Adoretini was closely related to the subfamily Dynastinae, and it is suggested that it be elevated to the subfamily level. Subchapter (2–1–1) and Kaneko and Kojima (2017) mentioned that the folding pattern has certain morphological features at the subfamily level in Scarabaeidae. Therefore, the unique characteristics observed in Adoretini also seem to support the need for treatment as an independent subfamily. Regarding the close relationship to Dynastinae, the additional irregular folds, which are unique synapomorphies in both groups, may augment this.

The genera *Malaia*, *Popillia* and *Spilopopillia*, have been considered as belonging to the tribe Anomalini (Smith 2006, Bouchard *et al*. 2011, Krajcik 2012, Bezděk *et al*. 2016, Scholtz and Grebennikov 2016). However, the folding pattern observed in the present study is typified in cetoniine-type. According to Kaneko and Kojima (2017) that the folding pattern shows certain morphological features at the subfamily level in Scarabaeidae; these genera are closely related to Cetoniinae and Trichiinae and may need to be removed from the Rutelinae. Scholtz (1990) examined the karyotype and, suggested that *Popillia* has different states from other species of the Anomalini.

In the genera *Dicaulocephalus*, *Kibakoganea*, *Parastasia*, and *Pelidnota*, the folding pattern is typified as dynastine-type, which contains members of Dynastinae. These genera have been considered as belonging to the subfamily Rutelinae (Smith 2006, Bouchard *et al*. 2011, Krajcik 2012, Bezděk *et al*. 2016, Scholtz and Grebennikov 2016), but Smith *et al*. (2006) and Wada (2015) suggested that the genus *Parastasia* is firmly placed in the subfamily Dynastinae. My observational results also show that the above genera have remarkably different features from other members of the Rutelinae and their characteristics were similar to those of the subfamily Dynastinae. On the premise that the folding pattern represents specific characteristics for each subfamily and closely related groups, I strongly support that *Parastasia* be included in the Dynastinae, and it has also been suggested that other groups with similar characteristics (genera *Dicaulocephalus*, *Kibakoganea*, and *Pelidnota*) are also closely related to the Dynastinae.

Subfamily Melolonthinae

The subfamily Melolonthinae is poorly defined, and several groups have been included and excluded at various stages by different authors. For example, the tribe Hopliini is regarded as the scarabaeid subfamily Hoplinae in Nel and DeVilliers (1988), d'Hotman and Scholtz (1990a), Nel and Scholtz (1990) and Pretorius and Scholtz (2001), and the Sericini is considered as scarabaeid subfamily Sericinae in Ritcher (1969a) and Coca-Abia (2007). Moreover, phylogenetic analyses have shown that Melolonthinae is polyphyletic (Browne and Scholtz 1998, Ahrens 2005, Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, Šípek *et al*. 2016, Eberte *et al*. 2019). Therefore, significant variation in the folding pattern of the hind wing has been observed. These variations can be loosely classified into three types: melolonthine, diplotaxine and hopline-types. Of these, the melolonthine type is characterized by many plesiomorphies such as Fba longer than Faa, Dp is triangularly shaped, An is quadrangular in shape, and Id tapered, making it difficult to show the independence of each group (tribes Melolonthini, Rhizotrogini, Sericini, and Tanyproctini) ascribed to this type. Whereas, the tribes Diplotaxini (diplotaxine type) and Hopliini (hopline type) are typified by some autapomorphies in the ratio of Fba to Faa, shape of Pr, anterior region of Faa, and specific additional folds. The folding pattern is a characteristic typifying subfamilies in the family Scarabaeidae, and it is considered reasonable to treat Diplotaxini and Hopliini, which have unique character states, as the independent subfamilies, Diplotaxinae and Hopliinae, respectively.

Subfamily Euchirinae

Various researchers have established the systematic position of the subfamily Euchirinae. Young (1989) conducted the most detailed recent study of the subfamily, treating it as a scarabaeid subfamily. Ahrens (2005) indicated a slight relationship with subfamily Dynastinae (genus *Oryctes*). Šípek *et al*. (2009) suggested that the subfamily is positioned as a sister group of pleurostict scarabs (Rutelinae, Dynastinae, Melolonthinae, and Cetoniinae), but in Šípek *et al*. (2011), Euchirinae is placed with the sister group of the clade Rutelinae, Dynastinae, and Melolonthinae. Ahrens *et al*. (2014) indicated that Euchirinae is related to the tribe Hopliini and Macrodactylini. The hind wing folding pattern of Euchirinae was categorized as dynastne-type. The most notable attribute of the dynastine-type is the tapered S, which is not observed in other scarabaeid groups. The results of this study suggest that the Euchirinae is relatively closely related to Dynastinae, as the folding pattern is considered to show the same characteristics among closely related groups (Kaneko and Kojima 2017, subchapter 2–1–1).

Tribe Rhyparini

The observational results based on the hind wing folding pattern indicated that the tribe Rhyparini has a remarkably different character state than other members of the Aphodiinae. Although the folding pattern in the Rhyparini is similar in many features to other coprophagous species, it is distinctly different in that the Wd is complexly folded (Fig. 23). This feature is an incredibly unique character state that is not observed in other coprophagous species and is a primary characteristic for determining the Rhyparini. In many cases, the Rhyparini is treated as one of the tribes in the subfamily Aphodiinae (Smith 2006, Bouchard *et al*. 2011, Krajcik 2012, Bezděk *et al*. 2016, Scholtz and Grebennikov 2016). However, some researchers may consider it an independent subfamily Rhyparinae (Galante *et al*. 2003, Pittino 2006, Mencl and Rakovič 2013). No research has revealed the specificity of this tribe, but the characteristics of the hind wing folding pattern suggest that the Rhyparini should be treated as a different category other than the Aphodiinae.

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Bolboceratidae	Bolboceratinae	Bolbelasmini	*Bolbelasmus* (*Kolbeus*) *minutus* Li et Masumoto, 2008
		Bolbochromini	*Bolbocerodema nigroplagiatum* (Waterhouse, 1875)
			Bolbochromus ryukyuensis Masumoto, 1984
Geotrupidae	Geotrupinae	Chromogeotrupini	*Enoplotrupes sharpi* Rothschild & Jordan, 1893
		Enoplotrupini	*Phelotrupes* (*Chromogeotrupes*) *auratus auratus* (Motschulsky, 1858)
			Phelotrupes (*Eogeotrupes*) *laevistriatus* (Motschulsky, 1866)
	Lethrinae		*Lethrus* (*Mesolethrus*) *microbuccis* Ballion, 1870
			Lethrus (*Ceratodirus*) *karelini* Gebler, 1845
			Lethrus (*Paralethrus*) *bituberculatus* Ballion, 1870
Glaresidae			*Glaresis beckeri* Solsky, 1870
Glaphyridae	Amphicominae		*Amphicoma pectinata* (Lewis, 1895)
			Amphicoma splendens (Yawata, 1942)
			Eulasia (*Trichopleurus*) *vittata* (Fabricius, 1775)
			Pygopleurus vulpes (Fabricius, 1781)
Hybosoridae	Ceratocanthinae	Ceratocanthini	*Madrasostes hisamatsui* Ochi, 1990
	Hybosorinae		*Phaeochrous emarginatus emarginatus* Laporte, 1840
			Phaeochroops sp.
Lucanidae	Aesalinae	Aesalini	*Aesalus asiaticus asiaticus* Lewis, 1883
		Nicagini	*Nicagus japonicus* Nagel, 1928
	Syndesinae		*Ceruchus lignarius lignarius* Lewis, 1883
	Lampriminae		*Lamprima adolphinae* (Gestro, 1875)
	Lucaninae	Lucanini	*Dorcus rectus rectus* (Motschulsky, 1858)
			Figulus binodulus Waterhouse, 1873
			Figulus punctatus Waterhouse, 1873
			Lucanus maculifemoratus maculifemoratus Motschulsky, 1861
			Prismognathus dauricus (Motschulsky, 1860)
			Prosopocoilus inclinatus inclinatus (Motschulsky, 1858)
		Platycerini	*Platycerus acuticollis* Y. Kurosawa, 1969
Ochodaeidae	Ochodaeinae	Ochodaeini	*Codocera ferruginea* (Eschscholtz, 1818)
			Notochodaeus maculatus maculatus (Waterhouse, 1875)
			Ochodaeus chrysomeloides (Schrank, 1781)
Passalidae	Aulacocyclinae	Ceracupini	*Ceracupes chingkini* Okano, 1988
			Cylindrocaulus patalis (Lewis, 1883)
	Macrolininae		*Macrolinus sikkimensis* Stoliczka, 1873
Pleocomidae			*Pleocoma dubitabilis dubitabilis* Davis, 1935
Trogidae	Troginae		*Glyptotrox uenoi uenoi* (Nomura, 1961)
			Omorgus (*Afromorgus*) *chinensis* (Boheman, 1858)
			Trox (*Niditrox*) *niponensis* Lewis, 1895

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Scarabaeidae	Aegialinae	Aegialiini	*Aegialia* (*Aegialia*) *comis* (Lewis, 1895)
			Aegialia (*Aegialia*) *nitida* Waterhouse, 1875
			Caelius denticollis Lewis, 1895
			Psammoporus nakanei nakanei Masumoto, 1986
	Aphodiinae	Aphodiini	*Aphodius* (*Agrilinus*) *breviusculus* (Motschulsky, 1866)
			Aphodius (*Brachiaphodius*) *eccoptus* Bates, 1889
			Aphodius (*Colobopterus*) *quadoratus* Reiche, 1850
			Aphodius (*Phaeaphodius*) *rectus* Motschulsky, 1866
			Aphodius (*Sinodiapterna*) *troitzyi* Jacobson, 1897
		Eupariini	*Ataenius picinus* Harold, 1867
			Saprosites japonicus Waterhouse, 1875
			Setylaides foveatus (Schmidt, 1909)
		Odochilini	*Odochilus convexus* Nomura, 1971
		Psammodiini	*Rakovicius coreanus* (Kim, 1980)
			Psammodius kobayashii Nomura, 1973
			Trichiorhyssemus asperulus (Waterhouse, 1875)
		Rhyparini	*Rhyparus azumai azumai* Nakane, 1956
			Sybacodes sp. 1
	Chironinae		*Chiron* sp. 1
	Scarabaeinae	Ateuchini	*Paraphytus dentifrons* Lewis, 1895
		Deltochilini	*Deltochilum* (*Calhyboma*) *variolosum* Burmeister, 1873
			Deltochilum (*Hybomidium*) *gibbosum* (Fabricius, 1755)
			Panelus rufulus Nomura, 1973
		Coprini	*Catharsius molossus* (Linnaeus, 1758)
			Copris (*Copris*) *ochus* (Motschulsky, 1860)
			Copris (*Copris*) *tripartitus* Waterhouse, 1875
			Heliocopris tyrannus (Thomson, 1859)
		Gymnopleurini	*Paragymnopleurus melanarius* (Harold, 1867)
		Oniticellini	*Liatongus minutus* (Motschulsky, 1860)
			Liatongus gagatinus (Hope, 1831)
			Scaptodera rhadamistus (Fabricius, 1775)
			Sinodrepanus falsus (Sharp, 1875)
		Onthophagini	*Caccobius* (*Caccobius*) *jessoensis* Harold, 1867
			Digitonthophagus gazella (Fabricius, 1787)
			Onthophagus (*Gibbonthophagus*) *apicetinctus* d'Orbigny, 1898
			Onthophagus (*Serrophorus*) *seniculus* (Fabricius, 1781)
			Onthophagus (*Strandius*) *lenzii* Harold, 1874
		Onitini	*Onitis virens* Lansberge, 1875
			Onitis falcatus (Wulfen, 1786)
		Phanaeini	*Coprophanaeus* (*Metallophanaeus*) *saphirinus* (Strum, 1826)
		Scarabaeini	*Scarabaeus radama* Fairmaire, 1895
			Scarabaeus sacer Linnaeus, 1758
		Sisyphini	*Sisyphus longipes* (Olivier, 1789)

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Scarabaeidae	Aclopinae		*Pachypus candidae* (Petagna, 1787)
	Cetoniinae	Cetoniini	*Cetonia* (*Eucetonia*) *roelofsi roelofsi* Harold, 1880
			Gametis forticula forticula (Janson, 1881)
			Gametis jucunda (Faldermann, 1835)
			Glycyphana (*Glycyphana*) *fulvistemma* Motschulsky, 1860
			Protaetia (*Liocola*) *brevitarsis brevitarsis* (Lewis, 1879)
			Protaetia (*Calopotosia*) *orientalis submarmorea* (Burmeister, 1842)
		Cremastocheilini	*Clinterocera jucunda* (Westwood, 1874)
		Diplognathini	*Anthracophora rusticola* Burmeister, 1842
		Goliathini	*Cosmiomorpha* (*Microcosmiomorpha*) *similis nigra* Niijima & Kinoshita, 1927
			Dicronocephalus wallichi Hope, 1831
			Pseudotorynorrhina japonica (Hope, 1841)
			Rhomborhina (*Rhomborhina*) *polita* Waterhouse, 1875
			Rhomborhina (*Rhomborhina*) *unicolor unicolor* Motschulsky, 1861
		Taenioderini	*Coilodera pseudoalveata* (Miksic, 1971)
	Dynamopodinae		*Orubesa ata* Semenov & Medvedev, 1929
	Dynastinae	Dynastini	*Dynastes tityus* (Linnaeus, 1763)
			Trypoxylus dichotomus septentrionalis Kôno, 1931
			Xylotrupes gideon (Linnaeus, 1767)
		Oryctini	*Oryctes rhinoceros* (Linnaeus, 1758)
		Pentodontini	*Alissonotum pauperum* (Burmeister, 1847)
		Phileurini	*Eophileurus chinensis* (Faldermann, 1835)
	Euchirinae	Euchirini	*Cheirotonus peracanus* Kriesche, 1919
			Euchirus longimanus Linnaeus, 1758
	Melolonthinae	Diplotaxini	*Apogonia bicarinata* Lewis, 1896
			Apogonia ishiharai Sawada, 1940
			Apogonia kamiyai Sawada, 1940
		Hoplini	*Ectinohoplia obducta* (Motschulsky, 1857)
			Hoplia communis Waterhouse, 1875
			Pachycnema sp.
		Melolonthini	*Melolontha* (*Melolontha*) *frater frater* Arrow, 1913
			Melolontha (*Melolontha*) *japonica* Burmeister, 1855
			Polyphylla (*Granida*) *albolineata* (Motschulsky, 1861)
			Polyphylla (*Gynexophylla*) *laticollis laticollis* Lewis, 1887
		Rhizotrogini	*Nigrotrichia kiotoensis* (Brenske, 1894)
			Pollaplonyx flavidus Waterhouse, 1875
			Pedinotrichia picea (Waterhouse, 1875)
			Sophrops konishii konishii Nomura, 1970
		Sericini	*Maladera* (*Omaladera*) *orientalis* (Motschulsky, 1860)
			Maladera (*Aserica*) *secreta secreta* (Brenske, 1897)
			Serica boops Waterhouse, 1875
			Sericania hidana Niijima & Kinoshita, 1923
		Tanyproctini	*Tanyproctus* sp.
	Orphninae	Orphnini	*Orphnus* sp.

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Scarabaeidae	Rutelinae	Adoretini	*Adoretus falciungulatus* Nomura, 1965
			Adorodocia vittaticollis Fairmaire, 1883
			Chaetadoretus formosanus sakishimanus Kobayashi, 1982
			Lepadoretus sinicus (Burmeister, 1855) Burmeister, 1855
			Lepadoretus tenuimaculatus (Waterhouse, 1875)
		Anastatini	*Spodochlamys cupreola* Bates, 1888
		Anoimalini	*Anomala albopilosa albopilosa* (Hope, 1839)
			Anomala edentula yaeyamana (Nomura, 1965)
			Anomala octiescostata (Burmeister, 1844)
			Exomala conspurcata (Harold, 1878)
			Exomala orientalis (Waterhouse, 1875)
			Malaia nigrita (Boisduval, 1835)
			Mimela confucius ishigakiensis Sawada, 1950
			Mimela splendens (Gyllenhal, 1817)
			Mimela testaceipes (Motschulsky, 1860)
			Popillia japonica Newman, 1838
			Popillia lewisi Arrow, 1913
			Popillia mutans Newman, 1838
			Phyllopertha diversa Waterhouse, 1875
			Phyllopertha intermixta (Arrow, 1913)
			Spilopopillia sexguttata (Fairmaire, 1887)
		Anoplognathini	*Anoplognathus brunnipennis* (Gyllenhal, 1817)
			Anoplognathus prasinus (Castelnau, 1840)
			Calloodes rayneri Mac Leay, 1864
			Repsimus manicatus manicatus (Swartz, 1817)
		Rutelini	*Chrysophora chrysochlora* (Latreille, 1812)
			Dicaulocephalus feae Gestro, 1888
			Kibakoganea tamdaoensis Miyake & Muramoto, 1992
			Parastasia ferrieri ferrieri Nonfried, 1895
			Parastasia sp.1 Westwood, 1841
			Pelidnota prasina Burmeister, 1844
			Pelidnota punctate (Linnaeus, 1758)
	Trichinae	Osmodermini	*Osmoderma opicum* Lewis, 1887
		Trichini	*Corynotrichius bicolor* Kolbe, 1892
			Epitrichius elegans Kano, 1931
			Gnorimus subopacus Motschulsky, 1860
			Lasiotrichius succinctus succinctus (Pallas, 1781)
			Paratrichius doenitzi (Harold, 1879)
			Trichius fasciatus (Linnaeus, 1758)
			Trichius japonicus Janson, 1885
		Incaini	*Inca bonplandi* (Gyllenhal, 1817)
	Valginae	Valgini	*Dasyvalgus tuberculatus* (Lewis, 1887)
			Neovalgus fumosus (Lewis, 1887)
			Nipponovalgus angusticollis angusticollis (Waterhouse, 1875)
			Nipponovalgus yonakuniensis Sawada, 1941
		Microvalgini	*Microvalgus* sp.

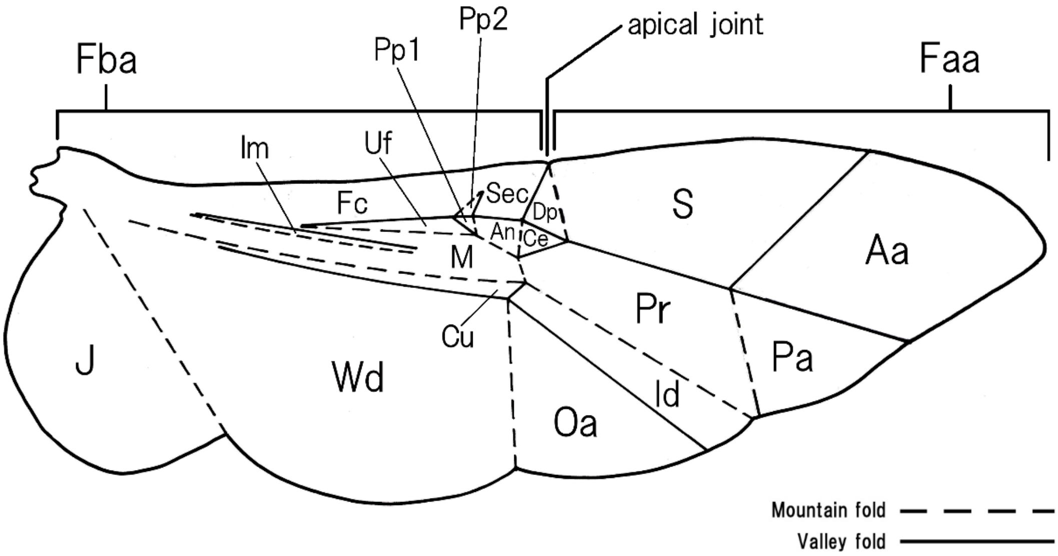
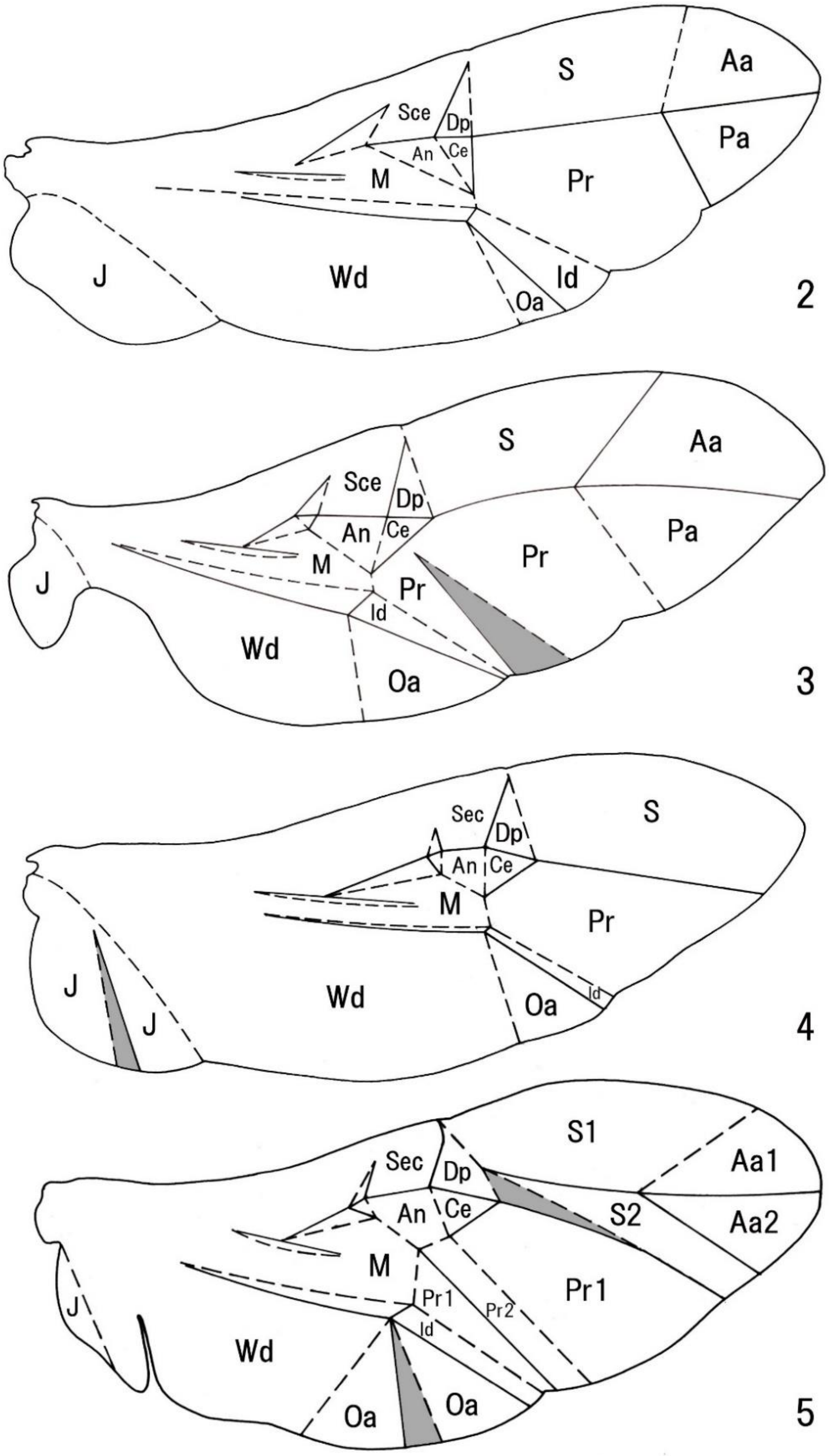
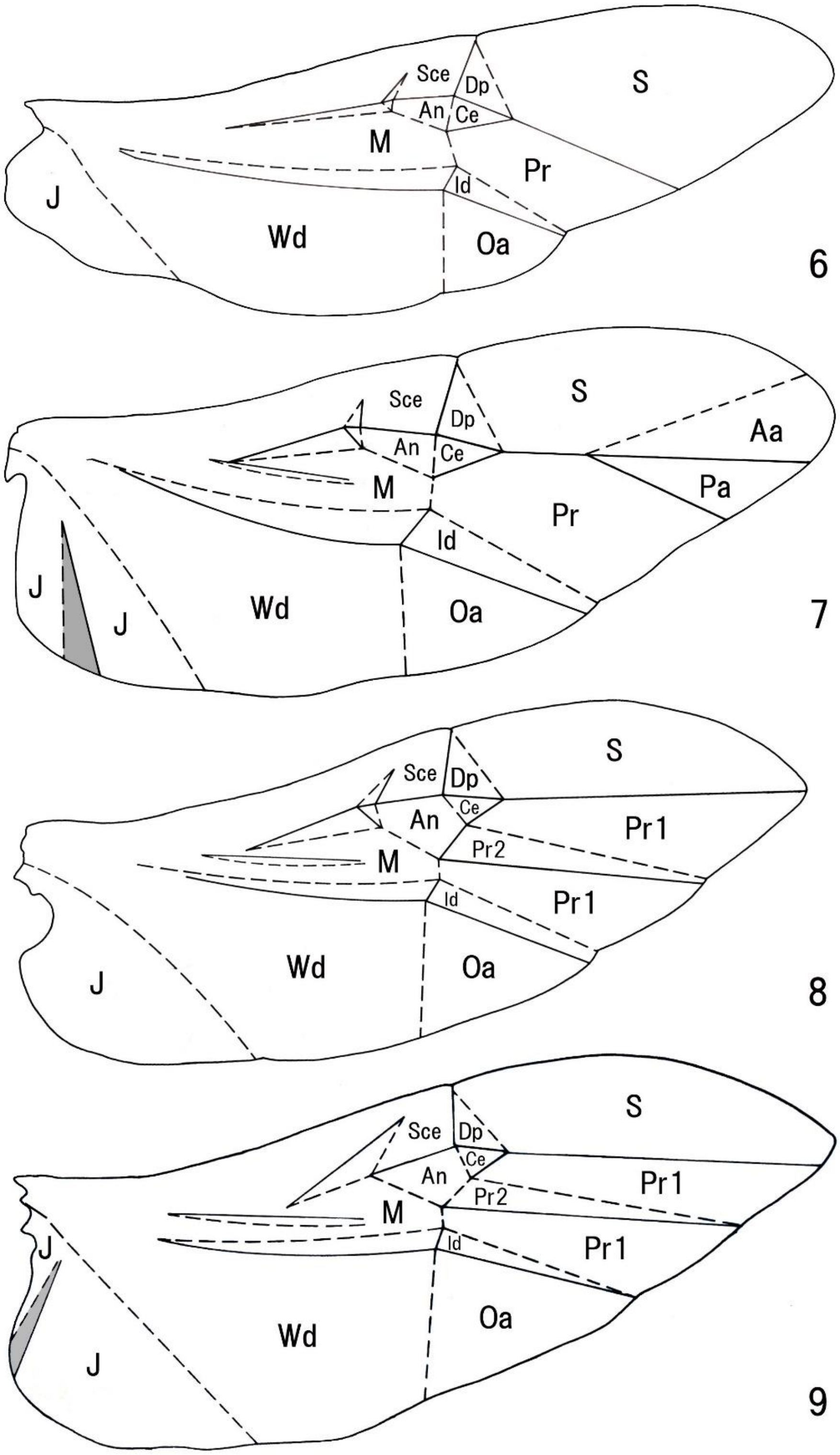


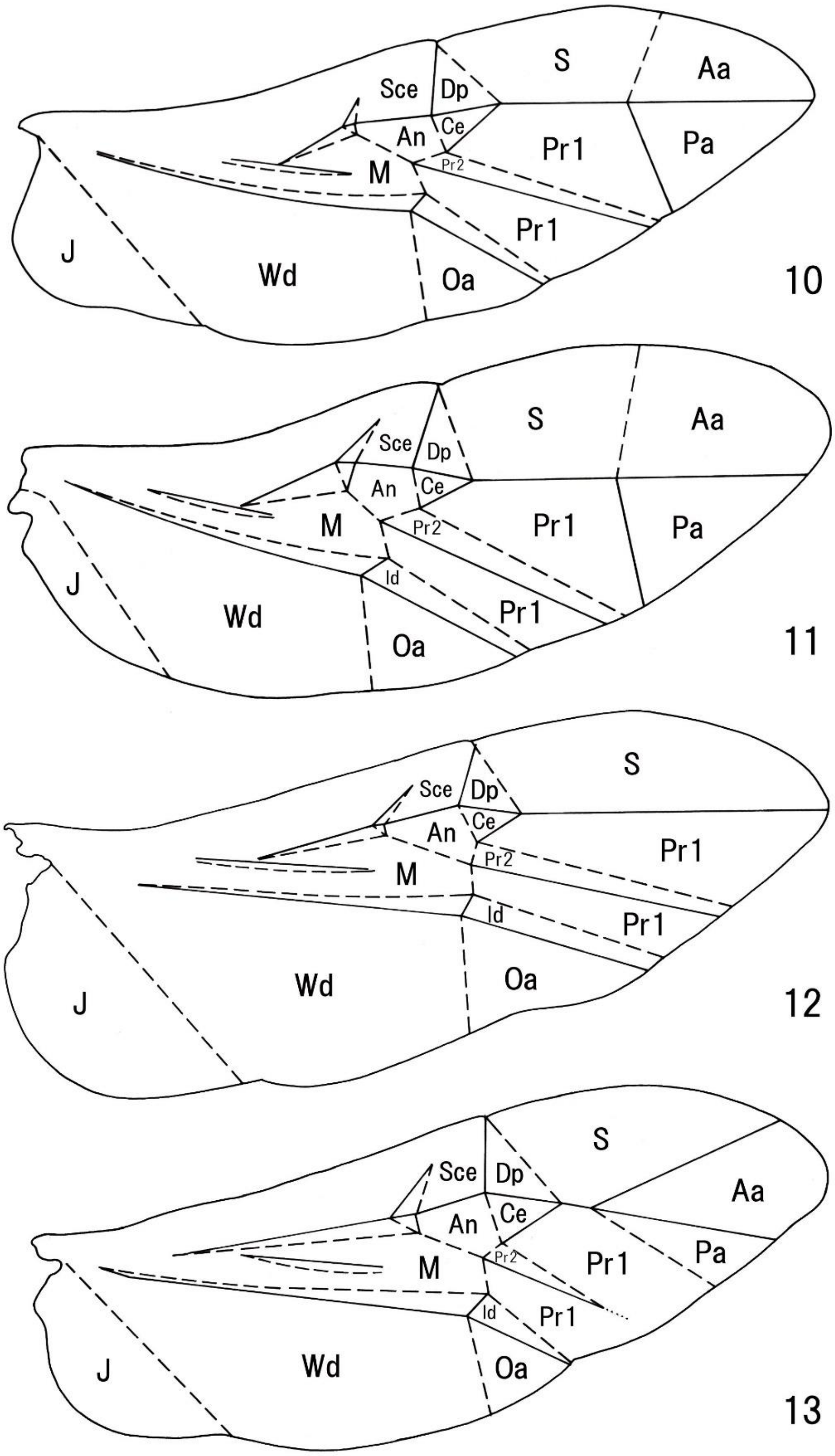
Figure 1. Schematics diagram of hind wing folding pattern in Scarabaeoidea. Abbreviations: Antero-apical (Aa), Antero medial (An), Central (Ce), Cubital (Cu), Distal pivot (Dp), First costal (Fc), Inside medial (Im), Intercubital distal (Id), Jugal (J), Medial (M), Outer anal (Oa), Postero-apical (Pa), Proximal pivot 1 (Pp1), Proximal pivot 2 (Pp2), Principal (Pr), Stigmatal (S), Second costal (Sc), Under first costal (Uf), Wedge (Wd).



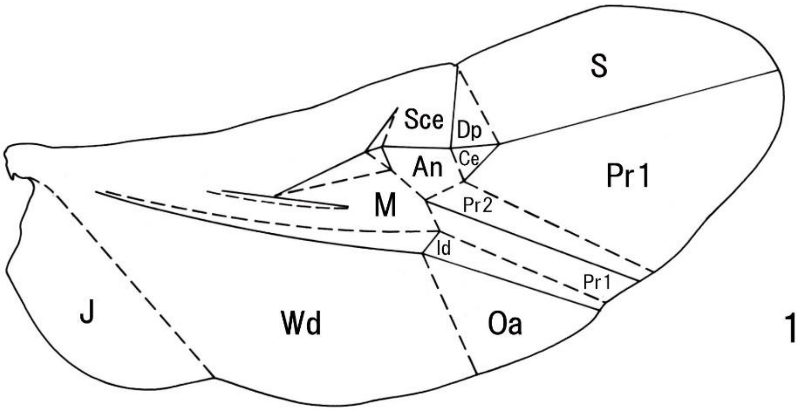
Figures 2–5. Hind wing folding patterns. **2** *Bolbocerosoma nigroplagiatum* (Waterhouse, 1875), **3** *Bolbelasmus minutus* Li et Masumoto, **4** *Phelotrupes laevistriatus* (Motschulsky), **5** *Glaresis beckeri* Solsky.



Figures 6–9. Hind wing folding patterns. **6** *Amphicoma splendens* (Yawata), **7** *Phaeochrous emarginatus* Laporte, **8** *Dorcus rectus* (Motschulsky), **9** *Lucanus maculifemoratus* Motschulsky.



Figures 10–13. Hind wing folding patterns. **10** *Ceruchus lignarius* Lewis, **11** *Aesalus asiaticus* Lewis, **12** *Lamprima adolphinae* (Gestro), **13** *Platycerus acuticollis* Y. Kurosawa.



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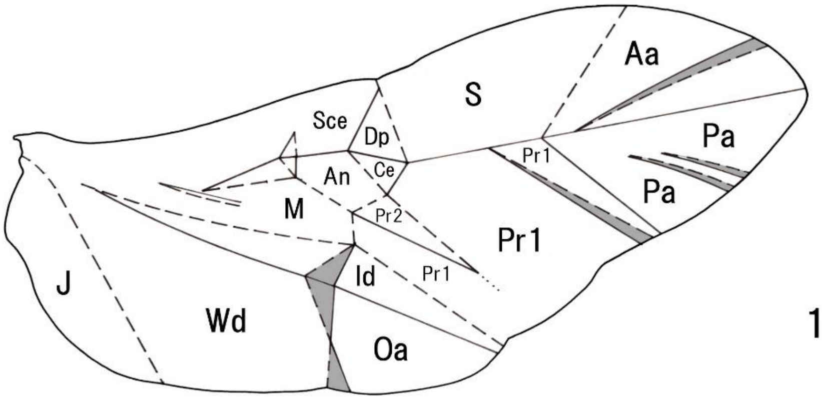

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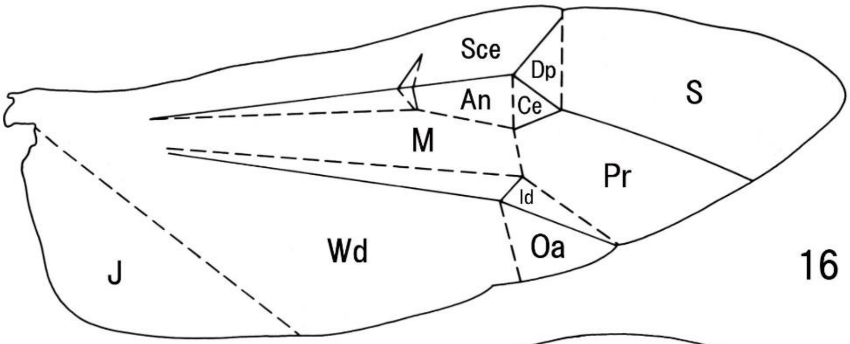

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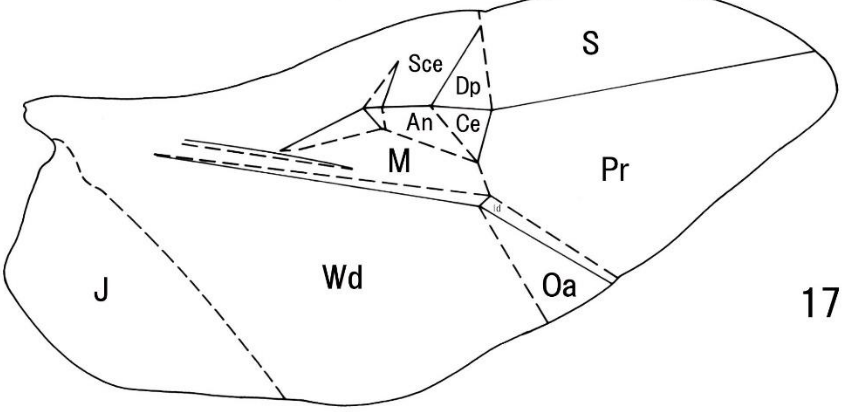

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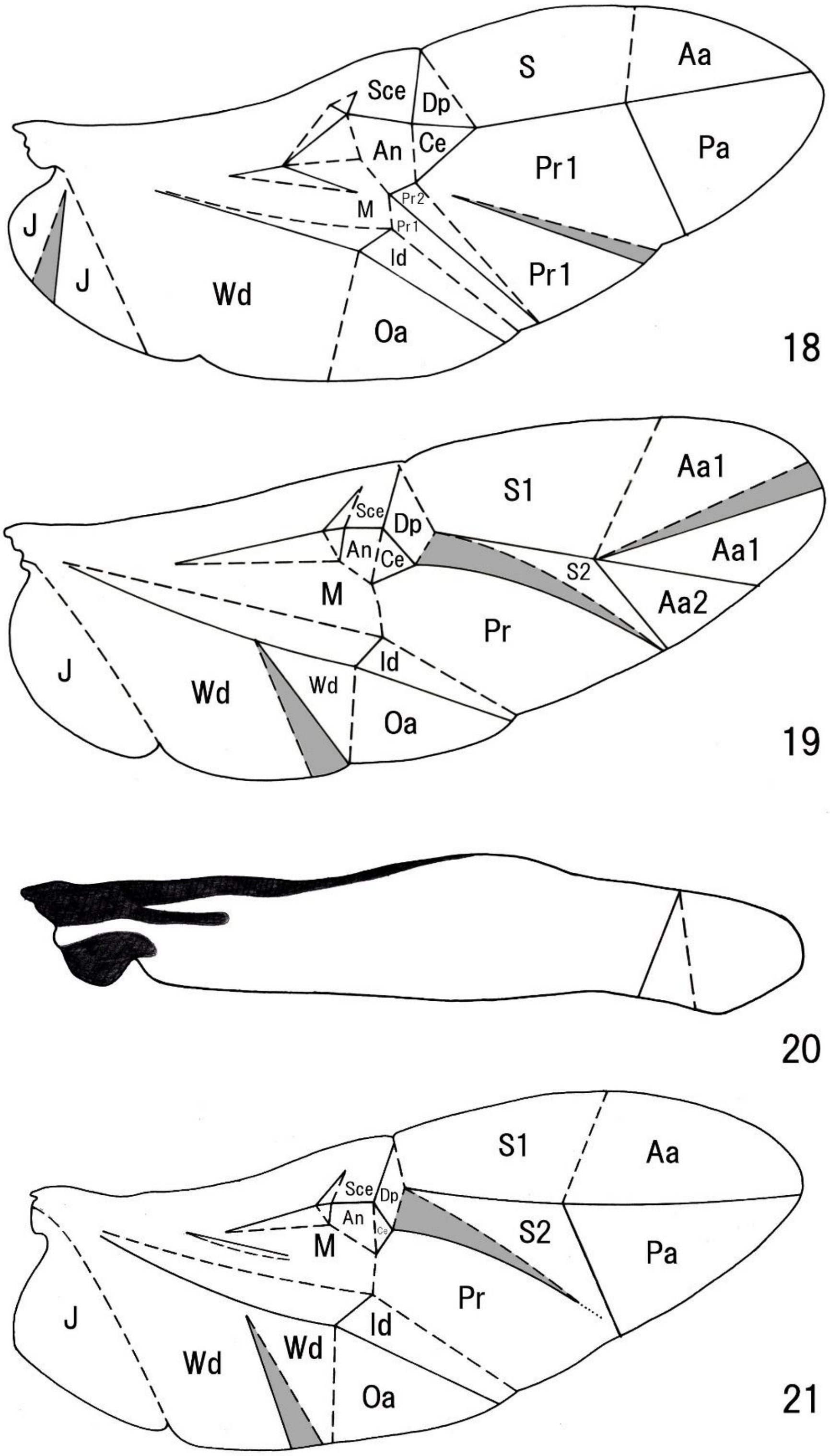
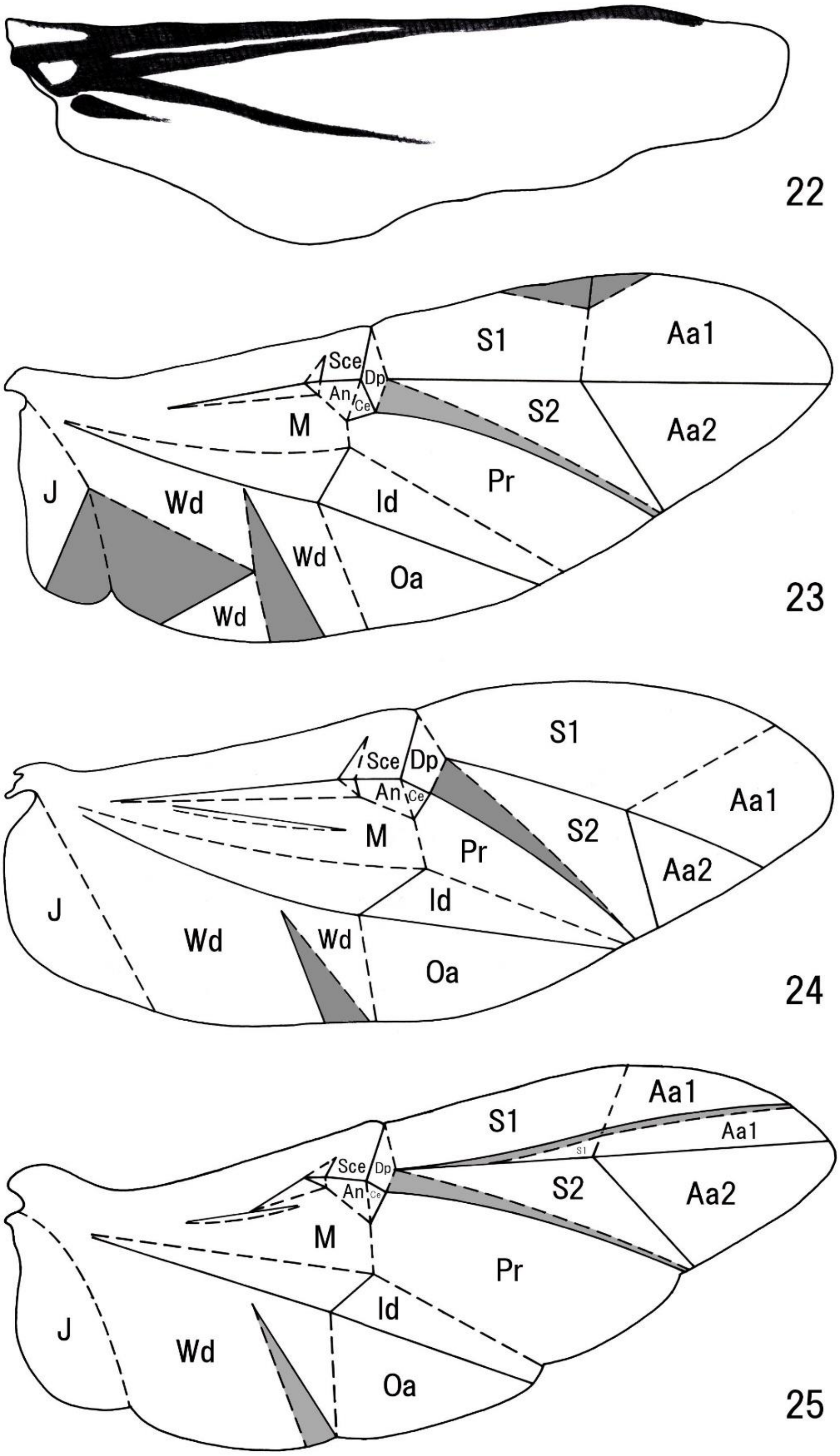
Figures 14–17. Hind wing folding patterns. **14** *Nicagus japonicus* Nagel, **15** *Ochodaeus chrysomeloides* (Schrank), **16** *Macrolinus sikkimensis* Stoliczka, **17** *Pleocoma dubitabilis* Davis.



Figures 18–21. Hind wing folding patterns. **18** *Glyptotrox uenoi* (Nomura), **19** *Caelius denticollis* Lewis, **20** *Aegialia nitida* Waterhouse, **21** *Aphodius breviusculus* (Motschulsky).



Figures 22–25. Hind wing folding patterns. **22** *Psammodius kobayashii* Nomura, **23** *Rhyparus azumai* Nakane, **24** *Chiron* sp., **25** *Copris ochus* (Motschulsky).

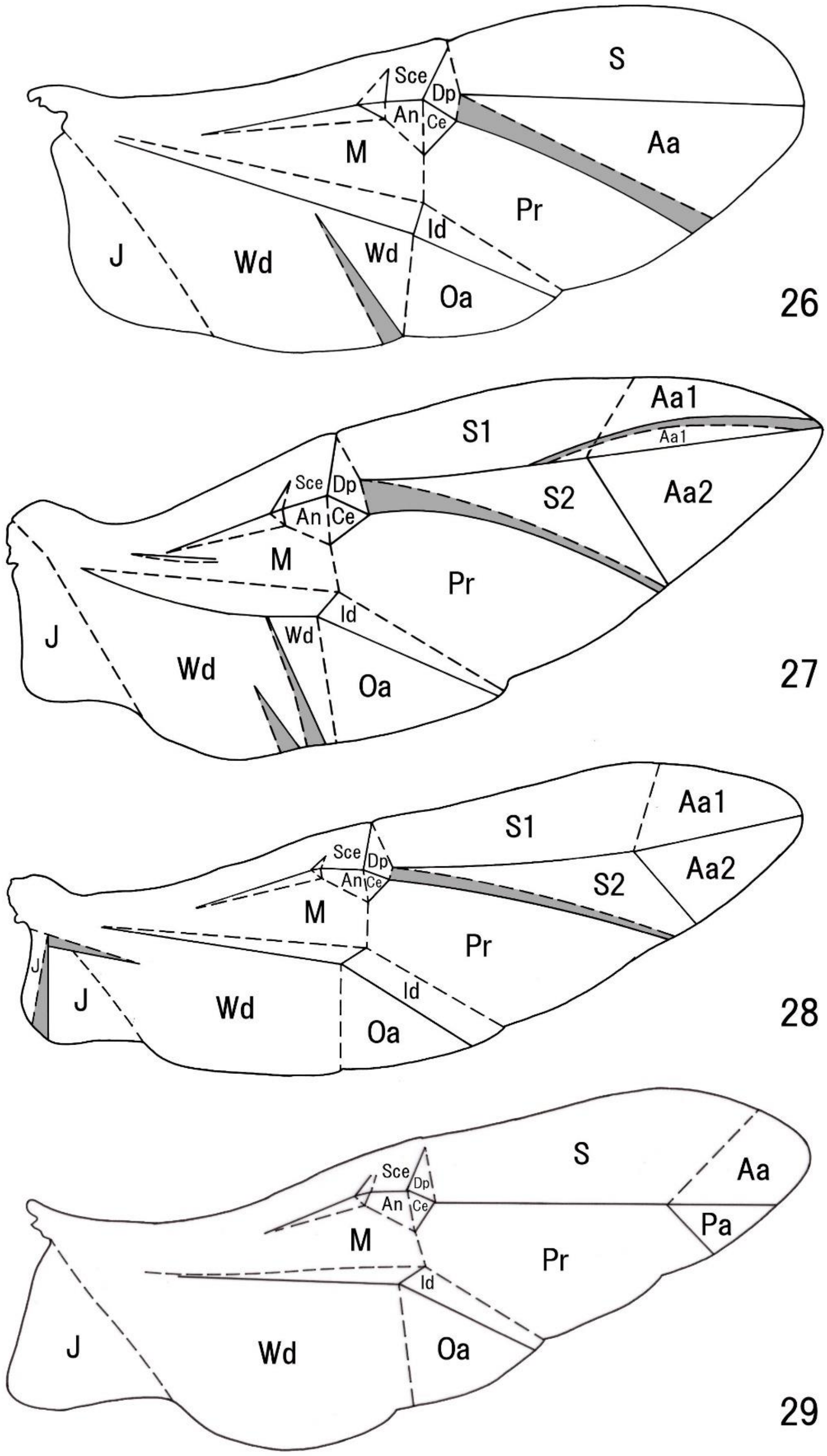


Figure 26−29. Hind wing folding patterns. **26** *Paraphytus dentifrons* Lewis, **27** *Dichotomius boreus* (Olivier), **28** *Paragymnopleurus melanarius* (Harold), **29** *Onitis virens* Lansberge.

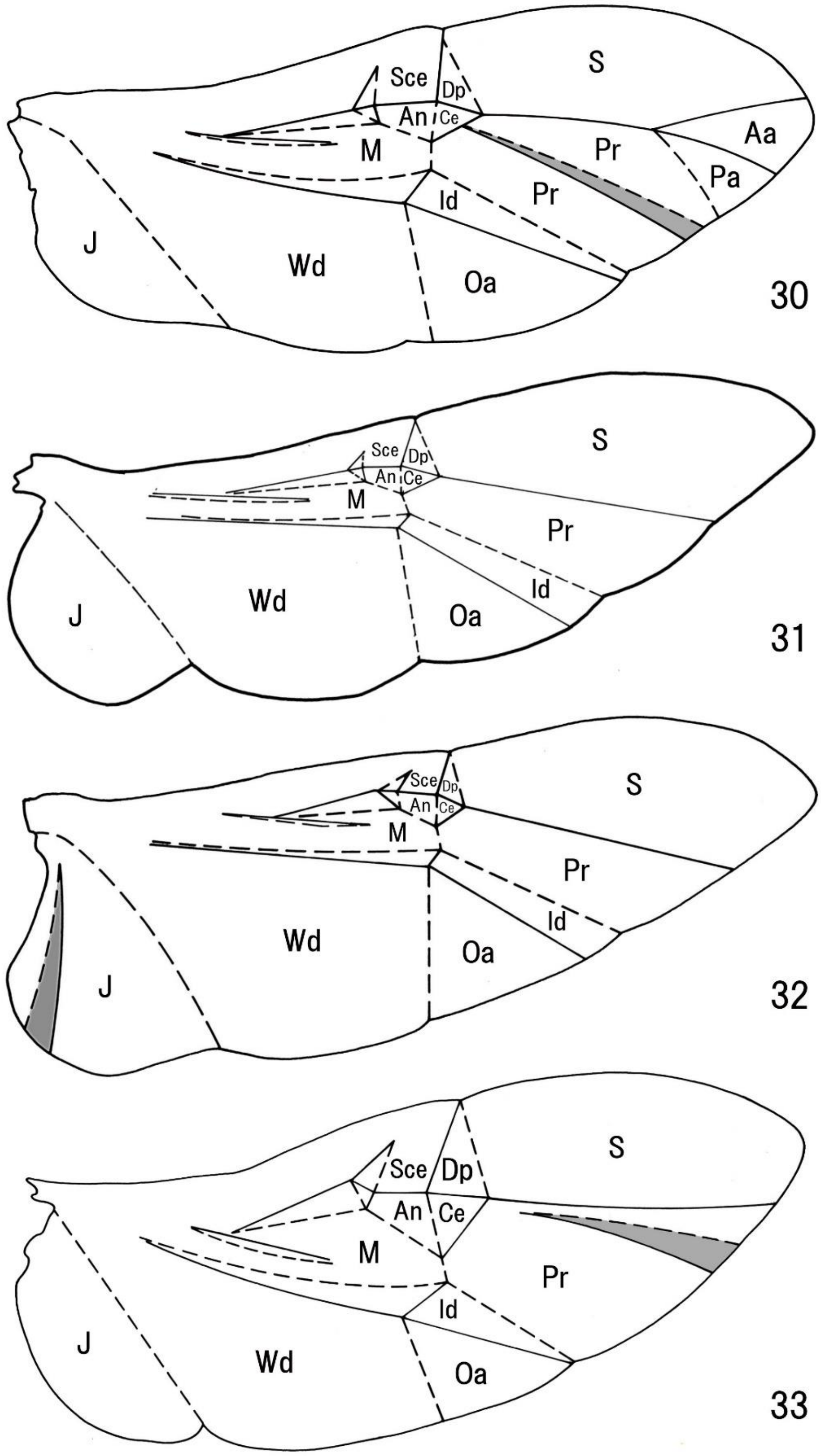
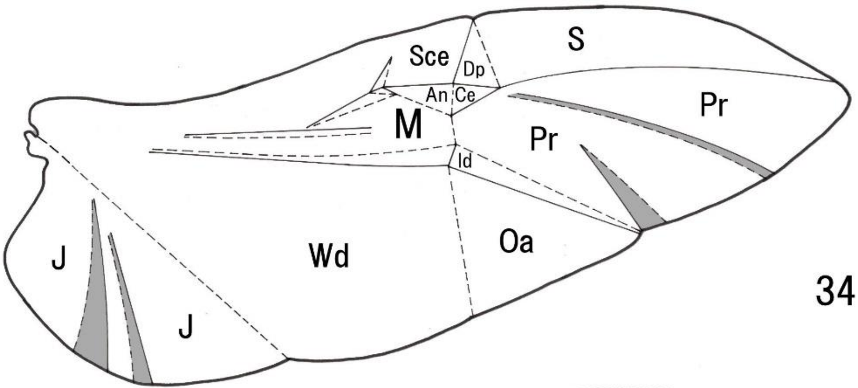


Figure 30−33. Hind wing folding patterns. **30** *Pachypus candidae* (Petagna), **31** *Gametis forticula* (Janson), **32** *Rhomborhina polita* Waterhouse, **33** *Orubesa ata* Semenov et Medvedev.



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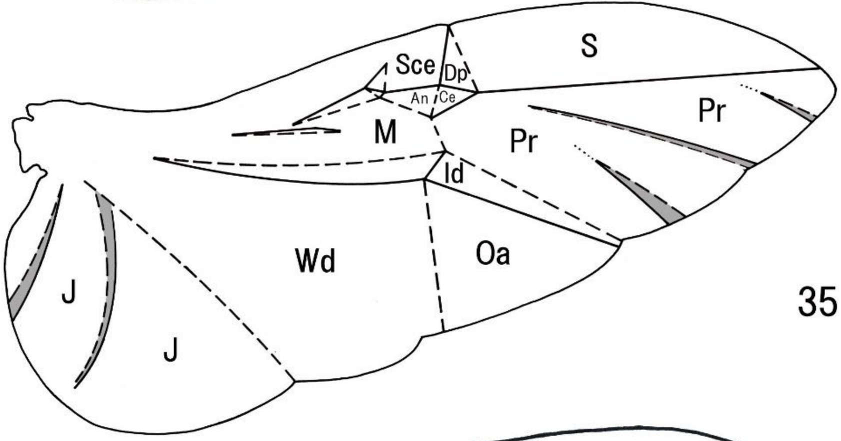

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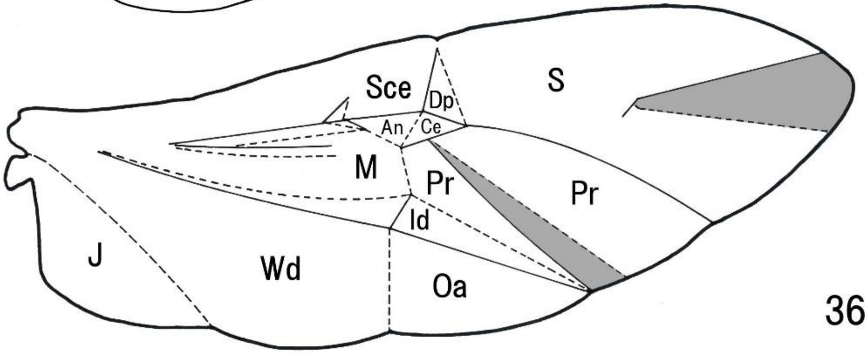

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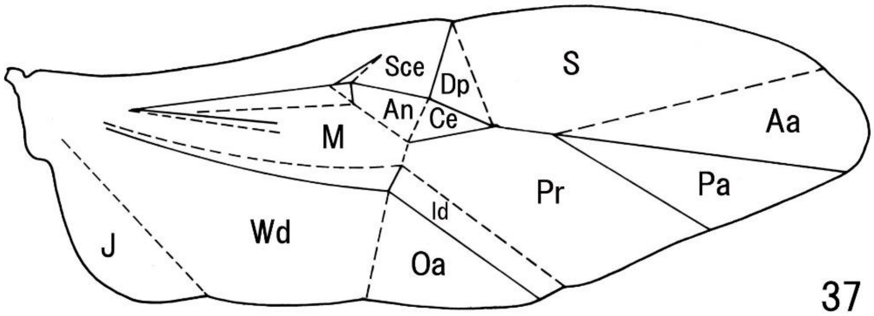

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Figure 34−37. Hind wing folding patterns. **34** *Trypoxylus dichotomus* Kôno, **35** *Cheirotonus peracanus* Kriesche, **36** *Apogonia bicarinate* Lewis, **37** *Hoplia communis* Waterhouse.

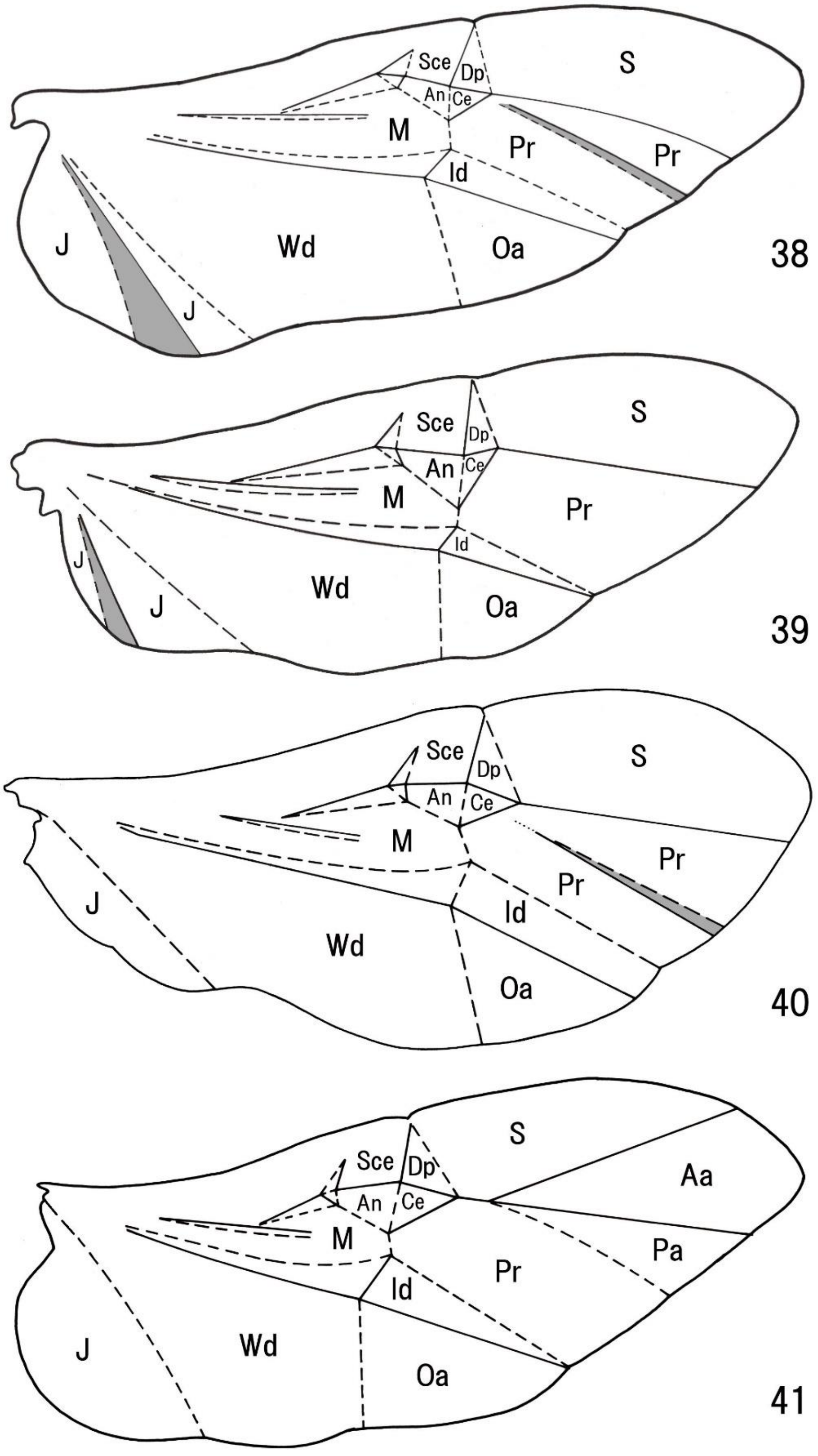


Figure 38−41. Hind wing folding patterns. **38** *Melolontha japonica* Burmeister, **39** *Maladera orientalis* (Motschulsky), **40** *Tanyproctus* sp., **41** *Orphnus* sp.

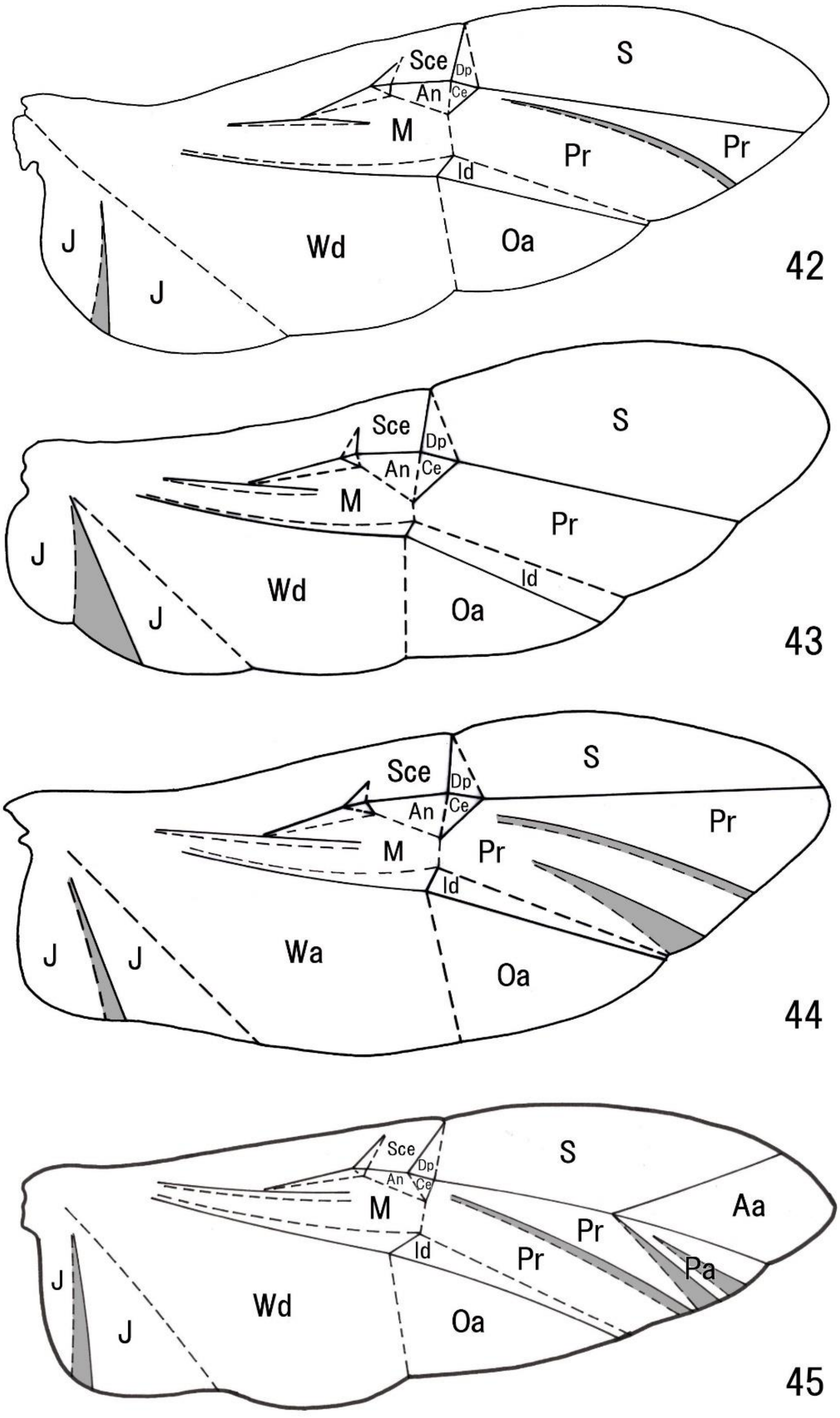


Figure 42−45. Hind wing folding patterns. **42** *Chrysophora chrysochlora* (Latreille), **43** *Popillia japonica* Newman, **44** *Parastasia ferrieri* Nonfried, **45** *Lepadoretus tenuimaculatus* (Waterhouse).

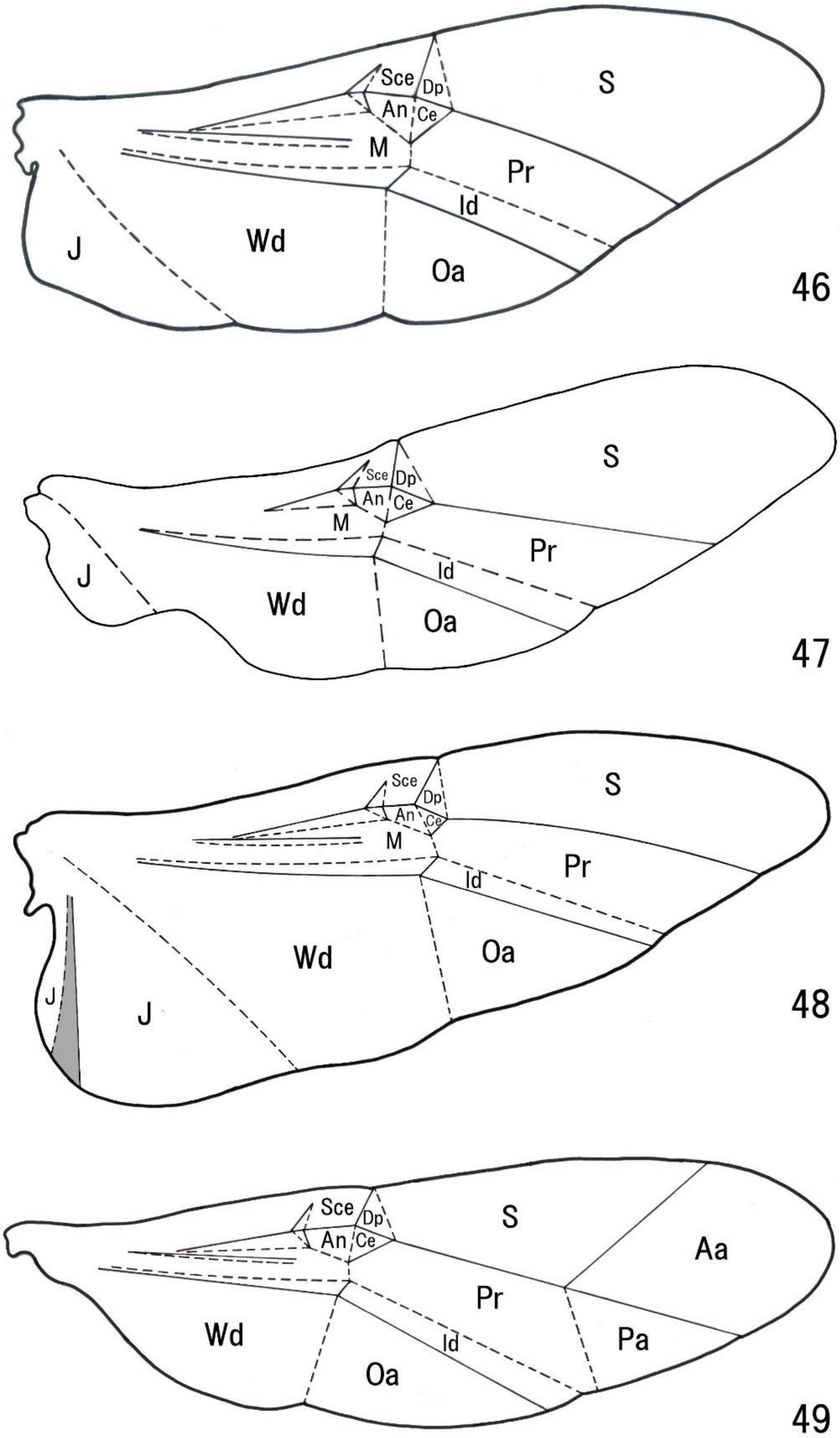


Figure 46–49. Hind wing folding patterns. **46** *Paratrichius doenitzi* (Harold), **47** *Lasiotrichius succinctus* (Pallas), **48** *Osmoderma opicum* Lewis, **49** *Nipponovalgus angusticollis* (Waterhouse).

