



Two new genera of Oriental xyleborine ambrosia beetles (Coleoptera, Curculionidae: Scolytinae)

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Abstract

As part of an ongoing revision of the Southeast Asian fauna two distinct species groups were identified and hypothesized as new genera. These species groups were monophyletic as evidenced by a Bayesian analysis of DNA sequences from four genes for 181 xyleborine taxa augmented by 18 species newly included in this phylogenetic analysis. The species groups and newly discovered species demonstrated unique combinations of diagnostic characters and levels of DNA sequence difference commensurable to other xyleborine taxa. Hence, two new genera and three new species were described: *Fraudatrix* **gen. n.**, *Tricosa* **gen. n.**, *Tricosa cattienensis* **sp. n.**, *T. indochinensis* **sp. n.**, *T. jacula* **sp. n.**. The following new combinations are proposed: *Fraudatrix cuneiformis* (Schedl, 1958) (*Xyleborus*) **comb. n.**, *Fraudatrix melas* (Eggers, 1927) **comb. n.**, *F. pileatula* (Schedl, 1975) (*Xyleborus*) **comb. n.**, *F. simplex* (Browne, 1949), (*Cryptoxyleborus*) **comb. n.**, *Tricosa mangoensis* (Schedl, 1942) (*Xyleborus*) **comb. n.**, *T. metacuneola* (Eggers, 1940) (*Xyleborus*) **comb. n.** Keys to the females of the species included in the new genera are presented. Diagnostic characters are given for the genera and species, and the distribution and biology of each taxon is discussed. The addition of these new genera increases the number of recognized genera of Xyleborini to 41.

Key words: new species, new combinations, new records, molecular phylogeny, taxonomy

Introduction

Xyleborine ambrosia beetles are a diverse group of scolytines represented by 1200 species (Hulcr *et al.* 2015). These beetles likely originated 20 million years ago and since dispersed and diversified into worldwide forests (Jordal & Cognato 2012). Their habits of inbreeding and feeding on symbiotic fungi have contributed to this diversification and many species remain undiscovered (Gohli *et al.* 2017; Smith *et al.* 2017). These species are currently divided into 39 genera, many of which may not represent monophyletic evolutionary lineages (Hulcr *et al.* 2007; Alonso-Zarazaga & Lyal 2009; Hulcr & Cognato 2010, 2013; Smith 2017; Cognato 2018; Mandelshtam *et al.* 2019).

Xyleborus was first described for five species (Eichhoff 1864). By 1986, a total of 45 genera of Xyleborini had been described (Wood 1986; Alonso-Zarazaga & Lyal 2009). Wood (1986) reviewed the genera, recognised only 24 and deemed his classification as “tentative and flawed”. Subsequent morphological and molecular phylogenies of the Xyleborini provided a template delimiting genera based on monophyly (Hulcr *et al.* 2007; Cognato *et al.* 2011). Also, a set of diagnostic morphological characters, including the antenna and mycangium, were established for the recognition of genera (Hulcr *et al.* 2007). Several studies since 1990 have removed *Premnobius* from Xyleborini, synonymized four genera, resurrected six and described 14 new genera (Wood and Bright 1992; Bright and Rabaglia 1999; Hulcr *et al.* 2007; Hulcr 2010; Hulcr & Cognato 2010, 2013; Cognato 2013; Storer *et al.* 2015; Smith 2017; Cognato 2018; Mandelshtam *et al.* 2019). Many of these new genera were described for known *Xyleborus* species.

The discovery of new genera continues and the complete diversity is not yet realized. Several *Xyleborus* species with autapomorphic features and/or phylogenetic placement sister to other genera suggest the existence of new genera (for example, Hulcr & Cognato 2013). Expeditions to under-collected regions in Southeast Asia and the Neotropics have uncovered specimens with little affinity to current genera (Smith & Cognato, personal ob-

servation). Recently, a combination of new collections from Vietnam and China, phylogenetics, and reevaluation of autapomorphies in certain *Xyleborus* species have yielded evidence for two new genera. These species include *Xyleborus metacuneolus* Eggers, 1940 and *X. cuneiformis* Schedl, 1958 whose generic placement was considered suspect, and which resemble some *Cyclorhipidion* Hagedorn, 1912 species (Hulcr & Cognato 2013; Smith, per. obs.). Given these preliminary data, we include additional specimens in a re-evaluated Xyleborini phylogeny, and review literature and worldwide scolytine collections to justify the erection of two new genera.

Methods

Type and non-type specimens were examined from the following institutions:

IZAS	Institute of Zoology, Chinese Academy of Sciences, Beijing, China
MSUC	A.J. Cook Arthropod Research Collection, Michigan State University, East Lansing, MI, USA
NMNH	National Museum of Natural History, Smithsonian Institution, Washington D.C., USA
RABC	Roger A. Beaver collection, Chiangmai, Thailand
UFFE	University of Florida Forest Entomology, University of Florida, Gainesville, FL, USA

Further specimens were recently collected from China and Vietnam and 18 specimens of *Xyleborus* and *Cyclorhipidion* representing potential species of the two new genera and *Cyclorhipidion* species were included in order to test the monophyly of the suspect species (Table 1). DNA was extracted, replicated for COI, CAD, EF-1 α , and 28S, in part, via PCR, and sequenced following the protocols of Cognato *et al.* (2018). Voucher specimens were pinned and deposited in MSUC. Based on prior studies, different alignments of 28S data for xyleborines (Cognato *et al.* 2011; Cognato *et al.* 2018) had little consequence on the resulting Bayesian phylogenies. Thus 28S sequences were aligned with the default settings of MUSCLE (Edgar 2004). This alignment along with the protein coding DNA sequences from an additional 163 specimens (Mandelstam *et al.* 2019 for details) were compiled into a NEXUS file which is available at <https://www.canr.msu.edu/hisl/research/>. These data were analyzed under maximum likelihood using Bayesian estimation of phylogeny (Mr. Bayes 3.2.6, Ronquist *et al.* 2012, run in parallel and enabled via CIPRES, www.phylo.org). The data were partitioned by gene, codon position, and 28S, resulting in 10 divisions, and were independently analyzed under a general time reversible model (GTR+ Γ +I), which was determined as best fit by AIC in MrModeltest v.2 (Nylander 2004). Four Metropolis-Coupled Markov Chain Monte Carlo searches (one cold, three heated) were run in two simultaneous analyses for 40 million generations. Each analysis was sampled every 100th iteration. All parameters reached stability within 40 million generations and the split distribution between analyses reached a mean standard deviation of 0.007184 suggesting little variation among the runs. Bayesian posterior probabilities of clades were calculated by a majority-rule consensus of those trees after a 25% burn-in (600,002 trees—the total of both runs).

