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EFFECT OF NEOTENY ON DIVERSIFICATION AND DISTRIBUTION OF NET-WINGED BEETLE *Scarelus* (COLEOPTERA: LYCIDAE)

Ph.D. Thesis

P1501 Zoology

Supervisor: Doc. Ing. Ladislav Bocák, Ph.D.

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Here undersigned Vladimír Malohlava I declare to have written this Ph.D. thesis alone during years 2006 – 2010 in the Department of Zoology and Anthropology under the supervision of Doc. Ing. Ladislav Bocák, Ph.D. and I have used the references enclosed in the Ph.D. thesis.

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Disertation Abstract

The Ph.D. Thesis deals with taxonomy, phylogeny and effect of ontogenetic modifications on speciation and distribution of a neotenic lineage of the family Lycidae (Coleoptera: Elateroidea). Further, I intended to study the potential conflict between organismic and species level selections. The tropical fauna of the family Lycidae is poorly known. Therefore, I had to start with the alpha-taxonomic work, which provides the basis for the second part of the study, which deals with evolution and speciation of *Scarelus*.

Taxonomical part: Alpha taxonomic revision of genera Scarelus and Paratelius (Coleoptera: Lycidae)

The taxonomical part provides comparative morphology of genera *Scarelus* and *Paratelius,* an alpha-taxonomic revision of thirty two species based on morphology, a key to all species, and illustrations of important taxonomic characters. The material was obtained either from the European Museums or the expeditions of the supervisor. Almost all primary types were available for taxonomic revision and the study was based on almost complete material of the known taxa from the Great Sundas, Malay Peninsula, the Philippines, and Southern Thailand.

The relationship among Ateliinae genera, their biology and distribution of the individual species is discussed in the first study of the morphological part of the Ph.D. Thesis.
As a result of the taxonomic revision and the study of the recently collected material, twenty seven species of *Scarelus* were recognized, eleven of these were described as new species: *S. baranciki, S. pseudoumbrosus, S. cibodasensis, S. flavicollis, S.loksadoensis, S. pahangensis, S. ruficollis, S. rufus, S. salvani, S. saranganensis, S. similis.* All species were defined by differencial diagnoses. Further, redescriptions, data on phenotypic variability, and distribution data were provided. Key to the identification of genera of the tribe Ateliini and the species of *Scarelus* were presented. The important diagnostical characters were ilustrated – mainly the male genitalia used as the most important character for species identification. The study is

supplemented by the distribution map of the species and the general morphology of both species is ilustrated in detail. This part of Thesis is submitted to Annales de la Sociéte entomologique de France under title "A revision of the neotenic net-winged beetle *Scarelus* (Coleoptera: Lycidae)".

The second study of the morphological part of the Ph.D. Thesis is the revision of genus *Paratelius* Kazantsev, 1992 (Coleoptera: Lycidae). I have revised the taxonomy of the genus and described several new species recently collected in northeastern Borneo. In total five species are classified in *Paratelius,* three of them were described as new species: *P. emasensis, P. snizeki, P. nigricornis.* The differential diagnosis, with description or redescription and data of their variability and distribution were provided. This part of Thesis was published in *Zootaxa*, 2306, 44 – 50 in 2009: "A revision of *Paratelius* Kazantsev, 1992 (Coleoptera: Lycidae)".

The molecular phylogeny and evolution: *„Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles".*

Molecular phylogenetic part of the Ph.D. Thesis deals with the phylogeny, phylogeography, and speciation process of the selected species representing genera *Scarelus* and *Paratelius*. The genera *Scarelus* and *Paratelius* are suitable as a model taxa for the study on the speciation of neotenic lineages. They share basic ecological traits with related fully metamorphosing lineages and their ancienty was inferred from the previously published comprehensive phylogeny of Lycidae (Bocak *et al.* 2008). Therefore, we can study them as a model of macroevolutionary consequences of ontogenetic modifications. Additionally, their extremely poor dispersal ability should preserve information on deep dispersal history and enable to couple climatic and tectonic processes with the speciation of *Scarelus.* The study focused on the following topics:

a/ Reconstruction of phylogeny as a basis for further considerations.

b/ Dating of principal evolutionary events from molecular data.

c/ Speciation process – the role of ecology in speciation, role of fragmentation and geographic isolation in genetic differentiation.

d/ Speciation rate in neotenics, dependence of speciation rate on extrinsic factors.

e/ Neotenics as potential indicators of the stable habitats.

Scarelus is an endemic of the Sundaland and the Philippines and it does not occur further than to the Isthmus Kra in the north despite absence of any physical barriere. Altogether, 32 species are known in the region and 18 of them were available for DNA isolations, usually each species represented by several specimens. The sampling represented approximately 60 per cent of known species *Scarelus* and *Paratelius* from Java, Sumatra, the Malay Peninsula, Borneo and the Philippines.

Five markers were used for building the phylogenetic hypothesis. We used the nuclear ribosomal genes: the full length of 18S rDNA (1900 bp) and the 640 bp fragment 28S rDNA. Further, three mitochondrial markers were sequenced: the 800 bp fragment of 16S rDNA, tRNA-Leu and ND1 mtDNA; the 1020 bp of COI/COII mtDNA genes with inserted tRNA-Leu, and the 1220 bp fragment of ND5 mtDNA and adjacent three tRNA genes.

The phylogenetic hypothesis was inferred using the Bayesian approach, maximum parsimony, and likelihood. The Bayesian approach was used for normalizing the tree as implemented in the Beast software package. The Geiger and Laser packages available in R programming language were employed for the analysis of the speciation process.

We have found that all closely related species have vicariant ranges although the scale of vicariance may be very small in some cases. Such pattern results from poor dispersal ability of all neotenic beetles. The estimation of diversification events supports previously inferred anciety of *Scarelus*.

Speciation as a core of evolutionary biology attracts wide attention. Although the numbers of molecular phylogenies provided a valuable insights in the history of speciation and speciation rate in recent years, many aspects remain controversal and hardly generalized across various animal lineages. Extending the analysis of species selection and diversification rates to the obligatory-neotenic beetles is important, because their extreme life history traits may provide new insight to the selection process. Considering the fact that organismic and species level selections are largely independent, we may ask how frequently may organismic selection produce, and eventually further escalate an trait decreasing the emergent fitness of the whole lineage.

The ontogenetic program plays an important role in determining the mode and diversification rate in neotenic *Scarelus*. Our results support predominance of the allopatric mode of speciation operating within short distances, rare expansions of ranges and extremely low morphological diversification. We postulate from the analysis of speciation, that morphological stasis is indicative about the completion of the speciation process in allopatry. Only two speciation events may indicate presence of sexual selection, when a new type of genitalia is established in the lineage, but the morphological stasis is re-established there after.

We expect that sea level fluctuations, uplifting of mountain ridges and tropical forest fragmentations during climatic changes contributed to observed diversity and high endemism. Neotenics speciate readily under influence of these extrinsic factors, but speciation may be halted under stable homogenous conditions very probably due to the low dispersal potential and small, genetically uniform populations. Although comparison with related lineages is beyond the scope of this study, we do not expect that neotenic lineages inherit low rate of diversification as an intrinsic trait, but the observed low diversity is a consequence of low emergent fitness caused by small ranges and small populations. The data suggest a conflict between organismic and species selection in the neotenic lineages. The organismic selection selects low dispersal activity of males to ensure their ability to find wingless female, i.e. to ensure survival and reproduction of individuals of neotenic lineages in a stable environment. On the other hand, this selection leads to vulnerabitility to extinctions. Neotenic lineages depend on extreme habitat stability and the changes in the extent and position of suitable habitats deeply threaten their existence.

At present, these narrowly endemic taxa are additionally highly endangered by deep disturbances of their habitats by human activities. Animals with similarly restricted ranges and limited dispersal abilities such as land snails have been assigned global conservation status ranking of ‘vulnerable’ or higher (IUCN, 2010), but neotenic lineages of elateroid beetles have been omitted from these lists due to our very limited knowledge. We believe, that the demonstrated congruence between distribution of neotenics and ancient refugia of rain forests make them very valuable for biodiversity conservation management.

The results of this study were accepted for publication to Molecular Ecology under title *„Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles “.*

Keywords: speciation, neoteny, phylogeny, rDNA, mtDNA, diversification, distribution, biodiversity

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Předmluva. – Preface.

Poznání mechanizmu speciace je zásadní pro pochopení mimořádné diverzity na Zemi. V této studii jsem se zaměřil na skupinu neotenních brouku čeledi Lycidae, kteří mohou objasnit postup speciace za podmínek extrémně nízké disperzní schopnosti. Tento projekt se zabývá především interakcí mezi ontogenetickým vývojem a speciací v rodu *Scarelus* Waterhouse, 1878 a vlivu ontogenetických modifikací na distribuci této skupiny. Tropická fauna je obecně málo prozkoumaná a Lycidae nejsou výjimkou. Proto byla vypracována alfa-taxonomická revize pojednávající o taxonomii, fylogenezi a distribuci neotenní linie čeledi Lycidae (Coleoptera: Elateroidea).

Speciace je velmi složitý proces, který může být podstatně modifikován v závislosti na biologii dané skupiny. Scarelus je vyjímečný velmi nízkou alfa diverzitou, malými areály jednotlivých druhů, celkově omezeným rozšířením a to v rozporu s dlouhou evoluční historií této linie. Proto mechanizmus speciace ovlivňuje i celkovou schopnost skupiny generovat nové druhy se schopností jednotlivých linií dlouhodobě přežívat. Dochází zde potenciálně ke konfliktu mezi individuálním a druhovým výběrem (Rabosky a McCune 2010). Hlavními otázkami byly fylogenetické vztahy mezi neotenickými liniemi rodu *Scarelus* z různých částí regionu souostroví Velkých Sund a jejich závislost na stabilním životním prostředí, jež by mělo být předmětem zvýšené ochrany. Srovnání fylogeneze a historie tektoniky regionu může osvětlit klíčové parametry, které byly důležité pro vývoj jednotlivých linií včetně jejich diverzifikace a původu lokální fauny. Studoval jsem faktory důležité pro proces speciace neotenických linií a vlivu na morfologickou rozdílnost. Vycházel jsem rovněž z publikovaných informací pojednávajících o morfologii, malé početnosti populací a areálů výskytů včetně nízké mobility této skupiny. I když problematika druhového výběru je diskutována v mnoha studiích, většina z nich pojednává o speciačním tempu a roli ekologických inovací v adaptivní speciaci (Jablonski 1986, Lloyd a Gould 1993, Coyne a Orr 2004) a někteří autoři výběr na úrovni druhu dosud zpochybňují (viz práce Rabosky a McCune 2010). Mnoho aspektů speciace napříč liniemi je stále kontroverzních a stěží zobecnitelných (Fitzpatrick a Turelli 2006) i přes rostoucí počet podrobných molekulárně fylogenetických a evolučních studií (Barraclough a Vogler 2002, Rabosky a McCune 2010). Studium speciačního procesu neotenních brouků proto může poskytnout nový pohled na proces selekce na různých úrovních a poznatky o speciaci linie s velmi modifikovanou ontogenezí mohou být velmi důležité i pro generalizaci speciačních procesů v rámci jiných skupin organismů.

Heterochronie a její význam.

Heterochronie je významný proces, který realokací začátku či konce vývoje je schopen generovat evoluční novinky. Modifikace doby vzniku určitých orgánů, včetně časování doby pohlavní dospělosti vůči době ukončení somatického vývoje, může rychle vytvořit odlišné fenotypy a tím změnit evoluci skupiny. Předpokládáme, že mutační změny se týkají regulačního genetického systému a tím náhle dochází u organismů ke změnám v ontogenezi. Heterochronické změny mohou způsobit zrychlování vývoje určitých struktur, nebo naopak zastavení vývoje adultních znaků i dlouho před dosažením dospělosti. Významnou charakteristikou heterochronických modifikací je náhlost (Gould 1977).

Zásadní změny v tělesné stavbě mohou vzniknout jako důsledek minimální genetické změny, někdy i změnou v regulační oblasti jediného genu (Flegr 2005). Geny zodpovědné za změny v tělesné stavbě, regulační geny, vznikly v evolučním procesu v raných stádiích evoluce organismů. Tyto geny proto také byly velmi dlouhou dobu vystaveny mutačním změnám a můžeme je pokládat za nejstarší složku genetické výbavy organismu (Gould 1977). Mutační změny zasahující velmi konzervativní geny řídící podstatné ontogenetické procesy jsou velmi často negativní nebo letální. Pravděpodobnost výhodnosti drastické změny ve stavbě těla je malá a proto je většina takových modifikací přírodním výběrem rychle odstraňována (Gould 1977). Na druhé straně je ovšem velmi důležité, že pokud v raných stádiích vývoje organismu vznikne mutace, která je pro organismus výhodná, nebo jak se budu snažit dále dokázat akceptovatelná, pak se může fixovat. Často stačí jen velmi malá genetická změna k tomu, aby určitý orgán začal v průběhu ontogeneze vznikat u jedinců určitého druhu dříve či naopak později a dospěl tak během ontogeneze do jiného stavu než u jeho fylogenetických předků. Drobná změna v načasování jednotlivých ontogenetických dějů tak může mít zásadní význam pro fenotyp příslušníků dané linie. (Wakahara 1996, Klingenberg 1998, Richardson 1995).

Typy heterochronie.

Můžeme rozlišit různé typy heterochronických změn (Flegr 2005). Peramorfózy jsou ontogenetické modifikace, při nichž je potomek ve vývoji na vyšším stupni než jeho předci. Například živočichové ze skupiny vymřelých amonitů – postupným vývojem docházelo ke zvyšování počtů rýh na jejich schránkách. Peramorfózy jsou často u recentních organismů popisovány například u ploštic – Heteroptera (Guilbert a kol. 2007).

Dalším typem ontogenetických modifikací jsou změny, kdy potomek nedojde do stádia vývoje svého předka a ontogenetický vývoj je neukončený při nástupu pohlavní dospělosti. Pedomorfní skupina je z ekologického hlediska r-stratég. Všichni r-stratégové se vyznačují rychlým ontogenetickým vývojem – produkcí velkého množství potomků s nízkými energetickými náklady na jedince a krátkým životním cyklem. Naopak, neotenní linie se vyznačují zpomaleným somatickým vývojem, který je prodloužen, ale přitom není ukončen morfologický vývoj v době dosažení sexuální dospělosti. Výsledkem je juvenilní nebo larvální forma schopná rozmnožování (Gould 1977). Neoteniky z čeledi Lycidae řadíme k tzv. K-stratégům, vyznačujících se velkou energetickou investicí do rozmnožování, produkcí malého množství potomků a relativně dlouhým životem jedinců (Bocák a kol. 2008). Dospělý jedinec schopný rozmnožování má znaky charakteristické pro mladší vývojová stádia nebo larvy příbuzných druhů.

Neotenie dosud byla studována především na modelu *Ambystoma* spp., který se podstatně liší od neotenie v řádu Coleoptera. Především, v Coleptera je neotenie obligatorní zatímco v *Amblystoma* fakultativní. *Ambystoma mexicanum* je po celý život vodní živočich a k dýchání používá žábra. Některé příbuzné formy prodělávají metamorfózu, vodní prostředí opouštějí a v dalším životě dýchají plícemi. Axolotl tedy zůstává morfologicky nedospělý v době sexuálního rozmnožování (Wakahara 1996). Pokud je do těla axolotla experimentálním zásahem vpraven extrakt hormonu štítné žlázy je indukována metamorfóza a adultní fenotyp se neliší od příbuzných druhů, u kterých k neotenii nedochází (Flegr 2005). Několikanásobný vznik způsobu tohoto rozmnožování indikuje jednoduchost jeho vzniku.

Mnoho případů pedomorfózy můžeme nalézt u hmyzu ze skupin, jako jsou například švábi či termiti, nebo u mšic a brouků. I tyto skupiny si zachovávají víceméně larvální způsob života a nikdy nedojde k přeměně do stádia imaga. U brouků byla neotenie popsána v několika čeledích, např.: Phengodidae, Lampyridae, Omalisidae, Telegeusidae, Rhagophtalmidae, Lycidae a další (Coleoptera, Elateriformia) (Bocák a kol. 2008).

Makroevoluční důsledky heterochronie.

Nové vyšší taxony mohou příležitostně vzniknout procesem heterochronie (Gould 1977). Morfologická disparita a kombinace juvenilních a adultních znaků otevírají nové evoluční trajektorie. Evoluce nové linie může být pak velice rychlá a náhodná, i když se přímo nevytvoří nové morfologické struktury (Gould 1977).

Ačkoliv ontogenetické reprogramování bylo široce studováno a existují odborné práce zabývající se tímto tématem, většina z nich byla zaměřena na modelové skupiny obratlovců

(Gould 1977). Pouze kusé informace byly dostupné v rámci skupiny hmyzu včetně neotenních linií a skupin brouků (Coleoptera) (např. Crowson 1972, Cicero 1988, 2008, Miller 1991). Bohužel byly dostupné pouze nekompletní informace týkající se distribuce a chaotická klasifikace bránila zobecnění důsledků ontogenetických modifikací na ekologii a distribuci jednotlivých linií. Bylo tudíž potřeba shromáždit více alfa-taxonomických a zoogeografických dat ke studiu takových témat, jako jsou procesy speciace a vztahy mezi neotenií a ekologií.

Čeleď Lycidae jako modelová skupina pro studium neotenie.

Lycidae jsou zkoumáni z evoluční perspektivy pouze v posledních letech a jako skupina velmi odlišná od dříve používaných modelů, může přinést její studium nové poznatky o vzniku neotenie a jejím vlivu na makroevoluci.

Čeleď Lycidae je zařazena do nadčeledi Elateroidea kam řadíme 15 čeledí *sensu lato*. Je obtížné najít synapomorfie, které by definovaly tuto nadčeleď díky mimořádné morfologické disparitě elateroidního komplexu. Pro tuto skupinu je morfologicky charakteristická absence mandibulární moly a primitivní způsob skládání křídel, úzké tělo s velmi dobře vyvinutým prothorakálním mechanismem zámku s různými modifikacemi „cvakání“. U larev můžeme pozorovat maximálně jedno stemma a ústní ústrojí modifikované k příjmu tekuté potravy. Čtyři čeledi reprezentují předpokládané bazální skupiny jejichž fylogenetické vztahy jsou stále poněkud nejisté: Cerophytidae, Eucnemidae, Throscidae a Elateridae (Crowson 1972). Jsou řazeny do původních Elateroidea do elateroidního komplexu (Lawrence 1995, Bocáková a kol. 2007). Ostatní čeledi jsou součástí původních Cantharoidea nebo též tzv. cantaroidního komplexu, kam náleží tato čeleď – Lycidae - spolu s čeleděmi: Plastoceridae, Drilidae, Omalisidae, Telegeusidae, Phengodidae, Rhagophthalmidae, Lampyridae, Omethidae a Cantharidae. Dospělá stádia těchto čeledí vykazují přítomnost larválních znaků. Cantaroidní linie byly rovněž svého času považovány za nejprimitivnější skupinu Polyphaga hlavně díky kompletní volné artikulaci abdominálních ventritů a dobře vyvinutým a exponovaným protrochantinům. Crowson (1972) považoval tyto znaky u neoteniků a přetrvávání larválních znaků do dospělosti za druhotně vyvinuté. Tato hypotéza byla podporována výskytem kompletně larviformních nebo brachelytrických samic minimálně u šesti čeledí patřících do této skupiny.

Fylogenetické vztahy v rámci této skupiny (Bocákova a kol. 2007): linie Elatoreidea + Cantharoidea (= Elateroidea *sensu lato*) je monofyletická se skupinou Omethidae + Telegeusidae. Rovněž byla monofylie prokázána u poněkud fylogeneticky vzdálenější skupiny Scirtoidea (včetně Decliniidae), což bylo popřeno Huntem a kol. (2007). Charakteristický znak omezené sklerotizace dospělců vyskytující se u čeledí je polyfyletického původu. Tím je popřeno původní umístění Cantharoidea ve stejné skupině. U minimálně sedmi linií je souvislost mezi výskytem měkkého těla a postupným či simultánním přechodem čeledí k neotennímu způsobu rozmnožování. U čeledi Lampyridae a u blízce příbuzných čeledí Phengodidae a Rhagophthalmidae bylo potvrzeno, že nemají monofyletický původ. Čeleď Lampyridae je příbuzná Lycidae a Cantharidae, zatímco čeledi Phengodidae a Rhagophthalmidae jsou vývojově blízké čeledi Elateridae.

Z morfologických znaků jsou pro čeleď Lycidae charakteristické štíhlé a dlouhé trochantery u dospělých jedinců, u larev jsou mandibuly rozděleny na dvě k sobě přiložené části používané k nasávání tekuté potravy. Na štítu a krovkách imag se většinou vyvinula zřetelná žebírka. Vývoj larev probíhá v tlejícím dřevě či v detritu ve svrchních vrstvách půdy. Dospělci se vyskytují na vegetaci či tlejícím dřevě, výjimečně jsou pak pozorováni na květech. Samice některých skupin čeledi Lycidae jsou neotenní. Vyskytují se převážně v tropických vlhkých oblastech. V České Republice se vyskytuje sedm druhů čeledi Lycidae, mezi nejhojnější patří *Dictyoptera aurora*, nebo *Lygistopterus sanguineus*. V této disertaci byly studovány rody *Scarelus* a *Paratelius* klasifikované v tribu Ateliini. Ten společně s tribem Dilophotini tvoří podčeleď Ateliinae (Bocák a Bocáková, 2008). Pro zástupce podčeledi Ateliinae jsou charakteristická dlouhá, úzká a plochá tykadla a pronotum s jednoduchým, středovým podélným kýlem. Všechny druhy mají charakteristický falus, který je trubicovitého tvaru s ostrým nebo tupým zakončením. Samice jsou neznámé, avšak panuje shoda, že budou neotenické (Bocák a kol. 2008, Bocák a Matsuda 2003, Wong 1996, Kazantsev 1992). V současnosti je v tribu Ateliini klasifikováno 36 druhů, tento tribus je druhově nejchudším v čeledi Lycidae.

Ekologická charakteristika čeledi Lycidae.

Zástupci čeledi Lycidae se vyskytují především ve vlhkých tropických oblastech. Nejčastější výskyt je v horách s celoroční vlhkostí. K dispozici nejsou informace o larvách, nicméně předpokládáme, že jejich životní nároky jsou podobné jako u jiných příbuzných neotenních skupin (Bocák a Matsuda 2003).

Linie, u kterých se vyskytuje největší stupeň neotenního rozmnožování, jsou nacházeny právě v čeledi Lycidae. Samice se nevyskytují v pupální fázi ani ve fázi dospělce. K rozmnožování u těchto skupin dochází v larválních formách po poslední ekdysi. Patří mezi nejnápadnější druhy brouků, jejich velikost dosahuje pěti i více centimetrů délky a často jsou nazývány „trilobitními larvami" díky jejich celkovému vzhledu, který tohoto vyhynulého živočicha připomíná. Neotenie byla již popsána v minulosti (např. Gravely 1915), ale pouze práce z nedávného období rozšířily naše znalosti o neotenii ve skupinách neotenických brouků ze všech hlavních tropických oblastí jejich výskytu (např. Bocák a Bocákova 1988, 1989, 1990, Wong 1996, Bocák 1995, 2001, Bocák a kol. 2008 etc.).

Rod *Scarelus* je široce rozšířen na jihovýchodě kontinentální Asie (Tenasserim, Malajský poloostrov) a na ostrovech Velké Sundy, díky historickému spojení s kontinentem pomocí asijského šelfu (Hall a Blundell 1996, Voris 2000). Dva druhy rodu *Scarelus* jsou známy z Palawanu a dva z Filipín, jež byly izolovány od Asijské pevniny po velmi dlouhou dobu (Voris 2000). Předpokládáme, že rozšíření neotenního rodu *Scarelus* na Filipíny bylo suchozemskou cestou (Hall a Blundell 1996). Část druhů rodu *Scarelus* se vyskytuje v oblasti Barisan Range podél západního pobřeží Sumatry. Celkem je z hor této oblasti popsáno devět druhů. Tyto oblasti byly identifikovány jako refugia tropických deštných pralesů během suchých a chladných období (Ray a Adams 2001). Z Malajského poloostrova je známo pět druhů rodu *Scarelus,* z Bornea bylo popsáno druhů šest a na Jávě se vyskytují druhy tři.

Rozmnožování neotenních druhů z ekologického hlediska řadíme do tzv. K-strategie (viz výše). Ztráta křídel či schopnosti létat u samic významně redukuje možnost rozšíření areálu výskytu druhu či kolonizování areálů nových a to i v případě, že existují disperzní mosty. Samičky kladou vajíčka bezprostředně po kopulaci a vylíhlé larvy se pohybují v omezeném prostoru, což rovněž omezuje velikost areálu. Změny prostředí vlivem působení suchých a chladných období v tropických oblastech v průběhu glaciálních maxim během Pleistocénu rovněž podstatným způsobem ovlivnily velikost ostrůvkovitých areálů (Tallis 1991, Ray a Adams 2000). Tato refugia tropických pralesů se vyznačují vysokou druhovou biodiverzitou (Mayers a kol. 2000).

