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World review of *Laricobius* (Coleoptera: Derodontidae)

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Abstract

The Holarctic genus *Laricobius* (Derodontidae) is reviewed and a key to the species provided. There are 21 known species and those with known life history are predators of adelgids. The type specimen of *L. minutus* Nikitsky was lost prior to this study and types of *L. caucasicus* Rost were never located, though one specimen which lacks the abdomen is attributed to this species. One new species is described (*Laricobius naganoensis* **n. sp.**) and lectotypes were designated for *L. erichsonii* Rosenhauer and *L. sahlberg* Reitter. Europe has one described species, North America 3, and Asia 17. A cladistic analysis, based on 20 species, resulted in two broad groups, one which is confined to south-eastern Asia and Himalaya and has more shortened species with a narrower pronotum lacking explanate margins, and a more widespread Holarctic group, which is more typical of the genus type, being more elongate, with a transverse, fully explanate pronotum. The latter group includes four Asian species without ocelli, collected from *Tsuga* (hemlock) infested with *Adelges tsugae* Annand.

Key words: *Laricobius*, Derodontidae, bio-control, phylogeny

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Introduction

Laricobius is one of four genera in the family Derodontidae (Leschen and Beutel 2010), all of which with known biologies prey on adelgids (Franz 1958; Clark and Brown 1960; Lawrence and Hlavac 1979; Montgomery *et al*. 2011). There are currently 20 species included in this exclusively Holarctic genus, with 11 of the species described since 1999—all from Asia. Reasons for the increased rate of *Laricobius* descriptions are two-fold: new (but scant) material gleaned from bulk collections made in montane areas in Asia and deposited unidentified in museums, and recent efforts to obtain biological controls for *Adelges tsugae* Annand (the hemlock woolly adelgid), an introduced pest of *Tsuga canadensis* (L.) Carr. and *Tsuga caroliniana* Engelm. in eastern North America.

This taxonomic study was prompted by the recent doubling of described species and interest in *Laricobius* as a biocontrol genus, including the pending release of further species to eastern North America (Montgomery *et al*. 2011). Two species have been introduced to eastern North America: *Laricobius erichsonii* Rosenhauer, 1846 from Europe for the control the balsam wooly adelgid, *Adelges piceae* (Ratz.) (see Clark & Brown 1958), and *Laricobius nigrinus* Fender, 1945, endemic to Western North America and released to control *A. tsugae* (e.g., Zilahi-Balogh *et al*. 2002a,b).The family review by Lawrence and Hlavac (1979) included a brief review of the six known species and a key to the North American species. Since Lawrence and Hlavac (1979), two species from the Russian Far-East were described by Nikitsky (1992) and what followed was a flurry of new species descriptions. Biocontrol researchers working in collaboration with taxonomists have described four Asian species: *Laricobius baoxingensis* Zilahi-Balogh & Jelínek, 2007 (China: Sichuan), *Laricobius kangdingensis* Zilahi-Balogh & Jelínek, 2007 (China: Sichuan), *Laricobius taiwanensis* Yu & Montgomery, 2007 (Taiwan), and *Laricobius osakensis* Montgomery and Shiyake, 2011 (Japan). The remaining Asian species were described by Jiri Háva in several papers (Háva 2008, 2009a–d, 2010; Háva & Jelínek 1999; Jelínek & Háva 2001). I review the described species, confirm their taxonomic status by examining type specimens, and provide a key to facilitate their identification world wide. A cladistic analysis of the known species based on adult characters is included to determine if these characters relate to monophyletic groups. Biogeographic patterns, plant- and adelgid-host relationships are also examined in the context of these reconstructed phylogenies.

Methods

Type specimens and representative specimens of all species have been examined, apart from *L. minutus* Nikitsky in Nikitsky & Lafer, 1992 of which the specimens were lost prior to this study (N. Nikitsky, personal communication). Queries at major European collections for type specimens of *L. caucasicus* Rost, 1893 were unsuccessful and a single specimen from Georgia matching the description of Rost (1893) is treated as a specimen of *L. caucasicus*. Because it lacks the abdomen, I decided not to name this as a neotype.

Collection acronyms are as follows, along with the primary museum contact:

Andreas Pütz Private Collection, Eisenhüttenstadt, Germany (APUC)
California Academy of Sciences, San Francisco (CAS, Dave Kavanaugh)
Canadian National Collection of Insects Arachnids and Nematodes, Ottawa, Canada (CNC, Serge LaPlante)
Field Museum of Natural History, Chicago, USA (FMNH, James Boone)
Natural History Musuem, London, United Kingdom (BMNH, Roger Booth)
Hungarian Natural History Museum, Budapest, Hungary (HNHM, Otto Merkl)
Institute of Zoology, Academia Sinica, Beijing, China (IZAS)
Jiří Háva Private Collection, Praha, Czech Republic (JHAC)
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZC, Phil Perkins)
Museum für Naturkunde (Humboldt), Berlin, Germany (MFNB, Bernd Jaeger)
Muséum d´Histoire Naturelle, Geneve, Switzerland (MHNG, Giulio Cuccudoro)
Museum d´Histoire Naturelle, Paris, France (MNHN, Azadeh Taghavian)
National Museum of Natural Science, Taichung, Taiwan (NMNS)
National Muzeum Praha, Czech Republic (NMPC, Jiří Hájek)

Naturhistorisches Museum, Basel, Swizterland (NHMB, Michel Brancucci and Isabelle Zürcher)
New Zealand Arthropod Collection, Auckland, New Zealand (NZAC, Rich Leschen)
Osaka Museum of Natural History, Osaka, Japan (OMNH, Shigehiko Shiyake)
Peabody Museum of Natural History, Yale University, New Haven (YPM, Ray Pupedis) (USDA, PMNH also in YPM)
Russian Academy of Sciences, Laboratory of Insect Systematics, St. Petersburg, Russia (RASC, Alexander G. Kirejtshuk)
Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS, Wolfgang Schawaller)
United States National Museum, Washington, DC (NMNH, Gary Hevel)
University of New Hampshire, Durham (UNHD, Don Chandler)
Virginia Tech Research Collection, Blacksburg (VTRC, Tom McAvoy)
Zoological Museum, University of Moscow, Russia (ZMUM, Nicolai Nikitsky)

Measurements were made on the types and additional individuals where available. For antennal ratios, images were made of the heads and ratios were derived from these. Morphological terms follow those by Lawrence *et al.* (2010). Details regarding character definitions used in the descriptions follow the generic description and the list of characters used for the cladistic analysis.

The examination of material yielded several specimens that could not be placed into existing species, and these, along with a couple of others noted by Háva (2010), are listed in Appendix 1.

Laricobius Rosenhauer, 1846

Type species by monotypy, *L. erichsonii* Rosenhauer

Description (based on Leschen and Beutel 2010). Total length 1.25–3.04 mm. Body elongate, dorsally slightly convex and ventrally flattened. Surface glabrous with vestiture of erect, suberect, or decumbent setae; foveae on head (between the antennal insertion and the eye, see Lawrence and Hlavac 1979), pronotum, and ventrites (figs 24–28), lacking tubercles or well-developed ridges; punctation consisting of large macropunctures dorsally (figs 22, 23, 31, 33) and smaller micropunctures dorsally and ventrally; surfaces with microsculpture (mostly apparent in dissections using compound microscope, see fig 33). Color variable. Head slightly declined and not srongly prognathous, not abruptly constricted to form a neck; temples, transverse occipital ridge and stridulatory files absent. Antennal insertions more or less exposed in dorsal view; antennal grooves absent. Compound eyes finely facetted; interfacetal setae present; two ocelli present (absent in some species). Mandible bidentate without well-developed mola and prostheca. Corporotentorium without median process. Prothorax quadrate to transverse. Pronotum with lateral carinae complete, weakly to strongly explanate, with or without a distinct bead and not dentate along entire margin. Procoxal cavities open. Protrochantin exposed with cavities strongly transverse and externally open, but narrowly so by acute hypomeral processes. Elytra with 10 punctate rows or striae, plus scutellary striole; suture not deflected at apex; epipleuron present in apical third (ending at level of metaventrite). Mesoventrite with paired procoxal rests (fig 24). Mesocoxae conical. Tibial apices with an apical comb of spines; tarsomeres 1–3 lobed below. Abdominal ventrites 1 and 2 connate (fig 28), lateral pores and canals present. Ovipositor short with short styli.

Comments. Species of *Laricobius* can be distinguished from other members of Derodontidae by the vestiture of long setae, lobed tarsomeres, open procoxal cavities, presence of a scutellary striole and 10 rows of punctures on the eyltra. A key to the genera is provided in Lawrence and Hlavac (1979).

A few characters in Leschen and Beutel (2010) require updating as follows. Ocelli, which are a diagnostic feature of Derodontidae, have recently been recorded as absent in a few species of *Laricobius* (Montgomery *et al.* 2011; see also C10, below in cladistic analysis). Franz (1958b) referred to the ocelli of *Laricobius* as "dorsal lobes" because they did not have a sense organ visible in serial sections. True ocelli are confirmed by the innervation of the optic nerve with the ocellus which was been demonstrated by Leschen and Beutel (2004) for *Derodontus* LeConte. The mesoventrite has paired procoxal rests (not absent, as stated in Leschen and Beutel 2010). The ostium of the ejaculatory duct in the male genitalia of all derodontids is large and striate (figs 29, 30), and the distribution of this character in Coleoptera is unknown, though it does not appear in Cucujiformia which I have examined.

Cuticular features of adult derodontids and their potential function as chemical defense organs were discussed by Lawrence and Hlavac (1979). *Laricobius* has a range of cuticular features that include microsculpture (fig 33), micropunctures, macropunctures (figs 21–23, 31–33), and foveae (or pits; figs 24–27, 29). The difference between foveae and macropunctures is one of comparable size and depth of penetration of the integument and while micropunctures have a limited depth, I restrict the term foveae to those deeper invaginations at the four corners of the pronotum (seen more clearly in lateral view), on the ventrites and pleura, and the postantennal region of the head (see Lawrence and Hlavac 1979). Usually, these larger invaginations have white secretions, and in the postantennal fovea there are setae (see fig 6 of Lawrence and Hlavac 1979). The macropunctures of the elytra have been called "window punctures," by Lawrence and Hlavac (1979) and these do not appear to have the annulation or multiple rings as seen in other foveae (compare figs 24 and 33). Franz (1958b) discussed the arrangement of the macropunctures (= pits) on the head of *L. erichsonii* and discovered that the number is variable and in remaining species these cephalic macropunctures may be connected by a weak to well-developed furrow, which may also vary within some species. By contrast, the foveature (number and position), though, is consistent among the material I have dissected.

Various characters are critical for the identification of *Laricobius* species, and these are presented in the diagnoses and keys for each species. Coloration of the body and appendages is useful and in the diagnoses and cladistic analysis I have referred to color value (light or pale versus dark) while in the descriptions the color is detailed. Elytral striae of Asian species without an explanate pronotum tend to have several macropunctures posteriorly confluent, especially in striae rows 1–4 and/or the punctures are contained within deep grooves. Stria 1 may also have punctures that are posteriorly confluent in species that have an explanate pronotum.

Detailed life history studies and descriptions of immature stages exist for two *Laricobius* species (i.e., Zilahi-Balogh *et al*. 2006) and like other members of the family (Lawrence & Hlavac 1979; Crowson 1980; Lawrence 1982; Leschen & Beutel 2009), larvae and adults occur together in the same habitat. The foremost work on *Laricobius* biology and morphology was done by Franz (1958a,b) for *L. erichsonii*, and his studies should be consulted for a detailed account of the life history of this species. Predatory behavior of *Laricobius* is thought to be derived in the family (Leschen 2000) from more primitive associations with fungi where the Holarctic genus *Derodontus* is found on homobasidiomycte fungi (Lawrence & Hlavac 1979; Leschen 1994, 2002; Dodelin 2004) and the south temperate genus *Nothoderodontus* Crowson, sister taxon to *Laricobius*, is associated with sooty molds (Lawrence 1985).

Larvae have been described and keyed by several authors (Franz 1958; Fukuda 1963, Lawrence & Hlavac 1979; Lawrence 1991; Lawrence *et al*. 1999b; Zilahi-Balogh *et al*. 2006).

The classification and phylogenetic relationships of Derodontidae, and within it, were summarized by Leschen and Beutel (2010). The family was removed from Bostrichiformia (Lawrence & Newton 1995) and is now included in Derodontiformia Lawrence *et al*. (2010) along with Nosodendridae and Jacobsoniidae. Larval and adult morphology suggests that derodontids may be the sister taxon to Nosodendridae (Beutel 1996; Ge *et al*. 2007), but this is an open question as phylogenetic results are mixed (Caterino *et al*. 2002; Beutel & Leschen 2005; Ge *et al*. 2007; Hunt *et al*. 2007).

Though only four genera, there are three subfamilies in Derodontidae: Peltasticinae LeConte contains the single genus *Peltastica* Mannerheim, Derodontinae LeConte contains *Derodontus*, and Laricobiinae Mulsant & Rey contains *Laricobius* and *Nothoderodontus*. Relationships among the genera have been proposed by Crowson (1959, 1980), Fukuda (1963), and Lawrence & Hlavac (1979). Based on larval characters, Fukuda (1963) divided the family into the *Laricobius* and *Derodontus* groups, the latter consisting of *Pelatistica* and a clade comprising *Derodontus* and *Nothoderodontus*, largely in agreement with Crowson (1955, 1959; but see 1981). Lawrence & Hlavac (1979) placed *Peltastica* at the base of their two preferred trees, with uncertain relationships among *Derodontus*, *Laricobius*, and *Nothoderodontus*. In the recent cladistic analysis using adult and larval characters, Ge *et al*. (2007) showed that *Peltastica* is the sister taxon to the remaining Derodontidae.

Key to the species of *Laricobius*

1. Lateral margins of prothorax explanate with lateral carina well developed (fig 10); anterior pronotal foveae visible in dorsal view 2
   Lateral margins of prothorax not strongly explanate with lateral carina reduced only to a bead (fig 12); anterior pronotal foveae

visible only in lateral view 13
2.(1) Ocelli absent from head 3
Ocelli present on vertex of head 6
3.(2) Tibiae pale (see fig 8); orange color of elytra more vivid (fig 14); apex of medium lobe acute (fig 43) .. *L. naganoensis* **n. sp.**
Tibiae dark, about same color as the ventrites (fig 4); lighter color of elytra less vivid (figs 9, 16, 20); apex of medium lobe rounded to subacute (figs 39, 45, 49) 4
4.(3) Posterior pronotal tooth absent (fig ~~80~~16) ..... *L. osakensis* Montgomery & Shiyake
Posterior pronotal tooth present (fig ~~14~~) .9, 20 5
5.(4) Median carina of basal piece present (fig 48); color of elytra mainly dark red-brown (fig ~~9~~); Taiwan .....
..... 20 . *L. taiwanensis* Yu & Montgomery
Median carina of basal piece absent (fig 39); color of elytra light red-brown to light tan (fig ~~20~~); China. . 9 .....
..... *L. kangdingensis* Zilahi-Balogh & Jelínek
6.(2) Head darker than pronotum (Fig 3); color of hypomera and proventrite dissimilar 7
Head the same color as pronotum (fig 5); color of hypomera and proventrite the same 9
7.(6) Anterior ½ of pronotum with sides subparallel (fig 1) ..... *L. baoxingensis* Zilahi-Balogh & Jelínek
Anterior ½ of pronotum with sides convex (fig 11) 8
8.(7) Pronotum with evenly rounded sides; Caucasus ..... *L. caucasicus* Rost
Pronotum with weakly angulate sides; western North America ..... *L. laticollis* Fall
9.(6) Tibiae pale, lighter than femora 10
Tibiae dark and same color as femora 11
10.(9) Most specimens bicolored (fig 5), otherwise black (fig 6); apex of median lobe acute to rounded (fig 36) .....
..... *L. erichsonii* Rosenhauer
Body unicolored dark brown (fig 18); apex of median lobe apiculate (fig 47) ..... *L. sahlbergi* Reitter
11.(9) Body unicolored black (fig 15) ..... *L. nigrinus* Fender
Body bicolored (figs 10, 17) 12
12.(11) Posterior pronotal tooth present (fig ~~14~~); apices of parameres with an internal ridge; median lobe rounded to subacute (fig 46)
..... 17 ..... *L. rubidus* LeConte
Posterior pronotal tooth absent (fig ~~80~~); apices of parameres without an internal ridge; median lobe acute (fig 40) .....
..... 10 ..... *L. kovalevi* Nikitsky
13.(1) Scutellum pale, body color uniform tan (fig 13) ..... *L. mirabilis* Háva & Jelínek
Scutellum dark, body color different and not completely tan 14
14.(13) Head and epipleura pale (fig 19); anterior pronotal tooth absent ..... *L. schawalleri* Háva & Jelínek
Head and epipleura dark; anterior pronotal tooth present (fig 13) 15
15.(14) Elytral punctures separate and not confluent (fig 21) ..... *L. wittmeri* Háva
Elytral punctures posteriorly confluent, or at least contained within deep grooves (fig 12) 16
16.(15) Elytra bicolored (fig 2) ..... *L. bicolor* Háva
Elytral color uniform 17
17.(16) Color of head darker than pronotum (fig 7) ..... *L. incognatus* Háva
Color of head the same as the pronotum, body unicolored 18
18.(17) Femora pale; prothorax transverse (fig 8) ..... *L. jizu* Háva
Femora dark; prothorax elongate to quadrate 19
19.(18) Tibiae dark (fig 4); elytral surface incurvate; median carina of basal piece absent (fig 35) ..... *L. daliensis* Háva
20.(19) Tibiae pale (fig 12); elytral surface flat; median carina of basal piece present (fig 42) ..... *L. loebli* Jelínek & Háva

1. *Laricobius baoxingensis* Zilahi-Balogh & Jelínek, 2007

(figs 1, 34)

Diagnosis. Body bicolored. Head dark; ocelli present. Prothorax transverse with well developed lateral carina and sides explanate. Pronotum dark; posterior tooth present. Scutellum dark. Surface of elytra incurvate; elytral punctures not confluent. Epipleura at base dark. Ventrites mostly dark. Femora dark. Tibiae light. Aedeagus without median carina on phallobase; medium lobe acute; apices of parameres without an internal ridge.

Description. Length 1.25–1.50 mm (x = 1.34, n = 5). Body bicolored, with head dark brown to black; pronotum, hypomeron, elytra caramel brown to dark tan, scutellum black, epipleuron at base dark brown to black, prosternum darker than hypomeron, ventrites dark brown, lighter brown on the tip of the abdominal ventrites; antenna tan with AI darker, palpi tan, femora dark brown with apices lighter, tibiae and tarsi light brown to tan. Head with ocelli; u-shaped furrow present; interocular distance about 4x the width of the eye; macropunctures irregular to ovate, present in central area of frons; micropunctures coarse; setae erect, moderately elongate with an average length as long as 2/3 the width of the eye. Antenna with length of A3 about equal to A4, ratios 1.7:1.4:1.2:1.3:1.4:1.1:1.2:1.0:1.4:1.4:1.7; A11 strongly asymmetrical. Prothorax transverse, dorsoventrally flat-

tened, and widest at middle, sides parallel and straight in apical half and strongly converging posteriorly, and not constricted apically; about 0.80 x as long as wide (pronotal length/greatest pronotal width = 0.75–0.88, x = 0.80); depth = 0.17–0.36 mm (x = 0.27); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle right and subrounded, not forming a tooth; posterior angle indistinct and broadly rounded and with a short tooth; foveae visible in dorsal view; macropunctures on disc of variable in size, narrowly to well separated or contiguous, micropunctures coarse; setae decumbent to erect, long and greater than width of eye. Elytra about 3.30 x as long as wide (elytral length/greatest elytral width = 3.13–3.57, x = 3.30) and 3.17 x as long as pronotum (elytral length/pronotal length = 2.59–3.29, x = 3.17); surface incurvate at basal third; macropunctures not coalescing to form grooves (apart from those of striae 1 along the suture at apical third), separated by ½ to 1 puncture diameter; micropunctures fine; microsculpture not visible; setae suberect and about as long as length of the eye. Aedeagus with phallobase transverse, about 1/3 the length of the median lobe, median carina absent; median lobe projecting slightly beyond apices of parameres, relatively narrow with its greatest width subequal to width of paramere, apex acute, median groove or carina absent, ostium subapical; parameres slender and acute, short setae present on apices, internal subapical ridge absent.

Comments. *Laricobius baoxingensis* is the only species of the genus with a subparallel-sided explanate margin (fig 1). The pronotal shape is somewhat similar to *L. taiwanensis*, but can easily be distinguished from it by the coloration of the head and elytra and presence of ocelli.

The holotype in IZAS was not examined. The dissected male for this study was not part of the type series and the illustrations published in Háva (2009a, Fig. 3; 2009c, Fig. 4) of the genitalia do not match the specimens here. The pinned specimens of the type series were covered with a residue making some of the cuticular and setal characters difficult to observe. The spiculum gastrale was not observed.

Hosts. Plant: *Tsuga chinensis* (Franch) Pritzel ex Diels Adelgid: *Adelges tsugae*. (Annand)

Biology. Habitat (Zilahi-Balogh & Jelínek, 2007).

Distribution. China: Sichuan.

Type material examined. PARATYPES: 4, NiBa Gorge Forestry Station, near Qiagi village, Baoxing, Sichuan, China 5–8 IV 2002 coll. G.Zilahi-Balogh/T. McAvoy/ Host: Adelges, Tsuga chinensis Lat. 30°41‘44“ N; 102° 41‘44“ E Elev. 8899 ft./ 2 (hw in pencil)/ Laricobius **sp. n.** Jelínek & Zilahi-Balogh / Laricobius baoxingensis PT (hw on red label) (1, HNHM, 1, NMPC, 2, NMNH; note that the sequence of label data is different from Zilahi-Balogh & Jelínek 2007).

