

## Systematics and biogeography of the Indo-Malaysian endemic *Neochauliodes sundaicus* species-group (Megaloptera: Corydalidae)

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**Abstract.** The *Neochauliodes sundaicus* species-group is newly proposed, containing six species and endemic to Indo-Malaysia. All six species are described and illustrated, including two new species: *Neochauliodes parvus* Liu, Hayashi & Flint, sp. n. and *N. peninsularis* Liu, Hayashi & Flint, sp. n. Full species status is given to *N. maculatus* Stitz, 1914, stat. n. and *N. borneensis* van der Weele, 1909, stat. n. A cladistic analysis is conducted to reconstruct the species level phylogeny of the *N. sundaicus* group based on the morphological data. Combining the present morphological phylogeny and historical geography of Indo-Malaysia, the origin and speciation of this species-group is briefly discussed.

### INTRODUCTION

The fishfly genus *Neochauliodes* van der Weele, 1909 is a highly diversified group of the subfamily Chauliodinae, with approximately 40 described species (including subspecies and varieties), ranging from South and Southeast Asia to the Russian Far East. The adult of *Neochauliodes* is characterized by distinct sexual dimorphism of the antenna (pectinate in male but subserrate in female), the straight 1A and 2A, and the wings possessing various pigment patterns. Since the taxonomic study of some early researchers (van der Weele, 1906a,b, 1907, 1909, 1910; Lestage, 1927; Kimmins, 1954), the genus *Neochauliodes* has been almost neglected for several decades. Yang & Yang (1991, 1992, 1993, 1997) described a few new species of *Neochauliodes* from China, and after that Liu & Yang (2005a, b, 2006a) and Liu et al. (2007) made a series of regional revisions on this genus from East Asia. However, the fauna of *Neochauliodes* from South and Southeast Asia is still poorly known; currently with 19 species and subspecies, most of which lack revision or modern redescription since their original publication early in 20th century.

During our current studies of the genus *Neochauliodes* from South and Southeastern Asia, we found that the faunas from the northern Indian subcontinent, Indochina and Indo-Malaysia were completely different, without any common species (Liu, unpubl. data). In Indo-Malaysia, three species, with one subspecies and one variety, were recorded previously, namely *Neochauliodes dispar* (van der Weele, 1906) from Sumatra, *N. sundaicus sundaicus* (van der Weele, 1906) from Malay peninsula, Sumatra, and Java, *N. sundaicus borneensis* van der Weele, 1909 from Borneo, *N. punctatoguttatus* (van der

Weele, 1906) from Java, and *N. punctatoguttatus* var. *maculatus* Stitz, 1914 from Sumatra. Based on our examination, *N. dispar* is quite different from the other four taxa but closer to *N. bowringi* group from China and Indochina because of the posteriorly inflated male tenth tergum and the male tenth sternum with narrowly extended connection to the lateral arms. Considering the appearance and genitalia, the Bornean *N. sundaicus borneensis* differs from *N. sundaicus sundaicus*, and the Sumatran *N. punctatoguttatus* var. *maculatus* can also be distinguished from the Javan *N. punctatoguttatus*; all of them are here regarded as four independent but closely related species. Additionally, two undescribed *Neochauliodes* species from Indo-Malaysia were found that resemble *N. sundaicus* and its three relatives. Therefore, a new *N. sundaicus* species-group is hereby defined by the similar angulately produced male tenth tergum, the male tenth sternum without connections to the lateral arms, and the longitudinally depressed female eighth sternum. The new species-group includes six species (two new to science) endemic to Indo-Malaysia. All are keyed, illustrated and described. A cladistic analysis using the morphological data of the adults is made to reveal the interspecific phylogeny of the *N. sundaicus* group. A brief discussion on the biogeography of this group is also made based on this phylogeny.

### MATERIAL AND METHODS

#### Taxa studied

The specimens used in the present study are deposited in the following collections: BPBM – Bishop Museum, Honolulu; DEIC – Deutsches Entomologisches Institut, MÜNCHENBERG; EUMJ – Ehime University Museum, Matsuyama; HC – Personal collection of Fumio Hayashi, Tokyo; ZMHB – Museum

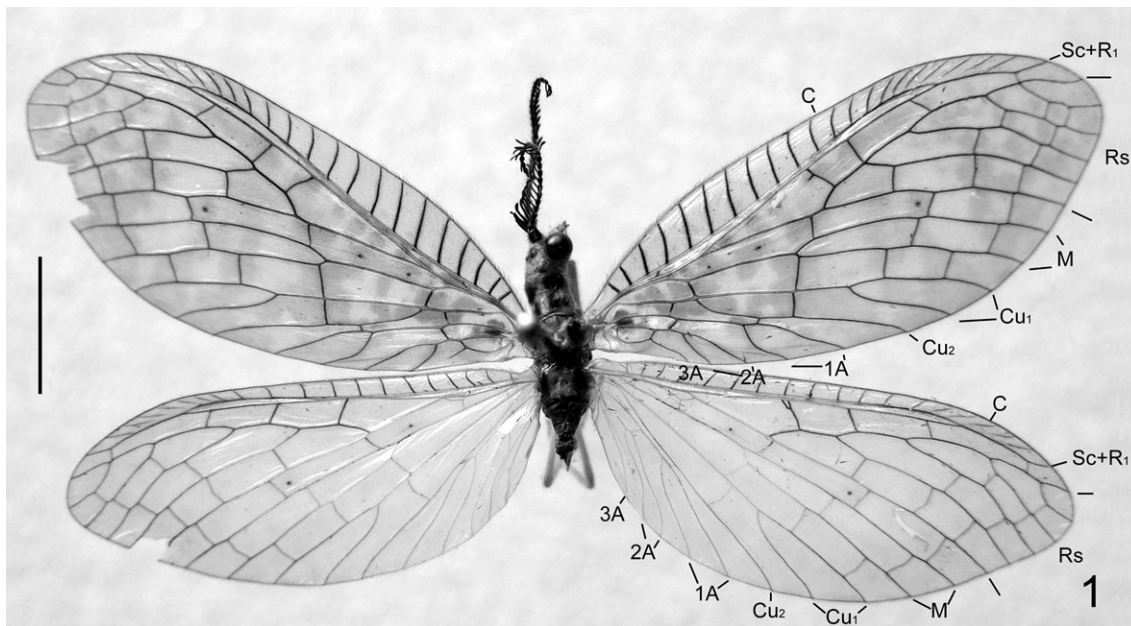


Fig. 1. Habitus photograph of *N. borneensis* van der Weele. Scale line 5.0 mm.

für Naturkunde, Berlin; MNHN – Muséum National d’Histoire Naturelle, Paris; NHMW – Naturhistorische Museum, Vienna; USNM – National Museum of Natural History, Smithsonian Institution, Washington D.C.; NSMT – National Science Museum, Tokyo; RMNH – Nationaal Natuurhistorisch Museum, Leiden.

Labels of the primary types are transcribed verbatim within quotation marks. Additional information that expands or augments the often cryptic text and provides the geographic coordinates is placed in square brackets.

Genitalic preparations were made by clearing the apex of the abdomen in a cold, saturated KOH solution for 8–10 h. After washing out the KOH with acetic acid and water, the apex of the abdomen was transferred to glycerin for further dissection and examination. After examination it was moved to fresh glycerin and stored in a microvial pinned below the specimen. The terminology of the genitalia follows that of Contreras-Ramos (2004).

#### Cladistic analysis

Sixteen adult morphological characters were numerically coded for all six species of the *N. sundaicus* group. *Sinochauliodes squalidus* Liu & Yang, 2006 in the *Parachauliodes* lineage, which was considered to be the sister clade of the *Neochauliodes* lineage (Liu & Yang, 2006b), was herein selected as an outgroup. *Neochauliodes bowringi* (McLachlan, 1867), a representative species from the mainland of East and Southeast Asia, was selected as another outgroup.

The present cladistic analysis was performed using PAUP\* version 4.0b10 (Swofford, 2002) by an exhaustive search, characters unordered and of equal weight because of the small dataset. Bremer’s decay index was calculated with Autodecay version 4.0 (Eriksson, 1998) and PAUP\* version 4.0b10. The unambiguous characters were mapped by MacClade version 4.0 (Maddison & Maddison, 2000).

## RESULTS

### The *Neochauliodes sundaicus* species-group

**Diagnosis.** Small sized, with male forewing length less than 30 mm. Head and prothorax yellow, but sometimes with blackish markings laterally. Wings hyaline;

forewings sparsely or densely dotted with brownish spots, but sometimes almost immaculate. Rs six- to eight-branched; four or five crossveins between  $R_1$  and Rs; M two-branched, but with posterior branch bifurcate distad in hindwing;  $Cu_1$  two- to four-branched; 1A two-branched. Male ninth tergum subquadrate in lateral view, with straight and thickened ventral margin; tenth tergum acutely produced posterodorsad, mostly with a ventral projection; tenth sternum elongate, subtriangular or subtrapezoidal, lateral portions expanded ventrad, forming a median longitudinal groove; lateral arms short and broad, fused with median plate. Female eighth sternum medially with a longitudinal depression, narrow areas laterally to depression much more sclerotized; ninth gonocoxite broad, slightly produced posteroventrad, sometimes with a small lobe at tip; tenth tergum short and stout, posterodorsal corners prominent to some degree.

**Distribution.** Currently, this species-group is only distributed in Indonesia (Sumatra, Java, central and southern Borneo) and Malaysia (Malay Peninsula and northern Borneo), which harbor the typical rain forest habitats of tropical Asia. Based on the scarcity of the specimens, the *N. sundaicus* group is probably rare in the field. The collecting dates of adults are recorded almost over a whole year, except March, April, and June ( $n = 20$ ), but more concentrated from July to December ( $n = 14$ , 70%).

### Key to species of the *N. sundaicus* species-group

- 1 Head laterally with blackish markings. . . . . 2
  - Head yellow, immaculate. . . . . 5
- 2 M with posterior branch bifurcate distad in hindwing. . . . . 3
  - M with posterior branch simple in hindwing. . . . . 4
- 3 Male tenth sternum directed posterodorsad, with median plate gradually narrowed toward apex (Figs 24, 27). . . . .
  - . . . . . *N. parvus* sp. n.
  - Male tenth sternum directed posteriad, with median plate widened at apex (Figs 18, 21). . . . . *N. maculatus*



Figs 2–4. Habitus photographs of the species in *N. sundaicus* group: 2 – *N. borneensis* van der Weele, female holotype; 3 – *N. maculatus* Stütz, male; 4 – ditto, female holotype. Scale lines: 5.0 mm.

