Journal of Insect Biodiversity

ISSN: 2147-7612

RESEARCH ARTICLE

Review of the subgenus *Granida* of the genus *Polyphylla* from Vietnam (Coleoptera, Scarabaeidae, Melolonthinae)

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Abstract: The species of *Polyphylla* Harris, 1841 of the subgenus *Granida* Motschulsky, 1862 recorded from Vietnam are redescribed, their known distribution is extended and affinities are rediscussed based on the evidence provided by correct attribution of aedeagi and new morphological characters. *Polyphylla* (*Granida*) vietnamica Kobayashi & Fujioka, 2016 is considered to be closely related to *P*. (*G*.) nikodymi de Wailly, 1993, known from southeast Myanmar, and its holotype is recognized to be an aberrant specimen. *Polyphylla* (*G.*) kontumensis Kobayashi & Fujioka, 2016 is considered closely related to *P*. (*G.*) simoni Sehnal & Bezděk, 2011 and treated as its subspecies; the latter is rediagnosed and the diagnostic value of elytral pattern in *Granida* is discussed.

Key words: Melolonthini, *Polyphylla*, *Granida*, diagnostic characters, taxonomy, new locality records, Vietnam.

Introduction

The recent revisions of the subgenus *Polyphylla* (*Granida*) published by de Wailly (1993) and by Sehnal & Bezděk (2011) did not report any representative of this taxon for the fauna of Vietnam. First records for this country were published by Prokofiev (2012), who noted specimens collected in Khanh Hoa and Lam Dong provinces under the name *P*. (*G*.) *minor* Nomura, 1977, although differences from typical *P. minor* were mentioned in the shape of male antennomere 3 (genitalia were not studied).

Additional specimens of *Granida* from different localities in Vietnam, belonging to two different taxa, were recently gathered by the first author. This stimulated us to review this subgenus in the fauna of Vietnam but prior to submission of our results, the same taxa

were described by Kobayashi & Fujioka (2016). Although their descriptions are clear and complete, their work is undermined by the diagnosis of a new species (*P*. (*G*.) vietnamica Kobayashi & Fujioka, 2016) based on a single aberrant male specimen, and by the misattribution of aedeagi in both the description and the pictures: each of the two new species had its aedeagus attributed to the other.

On these grounds, identification of the Vietnamese species from their original descriptions or from the key proposed by Kobayashi & Fujioka (2016) appears to be problematic. Therefore, we consider necessary to publish the results of our examination of the Vietnamese *Granida* in the present contribution.

Beside addressing the mentioned problems, that include the redescription of P. (G.) *vietnamica* based on a larger number of specimens, we also propose a different interpretation of their relations and, in one case, taxonomic rank.

Material and methods

The following abbreviations identify the collections housing the pinned and dry mounted specimens examined:

AMPC: Coll. A.M. Prokofiev, Moscow, Russia (will be housed in the Zoological Museum, Moscow State University, Russia)

BMNH: Natural History Museum, London, UK

- MKCL: Coll. M. Kuchař, Litoměřice, Czech Republic
- MNCR: Coll. M. Nikodým, Roztoky u Prahy, Czech Republic
- MNHN: Muséum national d'Histoire naturelle, Paris, France
- MUCC: Coll. M. Uliana, Codevigo, Italy
- MZUF: Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia, Italy
- NMPC: National Museum (Natural History), Praha, Czech Republic

Comparative material examined:

- Polyphylla (Granida) jessopi de Wailly, 1993: 1 ♂, holotype, Foochow, vi.1936, M.S. Yang (BMNH).
- *Polyphylla* (*Granida*) *minor* Nomura, 1977: 1 ♀, Formosa, coll. Oberthür (MNHN). Additional data were taken from Sehnal & Bezděk (2011).
- *Polyphylla* (*Granida*) *nikodymi* de Wailly, 1993: 2 ♂, paratype, Birmanie, Süd-Ost, 10.V.1990 (MNCR and NMPC, the latter examined by high resolution photographs in different positions).
- *Polyphylla (Granida) phongsali* Zídek, 2006: 1 ♂, holotype, N. Laos, Phongsali, Gnoi-ou, Li Jingke VI-2003 (BMNH); 15 ♂, 12 ♀, Laos, Khammouane prov., Pakhhene, 1-6.VI.2013 (AMPC).
- Polyphylla (Granida) simoni Sehnal & Bezdĕk, 2011: 1 ♂, holotype, N Thailand, 100 Km NE of Nan, Doi Phu Kha, N.P., 20-25.IV.2004, leg. F. Pavel (BMNH).

