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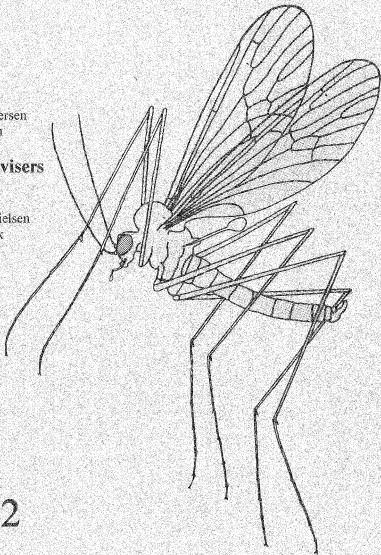
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## ENTOMOLOGICA SCANDINAVICA

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# Systematics of the genus *Colocasiomyia* de Meijere (Diptera: Drosophilidae): cladistics, a new generic synonym, new records, and a new species from Nepal

DAVID GRIMALDI

Ent. scand.



Grimaldi, D.: Systematics of the genus *Colocasiomyia* de Meijere (Diptera: Drosophilidae): cladistics, a new generic synonym, new records, and a new species from Nepal. *Ent. scand.* 22: 417–426. Copenhagen, Denmark January 1992. ISSN 0013–8711.

The fly species *crassipes* de Meijere is transferred from the Sphaeroceridae to the Drosophilidae since *Platyborborus* de Meijere, a monotypic genus, is a junior synonym of *Colocasiomyia* de Meijere. *Colocasiomyia crassipes* is a very highly modified member of the genus due to its flattened body, reduction and loss of many groundplan setae, deep antennal fossae, and crassate hind legs. The holotype and only known specimen, from Java, is redescribed in detail and illustrated. New records of *Colocasiomyia staminicola* (Carson & Okada) and *C. gigantea* (Okada) are reported from Guadalcanal, Solomon Islands, considerably outside their reported ranges. *Colocasiomyia nepalensis* sp. n. is described from Kathmandu, Nepal. Cladistic relationships in the genus are briefly examined and related to biogeography and aroid host use.

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## Introduction

The genus *Colocasiomyia* is a moderate sized group of drosophilids, but with a fascinating biology. Larvae and adults are found in strict association with the spadices of several aroid plants in the Old World tropics, such as *Aglanema*, *Alocasia*, *Colocasia*, and *Homalomena*. The larvae breed in the spike-like inflorescence and are sometimes restricted to even the upper or lower part of inflorescence, which may separate the male and female flowers. Only one species has not been found with aroids and several others have unknown hosts. Virtually all of the work, taxonomic and ecological, has been done by the Japanese (Carson & Okada 1980; Okada 1986; Okada 1987; Okada 1988; Okada & Yafuso 1989; Toda & Okada 1983; Yasufo & Okada 1990).

A list of the species in the genus is given by Okada (1988), with five more species having been added since then (Okada & Yafuso 1989; Okada 1990; Yasufo & Okada 1990). Presently there are 20 species in the genus, plus the two placed in the genus here.

*Colocasiomyia* is certainly a monophyletic genus since it bears a suite of distinctive autapomorphies (which are presented in the diagnosis), but these

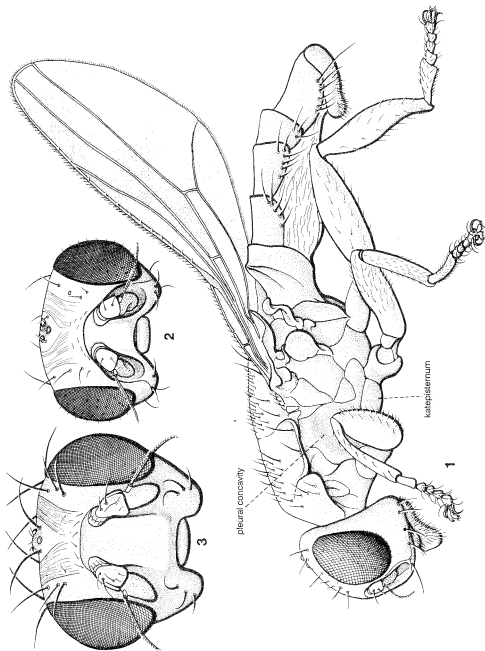
modifications have also probably resulted in a difficulty of placing a sister group to the genus. In the world catalogue of drosophilids by Wheeler (1981; 1986), the genus is placed incertae sedis to subfamily (under the synonym *Drosophilella* and as *Colocasiomyia*). Okada (1989), in a phenetic analysis of drosophilid genera, placed the genus as the sister group to *Calodrosophila*. Grimaldi's (1990) cladistic analysis placed the genus as the sister group to *Baedrosophila*. In the cladistic analysis *Baedrosophila* + *Colocasiomyia* represents a primitive clade in the subfamily Drosophilinae.

