

Ebbepterote, a new genus for the Australian ‘*Eupterote*’ *expansa* (T. P. Lucas), with a revised classification of the family Eupterotidae (Lepidoptera)

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Abstract. The single and endemic species of *Eupterote* Hübner recorded from Australia is shown not to possess the male genitalia typical of this genus, nor of any other genus of Eupterotidae, and it is consequently placed in a new genus, *Ebbepterote* Oberprieler, Nässig & Edwards, as *E. expansa* (T. P. Lucas, 1891), comb. nov. Its genitalia are compared with those of many Asian and African genera of Eupterotidae, resulting in a revised classification and redefinition of the major eupterotid lineages. Five groups are defined: a probably paraphyletic ‘basal’ *Ganisa*-group and likely monophyletic subfamilies Janinae (including *Tissanga* Aurivillius and *Hibrildes* Druce), Striphnopteryginae, Eupterotinae and Panacelinae. *Ebbepterote* and the New Guinean ‘*Eupterote*’ *styx* Bethune-Baker species-complex are included in Striphnopteryginae, which is otherwise restricted to Africa. *Cotana* Walker is reassigned to Eupterotinae from Panacelinae and *Sphingognatha* Felder is resurrected from synonymy with *Eupterote*. The genitalia of *Ebbepterote* and several other critical genera are illustrated, demonstrating that the shape of the uncus does not constitute a suitable synapomorphy for defining the Eupterotidae as a monophyletic group. Another alleged eupterotid synapomorphy, the presence of a row of midventral spurs on the apical tarsal segment of the hindleg of the female, is shown to occur only sporadically in the family but also outside of it, in the lemoniid–brahmaeid–sphingid clade of Bombycoidea. As a result, the monophyly of the Eupterotidae currently rests only on a single, cryptic character of the mesoscutum of the imago and is in urgent need of substantiation.

Introduction

The genus *Eupterote* Hübner, 1820 (‘1816’) (type species: *Phalaena fabia* Cramer, 1779; India) comprises an ill-defined complex of between 30 and 80 species in South and South-east Asia, spread over more than a dozen generic names and representing one of the few radiations in the small, largely Palaeotropical bombycoid family Eupterotidae. Some recent studies (Holloway 1982, 1987; Nässig 1995) have begun to develop a more natural concept of the genus, synonymising several generic names, but its proper delimitation as a monophyletic group has not yet been achieved. Similarly, the definition of a number of closely related genera, such as *Palirisa* Moore, 1884, *Nisaga* Walker, 1855, *Dreata* Walker, 1855 and *Sphingognatha* C. & R. Felder, 1874, and their proper distinction from *Eupterote* remain unresolved problems, as is the concept of this entire group of genera as constituting a natural (monophyletic) tribe or subfamily. Additional difficulties

are presented by some poorly studied south-eastern outliers placed in *Eupterote*, in particular the Australian ‘*Eupterote*’ *expansa* (T. P. Lucas, 1891) and the New Guinean ‘*Eupterote*’ *styx* Bethune-Baker, 1909. The latter species was included in *Sphingognatha* by Forbes (1955), but – tentatively – in *Tagora* Walker, 1855 by, for example, Holloway *et al.* (2001). The Australian-endemic species commonly placed in *Eupterote* was originally described in the anthelid genus *Darala* Walker, 1855 (a synonym of *Anthela* Walker, 1855, see Edwards and Fairey 1996) as *D. expansa* (Lucas 1891), and again, later, as *Eupterote doddi* by Turner (1911). Its placement in *Eupterote* has never been questioned, probably in part owing to a lack of specimens being available to European and American workers, such as Forbes. Illustrations of the species appeared only in the recent literature, D’Abrera (1974) figuring the male in colour and Common (1990) in monochrome. Its male genitalia have never been studied.

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The second author's visit to the Australian National Insect Collection (ANIC) in Canberra in January/February 2001 provided an opportunity to study this unique and taxonomically important species. Dissection of male and female specimens showed that it differs significantly from all other species of *Eupterote* and related genera in characters of the male genitalia and represents a distinct genus. We here describe this genus as new and name it for the eminent Danish-Australian lepidopterist Ebbe Schmidt Nielsen, who tragically died barely a month after the second author's visit to the ANIC and the discovery of the uniqueness of this Australian bombycoid taxon. In assessing the taxonomic placement and relationships of the new genus, we also studied representatives of other eupterotid genera from Asia and Africa, in particular species of the New Guinean '*Eupterote*' *styx*-complex. Even though it became evident that a separate genus is also required for this complex, we do not describe such a taxon here because this is meaningfully done only in a comprehensive study of the New Guinean Eupterotidae.

The poorly resolved classification of the mainly Afro-Asian family Eupterotidae (with only a few species in Australia/New Guinea and in Central America) posed severe difficulties in assessing the affinities and taxonomic placement of the new Australian genus, as of the '*Eupterote*' *styx*-complex. Aurivillius (1901) attempted the first comprehensive definition of the Eupterotidae (as Striphnopterygidae), dividing it into two subfamilies, Striphnopteryginae and Janinae, based on wing venation characters and, consequently, also including the genera *Lemonia* Hübner, 1820 ('1816'), *Sabalia* Walker, 1865 and *Spiramiopsis* Hampson, 1901 in Striphnopteryginae. These three genera have since been shown to belong to the lemoniid–brahmaeid–sphingid clade of Bombycoidea (Minet 1994), the former two placed in Lemoniidae and the latter – less securely (Oberprieler and Duke 1994) – in Brahmaeidae. In a detailed study of the Chinese eupterotid fauna, Mell (1930) found Aurivillius' venation characters to be variable and doubted their suitability to distinguish eupterotid subfamilies; however, owing to the geographical limitation of his study, he refrained from proposing an improved classification system. Gaede (1930), Pinhey (1975) and Vári and Kroon (1986) followed Aurivillius' classification, recognising subfamilies Eupterotinae, Striphnopteryginae and Janinae. In a major study of the world Eupterotidae with special emphasis on the structure of the male genitalia, Forbes (1955) adopted a different system that recognised the four subfamilies Eupterotinae (with tribes Janini, Tissangini, Eupterotini [including Striphnopterygini] and Cotanini), Panacelinae, Prismostictinae and Apatelodinae, and provided a catalogue of the genera of the family as distributed over these taxa. Forbes' system was, in essence, followed by Holloway (1987), Common (1990) and Edwards (1996), except for treating Apatelodinae as a separate family and Prismostictinae as a subfamily of

Bombycoidea. In a phylogenetically orientated study of the Bombycoidea, Minet (1994) proposed a new concept of the Eupterotidae. Minet's classification raised Forbes' tribes Janini, Tissangini and Eupterotini to subfamily-level, included Cotanini in Panacelinae, placed Prismostictinae and Apatelodinae in Bombycoidea and formally added the African *Hibrildes* Druce, 1888 to Eupterotidae, as a subfamily Hibrildinae (its affinity to Eupterotidae had already been suspected by Aurivillius and Forbes). Minet proposed a number of 'indisputable' to tentative synapomorphies for these various groups, including for the family itself, but a comprehensive analysis of eupterotid classification and phylogeny was outside the scope of his study. Minet's classification was adopted by Lemaire and Minet (1998), Holloway *et al.* (2001) and Vári *et al.* (2002). Our study of '*Eupterote*' *expansa* and its genital characters necessitates a reappraisal of these classification systems.