Some specimens of the treated taxa were examined based on photos only. They are listed separately from others and were considered to evaluate macroscopic characters only. Their identification was confirmed by the owner, Martin Kuchař, after examination of the parameres (for males) and other diagnostic characters indicated by us.

All measurements were made point to point to 0.1 mm.

Results

Polyphylla (Granida) vietnamica Kobayashi & Fujioka, 2016 (Figs 1-6, 10-12, 22-23)

Polyphylla (Granida) vietnamica Kobayashi & Fujioka, 2016: 16, figs 3, 4, 6 (original description; Ngoc Linh and Dalat in Vietnam; holotype "will be deposited in the Department of Zoology, Natural Museum of Nature and Science, Tsukuba", Japan; not available for us).

Polyphylla (Granida) minor: Prokofiev, 2012: 14 (Dalat Mts.; misidentification).

Diagnosis: A species of *Polyphylla*, subgenus *Granida*, with the following combination of characters. Elytral pattern striped, stripes regular, well developed. Labrum with medial incisure narrow, its sides straight, divergent. Clypeus with anterior margin having constant thickness. Third antennomere of the male elongated, roughly conical, lacking the anterodistal tooth, with maximum width at the distal end. Ratio antennal club/antennomere 3 in males = 3.9-4.6. Protibia bidentate. Parameres with ventral tooth parted from the apex, their shape distinctive from all other species. Pygidium with bare, impunctate medial line.

Material examined: Direct examination $(15 \bar{o}, 15 \bar{o})$: Vietnam, Kon Tum Prov., Ngọc Linh mt., 1700 m, V.2016, leg. local collector: 10 $\bar{o}, 9 \bar{o}$ (5 $\bar{o}, 4 \bar{o}$ MUCC; 5 $\bar{o}, 5 \bar{o}$ MKCL); same data as above, but IV.2016: 2 \bar{o} (MKCL); Vietnam, Lam Dong prov., Lac Duon distr., Bi Doup – Nui Ba Natl. Park, Hon Giao Pass, 12°10'58" N, 108°42'50" E, alt. 1625 m, at light, 13.05.2009, A.M. Prokofiev leg.: 1 $\bar{o}, 2 \bar{o}$ (AMPC); same data as previous specimens, but 22-24.04.2010: 1 \bar{o} , (AMPC); Vietnam, Khanh Hoa prov., Khanh Vinh distr., ~ 72 km E Da Lat, 12°14'08" N, 108°46'14" E, alt. 750-800 m, at light, 14-15.05.2009, A.M. Prokofiev leg.: 1 $\bar{o}, 3 \bar{o}$., (AMPC); Vietnam, Lam Dong prov., Lac Duong distr. Bi Doup – Nui Ba Natl. Park, VI. 2013, leg. local collector: 1 \bar{o} (MUCC); Vietnam, Tua Thien Hue prov., Bach Ma Natl. Park., surr. Hotel Morin (1350-1400 m), 16.2°N 107.85°E, 23-28.V.2014, at light, leg. L. Bartolozzi, G. Chelazzi, A. Bandinelli, S. Bambi, F. Fabiano: 1 \bar{o} (MZUF).

Other specimens, examined based on photos only $(5 \ 3, 11 \ 9, all MKCL)$: Vietnam, Kon Tum Prov., Ngọc Linh mt., 1700 m, IV.2016, leg. local collector: $5 \ 3, 2 \ 9$; Vietnam, Lam Dong prov., Da Lat env., 1500 m, VI.2014, leg. local collector: $3 \ 9$; Vietnam, Da Nang prov., Ba Na Hill, 1450 m, IV.2015, leg. local collector: $3 \ 9$; Vietnam, Kon Tum prov., Kon Tum env., IV.2015, leg. local collector: $3 \ 9$.

Redescription of males

Habitus as in Fig. 1. Body length 20.0-22.5 mm excluding pygidium; greatest width 9.5-10.8 mm. Body elongate, moderately convex. Integument reddish-brown, discal part of the head (except vertex) and of the pronotum sometimes black, elytra slightly lighter, with base, suture and basal half of the lateral margin dark brown to black. Color of vestiture (scales and hairs) varying from white to pale ochreous on all body parts, usually lighter on elytra.