Terminology for the descriptions follows that given in Grimaldi (1990). Ipsilateral refers to structures on the same side (e.g., ipsilateral dorsocentral setae). Decasternum refers to the small sclerite connecting the lobes of the surstyli, which may or may not be homologous to the tenth sternite. C.I. and 4-V are standard drosophilid wing ratios, the costal index and 4th vein index, respectively, as defined in Grimaldi (1987).

## Taxonomy

### Genus *Colocasiomyia* de Meijere

*Colocasiomyia* de Meijere, 1914: 272. Type species:



Figs 1-3. *Colocasiomyia* spp.: (1) *C. crassipes* (de Meijere), holotype, left lateral habitus, with positions of appendages slightly rearranged; (2) same, head in frontal view; (3) *C. gigantea* (Okada) from Guadalcanal Island, head in frontal view.

*Colocasiomyia cristata* de Meijere, by monotypy. Wheeler 1981: 82 (p.p., world catalogue).

*Platyborborus* de Meijere, 1914: 273. Type species: *Platyborborus crassipes* de Meijere, by monotypy (as Sphaeroceridae), *syn. n.*

*Drosophilella* Duda, 1923: 25. Type species: *Drosophilella seminigra* Duda, by monotypy. Wheeler 1981: 66 (world catalogue); Okada 1988: 34 (synonymy).

**Diagnosis.** – Arista pubescent in all but six species; antennal bases widely separated; facial carina high, very broad and flat; cheek deep; ocellar setae lying outside of ocellar triangle; eye usually without pile (pile present in four species); fore tarsomere II usually with apical-medial elongation, and one or two rows of thick, sclerotized teeth; pulvilli large; wing hyaline and with enlarged setae interspersed throughout other, smaller setae on costal edge; except for *C. arenga*, oviscapt without pegs, with just fine setulae; spermathecal capsules vestigial; male genitalia highly modified, usually with elongate and pointed ventral epandrial lobe, cercus with long ventral lobe; if surstylus present it is long and thin, and the aedeagus simple and tubular with a heavily scaled, membranous and eversible distiphallus.

### *Colocasiomyia crassipes* (de Meijere)

#### comb. n.

*Platyborborus crassipes* de Meijere, 1914: 273. Type locality: Java.

**Redescription.** – Body dorsoventrally flattened (Fig. 1), including head, thorax, and abdomen.

Head (Figs 1, 2): Ratio of head height to width = 0.63. Body mostly ochre in color. Eyes dark red; with sparse, long, thin interfacetal setulae. Ratio of cheek depth/eye depth = 0.26. Recline orbital setae erect, slightly laterocline; proclinate at normal angle of position. Orbital setae short, posterior 'reclinate' longest, then anterior 'reclinate', with proclinate shortest. Anterior 'recline' slightly closer to proclinate than to posterior 'recline'. Proclinate nearly in line with dorsal-most margin of pilinal suture. Ipsilateral orbitals in line with inner vertical seta. Intraocellar setulae lost. Ocellar setae small, about same length as proclinate; parallel; sockets lie outside of ocellar triangle, bordering anterior ocellus. Postocellar setae small, about same length as ocellars; convergent. Outer vertical setae lost. Inner vertical setae longest ones on head. Base of antenna (pedicel, flagellomere 1) recessed into deep fossa. Flagellomere 1 short, slightly shorter than pedicel. Bases of antennae separated by distance about equal to width of scape.

