

Systematics and biogeography of the dobsonfly genus *Neurhermes* Navás (Megaloptera: Corydalidae: Corydalinae)

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Abstract

The Oriental dobsonfly genus *Neurhermes* Navás is one of the most impressive megalopterans because of the striking coloration and marking patterns, which probably imitate some diurnal toxic moths. In this paper, all seven species of *Neurhermes* are described or re-described, and illustrated, with a new species, namely *Neurhermes nigerescens* **sp.n.**, described from northeastern India. Lectotypes of *Neurhermes costatostrata* (van der Weele, 1907) and *Neurhermes tonkinensis* (van der Weele, 1909) are herein designated. *Neurhermes bipunctata* Yang & Yang, 1988 is treated as a junior synonym of *Neurhermes selysi* (van der Weele, 1909). A phylogeny of *Neurhermes* is reconstructed based on the morphological data of the adults. Combining this phylogeny and the geographical distribution, *Neurhermes* is considered to have an origin and a historically widespread distribution in southern Eurasia at least during Eocene. The speciation within *Neurhermes* might have happened because of the Tertiary orogenic events after the collision between the Indian subcontinent and Eurasia. The separation of Sundaland from Eurasia and the island formation within Sundaland possibly shaped the fauna within the clade comprising the species, i.e. *Neurhermes maculipennis* (Gray in Cuvier, 1832), *Neurhermes sumatrensis* (van der Weele, 1909), and *Neurhermes tonkinensis* (van der Weele, 1909), from Indochina and Malesia.

Key words

Megaloptera, Corydalidae, *Neurhermes*, systematics, biogeography, new species, Oriental realm.

1. Introduction

The megalopteran genus *Neurhermes* Navás, 1915 belongs to the subfamily Corydalinae (dobsonflies) of the family Corydalidae. Species in this genus mainly live in the mountainous areas with subtropical or tropical rainforest, and rely on the clear lotic habitat for the larvae. The adults of *Neurhermes* are among the most impressive dobsonflies, having black body with bright orange prothorax and blackish wings with creamy white markings (Figs. 1–14). In contrast to the nocturnal habits of most dobsonfly species, *Neurhermes* adults are active during daytime, and their striking body and wing coloration

was considered to be a kind of mimicry for imitating some diurnal toxic moths (HAYASHI 1995).

Neurhermes is a replacement name for Gray's *Hermes*, homonymous with a gastropod genus (GLORIOSO 1981). The former is endemic to the Oriental realm and currently includes seven valid species. All *Neurhermes* species except *Neurhermes bipunctata* Yang & Yang, 1988 were originally described before 1910 mainly based on body coloration and wing marking patterns (VAN DER WEELE 1910). Except for the recent re-descriptions of *N. bipunctata*, *N. maculipennis* (Gray in Cuvier, 1832),

and *N. tonkinensis* (van der Weele, 1909) (GLORIOSO 1981; YANG & LIU 2010), all other species of *Neurhermes* are poorly known. A comprehensive taxonomic revision of *Neurhermes* therefore is desirable. Moreover, the phylogenetic relationships among the *Neurhermes* species have never been explored.

In the present paper, we review the genus *Neurhermes* based on the material from worldwide collections in order to give a modern and updated taxonomic system. We also describe a new species *Neurhermes nigerescens* sp.n. A phylogeny of the genus is reconstructed based on the adult morphological data. The biogeography of the genus is discussed according to their distribution pattern combined with the herein proposed phylogenetic relationships.

2. Material and methods

2.1. Taxonomic study

The specimens for the present study are deposited in the following collections: **BPBM** – Bishop Museum, Honolulu, U.S.A.; **CAU** – Entomological Museum, China Agricultural University, Beijing, China; **CNC** – Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada; **EUM** – Ehime University Museum, Matsuyama, Japan; **HFC** – Fumio Hayashi personal collection in Tokyo Metropolitan University, Tokyo, Japan; **HNHM** – Hungarian Natural History Museum, Budapest, Hungary; **IRSNB** – Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **IZCAS** – Institute of Zoology, Chinese Academy of Sciences, Beijing, China; **MFN** – Museum für Naturkunde, Berlin, Germany; **MNHN** – Muséum National d'Histoire Naturelle, Paris, France; **MZPW** – Warsaw Museum of the Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland; **NHM** – Natural History Museum, London, U.K.; **NMB** – Naturhistorisches Museum Basel, Basel, Switzerland; **NMW** – Naturhistorisches Museum Wien, Vienna, Austria; **NMPC** – Natural History Museum, National Museum, Prague, Czech Republic; **NSMT** – National Museum of Nature and Science, Tokyo, Japan; **RMNH** – Nationaal Natuurhistorisch Museum, Leiden, Netherlands; **SDEI** – Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; **SYSU** – Sun Yat-sen University, Guangzhou, China; **USNM** – National Museum of Natural History, Smithsonian Institutions, Washington, D.C., U.S.A.; **ZMA** – Zoological Museum Amsterdam, Leiden, Netherlands.

The label data of the name-bearing types are presented in quotation marks ‘ ’. Added information that expands or augments the often cryptic text and provides the geographic coordinates is placed in square brackets [].

Genitalia preparations were made by clearing the apex of the abdomen in a cold, saturated potassium hydroxide (KOH) solution for 8–10 h. After rinsing 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 genitalic structures follows ASPÖCK & ASPÖCK (2008).

2.2. Phylogenetic analysis

The analysis was performed using WinClada ver. 1.00.08 (NIXON 2002) and NONA ver. 2.0 (GOLOBOFF 1993). The heuristic search was used with maximum trees to keep setting to 10000 and number of replication setting to 100. We also analyzed the datasets by using TNT ver. 1.1 (GOLOBOFF et al. 2008) with an initial New Technology search set to 100 (using a driven search with sectorial search, ratchet, drift, and tree fusing; finding the minimum tree 10 times). The branch support values were calculated with the function implemented in TNT (TBR from existing trees, retain trees suboptimal by ten steps). All characters were treated as unordered and with equal weight. Character states were mapped on a most parsimonious tree (MPT) using WinClada ver. 1.0 (NIXON 2002), showing only unambiguous changes.

Chloroniella peringueyi Esben-Petersen, 1924 was selected as the outgroup taxon because it is considered to be the sister of all other dobsonfly genera (CONTRERAS-RAMOS 2011). *Protohermes davidi* van der Weele, 1909 was selected as another outgroup taxon for representing the genus *Protohermes* van der Weele, 1907, which is considered to be the sister of *Neurhermes* (CONTRERAS-RAMOS 2011). All *Neurhermes* species were included in the initial data matrix (matrix 1) as ingroup taxa. However, for *Neurhermes maculifera* (Walker, 1853) characters of male genitalia, which form the major part of the present dataset, are lacking. Therefore, another data matrix (matrix 2) excluding *N. maculifera* was analysed to find improvements in tree resolution and support by pruning certain wildcard taxon.

2.3. Characters

Twenty-four morphological characters of adults were coded as follows. Twenty were coded as binary and four as multistate. The matrix 1 is given in Table 1.

1. Postocular spines on head: (0) absent (Fig. 15); (1) present. — The postocular plane (indicated by arrow 2:1 in Fig. 15) is an apomorphy of Corydalinae (CONTRERAS-RAMOS 2011) and it bears a small spine in many dobsonfly genera, e.g. *Acanthacorydalis*

Table 1. Character matrix.

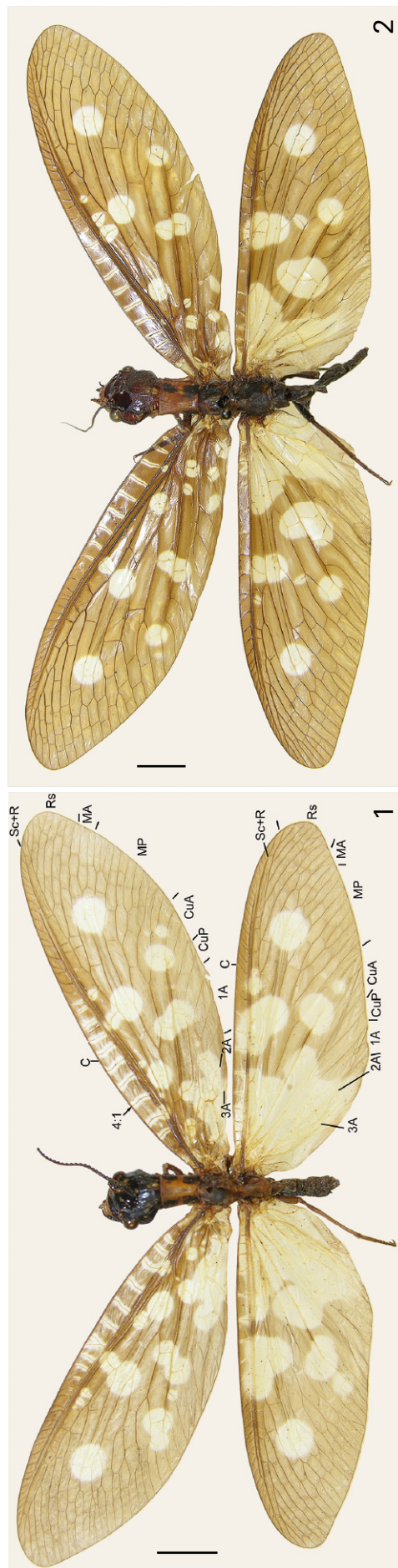
	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
<i>Chloroniella peringueyi</i>	1	1	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	
<i>Protohermes davidi</i>	1	1	0	0	1	0	0	0	0	—	—	2	0	0	0	0	0	0	0	0	1	1	0	
<i>Neurhermes costatostrata</i>	0	1	0	1	1	1	0	1	1	1	0	1	1	1	1	0	0	0	1	1	1	0	0	
<i>Neurhermes maculifera</i>	0	0	3	2	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	
<i>Neurhermes maculipennis</i>	0	0	1	2	1	1	0	1	1	1	1	2	1	0	1	1	1	0	1	1	1	0	0	
<i>Neurhermes nigerescens</i>	0	0	2	2	1	1	0	1	1	1	0	0	1	1	1	0	1	1	1	1	0	1	0	
<i>Neurhermes selysi</i>	0	0	1	2	1	2	0	1	1	0	1	0	0	0	1	0	1	0	1	0	0	1	0	
<i>Neurhermes sumatrensis</i>	0	0	3	2	1	2	0	1	1	1	1	2	1	0	1	1	1	0	1	1	1	0	0	
<i>Neurhermes tonkinensis</i>	0	0	3	2	1	2	0	1	1	1	1	2	1	0	1	1	1	0	1	1	1	0	0	

van der Weele, 1907, and some species of *Protohermes* (YANG & LIU 2010). However, the postocular spines are absent in all species of *Neurhermes*.

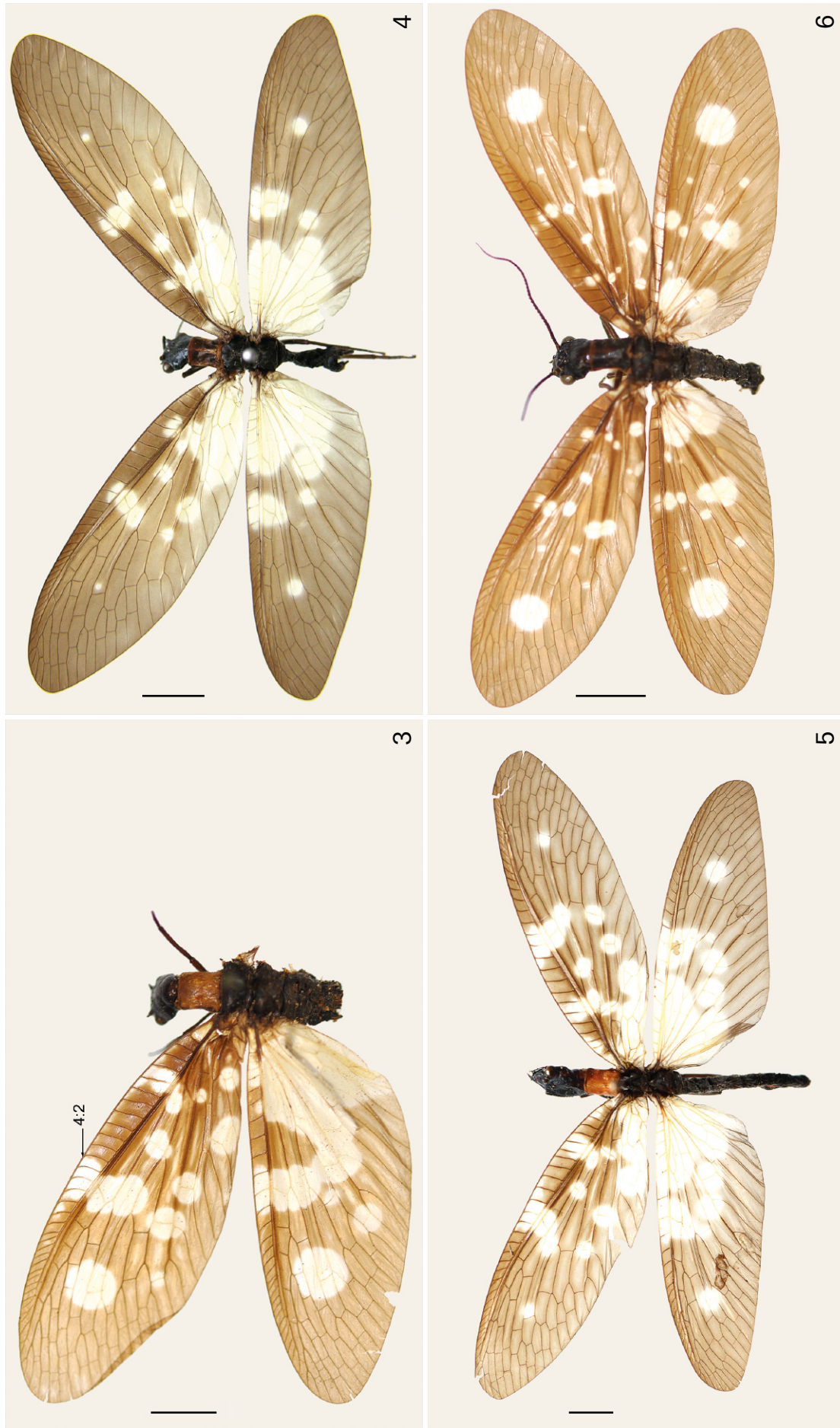
2. Postocular plane on head: (0) narrow (Fig. 16); (1) broad (Fig. 15). — The postocular plane is broad in *Neurhermes costatostrata* (van der Weele) but much narrower in other *Neurhermes* species.
3. Pronotum colouration: (0) with one or two pairs of lateral black markings (Fig. 15); (1) with one pair of median black markings (Figs. 16, 18); (2) almost entirely black (Fig. 17); (3) entirely orange (Fig. 19).
4. Forewing costal region: (0) transparent; (1) black proximally with white stripes on costal crossveins (Fig. 1); (2) black with two white markings (Fig. 3).
5. Forewing 1A: (0) 2-branched; (1) 3-branched. — The 3-branched forewing 1A is a synapomorphy of *Protohermes* and *Neurhermes* (CONTRERAS-RAMOS 2011).
6. Hindwing with proximal white marking: (0) absent; (1) present, narrow (Fig. 6); (2) present, wide (Fig. 14).
7. Male ninth tergum medially separated into a pair of semitergites: (0) absent; (1) present. — The male ninth tergum is longitudinally divided at midline into a pair of semitergites in most dobsonfly genera, while the sclerite is entire in *Neurhermes*, *Neoneuromus* van der Weele, 1909, *Nevromus* Rambur, 1842 and most species of *Protohermes*.
8. Male ninth tergum with posteromedian notch: (0) absent; (1) present. — The male ninth tergum has a posteromedian notch (indicated by arrow in Fig. 20) in *Neurhermes*, which is considered to be an apomorphy of this genus (GLORIOSO 1981), but a notch is also found in *Chloroniella peringueyi*.
9. Male ninth sternum, projections on posteromedian part: (0) absent; (1) present. — In *Neurhermes* the male ninth sternum is variably produced posteromedially. In some species, e.g. *N. maculipennis*, this is represented by a long projection. GLORIOSO (1981) considered this character state to be apomorphic for *Neurhermes*, but it is also present in *C. peringueyi* and some species of *Corydalus* Latreille, 1802.
10. Male ninth sternum, projections on posteromedian part: (0) paired (Fig. 45); (1) unpaired (Fig. 30). — The character can alternatively be viewed as the posteromedian projection either being deeply divided by a midline notch (state (1)) or being undivided (state (2)). Character only applicable to taxa with state (1) in character 9.
11. Male ninth sternum, posteromedian part: (0) feebly prominent (Fig. 38); (1) distinctly prominent (Fig. 30). — In *N. costatostrata* and *N. nigerescens*, the male ninth sternum is feebly prominent posteromedially, while in other *Neurhermes* species the posteromedian producing part is represented as one or two distinct projections.
12. Male ninth sternum, projections on posterolateral part: (0) feebly developed (Fig. 38); (1) well developed, slenderly digitiform (Fig. 21); (2) well developed, subtriangular (Fig. 60). — The male ninth sternum is more or less produced posterolaterally in some genera, e.g. *Chloroniella*, *Protohermes* and *Neurhermes*. In *Neurhermes nigerescens* and *N. selysi* (van der Weele) the posterolateral projections are indistinct, while in other *Neurhermes* species they are well developed. Furthermore, they are slenderly digitiform in *N. costatostrata* but subtriangular in *N. maculipennis*, *Neurhermes sumatrensis* (van der Weele), and *N. tonkinensis*.
13. Male ninth sternum, proportions: (0) nearly as long as wide (Fig. 45); (1) shorter than wide (Fig. 38). — The length of male ninth sternum is assessed from the anterior margin to the base of the posteromedian projections. In most *Neurhermes* species the male ninth sternum is short but transversely wide, while it is nearly as long as wide in *N. selysi*.
14. Male ninth sternum, inflation of central portion: (0) absent (Fig. 30); (1) present (Fig. 21). — In *N. costatostrata* and *N. nigerescens* the male ninth sternum is inflated in the central portion.
15. Male ninth gonocoxite and gonostylus: (0) short; (1) long. — The male ninth gonocoxite and gonostylus are generally integrated into a single unguiform sclerotised process. This process is much shorter than the ninth tergum in *C. peringueyi* and most *Protohermes* species, but prolonged and much longer than ninth tergum in *Neurhermes*.
16. Male ninth gonocoxite, distal inflation: (0) absent (Fig. 24); (1) present (Fig. 56). — In *N. maculipennis*, *N. sumatrensis*, and *N. tonkinensis*, the male