Neotenie ve vztahu k fylogenezi Lycidae.

V práci Bocáka a kol. (2008) bylo popsáno, že neotenie v rámci čeledi Lycidae vznikla třemi, vzájemně nezávislými původy, neboli není u této skupiny monofyletická avšak parafyletická. V čeledi Lycidae bylo identifikováno šest linií, které jsou klasifikovány jako podčeledi (Bocák a Bocáková 2008, Bocák a kol. 2008). Tři podčeledi obsahují neotenní linie: Lyropaeinae (všechny druhy), Scarelinae (tribus Scarelini) a Lycinae (Leptolycini). Dexorinae jsou další podčeledí obsahující výhradně neotenní formy a je klasifikována jako podčeleď v nespecifikovaném postavení (Bocák a Bocáková 1990, 2008). Molekulární studie prokázala starobylý vznik orientálních neotenních linií Lyropaeinae a Scarelini a výrazně mladší původ neotenních Leptolycini. Posledně jmenovaná linie je pravděpodobně součástí tribu Calopterini (Bocák a Bocáková 2008, Miller 2001). Neotenní linie podle současných znalostí vznikly několikanásobně. Lycidae poskytují široké možnosti výzkumu neotenie a makroevolučních následků tohoto modifikovaného způsobu rozmnožování. V čeledi Lycidae bylo dosud popsáno přes 4000 druhů, v blízce příbuzné čeledi Cantharidae pak přes 6000 druhů a 2000 druhů Lampyridae, z nichž je přibližně 25 % neotenních. Zbylé čeledi Elateroidea s měkkou tělní strukturou, kam zahrnujeme čeledi Phengodidae, Rhagophthalmidae, Drilidae, Telegeusidae a Omalisidae, jsou zastoupeny většinou jen několika desítkami či jednotkami doposud popsaných druhů. Jsou evidentně druhově chudšími čeleděmi a zahrnuji pouze neotenicky se rozmnožující druhy. Pouze čeleď Omethidae není neotenická, nicméně druhově také velice chudá (známo něco málo přes 40 druhů). Neoteničtí zástupci lycidů reprezentují pouze 2 % z celkového počtu známých druhů celé čeledi Lycidae, což opět podporuje trend možnosti velké redukce druhové diverzity (Bocáková a kol. 2008).

Speciační rychlost neotenních linií.

Neotenie u některých čeledí Lycidae je významným faktorem ovlivňujícím speciační procesy (Bocák a kol. 2008, Malohlava a Bocák v tisku). Neotenní linie Elateroidea se vyskytují v současnosti na místech se stabilním životním prostředím negativně neovlivněným střídáním vlhkých a suchých období během Pleistocénu, střídáním dob ledových a meziledových. Díky velmi omezené schopnosti pohybu neotenních brouků na větší vzdálenosti je jejich výskyt omezen na území s kontinuální přítomností vhodných podmínek pro život a rozmnožování. Samice neotenních brouků jsou penalizovány neschopností měnit významnějším způsobem svou lokalitu výskytu. Jsou bezkřídlé, často fysogastrické, žijí skrytě v hrabance v tlejícím listí a vlhku (Wong 1996). Zajímavostí je, že i samci, kteří jsou okřídlení, nebyli často pozorováni při letu a pokud ano, tak pouze pár desítek centimetrů při přeletech z vegetace na vegetaci a to pod ochranou pralesního krytu (Bocák 1995, 1997, 1998). I když je schopnost disperse takovýmto drastickým způsobem ovlivněna či zredukována, neznamená to na druhou stranu rychlé ohrožení linie či druhu (Bocák a Bocákova 2008). V průběhu historie došlo u neotenických skupin ke speciaci, často ani ne tak morfologické jako genetické a vzniku následných druhů. V rámci speciace můžeme pozorovat, že určité znaky u neotenických linií mohou přetrvávat i při razantní změně životních podmínek. Tyto znaky mohou přetrvávat poměrně dlouhou dobu. Podobný případ můžeme sledovat u neotenních brouků.

Přežívání skupin pouze v oblastech s velmi stabilním výskytem tropického deštného pralesa umožňuje využití neotenních brouků pro přesnou identifikaci pleistocénních refugií a zohlednění jemné struktury ekosystémů při praktické ochraně biodiverzity tropického pralesa. Předpokládáme, že v rámci evoluce není přechod k neotennímu způsobu života poznamenán ztrátou životaschopnosti druhu či schopnosti dále speciovat. Fitness broučích linií a druhů, pokud jsou v areálech s vyrovnanými životními a přírodními podmínkami, může být stabilní. Samozřejmě, pokud nastanou nepříznivé situace a areály výskytu těchto neoteniků jsou zničeny přírodními vlivy, jako jsou požáry, výlev lávy, záplavy, likvidace pralesa lidskou činností, aridizací apod., pak tyto druhy samozřejmě nemají vzhledem ke své omezené mobilitě šanci uniknout záhubě. Rovněž i díky jejich malému početnému zastoupení v omezených lokalitách může dojít k ohrožení přežívání linie.

Scarelus jako modelový příklad.

Zástupce čeledi Lycidae, rod *Scarelus,* je vhodným modelem pro studium těchto jevů. U těchto brouků jsou demonstrovány základní ekologické neotenické znaky s příbuznými liniemi a tyto u nich přetrvávají velice dlouhou dobu (Bocák 1995, Malohlava a Bocák v tisku). To byl důvod pro zaměření se v této disertační práci na studium rodu *Scarelus* jako modelového případu pro hlubší a další poznání makroevolučních důsledků změn v ontogenetickém vývoji. Díky velice omezené schopnosti pohybu tohoto rodu můžeme studovat dávnou historii jejich disperze a tyto informace pak zhodnotit a porovnat s historickými časovými událostmi ve smyslu tektonických a klimatických procesů a vztahu k vývoji druhů u rodu *Scarelus.*

Samice tohoto rodu, jak již bylo zmíněno, jsou zásadně larviformní, neokřídlené, extrémně nepohyblivé vyskytující se v tlejícím materiálu na zemi pod vegetačním spadem a s požadavkem na vlhké životní prostředí, v tropických deštných pralesích oblastí ostrovů Velkých Sund (Bocák a Matsuda 2003). Samci oproti tomu prodělávají úplnou, klasickou metamorfózu holometabolního hmyzu, jsou okřídlení a letu schopni. Předpokládáme, že v dospělosti nepřijímají potravu, snad pouze tekutou. Celkem je v současnosti popsáno z oblasti tropických deštných pralesů jihovýchodní Asie 32 druhů rodu *Scarelus,* přičemž většina druhů byla sbírána a popsána v posledních deseti letech. Díky tomu byla i potvrzena vysoká endemičnost těchto druhů. Nedávno sesbíraný materiál rovněž posloužil k výzkumům na molekulární úrovni, studiu DNA struktury a fylogenezi skupiny, datování vzniku druhů a speciačních procesů v rámci studované skupiny. Rod *Scarelus*, ale i jiné neotenické skupiny hmyzu jsou silně ohroženy lidskou činností, destrukcí pralesů, klimatickými změnami a dalšími negativními vlivy na jejich přírodní životní prostředí.

Modifikace – mimikry.

Zástupci rodu *Scarelus* mají většinou nenápadné, červenohnědé či hnědé zbarvení, jež je podobné zástupcům tribu Dilophotini, některým zástupcům Platerodini a nepříbuzné podčeledi

Libnetinae, jež se vyskytuje společně s Ateliini (Malohlava a Bocák, v tisku). U dalších zástupců čeledi Lycidae se setkáváme často se široce vyvinutými mimikry, což s největší pravděpodobností souvisí právě s jejich způsobem života a relativním vysokým nebezpečím ohrožení vyplývající z nízké mobility dospělců. Tato problematika a vliv mimikry na disperzi a speciaci byla například studována u rodu *Metriorrhynchus* v jihovýchodní Asii (Bocák a Yagi 2010). Byl prokázán vliv Müllerovské mimikry – tzv. synaposematismus (mimetizovaní jedinci jsou všichni pro predátory nepoživatelní a chráněné druhy si vytvářejí nepříjemný barevný vzorek) na speciaci a rozšíření tohoto rodu. U několika populací byl prokázán polymorfizmus. Na základě analýzy molekulárních dat bylo prokázáno, že spouštěcím mechanismem speciace byly rozdílné vzorce aposematických (výstražných) zbarvení brouků. Docházelo k pomalé akumulaci genetických rozdílností v podmínkách nedokonalé prostorové izolace jednotlivých populací. Následně pak morfologické rozdíly v genitáliích jednotlivých druhů posílily speciační proces, který byl iniciován rozdíly v mimikrách u jednotlivých populací.

Cíle disertační práce.

Předložená práce sleduje několik cílů, které jsou založeny na použití různých metod. Pro evoluční část práce bylo nutno zpracovat klasifikační základ spočívající v revizi známých druhů a popisu nových forem. Hlavním cílem práce je studium vlivu neotenických modifikací na makroevoluční procesy a ekologii studované skupiny.

Část disertační práce tvoří dvě alfa-taxonomické revize rodů *Scarelus* a *Paratelius* založené na morfologii. Materiál pro studie byl získán jednak z evropských muzeí a dále z expediční činnosti školitele. Práce proto mohla být založena na téměř kompletním zastoupení známých taxonů z oblasti Velkých Sund, Malajského poloostrova a Thajska.

V první studii morfologické části disertace je diskutován vztah rodů *Scarelus, Paratelius,* biologie skupiny a zoogeografie jednotlivých druhů rodu *Scarelus*. Celkem bylo rozpoznáno dvacet sedm druhů rodu *Scarelus,* z nichž jedenáct bylo popsáno jako nové druhy: *S. baranciki, S. pseudoumbrosus, S. cibodasensis, S. flavicollis, S.loksadoensis, S. pahangensis, S. ruficollis, S. rufus, S. salvani, S. saranganensis, S. similis.* Všechny známé druhy byly uvedeny s diferenciální diagnózou, redeskripcí a daty týkajících se jejich variability a rozšíření. Byl vytvořen určovací klíč rodů *Scarelus* a tribu Ateliini. Byly ilustrovány významné diagnostické znaky - jedná se především o samčí kopulační orgány, které slouží jako základní zdroj diferenciálních znaků v linii a umožňují identifikaci jednotlivých druhů. Práce obsahuje zoogeografická data a rozšíření jednotlivých druhů je kompilováno na základě literárních údajů, sbírek a nově studovaného materiálu. Dále je podrobně ilustrována morfologie obou studovaných rodů. Tato část disertace je předložena do tisku pod názvem: A revision of the neotenic net-winged beetle *Scarelus* (Coleoptera: Lycidae) v časopise Annales de la Sociéte entomologique de France. Druhou studií morfologické částí disertace je revize rodu *Paratelius* Kazantsev, 1992 (Coleoptera: Lycidae). Celkem bylo v rodu *Paratelius* klasifikováno pět druhů, z nichž tři byly popsány jako druhy nové: *P. emasensis, P. snizeki, P. nigricornis.* U všech známých druhů byla předložena diferenciální diagnóza, popis nebo redeskripce a zpracována data jejich variability a distribuce. Rovněž i zde byl vytvořen určovací klíč samčích znaků jednotlivých druhů tohoto rodu. Tato část byla publikována v časopise Zootaxa, 2306, 44 – 50 v roce 2009 pod názvem A revision of *Paratelius* Kazantsev, 1992 (Coleoptera: Lycidae).

Molekulárně fylogenetická část disertace se věnuje fylogeografii a procesu speciace vybraných druhů rodu *Scarelus* a *Paratelius* pod názvem: Evoluční analýza neotenického rodu *Scarelus* jako indikátoru extrémní stanovištní stability JV asijské biodiverzity a byla přijata k tisku do časopisu Molecular Ecology. Pro studii byl k dispozici poměrně rozsáhlý materiál fixovaný pro isolaci DNA, který reprezentoval cca 60 procent známých druhů rodů *Scarelus* a *Paratelius* z Jávy, Sumatry, Malajsie, Bornea a Filipín. Jako markery byla použita plná délka genu 18S rDNA (1900 bp), 640 bp fragment 28S rDNA, 800 bp 16S rDNA a ND1 mtDNA, 1020 bp COI/COII mtDNA geny a 1220 bp ND5 mtDNA a následující tRNA geny. *Scarelus* je v tomto regionu endemitem a nerozšířil se směrem na sever díky existenci geografických bariér. Většina druhů jsou vikarianti a z výsledků studia jejich fylogeneze vyplývá jejich raritní a pomalá schopnost disperze. Hlavními otázkami byly: fylogenetická příbuznost, tempo speciace kládů a datování jejich vzniku. Snažil jsem se objasnit, zda izolace jednotlivých linií v průběhu speciace má za důsledek neutrální genetickou diversifikaci bez uplatnění posilujících reprodukčně isolačních mechanismů, poněvadž jednotlivé druhy jsou velmi konzervativní morfologicky a to včetně kopulačních orgánů. Diskutovány pak byly vzájemné vztahy mezi druhy, jejich distribuce, otázka ekologické speciace versus geografické fragmentace, alopatrická speciace, selekce na úrovni druhu a linií a delimitace tzv. horkých míst biodiverzity a ochrany.

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Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles

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Abstract

The diversification of neotenic beetle lineages has not been studied, despite the potential for defining biodiversity hotspots and elucidating the history of regional faunas. Additionally, neotenics may provide insight into the process of speciation in small populations with extremely low dispersal ability and a limited range. Here, we used two rDNA and three mtDNA markers to investigate the phylogeny of *Scarelus,* a neotenic lineage endemic to Southeast Asian rainforests. Most genetic differentiation was associated with Palaeogene geographic divisions, which remain distinct despite temporary connections. Dispersal events were rare, with only two inferred for *Scarelus*: from Borneo to the Philippines 28.3 million years ago (mya) and from Sumatra to Java 13.9 mya. We suggest that speciation resulted from allopatric range fragmentation, and *Scarelus* diversified readily when conditions were favorable; in this case, at different times in the eastern (19.3–39.1 mya) and western (3.5–13.9 mya) parts of Sundaland. The observed similarity in general appearance and structure of the genitalia was preserved under speciation through complete allopatry. Neotenic Lycidae have survived for a long time in very stable habitats, and extremely low dispersal activity has not limited their persistence; however, the long-term diversification rate of neotenics is low and diversification is nonexistent under stable conditions. The modern ranges of neotenic lineages are indicative of ancient rainforest refugia, and may be used in biodiversity conservation management.

Keywords: Coleoptera, Lycidae, neoteny, phylogeny, speciation, dispersal, rain forest refugia

INTRODUCTION

Various traits may affect the speciation process and consequently the evolutionary success of individual lineages (Rabosky & McCune 2010). The fundamental modification of ontogeny in some net-winged beetles has resulted in completely larviform females and has set specific conditions for diversification (Bocak & Matsuda 2003; Bocak *et al.* 2008). These neotenics share basic ecological traits with related fully metamorphosing lineages; they persist for a long time; moreover, their extremely poor dispersal ability should preserve information related to their dispersal history, which may be used to couple climatic and tectonic processes with speciation in the lineage. Extending the analysis of speciation, diversification rates, and dispersal to obligatory neotenic beetles may provide new insights into the speciation process.

The multiple origins of neotenic beetle lineages were confirmed by recent, extensive molecular studies (Bocakova *et al.* 2007; Bocak *et al.* 2008). Neotenic females remain larviform or partially metamorphosed when sexually mature in some groups of net-winged beetles and fireflies, and in all glowworms, omalisids, and drilids. Conspecific males and females of neotenic net-winged beetles were identified by Mjöberg in 1925. It was only later that the females of some other net-winged beetles were found to be obligate larviforms (i.e., the females never metamorphose and maintain a larval morphology even when sexually mature) (Wong 1996; Miller 2001; Bocak & Bocakova 2008), while the conspecific adult males are fully metamorphosed and always winged (Fig. 1). Only a few females have been linked with conspecific males by collecting in the same place or breeding, including *Duliticola* (Mjöberg 1925; Wong 1996), *Leptolycus* (M. Ivie, personal communication), and two lyropaeine genera identified by molecular markers (Levkanicova & Bocak 2009). Most known females have extremely large bodies; only leptolycine neotenic females are similar in size to males. As all known neotenics live cryptically in leaf litter in tropical rainforests, females of many lineages have never been collected. One lineage known only through males and with a presumed obligatory female neoteny is Ateliini (*Scarelus* Waterhouse, 1879; *Atelius* Waterhouse, 1878). Besides a high number of collected males (~200 specimens) and unknown females, they share reduced mouthparts and other morphological characters with other neotenics, including Lyropaeini, Leptolycini, and Dexorini (Bocak *et al.* 2008). As a rule, neotenics occupy limited ranges, their populations are small, their genera are species-poor, and they occur only in the humid tropics (Bocak & Bocakova 2008).

The study of speciation in neotenic beetle lineages has been neglected since little is known about these groups and they are rarely collected (Bocak *et al.* 2008); only 15 specimens reside at the Natural History Museum of London. *Scarelus*, with 32 species occurring in the tropical rainforests of Southeast Asia, can be used as a model of ancient obligatory neotenic lineages (Bocak *et al.* 2008). Our understanding of *Scarelus* comparative morphology and taxonomy has improved over the last two decades (Malohlava & Bocak 2009, in press), and molecular analyses of recently collected materials have enabled us to investigate and date the species-level phylogeny.

In this study, we investigated the relationships among neotenic lineages of *Scarelus* from various parts of the range and their dependence on ancient stable habitats, which should be targeted by conservation efforts. Comparisons of phylogeny and tectonic history should elucidate key factors involved in lineage evolution, including the diversification rate and origins of local fauna. Based on previously published information about the low morphological disparity, small populations and ranges, and low dispersal potential in this group we investigated factors supporting the speciation of neotenic lineages and the consequences of speciation mode on morphological diversification.

MATERIAL AND METHODS

Sampling, distribution, molecular biology methods, and data compilation.

Altogether, 51 male species of *Scarelus*, representing 18 of 32 described species, were preserved in alcohol after collection (Malohlava & Bocak 2009, in press; Fig. 1, Table S1). There were at least some representatives from all major parts of the range: Sumatra (6 of 9 species), Java (2/2), Malaya (3/4), Borneo (5/11), and the Philippines (2/2). Distances among sampled localities are given in Table S3. Species from Palawan and Southern Thailand were unavailable. There is a relatively large proportion of species not included in the study as many species are available only in dry preserved type specimens. Altogether, 15 taxa were included in the analysis as an outgroup. The larger outgroup was chosen as the putative sister taxon *Atelius* was unavailable for DNA extraction and the relationships among main lycid lineages remain poorly supported (Bocak *et al.* 2008). The ingroup taxa, sequenced fragments, and Genbank Accession numbers are listed in Table S1, the sequences for the outgroup taxa were published by Bocak *et al.* (2008).

DNA extraction, PCR amplification, and DNA sequencing

Total DNA was extracted from thoracic muscles and legs using the phenol-chlorophorm protocol (as described by Vogler *et al.* 1993). Extraction yield was determined using a NanoDrop-1000 Spectrophotometer. PCR was performed using 0.5–0.6 U Taq polymerase, 1 mM $MgCl_2$, 50 mM each dNTP, 0.2 mM primer, and typically 0.03 mg of template in 50 microlitre reaction volume. Cycle conditions were 2 min at 94°C, 30–60 sec at 94°C, 30–60 sec at 45–52°C (depending on the melting temperatures of primer pairs used, Table S2), 1–2 min at 72°C (repeated for 30–40 cycles), and 10 min at 72°C. Five fragments were included in the study: the full length small subunit ribosomal DNA (18S rDNA) PCR-amplified in four fragments (~1900 base pairs, bp), a 630 bp fragment of the large subunit ribosomal DNA (28S rDNA), 780 bp of the mitochondrial large subunit ribosomal DNA (*rrnl*) with adjacent short fragment of the NADH dehydrogenase subunit 1 mtDNA, 1100 bp fragment of cytochrom oxidase subunit 1 mtDNA (*cox1*), tRNA-Leu gene, and cytochrom oxidase subunit 2 mtDNA (*cox2*), and 1180 bp of NADH dehydrogenase subunit 5 mtDNA (*nad*5) and adjacent tRNA-Phe, tRNA-Glu, and tRNA-Ser genes (multiple gene fragments are referred as *rrnl*, *cox1*, and *nad5* further). The used primers are listed in Table S2. Purified PCR products were sequenced by an ABI 3130 automated sequencer using a Big Dye Terminator Cycle Sequencing Kit v. 1.1.

Sequence handling, phylogenetic and historical biogeography analyses

Sequences were edited using Sequencher 4.6 software package (Gene Codes Corp.) and aligned by ClustalX 1.8 under default settings (Thompson *et al.* 1997). Mitochondrial genes showed minimum indels and the aligned sequences were subject to some minor adjustments guided by reading frames. The rDNA fragments showed a higher content of indels, but relatively high similarity of ingroup taxa simplified alignment and therefore only default settings were used. Long indels, which did not have a homologue in other taxa were deleted before analysis. Congruence of the phylogenetic signal from the individual fragments, protein coding (*nad1*, *cox1*, *cox2*, and *nad5* genes), nuclear rDNA genes (18S and 28S) and all rDNA genes was investigated by comparing results of partitioned analyses.

The phylogenetic analysis was carried out under the parsimony criterion using TNT 1.1 (Goloboff *et al.* 2003). All DNA fragments were combined, equal weights were assigned to all positions, and all gaps were treated as a fifth character state. For bootstrap analysis 1000 pseudoreplicates were generated. The concatenated matrix was also analyzed under the likelihood criterion using RAXML 7.2.3 (Stamatakis 2006a; Stamatakis *et al*. 2008). The dataset was partitioned by genes and by codons for cds mtDNA fragments and was analyzed for 100 bootstrap search replicates under the GTRCAT substitution model (Stamatakis 2006b). We used the majority consensus phylogram to infer relationships and to evaluate support for *Scarelus* clades. Additionally, the dataset was analyzed using MrBayes 3.1.2 (Huelsenbeck 2000), where tree topology and evolutionary model parameters were permuted using a Markov chain Monte Carlo method (MCMC). The MCMC was set for independent variability of parameters in individual coding and non-coding genes under the general time reversible model with estimation of the nucleotide rate substitution matrix, the PINVAR, and among-site rate heterogenity (GTR+I+G, Tavaré 1986). Four chains were run simultaneously for 12.10^6 generations, with trees being sampled each 1000 generations, all fragments partitioned and unlinked as above. The first 2000 trees were discarded as burn-in and posterior probabilities at nodes were determined from the remaining trees.

Ancestral zoogeographical areas of *Scarelus* were inferred using dispersal-vicariance analysis as implemented in DIVA 1.2 (Ronquist 1996). Six zoogeographical areas represented (a) the distribution of *Atelius* as the presumed outgroup in continental Asia (Bocak & Bocakova 2008) and the distributions *Scarelus* in (b) Borneo, (c) the Philippines, (d) Malaya, (e) Sumatra, and (f) Java (Figs 1–2).

A likelihood ratio test was used to test the molecular clock hypothesis. The null hypothesis L_0 is that molecular clock holds and L_1 hypothesis relaxes the clock constraint. The chi-square value is given by $2logL= 2(logL_0-logL_1)$ where L_0 and L_1 are likelihoods of the tree under given constraints. The p-value is counted for s-2 degrees of freedom where s is number of terminal branches on the tree (Felsenstein 1981). For the concatenated trees, samples were removed when they lacked some gene and a conspecific sample with complete set of genes was available. In a few cases a chimeric sample was assembled from sequences representing two specimens from the same population. The concatenated dataset missed two fragments: *S. loksadoensis* requires 28S rDNA and *nad5* sequence.

We estimated time to the most recent common ancestor for selected clades using a Bayesian approach implemented in Beast 1.4.8 (Drummond & Rambaut 2007). All analyses were performed using a GTR+I+G model of nucleotide substitution proposed by AICc criterion in JModelTest 0.1.1 (Posada 2008) (Table S5), using relaxed molecular clock (LRT values given in Table S6) and an uncorrelated lognormal model of rate variation among branches in the tree. No fossils are known for neotenic lycids, therefore the origin of the most recent common ancestor of the Bornean *Scarelus* clade was set to 67.3±3 my as was inferred in the previously published dated phylogeny of Lycidae for all-fragments dataset (Bocak *et al.* 2008). Alternatively, the substitution rate was fixed to 0.0115 substitutions per lineage and million year using the ‘universal’ insect molecular clock (Brower 1994) for the all-mtDNA and cds mtDNA datasets. A starting tree was used to improve likelihood of initial run trees. The genes and codon positions were partitioned, each partition was provided with its own parameters, and the monophyly of estimated clades was enforced. In all analyses 3.10^7 MCMC generations were run with trees being sampled each 1,000 generations. Convergence was assessed in Tracer 1.4 (Rambaut & Drummond 2004) after the first 3.10^6 generations were burned-in. The cds mtDNA dataset was run four times and results were combined. Pathd8 (Britton *et al.* 2007) was used to check molecular clock in the parts of the tree.