Arista pubescent, with mostly dorsal, fine, minute branches. Carina broad and flat, greatest width = 0.38 width of face at same level (between inner margins of eyes). Oral margin very deeply indented; height of indentation 0.48 that of face depth (to the dorsal margin of pilinal suture). Single pair of vibrissae, long, projected forward; pair slightly posterior to them, about one-half the size, slightly upturned. 2-3 subvibrissal setulae present, 2 long genals. Palpi small, yellow. Labellum yellow; fairly large, with long fine setulae; mostly recessed into oral cavity.

Thorax (Fig. 1): Mesonotum collapsed in type specimen, but noticeably flat and very broad in dorsal view. Mesonotum brown, with slight yellow along transverse suture. Width of mesonotum 1.54x height of thorax. Acrostichal setulae black, long, erect, not in any noticeable rows. Dorsocentral setae either lost or reduced to 2 pairs of setae in posterolateral corners of mesonotum; length and thickness of these setae barely longer than in acrostichals. Scutellum brown above; short; wide. Apical scutellar setae lost; preapicals parallel, directed posteriorly, length about equal to greatest length of scutellum. Postpronotal lobe large, with 3 larger setae, 2 smaller ones. Notum with 2 large notopleural setae, 1 large and 2 small supra-alar setae. Pleura yellowish, completely devoid of setae. Anterior leg lying in concave area in pleuron. Katepisternum ventrally positioned.

Legs (Figs 1, 4): yellow. Foreleg (Fig. 4): Fore femur stout, width is 0.35 the length (excluding trochanter). Fore coxae bulbous, distal ends pointed mesad and touching. Fore femur with only fine golden setae, no black ones. Relative lengths of foreleg segments: femur 2.8, tibia 2.6, tarsomere I 1.0, distal tarsomeres (II-V) 1.0. Ventral surface of tarsomeres I, II, III with comb of 7 heavily sclerotized, stout, sharp setae: 3 at distal end of t-I, 2 each on t-II and t-III. Fore tibia slightly clavate, with about 10 sparse, sharp curved setae on dorsal surface; no large apical/preapical setae. Fore tarsomere I laterally flattened. All pretarsi with 4 long setae on apical margin, lengths about equal to length of pretarsus. Pulvillus large, brush-like; empodium long, bristle-like; claws large, flattened, heavily sclerotized at tips. Mid leg: coxa small, buried in katepisternum. Relative lengths of segments: femur 2.25, tibia 2.0, tarsomere I 1.0, distal tarsomeres 1.0. Mid femur with fine golden setae; mid tibia with short, black, spinule-like setulae on ventral (adaxial) surface, denser at apex of tibia. Mid tarsomeres

II-IV with single, longitudinal row of minute cuneiform setulae along postero-lateral surface. Hind legs: long, 1.2x longer than fore, 1.7x longer than midlegs. Mesal surfaces of hind coxae contiguous for almost the entire length. Femur thick, with 0.25x length of femur; with mesal surface flat, lateral surface bowed. Tarsomere I laterally flattened. Relative lengths of hind leg segments: femur 2.6, tibia 2.4, tarsomere I 1.0; distal tarsomeres 1.0. Hind tarsi without row of cuneiform setulae.

Wing (Fig. 1): hyaline, no markings. Humeral break distal from humeral crossvein by distance about equal to its length. Wing base with 1 long seta. Humeral and subcostal breaks without enlarged setae. Subcostal vein apically fused to costal vein; vein thickness of fused area is about twice the normal thickness. Costa extended around to apex of  $R_{4+5}$ ; with fringe of long setulae on upper surface; row of 13-15 fine black setulae on lower surface, evenly spaced. Wing length 1.9x length of notum (including scutellum). Wing indices: C.I. = 2.33; 4-V = 3.0. Halter base yellow; knob narrow, light brown.

Abdomen (Fig. 1): tergites light brown, very broad; dorsally completely devoid of setae, 4-5 setae only on lateral edges of tergites 3,4,5 and (syn-tergite 6 + 7). Lateral setae long, thin, golden.

