The Epicopeiidae: phylogeny and a redefinition, with the description of new taxa (Lepidoptera: Drepanoidea)

Joël MINET

Muséum National d'Histoire Naturelle,
Laboratoire d'Entomologie, 45 rue Buffon,
F-75005 Paris, France.

Abstract – *Amana banghaasi* Hering, a poorly known species from central China (described in the "Epiplemidae", now Epipleminae [Uraniidae]), is transferred to a new genus, *Deuveia*, which belongs to the Epicopeiidae (Drepanoidea). This taxon turns out to be the sister-group of a clade consisting of all other members of the family. Another new epicopeiid genus, *Burmeia*, is proposed for *B. leesi* n. sp., a species described from northern Burma. Quite clearly, there is a sister-group relationship between *Burmeia* and *Psychostrophia*, but these genera differ markedly in certain characters, for example in the course of vein M2: in both pairs of wings, M2 arises distinctly closer to M3 than to M1 in *Burmeia*, unlike the condition found in all other Epicopeiidae. A key is provided for the identification of the species in these two genera. A manually derived cladogram may correctly sum up the phylogeny of the Epicopeiidae, a family now composed of nine genera. It matches exactly one of the two most parsimonious trees found with computer programs such as Hennig86 or PAUP (the second tree of minimal length being similar, except for the affinities of the monotypic genus *Amana*). For the software-based analyses, all the 34 (imaginal) characters taken into account were polarized and given equal weight. The "robustness" of each branch of the preferred cladogram was assessed by calculating the corresponding Bremer's support index, but also with non-quantifiable criteria. Six genera may form a clade, within which the following sister-group relationships can be considered well established: *Chatamla*/*Parabraxas*, *Nossa*/*Epicopeia*, and *Schistomitra*/*Nossa* + *Epicopeia* (whereas *Chatamla* + *Parabraxas* is only tentatively regarded as sister to *Amana*). Owing to the basal position of *Deuveia* within the Epicopeiidae, the morphology of this genus is of great significance to identify the autapomorphies of the Drepanoidea and those of the Epicopeiidae (respectively 5 and 12 in number at this stage of the investigations). With regard to the Drepanidae, an apomorphy of the male genitalia can be added to the definition of the family, whose basalmost lineage probably is the subfamily Cyclidiinae. The composition of the Thyatirinae is briefly discussed.

For long, the family Epicopeiidae has been restricted to the Asian genus *Epicopeia* Westwood, 1841 (e.g. Laithwaite *et al.* 1975), that is to a few large diurnal species, which mimic papilionids and whose taxonomy remains unclear (Inoue 1978; Endo & Kishida 1999). In 1979, Fletcher rightly placed *Nossa* Kirby, 1892, in this family but without giving any explanation, although these pierid-like moths were previously assigned to the Uraniidae or "Epiplemidae" (a group now regarded as a subfamily of the Uraniidae). Minet (1983, 1986) added to the Epicopeiidae five genera that had been maintained by Fletcher (1979) in the "Epiplemidae", namely *Amana* Walker, 1855, *Chatamla* Moore, 1881,

Parabraxas Leech, 1897, *Psychostrophia* Butler, 1877, and *Schistomitra* Butler, 1881. In the 1986 paper, seven epicopeiid genera were thus recorded, along with their synonyms, and the Schistomitrinae Inoue, 1982, were synonymized with the Epicopeiidae Swinhoe, 1892. It should be noted that, in 1972, Nakamura had already pointed out the existence of similarities – mainly in pupal morphology – between *Schistomitra* and *Epicopeia*, nevertheless without formally transferring *Schistomitra* or *Psychostrophia* (also considered) to the family Epicopeiidae. In the old literature, the "Epiplemidae" usually included most epicopeiid genera (e.g. Dalla Torre 1924) but as many as three "families" were used by Hampson (1895) to accommodate the Indian taxa currently placed in the Epicopeiidae, and *Schistomitra* – from Japan – was occasionally ascribed to the Callidulidae (Seitz 1911).

Compared with its sister-group – the Drepanidae (Minet 1991: 87) –, the family Epicopeiidae is a small Asian (palaearctic + oriental) lineage, henceforth composed of nine genera (Minet & Scoble [1998]). This figure takes into account the two monotypic genera described hereafter, one based on a Chinese species hitherto assigned to *Amana*, the other corresponding to a new species from northern Burma. All Epicopeiidae are day-flying moths, although *Nossa moorei* (Elwes) comes occasionally to U.V. lights at night (L. Beaudouin, *pers. comm.*). The early stages of these insects are known only in a limited number of instances (see e.g. Sugi *et al.* 1987, Yen *et al.* 1995, Minet & Scoble [1998], and Jaroš & Spitzer 1999). Their study is outside the scope of the present paper, unlike the imaginal morphology. To date, the latter has been surveyed very incompletely, even with regard to the wing venation (Hampson 1895; Janet & Wytsman 1903; Grünberg 1908; Handlirsch 1925; Minet & Scoble [1998]) or male genitalia (Okano 1964 and 1973; Kuznetzov & Stekolnikov 1988 and 1993; Inoue 1992).

