



## ***Doddifoenus wallacei*, a new giant parasitoid wasp of the subfamily Leptofoeninae (Chalcidoidea: Pteromalidae), with a description of its mesosomal skeletal anatomy and a molecular characterization**

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### **Abstract**

A third species of *Doddifoenus* Bouček (Pteromalidae: Leptofoeninae), is described from Laos and Thailand. *Doddifoenus wallacei* **sp. n.** is the first species of the genus occurring west of Wallace's Line, and with a body length of up to 4.2 cm it is among the longest known of any chalcidoid wasp. A differential key and distribution map for the world species of *Doddifoenus* are given. A detailed description of the mesosoma, including external and internal features, and molecular data (D2-D5 fragments of the 28S gene) are provided to facilitate future phylogenetic analyses. The phylogenetic placement of Leptofoeninae is briefly discussed, especially with respect to the pteromalid subfamilies Pteromalinae and Cleonyminae.

**Key words:** Pteromalidae, Leptofoeninae, *Doddifoenus*, new species, taxonomy, mesosoma, Indo-Malaya, Australasia, Wallace's Line

### **Introduction**

The Leptofoeninae is probably one of the least known of the 31 subfamilies of Pteromalidae (Chalcidoidea) recognized by Noyes (2009). Leptofoenines are very rarely collected but morphologically are of special interest because of their very large body size (Fig. 1) and a number of character states that are uncommon among chalcidoid wasps. Some, though not all, species appear to have a pigmented costal vein in the forewing, and a sclerotized area where the postulated basal and cubital veins meet (LaSalle & Stage 1985). The phylogenetic affinities of Leptofoeninae to other Chalcidoidea are uncertain, and placement in the family Pteromalidae is essentially a statement that there is no compelling information about the true relationships of the subfamily. Pteromalidae is widely recognized as the “garbage can” family within Chalcidoidea (Gibson *et al.* 1999), containing 31 potentially unrelated subfamilies, totaling about 590 genera and about 3,500 species (Noyes 2009). Gibson (2003), in an analysis of pteromalids that have been postulated as closely related to the subfamily Cleonyminae, hypothesized Leptofoeninae to be the monophyletic sister group of the Australasian subfamily Nefoeninae and, depending on rooting, as more closely related to Pteromalinae than to Cleonyminae. This would place it as a potential member of a yet to be defined “Pteromalidae s.str.”. The placement of Leptofoeninae therefore has significant value in unraveling the problem of the relationships of the disparate subfamilies of Pteromalidae, many of which are probably more closely related to other chalcidoid families than to Pteromalinae (see e.g., Krogmann & Vilhelmsen 2006).

Leptofoeninae comprises only seven described species in two genera (Noyes 2009). The genus *Doddifoenus* Bouček includes two Australasian species, whereas *Leptofoenus* Smith contains five described

species and is restricted to the New World. Bouček (1988) established *Doddifoenus* and distinguished it from *Leptofoenus* by its elongate epipygium, non-striate lateral pronotal surface, mandibles without denticles, and short basal tarsomeres relative to the other tarsomeres. *Doddifoenus* species are also shiny metallic, whereas members of *Leptofoenus* are blackish, brownish, or rusty (LaSalle & Stage 1985).

Here we describe a remarkable new species of *Doddifoenus*, the first species of that genus occurring west of Wallace's Line, and one of the longest known chalcidoid wasps. We provide a determination key and a distribution map for the genus and add extensive morphological data, including a detailed description of the mesosomal skeleton, and molecular data (D2-D5 fragments of the 28S gene) to facilitate future phylogenetic analyses.

## Material and methods

All measurements are given in millimeters. The units are omitted in the description to save space. Morphological terms follow primarily Huber & Sharkey (1993), but also Gibson (1997), Bouček (1988), or Krogmann & Vilhelmsen (2006) for terms that are not defined in the primary reference. Most measurements were taken as illustrated by Graham (1969). Measurements of forewing venation were taken as illustrated by Bouček (1988). Other terms are defined as follows. 'Alveolate' sensu Harris (1979) describes surfaces furnished with angular cavities which are separated by raised partitions. 'Coriaceous' describes sculpture consisting of rounded to pentagonal, nearly isodiametric meshes that are adjacent and delineated by grooves. Coriaceous is like alveolate in every way except that the cells comprising the sculpture are delineated by sunken instead of raised partitions. 'Striate' describes sculpture consisting of tiny straight carinae that are essentially parallel or that radiate from a point. The flagellar segments are numbered F1–F11. Abbreviations for morphological terms and ratios are: CX<sub>1</sub> = procoxa, CX<sub>2</sub> = mesocoxa, CX<sub>3</sub> = metacoxa, EH = eye height, EL = eye length (measured dorsally), FM<sub>1</sub> = profemur, FM<sub>2</sub> = mesofemur, FM<sub>3</sub> = metafemur, FW = forewing, HW = hind wing, IOD = interocular distance, ISD = interspiracular distance (shortest distance between the propodeal spiracles), ITD = intertorular distance (shortest distance between the toruli), MS = malar space, MTD = distance from bottom of torulus to mouth margin, MV = marginal vein length, MW = mouth width, OOL = ocell-ocular distance, PMV = postmarginal vein length, POL = post-ocellar distance, SV = total stigmal vein length, TB<sub>1</sub> = protibia, TB<sub>2</sub> = mesotibia, TB<sub>3</sub> = metatibia, TL = temple length measured dorsally from hind margin of eye to posterior edge of gena, VTD = distance from top of torulus to vertex.

Photographs were taken using Auto-Montage software (version 4.04.0128 BETA, Synoptics, Ltd., UK) through a 3-CCD digital videocamera attached to a stereoscope.

For the anatomical study, the mesosoma of one specimen was dissected into the following parts as described in Krogmann & Vilhelmsen (2006): 1) pronotum, 2) propectus (propleura and prosternum), 3) mesonotum (including pro- and mesophragma), 4) mesopectus, 5) metathorax-propodeum complex. The preparations were macerated in 10% potassium hydroxide in a heating cabinet at 40° C for 4 hours. The preparations were then rinsed in demineralised water and cleaned in 0.1% Triton X-100. Afterwards they were transferred from 70% to 99% ethanol in an ethanol series and critical-point dried. The preparations were mounted on SEM stubs, sputter-coated with gold and observed in a JEOL JSM-6335-F SEM unit.

One leg of the same specimen was stored at -80°F in 95% EtOH until DNA extraction, using the Chelex method (Walsh *et al.* 1991). Polymerase chain reactions were carried out in 20µl reaction volumes using Promega Taq DNA polymerase (Madison, WI), Qiagen 10x PCR buffer (15 mM MgCl<sub>2</sub>) and Qiagen 5x Q-solution (Valencia, CA) with an annealing Temperature of 48°C. Gene fragments were sequenced in the forward and reverse directions, and the resulting chromatograms were examined and compared in order to find potential PCR or reading errors. Primers used are given in Table 1. All PCR products were gene cleaned with the Bio 101 GeneClean Kit (Carlsbad, CA) using NaI and glassmilk. Cleaned samples were directly sequenced at the San Diego State Microchemical Core Facility.





**FIGURE 1.** *Doddifoenus wallacei* sp. n. female paratype specimen in natural habitat (photographed by G. Ballmer).

***Doddifoenus wallacei* Burks & Krogmann, sp. n.**

**Diagnosis.** Metasomal tergites without white spots (Fig. 2A). Antenna without white flagellomeres (Fig. 2D). Mesoscutellum with a faint mesal channel (Figs 3E, 4A). Parastigma of forewing without a sclerotized spur at origin of basal vein. Profemur with a distinct unsocketed ventral spine (Fig. 5C).