Male genitalia (Fig.5): Epandrium small, with fringe of fine, short setae on posterior margin. Genitalia held ventrally, directed anteriorly. Ventral epandrial lobes stout, broadly-attached, pendulous; each bearing c. 50 fine, long setae, principally on the mesal surface. Cerci mostly hidden within epandrium, ventral corner of each lobe extended to fine sclerotized point, directed inward. Hypandrium with flat anterior margin. Surstyli scoop-shaped, directed posteriorly, with fringe of long, fine setulae on mesal ridge. Surstyli basally connected to pair of lobes (gonopods) that connect behind distiphallus. Aedeagus spindle-shaped, typical of genus. 'Decasternum' present, connecting surstyli behind ventral lobes of cerci.

*Material examined.* - Holotype and only known specimen, a male with the following labels: Java II.II.06, Semarang, Jacobson / 30I. in Tjempaka blume / *Platyborborus crassipes* det. de Meijere [date illegible] / Type [red label].

The original description mentioned that *Michelia champapa* was the inflorescence ('Tjempaka') on which the specimen was caught. The left foreleg and terminal segments of the abdomen, with genitalia, were dissected and cleared in KOH by D. Grimaldi, and stored in glycerine and pinned in a microvial beneath the specimen.

Specimen is in the Zoologisch Museum, Entomologie,

Instituut voor Taxonomische Zoölogie, Universiteit van Amsterdam. Bächli (1987) catalogued the type collection of Drosophilidae in the Zoological Museum, Amsterdam, but no mention was made of this species.

*Discussion.* - This unusual drosophilid undoubtedly belongs in the genus *Colocasiomyia*, by its sharing characters given in the generic diagnosis above. Despite the fact that de Meijere described *Platyborborus* and *Colocasiomyia* on two consecutive pages, he probably confused the former as being a sphaerocerid because of the flattened and stout body, and the enlarged hind tarsomere I. The many autapomorphies of *C. crassipes* attests to the fact that it would not be immediately recognizable as being in *Colocasiomyia* nor the Drosophilidae. These are the following: A widened, flat body; 'reclinate' orbital setae erect; outer vertical setae lost; ocellar and postocellar setae minute; antennae recessed into deep fossae; postpronotal lobe large; foreleg recessed into concave area in pleura; all pleural setae lost, and katapisternum almost entirely ventral; dorsocentral setae lost or greatly reduced; legs stout and splayed, especially the hind pair which are also slightly crassate; black pegs on fore tarsomeres 1,2, and 3, instead of on just tarsomere 2; setae on abdominal tergites lost except at lateral margins.

A surprising result of the rediscovery of this type specimen is its origin: Java. Java has been probably the best studied area for *Colocasiomyia* (summarized in Yasufo & Okada 1990), and its fauna currently has 8 species compared to the 2 and 3 species each for the other localities in the range of *Colocasiomyia*. Despite the effort spent on the Javanese fauna, the type of *C. crassipes* is the only known specimen of the species. There was no citation of the species or genus in catalogues of Australasian Diptera (Marshall 1989) and Oriental Diptera (Hackman 1977).

### *Colocasiomyia nepalensis* sp. n.

*Type material.* - Holotype, male, NEPAL: Kathmandu: Godavari, 5000 ft., 19.vii.1967, Canadian Nepal Expedition. Not dissected. In the Canadian National Collection, Biosystematics Research Centre, Ottawa. Paratypes: 2 males, 2 females (1 of each completely cleared in KOH and stored in a microvial with glycerine), with same collection data as holotype. 1 male deposited in AMNH, remainder in CNC.

*Etymology.* - From Nepal.

*Description.* - Entire body in males and females evenly dark black-brown, except for tibiae and tarsi, which are ochre.