Materials and methods

The holdings of '*Eupterote*' *expansa* in the ANIC, consisting of 26 male and 22 female pinned specimens, were studied, including the genitalia of three males and three females. The male genitalia of the following other representatives of Eupterotidae were studied for comparative purposes.

'Ganisa-group'. Asia: *Apha* spp., *Ganisa* spp., *Apona* spp., *Pandala dolosa* Walker, 1855, *Pseudojana clemensi* Schultze, 1907, *Pseudojana* spp., *Melanothrix nymphaliaria* (Walker, 1866), *Melanothrix* spp., *Pseudoganisa currani* Schultze, 1910; Africa: *Poloma angulata* Walker, 1855, '*Hemijana*' *variegata* Rothschild, 1917 (as identified in the collection of the Transvaal Museum in Pretoria, South Africa, seemingly in 1965 by A. Watson at The Natural History Museum, London, by comparison with the type; it is very close to *Poloma* in wing pattern and male genitalia and does not belong in *Hemijana* or Janinae); America (Mexico): *Preptos* sp.

Janinae. Africa: *Jana eurymas* Herrich-Schäffer, [1854], *J. tantalus* Herrich-Schäffer, [1854], *Jana* sp., *Hoplojana rhodoptera* (Gerstäcker, 1871), *Hemijana subrosea* (Aurivillius, 1893), *Camerunia* sp., *Stenoglene hilaris* Felder, 1874, *S. obtusa* (Walker, 1865), *S. rosea* (Druce, 1886), *Hibrildes ansorgei* (Kirby, 1896), *H. norax* (Druce, 1888).

Striphnopteryginae. Africa: *Striphnopteryx edulis* (Boisduval, 1847), *Phyllalia alboradiata* Aurivillius, 1911 (listed as a synonym of *acuta* Strand, 1911 by Gaede (1930), but Strand's description does not agree with *P. alboradiata* in several details and indicates *P. acuta* to be a different species), *P. patens* (Boisduval, 1847), *P. thunbergii* (Boisduval, 1847), *Phyllalia* sp. nr. *flavicostata* Fawcett, 1903, *Phyllalia* sp. nr. *umbripennis* Strand, 1911, *Phiala arrecta* (Distant, 1899), *P. dasyopoda* Wallengren, 1860, *P. incana* (Distant, 1897), *Rhabdosia patagiata* (Aurivillius, 1911), *Trichophiala devylderii* Aurivillius, 1879, *Lichenopteryx despecta* Felder, 1874, *Stibolepis* sp., *Janomima mariana* (White, 1843), *J. westwoodi* Aurivillius, 1902, *Marmaroplegma paragarda* Wallengren, 1860; New Guinea: '*Eupterote*' *styx*-complex.

Eupterotinae. Asia: *Sphingognatha* cf. *asclepiades* C. & R. Felder, 1874, *Sphingognatha* sp., *Eupterote* (*Eupterote*) cf. *radiata* (Walker, 1866), *Eupterote* (*Eupterote*) spp., *Eupterote* (*Tagora*) *glaucescens* (Walker, 1855), *Eupterote* (*Tagora*) spp., *Palirisa lineosa* (Walker, 1855), *Palirisa* spp., *Dreata* spp., *Nisaga* spp. (numerous species studied of these taxa, many still undescribed); New Guinea/Australia: *Cotana serranotata* (T. P. Lucas, 1894).

Panacelinae. Australia: *Panacela lewinae* (Lewin, 1805), *P. nyctopa* (Turner, 1922), *P. syntropha* Turner, 1922, *Panacela* sp.

The genitalia were prepared and mounted in the standard manner for Lepidoptera (dissection nos. ANIC 16992 and 16993 for males, nos. W. Nässig 1480/01 and 1481/01 for females); however, those used for the illustrations (Figs 11–29) were not slide-mounted but preserved in their natural state in glycerine in microvials attached to the pins of the respective specimens. The illustrations were made from genitalia in glycerine, using a Zeiss ProgRes 3012 high-resolution digital camera and the software Automontage (Synoptics Ltd, Cambridge, UK) to compile a series of focus levels into a single image.

Taxonomy of the new Australian genus

Genus *Ebbepterote*, gen. nov.

Type species: *Darala expansa* T. P. Lucas, 1891 (= *Eupterote doddi* Turner, 1911, synonymised by Turner 1922).

Description

Male (Figs 1, 3–4)

Head. Densely covered with long hair scales, proboscis absent; labial palpi short, porrect, third segment less than one quarter length of second segment; antennae broadly bipectinate to tip, left and right rami of each segment ventrally confluent at the base, shaft dorsally covered with whitish scales for entire length.

Thorax. Stout, above with dense long hair scales, femur and tibia expanded with dense long hair scales, tarsal segments with few hair scales, tibial spurs 0–2–2, epiphysis large and well developed.

Forewing. Retinaculum absent; cell short, about a quarter length of wing, R2 absent, R5 stalked with R3+R4.

Hindwing. Cell broad, short, less than a third length of wing; Sc+R1 and Rs well separated, parallel; Rs, M1 and M2 arising in proximity but separated.

Genitalia (Figs 11–13). Obliquely slanted in lateral view; uncus very short and broad, fused with tegumen but fusion line distinct laterally, apex broadly shallowly emarginate, lateral processes forming weakly, irregularly sclerotised lobes protruding beyond uncus and there membranously connected to each other and to uncus (Fig. 13); gnathos absent; vinculum strongly fused to tegumen, gently sinuate in lateral view, saccus reduced to small point but with two adjacent, strong, broad, apically rounded, parallel processes ('pseudosacci') directed anteriorly; valves broad, single sclerites with distinct but blunt costal area, valvula produced into broadly acute point curved mesad but not downwards, sacculus strengthened into a right angle and forming a narrow cleft between the valves (Fig. 12), not striated or corrugated; valves at base broadly and firmly fused with vinculum and ventrally narrowly with each other; juxta an upright, even, shallowly cup-shaped disc with inflexed basal lip hinged to sacculus area of valves, dorsally fused with aedeagus; aedeagus stout and short, gently

curved, obliquely positioned in lateral view, base moderately inflated, apex ventrally extended into evenly rounded lip; vesica without distinct scobinations.

Female (Figs 2, 5–6)

