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## Phylogeny, Biogeography, and Revision of the Subfamily Dallatorrellinae (Hymenoptera: Liopteridae)

ZHIWEI LIU<sup>1,2</sup>

### ABSTRACT

A recent cladistic study suggested that the parasitoid wasp subfamily Dallatorrellinae is a monophyletic clade within the cynipoid family Liopteridae. The subfamily currently includes only four known species belonging to two genera, i.e., the monotypic genus *Mesocynips* Cameron, 1903 and the genus *Dallatorrella* Kieffer, 1911. The present study presents a revision of the subfamily, including descriptions of five new species in the genus *Dallatorrella*: *D. maculata*, *D. maxima*, *D. pulla*, *D. ronquisti*, and *D. sinica*. A key to the species of the subfamily is provided. Cladistic analysis of the subfamily at species level is undertaken and the biogeographic history of the subfamily Dallatorrellinae is reconstructed with respect to phylogeny. Contrary to an earlier assumption that the Dallatorrellinae originated in the Australian region, the phylogeny indicates that the Dallatorrellinae originated in southeastern Asia and dispersed to Australia at a later date. Consequently, the divergence between the Dallatorrellinae and the stem species of two other liopterid subfamilies, Liopterinae and Oberthuerellinae, corresponds with the separation between Laurasia and Gondwanaland.

### INTRODUCTION

The subfamily Dallatorrellinae belongs to the cynipoid family Liopteridae, together with Austrocynipidae and Ibalidae making up the macrocynipoids (Ronquist, 1995a). The macrocynipoid families are the paraphy-

letic basal branches of the Cynipoidea. Their species are typically large in size. Although the macrocynipoids are generally known as parasitoids of wood- or cone-boring insect larvae (Ronquist, 1999), the biology of the Dallatorrellinae is virtually unknown. Fe-

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males of one species of *Dallatorrella* have been collected on logs of *Syzygium* (Myrtaceae) in Papua New Guinea, suggesting an association with wood-boring insects on broadleaved trees. Such an association is characteristic of all other liopterids with known hosts (Ronquist, 1995a; Liu, personal observation).

Dallatorrellinae as currently understood includes two genera: *Dallatorrella* Kieffer, 1911 and *Mesocynips* Cameron, 1903 (Ronquist, 1995b). The subfamily was first established by Kieffer (1911) for his new genus *Dallatorrella* and was originally assigned to the family Cynipidae as then understood. Hedicke and Kerrich (1940) placed Dallatorrellinae and several other groups previously considered as subfamilies within the Cynipidae or Figitidae in a separate family, Liopteridae. In that paper, Kerrich included Dallatorrellinae and the previously recognized Mayrellinae Hedicke, 1922 in a new subfamily, Mesocynipinae, consisting of five genera, namely *Mesocynips* Cameron, 1903, *Paramblynotus* Cameron, 1908, *Dallatorrella* Kieffer, 1911, *Mayrella* Hedicke, 1922, and *Paribalia* Weld, 1922. The classification remained unchanged until recently. Based on a phylogenetic analysis of the family, Ronquist (1995b) revised the Liopteridae and split the Mesocynipinae once again into the two subfamilies recognized prior to Hedicke and Kerrich (1940), i.e., Mayrellinae and Dallatorrellinae. Phylogenetically, Mayrellinae is the basal clade of Liopteridae and is the sister group to all other liopterids, whereas Dallatorrellinae is the sister clade of Oberthuerellinae and Liopterinae (fig. 44).

Biogeographically, *Mesocynips* has been reported only from Southeast Asia while species of *Dallatorrella* are distributed in both the Australian and Oriental regions. Reconstructions of historical biogeography for the Liopteridae suggested that the Dallatorrellinae originated in southern Gondwanaland and subsequently dispersed into the Orient (Ronquist, 1995b). However, this hypothesis has not been tested by a phylogenetic reconstruction of relationships within the subfamily.

Taxonomic work on Liopteridae in general and on Dallatorrellinae in particular has been almost entirely restricted to alpha-level stud-

ies. Ronquist (1995b) revised the liopterid genera and studied phylogenetic relationships among them. Despite this encouraging development in liopterid systematics, revisions at the species level are still lacking, a situation common for cynipoid groups.

The genus *Dallatorrella* currently includes three named species. Ronquist (1995b) referred to five additional undescribed species, of which two are considered as conspecific here. An undescribed species was also subsequently discovered from China. The genus *Mesocynips* is monotypic.

The present study provides a revision of Dallatorrellinae, including a key to and diagnoses of all known species, analyzes the phylogenetic relationships among these species, and attempts to reconstruct the historical biogeography of the subfamily. The concepts of the subfamily and the genera studied here follow that of Ronquist (1995b), which should be consulted for detailed descriptions of the higher taxa.

## MATERIAL AND METHODS

### SPECIMENS

The present paper is based on 34 specimens of Dallatorrellinae borrowed from the world's major insect collections given below through the kindness of persons listed. Holotypes of all known species were studied except that of *Cynips insignis* Smith, 1903, which is believed to be lost (see below).

### LIST OF DEPOSITORIES

AEI	American Entomological Institute, Gainesville, FL, USA (D. Wahl)
ANIC	Australian National Insect Collection, Canberra, Australia (I. Naumann)
BPMB	Bernice P. Bishop Museum, Honolulu, HI, USA (K. Arakaki)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (P. Perkins)
NHM	The Natural History Museum, London, UK (T. Huddleston, S. Lewis)
USNM	Smithsonian Institution, Washington, DC, USA (D. Smith)
ZICA	Zoological Institute, Chinese Academy of Sciences, Beijing (X. Yang)
ZLMU	Zoological Laboratory, Meijo University, Nagoya, Japan (K. Yamagishi)

## METHODS

Phylogenetic analysis was carried out using parsimony as implemented in the computer package NONA 2.0 (Goloboff, 1999). Search options were: hold maximum number of trees, i.e., 100,000 trees, and mult\*1000. Characters with multiple states are treated as ordered when a trend is obvious, and they are so indicated in the character list. All characters were weighted equally. *Liopteron* and *Paramblynotus*, whose phylogenetic relationship with Dallatorrellinae are shown in figure 44, were chosen as outgroups and coded as collective units. The coding for *Paramblynotus* is based on an ongoing study on the subfamily Mayrellinae (Liu et al., in prep.), whereas coding for *Liopteron* is based on published information (Ronquist, 1995b) as well as on observations of three unidentified species in the Cynipoidea collection of the American Museum of Natural History and in the author's own collection. Since the relationship among the outgroups, *Liopteron* and *Paramblynotus*, and Dallatorrellinae is very strongly supported by previous studies (Ronquist, 1995a, 1995b), and, because the present analysis focuses on the relationships within the subfamily, the higher level relationship among the outgroups and Dallatorrellinae is constrained accordingly in the analysis.

The resulted trees were subsequently subjected to WinClada (Nixon, 1998) for character optimization. Bootstrap and Jackknife values were calculated with NONA and WinClada (1000 replications, each with 100 search replications).

The study is entirely based on adult external morphology. SEM images were taken with a Hitachi S4700 field emission scanning electron microscope (FE-SEM). Because of the scarcity of available material, specimens were examined unprepared and uncoated with emission current at 4500–7000 nA and accelerating voltage at 1–1.5 kV. Morphological terminology follows that proposed by Ronquist and Nordlander (1989) and Ronquist (1995b). Terms for surface sculpturing follow Harris (1979). Antennal flagellomeres and abdominal terga are represented in the text as, e.g., F1 and T3.

Since detailed descriptions of *Mesocynips*

and *Dallatorrella* have recently been presented by Ronquist (1995b), I limit the descriptions of taxa, including the new species, to the minimum. Instead, I provide a detailed key to species along with species diagnoses, supplemented by figures and SEM images.

## SYSTEMATICS

SUBFAMILY DALLATORRELLINAE  
KIEFFER

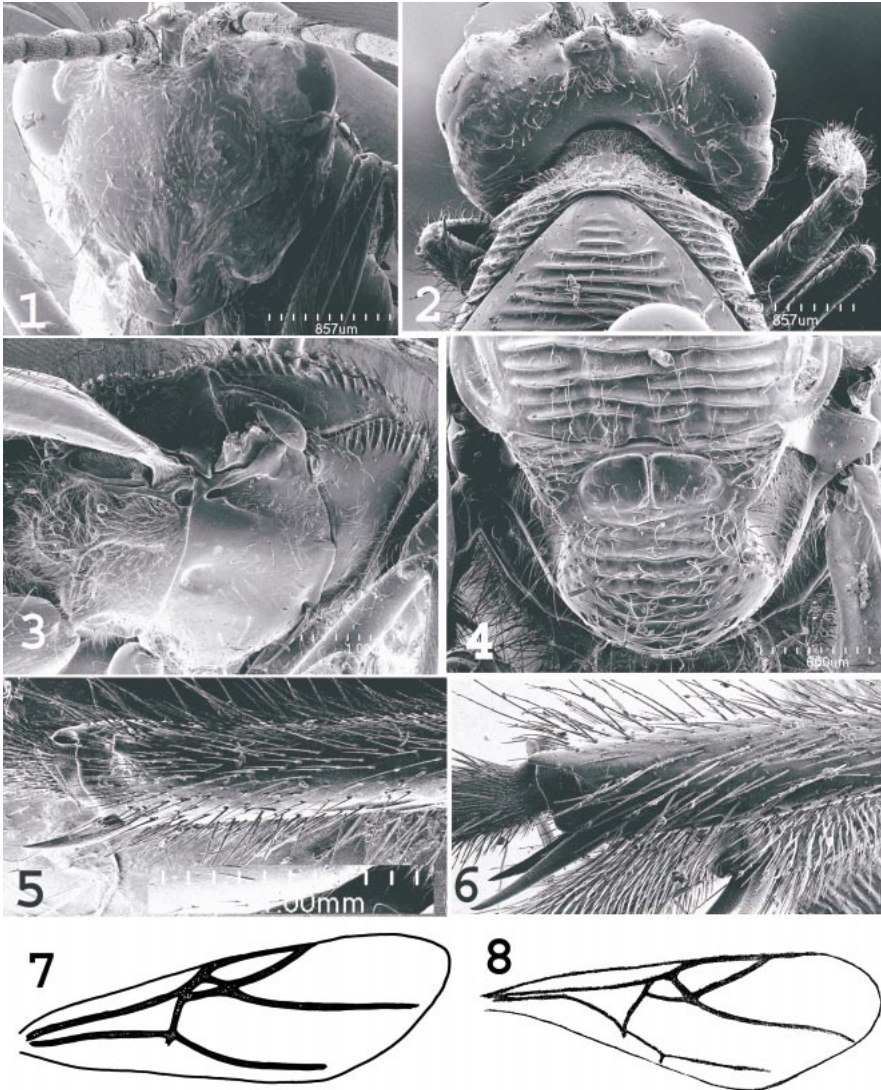
Dallatorrellinae Kieffer, 1911: 244. Type genus: *Dallatorrella* Kieffer, 1911. RESTABLISHED by Ronquist (1995b: 38).

