

An Attempt at the Higher Classification of the Carabina (Coleoptera,
Carabidae) Based on Morphology and Molecular Phylogeny,
with Special Reference to *Apotomopterus*,
Limnocarabus and *Euleptocarabus*

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Abstract Higher classification of the genus *Carabus* (s. lat.) is re-examined based on a phylogenetic tree constructed from the mitochondrial ND5 gene sequences of 45 species representing all the 8 subdivisions (IMURA, 1996 a) (see SU *et al.*, 1998). The subgenera belonging to these subdivisions emerged almost simultaneously and therefore further grouping of these subdivisions seems to have little phylogenetic significance. It seems more appropriate to regard them as equivalent divisions. Special attention is focused on the phylogenetic positions of *Apotomopterus*, *Limnocarabus* and *Euleptocarabus*. The species belonging to *Apotomopterus* form a single cluster on the ND5 tree, while those of *Limnocarabus* and *Euleptocarabus* constitute another monophyletic cluster. A new division is therefore proposed for the latter two subgenera under the name *Lepidospinulati* nov., together with a new term, *lepidospinula*, for their characteristic basal sclerite on the endophallus.

Introduction

Current higher classification of the genus *Carabus* (s. lat.) has been done mainly on the basis of endophallic characters of the male genital organ, the use of which was first proposed by ISHIKAWA (1973, '78, '79). A historical account after ISHIKAWA's proposal was already documented by IMURA (1996 a). IMURA (1996 a) proposed a new system, in which the genus *Carabus* (s. lat.) is first divided into two large divisions, namely, Carabogenici and Multistriati; the former is composed of three subdivisions containing 14 subgenera, and the latter comprises five subdivisions containing 80 subgenera.

In the first part of the present paper, the higher classification is evaluated by a

phylogenetic tree of the mitochondrial ND5 gene using 45 species of the genus *Carabus* (s. lat.) representing all the 8 subdivisions (sensu IMURA, 1996a) (SU *et al.*, 1998).

Apotomopterus is the largest subgenus in the genus *Carabus* (s. lat.), which contains nearly 100 species distributed in the southeastern part of the Eurasian Continent, mainly in China and the adjacent regions including Taiwan. It is characterised by the absence of an ostium lobe on the membranous preostium and the presence of a small sclerite at the basal part of the endophallus, a unique morphology of the male genital organ in *Carabus*.

These characters are also shared with the other two subgenera, *Limnocarabus* and *Euleptocarabus*. *Limnocarabus* is rather sporadically but widely distributed in the northern parts of the Eurasian Continent including several adjunctive islands, and is usually treated monotypical, though the type species, *Carabus* (*L.*) *clathratus*, shows marked geographical variation and is separated into several subspecies. For the reasons to be mentioned below, we regard *Limnocarabus* as containing at least two different species, *clathratus* and *maacki*. The population occurring in Japan is represented by subsp. *aquatilis*, belonging most likely to the latter species. *Euleptocarabus* is composed of a single type species, *C. (E.) porrecticollis*, which is endemic to Honshu, the mainland of Japan. It is separated into two local races, i.e., nominotypical subspecies and subsp. *kansaiensis*, but the geographical variation of the species is more complicated (KIM *et al.*, to be published).

ISHIKAWA (1978, p. 63) unified these three subgenera into a single group, Spinulati (=equivalent to the genus *Apotomopterus* in his sense), as one of his three divisions of the subtribe Carabina, mainly on the basis of unique characters of the male genitalia as mentioned above. This arrangement has been subsequently supported by such taxonomists as DEUVE (1991, '94, '97) and IMURA (1996a), though they ranked the Spinulati as one of the subdivisions between the genus and its component subgenera. However, phylogenetic relationships among the subgenera and/or species belonging to this subdivision have not been satisfactorily established.

SU *et al.* (1996) reported that two Japanese species, *Limnocarabus maacki* (= *Carabus* (*L.*) *maacki aquatilis* in the present sense) and *Euleptocarabus porrecticollis* (= *C. (Euleptocarabus) porrecticollis, idem.*) are clustered together, and clearly separated from the other Japanese carabine species on the phylogenetic tree of the mitochondrial ND5 gene sequences. Evolutionary distance between these two species is rather small, though they are morphologically separated from each other at the subgeneric level as noted above.

In the second part of the present study, we will analyse both morphologically and molecular phylogenetically 12 taxa belonging to the above three subgenera from China, Vietnam, Taiwan, Germany and Japan to clarify their appropriate phylogenetic positions.

Materials and Methods

A NJ-phylogenetic tree was used of the mitochondrial ND5 sequences (SU *et al.*, 1998) containing 45 species of the genus *Carabus* (s. lat.) representing all the 8 subdivisions (sensu IMURA, 1996a), and a higher system proposed in the present paper is shown in the right column. For morphological notes and collecting data of the specimens of *Apotomopterus*, *Limnocarabus* and *Euleptocarabus* used in this study, see Appendix.

Scanning electron microscopy. The male genital organ was dissected out from several specimens of *Apotomopterus*, *Limnocarabus* and *Euleptocarabus*. A small basal sclerite on the endophallus was cut out, air-dried, coated with gold and examined under a scanning electron microscope (SEM) (JEOL, JSM-5300LV).

Results and Discussion

Twenty-one clusters, which are supported by the branch length with the bootstrap value of more than 70%, were recognized on a ND5 phylogenetic tree of 45 species of the genus *Carabus* (s. lat.) representing all the 8 subdivisions (Fig. 1). The lineages so recognized are: 1) *Limnocarabus*+*Euleptocarabus*, 2) *Chaetocarabus*/*Platycarabus*, 3) *Hemicarabus*/*Homoeocarabus*, 4) *Apotomopterus*, 5) *Chrysocarabus*, 6) *Damaster* (s. lat.), 7) *Procrustes*/*Megodontus*, 8) *Ohomopterus*, 9) *Carabus* (s. str.)/*Eucarabus*, 10) *Isiocarabus*, 11) *Archaeocarabus**, 12) *Archicarabus*, 13) *Morphocarabus*, 14) *Mesocarabus*, 15) *Pentacarabus*, 16) *Tomocarabus*, 17) *Asthenocarabus*, 18) *Scambo-carabus*, 19) *Leptocarabus* (s. lat.), 20) *Oreocarabus* and 21) *Rhigocarabus*. The lineages 5)–7), 8)–11) and 14)–21) could respectively form one cluster. If so, the number of the lineage could be reduced to 9. IMURA (1996a) recognized two major divisions, the Carabogenici and the Multistriati, between the genus and the subdivisions. Since the branching order of these 9 lineages cannot be determined presumably because of their almost simultaneous emergence, they should be treated as “equivalent” taxa without further grouping. Thus, the bi-divisional classification seems to have little phylogenetic significance from the ND5 tree, and it would be appropriate to raise IMURA’s subdivisions to divisions directly above the subgenera (Fig. 1). These 9 lineages well correspond to the subdivisions of the Carabina proposed by IMURA (1996a) with only one exception. *Apotomopterus* (s. str.) (4) and *Limnocarabus*+*Euleptocarabus* (1) were combined by IMURA (1996a) in a single subdivision Spinulati, while these two are separated on the ND5 tree (see below).

