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A morphological and molecular description of a new *Teleopsis* species (Diptera: Diopsidae) from Thailand

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Abstract

A new species of *Teleopsis* (Diptera, Diopsidae) from Chiang Mai, Thailand is described and illustrated. *Teleopsis thaii* Földvári & Carr is shown to be a member of a species group, termed the dalmanni species group, along with three previously described species. Presented here are a morphological description of *T. thaii* and an allometric comparison of the species with other members of the *Teleopsis* genus. We also present multi-gene phylogenetic analyses to highlight the possible position of *T. thaii* within the dalmanni species group.

Key words: Diopsidae, *Teleopsis*, Thailand, new species, eye span allometry, molecular phylogeny, dalmanni species group

Introduction

The diopsid stalk-eyed flies are a morphologically distinct family of the Schizophoran diptera, with both males and females of all species possessing laterally extended head morphologies. There are approximately 160 described species within the family, although this figure is increasing (Papp *et al.* 1997, Feijen 1999, Carr *et al.* 2006a) and the family is currently undergoing taxonomic revision (Baker *et al.* 2001, Kotrba & Balke 2006). Recent molecular studies have shown that the genera *Teleopsis* and *Cyrtodiopsis* are in fact paraphyletic with respect to each other, form a monophyletic group and should be considered as a single genus (Baker *et al.* 2001, Meier & Baker 2002). Under this revision, species previously named as *Cyrtodiopsis* are now termed *Teleopsis* species.

Species from the genus *Teleopsis* are mainly found in South East Asia (Feijen 1998). Many of the described *Teleopsis* species show sexual dimorphism within their eyespan, with males showing the greater exaggeration in head morphology, a trait strongly linked to sexual selection. Sexually dimorphic species from Malaysia have been the focus of much of the research in the study of sexual selection within the stalk-eyed flies (David *et al.* 2000, Hingle *et al.* 2001, Cotton *et al.* 2004).

Here we describe a new species of *Teleopsis* from the Doi Suthep, Chiang Mai, Thailand. A viable laboratory population has been established at University College, London from individuals collected from this region. Using phylogenetic analysis of four partial gene sequences we have placed this species within a newly termed species group along with *T. currani* (Shillito), *T. dalmanni* (Wiedemann) and *T. whitei* (Curran). This new group has been named the dalmanni species group (after the species, *T. dalmanni*). We have described the

morphology of *T. thaii* and compared aspects of its morphology with the other members of the dalmanni species group. We have also performed an allometric analysis of *T. thaii*, with emphasis on its extreme sexual dimorphism, and compared its allometry to six other members of the *Teleopsis* genus.

Method and materials

All allometric and molecular work was performed on individuals taken from the same laboratory population as the morphologically described specimens.

Allometric Comparisons

T. thaii were reared in the laboratory under variable larval density to generate the variance in adult size required for the investigation of allometry (David *et al.* 1998, Cotton *et al.* 2004). Eclosing individuals (20 males and 25 females) were collected and measured to an accuracy of 0.01 mm using a monocular microscope and the image analysis program NIH Image (Version 1.55; National Institutes of Health, Bethesda, MD, USA). Measurements were taken of eye span (between the outermost lateral edges of the eye bulbs) and body length (from the front of the face to the tips of the wings; Baker & Wilkinson 2001).

Absolute trait size data were non-normally distributed so differences between sexes were detected using non-parametric Wilcoxon-tests. Eye span is a highly allometric trait in stalk-eyed flies (Baker & Wilkinson 2001), so we analysed sexual dimorphism of eye span using a General Linear Model (GLM) containing SEX and BODY LENGTH as fixed factors, their interaction, and an intercept. The significance of each effect (or interaction) was determined via *F*-tests on the change in explained variance upon removal of each term from the full model. A significant interaction implies that the *relationship* between eye span and body length (i.e. the allometric slope of eye span) differs between the sexes. We compared eyespan allometry and sexual dimorphism in *T. thaii* with that of its congeners using summary data published previously (Table 1 in Baker & Wilkinson 2001).

TABLE 1. List of PCR primers.

Gene	Sequence coordinate or primer name	Annealing temperature (°C)	Reference
<i>16S</i>	12727–12747(S) 13270–13290(A)	50.0	Baker <i>et al.</i> (2001)
<i>COII</i>	A3772 S3291	50.8	Brower (1994)
<i>w</i>	11404–11426(S) 11975–11997(A)	58.6	Baker <i>et al.</i> (2001)
<i>wg</i>	5'GTTAGAACATGTTGGATGCG3' 5'CGTTCAACGACAATGACCTC3'	53.3	Adapted from Baker <i>et al.</i> (2001)

Gene Cloning And Phylogenetic Analysis

Genomic DNA extractions, PCR and sequencing were performed using the protocol of Carr *et al.* (2006a). The primers used for *16S ribosomal RNA (16S)*, *cytochrome oxidase subunit II (COII)*, *white (w)* and *wingless (wg)* are listed in Table 1.

The sequences for each of the genes have been deposited into the GenBank database (Accession numbers DQ191299–DQ191302). Phylogenies were created from each individual gene and, in addition, from a concatenated four-gene alignment.

The nucleotide sequences produced from *T. thaii* were aligned against the orthologous sequences from seven other *Teleopsis*, two *Diopsis* and one *Eurydiopsis* species taken from GenBank. Recent studies have

shown that *Diopsis* and *Eurydiopsis* are closely related genera to *Teleopsis* (Baker *et al.* 2001) and therefore these sequences are appropriate to use to root the phylogenies of *Teleopsis*. Alignments were created using ClustalX (Thompson *et al.* 1997) and then edited by eye. Gaps present in coding regions were adjusted so that codons were maintained as intact. Both *w* and *wg* harbour introns in the regions amplified by PCR and these were retained in the alignments. However, both introns contained regions of low similarity possessing overlapping indels across the eleven species; these regions were excluded since they could not be unambiguously aligned.

The alignments were analysed with Modeltest 3.7 (Posada and Crandall 1998), which indicated that the General Time Reversible model (Rodríguez *et al.* 1990), with a designated proportion of invariant sites and a gamma correction for rate variation among sites (GTR+I+ Γ) was the most suitable nucleotide substitution model. In each of the analyses the gamma distribution was divided into four categories. Phylogenies were created using two likelihood methods, Bayesian Inference (BI) and Maximum Likelihood (ML). BI phylogenies were produced using MrBayes 3.1.1 (Ronquist & Huelsenbeck 2003) and ML trees from Phym1 2.4.4 (Guindon & Gascuel 2003). The parameters for each analysis were defined by the programs.

