A review of taxonomy and flower-breeding ecology of the *Colocasiomyia toshiokai* species group (Diptera: Drosophilidae), with description of a new species from Indonesia

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**Abstract.** Flies of the *Colocasiomyia toshiokai* species group depend exclusively on inflorescences/infructescences of the aroid tribe Homalomenae. The taxonomy and reproductive biology of this group is reviewed on the basis of data and samples collected from Southeast Asia. The species boundaries are determined by combining morphological analyses and molecular species delimitation based on sequences of the mitochondrial COI (cytochrome *c* oxidase subunit I) gene. For the phylogenetic classification within this species group, a cladistic analysis of all the member species is conducted based on 29 parsimony-informative, morphological characters. As a result, six species are recognised within the *toshiokai* group, including one new species, viz. *C. toshiokai*, *C. xanthogaster*, *C. nigricauda*, *C. erythrocephala*, *C. heterodonta* and *C. rostrata* sp. *n.* Various host plants are utilised by these species in different combinations at different localities: Some host plants are monopolized by a single species, while others are shared by two or three species. *C. xanthogaster* and *C. heterodonta* cohabit on the same host plant in West Java, breeding on spatially different parts of the spadix. There is a close synchrony between flower-visiting behaviour of flies and flowering events of host plants, which indicate an intimate pollination mutualism.

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**INTRODUCTION**

Flies of the family Drosophilidae principally feed/breed on fermenting or decaying organic matter such as fruit, tree sap, mushrooms and herbage (Kimura et al., 1977; Shorrockes, 1982). However, feeding on fresh flowers has evolved repeatedly in some lineages of Drosophilidae (Brncic, 1983). The genus *Colocasiomyia* de Meijere is one such group that obligatorily breeds in flowers. Currently there are 29 formally described species in this genus, mostly from the Asian tropics (Toda, 2018), which are classified into six species groups (Sultana et al., 2006; Fartyal et al., 2013). Each species group specialises on host plants...
of a particular taxon (Yafuso & Okada, 1990; Yafuso et al., 2000; Sultana et al., 2002, 2006; Toda & Lakim, 2011; Fartyal et al., 2013; Li et al., 2014): *crassipes* group (Sultana et al., 2006) the family Magnoliaceae, *zylanica* group (Sultana et al., 2006) the family Araceae (genus *Pinanga* Blume), *gigantea* group (Fartyal et al., 2013) the subfamily Monsteroideae (Araceae), *baechlii* group (Okada, 1990) the tribe Schizomatoglottideae (subfamily Aroidae, Araceae), *cristata* group (Okada, 1990) the *Colocasia* clade and genera *Alocasia* (Schott) G. Don and *Leucoca- sia* (sensu Cusimano et al., 2011; Aroidae, Araceae), and *toshiokai* group (Sultana et al., 2002) the genera *Homalo- mena* Schott (*Pholidenron* clade) and *Aglao- mena* Schott (tribe Aglaonemateae) of Aroidae (Araceae).

*Colocasiumyia* flies depend on specific host plants throughout their entire life cycle; their life histories from oviposition to adult eclosion are adapted to the flowering/fructifying of specific host plants, and vary depending on the number and combination of cohabiting fly species (Carson & Okada, 1980; Honda-Yafuso, 1983; Toda & Okada, 1983; Yafuso, 1994; Takenaka, 2006; Takenaka et al., 2006; Takano et al., 2012; Fartyal et al., 2013). In turn, the flies serve as specific, obligate pollinators of their host plants (Yafuso, 1993; Miyake & Yafuso, 2003; Takenaka, 2006; Takenaka et al., 2006; Takano et al., 2012).

The *toshiokai* group was established by Sultana et al. (2002) for five species: *C. toshiokai* (Okada, 1983) recorded from the Philippines, *C. xanthogaster* Yafuso & Okada, 1990 and *C. heterodonta* Yafuso & Okada, 1990 both from Java, *C. erythrocephala* Sultana & Yafuso, 2002 from Vietnam and *C. nigricauda* Sultana & Toda, 2002 from Sabah. All these species are recorded exclusively on inflorescences of the genera *Homalomena* and *Aglao mena*. However, the knowledge of their flower-visiting/breeding habits is still fragmentary (Yafuso & Okada, 1990).

In addition, Sultana et al. (2006) lists four undescribed, putative species (sp. *aff. heterodonta* from Java, sp. 2 *aff. heterodonta* and sp. 3 *aff. heterodonta* from Sumatra, and sp. *aff. xanthogaster* from Sumatra and Sulawesi) as members of the *toshiokai* group, but leave their species status uncertain. In the present study, the species delimitation and relationships within the *toshiokai* group are determined based on detailed morphology and mitochondrial COI (cytochrome *c* oxidase subunit I) sequences of populations from Malaysia and Indonesia. As a result, one new species is described and the descriptions of the five known species are revised. In addition, the reproductive ecology of this species group is summarized on the basis of all the available data and observations of flower-visiting behaviour in relation to heat generation by host plant inflorescences.

**MATERIAL AND METHODS**

**Insect specimens**

All of the specimens included in the present study were collected from inflorescences of *Homalomena* and *Aglao mena* in Malaysia and Indonesia (see the “Ecological observation” section for details). Specimens were preserved in Kahle’s solution followed by 70% ethanol for morphological observation, or in 100% ethanol for DNA sequencing. The specimens studied are deposited in the following institutions: Forest Research Center, Kuching, Sarawak, Malaysia (FRCK); Kinabalu Park, Sabah Parks, Sabah, Malaysia (KPSP); Institute for Tropical Biology and Conservation, Universiti Malaya Sabah, Kota Kinabalu, Sabah, Malaysia (BORN); Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB); Systematic Entomology, The Hokkaido University Museum, Hokkaido University, Sapporo, Japan (SEHU); Tsukuba Research Departments of National Museum of Nature and Science Tokyo, Japan (NSMT); and Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China (KIZ).

**Species delimitation and description**

We followed the same methods used by Sultana et al. (2002) and Li et al. (2014) for studying their external morphology, measuring and dissecting them. First, the intact whole body was observed under a stereoscopic microscope for determining the external morphology and measuring characters using an ocular micrometer. Then, the head, mouthparts, a foreleg and male/female terminalia were detached from the body of some specimens, treated with 10% KOH solution at 80–90 °C for a few minutes and mounted in a droplet of glycerin on a cavity slide to observe under a light microscope. The fine structures of these dissected organs were microphotographed (either following further dissection or not) using a DinoLite® Digital Eyepiece Camera or a HI- TACHI TM5000 tabletop scanning electron microscope (SEM), and drawn based on the resulting digital pictures using COREL-DRAW® X4 (Corel Corporation).

The specimens were first identified as members of the *C. toshioki* group and sorted into known and putatively new species based on their morphology. Then, a total of 38 specimens representing local populations of these morpho-species were selected for sequencing a 658-bp fragment of COI (Table S1). However, DNA was not available for two species, *C. toshiokai* and *C. erythrocephala*. Some DNA samples were extracted from whole bodies following the method of Boom et al. (1990), with some modifications (Kobayashi et al., 2009). The remaining DNA samples were extracted from a hindleg or small piece(s) of abdominal tissue extracted through the hole left after the removal of the terminalia, using the TIANamp® Genomic DNA Kit. We used the same methods for PCR and sequencing as in Li et al. (2014), with Folmer et al.’s (1994) primers: LCO1490, 5'- GGTCA ACAAA TCATA CAAAT CA -3'; HCO2198, 5'- TAAAC TTCAG GGTGA AGTGA-3'; and an ABI® 3730 DNA Analyzer. Sequences were edited in the SEQMAN module of the DNASTAR package (DNASTAR Inc. 1996) and aligned in MEGALIGN® (Kumar et al., 2016).

For the species delimitation based on molecular data, the COI sequences were analysed using three algorithms for OTU (Operational Taxonomic Unit) recognition: the Automatic Barcode Gap Discovery (ABGD; Puillandre et al., 2012), the Generalized Mixed Yule Coalescent (GMYC; Pons et al., 2006) and the Refined Single Linkage (RELS; Ratnasingham & Hebert, 2013). The ABGD analysis was done using the web interface (http://www.abgd.univ-jussieu.fr/public/abgd/abgdweb.html). The COI alignments were uploaded to this web-interface, and analysed under the default setting: *P* (prior maximum divergence of intraspecific diversity) ranges from 0.001 to 0.1; *Steps* = 10; *X* (a proxy for minimum gap width) = 1.5; *Nb* bins (for distance distribution) = 20; distance = Jukes-Cantor (JC69). For the GMYC analysis, an ultrametric tree was generated by BEAST v2.4.5 (Bouckaert et al., 2014) using the Yule prior and the HKY (Hasegawa et al., 1985) + Gamma model. The MCMC chains were run for 5,000,000 generations with a burn-in of the initial 10% of samples, then the output was
summarized using TreeAnnotator v2.4.8. The GMYC analysis was performed using the package “splits” (Species Limits by Threshold Statistics; available from http://r-forge.r-project.org/projects/splits) implemented in R software with default scaling parameters for the single- and multiple-threshold options. Ratnasingham & Hebert (2013) developed the Barcode Index Number (BIN) System within the Barcode of Life Data System (BOLD: http://www.barcodinglife.org; Ratnasingham & Hebert, 2007) to register the OTUs (hypothetical species) delineated by RESL. New barcode sequences uploaded to BOLD are analysed through the BIN pipeline (Ratnasingham & Hebert, 2013); the BIN assignments of all records in BOLD are updated regularly, and BIN clusters can be split farther or merged together. We used BIN assignments for our COI sequences as the results of RESL analysis, which were downloaded from BOLD on May 28, 2018. A maximum likelihood (ML) tree was constructed using the program RAxML HPC (Stamatakis, 2006). In the ML analysis, the data set of the COI sequences was partitioned into two: 1st + 2nd codon positions and 3rd codon position. We selected eight species, two from each of four other species groups, as outgroup taxa (Table S1). A total of 100 distinct ML trees were calculated from distinct random trees under the GTRGAMMA model of nucleotide substitution, with the gamma model of rate heterogeneity across sites. Branch confidence values (bootstrap percentages, BPs) were obtained by conducting rapid bootstrap analyses (1000 replicates), with bipartitions drawn from the 1000 boot strapped trees onto the best-scoring ML tree of the 100 calculated.

The species boundaries were determined integratively based on the results of the above molecular analyses and morphological comparison. In the description of a new species and redescriptions of known species, we followed McAlpine (1981) for the morphological terminology and Zhang & Toda (1992) for the definitions of measurements and indices.