- 4 Forewings with numerous distinct brownish spots in proximal costal areas (Figs 6–7); male ninth tergum with posterior margin prominent medially (Fig. 29); male tenth tergum without ventral projection (Fig. 28). . . . . *N. peninsularis* sp. n.
- Forewings with costal areas immaculate (Figs 1–2); male ninth tergum with posterior margin slightly concave medially (Fig. 13); male tenth tergum with a ventral projection (Fig. 13). . . . . *N. borneensis*
- 5 Forewings densely dotted with small brownish spots; male tenth tergum with feebly prominent ventral projection (Figs 8–9); male tenth sternum with median plate narrowed at apex (Fig. 36). . . . . *N. punctatoguttatus*
- Forewings sparsely dotted with several brownish markings, which are fused proximally as arched stripes (Figs 10–11); male tenth tergum with long and acutely pointed ventral projection; male tenth sternum with median plate slightly widened at apex (Fig. 42). . . . . *N. sundaicus*

***Neochauliodes borneensis* van der Weele, 1909, stat. n.**

(Figs 1, 2, 12–17)

*Neochauliodes sundaicus borneensis* van der Weele, 1909: 261.  
Type locality: Borneo (Mahakkam).

**Description. Male.** Body length 14–16 mm; forewing length 21–22 mm, hindwing length 20–21 mm.

Head yellow, vertex sometimes with a pair of tiny brownish markings laterally. Compound eyes black-brown; ocelli yellow, medially margined black. Antenna black except for scape and pedicel yellow. Mouthparts yellow, mandibles with distal half black.

Prothorax yellow, pronotum laterally with two pairs of broad black markings; meso- and metathorax yellow, with a pair of black-brown markings laterally. Legs yellow with short, dense, yellowish setae; tarsi slightly darkened distad. Wings rather short and broad, pale grayish, with several brownish markings. Forewing slightly darkened at pterostigmatic area and dispersedly dotted by indistinct brownish markings, but with a round spot much darker at extreme base; brownish markings on crossveins of  $r_1$ – $rs$ , proximal first  $r$ - $m$ , proximal second  $m$ - $cu$ , and  $cu$  arranged as a transverse band. Hindwing immaculate. Veins dark brown except for those on proximal half of hindwings, pale yellow.  $Rs$  six- or seven-branched; four or five crossveins between  $R_1$  and  $Rs$ ;  $M$  two-branched;  $Cu_1$  two-branched;  $1A$  two-branched.

Abdomen black-brown. Ninth tergum (Figs 12–13) strongly arched, with posterior margin arcuately concave medially in lateral view; in dorsal view posterior margin with a small median incision. Tenth tergum (Figs 13–14) laterally broad, with posterodorsal corner acutely tapered dorsad and with posteroventral corner produced ventrad into a short subtriangular process; in dorsal view acutely pointed and slightly curved medially at tip, with rows of brushy setae on inner portion. Tenth sternum (Figs 12, 15) strongly sclerotized and obliquely directed dorsad, with distal 1/3 narrowed in lateral view; in ventral view median plate slender, strongly narrowed distad with rounded tip, lateral portions expanded ventrad, leaving a median longitudinal groove, and with anteroventral corners acutely pointed.

**Female.** Body length 18–23 mm; forewing length 26–27 mm, hindwing length 23–24 mm.

Eighth sternum (Figs 16–17) in ventral view broad, slightly narrowed posteriad, medially depressed longitudinally, laterally with a pair of narrowly elongate sclerites, which slightly curve laterally on posterior half. Tenth tergum short and stout, with posterodorsal corner strongly produced in lateral view. Gonocoxite broad, posteroventrally with a rounded short process.

**Type material.** Holotype ♀, Indonesia: “Borneo Exped[ition]., Mahakkam [0°05’N, 116°14’E], 1894, Dr. [A.W.] Nieuwenhuis” [1st label, printed with Mahakkam handwritten] / “Museum Leiden” [printed] (RMNH).

**Additional material.** 1 ♀, Central eastern Borneo, 2.xi.1925, H.C. Siebers lgt. (RMNH); 2 ♂, Malaysia: Borneo, Sabah, 75 km Western Lahad Datu, confl. Southern Sabran, Southern Danum [4°34’N, 117°24’E], 200 m, 25.x.1987, J. Huisman & R. de Jong lgt. (RMNH); 1 ♂, Malaysia: Borneo, Sabah, Luasong [4°38’N, 117°23’E], 31.viii.1999, S. Matsumoto lgt. (HC); 1 ♀, Malaysia: Borneo, Sandakan [5°50’N, 118°03’E], ix.1880, Montano & Rey lgt. (MNHN); 1 ♂, Malaysia: Borneo, Tawau, Quoin Hill [5°18’N, 118°45’E], 15.–20.vii.1962, H. Holtmann lgt. (BPBM); 1 ♂, Malaysia: Borneo, Tawau, Quoin Hill, Cocoa Research Station, 19.ix.1962, Y. Hirashima lgt. (BPBM); 1 ♀, Malaysia: Borneo, Sabah, near Kinabalu, Ranau, Mamut copper Mine [5°56’N, 116°40’E], 1,300 m, 25.v.1979, S. Nagai lgt. (EUMJ); 1 ♀, Indonesia: Kalimantan, Balikpapan [1°16’S, 116°50’E] (MNHN).

**Distribution.** This species is endemic to Borneo and distributed both in the Malaysian and Indonesian parts (Kalimantan), but based on the current collecting data it seems to be more frequently encountered in the mountainous region of Sabah, north-eastern Borneo. The collecting dates of the adult range from July to November.

**Remarks.** This species was originally described as a subspecies of *N. sundaicus* based on only one female specimen from Borneo (van der Weele, 1909). However, it differs distinctly from *N. sundaicus* by the head and pronotum with dark patterns and by the small, subtriangular ventral projection of the male tenth tergum. Therefore, it is herein treated as an independent species of the *N. sundaicus* group. We found that the female specimen from Makkaham in RMNH (Leiden Museum) which was designated as type by van der Weele (1909) bears neither type label nor identification label, but by monotypy this female specimen is confirmed to be the holotype of *N. borneensis*.

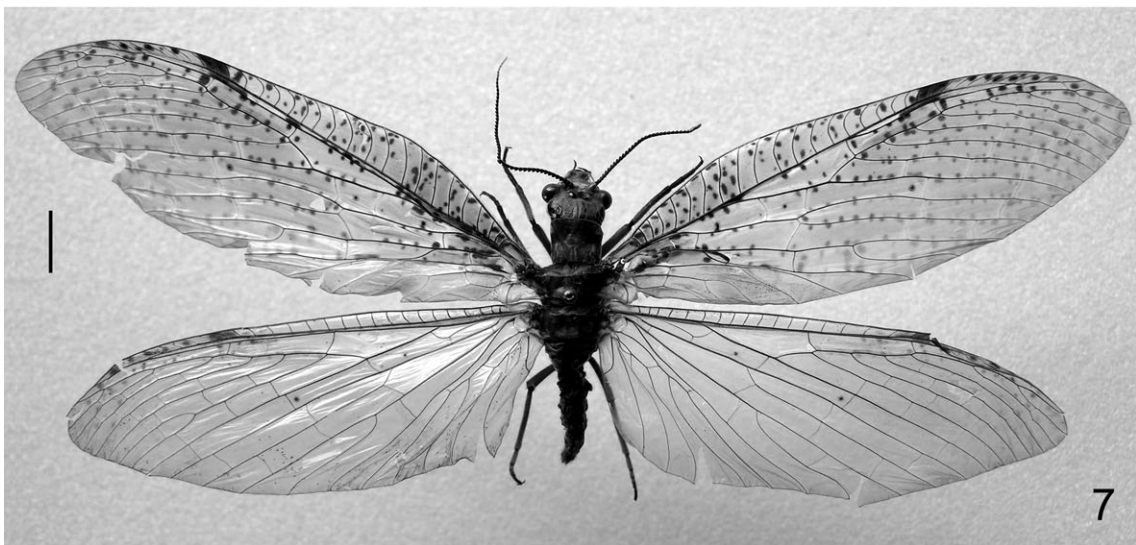
***Neochauliodes maculatus* Stitz, 1914, stat. n.**

(Figs 3, 4, 18–23)

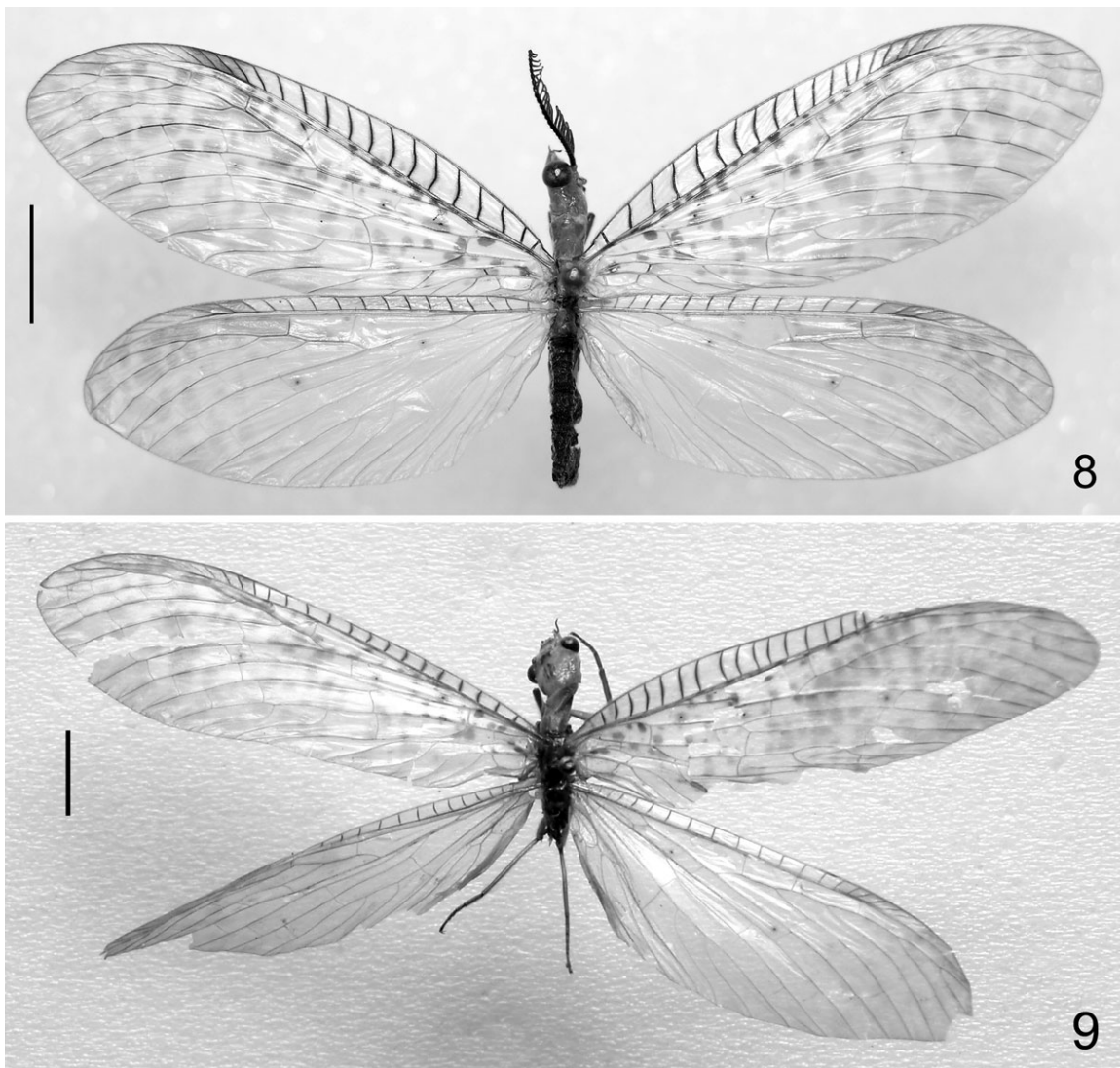
*Neochauliodes punctatoguttatus* var. *maculatus* Stitz, 1914: 204.  
Type locality: Sumatra.

