

**Morphological study and taxonomic revision
of the genus *Nipponocercyon*
(Coleoptera: Hydrophilidae: Sphaeridiinae)**

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Abstract. External morphology and male genitalia of the endemic Japanese genus *Nipponocercyon* Satô, 1963 are examined and the taxonomy of the genus revised based on specimens from nine localities at the islands of Kyushu, Shikoku and Honshu. All examined specimens are found to belong to the same species, *N. shibatai* Satô, 1963, which shows a considerable intraspecific geographic variability in the shape of the preepisternal elevation of the mesothorax, interstitial microsculpture of the mentum, pronotum and elytra and the morphology of the basal portion of the elytra. Two new synonyms of *N. shibatai* are proposed, *N. shibatai oyananum* Nakane, 1968, syn. nov. and *N. monticola* Nakane, 1968, syn. nov. Important diagnostic characters of the genus as well as the intraspecific variability of the above characters are illustrated in line drawings and SEM photographs. Geographic patterns of the variability are discussed.

Keywords. Megasternini, *Nipponocercyon*, morphology, taxonomy, intraspecific variability, synonymy, endemics, distribution, islands, Japan, Palaearctic Region

Introduction

The Japanese endemic megasternine genus *Nipponocercyon* Satô, 1963 was described on the basis of three specimens collected in the leaf litter in the Osaka Prefecture (Japan) by SATÔ (1963), who provided a rather detailed description of the species along with good drawings. Later, NAKANE (1968, 1977) described two additional taxa, *N. shibatai oyananum* Nakane, 1968 and *N. monticola* Nakane, 1968, both based on short series collected in the Nagano and Kanagawa Prefectures, respectively. However, NAKANE'S (1968) descriptions were very brief

and the description of *N. monticola* was split and the second part of the description containing the differential diagnosis was published nine years later. The genus remained known only from the three type localities in the central part of the Honshu Island and no additional specimens were available. Moreover, HANSEN (1991) only adopted data from the original description in his generic revision of the Hydrophiloidea without examining any specimen of the genus. *Nipponocercyon* therefore became enigmatic for entomologists outside Japan.

For the present study, we have accumulated representatives of the genus collected mostly during the last decades. Our aim is to provide a redescription of *Nipponocercyon*, update the diagnoses and revise the described species, including SEM photographs and illustrations of important characters.

Material and methods

We have examined 35 specimens of *Nipponocercyon*. Part of each type series and of the additional specimens was dissected and the genitalia were cleaned in 5% KOH solution for about 12 hours at room temperature. Drawings of male genitalia were prepared using a drawing tube attached to a compound microscope; drawings of preepisternal plates of mesothorax were drawn using a stereomicroscope with ocular grid. Habitus photographs were taken using an Olympus Camedia C-5060 camera attached to an Olympus SZX9 binocular microscope and subsequently edited in Adobe Photoshop 7.0 partly using the procedures described by Darci Kampschroeder at <http://nhm.ku.edu/illustration/>. SEM micrographs of uncoated specimens were prepared at the Department of Paleontology of the National Museum in Prague using a Hitachi S-3700N scanning electron microscope. Morphological terminology follows KOMAREK (2004) and FIKÁČEK (2010). Sternite 8 bearing important characters was erroneously called ‘tergite 8’ by FIKÁČEK & HEBAUER (2009); we refer to the sclerite correctly as ‘sternite 8’ in this paper. Morphological structures not mentioned in the redescriptions were not examined.

Examined material is deposited in the following collections:

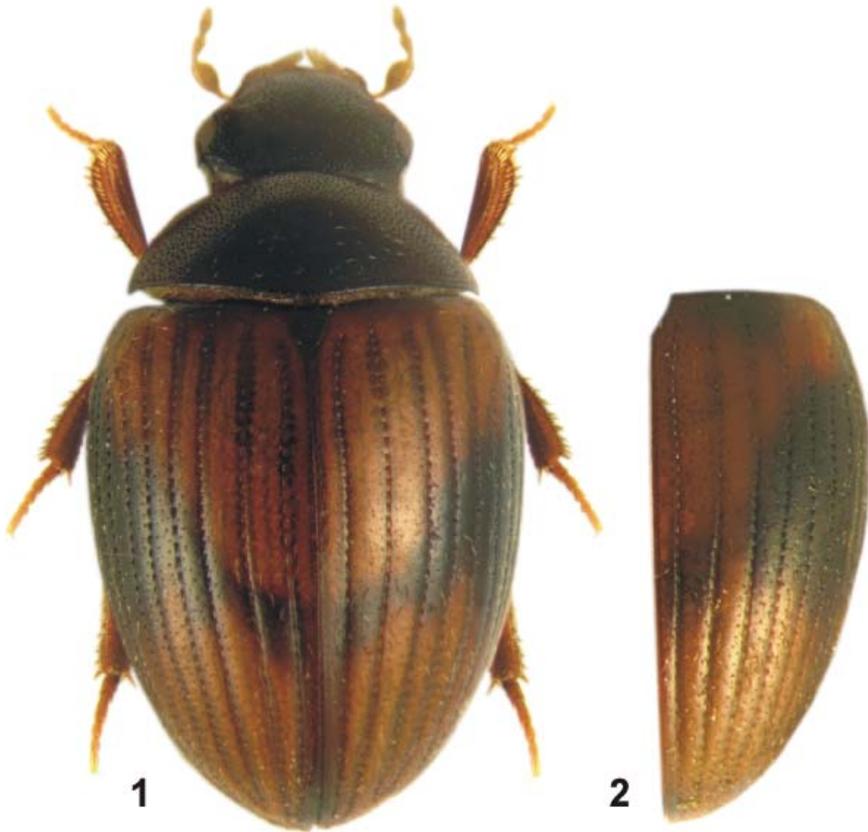
- EIHU Entomological Laboratory, Hokkaido University, Sapporo, Japan (M. Ôhara);
- EUMJ Entomological Laboratory, Ehime University, Matsuyama, Japan (M. Sakai);
- FEFU Faculty of Education & Regional Studies, Fukui University, Fukui, Japan (H. Hoshina);
- NMPC Department of Entomology, National Museum, Prague, Czech Republic (M. Fikáček);
- PJWP Paweł Jałoszyński collection, Włocławek, Poland;
- ZMUC Zoological Museum, University of Copenhagen, Copenhagen, Denmark (A. Solodovnikov).