The diversification rate analyses were conducted on the species-level tree created by pruning all but one specimen per species for all-data, all-mtDNA, and cds mtDNA datasets. Heights of nodes were provided by the Beast analysis and first, we considered the *Scarelus* diversity as a whole with *Dilophotes* used as an outgroup (Bocak *et al.* 2008). The Gamma statistics is a measure of relative node heights and we tested the robustness of results for chronograms produced from different datasets and using independent calibration methods. The test was corrected for random incomplete sampling using the Monte Carlo simulation (Pybus & Harvey 2000), when we considered the number of described species as the real number of species. Similarly, Gamma statistics was used to test the null constant-rates model separately for the subclades of the same tree to test if speciation history differs in various biogeographic regions. We assume, with other traits being the same, the difference in the speciation history in subclades should depend on extrinsic factors and may indicate events such as radiation after uplift of the mountain range or fragmentation of ranges. Gamma statistics, simulated gamma values for incomplete sampling and p-values were obtained with Geiger and Laser packages for the R programming language (Pybus & Harvey 2000; Rabosky 2006; Harmon 2008). Further, to distinguish between different models of diversification, we compared the fit of various models of diversification on the whole *Scarelus* tree and the subclades. We used the AIC criterion for comparing the likelihood values for each ultrametric tree and for the following models of diversification: pb - pure birth, bd - birth and death, ddl - logistic density dependent, ddx - exponential density dependent, spvar - variable speciation rate, exvar - variable extinction rate, both - variable both rates (Rabosky 2006).

RESULTS

DNA sequencing

DNA sequences were obtained for five fragments: 18S (48 spec.), 28S (46 spec.), *rrnl* (46 spec.), *cox1* (43 spec.), and *nad5* (47 spec.). Mitochondrial genes did not contain stop codons, indels, and frame-shift mutations indicative of the presence of numt pseudogenes (Triant & Dewoody 2007) and this dataset should not be affected also due to the short-term persistence of the numt pseudogenes in beetle genomes (Pons & Vogler 2005). Nucleotide composition of mitochondrial genes was characterized by a deficit of guanines (5.5-17.7%, Table S10) as previously reported for other net-winged beetles (Bocak et al. 2008). The number of base pairs and number of parsimony-informative characters determined under default alignment settings are given in Table S7. The rDNA fragments varied only slightly in length within the ingroup, and they were unambiguously aligned under the default settings of ClustalX. The concatenated dataset consisted of 5704 characters, 2020 and 2112 of which were parsimony informative when gaps were considered as missing and the fifth character, respectively (Table S7). Uncorrected pairwise distances among the ingroup taxa are given in Table S4.

Estimation of phylogeny

The phylogenetic reconstruction inferred by parsimony, likelihood, and Bayesian analyses resulted in essentially identical trees for the concatenated five-fragment dataset and the protein-coding genes dataset. Species level and deeper relationships were regularly recovered by the partial analyses (Table S8). The trees had fully resolved basal branches and polytomies were found only in intraspecific clades (Fig. 2). These trees indicate that *Scarelus* and *Paratelius* represent a monophyletic clade, with *Paratelius* appearing consistently as a terminal branch within *Scarelus* (henceforth, all species are considered to be members of *Scarelus*; see the Supplements for taxonomic considerations). Species with a pointed phallus (the *S. orbatus* species group [Malohlava & Bocak, in press]) formed a monophylum, which represented a terminal branch in the *Scarelus* clade. The *S. anthracinus* species group was a paraphyletic assemblage. All species defined based on morphology were recovered in the tree. Our analysis demonstrates striking monophyly in terms of phylogeographic divisions. The deepest split was detected between the Borneo/Philippines (BPh) and Malaysia/Sumatra/Java (MSJ) clades (Fig. 2). The eastern Bornean clade split into two well-supported subclades, one represented by two species previously classified as *Paratelius* (*S. nigricornis* and *S. emasensis*), and three Bornean species (*S. loksadoensis*, *S. similis*, and *S. baranciki*) along with two Philippine species (*S. crudus* and *S. salvani*) in the sister group position to *S. baranciki*. The western clade was also structured into well-supported geographically distinct subclades, one being centered on the Malay Peninsula (*S. anthracinus*, *S. pahangensis*, and *S. pseudoumbrosus*) and the other on Sumatra and Java (*S. sanguineus*, *S. ruficollis*, *S. brastagiensis*, *S. rufus*, *S. longicornis*, *S. flavicollis*, *S. cibodasensis*, and *S. saranganensis*) (Fig. 2). The clade defined by a short pointed phallus occurred on both Sumatra and Java and was part of the Sumatran clade and a sister group to all Sumatran species with a long, apically-rounded phallus (Fig. 2).

Divergence times and rate of speciation

The molecular clock was tested using a likelihood ratio test. With all fragments combined, a null model enforcing a molecular clock was rejected for all three datasets and separately considered BPh and MSJ clades (Table S6). A strict molecular clock rate was identified only in the Malay clade using Pathd8, while all other clades showed apparent rate variation (results not shown). Therefore, speciation events were dated using a relaxed molecular clock as implemented in Beast 1.4.8. Concerning the uncertainty of dating when there is significant heterogenity across lineages (Sanderson 2002) and no fossil calibration is available, we considered the results based on all three datasets (Fig. 4 and Table S8). After a comparison with tectonic information, we prefer the normalized tree inferred from the coding sequence (cds) mtDNA dataset and a fixed median mutation rate of 2.3% per million years (Fig. 3). The inferred dating of splits agrees at several crucial points with tectonic information: *Scarelus* originated on the Sunda Shelf 39.1 million years ago (mya) (95% HPD 32.3–46.5) when the shelf was subaerial; the Philippines were colonized 28.3 mya (22.1–35.1) when sea levels were much lower (Haq *et al.* 1987); the Sumatran clade diversified in the last 15 my in accordance with the uplift of the island; and Java was colonized 13.9 mya (11.0–17.3), soon after Java and Sumatra were established as islands (Hall 2002). This estimation suggests only slightly deeper dating than results inferred from all-mtDNA dataset when a slower *rrnl* mtDNA fragment was included. The all-data analysis calibrated by the origin of the Borneo clade inferred from the comprehensive phylogeny of Lycidae (Bocak *et al.* 2008) suggests the origin of *Scarelus* before the KT boundary, and a deeper position for all splits (Table S8).

The maximum likelihood tree pruned to one specimen per species was used as input for DIVA analysis, which identified Sundaland, minus Java, as the ancestral area for *Scarelus* and two dispersal events to Java and the Philippines (Fig. 3). The equally parsimonious solution included Java in the ancestral region of *Scarelus*.

Three chronograms were produced from (1) all five markers, (2) three mtDNA fragments, and (3) cds mtDNA genes using various calibration methods as described in the methods. Gamma statistics did not show a shift in diversification towards the base of any of the trees when considered as a whole. Further, we investigated the gamma values separately for the BPh and MSJ clades and found the early diversification of the BPh clade, although it was only marginally significant (Fig. 4 and Table S9). All three chronograms favored a logistic density-dependent model for the BPh clade and a pure birth model for the MSJ clade. A variable speciation rate was preferred for all considered chronograms (Table S9).

DISCUSSION

Relationships and distribution

Their long evolutionary history and extremely low dispersal ability makes neotenic beetles a promising source of information on ancient dispersal and vicariance events. Our data suggest that the *Scarelus* fauna originated after *in situ* diversification and rare dispersal events without migratory reversals (Fig. 2) and that the wide distribution of *Scarelus* in Sundaland was achieved early in its evolutionary history. We inferred the origin of the most recent common ancestor (mrca) of *Scarelus* to 42.6 mya in the subaerial Sunda Shelf (Cole & Crittenden 1997). Although dating without fossils is always prone to error, we consider our estimation based on cds mtDNA to be conservative and believe that all results confirm the antiquity of *Scarelus*. Both deep clades, occurring in Malaya, Sumatra, and Java (MSJ) and in Borneo and the Philippines (BPh), are mutually monophyletic (Fig. 2). The Bornean clade diversified earlier (Fig. 3), in agreement with the uninterrupted persistence of dry land in Borneo and formation of the Crocker Range during the Oligocene–Upper Miocene (Hall 2002). This region is regarded as a diversity hotspot for many plant and animal taxa (Davis *et al.* 1995; Brandon-Jones 1996; Quek *et al.* 2007), and its diversity may be a result of the uninterrupted persistence of the tropical rainforest there, not just during glacial periods (Tallis 1991; Cannon *et al.* 2009). The MSJ clade diversified much later. Sumatra was submerged 15–25 mya, and, in agreement with tectonic history, the origin of most lineages of Sumatran *Scarelus* was dated to the last 15 my (Fig. 3). The most basal split in the Sumatran clade predates the uplift of Sumatra to its present form, and supports the existence of an island chain in the region throughout the lower Miocene (Hall 2002).

We postulate that the cladogenesis of *Scarelus* was based mainly on range fragmentation and their rare expansion. The range of the ancestral species was fragmented following the separation of Borneo and Sumatra by rising sea levels (Haq *et al.* 1987). The MSJ and BPh clades as well as more recent clades (Figs. 1 and 2) have remained vicariant during several subsequent periods of low sea levels while other net winged beetles colonized whole region (Bocak & Yagi 2010). Separation by distance is supposed to be a primary cause of differentiation; however, dry lowland habitats may have played a role during the refugial phase in rainforests (e.g., Bird *et al.* 2005; Cannon *et al.* 2009). No data are available on the dispersal rate of neotenic lycids due to their rarity, but they may be compared with minute land snails for which a rate of 1–100 m/y has been proposed (Hausdorf & Hennig 2003). Both snails and small bodied, wingless beetles are limited by watercourses and dry habitats. Therefore, neotenic lycids might have missed dispersal opportunities explored by other lineages when isolation barriers temporarily ceased to exist.

Nevertheless, some range expansion was predicted, which is broadly consistent with the available geological data. Javanese species share a common ancestor with two other Sumatran species with a short pointed phallus (Figs. 2–3). These species split 13.9 mya (11.0–17.3), well after the clade of Sumatran *Scarelus* first diversified 33.0 mya (26.9–39.3). Although the inclusion of Java in the ancestral area (Fig. 2) is equally parsimonious, we prefer dispersal to vicariance as the lineage with a pointed phallus is known also in Malaya, and the Malay species may be a sister species of the Sumatra/Java clade as in the long-phallus clade. Additional material is needed for a more robust hypothesis. Java, as part of Sundaland, may have had some *Scarelus* before the dispersal of the species with a short pointed phallus, but only these relatively recent immigrants were present in our sampling and no species belonging to the lineage with a long phallus are known from Java (Bocak & Malohlava, in press). Therefore, either the older fauna went extinct or *Scarelus* colonized Java only once and quite recently.

Unambiguous dispersal from Borneo to the Philippines is inferred for the *crudus*/*salvani* clade (Fig. 2). Although some parts of the Philippines have a continental origin, these continental fragments were probably submerged for some time (Hall 1998) and did not bring neotenic lycids to the modern Philippines. The Philippine species split from its mrca *S. baranciki* 28.3 mya (22.1–35.1), well after the separation of Palawan and Mindoro from the continent. This date points to several tectonic and climatic events that may have enabled dispersal: a deep glacial maximum during the early Oligocene ~34–30 mya (Zachos *et al.* 2001), an Oligocene connection between proto-Luzon and Northern Borneo via the Sulu-Cagayan Arc (Hall 2002), and a concurrent global drop in sea level (Haq *et al.* 1987). Although a full subaerial connection between Borneo and the Philippines has never been explicitly proposed, a land bridge between Borneo and some parts of the modern Philippines is suggested by the life history of *Scarelus*. Assessing the origins of other neotenic net-winged beetles in the Philippines will test this hypothesis.

Scarelus are distributed in Palawan and may represent an independent dispersal event. Palawan was connected with Borneo by the subaerial Balabac Strait, but it likely remained isolated from Panay and Mindoro; therefore, it is an improbable stepping stone to the Philippines (Hall 1998). The island approached its present position close to Borneo about 10 mya, well after the inferred dispersal via the Sulu-Cagayan Arc (Hall 2002). Despite recent progress, our understanding of Philippine zoogeography remains poor. Jones and Kennedy (2008) reviewed recent contributions to the field; however, most cases referred to effective dispersers and more recent dispersal events. A phylogenetic approach and poor dispersers should be used to date these colonization events, which may reflect the much older Oligocene or Miocene colonization of the Philippines.

Speciation through allopatry

All net-winged beetles display a very conservative life history based on the unique modification of their larval mouthparts (Bocak & Matsuda 2003), and the adults are short-lived with low activity levels that are particularly pronounced in neotenic lineages (Bocak *et al.* 2008). Being short-lived and wingless, neotenic females must lay eggs close to the place where they mate, and larval dispersal and the search for new resources are limited by the mosaic structure of microhabitats, watercourses, and mountain ridges to small ecologically homogenous ranges. The phylogeny of *Scarelus* shows that most speciation events were completed via allopatry, although often within small geographic areas (Fig. 1). The differentiation of *Scarelus* within small areas is demonstrated by recent speciation events in allopatry [*S. anthracinus* clade in the mountain range of central Malaya or *S. crudus* and *S. salvani* in central Mindanao; Malohlava & Bocak (in press)]. Similarly, although the Crocker Range houses eight species of *Scarelus* in an area of ~500 km^2, none two of them are recently diversified sister species (Fig. 1 and Table S3). The ranges of sister species are vicariant and there is no indication of sympatric speciation (Fig. 2). If several species occur sympatrically, they are distantly related or diverged long time ago (e.g., the only sympatrically occurring sister species in the Crocker Range diversified 29.5 mya). Additionally, we do not know any ecological adaptation that might support a sympatric mode of speciation. Based on the absence of effective barriers between ranges of sister species, we consider isolation by distance as the major factor in *Scarelus* diversification.

We found early diversification in the BPh clade and delayed diversification in the MSJ clade (Fig. 4A–C). We suggest that this difference is caused by extrinsic influences as neotenic characteristics and life history traits remained constant within *Scarelus* (Bocak & Matsuda 2003; Bocak *et al.* 2008). Sumatra was established in its present form much later than Borneo (Hall 2002), and only the formation of the Barisan range provided the long term persisting dry land needed for the diversification of *Scarelus* (see Supplementary Information for tectonic history of the region). The ability of neotenic lineages to diversify is evident in the early origin of *Scarelus* diversity in Borneo or Sumatra after their uplift (Figs. 2–3).

Scarelus is characterized by a uniform, supposedly plesiomorphic morphology that is suggestive of complete morphological stasis over 40 my. We observed a widespread lack of diversification both in external characters and male genitalia (Fig. 2). As morphological differences evolve readily as adaptations to different environments (Mayr 1963) or to reinforce reproductive isolation when closely related species are in contact (Lukhanov *et al.* 2005; Bocak & Yagi 2010), strict geographic isolation throughout speciation and small, stable ecologically uniform ranges are consistent with low morphological divergence.

The marked similarity of male genitalia among distantly related species is unusual in net-winged beetles, and lycid male genitalia vary widely in shape (Bocak 2000). In contrast, many *Scarelus* have similar genitalia despite their advanced genetic distance (Fig. 2 and Table S4). The deep divergence and similarity of the Bornean species suggest that such a situation may be conserved for tens of millions of years (Figs. 2–3). In *Scarelus*, speciation by allopatry and low dispersal ability prevented secondary contact between incompletely reproductively isolated species, and the often hypothesized role of male genitalia in reproductive isolation (Eberhard 1985) is highly improbable. Additionally, the unusual male antennae with a large surface area suggest their role in pheromone communication, which may contribute to effective reproductive isolation early in the speciation process. Under these scenarios, there is no opportunity for other mechanisms to contribute to definitive reproductive isolation. Sexual selection as an alternative explanation of the diversification of genitalia requires multiple mating events with different males before fertilization (Hosken & Stockley 2004). Two factors may reduce the effectiveness of all mechanisms based on female choice and intrasexual competition: the extremely low population density of *Scarelus* and the short life span of adult neotenic females (observed in *Duliticola* by Wong [1996]). These traits lower the chance of multiple mating events, which are a necessary precondition for effective sexual selection.

The presence of three clearly defined types of male genitalia (Fig. 2) indicates the involvement of some diversifying process in two instances. Both shifts to a different type of genitalia were abrupt and were followed by the conservation of shape. Incomplete sampling and the antiquity of the new genital shapes prevent us from testing for possible secondary contact between incompletely isolated lineages; however, both origins are inferred in areas where a greater number of species are present.

The speciation rate in neotenic lineages

The inferred phylogenies of neotenic lineages (Bocak *et al.* 2008 and this study) show their antiquity (Fig. 3) and confirm that a severely limited dispersal ability does not necessarily threaten lineage survival as was previously proposed (Crowson 1972; Miller 2001). Nevertheless, all neotenic lineages, including *Scarelus*, are species-poor and limited to small ranges (Bocak *et al.* 2008; Bocak & Brlik 2008; Kundrata & Bocak 2007). Deep environmental changes, such as sea level fluctuation or large-scale aridization, may have caused the extinction of lineages of poor dispersers, which cannot react by dispersal, especially when they are limited to small forest refugia like *Scarelus* (Fig. 1). The dependence of diversification on extrinsic influences is demonstrated by differences in the timing of diversification in the MSJ and BPh clades, and by the absence of diversification in Borneo in the last 20 my (Figs. 3 and 4) when they occupied a stable, continuous habitat. Another trait strongly affected by neoteny is genetic variability. The restricted range and small population characteristic of *Scarelus* mean low intraspecific genetic variability, which may negatively affect species plasticity and survival (Lloyd & Gould 1993; Dobrzhansky 1937). The obligatory female neoteny of *Scarelus* defines the life history of the lineage and has resulted in the strong dependence of *Scarelus* diversification, in terms of species origin and extinction, on extrinsic influences. Habitat fragmentation generates specific diversity among neotenics; however, it produces species with restricted ranges and small populations, which are sensitive to disturbances. The confinement of neotenics to stable and geographically limited habitats may be responsible for the observed low level of specific diversity.

Delimitation of biodiversity hotspots and conservation

Although biodiversity hotspots are often defined as large homogenous regions (Myers *et al.* 2000), a much finer distinction of places with long-term stable habitats is necessary for conservation management. Neotenics have small ranges that are limited to ancient tropical rainforests, which may facilitate the design of effective conservation strategies for the most valuable biodiversity hotspots.

The distribution of *Scarelus* is consistent with the refugia of ancient tropical rainforests identified by previous studies: northeastern Indochina (i.e., range of *Atelius*, a presumed sister lineage of *Scarelus*), northwestern Sumatra (nine *Scarelus* spp.), the mountains of the Malay Peninsula (four spp.), and northern Borneo (eight spp.) (Brandon-Jones 1996; Quek *et al.* 2007; Bird *et al.* 2005; Tallis 1991; Gathorne-Hardy *et al.* 2002). The occurrence of several *Scarelus* spp. in the Crocker Range and their limited diversity elsewhere suggests that the present diversity of the Bornean clade is a subset of the pre-Quaternary Bornean fauna. Forests along the large rivers of the Sunda shelf may have served as refugia for a few lowland species. The rainforest refugia have preserved at least part of the specific diversity, which may have evolved during periods of favorable climatic conditions supporting large humid forests (Cannon *et al.* 2009). Concerning the limitation of *Scarelus* diversity to small refugia, deforestation in Southeast Asia (Sodhi *et al.* 2004) has resulted in a definitive loss of diversity, and conservation should be a priority in these areas.

CONCLUSIONS

The ontogenetic program determines the mode of speciation and diversification rate in neotenic *Scarelus*. Our results support an allopatric mode of speciation operating within short distances, with rare range expansions and extremely limited morphological diversification. We postulate that morphological stasis is indicative of the completion of speciation by allopatry and ineffective sexual selection. Although neotenics speciate readily due to habitat fragmentation, speciation may be halted under stable homogenous conditions due to a low dispersal potential and small, genetically uniform populations. Neotenic lineages depend on extreme habitat stability; thus, changes in the extent and position of suitable habitats deeply threaten their existence. We found that modern distribution patterns define the position of rainforest refugia, and pre-Quaternary dispersal events can be inferred from the phylogeny of neotenics.

At present, these narrowly endemic taxa are endangered by disturbances in their habitats due to human activity. Animals with similarly restricted ranges and limited dispersal abilities, such as land snails, have been assigned global conservation status rankings of “vulnerable” or higher (IUCN 2010); however, neotenic lineages of elateroid beetles have been omitted from these lists due to our limited knowledge. The demonstrated congruence between the distribution of neotenics and ancient refugia of rainforests makes them valuable for biodiversity conservation management.

ACKNOWLEDGEMENTS

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Author Information Box

This study was completed as a part of Vladimír Malohlava's Ph D thesis on systematics of *Scarelus* and diversification processes in neotenic net-winged beetles. Ladislav Bocák leads the Laboratory of Molecular Phylogenetics at the Palacky University of Olomouc and has research interests in the phylogeny of beetles and understanding of the evolutionary processes that affect net-winged beetle diversity and evolution of mimicry.

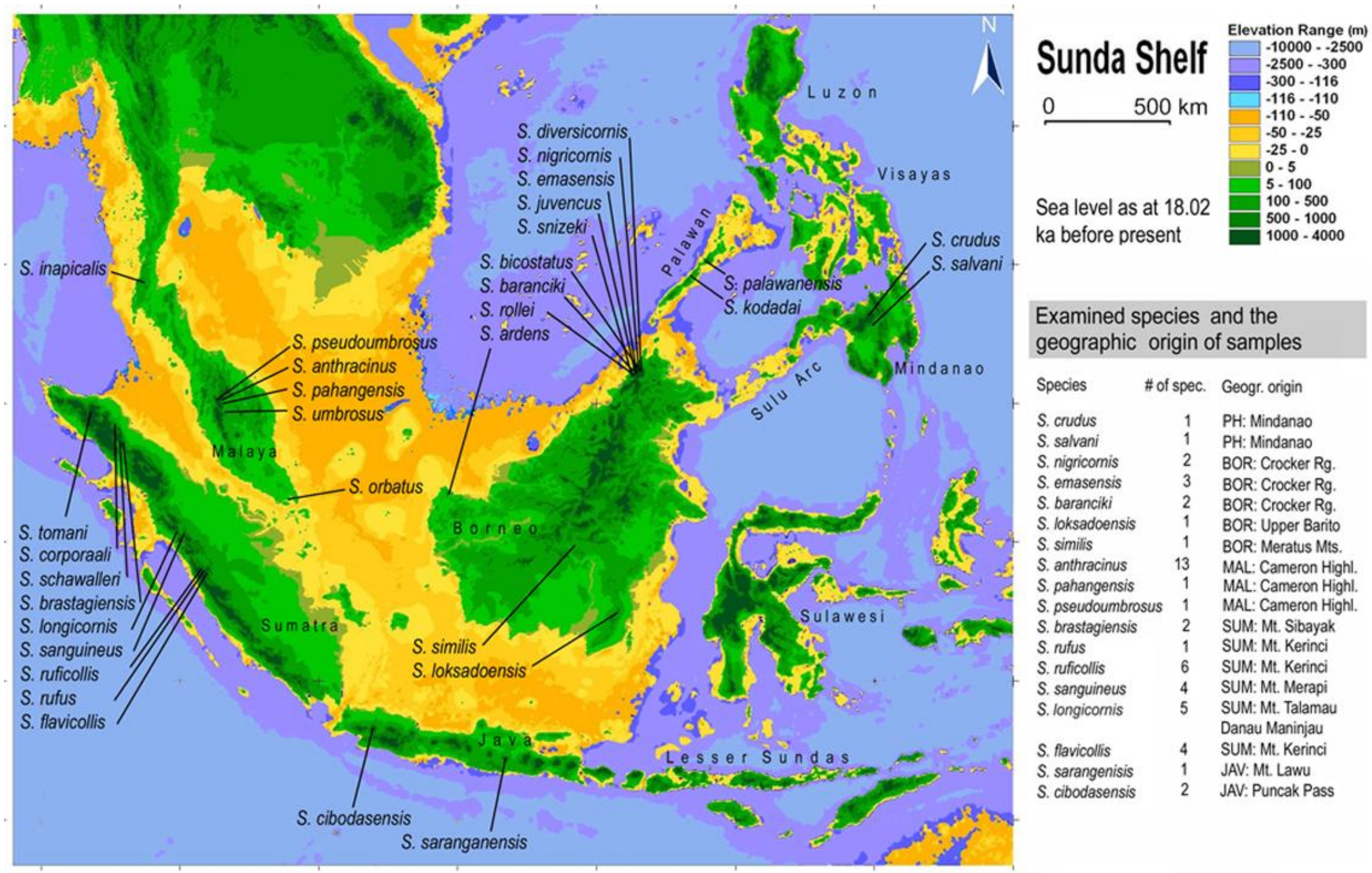
Fig 1. Extension of the continental shelf in the Pleistocene, the distribution of *Scarelus,* and the list of examined species. (The map of the Sunda Shelf the was derived from Sathiamurthy and Voris 2006, © 2006 Field Museum of Natural History, Chicago, Illinois USA).