ninth gonocoxites are strongly inflated distally, while such distal inflation is absent *N. costatostrata*, *N. nigerescens*, and *N. selysi*.

17. Male ninth gonocoxite with gonostylus vertically curved: (0) no (Fig. 24); (1) yes (Fig. 56). — In most *Neurhermes* species the male ninth gonostylus is at right angle to the ninth gonocoxite except *N. costatostrata*, in which the male ninth gonocoxite and gonostylus is continuously and arcuately curved.
18. Male ninth gonostylus: (0) slender with a claw-like tip (Fig. 56); (1) arrow-shaped without claw-like tip (Fig. 41).
19. Male ectoproct bilobed dorsoventrally: (0) no; (1) yes. — The male ectoproct is dorsoventrally separated into a dorsal and a ventral lobe in *Neurhermes*, which is considered to be the apomorphic state of this genus (GLORIOSO 1981). However, such state is also present in some species of *Protohermes*, e.g. the species of the *Protohermes channinganus* group (LIU et al. 2013).
20. Male tenth gonostylus flattened dorsoventrally: (0) no (Fig. 47); (1) yes (Fig. 40). — In most *Neurhermes* species the male tenth gonostyli are flattened dorsoventrally, but not in *N. selysi*.
21. Male tenth gonostylus moderately sclerotized with membranous edges: (0) no (Fig. 40); (1) yes (Fig. 32). — Generally, the male tenth gonostyli are feebly sclerotized in dobsonflies, while in some *Neurhermes* species the male tenth gonostyli are longitudinally sclerotized and bear membranous edges.
22. Female fused eighth gonocoxites: (0) posteriorly concave (Fig. 26); (1) posteriorly truncate (Fig. 28). — In *N. costatostrata*, *N. maculipennis*, *N. sumatrensis*, and *N. tonkinensis*, the female fused eighth gonocoxites are concaved posteriorly, while in other *Neurhermes* species they have a truncate posterior margin.
23. Female eighth gonapophyses: (0) present; (1) absent. — The sclerotized female eighth gonapophyses are absent in most dobsonfly species, while in *Neurhermes* they are present.
24. Female ninth gonocoxite produced anteriorly: (0) no (Fig. 25); (1) yes (Fig. 27). — The female ninth gonocoxite is not produced anteriorly in most dobsonfly species, but is produced in *N. maculifera*, *N. selysi*, *N. sumatrensis*, and *N. tonkinensis*.



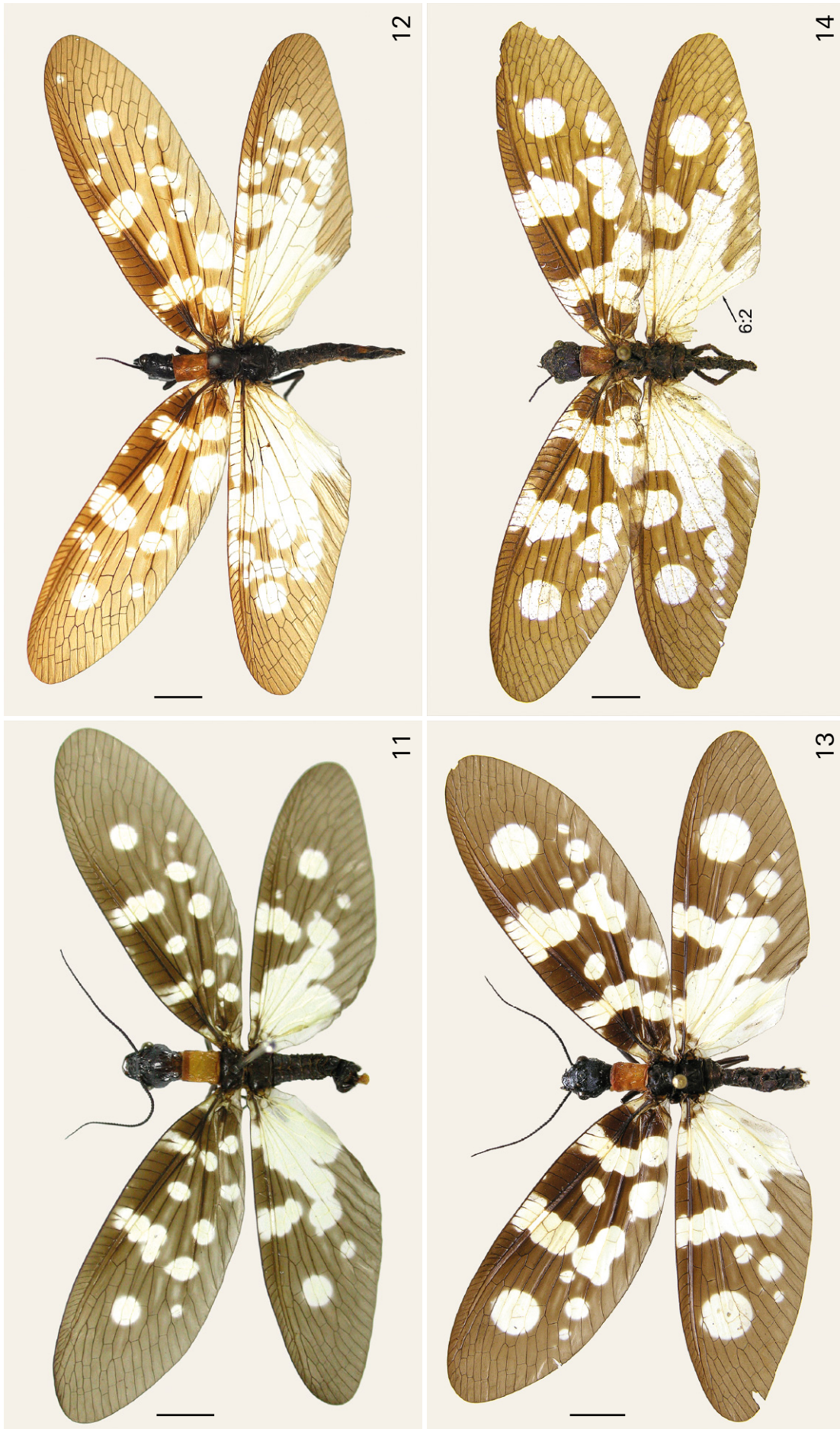
Figs. 1, 2. Habitus of *Neurhermes* species. **1:** *N. costatostrata* (van der Weele), lectotype male. **2:** *N. costatostrata*, paralectotype female. Scale bars: 5.0 mm.



Figs. 3–6. Habitus of *Neurhermes* species. **3:** *N. maculifera* (Walker), holotype female. **4:** *N. maculipennis* (Gray in Cuvier), male. **5:** *N. maculipennis*, female. **6:** *N. nigerescens* sp.n., holotype male. Scale bars: 5.0 mm.



Figs. 7–10. Habitus of *Neurhermes* species. **7:** *N. nigerescens*, paratype female. **8:** *N. selysi* (van der Weele), lectotype male, showing pronotum without black markings. **9:** *N. selysi*, female, showing pronotum with black markings. **10:** *N. selysi*, female. Scale bars: 5.0 mm.



Figs. 11–14. Habitus of *Neurhermes* species. **11:** *N. sumatrensis* (van der Weele), male from Malay peninsula. **12:** *N. sumatrensis*, female from Sumatra. **13:** *N. tonkinensis* (van der Weele), male from southern Vietnam. **14:** *N. tonkinensis*, lectotype female from northern Vietnam. Scale bars: 5.0 mm.

3. Results

3.1. Taxonomy

3.1.1. *Neurhermes* Navás

Neurhermes Navás, 1915: 391. **Type species:** *Chauliodes maculipennis* Gray in Cuvier, 1832: 332 (by monotypy).

Hermes Gray in Cuvier, 1832: 331. **Type species:** *Hermes maculipennis* Gray in Cuvier, 1832: 332 (orig. des.).

Diagnosis. Adults of this genus are very similar to those of *Protohermes* by having a 3-branched forewing 1A vein and digitiform female ninth gonostyli. However, *Neurhermes* can be distinguished from *Protohermes* by the male ninth tergum bearing a median projection and the male ectoproct being dorsoventrally bifurcated into a short dorsal and a long ventral lobe.

Redescription. Adults small to medium-sized (forewing length 25–34 mm in males and 28–44 mm in females). Body mostly black, usually with pronotum orange. Head robust without postocular spine. Ocelli rather small; lateral ocelli widely separated from median ocellus, distance between lateral ocelli approximately $4 \times$ width of median ocellus, but much shorter than distance between antennal fossae. Clypeus with anterior margin not concave at middle. Antennae subserrate. Wings grayish black, with several creamy white markings. 1A 3-branched. Male ninth tergum much wider than long, not separated by longitudinal incision, with anterior margin broadly concave; ninth sternum transversely broad, usually with median projection (which can be deeply notched at midline); ectoproct short, bifurcated dorsoventrally into short dorsal and long ventral lobe; ninth gonocoxite long and robust, ninth gonostylus slenderly elongated, angulately produced from ninth gonocoxite and directed dorsad; fused tenth gonocoxites narrowly arcuate, with pair of generally digitiform gonostyli. Female fused eighth gonocoxites broad, with posterior margin concave or truncate; eighth gonapophyses present as pair of small sclerotized sclerites posterior to eighth gonocoxite; ninth gonocoxites valvate with pair of slender digitiform gonostyli.

Distribution. This genus is endemic to the Oriental realm and is currently recorded in Bangladesh, China, India, Indonesia, Laos, Malaysia, Myanmar, Thailand, and Vietnam.

3.1.2. Key to species of *Neurhermes*

1 Pronotum orange, laterally with two pairs of black markings (Fig. 15); forewing with white stripes along costal crossveins on proximal half (Fig. 1); male ninth sternum with posterior margin feebly produced

medially but with posterolateral corners distinctly produced into digitiform processes (Fig. 21); male ninth gonocoxite and gonostylus continuous, without angulate articulation (Fig. 24)

..... *N. costatostrata* (van der Weele)

1' Pronotum entirely orange or with one pair of black markings or entirely blackish brown; forewing without white stripes along costal crossveins on proximal half; male ninth sternum with posterior margin strongly produced medially or if feebly produced medially posterolateral corners also feebly prominent; male ninth gonocoxite and gonostylus with angulate articulation 2

2 Pronotum entirely blackish brown, with only anterior and posterior margins orange (Fig. 17); hindwing with proximal white marking small, $\sim 1/5 \times$ length of hindwing (Fig. 6); male ninth sternum with both middle portion of posterior margin and posterolateral corners feebly produced (Fig. 38); male ninth gonostylus arrow-shaped (Fig. 41) *N. nigerescens* sp.n.