Mesocynipinae Kerrich in Hedicke and Kerrich, 1940: 178. Type genus: *Mesocynips* Cameron, 1903.

DIAGNOSIS: Median flagellomeres distinctly swollen submedially to somewhat swollen subapically, especially ventrally. First flagellomere of female with placodeal sensilla. Posterolateral pronotal margin distinctly incised in front of mesopleural triangle, the latter deeply impressed anteriorly. Scutellum laterally without impressed semilunar area. Ventral end of metapleural carina produced into a prominent process laterad to metacoxal foramen. Pro- and mesotarsal claws with basal, lamellate lobe. Laterobasal part of metacoxa with a lateral ridge and an anterolateral, pubescent depression. Metatibial lobe produced into distinct, slender, toothlike process (except *D. maxima*); petiolar annulus of female with ventral hump. Abdominal T3–T5 covered with conspicuous, erect pubescence; T7 larger than T5 and T6 in lateral view and with a patch of recumbent pubescence ventrolaterally.

KEY TO GENERA AND SPECIES OF  
DALLATORRELLINAE

1. Body entirely yellow to red-brown. Flagellum long and slender, F1 about 4 times as long as wide at midpoint; flagellomeres cylindrical. Eyes distinctly shorter than height of malar space (fig. 1) and protruding laterally, but not distinctly beyond temple (fig. 2). Clypeus only slightly emarginated anteriorly (fig. 1). Foveate sculpture absent or almost absent from head, pronotum, and mesoscutum (figs. 1–3). Lateral pronotal carina meeting pronotal crest dorsally; dorsal pronotal area behind pronotal crest indis-

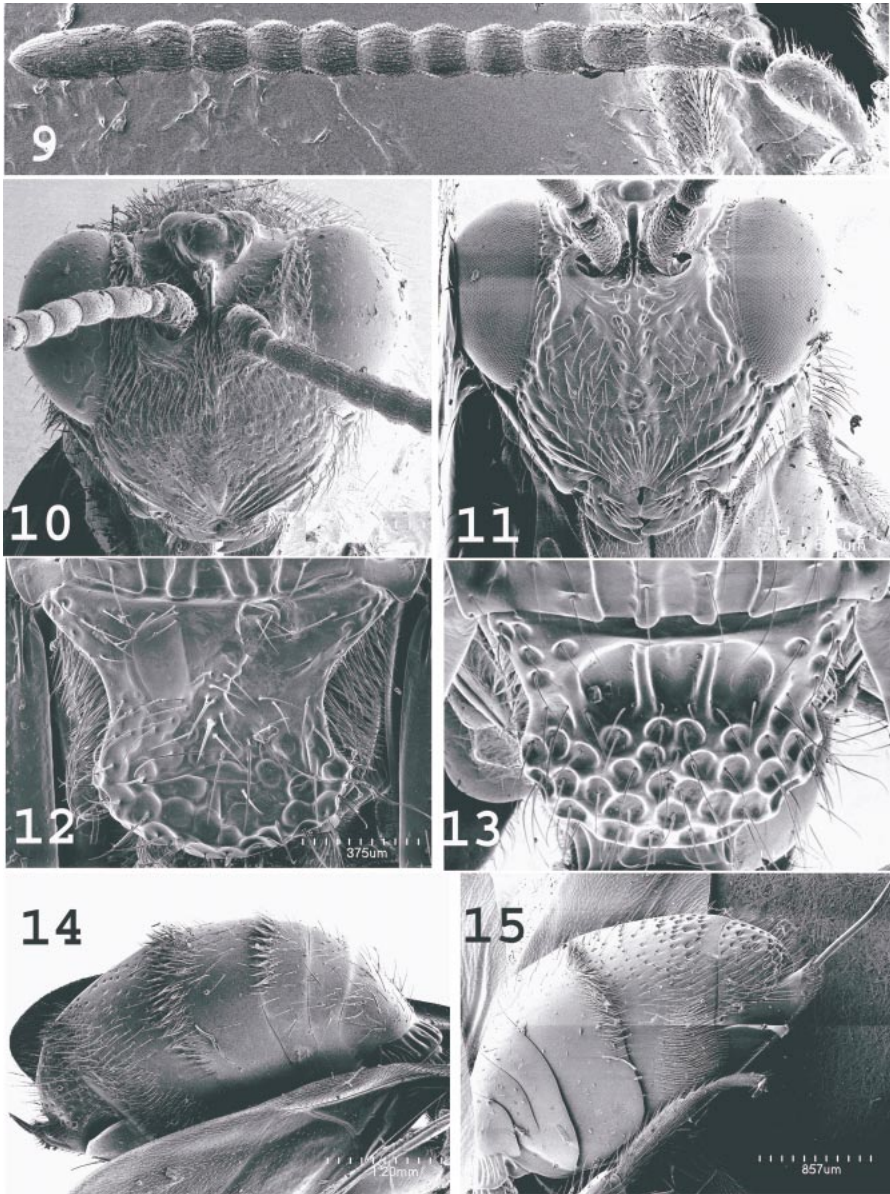


Figs. 1–8. 1–5, 7. *Mesocynips insignis*. 1. Head in frontal view; 2. Head and pronotum in dorsal view; 3. Mesosoma in lateral view; 4. Posterior part of mesoscutum and mesoscutellum in dorsal view; 5. Metatibia in laterodorsal view; 7. Forewing. 6, 8: *Dallatorrella albata*. 6. Metatibia in laterodorsal view; 8. Forewing.

tinct (fig. 2). Parascutal carinae of mesoscutum posterolaterally not produced, smooth and broadly rounded, scutellar sulcus divided into two foveae by median carina, mesoscutellum sloped laterally and posteriorly, dorsal surface transversely costate and lacking foveate structure (fig. 4). Metapleural sulcus abruptly bent at middle, metepisternum subrectangular (fig. 3).  $M+Cu_1$  of forewing straight, diverging from  $R+Sc$  at the base and not curved to-

ward  $R+Sc$  medially (fig. 7). Procoxa laterally without a vertical carina. T7–T8 fused .....

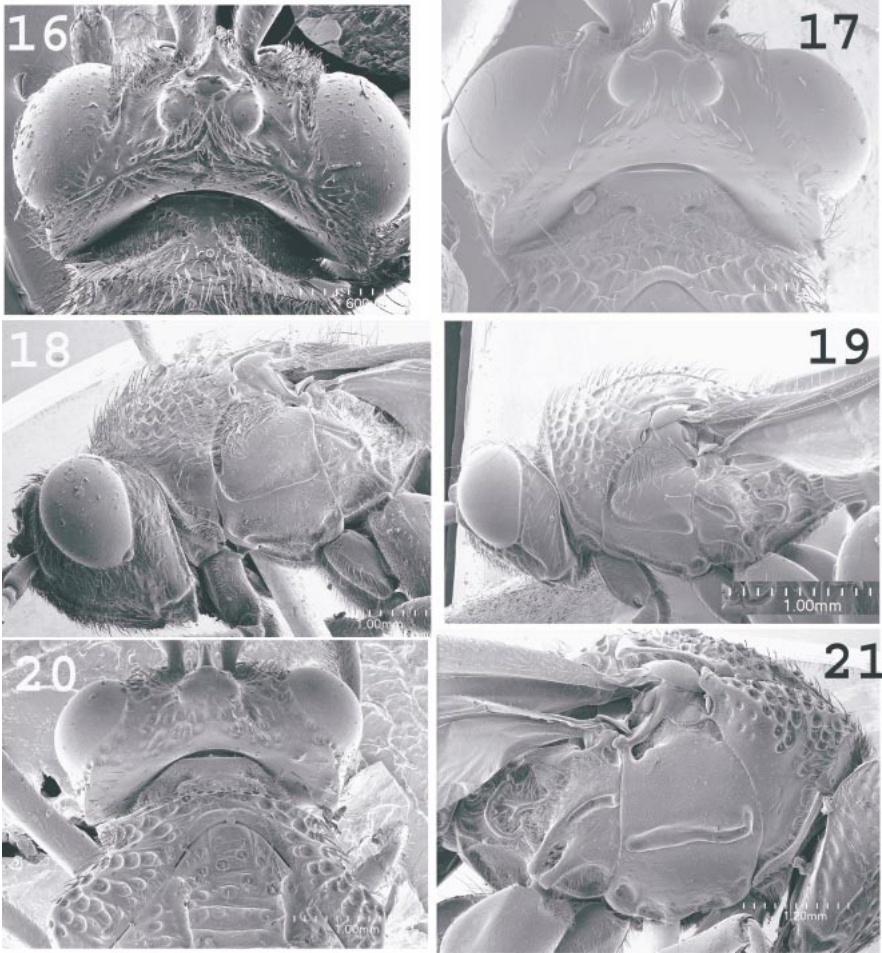
- ..... *Mesocynips insignis* (Smith)  
 — Body usually entirely black, or at least mesosoma black. Flagellum short and stout, F1 at most 1.7 times as long as wide at midpoint; flagellomeres distinctly constricted basally and apically (fig. 9). Eyes at least as long as height of malar space (e.g., figs. 10, 11) and distinctly protruding



Figs. 9–15. 9, 10, 12, and 14: *Dallatorrella albata*. 9. Female antenna. 10. Head in frontal view; 12, Mesoscutellum; 14. Metasoma in lateral view. 11, 13, 15: *Dallatorrella maculata*. 11. Head in frontal view; 13, Mesoscutellum; 15. Metasoma in lateral view.

laterally beyond temple (e.g., fig. 20). Clypeus anteriorly with a deep, broad triangular emargination (figs. 10, 11, 22, 23, 35–37). Foveate sculpture present on lower face, lateral surfaces of pronotum, mesoscutum, and scutellum (e.g., figs. 10–13). Lateral pronotal carina not meeting pronotal crest dorsally; dorsal pronotal