Taxonomy

Nipponocercyon Satô, 1963

Nipponocercyon Satô, 1963: 267. Type species: *Nipponocercyon shibatai* Satô, 1963 (by monotypy). Gender masculine.

Differential diagnosis. Head without distinct interantennal ridge; mentum weakly bisinuate on anterior margin; antennomeres 7–8 with groups of peg-like sensilla ventrally; maxilla with sucking disc in males; posterior tentorial pits minute; pronotum evenly convex, lateral margins not deflexed; transverse row of punctures along posterior margin of pronotum absent; median portion of prosternum elevated, bearing strong setiferous sculpture but not separated



Figs. 1–2. *Nipponocercyon shibatai* Satô, 1963. 1 – general habitus (Mt. Hikosan, Fukuoka Prefecture); 2 – right elytron, showing variability in colouration (Kanagawa Prefecture).

from lateral portion by a ridge; antennal grooves not reaching lateral margin of hypomeron; profemur with elongate ventral depression along anterior margin; elytron with 10 punctural series; elytral intervals not costate; lateral margins of elytra not denticulate or serrate; cavities for reception of procoxae large, reaching mesocoxae; preepisternal plate suboval to subrhomboid, widely contacting metaventrite; metaventrite with two short mesal ridges anteriorly; each anterolateral ridge of metaventrite lying along posterior margin of mesocoxa throughout the width of metaventrite, reaching anterolateral corner and not overlapping to lateral margin of metaventrite; lateral portions of metaventrite with coarse setiferous punctation consisting of two differently sized types of punctures; abdominal ventrite 1 pubescent, ventrites 2–5 bare; phallobase much shorter than parameres, slightly asymmetrical, not delimited from manubrium; corona of median lobe situated in basal half; lateral margin of median lobe lacking pubescence; male sternite 9 with large tongue-like projection; male sternite 8 without anterior narrow projection.

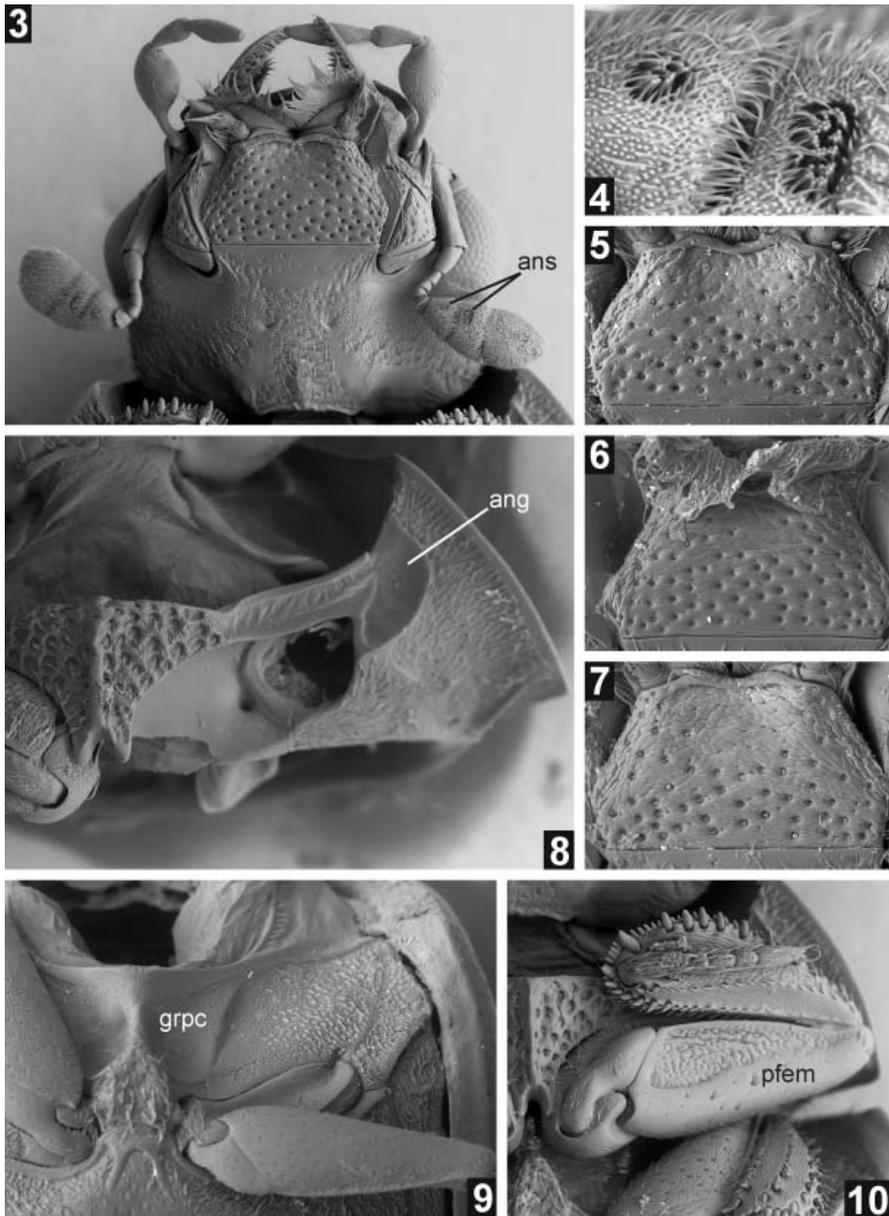
The genus is compared with other megasternine genera in the discussion below.

