

A revision of the neotenic genus *Scarelus* (Coleoptera: Lycidae)

VLADIMÍR MALOHLAVA & LADISLAV BOCAK

Department of Zoology, Faculty of Science, Palacký University, tř. Svobody 26, 771 46 Olomouc, Czech Republic.

Abstract. The neotenic net-winged beetle genus *Scarelus* Waterhouse 1878 is revised and its relationships to other genera of Ateliini, biology, and zoogeography are discussed. Twenty-seven species of *Scarelus* are recognized, of which eleven are described as new: *S. baranciki* n. sp. (Borneo), *S. pseudumbrosus* n. sp. (Malaysia), *S. cibodasensis* n. sp. (Java), *S. flavicollis* n. sp. (Sumatra), *S. loksadoensis* n. sp. (Borneo), *S. pahangensis* n. sp. (Malaysia), *S. ruficollis* n. sp. (Sumatra), *S. rufus* n. sp. (Sumatra), *S. salvani* n. sp. (Philippines), *S. saranganensis* n. sp. (Java), and *S. similis* n. sp. (Borneo). *Scarelus luchti* Kazantsev & Yang 1999 is considered to be a nomen nudum due to proposal without any description. All known species are listed with differential diagnoses, redescriptions, data on variability and distribution. A key to *Scarelus* species and Ateliini genera is provided.

Résumé. Une révision du genre néoténique *Scarelus* (Coleoptera : Lycidae). Le genre néoténique *Scarelus* Waterhouse 1878 est revu et ses relations avec les autres genres d'Atelini, leur biologie et leur zoogéographie sont discutées. Vingt-sept espèces de *Scarelus* sont reconnues, parmi lesquelles onze sont nouvellement décrites : *S. baranciki* n. sp. (Bornéo), *S. pseudumbrosus* n. sp. (Malaisie), *S. cibodasensis* n. sp. (Java), *S. flavicollis* n. sp. (Sumatra), *S. loksadoensis* n. sp. (Bornéo), *S. pahangensis* n. sp. (Malaisie), *S. ruficollis* n. sp. (Sumatra), *S. rufus* n. sp. (Sumatra), *S. salvani* n. sp. (Philippines), *S. saranganensis* n. sp. (Java), et *S. similis* n. sp. (Bornéo). *Scarelus luchti* Kazantsev & Yang 1999 est considéré comme nomen nudum du fait de l'absence de description. Toutes les espèces connues sont citées avec une diagnose différentielle, une redescription, des données sur leur variabilité et sur leur distribution. Une clef des espèces de *Scarelus* et des genres d'Atelini est fournie.

Keywords: Atelini, net-winged beetles, new species, zoogeography, Oriental Region.

The net-winged beetles, Lycidae, are one of elateroid lineages (Crowson 1972, Bocakova *et al.* 2007). Similarly with several families of Elateroidea, the metamorphosis of net-winged beetles is incomplete and results in morphological modifications, from widespread soft-bodiedness, to larviform females in some lineages including *Scarelus* Waterhouse 1878. Although ontogenetic reprogramming has been widely studied, most works have focused on vertebrates (Gould 1977) and fragmentary, mostly descriptive information is available on insects, including Lycidae (*e.g.*, Crowson 1972, Cicero 1988, 2008, Miller 1991). Multiple origins of soft-bodiedness and neoteny in Elateroidea and Lycidae were inferred from molecular phylogenies (Bocakova *et al.* 2007; Bocak *et al.* 2008). Unfortunately, incomplete information about distribution, natural history, and the chaotic classification, prevent detailed studies on the impact of ontogenetic modifications on ecology and

distribution. Therefore, we need to accumulate further alpha-taxonomic and zoogeographic data on *Scarelus* to address such topics as the speciation processes or interactions between neoteny and ecology.

Ateliini are species poor despite a hypothesized ancient origin (Bocak *et al.* 2008). We believe that it is not a bias caused by neglect of the group by taxonomists, as *Scarelus* was intensively studied in the last decade (Bocak 1995, 1997, 1998, Kazantsev 1992, 1997, Malohlava & Bocak 2009). At present, three genera are defined in Ateliinae: *Atelius* Waterhouse 1878, *Paratelius* Kazantsev 1997, and *Scarelus* Waterhouse 1878. Ateliinae are distinguishable by the long, slender, and usually strongly compressed antennae (fig. 2A), and the pronotum with a single median longitudinal keel (fig. 2E, 2F). All species have the characteristic phallus, which is either long and tubelike or shortened and pointed (fig. 3A–6H). Females are unknown and supposedly neotenic (Bocak *et al.* 2008; Bocak & Bocakova 2008, Bocak & Matsuda 2003; Wong 1996).

Ateliinae were proposed by Kleine (1928) to intercept the monotypic *Atelius* and seven species classified in *Scarelus*. Later, Kleine (1933) lowered the

E-mail: ink@volny.cz; ladislav.bocak@upol.cz

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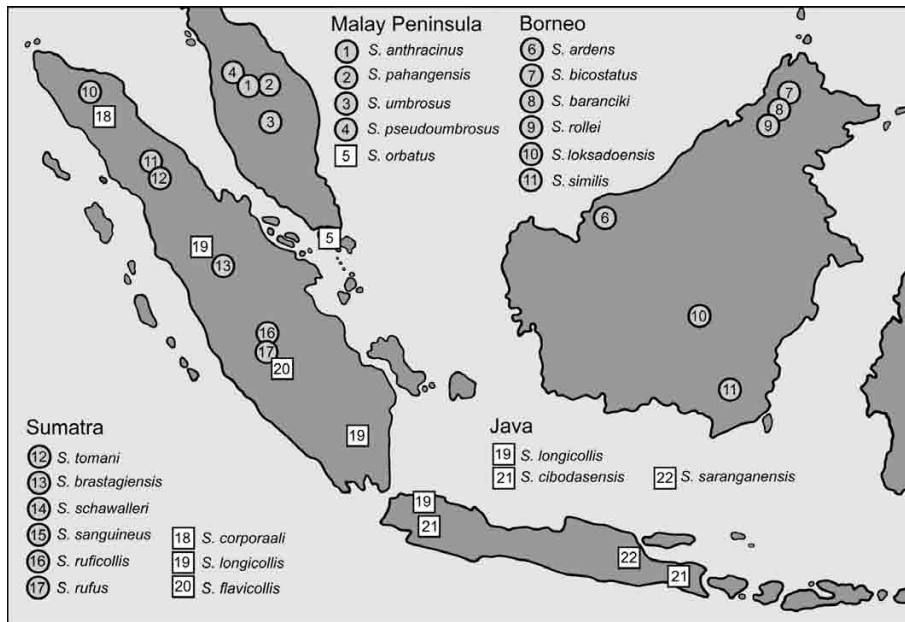


Figure 1
Map: Distribution of *Scarelus* spp. in Peninsular Malaysia and the Great Sundas. The numbers in circles designate species placed in the *S. anthracinus* group, numbers in rectangles the *S. orbatus* group.

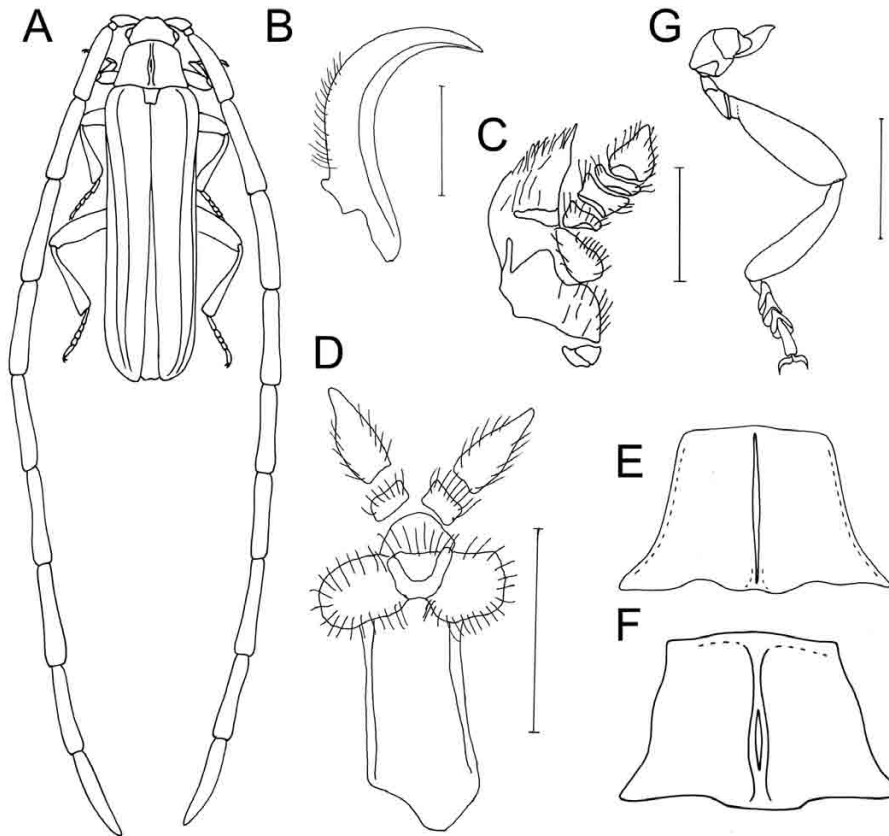


Figure 2
A, *Scarelus crudus* Kleine, general view; B, *Scarelus* sp., mandible; C, *Scarelus* sp., maxilla; D, *Scarelus* sp., hypopharynx; E-F, *Scarelus* sp., pronotum, E, *S. sanguineus*; pronotum; F, *S. brastagiensis*, pronotum; G, *Scarelus* sp: hind leg. Scales 0.5 mm.

status of all lycid subfamilies to tribes when he classified Lycinae and Homalisininae in one family (Crowson 1955, 1972, Bocak & Brlik 2008; Kleine 1933). Bocak & Bocakova (1990) proposed Ateliinae as one of six lycid subfamilies. A recently published molecular phylogeny of Lycidae suggested the relationships of Dilophotini and Ateliini, with these tribes forming the redefined subfamily Ateliinae (Bocak & Bocakova 2008). Despite similar biology, both morphology and molecular data suggests a distant position of Scarelini from the other lycid neotenic lineages (Bocak *et al.* 2008).

Altogether 36 species are now classified in Ateliini, making it one of the species poorest tribes in Lycidae. The observed low species level diversity of Ateliini is characteristic for all lycid lineages with proven or expected female neoteny (Bocak *et al.* 2008). Three genera, *Atelius*, *Scarelus*, and *Paratelius*, are placed in Ateliini. *Atelius* remained monotypic since it's proposal in the mid 19th century until the 90's (Kazantsev 1992; Bocak 1997). Five species are placed in *Paratelius* (Kazantsev 1997; Malohlava & Bocak 2009). *Scarelus* Waterhouse 1878 is the largest genus with 27 species. The first two species were described by Waterhouse (1878) from Singapore and Java and further species were added only in the beginning of 20th century (Pic 1911, 1912; Kleine 1926). Kazantsev (1992) reviewed the status and synonymized several species described by M. Pic. Further species were proposed by Kazantsev (1997), Kazantsev & Yang (1999), Bocak (1995, 1997, 1998) and Bocak & Bocakova (1999).

Herein, we present a detailed redescription of *Scarelus*, an alpha-taxonomic revision of twenty-seven species, a key to all species, and illustrations of important taxonomic characters. As no comprehensive study is available, the main goal is to provide a sound taxonomic basis for further studies on the impact of neotenic modifications on macroevolution and ecology. Additionally, the neotenic lineages are characteristic in restricted ranges, which may be used for identification of Pleistocene rain forest refugia as valuable areas for biodiversity conservation.

Material and methods

The revision is mostly based on the recently collected material from the Oriental region and several collections deposited in major European museums. All species were represented only by the male adult semaphoront. Male genitalia of all available type specimens were dissected after muscles and fat bodies were removed by short boiling of the abdomen in 10% KOH. Illustrations of important characters were derived from photographs taken with a digital camera attached to a stereoscopic microscope. Holotypes were used for descriptions when available. Measurements were taken under a dissecting microscope using an ocular eye piece with a scale bar. The following measurements were taken: BL-body length, measured

from the fore margin of head to the apex of the elytra; WH-width at humeri, measured at base of elytra at point where they become parallel-sided; PL-pronotum length, measured at midline; PW-pronotum width, measured at posterior angles; Edist-minimum interocular distance in frontal part of cranium; Ediam-maximum eye diameter in lateral view.