The species belonging to the subdivision Spinulati in IMURA’s sense appear on the tree as two separate clusters. All the species belonging to *Apotomopterus* form a clear single cluster (AP-cluster), while the species belonging to *Limnocarabus* and *Eulepto-*

* IMURA and MIZUSAWA (1996) treated *nanosomus* and *paris* as members of *Carabus* (s. str.), but they form an independent cluster from other *Carabus* (s. str.) spp. on the ND5 tree. Therefore, we tentatively adopt the subgenus *Archaeocarabus* (type species: *relictus*, male is unknown) for these Chinese species.

carabus constitute another monophyletic cluster (LE-cluster). There is no indication of any phylogenetic relatedness between these two lineages.

The AP-cluster is composed of three subclusters: the first cluster containing *C. (A.) clermontianus* from North Vietnam and two species from South China, i.e., *C. (A.) arrowi* and *C. (A.) laoshanicus* (containing two subspecies), the second one containing all the three subspecies of *C. (A.) sauteri* from the Chinese Continent and Taiwan, and the third one consisting of *C. (A.) tonkinensis* from North Vietnam and *C. (A.) toulgoeti* from South China. The LE-cluster contains *C. (Limnocarabus) clathratus clathratus* from Germany, *C. (L.) maacki aquatilis* from Japan, and *C. (Euleptocarabus) porrecticollis* from Japan.

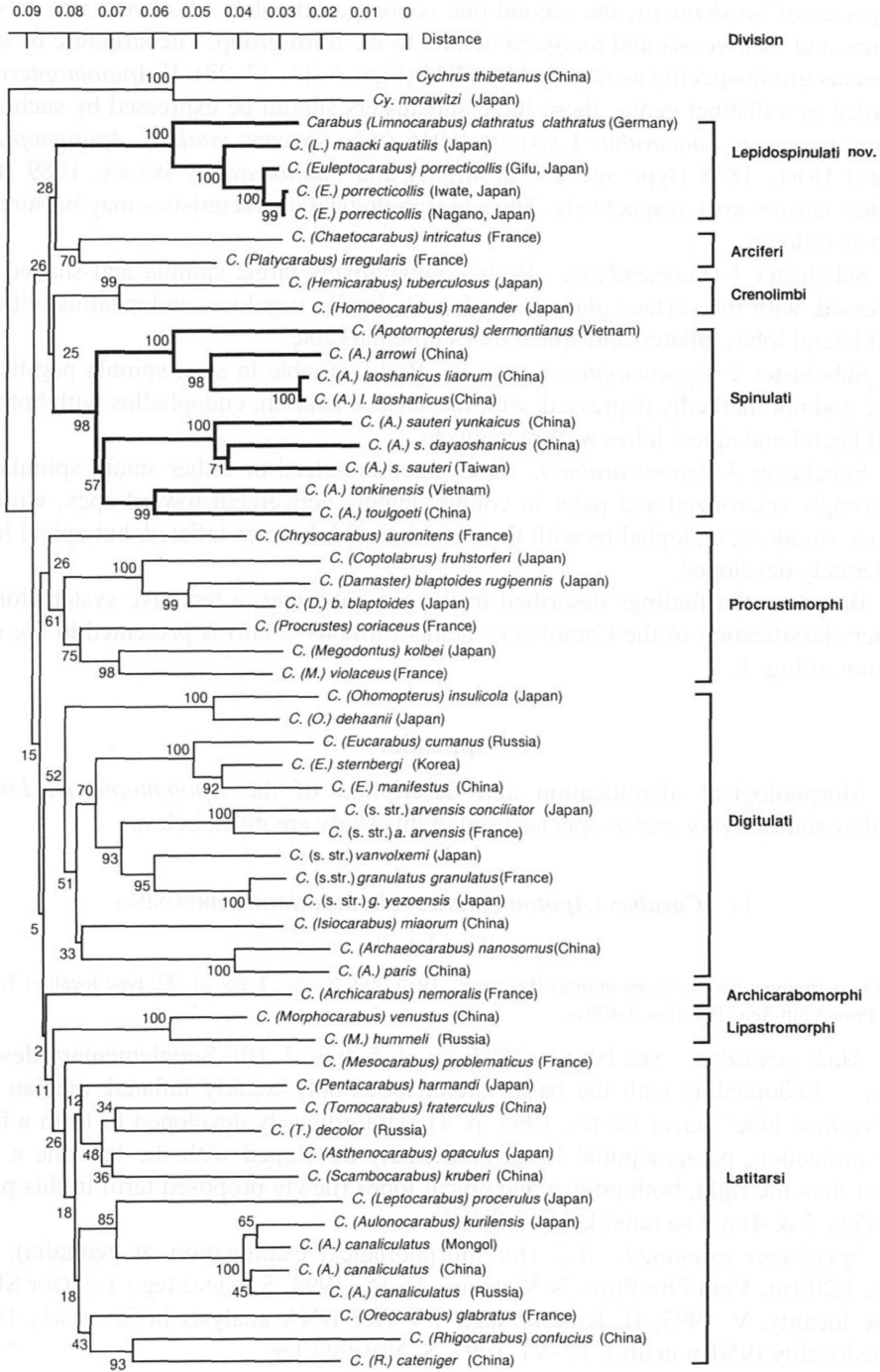
The *Apotomopterus* species are clearly monophyletic. In spite of morphological similarity of the male genital organ, *Limnocarabus* and *Euleptocarabus* are quite remote from *Apotomopterus*. This suggests that the unique morphology of the male genital organ must have developed in parallel in these two independent phylogenetic lines. We therefore consider that *Limnocarabus* and *Euleptocarabus* should not be included in the same lineage as *Apotomopterus*. By the same token, there would be no rationale to place the morphologically similar but phylogenetically independent groups in the Spinulati. Therefore, here we propose a new division for the LE-cluster under the name Lepidospinulati nov. As to the terminology for the basal sclerite of endophallus observed in the species belonging to the new division, we propose lepidospinula, named after scale-like microstructure on its surface.

The Lepidospinulati nov. is discriminated from the Spinulati not only molecular biologically but also morphologically as shown in the following key:

- 1 (2) Membraneous preostium not so strongly inflated and not markedly rugulose on the surface; basal sclerite of endophallus (=spinula) more or less leaf-shaped, widely connected with the membraneous wall, developed horizontally along there, without scale-like microstructure on the surface; parapraeputal lobes more or less developed; apical portion of endophallus not so remarkably inflated or rather deflated, with the apical lobes at most moderately developed. Southeast Eurasia. Spinulati
- 2 (1) Membraneous preostium apparently inflated, with the surface remarkably rugulose; basal sclerite (=lepidospinula) spine- or thorn-shaped, more narrowly connected with the membraneous wall, developed therefrom nearly vertically, and densely covered with scale-like microstructure at least partly; parapraeputal lobes vestigial or at most weakly developed; apical portion of endophallus disproportionately large, with the apical lobes extraordinarily inflated. North Eurasia. Lepidospinulati nov.

In the cluster of the Spinulati (= *Carabus (Apotomopterus)*), three distinct subclusters are recognized (Fig. 1): the first one contains *clermontianus*, *arrowi* and two

Fig. 1. Neighbor-joining (NJ) phylogenetic tree of the Carabina constructed from mitochondrial ND5 gene sequences (taken from SU *et al.*, 1998).



subspecies of *laoshanicus*, the second one is composed solely of *sauteri* and its subspecies, and *tonkinensis* and *toulgoeti* belong to the third group. The structure of spinula seems group-specific as revealed by SEM (Figs. 6–11, 17–22). If *Apotomopterus* is regarded as a distinct genus, these three subclusters should be expressed by such subgeneric names as *Laocarabus* LAPOUGE, 1916 (type species: *vitalisi*), *Apotomopterus* (s. str.) HOPE, 1838 (type species: *prodigus*) and *Siamocarabus* IMURA, 1989 (type species: *masumotoi*), respectively. Their morphological characteristics may be summarized as follows:

Subcluster 1 (*Laocarabus*). Body comparatively large; spinula leaf-shaped and depressed, with the surface glabrous or longitudinally rugulose; endophallus with the basal lateral lobes inflated and apical lobes unremarkable.