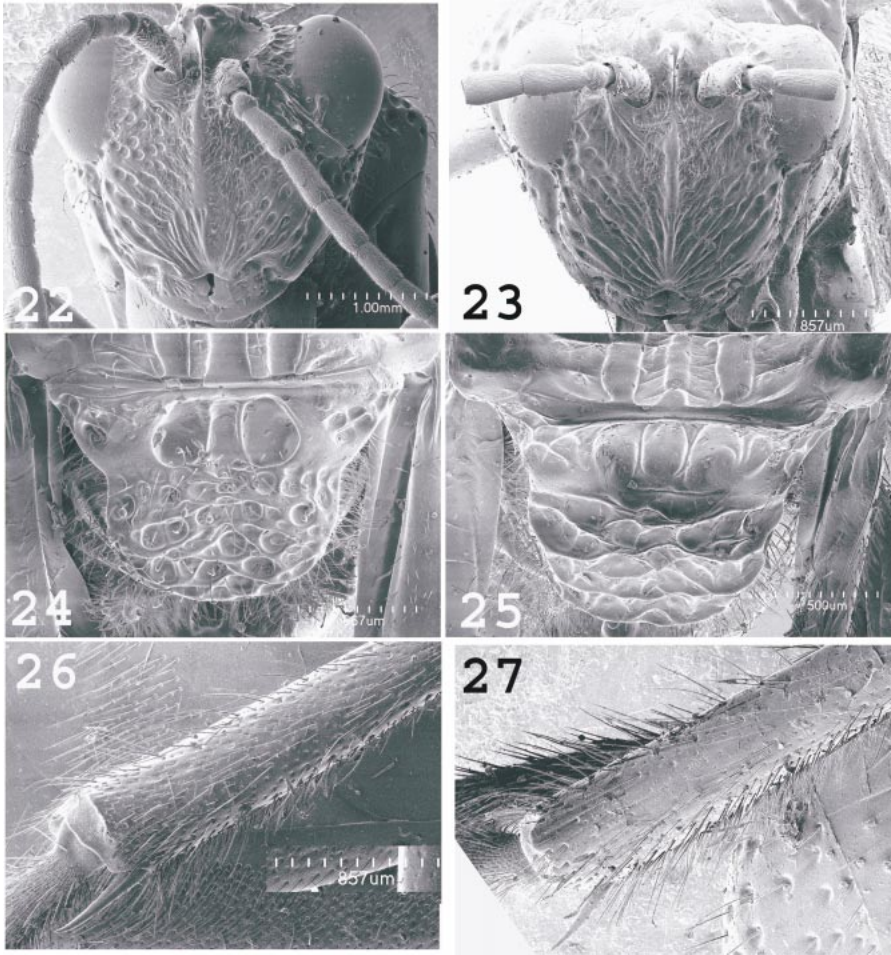
area behind pronotal crest distinct (figs. 17, 20). Parascutal carinae posterolaterally distinctly produced into a more or less triangular process (e.g., figs. 12, 13, 24, 25). Scutellar sulcus divided into several foveae by two or more longitudinal carinae. Mesocutellum at least raised laterally and sometimes also posteriorly; dorsal surface



Figs. 16–21. 16, 18: *Dallatorrella albata*. 16. Vertex; 18. Head and mesosoma in lateral view. 17, 19: *Dallatorrella maculata*. 17. Vertex; 19. Head and mesosoma in lateral view. 20, 21: *Dallatorrella maxima*. 20. Head and pronotum in dorsal view; 21. Mesosoma in lateral view.

- entirely foveate-reticulate or foveate-rugose and without transverse costae (e.g., figs. 12, 13). Metapleural sulcus slightly and evenly curved, metepisternum subtriangular (figs. 18, 19, 21).  $M+Cu_1$  of forewing run almost parallel to  $R+Sc$  basally and curved abruptly from  $R+Sc$  apically (fig. 8). Procoxa laterally with a vertical carina. T7–T8 not fused . . . . . *Dallatorrella*, 2
2. Median frontal carina distinctly percurrent to clypeus in lower face (figs. 22, 23). Pronotum strongly expanded posterolaterally (fig. 20). Posterolateral projection of parascutal carina apically rounded (figs. 24, 25). Mesosubpleuron in lateral view ventrally projected into a triangular process.

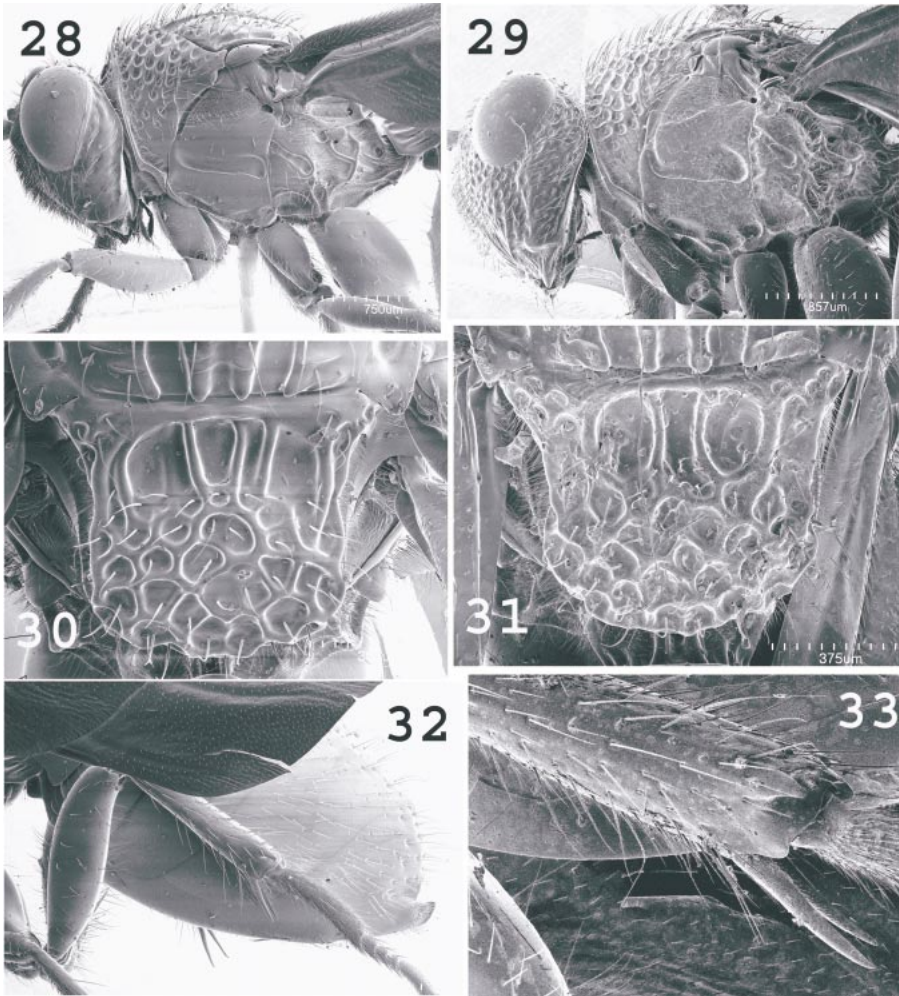
- Metepisternum with extra process laterad to metacoxal foramen, anterior to the prominent process that extends from metapleural carina (fig. 21). Apical process of metatibia absent or reduced, short and apically rounded (figs. 26, 27) . . . . . 3
- Median frontal carina not percurrent to clypeus, continuous at most to the middle of lower face. Pronotum not expanded posterolaterally. Posterolateral projection of parascutal carina apically angular (figs. 12, 13, 30, 31). Mesosubpleuron in lateral view nearly straight, not ventrally projected into triangular process. Metepisternum without an extra process laterad to metacoxal foramen, anterior to the prominent process that extends from metapleural ca-



Figs. 22–27. 22, 24, 26: *Dallatorrella maxima*. 22. Head in frontal view; 24. Mesoscutellum; 26. Metatibia in laterodorsal view. 23, 25, 27: *Dallatorrella pulla*. 23. Head in frontal view; 25. Mesoscutellum; 27. Metatibia in laterodorsal view.

- rina. Apical process of metatibia long and pointed apically (figs. 32, 33) . . . . . 4
- 3. Radiate-carinate sculpture present on almost entire lower face (fig. 23). Mesoscutellum transversely rugose and without distinct foveae (fig. 25). Wings ferruginous. Apical metatibial process present (fig. 27) . . . . . *Dallatorrella pulla*, new species
- Radiate-carinate sculpture present only on ventral one-third of lower face (fig. 22). Mesoscutellum distinctly foveate and without distinct transverse sculpture (fig. 24). Forewing with a wide band across middle and along outer margin, respectively, and hind wing with basal half transparent and distal half ferruginous except tip pale. Apical metatibial process absent (fig. 26) . . . . . *Dallatorrella maxima*, new species
- 4. Forewing with large, contrasting macula toward tip. Female metasoma dorsally with a band of dense hairs along posterior margin of T6 (figs. 14, 15) . . . . . 5
- Wings transparent or evenly ferruginous; forewing sometimes with darker areas, but they are never contrastingly so. Female metasoma dorsally without a band of dense hairs along posterior margin of T6 (fig. 30) . . . . . 6
- 5. Vertex (fig. 15), lower face (fig. 9), and pronotum (fig. 17) sparsely pubescent. Mesoscutellum distinctly narrower across scutellar sulcus than behind (fig. 12). Axillar area without conspicuous hair tuft (fig.

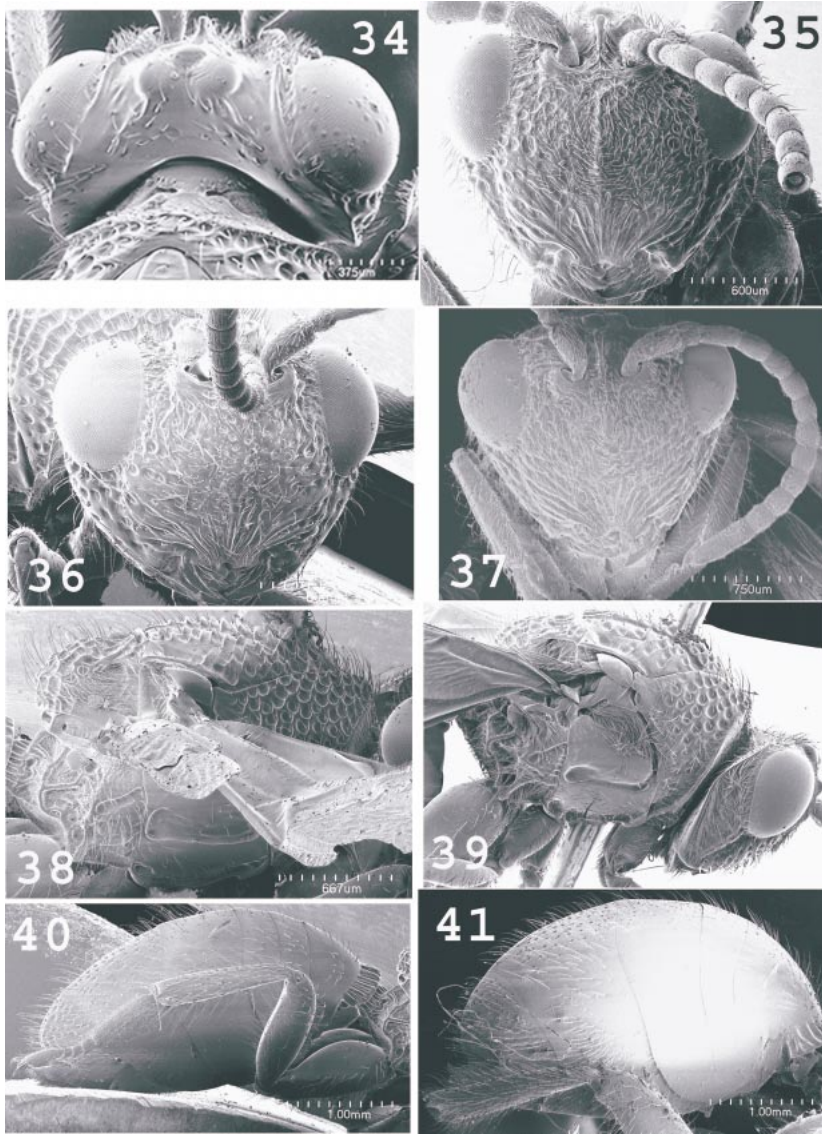




Figs. 28–33. 28, 30, 32: *Dallatorrella ronquisti*. 28. Head and mesosoma in lateral view; 30. Mesoscutellum; 32. Mesosoma and metatibia in lateral view. 29, 31, 33: *Dallatorrella sinica*. 29. Head and mesosoma in lateral view; 31. Mesoscutellum; 33. Metatibia in lateral view.