2' Pronotum entirely orange or with dark markings at middle; hindwing with proximal white marking broad, $\sim 1/3 - 1/2 \times$ length of hindwing; male ninth sternum with posterior margin strongly produced medially; male ninth gonostylus slenderly elongated with claw-like tip 3

3 Forewing with proximal white marking strongly extended distad, making anal area largely white (Fig. 4); distal round marking on forewing small, at most with two longitudinal veins crossing it (Fig. 4); male ninth sternum posteriorly with long digitiform median projection (Fig. 30)

..... *N. maculipennis* (Gray in Cuvier)

3' Forewing with several isolated proximal white markings, which do not extend distad; distal round marking on forewing large, at least with three longitudinal veins crossing it; male ninth sternum posteriorly with median projection variable but not long digitiform

..... 4

4 Pronotum orange, mostly with a pair of irregular-shaped black markings at middle (Fig. 18); male ninth sternum posteriorly with pair of short digitiform projections medially (Fig. 45)

..... *N. selysi* (van der Weele)

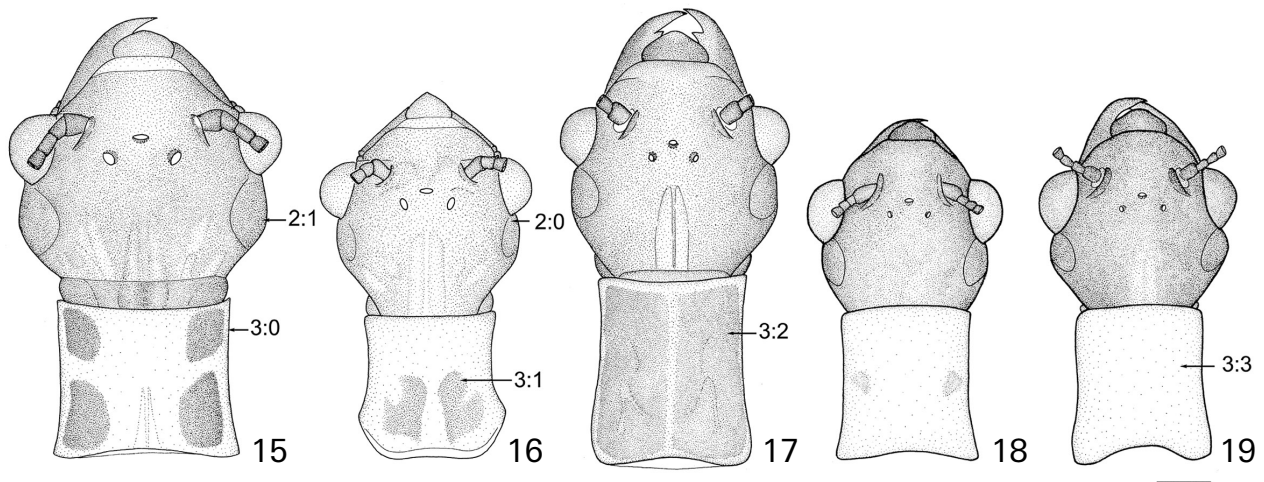
4' Pronotum entirely orange, without any dark markings; male ninth sternum posteriorly with only one median projection 5

5 Female fused eighth gonocoxites with posterior margin truncate in ventral view (Fig. 28); [southern India] *N. maculifera* (Walker)

5' Female fused eighth gonocoxites with posterior margin distinctly concaved medially in ventral view; [widespread in southern China, Indochina, Malay peninsula, and Sumatra] 6

6 Male ninth sternum posteriorly with large subtriangular median projection and with posterolateral corners strongly produced (Fig. 60); [widespread in southern China and Indochina]

..... *N. tonkinensis* (van der Weele)



Figs. 15–19. Head and pronotum of *Neurhermes* species. **15:** *N. costatostrata* (van der Weele). **16:** *N. maculipennis* (Gray in Cuvier). **17:** *N. nigerescens* sp.n. **18:** *N. selysi* (van der Weele). **19:** *N. tonkinensis* (van der Weele). Scale bar: 1.0 mm.

6' Male ninth sternum posteriorly with short tubercle-shaped or short digitiform median projection, and with posterolateral corners feebly produced (Fig. 52); [Malay peninsula and Sumatra]

..... *N. sumatrensis* (van der Weele)

3.1.3. *Neurhermes costatostrata* (van der Weele) Figs. 1–2, 15, 20–26

Hermes costatostrata van der Weele, 1907: 249. Type locality: India (Assam: Khasia Hills).

Diagnosis. This species is characterized by the pronotum having two pairs of black lateral markings (Fig. 15), the forewings with white stripes along costal crossveins on proximal half (Fig. 1), and the male ninth sternum with feebly produced posterior margin but having posterolateral corners distinctly produced into digitiform processes (Fig. 21).

Description. Male: Body length 23.8–25.0 mm; forewing length 33.3–33.7 mm, hindwing length 30.0–31.2 mm.

Head (Fig. 15) entirely black except for anterior margin of clypeus yellow. Compound eyes brown; ocelli yellow, medially margined black. Antenna black with scape and pedicel dark brown. Mouthparts yellow except for mandibles black with tips reddish brown.

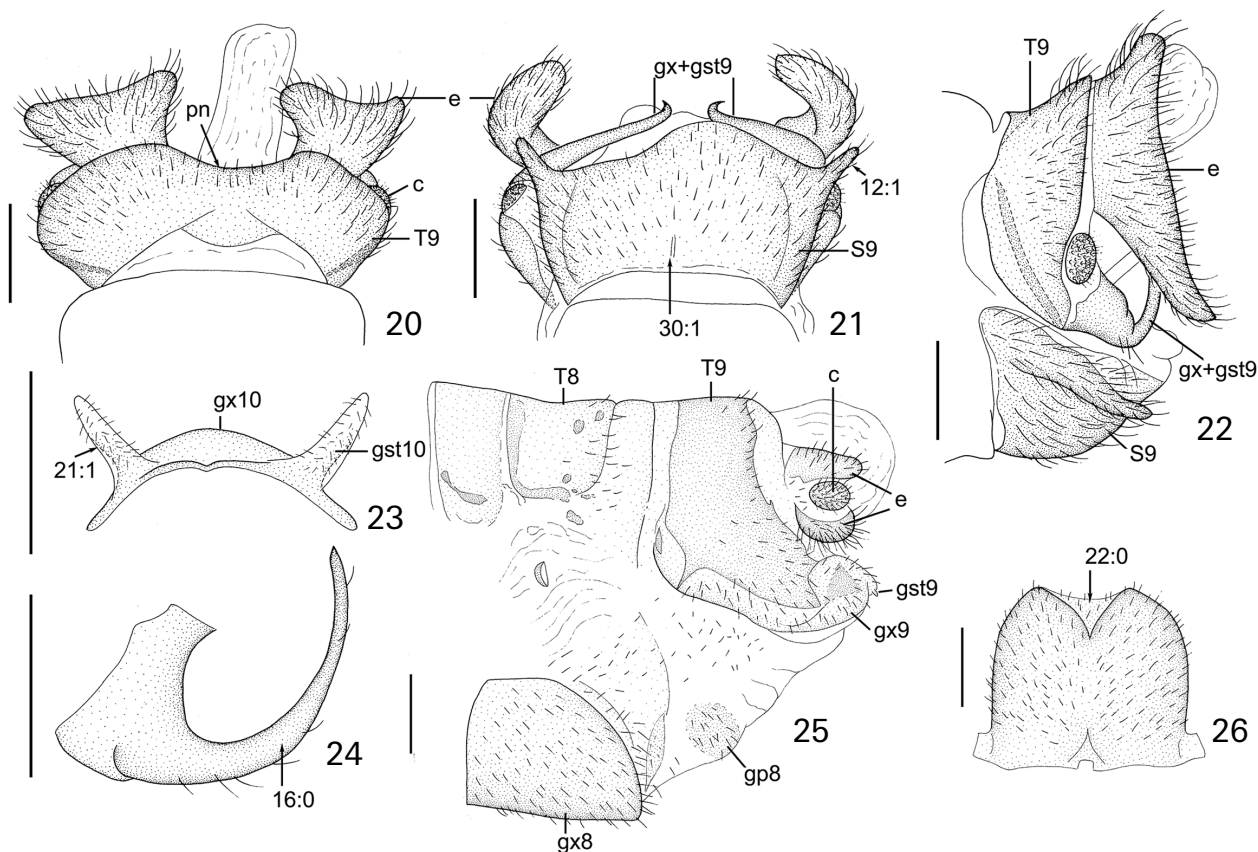
Prothorax (Fig. 15) orange, laterally with two pairs of broad black markings. Meso- and metathorax blackish brown. Thoracic pilosity pale yellow. Legs brown with short dense yellowish setae; tarsal claws reddish brown. Wings (Fig. 1) greyish black, with several creamy white markings. Forewing with creamy white stripes on costal crossveins on proximal half; proximally with a few small round markings, which are occasionally fused with each other, medially with three large, mostly round or ovoid markings and sometimes also with a few small mark-

ings, a round marking present at distal 1/3. Hindwing with proximal 1/3 creamy white, medially with three or four markings, two of which are much larger, and a round marking present at distal 1/3. Veins brown, except for those in creamy white markings yellow. Rs with 7–8 branches; 7–8 crossveins between R and Rs; anterior branch of MP with 4–7 branches, posterior branch of MP with 2–4 branches.

Abdomen black, but venter orange with black markings anteriorly. Ninth tergum (Fig. 20) short but rather deep, in dorsal view posteriorly widened, anterior margin broadly concave but roundly convex medially, posterior margin arcuately convex, medially with arcuate incision. Ninth sternum (Fig. 21) strongly sclerotized, slightly longer than ninth tergum, broadly subquadrate and feebly widened posteriad, median portion deeply inflated, posterior margin slightly produced medially, posterolateral corners distinctly produced into pair of digitiform processes. Ninth gonocoxite and gonostylus (Fig. 24) continuous as unguiform structure, which is extremely elongated, directed dorsomedially and arcuately curved. Ectoproct (Figs. 20, 22) short, much deeper than ninth tergum, dorsal lobe short and obtuse, ventral lobe long and medially curved distad. Fused tenth gonocoxites (Fig. 23) arched, dorsal and ventral margin slightly produced medially; tenth gonostyli digitiform, slightly flattened, directed posterolaterally.

Female: Body length 36.7–37.0 mm; forewing length 35.3–39.4 mm, hindwing length 31.7–35.8 mm.

Fused eighth gonocoxites (Figs. 25–26) broad and strongly sclerotized, in lateral view subtrapezoidal, posteriorly produced, in ventral view anterior and posterior margins medially with V-shaped incision; eighth gonapophyses present as pair of small sclerites posterior to eighth gonocoxite. Ninth gonocoxite (Fig. 25) short and broad, posterior portion ventrally incised, with small gonostylus. Ectoproct (Fig. 25) short with posterior margin incised, leaving thick digitiform and semicircular ventral lobes.



Figs. 20–26. *Neurhermes costatostrata* (van der Weele). **20:** Male genitalia, dorsal view. **21:** Male genitalia, ventral view. **22:** Male genitalia, lateral view. **23:** Male fused tenth gonocoxites, ventral view. **24:** Male ninth gonocoxite and gonostylus. **25:** Female genitalia, lateral view. **26:** Female fused eighth gonocoxites, ventral view. — S9: ninth sternum; T8–9: eighth to ninth tergum; gp8: eighth gonapophysis; gst9–10: ninth and tenth gonostylus; gx8–10: eighth to tenth gonocoxite; c: callus cerci; e: ectoproct; pn: posteromedian notch. Scale bars: 1.0 mm.

Distribution. India (Meghalaya).

Remarks. *Neurhermes costatostrata* is the most distinctive species in *Neurhermes* by having the broad head with distinctly expanded postocular planes, the pronotum with two pairs of black stripes, and the forewings with white stripes along costal crossveins.

Material. Lectotype ♂ [herein designated], ‘Khasia Hills. [= Khasi Hills, 25°35′N 91°38′E, Meghalaya, India]/leg. 1907 No. 6. Coll [ection]. v[an].d[er]. Weele/*Hermes costatostrata* [specific name originally published as *costatostrata*] Type v[an].d[er]. Weele’ (RMNH). Paralectotypes 2♀ [herein designated], same data as lectotype (RMNH). **INDIA:** 1♀, Meghalaya, U.J.K.H. [= United Khasi-Jaintia Hills District], Mawja [ca. 25°17′N 91°57′E], 30.iii.1960, F. Schmid (CNC); 1♂ 1♀, Meghalaya, Khasis [= Khasi Hills], Nat[ive]. Coll[ector] (NHM); 1♂ 1♀, Meghalaya, Khasia Hills [= Khasi Hills] (NHM); 1♂, without collecting label (NHM).

3.1.4. *Neurhermes maculifera* (Walker)

Figs. 3, 27–28

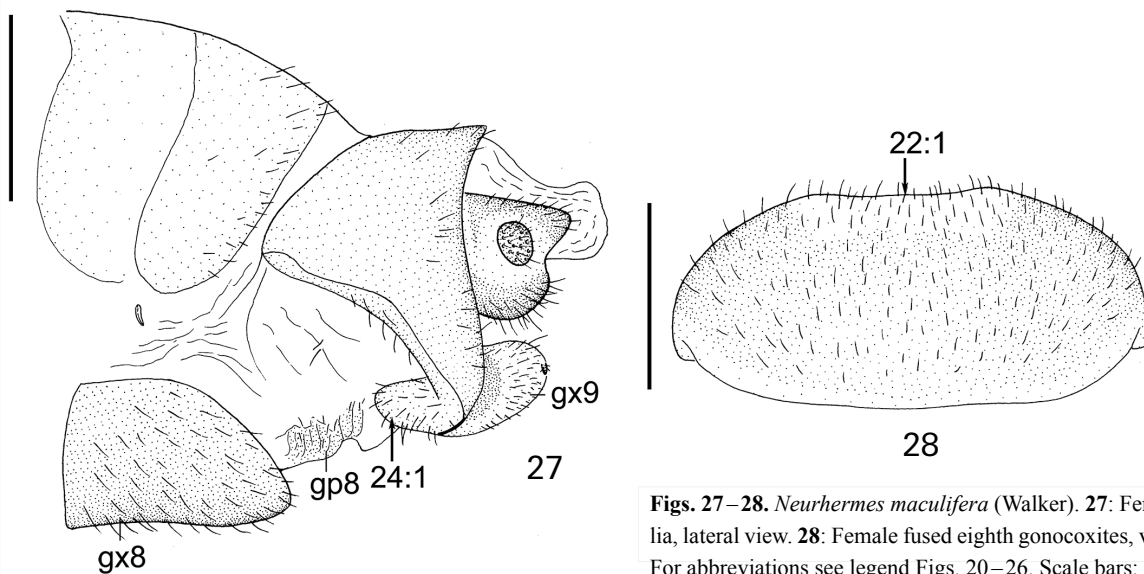
Hermes maculifera Walker, 1853: 203. Type locality: India (Kerala: Malabar).

Diagnosis. This species is characterized by the entirely orange pronotum, the presence of large white distal round markings, the broad proximal white markings on hindwings, and the female eighth gonocoxite with truncate posterior margin (Figs. 3, 27).

Description. Female: Forewing length 33.2–33.5 mm, hindwing length 30.0–31.4 mm.

Head (Fig. 3) entirely blackish brown. Compound eyes blackish brown; ocelli pale yellow, medially margined black. Antennae black. Mouthparts black.

Prothorax (Fig. 3) orange. Meso- and metathorax blackish brown. Thoracic pilosity white on prothorax but dark brown on meso- and metathorax. Legs blackish brown with short dense brownish setae; tarsal claws reddish brown. Wings (Fig. 3) blackish brown with several creamy white markings. Forewing proximally with 3–4 small ovoid markings, one of which extends to costal area; medially with several small round markings and 4 broader ovoid markings, one of which extends to costal area; a round marking present at distal 1/3. Hindwing proximally with rather broad creamy white marking, which strongly extends distad and bends toward costal area at middle, forming a hook-like pattern; 1 or several smaller markings present distal to proximal marking; a



Figs. 27–28. *Neurhermes maculifera* (Walker). **27:** Female genitalia, lateral view. **28:** Female fused eighth gonocoxites, ventral view. For abbreviations see legend Figs. 20–26. Scale bars: 1.0 mm.

round marking present at distal 1/3. Veins blackish brown except for those in creamy white markings yellow. Rs with 5–6 branches; 5–6 crossveins between R and Rs; anterior branch of MP with 4 branches, posterior branch of MP with 3 branches.

Abdomen blackish brown. Fused eighth gonocoxites (Figs. 27–28) broad and strongly sclerotized, in lateral view subtrapezoidal, posteriorly produced, in ventral view posterior margin truncate; eighth gonapophyses present as pair of small feebly sclerotized sclerites posterior to eighth gonocoxite. Ninth gonocoxite (Fig. 27) short and broad, strongly and roundly produced anteriorly, posterior portion roundly convexed, ventrally with small gonostylus. Ectoproct (Fig. 27) with dorsal lobes thick, digitiform, and with ventral lobes nearly semicircular, slightly shorter than dorsal lobes.