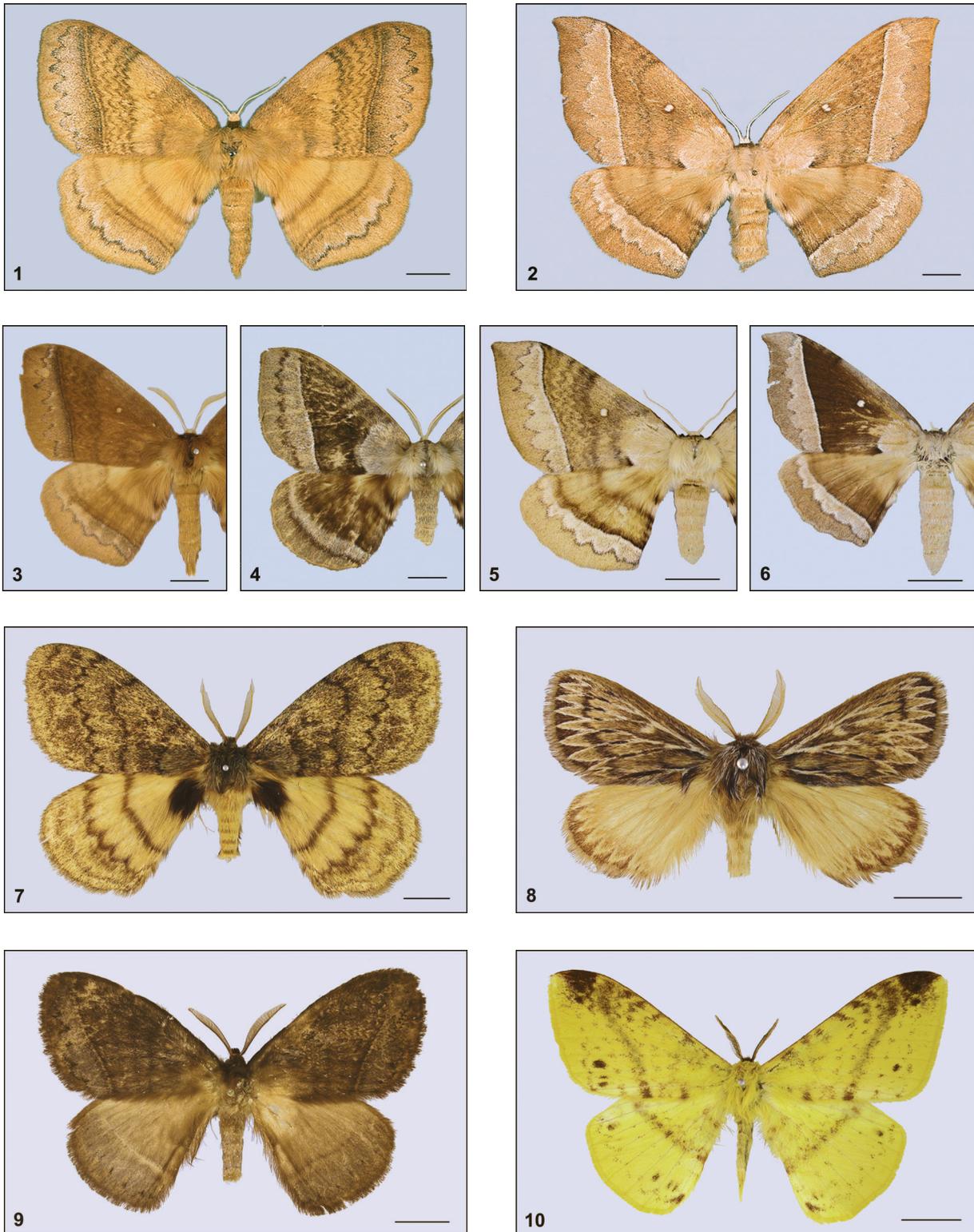
Head. Antennae shortly bipectinate to tip, shaft also covered with whitish scales to tip.

Thorax. Epiphysis absent, apical segment of metatarsus ('metathoracic distitarsus') ventrally with broad shallow depression carrying sparse, stiff setae and medially a single row of four strong, articulated spurs increasing in size towards apex (Fig. 30); wings more elongate than in male, apex of forewing produced, termen sinuate.

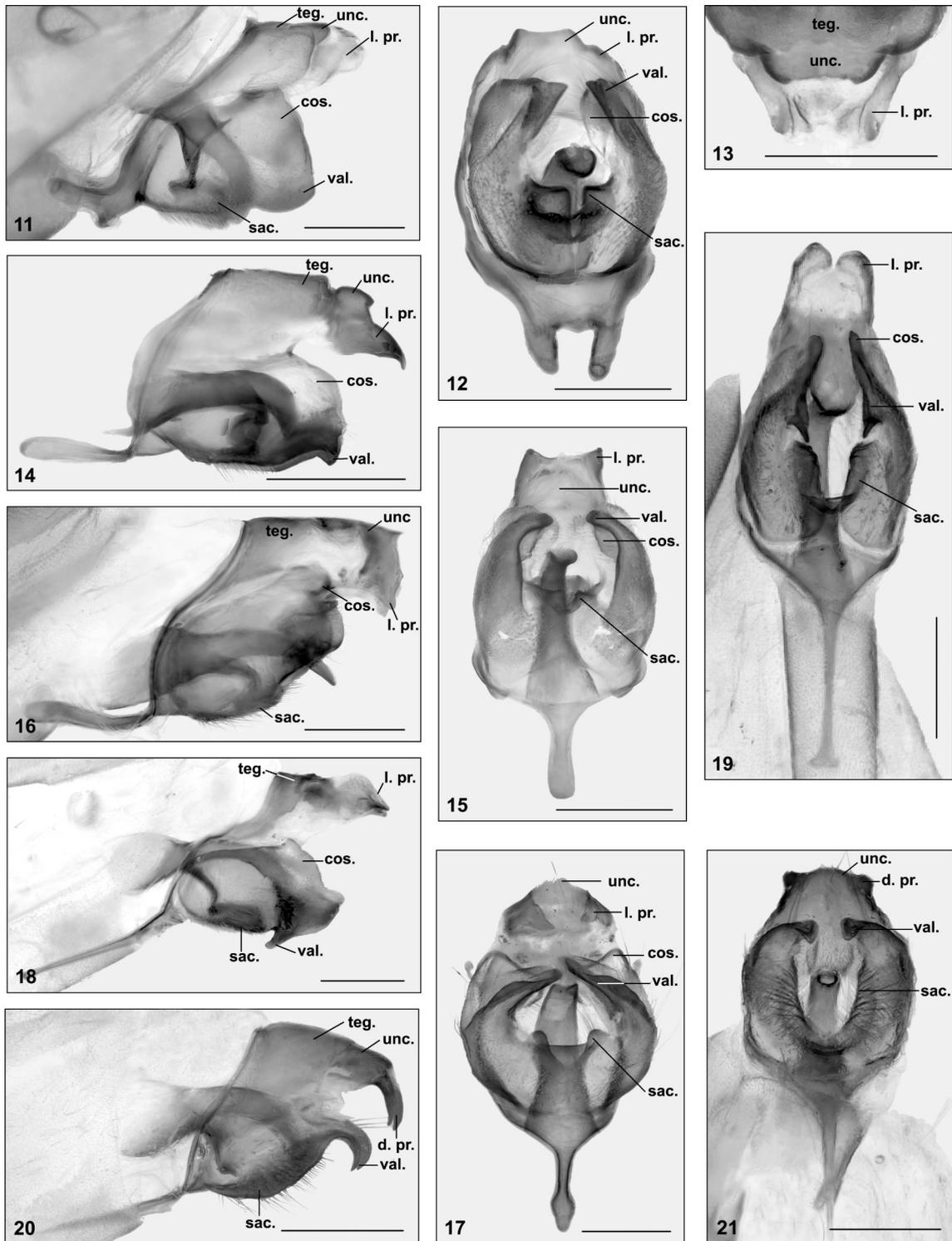
Genitalia (Figs 28–29). Ostium bursae a strongly sclerotised tube protruding about 0.8 mm above the body surface, outer walls nearly fully sclerotised, hindmargin ventrally notched, without separate lamellae ante- or postvaginales, slightly wider distally than proximally; fully integrated into a narrow but strongly sclerotised and quite rigid ventral band connecting to apophyses of 8th abdominal segment; together with sclerotised 8th tergite forming a closed, stiff ring around the 8th segment, in which the tube-like ostium bursae is embedded; remaining area of 7th, 8th and 9th/10th abdominal segments ventrally membranous; bursa copulatrix comparatively small, soft and membranous, without signum or any other sclerotisation.

