

## REVISION OF THE SOUTHEAST ASIAN SILKY LACEWING GENUS *BALMES* (NEUROPTERA: PSYCHOPSIDAE)

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The southeast Asian psychopsid genus *Balmes* is comprehensively revised for the first time. Four species are recognized: *birmanus*, *formosus*, *notabilis*, and *terissinus*. Each species is redescribed, illustrated, and keyed. *Balmes notabilis* is removed from the synonymy of *birmanus* and re-established as a valid species. The four species are phylogenetically (cladistically) related as follows: (*formosus* + (*terissinus* + (*notabilis* + *birmanus*))).

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The family Psychopsidae, silky lacewings, is a monophyletic (=holophyletic) clade containing five genera and 26 extant species (Oswald 1993). The distribution of extant psychopsids is relictual, being restricted to southern Africa, Australia, and southeast Asia. Fossil taxa attributed to this family are currently known from North America, Europe, Asia, and Australia. Psychopsids are of special interest because of their highly disjunct present geographic distribution, their unusual female ovipositional habits, and their phylogenetic position as the basalmost clade of the neuropterous superfamily Myrmeleontoidea, i.e., as the sister-group to the Nymphidae + Nemopteridae + Myrmeleontidae + Ascalaphidae (Mansell 1992; Oswald, unpublished data).

Since the publication of my earlier monograph of this family (Oswald 1993), I have had the opportunity to examine additional material of the little-known Oriental genus *Balmes* Navás. The recent taxonomic history of this genus can be summarized as follows. Kimmins (1939) recognized three *Balmes* species: *birmanus* (as '*birmanus*' [sic], with *terissinus* and *notabilis* as synonyms), *formosus* (as '*formosus*' [sic]), and *gallardi*. New ([1989]) demoted *Balmes* to a junior subjective synonym of the otherwise Australian endemic genus *Psychopsis*, and treated *birmanus*, *formosus*, and *gallardi* as valid species of *Psychopsis*. Oswald (1993) (1) re-erected the genus *Balmes* on the basis of evidence supporting its monophyly and the existence of a sister-group relationship between *Balmes* and *Psychopsis*, (2) established the va-

lidity of *B. terissinus* and removed it from the synonymy of *birmanus*, and (3) noted the existence of a fourth, at that time apparently undescribed, *Balmes* species in China (the 'bns1' of Oswald 1993).

The species 'bns1' has since proven to be conspecific with *notabilis*, which is herein recognized as a valid species and removed from synonymy with *birmanus*. Thus, four valid species of *Balmes* are treated here: *B. birmanus* (McLachlan), *B. formosus* (Kuwayama), *B. notabilis* Navás and *B. terissinus* Navás. The current revision contains redescrptions and illustrations of each species, a key to distinguish among the species, and a phylogenetic (cladistic) analysis of interspecific relationships within *Balmes*. The latter extends the prior analysis of Oswald (1993) through the incorporation of new data for the Taiwanese species *B. formosus*.

### MATERIALS AND METHODS

Material and collection acronyms. – This study is based upon approximately 40 adult *Balmes* specimens in the following collections: BMNH, The Natural History Museum, London, England; CUIC, Cornell University Insect Collection, Ithaca, NY, U.S.A.; EIHU, Insect Collection, Hokkaido University, Sapporo, Japan; MCZC, Museum of Comparative Zoology, Cambridge, MA, U.S.A.; MNHP, Muséum National d'Histoire Naturelle, Paris, France; USNM, National Museum of Natural History, Washington, DC, U.S.A.



**Illustrations.** – Line drawings were executed with the aid of a drawing tube attached to a dissecting microscope. Terminalic illustrations were made from cleared, and generally stained, preparations temporarily mounted in glycerin. Setae are not shown. In illustrations of the gonarcus/mediuncus/9th gonocoxite complex, membranes attached along the antextragonarcal commissure and the venter of the 9th gonocoxites are shown stretched in a manner calculated to best convey their lines of attachment, not necessarily as *in situ*.

**Terminology.** – General entomological terminology follows Nichols (1989). Terms for terminalic structures follow Oswald (1993).

**Annotations.** – The following annotations are used in the synonymical listings: Dst, distribution; FT, female terminalia; FW, forewing; H, habitus; Lst, list or listed; MT, male terminalia; Nom, nomenclature; OD, original publication/description; RD, redescription; Tax, taxonomy; W, wing. An asterisk (\*) following an annotation indicates a figure (e.g., FW\*, forewing figure).

**Miscellaneous.** – Species are treated in alphabetical order. Forewing lengths were measured from the proximal margin of the tegula to the wing apex ( $\pm 1$  mm). Unless otherwise cited, reported flight periods

are the earliest and latest dates of collection of adults as indicated by label data. Bracketed collection locality names and latitude and longitude coordinates found in the material examined sections have been taken principally from the Official Standard Names Gazetteers of individual southeast Asian countries, which were compiled by the U.S. Defense Mapping Agency Topographic Center for the U.S. Board on Geographic Names.

## SYSTEMATIC PART

### Genus *Balmes* Navás

*Balmes* Navás, 1910: 85 (Type species: *Balmes terissinus* Navás, 1910: 85, by monotypy): Navás 1917 (Tax); Kimmins 1939 (Tax); New [1989] (Nom); Oswald 1993 (RD, Tax).

**Diagnosis.** – The only extant genus of psychopids known from southeastern Asia. Distinguished from the Australian genus *Psychopsis* (except *P. gallardi*) by the absence in *Balmes* of a prominent dark macula situated distally on each hind wing (fig. 3). Based on illustrations contained in New ([1989]), males of *P.*