11). Female metasoma devoid of hairs on T3–T5, with only a band of dense hairs dorsally along posterior margin of T6; T3 only slightly longer than T4 along a lateral median line (fig. 13) . . . . .  
 . . . . *Dallatorrella maculata*, new species  
 — Vertex (fig. 14), lower face (fig. 8), and pronotum densely pubescent. Mesoscutellum only slightly narrower across scutellar sulcus than behind (fig. 13). Axillar area with conspicuous hair tuft (fig. 10). Female metasoma with more or less dense hairs on all terga, dorsally with a band of dense hairs along posterior margin of T5–T6; T3 distinctly longer than T4 along a lateral

median line (fig. 12) . . . . .  
 . . . . . *Dallatorrella albata* (Weld, 1944)  
 6. Face and gena orange. Lower face glabrate-punctate with sparse pubescence (fig. 36). Scutellar sulcus subdivided by three or more longitudinal carinae. Lateroposterior process of parascutal carina apically bent ventrally. Metasoma bright yellow . . . .  
*Dallatorrella rubriventris* Kieffer, 1911  
 — Face and gena black to dark brown. Lower face foveate and punctate with dense pubescence (figs. 28, 29, 35, 37). Scutellar sulcus subdivided by two submedian longitudinal carinae. Lateroposterior process of parascutal carina apically not bent ven-



Figs. 34–41. 34. *Dallatorrella ronquisti*, head in dorsal view. 35. *Dallatorrella sinica*, head in front view. 36, 38, 40: *Dallatorrella rubriventris*. 36. Head in frontal view; 38. Mesosoma in lateral view; 40. Metasoma in lateral view. 37, 39, 41: *Dallatorrella carinifrons*. 37. Head in front view; 39. Mesosoma in lateral view; 41. Metasoma in lateral view.

trally. Metasoma brown to dark brown . . . . . 7  
 7. Eyes prominent, 1.5 times as long as malar space (fig. 28). Mesoscutellum nearly truncate posteriorly (fig. 30). Metasoma light brown . . . . .  
 . . . . . *Dallatorrella ronquisti*, new species  
 — Eyes less prominent, 1.2 times as long as ma-

lar space (figs. 35, 37). Mesoscutellum broadly rounded posteriorly (fig. 31). Metasoma dark brown to black . . . . . 8  
 8. Genae in frontal view almost straight (fig. 37). Median frontal carina distinctly extended to middle of lower face. Mesoscutellum distinctly narrower across scutellar sulcus than behind. Metasoma

brown .....  
 .... *Dallatorrella carinifrons* (Cameron,  
 1910)

- Genae in frontal view distinctly curved laterally (fig. 35). Median frontal carina extended to lower face, but rather weak, and discontinuous beneath antennal sockets (fig. 35). Mesoscutellum across scutellar sulcus not distinctly narrower than behind (fig. 31). Metasoma black .....  
 ..... *Dallatorrella sinica*, new species

#### *Mesocynips* Cameron

*Mesocynips* Cameron, 1903: 91. Type species: *Mesocynips insignis* Cameron, 1903 (= *Cynips insignis* Smith, 1858) by monotypy.

DIAGNOSIS: Body entirely yellowish brown. Foveate sculpture absent or almost absent from head and pronotum. Flagellum long and slender, F1 about 4 times as long as wide at midpoint; flagellomeres cylindrical, swollen distally. Eyes shorter than height of malar space and laterally protruding, but not distinctly beyond temple. Lower face and lateral surface of pronotum almost entirely glabrous. Clypeus strongly projected into upturned trapezoid, anteriorly only slightly emarginated (fig. 1). Occipital carina present only ventrally; dorsally carina reaches only lower margin of compound eye. Parascutal carinae posterolaterally smoothly curved. Scutellar sulcus divided into two foveae by median carina. Scutellum transversely costulate, falling gradually laterally as well as posteriorly. Metapleural sulcus abruptly bent at middle, metepisternum subrectangular.  $M+Cu_1$  of forewing straight, not curved toward  $R+Sc$  (fig. 7). Procoxa laterally without a vertical carina. T7–T8 fused.

COMMENTS: Ronquist (1995a) listed a slightly and evenly curved metapleural sulcus and a subtriangular metepisternum as a synapomorphy for the family of Liopteridae. I have examined the four specimens of the only species of *Mesocynips* available to me and found, however, that the genus has a medially abruptly bent metapleural sulcus and a subrectangular metepisternum, a feature found only in the Iballiidae among the Cynipoidea (Ronquist, 1995b). Since the monophyly of the Liopteridae is well supported (Ronquist, 1995a), this feature has apparently developed independently in the two lineages.

#### *Mesocynips insignis* (Smith)

Figures 1–5, 7

*Cynips insignis* Smith, 1858: 117, ♀. Neotype (designated below).

*Mesocynips insignis* Cameron, 1903: 91, ♀. Objective synonym of *C. insignis* Smith (through neotype designation: see Comments below).

*Mesocynips insignis* (Smith); Weld, 1952: 161. Ronquist, 1995b: 38–40.

DESCRIPTION: Length: ♂ 9.0 mm, ♀ 9.0–14.0 mm. Body entirely yellow to yellowish brown. Basal half of wings clear and distal half ferruginous. The female specimen from the Philippines is darker on distal half of wings.

Face, gena, and vertex glabrous and sparsely punctate with hairs. Eyes only about two-thirds as long as height of malar space, slightly protruding laterally beyond temple. Median frontal carina present only as small triangular, lobular process between antennal sockets and completely lacking in lower face. Vertex glabrous, posteriorly with a rim of sparse long hairs. Occiput glabrous, laterally with sparse long hairs. Lateral pronotal carinae dorsally meeting pronotal crest, thus medially disconnecting lateral pronotal areas. Lateral surface of pronotum glabrous except elevated dorsal part transversely costate. Mesoscutum sparsely punctate with a pressed long hair and strongly costulate, except in a narrow glabrous anterolateral strip and a glabrous area laterad to parapsidal signum. Scutellum transversely costulate laterally with glabrate area. Mesopleuron glabrous; mesopleural impression only vaguely visible anteriorly and shallowly present posteriorly. Mesopleural triangle glabrous with sparse, short hairs. Process produced from metapleural carina laterad to metacoxal foramen short, slightly extended beyond ventroposterior margin of metepisternum. Metepisternum glabrous, sparsely punctate with hairs. Lateral propodeal carina raised dorsally into a laminate structure ending abruptly posteriorly. Apical metatibial process apically truncate, by far not reaching apex of metatibia.

DISTRIBUTION: Borneo and the Philippines (Mindanao).

MATERIAL EXAMINED: 3 ♀ 1 ♂. NHM: 1 ♀ (Type, #7.45.), Borneo; USNM: 1 ♀ 1 ♂, Borneo; ZLMU: 1 ♀, Philippines: Mindanao.

NEOTYPE DESIGNATION: First described by Smith (1858), the species was redescribed as *Mesocynips insignis* by Cameron (1903) based on specimens from the type locality. The latter author realized the possible synonymy between Smith's species and his "new species", and thus gave his species the same specific epithet as Smith's. The synonymy was formally established by Weld (1950).

The type of *Cynips insignis* Smith, 1858 could not be located and has apparently been lost. It is not in the Oxford University Museum (Ronquist, 1995b), nor in the Natural History Museum in London (Ronquist, 1995b, S. Lewis, personal commun.). Therefore, the designation of a neotype becomes necessary according to the ICZN: Article 75.3.4. (ICZN, 1999).

The type specimen of *Mesocynips insignis* Cameron, 1903 is hereby designated as the neotype of *Cynips insignis* Smith, 1858. It matches well with Smith's (1858) description, is from the same localities as *Cynipis insignis*, and is in good condition. The specimen is deposited in the Natural History Museum in London (Type, #7.45) and has labels reading "Type (in red circle)", "B. M. Type HYM 7.45", "*Mesocynips insignis* Cam. Type, Borneo [in Cameron's handwriting]", "Cameron Coll. 1903-121", and the neotype designation label of the current author (blue).

COMMENT ON ADDITIONAL MATERIAL: The male specimen from USNM is labeled as "type" (# 9939) and indicated as female. It bears Cameron's handwritten identification label. Weld (1950) stated that this specimen is a male "cotype" "sent by the Sarawak Museum in July 1906". However, in Cameron's (1903) original description of *M. insignis* he did not describe the male, which was subsequently described two years later (Cameron, 1905). Therefore, the specimen in USNM cannot be a type.

#### Genus *Dallatorrella* Kieffer

*Dallatorrella* Kieffer, 1911:244. Type species *Dallatorrella rubriventris* Kieffer, 1911, by monotypy.

DIAGNOSIS: Body usually entirely black to dark brown or at least so on mesosoma. Foveate sculpture present on lower face, lateral

surfaces of pronotum, and scutellum. Antenna short in both sexes, shorter than the length of head and mesosoma combined; F1 at most 1.7 times as long as wide at midpoint; flagellomeres distinctly swollen submedially. Eyes distinctly protruding laterally beyond temple. Parascutal carinae posterolaterally produced into a triangular process. Scuto-scutellar sulcus divided by two or more submedian carinae into three or more foveae; median carina absent. Mesoscutellum at least raised laterally and sometimes also posteriorly; dorsal surface entirely foveate-reticulate or foveate-rugose and without transverse costae. Metapleural sulcus straight to slightly bent at middle, metepisternum subtriangular.  $M+Cu_1$  of forewing run almost parallel basally to  $R+Sc$  before turning away abruptly from the latter apically. Procoxa anterolaterally with a vertical carina (figs. 18, 19, 28, 29). Median, ventral hump on petiolar annulus present in females but absent in males. T7-T8 not fused with each other.