2−2 Mesonotum

2−2−1

Comparison of mesonotal morphology in beetles of the coprophagous group of Scarabaeidae and other scarabaeoid taxa (Coleoptera, Scarabaeoidea)

Introduction

The coprophagous group of Scarabaeidae has long attracted the attention of numerous researchers, and several detailed comparative studies on various morphological structures have been conducted (Ritcher and Baker 1974, Yadav and Pillai 1979, Caveney and McIntyre 1981, Nel and Villiers 1988, Nel and Scholtz 1990, d'Hotman and Scholtz 1990a, Grebennikov and Scholtz 2004) [for more information see Scholtz (1990) and Scholtz and Grebennikov (2016)]. In contrast, however, there have been relatively few comparative studies that have focused on the mesonotal structures in scarabaeid beetles. The mesonotum of Coleoptera has been described by researchers such as Snodgrass (1909, 1935), Larsén (1966) and Matsuda (1970), who established basic terminologies, and some different researchers have indicated more detailed descriptions of mesonotal structures in some coleopteran species (El-Kifl 1953, Doyen 1966, Naomi 1988, Kazantsev 2003−2004, Beutel and Komarek 2004, Friedrich and Beutel 2006). Observations made in these studies tend to indicate that mesonotal structures mutate relatively frequently at the family level, and accordingly, comparative studies are necessary to establish the detailed structures in each taxon. Detailed studies that have examined these structures in the Scarabaeidae have been conducted for species such as *Melolontha vulgaris* Fabricius [synonym of *Melolontha melolontha* (Linnaeus)] (Snodgrass 1909), *Phanaeus vindex* MacLeay and *Coprophanaeus lancifer* (Linnaeus) (Edmonds 1972), and *Lagochile emarginata* (Gyllenhal) (Albertoni *et al*. 2014). However, although Philips *et al*. (2004, 2016) and Tarasov and Génier (2015) examined a range of characters in the Scarabaeinae and generated large data matrices, they did not present detailed descriptions. With respect to establishing phylogenetic relationships, the value of mesonotal characters has been proven in studies on other coleopteran groups (Beutel and Komarek 2004, Friedrich and Beutel 2006, Ge *et al*. 2007) and the Scarabaeinae (Philips *et al*. 2004, 2016, Tarasov and Génier 2015). The accumulation of new reliable morphological data, particularly for features that can be readily observed, will make an important contribution to molecular phylogenetic studies in recent years.

In this study, I examined details of the mesonotal structures of 31 genera from four subfamilies within the coprophagous group of Scarabaeidae, four genera from four subfamilies within the phytophagous group of Scarabaeidae, and five genera within other scarabaeoid families. Although the comparatively few representatives species examined are clearly inadequate and may thus not provide a totally reliable basis on which to discuss far-reaching phylogenetic and systematic implications, it has, nevertheless, been possible to identify similarities between the different subfamilies.

Material and methods

Preparation of specimens

All dissections were carried out on dried specimens. In order to relax the specimens, they were initially placed in 50% ethanol for a few minutes, after which the prothorax and abdomen were detached from the meso- and metathorax using fine forceps. The meso- and metathorax were placed in 5% KOH solution for 6 to 8 h to soften and dissolve the internal organs. Following pretreatment, these parts were washed several times in distilled water. Therefore, the mesonotum was detached from the meso- and metathorax, and the isolated mesonotum was soaked in 99% ethanol for 10 min to dehydrate the tissues.

Drawings were made with the aid of OLIMPAS SZX9 and, LEICA M165C microscopes and a KEYENCE VHX-1000 digital microscope. Fine structures such as hairs and punctates on the mesonotal surface were excluded from the diagrams as these tended to obscure structures required for comparative observation.

Terminology

The main morphological terminology used for the mosonotal structures of Scarabaeidae follows that of Larsén (1966) and Matsuda (1970), although the studies of other authors were also consulted (Doyen 1966, Edmonds 1972, Beutel and Komarek 2004, Albertoni *et al*. 2014).

In species of the Scarabaeidae, the mesonotum is located between the articular process of the elytra and mainly consists of the first phragma, prescutum, scutum, and scutellum (Fig. 3F). The first phragma has been observed in diverse coleopteran taxa (Larsén 1966, Matsuda 1970, Edmonds 1972, Albertoni *et al*. 2014), and some researchers have established different terminologies for the homologous trait, for example, prescutum + anterior phragma (Naomi 1988), anterior phragma (El-Kifl 1953), anterior phragma or prephragma (Snodgrass 1935), prephragma (Doyen 1966), and prophragma (Beutel and Komarek 2004). The prescutum is generally indistinguishably fused to scutum. According to Edmonds (1972), the scutum and scutellum form the scutum + scutellum owing to the absence of the scutoscutellar suture, which normally divides the scutum and scutellum. Furthermore, Edmonds (1972) mentions that internal ridges, which are termed the vertical and horizontal plates (Fig. 7F), are not indicative of basic notal divisions. On the lateral side of the scutum + scutellum there is generally a pair of postmedian notal processes (Matsuda 1970) (Fig. 3F). According to El-Kifl (1953) and Doyen (1966), these processes are referred to the posterior notal processes, although Matsuda (1970) has started that these processes are probably absent in many coleopteran species. On the ventral side of the scutum + scutellum, there is a pouch-like cavity referred to as the "mesonotal pouch" (Beutel and Komarek 2004) (Fig. 6A, 7F) and a pair of processes designated the "scutellar processes" (Doyen, 1966) (Fig. 7F), which are often referred to using different terminologies, such as the yoke plate (Snodgrass 1909, Matsuda 1970), lateral processes of the second phragma (Larsén 1966), and sclerite q (Edmonds 1972). The scutellar processes and posterior inflection of the mesonotal pouch are suggested to be remnants of the mesopostnotum (Snodgrass 1909, Larsén 1966, Matsuda 1970, Edmonds 1972), and the axillary cord, which is a weakly sclerotized flexible membrane (Doyen 1966, Friedrich and Beutel 2006) that is attached in many cases. The posterior inflection of the mesonotal pouch, yoke plate, and axillary cord are related to connect with the metathoracic notum.

Specimens studied

In the present study, I examined from 36 genera within four subfamilies of the coprophagous group of Scarabaeidae (Aegialiinae, Aphodiinae, Chironinae and Scarabaeinae), other scarabaeoid beetles in the families Geotrupidae, Glaphyridae, Hybosoridae, Pleocomidae and Trogidae, and four subfamilies within the phytophagous group of Scarabaeidae (Cetoniinae, Dynastinae, Rutelinae and Melolonthinae). Four species within three genera of the tribe Aegialiini were selected in the subfamily Aegialiinae. 14 species within 10 genera of five tribes (Aphodiini, Eupariini, Odochilini, Psammodiini, and Rhyparini) were selected in the subfamily Aphodiinae. One species in the genus *Chiron* MacLeay was selected in the subfamily Chironinae. 24 species within 17 genera of 10 tribes (Ateuchini, Coprini, Deltochilini, Gymnopleurini, Oniticellini, Onitini, Onthophagini, Phanaeini, Scarabaeini, and Sisyphini) were selected in the subfamily Scarabaeinae. For each of the following taxa, I examined single species: Geotrupidae, Glaphyridae, Hybosoridae, Pleocomidae, Trogidae, Cetoniinae, Dynastinae, Rutelinae and Melolonthinae (Table 1).

Results

The mesonotum in the Scarabaeoidea is located beneath the pronotum and lies between of elytral bases (Fig.1). Since the anterior half of the mesonotum is often covered by the pronotum, typically less than half of the entire structure is visible when observed dorsally. In some species within the coprophagous group of the Scarabaeidae, however, the entire extent of the mesonotum is completely hidden by the pronotum. The boundary demarcating the concealed and exposed portions is generally characterized by a transverse depression. The mesonotum and the elytral bases are articulated through the postmedian notal process, some axillary sclerites, and the axillary cord. The basic structure of the mesonotum in the Scarabaeoidea consist of four parts: the first phragma, prescutum, scutum, and scutellum, among which, the prescutum is substantially reduced in size or has been completely lost. The scutum and scutellum are completely fused, owing to disappearance of the scutoscutellar suture. Internal ridges (the vertical and horizontal plates) typically develop and form a mesonotal pouch, into which muscles associated with the back and forth movements of the mesonotum are inserted. The movement of the mesonotum is important with respect to fixation of the elytra. When the mesonotum is tilted forward, the elytra are extended and elevated, whereas when tilted backward, which is the normal position, the position of the elytra becomes fixed. This fixation mechanism is also observed in the subfamily Scarabaeinae, in which the mesonotum is completely covered by the pronotum (Fig. 1). The scutellar process and axillary cord on the ventral side of the scutum + scutellum function as a levering device for the back and forth movements. The axillary cord shows various morphological states, including thin membrane and sclerotized processes. The sclerotized axillary cord found in some groups, which is located at the base of the elytra and third axillary sclerites when the elytra are opened, is considered to play a role in adjusting the angle of the elytra, thereby functioning as balancer during flight.

Aegialiinae (Figs. 2A−C, 6A−C, 10A)

In the subfamily Aegialiinae (genera *Aegialia*, *Caelius,* and *Psammoporus*) the anterior two-thirds of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversally depressed. The first phragma is reduced, and the most part is unrecognizable from the dorsal side. The prescutum is completely lost. The scutum + scutellum is sagittate in shape, and the exposed portion is triangular. The postmedian notal process is obtuse, and in the genus *Caelius* (Fig. 2C) its base invaginate. The mesonotal pouch is inverted triangular shaped, but the vertical plate and horizontal plate is strongly reduced. The scutellar process is sclerotized rod-shaped and the attached axillary cord is present as a very thin membrane. The scutellar process is completely fused with the posterior inflection of mesonotal pouch.

In the *Aegialia nitida* (Fig. 2B), which has atrophied hind wing, the mesonotum length becomes extremely short for the width as compared to other species. The postmedian notal process is obtuse and the development is very weak compared to other winged species. The mesonotal pouch is semicircular shaped.

Aphodiinae (Figs. 2D–2I, 3A, 6D–6I, 7A, 10B–10C)

In the subfamily Aphodiinae, I examined the mesonotum of species in the following genera: *Aphodius* (*Agrilinus*), *Aphodius* (*Brachiaphodius*), *Aphodius* (*Colobopterus*), *Aphodius* (*Phaeaphodius*), *Aphodius* (*Sinodiapterna*), *Saprosites*, *Setylaides*, *Ataenius*, *Odochilus*, *Rakovicius*, *Psammodius*, *Trichiorhyssemus*, *Rhyparus*, and *Sybacodes*. The mesonotum in these species, at least the anterior half, is generally covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is weakly developed. The prescutum is completely lost. Generally, the scutum + scutellum is sagittate in shape, and the exposed portion has a triangular of pointed shape. The postmedian notal process is obtuse, and in the genus *Aphodius* (Fig. 2D–2F) its base invaginate. The mesonotal pouch is rounded or oval in shape. The vertical and horizontal plates generally developed, but in the genera *Psammodius*, *Saprosites*, *Setylaides*, and *Trichiorhyssemus* (Figs. 6G, 6I) the vertical plate tends to be poorly developed. The scutellar process is sclerotized rod-shaped and the attached axillary cord is present as a very thin membrane. The scutellar process is completely fused with the posterior inflection of mesonotal pouch. In the genus *Aphodius* (*Colobopterus*) (Figs. 2E, 6E), although the most common features are similar to those of other aphodiine species, the scutum + scutellum is diamond shaped. In the genus *Aphodius* (*Sinodiapterna*) (Figs. 2F, 6F, 10C), the most part of the mesonotum is exposed, with the visible portion being triangular in shape and elongating toward the posterior apex. The scutum + scutellum is hastate in shape. The mesonotal pouch is quadrangle in shape and opens forward owing to the decrease of the horizontal plate.

In the tribe Rhyparini (*Rhyparus* and *Sybacodes*) (Figs. 3A, 7A) the mesonotum is covered by the pronotum and elytra. The anterior half of the mesonotum is covered by the pronotum and each side of the exposed part is covered with an elytral base, with both boundaries being depressed. The mesonotal pouch is quadrangle in shape and opens forward owing to the decrease of the horizontal plate, whereas the vertical plate develops.

Chironinae (Figs. 3B, 7B, 10D)

In the subfamily Chironinae (genus *Chiron*) the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is reduced, and the most part is unrecognizable from the dorsal side. The prescutum is completely lost. The scutum + scutellum is sagittate in shape, and the exposed portion is strongly pointed. The postmedian notal process is obtuse, and its base weakly invaginate. The mesonotal pouch is oval shaped, with the developed vertical plate lying at the center. The scutellar process is sclerotized rod-shaped and the attached axillary cord is present as a very thin membrane. The scutellar process is completely fused with the posterior inflection of mesonotal pouch.

These features are similar to genus *Caelius* (Aegialiinae).

Scarabaeinae (Figs. 3C−4E, 7C−8E, 10E)

I examined the mesonotum of the following genera in the subfamily Scarabaeinae: *Paraphytus*, *Deltochilum*, *Panelus*, *Catharsius*, *Copris*, *Heliocopris*, *Paragymnopleurus*, *Liatongus*, *Scaptodera*, *Sinodrepanus*, *Caccobius*, *Digitonthophagus*, *Onthophagus*, *Onitis*, *Coprophanaeus*, *Scarabaeus*, and *Sisyphus*. The mesonotum is generally completely covered by the pronotum, in some tribes (Onitini and Oniticellini) (Figs. 3H, 4B), the posterior apex of the mesonotum is exposed. The boundary between the concealed and exposed portions is flat or slightly depressed. The first phragma is generally well-developed and is characterized by an anterior margin that is deeply emarginate at the center. However, in the genera *Deltochilum*, *Scaptodera*, and *Sisyphus* (Figs. 3D, 3H, 4E), the developed first phragma is difficult to observe from the dorsal view and the anterior margin is pointed. In certain genera such as the *Paraphytus* and *Panelus* (Figs. 3C, 3E, 7C, 7E), the development of the first phragma tend to be very weak. The prescutum is generally reduced and the remnant is visible at the anterior margin of the scutum + scutellum. However, in the genus *Paraphytus*, the prescutum has been completely lost. The scutum + scutellum is pentagonal, and in the tribes Onitini and Oniticellini the posterior apex is elongated and pointed (Figs. 3H, 4B). The postmedian notal process is generally obtuse, and is base is truncated. The mesonotal pouch is rounded or oval shaped. The vertical and horizontal plates develop strongly, with the former generally traversing the mesonotal pouch. Contrastingly, in the genera *Deltochilum*, *Paraphytus*, *Scaptodera*, and *Sisyphus* (Fig. 7C, 7D, 7H, 8E), the mesonotal pouch is incompletely divided by the vertical plate. The scutellar process is sclerotized triangular shaped and the attached axillary cord is usually present as a thin membrane, although weakly sclerotized axillary cord is observed in some genera such as *Catharsius*, *Copris*, *Coprophanaeus*, *Deltochilum*, *Heliocopris*, *Onitis*, and *Paragymnopleurus* (Figs. 7D, 7F, 7G, 8B, 8C), whereas in the genus *Panelus* (Fig. 7E), the axillary code is reduced. The sutural line between the scutellar process and the posterior inflection of the mesonotal pouch is clearly visible.

Phytophagous group of Scarabaeidae

Dynastinae, Rutelinae and Melolonthinae (Figs. 4F, 8F, 11)

In the phytophagous group of Scarabaeidae (genera *Anomala*, *Melolontha* and *Trypoxylus*) the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is well-developed, and is visible from the dorsal surface. The remnant of prescutum is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is shield-like in shape, and the exposed portion is diffusely triangular. The postmedian notal process is obtuse. The mesonotal pouch is oval in shape. The vertical and horizontal plates usually develop, but in the genus *Trypoxylus* the former is reduced. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process (Fig. 11). The posterior process is characterized by a pouch-like structure and is covered with long setae. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Cetoniinae (Figs. 4G, 8G)

In the subfamily Cetoniinae (genus *Cetonia*) the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is flat. The first phragma is well-developed, and is visible from the dorsal surface. The prescutum is completely lost. The scutum + scutellum is diamond shaped, and the exposed portion appears as a large triangle. The postmedian notal process is strongly reduced. The mesonotal pouch is oval shaped, but the vertical plate is completely lost. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process, whereas the development and sclerotized membranous state of the posterior arm corresponding to axillary cord is weak compared with that in other phytophagous groups of Scarabaeidae. The posterior process is characterized by a shallow pouch-like structure and is covered with long setae. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Geotrupidae (Figs. 4H, 8H)

In the family Geotrupidae (genus *Phelotrupes*) the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is well-developed, and the lateral ends protrude outside. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is shield-like in shape, and the exposed portion is diffusely triangle. The postmedian notal process is obtuse and its base invaginate. The mesonotal pouch is flabellate in shape. The vertical and horizontal plates that form the mesonotal pouch developed. The scutellar process is a sclerotized rod-shaped and completely fused with the posterior inflection of the mesonotal pouch, and the attached axillary cord is very thin membrane.

Glaphyridae (Figs. 4I, 8I, 10F)

In the family Glaphyridae (genus *Amphicoma*) the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is well-developed, and the lateral sides protrude to outside. The prescutum is completely lost. The scutum + scutellum is isosceles triangular, and the exposed portion is lingual shape. The postmedian notal process is reduced. The mesonotal pouch is oval and opens forward owing to the decrease of the horizontal plate, whereas the vertical plate develops. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process, but the development of the posterior process corresponding to axillary cord is weak. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Hybosoridae (Figs. 5A, 9A, 10G)

In the family Hybosoridae (genus *Phaeochrous*) the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed parts is transversely depressed. The first phragma is reduced the most part, but the lateral sides remain and protrude to forward. The prescutum is completely lost. The scutum + scutellum is isosceles triangular, and the exposed portion is lingual shape. The postmedian notal process is obtuse. The mesonotal pouch is oval in shape. The most parts of the vertical plate are fused with developed horizontal plate. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process, but the development of the posterior process corresponding to axillary cord is weak. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Pleocomidae (Figs. 5B, 9B, 10H)

In the family Pleocomidae (genus *Pleocoma*) the anterior two-thirds of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is well-developed, and the anterior margin is truncated. The prescutum is completely lost. The scutum + scutellum is shield-like in shape, and the exposed portion is diffusely triangular. The postmedian notal process is obtuse. The mesonotal pouch is oval in shape, with the developed vertical plate lying at the center. The rod-shaped scutellar process is sclerotized and completely fused with the posterior inflection of the mesonotal pouch, whereas the attached axillary cord is present as a very thin membrane.

Trogidae (Figs. 5C, 9C)

In the family Trogidae (genus *Glyptotrox*) the anterior two-third of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is marked by a transverse depression. The first phragma is well-developed, and is characterized by an anterior margin that is strongly emarginate. The prescutum is completely lost. The scutum + scutellum is sagittate in shape, and the exposed portion is lingual shape. The postmedian notal process is obtuse, and its base is weakly invaginate. The mesonotal pouch is oval in shape, with the developed vertical plate lying at the center. The scutellar process is a sclerotized rod-shaped and the attached axillary cord is present as a very thin membrane. The single scutellar process and posterior inflection of the mesonotal pouch are completely fused.

Discussion

On the basis of my examination of the mesonotum in the coprophagous group of Scarabaeidae and comparison with that in species in the phytophagous group of Scarabaeidae and other scarabaeoid families, I make the following inferences.

Types of mesonotum in the coprophagous group of Scarabaeidae

I suggest dividing the mesonotum in the coprophagous group of Scarabaeidae into aphodiine and scarabaeine types. Generally, the mesonotum play a role in fixing the elytra, although it has little influence on flight behavior. Indeed, as the mesonotum is not necessary for flight, it is typically considerably smaller than the metanotum. The following features are important with respect to distinguishing aphodiine and scarabaeine types: the development of the first phragma, the shape of the scutum + scutellum, the development of an internal ridge (horizontal and vertical plates), and the scutellar process and axillary cord.

Aegialiinae, Aphodiinae, and Chironinae belong to the aphodiine type. The mesonotum is concealed by the pronotum at least in the anterior half. The development of the first phragma is weak. The scutum + scutellum is sagittate shaped. Development of the vertical and horizontal plates tend to be weak. The scutellar process is rod-shaped and the attached axillary cord occurs as a is thin membrane. The scutellar process and the posterior inflection of mesonotal pouch are fused completely.

Scarabaeinae belong to the scarabaeine type. The mesonotum is completely concealed by the pronotum, excluding species of the tribe Oniticellini and Onitini. The development of the first phragma is strong. The remnant of the prescutum is present on the anterior margin of the scutum + scutellum. The scutum + scutellum is pentagonal in shape, and the base of the postmedian notal process is truncated. Development of the vertical and horizontal plates is strong. The scutellar process is triangular in shape and the attached axillary cord generally appears as a thin membrane, although in some genera it is weakly sclerotized. The sutural line between the scutellar process and the posterior inflection of mesonotal pouch can be clearly distinguished. Among the observed Scarabaeoidea, this feature is an autapomorphic character found only in Scarabaeinae.

Evolution of the mesonotal structure in Scarabaeidae

It is assumed that development of the mesonotum in the Pterygota is affected by environmental factors and behavioral traits, given that it is an attachment point for flight muscles that play some of the most important roles in flight behavior. However, in Coleoptera, the mesonotum is reduced, as a consequence of the loss of flight muscles and development of the elytra, and thus is affected to a lesser extent by environmental factors and behavioral traits. In most coleopteran species, the mesonotum functions primarily as a fixing device, to which the elytra are firmly fixed by engagement of the sutural line, metanotal alacrista, and mesonotal posterior margin (Larsen 1966, Nomura 2015). From the perspective of determining evolutionary trends in Scarabaeoidea, an important consideration is whether the mesonotum is exposed or concealed by the pronotum (Ochi *et al*. 2012). Complete concealed of the mesonotum by the pronotum is considered a unique state in the subfamily Scarabaeinae. In many coleopteran species, the mesonotum is generally exposed, and a completely concealed mesonotum state is considered to be a derived state. Consequently, species of the Onitini and Oniticellini, which are characterized by the exposed state, would appear to comprise an ancestral group of the Scarabaeinae. Contrastingly, however, the recent phylogenetic analyses (Monaghan *et al*. 2007, Mlambo *et al*. 2015, Tarasov and Génier 2015, Tarasov and Dimitrov 2016) have provided evidence indicating that the Ateuchini or Deltochilini (=Canthonini), which are characterized by a concealed mesonotum, form an ancestral group of the Scarabaeinae, whereas the Onitini and Oniticellini are clustered in a comparatively derived group. Accordingly, this would suggest that the exposed state of the Onitini and Oniticellini mesonotum has evolved secondarily from the covered state. With regards to estimating evolutionary trends, my observation indicate that the following characteristics are of more particular importance: development of the first phragma, presence of the prescutum, development of the internal ridge (vertical and horizontal plates), and variation in the scutellar process and attached axillary cord.

In species of the subfamilies Aegialiinae, Aphodiinae, and Chironinae, the first phragma is weakly developed or indistinguishable when viewed dorsally. In contrast, the first phragma in the Scarabaeinae is generally well-developed, although in the genus *Scaptodera*, it cannot be distinguished when viewed from the dorsal surface. In the Cetoniinae, Dynastinae, Melolonthinae, and Rutelinae within the phytophagous group of Scarabaeidae, the first phragma is developed and dorsally visible. The Geotrupidae, Pleocomidae, and Trogidae, which are considered be to ancestral in the Scarabaeoidea (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990) are characterized by a well-developed first phragma, a trait that is also observed in the family Scirtidae, which is considered the most primitive polyphagan (Friedrich and Beutel 2006, Mckenna *et al*. 2019). On the basis of the aforementioned state, I speculate that a well-developed dorsally visible first phragma appeared early in the Scarabaeoidea, and that a reduced first phragma evolved relatively late in certain lineages.

In the families Glaphyridae, Hybosoridae, Pleocomidae, and Trogidae, and some subfamilies within the Scarabaeidae (Aegialiinae, Aphodiinae, Chironinae, and Cetoniinae) the prescutum has been completely lost. However, the remnant of the prescutum has been identified in some subfamilies of Scarabaeidae (Scarabaeinae, Dynastinae, Melolonthinae, and Rutelinae) and in the family Geotrupidae. The prescutum has also been confirmed in the Staphylinidae (Larsén 1966; Matsuda 1970) within an out group of the Scarabaeoidea (McKenna *et al*. 2019) and presence of the prescutum is considered a typical thoracic structure of insects (Snodgrass 1935). Therefore, the remnant of the prescutum, which was confirmed in the Scarabaeidae (Scarabaeinae, Dynastinae, Melolonthinae, and Rutelinae) and Geotrupidae is considered to represent an ancestral state. However, as indicated in recent phylogenies, this structure it is not present in some scarabaeoid clades (Ahrens *et al*. 2014, Gunter *et al*. 2016), including the ancestral groups Pleocomidae and Trogidae. It is thus considered that a reduction in the prescutum has occurred convergently in multiple scarabaeoid clades.

In the development of the internal ridges, although I observed a number of different states, it was generally difficult to categorize these features. However, I speculate that differences in the degree of development may reflect an evolutionary tendency. Well-developed internal ridges are observed in most scarabaeoid beetles, particularly in species of the subfamily Scarabaeinae, whereas the internal ridges tend to be reduced in the subfamily Aegialiinae, Aphodiinae (genera *Odochilus*, *Psammodius*, *Saprosites*, *Setylaides* and *Trichiorhyssemus*), Cetoniinae, and Dynastinae. It is postulate that the internal ridge is a remnant of the scutoscutellar suture, and the aforementioned two character states are considered derived states observed in the Scarabaeoidea. On the basis of recent phylogenetic analyses, it would be appear that the family Scarabaeidae is one of the most derived groups within the Scarabaeoidea (Ahrens *et al*. 2014, Gunter *et al*. 2016). Notably, the derived state of the subfamilies Cetoniinae and Dynastinae has also been indicated by traditional morphological studies (Crowson 1981, Lawrence and Newton 1982, d'Hotman and Scholtz 1990a, Nel and Scholtz 1990, Scholtz 1990). I thus suggest that the ancestral state of the internal ridges in Scarabaeidae is the normal state of the Geotrupidae, Glaphyridae, Hybosoridae, Pleocomidae, Trogidae, and Aphodiinae (with the exception of the genera *Odochilus*, *Psammodius*, *Saprosites*, *Setylaides* and *Trichiorhyssemus*), Chironinae, and phytophagous group of Scarabaeidae (Rutelinae and Melolonthinae) (Figs. 6D, 6E, 6F, 7A, 7B, 8F, 8H, 8I, 9A, 9B, 9C). Interestingly, however, Edmonds (1972) mentioned that the internal ridges and scutoscutellar suture are unrelated traits in the subfamily Scarabaeinae. In the future, it will thus be necessary to examine a large number of taxonomic groups in order to gain a more complete image of the evolutionary trends.

Variations in the characteristics of the scutellar process and attached axillary cord are among the most important features defining mesonotum structures. In species of the Geotrupidae, Pleocomidae, Trogidae, Aegialiinae, Aphodiinae, and Chironinae, the scutellar processes are rod-shaped and the axillary cord is membranous. The scutellar process in the Scarabaeinae is triangular in shape with a membranous axillary cord, the axillary cord in the genera *Catharsius*, *Copris*, *Deltochilum*, *Heliocopris*, *Onitis*, and *Paragymnopleurus* comprises a weakly sclerotized membrane. In contrast to these two states, which are characterized by a single scutellar process and membranous axillary cord, the scutellar processes and axillary cord in the Hybosoridae, Glaphyridae, and phytophagous groups of Scarabaeidae (Cetoniinae, Dynastinae, Melolonthinae and Rutelinae) form a sclerotized dichotomous branching process. Among these groups, species of the subfamilies Cetoniinae, Dynastinae, Melolonthinae and Rutelinae possess a pouch-like structure on a part corresponding to the axillary cord (Fig. 11). The combination of a dichotomous branching process and pouch-like structure is considered to be the most derived state among the aforementioned character states, and is presumed to be related to an adjustment of the elytral angle during flight. Indeed, a dichotomous branching process co-existing with a pouch-like structure is observed in the subfamilies

Dynastinae, Melolonthinae, and Rutelinae, which are characterized by highly maneuverable flight. Although species of the subfamily Cetoniinae also have the same scutellar process and axillary cord, the development of the axillary cord is weaker than that observed in other members of phytophagous Scarabaeidae, and appears to reflect a process of atrophication. This may be associated with the unique form of flight displayed by the Cetoniinae that fly with the elytra closed, which contrasts with most scarabaeoid beetles that fly with opened elytra. Consequently, the Cetoniinae elytra are no longer used to aid balance, as in other scarabaeoid beetles, and thus the axillary cord may have atrophied secondarily. The phytophagous group of Scarabaeidae is among of the most derived groups in the Scarabaeoidea (Ahrens *et al*. 2014, Gunter *et al*. 2016, Neita-Moreno *et al*. 2019). Especially, the subfamily Cetoniinae is considered to be a sister group of the Dynastinae + Rutelinae clade (Browne and Scholtz 1998, Ahrens *et al*. 2014, Gunter *et al*. 2016, Šípek *et al*., 2016, Neita-Moreno *et al*. 2019), thereby suggesting that the Cetoniinae probably evolved from the Dynastinae + Rutelinae clade. Thus, a rod-shaped single process and membranous axillary cord (Geotrupidae, Pleocomidae, Trogidae, Aegialiinae, Aphodiinae, and Chironinae) are assumed to have appeared early time, and I regard this as a primary stage. The triangular shaped scutellar process with thin or sclerotized membranous axillary cord (Scarabaeinae) and the dichotomous branching process (Glaphyridae and Hybosoridae) are considered to be derived states, whereas the dichotomous branching process with a pouch-like structure found in the phytophagous group of Scarabaeidae is assumed to be the most recently developed.

Coprophagous and phytophagous groups of Scarabaeidae

Although the basic structure of the mesonotum is similar in the coprophagous and phytophagous groups of the Scarabaeidae, these groups can be distinguished based on by the characteristics of the scutellar process and axillary cord. In this regard, a dichotomous branching process, which consist of a sclerotized scutellar process and axillary cord with a pouch-like structure bearing long setae (Figs. 8F, 8G, 11), is recognizable only in phytophagous group of Scarabaeidae. Subfamilies of the coprophagous group of Scarabaeidae can be classified into two types based on mesonotal structures (the aphodiine and scarabaeine types), however, common features are observed in these types, notably the single scutellar process and a membranous axillary cord, indicating that these groups might be closely related. Indeed, evidence obtained from various molecular and morphological phylogenies indicate that the Aphodiinae and Scarabaeinae are sister groups (Smith *et al*. 2006, Philips 2011, Lawrence *et al*. 2011, Mckenna *et al*. 2019). Traditionally, the coprophagous and phytophagous groups of Scarabaeidae have been treated as sister groups based on morphological observations (Browne and Scholtz 1995, 1998) and some molecular phylogeny (Ahrens and Volger 2008, Gunter *et al*. 2016, Šípek *et al*. 2016, McKenna *et al*. 2019). However, the findings of some recent molecular phylogenetic analyses indicate that the coprophagous and phytophagous groups are not closely related, and that the phytophagous group is grouped within a clade that includes either Glaphyridae or Hybosoridae (Smith *et al*. 2006, Ahrens *et al*. 2014, Neita-Moreno *et al*. 2019). Indeed, I have confirmed that species belonging to Glaphyridae and Hybosoridae have intermediate features associated with a dichotomous branching scutellar process (Figs. 8I, 9A, 10F, 10G). Given that members of the families Geotrupidae, Pleocomidae, and Trogidae, and coprophagous group of Scarabaeidae are characterized by a single scutellar process and membranous axillary cord, I reason that the coprophagous and phytophagous groups of Scarabaeidae should be grouped in different clades.

Subfamilies Aphodiinae, Aegialiinae and Chironinae

The subfamilies Aegialiinae and Chironinae are closely related to the Aphodiinae, and consistently, the morphology of the mesonotum in these three subfamilies are observed to be highly similarly. In particular, the characteristics of Aegialiinae (Figs. 2A−2C, 6A−6C) are similar to those of the tribes Psammodiini and Odochilini (Figs. 2H−2I, 6H−6I), whereas these features in Chironinae are similar to those in the genus *Caelius* within the Aegialiinae (Figs. 2C, 6C). However, although the subfamilies Aegialiinae and Chironinae are often established as different families, Aegialiidae and Chironidae (Nel and Scholtz 1990, d'Hotman and Scholtz 1990a, Paulian and Baraud 1982, Carpaneto and Piattella 1995, Huchet 2000, 2002, 2003, 2004, 2019, Huchet and Lumaret 2002), I found that morphologically, variation in the mesonotum of these subfamilies is relatively low. Indeed, on the basis of a comparison of mesonotum morphology among the Aphodiinae, Aegialiinae and Chironinae, I conclude that Aegialiinae and Chironinae should be included in the subfamily Aphodiinae. In this regard, my findings are consistent with those of Browne and Scholtz (1998), Smith *et al*. (2006) and Ahrens *et al*. (2014), who showed that Aegialiinae and Chironinae are included in a clade with Aphodiinae, and also with the findings of Ritcher (1969a, 1974) and Stebnicka (1977), who, on the basis of morphological point of view, concluded that Aegialiinae and Chironinae are close to Aphodiinae. Collectively, these observations on the morphology of the mesonotum in Aphodiinae, Aegialiinae and Chironinae tend to indicate that these subfamilies comprise a single lineage.

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Geotrupidae	Geotrupinae	Enoplotrupini	*Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky, 1866)
Glaphiridae	Amphicominae		*Amphicoma splendens* (Yawata, 1942)
Hybosoridae	Hybosorinae		*Phaeochrous emarginatus emarginatus* Laporte, 1840
Pleocomidae			*Pleocoma dubitabilis dubitabilis* Davis, 1935
Trogidae	Troginae		*Glyptotrox uenoi uenoi* (Nomura, 1961)
Scarabaeidae	Aegialinae	Aegialini	*Aegialia* (*Aegialia*) *comis* (Lewis, 1895)
			Aegialia (*Aegialia*) *nitida* Waterhouse, 1875
			Caelius denticollis Lewis, 1895
			Psammoporus nakanei nakanei Masumoto, 1986
	Aphodiinae	Aphodiini	*Aphodius* (*Agrilinus*) *breviusculus* (Motschulsky, 1866)
			Aphodius (*Brachiaphodius*) *eccoptus* Bates, 1889
			Aphodius (*Colobopterus*) *quadoratus* Reiche, 1850
			Aphodius (*Phaeaphodius*) *rectus* Motschulsky, 1866
			Aphodius (*Sinodiapterna*) *troitzyi* Jacobson, 1897
		Eupariini	*Ataenius picinus* Harold, 1867
			Saprosites japonicus Waterhouse, 1875
			Setylaides foveatus (Schmidt, 1909)
		Odochilini	*Odochilus convexus* Nomura, 1971
		Psammodiini	*Rakovicius coreanus* (Kim, 1980)
			Psammodius kobayashii Nomura, 1973
			Trichiorhyssemus asperulus (Waterhouse, 1875)
		Rhyparini	*Rhyparus azumai azumai* Nakane, 1956
			Sybacodes sp. 1
	Chironinae		*Chiron* sp. 1
	Scarabaeinae	Ateuchini	*Paraphytus dentifrons* Lewis, 1895
		Deltochilini	*Deltochilum* (*Calhyboma*) *variolosum* Burmeister, 1873
			Deltochilum (*Hybomidium*) *gibbosum* (Fabricius, 1755)
			Panelus rufulus Nomura, 1973
		Coprini	*Catharsius molossus* (Linnaeus, 1758)
			Copris (*Copris*) *ochus* (Motschulsky, 1860)
			Copris (*Copris*) *tripartitus* Waterhouse, 1875
			Heliocopris tyrannus (Thomson, 1859)
		Gymnopleurini	*Paragymnopleurus melanarius* (Harold, 1867)
		Oniticellini	*Liatongus minutus* (Motschulsky, 1860)
			Liatongus gagatinus (Hope, 1831)
			Scaptodera rhadamistus (Fabricius, 1775)
			Sinodrepanus falsus (Sharp, 1875)
		Onthophagini	*Caccobius* (*Caccobius*) *jessoensis* Harold, 1867
			Digitonthophagus gazella (Fabricius, 1787)
			Onthophagus (*Gibbonthophagus*) *apicetinctus* d'Orbigny, 1898
			Onthophagus (*Serrophorus*) *seniculus* (Fabricius, 1781)
			Onthophagus (*Strandius*) *lenzii* Harold, 1874
		Onitini	*Onitis virens* Lansberge, 1875
			Onitis falcatus (Wulfen, 1786)
		Phanaeini	*Coprophanaeus* (*Metallophanaeus*) *saphirinus* (Strum, 1826)
		Scarabaeini	*Scarabaeus radama* Fairmaire, 1895
			Scarabaeus sacer Linnaeus, 1758
		Sisyphini	*Sisyphus longipes* (Olivier, 1789)
	Cetoniinae	Cetoniini	*Cetonia* (*Eucetonia*) *roelofsi roelofsi* Harold, 1880
	Dynastinae	Dynastini	*Trypoxylus dichotomus septentrionalis* Kôno, 1931
	Rutelinae	Anoimalini	*Mimela splendens* (Gyllenhal, 1817)
	Melolonthinae	Melolonthini	*Melolontha* (*Melolontha*) *frater* Arrow, 1913

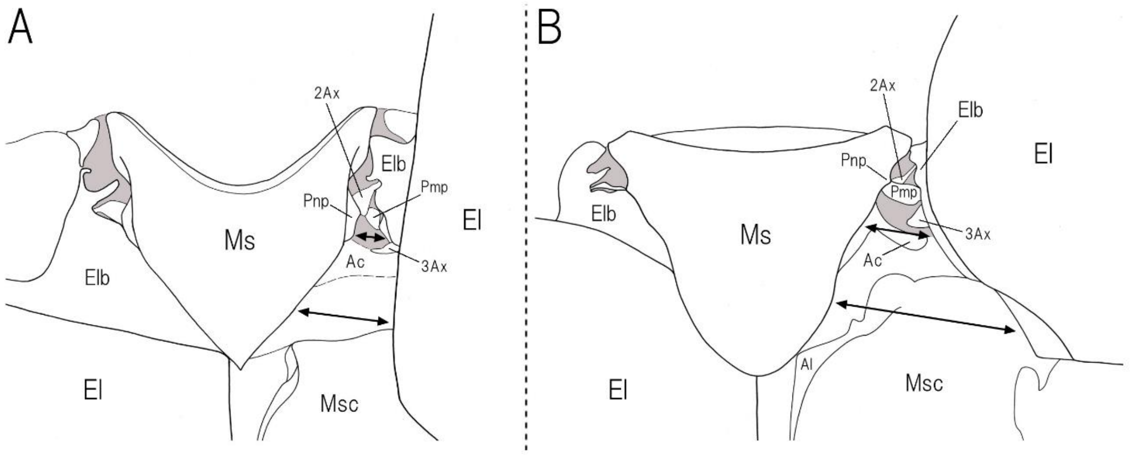
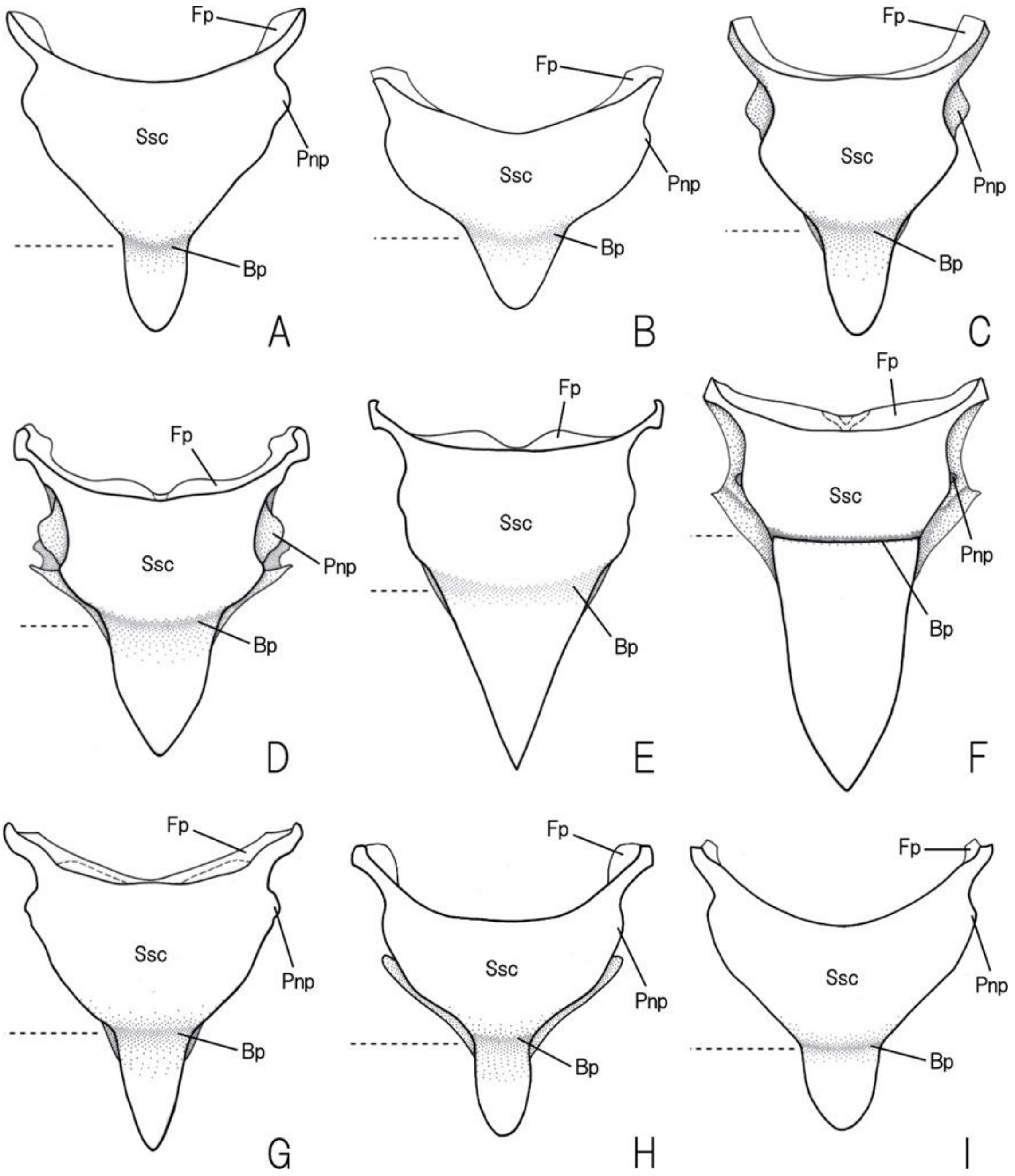
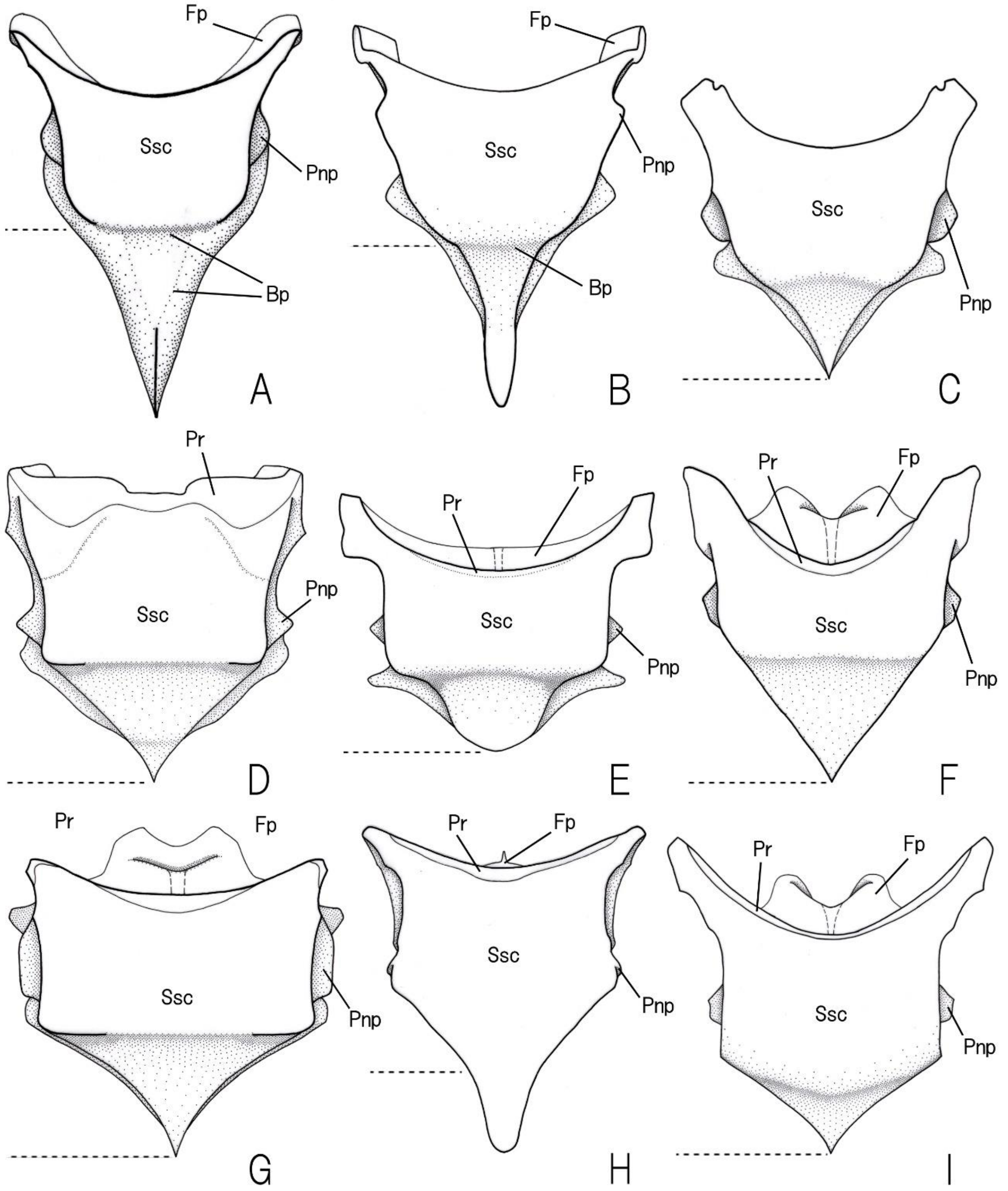


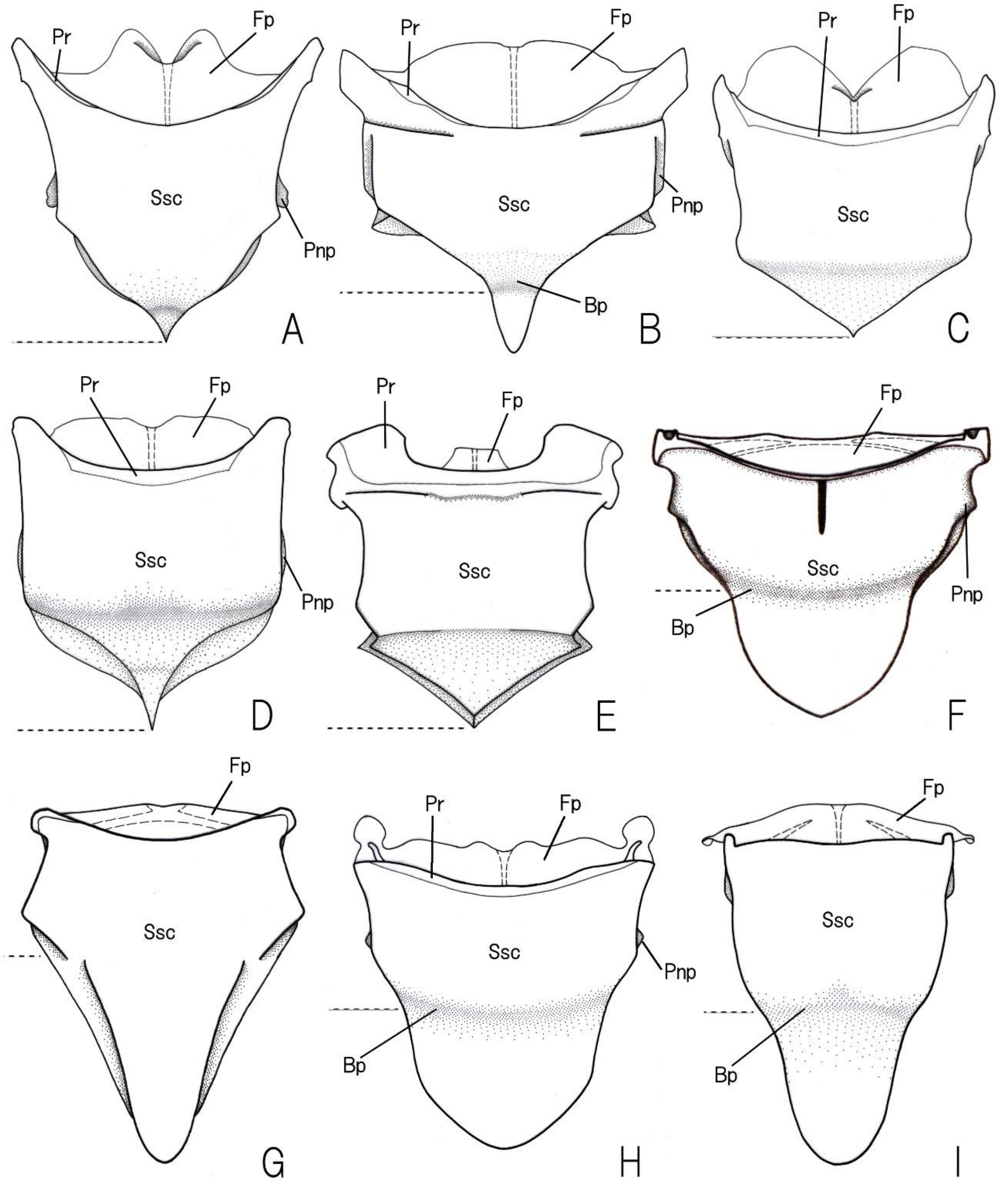
Figure 1. The position of the mesonotal characters in Scarabaeidae **A** *Copris ochus* (Motschulsky) **B** *Melolontha frater frater* Arrow. Abbreviations: alacrista (Al); axillary cord (Ac); elytron (El); elytral base (Elb); mesonotum (Ms); metascutum (Msc); proximal median plate (Pmp); postmedian notal process (Pnp); second axillary sclerite (2Ax); third axillary screlite (3Ax). The membranous parts are painted gray, and the fixed parts between the mesonotum and elytron are showed by arrow.



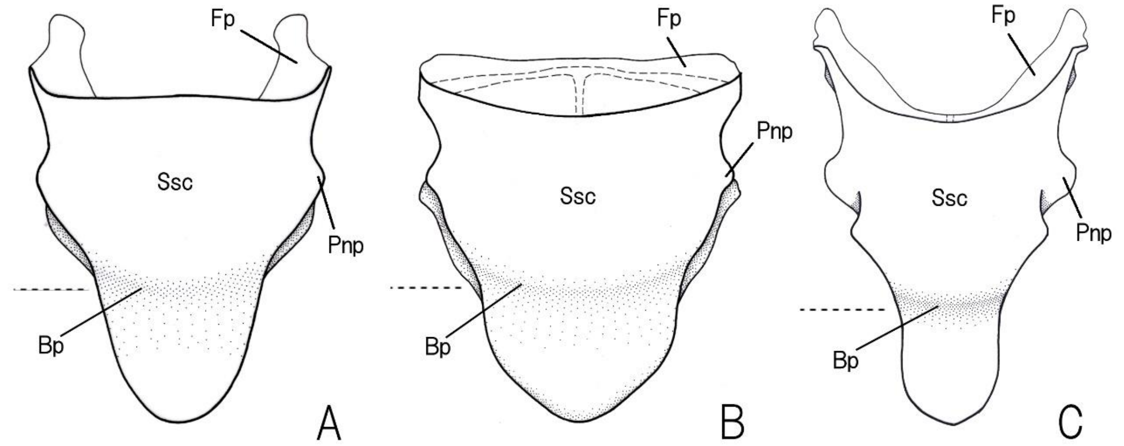
Figures 2A–I. Dorsal habitus of the mesonotum. **A** *Aegialia* (*Aegialia*) *comis* (Lewis) **B** *Aegialia* (*Aegialia*) *nitida* Waterhouse **C** *Caelius denticollis* Lewis **D** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **E** *Aphodius* (*Colobopterus*) *quadoratus* Reiche **F** *Aphodius* (*Sinodiapterna*) *troitzyi* Jacobson **G** *Saprosites japonicus* Waterhouse **H** *Odochilus convexus* Nomura **I** *Psammodius kobayashii* Nomura. Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



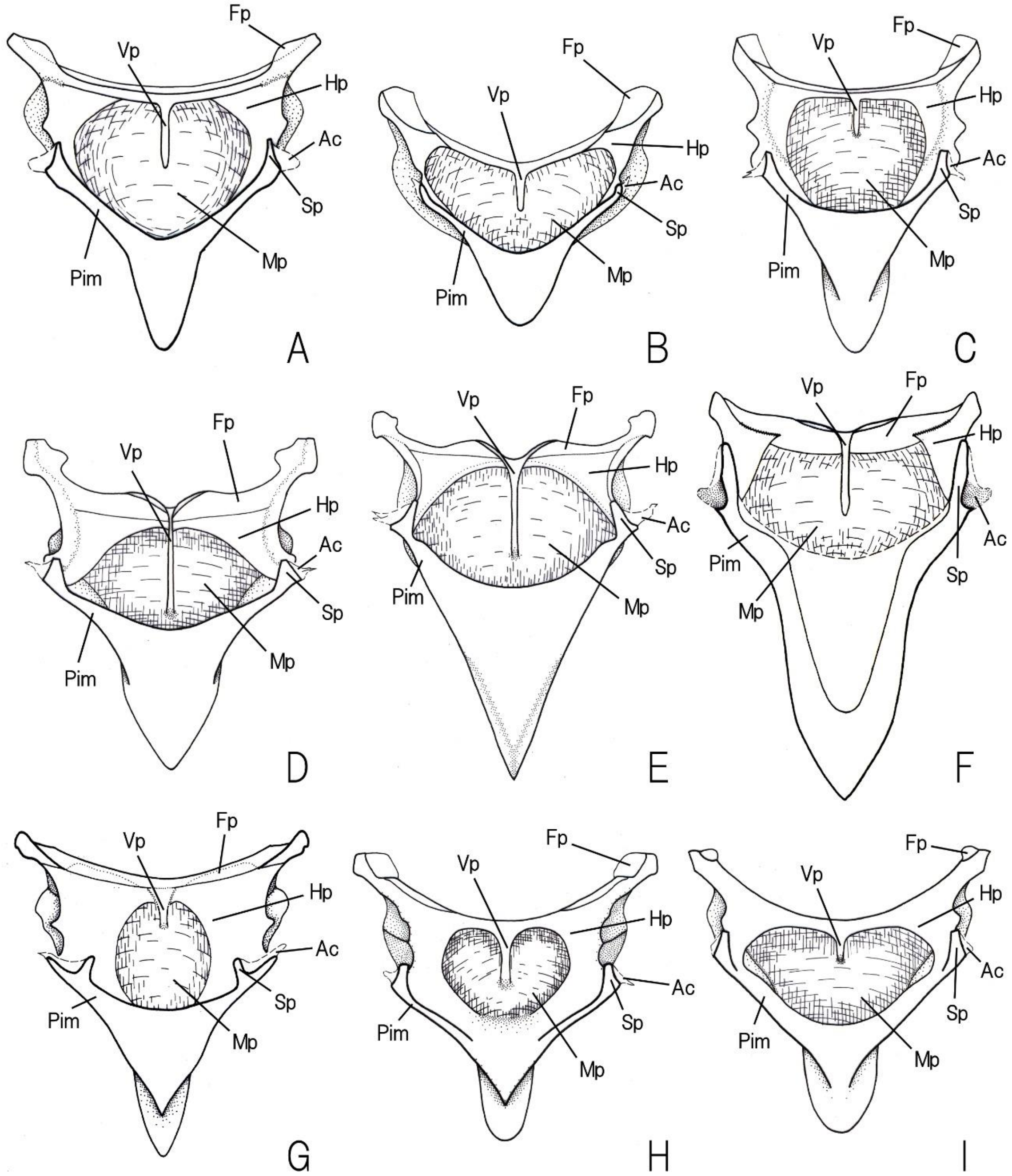
Figures 3A–I. Dorsal habitus of the mesonotum. **A** *Rhyparus azumai azumai* Nakane **B** *Chiron* sp. **C** *Paraphytus dentifrons* Lewis **D** *Deltochilum* (*Calhyboma*) *variolosum* Burmeister **E** *Panelus rufulus* Nomura **F** *Copris* (*Copris*) *ochus* (Motschulsky) **G** *Paragymnopleurus melanarius* (Harold) **H** *Scaptodera rhadamistus* (Fabricius) **I** *Caccobius* (*Caccobius*) *jessoensis* Harold. Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



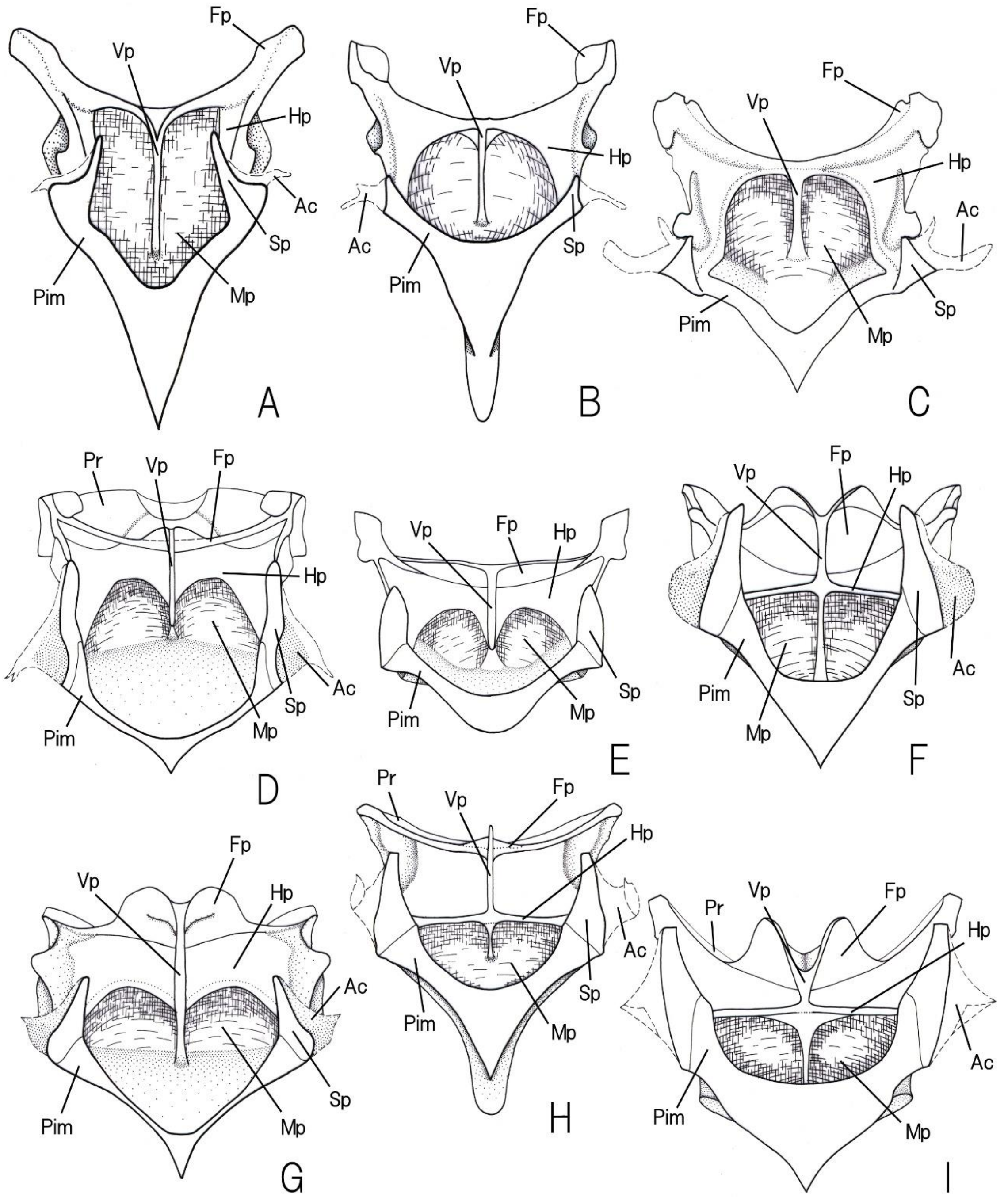
Figures 4A–I. Dorsal habitus of the mesonotum. **A** *Onthophagus* (*Serrophorus*) *seniculus* (Fabricius) **B** *Onitis virens* Lansberge **C** *Coprophanaeus* (*Metallophanaeus*) *saphirinus* (Strum) **D** *Scarabaeus radama* Fairmaire **E** *Sisyphus longipes* (Olivier) **F** *Mimela splendens* (Gyllenhal) **G** *Cetonia* (*Eucetonia*) *roelofsi roelofsi* Harold **H** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky) **I** *Amphicoma splendens* (Yawata). Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



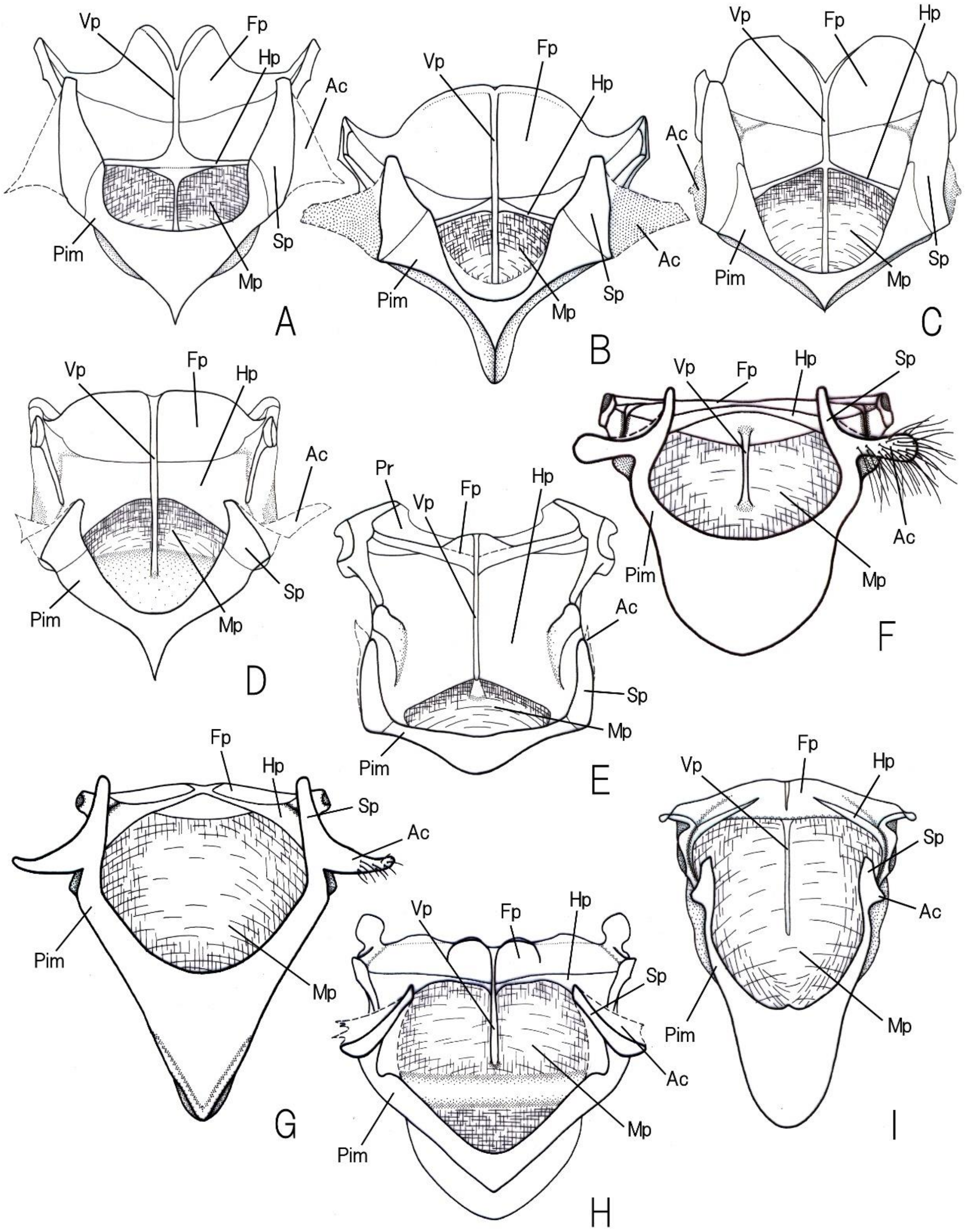
Figures 5A−C. Dorsal habitus of the mesonotum. **A** *Phaeochrous emarginatus emarginatus* Laporte **B** *Pleocoma dubitabilis dubitabilis* Davis **C** *Glyptotrox uenoi uenoi* (Nomura). Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



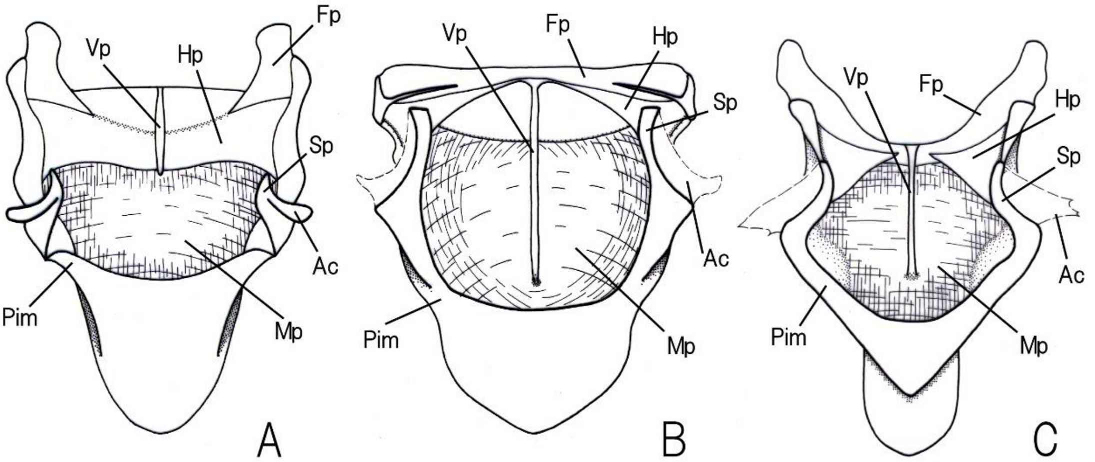
Figures 6A−I. Ventral habitus of the mesonotum. **A** *Aegialia* (*Aegialia*) *comis* (Lewis) **B** *Aegialia* (*Aegialia*) *nitida* Waterhouse **C** *Caelius denticollis* Lewis **D** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **E** *Aphodius* (*Colobopterus*) *quadoratus* Reiche **F** *Aphodius* (*Sinodiapterna*) *troitzyi* Jacobson **G** *Saprosites japonicus* Waterhouse **H** *Odochilus convexus* Nomura **I** *Psammodius kobayashii* Nomura. Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



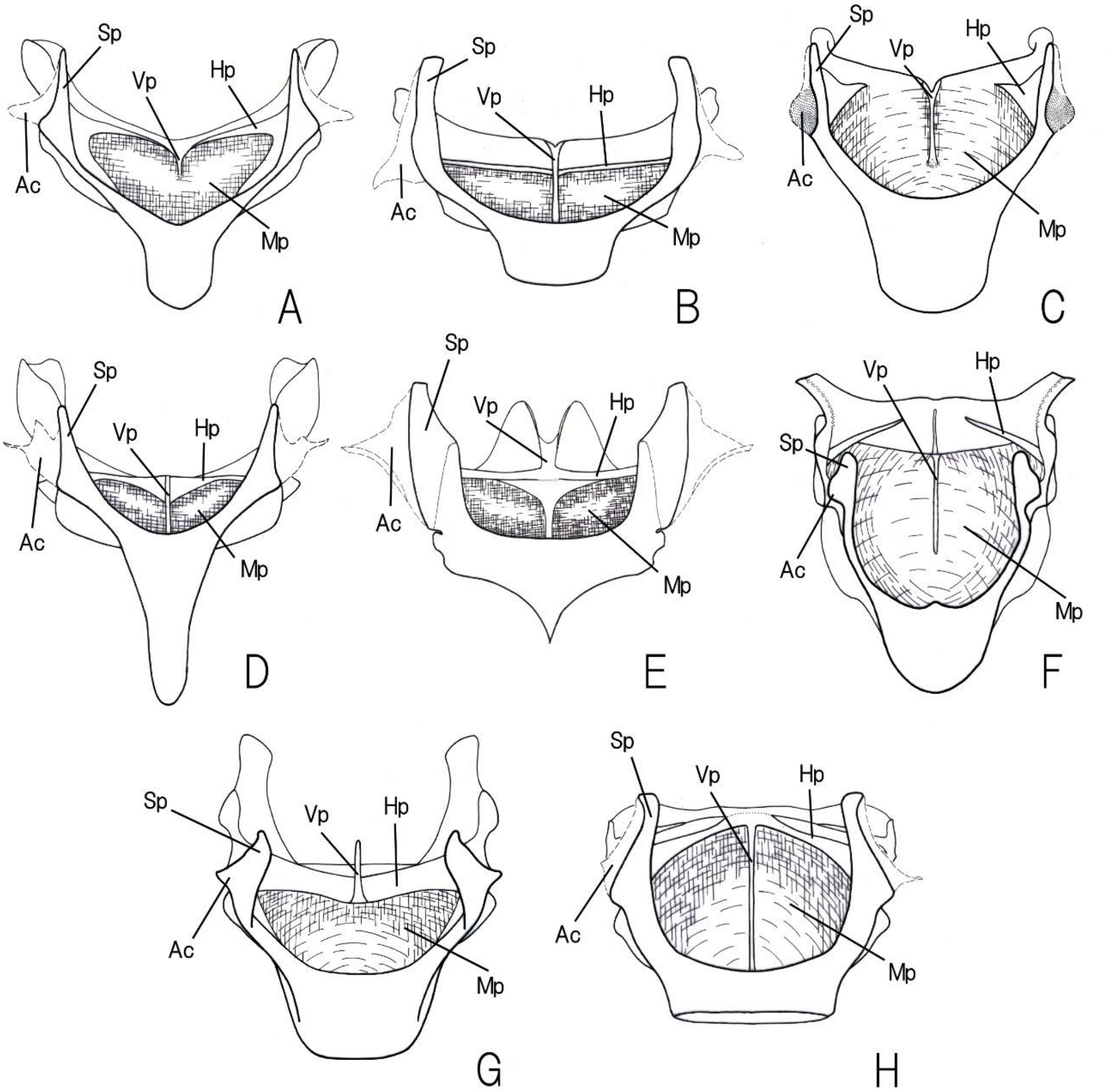
Figures 7A–I. Ventral habitus of the mesonotum. **A** *Rhyparus azumai azumai* Nakane **B** *Chiron* sp. **C** *Paraphytus dentifrons* Lewis **D** *Deltochilum* (*Calhyboma*) *variolosum* Burmeister **E** *Panelus rufulus* Nomura **F** *Copris* (*Copris*) *ochus* (Motschulsky) **G** *Paragymnopleurus melanarius* (Harold) **H** *Scaptodera rhadamistus* (Fabricius) **I** *Caccobius* (*Caccobius*) *jessoensis* Harold. Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



Figures 8A–I. Ventral habitus of the mesonotum. **A** *Onthophagus* (*Serrophorus*) *seniculus* (Fabricius) **B** *Onitis virens* Lansberge **C** *Coprophanaeus* (*Met allophanaeus*) *saphirinus* (Strum) **D** *Scarabaeus radama* Fairmaire **E** *Sisyphus longipes* (Olivier) **F** *Mimela splendens* (Gyllenhal) **G** *Cetonia* (*Eucetonia*) *roelofsi roelofsi* Harold **H** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky) **I** *Amphicoma splendens* (Yawata). Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



Figures 9A−C. Ventral habitus of the mesonotum. **A** *Phaeochrous emarginatus emarginatus* Laporte **B** *Pleocoma dubitabilis dubitabilis* Davis **C** *Glyptotrox uenoi uenoi* (Nomura). Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



Figures 10A–H. Posterior habitus of the mesonotum. **A** *Aegialia* (*Aegialia*) *comis* (Lewis) **B** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **C** *Aphodius* (*Sinodiapterna*) *troitzyi* Jacobson **D** *Chiron* sp. **E** *Caccobius* (*Caccobius*) *jessoensis* Harold **F** *Amphicoma splendens* (Yawata) **G** *Phaeochrous emarginatus emarginatus* Laporte **H** *Pleocoma dubitabilis dubitabilis* Davis. Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).