Cladistic analysis of morphological characters

In order to determine the phylogenetic positions of C. toshiokai and C. erythrocephala, for which no specimens were available for DNA sequencing, a cladistic analysis of all six species of the toshiokai group was conducted using morphological characters. Four outgroup taxa, C. baechlii (Okada, 1986), C. sp. 1 aff. bogneri, C. sp. 2 aff. bogneri and C. sp. 13 aff. bogneri, were selected from the baechlii group, which was proposed as the sister to the toshiokai group because of some synapomorphies and partial overlap in their host plant use with the toshiokai group. The character states for C. baechlii are based on its original description (Okada, 1986).

The parsimony analysis was performed using PAUP* v4.0a165 (Swofford, 2003). Maximum parsimony cladogram was generated by a heuristic search with 1000 replicates under the setting of “addition sequences at random” and “tree-bisection reconnection (TBR)” branch-swapping. All transformation series were assumed to be “unordered”. On the resulting tree, character optimization was performed by ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation). Branch support was assessed by a bootstrap analysis with 1000 replicates.

Ecological observations

In order to investigate the flower-visiting and reproductive habits of the species of the toshiokai group, field collections and observations were conducted at various localities in Vietnam, Malaysia (Sarawak and Sabah) and Indonesia (Sumatra, Java and Sulawesi). At each locality, host plant (Homalomena and Aglonema) inflorescences/infrutescences at different developmental stages were collected. The flowering/fruiteming of host inflorescences/infrutescences was divided into six stages (Fig. 1B): Stage I, inflorescence bud with spadix completely covered with spathe before anthesis; Stage II, flowering phase with spathe open and spadix exposed; Stage III, post-flowering phase with spathe closed and spadix covered; Stage IV, stamens decaying and pistils starting to grow within spathe; Stage V, stamen-remnants dried out and fruit growing; Stage VI, spathe detached and ripe fruitlets exposed. When Colocasiomyia flies were found visiting an inflorescence at Stage II, the inflorescence was enclosed within a plastic bag and all adult insects coming out of the inflorescence within the plastic bag were caught using an aspirator. The collected inflorescences/infrutescences were brought back to the laboratory and dissected under a stereomicroscope to determine the distribution of Colocasiomyia immature stages (eggs, larvae or puparia) on the spadix. In cases where C. xanthogaster and C. heterodonta coexisted, their immature stages were identified based on the morphological differences described for eggs and larvae.

Fig. 1. Homalomena megaloephlya M. Hotta in West Java. A – photograph of a complete plant; B – inflorescences and infrutescences at Stages I to V (see text for explanation of each stage) in a cluster of sequentially blooming inflorescences; C – an inflorescence at Stage II, with a Colocasiomyia fly on the spadix; D – a spadix with powdery pollen at Stage III, shown by removing the spathe: upper 3/5 of the spadix, the staminate region covered with male flowers (stamens); lower 2/5, the pistillate region covered with female flowers (pistils).
of these two species by Yafuso & Okada (1990). The distribution of C. nigricauda immatures was examined on inflorescences/infructescences of Homalomena lambirensis S.Y. Wong & P.C. Boyce in Lambir, Sarawak, where C. nigricauda monopolized this host plant. No inflorescences/infructescences were examined for immature distributions of the other Colocasiomyia species.

Flower-visiting behaviour of Colocasiomyia flies during the flowering of two host plants belonging to the Homalomena supergroup, Homalomena megalophylla M. Hotta (Fig. 1) and H. pendula (Blume) Bakh. f. (Fig. S4), was observed in the Bogor Botanical Garden (6°35´S, 106°47´E, 260 m a.s.l., West Java, Indonesia), from November 14 to 17, 2009 for H. megalophylla and from August 1 to 4, 2011 for H. pendula. Important flowering events, i.e., anthesis, heat generation, odour emission, pollen release and spathe closure, were observed on one inflorescence of each species. Inflorescences of H. megalophylla and H. pendula are nearly identical in structure. The spadix consists of a pistillate (lower female-flower) region covered with pistils and clavate, interpistillar staminodes, and a staminate (upper male-flower) region covered with stamens (Fig. 1D). There are two or three lines of relatively large, closely spaced staminodes at the border between the pistillate and staminate regions. The spathe covers the spadix and forms a spatheal chamber (Fig. 1C). Temperatures of the pistillate and the staminate regions were measured by inserting two thermo-couple sensors into the middle part of the respective regions through the spathe from the rear side. These temperatures were recorded along with nearby ambient temperature, every 2 min for 3 days covering the entire flowering process, using a data logger thermometer (Center® 309). At the same time, the behaviour of insects visiting the inflorescences, particularly that of Colocasiomyia, was recorded.

**RESULTS AND DISCUSSION**

**Species delimitation**

Fig. 2 shows the ML tree constructed using the COI sequences, along with the results of the ABGD and GMYC analyses and the BIN assignments. The monophyly of the toshiokai group was strongly supported (BP = 97). The 38 ingroup sequences were sorted into six OTUs by the ABGD analysis (see also Table S2). Each OTU represented a highly supported clade with BP ≥ 85. OTU1 (BP = 100) and OTU2 (BP = 99) each corresponded to a single morpho-species, “sp. 2 aff. xanthogaster” and “C. nigricauda”, respectively. OTU3 (BP = 100) included two morpho-species, “xanthogaster” from West Java (including the type locality of C. xanthogaster, Bogor) and West Sumatra and the dark form “sp. aff. xanthogaster” from West Sumatra and North Sulawesi. The sister relationship between OTU2 and OTU3 was strongly supported (BP = 100). The remaining three OTUs formed another highly supported cluster (BP = 99). Of the three OTUs, OTU6 (BP = 90) corresponded to the morpho-species “sp. 3 aff. heterodonta” representing a highland population on Mt. Kerinci, Jambi, Sumatra. Another morpho-species, “sp. aff. heterodonta”, which was recognised for highland populations with darker body col-
our in West Java, was assigned to OTU4 (BP = 85), together with populations of “heterodonta” in lowland West Java (including the type locality of *C. heterodonta*, Bogor) and Sumatra. However, the Bornean (Sabah and Sarawak) populations that had been identified as *C. heterodonta* (Sultana et al., 2002, 2006; Toda & Lakim, 2011) formed OTU5 (BP = 95) distinct from OTU4. However, the GMYC and BIN assignments lumped OTU5 and OTU6. Morphologically, the three OTUs of the “heterodonta” cluster were more or less different from each other (see Remarks for *C. heterodonta*). Especially, OTU6 was quite different in the morphology of its phallic organs from OTU4 and OTU5 (Fig. S2E, F, K, L, P, Q), suggesting that OTU6 is a distinct species. However, the molecular evidence contradicts the morphological resemblance: OTU5 and OTU6 were more similar in their COI sequences. A more critical point for the molecular species delimitation in this cluster is the insufficient sampling of OTU5 and OTU6 with only three and two specimens included in the analyses, respectively. Therefore, we refrained from taking any formal nomenclatural actions regarding the OTUs in this cluster and treated them as different forms of *C. heterodonta*: OTU4 = Form I (including the type of *C. heterodonta*), OTU5 = Form II (populations from Sarawak and Sabah, Borneo), and OTU6 = Form III (a highland population on Mt. Kerinci, Sumatra). As a consequence, we recognised four (one new and three known) species within the studied samples of the *C. toshiokai* species group: OTU1 = *C. rostrata* Shi, OTU2 = *C. heterodonta*, OTU3 = *C. erythrocephala* (paratype♂ from Lembah Anai, West Sumatra, Indonesia), and OTU4 = *C. nigricauda* (♂ from Inobong, Crocker Range, Sabah, Malaysia). All photographed specimens are the same as those in Fig. 3. Abbreviations: ar – arista, c – cavity, flgm 1 – first flagellomere, i – invaginated organ, p – pouch, ped – pedicel. Scale bars: 0.1 mm.

**Table 1.** Data matrix of 29 morphological characters of six species of the *Colocasiomyia toshiokai* species group (ingroup) and four species of the *C. baechlii* species group (outgroup). Character descriptions and polarity are fully detailed in the text (Cladistic analysis section).

| Character No. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 |
|--------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Outgroup     |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| C. sp. 1 aff. bogneri | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. sp. 2 aff. bogneri | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. baechlii      | ? | ? | ? | ? | 0 | 0 | ? | ? | ? | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. sp. 13 aff. bogneri | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 |

| Ingroup       |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| C. rostrata sp. n.       | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. heterodonta           | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 |
| C. erythrocephala        | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| C. toshiokai             | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. xanthogaster          | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. nigricauda            | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

a – 0 or 1; b – 1 or 2.
& Gao, sp. n., OTU2 = C. nigricauda, OTU3 = C. xanthogaster (but see Remarks for this species), and OTU4–6 = C. heterodonta.

**Cladistic analysis**

**Characters**

As a result of the morphological study, a total of 29 characters were included in the cladistic analysis (Table 1). The polarity of each character was determined using the outgroup comparison method (Watrous & Wheeler, 1981): all character states of C. sp. 1 aff. bogneri were coded as 0 (Table 1).

1. Antennal first flagellomere: (0) only slightly longer than pedicel (Fig. 3F); (1) 1.5 or more times as long as pedicel (Fig. 3A–E).

2. Small pouch on inner surface of first flagellomere: (0) absent (Fig. 3A–C, F); (1) present (Fig. 3D, E).

3. Longest branch of arista: (0) longer than upper, prominent seta on pedicel (Fig. 3B, C); (1) as long as (Fig. 3A, D, E) or shorter than (Fig. 3F) upper, prominent seta on pedicel.

4. Distance between antennal sockets: (0) greater than half of the diameter of the socket (Fig. 4B, C, E); (1) narrower than half the diameter of the socket (Fig. 4A, D, F).

5. Facial carina, width: (0) distinctly narrower than first flagellomere (Fig. 4A, F); (1) as wide as (Fig. 4E) or only slightly narrower than (Fig. 4B–D) first flagellomere.

6. Facial carina, length: (0) shorter than pedicel and first flagellomere combined (Fig. 4A, D–F); (1) as long as pedicel and first flagellomere combined (Fig. 4B, C).

7. Medial portion of clypeus: (0) thinner than distal portion of palpus (Fig. 5F); (1) as thick as distal portion of palpus (Fig. 5B, C); (2) thicker than distal portion of palpus (Fig. 5A, D, E).

