Taxonomy of the *Leptogenys modiglianii* species group from southeast Asia (Hymenoptera, Formicidae, Ponerinae)

Kôichi Arimoto

1 Entomological Laboratory, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University, Hakozaki 6-10-1, Fukuoka, 812–8581 Japan

Corresponding author: Kôichi Arimoto (antbeginning@gmail.com)

Academic editor: M. Borowiec | Received 30 August 2016 | Accepted 22 December 2016 | Published 2 February 2017

http://zoobank.org/53DC0CBC-09E7-41C8-91C8-27D31F3D99EE

Citation: Arimoto K (2017) Taxonomy of the *Leptogenys modiglianii* species group from southeast Asia (Hymenoptera, Formicidae, Ponerinae). ZooKeys 651: 79–106. https://doi.org/10.3897/zookeys.651.10336

Abstract

*Leptogenys breviloba* sp. n., *L. curva* sp. n., *L. itoi* sp. n., *L. kanaoi* sp. n., *L. malayana* sp. n., and *L. modiglianii* Emery, 1900 are described from southeast Asia. The *Leptogenys modiglianii* species group is proposed on the basis of similarities among the six species. An identification key to species in this group from southeast Asia is provided.

Keywords

Ants, new species, Oriental region, Ponerini, redescription, taxonomic revision

Introduction

The genus *Leptogenys* Roger, 1861 is one of the largest ant genera, and contains 302 species and 25 subspecies throughout the tropical and subtropical regions (Bolton 2016). In the Oriental region, approximately 70 *Leptogenys* species have been described. They have not been comprehensively studied, although Xu and He (2015) provided a preliminary key to the known Oriental species. There are no species groups well defined on the basis of worker morphology in this region. *Leptogenys modiglianii* Emery, 1900
was described from Engano Island, which is located southwest of Sumatra, Indonesia. Subsequently, Mann (1919) provided a key to species related to \textit{L. modiglianii} in the Australian region, but no additional species in this group have been found in the Oriental region. \textit{Leptogenys modiglianii} was not treated in Xu and He (2015). In this paper, the \textit{Leptogenys modiglianii} species group is proposed, and all species treated here are described from southeast Asia. An identification key is provided for all the species.

\textbf{Materials and methods}

Repositories of the type specimens are as follows:

\begin{itemize}
  \item \textbf{BLKU} Laboratory of Biology, Faculty of Agriculture, Kagawa University, Takamatsu, Japan.
  \item \textbf{BMNH} The Natural History Museum, London, United Kingdom.
  \item \textbf{ELKU} Entomological Laboratory, Kyushu University, Fukuoka, Japan.
  \item \textbf{FDS} Forest Department Sarawak, Kuching, Malaysia.
  \item \textbf{SKYC} Seiki Yamane Collection, Kagoshima, Japan.
  \item \textbf{MSNG} Museo Civico di Storia Naturale Giacomo Doria, Genova, Italy.
  \item \textbf{NHMW} Naturhistorisches Museum Wein, Vienna, Austria.
\end{itemize}

Colony codes and depositories are shown in round and square brackets, respectively. Photographs of specimens were taken with a Canon EOS 7D digital camera with a Canon macro photo lens MP-E 65mm (Canon Inc., Tokyo, Japan) and then combined using the CombineZM software. General structures of specimens were observed with an Olympus-SZX9 stereomicroscope (Olympus Corporation, Tokyo, Japan). Maps were generated using DIVA-GIS 7.5.0. Digital images of photographs and maps were edited with Adobe Photoshop 7.0 (Adobe, San Jose, CA, USA).

\textbf{Measurements and indices}

Measurements are shown in millimeters and were made with a micro ruler (MR-2, minimum scale value: 0.05 mm). The following measurements are visualized in Figures 1 and 2. The ratios were calculated from measurements and are denominated indices.

\begin{itemize}
  \item \textbf{HL} Head length: in full-face view, the maximum length of the head excluding the mandible, measured from the anterior margin of the clypeus to the nuchal carina.
  \item \textbf{HLL} Head lateral margin length: in full-face view, the head length measured from the mandible base to the nuchal carina.
  \item \textbf{HLA} Anterior head length: in full-face view, the head length measured from the mandible base to the anterior edge of the eye.
\end{itemize}
Figure 1. Measurements of worker of the *Leptogenys modiglianii* species group. A Head, full-face view B lateral view C petiole, lateral view D dorsal view. Abbreviations: HL: Head length, HLL Head lateral margin length, HLA Anterior head length, HW Head width, CML Clypeal median lobe length, SL Scape length, EL Eye length, PrL Pronotum length, PrH Pronotum height, PrW Pronotum width, WL Weber’s length, PeL Petiole length, PeH Petiole height, PeW Petiole width.

- **HW** Head width: in full-face view, the maximum width of the head excluding the eyes.
- **CML** Clypeal median lobe length: in full-face view, the straight-line length measured from the anterior margin of the clypeus to the anterior margin of the torulus.
- **CI** Cephalic index: HW/HL × 100.
- **CLI** Clypeus index: CML/HL × 100.
- **SL** Scape length: the straight-line length of the first antennal segment, excluding the neck and the basal condyle.
- **SI** Scape index: SL/HW × 100.
- **EL** Eye length: in full-face view, the vertical line length of the compound eye.
- **OI** Ocular index: EL/HLL × 100.
- **PrL** Pronotum length: in profile, the diagonal length of the pronotum, measured from the anterior margin of the pronotum excluding the collar to the posterior extremity of the pronotum.
Figure 2. Measurements of male of the *Leptogenys modiglianii* species group. A Head, full-face view B lateral view C petiole, lateral view D dorsal view. HL Head length, HW Head width, CML Clypeal median lobe length, EL Eye length, MeL Mesoscutum length, MeW Mesoscutum width, WL Weber’s length, PeL Petiole length, PeH Petiole height, PeW Petiole width.

**PrH** Pronotum height: in profile, the maximum height of the pronotum, measured from the posterior base of the lateral margin of the pronotum to the highest point of the pronotum.

**PrW** Pronotum width: in dorsal view, the maximum width of the pronotum.

**MeL** Mesoscutum length: in dorsal view, the maximum length of the mesoscutum.

**MeW** Mesoscutum width: in dorsal view, the maximum width of the mesoscutum.

**WL** Weber’s length: in profile, the diagonal length of the mesosoma, measured from the anterior margin of the pronotum excluding the collar to the posterior extremity of the propodeal lobe.