Fig. 2. Phylogenetic hypothesis for *Scarelus* based on a parsimony analysis of all available fragments (18S and 28S rDNA, *cox1*, *nad5* and *rrnl* mtDNA. Numbers at the branches are parsimony, bayesian, and likelihood frequencies (ingroup taxa only). The colours of branches indicate geographic origins and ancestral areas inferred from the DIVA analysis (areas are coded under branches, the distribution of *Atelius* in continental Asia was coded as the outgroup in the DIVA analysis). Male genitalia are illustrated for individual species groups (original illustrations by the authors).

Fig. 3. Timing of the *Scarelus* radiation in the Sundaland. Estimated mean ages of nodes are based on bayesian analysis of cds mtDNA fragments under the relaxed molecular clock model and the universal mitochondrial mutation rate proposed by Brower (1994). The bars and limits depict 95% confidence intervals.

Fig. 4. Logarithmic plots of the number of lineages through time for (1) all *Scarelus* in the Sundaland and the Philippines (2) *Scarelus* in Borneo and the Philippines, and (3) *Scarelus* in the Malay Peninsula, Sumatra and Java. The insertions depict the corresponding chronograms.

Fig. 1



Examined species and the geographic origin of samples

Species	# of spec.	Geogr. origin
S. crudus	1	PH: Mindanao
S. salvani	1	PH: Mindanao
S. nigricornis	2	BOR: Crocker Rg.
S. emasensis	3	BOR: Crocker Rg.
S. baranciki	2	BOR: Crocker Rg.
S. loksadoensis	1	BOR: Upper Barito
S. similis	1	BOR: Meratus Mts.
S. anthracinus	13	MAL: Cameron Highl.
S. pahangensis	1	MAL: Cameron Highl.
S. pseudoumbrosus	1	MAL: Cameron Highl.
S. brastagiensis	2	SUM: Mt. Sibayak
S. rufus	1	SUM: Mt. Kerinci
S. ruficollis	6	SUM: Mt. Kerinci
S. sanguineus	4	SUM: Mt. Merapi
S. longicornis	5	SUM: Mt. Talamau Danau Maninjau
S. flavicollis	4	SUM: Mt. Kerinci
S. sarangenisis	1	JAV: Mt. Lawu
S. cibodasensis	2	JAV: Puncak Pass

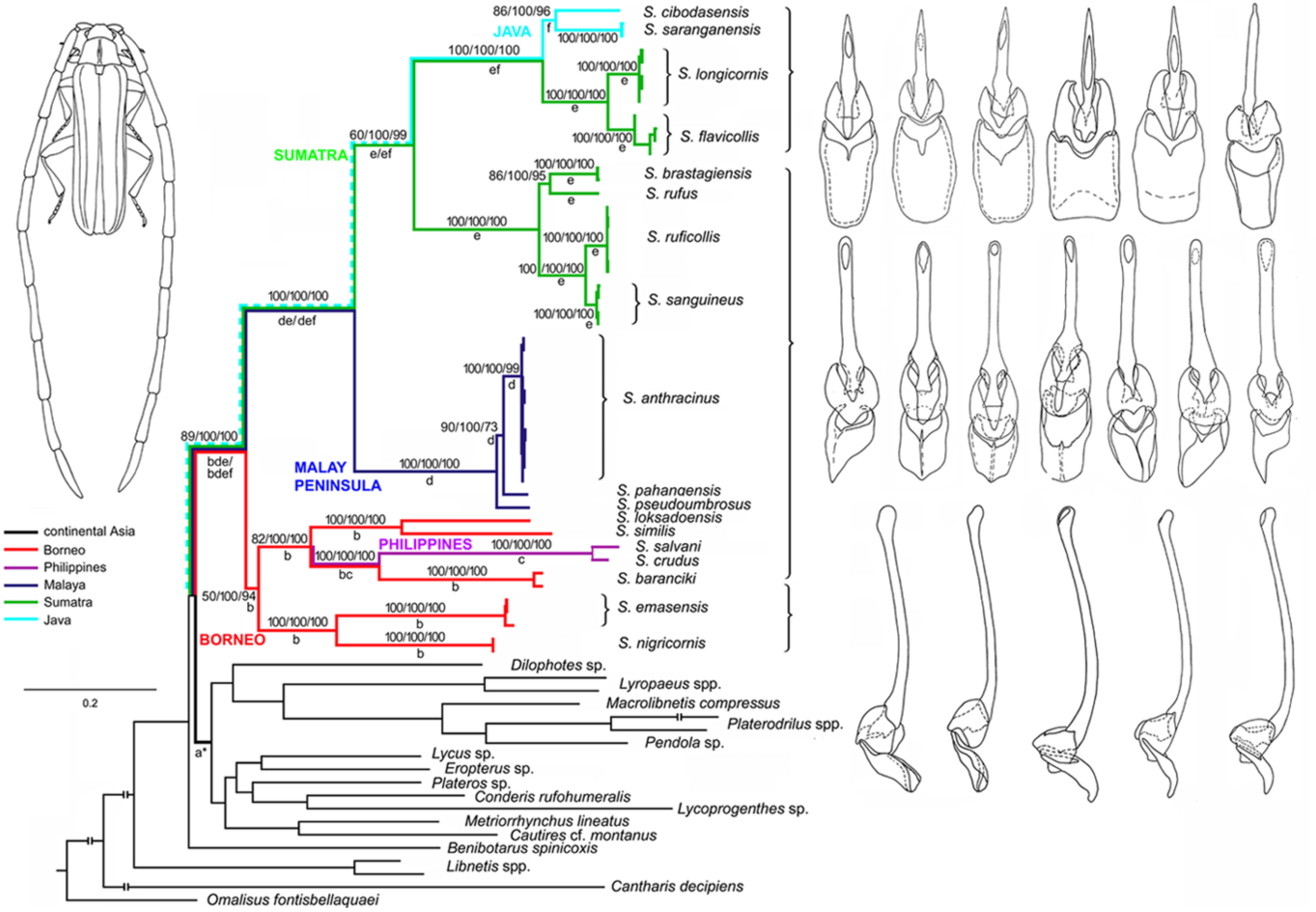
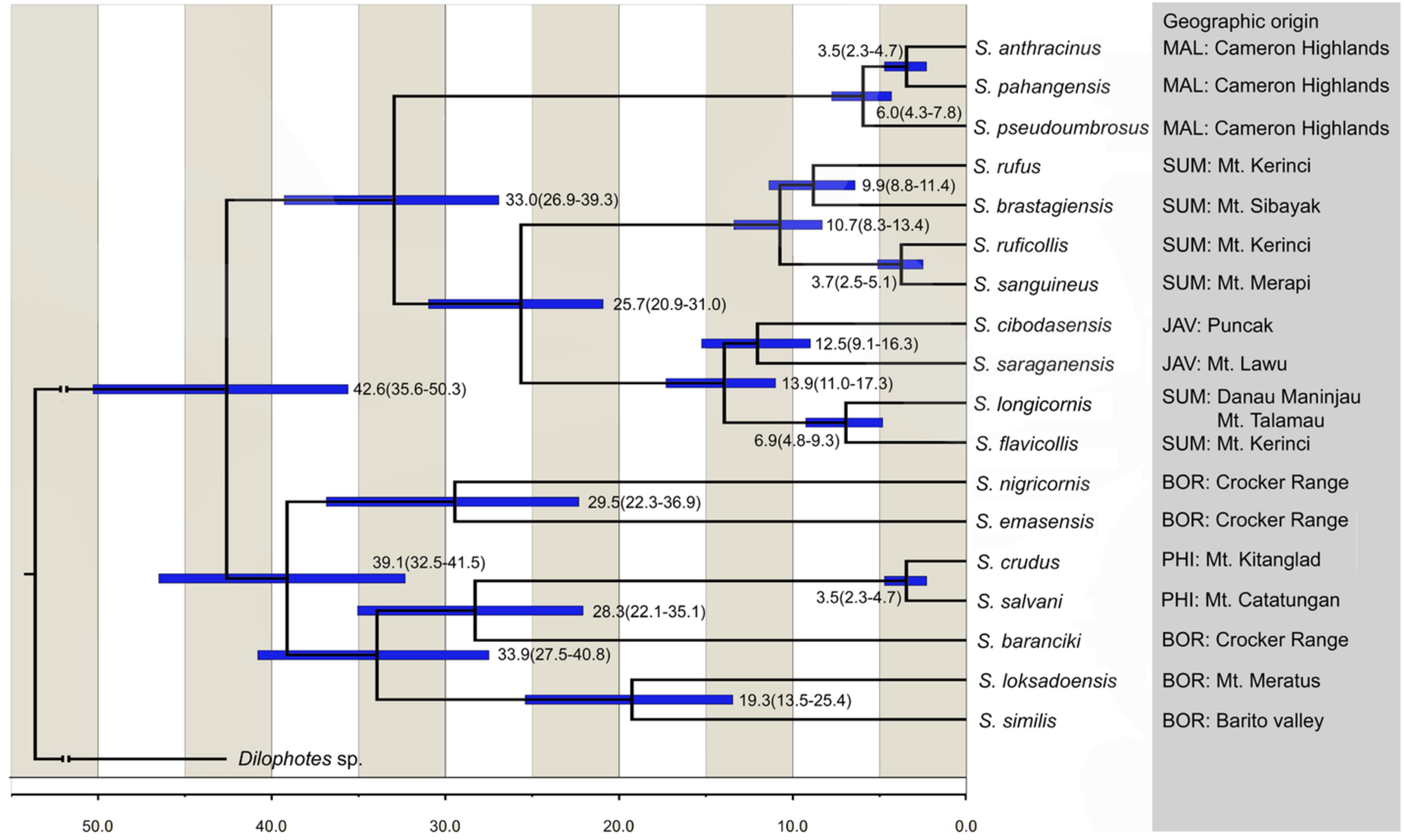

86/100/96
JAVA
f
S. cibodasensis
S. saranganensis
100/100/100
100/100/100
ef
100/100/100
e
S. longicornis
100/100/100
e
60/100/99
e/ef
100/100/100
e
S. flavicollis
SUMATRA
100/100/100
86/100/95
e
e
S. brastagiensis
S. rufus
100/100/100
e
100/100/100
e
S. ruficollis
100/100/100
e
100/100/100
de/def
S. sanguineus
100/100/100
e
100/100/99
d
S. anthracinus
90/100/73
d
89/100/100
bde/
bdef
MALAY
PENINSULA
100/100/100
d
S. pahangensis
S. pseudoumbrosus
S. loksadoensis
S. similis
100/100/100
b
82/100/100
b
100/100/100
bc
PHILIPPINES
100/100/100
c
S. salvani
S. crudus
100/100/100
b
S. baranciki
50/100/94
b
100/100/100
b
S. emasensis
100/100/100
b
BORNEO
b
100/100/100
b
S. nigricornis
Dilophotes sp.
Lyropaeus spp.
Macrolibnetis compressus
Platerodrilus spp.
Pendola sp.
a*
Lycus sp.
Eropterus sp.
Plateros sp.
Conderis rufohumeralis
Lycoprogenthes sp.
Metriorrhynchus lineatus
Cautires cf. montanus
Benibotarus spinicoxis
Libnetis spp.
Cantharis decipiens
Omalisus fontisbellaquaei
continental Asia
Borneo
Philippines
Malaya
Sumatra
Java
0.2

Fig. 2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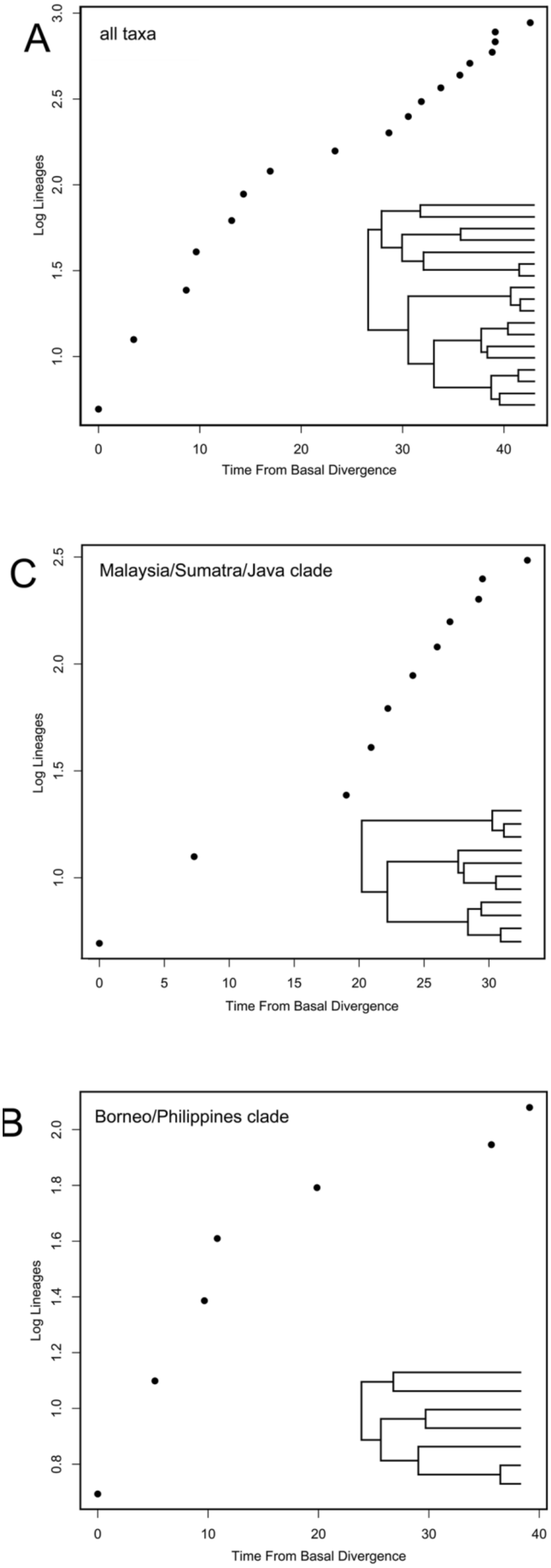
6.0(4.3-7.8)
9.9(8.8-11.4)
10.7(8.3-13.4)
3.7(2.5-5.1)
33.0(26.9-39.3)
25.7(20.9-31.0)
12.5(9.1-16.3)
13.9(11.0-17.3)
6.9(4.8-9.3)
42.6(35.6-50.3)
29.5(22.3-36.9)
39.1(32.5-41.5)
3.5(2.3-4.7)
28.3(22.1-35.1)
33.9(27.5-40.8)
19.3(13.5-25.4)
Dilophotes sp.
S. anthracinus
S. pahangensis
S. pseudoumbrosus
S. rufus
S. brastagiensis
S. ruficollis
S. sanguineus
S. cibodasensis
S. saraganensis
S. longicornis
S. flavicollis
S. nigricornis
S. emasensis
S. crudus
S. salvani
S. baranciki
S. loksadoensis
S. similis
Geographic origin
MAL: Cameron Highlands
MAL: Cameron Highlands
MAL: Cameron Highlands
SUM: Mt. Kerinci
SUM: Mt. Sibayak
SUM: Mt. Kerinci
SUM: Mt. Merapi
JAV: Puncak
JAV: Mt. Lawu
SUM: Danau Maninjau
Mt. Talamau
SUM: Mt. Kerinci
BOR: Crocker Range
BOR: Crocker Range
PHI: Mt. Kitanglad
PHI: Mt. Catatungan
BOR: Crocker Range
BOR: Mt. Meratus
BOR: Barito valley
50.0
40.0
30.0
20.0
10.0
0.0

Fig. 4


A
all taxa
Log Lineages
3.0
2.5
2.0
1.5
1.0
0
10
20
30
40
Time From Basal Divergence
C
Malaysia/Sumatra/Java clade
Log Lineages
2.5
2.0
1.5
1.0
0
5
10
15
20
25
30
Time From Basal Divergence
B
Borneo/Philippines clade
Log Lineages
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0
10
20
30
40
Time From Basal Divergence

The list of Supplementary Information

Tectonic and climatic history of Southeast Asia

The Malay Peninsula, Java, Sumatra, and Borneo are parts of the Sunda Shelf, which was land positive for significant periods during the past 50 million years (Hall 2002). The now submerged terrains of the shelf were exposed as dry land already in the Palaeocene and as recently as the Pleistocene glacial maxima (Hall 1998, Voris 2000), thus providing opportunities for dispersal between present islands (Bird *et al.* 2005; Heaney 1985). The northern part of Borneo was uplifted until the end of Eocene (Sarawak Orogeny) and the Crocker Range in the mid to late Miocene (Sabah Orogeny, Hutchinson *et al.* 2000). Subaerial Java and Sumatra existed as a part of the Sunda Shelf from the early Eocene (~50 Mya) to the late Oligocene (~25 Mya), after which both islands were submerged until the middle Miocene (~15 Mya) (Hall 1998). The Philippine Archipelago, located east of the Sunda Shelf, has a complex tectonic history. Some parts are of continental origin (Mindoro, Palawan, and the Zamboanga Peninsula) and there is a prevailing opinion that these continental fragments were submerged before they were accreted to the Philippines (Hall 1998, 2002), although previously they were considered to be subaerial during the drift (Mitchell *et al.* 1986, de Jong 1996). The other Philippine islands have been converging toward their present position from the south over the last ~35 my and they never had any contact with the Asian tectonic plate (Hall 2002). It is supposed that the Philippine fauna is thus derived from over-water colonization (Heaney 1985; Evans *et al.* 2003, but see Brown & Guttman 2002). The subduction of the proto-South China Sea margin 45 mya initiated the creation of the Sulu Arc extending from Sabah to the proto-Philippines (Hall, 2002), but the complete dry land connection between Borneo and any part of the Philippines through the Sulu Arc has never been hypothesized. The Palawan approached its present position ~10 mya and has been connected to Borneo by a land-positive aerial exposure during Pliocene and Pleistocene sea-level retreats (Hall 1998; Heaney 1985).

The extent of Pleistocene and older rain forest in the Sunda region may affect survival and speciation history of *Scarelus*. Some studies demonstrate a predominance of savanna vegetation in most of Sundaland during cold and dry periods (Morley, 1998), whereas others indicate that tropical rain forest was widely preserved and the lower mountain forests were less fragmented and more widely distributed (Cannon 2009). The riverine systems probably supported gallery forests, which may have provided refuge for rain forest fauna in dry regions (Sun *et al.*, 2000).

Supplementary Table 1. The list of examined specimens.

		Fragments					
Species	**Geographic origin**	**16S**	**18S**	**28S**	**COI**	**ND5**	**Voucher #**
S. brastagiensis	Sumatra, Utara, Brastagi, Gn. Sibayak	HM451006	HM451131	HM451088	HM451047	HM451217	VM012
	Sumatra, Utara, Brastagi, Gn. Sibayak	HM451007	HM451132	HM451089	HM451048	HM451218	VM013
S. flavicolis	Sumatra, Jambi, Kersik Tua. Gn. Kerinci	HM451020	HM451148	HM451103	HM451060	HM451231	VM030
	Sumatra, Jambi, Kersik Tua. Gn. Kerinci	HM451021	HM451149	HM451104	HM451061	HM451232	VM031
	Sumatra, Jambi, Kersik Tua. Gn. Kerinci	HM451022	HM451150	HM451105	HM451062	HM451233	VM032
	Sumatra, Jambi, Kersik Tua. Gn. Kerinci	HM451025	HM451155	HM451110	-	HM451238	VM037
S. longicornis	Sumatra, Gn. Talamau	HM451010	HM451135	HM451091	-	HM451220	VM017
	Sumatra, Barat Lake, Maninjau	HM451011	HM451136	HM451092	-	HM451221	VM018
	Sumatra, Barat Lake, Maninjau	HM451017	HM451143	HM451098	-	HM451226	VM025
	Sumatra, Barat Lake, Maninjau	HM451018	HM451144	HM451099	HM451057	HM451227	VM026
	Sumatra, Barat Lake, Maninjau	HM451019	HM451145	HM451100	-	HM451228	VM027
S. rufus	Sumatra, Jambi, Kersik Tua, Gn. Kerinci	HM451024	HM451152	HM451107	HM451064	HM451235	VM034
S. ruficollis	Sumatra, Jambi Prov, Kerinci Seblat N.P.	-	HM451127	HM451085	HM451078	HM451213	VM008
	Sumatra, Jambi, Kersik Tua, Gn. Kerinci	-	HM451147	HM451102	HM451059	HM451230	VM029
	Sumatra, Jambi, Kersik Tua, Gn. Kerinci	HM451023	HM451151	HM451106	HM451063	HM451234	VM033
	Sumatra, Jambi, Kersik Tua, Gn. Kerinci	-	HM451153	HM451108	HM451065	HM451236	VM035
	Sumatra, Jambi, Kersik Tua, Gn. Kerinci	-	HM451154	HM451109	HM451066	HM451237	VM036
S. sanguineus	Sumatra, Gn. Merapi, 5 km of Kotobaru	-	HM451122	HM451080	HM451039	HM451208	VM003
	Sumatra, Gn. Merapi, 5 km of Kotobaru	-	HM451128	HM451086	HM451044	HM451214	VM009
	Sumatra, Barat, 10 km of Bukittinggi	HM451016	HM451141	HM451096	HM451055	HM451224	VM023
	Sumatra, Sumatra, Barat, Bukittinggi	-	HM451142	HM451097	HM451056	HM451225	VM024
S. anthracinus	Malaysia, Pahang, Cameron Highl.	HM450998	HM451120	-	HM451037	HM451206	VM001
	Malaysia, Pahang, Cameron Highl.	HM451002	HM451125	HM451083	HM451042	HM451211	VM006
	Malaysia, Pahang, Cameron Highl.	HM451009	HM451134	HM451090	HM451050	HM451219	VM016
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451026	HM451156	HM451111	HM451067	HM451239	VM038
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451027	HM451157	-	HM451068	HM451240	VM039
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451028	HM451158	HM451112	HM451069	HM451241	VM040
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451029	HM451159	HM451113	HM451070	HM451242	VM043
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451030	HM451160	HM451114	HM451071	HM451243	VM044
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451031	HM451161	HM451115	HM451072	HM451244	VM045
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451032	HM451162	HM451116	HM451073	HM451245	VM046
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451033	HM451163	HM451117	HM451074	HM451246	VM047
	Malaysia, Pahang, Tanah Rata, Gn. Jasar	HM451034	HM451164	-	HM451075	HM451247	VM048

S. pahangensis	Malaysia, Kampong Kuala Boh	HM451000	HM451123	HM451081	HM451040	HM451209	VM004
S. pseudoumbrosus	Malaysia, W Pahang, Road Ipoh, Kg. Raja	HM450999	HM451121	HM451079	HM451038	HM451207	VM002
S. saranganensis	Java, C, Gn. Lawu, 8 km W of Sarangan	HM451005	HM451130	HM451087	HM451046	HM451216	VM011
	Java, C, Gn. Lawu, 8 km W of Sarangan	HM451004	HM451129	-	HM451045	HM451215	VM010
S. cibodasensis	Java, W, Puncak Pass	HM451003	HM451126	HM451084	HM451043	HM451212	VM007
S. crudus	Philippines, Mindanao, Bagongsilang	HM451035	HM451165	HM451118	HM451076	HM451248	VM049
S. salvani	Philippines, Mindanao, Mt. Kitanglad	HM451036	HM451166	HM451119	HM451077	HM451249	VM050
S. similis	Borneo,C Kalimantan Prov, Muara Teveh	HM451001	HM451124	HM451082	HM451041	HM451210	VM005
S. loksadoensis	Borneo,S Kalimantan Prov, Loksado	HM451008	HM451133	-	HM451049	-	VM014
S. baranciki	Borneo, Sabah, Road KK-Tambunan	HM451012	HM451137	HM451093	HM451051	-	VM019
S. emasensis	Borneo, Sabah	HM451013	HM451138	HM451094	HM451052	-	VM020
	Borneo, Sabah	HM451015	HM451140	-	HM451054	HM451223	VM022
S. nigricornis	Borneo, Sabah	HM451014	HM451139	HM451095	HM451053	HM451222	VM021

Voucher specimens are deposited at L. B. molecular systematics laboratory of the Zoology Department, Palacky University, Olomouc. The full Genbank Voucher Numbers consist of 'UPOL'+ a code given here.