Subcluster 2 (*Apotomopterus* s. str.). Body variable in size; spinula peg-like in shape and not markedly depressed, with the surface smooth; endophallus with both the basal lateral and apical lobes well-recognized.

Subcluster 3 (*Siamocarabus*). Body medium-sized or rather small; spinula not so strongly sclerotized and paler in colour, acutely convergent toward apex, with the surface rugulose; endophallus with the basal lateral lobes not inflated, but apical lobes moderately developed.

Based on the findings described in the present paper, a tentative system for the higher classification of the Carabina (=genus *Carabus* s. lat.) is presented in the right column of Fig. 1.

Appendix

Morphological identification and description of the *Apotomopterus*, *Limnocarabus* and *Euleptocarabus* species used in this study are given below.

1) *Carabus (Apotomopterus) clermontianus* BREUNING

(Figs. 2, 6–7)

Carabus (Apotomopterus) clermontianus BREUNING, 1933, Ent. Nachr., **7**, pp. 21–22; type locality: Tonkin, Prov. Vinh-Yen, Tam-dao, 1,400 m.

Male genitalia. See IMURA (1995, pp. 4–5, figs. 7–10). Supplementary descriptions:—Endophallus with the basal lateral lobes only weakly inflated, median lobe (=“vertical lobe” sensu IMURA, 1995, p. 4) extraordinarily developed to form a horn-like projection, parapraeputal lobes moderately developed with the left one a little larger than the right, both podian and apical lobes (newly proposed term in this paper, see Figs. 2 & 4) not so remarkably inflated.

Specimens examined. 1 ♂ (for morphological examination of genitalia), Tam Dao, 1,200 m, Vinh Phu Prov., N Vietnam, 24–IX–1994, S. UENO leg.; 1 ♂ (for SEM), same locality, V–1993, H. KARUBE leg.; 1 ♀ (for DNA analysis in SU *et al.*, 1998), same locality (950 m in alt.), 17–VI–1997, S. NOMURA leg.

2) *Carabus (Apotomopterus) arrowi arrogantior* DEUVE

(Figs. 3, 8–9)

Carabus (Apotomopterus) arrogantior DEUVE, 1991, *Nouv. Revue Ent.*, (N. S.), **8**, p. 102; type locality: Chine, Guangxi, Longsheng Gezu Zizhixian, Huaping.

Carabus (Apotomopterus) arrowi arrogantior: IMURA, 1996, *Elytra*, Tokyo, **24**, p. 187, fig. 7.

Male genitalia. See IMURA (1996 b, p.187, fig. 7). Supplementary descriptions:— Basal lateral lobes extraordinarily inflated on both sides, median lobe hardly developed, parapraeputial lobes rather strongly protrudent dorsad and almost symmetrical, apical portion of endophallus very short and undeveloped, both apical and podian lobes not swollen at all.

Specimens examined. 2 ♂♂ (for morphological examination of genitalia), 1 ♀ (for DNA analysis), above Antang Ping (1,820 m), on Mt. Miao'er Shan in Xing'an Xian of northeastern Guangxi, South China, 25~27-V-1996, Y. IMURA leg.

3) *Carabus (Apotomopterus) laoshanicus laoshanicus* IMURA

(Fig. 4)

Carabus (Apotomopterus) inagakii laoshanicus IMURA, 1995, *Gekkan-Mushi*, Tokyo, (287), p. 9, figs. 5–6, 13–15; type locality: Mt. Lao Shan on the Dayao Shan Mts., Jinxiu Xian, Guangxi, South China.

Carabus (Apotomopterus) laoshanicus: IMURA & MIZUSAWA, 1996, *The Carabus of the World*, p. 130, pl. 21, figs. 170–1, 2.

Male genitalia. See IMURA (1995, pp. 9–10, figs. 13–15). Supplementary descriptions on the endophallus:— Basal lateral lobes well-developed and strongly inflated laterad on both sides with the left lobe a little larger than the right, median lobe absent, parapraeputial lobes rather small and only weakly and roundly inflated dorsad, apical lobes rather remarkably protruded though small, podian lobes inconspicuous.

Specimens examined. 2 ♂♂ (1 ♂ for morphological examination of genitalia, 1 ♂ for DNA analysis), Dayao Shan Mts. in eastern Guangxi, South China, VIII-1996, collected by a native collector.

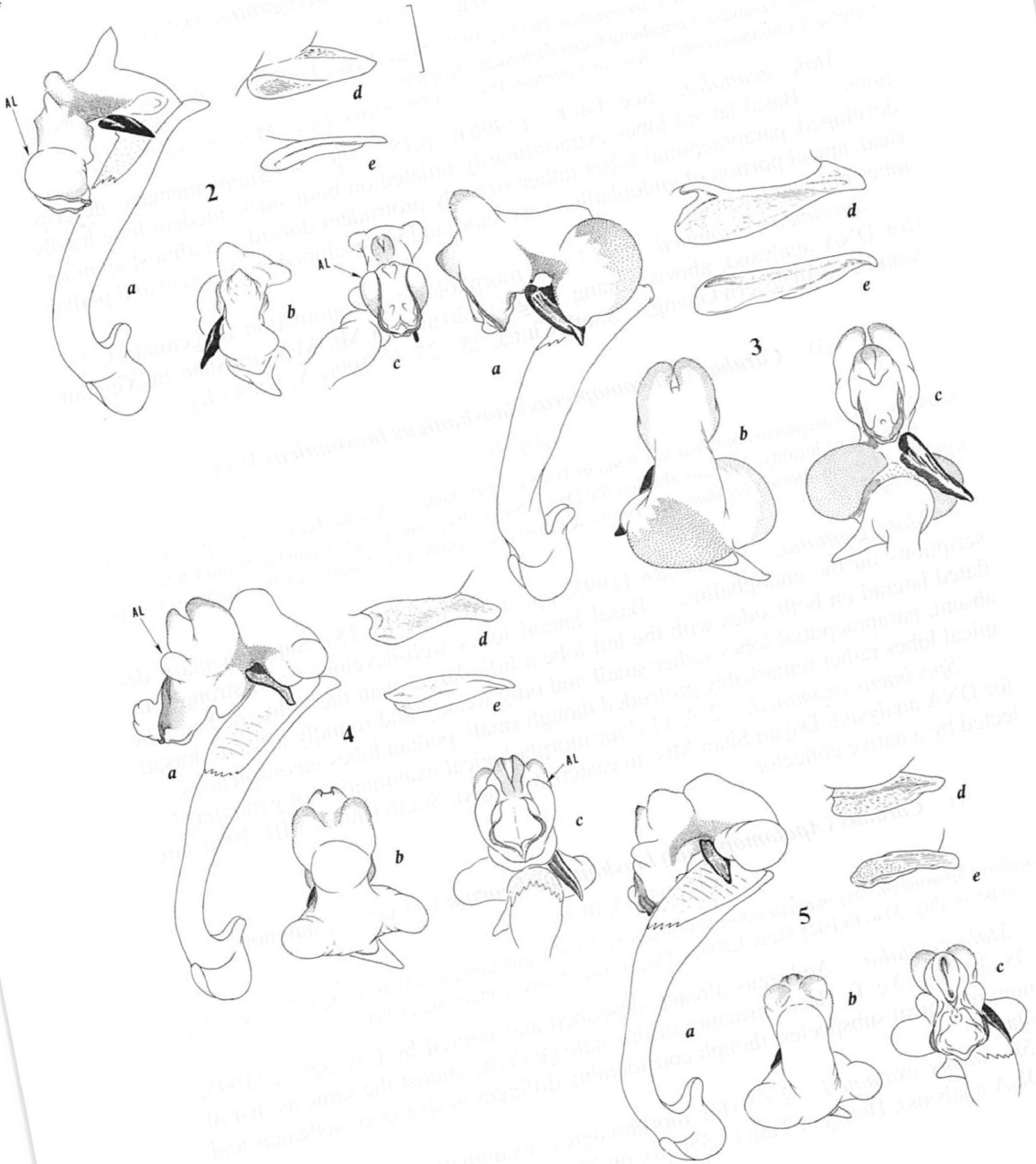
4) *Carabus (Apotomopterus) laoshanicus liaorum* CAVAZZUTI, stat. nov.

