

New taxa of the genus *Bareogonalos* from Asia with further information on the tribe Nomadinini (Hymenoptera, Trigonalidae)

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Abstract

A new subgenus of the nomadinine genus *Bareogonalos* (Trigonalidae) is described with *B. huisuni* Yamane et Yamane as the type species. A trigonalid obtained from a *Provespa* nest is described as *B. (Makotogonalos) provespae* sp. n. Further information on *B. (Bareogonalos) jezoensis* (Uchida) is given for distribution and behavior. A map is given showing the geographical distribution of *B. jezoensis*. Morphological characters important for the classification of Nomadinini are discussed.

Keywords: *Trigonalidae*, *Nomadinini*, *Bareogonalos*, new subgenus, new species, distribution, morphological characters.

Introduction

The wasps of the family Trigonalidae (=Trigonalidae) are distributed almost over the world, but most of them are rare insects probably reflecting their peculiar habits. They generally have intermediate hosts (lepidopteran and symphytan larvae) before reaching the final hosts (mainly hymenopterous parasitoids and social wasps). The taxonomy of this interesting family was initiated by Schulz (1907) and Bischoff (1933, 1938), and the current classification system was established by Carmean and Kimsey (1998), who reduced the number of subfamilies from six (Weinstein and Austin, 1991) to one, also combining several genera into fewer groups, while erecting a new subfamily and new genus. Although Popov (1945) suggested that the ancient hosts of the family were Vespidae rather than Ichneumonidae, Carmean's and Kimsey's (1998) phylogenetic analysis shows a reversed scenario.

The species of the trigonaline genus *Bareogonalos* parasitize the nest of vespid social wasps of the subfamily Vespinae. All the described species of this genus have been known from nests of the genera *Vespa*, *Vespula*, *Dolichovespula* and/or *Provespa* (Carmean, 1991; Carmean and Kimsey, 1998; Matsuura

and Yamane, 1990; Yamane, 1973; Yamane and Yamane, 1975; Weinstein and Austin, 1991). In this paper a new species of *Bareogonalos* is described that was reared from a nest of *Provespa* in Sumatra, Indonesia (Matsuura and Yamane, 1984). A new subgenus is established for two species, *B. huisuni* Yamane et Yamane and *B. provespae* sp. n., mainly based on the mandibular structure and palpal formula. Other information on the distribution and biology of *B. jezoensis* (Uchida) and a discussion on important morphological characters in the tribe Nomadinini are also given.

Materials and Methods

The holotype of *Bareogonalos huisuni* Yamane et Yamane was borrowed from the Entomological Collection of the Hokkaido University Museum (SEHU). The other material is now at the SKY Collection in Kagoshima, but will be deposited in SEHU in the near future. The holotype of *B. provespae* will be deposited in the Entomological Collection of Museum Zoologicum Bogoriense, Indonesia. Morphological characters were observed with a Nikon Stereomicroscope SMZ18. Information on the distribution and biology of *B. jezoensis* was

collected through previous literature, internet websites and with the help of my friends.

Taxonomy

Genus *Bareogonalos* Schulz

Bareogonalos Schulz, 1907: 18. Type species: *Trigonalyis canadensis* Harrington, 1896; Carmean and Kimsey, 1998: 60.

Nippogonalos Uchida, 1929: 79. Type species: *N. jezoensis* Uchida, 1929 by monotypy; Tsuneki, 1991: 4; Lelej, 1995: 12. Synonymized with *Bareogonalos* by Bischoff, 1938: 14.

Diagnosis. Antenna slender, forward-directed, with 19-23 segments in male and 19-21 segments in female; scape and pedicel smooth or very superficially punctate and shiny. Median furrow on frons indistinct. Mandible ‘schnabelform’; mandibles symmetrical or asymmetrical; right mandible with 4 teeth, left mandible with 3 or 4 teeth. Maxillary palpus with 5-6 segments; labial palpus with 3 segments. Eye normally positioned; its lower margin at the level above mandibular base. Deep depression behind ocelli absent. Pronotum normal, not overhanging anteriorly; its lower lateral lobe more or less incised. Parapsidal line on mesoscutum carinate, not excavated as in *Bakeronymus* and *Pseudonomadina*. Metanotum flat or pyramidal. Apical spur of foretibia shallowly bifid apically (in male smaller branch sometimes rudimentary). Gastral tergites with minute to small punctures, smooth or mat; female gaster thick, elongate-globular; its sternites 2 and 3 armed with posteriorly directed processes/lobes (armature sensu Carmean and Kimsey, 1998). Hind trochanter 2-segmented. Second and third cubital cells clearly separated.

All the known species have been collected from nests of vespine species (van der Vecht, 1933; Yamane, 1973; Yamane and Yamane, 1975).

***Makotogonalos* Yamane, subgen. nov.**

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Type species: *Bareogonalos huisuni* Yamane et Yamane, 1975.

Diagnosis. Antenna with 20-23 segments in male and 19-21 segments in female. Mandibles

symmetrical; both right and left mandibles with 4 teeth (Fig.1); basal tooth bifid apically. Maxillary palpus 5-segmented; labial palpus 3-segmented; terminal segment of labial palpus not modified (Figs. 2, 3). Anterior lateral lobe of pronotum distinctly incised below. Metanotum normal, not distinctly raised. Punctuation on gastral tergites small but distinct and dense; tergites mat, only weakly shiny. Sexual difference not strongly pronounced; male gaster weakly tapered posteriorly, with similar maculation to that of female.

Etymology. The subgeneric name is composed of ‘Makoto’ and ‘gonalos’, the latter having been frequently used as a suffix for trigonalid genera. ‘Makoto’ is the given name of the collector of the new Sumatran species, the late Dr. Makoto Matsuura, its meaning being ‘true’ or ‘faithfulness’.

The nominal subgenus *Bareogonalos* is characterized as follows: antenna 19-23 (usually 21) segments in male and 20-21 (usually 21) in female. Mandibles asymmetrical; right mandible with 4 teeth, left mandible with 3 teeth. Maxillary palpus 6-segmented; labial palpus 3-segmented; terminal segment of labial palpus strongly flattened, more or less spatulate (Fig. 4). Lower lateral lobe of pronotum only weakly incised. Metanotum pyramidal. Punctuation on gastral tergites minute; tergites nearly smooth and very shiny. Sexual difference more pronounced (in at least *B. jezoensis*); male gaster distinctly tapered posteriorly, with more or less reduced pale maculation.

Two species are included in the new subgenus, namely *Bareogonalos huisuni* Yamane et Yamane from Taiwan, and *B. provespae* Yamane, sp. n. from Sumatra, Indonesia.