Redescription. Body elongate oval, moderately convex in lateral view. Elytra gradually narrowing posteriorly.

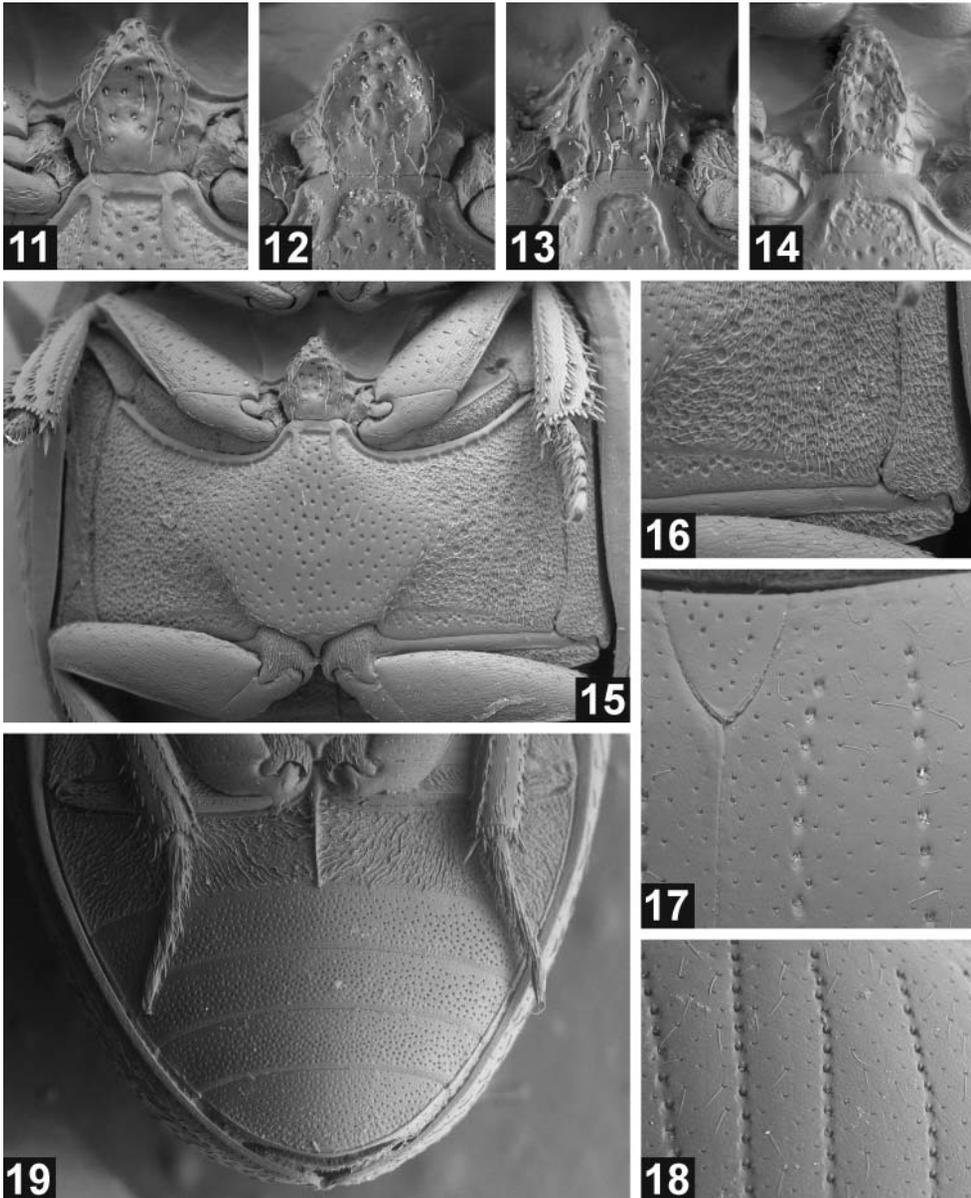
Head. Clypeus and frons with coarse setiferous punctures, anterior clypeal margin slightly convex, narrowly rimmed, very indistinctly widened laterad; frontoclypeal suture not visible; interantennal ridge not developed, visible only as small unpunctured area on each side of head. Interocular area not elevated. Eyes small, convex, separated by $9\times$ the width of one eye. Genae without distinct ocular ridge, bearing rugose setiferous microsculpture posteriorly of eyes, smooth in posterior portion. Gula distinct, wide, bearing posteromedian carina and narrow posterior collar; surface with rugose setiferous microsculpture. Posterior tentorial pits minute. Labrum retracted under clypeus, weakly sclerotized; anterior margin trilobate, with median lobe less protruding anteriorly than lateral lobes; chaetotaxy not examined. Mandibles not examined. Antenna with nine antennomeres; scapus long and thin, ca. as long as antennal club, longer than antennomeres 2–6 combined; cupula small; antennal club compact, elongate, ca. 2.3 times as long as wide, antennomeres 7 and 8 bearing groups of peg-like sensilla ventrally, antennomere 9 not constricted subapically, forming distal half of antennal club, bluntly rounded at apex. Maxilla with sucking disc in males; maxillary palpomeres 2 and 4 subequal in length, palpomere 3 distinctly shorter than palpomere 4; palpomere 2 strongly widened distally, palpomere 3 slightly widened distally, palpomere 4 spindle-like. Submentum slightly shorter than mentum, bearing sparse setiferous punctures, lacking microsculpture and disc-like fields; mentum 1.7 times as wide as long, slightly narrowing anteriorly, anterior margin slightly bisinuate, surface with weak transverse sulcus along anterior margin.