Material, methods and terminology

Material – The description of the genus *Deuveia* proposed hereafter is based on two Bouin-fixed male specimens, long kept in 70% ethanol (material got in 1987). One of these was "washed" by immersion in several ethanol baths, extracted from 95% ethanol (using glass coverslips to prevent any deformation of the wings), placed on damp sand in a relaxing container, and pinned and spread in a standard way. The second specimen was first used to examine the course of the aorta inside the mesothorax. With a razor blade, its body was incised longitudinally, in a parasagittal plane, after severance of two regions, an anterior one composed of the head and prothorax, and a posterior one corresponding to the abdomen caudad of A3. As recommended by Hessel (1966; 1969), a solution of trypan blue was chosen as the appropriate dye: the thorax being maintained in 70% alcohol, a jet of this staining solution was gently blown around the dorsal vessel, by means of a hypodermic syringe and after removal of the dorsolongitudinal muscles situated "above" (laterad of) the sagittal plane. Afterwards, the different parts of this specimen – wings excepted – were treated with a 10% potassium hydroxide solution and, after rinsing, dissected in 70% alcohol just like the other imagines studied, which all belong to the collections of two museums (viz. The Natural History Museum, London – BMNH – and the Muséum National d'Histoire Naturelle, Paris – MNHN).

The cuticular pieces were always stained with Chlorazol Black E. They were observed/drawn in either thickened cedar oil, a medium used for temporary preparations, or Euparal, a mounting medium suited to make permanent slide preparations (see e.g. p. 14-16 *in* Holloway *et al.* 1987).

Methods – Regarding the search for the interrelationships of the epicopeiid genera, two different methodological approaches were tried and compared. First a cladogram was constructed "manually", that is using the Hennigian method of phylogenetic analysis (Kitching *et al.* 1998: 38). It should be noted that, in this approach, certain characters are regarded as more significant than others insofar as they seem to be more reliable or even non-homoplastic. Accordingly they are given precedence for disclosing a number of possible clades, which implies that the Hennigian procedure usually relies on some sort of character weighting. Then computerized methods were used for the analysis of the same set of characters, this time without having recourse to any type of differential weighting. The computer programs Hennig86 (version 1.5) and PAUP (version 4) led, as expected, to the same results with search options based on exact methods (Kitching *et al.* 1998: 39-42). Use of the latter program was however essential to calculate the indices chosen for assessing the robustness of the different clades (viz. Bremer support – *ibid.*: 127-129). Each character included in the data matrix was polarized *a priori*, always by outgroup comparison, that is by taking into account as many outgroups as possible (not necessarily the same ones for all characters). In other words, the matrix starts with an all-zero "outgroup", which actually corresponds to a hypothetical ancestor. It comprises only binary characters to avoid certain difficulties that might result from the introduction of multistate characters (Barriel & Tassy 1993). "Inapplicable" character states were denoted by question marks (reductive coding: Strong & Lipscomb 1999) and such signs were also used for missing information (see section III: character 8).

Terminology – For most of the descriptive terms used in the present paper, a definition can be easily found in several general works (e.g. Nichols *et al.* 1989 and Scoble 1992). As a rule, the terminology for the thoracic morphology, wing venation, wing base, dorsal vessel, male abdominal brush-organs, and male genitalia follows – respectively – Brock (1971), Wootton (1979), Sharplin (essentially 1963a, b), Hessel (1966; 1969), Birch (e.g. 1972), and Klots (1970). Terms that may require explanations are listed hereafter, in a short glossary.

Anterior and posterior genae: respectively a narrow area between the compound eye and the lateroclypeal suture ("gena" of many authors) and a variously developed area between the eye and the occipital suture. Unlike the rather wide postgena, the posterior gena is often very narrow, inconspicuous (e.g. fig. 3 *in* Rouchy 1964). Occasionally it may be fairly broad (figs. 5 and 6 *in* Kristensen 1968).
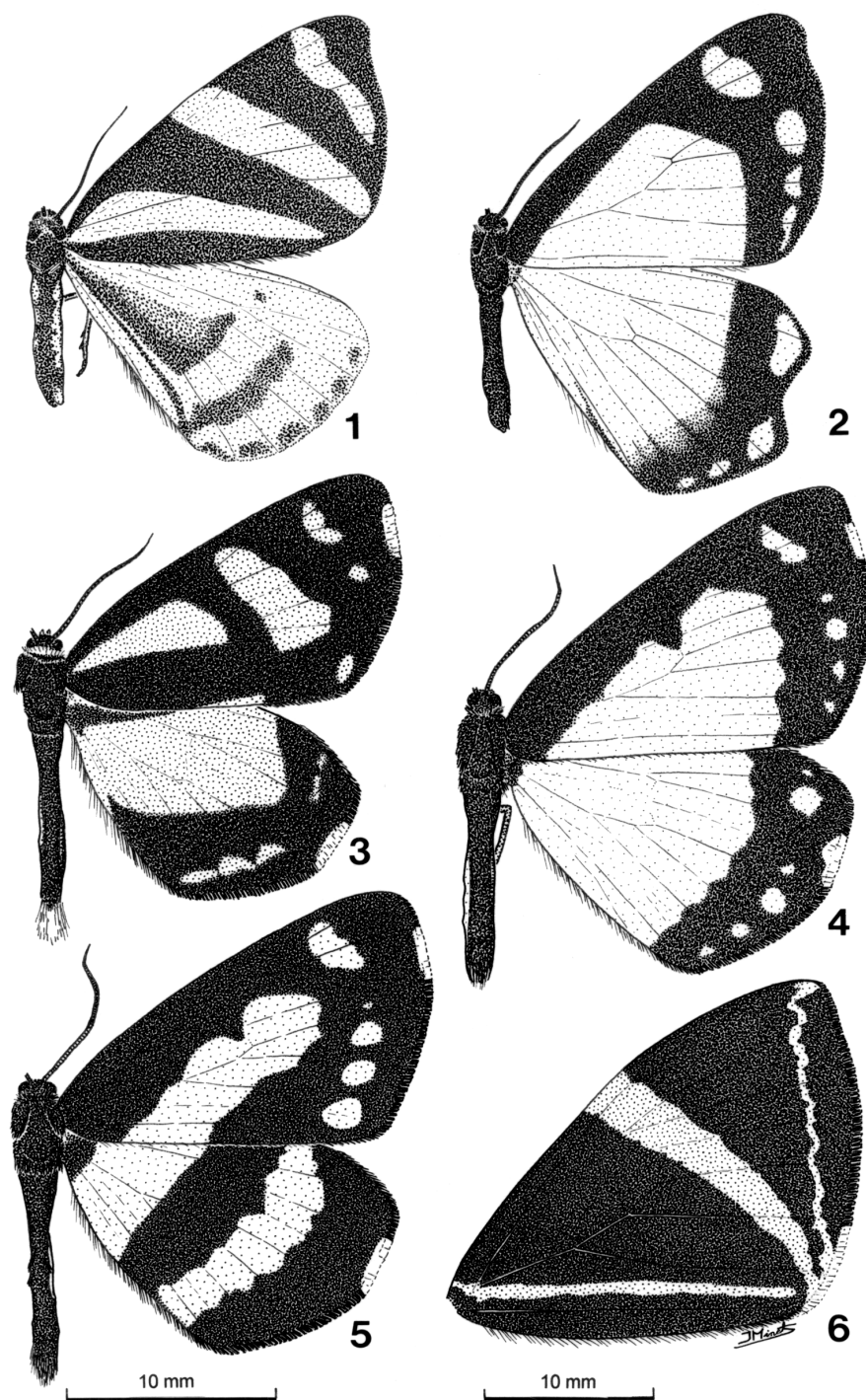
Anterolateral projection of sternum A3: an elongate extension of the anterior edge of this sternum (figs. 9, 10). Such projections, which are not internal structures, are sometimes improperly termed "apodemes" in moths provided with brush-organs (Birch 1972: figs. 2-4).