BI Monte Carlo Markov Chain analyses were performed with one cold and three hot chains, with a sample frequency of 10, until the two parallel runs had reached convergence (i.e. the average standard deviation of split frequencies <0.01). The first 25% of the sampled trees were discarded as burnin. ML trees were bootstrapped with 1000 replicates. The alignments used to produce the phylogenies are available from the authors upon request.

***Teleopsis thaii* Földvári & Carr, new species** (Figs 1–5)

Teleopsis sp. n.: Carr *et al.* 2006b, Carr 2007

Teleopsis sp. n. 1: Papp *et al.* 2006

Diagnosis: Inner vertical bristle (IVB) only 3–4 times as long as the width of eye stalks in the middle. Thorax shiny in general, scutellar spines up to 5 times as long as scutellum (longest among this four species group). Epandrium in dorsal view narrower than hypandrium. Only few hairs (8–10) at the base of hypandrium. Hypandrial bridge broad, widest at the middle.

Type material: Holotype, male (Hungarian Natural History Museum, Budapest). Paratypes 4 males, 5 females (Hungarian Natural History Museum, Budapest), 5 males, 5 females (Natural History Museum, London). All type specimens (dried, double mounted, excellent condition) taken from a laboratory culture housed at University College, London in July 2006. Parent specimens were collected at Doi Suthep National Park, Chiang Mai, Thailand. Label data: over and along a brook, above and below a small waterfall, Nov 9, 2004, leg. L. Papp & M. Földvári, No. 27.

Head: Yellowish red, with minute, whitish hairs, up to 1.5 times the width of eye stalks in the middle. No facial teeth, edges rounded. Outer vertical bristle (OVB) narrow, 1.5 times the width of eye stalks in the middle. IVB on a small tubercle black, 3–4 times the width of eye stalks in the middle.

Thorax: Generally shiny, Intra-alar spine (IAS) yellow, slightly curved posteriorly in dorsal view, flattened dorsoventrally. Scutellar spine up to 5 times longer than scutellum, yellow–brown, with hairs on the spine as long as the diameter of the spine.

Wing: Four dark bands, proximal band pale, only a dark spot visible above cell cup.

Legs: Covered with hairs (shorter than those on the head). Coxae and femora yellow, tibiae and tarsi brown, front femora with rows of peg-like black tubercles; mid femora slightly swollen in posterior view.

Praeabdomen: Tergites 1 and 2 completely yellow, first half of tergite 3 yellow, otherwise brown. Tergites 1 and 2 with brown spots dorsally in the middle; tergite 3 with grey pollinose spots on the sides. Hairs on the abdomen (as well as all over the body) moderately long, up to $\frac{1}{2}$ of the length of the first coxa

Genitalia: The epandrium and the cerci have long, dispersed setae along their surface. There are two hairs and four minute setae at the base of the hypandrium, the tip of the surstyli have numerous short, distinct hairs (Fig. 2). In lateral view the aedeagal apodeme is slightly curved, longest among the four species discussed here, not broadening towards tip (Fig. 3). The parameres in ventral view have two long and two minute hairs (Fig. 4). The hypandrium is connected to the aedeagal apodeme and the membranous tip of the hypandrium (hypandrial bridge) is continuous, not divided into two lobes anteriorly (Fig. 5). The genitalia in ventral view are broader at the membranous part of the hypandrium than at the surstyli, i.e. the epandrium (Fig. 4).

Etymology: The name refers to Thailand where the type locality can be found.