Prothorax. Pronotum arcuately narrowing anteriorly, anterior margin slightly bisinuate, posterior margin nearly simply arcuate; lateral margins not deflexed, not explanate, narrowly rimmed, not serrate; surface evenly convex, without elevated ridges or bulges; punctures with minute setae intermixed with those bearing long decumbent setae; posterior pronotal margin without distinct transverse row of punctures; posterior corners obtusely rounded. Hypomerion with very narrow lateral glabrous portion very indistinctly widening posteriorly; mesal portion with weakly developed intrahypomerion ridge, whole mesal hypomerion portion with equal rugose setiferous microsculpture; hypomerion process not developed. Prosternum carinate medially, with median part more elevated and bearing very coarse setiferous punctures and minute denticles on interstices, separated from lateral smooth impunctate portion by weak ridge; anterior margin slightly constricted at the border of median and lateral portions; deep pits at the border of lateral and mesal portion absent; posterior part forming prosternal process with large posterior notch. Antennal grooves large but not reaching lateral glabrous hypomerion portion, lateral margins of grooves rounded; notopleural suture indistinct. Coxal cavity closed internally; sclerotized postcoxal bridge reinforced mesally. Accessory ridge below posterior pronotal margin present, distinct even laterally as transverse fold. Profurca protruding outside of prothoracic cavity, composed of short and wide stalk and slightly asymmetrical extension with blunt apex.

Meso thorax. Scutellar shield triangular, slightly longer than wide, with few punctures present on surface. Elytron with 10 series of punctures, series 1–5 and 9–10 reaching elytral base, series 6–8 arising subbasally. Series 7 and 8 as widely separated from each other as other series; serial punctures with minute setae (indistinct under binocular microscope);



Figs. 3–10. Morphology of *Nipponocercyon shibatai* Satô, 1963. 3 – head, ventral view (Kanagawa Prefecture); 4 – detail of the sensilla on antennal club (Kanagawa Prefecture); 5–7 – mentum (5 – Hyogo Prefecture; 6 – Nagano Prefecture, paratype of *N. monticola* Nakane, 1968; 7 – Fukuoka Prefecture); 8 – prosternum (Tokushima Prefecture); 9 – mesoventrite (Tokushima Prefecture); 10 – anterior leg (Kanagawa Prefecture). Abbreviations: ang – antennal grooves; ans – sensilla on antennal club; grpc – grooves for reception of procoxae; pfem – profemur.