Additional material examined. 1, NiBa Gorge Forestry Station near Qiagi Village, Baoxing, Sichuan, China, 5–8 IV 2002, coll. G. Zilahi-Balogh/T. McAvoy, Laricobius **sp. n.** baoxingensis Jelínek & Zilahi-Balogh, 1 (VTRC); 1, IV 2005, Niba Gou, W Liu (VTRC); CHINA: Sichuan, Nibagou Jiaoqi Baoxing, 6 May 2007, Zhang G K from hemlock (IZAS).

2. *Laricobius bicolor* Háva, 2008

(fig 2)

Diagnosis. Body bicolored. Head dark; ocelli present. Prothorax quadrate without well developed lateral carina, sides not strongly explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra incurvate; elytral punctures posteriorly confluent. Epipleura dark. Ventrites dark. Femora dark. Tibiae dark.

Description. Length 3.04 mm. Body bicolored, mostly black, head, prothorax, scutellum, sides and apices of the elytra, and venter black, central disc of elytra red-brown; antenna tan with AI darker and club darker, palpi tan, femora and tibiae black, extreme base of tibiae and tarsi dark brown. Head with ocelli; u-shaped furrow absent; interocular distance about 2.5x the width of the eye; macropunctures distinctly ovate, somewhat shallowly impressed at middle and more impressed on the frons, scattered and present at the center of the frons; micropunctures coarse; setation short and decumbent, length shorter than 1/2 the width of the eye. Antenna with length of A3 about equal to A4, ratios 1.7:1.5:1.2:1.3:1.4:1.1:1.2:1.0:1.4:1.3:2.2; A11 strongly asymmetrical. Prothorax quadrate and highly convex, widest at middle, sides weakly constricted apically; about 0.81 x as long as wide (pronotal length/greatest pronotal width = 0.81); depth = 0.44 mm; pronotum not explanate, lateral carina without a distinct sharp edge; anterior angle acute, deflected, and forming a large lateroventrally directed tooth (the angle formed between the anterior margin and lateral carina, excluding the tooth, is about 65°); posterior angle indistinct and

broadly rounded and without a short tooth; anterior and posterior foveae visible only in lateral view; macropunctures ovate, deep, well separated to contiguous; micropunctures coarse; setae decumbent short and about half the width of eye. Elytra about 2.95 x as long as wide (elytral length/greatest elytral width = 2.95) and 3.47 x as long as pronotum (elytral length/pronotal length = 3.47); surface incurvate at basal third; macropunctures, especially of stria 1, coalescing posteriorly to form grooves, separated by an average of ½ to 1 puncture diameter; micropunctures fine; microsculpture not visible; setae suberect and shorter than half length of the eye.

Comments. *Laricobius bicolor* is the only species with bicolored elytra lacking an explanate pronotum. This species was described based on a single female.

Distribution. China: Sichuan.

Type material examined. HOLOTYPE (APUC). 1 female (card mounted and dissected), China: W Sichuan, Ya´an Prefecture, Tianquan Co., E Erlang Shan Pass/ 2900 m, 22.vi.1999 29.52.36N, 102.17.82E. leg A. Pütz/ Sammlung Andreas Pütz Eisenhüttenstadt (yellow label)/Laricobius **sp. n.** (hw) det. A. Pütz 2006 (hw)/ HOLOTYPE ♀ *Laricobius bicolor* **sp. n.** (hw) Jirí Háva 2007 (red label).

3. *Laricobius caucasicus* Rost, 1893

(figs 3)

Diagnosis. Body bicolored. Head dark; ocelli present. Prothorax transverse with well developed lateral carina and sides explanate. Pronotum light; posterior tooth absent. Scutellum dark. Surface of elytra not incurvate; elytral punctures not confluent. Epipleura light. Ventrites dark. Femora light. Tibiae light.

Description. Length 2.56 mm. Body bicolored, mostly dark tan above, head, scutellum, and ventrites black, hypomeron and epipleuron tan; antenna and legs tan with AI darker. Dorsal surfaces subglabrous. Head with ocelli; u-shaped furrow present; interocular distance about 4x the width of the eye; macropunctures ovate or fused, small to lineate and shallowly impressed, absent from central area of frons; micropunctures coarse; setation short, erect to suberect, length about half the width of the eye. Antenna with length of A3 about equal to A4, ratios 2.1:2.1:1.4:1.4:1.4:1.3:1.2:1.0:1.5:1.6:2.3; A11 not strongly asymmetrical. Prothorax transverse and dorsoventrally flattened, widest at middle, sides gradually narrowing anteriorly and more steeply convergent posteriorly; about 0.72 x as long as wide (pronotal length/greatest pronotal width = 0.72); depth = 0.24 mm; pronotum laterally broadly explanate with well developed lateral carina with a distinct sharp edge; anterior angle about 65° and not forming a tooth (may be obscured by setae); posterior angle indistinct and broadly rounded and without a short tooth; foveae visible in dorsal view; macropunctures ovate, deep, and well-separated; micropunctures coarse; setae erect and elongate, longer than half the width of eye. Elytra about 3.30 x as long as wide (elytral length/greatest elytral width = 3.30) and 3.41 x as long as pronotum (elytral length/pronotal length = 3.41); surface not incurvate at basal third; macropunctures not coalescing posteriorly to form grooves, separated by an average of 1 puncture diameter; micropunctures fine; microsculpture not visible; vestiture biseriate, mostly consisting of suberect setae, with scattered erect setae, elongate and about 2/3 the length of the eye.

Comments. Among the species that have an explanate pronotal margin, *L. caucasicus* is one of three species that has the head darker than the pronotum. It can be distinguished from *L. laticollis* and *L. baoxingensis* by the shape of the pronotum.

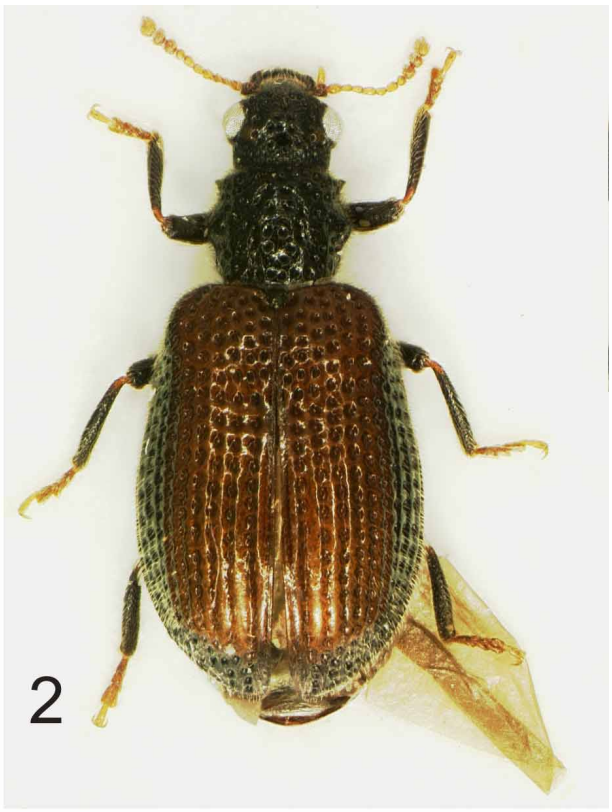
Rost (1893) mentions in the description that *L. caucasicus* that there is a shallow impression before the middle of the elytra; this feature is lacking in the specimen here examined.

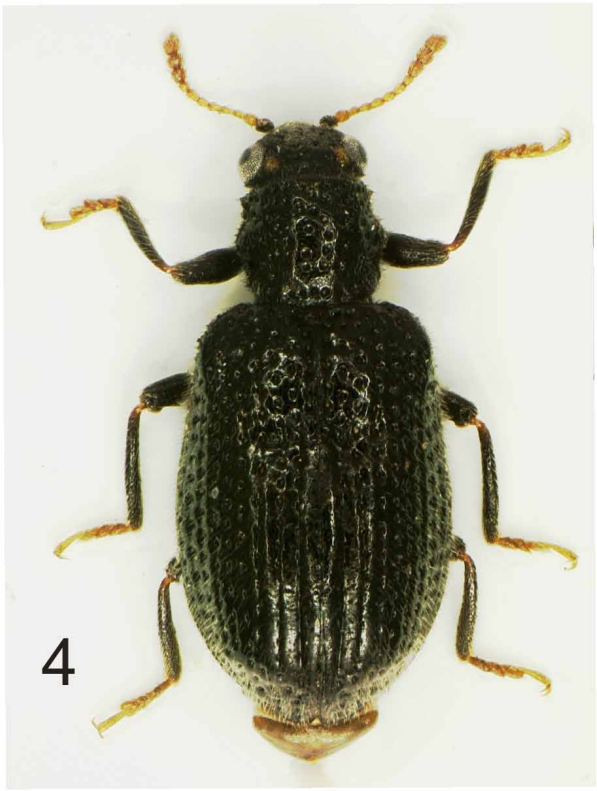
Háva (2006) listed the type deposition of Rost's specimen(s) of *L. caucasicus* as questionably in the MFNB, and queries for types to Berlin and Dresden where some of the Rost material was eventually deposited, either by direct deposition or by exchange (Horn *et al*. 1990), did not yield specimens. A single specimen that is provisionally identified as *L. caucasicus* based on the original description and matching the distribution recorded in Rost (1893) is described here. I decided not to name this specimen as a neotype because the abdomen and hind legs of the female specimen (N. Havill, pers. com.) were removed for DNA work prior to this study.

Hosts. Plant: *Abies nordmanniana* (Steven) Spach.

Distribution. Georgia: Guria.

Material examined. 1, GEORGIA: Guria Province Bakhmaro 9 June 2007 Coll. M. Kenis ex. Abies nordmanniana, Laricobius caucasicus?, Sample: Havill 07-66 (YPM)





FIGURES 1–4. Dorsal habitus. 1, *Laricobius baoxingensis*; 2, *L. bicolor*; 3, *L. caucasicus*; 4, *L. daliensis*.

4. *Laricobius daliensis* Háva, 2009b
(figs 4, 35)

Diagnosis. Body unicolored. Head dark; ocelli present. Prothorax quadrate without well developed lateral carina, sides not strongly explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra incurvate; elytral punctures posteriorly confluent. Epipleura dark. Ventrites dark. Femora dark. Tibiae dark. Aedeagus with median carina on phallobase; medium lobe subacute; apices of parameres without an internal ridge.

Description. Length 2.54. Body unicolored black; antenna with AI black, funicle light tan, club brown; palpi tan, extreme bases of tibiae and tarsi brown. Head with ocelli; u-shaped furrow indistinct; interocular distance about 2.5x the width of the eye; macropunctures ovate and shallowly impressed but slghtly more impressed on frons; micropunctures coarse; setation very short and suberect, length shorter than 1/3 the width of the eye. Antenna with length of A3 about equal to A4, ratios 1.9:1.5:1.2:1.3:1.4:1.3:1.3:1.0:1.6:1.6:2.2; A11 strongly asymmetrical. Prothorax quadrate and highly convex, widest at middle, sides sinuate; about 0.81 x as long as wide (pronotal length/greatest pronotal width = 0.81); depth = 0.36; pronotum not laterally explanate, lateral carina without a distinct sharp edge; anterior angle acute, deflected, and forming a short laterally directed tooth (the angle formed between the anterior margin and lateral carina, excluding the tooth is about 60°); posterior angle indistinct and broadly rounded and without a short tooth; anterior foveae visible only in lateral view, posterior fovea visible dorsally; macropunctures ovate, deep, anteriorly contiguous or well-separated; micropunctures coarse; setae short, erect, and about 1/3 the width of eye. Elytra about 3.16 x as long as wide (elytral length/greatest elytral width = 3.16) and 3.38 x as long as pronotum (elytral length/pronotal length = 3.38); surface incurvate at basal third; macropunctures, especially of striae 1–4, coalescing posteriorly to form grooves, separated by an average of ½ to 1 puncture diameter, but those of striae 1–3 fusing at incurvature; micropunctures sparse; microsculpture not visible; setae suberect and short, about 1/3 length of the eye. Aedeagus with phallobase subquadrate, about 2/3 the length of the median lobe, median carina present; median lobe projecting slightly beyond apices of parameres, apex subacute, median groove present; parameres broad and acute with a distinct subapical tooth, moderately short setae present on apices. Spiculum gastrale apically broad.

Comments. Among the species that have the elytral punctures posteriorly coalescing, *L. daliensis* is the only species with dark tibiae that is the same color as the femora. This species is known from a single specimen. The aedeagus of the type specimen was drawn and observed from its original placement on the card with the specimen, therefore some of the aedeagal characters were not observed (the width of the median lobe, the placement of ostium and presence of internal subapical ridge).

Distribution. China: Yunnan.

Type material examined. HOLOTYPE (APUC). 1 male (card mounted and dissected), China, Yunnan {CH07-03}, Dali Bai Auton. Pref., Diancang Shan W Dali, 25°41´49´´N, 100°06´24´´E, 2970 m, sifted at rock edges and under small shrubs, 28.V.2007, leg. A. Pütz/ Laricobius n. sp. ♂ (hw) det. A. Pütz 2007 (hw)/HOLOTYPE ♂ *Laricobius daliensis* **sp. n.** Jiří Háva 2009 (red label with thin black border).

5. *Laricobius erichsonii* Rosenhauer, 1846
(figs 5, 22, 24, 26, 31, 36)

Diagnosis. Body bicolored or unicolored. Head dark; ocelli present. Prothorax transverse with well developed lateral carina and sides explanate. Pronotum dark; posterior tooth usually present. Scutellum dark. Surface of elytra usually not incurvate; elytral punctures not confluent. Epipleura at base dark. Ventrites dark. Femora dark. Tibiae light. Aedeagus without median carina on phallobase; medium lobe acute; apices of parameres without an internal ridge.

Description. Length 2.36–2.78 mm (x = 2.55, n = 16). Body unicolored black (in southern European forms) or more typically bicolored with head, prothorax, scutellum, epipleura, and ventrites light brown to black, elytra along sides to apex (covering striae 7 or 8–10) and suture, and femora light brown to black, or sutural stripes distinct only to basal 1/3, with the broad central disc red brown; antenna reddish brown to light tan with AI and club often slightly darker, palpi, tibiae, and tarsi reddish brown to tan (tibiae lighter than femora). Head with ocelli; u-shaped furrow present; interocular distance about 4x the width of the eye; macropunctures weakly to strongly impressed,

ovate or fused and lineate, sometimes present at the center of the frons; micropunctures coarse; setation elongate, mostly erect to suberect, average length about 2/3 the width of the eye. Antenna with length of A3 about equal to A4, ratios 2.1:1.6:1.6:1.4:1.3:1.2:1.1:1.0:1.4:1.6:2.1; A11 not strongly asymmetrical. Prothorax transverse and dorsoventrally flattened, widest at middle, sides weakly sinuate or unevenly convex, with margin converging more sharply posteriorly than anteriorly; about 0.72 x as long as wide (pronotal length/greatest pronotal width = 0.72–0.80, x = 0.84); depth = 0.26–0.36 mm (x = 0.31); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle about 65° and forming a tooth; posterior angle indistinct and broadly rounded and often with a short tooth; foveae visible in dorsal view; macropunctures ovate, deep, usually well-separated, may sometimesbe contiguous; micropunctures coarse; setae erect and elongate, about as long as width of eye. Elytra about 3.30 x as long as wide (elytral length/greatest elytral width = 3.14–3.58, x = 3.30) and 3.17 x as long as pronotum (elytral length/pronotal length = 2.96–3.29, x = 3.17); surface typically not incurvate (present in some specimen, but usually very weak) at basal third; macropunctures not coalescing posteriorly to form grooves (apart from those of striae 1 along the suture at the apical 1/3 in some specimens), separated by an average of 1/2 puncture diameter; micropunctures fine; microsculpture present or absent; vestiture mostly consisting of suberect setae with scattered erect setae, elongate and average length about 2/3 the length of the eye. Aedeagus with phallobase transverse, about 1/2 the length of the median lobe, median carina absent; median lobe projecting slightly beyond apices of parameres, relatively broad with its greatest width larger than the width the parameres, apex acute, median groove or carina absent, ostium subapical; parameres moderately broad and subacute, long and short setae present on apices, internal subapical ridge absent. Spiculum gastrale apically acute and narrowed.

Comments. *Laricobius erichsonii* can be distinguished from other members having an explanate pronotal margin by the bicolored elytra, anterior lateral margin forming a tooth, and the tibiae pale, lighter than femora. The last character, in combination with the large elytral punctures that are uniform in size will separate *L. erichsonii* from the similar looking *L. rubidus*.

Gorham (1878) referred to a species in the Fry collection from France as possibly identical to "*lituratus,* Costa" and a "new species" supposedly listed in Chevrolat (1874: 28). Neither the species name "*lituratus*" nor the genus *Laricobius* was in Chevrolat (1874) cited by Gorham (1878) and the page referred to concerns Orthoptera. The Gorham reference was mistaken by Háva (2007) who incorrectly listed *L. lituratus* Gorham, 1878:156 as a synonymn of *L. erichsonii;* the former name originally described in *Salpingus* Illiger is now recognized as *Lissodema lituratum* (A. Costa, 1847:158; see Pollock and Löbl (2008)).

The type specimens of *L. erichsonii* were listed questionably in the MNHN by Háva (2009) but were obtained from MFNB. Pic (1895:88) named a variety from Southern Europe, the subspecies *niger*, that has black elytra and stronger punctation than the typical bicolored forms elsewhere. Háva (2009) listed the type depository of *L. erichsonii niger* as MNHN but specimens were not located there. Black specimens were examined from Switzerland and France, but the series are mixed with very dark forms, most with consistent elytral color patterns as seen in typical forms and there was no marked difference in the punctation among these specimens.

I have examined no recent specimens of *L. erichsonii* which was introduced to North America (Nova Scotia, New Brunswick, Newfoundland, Washington and Oregon, see Clark & Brown 1958, 1960, Hatch 1962, Lawrence & Hlavac 1979, and Majka 2007) after first being reported in Maine (Lovell 1915). This observation was followed up by collection queries to North American museums and literature searches (systematic, biocontrol, and faunistics). These data corroborate evidence that *L. erichsonii* was last observed in North America in 1974 and all vouchers of field recovery one or more years following release in eastern North America were *L. rubidus* (M. Montgomery, pers. com.).

Hosts (Franz 1958a). Plants: *Larix decidua* Mill., *Pinus cembra*, L., *Pinus mugo* Turra, *Pinus sylvestris* L. Adelgids: *Adelges nusslini* (Bomer), *Adelges piceae* (Ratzeburg) preferred host according to Franz 1958a), *Pineus pineoides* (Cholodkovsky), *Pineus strobi* (Hartig).

Biology. Natural history (Franz 1958a,b; Clark & Brown 1958).

Distribution (Háva 2007). Austria, Belgium, Bulgaria, Croatia, Czech Republic, Denmark, France, Great Britain, Germany, Hungary, Liechtenstein, Italy, The Netherlands, Poland, Romania, Slovakia, Switzerland, Serbia and Montenegro.

Type material examined. LECTOTYPE (MFNB). 1 (unknown sex, point mounted on very short point), 17843/ HIST.-Coll. (Coleoptera) Nr. 17843 Laricobius Erichsonii Rosenh. Tyrol. Rosenhauer Zool. Mus. Berlin (black bordered white label)/Erichsonii Rosenhauer* Tyrol. Rosenh. (elegant hw on black bordered faded white

label)/ SYNTYPUS Laricobius erichsonii Rosenhauer; 1846 labelled by MNHUB 2009/ LECTOTYPE Laricobius erichsonii Rosenhauer, desig, R. Leschen, 2009. PARALECTOTYPES (MFNB). 3, (unknown sex, point mounted on very short point), HIST.-Coll. (Coleoptera) Nr. 17843 Laricobius Erichsonii Rosenh. Tyrol. Rosenhauer Zool. Mus. Berlin (black bordered white label)/ SYNTYPUS Laricobius erichsonii Rosenhauer; 1846 labelled by MNHUB 2009/ PARALECTOTYPE Laricobius erichsonii Rosenhauer, desig, R. Leschen, 2009.

Additional material examined. EUROPE: Austria: 2, Zirbitzkogel, Eduard Knirsch (FMNH). Czech Republic: 3, Kostelec n. Boh. 7.53.; ex coll. Pfeffer (NMPC). England: 1, Shrubland Estate (ES) TM15., 31/V, C. Johnson (NZAC). France: 3, G. Serullaz, Modane, Laric. erichsonii vr niger, Coll. A. Méquignon (MHNG); 13, Alp. Hte Prov.; Col. d'Allos, 2150m; 12.IX.1982 Löbl (MHNG); 1, Gard, Mt. Aigual, 1300m, Col de Serreyrede, 6.IV.1980, Löbl (MHNG). Germany: 14 Süd-Tyrol, Reittter (1, CAS; 7, FMNH; 6 NMPC); 2, Hanau (RASC); 2, Limburg, Suffrian (MFNB); 1, Ex. Adelges, Black Forest, 4. 1969 (NZAC). Italy: 1, Torino, Sentriéne, 2150 m. 28.VIII.67, A. Comellini (MHNG). Sweden: 3, Sweden (NMNH). Swizerland: 2, Grisons, s/Samnaun, (2050 m) 26.VIII.68, Cl. Besuchet (MHNG); 1, Ti, Gambarogna, 1600 .6/38, Toumayeff (MHNG); 1, Grisons, Val Poschiavo, 2050 m, s/ Cavaione 27.VIII, C. Besuchet 83 (MHNG); Zuoz, Eng. Gr, Coll. 9/74 1640, Toumayeff (MHNG); 5, Enga din; Helena Pavlov; кол. РЭО (Елены Павл.) (RASC). NORTH AMERICA (all from lab colonies): Canada: Fredricton, New Brunswick, 1954 (CNC); 3, Vancouver, 1964 (CNC). United States: Bent Creek Lab, NC; 5-17-60, G.D. Amman (YPM).