***Bareogonalos huisuni* Yamane et Yamane (Figs. 1, 2, 6-9)**

Bareogonalos huisuni Yamane et Yamane, 1975: 456. Type locality: Kwantau-Shih, Taiwan; Carmean and Kimsey, 1998: 61; Chen *et al.*, 2014: 18 (redescription).

Female.

Measurements (in mm). Paratype from *Vespula flaviceps karenkona* nest: body length 11.1; head width including eyes 2.96; eye length 1.23; interocular distance at the level of anterior

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ocellus 1.96; distance between eye and posterior ocellus 0.75; distance between outer margins of posterior ocelli 0.73; scape length 0.43; mesonotal width just before tegulae 2.80; hind tibial length 2.68; forewing length 10.7. Specimens from *Vespa velutina flavitarsus* nests (n=5): body length 12.9-15.1 (mean: 14.8); head width 3.52-3.88 (3.75); interocular distance 2.28-2.60 (2.48); distance between eye and posterior ocellus 0.80-0.90 (0.88); distance between outer margins of posterior ocelli 0.83-0.98 (0.90); scape length 0.50-0.53 (0.52); mesonotal width 3.44-3.92 (3.78); hind tibial length 3.04-3.48 (3.31); forewing length 12.3-14.3 (13.8).

Description. (Larger specimens reared from *Vespa velutina flavitarsus*). Head distinctly broader than long; inner margins of eyes weakly convergent below. Clypeus transverse, with apical margin weakly emarginate medially and basal margin straight. Apical to third mandibular teeth bluntly pointed apically; basal tooth very broad at base and bifid shallowly at apex. Distance between outer margins of lateral ocelli almost as long as that between eye and posterior ocellus. Pair of small but distinct pits present behind ocelli (pits not connected by a narrow furrow); area behind ocelli not raised. Antenna with 19-20 segments. Median sulcus of mesoscutum located in a broader furrow margined laterally by low carinae that are less than half the mesoscutum length, not very clearly separated from rugoso-reticulum on its both sides, but complete, reaching the posterior margin of scutum; notaulix complete, its bottom with transverse carinae; parapsidal line carinate; notaulix and parapsidal line more parallel than in *B. provespae*; mesoscutellar disc roundly raised, with pair of distinct posterolateral tubercles; dorsal face of mesoscutellum gradually merging into posterior face. Metanotum demarcated from mesoscutellum and propodeum by deep sulci; its disc reversed-trapezoidal with flat dorsal surface, elevated from level of lateral parts of metanotum. Propodeum with same inclination as metanotum; dorsal face weakly produced laterally. First gastral tergite small and almost vertical; second tergite largest. Second and third sternites each apically with median process; that on second sternite broader than in *B. provespae* and medially weakly emarginate; that on third

sternite short.

Head including clypeus very minutely punctate, and moderately shiny; supra-antennal area irregularly sculptured (often transversely striate) and mat. Lateral face of pronotum coarsely rugose; dorsa of mesoscutum and mesoscutellum coarsely reticulate; lower half of mesopleuron weakly punctate and moderately shiny; posterior slope of mesoscutellum finely sculptured, mat. Median disc of metanotum finely sculptured, mat; lateral portion of metanotum rugose with large punctures along posterior margin but interspaces shiny. Propodeum coarsely reticulate; its ventrolateral portion with 2-3 strong carinae. Second and subsequent gastral tergites very finely and densely punctate, only slightly shiny; lateral portion of gaster, first tergite and sternites more shiny. Femora smooth and shiny, other parts of legs finely and densely sculptured and mat. Whole body with dense erect to suberect hairs; those on gastral tergites shorter than those on other parts of body; maxillary and labial palpi with strong erect hairs.

Body black, with the following parts yellowish to orange-yellow: antennal scape; upper lateral portion of pronotum close to tegula; pair of elongate cuneiform markings on mesonotum anteriorly; pair of smaller markings adjacent to notaulices; entire mesoscutellar disc and axilla largely; transverse line on metanotum (often interrupted medially); median spot (often lost) and pair of large lateral spots on propodeum; basal bands on second to fifth gastral segments, those on fourth and fifth with median extension toward their apical margin, small spot on sixth tergite; apical process of second sternite (often enlarged behind the lobe); upper face of hind coxa and hind trochanter entirely. Mandible and antenna (at least basal segments) reddish brown. Wings yellowish brown, particularly darker in anterior 2/3 of forewing; forewing with dark area near apex.

Male.

Measurements (in mm). Holotype from *Vespula flaviceps karenkona* nest: body length 11.0; head width including eyes 3.32; eye length 1.35; interocular distance at the level of anterior ocellus 2.16; distance between eye and posterior ocellus 0.80; distance between outer margins of posterior ocelli 0.73; scape length 0.48;

mesonotal width just before tegulae 3.08; hind tibial length 2.72; forewing length 10.6. Larger specimens reared from *Vespa velutina flavitarsus* (n=5): body length 12.9-15.0 (mean 13.7); head width including eyes 3.48-3.84 (3.60); eye length 1.4-1.53 (1.46); interocular distance at the level of anterior ocellus 2.24-2.52 (2.35); distance between eye and posterior ocellus 0.75-0.85 (0.79); distance between outer margins of posterior ocelli 0.83-0.88 (0.86); scape length 0.53-0.55 (0.54); mesonotal width just before tegulae 3.36-3.84 (3.58); hind tibial length 2.84-3.24 (3.04); forewing length 11.1-12.1 (11.7).

Description. (Larger specimens reared from *Vespa velutina flavitarsus*). Structure, sculpture and coloration similar to those of female. Antenna with 20-21 segments, in total length much longer than in the female. Distance between outer margins of lateral ocelli slightly longer than that between eye and posterior ocellus. Gaster narrowed both anteriorly and posteriorly; second and third sternites without apical processes. Fourth to seventh tergites extensively or entirely yellow. Body markings much reduced in some specimens.

Specimens examined (except for the holotype and paratypes): 1♀, Shanlinchi, Nantou Hsien, 16 ix 1995; 1♂, Kuantaushan, Lenai, Nantou Hsien, 23 ix 1996; 1♂, Sungkang, Nantou Hsien, Taiwan, 15 iv 1996; 1♀, Fenglin, Nantou Hsien, 13 ix 1997; 11♂9♀, Nanshanchi, Nantou Hsien, 13-19 xi 1997 (reared from a nest of *Vespa velutina flavitarsus* Sonan; all specimens collected by C.C. Luo).