**PeL** Petiole length: in profile, the maximum length of the petiole, measured from the anteriormost margin to the posteriormost margin of the petiole, including the peduncle.

**PeH** Petiole height: in profile, the height of the node, measured from the apex of the subpetiolar process to the highest point of the node.
PeW  Petiole width: in dorsal view, the maximum width of the node.
LPI  Lateral petiole index: PeH/PeL × 100.
DPI  Dorsal petiole index: PeW/PeL × 100.

Taxonomy

The modiglianii species group (proposed here)

Species included in southeast Asia. Six species: L. breviloba sp. n., L. curva sp. n., L. itoi sp. n., L. kanaoi sp. n., L. malayana sp. n., L. modiglianii Emery, 1900

Distribution (Fig. 3). Malaysia (Peninsular Malaysia, Borneo), Indonesia (Sumatra, Engano Island).

Worker (Figs 4, 6, 8, 11, 13–19). Diagnosis. Head widest just posterior to clypeus excluding eyes. Mandible sickle-shaped, elongate, without denticles. Anterior edge of torulus located anterior to mandible bases. Clypeus short, with apical median extension. Eye situated just posterior to clypeus, breaking outline of lateral head margin. Hypostomal teeth large, visible in full-face view. In profile, petioler node rectangular to fan-shape; subpetiolar process consisting of high anterior lobe and thin posterior extension. Body surface mostly areolate-rugose, extensively with standing long hairs.

Description. In full-face view, head either longer than wide or almost as long as wide (CI: 77-101), broadening anteriad, widest just posterior to clypeus excluding eyes; posterior margin broadly convex. Mandible sickle-shaped, elongate, curved near base and becoming straight apically or curved throughout, without denticles, subapical tooth either absent or present near apical tooth; internal margin with narrow lamella; large gap present between mandibular shaft and clypeus; mandibles with only their apical portions crossing each other when fully closed. Eye large (OI: 26–39), situated just posterior to clypeus, breaking outline of lateral margin of head. Antennal scape almost as long as width of head or longer (SI: 99-121), surpassing posterior margin of head by one-sixth to two-fifths of its length; antennomere III longer than II; antennomere XII shorter than III, longer than XI. Anterior edge of torulus located anterior to mandible base. Clypeus short, with longitudinal median carina; anterolateral margin broadly concave, either with or without lateral lobe; apical median extension (CLI: 12–21) with convex or truncate apex, fringed by narrow translucent lamella, with pair of peg-like setae. Hypostomal teeth large, visible in full-face view. Pronotum in profile longer than high, in dorsal view shorter than wide or longer. Mesonotum in dorsal view shorter than wide. Metanotal groove distinctly visible, weakly to strongly impressed. Meso-metapleural sulcus present. In profile, propodeal dorsum convex to straight, posteriorly rounding into declivity, longer than length of propodeal declivity; metapleural-propodeal sulcus shallow. Petiole in profile longer than high or shorter (LPI: 94–118), in dorsal view longer than wide (DPI: 71–87); node in profile either rectangular (dorsal face subhorizontal) or fan-shape (dorsal face distinctly sloping anteriad), highest posteriorly, with anterior and dorsal faces forming continuous curve or anterior face of node ventrally vertical and dorsally forming continuous curve with dor-
Figure 3. Collecting localities of species of the modiglianii species group. Black star: *L. breviloba* and *L. itoi*, white circle: *L. curva*, black triangle: *L. itoi*, black circle: *L. kanaoi*, white rectangle: *L. malayana*, white triangle: *L. modiglianii*.

sum, in dorsal view widening posteriad, with lateral margin broadly convex; posterior face flat, abruptly separated from lateral face, slightly inclined anteriad. Subpetiolar process consisting of high anterior lobe and thin posterior extension; anterior lobe fan-shaped, with continuously curved anteroventral margin and concave posterior margin. Anterior face of gastral tergite I flat; in profile, anteroventral edge of gastral sternite I shallowly indented just posterior to prora; in profile, prora long-rectangular, low; constriction between gastral segments I and II distinct.

Head, mesosoma, and petiole mostly areolate-rugose, superimposed with small piligerous punctures. Antennal scape and legs densely punctuated. Clypeus with oblique to longitudinal striae. Propodeal declivity with transverse crests. Postgenal bridge and prosternum sparsely with circular depressions, medially smooth and without punctures.
Mesosternum smooth and without punctures, sometime with transverse striate anteriorly and posteriorly. Ventrolateral and posterior faces of petiolar node smooth; subpetiolar process finely striate. Anterior face of gastral tergite I smooth; gastral segment I with scalloped depressions that are deepest anteriorly and sloping posteriad; segment II smooth or covered with scalloped depressions; constriction between gastral segments I and II finely scrobiculate; segments III–V smooth.

Body black and tinged with red, shiny. Hairs of various lengths, scattered, white-yellow; long hairs standing; short pubescence decumbent; antenna and legs with dense short pubescence, mixed with scattered long hairs.
Queen (Figs 5, 7, 9, 12). In general structure the queen is very similar to the worker (ergatoid queen) and lacks ocelli; it differs from the worker in having a higher and wider petiole (LPI: 105–132; DPI: 79–94) and voluminous gaster.

Male (Fig. 10). Only known from L. itoi (see below).

Key to species in the Leptogenys modiglianii species group from southeast Asia: worker

1 In profile, petiole longer than or almost as long as high (LPI: 94–102); dorsal face of node subhorizontal (Fig. 16A) ......................................................L. breviloba
   – In profile, petiole higher than long (LPI: 103–122); dorsal face of node distinctly sloping anteriad (Fig. 16B) .............................................................2

2 In full-face view, head shorter (CI: 88–101). Mandible curved near base, becoming straight apically. Clypeus with lateral lobe (Fig. 17A: arrow) .....3
   – In full-face view, head longer (CI: 77–83). Mandible distinctly curved throughout. Clypeus without lateral lobe (Fig. 17B: arrow) .................5

3 In full-face view, head almost as long as wide (CI: 98–101). Antennal scape distinctly long (SL: 1.83–1.95; SI: 115–121), surpassing posterior margin of head by two-fifths of its length. Median clypeal extension with truncate apex (Fig. 18A) .................................................................L. malayana
   – In full-face view, head longer than wide (CI: 88–95). Antennal scape long (SL: 1.40–1.80; SI: 99–110), surpassing posterior margin of head by one-fifth to one-third of its length. Median clypeal extension with convex apex (Figs 18B, C) .................................................................L. itoi