Morphological terminology follows Hulcr *et al.* (2007). Specimens were imaged using a Visionary Digital Passport II system (Palmyra, VA) using a Canon EOS 5D Mark II, 65.0 mm Canon Macro photo lens, Canon Speedlite transmitter ST-E2, DYNALITE MH2015 road flash heads (Union, NJ), and a Stack Shot (Cognisys, Inc, Kingsley, MI) controlled by Zerene Stacker 1.04 (Zerene Systems, Richland WA). Montages of the sliced images for each specimen were assembled using Helicon Focus Mac Pro 7.5.6 (Helicon Soft, Kharkov, Ukraine) and edited in Adobe Photoshop Creative Cloud 2019 (Adobe Systems, San Jose, CA).

Results

Phylogenetic analysis

The Bayesian analysis returned a topology and posterior probabilities (pp) (Fig. 1) similar to recent analyses of the xyleborine DNA (e.g., Cognato *et al.* 2018; Mandelstam *et al.* 2019). A well-supported clade (0.98 pp) consisted of seven known genera, *Amasa* Lea, 1894, *Arixyleborus* Hopkins, 1915, *Cyclorhipidion*, *Stictodex* Hulcr & Cognato 2013, *Streptocranus* Schedl, 1939, *Truncaudum* Hulcr & Cognato, 2010 and *Xyleborus*, and, in addition, four species representing the suspect new genera (Fig. 2). The suspect species did not group with *Xyleborus* or *Cyclorhipidion*

TABLE 1. Specimens, labels, collection location, and GenBank numbers. – = same as species name. N/A = not available.

Species	OTU label	Voucher code	Locality	GenBank			
				COI	CAD	EF-1alpha	28S
<i>Cyclorhipidion bodoanum</i>	–	SAX241	China: Hong Kong	N/A	MN199590	MN199557	MN199607
<i>Cyclorhipidion circumcisum</i>	–	SAX53	Thailand	MN199574	MN199591	MN199558	MN199608
<i>Cyclorhipidion distinguendum</i>	–	SAX54	United States: Florida	MN199575	MN199592	MN199559	MN199609
<i>Cyclorhipidion fukiense</i>	nsp5	SAX148	Vietnam: Thua Thien-Hue	N/A	N/A	MN199565	MN199615
<i>Cyclorhipidion fukiense</i>	–	SAX191	Vietnam: Cao Bang	MN199576	MN199593	MN199560	MN199610
<i>Cyclorhipidion fukiense</i>	–	SAX194	China: Yunnan	MN199577	MN199594	MN199561	MN199611
<i>Cyclorhipidion fukiense</i>	–	SAX240	China: Hong Kong	MN199578	MN199595	MN199562	MN199612
<i>Cyclorhipidion inarmatum</i>	–	SAX55	United States: Florida	MN199579	MN199596	MN199563	MN199613
<i>Cyclorhipidion n.sp.</i>	nsp2	SAX124	Vietnam: Cao Bang	MN199580	MN199597	MN199564	MN199614
<i>Cyclorhipidion perpilosellum</i>	–	SAX125	Vietnam: Cao Bang	MN199581	MN199598	MN199566	MN199616
<i>Cyclorhipidion perpilosellum</i>	–	SAX146	Vietnam: Thua Thien-Hue	MN199582	MN199599	MN199567	MN199617
<i>Cyclorhipidion perpilosellum</i>	–	SAX192	China: Yunnan	MN199583	MN199600	MN199568	MN199618
<i>Cyclorhipidion pilipenne</i>	–	SAX193	China: Yunnan	MN199584	MN199601	MN199569	MN199619
<i>Cyclorhipidion pruinosulum</i>	–	SAX147	Vietnam: Dong Nai	MN199585	MN199602	MN199570	MN199620
<i>Fraudatrix melas</i>	Cyclorhipidion nsp14	SAX356	China: Hong Kong	MN199586	MN199603	MN199571	MN199621
<i>Tricosa cattienensis</i>	Cyclorhipidion nsp9	SAX288	Vietnam: Dong Nai	MN199587	MN199604	N/A	MN199622
<i>Tricosa jacula</i>	Cyclorhipidion nsp13	SAX384	China: Guizhou	MN199588	MN199605	MN199572	MN199623
<i>Tricosa metacuneola</i>	Xyleborus metacuneolus	SAX100	Papua New Guinea	MN199589	MN199606	MN199573	MN199624