Figs. 11–19. Morphology of *Nipponocercyon shibatai* Satô, 1963. 11–14 – preepisternal plate of mesothorax (11 – Fukuoka Prefecture; 12 – Hyogo Prefecture; 13 – Nagano Prefecture, paratype of *N. monticola* Nakane, 1968; 14 – Kanagawa Prefecture); 15 – meso- and metaventrite (Fukuoka Prefecture); 16 – detail of lateral portion of metaventrite (Fukuoka Prefecture); 17–18 – basal portion of elytra (17 – Fukuoka Prefecture; 18 – Nagano Prefecture, paratype of *N. monticola*); 19 – abdominal ventrites (Kanagawa Prefecture).

elytral interstices flat to weakly convex, bearing fine setiferous punctures; alternate elytral intervals not more convex than adjacent ones; elytral margin slightly deflexed laterally, without denticulation or serration. Pseudepipleuron much wider than epipleuron subbasally, nearly horizontal, glabrous, reaching elytral apex; epipleuron pubescent, very narrow, oblique, reaching metathorax. Mesoventrite fused with anepisternum 2, anepisternal suture absent. Cavities for reception of procoxae deep and large, lacking pubescence, reaching mesocoxae. Preepisternal elevation not subdivided into short anterior and long posterior portion, bearing subrhomboid to suboval plate widely contacting but not overlapping anterior margin of metaventrite; posterolateral portion of preepisternal elevation with large tooth-like bulges separating the elevation from coxal lobe. Mesofurca not examined.

Metathorax. Metanotum not examined. Metaventrite with slightly raised subpentagonal median portion bearing finer punctures without setae, not depressed in both sexes; lateral portions except for narrow posterior part bearing very coarse setiferous punctation with punctures of two different sizes and without microsculpture, posterior part along metacoxae with a few smaller punctures without setae and with weak scale-like microsculpture. Antero-median part of metaventrite slightly projecting anteriad, reaching ca. posterior third of length of mesocoxal cavities. Anterior margin of metaventrite with very distinct anterolateral ridge along posterior margin of mesocoxal cavities, reaching but not overlapping anterolateral corner of metaventrite; mesal portions of anterolateral ridges bending posteriad, forming two short longitudinal mesal ridges on anterior part of metaventrite; posterior margin of anterolateral ridges weakly crenulate. Femoral lines absent. Anepisternum 3 narrow, 7.5 times as long as wide. Epimeron 3 with minute but distinct ventral portion. Metafurca not examined. Hind wings present, well developed, venation not examined.

Legs. Procoxae moderately transverse, narrowly separated; mesocoxae transverse, moderately separated by preepisternal elevation and anteromedian part of metaventrite; metacoxae transverse, contiguous medially. Proximal part of trochanters concealed by coxae, surface bearing few setiferous punctures. Profemur with very distinct tibial groove delimited by dorsal and ventral ridges; meso- and metafemora with weaker tibial grooves delimited throughout ventrally and in distal half dorsally; profemur with very distinct elongate depression on ventral surface along anterior margin, bearing dense mesh-like microsculpture, remaining surface bearing few setae and weak scale-like microsculpture; meso- and metafemur with sparse punctation bearing stiff semierect setae, surface with fine microsculpture consisting of elongate meshes. Protibia slightly widened apically, without lateral or laterodistal emargination, bearing two rows of stout setae along lateral margin and one row of fine setae along mesal margin, dorsal surface with three rows of fine setae, ventral surface with one oblique row of stout setae and weak, strongly sculptured tarsal groove. Mesotibia with one row of stout setae along lateral margin, three rows of partly fine and partly stout setae on ventral surface and one row of fine setae mesally, apical portion with a series of stout setae and moderately long tibial spurs; metatibia similar to mesotibia but with four ventral series of setae. Tarsi slightly shorter than tibiae, pro- and mesotarsomeres 1–4 short, subequal in length, tarsomere 5 ca. twice as long as tarsomere 4; metatarsomere 1 ca. as long as tarsomeres 2–3 combined, tarsomeres 2–5 subequal in length. All tarsi with rather sparse and short pubescence ventrally and few longer setae on each tarsomere dorsally. Claws small, arcuate.

Abdomen with five ventrites; ventrite 1 carinate medially, bearing coarse punctation with long setae; ventrites 2–5 not carinate, with finer punctation lacking setae and bare microdentulate portion along posterior margin; additional mesal ridges absent on all ventrites.

Male genitalia. Phallobase much shorter than parameres, asymmetrical, lacking median ridge, with weakly developed manubrium. Parameres slender, lacking median projections, each paramere bearing one seta at apex. Median lobe reaching deeply into phallobase, bearing distinct apophyses, not attached to bases of parameres and therefore freely movable within phallobase in anteroposterior direction; corona situated in basal half; lateral margins and apex lacking pubescence. Sternite 9 with long tongue-like posterior projection on median part. Sternite 8 without anterior projection.

Female genitalia. Not examined.

Nipponocerycon shibatai Satô, 1963

Nipponocerycon shibatai Satô, 1963: 267.