8. Projections on anterolateral corners of cibarium: (0) shorter than half the width of cibarial anterior margin (Fig. 6F); (1) longer than width of its anterior margin (Fig. 6A–E).

9. Rows of medial sensilla on cibarium: (0) wider than or (1) as wide as sensilla campaniformia (Fig. 6).

10. Supralateral pair of setae outside prementum plate: (0) present (Fig. 7E, F); (1) absent (Fig. 7A–D).

11. Acrostichal setulae, number of rows: (0) 2; (1) 4.

12. Additional pair of dorsocentral setae: (0) absent; (1) present.

13. Prominent seta(e) on postpronotal lobe: (0) 2; (1) 3; (2) 1; (3) not differentiated.

14. Costal setae, middle row from medial portion of 2nd costal section to proximal portion of 3rd section: (0) apically blunt, thick, peg-like setae interspersed with thin, trichoid setae; (1) all apically blunt, thick, peg-like; (2) all thin, trichoid.

15. Pegs on foreleg tarsomere II: (0) 1 long and many small, tooth-like spines (Fig. 8B, C); (1) 3 long, stout spines (Fig. 8A).
16. Long spine(s) on foreleg tarsomere II: (0) not sulcate (Fig. 8B); (1) sulcate (Fig. 8A, C).
17. Surstylus: (0) absent; (1) as narrow as ventral elongation of cercus (Fig. 2A–C in Sultana et al., 2002); (2) broader than ventral elongation of cercus (Fig. 10A; Fig. S3A; Fig. 2D, E in Sultana et al., 2002).
18. Thick, upright, claw-like prensisetae on apical margin of surstylus (nested to ch. 17-1, 2): (0) absent (Fig. 10A; Fig. S3A; Fig. 2A in Sultana et al., 2002); (1) present (Fig. 2B–E in Sultana et al., 2002).
19. Fusion of cercus to epandrium: (0) fused; (1) separated (Fig. 10A; Fig. S3A; Fig. 2 in Sultana et al., 2002).
20. Parameres: (0) absent; (1) basally fused to hypandrium (Fig. 10B, C; Fig. S3B, C; Figs 3, 4A, B in Sultana et al., 2002); (2) basally articulated with hypandrium (Fig. S2F, L, Q; Fig. 4C, D in Sultana et al., 2002).
21. Membranous distiphallus of aedeagus: (0) absent or very short (Fig. S2F, L, Q; Fig. S3B; Fig. 4A in Sultana et al., 2002); (1) long, tube-like (Fig. 3A, C, E in Sultana et al., 2002).
22. Aedeagus, length (aedL): (0) aedL ≥ apodeme (Fig. 3A, C, E in Sultana et al., 2002); (1) 1/2 apodeme ≤ aedL < apodeme (Fig. 10B; Figs S3B, S2F; Fig. 4A in Sultana et al., 2002); (2) aedL < 1/2 apodeme (Fig. S2F, L).
23. Apex of aedeagus: (0) narrow, pointed (Fig. 3A, C, E in Sultana et al., 2002); (1) broad, round (Fig. 10B; Figs S3B, S2F, L, Q; Fig. 4A in Sultana et al., 2002).
24. Aedeagus, beak-like projection between basal processes: (0) absent (Fig. 3A, C, E in Sultana et al., 2002); (1) present (Fig. 10B; Figs S3B, S2F, L, Q; Fig. 4A in Sultana et al., 2002).
25. Female sternite VII, caudomedial margin: (0) not deeply notched; (1) deeply notched.
26. Epiproct, pubescence: (0) present (Fig. S3D); (1) absent.
27. Hypoproct, pubescence: (0) absent; (1) present (Fig. S3E).
28. Apical portion of oviscapt: (0) more or less elongated, forming a projection (Fig. 10D; Fig. S3D, E; Fig. 5A–D in Sultana et al., 2002); (1) roundish, without distinct projection (Fig. 5E in Sultana et al., 2002); (2) truncate.
29. Long, upright seta on dorsosubapical corner of oviscapt: (0) absent (Fig. 5E in Sultana et al., 2002); (1) present (Fig. 10D; Fig. S3D; Fig. 5A–D in Sultana et al., 2002).

Cladogram

The parsimony analysis of the morphological data matrix (Table 1) resulted in a single most parsimonious clado-
gram with a length of 59 steps and the following statistics: CI (consistency index) = 0.610, RI (characters retention index) = 0.681 and RC (rescaled consistency index) = 0.415. The tree was rooted by outgroup rooting (Fig. 9). Apomorphies are indicated on each branch based on the ACCTRAN estimations. The results of character optimization were inconsistent for some transformation series between ACCTRAN and DELTRAN (not shown). Synapomorphies not identified by both ACCTRAN and DELTRAN are excluded from the following description.

The resulting cladogram (Fig. 9) was compatible with the COI tree (Fig. 2). The monophyly of the toshiokai group was supported with BP = 73. Although the tree topology within the toshiokai group was not so highly resolved in terms of BP values, some morphological characters suggested phylogenetic relationships for some species. Colocasiomyia rostrata sp. n. was placed as the most basal branch within the toshiokai group. This species lacks some synapomorphies of the sister clade comprised of all the other ingroup species: antennal first flagellomere at least 1.5 times as long as pedicel (ch. 1-1); medial portion of clypeus as thick as or thicker than distal portion of palpus (ch. 7-1, 2); and long spine(s) on foreleg tarsomere II sulcate (ch. 16-1). This species shares the plesiomorphic states for these characters with the outgroup species.

Of the remaining species, the sibling C. xanthogaster and C. nigricauda formed a compact clade (BP = 99) supported by the following apomorphies: facial carina as long as pedicel and first flagellomere combined (ch. 6-1); and medial portion of clypeus as thick as distal portion of palpus (ch. 7-1). However, the relationships of this clade to C. erythrocephala and C. toshiokai remain uncertain (but see Remarks for the latter two species).

**Taxonomic account**

**Genus Colocasiomyia de Meijere, 1914**

**Colocasiomyia toshiokai species group**

Colocasiomyia toshiokai species group, Sultana et al., 2002: 306; Sultana et al., 2006: 694 (revised).

One new and five known species are here described and redescribed, respectively, with reference to the previous taxonomic studies on this species group (Toda & Okada, 1983; Yafuso & Okada, 1990; Sultana et al., 2002, 2006).

**Diagnosis** (Sultana et al., 2002, 2006, with minor modifications). Palpus subapically with large cavity (Fig. 5). The characters described as shared among the known species in this species group by Sultana et al. (2002) are not referred to in the descriptions below if also present in the new species.

*Colocasiomyia toshiokai* (Okada, 1983)


**Diagnosis.** Acrostichal setulae in 4 rows. Surstylus basally with a pair of strongly scleritized processes (Figs 10B, S2E, K, P, S3C; Figs 3, 4 in Sultana et al., 2002).
cus, rounded at apex, with 4 minute, submedial to apical setulae (Fig. 2A in Sultana et al., 2002).

**Redescription.** Antennal first flagellomere approximately 1.5 times as long as pedicel, without small pouch on inner surface; longest branch of arista as long as upper, prominent seta on pedicel (Fig. 3A). Facial carina somewhat roundly demarcated below, much shorter than pedicel and first flagellomere combined (Fig. 4A). Clypeus medially much thicker than distal portion of palpus (Fig. 5A). Projections on anterolateral corners of cibarium longer than width of its anterior margin (Fig. 6A). Prementum with 3 (proximal, lateral and distal) pairs of setae, lacking supralateral pair of setae outside prementum plate (Fig. 7A). Foreleg tarsomere II with 3 long, stout, sulcate spines. Epiproct and hypoproct with pubescence. Female sternite VII deeply notched on caudomedial margin.

**Type material examined.** PHILIPPINES: 1 ♂, 1 ♀ (paratypes), Mindanao, Surigao, 17.vii.1981 (S. Toshioka) (NSMT).

**Distribution.** Philippines (Mindanao).

**Remarks.** This species was placed as the sister to the clade of *C. xanthogaster* and *C. nigricauda* in the most parsimonious cladogram (but BP = 52; Fig. 9), with the following synapomorphies: surstylus as narrow as ventral elongation of cercus (ch. 17-1); and aedeagus with long, tube-like, membranous distiphallus (ch. 21-1). On the other hand, this species also seems to be related to *C. rostrata* sp. n., sharing the following homoplastic apomorphies: acrostichal setulae in 4 rows (ch. 11-1); costal setae in middle row from medial portion of 2nd costal section to proximal portion of 3rd section all thin, trichoid (ch. 14-2); and hypoproct pubescent (ch. 27-1).

**Colocasiomyia xanthogaster** Yafuso & Okada, 1990
(Figs 3–7B, 8A, S1; Table S3)

**Diagnosis.** Additional pair of dorsocentral setae present before transverse suture, approximately 1.5 times as long as pedicel, without small pouch on inner surface; longest branch of arista as long as upper, prominent seta on pedicel (Fig. 2B in Sultana et al., 2002). Clypeus apically narrow and clawed (Fig. S1M–O).