Supplementary Table 2. Primers and conditions used for PCR amplifications

Fragment	Code	-mer	Sequence (5’ >> 3’)	PCR thermocycler program	
				Annealing temperature	Taq polymerase
18S rRNA	5’	24	GACAACCTGGTTGATCCTGCCAGT	all primer pairs 48°C	Bioline 0.6 U
	b5.0	19	TAACCGCAACAACTTTAAT		
	ai	22	CCTGAGAAACGGCTACCACATC		
	b2.5	20	TCTTTGGCAAATGCTTTCGC		
	a1.0	20	GGTGAAATTCTTGGACCGTC		
	bi	20	GAGTCTCGTTCGTTATCGGA		
	3’I	24	CACCTACGGAAACCTTGTTACGAC		
	a2.0	19	ATGGTTGCAAAGCTGAAAC		
28S rRNA	ff	20	TTACACACTCCTTAGCGGAT	52 °C	Bioline 0.6 U
	dd	19	GGGACCCGTCTTGAAACAC		
16S rDNA	16a	20	CGCCTGTTTAACAAAAACAT	all primer pairs 48 °C	Bioline 0.6 U
	16b	22	CCGGTCTGAACTCAGATCATGT		
	ND1A	27	GGTCCCTTACGAATTTGAATATATCCT		
cox1 mtDNA	JerM	23	CAACAYYTATTTTGRTTYTTTGG	all primer pairs 45 °C	Invitrogen Platinum 0.5 U
	Pat	25	TCCATTGCACTAATCTGCCATATTA		
	Marilyn	21	TCATAAGTTCAGTATCATTG		
	Marcy	27	TARTTCRTATGWTCAATAYCAYTGRTG		
nad5 mtDNA	OF1	29	CCTACTCCTGTTTCTGCTTTAGTTCATTC	45 °C	Invitrogen Platinum 0.5 U
	R6	29	GAAACGAAAAATCGTATTTAATTTCGACT		

Supplementary Table 3. Distances among sampled localities (km)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	SUM:Sibayak	0														
2	SUM:Kerinci	634	0													
3	SUM:Talamau	390	249	0												
4	SUM:Maninjau	440	202	50	0											
5	SUM:Merapi	455	180	71	26	0										
6	MAL:Cameron H	347	683	514	546	557	0									
7	MAL:Kg. Raja	346	695	523	556	546	13	0								
8	MAL:Kg. Kuala Boh	357	679	514	545	544	16	26	0							
9	JAV:Sarangan	1854	1270	1508	1460	1436	1728	1741	1716	0						
10	JAV:Puncak	1448	831	1079	1028	1007	1385	1398	1374	476	0					
11	PHI:Bagongsilang	2964	2814	2895	2880	2859	2627	2630	2614	2295	2576	0				
12	PHI:Kitanglad	2970	2827	2903	2891	2869	2634	2635	2616	2312	2559	20	0			
13	BOR:Muara Teweh	1882	1506	1667	1634	1609	1620	1630	1606	850	1086	1477	1492	0		
14	BOR:Loksado	2007	1576	1757	1722	1696	1768	1752	1777	718	1038	1577	1595	217	0	
15	BOR:Crocker	1997	1856	1924	1912	1892	1664	1669	1651	1596	1730	971	979	765	958	0

Supplementary Table 4. Uncorrected ("p") distance matrix among ingroup taxa

mtDNA fragments

	Vouch.#[1]	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	000L15	S. nigricornis	-																	
2	VM0019	S. baranciki	0.21908	-																
3	000583	S. emasensis	0.21417	0.23494	-															
4	VM0005	S. similis	0.24094	0.22095	0.25276	-														
5	VM0014	S. loksadoensis	0.18811	0.17382	0.20269	0.13789	-													
6	VM0049	S. crudus	0.24146	0.20696	0.25594	0.25271	0.21104	-												
7	VM0050	S. salvani	0.25006	0.21788	0.26577	0.25372	0.21357	0.05661	-											
8	VM0002	S. pseudoumbrosus	0.23734	0.22853	0.24461	0.23268	0.17469	0.25589	0.26197	-										
9	VM0004	S. pahangensis	0.24106	0.23005	0.24847	0.24224	0.18522	0.26225	0.27050	0.07527	-									
10	VM0047	S. anthracinus	0.24001	0.22792	0.24808	0.23641	0.17677	0.26365	0.26900	0.06583	0.05563	-								
11	VM0013	S. brastagiensis	0.24711	0.23698	0.26573	0.25140	0.20663	0.26107	0.27359	0.20891	0.21446	0.20931	-							
12	VM0023	S. sanguineus	0.24666	0.23590	0.26438	0.25782	0.20652	0.26081	0.27203	0.20881	0.21238	0.20750	0.11511	-						
13	VM0026	S. longicornis	0.25143	0.22336	0.25991	0.25099	0.21327	0.25977	0.26369	0.20291	0.20518	0.20156	0.20709	0.20024	-					
14	VM0032	S. flavicollis	0.25882	0.22995	0.26218	0.24801	0.20882	0.26342	0.27060	0.20012	0.21038	0.20404	0.20863	0.20040	0.07931	-				
15	VM0033	S. ruficollis	0.25196	0.23955	0.26254	0.25981	0.20759	0.26682	0.27718	0.21130	0.21549	0.21028	0.12262	0.05304	0.20972	0.20942	-			
16	VM0034	S. rufus	0.24630	0.23340	0.26723	0.25454	0.21406	0.26220	0.27609	0.20779	0.21227	0.20775	0.10394	0.11514	0.19625	0.20587	0.12562	-		
17	VM0011	S. saranganensis	0.24892	0.22628	0.26461	0.25505	0.20710	0.26170	0.26646	0.20497	0.20801	0.20500	0.20623	0.19720	0.12707	0.12666	0.19805	0.19927	-	
18	VM0007	S. cibodasensis	0.24945	0.23336	0.26502	0.25705	0.21243	0.26374	0.27220	0.21373	0.20942	0.21002	0.20452	0.20491	0.13006	0.12939	0.20499	0.20718	0.12737	-

18S and 28S rDNA fragments

	Vouch.#[1]	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	000L15	S. nigricornis	-																	
2	VM0019	S. baranciki	0.00967	-																
3	000583	S. emasensis	0.00363	0.01048	-															
4	VM0005	S. similis	0.00725	0.00846	0.00846	-														
5	VM0014	S. loksadoensis	0.00748	0.00847	0.00967	0.00955	-													
6	VM0049	S. crudus	0.00968	0.00927	0.01129	0.00928	0.01284	-												
7	VM0050	S. salvani	0.00886	0.00846	0.01048	0.00886	0.01284	0.00081	-											
8	VM0002	S. pseudoumbrosus	0.01210	0.01331	0.01210	0.01170	0.00747	0.01370	0.01371	-										
9	VM0004	S. pahangensis	0.01089	0.01290	0.01129	0.01049	0.00691	0.01330	0.01330	0.00121	-									
10	VM0047	S. anthracinus	0.01210	0.01331	0.01210	0.01170	0.00745	0.01330	0.01330	0.00081	0.00201	-								
11	VM0013	S. brastagiensis	0.00726	0.01129	0.00887	0.00928	0.01064	0.01007	0.01008	0.00927	0.00806	0.00927	-							
12	VM0023	S. sanguineus	0.00559	0.00772	0.00690	0.00689	0.00751	0.00991	0.00991	0.00472	0.00343	0.00471	0.00344	-						
13	VM0026	S. longicornis	0.01087	0.01249	0.01128	0.01169	0.00962	0.01169	0.01208	0.00645	0.00685	0.00645	0.00685	0.00474	-					
14	VM0032	S. flavicollis	0.01087	0.01249	0.01128	0.01169	0.00962	0.01169	0.01208	0.00645	0.00685	0.00645	0.00685	0.00474	0.00000	-				
15	VM0033	S. ruficollis	0.00806	0.00968	0.00887	0.00847	0.00904	0.01007	0.01008	0.00806	0.00685	0.00806	0.00322	0.00172	0.00645	0.00645	-			
16	VM0034	S. rufus	0.00588	0.00755	0.00717	0.00716	0.00910	0.00969	0.00969	0.00631	0.00505	0.00630	0.00211	0.00130	0.00424	0.00424	0.00043	-		
17	VM0011	S. saranganensis	0.00928	0.01049	0.01009	0.01048	0.00961	0.01088	0.01089	0.00846	0.00806	0.00846	0.00645	0.00344	0.00403	0.00403	0.00645	0.00421	-	
18	VM0007	S. cibodasensis	0.01008	0.01169	0.01089	0.01169	0.01065	0.01088	0.01128	0.00806	0.00846	0.00806	0.00564	0.00428	0.00363	0.00363	0.00564	0.00379	0.00161	-

[1] The full Genbank Voucher Numbers consist of 'UPOL'+ a code given here

Supplementary Table 5. The models of nucleotide substitution as proposed by AICc criterion in JModelTest 0.1.1 (Posada 2008)

Data sets Taxa sets + outgroup	rDNA and mtDNA	all mtDNA	cds mtDNA
all taxa +*Dilophotes*	GTR+I+G	GTR+I+G	GTR+I+G
Bornean clade + *S. anthracinus*	GTR+G	GTR+G	GTR+I+G
Malaya/Sumatra/Java clade + *S. nigricornis*	GTR+I+G	HKY+G	HKY+I+G

Supplementary Table 6. Likelihood ratio test of molecular clock for *Scarelus*.

	ln L1	ln Lo	d.f.	2logL=2 (lnLo-LnL1)	p-value	critical p0.05-value	strict clock
CDS matrices							
all taxa	19351.38	19375.74	17	48.72	0.00007	27.59	rejected
BorPhil	10665.59	10681.79	6	32.40	0.00001	12.59	rejected
MalSumJava	12191.88	12201.70	10	19.64	0.0328	18.31	rejected
all mtDNA matrices							
all taxa	26208.36	26237.81	17	58.90	0.0000	27.59	rejected
BorPhil	14843.65	14865.68	6	44.06	0.0000	12.59	rejected
MalSumJava	16614.53	16630.65	10	32.24	0.0004	18.31	rejected
allDNA matrices							
all taxa	32208.98	32244.34	17	70.72	0.0000	27.59	rejected
BorPhil	20024.23	20050.83	6	53.20	0.0000	12.59	rejected
MalSumJava	21738.82	21751.97	10	26.30	0.0034	18.31	rejected

Supplementary Table 7. Phylogeny of *Scarelus* inferred from partial and concatenated matrices: the presence of the selected clades in majority consensus trees produced by the parsimony analysis

Datasets	All data	nuclear rDNA 18S and 28S	all rDNA	all mtDNAs	mt *rrnl* & tRNAs	cds mtDNA
# of specimens	69	64	69	69	59	69
# of characters	5704	2513	3453	3191	938	2253
parsimony informative missing/5th char.	2020/2112	218/243	647/724	1802/1865	426/460	1350/1363
Clade						
	miss/5th	miss/5th	miss/5th	miss/5th	miss/5th	miss/5th
Scarelus	M/M	P/-	M/M	M/M	M/M	M/M
Borneo & Philippines	M/M	P/-	M/M	M/P	M/M	M/M
baranciki(crudus&salvani)	M/M	M/M	M/M	M/M	M/M	M/M
crudus&*salvani*	M/M	M/M	M/M	M/M	M/M	M/M
emasensis&*nigricornis*	M/M	M/M	M/M	M/M	M/M	M/M
Malaysia & Sumatra&Java	M/M	P/M	M/M	M/M	M/M	M/M
Malaysia	M/M	M/M	M/M	M/M	M/M	M/M
Sumatra & Java	M/M	P/P	M/M	M/M	M/M	M/M
Sumatra: long phallus	M/M	M/M	M/M	M/M	M/M	M/M
Sum&Java: short phallus	M/M	M/M	M/M	M/M	M/M	M/M
Java: *cibodas*&*sarangan*	M/M	M/M	M/M	M/M	M/M	M/M

(to be continued)

Supplementary Table 7. Phylogeny of *Scarelus* inferred from partial and concatenated matrices: the presence of the selected clades in majority consensus trees produced by the parsimony analysis (continued)

Datasets	*rrnl*	*cox1*	*nad5*
# of specimens	61	64	66
# of characters	621	1105	1255
parsimony informative	285/289	581/582	852/882
Clade			
	miss/5th	miss/5th	miss/5th
Scarelus	M/M	M/M	M/M
Borneo & Philippines	M/M	M/M	P/P
(*sim.&loks*.)(*bar*(*crud&salv*))	M/M	P/P	M/M
baranciki(*crudus*&*salvani*)	M/M	P/P	M/M
crudus&*salvani*	M/M	M/M	M/M
emasensis&*nigricornis*	M/M	M/M	M/M
Malaysia&Sumatra&Java	M/M	M/M	M/M
Malaysia	M/M	M/M	M/M
Sumatra & Java	M/M	M/M	M/M
Sumatra: long phallus	M/M	P/P	M/M
Sum&Java: short phallus	M/M	M/M	M/M
Java: *cibodas*&*sarangan*	M/M	M/M	M/M

Supplementary Table 8. Mean age of 95% HPD interval for internal nodes of *Scarelus* phylogeny in my

Analysis	complete nucl. rDNA and mtDNA		complete mtDNA**		cds_mtDNA**	
	mean age	95% HPD intervals	mean age	95% HPD intervals	mean age	95% HPD intervals
Node						
Scarelus_all	73.0	65.0-81.1	34.9	25.5-43.8	48.2	41.5-55.3
BorneoPhilipp	67.3*		32.1	23.1-40.4	42.0	37.3-51.0
Paratelius	49.5	40.0-58.8	23.4	15.9-31.4	33.1	25.9-40.7
SimLoksBarCruSal	58.7	51.5-65.9	27.8	19.7-35.3	38.2	31.9-44.9
SimLoks	33.0	24.3-42.1	14.6	9.3-20.0	21.7	15.3-28.1
BarCruSalv	47.2	39.0-55.6	22.0	15.0-28.9	31.8	25.5-38.7
CruSalv	7.2	4.7-10.0	2.9	1.7-4.1	3.9	2.7-5.3
MalSumJava	54.8	46.2-63.7	26.0	18.8-33.1	37.1	31.3-43.3
Mal	10.8	7.6-14.3	4.7	3.0-6.6	6.7	4.8-8.7
PahangAnthr	7.1	4.6-9.7	3.2	1.9-4.6	3.9	2.6-5.2
SumJava	44.6	36.7-52.6	20.6	14.8-26.4	28.9	24.0-33.9
SumLongPhal	20.1	15.5-25.1	8.7	5.9-11.4	12.1	9.5-14.9
RufusBrastag	15.3	11.0-19.6	6.5	4.2-8.9	9.9	7.3-12.6
SanguiRuficoll	7.1	4.6-9.8	2.9	1.8-4.3	4.2	2.8-5.8
SumJavaShortPhal	23.3	18.0-28.9	10.5	7.2-13.6	15.7	12.6-19.0
CibodSarang	18.2	13.1-23.3	8.4	5.5-11.3	14.1	10.4-18.1
FlavicollLongicoll	12.4	8.4-19.6	5.5	3.5-7.7	7.9	5.5-10.3

* Prior value set according to the estimation published by Bocak et al. 2008

** Fixed mean rate 2.3%/my proposed as general mutation rate for insects by Brower, 1994, applied in Lycidae by Bocak and Yagi, 2010

Supplementary Table 9. Results of the CR and MCCR tests

Dataset	Gamma statistics	MCCR crit. values	p-values	aic.pb	aic.bd	aic.ddl	aic.ddx	aic.spvar	aic.exvar	aic.both
all-data	-1.350359	-2.00109	0.167665	1.3	3.3	**0**	1.3	**4.2**	5.4	6.2
all-data_BPh	-1.730079	-1.72825	0.051896	7.5	9.5	**0**	4.3	**8.4**	12	10
all_data_MSJ	-0.460950	-2.01411	0.493014	**0**	2	0.9	1.7	**4**	**4**	6
mtDNA	-0.537904	-2.16338	0.497006	**0**	2	1.0	0.9	**3.7**	4	5.7
mtDNA_BPh	-1.633832	-1.85018	0.085828	6.3	8.3	**0**	3.8	**7.7**	10	9.7
amtDNA_MSJ	-0.145907	-1.683778	0.475050	**0**	2	1.5	1.9	**4**	**4**	6
cdsDNA	-0.931241	-2.10561	0. 349301	0.23	2.2	0.34	**0**	**3.3**	4.3	5.3
cdsDNA_BPh	-1.430240	-1.91050	0.119880	4.5	6.5	**0**	2.5	**6.4**	8.5	8.4
cdsDNA_MSJ	-0.069505	-1.97944	0.662675	**0**	2	1.6	1.9	**4**	**4**	6

Supplementary Table 10. Nucleotide frequencies across studied genes

Fragment	Genes	A	C	G	T	No of sites
18S rDNA	18S rDNA	0.23948	0.24469	0.27907	0.23667	1855
28S rDNA	28S rDNA	0.25096	0.24048	0.31334	0.19522	628
rrnl fragment	rrnl mtDNA	0.34403	0.09069	0.16358	0.40171	595
	tRNA-Leu	0.31710	0.05799	0.17732	0.44758	69
	nad1	0.24321	0.05828	0.14614	0.55237	117
cox1 fragment	cox1	0.34930	0.18568	0.12981	0.33521	812
	tRNA-Leu	0.35894	0.11223	0.16990	0.35894	57
	cox2	0.38148	0.18607	0.05519	0.37725	208
nad5 fragment	nad5	0.29325	0.08297	0.14288	0.48090	1031
	tRNA-Phe, Glu, Ser	0.39183	0.06368	0.11074	0.43460	160

Appendix. Taxonomical conclusion

***Scarelus* Waterhouse, 1878**
Scarelus Waterhouse, 1878: 100.
Type species: *Scarelus orbatus* Waterhouse, 1878
Paratelius Kazantsev, 1992: 99.
Type species: *Scarelus diversicornis* Pic, 1912.

Kasantsev (1992) treated some Bornean species as a separate genus *Paratelius* Kazantsev, 1992, but our result suggests that *Paratelius* is a part of the *Scarelus* clade (Figs 2-3) and we propose to treat *Scarelus* in the previous wider sense and to consider *Paratelius* to be a junior synonym of *Scarelus*. The analyses showed that *Paratelius* sensu Kazantsev (1992) is an internal branch within *Scarelus* and therefore this lineage cannot be accepted as a separate genus. Both *Scarelus* and *Paratelius* share the type of vestiture (Kazantsev 1992, Malohlava & Bocak in press). The presence of four elytral costae in *Paratelius* is a plesiomorphy shared with *Atelius* Waterhouse, 1878 and the reduction of the number of costae to two or three is supposedly a result of parallel origin of small and slender body as was observed in related *Dilophotes* Waterhouse, 1879, various genera of Metriorrhynchini and in other net-winged beetles lineages (Bocak and Bocakova, 2008).

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α – TAXONOMICAL PART-A OF THESIS

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A revision of the neotenic net-winged beetle *Scarelus* (Coleoptera: Lycidae)

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Running title:
Revision of *Scarelus*

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. Twentyseven species of *Scarelus* are recognized, of which eleven are described as new: *S. baranciki* n. sp., *S. pseudoumbrosus* n. sp., *S. cibodasensis* n. sp., *S. flavicollis* n. sp., *S. loksadoensis* n. sp., *S. pahangensis* n. sp., *S. ruficollis* n. sp., *S. rufus* n. sp., *S. salvani* n. sp., *S. saranganensis* n. sp., and *S. similis* n. sp. *Scarelus luchti* Kazantsev et Yang , 1999: 245 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.

Key words: new species, zoogeography, neoteny, Oriental Region.

Introduction

The net-winged beetles, Lycidae, is a lineage of former Cantharoidea (Crowson, 1972) and at present, they are placed in Elateroidea as one of soft-bodied lineages (Lawrence, 1995, Bocakova *et al.*, 2007). Similarly with several related families previously classified in Cantharoidea, such as Lampyridae, Phengodidae, Drilidae, and Omalisidae, the metamorphosis of net-winged beetles to the adult stage is incomplete and it results in morphological modifications, from widespread soft-bodiedness to the completely larviform females in several lycid lineages (*e.g., Platerodrilus* Pic, 1921, *Lyropaeus* Waterhouse, 1879, and supposedly *Scarelus* Waterhouse, 1878; Bocak *et al.*, 2008). Although ontogenetic reprogramming has been widely studied, most works have focused on vertebrate model groups (Gould, 1977) and only fragmentary, mostly descriptive, information is available on insects, including beetle neotenic lineages (*e.g.*, Crowson, 1972, Cicero, 1988, 2008, Miller, 1991). Only recently, 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 more detailed studies on the impact of ontogenetic modifications on ecology and distribution. Therefore, we need to accumulate further alphataxonomic and zoogeographic data to address such topics as the speciation processes or interactions between neoteny and ecology. Ateliini and Dilophotini form the subfamily Ateliinae (Bocak and Bocakova, 2008). This tribe, similarly to other lycid neotenic lineages, is species poor despite hypothesized ancient origin (Bocak *et al.*, 2008). We believe, that it is not a bias caused by neglecting of the group by taxonomists as *Scarelus* was intensively studied in the last decade (Bocak, 1995, 1997, 1998, Kazantsev, 1992, 1997). At present, three genera are defined in Ateliinae: *Atelius* Waterhouse, 1878 known from Ceylon, Vietnam and Hainan (Kazantsev, 1992; Bocak, 1997), *Paratelius* Kazantsev, 1997 from Northeastern Borneo (Malohlava and Bocak, 2009) and *Scarelus* Waterhouse, 1878 from Burma, Malaysia, Indonesia and the Philippines (Bocak, 1995, 1997). 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, tube-like or shortened and pointed (fig. 3A-6H). Females are unknown (Bocak and all, 2008; Bocak and Matsuda, 2003; Wong, 1996). 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.

History of the classification of Ateliinae

Ateliinae were proposed by Kleine (1928) to intercept the monotypic *Atelius* and seven species classified in *Scarelus*. Later, Kleine (1933) lowered the status of all lycid subfamilies to tribes when he classified Lycinae and Homalisinae in one family, but Homalisidae were soon classified as a separate family (Crowson, 1955, 1972, Bocak & Brlik, 2008). Bocak and Bocakova (1990) revised classification of Lycidae and proposed Ateliinae as one of six lycid subfamilies. Recently published molecular phylogeny of Lycidae suggested the relationships of Dilophotini and Ateliini and these tribes form the redefined subfamily Ateliinae (Bocak and Bocakova, 2008). Despite similar biology, both morphology and molecular data suggest distant position of Scarelini from the other lycids neotenic lineages (Bocak *et al.*, 2008). Altogether 36 species are now classified in Ateliini and it makes Ateliini one of the species poorest tribes in Lycidae. The observed low species level diversity of Ateliini is characteristic for all lycid lineages with proved or expected female neoteny (Bocak *et al.*, 2008). Three genera, *Atelius*, *Scarelus*, and *Paratelius,* are placed in Ateliini after Kazantsev (1992) proposed a separate genus *Paratelius. Atelius* remained monotypic since the proposal in the mid 19th century till 90's (Kazantsev, 1992; Bocak, 1997). *Paratelius* was monotypic when described and another species was described by Kazantsev (1997) and later synonymized with a species previously placed in *Scarelus* (Kazantsev and Yang, 1999).

Additional species have been described subsequently by Malohlava and Bocak (in press). *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). The World catalogue of Lycidae listed seven species of *Scarelus* (Kleine 1933). Kazantsev (1992) reviewed the status and synonymized several species described by M. Pic. Further species were proposed by Kazantsev (1997), Kazantsev and Yang (1999), Bocak (1995, 1997, 1998) and Bocak and Bocakova (1999).

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 whole year around, 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 season, most of these species were collected in very few specimens. There is no information available on larvae and their ecological requirements, but we may expect the similar requirements as in other net-winged beetles (Bocak and Matsuda, 2003). Adults are regularly collected in humid conditions, they never leave 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, but *Scarelus* species have usually quite inconspicuous reddish brown or testaceous elytra. These pattern 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. The bright colouration patterns characteristic for Oriental Metriorrhynchini or some Platerodini are unknown in Ateliini. 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 proved by observing copulating males and females of Ateliini.