Male: Unknown.

Distribution. India (Kerala, Karnataka).

Remarks. This species appears to be closely related to *N. sumatrensis* and *N. tonkinensis* by having similar orange pronotum without any black markings and wing marking patterns, but it can be distinguished from the latter two species by the female fused eighth gonocoxites with truncate posterior margin. In *N. sumatrensis* and *N. tonkinensis* the female fused eighth gonocoxites are distinctly concaved medially on the posterior margin. *Neurhermes maculifera* is the most poorly known species of *Neurhermes* due to the scarcity of the materials and the lack of male. However, it is the only species of *Neurhermes* from the southern India which harbours quite a few but endemic species of Megaloptera (Liu et al. 2008, 2012). The finding of the male of *N. maculifera* will further verify the validity of this species.

Material. Holotype ♀, 'Walker type label/Malabar [a region of Kerala, India, 10°00'N 76°15'E] [with on reverse] 'Ent. Club'/H.

maculifera, Malabar/*Hermes maculifera* Walker, ♀ Holotype, D. E. Kimmins det. 1969[†] (NHM). **INDIA:** 1♀, Karnataka, Bangalore, Mysore [12°17'N 76°38'E], X.1894 (NHM).

3.1.5. *Neurhermes maculipennis* (Gray in Cuvier) Figs. 4–5, 29–36

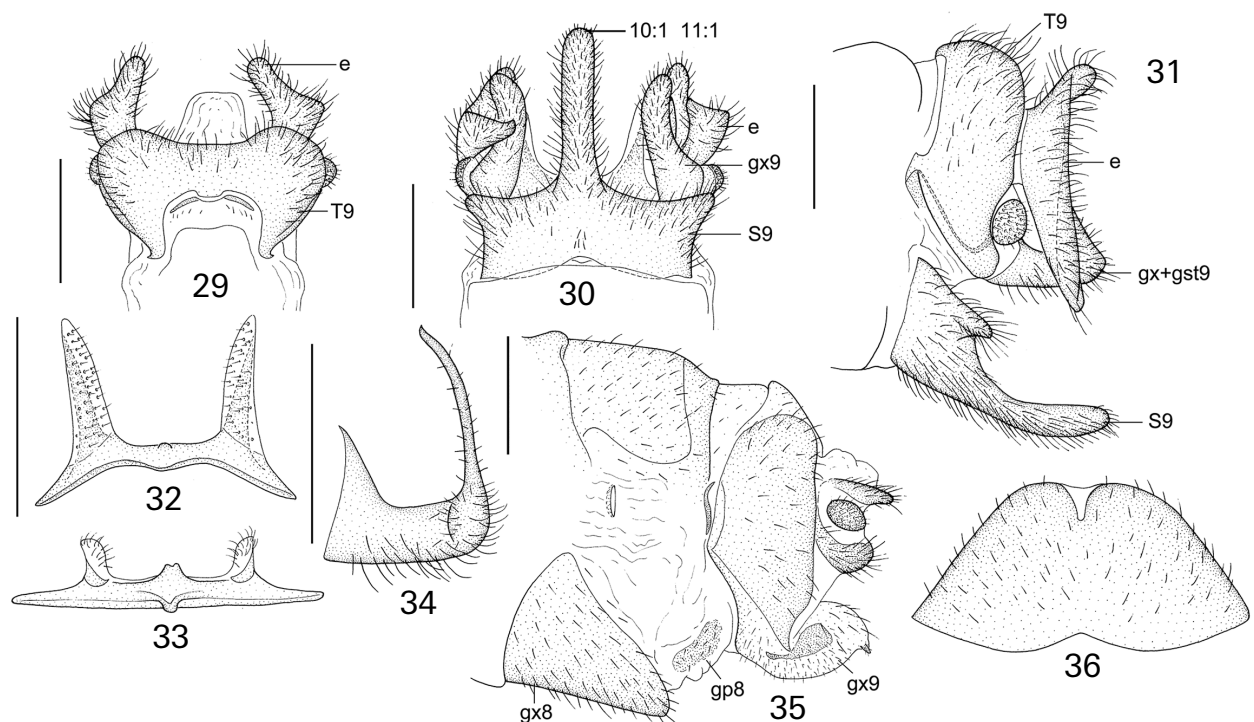
Chauliodes maculipennis Gray in Cuvier, 1932: 331. Type locality: Indonesia (Java).

Diagnosis. This species is characterized by the wings with very small white distal markings and the male ninth sternum with a long digitiform posteromedian projection (Figs. 4, 30).

Description. Male: Body length 15.0–23.0 mm; forewing length 25.0–32.0 mm, hindwing length 23.0–29.0 mm.

Head (Fig. 16) entirely black, with anterior clypeus and lateral margins of posterior clypeus slightly paler. Compound eyes brown; ocelli pale yellow, medially margined black. Antennae black. Mouthparts black.

Prothorax (Fig. 16) orange; pronotum mostly with pair of greyish markings, which are sometimes expanded to cover large part of pronotum. Meso- and metathorax black. Thoracic pilosity brown, much longer on meso- and metathorax. Legs black with short dense brownish setae; tarsal claws reddish brown. Wings (Fig. 4) blackish brown with several creamy white markings. Forewing proximally creamy white except for costal area with small markings at subproximal portion, two round markings present near white proximal area; medially with two suboval markings, one of which is extended to costal area; a small round marking present at distal 1/3. Hindwing proximally creamy white, including costal area; medially with two suboval markings, one of which is extended to costal area; a small round marking present



Figs. 29–36. *Neurhermes maculipennis* (Gray in Cuvier). **29:** Male genitalia, dorsal view. **30:** Male genitalia, ventral view. **31:** Male genitalia, lateral view. **32:** Male fused tenth gonocoxites, ventral view. **33:** Male tenth gonocoxite, caudal view. **34:** Male ninth gonocoxite and gonostylus. **35:** Female genitalia, lateral view. **36:** Female fused eighth gonocoxites, ventral view. For abbreviations see legend Figs. 20–26. Scale bars: 1.0 mm.

at distal 1/3. Veins blackish brown except for those in creamy white markings yellow. Rs with 6 branches; 5–7 crossveins between R and Rs; anterior branch of MP with 4 branches, posterior branch of MP with 2 branches.

Abdomen blackish brown. Ninth tergum (Fig. 29) short and rather deep, in dorsal view subtrapezoidal, anterior incision arched with short median projection, posterior margin shallowly incised medially. Ninth sternum (Fig. 30) short, nearly rectangular, about 3.0x as wide as long, posteriorly with blunt lateral corners and long digitiform median projection, which is about 1.5x length of lateral margin of ninth sternum. Ninth gonocoxite (Fig. 34) slightly curved laterally, ninth gonostylus vertically bended dorsad. Ectoproct (Fig. 31) with ventral lobe about 5.0x length of dorsal lobe. Fused tenth gonocoxites (Figs. 32–33) arched, anterior margin with small dorsomedian process, posterior margin with small ventromedian process; tenth gonostyli digitiform, somewhat flattened, slightly directed posterolaterally, with dorsal surface slightly sclerotized.

Female: Body length 29.0–35.0 mm; forewing length 38.0–44.0 mm, hindwing length 33.0–39.0 mm.

Fused eighth gonocoxites (Figs. 35–36) broad and strongly sclerotized, in lateral view subtriangular, posteriorly produced, in ventral view anterior margin shallowly incised medially, posterior margin with deeply V-shaped incision; eighth gonapophyses present as a pair of small sclerites posterior to eighth gonocoxite. Ninth gonocoxite (Fig. 35) short and broad, posterior portion ventrally incised, with small gonostylus. Ectoproct (Fig.

35) short with posterior margin incised, leaving digitiform dorsal and semicircular ventral lobes.

Distribution. Indonesia (Java, Sumatra?, East Kalimantan?); Malaysia (Malay peninsula?, Sabah?).

Remarks. This species can be easily distinguished from other *Neurhermes* species by the wings with rather small white distal markings, while in the other *Neurhermes* species the white round markings at distal 1/3 of both fore- and hindwings are much larger. Most of our examined materials of *N. maculipennis* were collected from Java, but there is one female collected from Sumatra and three males from Borneo. Moreover, BANKS (1931) recorded this species from the Malay peninsula based on one specimen. However, all these specimens collected beyond Java were obtained by certain European museums 70–110 years ago, and no new specimen of *N. maculipennis* was found in Malay peninsula, Borneo, and Sumatra despite the past long-term faunal investigation of these areas. Therefore, the distributions of *N. maculipennis* in Malay peninsula, Borneo and Sumatra needs further verification based on newly collected specimens. In the present biogeographic discussion, we consider *N. maculipennis* to be endemic to Java.

Material. Holotype ♂, '*H[ermes]. maculipennis (ruficollis* Ramb[ur])', Java/Holotype' (NHM). **INDONESIA:** 22♂ 1♀, West Java, Djampang [6°28'S 106°43'E] Tengah [= central], 6[00]–800 m, M.E. Walsh (RMNH); 1♂, West Java, Mt. Djampang Wetan, Tji-goia, ii.1939 (NMB); 1♂, West Java, 8–1500 ft [= 243–457 m],

Djampang Tengah, 11–18.x.1939, J.M.A. van Groenendael (ZMA); 1♀, West Java, Djampang Tengah, 8–1500 ft [= 243–457 m], 11–18.x.1939, J.M.A. van Groenendael (ZMA); 1♂, West Java, Djampang Tengah, 1800 ft [= 548 m], 24.iv.1939, J.M.A. van Groenendael (ZMA); 1♂, West Java, Djampang Tengah, Tjimerang, 1800 ft [= 548 m], 10–24.iv.1940, J.M.A. van Groenendael (ZMA); 1♂, West Java, Djampang, 1000' [= 305 m], 8.xi.1939, J.M.A. van Groenendael (ZMA); 1♀, West Java, Djampang Tengah, 1500 ft [= 457 m], 15–18.i.1940, J.M.A. van Groenendael (ZMA); 1♂, West Java, Djampang Tengah [= central], S. Malang, i.1940, M.E. Walsh (RMNH); 1♂, West Java, Malang (NMPC); 1♂, West Java, Mt. Djampang Wetan, Gonong Malang, viii.1937 (NMB); 1♂, West Java, Djampang Tengah, Gng Malang, 3500' [= 1066 m], 12.vii.1939, J.M.A. van Groenendael (ZMA); 1♂, West Java, Mt. Gedeh, Perbawati [6°46'S 106°57'E], 1000 m, xii.1930 (RMNH); 1♂, West Java, Mt. Gedeh, Perbawati, 9.viii.1938 (RMNH); 1♂, West Java, Mt. Gedeh, Perbawati, 1000 m, xii.1938 (RMNH); 1♂, West Java, Mt. Gedeh, Perbawati, 1000 m, 9.ix.1938 (RMNH); 2♂, West Java, Mt. Gedeh, Perbawati, 1000 m, ix.1938 (RMNH); 1♂ 1♀, West Java, Mt. Gedeh, Perbawati, Soekaboemi [= Sukabumi, 6°12'S 106°46'E], 1000 m, xii.1938 (RMNH); 1♀, West Java, Soekaboemi, 1938, Boger (NMB); 1♂, West Java, Soekaboemi, 2000' [= 609 m], 22.x.1935, J.M.A. van Groenendael (ZMA); 1♂, West Java, Soekaboemi, 2000' [= 609 m], 20.v.1936, J.M.A. van Groenendael (ZMA); 1♀, West Java, Soekaboemi, 2000' [= 609 m], 20.iv.1937, J.M.A. van Groenendael (ZMA); 1♂, West Java, Soekaboemi, 2000' [= 609 m], 29.iii.1937, J.M.A. van Groenendael (ZMA); 1♂, West Java, Soekaboemi, 2000' [= 609 m], 19.ii.1937, J.M.A. van Groenendael (ZMA); 1♂, West Java, Soekaboemi, 2000' [= 609 m], 2.ii.1937, J.M.A. van Groenendael (ZMA); 1♂, West Java, Soekaboemi, 2000' [= 609 m], 12.ii.1940, J.M.A. van Groenendael (ZMA); 1♂, West Java, Soekaboemi, 2000' [= 609 m], v.1941, J.M.A. van Groenendael (ZMA); 1♂, West Java, Mt. Sesoroer, Soekaboemi, 650 m, iii.1937 (RMNH); 1♂, West Java, Selabintanah, Soekaboemi, 900 m, 2.iv.1933, M.E. Walsh (RMNH); 1♂ 1♀, West Java, Soekaboemi (RMNH); 1♀, West Java, Soekaboemi, 22.vii, Le Moulit (DEI); 1♂, West Java, Mt. Gedeh, Selabintanah [6°47'S 108°58'E], 1000 m, vi.1939, Walsh (RMNH); 1♂, West Java, Mt. Djampang Wetan, Tjigocha, ii.1939 (RMNH); 1♂, West Java, Soekanegara [= Sukanegara, 7°04'S 107°12'E], 400–1000 m, ii.1940 (RMNH); 1♀, West Java, S of Sukanegara, Mt. Beng Bareng, ix.1938 (RMNH); 1♂, West Java, Gedeh, Tjibodas [6°30'S 107°42'E], 1400 m, iv.1937, F.C.v. Wagensveld (RMNH); 1♀, West Java, Gedeh, Tjibodas, 1400 m, i.1936, M.A. Lieftinck (RMNH); 1♀, West Java, Tjibodas, 5.i.1934, Toxopeus (RMNH); 1♀, West Java, Gedeh, Tjisaroa [6°39'S 106°54'E], 1200 m, 22.i.1939, M.A. Lieftinck (RMNH); 1♀, West Java, Tjisaroa Zd. (Gedeh 1100 m), 26.x.1947 (RMNH); 1♀, West Java, Gedeh, Tjisaroa z, 25.vi.1939, M.A. Lieftinck (RMNH); 1♀, West Java, Djampang, Wetan, Tjiajoenan, 800 m, Walsh, iv.1940 (RMNH); 1♀, West Java, Djampang Tengah, S. Malang [6°40'S 106°30'E], 2[00]–800 m, i.1940, M.E. Walsh (RMNH); 1♀, West Java, Mt. Gedeh (J.B. Ledru) [6°48'S 107°06'E], 1898, R. Oberthur (MNHN); 3♂, West Java, Mt. Gedeh (NHM); 1♂, West Java, Goalpara, Mt. Gedeh, 4000' [= 1219 m], 10.x.1935, J.M.A. van Groenendael (ZMA); 2♂, West Java, Mt. Medeh, ix.2004 (HFC); 2♂, West Java, Priangan [ca. 7°01'S 107°31'E], 9/10.viii.1937, J.M.A. van Groenendael (ZMA); 1♀, West Java, Priangan, Piepers (RMNH); 1♀, West Java, 1500' [= 457 m], 16.x.1939 (ZMA); 1♀, West Java, Siebert (MFN); 3♂ 1♀, West Java, Batavia [6°07'S 106°45'E] (IRSBN); 1♂, Central Java, res. Kedoe, Mt. Telamojo, 1200 m, 10.x.1939, M.A. Lieftinck (RMNH); 1♂, Central Java, C[entral].N[orthern]. Java, Marcodjambangan, G. Moeria [= Mt. Muria, ca. 6°36'S 110°53'E], 1200 m, xii.1935, M.E. Walsh (RMNH); 1♂, Java, Mega Mondoeng, M.C. Piepers (RMNH); 3♂, Java, M.C. Piepers (RMNH); 1♂, Java, De Haan (MFN); 1♂ 1♀, Java, Fruhstorfer, Gerstaecker, G. (MFN); 1♂, Java, 1892, Deyrolle (MNHN); 1♀, Java, Staudinger (DEI); 1♂, Java, Fruhstorfer (NMB); 2♂ 1♀, Java, 4000–6000' [= 1219–1828 m], [18]93, Fruhstorfer (NMW); 7♂ 3♀, Java, 1894, Fruhstorfer (NMW); 1♂, Java, 1895, Fruhstorfer (NMW); 5♂ 4♀, Java (1♂ 1♀ in IRSBN,

2♀ in MZPW, 4♂ 1♀ in NHM, 1♀ in NMPC, 1♂ in NMW, 1♀ in RMNH, 1♂ in ZMA); 1♂, Java, Kina Balu [probably wrongly labeled], Coll. Lacroix (MNHN); 1♀, Sumatra, 6/5 (NHM); 1♂, East Kalimantan, Samarinda [0°30'S 117°09'E], iv.1939, M.E. Walsh (RMNH); 1♂, Indes orient, 110-59 (arrived at collection in 1859), Mniszech (MNHN); **MALAYSIA**: 2♂, Sabah, Kina Balu [6°04'N 116°33'E], acq.1903, coll. Staudgr. [= Staudinger] (RMNH); 1♂, no collecting data, Children's coll. (NHM).