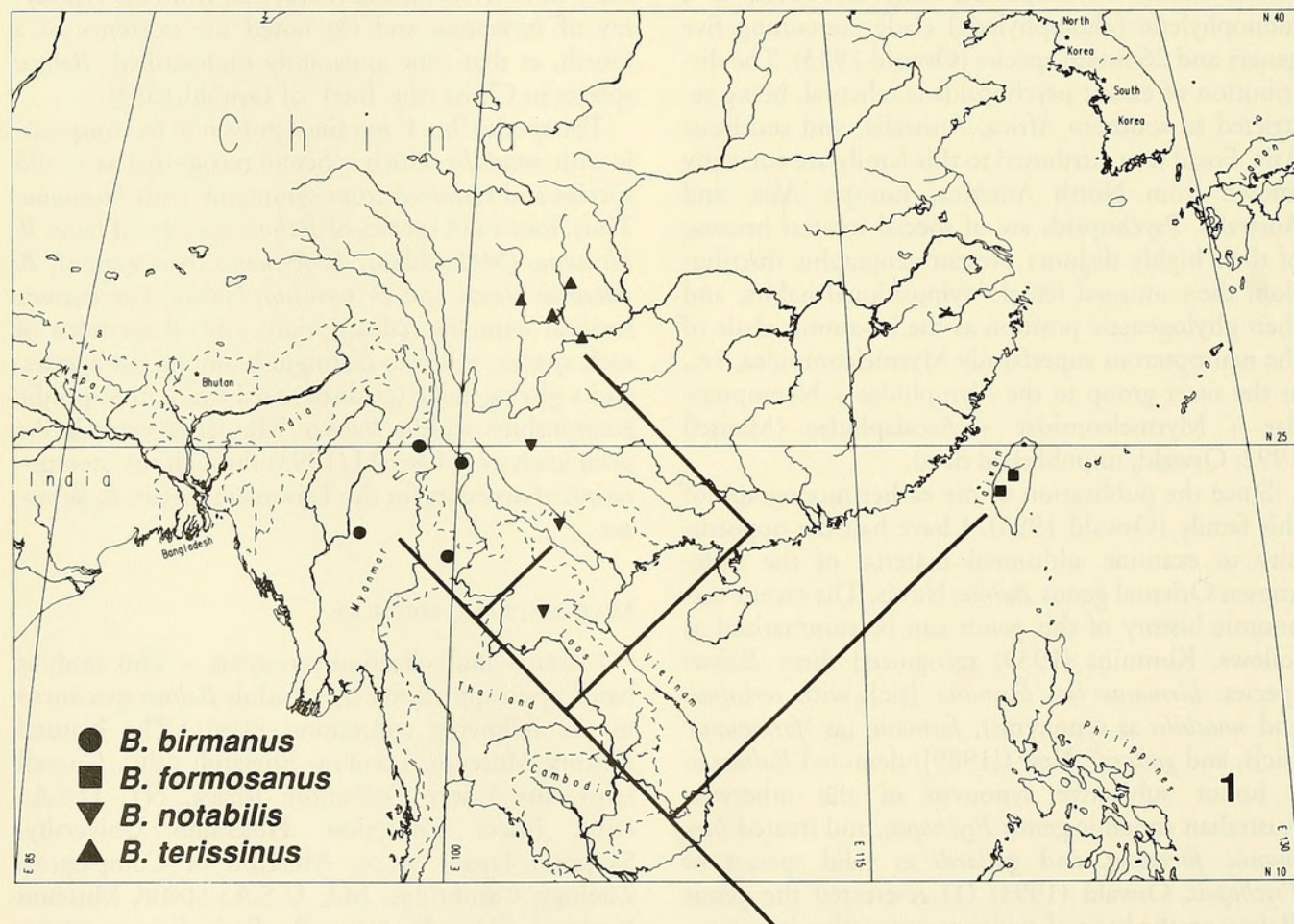


Fig. 1. Geographic distributions of *Balmes* species and cladogram of interspecific relationships. Only accurately located records have been plotted.



*gallardi* (unique holotype in BMNH, not examined) may be distinguished from males of *Balmes* species by (1) the presence in *gallardi* of an elongate [not short] 9th gonocoxite costa, and (2) the absence in *gallardi* of the male 9th gonocoxite superprocesses modified into a transverse tumulus.

Description. – Head: Ocelli absent, but vertex bearing 2 well-developed ocellar/cranial pulvinae. Forewing: length: 10.8 - ca. 21 mm; coloration: brown mottling on a hyaline ground; forewing costal gradate series absent or reduced (i.e., <6 crossveins), except in *formosus* where it is well developed (>20 crossveins).

Hind wing: hyaline, without a dark distal macula.

Male terminalia: 8th sternite (fig. 6): without a posteromedian lobe; 9th tergite (fig. 6): without free posteroventral processes; 9th sternite (figs. 6, 7): apex rounded (fig. 7) or emarginate (fig. 13), not narrow and parallel-sided in ventral view; gonarcus (figs. 9, 10): intragonarcus present but narrow relative to extragonarcus; extragonarcus composed of a posteriorly protruded dorsal plate, the extragonopons (egps), and a pair of lateral narrow to broad extrahemigonarcus (ehgs); mediuncus (med) weakly decurved, not recurved; 9th gonocoxites (figs. 10, 11): fused medially into a transverse sclerite which articulates with posteroventral angles of hemigonarcus; ventral costae (vc) absent or reduced to short thickenings; superprocesses (spp) present but fused into a transverse elevation on dorsal surface of conjoined gonocoxites (elevation produced as an attenuate process in *notabilis*); ventrolateral lobes (vll) sometimes present; miscellaneous: gonosaccal membrane bearing one (fig. 8) or two (figs. 21, 22) sets of bilaterally paired spiculate lobes; subanale (sa) present (figs. 9, 10).

Female terminalia: Posterior margin of 7th sternite medially depressed and emarginate (figs. 26, 27); 7th and 8th sternites fused, but path of fusion marked by a suture; copulatory fovea approximately hemispherical, overhung posteriorly by anteromedian margin of 8th sternite (figs. 26, 27); 9th gonocoxites: without a longitudinal row of stiff setae below each gonocoxal costa, without a compact aggregation of setae borne adjacent to insertion of stylus, suprastylar setae >50% cochleariform; bursa without lateral corniform diverticulae; spermatheca sigmoid in lateral view, lacking distinct hollow ventrolateral lobes; two bursal accessory glands present, but form and insertion of ducts on bursa varies interspecifically.

Distribution (fig. 1). – Southeast Asia (reported here from Taiwan, southern China, northeastern Burma, northern Laos, and northern Vietnam). The three southeast Asian species of *Balmes* appear to form a complex of allopatric or parapatric species. The few elevation records available for *Balmes* species (all for mainland species) range between 600 and 1825 me-

ters, suggesting that *Balmes* species are montane. This conclusion is also supported by the apparent geographic restriction of mainland *Balmes* species to the upland areas of the countries in which they occur.

Biology and immature stages. – Unknown.

Species (4). – *birmanus*: Burma, China [Yunnan Prov.]; *formosus*: Taiwan; *notabilis*: China [Yunnan Prov.], Laos, Vietnam; *terissinus*: China [Sichuan Prov.].

Classification. – The following sequenced classification is recommended for this genus:

Genus *Balmes* Navás

*B. formosus* (Kuwayama, 1927)

*B. terissinus* Navás, 1910

*B. notabilis* Navás, 1912

*B. birmanus* (McLachlan, 1891)