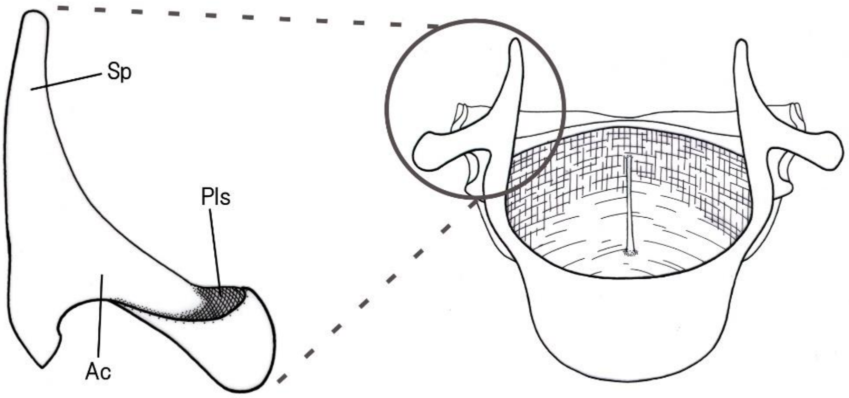


Figure 11. Pouch-like structure of dichotomous branching process in phytophagous group of Scarabaeidae, *Mimela splendens* (Gyllenhal). Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); pouch-like structure (Pls); scutellar process (Sp); vertical plate (Vp).

2−2−2

Comparison of mesonotal morphology in beetles of the phytophagous group of Scarabaeidae and other scarabaeoid taxa (Coleoptera, Scarabaeoidea)

Introduction

The phytophagous group of Scarabaeidae has long attracted the attention of numerous researchers, and several detailed comparative studies on various morphological structures have been conducted (Ritcher and Baker 1974, Yadav and Pillai 1979, Caveney and McIntyre 1981, Nel and Villiers 1988, Nel and Scholtz 1990, d'Hotman and Scholtz 1990a, Grebennikov and Scholtz 2004) [for more information see Scholtz (1990) and Scholtz and Grebennikov (2016)]. In contrast, however, there have been relatively few comparative studies that have focused on the mesonotal structures in scarabaeid beetles. Detailed mesonotal structures in some scarabaeid species have been examined by some researchers (Snodgrass 1909, Larsén 1966, Edmonds 1972, Albertoni *et al*. 2014). The first comparative study of the mesonotum based on the multiple scarabaeoid species was conducted in subchapter (2–2–1), however the examination was incompletely due to lacking many phytophagous group species and other scarabaeoid families. With respect to establishing phylogenetic relationships, the value of mesonotal characters has been proven in studies on other coleopteran groups (Beutel and Komarek 2004, Friedrich and Beutel 2006, Ge *et al*. 2007) and the Scarabaeinae (Philips *et al*. 2004, 2016, Tarasov and Génier 2015, subchapter 2–2–1). The accumulation of new reliable morphological data, particularly for features that can be readily observed, will make an important contribution to molecular phylogenetic studies in recent years. In this study, I examined details of the mesonotal structures of 69 genera from 10 subfamilies within the phytophagous group of Scarabaeidae, two genera from two subfamilies within the coprophagous group of Scarabaeidae, and 57 genera within other scarabaeoid families. Although the representatives examined are clearly an inadequate and may thus not provide a totally reliable basis on which to discuss far-reaching phylogenetic and systematic implications, it has, nevertheless, been possible to identify similarities between the different families and subfamilies.

Material and methods

Preparation of specimens

All dissections were carried out on dry specimens. In order to relax the specimens, they were initially placed in 50% ethanol for few minutes, after which the prothorax and the abdomen were detached from the meso- and metathorax using fine forceps. The meso- and metathorax were placed in 5% KOH solution for 6 to 8 hours to soften and dissolve the internal organs. Following pretreatment, these parts were washed several times in distilled water. Therefore, the mesonotum was detached from the meso- and metathorax, and the isolated mesonotum was soaked in 99% ethanol for 10 minutes to dehydrate the tissues.

Drawings were made with the aid of OLIMPAS SZX9 and LEICA M165C microscopes and a KEYENCE VHX-1000 digital microscope. Fine structures such as hairs and punctates on the mesonotal surface were excluded from the diagrams as these tended to obscure structures required for comparative observations.

Terminology

Terminology used in this paper was developed by subchapter 2–2–1.

Specimens studied

In the present study, I examined beetles from 102 genera within to 11 families of superfamily Scarabaeoidea (Bolboceratidae, Geotrupidae, Glaresidae, Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Passalidae, Pleocomidae, Trogidae and Scarabaeidae). Three species within three genera were selected in the family Bolboceratidae. Six species within three genera of two subfamilies (Geotrupinae and Lethrinae) were selected in the family Geotrupidae. One species within genus *Glaresis* Erichson, 1848 was selected in the family Glaresidae. Four species within three genera were selected in the family Glaphyridae. Three species within three genera of two subfamilies (Ceratocanthinae and Hybosorinae) were selected in the family Hybosoridae. 11 species within 10 genera of four subfamilies (Aesalinae, Syndesinae, Lamprinae and Lucaninae) were selected in the family Lucanidae. Three species within three genera were selected in the family Ochodaeidae. Three species within three genera of two subfamilies (Aulacocyclinae and Macrolinae) were selected in the family Passalidae. One species within genus *Pleocoma* LeConte, 1856 was selected in the family Pleocomidae. Three species within three genera were selected in the family Trogidae. 93 species within 71 genera of 12 subfamilies (Aphodiinae, Scarabaeinae, Aclopinae, Cetoniinae, Dynamopodinae, Dynastinae, Euchirinae, Melolonthinae, Orphninae, Rutelinae, Trichiinae and Valginae) were selected in the family Scarabaeidae (Table. 1).

Results

In the Scarabaeoidea, the mesonotum is located beneath the pronotum and lies between the elytral bases (Fig. 1). Given that the anterior half of the mesonotum is often covered by the pronotum, typically less than half of the entire structure is visible when observed dorsally. In some species within the family Passalidae and the subfamily Scarabaeinae (genus *Copris*), however, the entire extent of the mesonotum is completely hidden by the pronotum. The boundary demarcating the concealed and exposed portion is, generally characterized by a transverse depression, but in some phytophagous scarabaeid beetles it is represented completely flat or truncate states. The mesonotum and the elytral bases are articulated through the postmedian notal process, some axillary sclerites, and the axillary cord. The basic structure of the mesonotum in the Scarabaeoidea consists of four parts: the first phragma, prescutum, scutum, and scutellum, among which, the prescutum is substantially reduced in size or has been completely lost. The scutum and scutellum are completely fused, owing to disappearance of the scutoscutellar suture. Moreover, internal ridges (the vertical and horizontal plates) typically weakly develop and form a mesonotal pouch, into which muscles associated with the back and forth movements of the mesonotum are inserted. The movement of the mesonotum is important with respect to fixation of the elytra. When the mesonotum is tilted forward, causing an extension and elevation of the elytra, whereas when tilted backward, which is the normal position, the position of the elytra becomes fixed. The scutellar process and axillary cord on the ventral side of the scutum + scutellum function as a levering device for the back and forth movements. The axillary cord shows various morphological states, including thin membranes and sclerotized processes. The sclerotized axillary cord found in many phytophagous groups of Scarabaeidae (Fig. 14), which is located at the base of the elytra and third axillary sclerites when the elytra are opened, is considered to play a role in adjusting the angle of the elytra, thereby functioning as balancer during flight.

Scarabaeidae

Aclopinae (Figs. 2A, 8A)

In the subfamily Aclopinae (genus *Pachypus*) the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is developed and is characterized by an anterior margin that is broadly emarginated. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is shield-like in shape, and the exposed portion is diffusely triangular with a notch at the posterior apex. The postmedian notal process is obtuse. The mesonotal pouch is oval in shape. The vertical and horizontal plates that form the mesonotal pouch developed. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process. The posterior process is characterized by a pouch-like structure. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Cetoniinae (Figs. 2B−2E, 8B−8E)

In the subfamily Cetoniinae the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is typically flat, but in some tribal species such as Cremastocheilini and Taenioderini (Figs. 2C, 2D) the boundary portions is represented depressed state. The first phragma is developed and is characterized by an anterior margin that is broadly pointed forward at the center. The prescutum is completely lost. The scutum + scutellum is diamond in shape and the exposed portion appears as a large triangle. The postmedian notal process is strongly reduced. The mesonotal pouch is oval shaped, although whereas the horizontal plate develops, the vertical plate is typically completely lost. However, in the tribes Cremastocheilini and Diplognathini the vertical plate slightly develops (Figs. 8C, 8E). The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process, whereas the development and sclerotized membranous state of the posterior arm corresponding to axillary cord is weak compared with that in other phytophagous groups of Scarabaeidae. The posterior process is usually characterized by a shallow pouch-like structure and is covered with long setae, but in the tribes Cremastocheilini and Diplognathini the development of this process is very weak and the pouch-like structure is lost (Figs. 8C, 8E). The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Dynamopodinae (Figs. 2F, 8F)

In the subfamily Dynamopodinae (genus *Orubesa*) the anterior two-thirds of the mesonotum are covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is developed and is characterized by an anterior margin that is sags downward. The prescutum is completely lost. The scutum + scutellum is isosceles triangular, and the exposed portion is lingual shaped. The postmedian notal process is obtuse, and its base invaginate. The mesonotal pouch is oval shaped. The vertical and horizontal plates that form the mesonotal pouch developed. The scutellar process is a sclerotized rod-shaped and its base weakly protrudes to outside, and the attached axillary cord is very thin membrane. The single scutellar process and posterior inflection of the mesonotal pouch are completely fused.

These character states resemble to the subfamily Orphninae and family Hybosoridae.

Dynastinae (Figs. 2G–2H, 8G–8H)

In the subfamily Dynastinae the anterior two-thirds of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is developed and is characterized by various states anterior margin. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is shield-like in shape, and the exposed portion is triangle. The lateral sides of the boundary portion are strongly constricted, except in Dynastini (Fig. 2G). The postmedian notal process is obtuse. The mesonotal pouch is oval in shape. The vertical and horizontal plates that form the mesonotal pouch developed, but the development of the vertical plate varies between tribes. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process. The posterior process is characterized by a pouch-like structure, which is rounded and developing, and is covered with long setae. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Euchirinae (Figs. 2I, 3A, 8I, 9A)

In the subfamily Euchirinae the anterior two-thirds of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is developed and is characterized by an anterior margin that is broadly emarginated. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is shield-like in shape, and the exposed portion in the genus *Cheirotonus* (Fig. 2I) is diffusely triangular while in the genus *Euchirus* is triangle (Fig. 3A). The lateral sides of the boundary portion in the genus *Cheirotonus* are strongly constricted. The postmedian notal process is obtuse. The mesonotal pouch is oval in shape. The vertical and horizontal plates that form the mesonotal pouch developed. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process. The posterior process is characterized by a pouch-like structure, which in the genus *Cheirotonus* is well-developed with rounded, and is covered with long setae. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

These states, especially the genus *Cheirotonus*, resemble to the subfamily Dynastinae.

Melolonthinae (Figs. 3B–3G, 9B–9G)

The mesonotal structures in the subfamily Melolonthinae shows a unique character state between tribes.

Melolonthini, Rhizotrogini and Tanyproctini (Figs. 3B–3D, 9B–9D)

In the tribes Melolonthini, Rhizotrogini and Tanyproctini the anterior two-thirds of the mesonotum are covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is developed and is characterized by an anterior margin that is broadly emarginated. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is shield-like in shape, and the exposed portion is diffusely triangle. The postmedian notal process is obtuse and its base in the tribe Rhizotrogini invaginate (Fig. 3C). The mesonotal pouch is oval in shape. The vertical and horizontal plates that form the mesonotal pouch developed. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process. The posterior process is characterized by a pouch-like structure and is covered with long setae. However, in the tribe Tanyproctini the pouch-like structure is very shallow. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Diplotaxini (Figs. 3E, 9E)

In the tribe Diplotaxini the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is truncated. The first phragma is developed and is characterized by an anterior margin that is broadly emarginated and the surface invaginate at the fused point of vertical plate. The prescutum is completely lost. The scutum + scutellum is triangular, and the exposed portion is triangle. The postmedian notal process is obtuse and its base invaginate. The mesonotal pouch is oval in shape with the developed vertical plate lying at the center, and opens forward owing to the decrease of the horizontal plate. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process. The posterior process is characterized by a pouch-like structure but the development is weak. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Hopliini (Figs. 3F, 9F)

In the tribe Hopliini the anterior two-thirds of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is developed and is characterized by an anterior margin that is broadly emarginated. The prescutum is completely lost. The scutum + scutellum is sagittate in shape, and the exposed portion is lingual shaped. The lateral sides of the covered portion are strongly constricted. The postmedian notal process is well-developed with obtuse angle, and its base is invaginate. The mesonotal pouch is oval in shape with the developed vertical plate lying at the center, and opens forward owing to the decrease of the horizontal plate. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process. The posterior process is characterized by a pouch-like structure and is covered with a few long hairs. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Sericini (Fig. 3G, 9G)

In the tribe Sericini the anterior half or two-thirds of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is flat. The first phragma is developed and is characterized by an anterior margin that is broadly emarginated. The prescutum is completely lost. The scutum + scutellum is triangular, and the exposed part is triangle. The postmedian notal process obtuse and its base weakly invaginate, and has no undulations on the lateral sides of the scutum + scutellum except this process. The mesonotal pouch is oval in shape is formed by only a horizontal plate as the vertical plate is completely lost. The scutellar process is sclerotized rod-shaped and its base weakly protrudes to outside, and the attached axillary cord is very thin membrane. The single scutellar process and posterior inflection of the mesonotal pouch are completely fused.

Orphninae (Figs. 3H, 9H)

In the subfamily Orphninae (genus *Orphnus*) the anterior two-thirds of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is developed and is characterized by an anterior margin that is emarginated. The prescutum is completely lost. The scutum + scutellum is isosceles triangular, and the exposed portion is triangle. The postmedian notal process is obtuse and its base strongly invaginate. The mesonotal pouch is oval in shape. The vertical and horizontal plates that form the mesonotal pouch developed. The scutellar process is sclerotized rod-shaped and its base weakly protrudes to outside, and the attached axillary cord is very thin membrane. The single scutellar process and posterior inflection of the mesonotal pouch are completely fused.

These character states resemble to the subfamily Dynamopodinae and family Hybosoridae.

Rutelinae (Figs. 3I, 4A−4E, 9I, 10A−10E)
In the Rutelinae, I examined the mesonotum of species in the following genera: *Adoretus*, *Adorodocia*, *Chaetadoretus*, *Lepadoretus*, *Spodochlamys*, *Anomala*, *Exomala*, *Mimela*, *Malaia*, *Popillia*, *Phyllopertha*, *Spilopopillia*, *Anoplognathus*, *Calloodes*, *Repsimus*, *Chrysophora*, *Dicaulocephalus*, *Kibakoganea*, *Parastasia*, and *Pelidnota*. The anterior half of the mesonotum in these beetles is covered by the pronotum, and the boundary dividing the exposed and concealed portions is marked by a transverse depression, but in some genera it is represented as flat (*Malaia*, *Popillia*, and *Repsimus*) (Fig. 4A) or truncate statuses (*Dicaulocephalus*, *Kibakoganea*, and *Parastasia*) (Figs.4B−4D). The first phragma is developed and is characterized by various states anterior margin. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum, but in the genus *Dicaulocephalus* the remnant is completely lost. The scutum + scutellum is typically shield-like in shape and the exposed portion is diffusely triangle, but in the genera *Dicaulocephalus*, *Kibakoganea* and *Parastasia* (Figs. 4B−4D) the scutum + scutellum is lingual shaped. The lateral sides of the boundary portion in the tribe Adoretini are strongly constricted. The postmedian notal process is obtuse, and in the tribe Adoretini it is well-developed (Figs. 4E). The mesonotal pouch is oval in shape. The vertical and horizontal plates that form the mesonotal pouch developed, but the vertical plate in the genera *Malaia*, *Popillia*, *Calloodes*, *Repsimus* and *Parastasia* is obscure or completely lost (Figs. 10A). The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process. The posterior process is characterized by a pouch-like structure and is covered with long setae. With the exception of some genera such as *Adoretus*, *Adorodocia*, *Chaetadoretus* and *Lepadoretus* (Figs. 10E), the posterior process is developed with rounded. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused. Exceptionally, in *Dicaulocephalus* (Figs. 4B−4C, 10B−10C), a sexual dimorphism, which the female is smooths while the male is strongly concave at the dorsal surface of the mesonotum, is observed. As a result, the vertical plate in male is completely fused with scutum + scutellum.

Trichinae (Figs. 4F−4I, 10F−10I)
Triciini and Incaini (Figs. 4F−4H, 10F−10H)
In the tribes Triciini and Incaini the anterior half or two-thirds of the mesonotum is

covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed or truncated. The first phragma is developed and is characterized by an anterior margin that is typically broadly emarginated, but in the genus *Corynotrichius* (Fig. 4G) it is pointed forward. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The shape of scutum + scutellum is observed two types that is shield-like in shape and trapezoidal in shape. The shield-like shaped scutum + scutellum is observed in the genera *Corynotrichius*, *Epitrichius*, *Gnorimus*, *Paratrichius* and *Inca* (Figs. 4F−4G). The trapezoidal shaped scutum + scutellum is observed in the genera *Lasiotrichius* and *Trichius* (Figs. 4H). The exposed portions of each type in scutum + scutellum is typically semicircular, but in the genera *Lasiotrichius* and *Inca* it is lingual and diffusely triangular shaped, respectively. The postmedian notal process in the genera *Corynotrichius*, *Gnorimus* and *Inca* is obtuse and is visible from the dorsal side, while in the genera *Epitrichius*, *Paratrichius*, *Lasiotrichius* and *Trichius* it is invisible from the dorsal side. The mosonotal pouch is oval in shape. The vertical and horizontal plates that form the mesonotal pouch developed, but the vertical plate in the genera *Corynotrichius*, *Lasiotrichius* and *Trichius* is completely lost. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process. The posterior process is characterized by a pouch-like structure and is covered with long setae. With the exception of some genera such as *Lasiotrichius* and *Trichius*, the posterior process is developed with rounded. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Osmodermini (Figs. 4I, 10I)

In the tribe Osmodermini the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is weakly transversely depressed. The first phragma is developed and is characterized by an anterior margin that is broadly pointed forward. The prescutum is completely lost. The scutum + scutellum is diamond shaped and the exposed portion appears as a large triangle. The postmedian notal process is strongly reduced. The mesonotal pouch is oval in shape. The vertical and horizontal plates that form the mesonotal pouch developed, but the vertical plate does not fused with the internal surface of the scutum + scutellum and protrudes to ventral side. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process, but the development of the posterior process is very weak and the pouch-like structure is lost. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Valginae (Figs. 5A−5B, 11A−11B)

The subfamily Valginae showed the most unique characteristics in the family Scarabaeidae. The anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is typically completely lost, but in the tribe Microvalgini (Fig. 5B) it is weakly developed and is characterized by an anterior margin that is straight. The prescutum is completely lost. The scutum + scutellum is auriculate shaped, and the exposed portion is usually pointed but the tribe Microvalgini is triangle. The postmedian notal process is completely lost. The mesonotal pouch is inverted triangular or round in shape. The vertical and horizontal plates that form the mesonotal pouch developed, especially the vertical plate protrudes to ventral side. The scutellar process is sclerotized rod-shaped and the attached axillary cord is completely lost. The single scutellar process and posterior inflection of the mesonotal pouch are completely fused.

Coprophagous group of Scarabaeidae

Aphodiinae (Figs. 5C, 11C)

In the subfamily Aphodiinae (genus *Aphodius*) the anterior half of the mesonotum is covered by the pronotum, and the boundary dividing the exposed and concealed portions is marked by a transverse depression. The development of first phragma is weakly. The prescutum is completely lost. The scutum + scutellum is sagittate in shape, and the exposed portion has a triangular shape. The postmedian notal process is obtuse and its base is invaginate. The mesonotal pouch is oval shape. The vertical and horizontal plates that form the mesonotal pouch developed. The scutellar process is a sclerotized rod-shape and completely fused with the posterior inflection of the mesonotal pouch, and the attached axillary cord appears as a very thin membrane.

Scarabaeinae (Figs. 5D, 11D)

In the subfamily Scarabaeinae (genus *Copris*) the mesonotum is completely covered by the pronotum. The first phragma is well-developed and is characterized by an anterior margin that is deeply emarginate at the center. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is pentagonal in shape. The postmedian notal process is obtuse, and its base is strongly concave and truncated. The mesonotal pouch is oval shaped. The vertical and horizontal plates develop strongly, with the former traversing the mesonotal pouch, dividing the pouch into two sections. The scutellar process is sclerotized and triangular shape and the attached axillary cord is weakly sclerotized membrane. Furthermore, the sutural line between the scutellar process and the posterior inflection of mesonotal pouch is clearly visible.

Bolboceratidae (Figs. 5E−5F, 11E−11F)

In the family Bolboceratidae the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is well developed, and the lateral parts of the anterior margin protrude forward. The prescutum is completely lost. The shape of scutum + scutellum is sagittate and the exposed portion is observed two types that are rounded triangular (tribe Bolbochromini) (Fig. 5E) and lingual shape (tribe Bolbelasmini) (Fig. 5F). The postmedian notal process is obtuse, and its base invaginate. The mesonotal pouch is oval shape. The vertical and horizontal plates that form the mesonotal pouch developed, but in the genera *Bolbelasmus* and *Bolbochromus* the mesonotal pouch slightly opens forward owing to the decrease of the horizontal plate (Fig. 11F). The scutellar process is a sclerotized rod-shaped and completely fused with the posterior inflection of the mesonotal pouch, and the attached axillary cord appears as a very thin membrane.

Geotrupidae (Figs. 5G−5H, 11G−11H)

Geotrupinae (Figs. 5G, 11G)

In the subfamily Geotrupinae the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is well-developed, and the lateral ends protrude outside. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is shield-like in shape, and the exposed portion is diffusely triangle. The postmedian notal process is obtuse and its base invaginate. The mesonotal pouch is flabellate in shape. The vertical and horizontal plates that form the mesonotal pouch developed. The scutellar process is a sclerotized rod-shaped and completely fused with the posterior inflection of the mesonotal pouch, and the attached axillary cord is very thin membrane.

Lethrinae (Figs. 5H, 11H)

In the Lethrinae (genus *Lethrus*) the mesonotum shows very unique states compared to other species in Geotrupidae by the completely lose of hind wing. The mesonotum is exposed the most part. The first phragma is strongly reduced and amalgamate to the horizontal plate. The prescutum is completely lost. The scutum + scutellum is isosceles right triangularly shaped. The postmedian notal process is strongly reduced. The mesonotal pouch is isosceles right triangular and occupies the most of ventral surface. The development of the vertical plate and horizontal plate that form the mesonotal pouch are very weak. The scutellar process is sclerotized membrane, and is completely fused with the posterior inflection of mesonotal pouch.

Glaresidae (Figs. 5I, 11I)

In the family Glaresidae (genus *Glaresis*) the anterior half of the mesonotum is covered by the pronotum, and the center of the boundary dividing the exposed and concealed portions is marked by a slightly depression. The first phragma is developed but is invisible from the dorsal surface, and is characterized by an anterior margin that is sags downward. The prescutum is reduced and the remnant is visible at the anterior margin of the scutum + scutellum. The scutum + scutellum is sagittate in shape, and the exposed portion is lingual shape. The postmedian notal process is obtuse. The mesonotal pouch is inverted triangularly shaped is formed by only a horizontal plate as the vertical plate is completely lost. The scutellar process is a sclerotized rod-shaped and completely fused with the posterior inflection of the mesonotal pouch, and the attached axillary cord is very thin membrane.

Glaphyridae (Figs. 6A, 12A)

In the family Glaphyridae the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is well-developed, and the lateral sides protrude to outside. The prescutum is completely lost. The scutum + scutellum is isosceles triangular, and the exposed portion is lingual shape. The postmedian notal process is reduced. The mesonotal pouch is oval and opens forward owing to the decrease of the horizontal plate, whereas the vertical plate develops. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process, but the development of the posterior process corresponding to axillary cord is weak. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Hybosoridae (Figs. 6B−6C, 12B−12C)

Hybosorinae (Figs. 6B, 12B)

In the subfamily Hybosorinae the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is reduced the most part, but the lateral sides remain and protrude to forward. The prescutum is completely lost. The scutum + scutellum is isosceles triangular, and the exposed portion is lingual shape. The postmedian notal process is obtuse. The mesonotal pouch is oval in shape. The most parts of the vertical plate are fused with developed horizontal plate. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process, but the development of the posterior process corresponding to axillary cord is weak. The dichotomous branching process and posterior inflection of the mesonotal pouch are completely fused.

Ceratocanthinae (Figs. 6C, 12C)

In the subfamily Ceratocanthinae the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is marked by a weakly transverse depression. The first phragma is almost completely reduced and its remnant is visible on the lateral sides. The prescutum is completely lost. The scutum + scutellum is isosceles triangular, and the exposed portion is strongly pointed. The postmedian notal process is strongly reduced. The mesonotal pouch is oval and is formed by only a developed horizontal plate as a vertical plate is completely lost. The scutellar process and the attached axillary cord are sclerotized and completely fused to form a dichotomous branching process, but the development of the posterior process corresponding to axillary cord is weak. The dichotomous branching process and the posterior inflection of mesonotal pouch are completely fused.

Lucanidae (Figs. 6D−6I, 7A, 12D−12I, 13A)

Aesalinae and Syndesinae (Figs. 6D−6F, 12D−12F)

In the subfamilies Aesalinae and Syndesinae the anterior half of the mesonotum is covered by the pronotum, and the boundary dividing the exposed and concealed portions is marked by a transverse depression, but in the genus *Aesalus* the boundary portion is presented a truncate state (Fig. 6D). The first phragma is well-developed and the lateral parts of the anterior margin protrude forward, except in the genus *Aesalus*. The first phragma in the genus *Aesalus* also well-developed but is characterized by an anterior margin that is emarginated. The prescutum is completely lost. The scutum + scutellum is isosceles triangular and the exposed portion is lingual shape. The postmedian notal process is obtuse and its base is invaginate. The mesonotal pouch is rounded, with the developed vertical plate lying at the center. The scutellar process is a sclerotized rod-shaped and its base expand to outside, and the attached axillary cord is very thin membrane. The single scutellar process and posterior inflection of the mesonotal pouch are completely fused.

Lucaninae and Lamprinae (Figs. 6G−6I, 7A, 12G−12I, 13A)
In the subfamilies Lucaninae and Lamprinae the anterior two-thirds of the mesonotum are covered by the pronotum, and the boundary dividing the exposed and concealed portions is marked by a transverse depression. The first phragma is well-developed and the lateral parts of the anterior margin protrude forward. The prescutum is completely lost. The scum + scutellum is sagittate in shape, and the exposed portion is lingual shape, but in the genus *Figulus* (Fig. 6H) the exposed part is strongly pointed. The postmedian notal process is obtuse and its base is invaginate. The mesonotal pouch is round and typically opens forward owing to the decrease of the horizontal plate, but in the genus *Platycerus* the horizontal plate is developed (Fig. 12I). The developed vertical plate lying at the center of the mesonotal pouch. The scutellar process is a sclerotized rod-shaped and its base expand to outside, and the attached axillary cord is very thin membrane. The single scutellar process and posterior inflection of the mesonotal pouch are completely fused.

Ochodaeidae (Figs. 7B, 13B)
In the family Ochodaeidae the anterior half of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is developed and is characterized by an anterior margin that is sags downward. The prescutum is completely lost. The scutum + scutellum is sagittate in shape, and the exposed portion is triangular shape. The postmedian notal process is obtuse and its base is invaginate. The mesonotal pouch is rounded and typically opens forward owing to the decrease of the horizontal plate, but in the genus *Notochodaeus* the mesonotal pouch is complete. The developed vertical plate lying at the center of the mesonotal pouch. The scutellar process is a sclerotized rod-shaped and its base expand to outside, and the attached axillary cord is very thin membrane. The single scutellar process and the posterior inflection of the mesonotal pouch are fused completely.

Passalidae (Figs. 7C, 13C)
In the family Passalidae the mesonotum is completely covered by the pronotum. The first phragma is developed and is strongly sclerotized but is almost invisible from dorsal surface, and is characterized by an anterior margin that is sags downward. The prescutum is completely lost. The scutum + scutellum is cordate in shape and the remnant of the mesopostnotum is observed from the posterior apex. The postmedian notal process is

obtuse and its base is invaginate. The mesonotal pouch is very large and opens forward owing to the decrease of the horizontal plate, and the vertical plate also completely lost. The scutellar process is a sclerotized rod-shaped and its base expand to out sides, and the attached axillary cord is very thin membrane. The single scutellar process and the posterior inflection of the mesonotal pouch is completely fused.

Pleocomidae (Figs. 7D, 13D)

In the family Pleocomidae (genus *Pleocoma*) the anterior two-thirds of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is transversely depressed. The first phragma is well-developed, and the anterior margin is truncated. The prescutum is completely lost. The scutum + scutellum is shield-like in shape, and the exposed portion is diffusely triangular. The postmedian notal process is obtuse. The mesonotal pouch is oval in shape, with the developed vertical plate lying at the center. The rod-shaped scutellar process is sclerotized and completely fused with the posterior inflection of the mesonotal pouch, whereas the attached axillary cord is present as a very thin membrane.

Trogidae (Figs. 7E, 13E)

In the family Trogidae the anterior two-third of the mesonotum is covered by the pronotum, and the boundary between the concealed and exposed portions is marked by a transverse depression. The first phragma is well-developed, and is characterized by an anterior margin that is strongly emarginate. The prescutum is completely lost. The scutum + scutellum is sagittate in shape, and the exposed portion is lingual shape. The postmedian notal process is obtuse, and its base is weakly invaginate. The mesonotal pouch is oval in shape, with the developed vertical plate lying at the center. The scutellar process is a sclerotized rod-shaped and the attached axillary cord is present as a very thin membrane. The single scutellar process and posterior inflection of the mesonotal pouch are completely fused.

Discussion

On the basis of my examination of the mesonotum in the phytophagous group of Scarabaeidae and comparison with that in species in the phytophagous group of Scarabaeidae and other scarabaeoid families, I make the following inferences.

Types of mesonotum in the phytophagous group of Scarabaeidae

I suggest dividing the mesonotum in the phytophagous group of Scarabaeidae into nine types: melolonthine, ruteline, tricine, cetoniine, valgine, sericine, hopline, diplotaxine, and orphnine types. According to subchapter 2–2–1, the mesonotum plays a role in fixing the elytra, although it has little influence on flight behavior in the coprophagous group of Scarabaeidae. This is also the case for the phytophagous group of Scarabaeidae, where the mesonotum is usually much smaller than the metanotum due to hardly necessary for flying. The following features are important to distinguish each type: shape of scutum + scutellum, state of boundary portion, development of internal ridges (horizontal and vertical plates), and scutellar process and axillary cord.

The Aclopinae, Melolonthinae (Melolonthini, Rhizotrogini, and Tanyproctini), and Rutelinae (Adoretini) belong to the melolonthine type. The scutum + scutellum is shield-like in shape. The boundary between the concealed and exposed portions was transversely depressed. The horizontal plate forms a mesonotal pouch by closing forward, and the vertical plate develops and elongated. The scutellar process and attached axillary cord form a dichotomous branching process. The axillary cord has a pouch-like structure and is covered with long setae, however these setae were not observed in the subfamily Aclopinae.

The Rutelinae, Dynastinae, Euchirinae, and Trichiinae (*Corynotrichius*, *Epitrichius*, *Gnorimus*, *Paratrichius* and *Inca*) belong to the ruteline type. The scutum + scutellum is shield-like in shape. The boundary between the concealed and exposed portions is marked by a transverse depression, but some genera such as *Dicaulocephalus*, *Kibakoganea*, *Parastasia*, *Malaia* and *Popillia* (Figs. 4A−4D) are presented by truncate or flat states. The horizontal plate forms a mesonotal pouch by closing forward, and a vertical plate is more or less observed. The scutellar process and attached axillary cord form a dichotomous branching process. The axillary cord has a pouch-like structure and is largely rounded. The surface of the axillary cord was covered with long setae.

Some Trichiinae (*Lasiotrichius* and *Trichius*) belong to the triciine type. The scutum + scutellum is trapezoidal in shape. The boundary between the concealed and exposed portions was transversely depressed. The horizontal plate forms a mesonotal pouch by closing forward and the vertical plate is completely lost. The scutellar process and attached axillary cord form a dichotomous branching process. The axillary cord has a pouch-like structure and is covered with sparse long setae.

The Cetoniinae and Osmodermini belong to the cetoniine type. The scutum + scutellum is diamond in shape. The boundary between the concealed and exposed portions is typically flat, but the genera *Clinterocera*, *Coilodera*, and *Osmoderma* are characterized by depression. The horizontal plate forms a mesonotal pouch by closing forward and the vertical plate is completely lost. The scutellar process and attached axillary cord form a dichotomous branching process. The axillary cord is represented by a sclerotized membranous state and has a shallow elongated pouch-like structure and sparse setae. As an exception, the development of the axillary cord in the genera *Anthracophora*, *Clinterocera*, and *Osmoderma* was very weak and the pouch-like structure was completely lost (Figs. 8C, 8E, 10I).

The Valginae belongs to the valgine type. The scutum + scutellum is auriculate in shape. The boundary between the concealed and exposed portions was marked by transverse depression. The horizontal plate forms a mesonotal pouch by closing forward, and the vertical plate develops and protrudes to the ventral side. The scutellar process is sclerotized rod-shaped, and the axillary cord is completely lost.

The tribe Sericini belongs to the sericine type. The scutum + scutellum is triangular and has no undulations on the lateral sides except for the postmedian notal process. The boundary between the concealed and exposed portions is flat. The horizontal plate forms a mesonotal pouch by closing forward and the vertical plate is completely lost. The scutellar process is sclerotized rod-shaped, and its base weakly expands to the outside. The axillary cord is a thin membrane.

The tribe Hopliini belongs to the hopline type. The scutum + scutellum is sagittate in shape and the lateral sides of the covered part are strongly constricted. The boundary between the concealed and exposed portions was transversely depressed. The mesonotal pouch opens forward owing to the decrease in the horizontal plate, whereas the vertical plate develops elongate. The scutellar process and attached axillary cord form a dichotomous branching process. The axillary cord has a pouch-like structure and few long setae.

The tribe Diplotaxini belongs to the diplotaxine type. The scutum + scutellum is triangular in shape. The boundary between the concealed and exposed portions was transversely depressed. The mesonotal pouch opens forward owing to the decrease in the horizontal plate, while the vertical plate develops elongate, and the fused point of the vertical plate to the first phragma is characterized by an invaginate. The scutellar process and the attached axillary cord form a dichotomous branching process, but the development of the axillary cord is weak. The axillary cord has a small pouch-like structure.

The Orphninae and Dynamopodinae belong to the orphnine type. The scutum + scutellum is isosceles triangularly shaped. The boundary between the concealed and exposed portions was marked by transverse depression. The horizontal plate forms a mesonotal pouch by closing forward, and the vertical plate develops and elongated. The scutellar process and the attached axillary cord form a dichotomous branching process by sclerotization and complete fusion with each other, but the development of the posterior process corresponding to the axillary cord is weak. These character states are similar to those of the families Hybosoridae and Glaphyridae.

Phytophagous and coprophagous groups of Scarabaeidae

According to subchapter (2–2–1), phytophagous and coprophagous groups of Scarabaeidae can be distinguished based on the characteristics of the scutellar process and attached axillary cord. Phytophagous groups are indicated by a dichotomous branching process (Fig. 14), which consists of a sclerotized scutellar process and axillary cord with a pouch-like structure bearing long setae, whereas coprophagous groups are indicated by a single rod-shaped or triangular scutellar process and a membranous axillary cord (subchapter 2–2–1). However, in this study, a single rod-shaped process and an intermediate feature of the dichotomous branching process, which is observed in the families Hybosoridae and Glaphyridae, are observed in some species of the phytophagous group of Scarabaeidae.

The single rod-shaped process was confirmed in the tribe Sericini and subfamily Valginae. Since the single rod-shaped process usually indicates an ancestral state, it was regarded that the Sericini is an ancestral group compared to other phytophagous groups. However, reference to recent phylogenetic analyses (Ahrens *et al*. 2014, Gunter *et al*. 2016, Šípek *et al*. 2016) showed that the tribe Sericini is positioned at the early diverging lineages in the phytophagous group of Scarabaeidae, and that the phytophagous group were derived lineages from the families Glaphyridae and Hybosoridae, which have intermediate dichotomous branching process. Therefore, the single rod-shaped process in the Sericini is regarded as occurring from the intermediate dichotomous branching process by secondary atrophy. The single rod-shaped process observed in the Valginae is also thought to have occurred due to secondary atrophy. The subfamily Valginae is known as the sister group of the subfamily Cetoniinae (Browne and Scholtz 1998, Smith *et al*. 2006, Gunter *et al*. 2016). Subchapter (2–2–1) mentioned that the development of the axillary cord in Cetoniinae is weaker than that observed in other members of the phytophagous Scarabaeidae and appears to reflect a process of atrophication. Indeed, a remarkably atrophied axillary cord is observed in some tribes of Cetoniinae, implying that the single rod-shaped process found in the Valginae was derived from Cetoniinae.

The intermediate dichotomous branching process was confirmed in the subfamilies Dynamopodinae and Orphninae. Of these, the Orphninae is presented as an ancestral group of the phytophagous group of Scarabaeidae based on by some phylogenetic studies (Browne and Scholtz 1998, Ahrens 2005, Ahrens *et al.* 2014), and tends to form the early diverging lineages of phytophagous groups of Scarabaeidae (Paulian and Lumaret 1982) with the families Glaphyridae and Hybosoridae, which also have an intermediate branching process. From the above, it seems that the intermediate features found in the Dynamopodinae and Orphninae clearly indicate the relationships between the phytophagous groups of Scarabaeidae and Hybosoridae and Glaphyridae.

These results, with some exceptions, generally follow subchapter (2–2–1) which is suggests that the phytophagous and coprophagous groups of Scarabaeidae can be divided by the differences in the scutellar process and axillary cord. In addition, the intermediate dichotomous branching process of the subfamilies Dynamopodinae and Orphninae strongly supported the relationship between the phytophagous groups and the families Glaphyridae and Hybosoridae. On the other hand, the close relationship between the phytophagous and coprophagous groups is denied, which supports the results the recent phylogenetic analyses (Smith *et al.* 2006, Ahrens *et al.* 2014).

Evolution of the mesonotal structure and the most ancestral states of mesonotum in Scarabaeoidea

The mesonotum in Coleoptera is reduced by loss of flight muscle with developing the elytra, and was less affected by environmental factors and behavioral traits. Therefore, the characteristics of the mesonotum, which show a moderate evolutionary rate compared to other variable morphological traits, such as a mouth parts and legs, are considered to be useful for estimating evolutionary trends. In most coleopteran species, the mesonotum functions only as a fixing device, and the elytra are firmly fixed by the engagement of the sutural line and metanotal alacrista, and the posterior margin of the mesonotum (Larsen 1966, Nomura 2015). According to Ochi *et al.* (2012), the importance of mesonotal features for estimating evolutionary directions in Scarabaeoidea tends to consider whether the mesonotum is covered or exposed by the pronotum. However, its characteristics depend on the shape of the pronotum, and it was suggested in subchapter (2–2–1) that the exposed or covered state is inappropriate for considering evolutionary trends. My observations and the results of subchapter (2–2–1) found that the following characteristics are more important in estimating evolutionary trends: development of first phragma, presence of prescutum, shape of scutum + scutellum, and variation of scutellar process and attached axillary cord.

In the members of the Scarabaeoidea, the first phragma is also generally well-developed when viewed dorsally. The first phragma in the phytophagous and coprophagous groups of the Scarabaeidae are generally well-developed and present various character states, although in the subfamilies Valginae and Aphodiinae (*Aphodius*) it was strongly reduced or completely lost. In the other scarabaeoid families Bolboceratidae, Geotrupidae (Geotrupinae), Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Pleocomidae, and Trogidae also have well-developed first phragma, whereas the first phragma tends to be reduced or completely lost in the Geotrupidae (Lethrinae), Glaresidae, and Passalidae. According to subchapter (2–2–1), the ancestral state of the first phragma in the Scarabaeoidea indicates a well-developed state, and the reduced first phragma evolved relatively late. Indeed, a well-developed first phragma is observed in the groups (families Geotrupidae, Hybosoridae, Lucanidae, Ochodaeidae, Pleocomidae, and Trogidae) that are considered to be ancestral scarabaeoid families (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990, Browne and Scholtz 1999, Ahrens *et al*. 2014, Gunter *et al*. 2016). This implies that the reduced or completely lost first phragma indicates a more derived state. However, the reduced first phragma was also confirmed in the Glaresidae and Passalidae, which are generally included in the ancestral group of the Scarabaeoidea. Consequently, it may not be possible to conclude that the reduced first phragma indicates a relatively derived state, however these reductions in the Glaresidae and Passalidae may have been affected by a behavioral traits and environmental factors. Species of the Glaresidae usually prefer xerothermic, often sandy habitats (Scholtz and Grebennikov 2016, Král *et al*. 2017), and Scholtz *et al*. (1987), based on the shape of the maxillar lacinia, believe that the adults feed on underground mushrooms. Species of the Passalidae are often found in rotting hardwood logs and feed on wood (Scholtz and Grebennikov 2016). Owing to these ecological interactions, the flight frequency in each group was considered to have decreased markedly. For example, the species of the subfamily Lethrinae (*Lethrus karelini*, *L. microbuccis*, and *L. bituberculatus*) and Aegialiinae (*Aegialia nitida*) (subchapter 2–2–1), which is entirely comprised of flightless beetles, appear with remarkably reduced first phragma. On the basis of the aforementioned states and results of subchapter (2–2–1), I also conclude that the well-developed first phragma appears early in the Scarabaeoidea, and that a reduced first phragma evolved relatively late in certain lineages.

In the families Bolboceratidae, Geotrupidae (Lethrinae), Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Passalidae, Pleocomidae, and Trogidae, and some subfamilies within the Scarabaeidae [Aphodiinae, Cetoniinae, Dynamopodinae, Melolonthinae (Diplotaxini, Hopliini, Sericini), Orphninae, Rutelinae (*Dicaulocephalus*), Trichiinae (Osmodermini), and Valginae], the prescutum was completely lost. However, the remnant of the prescutum has been identified in the Geotrupidae (Geotrupinae) and

Glaresidae, and some subfamilies within the Scarabaeidae [Aclopinae, Dynastinae, Euchirinae, Melolonthinae (Melolonthini, Rhizotrogini, and Tanyproctini), Rutelinae, Trichinae (Triciini and Incaini), and Scarabaeinae]. Prescutum have also been confirmed in the Staphylinidae (Larsén 1966, Matsuda 1970) within an out group of the Scarabaeoidea (McKenna *et al*. 2019), and is considered a typical thoracic structure of insects (Snodgrass 1935). Therefore, the remnant of the prescutum, which was confirmed in the Geotrupidae (Geotrupinae) and Glaresidae, and some subfamilies within the Scarabaeidae [Aclopinae, Dynastinae, Euchirinae, Melolonthinae (Melolonthini, Rhizotrogini, and Tanyproctini), Rutelinae, Trichinae (Triciini and Incaini), and Scarabaeinae], are considered to represent an ancestral state. However, as indicated in recent phylogenies (Ahrens *et al*. 2014, Gunter *et al*. 2016), this structure it is not present in some scarabaeoid clades including the ancestral groups Geotrupidae, Hybosoridae, Ochodaeidae, Pleocomidae, and Trogidae. It is thus considered that a reduction in the prescutum occurred convergently in multiple scarabaeoid clades.

A diversity of shapes of scutum + scutellum is observed in various types of Scarabaeoidea, but the shape of the mesonotum was categorized into three major shape types (sagittate, isosceles triangular, and shield) based on examination. In species of the Bolboceratidae, Glaresidae, Lucanidae (Lucaninae and Lamprinae), Ochodaeidae, and Trogidae, and some groups of the Scarabaeidae [Aphodiinae and Melolonthinae (Hopliini)], the mesonotum is sagittate shaped. The above groups, excluding the Scarabaeidae have been traditionally treated as ancestral groups of the Scarabaeoidea (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990) and are presumed to establish early diverging lineages in molecular phylogenetic analyses (Ahrens *et al*. 2014, Gunter *et al*. 2016). In species of the Glaphyridae, Hybosoridae, and Lucanidae (Aesalinae and Syndesinae), and some groups of the Scarabaeidae (Dynamopodinae and Orphninae), the shape of the mesonotum is isosceles triangular in shape. Among these groups, the Hybosoridae and Lucanidae have been treated with ancestral groups, and the Glaphyridae and Orphninae have been treated as intermediate groups of Scarabaeoidea (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990). In recent phylogenetic analyses, the Hybosoridae, Glaphyridae, and Orphninae were placed around the turning-points between the phytophagous groups of Scarabaeidae and other scarabaeoid groups. In species of the Geotrupidae and Pleocomidae, and many groups of the Scarabaeidae [Aclopinae, Dynastinae, Euchirinae, Melolonthinae (Melolonthini, Rhizotrogini, and Tanyproctini), Rutelinae, and Trichinae (Triciini and Incaini)], the mesonotum is shield-like shaped. Among these groups, Geotrupidae and Pleocomidae are generally considered to be the ancestral group of

Scarabaeoidea, whereas the phytophagous group of Scarabaeidae is considered to be the most derived group (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990, Ahrens *et al*. 2014, Gunter *et al*. 2016). Based on the aforementioned results, the evolutionary tendency of the mesonotum in Scarabaeoidea concluded that the sagittate mesonotum appeared in the early diverging lineages, followed by the isosceles triangular mesonotum, and that the shield-like shaped mesonotum occurred rather late. The other uniquely shaped mesonotum is thought to be derived from some stages of the above shapes.

The variation of the scutellar process and attached axillary cord is suggested in subchapter (2–2–1) as the most important features defining mesonotal structures in the Scarabaeoidea. According to subchapter (2–2–1), the scutellar process and axillary cord are broadly distinguishable as a single process (single rod or triangular) with thin membranous axillary cord, and a dichotomous branching process, of which the latter indicates a derived state. As a matter of fact, the dichotomous branching process is observed in most of the phytophagous group of Scarabaeidae (Figs. 8A−8I, 9A−9F, 9I, 10A−10I), which is a relatively late group, and a single rod-shaped process with a thin membranous axillary cord are found in most ancestral groups such as the families Bolboceratidae, Geotrupidae, Glaresidae, Lucanidae, Ochodaeidae, Passalidae, Pleocomidae, and Trogidae. Consequently, it was definite that the single rod-shaped process with a thin membranous axillary cord indicated ancestral features, and thus, the dichotomous branching process and single triangular process with membranous axillary cord indicate derived features. However, in the subfamily Cetoniinae the development of the dichotomous branching process tends to be weaker than that of other members of the phytophagous group of Scarabaeidae (subchapter 2–2–1). As a result of observing additional groups in this study, the single scutellar process was also observed in some phytophagous groups (tribe Sericini, and subfamilies Cetoniinae and Valginae) (Figs. 8C, 8E, 9G, 11A−B). Since most species of the phytophagous members closely related to these groups have a dichotomous branching process, it is considered that the above single process was caused by the secondary atrophy of the dichotomous branching process. Therefore, the single process indicates an ancestral state, but in some phytophagous groups, it appears to be the most derived state.

My observation concludes that the most ancestral scarabaeoid species are characterized by the following characteristics of the mesonotum: well-developed first phragma, remnant of the prescutum, sagittate scutum + scutellum, and single rod-shaped scutellar process and thin membranous axillary cord.

Families Bolboceratidae and Geotrupidae

The families Bolboceratidae and Geotrupidae had been treated as a single family (Geotrupidae) within Scarabaeoidea in early studies. However, since Scholtz and Browne (1996) the Bolboceratidae and Geotrupidae have been accorded as an independent family, respectively. Besides, in other recent studies, the relationship between Bolboceratidae and Geotrupidae is not supported and a molecular phylogenetic analysis conducted by Ahrens *et al*. (2014) indicated the monophyly of the Bolboceratidae. The mesonotal characteristics observed in this examination also indicates different features between Bolboceratidae and Geotrupidae, that are characterized by a sagittate and a shield-like shaped scutum + scutellum, respectively. On the contrary, the members in Bolboceratidae shared the same characteristics as the families Glaresidae, Lucanidae, Ochodaeidae, and Trogidae.

Family Hybosoridae, and subfamilies Dynamopodinae and Orphninae

The mesonotal structures in the subfamilies Dynamopodinae and Orphninae presents the same features as that in the family Hybosoridae. Specifically, the prescutum is completely lost, the scutum + scutellum is isosceles triangular, the first phragma is well-developed, and the scutellar process and axillary cord form an intermediate dichotomous branching process. About the affiliation of the subfamily Dynamopodinae had been proposed some hypothesis. According to Fairmaire (1897), the Dynamopodinae is placed to the subfamily Dynastinae, whereas Balthasar (1971) and Nikolayev (1993) treated it as the family Hybosoridae. Li *et al*. (2019) a close relationship between Dynamopodinae and Pleocomidae. The subfamily Orphninae has been associated with the Hybosoridae based on prominent mandibles and labrum (Iablokoff-Khnzorian 1977, Paulian 1984, Scholtz and Grevennikov 2016). My examination results supported to the closely relation between the family Hybosoridae and subfamilies Dynamopodinae and Orphninae.

Subfamilies Rutelinae and Dynastinae

The closely relation between the subfamilies Rutelinae and Dynastinae have been indicated by the morphological (Browne and Scholtz 1998) and molecular phylogenetic analyses (Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, Eberle *et al*. 2019). Indeed, typically, the species of Rutelinae and Dynastinae are shared the ruteline typed mesonotum, however some unique character states are observed in the following groups: Rutelini (genera *Parastasia*, *Kibakoganea*, and *Dicaulocephalus*) and Adoretini.

In the genera *Parastasia*, *Kibakoganea*, and *Dicaulocephalus*, the boundary between the concealed and exposed portions of the mesonotum is truncated, and the exposed portion is characterized by lingual in shape. These genera, generally, have been treated as the members of subfamily Rutelinae (Smith 2006, Bouchard *et al*. 2011, Krajcik 2012, Bezděk *et al*. 2016, Scholtz and Grebennikov 2016). However, Smith *et al*. (2006) and Wada (2015) regarded that the genus *Parastasia* is firmly placed in the subfamily Dynastinae. My observational results present that the above genera have obviously different features from other members of the Rutelinae and may need to be moved to another group. However, the relationship between the genus *Parastasia* and the subfamily Dynastinae were not well supported.

In the Adoretini, the mesonotum is characterized by a strongly constricted lateral sides of the boundary portion, and a undeveloped axillary cord. This tribe also has been considered as belonging to the subfamily Rutelinae (Smith 2006, Bouchard *et al*. 2011, Krajcik 2012, Bezděk *et al*. 2016, Scholtz and Grebennikov 2016). However, according to recent molecular phylogenetic analyses (Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, Šípek *et al*. 2016, Eberte *et al*. 2019), the systematic position is suggested that needed to be elevated to the subfamily level. Moreover, the relationships with the subfamily Dynastinae are strongly supported. A similarity of the strongly constricted boundary portion may indicate the closely relation between the Dynastinae and Adoretini.

Subfamily Melolonthinae

This is the largest subfamily of Scarabaeidae. Typical Melolonthinae is without doubt basal to the large "phytophagous" clade of Dynastinae, Rutelinae, and Cetoniinae (Browne and Scholtz 1998, Ahrens *et al*. 2014, Scholtz and Grebennikov 2016). However, the Melolonthinae is poorly defined yet, and several groups have been included and excluded at various stages by different authors. To give some example, Nel and De Villiers (1988), d'Hotman and Scholtz (1990a), Nel and Scholtz (1990) and Pretorius and Scholtz (2001) treated tribe Hopliini as scarabaeid subfamily Hoplinae, and the tribe Sericini is regarded as scarabaeid subfamily Sericinae in Ritcher (1969a) and Coca-Abia (2007). Moreover, some phylogenetic analyses have shown that present Melolonthinae is polyphyletic group (Browne and Scholtz 1998, Ahrens 2005, Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, Šípek *et al*. 2016, Eberte *et al*. 2019). Therefore, considerable variation in the mesonotum also has been founded such as the melolonthine, sericine, hopline, diplotaxine types. Among these, probably, the melolonthine type is the basic form that defines authentic Melolonthinae. Since the mesonotal features were considered as a crucial characteristic for estimate a relationship among subfamilies in the Scarabaeidae, it may be reasonable to treat each group, which show unique mesonotal types such as sericine, hopline and diplotaxine, as the independent subfamilies.

Subfamily Aclopinae

The systematic treatment of the subfamily Aclopinae is still incompletely understood. Erichson (1845-1847) treated the Aclopinae as the family Glaphyridae, but Lacordaire (1856) suggested that the Aclopinae be moved to the Melolonthinae based on the position of the spiracles. Scholtz and Grebennikov (2016) mentioned that Aclopinae resembles members of the Hybosoridae based on prominent mandibles and labrum.

The mesonotal structures of the Aclopinae are similar to those of melolonthine tribes Melolonthini, Rhizotrogini, and Tanyproctini, which present the melolonthine typed mesonotum. However, unique characteristics, such as no hair on the axillary cord, were observed in the Aclopinae. Since the dichotomous branching process with long hair shows a rather derived state, the Aclopinae is considered to be an ancestral taxon compared to the above melolonthine groups.

Subfamilies Cetoniinae, Trichinae, and Valginae

Subfamilies Cetoniinae, Trichinae, and Valginae, are often treated as a single subfamily Cetoniinae (Ahrens *et al*. 2014, Bezděk 2016, Šípek *et al*. 2016). However, the characteristics of the mesonotum were showed remarkably differences between subfamilies (Figs. 2B, 4F, 5A). Accordingly, this observational results conclude that the Cetoniinae, Trichinae, and Valginae should be defined as independent subfamilies. Moreover, unique characteristics were founded in some members such as the tribe Osmodermini and genus *Corynotrichius*.

The tribe Osmodermini has been considered as one of the tribes in Trichinae (Krikken 1984, Krajcik 2012). However many phylogenetic hypotheses, are established based on morphological and molecular data, have indicated a close relationship between subfamily Cetoniinae (Micó *et al*. 2008, Šípek *et al*. 2009, Šípek *et al*. 2011, Šípek *et al*. 2016), since Browne and Scholtz (1998) suggested that the tribe Osmodermini is the sister group of Cetoniinae. The mesonotal structures are also supported the closely relationships to the Cetoniinae, notably the tribes Cremastocheilini and Taenioderini have many same characteristics.

A systematic position of the genus *Corynotrichius* has been placed in the tribe Triciini within subfamily Trichinae (Krikken 1982, Krajcik 2012). However, the mesonotum is similar to the features of the Rutelini (genera *Kibakoganea* and *Parastasia*), that is may representing a close relation each other.

Systematic position of the subfamily Euchirinae

The systematic treatment of the subfamily Euchirinae has been changed through time. Young (1989) conducted the most detailed study of the subfamily, treating it as one of scarabaeid subfamily. Ahrens (2005) indicated a slight the relationship with subfamily Dynastinae (genus *Oryctes*). Šípek *et al*. (2009) mentioned that the subfamily is positioned as a sister group of pleurostict scarabs (Rutelinae, Dynastinae, Melolonthinae, and Cetoniinae), however in Šípek *et al*. (2011) the Euchirinae is placed on a sister group of the clade Rutelinae + Dynastinae + Melolonthinae. Ahrens *et al*. (2014) suggested that Euchirinae is related to the tribes Hopliini and Macrodactylini. The mesonotal structure of Euchirinae is similar to characteristics of Dynastinae and Rutelinae, especially the dynastine features are almost conformity, that may indicate to closely relation of each other.

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Bolboceratidae	Bolboceratinae	Bolbelasmini	*Bolbelasmus* (*Kolbeus*) *minutus* Li et Masumoto, 2008
		Bolbochromini	*Bolbocerodema nigroplagiatum* (Waterhouse, 1875)
			Bolbochromus ryukyuensis Masumoto, 1984
Geotrupidae	Geotrupinae	Chromogeotrupini	*Enoplotrupes sharpi* Rothschild & Jordan, 1893
		Enoplotrupini	*Phelotrupes* (*Chromogeotrupes*) *auratus auratus* (Motschulsky, 1858)
			Phelotrupes (*Eogeotrupes*) *laevistriatus* (Motschulsky, 1866)
	Lethrinae		*Lethrus* (*Mesolethrus*) *microbuccis* Ballion, 1870
			Lethrus (*Ceratodirus*) *karelini* Gebler, 1845
			Lethrus (*Paralethrus*) *bituberculatus* Ballion, 1870
Glaresidae			*Glaresis beckeri* Solsky, 1870
Glaphyridae	Amphicominae		*Amphicoma pectinata* (Lewis, 1895)
			Amphicoma splendens (Yawata, 1942)
			Eulasia (*Trichopleurus*) *vittata* (Fabricius, 1775)
			Pygopleurus vulpes (Fabricius, 1781)
Hybosoridae	Ceratocanthinae	Ceratocanthini	*Madrasostes hisamatsui* Ochi, 1990
	Hybosorinae		*Phaeochrous emarginatus emarginatus* Laporte, 1840
			Phaeochroops sp.
Lucanidae	Aesalinae	Aesalini	*Aesalus asiaticus asiaticus* Lewis, 1883
		Nicagini	*Nicagus japonicus* Nagel, 1928
	Syndesinae		*Ceruchus lignarius lignarius* Lewis, 1883
	Lampriminae		*Lamprima adolphinae* (Gestro, 1875)
	Lucaninae	Lucanini	*Dorcus rectus rectus* (Motschulsky, 1858)
			Figulus binodulus Waterhouse, 1873
			Figulus punctatus Waterhouse, 1873
			Lucanus maculifemoratus maculifemoratus Motschulsky, 1861
			Prismognathus dauricus (Motschulsky, 1860)
			Prosopocoilus inclinatus inclinatus (Motschulsky, 1858)
		Platycerini	*Platycerus acuticollis* Y. Kurosawa, 1969
Ochodaeidae	Ochodaeinae	Ochodaeini	*Codocera ferruginea* (Eschscholtz, 1818)
			Notochodaeus maculatus maculatus (Waterhouse, 1875)
			Ochodaeus chrysomeloides (Schrank, 1781)
Passalidae	Aulacocyclinae	Ceracupini	*Ceracupes chingkini* Okano, 1988
			Cylindrocaulus patalis (Lewis, 1883)
	Macrolininae		*Macrolinus sikkimensis* Stoliczka, 1873
Pleocomidae			*Pleocoma dubitabilis dubitabilis* Davis, 1935
Trogidae	Troginae		*Glyptotrox uenoi uenoi* (Nomura, 1961)
			Omorgus (*Afromorgus*) *chinensis* (Boheman, 1858)
			Trox (*Niditrox*) *niponensis* Lewis, 1895

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Scarabaeidae	Aclopinae		*Pachypus candidae* (Petagna, 1787)
	Cetoniinae	Cetoniini	*Cetonia* (*Eucetonia*) *roelofsi roelofsi* Harold, 1880
			Gametis forticula forticula (Janson, 1881)
			Gametis jucunda (Faldermann, 1835)
			Glycyphana (*Glycyphana*) *fulvistemma* Motschulsky, 1860
			Protaetia (*Liocola*) *brevitarsis brevitarsis* (Lewis, 1879)
			Protaetia (*Calopotosia*) *orientalis submarmorea* (Burmeister, 1842)
		Cremastocheilini	*Clinterocera jucunda* (Westwood, 1874)
		Diplognathini	*Anthracophora rusticola* Burmeister, 1842
		Goliathini	*Cosmiomorpha* (*Microcosmiomorpha*) *similis nigra* Niijima & Kinoshita, 1927
			Dicronocephalus wallichi Hope, 1831
			Pseudotorynorrhina japonica (Hope, 1841)
			Rhomborhina (*Rhomborhina*) *polita* Waterhouse, 1875
			Rhomborhina (*Rhomborhina*) *unicolor unicolor* Motschulsky, 1861
		Taenioderini	*Coilodera pseudoalveata* (Miksic, 1971)
	Dynamopodinae		*Orubesa ata* Semenov & Medvedev, 1929
	Dynastinae	Dynastini	*Dynastes tityus* (Linnaeus, 1763)
			Trypoxylus dichotomus septentrionalis Kôno, 1931
			Xylotrupes gideon (Linnaeus, 1767)
		Oryctini	*Oryctes rhinoceros* (Linnaeus, 1758)
		Pentodontini	*Alissonotum pauperum* (Burmeister, 1847)
		Phileurini	*Eophileurus chinensis* (Faldermann, 1835)
	Euchirinae	Euchirini	*Cheirotonus peracanus* Kriesche, 1919
			Euchirus longimanus Linnaeus, 1758
	Melolonthinae	Diplotaxini	*Apogonia bicarinata* Lewis, 1896
			Apogonia ishiharai Sawada, 1940
			Apogonia kamiyai Sawada, 1940
		Hoplini	*Ectinohoplia obducta* (Motschulsky, 1857)
			Hoplia communis Waterhouse, 1875
			Pachycnema sp.
		Melolonthini	*Melolontha* (*Melolontha*) *frater frater* Arrow, 1913
			Melolontha (*Melolontha*) *japonica* Burmeister, 1855
			Polyphylla (*Granida*) *albolineata* (Motschulsky, 1861)
			Polyphylla (*Gynexophylla*) *laticollis laticollis* Lewis, 1887
		Rhizotrogini	*Nigrotrichia kiotoensis* (Brenske, 1894)
			Pollaplonyx flavidus Waterhouse, 1875
			Pedinotrichia picea (Waterhouse, 1875)
			Sophrops konishii konishii Nomura, 1970
		Sericini	*Maladera* (*Omaladera*) *orientalis* (Motschulsky, 1860)
			Maladera (*Aserica*) *secreta secreta* (Brenske, 1897)
			Serica boops Waterhouse, 1875
			Sericania hidana Niijima & Kinoshita, 1923
		Tanyproctini	*Tanyproctus* sp.
	Orphninae	Orphnini	*Orphnus* sp.

