

Phylogenetic Studies of the Subgenus *Nialoe* (s. lat.) (Coleoptera, Carabidae, Genus *Pterostichus*), Part 2: The *Asymmetricus* Species Group

Kôji Sasakawa*

Graduate School of Agricultural and Life Sciences, The University of Tokyo, Yayoi 1-1-1,
Bunkyo-ku, Tokyo 113-8657, Japan

ABSTRACT—*Pterostichus* (*Nialoe*) *asymmetricus* Bates and its allies are revised based on the membranous parts of their genitalia. Four new taxa, *P. (N.) ovaliphallus* sp. nov., *P. (N.) fujimurai ibukiyamanus* ssp. nov., *P. (N.) shotaroi kiimontanus* ssp. nov., and *P. (N.) basilobatus* sp. nov. are described. A cladistic analysis based on 31 morphological characters reveals that *Daisenilaoe* (s. str.) Nakane and Straneo is included as one clade within *Nialoe* (s. str.). The speciation and dispersal process of this species group are also discussed.

Key words: *asymmetricus* species group, *Nialoe* (s. str.), *Daisenilaoe* (s. str.), new taxa, phylogeny

INTRODUCTION

Pterostichus (*Nialoe*) *asymmetricus* Bates, 1883 and its allied species are one of the most differentiated groups in the subgenus *Nialoe* (s. lat.). This apterous group is endemic to the Island of Honshu, in the Japanese Archipelago, and comprises approximately 40 species and subspecies (Tanaka, 1985; Kasahara, 1988b).

Tanaka (1958a, b, c) provided the first synopsis of this group with his descriptions of numerous pterostichine beetles from many areas of Japan. He erected the new subgenus *Nialoe* for *P. (N.) asymmetricus* and described a new species, *P. muranishii* (= *P. fujimurai* Habu, 1958 [Bousquet, 2003]). Despite much differentiation in external structures between them, Tanaka attached importance to the similarity of their aedeagi and included *P. muranishii* in *Nialoe*.

In 1979, Nakane and Straneo erected the new subgenus *Daisenilaoe* for *P. fujimurai*, emphasizing its external peculiarities. Later, Morita (1987) described a second species of *Daisenilaoe* from the Kii Peninsula, *P. shotaroi*.

In his overview of the subgenus *Pterostichus* (s. lat.) of Japan (=the subgenus *Nialoe* (s. lat.) in the present study), Kasahara (1988b) recognized the validity of both the subgenus *Daisenilaoe* (s. str.) and the subgenus *Nialoe* (s. str.). In addition, he divided *Nialoe* (s. str.) into two species groups, the *asymmetricus* species group and the *latistylis* species group. After Kasahara's (1988b) study, many authors

described new taxa under his classification system. In these studies, however, the membranous parts of the genitalia were not fully examined, although they were known to be useful taxonomic characters in *Pterostichini*.

Recently, Sasakawa (2005b) revealed that *P. (N.) fujimurai*, the type species of *Daisenilaoe*, is actually a member of *Nialoe* (s. str.), by cladistic analysis based on morphological characters. Thus, the taxonomy of *Nialoe* (s. str.) and *Daisenilaoe* (s. str.) remains to be revised at the subgeneric and specific levels.

The primary aim of the present study was to clarify the species relationships of *P. (N.) asymmetricus* and its allied species (the *asymmetricus* species group as treated here). A phylogenetic analysis based on 31 morphological characters (17 male genitalia, 4 female genitalia and 10 external structures) revealed that this species group is composed of three clades; *Daisenilaoe* (s. str.) is included within *Nialoe* (s. str.) as one clade. Two new species and two new subspecies are described, and the dispersal process of this species group on Honshu is discussed in relation to their phylogenetic relationships.

MATERIALS AND METHODS

There is currently little consistency among authors in the definitions of species and subspecies in the subgenus *Nialoe* (s. lat.). In the present study, taxa whose differences from their closest relative are qualitative (presence vs. absence of a structure) are tentatively described as species, whereas taxa whose differences from their closest relative are quantitative (e.g., size variation in a structure) are tentatively described as subspecies.

* Corresponding author. Phone: +81-3-5841-5227;
Fax : +81-3-5841-7555;
E-mail: ksasa@fr.a.u-tokyo.ac.jp

To reconstruct the phylogeny of the *asymmetricus* species group (defined below), the 28 ingroup species and subspecies listed in Table 1 were analyzed. Most specimens used in the present study were obtained from the author's collection. The remaining specimens were loaned from the following public or private collections: Laboratory of Forest Zoology, Department of Forest Science, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan (FZUT); Lake Biwa Museum, Shiga, Japan (LBM); The Museum of Nature and Human Activities Hyogo, Hyogo, Japan (MNHAH); The National Science Museum, Tokyo, Japan (NSMT); and the collection of Mr. K. Akita, Mie, Japan.

The distribution pattern of each ingroup species is indicated in Fig. 5. Five species, *P. (N.) bisetosus* (Straneo, 1938), *P. (N.) daisenicus* Ishida, 1958, *P. (N.) dandonis* Kasahara, 1989, *P. (N.) spiculifer yatsuensis* Straneo, 1955 and *P. (N.) mashidai* Ishida, 1959, were used for outgroup comparison. Except for *P. (N.) mashidai*, these species are members of the *uenoi* group (*bisetosus* and *daisenicus*) and the *spiculifer* group (*dandonis* and *spiculifer yatsuensis*) *sensu* Kasahara (1988b), whose relationships to the *asymmetricus* species group were shown by Sasakawa (2005b). The methods of phylogenetic analysis, and the homology and terminology of the component parts of the endophallus (Fig. 6) follow Sasakawa (2005b).

Table 1. List of species or subspecies used in the phylogenetic analysis.

Species or subspecies	Locality [collector or depositories*]
<i>Pterostichus fujimurai fujimurai</i> Habu	Akawase, Kamisaibara-mura, Okayama [OY]
<i>P. fujimurai ibukiyamanus</i> Sasakawa	Mt. Ibukiyama, Gifu [KA]
<i>P. shotaroi shotaroi</i> Morita	Mt. Gyôtokusan (♂) [KA], Kawara-dani Vally (♀) [NSMT], Wakayama
<i>P. shotaroi kiimoutanus</i> Sasakawa	Mts. Ôdaigahara, Nara-Mie [KA]
<i>P. ovaliphallus</i> Sasakawa	Mokkadaira, Fukui [HO]
<i>P. shibatai</i> Ishida	Komoridani Vally, Wakayama [MNHAH]
<i>P. latistylis</i> Tanaka	Mt. Hakutaisan, Saitama [KS]
<i>P. taoi</i> Kasahara	Seto-shi, Aichi [KeM]
<i>P. ohdaisanus</i> Nakane	Mts. Ôdaigahara, Nara [KK&HI]
<i>P. naokii</i> Morita	Fujiwara-chô, Mie [KK]
<i>P. kongosanus</i> Nakane	Mt. Kongôsan, Nara [MNHAH]
<i>P. tottoriensis</i> Morita	Mt. Daisen, Tottori [TS]
<i>P. rhanis kantous</i> Tanaka	Mt. Hakutaisan, Saitama [KS]
<i>P. rhanis angustistylis</i> Tanaka	Mt. Fujisan, Shizuoka [KS]
<i>P. katashinensis katashinensis</i> Habu	Suganuma, Katashina, Gunma [SK]
<i>P. katashinensis naganoensis</i> Tanaka	Karasawa-kôsen, Mts. Yatsu [KS]
<i>P. brunneipennis</i> Straneo	Karasawa-kôsen, Mts. Yatsu [KS]
<i>P. mitoyamanus</i> Tanaka	Name-sawa, Ôtaki-mura, Saitama [TM]
<i>P. musashiensis</i> Kasahara	Hachiôji-shi, Tokyo [KaM]
<i>P. okutamae</i> Tanaka	Mt. Hakutaisan, Saitama [KS]
<i>P. basilobatus</i> Sasakawa	Mt. Chausudake, Tochigi [KS]
<i>P. masahiroi</i> Kasahara	Kôkura-Pass, Fukui [SI]
<i>P. fujisanus</i> Tanaka and Suga	Abe-tôge Pass, Shizuoka [KS]
<i>P. asymmetricus</i> Bates	Kinshô-Pass, Mts. Nikko, Tochigi [RI]
<i>P. tokejii</i> Yoshida and Tanaka	Mt. Hakutaisan, Saitama [KS]
<i>P. nishiyamai</i> Kasahara	Miharu-chô, Fukushima [KS]
<i>P. yokohamae</i> Nakane and Straneo	Yokohama-shi, Kanagawa [KS]
<i>P. isumiensis</i> Kasahara and Saito	Isumi-chô, Chiba [KS]
<i>P. bisetosus</i> (Straneo)	Mts. Ôdaigahara, Nara [KK&HI]
<i>P. daisenicus</i> Ishida	Mt. Daisen, Okayama [OY]
<i>P. dandonis</i> Kasahara	Mt. Dantosan, Aichi [KS]
<i>P. spiculifer yatsuensis</i> Straneo	Karasawa-kôsen, Mts. Yatsu [KS]
<i>P. mashidai</i> Ishida	Mt. Yamanoriyama, Chuka-son, Okayama [OY]