**Description. Male.** Body length 19 mm; forewing length 30 mm, hindwing length 26 mm.

Head pale yellow-brown; vertex laterally with two pairs of black-brown markings and medially with a pair of brownish vittae. Compound eyes black-brown; ocelli yellow, medially margined black. Antenna black-brown except for scape and pedicel yellow-brown. Mouthparts yellow, mandibles with apices black-brown.



Figs 5–7. Habitus photographs of the species in *N. sundaicus* group: 5 – *N. parvus* sp. n., male holotype; 6 – *N. peninsularis* sp. n., male holotype; 7 – ditto, female paratype. Scale lines: 5.0 mm.



Figs 8, 9. Habitus photographs of the species in *N. sundaicus* group: 8 – *N. punctatoguttatus* (van der Weele), male; 9 – ditto, female lectotype. Scale lines: 5.0 mm.

Thorax pale yellow-brown; pronotum anteromedially with a much paler triangular area; meso- and metanota black-brown laterally. Legs yellow, with short, dense, yellowish setae; tibiae with extreme bases black, fore and midtibiae as well as all tarsi brown, tarsal claws red-brown. Wings hyaline, with indistinct brownish markings; pterostigmatic area short and whitish. Forewing respectively with a long and a short brownish stripe beside pterostigmatic area, and with numerous indistinct brownish markings on distal half. Hindwing almost immaculate, with stripes beside pterostigmatic area similar to that on forewing. Veins brown but much darker on forewings. Rs eight-branched; four crossveins between  $R_1$  and Rs; M two-branched in forewing, but with posterior branch bifurcate distad on hindwing;  $Cu_1$  three or four-branched; 1A two-branched.

Abdomen black-brown with yellowish brown venter. Ninth tergum (Figs 18–19) arched, with posterior and ventral margins nearly straight in lateral view. Tenth tergum (Figs 19–20) in lateral view subtrapezoidal, with posterodorsal corner acutely tapered posteriad and with

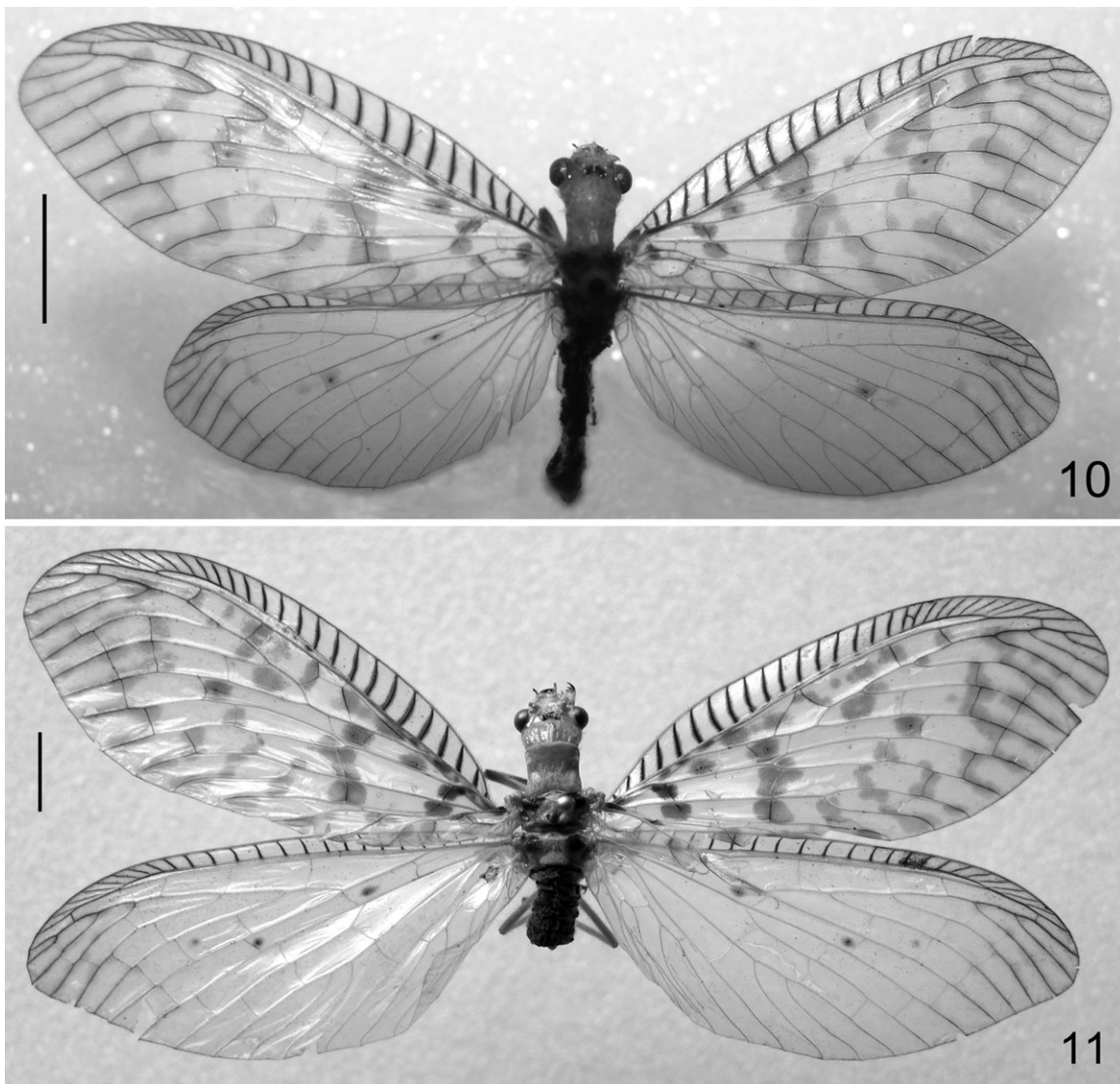
posteroventral corner slightly and roundly prominent; in dorsal view acutely pointed distad, with rows of brushy setae on inner portion. Tenth sternum (Figs 18, 21) strongly sclerotized, in lateral view directed posteriad, with distal 1/3 strongly narrowed and acutely pointed; in ventral view median plate elongatedly trapezoidal, lateral portions expanded ventrad, leaving a median longitudinal groove, distal portion slightly widened with truncate tip.

**Female.** Body length 29 mm; forewing length 32 mm, hindwing length 28 mm.

Appearance similar to male, but wings with much darker pattern, and forewings with some small brownish spots on proximal half of costal areas.

Eighth sternum (Figs 22–23) in ventral view broad, slightly narrowed posteriad, medially depressed longitudinally, laterally with a pair of narrowly elongate sclerites, which gradually widen posteriad. Tenth tergum rather short and stout, with posterodorsal corner rounded and feebly produced. Gonocoxite broad, subquadrate, feebly and roundly prominent posteroventrad.





Figs 10, 11. Habitus photographs of the species in *N. sundaicus* group: 10 – *N. sundaicus* (van der Weele), male lectotype; 11 – ditto, female. Scale lines: 5.0 mm.

**Type material.** Holotype ♀, Indonesia: “Sumatra [no specific locality], coll. v. Studt G[eber (= donor)]” [1st label, yellow, handwritten] / “Type” [2nd label, red, printed] / “*Neochauliodes punctoguttatus* Weele maculatus St[it]z” [3rd label, handwritten] (ZMHB).

**Additional material.** 1 ♂, Indonesia: Sumatra, E. Jacobson & E. Teleman lgt. (RMNH).

**Distribution.** This species is endemic to Sumatra, but due to the insufficient collecting data its detailed distribution in Sumatra is still unknown.