**Specimens examined.** Holotype ♀: THAILAND. *Songkhla*: Thale Ban National Park, Nam Tok Ton Pliu, 100m, 7°00′02″N 100°14′07″E, 17.ii.2005, D.Yanega. (UCRC, accession no. 104069). 2 paratype ♀♀: same data as holotype (UCRC, accession nos. 104070, 142549). 1 paratype ♂: same data as before, but collected by G. Ballmer (UCRC, accession no. 142548). 1 paratype ♀: LAOS. *Khammouane*: Ban Khounkham [Khun Kham] (Nahin), 300m, 18°13′027″N 104°30′880″E, 3–5.vi.2008, disturbed primary rainforest, A. Solodovnikov & J. Pedersen (ZMUC). The paratype with the accession no. 142549 was used for morphological dissection and DNA extraction.

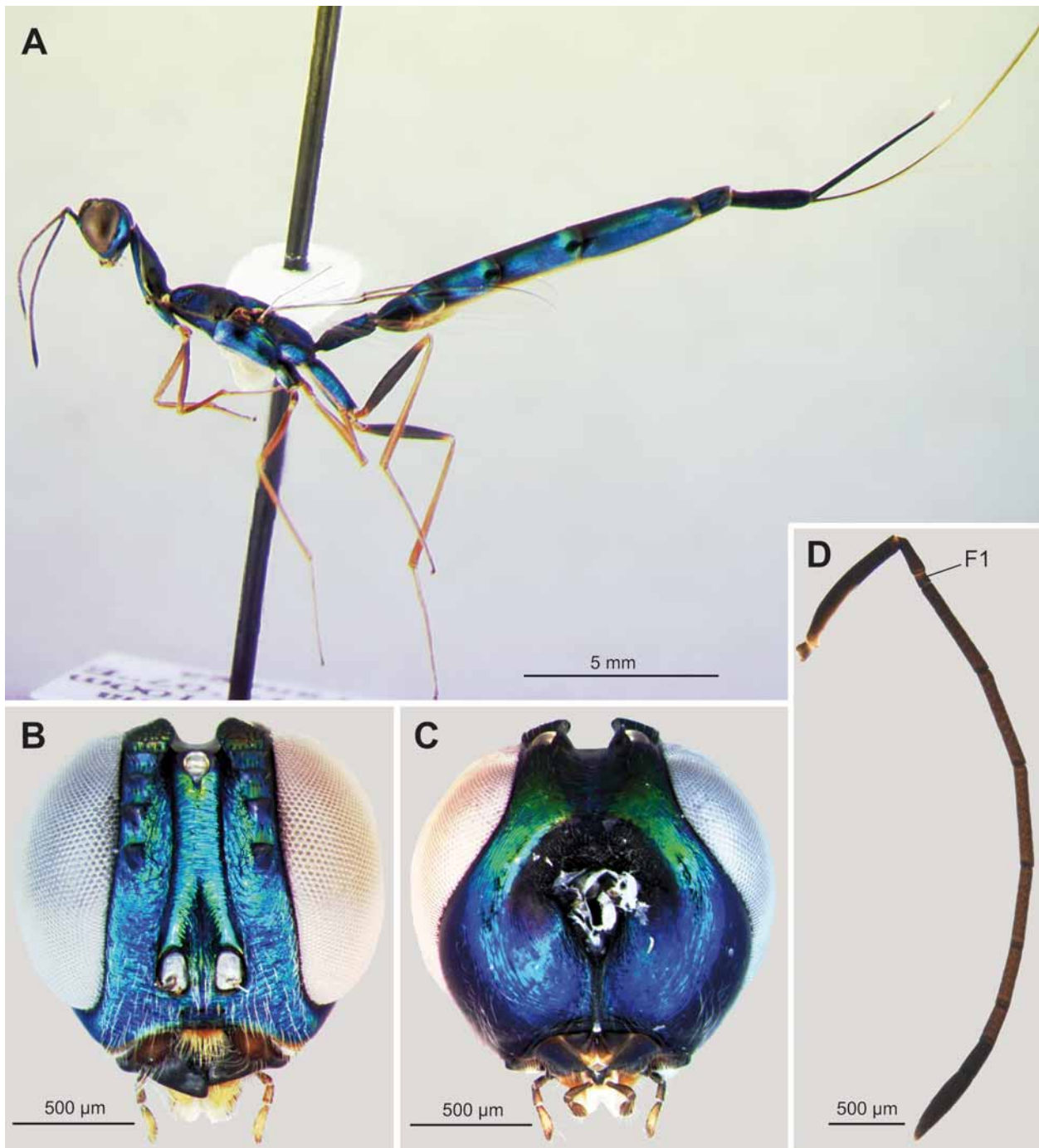
**Etymology.** Named in honour of Dr Alfred Russel Wallace, one of the most influential biologists of all time and co-founder of the theory of evolution by natural selection.

**Description.** Female (Figs 1-5): Body length: 17.1–19.6 mm without ovipositor, 34.6–41.7 mm including ovipositor. All measurements below are given in millimeters.

**Color:** Head and body metallic blue, tending to greenish or purplish; ventral edges of metasomal tergites becoming brownish; ovipositor sheath with long white band subapically (tip of ovipositor sheath darkened); epipygium with white stripe along apex; eyes and ocelli brown or red-brown; ventral surface of scape creamy white along basal half to two-thirds, rest of antenna brown except apical four flagellomeres dark brown; all legs beyond coxae rusty brown, except metafemur mostly dark brown, rusty brown at the tip and base.

Head (Figs 2B,C; 3A) width 1.48–1.64, height 1.37–1.56, length 1.20–1.25; EH 1.11–1.20; EL 0.86–1.03; MS 0.19–0.22; TL 0.17–0.22; MW 0.75–0.89; POL 0.25–0.31; OOL 0.03–0.04; dorsal IOD 0.53–0.59; ventral IOD (from one malar sulcus base to the other) 0.94–1.00; bottom of toruli about one torular height above lower eye margin; ITD 0.09–0.11; VTD 0.86–0.94; MTD 0.16–0.22; median ocellus within scrobal

channel and lateral ocelli immediately posterior end of the parascrobal crests; malar sulcus present but extremely faint and fine; ocular setae very short and sparse, almost not visible under normal stereoscope magnifications; setae of lower face highly variable. Most of head finely, transversely rugulose with underlying finely alveolate areas visible between rugulae, the rugulae usually subparallel but occasionally branching, except as follows: parascrobal area of head with raised cristae formed by 5 distinct carinate elevations, and with several smaller and less distinct carinae dorsad these; vertex with smooth area between the parascrobal crests from median ocellus to slightly beyond posterior limit of the crests; interantennal region with sharp carina between toruli reaching less than halfway to median ocellus; gena with smooth and bare area adjacent to eye, but the area gradually becoming setose posteriorly; occipital carina absent, although occiput relatively distinctly differentiated from vertex by an abrupt change in curvature and sculpture.



**FIGURE 2.** *Doddifoenus wallacei* sp. n. female paratypes. A. habitus, lateral view; B. head, anterior view; C. head, posterior view; D. antenna, lateral view. F1 = first flagellomere.

Clypeus not distinct, distance between anterior tentorial pits to mouth margin less than width of scape; clypeal margin broadly and shallowly concave, not distinct from curvature forming rest of the mouth margin. Labrum partially visible in non-dissected specimens, with thick golden setae (Fig. 2B). Mandible with an undivided cutting edge, with numerous long setae arising from contour that contacts mouth margin when mandibles are fully open. Antenna (Fig. 2D) with tip of scape reaching or slightly exceeding median ocellus height but not extending above vertex; F1 (anellus) without evident placoid or socketed sensilla but with a few tiny setae; all funicular segments cylindrical, with numerous rows of longitudinal sensilla and appressed dark setae; F9–F11 forming club, with a small micropilose region subapico-ventrally on F11. Length:width ratios of antennal segments as follows: scape (0.84–0.97:0.11–0.16), pedicel (0.20–0.27:0.09–0.11), F1 (0.08–0.09:0.08–0.11), F2 (0.62–0.69:0.09–0.11), F3 (0.61–0.67:0.09–0.11), F4 (0.61–0.67:0.09–0.10), F5 (0.50–0.58:0.09–0.10), F6 (0.39–0.42:0.11–0.12), F7 (0.23–0.26:0.12), F8 (0.20–0.25:0.12), F9 (0.27–0.30:0.16–0.17), F10 (0.16:0.14–0.16), F11 (0.12:0.09–0.11).