3.1.6. *Neurhermes nigerescens* sp.n.

Figs. 6–7, 17, 37–43

Diagnosis. This species is characterized by the largely blackish brown pronotum, the hindwings with rather small proximal white markings, and the male ninth gonostylus with arrow-shaped apex (Figs. 6, 41).

Description. Male: Body length 15.1–19.4 mm; forewing length 24.7–28.3 mm, hindwing length 21.5–25.1 mm.

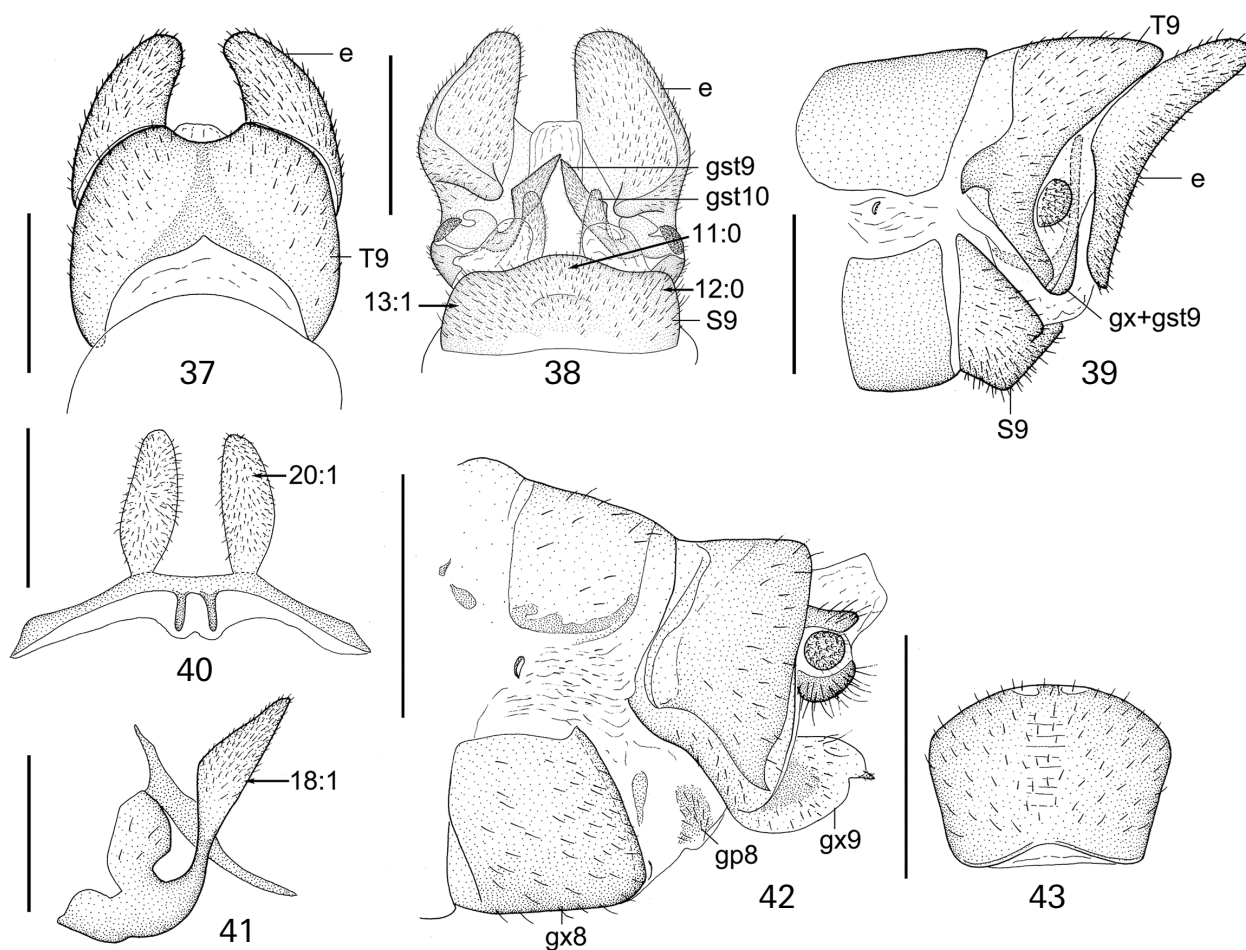
Head (Fig. 17) entirely blackish brown. Compound eyes grayish brown; ocelli yellow, medially margined black. Antennae blackish brown throughout. Mouthparts blackish brown.

Thorax blackish brown except for anterior and posterior margins of pronotum orange (Fig. 17). Thoracic pilosity yellowish brown. Legs blackish brown with short dense yellowish brown setae; tarsal claws reddish brown. Wings (Fig. 6) greyish black, with several creamy white markings. Forewing with proximal 1st costal cellule creamy white and with additionally two markings on costal area; proximally with five or six small markings, medially with two suboval large markings and a few small markings, and a round marking present at distal 1/3. Hindwing with proximal 1/5 creamy white, medially with two large irregular-shaped markings and a few small markings, and a round marking present at distal 1/3. Veins blackish brown, except for those in creamy white markings pale yellow. Rs with 6–7 branches; 5–7 crossveins between R and Rs; anterior branch of MP with 4 branches, posterior branch of MP with 2 branches.

Abdomen blackish brown. Ninth tergum (Fig. 37) short and rather deep, in dorsal view subquadrate, anterior incision broadly arcuate, posterior margin slightly convex with shallow median incision. Ninth sternum (Fig. 38) short, nearly rectangular, about 3.0 × as wide as long, posteriorly very weakly convex at middle. Ninth gonocoxite (Fig. 41) strongly curved, ninth gonostylus arrow-shaped and strongly bended dorsad. Ectoproct (Fig. 39) with ventral lobe about 2.0 × length of dorsal lobe. Fused tenth gonocoxites (Fig. 40) arched, anterior margin with small dorsomedian process, posterior margin truncate; tenth gonostyli thickly digitiform, somewhat flattened.

Female: Body length 22.0–25.3 mm; forewing length 30.0–31.1 mm, hindwing length 25.0–27.8 mm.

Fused eighth gonocoxites (Figs. 42–43) broad and strongly sclerotized; in lateral view subtrapezoidal, feebly produced posteriorly; in ventral view anterior margin



Figs. 37–43. *Neurhermes nigerescens* sp.n. **37:** Male genitalia, dorsal view. **38:** Male genitalia, ventral view. **39:** Male genitalia, lateral view. **40:** Male fused tenth gonocoxites, ventral view. **41:** Male ninth gonocoxite and gonostylus. **42:** Female genitalia, lateral view. **43:** Female fused eighth gonocoxites, ventral view. For abbreviations see legend Figs. 20–26. Scale bars: 1.0 mm.

slightly concaved, posterior margin arcuately convex; eighth gonapophyses present as pair of small sclerites posterior to eighth gonocoxite. Ninth gonocoxite (Fig. 42) short and broad, posterior portion ventrally incised, with small gonostylus. Ectoproct (Fig. 42) short with posterior margin incised, leaving short digitiform and semicircular ventral lobes.

Distribution. India (Manipur, Meghalaya).

Etymology. The specific epithet “*nigerescens*” refers to the almost entirely blackish brown pronotum in the new species.

Remarks. This northeastern Indian endemic species can be easily distinguished from other *Neurhermes* species by the almost entirely blackish brown pronotum and the male ninth gonostylus with arrow-shaped apex.

Material. Holotype ♂, ‘Khasis [= Khasi Hills, Meghalaya, India], Nat[ive]. Coll[ector]/McLachlan Coll[ection]. B[ritish]. M[useum]. 1938-674.’ (NHM). Paratypes, **INDIA:** 6♂ 4♀, same data as holotype (NHM); 1♂ 4♀, Meghalaya, Khasia Hills [= Khasi Hills] (2♀ as paralectotypes of *Neurhermes selysi* van der Weele in RMNH, 1♀ as a paralectotype of *Neurhermes selysi* van der Weele in

NHM, 1♂ 1♀ in NHM); 1♀, Meghalaya, Cherrapunji [25°18’N, 91°42’E], Heyne (MFN); 1♀, Manipur, Kambiron [24°43’N 93°22’E], 24.v.1960, F. Schmid (CNC); 1♀, Manipur, Lagairong [24°42’N 93°32’E], 26.v.1960, F. Schmid (CNC); 1♂, without collecting label (NHM).

3.1.7. *Neurhermes selysi* (van der Weele)

Figs. 8–10, 18, 44–50

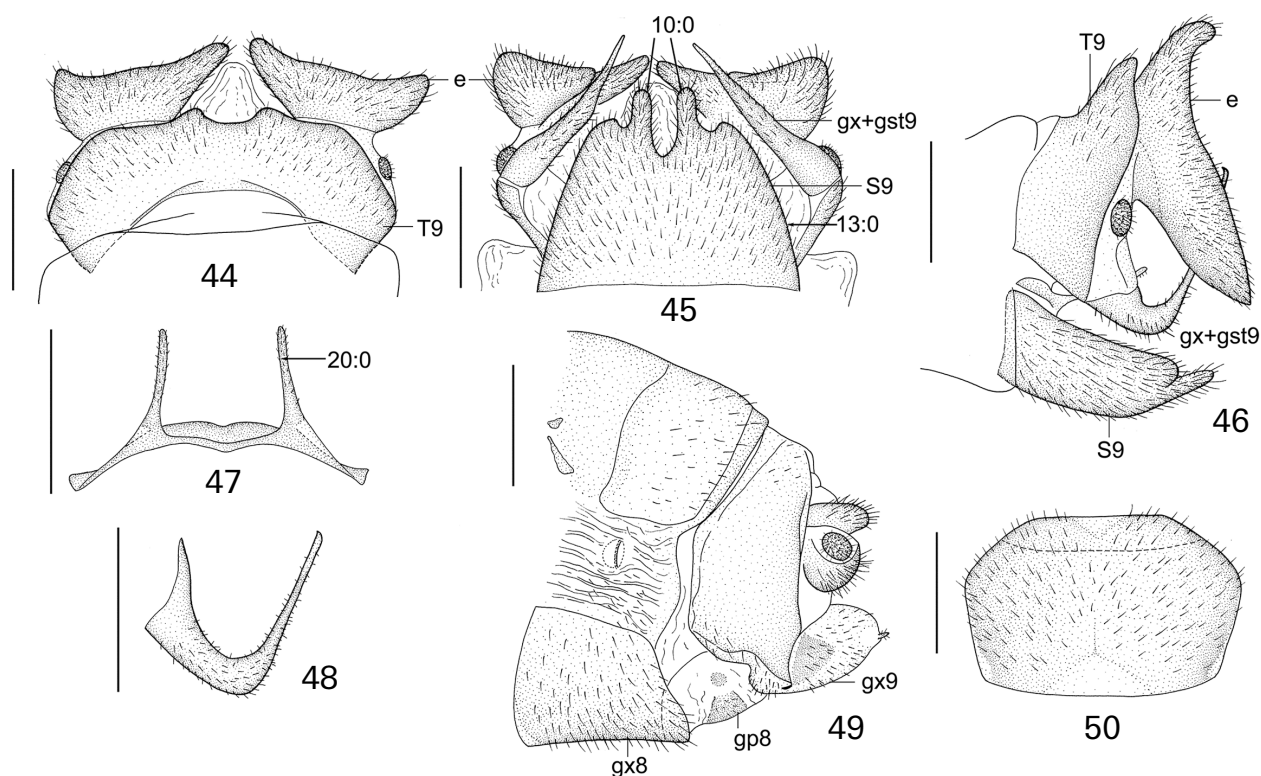
Hermes selysi van der Weele, 1909: 256. Type locality: Bangladesh (Sylhet); India (Meghalaya: Khasia Hills, Assam).

Neurhermes bipunctata Yang & Yang, 1988: 56. Type locality: China (Yunnan: Tengchong). **syn.n.**

Diagnosis. This species is characterized by the orange pronotum often with a pair of black markings medially and the male ninth sternum with a pair of short digitiform posteromedian projections (Figs. 18, 45).

Description. Male: Body length 15.4–20.0 mm; forewing length 25.1–26.9 mm, hindwing length 22.6–25.3 mm.

Head (Fig. 18) entirely blackish brown. Compound eyes blackish brown; ocelli pale yellow, medially margined black. Antennae black. Mouthparts black.



Figs. 44–50. *Neurhermes selysi* (van der Weele). **44:** Male genitalia, dorsal view. **45:** Male genitalia, ventral view. **46:** Male genitalia, lateral view. **47:** Male fused tenth gonocoxites, ventral view. **48:** Male ninth gonocoxite and gonostylus. **49:** Female genitalia, lateral view. **50:** Female fused eighth gonocoxites, ventral view. For abbreviations see legend Figs. 20–26. Scale bars: 1.0 mm.

Prothorax (Fig. 18) orange, generally with pair of black markings medially, but sometimes these markings absent. Meso- and metathorax blackish brown. Thoracic pilosity white on prothorax but dark brown on meso- and metathorax. Legs blackish brown with short dense brownish setae; tarsal claws reddish brown. Wings (Fig. 9) blackish brown with several creamy white markings. Forewing proximally with 6–7 small ovoid markings, one of which is presented on costal area; medially with several small round markings and two broader ovoid markings, one of which extends to costal area; a round marking present at distal 1/3. Hindwing proximally with broad creamy white marking, which strongly extends distad and bends toward costal area at middle, forming hook-like pattern, but sometimes such extension absent; a round marking present at distal 1/3. Veins blackish brown except for those in creamy white markings yellow. Rs with 6 branches; 5–7 crossveins between R and Rs; anterior branch of MP with 4 branches, posterior branch of MP with 2 branches.

Abdomen blackish brown. Ninth tergum (Fig. 44) short, transversely wide and rather deep, in dorsal view arcuate, with broadly arcuate anterior incision, and with posterior margin arcuately incised medially. Ninth sternum (Fig. 45) broad, subtrapezoidal, posteriorly deeply concaved, forming pair of short digitiform processes, posterolateral corners bluntly produced. Ninth gonocoxite (Fig. 48) gradually narrowed distad and bearing slenderly elongate gonostylus, which is arcuately curved

dorsad. Ectoproct (Fig. 46) with ventral lobe about 2.5 × length of dorsal lobe. Fused tenth gonocoxites (Fig. 47) arcuate, anterior margin slightly prominent medially, posterior margin feebly concaved medially; tenth gonostylus digitiform and slenderly elongated.