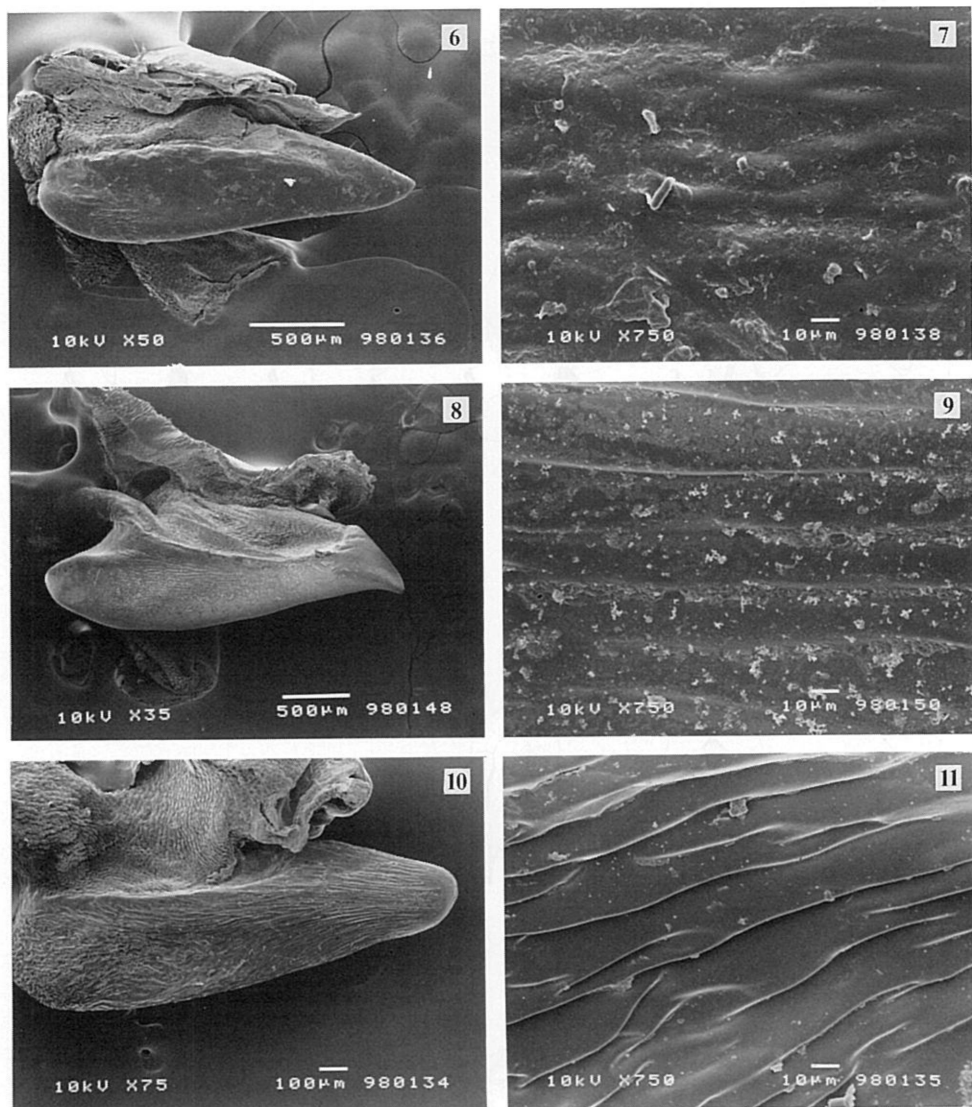
(Figs. 5, 10–11)

Carabus (Apotomopterus) inagakii liaorum CAVAZZUTI, 1995, *Lambillionea*, (95), p. 38, figs. 2 b, 3 e–f, 4 c; type locality: Mao Er [sic] Shan, 1,500 m, Guanxi [sic] N-occidentale [sic], Cina.

Male genitalia. Aedeagus already described and figured by CAVAZZUTI, (1995, pp. 38–39, figs. 3 e–f). Basic structure of the male genitalia almost the same as that of the nominotypical subspecies, though considerably different in shapes of aedeagus and spinula.

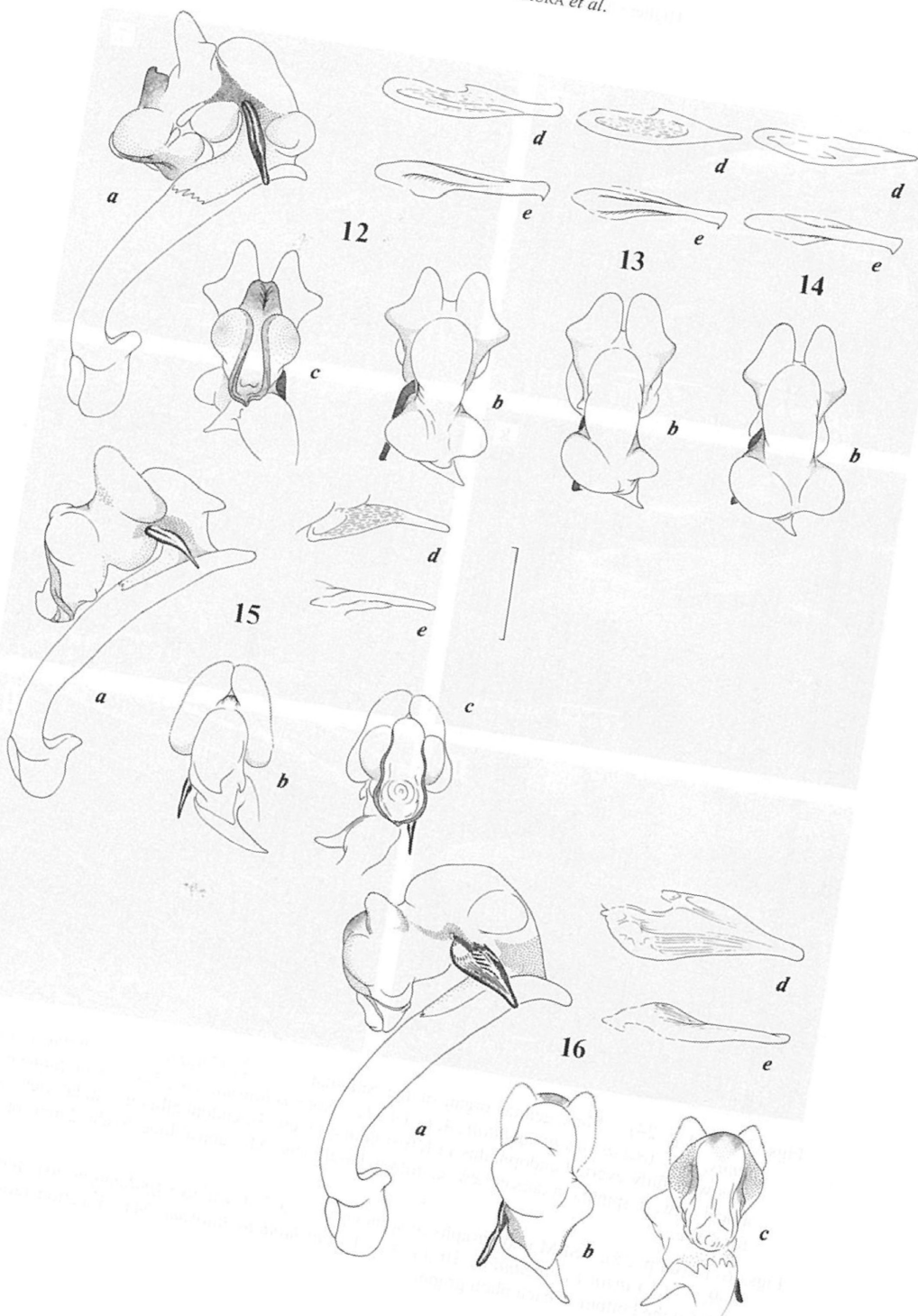
Specimens examined. 2 ♂♂ (for morphological examination of genitalia), 1 ♀ (for DNA analysis), Hongjun Ting (1,550 m), on Mt. Miao'er Shan in Xing'an Xian of