*Abbreviation of collectors or depositories: MNHAH, The Museum of Nature and Human Activities, Hyogo; NSMT, The National Science Museum, Tokyo; HI, Hiroshi Ikeda; HO, Hiroshi Otobe; KA, Katsumi Akita; KK, Kôhei Kubota; KaM, Kazuma Matsumoto; KeM, Keiichi Matsumoto; KS, Kôji Sasakawa; OY, Osamu Yamaji; RI, Ryôtsuke Ishikawa; SI, Shigeki Inoue; SK, Satoshi Kakishima; TM, Tadashi Maehara; TS, Teiji Sota.

SYSTEMATIC ACCOUNT

The *asymmetricus* species group

The *asymmetricus* species group is distinguished from other *Nialoe* (s. lat.) species by a number of character states. In particular, the tubercle on the aedeagus is a synapomorphy, and strongly suggests monophyly of this species group.

This species group is assumed to include 41 species (or subspecies). The 28 species used in the phylogenetic analyses (Table 1), as well as *P. (N.) nakanei* Straneo, 1955, *P. (N.) rhanis rhanis* Tschitschérine, 1902, *P. (N.) brunneipennis akaishicus* Tanaka, 1958, for which I was able to examine only male individuals, doubtlessly belong to this species group. The following ten species might also be included in this group because of the similarity of some external or genital structures: *P. (N.) tahirai* Kasahara, 1992, *P. (N.) ogaensis* Morita, 1995, *P. (N.) watanabei* Tanaka, 1960, *P. (N.) cordatissimus* (Straneo, 1937), *P. (N.) rhanis katoi* Kasahara, 1992, *P. (N.) hozumii* Ishida, 1961, *P. (N.) ishizukai* Kasahara, 1995, *P. (N.) uchiyamai* Morita, 1987, *P. (N.) napaea* Kasahara, 1988, *P. (N.) ohkurai* Morita, 1996. However, both the original descriptions and the redescrptions by subsequent authors (Morita, 1996a, 2004) lack information on most of the important characters, so these species' phylogenetic relationships to the *asymmetricus* species group are unclear.

Diagnosis. Setae of antennal segment 2 more than two. Male sternum 7 with an asymmetrical sexual character that varies morphologically at the subspecific level. Aedeagus strongly bent near basal third; tubercle present on right ventral surface of aedeagus. Endophallus relatively short, not in touch with ventral surface of aedeagus; conspicuous sclerite on endophallus (median pigmented lobe, basal sclerite, and pigmentation of left preapical lobe) absent except for left pigmented band, which is shown in most species. Spermatheca almost straight.

Affinity. According to Sasakawa (2005b), this species group is the sister group to the *spiculifer* group + the *uenoi* group *sensu* Kasahara (1988b). This sister-group relationship is supported by the following characters: right paramere

moderately long and pointed apically (never short and rounded apically); more or less developed left preapical lobe; sexual character on male sternum 7.

***Pterostichus (Nialoe) ovaliphallus* sp. nov.** (Fig. 1)

Diagnosis. This species is externally similar to *P. (N.) latistylis* Tanaka, 1958 and *P. (N.) shibatai* Ishida, 1961, but is easily distinguished from them by the endophallus without lobes.

Description. [External structures]: Length: ♂, 11.5–12.0 mm (mean±SD: 11.7±0.20 mm, n=5), ♀, 11.9–12.7 mm (mean±SD: 12.3±0.38 mm, n=3). Dorsal surface black, shiny. Legs dark brown. Head normal-sized. Pronotum cordate; surface smooth. Elytra elongated-ovate; three dorsal pores on interval 3. Ventral side almost smooth; male sternum 7 with a very short apical prominence; prominence wide, with left corner little produced. [Male genitalia]: Aedeagus with tubercle on right ventral side; left paramere square; right one slightly arcuate and rounded at apex. Endophallus small, without distinct lobe on its right side; left pigmented band rudimentary and weakly pigmented over apical half; left preapical lobe large, weakly sclerotized. [Female genitalia]: Vagina with slightly sclerotized part around median oviduct; spermatheca almost straight, but weakly curved at connected part of spermathecal canal.

Range. Mokkadaira, Fukui.

Holotype. ♂, Mokkadaira, Ôno-shi, Fukui, 19. v. 2002, (H. Otobe), in FZUT collection.

Paratypes. 4 ♂3 ♀, same data as holotype, in collection of H. Otobe and K. Sasakawa.

Other species examined. *P. (N.) latistylis*: 1 ♂1 ♀, Irikawa forest road, ca 1300m, Mt. Hakutaisan, Ôtaki-mura, Saitama, (K. Sasakawa). *P. (N.) shibatai*: 1 ♂ (Holotype), "Mt. Gomanodan (Komoridani), Wakayama, Japan", (MNHAH); 2 ♂1 ♀, Komoridani, alt. 800m, Ryûjin-mura, Wakayama, (MNHAH); 2 ♂, Sakataidani, Ryûjin-mura, Wakayama, (MNHAH), 2 ♂1 ♀, Rv. Chayagawa, Mandokoro, Eigenji-chô, Shiga, (LBM); 1 ♀, Mt. Ôginosen, Wakasa-chô, Tottori, (O. Yamaji); 1 ♂, Yakôdani, Chizu-chô, Tottori, (O. Yamaji); 1 ♂, Mt. Yamanoriyama, Chûka-son, Okayama, (O. Yamaji). *P. (N.) taotai*: 1 ♂1 ♀, Seto-shi, Aichi, (K. Matsumoto); 1 ♂1 ♀, Men'noki-Pass,

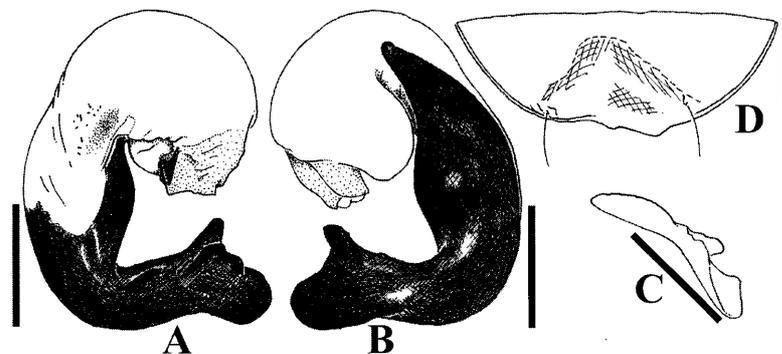


Fig. 1. *Pterostichus (Nialoe) ovaliphallus* sp. nov. (A) endophallus, left lateral view; (B) endophallus, right lateral view; (C) right paramere; (D) male sternum 7, ventral view. Scale line: 1 mm.

Inabu-chô, (K. Sasakawa).

Remarks. Two allied species that I was not able to examine directly have been described from Chûbu District (*P. (N.) napaea* Kasahara, 1988 from Mt. Kisokomagatake and *P. (N.) ohkurai* Morita, 1996 from Kumonotaira near Mt. Jiidake). *P. (N.) ovaliphallus* sp. nov. is distinguished from them by a larger body and shape of the right paramere. However, because the descriptions of the endophalli are lacking in the original descriptions (Kasahara 1988a; Morita 1996b), the relationships these two species to *P. (N.) ovaliphallus* are unresolved.