Nipponocerycon shibatai oyamanum Nakane, 1968: 86, **syn. nov.**

Nipponocerycon monticola Nakane, 1968: 86 (second part of description published in NAKANE (1977: 87)), **syn. nov.**

Nomenclatorial note. The description of *Nipponocerycon monticola* was divided into two parts: NAKANE (1968: 86) published the first part of the description containing the information about the colouration and about the morphology of the head and antennae and explicitly indicated that the remaining part of the description will be published later. The second part of the description containing the information about the morphology of remaining head appendages and the rest of the body, the differential diagnosis of the species and the list of type material examined was published nine years later by NAKANE (1977: 87). As the ICZN (1999: Art. 13.1) requires only a description or a definition for species names published before 2000, the name *N. monticola* is available already from NAKANE (1968).

Type locality. Japan, Honshu, Ôsaka Prefecture, Minoo.

Type material examined. *Nipponocerycon shibatai*: HOLOTYPE: ♂ (EUMJ), Minoo, Osaka Pref., Honshu, iv.1959, K. Ueda leg. PARATYPE: 1 spec. (ZMUC), Kasuga, Nara, I.xii.1957, T. Shibata leg.

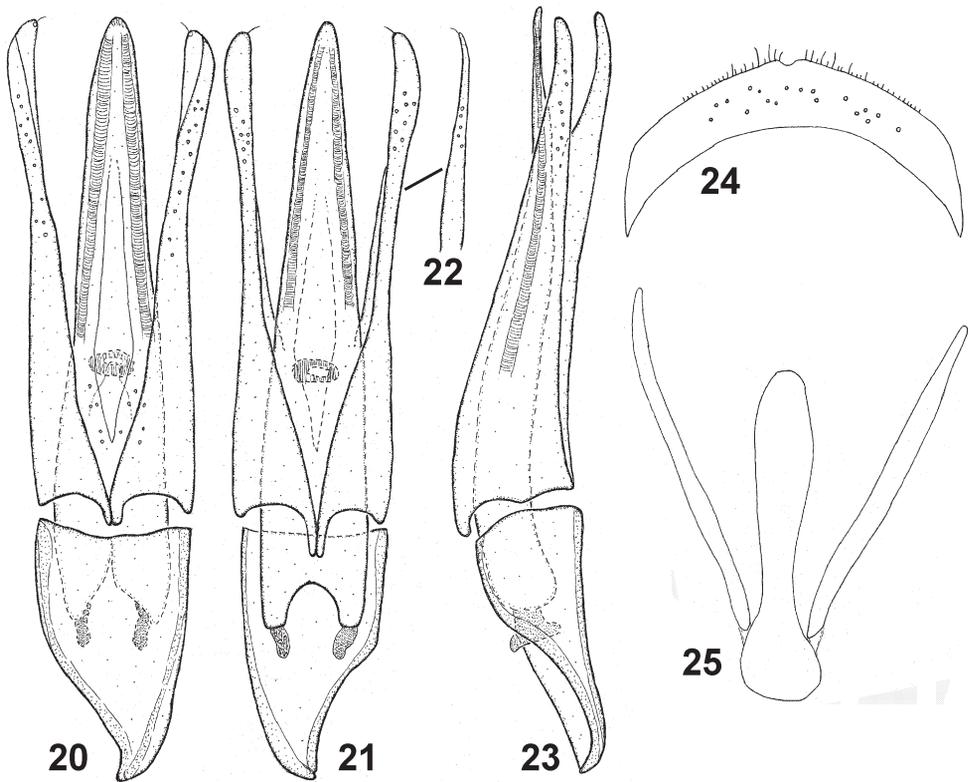
Nipponocerycon shibatai oyamanum: HOLOTYPE: ♂ (EIHU), Sagami-oyama, Kanagawa Pref., Honshu, 15.iv.1967, K. Masumoto leg. PARATYPE: 1 spec. (ZMUC), same data as holotype.

Nipponocerycon monticola: HOLOTYPE: ♀ (EIHU), Mt. Jônen, Nagano Pref., Honshu, 1.xi.1960, K. Kamimura leg. PARATYPE: 1 spec. (ZMUC), Mt. Jônen, Nagano Pref., Honshu, 16.x.1960, K. Kamimura leg.