Female: Body length 17.5–31.0 mm; forewing length 29.4–36.0 mm, hindwing length 27.2–32.4 mm.

Fused eighth gonocoxites (Figs. 49–50) broad and strongly sclerotized, in lateral view subtriangular, posteriorly produced, in ventral view anteromedially with feebly sclerotized subtriangular area, posterior margin truncate; eighth gonapophyses present as pair of small sclerites posterior to eighth gonocoxite. Ninth gonocoxite (Fig. 49) short and broad, anteriorly roundly convexed, posterior portion subquadrate, ventrally with small gonostylus. Ectoproct (Fig. 49) with dorsal lobes thick, digitiform, and with ventral lobes nearly semicircular, slightly shorter than dorsal lobes.

Distribution. Bangladesh (Sylhet); China (Yunnan); India (Assam, Manipur, Meghalaya); Myanmar (Mandalay, Shan).

Remarks. This species appears to be closely related to *N. nigerescens* by having similar wing marking patterns, but can be distinguished from the latter species by the orange pronotum medially with or without black markings and the male ninth sternum with a pair of short digitiform posteromedian projections. In *N. nigerescens* the pron-

tum are largely or entirely blackish brown and the male ninth sternum has its posterior margin only feebly convexed. The lectotype of *N. selysi* designated by VAN DER WEELE (1910) is an adult with entirely orange pronotum but lacking genitalia. All paralectotypes of *N. selysi* are females and have almost entirely blackish brown pronotum. Based on our examination of the male specimens of these two forms from northeastern India, we attribute the lectotype and the paralectotypes of *N. selysi* to *N. selysi* and *N. nigerescens*, respectively. *Neurhermes bipunctata* Yang & Yang was originally described by YANG & YANG (1988) based on a single male with partly damaged genitalia from western Yunnan, China. However, the holotype of *N. bipunctata* has an orange pronotum medially with blackish spots and similar wing marking patterns with *N. selysi*. Therefore, herein we treat *N. bipunctata* to be a junior synonym of *N. selysi*.

Material. Lectotype ex [sex unknown], ‘Silhet [= Sylhet, ca. 24°53'N 91°52'E, in Bangladesh]/*C. maculipennis* Gray/Collection Selys, *Corydalus maculipennis* Gray, Révision van der Weele 1908, *Corydalus selysi* van der Weele, Type/*Hermes selysi* Weele Type/Type' (IRSNB). 1♂ [Holotype of *Neurhermes bipunctata* Yang & Yang], CHINA: Yunnan, Tengchong [25°01'N 98°30'E], 1800 m, 31.v.1979 (CAU); INDIA: 1♂ 1♀, Meghalaya, U.J.K.H. [= United Khasi-Jaintia Hills District], Mawpran [25°17'N 91°57'E], 6/8. iv.1960, F. Schmid (CNC); 1♂, Meghalaya, Khasis [= Khasi Hills, 25°35'N 91°38'E], Nat[ive] Coll[ector] (NHM); 1ex, Meghalaya, Khasia [Khasi] Hills (RMNH); 2♀, Manipur, Luang Long Khunou [ca. 24°24'N 93°53'E], 28/29.v.1960, F. Schmid (CNC); 1♀, Assam (NHM); MYANMAR: 3♀, Burma [= Myanmar] (NHM); 4♂, Mandalay, Anisakan N.S.S. [22°03'N 96°30'E], vi.1920 (NHM); 1♂ 1♀, Ruby Mines [probably a locality near Mogok, Mandalay, 22°55'N 96°30'E] (NHM); 1♂ 1♀, Shan, Kolaw [ca. 20°37'N 96°33'E], 4000 ft [= 1219 m], iv.1916, F.M. Mackwood (NHM); 1♀, without collecting label (NHM).

3.1.8. *Neurhermes sumatrensis* (van der Weele) Figs. 11–12, 51–58

Hermes sumatrensis van der Weele, 1909: 255. Type locality: Indonesia (Sumatra).

Diagnosis. This species is characterized by the entirely orange pronotum, the presence of large white round markings at distal 1/3 of both fore- and hindwings, the hindwings with broad proximal white markings, and the male ninth sternum with a short posteromedian projection (Figs. 11, 52).

Description. Male: Body length 19.6–20.9 mm; forewing length 28.8–37.0 mm, hindwing length 26.3–35.0 mm.

Head (Fig. 11) entirely blackish brown. Compound eyes blackish brown; ocelli pale yellow, medially margined black. Antennae black. Mouthparts black.

Prothorax (Fig. 11) orange. Meso- and metathorax blackish brown. Thoracic pilosity white on prothorax but dark brown on meso- and metathorax. Legs blackish brown with short dense brownish setae; tarsal claws reddish brown. Wings (Fig. 11) blackish brown with several

creamy white markings. Forewing proximally with 5–6 ovoid markings, one of which extends to costal area; medially with 1 rather small and 4 larger ovoid markings, one of which extends to costal area; a round marking present at distal 1/3. Hindwing proximally with rather broad creamy white marking, which strongly extends distad and bends toward costal area at middle, forming hook-like pattern, but sometimes median extending white marking separated from proximal marking; a round marking present at distal 1/3. Veins blackish brown except for those in creamy white markings yellow. Rs with 6–7 branches; 5–7 crossveins between R and Rs; anterior branch of MP with 3–4 branches, posterior branch of MP with 2–3 branches.

Abdomen blackish brown. Ninth tergum (Fig. 51) short, transversely wide and rather deep, in dorsal view arcuate, with broadly arcuate anterior incision, and with posterior margin arcuately incised medially. Ninth sternum (Figs. 52, 54) transversely wide, nearly as long as ninth tergum, posteriorly produced medially into short obtuse projection, posterolateral corners bluntly produced. Ninth gonocoxite (Fig. 56) slightly inflated distad and bearing slenderly elongate gonostylus, which is vertical to ninth gonocoxite and straightly directed dorsad. Ectoproct (Fig. 53) with ventral lobe about 4.0 × length of dorsal lobe. Fused tenth gonocoxites (Fig. 55) arcuate, anterior margin slightly prominent medially, posterior margin feebly concaved medially; tenth gonostylus digitiform and directed posterolaterally.

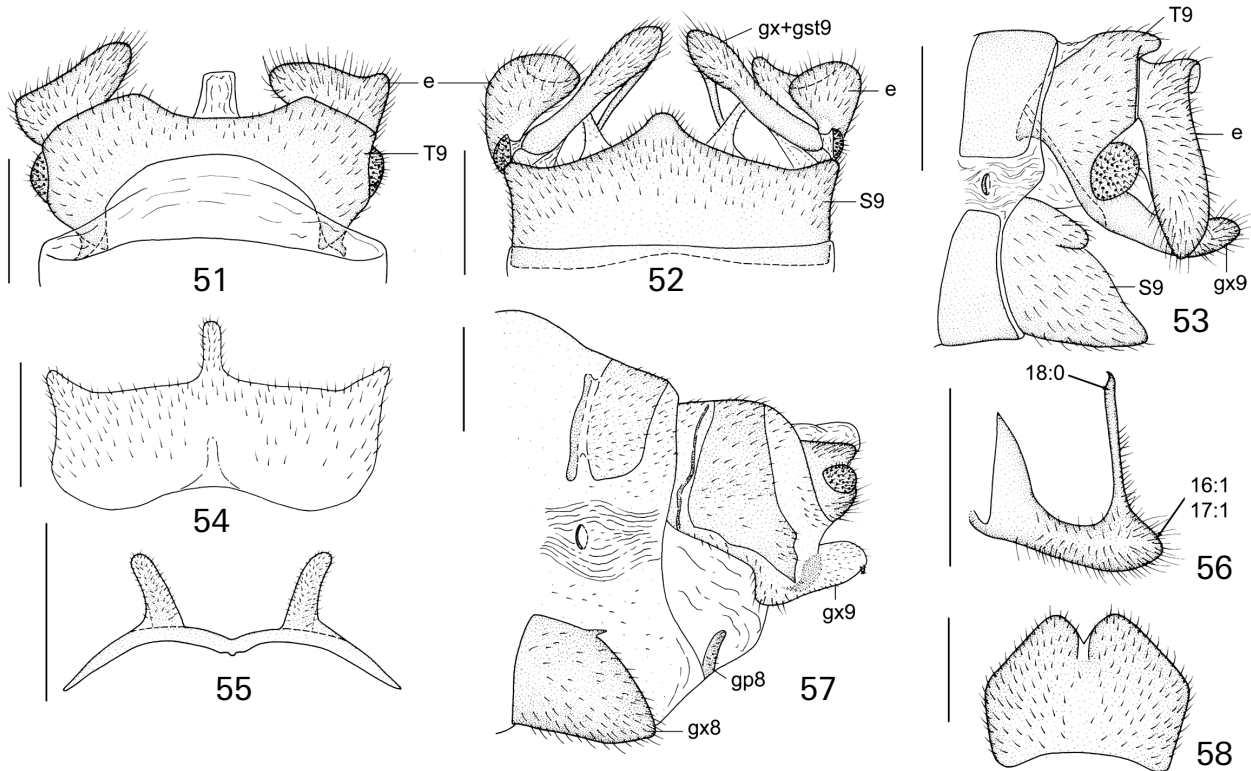
Female: Body length 19.9–30.5 mm; forewing length 28.8–42.0 mm, hindwing length 30.1–38.0 mm.

Fused eighth gonocoxites (Figs. 57–58) broad and sclerotized, subtrapezoidal in lateral view, posterior margin with V-shaped incision; eighth gonapophyses present as pair of small sclerites posterior to eighth gonocoxite. Ninth gonocoxite (Fig. 57) short and broad, anteriorly slightly convexed, posterior portion rounded, ventrally with small gonostylus. Ectoproct (Fig. 57) short, with posterior margin incised, leaving subtriangular dorsal and semicircular ventral lobes.

Distribution. Indonesia (Sumatra); Malaysia (Malay peninsula); Thailand (southern region).

Remarks. This species appears to be closely related to *N. tonkinensis* by having similar orange pronotum without black markings and similar wing marking patterns, but it can be distinguished from the latter species by the male ninth sternum with a short posteromedian projection. In *N. tonkinensis* the male ninth sternum possesses a long subtriangular posteromedian projection. This species is herein newly recorded from Thailand. In males of *N. sumatrensis* from southern Thailand, the posteromedian projection of ninth sternum is sometimes short and digitiform, which is considered to be intraspecific variation.

Material. Holotype ♀, ‘Sumatra, Pajakombo [0°15'S 100°33'E], H. Rouyer/Holotype/Museum Leiden' (RMNH). INDONESIA:



Figs. 51–58. *Neurhermes sumatrensis* (van der Weele). **51:** Male genitalia, dorsal view. **52:** Male genitalia, ventral view, based on a male from western Malaysia. **53:** Male genitalia, lateral view. **54:** Male ninth sternum, ventral view, based on a male from southern Thailand. **55:** Male fused tenth gonocoxites, ventral view. **56:** Male ninth gonocoxite and gonostylus. **57:** Female genitalia, lateral view. **58:** Female fused eighth gonocoxites, ventral view. For abbreviations see legend Figs. 20–26. Scale bars: 1.0 mm.

Sumatra: 1♀, Sibolangit [3°18'N 98°34'E], ix–x.1929, D.v. Leeuwen (RMNH); 1♀, S. Sumatra, S.W. Lampongs [= Lampung], Mt. Tanggamoes [ca. 4°33'S 105°24'E], 600 m, 24.xii.1934, Giesting, Lieftinck (RMNH); 1♀, Wai Lima Z [= South] Sum[atra]. Lampongs [= Lampung], 11.xii.1921, Siebers (DEI); 2♀, N. Sumatra, Berastagi [3°11'N 98°30'E], 25.vii.1995, L. Köteles (HNHM); 1♀, V. Studt G. (MFN); 6♀, W. Sumatra, Panty near Padang [ca. 0°57'S 100°21'E], 4.v.1992, H. Karube (HFC); 1♀, Sumatra, Delhi (NMPC); 1♀, Sumatra, don[ated] 1914, A. Weiss (ZMA); 1♀, Beli Sumatra, Walveck (ZMA); 1♀, Sumatra Deli, 1902, Grubauer (NMW); **MALAYSIA:** W. Malaysia [= Malay peninsula]: 1ex, Negri Sembilan, Gunung Angsi [2°41'N 102°02'E], 2000'–2700' [= 609–822 m], iv.1918 (NHM); 1♀, Pahang, Cameron Highland, Point of 19 miles from Tapha [ca. 4°28'N 101°23'E], 23.iv.1976, Sinji Nagai (EUM); 2♀, Pahang, Cameron Highland, v.1975 (NSMT); 1♀, Pahang, 20.iv.1979 (NSMT); 1♂, Pahang, Kuala Jeku, 16.ii.1920 (NHM); 3♂ 3♀, Pahang, Genting Tea Estate, 2000 ft [= 609 m], 11/29.xi.1981, K.R. Tuck (NHM); 1♀, Pahang, Genting Simpah [3°20'N 101°47'E], 2080 ft [= 633 m], 3.vi.1929, A.S. Corbet (NHM); 1♀, Perak, Batang Padang [4°11'N, 101°15'E], vi.1923, F.N.C. (NHM); 1ex, Perak, Batang Padang, Jor Camp., 1800 ft [= 548 m], 9.vi.1923, H.M. Pendlebury (NHM); 1♀, Perak, Tasek Temenggong, Sungei Halong [ca. 5°18'N 101°12'E], 250 m, xi/xii.1993 (NHM); 1♀, Perak, Hartert (MFN); 1♀, Johor, Mt. Ophir [2°22'N 102°36'E], viii.1905, P.B. Johore (NHM); 2♂ 1ex, Perak, Gunong Kledang [= Gunung Keledang, 4°35'N 101°00'E], 2646' [= 806 m], xi.1916 (NHM); 1ex, Selangor, Selangor Waterfall, Banlong Road [ca. 3°19'N 101°34'E], ix.1941 (NHM); 1ex, Selangor, Ginling Sampak, iv.1916 (NHM); 1ex, Kedah, Kedah Peak [5°47'N 100°26'E], 3500 ft [= 1066 m], 20.iii.1928 (NHM); 1♀, Kedah, Kedah Peak, 3950 ft [= 1204 m], 27.iii.1928 (NHM); 1♂ 1♀, Selangor, Bukit Kutu [3°32'N 101°43'E], 3300–3500 ft [= 1005–1066 m], 23.ix.1932, H.M. Pendlebury (NHM); 1♀, Selangor, Bukit Kutu, 3360 ft [= 1024 m], A.R. Sanderson (NHM);