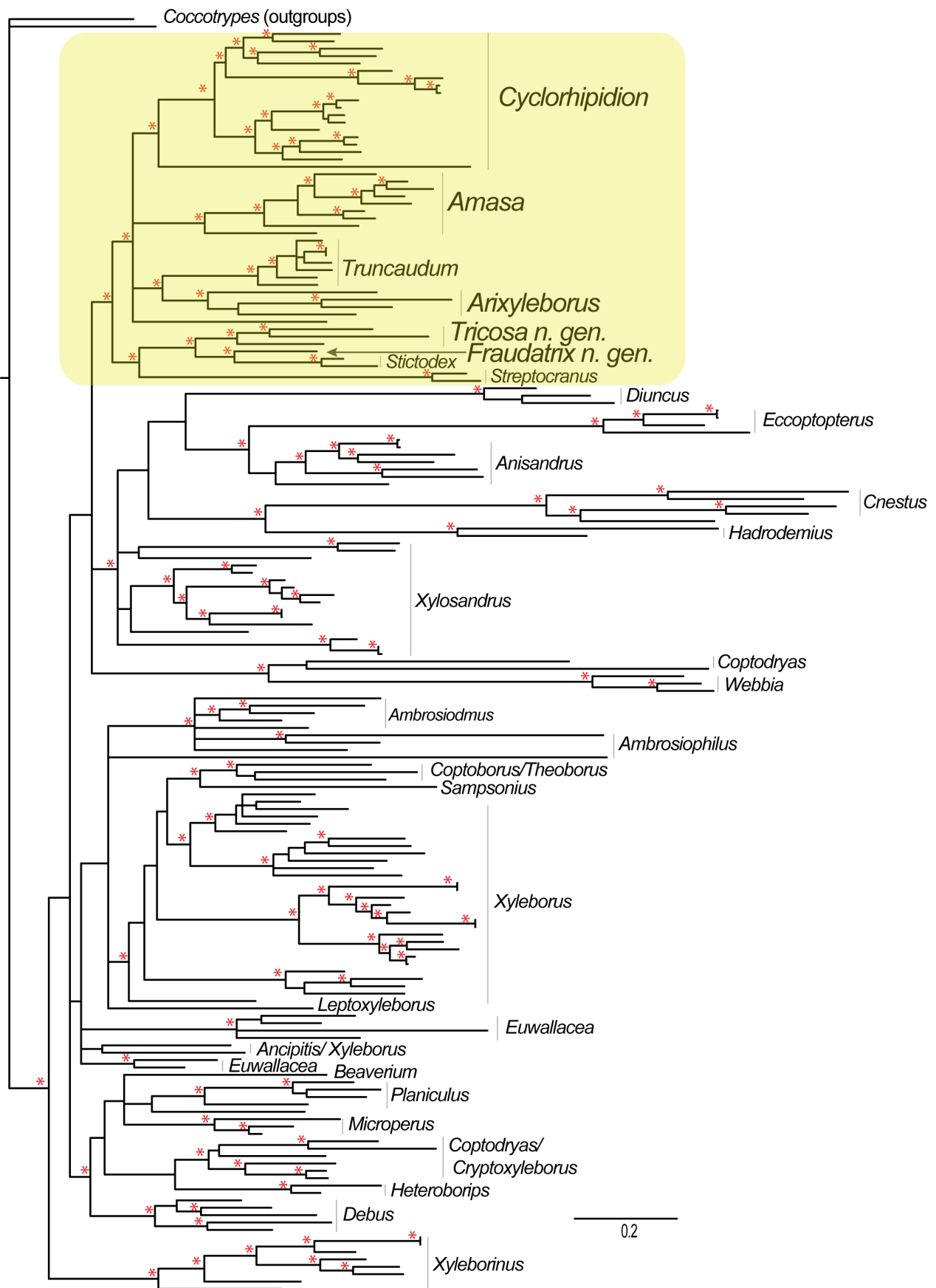


FIGURE 1. Majority-rule consensus tree of 600,002 trees found in the Bayesian analysis of DNA sequences from four genes for 181 xyleborine species. Red asterisks indicate nodes with 0.9–1.0 posterior probability. Taxa highlighted in yellow are detailed in Fig. 2.

(Fig. 1). Three of these species formed a clade (1.0 pp) and the fourth species was sister to *Stictodex* species (1.0 pp). Together these species formed a clade (1.0 pp) which was sister to *Streptocranus* (0.98 pp) (Fig. 2). The species of the *Tricosa* gen. n. and *Fraudatrix* gen. n. lineages have unique combinations of generic diagnostic characters. Given a combination of phylogenetic placement, monophyly and diagnostic morphology, these lineages are described below as new genera along with associated new species. Known *Xyleborus*, *Cryptoxyleborus* and *Cyclorhiphidion* species were reviewed for these characters and included within the appropriate genus.