Depositories

BMNH- Natural History Museum, London, United Kingdom; LMBC- Department of Zoology, Palacky University, Olomouc, Czech Republic; MZIW- Museum and Institute of Zoology, Polish Academy of Sciences, Poland; NHMP- National Museum of Natural History, Prague, Czech Republic; SMNS- Staatliches Museum für Naturkunde, Stuttgart, Germany.

Taxonomy

Scarelus Waterhouse 1878

Scarelus Waterhouse 1878: 100.

Type species: *Scarelus orbatus* Waterhouse 1878.

Redescription. Body small, slender, uniformly dark brown to black, seldom orange brown. Elytra and pronotum testaceous or with variable extension of light brown humeral part and dark apex of elytra; few species with upper side reddish brown or concolour black.

Head small (fig. 2A), hypognathous, freely movable, slightly retractable into pronotum, without rostrum. Cranium with fine microstructure, surface slightly shiny, pubescent; frons convex. Antennal tubercles inconspicuous, divided by shallow longitudinal depression, antennal cavities very close each to other, separated by narrow cranial bridge. Eyes small, hemispherically prominent. Antennae slender, long, surpassing elytral apex by 0.5 to 5 antennomeres (fig. 2A). Scapus robust, pear-shaped, pedicel trasverse, more than 3 times shorter than scapus, antennomeres 3–11 long, slender, strongly compressed to rounded in cross-section, parallel-sided to slightly serrate, apical antennomere longest, elliptical (fig. 2A). Antennomeres covered with dense recumbent pubescence. Mouthparts hypognathous; maxillae, labium, and both palpi tiny. Oral cavity rounded, slightly emarginate where mandibles are attached. Mandibles stout, long, slightly curved, without teeth (fig. 2B). Labium and maxillae separated (fig. 2C, D). Maxillary palpi 4-segmented (fig. 2C), labial palpi 2-segmented (fig. 2D), both palpi with apical palpomeres stoutest. Labrum triangular. Pronotum trapezoidal, flat, posterior margin wider than frontal one, disc with single stout, longitudinal carina bearing very deep and narrow depression in middle (fig. 2E-F). Frontal margin of pronotum slightly rounded, anterior angles obtuse, lateral margins convex to straight, posterior angles acutely prominent. Posterior margin almost straight. Scutellum flat, shiny, sparsely pubescent, usually weakly emarginate at apex. Elytra flat, with two or three longitudinal costae in most of elytral length, costa 1 weak to vestigial, reaching one to nine tenths of elytral length, stout only at base, costae 2 and 4 much stouter, costa 4 forms edge of humeri (fig. 2A), costa 3 vestigial, fused with base of costa 4, identifiable only at very base. Longitudinal costae connected by transverse ridges forming rectangular cells, whole elytra densely pubescent, without long, erected setae. Legs slender, compressed, densely pubescent. All tarsi with five tarsomeres, tarsomeres 1 and 2 slender, almost

parallel-sided, slightly emarginate at apex, tarsomeres 3 and 4 wider, triangular, deeply emarginate, tarsomere 5 very slender, almost twice longer than preceding, claws simple (fig. 2G). Male genitalia of two types: either phallus long and widened basally, slightly to strongly curved (e.g. fig. 4H-I), *S. anthracinus* species group), or phallus short and acutely pointed at apex (fig. 6A-D), *S. orbatus* species group). Female unknown.

Remark. The elytral costae have often been considered as a conservative character within Lycidae and they have been used for definitions of genera (e.g., *Paratelius* Kazantsev 1992). The comparison of Ateliini with Dilophotini as their hypothesized sister group does not help with polarization of this character as a similar tendency of shortening and reduction of the number of costae is found also in *Dilophotes* Waterhouse 1879, a presumed sister group of Ateliini (Bocak & Bocakova

2008). Considering the regular presence of fully developed four costae in various lineages of Lycidae, we hypothesize the pattern of four longitudinal costae as an ancestral state in Ateliini (Bocak & Bocakova 1990 2008), and the lower numbers of costae are considered to be reductions. Ateliine genera are based on the presence of four costae in *Atelius* and *Paratelius*, three costae in *Scarelus*. In *Atelius*, all costae are fully developed, unlike *Paratelius* whose costa 1 and 3 is much weaker than costae 2 and 4, in congruence with conditions found in *Scarelus*. Although the character has been used for classification, we found a remarkable variability in development of the elytral costae in *Scarelus* with an apparent tendency for further, possibly multiple, reductions of costae in connection

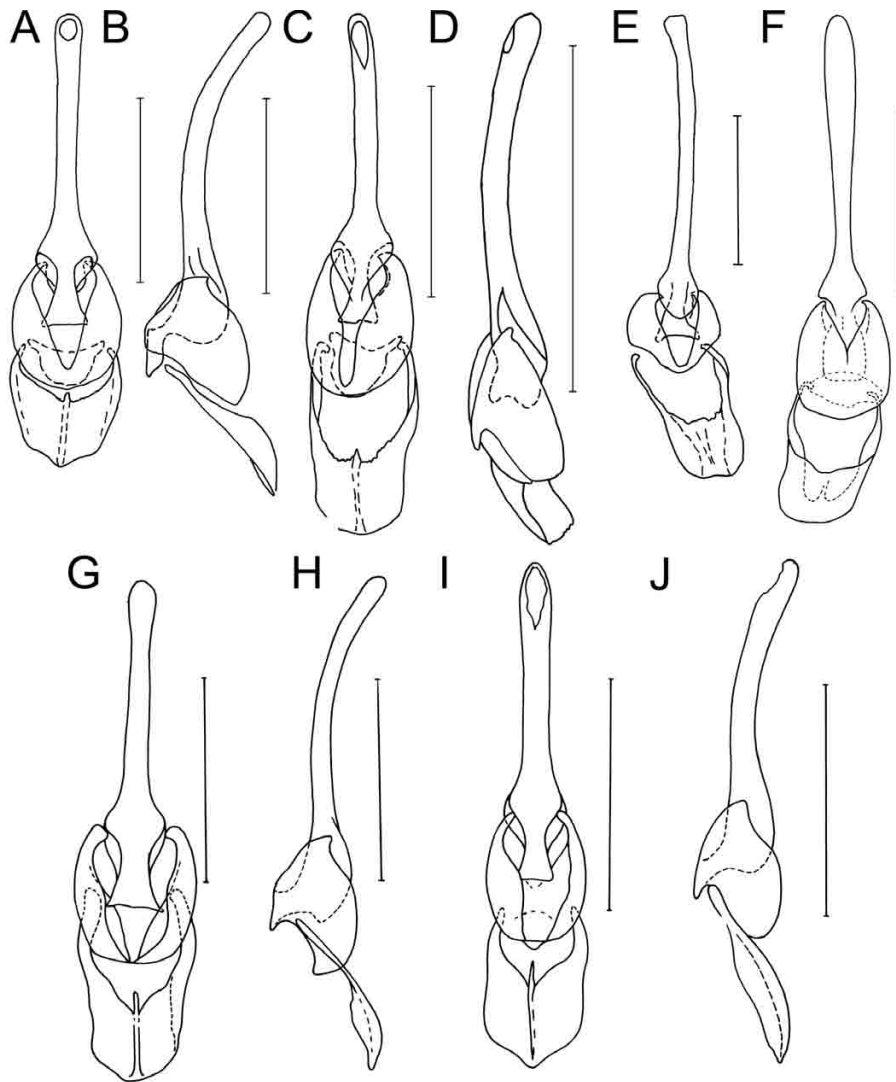


Figure 3
Male genitalia. A-B, *S. ruficollis* n. sp.; C-D, *S. brastagiensis*; E, *S. tomani*; F, *S. schawalleri*; G-H, *S. sanguineus*; I-J, *S. rufus* n. sp.. Scales 0.5 mm.

with a small and slender body. Therefore, we assume that their value for higher classification is limited. The costae are supposed to have a strengthening function in the generally soft-bodied lycids and their presence and/or absence can be selected differently in the small and slender bodied lineages, such as *Scarelus* or *Dilophotes*, than in other lineages. The supposed evolution of elytral costae leaves *Paratelius* as a taxon defined exclusively by symplesiomorphies.

The *S. anthracinus* species group

Differential diagnosis. Species classified in both the species groups proposed here are similar in the general body form, and they differ substantially only in the shape of male genitalia. The *S. anthracinus* group has a long, almost straight or slightly curved phallus, which is much longer than the phallobase and

always obtuse at apex (e.g. fig. 3A-J, 4B-J, 5A-L, 6E). This form of the phallus is reminiscent of those of the closely related *Paratelius* (Malohlava & Bocak 2009). Although both species groups within *Scarelus* are well defined by the morphology of genitalia, we prefer to assign species to informal groups as the long form of the phallus is similar to those of *Paratelius*, and therefore there is no evidence that the *S. anthracinus* species group represents a monophylum. The species from Borneo/Philippines and Sumatra/Peninsular Malaysia/Burma differ in the shape of the phallobase. The species from the western part of the range have a well-developed median longitudinal keel in the phallobase which is similar to those of *Paratelius* (e.g., fig. 3A-J; Malohlava & Bocak 2009). The Bornean and Philippine species have strongly asymmetrical phallobase without any keel (fig. 5A-L). No other character supports these species groups. The geographically structured variation on morphology suggests lack of dispersal between Borneo and Sumatra.

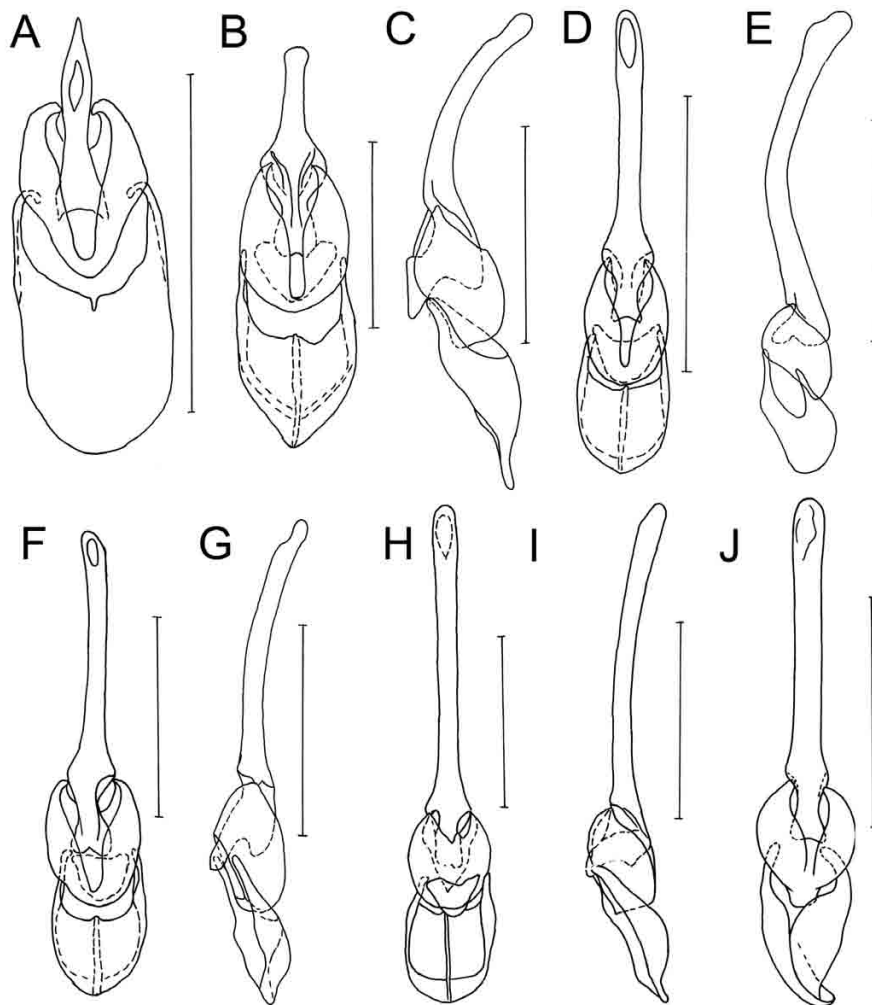


Figure 4
Male genitalia. A, *S. orbatus*; B-C, *S. umbrosus*; D, *S. pahangensis* n. sp.; E, *S. ardens*; F-G, *S. pseudoumbrosus* n. sp.; H-I, *S. anthracinus*; J, *S. baranciki* n. sp.. Scales 0.5 mm.