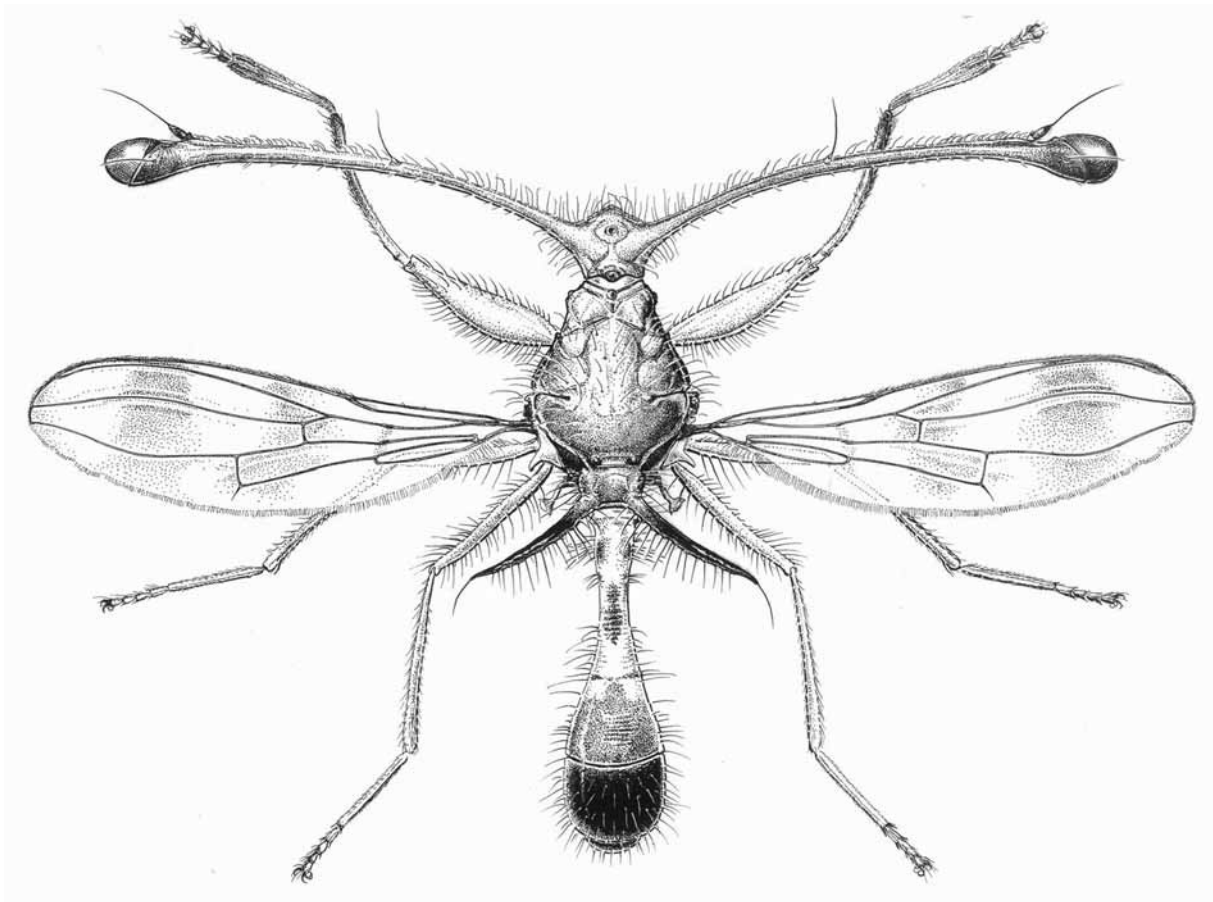
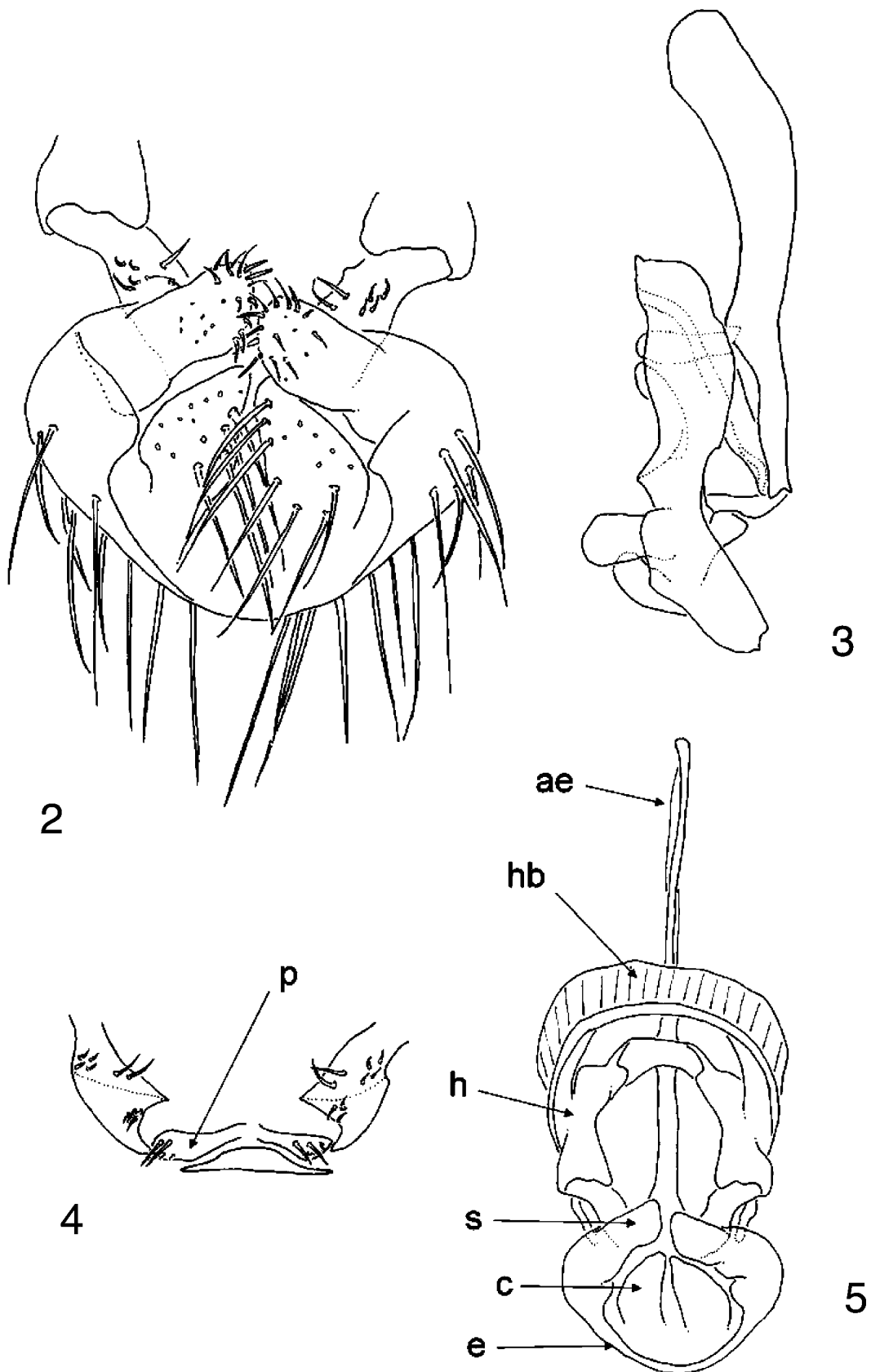


FIGURE 1. *T. thaii*, habitus, specimen collected at the type locality.

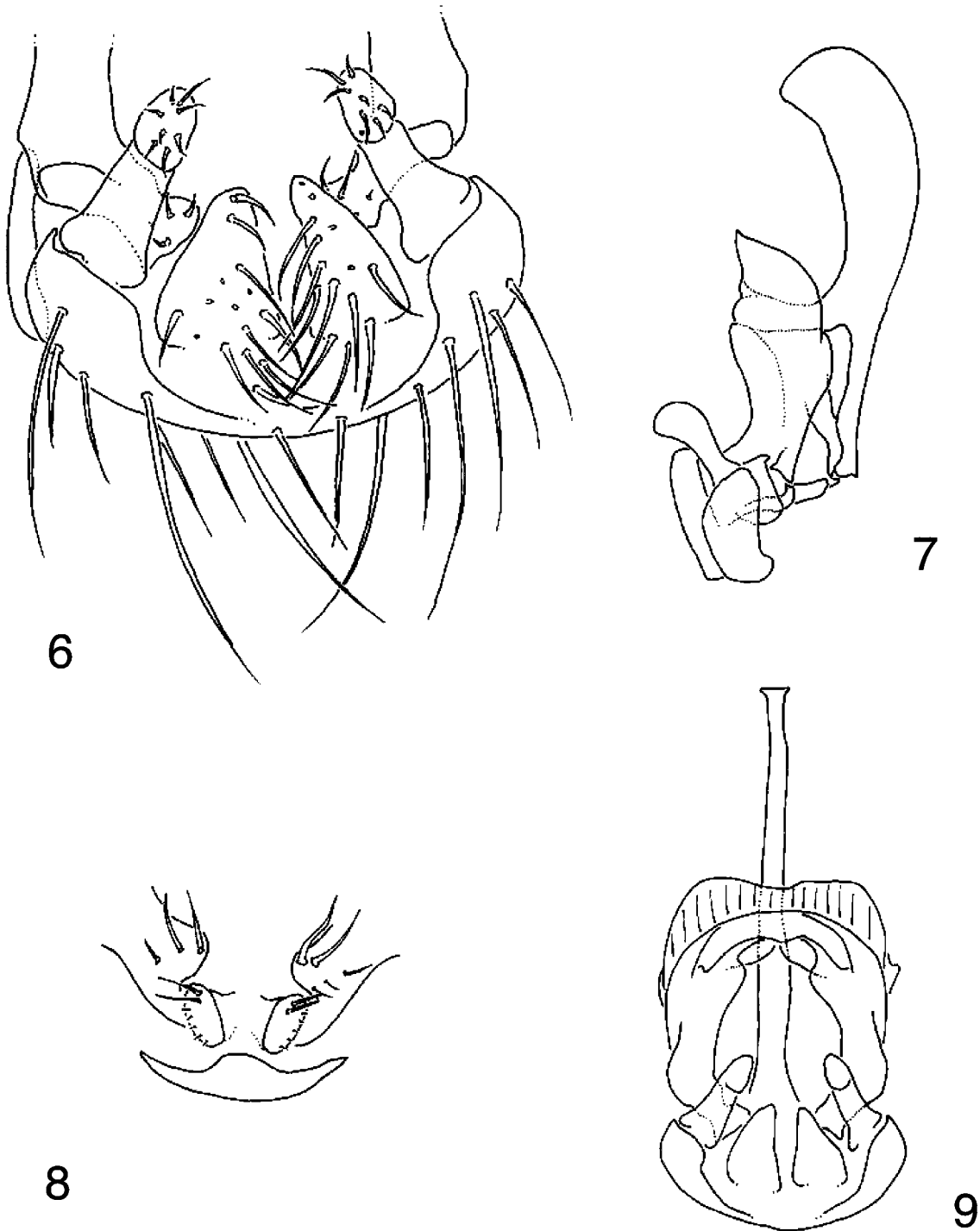
***Teleopsis whitei* (Curran, 1936)**
(Figs 6–9)