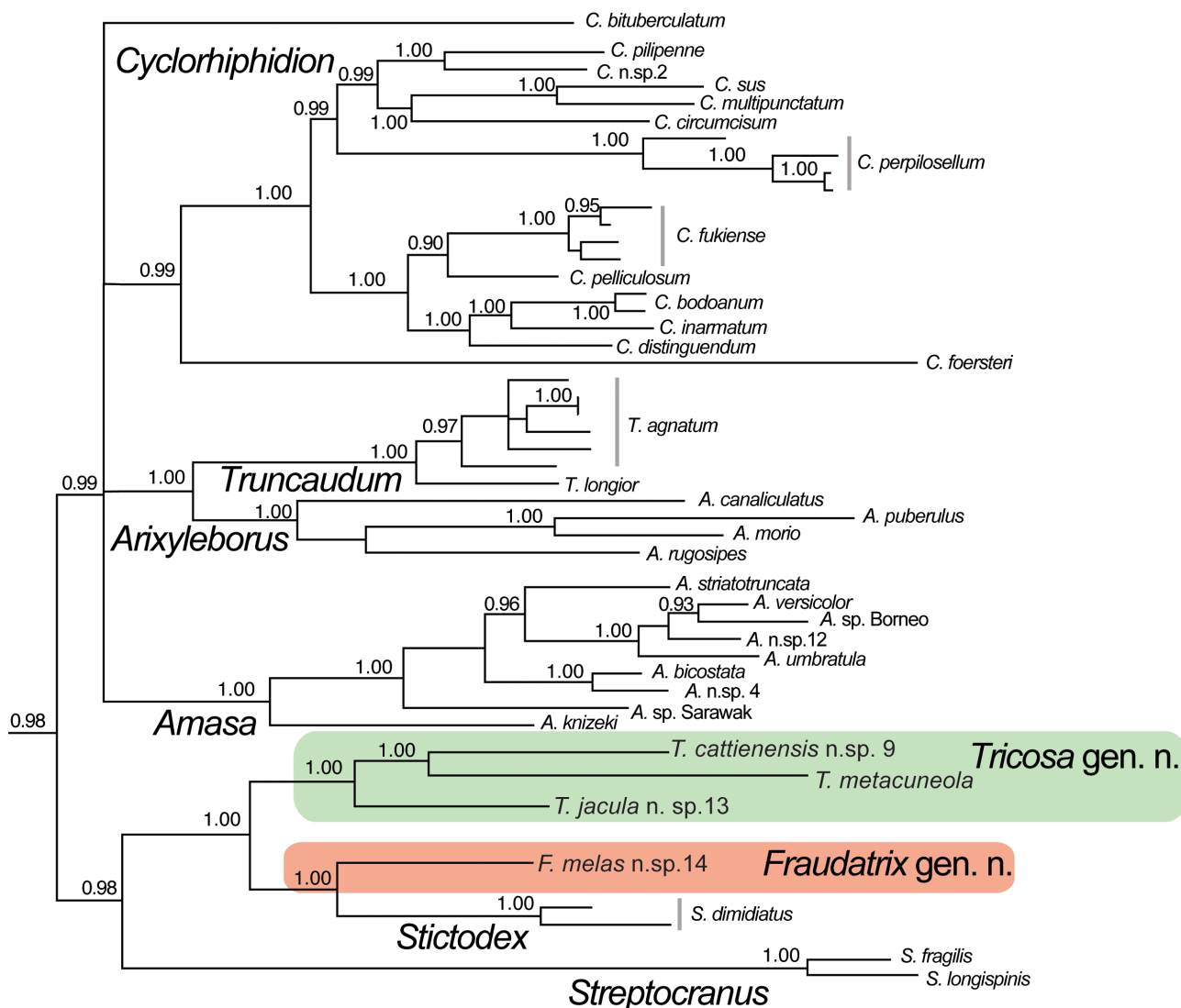


FIGURE 2. Details of taxa highlighted in Fig.1. New genera are highlighted and numbers at nodes indicate specific posterior probabilities.

Taxonomy

Fraudatrix, gen. n.

(Figs 3–18)

Type species. *Fraudatrix melas* (Eggers, 1927).

Description. Female. Length 1.75–2.50 mm and 2.86–3.33 times as long as wide. Body sparsely setose; color light to dark brown; legs and antennae yellow brown to brown. Appearing very slender, elytra attenuate. Mycangial tufts absent.

Head. Epistoma entire, transverse, lined with a row of hair-like setae. Frons slightly convex from epistoma to upper level of eyes; surface shagreened, dull, punctate; punctures above epistoma small, fine, shallow, punctures

larger, deeper on frons. Eyes moderately emarginate above level of antennal insertion, upper portion of eyes smaller than lower part. Submentum slightly impressed below genae, narrowly triangular. Scape short and thick or long and slender, about as long as club. Antennal funicle two-segmented, segments equal in size. Pedicle longer than funicle. Club obliquely truncate, approximately circular; segment 1 corneous, transverse on anterior face, nearly covering all of posterior face; segment 2 slightly procurved, corneous, visible on anterior side of club (type 2, Hulcr *et al.* 2007).

Pronotum. 1.06–1.5 times as long as wide. Pronotum from lateral view prolonged posteriorly (type 8; Hulcr *et al.* 2007). In dorsal view more or less elongate, parallel-sided (types 8 or 9; Hulcr *et al.* 2007), with or without a row of serrations on rounded or subquadrate anterior margin. Surface alutaceous, anterior half finely asperate, asperities close, arranged in concentric arcs from midpoint of pronotum to anterior and anterolateral areas; disc finely and evenly punctate. Lateral margins rounded without a carina. Base transverse.

Elytra. 1.61–2.14 times as long as wide. Elytral base transverse, margin oblique; humeral angles rounded. Scutellum small, triangular, flat, flush with elytra. Sides straight from base to apical half of declivity; attenuate beginning at apical third, apex acute. Disc longer than declivity. Disc smooth, shining, finely punctate; interstitial punctures seriate, each puncture bearing a single erect, fine, golden, hair-like seta (may be abraded); interstriae two times width of striae. Interstriae parallel along their length. Declivital interstriae impunctate, granulate. Posterolateral margins rounded, costa absent.

Legs. Procoxae contiguous, prosternal posterocoxal piece conical, slightly inflated. Protibiae obliquely triangular, broadest at apical third, posterior face flat, unarmed; 5 or 6 large denticles present on outer margin of apical third. Meso- and metatibiae obliquely triangular, flattened, posterior face unarmed.

Diagnosis. *Fraudatrix* can be distinguished from all other Xyleborini genera by the following combination of characters: antennal funicle two-segmented, antennal club type 2 (Hulcr *et al.* 2007) with one suture visible on the posterior face, protibia obliquely triangular with 6 or fewer denticles on outer margin, posterior face flattened and unarmed, elytra with first and second interstriae parallel, scutellum small, flush with elytral surface, mycangial tufts absent, elytra attenuate and pronotal disc longer than anterior slope.

Fraudatrix most closely resembles *Cryptoxyleborus* with which it shares an attenuate appearance and small size. It can be distinguished from *Cryptoxyleborus* by the following diagnostic characters (*Fraudatrix* given first). Scutellum visible *vs* scutellum not apparent, antennal club obliquely truncate and type 2 (Hulcr *et al.* 2007) *vs* flattened and type 4, antennal funicle two segmented *vs* three or four segmented, no more than one suture visible on the posterior face *vs* three sutures visible.

Etymology. *F. fraudatrix* (L.) = cheater, liar. In reference to its confusing similarity to *Cryptoxyleborus*.

Remarks. *Fraudatrix* was recovered as sister to *Stictodex* (Figure 2) and they share a type 2 antennal club, two-segmented funicle and obliquely triangular protibia. *Stictodex* is easily distinguished from *Fraudatrix* by the following combination of characters: larger size and stouter form (2.40–3.30 mm long; 2.54–2.89 times as long as wide), antennal club very broad, protibiae with 6–8 denticles on outer margin and inflated and granulate on posterior face, elytra with first and second interstriae divergent, broadest at elytral summit, and declivity truncate or broadly rounded.

***Fraudatrix cuneiformis* (Schedl) comb. n.**

(Figs 3–6)

Xyleborus cuneiformis Schedl, 1958: 104.

Diagnosis: 1.90–2.15 mm long (mean = 2.02 mm; n = 5); 2.86–3.07 times as long as wide. This species is distinguished by the anterior margin of the pronotum rounded, declivital striae punctures indistinct, interstitial granules large, distinct, elytral apex narrowly attenuate and stouter form.

Material examined: Lectotype, female, MALAYSIA: Selangor, Kepong, 6.x.1949, F.G. Browne, ex *Shorea macroptera* (NHMW); Sabah, Sipitang, Mendolong, 11.v.1988, leg. S. Adebratt (RABC, 1). TAIWAN: Nantou Co., Sun Moon Lake, EtOH trap, 3.x.2013, C-S. Lin (RABC, 1); as previous except: Hui Son, EtOH [trap], 10.viii.2006, Liu, L-Y. (RABC, 1).

Distribution: Brunei, East & West Malaysia, Singapore, Taiwan.