***Scarelus anthracinus* Bocak & Bocakova 1999**

Scarelus anthracinus Bocak & Bocakova 1999: 38.

= *Scarelus maxwelli* Kazantsev & Yang 1999: 245; Bocakova & Bocak 2000: 44.

= *Scarelus peddenburyi* Kazantsev & Yang 1999: 246, nomen nudum; Bocakova & Bocak 2000: 44.

Type material. Holotype. Male, Malaysia, Perak, Cameron Highlands, Mt. Beremban, 4°28'N 101°23'E, 1.-3. IV.1990, leg. A. Riedel (SMNS). Paratype. 2 males, ditto, 19.-23.III.1998, leg. L. Bocak; male, ditto, 13.-17.II.1997, leg. Ivo Jeniš; male, ditto, Mt. Jasar, 12.-15.II.1998, leg. S. Becvar; male, ditto, 20.II.-3.III.1998, leg. P. Cechovsky; male, Malaysia, Pahang, 30 km W Ipoh, 1500 m (all paratypes LMBC). *Other material examined.* Male, Malaysia, Pahang, Cameron Highland, Tanah Rata, 1.-13.II.2003, leg. P. Pacholatko; 7 males, ditto, 11.-

27.II.2000, leg. P. Pacholatko; 3 males, ditto, 11.-27.II.2000, leg. J. Horak; 2 males, ditto, 2.-26.II.2004, leg. P. Pacholatko; 4 males, ditto, 3.I.2005, leg. Bolm; 8 males, ditto, 3.-9.II.2005, leg. Bolm; male, ditto, 18.-22.IV.2000, leg. Bolm; male, ditto, 19.-23.III.1998, leg. Bolm (all LMBC).

Differential diagnosis. *S. anthracinus* is a species easily distinguishable by the uniformly black elytra and dark reddish brown sutural margins. The species does not resemble in colouration any other *Scarelus*. The phallus resembles those of *P. pahangensis* n. sp. (fig. 4H-I, 4D).

Redescription. Male. Body small-sized, slender; body black, only sutural margins of elytra and partly bases of elytral costae reddish brown. Head small with hemispherically prominent eyes, their distance 3.05 times maximum eye diameter. Antennae slender, compressed, surpassing apex of elytra by two

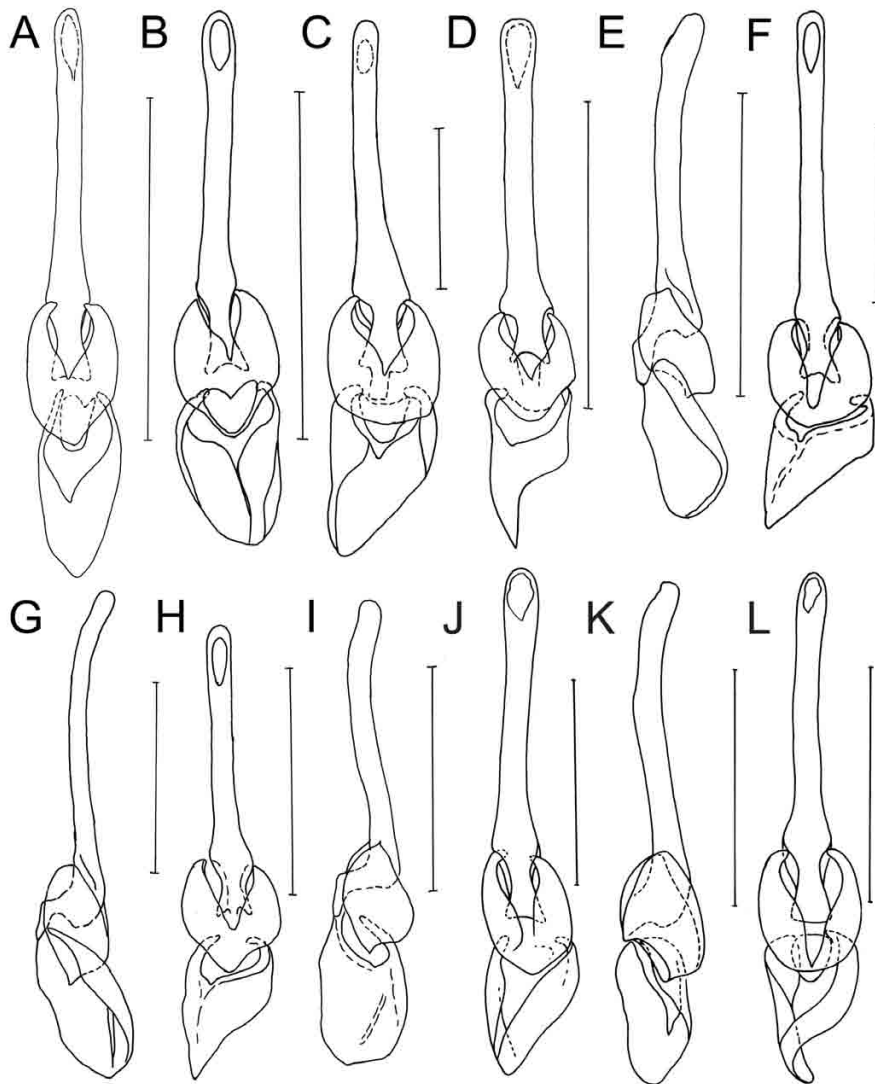


Figure 5
Male genitalia. A, *S. kodadai*; B, *S. palawensis*; C, *S. crudus*; D-E, *S. bicostatus*; F-G, *S. rollei*; H-I, *S. similis* n. sp.; J, *S. loksadoensis* n. sp.; K-L, *S. salvani* n. sp.. Scales 0.5 mm.

apical antennomeres. Antennomeres 3–11 gradually slenderer, almost parallel-sided. Elytra slender, 3.5 times longer than width at humeri, parallel-sided. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus very long, slightly turned upwards, parameres short, reaching to one fifth of phallic length, phallobase short (fig. 4H-I).

Measurements. BL 5.52 mm, PW 1.02 mm, PL 0.83 mm, WH 1.32 mm, Edist 0.64 mm, Ediam 0.21 mm.

Distribution. Malaysia, Pahang.

Scarelus ardens Kleine 1926

Scarelus ardens Kleine 1926 b: 360.

Material examined. Holotype. Male, [Malaysia]. Paratype. Malaysia, W. Sarawak. Quop, G. E. Bryant, iv 1914. (BMNH). *Other material examined.* Malaysia, Sarawak, Kuching dist., Mt. Penrisen, 1000 m, 24.-26.III.1994, leg. J. Horak (LMBC).

Differential diagnosis. *S. ardens* belongs to a group of the Bornean species with bright orange to reddish brown colouration of the thorax, elytra and head, but it is the only such coloured species occurring in Sarawak. In addition, the phallus of *S. ardens* is long, robust, and apparently curved (fig. 4E).

Redescription. Male. Body small-sized, slender, thorax and elytra brightly reddish brown, appendages similarly coloured, eyes black. Head small, eyes hemispherically prominent, their distance 2.48 times eye diameter. Antennae slender, compressed, surpassing elytral apex by 4.5 antennomeres. Antennomeres 3–11 gradually slenderer. Elytra 2.9 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae, covered with bright reddish pubescence. Legs moderately long, slender. Male genitalia trilobate, phallus strong, long, 4.2 times longer than parameres, slightly curved, phallobase short (fig. 4E).

Measurements. BL 4.50 mm, PW 1.06 mm, PL 0.84 mm, WH 1.22 mm, Edist 0.57 mm, Ediam 0.23 mm.

Distribution. Malaysia, Borneo, Sarawak.

Scarelus baranciki n. sp.

Type material. Holotype. Male, Malaysia, Sabah, Mt. Emas, 5°50'N 116°19'E, 1700 m, 22.III.-8.IV.2000, leg. Bolm (LMBC), DNA Isolation Voucher Number UPOL 000582.

Differential diagnosis. *S. baranciki* n. sp. belongs to an assemblage of the Bornean species with the orange brown elytra, pronotum and head. It differs from the syntopically occurring *S. rollei* in the obtuse transversae costae in elytra and in the shape of male genitalia (fig. 4J).

Description. Male. Body small-sized; head, thorax, elytra and appendages orange brown, femora and tibiae of 2nd and 3rd pairs of legs and abdomen dark brown. Head small, hypognathous, eyes hemispherically prominent, their distance 2.46 times maximum eye diameter. Antennae slender, flattened, 1.3 times longer than body. Antennomeres 3–11 gradually slenderer, approximately rounded in cross-section, only slightly widened apically, apical antennomere elliptical. Pronotum 1.5 times wider at base than long at midline, longitudinal keel complete, with short narrow groove in basal third. Elytra slender, 3.3 times longer than width at humeri, parallel-sided, with two full length longitudinal costae, costa 1 very short, reaching one tenth of elytral length, whole elytra covered with short, dense,

orange pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus stout, 2.9 longer than parameres, rounded at apex, phallobase short, asymmetrical (fig. 4J).

Measurements. BL 5.20 mm, PW 1.05 mm, PL 0.69 mm, WH 1.40 mm, Edist 0.59 mm, Ediam 0.24 mm.

Distribution. Malaysia, Sabah.

Name derivation. The specific epithet is a patronym in honour of F. Barancik (Chorelice, Czech Republic).

Remark. The DNA was isolated from the holotype and sequences of several mtDNA and rRNA genes are accessible in the GenBank under the voucher number UPOL 000582 (Bocak *et al.* 2008).

Scarelus bicostatus Pic 1912

Scarelus bicostatus Pic 1912: 5.

Material examined. Male. Malaysia, Borneo, W. Sabah, Crocker Range, W of Apin, 5°29'N 116°12'E, II.2000, leg. M. Snizek (LMBC).

Differential diagnosis. *S. bicostatus* is the only species occurring in Sabah, which resembles in colour pattern an assemblage of the similarly coloured species from the Malay Peninsula. The male genitalia of *S. bicostatus* are characteristic in the slender and straight phallus (fig. 5D-E).

Redescription. Male. Body small-sized, slender, dark brown, humeral quarter of elytra brown, scapus and pedicel testaceous, antennomeres 3–11 and legs brown. Head small, eyes hemispherically prominent, their frontal distance 3.0 times eye diameter. Antennae slender, compressed, surpassing elytral apex by more than four antennomeres. Antennomeres 3–11 gradually slenderer, slightly serrate. Elytra wide, 2.92 times longer than width at humeri, parallel-sided, with well developed longitudinal costa 2 and 4, densely pubescent. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus four times longer than parameres, phallobase short, slightly asymmetrical (fig. 5D-E).

Measurements. BL 4.83 mm, PW 1.11 mm, PL 0.83 mm, WH 1.32 mm, Edist 0.57 mm, Ediam 0.19 mm.

Distribution. Malaysia, Borneo, Sabah.

Scarelus brastagiensis Bocak 1995

Scarelus brastagiensis Bocak 1995: 5.

Type material. Holotype. Male, Indonesia, Sumatra, Brastagi, G. Sibayak, 3°13'N 98°30'E, 1450–1900 m., 19.-23.II.1991, leg. L. Bocak & M. Bocakova (LMBC). Paratypes, 2 males, Indonesia, Sumatra, Brastagi, G. Sibayak, 1450-1900 m., 19.-23.II.1991, leg. L. Bocak & M. Bocakova, (LMBC, SMNS). *Other material examined:* 3 males, Indonesia, Sumatra, Brastagi, Mt. Sibayak, 19.-23.II.1998, leg. L. Bocak, 1700–2000 m (LMBC); 2 males, Indonesia, Sumatra, Brastagi, Mt. Sibayak, 26.I.-1.II.2005, 1600-220 m, leg. Bolm (LMBC).