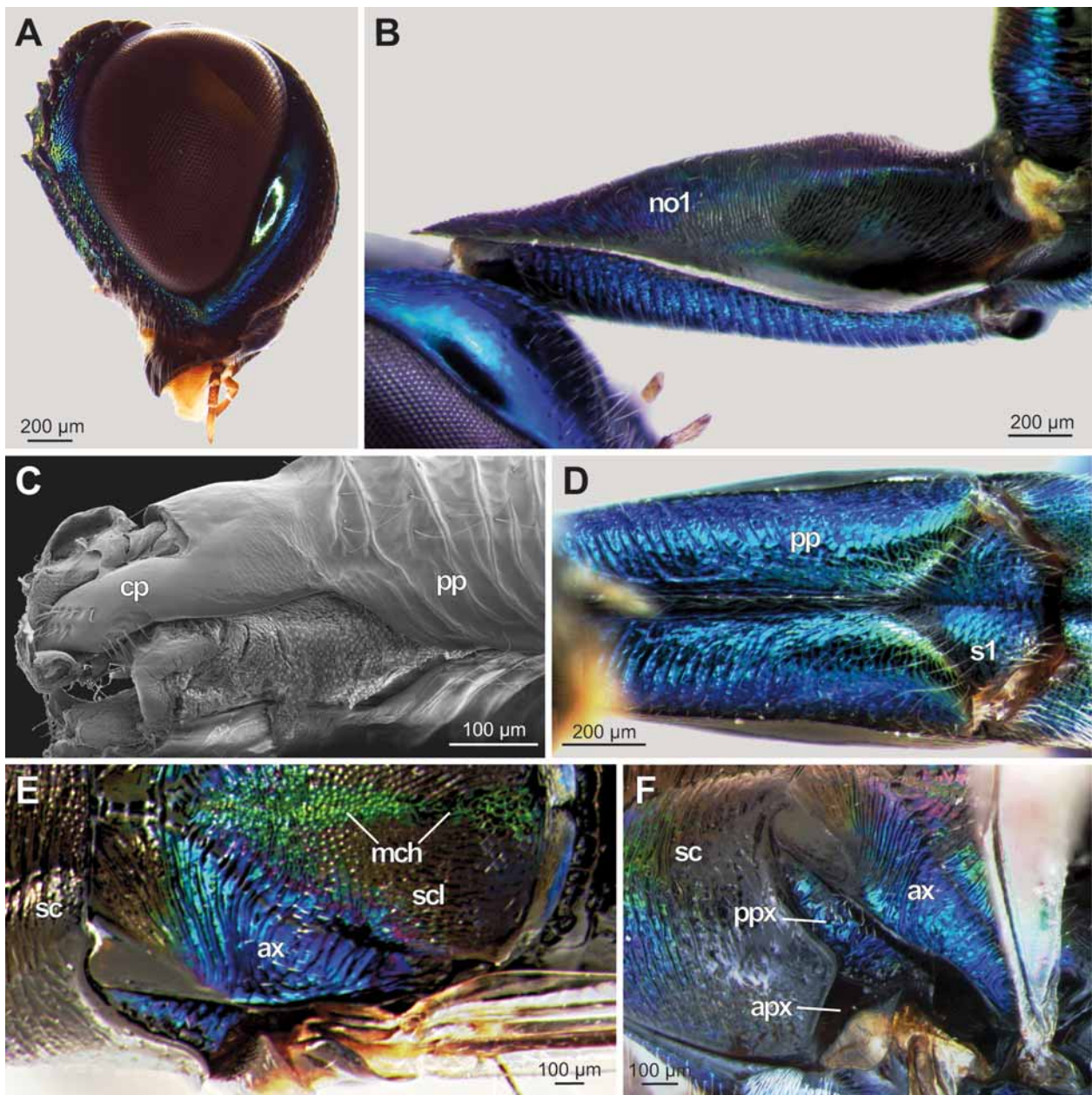
Mesosoma (Figs 2A; 3B–F; 4; 5). Mesosoma mainly finely transversely rugulose with underlying finely alveolate areas visible between the rugulae. Pronotum with smooth area on lateral surface in posterior half (Fig. 3B). Pronotum length:width = 2.00–2.14:0.65–0.95, not differentiated into collum and collar, anteriorly very narrow, almost tongue-like, and with narrow hyaline rim, but gradually becoming broader and higher posteriorly with a slight dorsal concavity before posterior margin; pronotal incisions for mesothoracic spiracles not developed. Propleuron length:width = 1.40–1.50:0.30–0.36, medioventral margins straight and closely abutting along major part of propleura but diverging posteriorly and leaving most of prosternum exposed (Fig. 3D: s1); ventral surface sparsely pilose and mostly covered by coarse striae but with fine reticulation posteriorly; lateral surface also finely reticulate, but anterodorsal surface completely smooth; cervical prominence (Fig. 3C: cp) exposed at anterior margin of propleuron, anteriorly elongate and slightly upcurved, with three rows of short setae: one row along mesal ventral margin and two parallel rows extending ventrally from anterodorsal margin (Fig. 3C). Prosternum (total) length:width = 0.37–0.42:0.44–0.51; only anterior margin covered by propleura, posterior margin straight, carinate without median process (Fig. 3D); ventral prosternal surface slightly reticulate, pilose, completely divided by medial prodiscriminal line.

Mesoscutum length:width = 1.22–1.45 (midlobe length only):1.26–1.54 (total width); sidelobe extending far past the apex of midlobe and forming a flange at tegula; anterior mesoscutal margin exposed, not overlapped by pronotum; with deep, foveolate notauli reaching transscutal articulation (Fig. 4A: not); transscutal articulation deep except for slight discontinuity at level of axillae lateral to notauli; parascutal carina upright in lateral view, posteriorly shifted and continuous with transscutal articulation; preaxilla extended posterodorsally, with anterior portion (covered by tegula) smooth and extended posterior portion reticulate (Fig. 3F: apx, ppx), only posterior portion covered with tiny setae and posterolaterally with long stalked setae. Mesoscutal midlobe more strongly rugulose in posterior half than anterior half, the sidelobes more uniformly strongly rugulose.