Additional material examined. **KYUSHU: FUKUOKA PREF.:** 1 spec. (FEFU), Mt. Hikosan, 31.v.1995, sifting of leaf litter, H. Hoshina leg.; 1 spec. (FEFU), same locality and collector, 26.vi.1995, sifting of leaf litter; 3 spec. (FEFU), same locality and collector, 20.xi.1995, sifting of leaf litter; 2 spec. (FEFU), Mt. Inunaki, 18.xii.1995, sifting of leaf litter, H. Hoshina leg. **SHIKOKU: TOKUSHIMA PREF.:** 1 spec. (FEFU), Dosu-tôge, Kisawa-village, 23.–31.v.1998, M. Yoshida leg.; 1 spec. (FEFU), Okuyarito, Kisawa-village, 28.–31.v.2004, flight intercept trap, K. Tanaka leg.; 2 spec. (FEFU), same locality and collector, flight intercept trap, 31.v.–4.vi.2004; 1 spec. (FEFU), same locality and collector, flight intercept trap, 4.–8.vii.2004, K. Tanaka leg.; 3 spec. (FEFU), Mt. Takashiro, Kisawa-village, 29.v.–19.vii.2004, M. Yoshida leg. **HONSHU: HYÔGO PREF.:** 2 spec. (FEFU), Mt. Nagusayama, 10.v.1997, sifting of leaf litter, H. Hoshina leg.; 3 spec. (FEFU), Tentaki, Ôya-town, 10.v.1997, sifting of leaf litter, H. Hoshina leg. **FUKUI PREF.:** 4 spec. (FEFU), Katsumi, Obama-City, 24.–31.v.2007, urea traps, H. Hoshina leg. **ISHIKAWA PREF.:** 1 spec. (FEFU), Mt. Hakusan, 18.–31.x.2002, urea traps, H. Hoshina leg. **KANAGAWA PREF.:** 1 spec. (FEFU), Tanzawa-ôyama, 14.iv.1973, K. Masumoto leg.; 2 spec. (FEFU), Aikawa-town, 20.xi.1994, T. Shimano leg.; 1 spec. (FEFU), Inugoeji, Tanzawa, 5.v.1993, Y. Hirano leg.; 1 spec. (PJWP), Nishi-Tanzawa, 9.xi.2002, P. Jałoszyński leg.

Differential diagnosis. See the differential diagnosis of the genus.

Redescription. Body widest in anterior third of elytra. Body length: 2.1–2.7 mm (holotype: 2.25 mm); body width: 1.3–1.5 mm (holotype: 1.35 mm).



Figs. 20–25. Male genitalia and abdominal sclerites of *Nipponocercyon shibatai* Satô, 1963. 20–23 – aedeagus (20 – ventral view; 21 – dorsal view; 22 – variable shape of the apical portion of the paramere; 23 – lateral view); 24 – sternite VIII; 25 – sternite IX. 20–21, 23–25 – specimen from Kanagawa Prefecture; 22 – specimen from Tokushima Prefecture.

Colouration. Head brown with reddish anterior margin of clypeus and small reddish spot in front of each eye. Pronotum dark reddish to brown, lateral portions paler, reddish to dark reddish. Scutellar shield brown. Elytron bicolored, reddish with rather sharply limited dark brown to black lateral triangular spot arising from ca. midlength of elytral interval 3 and reaching basalmost part of series 9 and posterior fourth of elytral interval 9 (= ‘large lateral spot’); additional small spots situated at posterior third of elytral interval 1 (‘small sutural spot’, sometimes joint with large lateral spot through otherwise completely pale interval 2) and at the bases of intervals 2–4 (‘small basal spot’, obsolete in some specimens); lateralmost elytral interval pale; pseudepipleuron and epipleuron pale. Ventral surface dark brown except for slightly paler posterior and lateral portions of abdominal ventrites. Legs and head appendages reddish, antennal club brown.

Head. Clypeus with moderately dense punctation consisting of rounded setiferous punctures; interstices without microsculpture. Frons with punctation similar to that on clypeus, punctures

Table 1. Geographical patterns of observed variability in *Nipponocercyon shibatai*. Explanations: + = present, (+) = weakly developed, – = absent.

| Locality | Preepisternal plate length/width ratio | Microsculpture on interstices | | | Elytra mesally | |
|-----------|--|-------------------------------|----------|--------|----------------------------|------------------|
| | | Mentum | Pronotum | Elytra | Impressed punctural series | Convex intervals |
| Fukuoka | 1.6 | + | (+) | + | – | – |
| Tokushima | 1.6 | – | (+) | + | + | + |
| Hyôgo | 1.2-1.4 | – | + | + | (+) | (+) |
| Fukui | 1.5-1.7 | – | (+) | + | – | – |
| Nara | 1.6 | + | (+) | + | (+) | – |
| Osaka | 1.4 | – | (+) | + | + | (+) |
| Ishikawa | 1.7 | – | (+) | + | (+) | + |
| Nagano | 1.8 | (+) | (+) | + | + | + |
| Kanagawa | 2.1-2.2 | – | – | (+) | (+) | – |

of same shape medially and laterally; interstices without microsculpture. Surface of mentum flat, bearing moderately dense punctation consisting of rounded punctures without longer setae, anteromedian portion lacking punctation; interstices with or without microsculpture (see Variability).

Thorax. Pronotum with dense punctation consisting of rounded punctures similar to those on head; all punctures similar in size, slightly coarser towards lateral margins; interstices with or without weak mesh-like microsculpture (see Variability). Elevated median portion of prosternum 1.45 times as wide as long, median carina slightly concave in lateral view. Scutellar shield bearing moderately dense rounded punctures lacking setae; interstices without microsculpture. Punctures of elytral series moderately large and rather dense, elytral series not impressed or weakly impressed (see Variability); elytral intervals flat near scutellar shield, becoming slightly convex laterad and posteriad; punctation sparse, consisting of fine irregularly arranged scar-like setiferous punctures; interstices with more or less developed mesh-like microsculpture. Preepisternal plate of mesothorax 1.2–2.2 times as long as wide (see Variability), central portion weakly convex in some specimens; surface with moderately dense punctures bearing long setae, interstices smooth. Median portion of metaventrite with coarse and dense punctation lacking setae; interstices without microsculpture.