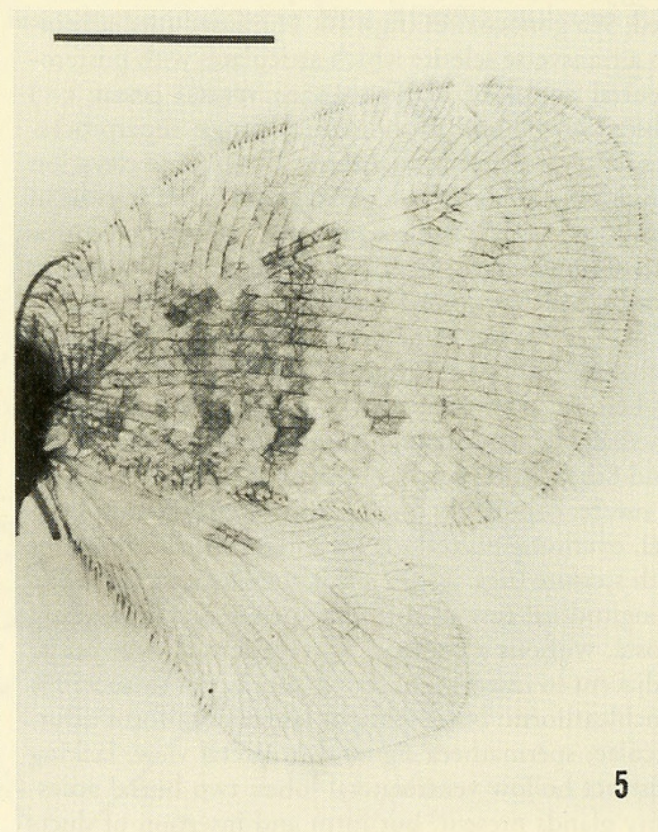
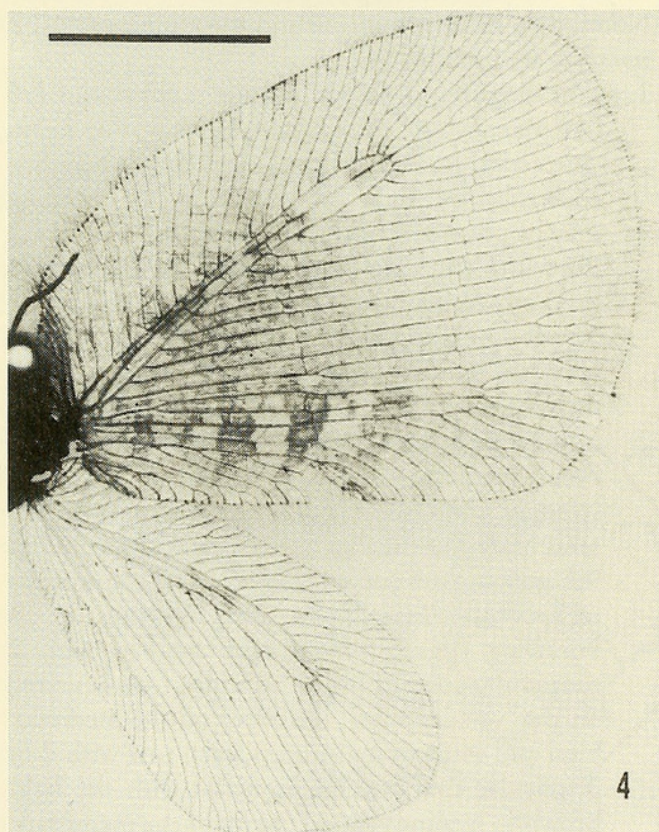
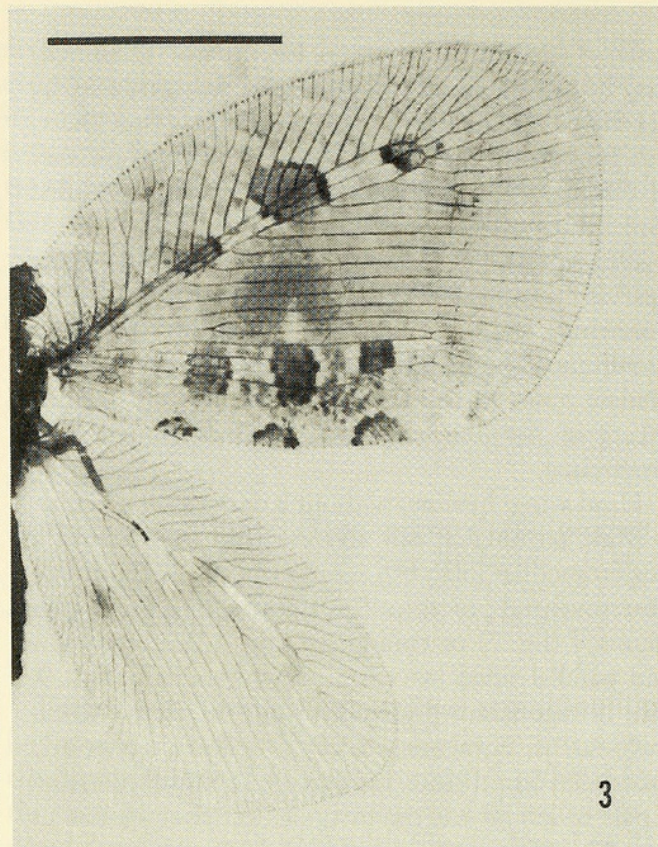
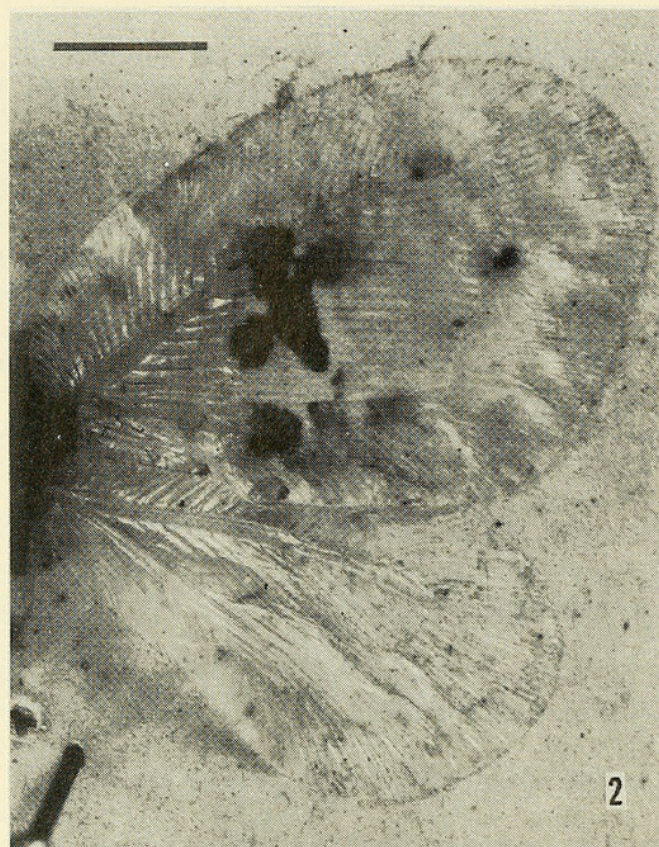
Etymology. – From the surname of Catalan philosopher Jaime Luciano Balmes [1810-1848], see Navás 1910: 85. Gender: Masculine, implied from the original combination *Balmes terissinus*, Art. 30d.

### Key to adult *Balmes* species

Notes: The male of *formosus* and the female of *notabilis* are unknown.

1. Forewing (fig. 3): costal gradate series absent (<6 crossveins/wing), intraradial area crossed by 2 gradate series, innermost series not bordered by fuscous maculae (light brown shading or mottling may be present) [continental southeast Asia].....2
  - Forewing (fig. 2); costal gradate series present (>20 crossveins/wing), intraradial area crossed by 3 well-developed gradate series, innermost series bordered by fuscous maculae [Taiwan and continental southeast Asia] .....*B. formosus*
2. Forewing (figs. 4, 5): membrane immaculate or evenly patterned with light brown mottling, strongly contrasting darker brown maculae absent; Male Terminalia: ventrolateral lobes of male 9th gonocoxites present (figs. 11, 18) [continental southeast Asia] ..... 3
  - Forewing (fig. 3): membrane marked with 2 prominent rows of brown maculae (one centered on the 'vena triplica', the other on the mediocubital and intracubital spaces), each row with 2 or 3 maculae that strongly contrast with the light brown to hyaline ground colour of the membrane (fig. 3); hind margin of wing also often with a row of contrasting maculae; Male Terminalia: ventrolateral lobes of male 9th gonocoxites absent (figs. 24, 25) [China: Sichuan Province] .....  
..... *B. terissinus*
3. Male 9th sternite: apex rounded (fig. 7); Male 9th gonocoxites: ventrolateral lobes digitate and bluntly pointed distally, apices not membrane





Figs. 2-5. *Balmes* spp., wings. 2, *B. formosus* (paratype); 3, *B. terissinus*; 4, *B. notabilis*; 5, *B. birmanus*. Scale bars = 5 mm.

margined (fig. 11); superprocesses fused into a broad transverse prominence (fig. 11) [Burma, China: Yunnan Province] ..... *B. birmanus*