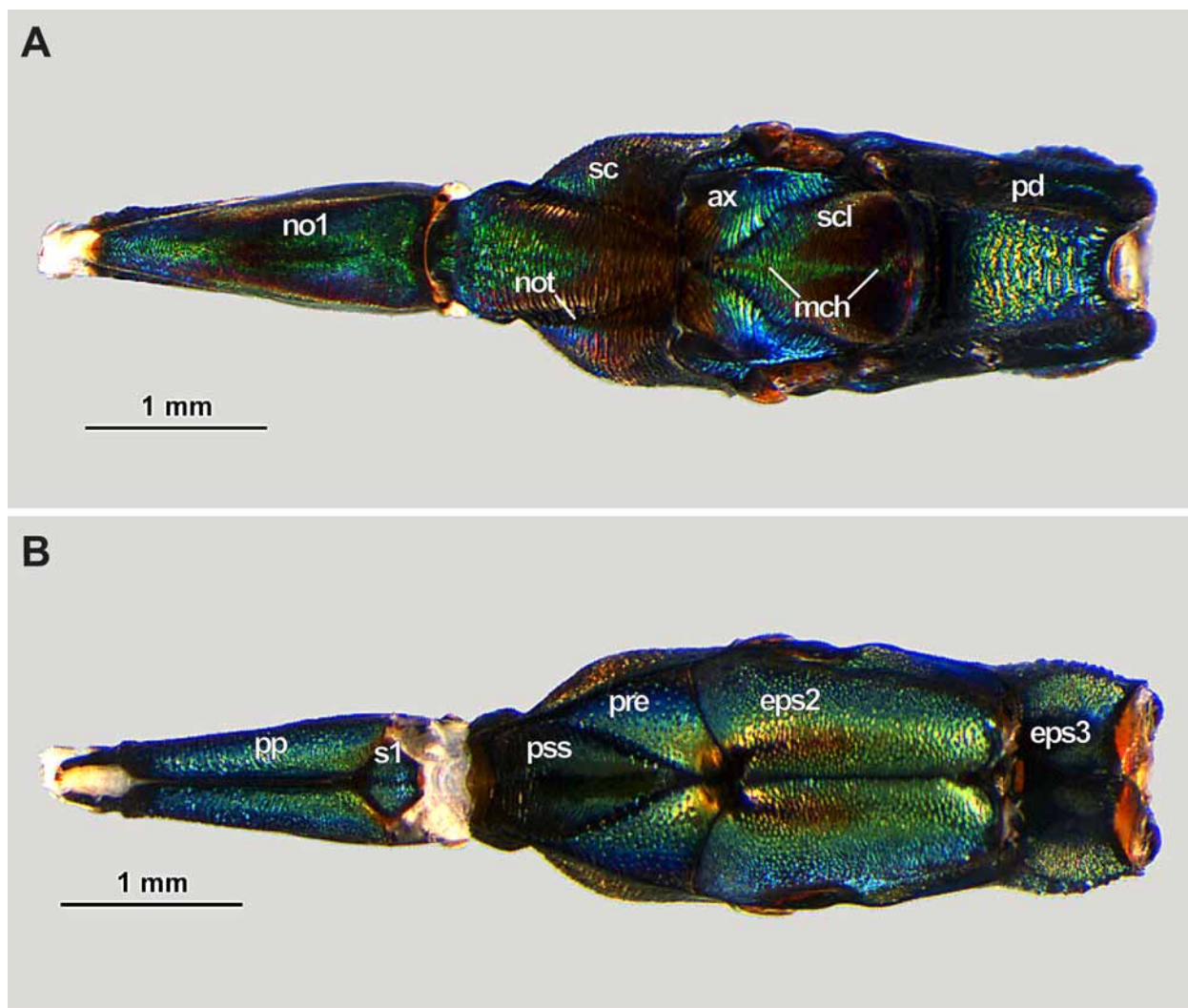
Mesoscutellar-axillar complex length:width = 1.17–1.39:0.78–0.89. Mesoscutellum mostly finely and densely alveolate except for occasional rugula extending from axilla, but with a shallow, broad, posteriorly narrower and shallower mesal longitudinal depression extending to frenal groove, the depression with finer alveolate sculpture than rest of mesoscutellum. Frenum with very fine and shallow sculpture, less alveolate than for rest of mesoscutellum. Axillae with dorsal surfaces large and abutting medially, finely transversely rugulose with underlying finely alveolate areas visible between rugulae except with nearly rectangular smooth depression anterolaterally (Fig. 3E: ax), the smooth depression bordered posteriorly by a carina that extends medially partly across the axillae; dorsal axillar surface with posterior half much more densely setose than anterior half, lateral panel of axilla mainly smooth, but with tiny punctures dorsally and with slight reticulation ventrally. Mesoscutellum with axillulae barely differentiated and with flat surface; frenum less than one tenth mesoscutellar length, with frenal line extremely shallow and abruptly arching posteriad at point where tiny posterior pair of mesoscutellar setae are positioned.

Prepectus (Fig. 4B: pre) greatly enlarged and fused with prospinasternum (Fig. 4B: pss), the line of fusion externally indicated by foveolate sulcus (Fig. 4B), and combined structure forming broad plate that is fused

with mesepisternum posteromedially; lateral panel of prepectus closely abutting but not overlapping mesopleuron (Fig. 5A: pre); prepectus with scattered punctures, but prospinasternum striate anteriorly and smooth posteriorly. Posterior edge of mesopleuron (what may be mesepimeron) mostly smooth and bare, but with some rugae and setae in a middle strip that becomes broader dorsally. Mesopleural sulcus obscure, but marked by sunken area that is sculptured in dorsal half and smooth and broadened in ventral half. Transepimeral and transepisternal divisions not apparent. Acropleuron small, transverse without distinct margins (acropleural sulcus), the posteroventral margin indicated by round depression and surface striate; mesopleuron otherwise with smooth area below acropleuron, posterolaterally with fine reticulation, and anterolaterally and ventrally with tiny piliferous punctures; mesopleural sulcus, transepimeral sulcus and transepisternal sulcus absent externally; mesodiscriminal line developed as shallow sulcus with mesofurcal pit just anterior to carinate mesotrochantal plate; mesocoxal foramina completely enclosed by sclerotized cuticle.



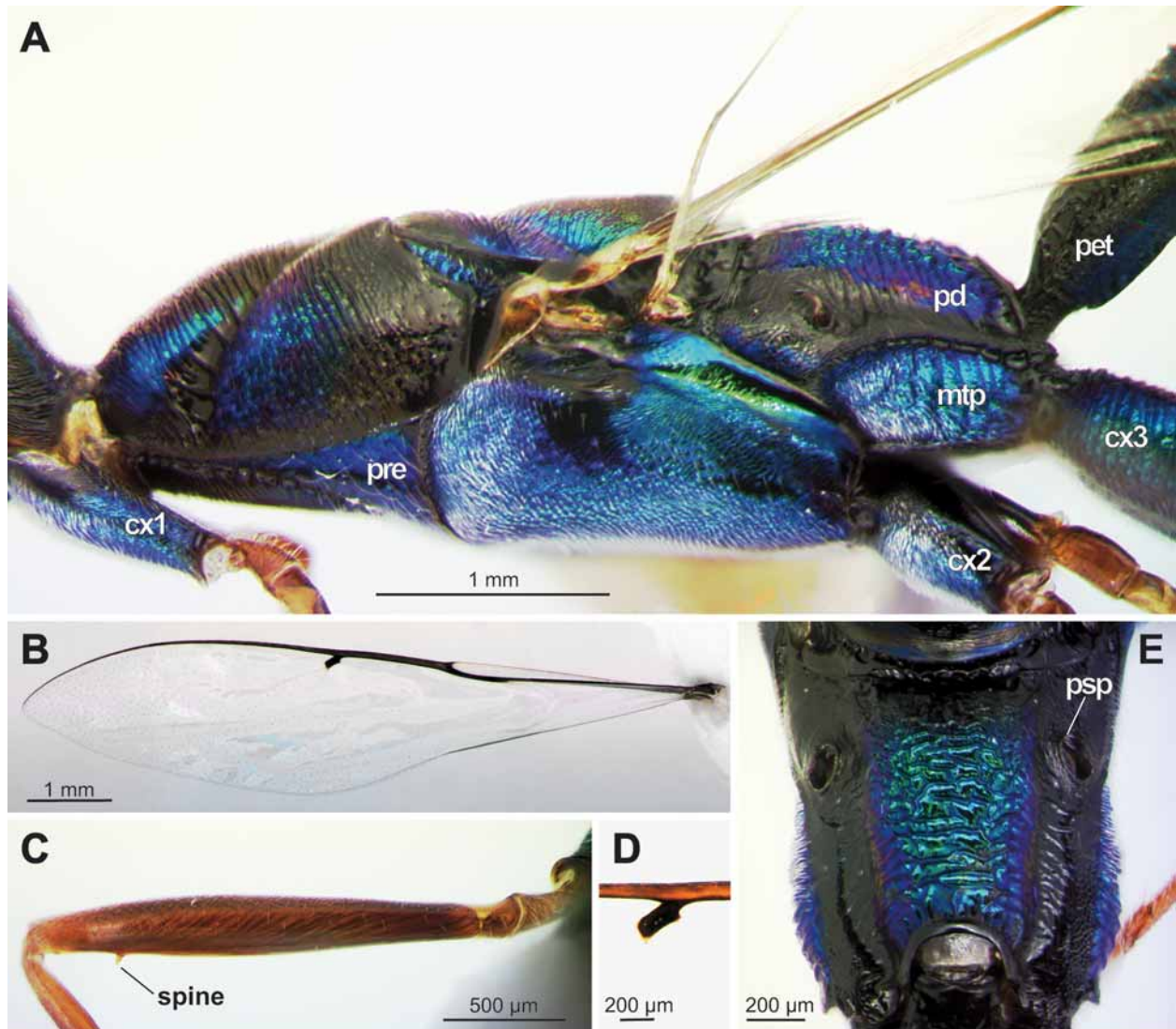
**FIGURE 3.** *Doddifoenus wallacei* sp. n. female paratypes. A. head, lateral view; B. prothorax, lateral view; C. anterior prepectus, ventrolateral view; D. prothorax, ventral view; E. mesoscutellum, dorsal view; F. mesonotum, lateral view. apx = anterior portion of preaxilla, ax = axilla, cp = cervical prominence, mch = mesal channel, no1 = pronotum, pp = propleuron, ppx = posterior portion of preaxilla, s1 = prosternum, sc = mesoscutum, scl = mesoscutellum.