4 In full-face view, head distinctly longer than wide (CI: 88–90). Clypeus with blunt angle between lateral lobe and median extension (Fig. 18B: arrow). In profile, petiole distinctly higher than long (LPI: 109–118); in profile, anterior face of node ventrally vertical and dorsally forming continuous curve with dorsum .................................................................L. modiglianii
   – In full-face view, head distinctly longer than wide (CI: 88–90). Clypeus smoothly incurved between lateral lobe and median extension (Fig. 18C). In profile, petiole slightly higher than long (LPI: 103–108); in profile node with anterior and dorsal faces forming continuous curve ..................L. curva

5 In profile, petiolar node with anterior and dorsal faces forming continuous curve. Gastral segment II covered with scalloped depressions, which close to each other. Body covered with understory layer of short dense hairs (Fig. 19A) .................................................................................................L. curva
   – In profile, anterior face of petiolar node ventrally vertical and dorsally forming continuous curve with dorsum. Gastral segment II smooth. Short hairs not forming understory layer. (Fig. 19B) ........................................L. kanaoi
Leptogenys breviloba sp. n.
http://zoobank.org/0697F839-348F-4C90-AEC7-C2CF2EBE68C3
Figures 3, 4, 5, 15B, 15D, 16A

**Etymology.** A combination of the Latin *brevis* (short), and the Latin *loba* (lobed), referring to the short clypeal lobe.

**Type material.** Holotype. Worker (AK18), under the bark of rotted wood, secondary rainforest, Ulu Gombak, Gombak, Selangor, Malaysia, 3.32°N, 101.75°E, 230–350 m, 23 V 2012, Taku Shimada leg. [ELKU]. **Paratypes** (6 workers, 2 queens). 2 workers, same colony as the holotype [ELKU]; 4 workers, 2 queens (FI99-402), same place as the holotype, 20 VIII 1999, Fuminori Itô leg. [BLKU].

**Type locality.** Ulu Gombak, Gombak, Selangor, Malaysia.

**Distribution.** Malaysia: Peninsular Malaysia (Selangor).

**Worker.** **Diagnosis.** In full-face view, head distinctly longer than wide (CI: 82–84). Mandible broadly curved throughout. Clypeus with lateral lobe, smoothly incurved between lateral lobe and median extension; apex of median extension convex. In profile, petiole longer than or almost as long as high (LPI: 94–102), highest near middle, with subhorizontal dorsal face.

**Measurements** (n = 5, holotype in parentheses). HL: 1.35–1.42 (1.39), HLL: 1.07–1.09 (1.09), HLA: 0.12–0.16 (0.16), HW: 1.11–1.20 (1.14), CML: 0.18–0.21 (0.21), CI: 82–84 (82), CLI: 12–15 (15), SL: 1.32–1.38 (1.38), SI: 112–121 (121), EL: 0.34–0.37 (0.36), Ol: 32–34 (33), PrL: 0.84–0.95 (0.84), PrH: 0.59–0.67 (0.67), PrW: 0.87–0.97 (0.90), WL: 2.22–2.37 (2.27), PeL: 0.85–0.88 (0.85), PeH: 0.81–0.89 (0.81), PeW: 0.60–0.67 (0.62), LPI: 94–102 (94), DPI: 71–76 (72).

**Description.** In full-face view, head distinctly longer than wide. Mandible broadly curved throughout, with subapical tooth near apical tooth. Eye strongly prominent, measuring one-third of head lateral margin length. Antennal scape distinctly longer than width of head, surpassing posterior margin of head by one-fourth of its length; antennomere III ca. 1.6 times as long as wide. Clypeus with lateral lobe, smoothly incurved between lateral lobe and median extension; median extension short, with convex apex. In dorsal view, pronotum shorter than or slightly longer than wide. Metanotal groove weakly impressed. In profile, propodeal dorsum almost straight. Petiole in profile longer than or almost as long as high, highest near middle, with subrectangular node; anterior face of node ventrally vertical and dorsally forming continuous curve with dorsum; dorsal face subhorizontal, but weakly sloping anteriad; posterior margin almost straight to slightly concave.

Head distinctly areolate-rugose. Mandible smooth. Gastral segment I with scalloped depressions, which are irregular in size but generally small; distance between small depressions greater than diameter of depressions; large depressions close to each other; segments II smooth.

Body black, slightly tinged with red; clypeus, mandible, antenna, legs and ventral half of petiole dark-red. Apical two or three segments of gaster red-brown. Scalloped depressions on gastral segments I bearing hairs.
Figure 5. Leptogenys breviloba sp. n., paratype, queen; gastral apical segments removed. A head, full-face view B lateral view C dorsal view.

**Queen.** Measurements (n = 2). HL: 1.32–1.46, HLL: 1.05–1.12, HLA: 0.15–0.16, HW: 1.14–1.21, CML: 0.21, CI: 83–87, CLI: 14–16, SL: 1.25–1.36, SI: 110–112, EL: 0.35–0.39, OI: 33–35, PrL: 0.88–0.98, PrH: 0.66–0.76, PrW: 0.94–0.98, WL: 2.27–2.41, PeL: 0.83–0.88, PeH: 0.87–0.95, PeW: 0.68–0.70, LPI: 105–108, DPI: 79–82. Mandible shorter than that of worker. Petiole in profile shorter than high, in dorsal view distinctly longer than wide.

**Male.** Unknown.

**Remarks.** The colony (AK18), including the holotype, was collected under the bark of rotted wood.
**Leptogenys curva** sp. n.
http://zoobank.org/2FE7314C-1CBC-4D18-B13E-A2E6F1D9A491
Figures 3, 6, 7, 19A

**Etymology.** From the Latin *curvus*, meaning curved, referring to the curved mandible.

**Type material.** Holotype. Worker (FI93-34), Sitiung, Dharmasraya, West Sumatra, Indonesia, I 1993, Fuminori Itô leg. [BLKU]. Paratype. 2 workers, 1 queen, same colony as the holotype [1 worker: BLKU; 1 worker, 1 queen: SKYC].