Diopsis whitei Curran 1936: 1.

Diagnosis: IVB length up to 4.5 times as long as width of eye stalk in the middle. Thorax pollinose on posterior part, scutellar spines up to 3.5 times as long as length of scutellum. Epandrium in dorsal view as wide as hypandrium. Only few hairs (4–6) at the base of hypandrium. Hypandrial bridge broad, slightly narrowed at the middle.



FIGURES 2–5. *T. thaii* sp. n. male genitalia. 1: detailed ventral view with surstyli, gonopods, cerci, 2: lateral view with aedeagal apodeme, hypandrium and epandrium, 3: detailed ventral view with base of hypandrium and parameres, 4: ventral view. Legend: ae: aedeagal apodeme, c: cercus, e: epandrium, h: hypandrium, hb: hypandrial bridge, p: paramere, s: surstylus.



FIGURES 6–9. *T. whitei* male genitalia. 5: detailed ventral view with surstyli, gonopods, cerci, 6: lateral view with aedeagal apodeme, hypandrium and epandrium, 7: detailed ventral view with base of hypandrium and parameres, 8: ventral view.

Material examined: 5 males, 5 females taken from a laboratory culture housed at University College, London in July, 2006. This culture was founded from individuals caught in Ulu Gombak, Malaysia by Andrew Pomiankowski and Samuel Cotton in April 2005. The dried, double-mounted specimens are deposited in the Hungarian Natural History Museum, Budapest.

Head: Yellow-brown, covered with white hairs up to as long as width of eye-stalk in the middle. No facial teeth, face rounded at the edges. OVB black, slightly larger than width of eye-stalk in the middle. IVB on a

small tubercle in the middle of eye stalk. IVB length up to 4.5 times as long as width of eye-stalk in the middle.

Thorax: Shiny yellow-brown on sides, anepimeron and posterior half of meron grayish pollinose. Scutum somewhat golden pollinose. IAS yellow, flattened dorsoventrally. Scutellar spines up to 3.5 times as long as length of scutellum.

Wing: Hyaline with 4 bands; proximal and distal bands are narrow and pale, 2nd band includes distal part of cell dm and R-M cross vein; 3rd band attaches to the 2nd along vein M.

Legs: Covered with hairs (shorter than those on the head). Coxae and femora yellow, tibiae and tarsi brown, front femora with rows of peg-like black tubercles.

Praeabdomen: Covered with hairs (shorter than those on the head). Tergites generally brown with yellow stripe on front half of T3 and sides of T1–3.

Genitalia: The epandrium and the cerci have long, dispersed setae along their surface. There are two hairs (longer than *T. thaii*) and two minute setae at the base of the hypandrium, the tip of the surstyli have numerous short, distinct hairs, surstyli broadened at tip (Fig. 6). In lateral view the aedeagal apodeme is curved (more than that of *T. thaii*), broad at distal one third (Fig. 7). The parameres in ventral view have two long and 4–6 minute hairs (Fig. 8). The hypandrium is connected to the aedeagal apodeme and the membranous tip of the hypandrium (hypandrial bridge) is slightly divided into two parts anteriorly (Fig. 9). The genitalia in ventral view are as broad at the membranous part of the hypandrium as at the surstyli, i.e. the epandrium (Fig. 9).

Teleopsis dalmanni (Wiedemann, 1830)

(Figs 10–13)

Diopsis dalmanni Wiedemann 1830: 560.

Diagnosis: The most densely haired among the four species, front femur apically strongly incrassate, mid femur distally swollen. IVB up to 4–5 times as long as width of eye stalk in the middle, scutellar spines up to 4 times as long as length of scutellum. Epandrium in dorsal view wider than hypandrium. Two thick setae at the base of hypandrium. Hypandrial bridge broad and with incision at the middle.

Material examined: 5 males, 5 females taken from a laboratory culture housed at University College, London in July, 2006. This culture was founded from individuals caught in Ulu Gombak, Malaysia by Andrew Pomiankowski and Samuel Cotton in April 2005. The dried, double-mounted specimens are deposited in Hungarian Natural History Museum, Budapest.