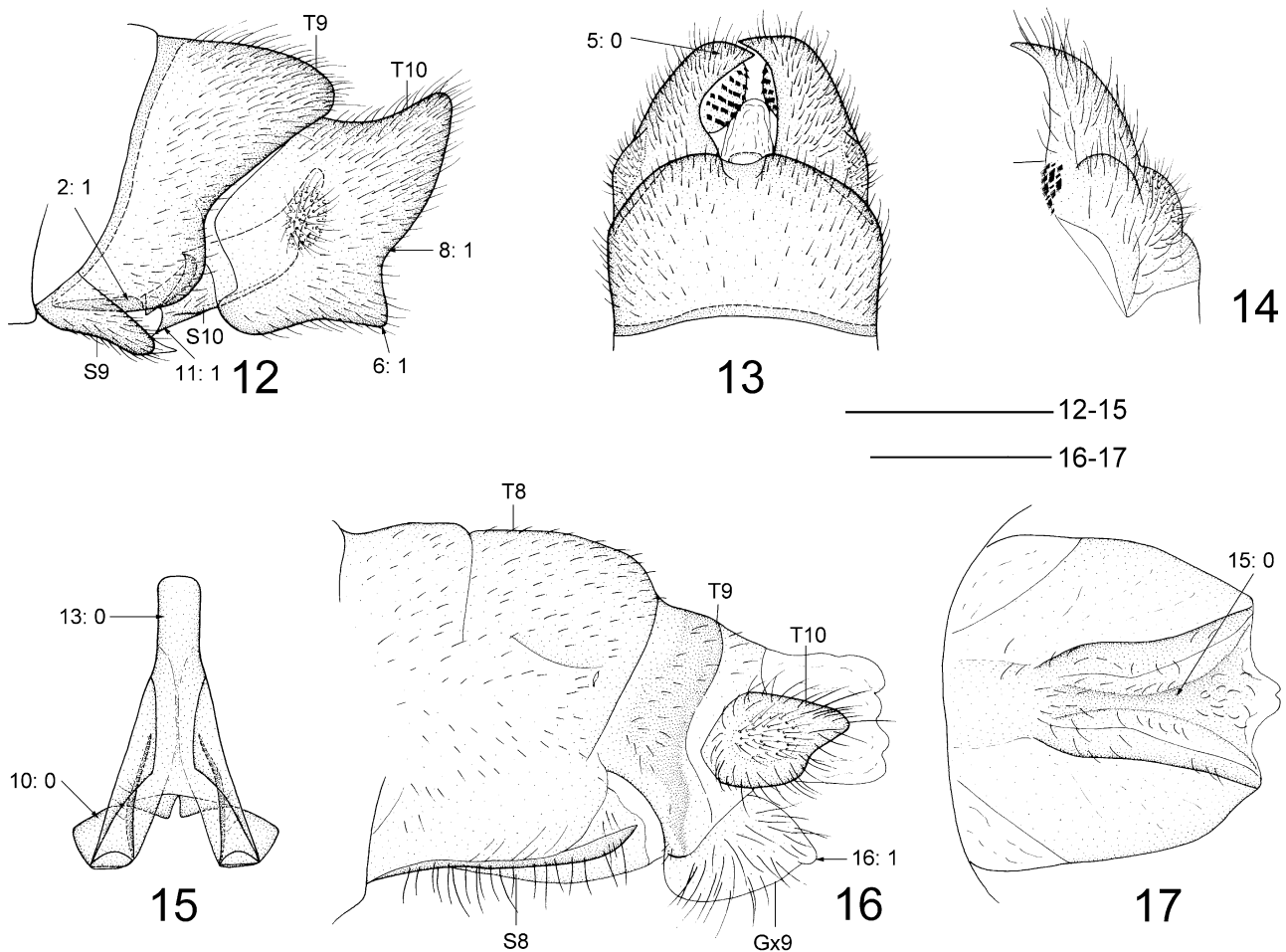
**Remarks.** This species was originally described as a variety of *N. punctatoguttatus* based on only one female specimen from Sumatra (Stitz, 1914). However, it differs distinctly from *N. punctatoguttatus* because the head has a dark pattern. The male of this species is herein described for the first time and the male genitalia are distinguished from those of *N. punctatoguttatus* by the slightly widened and truncate apex of the male tenth sternum. Therefore, we herein treat this as a valid species of the *N. sundaicus* group.

***Neochauliodes parvus* Liu, Hayashi & Flint, sp. n.**  
(Figs 5, 24–27)

**Description. Male.** Body length 14–18 mm; forewing length 18–19 mm, hindwing length 15–16 mm.

Head pale yellow-brown; vertex posterolaterally with a pair of blackish markings. Compound eyes black-brown; ocelli yellow, medially margined dark brown. Antenna black-brown, with scape and pedicel yellow. Mouthparts yellow, mandibles with apices red-brown.

Thorax pale yellow-brown; meso- and metanota laterally black-brown. Legs yellow, with short, dense, yellowish setae; fore- and midtarsi slightly black-brown, tarsal claws red-brown. Wings hyaline, slightly grayish distad; pterostigmatic area short and whitish. Forewing with a brownish stripe proximally to pterostigmatic area, and with a few rather indistinct brownish markings along  $R_1$  and  $R_s$ . Hindwing immaculate throughout. Veins yellow but much darker distad, with costal crossveins mostly black-brown on forewings.  $R_s$  seven- to eight-branched; four crossveins between  $R_1$  and  $R_s$ ; M two-



Figs 12–17. *Neochauliodes borneensis* van der Weele: 12 – male genitalia, lateral view; 13 – ditto, dorsal view; 14 – male tenth tergum, ventral view; 15 – male tenth sternum, ventral view; 16 – female genitalia, lateral view; 17 – female eighth sternum, ventral view. T8–10 – eighth to tenth tergum; S8–10 – eighth to tenth sternum; Gx9 – ninth gonocoxite. Scale lines: 1.0 mm.

branched, but with posterior branch bifurcate distad;  $Cu_1$  three-branched on forewing and four-branched on hindwing; 1A two-branched.

Abdomen black-brown. Ninth tergum (Figs 24–25) arched, with posterodorsal corner distinctly produced, and with anteroventral corner obtusely produced in lateral view. Tenth tergum (Figs 25–26) in lateral view subtrapezoidal, with posterodorsal corner obtusely tapered posteriorly and with posteroventral corner roundly prominent; in dorsal view distal portion acutely pointed, with rows of brushy setae on inner portion. Tenth sternum (Figs 24, 27) strongly sclerotized, in lateral view obliquely directed dorsad, with distal 1/3 strongly narrowed and acutely pointed; in ventral view median plate elongate, subtriangular, gradually narrowed distad with round tip, lateral portions expanded ventrad, leaving a median longitudinal groove.

**Female.** Unknown.

**Type material.** Holotype ♂, Indonesia: “Sipora Island [2°06’S, 99°38’E], West Sumatra, Oct. 1924., C.B.K. and N.S.” [1st label, printed] / “Megaloptera, 15.10[=October].24[=1924]” [2nd label, handwritten] (RMNH). Paratype 1 ♂, same data as holotype (RMNH).

**Distribution.** This species is currently known only from the Sipora Island, a small island located westward to Sumatra.

**Etymology.** The specific epithet “parvus” refers to the rather small body size of the new species.

**Remarks.** This species seems to be closely related to *N. maculatus* by the similar blackish patterned head and dense venation, but it can be distinguished from the latter species by the pale coloration of the wings and the male tenth sternum with narrowed and rounded apex.

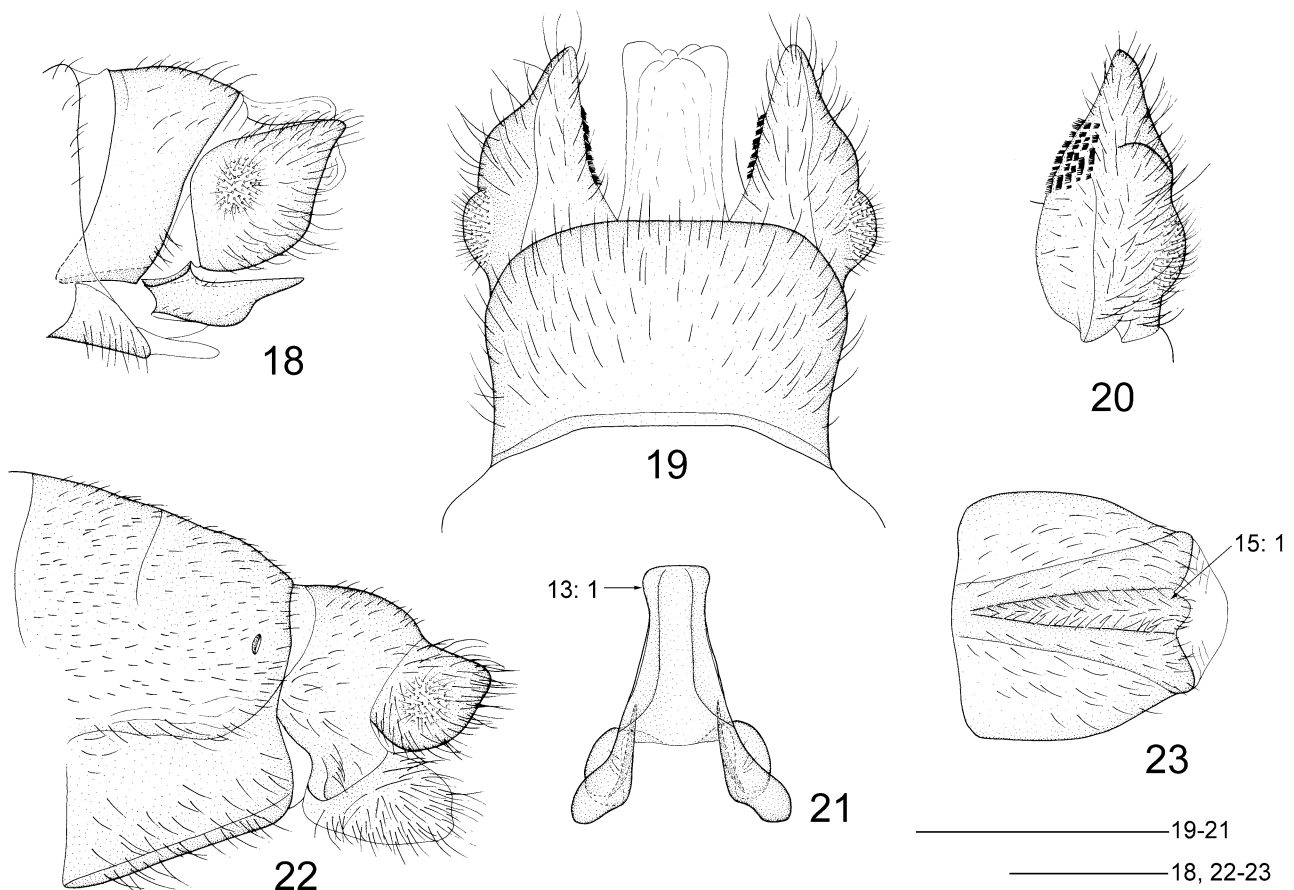
***Neochauliodes peninsularis* Liu, Hayashi & Flint, sp. n.** (Figs 6, 7, 28–32)

**Description. Male.** Body length 22 mm; forewing length 29 mm, hindwing length 24 mm.

Head yellow-brown, vertex laterally with two pairs of brownish markings. Compound eyes brown, ocelli yellow, medially margined black. Antenna black-brown, with scape and pedicel yellow-brown. Mouthparts yellow-brown, mandibles with tips red-brown.