Host plants: Recorded only from two species of *Shorea* (Dipterocarpaceae) (Schedl 1958).

Remarks: The gallery system has branched tunnels with small brood chambers in the longitudinal plane (Browne 1961).

***Fraudatrix melas* comb. n.**

(Figs 7–10)

Xyleborus melas Eggers, 1927: 93

Coptoborus melas (Eggers): Wood & Bright 1992: 663.

Diagnosis: 2.30 mm long (n = 2); 3.29 times as long as wide. This species is distinguished by the anterior margin of the pronotum rounded, declivital stria punctures distinct, nearly as large as interstitial granules, bearing a short recumbent seta, and more slender form.

Material examined: Lectotype, PHILIPPINES: [Luzon, Provinz Mountain], Balbalan (NMNH). CHINA: Hong Kong, Shing Mun Country Park, 5.vi.2017, Rui'e Nie, ex FIT (IZAS, 1; MSUC, 1).

Distribution: China (Hong Kong), Philippines (Wood & Bright 1992). The record from American Samoa (Schedl 1972) needs confirmation. The species has not been found in extensive recent collecting in the country.

Host plants: Unknown.

***Fraudatrix pileatula* Schedl comb. n.**

(Figs 11–14)

Xyleborus pileatulus Schedl, 1975: 369.

Diagnosis: 2.10–2.50 mm long (mean = 2.30 mm; n = 2); 3.13 times as long as wide. This species is distinguished by the anterior margin of the pronotum rounded, declivital stria punctures indistinct, declivital interstitial granules small, elytral apex broadly attenuate and slender form.

Material examined: AUSTRALIA: N. Qld, Cow Bay, N. of Daintree R, 17-29.vi.1990, Cunningham & De Faveri (RABC, 1). [PAPUA] NEW GUINEA: Morobe Dist., Wau Field Stn., 1200 m, 12.ix.[19]72, R. Beaver, at light (RABC, 1).

Distribution: Australia, Papua New Guinea.

Host plants: Unknown.

Remarks: Hulcr & Cognato (2013) state that the species has a type 1 (Hulcr *et al.* 2007) antennal club with segment 1 covering the entire posterior face. This species has a type 2 antennal club with segment 1 nearly covering all of the posterior face.

***Fraudatrix simplex* (Browne) comb. n.**

(Figs 15–18)

Cryptoxyleborus simplex Browne, 1949: 902.

Webbia simplex (Browne): Wood & Bright, 1992: 833.

Cryptoxyleborus simplex Browne: Bright & Skidmore, 1997: 5, 176.

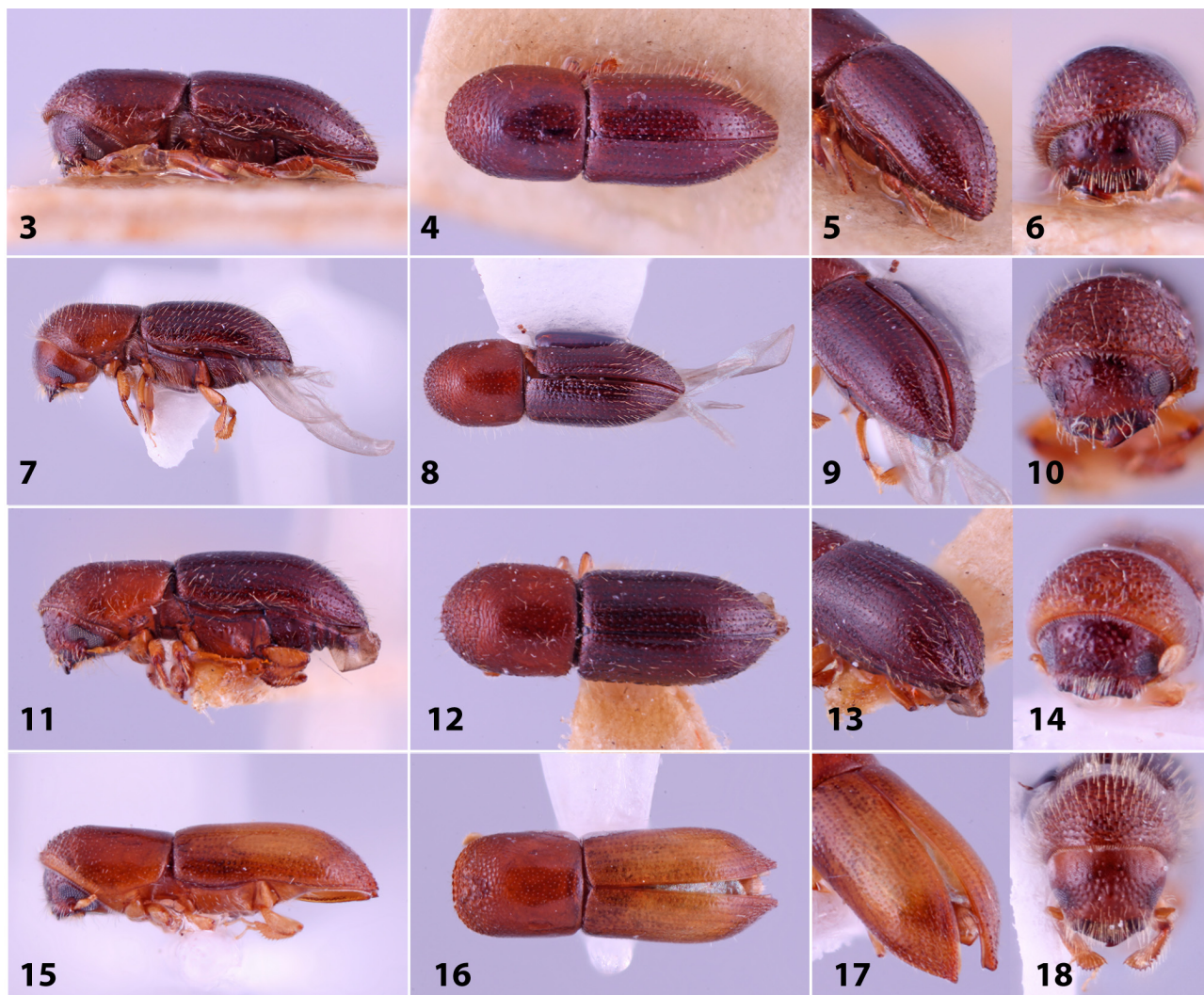
Diagnosis: 1.75–2.00 mm long (mean = 1.92 mm; n = 5); 3.08–3.33 times as long as wide. This species is distinguished by the anterior margin of the pronotum subquadrate, short semi-recumbent interstitial setae and minute size.