Labrum (Fig. 12) deeply bilobed, medial incisure narrow, about $1.5 \times$ as deep as its maximum (distal) width, with divergent sides. Clypeus transverse with anterior margin considerably upturned and protruded medially (Fig. 10), almost flat at the anterior angles, having constant thickness in lateral and frontal view (Figs 11, 12), anterior angles straight and broadly rounded, sides parallel; surface with coarse sparse punctures bearing setiform scales; scales denser marginally, especially in the middle of the anterior edge, much sparser on disc

of clypeus. Fronto-clypeal suture raised, ridge-like, straight to slightly bisinuated, with mid point slightly protruding towards vertex. Frons weakly impressed medially, similarly punctured as clypeus, with dense patches of elongate-lanceolate to setiform scales at sides continuing onto lateral sides of vertex, and with similar a medial patch in the central impression. Central part of vertex smooth and bare. Canthus ocularis narrow, reaching about half of eye length, with several short, erect, elongate-lanceolate scales. Antenna 10-jointed, with 7-jointed club approximately twice longer than antennomeres 1-3 combined and 3.9- $4.7 \times$ (average $4.3 \times$) as long as antennomere 3; antennomere 3 about twice longer than antennomere 2, considerably broadened at distal tip, with anterodistal angle only slightly more pronounced than posterodistal, and not toothed on its anterior margin, broadest at the distal end (Fig. 6). Last joint of maxillary palpi very sparsely covered with tiny semi-erect setae.

Pronotum transverse (1.6-1.8× as wide as long), widest approximately at the middle, moderately convex, with an impression on each side at anterior margin just medial from anterior angles. Sides straight to weakly concave in the anterior third, concave backwards; anterior angles prominent, obtuse, with rounded apex; posterior angles obtusely angulate with slightly upturned apex. Anterior margin of pronotum slightly bisinuate, thinly bordered. Posterior margin convex, with basal border conspicuously thinned in middle but not interrupted. Surface of pronotum rather coarsely but sparsely punctate, punctures bearing elongate-lanceolate scales forming a complex pattern: an almost straight well-delimited longitudinal stripe along midline; an irregularly-shaped longitudinal stripe on each side of disc interconnected by dispersed scales with an irregularly-shaped and less delimited patch along lateral side with formation of bare spaces separated by groups of setiform scales; in addition, isolated setiform scales distributed between middle and lateral discal stripes.

Scutellum parabolic, with disc bare and impunctate, margin bearing narrow-lanceolate scales interspersed with few setae, apex broadly rounded.

Elytra almost parallel-sided in basal half, weakly convergent toward rounded apex. Elytral length = $3.4-3.7 \times$ pronotal length, $1.5 \times$ greatest elytral width. Surface irregularly punctate, with punctures somewhat rugose, covered with longitudinal stripes of elongatelanceolate scales. Pattern of each elytron is the following: a fringe of short scales along sutural margin and a narrow stripe of larger scales along outer margin of sutural rib, present only in the basal half and bearing irregular interruptions; a pair of rather broad parallel stripes of dense scales on disc (inner stripe slightly broader than outer one), coalescing towards the apex; a narrow stripe of dense scales along lateral margins, starting humeral at the humeral umbone, with few short interruptions along its length, and isolated scales between outer discal and marginal stripes, forming a trace of an additional narrow stripe between them. In addition to aforementioned stripes, sparse scales are present along basal and apical margins of elytra.

Ventral surface of thorax densely covered with long hair-like setae. Abdominal sternites densely covered with short recumbent setiform to narrow-lanceolate scales, anterior margins impunctate. Pygidium triangular, broadly rounded at apex, densely covered with elongate-lanceolate scales but with bare and impunctate medial stripe. Rarely, bare area on the midline of pygidum extremely narrow.

Legs covered with short recumbent lanceolate to elongate-lanceolate scales and long erect hair-like setae. Protibia bidentate, basal tooth weak, obtuse, extreme variations are shown in Figs 3-4; inner spur inserted in the gap between the teeth. Meso- and metatibia gracile, weakly expanded distally. Posterior border of metatibia with 12-22 bristles and two

spine-like apical spurs. Tarsal claws with distinct basal tooth ventrally, teeth of the two claws unequal in all legs although difference is weaker on posterior ones.

Aedeagus as in Fig. 5; shape of paramere "crests" somewhat variable.

Redescription of females

Only relevant differences from male specimens are noted.