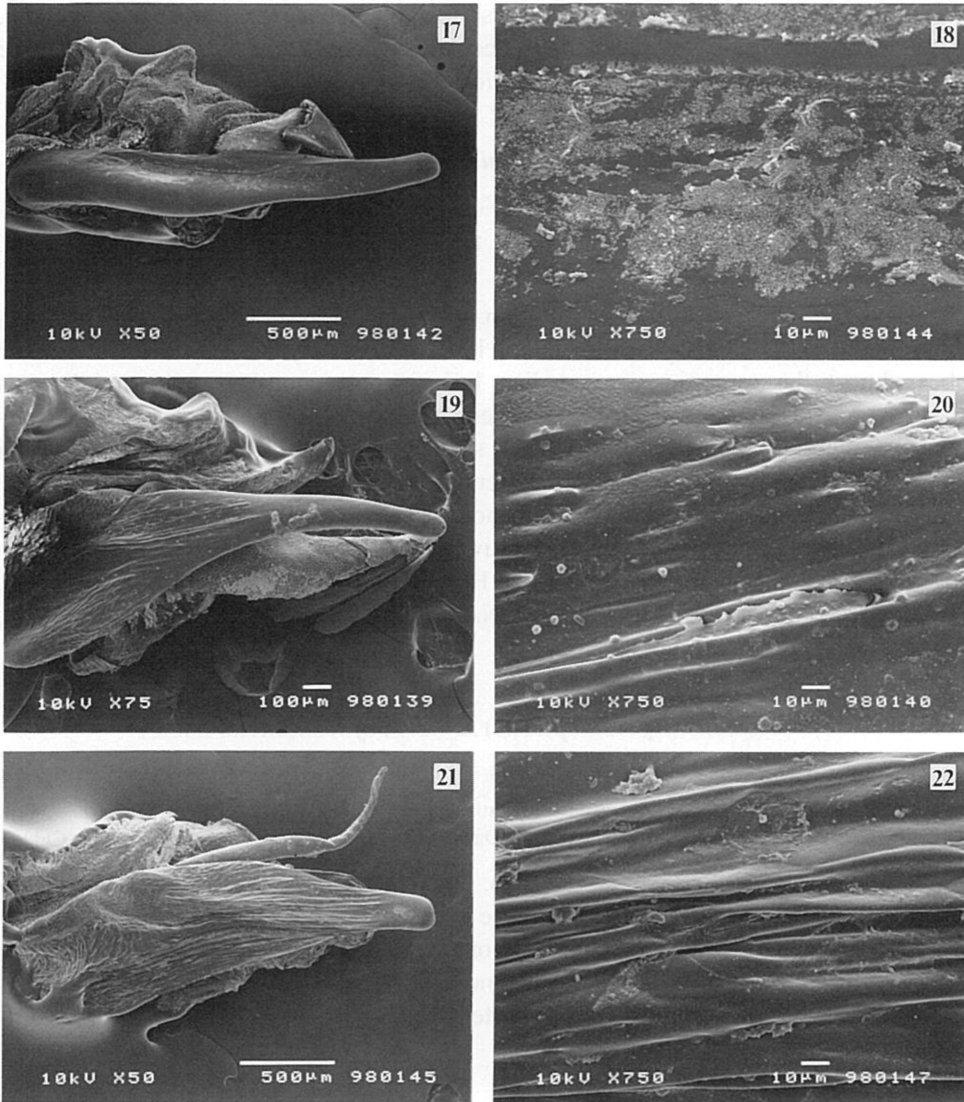




Figs. 2–5 (on p. 24). Male genital organ of the Spinulati. — 2, *Carabus (Apotomopterus) clermontianus*; 3, *C. (A.) arrowi arrogantior*; 4, *C. (A.) laoshanicus laoshanicus*; 5, *C. (A.) l. liaorum*; a, aedeagus with fully everted endophallus in left subdorsal view; b, endophallus in caudal view; c, ditto in apical view; d, spinula in dorsal view; e, ditto in basal view; AL=apical lobe. Scale: 2 mm for a–c, 1 mm for d & e.

Figs. 6–11 (on p. 25). SEM photographs of spinula. — 6–7, *Carabus (Apotomopterus) clermontianus*; 8–9, *C. (A.) arrowi arrogantior*; 10–11, *C. (A.) laoshanicus liaorum*. Magnification ratios are indicated at the bottom of each photograph.





Figs. 12–16 (on p. 26). Male genital organ of Spinulati. — 12, *Carabus (Apotomopterus) sauteri sauteri*; 13, *C. (A.) s. dayaoshanicus*; 14, *C. (A.) s. yunkaicus*; 15, *C. (A.) tonkinensis*; 16, *C. (A.) toulgoeti*; a, aedeagus with fully everted endophallus in left subdorsal view; b, endophallus in caudal view; c, ditto in apical view; d, spinula in dorsal view; e, ditto in basal view. Scale: 2 mm for a–c, 1 mm for d & e.

Figs. 17–22 (on p. 27). SEM photographs of spinula. — 17–18, *Carabus (Apotomopterus) sauteri sauteri*; 19–20, *C. (A.) tonkinensis*; 21–22, *C. (A.) toulgoeti*. Magnification ratios are indicated at the bottom of each photograph.

northeastern Guangxi, South China, 27-V-1996, Y. IMURA leg.

Notes. This taxon was originally described as a subspecies of *C. (A.) inagakii*. Judging from both morphological and molecular phylogenetic viewpoints, it should be regarded as a subspecies of *C. (A.) laoshanicus*.

5) *Carabus (Apotomopterus) sauteri sauteri* ROESCHKE

(Figs. 12, 17–18)

Carabus Sauteri ROESCHKE, 1912, Suppl. ent., Berlin, 1, pp. 4–6; type locality: Suisharyo (=Shui-she-liao), Taiwan.