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Scarabaeidae	Rutelinae	Adoretini	*Adoretus falciungulatus* Nomura, 1965
			Adorodocia vittaticollis Fairmaire, 1883
			Chaetadoretus formosanus sakishimanus Kobayashi, 1982
			Lepadoretus sinicus (Burmeister, 1855) Burmeister, 1855
			Lepadoretus tenuimaculatus (Waterhouse, 1875)
		Anastatini	*Spodochlamys cupreola* Bates, 1888
		Anoimalini	*Anomala albopilosa albopilosa* (Hope, 1839)
			Anomala edentula yaeyamana (Nomura, 1965)
			Anomala octiescostata (Burmeister, 1844)
			Exomala conspurcata (Harold, 1878)
			Exomala orientalis (Waterhouse, 1875)
			Malaia nigrita (Boisduval, 1835)
			Mimela confucius ishigakiensis Sawada, 1950
			Mimela splendens (Gyllenhal, 1817)
			Mimela testaceipes (Motschulsky, 1860)
			Popillia japonica Newman, 1838
			Popillia lewisi Arrow, 1913
			Popillia mutans Newman, 1838
			Phyllopertha diversa Waterhouse, 1875
			Phyllopertha intermixta (Arrow, 1913)
			Spilopopillia sexguttata (Fairmaire, 1887)
		Anoplognathini	*Anoplognathus brunnipennis* (Gyllenhal, 1817)
			Anoplognathus prasinus (Castelnau, 1840)
			Calloodes rayneri Mac Leay, 1864
			Repsimus manicatus manicatus (Swartz, 1817)
		Rutelini	*Chrysophora chrysochlora* (Latreille, 1812)
			Dicaulocephalus feae Gestro, 1888
			Kibakoganea tamdaoensis Miyake & Muramoto, 1992
			Parastasia ferrieri ferrieri Nonfried, 1895
			Parastasia sp.1 Westwood, 1841
			Pelidnota prasina Burmeister, 1844
			Pelidnota punctate (Linnaeus, 1758)
	Trichinae	Osmodermini	*Osmoderma opicum* Lewis, 1887
		Trichini	*Corynotrichius bicolor* Kolbe, 1892
			Epitrichius elegans Kano, 1931
			Gnorimus subopacus Motschulsky, 1860
			Lasiotrichius succinctus succinctus (Pallas, 1781)
			Paratrichius doenitzi (Harold, 1879)
			Trichius fasciatus (Linnaeus, 1758)
			Trichius japonicus Janson, 1885
		Incaini	*Inca bonplandi* (Gyllenhal, 1817)
	Valginae	Valgini	*Dasyvalgus tuberculatus* (Lewis, 1887)
			Neovalgus fumosus (Lewis, 1887)
			Nipponovalgus angusticollis angusticollis (Waterhouse, 1875)
			Nipponovalgus yonakuniensis Sawada, 1941
		Microvalgini	*Microvalgus* sp.
	Aphodiinae	Aphodiini	*Aphodius* (*Brachiaphodius*) *eccoptus* Bates, 1889
	Scarabaeinae	Coprini	*Copris* (*Copris*) *ochus* (Motschulsky, 1860)

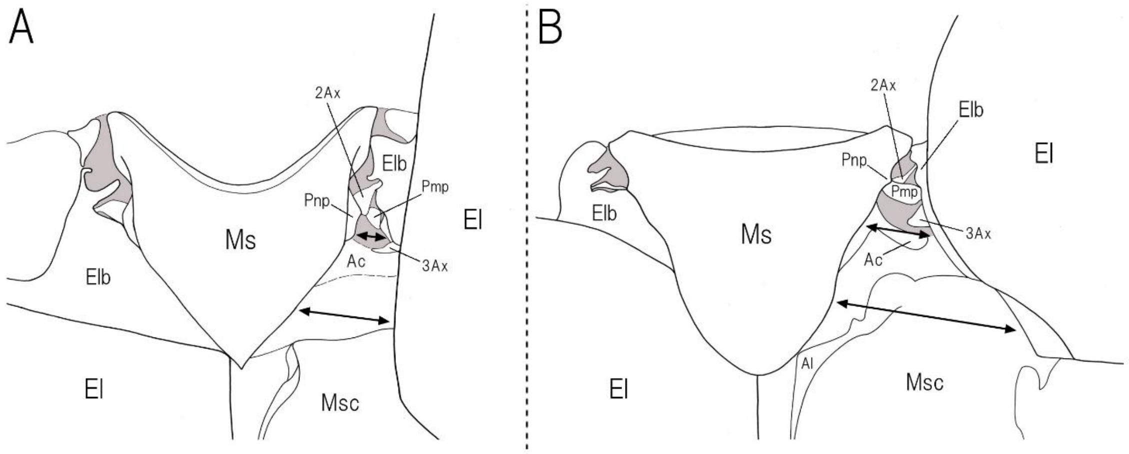
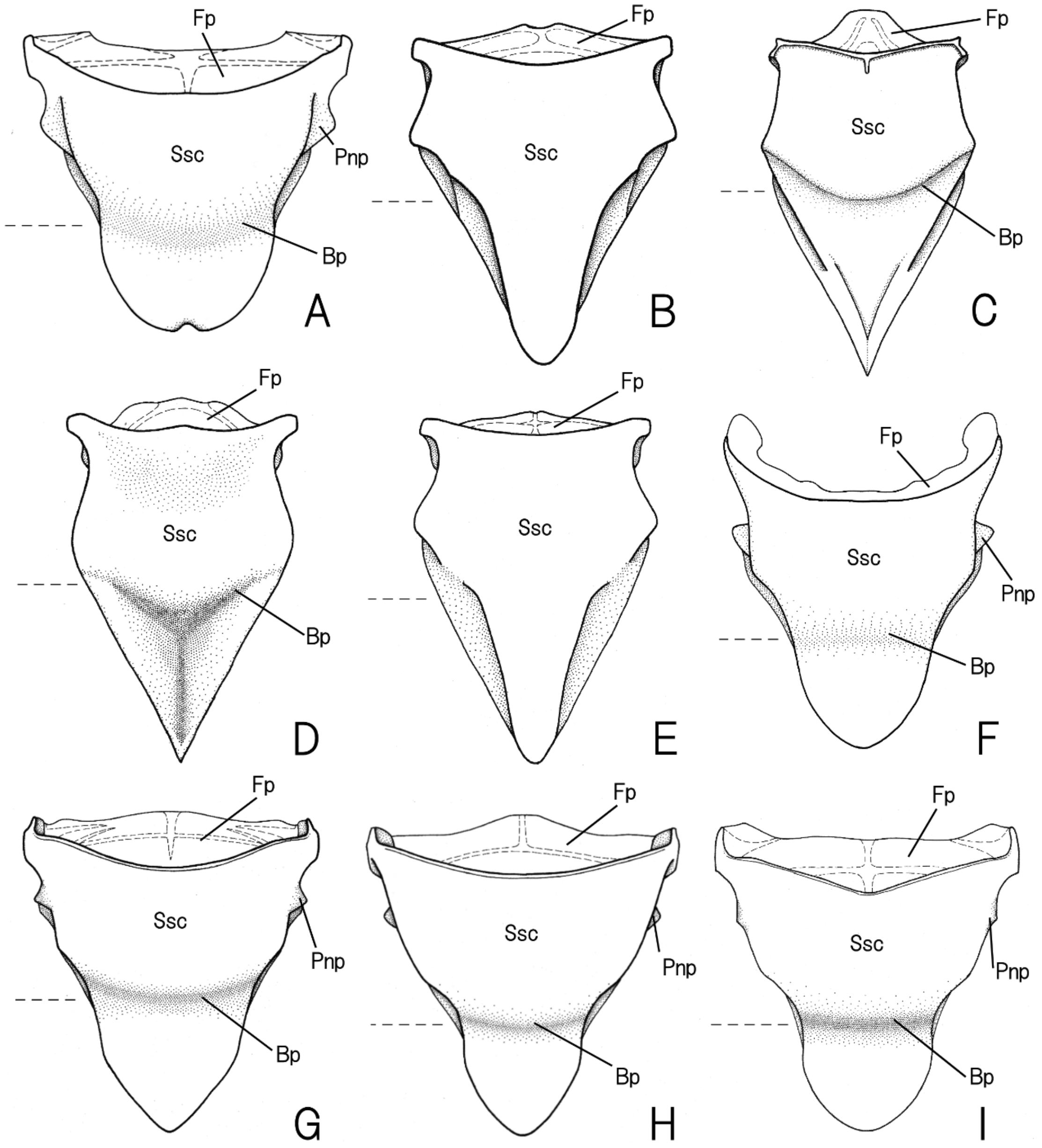
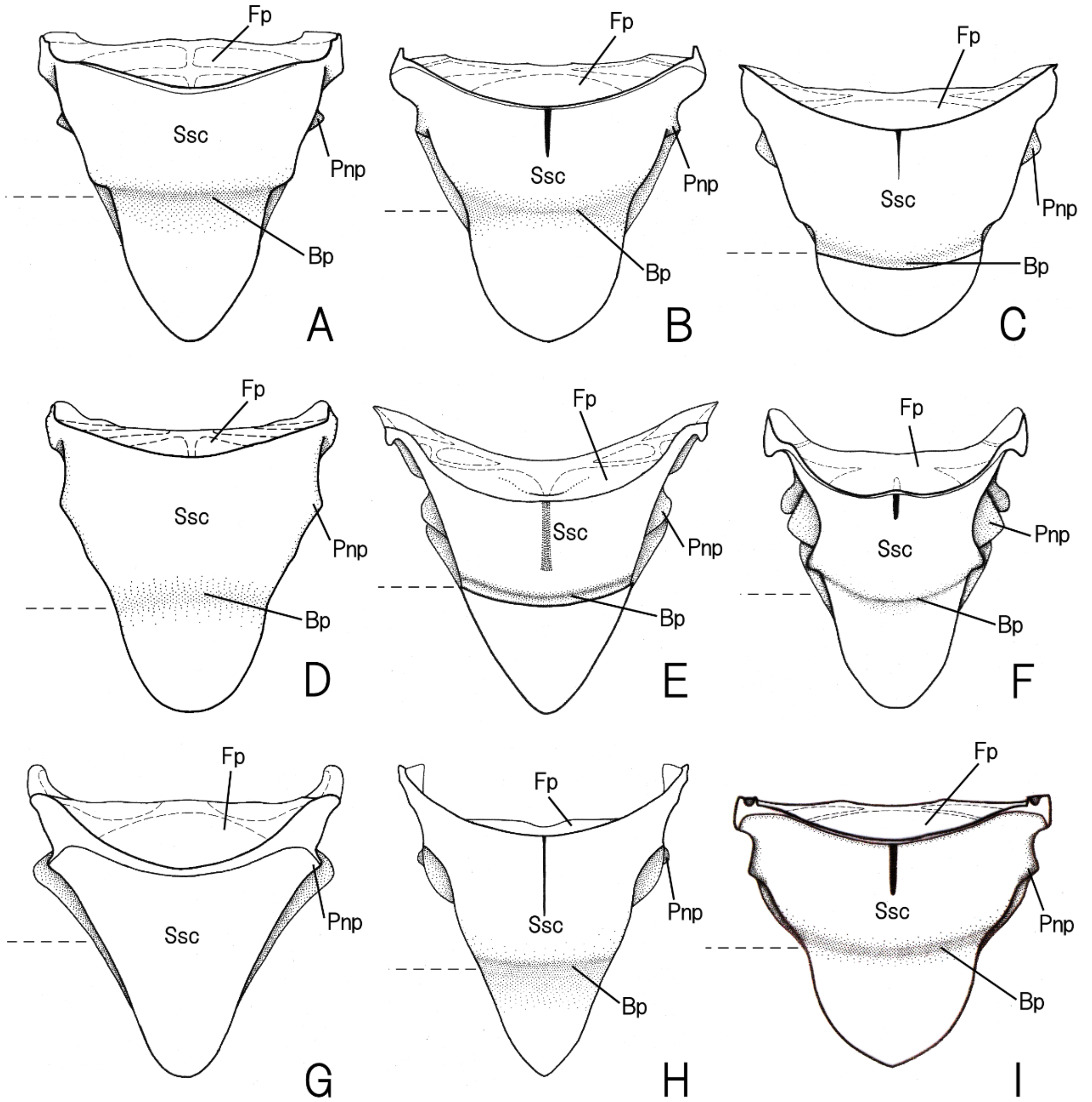


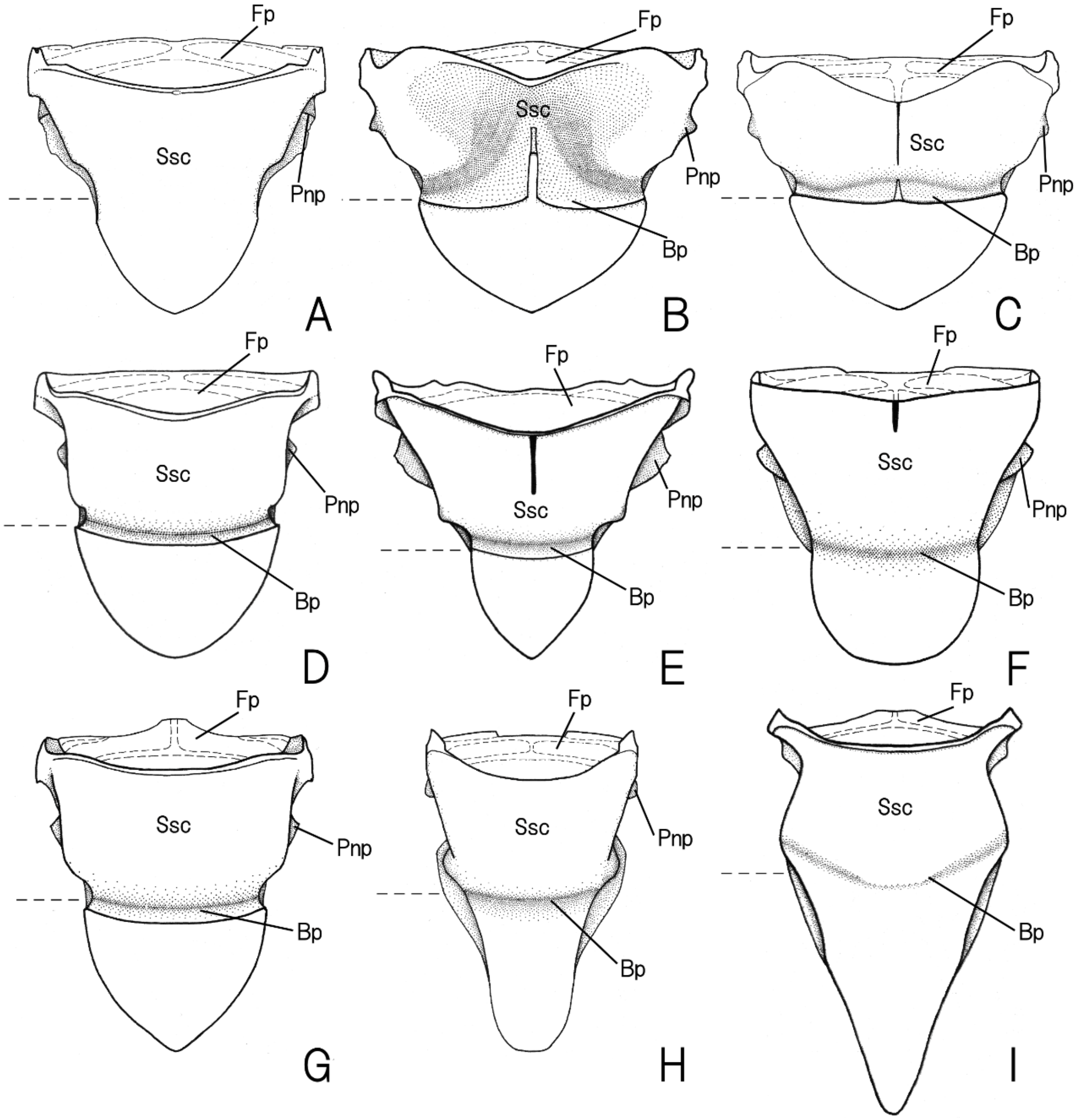
Figure 1. The position of the mesonotal characters in Scarabaeoidea **A** *Copris ochus* (Motschulsky) **B** *Melolontha frater frater* Arrow. Abbreviations: alacrista (Al); axillary cord (Ac); elytron (El); elytral base (Elb); mesonotum (Ms); metascutum (Msc); proximal median plate (Pmp); postmedian notal process (Pnp); second axillary sclerite (2Ax); third axillary screlite (3Ax). The membranous parts are painted gray, and the fixed parts between the mesonotum and elytron are showed by arrow.



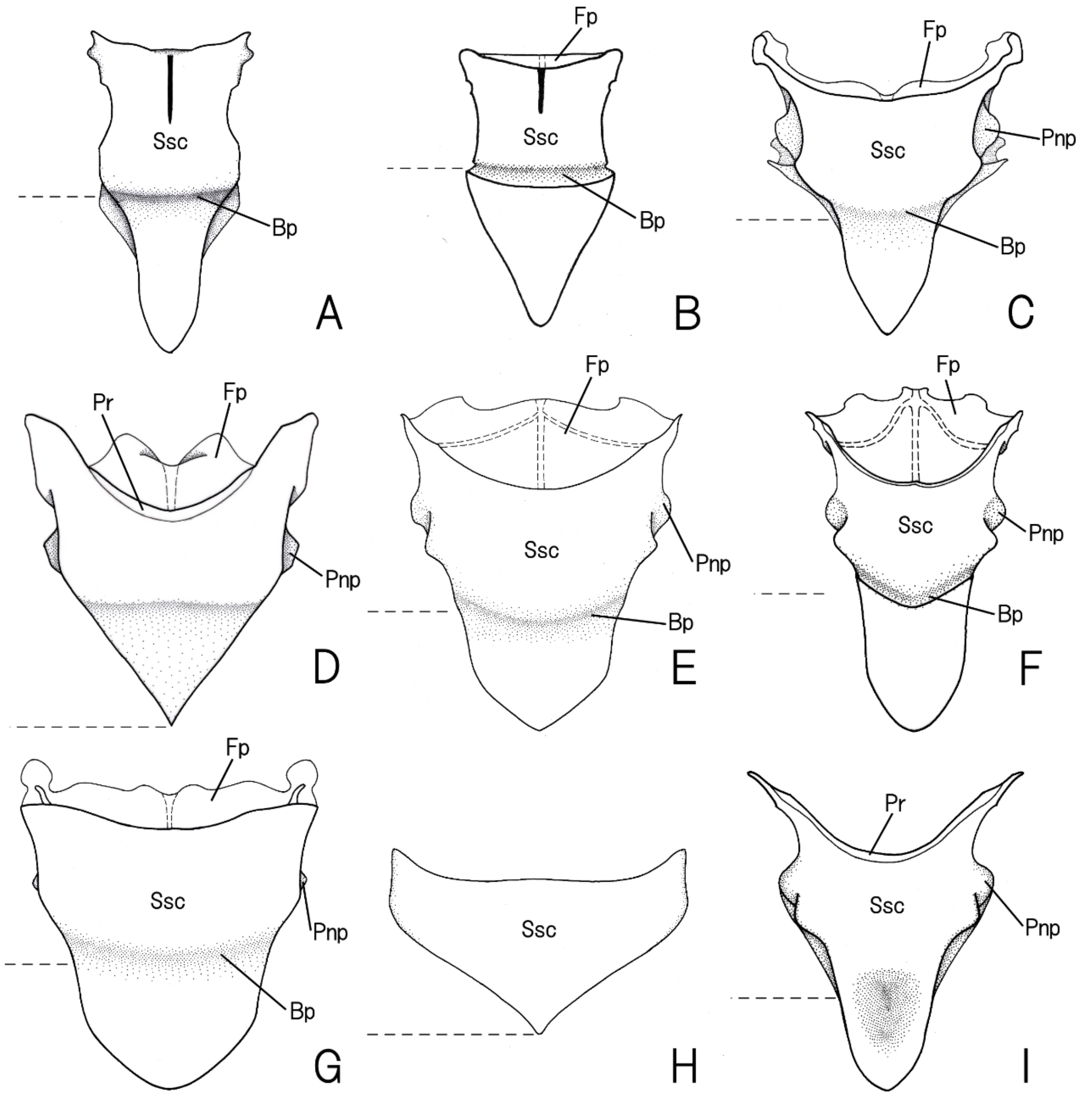
Figures 2A–I. Dorsal habitus of the mesonotum. **A** *Pachypus candidae* (Petagna) **B** *Protaetia brevitarsis* (Lewis) **C** *Clinterocera jucunda* (Westwood) **D** *Coilodera pseudoalveata* (Miksic) **E** *Anthracophora rusticola* Burmeister **F** *Orubesa ata* Semenov et Medvedev **G** *Xylotrupes gideon* (Linnaeus) **H** *Eophileurus chinensis* (Faldermann) **I** *Cheirotonus peracanus* Kriesche. Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



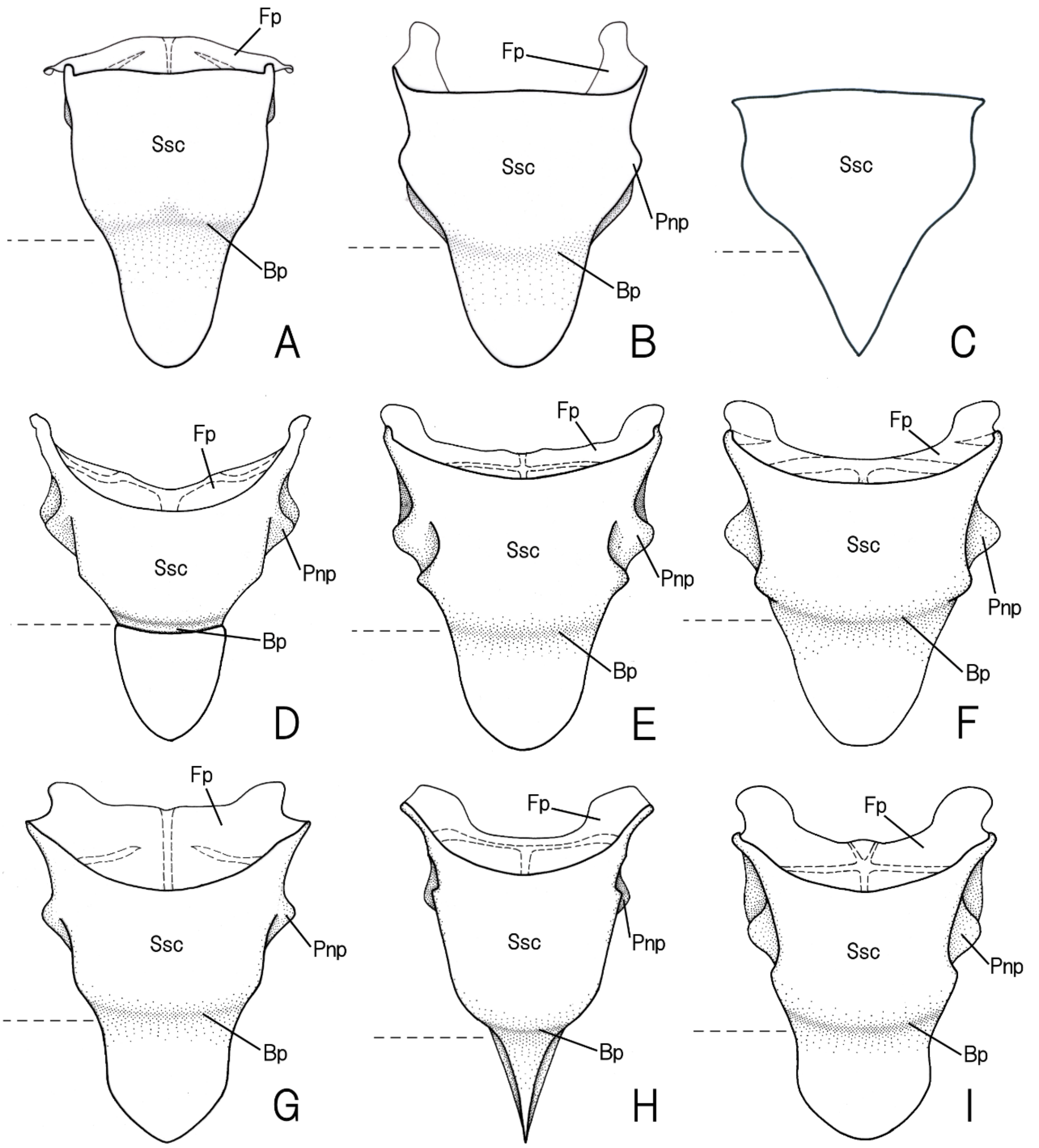
Figures 3A–I. Dorsal habitus of the mesonotum. **A** *Euchirus longimanus* Linnaeus **B** *Melolontha frater* Arrow **C** *Nigrotrichia kiotoensis* (Brenske) **D** *Tanyproctus* sp. **E** *Apogonia bicarinate* Lewis **F** *Hoplia communis* Waterhouse **G** *Maladera orientalis* (Motschulsky) **H** *Orphnus* sp. **I** *Mimela splendens* (Gyllenhal). Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



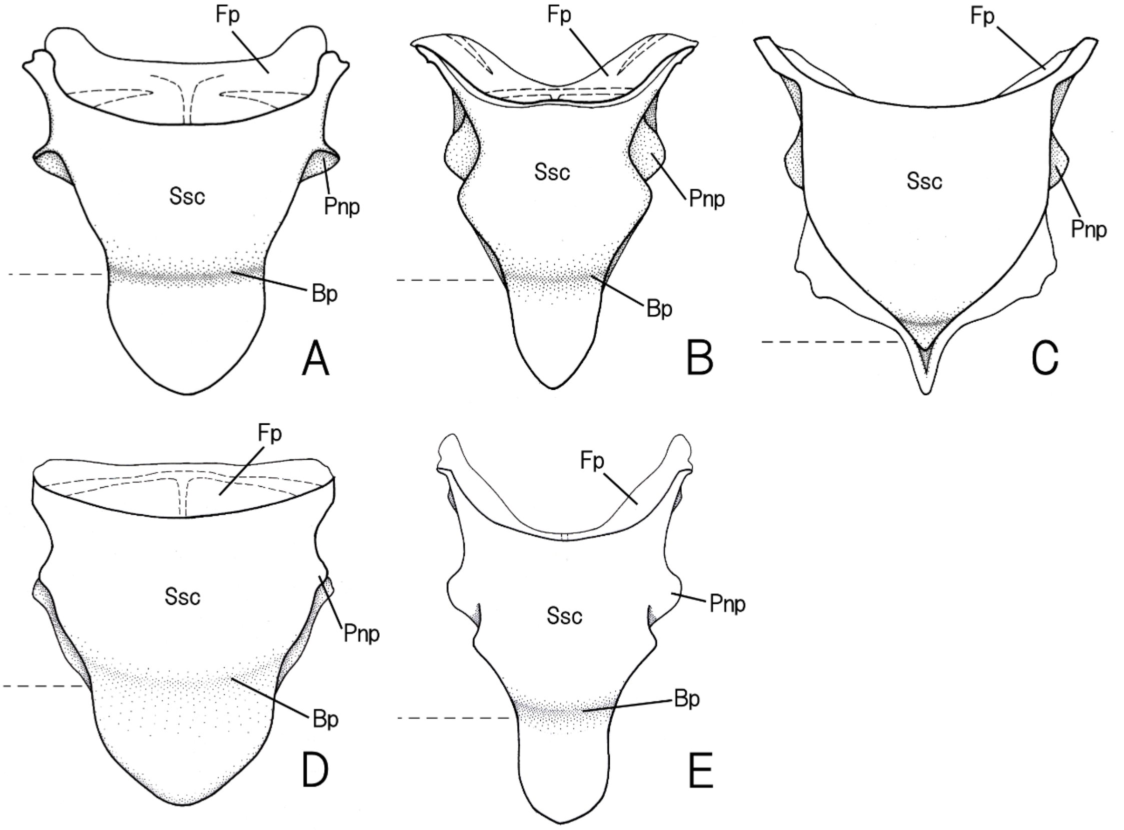
Figures 4A–I. Dorsal habitus of the mesonotum. **A** *Popillia mutans* Newman **B** *Dicaulocephalus feae* Gestro ♂ **C** *Dicaulocephalus feae* Gestro ♀ **D** *Parastasia ferrieri* Nonfried **E** *Lepadoretus tenuimaculatus* (Waterhouse) **F** *Gnorimus subopacus* Motschulsky **G** *Corynotrichius bicolor* Kolbe **H** *Lasiotrichius succinctus* (Pallas) **I** *Osmoderma opicum* Lewis. Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



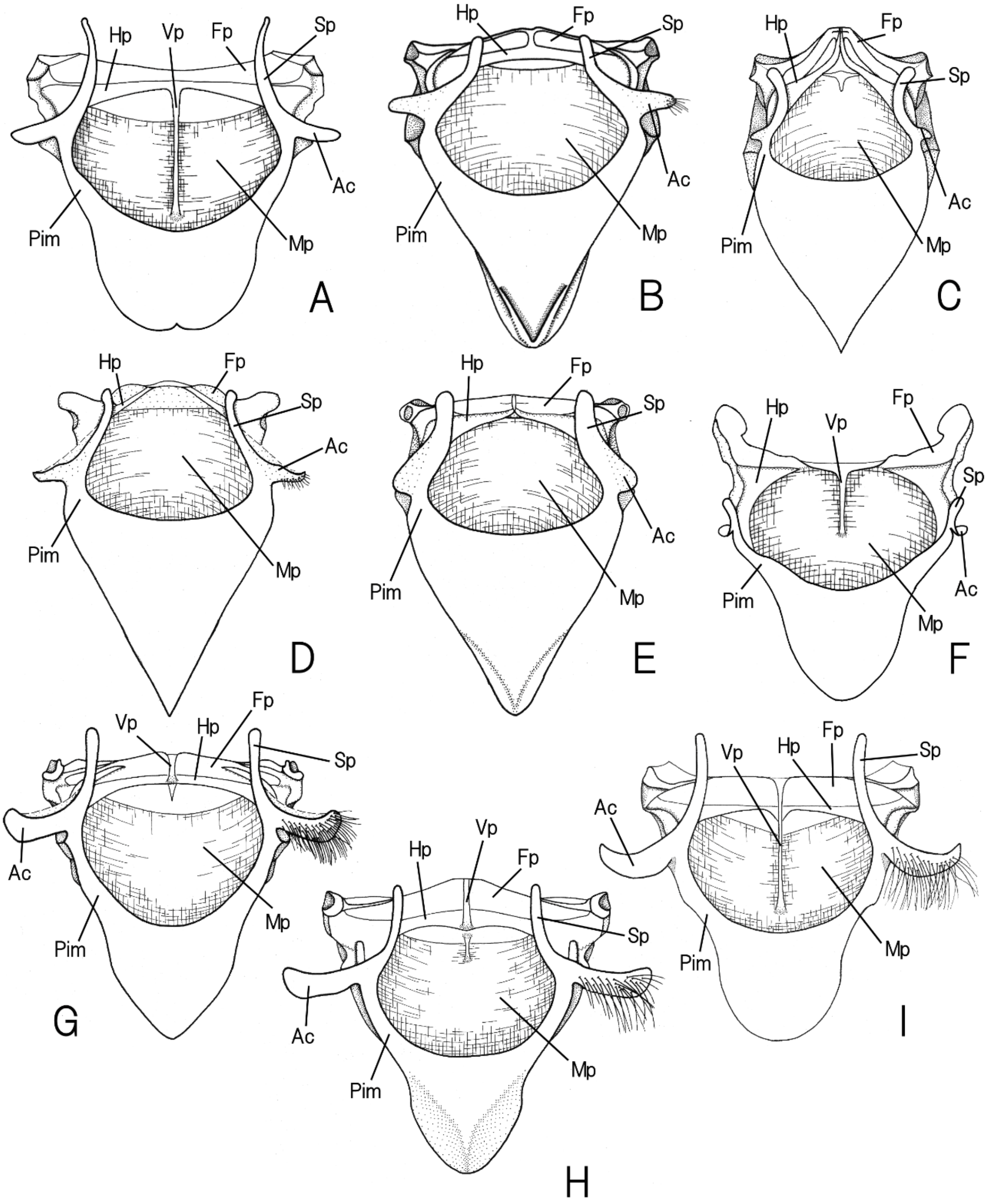
Figures 5A–I. Dorsal habitus of the mesonotum. **A** *Nipponovalgus angusticollis* (Waterhouse) **B** *Microvalgus* sp. **C** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **D** *Copris* (*Copris*) *ochus* (Motschulsky) **E** *Bolbocerodema nigroplagiatum* (Waterhouse, 1875) **F** *Bolbelasmus* (*Kolbeus*) *minutus* Li et Masumoto **G** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky) **H** *Lethrus* (*Paralethrus*) *bituberculatus* Ballion **I** *Glaresis beckeri* Solsky. Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



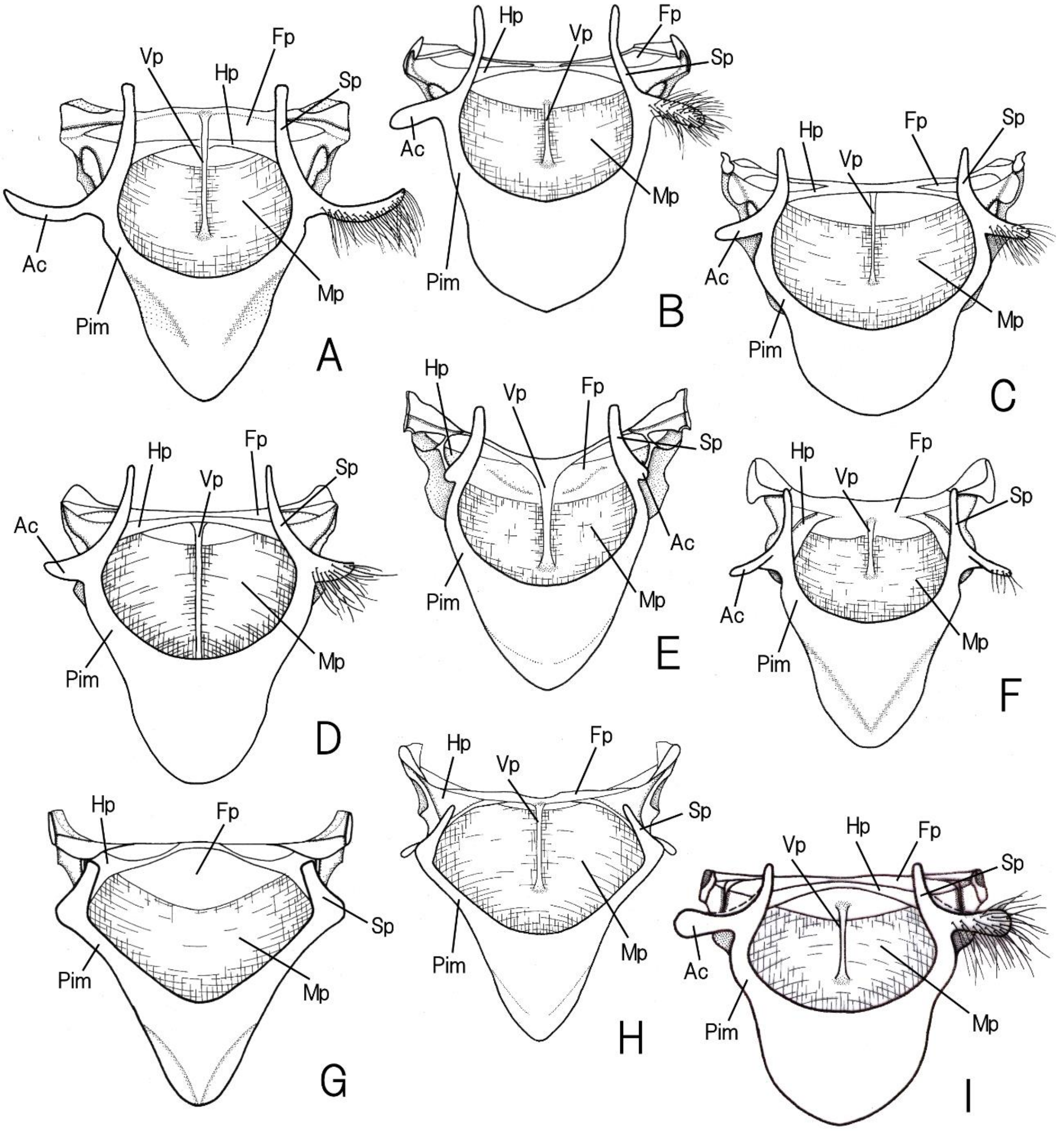
Figures 6A−I. Dorsal habitus of the mesonotum. **A** *Amphicoma splendens* (Yawata) **B** *Phaeochrous emarginatus* Laporte **C** *Madrasostes hisamatsui* Ochi **D** *Aesalus asiaticus asiaticus* Lewis **E** *Nicagus japonicus* Nagel **F** *Ceruchus lignarius lignarius* Lewis **G** *Dorcus rectus rectus* (Motschulsky) **H** *Figulus punctatus* Waterhouse **I** *Platycerus acuticollis* Y. Kurosawa. Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



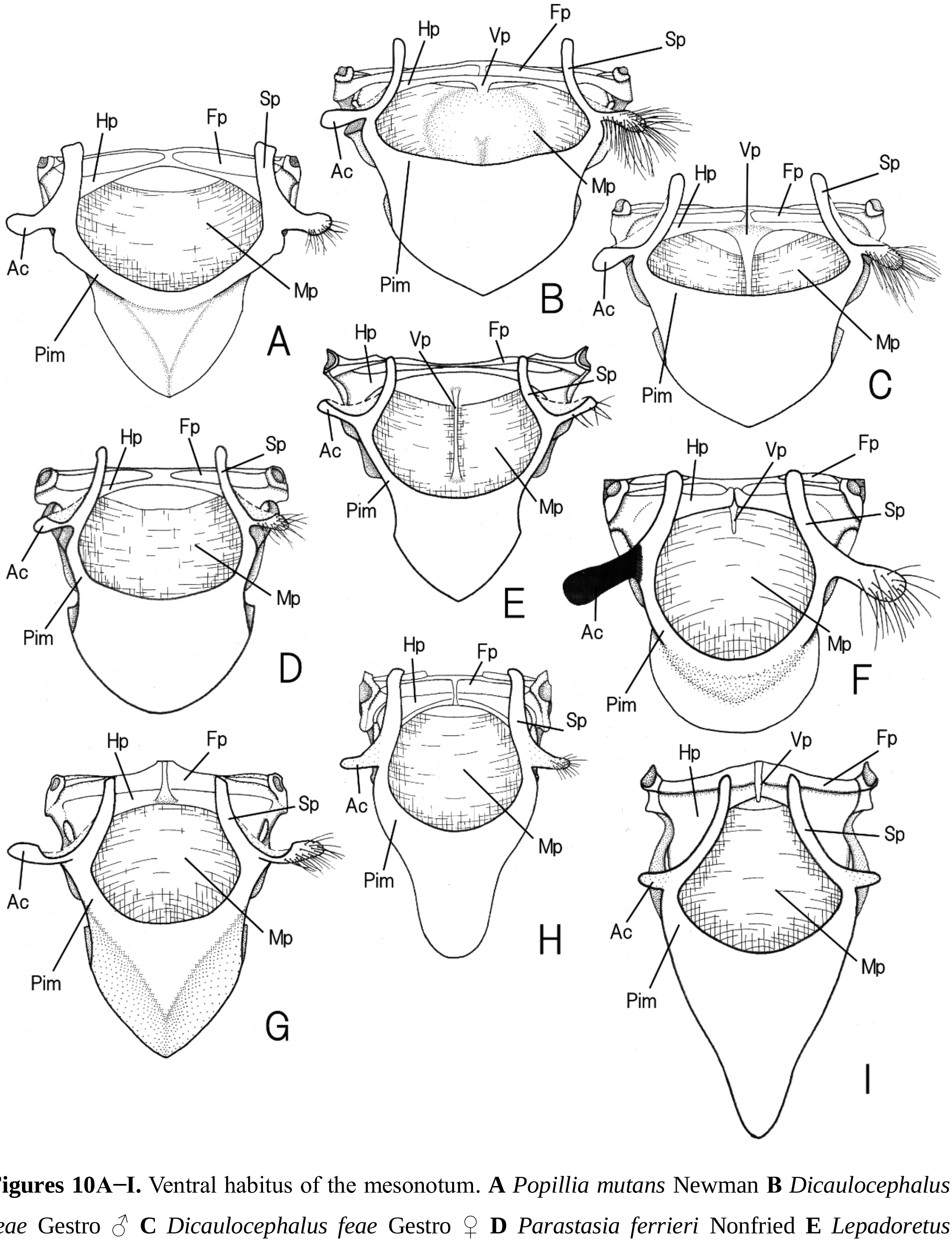
Figures 7A−I. Dorsal habitus of the mesonotum. **A** *Lamprima adolphinae* (Gestro) **B** *Ochodaeus chrysomeloides* (Schrank) **C** *Macrolinus sikkimensis* Stoliczka **D** *Pleocoma dubitabilis dubitabilis* Davis **E** *Glyptotrox uenoi uenoi* (Nomura). Abbreviations: boundary part (Bp); first phragma (Fp); postmedian notal process (Pnp); prescutum (Pr); scutum + scutellum (Ssc). The broken lines at the left side of each figures show the position of the posterior margin of pronotum.



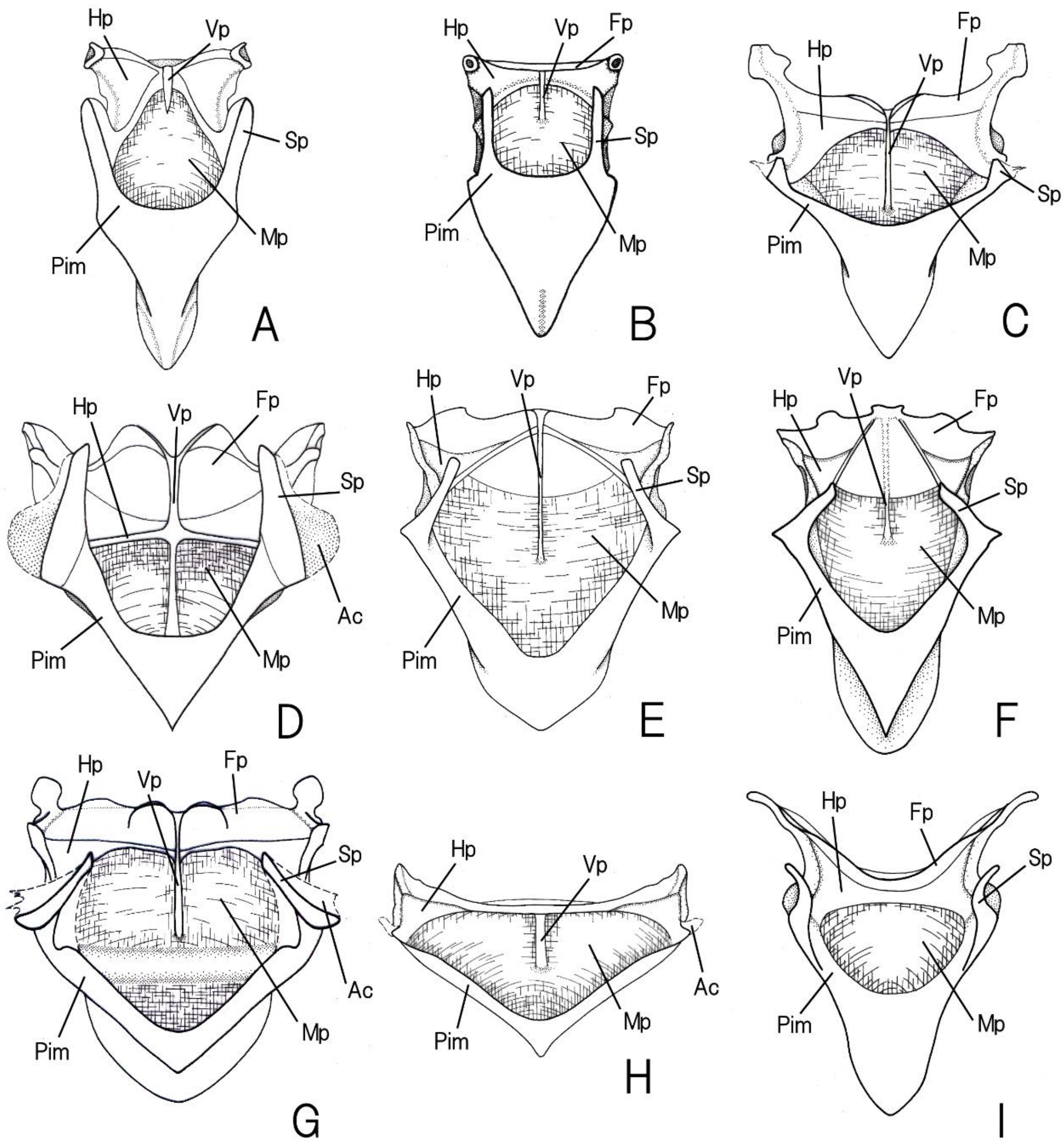
Figures 8A−I. Ventral habitus of the mesonotum. **A** *Pachypus candidae* (Petagna), **B** *Protaetia brevitarsis* (Lewis) **C** *Clinterocera jucunda* (Westwood) **D** *Coilodera pseudoalveata* (Miksic) **E** *Anthracophora rusticola* Burmeister **F** *Orubesa ata* Semenov et Medvedev **G** *Xylotrupes gideon* (Linnaeus) **H** *Eophileurus chinensis* (Faldermann) **I** *Cheirotonus peracanus* Kriesche. Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



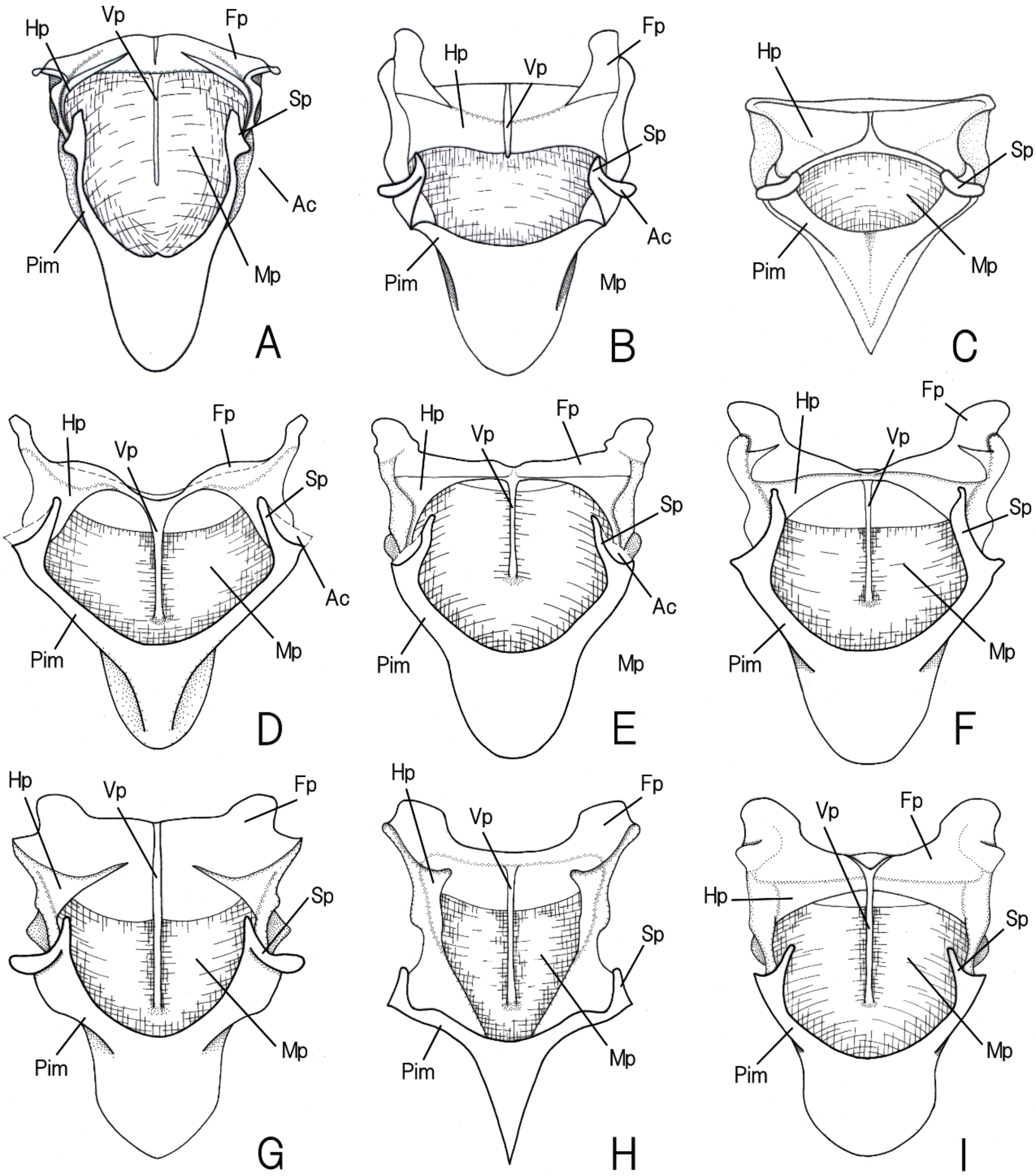
Figures 9A−I. Ventral habitus of the mesonotum. **A** *Euchirus longimanus* Linnaeus **B** *Melolontha frater* Arrow **C** *Nigrotrichia kiotoensis* (Brenske) **D** *Tanyproctus* sp. **E** *Apogonia bicarinate* Lewis **F** *Hoplia communis* Waterhouse **G** *Maladera orientalis* (Motschulsky) **H** *Orphnus* sp. **I** *Mimela splendens* (Gyllenhal). Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



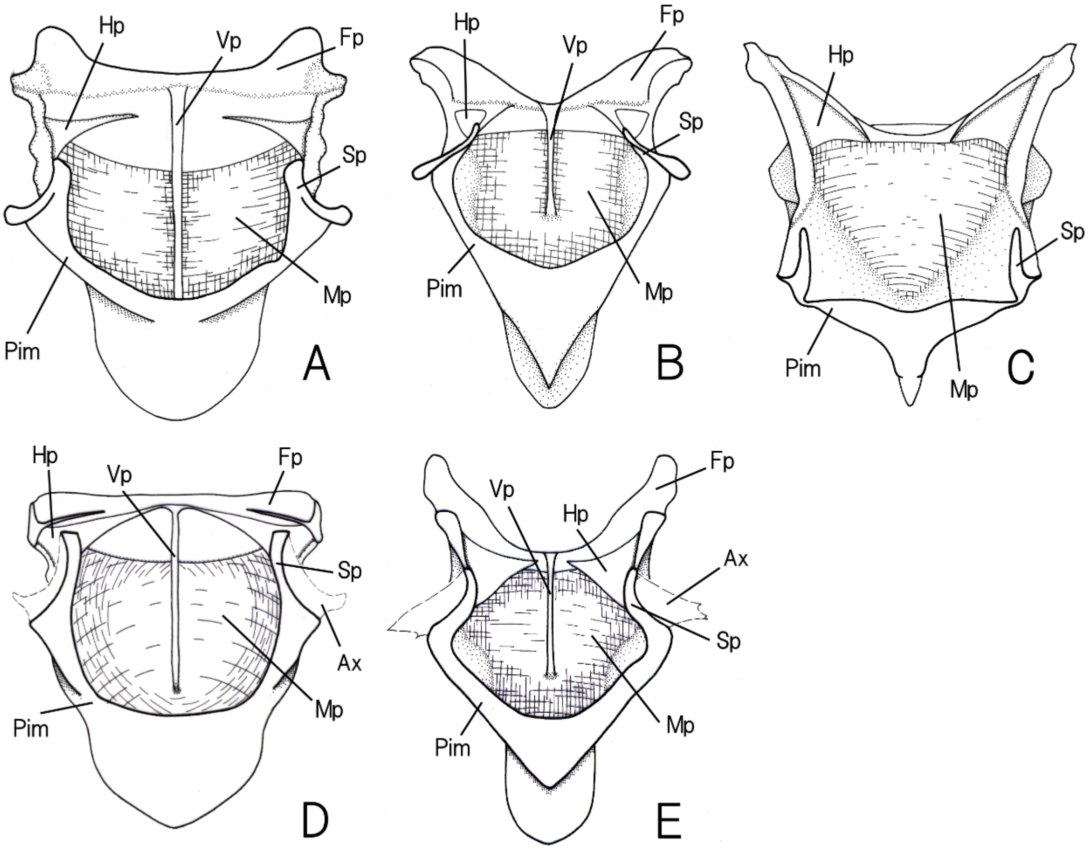
Figures 10A–I. Ventral habitus of the mesonotum. **A** *Popillia mutans* Newman **B** *Dicaulocephalus feae* Gestro ♂ **C** *Dicaulocephalus feae* Gestro ♀ **D** *Parastasia ferrieri* Nonfried **E** *Lepadoretus tenuimaculatus* (Waterhouse) **F** *Gnorimus subopacus* Motschulsky **G** *Corynotrichius bicolor* Kolbe **H** *Lasiotrichius succinctus* (Pallas) **I** *Osmoderma opicum* Lewis. Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



Figures 11A−I. Ventral habitus of the mesonotum. **A** *Nipponovalgus angusticollis* (Waterhouse) **B** *Microvalgus* sp. **C** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **D** *Copris* (*Copris*) *ochus* (Motschulsky) **E** *Bolbocerodema nigroplagiatum* (Waterhouse, 1875) **F** *Bolbelasmus* (*Kolbeus*) *minutus* Li et Masumoto **G** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky) **H** *Lethrus* (*Paralethrus*) *bituberculatus* Ballion **I** *Glaresis beckeri* Solsky. Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



Figures 12A–I. Ventral habitus of the mesonotum. **A** *Amphicoma splendens* (Yawata) **B** *Phaeochrous emarginatus* Laporte **C** *Madrasostes hisamatsui* Ochi **D** *Aesalus asiaticus asiaticus* Lewis **E** *Nicagus japonicus* Nagel **F** *Ceruchus lignarius lignarius* Lewis **G** *Dorcus rectus rectus* (Motschulsky) **H** *Figulus punctatus* Waterhouse **I** *Platycerus acuticollis* Y. Kurosawa. Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).



Figures 13A−I. Ventral habitus of the mesonotum. **A** *Lamprima adolphinae* (Gestro) **B** *Ochodaeus chrysomeloides* (Schrank) **C** *Macrolinus sikkimensis* Stoliczka **D** *Pleocoma dubitabilis dubitabilis* Davis **E** *Glyptotrox uenoi uenoi* (Nomura). Abbreviations: axillary cord (Ac); first phragma (Fp); horizontal plate (Hp); mesonotal pouch (Mp); posterior inflection of mesonotal pouch (Pim); scutellar process (Sp); vertical plate (Vp).

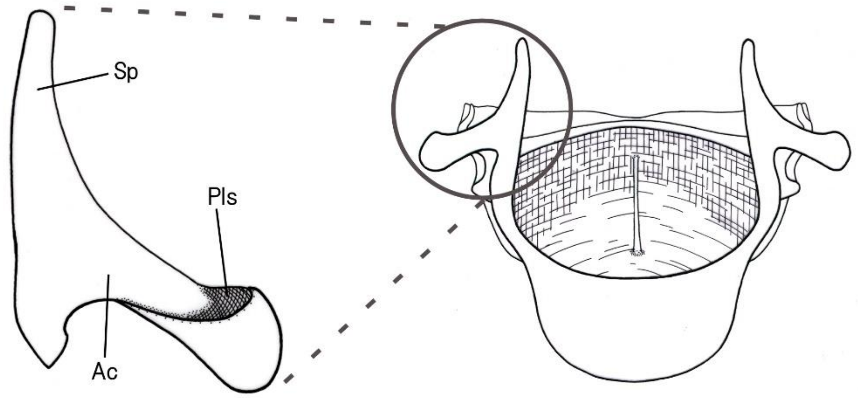


Figure 14. Pouch-like structure of dichotomous branching process in phytophagous group of Scarabaeidae, *Mimela splendens* (Gyllenhal). Abbreviations: axillary cord (Ac); pouch-like structure (Pls); scutellar process (Sp).

2−3 Metanotum

2−3−1

Comparative study of the metanotal structures in the coprophagous group of Scarabaeidae and some scarabaeoid beetles (Coleoptera, Scarabaeoidea)

Introduction

The coprophagous group of Scarabaeidae has long attracted the attention of numerous researchers, and several detailed comparative studies on various morphological structures have been conducted: ovariole (Ritcher and Baker 1974), karyotypes (Yadav and Pillai 1978), compound eye (Caveney and Mcintyre 1981), mouth parts (Nel and Villiers 1988, Nel and Scholtz 1990), male genitalia (d'Hotman and Scholtz 1990a, b), larval morphology (Grebennikov and Scholtz 2004) [for more information see Scholtz (1990) and Scholtz and Grebennikov (2016)]. In contrast, however, there have been relatively few comparative studies that have focused on the metanotal structures in scarabaeid beetles. The metanotum of Coleoptera has been described by researchers such as Snodgrass (1909, 1935), Larsén (1966) and Matsuda (1970), who established basic terminologies, and some different researchers have indicated more detailed descriptions of metanotal structures in some coleopteran species (El-Kifl 1953, Doyen 1966, Naomi 1988, Kazantsev 2003−2004, Beutel and Komarek 2004, Friedrich and Beutel 2006). Observations made in these studies tend to indicate that metanotal structures mutate relatively frequently at the family level, and accordingly, comparative studies are necessary to establish the detailed structures in each taxon. Detailed studies that have examined these structures in the Scarabaeidae have been conducted for species such as *Melolontha vulgaris* Fabricius [synonym of *Melolontha* (Linnaeus)] (Snodgrass 1909), *Phanaeus vindex* MacLeay and *Coprophanaeus lancifer* (Linnaeus) (Edmonds 1972), and *Lagochile emarginata* (Gyllenhal) (Albertoni *et al*. 2014). However, although Philips *et al*. (2004, 2016), Tarasov and Solodovnikov (2011), and Tarasov and Génier (2015) examined a range of characters in the Scarabaeinae and generated large data matrices, they did not present detailed descriptions. With respect to establishing phylogenetic relationships, the value of metanotal characters has been proven in studies on other coleopteran groups (Beutel and Komarek 2004, Friedrich and Beutel 2006, Ge *et al*. 2007) and Scarabaeinae (Philips *et al*. 2004, 2016, Tarasov and Solodovnikov 2011, Tarasov and Génier 2015). The accumulation of new reliable morphological data, particularly morphological ones highly accessible to human perception, will make an important contribution to molecular phylogenetic studies in recent years.

In this study, I examined details of the metanotal structures of 31 genera from four subfamilies within the coprophagous group of Scarabaeidae, four genera from four subfamilies within the phytophagous group of Scarabaeidae, and five genera within other scarabaeoid families. Although the comparatively few representatives species examined are clearly inadequate and may thus not provide a totally reliable basis on which to discuss far-reaching phylogenetic and systematic implications, it has, nevertheless, been possible to identify similarities between the different subfamilies.

Material and methods

Preparation of specimens

All dissections were carried out on dried specimens. In order to relax the specimens, they were initially placed in 50% ethanol for a few minutes, after which the prothorax and abdomen were detached from the meso- and metathorax using fine forceps. The meso- and metathorax were placed in 5% KOH solution for 6 to 8 hours to soften and dissolve the internal organs. Following pretreatment, these parts were washed several times in distilled water. Therefore, the metanotum was detached from the meso- and metathorax, and the isolated metanotum was soaked in 99% ethanol for 10 minutes to dehydrate the tissues.

Drawings were made with the aid of OLIMPAS SZX9 and, LEICA M165C microscopes and a KEYENCE VHX-1000 digital microscope. Fine structures such as hairs and punctates on the mesonotal surface were excluded from the diagrams as these tended to obscure structures required for comparative observation.

Terminology

Key morphological terminologies for the metanotal structures of Scarabaeidae follow Larsén (1966) and Matsuda (1970), although other literature was also referred (Doyen 1966, Edmonds 1972, Beutel and Komarek 2004, Albertoni *et al*. 2014).

The metanotum is typically hidden under the mesonotum and elytra. The metanotal structures are highly complex and widely vary across family or superfamily groups, however the main structure in the Scarabaeoidea is the same as the basic structure in Coleoptera, comprising the first phragma, prescutum, scutum, scutellum and postnotum (Fig.1). The first phragma is a well-developed sclerotized membrane and is distinctly separated by the antecostal suture from the other parts. The antecostal suture serves as a connection between the posterior inflection of the mesonotal pouch. The first phragma is surrounded by the prescutum and prescutal membrane, which are divided by the prescutoscutal and parapsidal sutures. The acrotergite, where the scutellar process of the mesonotum is attached, is located adjacent to the prescutum. This part has diverse names in the literature, including prealar (El-Kifl 1953), prephragmal area (Doyen 1966, Edmonds 1972) or lateral mesopostnotum (Albartoni 2014). The scutum and scutellum form the largest sclerites of the metanotum, and the middle part is divided into two areas by the medianlongitudinal groove, which corresponds to the scutellum (Doyen 1966, Larsén 1966, Edmonds 1972). The alacrista, or alar ridge (El-Kifl 1953, Doyen 1966), corresponding to the scutum is elevated and fairly sclerotized and form walls that divide the scutum and medianlongitudinal groove. The medianlongitudinal groove and alacrista are involved in the fixing mechanism of the elytra at rest (Crampton 1918, El-Kifl 1953, Doyen 1966, Larsén 1966, Matsuda 1970). According to Albertoni (2014), at the anterior end of the alacrista in Scarabaeidae, there is a rounded process called the "anterior lobe of metanotum". The anterior notal process, which is associated with the articulation of the hind wing, is present on the anterior lateral parts of the scutum. The anterior notal wing process and scutum are divided by the anterolateral scutal suture, which is fused with the prescutoscutal suture at the anterior end (Matsuda 1970). The posterior lateral sides of the scutum form a triangular area, called "posterolateral scutal area" (Edmonds 1972), defined by an oblique suture. This area is also observed in Teneblionidae and called lateral lobe of the scutum (El-Kifl 1953). The remnant of the posterolateral scutal suture is present at the lateral margin of the posterolateral scutal area, but it is lost in many coleopteran species (Matsuda, 1970). The posterior notal wing process arises from the posterolateral scutal area. The ventral side of the metanotum shows a deep cavity, and the many sutural ridges are observed on the internal surface. In particular, the scutoscutellar and prescutoscutal sutural ridges tend to develop strongly. The scutoscutellar suture is sometimes called a "V-shaped suture" based on its shape (Larsén 1966). A muscle attachment point called the anterior muscle disk is observed on the ventral side of the acrotergite. The postnotum is well-developed and divided from the lateral posterior margin of the scutum by the postnotal cleft. Both lateral sides of the postnotum protrude outside and form three processes: subalar tendon, anterior postnotal process, and posterior postnotal process (Doyen, 1966). In addition, the well-developed phragma appears form the posterior margin of the postnotum, and it is divided into two areas: mediophragmite and laterophragmite (Doyen, 1966). According to Larsen (1966), these phragmas show a greater variability in size and shape in Polyphaga and are strongly developed in Scarabaeidae.

Specimens studied

In the present study, I examined from 36 genera within four subfamilies of the coprophagous group of Scarabaeidae (Aegialiinae, Aphodiinae, Chironinae and Scarabaeinae), other scarabaeoid beetles in the families Geotrupidae, Glaphyridae, Hybosoridae, Pleocomidae and Trogidae, and four subfamilies within the phytophagous group of Scarabaeidae (Cetoniinae, Dynastinae, Rutelinae and Melolonthinae). Four species within three genera of the tribe Aegialiini were selected in the subfamily Aegialiinae. 14 species within 10 genera of five tribes (Aphodiini, Eupariini, Odochilini, Psammodiini, and Rhyparini) were selected in the subfamily Aphodiinae. One species in the genus *Chiron* MacLeay was selected in the subfamily Chironinae. 24 species within 17 genera of 10 tribes (Ateuchini, Coprini, Deltochilini, Gymnopleurini, Oniticellini, Onitini, Onthophagini, Phanaeini, Scarabaeini, and Sisyphini) were selected in the subfamily Scarabaeinae. For each of the following taxa, I examined single species: Geotrupidae, Glaphyridae, Hybosoridae, Pleocomidae, Trogidae, Cetoniinae, Dynastinae, Rutelinae and Melolonthinae (Table 1).