Abdomen. Ventrites 2–4 with moderately dense and coarse punctation bearing short setae; interstices with distinct mesh-like microsculpture.

Male genitalia. Aedeagus 0.95–1.00 mm long (holotype: 0.95 mm). Parameres 2.1 times as long as phallobase, slender, continually narrowing from base to apex or slightly expanded apically (see Variability); phallobase 1.75 times as long as wide. Median lobe slightly longer than parameres, continually narrowing from base to apex; corona situated in basal 0.4 of median lobe.

Variability. Considerable variability was observed in the proportions of the preepisternal elevation of the mesothorax, in the development of interstitial microsculpture on the mentum, pronotum and elytra and in the shape of the basal portions of the elytral series. While specimens from one locality are identical or vary only very slightly, specimens from different

Machilus spp. and other species of Lauraceae (Fukui Prefecture), and in deciduous beech (with *Fagus crenata*) and oak (with *Quercus* spp.) forests (Ishikawa, Fukuoka and Hyôgo Prefectures). Other specimens were collected by sifting leaf litter or using flight intercept traps and urea traps.

Distribution. Endemic to Japan and known from the islands of Kyushu, Shikoku and Honshu.

Discussion

Recognition of *Nipponocercyon* and its position within Megasternini

The genus *Nipponocercyon* is well delimited from all other genera of the Megasternini and may be easily recognized by the combination of the following characters: i) presence of two short mesal ridges on the anteromedian part of the metaventrite (unique character), ii) antennae with groups of peg-like sensilla on ventral surface of antennomeres 7–8 (unique character), iii) presence of shallow depressions on the ventral surface of the profemora, iv) the shape of the median portion of the prosternum, v) antennal grooves not reaching the lateral margins of the hypomerion, and vi) abdominal ventrites 2–5 bare in contrast to ventrite 1. Characteristic is also the colouration of elytra, in which *N. shibatai* is only similar to *Cercyon alinae* Ryndevich, 2004; this character may help in routine identification.

FIKÁČEK (2007, 2010) discussed two broadly defined groups of megasternine genera. *Nipponocercyon* belongs neither to the ‘*Megasternum* group of genera’ (based on the antennal grooves not reaching lateral margins of the hypomerion and the well-developed anepisternum 3) nor to the ‘Gondwanan group of genera’ (based on the morphology of the male genitalia: median lobe not attached to the base of parameres and freely movable inside of the phallobase, sternite 9 with a large median tongue-like projection and sternite 8 without a narrow anterior projection). The precise position of *Nipponocercyon* is at present unclear.

Besides the above characters, *Nipponocercyon* is very unusual in having very large mesothoracic cavities for the reception of the procoxae. The cavities reach the mesocoxae, which is otherwise known only in the genus *Australocyon* Hansen, 1990. *Nipponocercyon* might be related especially to the *A. pilocnemoides* species group (sensu HANSEN 2003), which seems unrelated to other Australian or Neotropical species of *Australocyon*. There are also similarities with the Afrotropical genus *Pseucyon* d’Orchymont, 1948 (similar morphology of the preepisternal plate, pubescence and punctation of the abdominal ventrites and presence of a ridge delimiting the median portion of the prosternum from the lateral parts) and with the Oriental genus *Gillisius* d’Orchymont, 1925 (similar morphology of the preepisternal plate and presence of a ridge delimiting the median portion of prosternum from the lateral parts). However, both *Pseucyon* and *Gillisius* have much smaller mesothoracic cavities for the reception of the procoxae, i.e. not reaching the mesocoxae.

Intraspecific variability of *Nipponocercyon shibatai*

Several characters vary considerably in *Nipponocercyon shibatai* (see Variability). However, each of them seems to vary independently (see Table 1). Therefore, subspecies based

on morphological characters cannot be established at present. The differences in pronotal and elytral microsculpture were used by NAKANE (1968, 1977) to define *N. shibatai oyamanum* and *N. monticola*, whose separate status now appears unjustified. This is supported also by the morphology of the male genitalia, which are very similar in all examined males and show only slight variability in the shape of parameres (which vary even within populations; see above for details). We thus consider both taxa by NAKANE (1968, 1977) as junior synonyms of *N. shibatai*.

On the other hand, the differences of specimens from the Kanagawa Prefecture (absence of dorsal microsculpture, very narrow preepisternal plate) and the Hyogo Prefecture (very wide preepisternal plate) seem to be larger than differences observed among other populations. However, morphological characters alone cannot show if these populations represent separate clades. This has to be clarified by a future phylogenetic analysis based on additional characters and samples from additional areas. Such an analysis may also reveal the degree of isolation of particular populations, which remains unclear at present. It seems that the species is not primarily limited by the lack of dispersal abilities, as all examined specimens were macrop-terous and many were collected using flight intercept traps. Expansions and contractions of the *Nipponoceryon* range during glacial and interglacial cycles might have also lead to the high morphological variability in the known populations of *N. shibatai*.

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