***Pterostichus (Nialoe) fujimurai ibukiyamanus* ssp. nov.**
(Fig. 2)

Diagnosis. This subspecies is easily distinguished from the nominotypical subspecies by the larger body and the shape of the endophallus.

Description. [External structures]: Length: ♂, 14.6–17.0 mm (mean±SD: 15.6±0.68 mm, n=15), ♀, 16.5–17.5 mm (mean±SD: 17.0±0.35 mm, n=11). Dorsal surface black, shiny. Legs reddish brown. Head normal-sized. Pronotum cordate; surface smooth except for laterobasal impressions that are slightly punctate. Elytra long-oval; three dorsal pores on interval 3. Ventral side almost smooth; male sternum 7 with apical prominence; prominence narrower, almost symmetrical. [Male genitalia]: Aedeagus weakly swollen on right ventral side, with apex hooked; left paramere square; right one short and spatular. Endophallus large; left pigmented band wide and strongly pigmented; right preapical lobe small; left preapical lobe cup-shaped, weakly sclerotized on the inner surface; left apical lobe present, with apex toward ventral side of endophallus. [Female genitalia]: Vagina with slightly sclerotized part around median oviduct; spermatheca almost straight, but weakly curved at connected part of spermathecal gland.

Range. Mt. Ibukiyama, the border between Gifu and Shiga.

Holotype. ♂, Mt. Ibukiyama, 1020–1170m, Kasugamura, Gifu, 7–21. ix. 2003, (K. Akita), in FZUT collection.

Paratypes. 3 ♂4 ♀, same data as holotype; 11 ♂7 ♀,

ditto, (N. Toda), in collection of N. Toda, K. Akita, and K. Sasakawa.

Other species examined. *P. (N.) fujimurai*: 1 ♂2 ♀, Mt. Daisen, Hôki-chô, Tottori, (H. Ikeda); 1 ♂1 ♀, Akawase, Kamisaibara-mura, Okayama, (O. Yamaji).

***Pterostichus (Nialoe) shotaroi kiimontanus* ssp. nov.**
(Fig. 3)

Diagnosis. This subspecies is easily distinguished from the nominotypical subspecies by having a broader pronotum and by the shape of the endophallus.

Description. [External structures]: Length: ♂, 15.8–17.2 mm (mean±SD: 16.3±0.65 mm, n=4), ♀, 16.6–17.8 mm (mean±SD: 17.0±0.39 mm, n=9). Dorsal surface of body dark brown, shiny. Legs reddish brown. Head normal-sized. Pronotum cordate; surface smooth except for weakly punctate laterobasal impressions. Elytra long-oval; four to six dorsal pores on interval 3. Ventral side almost smooth; male sternum 7 with apical prominence; prominence wide, almost symmetrical. [Male genitalia]: Aedeagus weakly swollen on right ventral side, with apex hooked; left paramere square; right one short and spatular. Endophallus large; left pigmented band wide and strongly pigmented; right preapical lobe rudimentary; left preapical lobe cup-shaped, weakly sclerotized on the inner surface; apical part of left preapical lobe absent; left apical lobe present. [Female genitalia]: Vagina with slightly sclerotized part around median oviduct; spermatheca almost straight, but weakly curved at connected part of spermathecal gland.

Range. Ôdaigahara and Ômine Mts., Nara and Mie.

Holotype. ♂, Mt. Ôdaigahara, Kamikitayama-mura, Nara, 29–30. viii. 2001, (K. Akita), in FZUT collection.

Paratypes. 1 ♀, Mt. Ôdaigahara, Miyagawa-mura, Mie, 30. ix. 2001, (K. Akita); 3 ♂5 ♀, Mt. Misen, Tenkawa-mura, Nara, 10–24. viii. 2003, (N. Toda); 3 ♀, ditto, 27. vii.-10. viii. 2003 (N. Toda), in collection of N. Toda, K. Akita and K. Sasakawa.

Other species examined. *P. (N.) shotaroi*: 1 ♂, Mt. Gyôtokusan, Shirahama-machi, (K. Akita); 1 ♀ (paratype), Kawara-dani Vally, Hikigawa-chô, Wakayama, (NSMT).

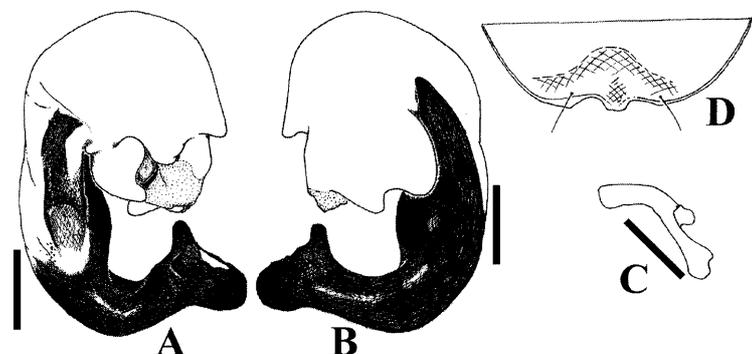


Fig. 2. *Pterostichus (Nialoe) fujimurai ibukiyamanus* ssp. nov. (A) endophallus, left lateral view; (B) endophallus, right lateral view; (C) right paramere; (D) male sternum 7, ventral view. Scale line: 1 mm.

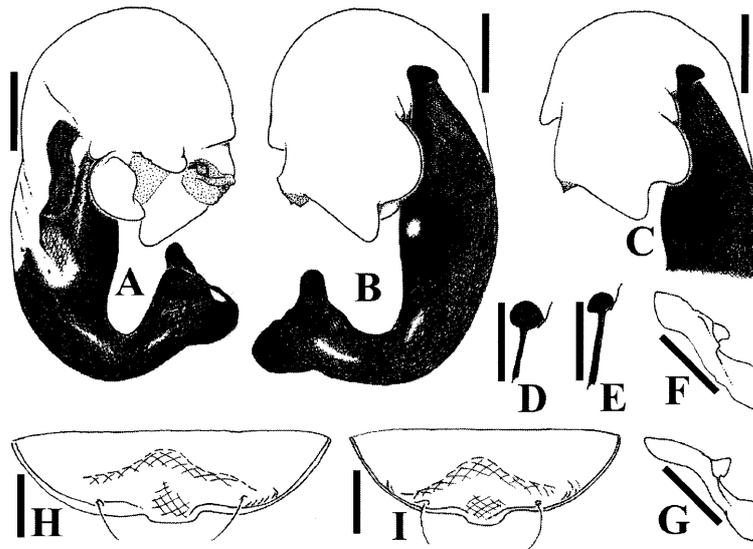


Fig. 3. *Pterostichus (Nialoe) shotaroi*, ssp. *kiimontanus* nov. (A, B, D, F, H) and ssp. *shotaroi* (C, E, G, I). (A) endophallus, left lateral view; (B–C) endophallus, right lateral view; (D–E) apical parts of aedeagus, dorsal view; (F–G) right parameres; (H–I) male sternum 7, ventral view. Scale line: 1 mm.

***Pterostichus (Nialoe) basilobatus* sp. nov.** (Fig. 4)

Diagnosis. This species is externally closely similar to *P. (N.) tokejii* and its allied species (*P. (N.) nishiyamai*, *P. (N.) yokohamae* and *P. (N.) isumiensis*), but is easily distinguished from them by the narrower apical prominence of male sternum 7.

Description. [External structures]: Length: ♂, 18.8–19.1 mm (mean±SD: 18.9±0.24 mm, n=2), ♀, 19.0–20.7 mm (mean±SD: 19.8±1.21 mm, n=2). Dorsal surface of body black, shiny. Legs reddish-brown. Head normal-sized. Pronotum cordate; surface smooth, without punctures. Elytra elongated-ovate; three dorsal pores on interval 3. Ventral side almost smooth; sternum 7 of male with apical prominence; prominence narrower, asymmetrical. [Male genitalia]: Aedeagus with tubercle on right ventral side; left paramere square; right one slender. Endophallus slender; left pigmented band rudimentary and weakly pigmented over apical

half; ostium lobe swollen; hind lobe weakly swollen; left basal and median lobes present, but only slightly swollen; right median lobe present; right preapical lobe small, but distinctly lobate; left preapical lobe large, with surface weakly sclerotized; right apical lobes weakly hooked, left apical lobe present, but not hooked. [Female genitalia]: Vagina with slightly sclerotized part around median oviduct; spermatheca almost straight.