Prothorax yellow, pronotum laterally with a pair of brownish vittae. Meso- and metathorax pale yellow, but laterally pale brown. Legs pale yellow, with short, dense, yellowish setae; joints of femora and tibiae black; fore- and midlegs with distal half of tibiae and entire tarsi





Figs 18–23. *Neochauliodes maculatus* Stitz: 18 – male genitalia, lateral view; 19 – ditto, dorsal view; 20 – male tenth tergum, ventral view; 21 – male tenth sternum, ventral view; 22 – female genitalia, lateral view; 23 – female eighth sternum, ventral view. Scale lines: 1.0 mm.

black-brown; hindlegs with 5th tarsomere brown; tarsal claws red-brown. Wings hyaline, slightly grey-brown; pterostigmatic area short, pale yellow. Forewing with costal area inflated at proximal 1/3, and with a short brownish stripe proximally to pterostigmatic area and numerous small brownish spots, which are mainly along longitudinal veins and much darker proximally. Hindwing mostly immaculate, but with a short brownish stripe proximally to pterostigmatic area and a few indistinct markings along  $R_1$  distad. Veins brown except for veins on anal areas much paler. Rs seven-branched; three or four crossveins between  $R_1$  and Rs; M two-branched;  $Cu_1$  two-branched; 1A two-branched.

Abdomen brown. Ninth tergum (Figs 28–29) arched, posterior margin medially prominent in dorsal view, anteroventral corner rounded in lateral view. Tenth tergum (Figs 28–30) in lateral view subquadrate, slightly widened posteriad, with posterodorsal corner distinctly produced dorsad and distally bearing rows of brushy setae on inner portion. Tenth sternum (Figs 28, 30) strongly sclerotized, extremely elongate; in lateral view median plate gradually narrowed distad and strongly curved dorsad on distal half; in ventral view lateral arms broadly subtriangular, median plate slender, moderately narrowed on distal 1/3 with rounded tip, lateral portions slightly expanded ventrad on proximal half.

**Female.** Body length 26 mm; forewing length 46 mm, hindwing length 41 mm.

Appearance similar to male, with Rs eight- to ten-branched.

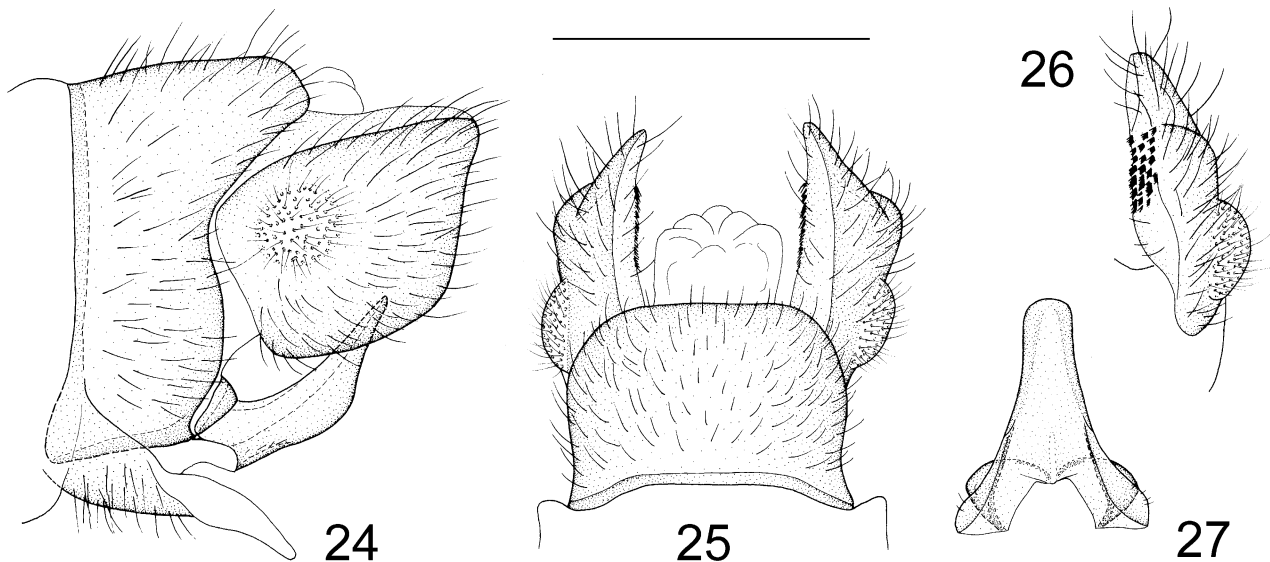
Eighth sternum (Figs 31–32) in ventral view broad, much more sclerotized medially; posteriorly separated, leaving a V-shaped and rugose depression; posterolateral corners slightly prominent. Tenth tergum much longer than gonocoxite, subuliform with tip acutely pointed. Gonocoxite subquadrate, slightly and roundly prominent posteroventrad.

**Type material.** Holotype ♂, Malaysia: “Pahang, Cameron Highlands, Tanah Rata Holiday Chalet [4°28'N, 101°22'E], 19.V.1987, Lee Guidry” [1st label, printed] (USNM). Paratype 1 ♀, Malaysia: “Pahang, Cameron Highland, 4.I.1985” (NSMT).

**Distribution.** This species is endemic to the Cameron Highlands of Malay Peninsula.

**Etymology.** The specific epithet “peninsularis” refers to the distribution of the new species in Malay Peninsula.

**Remarks.** In appearance this species somewhat resembles *N. maculatus* because the head has a dark pattern and the wings with numerous brownish spots. However, the male ninth tergum is produced posteromedially and the posterodorsal corner of the male tenth tergum is vertically produced dorsad, which is unique in the *N. sundaicus* group.



Figs 24–27. *Neochauliodes parvus* sp. n.: 24 – male genitalia, lateral view; 25 – ditto, dorsal view; 26 – male tenth tergum, ventral view; 27 – male tenth sternum, ventral view. Scale lines: 1.0 mm.

***Neochauliodes punctatoguttatus* (van der Weele, 1906)**

(Figs 8, 9, 33–38)

*Chauliodes punctatoguttatus* van der Weele, 1906b: 143. Type locality: Java.

**Description. Male.** Body length 14–16 mm; forewing length 24–25 mm, hindwing length 21–22.

Head yellow throughout. Compound eyes black-brown; ocelli yellow, medially margined black. Antenna black-brown, with scape and pedicel yellow. Mouthparts yellow, mandibles with distal half black-brown.

Thorax yellow; pronotum with anterolateral corners somewhat grayish, meso- and metanota laterally brown. Legs pale yellow-brown, with short, dense, yellowish setae; fore- and midlegs with tibiae and tarsi brown; hind-legs with tips of tibiae and entire tarsi brown; tarsal claws red-brown. Wings hyaline with brownish markings; pterostigmatic area short, whitish. Forewing with a short brownish stripe proximally to pterostigmatic area and densely dotted by numerous small brownish markings, which are usually darkened and fused with each other along first branch of Rs, forming an oblique band extending to M. Hindwing mostly immaculate, with a short brownish stripe proximally to pterostigmatic area and a few indistinct brownish markings along Rs. Veins yellow to brown, with costal crossveins much darker. Rs six-branched; four or five crossveins between R<sub>1</sub> and Rs; M two-branched; Cu<sub>1</sub> two to three-branched; 1A two-branched.

Abdomen dark brown. Ninth tergum (Figs 33–34) arched, with posterior and ventral margins nearly straight, anteroventral corner slightly produced. Tenth tergum (Figs 34–35) in lateral view subquadrate, with posterodorsal corner bluntly tapered posteriad and with posteroventral corner roundly prominent; in dorsal view distal portion acutely pointed and slightly curved medially, with rows of brushy setae on inner portion. Tenth sternum (Figs 33, 36) strongly sclerotized, in lateral view

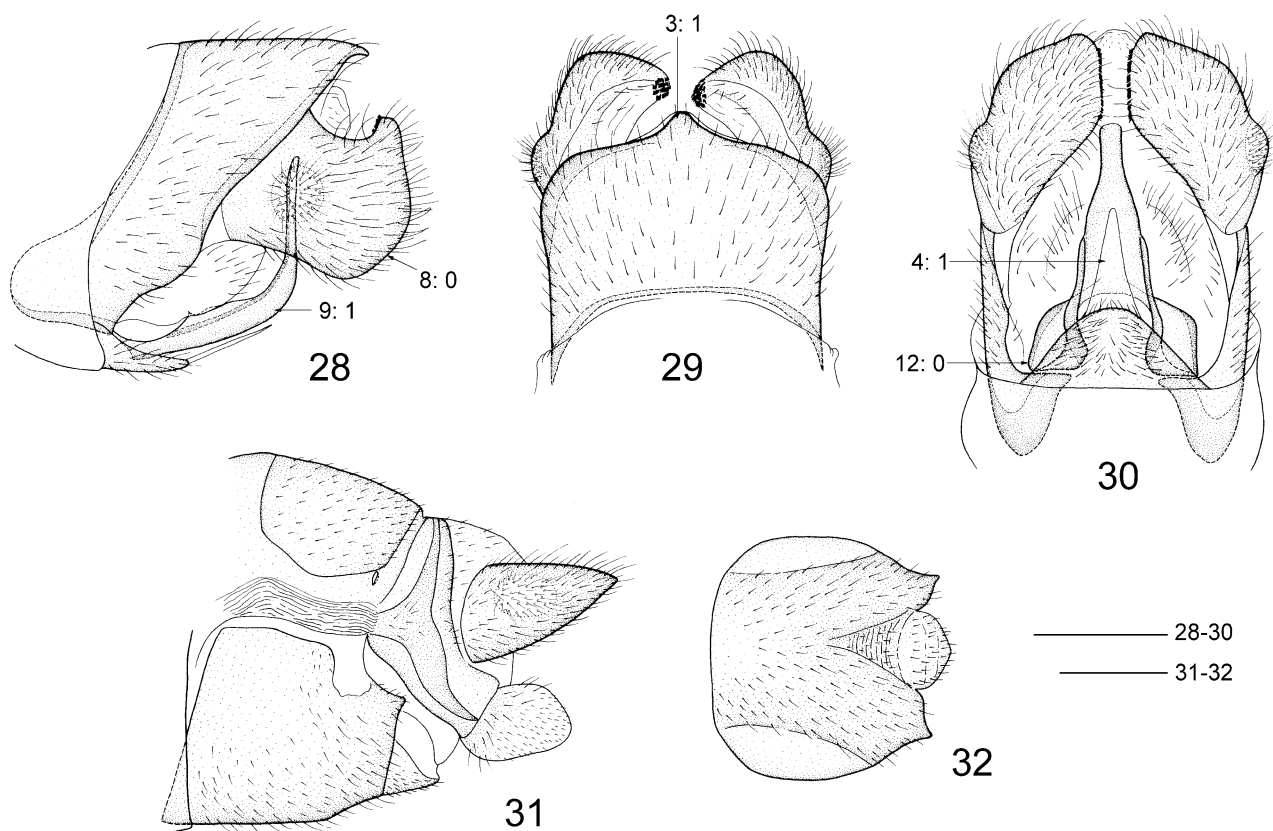
obliquely directed posteroventrad, with distal portion strongly narrowed, acutely produced dorsad; in ventral view median plate elongate, subtriangular, lateral portions expanded ventrad, leaving a deep median longitudinal groove, distal portion distinctly narrowed with round tip.