Basal sclerite of CuP (forewing base): a convex sclerite lying distad of the median and radial plates. Previously referred to as the "base of the second cubitus" or "Cu2" (Sharplin 1963).

Basal section of R + Rs (wing base): the very base of stem R + Rs, in forewing (Sharplin 1963a: figs. 26, 27, "R") as also in hindwing (Sharplin 1963b: fig. 11, "R + Sc").

Basisternal mesal ridge: see mesal ridge of basisternum.

Cibarial plate (hypopharynx): the sclerotized floor of the sucking pump (e.g. fig. 10 *in* Kristensen 1968), which bears variously arranged sensilla basiconica (Faucheux 1999).

Costula (male genitalia): the basal process of the costa, which extends mesad and/or cephalad (Weller 1990: 38), and to which are attached, typically, muscles m2 and m4 (numbering of Kuznetzov & Stekolnikov: e.g. 1993, fig. 5). This structure has been given other names that I consider less appropriate, for example "tendon" (Forbes 1923: fig. 21) or "transtilla" (*sensu* Sibatani *et al*. 1954). In fact, the latter term usually refers to an unpaired bridge connecting the right and left costae.

Coxal membrane: in metathorax, a membranous, posterodorsal extension of the meron (Minet 1982: fig. 5, m.cx.).

Endodont: a medial, ventral tooth on a pretarsal claw (Clench 1955).

Fenestra lateralis (pl., *fenestrae laterales*) and ***fenestra media***: in many Ditrysia, lateral and median membranes (Minet 1982) corresponding to fragments of the undivided fenestra (*fenestra unica*), which occurs in primitive Lepidoptera, caudad/ventrad of the metascutellum (Brock 1971: fig. 9).

Frontoclypeus: the large anteromedian sclerite of the imaginal head capsule of most lepidopterans (e.g. Kristensen 1968). Less accurately termed "clypeus" by certain authors (Short 1951; Goyle 1990). In actual fact, the glossatan head lacks a distinct suture between the frons and the clypeus (Eassa 1963b, Rouchy 1964, Kristensen [1998], etc.).

Furco-epimeral band (metathorax): an external sclerotized bridge, essentially of epimeral origin, which runs dorsad of the coxal membrane, along one of the internal ridges termed by Brock (1971) "laminae of secondary furcal arms". As defined here, the furco-epimeral bands correspond to the "secondary arms of the furca" *sensu* Brock. In my opinion, the term "secondary furcal arms" should preferably be used to designate the above-mentioned internal ridges.

Geometromorpha: a name proposed by Fänger (1999) for a clade considered by Minet (1991: "group A-G"). The taxon consists of seven superfamilies, namely the Axioidea, Calliduloidea, Hedyloidea, Hesperioidea, Papilionoidea, Drepanoidea, and Geometroidea.

Interommatidial sensilla: the short to long sensilla chaetica present between some corneal lenses of the compound eyes (Faucheux 1999). Also termed "interommatidial setae".

Intersaccular sclerite (male genitalia): in many Epicopeiidae and a few other moths, a median sclerite (*is*) situated ventrad of the juxta, between the sacculi, and separated from the ventral part of the vinculum by a fold or a narrow membranous area. A new (more precise) term for the "intervalvar sclerite" of Kuznetzov & Stekolnikov (1988, 1993).

Junction piece (male genitalia): in *Deuveia*, an unpaired sclerite, which is located immediately dorsad of the juxta and reaches the ventral region of the phallus (fig. 17: *jp*).

Lateroclypeal suture: in most Lepidoptera, the suture separating the frontoclypeus from the anterior gena. A "descriptive" term here proposed for a boundary sometimes regarded as a preantennal suture (Rouchy 1964: "suture préantennaire"), sometimes as part of the epistomal suture (e.g. Goyle 1990).

Marginotergite: Brock's term (1971: fig. 9 a) for each lateral bar of dorsum A1 (fig. 11: *mt*). Marginotergites have also been referred to as "tergal braces" (Nielsen & Kristensen 1989).