Distribution

Ateliini are known exclusively from the Oriental region and both genus and species level ranges are regularly limited to restricted areas. *Atelius* has the disjunctive range with two species in Sri Lanka, two in Vietnam and one in Hainan. Such pattern of the distribution suggests relict refugia after extinction, which may be caused by aridisation of the region during the late Tertiary and Quaternary (Logachev *et al.*, 1998; Vanderberghe, 2004). More extensive, but similarly disjunctive distribution is known in the neotenic *Lyropaeus* Waterhouse, 1878 (Lyropaeinae). Both, *Paratelius* and *Scarelus* occur in only the eastern part of the Oriental region. *Scarelus* is widespread in the southeast of continental Asia (Tenasserim, the Malay Peninsula) and all Great Sunda Islands, which were connected with the continent when the Asian shelf was subaerial (Sumatra, Borneo and Java; Hall and Blundell, 1996, Voris, 2000). Additionally, four species of *Scarelus* are known from the Philippines and Palawan, which have been isolated from continental Asia for a long time (Voris, 2000). The dispersal of neotenic *Scarelus* across the sea is improbable and the Philippine species may be taken to the Philippines on some continental fragments (Hall and Blundell, 1996). Although an Asian continental fragment was also accreted to the present day Sulawesi (Hall, 2002), no *Scarelus* occurs east of the Wallace line. *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 and no material is available from some parts of the region, e.g. Southern Sumatra, the Mt. Dempo massive or mountain ranges in Central Sumatra between Bukittinggi and the Lake Toba. Two species are known from northernmost Sumatra (Aceh Province): *S. tomani* from lower mountain elevation near Takengon and widespread *S. corporaali* from lower elevation south of Lhokseumawe (fig. 1). Two species are known from the volcanic massifs of Mts Sinabung and Sibayak (*S. brastagiensis* and *S. schawalleri*). Two species were reported from the area of Bukittinggi: one species from the Mt. Merapi (*S. sanguineus*), and the second from lower elevations in the vicinity of Bukittinggi (the widespread *S. longicornis*). Another three species, *S. flavicollis*, *S. ruficollis* and *S. rufus*, 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 and Adams, 2001). Only two Sumatran species, *S. corporaali* and *S. longicornis*, were collected in lover 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* is widespread in lower mountain forests of the Malay Peninsula, *S. anthracinus* occurs in the Cameron Highlands, *S. pahangensis* is known from the eastern slope of a mountain range between Perak and Pahang and *S. pseudoumbrosus* is known from the western slope of the same range (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 similarly to the Barisan Range in Sumatra. These mountain kept the humid forest during the aridisation of South East Asia in the Pleistocene (Tallis, 1991). Another species was collected in the mountains of Sarawak (*S. ardens*). Two species, *S. similis* and *S. loksadoensis* are known from the lowlands of central Borneo and lower elevations of the Meratus Mts. Surprisingly, no endemic species has been collected in the higher elevations of this range. Concerning the limited collecting activity in the region, we are not sure if the missing record from the mountainous region southern Borneo reflects the supposed aridisation of the region during Pleistocene. Three 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). One species was collected in the high mountain forests of Mt. Lawu in Central Java (*S. saranganensis*). *S. longicornis* was reported from Java by Waterhouse (1879), but this species was recently collected only in Sumatra. Neotenic lycids have very low vagility. Their ranges are often allopatric and typically contain a single mountain chain. Only a few species, such as *S. crudus* in the Philippines, *S. cibodasensis* in Java, and *S. orbatus* in Malaysia have more extensive ranges (fig. 1). The observed pattern of high endemicity and very restricted ranges is unlikely the result of the collecting bias as most localities were visited several times during the last two decades and the same species were repeatedly collected in the same place. A pattern of isolated volcanoes and mountain chains in combination with limited ability to disperse may support the diversification of *Scarelus*. We believe, that limited ability to re-invade newly established rain forest ecosystems after climatic fluctuations explains the isolated centres of diversity in Western Sumatra and Northeast Borneo with no overlap in the species spectrum. These centres of high diversity agree with refugia of the tropical rain forest preserved during much drier cold periods in Pleistocene (Tallis, 1991; Ray & Adams, 2000) and represent biodiversity hot spots (Myers, 2000).

Conservation

The high endemicity 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.

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 apical part 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
NHMP- National Museum of Natural History, Prague, Czech Republic
SMNS- Staatliches Museum für Naturkunde, Stuttgart, Germany
MZIW- Museum and Institute of Zoology, Polish Academy of Sciences, Poland
LMBC- Department of Zoology, Palacky University, Olomouc, Czech Republic

Taxonomy

Scarelus Waterhouse, 1878

Scarelus Waterhouse, 1878: 100.

Type species: *Scarelus orbatus* Waterhouse, 1878.

Redescription. Body small, slender, usually uniformly dark brown or black, seldom orange brown. Elytra and pronotum testaceous or with variable extension of light brown humeral part and dark brown to black apex of elytra; few species with upper side reddish brown or concolour black. Head small (fig. 2A), hypognathous, freely movable, only slightly retractable into pronotum, without rostrum. Cranium with fine microstructure, surface slightly shiny, shortly 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, narrowed to apex, eliptical (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, quite long, slightly curved, with shining inner margin, 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, trapezoidal, shiny, sparsely pubescent, usually weakly emarginate at apex. Elytra flat, with two or three longitudinal costae in most of elytral length, costa 1 usually weak to vestigial, reaching one to nine tenths of elytral length, stout only at base of elytra, 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 longitudinal elytral costae have been often 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 the similar tendency to shortening and reduction of the number of costae is found also in *Dilophotes*, a presumed sister group of Ateliini (Bocak and 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 and 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 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 and it may form a paraphylum in respect with *Scarelus*.

The *S. anthracinus* species group.

Differential diagnosis. Species classified in both here proposed species groups 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 reminds those of the closely related *Paratelius* (Malohlava and 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 and Bocak 2009). The species from Borneo and the Philippines have strongly assymetrical phallobase without any keel (fig. 5A-L). No other character supports the separation of these species groups. The geographically structured variation on morphology suggests lack of dispersal between Borneo and Sumatra and in site speciation within respective assemblages of species. The following twenty-one species are classified in the *S. anthracinus* group: *S. anthracinus* Bocak and Bocakova, 1999 (Peninsular Malaysia), *S. bicostatus* Pic 1912 (Borneo), *S. ardens* Kleine, 1926 (Malaysia), *S. baranciki* n. sp. (Borneo), *S. brastagiensis* Bocak, 1995 (Sumatra), *S. crudus* Kleine, 1926 (Philippines), *S. inapicalis* Pic, 1925 (Burma, Tenasserim), *S. loksadoensis* n. sp. (Borneo), *S. kodadai* Bocak, 1999 (Palawan), *S. pahangensis* n. sp. (Malaysia), *S. palawanensis* Bocak, 1999 (Palawan), *S. pseudoumbrosus* n. sp. (Peninsular Malaysia) *S. rollei* Pic, 1912 (Borneo), *S. ruficollis* n. sp. (Sumatra), *S. rufus* n. sp. (Sumatra), *S. salvani* n. sp. (Mindanao), *S. sanguineus* Bocak, 1995 (Sumatra), *S. schawelleri* Bocak, 1999 (Sumatra), *S. similis* n. sp. (Borneo), *S. tomani* Bocak, 1998 (Sumatra), and *S. umbrosus* Kleine, 1932 (Malaysia).

***Scarelus anthracinus* Bocak et Bocakova, 1999**

Scarelus anthracinus Bocakova et Bocak, 1999: 38.

= *Scarelus maxwelli* Kasantsev et Yang, 1999: 245; Bocakova and Bocak, 2000: 44. = *Scarelus pedlenburyi* Kazantsev et Yang 1999: 246, nomen nudum; Bocakova and Bocak, 2000: 44.

Type material. Holotype. Male, Malaysia, Perak, Cameron Highlands, Mt. Beremban, 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. 4HI, 4D). *Redescription*. Male. Body small-sized, slender; all body parts including appendages black, only sutural margins of elytra and partly bases of elytral costae reddish brown. Head small, densely pubescent. Eyes small, hemispherically prominent, their frontal interocular distance 3.05 times maximum eye diameter in lateral view. Antennae slender, compressed, surpassing apex of elytra by two apical antennomeres. Antennomeres 3-11 gradually slenderer, almost parallel-sided, apical antennomere eliptical. Elytra slender, 3.5 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae, covered with dense, short, black pubescence. 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 1.02mm, 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: 360.

Material examined. Male, Malaysia, Sarawak, Kuching dist., Mt. Penrissen, 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 similiarly coloured, eyes black. Head small, densely pubescent, eyes small, hemispherically prominent, their distance 2.48 times maximum eye diameter. Antennae slender, compressed, surpassing elytral apex by 4.5 antennomeres. Antennomeres 3-11 gradually slenderer, apical antennomere eliptical. Elytra slender, 2.9 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae, covered with bright reddish brown pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus strong, long, 4.2 times longer than parameres, sligtly 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. Borneo, Sarawak.

Scarelus baranciki n. sp.

Type material. Holotype. Male, Malaysia, Sabah, Mt. Emas, 1700 m, 22.III.-8.IV.2000, leg. Bolm (LMBC), DNA Isolation Voucher Number UPOL 000582.

Differential diagnosis. *S. baranciki* 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 eliptical. 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, assymetrical (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, 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, hypognathous, eyes small, hemispherically prominent, their frontal distance 3.0 times maximum eye diameter. Antennae slender, compressed, surpassing elytral apex by more than four antennomeres. Antennomeres 3-11 gradually slenderer, slightly serrate, apical antennomere eliptical. 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 assymetrical (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. Borneo, Sabah.

Scarelus brastagiensis Bocak, 1995

Scarelus brastagiensis Bocak, 1995: 5.

Type material. Holotype. Male, Sumatra, Brastagi, G. Sibayak, 1450-1900 m., 19.-23.II.1991, leg. L. Bocak and M. Bocakova (LMBC). Paratypes, 2 males, ditto (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, Sumatra, Brastagi, Mt. Sibayak, 26.I.-1.II.2005, 1600-220 m, leg. Bolm (LMBC).

Differential diagnosis. *S. brastagiensis* reminds in the general body form 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. 3CD).

Redescription. Male. Body small-sized, humeral part of elytra, head and thorax brown, abdomen black, pronotum black, scutellum and apical third dark brown to black. Antennae, mouthparts and legs brown. Head small, eyes small, hemispherically prominent, their distance twice maximum eye diameter. Antennae slender, flattened, 1.2 times longer than body. Antennomeres 3-11 gradually slender, apical antennomere eliptical. Elytra slender, 3.5 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae covered with reddish pubescence. Legs moderately long, slender, flattened, 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. Sumatra. *S. brastagiensis* is known only from the vicinity of Brastagi in the Northern Sumatra province.

Scarelus crudus Kleine, 1926

Scarelus crudus Kleine, 1926: 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$_o$52´E, 124 $_o$54´E, 17.-20.I.2007, leg. Bolm (all LMBC).

Differential diagnosis. *Scarelus crudus* and *S. salvani* 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* 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, 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 eliptical. 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 eliptical, parameres short reaching one fourth of phallic length, phallobase short, slightly assymetrical (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 *Scarelus* occuring in the Malay Peninsula.

Redescription. Male. Body small-sized, robust, brown, eyes black, appendages dark brown. Head small, eyes small, hemispherically prominent, their distance 2.63 times maximum eye diameter. Antennae slender, compressed, flattened, 1.43 times longer than the body. Antennomeres 3-11 gradually slender, apical antennomere eliptical. 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, flattened, densely pubescent. Male genitalia trilobate, phallus very long, apex eliptical, parameres short, 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 Myamar in the type specimen collected already in the xixth century in Tenasserim by the Czech entolomologist J. W. Helfer. Futher 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, 1999**

Scarelus kodadai Bocak, 1999: 177.

Type material. Holotype. Male, Palawan centr., env. Lion´s Cave near Cabayuga, 1.XII.1995, primary forest on limestone, leg. Jan Kodada (LMBC). Paratype, male, Palawan, Tanabank river, 20.XII.1991, leg. Bolm (LMBC). Paratype, male, Phillippines, 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 including coxae brown. Head small, eyes small, hemispherically prominent, their distance 3.42 times maximum eye diameter. Antennae slender, flattened, 2.1 times longer than body. Antennomeres 3-11 gradually slender, apical antennomere eliptical. Elytra slender, 2.85 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae, covered with brown pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus very long, eliptically 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.

S. loksadoensis **n. sp.**

Type material. Holotype. Male, S Kalimantan Province, 10 km E of Loksado, 600-1100 m, 2° 43´S 115° 32´E, 18.-23.VI.2001, leg. Bolm (LMBC).

Differential diagnosis. *S. loksadoensis* reminds other similarly coloured species, *S. baranciki*, *S. rollei* and *S. loksadoensis*. 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 small hemispherically prominent, their distance 3 times maximum eye diameter. Antennae slender, flattened, twice longer than body. Antennomeres 3-11 gradually slenderer, apical antennomere eliptical. 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 trilobate, phallus long, apex rounded, phallobase assymetrical 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, 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$_{o}$53´N 102$_{o}$01´E, 1.IV.1998, leg. Dembicky and Pacholatko (LMBC).

Differential diagnosis. *S. pahangensis* belongs to an asseblage 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* 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 slender, flattened, 1.5 times longer than body, mouthparts and legs black. Antennomeres 3-11 gradually slenderer, apical antennomere eliptical. Elytra slender, 3.6 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae covered with testaceous pubescence. Legs moderately long, slender, 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, 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 eliptical. 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 assymetrical (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 pseudoumbrosus* n. sp.**

Type material. Holotype. Male, Malaysia, Pahang, 20 km E of Ringlet, Kampong Kuala Boh, 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. pseudoumbrosus* is a species with a major part of elytra black and only a small humeral part of elytra brown. *S. pahangensis* resembles to *S. pseudoumbrosus* and it 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 slender, compressed, reaching over apex of elytra by 2 antennomeres. Antennomeres 3-11 gradually slenderer, apical antennomere eliptical. Elytra slender, 2.86 times longer than width at humeri, parallel-sided, with three well developed 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 to one fourth of phallic length, phallobase as long as the 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, Pahang.

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

Scarelus rollei **Pic**

Scarelus rollei Pic, 1912: 4.

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

Material examined. 4 males, Borneo, Sabah, M. Kinabalu N. P., II.2000, leg. M. Snizek; 2 males, ditto, 28.V.1999, leg. M. Snizek; 1 Borneo, 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* (fig. 5F-G).

Description. Male. Body small-sized, head red, thorax brown, abdomen black, scutellum, pronotum, elytra, antennae, mouthparts and legs red. Head small, eyes small, hemispherically prominent, their distance 2.5 times maximum eye diameter. Antennae slender, flattened, 2.2 times longer than body. Antennomeres 3-11 gradually slenderer, apical antennomere eliptical. Elytra slender, 2.47 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae covered with red pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate, phallus three times longer than pallobase, apex eliptical, 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. Borneo, Sabah area.

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

Description. Male. Body small-sized, head and thorax dark brown, abdomen black, pronotum, scutellum and elytra greyish brown. Antennae, mouthparts and legs black. Head small, eyes small, 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 eliptical. Elytra slender, 3.75 times longer than width at humeri, parallelsided, with well developed three longitudinal costae covered with brown pubescence. Legs moderately long, slender, flattened, 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. Philippines, 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, Sumatra, Mt. Singgalang, S of Bukittinggi, 1300 m, 14.-16.II.1991, leg. L. Bocak and M. Bocakova (LMBC). *Other material examined*. 2 males, Sumatra, Gn. Merapi, 5 km E of Kotobaru, 1600 m, 18.-25.V.2001, leg. Bolm; 2 males, 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* and *S. rufus* in general appearance and the slightly curved free part of the phallus. The phallus of *S. sanguineus* is slenderer than those of *S. ruficollis* (fig. 3H).

Redescription. Male. Body small-sized, head, thorax and abdomen black, only elytra red. Antennae, mouthparts and legs black. 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 eliptical. 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. Sumatra, Mts. Merapi and Singgalang.

Scarelus ruficollis **n. sp.**

Type material. Holotype. Male, Sumatra, Jambi, Kersik Tua, Mt. Kerinci, 1600-2200 m, 19.-22.I.2005, leg. Bolm (LMBC). Paratypes, 6 males, same locality data (LMBC).

Differential diagnosis. *S. ruficollis, S. rufus* 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 characters separating these species. The phallus of *S. ruficollis* is relatively more robust (fig. 3A-B).

Redescription. Male. Body small-sized, black colouration, only elytra red. The body appendages black. Head and eyes small, hemispherically prominent, their mutual distance 2.75 times maximum eye diameter. Antennae slender, flattened, 1.2 times longer than body. Antennomeres 3-11 gradually slenderer, apical antennomere eliptical. Elytra slender, 3.81 times longer than width at humeri, parallel-sided. Similarly as in *S. sanguineus* well developed three longitudinal costae also covered with reddish pubescence. Legs moderately long, slender, flattened, and 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. Sumatra, Mt. Kerinci Massif.

Scarelus rufus n. sp.

Type material. Holotype. Male, Sumatra, Jambi, Kersik Tua, Mt. Kerinci, 1600-2200 m, 19.-22.I.2005, leg. Bolm (LMBC).

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

Redescription. Male. Body small-sized, head, thorax and abdomen black, elytra red. Antennae, mouthparts and legs black. Very similarly as in the previous species described. Head small and eyes small. Eyes hemispherically prominent, their mutual interocular distance 3.06 times maximum eye diameter. Antennae slender, flattened 1.2 times longer than body. Antennomeres 3-11 gradually slenderer with apical antennomere eliptical. Elytra slender, 3.38 times longer than width at humeri, parallel-sided. Well developed three longitudinal costae which are red pubescent. Legs moderately long, slender, flattened and covered scarse pubescence. Male genitalia trilobate, phallus long, at the end rounded, upword rounded, phallobase and parameres similar in length, as long as wide. 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. Sumatra, Mt. Kerinci Massif.

Scarelus schawalleri Bocak, 1995

Scarelus schawalleri Bocak, 1995: 8.

Type material. Holotype. Male, Sumatra, Kabanjahe, Gn. Sinabung, 7.-10.X.1990, leg. A. Riedel (SMNS).

Differential diagnosis. *S. schawalleri* may be easily separated from other *Scarelus* species by the shortest antennae within the genus. 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, scutellum dark at apex, apical third of elytra black, basal part testaceous. Head small, slightly broader than frontal margin of pronotum, mouthparts testaceous, antennae reaching over elytral apex by less than one antennomere. Eyes small, hemispherically prominent, their distance 2.57 times maximum eye diameter. Pronotum 1.48 times broader at base than long at midline. Elytra with two distinct 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 to apical third (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. Northern Sumatra.

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

Type material. Holotype. Male, Central Kalimanten 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* reminds other similarly coloured Bornean species, *S. baranciki*, *S. rollei* and *S. loksadoensis*. These species differ only slightly in the shape of male genitalia (fig. 5H-I, 4J, 5F-G, 5J).

Description. Male. Body small-sized, head, thorax bright red, abdomen brown, scutellum and pronotum reddish brown and elytra bright red. Whole antennae, mouthparts and legs red. Head small, eyes small 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 eliptical. 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 assymetrical, 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. Borneo, Central Kalimantan Province.

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

***Scarelus tomani* Bocak, 1998**

Scarelus tomani Bocak, 1998: 24.

Type material. Holotype. Male, Indonesia, Sumatra, Aceh, 15 km SSE Takengon, 1600 m, 26.II.-13.III. 1998, leg. L. Bocak and 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, slender, black, only cranium, pronotum, prothoracal pleurons, scutellum and basal two third of elytra yellowish brown. Head small, frons convex, with shallow rounded depression in middle, covered with long brownish pubescence, antennal tubercles inconspicuous. Eyes small, interocular distance 3.0 times maximum eye diameter. Antennae surpassing elytral length by 2.5 segments, very slender, only slightly compressed, antennomeres 3-11 subequal in length, gradually shortening towards apex of antennae. Pronotum with flat disc, median longitudinal keel well developed, Elytra parallel-sided, with three longitudinal costae. Longitudinal costa 1 weakest, 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. Sumatra, Aceh Province.

Scarelus umbrosus **Kleine, 1932**

Scarelus umbrosus Kleine, 1932: 535

= *Scarelus riedeli* Bocak et Bocakova, 1995 : Bocakova and Bocak, 1999: 109. *Type material*. Holotype. Male, 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$_o$53´N 102$_o$01´E 1.IV.1998, leg. Dembicky and 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, head and thorax brown, abdomen dark brown, humeral half of elytra testaceous, apical part dark brown to black. Antennae, mouthparts and legs brown. Head small, eyes small, hemispherically prominent, their distance 3.38 times maximum eye diameter. Antennae slender, flattened, 1.5 times longer than body. Antennomeres 3-11 gradually slenderer. Elytra slender, 2.94 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae covered with brown pubescence. Legs moderately long, slender, flattened, 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. 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* and *S. saranganensis*, share a similarly widened phallic base (fig. 6BC, 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. The following six species are classified in the *S. orbatus* species group: *S. cibodasensis* n. sp. (Java), *S. corporaali* Kazantsev, 1992 (Sumatra), *S. flavicollis* n. sp. (Sumatra), *S. longicornis* Waterhouse, 1878 (Sumatra), *S. orbatus* Waterhouse, 1878 (Malaysia, Singapore), and *S. saranganensis* n. sp. (Java).

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

= *Scarelus longicornis*: Kazantsev, 1992: 101 nec Waterhouse, 1879. = *Scarelus luchti* Kazantsev et Yang , 1999: 245 - nomen nudum.

Type material. Holotype. Male, Indonesia, Java, Puncak Pass, 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* resembles *S. saranganensis* in the uniformly testaceous elytra and these species differ in the shape of their male genitalia. The paramerae of *S. saranganensis* are slenderer and the phallus shorter than in *S. cibodasensis* (fig. 6B-C).

Description. Male. Body small-sized, slender, brown, head, eyes, antennae, and legs including coxae black. Head small, eyes small, hemispherically prominent, their interocular distance 2.55 times maximum eye diameter. Antennae slender, compressed, reaching over apex of elytra by two segments. Antennomeres 3-11 gradually slenderer, apical antennomere eliptical. Elytra slender, 3.43 times longer than width at humeri, parallel-sided, with well developed three longitudinal costae covered with brown pubescence. Legs moderately long, slender, flattened, 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* is known only from several localities in 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 et Yang, 1999 in a study coauthored 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 et Yang, 1999 the name is invalid (ICZN 1999, Art. 13.1).

Scarelus corporaali **Kasantsev, 1992**

Scarelus corporaali Kasantsev, 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, 4.85-5.90 mm long, 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, mouthparts testaceous, legs brown. Head small, eyes hemispherically prominent, their frontal distance 2.91 times maximum eye diameter. Antennae slender, flattened, 1.2 times longer than body. Antennomeres 3-11 gradually slender, slightly compressed, apical antennomere eliptical. 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, slender, compressed, densely pubescent. Male genitalia trilobate, phallus long, parameres short reaching one fourth of phalic 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. Nothern Sumatra and Aceh provinces.

Scarelus flavicollis **n. sp.**

Type material. Holotype. Male, Sumatra, Jambi, Kersik Tua, Mt. Kerinci, 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* 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, head, thorax, abdomen and appendages black, scutellum and elytra reddish brown. Head small, eyes hemispherically prominent, small, their frontal distance 2.21 times maximum eye diameter. Antennae slender, compressed, almost 1.5 times longer than body. Antennomeres 3-11 gradually slenderer, parallel-sided, apical antennomere eliptical. Elytra slender, 3.7 times longer than width at humeri, parallel-sided, with three well developed longitudinal costae. Legs moderately long, slender, compressed, 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. 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; Kasantsev, 1992: 20.

Material examined. 2 males, Western Sumatra Province, Batang Palupuh Nature Reserve, 25 km of Bukittinggi, 15.II.1991, leg. Bocak and M. Bocakova (LMBC); 1 male, Sumatra (Z.W.K.), Boekit Gabah, IV.1919, leg. Lucht (ZIW); 2 males, Sumatra, Barat, Lake Maninjau, E coast, 800 m, 12.-23.I.2005, leg. Bolm (LMBC); 1 male, Sumatra, Ophir mts., Mt. Talamau, 17 km E Simpangempat, 21.-25.V.2001, 750 m, leg. Bolm (LMBC); 1 male, 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, slender, testaceous, abdomen and apical third of elytra dark brown, eyes black, head, antennae and legs darker than other body parts. Hlad small, sparsely pubescent, eyes small, hemispherically prominent, their frontal distance 2.8 times maximum eye diameter. Antennae slender, compressed, surpassing apex of elytra by almost three antennomeres. Antennomeres 3-11 gradually slenderer, slightly compressed, almost parallel-sided, apical antennomere eliptical. 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, slender, flattened, 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. Sumatra. *Remark*. Specimens collected in lower elevations in the westerns 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. 1 male, Singapore, Coll. Baker (ZIW); 4 males, Malaysia, Tioman Isl. 400 m, Kampong Telek-K. Juara, 9.III.1998, 2o48´N 104o11´E, leg. Dembicky & Pacholatko (LMBC); 13 males, Malaysia Pahang, Tioman Isl., 7.-25.II.2000, Kampong Telek-Kampong Juara, 2o48´N 104o11´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 which is well characterized by the pointed apex of the phallus. The closely related Sumatran species differ in the uniformly coloured elytra (*S. flavicollis*), only the apical third of elytra dark (*S. longicornis*) or a very long phallus (*S. corporaali*).