Range. Mt. Chausudake, Nasudake Mts., along border between Tochigi and Fukushima.

Holotype. ♂, Hachiman-Spa, Mt. Chausudake, Nasu-machi, Tochigi, 3–4. ix. 2002, (K. Sasakawa), in FZUT collection.

Paratypes. 1 ♂ 2 ♀, same data as holotype, in collection of K. Sasakawa.

Other species examined. *P. (N.) tokejii*: 1 ♂ 1 ♀, Irikawa forest road, ca 1300m, Mt. Hakutaisan, Ôtaki-mura, Saitama

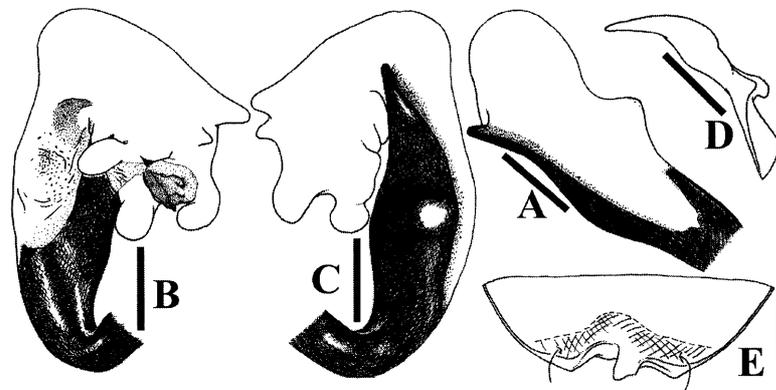


Fig. 4. *Pterostichus (Nialoe) basilobatus* sp. nov. (A) endophallus (basal part was omitted), dorsal view; (B) endophallus, left lateral view; (C) ditto, right lateral view; (D) right paramere; (E) male sternum 7, ventral view. Scale line: 1 mm.

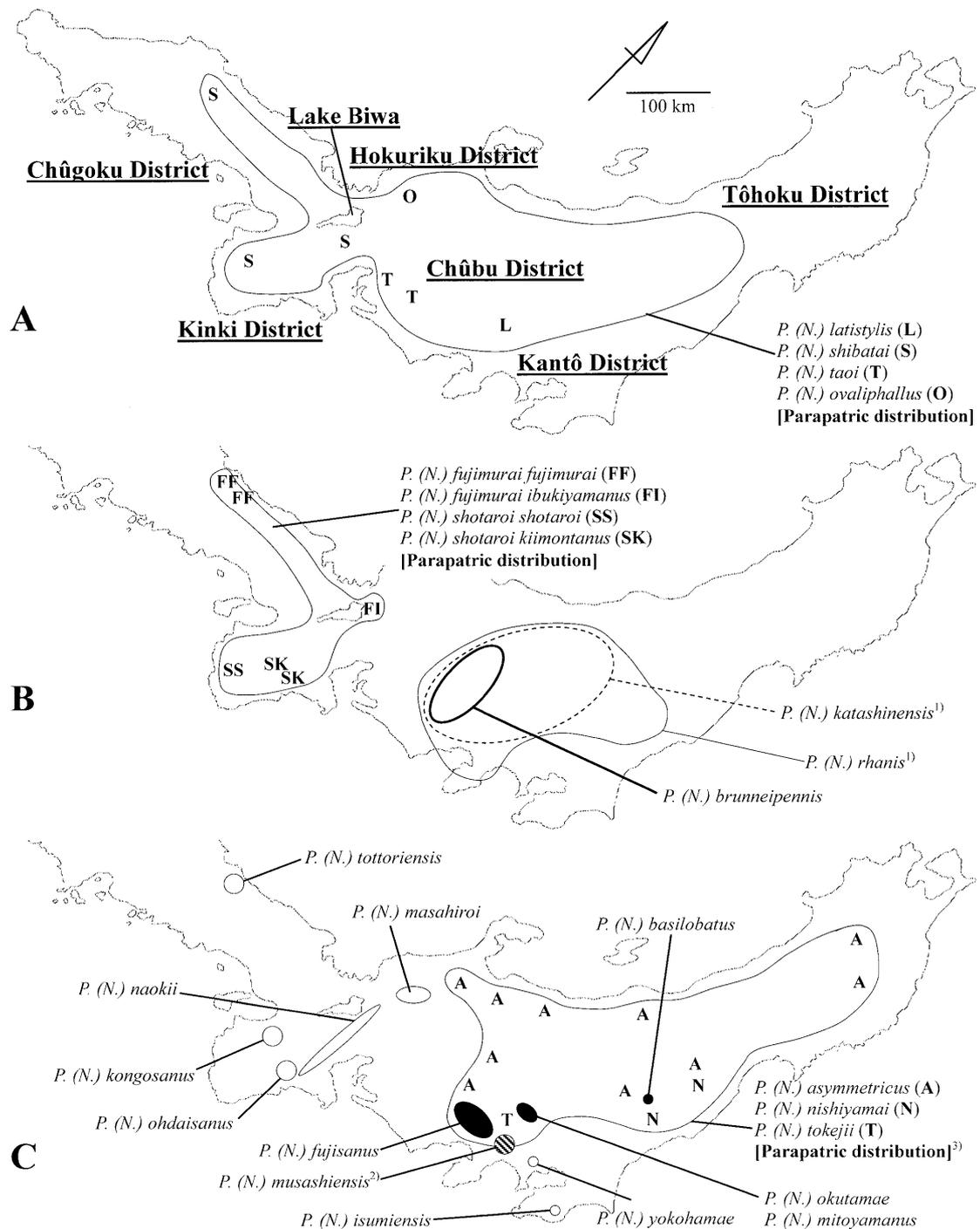


Fig. 5. Distribution of species used in the present study (compiled from Tanaka (1958b, c, 1985), Habu and Baba (1971), Kasahara (1988a, b, 1993), Kasahara and Nishiyama (1990), Kasahara and Saito (1997), Maehara (1998), Mori (2001), Morita (2003) and Sasakawa (unpublished data)). (A) Lineage A species (see phylogenetic part); (B) Lineage B and part of Lineage C species; (C) Part of Lineage C species. The species shown separately in A–C are sympatric.

¹⁾ The distributions of *P. (N.) katashinensis* and *P. (N.) rhanis* at the subspecific level are not shown because the determinations of the subspecies by the senior author were without reliable morphological evidence (e.g., endophallic structure examined in the present study).

²⁾ Though the distribution overlaps with *P. (N.) asymmetricus* and its allies on the map, this species inhabits low mountains, and does not coexist with them.

³⁾ *P. (N.) nishiyamai* and *P. (N.) asymmetricus* have been recognized as distinct species which coexist in the Abukuma Mountains (Kasahara 1986; Kasahara and Nishiyama 1990). However, further study is needed, because "*P. (N.) asymmetricus*" of the Abukuma Mountains has no differences with *P. (N.) nishiyamai* in the endophallus.