**Female.** Body length 17–22 mm; forewing length 28–34 mm, hindwing length 26–31 mm.

Eighth sternum (Figs 37–38) in ventral view subquadrate, medially depressed longitudinally, laterally with a pair of narrow, elongate sclerites, which are widened posteriad. Tenth tergum short and stout, with posterodorsal corner prominent in lateral view. Gonocoxite broad and subquadrate, with posteroventral corner slightly produced.

**Type material.** Lectotype ♀ (present designation), Indonesia: “Java [no specific locality]” [1st label, printed] / “♀” [2nd label] / “dispar v[an]d[er] Weele, T, det. v[an]. d[er]. Weele” [3rd label, handwritten with name of identifier printed] / “punctatoguttatus v[an]d[er] Weele, type ♀, det. v[an]. d[er]. Weele” [4th label, handwritten with name of identifier printed] (NHMW). Paralectotype 1 ♀ (present designation), “Sunda Yns? [obscure locality]” [1st label, handwritten] / “♀” [2nd label] / “dispar v[an]d[er] Weele, T, det. v[an]. d[er]. Weele” [3rd label, handwritten with name of identifier printed] / “punctatoguttatus v[an]d[er] Weele, ♀, det. v[an]. d[er]. Weele” [4th label, handwritten with name of identifier printed] (NHMW).

**Additional material.** 1 ♀, Indonesia: Java, Sukabumi [6°12'S, 106°46'E], M.E. Walsh lgt. (NSMT); 2 ♀, Indonesia: Java, Sukabumi, J. Lindemans lgt. (RMNH); 1 ♀, Indonesia: Java, Sukabumi, i.1935, Groenendaal lgt. (RMNH); 5 ♂, 5 ♀, Indonesia: Java, Sukabumi (RMNH and DEIC); 13 ♂, 6 ♀, Indonesia: Java, Central Djampang [6°28'S, 106°43'E], 600–800 m, M.E. Walsh lgt. (RMNH); 1 ♀, Indonesia: Java, Djampang, x.1933, M.E. Walsh lgt. (RMNH); 2 ♂, Indonesia: Java, Djampang, xii.1934, M.E. Walsh lgt. (RMNH); 1 ♂, 1 ♀, Indonesia: Java, Djampang, Bantam, Bibidjilan, x.1935 (RMNH); 1 ♀, Indonesia: Java, Djampang, Bantam, Bibidjilan, vii.1938 (RMNH); 1 ♀, Indonesia: Java, Djampang, Bantam, Bibidjilan (RMNH); 1 ♂, Indonesia: Java, Djampang, Bantam, Bibidjilan, xii.1938 (RMNH); 1 ♂, Indonesia: Java, Djampang, Bantam,



Figs 28–32. *Neochauliodes peninsularis* sp. n.: 28 – male genitalia, lateral view; 29 – ditto, dorsal view; 30 – ditto, ventral view; 31 – female genitalia, lateral view; 32 – female eighth sternum, ventral view. Scale lines: 1.0 mm.

Bibidjilan, xi.1935 (RMNH); 1 ♀, Indonesia: Java, Mt. Gedeh, Selabintanah [6°47'S, 108°58'E], 1,200 m, ix.1935 (RMNH); 1 ♂, Indonesia: Java, Oedjoeng Genteng [6°48'S, 107°36'E], v.1939, M.E. Walsh lgt. (RMNH); 1 ♂, 2 ♀, Indonesia: Java (ZMHB); 1 ♀, Indonesia: Java, Tjipanas [6°34'S, 106°25'E], 6.ii.1965, J. Winkler lgt. (BPBM); 1 ♂, Borneo [probably mislabeled] (ZMHB); 7 ♂, 4 ♀, Tonkin [probably mislabeled] (MNHN).

**Distribution.** This species seems to be endemic to Java and mainly occurs in the western part of this island according to the present detailed collecting data. The specimens labeled as collected from Borneo and Tonkin (Northern Vietnam) are probably mislabeled.

**Remarks.** This species seems related to *N. maculatus* in having similar wing patterns, but it can be distinguished from the latter species by the immaculate yellowish head and the male tenth sternum with narrowed apex. In *N. maculatus* the head possesses black markings and the male tenth sternum is widened on apex.

***Neochauliodes sundaicus* (van der Weele, 1906)**

(Figs 10, 11, 39–44)

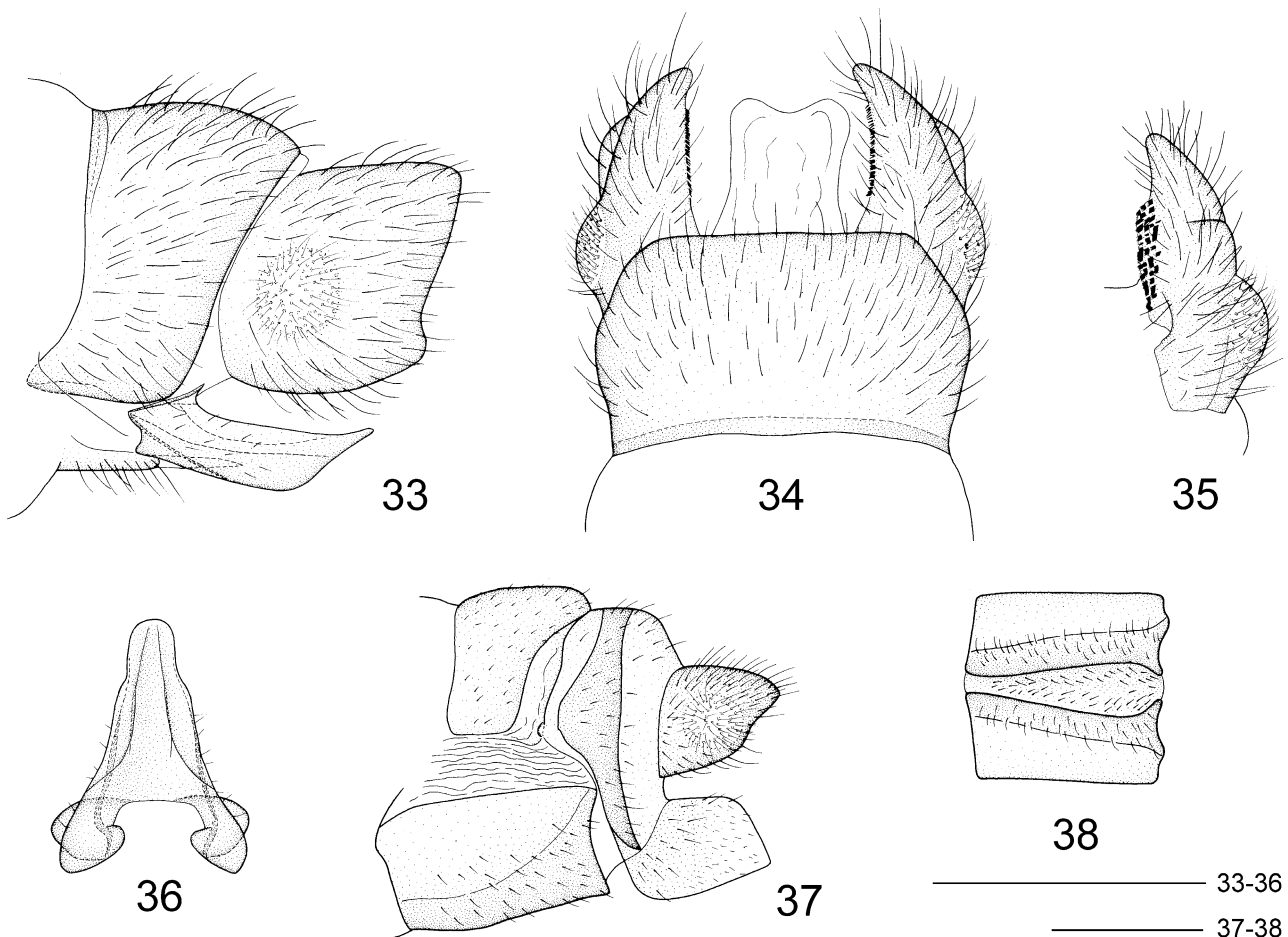
*Chauliodes sundaicus* van der Weele, 1906b: 143. Type locality: Sumatra and Java.

**Description. Male.** Body length 14–20 mm; forewing length 22–26 mm, hindwing length 21–23.

Head yellow throughout. Compound eyes black-brown; ocelli yellow, medially margined black. Antenna black with scape and pedicel yellow. Mouthparts yellow, mandibles with distal half black.

Thorax yellow; meso- and metanota laterally black-brown. Legs yellow, with short, dense, yellowish setae; foreleg with distal 1/3 of femora, as well as entire tibia and tarsi, black-brown; mid- and hindlegs with only tips of femora and tibiae darkened, and with tarsi mostly black-brown; tarsal claws reddish brown. Wings hyaline, with brownish markings; pterostigmatic area indistinct. Forewing sparsely dotted by a few brownish markings, which are much darker on base and fused as an arched band along the proximal r-m, m-cu and cu; distal markings much paler and extending along longitudinal veins as several narrow stripes. Hindwing mostly immaculate, with two brownish spots on nygmata between Rs and M, and distally with indistinct stripes along longitudinal veins. Veins yellow but brownish distad, with costal crossveins blackish brown. Rs six- to seven-branched, distinctly curved posteriad; four or six crossveins between R<sub>1</sub> and Rs; M two-branched; Cu<sub>1</sub> two-branched on forewing and three-branched on hindwing; 1A two-branched.