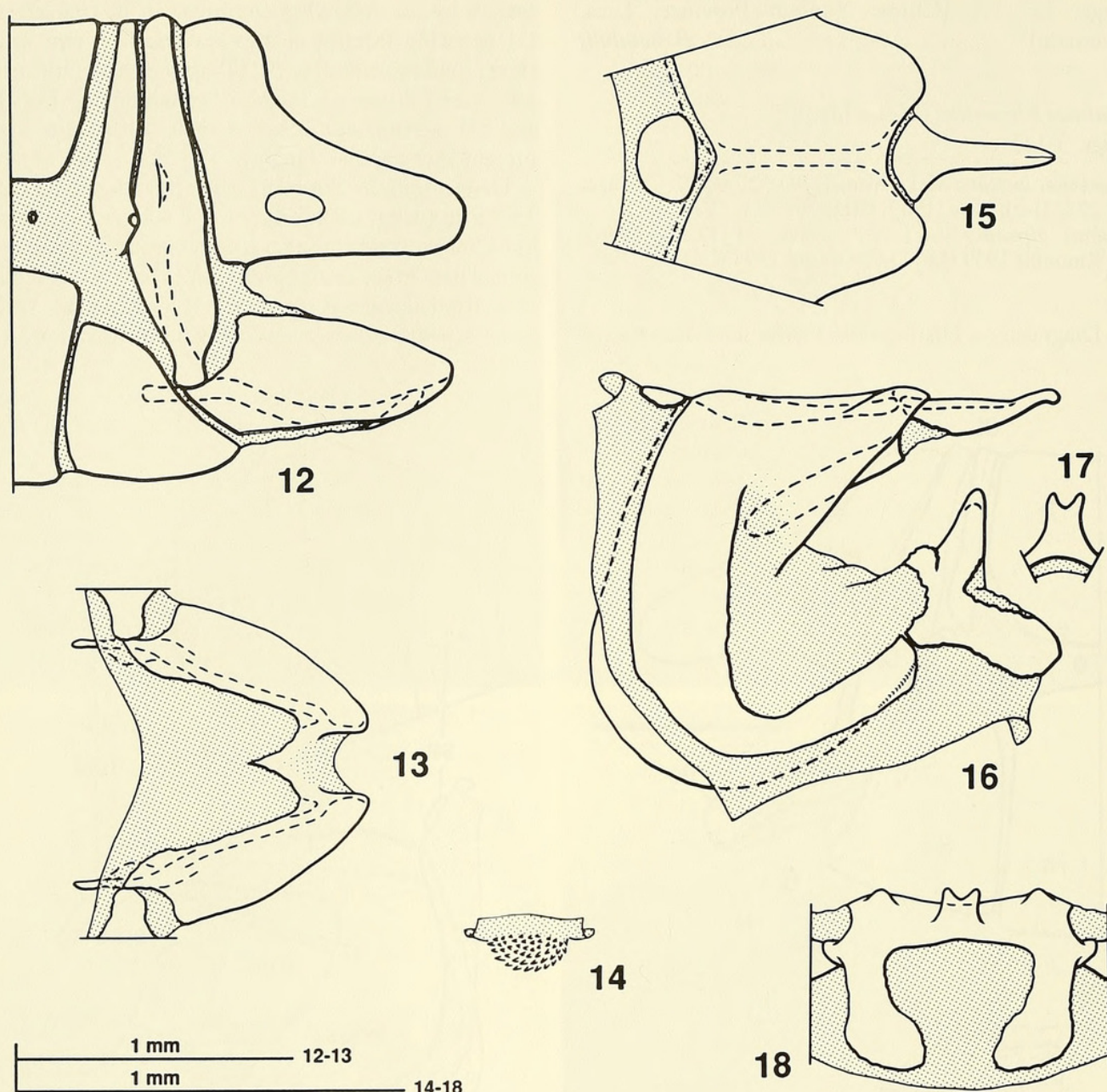
– Male 9th sternite: apex conspicuously emarginate

(fig. 13); Male 9th gonocoxites: ventrolateral lobes plate like and broadly rounded distally, apices membrane margined (fig. 18); superprocesses fused and projecting medially as a short process









Figs. 12-18. *Balmes notabilis*, male terminalia. 12, abdominal apex, lateral; 13, 9th sternite, ventral; 14, ventral spiculate lobe of gonosaccus, lateral; 15, medial portion of gonarcus, dorsal; 16, gonarcus / 9th gonocoxite complex, lateral; 17, medial process of 9th gonocoxites, posterior; 18, fused 9th gonocoxites, posterodorsal.

(these lacking or inconspicuous in rubbed wings); costal gradate series absent (1-2 adventitious costal crossveins occasionally present); intraradial area traversed by two gradate series.

Male terminalia (figs. 6-11): 9th sternite: posterior margin rounded, not sagittally emarginate; gonarcus: intragonarcus narrow dorsally, broadened toward anteroventral angles, anterior and ventral margins marked internally by thickened costae; extrahemigonarcus broad; midline and posterior margin of extragonopons marked by a T-shaped costa internally, posterior margin transverse; mediuncus: length approximately twice average width, slightly constricted basally; apex rounded or obtusely angulate with a nar-

row sagittal emargination; 9th gonocoxites: superprocesses united sagittally to form a low transverse elevation; elevation bilobed in posterior view due to a shallow median emargination; ventrolateral lobes present as a pair of free, attenuated, and medially convergent lobes; spiculate gonosaccal lobes: one pair present on ventral surface of bursa.

Female terminalia: 7th sternite: parafoveal lobes weakly developed, not prominently projecting; 8th sternite: reduced, transverse, expanded medially, attenuate laterally, anterior margin not emarginate sagittally; bursal accessory gland ducts: fused proximally, attached to sagittodorsal surface of bursa as a single common duct.



Distribution (fig. 1). – Mainland southeast Asia (reported here from northeastern Burma and the adjacent portions of Yunnan Province, China).

Flight period. – 14 March - April (no day recorded).

Primary type. – *Psychopsis birmana*. Holotype ♀ (BMNH), examined. Type locality: 'Birmah' [=BURMA, precise locality unknown]. Verbatim label data: 'Type.' [pink rectangle], 'Type' [white circle with red border], 'Birmah' [script, white rectangle], 'McLachlan Coll. / B.M. 1938-674' [blue rectangle], 'Psychopsis / birmana ML.' [McLachlan script, white rectangle], 'Holotype / Psychopsis / birmana det. / J.D. Oswald 1994' [red rectangle]. Condition: parts of the following missing – both antennae, left fore- and hind legs and right foreleg. Minor insect pest damage. Pinned through thorax, wings spread. Terminalia macerated in KOH by Oswald in 1994, stained with Chlorazol Black, and placed in a glycerin-filled microvial pinned below specimen. This is the single specimen upon which the description of *birmana* was based (McLachlan 1891: 321).

Other material examined (6♂, 3♀ = 9). – BURMA: *Mandalay division*: 1♂, 2♀, Maymyo [22°02'N 96°28'E], iv.1912, Mackwood; 14.iii.[19]01, Barrow; no date, Scott (BMNH). *Shan state*: 2♂, Kolaw, S. Shan States, iv.1916, 1215m (4000'), Mackwood (BMNH); 1♀, Loimwe [Loi Mwe, 21°11'N 99°46'E], iv, 1520-1825m (5000-6000'), Kingford (MCZC). CHINA: *Yunnan province*: 1♂, bet[ween]. Tengyueh [=Tengchong, 25°02'N 98°28'E] and Nan Tien, '1909-10', Brown (CUIC); 2♂, Yun Hsien [=Yunxian, 24°25'N 100°06'E], iv.1942, Jellison (USNM).

Etymology. – Unexplained, probably derived from the type locality 'Birmah' [=Burma].