Redescription. Male. Body small-sized, slender, testaceous, only eyes black, antennae and legs dark brown. Head small, sparsely pubescent, eyes small, hemispherically prominent, their frontal distance 2.91 times maximum eye diameter. Antennae slender, compressed, surpassing elytra by three antennomeres. Antennomeres 3-11 gradually slenderer, slightly compressed, almost parallel-sided, apical antennomere eliptical. Elytra slender, 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, Java, Mt. Lawu, 8 km W of Sarangan, 10.-11.V.2001, leg. Bolm. Paratype. Male, ditto (LMBC).

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

Description. Male. Body small-sized, head, thorax, abdomen and appendages black, scutellum and pronotum dark brown to black with narrow reddish margins; elytra reddish brown. Head small, hypognathous, eyes small, hemispherically prominent, their frontal distance 2.53 times maximum eye diameter. Antennae slender, compressed, 1.6 times longer than body. Antennomeres 3-11 gradually slenderer, apical antennomere eliptical. 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. 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, phallus at least 3 times longer than the phallobase, four longitudinal costae in each elytron ..…………….. ***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 that 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 et 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 ……………………………………………………………………………...… ***S. bicostatus* Pic**

- Phallobase with longitudinal median keel (fig. 4B-C, 3E, 3H, 3C-D, 4D, 4F ……..………………………………………………………………………………… 7

7. Phallus short, strongly curved (fig. 4B-C)…………………………….... ***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 ……………………………………..………. ***S. tomani* Bocak**

- Phallus shorter, more robust, head dark brown to black ………………………...………. 9

9. Phallus slender in middle of its length (fig. 3H) ………………....…. ***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) ………………………………………………...……...…. ***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) …………..………………………...…… ***S. pahangensis* n. sp.**

- Phallus slender (fig. 4F-G) …………………………..……….. ***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, pronotum 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 infuscate, male genitalia as in fig. 5B ………………..…………………………….… ***S. palawensis*** **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), 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) ……………………………………………………………..…………… ***S. crudus*** **Kleine**

- Pronotum and elytra greyish brown, phallus moderately widened at base (fig. 5K-L) ……………………………………………………………………….... ***S. salvani*** **n. sp.**

18. Phallus apparently curved in lateral view (fig. 4E), Sarawak ………..…. ***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 testaceously 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 ……………………………..….… ***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 …………………………...…….. ***S. baranciki*** **n. sp.**

21. Parameres wide, rounded (fig. 5H-I) ……………………..……..……... ***S. similis*** **n. sp.**

- Parameres slender (fig. 5J) ………………………………..………. ***S. loksadoensis* n. sp.**

22\. Phallus almost straight in lateral view (fig. 3I) ……………………….……. ***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. 3GH), 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), 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. Sumatra: Kerinci massif ………....… ***S. flavicollis* n. sp.**

- Elytra dark brown to black apically ……………………………….………...…….. 26

26\. Phallus longer than phallobase (fig. 6F) ………………..……. ***S. corporaali* Kasantsev**

- 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, eadeagus 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,D) ………………………………...……………………..… ***S. longicornis* Waterhouse**

28\. Pronotum light brown, head and antennae brownish black, aedeagus with short phallus (fig. 6A) ………………………………...……………………..… ***S. saranganensis* n. sp.**

- Pronotum dark brown, head, antennae and legs black, aedeagus with long phallus (fig. 6B,C) ……………………..……………………………………………….... ***S. cibodasensis* n. sp.**

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We are obliged to the curators and institutions who enabled us to study the material in their care: M. L. V. Barclay (The Natural History Museum, London), Th. Deuve (Muséum National d’Histoire Naturelle, Paris), W. Tomaszewska and T. Huflejt (Museum and Institute of Zoology, Warszawa). We are also obliged to our colleagues who donated material from their field expeditions: P. Pacholatko, L. Dembicky, and J. Kodada. The study was supported by grants to L. B. from the Czech Grant Agency (Project 206/09/0015) and Ministry of Education of the Czech Republic (MSMT 6198959212). This research received support from the SYNTHESYS Project http://www.synthesys.info/ which is financed by European Community Research Infrastructure Action under the FP6 “Structuring the European Research Area“ Programme. All agencies are gratefully acknowledged for their support.

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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.

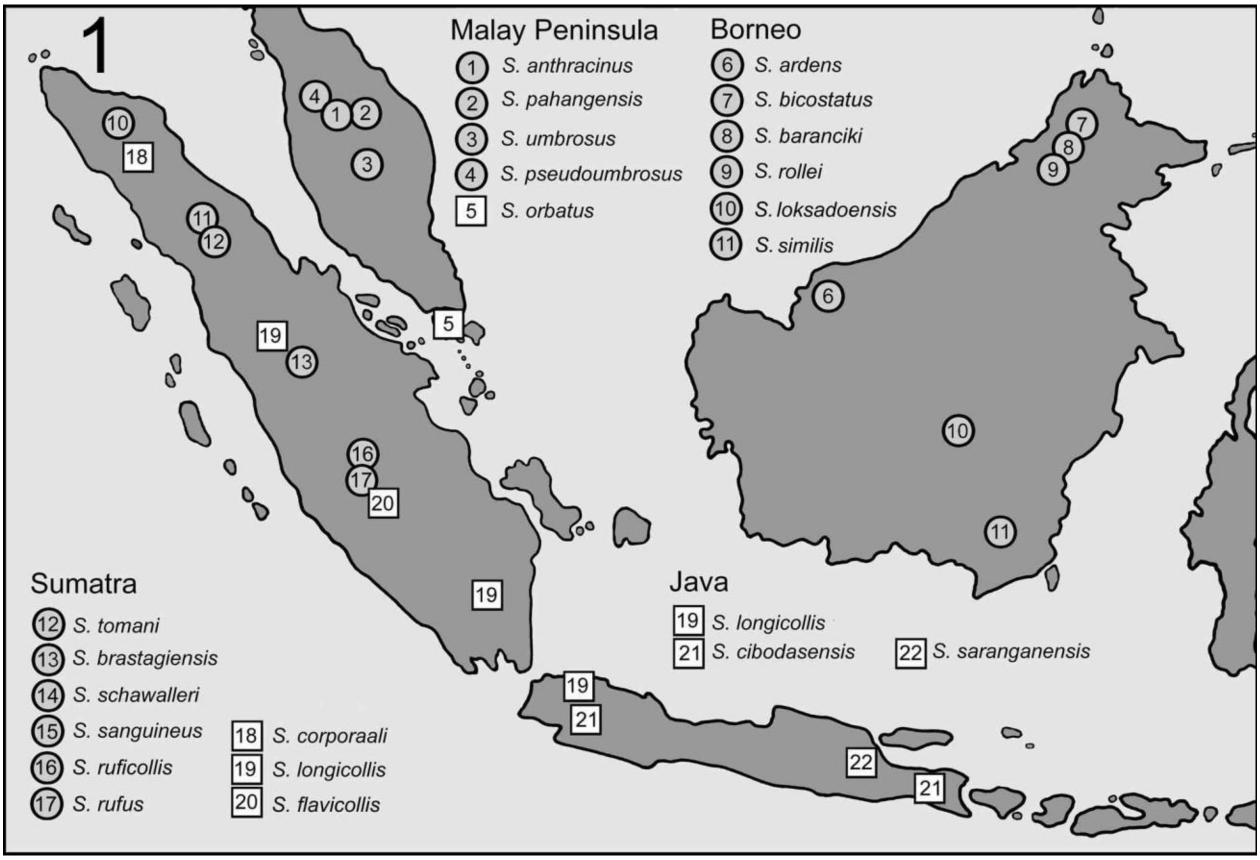
Figure 3. Male genitalia. (A-B) *S. ruficollis*; (C-D) *S. brastagiensis*; (E) *S. tomani*; (F) *S. schawalleri*; (G-H) *S. sanguineus*; (I-J) *S. rufus*. Scales 0.5 mm.

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

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*; (J) *S. loksadoensis*; (K-L) *S. salvani*. Scales 0.5 mm.

Figure 6. Male genitalia. (A) *S. sarangensis*; (B-C) *S. cibodasensis*; (D) *S. longicornis*; (E) *S. inapicalis*; (F) *S. corporaali* ; (G) *S. longicornis* ; (H) *S. flavicollis*. Scales 0.5 mm.

Figure 1


1
Malay Peninsula
1 S. anthracinus
2 S. pahangensis
3 S. umbrosus
4 S. pseudoumbrosus
5 S. orbatus
Borneo
6 S. ardens
7 S. bicostatus
8 S. baranciki
9 S. rollei
10 S. loksadoensis
11 S. similis
Sumatra
12 S. tomani
13 S. brastagiensis
14 S. schawalleri
15 S. sanguineus
16 S. ruficollis
17 S. rufus
18 S. corporaali
19 S. longicollis
20 S. flavicollis
Java
19 S. longicollis
21 S. cibodasensis
22 S. saranganensis

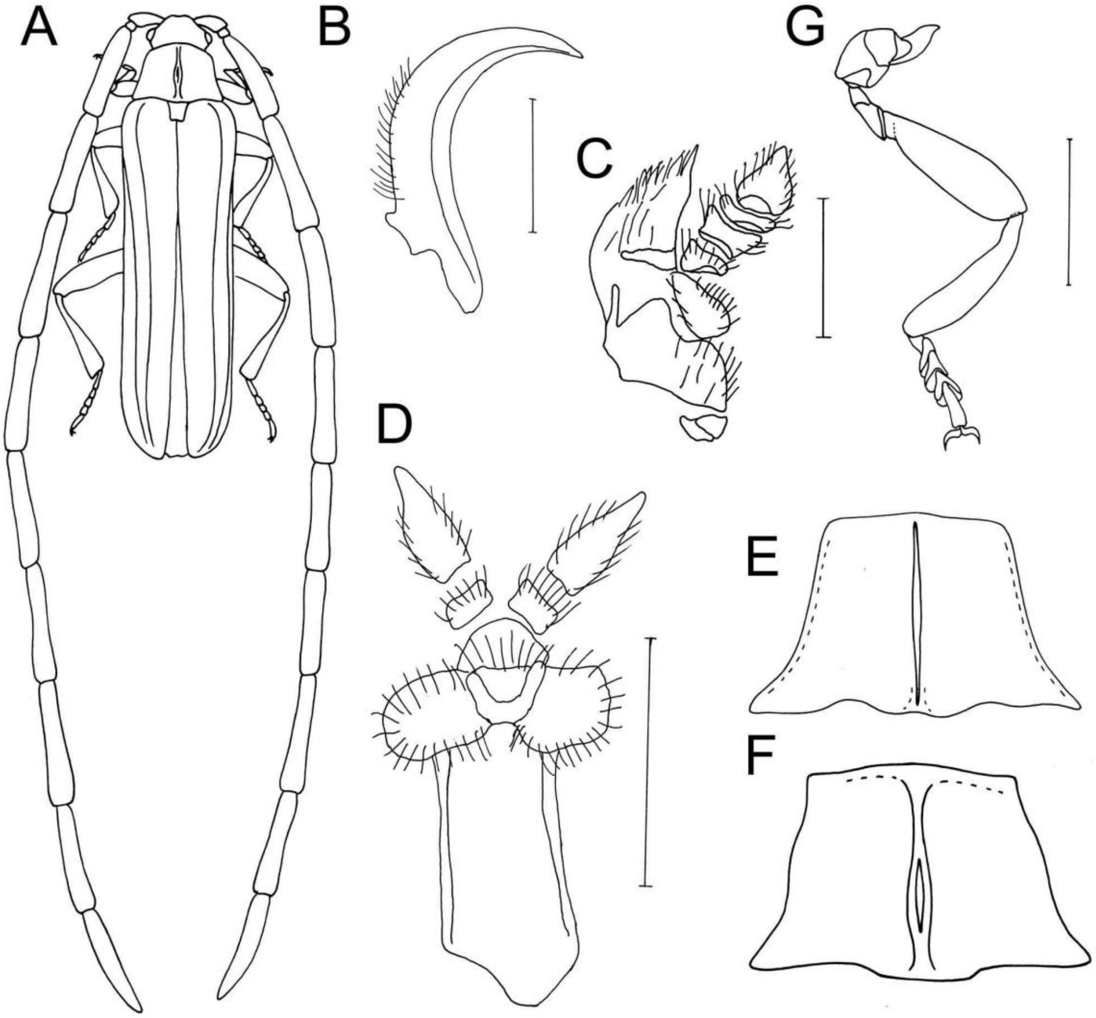


Figure 2

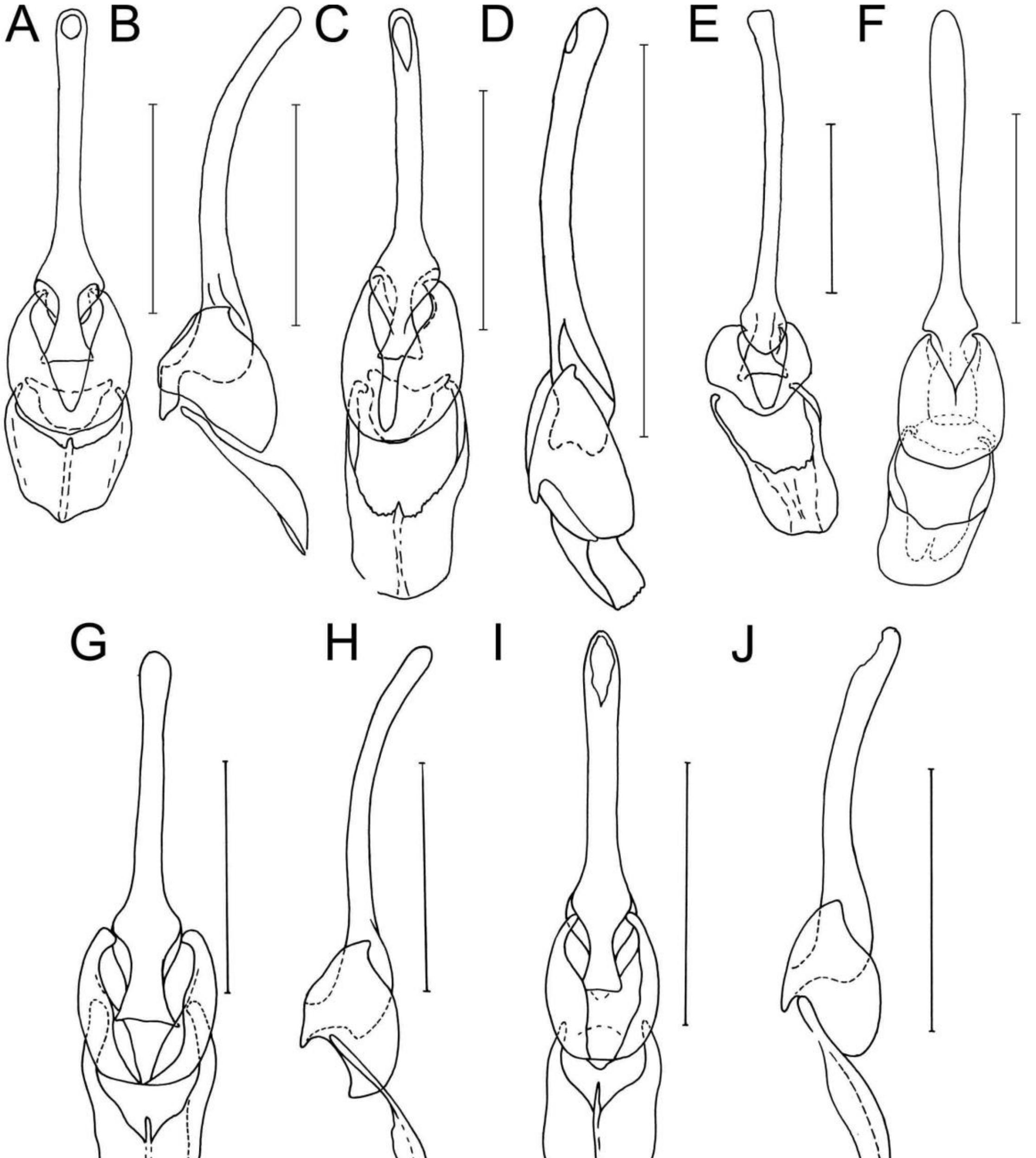


Figure 3

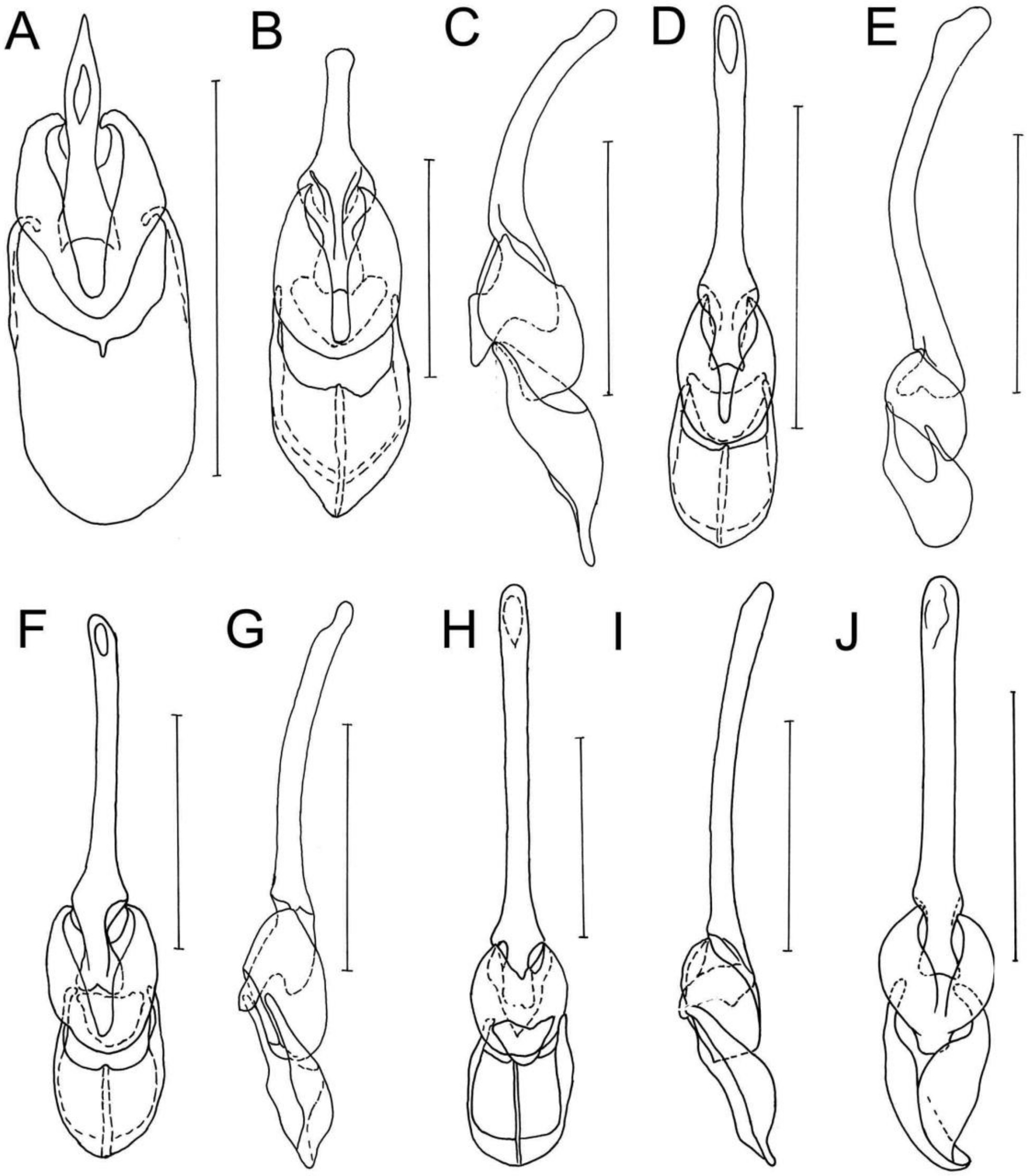


Figure 4

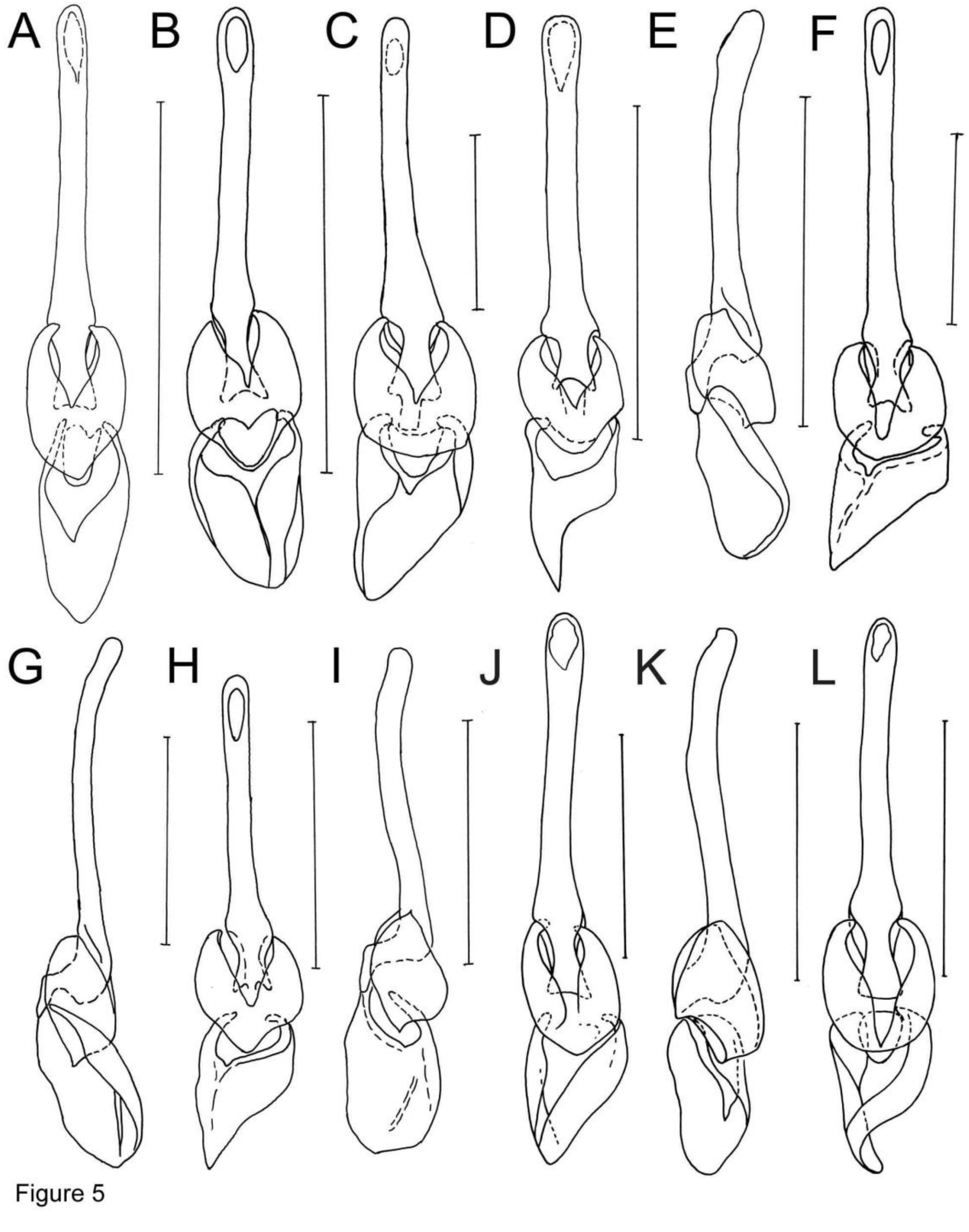


Figure 5

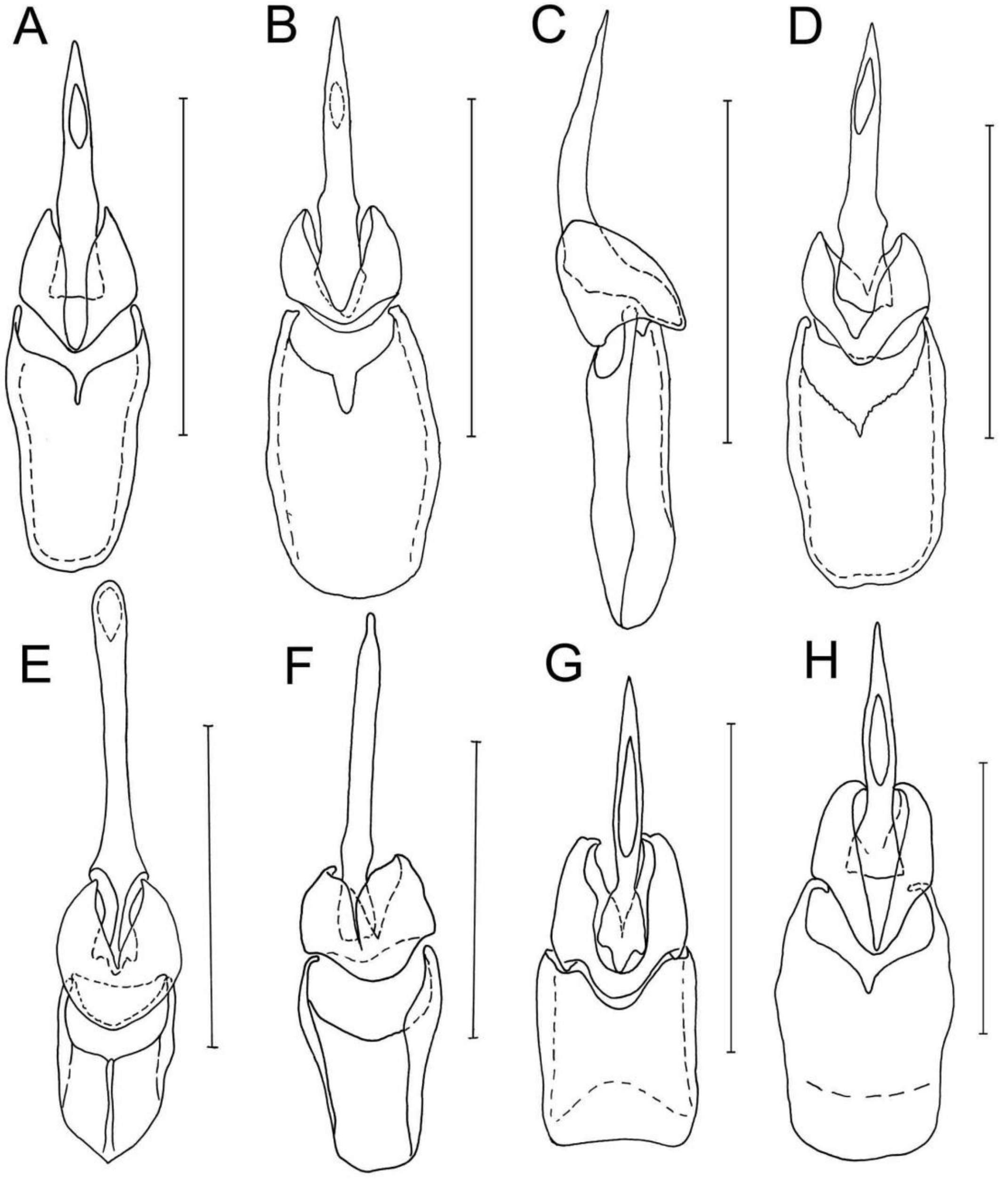


Figure 6

α – TAXONOMICAL PART-B OF THESIS

Note: This part of thesis was published in Zootaxa paper, 2306, 44 – 50 in 2009 named: A revision of *Paratelius* Kazantsev, 1992 (Coleoptera: Lycidae).