Differential diagnosis. *S. brastagiensis* body form is reminiscent of other Sumatran species with a darker apical part of elytra. Close examination of male genitalia is necessary for reliable identification. *S. brastagiensis* may be distinguished by the short phallus (fig. 3C-D).

Redescription. Male. Body small-sized, humeral part of elytra, head and thorax brown, pronotum, abdomen, and apical third of elytra dark brown to black. Head small, eyes hemispherically prominent, their distance twice maximum eye diameter. Antennae slender, 1.2 times longer than body. Antennomeres 3–11 gradually slender. Elytra 3.5 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae covered with reddish pubescence. Legs moderately long, densely pubescent. Phallus short, 1.96 times longer than paramerae (fig. 3C-D).

Measurements. BL 6.63 mm, PW 0.83 mm, PL 0.84 mm, WH 1.64 mm, Edist 0.42 mm, Ediam 0.21 mm.

Distribution. Indonesia, Sumatra. *S. brastagiensis* is known only from the vicinity of Brastagi in the Northern Sumatra province.

Scarelus crudus Kleine 1926

Scarelus crudus Kleine 1926 a: 77.

Material examined. 4 males, Philippines, Mindanao, 30 km W of Maramag, 1600 m, 28.-30.XII.1991, leg. Bolm; male, 1 male, Philippines, Leyte, above Visayas State College of Agriculture, N Baybay, 27.II.1991, leg. Schawaller; 7 males, Philippines, Mindanao, 30 km W of Maramag, 28.-30.XII.1990, 1600 m, leg. Bolm; male, Philippines, Mindanao, Bagongsilang, 1500 m, N7 55'52"E, 124 54'E, 17.-20.I.2007, leg. Bolm (all LMBC).

Differential diagnosis. *Scarelus crudus* and *S. salvani* n. sp. are the only two species known from the Philippines. They differ in the colouration: *S. crudus* has the light yellow pronotum and elytra and *S. salvani* n. sp. is much darker, brown coloured. The similarities in the shape of male genitalia suggest that they may be the sister species.

Redescription. Male. Body small-sized, slender, testaceous,

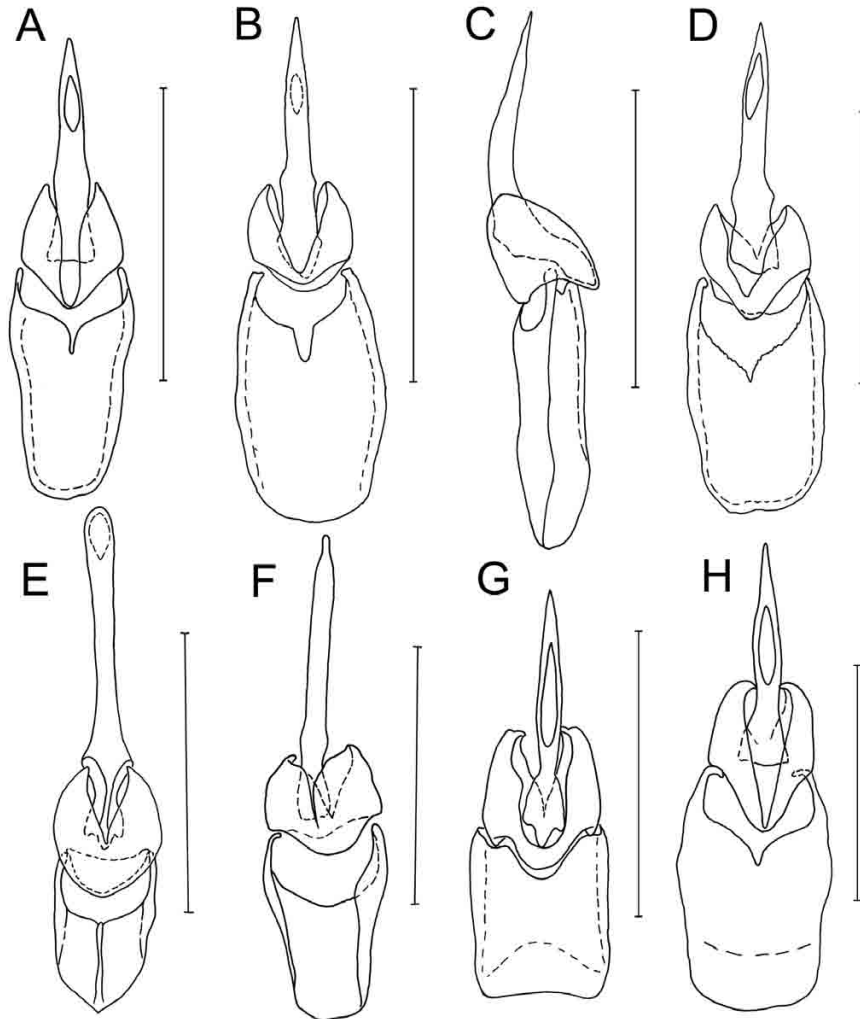


Figure 6
Male genitalia. A, *S. sarangensis*; B-C, *S. cibodasensis* n. sp.; D, *S. javanus*; E, *S. inapicali*; F, *S. corporaali*; G, *S. longicornis*; H, *S. flavicollis* n. sp.. Scales 0.5 mm.

eyes black, scapus and pedicel testaceous, rest of antennae black, legs including coxae dark brown. Head small, eyes small, hemispherically prominent, their distance 2.58 times maximum eye diameter. Antennae slender, compressed, reaching over elytrae apex by more than five antennomeres. Antennomeres 3–11 gradually slender, apical antennomere elliptical. Elytra slender, 4.2 times longer than width at humeri, parallel-sided, with fully developed three longitudinal costae, covered with brown pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus long, apex elliptical, parameres short reaching one fourth of phallic length, phallobase short, slightly asymmetrical (fig. 5C).

Measurements. BL 6.07 mm, PW 1.13 mm, PL 0.84 mm, WH 1.21 mm, Edist 0.67 mm, Ediam 0.26 mm.

Distribution. Philippines, Mindanao.

Scarelus inapicalis Pic 1925

Scarelus inapicalis Pic 1925: 161.

Type material. Holotype. Male, [Burma] 'Museum Pragense, Tenasserim, coll. Helfer' (NHMP). *Other material examined.* 2 males. [Thailand] Siam, Renong, Doherty (BMNH).

Differential diagnosis. *S. inapicalis* may be easily distinguished by the uniformly brown colouration of elytra and a robust body form from Malayan species.

Redescription. Male. Body small-sized, robust, brown. Head small, eyes hemispherically prominent, their distance 2.63 times maximum eye diameter. Antennae slender, flattened, 1.43 times longer than body. Antennomeres 3–11 gradually slender. Elytra slender, 2.9 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae, covered with brown pubescence. Legs moderately long, slender. Male genitalia with very long phallus, its apex elliptical, parameres reaching one third of phallic length, phallobase short (fig. 6E).

Measurements. BL 3.94 mm, PW 0.81 mm, PL 0.82 mm, WH 1.09 mm, Edist 0.54 mm, Ediam 0.19 mm.

Distribution. *S. inapicalis* is known from Myanmar in the type specimen collected already in the sixteenth century in Tenasserim by the Czech entomologist J. W. Helfer. Further two specimens were identified from an old material from southern Thailand (the Ranong Province). It is the only *Scarelus* species occurring north of the Isthmus Kra.

Scarelus kodadai Bocak 1998

Scarelus kodadai Bocak 1998: 177.

Type material. Holotype. Male, Philippines, Palawan centr., env. Lion's Cave near Cabayuga, 10°10'N 118°54'E, 1.XII.1995, primary forest on limestone, leg. Jan Kodada (LMBC). Paratype, male, Philippines, Palawan, Tanabank river, 20.XII.1991, leg. Bolm (LMBC). Paratype, male, Philippines, Palawan, Puerto Princessa env., 300–500 m, II.1999, local collector (LMBC).

Differential diagnosis. *S. kodadai* belongs to an assemblage of the species from Palawan and the Philippines with uniformly light brown colouration of the pronotum and elytra. It resembles *S. crudus*, but the colouration of elytra and the body is darker and phallus is stouter and less curved (fig. 5A).

Redescription. Male. Body small-sized, slender, brown, eyes black, scapus and pedicel bright brown, the rest of antennae and

legs brown. Head small, eyes hemispherically prominent, their distance 3.42 times maximum eye diameter. Antennae slender, 2.1 times longer than body. Elytra slender, 2.85 times longer than width at humeri, parallel-sided, with three longitudinal costae, covered with brown pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus very long, elliptically pointed, parameres short, about one fourth of phallic length, phallobase short (fig. 5A).

Measurements. BL 4.74 mm, PW 1.13 mm, PL 0.82 mm, WH 1.33 mm, Edist 0.65 mm, Ediam 0.19 mm.

Distribution. Philippines, Palawan Isl.

Scarelus loksadoensis n. sp.

Type material. Holotype. Male, Indonesia, S Kalimantan Province, 10 km E of Loksado, 4°27'N 101°34'E, 600–1100 m, 2°43'S 115° 32'E, 18.–23.VI.2001, leg. Bolm (LMBC).

Differential diagnosis. *S. loksadoensis* n. sp. is reminiscent of other similarly coloured species, *S. baranciki* n. sp., *S. rollei* and *S. loksadoensis* n. sp. These species differ only slightly in the shape of male genitalia (fig. 5J).

Description. Male. Body very small-sized, head, thorax and elytra bright orange red, abdomen brown, scutellum and pronotum reddish brown and elytra bright orange red. Whole antennae, mouthparts, and legs red. Head small, eyes hemispherically prominent, their distance 3 times maximum eye diameter. Antennae slender, flattened, twice longer than body. Antennomeres 3–11 gradually slender, apical antennomere elliptical. Elytra slender, 3.7 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae, covered with reddish pubescence. Legs moderately long, slender, flattened, scarcely pubescent. Male genitalia with long phallus, its apex rounded, phallobase asymmetrical and parameres small, reaching one third of phallic length (fig. 5J).

Measurements. BL 4.60 mm, PW 1.06 mm, PL 0.74 mm, WH 1.20 mm, Edist 0.49 mm, Ediam 0.17 mm.

Distribution. Indonesia, Southern Kalimantan.

Name derivation. The specific epithet refers to the type locality of this species.

Scarelus pahangensis n. sp.

Type material. Holotype. Male, Malaysia, Pahang, 20 km E of Ringlet, Kg. Kuala Boh, 4°27'N 101°34'E, 800 m, 4.I.2005, leg. Bolm (LMBC). *Other material examined.* Male, Malaysia, Pahang distr., Cam. Highlands, Campung Kuala Boh vill. env., 850–1050 m, 4°27'N, 101°34'E, 26.III.–3.IV.2001, leg. M. Strba (LMBC); male, Malaysia, Benom Mts., 700 m, 15 km E Kampong Dong, 3°53'N 102°01'E, 1.IV.1998, leg. Dembicky & Pacholatko (LMBC).

Differential diagnosis. *S. pahangensis* n. sp. belongs to an assemblage of the Malayan species with the brown pronotum and humeri and the dark coloured apex of elytra. This species can be distinguished from the closely related *S. pseudoumbrosus* n. sp. by the stouter phallus (fig. 4D).

Description. Male. Body small-sized, head, and thorax light brown, abdomen black, scutellum and humeral part of elytra testaceous, apical third dark brown to black. Head small, eyes hemispherically prominent, their distance 2.48 times maximum eye diameter. Antennae 1.5 times longer than body.

Antennomeres 3–11 gradually slenderer. Elytra 3.6 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae covered with testaceous pubescence. Legs moderately long, flattened, densely pubescent. Male genitalia trilobate, phallus stout, 5.6 times longer than width at widest part at its base, parameres short, reaching one third of phallic length, phallobase short (fig. 4D).