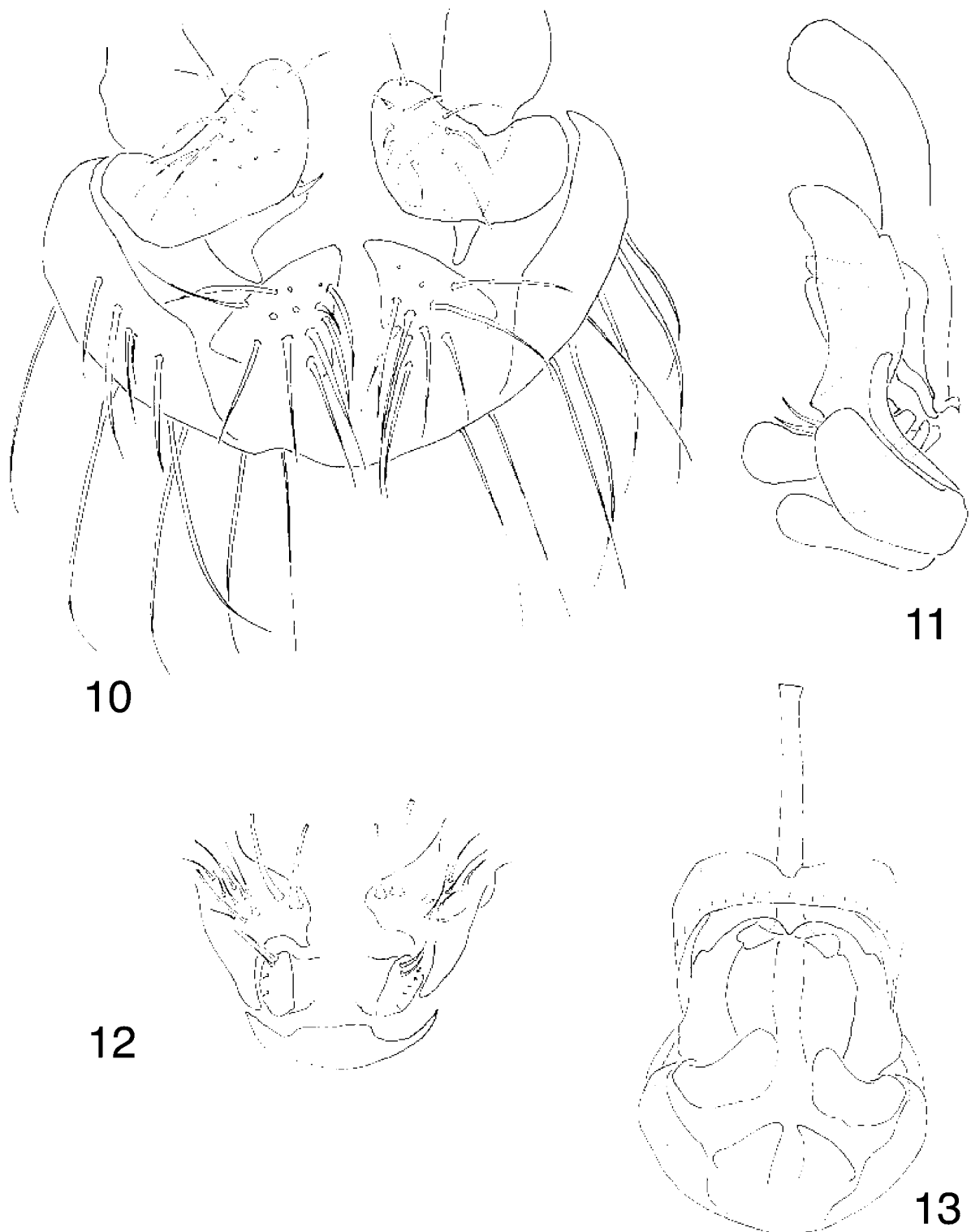
Head: Yellow-brown, covered with brown hairs up to 3 times as long as width of eye-stalk in the middle. No facial teeth, edge rounded. OVB black twice as long as width of eye-stalk in the middle. IVB up to 4.5–5 times as long as width of eye-stalk in the middle; on a small tubercle.

Thorax: Shiny yellow, without pollinosity. Intra-alar spine (IAS) yellow, dorsoventrally flattened, blunt in dorsal view. Scutellar spines up to 4 times as long as length of scutellum.

Wing: Hyaline with only 3 bands (distal fourth is missing). Proximal band continuing in the area of the cell cup, 2nd band includes distal part of cell dm and R-M cross vein; 3rd band attaches to the 2nd along vein M.

Legs: Covered with hairs (shorter than those on the head). Coxae and femora yellow, tibiae and tarsi brown, front femora with rows of peg-like black tubercles. Front femur apically strongly incrassate, mid femur distally swollen (best seen in posterior view). Distal 2/5 of the first tarsus broad, dark brown to black ventrally on the front leg.

Praeabdomen: Tergites 1 and 2 completely yellow, first half of tergite 3 yellow, otherwise brown. Tergites 1 and 2 with brown spots dorsally in the middle; tergite 3 with grey pollinose spots on the sides. Hairs on the abdomen (as well as all over the body) very long, up to the length of the first coxa.



FIGURES 10–13. *T. dalmanni* male genitalia. 9: detailed ventral view with surstyli, gonopods, cerci, 10: lateral view with aedeagal apodeme, hypandrium and epandrium, 11: detailed ventral view with base of hypandrium and parameres, 12: ventral view.

Genitalia: The epandrium and the cerci have long, dispersed setae along their surface. There are two thick setae and 7–10 long hairs at the base of the hypandrium, the tip of the surstyli have numerous longer hairs, more dispersed than *T. thaii* and *T. whitei*). Surstyli broad in general, broadest among the four species (Fig.

10). In lateral view the aedeagal apodeme is curved (as in *T. whitei*), not broadened at distal one third (Fig. 11). The parameres in ventral view have two long and 2–4 minute hairs (Fig. 12). The hypandrium is connected to the aedeagal apodeme and the membranous tip of the hypandrium (hypandrial bridge) is clearly divided into two parts anteriorly by an incision (Fig. 13). The genitalia in ventral view are narrower at the membranous part of the hypandrium than at the surstyli, i.e. the epandrium (Fig. 13).

***Teleopsis currani* (Shillito, 1940)**
(Figs 14–17)

Cyrtodiopsis currani Shillito 1940: 159.

Diagnosis: IVB on large protuberance, that is up to $\frac{3}{4}$ of the width of eye stalk in the middle, length of IVB 4–5 times as long as eye stalk in the middle. OVB: 3–4 times the width of eye stalks in the middle (much longer than in other species), IAS not flattened (unlike in other three species). Scutellar spines 3–3.5 times as long as length of scutellum. Epandrium in dorsal view as wide as hypandrium. Only few hairs (8–10) at the base of hypandrium. Hypandrial bridge narrow.

Material examined: 2 males, 2 females, Thailand, Bangkok, 1–7 March 1971, [leg.] P. & P. Spangler (National Museum of Natural History, Washington D.C.)

Head: Yellow-brown, covered with minute whitish hairs up to $\frac{1}{2}$ of the width of eye stalk in the middle. No facial teeth, edge rounded. OVB black, 3–4 times as long as width of eye stalk in the middle. IVB on large protuberance, that is up to $\frac{3}{4}$ of the width of eye stalk in the middle, length of IVB 4–5 times as long as eye stalk in the middle.

Thorax: Shiny yellow-brown, pollinosity only on the sides, posteriorly. IAS yellow-brown, not flattened. Scutellar spines 3–3.5 times as long as length of scutellum, darker towards tip.

Wing: Four dark bands (appearing as a dark wing with 3 white bands). The second dark band is continuous with the third, 3 white spots in the middle of the wing (border of the two dark bands).