***Balmes formosus*** (Kuwayama)  
(figs. 2, 27)

*Psychopsis* (*Orientichopsis*) *formosa* Kuwayama, 1927: 123 (OD, H\*).

*Balmes formosana* [sic]. – Kimmins 1939 (Lst, Dst).

*Psychopsis formosa*. – New [1989] (RD, Dst, FT\*, W\*).

*Balmes formosa* [sic]. – Oswald 1993 (Lst).

Diagnosis. – Distinguished from all other *Balmes* species by the presence of three [not two] gradate series traversing the intraradial area of the forewing (fig. 2).

Description. – Forewing (fig. 2): length: ca. 21 mm (n = 1 wing); markings: predominantly hyaline, center of disk with two fuscous maculae, one (proximal) nearly circular and one (distal) elongate and continued anteriorly across 'vena triplica', an additional small fuscous dot in middle of intraradial space just beyond middle gradate series, also with scattered pal-

er brown markings, particularly along cubital and mediocubital spaces; costal gradate series with more than 20 crossveins; intraradial area traversed by three gradate series.

Male: Unknown.

Female terminalia (fig. 27): 7th sternite: parafoveal lobes strongly developed, prominently projecting; 8th sternite: a small cordate plate, anterior margin sagittally emarginate; bursal accessory gland ducts: two free ducts inserted bilaterally symmetrically on dorsal surface of bursa at a pair of widely separated (more than two duct diameters) points.

Distribution (fig. 1). – Taiwan.

Flight period. – August.

Primary type. – Holotype ♀ [not ♂] (EIHU), not examined. Type locality: TAIWAN: 'Rengechi, near Horisha, Taichiu-district, Formosa' [Horisha = TAIWAN: *Nan-t'ou hsien*: Pu-li, 23°58'N 120°57'E].

Material examined (1♀ paratype). – TAIWAN: *Chia-i hsien*: 1♀, 'Kagi' [=Chia-i, 23°29'N 120°27'E], viii.1921, Hirayama (EIHU).

Etymology. – Unexplained, probably derived either from Latin *formosus*, beautiful, or the island name Formosa (=Taiwan). Name incorrectly treated by Oswald (1993) as a noun in apposition, based on the island name Formosa. Since 'formosa' is a valid Latin adjective, the termination of a species-group name based on this word must match the gender of the genus-group name with which it is combined, Art. 31b.

Comments. – *Balmes formosus* is known only from the two females (not males as stated by Kuwayama) of the type series.

***Balmes notabilis*** Navás, **stat. n.**  
(figs. 4, 12-18)

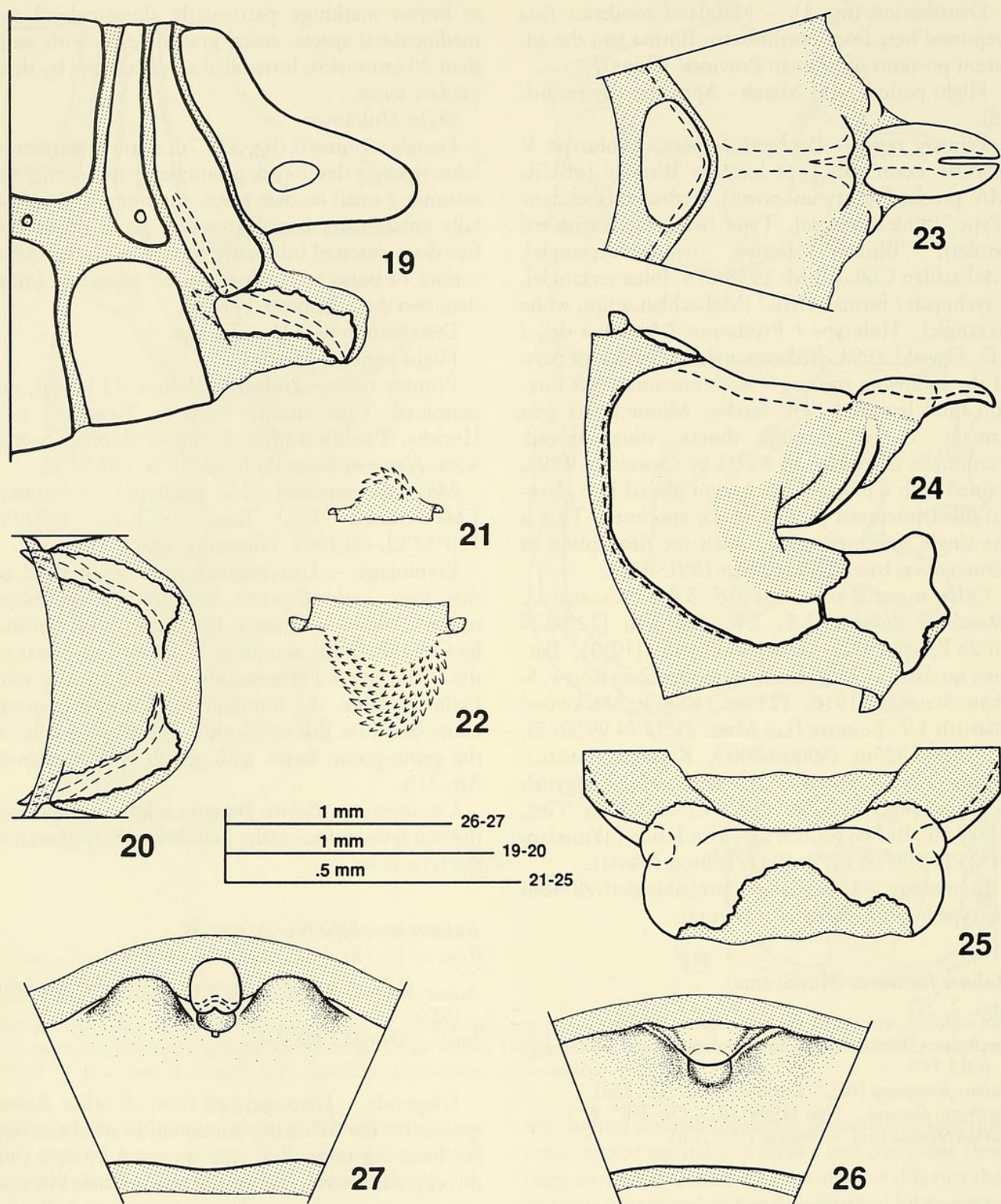
*Balmes notabilis* Navás, 1912: 197 (OD). – Navás 1917 (RD).

'bns1'. – Oswald 1993 (Lst).

Diagnosis. – Distinguished from all other *Balmes* species by the following combination of characters: (1) forewing intraradial area traversed by two [not three] gradate series (fig. 4), (2) apex of male 9th sternite conspicuously emarginate [not rounded] (fig. 13).

Description. – Forewing (fig. 4): length 12.5 - 14.0 mm (mean = 13.2 mm, n = 4 wings); markings: very similar to *birmanus*, light brown mottling on a hyaline ground, markings somewhat darker along 'vena triplica' and along cubital and mediocubital spaces, hyaline-bounded brown patches of distal margin (see *birmanus* description) obscure to absent; costal gradate series absent; intraradial area traversed by two gradate series.





Figs. 19-27. *Balmes terissinus*, male terminalia. 19, abdominal apex, lateral; 20, 9th sternite, ventral; 21, dorsal spiculate lobe of gonosaccus, lateral; 22, ventral spiculate lobe of gonosaccus, lateral; 23, medial portion of gonarcus, dorsal; 24, gonarcus / 9th gonocoxite complex, lateral; 25, fused 9th gonocoxites, posterodorsal. 26-27, *Balmes* spp., female 7th (medial portion) and 8th sternites, ventral. 26, *B. terissinus*, 27, *B. formosus*.