6. *Laricobius incognatus* Háva, 2009a

(figs 7, 37)

Diagnosis. Body bicolored. Head dark; ocelli present. Prothorax transverse without well developed lateral carina, sides not strongly explanate. Pronotum light; posterior tooth absent. Scutellum dark. Surface of elytra incurvate; elytral punctures posteriorly confluent. Epipleura dark. Ventrites dark. Femora light. Tibiae light. Aedeagus with medium lobe subacute.

Description. Length 2.64 mm. Body bicolored, mostly dark tan dorsally and the hypomera, head, venter, scutellum, and epipleura chocolate brown; antenna with AI dark tan, funicle light tan, club dark tan; palpi light tan, femora, tibiae and tarsi tan, with the metafemora brown to apical 1/3. Head with ocelli; u-shaped furrow absent; interocular distance about 2x the width of the eye; macropunctures ovate and deeply impressed and present at the center of the frons; micropunctures coarse; setation short, length shorter than 1/3 the width of the eye. Antenna with length of A3 about equal to A4, ratios 2.0:1.7:1.3:1.4:1.5:1.3:1.2:1.0:1.6:1.5:2.2; A11 strongly asymmetrical. Prothorax slightly transverse and moderately convex, widest at middle, sides sinuate, but not constricted greatly; about 0.79 x as long as wide (pronotal length/greatest pronotal width = 0.79); depth = 0.32; pronotum not laterally explanate, lateral carina without a distinct sharp edge; anterior angle acute, deflected, and forming a short laterally directed tooth (the angle formed between the anterior margin and lateral carina, excluding the tooth is about 90°); posterior angle indistinct and broadly rounded and without a short tooth; anterior foveae visible only in lateral view, posterior foveae visible in dorsal view; macropunctures ovate, deep, and well-separated, micropunctures present but sparse; setae short, and about 1/2 the width of eye. Elytra about 2.76 x as long as wide (elytral length/ greatest elytral width = 2.76) and 3.40 x as long as pronotum (elytral length/pronotal length = 3.40); surface incurvate at basal third; macropunctures, especially of striae 1–4, coalescing posteriorly to form grooves, separated by an average of ½ of a puncture diameter; micropunctures fine; microsculpture not visible; setae suberect and short, about 1/3 length of the eye. Aedeagus with phallobase slightly transverse and rectangular, about 2/3 the length of the median lobe; median lobe projecting significantly beyond apices of parameres, relatively narrow, apex subacute; parameres broad and apically blunt, apices curving towards midline and ending in a sharp point, asetose. Spiculum gastrale apically broad.

Comments. *Laricobius incognatus* can be distinguished from other species having posteriorly confluent elytral punctures by its bicolored body and uniformly colored elytra; the relatively more transverse prothorax and black scutellum will also separate this species from the similar-looking *L. mirabilis*.

This species was described from two male specimens from the Shennongjia Mountains and I examined the holotype which was covered with a residue making the cuticular and setal characters difficult to assess (the setae were stuck flat against the cuticle). The genitalia was not cleared and was drawn from the card mount, so some of

the characters were not examined (the width of the median lobe, presence of median carina, and the placement of ostium and presence of internal subapical ridge).

FIGURES 5–8. Dorsal habitus. 5, *Laricobius erichsonii*; 6, *L. erichsonii* (dark form); 7, *L. incognatus*; 8, *L. jizu*.

Distribution. China: Hubei.

Type material examined. HOLOTYPE (JHPC). 1, male (card mounted and dissected, right metatarsus missing), China, W Hubei, 10.–14.VI. **DASHENNONGJIA** mts. 31.5N 110.3E, 2100–2900m Jaroslav Turna leg., 2002/HOLOTYPE Laricobius incognatus **sp. n.** Jiři Háva 2009 (name hw, red label).

7. *Laricobius jizu* Háva, 2010a

(figs 8, 38)

Diagnosis. Body unicolored. Head dark; ocelli present. Prothorax quadrate without well developed lateral carina, sides not strongly explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra incurvate; elytral punctures posteriorly confluent. Epipleura dark. Ventrites dark. Femora light. Tibiae light. Aedeagus with medium lobe acute.

Description. Length 2.40 mm. Body unicolored chocolate brown; antenna with AI dark tan, funicle light tan, club dark tan; palpi light tan; legs unicolored tan. Head with ocelli; u-shaped furrow absent; interocular distance about 2x the width of the eye; macropunctures ovate and deeply impressed, scattered and present at center of frons; micropunctures fine; setation short, decumbent, length about 1/3 the width of the eye. Antenna with length of A3 distinctly shorter than A4, ratios 2.0:2.0:1.0:1.4:1.6:1.2:1.6:1.2:1.8:2.0:2.4; A11 strongly asymmetrical. Prothorax quadrate and convex, widest at middle, sides sinuate; about 0.8 x as long as wide (pronotal length/greatest pronotal width = 0.8); depth = 0.5 mm; pronotum not laterally explanate, lateral carina poorly developed; anterior angle acute and deflected, forming a short tooth (the angle formed between the anterior margin and lateral carina, excluding the tooth, is about 90°); posterior angle indistinct and broadly rounded and without a short tooth; anterior foveae visible only in lateral view, posterior foveae visible in dorsal view; macropunctures ovate, deep, and well-separated, micropunctures fine; setae short, decumbent and about 1/3 to 1/2 the width of eye. Elytra about 1.43 x as long as wide (elytral length/greatest elytral width = 1.43) and 2.8 x as long as pronotum (elytral length/pronotal length = 2.80); surface incurvate at basal third; macropunctures, especially of striae 1–4, coalescing posteriorly to form grooves, separated by an average of ½ of a puncture diameter; micropunctures fine; microsculpture not visible; setae suberect, short, about 1/3 length of the eye. Aedeagus with phallobase slightly transverse and rectangular, about 2/3 the length of the median lobe; median lobe projecting significantly beyond apices of parameres, apex acute and triangulate with a dorsal carina; parameres broad and apically blunt, and anvil-shaped with laterally directed tooth, subapical setae present and moderately elongate. Spiculum gastrale apically broad.

Comments. *Laricobius jizu* can be distinguished from the similar-looking species *L. daliensis* and *L. loebli* by the unicolored, tan legs. This species is known from a single male specimen. The genitalia were drawn from the carded specimen and the width of the median lobe, presence of median carina, the placement of ostium and presence of internal subapical ridge were not observed.

Hosts. Plant: *Tsuga*.

Distribution. CHINA: Sichuan, Yunnan.

Type material examined. HOLOTYPE (NHMB): YUNNAN, 30 May–3Jun JIZU MTS., 1983 25.58N 100.21E, Bolm lgt., 2800/HOLOTYPE ♂ *Laricobius jizu* **sp. n.** J. Háva det. 2009 (red label with narrow black border).

Additional material examined. CHINA Sichuan, Goudingshan Danba, 19 Oct 2006, Lu, W H, from hemlock (IZAS).

8. *Laricobius kangdingensis* Zilahi-Balogh & Jelínek, 2007

(figs 9, 39)

Diagnosis. Body bicolored. Head dark; ocelli absent. Prothorax transverse with well developed lateral carina and sides explanate. Pronotum dark; posterior tooth present. Scutellum dark. Surface of elytra incurvate; elytral punctures not confluent. Epipleura at base dark. Ventrites dark. Femora dark. Tibiae light. Aedeagus without median carina on phallobase; medium lobe subacute; apices of parameres without an internal ridge.

Description. Length 2.36–2.80 mm (x = 2.59, n = 8). Body bicolored with head, prothorax, scutellum, elytra along sides to level of abdominal ventrite 2 (covering striae 9–10, sometimes striae 8) and suture along scutellary

striole (sometimes to apex or absent), epipleuron, and venter chocolate brown; elytra reddish brown to dark tan; antenna reddish brown to dark brown with AI darker (not the club), palpi, femora, and tibiae dark brown, tarsi lighter. Head without ocelli; u-shaped furrow present, but very shallow and broad; interocular distance about 4x the width of the eye; macropunctures rounded distinct to indistinct and not rounded, fusing sometimes to form irregular trenches; micropunctures fine to coarse; setae erect, moderately elongate with an average length as long as 2/3 the width of the eye. Antenna with length of A3 about equal to A4, ratios 1.7:1.4:1.3:1.2:1.2:1.0:1.1:1.0:1.2:1.2:1.7; A11 not strongly asymmetrical. Prothorax slightly transverse and rectangular, dorsoventrally flattened, and widest at basal third, sides converging anteriorly from widest point and weakly convex posteriorly; about 0.81 x as long as wide (pronotal length/greatest pronotal width = 0.76–0.87, x = 0.81); depth = 0.24–0.40 mm (x = 0.33); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle 90º to about 80° and subacute, not forming a tooth; posterior angle distinct and marked by a short tooth; foveae visible in dorsal view; macropunctures on disc indistinct, shallowly to well-impressed and well-separated; micropunctures coarse; setae erect, long and 2/3 or equal to width of eye. Elytra about 3.32 x as long as wide (elytral length/greatest elytral width = 2.97–3.79, x = 3.32) and 3.15 x as long as pronotum (elytral length/pronotal length = 3.06–3.25, x = 3.15); surface weakly incurvate at basal third; macropunctures not coalescing to form grooves, separated by 1/2 puncture diameter; micropunctures fine; microsculpture not visible; setae suberect and long, about 2/3 length of the eye. Aedeagus with phallobase quadrate, about 1/2 the length of the median lobe, median carina absent; median lobe projecting slightly beyond apices of parameres, narrow with its greatest width larger than the width of the parameres, apex subacute, median groove or carina absent, ostium subapical; parameres slender and acute, very short setae present on apices (visible under high magnification), internal subapical ridge absent. Spiculum gastrale apically narrow.

Comments. *Laricobius kangdingensis* can be distinguished from most species by the lack of ocelli. It can be reliably distinguished from the other ocelli-lacking species by its genitalia and distribution.

The holotype (IZAS) was not examined, but several paratypes were available for study. The sequence of information on the label data of the type specimens I examined were not as they appear in Zilahi-Balogh & Jelínek (2007).

Hosts. Plant: *Tsuga chinensis, Tsuga dumosa* (D. Don) Eichler. Adelgid: *Adelges tsugae*.

Biology. Habitat and rearing under quarantine (Zilahi-Balogh & Jelínek, 2007).

Distribution. China: Sichuan.

Type material examined. PARATYPES. 12IV2002 Luoxiba Deng, Kangding Co. Sichuan Prov. China, coll. T. McAvoy/G. Zilahi-Balogh/ Host: Adelges infested Tsuga chinenis [sic] Lat/long: 30º03‘00“N/102º02‘00“ elev: 2840 m/ Paratype 5 ♀ (5 ♀ hw)/ / Laricobius kangdingensis PT (hw on red label) (1, NMPC, 2, NMNH).

Additional material examined. 4, 12 IV 2002, Luoxiba Deng, Kangding Co. Sichuan Prov, China; coll: T. McAvoy/G. Zilahi-Balogh, Host: Adelges infested Tsuga chinensis, Lat/long: 30º 03' 00" N/102° 02' 00" E, elev: 2840 m, Laricobius **sp. n.** kangdingensis Zilahi-Balogh & Jelínek (VTRC); 3, Houditong, Ningshan Co., Shaanxi, 17 Oct. 2002, G Yu (YPM); 3, Sichuan Province, Danba County, Donggu town, Maoniugou, 1 December 2007, Zhang Dekui, Havill Sample # 08-267 (YPM); 2, same but Havill Sample # 08-269 (YPM); 5, same but 30.61 N 101.76 E, 2710 m, Havill sample 08- (YPM); 2, Sichuan Province, Lixian, Duergou; downtown Dagou, 31.58 N 102.95 E, 2670 m, 21 August 2008, Coll.: Feng Bo, Havill sample 08-268 (YPM); 1, Sichuan, Kuiyonggou Danba, 15 Dec 2006, Lu W H, from hemlock (IZAS); 1, same but 10 Feb 2007 (IZAS); 1, Sichuan, Dagou Lixian, 10 May 2006, Xiao N P, from hemlock (IZAS); 1, same but 22 Sep 2006, Zhou J H, from hemlock (IZAS). *Lab colony:* 2, USA Virginia Blacksburg,VA Tech, From lab colony, 2004, Coll.: H. Gatton (VTRC); 6, CHINA, Sichuan Province, Laboratory reared, 11 October 2007, J. Zhou, Havill Sample # 08-266 (YPM); 1, CHINA, from Lab, Liu Y, 18 Apr 2007, from hemlock (IZAS).

9. *Laricobius kovalevi* Nikitsky in Nikitsky & Lafer, 1992

(figs 10, 40)

Diagnosis. Body bicolored. Head dark; ocelli present. Prothorax transverse with well developed lateral carina and sides explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra not incurvate; elytral punctures not confluent. Epipleura at base dark. Ventrites dark. Femora light. Tibiae light. Aedeagus without median carina on phallobase; medium lobe subacute; apices of parameres without an internal ridge.

Description. Length 2.80 mm. Body bicolored with head, prothorax, scutellum, elytra along sides to level above abdominal ventrite 2 (covering stria 10), epipleuron, and venter chocolate brown; elytra reddish brown to dark tan; antenna reddish brown to dark brown with AI and club darker, legs reddish brown to dark tan. Head with ocelli; u-shaped furrow present; interocular distance about 4x the width of the eye; macropunctures rounded, distinct to indistinct and not rounded, fusing sometimes to form irregular trenches and present at the center of the frons; micropunctures coarse; setae erect, moderately elongate with an average length as long as 2/3 the width of the eye. Antenna with length of A3 about equal to A4, ratios 1.9:1.6:1.4:1.3:1.3:1.2:1.1:1.0:1.5:1.6:2.4; A11 not strongly asymmetrical. Prothorax transverse and rectangular, dorsoventrally flattened, and widest at middle, sides evenly rounded; about 0.73 x as long as wide (pronotal length/greatest pronotal width = 0.73); depth = 0.42; pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle variable (90º to about 60° and rounded), not forming a tooth; posterior angle indistinct, short tooth absent at the posterior of the lateral margin; foveae visible dorsally; macropunctures on disc distinct, well-impressed and well-separated; micropunctures coarse; setae erect, long with average length 2/3 or equal to width of eye. Elytra about 3.48 x as long as wide (elytral length/greatest elytral width = 3.48) and 3.37 x as long as pronotum (elytral length/pronotal length = 3.37); surface not incurvate at basal third; macropunctures not coalescing to form grooves, separated by an average of 1/2 puncture diameter; micropunctures fine; microsculpture visible; setae suberect to erect, moderately long averaging about 2/3the length of the eye. Aedeagus with phallobase quadrate, about 1/2 the length of the median lobe, median carina absent; median lobe not projecting beyond apices of parameres, narrow with its greatest width less than the width of the parameres, apex subacute and converging apically at about apical 1/3, median groove or carina absent, ostium subapical; parameres broad and subacute, short setae present on apices and along inner margin, internal subapical ridge absent. Spiculum gastrale apically narrow.

Comments. Among the ocelli-bearing species with an explanate pronotal margin, *L. kovalevi* can be distinguished by the black head and pronotum and lighter elytra. The posterior pronotal tooth is absent in *L. kovalevi*, which is present in *L. rubidus*, while the femora and tibiae are light which can distinguish *L. kovalevi* from *L. erichsonii*.

I had two paratypes in relatively poor condition from ZMUM for study and only the male genitalia were dissected from one of these. A single measured specimen fell outside of the published size range of the species (2.1–2.5 mm). At the time this manuscript was in review, additional specimens of this species from Japan were sent sent to N. Havill (USDA) and myself by S. Shiyake (OMNH), and based on dissection, this species is confirmed as a *L. kovalevi*.

Hosts. Plant: *Pinus pumila* (Pall.) Regel.

Distribution. Russia: Far East. Japan: Honshū.

Type material examined. PARATYPES (ZMUM): 2, ИАГАД. обп. ЛГ–19 Стоковое, 11 КМ ЮВ КУЛУ, 14 06 1976, Л. Глумкова, Paratypus Laricobius kovalevi Nikitsky (red label with name hw).

Additional material examined. 5, Tekari-dake, Senzu, Honkawane-cho, Haibara-gun, Shizuoka Pref., Japan, 24. September, 2001, Y. Tahira leg., altitude 2,540m, on Pinus pumila (2, OMNH; 2, NZAC; 1, YPM); 1, Mt. Hakkoda, Aomori Pref., Japan, 4 October 2007, S. Shiyake leg., altitude 1,520 m, on Pinus pumila (1, YPM).

10. *Laricobius laticollis* Fall, 1916

(figs 11, 41)

Diagnosis. Body bicolored. Head dark; ocelli present. Prothorax transverse with well developed lateral carina and sides explanate. Pronotum light; posterior tooth present or absent. Scutellum usually dark. Surface of elytra weakly incurvate; elytral punctures not confluent. Epipleura dark. Ventrites dark. Femora light. Tibiae light. Aedeagus without median carina on phallobase; medium lobe apiculate; apices of parameres without an internal ridge.

Description. Length 2.30–2.76 mm (x = 2.52, n = 15). Body bicolored with head, scutellum (usually), epipleuron, and venter chocolate brown; pronotum, elytra, and hypomeron light brown or tan; antenna light brown or tan with AI usually darker, legs reddish light brown or tan, bases and apices of the femora and tibiae may be darker. Head with ocelli; u-shaped furrow present; interocular distance about 4x the width of the eye; macropunctures rounded and distinct, sometimes fusing and sometimes present at the center of the frons; micropunctures coarse; setae erect, moderately elongate with an average length as long as 2/3 the width of the eye. Antenna with length of

A3 about equal to A4, ratios 2.1:1.6:1.3:1.4:1.4:1.1:1.1:1.0:1.6:1.4:2.1; A11 not strongly asymmetrical. Prothorax transverse and rectangular, dorsoventrally flattened, and widest at middle, sides converging anteriorly from widest point and weakly convex posteriorly; about 0.68 x as long as wide (pronotal length/greatest pronotal width = 0.63–0.71, x = 0.68); depth = 0.26–0.40 mm (x = 0.32); pronotum laterally explanate, lateral carina with a distinct sharp edge; anterior angle about 60° and subacute, not forming a tooth; foveae visible in dorsal view; posterior angle indistinct or distinct with short tooth present or absent; macropunctures on disc distinct, well-impressed and well-separated or contiguous at the anterior middle of disc, micropunctures coarse; setae suberect, short and average length about 1/2 width of eye. Elytra about 3.22 x as long as wide (elytral length/greatest elytral width = 3.00–3.47, x = 3.22) and 3.35 x as long as pronotum (elytral length/pronotal length = 3.20–3.54, x = 3.35); surface weakly incurvate at basal third; macropunctures not coalescing to form grooves (apart from those of striae 1 along the suture near apex in some specimens), separated by an average of 1/2 puncture diameter; micropunctures fine; microsculpture visible on some specimens; setae suberect, short and an average of about 1/2 the length of the eye. Aedeagus with phallobase transverse, about 1/2 the length of the median lobe, median carina absent; median lobe projecting slightly beyond apices of parameres, moderately broad with its greatest width subequal to parameres, sides gradually narrowing posteriorly with the apex apiculate, median groove or carina absent; ostium subapical; parameres broad and rounded apically, short setae present on apices and along inner margin, internal subapical ridge absent. Spiculum gastrale apically narrowed.

Comments. Among the species having an explanate pronotal margin, *L. laticollis* is one of three species with the head dark and pronotum light. It can be distinguished from *L. caucasicus* by having an incurvate elytral surface and from *L. baoxingensis* by the shape of the pronotum.

Fall (1916) had 14 specimens, taken at the University of Washington Campus February and April, but I have only examined specimens collected in February 1911. The single specimen labelled as "type" is here designated as the lectotype, this does not have a black scutellum; the remaining syntypes are mixed.

Hosts. Plants: *Pseudotsuga menzeseii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg. Adelgid: *Adelges cooleyi* (Gillette) (M. Montgomery, pers. com.).

Distribution. United States: California, Idaho, Oregon, Washington. Canada: Alberta, British Columbia.

Type material examined. 7 syntypes (all pointed MCZ): 1, Seattle, II-12-11 (hw)/H. C. FALL COLLECTION/W. T./TYPE laticollis. (name hw)/ M.C.Z. Type 24993 (red label, number hw)/ Aug–Dec 2005 MCZ Image Database (bordered label with camera icon)/LECTOTYPE, designated by R. Leschen 2009; 1, W. T./Univ. of W. Campus. Seattle. IV–6–12 (hw)/ H. C. FALL COLLECTION/ Laricobius laticollis Fall. (hw); 2, Seattle Wash. (hw)/ H. C. FALL COLLECTION; 1, W. T./Seattle, Campus Univ. of W., II-12-11 (hw)/ H. C. FALL COLLECTION; 1, W. T./Seattle, II-12-11 (hw)/ H. C. FALL COLLECTION; 1, "Campus" (hw), Seattle, Wash (printed) II-12-11 T. C. K. (hw)/ H. C. FALL COLLECTION.