**Redescription.** Antennal first flagellomere approximately 1.5 times as long as pedicel, without small pouch on inner surface; longest branch of arista as long as upper, prominent seta on pedicel (Fig. 3B). Clypeus medially nearly as thick as distal portion of palpus (Fig. 5B). Projections on anterolateral corners of cibarium longer than width of its anterior margin; medial and posterior cibarial sensilla 3–6 and 4–6 per side, respectively (Fig. 6B). Prementum with 3 (proximal, lateral and distal) pairs of setae, lacking supralateral pair of setae outside prementum plate (Fig. 7B).
**Material examined.** INDONESIA: 1♂ (Light), West Java, Bogor, Bogor Botanical Garden, 6°36’9.9”S, 106°47’47.8”E, 273 m a.s.l., 22.1.2004, ex *H. pendula* (M.J. Toda) (SEHU); 1♀, 1♂ (Light), ditto, except 27.1.2004 (MZB); 2♂ (1 Light, 1 Dark I), West Sumatra, Padang Panjang, Batangang, 5.1.2004, ex *Homalomena* sp. (M.J. Toda) (SEHU); 1♂ (Light), West Sumatra, Sungai Penuh – Tapan, 700 m a.s.l., 7.xii.2004, ex *Homalomena* sp.P (Fig. S5) (K.T. Takano) (MZB); 1♀ (Dark I), West Sumatra, Lembah Anai, 0°28’55.3”S, 100°20’17.7”E, 250 m a.s.l., 19.xii.2003, ex *Homalomena* sp. (M.J. Toda) (SEHU); 1♂, 2♀ (Dark I), West Sumatra, Lembah Anai, 9.xii.2004, ex *Homalomena* sp.L c.f. *megalophylla* (Fig. S6) (K.T. Takano) (SEHU); 25♂, 23♀ (#02778–2825, Dark II), North Sulawesi, Dumoga Bone National Park, Tumokang, 0°32’49.3”S, 123°49’7.6”E, 587 m a.s.l., 19.xii.2003, ex *Homalomena* sp. aff. alba (Fig. S7) (K.T. Takano) (KIZ); 12♂, 18♀ (#02826–2855, Dark II), 1♂, 2♀ (Dark II), North Sulawesi, Toraut, 0°32’43.9”N, 123°49’7.6”E, 587 m a.s.l., 19.xii.2003, ex *Homalomena* sp.T (Fig. S8) (K.T. Takano) (SEHU); 8♂, 19♀ (#02856–2882, Dark II), North Sulawesi, Desa Tinoor, 22.xii.2003, ex *Homalomena* sp. (K.T. Takano) (SEHU). MALAYSIA: 1♂ (Light), Sarawak, Kuching, Siburan, Kampung Giam, Air Terjun, 1°19’11.2”N, 100°16’11.4”E, 37 m a.s.l., xii.2009, ex *Homalomena giamensis* L.S. Tung, S.Y. Wong & P.C. Boyce (S.Y. Wong) (SEHU).

**Distribution** (*new record*). Indonesia (Java, West Kalimantan, Sumatra*, Sulawesi*, Malaysia* (Sabah)).

**Remarks.** Some local populations vary morphologically. The light form (including the holotype) has light (pale yellow in female and pale brown in male) abdominal tergites, as reflected in the specific name *xanthogaster*, and its foreleg tibia lacks dark patch on apical portion of inner surface (Fig. S1A). The dark form, which is regarded as a different morpho-species, ”sp. aff. *xanthogaster*”, by Sul- tana et al. (2006), has nearly entirely dark grey to black abdominal tergites and a dark patch on apical portion of inner surface of the foreleg tibia (Fig. S1B, C). Specimens of the light form have been collected in West Java, West Sumatra, West Kalimantan and Sarawak, and those of the dark form in West Sumatra and North Sulawesi. In the present study the detailed morphological comparison revealed that some characters other than body colour are different between Sumatran and Sulawesian populations of the dark form. Thus, three morphological forms, Light, Dark I (Sumatra) and Dark II (Sulawesi) are recognised within *C. xanthogaster*, and Light and Dark I forms co-occur in West Sumatra (see Table S3 and Fig. S1 for details). Although intraspecific pigmentation polymorphisms have been repeatedly observed in drosophilid species (e.g., Gibert et al., 1999; Wittkopf et al., 2003), the observed differences in structures and setation of some organs suggest a possibility that the three forms are good sibling species. However, the COI barcoding detected no distinct genetic differentiation among them. Therefore, we refrain from treating the two Dark forms as good species until more crucial evidence is obtained.

**Colocasiomyia nigricauda Sultana & Toda, 2002**

(Figs 3–7C)

**Colocasiomyia nigricauda Sultana & Toda in Sultana et al., 2002: 309.**

**Diagnosis.** Additional pair of dorsocentral setae present before transverse suture, approximately 3/4 as long as anterior dorsocentral setae. Surstylus gently curved downwards, apically triangular (Fig. 2C in Sultana et al., 2002). Aedeagus shaped like thick claw apically (Fig. 3E in Sultana et al., 2002).

**Redescription.** Antennal first flagellomere approximately 1.5 times as long as pedicel, without small pouch on inner surface; longest branch of arista longer than upper, prominent seta on pedicel (Fig. 3C). Facial carina as long as pedicel and first flagellomere combined, somewhat truncate demarcated below (Fig. 4C). Clypeus medially nearly as thick as distal portion of palpus (Fig. 5C). Projections on anterolateral corners of cibarium longer than width of its anterior margin; medial, cibarial sensilla 3–8 per side (Fig. 6C). Prementum with 3 (proximal, lateral and distal) pairs of setae, lacking supralateral pair of setae outside prementum plate (Fig. 7C). Foreleg tarsome II with 3 long, stout, sulcate spines (Fig. 1E in Sultana et al., 2002). Aedeagus without beak-like projection between basal processes (Fig. 3E in Sultana et al., 2002). Epiproct and hypoproct not pubescent. Female sternite VII deeply notched on caudomedial margin.

**Material examined.** MALAYSIA: 1♂, Sabah, Crocker Range, Inobong, 5°51’22.2”N, 116°8’13.4”E, 500 m a.s.l., 7. viii. 2003, ex *Homalomena* sp.P belonging to the Hanneae complex (Fig. S9) (M.J. Toda) (SEHU); 1♂, Sarawak, Lambir, 4°11’54.14”N, 114°2’34.34”E, 68 m a.s.l., 17.xi.2004, ex *H. lambirensis* (Fig. S10) (K.T. Takano) (FRCK). INDONESIA: 1♂, West Sumatra, Sungai Penuh – Tapan, 7.xii.2004, ex *Homalomena* sp.P (K.T. Takano) (MZB); 1♂, West Java, Mt. Halimun, Cikaniki, 6°44’42.5”S, 106°32’14.5”E, 1051 m a.s.l., 7.xi.2009, ex *H. megalophylla* (M.J. Toda) (SEHU).

**Distribution.** Malaysia (Sabah, Sarawak), Indonesia* (Sumatra, Java).

**Remarks.** The specimens collected from Indonesia were identified as being conspecific with those from the type locality, i.e., Poring, Sabah, Malaysia, based on morphology and DNA barcoding (Fig. 2).

**Colocasiomyia erythrocephala Sultana & Yafuso, 2002**

(Figs 3–7D)

**Colocasiomyia erythrocephala Sultana & Yafuso in Sultana et al., 2002: 311.**

**Diagnosis.** Three stout spines on foreleg tarsomere II slightly longer than tarsomeres III and IV combined. Surstylus straight, as long as but slightly broader than ventral elongation of cercus, rounded at apex (Fig. 2D in Sultana et al., 2002). Aedeagus broad, apically thick and rounded, with beak-like projection between a pair of strongly sclerotized, basal processes (Fig. 4A in Sultana et al., 2002).
Redescription. Supracervical setae 3–5 per side. Antennal first flagellomere approximately twice as long as pedicel, with small pouch on inner surface; longest branch of arista as long as upper, prominent seta on pedicel (Fig. 3D). Facial carina roundly demarcated below, shorter than pedicel and first flagellomere combined (Fig. 4D). Clypeus medi- ally thicker than distal portion of palpus (Fig. 5D). Projections on anterolateral corners of cibarium longer than width of its anterior margin; posterior, cibarial sensilla 3–5 per side (Fig. 6D). Prementum with 3 (proximal, lateral and distal) pairs of setae, lacking supralateral pair of setae outside prementum plate (Fig. 7D). Foreleg tarsomere II with 3 long, stout, sulcate spines. Epiproct and hypoproct not pubescent. Female sternite VII deeply notched on caudomedial margin.

Type material examined. VIETNAM: 3 ♂, 1 ♀ (paratypes), Cuc Phuong, 19.vi.2000, ex Homalomena vietnensis Bogner & V.D. Nguyen (Fig. S11) (M. Yafuso) (SEHU). Distribution. Vietnam.

Remarks. This species seems to be intermediate in morphology between C. heterodonta and the clade of C. xanthogaster and C. nigricauda, sharing two apomorphies (ch. 2–1, antennal first flagellomere with small pouch on inner surface; and ch. 17-2, surstylus broader than ventral inner surface; and ch. 17-2, surstylus broader than ventral xanthogaster Colocasiomyia: Sultana et al., 2006: 694; Colocasiomyia heterodonta (Figs 3–7E, 8C, S2; Table S4) Colocasiomyia heterodonta Yafuso & Okada, 1990: 140; Sultana et al., 2006: 694. Additional pair of dorso-central setae absent. Acrostichal setulae in 2 rows. Basal and apical scutellar setae convergent; apicals not cruciate. Wing nearly hyaline, apically more or less clouded. Costa with apically blunt, heavy, peg-like setae interspersed with weak, trichoid setae in middle row. Epandrium pubescent except for anterior margin and ventral portion (Fig. 2E in Sultana et al., 2002). Surstylus broader than ventral elongation of cercus (Fig. 2E in Sultana et al., 2002). Paramere basally articulated with aedeagal guide (Fig. S2F, L, Q; Fig. 4C in Sultana et al., 2002). Aedeagus apically broad and round, with strongly sclerotized, apically pointed (in lateral view), beak-like projection between basal processes; membranous distiphallus very short (Fig. S2F, L, Q). Female sternite VII not deeply notched on caudomedial margin. Epiproct slightly pubescent; hypoproct not pubescent. Oviscapt without long, upright seta on dorsosubapical corner (Fig. 5E in Sultana et al., 2002).