**FIGURE 4.** *Doddifoenus wallacei* sp. n. female paratype. A. mesosoma, dorsal view; B. mesosoma, ventral view. ax = axilla, eps2 = mesepisternum, eps3 = metepisternum, mch = mesal channel, no1 = pronotum, not = notaulus, pd = propodeum, pp = propleuron, pre = prepectus, pss = prospinasternum, s1 = prosternum, sc = mesoscutum, scl = mesoscutellum.

Metanotum with metascutellum (=dorsellum) extremely shortened, forming a carina that is anteriorly and posteriorly bordered by row of foveolae; metascutellum laterally continuous with smooth metascutellar arms; metascutellar arms broad anterior with inconspicuous row of foveolae. Metapleuron (=lateral metepisternum) quadrangular with a curved dorsal margin, separated from propodeum by carina forming dorsal margin of foveolate sulcus extending from metacoxal foramen to anterior margin of metapectus; anteriorly with fine reticulation and conspicuous white pilosity, posteriorly with coarse irregular reticulation and reduced pilosity. Ventral metepisternum (=metasternum) greatly enlarged and separated by carina from metapleuron; with fine reticulation and pilosity laterally but medially bare with traces of reticulation and two submedian metafurcal pits close to anterior margin (Fig. 6F: f3p), the pits very close to each other within single depression. Propodeum length:width = 1.22–1.43:1.17–1.26, propodeal surface with strong and anastomose rugae (Fig. 5E), areas around spiracle less rugulose and more strongly alveolate; entire surface laterad postspiracular furrow densely alveolate; margin of propodeal foramen carinate (Fig. 5E); anterior edge of propodeum with a deep trough along width of metascutellum; with short tongue-like rim extending anteriorly partially over propodeal spiracle, the spiracle appearing elongate-ovoid in shape if rim ignored (Fig. 5E), ISD 0.80–0.86, spiracle about 1/3 propodeal length from anterior margin of propodeum; postspiracular furrow shallow and

broad but complete to posterior margin of propodeum; nucha distinct but extremely short, not convex; propodeal callus divided into two sections: an anterior smooth region with numerous posteroclinate setae and a posterior alveolate region having a few long laterocline setae immediately posterior to the spiracle; propodeal foramen large, pear-shaped, dorsally extended to form high articulation point for metasoma (Fig. 5A).



**FIGURE 5.** *Doddifoenus wallacei* sp. n. female paratypes. A. mesosoma, lateral view; B. forewing, dorsal view; C. profemur, lateral view; D. stigmal vein, dorsal view; E. propodeum, dorsal view. cx1 = procoxa, cx2 = mesocoxa, cx3 = metacoxa, mtp = metapleuron, pd = propodeum, pet = petiole, pre = prepectus, psp = propodeal spiracle.

Legs (Figs 2A; 5A,C). Coxae densely covered with white setae in contrast to nearly bare ventral surfaces of femora. Length to wide ratios of fore leg:  $CX_1$  0.90–0.98:0.31–0.36;  $FM_1$  1.79–2.06:0.23–0.28,  $TB_1$  1.65–1.84:0.12–0.14. Profemur with an isolated, short, unsocketed spine preapically; protibia with a very small set of apical spinules extending on lateral side between protibial spur socket and tarsal socket, with an abruptly longer spinule nearest the spur dorsal surface of protibial apex with thick socketed spine, giving apex a trilobed appearance when viewed from above; protibial spur not cleft, without a fringe; basal protarsomere with a fine ventral fringe in area used for antennal grooming, but smooth immediately above fringe; 2<sup>nd</sup> protarsomere the longest, longer than apical three tarsomeres combined. Length to wide ratios of middle leg:

CX<sub>2</sub> 0.70–0.90:0.39–0.51; FM<sub>2</sub> 2.14–2.44:0.14–0.22; TB<sub>2</sub> 2.45–2.75:0.10–0.15. Mesotibia with apical spinules of nearly equal length and not stout, and with a dorsal socketed spine as for protibia; mesotibial spur 0.23–0.27, simple and with only extremely short setae as viewed under stereoscope magnification; 2<sup>nd</sup> mesotarsomere the longest, all segments similar in proportion as protarsus. Length to wide ratios of hind leg: CX<sub>3</sub> 1.50–1.80; FM<sub>3</sub> 2.68–3.10; TB<sub>3</sub> 3.29–3.76:0.25–0.28 (apically). Metacoxa without dorsal groove or carina for accommodating metafemur, ventral surface of metacoxa much more finely sculptured and more alveolate than coarsely rugose dorsal surface; metatibia with a set of apical spinules medially of nearly equal length, 1<sup>st</sup> metatibial spur 0.27–0.31, 2<sup>nd</sup> metatibial spur 0.12–0.14, both simple and with only very tiny setae, 2<sup>nd</sup> metatarsomere the longest, with all metatarsomeres with similar proportions as protarsomeres.

Wings (Figs 5B,D). Forewing length:width 6.5–7.5:1.5–1.69; tegula with some fine setae anteriorly but without spines; humeral plate with very few setae and no spines; costal cell length: width = 2.38–2.70:0.12–0.15, without pigmented costal vein, bare dorsally but ventrally with one line of setae and an isolated seta near midlength posterior to setal line; without parastigmal sensilla or sclerotization of basal vein evident; marginal vein length:width = 1.12–1.33:0.08–0.10, with very weak setae; postmarginal vein curved and extending to just short of wing apex, length about 3.00–3.47; stigmal vein rhomboidal, with three or four uncal sensilla; basal cell bare; speculum present; cubital vein absent but position may be indicated by raised folds; fringe setae extremely short but present. Hind wing length:width = 3.41–3.85:0.59–0.69; basal plate without setae or spines; costal cell distinct; marginal vein sclerotized; three hamuli present; fringe setae present except for a short region starting at the hamuli and ending before the wing apex.