**Type locality.** Sitiung, West Sumatra, Indonesia.

**Distribution.** Indonesia (West Sumatra).

**Worker.**
**Diagnosis.** In full-face view, head distinctly longer than wide (CI: 77–78). Mandible distinctly curved throughout. Clypeus without lateral lobe; apex of median extension strongly projecting. In profile, petiole higher than long (LPI: 115–117), highest just anterior to posterodorsal angle; anterior and dorsal faces of node forming continuous curve; dorsal face distinctly sloping anteriad. Gastral segment II extensively covered with scalloped depressions. Body covered with understory layer of short, dense and recumbent pubescence.

**Measurements** (n = 3, holotype in parentheses). HL: 1.71–1.75 (1.75), HLL: 1.18–1.22 (1.22), HLA: 0.14–0.15 (0.15), HW: 1.32–1.35 (1.35), CML: 0.29–0.31 (0.31), CI: 77–78 (77), CLI: 17–18 (18), SL: 1.43–1.52 (1.52), SI: 108–113 (113), EL: 0.34–0.36 (0.34), OI: 28–31 (28), PrL: 1.03–1.06 (1.03), PrH: 0.63–0.64 (0.64), PrW: 0.97–1.00 (0.97), WL: 2.48–2.53 (2.48), PeL: 0.81–0.82 (0.82), PeH: 0.93–0.95 (0.95), PeW: 0.65–0.67 (0.65), LPI: 115–117 (116), DPI: 80–82 (80).

**Description.** In full face view, head distinctly longer than wide. Mandible distinctly curved throughout, with subapical tooth near apical tooth. Eye prominent, measuring one-fourth to one-third of head lateral margin length. Antennal scape longer than width of head, surpassing posterior margin of head by less than one-fifth of its length; antennomere III ca. 2.2 times as long as wide. Clypeus without lateral lobe; median extension moderately long, with apex strongly projecting. In dorsal view, pronotum longer than wide. Metanotal groove distinctly impressed. In profile, propodeal dorsum broadly convex. Petiole in profile higher than long, with fan-shaped node, highest just anterior to posterodorsal angle of node; anterior and dorsal faces of node forming continuous curve; dorsal face distinctly sloping anteriad; posterior face almost straight.

Head weakly areolate-rugose, longitudinally striate anteriorly; vertex weakly and transversely striate. Mandible longitudinally striate. Prosternum weakly rugose. Gastral segments I–II extensively covered with scalloped depressions that are irregular in size and close to each other; generally depressions on segment I larger than those on segment II.

Body black-gray; clypeus, mandible, antenna, legs, and ventral half of petiole dark-red. Body covered with understory layer of short, dense and recumbent pubescence. Scalloped depressions on gastral segments I–II bearing hairs.
Figure 6. *Leptogenys curva* sp. n., holotype, worker; gastral apical two segments removed. A head, full-face view B lateral view C dorsal view.

Queen. Measurements (n = 1). HL: 1.65, HLL: 1.19, HLA: 0.17, HW: 1.30, CML: 0.32, CI: 79, CLI: 20, SL: 1.41, SI: 109, EL: 0.36, OI: 31, PrL: 1.05, PrH: 0.75, PrW: 0.99, WL: 2.50, PeL: 0.76, PeH: 1.01, PeW: 0.74, LPI: 132, DPI: 97. Petiole in profile distinctly higher than long, in dorsal view almost as long as wide.

Male. Unknown.

Remarks. Gastral segments IV and V of the specimen examined were removed to confirm the genitalia by the collector.
Figure 7. *Leptogenys curva* sp. n., paratype, queen; gastral apical two segments removed. **A** head, full-face view **B** lateral view **C** dorsal view.

*Leptogenys itoi* sp. n.
http://zoobank.org/E07CBB4D-A7D1-4E99-98AF-F83BBB012EBF
Figures 3, 8, 9, 10, 15A, 16B, 17A, 18B

**Etymology.** Dedicated to Professor Fuminori Itô, collector of the material examined.

**Type material. Holotype.** Worker (FI99-240), transporting woodlouse, secondary rainforest, Ulu Gombak, Gombak, Selangor, Malaysia, 3.32°N, 101.75°E, 230–350 m, 3 VI 1999, Fuminori Itô leg. [BLKU]. **Paratypes** (47 workers, 6 queens, 2 male). 1 worker (FI92MG-270-5), same place as the holotype, VII-X 1992,
Figure 8. Leptogenys itoi sp. n., holotype, worker. A head, full-face view B lateral view, C dorsal view.

Fuminori Itô leg. [BLKU]; 1 worker (FI92MG-270-7), same place, VII-X 1992, Fuminori Itô leg. [BLKU]; 2 workers, 1 queen (FI92MG-366), same place, VII-X 1992, Fuminori Itô leg. [1 worker, 1 queen: BLKU; 1 worker: SKYC]; 6 workers (FI92MG-456), 2 workers (FI92MG-463), same place, VII-X 1992, Fuminori Itô leg. [BLKU]; 4 workers (FI92MG-518), same place, VII-X 1992, Fuminori Itô leg. [3 worker: BLKU; 1 worker: SKYC]; 4 workers, 1 male (BG99-2), same place, V 1999, Bruno Gobin leg. [BLKU]; 4 workers (FI04-119), same place, 19 XII 2004, Fuminori Itô leg. [BLKU]; 6 workers, 1 queen, 1 male (FI04-120), same place, 17 XII 2004, Fuminori Itô leg. [BLKU]; 8 workers, 1 queen (AG05-20), same place, VII 2005, Ayako Gotô leg. [BLKU]; 1 worker, same place, 3 XII 2005, Seiki Yamane leg.
Figure 9. *Leptogenys itoi* sp. n., paratype, queen; gastral apical two segments removed. **A** head, full-face view **B** lateral view **C** dorsal view.

Type locality. Ulu Gombak, Gombak, Selangor, Malaysia.

Distribution. Malaysia: Peninsular Malaysia (Selangor and Pahang).

Worker. Diagnosis. In full-face view, head slightly longer than wide (CI: 93–95). Mandible curved near base, becoming straight apically. Antennal scape long (SI:
surpassing posterior margin of head by two-fifths to one-third of its length. Clypeus with lateral lobe, with blunt angle between lateral lobe and median extension; median extension long, with broadly convex apex. In profile, petiole distinctly higher than long (LPI: 109–118), highest just anterior to posterodorsal angle; anterior face of node ventrally vertical and dorsally forming continuous curve with dorsum; dorsal face distinctly sloping anteriad.