Remarks. This species was originally described based on the specimens obtained from *Vespula flaviceps karenkona* Sonan nests in Taiwan (Yamane and Yamane, 1975). These specimens are naturally small in size as in the specimens of *B. jezoensis* collected from *Vespula* and *Dolichovesoula* nests in Japan. In 1985 additional specimens were collected by Mr. C. C. Luo (Puli, Taiwan) also in Taiwan. They are comparable in size to the specimens of *B. jezoensis* from *Vespa* species in Japan. The larger and smaller specimens of *B. huisuni* differ from each other only in size; distinct differences have not been detected in basic structure and

coloration between them.

Chen *et al.* (2013) stated that the illustrated paratype in Yamane and Yamane (1995) is a female not a male as reported by Yamane and Yamane (1975), and that the male is unknown (they even changed the sex of the holotype from the male to female, surprisingly, without examining it). Their view is very strange, because sexual differences are clearly mentioned in the original description. The illustrated paratype (Fig. 2 in Yamane and Yamane, 1975) is, of course, a female as was mentioned by the authors, who never said that the specimen is a male. The holotype is a male (Fig. 1), which was examined again this time. Probably Chen *et al.* (2013) did not read the original description at all, or were unable to recognize differences between the sexes. The male and female of this species are very easily distinguished based on the characters mentioned in the original description and redescription given above. Even just a glance at Fig. 1 (male) and Fig. 2 (female) in the original description is enough to identify the sex.

***Bareogonalos provepae* Yamane, sp. n.**
(Figs. 3, 10-13)

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Female (paratype).

Measurements (in mm). Body length 13.4; head width including eyes 3.52; eye length 1.43; interocular distance at the level of anterior ocellus 2.44; distance between eye and posterior ocellus 0.83; distance between outer margins of posterior ocelli 1.00; scape length 0.50; mesonotal width just before tegulae 3.56; hind tibial length 3.20; forewing length 12.0.

Description. Head distinctly broader than long; inner margins of eyes weakly convergent below. Clypeus transverse, with apical margin more deeply emarginate medially than in *B. huisuni* and basal margin weakly emarginate. Apical to third mandibular teeth pointed apically; basal tooth very broad at base and bifid shallowly at apex. Distance between outer margins of posterior ocelli distinctly longer than that between eye and lateral ocellus. Pair of small pits behind posterior ocelli indistinct; the pits

connected by a narrow groove; area behind lateral ocelli raised to form square platform. Antenna with 21 segments. Median sulcus of mesonotum obsolete, located in broader furrow that reaches midlength of mesonotum and is margined laterally by carinae; notaulix complete, its bottom with transverse carinae; parapsidal carina forming triangular area together with notaulix, opened anteriorly; mesoscutellum only feebly convex dorsad, without distinct posterior tubercles; dorsal face of mesoscutellum demarcated from steeper posterior face only by sculpturation. Metanotal disc transversely rectangular with flat dorsal surface, elevated from lateral parts of metanotum. Propodeum with same inclination as metanotal disc and mesoscutellum, with lateral triangular area that is depressed. First gastral tergite small and steep; second tergite largest. Second sternite apically with median process that has round apex; that on third sternite shorter.

Head very minutely and densely punctate, weakly shiny; mandible, vertex, temple and gena more strongly shiny. Lateral face of pronotum coarsely rugose; dorsa of mesoscutum and mesoscutellum coarsely reticulate; lower half of mesopleuron and metapleuron smooth to weakly sculptured; posterior slope of mesoscutellum finely sculptured. Median disc of metanotum finely sculptured, mat; lateral portion of metanotum nearly smooth with large punctures along posterior margin. Propodeum very coarsely rugoso-reticulate. Gastral tergites finely and densely punctate and mat, but lateral portion and sternites more shiny. Femora rather smooth and shiny; other parts of legs finely and densely sculptured and mat. Whole body with dense erect to suberect hairs; those on gastral tergites shorter than those on other parts of body; maxillary and labial palpi with strong erect hairs.

Body black, with the following parts yellowish or orange-yellow: posterior face of propodeum, first gastral segment, second tergite basally, second sternite except for lateral portion, upper face of hind coxa and hind trochanter entirely. Mandible and antennal flagellum reddish brown. Anterior 2/3 of forewing yellowish brown. The single female specimen is somewhat teneral so that the lighter body portions might be slightly darker in

maturation.

Male (holotype and paratype).

Head of the paratype missing.

Measurements (in mm; n=1). Body length 12.3; head width including eyes 3.44; eye length 1.48; interocular distance at the level of anterior ocellus 2.20; distance between eye and posterior ocellus 0.78; distance between outer margins of posterior ocelli 0.90; scape length 0.50; mesonotal width just before tegulae 3.40; hind tibial length 3.00; forewing length 10.9.

Description. Structure, sculpture and coloration similar to those of female. Antenna with 22-23 segments. Caphalic pits behind ocelli very obsolete. Gaster distinctly narrowed both anteriorly and posteriorly; second and third gastral sternites without armature (processes).

Holotype: male, collected from a *Provespa nocturna* Vecht nest (No. 8101), 15.xi.1981, Kotabumi, West Sumatra, Indonesia, M. Matsuura leg. (MZB, Indonesia). Paratypes: 1 male, same data as above, but emerged on 22.xi.1981; 1 female, same data as holotype.

Etymology. The specific epithet is named after the host vespid *Provespa*.

Remarks. It was rather unexpected that the two species of the subgenus *Makotogonalos* use very different groups of Vespinae as their hosts (*Vespa* and *Vespula* by *B. huisuni*, and *Provespa* by *B. provespae*). Furthermore, the other Indonesian species *B. jezoensis* known from Java belongs to the other subgenus (*Bareogonalos*). The latter species is originally recorded from temperate Japan (Uchida, 1929; Yamane, 1973) and Russian Far East (Lelej, 2003), located very far from Java, but the two populations use *Vespa* species as hosts; the other hosts for the Japanese population, i.e. *Vespula* and *Dolichovespula*, are absent from Java. With very scanty information I cannot say with certainty that in Indonesia the two *Bareogonalos* species overlap in both their hosts and distribution, but this may be possible. On the other hand, Carmean (1991) suggested the possibility that *B. jezoensis* had been introduced to Java with ornamental plants carrying trigonalid eggs deposited in their foliage, because no locality had been known between