Head (Fig. 6): Eyes dark red, apparently with sparse, very short but stout interfacetal setulae. Ocelli clear, not red. 2 pairs intraocellar setulae present. Ocellar setae parallel, projected forward, apices extended to about level of proclinate sockets; base of ocellar seta antero-lateral to anterior ocellus. Postocellar setae of moderate length, parallel, projected slightly posteriorly. Inner vertical seta in line with ipsilateral orbitals; thick, pointed; longest setae on head. Inner verticals convergent. Outer verticals c. one-half the length and thickness of inner verticals, projected postero-laterad. Proclinate and posterior reclinate orbital setae very similar in size; anterior reclinate c. one-third the length and thickness of these setae and slightly closer to proclinate. Proclinate midway between ptilinal suture and posterior reclinate. Posterior reclinate slightly closer to proclinate than to inner vertical. 2-3 pairs fine short interfrontal setulae present, very close to ptilinal suture. Ocellar triangle without discrete edge, shiny. Frontal vitta flat black. Frontal orbital plates c. one-half the thickness of frontal vitta; shiny. Carina extended to ptilinal suture, separating antennal bases by distance about equal to diameter of scape (Fig. 6). Carina broad, flat, extended to oral margin, width c. equal to that of pedicel. Arista 2.5x the length of flagellomere I, pubescent. Pedicel and flagellomere I lie in rounded, deep cavity. Clypeus deep. 1 pair vibrissae present, with 3 prs. subvibrissal setulae. Cheek moderately deep.

Proboscis (Fig. 7): Floor of cibarium oval, without proximal bulb or dorsal keeled apodeme. Cibarial floor with 3 pairs of median and 1 pair of anterior (distal) sensilla; with 3 proximal (posterior) sensilla, forming a triangle. Palp drop-shaped (Fig. 7), with 1 large apical seta and 1 seta dorsal and 3 setae ventral to it, c. one-half the size. Dorsal arm of stipes long and thin, length c. 0.75x that of lacinia (anterior arm); ventral arm of stipes c. 0.6x the length of dorsal arm (Fig. 8). Labium broad, saddle-shaped, with indented posterior margin.

Thorax: Notum shiny, but with microtomentum. Acrostichals thick, in 6 even rows. Pair of prescutellar acrostichals c. 2x the length of anterior ones. Anterior dorsocentral slightly more than one-third the length of posterior. Distance between ipsilateral dorsocentrals slightly greater than length of anterior dorsocentral. Anterior scutellar setae very close to anterolateral corner of scutellum: distance from corner only c. 2x diameter of seta base. Dorsal surface of scutellum flat. Postpronotal lobe small, dis-

placed laterally, with 2 medium setae. Notopleural suture also displaced laterally, with 2 stout setae on edge plus one dorsal to these. 2 large supra-alar setae present. Katepisternum mostly ventral, with 1 large seta.

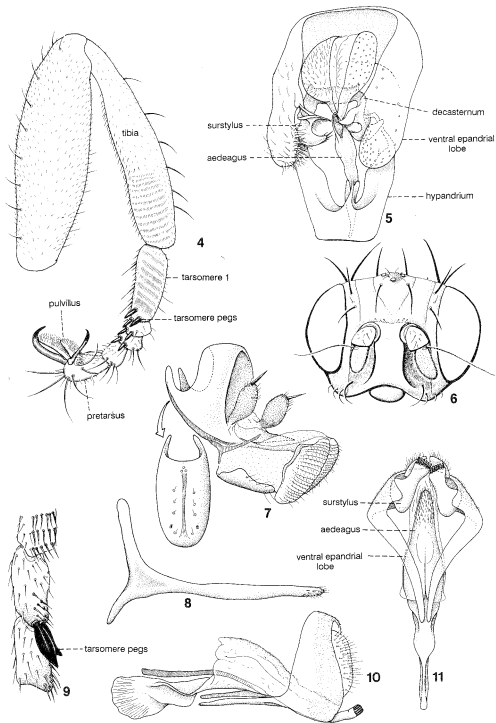
Wing: Hyaline. Stout seta proximal to humeral break (1 ventral, 1 dorsal) and one at apex of costal break. Setae on costal edge between breaks c. 2x size of setae on distal parts of costa. Costa extended to apex of  $M_2$ . Ventral surface of costa with a row of fine, long setae interspersed between 5-8 normal setae; dorsal surface with same setae of similar spacing. Base and knob of halter dark brown.