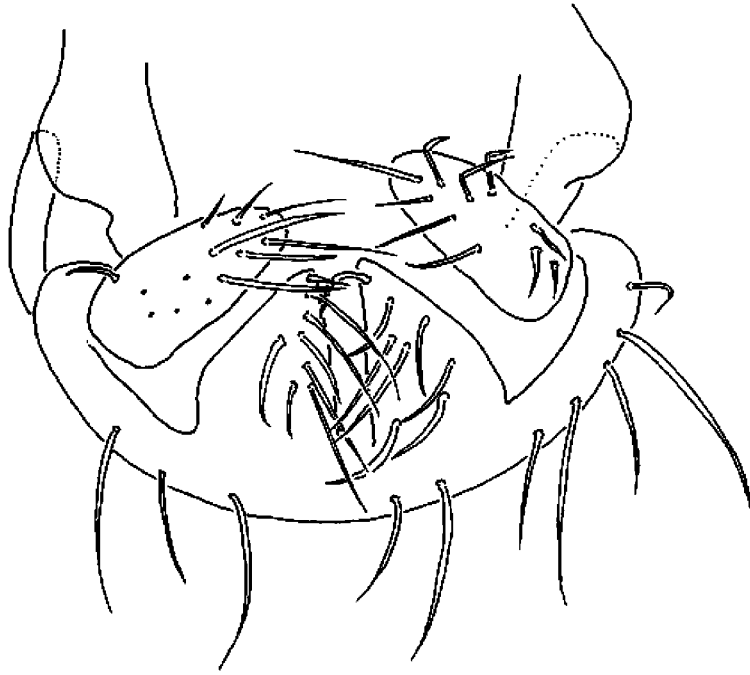
Legs: Covered with hairs (shorter than those on the head). Coxae and femora yellow, tibiae and tarsi brown, front femora with rows of peg-like black tubercles. Front femora similar to those of *T. whitei*, but shorter.

Praeabdomen: Tergites 1 and 2 yellow, otherwise brown, anterior part of tergite 2 brown, tergite 4 grayish pollinose. Hairs dispersed, short, the longest up to $\frac{1}{3}$ of the length of first coxa.

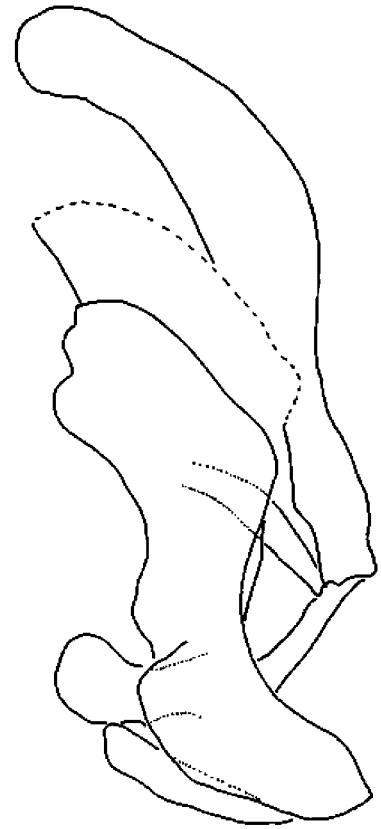
Genitalia: The epandrium and the cerci have long, dispersed setae along their surface. There are two hairs (as long as *T. whitei*) and 6–8 minute setae at the base of the hypandrium, the tip of the surstyli have numerous longer hairs, more dispersed than *T. thaii* and *T. whitei*), i.e. not restricted to the tip. Surstyli slightly broadened in apical part (Fig. 14). In lateral view the aedeagal apodeme is curved (as in *T. thaii*), broadest in the middle (Fig. 15). The parameres in ventral view have two long and 2–4 minute hairs (Fig. 16). The hypandrium is connected to the aedeagal apodeme and there is no membranous part of the hypandrium, the hypandrial bridge is narrow (Fig. 17). The genitalia in ventral view are as broad at the membranous part of the hypandrium as at the surstyli, i.e. the epandrium, comparable to *T. whitei* (Fig. 17).

Allometry of *Teleopsis thaii*

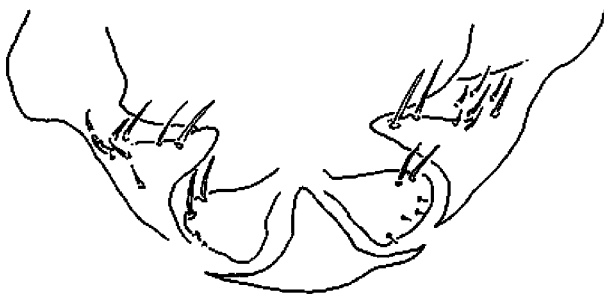
Male *T. thaii* were significantly larger than females for both eyespan and body length (Fig. 18; Table 2; $\chi^2 = 25.02$, d.f. = 1, $P < 0.001$ and $\chi^2 = 7.52$, d.f. = 1, $P = 0.006$, respectively). There was significant difference in the slope of eyespan allometry between male and female *T. thaii*, with males having a steeper scaling relationship (Fig. 18; SEX \times BODY LENGTH interaction term in Table 3).



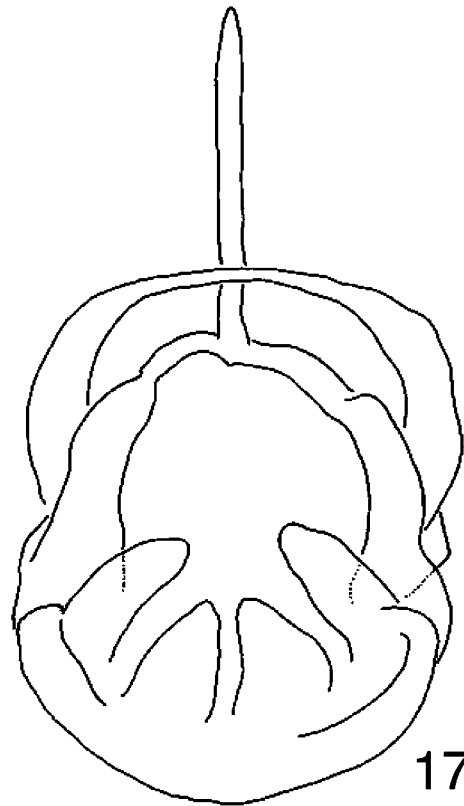
14



15



16



17

FIGURES 14–17. *T. currani* male genitalia. 13: detailed ventral view with surstyli, gonopods, cerci, 14: lateral view with aedeagal apodeme, hypandrium and epandrium, 15: detailed ventral view with base of hypandrium and parameres, 16: ventral view.

Male *T. thaii* have the largest mean eyespan of all the species available for phylogenetic and morphological comparisons (Table 2). In addition, the slope of male eyespan allometry and the degree of sexual dimorphism observed in *T. thaii* is greater than that of all other recorded species except *T. breviscopium* (Table 2).