Material examined: MALAYSIA: Penang, Muka Head, 23.iv.[19]75, R. A. Beaver (RABC, 5). THAILAND: Chiang Mai, C[hiang] M[ai] Univ[ersity], 300m, ex EtOH trap, 27.iii.–17.iv.[20]06, W. Puranasakul (RABC, 1); Nakhon Sri Thammarat, EtOH trap, 1.i.2010, W. Sittichaya (RABC, 1); as previous except: 1.xi.[20]10 (MSUC, 1).

Distribution: Brunei, Indonesia (Sumatra), East & West Malaysia, Thailand.

Host plants: Recorded from *Dipterocarpus*, *Dryobalanops*, *Hopea* and *Shorea* (Dipterocarpaceae) (Beaver & Hulcr 2008).

Remarks: Browne (1961) notes that brood size can exceed 50.



FIGURES 3–18. Lateral, dorsal, posterior oblique and anterior view of *Fraudatrix cuneiformis* (3–6), *F. melas* (7–10), *F. pileatula* (11–14), *F. simplex* (15–18).

Key to *Fraudatrix* species (females only)

- 1 Pronotum anterior margin subquadrate *simplex* (Browne)
- Pronotum anterior margin rounded. 2
- 2 Declivital stria punctures distinct, nearly as large as interstitial granules, elytral disc setose. *melas* (Eggers)
- Declivital stria punctures indistinct, much smaller than interstitial granules, elytral disc asetose 3
- 3 Declivital interstitial granules large, elytral apex narrowly attenuate. Smaller size, 1.90–2.15 mm *cuneiformis* (Schedl)
- Declivital interstitial granules small, elytral apex broadly attenuate. Larger size, 2.10–2.50. *pileatula* (Schedl)

***Tricosa*, gen. n.**

(Figs 19–38)

Type species. *Tricosa metacuneola* (Eggers, 1940).

Description. Female. Length 2.20–3.80 mm and 2.50–3.00 times as long as wide. Body sparsely to densely

setose; color light brown to ferruginous. Appearing moderately slender, elytra attenuate. Mycangial tufts absent.

Head. Epistoma entire, transverse, lined with a row of hair-like setae. Frons slightly convex from epistoma to upper level of eyes; surface shagreened, dull, punctate; punctures above epistoma small, fine, shallow, punctures larger, deeper on frons. Eyes weakly emarginated above level of antennal insertion, upper portion of eyes smaller than lower part. Submentum slightly impressed below genae, narrowly triangular. Scape regularly thick, shorter than club. Antennal funicle four-segmented, segments equal in size. Pedicel shorter than funicle. Club flattened, approximately circular; segment 1 corneous, transverse on anterior face, nearly covering all of posterior face; segment 2 slightly procurved, corneous, always visible on both sides (type 3, Hulcr *et al.* 2007).

Pronotum. 1.05–1.25 times as long as wide. Pronotum from lateral view with disc as long or shorter than anterior slope (type 7, Hulcr *et al.* 2007). In dorsal view, elongate, parallel-sided, anterior margin rounded (type 7; Hulcr *et al.* 2007), with or without a row of serrations. Surface alutaceous, anterior half asperate, asperities close, arranged in concentric arcs from midpoint of pronotum to anterior and anterolateral areas; disc finely and evenly punctate. Lateral margins rounded without carina. Base transverse.

Elytra. 1.26–2.0 times as long as wide. Elytral bases transverse, margins oblique; humeral angles rounded. Scutellum small, triangular, flat, flush with elytra. Sides straight from base to apical half of declivity; attenuate at apical third, apex attenuate and rounded. Interstriae parallel along their length. Disc longer than declivity. Disc smooth, shining, finely punctate; discal interstriae punctures seriate or confused. Interstriae parallel along their length. Declivital interstriae impunctate, granulate, densely setose. Posterolateral margins rounded, costa absent.

Legs. Procoxae contiguous, prosternal posterocoxal piece conical, slightly inflated. Protibiae distinctly triangular, broadest at apical third, or obliquely triangular, posterior face flat, unarmed; 5 or 6 large denticles present on outer margin of apical third. Meso- and metatibiae obliquely triangular, flattened, posterior face unarmed.

Diagnosis. *Tricosa* can be distinguished from all other Xyleborini genera by the following combination of characters: antennal funicle four segmented, antennal club type 3 (Hulcr *et al.* 2007) with one or two sutures visible on the posterior face, protibia distinctly or obliquely triangular with 6 or fewer denticles on outer margin and posterior face flattened and unarmed, scutellum small, flush with elytra surface, mycangial tufts absent, elytra attenuate, discal punctures seriate and posterolateral costa absent.

Tricosa resembles *Cyclorhipidion*, *Cryptoxyleborus* and *Fraudatrix* **gen. n.**, with which it shares either a setose and/or an attenuate appearance. *Tricosa* is most similar to *Cyclorhipidion* and they share a setose appearance and can be distinguished from *Cryptoxyleborus* and *Fraudatrix* **gen.n.** by the following diagnostic characters (*Tricosa* given first): protibia obliquely triangular *vs* semi-circular with evenly rounded outer edge; typically attenuate elytra *vs* rounded, truncate or excavated; outer margin of protibia with 5–6 socketed denticles *vs* 6–9+; anterior margin of the pronotum typically serrate *vs* unarmed (rarely serrate). *Tricosa* can be distinguished from *Cryptoxyleborus* by the visible scutellum, and from *Fraudatrix* by the four segmented antennal funicle and antennal club type 3 with one or two sutures visible on the posterior face, and the pronotal disc being as long as or shorter than the anterior slope.

Etymology. *F. tricosa* (L.) = trickster. In reference to its confusing similarity to *Cryptoxyleborus* and *Cyclorhipidion*.

Tricosa cattienensis sp. n.