Legs: Femora dark brown; all tibiae and tarsi ochre. Tarsal segment on foreleg with slight ventral elongation bearing a pair of black, spine-like setae; medial one slightly longer, flat and wide, lanceolate, and with slightly median ridge (Fig. 9). Mid tarsomeres I, II, and III with pair of stout, peg-like black setae on ventro-apical margin. Pulvilli and claws of moderate size.

Abdomen: Dull black-brown, with 4 uniform transverse rows of short stout setae on each tergite. Female tergite 7 with dorsal surface interrupted medially. Oviscapit long, thin, apically pointed; with fine long apical setae, no pegs. Male (Figs 10, 11): Epandrium with 3-4 small setae on postero-lateral corner. Ventral epandrial lobes very long, thin, projected anteriorly and ventral to aedeagus; convergent and touching near base of aedeagal apodeme (Figs 10, 11). Surstyli flat, pointed posteriorly, in line with flat surface formed from ventral surface of epandrium, epandrial lobes, and aedeagus. Surstylus with comb of 6 equal-sized, finger-like prenisetae (Fig. 11). No process on posterior margin of sternite 7. No long, ventral process of cerci. Decasternum small. Aedeagal apodeme laterally flattened and apically flared into a flange. Long, thin sclerotized rod (ejaculatory apodeme? endophallus?) inserted proximally into membranous base of endophallus (Fig. 10). Distiphallus fusiform, apically with fine spicules, covered with membrane (Fig. 11).

### New records from Solomon Islands

Mr N. Sui had reared Diptera from female flowers of *Colocasia esculenta* (Araceae) on Guadalcanal, Solomon Islands, on 28.viii.1985, and found two species of *Colocasiomyia* which were then sent to me for identification. The new records are notable since Guadalcanal lies some 1800 and 5200 km east





of where the two species had previously been reported, thus considerably extending their range. Below are brief treatments of each species. Specimens are in the American Museum of Natural History and the Natural History Museum, London.

*Colocasiomyia stamenicola* (Carson & Okada, 1980): A large series of over 100 males and females reared from the female flowers of *C. esculenta*. Material is identical to that described by Carson & Okada (1980) and with material examined by myself from New Guinea. New Guinea was the known range prior to this record and *C. stamenicola* from there had also been reared from *C. esculenta*.

*Colocasiomyia gigantea* (Okada, 1987): A series of 11 males and females found co-occurring with *C. stamenicola* on Guadalcanal was examined. Dr Toyohi Okada provided a series of male and female paratypes of *C. gigantea* for closer comparisons. *C. gigantea* had originally been known only from the Bogor Botanical Garden, Java, where it had been reared from *Colocasia gigantea*. The material at hand differs slightly in the following details (features in parentheses refer to Javan specimens): face and cheeks are ochre (instead of dark brown like the rest of the body); lower margin of carina is square (vs. the lower corners oblique, making the carina slightly rounded); anterior reclinate is slightly closer to the proclinate (vs. midway between proclinate and post. reclinate); ends of all tibiae and all the tarsi are ochre (vs. uniformly dark brown); body size is slightly larger in Guadalcanal specimens. No differences in male genitalia, female genitalia, or the foretarsal comb was found between the two series. Thus, with the exception of the slight differences in the carina and orbital chaetotaxy, the main differences between the two populations is one of color and size, which are known to be very susceptible to environmental influences during larval development. It is quite likely that this species will eventually be found in New Guinea, since that island lies between Guadalcanal and Java.

### Cladistics

A matrix of 22 adult morphological characters and 20 species was constructed, using all binary states.

Some of the data came from the publications of Okada, Toda, and others, as well as from specimens in the AMNH. *Colocasiomyia seminigra* Duda, 1923 was not analyzed since an insufficient amount of data was in the original description and little museum material of this species is available. The matrix was run on the program HENNIG86 (courtesy of J. S. Farris), using the most exhaustive branch and bound algorithm, implicit enumeration ('i.e.'). This analysis yielded two most parsimonious trees, with a length of 47, a consistency index of 48, and retention index of 68. Synapomorphies on the tree were then analyzed by hand and their arrangement slightly modified since the computer analysis forced a reinterpretation of some of the original homologies. The choice between the two competing cladograms was made on the basis of apomorphy three. This is a unique modification of the ventral margin of the epandrium linking three species; instead of it being convergent on the cladogram, my preference was to have it appear once (homology of the character is in little doubt). This forced character four to appear twice. Since character four is a loss character, it is very difficult to homologize the independent loss of the character. Fig. 12 shows the resultant cladogram. Below is a description of the characters used, with numbers referring to the apomorphy numbers on the cladogram.