Additional material examined. CANADA. Alberta: 1, Truner V., Alta. VI.1.1933, Owen Bryant (CAS); 20, Ghost Dam, Alberta, several dates, BF and JL Carr (CNC); 2, Calgary, 1973, BF and JL Carr (CNC); 1, Coleman, Alberta (CNC). British Columbia: 2, Salmon Arm, 3.V.35, Hugh Leech, 10351; 1, same but 30.IV.1930 (CAS); 1, same but 30.IV.1933 on Douglas fir boughs, 23.III.34, beating Douglas fir branches, E. S. Ross Collection (CAS); 1, Sanca, 22.IV.1933 G. Stace Smith, from swift stream (1, CAS; 4, CNC). UNITED STATES. California: 8, Fieldbrook, Humboldt Co., Mar.27, '38, B. P. Bliven No. 801(CAS); Humbolt Co., v .3.17, F.W. Nunenmacher (FMNH). Idaho: 1, Moscow, v-28 1950, N.M. Downie (FMNH); 1, same but v-20, 1950 (FMNH); 1, Troy, v-14, 1950, N.M. Downie (FMNH); 1, Deary, v-14, 1950, N.M. Downie (FMNH); 1, Moscow Mts, II.10.1934, I.W. Bales (FMNH). Oregon: 7, Milton, Ore, G. H. Nelson, IV-3-49, G. W. Green collection (CAS). Washington: 1, Fort Lewis, Pierce Co. V-3.1946, P. H. arnaudf (CAS); 2, Seattle, VII-13 on Douglas Fir, Van Dyke Collection (CAS); 1, Seattle, Wash. III-7-13, sweeping Douglas fir (CAS); 3, Grand Coulee, Washington, BF and JL Carr (CNC); 11, King Co., Seattle; 17-24 February 2007, D. McDonald, Havill Samples # 07-01, 07-01A, 07-01B, 07-01.1 (YPM).

11. *Laricobius loebli* Jelínek & Háva, 2001

(figs 12, 42, 50)

Diagnosis. Body unicolored. Head dark; ocelli present. Prothorax quadrate without well developed lateral carina, sides not strongly explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra not incur-

vate; elytral punctures posteriorly confluent. Epipleura dark. Ventrites dark. Meso- and metafemora dark (profemora light). Tibiae light. Aedeagus with median carina on phallobase; medium lobe acute; apices of parameres without an internal ridge.

Description. Length 2.36–2.86 mm (x = 2.56, n= 3). Body unicolored chocolate brown; antenna with AI dark tan, funicle light tan, club dark tan; palpi light tan; legs bicolored with prolegs light brown or tan, with apex of tibiae darker; midleg light to dark brown with femora darker at apical 1/3 or 2/3 darker, tibiae slightly darker and tarsi lighter; hindleg with femora brown, tibiae slightly lighter and tarsi light brown or tan. Head with ocelli; u-shaped furrow absent; interocular distance about 2x the width of the eye; punctures ovate and deeply impressed, present at the center of the frons; micropunctures moderately coarse; setation short, decumbent, length about 1/3 the width of the eye. Antenna with length of A3 shorter than A4, ratios 1.7:1.4:1.0:1.4:1.4:1.2:1.2:1.0:1.3:1.3:1.8; A11 strongly asymmetrical. Prothorax quadrate and convex, widest at middle, sides sinuate; about 0.81 x as long as wide (pronotal length/greatest pronotal width = 0.78–0.84, x = 0.81); depth = 0.30–0.40 mm (x = 0.35); pronotum not laterally explanate, lateral carina without a distinct sharp edge and reduced to a narrow bead; anterior angle acute and deflected, forming a short tooth (the angle formed between the anterior margin and lateral carina, excluding the tooth, is about 90°); posterior angle indistinct and broadly rounded and without a short tooth; anterior foveae visible only in lateral view, posterior foveae visible in dorsal view; macropunctures ovate, deep, and well-separated, micropunctures moderately coarse; setae short, decumbent to suberect, and about 1/3 to 1/2 the width of eye. Elytra about 2.98 x as long as wide (elytral length/greatest elytral width = 2.65–3.23, x = 2.98) and 3.17 x as long as pronotum (elytral length/pronotal length = 2.90–3.33, x = 3.17); surface not incurvate at basal third; macropunctures, especially of striae 1–5, coalescing posteriorly to form grooves, separated by an average of ½ of a puncture diameter; micropunctures fine; microsculpture not visible; setae suberect, short, about 1/3 the length of the eye. Aedeagus with phallobase slightly transverse and rectangular, about 1/2 the length of the median lobe, median carina present; median lobe projecting significantly beyond apices of parameres, relatively narrow with its greatest length narrower than the parameres, apex acute and attenuate, median carina or groove absent, placement of ostium basal; parameres moderately broad and apically blunt, and anvil-shaped with laterally directed tooth, apical setae present and moderately elongate, internal subapical ridge absent. Spiculum gastrale apically broad.

Comments. Among species with coalescent elytral punctuation *L. loebli* is the only species with the coloration of the prolegs different from the middle and hindlegs. This species was described based on a single female.

Distribution. Nepal.

Type material examined. HOLOTYPE (MHNG). 1 female (card mounted and dissected), NEPAL: distr. Kathmandu: Phulcoki 2500 m, 28–29.IV.84 Löbl–Smetana/Laricobius **sp. n.** (hw) det. Löbl 19/ HOLOTYPE ♀ *Laricobius loebli* **sp. n.** J. Háva & J. Jelínek det. 2000 (red label).

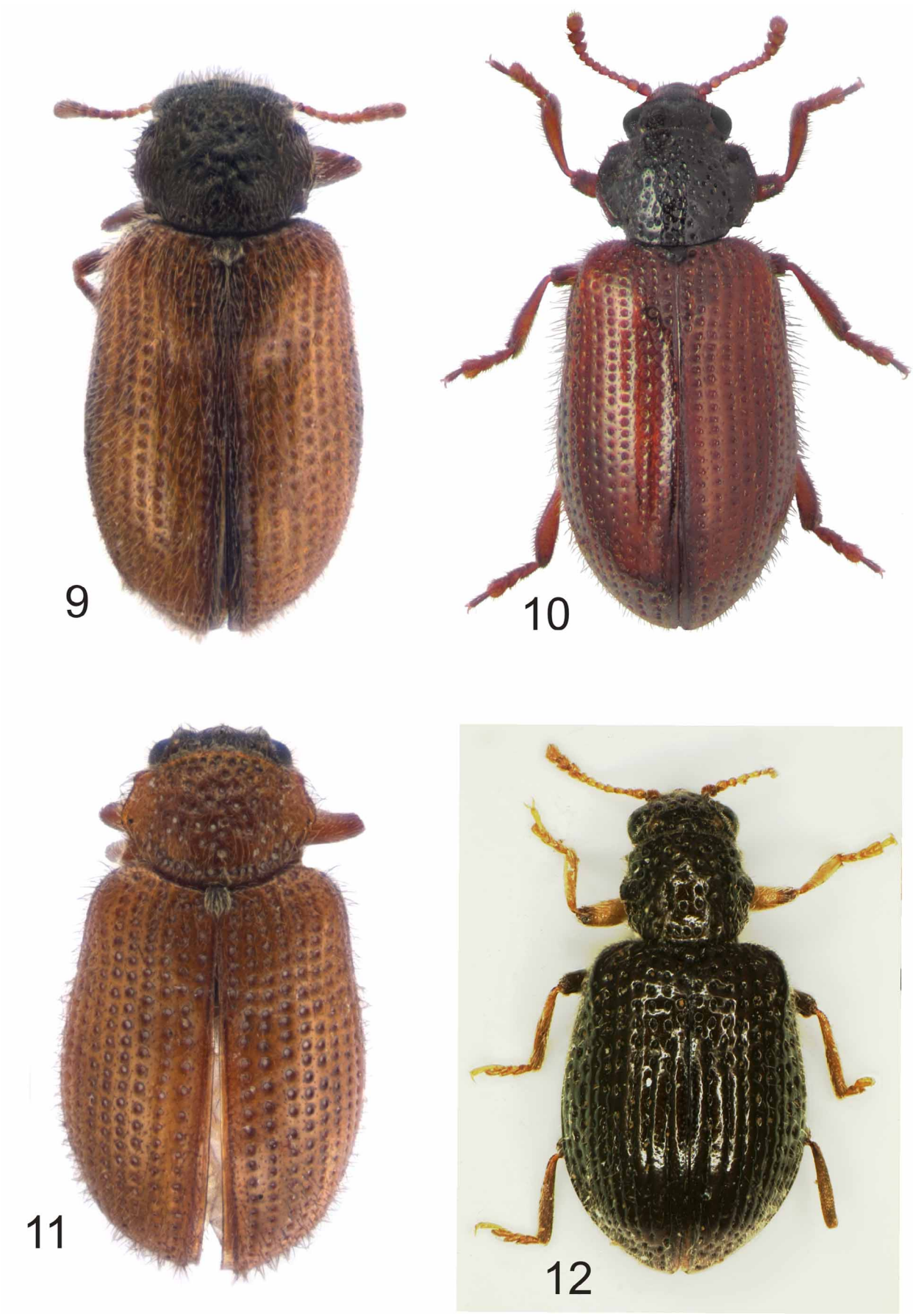
Additional material examined. 1, 525 NEPAL: Solukhumbu Distr. Hinku Dranka Khola Bridge, 2000 m, 18–19 V.1997 leg. W. SCHAWALLER (SMNS); 2, 564 NEPAL: Dailekh Distr. Dailekh to Mabuchin Pass, 2300 m, 3.–4.VI.1998 leg. W. SCHAWALLER (SMNS).

12. *Laricobius minutus* Nikitsky in Nikitsky & Lafer, 1992

Diagnosis (based on Nikitsky & Lafer, 1992). Length 2.1 mm. Body rusty brown, with the thorax a little darker ventrally, elytra bicolored with a black-brown or black stripe along the suture; antennae yellow-brown, legs partially darkened; dorsal vestiture erect. Ocelli present but difficult to distinguished from the rusty color of the head. Prothorax transverse (longer than wide), sides almost evenly convex and converging from middle, with anterior angles rounded and posterior angles "visible". Elytra elongate (1.5–1.6 X longer than wide).

Comments. No specimen of this species was examined. The description of the species was based on a single male specimen originally deposited in the ZMUM. It was subsequently lost in mail prior to this study (Nikitsky, personal communication). The diagnosis above was based on the figure of the head and prothorax and the key in Nikitsky and Lafer (1992), I provide the diagnosis above that will help to distinguish this species from *L. kovalevi* and *L. sahlbergi*.

Distribution. Russia: Far East.



FIGURES 9–12. Dorsal habitus. 9, *Laricobius kangdingensis*; 10, *L. kovalevi*; 11, *L. laticollis*; 12, *L. loebli*.

13. *Laricobius mirabilis* Háva & Jelínek, 1999
(fig 13)

Diagnosis. Body unicolored. Head light; ocelli present. Prothorax quadrate without well developed lateral carina, sides not strongly explanate. Pronotum light; posterior tooth absent. Scutellum light. Surface of elytra incurvate; elytral punctures posteriorly confluent. Epipleura light. Ventrites dark. Femora light. Tibiae light. Aedeagus with medium lobe acute.

Description. Length 2.86 mm. Body unicolored, mostly light brown or tan dorsally, prosternum light brown, thoracic and abdominal ventrites dark brown; antenna (with A1 slightly darker), palpi, and legs light tan. Head with ocelli; u-shaped furrow absent; interocular distance about 2x the width of the eye; macropunctures ovate and deeply impressed, scattered and present at center of frons; micropunctures coarse; microsculpture visible; setation short, length shorter than 1/3 the width of the eye. Antenna with length of A3 shorter than A4, ratios 1.6:1.3:1.0:1.3:1.5:1.4:1.5:1.0:1.4:1.3:1.8; A11 strongly asymmetrical. Prothorax quadrate and convex, widest just antemedially, sides sinuate; about 0.82 x as long as wide (pronotal length/greatest pronotal width = 0.82); depth = 0.40 mm; pronotum not laterally explanate, lateral carina poorly developed and reduced to a narrow bead; anterior angle acute, deflected, and forming a short laterally directed tooth (the angle formed between the anterior margin and lateral carina, excluding the tooth, is about 90°); anterior foveae visible in lateral view only, posterior foveae visible dorsally; posterior angle indistinct and broadly rounded and without a short tooth; macropunctures ovate, deep, and well-separated; micropunctures coarse; microsculpture visible; setae short, and about 1/2 the width of eye. Elytra about 3.23 x as long as wide (elytral length/greatest elytral width = 3.23) and 3.33 x as long as pronotum (elytral length/pronotal length = 3.33); surface weakly incurvate at basal third; macropunctures, especially of striae 1–2, coalescing posteriorly to form grooves, separated by an average of 1/3 of a puncture diameter; micropunctures fine; setae decumbent and short, about 1/2 length of the eye. Aedeagus (based on Háva 2009a) with phallobase slightly transverse and rectangular, about 2/3 the length of the median lobe, median lobe projecting significantly beyond apices of parameres, relatively broad and apically arrowshape-d with its greatest width about that of the parameres, apex acute; parameres broad and apically acute, internal subapical ridge absent.

Comments. *Laricobius mirabilis* is the only species with coalescent elytral punctuation that is unicolorous tan in color. It was described based on a single female, which was covered with a thin clear residue making some of the characters difficult to observe. The male genitalia was drawn by Háva (2009a), presumably from an additional specimen that was recorded by Háva (2009b), and was not made available for study.

Distribution. China: Shaanxi, Yunnan.

Type material examined. HOLOTYPE (NMPC). 1 female (card mounted and dissected), CHINA, Shangxi prov. Qing Ling Shan Mts., track Hou Zen Zi vill. to Taibai Shan, 3500 m, / 2–4 July 1998, alpina meadows, Z. Jindra, O. Šafránek, et M. Trýzna leg./ HOLOTYPE (red label) / *Laricobius mirabilis* **sp. n.** J. Háva & J. Jelínek det. 1999/ Mus. Nat. Pragae 66130 (number handwritten) Inv. (red label).

Material not examined (see Háva 2009b). China, N-Yunnan [C2005-05A], Diqing Tibet. Aut. Pref., Zhongdian Co., Xue Shan near lake 23 km S Zhongdian, 3895 m / 27°37.1´N, 99°38.5´E, devast mixed forest, meadows, lake border leaf litter, dead wood, sifted, 6.vi.2005, M. Schülke leg., 1 ♀, J. Háva det. (SMNS).

14. *Laricobius naganoensis* n. sp.
(figs 14, 29, 30, 43)

Diagnosis. Body bicolored. Head dark; ocelli absent. Prothorax transverse with well developed lateral carina and sides explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra usually incurvate; elytral punctures not confluent. Epipleura dark. Ventrites dark. Femora dark. Tibiae light. Aedeagus with median carina on phallobase; medium lobe acute; apices of parameres without an internal ridge.

Description. Length 2.40–2.84 mm (x = 2.58, n = 9). Body bicolored with head, prothorax, scutellum, elytra along sides to level of abdominal ventrite 3 (usually covering striae 7–10) and usually along suture and scutellary striole (but may be reduced to the area surrounding the scutellum), epipleuron, venter, and usually the femora chocolate brown; elytra orange-red to dark or reddish tan; antenna reddish brown to dark brown with AI and club usually darker, palpi, and tibiae light to reddish brown, tarsi lighter. Head without ocelli; u-shaped furrow present;

interocular distance about 4x the width of the eye; macropunctures rounded and distinct to indistinct and shallowly impressed, scattered and present at the center of dronsf; micropunctures coarse; setae erect, moderately elongate with an average length as long as 2/3 to full width of the eye. Antenna with length of A3 about equal to A4, ratios 1.8:1.5:1.3:1.2:1.2:1.1:1.1:1.0:1.2:1.3:1.9; A11 not strongly asymmetrical. Prothorax transverse and rectangular, dorsoventrally flattened, and widest at middle, sides weakly convex, converging anteriorly from widest point and weakly convex or convergent posteriorly; about 0.74 x as long as wide (pronotal length/greatest pronotal width = 0.67–0.77, x = 0.74); depth = 0.28–0.44 mm (x = 0.37); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle 90º to about 80° and subacute, not forming a tooth; posterior angle indistinct, rounded, and without a short tooth; foveae visible in dorsal view; macropunctures on disc distinct, usually weakly-impressed and well-separated; micropunctures strong; setae erect, moderately long and 2/3 to full width of eye. Elytra about 3.41 x as long as wide (elytral length/greatest elytral width = 3.13–3.73, x = 3.41) and 3.39 x as long as pronotum (elytral length/pronotal length = 3.13–3.71, x = 3.39); surface weakly incurvate at basal third; macropunctures not coalescing to form grooves, separated by 1/2 puncture diameter; micropunctures fine; microsculpture not visible; setae suberect to subdecumbent, short and on average about 2/3 length of the eye. Aedeagus with phallobase slightly elongate (longer than wide), about 2/3 the length of the median lobe, median carina present; median lobe projecting very slightly beyond apices of parameres, relatively narrow with its greatest width larger than the width of the parameres, apex acute and attenuate, median groove and carina absent, ostium subapical; parameres slender and acute, very short setae present on apices and along inner margin, internal subapical ridge absent. Spiculum gastrale apically narrow.

Comments. *Laricobius naganoensis* can be distinguished from most species by the lack of ocelli. It can be reliably distinguished from the remaining species that lack ocelli by having pale tibiae and the acute median lobe of the male genitalia. *Laricobius naganoensis* can also be distinguished from these species, as well as the sympatric species *L. osakensis*, by the more vivid orange-red coloration of the elytra.

This new species is based on specimens collected from relatively high altitude areas in Nagano Prefecture where it is sympatric with *L. osakensis*.

Hosts. Plant: *Tsuga diversifolia* (Maxim.) Mast. Adelgid: *Adelges tsugae*.

Distribution. Japan: Honshū.

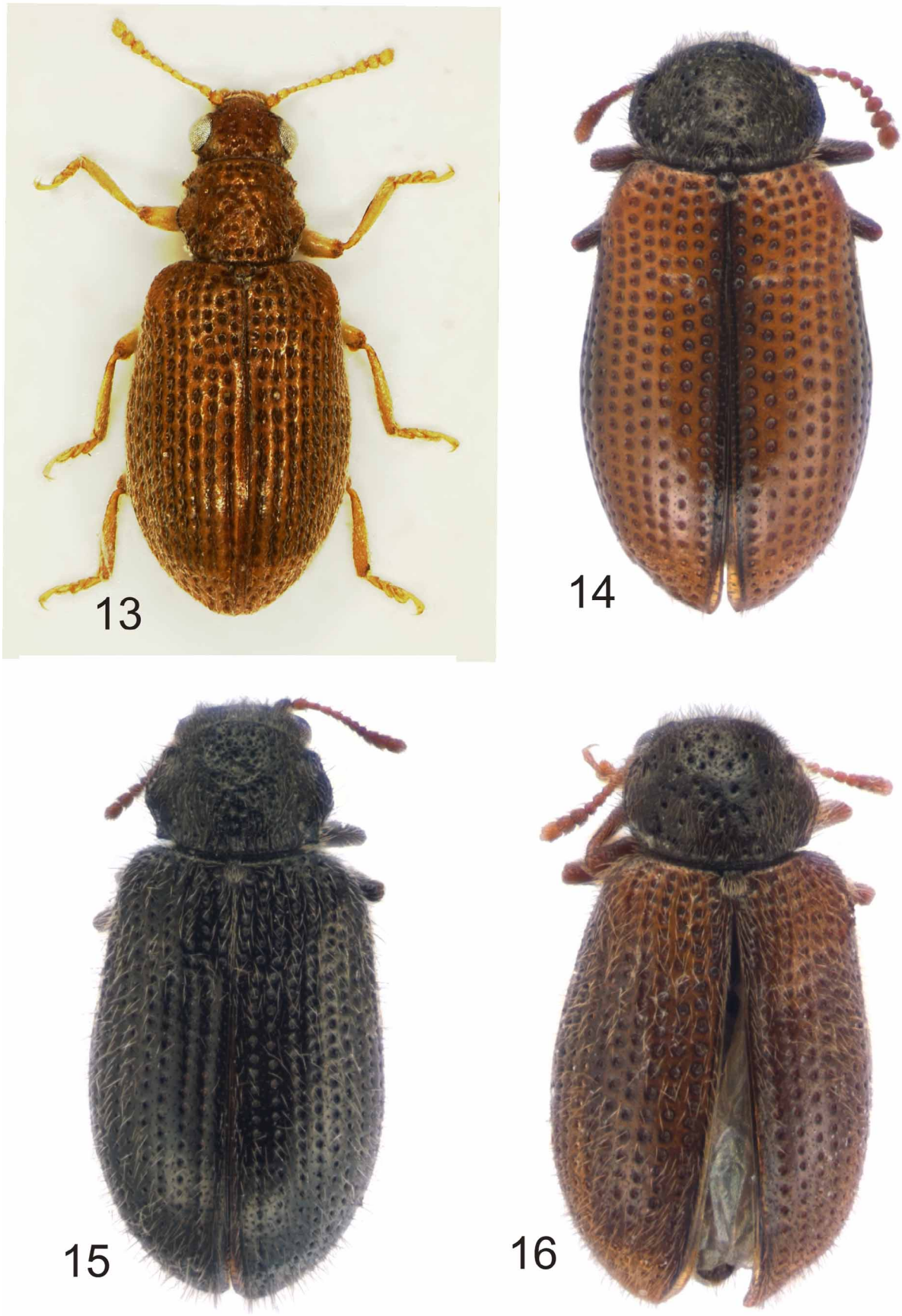
Type material examined. HOLOTYPE (OMNH): JAPAN Nagano Prefecture Ootaki Mt Ontake 35.86938 N 137.51064 E 2050 m 29 October 2009 A. Lamb S. Shiyake/Beaten from Tsuga diversifolia Havill Sample # 09-215.7/HOLOTYPE Laricobius naganoensis design. R. Leschen 2010.