Material examined. Form I – INDONESIA: 2 ♂, West Java, Bogor, Bogor Botanical Garden, 21.vii.2005, ex H. pendula (M.J. Toda) (SEHU); 4 ♂, 5 ♀, West Java, Bogor, Bogor Botanical Garden, 22.i.2004, ex Homalomena sp. (M.J. Toda) (MBZ); 2 ♂, 6 ♂, West Java, Bogor, Bogor Botanical Garden, 22.xii.2003, ex Aglaonema simplex (Blume) Blume (M.J. Toda) (SEHU); 10 ♂, 18 ♂, West Java, Mt. Gede-Pangarango National Park, Salabintana, 6°49′54.3″S, 106°58′17.2″E, 1100 m a.s.l., 1.i.2004, ex Homalomena sp. (M.J. Toda) (MBZ); 26 ♂, 21 ♂, West Java, Mt. Halimun, Cikanki, 18.i.2004, ex H. megalophylla (M.J. Toda) (SEHU); 1 ♂, West Java, Kelapa Nunggal, 6°50′1.2″S, 106°38′59.5″E, 567 m a.s.l., 31.x.2009, ex H. megalophylla (M.J. Toda) (SEHU); 2 ♂, 1 ♂, West Sumatra, Sungai Penuh – Tapan, 7.xii.2004, ex Homalomena sp. PT (K.T. Takano) (MBZ); 7 ♂, 8 ♂, West Sumatra, Padang Panjang, Batanggang, 5.i.2004, ex Homalomena sp. (M.J. Toda) (SEHU). Form II – MALAYSIA: 2 ♂, 1 ♂ (02755–2757), Sarawak, Betong, Roban, Sebankoi, Taman Rekreasi Sebankoi, 01°57′27.4″N, 106°38′59.5″E, 154 m a.s.l., 5.xii.2005, ex Homalomena ibanorum S.Y. Wong & P.C. Boyce (P.C. Boyce, Jeland ak Kisai, Jepom ak Tisai, Mael ak Late and Wong Sin Yeng) (UNIMAS); 1⎷ (02752), Sarawak, Kuching, Siburan, Kampung Giam, Sungun Jawan, 1°19′16.1″N, 110°16′16.7″E, 50 m a.s.l., 31.x.2012, ex Homalomena cf. borneensis (P.C. Boyce and Wong Sin Yeng) (UNIMAS); 14 ♂, 6 ♂ (02758–2777), Sarawak, Kuching, Siburan, Kampung Giam, Air Terjun Giam, 1°19′11.2″N, 110°16′11.4″E, 37 m a.s.l., 12.i.2011, ex H. giamensis (P.C. Boyce, Jeland ak Kisai and Wong Sin Yeng) (7 ♂, 3 ♂, KIZ; 7 ♂, 3 ♂, SEHU); 1 ♂, 1 ♂, Sabah, Crocker Range, Inobong, 7.vii.2003, ex Homalomena sp. (M.J. Toda) (BORN); 1 ♂ (identified as C. heterodonta by Sultana et al. [2002]), Sabah, Crocker Range, Ulu Senangang, 500 m a.s.l., 18.x.1999, ex Homalomena sp. (P.M. Toda) (SEHU); 3 ♂, 1 ♂, Sabah, Mabau, Poring, 6°2′55.5″N 116°42′8.2″E, 500 m a.s.l., 11.i.2000, ex Homalomena sp. (M.J. Toda) (1 ♂, 1 ♂, KPPS; 2 ♂, SEHU). Form III – INDONESIA: 1 ♂, 2 ♂ (02751–2753), Sumatra, Jambi, Mt. Kerinci, 1°45′5.9″S, 101°15′34.6″E, 1800–2000 m a.s.l., 7.x.2004, ex Homalomena sp.K (Fig. S12) (M.J. Toda) (1 ♂, 1 ♂, MZB; 1 ♂, SEHU).

Distribution. Malaysia (Sabah, Sarawak*), Indonesia (Java, Sumatra).

Remarks. Morphological differences among the Forms I–III of this species are summarized in Table S4 and Fig. S2. Form III is specifically different from the other two forms in the structure of the male phallic organs, with a longer aedeagus, longer and more strongly curved basome-
dial, beak-like projection on aedeagus, and an apicollaterally extended paramere (Fig. S2P, Q). On the other hand, Forms I and II are almost identical in the detailed structure of male genitalia (Fig. S2E, F, K, L), although there are subtle differences in a few of their external characters (Table S4).

**Colocasiomyia rostrata** Shi & Gao, sp. n.  
(Figs 3–7F, 8B, 10, S3)

ZooBank taxon LSID: E25FA47-4241-4642-A00A-801A8FE5FF24

Colocasiomyia sp. 2 aff. heterodonta: Sultana et al., 2006: 694.

**Diagnosis.** Antennal aristal branches minute; first flagellomere only slightly longer than pedicel, without small pouch on inner surface (Fig. 3F). Projections on anterolateral corners of cibarium shorter than half the width of cibarial, anterior margin (Fig. 6F). Lateral bumps on prementum covered with short, thin setae (Figs 5F, 7F). Postpronotal lobe with approximately 10 setae; longest one not prominent, as thin as others. Long spine on foreleg tarsomere II thin, simple, not sulcate (Fig. 8B). Aedeagal basal beak-like projection longer than aedeagus proper, apically rounded (Fig. 10B). Oviscapt apically bilobed: dorsal lobe with 1 long, upright seta on dorsosubapical corner, 1 peg-like, upward-curved ovisensillum at apex, 1 short seta dorsosubapically near base of apical, peg-like ovisensillum and 1 or 2 setae on ventrosubapical margin; ventral lobe with 7–8 short setulae along caudoventral margin (Figs 10D, S3E, D).

**Description. Male.** Head: Eye brownish red. Supracervical setae 2–4, and postoculars 18–19 per side. Frontal vittae mat, greyish yellow. Distance between antennal sockets narrower than half of socket width (Fig. 4F); pedicel greyish yellow, dorsally with a few stout setae approximately half as long as prominent setae; aristata with 3–4 dorsal and 2–3 ventral branches (Fig. 3F). Facial carina less demarcated below, slightly shorter than pedicel and first flagellomere combined, narrower than first flagellomere (Fig. 4F). Gena greyish brown. Palpus greyish yellow, much dilated distally (Fig. 5F). Clypeus medially thinner than distal portion of palpus (Fig. 5F). Cibarial, medial and posterior sensilla 4 and 2–4, respectively, per side; posterior sensilla much shorter than medial ones; 4 anterior sensilla arranged in somewhat irregular, transverse row (Fig. 6F). Prementum with 3 (lateral, supralateral and distal) pairs of setae nearly arranged in a transverse row (Fig. 7F). Labelum with 11–12 pseudotracheae per side.


Wing: hyaline, apically not clouded. Veins pale brown; R₄₊₅ and M₁ slightly converging apically. Costal setae in middle row all weak, trichoid. Halter dark brown.

Legs: Foreleg tarsomere II with 1 long and 9–14 short, stout spines (Fig. 8B).

Abdomen: Tergites blackish brown. Sternites greyish brown.

Terminalia (Figs 10A–C, S3A–C): Epandrium with 8–9 setae on dorsal to lateral portion and approximately 5 near base of surstylist. Surstylus blade-shaped, apically somewhat triangular, with 3 minute setae on apical portion. Cercus with approximately 37 setae; ventral elongation with approximately 2 minute tooth-like setulae on dorsosubapical margin. Paramere basally fused to hypandrium, slightly shorter than aedeagus, distally curved inwards, apically rounded, with 4 minute sensilla. Aedeagus approximately half as long as apodeme, apically broad and round, with short but broad, aedeagal guide; membranous distiphallus very short.

Measurements (holotype/range in 5♀ paratypes, in mm): BL = 2.00/1.90–2.00, ThL = 0.87/0.80–0.87, WL = 1.77/1.60–1.87, WW = 0.77/0.77–0.93.

Indices (holotype/range in 5♀ paratypes, in ratio): FW/ HW (frontal width/head width) = 0.53/0.56–0.63, ch/o (maximum width of gena/maximum diameter of eye) = 0.39/0.28–0.44, prob (proclinate orbital seta length/posterior reclinate orbital seta length) = 0.83/(n/a), rcorb (anterior reclinate orbital seta length/posterior reclinate orbital seta length) = 0.25/0.42–0.56, vb (subvibrissal seta length/vibrissa length) = 0.21/0.23–0.25, dcl (anterior dorsocentral seta length/posterior dorsocentral seta length) = (n/a)/0.56–0.74, presctl (prescutellar seta length/posterior dorsocentral seta length) = 0.62/0.63–0.78, sclt (basal scutellar seta length/apical scutellar seta length) = 0.49/0.50–0.65, snr (anterior katepisternal seta length/posterior katepisternal seta length) = 0.67/0.47–0.60, orbito (distance between procline and posterior reclinate orbital seta/distance between inner vertical and posterior reclinate orbital seta) = 1.00/0.82–1.00, dcps (distance between ipsilateral dorsocentral seta/distance between anterior dorsocentral seta) = 1.05/0.75–1.06, scpt (distance between subcostal break and R₂+₃/3rd costal section between R₂+₃ and R₄+₅) = 1.59/1.56–1.91, 4c (3rd costal section between R₂+₃ and R₄+₅/M₁ between r-m and dm-cu) = 1.46/1.33–2.00, 4v (M₁ between dm-cu and wing margin/M₁ between r-m and dm-cu) = 2.18/2.13–3.13, 5x (Cu₄A, between dm-cu and wing margin/dm-cu between M₁ and Cu₄A) = 1.20/1.00–1.46, ac (3rd costal section between R₂+₃ and R₄+₅/distance between distal ends of R₄+₅ and M₁) = 3.20/2.55–3.09, M (Cu₄A, between dm-cu and wing margin/M₁ between r-m and dm-cu) = 0.21/0.22–0.24.

**Female.** Head, thorax, legs and wings as in male.

Terminalia (Figs 10D, E, S3D, E): Sternite VII slightly concave on caudal margin. Epiproct nearly entirely pubescent; hypoproct laterally with a pair of small patches of pubescence. Oviscapt with 1–2 peg-like ovisensillum(a) on submedial surface.

Measurements (range in 5♀ paratypes, in mm): BL = 1.75–2.05, ThL = 0.80–0.87, WL = 1.43–1.73, WW = 0.70–0.80.

Indices (range in 5♀, or less if noted, paratypes, in ratio): FW/HW = 0.51–0.66, ch/o = 0.25–0.42, prob = 0.76–0.86 (2♀), rcorb = 0.16–0.24 (3♀), vb = 0.20–0.26, dcl
members of this species group.

In addition, it is unique in having many species-specific, diagnostic characters among the members of this species group.