Remarks

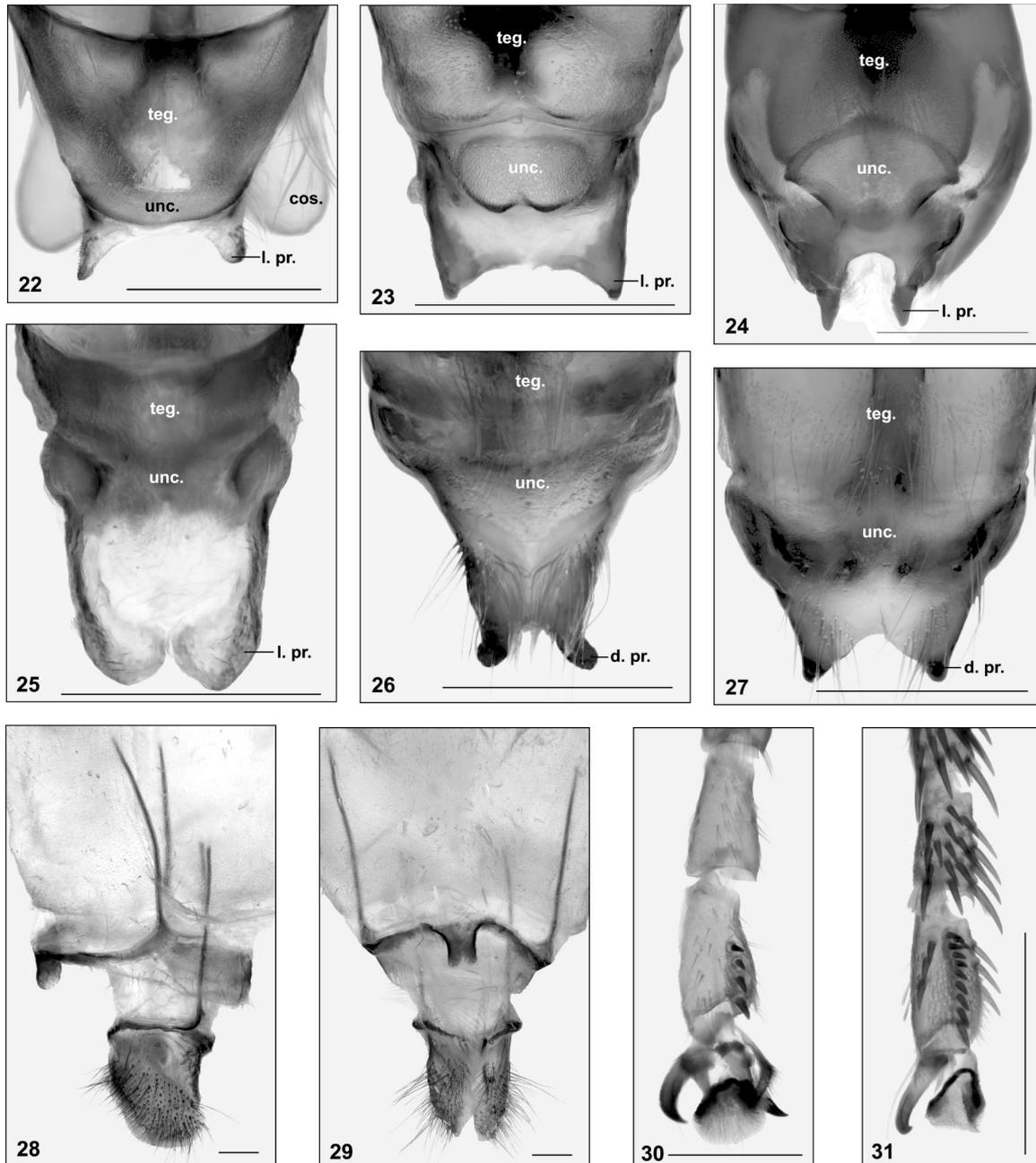
Ebbepterote is readily distinguishable from all other genera of Eupterotidae by the double projections of the saccus in its male genitalia. The deep narrow cleft between the sacculus area of the fused valves and the corresponding protruding ostium bursae in the female, which seemingly locks into this cleft during copulation, are also most unusual features, serving to distinguish *Ebbepterote* from other genera as far as their genitalia have been studied. Among the groups of Eupterotidae as characterised below, *Ebbepterote* differs as follows: from the *Ganisa*-group in its strongly fused valve–vinculum–juxta–aedeagus complex and its reduced uncus; from the Janinae (including Tissanginae and Hibridinae) in its undivided valves; from the Eupterotinae in its short, truncate uncus without dorsal processes (possessing instead a pair of weak lateral processes joined mesally beyond the uncus) and in its valves having a distinct costal area; and from *Panacelinae* in its valves not having the costal area inflated into membranous lobes. In the shape of its uncus, being short and broad without apical prongs but possessing a pair of lateral processes instead, and also in its valves having a distinct costal area, *Ebbepterote* agrees with the Striphnopteryginae, in which its fused valve–vinculum–juxta–aedeagus complex places it near the genera *Marmaroplegma* Wallengren, 1860 (Figs 14–15) and *Janomima* Aurivillius, 1901 (Figs 16–17). Its wing venation, having M1 in both wings arising close to M2 from the cell



Figs 1–10. Habitus of imagines of *Ebbepeterote expansa* (showing species variability) and compared taxa of Eupterotidae. 1–6, *Ebbepeterote expansa*: 1, male (Mossman); 2, female (Paluma Range); 3, male (Mt Spurgeon); 4, male (Eungella Nat. Park); 5, 6, females (Paluma Range). 7, *Janomima mariana*, male (South Africa); 8, *Marmaroplegma paragarda*, male (South Africa); 9, ‘*Eupterote*’ *styx*, male (Morobe, New Guinea); 10, *Eupterote* sp., male (Yunnan, China). Scale bars: 10 mm.



Figs 11–21. Male terminalia of *Ebbepterote expansa* and compared taxa of Eupterotidae. 11–12, *Ebbepterote expansa* (Kuranda), lateral and ventro-caudal views; 13, uncus of *E. expansa* (Kuranda), dorsal view; 14–15, *Marmaroplegma paragarda* (South Africa), lateral and ventro-caudal views; 16–17, *Janomima mariana* (South Africa), lateral and ventro-caudal views; 18–19, ‘*Eupterote*’ *styx* (Morobe, New Guinea), lateral and ventro-caudal views; 20–21, *Eupterote* sp. (India), lateral and ventro-caudal views. teg., Tegumen; unc., uncus; l. pr., lateral process; cos., costal area; val., valvula; sac., sacculus area; d. pr., dorsal process. Scale bars: 1 mm.



Figs 22–31. Terminalia and metatarsi of *Ebbeterote expansa* and compared taxa of Eupterotidae. 22–27, Uncus and tegumen, dorsal view: 22, *Phyllalia cf. umbripennis* (South Africa); 23, *Marmaroplegma paragarda* (South Africa); 24, *Janomima westwoodi* (Congo); 25, ‘*Eupterote*’ *styx* (Morobe, New Guinea); 26, *Sphingognatha cf. asclepiades* (Java, Indonesia); 27, *Eupterote* sp. (Myanmar). 28–29, Female terminalia of *Ebbeterote expansa* (Mt Spurgeon), lateral and ventral views. 30–31, Distal segments of female metatarsus, ventro-lateral view: 30, *E. expansa* (Mt Spurgeon); 31, *Spiramiopsis comma* (Swaziland), Brahmaeidae. teg., Tegumen; unc., uncus; l. pr., lateral process; cos., costal area; d. pr., dorsal process. Scale bars: 1 mm.