PARATYPES: 1, JAPAN Nagano Prefecture Matsumoto Mt. Norikura 15 October 2008 Coll.: S. Shiyake A. Lamb Beaten from Tsuga diversifolia male Havill sample 08-291.1 (genitalia mounted separately on microslide, YPM); 1, JAPAN Nagano Prefecture Matsumoto Mt. Norikura 36.12 N 137.59 E 2030 m 28 October 2009 Coll.: A. Lamb S. Shiyake Laricobius sp. Female Beaten from Tsuga diversifolia Havill sample 09-214.2 (OMNH); 1, JAPAN Nagano Prefecture Ootaki Mt Ontake 35.87 N 137.51 E 2050 m 29 October 2009 Coll.: A. Lamb, S. Shiyake; Laricobius sp. Female Beaten from Tsuga diversifolia Havill sample 09-215.2 (OMNH); 5, JAPAN Nagano Prefecture Ootaki Mt Ontake 35.86938 N 137.51064 E 2050 m 29 October 2009 A. Lamb S. Shiyake Beaten from Tsuga diversifolia Havill Sample # 09-215 (2, OMNH; 1, YPM; 1 BMNH; 1 NMNH); 1, JAPAN; Nagano Prefecture Shiga-kogen 17 October 2008 Coll. S. Shiyake A. Lamb Laricobius osakensis Beaten from Tsuga diversifolia male Havill Sample # 08- (OMNH); 1, JAPAN Nagano Prefecture Matsumoto Mt. Norikura 15 October 2008 Coll.: S. Shiyake A. Lamb Beaten from Tsuga diversifolia female Havill sample # 08-291.2 (OMNH); 1, JAPAN Nagano Prefecture Ootaki Mt Ontake 35.87 N 137.51 E 2050 m 29 October 2009 Coll. A. Lamb S. Shiyake Laricobius sp. Male Beaten from Tsuga (OMNH).

15. *Laricobius nigrinus* Fender, 1945

(figs 15, 44)

Diagnosis. Body unicolored. Head dark; ocelli present. Prothorax transverse with well-developed lateral carina and sides explanate. Pronotum dark; posterior tooth present. Scutellum dark. Surface of elytra not incurvate; elytral punctures not confluent. Epipleura dark. Ventrites dark. Femora dark. Tibiae dark. Aedeagus with median carina on phallobase; medium lobe subacute; apices of parameres with an internal ridge.



FIGURES 13–16. Dorsal habitus. 13, *Laricobius mirabilis*; 14, *L. naganoensis*; 15, *L. nigrinus*; 16, *L. osakensis*.

Description. Length 2.02–2.73 mm (x = 2.49, n = 16). Body unicolored black; palpi and tarsi red or dark brown, tibiae black or dark brown and lighter at near the joints. Head with ocelli; u-shaped furrow present but shallow; interocular distance about 4x the width of the eye; macropunctures rounded and distinct to indistinct and shallowly impressed and absent from the center of frons; micropunctures very coarse, especially posteriorly; setae erect, moderately elongate with an average length as long as 2/3 to full width of the eye. Antenna with length of A3 about equal to A4, ratios 1.7:1.6:1.6:1.5:1.5:1.1:1.2:1.0:1.4:1.4:1.9; A11 generally not strongly asymmetrical. Prothorax transverse and rectangular, dorsoventrally flattened, and widest at middle, sides weakly convex, converging anteriorly from widest point and weakly convex or convergent posteriorly; about 0.76 x as long as wide (pronotal length/greatest pronotal width = 0.70–0.85, x = 0.76); depth = 0.28–0.44 mm (x = 0.34); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle 90º to about 60° and acute, not forming a tooth; posterior angle distinct and marked by a tooth which may be reduced; foveae visible dorsally; macropunctures on disc distinct to poorly defined, and shallowly impressed, well-separated; micropunctures coarse to moderately coarse; setae erect, moderately long and 2/3 to full width of eye. Elytra about 3.20 x as long as wide (elytral length/greatest elytral width = 2.91–3.56, x = 3.20) and 3.35 x as long as pronotum (elytral length/pronotal length = 2.81–3.64, x = 3.35); surface weakly incurvate at basal third; macropunctures not coalescing to form grooves (apart from those of striae 1 along the suture near apex), separated by 1/2 puncture diameter; micropunctures fine; microsculpture not visible; setae mostly suberect with scattered erect setae, elongate and on average about 2/3 to full length of the eye. Aedeagus with phallobase slightly transverse (wider than long), about 2/3 the length of the median lobe, median carina present; median lobe projecting beyond apices of parameres, relatively broad with its greatest width larger than the width of the parameres, gradually tapering apically with apex subacute, median carina or groove absent; ostium subapical; parameres moderately slender, and acute, short setae present on apices and along inner margin, internal subapical ridge present. Spiculum gastrale apically narrow and acute.

Comments. *Laricobius nigrinus* is the only unicolorous black species with a well-developed explanate pronotal margin. It can be distinguished from unicolorous *L. sahlbergi* and melanistic *L. erichsonii* by the dark femora and tibiae.

Fender (1945) clearly states that the holotype, allotype, and five paratypes were collected from Bear Springs, Oregon, June 20, 1904, and one paratype from Creston, British Columbia, collected by G. Stace Smith October 29, 1933. The type material in the CAS and MCZ from Oregon are of different dates and the date given in the original description is probably a combination of a typo of "1904" and a simple error of "10" instead of "20" (the BC type was not recovered). Despite these and other inconsistencies among the labels, I consider that those below were part of the type series.

After studies to determine its efficacy as a biocontrol agent for *A. tsugae* (Zilahi-Balogh *et al*. 2002a,b), *L. nigrinus* was introduced the mid-Atlantic states in 2003 (Zilahi-Balogh *et al*. 2006) and is now widespread throughout eastern North America where hybridization between *L. nigrinus* and the native *L. rubidus* has been detected using microsatellite markers (Havill *et al*. in press). The external morphology of the hybrid individuals matches *L. rubidus*.

Hosts. Plants: *Larix* sp., *Larix occidentalis* Nutt., *Pinus monticola* Douglas ex D. Don, *Tsuga heterophylla*. Adelgids: *Adelges tsugae*, *Adelges lariciatus* (Patch) *Pineus* sp.

Biology. Natural history, larvae, morphology (Zilahi-Balogh *et al*. 2002a,b, 2003, 2006).

Distribution. United States*:* Alaska, California, Idaho, Oregon, Washington, Wyoming (*intoduced to eastern North America and now in Delaware, Georgia, Kentucky, Maine, Massachusettes, Maryland, North Carolina, New Hampshire, New Jersey, New York, Pennsylvania, Tennessee, Vermont, Virginia, West Virginia. Canada: Alberta, British Columbia).

Type material examined. HOLOTYPE (CAS): BearSpringsOre; VI-10-1940 [hw]; KM & DM Fender / Laricobius nigrinus Fender [hw], HOLOTYPE / California Academy of Sciences; Type No. 5527 [hw] / [hw label] Holotype [vertical with red highlight] Laricobius nigrinus Fender. PARATYPES: BearSpringsOre; VI-10-1940 [hw]; KM & DM Fender / Laricobius nigrinus Fender [hw], ALLOTYPE / [hw label] Allotype [vertical w red highlight] Laricobius nigrinus Fender / Collection of the CALIFORNIA ACADEMY OF THE SCIENCES; San Francisco, California / [2nd hw label] Allotype [vertical w red highlight], No. 5528, Laricobius nigrinus Fender (CAS). 1, Bear Springs Ore, 01-10. 1940, KM & DM Fender (printed and hw date)/Paratype (red label, hw)/Laricobius nigrinus Fender (red label, hw)/C. A. Frost Collection 1962 (MCZ). 1, same but 10/6/1940 (MCZ).

Additional material examined. CANADA. Alberta: 11, Ghost Dam, Alberta (CNC). British Columbia: 4, Victoria, 20–21 Oct 1994, leg. L.M. Humble, FSQF-94-3052 (VTRC); Saanichton, 12 IV 1991, T. heterophylla, L. Humble, CPFP Seed Orchard (VTRC); 5, Victoria, ex *Tsugae heterophylla*, *Adelges tsugae* (CNC); Vancouver, 3.IV.1931, H. B. Leech, Blaisdell Collection (CAS); 1, Vancouver (CNC); 3, Victoria, 2 II 2002, A. Lamb, Tsuga heterophylla, Adelges tsugae (VTRC); 1, near Vernon, 10 May 2007, G. Zilahi-Balogh, Late instar collected in May, reared in lab to adult, ex. Larix oxidentalis (VTRC); 1, Vernon, Kalamalka Seed Orchard, ex larch cone hit by adelgids, collected as larva 7 May, live adult recovered 27 Aug 2007, J.E. Corrigan (VTRC). UNITED STATES. Alaska: 1, Whitehorse, Yukon Territory (NMNH). California: 1, Teh. Co., California (UNHD). Idaho: 13, Bonner Co. Sandpoint, 8 Oct 2008, D. Mausel, beating western hemlock with A. tsugae (VTRC); 2, Moscow (MCZ); 1, Kootenai County, Coeur d'Alene, Couger Gulch, 9 March 2007, D. Mausel, ex. Tsuga heterophylla, Sample: Havill 07-03.3 (PBNH); 9, same but Sample: Havill 07-03.1 (PNHM); 8, same but Sample: Havill 07-04 (PNHM); 3, Latah County, Moscow, 9 November 2007, Coll. S. Cool, D. Mausel, ex. Pinus monticola, Sample: Havill 07-134 (PNHM); 1, same but Sample: Havill 07-134.3 (PNHM). Oregon: 6, Oregon, Portland, Grant Park, 23 January 2006, Coll. D. Ross, Havill Sample # 06-119 (PNHM); 1, Polk Co. Bethel Heights, 45° 02.750' N,123° 08.000' W, 26.X .2007, Coll. Glen Kohler, Sample: Havill 07-135(PNHM). Washington: 54, King Co. Seattle, 12 Oct 2008, D. Mausel, beating western hemlock with A. tsugae, 77m, 47° 39' 58.62 N, 122° 20' 37.69 W (VTRC); 1, Grand Coulee (CNC); 7, King County, Seattle, 18 January 2007, coll. D. Mausel, C. Jubb, ex. Tsuga heterophylla; Sample: Havill 07-02 (PNHM); 1, same but Sample: Havill 07-02.2 (PBNH); 18, same but Sample: Havill 07-138 (PBNH); King Co.; Seattle; Marymoore Park, 7 April 2008, Coll. R.C. McDonald, ex. Tsuga heterphyllia, Sample 08-54.1 (VTRC); 4, Thurston Co. Olympia, 26 October 2007, Coll. G. Kohler, ex. Tsuga heterophylla, Sample: Havill 07-136 (PNHM); 1, same but Sample: Havill 07-136.6 (PNHM); 1, same but Sample: Havill 07-136.7 (PNHM).; Longmire Spgs VII-12-19, Blaisdell Collection (CAS). Wyoming: 1, Saratoga, (NMNH). Lab reared: Virginia: 23, Blacksburg, VA; 10 IV 2003 (VTRC); 4, Washington, King Co., F1 reared in VA Tech Lab, June 2006, Coll. D. Mausel, Havill Sample # 06-115 (PNHM).

16. *Laricobius osakensis* Montgomery and Shiyake, 2011, in Montgomery *et al.* 2011

(figs 16, 43, 51)

Diagnosis. Body bicolored. Head dark; ocelli absent. Prothorax transverse with well-developed lateral carina and sides explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra incurvate; elytral punctures not confluent. Epipleura at base dark. Ventrites dark. Tibiae and femora dark. Aedeagus with median carina on phallobase; medium lobe subacute; apices of parameres without an internal ridge.

Description. Length 2.18–2.82 mm (x = 2.50, n = 15). Body bicolored with head, prothorax, scutellum, elytra along sides to level of abdominal ventrite 3 (usually covering striae 7–10) and suture along scutellary striole, epipleuron, venter, and usually the femora brown to black; elytra dark to light tan; antenna tan with AI dark tan and club usually darker than funicle but lighter than A1, palpi, and tarsi tan, femora and tibiae dark tan or brown. Head without ocelli; u-shaped furrow present, but very weak or absent; interocular distance about 4x the width of the eye; macropunctures rounded and distinct to indistinct and shallowly impressed; micropunctures coarse; setae erect, moderately elongate with an average length as long as 2/3 the width of the eye. Antenna with length of A3 about equal to A4, ratios 2.0:1.7:1.4:1.5:1.5:1.1:1.2:1.0:1.4:1.5:2.1; A11 not strongly asymmetrical. Prothorax transverse and rectangular, dorsoventrally flattened, and widest at middle, sides weakly convex, converging anteriorly from widest point and weakly convex or convergent posteriorly; about 0.77 x as long as wide (pronotal length/greatest pronotal width = 0.68–0.87, x = 0.77); depth = 0.25–0.38 mm (x = 0.32); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle 90º to about 80° and subacute, not forming a tooth; posterior angle distinct, rounded, and without a short tooth; foveae visible dorsally; macropunctures on disc distinct, usually weakly-impressed and well-separated; micropunctures coarse; setae erect, moderately long and 2/3 to full width of eye. Elytra about 3.24 x as long as wide (elytral length/greatest elytral width = 2.81–3.53, x = 3.24) and 3.20 x as long as pronotum (elytral length/pronotal length = 2.81–3.61, x = 3.20); surface weakly incurvate at basal third; macropunctures not coalescing to form grooves, separated by 1/2 puncture diameter; micropunctures sparse; microsculpture visible in some specimens (but usually absent); setae suberect to subdecumbent, short and on average about 1/3 to 2/3 length of the eye. Aedeagus with phallobase transverse (wider than long), just

over 2/3 the length of the median lobe, median carina present; median lobe projecting slightly beyond apices of parameres, relatively broad with its greatest width larger than the width of the parameres, apex subacute, median carina or groove absent, ostium subapical; parameres narrow, slender and acute, very short setae present on apices and not along inner margin, internal subapical ridge absent. Spiculum gastrale apically narrow.

Comments. *Laricobius osakensis* lacks ocelli and can be distinguished from other species with this character by the absence of a well-developed posterior tooth on the pronotal margin. The dark tibiae and red-brown rather than vivid orangish elytral coloration distinguish it from *L. naganoensis*: but to confirm the species collected in higher altitudes of Nagano Japan, dissection of males is recommended.

Hosts. Plants: *Tsuga diversifolia*, *Tsuga sieboldii* Carr. Adelgids: *Adelges tsugae*.

Biology. Natural history notes (Montgomery *et al*. 2011).

Distribution. Japan: Honshū, Shikoku.

Type material examined. PARATYPES. 14, JAPAN, Gunma Prefecture, Katashina, Mt. Nikko-Shirane, 36.81287 N, 139.34099 E, 1550 m, 31 October 2009, Coll.: A. Lamb & S. Shiyake, Havill Sample #09-219 (2, NZAC; 2, OMNH; 10, YPM); 1 JAPAN, Nagano Prefecture, Shiga-kogen, 17 October 2008, Coll.: S. Shiyake & A. Lamb, Havill Sample #08-289.2 (YPM); 1, JAPAN, Nagano Prefecture, Matsumoto, Mt. Norikura, 36.11419 N, 137.61401 E, 1590 m, 28 October 2009, Coll.: A. Lamb & S. Shiyake, Havill Sample #09-213 (YPM); 3, JAPAN, Nagano Prefecture, Matsumoto, Mt. Norikura, 36.12203 N, 137.58749 E, 2030 m, 28 October 2009, Coll.: A. Lamb & S. Shiyake, Havill Sample #09-214 (YPM); 3, JAPAN, Nagano Prefecture, Ootaki, Mt. Ontake, 35.86938 N, 137.51064 E, 2050 m, 29 October 2009, Coll.: A. Lamb, & S. Shiyake, Havill Sample #09-215 (YPM); 4, JAPAN, Nagano Prefecture, Yamanouchi, Shiga-kogan, 36.68213 N, 138.50032 E, 1720 m, 30 October 2009, Coll.: A. Lamb & S. Shiyake, Havill Sample #09-218 (YPM); 4, JAPAN, Osaka Prefecture, Kawachi Nagano, Site # 1 Kita-san, 34º 24.150'N, 135º 33.761'E, 231 m, 27 Feb 2006, Coll.: T. McAvoy & A. Lamb, Virginia Tech nos. 147–150 (YPM); 3, JAPAN, Tochigi Prefecture, Nikko, Konsei Pass, 36.81883 N, 139.39461 E, 2020 m, 1 November 2009, Coll.: A. Lamb & S. Shiyake, Havill Sample #09-216 (YPM); 4, JAPAN, Tochigi Prefecture, Nikko, Nikko-Yumoto Spa, 36.80325 N, 139.4203 E, 1485 m, 31 October 2009, Coll.: A. Lamb & S. Shiyake, Havill Sample #09-22 (YPM).

Additional material examined. JAPAN. 2, various localities in Osaka Prefecture and Shikoku (Kansai area?), January 2008, A. Lamb, Havill Sample #08-263.1 (PNHM); 2, JAPAN, Osaka Prefecture, Kobe Municipal Arboretum, 34° 44.445' N, 135° 10.566' E, 2-III-2006–7-III-2006, Coll.: T. McAvoy, A. Lamb & S. Shigehiko, Virginia Tech nos. 177–178 (YPM). UNITED STATES. Virginia (lab reared): 6, Nov. 2007, M. Beck, F2 originally from Osaka Pre., Virginia Tech nos. 171–176; 1, Virginia Tech rearing facility, 2007–2008, A. Lamb, Havill Sample #08-264 (YPM); 2, same but October to November 2006, A. Lamb, F1 generation; emerged as adults in Oct. to Nov. 2006, parents from various sites in Japan; Honshu, Havill Sample #06-117 (YPM).

17. *Laricobius rubidus* LeConte, 1861

(figs 17, 24, 25, 32, 46)

Diagnosis. Body bicolored. Head dark; ocelli present. Prothorax transverse with well-developed lateral carina and sides explanate. Pronotum dark; posterior tooth usually present. Scutellum dark. Surface of elytra incurvate; elytral punctures not confluent. Epipleura at base dark. Ventrites dark. Femora dark. Tibiae dark. Aedeagus without median carina on phallobase; medium lobe subacute; apices of parameres with an internal ridge.

Description. Length 2.03–2.50 mm (x = 2.32, n = 16). Body bicolored, with head, prothorax, scutellum, and ventrites light brown to black, elytra along sides to apex (covering striae 7–10 or 8–10) and suture dark brown to black, or sutural stripes distinct and present only to basal 1/3 or less, with the broad central disc dark tan to deep red brown; antenna light to dark brown with AI and club sometimes darker, rarely the funicle dark brown to black, palpi, and tarsi reddish brown to tan, femora and tibiae light to chocolate brown (tibiae same color as femora). Head with ocelli; u-shaped furrow present but weakly impressed; interocular distance about 4x the width of the eye; macropunctures weakly to strongly impressed, ovate; micropunctures coarse; setation elongate, erect, average length about 2/3 to full width of the eye. Antenna with length of A3 about equal to A4, ratios 1.9:1.7:1.4:1.3:1.4:1.2:1.2:1.0:1.3:1.4:1.8; A11 not strongly asymmetrical. Prothorax transverse and dorsoventrally flattened, widest at middle, sides weakly sinuate or unevenly convex, with margin converging more sharply poste-

riorly than anteriorly; about 0.75 x as long as wide (pronotal length/greatest pronotal width = 0.67–0.81, x = 0.75); depth = 0.25–0.39 mm (x = 0.30); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle variable from 90º to about 65°, acute but not forming a tooth; posterior angle distinct and marked by a short tooth that may be weakly formed; foveae visible in dorsal view; macropunctures ovate, deep, usually well-separated but sometimes contiguous; micropunctures coarse; setae erect and elongate, length about 2/3 to full width of eye. Elytra about 3.22 x as long as wide (elytral length/greatest elytral width = 2.75–3.65, x = 3.22) and 3.25 x as long as pronotum (elytral length/pronotal length = 3.00–3.67, x = 3.25); surface strongly to weakly incurvate at basal third; macropunctures not coalescing posteriorly to form grooves (apart from those of striae 1 along the suture at the apical 1/3 in some specimens), separated by an average of 1/2 puncture diameter; micropunctures fine; microsculpture visible or not; vestiture mostly consisting of suberect setae with scattered erect setae, elongate and average length about 2/3 to full width of eye. Aedeagus with phallobase transverse (wider than long), about 2/3 the length of the median lobe, median carina absent; median lobe projecting beyond apices of parameres, relatively broad with its greatest width larger than the width of the parameres, gradually tapering apically with apex subacute, median carina or groove absent, ostium subapical; parameres moderately broad, apex angulate, short setae present on apices and absent along inner margin, internal subapical ridge present. Spiculum gastrale apically acute.

Comments. *Laricobius rubidus* can be distinguished from other bicolored species with ocelli and explanate pronotal margins (especially the similar looking *L. erichsonii*) by the dark-colored tibiae which is the same color as the femora, by the punctures on the head shallowly impressed, the anterior angle not forming a tooth, and most easily by the aedeagal characters. The internal subapical ridge on the parameres is shared only with the species *L. nigrinus*. Preliminary genetic data suggest that *L. nigrinus* and *L. rubidus* can successfully reproduce in the field (Havill *et al*. in press). Host plants and distributions were recently included in the study by Majka (2007).

Hosts. Plants: *Abies fraseri* (Pursh) Poir., *Abies balsamaea* (L.) Mill., *Pinus strobus* L., *Pinus banksiana* Lamb., *Tsuga canadensis* (L.) Carriére, *Picea rubens* Sarg. Adelgids: *Adelges tsugae*, *Adelges piceae* (Ratzeburg), *Pineus strobi*.

Biology. Natural history (Clark & Brown 1960, Lawrence & Hlavac 1979).

Distribution. Canada: New Brunswick, Nova Scotia, Ontario, Quebec. United States: Connecticut, Georgia, Maine, Maryland, Massachusettes, New Hampshire, New York, North Carolina, Pennsylvania, Rhode Island, Tennessee, Vermont, West Virginia.