**Measurements** (n = 5, holotype in parentheses). HL: 1.66–1.73 (1.73), HLL: 1.12–1.18 (1.18), HLA: 0.13–0.15 (0.14), HW: 1.54–1.64 (1.64), CML: 0.29–0.36 (0.35), CI: 93–95 (95), CLI: 17–21 (20), SL: 1.57–1.80 (1.80), SI: 99–110 (110), EL: 0.31–0.35 (0.35), OI: 28–30 (30), PrL: 0.99–1.10 (1.10), PrH: 0.67–0.80 (0.79), PrW: 1.00–1.07 (1.05), WL: 2.47–2.72 (2.72), PeL: 0.84–0.95 (0.95), PeH: 0.99–1.04 (1.04), PeW: 0.68–0.74 (0.74), LPI: 109–118 (109), DPI: 76–84 (78).

**Description.** In full face view, head slightly longer than wide. Mandible curved near base, becoming straight apically; subapical tooth obsolete. Eye prominent, measuring one-fourth to one-third of head lateral margin length. Antennal scape longer than width of head, surpassing posterior margin of head by two-fifths to one-third of its length; antennomere III ca. 2.5 times as long as wide. Clypeus with lateral lobe, with blunt angle between lateral lobe and median extension; median extension long, with broadly convex apex. In dorsal view, pronotum almost as long as wide. Metanotal groove slightly impressed. In profile, propodeal dorsum almost straight. Petiole in profile distinctly higher than long, highest just anterior to posterodorsal angle of node, with fan-shaped node; anterior face of node ventrally vertical and dorsally forming continuous curve with dorsum; dorsal face distinctly sloping anteriad; posterior face slightly concave dorsally and slightly convex ventrally.

Head strongly areolate-rugose, longitudinally striate near clypeus; vertex weakly and transversally striate. Mandible weakly striate longitudinally. Prosternum smooth and without punctures. Gastral segment I with scalloped depressions that are irregular in size; distance between depressions distinctly greater than diameter of depressions; interspace between depressions with small punctures; segments II smooth.

Body black, slightly tinged with red; clypeus, mandible, antenna, legs and ventral half of petiole dark-red. Apical two or three segments of gaster red-brown. Scalloped depressions on gastral segment I bearing hairs; small punctures without hairs.

**Queen. Measurements** (n = 5). HL: 1.58–1.68, HLL: 1.07–1.14, HLA: 0.10–0.14, HW: 1.43–1.59, CML: 0.29–0.34, CI: 89–94, CLI: 18–20, SL: 1.51–1.62, SI: 102–107, EL: 0.30–0.36, OI: 27–31, PrL: 0.98–1.09, PrH: 0.66–0.79, PrW: 1.01–1.09, WL: 2.40–2.72, PeL: 0.84–0.90, PeH: 1.02–1.07, PeW: 0.72–0.78, LPI: 119–126, DPI: 85–90. Mandible shorter than that of worker. Petiole in profile distinctly higher than long, in dorsal view distinctly longer than wide.

**Male. Measurements** (n = 2). HL: 1.08–1.17, HW: 0.83–0.87, CML: 0.35–0.38, CI: 75–77, CLI: 33, EL: 0.63–0.64, MeL: 1.01–1.10, MeW: 1.05–1.20, WL: 2.44–2.59, PeL: 0.68–0.75, PeH: 0.81–0.85, PeW: 0.54, LPI: 113–120, DPI: 71–80.

**Description.** In full-face view, head longer than wide excluding eyes, wider posteriorly; posterior margin distinctly rounded. Mandible small, without basal angle and
denticles, with rounded apex. Eye occupying over half of head length. Three prominent ocelli present; maximum length of lateral ocellus shorter than minimum distance between lateral ocellus and eye. Antenna 13-segmented; scape distinctly shorter than width of head; antennomere II shortest, roughly as long as wide; III longest; XIII shorter than III. Clypeus triangular and projecting anteriad, convex on midline; anterolateral margin straight; apex moderately acute; epistomal suture broadly rounded. Mesoscutum in profile convex, in dorsal view shorter than wide, widest posterior to mid-length; notaulus weakly notable; parapsidal line more than half of mesoscutal length; transscutal line almost straight. Anterior margin of mesoscutellar disc rounded.

Figure 10. *Leptogenys itoi* sp. n., paratype, male. A head, full-face view B lateral view C petiole, lateral view D dorsal view E forewing F hindwing.
In profile, propodeal dorsum forming continuous curve with declivity; metapleural-propodeal sulcus present. Forewing ca. 3.0 times as long as wide, with stigma. Hindwing less than 0.8 times as long as forewing. Petiole in profile higher than long, in dorsal view longer than wide, highest posteriorly, with short peduncle, with fan-shaped node; anterior and dorsal faces forming convex line; dorsal face sloping anteriad; posterior face convex; in dorsal view, lateral margin broadly convex. With waist in profile, anterior lobe of subpetiolar process short-subtriangular, anterior margin convex, ventral apex moderately acute, posterior margin concave. With gaster in profile, prora low, long; continuously curved between prora and anteroventral edge of gastral sternite I. Constriction between gastral segments I and II distinct.

Head, mesosoma, and petiole weakly rugose, with piligerous small punctures. Mandible smooth. Clypeus with oblique to longitudinal striae. Subpetiolar process finely striate. Gastral segment I with irregularly sized depressions; distance between depressions distinctly greater than diameter of depressions; interspace between depressions with small punctures; segments II–V smooth; constriction between gastral segments I and II finely scrobiculate.

Body black, tinged with red; clypeus, mandible, antenna, legs, subpetiolar process, and gaster red-brown. Hairs of various lengths, scattered, white-yellow; antennal scape and legs with dense short pubescence, mixed with long scattered hairs. Scalloped depressions and small punctures on gastral segment I bearing hairs.

Remarks. This species corresponds to Leptogenys sp. 35 in Itô (1996). Workers selectively attack Isopoda, in which this species is thought to specialize (Itô, 2000).

**Leptogenys kanaoi** sp. n.
http://zoobank.org/6E7E651D-FCEF-445A-A775-F44FB961D35D
Figures 3, 11, 12, 17B, 19B

Etymology. Dedicated to Dr. Taisuke Kanoa, collector of the material examined.