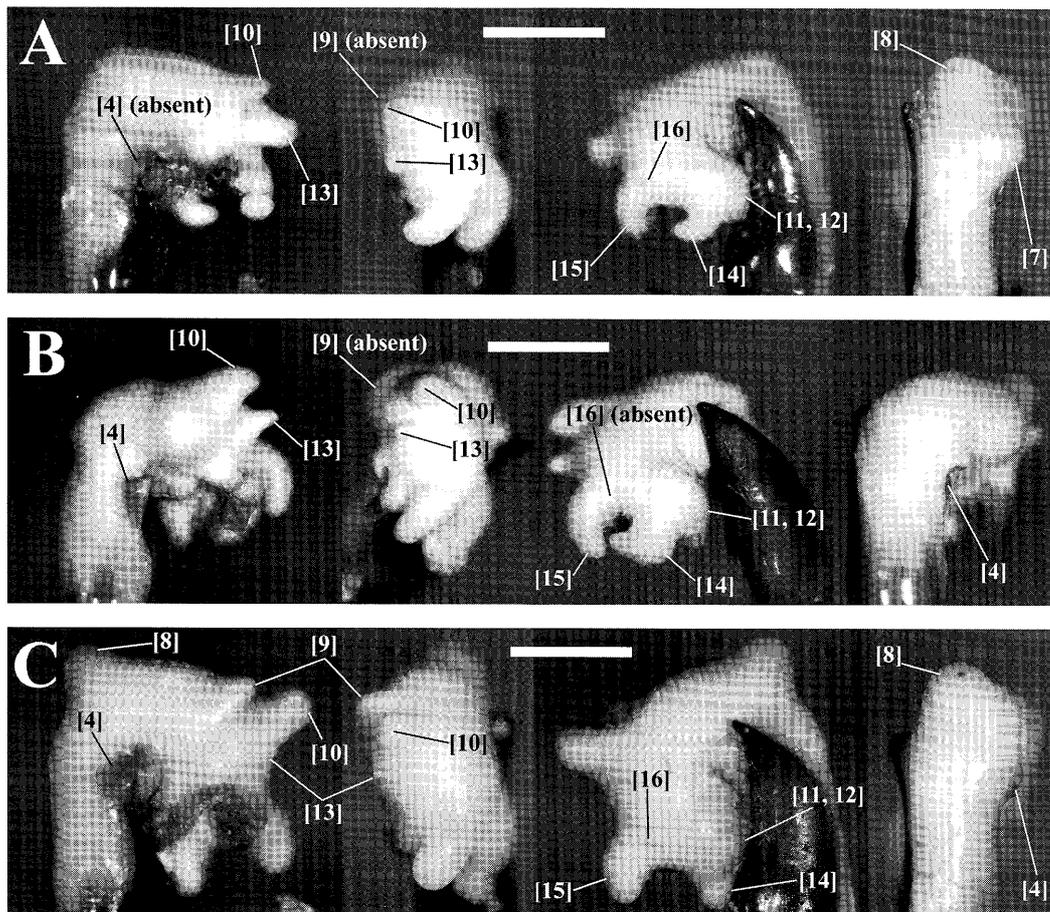


Fig. 6. Homology of the characters of the endophallus (dorsal view of apical half, posterior view, ventral view and dorsal view of basal half). (A) *Pterostichus (Nialoe) ohdaisanus*. (B) *P. (N.) tokejii*. (C) *P. (N.) katashinensis naganoensis*. Numbers in the bracket represent characters in Table 2. Note that homology of lobes on the right side of the endophallus (character numbers 9, 10 and 13) can be revealed by only alignment of lobes seen from posterior view. Scale lines: 1 mm.

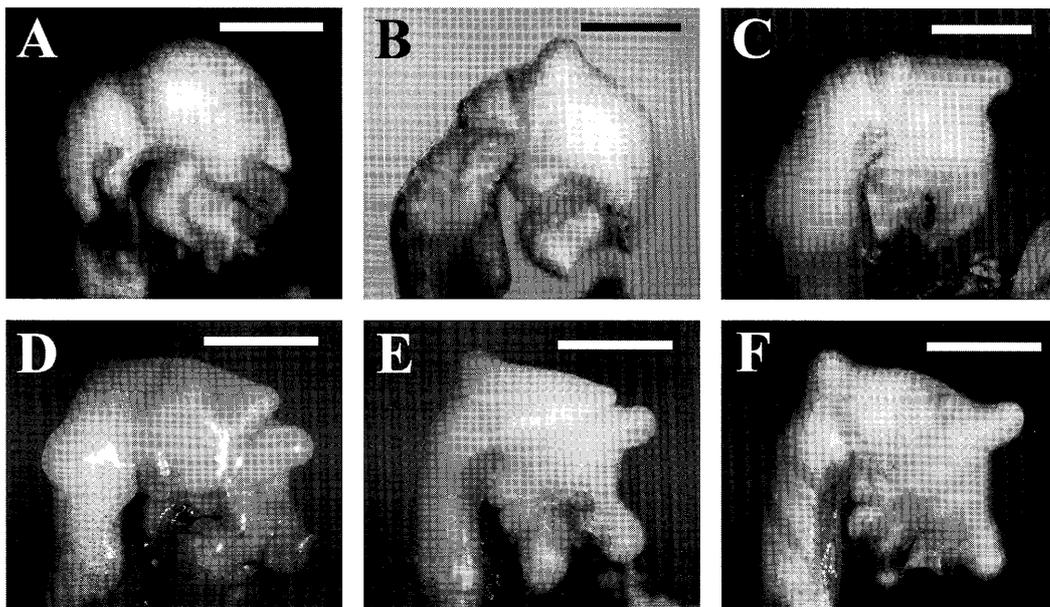


Fig. 7. Endophalli of the *asymmetricus* species group. (A) *P. (N.) fujimurai fujimurai*. (B) *P. (N.) shibatai*. (C) *P. (N.) latistylis*. (D) *P. (N.) totoriensis*. (E) *P. (N.) rhanis kantous*. (F) *P. (N.) brunneipennis*. Scale lines: 1 mm.

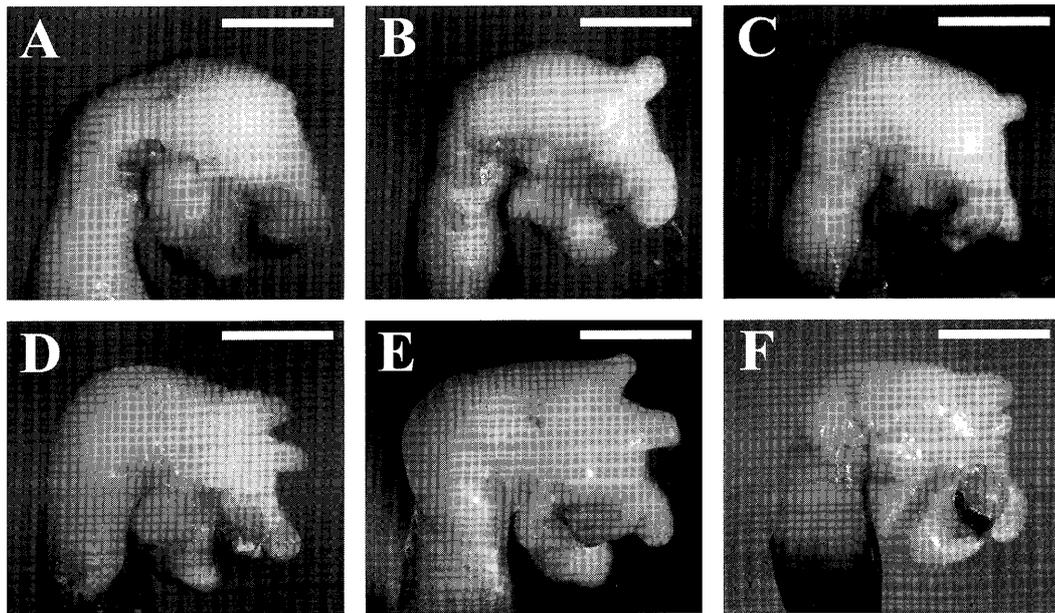


Fig. 8. Endophalli of the *asymmetricus* species group. (A) *P. (N.) mitoyamanus*. (B) *P. (N.) musashiensis*. (C) *P. (N.) okutamae*. (D) *P. (N.) masahiroi*. (E) *P. (N.) fujisanus*. (F) *P. (N.) asymmetricus*. Scale lines: 1 mm.

Table 2. Character matrix for cladistic analyses of the *asymmetricus* species group and outgroup species.