Type material examined. Holotype (MCZ). 1, pointed, D. C/Laricobius rubidus Lec. (hw)/ erichsonii 2 (hw)/ M.C.Z. Type 32369 (red label, number hw)/LARICOBIUS RUBIDUS LEC. Det. J. F. Lawrence (bordered det. label, name hw)/Holotype (red label)/Jan–Jul 2005 MCZ Image Database (bordered label with camera icon).

Additional material examined. CANADA. New Brunswick: 1 (CNC). Ontario: 1, Constance B., 16.v 1933, W. J. Brown (CAS); 2, Ottawa (CAS); 5, Toronto, R. J. Crew (CAS); 24 (CNC). Quebec: 4, Aylmer, Que., 1.V 1933, W. J. Brown / [hw label] Det. 1934 W. J. B. (CAS); 1, same but 18-v-1934 (CAS); 1, same but 9.v 1932 (CAS); 1, same but 1.v 1933 (CAS); 1, Aylmer, 12.v 1932, W. J. Brown (CAS); 2, Lanoraie, 13 iii 77, F. Liard, 1992 Acc. Z-18,343 (FMNH). UNITED STATES. Connecticut: 1, New Haven Co., New Haven, 30 March 1994, Coll.: S. Lyon (USDA); same but 19 April 1994 (USDA); 6, New Haven Co, Lake Whitney, 31 X 1997, M. Montgomery, W. Lu (USDA); 1, same but 14 vii 1993 (USDA); 1, Hamden, end of Ingram St., Water Co. property, 27 March 2007, Coll.:N. Havill, ex. Tsuga canadensis, Sample: Havill 07–14 (YPM); 1, Hamden, USDA Forest Service Northern Research Stn., 51 Mill Pond Rd., 17 April 2008, Coll.: N. Havill, A. Serafin, ex. Pinus strobus, Sample 08-57.1 (YPM). Maryland: 1, Allegany County, Rocky Gap, 3 May 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM 4397022N, 0699934E, Sample: Havill 06-126 (YPM). Massachusettes: 1 (CAS); 1, Holyoke, Mt. Tom State Park, 5 May 2008, Coll.: J. Biroscak, ex. Pinus strobus, Sample 08-71.1 (YPM). Michigan: 1 (CAS). Minnesota: 1, on *Pinus strobes* (CNC). New Hampshire: 53, (UNHD). New York: 1 (CNC). North Carolina: 1, Watauga County, Holloway Gap, 16 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM 4000032N, 0431471E, Sample: Havill 06-122.3 (YPM); 1, same but Sample: Havill 06-122.4 (YPM); 3, Watauga County, Fosco, Holloway Mountain Road, 17 April 2008, Coll.: M.E. Montgomey, R.C. McDonald, ex. Pinus strobus; 36.14 N: 81.76 W, Sample 08-61 (YPM); 1, same but Sample 08-61.1 (YPM); 2, Yancey County, Locust Creek, 16 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM 3964523N, 0390540E, Sample: Havill 06-123 (YPM); 1, same but Sample: Havill 06-124.1 (YPM). Pennsylvania: 1, Cumberland Co., Hogestown, 12 April 1994, Coll.: S. Lyon (USDA); 3, Huntingdon Co., Rothrock State Forest, 4 May 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM

4504040N, 0268595E, Sample: Havill 06-128 (YPM). Tenessee: 7, Sevier Co., Smokies Nat. Park, Laurel Creek, 9 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab; UTM 3943370N, 0250526E, Sample: Havill 06-125 (YPM); 1, same but Sample: Havill 06-125.5 (YPM); 1, same but Sample: Havill 06-125.6 (YPM). Virginia: 6, Montgomery Co. Blacksburg, 6-30 IV 2001, coll. G. Zilahi-Balogh, Host tree: Tsuga canadensis, Host: Adelges tsugae, Habitat: plantation <10 yr. mixed, w/ Abies fraseri, Pinus strobus (VTRC); 3, Montgomery Co. Prices Fork, 6–30 IV 2001, G. Zilahi-Balogh, Host: Tsuga canadensis infested w/ Adelges tsugae (VTRC); 7, Smyth Co., Hurricane Camp, 20 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM 4064121N; 0456464E, Sample: Havill 06-129 (YPM); 6, Montgomery Co. Kentland Farm, 28 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM 4118054N, 0536469E, Sample: Havill 06-132 (YPM); 1, Bland Co., Lick Creek, 18 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM 4096147N; 0461976E, Sample: Havill 06-130 (YPM); 8, Giles Co., North Fork, 15 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM 4144202N, 0542872E, Sample: Havill 06-133 (YPM); 1, same but Sample: Havill 06-133.9 (YPM); 7, Giles Co., Big Stony, 15 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected, reared in lab, UTM 4141138N, 0538027E, Sample: Havill 06-135 (YPM); 1, Grayson Co., Highland Trail, 24 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected, reared in lab, UTM 4060842N, 0453808E; Sample: Havill 06-134 (YPM). Vermont: 1 (CNC). West Virginia: 15, Pocahontas Co., Seneca State Forest, 27 April 2006, Coll.: D. Mausel, ex. Tsuga conadensis, larva collected. reared in lab, UTM 4239369N, 0594329E; Sample: Havill 06-120 (YPM); 1, Pocahontas Co., Watoga State Park, 27 April 2006, Coll.: D. Mausel, ex. Tsuga canadensis, larva collected. reared in lab, UTM 4217462N, 0579409E, Sample: Havill 06-121.10 (YPM); 20, but Sample: Havill 06-121 (YPM). Laboratory reared: 3, Blacksburg, VA; 10 IV 2003 (VTRC).

18. *Laricobius sahlbergi* Reitter, 1883
(figs 18, 47)

Diagnosis. Body unicolored. Head dark; ocelli present. Prothorax transverse with well-developed lateral carina and sides explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra incurvate; elytral punctures not confluent. Epipleura dark. Ventrites dark. Femora dark. Tibiae light. Aedeagus without median carina on phallobase; medium lobe subapiculate; apices of parameres without an internal ridge.

Description. Length 2.58–2.72 mm (x = 2.63, n = 4). Body unicolored dark brown; palpi, tibiae, and tarsi tan or yellow brown, antennae yellow with A1 darker and club yellow brown. Head with ocelli; u-shaped furrow present; interocular distance about 4x the width of the eye; macropunctures distinct to indistinct, impressed; micropunctures coarse; setae erect, moderately short with an average length as long as 1/2 width of the eye. Antenna with length of A3 about equal to A4, ratios 1.8:1.5:1.3:1.2:1.2:1.0:1.1:1.0:1.3:1.4:2.4; A11 not strongly asymmetrical. Prothorax transverse and rectangular, dorsoventrally flattened, and widest at middle, sides weakly convex, converging anteriorly from widest point and more steeply convergent posteriorly; about 0.73 x as long as wide (pronotal length/greatest pronotal width = 0.71–0.76, x = 0.73); depth = 0.30–0.40 mm (x = 0.35); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle about 60° and acute, not forming a tooth; posterior angle distinct and not marked by a short tooth; foveae visible dorsally; macropunctures on disc distinct, well-impressed, and well-separated; micropunctures coarse; setae erect, moderately long and the average length 2/3 width of eye. Elytra about 3.17 x as long as wide (elytral length/greatest elytral width = 3.00–3.30, x = 3.17) and 3.32 x as long as pronotum (elytral length/pronotal length = 3.19–3.47, x = 3.32); surface weakly incurvate at basal third; macropunctures not coalescing to form grooves, separated by an average of 1 puncture diameter; micropunctures fine; microsculpture not visible; setae suberect and erect, short and on average about 1/2 the length of the eye. Aedeagus with phallobase transverse (wider than long), about 2/3 the length of the median lobe, median carina absent; median lobe not projecting beyond apices of parameres, relatively broad with its greatest width subequal to the width of the parameres, gradually tapering apically with apex subapiculate, median carina or groove absent, ostium subapical; parameres broad, apices rounded, short apical and subapical setae present, internal subapical ridge absent. Spiculum gastrale apically narrow or acute.

Comments. *Laricobius sahlbergi* is the only unicolorous dark brown species with a well-developed explanate pronotal margin. It can be distinguished from unicolorous *L. nigrinus* by its pale femora and from melanistic *L. erichsonii* by the absence of posterior pronotal teeth and the acute median lobe of the male.

I obtained four specimens from the HNMH, not all having the same labelling. Reitter (1883) gave a size range, so it is likely he had a series (only one specimen had a label bearing the type locality) and all the HNMH specimens, including one from the E. Frivaldszky collection, are considered part of the syntype series. The locality abbreviated on the lectotype label (Fatjanovsk.) may be the modified German translation of the Russian place name listed as Fatjanowskaja in Andree (1896). This may also be written as Fatianowskaya in older literature, but in modern maps and literature it is written as Fatianowo (or Fatianovo which means the same as Fatianovskaya) in Yaroslavl Oblast in European Russia with the coordinates 57.01'.45.64"N, 38.54'49.77"E (A. Solodovnikov, pers. com.). Nikitsky (1992) listed the species range as middle Siberia in Krusnayerskykry (= Krasnoyarskij of Krasnoyarskij Kraj; A. Solodovnikov, pers. com.).

Distribution. Russia: East Siberia. China: Mongolia.

Type material examined. LECTOTYPE (HNHM). 1 female (card mounted and dissected), Fatjanovsk./J. Sahlb./Laricobius sahlbergi m. (hw)/Coll. Reitter/ Holotypus (red) Laricobius sahlbergi 1883 Reitter (name and date hw on white label with red border)/ Laricobius sahlbergi Reitter det. Nikitsky, 1992 (hw)/ Laricobius ♀ sahlbergi Rtt. Jirí Háva det. 03 (hw and printed)/ LECTOTYPE Laricobius sahlbergi Reitter desig, R. Leschen, 2009. PARALECTOTYPES (HNHM). 1, male (card mounted and dissected, genitalia in glycerin pinned below specimen), Sibir. arct./ Paratypus (red) Laricobius sahlbergi 1883 Reitter (name and date hw on white label with red border)/ Coll. Reitter/ PARALECTOTYPE Laricobius sahlbergi Reitter desig, R. Leschen, 2009. 1, sex unknown (card mounted), Sibir. arct./ J. Sahlb./Paratypus (red) Laricobius sahlbergi 1883 Reitter (name and date hw on white label with red border)/ Coll. Reitter/ PARALECTOTYPE Laricobius sahlbergi Reitter desig, R. Leschen, 2009. 1, sex unknown (card mounted), Sibir. arct./ J. Sahlb./L. Sahlbergi (hw) coll. E. Frivaldszky/ 660 b5 (hw on small folded black bordered label)/ Sahlbergi Reitt Sibir. arct. (hw)/PARALECTOTYPE Laricobius sahlbergi Reitter desig, R. Leschen, 2009

Additional material examined. CHINA. 1, Mongolia, Central aimak Chentej Gebirge 25.IV.1971 leg. Zs. Peregi/Laricobius sahlbergi Reitt. V. Richter det. 1973 (HNHM).

19. *Laricobius schawalleri* Háva & Jelínek, 2000

(fig 19)

Diagnosis. Body bicolored. Head light; ocelli present. Prothorax transverse without well-developed lateral carina, sides not strongly explanate. Pronotum light; posterior tooth present. Scutellum dark. Surface of elytra incurvate; elytral punctures posteriorly confluent. Epipleura dark. Ventrites dark. Femora dark. Tibiae light.

Description. Length 2.24 mm. Body bicolored, mostly yellowish tan apart from the meso- and metaventrites-that are completely black, the abdominal ventrites which are infuscate, and most of the elytra which is mostly black to the apical 1/3 along suture, then expanding obliquely to apex to level of stria 5; antenna with AI and club slightly darker. Head with ocelli; u-shaped furrow absent; interocular distance about 2x the width of the eye; macropunctures ovate and well-impressed, scattered and present at center of frons; micropunctures moderately coarse; setation short, decumbent, length about 1/3 the width of the eye. Antenna with length of A3 about equal to A4, ratios 2.1:1.8:1.7:1.7:1.6:1.2:1.2:1.0:1.4:1.3:2.2; A11 strongly asymmetrical. Prothorax transverse and moderately convex, widest at apical 1/3, sides sinuate, and strongly convergent posteriorly; about 0.78 x as long as wide (pronotal length/greatest pronotal width = 0.78); depth = 0.32 mm; pronotum not laterally explanate, lateral carina narrow and reduced to a bead; anterior angle deflected, forming a short ridge and not dentate (the angle formed between the anterior margin and lateral carina, excluding the ridge, is about 60°); posterior angle indistinct and broadly rounded and with a very short tooth; anterior foveae visible only in lateral view, posterior foveae visible in dorsal view; macropunctures ovate, deep, and generally well-separated; micropunctures moderately coarse; setae short, decumbent, and about 1/2 the width of eye. Elytra about 2.80 x as long as wide (elytral length/greatest elytral width = 2.80) and 3.00 x as long as pronotum (elytral length/pronotal length = 3.00); surface incurvate at basal third; macropunctures, especially of striae 1–3, coalescing posteriorly to form grooves, separated by an average of 2/3 of a puncture diameter; micropunctures fine; microsculpture not visible; setae suberect to subdecumbent, short, about 1/2 length of the eye.

Comments. *Laricobius schawalleri* is a distinctive species within the group with confluent elytral punctures by having a transverse prothorax and the apical and posteromedial portions of the elytra yellowish tan. This species was described based on a single female.

Distribution. Nepal.

Type material examined. HOLOTYPE (SMNS). 1 (card mounted and dissected), 564 NEPAL: Dailekh Distr. Dailekh to Mabuchin Pass, 2500 m, 3.–4.VI.1998 leg. W. SCHAWALLER/ Laricobius sp. (hw) det. SCHAWALLER 1999/ HOLOTYPE *Laricobius schawalleri* **sp. n.** J. Jelínek & J. Háva 2000 (red label).

20. *Laricobius taiwanensis* Yu & Montgomery, 2007

(figs 20, 48)

Diagnosis. Body bicolored. Head dark; ocelli absent. Prothorax transverse with well-developed lateral carina and sides explanate. Pronotum dark; posterior tooth present. Scutellum dark. Surface of elytra usually not incurvate; elytral punctures not confluent. Epipleura dark. Ventrites dark. Femora dark. Tibiae usually dark. Aedeagus with median carina on phallobase; medium lobe subacute; apices of parameres without an internal ridge.

Description. Length 1.58–2.54 mm (x = 2.67, n = 15). Body bicolored with head, prothorax, scutellum, elytra along sides to level of abdominal ventrite 5 (usually extending to stria 4 and covering striae 5–10), along suture (though maybealit reduced or absent), epipleuron, and venter black or chocolate brown; elytra dark red brown; antenna with A1 dark brown, funicle yellow brown, and club red-brown; palpi and legs dark brown, tarsi brown, but lighter in some specimens. Head without ocelli; u-shaped furrow present; interocular distance about 4x the width of the eye; macropunctures rounded and distinct, impressed and sometimes fused into trenches and set into depressions; micropunctures moderately coarse; setae erect, elongate with an average length as long as 2/3 to full width of the eye. Antenna with length of A3 about equal to A4, ratios 2.1:1.4:1.1:1.2:1.3:1.1:1.1:1.0:1.3:1.2:1.9; A11 not strongly asymmetrical. Prothorax transverse and rectangular, dorsoventrally flattened, and widest at middle, sides weakly convex, converging anteriorly from widest point and weakly convex, subparallel anteriorly and convergent posteriorly; about 0.79 x as long as wide (pronotal length/greatest pronotal width = 0.75–0.83, x = 0.79); depth = 0.16–0.38 mm (x = 0.29); pronotum laterally broadly explanate, lateral carina with a distinct sharp edge; anterior angle 90º to about 80° and subacute, not forming a tooth; posterior angle distinct, rounded, and with a short tooth; foveae visible in dorsal view; macropunctures on disc distinct, well-impressed and well-separated; micropunctures coarse; setae erect, moderately long with length 2/3 to full width of eye. Elytra about 2.91 x as long as wide (elytral length/greatest elytral width = 1.86–3.71, x = 2.91) and 2.92 x as long as pronotum (elytral length/pronotal length = 1.73–3.30, x = 2.12); surface not or weakly-incurvate at basal third; macropunctures not coalescing to form grooves, separated on an average by 1/2 puncture diameter; micropunctures fine; microsculpture not visible; setae suberect to decumbent, short and on average about 2/3 to full length of the eye. Aedeagus with phallobase transverse (wider than long), 2/3 the length of the median lobe, median carina present; median lobe projecting slightly beyond apices of parameres, somewhat narrow with its greatest width equal to width of the parameres at their basal 1/3, apex subacute, median groove or carina absent, ostium subapical; parameres, slender and narrow, apically acute, very short setae present apically and along inner margin, internal subapical ridge absent. Spiculum gastrale narrow.

Comments. There are no discernable ocelli in this species, though the color of the cuticle that surrounds the deeper cephalic macropunctures may be lighter. Among the species that lack ocelli, *L. taiwanensis* has the sides of the prothorax weakly convex, which will distinguish this species from the others. Having the dark tibiae will distinguish *L. taiwanensis* from *L. naganoensis*, the presence of of the posterior pronotal tooth will distinguish *L. taiwanensis* from *L. osakensis*, and the dark red coloration and presence of a median carina on the basal piece will distinguish *L. taiwanensis* from *L. kangdingensis*.

The holotype (NMNS) was not examined, but several paratypes were, belonging to the same series.

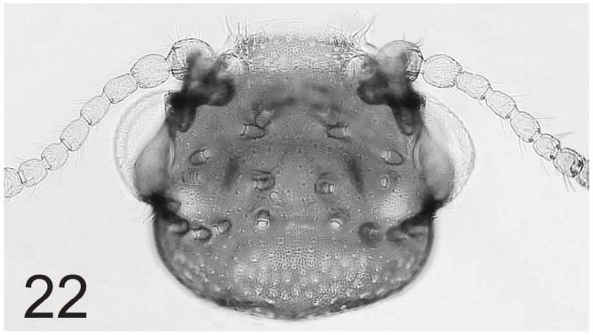
Hosts. Plants: *Tsuga chinensis*. Adelgid: *Adelges tsugae*.

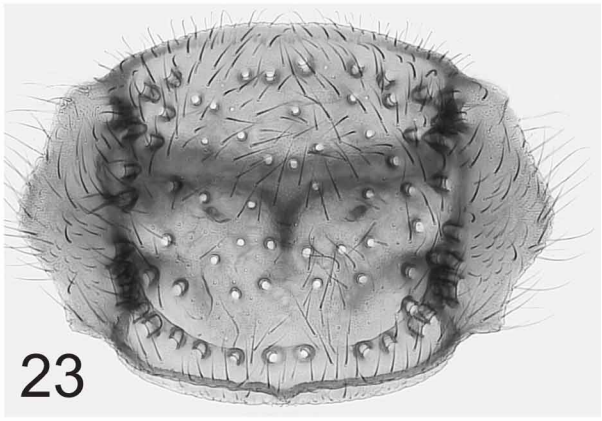
Biology. Habitat and rearing (Yu & Montgomery 2007).

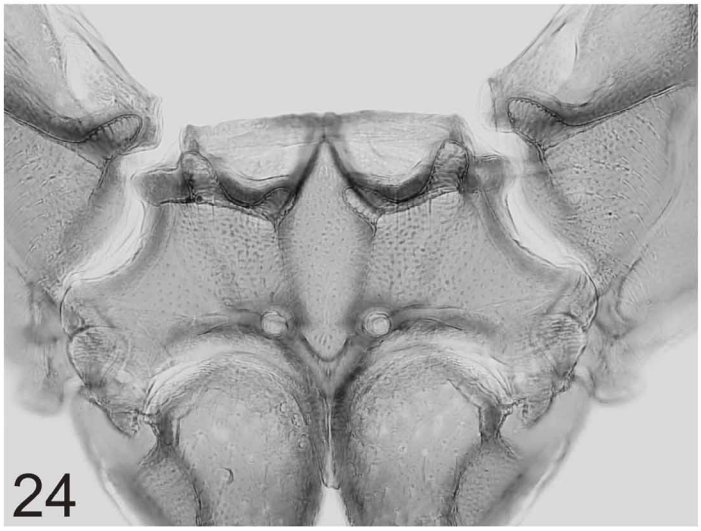
Distribution. Taiwan: Kao Hsiung.

Type material examined. PARATYPES: 21 (10, BMNH [with all original labels hw]; 4, NMNH; 3, YPM; 4, USDA, one each with Havill Sample # 08-50, Havill Sample # 08-51), TAIWAN Kao Hsiung Co. Road 20, 2 Km west of Ya Kou Hotel 26 May 1994 S.T. Murphy/PARATYPE Laricobius taiwanensis, Yu and Montgomery (yellow green label).

FIGURES 17–20. Dorsal habitus. 17, *Laricobius rubidus*; 18, *L. sahlbergi*; 19, *L. schawalleri*; 20, *L. taiwanensis*.