Results

In the Scarabaeoidea, the metanotum is located under the elytra and pronotum (Fig. 1), and it is one of the largest attachment points of flight muscles. The lateral sides are connected to the hind wing and epimeron via the anterior and posterior notal wing processes and the anterior postnotal process, respectively. The basic structure of the metanotum in Scarabaeoidea comprises seven parts: first phragma, acrotergite, prescutum, prescutal membrane, scutum, scutellum, and postnotum. Of these, the prescutum is remarkably reduced and even lost in some groups. The first phragma develops strongly, because it becomes an attachment point for longitudinal muscles, therefore, it is remarkably reduced in some species with atrophied hind wings. The acrotergite on the lateral sides of the first phragma is elongated. The prescutal membrane is typically thin and membranous state, but in some groups, it comprises a sclerotized area. The scutum and scutellum are completely fused with each other, and there is a strongly developed internal ridge on the ventral side of the sutural part. The medianlongitudinal groove of the scutum + scutellum is generally large, and well-developed alacrista is usually observed on the lateral side bump. In some groups, the anterior lobe of metanotum is present at the anterior part of the alacrista. The anterior notal wing process is triangular or trapezoidal. The posterolateral scutal area is usually wedge-shaped and divided from the scutum by an oblique suture and a deep groove. However, the posterolateral scutal area is completely divided into some scarabaeid groups. The posterior notal wing process is sharply pointed. Postnotum is usually strongly developed and comprises six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process).

Coprophagous Scarabaeidae

Aegialiinae (Fig. 2A−2C, 3A, 7A, 9A)

In Aegialiinae the metanotum is rectangular, and the length-to-width ratio is usually approximately 1:2.4 (Fig. 2A), but this ratio in the genus *Caelius* is approximately 1:1.7 (Fig. 2C). The first phragma is usually semicircular, and bilobed phragma is present on the anterior margin. The prescutum develops strongly and is triangular in shape. The prescutal membrane is typically oblong in shape. The acrotergite is rectangular, and the anterior part protrudes and points. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is the widest in the middle part. The posterior apex of the scutum and scutellum is protruded. The alacrista and the anterior lobe of metanotum are almost completely lost. The anterior notal wing process is typically trapezoidal in shape. The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side, and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process develops and is sharply pointed outward. The scutoscutellar suture and prescutal suture are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is developed and usually comprises six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which are V-shaped (Fig. 9A). The mediophragmite and laterophragmite are strongly reduced, whereas the anterior and posterior postnotal processes are strongly developed.

These character states are similar to the subfamily Aphodiinae.

Aegialia nitida has reduced hind wings and shows remarkably different character states compared to other species (Fig. 2B). The length-to-width ratio of the metanotum is approximately 1:7.1. The first phragma is strongly reduced, and the bilobed phragma on the anterior margin is completely lost. The prescutum, prescutal membrane, and acrotergite are strongly reduced. The scutum + scutellum, which is divided by the nearly straight medianlongitudinal groove, is quadrangular in shape. The posterior apex of the scutum and scutellum is protruding. The alacrista and anterior lobe of the metanotum are completely lost. The anterior notal wing process is triangular and strongly reduced. The posterolateral scutal area is completely fused with the scutum. The posterior notal wing process is strongly reduced. The scutoscutellar suture and prescutal suture are strongly reduced. The postnotum is developed, but the mediophragmite and laterophragmite are completely lost.

Aphodiinae (Fig. 2D−2F, 5B, 7B, 9B−9C)

In the Aphodiinae the metanotum is typically rectangular, and the length-to-width ratio is usually approximately 1:2, but this ratio in the tribes Odochilini and Psammodiini is approximately 1:3 (Fig. 2E). The first phragma is semicircular, and bilobed phragma is present on the anterior margin. In the genus *Aphodius* (*Brachiaphodius*), sclerotized ridges develop in the middle part of the first phragma (Fig. 7B). *Psammodius kobayashii*, which has a reduced hind wing, shows a strongly reduced first phragma. The prescutum develops strongly and is triangular in shape. The prescutal membrane is usually oblong in shape. In the genera *Aphodius* (*Phaeaphodius*) and *Aphodius* (*Agrilinus*) the prescutal membrane comprises a sclerotized and a thin membranous areas. The acrotergite is rectangular and the anterior part protrudes and points. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is the widest in the middle part. The posterior apex of the scutum + scutellum in the genera *Aphodius* (*Colobopterus*) and *Aphodius* (*Sinodiapterna*) is strongly protruded (Fig. 2F). The alacrista and the anterior lobe of metanotum are almost completely lost. The anterior notal wing process is usually trapezoidal, but it is triangular in the tribes Psammodiini and Rhyparini (genus *Sybacodes*). The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side, and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process develops and is sharply pointed outward. The scutoscutellar suture and prescutal suture are developed, and each suture is fused at the middle portion to form an “X” shape. The postnotum is developed and usually comprises six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which are V-shaped (Fig. 9B). The mediophragmite and laterophragmite are strongly reduced, whereas the anterior and posterior postnotal processes are strongly developed. The mediophragmite and laterophragmite are lost in the species *Psammodius kobayashii* and *Odochilus convexus* (Fig. 9C). The posterior postnotal process in the tribe Rhyparini is strongly reduced.

Chironinae (Fig. 2G, 5C, 7C, 9D)

In the Chironinae (genus *Chiron*) the metanotum is dome-like in shape, and the length-to-width ratio is approximately 1:1.3. The first phragma is semicircular, and bilobed phragma is present on the anterior margin. The prescutum is rounded, and is thin membranous. The prescutal membrane is rhomboidal in shape. The acrotergite is rectangular, and the anterior part protrudes. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is the widest in the middle part. The posterior apex of the scutum + scutellum is weakly protruded. The alacrista is remarkably reduced and the anterior lobe of metanotum is completely lost. The anterior notal wing process is triangular, and the anterior margin is characterized by a curve. The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side, and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process develops and is sharply pointed outward. The scutoscutellar suture and prescutal suture are developed, and each suture is fused at the middle portion to form an “X” shape. The postnotum is developed and comprises six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which are formed V-shaped. The mediophragmite, laterophragmite, and posterior postnotal process are strongly reduced.

These character states are similar to the subfamily Aphodiinae, especially tribe Rhyparini.

Scarabaeinae (Fig. 2H, 3A−3B, 5D, 7D, 9E−9F)

In the Scarabaeinae the metanotum is rectangular, and the length-to-width ratio is typically approximately 1:4−5. The first phragma shows various shapes such as semicircular (genus *Paraphytus*), oval (tribes Deltochilini and Gymnopleurini, and genus *Catharsius*), or inverted trapezoidal shaped (tribes Dichotomini, Oniticellini, Onthophagini, Phanaeini, Scarabaeini, Onitini and Sisyphini, and genera *Copris* and *Heliocopris*). A developed bilobed phragma is present on the anterior margin (Fig. 7D), but in some groups (tribes Ateuchini, Onitini, Oniticellini, Onthophagini, Phanaeini, Scarabaeini and Sisyphini, and genus *Panelus*), the phragma is strongly reduced. The sclerotized ridge usually develops in the middle part of the first phragma, but it is completely lost in members of the tribes Deltochilini (genus *Panelus*) and Ateuchini (genus *Paraphytus*). The prescutum is usually triangular in shape (Fig. 5D), but in some groups such as Onthophagini, Oniticellini, Onitini, Phanaeini, and *Panelus* the prescutum is completely lost (Fig. 3A). The prescutal membrane is oblong in shape. The acrotergite is rectangular, and the anterior part protrudes and points. Usually, the scutum + scutellum divided by a medianlongitudinal groove is quadrangular, and the groove is the widest in the middle part and the posterior apex is somewhat protruding. Notably, in the tribe Onthophagini the posterior apex is strongly pointed (Fig. 3A). However, in the tribe Oniticellini, the medianlongitudinal groove is wide and inverted trapezoidal and the scutum + scutellum is triangular and the posterior apex is flat (Fig. 3B). In the tribe Phanaeini, the posterior apex of the scutum and scutellum does not protrude and instead has long setae. The alacrista is remarkably reduced, and the anterior lobe of metanotum is completely lost. The anterior notal wing process shows various shapes. In Ateuchini (genus *Paraphytus*), Deltochilini (genus *Panelus*), Oniticellini, Onitini, Onthophagini, Scarabaeini, and Coprini (genus *Heliocopris*), this process is triangular with a small apophysis. In Deltochilini (genus *Deltochilum*), Dichotomini, Coprini (genera *Copris* and *Catharsius*), Gymnopleurini, and Sisyphini, this process is trapezoidal shaped with a small apophysis. In Phanaeini, this process is a trapezoidal with a winding anterior margin. The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side and this area is completely divided from the scutum by an oblique suture and a cleft (Fig. 2H). The posterior notal wing process is strongly reduced. The scutoscutellar suture and prescutal suture are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process) (Fig. 9E), which show various characteristics. In Onthophagini, Oniticellini, and Sisyphini, these are cingulate, with strongly reduced mediophragmite and laterophragmite. In tribes Deltochilini, Dichotomini, Coprini, and Phanaeini, the postnotum is V-shaped, with strongly reduced mediophragmite and laterophragmite, but the subalar tendon is strongly developed. In the tribe Gymnopleurini and Onitini, the postnotum is developed, with strongly reduced laterophragmite, but the subalar tendon and laterophragmite are strongly developed (Fig. 9F). The postnotum in the tribe Ateuchini is similar to that in the tribes Deltochilini, Dichotomini, Coprini and Phanaeini, but the anterior and posterior postnotal processes are strongly developed.

Phytophagous groups of Scarabaeidae

Cetoniinae (Figs. 3C, 5E, 7E, 9G)

In the Cetoniinae (genus *Gametis*) the metanotum is rhomboidal, and the length-to-width ratio is approximately 1:1.6. The first phragma is semicircular, and bilobed phragma is present on the anterior margin. The prescutum develops and is elongate shape. The prescutal membrane is rectangular and consists of thin membrane. The acrotergite is triangular, and the anterior part is protruding and elongated. The one side of the scutum + scutellum divided by a medianlongitudinal groove is parallelogram, and the groove expanding forward. The alacrista is recognizable on the lateral margin of the medianlongitudinal groove, but the development is confined to the posterior apex to the middle portion. The anterior lobe of metanotum is completely reduced. The anterior notal wing process is triangular in shape. The posterolateral scutal area is triangular, somewhat bulging on the dorsal side and this area is completely divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is strongly reduced.

The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which are bow-shaped. The mediophragmite, laterophragmite, and anterior postnotal process are strongly developed. Of these, the mediophragmite and laterophragmite are clearly separated.

Dynastinae, Rutelinae, and Melolonthinae (Figs. 3D, 5F, 7F, 9H)

In the phytophagous group of Scarabaeidae (genera *Anomala*, *Melolontha* and *Trypoxylus*) the metanotum is dome-shaped, and the length-to-width ratio is approximately 1:1.3−1.5. The first phragma is oval, and there is a weakly developed sclerotized ridge in the middle part. The weakly developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is strongly developed and is triangular in shape. The prescutal membrane is rectangular and consists of thin membranous and sclerotized areas. The acrotergite is triangular, and the anterior part is protruding and elongated. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is triangular, with a winding anterior margin. The posterolateral scutal area is usually wedge-shaped, somewhat bulging on the dorsal side and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is developed and sharply pointed outward. The scutoscutellar and prescutal sutures are well-developed, and each suture is fused at the middle portion to form an “X” shape. The postnotum is developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which are trapezoidal in shape. The mediophragmite, laterophragmite, and anterior postnotal processes are strongly developed.

Geotrupidae (Fig. 3E, 5G, 7G, 10A)

In the family Geotrupidae (genus *Phelotrupes*) the metanotum is dome-shaped, and the length-to-width ratio is approximately 1:1.6. The first phragma is rounded, with a sclerotized ridge in the middle part. The developed sclerotized bilobed phragma is present on the anterior margin of the first phragma. The prescutum is sclerotized and is triangular in shape. The prescutal membrane is oblong, and consists of thin membranous and sclerotized areas. The acrotergite is rectangular, and the anterior part is slightly protruding. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal and the groove gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is trapezoidal in shape. The posterolateral scutal area is wedge-shaped, and is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is recognizable on the lateral margin of the posterolateral scutal area. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). Among these, the mediophragmite and laterophragmite are strongly developed, but the development of the subalar tendon is very weak.

Glaphyridae (Fig. 3F, 5H, 7H, 10B)

In the family Glaphyridae (genus *Amphicoma*) the metanotum is dome-shaped, and the length-to-width ratio is approximately 1:1.2. The first phragma is oblong, with a rudimentary sclerotized ridge in the middle part and a developed sclerotized bilobed phragma is present on the anterior margin. The prescutum is triangular and strongly developed. The prescutal membrane is trapezoidal or oblong, with a very thin membranous state. The acrotergite is rectangular with a small apophysis, and no protrusion at the anterior part. The one side of the scutum + scutellum divided by a medianlongitudinal groove is rectangular and the groove greatly expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is trapezoidal in shape. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of an oblique suture. The weakly protruding posterior notal wing process is recognizable on the lateral margin of the posterolateral scutal area. The scutoscutellar suture and prescutal suture are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). The median postnotum, mediophragmite, and anterior postnotal processes are strongly developed.

Hybosoridae (Fig. 3G, 6A, 8A, 10C)

In the family Hybosoridae (genus *Phaeochrous*) the metanotum is dome-shaped, and the length-to-width ratio is approximately 1:1.5. The first phragma is semicircular, and the sclerotized ridges develop in the middle part. The weakly developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is developed and triangular in shape. The prescutal membrane is oblong and consists of thin membranous and sclerotized areas. The acrotergite is rectangular, and the anterior part is protruding in trapezoid. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal and the groove gradually expanding forward, and the posterior apex slightly protrudes. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular, with a slightly winding anterior margin. The posterolateral scutal area is wedge-shaped and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). However, the development of the mediophragmite and laterophragmite is weak, whereas the anterior postnotal process is strongly developed.

Pleocomidae (Fig. 3H, 6B, 8B, 10D)

In the family Pleocomidae (genus *Pleocoma*) the metanotum is dome-shaped and the length-to-width ratio is approximately 1:1.3. The first phragma is oblong in shape and there is a weakly developed bilobed phragma on the anterior margin. The prescutum is elongated triangular. The prescutal membrane is square with a very thin membranous state. The acrotergite is elongated rectangular and does not protrude in the anterior part. The scutum + scutellum divided by a medianlongitudinal groove is pentagonal and the groove gradually expanding forward. The scutellum is developed at the posterior part. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the posterior apex does not reach the posterior margin of the metanotum. The anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular, and the anterior margin is almost straight. The posterolateral scutal area is triangular, is divided from the scutum by an oblique suture and a deep groove. The weakly protruding posterior notal wing process is recognizable on the lateral margin of the posterolateral scutal area. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). The mediophragmite and laterophragmite are strongly developed, but the subalar tendon is very weakly developed.

Trogidae (Fig. 4A, 6C, 8C, 10E)

In the family Trogidae (genus *Glyptotrox*) the metanotum is rectangular and the length-to-width ratio is approximately 1:1.6. The first phragma is semicircular and the sclerotized ridges develop in the middle part, and there is a developed bilobed phragma on the anterior margin. The prescutum is triangular in shape. The prescutal membrane is oblong and consists of thin membranous areas. The acrotergite is rectangular and the anterior part is protruding in trapezoidal in shape. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular and is characterized by an almost straight anterior margin. The posterolateral scutal area is wedge-shaped and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is recognizable on the lateral margin of the posterolateral scutal area. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). Among these, the development of the mediophragmite and laterophragmite are weak.

Discussion

Based on the examination of the metanotum in the coprophagous groups of Scarabaeidae and its comparison with the metanotum in the phytophagous groups of Scarabaeidae and other scarabaeoid families, I make the following inferences.

Types of metanotum in coprophagous groups of Scarabaeidae

Owing to its great importance for flight, the metanotum is well-developed and large, accommodating the powerful muscles that move the hind wings (Larsén 1966). Therefore, metanotal structures are considered to correspond to behavioral traits. Indeed, flight-less species such as *Aegialia nitida* and *Psammodius kobayashii* (Figs. 2B, 2E) have remarkably reduced metanotum composed to other species that can fly. However, the basic metanotal structures in the coprophagous group can be divided into two types according to their characteristics. I suggest dividing the metanotum in the coprophagous groups of Scarabaeidae into the aphodiine and scarabaeine types. The following characteristics are important for distinguishing the aphodiine and scarabaeine types: length-to-width ratio of the metanotum, shape of medianlongitudinal groove, shape of scutum + scutellum, and posterolateral scutal area.

Members of Aegialiinae, Aphodiinae, and Chironinae within the aphodiine type. The length-to-width ratio of the metanotum is approximately 1:2−3. The medianlongitudinal groove gradually widens near the middle portion of the metanotum. The divided scutum + scutellum is pentagonal in shape (Figs. 2A−2G). The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side, and this area is divided from the scutum by an oblique suture and a deep groove.

Members of Scarabaeinae within the scarabaeine type. The length-to-width of the metanotum is approximately 1:4−5. The medianlongitudinal groove generally widens near the middle portion of the metanotum. The divided scutum + scutellum is quadrangular or triangular in shape (Figs. 2H, 3A−3B). The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side, and this area is completely divided from the scutum by an oblique suture and a cleft.

Evolution of the mesonotal structure in Scarabaeidae

The development of the metanotum in Pterygota may be affected by environmental factors and behavioral traits, given that it is an attachment point for flight muscles that play pivotal roles in flight behavior. In Coleoptera, the metanotum may be strongly affected by the aforementioned factors, because the mesonotum, which is one of an important muscles attachment point, is strongly reduced. In studies by Philips *et al*. (2004), Tarasov and Solodovnikov (2011), and Tarasov and Génier (2015), some metanotal features were used for estimating a phylogenetic relationship. However, these studies were limited to Scarabaeinae species and used only few characteristics. Regarding evolutionary trends, my observation indicates that the following characteristics are particularly important: shape of the acrotergite, development of the alacrista, presence of the anterior lobe of the metanotum, and posterolateral scutal area.

The presence of acrotergite was confirmed in all examined taxa, but its shape and development showed various characteristics. In species of the coprophagous and phytophagous groups of Scarabaeidae, and families Hybosoridae and Trogidae, the acrotergite was developed with a protruding anterior part. Among these, in coprophagous Scarabaeidae, Hybosoridae, and Trogidae, the acrotergite is rectangular and the protrusion is characterized by a trapezoid or triangular. In phytophagous Scarabaeidae, the acrotergite is triangular and the protrusion is characterized by a elongate-shape. In contrast, the acrotergite in the families Geotrupidae, Glaphyridae, and Pleocomidae is represent rectangular, but the anterior part does not protrude. Geotrupidae and Pleocomidae, which are considered to be ancestral among Scarabaeoidea (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990), are characterized by a non-protruding rectangular acrotergite. A non-protruding acrotergite is also observed in the family Staphylinidae (Naomi 1988) within the superfamily Staphylinoidea, which is the sister group of Scarabaeoidea (McKenna *et al*. 2019), as well as in the family Scirtidae, which is the most primitive polyphagan beetle (Friedrich and Beutel 2006, Mckenna *et al*. 2019). However, the Hybosoridae and Trogidae, which are also considered to be ancestral among the Scarabaeoidea (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990) were characterized by a trapezoidal protruding acrotergite. Based on the aforementioned state, I speculate that non-protruding acrotergite appeared early in Scarabaeoidea and that a protruding acrotergite evolved relatively late in certain lineages. Notably, the triangular shaped and elongated protruding acrotergite observed in the phytophagous groups of Scarabaeidae was considered to be the most derived state.

The alacrista was usually recognizable in the examined species, but unique characteristics were observed in some groups. In the coprophagous groups of Scarabaeidae, the alacrista is remarkably reduced. In contrast, in the phytophagous groups of Scarabaeidae, the alacrista is strongly developed. However, the development of the acrotergite in the subfamily Cetoniinae is limited from the posterior apex to the middle part of the scutum + scutellum. In the family Pleocomidae, the alacrista is clearly recognizable, but the development is limited from the anterior to middle parts of the scutum + scutellum. A developed acrotergite is generally observed in many coleopteran lineages, including Cantharidae (Matsuda 1970), Gyrinisae (Larsén 1966), Lycidae (Kazantsev 2003-2004), Teneblionidae (El-Kifl 1953, Doyen 1966), Scirtoidea (Friedrich and Beutel 2006), and Staphylinidae (Naomi 1988). Consequently, the unique characteristics observed in the subfamily Cetoniinae and family Pleocomidae are the derived states of the alacrista. In particular, the almost completely lost state observed in the coprophagous groups of Scarabaeidae may have evolved relatively late.

The anterior lobe of metanotum was observed only in the phytophagous groups of Scarabaeidae, except in the subfamily Cetoniinae. Since this characteristic was not observed in other examined scarabaeoid species, it is probably an autapomorphic character present only in the phytophagous groups of Scarabaeidae. The subfamily Cetoniinae is traditionally placed as a sister group of the Rutelinae + Dynastinae clade

(Browne and Scholtz 1998, Ahrens *et al*. 2014, Šípek *et al*. 2016, Gunter *et al*. 2016). Accordingly, the anterior lobe of metanotum in the subfamily Cetoniinae likely represents a secondary atrophied state.

The characteristics of the posterolateral scutal area could be roughly divided into three types. In the families Glaphyridae, Hybosoridae, and Trogidae, this area is completely fused with the scutum owing to a decrease of the oblique suture. However, in the families Geotrupidae, Pleocomidae, and Scarabaeidae, this area is divided from the scutum. Of these, the families Geotrupidae and Pleocomidae, and the scarabaeid subfamilies Aegialiinae, Aphodiinae, Chironinae, Cetoniinae, Dynastinae, Melolonthinae, and Rutelinae are characterized by the presence of a developed oblique suture and deep groove, while the subfamily Scarabaeinae is characterized by the presence of a developed oblique suture and cleft. The divided posterolateral scutal area is not observed in the most ancestral polyphagan beetle (Friedrich and Beutel 2006) and Staphylinoidea (Naomi 1988), an outgroup of Scarabaeoidea. Therefore, the undivided state observed in the Glaphyridae, Hybosoridae, and Trogidae may have appeared early, and I regard this as a primary stage. The divided state by an oblique suture and a deep groove (Geotrupidae, Pleocomidae, Aegialiinae, Aphodiinae, Chironinae, Cetoniinae, Dynastinae, Melolonthinae, and Rutelinae) may derived, whereas the divided state by an oblique suture and a cleft (Scarabaeinae) may be the most recent.

Coprophagous and phytophagous groups of Scarabaeidae

Although the basic structure of the mesonotum is similar in the coprophagous and phytophagous groups of Scarabaeidae, these groups can be distinguished based on the characteristics of the acrotergite, alacrista, anterior lobe of metanotum, and medianlongitudinal groove.

The species of the coprophagous group are defined by the following features: acrotergite is rectangular and protrudes in a trapezoid or triangle; alacrista is remarkably reduced; anterior lobe of metanotum is unrecognizable; and the medianlongitudinal groove is the widest at the middle part. Among these, the remarkably reduced alacrista and the unique characteristic of the medianlongitudinal groove are considered to be autapomorphies in the coprophagous groups. In contrast, the species of the phytophagous groups are defined by the following features: acrotergite is triangular and protrudes in an elongated shape; alacrista is usually strongly developed; anterior lobe of metanotum is usually strongly developed; and the medianlongitudinal groove is gradually expanding forward. Among these, the acrotergite features and presence of the anterior lobe of metanotum are considered to be autapomorphies in the phytophagous groups.

Traditionally, the coprophagous and phytophagous groups of Scarabaeidae have been treated as sister groups based on morphological observations (Browne and Scholtz 1995, 1998) and some molecular phylogenetic studies (Ahrens and Volger 2008, Gunter *et al.* 2016, Šípek *et al.* 2016, McKenna *et al.* 2019). However, the findings of some recent molecular phylogenetic analyses indicated that the coprophagous and phytophagous groups are not closely related and that the phytophagous group is nested within a clade including the families Glaphyridae and Hybosoridae (Smith *et al.* 2006, Ahrens *et al.* 2014, Neita-Moreno *et al.* 2019). The common features of the phytophagous groups and the families Hybosoridae and Glaphyridae include the presence of alacrista and a developed triangular prescutum. However, since these features are plesiomorphic characteristics in a large group, they are not significant enough to support the relationship. Furthermore, even though some autapomorphies that define the coprophagous and phytophagous groups are observed, it is difficult to identify synapomorphies that indicate the relationships with other groups. Consequently, the present observations do not support the previous phylogenetic hypothesis.

Subfamilies Aphodiinae, Aegialiinae, and Chironinae

The subfamilies Aegialiinae and Chironinae are closely related to Aphodiinae, and consistently, the morphology of the metanotum in these three subfamilies are observed to be highly similarly, except in the flight-less species. Notably, the characteristics of the postnotal structures, which are observed various character states between different taxa, are indicated similar characteristics among these subfamilies. Although the subfamilies Aegialiinae and Chironinae are often established as different families, namely Aegialiidae and Chironidae (Nel and Scholtz 1990, d'Hotman and Scholtz 1990, Paulian and Baraud 1982, Carpaneto and Piattella 1995, Huchet 2000, 2002, 2003, 2004, 2019, Huchet and Lumaret 2002), I found that morphologically, variation in the metanotum of these subfamilies is relatively low. Indeed, on the basis of a comparison of metanotal morphology among the Aphodiinae, Aegialiinae and Chironinae, I conclude that Aegialiinae and Chironinae should be included in the subfamily Aphodiinae, similar to the results of a comparative study in mesonotum (subchapter 2–2–1). In this regard, my findings are consistent with those of Browne and Scholtz (1998), Smith *et al.* (2006), Ahrens *et al.* (2014), and subchapter (2–2–1), that showed that Aegialiinae and Chironinae are included in a clade with Aphodiinae, and also with the findings of Ritcher (1969a, 1974) and Stebnicka (1977), who, on the basis of morphological point of view, concluded that Aegialiinae and Chironinae are close to Aphodiinae. Collectively, these observations on the morphology of the mesonotum in Aphodiinae, Aegialiinae and

Chironinae tend to indicate that these subfamilies comprise a single lineage.

Unique features of the medianlongitudinal groove in the tribes Onthophagini, Oniticellini, and Phanaeini

In Scarabaeoidea species, the characteristics of the medianlongitudinal groove varied widely. In particular, conspicuous and unique character states are noted in some members of the subfamily Scarabaeinae (tribes Oniticellini, Onthophagini, and Phanaeini). In members of the tribe Oniticellini, the medianlongitudinal groove is wide, with an inverted trapezoidal shape, and does not protrude backward (Fig. 3B). In the tribe Onthophagini, the medianlongitudinal groove is of an inverted triangular in shape, and the posterior apex strongly protrudes and points backward (Fig. 3A). Similarly, in the tribe Phanaeini, the medianlongitudinal groove is of an inverted triangular in shape, but the posterior apex is non-protruding and has a tuft of long setae (Edmonds 1972). Since these character states are established in each tribe, they are considered useful for distinguishing the corresponding tribes. Moreover, the aforementioned tribes may have evolved relatively late in the scarabaeine lineage (Philips *et al*. 2004, Monaghan *et al*. 2007, Philips 2011, Tarasov *et al*. 2015, Mlambo *et al*. 2015, Gunter *et al*. 2016). These unique characteristics observed in the present study suggest the derived state of the tribes above Scarabaeinae.

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Geotrupidae	Geotrupinae	Enoplotrupini	*Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky, 1866)
Glaphiridae	Amphicominae		*Amphicoma splendens* (Yawata, 1942)
Hybosoridae	Hybosorinae		*Phaeochrous emarginatus emarginatus* Laporte, 1840
Pleocomidae			*Pleocoma dubitabilis dubitabilis* Davis, 1935
Trogidae	Troginae		*Glyptotrox uenoi uenoi* (Nomura, 1961)
Scarabaeidae	Aegialinae	Aegialiini	*Aegialia* (*Aegialia*) *comis* (Lewis, 1895)
			Aegialia (*Aegialia*) *nitida* Waterhouse, 1875
			Caelius denticollis Lewis, 1895
			Psammoporus nakanei nakanei Masumoto, 1986
	Aphodiinae	Aphodiini	*Aphodius* (*Agrilinus*) *breviusculus* (Motschulsky, 1866)
			Aphodius (*Brachiaphodius*) *eccoptus* Bates, 1889
			Aphodius (*Colobopterus*) *quadoratus* Reiche, 1850
			Aphodius (*Phaeaphodius*) *rectus* Motschulsky, 1866
			Aphodius (*Sinodiapterna*) *troitzyi* Jacobson, 1897
		Eupariini	*Ataenius picinus* Harold, 1867
			Saprosites japonicus Waterhouse, 1875
			Setylaides foveatus (Schmidt, 1909)
		Odochilini	*Odochilus convexus* Nomura, 1971
		Psammodiini	*Rakovicius coreanus* (Kim, 1980)
			Psammodius kobayashii Nomura, 1973
			Trichiorhyssemus asperulus (Waterhouse, 1875)
		Rhyparini	*Rhyparus azumai azumai* Nakane, 1956
			Sybacodes sp. 1
	Chironinae		*Chiron* sp. 1
	Scarabaeinae	Ateuchini	*Paraphytus dentifrons* Lewis, 1895
		Deltochilini	*Deltochilum* (*Calhyboma*) *variolosum* Burmeister, 1873
			Deltochilum (*Hybomidium*) *gibbosum* (Fabricius, 1755)
			Panelus rufulus Nomura, 1973
		Coprini	*Catharsius molossus* (Linnaeus, 1758)
			Copris (*Copris*) *ochus* (Motschulsky, 1860)
			Copris (*Copris*) *tripartitus* Waterhouse, 1875
			Heliocopris tyrannus (Thomson, 1859)
		Gymnopleurini	*Paragymnopleurus melanarius* (Harold, 1867)
		Oniticellini	*Liatongus minutus* (Motschulsky, 1860)
			Liatongus gagatinus (Hope, 1831)
			Scaptodera rhadamistus (Fabricius, 1775)
			Sinodrepanus falsus (Sharp, 1875)
		Onthophagini	*Caccobius* (*Caccobius*) *jessoensis* Harold, 1867
			Digitonthophagus gazella (Fabricius, 1787)
			Onthophagus (*Gibbonthophagus*) *apicetinctus* d'Orbigny, 1898
			Onthophagus (*Serrophorus*) *seniculus* (Fabricius, 1781)
			Onthophagus (*Strandius*) *lenzii* Harold, 1874
		Onitini	*Onitis virens* Lansberge, 1875
			Onitis falcatus (Wulfen, 1786)
		Phanaeini	*Coprophanaeus* (*Metallophanaeus*) *saphirinus* (Strum, 1826)
		Scarabaeini	*Scarabaeus radama* Fairmaire, 1895
			Scarabaeus sacer Linnaeus, 1758
		Sisyphini	*Sisyphus longipes* (Olivier, 1789)
	Cetoniinae	Cetoniini	*Cetonia* (*Eucetonia*) *roelofsi roelofsi* Harold, 1880
	Dynastinae	Dynastini	*Trypoxylus dichotomus septentrionalis* Kôno, 1931
	Rutelinae	Anoimalini	*Mimela splendens* (Gyllenhal, 1817)
	Melolonthinae	Melolonthini	*Melolontha* (*Melolontha*) *frater* Arrow, 1913

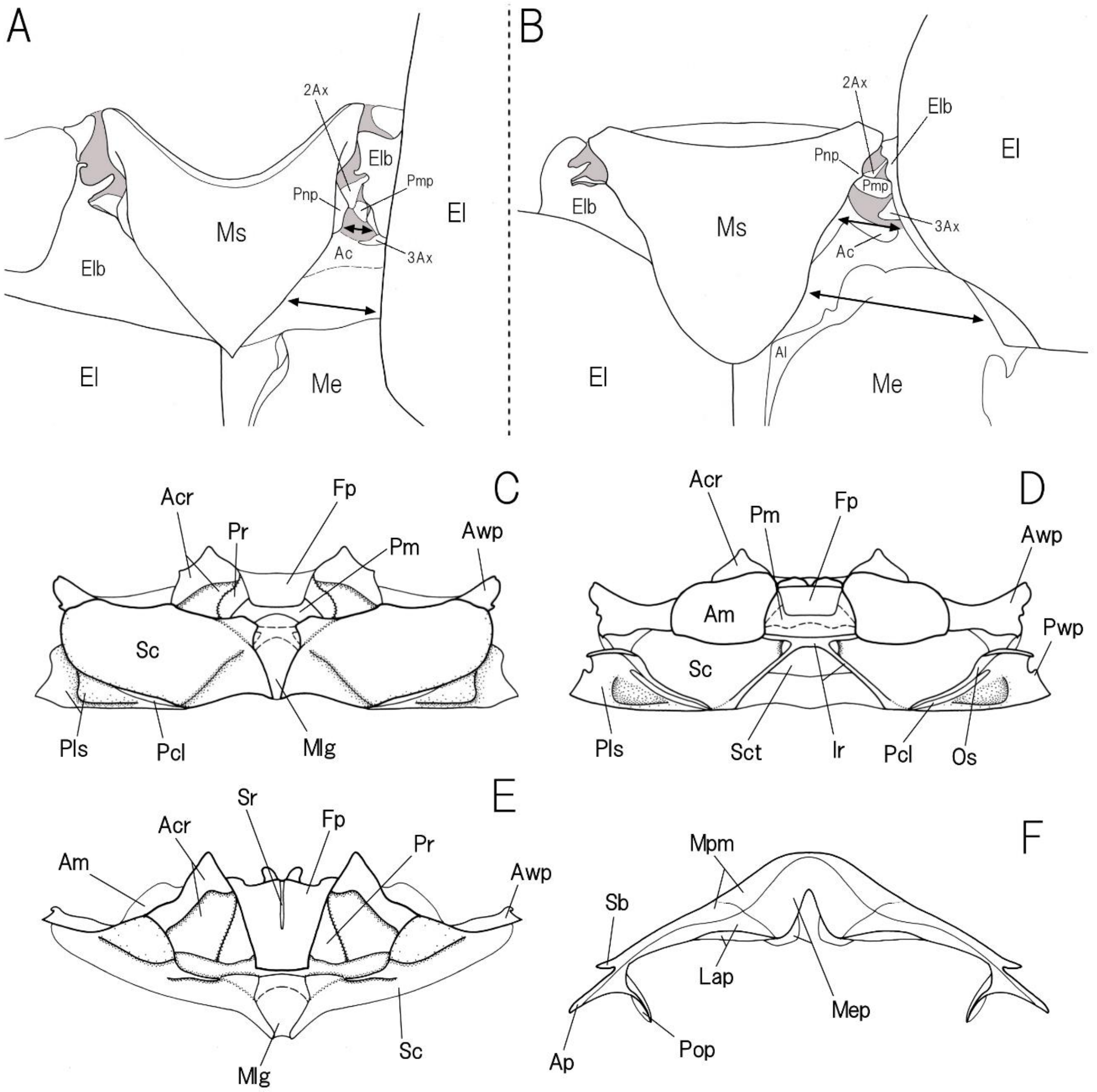


Figure 1. The position of the metanotum in Scarabaeoidea **A** *Copris ochus* (Motschulsky) **B** *Melolontha frater frater* Arrow **C–F** Schematics diagram of metanotum: **C** Dorsal **D** Ventral **E** Frontal **F** Postnotum. Abbreviations: acrotergite **(Acr)**; alacrista **(Al)**; anterior muscle disc **(Am)**; anterior notal wing process **(Awp)**; anterior postnotal process **(Ap);** axillary cord **(Ac)**; elytral base **(Elb)**; elytron **(El)**; first phragma **(Fp)**; internal ridge **(Ir)**; laterophragmite **(Lap)**; median longitudinal groove **(Mlg)**; median postnotum **(Mpm)**; mediophragmite **(Mep);** mesonotum **(Ms)**; metanotum **(Me)**; oblique suture **(Os)**; posterior notal wing process **(Pwp)**; postnotal cleft **(Pcl)**; postmedian notal process **(Pnp)**; posterolateral scutal area **(Pls)**; prescutal membrane **(Pm)**; prescutum **(Pr)**; proximal median plate **(Pmp)**; posterior postnotal process **(Pop)**; sclerotized ridge **(Sr)**; scutellum **(Sct)**; scutum **(Sc)**; subalar tendon **(Sb)**; second axillary sclerite **(2Ax)**; third axillary screlite **(3Ax)**. The membranous parts are painted gray, and the fixed parts between the mesonotum and elytron are showed by arrow.

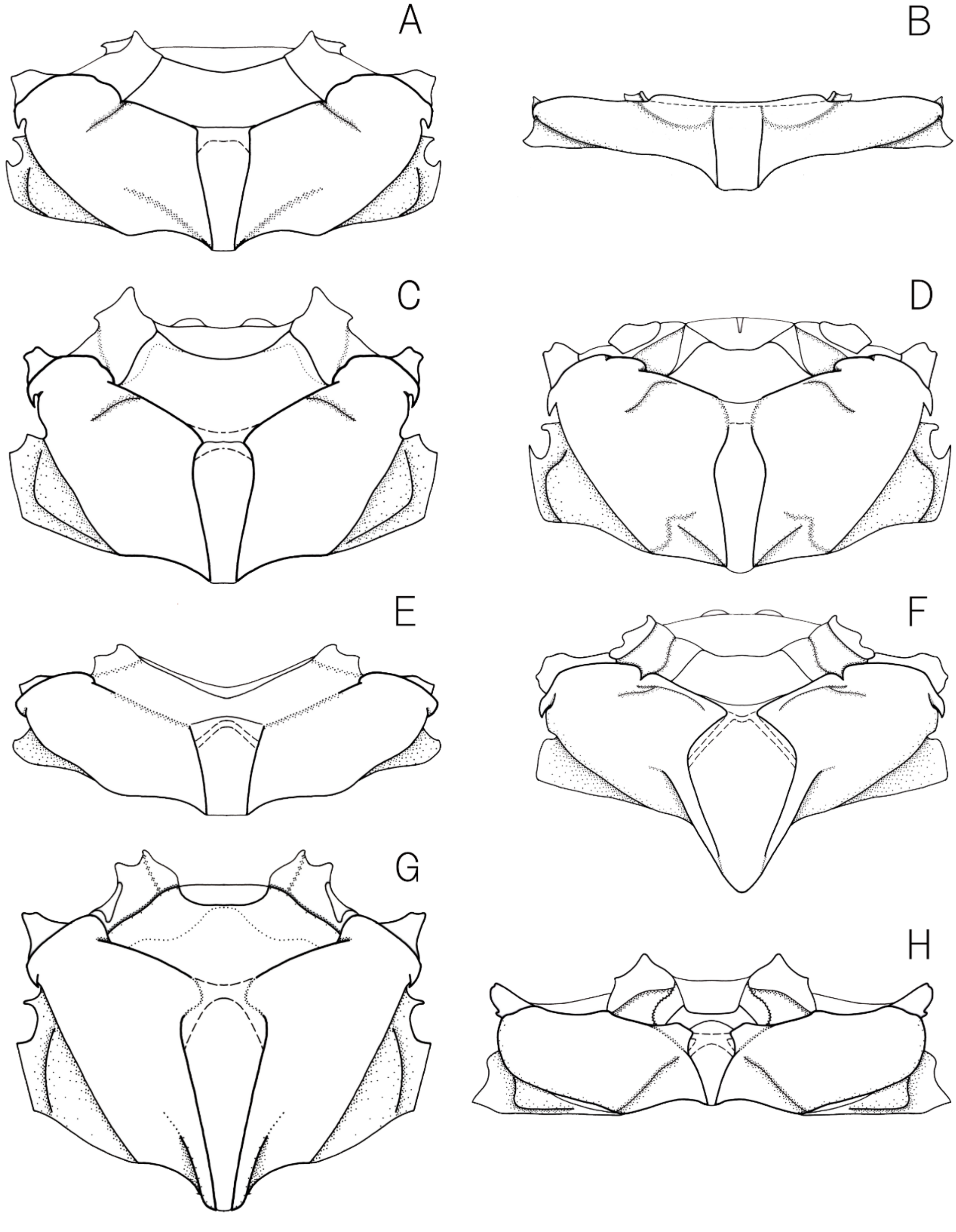


Figure 2A−H. Dorsal habitus of the metanotum. **A** *Aegialia* (*Aegialia*) *comis* (Lewis) **B** *Aegialia* (*Aegialia*) *nitida* Waterhouse **C** *Caelius denticollis* Lewis **D** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **E** *Psammodius kobayashii* Nomura **F** *Aphodius* (*Sinodiapterna*) *troitzyi* Jacobson **G** *Chiron* sp. **H** *Copris* (*Copris*) *ochus* (Motschulsky).

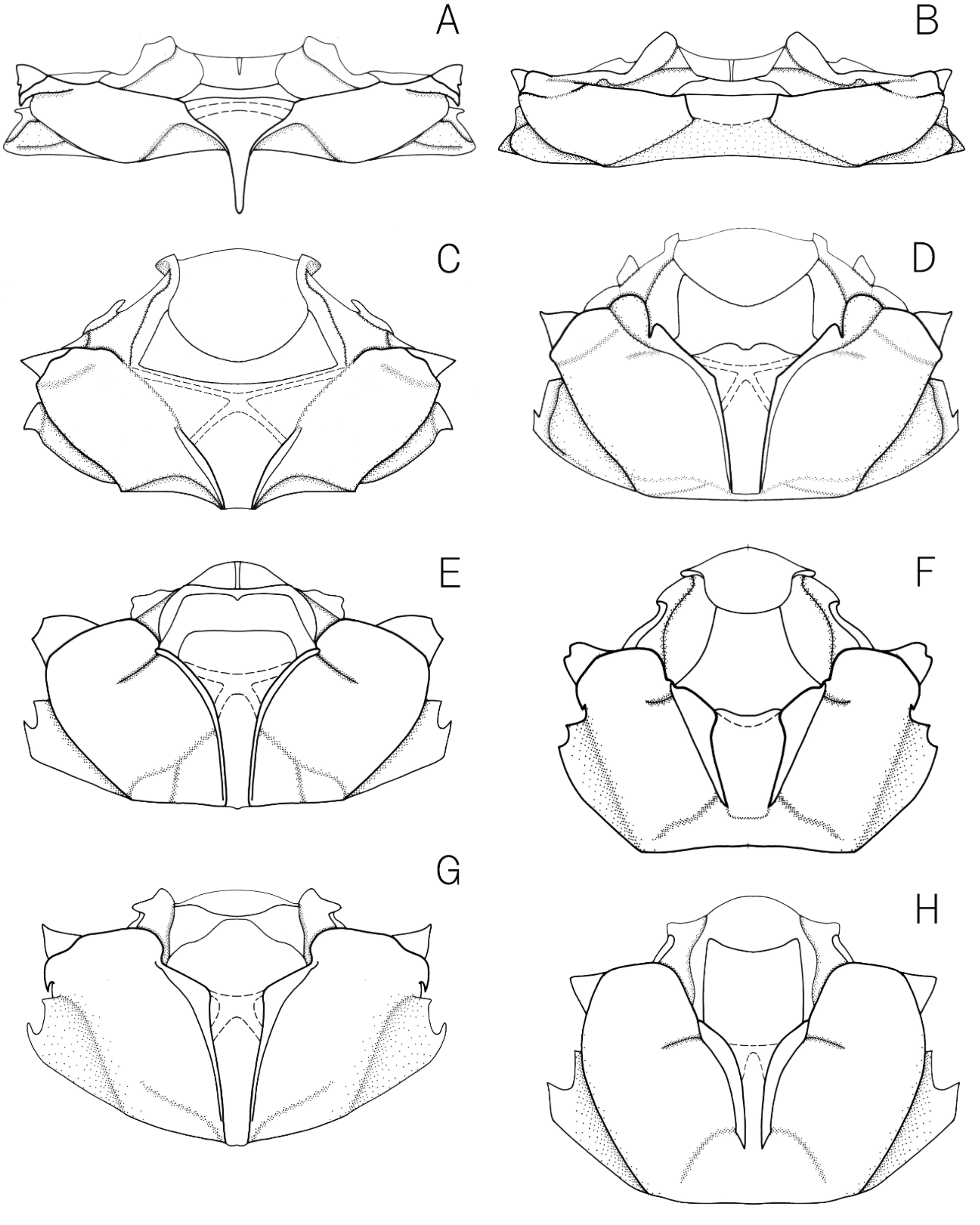


Figure 3A−H. Dorsal habitus of the metanotum. **A** *Caccobius* (*Caccobius*) *jessoensis* Harold **B** *Scaptodera rhadamistus* (Fabricius) **C** *Gametis jucunda* (Faldermann) **D** *Mimela splendens* (Gyllenhal) **E** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky) **F** *Amphicoma splendens* (Yawata) **G** *Phaeochrous emarginatus* Laporte **H** *Pleocoma dubitabilis* Davis.

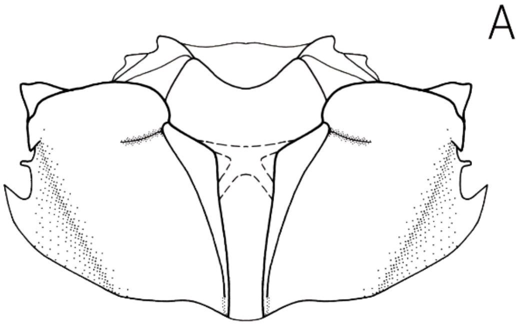


Figure 4A. Dorsal habitus of the metanotum. **A** *Glyptotrox uenoi* (Nomura).

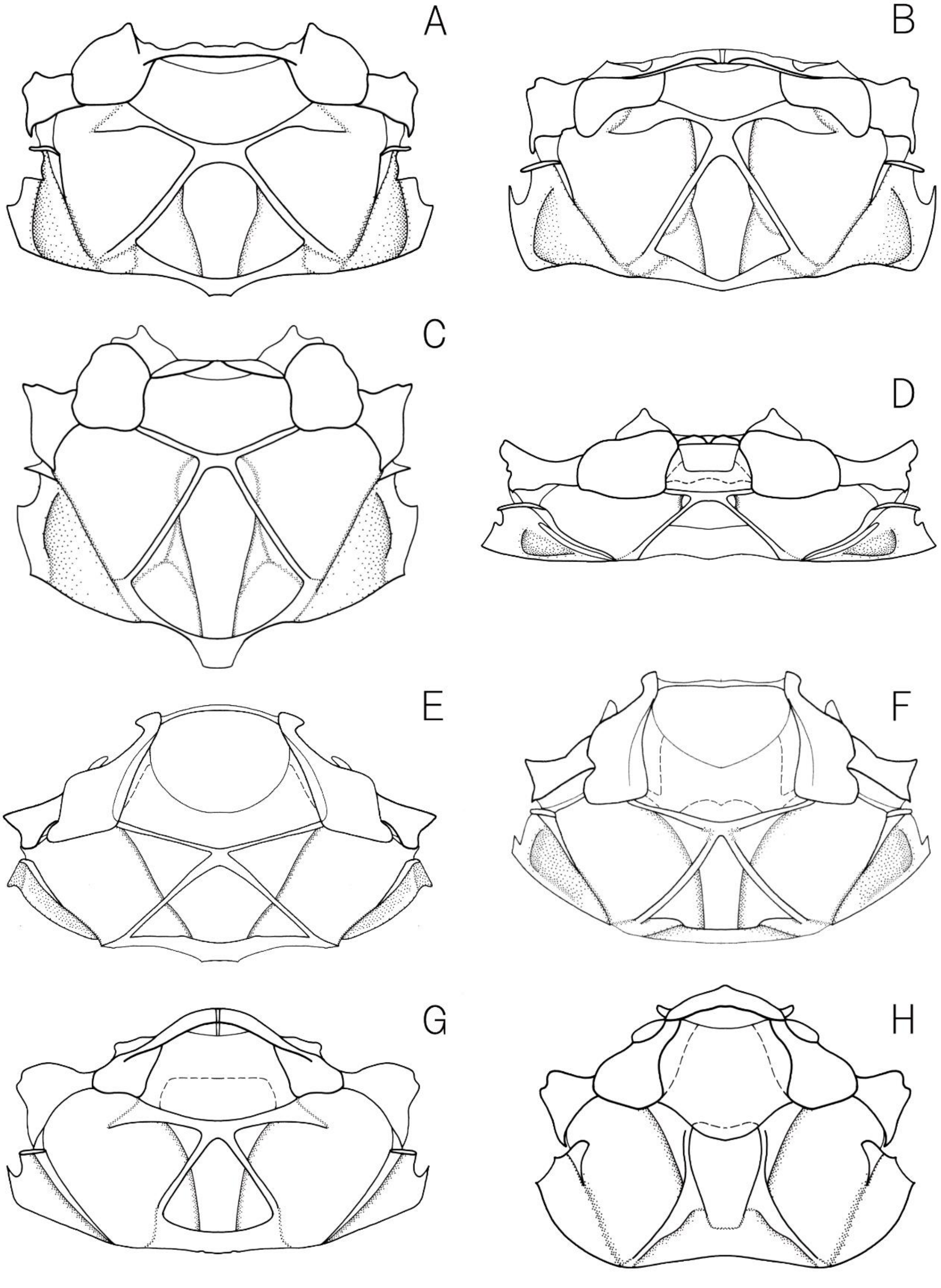


Figure 5A–H. Ventral habitus of the metanotum. **A** *Caelius denticollis* Lewis **B** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **C** *Chiron* sp. **D** *Copris* (*Copris*) *ochus* (Motschulsky) **E** *Gametis jucunda* (Faldermann) **F** *Mimela splendens* (Gyllenhal) **G** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky) **H** *Amphicoma splendens* (Yawata).

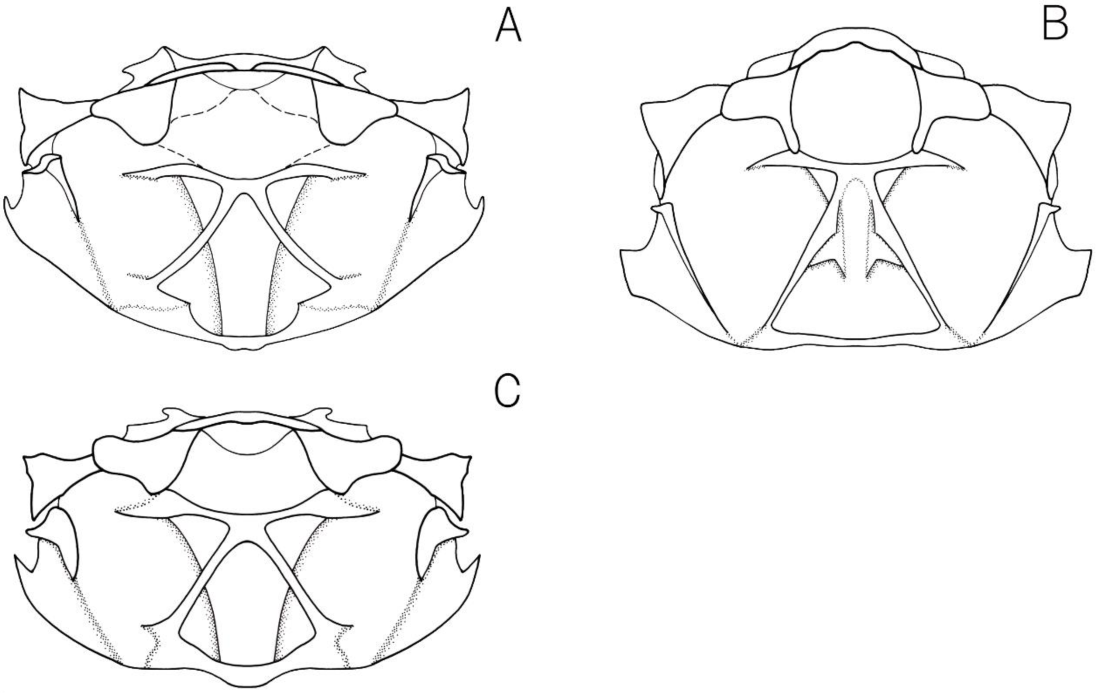


Figure 6A−B. Ventral habitus of the metanotum. **A** *Phaeochrous emarginatus* Laporte **B** *Pleocoma dubitabilis* Davis **C** *Glyptotrox uenoi* (Nomura).

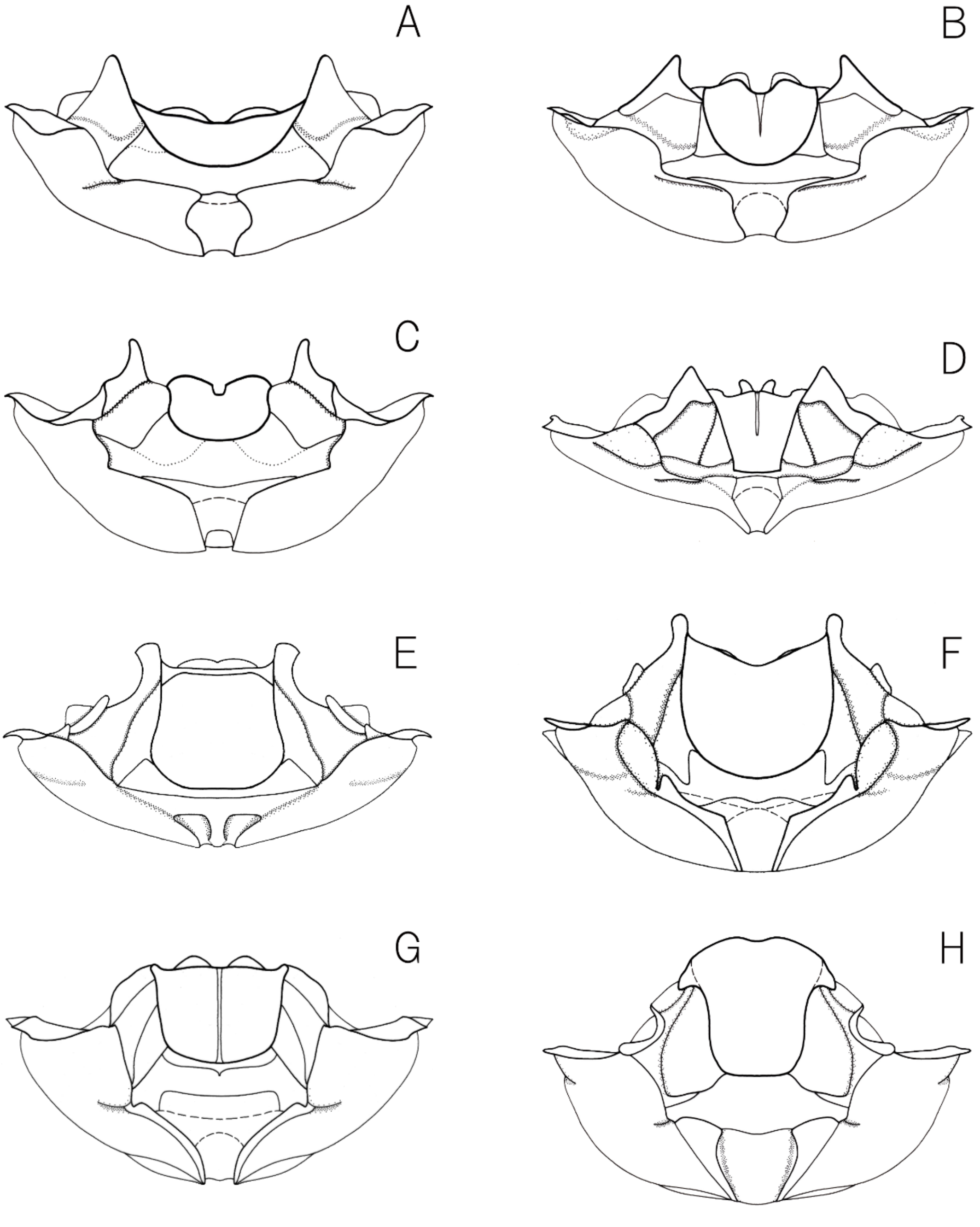


Figure 7A–H. Frontal habitus of the metanotum. **A** *Caelius denticollis* Lewis **B** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **C** *Chiron* sp. **D** *Copris* (*Copris*) *ochus* (Motschulsky) **E** *Gametis jucunda* (Faldermann) **F** *Mimela splendens* (Gyllenhal) **G** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky) **H** *Amphicoma splendens* (Yawata).

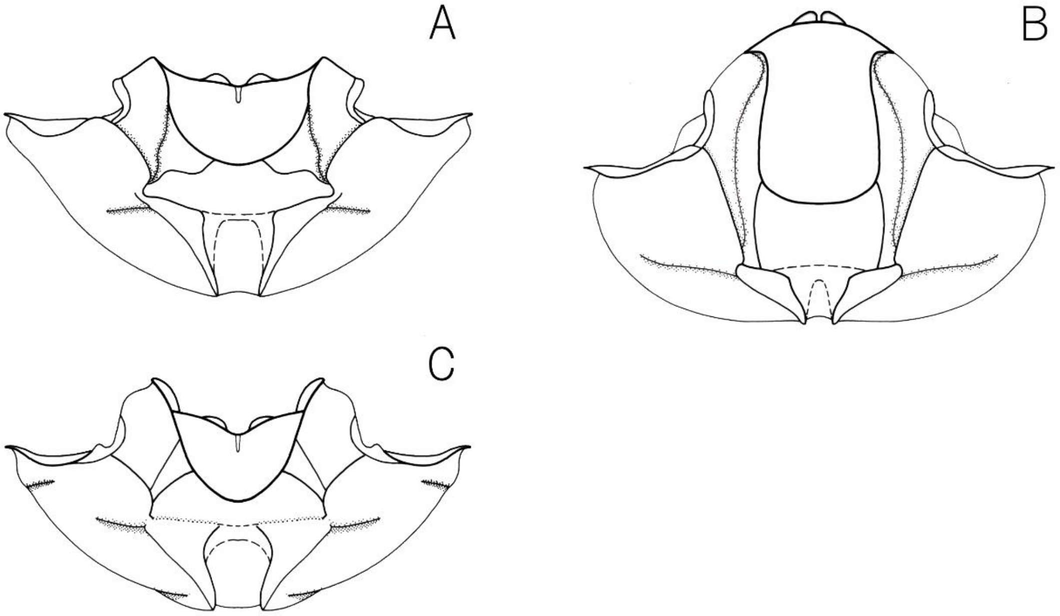


Figure 8A–B. Frontal habitus of the metanotum. **A** *Phaeochrous emarginatus* Laporte **B** *Pleocoma dubitabilis* Davis **C** *Glyptotrox uenoi* (Nomura).

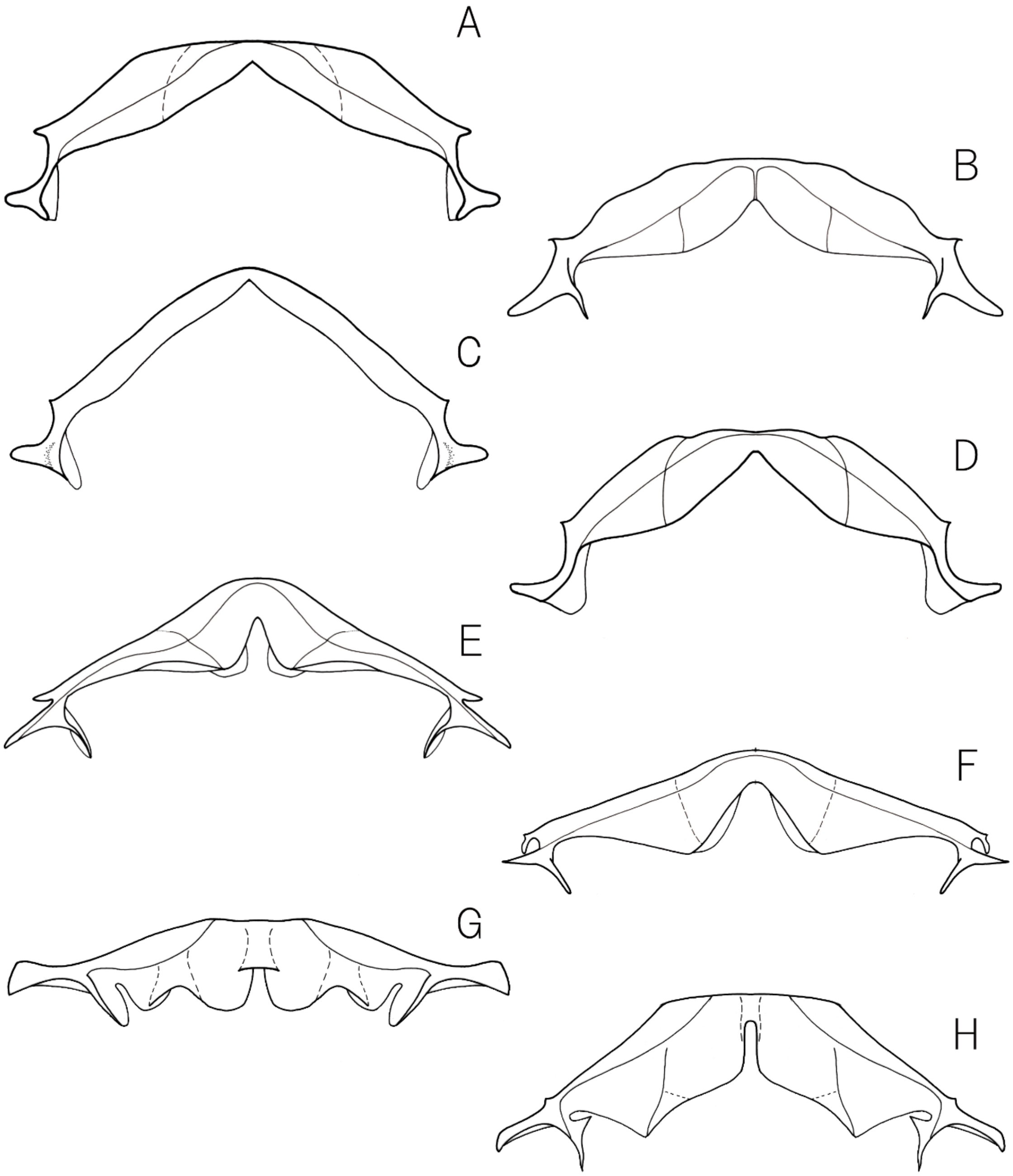


Figure 9A–H. Habitus of the postnotum. **A** *Caelius denticollis* Lewis **B** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates **C** *Psammodius kobayashii* Nomura **D** *Chiron* sp. **E** *Copris* (*Copris*) *ochus* (Motschulsky) **F** *Paragymnopleurus melanarius* (Harold) **G** *Gametis jucunda* (Faldermann) **H** *Mimela splendens* (Gyllenhal).

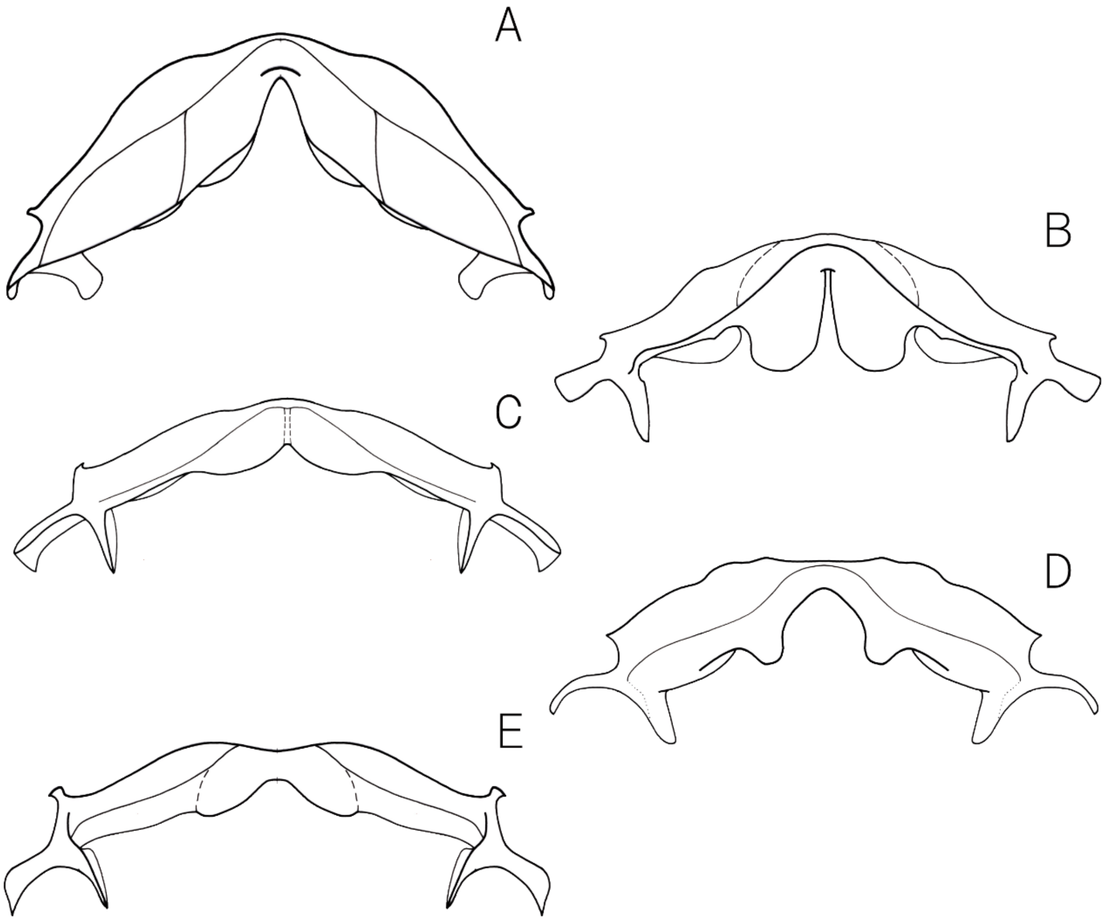


Figure 10A−H. Habitus of the postnotum. **A** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky) **B** *Amphicoma splendens* (Yawata) **C** *Phaeochrous emarginatus* Laporte **D** *Pleocoma dubitabilis* Davis **E** *Glyptotrox uenoi* (Nomura).

2−3−2

Comparative study of the metanotal structures in the phytophagous group of Scarabaeidae and some scarabaeoid beetles (Coleoptera, Scarabaeoidea)

Introduction

The phytophagous group of Scarabaeidae has long attracted the attention of numerous researchers, and several detailed comparative studies on various morphological structures have been conducted (Scholtz 1990, Scholtz and Grebennikov 2016).Nevertheless, there have been relatively few comparative studies that have focused on the metanotum in Scarabaeidae. Detailed metanotal structures in some scarabaeid species have been examined by some literatures (Snodgrass 1909, Larsén 1966, Edmonds 1972, Albertoni *et al*. 2014). Moreover, the first comparative study of the metanotum based on the multiple scarabaeoid species was conducted in subchapter (2–3–1), however this examination was incompletely owing to lack many phytophagous group species and other families of Scarabaeoidea. With respect to establishing phylogenetic relationships, the value of metanotal characters has been proven in studies on other coleopteran groups (Beutel and Komarek 2004, Friedrich and Beutel 2006, Ge *et al*. 2007) and the Scarabaeinae (Philips *et al*. 2004, 2016, Tarasov and Solodovnikov 2011, Tarasov and Génier 2015, subchapter, 2–3–1). In order to construct a more accurate phylogenetic hypothesis by comparison with molecular phylogenetic analyses, which has been frequently conducted in recent years, it is vital to find novel morphological traits to augment the data. In this study, I examined details of the metanotal structures of 69 genera from 10 subfamilies belong to the phytophagous group of Scarabaeidae, two genera from two subfamilies belong to the coprophagous group of Scarabaeidae, and 57 genera belong to other scarabaeoid families. Although the representatives species examined are clearly inadequate and may thus not provide a totally reliable basis on which to discuss far-reaching phylogenetic and systematic implications, it has, nevertheless, been possible to identify similarities among the different subfamilies.