Median arm (hindwing base): in most Lepidoptera, a sclerite situated distad of the second axillary sclerite and attached to the "radial bridge" which connects the latter to the very base of R + Rs (Sharplin 1963b: e.g. fig. 6, "m.arm", and fig. 12, "M + Cu1").

Median labral process: a median, anterior extension of the imaginal labrum, typically subtriangular in shape (Eassa 1963a: fig. 5B).

Merocosta (pterothoracic legs): the suture separating the meron from the eucoxa (Matsuda 1970: 46).

Mesal ridge of basisternum (mesothorax): the "basisternal discrimen" of Nielsen & Kristensen (1989: fig. 76).

Mesoclidium (mesothorax): a ventral, typically Y-shaped sclerite, which may connect the anterior edge of the mesobasisternum to the prothoracic spinasternum (Jordan 1902). This structure is absent from the ground plan of the Lepidoptera (Nielsen & Kristensen 1996). It has often been confused with the spinasternum and was inaccurately regarded as a presternum by Weber (1928).

Mesocuticular: an area of the exoskeleton that is "mesocuticular" stains intensely with Chlorazol Black E (e.g. Nielsen & Kristensen 1989: 21). By contrast, membranous areas turn rather pale blue with this dye.

Metascutellar height index: here defined as the ratio (MHI) between two measurements of the scutellum, in a metathorax observed in posterior view, after removal of the abdomen. MHI = height of metascutellum (in the sagittal plane): width of metascutellum (measured in a horizontal plane midway between the top of the scutellum and the mid-point of the posteroventral boundary of this sclerite).

Neotergite: the median or posteromedian sclerite of dorsum A1 (Fänger 1999; *nt*), which is usually present between the marginotergites.

Ocular ridge: the term used by Short (1951: 86) for the "ocular diaphragm" of Ferris (1940: 34). In fact, the infolded part of the ocular suture.

Oculo-facial index: a new name for the "interocular index" of Davis (1975: 5). The latter name might be misleading since the index in question (OFI) is inversely proportional to the interocular distance. OFI = vertical eye diameter: interocular distance (measured midway between the antennal sockets and the anterior tentorial pits).

Postantennal suture: a suture running laterad of the vertex and occiput, from the antennal socket to the postoccipital suture (Short 1951; Rouchy 1964: figs. 1-3, spsant). The temporal sulcus, as delimited by Kristensen (1968) in a neopseustid, can be regarded as the posterior part of the postantennal suture.

Posterior gena: see anterior and posterior genae.

Praesacculus (male genitalia): a free apical process of the sacculus (Werny 1966: fig. 1).

Precoxal bridge (prothorax): in most heteroneurous Lepidoptera, a sclerotized bridge between the probasisternum and the anepisternum, ventrad of the laterocervicale (e.g. fig. 1 *in* Minet 1984).

Secondary longitudinal ridges (on wing scales): stronger ridges on a scale provided with dimorphic longitudinal ridges (Kristensen 1978a). Such scales occur mainly in exoporian moths.

Spinarea (forewing): on forewing under surface – in many moths – a dense group of spine-like microtrichia, which forms an oval or elongate area along the inner margin, near wing base (Minet 1990: 355).

Subalar membrane: in meso- and metathorax, the membrane dorsal to the epimeron (see e.g. Yack & Fullard 1993).

Supraocular index: an index (SI) proposed by Kristensen & Nielsen (1979: 75) for appraising the development of the dorsal region of a lepidopteran head. SI = height of head capsule above compound eyes: total height of head capsule.

Tuberculum (pl., *tubercula*): the Latin name (Minet 1985: 81) for the "tuberculate plate(s)" of Kristensen (1978b). Tubercula were discovered in primitive moths (see e.g. Scoble 1992: 95-96) but actually occur in all lepidopterans. They are very small sclerotized patches basically located in the pleural membranes of certain abdominal segments, notably A2 and A3 (figs. 9-11, *tb*). Typically, the pleural membrane of such a segment bears a dorsal tuberculum caudad of the spiracle, near the tergum, and a ventral tuberculum below the dorsal one, near the sternum. Sometimes, the tubercula lie on the sterna and/or terga rather than in the vicinity of these sclerites.

Venula (pl., *venulae*): a lateral, longitudinal "rod" on the surface of sternum A2 (Minet 1982). The venulae have also been termed "sternal rods" (Kyrki 1984).

Figures 1-6

Epicopeiidae: male adults (1-5)/ forewing upperside (6). − 1, *Deuveia banghaasi* (Hering). − 2, *Burmeia leesi* n. sp. (habitus reconstruction based on a comparison between the left and right sides of the holotype; antenna length hypothetical). − 3, *Psychostrophia melanargia* Butler. − 4, *Psychostrophia nymphidiaria* (Oberthür). − 5, *Psychostrophia picaria* Leech. − 6, *Amana angulifera* Walker. (Uniform magnification for figs 1-5)

I. – NEW GENERA AND SPECIES

Deuveia n. gen.

Type-species: *Amana banghaasi* Hering, 1932, *Mitt. dt. ent. Ges.*, 3: 28 (by present designation).

Diagnosis – *Deuveia* retains a few plesiomorphies that distinguish it from all other epicopeiid genera, in particular the absence of complete, antero-abdominal, tergosternal sclerites (fig. 9), and the unmodified condition of the posteromesal region of the vinculum (which is not differentiated into an "intersaccular sclerite" – fig. 16). Like *Psychostrophia* and *Burmeia*, *Deuveia* shows, in the forewing venation (fig. 7), a fairly straight stem Rs1 + 2 + 3, which diverges progressively from vein R. By contrast, the median region of Rs1 + 2 + 3 is approximated to R in *Amana*, *Chatamla*, *Parabraxas*, *Schistomitra*, *Nossa*, and *Epicopeia*. Unlike *Burmeia* and *Psychostrophia*, the genus *Deuveia* has 2-segmented (not 3-segmented) labial palpi, hindwings with the veins Rs and M1 distinctly stalked, a sternum A4 without lateral folds (in the male), a well developed gnathos, etc.