(not stalked with Rs) and Sc+R1 in the hindwing not connected to Rs, is very similar to that of *Janomima*. The New Guinean ‘*Eupterote*’ *styx* also has a similar genital apparatus (Figs 18–19), in particular the same striphnopterygine type of uncus and valves (see below), but differs from *Ebbeterote* in that the costal area of its valves

is more prominent and produced caudad, the valvula forms a prominent hook overhanging a deep median notch and the valve bases are only weakly fused with the vinculum and mesally with each other. *Ebbeterote* is also distinguishable from *Janomima*, ‘*Eupterote*’ *styx* and *Eupterote* by its wing shape and pattern (compare Figs 1–6 with 7, 9–10).

Etymology

This new genus is dedicated to Ebbe Schmidt Nielsen, late Director of the Australian National Insect Collection (ANIC) at CSIRO Entomology and leader of the Lepidoptera project, in recognition of his major contributions to the study of Lepidoptera in Australia and the world. The second part of the generic name recalls the stem of the generic name *Eupterote*, the type genus of the family Eupterotidae. The gender of *Ebbepterote* is to be considered feminine.

Included species

Ebbepterote is a monotypic genus, including only the type species, *Ebbepterote expansa* (T. P. Lucas, 1891), comb. nov. The type locality of *Darala expansa* is given as the Dawson River (Lucas 1891), but this is far south of the distribution range of the species and Lucas' locality record is deemed to be an error (Turner 1922). The type locality of the synonym *Eupterote doddi* is the Evelyn Scrub near Herberton on the Atherton Tablelands (Turner 1911). The male holotype of *Eupterote doddi* is in the ANIC, but the female holotype of *Darala expansa* has not been located and appears lost.

The species is variable in size and colour pattern (Figs 1–6). In the male, the forewing length ranges between 40 and 50 mm (mean 45.9 mm, standard deviation 2.0, $n = 24$), in the female, between 50 and 64 mm (mean 56.3 mm, standard deviation 3.9, $n = 17$). The ground colour in both sexes ranges from pale greyish-brown to reddish-brown and the markings vary in intensity and in colour from brown to dark brown, dark grey and deep reddish-brown. In some individuals, the median area of the wing, between the innermost wavy transverse line at one third to the straight transverse line at 5/6 costa and 4/5 inner margin is entirely dark brown or dark grey from costa to inner margin (Figs 4, 6). The single male specimen available to us from Eungella (Fig. 4), evidently representing an isolated southern population, differs from all other specimens examined in having the outermost line of both wings (the dark outer margin of the pale outer band) much more diffused and regular and the wavy lines on the wing undersides closer to the wing bases. It does not differ in its male genitalia, however.

Distribution

The known distribution of *E. expansa* (Fig. 32) covers a small strip of rainforest along the Queensland coast, from Mt Lewis near Mossman in the north and southwards across the Atherton Tableland to the Paluma Range near Townsville, with an isolated record from Eungella near Mackay. This area includes the tropical and subtropical rainforests of north-eastern Queensland but does not extend onto the Cape York Peninsula. A similar distribution pattern is found in many other Australian moths, identifying a northern Australian rainforest element that typically does not extend

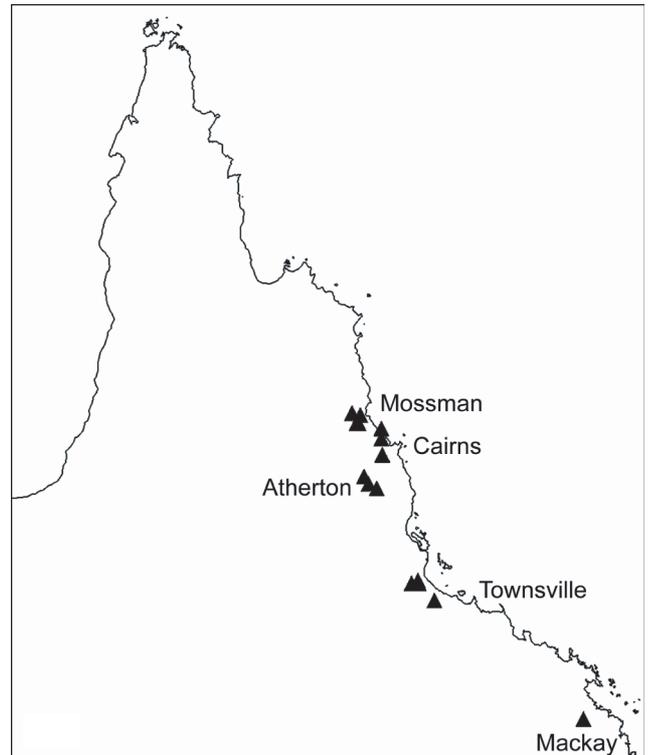


Fig. 32. Distribution records of *Ebbepterote expansa* in northern Queensland, Australia.

north into the tropical rainforests of the Iron Range (which harbours a fauna much more New Guinean in character), nor south into the subtropical rainforests that extend from Gympie through Brisbane to northern New South Wales.

The collection records range from about 700 m to 1300 m in altitude, the latter pertaining to mountaintops such as Mt Lewis and Mt Spurgeon, where *E. expansa* has been taken at light near the summit in *Eucalyptus–Casuarina* forest habitats. Its precise habitats as well as its larva and larval foodplants are unknown, although Turner (1911) records part of the type series of *Eupterote doddi* as having been bred by F. P. Dodd. Both sexes are nocturnal in habit and attracted to light.

Classification of the family Eupterotidae

The greater similarity of the male genitalia (especially of the uncus) of *Ebbepterote* to those of the African *Janomima* and *Marmaroplegma*, rather than the Asian *Eupterote*, raises questions not only about the distinction of the African Striphnopteryginae from the Asian Eupterotinae, but also about the definition of the entire family Eupterotidae, as the condition of the uncus ('mesally reduced') has been proposed as one of three synapomorphies delimiting the Eupterotidae as a monophyletic group (Minet 1994; Lemaire and Minet 1998). The value of this character as a synapomorphy is, however, compromised by (a) it suffering

from a poor concept and definition (assessment of when the condition actually occurs), (b) involving a reduction (losses having a high probability of homoplasy), (c) problems in determining homology in the various developments of the uncus as occur in the family, and (d) similar conditions occurring also in other bombycoid groups.

The uncus, representing the tergum of the 10th abdominal segment, is seemingly primitively apically divided (bifid or bilobed) in the Bombycoidea *sensu lato* (*sensu* Brock 1971, Scoble 1992, i.e. including Mimallonoidea and Lasiocampoidea *sensu* Minet 1994), an entire apex being a derived condition (Holloway 1987). However, in the Mimallonidae, the indicated most basal bombycoid lineage (Minet 1994), the uncus is single pointed (Franclemont 1973). In the Lasiocampidae, an apically bifid uncus occurs in the primitive subfamilies Chionopsychinae, Chondrosteginae and Poecilocampinae, whereas it is reduced in the Macromphaliinae – but with a pair of strongly developed processes (*socii* after Franclemont 1973, but probably extensions of the uncus), resulting in a ‘mesally reduced’ condition – and mostly totally lost in the derived Lasiocampinae (with true *socii* generally present). In the Anthelidae, the uncus is well developed and apically mostly strongly divided or bilobed (Common 1990: fig. 117.6), sometimes short with the two prongs widely separated (e.g. in the *Anthela ocellata* (Walker, 1855) group) to also result in a ‘mesally reduced’ condition. In the Apatelodidae (or Bombycidae: Apatelodinae), the uncus is bifid (*Apatelodes* Packard, 1864) to deeply cleft into a pair of strong processes (*Olceclostera* Butler, 1874) (*socii* after Franclemont 1973), again representing a ‘mesally reduced’ condition.