Male genitalia. See IMURA (1994, pp. 4–6, figs. 32–33). Supplementary descriptions on the endophallus:— Basal lateral lobes moderately developed and both the lobes almost the same in size, median lobe inconspicuous, parapraeputal lobes strongly protruded dorsad with weaker lateral projections on both sides at basal portions, praeputal pad remarkably raised and strongly pigmented, both apical and podian lobes not so strongly inflated though apparently recognizable.

Specimens examined. 1 ♂ (for morphological examination of genitalia), Mt. Pei-chatien Shan in Taipei Hsien, northern Taiwan, 9–VII–1994, M. TANIKADO leg.; 1 ♂ (for SEM), Mt. Kuan-tao Shan in Jen-ai Hsiang of Nan-tou Hsien, central Taiwan, 5–V–1981, M. TANIKADO leg.; 1 ♂ (for DNA analysis), Nanshanchi in Nantou Hsien, central Taiwan, H. NARA leg.

6) *Carabus (Apotomopterus) sauteri dayaoshanicus* IMURA

(Fig. 13)

Carabus (Apotomopterus) sauteri dayaoshanicus IMURA, 1995, Gekkan-Mushi, Tokyo, (287), p. 9, figs. 3–4, 10–12; type locality: Mt. Lao Shan on the Dayao Shan Mts., Jinxiu Xian, Guangxi, South China.

Male genitalia. See IMURA (1995, p. 9, figs. 10–12). Basal lateral lobes of endophallus with the left one larger than the right, parapraeputal lobes more roundly shaped at tips with the basal lateral projections weaker.

Specimens examined. 2 ♂♂ (1 ♂ for morphological examination of genitalia, 1 ♂ for DNA analysis), Dayao Shan Mts. in eastern Guangxi, South China, VIII–1996, collected by a native collector.

7) *Carabus (Apotomopterus) sauteri yunkaicus* DEUVE

(Fig. 14)

Carabus (Apotomopterus) yunkaicus DEUVE, 1991, Bull. Soc. ent. Fr., 96, pp. 224, 226, fig. 3; type locality: Chine, Guangxi, Longsheng Xian, 1,420 m.

Carabus (Apotomopterus) sauteri yunkaicus: IMURA, 1994, Elytra, Tokyo, 22, pp. 12–13, figs. 14–15, 23–31, 40.

Male genitalia. See IMURA (1994, pp. 12–13, fig. 40). Supplementary descrip-

tions:— Membraneous preostium obviously swollen in fully everted condition, basal lateral lobes a little more strongly inflated than in the above two subspecies, parapraeputal lobes almost the same in shape as those of subsp. *dayaoshanicus*.

Specimens examined. 1 ♂ (for morphological examination of genitalia), 1 ♀ (for DNA analysis), above Antang Ping (1,820 m), on Mt. Miao'er Shan in Xing'an Xian of northeastern Guangxi, South China, 25~27-V-1996, Y. IMURA leg.

8) *Carabus (Apotomopterus) tonkinensis* DEUVE

(Figs. 15, 19–20)

Carabus (Apotomopterus) tonkinensis DEUVE, 1990, Bull. Soc. Sci. Nat. (65), p. 26, figs. 1, 4; originally designated type locality: "Vietnam Tonkin, Tam Dao".

Carabus (Apotomopterus) tonkinensis: IMURA, 1995, Bull. natn. Sci. Mus., Tokyo, (A), **21**, pp. 2–4, figs. 1–6; most probable distributional area: the high altitudinal area of the northwestern part of N Vietnam around Phang Si Pang.

Male genitalia. See IMURA (1995, pp. 2–4, figs. 3–6). Supplementary descriptions:— Endophallus with the basal lateral lobes not swollen at all, median lobe apparently recognized, with a small accessory projection at a little right side, parapraeputal lobes well-developed and symmetrical, with the basal portions strongly inflated ventrad, praeputal pad vestigial, apical lobes roundly inflated, podian lobes very small but clearly recognizable.

Specimens examined. 1 ♂ (for morphological examination of genitalia), Hoang Lien Son Mts., N of Phang Si Pang, 1,920 m, Lao Cai Prov., N Vietnam, 10-X-1994, S. UÉNO, M. SATÔ & Y. NISHIKAWA leg.; 1 ♂ (for SEM), Sa Pa, 2,300 m, SW of Lao Cai, 20~26-VI-1991, M. ITÔ leg.; 1 ♀ (for DNA analysis), Deo Tram Ton, 1,950 m, Lao Cai Prov., N Vietnam, 29-VI-1997, S. NOMURA leg.

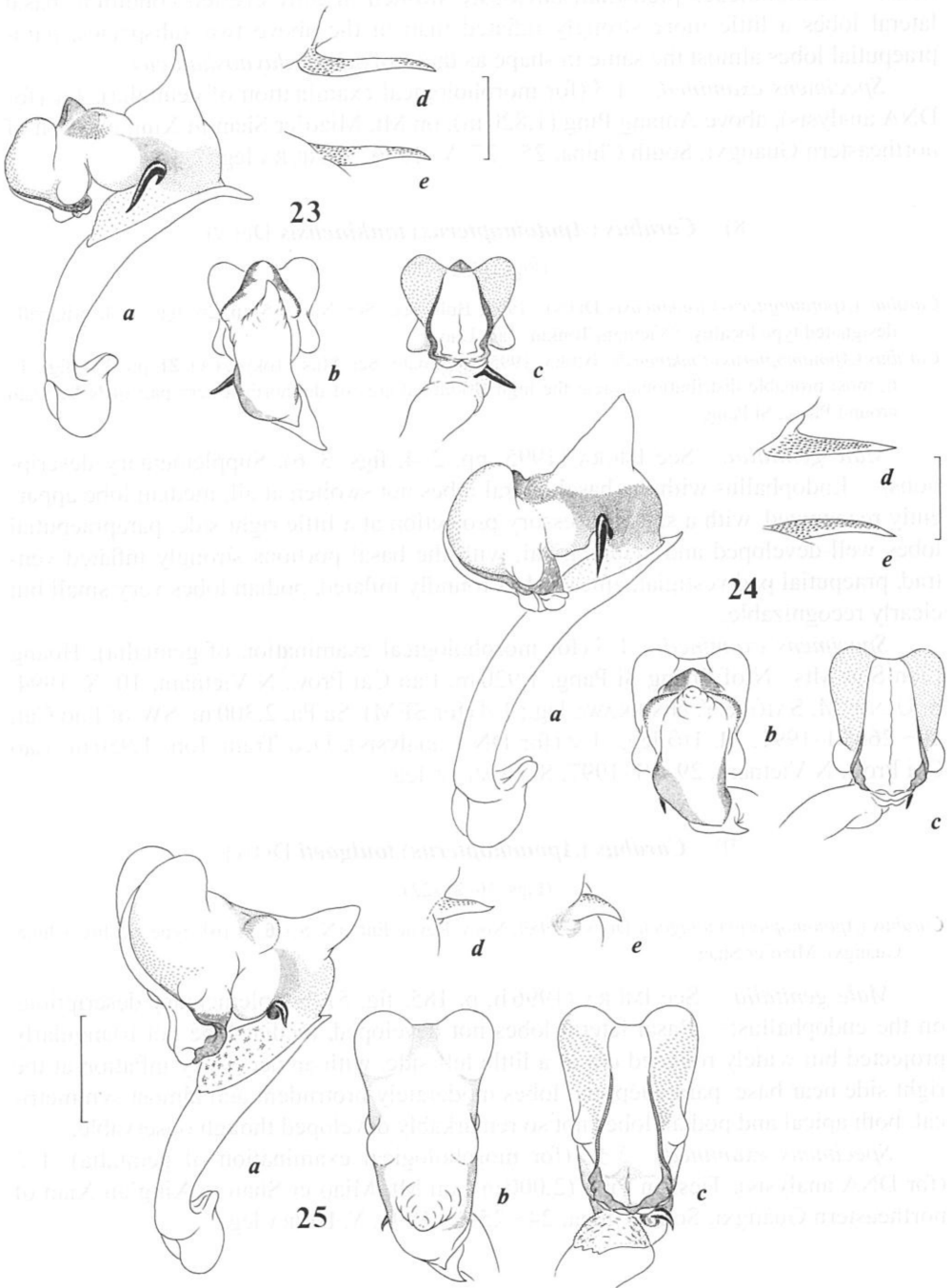
9) *Carabus (Apotomopterus) toulgoeti* DEUVE