Description – **Male**. *Head*. Compound eyes small, obtusely angulate posterodorsally. Posterior limits of the eyes in line with the posteriormost points of the antennal sockets when head is examined in dorsal view. Oculo-facial index: 0.75. Supraocular index: 0.24. Interommatidial sensilla minute, inconspicuous. Ocular ridge comparatively narrow and pigmented only anteriorly. Ocelli absent. Chaetosemata: two transverse rows of long "setae" (among lamellar scales), which come fairly close to each other mesally. Frontoclypeus wide, evenly and moderately convex; its wall slightly less dark than the narrow anterior genae. Lateroclypeal sutures without internal ridges. Vertex wall weakly pigmented, except for a central, nearly oval area. Postantennal sutures remote from the eyes and provided with weak ridges. Posterior genae very broad, each of them being divided into an anterior, deeply pigmented band and a posterior (wider), weakly pigmented area. On dorsomeson, postocciput broader than the occiput and postoccipital ridge well indicated, although rather narrow. Postgenae heavily pigmented and narrower than the posterior genae. Dorsal tentorial arms absent. Anterior tentorial arms divergent forwards and fairly thin (a little thicker caudad of their mid-points). Pretentorinae lying lower than the metatentorinae. Antennae lamellate, tapering distally; scape neither squat nor elongate, with a proximal constriction; intercalary sclerite rounded, fairly large; pedicel short; first flagellomere moderately long, although it results from the fusion of two segments (as indicated by the presence of lateral, transverse furrows); flagellum lateroventrally covered with very short trichoid sensilla. Pilifers moderately produced, with numerous well developed bristles. Median labral process triangular, comparatively short. Mandibles obsolete. Proboscis length: approximately three times height of head capsule. Proboscis base rather broad, tending to flatten laterally. Each galea with many basiconic, styloconic and trichoid sensilla, the last-named being easily detectable proximally, on the anterodorsal surface; styloconic sensilla long,

conspicuously carinate, arranged in a dense, distal group. Maxillary palpus consisting of one globular segment whose diameter equals half the length of the distal labial palpus segment. Labial palpus short, drooping, 2-segmented; distal half of terminal segment with a very shallow dorsal depression representing the vom Rath's organ. Cibarial plate large, heavily pigmented, with four groups of basiconic sensilla.

Thoracic exo- and endoskeleton. Patagia medium-sized, regularly arched dorsally, about three times as wide as high. Parapatagia narrow, inconspicuous. Laterocervicale with its dorsal and ventral arms at right angles; dorsal arm with a well developed proprioceptive "hair plate"; ventral arm elongate, reaching the anterodorsal point of the probasisternum. Mesal suture of the probasisternum reinforced by an internal ridge. Precoxal bridge showing a small unsclerotized "window" near the sclerotized (posterior) part of the prokatepisternum. Ventral process of the tegula rather short, with a moderately pointed apex (fig. 29). Mesonotum: prescutal clefts slightly convergent dorsad (approximately as in *Axia margarita* (Hübner): Minet 1991: fig. 39); scutal mediolongitudinal suture heavily pigmented, though practically devoid of internal ridge; scutellum with an anteromedian angle of about 90°. Mesopleurosternum: ventral arms of mesoclidium with widely separated extremities; anepisternum well developed; upper sector of the precoxal suture wholly absent; marginopleural suture long, reaching the broad, membranous parepisternal suture; parepisternum narrower than the latter; basisternal margin concave between the arms of the mesoclidium; basisternal mesal suture and its ridge ending a short distance before the anterodorsal margin of the basisternum; dorsal edge of the meron ascending cephalad, reinforced by an internal ridge; meron and epimeron sharing a short line of junction (shorter than half the length of the dorsal edge of the meron when this is observed in lateral view); posterior "arm" of the epimeron divided by a mesocuticular area. Metanotum: scutum entire, though very strongly constricted mesally; scutellum with a large posteroventral area devoid of scales. Metascutellar height index: about 0.47. Fenestrae laterales small; fenestra media well developed. Metepimeron divided by a vertical mesocuticular band (as in certain Bombycoidea: see figs. 25 and 26 *in* Minet 1994), and forming – posteriorly – a broad, well sclerotized furco-epimeral band (broader than the coxal membrane lying ventrad of it). Metafurca with a minute mesal lamella that connects the anterior ventral laminae with a pair of long furcal struts. Ventralmost region of the metathoracic meron slightly raised, delimited by a complete, rounded suture.

Legs. Tibiae and tarsi smooth-scaled; the latter ventrally provided with moderately developed spines (less numerous on distitarsi). Epiphysis medium-sized, arising just beyond the middle of the fore tibia and going a little beyond the tibial apex. Tibial spurs medium-sized, unspined, with tiny apical points; spur formula: 0-2-4. Hind tibia with the medial spurs arising one-fourth from its apex. Basitarsus of the hindleg bent, compressed, weakly sclerotized (except for its proximal third), with its dorsal edge slightly concave and its ventral edge distinctly convex. Pretarsus with only one pseudempodial seta; arolium present, poorly pigmented; pulvilli not bifid; claws simple (i.e. without endodont and with non-serrate ventral edge).