Material and methods

Preparation of specimens

All dissections were carried out on dried specimens. In order to relax the specimens, they were initially placed in 50% ethanol for a few minutes, after which the prothorax and abdomen were detached from the meso- and metathorax using fine forceps. The meso- and metathorax were placed in 5% KOH solution for 6 to 8 hours to soften and dissolve the internal organs. Following pretreatment, these parts were washed several times in distilled water. Therefore, the metanotum was detached from the meso- and metathorax, and the isolated metanotum was soaked in 99% ethanol for 10 minutes to dehydrate the tissues.

Drawings were made with the aid of OLIMPAS SZX9 and, LEICA M165C microscopes and a KEYENCE VHX-1000 digital microscope. Fine structures such as hairs and punctates on the metanotal surface were excluded from the diagrams as these tended to obscure structures required for comparative observation.

Terminology

Terminology used in this paper was developed by subchapter 2–3–1 (Fig. 1).

Specimens studied

102 genera within 11 families of superfamily Scarabaeoidea, which is Bolboceratidae, Geotrupidae, Glaresidae, Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Passalidae, Pleocomidae, Trogidae and Scarabaeidae, were examined in this study. Two species within two genera of subfamily Bolboceratinae were selected in the family Bolboceratidae. Six species within three genera of two subfamilies (Geotrupinae and Lethrinae) were selected in the family Geotrupidae. One species within genus *Glaresis* Erichson, 1848 was selected in the family Glaresidae. Four species within three genera were selected in the family Glaphyridae. Three species within three genera of two subfamilies (Ceratocanthinae and Hybosorinae) were selected in the family Hybosoridae. 11 species within 10 genera of four subfamilies (Aesalinae, Syndesinae, Lamprinae and Lucaninae) were selected in the family Lucanidae. Three species within three genera were selected in the family Ochodaeidae. Three species within three genera of two subfamilies (Aulacocyclinae and Macrolinae) were selected in the family Passalidae. One species within genus *Pleocoma* LeConte, 1856 was selected in the family Pleocomidae. Three species within three genera were selected in the family Trogidae. 134 species within 101 genera of 14 subfamilies (Aegialiinae, Aphodiinae, Chironinae, Scarabaeinae, Aclopinae, Cetoniinae, Dynamopodinae, Dynastinae, Euchirinae, Melolonthinae, Orphninae, Rutelinae, Trichiinae and Valginae) were selected in the family Scarabaeidae (Table. 1).

Results

Scarabaeidae

Aclopinae (Figs. 2A, 7A, 11A, 15A)

In the Aclopinae (genus *Pachypus*) the metanotum is dome-shaped and, the length-to-width ratio is approximately 1:1.3. The first phragma shows trapezoidal and bilobed phragma is present on the anterior margin. The prescutum develops and elongate shape. The prescutal membrane is oblong and comprises a thin membranous and sclerotized areas. The acrotergite is triangular and the anterior part is slightly protruding. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is recognizable on the lateral margin of the medianlongitudinal groove, and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is triangular with a winding anterior margin. The posterolateral scutal area is wedge-shaped and this area is completely fused with the scutum owing to a decrease of an oblique suture. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is bow-shaped (Fig. 15A). The mediophragmite and anterior postnotal process are strongly developed, whereas the development of laterophragmite is weak. Of these, the mediophragmite and laterophragmite are clearly separated.

Cetoniinae (Figs. 2B−C, 7B, 11B, 15B)

In the Cetoniinae the metanotum is rhomboidal and the length-to-width ratio is typically approximately 1:1.6−1.7, however in the genera *Clinterocera* (approximately 1:1.3) (Fig. 2C) and *Coilodera* (approximately 1:1.2) represent low aspect ratio. The first phragma is typically trapezoidal and bilobed phragma is present on the anterior margin. The prescutum develops and is elongate shape. The prescutal membrane is rectangular and consists of thin membrane. The acrotergite is triangular and the anterior part is protruding and elongated. The scutum + scutellum divided by a medianlongitudinal groove is parallelogram and the groove expanding forward. The alacrista is recognizable on the lateral margin of the medianlongitudinal groove, but the development is confined to the posterior apex to the middle portion. The anterior lobe of metanotum is completely reduced. The anterior notal wing process is triangular (Cetoniini, Cremastocheilini, and Taenioderini) or trapezoidal (Goliathini and Diplognathini) in shape. The posterolateral scutal area is triangular, somewhat bulging on the dorsal side and this area is completely divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is strongly reduced (Cetoniini) or weakly developed and pointing outward (Goliathini, Cremastocheilini, Diplognathini, and Taenioderini). The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form a "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is bow-shaped (Fig. 15B). The mediophragmite, laterophragmite, and anterior postnotal process are strongly developed. Of these, the mediophragmite and laterophragmite are clearly separated.

Dynamopodinae (Figs. 2D, 7C, 11C, 15C)

In the subfamily Dynamopodinae (genus *Orubesa*) the metanotum is dome-shaped and the length-to-width ratio is approximately 1:1.5. The first phragma is rounded and bilobed phragma is present on the anterior margin. The prescutum is developed and is triangular in shape. The prescutal membrane is rounded and consists of thin membrane. The acrotergite is rectangular and the anterior part is protruding in trapezoidal in shape. The scutum + scutellum divided by a medianlongitudinal groove is pentagonal and the groove gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular with a slightly winding anterior margin. The posterolateral scutal area is wedge-shaped and this area is completely fused with the scutum owing to a decrease of an oblique suture. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an "X" shape. The postnotum is developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process) (Fig. 15C). The anterior postnotal process is strongly developed, whereas the mediophragmite and laterophragmite are without strongly developed. These character states are similar to the family Hybosoridae.

Dynastinae (Figs. 2E, 7D, 11D, 15D)

In the subfamily Dynastinae is dome-shaped and the length-to-width ratio is typically approximately 1:1.2−1.3, but in the tribe Pentodontini it is approximately 1:1.5. The first phragma is oval and bilobed phragma is present on the anterior margin. The prescutum develops strongly and is triangular in shape. The prescutal membrane is rectangular and comprises a thin membranous and sclerotized areas. The acrotergite is triangular and the anterior part is protruding and elongated. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is triangular with a winding anterior margin. The posterolateral scutal area is typically wedge-shaped, somewhat bulging on the dorsal side and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is developed and sharply pointed outward. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is trapezoidal in shape (Fig. 15D). The mediophragmite, laterophragmite, and anterior postnotal process are strongly developed.

These character states are similar to the subfamily Rutelinae.

Euchirinae (Figs. 2F, 7E, 11E, 15E)

In the subfamily Euchirinae the metanotum is dome-shaped and the length-to-width ratio is approximately 1:1.1−1.2. The first phragma is oval and bilobed phragma is present on the anterior margin. The prescutum is strongly developed and is trapezoidal in shape. The prescutal membrane is rectangular and consists of thin membranous and sclerotized areas. The acrotergite is triangular and the anterior part is slightly protruding and elongated. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is triangular with a winding anterior margin. The posterolateral scutal area is typically wedge-shaped, somewhat bulging on the dorsal side and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is slender trapezoidal in shape (Fig. 15E). The mediophragmite, laterophragmite, and anterior postnotal process are strongly developed. Of these, the mediophragmite and laterophragmite are clearly separated.

These character states are similar to the subfamily Dynastinae.

Melolonthinae (Figs. 2G−2H, 3A−3C, 7F−7H, 8A−8B, 11F−11H, 12A−12B, 15F−15H, 16A−16B)

In the subfamily Melolonthinae, the metanotum structure widely various across different tribes.

Diplotaxini (Figs. 2G, 7F, 11F, 15F)

In the tribe Diplotaxini (genus *Apogonia*) the metanotum is dome-shaped and the length-to-width ratio is approximately 1:1.6−1.7. The first phragma is semicircular with a sclerotized ridge in the middle part. The weakly developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is well-developed and is triangular in shape. The prescutal membrane is oblong and consists of thin membrane. The acrotergite is triangular and the anterior part is protruding and elongated. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is triangular and the anterior margin is almost straight. The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side, and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is developed and composed of five parts (mediophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is slender trapezoidal in shape. The laterophragmite is completely lost and the mediophragmite is strongly reduced.

Sericini (Figs. 2H, 7G, 11G, 15G)

In the tribe Sericini is dome-shaped and the length-to-width ratio is typically approximately 1:1.6, however in the genera *Serica* and *Sericania* which comprise elongated species, this ratio is approximately 1:1.3. The first phragma is oval and a developed bilobed phragma is present on the anterior margin. The prescutum is developed and is triangular in shaped. The prescutal membrane is oblong, with a very thin membrane. The acrotergite is rectangular and the anterior part is weakly protruding. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is rounded triangular in shape. The posterolateral scutal area is wedge-shaped and this area is completely fused with the scutum owing to a decrease of an oblique suture. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), forming a slender trapezoidal in shape. The anterior postnotal process is strongly developed, whereas the mediophragmite and laterophragmite are weakly developed compared to those in other subfamilies.

Hopliini (Figs. 3A, 7H, 11H, 15H)

In the tribe Hopliini is dome-shaped and the length-to-width ratio is approximately 1:1.5−1.6. The first phragma is rectangular with a sclerotized ridge in the middle part. The developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is well-developed and is triangular in shape. The prescutal membrane is rectangular and consists of thin membranous and sclerotized areas. The acrotergite is triangular and the anterior part is protruding and elongated. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is triangular with an almost straight or winding anterior margin. The posterolateral scutal area is flabellate-shaped with concave on the dorsal side and this area is completely fused with the scutum owing to a decrease of an oblique suture. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), forming a slender trapezoidal in shape. The anterior postnotal process is strongly developed, whereas the mediophragmite and laterophragmite are strongly reduced compared to those in other subfamilies.

Melolonthini and Rhizotrogini (Figs. 3B, 8A, 12A, 16A)

In the tribes Melolonthini and Rhizotrogini the metanotum is dome-shaped and the length-to-width ratio is typically approximately 1:1.2−1.3. The first phragma is oval with a V-shaped sclerotized ridge in the middle part. The weakly developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is well-developed and is triangular in shape. The prescutal membrane is oblong and consists of very thin membrane. The acrotergite is triangular and the anterior part is protruding and elongated. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, and the anterior part is connected to the weakly developed anterior lobe of metanotum. The anterior notal wing process is triangular with an almost straight or winding anterior margin. The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), forming a trapezoidal in shape. The mediophragmite, laterophragmite, and anterior postnotal process are strongly developed.

These character states are similar to the subfamily Rutelinae.

Tanyproctini (Figs. 3C, 8B, 12B, 16B)

In the tribe Tanyproctini (genus *Tanyproctus*) is dome-shaped and the length-to-width ratio is approximately 1:1.2. The first phragma is oblong with a sclerotized ridge in the middle part. The developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is triangular and elongated. The prescutal membrane is oblong and consists of thin membranous and sclerotized areas. The acrotergite is elongated triangular and the anterior part is weakly protruding. The scutum + scutellum divided by a medianlongitudinal groove is rectangular and the groove is gradually expanding forward. The developed scutellum is observed at the posterior part. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove but the posterior apex does not reach the posterior margin of the metanotum. The anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular with a winding anterior margin. The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is weakly developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). The mediophragmite and laterophragmite are strongly developed, however the development of the subalar tendon is very weak.

These character states are similar to the family Pleocomidae.

Orphninae (Figs. 3D, 8C, 12C, 16C)

The metanotum in the Orphninae (genus *Orphnus*) is dome-shaped and the length-to width-ratio is approximately 1:1.7. The first phragma is rounded with a sclerotized ridge in the middle part. The bilobed phragma on the anterior margin of the first phragma is completely lost. The prescutum is developed and is triangular in shape. The prescutal membrane is oblong and consists of thin membrane. The acrotergite is rectangular and the anterior part protrudes to form a trapezoid. The scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, however the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular with a slightly winding anterior margin. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), forming a slender trapezoidal in shape. The anterior postnotal process is strongly developed, whereas the mediophragmite and laterophragmite are strongly developed compared to those in other subfamilies.

Rutelinae (Figs. 3E−3G, 8D−8F, 12D−12F, 16D−16F)

In the Rutelinae the metanotum is typically dome-shaped and the length-to-width ratio is approximately 1:1.2−1.4, however in the genus *Popillia* and *Malaia* this ratio is approximately 1:2 (Fig. 3F). The first phragma shows various states, such as rounded or rectangular with sclerotized ridges in the middle part in some genera (*Anomala*, *Phyllopertha*, *Chrysophora*, *Parastasia*, *Repsimus*, *Calloodes*, *Adoretus, Adorodocia*, *Chaetadoretus*, and *Lepadoretus*) (Fig. 12F). However, the presence of sclerotized ridges is a very ambiguous characteristic between species, except in the genera of the tribe Adoretini. A weakly developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is strongly developed and is triangular in shape. The prescutal membrane is oblong and comprises a thin membranous and sclerotized areas. The acrotergite is triangular and the anterior part is usually protruding and elongated, however in genera *Parastasia*, *Kibakoganea*, and *Dicaulocephalus* the anterior part of the acrotergite is non-protruding (Fig. 12F). The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is triangular and the anterior margin is almost straight or winding. The posterolateral scutal area is usually wedge-shaped, somewhat bulging on the dorsal side and this area is divided from the scutum by an oblique suture and a deep groove. In the genus *Popillia* and *Malaia*, this area shows is stout with a concave dorsal side (Fig. 3F). The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is trapezoidal in shape. The mediophragmite, laterophragmite, and anterior postnotal process are strongly developed.

Trichinae (Figs. 3H, 8G, 12G, 16G)

In the Trichinae (except in the tribe Osmodermini) the metanotum is dome-shaped and the length-to-width ratio is typically approximately 1:1.3−1.6. The first phragma is trapezoidal with a sclerotized ridge in the middle part, except in the genus *Lasiotrichius*. A developed bilobed phragma is present on the anterior margin of the first phragma, however in the genera *Corynotrichius* and *Inca* the phragma lobed. The prescutum is strongly developed and is elongated triangular in shape. The prescutal membrane is oblong and comprises thin membranous and sclerotized areas. The acrotergite is triangular and the anterior part is usually protruding and elongated, however in the genus *Paratrichius* the anterior part of the acrotergite is non-protruding (Fig. 12G). The scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove and the anterior part is connected to the developed anterior lobe of metanotum. The anterior notal wing process is usually triangular with a winding anterior margin, except the genus *Lasiotrichius*, in which the anterior notal wing process is trapezoidal in shape. The posterolateral scutal area is wedge-shaped and this area is divided from the scutum by an oblique suture and a deep groove. The dorsal surface of the posterolateral scutal area shows various character states, such as bulging (genera *Lasiotrichius* and *Trichius*), flat (genus *Inca*), and sclerotized (genera *Corynotrichius*, *Epitrichius*, *Gnorimus*, and *Paratrichius*). The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is trapezoidal in shape. The mediophragmite, laterophragmite, and anterior postnotal process is strongly developed.

These character states are similar to the subfamily Rutelinae.

Osmodermini (Figs. 4A, 8H, 12H, 16H)

In the Osmodermini (genus *Osmoderma*) the metanotum is rhomboidal and the length-to-width ratio is approximately 1:1.6. The first phragma is trapezoidal with a slightly developed sclerotized ridge in the middle part. A developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum develops and is elongate shape. The prescutal membrane is rectangular and consists of thin membrane. The acrotergite is triangular and the anterior part is protruding and elongated. The one side of the scutum + scutellum divided by a medianlongitudinal groove is parallelogram, and the groove is greatly expanding forward. The alacrista is recognizable on the lateral margin of the medianlongitudinal groove, but the development is confined to the posterior apex to the middle portion. The anterior lobe of metanotum is completely reduced. The anterior notal wing process is trapezoidal in shape. The posterolateral scutal area is triangular, somewhat bulging on the dorsal side and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is strongly reduced. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is bow-shaped. The mediophragmite, laterophragmite, and anterior postnotal process are strongly developed.

These character states are remarkably similar to the subfamily Cetoniinae.

Valginae (Figs. 4B, 9A, 13A, 17A)

In the Valginae is rectangular and the length-to-width ratio is typically approximately 1:2. The first phragma is oblong with a developed sclerotized ridge in the middle part. A developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is elongated triangular but in the genus *Microvalgus* the prescutum is completely lost. The prescutal membrane is trapezoidal and consists of thin membranous and sclerotized areas. The acrotergite is rectangular, and the anterior part is protruding and elongated. The scutum + scutellum divided by a medianlongitudinal groove is quadrangular and the groove is gradually expanding forward, but in the genus *Microvalgus* the width of the medianlongitudinal groove is represented remarkably wide state. Moreover, the posterior apex of the scutum and scutellum is separated, respectively. The alacrista and anterior lobe of metanotum are completely lost. The anterior notal wing process typically strongly points, but the process in the genus *Microvalgus* forms by two protrusions. The posterolateral scutal area is isosceles triangular, somewhat bulging on the dorsal side and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process is strongly reduced. The scutoscutellar and prescutal sutures are fused at the middle portion to form an "X" shape, but the development of the prescutal suture is weak. The postnotum is well developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which is bow-shaped. The mediophragmite, laterophragmite, and anterior postnotal process are strongly developed. Of these, the mediophragmite and laterophragmite are clearly separated and are strongly reduced.

Coprophagous group of Scarabaeidae

Aphodiinae (Figs. 4C, 9B, 13B, 17B)

In the Aphodiinae (genus *Aphodius*) the metanotum is typically rectangular and the length-to-width ratio is usually approximately 1:2. The first phragma is semicircular and bilobed phragma is present on the anterior margin. The prescutum develops strongly and is triangular in shape. The prescutal membrane is oblong and consists of thin membrane. The acrotergite is rectangular and the anterior part protrudes and points. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is the widest in the middle part. The alacrista and the anterior lobe of metanotum are almost completely lost. The anterior notal wing process is trapezoidal in shape. The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side, and this area is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process develops and is sharply pointed outward. The scutoscutellar suture and prescutal suture are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is developed and usually comprises six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), which are V-shaped. The mediophragmite and laterophragmite are strongly reduced, whereas the anterior and posterior postnotal processes are strongly developed.

Scarabaeinae (Figs. 4D, 9C, 13C, 17C)

In the Scarabaeinae (genus *Copris*) the metanotum is rectangular, and the length-to-width ratio is approximately 1:4. The first phragma is inverted trapezoidal with a developed sclerotized ridge in the middle part. A developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is developed and triangular in shape. The prescutal membrane is oblong and consists of thin membrane. The acrotergite is rectangular and the anterior part protrudes and points. The scutum + scutellum divided by a medianlongitudinal groove is quadrangular, and the groove is the widest in the middle part and the posterior apex is somewhat protruding. The alacrista is remarkably reduced, and the anterior lobe of metanotum is completely lost. The anterior notal wing process is trapezoidal with a small apophysis. The posterolateral scutal area is wedge-shaped, somewhat bulging on the dorsal side and this area is completely divided from the scutum by an oblique suture and a cleft. The scutoscutellar suture and prescutal suture are developed, and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process), forming a V-shaped. The mediophragmite and laterophragmite are strongly reduced, but the subalar tendon is strongly developed.

Bolboceratidae (Figs. 4E, 9D, 13D, 17D)

In the family Bolboceratidae the metanotum is dome-shaped and the length to width ratio is approximately 1:1.6−1.7. The first phragma is rounded and developed sclerotized bilobed phragma is present on the anterior margin. In the genus Bolbochromus, a developed sclerotized ridge is present at the middle part of the first phragma. The prescutum is reduced. The prescutal membrane is square and consists of thin membrane. The acrotergite is rectangular and the anterior part is non-protruding. The scutum + scutellum divided by a medianlongitudinal groove is trapezoidal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular in shape. The posterolateral scutal area is wedge-shaped and this area is completely fused with the scutum owing to a decrease of an oblique suture. The posterior notal wing process is strongly reduced. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). The mediophragmite and laterophragmite are strongly developed, but the development of subalar tendon is weak.

Geotrupidae (Figs. 4F−G, 9E, 13E, 17E)

Geotrupinae (Figs. 4F, 9E, 13E, 17E)

In the family Geotrupidae the metanotum is dome-shaped, and the length-to-width ratio is approximately 1:1.6–1.7. The first phragma is rounded with a sclerotized ridge in the middle part. The developed sclerotized bilobed phragma is present on the anterior margin of the first phragma. The prescutum is sclerotized and is triangular in shape. The prescutal membrane is oblong, and consists of thin membranous and sclerotized areas. The acrotergite is rectangular and the anterior part is slightly protruding. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is trapezoidal in shape. The posterolateral scutal area is wedge-shaped, and is divided from the scutum by an oblique suture and a deep groove. The posterior notal wing process develops and is sharply pointed outward. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an “X” shape. The postnotum well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). Among these, the mediophragmite and laterophragmite are strongly developed, but the development of the subalar tendon is very weak.

Lethrinae (Fig. 4G)

Members of the subfamily Lethrinae, which show reduced hind wings, possess a remarkably reduced metanotum. The metanotum consists only of the scutum + scutellum and the remaining parts are reduced. The length-to-width ratio of the metanotum is approximately 1:4. The remnant of the medianlongitudinal groove is observed at the middle part of the scutum + scutellum, but the alacrista and anterior lobe of metanotum are completely lost. The remnants of the anterior notal wing process and posterolateral scutal area are observed at the lateral side. The postnotum is almost completely lost, leaving only the anterior postnotal process.

Glaresidae (Figs. 4H, 9F, 13F, 17F)

In the family Glaresidae is rectangular, and the length-to-width ratio is approximately 1:2. The first phragma is semicircular and a weakly developed bilobed phragma is present on the anterior margin. The prescutum is triangular and weakly sclerotized. The prescutal membrane is oblong and consists of thin membrane. The acrotergite is rhomboidal and the anterior part protrudes in a trapezoid. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward with a slightly protruding posterior apex. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular and the anterior margin is almost straight. The posterolateral scutal area is flabellate and this area is completely fused with the scutum owing to a decrease of an oblique suture. The posterior notal wing process weakly develops and is pointed outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). The mediophragmite and laterophragmite are weakly developed.

Glaphyridae (Figs. 5A, 9G, 13G, 17G)

In the family Glaphyridae the metanotum is dome-shaped, and the length-to-width ratio is approximately 1 : 1.2−1.3. The first phragma is oblong with a rudimentary sclerotized ridge in the middle part, and a developed sclerotized bilobed phragma is present on the anterior margin. The prescutum is triangular and strongly developed. The prescutal membrane is trapezoidal or oblong and consists of very thin membrane. The acrotergite is rectangular with a small apophysis, and no protrusion at the anterior part. The one side of the scutum + scutellum divided by a medianlongitudinal groove is rectangular, and the groove is greatly expanding forward. In the genus *Pygopleurus* the posterior apex of the medianlongitudinal groove protrudes. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is trapezoidal in shape. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process weakly develops and is slightly pointed outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). The median postnotum, mediophragmite, and anterior postnotal process are strongly developed.

Hybosoridae (Figs. 5B, 9H, 13H, 17H)

In the family Hybosoridae the metanotum is dome-shaped, and the length-to-width ratio is approximately 1:1.6−1.7, but in the genus *Madrasostes*, this ratio is approximately 1:2. The first phragma is semicircular, and the sclerotized ridges usually develop in the middle part, however, in the genus *Madrasostes* the sclerotized rides are absent. The weakly developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is developed and triangular in shape, but in the genus *Madrasostes* the prescutum is completely lost. The prescutal membrane is oblong and comprises thin membranous and sclerotized areas. The acrotergite is rectangular and the anterior part is protruding in trapezoid. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal and the groove gradually expanding forward, and the posterior apex slightly protrudes. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular, with a slightly winding anterior margin. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is developed and sharply pointing outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). However, the development of the mediophragmite and laterophragmite is weak, whereas the anterior postnotal process is strongly developed.

Lucanidae (Figs. 5C−5F, 10A−10D, 14A−14D, 18A−18D)

Aesalinae (Figs. 5C, 10A, 14A, 18A)

In the subfamily Aesalinae the metanotum is rectangular and the length-to-width ratio is approximately 1:1.8 (genus *Aesalus*) or 1:1.4 (genus *Nicagus*). The first phragma in the genus *Aesalus* is semicircular, while the genus *Nicagus* is characterized by rectangular with a sclerotized ridge in the middle part. The developed bilobed phragma is present on the anterior margin of the first phragma. The prescutum is well-developed and is triangular in shape. The prescutal membrane is trapezoidal and comprises thin membranous and sclerotized areas. The acrotergite is rectangular and the anterior part is protruding in trapezoid. The one side of the scutum + scutellum divided by a medianlongitudinal groove is rhomboidal and the groove is gradually expanding forward, but in the genus *Nicagus* the divided scutum + scutellum is pentagonal. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular, with an almost straight anterior margin. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is weakly developed and pointed outward. The scutoscutellar and prescutal sutures are well-developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum well develops and composed to six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). The subalar tendon and anterior postnotal process are strongly developed, but the mediophragmite is strongly reduced compared to those in other subfamilies.

Syndesinae (Figs. 5D, 10B, 14B, 18B)

In the subfamily Syndesinae (genus *Ceruchus*) the metanotum is square and the length-to-width ratio is approximately 1:1.2. The first phragma is oblong and bilobed phragma is present on the anterior margin. The prescutum is well-developed and is triangular in shape. The prescutal membrane is trapezoidal and comprises thin membranous and sclerotized areas. The acrotergite is rectangular and the anterior part is non-protruding. The one side of the scutum + scutellum divided by a medianlongitudinal groove is rhomboidal, and the groove is gradually expanding forward with a protruding posterior apex. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular, with an almost straight anterior margin. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is developed and pointed outward. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed to six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). Among these, the mediophragmite, subalar tendon, and anterior postnotal process are strongly developed.

Lamprinae (Figs. 5E, 10C, 14C, 18C)

In the subfamily Lamprinae is square and the length-to-width ratio is approximately1:1.5. The first phragma is rounded with a slightly developed sclerotized ridge in the middle part. The bilobed phragma is present on the anterior margin of the first phragma. The prescutum is well-developed and is triangular in shape. The prescutal membrane is trapezoidal and consists of thin membrane. The acrotergite is rectangular and the anterior part is non-protruding. The scutum and scutellum divided by a medianlongitudinal groove is rhomboidal, and the groove is gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is rounded triangular in shape. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is weakly developed and slightly pointed outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form a “X” shape. The postnotum is well-developed and composed to six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). Among these, the mediophragmite and subalar tendon are strongly developed, and the anterior postnotal and posterior postnotal processes get stout.

Lucaninae (Figs. 5F, 10D, 14D, 18D)

In the subfamily Lucaninae the metanotum is square and the length-to-width ratio is typically approximately 1.2−1.3. The first phragma is rounded, with a developed sclerotized ridge in the middle part, except for the genus *Lucanus*. The sclerotized bilobed phragma is present on the anterior margin of the first phragma. The prescutum is well-developed and is triangular in shape. The prescutal membrane is trapezoidal and comprises thin membranous and sclerotized areas. The acrotergite is rectangular and the anterior part is slightly protruding. The one side of the scutum + scutellum divided by a medianlongitudinal groove is rhomboidal, and the groove is gradually expanding forward. In the genera *Figulus* and *Platycerus*, the posterior apex of the medianlongitudinal groove is slightly protruding. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular with a winding anterior margin. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is strongly developed and sharply pointed outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum well develops and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). Among these, the mediophragmite and subalar tendon are strongly developed.

Ochodaeidae (Figs. 5G, 10E, 14E, 18E)

In the family Ochodaeidae the metanotum is dome-shaped and the length-to-width ratio is typically approximately 1:1.7−1.8. The first phragma is rounded with a sclerotized ridge in the middle part, but a bilobed phragma on the anterior margin is absent. The prescutum is triangular but is strongly reduced. The prescutal membrane is oblong and consists of thin membrane. The acrotergite is rectangular and the anterior part is protruding in trapezoid. The one side of the scutum +scutellum divided by a medianlongitudinal groove is pentagonal, and the groove is gradually expanding forward with a slightly protruding posterior apex. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular with an almost straight anterior margin. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is developed and sharply pointed outward. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an "X" shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). Among these, the mediophragmite, laterophragmite, and anterior postnotal process are strongly developed.

Passalidae (Figs. 5H, 10F, 14F)

In the family Passalidae the metanotum is square and very flat, with a length-to-width ratio of approximately 11.3. The first phragma is typically strongly sclerotized and semicircular, with a developed sclerotized lobed phragma on the anterior margin. The prescutum and acrotergite are fused with each other to form a single plate, which protrudes forward in a trapezoid. The prescutal membrane is square, with a very thin membranous state. The one side of the scutum + scutellum divided by a medianlongitudinal groove is square, and the groove is almost straight, with a protruding posterior apex. The scutum + scutellum forms a plate-like structure by remarkably reduced internal ridges. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is sharply pointing outward. The posterolateral scutal area is completely fused with the scutum by reducing the oblique suture. The posterior notal wing process is elongated. The scutoscutellar and prescutal sutures are remarkably reduced. The postnotum is remarkably reduced and composed of three parts (median postnotum, subalar tendon, and anterior postnotal process). The subalar tendon is strongly developed, while the mediophragmite, laterophragmite, and posterior postnotum process are completely lost.

Cylindrocaulus patalis belonging to the subfamily Aulacocyclinae has reduced hind wings and shows some different characters from other species. The length-to-width ratio of the metanotum is approximately 1:1.6. The first phragma is completely lost. The prescutum, acrotergite, and prescutal membrane are fused with each other to form a single plate, which protrudes forward. The anterior notal wing process is triangular, but weakly developed. The posterior notal wing process is completely lost. The scutoscutellar and prescutal sutures are remarkably reduced. The postnotum is remarkably reduced and composed of two parts (median postnotum and anterior postnotal process). The mediophragmite, laterophragmite , subalar tendon, and posterior postnotal process are completely lost.

Pleocomidae (Figs. 6A, 10G, 14G, 18F)

In the family Pleocomidae (genus *Pleocoma*) the metanotum is dome-shaped and the length-to-width ratio is approximately 1:1.3. The first phragma is oblong in shape and there is a weakly developed bilobed phragma on the anterior margin. The prescutum is elongated triangular. The prescutal membrane is square with a very thin membranous state. The acrotergite is elongated rectangular and does not protrude in the anterior part. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal and the groove gradually expanding forward. The scutellum is developed at the posterior part. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the posterior apex does not reach the posterior margin of the metanotum. The anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular, and the anterior margin is almost straight. The posterolateral scutal area is triangular, is divided from the scutum by an oblique suture and a deep groove. The weakly protruding posterior notal wing process is recognizable on the lateral margin of the posterolateral scutal area. The scutoscutellar and prescutal sutures are developed, and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). The mediophragmite and laterophragmite are strongly developed, but the subalar tendon is very weakly developed.

Trogidae (Figs. 6B, 10H, 14H, 18G)

In the family Trogidae the metanotum is rectangular and the length-to-width ratio is approximately 1:1.7–1.8. The first phragma is semicircular and the sclerotized ridges develop in the middle part, and there is a developed bilobed phragma on the anterior margin. The prescutum is triangular in shape. The prescutal membrane is oblong and consists of thin membranous areas. The acrotergite is rectangular and the anterior part is protruding in trapezoidal in shape. The one side of the scutum + scutellum divided by a medianlongitudinal groove is pentagonal, and the groove gradually expanding forward. The alacrista is clearly recognizable on the lateral margin of the medianlongitudinal groove, but the anterior lobe of metanotum is unrecognizable. The anterior notal wing process is triangular and is characterized by an almost straight anterior margin. The posterolateral scutal area is wedge-shaped, and this area is completely fused with the scutum owing to a decrease of the oblique suture. The posterior notal wing process is recognizable on the lateral margin of the posterolateral scutal area. The scutoscutellar and prescutal sutures are developed and each suture is fused at the middle portion to form an “X” shape. The postnotum is well-developed and composed of six parts (mediophragmite, laterophragmite, median postnotum, subalar tendon, anterior postnotal process, and posterior postnotal process). Among these, the development of the mediophragmite and laterophragmite are weak.

Discussion

Based on the examination of the metanotum in the phytophagous groups of Scarabaeidae and its comparison with the metanotum in the coprophagous groups of Scarabaeidae and other scarabaeoid families, I make the following inferences.

Types of metanotum in phytophagous groups of Scarabaeidae

I suggest dividing the metanotum in the phytophagous group of Scarabaeidae into five types: melolonthine, sericine, orphnine, cetoniine, and valgine. Owing to its great importance for flight, the metanotum is highly developed and large, accommodating the powerful muscles for moving the hind wings (Larsén 1966). Therefore, it is considered that the metanotal structures are commonly affected by behavioral traits. However, the metanotum in the coprophagous groups may be divided into several types based on their characteristics, which are not affected by behavioral traits (subchapter 2–3–1). This also seems to apply to the phytophagous groups. The following features are important to distinguishing the five types: shape of the metanotum, acrotergite, medianlongitudinal groove, shape of the one side of the scutum + scutellum divided by a medianlongitudinal groove, alacrista, anterior lobe of metanotum, posterolateral scutal area, and postnotum.

Members of the subfamilies Aclopinae, Dynastinae, Euchirinae, some of Melolonthinae (tribes Diplotaxini, Hopliini, Melolonthini, Rhizotrogini, and Tanyproctini), Rutelinae, and Trichinae belong to the melolonthine type. In these, the metanotum is dome-shaped. The acrotergite is triangular, and the anterior part is protruding and elongated. The medianlongitudinal groove is gradually expanding. The one side of the scutum + scutellum is pentagonal in shape. The alacrista is present on the lateral sides of the medianlongitudinal groove. The anterior lobe of metanotum is developed. The posterolateral scutal area is divided from the scutum by an oblique suture and a deep groove. The postnotum is usually well-developed.

Members of tribe Sericini belong to the sericine type. In these, the metanotum is dome-shaped. The acrotergite is rectangular and the anterior part is protruding in a trapezoid. The medianlongitudinal groove is gradually expanding. The one side of the scutum + scutellum is pentagonal in shape. The alacrista is present on the lateral sides of the medianlongitudinal groove. The anterior lobe of metanotum is developed. The posterolateral scutal area is completely fused with the scutum owing to a decrease of the oblique suture. The medio- and laterophragmite of the postnotum are reduced.

Members of subfamilies Dynamopodinae and Orphninae belong to the orphnine type. This type is similar to the sericine type, however differs in the lack of the anterior lobe of metanotum. Moreover, these character states are remarkably similar to the characteristics of the family Hybosoridae.

Members of subfamily Cetoniinae, and tribe Osmodermini belong to the cetoniine type. In these, the metanotum is rhomboidal in shape. The acrotergite is triangular and the anterior part is protruding and elongated. The medianlongitudinal groove is greatly expanding. The one side of the scutum + scutellum is parallelogram in shape. The alacrista is recognizable on the lateral margin of the medianlongitudinal groove, but the development is confined to the posterior apex to the middle portion. The development of the anterior lobe of metanotum is strongly reduced. The posterolateral scutal area is divided from the scutum by an oblique suture and a deep groove or cleft. The postnotum is usually well-developed.

Members of subfamily Valginae belong to the valgine type. In this, the metanotum is rectangular in shape. The acrotergite is rectangular and the anterior part is protruding and elongated. The medianlongitudinal grove is gradually expanding, and the posterior apex of the scutum and scutellum is separated, respectively. The alacrista is completely lost. The anterior lobe of metanotum is unrecognizable. The posterolateral scutal area is divided from the scutum by an oblique suture and a deep groove. The postnotum is usually well-developed.

Evolution of the metanotal structure and the most ancestral metanotal states in Scarabaeoidea

As mentioned in subchapter (2–3–1), the metanotum is strongly affected by environmental factors and behavioral traits, whereas it a reliable characteristic for estimating the phylogenetic relationships and evolutionary trends. However, since the examination in that subchapter mainly focused on the coprophagous group of Scarabaeidae, only a few species in the phytophagous group of Scarabaeidae and other families of Scarabaeoidea were observed. To estimate the evolutionary trends and phylogenetic relationships, the morphological data of the phytophagous group, member of which show various body shapes and behaviors, as well as of multiple ancestral groups, such as families Glaresidae, Ochodaeidae, and Pleocomidae are indispensable. Based on the present observations and findings reported in subchapter (2–3–1), the following characteristics are crucial for estimating evolutionary trends: shape of the metanotum, shape of the acrotergite, presence of alacrista, presence of the anterior lobe of metanotum, shape of the anterior notal wing process, and posterolateral scutal area.

There are four shapes of the metanotum: dome, rectangle, square, and rhomboidal. A dome-shaped metanotum is observed in members of the families Bolboceratidae, Geotrupidae, Glaphyridae, Hybosoridae, Ochodaeidae, and Pleocomidae, as well as majority of the phytophagous Scarabaeidae [Aclopinae, Dynamopodinae, Dynastinae, Euchirinae, Melolonthinae, Orphninae, Rutelinae, Trichinae (except in the tribe Osmodermini)]. A rectangular metanotum is observed in members of the families Glaresidae, Lucanidae (Aesalinae), and Trogidae, as well as in some subfamilies within Scarabaeidae (Aphodiinae, Scarabaeinae, and Valginae). A square metanotum is observed in some families such as Lucanidae (Syndesinae, Lamprinae, and Lucaninae) and Passalidae. A rhomboidal metanotum is observed only in the subfamily Cetoniinae and tribe Osmodermini. Generally, the families Bolboceratidae, Geotrupidae, Glaresidae, Hybosoridae, Ochodaeidae, Pleocomidae, and Trogidae are treated as the ancestral groups in Scarabaeoidea (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990). Of these, members of families Bolboceratidae, Geotrupidae, Hybosoridae, Ochodaeidae, and Pleocomidae have a dome-shaped metanotum, and this feature is also observed in many derived groups of Scarabaeidae. Therefore, the dome-shaped metanotum may be the most primitive state in the Scarabaeoidea, as observed in several different lineages. In fact, however, a dome-shaped metanotum is considered an intermediate state, while a rectangular metanotum is considered the true primitive state. A rectangular metanotum is observed in the families Glaresidae and Trogidae and the subfamily Aesalinae. Glaresidae is considered to be the most ancestral family within Scarabaeoidea (Scholtz *et al*. 1994, Browne and Scholtz 1999, Scholtz and Grebennikov 2005, Bai *et al*. 2013), and Aesalinae has been proposed as the most primitive group within Lucanidae (Kim and Farrell 2015). Furthermore, rectangular metanotum is observed in Staphylinidae (Naomi 1988), which is placed as the sister group of Scarabaeoidea (McKenna *et al*. 2019), and the most ancestral polyphagan group Scirtidae (Friedrich and Beutel 2006, McKenna *et al*. 2019). In contrast, the features observed only in some groups such as a square or rhomboidal metanotum, may be considerably derived states. Consequently, based on the shape of the metanotum within Scarabaeoidea, rectangular is the primitive state and other remaining characteristics are derived states. Notably, square and rhomboidal metanotum evolved relatively late in certain lineages. A rectangular metanotum is observed in Valginae, which is a highly divergent lineage within Scarabaeidae, however, this is considered to be homoplasy due to convergence.

According to subchapter (2–3–1), the acrotergite are recognized following three types: rectangular and protruding in a trapezoid, triangular and elongated, and rectangular and non-protruding. Among these, a rectangular and non-protruding acrotergite may be the most primitive character state. Examination of the phytophagous group of Scarabaeidae and many other families of Scarabaeoidea also supported that a rectangular and non-protruding acrotergite is the most primitive state. In members of the families Glaresidae, Hybosoridae, Lucanidae (Aesalinae), Ochodaeidae, Passalidae, Trogidae, and Scarabaeidae [Dynamopodinae, Melolonthinae (Sericini), Orphninae, Aphodiinae, Scarabaeinae], the acrotergite is rectangular and protrudes in a trapezoid. In most species of the phytophagous groups of Scarabaeidae [Aclopinae, Cetoniinae, Dynastinae, Euchirinae, Melolonthinae (Diplotaxini, Hopliini, Melolonthini, Rhizotrogini, and Tanyproctini), Rutelinae, Trichinae, and Valginae], the acrotergite is triangular and elongated. Among these, protrusion in Aclopinae, Rutelinae (genera *Parastasia*, *Kibakoganea*, and *Dicaulocephalus*), and Trichinae (genus *Paratrichius*) is very weak. In members of the families Bolboceratidae, Geotrupidae, Glaphyridae, Lucanidae (Syndesinae, Lamprinae, and Lucaninae), and Pleocomidae, the acrotergite is rectangular and non-protruding. Since a rectangular acrotergite with a trapezoidal protrusion is observed in many ancestral groups [Glaresidae, Lucanidae (Aesalinae), Ochodaeidae, Passalidae, and Trogidae], this character state may be considered the most primitive state. Families Glaresidae, Lucanidae, Passalidae, and Trogidae were placed as the basal lineages of Scarabaeoidea in some recent phylogenetic analyses (Smith *et al*. 2006, Bai *et al*. 2013, Ahrens *et al*. 2014, Gunter *et al*. 2016). However, as mentioned in the subchapter (2–3–1), the superfamilies Staphylinoidea and Scirtoidea, which are placed as the sister group of Scarabaeoidea and the most ancestral group within Polyphaga respectively, are represented by the non-protruding state. Therefore, I conclude that the rectangular and non-protruding states is the most primitive. A slightly protruded state is observed in some phytophagous groups such as Aclopinae, Rutelinae (genera *Parastasia*, *Kibakoganea*, and *Dicaulocephalus*), and Trichinae (genus *Paratrichius*), which is probably a further derivative of the triangular and elongated acrotergite.

The primitive and derived characteristics of the alacrista are described in subchapter (2–3–1). The primitive state is represented by the presence of a developed alacrista, while the derived states are represented by other unique features, such as a partial disappearance or complete reduction. Examination based on the phytophagous groups of Scarabaeidae and many other families of Scarabaeoidea also supported findings reported in subchapter (2–3–1). A developed alacrista is observed in most species belonging to Scarabaeoidea, whereas unique character states are observed in only a few groups. In members of the family Pleocomidae and tribe Tanyproctini, the alacrista is clearly recognizable, but the posterior apex does not reach the posterior margin of the metanotum. In members of the subfamily Cetoniinae and tribe Osmodermini, development is limited from the posterior apex to the middle part of the scutum + scutellum. In members of the coprophagous group of Scarabaeidae, the alacrista is remarkably reduced. In members of subfamily Valginae, the alacrista is completely lost. Among these, the completely lost state in Valginae is likely to be the most derived state.

The presence of the anterior lobe of the metanotum has been considered a rather derived state observed only in the phytophagous group of Scarabaeidae, and the complete loss of this lobe in members of the Cetoniinae is considered a secondary atrophied state (subchapter 2–3–1). Based on the present examination of many phytophagous groups, the presence of the anterior lobe of the metanotum is indeed a unique characteristic to these group. However, in the subfamilies Dynamopodinae, Orphninae, and Valginae, this structure is completely lost, as observed in Cetoniinae. Of these, the features observed in the Valginae are considered a secondary atrophied state, similar to that in Cetoniinae. In contrast, the loss in Dynamopodinae and Orphninae is regarded as representing the primitive state in Scarabaeoidea. In recent phylogenetic analyses, the close relationship between Valginae and Cetoniinae has been strongly supported, and both groups are placed within derived lineages (Browne and Scholtz 1998, Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, Šípek *et al*. 2016, Eberte *et al*. 2019). However, Orphninae has been placed within early diverging lineages of the phytophagous group (Browne and Scholtz

1998, Ahrens *et al*. 2014, Neita-Moreno *et al*. 2019). Moreover, Dynamopodinae and Orphninae were previously treated as the family Hybosoridae (Balthasar 1971, Iablokoff-Khnzorian 1977, Paulian 1984, Nikolayev 1993, Scholtz and Grevennikov 2016), which has been placed at intermediate lineage in scarabaeoid clade. Overall, these results indicate that an unrecognizable anterior lobe of metanotum usually indicates a primitive character state, although it is considered to represent a highly derived state in some coprophagous groups.

The shape of the anterior notal wing process represented various character states, which were distinguished into four types: triangular with a straight anterior margin, triangular with a winding anterior margin, trapezoidal, and sharply pointed. In members of the families Bolboceratidae, Glaresidae, Lucanidae (subfamilies Aesalinae and Syndesinae), Ochodaeidae, Pleocomidae, Trogidae, and Scarabaeidae (tribes Diplotaxini, Hopliini, and Sericini), the anterior notal wing process is triangular shape with a straight anterior margin. In members of the families Hybosoridae, Lucanidae (subfamilies Lucaninae and Lamprinae), and Scarabaeidae [subfamilies Aclopinae, Dynamopodinae, Dynastinae, Euchirinae, Melolonthinae (tribes Melolonthini, Rhizotrogini, and Tanyproctini), Orphninae, Rutelinae, and Trichinae (except in the tribe Osmodermini and genus *Lasiotrichius*)], the anterior notal wing process is triangular with a winding anterior margin. In members of the families Geotrupidae, Glaphyridae, and Scarabaeidae [subfamilies Cetoniinae, Trichinae (tribe Osmodermini and genus *Lasiotrichius*), Aphodiinae, and Scarabaeinae], the anterior notal wing process is trapezoidal. In members of the families Passalidae and Scarabaeidae (Valginae), the anterior notal wing process is sharply pointed. Among these, a triangular anterior notal wing process with a straight anterior margin is considered to be the most primitive state. Most families that are characterized by a triangular anterior notal wing process with a straight anterior margin, including families Bolboceratidae, Glaresidae, Hybosoridae, Lucanidae, Ochodaeidae, Pleocomidae, and Trogidae, have traditionally been considered primitive group (Crowson 1981, Lawrence and Newton 1982, Nel and Scholtz 1990, Scholtz 1990), and they have been placed as the basal lineages within Scarabaeoidea in recent phylogenetic analyses (Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, McKenna *et al*. 2015, 2019). In particular, the family Glaresidae has been treated as the most ancestral group within Scarabaeoidea (Scholtz *et al*. 1994, Browne and Scholtz 1999, Scholtz and Grebennikov 2005, Bai *et al*. 2013). Furthermore, Staphylinoidea and Scirtoidea are characterized by a simple triangular anterior notal wing process. As mentioned above, a triangular process with a straight anterior margin is the most primitive character state.

According to subchapter (2–3–1), the posterolateral scutal area can be roughly divided into three types (undivided, divided by an oblique suture and a deep groove, and divided by an oblique suture and a cleft). The undivided state observed in families Glaphyridae, Hybosoridae, and Trogidae is considered to be the most primitive state. Examination based on the phytophagous group and many other families of Scarabaeoidea also supported that an undivided posterolateral scutal area represents the most primitive state, and the posterolateral scutal area divided by an oblique suture and a deep groove or a cleft represent the most recent derived state. The undivided state is observed in families Bolboceratidae, Glaresidae, Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Passalidae, and Trogidae as well as in some groups within Scarabaeidae [Aclopinae, Dynamopodinae, Melolonthinae (tribes Sericini and Hopliini), and Orphninae]. The posterolateral scutal area divided by an oblique suture and a deep groove is observed in families Geotrupidae and Pleocomidae as well as in many groups within Scarabaeidae [Cetoniinae, Dynastinae, Euchirinae, Melolonthinae (tribes Diplotaxini, Melolonthini, Rhizotrogini, and Tanyproctini), Rutelinae, Trichinae, Valginae, and Aphodiinae]. The divided state characterized by an oblique suture and a cleft is observed only in the subfamily Scarabaeinae. Since the families Bolboceratidae, Glaresidae, Lucanidae, Passalidae, and Trogidae diverged early as per recent phylogenetic analyses, the undivided posterolateral scutal area represents a plesiomorphic state. Together, these results suggest that the most ancestral scarabaeoid species exhibit the following characteristics: the metanotum is rectangular in shape, the acrotergite is rectangular and non-protruding, the alacrista is developed, the anterior lobe of metanotum is unrecognizable, the anterior notal wing process is triangular with a straight anterior margin, and the posterolateral scutal area is completely fused with the scutum by reducing the oblique suture.

Phytophagous and coprophagous groups of Scarabaeidae

According to subchapter (2–3–1), the phytophagous and coprophagous groups of Scarabaeidae can be distinguished based on the characteristics of the acrotergite, alacrista, anterior lobe of metanotum, and medianlongitudinal groove. The phytophagous groups are characterized by the following features: acrotergite is triangular and protrudes in an elongated, alacrista is typically strongly developed, anterior lobe of metanotum is well-developed, and medianlongitudinal groove is gradually expanding forward. Conversely, the coprophagous groups are characterized by the following features: acrotergite is rectangular and protrudes in a trapezoid or triangle, alacrista is usually strongly reduced, anterior lobe of metanotum is unrecognizable, medianlongitudinal groove is the widest at the middle part (subchapter 2–3–1). However, in some phytophagous groups, exceptional character states of the acrotergite, alacrista, and anterior lobe of the metanotum were found.

Usually, the acrotergite in the phytophagous groups is triangular and protrudes in an elongated. However, in the subfamilies Dynamopodinae and Orphninae and tribe Sericini, the acrotergite is rectangular and is protruding in a trapezoid. Of these, Orphninae and Sericini represent the early diverging lineage of the phytophagous groups, and the phytophagous group was derived from the family Hybosoridae (Ahrens *et al.* 2014, Mckenna *et al.* 2019), members of which also have a rectangular acrotergite. Therefore, a triangular acrotergite with an elongated protrusion is characteristic to recently derived phytophagous taxa.

A remarkably reduced alacrista was considered to be unique to the coprophagous group (subchapter 2–3–1), however, a similar characteristic, that is complete loss, was found in the subfamily Valginae (Fig. 4B). Despite the similarity in such characteristics, close relationships among these groups have never been indicated in previous studies, although a close relationship between the subfamilies Cetoniinae and Valginae has been strongly supported (Browne and Scholtz 1998, Smith *et al.* 2006, Ahrens *et al.* 2014, Mckenna *et al.* 2015, Gunter *et al.* 2016). Consequently, completely loss of alacrista in Valginae is a derived characteristic from Cetoniinae, in which the alacrista development is limited from the posterior apex to the middle part of the medianlongitudinal groove, and the similarity between the coprophagous group and Valginae is due to convergence.

These results, albeit with some exceptions, generally corroborate findings reported in subchapter (2–3–1), suggesting that the phytophagous and coprophagous groups of Scarabaeidae can be divided based on differences in the acrotergite, alacrista, anterior lobe of the metanotum, and medianlongitudinal groove.

Families Bolboceratidae and Geotrupidae

The family Bolboceratidae had been treated as a subfamily of family Geotrupidae in early studies. However, since the study of Scholtz and Browne (1996), it has been considered as an independent family. In other recent studies, the relationship between Bolboceratidae and Geotrupidae is not supported and a molecular phylogenetic analysis conducted by Ahrens *et al.* (2014) shows the monophyly of the Bolboceratidae. The metanotal characteristics observed in this examination also indicates different features between the Bolboceratidae and Geotrupidae. The Bolboceratidae is characterized by a triangular anterior notal wing process and the undivided posterolateral scutal area, whereas the Geotrupidae is characterized by the trapezoidal anterior notal wing process and divided posterolateral scutal area. Usually, these characteristics are not caused remarkably difference among groups included in single family. This result may indicate that Bolboceratidae and Geotrupidae are positioned in different clade, similar to the hypothesis of Ahrens *et al*. (2014).

Family Glaresidae

The family Glaresidae has been treated as the most ancestral extant scarabaeoid taxon (Scholtz *et al*. 1994) and has been considered to be a sister group of the remaining Scarabaeoidea (Scholtz *et al*. 1994, Browne and Scholtz 1999, Scholtz and Grebennikov 2005, Bai *et al*. 2013). However, a morphological study based on the adult head structure (Anton and Beutel 2012) and a recent phylogenetic analysis (Smith *et al*. 2006) have indicated that the families Glaresidae and Trogidae are sister groups. Meanwhile, in a previous phylogenetic analysis, Ahrens *et al*. (2014) proposed a close relationship between Glaresidae and Lucanidae. The metanotal structures observed in the present examination indicated that Glaresidae, Trogidae, and Lucanidae (subfamily Aesalinae) shared the following characteristics: the metanotum is rectangular, the acrotergite is rectangular and is protruding in a trapezoid, the alacrista is developed, the anterior lobe of metanotum is unrecognizable, the anterior notal wing process is triangular with a straight anterior margin, and the posterolateral scutal area is completely fused with the scutum. All characteristics, except acrotergite shape, are plesiomorphic. Thus, it was difficult to define the close relationships among groups based on these characteristics. However, Glaresidae, Trogidae, and Lucanidae (Aesalinae) are placed as basal divergence lineages within Scarabaeoidea.

Family Hybosoridae, and subfamilies Dynamopodinae and Orphninae

The mesonotal structure in the subfamilies Dynamopodinae and Orphninae presents the same features as that in the family Hybosoridae. Specifically, the metanotum is dome-shaped, the acrotergite is rectangular and is protruding in a trapezoid, the alacrista is developed, the anterior lobe of metanotum is unrecognizable, and the posterolateral scutal area is undivided. Some hypotheses regarding the phylogeny of the subfamily Dynamopodinae have been put forth. According to Fairmaire (1897) placed Dynamopodinae within the subfamily Dynastinae, whereas Balthasar (1971) and Nikolayev (1993) treated it as the family Hybosoridae. Li *et al*. (2019) suggested a close relationship between Dynamopodinae and Pleocomidae. The subfamily Orphninae has been associated with Hybosoridae based on prominent mandibles and labrum (Iablokoff-Khnzorian 1977, Paulian 1984, Scholtz and Grevennikov 2016). The results of the present examination based on the metanotal structure support a close relationship between the family Hybosoridae and subfamilies Dynamopodinae and Orphninae.

Relationship between the subfamilies Rutelinae and Dynastinae

The close relationships between the subfamilies Rutelinae and Dynastinae have been suggested by morphological (Browne and Scholtz 1998) and molecular phylogenetic analyses (Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, Eberle *et al*. 2019). Indeed, the members of Rutelinae and Dynastinae are shared the melolonthine typed mesonotum, however in the tribes Anomalini (genera *Popillia* and *Malaia*) and Rutelini (genera *Parastasia*, *Kibakoganea*, and *Dicaulocephalus*) some of unique character states are observed.

In the genera *Popillia* and *Malaia*, the length-to-width ratio of the metanotum is approximately 1:2, and the posterolateral scutal area is stout with a concave dorsal side. These genera have been considered as belonging to the tribe Anomalini (Smith 2006, Bouchard *et al*. 2011, Krajcik 2012, Bezděk *et al*. 2016, Scholtz and Grebennikov 2016), however in the Scholtz (1990) who examined the karyotype, *Popillia* had different states from other species of the Anomalini. The metanotal structures also suggested the specificity of the *Popillia* and *Malaia*.

In the genera *Parastasia*, *Kibakoganea*, and *Dicaulocephalus*, the acrotergite is triangular but the anterior part is non-protruding. These genera have been considered as belonging to the subfamily Rutelinae (Smith 2006, Bouchard *et al*. 2011, Krajcik 2012, Bezděk *et al*. 2016, Scholtz and Grebennikov 2016), but Smith *et al*. (2006) and Wada (2015) suggested that the genus *Parastasia* is firmly placed in the subfamily Dynastinae. These observational results show that the above genera have some little different features from other members of the tribe Rutelini and may need to be moved to another group. However, the close relationship between genus *Parastasia* and subfamily Dynastinae were not well supported.

Relationships between the subfamilies Cetoniinae, Trichinae, and Valginae

The subfamilies Cetoniinae, Trichinae, and Valginae are often treated as a single subfamily Cetoniinae (Ahrens *et al*. 2014, Bezděk 2016, Šípek *et al*. 2016). However, the characteristics of the metanotum were observed remarkably differences among subfamilies (Figs. 2B, 3H, 4B). Consequently, my observational results in the metanotum conclude that Cetoniinae, Trichinae, and Valginae should be treated as independent subfamilies. Moreover, unique characteristics were observed in tribe Osmodermini within subfamily Trichinae.

The tribe Osmodermini has been regarded as one of the tribes in subfamily Trichinae (Krikken 1984, Krajcik 2012). However, many recent phylogenetic studies have indicated a close relationship between subfamily Cetoniinae (Micó *et al*. 2008, Šípek *et al*. 2009, Šípek *et al*. 2011, Šípek *et al*. 2016), since Browne and Scholtz (1998) suggested that the tribe Osmodermini is the sister group of Cetoniinae. The metanotal structures are also support the close relationships to the Cetoniinae.

Subfamily Melolonthinae

The subfamily Melolonthinae is poorly defined, and several groups have been included and excluded at various stages by different authors. For example, tribe Hopliini is treated as the scarabaeid subfamily Hoplinae in Nel and De Villiers (1988), d'Hotman and Scholtz (1990b), Nel and Scholtz (1990) and Pretorius and Scholtz (2001), and the Sericini is considered as the scarabaeid subfamily Sericinae in Ritcher (1969a) and Coca-Abia (2007). Moreover, phylogenetic analyses have shown that Melolonthinae is polyphyletic (Browne and Scholtz 1998, Ahrens 2005, Smith *et al*. 2006, Ahrens *et al*. 2014, Gunter *et al*. 2016, Šípek *et al*. 2016, Eberte *et al*. 2019). Thus, remarkable variation in the metanotum has been observed. These variations are loosely categorized into two types as melolonthine and sericine types, and there were some groups within the melolonthine type showed unique characteristics. In the members of the tribes Melolonthini and Rhizotrogini, the first phragma is characterized by a V-shaped sclerotized ridge in the middle part. In the members of the tribe Tanyproctini, the posterior apex of the alacrista does not reach the posterior margin of metanotum, which is similar to the characteristic in the family Pleocomidae.

Subfamily Aclopinae

The systematic position of the subfamily Aclopinae remains largely unknown. Erichson (1845–1847) treated it as the family Glaphyridae, while Lacordaire (1856) suggested that Aclopinae should be moved to Melolonthinae based on the position of the spiracles. According to Scholtz and Grebennikov (2016), Aclopinae resembles Hybosoridae based on prominent mandibles and labrum.

The metanotal structures of Aclopinae are belong to the melolonthine type. The presence of a developed anterior lobe of the metanotum is an autapomorphic character observed only in the phytophagous groups of Scarabaeidae. Consequently, it is considered that Aclopinae is closely related to the phytophagous groups.

Systematic position of the subfamily Euchirinae

The systematic position of Euchirinae is established various hypotheses by some literatures. Young (1989) conducted the most detailed recent study of the subfamily, treating it as one of scarabaeid subfamily. Ahrens (2005) suggested a slight the relationship with subfamily Dynastinae (genus *Oryctes*). Šípek *et al*. (2009) mentioned that the subfamily is positioned as a sister group of pleurostict scarabs (Rutelinae, Dynastinae, Melolonthinae, and Cetoniinae), however in Šípek *et al*. (2011) Euchirinae is placed on a sister group of the clade Rutelinae + Dynastinae + Melolonthinae. Ahrens *et al*. (2014) indicated that Euchirinae is related to the tribes Hopliini and Macrodactylini.

The metanotal structure of Euchirinae is similar to characteristics of the melolonthine typed metanotum, which including subfamilies Dynastinae and Rutelinae. This similarity is may indicate to closely relation of those groups.

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Bolboceratidae	Bolboceratinae	Bolbelasmini	*Bolbelasmus* (*Kolbeus*) *minutus* Li et Masumoto, 2008
		Bolbochromini	*Bolbocerodema nigroplagiatum* (Waterhouse, 1875)
			Bolbochromus ryukyuensis Masumoto, 1984
Geotrupidae	Geotrupinae	Chromogeotrupini	*Enoplotrupes sharpi* Rothschild & Jordan, 1893
		Enoplotrupini	*Phelotrupes* (*Chromogeotrupes*) *auratus auratus* (Motschulsky, 1858)
			Phelotrupes (*Eogeotrupes*) *laevistriatus* (Motschulsky, 1866)
	Lethrinae		*Lethrus* (*Mesolethrus*) *microbuccis* Ballion, 1870
			Lethrus (*Ceratodirus*) *karelini* Gebler, 1845
			Lethrus (*Paralethrus*) *bituberculatus* Ballion, 1870
Glaresidae			*Glaresis beckeri* Solsky, 1870
Glaphyridae	Amphicominae		*Amphicoma pectinata* (Lewis, 1895)
			Amphicoma splendens (Yawata, 1942)
			Eulasia (*Trichopleurus*) *vittata* (Fabricius, 1775)
			Pygopleurus vulpes (Fabricius, 1781)
Hybosoridae	Ceratocanthinae	Ceratocanthini	*Madrasostes hisamatsui* Ochi, 1990
	Hybosorinae		*Phaeochrous emarginatus emarginatus* Laporte, 1840
			Phaeochroops sp.
Lucanidae	Aesalinae	Aesalini	*Aesalus asiaticus asiaticus* Lewis, 1883
		Nicagini	*Nicagus japonicus* Nagel, 1928
	Syndesinae		*Ceruchus lignarius lignarius* Lewis, 1883
	Lampriminae		*Lamprima adolphinae* (Gestro, 1875)
	Lucaninae	Lucanini	*Dorcus rectus rectus* (Motschulsky, 1858)
			Figulus binodulus Waterhouse, 1873
			Figulus punctatus Waterhouse, 1873
			Lucanus maculifemoratus maculifemoratus Motschulsky, 1861
			Prismognathus dauricus (Motschulsky, 1860)
			Prosopocoilus inclinatus inclinatus (Motschulsky, 1858)
		Platycerini	*Platycerus acuticollis* Y. Kurosawa, 1969
Ochodaeidae	Ochodaeinae	Ochodaeini	*Codocera ferruginea* (Eschscholtz, 1818)
			Notochodaeus maculatus maculatus (Waterhouse, 1875)
			Ochodaeus chrysomeloides (Schrank, 1781)
Passalidae	Aulacocyclinae	Ceracupini	*Ceracupes chingkini* Okano, 1988
			Cylindrocaulus patalis (Lewis, 1883)
	Macrolininae		*Macrolinus sikkimensis* Stoliczka, 1873
Pleocomidae			*Pleocoma dubitabilis dubitabilis* Davis, 1935
Trogidae	Troginae		*Glyptotrox uenoi uenoi* (Nomura, 1961)
			Omorgus (*Afromorgus*) *chinensis* (Boheman, 1858)
			Trox (*Niditrox*) *niponensis* Lewis, 1895

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Scarabaeidae	Aclopinae		*Pachypus candidae* (Petagna, 1787)
	Cetoniinae	Cetoniini	*Cetonia* (*Eucetonia*) *roelofsi roelofsi* Harold, 1880
			Gametis forticula forticula (Janson, 1881)
			Gametis jucunda (Faldermann, 1835)
			Glycyphana (*Glycyphana*) *fulvistemma* Motschulsky, 1860
			Protaetia (*Liocola*) *brevitarsis brevitarsis* (Lewis, 1879)
			Protaetia (*Calopotosia*) *orientalis submarmorea* (Burmeister, 1842)
		Cremastocheilini	*Clinterocera jucunda* (Westwood, 1874)
		Diplognathini	*Anthracophora rusticola* Burmeister, 1842
		Goliathini	*Cosmiomorpha* (*Microcosmiomorpha*) *similis nigra* Niijima & Kinoshita, 1927
			Dicronocephalus wallichi Hope, 1831
			Pseudotorynorrhina japonica (Hope, 1841)
			Rhomborhina (*Rhomborhina*) *polita* Waterhouse, 1875
			Rhomborhina (*Rhomborhina*) *unicolor unicolor* Motschulsky, 1861
		Taenioderini	*Coilodera pseudoalveata* (Miksic, 1971)
	Dynamopodinae		*Orubesa ata* Semenov & Medvedev, 1929
	Dynastinae	Dynastini	*Dynastes tityus* (Linnaeus, 1763)
			Trypoxylus dichotomus septentrionalis Kôno, 1931
			Xylotrupes gideon (Linnaeus, 1767)
		Oryctini	*Oryctes rhinoceros* (Linnaeus, 1758)
		Pentodontini	*Alissonotum pauperum* (Burmeister, 1847)
		Phileurini	*Eophileurus chinensis* (Faldermann, 1835)
	Euchirinae	Euchirini	*Cheirotonus peracanus* Kriesche, 1919
			Euchirus longimanus Linnaeus, 1758
	Melolonthinae	Diplotaxini	*Apogonia bicarinata* Lewis, 1896
			Apogonia ishiharai Sawada, 1940
			Apogonia kamiyai Sawada, 1940
		Hoplini	*Ectinohoplia obducta* (Motschulsky, 1857)
			Hoplia communis Waterhouse, 1875
			Pachycnema sp.
		Melolonthini	*Melolontha* (*Melolontha*) *frater frater* Arrow, 1913
			Melolontha (*Melolontha*) *japonica* Burmeister, 1855
			Polyphylla (*Granida*) *albolineata* (Motschulsky, 1861)
			Polyphylla (*Gynexophylla*) *laticollis laticollis* Lewis, 1887
		Rhizotrogini	*Nigrotrichia kiotoensis* (Brenske, 1894)
			Pollaplonyx flavidus Waterhouse, 1875
			Pedinotrichia picea (Waterhouse, 1875)
			Sophrops konishii konishii Nomura, 1970
		Sericini	*Maladera* (*Omaladera*) *orientalis* (Motschulsky, 1860)
			Maladera (*Aserica*) *secreta secreta* (Brenske, 1897)
			Serica boops Waterhouse, 1875
			Sericania hidana Niijima & Kinoshita, 1923
		Tanyproctini	*Tanyproctus* sp.
	Orphninae	Orphnini	*Orphnus* sp.

Table 1. Examined species of Scarabaeoidea.