Habitus as in Fig. 2. Body length 22.0-25.0 mm excluding pygidium; greatest width 10.0-12.0 mm, more convex than male.

Medial part of the clypeus sometimes slightly convex, anterior angles on average more broadly rounded, anterior border of clypeus (upturned middle portion) sometimes weakly incised in midline.

Antennal club 5-jointed, about $0.8-0.9 \times$ as long as antennomeres 1-3 combined and $1.8-2.2 \times$ as long as antennomere 3, antennomere 3 equal to $2.1-2.8 \times$ the length of antennomere 2. Antennomere 5 partially expanded and about $1/3-1/4 \times$ as long as the rest of the club.

Protibia less slender, with basal tooth more developed, acute. Posterior border of metatibia with 24-29 bristles. Apical spurs of posterior tibia broad and flat. Each tarsus bears two claws similar to each other.

Genital sclerites as in Fig. 23.

Distribution: *Polyphylla* (*G.*) *vietnamica* is currently known from the Annam (= Truong Son) Mountain Chain in Thua Thien province southward to the Dalat (= Langbian) Plateau in Lam Dong province, Vietnam.

Remarks

Original description of *P*. (*G*.) *vietnamica* was based on a single male from Mt. Ngoc Linh and eight females from the same locality and "near Dalat" (Kobayashi & Fujioka 2016). The male holotype possesses an untraceable basal tooth of the protibia (Kobayashi & Fujioka 2016: fig. 3), which led the authors to classify this species within the group of insular species composed by *P*. (*G*.) *albolineata* (Motschulsky, 1862), *P*. (*G*.) *schoenfeldti* Brenske, 1890 and *P*. (*G*.) *taiwana* (Sawada, 1950), characterized by the unidentate protibia. However, all male specimens (totally 20) that we examined, including those from Mt. Ngoc Linh, constantly show an obvious second (basal) tooth of the protibia, whose development can be variable (Figs 3-4). All other characters in the original description well correspond with our specimens.

Therefore, we confidently point out that the unidentate protibiae of the holotype represent an aberration and not a characteristic of this species. Furthermore, the description and figures of the aedeagus attributed to P. (G.) vietnamica by Kobayashi and Fujioka (2016) actually correspond to the aedeagus of P. (G.) kontumensis (and vice versa).

According to our observations, P. (G.) vietnamica belongs to a group of species characterized by the bidentate protibia and the parameres bearing a pronounced ventral tooth well before the apex; included species are P. (G.) minor, P. (G.) nikodymi, P. (G.) jessopi and P. (G.) phongsali. The striped elytral pattern may allow to easily exclude P. (G.) phongsali from the most similar species, since the latter is known on marbled specimens only. However, the intraspecific variation of this condition, documented in other species of the same subgenus (see description of Polyphylla (G.) simoni kontumensis), suggests to take with extreme care the diagnostic utility of this character.

Shape of parameres (Fig. 5) allow to easily separate this taxon from P. (G.) minor, P. (G.) jessopi and P. (G.) phongsali, while it is evidently similar to P. (G.) nikodymi (Fig. 8). Diagnostic differences between P. (G.) vietnamica and the latter mostly consist in their shape in dorsal view, with parameres less divergent and right paramere evidently less broad in P. (G.) vietnamica; minor and more variable differences are found also in the shape of the apex in lateral view (more expanded in P. (G.) vietnamica) and of the ventral tooth (larger in P. (G.) vietnamica); the shape of the paramere "crest" is considerably variable.



Figures 1–9. *Polyphylla (Granida) vietnamica* (1-6, topotypes, MUCC) and *P. (G.) nikodymi* (7-9, paratype, MNCR). 1, 7: habitus of male; 2: habitus of female; 3, 4: variability of anterior tibia; 5, 8: parameres in right, dorsal and left view. In grey, parts of the opposite paramere. In fig. 8, right and dorsal view, the damaged right paramere of the NMPC paratype is reconstructed after NMPC paratype); 6, 9: detail of antenna, with evidence on the shape of the antennomere 3.



Figures 10–15. *Polyphylla (Granida) vietnamica* (**10-12,** topotypes, MUCC) and *P. (G.). nikodymi* (**13-15,** paratype, MNCR). Head in postero-dorsal (inclination about 45°), lateral and frontal view. In grey, symmetrization of damaged parts.