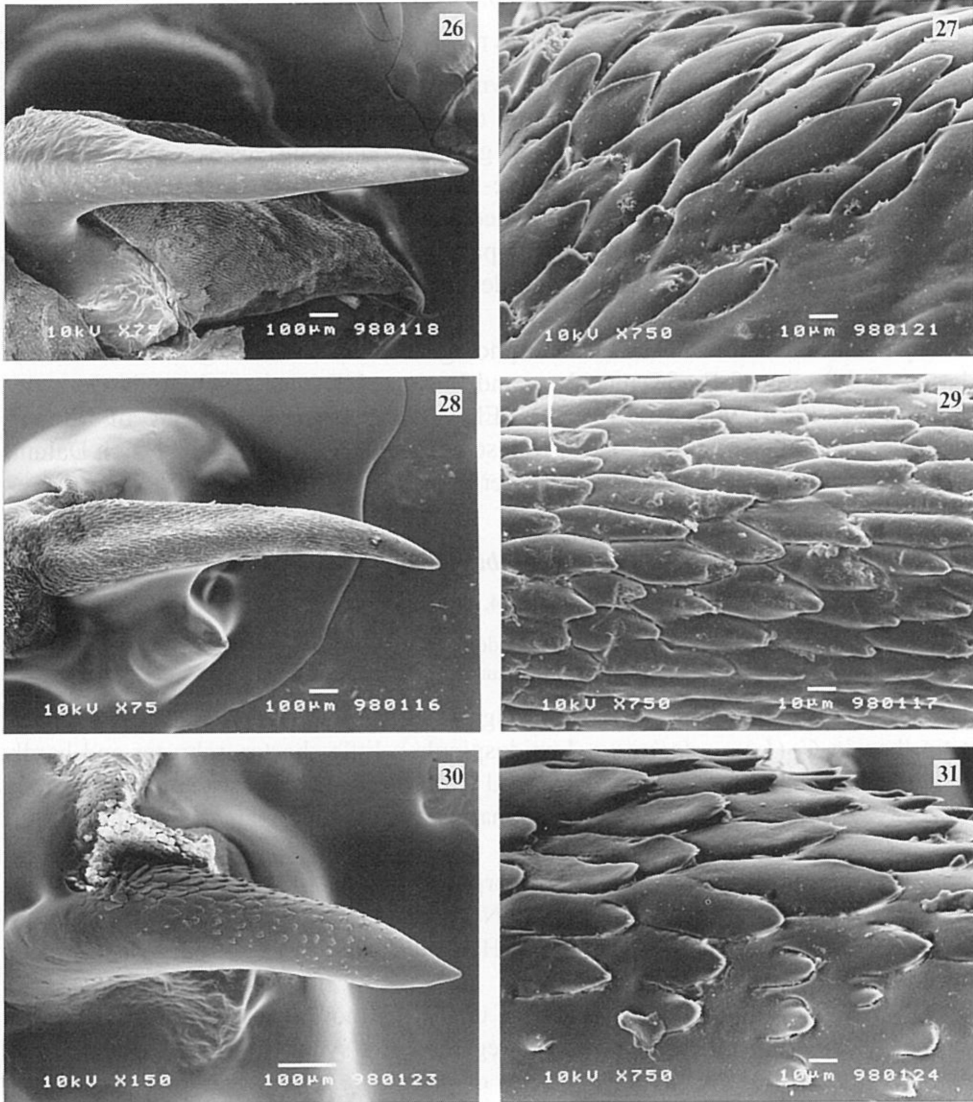
(Figs. 16, 21–22)

Carabus (Apotomopterus) toulgoeti DEUVE, 1989, Nouv. Revue Ent., (N. S.), **6**, p. 161; type locality: Chine, Guangxi, Miao'er Shan.

Male genitalia. See IMURA (1996 b, p. 185, fig. 5). Supplementary descriptions on the endophallus:— Basal lateral lobes not developed, medial lobe not triangularly projected but widely rounded out at a little left side, with an accessory inflation at the right side near base, parapraeputal lobes moderately protrudent and almost symmetrical, both apical and podian lobes not so remarkably developed though observable.

Specimens examined. 2 ♂♂ (for morphological examination of genitalia), 1 ♀ (for DNA analysis), Tieshan Ping (2,000 m), on Mt. Miao'er Shan in Xing'an Xian of northeastern Guangxi, South China, 24~25-V-1996, Y. IMURA leg.





Figs. 23–25 (on p. 30). Male genital organ of *Lepidospinulati* nov. — 23, *Carabus (Limnocarabus) clathratus clathratus*; 24, *C. (L.) maacki aquatilis*; 25, *C. (Euleptocarabus) porrecticollis*; a, aedeagus with fully everted endophallus in left subdorsal view; b, endophallus in caudal view; c, ditto in apical view; d, lepidospinula in dorsal view; e, ditto in basal view. Scale: 2 mm for a–c, 1 mm for d & e.

Figs. 26–31 (on p. 31). SEM photographs of lepidospinula. — 26–27, *Carabus (Limnocarabus) clathratus clathratus*; 28–29, *C. (L.) maacki aquatilis*; 30–31, *C. (Euleptocarabus) porrecticollis*. Magnification ratios are indicated at the bottom of each photograph.

10) *Carabus (Limnocarabus) clathratus clathratus* LINNÉ

(Figs. 23, 26–27)

Carabus clathratus LINNÉ, 1761, Faun. succ., 2nd ed., p. 218; presumable type area: North Germany.

Male genitalia. Aedeagus as shown in Fig. 10a. Membraneous preostium strongly inflated and remarkably rugulose on the surface. Endophallus with a spine-like basal sclerite (=lepidospinula) almost glabrous on the surface except for the basal part which is densely covered with scale-like microstructure as observed by SEM (Figs. 26–27), basal lateral lobes absent, median lobe markedly developed and triangularly shaped, with sharply pointed apex, parapraeputal lobes vestigial, apical lobes strongly inflated, podian lobes also well-developed though much smaller than apical lobes.

Specimens examined. 1 ♂ (for morphological examination of genitalia), between Gartow and Pevestorf, E of Dannenberg and Lüchow, NE Niedersachsen, N Germany, 18–VI–1986, K. STAVEN leg.; 1 ♂ (for SEM), Oppenweher Moor, NW of Minden, Niedersachsen, N Germany, V–1977, REBISCHKE leg.; 1 ♀ (for DNA analysis), Dalums Moor near Lingen, W Niedersachsen, N Germany, 17–VII–1997, K STAVEN leg.