Family	Subfamily	Tribe	Species
Scarabaeidae	Rutelinae	Adoretini	*Adoretus falciungulatus* Nomura, 1965
			Adorodocia vittaticollis Fairmaire, 1883
			Chaetadoretus formosanus sakishimanus Kobayashi, 1982
			Lepadoretus sinicus (Burmeister, 1855) Burmeister, 1855
			Lepadoretus tenuimaculatus (Waterhouse, 1875)
		Anastatini	*Spodochlamys cupreola* Bates, 1888
		Anoimalini	*Anomala albopilosa albopilosa* (Hope, 1839)
			Anomala edentula yaeyamana (Nomura, 1965)
			Anomala octiescostata (Burmeister, 1844)
			Exomala conspurcata (Harold, 1878)
			Exomala orientalis (Waterhouse, 1875)
			Malaia nigrita (Boisduval, 1835)
			Mimela confucius ishigakiensis Sawada, 1950
			Mimela splendens (Gyllenhal, 1817)
			Mimela testaceipes (Motschulsky, 1860)
			Popillia japonica Newman, 1838
			Popillia lewisi Arrow, 1913
			Popillia mutans Newman, 1838
			Phyllopertha diversa Waterhouse, 1875
			Phyllopertha intermixta (Arrow, 1913)
			Spilopopillia sexguttata (Fairmaire, 1887)
		Anoplognathini	*Anoplognathus brunnipennis* (Gyllenhal, 1817)
			Anoplognathus prasinus (Castelnau, 1840)
			Calloodes rayneri Mac Leay, 1864
			Repsimus manicatus manicatus (Swartz, 1817)
		Rutelini	*Chrysophora chrysochlora* (Latreille, 1812)
			Dicaulocephalus feae Gestro, 1888
			Kibakoganea tamdaoensis Miyake & Muramoto, 1992
			Parastasia ferrieri ferrieri Nonfried, 1895
			Parastasia sp.1 Westwood, 1841
			Pelidnota prasina Burmeister, 1844
			Pelidnota punctate (Linnaeus, 1758)
	Trichinae	Osmodermini	*Osmoderma opicum* Lewis, 1887
		Trichini	*Corynotrichius bicolor* Kolbe, 1892
			Epitrichius elegans Kano, 1931
			Gnorimus subopacus Motschulsky, 1860
			Lasiotrichius succinctus succinctus (Pallas, 1781)
			Paratrichius doenitzi (Harold, 1879)
			Trichius fasciatus (Linnaeus, 1758)
			Trichius japonicus Janson, 1885
		Incaini	*Inca bonplandi* (Gyllenhal, 1817)
	Valginae	Valgini	*Dasyvalgus tuberculatus* (Lewis, 1887)
			Neovalgus fumosus (Lewis, 1887)
			Nipponovalgus angusticollis angusticollis (Waterhouse, 1875)
			Nipponovalgus yonakuniensis Sawada, 1941
		Microvalgini	*Microvalgus* sp.
	Aphodiinae	Aphodiini	*Aphodius* (*Brachiaphodius*) *eccoptus* Bates, 1889
	Scarabaeinae	Coprini	*Copris* (*Copris*) *ochus* (Motschulsky, 1860)

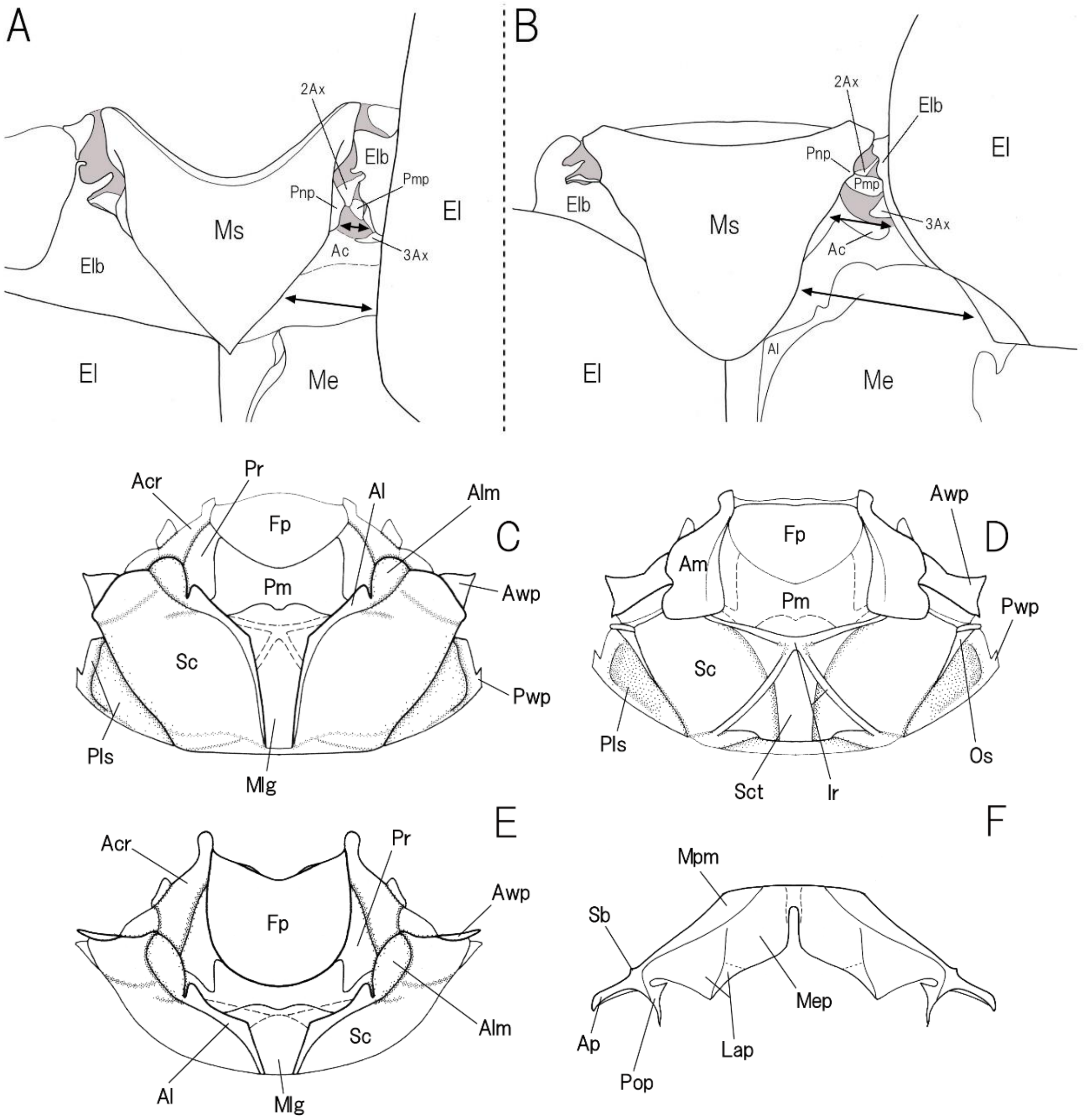


Figure 1. The position of the metanotum in Scarabaeoidea **A** *Copris ochus* (Motschulsky) **B** *Melolontha frater frater* Arrow **C−F** Schematics diagram of metanotum: **C** Dorsal **D** Ventral **E** Frontal **F** Postnotum. Abbreviations: acrotergite **(Acr)**; alacrista **(Al)**; anterior lobe of metanotum **(Alm)**; anterior muscle disc **(Am)**; anterior notal wing process **(Awp)**; anterior postnotal process **(Ap);** axillary cord **(Ac)**; elytral base **(Elb)**; elytron **(El)**; first phragma **(Fp)**; internal ridge **(Ir)**; laterophragmite **(Lap)**; median longitudinal groove **(Mlg)**; median postnotum **(Mpm)**; mediophragmite **(Mep);** mesonotum **(Ms)**; metanotum **(Me)**; oblique suture **(Os)**; posterior notal wing process **(Pwp)**; postmedian notal process **(Pnp)**; posterolateral scutal area **(Pls)**; prescutal membrane **(Pm)**; prescutum **(Pr)**; proximal median plate **(Pmp)**; posterior postnotal process **(Pop)**; scutellum **(Sct)**; scutum **(Sc)**; subalar tendon **(Sb)**; second axillary sclerite **(2Ax)**; third axillary screlite **(3Ax)**. The membranous parts are painted gray, and the fixed parts between the mesonotum and elytron are showed by arrow.

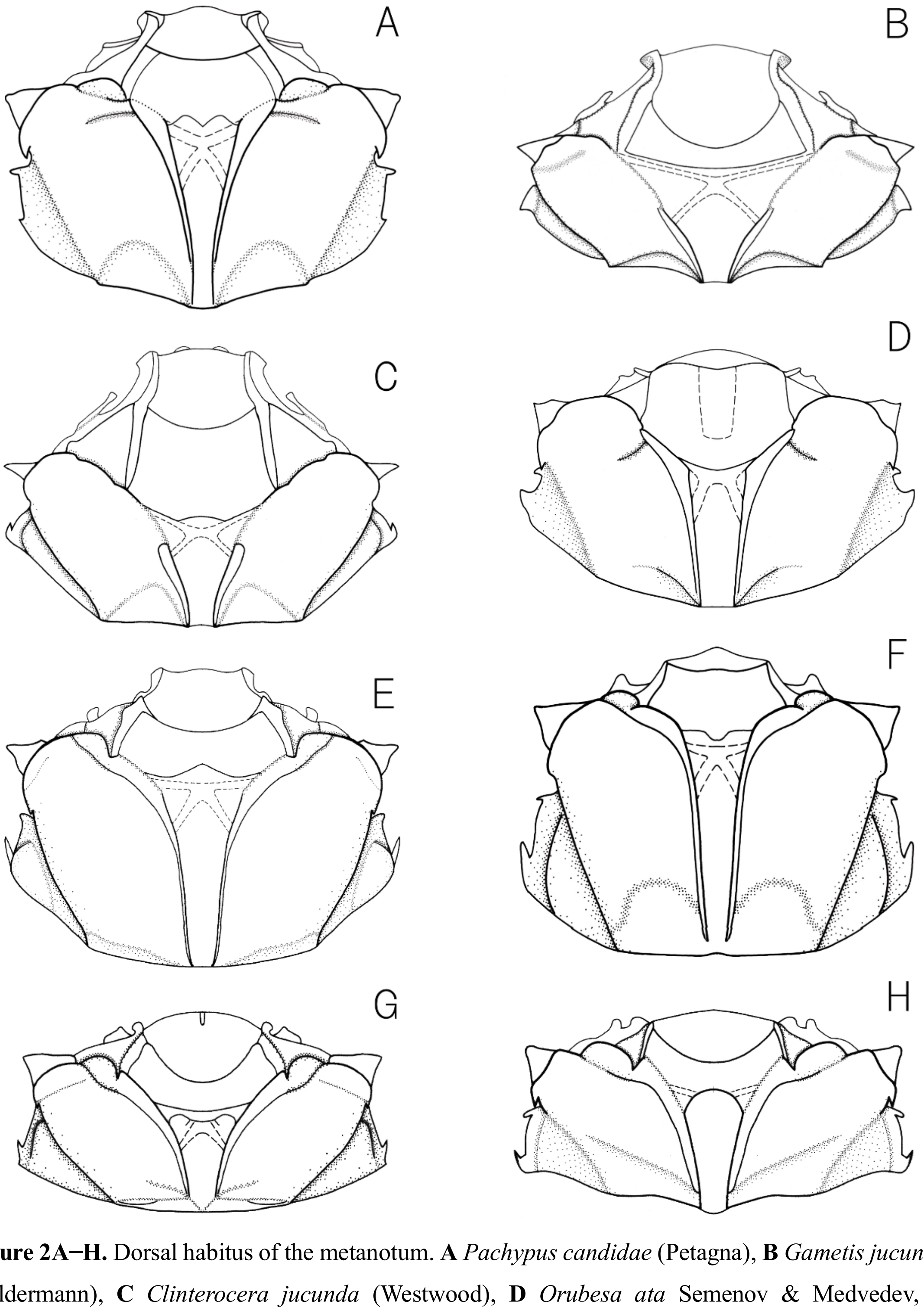


Figure 2A–H. Dorsal habitus of the metanotum. **A** *Pachypus candidae* (Petagna), **B** *Gametis jucunda* (Faldermann), **C** *Clinterocera jucunda* (Westwood), **D** *Orubesa ata* Semenov & Medvedev, **E** *Trypoxylus dichotomus septentrionalis* Kôno, **F** *Euchirus longimanus* Linnaeus, **G** *Apogonia bicarinata* Lewis, **H** *Maladera* (*Omaladera*) *orientalis* (Motschulsky).

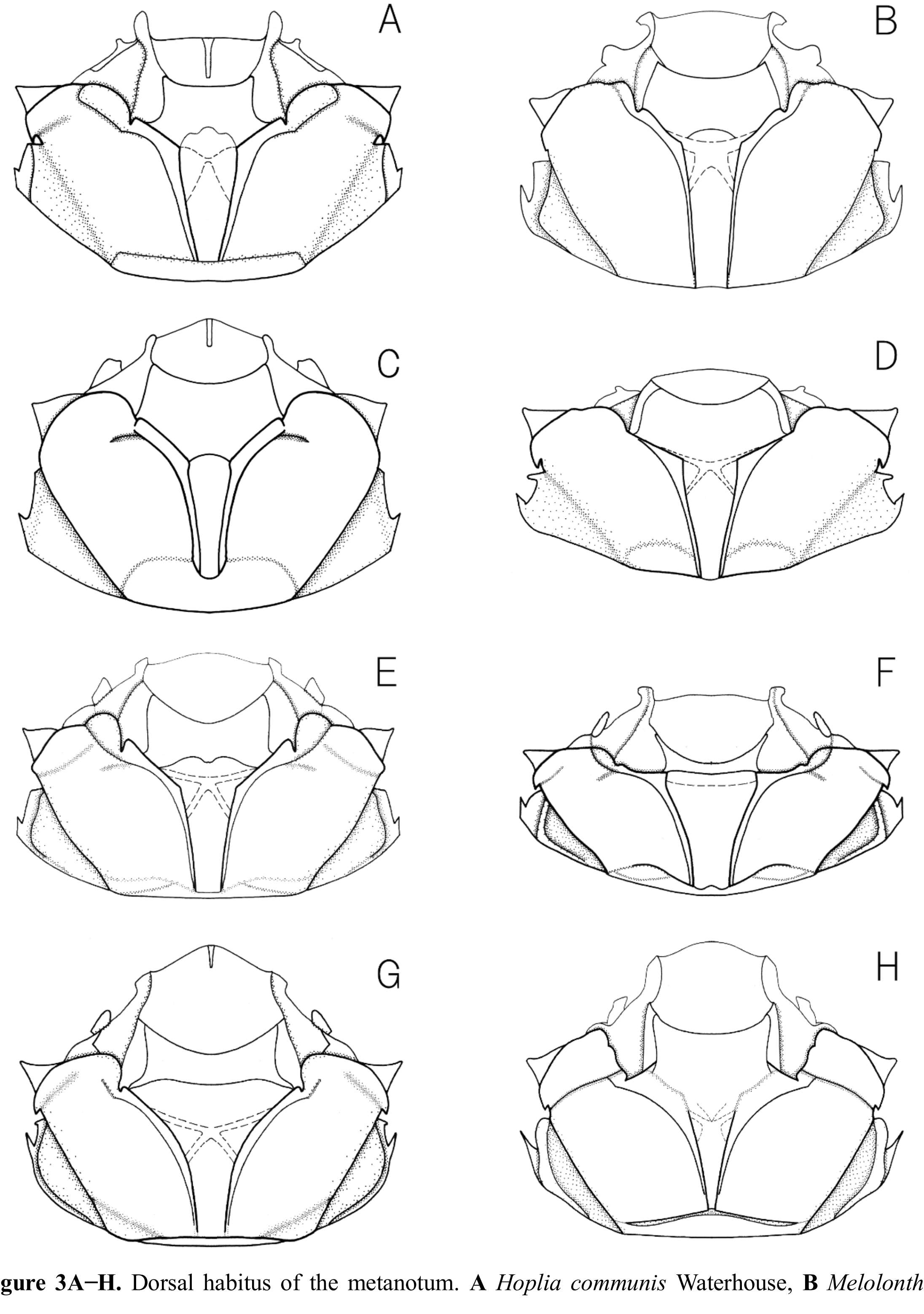


Figure 3A−H. Dorsal habitus of the metanotum. **A** *Hoplia communis* Waterhouse, **B** *Melolontha* (*Melolontha*) *japonica* Burmeister, **C** *Tanyproctus* sp., **D** *Orphnus* sp., **E** *Mimela splendens* (Gyllenhal), **F** *Popillia japonica* Newman, **G** *Parastasia ferrieri* Nonfried, **H** *Paratrichius doenitzi* (Harold).

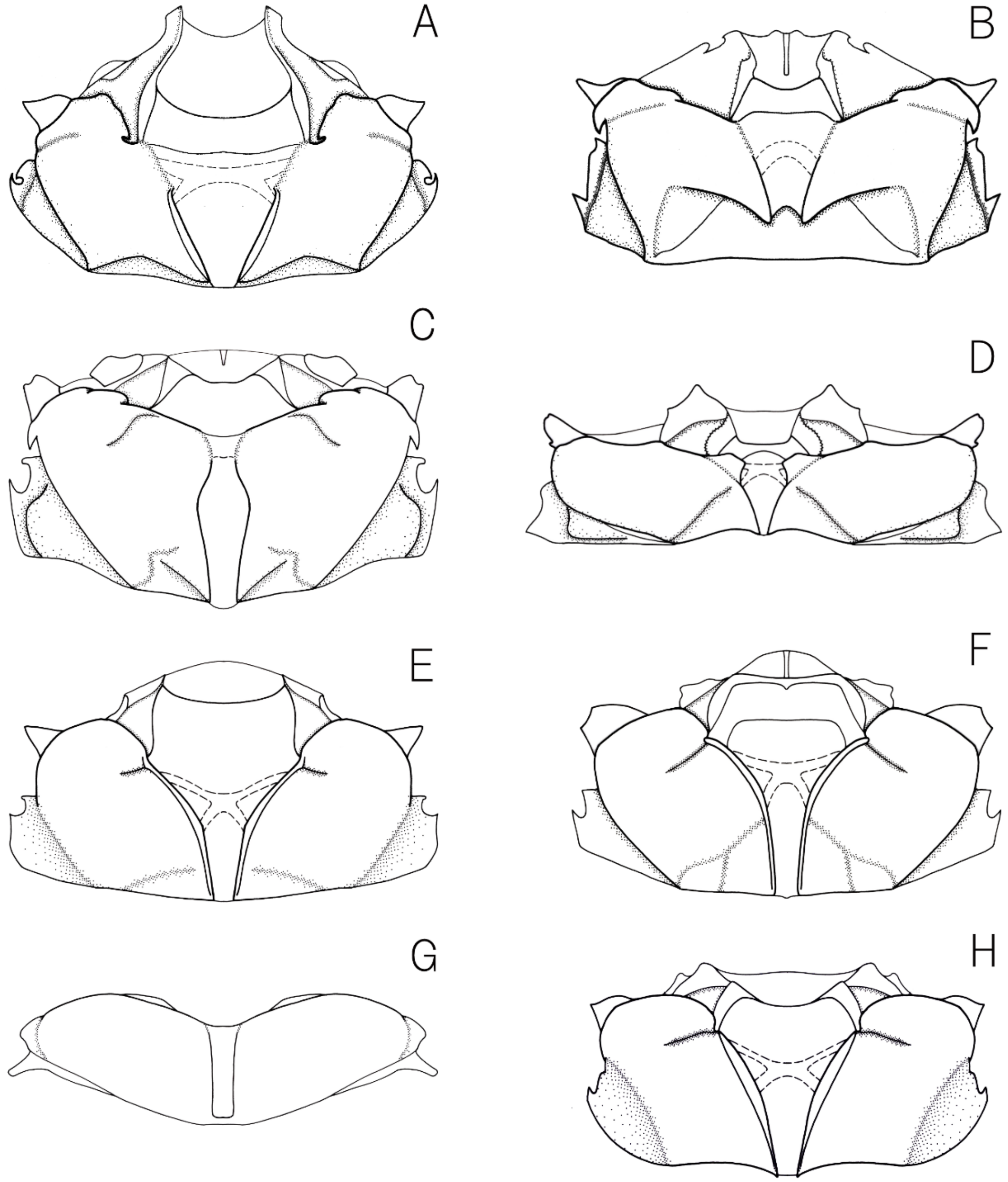


Figure 4A–H. Dorsal habitus of the metanotum. **A** *Osmoderma opicum* Lewis, **B** *Nipponovalgus angusticollis* (Waterhouse), **C** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates, **D** *Copris* (*Copris*) *ochus* (Motschulsky), **E** *Bolbocerodema nigroplagiatum* (Waterhouse), **F** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky), **G** *Lethrus* (*Paralethrus*) *bituberculatus* Ballion, **H** *Glaresis beckeri* Solsky.

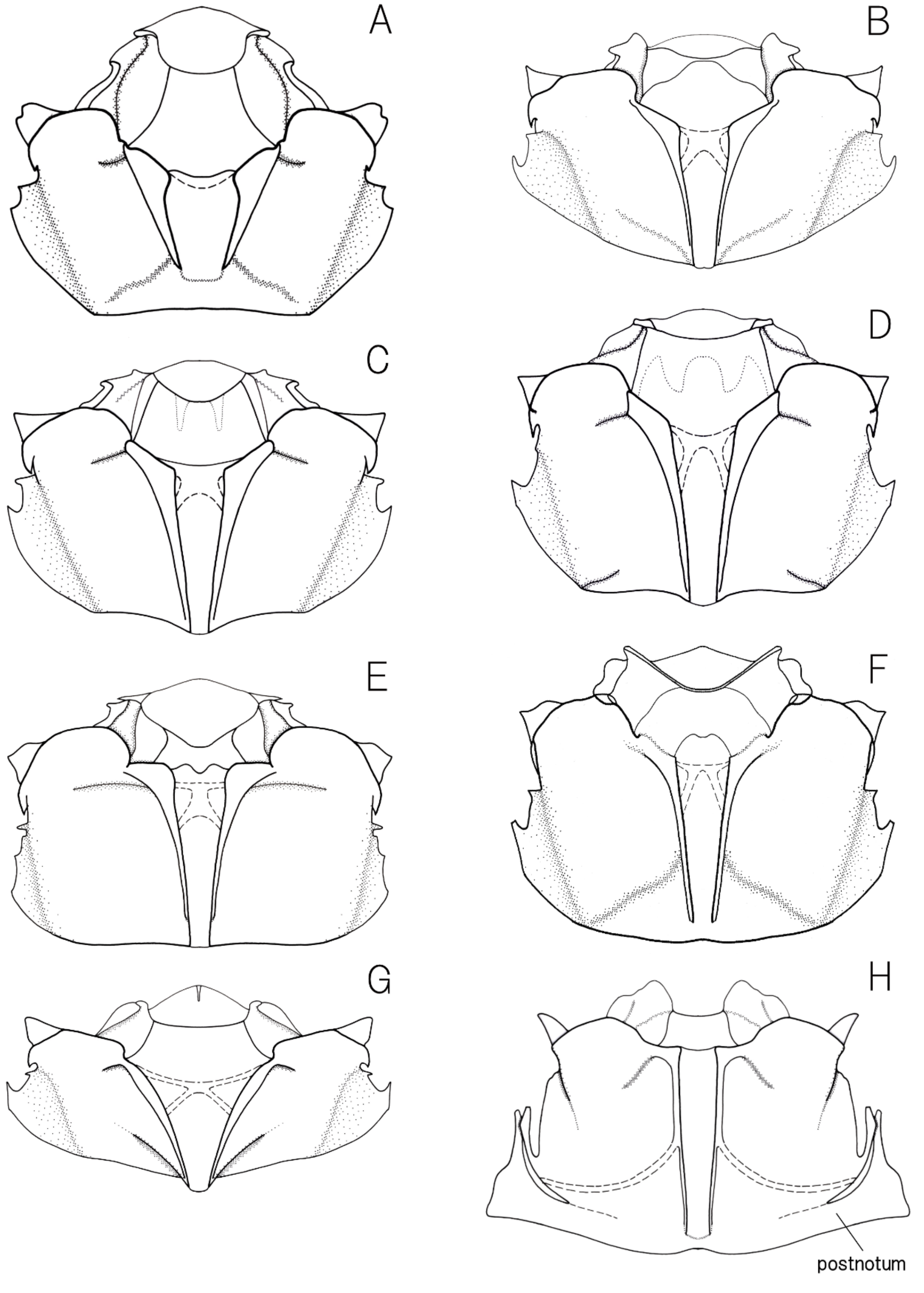


Figure 5A−H. Dorsal habitus of the metanotum. **A** *Amphicoma splendens* (Yawata), **B** *Phaeochrous emarginatus* Laporte, **C** *Nicagus japonicus* Nagel, **D** *Ceruchus lignarius* Lewis, **E** Lamprima adolphinae (Gestro), **F** *Lucanus maculifemoratus* Motschulsky, **G** *Notochodaeus maculatus* (Waterhouse), **H** *Macrolinus sikkimensis* Stoliczka.

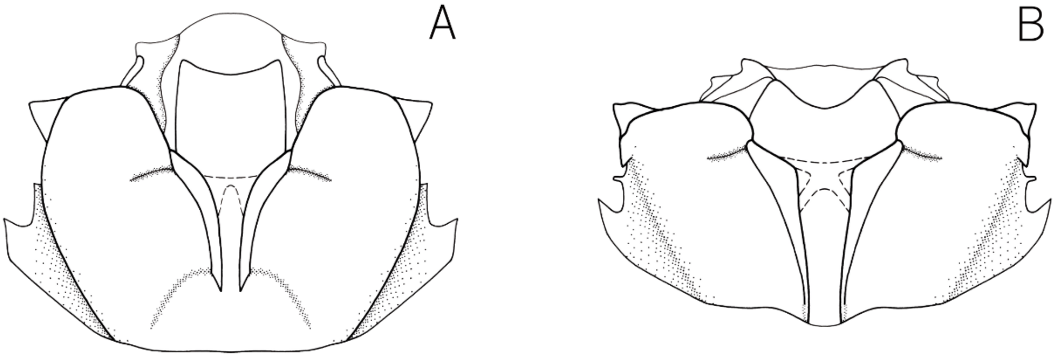


Figure 6A−B. Dorsal habitus of the metanotum. **A** *Pleocoma dubitabilis* Davis, **B** *Glyptotrox uenoi* (Nomura).

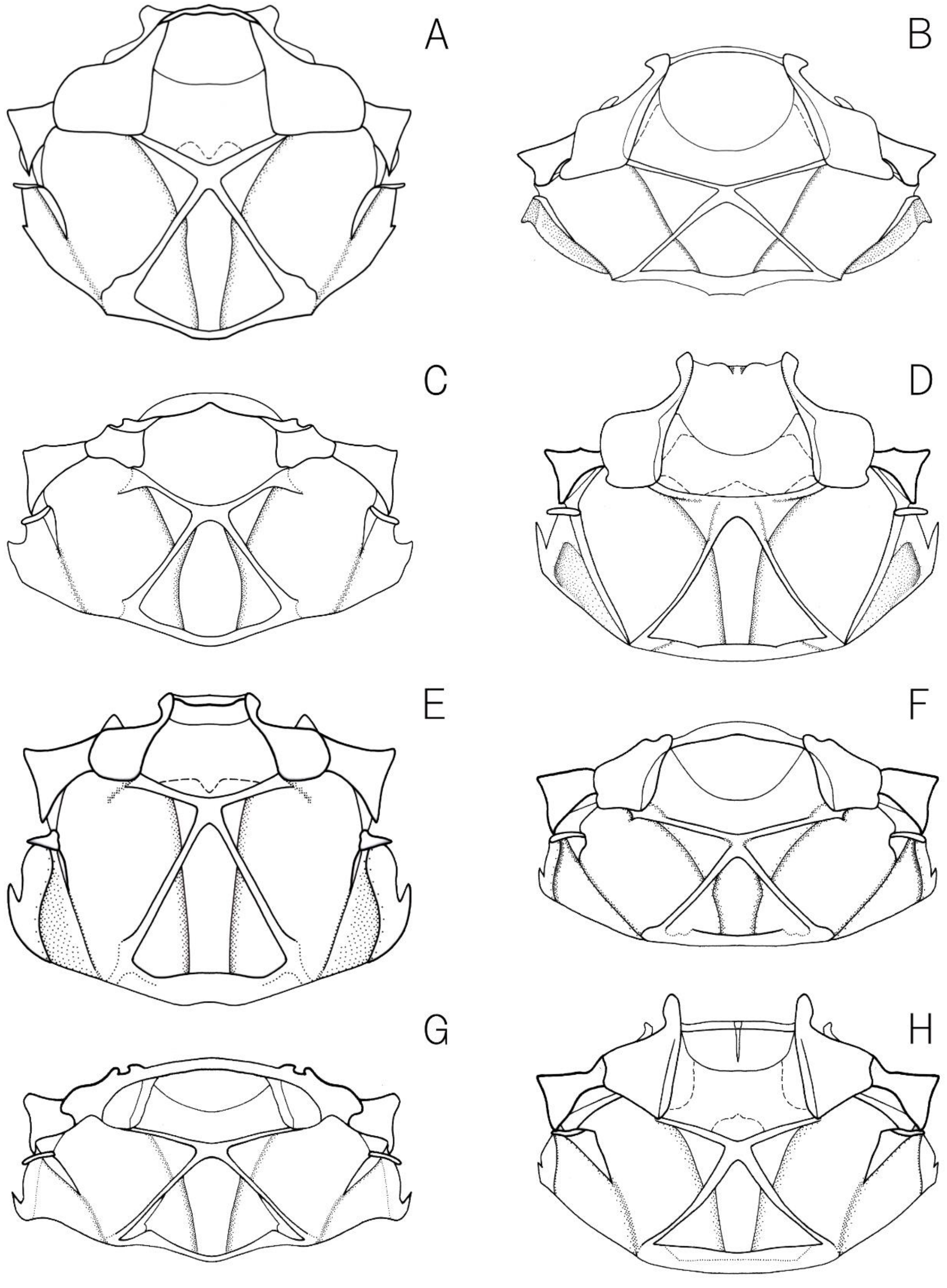


Figure 7A−H. Ventral habitus of the metanotum. **A** *Pachypus candidae* (Petagna, 1787), **B** *Gametis jucunda* (Faldermann), **C** *Orubesa ata* Semenov & Medvedev, **D** *Trypoxylus dichotomus* Kôno, **E** *Euchirus longimanus* Linnaeus, **F** *Apogonia bicarinata* Lewis, **G** *Maladera* (*Omaladera*) *orientalis* (Motschulsky), **H** *Hoplia communis* Waterhouse.

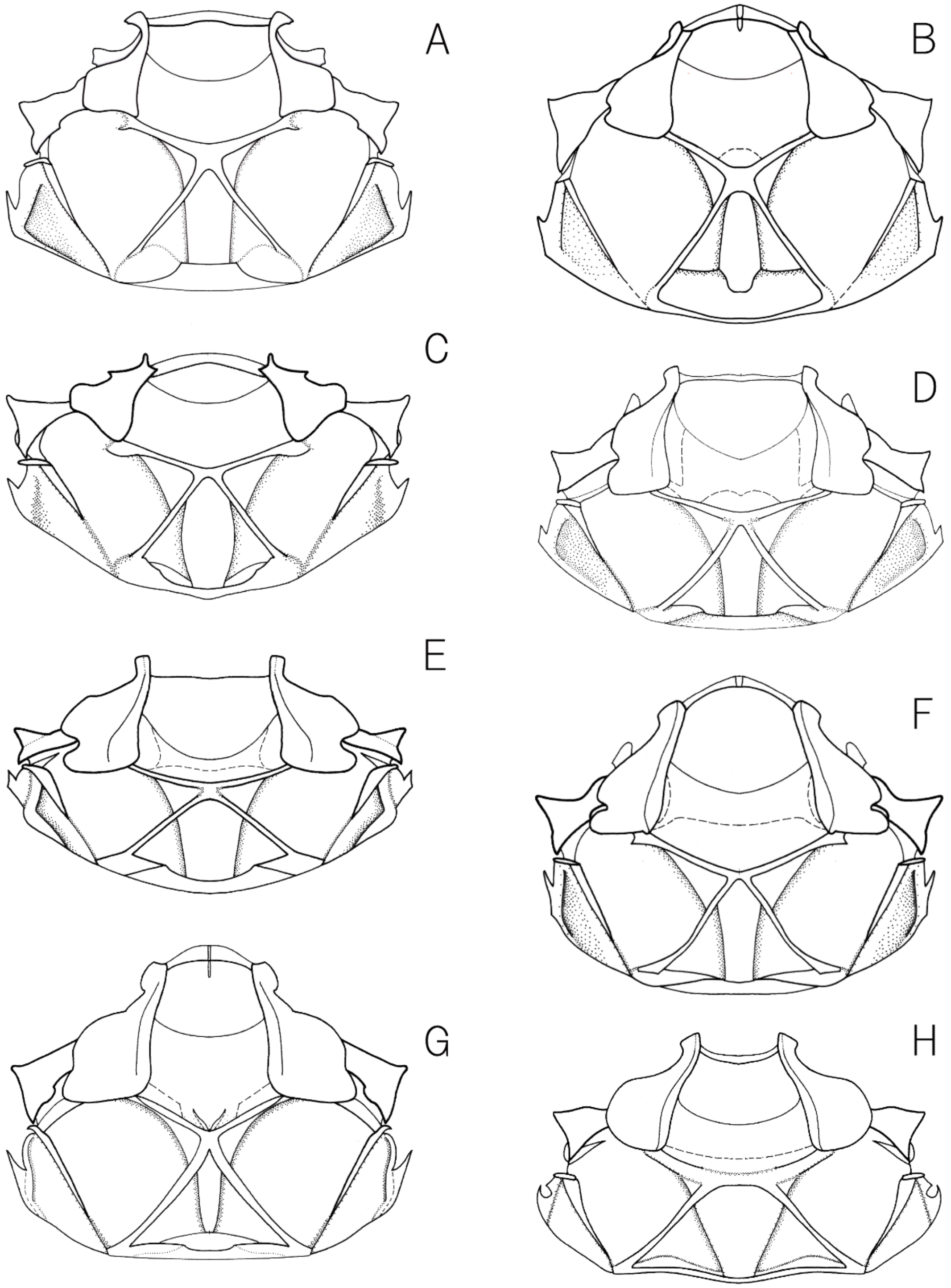


Figure 8A–H. Ventral habitus of the metanotum. **A** *Melolontha* (*Melolontha*) *japonica* Burmeister, **B** *Tanyproctus* sp., **C** *Orphnus* sp., **D** *Mimela splendens* (Gyllenhal), **E** *Popillia japonica* Newman, **F** *Parastasia ferrieri* Nonfried, **G** *Paratrichius doenitzi* (Harold), **H** *Osmoderma opicum* Lewis.

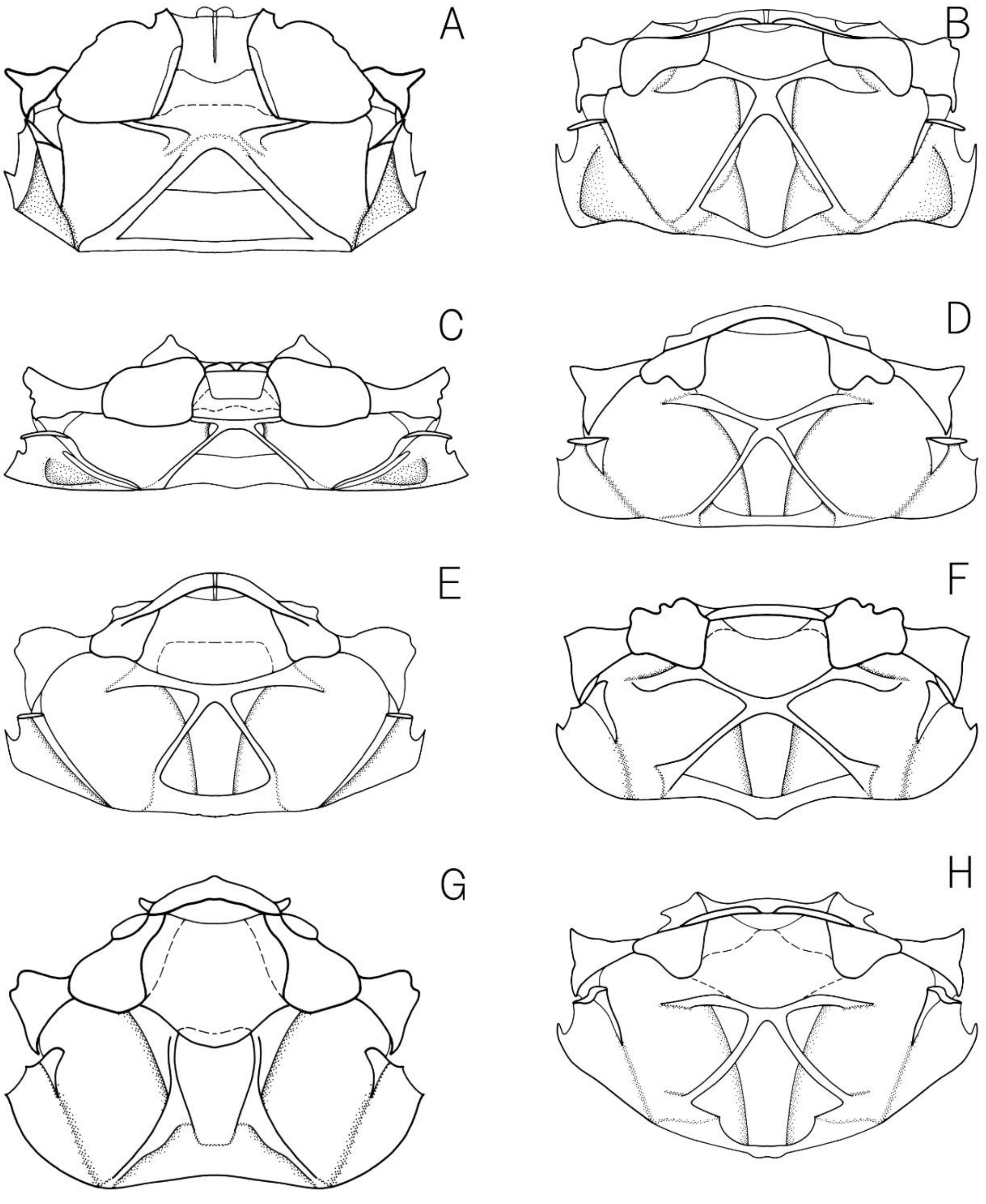


Figure 9A−H. Ventral habitus of the metanotum. **A** *Nipponovalgus angusticollis* (Waterhouse), **B** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates, **C** *Copris* (*Copris*) *ochus* (Motschulsky), **D** *Bolbocerodema nigroplagiatum* (Waterhouse), **E** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky), **F** *Glaresis beckeri* Solsky, **G** *Amphicoma splendens* (Yawata), **H** *Phaeochrous emarginatus* Laporte.

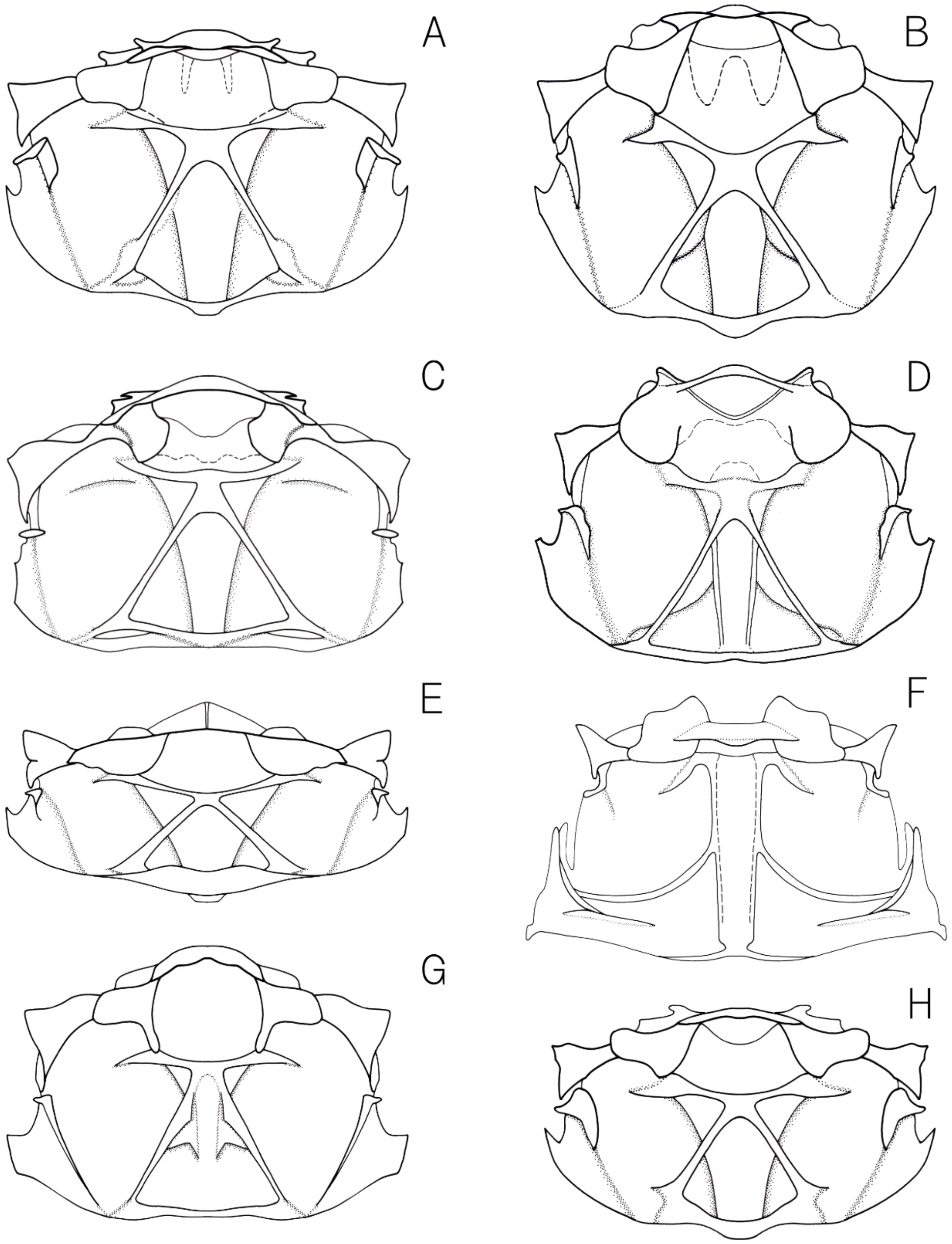


Figure 10A–H. Ventral habitus of the metanotum. **A** *Nicagus japonicus* Nagel, **B** *Ceruchus lignarius* Lewis, **C** *Lamprima adolphinae* (Gestro), **D** *Lucanus maculifemoratus* Motschulsky, **E** *Notochodaeus maculatus* (Waterhouse), **F** *Macrolinus sikkimensis* Stoliczka, **G** *Pleocoma dubitabilis* Davis, **H** *Glyptotrox uenoi* (Nomura).

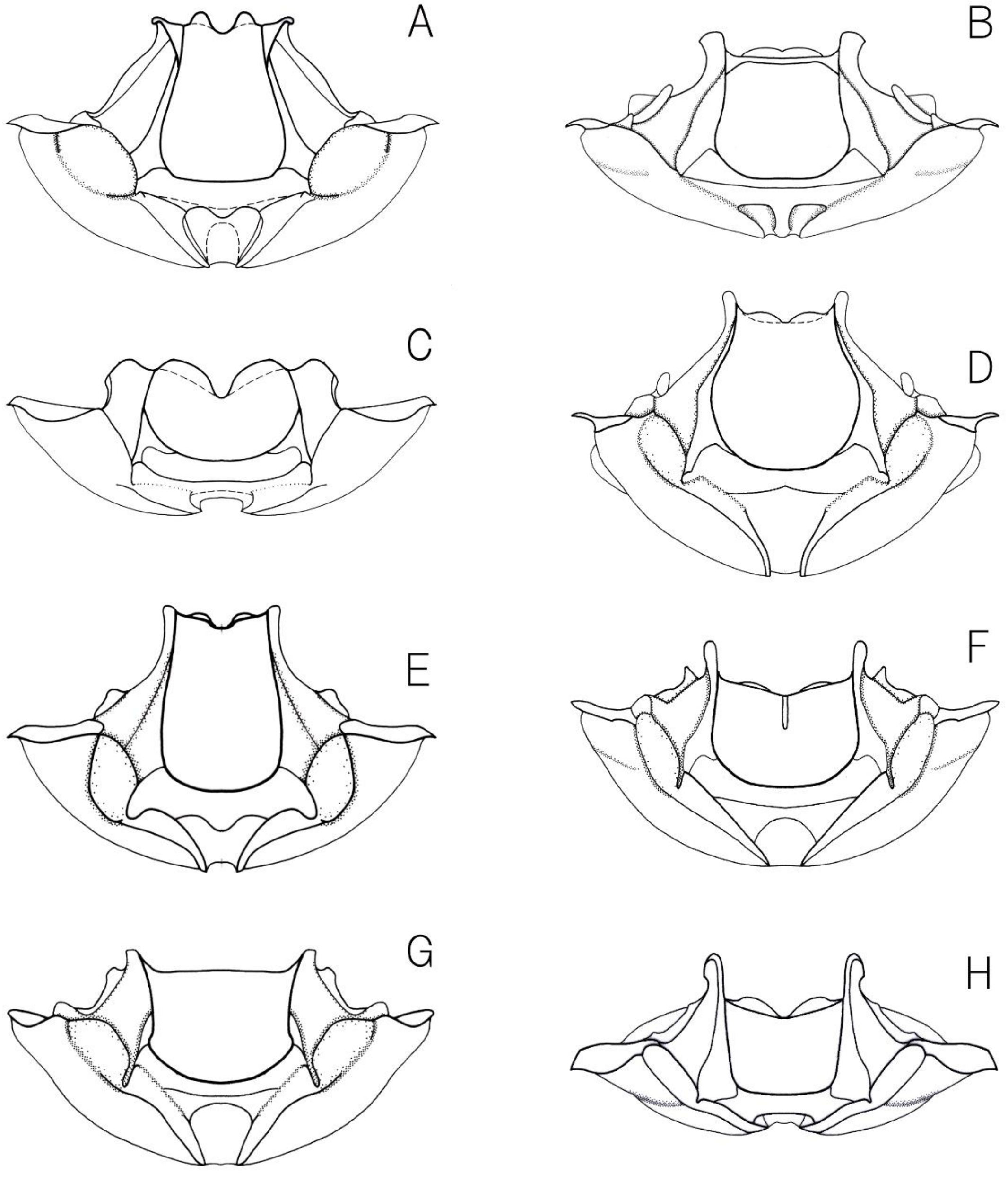


Figure 11A−H. Frontal habitus of the metanotum. **A** *Pachypus candidae* (Petagna), **B** *Gametis jucunda* (Faldermann), **C** *Orubesa ata* Semenov & Medvedev, **D** *Trypoxylus dichotomus* Kôno, **E** *Euchirus longimanus* Linnaeus, **F** *Apogonia bicarinata* Lewis, **G** *Maladera* (*Omaladera*) *orientalis* (Motschulsky), **H** *Hoplia communis* Waterhouse.

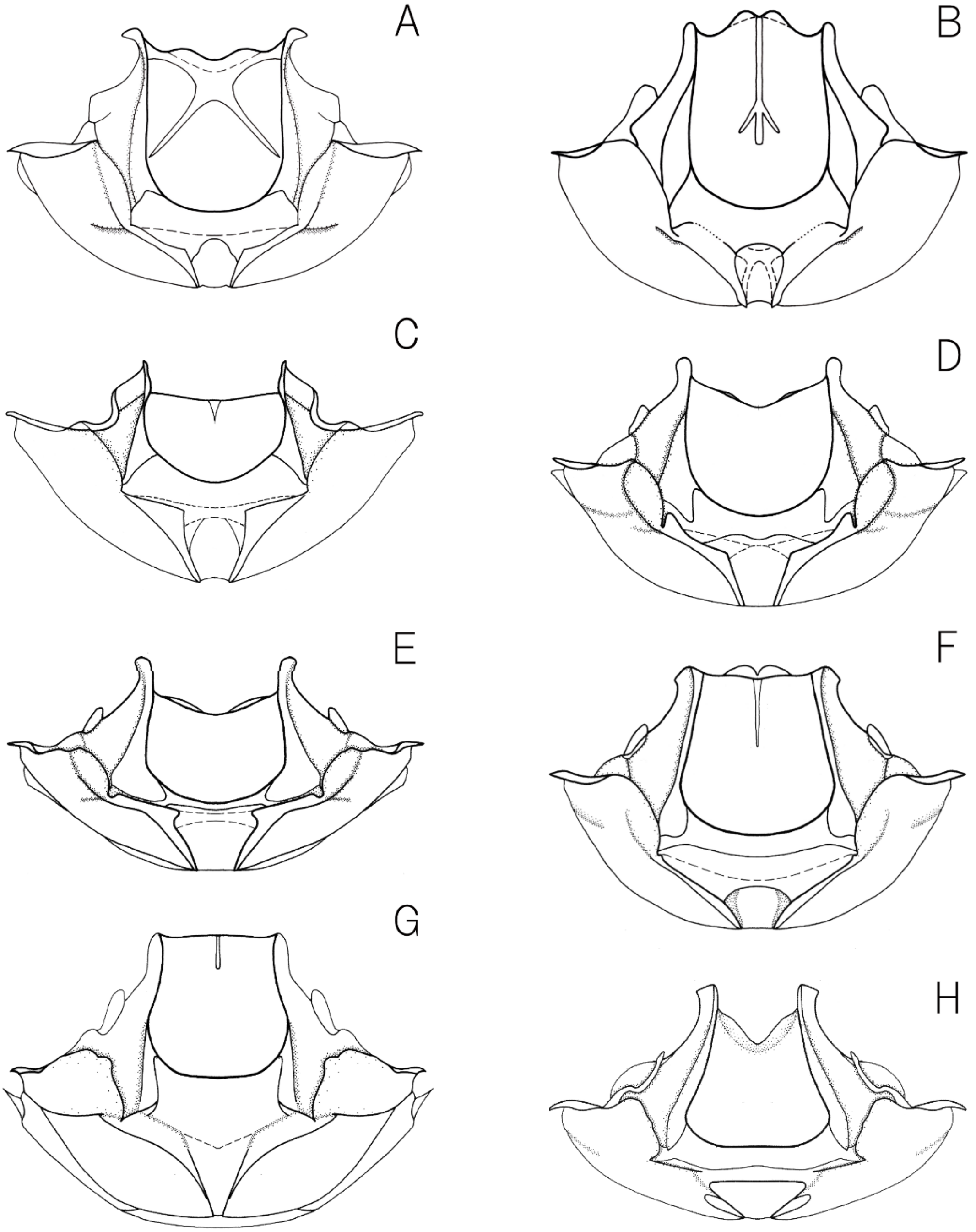


Figure 12A–H. Frontal habitus of the metanotum. **A** *Melolontha* (*Melolontha*) *japonica* Burmeister, **B** *Tanyproctus* sp., **C** *Orphnus* sp., **D** *Mimela splendens* (Gyllenhal), **E** *Popillia japonica* Newman, **F** *Parastasia ferrieri* Nonfried, **G** *Paratrichius doenitzi* (Harold), **H** *Osmoderma opicum* Lewis.

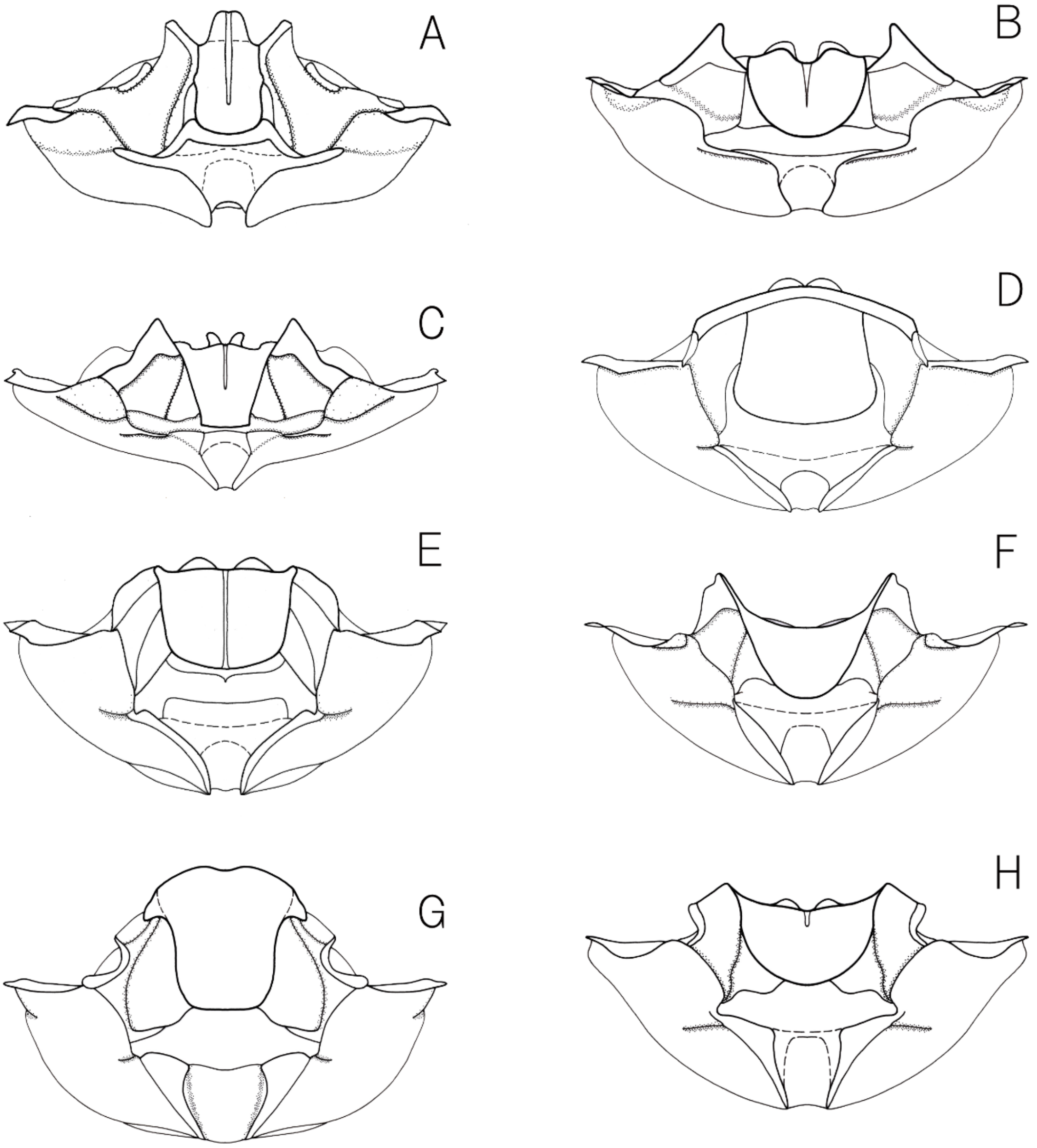


Figure 13A−H. Frontal habitus of the metanotum. **A** *Nipponovalgus angusticollis* (Waterhouse), **B** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates, **C** *Copris* (*Copris*) *ochus* (Motschulsky), **D** *Bolbocerodema nigroplagiatum* (Waterhouse), **E** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky), **F** *Glaresis beckeri* Solsky, **G** *Amphicoma splendens* (Yawata), **H** *Phaeochrous emarginatus* Laporte.

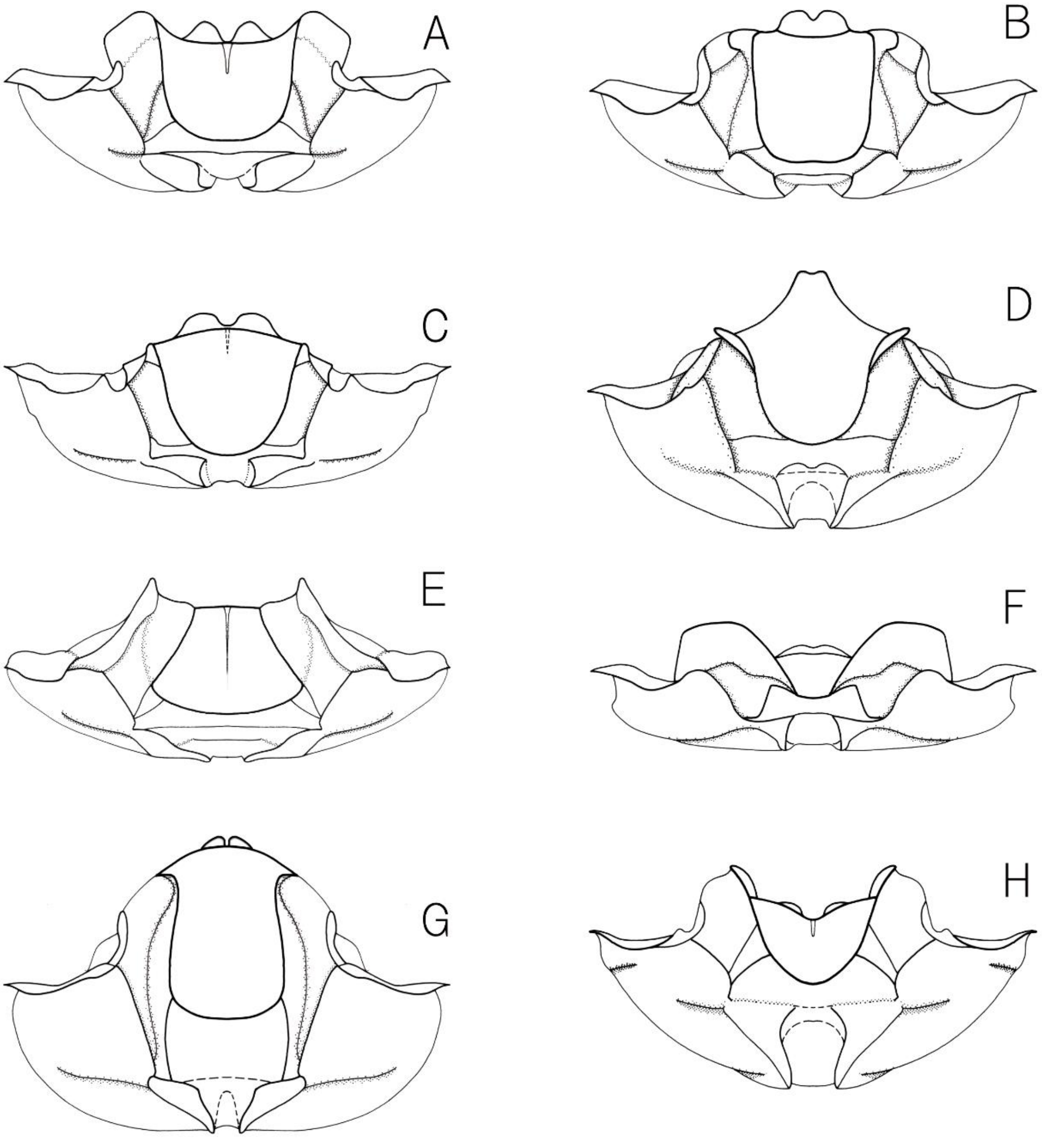


Figure 14A−H. Frontal habitus of the metanotum. **A** *Nicagus japonicus* Nagel, **B** *Ceruchus lignarius* Lewis, **C** *Lamprima adolphinae* (Gestro), **D** *Lucanus maculifemoratus* Motschulsky, **E** *Notochodaeus maculatus* (Waterhouse), **F** *Macrolinus sikkimensis* Stoliczka, **G** *Pleocoma dubitabilis* Davis, **H** *Glyptotrox uenoi* (Nomura).

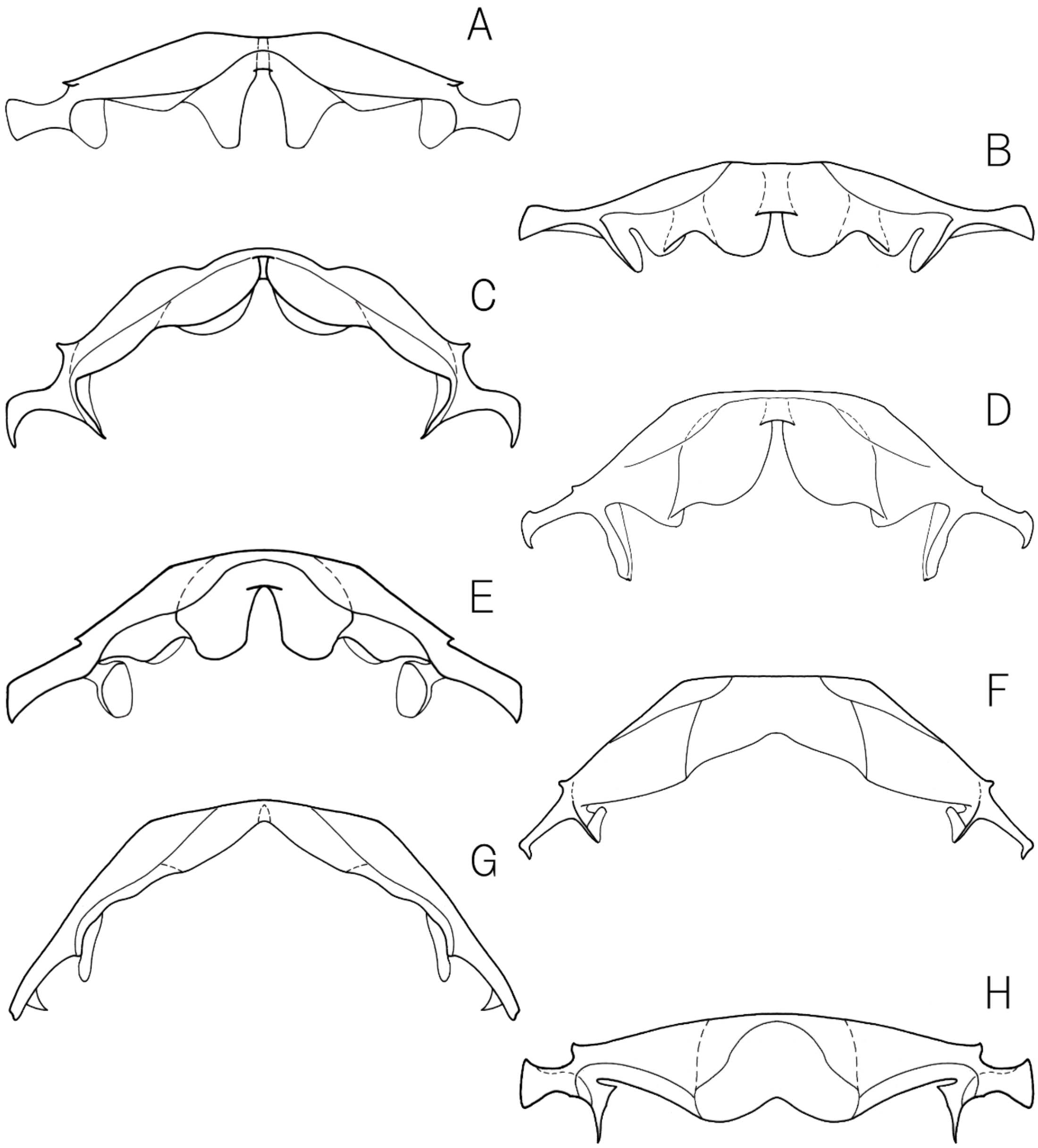


Figure 15A−H. Habitus of the postnotum. **A** *Pachypus candidae* (Petagna, 1787), **B** *Gametis jucunda* (Faldermann), **C** *Orubesa ata* Semenov & Medvedev, **D** *Trypoxylus dichotomus* Kôno, **E** *Euchirus longimanus* Linnaeus, **F** *Apogonia bicarinata* Lewis, **G** *Maladera* (*Omaladera*) *orientalis* (Motschulsky), **H** *Hoplia communis* Waterhouse.

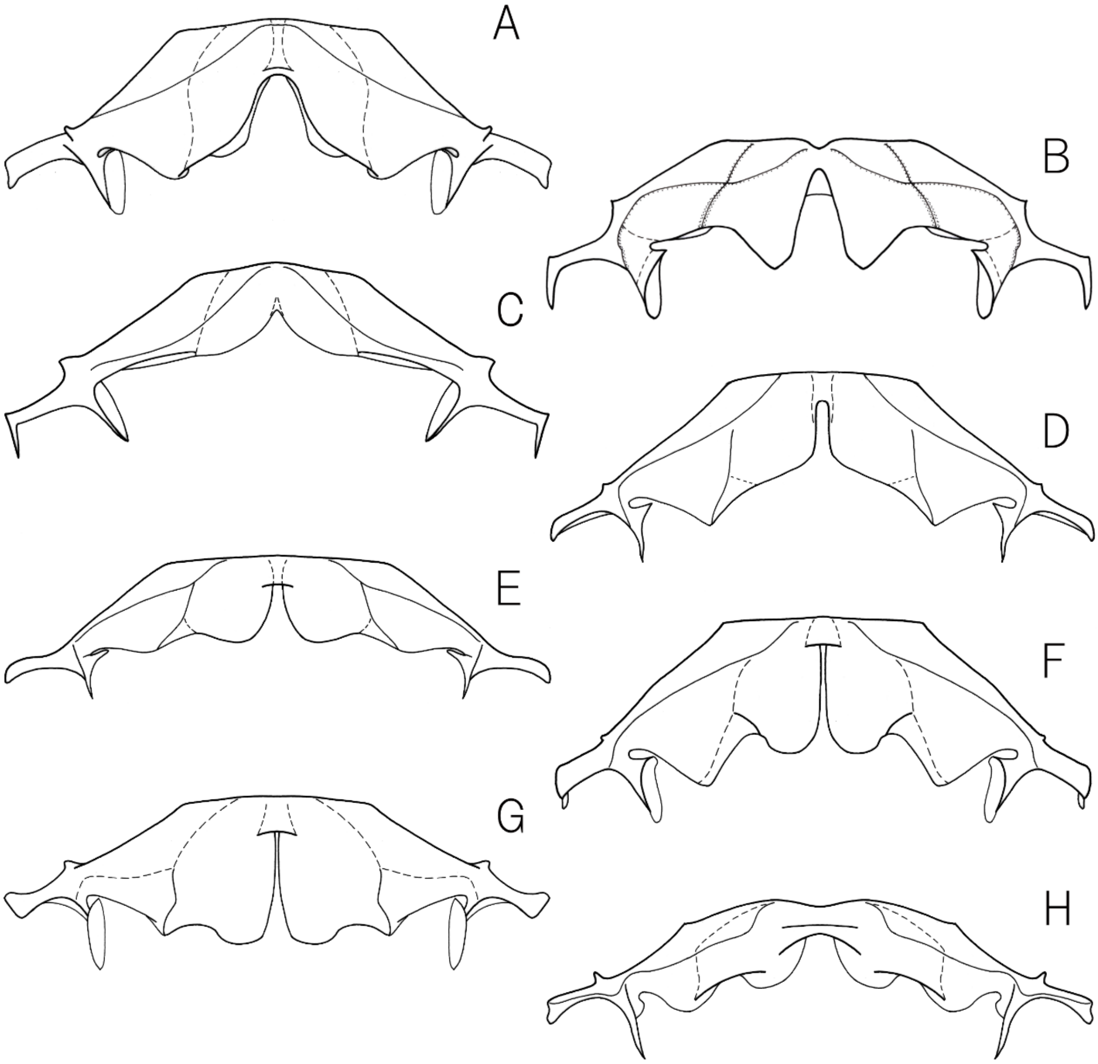


Figure 16A−H. Habitus of the postnotum. **A** *Melolontha* (*Melolontha*) *japonica* Burmeister, **B** *Tanyproctus* sp., **C** *Orphnus* sp., **D** *Mimela splendens* (Gyllenhal), **E** *Popillia japonica* Newman, **F** *Parastasia ferrieri* Nonfried, **G** *Paratrichius doenitzi* (Harold), **H** *Osmoderma opicum* Lewis.