Type material. Holotype. Worker (AK92), from rotted wood, mixed dipterocarp forest, Lambir Hills National Park, Miri, Sarawak, East Malaysia (Borneo), Malaysia, 4.20°N, 114.04°E, 90m, 4 X 2012, Taisuke Kanoa leg. [FDS]. Paratypes (12 workers, 8 queens). 8 workers, 4 queens, same colony as the holotype [4 workers, 2 queens: FDS; 4 workers, 2 queens: ELKU]; 1 worker, Tower Region, same park, 16 VIII 1995, Seiki Yamane leg. [SKYC]; 3 workers, 4 queens (Eg98-BOR-868), Seipilok Forest, Sabah, East Malaysia (Borneo), Malaysia, 4 VII 1998, Katsuyuki Eguchi leg. [SKYC].

Type locality. Lambir Hills National Park, Miri, Sarawak, East Malaysia (Borneo), Malaysia.

Distribution. Malaysia: Borneo (Sarawak and Sabah).

Worker. Diagnosis. In full-face view, head distinctly longer than wide (CI: 78–83). Mandible strongly curved throughout. Clypeus without lateral lobe; apex of median extension strongly projecting. Petiole in profile higher than long (LPI: 112–122), highest just anterior to posterodorsal angle; anterior face of node ventrally vertical and dorsally
forming continuous curve with dorsum; dorsal face sloping anteriad. Gastral segment II smooth.

**Measurements** (n = 5, holotype in parentheses). HL: 1.66–1.78 (1.77), HLL: 1.18–1.29 (1.24), HLA: 0.16–0.19 (0.19), HW: 1.34–1.43 (1.43), CML: 0.30–0.34 (0.34), CI: 78–83 (81), CLI: 17–19 (19), SL: 1.50–1.63 (1.56), SI: 109–116 (109), EL: 0.34–0.39 (0.36), OI: 27–30 (29), PrL: 1.04–1.09 (1.09), PrH: 0.69–0.74 (0.69), PrW: 1.03–1.07 (1.07), WL: 2.57–2.69 (2.69), PeL: 0.83–0.91 (0.91), PeH: 0.96–1.06 (1.02), PeW: 0.70–0.75 (0.75), LPI: 112–122 (112), DPI: 78–87 (82).

**Description.** In full face view, head distinctly longer than wide. Mandible strongly curved throughout, with subapical tooth near apical tooth. Eye prominent, measuring...
one-fourth to one-third of head lateral margin length. Antennal scape distinctly longer than width of head, surpassing posterior margin of head by one-fifth of its length; antennomere III ca. 2.2 times as long as wide. Clypeus without lateral lobe; median extension moderately long, with apex strongly projecting. In dorsal view, pronotum longer than wide. Metanotal groove distinctly impressed. In profile, propodeal dorsum broadly convex. Petiole in profile higher than long, highest near mid-length, with roughly fan-shaped node; anterior face of node ventrally vertical and dorsally forming continuous curve with dorsum; dorsal face sloping anteriad; posterior face almost straight.

Head weakly areolate-rugose, longitudinally striate anteriorly; vertex weakly and transversally striate. Mandible weakly and longitudinally striate. Prosternum weakly
Taxonomy of the Leptogenys modiglianii species group from southeast Asia...

rugose. Gastral segment I with scalloped depressions that are irregular in size and close to each other; segments II smooth.

Body black, gaster slightly tinged with red; clypeus, mandible, antenna, legs and ventral half of petiole dark-red. Apical two or three segments of gaster red-brown. Scallop depressions on gastral segment I bearing hairs.

**Queen. Measurements** (n = 5). HL: 1.59–1.74, HLL: 1.13–1.26, HLA: 0.16–0.18, HW: 1.30–1.39, CML: 0.26–0.33, CI: 80–82, CLI: 15–19, SL: 1.39–1.52, SI: 107–110, EL: 0.33–0.40, OI: 29–32, PrL: 0.96–1.03, PrH: 0.65–0.71, PrW: 1.00–1.06, WL: 2.39–2.56, PeL: 0.82–0.86, PeH: 1.03–1.09, PeW: 0.72–0.78, LPI: 123–126, DPI: 88–94. Petiole in profile distinctly higher than long, in dorsal view longer than wide.

**Male.** Unknown.

**Remarks.** The colony (AK92), including the holotype, was collected from rotted wood. It was composed of four queens, nine workers, and two pupae.

**Leptogenys malayana sp. n.**
http://zoobank.org/AB930BCD-8634-46EB-86BE-7E9A74D75B30
Figures 3, 13, 18A

**Etymology.** The species epithet, *malayana*, refers to the fact that this species was found on Peninsular Malaysia.

**Type material. Holotype.** Worker, Trengganu, Malaysia, 1974, T. Clay leg. [BMNH]. **Paratypes.** 2 workers, same data as the holotype [BMNH].

Detailed collecting locality of the types is unknown. For convenience, the location of this species is marked at the center of Trengganu Province, Malaysia, on the distribution map (Fig. 3).

**Type locality.** Trengganu, Malaysia.

**Distribution.** Malaysia: Peninsular Malaysia (Trengganu).

**Worker. Diagnosis.** In full-face view, head almost as long as wide (CI: 98–101). Mandible curved near base, becoming straight apically. Antennal scape distinctly longer than width of head (SI: 115–121), surpassing posterior margin of head by two-fifths of its length. Clypeus with lateral lobe, with blunt angle between lateral lobe and median extension; apex of median extension truncate. Petiole in profile distinctly higher than long (LPI: 112–116), highest just anterior to posterodorsal angle; anterior face of node ventrally vertical and dorsally forming continuous curve with dorsum; dorsal face distinctly inclined anteriad.