1. Presence of a broad facial carina (carina plesiomorphically narrow or flat, but not very broad).
2. Presence of heavily sclerotized, socketed pegs on at least fore tarsomere II (plesiomorphically these pegs are absent).
3. Presence of a thin, curved 'hook' on the antero-ventral corner of the epandrium (plesiomorphically absent).
4. Pegs on the ovicapt lost (plesiomorphically they are present).
5. Arista is pubescent (plesiomorphically with short or long dorsal and ventral branches).
6. Ovicapt long and narrow (plesiomorphically short and blunt, although a reversion to the ancestral state appears to have occurred in *C. baechlii*, *gigantea*, and *diconica*).
7. Ventral margin of male cercus with long lobe (plesiomorphically the lobes are absent).
8. Hypandrium vestigial or completely lost (plesiomor-

Figs 4-11. *Colocasiomyia* spp.: (4) *C. crassipes* (de Meijere), holotype, mesal view of left foreleg, showing arrangement of tarsal pegs and structure of pretarsus; (5) same, male genitalia, oblique terminal view; (6) *C. nepalensis* sp. n., head, frontal view; (7) same, proboscis, oblique lateral view, showing full view of cibarial floor; (8) same, lacinia and stipes; (9) same, fore tarsomere II, with pair of spine-like setae; (10) same, male genitalia, lateral view; (11) same, male genitalia, ventral view.

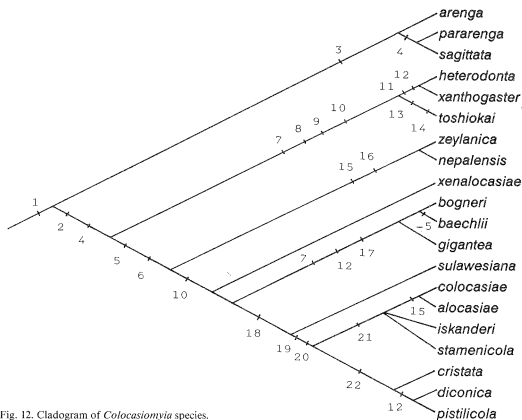


Fig. 12. Cladogram of *Colocasiomyia* species.

phically it is as in *C. arenga* or *crassipes*, which is plate-like).

9. Fore tarsal pegs are very long, at least four times the width (plesiomorphically the length of the pegs is only about two to three times the width).

10. Loss of prensisetæ pegs on the surstylus (plesiomorphically the surstylus in males has stout, sclerotized pegs). This apomorphy has occurred independently twice on the cladogram.

11. Wing with light apical infuscation (plesiomorphically completely hyaline).

12. Acrostichal setulae in 2 rows (plesiomorphically they run in 4 or more rows between the anterior dorso-central setae).

13. Oviscapt with a peculiar, narrow, finger-like process at apex (plesiomorphically without this process).

14. Surstylus very long and thin (plesiomorphically not lobe-like, length barely longer than thickness).

15. Eyes pubescent, with 3 stout ribbed setulae surrounding each ommatidium (plesiomorphically the eyes are without interfacetal setulae, or with sparse, thin setulae). This feature seems to be independently derived in the *C.*

*zeylanica* + *nepalensis* clade, in *C. xenalocasiae*, and again in the *C. colocasiae* + *alocasiae* clade. It needs careful study by scanning electron microscopy to determine if the condition is homologous or not in these three clades and other drosophilines (e.g., Grimaldi 1990).

16. Foretarsal pegs in a single pair on fore tarsomere II (plesiomorphically there at least 3, usually more, pegs).

17. Pegs in 5 pairs on fore tarsomere II (plesiomorphically there are 2–4 pairs).

18. Surstylus vestigial or lost (plesiomorphically surstylus is present).

19. Chaetotaxy of costal vein with series of long erect setulae interspersed with shorter, spinule-like setulae (plesiomorphically without the longer setulae).