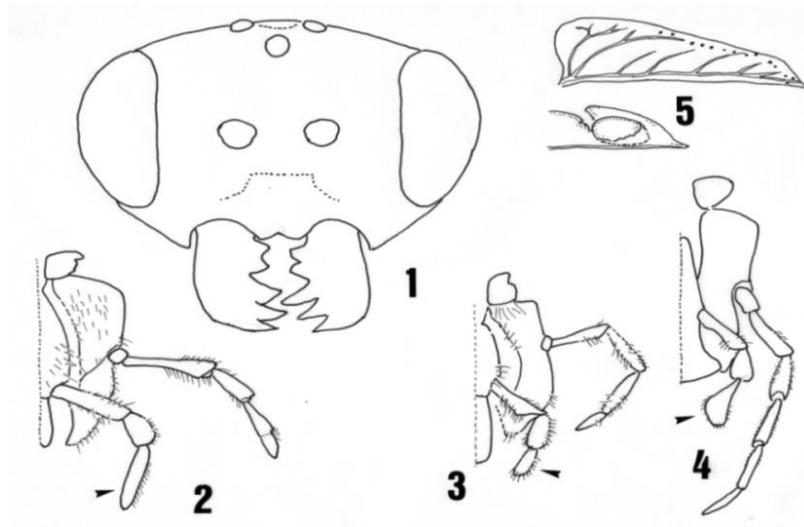
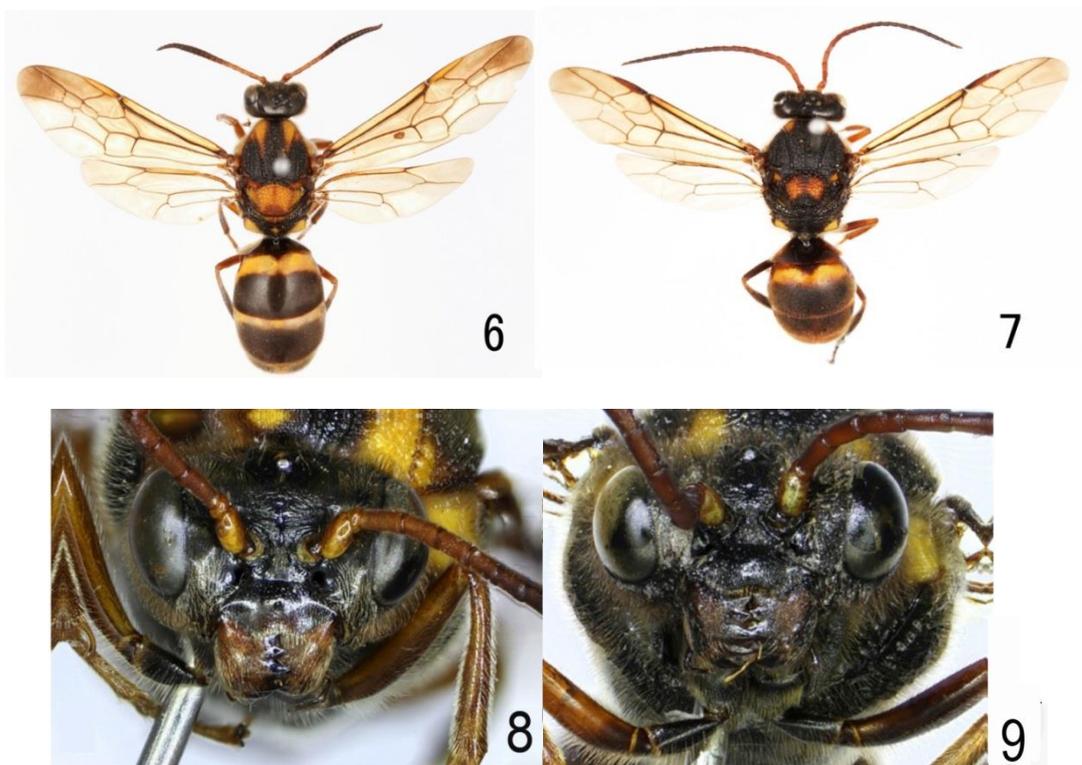
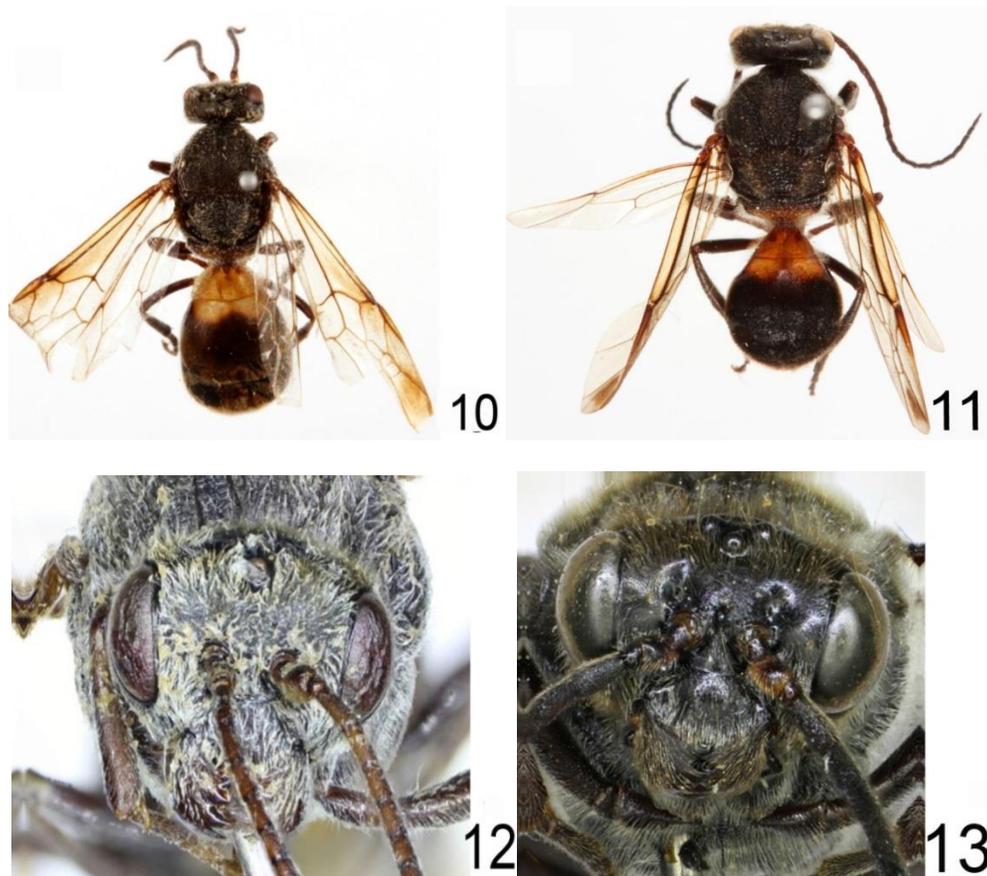


Fig. 1. Head of *Bareogonalos provespae* sp. n. (male) in frontal view. 2. Maxillary and labial pulpi of same specimen in ventral view. 3. Same, *B. huisuni* (male). 4. Same, *B. jezoensis* (male). 5. Mimosa leaf receiving *B. jezoensis* eggs (above) and an egg (below) (redrawn from Nozaka, 1976 with permission).