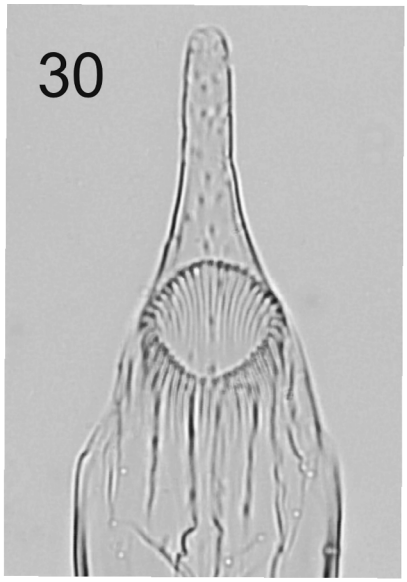


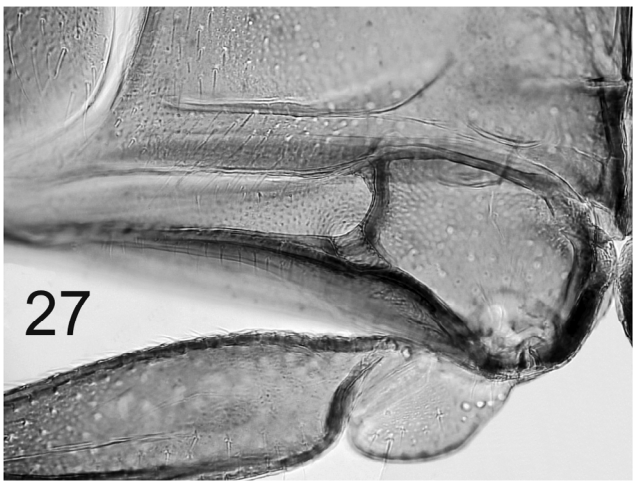
FIGURES 21–25. Dorsal habitus and morphological features. 21, habitus of *Laricobius wittmeri*; 22, head of *L. erichsonii*; 23, prothorax of *L. rubidus*; 24, mesoventrite of *L. erichsonii*; 25, metanepisternum of *L. rubidus*.

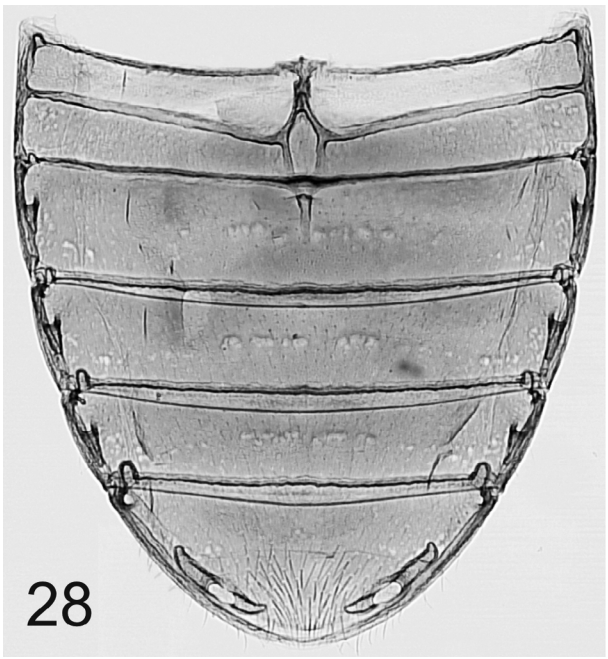
21. *Laricobius wittmeri* Háva 2010b

(figs 21, 49)

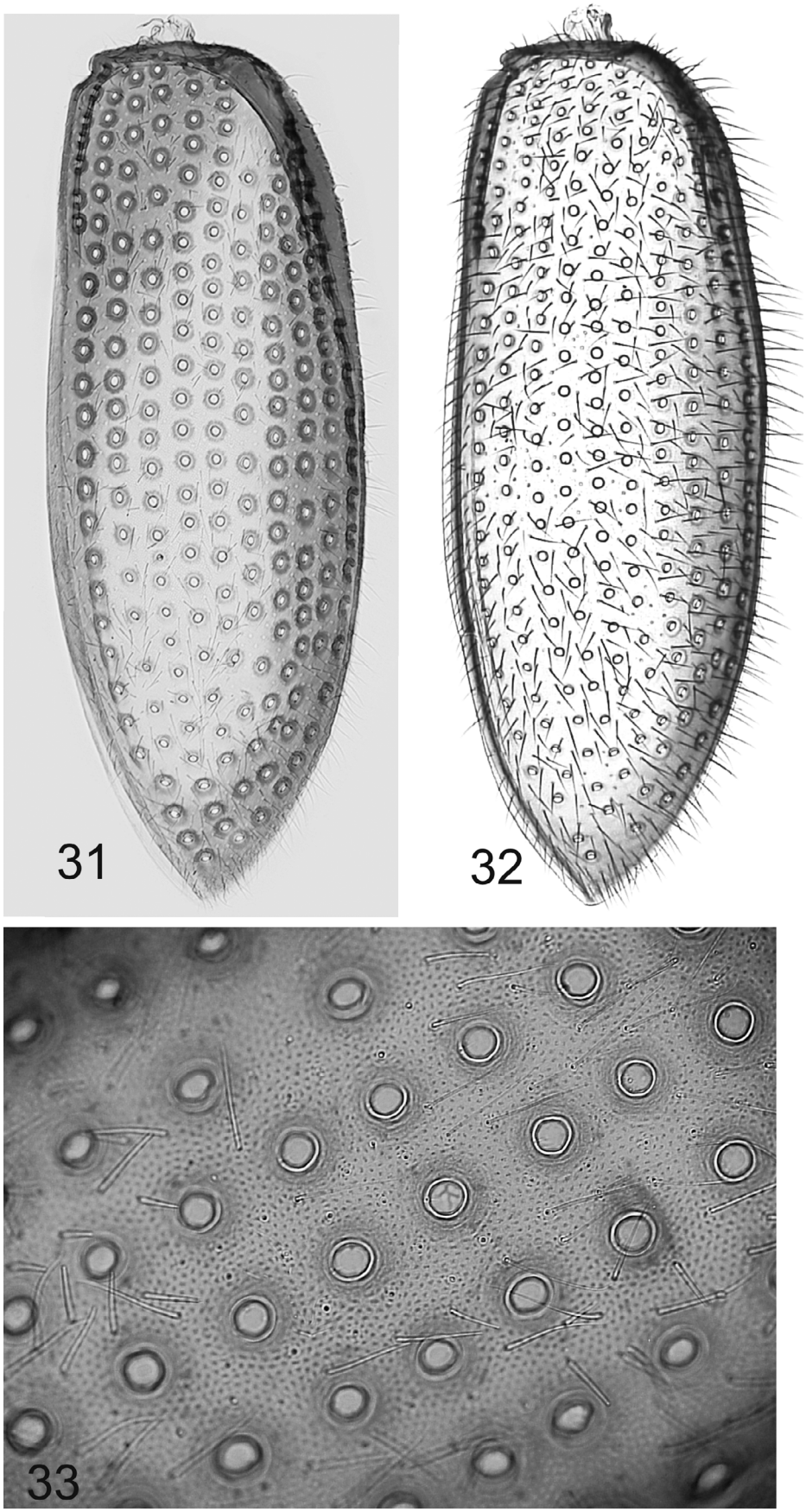
Diagnosis. Body bicolored. Head dark; ocelli present. Prothorax quadrate without well-developed lateral carina, sides not strongly explanate. Pronotum dark; posterior tooth absent. Scutellum dark. Surface of elytra incurvate; elytral punctures not posteriorly confluent. Epipleura dark. Ventrites dark. Femora light. Tibiae light. Aedeagus with medium lobe acute; apices of parameres without an internal ridge.



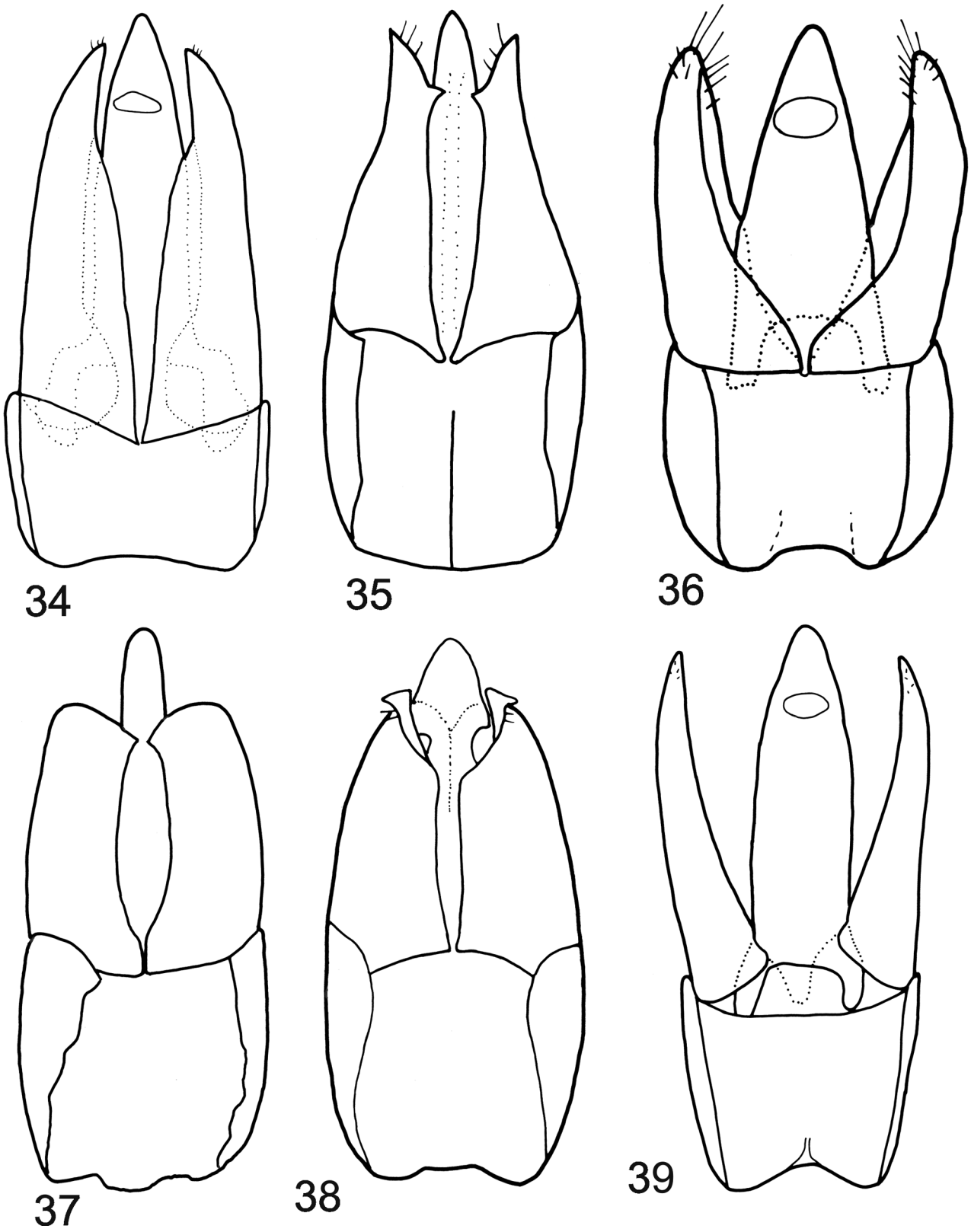




FIGURES 26–30. Morphological features. 26, metaventrite of *Laricobius erichsonii*; 27, right metacoxa of *L. erichsonii*; 28, abdomincal ventrites of *L. erichsonii*; 29, aedeagus of *L. naganoensis*; 30, apex of median lobe (penis) of *L. naganoensis*.

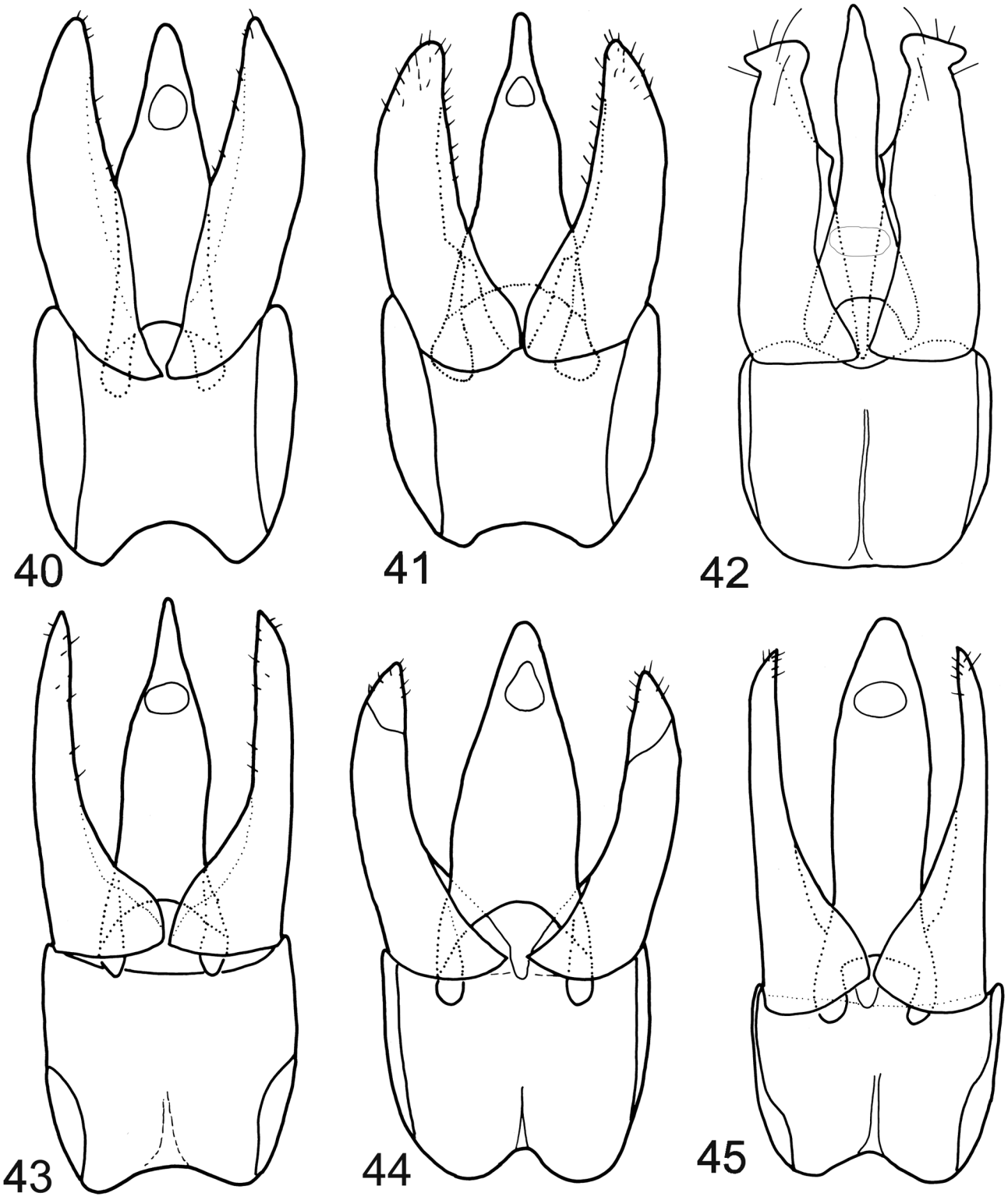


FIGURES 31–33. Elytra. 31, left elytron of *Laricobius erichsonii*; 32, left elytron of *L. rubidus*; 33, detail showing surface of elytron of *L. erichsonii*.



FIGURES 34–39. Dorsal views of genitalia. 34, *Laricobius baoxingensis*; 35, *L. daliensis*; 36, *L. erichsonii*; 37, *L. incognatus*; 38, *L. jizu*; 39, *L. kangdingensis*.

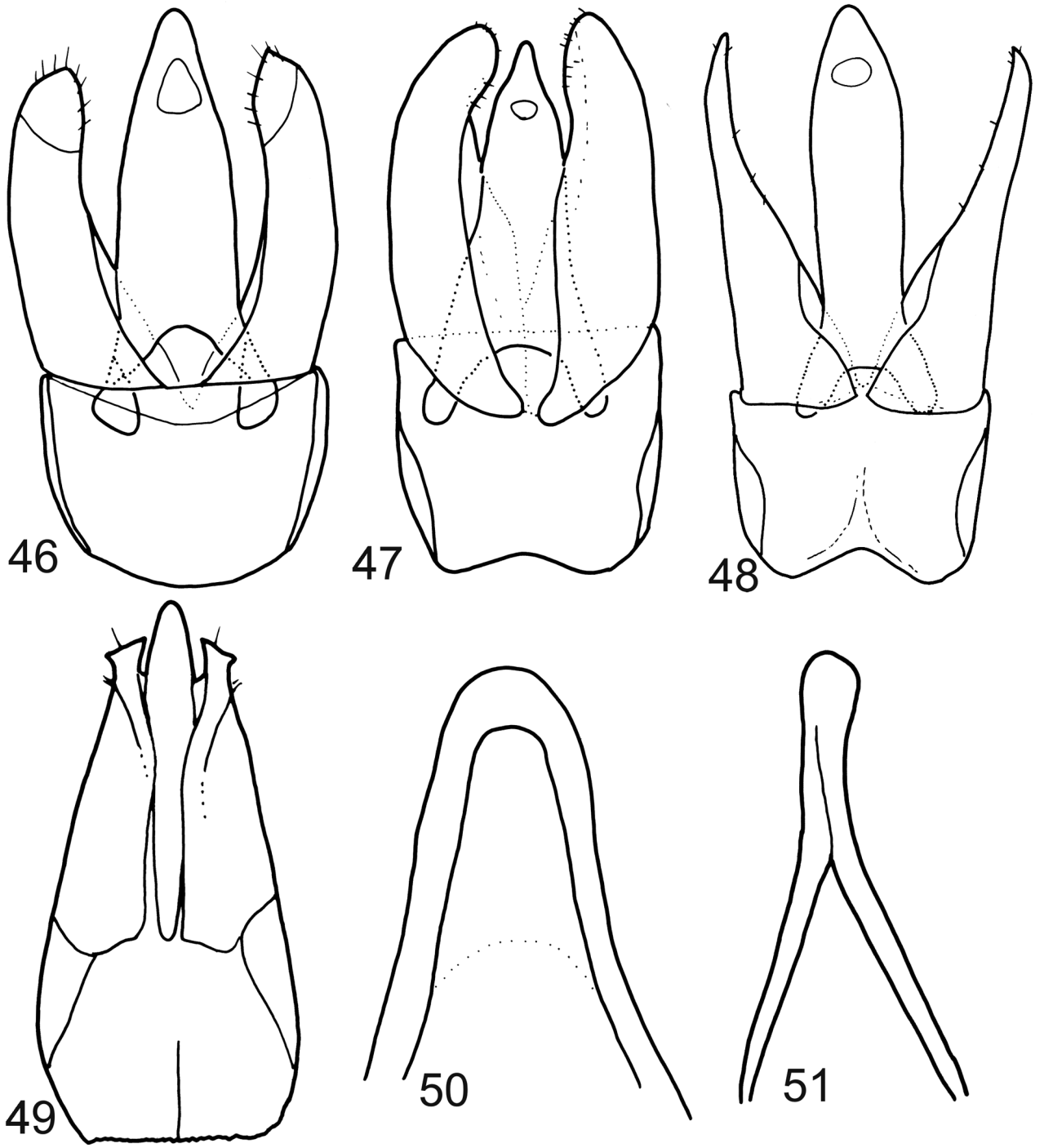
Description. Length 2.00. Body bicolored with chocolate brown head, prothorax, ventrites, scutellum, and flanks of elytra to striae 7 and remaining areas and appendages light tan; antenna with AI and club darker. Head with ocelli; u-shaped fovea absent; interocular distance about 2x the width of the eye; macropunctures ovate and well impressed; micropunctures coarse; setation short and decumbent, length about 1/3 the width of the eye.



FIGURES 40–45. Dorsal views of genitalia. 40, *Laricobius kovalevi*; 41, *L. laticollis*; 42, *L. loebli*; 43, *L. naganoensis*; 44, *L. nigrinus*; 45, *L. osakensis*.

Antenna with length of A3 less than A4, ratios 1.8:1.7:1.0:1.5:1.7:1.5:1.3:1.1:1.7:1.7:2.1; A11 strongly asymmetrical. Prothorax quadrate and highly convex, widest at middle, sides sinuate; about 0.84 x as long as wide (pronotal length/greatest pronotal width = 0.84); depth = 0.45; pronotum not laterally explanate, lateral carina reduced to a narrow bead; anterior angle acute, deflected, and forming a short laterally directed tooth (the angle formed between the anterior margin and lateral carina, excluding the tooth, is about 90°); posterior angle indistinct and broadly

rounded and without a short tooth; anterior foveae visible only in lateral view, posterior foveae visible in dorsal view; macropunctures ovate, deep, and well-separated; micropunctures moderately coarse; setae short, decumbent, and lengths about 1/3 the width of eye. Elytra about 1.6 x as long as wide (elytral length/greatest elytral width = 1.6) and 3.40 x as long as pronotum (elytral length/pronotal length = 3.40); surface incurvate at basal third; macropunctures of striae 1 coalescing posteriorly to form grooves, separated by an average of 1 puncture diameter; micropunctures sparse; microsculpture not visible; setae suberect and short, about 1/3 length of the eye. Aedeagus with phallobase transverse, about 2/3 the length of the median lobe; median lobe projecting beyond apices of parameres, apex acute, median groove present; parameres broad, apically acute and anvil-shaped with a distinct subapical tooth, moderately short setae present subapically, internal subapical ridge absent. Spiculum gastrale apically broad.



FIGURES 46–51. Dorsal views of terminalia. 46, genitalia of *Laricobius rubidus*; 47, genitalia of *L. sahlbergi*; 48, genitalia of *L. taiwanensis*; 49, genitalia of *L. wittmeri*; 50, spiculum gastrale of *L. loebli*; 51, spiculum gastrale of *L. osakensis*.

Comments. Among the species without explanate pronotal margins, *L. wittmeri* is the only member of the group that lacks confluent elytral punctures (apart from the sutural striae).

This species was described from two specimens (one male and one female), and only the male type was examined, the other was not made available for study. The Holotype is subteneral, and not fully pigmented. An additional specimen that was completely teneral was located in the CNC. The previously extracted genitalia of the Holotype was distorted and the width of the median lobe, presence of the median carina, ostium, and presence of internal subapical ridge were not observed.