#### *Dallatorrella albata* (Weld)

Figures 6, 8-10, 12, 14, 16, 18

*Mesocynips albata* Weld, 1944: 55, ♀.

*Dallatorrella albata* (Weld); Ronquist, 1995b: 43.

DESCRIPTION: Length: ♀ 9.0 mm. Body almost entirely black, except antennae, legs, and metasoma ventrally dark brown. Forewing clear with a distal, ferruginous macula, and hind wing entirely transparent.

Face between eyes and vertex densely punctate with long hairs; antennal scrobes glabrous; lower face glabrate, with sparse hairs. Median frontal carina almost percurrent, indistinct only shortly at middle of lower face, and strongly raised into a laminate, apically round triangular process between ocellar plate and antennal sockets. Eyes prominent, strongly protruding beyond temple and 1.2 times as long as height of malar space. Gena and malar space glabrate and sparsely punctate with hair; malar space with a vertical, almost linear shallow impression beneath eye. Clypeus laterally not curved and anteroventrally with a broad triangular emargination, with radiating striation continued to lower face. Lateral pronotal carina slightly not reaching pronotal crest dorso-medially. Lateral pronotal area mostly fove-

ate-reticulate except ventral one-fourth or so glabrous; lateroventral margin roundly emarginated. Mesoscutum strongly costulate transversely and sparsely foveate with long hairs; median mesoscutal impression only present as a short impression posteriorly; notauli percurrent, diverging anteriorly; parascutal carina conspicuously raised and produced posteriorly into a triangle. Lateral margin of axilla raised. Lateral bar laterally curved inward, shortest distance between lateral margins of lateral bar distinctly narrower than maximal width of scutellum behind. Scutellar sulcus divided by two submedian carinae into three large foveae. Dorsal surface of foveate-reticulate with sparse long hairs. In dorsal view, scutellum broadly rounded posteriorly. Axillula with conspicuous white pubescence. Mesopleuron glabrous; mesopleural triangle with conspicuous white pubescence. Metepisternum glabrous, process ventrally projected from metapleural carina small. Lateral propodeal carina strongly raised anterodorsally into laminate process. Metasomal T3 distinctly longer than T4 along a dorsal median line; all postpetiolar metasomal terga with more or less dense hairs; T5–T6 dorsally with a band of dense hairs along posterior margin. Apical metatibial process apically tapering, reaching slightly beyond apex of metatibia. Pubescence sparse on femurs and conspicuous on tibiae and tarsomeres.

DIAGNOSIS: *Dallatorrella albata* is similar to *D. maculata*, can be distinguished from the latter by (1) female metasoma with more or less dense hairs on all terga, (2) dorsally with a band of dense hairs along posterior margin of T5–T6, and (3) T3 distinctly longer than T4 along a lateral median line. In fact, the species can be easily distinguished from all other species by its band of dense, long hairs along posterior margin of metasomal T5–T6.

DISTRIBUTION: Philippines: Mindanao.

MATERIAL EXAMINED: 2♀. USNM: 1♀ (Type, #56810), Mindanao: Surigao; 1♀ (NHM), locality as type.

*Dallatorrella carinifrons* (Cameron)

Figures 37, 39, 41

*Paramblynotus carinifrons* Cameron, 1910a: 132, ♀.

*Dallatorrella carinifrons* (Cameron); Weld, 1952: 162. Ronquist, 1995b: 42.

DESCRIPTION: Length: ♀ 9.0 mm. Head and mesosoma including legs entirely black, metasoma brown. Wings ferruginous and somewhat lighter toward base.

Face, most of gena, and vertex moderately punctate with long hairs; antennal scrobes glabrous; lower face less hairy, with distinct, extensive radiating striations that reach laterally lower margin of eye. Median frontal carina almost percurrent, discontinued only at middle of lower face, and strongly raised into a laminate, dorsally somewhat flattened triangular process between ocellar plate and antennal sockets. Eyes prominent, strongly protruding beyond temple and 1.2 times as long as height of malar space. Malar space glabrate and sparsely punctate with hairs; malar space with a distinct vertical, almost linear impression beneath eye. Clypeus laterally distinctly incised, anteroventrally with a broad triangular emargination, and with radiating striation continued to lower face. Lateral pronotal carina laterally strong and crest-like, dorsomedially not quite reaching pronotal crest. Lateral pronotal area mostly foveate-reticulate except a small area ventrally glabrate; lateroventral margin straight. Mesoscutum strongly costulate transversely and sparsely foveate with long hairs; median mesoscutal impression only present as a short impression posteriorly; notauli percurrent, diverging anteriorly; parascutal carina conspicuously raised and produced posteriorly into a triangle. Lateral margin of axilla raised. Lateral bar broad, laterally almost straight, shortest distance between lateral margins of lateral bar as wide as maximal width of scutellum behind. Scutellar sulcus subdivided by two submedian carinae into three large foveae. Dorsal surface of scutellum foveate-reticulate with sparse long hairs. In dorsal view, scutellum broadly rounded posteriorly. Axillula with conspicuous white pubescence. Mesopleuron glabrous; mesopleural triangle with conspicuous white pubescence. Metepisternum punctate with hairs in upper part and strongly depressed with conspicuous pubescence in lower part, process ventrally projected from metapleural carina well developed. Lateral propodeal carina evenly raised

and dorsally with dense pubescence. Metasomal T3 distinctly longer than T4 along dorsal median line; T3-T6 with only sparse long hairs dorsally, T7-T8 with more or less evenly distributed long hairs, and tend to be congregated into a medial band lateroventrally on T7. Apical metatibial process tapering apically, reaching slightly beyond apex of metatibia. Pubescence sparse on femurs and conspicuous on tibiae and tarsomeres.

DIAGNOSIS: *D. carinifrons* is very similar to *D. sinica*, and can be distinguished from the latter by the following characters (1) gena in front view almost straight (fig. 37), (2) median frontal carina continuous to middle of lower face, and (3) lateral margin of axilla laterally distinctly narrower than scutellum behind. In addition, metasoma of *D. carinifrons* is light brown, differing from *D. sinica*, which has black metasoma. The last flagellomere of female antennae has a more or less distinct segmentation.

DISTRIBUTION: Malaysia: Borneo; Singapore.

MATERIAL EXAMINED: 4♀: 1♀ (holotype, NHM, #7.10.), Malaysia: Kuching; 1♀ (AEI), Malaysia: Negri S., Pasoh Forest Reserve; 1♀ (NHM), Sarawak: Mt. Matang; 1♀ (NHM), Singapore.

*Dallatorrella maculata* Liu, new species

Figures 11, 13, 15, 17, 19

DESCRIPTION: Length: ♀ 6.5–10.0 mm. Body almost entirely black, except metasoma ventrally somewhat brownish; fore- and middle legs dark brown and hindlegs black. Wings transparent, forewing with a distinctly contrasting, ferruginous macula distally.

Vertex, face, and gena glabrous; vertex and gena sparsely punctate with long hairs along margins and lower face evenly punctate with hairs; antennal scrobes glabrous. Median frontal carina present only as a linear, slight elevation in lower face and strongly raised into a prominent laminate, dorsally somewhat flattened triangular process between ocellar plate and antennal sockets. Eyes prominent, strongly protruding beyond temple and 1.5 times as long as height of malar space. Malar space glabrate and sparsely punctate with hair, and with a distinct vertical, almost linear impression be-

neath eye. Clypeus laterally distinctly incised, anteroventrally with a broad triangular emargination, and with radiating striation. Lateral pronotal carina distinct, but not crest-like, dorsomedially not reaching pronotal crest. Lateral pronotal area mostly foveate-reticulate except a small area ventrally glabrate; lateroventral margin straight. Mesoscutum strongly costulate transversely within area delimited by notauli; costulae in area laterad to notauli diminutive; whole surface of mesoscutum sparsely, weakly foveate with long hairs; median mesoscutal impression only present as a short impression posteriorly; notauli percurrent, diverging anteriorly; parascutal carina conspicuously raised and produced posteriorly into a nearly right angle. Lateral margin of axilla raised. Lateral bar broad with foveae, laterally slightly curved inward, shortest distance between lateral margins of lateral bars slightly smaller than maximal width of scutellum behind. Scutellar sulcus subdivided by two submedian carinae into three large foveae. Dorsal surface of scutellum foveate-reticulate with sparse, long hair. In dorsal view, scutellum broadly rounded posteriorly. Axillula with conspicuous white pubescence. Mesopleuron glabrous; mesopleural triangle with conspicuous white pubescence. Metepisternum glabrous; metapleural carina projected ventrally into a robust process and posterior to it present an additional, less prominent process. Lateral propodeal carina slightly raised anterodorsally. Metasomal T3 longer than T4 along dorsal median line; T6 as large as T4 and T5 combined, T7 posteriorly oblique and broadly curved, about 1.25 times as long as T6 and 2 times as long as T8. T3-T5 glabrous; T6 largely glabrous with a conspicuous band of pubescence dorsolaterally along posterior margin; T7-T8 more or less evenly punctate with long hair; T7 also with a conspicuous patch of pubescence lateroventrally. Apical metatibial process tapering apically, distinctly reaching beyond apex of metatibia. Pubescence sparse on femurs and conspicuous on tibiae and tarsomeres.

DIAGNOSIS: This new species is similar to *D. albata*, differing from other species of the genus in that both species have distally maculated forewing and T6 of female metasoma dorsally with a band of dense pubescence

along posterior margin. The new species can be further separated from *D. albata* by lack of pubescence on T3–T5 of female metasoma, and T3 being only slightly longer than T4 along a lateral median line.

Male unknown.

DISTRIBUTION: Borneo: Sulawesi.

MATERIAL EXAMINED: Holotype ♀, Sulawesi: Tengah, Mt. Morowali, Ranu River Area, 27 January–20 April 1980, M. Brendell coll. (NHM, London). Paratypes 6 ♀: 5 ♀, data as holotype (NHM, London); 1 ♀, Indonesia: Moluccas Bacan Island, Kampung, Wayamiga, VII-27–31 July 1981, A. C. Messer coll. (USNM, Washington, DC).

ADDITIONAL MATERIAL: 1 ♀, no collection data available.

ETYMOLOGY: The name *maculata* is from Latin, meaning spotted.

*Dallatorrella maxima* Liu, new species

Figures 20–22, 24, 26

DESCRIPTION: Length: ♀ 14.0 mm. Body and all legs entirely black, eyes brown. Wings transparent, forewing with a broad distinct ferruginous band across the middle and along outer margin.