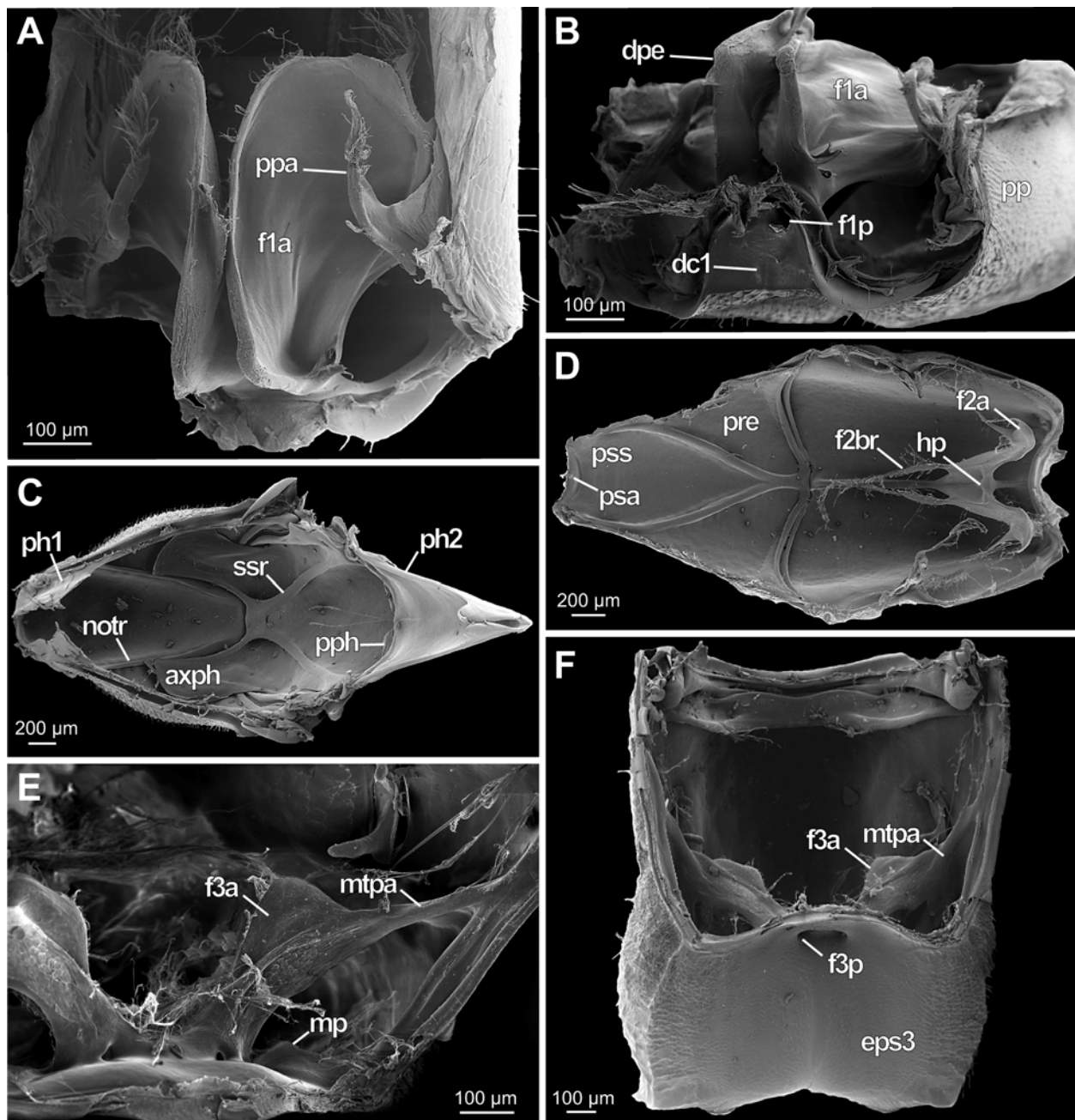
Metasoma (Figs 2A; 5A). 1<sup>st</sup> metasomal tergite (petiole) length:width = 1.34–1.58:0.42–0.50, with several long lateral setae; rugae of petiole strong, anastomosing in anterior half but more parallel and rarely branching in posterior half; ventral surface with an irregular mesal keel. Second metasomal tergite shallowly coriaceous, the remaining tergites very finely and shallowly rugulose-alveolate; 2<sup>nd</sup> metasomal tergite the shortest, 5<sup>th</sup> metasomal tergite the longest, all metasomal tergites except the 1<sup>st</sup> and 6<sup>th</sup>–8<sup>th</sup> with a posterior incision mesally; cercal setae short and of about same length; epipygium (Mt9) length:width = 3.79–4.60, with curved or sinuate setae that become longer and more sinuate apically; ovipositor sheaths length about 17.50–22.13, with a tiny fringe of apical setae.

Male: Differs from female as follows: micropilose sensory area of antennal club much larger, comprising more than half ventral surface of F11; legs slightly darker, with metatibia much darker; 1<sup>st</sup> metasomal tergite with a posterior mesal incision similar to other tergites; 8<sup>th</sup> metasomal tergite separated from 7<sup>th</sup> by a very faint groove and with a pair of elongate, dark, sinuate setae at apex; genitalia with digital spines and a spine arising at base of each volsella.

### **Internal skeletal anatomy of mesosoma**

(Figs 6A–F)

Prothorax (Figs 6A,B). Pronotum internally with short phragma anteriorly. Propectus with dorsally carinate, well developed propleural arm lateral to articulation between profurca and propleuron, the arm distinctly curved and protruding anterodorsally (Fig. 6A: ppa). Prosternum posteriorly inflected at an angle of about 90 degrees relative to ventral surface; smooth, with slight indication of prodiscriminal line (Fig. 6B: dc1); outer margin with complete carina lateral to procoxal articulation extending to lateral margin of ventral surface; with pair of submedian profurcal pits at dorsal margin posteriorly (Fig. 6B: flp). Profurcal arms separated from each other (Fig. 6B: fla), proximally with conspicuous dorsal extensions (Fig. 6B: dpe) extending far beyond dorsal margin of propleura and giving rise to large shovel-shaped, anteriorly projecting region of profurcal arms; profurcal arms with rounded opening at lateral margin.



**FIGURE 6.** *Doddifoenus wallacei* sp. n. female paratype. Dissected mesosomal skeleton (musculature and tissue removed). A. propectus, dorsal view; B. propectus, posterior view; C. mesonotum, ventral view; D. mesopectus, dorsal view; E. metafurca, anterior view; F. metathorax-propodeum complex, ventral view. axph = axillar phragma, dc1 = prodiscriminal line, dpe = dorsal profurcal extension, eps3 = metepisternum, f1a = profurcal arm, f1p = profurcal pit, f2a = mesofurcal arm, f2br = mesofurcal bridge, f3a = metafurcal arm, f3p = metafurcal pit, hp = horizontal plate, mp = metapectal plate, mtpa = metapleural apodeme, notch = notaular ridge, ph1 = prophragma, ph2 = mesophragma, pp = propleuron, ppa = propleural arm, pph = pseudophragma, pre = prepectus, psa = prospinasternal apodeme, pss = prospinasternum, ssr = scutoscutellar ridge.

Mesothorax (Figs 6C, D). Mesonotum with conspicuous, medially incised prophragma articulating with extended part of mesoscutal lobe (Fig. 6C: ph1); with distinct, complete notaular ridges; axillar phragma elongate (Fig. 6C: axph), lying adjacent to notaular ridges (Fig. 6C: notch). Scutoscutellar ridge distinct (Fig. 6C: ssr), abruptly widened laterally. Mesophragma elongate (Fig. 6C: ph2), extending towards propodeum;

anterior margin attached to inner surface of mesoscutellum, bilobed and forming short pseudophragma (Fig. 6C: pph); posterior margin deeply incised medially. Prepectus internally separated from mesepisternum and prospinasternum by complete ridges (Fig. 6D: pre), the prospinasternum with tiny prospinasternal apodeme (Fig. 6D: pss, psa). Acropleural ridge short, ventral limit corresponding to round (external) depression. Mesopleural and transepimeral ridge not developed. Mesodiscriminal lamella straight, extending to anterior margin of mesepisternum; mesofurca with complete, anteriorly elongate mesofurcal bridge (Fig. 6D: f2br), the bridge subtriangular in dorsal view due to straight apodemes that are fused at an acute angle; horizontal plate not extended anteriorly (Fig. 6D: hp).