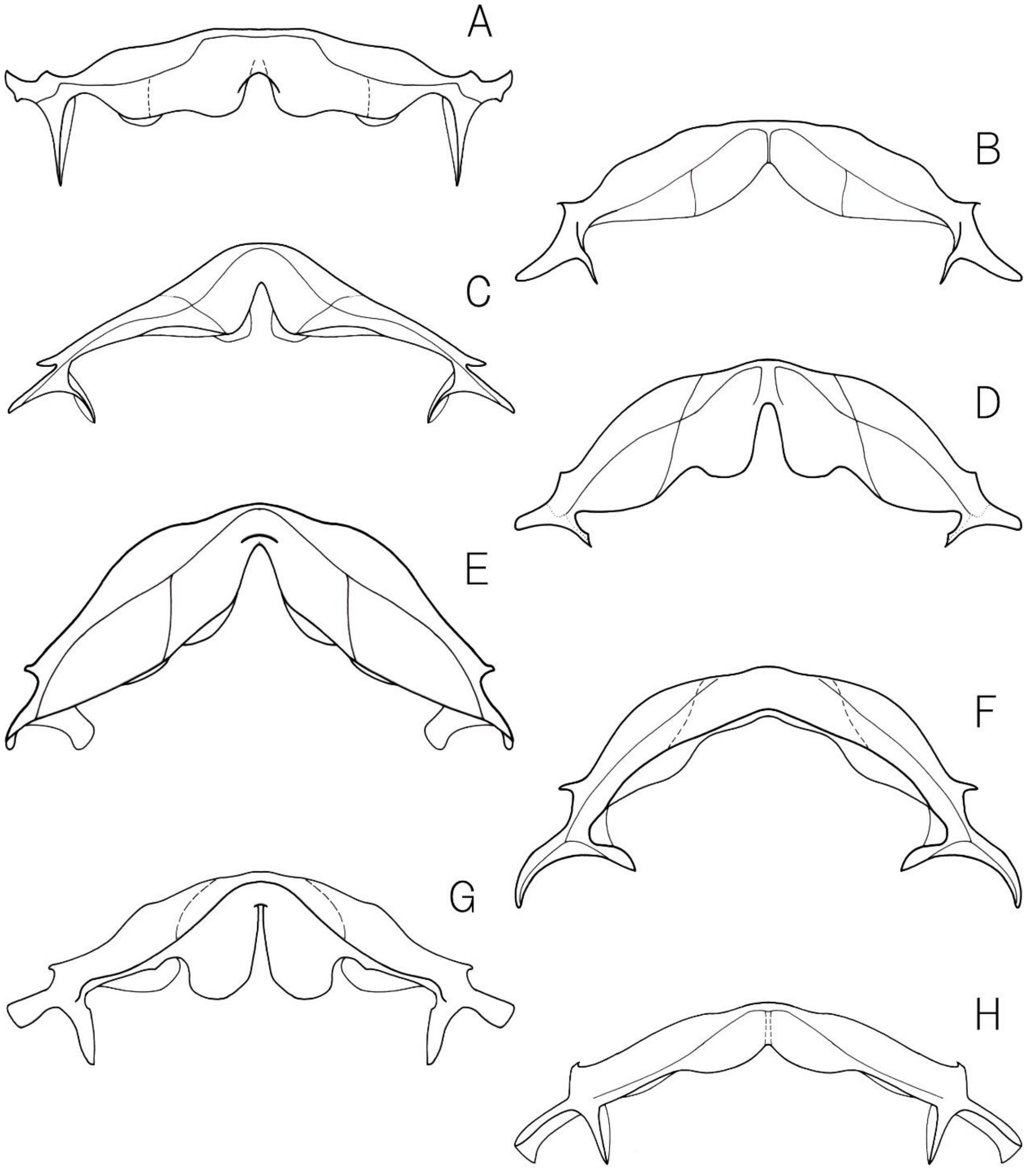


Figure 17A–H. Habitus of the postnotum. **A** *Nipponovalgus angusticollis* (Waterhouse), **B** *Aphodius* (*Brachiaphodius*) *eccoptus* Bates, **C** *Copris* (*Copris*) *ochus* (Motschulsky), **D** *Bolbocerodema nigroplagiatum* (Waterhouse), **E** *Phelotrupes* (*Eogeotrupes*) *laevistriatus* (Motschulsky), **F** *Glaresis beckeri* Solsky, **G** *Amphicoma splendens* (Yawata), **H** *Phaeochrous emarginatus* Laporte.

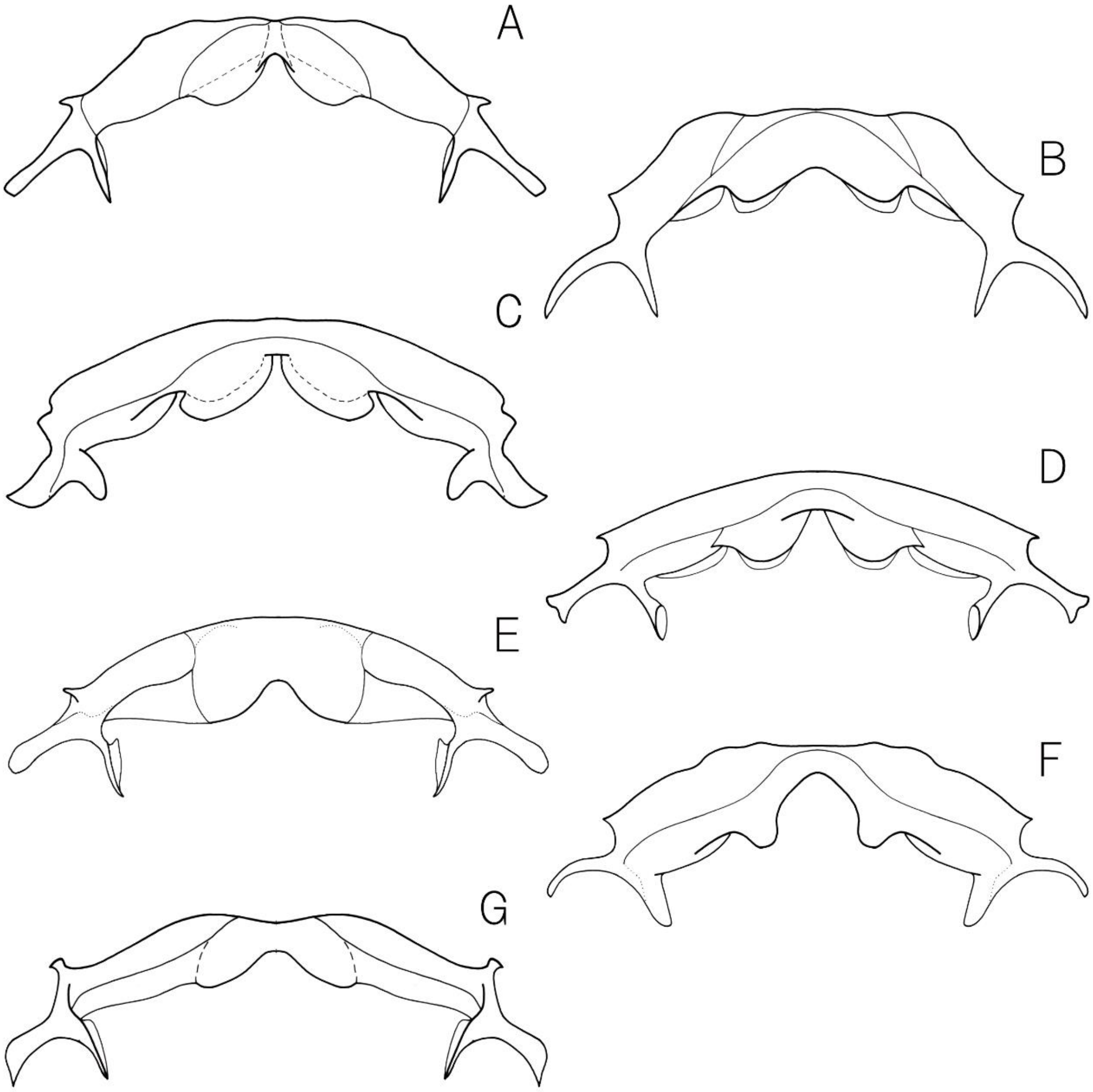


Figure 18A−H. Habitus of the postnotum. **A** *Nicagus japonicus* Nagel, **B** *Ceruchus lignarius* Lewis, **C** *Lamprima adolphinae* (Gestro), **D** *Lucanus maculifemoratus* Motschulsky, **E** *Notochodaeus maculatus* (Waterhouse), **F** *Pleocoma dubitabilis* Davis, **G** *Glyptotrox uenoi* (Nomura).

第 3 章

総合考察

緒言

コガネムシ上科は古くから多くの研究者の手によって研究が行われてきたこともあり，分類学における最も基礎の研究段階であるα分類は他のコウチュウ目と比較しても，よく進んだ状態にあると言える（Scholtz and Grebennikov 2016）．そのため，近年は種・属・科といった分類群間の系統関係を解明し，整理を行うβ分類が頻繁に行われるようになってきている．Browne and Scholtz (1995)において初めて形態形質を基に系統解析が行われて以降，より詳細な系統関係の解明へ向けた研究が行われてきており（Browne and Scholtz 1998, 1999, Ahrens 2005, Bai *et al*. 2013），最近では DNA などの分子データを基に系統解析行う分子系統学的研究が多く行われている（Smith *et al*. 2006, Hunt *et al*. 2007, Ahrens *et al*. 2014, McKenna *et al*. 2015, 2019, Neita-Moren *et al*. 2019）．これらの研究によって，非常に詳細な系統関係が明らかとなってきている反面，形態と分子の間で異なる系統仮説が提示される問題や，信憑性が高い系統仮説が得られるとされる分子系統解析においても，研究者ごとに異なる系統仮説が示されるなど，新たな問題が生じてきている．形態と分子の双方から支持される系統仮説の構築には従来の形質データに加えて，新たな系統的に有用と考えられる形質データを含めた解析が必要であり，異なる分子系統仮説が提示された場合には，どちらがより信憑性の高い系統仮説かを判断するためにも形態形質による証明が必要不可欠である．そこで本章では，今回観察された３つの形態形質【後翅折り畳み様式】,【中胸背板】,【後胸背板】から得られた形質データを基に，既存の分子系統仮説と比較・検証することで，その系統仮説の信憑性の検証，ならびに新たな系統類縁関係の探索を行った．

材料と方法

第２章の「２－１後翅折り畳み様式 hind wing folding pattern」，「２－２中胸背板 mesonotum」，そして「２－３後胸背板 metanotum」において得られた形態学的成果をまとめることで，科・亜科を特徴づける形質状態の整理を行った．そして，これらの形質データと分子データを基に構築された既存の系統仮説とを比較・検討することで，観察された形態形質の系統的有用性の証明，および対象とした分子系統仮説の信憑性の検証を行いつつ，新たな系統類縁関係の探索を行った．主な比較・検討には Ahrens *et al*. (2014)によって示された分子系統仮説を参考に作成したクラドグラム（Fig. 1）を用いたが，異なる系統仮説を示す分子系統学的研究が存在する場合は合わせて考察を行った．また，Ahrens *et al*. (2014) において扱われていない分類群については，その他の形態および分子系統仮説の情報を用いることで，系統類縁関係の考察を行い，詳細な系統情報が判明していない分類群については，クラドグラムを用いた分岐パターンの相違に関する考察は行わず，既知の形態情報と照合することで考察を行った．なお Ahrens *et al*. (2014)の系統仮説は，コガネムシ上科を構成する主要グループの多くが含まれていることに加え，４つの核およびミトコンドリア DNA

（18S ribosomal DNA (18S), 2364 bp; 28S ribosomal DNA (28S), 941 bp; 16S ribosomal DNA (16S), 484 bp; cytochrome oxidase subunit 1 (CO1), 826 bp）計 4615 塩基対 base pairs を基に解析を行っていることから，信頼性の高い系統情報であると考えられている．

結果および考察

ムネアカセンチコガネ科 Bolboceratidae

ムネアカセンチコガネ科は全世界に約 50 属 621 種が知られる分類群である．古くはセンチコガネ科に含まれる一つの分類群と考えられていたが，Scholtz and Browne (1996)以降，異なる独立の科として扱われている（Scholtz and Grebennikov 2016）．また，後翅翅脈と後翅基底骨を主体として行われた形態系統解析の結果においては，フユセンチコガネ科との姉妹群関係が示唆されている（Browne 1991, Browne and Scholtz 1995, 1999, Scholtz and Browne 1996）が，その一方で，Ahrens *et al.* (2014)(Fig. 1)の分子系統仮説においては，他の分類群との近縁性は示されておらず，本科のみで単系統群を形成することが示唆されている．ムネアカセンチコガネ科の単系統性を支持する特徴としては，後翅翅脈と後翅基底骨に見られる一連の派生形質（Browne and Scholtz 1994, 1995, 1997, 1998）と腹部気門，食性，幼虫形態が確認されている（Scholtz and Grebennikov 2016）．ただし，Neita-Moren *et al.* (2019)の分子系統解析においては，クロツヤムシ科と姉妹群関係にある事が示唆されている．今回観察された 3 つの形質からは以下の形質状態によって特徴づけられた．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 2）
Fba と Faa の比率は通常 Fba >> Faa（約 1.4–2 : 1）となる；Dp が三角形で先端領域は S と Aa で構成される；An は四角形；Id は平行型；Wd は細長い台形状で，Fba 領域の約半分を占める；S は長方形.

【中胸背板】（Figs. subchapter 2–2–2: 5E, 11E）
First phragma は大きく発達し，前縁側方部分は前方に向かって突出する；prescutum は完全に消失する；scutum＋scutellum は矢じり型；scutellar process は硬化した棒状で，付随する axillary code は非常に薄い膜状；internal ridge（horizontal plate と vertical plate）は発達して mesonotal pouch を形成する．

【後胸背板】（Figs. subchapter 2–3–2: 4E, 9D, 13D, 17D）
背面から見た基本となる形状はドーム型；acrotergite は矩形型で，前方に向かって突出しない；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は三角形状で前縁は平坦となる；posterolateral scutal area は分断されない；postnotum はよく発達し，特に mediophragmite と laterophragmite は強く発達する．しかし，subalar tendon の発達は弱い．

センチコガネ科 Geotrupidae

センチコガネ科は全世界に約34属460種が知られる分類群である（Schoolmeesters 2020）．古くから独立の科としての単系統性が支持されている分類群であり，形態形質の面からは，口器形態や後翅基底骨に固有の特徴を有するとされ，Ahrens *et al*. (2014)においても同様に本科は単系統群を形成することが示されている．しかし，以降に行われた分子系統解析（McKenna *et al*. 2015, Neita-Moren *et al*. 2019）においては異なる系統関係が示されており，McKenna *et al*. (2015)においてはコブスジコガネ科との近縁性が示唆され，Neita-Moren *et al*. (2019)では支持率が低いものの，クワガタムシ科と姉妹群を形成することが示唆されている．今回観察された３つの形質からは以下の形質状態によって特徴づけられた．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 4）
Fba と Faa の比率は Fba >> Faa（約 1.4–2 : 1）；DP が三角形で先端領域は S のみで構成される；An は四角形；Id は平行型；Wd は細長い台形状で，Fba 領域の約半分を占める；S は長方形．

【中胸背板】（Figs. subchapter 2–2–2: 5G, 11G）
First phragma は大きく発達し，前縁側方部分は前方に向かって突出する；prescutum は完全に退化せず，scutum＋scutellum の前縁にその名残が観察できる；scutum＋scutellum は盾型；scutellar process は硬化した棒状で，付随する axillary code は非常に薄い膜状；internal ridge（horizontal plate と vertical plate）は発達して mesonotal pouch を形成する．

【後胸背板】（Figs. subchapter 2–3–2: 4F, 9E, 13E, 17E）
背面から見た基本となる形状はドーム型；acrotergite は矩形型で，前方に向かって突出しない；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は台形状となる；posterolateral scutal area は oblique suture と深い溝によって分断される；postnotum はよく発達し，特に mediophragmite と laterophragmite は強く発達する．しかし，subalar tendon の発達は弱い．

ニセコブスジコガネ科 Glaresidae

ニセコブスジコガネ科は，オーストラリアとニュージーランドを除く全世界に 4 属 93 種が観察される，小さな分類群である．日本における分布は 2018 年まで確認されていなかったが，Ochi *et al*. (2019)によって初めて国内にも分布することが明らかとなった．本科は，近年までコブスジコガネ科に含まれる一つの分類群として扱われていたが，Scholtz (1986)の形態研究の結果から，コブスジコガネ科との近縁性を示す共有派生形質を有していないことが明らかとなり，Scholtz *et al*. (1994)において，残りのコガネムシ上科と姉妹群関係にある単系統の分類群であることが示された．ニセコブスジコガネ科がコガネムシ上科の基部に位置する単系統群であることは，以降の形態研究（Bai *et al*. 2013）からも支持されている一方で，近年の分子系統解析の結果からは異なる系統関係が示されている．Smith *et al*. (2006), McKenna *et al*. (2019), Neita-Moren *et al*. (2019)の結果は，コブスジコガネ科と姉妹群を形成することを示しており，さらに Smith *et al*. (2006)と McKenna *et al*. (2019)はクワガタムシ科とニセコブスジコガネ科＋コブスジコガネ科系統が近縁となり，一つの系統群を形成するとしている．その一方で，Ahrens *et al*. (2014)の提示した系統仮説においては，ニセコブスジコガネ科とクワガタムシ科の近縁性が示唆され，コブスジコガネ科は完全に異なる系統群に位置することが示されている．今回観察された 3 つの形質からは以下の形質状態によって特徴づけられた．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 5）
Fba と Faa の比率は Fba ≒ Faa（約 1–1.1 : 1–1.1）；Dp が四角形で先端領域は S1，S2，Aa1，Aa2 で構成される；An は五角形で Pr2 領域が付随する；Id は平行型；Wd は Fba 領域の約半分を占め，深い切れ込みを有する；S（S1 と S2）と Aa（Aa1 と Aa2）はヘラ型を形成する；明確な Additional fold が Oa と S2 に生じ，S2 は Dp から生じる．

【中胸背板】（Figs. subchapter 2–2–2: 5I, 11I）
First phragma は発達するが，背面からはほとんど確認できず，前縁中央が下方に陥入している；prescutum は完全に退化せず，scutum＋scutellum の前縁にその名残が観察できる；scutum＋scutellum は矢じり型；scutellar process は硬化した棒状で，付随する axillary code は非常に薄い膜状；horizontal plate は発達し，mesonotal pouch を形成するが，vertical plate は完全に消失する．

【後胸背板】（Figs. subchapter 2–3–2: 4H, 9F, 13F, 17F）
背面から見た基本となる形状は矩形型 rectangle；acrotergite は矩形型で，前方に向かって台形状に突出する；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は三角形状で前縁は平坦となる；posterolateral scutal area は分断されない；postnotum はよく発達するが，mediophragmite と laterophragmite の発達は弱い．

ヒゲブトハナムグリ科 Glaphyridae

ヒゲブトハナムグリ科は全北区を中心に約 13 属 230 種が知られる，比較的小さな分類群である（Schoolmeesters 2020）．本科の系統的位置については古くから議論が行われており，コガネムシ上科に含まれる分類群の中で「中間的な intermediate」分類群であると考えられる傾向が強い（Nel and Scholtz 1990, Scholtz 1990, d’Hotman and Scholtz 1990a）．Zunino (1988)にて行われた雌雄交尾器形態の比較研究からは，コガネムシ科に含まれることが示唆されていたが，以降に行われた多くの形態研究（d’Hotman and Scholtz 1990a, b, Scholtz 1990）の結果は，コガネムシ科などの派生グループに含むべきではないとしている．近縁と考えられる分類群についても複数の仮説が存在し，後翅基底骨の形質情報を基に構築された系統仮説（Browne and Scholtz 1995）では，コブスジコガネ科＋ムネアカセンチコガネ科＋フユセンチコガネ科系統群の姉妹群に当たることが示唆されており，その後の多様な形態形質を

含めた解析（Browne and Scholtz 1999）においては，コブスジコガネ科＋ムネアカセンチコガネ科系統群と姉妹群を形成するとしている．また，分子系統仮説 Ahrens *et al*. (2014)ではコガネムシ科食葉群 pleurosticti との姉妹群関係が示されている他，McKenna *et al*. (2015)と Neita-Moren *et al*. (2019)においては非常に弱いながらもアカマダラセンチコガネ科との近縁性が示唆されている．今回観察された３つの形質からは以下の形質状態によって特徴づけられた．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 6）

Fba と Faa の比率は Fba > Faa（約 1.2-1.3 : 1）；Dp が三角形で先端領域は S のみで構成される；An は四角形；Id は後縁に向かって先細りとなる；Wd は Fba 領域の約半分を占める；S はヘラ型を形成する．

【中胸背板】（Figs. subchapter 2–2–2: 6A, 12A）

First phragma は大きく発達し，前縁側方部分は前方に向かって突出する；prescutum は完全に消失する；scutum＋scutellum は二等辺三角形型；scutellar process と axillary cord は硬化して完全に癒合することで二股分岐の突起を形成するが，axillary cord に対応する後方突起の発達は弱い；internal ridge（horizontal plate と vertical plate）は発達して mesonotal pouch を形成する．

【後胸背板】（Figs. subchapter 2–3–2: 5A, 9G, 13G, 17G）

背面から見た基本となる形状はドーム型；acrotergite は矩形型で，前方に向かって突出しない；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は台形状となる；posterolateral scutal area は分断されない；postnotum はよく発達し，特に median postnotum，mediophragmite，anterior postnotal process が大きく発達する．

アツバコガネ科 Hybosoridae

アツバコガネ科は基本的に汎熱帯地域 pantropical に広く生息し，新熱帯区で爆発的な多様性を示すことが知られる分類群であり，現在までに約 101 属 700 種が知られている（Schoolmeesters 2020）．古くからアカマダラセンチコガネ科との近縁性が示唆されているが（Scholtz 1988, Ocampo and Hawks 2006），Ahrens *et al*. (2014)においては，他の分類群と姉妹群関係になることはなく，アツバコガネ科のみで単系統群を形成することが示されている．その一方で，Neita-Moren *et al*. (2019)の解析結果においては，その支持率は弱いものの，コガネムシ科の食葉群と元も近縁であることが示されている．今回観察された３つの形質からは以下の形質状態によって特徴づけられた．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 7）

Fba と Faa の比率は Fba ≒ Faa（約 1–1.1：1–1.1）；Dp が三角形で先端領域が S と Aa で構成される；An は四角形；Id は後縁に向かって先細りとなる；Wd は Fba 領域の約半分を占める；S と Aa は長方形はとなる.

【中胸背板】（Figs. subchapter 2–2–2: 6B, 12B）

First phragma の大半は減少するが，両側部は発達し，前方に向かって突出する；prescutum は完全に消失する；scutum＋scutellum は二等辺三角形型；scutellar process と axillary cord は硬化して完全に癒合することで二股分岐の突起を形成するが，axillary cord に対応する後方突起の発達は弱い；horizontal plate は発達して mesonotal pouch を形成し，vertical plate の大部分は horizontal plate に癒合している.

【後胸背板】（Figs. subchapter 2–3–2: 5B, 9H, 13H, 17H）

背面から見た基本となる形状はドーム型；acrotergite は矩形型で，前方に向かって台形状に突出する；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は三角形状で前縁は波打つ；posterolateral scutal area は分断されない；postnotum はよく発達し，特に anterior postnotal process が大きく発達する．しかし，mediophragmite と laterophragmite の発達は弱い.

クワガタムシ科 Lucanidae

クワガタムシ科は全世界に約 136 属 1700 種が知られる，コガネムシ上科の極めて大きな分類群の一つである（Schoolmeesters 2020）．古くはクロツヤムシ科との近縁性が示唆されていたが（Howden 1982），その後の単眼や後翅基底骨の形態研究から Diphyllostomatidae 科とより近縁であることが示唆され，クロツヤムシ科とは進化の初期段階で分岐し，それぞれ別の進化経路をたどったと考えられている（Browne and Scholtz 1995）．その一方で， Kim and Farrell (2015)にて行われた分子系統解析によると，クワガタムシ科と Diphyllostomatidae 科に含まれる種は，コガネムシ上科内で入れ子状に配置されることから，仮に Diphyllostomatidae 科を取り除いた場合，現在のクワガタムシ科は多系統群となる事を指摘しています．また，その他の分子系統仮説においては，ニセコブスジコガネ科（Ahrens *et al.* 2014）やセンチコガネ科（Neita-Moren *et al.* 2019）との近縁性が示唆されている．今回観察された 3 つの形質からは以下の形質状態によって特徴づけられた.

【後翅折り畳み様式】（Figs. subchapter 2–1–2: 9,10）

Fba と Faa の比率は Fba > Faa（約 1.2–1.3：1）；Dp 三角形で先端領域は S または S と Aa で構成される；An は五角形で Pr2 領域が付随する；Id は後縁に向かって先細りとなる；Wd は Fba 領域の約半分を占める；S または S と Aa は一般的に先端に向かって先細りとなる.

【中胸背板】（Figs. subchapter 2–2–2: 6E–6G, 12E–12G）

First phragma は大きく発達し，前縁側方部分は前方に向かって突出する；prescutum は完全に消失する；scutum＋scutellum は通常矢じり型だが，マダラクワガタ亜科 Aesalinae とツヤ

ハダクワガタ亜科 Syndesinae は二等辺三角形型を示す；scutellar process は硬化した棒状で，基部が外側に向かって突出し，付随する axillary code は非常に薄い膜状；internal ridge は発達し，mesonotal pouch を形成するが，マダラクワガタ亜科とツヤハダクワガタ亜科を除いて horizontal plate の中央部が消失することで，mesonotal pouch は前方に開く．

【後胸背板】（Figs. subchapter 2–3–2: 5C, 5F, 10A, 10D, 14A, 14D, 18A, 18D）

背面から見た基本となる形状は正方形型 square だが，マダラクワガタ亜科のみ矩形型を示す；acrotergite は矩形型で基本的に突出しないが，マダラクワガタ亜科のみ前方に向かって台形状に突出する；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は三角形状で通常前縁は波打つが，マダラクワガタ亜科とツヤハダクワガタ亜科においては平坦となる；posterolateral scutal area は分断されない；postnotum はよく発達し，特に mediophragmite，subalar tendon，anterior postnotal process が大きく発達する．

アカマダラセンチコガネ Ochodaeidae

アカマダラセンチコガネ科は，オーストラリアとニュージーランドを除く全世界に約 21 属 147 種が知られる，小さな分類群である．古くはコガネムシ科の Aclopinae 亜科の近縁グループと考えられていたが（Iablokoff-Khnzorian 1977），Crowson (1981)によって初めてアツバコガネ科とセンチコガネ科との近縁性が示唆され，Lawrence and Newton (1982)および Browne and Scholtz (1995, 1999)によってアツバコガネ科との近縁性が強く支持されるようになった．分子系統解析による明確な系統位置は未だ定まっていないが，Ahrens *et al.* (2014)と Neita-Moren *et al.* (2019)において構築された系統仮説は，ヒゲブトハナムグリ科との近縁性を弱くではあるが示している．今回観察された 3 つの形質からは以下の形質状態によって特徴づけられた．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 15）

Fba と Faa の比率は Fba < Faa（約 1 : 1.2–1.3）；Dp が三角形で先端領域は S と Aa で構成される；An は五角形で Pr2 領域が付随する；Id は後縁に向かって先細りとなる；Wd は Fba 領域の約半分を占める；S または S と Aa は先端に向かって先細りとなる；連続した additional fold が Cu, Wd, Oa に生じる；Aa, Pa, and Pr1 には複数の不規則な additional fold が生じる．

【中胸背板】（Figs. subchapter 2–2–2: 7B, 13B）

First phragma は発達し，前縁中央が下方に陥入している；prescutum は完全に消失する；scutum ＋scutellum は矢じり型；scutellar process は硬化した棒状で，付随する axillary code は非常に薄い膜状；internal ridge は発達し，mesonotal pouch を形成するが，通常 horizontal plate の中央部が消失することで，mesonotal pouch は前方に開く．

【後胸背板】（Figs. subchapter 2–3–2: 5G, 10E, 14E, 18E）

背面から見た基本となる形状はドーム型；acrotergite は矩形型で，前方に向かって台形状に突出する；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は三角形状で前縁は平坦となる；posterolateral scutal area は分断されない；postnotum はよく発達し，特に mediophragmite，laterophragmite，anterior postnotal process は大きく発達する．

クロツヤムシ科 Passalidae

クロツヤムシ科は汎熱帯地域に主に分布し，現在までに約 72 属 840 種が記録される，コガネムシ上科の中でも比較的大きな分類群である．本科は多くの固有派生形質によって特徴づけられる分類群であることから，単系統群として扱うことに関して疑いはないと考えられており，非常によくまとまった分類群であるとされている（Browne and Scholtz 1995, 1997, 1999, Grebennikov and Scholtz 2004, Boucher 2006, Scholtz and Grebennikov 2016）．Boucher (2006)は生物地理学と生態の多様性からコブスジコガネ科と Chironidae 科（Chironinae 亜科）と姉妹群関係にあると考えた．一方で，分子系統学的観点からは異なる見解が得られており，Smith *et al*. (2006)と McKenna *et al*. (2015)ではムネアカセンチコガネ科およびフユセンチコガネ科との近縁性が示唆され，Ahrens *et al*. (2014)はムネアカセンチコガネ科およびコブスジコガネ科と，Neita-Moren *et al*. (2019)はムネアカセンチコガネ科のみとの近縁性を示唆している．今回観察された 3 つの形質からは以下の形質状態によって特徴づけられた．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 16）
Fba と Faa の比率は Fba >> Faa（約 1.4–2 : 1）；Dp が三角形状で先端領域は S のみで構成される；An は四角形；Id は後縁に向かって先細りとなる；Wd は細長い台形状で，Fba 領域の約半分を占める；S は長方形.

【中胸背板】（Figs. subchapter 2–2–2: 7C, 13C）
First phragma は強く硬化して発達するが，背面からは観察できず，前縁中央は下方に陥入している；prescutum は完全に消失する；scutum＋scutellum は心臓型 cordate で，背面から mesopostnotum の名残が確認できる；scutellar process は硬化した棒状で，基部が外側に向かって突出し，付随する axillary code は非常に薄い膜状；internal ridge は著しく退化し，mesonotal pouch は完全に開く.

【後胸背板】（Figs. subchapter 2–3–2: 5H, 10F, 14F）
背面から見た基本となる形状は正方形型；acrotergite は矩形型で，前方に向かって台形状に突出する；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は鋭くとがる；posterolateral scutal area は分断されない；postnotum は著しく退化し，median postnotum，subalar tendon，anterior postnotal process のみで構成される．この内，subalar tendon が大きく発達する.

フユセンチコガネ科 Pleocomidae

フユセンチコガネ科は新北区 neoarctic と新熱帯区 neotropical にのみ生息が確認されている，コガネムシ上科の中でも極めて小さな分類群であり，現在までに3属32種が確認されている．古くはセンチコガネ科に含まれる分類群の一つとして扱われていたが（Paulian 1941），Crowson (1981)や Lawrence (1982)，Lawrence and Newton (1982)によって検討が行われた結果，独立の科として扱うべきであるとされている（Hovore 2002, Scholtz and Grebennikov 2016）．Browne and Scholtz (1995, 1999)と Scholtz and Browne (1996)において行われた系統解析の結果からは，ムネアカセンチコガネ科との近縁性が示唆されている．また，McKenna *et al*. (2015)の分子系統解析の結果においても，弱くだがムネアカセンチコガネ科との姉妹群関係が示唆されている．今回観察された3つの形質からは以下の形質状態によって特徴づけられた．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 17）
Fba と Faa の比率は Fba > Faa（約 1.2–1.3 : 1）；Dp が三角形状で先端領域は S のみで構成される；An は四角形；Id は平行型；Wd は Fba 領域の約半分を占める；S は先端に向かって先細りとなる．

【中胸背板】（Figs. subchapter 2–2–2: 7D, 13D）
First phragma は大きく発達し，前縁は裁断状となる；prescutum は完全に消失する；scutum ＋scutellum は盾型；scutellar process は硬化した棒状で，付随する axillary code は非常に薄い膜状；internal ridge（horizontal plate と vertical plate）は発達して mesonotal pouch を形成する．

【後胸背板】（Figs. subchapter 2–3–2: 6A, 10G, 14G, 18F）
背面から見た基本となる形状はドーム型；acrotergite は矩形型で，前方に向かって突出しない；alacrista は明確に発達するが，後端は後縁に達しない；anterior lobe of metanotum は発達しない；anterior notal wing process は三角形状で前縁は平坦となる；posterolateral scutal area は oblique suture と深い溝によって分断される；postnotum はよく発達し, 特に mediophragmite と laterophragmite が大きく発達する．しかし，subalar tendon の発達は著し弱い．

コブスジコガネ科 Trogidae

コブスジコガネ科は全世界に約9属300種が記録される，比較的小さな分類群である．本科の単系統性は多くの派生形質によってよく定義されており（Scholtz 1986, 1990, Scholtz and Peck 1990, Browne *et al*. 1993），Ahrens *et al*. (2014)の分子系統解析の結果からもその単系統性は強く支持されている．系統的位置については研究者ごとに異なる見解が存在し，Crowson (1967, 1981)や Scholtz (1986)はコガネムシ上科における最も原始的な分類群の一としていたが，Browne and Scholtz (1995)にて行われた，後翅基底骨の形質データを基にした系統解析の結果からは，ヒゲブトハナムグリ科系統群とムネアカセンチコガネ科＋フユセンチコガネ科系統群の中間に位置するとしている．また，Howden (1982)は複数の派生形質の存在から，

フチトリアツバコガネ科との近縁性を示唆しているが，Ahrens *et al*. (2014)はムネアカセンチコガネ科との強い近縁性を示し，Neita-Moren *et al*. (2019)の解析結果からは支持率が弱いものの，ニセコブスジコガネ科との近縁性が示されている．

【後翅折り畳み様式】（Fig. subchapter 2–1–2: 18）
Fba と Faa の比率は Fba > Faa （約 1.2–1.3 : 1）；Dp が三角形状で先端領域は S のみで構成される；An は五角形で Pr2 領域が付随する；Id は後縁に向かって先細りとなる；Wd は Fba 領域の約半分を占め，浅い切れ込みを有する；S は先端へ向かって先細りとなる．

【中胸背板】（Figs. subchapter 2–2–2: 7E, 13E）
First phragma は大きく発達し，前縁中央が下方に陥入している；prescutum は完全に消失する；scutum＋scutellum は矢じり型；scutellar process は硬化した棒状で，付随する axillary code は非常に薄い膜状；internal ridge（horizontal plate と vertical plate）は発達して mesonotal pouch を形成する．

【後胸背板】（Figs. subchapter 2–3–2: 6B, 10H, 14H, 18G）
背面から見た基本となる形状は矩形型；acrotergite は矩形型で，前方に向かって台形状に突出する；alacrista は明確に発達する；anterior lobe of metanotum は発達しない；anterior notal wing process は三角形状で前縁は平坦となる；posterolateral scutal area は分断されない；postnotum はよく発達するが，mediophragmite と laterophragmite の発達は弱い．

コガネムシ科 Scarabaeidae

コガネムシ科は全世界に約 1600 属 27000 種が知られるコガネムシ上科最大の分類群であり，極めて多様な生態と形態的特徴を有することから，主要な分類群として 14 亜科に分けられている．本科の単系統性は後翅基底骨と翅脈に観察される数多くの派生形質（Browne and Scholtz 1995, 1999）によって支持されており，これは Gunter *et al*. (2016)や McKenna *et al*. (2015, 2019)などの分子系統解析の結果からも支持されていることから，現在のコガネムシ科はよくまとまった単系統の分類群であるという認識が一般となっている．しかし，一部の分子系統解析の結果は，全く異なる見解を示しており，現行のコガネムシ科はダイコクコガネ亜科＋マグソコガネ亜科系統群（食糞群）とコフキコガネ亜科＋スジコガネ亜科＋カブトムシ亜科＋ハナムグリ亜科系統群（食葉群）の二つのグループに大別され，むしろ食葉群はアツバコガネ科やヒゲブトハナムグリ科，アカマダラセンチコガネ科に近縁であることが示される傾向にある（Hunt *et al*. 2007, Ahrens *et al*. 2014, Neita-Moren *et al*. 2019）．こうした背景から、今回コガネムシ科において観察された形態的特徴は多岐にわたり，亜科または一部の族ごとに固有の形質状態が観察され，科を特徴づける明確な形質状態を特定することは困難であった．そのためここでは，近年の分子系統学的研究において最も大きな問題となっている，食糞群 coprophagous group と食葉群 phytophagous group が明確に異なる分類群であることを証明する形質状態を中心に整理を行った．

【後翅折り畳み様式】

食糞群（Fig. subchapter 2–1–2: 21）：Dp が四角形状で先端領域は S1 と S2 または S1, S2, Aa1, Aa2 で構成される；Wd は Fba の約三分の一を占め，通常明確な additional fold が確認される．

食葉群（Figs. subchapter 2–1–2: 31, 41, 42）：Dp が三角形状で先端領域は S または S と Aa で構成される；Wd は通常 Fba の約半分を占め，ハナムグリ亜科においてのみ約三分の二を占める．

【中胸背板】

食糞群（Figs. subchapter 2–2–2: 11C, 11D）：scutellar process は硬化した単一の突起で，付随する axillary cord は硬化した膜質または非常に薄い膜質状を示す．ダイコクコガネ亜科の scutellar process は三角形のプレート状に発達し，posterior inflection of mesonotal pouch との縫合線が明確に確認できる．

食葉群（Figs. subchapter 2–2–2: 9G, 9H, 9I）：一部の分類群に含まれる種（Orphninae 亜科とビロウドコガネ族 Sericini）を除き，scutellar process と axillary cord は硬化して完全に癒合することで二股分岐の突起を形成する．axillary cord に対応する後方突起は大きく発達し，袋状の構造を形成する．

【後胸背板】

食糞群（Figs. subchapter 2–3–2: 4C, 4D, 13B, 13C）：背面から見た基本となる形状は矩形型；acrotergite は矩形型で，前方に向かって台形状に突出する；alacrista は著しく減少した状態を示す；anterior lobe of metanotum は発達しない；anterior notal wing process は台形状となる；posterolateral scutal area は oblique suture と深い溝によって分断され，Scarabaeinae においては明確な裂け目が確認できる；medianlongitudinal groove は中央部分で最も広くなる．

食葉群（Figs. subchapter 2–3–2: 2B, 2D, 3E, 4B, 11C, 12D）：ハナムグリ亜科とヒラタハナムグリ亜科を除き，背面から見た基本となる形状はドーム型；acrotergite 基本的に三角形型で前方に向かって細長く突出するが，一部の分類群（Dynamopodinae 亜科，Orphninae 亜科，ビロウドコガネ族）では矩形型で，前方に向かって台形状に突出する；alacrista は通常明確に発達する；anterior lobe of metanotum は通常発達するが，一部の分類群（ハナムグリ亜科，Dynamopodinae 亜科，Orphninae 亜科，ヒラタハナムグリ亜科）では著しく減少する；anterior notal wing process はハナムグリ亜科と一部のトラハナムグリ亜を除いて三角形状となる；posterolateral scutal area は通常 oblique suture と深い溝によって分断されるが，一部の分類群（Aclopinae 亜科，Dynamopodinae 亜科，Orphninae 亜科，ビロウドコガネ族，アシナガコガネ族 Hopliini）では分断されない；medianlongitudinal groove は後方から前方に向かって緩やかに広くなる．

ムネアカセンチコガネ科 Bolboceratidae，クロツヤムシ科 Passalidae，コブスジコガネ科 Trogidae について

近年の分子系統学的研究の結果，これらの分類群は少なからず近縁な関係にあることが示唆されており，特にムネアカセンチコガネ科とクロツヤムシ科に関しては姉妹群関係にあることが，Ahrens *et al*. (2014)（Fig. 1）や Neita-Moren *et al*. (2019)（Fig. 2）の分子系統仮説によって示されている．

今回観察された 3 つの形態形質において，複数の共有原始形質および派生形質を確認することが出来たが，上記の 3 科のみを特徴づける共有派生形質は観察されず，これらの近縁性を示すことはなかった．しかしながら，姉妹群関係にあるとされるムネアカセンチコガネ科とクロツヤムシ科においては，【後翅折り畳み様式】Fba >> Faa (約 1.4-2 : 1)，Wd が細長い台形状，という特異な形質状態が観察されており，本特徴は両分類群間の近縁性を示している可能性が示唆された．またこの場合，【後翅折り畳み様式】Fba >> Faa (約 1.4-2 : 1)の特徴は，センチコガネ科においても観察されており，これまでにムネアカセンチコガネ科，クロツヤムシ科，センチコガネ科間の近縁性に関する言及は確認されないが，今回初めてこれらの分類群が近縁となる可能性が示唆された．

センチコガネ科 Geotrupidae について

多くの場合，センチコガネ科は独立の単系統群を構成することが示唆されているが（Ahrens *et al*. 2014）（Fig. 1），一部の分子系統仮説において，その支持率は低いものの，異なる見解が示されており，クワガタムシ科（Neita-Moren *et al*. 2019）（Fig. 2）との近縁性が示唆されている．

今回観察された系統的に重要と考えられる形質状態の内，ほぼすべての項目において異なる形質状態を示していることが確認された．顕著な差異として，【後翅の折り畳み様式】Fba：Faa の比率，Wd の形状，An の形状と S2 領域の有無，Id の形状，先端領域の形状，【中胸背板】prescutum の有無，scutum＋scutellum の形状，mesonotal pouch の形状，【後胸背板】posterolateral scutal area の特徴，など極めて多くの差異が確認されている．上記の分子系統仮説における分類群間の支持値も総じて低いことから，センチコガネ科とコブスジコガネ科およびクワガタムシ科を近縁とする考察は誤りであると考えられる．

ニセコブスジコガネ科 Glaresidae，クワガタムシ科 Lucanidae，コブスジコガネ科 Trogidae，アカマダラセンチコガネ科 Ochodaeidae について

これらの分類群の系統学的扱いには様々な仮説が存在するものの，近年公表されている分子系統仮説の多くで，ニセコブスジコガネ科とコブスジコガネ科(Neita-Moren *et al*. 2019)，（Fig. 2）およびニセコブスジコガネ科＋コブスジコガネ科とクワガタムシ科間の近縁性（Smith *et al*. 2006, McKenna *et al*. 2015, 2019）（Fig. 3）が示唆される傾向にある．

比較観察の結果，ニセコブスジコガネ科，コブスジコガネ科，クワガタムシ科の近縁性を

補完する極めて重要な形質が【後翅の折り畳み様式】に存在することが明らかとなった．これらの分類群は An 領域が五角形状を示し，それに伴って Pr2 領域が生じるという特徴を有している．この特徴は，コガネムシ上科の折り畳み様式において，極めて特異な形質状態であると考えられることから，上記３科の近縁性が強く支持された（Fig. 4）．また，本特徴はアカマダラセンチコガネ科においても観察されていることから，ニセコブスジコガネ科，コブスジコガネ科，クワガタムシ科，アカマダラセンチコガネ科の近縁な関係にあると共に，An の特徴によってくくられる一つの系統群を形成すると考えられる．ただし，アカマダラセンチコガネ科は一般的に，ヒゲブトハナムグリ科（Ahrens *et al.* 2014, Neita-Moren *et al.* 2019）やアツバコガネ科（Lawrence and Newton 1982, Browne and Scholtz 1995, 1999）との近縁性が示されていることに加え，Ahrens *et al.* (2014)の系統仮説（Fig. 1）においては，その支持率は低いものの，コブスジコガネ科はニセコブスジコガネ科やクワガタムシ科とは異なる系統に位置すること示されている．そのため今後は，今回の観察によって得られた形質データと先行する形態研究によって得られている形質データを合わせて解析する必要があるかもしれない．

アツバコガネ科 Hybosoridae とヒゲブトハナムグリ科について

アツバコガネ科とヒゲブトハナムグリ科の系統的配置に関しては，上述した通り，様々な仮説が提案されているが，近年は Ahrens *et al.* (2014)や Neita-Moren *et al.* (2019)の系統仮説で示されているように，両分類群ともにコガネムシ上科の中間的系統に位置する分類群でとする認識が一般的になっている（Figs. 1, 2）．また両者の系統仮説では，一貫してアツバコガネ科とヒゲブトハナムグリ科はコガネムシ科食糞群以上に食葉群と近縁であることを示しており，この場合現行のコガネムシ科は多系統の分類群として扱われる．

今回観察を行った３つの形質においても，アツバコガネ科とヒゲブトハナムグリ科が食葉群と近縁であることを示す特徴が観察されたことに加え，両科が互いに近縁となる可能性が強く示唆された．共有する特徴として、【後翅折り畳み様式】Dp が三角形，An が四角形，Id は先細りとなる，Wd は Fba 領域の約半分を占める，【中胸背板】prescutum は完全に消失する，scutum＋scutellum は二等辺三角形型，scutellar process と axillary cord は二分岐突起を形成するが，後方突起の発達が弱い不完全なものとなる，mesonotal pouch は閉じる，【後胸背板】形状はドーム型，acrotergite は長方形，alacrista は発達する，anterior lobe of metanotum は発達しない，posterolateral scutal area は完全に癒合する，postnotum は発達する，が挙げられる．これらの形質状態の内，【中胸背板】に観察される不完全な二分岐突起と二等辺三角形型の scutum＋scutellum は両科の近縁性を示す重要な特徴であった．前者に関しては両科にのみ観察される共有派生形質であると共に，コガネムシ科食葉群の保有する完全な二分岐突起の前形質であると考えられることから，この特徴はヒゲブトハナムグリ科＋アツバコガネ科と食葉群を近縁とする系統仮説（Ahrens *et al.* 2014, Neita-Moren *et al.* 2019）を強く支持するものとなった（Fig. 5）．しかし，これらの系統仮説の中で非常に

弱くだが示唆されている，アカマダラセンチコガネ科とヒゲブトハナムグリ科の近縁性を支持する形質状態は確認することが出来なかった．

フユセンチコガネ科について

本科は先述の通り，形態および分子系統解析の結果から，ムネアカセンチコガネ科と近縁な関係にあることが示唆されているが，今回観察された３つの形質からは，両分類群の近縁性を示す特徴を見出すことはできなかった．むしろ，【中胸背板】scutum＋scutellum が盾型，【後胸背板】posterolateral scutal area が oblique suture と深い溝によって分断される，という特徴を有することから，センチコガネ科と近縁である可能性が高いと考えられる．しかし，これらの特徴も幅広い分類群に観察される共有派生形質であることから，明確な系統関係の解明には更なる検討が必要である．

コガネムシ科 Scarabaeidae 食葉群 phytophagous group と食糞群 coprophagous group について

上述の結果の通り，食糞群と食葉群の間には多くの形態的差異が確認されたことから，それぞれが明確に異なる系統群を構築することが本研究からも示された．また，Ahrens *et al.* (2014)や Neita-Moren *et al.* (2019)の分子系統仮説において，食葉群とアツバコガネ科またはヒゲブトハナムグリ科との近縁性が示唆されているが，これは【中胸背板】に観察される，硬化した scutellar process と axillary cord からなる発達した二分岐突起の特徴によって補間されることが明らかとなった．食葉群を明確に特徴づける形質状態の一つに大きく発達した二分岐突起の特徴が認められるが，アツバコガネ科とヒゲブトハナムグリ科および一部の祖先的な食葉群（Dynamopodinae 亜科）において，この前段階の形質状態と考えられる，不完全な二分岐突起が観察されている．これらの二分岐突起はコガネムシ上科において食葉群とアツバコガネ科，ヒゲブトハナムグリ科にのみ観察される極めて特異な共有派生形質であることから，本特徴によって各分類群の近縁性が強く支持された（Fig. 5）．一部の食葉群（ビロウドコガネ族や Orphninae 亜科）において単一突起の scutellar process が観察されるが，上記二つの分類群が食葉群とは異なる系統群として扱われた研究例は過去になく，形態および分子系統解析の結果からも，これらを含めて食葉群として扱うべきである事が強く支持されている（Browne and Scholtz 1998, Hunt *et al.* 2007, Ahrens *et al.* 2014, McKenna *et al.* 2015, 2019, Neita-Moren *et al.* 2019）．このことから，ビロウドコガネ族と Orphninae 亜科に観察される単一突起の scutellar process は，アツバコガネ科やヒゲブトハナムグリ科，Dynamopodinae 亜科に観察される不完全な二分岐突起に生じた形質変化の初期段階において，二次的に退化して生じたものであると考えられる．

以上のことから，本研究結果は現行のコガネムシ科を多系統の分類群であるとし，食糞群と食葉群は完全に異なる系統群であるとする Ahrens *et al.* (2014)や Neita-Moren *et al.* (2019)の分子系統仮説を強く支持するものとなった．

コガネムシ科食葉群 phytophagous group の多様化と害虫化に関わる形態形質について

コガネムシ上科の中でもコガネムシ科食葉群は，もっとも多様化した一群で，農林業害虫として扱われる種の大半はこの食葉群に含まれる．特に重大な害虫として，スジコガネ亜科 Rutelinae に属するスジコガネ類 Anomalini（*Anomala* 属や *Popillia* 属）や，コフキコガネ亜科 Melolonthinae に含まれるコフキコガネ類 Melolonthini（*Melolontha* 属）とクロコガネ類 Rhizotrogini（*Phyllophaga* 属）の種が世界的にも認識されている（Scholtz and Grebennikov 2016）．これらの種が害虫として扱われる主な要因には，突発的に大発生する傾向があるとともに，様々な環境に進出して繁殖することを可能とする高い適応能力が挙げられる（Ritcher 1966, Eberhard 1993, Yeates *et al.* 1999）．しかし，今回行った胸部形態の比較観察の結果，そうした高い繁殖能力に加えて，高い移動分散能力を獲得したことが害虫化の一つの大きな要因となっている可能性が示された．食葉群を特徴づける非常に重要な形質状態として，【中胸背板】に観察される発達した scutellar process と axillary cord（二分岐突起）の存在がある（Fig. 5）．通常，コガネムシ上科甲虫に観察されるのは単一の硬化した scutellar process と膜質化した axillary cord であり，この内，前者のみが後胸背板の acrotergite に接続されることで，鞘翅を固定する前後運動の操作棒 levering device となり，後者は鞘翅基底部の膜質部分と結合している．しかし食葉群においては，scutellar process が後胸背板に接続されると共に，axillary cord に該当する発達した後方突起が鞘翅の基部にあてがわれることで，鞘翅の展開時にその角度を調整する役割を果たしていると考えられる．甲虫の鞘翅は飛翔時に揚力を発生させると共に，体の平行を保つバランサーとして機能しており，一部の例外を除き飛翔行動における極めて重要な役割を担っている（Sitorus *et al.* 2010）．食葉群に含まれる種は発達した二分岐突起を獲得したことで，飛翔時に鞘翅の角度を調整することが可能となり，高い機動性を獲得し多様化したと考えられる．また，実際に害虫として扱われる上述のグループに含まれる種は，総じてよく発達した二分岐突起を保有していることが今回確認されている．

以上のことから，コガネムシ科食葉群が多様化したことに加え、多くの害虫種が含まれる要因として，コガネムシ類が本来持ち合わせる高い繁殖能力に加えて，中胸背板に発達した二分岐突起を獲得したことにより，飛翔制御能力が向上し，広範囲への移動が容易となったことが今回初めて示唆された．本研究では飛翔能力に関する詳細な実験を行っていないため，これらの考察は憶測の域を出ないが，今後生体を用いた実験によるデータを蓄積することが出来れば，確信に至ることができるだろう．また，本形態的特徴が真に害虫化の要因となる場合，今後，新たな害虫種の出現時に，その種の害虫としての危険度を標本の情報のみからある程度推測することが出来るようになると思われる．

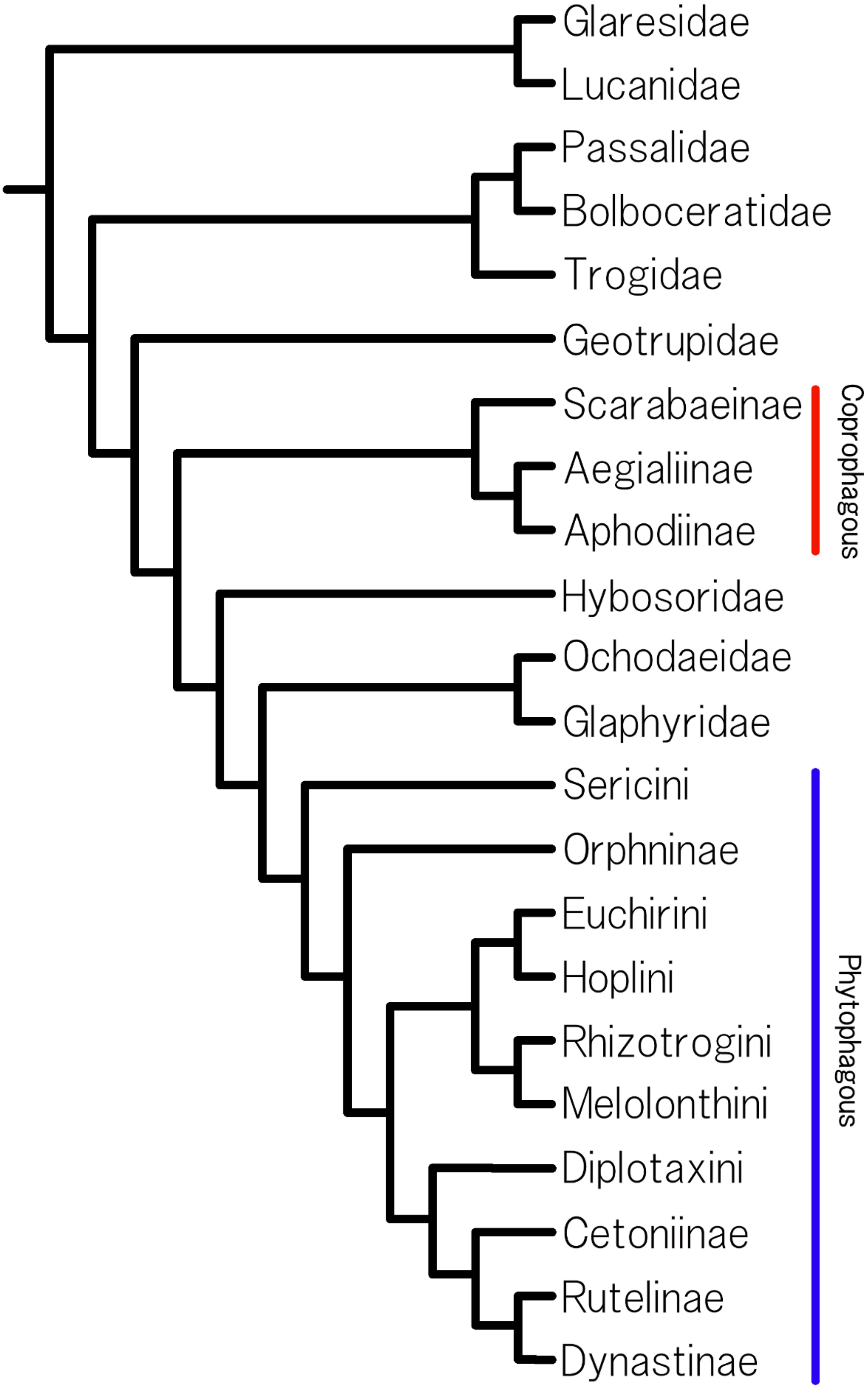


Figure 1. A molecular phylogenetic hypothesis of Ahrens *et al*. (2014), partly modified.

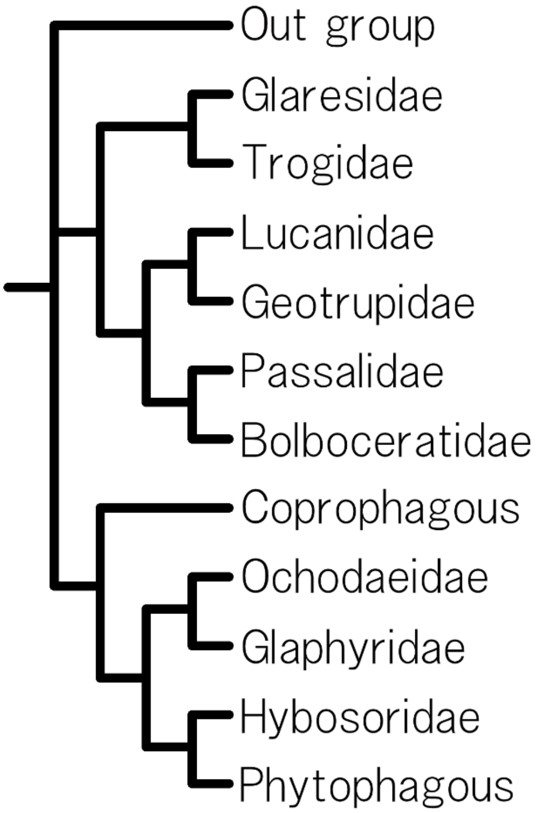


Figure 2. A molecular phylogenetic hypothesis of Neita-Moren *et al*. (2019), partly modified.

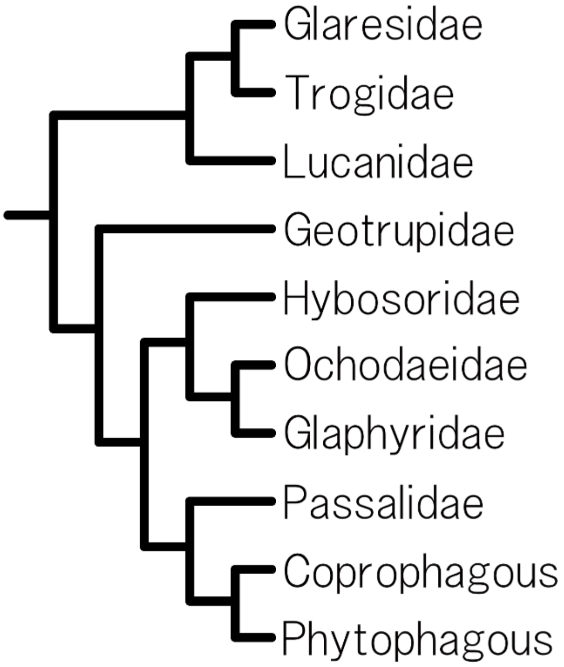


Figure 3. A molecular phylogenetic hypothesis of McKenna *et al*. (2015), partly modified.

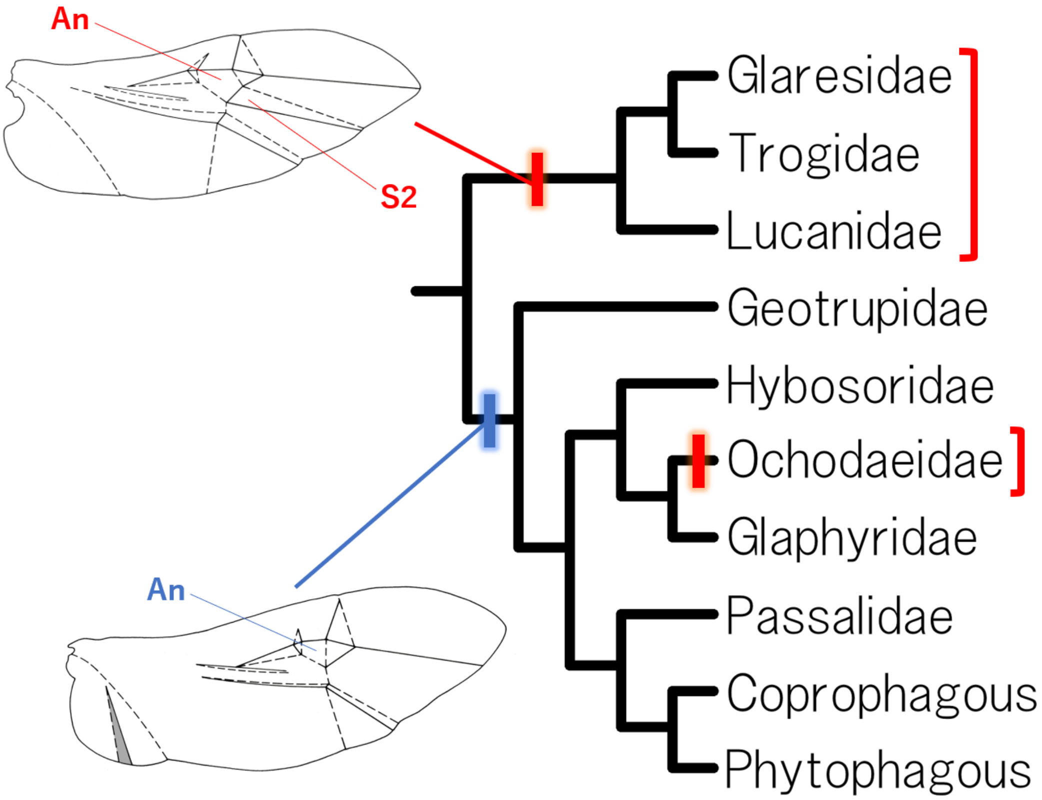


Figure 4. Mapping of characteristics of the hind wing folding pattern on the molecular phylogenetic tree of McKenna *et al*. (2015).

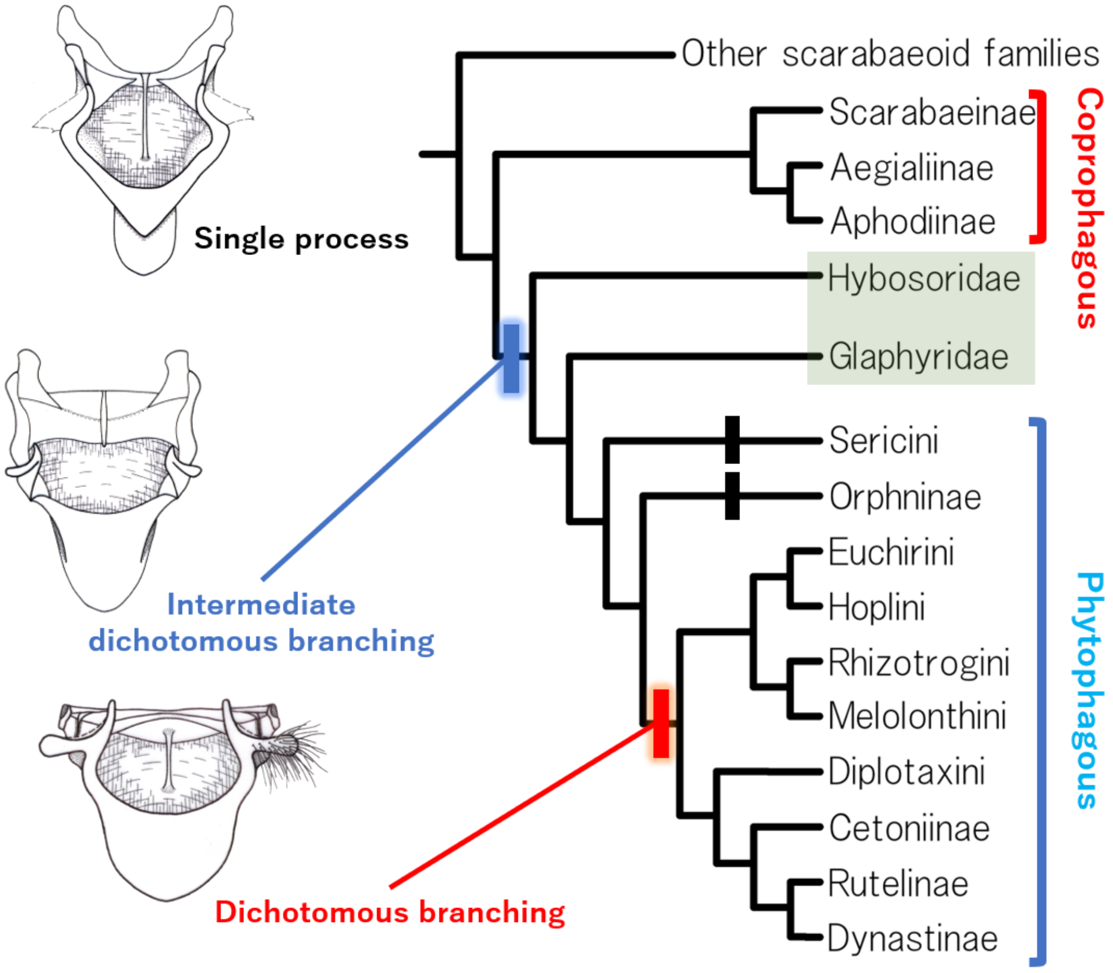


Figure 5. Mapping of characteristics of the mesonotum on a molecular phylogenetic tree of Ahrens *et al*. (2014).

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Summary

The superfamily Scarabaeoidea is a large group of Coleoptera including many agricultural and forest pests. This group has long attracted the attention of numerous researchers, and several detailed comparative studies on various morphological structures have been conducted. In this study, I examined in detail three novel characters (hind wing folding pattern, mesonotum, and metanotum) of 132 genera from 11 families of Scarabaeoidea (Bolboceratidae, Geotrupidae, Glaresidae, Glaphyridae, Hybosoridae, Lucanidae, Ochodaeidae, Passalidae, Pleocomidae, Trogidae, and Scarabaeidae). Moreover, I verified the credibility of the phylogenetic hypotheses presented in recent years and searched new phylogenetic relationships by using the morphological data (synapomorphy) obtained in this research.

Chapter 2−1. Hind wing folding pattern: Many functional and comparative morphological studies concerning hindwing shape and venation have been conducted in Coleoptera. However, there are few researches on hind wing folding pattern, and it is poorly understood in the scarabaeoid species. As a result of this examination, the hind wing folding patterns were similar within each family or subfamily independently from body size or habitats and behavioral traits. These results suggest that hind wing folding patterns are one of the steady characters limited by phylogenetic constraint within each family or subfamily and may become a key characteristic that can help to identify higher taxa.

Chapter 2−2. Mesonotum: In Coleoptera, the mesonotum is located beneath the pronotum and lies between elytral bases, and has the primarily function as a fixing device of elytra. Thus, it is regarded to be affected to a lesser extent by environmental factors and behavioral traits. In the primitive Scarabaeoidea, many character states observed were plesiomorphic state. Whereas, in the intermediate and higher groups such as phytophagous group of Scarabaeidae, many observed character states were apomorphic state. A particularly important feature was observed in the scutellar process and axillary cord, which are considered to play a role in adjusting the angle of the elytra in flight time. In the phytophagous group, the scutellar process and axillary cord greatly develop to form dichotomous branching process, and it was revealed as a unique character state to distinguish this group.

Chapter 2−3. Metanotum: Since the metanotum is one of the largest attachments point of the muscles relating to flight, it was considered that there are remarkably differences between higher taxa. However, the observed character states represented a stable state with the fewest mutations among the characters observed in this research.

Most of the observed character states were considered to be plesiomorphic, and were not useful as a feature characterizing particular family or subfamily, except in the derived group such as Scarabaeinae and Cetoniinae. However, the acrotergite, alacrista, anterior lobe of metanotum, and posterolateral scutal area were useful features for considering the phylogenetic relationships and evolutionary tendencies of families and subfamilies.

Chapter 3. Based on the aforementioned results, it was concluded that the characteristics observed in the hind wing folding pattern, mesonotum and metanotum are useful for characterizing the families and subfamilies of the superfamily Scarabaeoidea, and are also important features for considering their evolutionary tendencies and phylogenetic relationships. Furthermore, many morphological data obtained in this study strongly supports some existing molecular phylogenetic hypothesis, and in some groups such as the family Scarabaeidae, it is possible to complement hypotheses that have not been supported from the viewpoint of morphology for the first time.

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