In the Eupterotidae, the uncus is quite differently constructed among the various groups (as characterised below). In the *Ganisa*-group, it typically carries a dorsal and a lateral pair of processes, which are equally strongly developed in *Pseudojana* Hampson, 1893 and *Poloma* Walker, 1855, but with the dorsal pair smaller in *Melanothrix* C. & R. Felder, 1874, much reduced in *Ganisa* Walker, 1855, *Apona* Walker, 1856 and *Pandala* Walker, 1855 and completely lost (together with the whole dorsum of the uncus) in *Pseudoganisa* Schultze, 1910. In *Apha* Walker, 1855, there are only two long, thin parallel processes dorsally, with a non-sclerotised window between them, perhaps representing the dorsal rather than the lateral prongs. In the Janinae, the uncus is mesally usually weakly developed (but not so in *Acrojana* Aurivillius, 1901, *Epijana* Holland, 1893 and some *Stenoglene* C. & R. Felder, 1874) and often forms a short, broad lobe (a narrow strip only in *Hibrildes*), while from its sides arise one or two pairs of strong, often long and spike-like lateral processes (possibly representing *socii* fused to the uncus). In the Striphnopteryginae, the uncus itself carries no processes at all but forms a transverse, often doubly buckled sclerite (Figs 22–24). However, a pair of processes

(*socii*) arises from its lateral membranes to form soft, loose protuberances (in *Phyllalia* Walker, 1855, Fig. 22) that can join mesally beyond the uncus and become more strongly sclerotised and pointed, but always leaving a weakly or unsclerotised area mesally (*Marmaroplegma*, *Janomima*, Figs 23–24). These processes never carry any scales, but, when small as in *Phyllalia*, sometimes a few setae. In the *Phiala* section of Striphnopteryginae, both these processes and the uncus itself are only small, weak sclerites connected by a membrane. In the Eupterotinae, the uncus is a strong sclerite with a prominent apical bifurcation (Figs 26–27), basically identical to that of other bombycoids, such as Anthelidae. These prongs are covered with scales to nearly the apex and also carry several strong dorsal setae, and there is no indication of them being lateral rather than dorsal in origin, or of an additional lateral pair of processes being present. *Cotana* Walker, 1865 has this latter type of uncus as well, the apical prongs being further separated than in *Eupterote*, whereas the uncus of *Panacela* Walker, 1865 is a small, weak, triangular, single-pointed sclerite or totally absent.

Taking the apically bifid anthelid uncus as a reference point (or that of the saturniid or brahmaeid clades of Bombycoidea), a ‘mesal reduction’ of the uncus can only be said to occur in some members of the *Ganisa*-group and in some Janinae and Striphnopteryginae, but not in Eupterotinae or Panacelinae. In Striphnopteryginae, this reduction appears to have been accompanied by a development of the *socii* into auxiliary lateral lobes or prongs, in Janinae such lateral processes have developed into strong spines firmly fused to the uncus, whereas in the *Ganisa*-group the original dorsal processes have mostly been retained in addition to the lateral ones. The surface sculpture of the uncus, tegumen and *socii* is a useful aid in establishing homology between these various structures and modifications, but a more intensive study is required to clarify the homology in all instances. It is evident that the structure of the eupterotid uncus is quite diverse and does not yield any single synapomorphy (such as a ‘mesal reduction’) that can be used to delimit the family as a monophylum. However, the uncus is useful in assisting the characterisation of the following subgroups in Eupterotidae.

Ganisa-group. Uncus distinct from tegumen to more or less fused dorsally, typically large and strongly 4-pronged (*Pseudojana*, *Poloma*, *Melanothrix*), but the dorsal prongs reduced in *Ganisa*, *Pandala* and *Apona* to absent in *Pseudoganisa* and only two dorsal processes present in *Apha* (long) and *Preptos* (short); gnathos generally present, large to strip-like; valves single but generally 3-pointed, not fused with vinculum or juxta or each other; juxta free, flat, broad to small to absent; aedeagus free; vesica with or without scobinations; vinculum narrow, fused with tegumen except in *Apha*; saccus mostly absent (present in *Apha* and *Poloma*).

As here delimited, this group includes *Pseudojana*, *Ganisa*, *Apona*, *Pandala*, *Apha*, *Melanothrix*, *Pseudoganisa*, the African *Poloma*, '*Hemijana*' *variegata* and, seemingly, *Sarvena* Walker, 1865 (not seen). The Central American *Preptos* Schaus, 1892 and *Neopreptos* Draudt, 1930 are also tentatively included. These few and isolated eupterotids are not true members of the Neotropical bombycoid fauna (as stated by, for example, Common 1990) but originate from the subtropical part of the North American continent and have barely spread into the Neotropics. Forbes (1955) related *Preptos* to *Apona*. Its genitalia are somewhat aberrant in comparison with those of the other members of the *Ganisa*-group, and further studies based on more material and a broader character set are necessary to determine the relationships of these two American genera.

No synapomorphies are currently evident to indicate the *Ganisa*-group to be monophyletic; it may indeed form the paraphyletic stock from which some or all the other eupterotid groups could have arisen. In this group also, the male antenna is mostly (in *Ganisa*, *Apona*, *Pseudojana* and *Melanothrix*) distinctly tripectinate, carrying a prominent ventral process between the bases of the rami. This antennal type is indicated to be a bombycoid symplesiomorphy, occurring also in Anthelidae (all genera, but with the ventral process reduced in some *Anthela* and in *Chenuala* Swinhoe, 1892, *Omphaliodes* C. & R. Felder, 1874, *Munychryia* Walker, 1865 and *Gephyroneura* Turner, 1920), in phiditiine Bombycidae (Minet 1994) and in all basal members of Minet's (1994) '*Carthaea*-L-S clade', i.e. in *Carthaea* Walker, 1858, *Lemonia*, *Sabalia*, *Spiramiopsis*, *Dactyloceras* Mell, 1930, *Brahmaea* Walker, 1855, and in the sphingids *Xenosphingia janseni* Jordan, 1920, *Ceridia mira* Rothschild & Jordan, 1903 and *Smerinthus jamaicensis* (Drury, 1773). A small hump or ridge between the bases of the rami in *Apha* and *Pseudoganisa* indicates that the ventral process may have been reduced in these genera (as has occurred in some Anthelidae), whereas in *Poloma* the rami are still separate at their bases (confluent to prominently bridged in other Eupterotidae).

Janinae. Uncus firmly fused with tegumen so that fusion line mostly indiscernible, mesally generally short with no or only a small pair of processes (but forming a strong, bifid or flared median structure in *Stenoglene* and *Epijana*) and always with a lateral pair of strong spike-like processes (sometimes forked); gnathos varying from large and multi-spined to small or absent; valves movable (occasionally weakly fused at their bases and with juxta, opening only partially), deeply divided to fully cleft into a dorsal, mostly slender costa and a ventral, broader sacculus, the latter generally with an upper inner point (a long separate spike in *Hibrildes*) probably representing the valvula; juxta a broad, flat or saddle-shaped plate, mostly free but sometimes weakly fused with valves; aedeagus always free; vesica with scobinate lining or a single apical cornutus; vinculum narrow; saccus short and stout, often elongate triangular.