Species or subspecies	1	5	10	15	20	25	30																									
<i>Pterostichus fujimurai fujimurai</i>	0	1	0	1	0	0	0	0	0	0	2	1	2	1	0	0	0	1	1	1	0	1	1	0	0	0	1	1	0			
<i>P. fujimurai ibukiyamanus</i>	0	1	0	1	0	0	0	0	0	0	2	1	2	1	0	0	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	
<i>P. shotaroi shotaroi</i>	0	1	1	1	0	0	0	0	0	0	2	1	2	1	0	0	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	
<i>P. shotaroi kiimontanus</i>	0	1	1	1	0	0	0	0	0	0	2	1	1	1	0	0	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	
<i>P. ovaliphallus</i>	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	2	0	0	1	0	0	0	0	0	0	0	1	
<i>P. shibatai</i>	0	1	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	2	0	2	0	0	1	0	0	0	0	0	0	0	1	
<i>P. latistylis</i>	0	1	0	1	0	0	0	0	1	2	1	0	1	0	0	0	0	2	0	2	0	0	1	0	0	0	0	0	0	0	1	
<i>P. taoi</i>	0	1	0	1	0	0	0	0	2	2	1	0	0	0	0	0	0	2	0	2	0	0	1	0	0	0	0	0	0	0	1	
<i>P. ohdaisanus</i>	2	1	0	0	0	0	2	1	0	2	2	1	3	2	2	1	2	0	0	0	0	0	1	0	2	0	1	0	0	3	1	
<i>P. naokii</i>	2	1	0	0	0	0	2	1	0	2	2	1	3	2	2	1	2	0	1	1	0	0	1	0	2	0	1	0	0	3	1	
<i>P. kongosanus</i>	2	1	0	0	0	0	2	2	0	2	2	1	3	2	3	1	2	0	1	1	0	0	1	0	2	0	1	0	0	3	1	
<i>P. tottoriensis</i>	2	1	0	0	0	0	2	1	0	2	2	1	3	2	3	0	2	0	1	1	0	0	1	0	2	0	1	0	0	3	1	
<i>P. rhanis kantous</i>	1	1	0	1	0	0	0	2	2	2	2	1	1	1	2	0	2	1	1	1	0	0	1	0	1	1	0	0	0	3	1	
<i>P. rhanis angustistylis</i>	2	1	0	1	0	0	0	2	2	2	2	1	1	1	2	0	2	1	1	1	0	0	1	0	1	2	1	0	0	3	1	
<i>P. katashinensis katashinensis</i>	1	1	0	1	0	0	0	2	2	2	2	1	1	1	2	1	2	0	0	0	0	0	1	0	0	2	0	0	0	2	1	
<i>P. katashinensis naganoensis</i>	1	1	0	1	0	0	0	2	2	2	2	1	1	1	2	1	2	1	1	1	0	0	1	0	0	2	0	0	0	2	1	
<i>P. brunneipennis</i>	1	1	0	1	0	0	0	2	2	2	2	1	1	1	2	0	1	0	0	0	0	0	1	0	1	1	0	1	0	3	1	
<i>P. mitoyamanus</i>	2	1	0	1	0	0	0	0	1	2	1	1	0	1	1	2	1	0	1	0	0	1	0	1	1	0	0	0	4	1		
<i>P. musashiensis</i>	2	1	0	1	0	1	0	0	0	2	2	1	0	2	2	0	2	0	1	1	0	0	1	0	0	1	0	0	0	2	1	
<i>P. okutamae</i>	1	1	0	1	0	0	0	0	1	2	2	1	1	0	1	1	1	0	1	0	0	1	1	1	1	0	0	0	3	1		
<i>P. basilobatus</i>	1	1	0	1	0	1	0	1	0	2	2	1	2	1	2	0	2	1	1	1	0	0	1	0	0	0	0	0	0	2	1	
<i>P. masahiroi</i>	2	1	0	0	0	0	1	0	0	2	2	1	2	1	2	0	2	0	1	1	0	0	1	0	2	1	0	0	0	3	1	
<i>P. fujisanus</i>	2	1	0	1	0	0	0	0	0	2	2	1	3	0	2	1	2	1	1	1	0	0	1	0	2	1	1	0	0	1	1	
<i>P. asymmetricus</i>	2	1	0	0	0	0	0	0	0	2	2	1	2	2	2	0	2	0	1	1	0	0	1	0	1	1	0	0	0	4	1	
<i>P. tokejii</i>	2	1	0	2	0	0	0	0	0	2	2	1	2	2	2	1	2	1	1	1	0	0	1	0	1	0	0	0	0	4	1	
<i>P. nishiyamai</i>	2	1	0	2	0	0	0	0	0	2	2	1	2	2	2	1	2	1	1	1	0	0	1	0	1	1	0	0	0	4	1	
<i>P. yokohamae</i>	2	1	0	2	0	0	0	0	0	2	2	1	2	2	2	0	2	1	1	1	0	0	1	0	1	1	0	0	0	4	1	
<i>P. isumiensis</i>	2	1	0	2	0	0	0	0	0	2	2	1	2	2	2	0	2	1	1	1	0	0	1	0	0	1	0	0	0	4	1	
<i>P. bisetosus</i>	2	0	0	0	0	0	2	0	3	0	0	1	0	0	1	0	0	2	0	2	1	0	1	1	1	0	0	0	1	0	1	
<i>P. daisenicus</i>	2	0	0	2	0	0	2	0	2	0	0	1	0	0	0	0	0	2	1	2	0	0	1	0	0	0	0	0	0	1	1	
<i>P. dandonis</i>	2	0	0	2	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	
<i>P. spiculifer yatsuensis</i>	2	0	0	2	2	0	0	0	1	0	1	1	0	0	0	1	0	2	0	1	0	0	0	0	0	1	1	0	0	0	1	1
<i>P. mashidai</i>	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0

(K. Sasakawa). *P. (N.) yokohamae*: 1 ♂ 1 ♀, Kanagawa (K. Sasakawa). *P. (N.) isumiensis*: 1 ♂ 1 ♀, Mangi, Isumi-chō, Chiba (K. Sasakawa). *P. (N.) nishiyamai*: 1 ♂ 1 ♀, Miharu-Dam, Miharu-chō, Fukushima (K. Sasakawa).

PHYLOGENY AND CHARACTER EVOLUTION

Thirty-one variable characters (17 male genitalia, 4 female genitalia and 10 external structures) were observed on adult beetles and coded for phylogenetic analyses (Table 2, Appendix 1).

Both the EW and SW analyses supported monophyly of the *asymmetricus* species group (Fig. 9). However, reliability of the EW analysis was low (bootstrap values < 50%), while that of the SW analysis was relatively high (75%). There were some topological conflicts in the outgroup between the two analyses; however, the ingroup showed no conflicts. The difference in tree length between two analyses may have been due to the change in outgroup topology. Three lineages (A, B and C) emerged in both analyses. The relationships among the three lineages, and the monophyly of each lineage, were supported by high bootstrap values (78–100%).

In the EW analysis, 30 trees of 121 steps were obtained, with CI=0.438 and RI=0.737. Species relationships in Lineages A and B were well resolved and congruent with those of the SW analysis. In contrast, species relationships in Lineage C were mostly unresolved, although monophyly of *P. (N.) kongosanus* + *P. (N.) tottoriensis* + *P. (N.) ohdaisanus* + *P. (N.) naokii*, *P. (N.) okutamae* + *P. (N.)*

mitoyamanus, and two subspecies of *P. (N.) katashinensis* were supported; the remaining species formed an unresolved polytomy.

In the SW analysis, six trees of 125 steps were obtained, with CI=0.424 and RI=0.722. Resolution of Lineage C was improved. *Pterostichus (N.) fujisanus* formed the most basal branch. *P. (N.) katashinensis*, *P. (N.) rhanis*, *P. (N.) brunneipennis*, *P. (N.) mitoyamanus*, and *P. (N.) okutamae* constituted a monophyletic sister group to a clade containing the rest of the species. In the latter group, a *P. (N.) musashiensis* + *P. (N.) basilobatus* clade was situated in the most basal position. Other species were divided into two clades. One clade contained *P. (N.) tokejii*, *P. (N.) nishiyamai*, *P. (N.) yokohamae*, *P. (N.) isumiensis*, and *P. (N.) asymmetricus*, with *P. (N.) asymmetricus* most basal. The other clade included *P. (N.) kongosanus*, *P. (N.) tottoriensis*, *P. (N.) ohdaisanus*, *P. (N.) naokii*, and *P. (N.) masahiroi*, with *P. (N.) masahiroi* in the basal position.