Metathorax-propodeum complex (Figs 6E,F). Metafurcal arms broad (Fig. 6F: f3a), medially fused into u-shaped metafurca; metafurcal arm broadly fused with metapleural apodeme, the line of fusion indiscernible (Fig. 6E: f3a, mtpa), basally with distinct round pit anteriorly; metadiscriminal lamella indistinct, covered by bunch of tendons; metapectal plate short, acute dorsally, separate from metafurcal arm (Fig. 6E: mp).

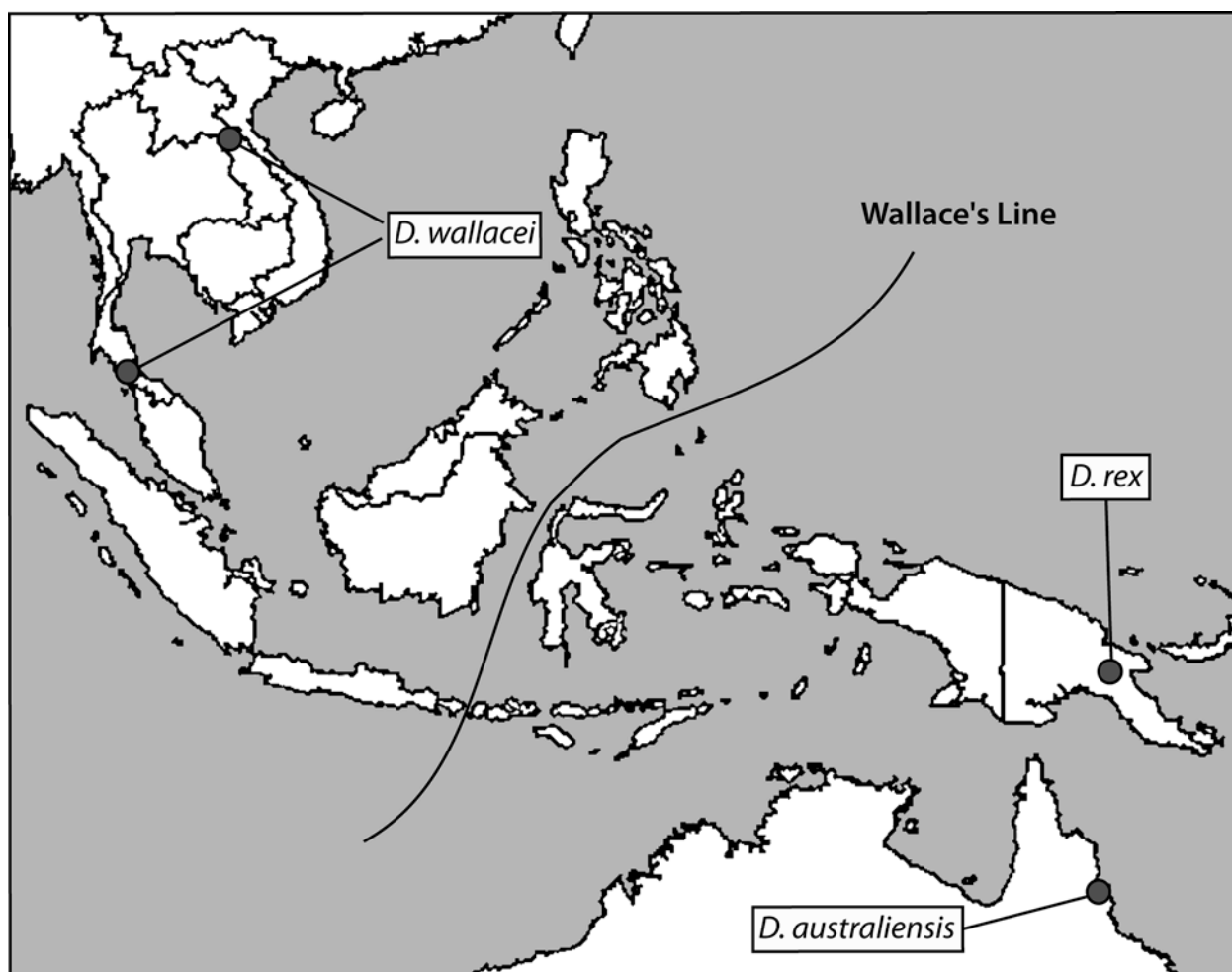
**Molecular sequences.** The 28S D2-D5 ribosomal DNA, amplified by the primers described were sequenced and posted to GenBank (accession numbers 28S D2: FJ859012 and 28S D3-D5: FJ859013). A phylogenetic analysis is beyond the scope of this article, but some information can be provided regarding the sequences themselves.

Helix 3-2 of the 28S D2 sequence (using nomenclature established by Gillespie *et al.* 2005) is unusual for Chalcidoidea in that there are only three bases between the presumed 3l helix and its complement 3l', meaning that helices 3m, 3n, 3o and 3p are missing. Admittedly, the bases assignable to 3l may actually belong to one of the presumed missing helices. Regardless, helix 3-2 is unusually short for *D. wallacei* in comparison to other Chalcidoidea. The three bases between the presumed 3l and 3l' do not seem to pair with any other part of the ribosomal sequence and were assigned to a region of ambiguous alignment.

**Biology.** All specimens of *D. wallacei* were collected from naturally fallen trees in a primary tropical rainforest (Yanega & Ballmer, pers. comm. and collection data). No host records are known for *Doddifoenus* or any other Leptofoeninae, but they are presumed to be parasitoids of wood-boring insects. This hypothesis is based on the frequency that specimens are collected from dead and felled trees, and on the long ovipositor (LaSalle & Stage 1985). Furthermore, some morphological features of *D. wallacei* are similar to other hymenopteran parasitoids of endoxylous hosts, such as Orussidae, Stephanidae, Rhyssinae (Ichneumonidae), Calosotinae (Eupelmidae), and a few Cleonyminae (Pteromalidae). Although the similarities are probably convergent they support an hypothesis that *D. wallacei* is also a parasitoid of wood-boring insects. The shared morphological features include: 1) rows of transverse parascrobal crests or denticles on upper frons and vertex parallel to eyes, and 2) transverse ridges forming the most prominent sculpture of the mesoscutum. The parascrobal crests have been hypothesized to have a potential use in moving debris from blocked channels inside the log, in addition to strengthening the head capsule (Gibson 2003). The transverse ridges on the mesoscutum may serve to provide additional purchase to the top of the channel to provide better leverage for moving clumps of debris, but at least they would seem to serve well in strengthening the mesoscutum. Potential morphological adaptations of various parasitoid wasp groups to endoxylous hosts are summarized in Quicke (1997).

Final determination of hosts will necessitate rearing the parasitoids from field-collected logs and being able to unambiguously match them to the host. It is also necessary to determine if leptofoenines are primary, facultative secondary, or obligate secondary parasitoids, through rearing of several individuals and dissection of the host material. The labor-intensiveness of this process, along with the extreme rarity with which leptofoenines are encountered probably are the chief reasons for our lack of knowledge of leptofoenine biology.

**Distribution** (Fig. 7). *D. wallacei* is known from two localities in Laos and Thailand. Previously, *Doddifoenus* was solely known to occur east of Wallace's Line. *Doddifoenus rex* and *D. australiensis* are both only known from their respective type localities in Papua New Guinea and Northeastern Australia.



**FIGURE 7.** Distribution of world *Doddifoenus* species: *D. wallacei* (Laos and Thailand), *D. rex* (Papua New Guinea), *D. australiensis* (Northeastern Australia).