Male terminalia (figs. 12-18): 9th sternite: posterior margin prominently emarginate medially; gonarcus: intragonarcus narrow throughout, broadest at anteroventral angle; extragonopons with a strong sagittal costa internally, posterior margin with a pair of

rounded lobes divided by a broad medial excavation; extrahemigonarcus composed of a broad proximal region and a narrower distal region, the two regions being continuous anteroventrally but separated distal to this region by an approximately 60° angle in the pos-



terior margin of the hemigonarcus; mediuncus: apical 2/3 to 3/4 slender and nearly parallel sided, base flared and broader; apex bifid (condition usually not obvious because paired apical lobes usually lie parallel with their medial margins adpressed); 9th gonocoxites: superprocesses united and produced medially to form a short digitate process; apex of process distinctly forked (as shown in fig. 17) to only slightly emarginate; anterior margin of transverse gonocoxal bar lateral to median process usually with a pair of low, setose, convexities; ventrolateral lobes present as a pair of shallowly concavo-convex, membrane-margined, spathulate lobes; spiculate gonosaccal lobes: one pair present on ventral surface of bursa.

Female: Unknown.

Distribution (fig. 1). – Mainland southeast Asia (reported here from southern China [Yunnan Province], northern Laos and northern Vietnam).

Flight period. – 22 April - 2 June.

Primary type. – Lectotype ♂ (BMNH), designated by New ([1989]) by inference of holotype, examined. Type locality: PEOPLE'S REPUBLIC OF CHINA: probably Yunnan Province, see discussion below. Verbatim label data: 'Type' [white circle with red border], 'mamun[?], yuman [=? Yunnan] / H. E. Hobson / 1900-192' [white rectangle, text in somewhat illegible script], '*Balmes* / *notabilis* / Nav[ás].' [blue-lined white notebook paper, rectangle with corners clipped, in Navás' (?) script], 'Lectotype / *Balmes* / *notabilis* det. / J.D. Oswald 1994' [red rectangle]. Condition: parts of left fore- and midlegs and right midleg missing, wings somewhat tattered. Stage mounted, wings spread, probably formerly extracted from alcohol. Terminalia macerated in KOH and placed in a glycerin-filled microvial pinned below specimen.

Navás (1912) cited two specimens in the type series of *notabilis*, one in the British Museum and one in his personal collection. The BMNH specimen cited by New ([1989]:845) as the 'holotype' must, consequently, be considered a lectotype, Art. 74b. The specimen stated to have been in Navás' collection has not been traced. The precise type locality of *notabilis* is uncertain. In the original description Navás cited a single locality, 'China, Junam' (referred to by Navás 1917 as 'China: Yu-nam'), but this site does not match the text of the lectotype's locality label. It is possible that this locality was taken from the unseen specimen retained in Navás' collection. Attempts to identify 'Junam' or 'Yu-nam' in several Chinese gazetteers have failed. In the present work I interpret the word 'yuman' on the lectotype locality label to be a variant or erroneous spelling of 'Yunnan', in reference to the Chinese province of Yunnan, where *notabilis* has been confirmed to occur. The significance of the word 'mamun[?]' is unknown. It could not be traced in the available gazetteers.

Other material examined (3♂). – CHINA (Mainland): *Yunnan Prov.*: 1♂, Kunming [25°04'N 102°41'E], 2.vi.1941 (USNM). LAOS: *Xieng khouang*: 1♂, Xieng Khouang [19°20'N 103°22'E], 22.iv.1919, Salvaza (BMNH). VIETNAM: *Hoang lien son*: 1♂, 'Chapa' [=Sa Pa, 22°21'N 103°50'E], Tonkin, v.-vi.1916, Salvaza (BMNH).

Etymology. – Unexplained, probably derived from Latin, *notabilis*, noteworthy.

Comments. – Based on its distinctive male terminalia, *B. notabilis* is here recognized as a valid species and is resurrected from the synonymy of *birmanus*, where it was placed by Kimmins (1939) and subsequent authors.

### *Balmes terissinus* Navás

(figs. 3, 19-26)

*Balmes terissinus* Navás, 1910: 85 (OD, FW\*). – Navás 1917 (RD); Oswald 1993 (Lst).

Diagnosis. – Distinguished from all other *Balmes* species by the following combination of characters: (1) forewing intraradial area traversed by two [not three] gradate series (fig. 3), (2) apex of male 9th sternite rounded [not conspicuously emarginate] (fig. 20), and (3) ventrolateral lobes of male 9th gonocoxites absent [not present] (fig. 25).

Description. – Forewing (fig. 3): length 10.8 - 15.7 mm (mean = 13.1 mm, n = 22 wings); markings: pattern similar to *birmanus* with brown mottling on a hyaline ground, but markings along 'vena triplica' and cubital and mediocubital spaces usually strongly contrasting with adjacent membrane, hyaline-bound brown patches of distal margin (see *birmanus* description) obscure to absent; costal gradate series absent (1 or 2 adventitious costal crossveins occasionally present); intraradial area traversed by two gradate series.

Male terminalia (figs. 19-25): 9th sternite: posterior margin rounded, not sagittally emarginate; gonarcus: intragonarcus expressed as a narrow internal costa following course of antextragonarcus commissure; extragonopons not prominently produced, midline marked internally by a thickened costa which divides posteriorly, distomedial margin of extragonopons narrowly emarginate; extrahemigonarcus broad dorsally, tapering toward articulation with 9th gonocoxites; postextragonarcus commissure often poorly defined; mediuncus: length 1 1/2 to 2 times width, nearly parallel-sided proximally, attenuated distally; apex bifid with a narrow but distinct separation between the tines; 9th gonocoxites: superprocesses united sagittally to form a low transverse elevation; ventrolateral lobes absent; spiculate gonosaccal lobes: two pairs present – an inconspicuous pair on dorsal



surface of bursa adjacent to ventral margin of fused 9th gonocoxites, and a second larger pair on ventral surface.

Female terminalia (fig. 26): 7th sternite: parafoveal lobes weakly developed, not prominently projecting; 8th sternite: reduced, transverse, expanded medially, attenuate laterally, anterior margin not emarginate sagittally; bursal accessory gland ducts: two free ducts inserted bilaterally symmetrically on dorsal surface of bursa at a pair of closely adjacent (less than two duct diameters) points.

Distribution (fig. 1). – Mainland southeast Asia (reported here only from Sichuan Province, China [some imprecise records may also refer to far northern Yunnan Province]).

Flight period. – April (no date) - 21 July.

Primary type. – Holotype ♂? (MNHP?), not examined. Type locality: ‘Tibet, Ta-Tsien-lou’ [=CHINA: *Sichuan province*: Lucheng (=Tatsienlu, Tatsientu, Kangting, and Kangding, 30°03’N 102°02’E)].

The presumptive holotype of *terissinus*, stated by Navás to reside in the Paris Museum, was not available for examination. The forewing maculation patterns of the material attributed here to this species closely match the maculation pattern shown in Navás’ (1910:86, fig. 24) figure of the forewing of *terissinus*. Particularly apparent are: (1) the strong contrast between the wing’s dark macula and its light ground colour, and (2) the well-developed row of macula along the hind margin of the forewing. The identification of this material is also supported by distributional evidence. All of the specimens attributed here to *terissinus* were collected in China in either Sichuan province or, possibly for some specimens, far north-

ern Yunnan province. The combined distribution of this material and the type locality of *terissinus* (from Sichuan province) form a compact range which is allopatric relative to the ranges of other *Balmes* species.