Measurements. BL 5.13 mm, PW 0.82 mm, PL 0.71 mm, WH 1.13 mm, Edist 0.57 mm, Ediam 0.23 mm.

Distribution. Malaysia, Pahang.

Name derivation. The specific epithet refers to the Malay State Pahang, where the type series was collected.

Scarelus palawanensis Bocak 1999

Scarelus palawanensis Bocak 1999: 175.

Type material. Holotype. Male, Philippines, Palawan Isl., Cleopatra Needle N. P., Tanabank River Valley, 300 m, 20.-22.XII.1990, leg. Bolm (LMBC).

Differential diagnosis. *S. palawensis* is one of two species known from Palawan and it differs from *S. kodadai* in the dark apical part of elytra. The male genitalia are similar in general shape to those of *S. crudus* (fig. 5B).

Redescription. Male. Body very small, slender, brown, eyes black, antennae and legs including coxae brown. Head small, eyes small, hemispherically prominent, their distance 3.29 times maximum eye diameter. Antennae slender, compressed, flattened, surpassing apex of elytra by more than three antennomeres. Antennomeres 3–11 gradually slenderer, apical antennomere elliptical. Elytra slender, 2.7 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae, brown pubescent. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus long, parameres short, reaching one fourth of phallic length, phallobase short, slightly asymmetrical (fig. 5B).

Measurements. BL 3.44 mm, PW 0.64 mm, PL 0.63 mm, WH 0.94 mm, Edist 0.46 mm, Ediam 0.14 mm.

Distribution. Philippines, Palawan Isl.

Scarelus pseudombrosus n. sp.

Type material. Holotype. Male, Malaysia, Perak, Road Ipoh - Kg. Raja, km 35 E of Ipoh, 4°35'N 101°19'E, 800 m, 8.II.2005, leg. Bolm (LMBC). Paratype. Male, Malaysia, W Perak, 25 km NE Ipoh, 1200 m, Korbu mts., 17.I-2.II.1999, leg. P. Pacholatko (LMBC).

Differential diagnosis. *S. pseudombrosus* n. sp. is a species with a major part of elytra black and only a small humeral part of elytra brown. *S. pahangensis* n. sp. resembles *S. pseudombrosus* n. sp. and is distinguishable by the stouter phallus (fig. 4F-G). The ranges of these two species are allopatric.

Redescription. Male. Body small-sized, slender, brown, only eyes black, antennae and legs including coxae darker than body. Head small, sparsely pubescent, eyes small, hemispherically prominent, their interocular distance 3.04 times maximum eye diameter. Antennae surpassing apex of elytra by 2 antennomeres. Antennomeres 3–11 gradually slenderer. Elytra slender, 2.86 times longer than width at humeri, parallel-sided, with three longitudinal costae, these slightly lighter than bottoms of reticulate cells, covered with brown pubescence.

Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus slender, 7.0 times longer than width at widest part, parameres short, reaching one fourth of phallic length, phallobase as long as parameres (fig. 4F-G).

Measurements. BL 5.21 mm, PW 1.14 mm, PL 0.83 mm, WH 1.44 mm, Edist 0.64 mm, Ediam 0.21 mm.

Distribution. Malaysia, Perak, Pahang.

Name derivation. The species resembles *S. umbrosus* in the general body form and colouration.

Scarelus rollei Pic 1912

Scarelus rollei Pic 1912: 4.

=*S. testaceus* Pic 1912: 4; Kazantsev 1992: 103.

Material examined. 4 males, Malaysia, Sabah, M. Kinabalu N. P., II.2000, leg. M. Snizek; 2 males, ditto, 28.V.1999, leg. M. Snizek; 1 Malaysia, Sabah, Mt. Emas, 22.III.-8.IV.2003 (LMBC).

Differential diagnosis. *S. rollei* belongs to a group of orange brown species from Borneo. It differs from the similarly coloured species in the well developed, stout transverse costae in elytra. The phallus is slightly slenderer than those of *S. similis* n. sp. (fig. 5F-G).

Description. Male. Body small-sized, reddish, only thorax brown and abdomen black. Head small, eyes hemispherically prominent, their distance 2.5 times maximum eye diameter. Antennae slender, 2.2 times longer than body. Antennomeres 3–11 gradually slenderer. Elytra 2.47 times longer than width at humeri, parallel-sided, with three longitudinal costae covered with red pubescence. Legs moderately long, slender, densely pubescent. Male genitalia trilobate, phallus three times longer than phallobase, apex elliptical, slightly curved, phallobase small, assymetrical, parameres short reaching to one third of phallic length (fig. 5F-G).

Measurements. BL 5.71 mm, PW 1.09 mm, PL 1.11 mm, WH 1.94 mm, Edist 0.71 mm, Ediam 0.29 mm.

Distribution. Malaysia, Borneo (Sabah).

Scarelus salvani n. sp.

Type material. Holotype. Male, Philippines, Mindanao, Mt. Kitanglad, 1800 m, 8°05'N 124° 56'E, 14.-15.I.2007, leg. Bolm (LMBC).

Differential diagnosis. *Scarelus salvani* n. sp. and *S. crudus* are the only two species recorded from the Philippines. They differ in the colouration of the pronotum and elytra, which is bright yellow in *S. crudus* and greyish brown in *S. salvani* n. sp. Additionally, the stouter phallus of *S. salvani* n. sp. supports its separation from the widespread *S. crudus* (fig. 5K-L).

Description. Male. Body small-sized, body dark brown to black, pronotum, scutellum and elytra greyish brown. Head small, eyes hemispherically prominent, their distance 2.5 times maximum eye diameter. Antennae slender, flattened, 1.79 times longer than the body. Antennomeres 3–11 gradually slenderer, apical antennomere elliptical. Elytra slender, 3.75 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae covered with brown pubescence. Legs moderately long, sparsely pubescent. Male genitalia trilobate, phallus long, stout, phallobase and parameres similar in length. Phallobase assymetrical. Parameres short, reaching one third of

phallic length. Phallobase rounded and stout (fig. 5K-L).

Measurements. BL 5.52 mm, PW 0.92 mm, PL 0.73 mm, WH 1.23 mm, Edist 0.63 mm, Ediam 0.19 mm.

Distribution. Phillipines, Mindanao.

Name derivation. The specific epithet is a patronym in honour of Eugene Salvan, Sr. (Bagongsilang, Bukidnon) who provided the collectors with an invaluable help during their field trips to the Central Mindanao.

Scarelus sanguineus Bocak 1995

Scarelus sanguineus Bocak 1995: 6.

Type material. Holotype. Male, Indonesia, Sumatra, Mt. Singgalang, S of Bukittinggi, 0°26'N 100°21'E, 1300 m, 14.-16.II.1991, leg. L. Bocak & M. Bocakova (LMBC). *Other material examined.* 2 males, Indonesia, Sumatra, Gn. Merapi, 5 km E of Kotobaru, 1600 m, 18.-25.V.2001, leg. Bolm; 2 males, Indonesia, Sumatra Barat, 10 km S of Bukittinggi, 1600 m, Gn. Merapi, 10.-11.I.2005, leg. Bolm (LMBC).

Differential diagnosis. *S. sanguineus* closely resembles *S. ruficollis* n. sp. and *S. rufus* n. sp. in general appearance and the slightly curved free part of the phallus. The phallus of *S. sanguineus* is slenderer than those of *S. ruficollis* n. sp. (fig. 3H).

Redescription. Male. Body small-sized, head, body and appendages black, elytra red. Head small, eyes small, hemispherically prominent, their interocular distance 2.5 times maximum eye diameter. Antennae slender, flattened, 1.2 times longer than body. Antennomeres 3–11 gradually slenderer, apical antennomere elliptical. Elytra slender, 3.85 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae covered with reddish pubescence. Legs moderately long, slender, flattened, sparsely pubescent. Male genitalia trilobate, phallus long, slightly curved, phallobase and parameres similar in length, as long as wide. Parameres short, reaching to one third of phallic length (fig. 3G-H).

Measurements. BL 6.40 mm, PW 1.16 mm, PL 0.64 mm, WH 1.42 mm, Edist 0.42 mm, Ediam 0.17 mm.

Distribution. Indonesia, Sumatra, Mts. Merapi and Singgalang.

Scarelus ruficollis n. sp.

Type material. Holotype. Male, Indonesia, Sumatra, Jambi, Kersik Tua, Mt. Kerinci, 1°41'S 101°22'E, 1600–2200 m, 19.-22.I.2005, leg. Bolm (LMBC). Paratypes, 6 males, same locality data (LMBC).

Differential diagnosis. *S. ruficollis* n. sp., *S. rufus* n. sp. and *S. sanguineus* are the only Sumatran species with completely reddish brown elytra, and these species are very similar in general appearance. The ratio between length of the free part of the phallus and its width and position of widened part of the phallus are the only separating characters. The phallus of *S. ruficollis* n. sp. is relatively more robust (fig. 3A-B).

Redescription. Male. Body small-sized, black, only elytra red. Head small, eyes hemispherically prominent, their distance 2.75 times eye diameter. Antennae slender, flattened, 1.2 times longer than body. Antennomeres 3–11 gradually slenderer, apical antennomere elliptical. Elytra slender, 3.81 times longer than width at humeri, parallel-sided. Longitudinal costae well

developed, covered with reddish pubescence. Legs moderately long, slender, sparsely pubescent. Male genitalia trilobate, phallus long, obtuse at apex, slightly curved, phallobase and parameres similar in length, as long as wide. Parameres short reaching to one third of phallic length (fig. 3A-B).

Measurements. BL 6.43 mm, PW 1.22 mm, PL 0.61 mm, WH 1.44 mm, Edist 0.44 mm, Ediam 0.16 mm.

Distribution. Indonesia, Sumatra, Mt. Kerinci Massif.

Scarelus rufus n. sp.

Type material. Holotype. Male, Indonesia, Sumatra, Jambi, Kersik Tua, Mt. Kerinci, 1°41'S 101°22'E, 1600–2200 m, 19.-22.I.2005, leg. Bolm (LMBC).

Differential diagnosis. *S. rufus* n. sp. is very similar in general appearance to syntopically occurring *S. ruficollis* n. sp. and these species differ only in the shape of male genitalia. The phallus of *S. rufus* n. sp. is shorter more robust and less curved in the lateral view (fig. 3I-J).

Redescription. Male. Body small-sized, head, thorax, abdomen and appendages black, elytra red. Head small, eyes hemispherically prominent, their distance 3.06 times eye diameter. Antennae slender, flattened, 1.2 times body length. Antennomeres 3–11 gradually slenderer with apical antennomere elliptical. Elytra slender, 3.38 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae. Legs moderately long, covered with scarce pubescence. Male genitalia trilobate, phallus long, rounded apically, phallobase and parameres similar in length. Parameres short, reaching one third of phallic length (fig. 3I-J).

Measurements. BL 6.13 mm, PW 1.04 mm, PL 0.74 mm, WH 1.48 mm, Edist 0.57 mm, Ediam 0.19 mm.

Distribution. Indonesia, Sumatra, Mt. Kerinci Massif.

Scarelus schawalleri Bocak 1995

Scarelus schawalleri Bocak 1995: 8.

Type material. Holotype. Male, Indonesia, Sumatra, Kabanjahe, Gn. Sinabung, 3°11'S 92°22'E, 7.-10.X.1990, leg. A. Riedel (SMNS).

Differential diagnosis. *S. schawalleri* can be easily separated from other species by the shortest antennae. Compared with other Sumatran species, its antennae are almost rounded in cross section. The shape of the male genitalia supports the distant position of this species (fig. 3F).

Redescription. Small bodied, slender, body dark brown to black, pronotum brown, its margins and carinae darker, apical third of elytra black, basal part testaceous. Head small, slightly broader than frontal margin of pronotum, antennae reaching over elytral apex by less than one antennomere. Eyes hemispherically prominent, their distance 2.57 times eye diameter. Pronotum 1.48 times broader at base than long at midline. Elytra with two longitudinal costae on each elytron, costa 1 inconspicuous, partly missing, second costa prominent basally, very weak in apical third of length. Costa 4 stout, transverse costae weak, incomplete and irregular. Legs slender, flattened. Phallus slender in middle, slightly widened apically (fig. 3F).