This group contains the genera included by Forbes (1955) in his Janini, but also *Parajana* Aurivillius, 1906, *Pterocerota* Hampson, 1905 (after Minet 1994), *Tissanga* Aurivillius, 1903 (Tissangini of Forbes, Tissanginae of Minet) and *Hibrildes* (Hibrildinae of Minet). The common genital feature of all these genera is the deep, cleft-like to complete division of the valves, which does not occur in any other eupterotid genera and seems to constitute a synapomorphy for the Janinae in this sense. *Tissanga* appears to have the most plesiomorphic genital structure of the group, whereas the genitalia of *Hibrildes* are evidently highly derived, featuring not only fully tripartite valves but an uncus reduced to a thin dorsal strip and a pair of long lateral processes (comparable to the condition in *Pseudoganisa*).

Striphnopteryginae. Uncus fused with tegumen but fusion line generally discernible, often evenly convex or doubly bulged, apically broadly rounded to truncate, without any median processes but with a pair of lateral processes (socii?) arising from membrane at base of uncus, these processes soft and loose or joining mesally beyond uncus and becoming more strongly sclerotised and pointed, never squamose; gnathos obsolete; valves single, short and broad (high), free or weakly to strongly fused with vinculum, at base with each other and with juxta, costa area distinct and often membranously inflated (e.g. in *Phyllalia*, Fig. 22), valvula forming a sharp stout process pointed mesad or a hook pointed ventrad and overhanging a deep notch in inner margin (Fig. 19), ventral margin of notch formed by rounded to angled upper edge of sacculus, which is often corrugate or striate (not so in the *Janomima* section); juxta fused with aedeagus and valves; aedeagus basally inflated, apex sharply pointed ventrad; vesica without distinct scobination; vinculum narrow; saccus mostly long and slender.

In this definition, this group incorporates the genera included by Forbes (1955) in his tribe Phialini and also *Janomima*, *Marmaroplegma* and *Cyrtोजना* Aurivillius, 1911 from Africa and *Ebbepterote* and the '*Eupterote*' *styx*-complex from Australia/New Guinea. Three groups of genera are indicated: one including *Striphnopteryx* Wallengren, 1858, *Phyllalia*, *Schistissa* Aurivillius, 1901 and *Paraphyllalia* Gaede, 1927 (*Striphnopteryx* section); another group including *Phiala* Wallengren, 1860, *Stibolepis* Butler, 1878, *Rhabdosia* Hübner, [1820], *Trichophiala* Aurivillius, 1879, *Lichenopteryx* C. & R. Felder, 1874 and probably *Bantuana* Distant, 1906 (*Phiala* section); and the last group including *Janomima*, *Marmaroplegma*, seemingly *Cyrtोजना*, the '*Eupterote*' *styx*-complex and *Ebbepterote* (*Janomima* section). The most distinctive genital features of the Striphnopteryginae in this concept are the reduction of the uncus and the development of a pair of lateral processes from the membrane at the base of the uncus. The latter feature appears to constitute a suitable synapomorphy to define the group as monophyletic, unless these processes can

be shown to be homologous with the stiff lateral prongs of the uncus in Janinae and the *Ganisa*-group. The Striphnopteryginae are also characterised by a well-developed costal area of the valves (often membranously inflated), which otherwise only occurs in *Panacela* (Panacelinae).

With the Eupterotinae, the Striphnopteryginae (except the *Janomima* section) share the striations on the inner border of the sacculus area of the valves (Fig. 21), but it is unlikely that this feature represents a synapomorphy linking these two groups, as inferred by Minet (1994). Forbes (1955) referred to it as a stridulating area, but, judging from the development and apparent function of this sacculus area in *Ebbepterote*, the striation is more likely to play a role in holding the ostium bursae of the female in place during copulation, and it may thus develop whenever the valves become fused and lose their clamping action. In Eupterotinae, this striation does not occur when the valves are only weakly fused at their base and partially movable (*Palirisa*) or when the aedeagus is movable (*Sphingognatha*) or the sacculus is extended (*Cotana*). In the *Janomima* section of Striphnopteryginae, in which the striation is also absent, either the valves are again partly movable ('*Eupterote*' *styx*, Fig. 19), or the sacculus area is broadly fused to leave a strengthened distal cleft or notch (Figs 12, 15, 17) that seemingly achieves this holding function in a different way.

Eupterotinae. Uncus broad and strongly developed, uniformly sclerotised, firmly fused with tegumen to leave no or only a weak suture line (in *Sphingognatha*, *Palirisa*, *Dreata*, *Cotana*), ending distally in a pair of strong points or hook-like prongs, which are dorsally closely approximated in *Sphingognatha* (Fig. 26) but widely separated in the other genera (Figs 21, 27), these prongs at base squamose and with sparse or densely clustered strong setae (Figs 26–27); gnathos obsolete to absent; valves short but narrower than in Striphnopteryginae, weakly (*Sphingognatha*, *Palirisa*, *Dreata*, *Cotana*) to strongly (*Eupterote*, *Nisaga*) fused with vinculum and with each other at base, costa not developed, valvula forming a sharp stout process pointed caudo-mesad (*Sphingognatha*, *Cotana*) or ventrad, with the apex sometimes flattened and/or twisted (*Palirisa*, *Dreata*, *Nisaga*), sacculus area mostly not prominent and with strong transverse striations (Fig. 21) but extended and without striations in *Sphingognatha*, *Palirisa* and *Cotana*; juxta fused with aedeagus (except in *Sphingognatha*) and valves; aedeagus basally inflated, apex acute; vesica with fine to strong scobination (except *Nisaga* and *Dreata*); vinculum narrow, saccus varying from short and broad to long and thin.

This group includes *Sphingognatha*, *Dreata*, *Palirisa*, *Nisaga*, *Eupterote* (including *Sarmalia*, *Tagora*) and *Cotana*. Its most distinctive genital feature is the large uncus with its pair of squamose, setose dorsal processes, but while this uncus distinguishes the Eupterotinae well from all other

members of the Eupterotidae, it is not much different from the typical bombycoid uncus (as in Anthelidae) and not clearly definable as a synapomorphy for the group. The reduction of the costa area of the valves is also a characteristic feature of the Eupterotinae in this concept, but again not an unambiguous synapomorphy. Although the group is thus distinctive within the Eupterotidae, its monophyly remains to be clearly demonstrated.

Within the Eupterotinae, the male genitalia provide useful characters to delimit genera. *Sphingognatha* is indeed a 'well-marked genus' (Forbes 1955) by its free aedeagus, narrow uncus and elongated valve apex, and its synonymy with *Eupterote* (Holloway 1987) cannot be upheld. We here reinstate it as a valid genus. Unique configurations of mainly the valve apex characterise *Palirisa*, *Dreata* and *Nisaga*, whereas *Tagora* and *Sarmalia* are indistinguishable from *Eupterote* on genital characters (see also Nässig 1995). However, the proper delimitation of these genera requires a more comprehensive investigation than was within the scope of our study. *Cotana* clearly belongs to the Eupterotinae on genital characters, which differ strongly from those of *Panacela* (Panacelinae, below), and we here again place it in this group, although a separate tribe, Cotanini of Forbes (1955), for the genus is not definable without a more comprehensive study of *Cotana* and its indicated New Guinean relatives *Melanergon* Bethune-Baker, 1904, *Paracydas* Bethune-Baker, 1908 and seemingly also *Rarisquamosa* Bethune-Baker, 1910 and *Lasiomorpha* Joicey & Talbot, 1916 (Holloway *et al.* 2001).