Material examined (18♂, 3♀, 5?). – CHINA: *Sichuan* [=Szechwan] *province*: 1?, Suifu [=Yibin, 28°46’N 104°34’E], 30.v.1925, 610m (2000’), Graham (MCZC); 17♂, 4?, Yunnan border S of Suifu, iv.[19]29, Graham (MCZC, USNM); 1♀, Chengtu [=Chengdu, 30°40’N 104°04’E], 21.v.1929, Parish? (CUIC); 1♂, 1♀, Chengtu, v.1934, Graham (MCZC, USNM); 1♀, Mt. Omei [=Emei Shan, 29°32’N 103°21’E], 21.vii.[19]35, 1215m (4000’), Graham (USNM).

Etymology. – Derived from the surname of J. Terisse, collector of the holotype (see Navás 1910:85).

### PHYLOGENETIC ANALYSIS

Overview. – A cladistic analysis was used to estimate relative interspecific relationships within the genus *Balmes* and the position of *Balmes* within the family Psychopsidae.

Computational methods. – Cladograms were generated by application of the ‘ie’ (implicit enumeration) tree calculation option of HENNIG86 (Farris 1988) to the input data file described under *Data* below. The ‘ie’ tree calculation option guarantees identification of the minimal length tree(s) for a given input matrix.

Characters. – The characters and character states used in the present analysis are identical to those used in the earlier analysis of Oswald (1993), except for the addition of a fifth state to character 44, see below. See Oswald (1993) for detailed definitions and discussions of characters and their states.

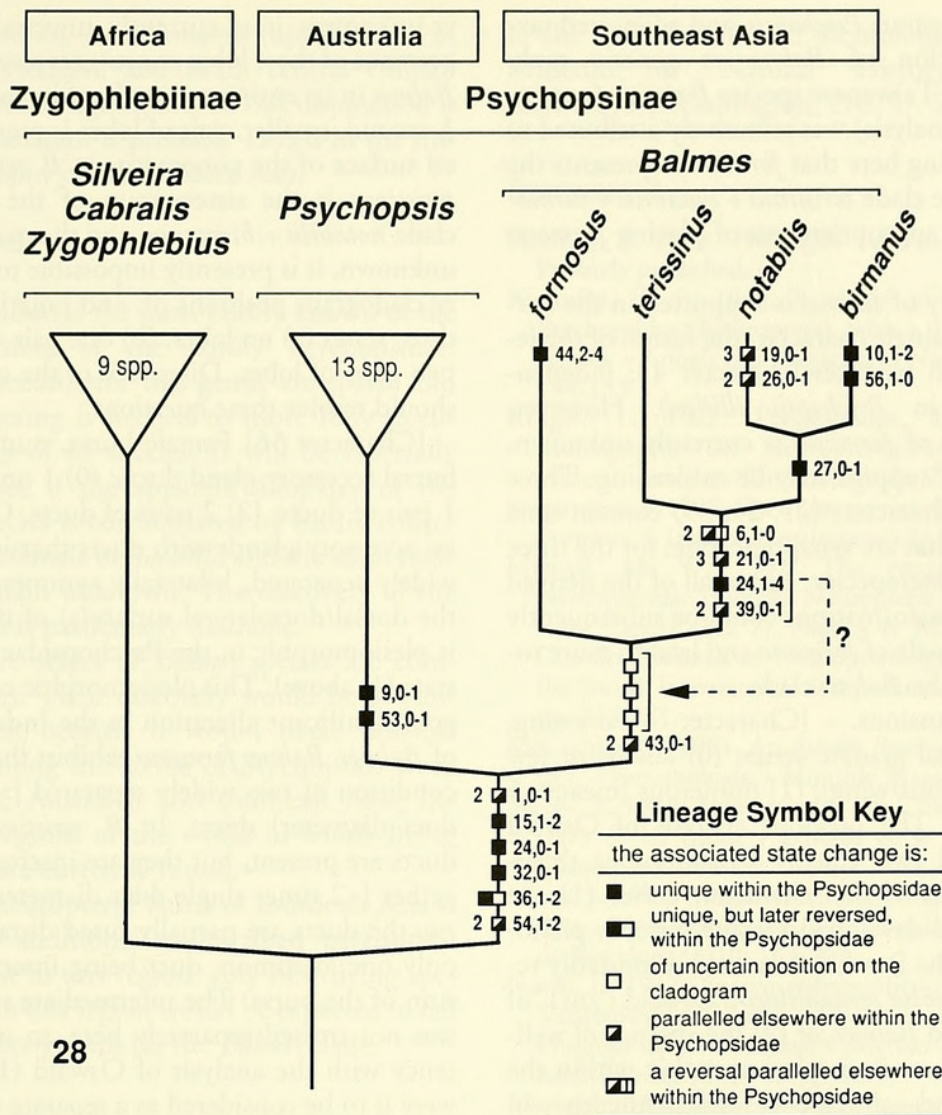
Character 44. Female 8th sternite. (state 4 [new state]) present, a small cordate plate, emarginate anteromedially. Oswald (1993) attributed four unordered states to this character. Because the female 8th sternite state found in *formosus* does not fit well into any of those states, the preceding state is added here to accommodate *formosus* into the present analysis. This state is an autapomorphy of *formosus*.

Data. – The input data matrix contained numerically-coded morphological character data derived from: (1) Oswald (1993: Appendix 2), for 21 previously character-scored psychopsid species and the hypothetical ancestor used to root the tree, and (2) a row of newly coded data (Table 1) for *B. formosus*. Characters 10-39 in table 1 pertain to the unknown male of *formosus* and were coded as unknown data (?). The following two additional *formosus* characters were coded as unknown: [1] Shape of forewing humeral plate (character 7) – the humeral plates of the

Table 1. Coded character state data for *Balmes formosus*. Characters (left numbers) and states (right numbers) are identical to those given by Oswald (1993:28-40), except as noted in the text under ‘Phylogenetic Analysis: Characters’. Matrix symbols: 0, 1, 2, 4 character state numbers; ?, missing data (i.e., missing female data [characters 7 and 49] and unknown male data [characters 10-39]).

1	1	16	?	31	?	46	1
2	0	17	?	32	?	47	1
3	0	18	?	33	?	48	1
4	0	19	?	34	?	49	?
5	1	20	?	35	?	50	1
6	1	21	?	36	?	51	1
7	?	22	?	37	?	52	0
8	1	23	?	38	?	53	0
9	0	24	?	39	?	54	2
10	?	25	?	40	1	55	1
11	?	26	?	41	0	56	1
12	?	27	?	42	1	57	0
13	?	28	?	43	1	58	0
14	?	29	?	44	4	59	0
15	?	30	?	45	0	60	1





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Fig. 28. Cladogram showing relative interspecific relationships within *Balmes*, and the position of *Balmes* relative to the other higher taxa of extant psychopids. Character data are mapped only for *Balmes* and immediately adjacent lineages. Character state changes are shown in the following format [left to right]: (1) number of occurrences on the cladogram, including those on lineages not fully illustrated (see *Phylogenetic Analysis: Results*), (2) lineage symbol, (3) character number, (4) state numbers [ancestral state - derived state]. Male terminalic characters 21, 24, and 39 cannot be unambiguously mapped within *Balmes* because the male of *formosus* is unknown.

available paratype of *formosus* are obscured, consequently, this character could not be coded, and [2] Distal apodemes of female 9th tergite (character 49) – no distal apodemes could be located in *formosus*; however, because the membranous region where these apodemes are located is poorly preserved in the available paratype, the apparent absence of these structures may be an artifact, particularly since they are frequently difficult to observe even in well-preserved material. In the analysis of Oswald (1993), distal apodemes were shown to be a synapomorphy of the Psychopsidae, and it is strongly suspected that they will subsequently be found to be present in *formosus*. To indicate the present unreliability of the coding of this character in *formosus*, it has been coded as an unknown datum in the present analysis.