TABLE 2. Mean trait size (mm) for eyespan (ES), body length (BL) and allometric slope (\pm S.E.) of male and female *T. thaii* (N = sample size). Allometric slope is the least-squares regression coefficient of eyespan on body length. Sexual dimorphism is computed as the difference between male and female slopes. For comparison, the same metrics are given for other members of the *Teleopsis* genus (data from Baker & Wilkinson 2001).

Species	Males				Females				Sexual dimorphism
	N	Mean ES	Mean BL	Allometric slope	N	Mean ES	Mean BL	Allometric slope	
<i>T. thaii</i>	20	11.18	8.03	2.50 ± 0.13	25	6.86	7.46	0.97 ± 0.05	1.531
<i>T. dalmanni</i>	93	7.49	6.23	2.31 ± 0.07	91	5.20	5.86	1.14 ± 0.03	1.168
<i>T. quinqueguttata</i>	102	4.26	6.97	0.69 ± 0.03	66	4.28	7.15	0.67 ± 0.04	0.024
<i>T. whitei</i>	86	7.97	6.37	2.13 ± 0.05	86	4.67	5.55	1.12 ± 0.02	1.006
<i>T. breviscopium</i>	60	10.98	6.32	2.73 ± 0.30	30	6.09	6.38	0.95 ± 0.11	1.779
<i>T. quadriguttata</i>	29	3.33	4.98	0.71 ± 0.04	18	3.37	5.21	0.63 ± 0.04	0.084
<i>T. rubicunda</i>	89	4.97	4.92	1.73 ± 0.08	52	4.65	5.45	1.15 ± 0.05	0.579

TABLE 3. General Linear Model of body length and sex effects on eyespan in *T. thaii*.

Factor	SS	d.f.	MS	F -ratio	Prob > F
body length	191.79	1	191.79	1892.67	< 0.001
sex	91.95	1	91.95	907.40	< 0.001
sex \times body length	9.09	1	9.09	89.75	< 0.001
error	4.15	41	0.10		
Total	292.83	44			

Gene sequencing and phylogenetic analysis

Two likelihood methods were employed to create phylogenies for each of the four genes (data not shown). None of the single gene phylogenies showed strong support for the position of *T. thaii*, however seven out of the eight trees group *T. thaii* with *T. currani*, *T. dalmanni* and *T. whitei*. This four species group is robustly supported for the two nuclear protein-encoding genes (BI posterior probability=1.00, ML bootstrap support=100%), but only with weak support in the *16S* and Bayesian *COII* trees.

A concatenated four-gene alignment was constructed and in both the Bayesian and ML phylogenies the four species clade was recovered (see Figure 19). None of the internal branches in the concatenated phylogenies showed strong support (i.e. BI posterior probability ≥ 0.97 , ML bootstrap support $\geq 75\%$) in the species group, however weak support was given for *T. thaii* being the sister-species to *T. dalmanni* + *T. whitei*.

Comments

Morphologically the genitalia of the four species are very similar and there are small differences to separate them. Based on the shape of the different parts the species can be aligned in a row of gradual change. Accord-

ing to the shape in ventral view: *T. thaii* – *T. currani* – *T. whitei* – *T. dalmanni* from the narrowest to the broadest epandrium compared to the width of the hypandrium (Figs 4, 8, 12, 16). According to the shape of the aedeagal apodeme: *T. thaii* – *T. currani* – *T. dalmanni* – *T. whitei* from the longest and narrowest to the most curved and broadest (Figs 2, 6, 10, 14). According to the shape of the surstylus: *T. whitei* – *T. currani* – *T. thaii* – *T. dalmanni* from the narrowest to the broadest (Figs 2, 6, 10, 14). It is not known whether these characters contain phylogenetic information, only a detailed morphological study of features in numerous populations would allow us to draw the conclusions.

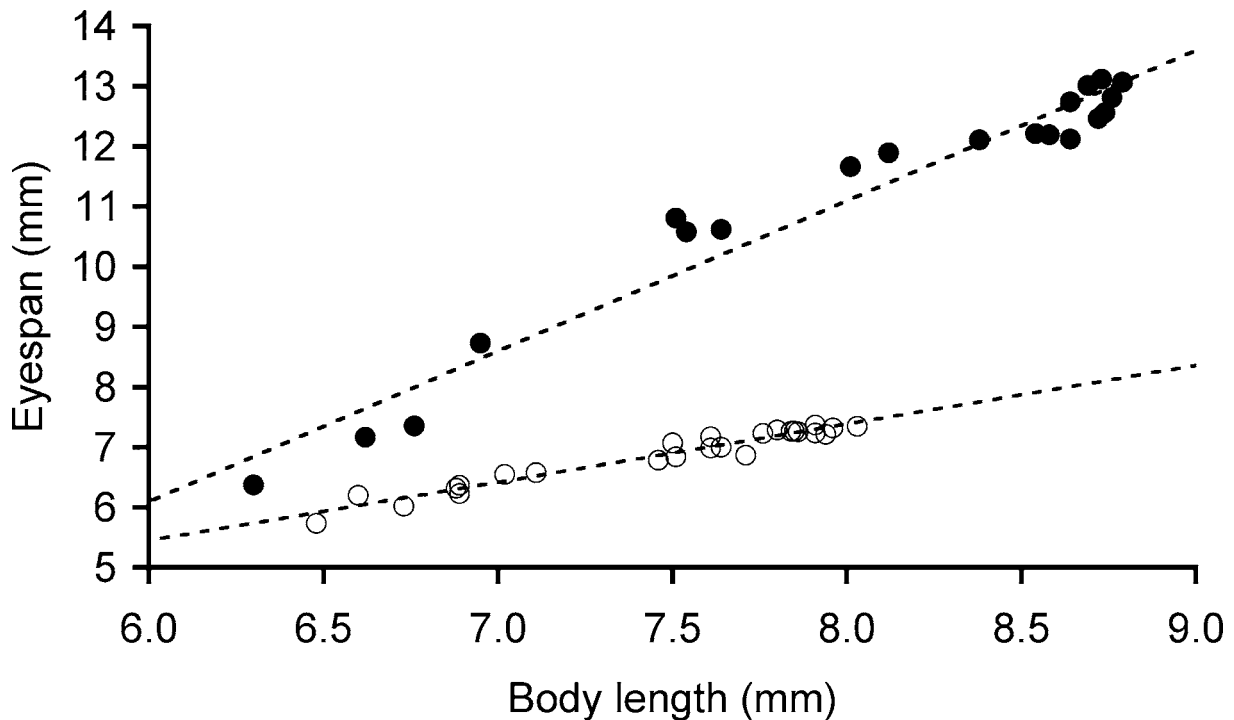


FIGURE 18. Eyespan allometry in *T. thaii*. Males = closed circles, females = open circles. Least-squares regression lines are given for heuristic purposes.