Wings. Forewing and hindwing membranes showing an irregular arrangement of the scale sockets. Scales never deeply cleft. Scale blade without secondary longitudinal ridges and never produced basad of the blade-pedicel junction. Forewing upper surface with two commonest types of scales: 1 − scale roughly oval/round with 5-8 short, blunt apical teeth; 2 − scale elongate with 3-4 teeth, among which the lateral ones are shorter and sharper. Vestiture similar on hindwing upper surface, but with the type 2 scales often rounded distally and with the occurrence of a number of piliform scales. Type 2 scales tending to be lanceolate on fore-/hindwing under surfaces. Forewing base: basal section of R + Rs with a conspicuous transverse partition; base of 1A produced anteriorly (i.e. towards costa), overlying the apex of the basal sclerite of CuP; spinarea absent; subcostal retinaculum oblique to Sc, a little longer than broad. Hindwing base: frenulum well developed, with tapering apex and ovate sclerotized base; greatest diameter of the latter slightly exceeding one third of the distance separating this sclerite from the basal section of R + Rs; "median arm" conspicuous. Forewing termen slightly concave below apex (fig. 7); tornus broadly rounded; vein Sc ending near middle of costa; R free; Rs1, Rs2 and Rs3 stalked together (normally, Rs2 and Rs3 are stalked for a longer distance than Rs1 and Rs2); stem Rs1 + 2 + 3 fairly straight, with its base close to R and remote from the upper angle of the discal cell; Rs4 and M1 short-stalked; M2 arising about midway between M1 and M3 or slightly closer to M1 than to M3; M3 and CuA1 separate; stem of M and vein CuP replaced by folds; "basal fork" of 1A + 2A with very thin lower branch. Hindwing with rounded apex and tornus; termen convex, neither "tailed" nor angulate; subcosta and upper edge of discal cell diverging, except near wing base where they are bent and connected by a minute (practically dotlike) crossvein; Rs and M1 short-stalked; M2 arising closer to Rs + M1 than to M3; veins M3 and CuA1 separate; stem of M replaced by a fold in discal cell; no tubular CuP; 3A present, slightly exceeding half the length of 1A + 2A.

Dorsal vessel. In mesothorax, ascending and descending aortal branches diverging moderately, ventrad of a short fused section that forms an extension of the dorsal chamber. The latter lies immediately caudad of the scutoscutellar suture and is associated with the pulsatile diaphragma which underlies the anterior half of the mesoscutellum. This aortal arrangement is clearly not of the butterfly type.

Pregenital abdomen (figs. 9, 12, 13). Ventral part of the intersegmental thoraco-abdominal membrane distinctly scaled. Abdomen mainly clothed with appressed lamellar scales (but with a number of piliform scales anteroventrally); terga without posterior rows/strips of lanceolate scales. Dorsum A1: neotergite large, broader (on meson) than the membrane anterior to it, and laterally broadly fused with the marginotergites; the latter narrow, slightly produced ventrad posteriorly, along the anterolateral angles of tergum A2. No distinct lateral rods on tergum A2, which is subrectangular and has a moderately developed, continuous antecostal phragma (with shallow ventral notch mesally). Sternum A2: anterior edge weakly concave; anterolateral processes arched and elongate, though not connected to the faintly developed anterior lobes of the marginotergites; apodemes (*ap*) short, conical; venulae indistinct, replaced by a pair of shallow anterior grooves; posterolateral angles/areas of the sternum broadly rounded; each of these produced, cephalad, into a sclerotized arm that bears, distally, a thin, long hairpencil (the arm and hairpencil correspond, respectively, to the lever and brush of noctuid "brush-organs": see e.g. Birch 1972). A2 and A3 with the ventral and dorsal tubercula (*tu*) well developed, lying in the pleural membranes, near the edges of the corresponding sterna or terga (the ventral tubercula of A2 lie dorsad of the enlarged bases of the levers). Sternum A3 broader than long, with narrow anterolateral projections and parallel lateral edges that are folded in (fig. 9: pecked line) to form longitudinal furrows, which shelter the distal parts of the hairpencils. Sternum A4 without lateral folds. Sterna A4-A7 narrower (transversely) than sterna A2-A3, though still broader than long; sterna A4-A7 slightly (A7) to markedly (A4-A6) narrowed cephalad. Terga A3-A7 about twice to three times as broad as long, and always broader anteriorly than posteriorly. Terga A4-A7 (notably A4-A6) with an irregular dark line running along the anterior margin; this line replaced on tergum A3 by a pair of evenly arched shadows (joined, mesally, by a short dark dash). A8 (fig. 12) with the tergum and sternum distinctly narrowed posteriorly; tergum trapezoidal; lateral edges of sternum strongly concave (fig. 13). Intersegmental membrane A8-A9 devoid of scales.

Genitalia (figs. 12, 14-17). Tegumen (*tg*) small, subrectangular, mesally provided (near its posterior boundary) with a minute, finger-like, internal projection (fig. 14). Vinculum (*vi*) conspicuously extended dorsad and separated from the tegumen by long, well indicated, longitudinal furrows (these sutures are not membranous however). Saccus absent: median part of vinculum with a shallow anterior notch (fig. 15). Valva (*va*) entire, with broad base and sparsely setose inner surface (fig. 16); costa short, concave; sacculus ill-delimited distally, touching juxta proximally (at one point). Costulae very small, remote from each other. Juxta, or main part of it (fig. 12: *jx*), represented by a large sclerite that is heavily pigmented − except for its ventralmost area, between the sacculi −, posteriorly produced into a pair of huge, spoon-shaped projections, and anterodorsally provided with a pair of strong apodemes. This conspicuous structure articulates, dorsally, with a narrow sclerite (part of juxta? − fig. 17, junction piece: *jp*), which runs along the meson and reaches the phallus, with which it is fused. Uncus (*un*) subtriangular, with fairly elongate distal half and hook-like, ventrally directed apex; no distinct socii; tegumen-uncus suture: a shallow sclerotized groove that is arched in dorsal view. Gnathos complete, with pointed, upcurved apex and strongly bent long narrow arms; base of each arm (fig. 14: *bg*) separated from the uncus by a narrow membrane and fused with the tegumen for only an extremely short distance. Subscaphium absent. Phallus arched distally (fig. 17) and provided with a well developed anteroventral coecum and two groups of cornuti.