Key to species of the *Colocasiomyia toshiokai* species group

1 Foreleg tarsomere II apically with 3 long, stout spines (Fig. 8A) .............................................. 2
   - Foreleg tarsomere II apically with 1 long and many small, tooth-like spines (Figs 8B, C, S2C, D, I, J, O) ............. 5

2 Additional pair of dorsocentral setae present .......................................................... 3
   - Additional pair of dorsocentral setae absent .................................................. 4

3 Surstylus apically round (Fig. 2B in Sultana et al., 2002); paramere half as long as aedeagus; aedeagus apically narrow in lateral view (Fig. S1M–O). ............................................ C. xanthogaster Yafuso & Okada
   - Surstylus apically triangular (Fig. 2C in Sultana et al., 2002); paramere 2/3 as long as aedeagus; aedeagus apically thick (Fig. 3E in Sultana et al., 2002) ........................................... C. nigricauda Sultana & Toda

4 Acrostichal setae in 4 rows; foreleg tarsomere II slightly shorter than tarsomeres III and IV combined; antennal first flagellomere without small pouch on inner surface (Fig. 3A); surstylus and ventral elongation of epandrium narrower than ventral elongation of epandrium (Fig. 2A in Sultana et al., 2002); aedeagus basally without beak-like projection (Fig. 3A in Sultana et al., 2002); oviscapit with small patch of pubescence (Fig. 5A in Sultana et al., 2002) ............ C. toshiokai (Okada)
   - Acrostichal setae in 2 rows; foreleg tarsomere II slightly longer than tarsomeres III and IV combined; antennal first flagellomere with small pouch on inner surface (Fig. 3D); surstylus and ventral elongation of epandrium broader than ventral elongation of epandrium (Fig. 2D in Sultana et al., 2002); aedeagus basally with beak-like projection (Fig. 4A in Sultana et al., 2002); oviscapit without pubescence (Fig. 5D in Sultana et al., 2002) ............ C. erythrocephala Sultana & Toda

5 Antennal aristal branches minute (Fig. 3F); thoracic pleura entirely dark brown; costal setae in middle row all weak, trichoid; long spine on foreleg tarsomere II thin, not sulcate (Fig. 8B); postpronotal lobe with approximately 10 setae nearly equal in thickness; oviscapit apically bilobed (Figs 10D, S3E) .......... C. rostrata Shi & Gao, sp. n.
   - Longest branch of aristae as long as prominent setae on pedicle (Fig. 3E); thoracic pleura largely (at least anepisternum and anepimeron) pale yellow; costa with apically blunt, heavy, peg-like setae interspersed between weak, trichoid ones in middle row; long spine on foreleg tarsomere II thick, sulcate (Figs 8C, S2O); postpronotal lobe with 2 prominent setae and 2–3 short setulae; oviscapit apically not bilobed (Fig. 5E in Sultana et al., 2002) ............ C. heterodonta Yafuso & Okada

Reproductive ecology

Fig. 11 shows almost all the data on the composition of *Colocasiomyia* flies collected from individual inflorescences of *Homalomena* and *Aglaonema* in Vietnam, Malaysia and Indonesia. In lowlands of West Java, host inflorescences were usually occupied by two species of the *toshiokai* group, *C. xanthogaster* (Light form) and *C. heterodonta* (Form I), with *baechlii*-group species occasional cohabitants. In the Bogor Botanical Garden, *C. xanthogaster* tended to be more abundant than *C. heterodonta* on individual inflorescences of *Homalomena*, while the opposite was recorded on *Aglaonema* inflorescences. In the highlands of West Java, however, *Homalomena* inflorescences were almost monopolized by *C. heterodonta*. In Sarawak and Sabah, inflorescences of various *Homalomena* species were shared by another pair of species, *C. nigricauda* and *C. heterodonta* (Form II), of which the former was more abundant on all the host species studied except *H. matangae*. However, inflorescences of *H. lambirensis* in Lambir, which was misidentified as *H. propinquua* Schott by Kuman & Yamaoka (2006) and Kuman-Nomura & Yamaoka (2009) (Wong & Boyce, 2017), were monopolized by...
C. nigricauda. In North Sulawesi and Vietnam, Homalomena inflorescences were monopolized by C. xanthogaster (Dark II form) and C. erythrocephala, respectively. In Sumatra there is the highest species richness of the toshio-kai group, with three species including two Forms of C. heterodonta and two colour forms of C. xanthogaster. These species/forms used different Homalomena species as hosts in different combinations: a Homalomena inflorescence in Padang Panjang, West Sumatra was shared by C. heterodonta Form I, C. xanthogaster Light form and C. xanthogaster Dark I form, an inflorescence of H. sp.PT in Sungai Penuh-Tapan, West Sumatra by C. heterodonta Form I, C. xanthogaster Light form and C. nigricauda, an inflorescence of H. sp.L.c.f. megalophylla in Lembah Anai, West Sumatra by C. rostrata and C. xanthogaster Dark I form and an inflorescence of H. sp.K on Mt. Kerinci, Jambi monopolized by C. heterodonta Form III.

Fig. 11 shows the distribution of Colocasiomyia eggs and larvae over the spadix of host inflorescences/infructescences collected in West Java. The eggs were counted on each 1 cm section of the pistillate and staminate regions from the border of the two regions. However, the larvae were counted separately only for each of the pistillate and staminate regions, because they were very actively moving. In lowland West Java where C. xanthogaster (Light form) and C. heterodonta (Form I) cohabited in the same host inflorescences (Fig. 11), both species laid their eggs in the narrow spaces between pistils and/or staminodes mainly on the middle to upper portion of the pistillate region of Homalomena inflorescences, but C. heterodonta sporadically oviposited also on the basal border zone composed of relatively large, interstice staminodes in the staminate region. In the highlands where inflorescences of H. megalophylla collected on Mt. Halimun were almost monopolized by C. heterodonta (Fig. 11), the eggs of this species were found mainly on the pistillate middle portion to the staminate basal portion, but also sporadically on the staminate upper portions of the inflorescence. On an inflorescence of Aglaonema pictum (Roxb.) Kunth. in the Bogor Botanical Garden, which was visited by both C. xanthogaster and C. heterodonta, the eggs of only C. heterodonta were found and more abundant on the staminate lower portion than on the pistillate region. On Homalomena infructescences at Stage IV (Fig. 1B), Colocasiomyia larvae were found. Within an infructescence of H. pendula collected from the Bogor Botanical Garden, larvae (2nd and 3rd instars) of C. xanthogaster were observed feeding mostly on exudates in the pistillate region, while those of C. heterodonta fed on
decaying tissues in the staminate region. Only *C. heterodonta* larvae were found in Stage-IV infructescences of *H. megalophylla* collected on Mt. Halimun: 2nd instars were restricted to the pistillate region and 3rd instars were recorded in both pistillate and staminate regions. However, neither larvae nor puparia (or empty puparial capsules) were found in any of the infructescences at Stage V. This implies that full-grown larvae of the *toshiokai* group leave their host infructescence via the decayed and exposed apex portion of the staminate region and pupate elsewhere. Some larvae showed skipping behaviour in the laboratory. Actually, larvae of *C. alocasiae* (Okada, 1975) of the *cristata* group were observed “popping out” of host infructescence and pupating elsewhere by Yafuso (1993).

Inflorescences/infructescences of *H. lambirensis* in Lambir, Sarawak were monopolized by *C. nigricauda*, the closest relative of *C. xanthogaster*. To determine the distribution of *C. nigricauda* immature stages (eggs, 1st and 2nd instars) on the spadix, spadices of inflorescences (Stage II) and young infructescences (Stage III and early IV) were separated into seven parts: upper 1/3, middle 1/3 and lower 1/3 of staminate region, intermediate sterile region, and upper 1/3, middle 1/3 and lower 1/3 of pistillate region. However, spadices of infructescences at late Stage IV, with 3rd instar larvae, were separated into three parts: staminate, intermediate and pistillate regions. There is a distinct intermediate region composed only of staminodes between the staminate and the pistillate regions on the spadix of *H. lambirensis* (Fig. 1b in Kumano & Yamaoka, 2006). Eggs were laid mostly on the pistillate and intermediate regions, but also sporadically on the staminate region; 1st instar larvae were recorded mainly on the pistillate region, being most abundant on its lower 1/3, but also sporadically on the intermediate and the staminate regions; 2nd instar larvae were recorded on the basal pistillate and intermediate region, rarely on the basal staminate region; 3rd instar larvae were recorded on the pistillate and staminate regions (Fig. 13).

Thus, when the two species, *C. xanthogaster* and *C. heterodonta*, cohabit inflorescences/infructescences of the same host plant, a slight difference was recorded in their utilization of the spadix for breeding. Although both species mainly used the pistillate region for oviposition and as a source of food for young larvae, *C. heterodonta* had a slightly wider niche in also sporadically using the basal staminate region. This difference, which is reported on the basis of incomplete data by Yafuso & Okada (1990), is confirmed by the data collected in the present study. Furthermore, the present study suggests spatio-temporal separation of the feeding sites of the older larvae between these
two species. Larvae of *C. heterodonta* may first move from the pistillate region to the staminate region and feed there on the decaying stamens. Larvae of *C. xanthogaster* may follow them, or complete their growth within the pistillate region. Although much more data are needed to reveal the interspecific differences in larval food habits, it can be said that *C. xanthogaster* is more pistilicolous and *C. heterodonta* more stamenicolous. Good examples of breeding niche separation in two cohabiting species are reported for some species pairs of the *crisata* group: one species uses exclusively the pistillate region for oviposition and larval development and pupates within the infructescence chamber, whereas the other uses mostly the stamate region and pupates elsewhere (Carson & Okada, 1980; Honda-Yafuso, 1983; Toda & Okada, 1983; Okada & Yafuso, 1989; Yafuso, 1994). In comparison to these species, the niche separation between *C. xanthogaster* and *C. heterodonta* is slight and both species do not pupate in the host infructescence. Another case of slight niche separation is reported for two undescribed species, *C.* sp. 1 aff. *sulawesiana* and *C.* sp. 2 aff. *sulawesiana*, of the *crisata* group: both are principally pistilicolous and pupate within the host infructescence, but the two species show the different distributions of the adult flies within the host infructescences and consequently oviposit on different parts of the spadix (Takano et al., 2012). In this case, one species (sp. 1) is also more pistilicolous than the other (sp. 2). When two *Colocasiomyia* species cohabit infructescences/infructescences of the same Araceae host plant, breeding niche separation along the axis of the spadix seems to be a general pattern, probably resulting from convergence (e.g., parallel evolution) in different lineages. In relation to this niche separation, cohabitating species show different reproductive strategies in terms of a trade-off in “egg size vs. number”: the stamenicolous species lay “more smaller eggs” than the pistilicolous species (Fartyal et al., 2013). The difference in this trade-off between *C. xanthogaster* and *C. heterodonta* is consistent with the general pattern, though smaller than in other pairs the niche separation of which is more marked (Fartyal et al., 2013).