11) *Carabus (Limnocarabus) maacki aquatilis* BATES

(Figs. 24, 28–29)

Carabus aquatilis BATES, 1883, Trans. ent. Soc. London, 1883, p. 224; type locality: "Shimonosuwa Lake" (=presumably Lake Suwa-ko in Nagano Prefecture, central Honshu, Japan).

Male genitalia. Aedeagus much longer, slenderer and less acutely bent ventrad at tip than in *C. (L.) c. clathratus*. Lepidospinula a little shorter, robuster and hardly sinuate throughout, its surface fully covered with scale-like microstructure as shown in Figs. 28–29. Membraneous part of endophallus as in the German species, though the median lobe a little larger and robuster.

Specimens examined. 2 ♂♂ (for morphological examination of genitalia), the riverside marsh of the Riv. Iwaki-gawa, in Nakasato Town of Kita-tsugaru County, Aomori Prefecture, near the northern end of Honshu, Japan, 5–VII–1987, Y. IMURA leg.; 1 ♀ (for DNA analysis), same locality.

Notes. The taxon *aquatilis* has been treated by most authors as one of the local races of *C. clathratus*, though sometimes regarded as a synonym of subsp. *maacki* (cf. NAKANE, 1962, p. 44), or as a subspecies of *Apotomopterus (Limnocarabus) maacki* (cf. ISHIKAWA, 1985, pp. 32–33). Here we regard *maacki* as a race specifically differentiated from *C. clathratus*, and place *aquatilis* as a subspecies of *C. (L.) maacki*, based upon both morphological and molecular phylogenetic findings.

12) *Carabus (Euleptocarabus) porrecticollis* BATES

(Figs. 25, 30–31)

Carabus porrecticollis BATES, 1883, Trans. ent. Soc. London, **1883**, p. 228; type locality: "Urasa, and on the north-west coast at Akita and Sakata" (Urasa is situated in Yamato Town of Minami-Uwonuma County, Niigata Prefecture, central Honshu, Japan).

Male genitalia. Aedeagus as shown in Fig. 13 a, which is very small as compared with the body size. Membraneous preostium strongly inflated and remarkably rugulose as in the above two species. Endophallus with lepidospinula as figured in Figs. 13 d–e, very small, short and thorn-shaped, with the surface rather sporadically covered with scale-like microstructure as observed by SEM (Figs. 30–31), basal lateral lobes absent, median lobe large and triangularly shaped, parapraeputal lobes recognized though small, praeputal pad vestigial, apical portion disproportionately large, with extraordinarily inflated apical lobes and relatively small podian lobes.

Specimens examined. 1 ♂ (for morphological examination of genitalia), Kamado in Mizunami City, Gifu Prefecture, central Honshu, Japan, 9–IV–1975, Y. IMURA leg.; 1 ♂ (for SEM), southern slope of Mt. Ogura-yama near Nikkō City, Tochigi Prefecture, central Honshu, Japan, 11–III–1973, Y. IMURA leg.; 1 ♀ (for DNA analysis), be-

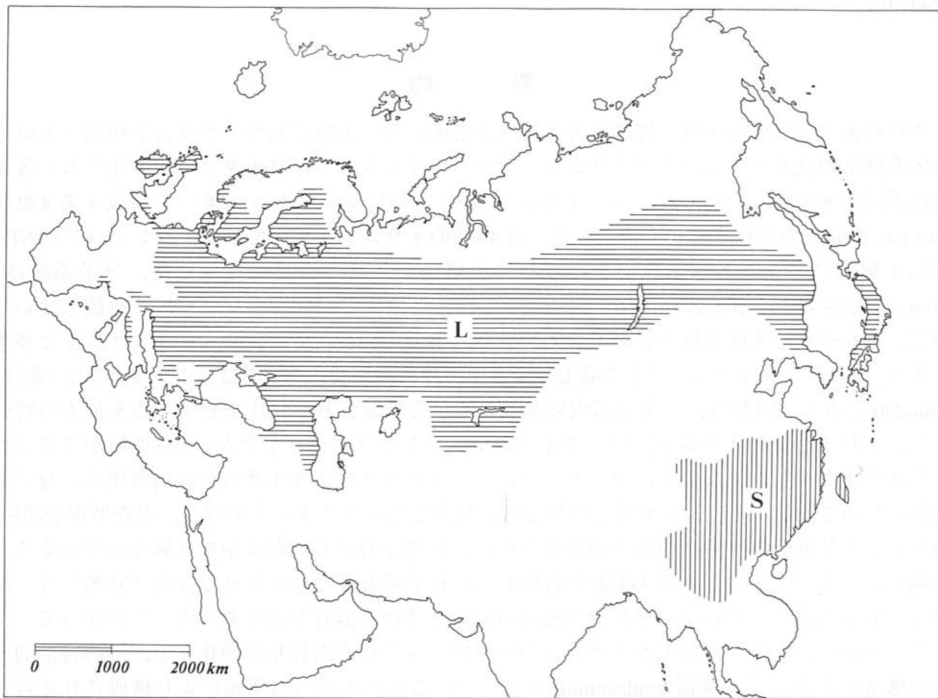


Fig. 32. Map showing the distributional range of Spinulati (S) and Lepidospinulati nov. (L).

tween Nenoue-kôgen and Agi in Nakatsugawa City, Gifu Prefecture, central Honshu, Japan, 10-X-1997, O. TOMINAGA leg.; 1 ♀ (*idem.*), Hiraizumi-chô, Iwate Prefecture, northern Honshu, Japan, 22-XI-1996, O. TOMINAGA leg.; 1 ♀ (*idem.*), Komagane City, Nagano Prefecture, central Honshu, Japan, 24-XII-1996, O. TOMINAGA leg.

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要 約

井村有希・金 衝坤・蘇 智慧・大澤省三：形態と分子系統に基づくオサムシ亜族の上位分類体系構築の試み—とくにトゲオサムシ、マークオサムシおよびアキタクロナガオサムシ各亜属の系統的位置について。——オサムシ亜族（＝広義のオサムシ属）を構成する8亜群（IMURA, 1996）のそれぞれから抽出した、計45種のオサムシを用いて、ミトコンドリアのND5遺伝子解析に基づく分子系統樹を作成し、上位分類体系の再検討を行った。分子系統は、IMURAの形態学的分類におおむね一致しているが、各亜群はほぼ同時期に分岐、放散しているので、それぞれを等価な群と認めてよく、さらに上位のレベルでこれらを真正オサムシと多条オサムシの2群にグルーピングする必要はなさそうである。唯一の例外は、トゲオサムシ（亜）群 Spinulatiである。同群は、♂交尾器内袋基部に基棘と呼ばれる硬化片を有する点を最大の特徴とし、これまでトゲオサムシ、マークオサムシ、アキタクロナガオサムシの3亜属がここに含められてきた。しかしながら、マークオサムシとアキタクロナガオサムシの両亜属は、分子系統樹において、トゲオサムシ亜属とは異なる、独立したクラスターを形成し、走査型電子顕微鏡を用いた基棘表面の微細構造の観察などから、形態学的にも両者はかなり異なっていることが明らかになった。これらの3亜属が共有する固有子孫形質と考えられてきた“基棘”は、ふたつの異なる系列において、それぞれ独自の発達を遂げた器官なのであろう。したがって、マークオサムシ、アキタクロナガオサムシの両亜属にみられる内袋基部硬化片を、その特徴的な表面構造にちなんで、鱗棘 *lepidospinula* と名づけ、これらふたつの亜属により構成される新しい上位分類単位、*Lepidospinulati* nov.（マークオサムシ群）を設立した。

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