Abdomen black-brown. Ninth sternum (Figs 39–40) arched, with slightly concave posterior margin and truncate ventral margin, anteroventral corner roundly produced. Tenth tergum (Figs 40–41) in lateral view suboblong, posteriorly bifurcate into two processes; dorsal process short, blunt, directed medially; ventral process long, acutely pointed; inner portion with rows of brushy setae. Tenth sternum (Figs 39, 42) strongly sclerotized; in lateral view slightly curved dorsad, with distal



Figs 33–38. *Neochauliodes punctatoguttatus* (van der Weele): 33 – male genitalia, lateral view; 34 – ditto, dorsal view; 35 – male tenth tergum, ventral view; 36 – male tenth sternum, ventral view; 37 – female genitalia, lateral view; 38 – female eighth sternum, ventral view. Scale lines: 1.0 mm.

half slightly narrowed; in ventral view median plate elongate, subtrapezoidal, gradually narrowed distad, with slightly widened and truncate apex, lateral portions expanded ventrad, leaving a median longitudinal groove.

**Female.** Body length 26–27 mm; forewing length 33–35 mm, hindwing length 30–31 mm.

Eighth sternum (Figs 43–44) in ventral view broad, slightly narrowed posteriorly, medially much more sclerotized, posterior half medially depressed longitudinally. Tenth tergum stoutly ovoid with rounded tip in lateral view. Gonocoxite broad, posteroventrally with a rounded short process.

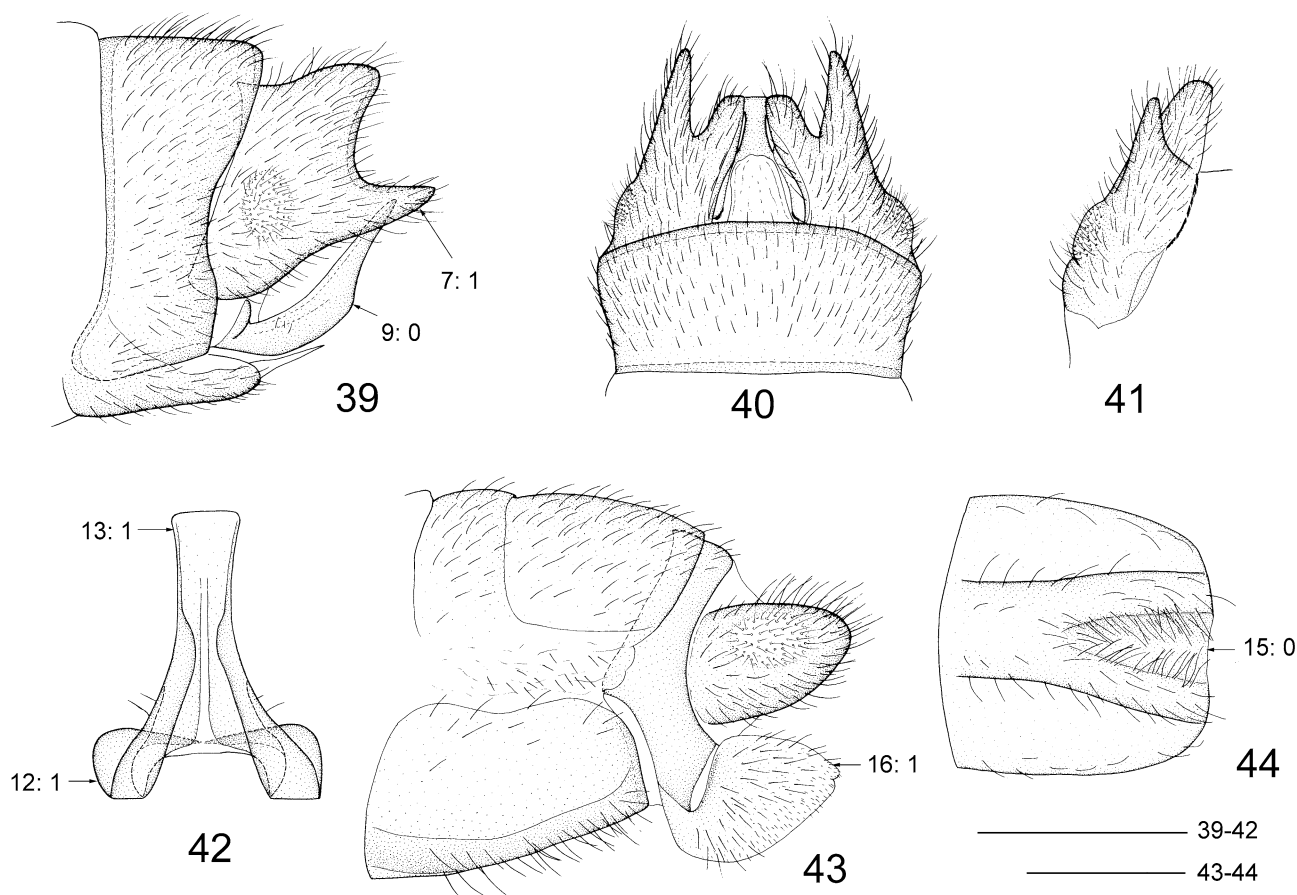
**Type material.** Lectotype ♂ (present designation), Indonesia: “N[ord]O[sten] (=northeastern). Sumatra, Deli [=Labuhandeli, 3°45’N, 98°41’E], L. Martin S[ammler] (=collector)” [1st label, yellow, printed] / “Type” [2nd label, red, printed] / “Chauliodes *sundaicus* Type v[an]d[er]Weele” [3rd label, handwritten] (ZMHB). Paralectotypes: 1 ♀ (present designation), Indonesia: “Sumatra [no specific locality]” [1st label, handwritten] / “Mus[eum]. Berol[in] (=Berlin).” [2nd label, printed] / “Chauliodes *sundaicus* Type v[an]d[er]Weele” [3rd label, handwritten] / “Museum Leiden” [4th label, printed] (RMNH); 1 ♀ (present designation), Indonesia: “Java, Buitenzorg [=Bogor, 6°35’S, 106°47’E], Ude S[ammler] (=collector).” [1st label, yellow, handwritten] / “Type” [2nd label, red, printed] / “Chauliodes

*sundaicus* Type v[an]d[er]Weele” [3rd label, handwritten] (ZMHB).

**Additional material.** 1 ♂, Indonesia: Sumatra? (ZMHB); 1 ♀, Malaysia: Selangor, Hulu Langat [3°06’N, 101°48’E], x.1990, H.S. Yong lgt. (HC); 1 ♂, 1 ♀, Malaysia: Cameron Highlands, v.1988 (HC).

**Distribution.** This species is widely spread from Malay Peninsula through Sumatra to western Java.

**Remarks.** This species can be easily distinguished from the other members of the *N. sundaicus* group by the remarkable arched stripe on the forewing and the male tenth tergum with a long and acutely produced ventral projection. Ohl & Oswald (2004) listed three syntypes of *N. sundaicus* in ZMHB (Berlin Museum) but did not designate holotype or lectotype. Based on our examination of the collection in RMNH (Leiden Museum), we found a female specimen from Sumatra with an original handwritten identification and type label of van der Weele. So, we consider that the three syntypes mentioned to be in Berlin Museum by van der Weele (1906b, 1910) are respectively deposited in ZMHB and RMNH currently. The male specimen with a single collecting label as “Sumatra?”, which was considered as one of the syntypes, should be excluded from the type series of *N. sundaicus*.



Figs 39–44. *Neochauliodes sundaicus* (van der Weele): 39 – male genitalia, lateral view; 40 – ditto, dorsal view; 41 – male tenth tergum, ventral view; 42 – male tenth sternum, ventral view; 43 – female genitalia, lateral view; 44 – female eighth sternum, ventral view. Scale lines: 1.0 mm.

### Characters of cladistic analysis

Morphological characters used in the phylogenetic analysis are listed below. 0 = plesiomorphic state, 1 = apomorphic state, ? = unavailable. The character matrix is given in Table 1.

1. Posterior branch of M vein in hind wing: (0) simple; (1) bifurcate distad (Figs 3–5). In the subfamily Chauliodinae, the M vein is proximally bifurcate into two long branches and the posterior branch on the hindwing is mostly simple. However, in *N. maculatus* and *N. parvus*, the posterior branch of M apomorphically possesses a distal bifurcation in the hindwing.

2. Male ninth tergum in lateral view: (0) narrowed and pointed ventrad; (1) not narrowed ventrad, with truncated and thickened ventral margin (Figs 12, 18, 24, 28, 33, 39). The male ninth tergum of most groups of Chauliodinae is an arched structure, laterally narrowed and pointed ventrad, while in the *N. sundaicus* group the male ninth tergum is not pointed ventrad but possesses a truncate and thickened ventral margin.

3. Male ninth tergum in dorsal view: (0) without median projection; (1) with a median projection (Fig. 29).

4. Male ninth sternum: (0) with short subtriangular membranous lobe (Figs 12, 39); (1) with long subtriangular membranous lobe (Figs 18, 24, 28, 33). In the *Neochauliodes* lineage and *Parachauliodes* lineage, the male

ninth sternum bears a subtriangular membranous lobe posteriad. In *N. borneensis* and *N. sundaicus*, the lobe is short, less than a half of the length of the male ninth sternum, which is considered to be plesiomorphic. However, in the other members of *N. sundaicus* group, the lobe is well developed, nearly as long as the male ninth sternum.

5. Male tenth tergum: (0) with apex produced posteriad (Figs 13, 19, 25, 29, 34, 40); (1) with apex inflated. The male tenth tergum in most groups of Chauliodinae is plesiomorphically presented as a pair of claspers with the apices produced posteriad. In the *Neochauliodes* lineage and *Parachauliodes* lineage, however, the male tenth tergum is inflated apically, except for the *N. sundaicus* group with a posteriorly produced tenth tergum.

6. Male tenth tergum: (0) without ventral projection (Fig. 30); (1) with ventral projection (Figs 14, 20, 26, 35, 41). The male tenth tergum in *Neochauliodes* is mostly a simple structure without additional projections, while five species of the *N. sundaicus* group possess a modified male tenth tergum, which bears a projection ventrad.

7. Male tenth tergum with ventral projection: (0) feebly prominent (Figs 20, 26, 35); (1) strongly prominent (Figs 14, 41). The ventral projection of the male tenth tergum in the *N. sundaicus* group is feebly prominent in *N. maculatus*, *N. parvus*, and *N. punctatoguttatus*, while it is

TABLE 1. Character matrix.