**Flower-visiting behaviour**

Fig. 14 shows changes in the temperature of the pistillate and staminate regions of the two infructescences of *H. megalophylla* and *H. pendula* recorded over the course of flowering, which lasted for two days, along with records of the important flowering events and behaviour of *Colocasiomyia* flies. The extent of heat generation by the infructescence is expressed in terms of the differences between the pistillate (*T_p*) or staminate (*T_s*) temperatures and the ambient air temperature (*T*). The general pattern in the flowering process and fly behaviour was almost identical on the two host plants. The heat generation was detected only in the staminate region of both species of plants. *T_s* began to be higher than *T* from dusk or early in the night of the day before anthesis, and the difference became about 1°C in the middle of the night. Synchronized with this increase in temperature was a loosening of the spathe. The dramatic process of anthesis started in the dark around 4:00 (in 24-hour notation; in November, for *H. megalophylla* or 4:30 (in August, for *H. pendula*) in synchronization with the distinct increase in temperature recorded in the staminate region. The spathe became fully open within 30–60 min, but no *Colocasiomyia* flies visited the infructescence in the dark. Around dawn at 4:50 or 5:20, *T_s* was 5 and 9°C higher than *T* in *H. megalophylla* and *H. pendula*, respectively, and the infructescence started to emit an odour. Soon after that, around sunrise (5:25 in November and 6:05 in August), *Colocasiomyia* flies successively visited the infructescence of *H. megalophylla* from 5:20 to 5:45 and that of *H. pendula* from 5:40 to 6:30 when *T_s* peaked at about 38°C, which was 14°C higher than *T*, and there was a strong emission of odour. *T_p* was only 2 or 3°C higher than *T* during this period, which could have been caused by the conduction of heat from the staminate region. The flies alighted on the spathe or the staminate region but immediately moved to the pistillate region. Thereafter, *T_p* gradually decreased, but remained about 5°C higher than *T* at 7:30 in *H. megalophylla* or at 8:00 in *H. pendula*; the flies stayed in the pistillate region, mostly on the rear of its upper portion, sometimes ovipositing on the upper half of

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**Fig. 13.** Distribution of *Colocasiomyia nigricauda* eggs and larvae over the spadix of infructescences of *Homalomena lambirensis* collected in Lambir, Sarawak.
pistillate region and/or attempting to mate. The difference between \( T_s \) and \( T \) decreased to about 2°C from 9:00 in *H. megalophylla* or 1°C from 9:30 in *H. pendula*, and then remained relatively constant during the daytime; the flies seemed to be resting together on the rear of the inner wall of the spathe surrounding the pistillate region. In the evening, the flies resumed activity, feeding exclusively around the border zone between the pistillate and staminate regions, ovipositing on the pistillate region and in the border zone and mating; these activities continued throughout the night. The second increase in the \( T_s - T \) temperature was recorded from 3:30 in both inflorescences, though it was less pronounced in *H. megalophylla*. This coincided with the spathe beginning to close and pollen release. *Colocasiomyia* flies successively left the inflorescence of *H. megalophylla* between 4:10 and 5:05 and that of *H. pendula* between 5:15 and 5:40. Although a few flies left the inflorescence of *H. megalophylla* during the middle of the night, this may have been due to disturbance or the effect of the headlamp used for nighttime observation: in the case of the *H. pendula* inflorescence, which was not observed at night, the same number of *Colocasiomyia* flies that visited the inflorescence in the previous morning left together the following day. There was no longer a difference between \( T_s \) and \( T \) recorded around 8:00 to 10:00, and by this time the spathe was completely closed, leaving the front-side, middle to upper portion of the staminate region uncovered; this exposed portion of the staminate region gradually decreased in area and finally only the apical portion remained exposed.

The two species of *Homalomena* studied are protogynous like other Araceae plants (Mayo et al., 1997): the female phase (stigma receptivity) of the inflorescence precedes the male phase (anther dehiscence). The first thermogenesis occurred in the female phase and was intimately associated with emission of a strong odour and the attraction of *Colocasiomyia* flies. Some studies have shown histologically that the generation of heat is associated with the volatilization of floral scent molecules (Skubatz et al., 1995; Skubatz & Kunkel, 1999) and that *Colocasiomyia* flies are attracted to specific volatiles (Miyake & Yafuso, 2003, 2005). In the present study, *Colocasiomyia* flies were observed immediately moving to the pistillate region and remaining there after alighting on the spathe or the staminate region. This behaviour would enable them to avoid exposure to the high temperature (about 38°C at the peak) conditions in the staminate region at this phase, as suggested by Ivancic et al. (2004): the pistillate temperature was about 12°C lower than the staminate temperature even at the peak of heat generation (Fig. 14). The second thermogenesis corresponded to the male phase and was synchronized with the spathe closing followed by pollen release and the flies leaving. Closing of the spathe stimulates the flies to crawl up from the pistillate region to the staminate region to avoid being imprisoned within the closed inflorescence chamber (cf. Bröderbauer et al., 2012). Then, the flies are dusted with pollen grains released in the staminate region and ultimately leave the inflorescence and then search for and are attracted by surrounding female-phase inflorescences. In the pollen-releasing phase, stingless bees were often observed visiting the inflorescence to collect pollen, even after the spathe was completely closed, but never entered the pistillate region. Thus, *C. heterodonta* and *C. xanthogaster* seem to be the most effective, specific pollinators of *H. megalophylla* and *H. pendula*, in their response to the characteristic flowering-events related to thermogenesis in the female and male phases. However, their efficiency as pollinators should be evaluated by field bagging experiments.

Plant-pollinator interactions in Homalomeinae: a short review

*Homalomena* is a large genus with more than 350 described and formally undescribed species (Boyce et al., 2010). Contrary to our observations of possible fly-pollination in *H. megalophylla* and *H. pendula*, both of which belong to the Homalomena section (sensu Wong et al., 2016), in Java, beetle-pollination is strongly suggested for *H. lambirensis* (Kumano & Yamaoka, 2006), *H. giamensis* (Tung et al., 2010) and six other *Homalomena* species (Hoe et al., 2016) in Sarawak, Malaysian Borneo. Although these *Homalomena* species attract not only beetles but also *Colocasiomyia* flies, Kumano & Yamaoka (2006) report pollen only attached to the bodies of two beetle species, *Parastasia bimaculata* Guerin (Scarabaeidae) and *Dercetina* sp. (Chrysomelidae), and Tung et al. (2010) and Hoe et al. (2016) report that only *Parastasia* species behave as possible effective pollinators of their host plants. It seems that species in the Homalomena and the Chamaeleadon sections (sensu Wong et al., 2016) tend to be pollinated by *Colocasiomyia* flies, whereas species in the Cyrtocladon section (sensu Wong et al., 2016) tend to be pollinated by Scarabaeidae, Chrysomelidae and Hydrophilidae beetles (Wong et al., 2013; Hoe et al., 2016).

Chartiér et al. (2014) categorize the genus *Homalomena* as plants “pollinated by fly and beetle”, and its closely related genera *Philodendron* as those “pollinated by beetle” and *Furtdaoa* as those “pollinated by fly”. Mapping these pollination interaction types on a phylogenetic tree, they inferred that beetle pollination would have been the ancestral state for these related taxa.

The diurnal timing of anthesis varies among these aroid plants. Inflorescences of “beetle-pollinating” *Philodendron* species open in the evening and attract beetles at dusk (e.g., Gottsberger et al., 2013), whereas “beetle-pollinating” *Homalomena* species begin flowering in the morning (Kumano & Yamaoka, 2006; Tung et al., 2010; Hoe et al., 2016) as well as other “fly-pollinating” *Homalomena* species, *H. megalophylla* and *H. pendula* (the present study), and *Furtdaoa sumatrensis* M. Hotta (Mori & Okada, 2001), which attract *Colocasiomyia* flies in the early morning when drosophilid flies are active. As for the tribe Schismatoglottideae, Low et al. (2016) report that *Aridarum nicosionii* Bogner, *Phymatarum borneense* M. Hotta and *Schottarum sarkeense* (Bogner & M. Hotta) P.C. Boyce & S.Y. Wong are pollinated by *Colocasiomyia* flies and that the first and the second species bloom at dawn.
Fig. 14. Flowering-events, especially temperature changes recorded in the pistillate and staminate regions of spadix, and behaviour of Colocasiomyia flies observed during the flowering of inflorescences of Homalomena megalophylla (upper) and H. pendula (below) in the Bogor Botanical Garden, West Java.
whereas the third species flowers at dusk. They state: “It seems that Schismatoglottiditaeae and Homalomenaeae tend to flower at dawn in the Old World tropics but related taxa in the Neotropics flower at dusk. This requires further investigation.”

Not only the timing of anthesis but also other floral traits vary among aroid plants in relation to pollinator types. Gibernau et al. (2010) investigated 68 species of Araceae and found correspondence between pollinator types (i.e., bee-, fly- or beetle-pollination) and floral traits, such as pollen volume and number, the number of female flowers and flower sexual types (unisexual or bisexual). Differences in such floral syndromes are reported between “beetle-pollinating” and “fly-pollinating” species even within the genus *Homalomena*.

Grayum (1986) report that the texture of Araceae pollen would have differentiated in adaptation to different types of pollinators: echinate (i.e., spiny) pollen is more effective for attaching to the hairs or bristles of flies and bees, whereas sticky secretions from the stigma or inner surface of spathe help psilate (i.e., smooth and lacking ornamentation) pollen to attach to smooth, hard bodies of beetles. Sannier et al. (2009) infer that psilate and foveolate/reticulate pollen ornamentations are ancestral character states in Araceae, and that evolutionary shifts to fly pollination are probably followed by transitions towards echinate pollen. Pollen of all the species of the genus *Schismatoglottis* Zoll. & Moritzi investigated is psilate, and Hoe & Wong (2016) infer mixed pollination of *Schismatoglottis baangongensis* S.Y. Wong, Y.C. Hoe & P.C. Boyce (tribe Schismatoglottitaeae, Araceae) by *Cycreon* beetles (Hydropididae) and *Colocasioymia* aff. *bogneri*. Such mixed pollination may represent a transitional state in an evolutionary shift in pollinator type. In our observations, *H. megalophylla* (Fig. 1), *H. pendula* (Fig. S4), *Homalomena* sp. L cf. *megalophylla* (Fig. S6), *H. sp. aff. alba* (Fig. S7), *Homalomena* sp. T (Fig. S8) and *Homalomena* sp. K (Fig. S12) produced powdery pollen, although we did not investigate ultra-structure of the ornamentation on the pollen. On the other hand, *H. lambirensis* (Kumano & Yamaoka, 2006) and another seven *Homalomena* species (Hoe et al., 2016) in Sarawak secrete resin in the staminode region before the male phase (Fig. S10A), which makes the pollen sticky (Fig. S10C).