Distinction of *P*. (*G*.) vietnamica from *P*. (*G*.) nikodymi (habitus as in Fig. 7) is better supported by various external characters: incision of labrum with divergent sides and

augmenting breadth in *P*. (*G*.) *vietnamica* vs. incision of labrum with parallel sides and costant breadth in P. (G.) nikodymi (Figs 12, 15); anterior margin of clypeus, in postero-dorsal view, convex in *P*. (*G*.) *vietnamica* vs. straight in *P*. (*G*.) *nikodymi* (Figs 10, 13); margin of clypeus with regular, constant thickness in P. (G.) vietnamica vs. about twice thicker at the angles than in the middle in *P*. (*G*.) *nikodymi* (Figs 11-12, 14-15); frontoclypeal suture raised and straight in, or almost so, P. (G.) vietnamica vs. convex and flat in *P*. (*G.) nikodymi*; in males, antennomere 3 without dorsal tooth and more elongate (club = $3.9-4.7 \times$ its length) in *P*. (*G.*) *vietnamica*, with dorsal tooth and less elongate (club = $5.9-6.6 \times$ its length) in *P*. (*G.*) *nikodymi* (Figs 6, 9); in males, anterior tibiae more slender, with second tooth less protruding in *P*. (*G.*) *vietnamica* than in *P*. (*G.*) *nikodymi* (pygidium with bare and impunctate midline (occasionally poorly evident) vs. entirely covered with recumbent scales in *P*. (*G.*) *nikodymi* (scales less dense on the midline, but present).

For differences between females of P. (G.) vietnamica and the syntopic P. (G.) simoni kontumensis, see discussion about the latter taxon.

Ecological notes: Specimens collected by AP were attracted by light exposed on the disturbed margins of primary montane cloud forests at altitudes 750-1625 m above sea level. Only few specimens came per night, females prevailed.

Polyphylla (Granida) simoni kontumensis Kobayashi & Fujioka, 2016, new status (Figs 16-19, 24-25)

Polyphylla (Granida) kontumensis: Kobayashi & Fujioka, 2016: 17, figs 1, 2, 5 (original description; Ngoc Linh and "Ngoe Thinh" in Central Vietnam; holotype "will be deposited in the Department of Zoology, Natural Museum of Nature and Science, Tsukuba", Japan; not examined).

Diagnosis

Polyphylla (Granida) simoni s.l.: a species of Polyphylla, subgenus Granida with the following combination of characters. Elytral pattern striped to marbled. Labrum with medial incisure broad, with roughly semicircular shape. Clypeus slightly thicker at the angles than in the middle in frontal view. Third antennomere of the male elongated, broadened at distal tip, with anterodistal angle only slightly more pronounced than posterodistal one, not toothed on its anterior margin. Ratio antennal club/antennomere 3 in males = 3.4-4.0. Protibia bidentate. Parameres with a minute ventral indentation immediately behind the apex. Pygidium with medial line impunctated, bare or with few isolated setae.

ssp. *simoni* **Sehnal & Bezděk, 2011** (Figs 20, 21): populations of *Polyphylla* referable to *Polyphylla simoni* from North Thailand with elytral pattern striped, and stripes regular, well developed.

ssp. *kontumensis* **Kobayashi & Fujioka, 2016** (Figs 16-19, 24-25): populations of *Polyphylla* referable to *Polyphylla simoni* from Central Vietnam, and distinct from the nominotypical population for the marbled elytral pattern shown by most of specimens.

Distribution: *P. simoni kontumensis* is known from the mountains in Thua Thien and Kon Tum provinces of Central Vietnam. We are unable to locate the collecting site "Ngoe Thinh, Kon Tan Dist." listed in the original description: there is no such district in the current

administrative division of Vietnam (Anonymous 2009) and we tentatively consider it as a mistake in the transcription of specimens collected in "Ngoc Linh, Kon Tum" (type locality).



Figures 16–21. *Polyphylla* (*Granida*) *simoni kontumensis* (16-19, MUCC, MKCL) and *P*. (*G*.) *simoni simoni* (20-21, holotype, BMNH). 16, 17, 20: habitus of male; 18: habitus of female; 19, 21: parameres in right, dorsal and left view. In grey, parts of the opposite paramere.