20. Male abdominal sternite 6 modified, as diagnosed below into characters 20 and 21 (plesiomorphically sternite 6 is an unmodified plate similar to proximal sternites).

21. Male abdominal sternite 6 with a conical process on the posterior margin (plesiomorphically without the process).

22. Male abdominal sternite 6 deeply bifurcate on the posterior margin (plesiomorphically without the bifurcation).

The resulting cladogram (Fig. 12) is almost entirely resolved, except for one trichotomy at a higher-level node. It is important to point out that there is little congruence between this phylogeny and the trees presented by Okada (1986; 1987; 1990). One reason for the major discrepancy lies in differences of analysis. Okada's methods are phenetic, specifically a modified UPGMA analysis. There are some agreements, however. For example, both Okada and the cladistic analysis are in agreement that *C. baechlii* and *bogneri* are sister species, that *C. colocasiae*, *alocasiae*, and *stamenicola* are very closely related, as are *C. arena*, *pararenga*, and *sagittata*. It is important to scrutinize hypotheses of relationships in *Colocasiomyia*, since there are hypotheses on geographical and host evolutionary trends in the genus (Okada 1986; Yasufo & Okada 1990), and these hypotheses depend critically on a phylogeny.

*Colocasiomyia arenga*, *C. pararenga*, and *C. sagittata* from Java, appear on most grounds to be the most primitive members of the genus, but *C. arenga* has also a derived type of oviscapt. Considered to be the ground plan of the genus is an oviscapt with long fine apical setae, which is plesiomorphic with respect to the subtribe Drosophilina (sensu Grimaldi 1990). The prenisetae on the surstylus (male) likewise are modified into pegs. The Drosophilina are characterized mainly by possession of pegs on the ventral and apical margin of the oviscapt (character 212 in Grimaldi 1990). The tribe Drosophilini (comprised of subtribes Drosophilina and Colocasiomyina) is characterized in part by pegs on the prenisetae (character 200 in Grimaldi 1990); absence of the pegs was considered to have been a loss for *Colocasiomyia*. A plesiomorphic position of *C. arenga* would throw into doubt the supposed plesiomorphic state of the oviscapt sensilla in *Colocasiomyia*: instead of the pegs being primitively absent, they would be lost. This would correspond to the hypothesis about the loss of prenisetae in the subtribe Colocasiomyina. Features of *C. arenga*, *pararenga*, and *sagittata* that are plesiomorphic with respect to most other members of the genus are the following: arista short plumose, instead of pubescent; 2nd foretarsal segment not modified (otherwise with two or more black, spine-like setae and usually prolonged); and *C. arenga* is from a palm inflorescence, not an aroid.

*Colocasiomyia nepalensis* is similar to *C. arenga* and its sister species by possession (retention?) of the prenisetae pegs. I have noted elsewhere (in litt.)

the loss of prenisetae pegs that are correlated with the loss of oviscapt pegs in drosophilids, which occurs repeatedly in the Drosophilidae. However, as shown by *C. nepalensis*, prenisetae pegs can be present without the female having oviscapt pegs, so it is not a perfectly functional association between the two sexes.

There seemed to be few patterns in biogeography and host use that emerged from the cladogram. Obvious features are that the *C. heterodonta* + *xanthogaster* + *toshiokai* clade all breed in *Homalomena* (and either *Aglaonema* or *Colocasia*). Likewise, the *C. bogneri* + *baechlii* clade is a *Homalomena* associate. At least one of the most primitive species presumably breeds in palms, not aroids. No other host use pattern emerged, suggesting (if the cladistic analysis is accurate) that either shifts in the use of *Alocasia* and *Colocasia* hosts are frequent and stochastic, or that sampling of species and host use are insufficient. New findings of *C. gigantea* 5200 km east of its original distribution and such a distinctive fly as *C. crassipes* in a fauna as well known as that of Java certainly attests to our limited faunal knowledge of the genus at this point.

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