## Discussion

Females of *D. wallacei* vary in length from 34.6–41.7 mm, and therefore the species is among the longest species ever described within the superfamily Chalcidoidea. It is distinctly longer than its congeners *D. australiensis* (female: 24.2 mm) and *D. rex* (females 25–28 mm).

*Doddifoenus* exhibits strong elongation of some regions of the mesosoma and metasoma relative to other potentially related pteromalid groups. The areas of the propleuron and pronotum anterior to the prosternum (Figs 3D; 4A,B), the anterior part of the mesoscutal midlobe (Fig. 4A) and transverse section flanking the preaxillae (Fig. 3F), the prepectus and associated prospinasternum (Fig. 4B), and the ventral portion of the metepisternum (Fig. 4B) are all conspicuously elongate. The elongation of areas in line with the preaxilla is interesting because it involves elongation of such diverse structures as the anterior portion of the preaxilla, axillae, and posterior lateral corners of the mesoscutal sidlobe. However, the rest of the mesoscutal sidlobe is not noticeably elongate, and the frenum and metanotum are extremely short. Metasomal tergites 4–6 and 8 and 9 are elongate relative to tergites 2, 3 and 7 and to the same tergites in non-leptofoenines. *Doddifoenus* also exhibits an elongate petiole, but this character occurs frequently in Pteromalinae and other Chalcidoidea. The selective pressure for the elongation of various body parts in Leptofoeninae is unknown, as such a conspicuously elongate-slender body does not fully correlate with the morphology of parasitoids of wood-boring beetles, which are presumed to have similar life histories to *Doddifoenus*.

Leptofoeninae possess several conspicuous and/or rare, putative plesiomorphies and apomorphies. Some of the putative plesiomorphies, such as the pigmented and partially sclerotized basal and cubital forewing veins, may be correlated with less morphological reduction than for most other, much smaller chalcidoids. However, these structures may also be secondarily regained to strengthen the enlarged forewing, and thus apomorphic. Within Chalcidoidea, basal and cubital forewing veins are also pigmented in some Melanosomellini (Pteromalidae: Ormocerinae) (Yoshimoto 1972), some miscogasterine and trigonoderine pteromalids, Rotoitidae, Leucospidae, and sporadically in many other groups.

The posterior (reticulate) portion of the preaxilla is greatly extended dorsally in *Doddifoenus* (Fig. 3F). It is also distinctly extended dorsally in at least some Cleonyminae such as *Thaumasura* Westwood (Krogmann & Vilhelmsen 2006: Fig. 11A) and *Notanisus* Walker (unpublished observation). Although this structure might have some phylogenetic value it is premature to use it as evidence of a relationship between Leptofoeninae and Cleonyminae because the character state distribution within Chalcidoidea is otherwise still uncertain.

There are several internal morphological structures in *Doddifoenus* that exhibit putative apomorphic character states. Although the profurca bears several features that are most likely plesiomorphic within Chalcidoidea (e.g., profurcal arms and pits separated), the dorsal extension of the profurcal arms (Fig. 6B) is more pronounced than in other chalcidoid groups (Krogmann & Vilhelmsen 2006) and this is most likely an autapomorphic character state. The metafurca of Chalcidoidea has been comprehensively studied by Krogmann & Vilhelmsen (2006) and was revealed as highly variable and more phylogenetically informative than the pro- or mesofurca. The complete fusion between the metafurcal arms and metapleural apodemes (Fig. 6E) is an apomorphic character state of *Doddifoenus* that has not been found in any other Chalcidoidea (Krogmann & Vilhelmsen 2006) although it occurs sporadically in other apocritan taxa (Weber 1926; Vilhelmsen *et al.* in press). The metafurca of *Doddifoenus* is further characterized by basally fused metafurcal arms, which corresponds to metafurcal Type 2 of Krogmann & Vilhelmsen (2006). This type differs from Type 3, the most common type in Chalcidoidea, which is characterized by separate metafurcal arms lateral to the metadiscal lamella. Interestingly, Cleonyminae have either Type 2 or Type 3 metafurca, whereas all Pteromalinae they examined for their study shared Type 2. Even though it is not possible to definitely ascertain the polarity of the metafurcal characters, the proposed transformation series of Krogmann & Vilhelmsen (2006: Fig. 24) may indicate a plesiomorphic condition in *Doddifoenus* and (some) Cleonyminae relative to the condition in Pteromalinae.

The lack of fusion between metasomal tergites 8 and 9 in *Doddifoenus* is another likely plesiomorphic state. The two tergites are partially fused in *Leptofoenus* (Gibson 2003). Separate Mt8 and Mt9 occur sporadically across the Chalcidoidea, known in Torymidae, Agaonidae, Pteromalidae (Sycophaginae (Grissell 1995), Chromeurytominae (Bouček 1988), and some Cleonyminae, Colotrechninae and Nefoeninae (Gibson 2003)), Signiphoridae (Woolley 1988), Aphelinidae (Azotinae (Munro, pers. comm.)), Eulophidae (Euderinae (Coote 1994)), and some Eupelmidae (Gibson 1989). The tergites are also partially to fully separated in some Pireninae (Pteromalidae). A complete survey has not been made across Chalcidoidea for this character state and any speculation on its phylogenetic significance is preliminary. However, the character state distribution throughout Chalcidoidea indicates that fusion of the Mt8 and Mt9 happened multiple times.

Gibson's (2003: Figs 1b, d) analysis of Cleonyminae and similar pteromalids indicated that Leptofoeninae is the sister group to Nefoeninae, and that this clade could be the sister group of Pteromalinae + Macromesinae, or of a non-monophyletic Cleonyminae + Louriciinae + Hetreulophini (Colotrechninae), depending upon rooting. Although that analysis was mainly intended to determine relationships within Cleonyminae, these alternative hypotheses have very different implications for chalcidoid phylogeny and for polarization of morphological characters within pteromalid subfamilies. The chief characters placing Leptofoeninae between Pteromalinae and Cleonyminae in Gibson's (2003) phylogeny appear to be the divergence of the inner eye orbits and forewing setation patterns, and to a lesser degree mesoscutellar setation patterns. Gibson (2003) pointed out that divergence of the inner eye margins was difficult to divide into discrete states, but he interpreted them as being "slightly divergent" in *Doddifoenus* (inner margins ventrally

divergent along most of their height, Fig. 2B). This state is different to the condition found in *Leptofoenus*, which has nearly parallel inner orbits (Gibson 1993, Fig. 4) and also differs from *Nefoenus* Bouček, which has more rounded eyes. However, it seems that this character is difficult to code and of unclear polarity and it may not provide conclusive evidence for the phylogenetic relationships of *Doddifoenus* or Leptofoeninae.

The setal patterns of the mesoscutellum and forewing did not fully unite Leptofoeninae + Nefoeninae with Pteromalinae or Cleonyminae either, as *Doddifoenus* and *Leptofoenus* differ from one another in both of these characters. *Doddifoenus* has a mesally bare mesoscutellum like most Pteromalinae, but unlike *Leptofoenus*, *Nefoenus*, and most Cleonyminae. The forewing of *D. rex* was interpreted as “entirely bare” by Gibson. However, very short dorsal and ventral discal setae are visible in *D. rex*, *D. australiensis* and *D. wallacei*. The setal pattern is like that of *Leptofoenus* and most Pteromalinae in that there is a speculum and reduced basal cell setation, but the basal fold has few or no setae in *Doddifoenus*. In *Nefoenus* (as in most Cleonyminae) the forewing is essentially entirely setose. This leaves no known morphological character consistently uniting all Leptofoeninae + Nefoenine with either Pteromalinae or Cleonyminae. The solution to this problem likely requires a broader analysis of Pteromalinae and additional pteromalid subfamilies that could be closely related to it, such as Miscogasterinae, Ormocerinae, Pireninae, Austrosystasinae, Austroterobiinae, and additional Colotrechninae.

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