Figs. 6-9. *Bareogonalos huisuni* (ex. *Vespa velutina* nest). 6, 8. Female. 7, 9. Male.



Figs. 10-13. *Bareogonalos provespae*. 10, 12. Female. 11, 13. Male.

Japan and Java, and because the collection site in Java was a tourist site.

Additional information on *Bareogonalos* (*Bareogonalos*) *jezoensis* (Uchida)

Distribution. After the publication of Yamane (1973) many localities have been added to the distribution of this species (Fig. 14):

Primori'e (Russian Far East). Kamenushka, Ussuriysk Reserve (Lelej, 2003); Vysokogsk (A.S. Lelej, pers. comm., 5 Oct. 2014).

Hokkaido. Hamamasu and Atsuta, Ishikari-shi (Matsuura, 1995); Otaru, ix.1984, T. Ban leg., reared from *Vespa simillima* nest; Akanuma, Assabu-cho (Akihide Nomura: arisuabu.exblog.jp, 15.x.2014; Fig. 15).

Honshu. Fukushima Pref.: Kohri-machi, Date-gun (Ono, 1988); Kurotanikawa, Tadami, 14.ix.1963, M. Kanno. Niigata Pref.: Muroya, Aga-machi; Yagisawa and Kaigake Spa, Yuzawa-machi (Itami, 2011); Yunotani and

Maruyama, Uonuma-shi (Iwata and Fukada, 2010). Nagano Pref.: Tokuhara (Tsuneki, 1991); Seinaiji-mura, Shimoina-gun (Ono, 1987); 2 males & 3 females, Hakuba, 12.x.1990, reared from *V. simillima* nest; 1 male, Tokisato, Iiyama-shi, Nagano Pref., 18–24.viii.1998, A. Shimizu (Shimizu Collection). Toyama Pref.: Arimine, Toyama-shi (Matsuura, 1991). Fukui Pref.: Ohno-shi (Nozaka, 1976); 1 male, Hatogayu, 26-30.ix.1982, T. Tano leg.; 1 female, Satsura, Izumi-mura, 18.ix.1982, T. Tano leg.; 1 female, Taniyama, 5.x.1972, T. Tano leg.; 1 male, Arashi, 23.ix.1977, H. Kurokawa leg. Ishikawa Pref.: Hakusan (Nakamura, 1978).

Kyushu. Miyazaki Pref.: Fudono, Shiiba-son, Higashiusuki-gun (from a *Vespa simillima* nest; 1 female, photograph taken on 10 Oct. 2003; N. Nasu, pers. comm., 13 Oct., 2014).

In Northeastern Asia this species occurs in Primori'e (Russian Far East), Hokkaido, Honshu and Kyushu, with the southernmost locality in a mountain range in Kyushu (Shiiba-son,

Miyazaki Pref.). Shikoku apparently lacks it. Up to now no record of this species is available in the Korean Peninsula (J. K. Kim, personal comm., 13 Oct. 2014).

Biological notes. An Australian species, *Taeniogonlos maculata* (F. Smith), and some others are known to be primary parasites of sawflies and probably of lepidopteran larvae (Carmean and Kimsey, 1998; Raff, 1934). Other species are parasitoids of parasitic wasps and tachinid flies that attack larvae of lepidopterans and sawflies (Clausen, 1940). Not a few species, however, have been found from nests of solitary and social wasps such as eumenids, polistines and vespines (Bischoff, 1938; Iwata, 1971; Carmean, 1991; Weinstein and Austin, 1996). Among them are *Licogaster*, *Xanthogonalos*, *Seminota* (S. America), *Bakeronyms*, *Nomadina*, *Pseudonomadina* (S. America and SE Asia), and *Boreogonalos* (N. and C. Americas, and E. Asia).

The life cycle of *Bareogonalos jezoensis* was briefly discussed by Yamane (1973) with reference to Clausen's (1931) observations on *Poecilogonalos maga* Teranishi (currently *Taeniogonalos maga*). Probably first instar larvae are carried to vespine nests in food pellets

made of parasitized caterpillars that are captured and chewed by vespine workers. After entering a host wasp larva (or prepupa) planidium first instar larvae, though not yet observed actually, probably moult into second instar larvae that might moult into third instar shortly. Third instar larvae are of mandibulate type, fighting with each other leaving only one individual in the host. The survived fourth instar larva grows inside the host and come out to host's body surface and moults into a fifth (final) instar larva that consumes the host from outside (Yamane, 1973).

Adult trigonalids are collected in the field and from vespine nests during June to October in temperate Japan (Yamane, 1973; Tsuneki, 1973, 1991; Nozaka, 1976; Iwata and Fukada, 2010). Some males were collected in early June when prepupae are generally not available in the nests of vespines in Hokkaido. Yamane (1973) suggested the possibility that this species overwinters as adults. However, later observations made by Nozaka (1976) disagree with this view because the oviposition was conducted during October to leaves of the mimosa *Albizia julibrissin* Durazz. (Fabaceae) native to Japan (Fig. 5). Tsuneki (1973) listed other deciduous trees such as willows,

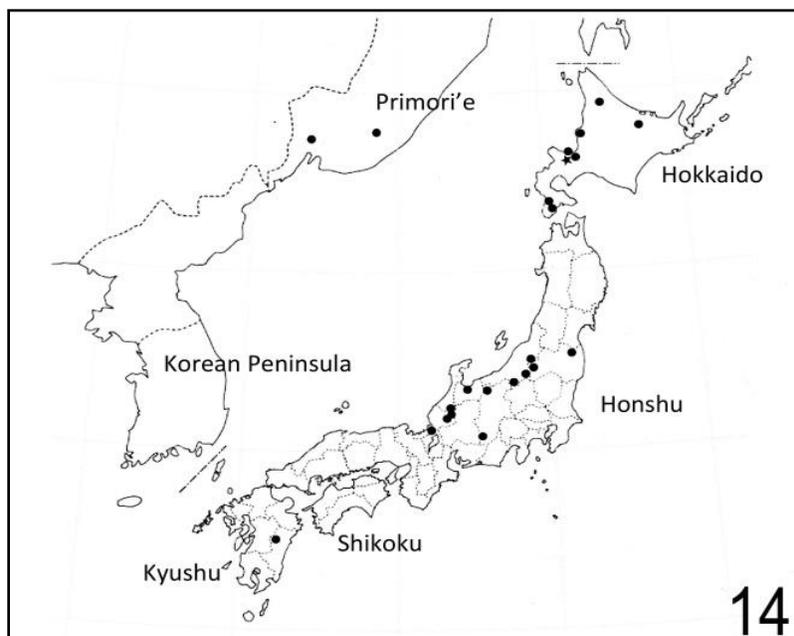


Fig. 14. Distribution of *Bareogonalos jezoensis* in Far Eastern Asia. ★ indicates the type locality (Jozankei, Sapporo, Hokkaido)