(Figs 19–22)

Diagnosis: 2.70–3.10 mm long (mean = 2.98 mm; n = 5); 2.50–2.70 times as long as wide. This species is distinguished by the discal interstitial punctures confused, protibia distinctly triangular, anterior margin of pronotum with a clear row of six moderate serrations. This species is very similar to *C. indochinensis* but can be distinguished by the smaller size and stouter form.

Type material: Holotype, female: VIETNAM: Dong Nai prov., Cat Tien NP, 11.42232, 107.42834, 128 m, 25.ii.2017, VN103, A.I. Cognato, T.A. Hoang, ex 1–3 cm dia branch (MSUC). Paratypes, female: CHINA: Hong Kong, Kadoorie Farm, vi.2016, J. Skelton, P. Carlson, Y. Li, J. Hulcr (IZAS, 1). JAPAN: Okinawa Pref., Iriomotejima Island, 20.ix.2016, H. Kajimura, ex *Machilus thunbergii* (MSUC, 1); as previous except Okinawa, Yona, 1.xi.2011, J. Hulcr, ex *Castanopsis*, uffeld 7388 (UFFE, 1). THAILAND: Chiang Mai, Doi Suthep, 7.viii.2002, R.A. Beaver, K. Koivisto (RABC, 1); Phetchaburi, Kaeng Krachan NP, Ban Krang, ex *Pterocarpus macrocar-*

pus, x.2017, S. Sanguansub (RABC, 1); Surat Thani, Ratchaprapa Reservoir, ex cut liana, 24.ii.2012, R.A. Beaver (RABC, 1).

Description (Female): 2.70–3.10 mm long (mean = 2.98 mm; n = 5); 2.50–2.70 times as long as wide. Body densely setose; color ferruginous; appearing moderately slender, elytra attenuate. Mycangial tufts absent.

Head. As described for genus.

Pronotum. As described for genus except: 1.05 times as long as wide. Pronotum from lateral view with disc as long as anterior slope (type 7, Hulcr *et al.* 2007). In dorsal view, elongate, parallel-sided, anterior margin rounded (type 7; Hulcr *et al.* 2007), with a row of six serrations.

Elytra. As described for genus except: 1.71 times as long as wide. Discal interstriae punctures confused.

Legs. As described for genus except: protibiae distinctly triangular with 6 large denticles present on outer margin of apical third.

Etymology: In reference to the type locality, Cat Tien National Park, Vietnam.

Distribution: China (Hong Kong), Japan, Thailand, Vietnam.

Host plants: Known only from *Pterocarpus* (Fabaceae), *Castanopsis* (Fagaceae), *Machilus* (Lauraceae), and an unknown cut liana.

Tricosa indochinensis sp. n.

(Figs 23–26)

Diagnosis: 3.20–3.40 mm long (mean = 3.32 mm; n = 5); 2.83–2.91 times as long as wide. This species is distinguished by the discal interstitial punctures confused, protibia distinctly triangular, anterior margin of the pronotum with a clear row of eight moderate serrations. This species is very similar to *C. cattienensis* and can be distinguished by the larger size and narrower form.

Type material: Holotype, female: CHINA: Yunnan, Mengyang, 950 m, 2.v.1962, Shimei Song (NMNH). Paratypes, female: CHINA: Yunnan, Mengyang, 950 m, 2.v.1962, Shimei Song (NMNH, 1; IZAS, 1). INDIA: Bengal, Kalimpong, Samsingh, 1800', I.1934, Mohan Lall, ex unknown wood (NMNH, 3). THAILAND: Chiang Mai, Doi Pui, 28°50'23"N, 98°53'53"E, 1200–1300 m, ex *Pterocarpus* sp. coll. ix.2014, S. Sanguansub *et al.* (RABC, 1).

Description (Female): 3.20–3.40 mm long (mean = 3.32 mm; n = 5); 2.83–2.91 times as long as wide. Body densely setose; color ferruginous. Appearing moderately slender, elytra attenuate. Mycangial tufts absent.

Head. As described for genus.

Pronotum. As described for genus except: 1.25 times as long as wide. Pronotum from lateral view with disc as long as anterior slope (type 7; Hulcr *et al.* 2007). In dorsal view, elongate, parallel-sided, anterior margin rounded (type 7; Hulcr *et al.* 2007), with a row of eight serrations.

Elytra. As described for genus except: 1.6 times as long as wide. Discal interstriae punctures confused.

Legs. As described for genus except: protibiae distinctly triangular with 6 large denticles present on outer margin of apical third.

Male: Unknown.

Etymology: In reference to the species occurrence in Southeast Asia.

Distribution: China (Yunnan), India (Bengal), Thailand.

Host plants: Known only from *Pterocarpus* (Fabaceae).

Tricosa jacula sp. n.

(Figs 27–30)

Diagnosis: 3.20 mm long (n = 1); 2.91 times as long as wide. This species can be distinguished by the elytral discal striae and interstriae clearly uniseriate punctate, anterior margin of the pronotum unarmed, and protibia distinctly triangular.

Type material: Holotype, female: CHINA: Guizhou, Guiyang, Huaxi, 20.x.2015, Y. Li, ex poplar (IZAS).

Description (Female): Female. 3.20 mm long (n = 1); 2.91 times as long as wide. Body sparsely setose; color ferruginous. Appearing moderately slender, elytra attenuate. Mycangial tufts absent.

Head. As described for genus.

Pronotum. As described for genus except: 1.06 times as long as wide. Pronotum from lateral view with disc as long as anterior slope (type 7; Hulcr *et al.* 2007). In dorsal view, elongate, parallel-sided, anterior margin rounded (type 7; Hulcr *et al.* 2007), without a row of serrations.

Elytra. As described for genus except: 2.0 times as long as wide. Discal interstriae punctures uniseriate.

Legs. As described for genus except: protibiae distinctly triangular with 6 large denticles present on outer margin of apical third.

Male: Unknown.

Etymology: *L. jacula* = dart. In reference to the attenuate elytral apex.

Distribution: China (Guizhou).

Host plants: Known only from *Populus* (Salicaceae).

***Tricosa mangoensis* (Schedl) comb. n.**

(Figs 31–34)

Xyleborus mangoensis Schedl, 1942: 189.

Cyclorhipidion mangoense (Schedl): Wood & Bright, 1992: 700.

Diagnosis: 3.80 mm long; 2.53 times as long as wide. This species is distinguished by its very large size, and declivital striae and interstriae densely setose.