Distribution. Nepal.

Type material examined. HOLOTYPE (NHMB). O Nepal 1980 W. Wittmer/ Mumbug, O Makalu 3500 m, 9.6./HOLOTYPE ♂ *Laricobius wittmeri* **sp. n.** J. Háva det. 2009 (red label with narrow black border).

Additional material examined. Nepal: 1, 27°58'N. 85°00'E. Mal. Tr. 2, 11, 200', 28 May 1967, Can. Nepal Exped. (CNC).

Cladistic analysis

Twenty terminal taxa were scored for adult characters based on the material available for this study (Table 1). Multistate characters were treated as polymorphic and unknown states were treated as missing (?). The data were coded and entered into MacClade version 3 (Maddison and Maddison 1992) for character analysis and tree construction in Paup*4.0b10 (Swofford 1998). The settings used in Paup*4.0b10 for heuristic tree searches include swapping on all trees and random addition sequences (100 replicates). Character states were unordered. Branch support was examined using decay indices (DI; Bremer 1994) calculated by TreeRot (Sorenson 1999). Bootstrap values (BS; Felsenstein 1985, Sanderson 1995) were calculated by resampling at 100 replications using simple searches while holding one tree at each step and swapping on the best tree. Ambiguous characters were optimized onto trees using standard ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) optimizations (Maddison *et al*. 1984).

TABLE 1. Data matrix with characters grouped by tens. * = Polymorphisms.

										10										20				
baoxingensis	1	0	1	1	1	?	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	
bicolor	1	1	0	1	1	?	1	1	1	0	0	1	1	1	1	0	1	1	?	?	?	?	?	
caucasicus	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	?	?	?	?	?	
daliensis	1	1	0	1	0	1	1	1	1	0	0	1	1	1	1	0	1	1	0	1	?	1	1	
erichsonii	1	1	0	1	*	?	1	1	0	0	1	0	0	0	0	1	*	0	0	0	0	0	0	
incognatus	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	1	1	?	2	?	1	1	
jizu	1	1	0	1	0	1	1	0	0	0	0	0	1	1	1	0	1	1	?	1	?	0	1	
kangdingensis	1	1	0	1	1	?	1	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	
kovalevi	1	1	0	1	1	?	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	
laticollis	1	0	1	*	0	0	0	0	0	0	1	0	0	0	0	*	1	0	0	0	0	1	0	
loebli	1	1	0	1	0	1	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	1	1	
mirabilis	0	0	0	0	1	?	0	0	0	0	0	0	1	1	1	0	1	1	?	?	?	?	?	
naganoensis	1	1	0	1	1	?	1	1	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	
nigrinus	1	1	0	1	0	1	1	1	1	0	1	0	0	0	0	*	1	0	1	0	1	0	0	
osakensis	1	1	0	1	1	?	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	
rubidus	1	1	0	1	1	?	1	1	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	
sahlbergi	1	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	
schawalleri	0	0	0	1	1	?	0	0	0	0	0	0	0	1	1	1	0	1	?	?	?	?	?	
taiwanesnsis	1	1	0	1	1	?	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	
wittmeri	1	1	0	1	1	?	1	0	0	0	0	0	1	1	1	0	1	0	?	1	?	1	1	
Nothoderodontus	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	

Nothoderodontus is the sister species of *Laricobius*, both are placed in the subfamily Laricobiinae (Ge *et al*. 2007, Leschen and Beutel 2010) and share various features (Crowson 1980), including the foveae and pore systems on the ventrites (Lawrence and Hlavac 1979). Lawrence (1985) provided a list of synapomorphies for Laricobiinae: body with a vestiture of setae, pits or foveae (eg, fig 24) present at each corner of the pronotal disc, on the metanepisternum, and on the metaventrite, discrimen not reaching anterior edge of metaventrite (fig 26) and tarsomere 4 shorter and narrower than T3. I examined material of most species of *Nothoderodontus*, including a new species from New Zealand, but the trees were rooted using *Nothoderodontus dentatus* Lawrence, as this species (along with *N. chilensis* Lawrence, both from Chile), were considered by Lawrence (1985) to be the most primitive members of the genus.

List of characters

Though many of the species of *Laricobius* are distinctive, character scoring was limited by the number of available specimens, especially where males are unknown. Nine characters were based on color and restricted to homologous segments and comparisons across species. These colors are simply classified as pale and dark, without specifying exact color.

1. Color of head. 0, pale (fig 13); 1, dark (fig 20).
2. Color of pronotum. 0, pale (fig 13); 1, dark (fig 20).
3. Coloration of proventer and hypomeron. 0, same; 1, different. Taxa coded as 3-1 the hypomeron is tan and proventrite is dark. In most species the meso-, meta- and abdominal ventrites are dark.
4. Coloration of scutellum. 0, pale (fig 13); 1, dark (fig 18). This character is coded as polymorphic in *L. laticollis*.
5. Coloration of elytra. 0, unicolored (fig 13); 1, bicolored (fig 20). The color of the elytra is variable and in those species coded as 5-1 include *L. baoxingensis* and *L. kovalevi* which have the lateral dark maculae restricted to an area on the anterior portion above the epipleuron. This reduced maculation also occurs in other bicolored species with more conspicuous bicoloration (e.g., see variation under *L. erichsonii* and *L. rubidus*.)
6. Main color of elytra. 0, pale (fig 17); 1, dark (fig 18).
7. Coloration of epipleura. 0, pale; 1, dark. This character treats the epipleural color at the base.
8. Coloration of midfemora. 0, pale (fig 19); 1, dark (fig 2).
9. Coloration of midtibiae. 0, pale (fig 19); 1, dark, (fig 4).
10. Ocelli. 0, present; 1, absent.
11. U-shaped furrow of head. 0, absent (fig 2); 1, present (fig 20). There is a furrow on the head of some species of *Nothoderodontus*, but these do not appear to be composed of deep foveae or macropunctures (like that in *Laricobius*) that are joined by channels, nor do they ring the lateral margins of the disc of the frons, but rather run transversely. These furrows are weak or shallowly impressed in *L. nigrinus*, *L. osakensis*, and *L. rubidus*, and coded as present.
12. Prothorax. 0, transverse (wider than long, fig 12); 1 elongate (longer than wide, fig 11). The shape of the prothorax of *L. loebli* is more or less quadrate and I chose to code this species as state 1.
13. Anterior pronotal tooth. 0, absent (fig 3); 1, present (fig 2). There is a small tooth at the anterior angle of some specimens of *L. erichsonii*, but this tooth is not in the form of a well-defined anterolateral tooth present in the remaining species coded as 13-1.
14. Anterior pronotal fovea. 0, visible in dorsal view; 1, visible in lateral view. This character is coded as 14-0 *Nothoderodontus* because these are present in New Zealand species, though absent in the specimens I have of *N. dentatus*.
15. Pronotal carina. 0, well developed (fig 11); 1, reduced (fig 12). In the group lacking a well-developed explanate pronotum, the prothorax has a higher pronotal volume and, in general, more convex (coded here as 15-1).
16. Posterior pronotal tooth. 0, absent (fig 12); 1, present (fig 17). The posterior tooth arises from the posterior angle of the lateral carina (or bead). In some specimens of *L. erichsonii* the tooth may be reduced, but present and this character is coded as polymorphic for *L. laticollis* and *L. nigrinus*.
17. Elytral surface. 0, flat; 1, incurvate. This character is coded as polymorphic for *L. erichsonii* and *L. taiwanensis*.
18. Elytral punctures. 0, posteriorly separate (fig 3); 1, posteriorly confluent (fig 8). In most species of *Nothodero-*

dontus there is no vestige of punctures at the basal third of the elytra.

19. Median carina of phallobase. 0, absent (fig 34); 1, present (fig 35). This character is coded as unknown for *L. bicolour*, *L. caucasicus*, *L. incognatus*, *L. jizu*, *L. mirabilis*, *L. schawalleri*, and *L. wittmeri*.
20. Apices of parameres. 0, acute or rounded (fig 35); 1, anvil-shaped (fig 38); 2, broad (fig 37). The shape of the parameres are variable and I restrict coding to the shape of the apices. This character is coded as unknown for *L. bicolor*, *L. caucasicus*, *L. daliensis*, *L. mirabilis*, *L. schawalleri*, and *L. wittmeri*.
21. Subapical ridge of parameres. 0, absent (fig 44); 1, present (fig 41). This character is coded as unknown for *L. bicolor*, *L. caucasicus*, *L. incognatus*, *L. jizu*, *L. mirabilis*, *L. schawalleri*, and *L. wittmeri*.
22. Median lobe. 0, rounded (fig 45); 1, acute (fig 41). The shape of the median lobe is variable and I restricted coding to the shape of the apices. The apex of the median lobe of *L. jizu* is arrow-shaped and coded as rounded (23-0) while it is apiculate in *L. laticollis* and it is coded as acute (23-1).
23. Spiculum gastrale. 0, apically narrow (fig 50); 1, apically broad (fig 51). This character is coded as unknown for *L. bicolor*, *L. caucasicus*, *L. mirabilis*, and *L. schawalleri*.

Results

The cladistic analysis resulted in 14 trees (Tree length = 50, Consistency index = 0.48, Retention index = 0.75): the 50% majority-rule consensus tree is shown in fig 52 and strict consensus tree shown in fig 53. Two broad groups are shown in the reconstructions. Group A consists of a fully resolved lineage of species from China and the Himalayan Plateau and supported by 3 unambiguous characters: u-shaped furrow of head absent (11-0), anterior pronotal fovea visible in lateral view (14-1), and pronotal carina reduced (15-1). Character 13-1 (anterior pronotal tooth present) supports this group by ACCTRAN when polytomies are fixed. Group B consists of the remaining species which are widespread: elytral punctures posteriorly separate (18-0) and spiculum gastrale narrow (23-0, coded as unknown for several Himalayan-Chinese species). The relationships are relatively well resolved in the tree (fig 52), apart from a large terminal multichotomy. Three sister groups are supported: *L. laticollis* + *L. caucausicus* (3-1, coloration of hypomeron and proventer different); *L. rubidus* + *L. nigrinus* (21-1, internal ridge of parameres present); *L. baoxingensis* + *L. erichsoni* (no unambiguous changes, though 9-0, dark tibiae supports this group in some of the resolutions of the polytomy). To further resolve the relationships I used Successive Approximations Weighting (Farris 1969, Carpenter 1988, 1994) based on recalculating the weight by the CI (base weight of 10) and using the best fit option in PAUP*. Six trees resulted by two iterations (strict consensus shown in fig 54) showing further resolution, in the group B crown groups, and the grouping of *L. naganoensis* and *L. osakensis* is supported by a reversal (16-0, posterior pronotal tooth absent). The grouping of taxa that lack ocelli (10-1) is shown as a monophyletic group in this weighted tree. It is interesting to note that if all color characters are removed (C1-9) and the analysis is rerun, this results in 10 trees (TL = 24, CI = 0.62, RI = 0.86) with minor rearrangements among group A and in group B supports a monophyletic group lacking ocelli, and the group *L. laticollis*, *L. sahlbergi*, *L. caucausicus* + *L. kovalevi* are sister taxon to the remaining taxa as shown in fig 54. In these latter analyses *L. baoxingensis* and *L. erichsoni* are not shown as sister taxa, suggesting that this sister relationship in some of the initial trees is tenuous.

Discussion

Two morphologically distinct lineages exist, with group A having more elongate bodies with a generally more transverse prothorax with well-developed lateral carinae. Group A is widely distributed in the Holarctic. By contrast, group B has shorter bodies with a more convex prothorax and reduced lateral carinae, and is confined to the ranges of the western Himalaya and the Sichuan Basin. Group B also lacks well-developed furrows of the head, but this reduction of foveae also occurs within group A.

The character matrix is limited with an almost equal ratio of taxa to characters (20:23) which can be improved by increasing the number of specimens, especially of males for specimen-limited species. Color variation has provided a good source of informative characters especially resolving the relationships within the major groups. But due to the lack of hard characters and especially genitalic characters, the high number of “soft”color characters (9

of 23) may have swamped the information contributed from morphological characters, such as the loss of ocelli. Apart from the major differences in the prothorax between groups A and B, there seems to be few overall phylogenetic changes of "hard" morphological characters within each group like the location and number of major foveae which are consistent among all species of *Laricobius* (as they are in *Nothoderodontus*). Meanwhile, ocelli are absent in a great majority of beetles (Leschen and Beutel 2004) and the loss of these may have occurred once in group B and only among the eastern Asian species. Additional specimens of males for species known only by females will help further resolve species relationships.

While this study is a first attempt at reconstructing the relationships of all *Laricobius* species, the genetic study included in Montgomery *et al*. (2011) is a first attempt to reconstruct the relationships of seven species of group B based on four genes (COI, wingless, EF1α, and ITS2; see fig 52). There is little congruence between the two studies in their basal relationships though they both support a monophyletic *L. nigrinus* + *L. rubidus*. A single loss of ocelli is shown in the molecular trees, which is only shown the weighted morphological trees (fig 54).

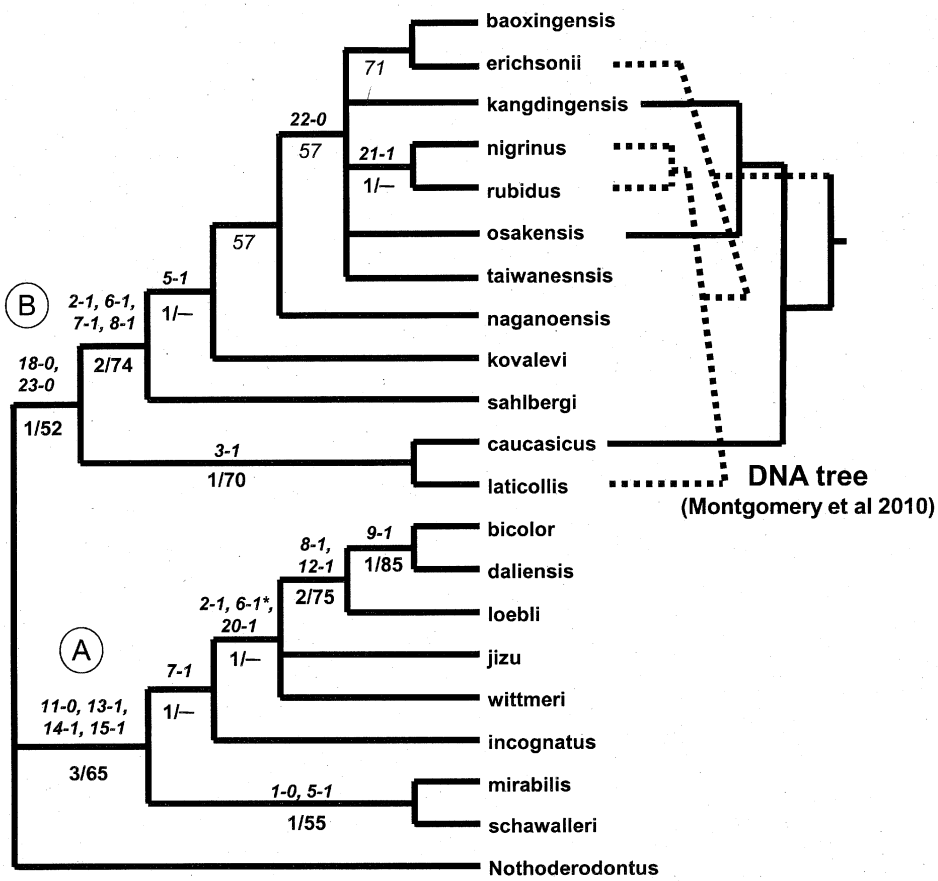


fig 52

FIGURE 52. Cladogram showing reconstructed relationships among *Laricobius* species. Character changes are provided above the nodes and Bremer /Bootstrap values are below. Note that 6-1, unknown in *L. wittmeri* and *L. bicolor*, 13-1 by ACCTRAN when polytomies are fixed, 20-1 (unknown in *L. bicolor*, *L. mirabilis* and *L. schawalleri*). The DNA tree published by Montgomery *et al*. (2011) is shown at right.

Host plant and adelgid associations are known for only a few members of group B, and none for group A, making the phylogenetic assessment of the evolution of these characters difficult. Based on the scant data, members of group B that have known host data suggest that they will be found on both primary and secondary aldelgid hosts (see host list of adelgids in Havill & Foottit 2007). By contrast, comments about biogeography are more compelling.

Based on the cladograms, it can be inferred that there was a split between a widespread lineage (group B, with basal taxa found in central Asia and western North America) and a restricted Asian lineage (group A, with basal

taxa found in Nepal and central China) which diversified further in areas of the Himalaya (Nepal) and the Sichuan Basin. The rather scattered occurrence of Nepalese taxa among more easterly species may be more an artefact from the lack of "hard" characters, rather than a true biogeographic pattern in group A. Phylogenetic relationships are ambiguous for nodes above *L. sahlbergi* in the morphology trees (see also trees in Figs. 53 and 54).

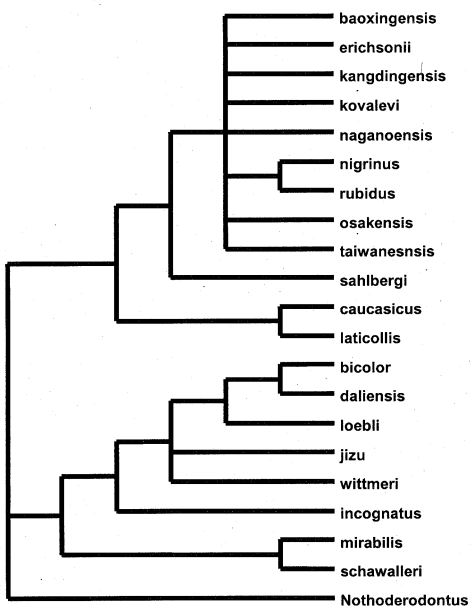


fig 53

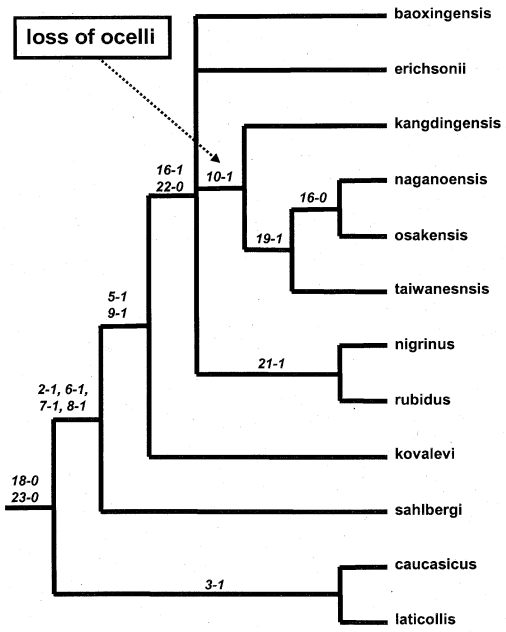


fig 54

FIGURES 53, 54. 53, strict consensus tree with characters unweighted; 54, portion of tree (group A) based on successive approximations character weighting (character support at relevant nodes).

Holactic faunas share a long biogeographic history (Allen 1983; Sanmartín at al. 2001) with ancient patterns of widespread Holarctic Laurasian ancestry, trans-Beringian exchanges, and recent long-distance dispersal events (e.g., Hendrixson and Bond 2007; Drovetski 2003; Meng *et al*. 2008; Vila *et al*. 2011). An Old World to New World dispersal route is predominant in *Bombus* bees (Hines 2008) and has been shown in *Tsuga* (Havill *et al*. 2008) and other plants (Wen *et al*. 1998; Donoghue and Smith 2004). There may have been a divergence between western North America (*L. laticollis*) and Asia (*L. caucasicus*) or a central/eastern Asian ancestor located near the base of group B inferred from the placements of *L. sahlbergi* and *L. kovalevi* (Figs. 52 and 54). *Tsuga,* a host of some *Laricobius* and one adelgid (Havill and Foottit 2007), does not support an hypothesis for Asian ancestors, but rather, Havill *et al*. (2008) found that ancestral *Tsuga* species had widespread distributions which contracted and split through time. Havill *et al*. (2008) suggest that "out of Asia" patterns are often inferred using methods that do not take into account fossils and the retention of widespread ranges through time. The taxon-limited molecular data which have *L. laticollis* and *L. caucasicus* grouped separately is in favor of a split between Europe + North America and Asia.

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APPENDIX 1. Undetermined species.

Laricobius* sp. nr. *baoxingensis
Label data: 1, China: Shaanxi Qing Ling Shan, 108.47E, 33.51N, Mountain W Pass, at Autoroute km 70, 47 km S Xian 2300–2500m, sifted 26–30.08.1995 leg. A. Pütz (APUC).

Laricobius* sp. nr. *loebli
Label data: 1, INDIA, W. Bengal, Darjeeling Distr., Ghum, 2200 m leg. Gy. Topál, No. 771 sifted moss samples 7.X.1967, Derodontidae Laricobius sp. N. Det. A. S. Slipinski 96 (HNHM).

Laricobius* sp. nr. *mirabilis
Label data (Háva 2010): 1, China, Yunnan, Hengduan Mts.—part Baima, 28°20´N 99°03´E, 4300 m, 23.vi.– 2.vii.1996, V. Kubán lgt. (NHMB).

Laricobius* sp. 1 nr. *jizu
Label data (Háva 2010)**:** 1, China, W Guizhou prov., Leigongshan, Xijiang, 1200–1900 m, 29.v.–2.vi.1997, Bolm lgt. (NHMB).

Laricobius* sp. 2 nr. *jizu
Label data: Distr. Darjeeling India, W. Wittmer, Tiger Hill, 2150 m, 7.5.75 (NHMB).