Characters	0000000001111111 1234567890123456
Taxa	
<i>Sinochauliodes squalidus</i>	0000100000000000
<i>Neochauliodes bowringi</i>	0000100011010000
<i>Neochauliodes borneensis</i>	0100011100110101
<i>Neochauliodes maculatus</i>	1101010100111110
<i>Neochauliodes parvus</i>	1101010100110???
<i>Neochauliodes peninsularis</i>	0111000010000100
<i>Neochauliodes punctatoguttatus</i>	0101010100110110
<i>Neochauliodes sundaicus</i>	0100011100011101

strongly prominent in *N. borneensis* and *N. sundaicus*, which is considered to be apomorphic.

8. Male tenth tergum: (0) dorsoventrally narrow, nearly as wide as 1/2 of ninth tergum (Fig. 28); (1) dorsoventrally broadened, nearly as wide as 2/3 of ninth tergum (Figs 12, 18, 24, 33, 39). The male tenth tergum is basically narrow dorsoventrally in Chauliodinae, barely as wide as 1/2 of the ninth tergum. However, in *N. borneensis*, *N. maculatus*, *N. parvus*, *N. punctatoguttatus*, and *N. sundaicus*, the male tenth tergum is broadened dorsoventrally, nearly equal to 2/3 of the ninth tergum in width.

9. Male tenth sternum: (0) short (Figs 12, 18, 24, 33, 39); (1) long (Fig. 28). The male tenth sternum is a strongly sclerotized structure with a median plate and a pair of lateral arms in Chauliodinae. The short male tenth sternum, which is shorter than the length of male ninth plus tenth tergum, is shared by many genera of Chauliodinae and considered to be plesiomorphic. However, most species of *Neochauliodes* possess a long male tenth sternum, which is as long as male ninth plus tenth tergum, except for some species of the *N. sundaicus* group retaining the plesiomorphic short tenth sternum.

10. Male tenth sternum with lateral arm: (0) fused with median plate, without narrow structure for connection (Figs 15, 21, 27, 30, 36, 42); (1) connected to median plate by a narrow extended structure. The lateral arms of the male tenth sternum in Chauliodinae are mostly fused with the median plate by no structure for connection, while in *Neochauliodes* the lateral arms are generally fused with the median plate by a narrow extended structure except for the species of the *N. sundaicus* group.

11. Male tenth sternum with median plate: (0) not protruding anterolaterally (Figs 28, 39); (1) angulately protruding anterolaterally (Figs 12, 18, 24, 33). The median plate of the male tenth sternum in Chauliodinae generally has its lateral margins slightly expanded ventrad but without anterolateral protrusion, while in *N. borneensis*, *N. maculatus*, *N. parvus*, and *N. punctatoguttatus*, the lateral margins of the male tenth sternum are angulately protruding anteroventrally.

12. Male tenth sternum with lateral arm: (0) angulate anterolaterally (Fig. 30); (1) rounded anterolaterally (Figs 15, 21, 27, 36, 42). The lateral arms of the male tenth sternum are generally angulate anterolaterally in Chauliodinae, but usually rounded in *Neochauliodes*. However,

*N. peninsularis* in the *N. sundaicus* group still retains the plesiomorphic angulate lateral arms.

13. Male tenth sternum with median plate: (0) narrowed on apex (Figs 15, 27, 30, 36); (1) widened on apex (Figs 21, 42).

14. Female eighth sternum: (0) without median depression; (1) with a median depression (Figs 17, 23, 32, 38, 44). The female eighth sternum is a broad sclerotized plate, with posterior portion more or less produced. In *N. sundaicus* group, the female eighth sternum is longitudinally depressed medially, while in the other *Neochauliodes* species, as well as other genera of Chauliodinae, such a median depression is absent.

15. Female eighth sternum with median depression: (0) extending from middle to posterior margin (Figs 17, 32, 44); (1) extending from anterior margin to posterior margin (Figs 23, 38).

16. Female ninth gonocoxite: (0) without additional lobe at posteroventral tip (Figs 22, 31, 37); (1) with a small lobe at posteroventral tip (Figs 16, 43). The female ninth gonocoxite (ovipositor) in Chauliodinae is a pair of membranous valvate structure, with or without a pair of articulate styli posteroventrally. In *Neochauliodes*, the female ninth gonocoxite mostly lacks the styli, while in *N. borneensis* and *N. sundaicus* the female ninth gonocoxite bears a pair of small lobes posterolaterally, which are fused with the gonocoxite.

### Results of cladistic analysis

The exhaustive search resulted in a single most parsimonious tree (length = 21, consistency index (CI) = 0.7619, retention index (RI) = 0.7500) (Fig. 45). The monophyly of the *N. sundaicus* group was well supported by the male ninth tergum not produced ventrad (character 2:1) and the longitudinally depressed female eighth sternum (character 14:1). *Neochauliodes peninsularis* occurred as a sister to all the other five group members, which formed a monophyletic subclade defined by the dorsoventrally broadened male tenth tergum with ventral projection (characters 6:1, 8:1). Within this subclade, *N. borneensis* and *N. sundaicus* grouped as a sister pair by the strongly produced ventral projection of the male tenth tergum (character 7:1) and the female ninth gonocoxite with an additional lobe posteroventrad (character 16:1), while *N. punctatoguttatus*, *N. maculatus*, and *N. parvus* formed another monophyletic group due to the female eighth sternum thoroughly separated by the longitudinal depression (character 15:1).

## DISCUSSION

### Phylogenetic affinities

The species-level phylogeny of *Neochauliodes* has been poorly studied so far. The present phylogeny on the *N. sundaicus* group is the first but preliminary attempt to reveal the interspecific relationships among some *Neochauliodes* species. Although the current monophyly of the *N. sundaicus* group is not rigorously tested in a comprehensive phylogeny including all the *Neochauliodes* species, the assemblage of the synapomorphic characters



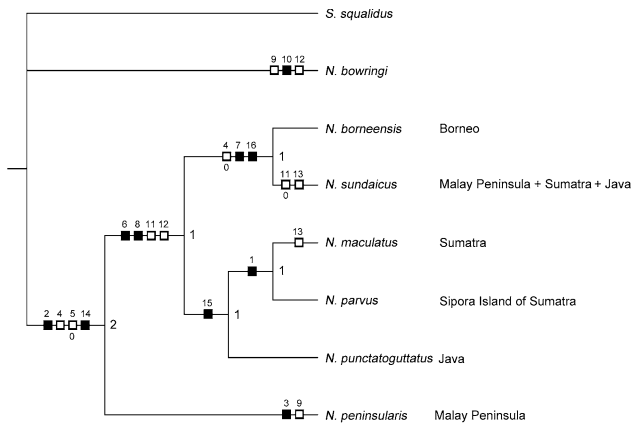


Fig. 45. Phylogeny of the *N. sundaicus* group: The most parsimonious tree, with assigned apomorphic characters shown on the branches. ■ – apomorphic characters, □ – parallelisms or reversals, with reversal character states shown below the open squares. Bremer's decay indices are shown at nodes.

is distinguishable and not shared by any other known species. A seemingly related species, *N. indicus* (van der Weele, 1907) from India, which possesses a male ninth tergum and tenth sternum similar to those of the *N. sundaicus* group, differs in that the apically rounded tenth tergum (Kimmins, 1954) is more like the other *Neochauliodes* species and the female eighth sternum lacks the longitudinal groove (Liu, pers. observ.). Generally, compared with the other *Neochauliodes* species, the members of the *N. sundaicus* group retain many more plesiomorphic characters, e.g., the angulately produced male tenth tergum, the short male tenth sternum, and the lateral arms of male tenth sternum without extended structure for connection to the median plate, which indicate that the *N. sundaicus* group might be a clade of *Neochauliodes* that diverged early.

### Biogeography

The genus *Neochauliodes* is the single representative of the subfamily Chauliodinae in Indo-Malaysia and mostly composed of the species of the *N. sundaicus* group. Besides *Neochauliodes*, four other genera of Megaloptera occur in Indo-Malaysia: The Corydalinae genera *Nevromus* Rambur, 1842 from Sumatra, Java, and Borneo (Glorioso, 1981), *Neurhermes* Navás, 1932 from Malay Peninsula, Sumatra, and Java (Glorioso, 1981), and *Protohermes* van der Weele, 1907 from Borneo (Liu et al., 2008a), and the Sialidae genus *Indosialis* Lestage, 1927 from Malay Peninsula and Borneo (Liu et al., 2008). Compared with the other megalopteran genera from Indo-Malaysia, the distribution of the *N. sundaicus* group is relatively wider, occupying most of main insular regions to the west of the Wallace line (Fig. 46).

Due to the freshwater habitats, the speciation of Megaloptera is probably prone to be affected by the geographical vicariance. As noted by Liu & Yang (2006b) and Liu et al. (2008b), the genus *Neochauliodes* together with its sister genus *Nigronia* Banks, 1908 from eastern Nearctic realm (Liu & Yang, 2006b) might have diverged during or even before Eocene due to the isolation



Fig. 46. Distribution map of species in the *N. sundaicus* group: ● – *N. borneensis*; ★ – *N. maculatus*; ▲ – *N. parvus* sp. n.; ■ – *N. peninsularis* sp. n.; + – *N. punctatoguttatus*; ⊙ – *N. sundaicus*.

between Eurasia and North America. Moreover, as an early divergent group of *Neochauliodes*, the *N. sundaicus* group might have been formed as a distinct clade by the transgressive events between Sundaland (Malay Peninsula, Sumatra, Java, and Borneo) and Eurasia during Eocene (Hall, 2001). Subsequently, the speciation of this species-group may have been caused by a series of insular geographical vicariations in the Cenozoic based on the currently obtained interspecific phylogeny. From Early to Middle Miocene, Sumatra and Java were mostly submerged by shallow sea, remaining a few small islands southwestern to a land mass formed by the fusion of the Malay Peninsula and Borneo during that period (Hall, 2001). This might be related to the separation of *N. peninsularis* from the other group members and might initiate the speciation among different islands, presumably involving the speciation of *N. sundaicus*, *N. maculatus*, and *N. punctatoguttatus*. The wide distribution of *N. sundaicus* might fit with the event of reconnection of Sumatra and Java to the Malay Peninsula by a land bridge in Late Miocene (Hall, 2001), which made faunal introductions possible from Sumatra and Java to Malay Peninsula and Borneo. Furthermore, the divergence between *N. borneensis* and *N. sundaicus* might be caused by the isolation of Borneo after the Pleistocene, while the origin of *N. parvus* might be associated with the vicariance between Sumatra and the Sipora Island, which has happened more recently. However, this matching between the speciation of the *N. sundaicus* group and the formation of the Indo-Malaysian islands was made according to the morphological phylogeny, which cannot be used to estimate the timing of divergence, so that further verification should be made when a molecular phylogeny is available in the future.

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