Panacelinae. Uncus short and weak to strongly reduced (*Panacela lewinae*), broadly fused with tegumen but suture line visible, ending distally in a single blunt point or lobe, lateral membranes weakly but distinctly sclerotised with a few setae to sometimes being the most prominent part of the uncus (*P. syntropha*); gnathos obsolete; valves broadly and firmly fused with vinculum and basally with each other, costa area strongly membranously inflated, valvula a broad, blade-like twisted point to spike-like extended (in *P. lewinae*), sacculus a broadly inflexed, flat, setose, non-striated plane (modified into two distinct ventral lobes in *P. lewinae*); juxta fused with aedeagus and valves; aedeagus large, basally inflated, apex with large ventral tooth but modified into caudadly pointing spike in *P. lewinae*; vesica without scobinations; vinculum broad or narrow, saccus long and thin but short and stout in *P. lewinae*.

The Panacelinae are here again restricted to include only the small Australian genus *Panacela* (Forbes' concept) rather than also *Cotana*, as contended by Minet (1994). The male genitalia of *Panacela* are unique among the Eupterotidae in having a single-pointed uncus, although it is uncertain whether this may be secondary reduction from an originally bifurcate apex, or a secondary extension from a broadly rounded or truncate apex as it occurs in Striphnopteryginae.

The genitalia of *Panacela* also share two other characters with those of Striphnopteryginae, namely the sclerotisation of the lateral uncus membranes and the membranous inflation of the costal area of the valves. It is unclear whether these similarities indicate a close relationship between Striphnopteryginae and Panacelinae, and further study of other character complexes is required to test this possibility. *Cotana* cannot be related to *Panacela* on genital characters at all, and there are also major differences in the larvae of these two genera. The larva of *P. lewinae* has the SV sclerite of its prolegs divided by a membranous strip, its procoxae not fused and its D1 and D2 scoli distinct on all segments, whereas the putative *Cotana* larva (a specimen collected in the Iron Range, northern Queensland, in ANIC) has undivided SV sclerites, fused procoxae and the D2 scoli strongly reduced and absent on A9. On the first two of these larval characters, *Panacela* belongs to Lasiocampoidea *sensu* Minet (1994), rather than Bombycoidea (and thus Eupterotidae), although divided SV sclerites and free procoxae also occur in other Eupterotidae (the *Phiala* section of Striphnopteryginae) and in Apatelodinae (*Apatelodes*, *Olceclostera*) and divided SV sclerites also occur in other Bombycidae (*Bombyx* Linnaeus, 1758, *Ocinara* Walker, 1856). The wing venation characters of *Panacela* and *Cotana* that were seen as similar and interpreted as synapomorphies by Minet (1994) are not identical and probably not homologous, and are contra-indicated by differences in other venation characters (e.g. the stalking of M3 and CuA1 in *Panacela* but not *Cotana*, see Common 1990, Holloway *et al.* 2001). They are also compromised by the great variability of venation characters in Eupterotidae as a whole.

Our study of *Ebbepterote* and its characters, particularly of the uncus and its suitability in defining the family Eupterotidae and its subgroups, raises one more important character issue that requires comment. Apart from the 'mesally reduced' uncus, Minet (1994) proposed two other synapomorphies identifying the family Eupterotidae as a monophyletic group: the mesoscutum having elongate and dorsally pointed notal incisions; and the last tarsal segment of the hind leg ('metathoracic distitarsus') in the female having a midventral row of spines (articulated spurs, to be precise). The latter character is conspicuously present in *Ebbepterote* (Fig. 30), but not universally so in the Eupterotidae. We found it to occur also in *Melanothrix* (as in Minet 1994: fig. 10) and *Poloma* of the *Ganisa*-group, in *Hibrildes* (as in Minet 1994: fig. 14) and *Stenoglene* of the Janinae, in *Phiala* and *Lichenopteryx* of the Striphnopteryginae (here on the middle leg as well), in *Cotana* and in *Panacela* (as in Minet 1994: fig. 15). It is not present in the striphnopterygines *Phyllalia*, *Trichophiala* (which, however, has the same setose depression in which these spurs occur in the other genera), *Marmaroplegma* and in the eupterotine *Palirisa*. However, an almost identical row

of spurs (Fig. 31) occurs in *Spiramiopsis* (included in Eupterotidae by older authors, but now placed in Brahmaeidae, see above) and also in *Lemonia* and *Sabalia* of the closely related Lemoniidae as well as in the sphingid *Xenosphingia janseni*. Minet (1994) furthermore reports it from the African brahmaeid *Dactyloceras*, as 'a simple case of convergence'. A similar condition is present in the Apatelodinae (*Apatelodes*, *Olceclostera*), where such a row of spurs is present on the outside of the apical tarsal segment (Minet 1994: fig. 11) and occurs on all legs. Although the apatelodine spurs may be interpreted as a different, convergently evolved character, this is less convincing for the midventral row in the lemoniid–brahmaeid clade. Unless it can be demonstrated that this extraordinary feature is truly non-homologous in Eupterotidae and Lemoniidae/Brahmaeidae, the possibilities that it is either a synapomorphy uniting Eupterotidae and Lemoniidae/Brahmaeidae (perhaps together with Bombycidae and Sphingidae) into a monophyletic lineage, or a bombycoid symplesiomorphy that is sporadically retained in a number of now disparate groups, cannot be discounted. Either way, this feature cannot currently be regarded as a synapomorphy for the family Eupterotidae.

Conclusions

It is evident that the new Australian genus *Ebbepterote* is not related to the Asian *Eupterote* or to the Eupterotinae as here delimited, but represents an isolated lineage with closer affinities to the African Striphnopteryginae. Whether its closest relatives are the African genera *Janomima* and *Marmaroplegma*, which have similar male genitalia, or rather the New Guinean 'Eupterote' *styx*-complex, remains to be determined. The latter complex also belongs to Striphnopteryginae rather than Eupterotinae and requires placement in a new genus, but this should only be done in the context of a proper study of the New Guinean eupterotid fauna.

The structure of the eupterotid uncus is unsuitable as a synapomorphy for the family, but it provides useful characters in delimiting natural groups (subfamilies) within the Eupterotidae. On its basis and that of the development of the valves, five lineages are definable: an African–Asian *Ganisa*-group (retaining many plesiomorphies and probably constituting a basal, paraphyletic group); a wholly African Janinae (likely monophyletic when including *Tissanga* and *Hibrildes*); an African–Australian Striphnopteryginae (probably also monophyletic but sharing some genital and perhaps larval characters with *Panacela*); an Asian–Australian Eupterotinae (not yet demonstrably monophyletic); and a monotypic Australian Panacelinae (possibly related to Striphnopteryginae). Several evolutionary and zoogeographical implications arise out of this classification and the apparent affinities of the Australian eupterotid genera, but a comprehensive

phylogenetic study of the family is required to investigate these.

A second alleged synapomorphy of the family Eupterotidae, the midventral row of spurs on the apical tarsal segment of the female hind leg, occurs only sporadically in the family but also in several genera of the lemoniid–brahmaeid–sphingid clade, making the character unsuitable as a eupterotid synapomorphy. This leaves the Eupterotidae defined on a single alleged synapomorphy (the structure of the notal incisions of the mesoscutum) and, together with the occurrence of ‘lasiocampoid’ characters in some eupterotid larvae, raises doubts about its monophyly.

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