A revision of *Paratelius* Kazantsev, 1992 (Coleoptera: Lycidae)

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Abstract

The neotenic net-winged beetle *Paratelius* Kazantsev, 1992 is revised. Five species are placed in *Paratelius,* three of which are described as new: *P. emasensis* **n. sp.**, *P. snizeki* **n. sp.**, and *P. nigricornis* **n. sp.** All known species are treated with diagnoses, redescriptions, and data on variability and distribution. A key to the males of *Paratelius* species and the genera of Ateliini is provided.

Key words: Coleoptera, Lycidae, *Paratelius*, taxonomy, new species, key, Oriental Region

Introduction

The diversity of most groups of Oriental net-winged beetles remains insufficiently known, even though they are easily recognizable and interesting due to their biology. One such taxon is the neotenic net-winged beetle genus *Paratelius*. The genus was described by Kazantsev (1992) for a single ateliine species formerly placed by Pic (1912) in *Scarelus* Waterhouse, 1879. *Paratelius* is similar in general appearance to Indochinese species of *Atelius* Waterhouse, 1879 (Kazantsev, 1992, Bocak, 1997) and several species of *Scarelus*. The genus is defined by the presence of long setae on the elytra, which is shared with *Scarelus*, and by four longitudinal costae in the basal part of the elytra, which is similar to *Atelius* (Kazantsev, 1992). Although well defined by the combination of these characters, none of these characters appear to be synapomorphies for the genus, suggesting the genus may not be monophyletic. On the other hand, all *Paratelius* species share similar male genitalia with a very long, slightly curved phallus, which may help to distinguish them from both *Scarelus* and *Atelius*. *Paratelius* along with *Scarelus* and *Atelius* comprise the tribe Ateliini in the subfamily

Ateliinae (Bocak & Bocakova, 1990, 2008) *Paratelius* has a very similar biology to *Scarelus*. Adults are short lived as is a rule in the net-winged beetles and are slow moving on leaves of the lowest forest stratum and seldom fly. No specimens have been collected in degraded secondary forests or in open, sunny areas. The subfamily Ateliinae is known only from males, and we hypothesize that females are neotenic, as was found in the Lyropaeinae (Wong, 1996, Bocak et al., 2008, Levkanicova & Bocak, 2009). Larvae are unknown and, if similar to other net-winged beetles, develop in rotten wood and soil with a high content of organic matter (Bocak & Matsuda, 2003). All known species of *Paratelius* have been collected only in the Mount Kinabalu and Crocker Range in northeastern Borneo. The range of the genus is very small compared to the widespread *Scarelus* (the Great Sundas, Philippines, Myanmar and Malay Peninsula) and *Atelius* (Sri Lanka, Vietnam, and China: Hainan). The goal of this paper is to revise the taxonomy of the genus and to describe several new species recently collected in northeastern Borneo. Although neotenic lycids are known, current knowledge is insufficient to determine the degree to which neotenic development may have affected the macroevolution, distribution and speciation in these lineages.

Material and methods

This revision is based on recently collected material from the Oriental region. All species are represented only by adult males, as females and larvae of Ateliinae remain unknown. Male genitalia of all available specimens were dissected after muscles and fat bodies were removed by briefly boiling the apical part of the abdomen in 10% KOH. Illustrations were derived from photographs taken with a digital camera attached to a stereoscopic microscope. Holotype specimens were used for descriptions when available. Locality data were cited as given in original labels. Measurements were taken under a dissecting microscope using an ocular micrometer. The following measurements were taken: BL – body length; WH – width at humeri, PL – pronotum length; PW – pronotum width; Edist – minimum interocular distance in the frontal part of the cranium, Ediam – maximum eye diameter in a lateral view.

Depositories:

BMNH	Natural History Museum, London, United Kingdom
LMBC	Department of Zoology, Palacky University, Olomouc, Czech Republic

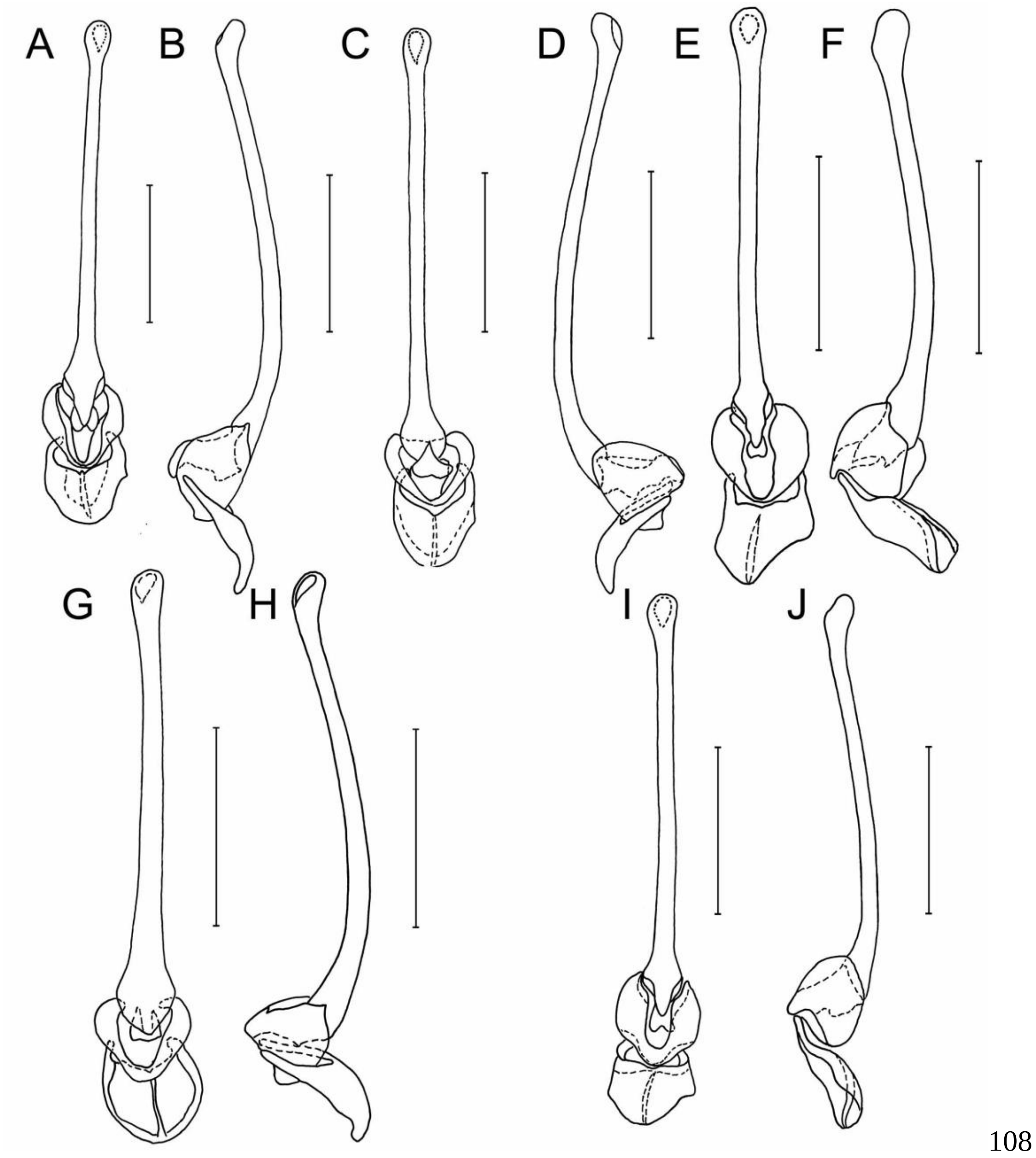
Genus *Paratelius* Kazantsev, 1992

Diagnosis: *Paratelius* resembles *Scarelus* in general appearance and has similar long setae between dense, short pubescence on elytra. *Paratelius*, like *Atelius*, bears four longitudinal costae on each elytron. In all known species the phallus is very long, slender and slightly curved (Figs 1A–1J).

Redescription: Similar to *Scarelus* in general appearance. Small-bodied, slender, 5.8–7.0 mm long. Most species brown to reddish brown colored, some uniformly testaceous; when dark colored, humeral part of elytra lighter and apical half of elytra dark. Head small, free, hypognathous, covered with short pubescence, surface mat, with fine structure. Frons convex; eyes small; antennal tubercles inconspicuous, divided by shallow depression; antennal cavities very close each to other, separated by narrow cranial bridge. Antennae 11-segmented, compressed, slightly serrate, long, surpassing elytral apex by 3 to 5 antennomeres, covered with dense, recumbent pubescence; apical antennomere longest, narrowed to the apex, pointed. Mandibles stout, quite long, slightly curved, shining, with smooth internal margin. Other mouthparts tiny. Labium and maxillae clearly visible without dissecting, reduced. Labium reaching from gular margin of mouth cavity to one third of its diameter: maxillae reaching to a half of diameter. Labial palpi 2-segmented, maxillary palpi 4- segmented, apical palpomere stoutest in both palpi. Labrum projected forwards, triangular. Pronotum trapezoidal, flat, posterior margin wider than frontal one, frontal margin slightly rounded, lateral margins convex, posterior angles acutely projected, posterior margin almost straight. Pronotal disc with single median longitudinal carina with very deep and narrow depression in middle part. Scutellum flat, trapezoidal, shiny, sparsely pubescent, usually emarginate at apex. Elytra flat, with four longitudinal costae. Costae connected by regular transverse ridges, whole elytra densely and shortly pubescent, also bearing sparse, stout, long, erect setae. Legs slender, compressed, densely pubescent. Tarsus with 5 tarsomeres. Male genitalia trilobate, uniform in general shape (Figs 1A-J). Phallus very long, widest at base, paramerae very short, globular in shape, phallobase longer than paramerae.

Distribution: Malaysia: Sabah State. Distribution is limited to mountain ranges in northeastern Borneo. These mountains were produced by a counterclockwise rotation of Borneo since the Late Miocene (Hall & Blundell, 1996). Based on the endemic occurence in a single mountain range, we may suppose speciation of all *Paratelius* species occurred in this region. *Paratelius* has not been recently collected in the lowlands of Borneo, and only the type specimen of *P. diversicornis* is recorded from Brunei without precise locality data.

Although Borneo was connected during the last glacial maximum to Indochina (Voris, 2000) and the generic structure of both faunas is similar, neither *Paratelius* from Borneo nor related *Atelius* from Vietnam expanded their ranges over the subaerial shelf of the Asian continent.



FIGURES 1A–J. Male genitalia in the ventral and lateral views. A, B *Paratelius snizeki* **n. sp.**; C, D *P. emasensis* **n. sp.**; E, F *P. nigricornis* **n. sp.**; G, H *P. diversicornis* (Pic).; I, J. *P. juvencus* (Kleine). Scales 0.5 mm.

Included species

Paratelius diversicornis (Pic, 1912)

Scarelus diversicornis Pic, 1912: 5. *Paratelius diversicornis* (Pic, 1912): Kazantsev, 1992: 100.

Material examined: Male. Malaysia, Borneo, W. Sabah, Crocker Range, road Keningau – Papan, v. 1999, leg. M. Snizek. (LMBC).

Diagnosis: *P. diversicornis* differs from all known *Paratelius* in the characteristic dark coloration of the elytra.

Redescription: Male. Body small, head and thorax dark brown; abdomen black; pronotum slightly lighter than elytra; elytra lighter at humeri, dark brown to black apically; eyes and anntennae black. Head small, densely pubescent; eyes small, hemispherically prominent, their interocular distance 3.4 times maximum eye diameter. Antennae slender, compressed, moderately flattened, surpassing apex of elytra by 3 antennomeres. Antennomeres 3–11 gradually more slender; apical antennomere eliptical. Elytra slender, parallel-sided, 3.47 times longer than width at humeri, with four well developed primary costae, covered with reddish pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate; phallus very long, slender, slightly curved; parameres short, reaching to one sixth of phallic length; phallobase short, subtle (Figs 1G-H).

Measurements: BL 6.2 mm, PW 1.2 mm, PL 0.8 mm, WH 1.5 mm, Edist 0.71 mm, Ediam 0.21 mm.

Distribution: Malaysia: Sabah: western part of the Crocker Range; Brunei (type locality).

Paratelius emasensis Malohlava et Bocak, n. sp.

Type material: Holotype, male. Borneo, Sabah, km 53 KK-Tambunan, 1650 m, Gn. Emas, 22. iii. – 6. iv. 2000, leg. Bolm. (LMBC); 2 paratypes, males. Same locality data (LMBC).

Diagnosis: *P. emasensis* **n. sp.** is similar to *P. nigricornis* **n. sp.** in possessing elytra with bright reddish coloration. These species differ in the dark brown to black head, pronotum, and antennae in *P. nigricornis* **n. sp.** and testaceous to reddish brown in *P. emasensis* **n. sp.** The slightly more curved phallus in *P. emasensis* supports separation of these species (Figs. 1C-D and 1E-F).

Description: Male. Body small, slender. Head and thorax red; abdomen dark brown; eyes black; scapus, pedicel, antennomeres 3–11 and legs light brown, coxae and mouth parts brown. Head small, densely pubescent; eyes small, hemispherically prominent, frontal interocular distance 3.4 times maximum eye diameter. Antennae compressed, slender, flattened, reaching over apex of elytra by 1.5 apical antennomeres. Antennomeres 3–11 gradually slender; apical antennomere eliptical. Elytra slender, 3.1 times longer than width at humeri, parallel sided, with four well developed primary costae, covered with red pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate; phallus very long, slightly turned upward; parameres short reaching one sixth of phallic length. Phallobase small, subtle (Figs 1C-D).

Measurements: BL 6.0 mm, PW 1.3 mm, PL 1.0 mm, WH 1.6 mm, Edist 0.71 mm, Ediam 0.21 mm.

Distribution: Malaysia: Sabah.

Etymology: The species epithet refers to type locality of this species, Gunung Emas in Sabah.

Remarks. The coloration of the antennomeres is slightly variable, and some specimens may have slightly darker apical antennomeres. However, it is notable that several basal antennomeres are brightly coloured in all available specimens of *P. emasensis* **n. sp.** DNA was isolated from one paratype, and sequences of several mtDNA and rRNA genes are accessible in the GenBank under the voucher number UPOL 000583 (Bocak et al., 2008).

***Paratelius juvencus* (Kleine, 1932)**

Scarelus juvencus Kleine, 1932 : 37–38. = *Paratelius iunius* Kazantsev, 1997: 184; Kazantsev & Yang, 1999: 246.

Type material: Holotype, male. B. N. Borneo, Mt. Kinabalu, Keuokok, 3.300 ft, 26 April 1929, H. M. Pendlebury coll., F. M. S. Museum (BMNH). **Other material examined:** Male, Borneo, Sabah, km 55 KK Tambunan, 1650 m, Gn. Emas, 22. iii. – 6. iv. 2000, leg. Bolm (LMBC); male, Borneo, Sabah, Mt. Kinabalu N. P., Feb 2000, M. Snizek (LMBC).

Diagnosis: *P. juvencus* is similar to *P. nigricornis* **n. sp.** in the coloration of pronotum and head. *P. juvencus* has more robust body with elytron less than 6 times longer than its width in the middle part and darker. The male genitalia of both species are similar (Figs 1I-J).

Redescription: Male. Body small, robust, head, thorax and abdomen black; elytra dark cinnamon brown; antennae, mouth parts and legs black. Head small, densely pubescent; eyes small, hemispherically prominent, frontal distance 3.4 times maximum eye diameter. Antennae slightly serrate, slender, flattened, antennomeres 3-10 triangular; last antennomere eliptical. Antennae reaching over apex of elytra by four antennomeres. Elytra wide, 3.1 times longer than width at humeri, parallel-sided, with four well developed primary costae, covered with reddish pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate; phallus very long, slightly turned upwards; parameres short, reaching one sixth of phallic length; phalobase very small, short and subtle (Figs 1I-J).

Measurements: BL 6.2 mm, PW 1.0 mm, PL 0.8 mm, WH 1.5 mm, Edist 0.71 mm, Ediam 0.21 mm.

Distribution: Malaysia: Sabah: Mt. Kinabalu, Crocker Range.

Paratelius nigricornis **Malohlava et Bocak, n. sp.**

Type material: Holotype, male. Borneo, Sabah, km 53, KK-Tambunan, 1650 m, Gn. Emas, 22. iii. – 6. iv. 2000, leg. Bolm (LMBC). Paratype: Same locality data (LMBC).

Diagnosis: *P. nigricornis* **n. sp.** is similar to *P. juvencus* in its dark colored pronotum. It differs mainly in the bright reddish coloration of the elytra and more slender body (the elytron about 8 times longer than the width in the middle part). The differences in male genitalia are very subtle (Figs 1E-F).

Description: Male. Body small; head, and thorax black; abdomen brown; elytra bright reddish brown; eyes black; scapus and pedicel brown; anntennae completely black; legs brown. Head small, densely pubescent; eyes small, hemispherically prominent, their distance 2.53 times maximum eye diameter. Antennae slender, flattened, reaching over apex of elytra by 3 antennomeres. Antennomeres 3–11 gradually slender; apical antennomere eliptical. Elytra slender, 3.16 times longer than width at humeri, parallel sided, with four well developed primary costae, covered with reddish pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate; phallus very long, slightly turned upwards; parameres short, subtle, reaching one fifth of phallic length; phallobase short, subtle (Figs 1E-F).

Measurements: BL 7.0 mm, PW 1.4 mm, PL 1.0 mm, WH 1.9 mm, Edist 0.71 mm, Ediam 0.28 mm.

Distribution: Malaysia: Sabah.

Etymology: The specific epithet refers to the black coloration of antennae.

Remark. DNA was isolated from the paratype, and sequences of several mtDNA and rRNA genes are accessible in the GenBank under the voucher number UPOL 000L15 (Bocak et al., 2008).

***Paratelius snizeki* Malohlava et Bocak, n. sp.**

Type material: Holotype, male. Borneo, Sabah, Crocker Mt., Gunung Emas env., 15.-27. iv. 1993, leg. Jenis & Strba (LMBC). Paratype: male, Borneo, Sabah, Mt. Kinabalu, 28 May 1999, M. Snizek lgt. (LMBC).

Diagnosis: *Paratelius snizeki* **n. sp.** is similar to *P. emasensis* **n. sp.** in the testaceous to reddish brown coloration of the cranium and pronotum. These species differ in the shape of antennomeres, which are more robust and acutely serrate in *P. snizeki*. Male genitalia differ in the relatively shorter phallus of *P. snizeki* (Figs 1A-B and 1C-D).

Description: Male. Body small, moderately slender; head, thorax, elytra reddish brown; abdomen dark brown; eyes black; antennae, mouth parts and legs brown. Head small, hypognathous; eyes small, hemispherically prominent; frontal interocular distance 3.04 times maximum eye diameter. Antennae slender, flattened, surpassing by 3 antennomeres apex of elytra. Antennomeres 3–11 gradually more slender; apical antennomere eliptical. Elytra slender, 3.69 times longer than width at humeri, parallel-sided, with four well developed primary costae, covered with dense brown pubescence. Legs moderately long, slender, flattened, densely pubescent. Male genitalia trilobate; phallus very long, slightly turned upwards; parameres short, reaching one fifth of phallic length; phallobase small and subtle (Figs 1A-B).

Measurements: BL 5.8 mm, PW 1.0 mm, PL 0.8 mm, WH 1.3 mm, Edist 0.64 mm, Ediam 0.21 mm.

Distribution: Malaysia: Sabah.

Etymology: The specific epithet is a patronym in honor of M. Snizek, the collector of the type specimen.

Key to genera of Ateliini and males of *Paratelius*

1.Elytra with long, erect setae......................................……………………............................... **2**

1'. Elytra without long erect setae, only short, dense pubescence present in whole elytra. Male genitalia with robust straight phallus, antennae often with widely triangular antennomeres 3-11 (Sri Lankan species), or at least slightly triangular in Indochinese species…... ***Atelius* Waterhouse**

2. Each elytron with three longitudinal costae, phallus straight, robust with obtuse apex or short, slender, and pointed at apex ....***Scarelus* Waterhouse**

2'. Each elytron with four longitudinal costae. Male genitalia with very slender, curved phallus (Figs 1A-J) (*Paratelius* Kazantsev)...............................…………………................. **3**

3. Head dark brown to black, pronotum similarly colored to or slightly lighter than head, antennae completely dark colored……………………... **4**

3'. Head testaceous to reddish brown, pronotum similarly colored………………................ **5**

4. Pronotum dark brown, usually lighter than coloration of head; elytra cinnamon brown; body robust, elytra 5.8 times longer than width at m.................................***P. juvencus* (Kleine)**

4'. Pronotum black, same color as head, elytra reddish brown, body slender, elytra 8.0 times longer than width at middle...............................……................................. ***P. nigricornis* n. sp.**

5. Elytra dark brown to black, slightly lighter at humeri, phallus slender, curved as in Figs 1G-H ……………………………………………………………………………… ***P. diversicornis* Pic**

5'. Elytra completely light brown to light reddish brown………………............................. **6**

6. Antennomeres 3-11 slender, antennomere 6 4.2 times longer than wide at middle, phallus very long and slender(Figs 1C-D) ....………..................................***P. emasensis* n. sp.**

6'. Antennomeres 3-11 more robust, antennomere 6 3.8 times longer than wide at middle, phallus slightly shorter that in *P. emasensis* (Figs 1A-B) .... ***P. snizeki* n. sp.**

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