**Measurements** (n = 3, holotype in parentheses). HL: 1.57–1.63 (1.63), HLL: 1.16–1.21 (1.18), HLA: 0.17–0.19 (0.17), HW: 1.59–1.61 (1.60), CML: 0.23–0.24 (0.23), CI: 98–101 (98), CLI: 14–15 (14), SL: 1.83–1.95 (1.91), SI: 115–121 (120), EL: 0.36–0.38 (0.37), OI: 31 (31), PrL: 1.01–1.09 (1.09), PrH: 0.74–0.89 (0.89), PrW: 1.12–1.14 (1.14), WL: 2.57–2.78 (2.78), PeL: 0.88–0.97 (0.97), PeH: 1.02–1.10 (1.09), PeW: 0.72–0.76 (0.76), LPI: 112–116 (112), DPI: 77–82 (78).
**Description.** In full face view, head almost as long as wide. Mandible curved near base, becoming straight apically; subapical tooth distinct in holotype or absent in paratypes. Eye prominent, measuring one-third of head lateral margin length. Antennal scape distinctly longer than width of head, surpassing posterior margin of head by two-fifths of its length; antennomere III ca. 2.7 times as long as wide. Clypeus with lateral lobe, with blunt angle between lateral lobe and median extension; median extension short, with truncate apex. In dorsal view, pronotum shorter than wide. Metanotal groove slightly impressed. In profile, propodeal dorsum weakly convex to almost straight. Petiole in profile distinctly higher than long, highest just anterior to posterodorsal angle, with fan-shaped node; anterior face of node ventrally vertical and
dorsally forming continuous curve with dorsum; dorsal face distinctly inclined anteriorly; posterior face slightly concave dorsally and slightly convex ventrally.

Head strongly areolate-rugose, longitudinally striate near clypeus; vertex weakly and transversally striate. Mandible distinctly striate longitudinally. Gastral segment I with scalloped depression that are irregular in size but generally large; large depressions close to each other; distance between small depressions greater than diameter of depressions; segments II smooth.

Body black, gaster slightly tinged with red; clypeus, mandible, antenna, legs and ventral half of petiole dark-red. Apical two or three segments of gaster red-brown. Scalloped depressions on gastral segment I bearing hairs.

**Queen and male.** Unknown.

*Leptogenys modiglianii* Emery, 1900

Figures 3, 14, 15C, 18C

*Leptogenys modiglianii* Emery, 1900: 13 (original description of workers; type locality: Malaconni, Enggano Is., Indonesia); Bolton 1995: 232 (catalogue).

*Leptogenys* (*Leptogenys*) *modiglianii* Emery, 1900: Emery 1911: 100 (catalogue); Mann 1919: 298 (in key); Chapman and Capco 1951: 31 (checklist).

**Type material.** Lectotype (present designation). Worker, Malaconni, Enggano Island, off the west coast of Sumatra, Indonesia, VI 1891, Elio Modigliani leg., specimen code: ANTWEB CASENT 0903974 [MSNG]. **Paralectotypes.** 4 workers, same data as the holotype [3 workers: MSNG; 1 worker: NHMW].

**Distribution.** Indonesia: Enggano Island.

**Worker.** Diagnosis. In full-face view, head distinctly longer than wide (CI: 88–90). Mandible curved near base, becoming straight apically. Antennal scape slightly longer than width of head (SI: 103–105), surpassing posterior margin of head by one-fifth to one-fourth of its length. Clypeus with lateral lobe, smoothly incurved between lateral lobe and median extension; median extension with convex apex. In profile, petiole slightly higher than long (LPI: 103–108), highest just anterior to posterodorsal angle; anterior and dorsal faces forming continuous curve; dorsal face distinctly sloping anteriad.

**Measurements** (n = 5, lectotype in parentheses). HL: 1.52–1.68 (1.68), HLL: 1.11–1.22 (1.22), HLA: 0.18–0.20 (0.18), HW: 1.34–1.50 (1.50), CML: 0.25–0.28 (0.28), CI: 88–90 (90), CLI: 15–17 (17), SL: 1.40–1.58 (1.58), SI: 103–105 (105), EL: 0.30–0.34 (0.34), OI: 26–28 (28), PrL: 0.99–1.09 (1.09), PrH: 0.59–0.75 (0.75), PrW: 0.95–1.02 (1.02), WI: 2.49–2.68 (2.68), PeL: 0.85–0.92 (0.92), PeH: 0.91–0.98 (0.98), PeW: 0.64–0.67 (0.67), LPI: 103–108 (106), DPI: 73–76 (73).

**Redescription.** In full-face view, head distinctly longer than wide. Mandible curved near base, becoming straight apically; subapical tooth absent. Eye prominent, measuring one-fourth to one-third of head lateral margin length. Antennal scape slightly longer than width of head, surpassing posterior margin of head by one-fifth...
Figure 14. *Leptogenys modiglianii* Emery, 1900, lectotype, worker, specimen code: ANTWEB CASENT 0903974. **A** head, full-face view **B** lateral view **C** dorsal view **D** labels.
Figure 15. A, B Apex of mandible C, D Antenna. A *Leptogenys itoi*, subapical tooth absent B *L. breviloba*, subapical tooth present near apical tooth C *L. modiglianii*, antennoreme III ca. 2.3 times as long as wide D *L. breviloba*, antennoreme III ca. 1.6 times as long as wide.

Figure 16. Petiole, lateral view. A *L. breviloba* B *L. itoi*.

Figure 17. Clypeus and mandible, full-face view. A *L. itoi* B *L. kanaoi*. 
to one-fourth of its length; antennomere III ca. 2.3 times as long as wide. Clypeus with lateral lobe, smoothly incurved between lateral lobe and median extension; median extension moderately long, with convex apex. In dorsal view, pronotum longer than wide. Metanotal groove weakly impressed. In profile, propodeal dorsum almost straight. Petiole in profile slightly higher than long, highest just anterior to posterodorsal angle, with fan-shaped node; anterior and dorsal faces forming continuous curve; dorsal face distinctly sloping anteriad; posterior face almost straight but slightly convex.

Head weakly areolate-rugose, longitudinally striate anteriorly; vertex weakly and transversally striate. Mandible smooth. Gastral segment I with scalloped depressions that are irregular in size; distance between depressions distinctly greater than diameter of depressions; interspace between depressions with small punctures; segment II smooth.

Body black, slightly tinged with red; clypeus, mandible, antenna, legs and lower half of petiole dark-red. Apical two or three segments of gaster red-brown. Scalloped depressions on gastral segment I bearing hairs, small punctures without hairs.

**Queen and male.** Unknown.

**Discussion**

In the Oriental region, the members of the *Leptogenys modiglianii* species group are similar to those of the *L. maxillosa* species group, which includes two species, *L. falcigera* Roger, 1861 and *L. pruinosa* Forel, 1900 in the region. They share several features such as the elongate and curved mandible, anterior edge of torulus located anterior to mandible base, short clypeus, eye situated just posterior to clypeus and
breaking outline of lateral margin of head, hypostomal teeth visible in full-face view, petioler node subrectangular in profile, and subpetiolar process consisting of high anterior lobe and thin posterior extension. However, the *L. modiglianii* species group is distinguished from the *L. maxillosa* group by the following contrasting character states (*maxillosa* group in parentheses): clypeus with apical median extension (without median extension), body surface mostly areolate-rugose (with shagreened sculpture), and body extensively covered with standing hairs (without standing hairs).