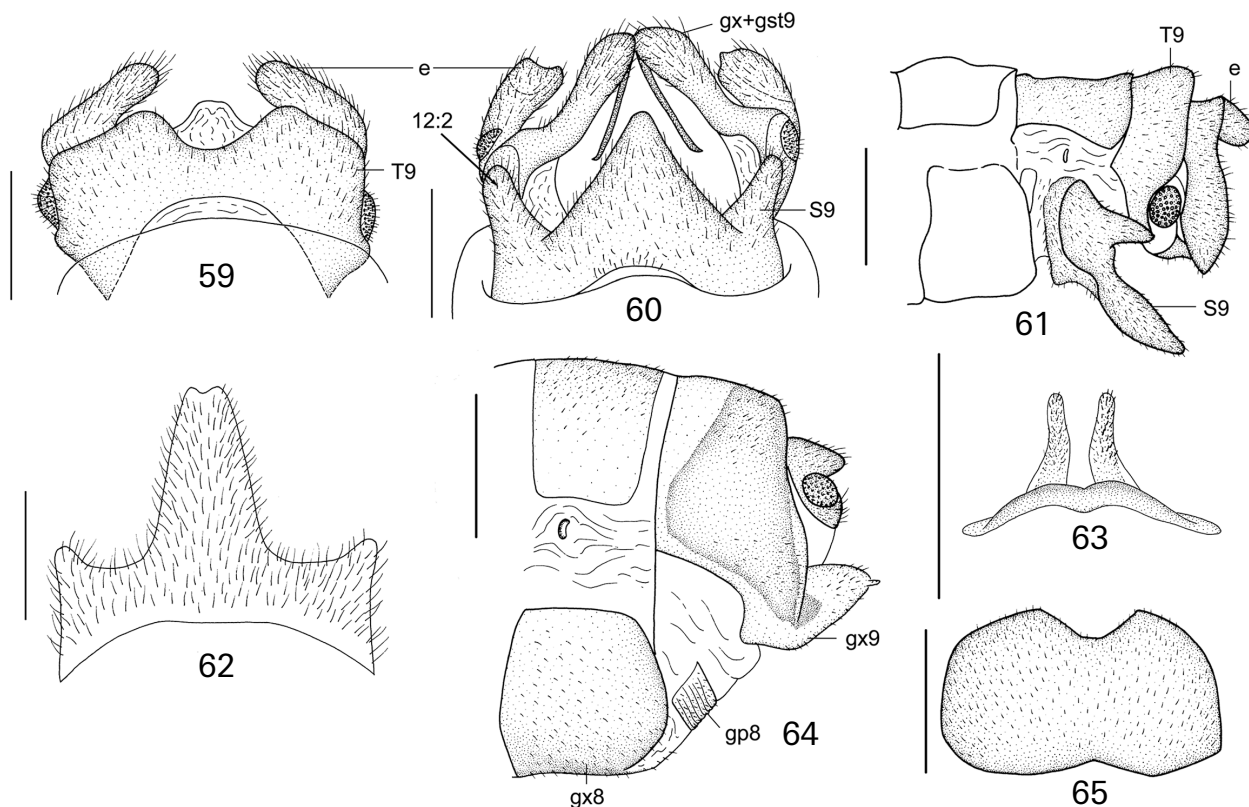
1♀, Bukit Kutu, 3300 ft [= 1005 m], A.R. Sanderson (NHM); 1ex, Selangor, Ulu Langat [3°06'N 101°50'E], 31.viii.1934 (NHM); 3♀, Selangor, Ulu Langat, reared from larvae and emerged in 1997 (HFC); **THAILAND:** 1ex, S. Siam [southern region of Thailand], Trang, Trang water fall [ca. 7°26'N 99°45'E], 23.vii.1935, Dajak Layang Gaddi (IRSNB); 1♂, Siam [southern region of Thailand], Songkhla, Khao Ram [7°04'N 100°37'E], 1200 ft [= 365 m], 23.ii.1922, J.X. Coll. (NHM); 1♂, Trong Lr Siam [an unknown locality in southern region of Thailand], i–ii.1899, W.L. Abbott (USNM); 1♂ 4♀, Trong Lr Siam, Khaw Sai Dow [an unknown locality in southern region of Thailand], 1000 ft [= 304 m]/i–ii.1899, W.L. Abbott (USNM).

3.1.9. *Neurhermes tonkinensis* (van der Weele) Figs. 13–14, 19, 59–65

Hermes maculifera tonkinensis van der Weele, 1909: 255. Type locality: Vietnam.

Diagnosis. This species is characterized by the entirely orange pronotum, the presence of large white round markings at distal 1/3 of both fore- and hindwings, the hindwings with broad proximal white markings, and the male ninth sternum with a large subtriangular posteromedian projection (Figs. 13, 60).

Description. Male: Body length 22.0–23.0 mm; forewing length 30.0–36.2 mm, hindwing length 28.0–31.1 mm.



Figs. 59–65. *Neurhermes tonkinensis* (van der Weele). **59:** Male genitalia, dorsal view. **60:** Male genitalia, ventral view, based on a male from southern China. **61:** Male genitalia, lateral view. **62:** Male ninth sternum, ventral view, based on a male from southern Vietnam. **63:** Male fused tenth gonocoxites, ventral view. **64:** Female genitalia, lateral view. **65:** Female fused eighth gonocoxites, ventral view. For abbreviations see legend Figs. 20–26. Scale bars: 1.0 mm.

Head (Fig. 19) entirely blackish brown. Compound eyes brown; ocelli pale yellow, medially margined black. Antennae black. Mouthparts black.

Prothorax (Fig. 19) orange. Meso- and metathorax blackish brown. Thoracic pilosity white on prothorax but dark brown on meso- and metathorax. Legs blackish brown with short dense brownish setae; tarsal claws reddish brown. Wings (Fig. 13) blackish brown with several creamy white markings. Forewing proximally with markings fused into arcuate band, but also with two markings distal to this band; medially with 5 large ovoid markings, one of which extends to costal area; a round marking present at distal 1/3. Hindwing proximally with rather broad creamy white marking, which strongly extends distad and bends toward costal area at middle, forming hook-like pattern, but sometimes median extending white marking separated from proximal marking; a round marking present at distal 1/3. Veins blackish brown except for those in creamy white markings yellow. Rs with 6–7 branches; 6–8 crossveins between R and Rs; anterior branch of MP with 4 branches, posterior branch of MP with 2 branches.

Abdomen brown with venters mostly yellow. Ninth tergum (Fig. 59) subquadrate and rather deep, in dorsal view with broadly arcuate anterior incision, and with posterior margin arcuately incised medially. Ninth sternum (Figs. 60, 62) posteriorly produced medially into

large subtriangular projection, posterolateral corners also strongly produced. Ninth gonocoxite (Fig. 60) slightly inflated distad and bearing slenderly elongate gonostylus, which is vertical to ninth gonocoxite and straightly directed dorsad. Ectoproct (Fig. 61) with ventral lobe about $4.0 \times$ length of dorsal lobe. Fused tenth gonocoxites (Fig. 63) arcuate, anterior margin slightly prominent medially, posterior margin feebly concaved medially; tenth gonostylus digitiform and directed posteriad.

Female: Body length 23.0–25.0 mm; forewing length 34.0–35.0 mm, hindwing length 29.0–31.0 mm.

Fused eighth gonocoxites (Figs. 64–65) broad and sclerotized, subtrapezoidal in lateral view, posterior margin medially with V-shaped incision; eighth gonapophyses present as pair of small sclerites posterior to eighth gonocoxite. Ninth gonocoxite (Fig. 64) short and broad, anteriorly bluntly prominent, posterior portion rounded, with small gonostylus. Ectoproct (Fig. 64) short, with posterior margin incised, leaving subtriangular dorsal and semicircular ventral lobes.

Distribution. China (Fujian, Guangdong, Guangxi, Guizhou, Yunnan); Laos (Hua Phan, Luang Namtha, Xieng Khouang); Thailand (Chantaburi, Chiang Mai, Chiang Mai, Mae Hong Son); Vietnam (Bac Kan, Ha Giang, Ha Tay, Hoa Binh, Lam Dong, Lang Son, Lao Cai, Vinh Phuc).

Remarks. This is the most widespread species of *Neurhermes*. It seems to be closely related to *N. sumatrensis* (see Remarks under *N. sumatrensis* for interspecific comparison). Males of *N. tonkinensis* from southern Vietnam have the posteromedian projection slightly narrowed proximally and feebly notched at tip, which is considered to be intraspecific variation.

Material. Lectotype ♀ [herein designated], ‘Tonkin [= Northern Vietnam], 1907, Ch. Alluaud, Museum Paris/Tonking [= Tonkin]/Type/*Hermes maculifera tonkinensis* v[an]d[er] Weele, Type’ (MNHN). Paralectotype 1 ♀ [herein designated], Haut-Tonkin et Bas-Yunnan, Entre Man-Had, Muong-Mum (Prés-Lao-Xay) et Ban-Mam-Coun [a locality in Lao Cai Prov. or Lai Chau Prov., Vietnam], 1905, Lieut Lesourt (RMNH). **CHINA:** 1 ♀, Yunnan, Mengla [21°27'N 106°33'E], 28.iv.2011, Hailin Yang & Jianyun Wang (CAU); 1 ♀, Yunnan, Gejiu, Longjing [23°25'N 103°09'E], 22.v.1979, Zhiyuan Wu (CAU); 1 ♂, Yunnan, Funing [23°37'N 105°37'E], 600 m, 6.v.1979, Jiafeng Wei (CAU); 1 ♀, Guizhou, Luodian [25°25'N 106°44'E], 12.vi.1963 (CAU); 1 ♂, Guangxi, Longzhou, Daqingshan [22°20'N 106°51'E], 5.v.1983 (CAU); 1 ♂, Guangxi, Longzhou, 22.v.1982, Xinli Wang (CAU); 1 ♂, Guangxi, Longsheng, Zuohushan [25°38'N 109°53'E], 23.vi.1982, Chikun Yang (CAU); 1 ♂, Guangxi, Longsheng, Tianpingshan [ca. 25°36'N 109°54'E], 740 m, 6.vi.1963, Yongshan Shi (IZCAS); 1 ♀, Guangxi, Fangcheng, Fulong [21°48'N 107°57'E], 200 m, 23.v.1999, Yanzhou Zhang (IZCAS); 1 ♀, Guangdong, Zhaoqing, Dinghushan, Xiuyangsuo, 1962, Zhaoxia Li (SYSU); 1 ♀, Guangdong, Zhaoqing, Dinghushan, Xiuyangsuo [21°30'N 112°33'E], 7.vi.1962, Wensheng Li (SYSU); 1 ♀, Guangdong, Dinghu [= Dinghushan] (SYSU); 1 ♀, Guangdong, Xinfeng, Simaping Linchang [24°03'N 114°12'E], 28.v.1991 (SYSU); 1 ♂, Guangdong, Nan Shan, Ho-yün, 30.iv.1938, W.T. Taang (SYSU); 1 ♀, Guangdong, Nan Shan, Ho-yün, 2.v.1938, W.T. Taang (SYSU); 1 ♀, Fujian (CAU); **LAOS:** 1 ♀, Hua Phan, Xamneua, Mt. Phu Pan Saluei [20°25'N 104°02'E], v.2003 (EUM); 1 ♂, Hua Phan, Ph-Pan, 30.iv.2003 (HFC); 1 ♂, Hua Phan, Xamneua, 15.iv.2001 (HFC); 7 ♂ 3 ♀, Hua Phan, Phou Pane Mt., 20°13'09–19°N 103°59'54"–104°00'03"E, 1480–1510 m, 1–16.vi.2009, Vit. Kubán (NMPC); 2 ♂ 5 ♀, Hua Phan, Phou Pane Mt., ~20°13'N 104°00'E, 1350–1500 m, 1–16.vi.2009, M. Brancucci (NMB); 2 ♀, Hua Phan, Ban Saleuy—Phou Pane Mt., 20°12–13.5'N 103°59.5'–104°01'E, 1340–1870 m, 2–22.vi.2011, Vit. Kubán & Lao coll[ector]. (NMPC); 1 ♀, Luang Namtha, Muang Sing [21°11'N 101°08'E], 650 m, 8.vi.1960, L.W. Quate (BPBM); 1 ♀, Xiang Khouang, 30 km NE Phonsavan: Ban Na Lam—Phou Sane Mt., 19°37–38'N 103°20'E, 1300–1500 m, 10–30.v.2009, M. Brancucci (NMB); **THAILAND:** 1 ♀, Chantaburi, Khao Soi Dao [12°56'N 102°13'E], 12.v.1984, A.M. Cotton (NSMT); 1 ♀, Chiang Mai, Mt. Doi Pui [18°49'N 98°53'E], 1400–1500 m, 30.iv.1982, T. Shimomura (NSMT); 4 ♀, Chiang Mai, Mae Sa Water-fall [18°54'N 98°54'E], 16.vi.1965, S. Asahina (NSMT); 1 ♀, Chiang Rai, Wien Papao [19°16'N 99°30'E], 1.v.1997, M. Takakuwa (HFC); 1 ♀, Mae Hong Son, Ban Huai Po, 800–1600 m, 1991, S. Bily (NMPC); 1 ♀, Pupin, 21.iv.1985, M. Tao (NSMT); **VIETNAM:** 3 ♀, Ha Giang, Dong Van [23°16'N 105°22'E], 6/7.v.2011, F. Hayashi (HFC); 1 ♀, Bac Kan, Ba Be [22°24'N 105°37'E], 4.vi.2012, F. Hayashi (HFC); 1 ♀, Hoa Binh, 6–9.vi.1986, J. Macek (NMPC); 1 ♂ 1 ♀, Lang Son, Montes Mauson [21°52'N 107°00'E], iv–x, 2[000]–3000' [= 609–914 m], H. Fruhstorfer (MFN); 1 ♀, Lang Son, Than-Moi [= Dong Mo, 21°46'N 106°05'E], vi–vii, H. Fruhstorfer (ZMA); 2 ♂, Lao Cai, Chapa [= Sa Pa, 22°20'N 103°50'E], viii.1936, S. Masseyeff (NHM); 1 ♂, Lao Cai, Sa Pa, Deo O Quy Ho, 1750 m, 1/3.vi.1999, M. Owada (NSMT); 2 ♂, Vinh Phuc, Mt. Tam Dao [21°45'N 105°64'E], v.1993, H. Karube (1 ♂ in CAU, 1 ♂ in HFC); 1 ♂, Vinh Phuc, Tam Dao, 25.iv.1995 (NSMT); 1 ♂, Ha Tay, Ba Vi, Mt. Tan Vien [21°04'N 105°21'E], 690–1150 m, 28.iv.1995, A. Shinohara (NSMT); 1 ♂, Ha Tay, Ba Vi, Tam Bien [= Tan Vien], 28.iv.1995, M. Sato (EUM); 17 ♂ 2 ♀, Ha Tay, Ba Vi, Tan Vien, 14.iv/1.v.1995 (NSMT); 2 ♂, Lam Dong, Bao Loc, Dambri [ca. 11°53'N 107°41'E], 800 m, 30.iv/4.v.2000, M. Owada (NSMT).