Genetic data gave different results, since partial sequences from four genes, analysed as individual and concatenated alignments, failed to confidently place *T. thaii* within the *Teleopsis* genus. A consistent result in the phylogenies produced was a clade made up of *T. currani*, *T. dalmanni*, *T. thaii* and *T. whitei*. We have termed this clade the dalmanni species group (named after the first species in the group to be described).

The concatenated dataset weakly place *T. thaii* as the outgroup to *T. dalmanni* and *T. whitei*. Within all of the trees the dalmanni species group shows short internal branches and long terminal branches suggesting, irrespective of the branching order, all species in the group diverged rapidly.

There are a number of possible, not mutually exclusive, explanations for the lack of resolution within the species group. A rapid radiation of the four species is likely to have produced little phylogenetic signal and any trace of this signal may have been swamped by mutations that have occurred on the long terminal branches. It is also possible that ancestral polymorphisms may have segregated unevenly amongst the lineages resulting in a “noisy” phylogeny. A third explanation could be limited gene flow between the four closely related species, which could produce the incongruencies observed between the different gene phylogenies. Given the apparent rapid radiation of the dalmanni species group, highlighted by the four genes sequenced here, it may not be possible to robustly determine the phylogenetic position of *T. thaii* without the sequencing of a large number of informative genes in all four member species.

T. thaii are, on average, larger than the other *Teleopsis* species presented here for both eyespan and body length. Such differences do not result from simple changes in scale, as eyespan in *T. thaii* also has a much

steeper male (but not female) allometric slope and hence shows much greater sexual dimorphism than those of other members of the dalmanni species group. It is likely that such morphological differences have resulted from current or past episodes of sexual selection for increased male eyespan, as all sexually-selected diopsids studied thus far exhibit an elevated male eye span allometry (Burkhardt & de la Motte 1985; Wilkinson & Dodson 1997; Baker & Wilkinson 2001; Cotton *et al.* 2006). However, without additional experiments this hypothesis cannot be tested.

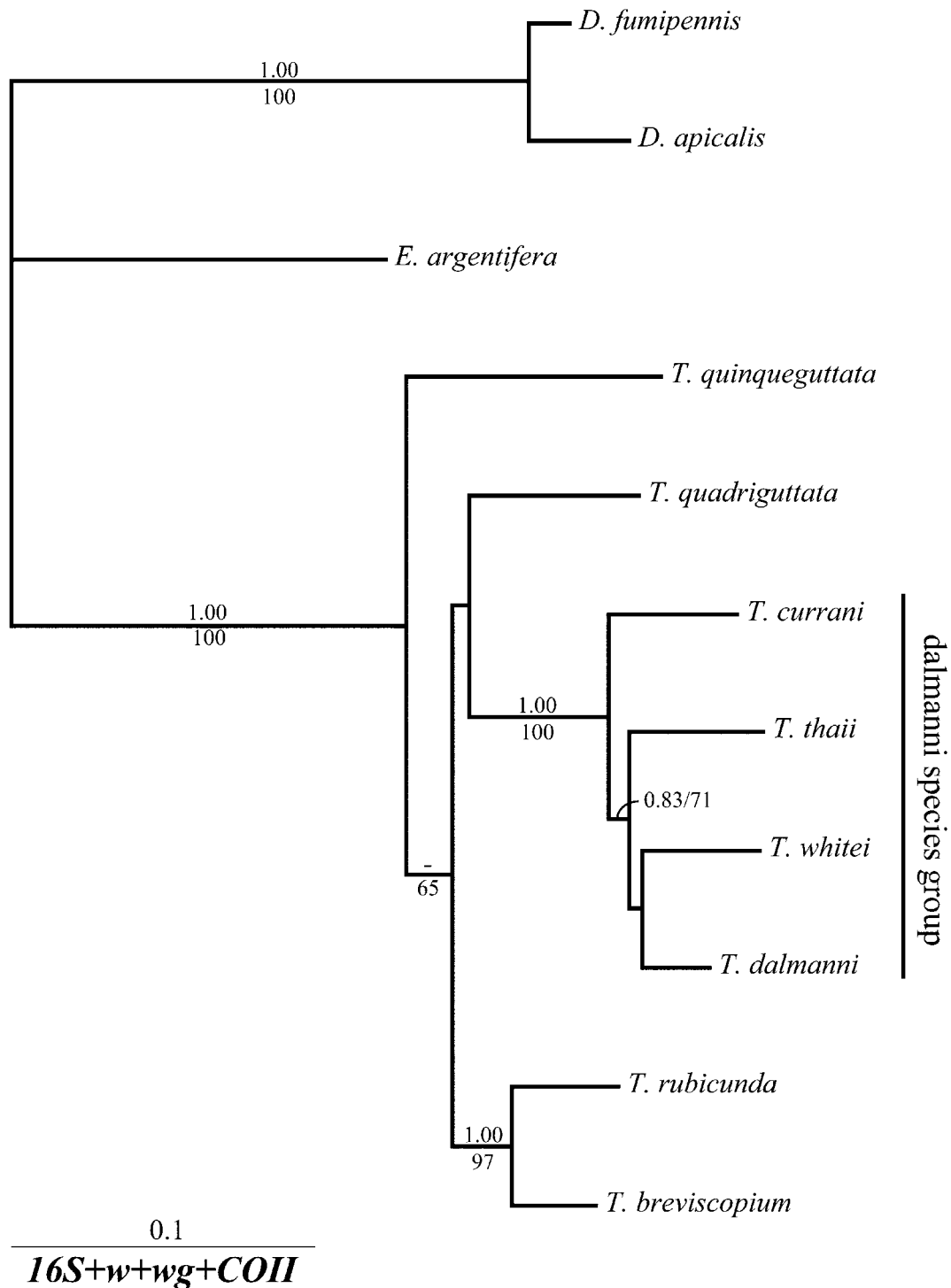


FIGURE 19. Bayesian phylogeny of the *Teleopsis* genus created using $16S+w+wg+COII$. Bayes Posterior Probabilities and Maximum Likelihood Bootstrap Support values are given above and below each branch respectively. Unsupported branches are unlabeled, Posterior Probabilities values below 0.70 and Bootstrap Support values below 50% are represented by “-”. The bar represents the number of nucleotide substitutions per site.

Male eyespan allometry and sexual dimorphism in *T. thaii* is not as pronounced as that reported for its congener, *T. breviscopium*. However, given that *T. thaii* and *T. breviscopium* are quite distantly related within the *Teleopsis* genus, the most parsimonious explanation for the existence of the large eyespan seen in *T. thaii* is that of independent evolution. The alternative hypothesis, that the large eyespans seen in these species are the result of a single evolutionary event in a common ancestor, is unlikely, as it requires a large number of reductions in eyespan size, scaling relationships and sexual dimorphism across the rest of the *Teleopsis* phylogeny.

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