Antenna slender in comparison with most species of the genus; median flagellomeres not distinctly constricted basally and apically. Vertex glabrous with shallow foveae behind ocellar plate and a few less distinct foveae along eye. Gena glabrous with evenly distributed shallow foveae, with or without hair. Upper face areolate-rugose except antennal scrobe glabrous. Lower face evenly foveate with dense pubescence in upper part and with radiating striation running from clypeus in lower one-third. Median frontal carina percurrent and strongly raised into a prominent laminate, dorsally somewhat flattened triangular process between ocellar plate and antennal sockets. Eyes prominent, strongly protruding beyond temple and slightly longer than height of malar space. Malar space glabrate and sparsely punctate with hair, with a distinct vertical, almost linear impression beneath eye. Clypeus laterally distinctly incised, anteroventrally with a broad triangular emargination and with radiating striation. Pronotum strongly expanded posterolaterally to form a wide, flat dorsal

area. Lateral pronotal carina distinct, dorsally widened ventrally and raised dorsally into a submedial lobular structure, and dorsomedially nearly reaching pronotal crest. Lateral pronotal area foveate-reticulate anterodorsally and glabrous lateroposteriorly; lateroventral margin straight. Mesoscutum strongly transversely costulate and foveate; foveae less distinct posteriorly; median mesoscutal impression only present as a short impression posteriorly; notauli percurrent, moderately diverging anteriorly; parascutal carina conspicuously raised and posteriorly rounded, not produced into an angle. Lateral margin of axilla not raised. Lateral bar broad and glabrous, laterally converging posteriorly, shortest distance between lateral margins of lateral bars distinctly larger than maximal width of scutellum. Scutellar sulcus subdivided by two longitudinal submedian carinae into three foveae. Dorsal surface of scutellum foveate-reticulate with sparse long hair; foveae more or less set in rows. In dorsal view, scutellum rounded posteriorly. Axillula without conspicuous pubescence. Mesopleuron glabrous; mesopleural triangle reduced into a narrow strip, without conspicuous pubescence. Metepisternum glabrous; metapleural carina projected ventrally into a robust process and posterior to it present an additional, less prominent process. Lateral propodeal carina dorsomedially strongly raised into a conspicuous hump and densely pubescent. Metasomal T3 distinctly longer than T4 along dorsal median line; T6 shorter than T4 and T5 combined, T7 posteriorly oblique and almost straight, twice as long as either T6 or T8. T3–T4 glabrous. T5 sparsely, finely punctate. T6 densely, finely punctate with pubescence dorsolaterally in anterior two-thirds. T7 densely and finely punctate with pubescence anteriorly. T8 sparsely and coarsely punctate with pubescence, lateroventrally with a conspicuous patch of white pubescence. Apical metatibial process absent, only indicated by a long, slightly elevated transverse carina. Pubescence sparse on femurs and conspicuous on tibiae and tarsomeres.

DIAGNOSIS: This new species and *D. pulla* are similar to each other and differ from all other species of the genus in having (1) median frontal carina distinctly extended to

clypeus in lower face (fig. 22), (2) pronotum strongly expanded posterolaterally (fig. 20), (3) mesosubpleuron ventrally projected into a triangular process, and (4) metepisternum with an extra process laterad to metacoxal foramen anterior to the prominent process extended from metapleural carina. *D. maxima* differs from *D. pulla* by having (1) lower face densely punctate with pubescence in upper half, (2) Mesoscutellum distinctly foveate-reticulate; without obvious transverse rugosity (fig. 24), (3) apical process of metatibia absent (fig. 26), and (4) Forewing with a wide band across middle and along outer margin, respectively, and hind wing with basal half transparent and distal half ferruginous except tip pale.

Male unknown.

DISTRIBUTION: Laos.

MATERIAL EXAMINED: Holotype ♀, Laos: Ban Van Heue, 20 km east of Phou-kow-kuei, 15–31 June 1965, native collector coll. (BPBM).

ETYMOLOGY: The name *maxima* is from Latin, meaning largest.

*Dallatorrella pulla* Liu, new species

Figures 23, 25, 27

DESCRIPTION: Length: ♂ 13.0 mm. Body and all legs almost entirely black, except metasoma slightly brownish ventrally. Wings evenly ferruginous.

Vertex mostly foveate, with small glabrous areas submedially. Gena glabrous with evenly distributed shallow foveae, with or without hair. Upper face areolate-rugose except antennal scrobes glabrous. Lower face with dense pubescence in a triangular area beneath antennal sockets and mostly with strong radiating striation running from clypeus. Median frontal carina percurrent and slightly weakened beneath antennal sockets; strongly raised into a distinct, dorsally rounded process between ocellar plate and antennal sockets; and raised beneath antennal sockets into a prominent ridge diminishing ventrally. Eyes prominent, only moderately protruding beyond temple and slightly longer than height of malar space. Malar space glabrate and sparsely punctate with hair, with a distinct, vertical, almost linear impression beneath eye. Clypeus laterally distinctly in-

cised, anteroventrally with a broad triangular emargination and with radiating striation. Pronotum strongly expanded posterolaterally to form a wide, flat dorsal area. Lateral pronotal carina distinct, dorsomedially not reaching pronotal crest; dorsally raised into a submedial lobular structure and thickened ventrally. Lateral pronotal area foveate-reticulate anterodorsally and glabrous lateroposteriorly; lateroventral margin straight. Mesoscutum strongly transversely costulate and mostly with foveae set in rows; median mesoscutal impression only present as a short impression posteriorly; notauli percurrent, moderately diverging anteriorly; parascutal carina conspicuously raised and posteriorly rounded, not produced into an angle. Lateral margin of axilla not raised. Lateral bar broad, with large fovea, laterally converging posteriorly, shortest distance between lateral margins of lateral bars distinctly larger than maximal width of scutellum. Scutellar sulcus subdivided by two submedian carinae into three foveae. Dorsal surface of scutellum scabrous to foveate-reticulate with sparse long hairs; foveae more or less set in rows without distinct division. In dorsal view, scutellum rounded posteriorly. Axillula without conspicuous pubescence. Mesopleuron glabrous; mesopleural triangle reduced into a narrow strip, without conspicuous pubescence. Metepisternum glabrous; metapleural carina projected ventrally into a robust process and posterior to it present an additional, less prominent process. Lateral propodeal carina evenly raised dorsally into a ridge and pubescent along base. Apical metatibial process present, but only as a blunt, short process. Pubescence sparse on femurs and conspicuous on tibiae and tarsomeres.

DIAGNOSIS: The new species is similar to *D. maxima* (see above), but differs from the latter in (1) lower face nearly entirely radiate-carinate, (2) forewing evenly ferruginous, mesoscutellum distinctly foveate-reticulate and not distinctly transversely rugose, (3) metatibia with a short, distally rounded apical process, and (4) dorsal surface of mesoscutellum scabrous (fig. 25).

Female unknown.

DISTRIBUTION: Malay.

MATERIAL EXAMINED: Holotype ♂, Malay: Pahang, F.M.S. Fraser's Hill, 4000 ft, 6



March 1946, no data on collector, with an extra label "Ex F.M.S. Museum, B.M. 1955-354" (NHM, London).

ETYMOLOGY: The name *pulla* is from Latin, meaning dark-colored, blackish, grayish black.

*Dallatorrella ronquisti* Liu, new species

Figures 28, 30, 32

DESCRIPTION: Length: ♀ 6.0–9.0 mm. Head and mesosoma black; legs brown to dark brown. Metasoma brown to dark brown. Wings evenly ferruginous.

Vertex glabrous and sparsely punctate with hair. Gena glabrous and shallowly foveate to punctate with hair; face foveate with dense pubescence; antennal scrobe glabrous and relatively densely punctate with hair close to base antennal socket. Median frontal carina strongly raised into a prominent laminate, dorsally slightly flattened and trapezoid (in lateral view) process between ocellar plate and antennal sockets; indistinct in upper lower face and raised to a low ridge ventrally in lower face. Lower face with conspicuous pubescence, which makes sculpture not easily observable. Eyes prominent, strongly protruding beyond temple and 1.5 times as long as height of malar space. Malar space glabrate and sparsely punctate with hair; vertical impression beneath eye absent. Clypeus laterally distinctly incised, anteroventrally with a broad triangular emargination and with radiating striation. Lateral pronotal carina distinct, crest like lateroventrally, dorsomedially not reaching pronotal crest. Lateral pronotal area mostly foveate-reticulate except one third lateroventrally glabrate; lateroventral margin straight. Mesoscutum strongly costulate transversely and sparsely punctate with long hair; median mesoscutal impression only present as a short impression posteriorly; notauli percurrent, strongly diverging anteriorly; parascutal carina conspicuously raised and produced posteriorly into a triangular process. Lateral margin of axilla not raised. Lateral bar moderately wide and longitudinally costate, laterally straight; shortest distance between lateral margins of lateral bars as large as maximal width of scutellum. Scutellar sulcus subdivided by two submedian carinae into three large foveae. Dorsal

surface of scutellum foveate-reticulate with long hair. In dorsal view, scutellum nearly truncate posteriorly, only rounded posterolaterally. Axillula with inconspicuous, whitish pubescence. Mesopleuron glabrous; mesopleural triangle with inconspicuous whitish pubescence. Metepisternum glabrous; metapleural carina projected ventrally into a robust, short process. Lateral propodeal carina raised dorsally throughout. Metasomal T3 longer than T4 along dorsal median line. T6 slightly shorter than T4 and T5 combined. T7 posteriorly oblique and nearly straight, slightly longer than T6 and about 1.4 times as long as T8. T3–T6 sparsely punctate with hair laterodorsally and glabrous lateroventrally. T7–T8 evenly, sparsely punctate with long hair. Apical metatibial process apically tapering, not reaching apex of metatibia. Pubescence sparse on femurs and tibiae, conspicuous on tarsomeres.

DIAGNOSIS: The new species is similar to *D. carinifrons*, *D. rubriventris*, and *D. sinica*, but differs from them by having eyes prominent and distinctly longer than malar space (fig. 28), lower part of lateral surface of pronotum glabrous (fig. 28), and mesoscutellum truncate posteriorly (fig. 30).

Male unknown.

DISTRIBUTION: Papua New Guinea.

MATERIAL EXAMINED: Holotype ♀, Papua New Guinea, Bulolo, 21 October 1981, Mani L. A. coll. (NHM, London). Paratypes 4♀: 2♀, data as holotype (NHM, London); 1♀, no collection data available, presumably from Aru (Ronquist, 1995b); 1♀, New Guinea, NE Green River Post, 200 m, Wet Forest, 26 June 1963, S. Straatman coll. (BPBM).

COMMENTS: The paratype in BPBM differs from the other type specimens in that the transverse sculptures on the lateral sides of pronotum are more obvious and the abdomen is darker.

ETYMOLOGY: This species is named after F. Ronquist for his contributions to the systematic studies on the Liopteridae, which facilitated this present work and my other ongoing researches on the family.