The constriction in the spathe between the staminate and pistillate regions of the spadix is seen in many genera of Araceae (Bröderbauer et al., 2012; Wong et al., 2013). Spathe constriction facilitates effective pollination by specific insects (e.g., Takenaka, 2006; Bröderbauer et al., 2014) but restricts access by non-pollinators to the pistillate region (e.g., Takano et al., 2012) by functioning as a sieve (Low et al., 2016). The spathe is swollen below the constriction (Figs S5B, S9, S10). Such more or less closed spathe chamber serves as a safe mating arena for pollinators (Kumano-Nomura & Yamaoka, 2009). In general, the space between the spathe and the spadix is the site where visiting insects feed, breed, mate and rest. Therefore, the size and shape of spathe chamber should be strongly related to pollinator type. Wong et al. (2013) infer that the constricted spathe is plesiomorphic for *Homalomena* and has been lost once in the clade comprising the Homalomena and the Chamaeladon sections. Our observations indicate that the spathe is not constricted in all the *Homalomena* species that produce powdery pollen (Figs 1, S2, S4–6, S10). Thus, the loss of the spathe constriction and reduction in spathe chamber space would have been caused by the pollinator shift from large-bodied beetles to small-bodied flies.

The resurrection of the genus *Adelonema* Schott (Wong et al., 2016), which is the former New World *Homalomena* and closely related to *Philodendron*, implies a necessity to reassess the phylogenetic context of plant-pollinator interactions in these related genera. Further studies on evolutionary changes in floral traits, such as diurnal time of flowering, pollen characters and spathe size and shape, along with the change in role of *Colocasioymia* flies from commensalist to mutualist would shed more light on the entangled evolution of intimate pollination mutualisms between the flower-breeding fly genus and Araceae plants.

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* Sequence determined by Li et al. (2014).
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| Table S3. Morphological comparison of the three forms of *Colocasiomyia xanthogaster*. |
|---------------------------------|-----------------|-----------------|-----------------|
| **Form**                        | **Light***      | **Dark I**      | **Dark II**     |
| **Distribution**                | West Java, West Sumatra, West Kalimantan, Sarawak | West Sumatra | North Sulawesi |
| **Abdominal tergites**          | Pale yellow (female) or pale brown (male; Fig. S1A) | Nearly entirely dark gray to black (Fig. S1B) | Nearly entirely dark gray to black (Fig. S1C) |
| **Dark patch on apical portion of inner surface of foreleg tibia** | Absent (Fig. S1A) | Present (Fig. S1B) | Present (Fig. S1C) |
| **Space between antennal sockets** | Broader than half of socket width (Fig. S1D) | Narrower than half of socket width (Fig. S1E) | Narrower than half of socket width (Fig. S1F) |
| **Facial carina**               | As long as antennal pedicel + first flagellomere, slightly narrower than first flagellomere, more or less truncately demarcated below (Fig. S1D) | As long as antennal pedicel + first flagellomere, as wide as first flagellomere, roundly demarcated below (Fig. S1E) | Shorter than antennal pedicel + first flagellomere, as wide as first flagellomere, truncately demarcated below (Fig. S1F) |
| **Number of supracervical setae per side** | 2–4 (Fig. S1G) | 3–5 (Fig. S1H) | 4–7 (Fig. S1I) |
| **Number of pseudotracheae per side in labelum** | 16–18 (West Java), 12–15 (West Sumatra) | 16–17 | 12–13 |
| **Number of rows of acrostichal setulae around anterior and extra dorsocentral setae** | 2 | 4 | 2 |
| **Density of heavy, peg-like setae on distal portion of costa** | Dense (Fig. S1J) | Sparse (Fig. S1K) | Dense (Fig. S1L) |
| **Paramere**                    | Broader than aedeagal basal process (Fig. S1M) | As narrow as aedeagal basal process (Fig. S1N) | As narrow as aedeagal basal process (Fig. S1O) |
| **Ventral subapical margin of aedeagus** | Slightly notched and/or finely serrated (Fig. S1M) | Smooth (Fig. S1N) | Coarsely serrated (Fig. S1O) |

* Including the holotype.
Table S4. Morphological comparison of the three forms of *Colocasiomyia heterodonta*.

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<td>Antennal first flagellomere</td>
<td>Approximately 1.5 times as long as pedicel (Fig. S2A)</td>
<td>Approximately 1.5 times as long as pedicel (Fig. S2G)</td>
<td>Twice as long as pedicel (Fig. S2M)</td>
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<td>Facial carina</td>
<td>Much shorter than antennal pedicel + first flagellomere, as wide as first flagellomere (Fig. S2B)</td>
<td>Slightly shorter than antennal pedicel + first flagellomere, slightly narrower than first flagellomere (Fig. S2H)</td>
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<td>Number of pseudotracheae per side in labellum</td>
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<td>11–12</td>
<td>13–14</td>
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<td>Long spine on foreleg tarsomere II</td>
<td>Not reaching to tip of tarsomere IV (Fig. S2C)</td>
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<td>Number of small, tooth-like spines on foreleg tarsomere II</td>
<td>12–40 (Fig. S2D)</td>
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<td>Paramere</td>
<td>Obliquely truncate apically (Fig. S2F)</td>
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<td>Aedeagus</td>
<td>Shorter than 1/2 apodeme (Fig. S2F)</td>
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<td>Approximately half as long as apodeme (Fig. S2Q)</td>
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<td>Aedeagal, basal, beak-like projection</td>
<td>As long as aedeagus proper, gently curved (Fig. S2F)</td>
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<td>As long as aedeagus proper, strongly curved (Fig. S2Q)</td>
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* Including the holotype.
Fig. S1. Morphological differences in the body colour (A–C; dark patch on apical portion of foreleg tibia indicated with arrowhead), the facial carina (D–F), the number of supracervical setae on the occiput (G–I), the setation on the costa (J–L), and the paramere and the aedeagus (M–O) of the three forms, Light (♂ from the type locality, i.e., Bogor Botanical Garden, Bogor, West Java, Indonesia), Dark I (B, K, N: ♂ from Lembah Anai, West Sumatra, Indonesia; E, H: ♂ from Batangang, Padanpanjang, West Sumatra, Indonesia) and Dark II (C, L, O: ♂, F, I: ♀ from Toraut, North Sulawesi, Indonesia), of Colocasiomyia xanthogaster. Abbreviations: aed = aedeagus, aed b p = aedeagal basal process, pm = paramere. Scale bars: 0.1 mm.
Fig. S2. Morphological differences in the antenna (A, G, M), the facial carina (B, H, N), the pegs on the foreleg tarsomere II (C, D, I, J, O) and the phallic organs (E, F, K, L, P, Q) of the three forms, Form I (A–F: ♂ from the type locality, i.e., Bogor Botanical Garden, Bogor, West Java, Indonesia), Form II (G–L: ♂ from Inobong, Crocker Range, Sabah, Malaysia) and Form III (M–Q: ♂ from Mt. Kerinci, Jambi, Sumatra, Indonesia; distinct characters are shown with yellow arrowheads), of *Colocasiomyia heterodonta*. Abbreviations: aed = aedeagus, aed b p = aedeagal basal process, aed bm p = aedeagal basomedial projection, aed gd = aedeagal guide, fc car = facial carina, pm = paramere. Scale bars: 0.1 mm.
Fig. S3. Microphotographs of the male (A, periphallic organs in caudolateral view; B, phallic organs in lateral view; C, ditto in ventral view) and female (D, lateral view; E, ventral view) terminalia of *Colocasiomyia rostrata* sp. n. Abbreviations: epiproct = epiprct, hypoproct = hyprct. Scale bars: 0.1 mm.
Fig. S4. Inflorescences of *Homalomena pendula* (Blume) Bakh.f. in the Bogor Botanical Garden, West Java. A, The flowering inflorescence (left) of which thermogenesis was recorded and an inflorescence bud (right); B, the spadix of the former, the spathe having been removed.
Fig. S5. *Homalomena* sp.PT (the Hanneae group) at a location between Sungai Penuh and Tapan, West Sumatra, photographed on 7.xii.2004. A, An overview of the plant; B, an inflorescence before pollen release at Stage II, with *Colocasiomyia* flies on the spadix.
Fig. S6. *Homalomena* sp.L c.f. *megalophylla* in Lembah Anai, West Sumatra, photographed on 9.xii.2004. A, An overview of the plant; B, an inflorescence (right) presumably just before the spathe opening at Stage I, with *Colocasiomyia* flies on the spathe.
Fig. S7. *Homalomena* sp. aff. *alba* (the *Homalomena* section) in Tumokang, Dumoga Bone National Park, North Sulawesi, photographed on 21.xii.2003. A, An inflorescence at Stage II, with *Colocasiomyia* flies on the spathe; B, an overview of the plant; C, the underside of a leaf.
Fig. S8. Homalomena sp.T (the Homalomena section) in Toraut, North Sulawesi, photographed on 19.xii.2003. A, An inflorescence at Stage II, with the spathe partly removed; B, an inflorescence at Stage II; C, a cluster of inflorescences/infructescences sequentially blooming/having bloomed; D, an overview of the plant; E, the upperside of a leaf; F, the underside of a leaf.
Fig. S9. Homalomena sp.P (the Hanneae group) belonging to the Hanneae complex in Poring, Mt. Kinabalu, Sabah, photographed on 11.iii.2000. A, An inflorescence at Stage II, with Colocasiomyia flies on the spadix; B, an overview of the plant; C, a cluster of inflorescences/infructescences sequentially blooming/having bloomed.
Fig. S10. Homalomena lambirensis S.Y.Wong & P.C.Boyce in the Lambir Hills National Park, Sarawak, photographed on 17.xi.2004. A, An inflorescence before pollen release at Stage II, with Colocasiomyia nigricauda flies on the spathe and resin droplets excreted on the spadix; B, an overview of the plant; C, an inflorescence after pollen release at Stage II, with C. nigricauda flies on the spathe and spadix, mating Parastasia bimaculata (Scarabaeidae) beetles on the spadix, and Dercetina sp. (Chrysomelidae) beetles on the spathe.
Fig. S11. *Homalomena vietnamensis* Bogner & V.D.Nguyen in Cuc Phuong, Vietnam. A, An overview of the plant; B, collected inflorescences and a leaf; C, an inflorescence at Stage II, with *Colocasiomyia erythrocephala* flies on the spadix.
**Fig. S12.** *Homalomena* sp.K (the Homalomena section) on Mt. Kerinci, Jambi, Sumatra, photographed on 7.x.2004. A, An inflorescence at Stage III (right) with powdery pollen grains on the spadix, and an inflorescence bud; B, an overview of the plant; C, a collected inflorescence and a leaf.
Fig. S13. *Homalomena* sp.BP in Bukit Punai, West Sumatra, photographed on 8.xii.2004.