Female unknown to me.

Etymology – The genus is dedicated to my colleague Dr Thierry Deuve (MNHN), who entrusted to me two specimens of the type-species.

Gender: feminine.

Remarks about *Deuveia banghaasi* (Hering) n. comb.

Original description – The original description of this very characteristic species (Hering 1932) is based on three male specimens kept in Berlin and London (respectively: Museum für Naturkunde, Humboldt-Universität, and BMNH). It is detailed and accurate for the pattern and coloration of the wings, but quite insufficient for the coloration of the other structures. Further information about the latter is proposed hereafter, taking into account the two specimens acquired by the MNHN in 1987 (see "Distribution and biology" and the section "Material, methods and terminology").
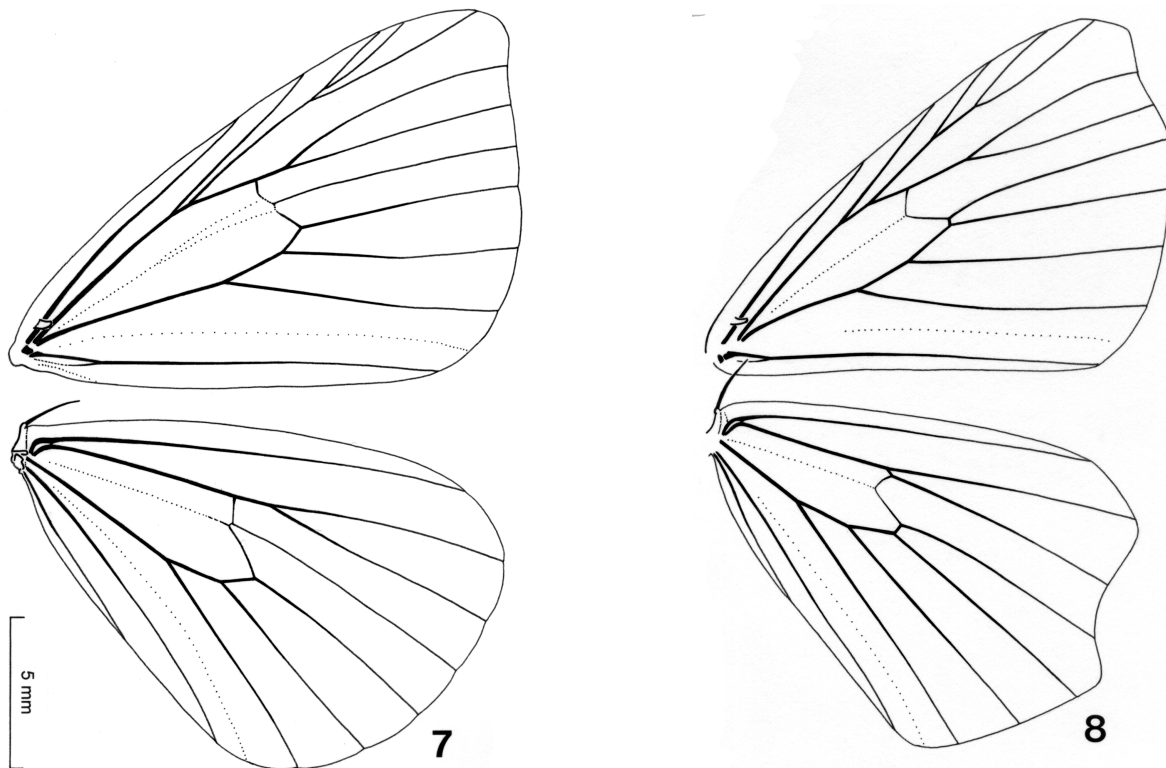
Diagnostic characters – *Deuveia banghaasi* (fig. 1) and *Amana angulifera* Walker, 1855 (fig. 6) are the only epicopeiids with a distinctive forewing pattern of three yellow stripes, which converge towards the tornus and contrast with a dark ground. The former species differs clearly from the latter in its smaller size (comparable to that of *Psychostrophia* species: figs. 3-5) and chiefly yellow hindwings (the hindwings of *Amana angulifera* are dark brown with orange marginal/submarginal markings: fig. 69 *in* Hampson 1895).

Partial redescription of the male – Wingspan: 31-34 mm. Forewing length: 17.5-20 mm.

Head vestiture. Chaetosema setae pale yellow. Ventralmost region of the frontoclypeus unscaled, glossy brown. Frontoclypeus clothed with appressed lamellar scales for its dorsal three quarters; these scales dark brown, except near the bare area, where they are yellow. Vestiture of vertex mainly appressed, dark brown; a crest of yellow scales caudad of the chaetosemata. Posterior genae with dark brown scales dorsally, with yellow (elongate) scales elsewhere. Antennae dark; scape vestiture essentially brown; flagellum with a dorsal band of dark brown scales. Maxillary palpi clothed with brown scales. Labial palpi with elongate yellow scales proximally, with dark brown scales distally.