*Dallatorrella rubriventris* Kieffer, 1911

Figures 23–25, 38, 40

*Dallatorrella rubriventris* Kieffer, 1911: 244, ♂.

DESCRIPTION: Length: ♂ 5.5–8.0 mm; ♀

5.0–8.0 mm. Head yellow, except vertex dark brown. Mesosoma black; legs black to dark brown. Metasoma yellow. Wings transparent, forewing with a very faint ferruginous mark distally along anterior margin.

Vertex foveate-reticulate with hair. Gena mostly glabrous and shallowly foveate with hair anteriorly and posteriorly; upper face rugose and sparsely pubescent; antennal scrobe glabrous and somewhat punctate with hair close to base antennal socket. Median frontal carina strongly raised into a prominent laminate, dorsally slightly flattened and triangular (in lateral view) process between ocellar plate and antennal sockets, indistinct in upper lower face and distinct in lower part of lower face. Lower face mostly glabrate and relatively densely punctate with hair in upper part and ventrally radiating striate. Eyes prominent, strongly protruding, but not so much beyond temple as in the other congeneric species, 1.2 times as long as height of malar space. Malar space glabrate and sparsely punctate with hair, with very faint vertical impression beneath eye. Clypeus laterally distinctly incised, anteroventrally with a broad triangular emargination, with radiating striation. Lateral pronotal carina distinct, but not crest like lateroventrally, dorso-medially not reaching pronotal crest. Lateral pronotal area almost entirely foveate-reticulate, foveae less prominent lateroventrally; lateroventral margin straight. Mesoscutum strongly costulate transversely and sparsely punctate with long hair; median mesoscutal impression only present as a short impression posteriorly; notauli percurrent, strongly diverging anteriorly; parascutal carina conspicuously raised and produced posteriorly into a triangular process ventrally turned apically. Lateral margin of axilla not raised. Lateral bar moderately wide and foveate, laterally slightly curved inward, shortest distance between lateral margins of lateral bars distinctly smaller than maximal width of scutellum. Scutellar sulcus subdivided by a median and two or more submedian carinae into multiple large foveae. Dorsal surface of scutellum foveate-reticulate with long hair, strongly sloping posteriorly. In dorsal view, scutellum rounded posteriorly. Axillula with inconspicuous whitish pubescence. Mesopleuron glabrous; mesopleural triangle with

sparse pubescence. Metepisternum scabrous; metapleural carina projected ventrally into a robust, short process. Lateral propodeal carina slightly raised dorsally throughout. Metasomal T3 only slightly shorter than T4–T5 combined. T6 slightly longer than T4 and T5 combined. T7 posteriorly oblique and nearly straight, 1.6 as long as T6 and about twice as long as T8. All post petiolar terga dorso-laterally punctate with hair; punctures coarser and denser on T7 and T8. Apical metatibial process apically tapering, distinctly reaching beyond apex of metatibia. Pubescence sparse on femurs and tibiae, denser ventrally, conspicuous on tarsomeres.

**DIAGNOSIS:** The species is most easily distinguished from other species of the genus by its body color pattern and its glabrate-punctate lower face (fig. 36).

**DISTRIBUTION:** Australia.

**MATERIAL EXAMINED:** 3♀5♂: 1♂ (holotype, NHM #7.12.), Australia: New South Wales; 3♂, Australia: New South Wales (MCZ), 1♂, Australia (NHM, London), 3♀, Australia: New South Wales and New Queensland (ANIC).

*Dallatorrella sinica* Liu, new species

Figures 29, 31, 33, 35

**DESCRIPTION:** Length: ♀ 8.0 mm. Body and legs almost entirely black, except metasoma dark brownish ventrally. Wings evenly ferruginous.

Vertex densely foveate with hair, except area continued posteriorly from antennal scrobe glabrous. Gena foveate-punctate with hairs. Upper face more or less scrobiculate with dense pubescence laterad to antennal scrobe. Antennal scrobe mostly glabrous and ventrally with dense pubescence. Median frontal carina extended in lower face to the level of ventral margin of eye, distinctly discontinuous beneath antennal socket, strongly raised into a prominent laminate, dorsally slightly flattened and triangular (in lateral view) process between ocellar plate and antennal sockets. Lower face punctate-foveate with dense pubescence in upper two-thirds and ventrally radiating-striate. Eyes prominent, strongly protruding beyond temple, 1.2 times as long as height of malar space. Malar space punctate-foveate with hair, with dis-

tinct vertical impression beneath eye. Clypeus laterally distinctly incised, anteroventrally with a broad triangular emargination, radiating-striate. Lateral pronotal carina distinct, but not crest like lateroventrally, almost reaching pronotal crest dorsomedially. Lateral pronotal area almost entirely foveate-reticulate, except a very small glabrous area lateroventrally; lateroventral margin straight. Mesoscutum strongly costulate transversely and sparsely punctate with long hair; median mesoscutal impression only present as a short impression posteriorly; notauli percurrent, strongly diverging anteriorly; parascutal carina conspicuously raised and produced posteriorly into a triangular process. Lateral margin of axilla slightly raised. Lateral bar moderately wide and foveate, laterally not curved inward, shortest distance between lateral margins of lateral bars as wide as maximal width of scutellum. Scutellar sulcus subdivided by two submedian carinae into three large foveae. Dorsal surface of scutellum foveate-reticulate with long hair. In dorsal view, scutellum rounded posteriorly. Axillula with conspicuous whitish pubescence. Mesopleuron glabrous; mesopleural triangle strongly depressed, with conspicuous white pubescence in anterior half and nearly nude posteriorly. Metepisternum glabrate and sparsely punctate with hair; metapleural carina projected ventrally into a robust, short process. Lateral propodeal carina slightly raised dorsally throughout and densely pubescent. Metasomal T3 approximately as long as T4 and T5 combined, as long as T6. T7 posteriorly oblique and nearly straight, 1.5 as long as T6 and about 2 twice as long as T8. All post petiolar terga laterodorsally punctate with hair, punctures coarser and denser on T7 and T8. Apical metatibial process apically tapering, distinctly reaching beyond apex of metatibia. Pubescence sparse on femurs and tibiae, being denser ventrally and conspicuous on tarsomeres.

**DIAGNOSIS:** This new species is close to *D. carinifrons*, but with median frontal carina distinctly discontinuous beneath antennal sockets; genae, in front view, distinctly curved medially (fig. 35); and lateral margin of axilla laterally as wide as scutellum behind (fig. 31). In addition, metasoma of the new species is dark brown.

Male unknown.

**DISTRIBUTION:** China.

**MATERIAL EXAMINED:** Holotype ♀, China: Yunnan, Xishuangbanna, Meng'a, 1050–1080 m, 11 May 1958, S.-Y. Wang coll. (ZICA, Beijing).

**ETYMOLOGY:** The name *sinica* is from Latin, meaning of China, referring to the northernmost distribution of the genus in southwestern China.

#### PHYLOGENY AND HISTORICAL BIOGEOGRAPHY

Cladistic analysis found three most parsimonious trees with length of 63 steps (CI = 74; RI = 71). The topology of all trees is the same at the base but differs toward the top. The monophyly of *Dallatorrella* is well supported by seven apomorphic character changes (figs. 42, 43), and relatively high bootstrap and jackknife values (fig. 42).

Biogeographically, seven of the nine species of Dallatorrellinae recognized in this paper are distributed in southeast and eastern Asia. The two species of the subfamily that do not occur in this region are from Australia and Papua New Guinea, and they nest in an unresolved terminal cluster with three others from the Oriental region in the strict consensus tree. The cladogram suggests that Dallatorrellinae originated in the Oriental region and subsequently dispersed to the Australian region, contrary to an earlier hypothesis by Ronquist (1995a). Ronquist suggested the Dallatorrellinae originated in the Australian region and subsequently dispersed to the Oriental region. However, Ronquist's hypothesis was not based on a phylogenetic analysis of relationships within the subfamily.

Ronquist (1995b) also reconstructed the historical biogeography of the Liopteridae based on his phylogenetic analysis of the family. Since Ronquist (1995b), more work has been done on the phylogeny and historical biogeography of several of the major lineages of Liopteridae. In addition to the present study, a forthcoming study on the subfamily Mayrellinae suggests that the Mayrellinae has originated in either the Nearctic or eastern Palearctic, with a clade subsequently dispersed to Africa (Liu et al., in prep.). Thus, both Mayrellinae and Dallatorrellinae

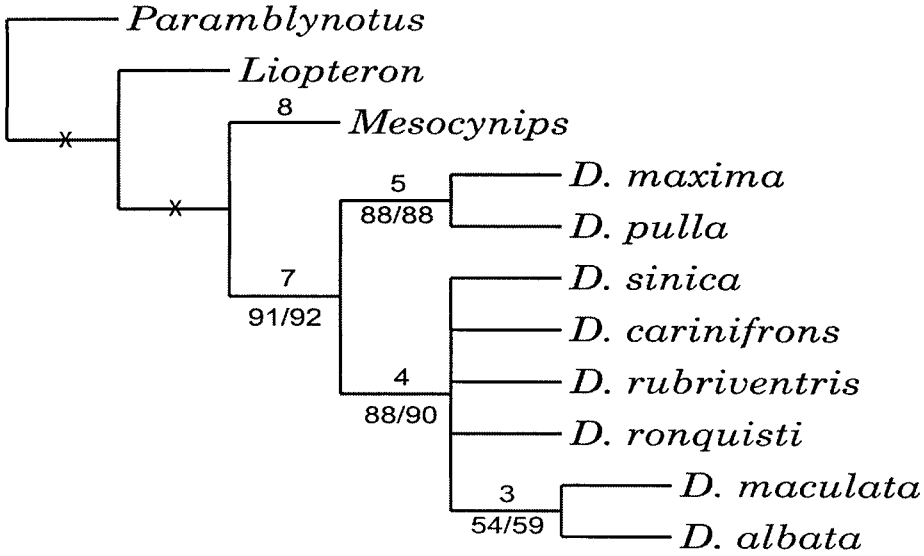


Fig. 42. Strict consensus of the three shortest trees (length 62, CI = 78, RI = 72) resulting from parsimony analysis using NONA (options: hold at maximum 1000 trees in memory, 100 replications of tree bisection—reconnection search). Branches marked with X indicate phylogenetic relationships constrained during the search according to earlier studies (Ronquist, 1995a, 1995b). Numbers above clades are the number of unambiguous character changes on the clade; numbers below the clades are bootstrap and jackknife values (1000 replications, each with the same options as the original tree search).