Character changes were reconstructed on one of the most parsimonious trees obtained by the SW analysis (Fig. 10). The monophyly of the *asymmetricus* species group is supported by four character changes: shortening of the right paramere (character 1: state 2→0), presence of a tubercle on the right ventral surface of the aedeagus (character 2: state 0→1), reduced sclerotization of the left pigmented band (character 4: state 2→1), and absence of the right basal lobe (character 9: state 1→0). Four characters (12, 20, 25 and 30), three of which are uniform within the lineage, provide support for the monophyly of Lineage A. Four characters support the monophyly of Lineage B + Lineage

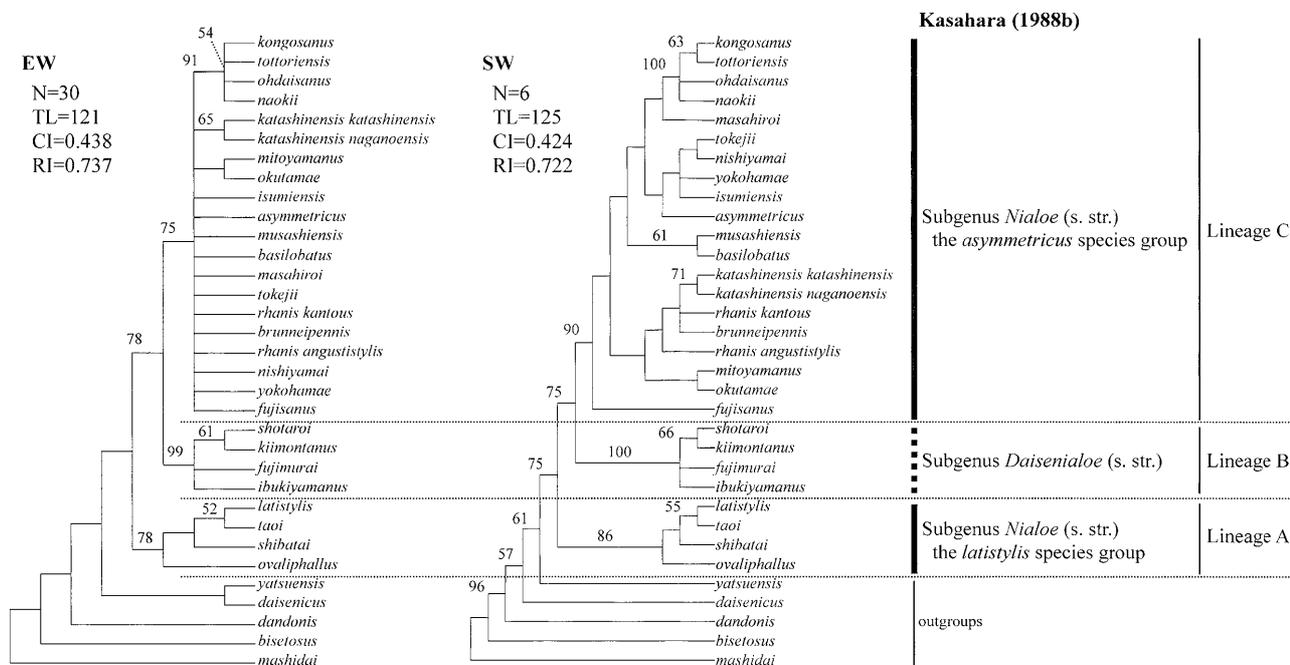


Fig. 9. Consensus trees of the most parsimonious trees obtained by the equal weighting method (EW) and the successive weighting method (SW). The taxonomy of Kasahara (1988) is presented for comparison. Note that subgenus *Nialoe* (s. str.) *sensu* Kasahara, 1988b is non-monophyletic. N, number of equally parsimonious trees; TL, tree length calculated with equally weighted characters; CI, consistency index; RI, retention index. The numbers above the branches indicate bootstrap values >50%.

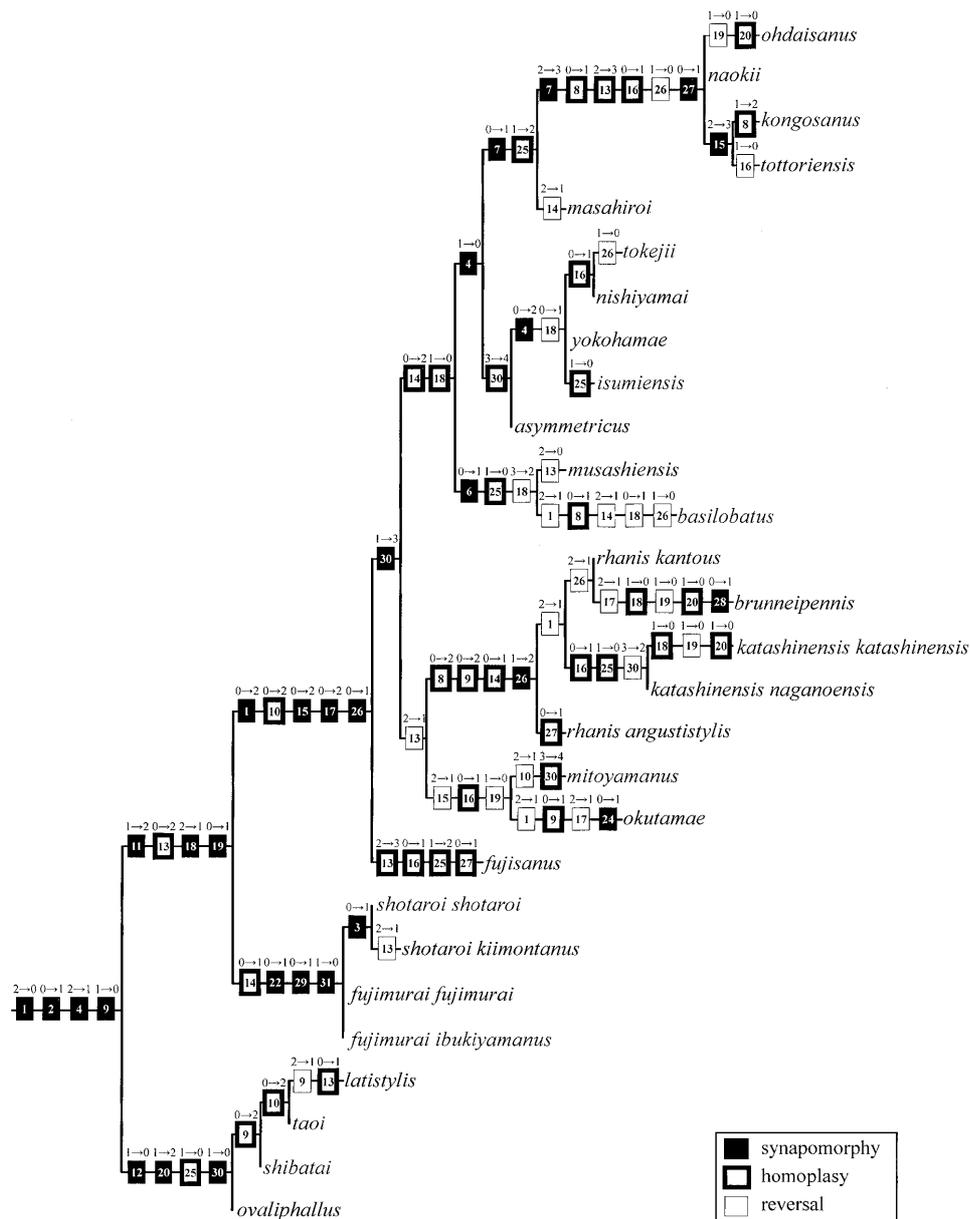


Fig. 10. Phylogeny and possible character evolution of the *asymmetricus* species group, based on one of the most parsimonious trees obtained by the successive weighting methods. Numbers in the squares indicate characters in Table 2, and numbers above the squares indicate character-state changes. Character-state changes were reconstructed with ACCTRAN optimization.