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Table 1. Hosts of *Bareogonalos* species in Asia

<i>B. jezoensis</i>	<i>Vespa analis analis</i>	Vecht 1933 (West Java)
	<i>Vespa analis insularis</i>	Haneda 1993 (Honshu), Sayama 1999 (Hokkaido)
	<i>Vespa crabro flavofasciata</i>	Yamane 1973 (Hokkaido), Sayama unpubl. (Hokkaido)
	<i>Vespa dybowskii</i>	Matsuura 1995 (Hokkaido), Sayama unpubl. (Hokkaido)
	<i>Vespa mandarinia japonica</i>	Ono 1988 (Honshu)
	<i>Vespa simillima simillima</i>	Yamane 1973 (Hokkaido)
	<i>Vespa simillima xanthoptera</i>	Ono 1987 (Honshu), Iwata and Fukada 2010 (Honshu), this paper (Kyushu)
	<i>Vespa velutina velutina</i>	Vecht 1933 (West Java)
	<i>Vespula shidai</i>	Yamane 1973 (Hokkaido; as <i>Vespula</i> sp.)
	<i>Vespula vulgaris</i>	Yamane 1973 (Hokkaido)
	<i>Vespula schrenckii</i>	Yamane 1973 (Hokkaido; as <i>V. rufa</i>)
	<i>Dolichovespula media media</i>	Sayama unpubl. (Hokkaido)
	<i>Dolichovespula media sugare</i>	Matsuura 1995 (Honshu)
	<i>Dolichovespula saxonica nipponica</i>	Yamane 1973 (Hokkaido; as <i>D. pacifica</i>), Makino 1982 (Hokkaido), Sayama (unpubl., Hokkaido)
<i>B. huisunu</i>	<i>Vespa velutina flavitarsus</i>	This paper (Taiwan)
	<i>Vespula flaviceps karenkona</i>	Yamane & Yamane 1975 (Taiwan)
<i>B. provespae</i>	<i>Provespa nocturna</i>	Matsuura & Yamane 1990 (West Sumatra)



Fig. 15. A *Bareogonalos jezoensis* female ovipositing on a leaf of *Atremisia montana* (6 Oct. 2013, Assabu-cho, Hokkaido, Japan; photo by Akihide Nomura; arisuabu.exblog.jp 15 Oct. 2014). 16. A teneral female of the same species collected from a *Vespa simillima* comb cell (18 Oct. 2003, Shiiba-son, Miyazaki Pref., Kyushu; photo by Naoko Nasu).

walnuts, alders etc., in which oviposition behavior was confirmed. Furthermore, overwintering adult trigonalids have never been found in Japan.

The oviposition found during autumn poses another problem. *Albizia julibrissin* is a deciduous tree, shedding all the leaves before winter so that all the eggs laid in the leaves would not survive. An important hint was presented for the North American congener *B. canadensis* by Carmean (1988, 1991). He studied the biology of *B. canadensis* in Oregon, USA, where the oviposition was seen in some plants and even paper under laboratory condition. Among the presented plants female wasps laid eggs more frequently in the leaves of Douglas-firs (*Pseudotsuga menziesii*) and Western hemlocks (*Tsuga heterophylla*), both being conifers with evergreen leaves. These eggs can survive on the trees until next spring. On the other hand, all the trees used for the oviposition by *B. jazoensis* are deciduous (Carmean's citation of bamboo and fern from Tsuneki, 1973, is not correct). I strongly suggest that lepidopteran larvae, or even leaf litter arthropods, which feed on live or fallen leaves during autumn and having overwintered, and those feeding fallen leaves next spring are candidates for the intermediate hosts of this species.

Several final host species have been found after Yamane (1973). All the host species are listed in Table 1.

Important characters in the classification of the nomadinine genera

In the course of taxonomic studies of social wasps of the Old World I have paid attention to their enemies especially of the family Trigonalidae (e.g., Yamane, 1973; Yamane and Terayama, 1983); some new taxa have been described in the tribe Nomadinini and their hosts revealed. It has become evident that some species have unusual numbers of mandibular teeth, and palpal segments of maxilla and labium; reduction in wing venation, thickening of antennae, etc. have also been noticed. Although the biological significance of these characters is not known, these characters seem to be important in the classification of the tribe Nomadinini (sensu Carmean and Kimsey, 1998).

Groups discussed.

1. Genus *Licogaster* Shuckard, 1841 (3 spp.)
2. Genus *Xanthogonalos* Schulz, 1907 (1 sp.)
3. Genus *Seminota* Spinola, 1840 (5 species in the world)
4. Genus *Nomadina* Westwood, 1868 (4 spp.)
5. Genus *Pseudonomadina* Sk. Yamane et Kojima, 1982 (1 sp.)
6. Genus *Bakeronymus* Rohwer, 1922 (2 spp.)
7. Genus *Bareogonalos* Schulz, 1907 (4 spp.)

The characters were observed with dry specimens or cited from previous literature. Although Carmean and Kimsey (1998) listed only one species for *Bakeronymus*, *B. typecus seidakka* Yamane et Terayama was raised to full species (Chen *et al.*, 2014).

1. Mandibular shape. Schulz (1907) mentioned that in the 'Nomadinae' and 'Bareogonalinae' the mandibles are much constricted and produced downward (schnabelform) like a beak. This condition is peculiar to these wasps and no doubt derived, though in *Bareogonalos* the condition is less distinct than in *Bakeronymus*, *Nomadina* and *Pseudonomadina*.