Measurements. BL 4.95 mm, PW 0.86 mm, PL 0.58 mm, WH 1.08 mm. Edist 0.54 mm, Ediam 0.21 mm.

Distribution. Indonesia, Northern Sumatra.

***Scarelus similis* n. sp.**

Type material. Holotype. Male, Indonesia, Central Kalimantan Prov., 60 km SE Muara Teweh, 150 m, 1°20'S 115°20'E, 24.-28.VI.2001, leg. Bolm (LMBC).

Differential diagnosis. *S. similis* n. sp. is reminiscent of other similarly coloured Bornean species, *S. baranciki* sp. n., *S. rollei* and *S. loksadoensis* n. sp. These species differ only slightly in the shape of male genitalia (fig. 5H-I, 4J, 5F-G, 5J).

Description. Male. Body small-sized, body and appendages bright red, abdomen brown. Head small, eyes hemispherically prominent, their distance 1.79 times maximum eye diameter. Antennae slender, flattened, 2.1 times longer than body. Antennomeres 3–11 gradually slenderer, apical antennomere elliptical. Elytra slender, 3.7 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae covered with reddish pubescence. Legs moderately long, slender, flattened, sparsely pubescent. Male genitalia trilobate, phallus long, obtuse at apex, phallobase asymmetrical, parameres small, reaching to one third of phallic length (fig. 5H-I).

Measurements. BL 4.72 mm, PW 0.82 mm, PL 0.73 mm, WH 1.06 mm, Edist 0.25 mm, Ediam 0.14 mm.

Distribution. Indonesia, Borneo, Central Kalimantan Province.

Name derivation. The specific epithet refers to a high degree of similarity with *S. loksadoensis* n. sp.

***Scarelus tomani* Bocak 1998**

Scarelus tomani Bocak 1998: 24.

Type material. Holotype. Male, Indonesia, Sumatra, Aceh, 15 km SSE Takengon, 4°35'S 9°53'E, 1600 m, 26.II.-13.III. 1998, leg. L. Bocak & V. Toman (LMBC). Paratype, 1 male, same locality data (LMBC).

Differential diagnosis. *S. tomani* is very similar in general body form and colouration to other North Sumatran species. It differs in a very long, slightly curved phallus (fig. 3E).

Description. Male. Body small, black, only cranium, pronotum, scutellum and basal two third of elytra yellowish brown. Head small, antennal tubercles inconspicuous. Eyes hemispherically prominent, interocular distance 3.0 times eye diameter. Antennae surpassing elytral length by 2.5 segments, slender, only slightly compressed, antennomeres 3–11 subequal in length. Pronotum with flat disc, median longitudinal keel well developed, elytra parallel-sided, with three longitudinal costae, transverse costae regular, reticulate cells transverse. Legs slender, slightly compressed. Male genitalia with very slender, moderately curved, long phallus (fig. 3E).

Measurements. BL 4.90 mm, WH 2.65 mm, PL 1.30 mm, PW 2.15 mm, Edist 0.63 mm, Ediam 0.21 mm.

Distribution. Indonesia, Sumatra, Aceh Province.

***Scarelus umbrosus* Kleine 1932**

Scarelus umbrosus Kleine 1932a: 535

= *Scarelus riedeli* Bocak 1995: 535; Bocakova & Bocak 1999: 109.

Type material. Holotype. Male, Malaysia, Malay Penin. F. M. S., Fraser Hills, 4200 ft., 26.VI.1931; H. M. L. Pendlebury, B. M. 1933-87 (BMNH). *Other material examined.* 1 male,

Malaysia, Benom Mts., 15 km E Kampong Dong, 700 m, 3°53'N 102°01'E 1.IV.1998, leg. Dembicky & Pacholatko (LMBC); 1 male, Malaysia, Cameron Highlands, Power station km 29, 21.IV.1990, leg. A. Riedel (the paratype of *S. riedeli*; LMBC).

Differential diagnosis. *S. umbrosus* belongs to a group of Malayan species with lighter humeri and infuscated apical part of the phallus. This species may be easily distinguished by the strongly curved, short phallus (fig. 4B-C).

Description. Male. Body small-sized, body brown, humeral half of elytra testaceous, apical part dark brown to black. Head small, eyes hemispherically prominent, their distance 3.38 times eye diameter. Antennae slender, flattened, 1.5 times longer than body. Elytra 2.94 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae covered with brown pubescence. Legs moderately long, densely pubescent. Male genitalia trilobate, phallus short, obtuse at apex, considerably curved, parameres short reaching one third of phallic length, phallobase and parameres similar in length.

Measurements. BL 6.05 mm, PW 1.41 mm, PL 0.82 mm, WH 1.71 mm, Edist 0.71 mm, Ediam 0.21 mm.

Distribution. Malaysia, Malay Peninsula, Fraser Hills, Benom Mts., and the Cameron Highlands.

The *S. orbatus* group

Differential diagnosis. All species placed in the here proposed *S. orbatus* species group have similar shape of male genitalia with a quite short, slender and apically pointed phallus. The form of the phallus is unique and defines the species groups as a monophylum. The Javanese species, *S. cibodasensis* n. sp. and *S. saranganensis* n. sp., share a similarly widened phallic base (fig. 6B-C, 6A). This structure may be homologous with the robust base of phallus present in all species from the *S. anthracinus* species group (e.g. fig. 3A-F, 4B-J). The Sumatran and Malayan species have parallel-sided basal part of the phallus and may form a monophylum within this species group.

***Scarelus cibodasensis* n. sp.**

= *Scarelus longicornis*: Kazantsev 1992: 101 nec Waterhouse 1879.

= *Scarelus luchti* Kazantsev & Yang 1999: 245 - nomen nudum.

Type material. Holotype. Male, Indonesia, Java, Puncak Pass, 6°42'S 107°00'E, 1250–1600 m, 10 km of Cipanas, 8.-20.X.2002, leg. Bolm (LMBC). Paratype. 1 male, Indonesia, W. Java, Mt. Gede, Cibodas, 1500 m, II.1996, leg. S. Jakl (LMBC).

Differential diagnosis. *S. cibodasensis* n. sp. resembles *S. saranganensis* n. sp. in the uniformly testaceous elytra and these species differ in the shape of their male genitalia. The paramerae of *S. saranganensis* n. sp. are slenderer and the phallus shorter than in *S. cibodasensis* n. sp. (fig. 6B-C).

Description. Male. Body small-sized, brown, elytra testaceous. Head small, eyes hemispherically prominent, their interocular distance 2.55 times eye diameter. Antennae compressed, reaching over apex of elytra by two segments. Antennomeres 3–11 gradually slenderer. Elytra 3.43 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae. Legs moderately long, densely pubescent. Male genitalia trilobate, phallus short, apically pointed, slightly curved in

lateral view, parameres short, reaching to one fourth of phallic length, phallobase as long as wide, oval (fig. 6B-C).

Measurements. BL 5.80 mm, PW 1.21 mm, PL 0.84 mm, WH 1.43 mm, Edist 0.64 mm, Ediam 0.21 mm.

Distribution. *S. cibodasensis* n. sp. is known only from several localities in Indonesia, Java (fig. 1).

Name derivation. The species name refers to the type locality, the town Cibodas in Western Java.

Remark. Kazantsev (1992) figured the male genitalia of a specimen of *Scarelus* from Kleine's collection in Warsaw identified as *S. longicornis* Waterhouse and gave locality data for the single specimen he studied. Unfortunately, he did not mention any further information, which may define the species. Later, when he found out that this specimen is not conspecific with the holotype of *S. longicornis* deposited in the collection of the Natural History Museum in London he proposed a new species, *Scarelus luchti* Kazantsev & Yang 1999 in a study co-authored by Ping-Shin Yang (Kazantsev & Yang 1999). No description was given by Kazantsev & Yang (1999) and besides "Type material" and "Etymology", they only mentioned that "*S. luchti* is separable from other *Scarelus* species by details specified in Kazantsev (1992) for *S. longicornis*". As no description was ever published for *S. luchti* Kazantsev & Yang 1999 the name is invalid (ICZN 1999, Art. 13.1).

Scarelus corporaali Kazantsev 1992

Scarelus corporaali Kazantsev 1992: 535.

Material examined. Male, Indonesia, Sumatra, Southern Aceh, Babahrot, 15.-20.VIII.1983, leg. Klapperich (SMNS); 2 males, Indonesia, Sumatra, Aceh Province, 20 km S of Blangkejeren, Kedah, 1700 m, 4.-8.III.1998, leg. L. Bocak; 2 males, Indonesia, Sumatra, Aceh Province, 20 km N Ronga Ronga, 800 m, 26.II.1998, leg. L. Bocak (LMBC).

Differential diagnosis. *S. corporaali* is a Sumatran species with almost whole elytra reddish brown and similarly coloured body. It resembles *S. longicornis* in general appearance and these species can easily be distinguished by the length of phallus (fig. 6F and 6G).

Redescription. Male. Body small-sized, head, thorax, and humeral part of elytra testaceous, apical part of elytra and abdomen black. Scapus and pedicel light brown, antennomeres 3–11 black, sometimes apical antennomere light brown. Head small, eyes hemispherically prominent, their distance 2.91 times eye diameter. Antennae slender, flattened, 1.2 times longer than body. Antennomeres 3–11 gradually slender, slightly compressed. Elytra slender, 3.75 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae, covered with testaceous pubescence. Legs moderately long, densely pubescent. Male genitalia trilobate, phallus long, parameres short reaching one fourth of phallic length, phallobase more than twice longer than parameres (fig. 6F).

Measurements. BL 5.53 mm, PW 1.12 mm, PL 0.73 mm, WH 1.21 mm, Edist 0.64 mm, Ediam 0.22 mm.

Distribution. Indonesia, Northern Sumatra and Aceh provinces.

Scarelus flavicollis n. sp.

Type material. Holotype. Male, Indonesia, Sumatra, Jambi, Kersik Tua, Mt. Kerinci, 1°41'S 101°22'E, 19.-22.I.2005,

1600–2200 m, leg. Bolm (LMBC). Paratypes. 3 males, the same locality data as the holotype (LMBC).

Differential diagnosis. *S. flavicollis* n. sp. is the only Sumatran species belonging to the *S. orbatus* group with uniformly reddish brown elytra, scutellum and pronotum. The male genitalia are similar to those of *S. longicornis* and support close relationships of these species (fig. 6H).

Description. Male. Body small-sized, body and appendages black, scutellum and elytra reddish brown. Head small, eyes hemispherically prominent, their frontal distance 2.21 times eye diameter. Antennae slender, compressed, almost 1.5 times longer than body. Antennomeres 3–11 gradually slenderer, parallel-sided. Elytra slender, 3.7 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae. Legs moderately long, densely pubescent. Male genitalia trilobate, phallus short, apically pointed, parameres short, reaching half of phallic length, phallobase long, slender (fig. 6H).

Measurements. BL 6.53 mm, PW 1.11 mm, PL 1.12 mm, WH 1.83 mm, Edist 0.64 mm, Ediam 0.29 mm.

Distribution. Indonesia, Sumatra, Jambi province, known only from the massive of Mt. Kerinci.

Name derivation. The specific name refers to the colouration of elytra.

Scarelus longicornis Waterhouse 1878

Scarelus longicornis Waterhouse 1878: 116.

= *sumatrensis* Pic 1912: 4; Kazantsev 1992: 20.

= *gracilicornis* Pic 1942: 7; Kazantsev 1992: 20.

Material examined. Holotype. Male. [Java], Bowring 63.47. *Other material examined.* 2 males, Indonesia, Western Sumatra Province, Batang Palupuh Nature Reserve, 25 km of Bukittinggi, 15.II.1991, leg. Bocak & M. Bocakova (LMBC); 1 male, Indonesia, Sumatra (Z.W.K.), Boekit Gabah, IV.1919, leg. Lucht (ZIW); 2 males, Indonesia, Sumatra, Barat, Lake Maninjau, E coast, 800 m, 12.-23.I.2005, leg. Bolm (LMBC); 1 male, Indonesia, Sumatra, Ophir mts., Mt. Talamau, 17 km E Simpangempat, 21.-25.V.2001, 750 m, leg. Bolm (LMBC); 1 male, Indonesia, Sumatra, Barat, Pasaman, Mt. Talamau, 1000 m, 14.-15.I.2005, leg. Bolm (LMBC).