**Results.** – A single most parsimonious tree (length = 105, c.i. = 0.83, r.i. = 0.91) was found. This tree is shown in fig. 28 in a reduced form that illustrates character data only for lineages within *Balmes* and those that immediately surround its attachment site to the more general tree. The branching patterns and character distributions of species within *Psychopsis* and the Zygophlebiinae are identical to those presented by Oswald (1993: 43, fig. 53). The tree shown in fig. 28 places *Balmes* as the sister-group to the genus *Psychopsis* and resolves relative interspecific relationships within *Balmes* as follows: (*formosus* + (*terissinus* + (*notabilis* + *birmanus*))).

**General discussion.** – Oswald (1993) depicted the southeast Asian species clade *terissinus* + *notabilis* [as 'bns1'] + *birmanus* as the monophyletic sister-group



of the Australian genus *Psychopsis*, and advocated taxonomic recognition of *Balmes* at generic rank. Additionally, the Taiwanese species *formosus* (not examined for that analysis) was tentatively attributed to *Balmes*. The finding here that *formosus* represents the sister-group to the clade *terissinus* + *notabilis* + *birmanus* confirms the appropriateness of placing *formosus* within *Balmes*.

The monophyly of *Balmes* is supported in the current analysis by a single character: the fusion of the female 7th and 8th sternites (character 43; independently derived in *Psychopsis illidgei*). However, because the male of *formosus* is currently unknown, this weak level of support may be misleading. Three male terminalic characters (21, 24, 39) contain state transformations that are synapomorphic for the three non-*formosus* *Balmes* species; any or all of the derived states of these transformations could be subsequently identified in the male of *formosus* and lead to more robust support for the *Balmes* clade.

Character discussions. – [Character 6] Forewing, crossveins of costal gradate series: (0) absent or few [mean  $\leq 5$  crossveins/wing]; (1) numerous [mean  $> 5$  crossveins/wing]. The previous analysis of Oswald (1993) identified two equally parsimonious three-step optimizations of this character, either (1) the presence of a well-developed gradate series is plesiomorphic within the Psychopsidae and secondarily reduced in *Zygophlebius pseudosilveira* Oswald ['zns1' of Oswald 1993] and *Balmes*, or (2) the absence of well-developed gradate series is plesiomorphic within the Psychopsidae and developed independently in *Psychopsis* and the Zygophlebiinae, but subsequently lost in the zygophlebiine species *Zygophlebius pseudosilveira*. The presence of a well-developed gradate series in *Balmes formosus*, and its inferred position here as the sister-group to the three *Balmes* species treated by Oswald (1993), now renders the first optimization more parsimonious than the second. The current cladogram unambiguously supports the first optimization as the better interpretation of costal gradate series evolution within the Psychopsidae, with the minor modification that the loss of the costal gradate series in *Balmes* is now seen as a synapomorphy of only the three Indochinese *Balmes* species, rather than as a synapomorphy of the entire genus.

[Character 39] Male gonosaccal membrane, rounded spiculate lobes: (0) absent; (1) present. The presence of a pair of spiculate lobes on the venter of the eversible male gonosaccus is an interesting feature of the male terminalia of the Indochinese species of *Balmes*. A similar pair of lobes has been developed independently in *Psychopsis insolens*. These lobes probably function during copulation and insemination to anchor the everted male gonosaccus within the female bursa (Oswald 1993). Because the male of *B. formosus*

is unknown, it is currently uncertain whether the presence of these lobes constitutes a synapomorphy of *Balmes* in its entirety, or only of its mainland species. A second, smaller, pair of lobes is present on the dorsal surface of the gonosaccus in *B. terissinus*. Because *terissinus* is the sister-group of the one-pair-lobed clade *notabilis* + *birmanus*, and the male of *formosus* is unknown, it is presently impossible to infer the proper cladogram positions of, and polarities among, the three states (a) no lobes, (b) one pair of lobes, and (c) two pairs of lobes. Discovery of the male of *formosus* should resolve these questions.

[Character 56] Female bursa, number of inserted bursal accessory gland ducts: (0) 1 unpaired duct; (1) 1 pair of ducts; (2) 2 pairs of ducts. One pair of bursal accessory glands with ducts that insert at a pair a widely separated, bilaterally symmetrical, points on the dorsal/dorsolateral surface(s) of the female bursa is plesiomorphic in the Psychopsidae (Oswald 1993; state (1) above). This plesiomorphic condition undergoes significant alteration in the Indochinese species of *Balmes*. *Balmes formosus* exhibits the plesiomorphic condition of two widely separated [ $> 2$  times single duct diameter] ducts. In *B. terissinus* two separate ducts are present, but they are inserted very close together [ $< 2$  times single duct diameter]. In *B. birmanus* the ducts are partially fused distally, resulting in only one, common, duct being inserted on the dorsum of the bursa. The intermediate state of *terissinus* was not treated separately here, to maintain consistency with the analysis of Oswald (1993); however, were it to be considered as a separate state, the narrowing of the interduct insertion distance would map on fig. 28 as another synapomorphy of the clade *terissinus* + *notabilis* + *birmanus*. Since the female of *notabilis* is unknown, it is uncertain whether the fusion of the bursal accessory gland ducts should be considered a synapomorphy of *notabilis* + *birmanus*, or simply an autapomorphy of *birmanus*. The distal fusion of bursal accessory gland ducts is an unusual condition, which, to my knowledge, has not been reported in any other neuropteran.

#### BIOGEOGRAPHY

The placement of *formosus* within *Balmes* is consistent with the biogeographic hypothesis advanced by Oswald (1993), which suggested that southeast Asian psychopids constituted a monophyletic group that could be traced to a common ancestor that reached Asia either by active dispersal from Australia or by transport on an ancient rift fragment derived from the northern margin of Gondwanaland in the vicinity of present-day Australia. Additionally, the basal position of *formosus* within *Balmes* correlates with the marked disjunction between the known distributions of *formosus* (Taiwan) and the mainland *Balmes* clade composed



of *terissinus*, *notabilis*, and *birmanus* (upland areas in Burma, Laos, Vietnam, and south central China). Although the precise significance of this disjunction is unclear, its explanation is probably rooted in the historical biogeography of southeastern Asia.

#### FUTURE RESEARCH

The genus *Balmes* is the most poorly known of the five extant genera of the family Psychopsidae. Distributional records for this genus are sparse and additional collecting is needed to more fully document the ranges of its species. It will be especially interesting to see if the apparent allopatry of the Indochinese species is corroborated by future collections. The adult female of *notabilis* and the adult male of *formosus*, remain unknown. The discovery of the male of *formosus* is particularly desirable.

The immature stages of *Balmes* species are completely unknown. Their discovery would be of considerable interest because it would make possible comparisons among the larvae of psychopsids from southern Africa, Australia, and southeast Asia, the three disjunct regions of the world in which living silky lacewings are currently found.

Because the neuropterid fauna of southeast Asia is poorly known, additional undescribed psychopsid species may exist in this region. Any new living species discovered in this region would be expected to fall within, or as sister-groups to, the *Balmes* clade.

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