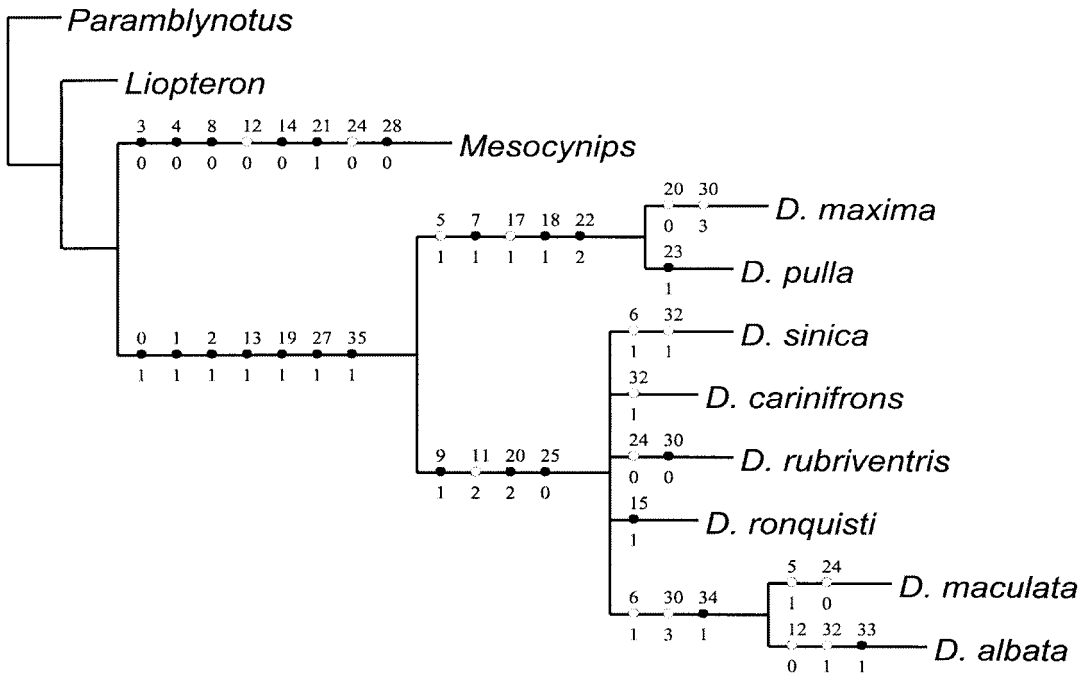


Fig. 43. Strict consensus tree of the shortest trees with character changes that can be mapped unambiguously. Character changes that are uniquely derived on the branches of the strict consensus tree are indicated as filled circles and those are not uniquely derived are indicated as empty circles.

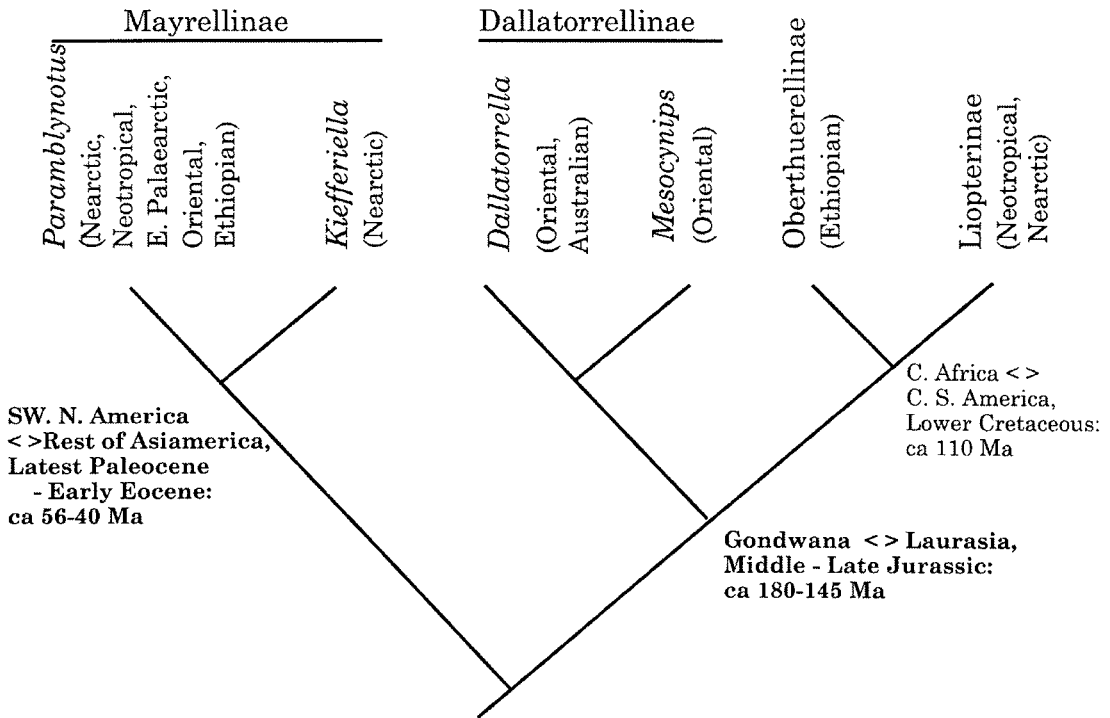


Fig. 44. Reconstruction of the historical biogeography of Liopteridae. Geological events are suggested to have possibly led to the vicariations in the higher level phylogeny. < > indicates a split between land masses. Related events in bold are based either on reconstruction of this study or on a concurrent study by Liu et al. (in prep.); and the events in lightface type were first suggested by Ronquist (1995b).

have a Laurasian origin. Consequently, the split of the Dallatorrellinae from the stem species of the two Gondwanian subfamilies Liopterinae and Oberthuerellinae probably corresponds to the breakup of Pangea into Gondwana and Laurasia in the Middle to Late Jurassic (180–145 mybp) (fig. 44).

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## APPENDIX 1. LIST OF CHARACTERS

### MAIN STRUCTURE

1. **Length of flagellum:** 0, long and slender, F1 is about 4 times as long as wide at middle; 1, short and stout, F1 is at most 1.7 times as long as wide at middle.
2. **Shape of flagellomeres:** 0, cylindrical; 1, constricted toward ends (fig. 9).
3. **Shape of ocellar triangle:** 0, not distinctly raised (fig. 2); 1, strongly raised (e.g., fig. 16).
4. **Prominence of eye:** 0, prominent, distinctly wider than temple laterally (figs. 35–37); 1, not prominent, narrower than or as wide as temple laterally (fig. 2).
5. **Foveate sculpture on lower face:** 0, absent; 1, present.
6. **Vertical impression beneath eye:** 0, indistinct; 1, distinct (figs. 22, 23).
7. **Dorsal area of pronotum:** 0, open posteriorly, not delimited by lateroposterior extension of pronotal crest; 1, closed posteriorly, delimited by lateroposterior extension of pronotal crest.
8. **Posterior part of dorsal pronotal area:** 0, not expanded laterally; 1, prominently expanded laterally (fig. 20).
9. **Foveate sculpture on lateral surface of pronotum:** 0, absent; 1, present.
10. **Secondary sculpture on lateral surface of pronotum:** 0, more or less transversely costulate; 1, without transverse costulation.
11. **Mesopleural triangle:** 0, large (e.g., figs. 3, 28, 29), 1, small (fig. 21).
12. **Shape of parascutal carinae:** 0, parascutal carinae broadly not produced lateroposteriorly (fig. 4); 1, parascutal carinae expanded lateroposteriorly into a rounded triangle (figs. 24, 25); 2, parascutal carinae expand-

- ed lateroposteriorly into an acute triangle. Ordered.
13. **Shape of mesoscutellum:** 0, sloped laterally and posteriorly (fig. 4); 1, at least laterally distinctly raised (e.g.; fig. 30).
  14. **Scutellar sulcus:** 0, divided by a longitudinal median carina (fig. 4); 1, divided by at least two equally strong longitudinal carinae (e.g., fig. 30).
  15. **Surface sculpture of mesoscutellum:** 0, transversely carinate (fig. 4); 1, foveate-reticulate or foveate and rugose (e.g., figs. 25, 30).
  16. **Shape of mesoscutellum posteriorly:** 0, broadly rounded (fig. 31); 1, almost truncate (fig. 30).
  17. **Shape of lateral margin of axilla:** 0, not raised (fig. 4); 1, raised (e.g., fig. 13).
  18. **Shape of mesosubpleuron:** 0, ventrally straight or very slightly curved medially; 1, ventrally projected medially into a triangular process.
  19. **Presence of additional process laterad to metacoxal foramen anterior to the prominent process extended from meta-pleural carina:** 0, absent; 1, present (fig. 21).
  20. **Presence of vertical carina on lateral side of procoxa:** 0, absent; 1, present.
  21. **Shape and size of apical process of metatibia:** 0, absent (fig. 26); 1, short and truncate apically (figs. 5, 27); 2, long and pointed apically (fig. 33). Ordered.
  22. **Abdominal T7–T8:** 0, separate; 1, fused with each other.

#### SURFACE SCULPTURE AND WING VENATION

23. **Extension of median frontal carina in lower face:** 0, absent; 1, to the middle or at least broken medially; 2, complete to clypeus.
24. **Radiating striate sculpture on lower face:** 0, present only on lower half; 1, present nearly on entire lower face.

25. **Secondary sculpture on lower face:** 0, coriaceous; 1, foveate; 2, foveate and densely punctate with pubescence.
26. **Glabrous area on lateral surface of pronotum:** 0, small, at most limited to ventral one-third; 1, large, occupying posteroventral half (fig. 19); 2, extensive, covering most of lateral surface of pronotum except upper one-fifth (fig. 4). Ordered.
27. **Direction of vein  $R_s+M$  and shape of submarginal of forewing:** 0,  $R_s+M$  arising proximally from middle or anterior one third of basalis, submarginal trapezoid (fig. 8); 1,  $R_s+M$  arising proximally from anterior end of basalis, submarginal subtriangular (fig. 7).
28. **Shape of  $M+Cu_1$  of forewing:** 0, straight or slightly curved with basal half divergent from  $R+Sc$  vein distally (fig. 7); 1, abruptly curved in the middle with basal half parallel with  $R+Sc$  vein distally (fig. 8).

#### COLOR AND PUBESCENCE

29. **Color of head:** 0, yellow; 1, black.
30. **Color of metasoma:** 0, yellow to brown; 1, black.
31. **Color pattern of forewings:** 0, nearly clear; 1, evenly ferruginous; 2, distally banded broadly; 3, distally maculate.
32. **Hair patch in mesopleural triangle:** 0, sparse or absent; 1, conspicuous.
33. **Conspicuous pubescence in axillula:** 0, absent; 1, present.
34. **Band of dense hairs in coarse punctures dorsally along posterior margin of abdominal T5 (female):** 0, absent; 1, present.
35. **Band of dense hairs in coarse punctures dorsally along posterior margin of abdominal T6 (female):** 0, absent; 1, present (figs. 14, 15).
36. **Band of dense hairs in coarse punctures ventrolaterally along posterior margin of abdominal T7 (female):** 0, absent; 1, present (fig. 14).