2. Number of mandibular teeth. Although Schulz (1907) counted the asymmetrical mandibles (right with 4 teeth, left with 3) as a characteristic defining the family, symmetrical mandibles occur in Nomadinini. In *Bakeronymus* and *Makotogonalos* (subgenus of *Bareogonalos*) (these taxa were not known to Schulz) both the mandibles have four teeth, and in *Pseudonomadina* (also not known to Schulz) both have three. I have not examined specimens of any species of *Nomadina*, but Westwood (1868) in his original description of the genus wrote "mandibulae 4-dentatae", and Carmean (1995) states that the mandibles are symmetrical. I consider the asymmetrical mandibles to be the ground plan for Trigonalidae, the symmetrical ones being regained within this family (see also Carmean and Kimsey, 1998).

3. Vertical furrow on frons. In *Bakeronymus* and *Pseudonomadina* the frons has a broad vertical furrow from the upper margin of clypeus to just below the anterior ocellus. Schulz's (1907) description of *Nomadina cisandina* (Schulz, 1905) and Bischoff's (1933) description of

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N. nasuta Bischoff, 1933 (= *N. balteata* (Cameron, 1899)) suggest that this condition also occurs in at least some species of *Nomadina*. This character state is peculiar to *Bakeronymus*, *Nomadina* and *Pseudonomadina* and no doubt represents a derived condition.

4. Clypeal shape. In *Bakeronymus* and *Pseudonomadina* the clypeus is completely flat, continued from the supraclypeal area that is part of the frontal furrow. This condition very probably occurs also in *Nomadina*. In *Seminota*, *Xanthogonalos* and *Bareogonalos*, the clypeus is raised, seen in profile higher than the supraclypeal area. The flat clypeus uniquely occurs in *Bakeronymus*, *Nomadina* and *Pseudonomadina*, and is considered to be derived.

5. Position of eyes. In *Bakeronymus* and *Pseudonomadina* the eyes are very large, and the lower margin of the eye is below the level of the mandibular base; the oculo-malar space is quite short. This condition is only found in these genera among Trigonalidae, and seems derived.

6. Deep depression behind ocelli. Vertex behind ocelli is generally flat or roundly convex in this tribe. Only in *Bakeronymus* and *Pseudonomadina* this area has a deep depression (Yamane and Kojima, 1982); this state may be derived.

7. Antennal shape. In most of the genera treated here the antennae are slender; flagellar segments are rarely moniliform (beadlike). In *Bakeronymus*, *Nomadina* and *Pseudonomadina* the antennae are thick (especially in the female) and relatively short; the segments are often strongly moniliform (see Fig 3 in Yamane and Kojima, 1982). The moniliform flagellar segments are another derived condition within the Nomadini.

8. Number of antennal segments. The number may vary even in a single species as well as within a genus (for *Bareogonalos*, see Yamane, 1973; Yamane and Yamane, 1975). However, generic differences are also noted. In *Seminota* and *Xanthogonalos* it is always more than 21 and in *Lycogaster* 22-24; in *Bareogonalos* it

varies between 19 and 23. In *Bakeronymus*, *Nomadina* and *Pseudonomadina*, however, it ranges from 13 to 16. The reduced number of antennal segments represents a derived condition among the Trigonalidae.

9. Number of segments in maxillary and labial palpi. Generally in the Trigonalidae the maxillary palp has 6 and labial palp 3 segments (Schulz, 1907). *Seminota*, *Xanthogonalos* and *Bareogonalos* (s. str.) have the same numbers (6, 3), while in the subgenus *Makotogonalos* they are 5 and 3 respectively. In *Bakeronymus* and *Pseudonomadina*, the numbers are further smaller, 4 and 2 respectively; in the latter these palpi are much reduced in size. In *Nomadina* the maxillary and labial palpi are dwarf or even lost (Carmean, 1995; Schulz, 1907, did not mention the precise numbers of palp segments). The reduction in both the number and size of segments may be derived for the nomadinine genera.

10. Anterior part of pronotum. In some trigonalid genera the pronotum anteriorly weakly overhangs, but in many others this condition is not observed. *Bakeronymus* and *Pseudonomadina* have a strongly overhanging pronotum (seen in profile the upper portion of the anterior part strongly protruding anteriorly). This is probably a derived condition.

11. Lower lateral lobe of pronotum. This part is distinctly incised in *Makotogonalos* and at least weakly incised in *Bareogonalos* (s. str.) (see Figs. 14 and 15 in Yamane and Yamane, 1975). The condition is peculiar to *Bareogonalos* and considered derived.

12. Shape of metanotum (postscutellum). The metanotum is flat and roundly convex in all the trigonalid genera except in *Bareogonalos* (s. str.), the members of which have a pyramidal metanotum with a bifid apex. Although this condition is very distinct in *B. canadensis* (Harrington, 1896) and *B. jezoensis* (Uchida, 1929), Cameron's (1897) original description of the Mexican *Trigonalys scutellaris* (= *Bareogonalos scutellaris*) leaves some doubt about the constant occurrence of this state in this species. At any rate the pyramidal metanotum is

confined to this subgenus and no doubt represents a derived condition.

13. Cubital cell of forewing. Distinction of second from third cubital cell is constant through most of the trigonalid genera, but is often absent in *Nomadina* and *Pseudonomadina*. The absence of the separation represents a derived condition.

14. Hind trochanter. In the Symphyta and some Apocrita there is an apparent second segment to the trochanter (trochantellus) that is morphologically a piece cut off the proximal end of the femur (Richards, 1977). In the Trigonalidae there often is an additional subdivision of the trochantellus so that the trochanter appears 3-segmented. The hind trochanter is '2-segmented' only in *Bakeronymus*, *Nomadina*, *Pseudonomadina* and *Bareogonalos* (Carmean and Kimsey, 1998). The frequent occurrence of the '2-segmented' hind trochanter in Ichneumonidae suggests that it represents an ancestral condition, but in *Seminota* and *Xanthogonalos* (closely related to these four genera) the hind trochanter is '3-segmented'. This means that the '2-segmented' hind trochanter in Nomadinini might be a regained condition within the Trigonalidae.

15. Apical spur on foretibia. In some nomadinine groups the apical spur of the foretibia is bifid apically; this condition is more distinct in the female. In other groups the spur is simple or missing.