Differential diagnosis. *S. longicornis* resembles *S. corporaali* in general body form and colouration, but it can be easily distinguished by the length of the phallus (fig. 6G and 6F).

Redescription. Male. Body small-sized, testaceous, abdomen and apical third of elytra dark brown, antennae and legs darker than other body parts. Head small, eyes hemispherically prominent, their distance 2.8 times eye diameter. Antennae slender, compressed, surpassing apex of elytra by almost three antennomeres. Antennomeres 3–11 gradually slenderer, slightly compressed, almost parallel-sided. Elytra slender, 3.33 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae, covered with brown pubescence. Legs moderately long, densely pubescent. Male genitalia trilobate, phallus short, apically pointed, parameres reaching half of phallic length, phallobase as long as parameres (fig. 6G).

Measurements. BL 6.07 mm, PW 1.32 mm, PL 0.82 mm, WH 1.51 mm, Edist 0.57 mm, Ediam 0.22 mm.

Distribution. Indonesia, Sumatra.

Remark. Specimens collected in lower elevations in the western slopes of the Barisan range (Lake Maninjau, Mt. Talamau) have very small body (cca 4 mm), but they resemble in all characters specimens from other regions.

Scarelus orbatus Waterhouse 1878

Scarelus orbatus Waterhouse 1878: 535.

Material examined. Holotype. Male, [Singapore], Coll. Baker (ZIW); *Other material examined.* 4 males, Malaysia, Tioman Isl. 400 m, Kampong Telek-K. Juara, 9.III.1998, 2°48'N 104°11'E, leg. Dembicky & Pacholatko (LMBC); 13 males, Malaysia, Pahang, Tioman Isl., 7.-25.II.2000, Kampong Telek-Kampong Juara, 2°48'N 104°11'E, 5–295 m, leg. M. Strba (LMBC).

Differential diagnosis. *S. orbatus* resembles in general appearance other *Scarelus* species from Peninsular Malaysia, but it is the only species in the area belonging to the *S. orbatus* group. The closely related Sumatran species differ in the uniformly coloured elytra (*S. flavicollis* n. sp.), only the apical third of elytra dark (*S. longicornis*) or a very long phallus (*S. corporaali*).

Redescription. Male. Body small-sized, testaceous, only antennae and legs dark brown. Head small, eyes hemispherically prominent, their distance 2.91 times eye diameter. Antennae slender, compressed, surpassing elytra by three antennomeres. Antennomeres 3–11 gradually slenderer, slightly compressed, almost parallel-sided. Elytra 3.3 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae, covered with brown pubescence. Legs moderately long, compressed, densely pubescent. Male genitalia trilobate, phallus short, apically pointed, slightly curved, parameres long reaching to half of phallic length, phallobase twice longer than parameres (fig. 4A).

Measurements. BL 5.32 mm, PW 1.12 mm, PL 0.82 mm, WH 1.51 mm, Edist 0.64 mm, Ediam 0.22 mm.

Distribution. Singapore, Malaysia: Tioman Isl.

Scarelus saranganensis n. sp.

Type material. Holotype. Male, Indonesia, Java, Mt. Lawu, 8 km W of Sarangan, 77°39'S 111°12'E, 10.-11.V.2001, leg. Bolm. Paratype. Male, ditto (LMBC).

Differential diagnosis. *S. saranganensis* n. sp. resembles *S. cibodasensis* n. sp. in general appearance and the widened basal part of the phallus (fig. 6A, 6B-C). These species can be distinguished by the colouration of the pronotum with those of *S. saranganensis* n. sp. being lighter brown. Additionally, *S. saranganensis* n. sp. has a shorter phallus and narrower paramerae (fig. 6A). The related Sumatran species with uniformly reddish brown elytra, *S. flavicollis* n. sp., differ in the parallel-sided basal part of phallus.

Description. Male. Body small-sized, body and appendages black, scutellum and pronotum dark brown to black with narrow reddish margins; elytra reddish brown. Head small, hypognathous, eyes hemispherically prominent, their distance 2.53 times eye diameter. Antennae slender, compressed, 1.6 times longer than body. Elytra slender, 4.0 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae covered with reddish pubescence. Legs moderately long, slender, flattened, densely pubescent. Male

genitalia trilobate, phallus short, apically pointed, parameres reaching to one third of phallic length, phallobase long, slender (fig. 6A).

Measurements. BL 5.11 mm, PW 0.62 mm, PL 0.61 mm, WH 1.08 mm, Edist 0.29 mm, Ediam 0.14 mm.

Distribution. Indonesia, Central Java, Mt. Lawu.

Name derivation. The specific epithet refers to the town Sarangan, that lies vicinity of Mt. Lawu.

Key to the identification of genera the Ateliini and species of *Scarelus*

1. Elytra with long erected setae 2
 - Elytra without long erected setae **3 (*Scarelus* Waterhouse)**
2. Male genitalia with robust straight phallus ***Atelius* Waterhouse**
 - Male genitalia with slender, considerably curved phallus ***Paratelius* Kazantsev**
3. Phallus obtuse at apex, long, at least three times longer than paramerae (fig. 3A-J, 4B-J, 5A-L, 6E) 4
 - Phallus pointed at apex, short, less than three times longer than paramerae (fig. 4A, 6A-D, 6F-H) **24**
4. Body and elytra uniformly black, aedeagus as in fig. 4H-I. Peninsular Malaysia ***S. anthracinus* Bocak & Bocakova**
 - At least humeri of elytra light brown to red 5
5. Elytral humeri lighter than the rest of elytra 6
 - Elytra concolour, testaceous or red coloured **12**
6. Phallobase without longitudinal median keel (fig. 5D-E), scapus and pedicel light brown. Malaysia, Borneo, Sabah ***S. bicostatus* Pic**
 - Phallobase with longitudinal median keel, scapus and pedicel dark coloured (fig. 4B-C, 3E, 3H, 3C-D, 4D, 4F) 7
7. Phallus short, strongly curved (fig. 4B-C). Malaysia, Malay Peninsula ***S. umbrosus* Kleine**
 - Phallus only slightly curved, moderately long, slender (fig. 3E, 3H, 3C-D, 4D, 4F-G) 8
8. Phallus very long compared with the length of paramerae (fig. 3E), head testaceous, similarly coloured as humeri. Indonesia, Sumatra, Aceh Province ***S. tomani* Bocak**
 - Phallus shorter, more robust, head dark brown to black 9
9. Phallus slender in middle of its length (fig. 3H). Indonesia, Northern Sumatra ***S. schawalleri* Bocak**
 - Phallus approximately parallel-sided in middle part (fig. 3C-D, 4D, 4F-G) **10**
10. Free part of phallus forms about half of the length of male genitalia (including phallobase) (fig. 3C-D). Indonesia, Sumatra ***S. brastagiensis* n. sp.**
 - Free part of phallus longer than the rest of male genitalia (fig. 4D, 4F-G) **11**

11. Phallus robust (fig. 4D). Malaysia, Pahang ***S. pahangensis* n. sp.**
- Phallus slender (fig. 4F-G). Malaysia, Pahang ***S. pseudoumbrosus* n. sp.**
12. The elytra and pronotum similar in colouration, phallus without longitudinal median keel, (fig. 5A-L), Philippines, Borneo, Thailand, Burma **13**
- Elytra reddish brown, pronotum dark brown to black, antennae and legs dark brown to black, phallus with strong median longitudinal keel in phallobase (fig. 5A-B, G-J), Sumatra **24**
13. Pronotum and elytra testaceous, antennae and legs dark brown, Philippines, Thailand, Burma **14**
- Pronotum and elytra brightly orange, antennae and legs at least partly similar coloured, Borneo **18**
14. Phallobase with strong longitudinal keel (fig. 6E), Thailand, Burma ***S. inapicalis* Pic**
- Phallobase without strong longitudinal keel (fig. 5A-C), Philippines **15**
15. Body very small, cca 3.5 mm long, apical margin of elytra very slightly infusate, male genitalia as in fig. 5B. Philippines, Palawan ***S. palawanensis* Bocak**
- Body medium sized, 5–6 mm long, apex of elytra lightly coloured **16**
16. Pronotum and elytra dark reddish brown, phallus straight, only slightly widened at base (fig. 5B), Philippines, Palawan ***S. kodadai* Bocak**
- Pronotum and elytra either light yellow or greyish brown, phallus wider at base (fig. 5C, 5L) **17**
17. Pronotum and elytra light yellow, phallus considerably widened at base (fig. 5C). Philippines, Mindanao ***S. crudus* Kleine**
- Pronotum and elytra greyish brown, phallus moderately widened at base (fig. 5K-L) Philippines, Mindanao ***S. salvani* n. sp.**
18. Phallus apparently curved in lateral view (fig. 4E), Malaysia, Saraw ***S. ardens* Kleine**
- Phallus almost straight in lateral view (e.g. fig. 5F-G, 4J, 5H-I, 5J), Sabah, Kalimantan **19**
19. Middle and posterior pair of legs with dark coloured femora and tibiae **20**
- Middle and posterior pair of legs with light testaceous coloured femora and tibiae **21**
20. Phallus slender, gradually narrowing to apex (fig. 5F-G), transverse costae in elytra well developed, reticulate cells mostly transverse. Malaysia, Borneo, Sab ***S. rollei* Pic**
- Phallus robust, parallel-sided in most of its length (fig. 4J), transverse costa in elytra obtuse, reticulate cells often quadrate in shape. Malaysia ***S. baranciki* n. sp.**
21. Parameres wide, rounded (fig. 5H-I) Indonesia, Borneo, Central Kalimantan Province ***S. similis* n. sp.**
- Parameres slender (fig. 5J). Indonesia, Southern Kalimantan ***S. loksadoensis* n. sp.**
22. Phallus almost straight in lateral view (fig. 3I). Indonesia, Sumatra, Mt. Kerinci Massif ***S. rufus* n. sp.**
- Phallus considerably curved in lateral view (fig. 3B, 3H) **23**
23. Phallus slender, widened part of phallus located at basal third of phallic length (fig. 3G-H), Indonesia, Central Sumatra, Gn. Merapi ***S. sanguineus* Bocak**
- Phallus more robust, widened part of phallus located at basal fourth of the phallic length (fig. 3A-B), Indonesia, Southern Sumatra, Gn. Kerinci ***S. ruficollis* n. sp.**
24. Phallus slightly widened in basal third of its length (fig. 6A, 6B-C) **28**
- Phallus parallel-sided in basal half of its length (fig. 6F, 4A, 6G) **25**
25. Elytra uniformly reddish brown. Indonesia, Sumatra: Kerinci massif ***S. flavicollis* n. sp.**
- Elytra dark brown to black apically **26**
26. Phallus longer than phallobase (fig. 6F). Indonesia, Northern Sumatra and Aceh provinces ***S. corporaali* Kazantsev**
- Phallus as long as phallobase or slightly shorter **27**
27. Body dark brown to black, proximal part of elytra brightly coloured, thorax and head similarly coloured, aedeagus as in fig. 4A, Malaysia, Tioman Island, Singapore ***S. orbatus* Waterhouse**
- More than basal half of elytra testaceous, apical part of elytra black, border between dark and light part of elytra distinct, aedeagus becoming narrower in apical half (fig. 6G). Indonesia, Sumatra ***S. longicornis* Waterhouse**
28. Pronotum light brown, head and antennae brownish black, aedeagus with short phallus (fig. 6A). Indonesia, Central Java, Mt. Lawu ***S. saranganensis* n. sp.**
- Pronotum dark brown, head, antennae and legs black, aedeagus with long phallus (fig. 6B-C). Indonesia ***S. cibodasensis* n. sp.**

Discussion

Natural history

Ateliini are lycids with a strong preference for humid tropical forest habitats. They have not yet been collected in semidry areas of the Oriental region, even when these are forested as Thailand or Southern India. Ateliini are most common in mountains with high humidity the whole year round, but compared with other lycid lineages they are rare, and most species are poorly represented even in major collections. Although some species occur in lowlands and regions with pronounced dry seasons, most of these species were collected with very few specimens. There is no information available on larvae and their ecological requirements, but we may expect similar requirements, as with other net-winged beetles (Bocak & Matsuda 2003). Adults never leave the dense canopy of rain forests and do not visit flowers. We observed very low flying activity during daylight, and adults mostly

stayed motionless on the leaves of the lowest herb stratum. Such behavior is typical for all neotenic lycids. Although detailed observations are unavailable, our collecting experience suggests that, similarly with other lycids, Ateliini are short lived and do not feed in the adult stage.