Material examined. MALAYSIA: Sabah, Sipitang, Mendolong, 12.i.1987, S. Adebratt (RABC, 1).

Distribution: East & West Malaysia.

Host plants: *Mangifera indica* (Anacardiaceae).

***Tricosa metacuneola* (Eggers) comb. n.**

(Figs 35–38)

Xyleborus metacuneolus Eggers, 1940: 150.

Xyleborus kaimochii Nobuchi, 1981: 143. Synonymy: Smith *et al.*, 2018: 397.

Diagnosis: 2.40–2.50 mm long (mean = 2.46 mm; n = 5); 2.67–2.78 times as long as wide. This species is distinguished by elytral discal striae and interstriae clearly uniseriate punctate, anterior margin of pronotum with a row of serrations, and protibia obliquely triangular.

Material examined: Paratype *Xyleborus metacuneolus*, [INDONESIA]: Java, Buitenzorg, 15.x.1923 (NMNH, 1). [INDONESIA]: Java, Boger [sic] viii.1964, N.L.H. Krauss (NMNH, 4). MALAYSIA: Sabah, Sipitang, Mendolong, 19.iv.1988, S. Adebratt (RABC, 1). PAPUA NEW GUINEA: Madang, Ohu, J. Hulcr, ex *Gymnacranthera paniculata* (MSUC, 1). SINGAPORE: Bukit Timah, 50m, 25–27.x.1998, B. H. Jordal (RABC, 2).

Distribution: Brunei, Indonesia (Java, Sulawesi), Japan, East & West Malaysia, New Guinea, Philippines, Singapore, Sri Lanka, Taiwan, Thailand.

Host plants: Probably polyphagous. Recorded from *Buchanania*, *Mangifera* (Anacardiaceae), *Swietenia* (Meliaceae), *Castanopsis* (Fagaceae) (Nobuchi 1981; Beaver & Liu 2010) and *Gymnacranthera* (Myrsicaceae).

Remarks: The paratype from Indonesia (Java; NMNH) and two specimens from Singapore and Malaysia (Sabah; RABC) were all found to have different pronotal length/width ratios of 1.08, 1.23 and 0.88 respectively. It is unclear whether the species is morphologically variable or if this species may be a species complex. At the time of this study DNA data was only available for *T. metacuneola s.s.* Future research is necessary to determine species limits.

Key to *Tricosa* species (females only)

1 Elytral discal striae and interstriae clearly uniseriate punctate 2

- Elytral discal striae and interstriae punctures confused 4
- 2 Pronotum anterior margin unarmed, protibia broad, appearing distinctly triangular *jacula* sp. n. 3
- Pronotum anterior margin serrate, protibia narrow, appearing obliquely triangular 3
- 3 Smaller size, 2.40–2.50 mm and declivital interstriae moderately setose *metacuneola* (Eggers)
- Larger size, 3.80 mm and declivital striae and interstriae densely setose *mangoensis* (Schedl)
- 4 Pronotum anterior margin armed by a row of six serrations. Smaller, 2.70–3.10 mm long, and stouter 2.50–2.70 times as long as wide *cattienensis* sp. n.
- Pronotum anterior margin armed by a row of eight serrations. Larger, 3.20–3.40 mm long and more slender, 2.83–2.91 times as long as wide *indochinensis* sp. n.



FIGURES 19–38. Lateral, dorsal, posterior oblique and anterior view of *Tricosa cattienensis* (19–22), *T. indochinensis* (23–26), *T. jacula* (27–30), *T. mangoense* (31–34), *T. metacuneola* (35–38).

Discussion

This study is the latest of an increasing number that have demonstrated an underestimation of Xyleborini genera (Hulcr *et al.* 2007; Cognato *et al.* 2011; Cognato *et al.* 2018; Mandelshtam *et al.* 2019). Convergent evolution of

few morphological characters and lack of phylogenies delayed the realization that a combination of plesiomorphic and autapomorphic characters diagnose Xyleborini genera (Hulcr *et al.* 2007). The advent of phylogenetic analysis provided the criteria of monophyly for the delimitation of generic limits which have resulted in the illumination of an increasing diversity of genera and an improved concept of *Xyleborus*.

Pre-21st century scolytine taxonomists were conservative and, at times, uncertain of generic determinations and often placed “odd” species without clear generic affinities into *Xyleborus* resulting in a bloated genus with a broad generic concept (Wood, 1986). Molecular phylogenies of Xyleborini have repeatedly demonstrated the polyphyly of *Xyleborus* (Hulcr *et al.* 2007; Cognato *et al.* 2011; Cognato *et al.* 2018; Mandelshtam *et al.* 2019) with the placement of “odd” species outside of the core *Xyleborus* clade which includes species similar to *X. affinis* Eichhoff, 1868. More of these “odd” species which may represent additional genera are evident in the current phylogeny (Fig. 1) and taxonomic literature (e.g. Hulcr & Cognato 2013). For example, a weakly supported clade of *Ancipitis/Xyleborus* occurs outside of the core *Xyleborus* clade (Fig. 1). This species, *Xyleborus granulatus* Schedl, 1975, is considered *Xyleborus sensu lato* and exhibits autapomorphic morphological characters (Hulcr & Cognato 2013). However taxonomic action to erect genera for these “odd” species will require their inclusion in the Xyleborini phylogeny and detailed morphological study.

The new genera *Fraudatrix* and *Tricosa* represent small radiations of similar but unrelated species. The species of both genera are differentiated by subtle characters such as size, length/width ratios, elytral vestiture, protibial denticle number and interstrial puncture arrangement. Similar amounts of morphological differentiation have been observed for species in other genera (e.g., Smith 2017; Cognato *et al.* 2018). The long branches for the species included in the phylogeny average 16% and 4% nucleotide difference for COI and CAD respectively. These values are greater than the average interspecific difference for Xyleborini (10% COI and 2% CAD) (Cognato *et al.* 2018). *Fraudatrix* and *Tricosa* species range from southern Japan to Australia to India and some species have been so far collected only from Dipterocarpaceae. Only *F. simplex* and *T. metacuneola* have broad ranges which suggest that geographic, and possibly tree host isolation, play an important role in speciation, as for many other organisms. These observations suggest that there are more species to discover; beginning with *T. metacuneola* where different body size ratios are observed in different localities.

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