3.2. Phylogenetic analysis

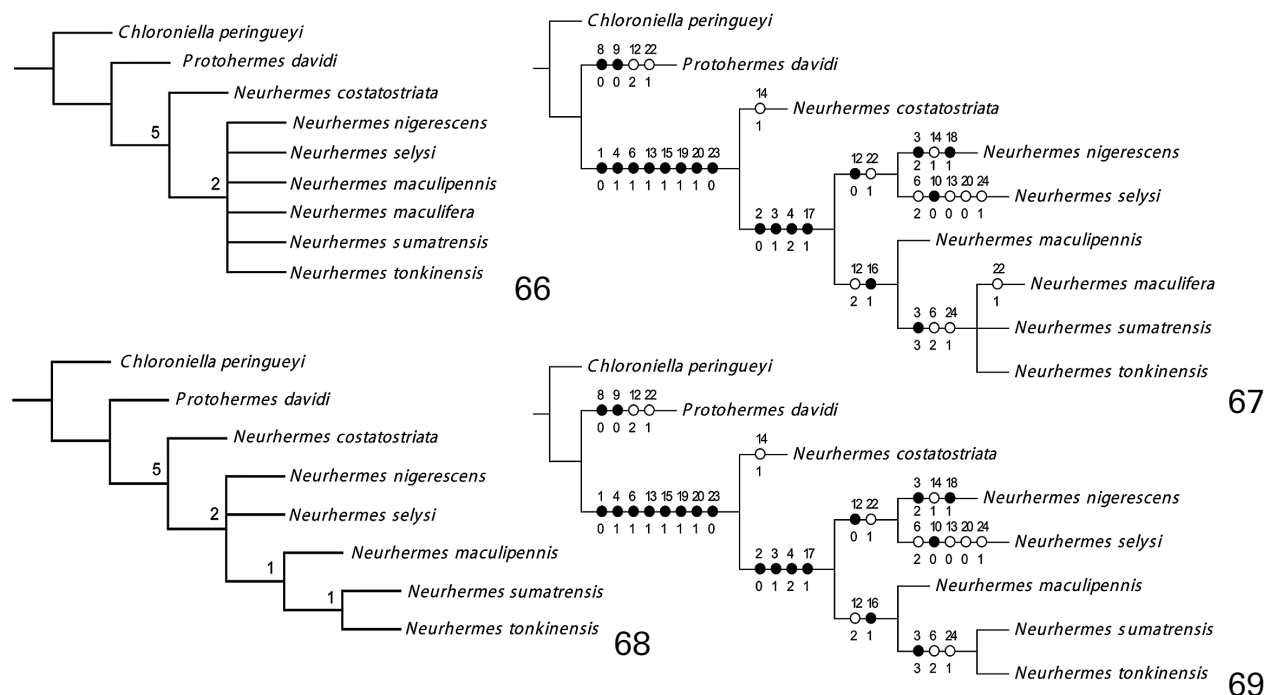
Phylogenetic analysis of matrix 1 using NONA yielded single most parsimonious tree (MPT) (length = 40, consistency index = 72, retention index = 75) (Fig. 67). However, the phylogenetic analysis of matrix 1 using TNT yielded four MPTs, and one of the four MPTs has an identical topology to the single MPT obtained with NONA. The strict consensus tree of the four MPTs is shown in Fig. 66. The resolution of relationships among most *Neurhermes* species is poor in the analysis with TNT probably due to the lack of male genitalic characters in *N. maculifera*. The analysis of matrix 2 with NONA yielded single MPT (length = 39, consistency index = 74, retention index = 74) (Fig. 69). The topology of this MPT is nearly identical to that obtained from matrix 1. *Neurhermes sumatrensis* and *N. tonkinensis* are sister groups, their clade being sister to *N. maculipennis*. The analysis of matrix 2 using TNT yielded two MPTs, one of the MPTs with identical topology to the single MPT obtained from matrix 2 with NONA. By excluding *N. maculifera*, the internal relationships among *Neurhermes* become well resolved (Fig. 68). The only difference between the results from TNT and NONA analyses refers to the sister relationship of *N. nigerescens* and *N. selysi*, which is recovered with NONA but not with TNT. According to the largely identical phylogenetic results from matrix 1 and matrix 2 with NONA, we discussed the interspecific relationships and biogeography of *Neurhermes* based on NONA trees (see Figs. 67, 69).

4. Discussion

4.1. Phylogenetic status of *Neurhermes*

The synapomorphies herein supporting the grouping of all *Neurhermes* species are the head without postocular spines (char. 1:0), the forewing costal region black proximally with white stripes on crossveins (char. 4:1), the hindwing with proximal white marking (char. 6:1), the short and transversely wide male ninth sternum (char. 13:1), the prolonged male ninth gonocoxite and gonostylus (char. 15:1), the dorsoventrally bilobed male ectoproct (char. 19:1), the dorsoventrally flattened male tenth gonostylus (char. 20:1) and the presence of female eighth gonapophyses (char. 23:1). However, many of these characters are shared by some species of *Protohermes* or *Chloroniella*, and only the long male ninth gonocoxite with an elongate gonostylus is probably a unique autapomorphy of *Neurhermes*.

The monophyly of *Neurhermes* should be further verified under an analysis including all species of *Protohermes* and representative species of other Corydalinae



Figs. 66–69. Reconstructed interspecific relationships among *Neurhermes* species. **66:** Strict consensus tree based on 4 MPTs inferred from matrix 1 with TNT. **67:** Single MPT inferred from matrix 1 with NONA. **68:** Strict consensus tree based on 2 MPTs inferred from matrix 2 with TNT. **69:** Single MPT inferred from matrix 2 with NONA. Bremer support values are shown at nodes on strict consensus trees. Only unambiguous character changes are shown on MPTs generated from NONA. Black circles represent unique changes, while white circles represent homoplasious changes.

genera, which is not yet possible at present due to lacking data. In addition, it should also be tested whether *Neurhermes* might be subordinate in some other genus, especially *Protohermes*. All previous phylogenetic analyses of Corydalinae recovered *Neurhermes* to be the sister of *Protohermes* (GLORIOSO 1981; PENNY 1993; CONTRERAS-RAMOS 1998, 2011). However, due to the morphological resemblance between *Neurhermes* and the *Protohermes guangxiensis* species-group or the *Protohermes differentialis* species-group, LIU & YANG (2006) indicated that *Neurhermes* might be derived forms inside of *Protohermes*. Nevertheless, the test of the generic status of *Neurhermes* and *Protohermes* should be made at species level by a phylogenetic analysis with a comprehensive sampling of characters and taxa, which is out of the scope of present study.

4.2. Interspecific relationships within *Neurhermes*

Within *Neurhermes*, *N. costatostrata* is the sister of the remaining species. The clade comprising *N. nigerescens*, *N. selysi*, *N. maculipennis*, *N. sumatrensis*, and *N. tonkinensis* is supported by the head with narrow postocular plane (char. 2:0), the pronotum with one pair of median black markings (char. 3:1), the black forewing costal region with two white markings (char. 4:2), and the male

ninth gonostylus being right angle to ninth gonocoxite (char. 17:1). Within this clade, *N. nigerescens* and *N. selysi* form a clade sister to the monophyletic group including *N. maculipennis*, *N. sumatrensis*, and *N. tonkinensis*. The synapomorphies supporting *N. nigerescens* + *N. selysi* are the male ninth sternum with feebly developed posterolateral projections (char. 12:0) and the female eighth gonocoxite with truncate posterior margin (char. 22:1). The synapomorphies supporting the monophyletic group comprising *N. maculipennis*, *N. sumatrensis*, and *N. tonkinensis* are the male ninth sternum with well developed subtriangular posterolateral projections (char. 12:2) and the distally strongly inflated male ninth gonocoxite (char. 16:1). Within this group *N. sumatrensis* and *N. tonkinensis* are sister species supported by the entirely orange pronotum (char. 3:3), the proximal white marking extending distally on hindwing (char. 6:2), and the anteriorly produced female ninth gonocoxite (char. 24:1). By having these three character states, *N. maculifera* is also grouped with *N. sumatrensis* and *N. tonkinensis*, which however needs further testing when the male of *N. maculifera* is found.

4.3. Biogeography

Neurhermes is widely distributed in almost all the major regions of the Oriental realm, including the southern and

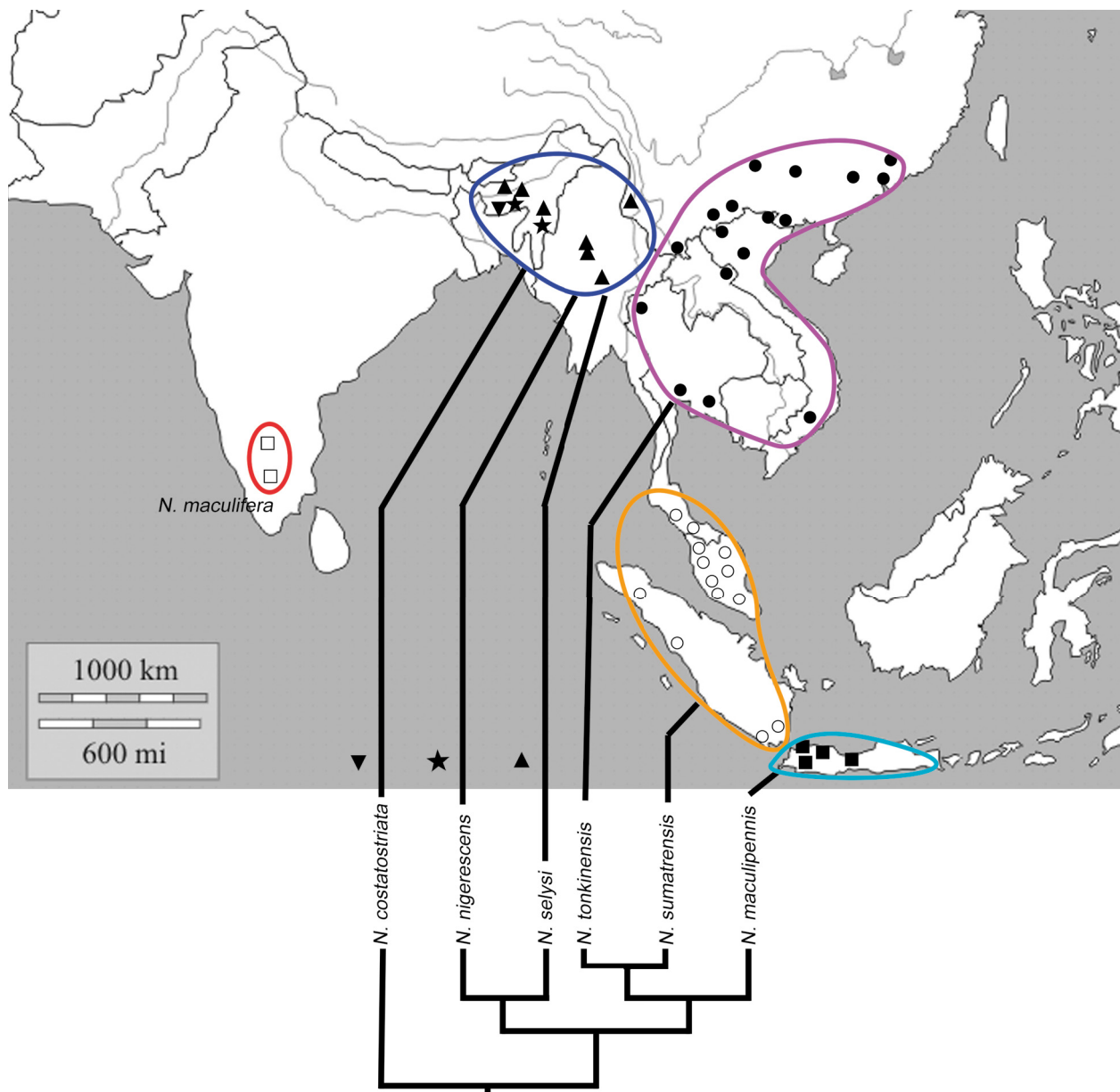


Fig. 70. Geographical distribution of *Neurhermes* species, mapped onto the phylogenetic tree from Fig. 69. *Neurhermes maculifera* not shown in the phylogeny due to unclear phylogenetic position.

northern Indian subcontinent, southern edge of China, large parts of Indochina, and two islands (i.e. Sumatra and Java) of the Malay Archipelago (Fig. 70). Irrespective of the doubtful record of *N. maculipennis* from the Malay Peninsula, Borneo and Sumatra, four *Neurhermes* species, i.e. *N. maculipennis*, *N. maculifera*, *N. sumatrensis*, and *N. tonkinensis*, allopatrically occur in Java, southern India, Sumatra + Malay Peninsula, and Indochina Peninsula + southern China. However, *N. costatostrata*, *N. nigerescens* and *N. selysi*, all endemic to northeastern India and adjacent areas, are sympatric in some localities, e.g. the Khasi Hills of northeastern India.

The range of *Neurhermes* largely overlaps with that of the Oriental endemic dobsonfly genus *Nevromus* (LIU et al. 2012). Based on the disjunct distribution of *Nevromus*, LIU et al. (2012) proposed an Indian origin of this

genus and considered that it dispersed in the southern part of Eurasia before middle Eocene when Sundaland (the Malay Peninsula, Sumatra, Java, and Borneo) was connected with Indochina. This hypothesis is probably also suitable for explaining the present distribution pattern of *Neurhermes*. Moreover, this origin-dispersal pattern is generally consistent to the “eastward” dispersal track (from the southeastern part of Asian mainland through the Malay Peninsula to the eastern part of Indonesia) mentioned by New (2003) for some groups of Malesian Neuroptera, which is the sister order of Megaloptera. However, the Indian origin of *Neurhermes* has not been corroborated due to the obscure status of the southern Indian species *N. maculifera*. If discovery of its male suggests sister relation of this species with the rest of *Neurhermes* by the finding of its male, the Indian ori-

gin of *Neruhermes* could be convincing. Whereas, if *N. maculifera* is truly grouped with *N. sumatrensis* from Malay Peninsula + Sumatra and *N. tonkinensis* from Indochina + southern China, it would be difficult to reconstruct the origin area of this genus.

Similar to *Nevromus*, *Neurhermes* also have poor capacity of dispersal due to the weak flight ability and the restriction to aquatic habitats, so geographical vicariance probably accounts for major divergence events of this genus. It is well known that series of orogenic events happened during Miocene after the collision between Indian subcontinent and Eurasia yielded many high mountains, e.g. the Himalayan Mountain Range and the Hengduan Mountain Range (WANG 2006). These mountains in the northeastern Indian subcontinent as well as in northern Myanmar and southwestern China might have caused vicariance-induced speciation of *Neurhermes*. Actually, the extraordinarily rich species diversity of Corydalidae in the northeastern Indian subcontinent and its adjacent areas to the east, which is considered to be the diversification centre of Asian Corydalidae (YANG & LIU 2010), was probably formed meanwhile with the uplift of numerous high mountains. The divergence of *N. costatostrata* and the splitting between *N. nigerescens* and *N. selysi* might be due to the isolation by certain mountains in the area around northeastern India. However, concerning the early origin of *Neurhermes* (possibly during or even before Eocene), it is difficult to trace the past vicariance events. Sympatric distribution of *N. costatostrata*, *N. nigerescens* and *N. selysi* suggests that their secondary dispersal beyond the areas of the original isolation. On the other hand, the divergence between the clade comprising *N. maculipennis*, *N. sumatrensis* and *N. tonkinensis* and the clade of *N. nigerescens* + *N. selysi* might be also due to the mountainous isolation around northeastern India, which formed different fauna from northeastern India and Indochina + Malesia. The transgressive event between Sundaland and Eurasia in late Eocene (HALL 2001) is considered to be a significant vicariance factor for the early divergence of various groups of the Asian Megaloptera (LIU et al. 2010, 2012), and the separation of Sundaland into several islands, e.g. Borneo, Java, and Sumatra etc., is probably the main reason for the speciation of Corydalidae from Malesia. Consequently, these tectonic events might account for the speciation of the Javanese endemic species *N. maculipennis* as well as the divergence between *N. tonkinensis* from Indochina and *N. sumatrensis* from the Malay Peninsula and Sumatra. Nevertheless, the test or corroboration of the present phylogenetic and biogeographical implications is to be made by a molecular systematic study with the estimation of divergence time.

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