16. Median processes (armature) on gastral sternites. The female trigonalids except for those of 'Trigonaloinae' have a median process either on the gastral sternite 2 or 3, or on both (Schulz, 1907). It is thought to function as an anchor for the basal part of the gaster to the upper surface of plant leaves during oviposition (Riek, 1970). In the 'Lycogastrinae' (heterogeneous group including *Lycogaster*) and 'Seminotinae' (*Seminota* + *Xanthogonalos*) the structure is more or less developed on both the sternite 2 and 3 (Schulz, 1907) (*Xanthogonalos fasciatus* Bertoni, 1912, which has the process only on sternite 3, was moved under *Trigonalys* by Carmean and Kimsey, 1998). In

Bakeronymus, *Nomadina* and *Pseudonomadina* it is seen only on sternite 3 (*Nomadina*), or the process on sternite 2 is much reduced to a pair of minute spines (*Bakeronymus* and *Pseudonomadina*). In the latter two genera the process on sternite 3 is bifid apically. It is more developed on sternite 2 than on sternite 3 in *Bareogonalos*. The bifid process on sternite 3 and minute spinous ones on sternite 2 should represent a derived condition among the Nomadinini.

17. Punctures on gastral tergites. Punctures on gastral tergites are minute in *Nomadina*?, *Bakeronymus*, *Pseudonomadina* and *Bareogonalos* (s. str.) (in the last the gaster is smooth and very polished), or small but distinct and dense in *Makotogonalos* (the tergites are only weakly shiny). The fine punctation may represent a derived condition among the Nomadinini.

18. Final hosts. For *Afrigonalos* Carmean and Kimsey, 1998, and *Xanthogonalos*, nothing is known for intermediate and final hosts. Among *Lycogaster* ichneumonid wasps, eumenid wasps and social vespids are known as final hosts. All the species of the Neotropical genus *Seminota* parasitise polistine wasps (Weinstein and Austin, 1991). Final hosts are also polistines in the Neotropical genus *Nomadina*, and the Southeast Asian *Bakeronymus* and *Pseudonomadina* (Carmean and Kimsey, 1998; Weinstein and Austin, 1991; Yamane and Terayama, 1983). The species of *Bareogonalos* have been known from vespine species, but the host is not known for *B. scutellaris* from Mexico (Carmean and Kimsey, 1998).

The Nomadinini forms a natural group with the female having the primary armature (process/lobe) generally on gastral sternum 2 and secondary armature on sternum 3, and the male secondarily having lost tyloids on antennae (Carmean and Kimsey, 1998). Many characters analyzed above suggest that *Bakeronymus*, *Nomadina* and *Pseudonomadina* can be recognized as a natural group, and grouped with *Bareogonalos* based on the "2-segmented" hind trochanter and beak-shaped mandibles. However, *Bareogonalos* contains two distinct groups that can be treated as subgenera.

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Table 2. Comparison of important morphological characters among some nomadine genera.

	<i>Nomadina</i>	<i>Pseudonomadina</i>	<i>Bakeronymus</i>	Subgen. <i>Bareogonalos</i>	Subgen. <i>Makotogonalos</i>
Mandibular shape	Schnabelform	Schnabelform	Schnabelform	Schnabelform	Schnabelform
No. of mandibular teeth	Right: 4, Left: 4,	Right: 3, Left: 3	Right: 4, Left: 4	Right: 4, Left: 3	Right: 4, Left: 4
Vertical furrow on frons	Present?	Broad, distinct	Broad, distinct	Not distinct	Not distinct
Clypeus	Flat?; longer than broad	Flat, in profile continued from supraclypeal area; broader than long	Flat, in profile continued from supraclypeal area; broader than long	Normal; broader than long	Normal; broader than long
Position of eye	Oculo-malar space short?	Lower margin of eye below level of mandibular base	Lower margin of eye below level of mandibular base	Normal	Normal
Deep depression behind ocelli	Absent	Distinct in male and female	Distinct in male, shallow in female	Absent	Absent
Shape of antenna	Thick, short particularly in female	Thick, short	Slender	Slender	Slender
Direction of antenna	?Forward	Downward	Downward	Forward	Forward
No. of antennal segments	11-16 (generally 16) in both sexes	14 in male, 13 in female	14 in male, 14-15 in female	19-23 (basically 21) in male, 20-21 (basically 21) in female	20-23 in male, 19-21 in female
No. of maxillary palpus segments	Palpus rudimentary	4 (segments small)	4	6	5
No. of labial palpus segments	Palpus rudimentary	2 (segments small)	2	3	3
Pronotum	Normal	Anteriorly overhanging	Anteriorly overhanging	Normal	Normal
Lower lateral lobe of pronotum	Normal	Normal	Normal	At least slightly incised	Distinctly incised
Shape of metanotum	Normal	Normal	Normal	Pyramidal	Normal
2nd & 3rd cubital cells	Not separated	Often not separated	Distinctly separated	Distinctly separated	Distinctly separated
Hind trochanter	2-segmented	2-segmented	2-segmented	2-segmented	2-segmented
Apical spur of foretibia	?	Absent	Simple	Apically bifid	Apically bifid
Female gastral shape	Rather flattened	Rather flattened	Rather flattened	Thick	Thick
Sternal armature (processes) in female	Present on 3rd	Present on 3rd	Present on 3rd	Present on 2nd and 3rd	Present on 2nd and 3rd
Punctuation on gastral tergites	Tergites smooth	Fine and superficial; tergites weakly shiny	Fine and superficial; tergites weakly shiny	Very fine and sparse; tergites almost smooth and very shiny	Fine but distinct and dense; tergites mat and weakly shiny
Hosts	<i>Agelaisia</i> , <i>Polybia</i> , or <i>Stelopolybia</i>	<i>Ropalidia</i>	<i>Parapolybia</i>	<i>Vespa</i> , <i>Vespula</i> , <i>Dolichovespula</i>	<i>Vespa</i> , <i>Vespula</i> , or <i>Provespa</i>

Acknowledgements

I would like to thank Dr. David Carmean (Simon Fraser University) for his kind offer of some important publications. Mr. Taisuke Kawano (Kyushu University) kindly took the photographs of specimens and provided me with useful information. Dr. Masahiro Ohara (Hokkaido University Museum) lent me the type material of *B. huisuni* under his care. Dr. A. S. Lelej (Institute of Pedology and Biology, Vladivostok) offered me an unpublished record of *Bareogonalos jezoensis* from Russian Primori'e. Dr. Mamoru Terayama (University of Tokyo) helped me with the material of *B. huisuni*. The following persons kindly offered me valuable information (including photographs) on *B. jezoensis*: Prof. Fuminori Ito (Kagawa University), Prof. Jeong-kyu Kim (Hanseong University, Korea), Ms. Naoko Nasu (Fukuoka, Japan), Mr. Akihito Nomura (Assabu, Hokkaido), Ms. Chizuko Nozaka (Sabae, Japan), Dr. Katsuhiko Sayama (Forestry and Forest Products Research Institute, Sapporo), Dr. Akira Shimizu (Tokyo Metropolitan University), and Mr. Tadashi Tano (Fukui, Japan).

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