Material examined: Direct examination $(10 \circlessift)$, $1 \circlessift)$: Vietnam, Kon Tum Prov., Ngọc Linh mt., 1700 m, V.2016, leg. local collector: $4 \circlessift)$ (MUCC); same data as above, but IV.2016: $4 \circlessift)$, $1 \circlessift)$ (MKCL); Vietnam, Thua Thien-Hue prov., Bach Ma mt., 1400 m, IV.2016: $2 \circlessift)$ (MKCL); Vietnam, Gia Lai Prov., Kon Chu Rang Nature Reserve, about 8 Km from HQ, m 1100, 14°30,256'N 108°30,109'E, 8-12.V.2016, at light, leg. L. Bartolozzi, A. Bandinelli, S. Bambi, V. Sbordoni: $1 \circlessift)$ (MZUF).

Other specimens, examined based on photos only (5 3, 4 9, all MKCL): Vietnam, Kon Tum Prov., Ngọc Linh mt., 1700 m, IV.2016: 2 3, 2 9; Vietnam, Kon Tum Prov., Ngọc Linh mt., 1900 m, III.2016: 2 3, 2 9; Vietam, Kon Tum prov., Kon Tum env., IV.2015, 1 3, leg. local collector.



Figures 22–25. *Polyphylla (Granida) vietnamica* (**22-23**) and *P. (G.). simoni kontumensis* (**24-25**), females, both from Kon Tum Prov., Ngọc Linh mt. (MUCC, MKCL). Dorsal view of pronotum, showing evident difference in punctures between syntopic females, and genital sclerites of female.

Remarks

Our specimens, including topotypical ones, well agree in characters with the original description of P. (G.) *kontumensis*, except the aedeagus: description and figures attributed to P. (G.) *kontumensis* by Kobayashi and Fujioka (2016) actually correspond to the aedeagus of P. (G.) *vietnamica* (and vice versa).

Kobayashi & Fujioka (2016: 20) compared this taxon only with P. (G.) phongsali (having a similar marbled elytral pattern). However, they overlooked that in all other characters, including the almost identical aedeagus, P. (G.) kontumensis well corresponds to

P. (*G.*) *simoni*. The latter is unique among the continental *Granida* in its characteristic aedeagus having only a minute ventral indentation just behind apex of the parameters.

To date, typical *P*. (*G*.) *simoni* is known only on the type series, counting 6 specimens, all males, collected in North Thailand; according to the original description they are all characterized by a striped pattern (Fig. 20), with no relevant variation. On the contrary, 20 out of 23 specimens from Vietnam known to us have the typical marbled pattern common to several other species of *Polyphylla*, with no trace of stripes at all (Figs 16, 18), while three (all males) have a striped pattern. The latter appears however significantly different from that of the typical population due to the grossly irregular structure of stripes, which have uneven thickness and coalesce to each other in random positions (Fig. 17). Apart from the elytral pattern, we could not observe any relevant difference between Vietnamese specimens and the holotype of *P. simoni*, including parameres (Figs 19, 21).

Although Vietnamese and Thailandese populations according to the present-day knowledge have a disjunct distribution and relevant differences on scale pattern, we consider these conditions not enough to attribute them to two different species. Instead, the lack of morphological differences and the syntopic presence of striped specimens among marbled ones are rather suggestive of a genetic flow still active or only recently interrupted. Therefore, in our opinion, the taxon *kontumensis* is better considered as a subspecies of *P*. (*G*.) simoni.

A variation of the elytral pattern similar to that of P. (G.) simoni kontumensis is known for P. (G.) jessopi (Sehnal & Bezděk 2011), but the few known specimens do not allow any inference about geographical variations.

Polyphylla (G.) simoni kontumensis occur in sintopy with P. (G.) vietnamica; in addition to differences in parameres and, as far as known, elytral pattern, the two species can be separated based on shape of labrum, margin of clypeus, puncture of pronotum (Figs 22-24), and presence/absence of basal border in the medial part of pronotum, all characters that apply to both sexes.

Acknowledgements

Our gratitude goes to all museum curators that assisted us for the study of the examined material: M. Barclay and M. Geiser (BMNH), A. Mantilleri and O. Montreuil (MNHN), L. Bartolozzi (MZUF) and J. Hájek (NMPC), who kindly provided us with high quality photographs of the paratype of *P. nikodymi*. We also thank M. Nikodým and M. Kuchař for sending us specimens from their private collections, and A. Bezděk (Biology Centre CAS, Institute of Entomology, České Budějovice) for his kind support and advice. Two anonymous referees improved the quality of the manuscript.

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