C (characters 11, 13, 18, and 19). In particular, the left preapical lobe that is more or less cup-shaped with a distinct rim (character 11) is a unique feature of this lineage. Four characters (14, 22, 29 and 31), all of which are uniform within the lineage, provide support for the monophyly of Lineage B. Five characters (1, 10, 15, 17 and 26) support the monophyly of Lineage C.

DISCUSSION

Phylogenetic relationships between *Nialoe* (s. str.) and *Dasenialoe* (s. str.)

The present study provides a phylogenetic hypothesis

for the *asymmetricus* species group of the subgenus *Nialoe* (s. lat.) for the first time, based on the cladistic analyses of 31 morphological characters. Such analyses are effective in distinguishing hidden para- or polyphyletic taxa that result from symplesiomorphies (Sasakawa, 2005a, b).

The present results are congruent with Kasahara (1988b) in the groupings at the species-group level, but not with respect to the subgeneric level (Fig. 9). Lineage A, which is a sister group to the other ingroup species, corresponds to the *latistylis* species group of the subgenus *Nialoe* (s. str.) *sensu* Kasahara, 1988b. Lineage B, including *P. (N.) fujimurai* and *P. (N.) shotaroi*, corresponds to the subgenus *Dasenialoe* (s. str.) *sensu* Kasahara, 1988b, and is a sister

group to Lineage C. Lineage C includes all remaining species, and corresponds to the *asymmetricus* species group of the subgenus *Nialoe* (s. str.) *sensu* Kasahara, 1988b. Thus, cladistic analysis on the basis of both external and internal characters revealed that *Daisenilaoe* (s. str.) is monophyletic, defined by pubescence of antennal segment 3 and sulcate dorsal tarsi, and is included within *Nialoe* (s. str.) as one clade.

Biogeography of the *asymmetricus* species group

Character states and species phylogeny give insights into the speciation and dispersal processes of this species group. In Lineage A, *P. (N.) ovaliphallus* in Fukui (area around "O" in Fig. 5A) is in the most basal position, and has the most ancestral endophallus (Fig. 1). Remaining species occupy the majority of the range of this lineage, and have a derivative endophallus with one (character 9 in *P. (N.) shibatai* [Fig. 7B]) or two lobes (characters 9 and 10 in *P. (N.) latistylis* [Fig. 7C] and *P. (N.) taoi*). The distributional boundary between *P. (N.) shibatai* and *P. (N.) latistylis* + *P. (N.) taoi* is located around the east side of Lake Biwa. These patterns suggest that Lineage A originated around Hokuriku District and dispersed to other areas.

In Lineage B, the species *P. (N.) fujimurai* is ancestral because it lacks the hooked apex of the aedeagus, while the species *P. (N.) shotaroi* possesses it. Between the two subspecies of *P. (N.) fujimurai*, *P. (N.) f. ibukiyamanus* has a rather ancestral endophallus with less developed lobes, although their subtle differences are not represented in the character coding in the present analysis. It is notable that *P. (N.) f. ibukiyamanus*, presumably most ancestral in Lineage B, is distributed close to *P. (N.) ovaliphallus*, ancestral in Lineage A, suggesting that initial differentiation of the *asymmetricus* species group occurred in this region.

Most of the basal positions in Lineage C are occupied by species of the East Kantô Mountains (Figs. 5). These species, *viz.* *P. (N.) fujisanus*, *P. (N.) mitoyamanus*, *P. (N.) okutamae*, and *P. (N.) musashiensis*, have the most ancestral endophallic structures in this lineage. This pattern suggests the initial speciation of Lineage C took place in the East Kantô Mountains. Remaining species distributed in other areas have derived morphologies, and are assumed to have dispersed from the East Kantô Mountains. A similar dispersal pattern is shown in the clade including *P. (N.) masahiroi* and its allies, in which *P. (N.) masahiroi* is most ancestral and originated near Mt. Hakusan. Thereafter, *P. (N.) ohdaisanus* and its allies originated and dispersed into the Kinki and Chûgoku districts. These results suggest that the initial speciation of Lineage C occurred around the Kantô Mountains, and then derived species dispersed in two directions: most species (*e.g.*, *P. (N.) asymmetricus*) dispersed northward into the Kantô and Tôhoku districts, and several species (*e.g.*, *P. (N.) ohdaisanus*) dispersed westward into the Kinki and Chûgoku districts.

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Appendix 1. Character evaluation and coding. All characters were treated as unordered.

Male genitalia (Figs. 6–8)

1. Right paramere: short with rounded to spatular apical part (0) (Figs. 1C, 2C, 3F, 3G); moderately long with narrow apical part that is differentiated from its basal part (1) ([D] in Fig. 4); long with narrow apical part that is not differentiated from its basal part (2).
2. Tubercle of the right ventral side of the aedeagus: absent (0); present (1) (Figs. 1B, 2B, 3B–C, 4C).
3. Apex of the aedeagus: not hooked (0) (Figs. 1B, 2B, 4A, 4C); hooked (1) (Figs. 3B–E).
4. Left pigmented band: absent (0); present, without apical fold (1) ([4] in Fig. 6C); present with apical fold (2) ([4] in Fig. 6B).
5. Basal sclerite: absent (0); present, but small (1); present and large (2).
6. Ostium lobe: absent (0); present (1) (Fig. 6A).
7. Left basal swelling: absent (0); weakly swollen (1); strongly swollen (2) ([7] in Fig. 6A).
8. Right basal swelling: absent (0); slightly swollen (1) ([8] in Fig. 6A); strongly lobate (2) ([8] in Fig. 6C).
9. Right basal lobe: absent (0); rudimentary (1); small but distinctly present (2) ([9] in Fig. 6C); large (3).
10. Right median lobe: absent (0); present (1) ([10] in Fig. 6).
11. Shape of left preapical lobe: almost flat (0); swollen, without distinct rim (1); cup-shaped (2) ([11] in Fig. 6).
12. Sclerotization of left preapical lobe: not sclerotized (0); weakly sclerotized (1) ([11] in Fig. 6).
13. Right preapical lobe: absent (0); present, but rudimentary (1) ([13] in Fig. 6C); present and distinct, but small (2) ([13] in Fig. 6B); present and large (3) ([13] in Fig. 6A).
14. Left apical lobe: absent or barely swollen (0); swollen but not hooked (1) ([14] in Fig. 6C); swollen and hooked (2) ([14] in Fig. 6A, C).
15. Right apical lobe: absent (0); simply swollen (1); swollen and bent to dorsal side (2) ([15] in Fig. 6); swollen and bent to dorsal side, with additional rudimentary lobe (3).
16. Apical sclerite: absent (0); present, but rudimentary to distinct (1) ([16] in Fig. 6A, C).
17. Left ventral edge of gonopore: not sclerotized (0); weakly sclerotized (1); strongly sclerotized (2).

Female genitalia

18. Sclerotization of apophysis of median oviduct: weakly and partly sclerotized (0); weakly and wholly sclerotized (1); strongly and wholly sclerotized (2).
19. Shape of apophysis of seminal canal: almost oval (0); crescent shape (1).
20. Sclerotization of apophysis of seminal canal: weakly and partly sclerotized (0); weakly and wholly sclerotized (1); strongly and wholly sclerotized (2).
21. Spermatheca: almost straight (0); weakly bent (1).

External structures

22. Pubescence of antennal segment 3: absent (0); present (1).
23. Setae of antennal segment 2: one seta (0); more than two setae (1).
24. Anterolateral setae on pronotum: one (0); more than two (1).
25. Punctures of laterobasal impression of pronotum: absent (0); weakly punctured (1); densely punctured (2).
26. Wrinkles of pronotum disk: absent (0); slightly wrinkled (1); strongly wrinkled (2).
27. Female elytra: shiny (0); opaque (1).
28. Color of elytra: black (0); reddish-brown (1).
29. Dorsal surface of tarsi: not sulcate (0); sulcate (1).
30. Male sternum 7: barely truncate (0) (Fig. 1D); moderately truncate, with narrow, almost symmetrical prominence (1) (Fig. 2D, Fig. 3H–I); moderately truncate, with narrow, asymmetrical prominence (2) (Fig. 4E); moderately truncate, with broader, asymmetrical prominence (3); strongly truncate, with broad asymmetrical prominence (4).
31. Rift in female tergum 8: absent (0); present (1).