Most Lycidae are aposematically coloured and unpalatable for potential predators (Bocak & Yagi 2010), but *Scarelus* species have usually quite inconspicuous reddish brown or testaceous elytra. These patterns resemble Dilophotini, some Platerodini, and unrelated subfamily Libnetinae, which occur syntopically with Ateliini. Although the resemblance of Ateliini to the local aposematic patterns is usually imperfect, the high similarity of syntopically occurring species of *Paratelius* and *Scarelus* in Borneo, or high similarity of all species in Sumatra and Malaysia, indicate the signaling function of these colour patterns.

All available specimens of Ateliini are males, and we suppose that sexually mature females remain larviform and live cryptically in forest litter similarly with Oriental Lyropaeinae (Wong 1996). Unfortunately, female neoteny has not yet been proven by observing copulating males and females of Ateliini.

Distribution

Ateliini are known exclusively from the Oriental region and *Scarelus* occurs in the southeast of continental Asia (Burma, the Malay Peninsula) and the Great Sunda Islands, which were connected with the continent when the Asian shelf was subaerial (Sumatra, Borneo and Java; Hall & Blundell 1996, Voris 2000). Four *Scarelus* are known from the Philippines and Palawan. The species level ranges are regularly limited to restricted, sometimes disjunctive areas. Neotenic lycids have very low vagility and therefore the ranges are often allopatric and typically contain a single mountain chain. Only a few species, such as *S. crudus* in the Philippines, *S. cibodasensis* n. sp. in Java, and *S. orbatus* in Malaysia are more widely distributed (fig. 1). The phylogeography of *Scarelus* was analyzed by Malohlava & Bocak (2010).

Scarelus is particularly species rich in the Barisan Range along the western coast of Sumatra. Altogether nine species are known from these mountains, and discovery of additional species can be expected as all known species have very restricted ranges with no material available from some parts of the region. Two species are known from northernmost Sumatra (Aceh Province), two species from the volcanic massifs of Mts Sinabung and Sibayak (*S. brastagiensis* and *S. schawalleri*) and another two species were reported from the area of Bukittinggi (*S. sanguineus* and *S.*

longicornis). Another three species, *S. flavicollis* n. sp., *S. ruficollis* n. sp. and *S. rufus* n. sp., are reported from higher mountain forests in the Kerinci massif. These areas were identified as refugia of the tropical rain forests during drier and colder periods (Ray & Adams 2001). Only two Sumatran species, *S. corporaali* and *S. longicornis*, were collected in lower elevations up to 850 m. Other species occur in the mountainous regions between 1000 and 2000 m above sea level.

The Malay Peninsula hosts several species of *Scarelus*: *S. orbatus* occurs in the lowlands (Singapore and Tioman); four species were recorded in the highlands: *S. umbrosus*, *S. anthracinus*, *S. pahangensis* n. sp. and *S. pseudoumbrosus* n. sp. (fig. 1).

Six *Scarelus* species are known from Borneo. Three records refer to the mountains in the northwest, which are considered as the Pleistocene rain forest refugium and the centre of biodiversity (in similarly to the Barisan Range in Sumatra). Another species was collected in the mountains of Sarawak (*S. ardens*) and two species, *S. similis* n. sp. and *S. loksadoensis* n. sp. are known from the lowlands of central Borneo and lower elevations of the Meratus Mts.

Only two species are known from Java. *Scarelus cibodasensis* is widespread and was collected by Dutch entomologists in mountainous Western Java in vicinity of Bandung, and in the Ijen Plateau in the easternmost part of the island, and recently in the eastern slope of Mt. Gede (fig. 1). *S. saranganensis* n. sp. was collected in the high mountain forests of Mt. Lawu in Central Java.

Conservation

The high endemism and small ranges make *Scarelus* as well as other neotenic lineages of net-winged beetles highly vulnerable to extinction. Only a few species are widespread and they are exclusively distributed in lowlands (*S. orbatus* in the Malay Peninsula, *S. longicornis* in Sumatra). Although damaged by logging, the lowlands in the region are sparsely populated and under most logging practices the populations of net-winged beetles may be preserved, as we witnessed in Southern Kalimantan. Most species occur in lower mountain forest at elevations 1300-1800 m. These habitats lie in the densely populated regions and even when formally protected as natural reserves they are often rendered in fields. The mountain species of *Scarelus* are limited to a single range as a rule and destruction of the original habitat would make them extinct.

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References

- Bocak L. 1995.** Review of the genus *Scarelus* Waterhouse from Sumatra and Malaysia (Coleoptera: Lycidae). *Stuttgarter Beiträge zur Naturkunde Serie A* **535**: 1-10.
- Bocak L. 1997.** New and poorly known Ateliinae (Coleoptera: Lycidae). *Annales Zoologici* **47**: 175-178.
- Bocak L. 1998.** New and little known species of Conderini and Ateliini (Coleoptera: Lycidae) *Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium* **36**: 7-26.
- Bocak L., Bocakova M. 1990.** Revision of the supergeneric classification of the family Lycidae (Coleoptera). *Polskie Pismo Entomologiczne* **59**: 623-676.
- Bocak L., Bocakova M. 1999.** New taxa of Lycidae from Indonesia, China and Nepal. *Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium* **37**: 47-55.
- Bocak L., Bocakova M. 2000.** Nomenclatur notes on Lycidae with description of a new species (Coleoptera). *Acta Universitatis Palackianae Olomucensis Faculta Rerum Naturalium* **38**: 41-46.
- Bocak L., Bocakova M. 2008.** Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). *Annales Zoologici* **58**: 695-720.
- Bocak L., Bocakova M., Hunt T., Vogler A.P. 2008.** Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proceedings of the Royal Society B* **275**: 2015-2023.
- Bocak L., Brlik M. 2008.** Revision of the family Omalidae (Coleoptera, Elateroidea). *Insect Systematics and Evolution*, **39**: 189-212.
- Bocak L., Matsuda K. 2003.** Review of immature stages of the family Lycidae (Insecta: Coleoptera). *Journal of Natural History* **37**: 1463-1507.
- Bocak L., Yagi T. 2010.** Evolution of mimicry patterns in Metriorrhynchus (Coleoptera: Lycidae): the history of dispersal and speciation in Southeast Asia. *Evolution* **64**: 39-52.
- Bocakova M., Bocak L. 1999.** New Lycidae from Peninsular Malaysia (Coleoptera). *Entomologica Basiliensia* **21**: 105-109.
- Bocakova M., Bocak L., Hunt T., Taravainen M., Vogler A.P. 2007.** Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics* **23**: 477-496.
- Cicero J.M. 1988.** Ontophylogenetics of cantharoid larviforms (Coleoptera: Cantharoidea). *Coleoptera Bulletin* **42**: 105-151.
- Cicero J.M. 2008.** Ontophylogenetic character analysis of *Diaphanes* (Coleoptera: Lampyridae) and extrapolation to the broader Coleoptera. *Pan-Pacific Entomologist* **84**: 200-219.
- Crowson R.A. 1955.** *The natural classification of the families of Coleoptera*. Nathaniel Lloyd & Co. Ltd., London, 187 p.
- Crowson R.A. 1972.** A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families: Cneoglossidae and Omethidae. *Revista Universidad Madrid* **21**: 35-71.
- Gould S.J. 1977.** *Ontogeny and Phylogeny*. Harvard University Press, Cambridge, 501 p.
- Hall R. 2002.** Coenozoic geological and plate tectonics evolution of SE Asia and the SW Pacific: computer based reconstructions, model and animations. *Journal of Asian Earth Sciences* **20**: 353-431.
- Hall R., Blundell D. 1996.** Tectonic Evolution of Southeast Asia. *Geological Society Special Publications* **106**. London. 432 pp.
- ICZN. 1999.** *International Code of Zoological Nomenclature, fourth edition*. The International Trust for Zoological Nomenclature, London, 305 p.
- Kazantsev S.V. 1992.** Contribution à l'étude des lycides orientaux. Les Ateliini (Coleoptera). *Revue Française d'Entomologie (nouvelle série)* **14**: 97-104.
- Kazantsev S.V. 1997.** New and little known Lycidae (Coleoptera) from Southeast Asia. *Raffles Bulletin of Zoology* **45**: 184-185.
- Kazantsev S.V., Yang P.S. 1999.** Taxonomic and synonymic notes on Lycidae (Coleoptera) with descriptions of new species from Taiwan. *Chinese Journal of Entomology* **19**: 239-247.
- Kleine R. 1926a.** Die Lyciden der Philippinen-Inseln. *Philippine Journal of Science* **31**: 33-114.
- Kleine R. 1926b.** Some Lycid beetles from Mt. Poi and Mt. Penrissen in Sarawak. *Sarawak Museum Journal* **3**: 359-361.
- Kleine R. 1928.** Neue Indische Lycidae nebst faunistischen Bemerkungen. *Indian Forest Records* **13**: 221-268.
- Kleine R. 1932a.** Sieben neue Lyciden von den Malayischen Halbinseln. *Bulletin Raffles Museum Singapore (Straits. settl.)* **7**: 117-123.
- Kleine R. 1933.** Lycidae. Pars 128. In: **Junk W., Schenkling S. (eds)**. *Coleopterorum Catalogus*. W. Junk, Berlin, 145 p.
- Malohlava V., Bocak L. 2009.** A revision of *Paratelius* Kazantsev 1992 (Coleoptera: Lycidae). *Zootaxa* **2306**: 44-50.
- Malohlava V., Bocak L. 2010.** Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. *Molecular Ecology* **19**: 4800-4811.
- Miller R.S. 1991.** *A revision of the Leptolycini (Coleoptera: Lycidae) with a discussion of paedomorphosis*. Dissertation. The Ohio State University, Columbus, 403 p.
- Pic M. 1911a.** Coléoptères exotiques nouveaux ou peu connus. *L'Échange* **321**: 164-167.
- Pic M. 1911b.** Trois Lycides exotiques nouveaux (Col.). *Bulletin de la Société Entomologique de France* [1911b]:331-332.
- Pic M. 1912.** Contribution à l'étude du genre "*Scarelus*" Waterh. *Mélanges Exotico-entomologiques* **3**: 4-5.
- Pic M. 1925.** Coléoptères nouveaux des chasses de Helfer aux Indes et Birmanie. *Sborník entomologického oddělení Národního Muzea v Praze* **21**: 161-163.
- Pic M. 1942.** Coléoptères du Globe. *L'Échange* **488**: 7.
- Ray N., Adams J. M. 2001.** A GIS-based Vegetation Map of the World at the last Glacial Maximum (25,000-15,000 BP). *Internet Archaeology* **11**: 1-44.
- Voris H.K. 2000.** Maps of Pleistocene sea levels in south-east Asia: shorelines, river systems and time duration. *Journal of Biogeography* **27**: 1153-1167.
- Waterhouse C.O. 1878.** On the different form occurring in the coleopterous family Lycidae, with descriptions of new genera and species. *Transactions of the Entomological Society of London* [1878]: 95-118.
- Waterhouse C.O. 1879.** *Illustrations of typical specimens of Coleoptera in the Collection of the British Museum. Part i. Lycidae*. British Museum, London, 83 p.
- Wong A. T. C. 1996.** A new species of neotenus beetle, *Dulitcola hoiseni* (Insecta: Coleoptera: Cantharoidea: Lycidae) from Peninsular Malaysia and Singapore. *Raffles Bulletin of Zoology* **44**: 173-187.