Mann (1919) indicated that *L. modiglianii* is related to four species in the Australian region: *L. emeryi* Forel, 1901 from Bismarck Islands, *L. foreli* Mann, 1919 from Solomon Islands, *L. triloba* Emery, 1901 from New Guinea, and *L. truncate* Mann, 1919 from Santa Cruz Islands. These four species share the above diagnostic characters with the *modiglianii* species group defined in this paper and possibly belong to this species group.

There is little information about this species group. Most of the specimens examined in this study were collected in one place: Ulu Gombak on the Peninsular Malaysia. This species group may also occur in Java, Kalimantan, and Sulawesi, Indonesia, and additional as-yet undescribed species may be found in Sundaland and New Guinea.

This species group in southeast Asia is divided into three subgroups. One, which contains *L. itoi*, *L. malayana* and *L. modiglianii*, is recognized by elongate antennomere III that is ca. 2.3–2.7 times as long as wide (Fig. 15C), presence of the lateral lobe on the anterior margin of the clypeus (Fig. 17A), short petiole (LPI: 103–118), and fan-shaped petiolar node. The second group, which contains *L. kanaoi* and *L. curva*, is recognized by the strongly curved mandible, relatively short antennomere III that is ca. 2.2 times as long as wide, absence of the lateral lobe on the anterior margin of the clypeus (Fig. 17B), short petiole (LPI: 112–122), and fan-shaped petiolar node. *Leptogeny breviloba* is a remarkable species among this species group, with very short antennomere III that is ca. 1.6 times as long as wide (Fig. 15D), anterior margin of the clypeus with lateral teeth, long petiole (LPI: 94–102), and rectangular petiolar node.

**Acknowledgements**

I would like to express my deep gratitude to Prof. Fuminori Itô (Faculty of Agriculture, Kagawa University, Japan), Ms. Suzanne Ryder (The Natural History Museum, UK), Dr. Maria Tavano (Museo Civico di Storia Naturale Giacomo Doria, Italy), and Mag. Dominique Zimmermann (Naturhistorisches Museum Wein, Austria) for providing access to their facilities and type material. I am also grateful to Dr. Taisuke Kanao (Kyoto University, Japan) and Mr. Taku Shimada (Tokyo, Japan) for help with collecting during field work, and to Mr. Paulus Meleng (Forest Research Centre, Forest Department Sarawak, Malaysia), Prof. Takao Itioka (Kyoto University, Japan), Dr. Munetoshi Maruyama (Kyushu University Museum, Japan) and, Dr. Rosli Hashim (University of Malaya, Malaysia) for help with obtaining permission to conduct my research at the field station of the University of Malaya and in Lambir Hills National Park. The research activities at Lambir Hills National Park were in accordance with the Memorandum of Understanding, signed by the Sarawak Forest Department and the Japan
Research Consortium for Tropical Forests in Sarawak in November 2012, on a joint research in tropical forests in Sarawak. I greatly thank Dr. Seiki Yamane (Kagoshima University Museum, Japan) for reading through an earlier draft of this paper, and Dr. Brian L. Fisher (California Academy of Sciences, USA) and Dr. John E. Lattke (Universidad Central de Venezuela, Venezuela) for the improvement of the manuscript. This work was partly supported by a Grant-in-Aid from the Japanese Society for the Promotion of Science (JSPS) Fellows (no. 26.1907). This is a contribution from the Entomological Laboratory, Kyushu University, Fukuoka (Ser.7, No. 45).

References

Bolton B (1995) A new general catalogue of the ants of the world. Harvard University Press, Cambridge, MA, 504 pp.
Bolton B (2016) An online catalog of the ants of the world. http://www.antcat.org [accessed 22 December 2016]
Chapman JW, Capco SR (1951) Check list of the ants (Hymenoptera: Formicidae) of Asia. Monographs of the Institute of Science and Technology 1: 1–327.
Emery C (1900) Formiche raccolte da Elio Modigliani in Sumatra, Engano e Mentawei. Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova) 20: 661–722. http://doi.org/10.5281/zenodo.25488
Emery C (1901) Formicidarum species novae vel minus cognitae in collectione Musaei Nationalis Hungarici, quas in Nova-Guinea, colonia germanica, collegit. L. Biró. Publicatio tertia. Természetrájzi Füzetek 25: 152–160. http://doi.org/10.5281/zenodo.25495
Emery C (1911) Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. Genera Insectorum 118: 1–125.
Forel A (1900) Les formicides de l’Empire des Indes et de Ceylan. Part VII. Journal of the Bombay Natural History Society 13: 303–332. http://doi.org/10.5281/zenodo.14396
Forel A (1901) Formiciden aus dem Bismarck-Archipel, auf Grundlage des von Prof. D. F. Dahl gesammelten Materials bearbeitet. Mitteilungen aus dem Zoologische Museum in Berlin 2: 1–37. http://doi.org/10.5281/zenodo.14522
Itô F (1996) Colony composition and morphological caste differentiation between ergatoid queens and workers in the ponerine ant genus *Leptogenys* in the Oriental tropics. Ethology Ecology Evolution 9: 335–343.
Itô F (2000) Bionomics of ants in Southeast Asia Tropics [3] –Biology of a ponerine ant genus *Leptogenys*. Insectarium 379: 278–283. https://doi.org/10.1080/08927014.1997.9522876 [In Japanese, with English title]
Mann WM (1919) The ants of the British Solomon Islands. Bulletin of the Museum of Comparative Zoology 63: 273–391. http://doi.org/10.5281/zenodo.25890
Roger J (1861) Die Ponera-artigen Ameisen. (Schluss.) Berliner Entomologische Zeitschrift 5: 1–54. http://doi.org/10.5281/zenodo.25617
Xu Z, He Q (2015) Taxonomic review of the ponerine ant genus *Leptogenys* Roger, 1861 (Hymenoptera: Formicidae) with a key to the Oriental species. Myrmecological News 21: 137–161.