Thorax (wings excepted). Tegulae mainly brown (yellow anteroventrally). Dorsal region of the thorax dark brown, except for an anterior group of yellow scales – basically corresponding to the patagia – and a number of elongate yellowish scales visible posterolaterally (on metascutum). Lateroventral vestiture of thorax composed of variously shaped yellow scales. Foreleg: coxa yellow; femur mainly yellow; tibia and tarsus yellow ventrally,

Figures 7-8
Wing venation. – 7, *Deuveia banghaasi* (Hering), male (specimen atypical with regard to the arrangement of forewing veins Rs1, Rs2 and Rs3). – 8, *Burmeia leesi* n. sp., male. (Same magnification for both figures)

brown dorsally (with a few yellow apical scales to the tibia and most tarsomeres). Midleg: femur yellow on its inner surface, sprinkled with numerous brown scales on its outer lateral surface; tibia and tarsus brown, with yellow ventral surfaces and only a few yellowish dorsal scales (apically on tibia and certain tarsomeres); spurs yellow, with a few brown scales. Hindleg mainly yellow; tibia dorsally provided with a narrow brown band (wider basally; absent distally); basitarsus essentially yellow; other tarsomeres brown, with a number of yellow scales (ventrally and/or distally); spurs yellow.

Abdomen. Dorsal region with a mediolongitudinal brown band, which has irregular edges and is fairly narrow anteriorly, especially on A1. Terga with a number of lateral yellow scales that may, or may not, form well defined patches. Pleural regions brown dorsally, yellow ventrally. Sterna yellow. Brush-organs with yellowish hairpencils. External surfaces of the valvae mainly yellow, though distinctly brownish dorsally.

Distribution and bionomics – *Deuveia banghaasi* occurs in central China, at rather high elevations (2000-3100 m approximately). The syntypes are from two areas near Baoji (Hering 1932), namely the surroundings of Lixian ("Lihsien", 34°05'N, 105°00'E) and the mountains to the east of Lüeyang ("Liojang", 33°20'N, 106°10'E). Further information about the distribution of the species should be soon provided by Dr Dieter Stüning (*pers. comm.*), who also intends to designate a lectotype for this taxon. The two specimens kept in MNHN – got by Dr Thierry Deuve from an anonymous Chinese collector – were found near the skirts of a forest of firs, in northern Sichuan (SW of Nanping, approximately 33°N, 104°E; 3100 m). They were flying by day, at around noon, in the month of June (10/15.vi.1987). Hering's paper also mentions June for the flight period.

Burmeia n. gen.

Type-species: *Burmeia leesi* n. sp. (by present designation).

Diagnosis – This monotypic genus is unique among epicopeiids with regard to the course of vein M2, which, in both pairs of wings, arises much closer to M3 than to M1 (fig. 8). *Burmeia* shares with *Psychostrophia* a few traits that do not occur elsewhere in the family, in particular the loss of the gnathos (figs. 18, 24) and a lengthening of the longitudinal furrows (pockets) that shelter the antero-abdominal, androconial hairpencils (fig. 10; caudad, these furrows reach the intersegmental fold A4-A5 while they do not extend beyond A3 in *Deuveia*, *Schistomitra*, *Nossa*, and *Epicopeia*). Several characters, however, distinguish *Burmeia* from *Psychostrophia*: in the male, the antennal flagellum lacks scales on most of its dorsal surface (it is continuously scaled dorsally in *Psychostrophia*); the hindwing termen is angulate between

M2 and M3 (rather than straight or weakly convex between these two veins); sternum A2 of the male does not show any reinforcement of its lateral edges; in the male, the intersegmental membrane A8-A9 is wholly unscaled (rather than provided with piliform scales near the tegumen); the tegumen and vinculum are synscleritous (rather than delimited laterally by a pair of short, narrow sutures); the thin, tubular part of the uncus is relatively short and restricted to the distal half of this sclerite (rather than long and extending cephalad of uncus mid-point; cf. figs. 22, 24); etc.

Description – Male. *Head.* Compound eyes small (smaller than in *Psychostrophia*, though slightly larger than in *Deuveia*); ocular margin angulate posterodorsally. Posterior limits of the eyes in line with the posteriormost points of the antennal sockets (when head is observed in dorsal view). Oculo-facial index: 0.95. Supraocular index: 0.25. Interommatidial sensilla very short. Ocelli absent. Chaetosemata well developed, lying postero-laterad of the scapes – hence remote from each other – and fairly remote from the eyes. Frontoclypeus wide, regularly convex, with its ventralmost area slightly produced in lateral view. Vertex strongly convex when examined in anterior view. Posterior genae very broad. Pretentorinae represented by a pair of oblique slits, strongly convergent ventrad. Distance between the scapes only slightly longer than the distance separating the right (or left) scape from the right (/left) compound eye. Antennae roughly lamellate (although the lateroventral surfaces of a given flagellomere are distinctly convex in cross-section – at least proximally; the antennae of the holotype are both incomplete, the longest one having eleven flagellomeres); scape medium-sized, with a proximal constriction; pedicel fairly short; flagellum mostly unscaled, only basally provided with a narrow dorsal row of scales; distad of the basalmost section of the antenna, flagellomeres wholly covered with fairly short trichoid sensilla that are close-set laterally and ventrally (these sensilla are longer than in *Deuveia* and approximately as long as in *Psychostrophia*). Pilifers: a pair of well developed lobes with rather long bristles. Median labral process distinctly triangular. Proboscis well developed; its proximal section somewhat flattened laterally; distal section with elongate styloconic sensilla. Maxillary palpus with only one segment apparently. Labial palpus 3-segmented, approximately as long as vertical eye diameter; segment 1 markedly curved, a bit longer than segment 2; segments 2 and 3 more or less porrect; segment 2 fairly thin, relatively straight; segment 3 thicker and shorter than the latter, and roughly spindle-shaped.
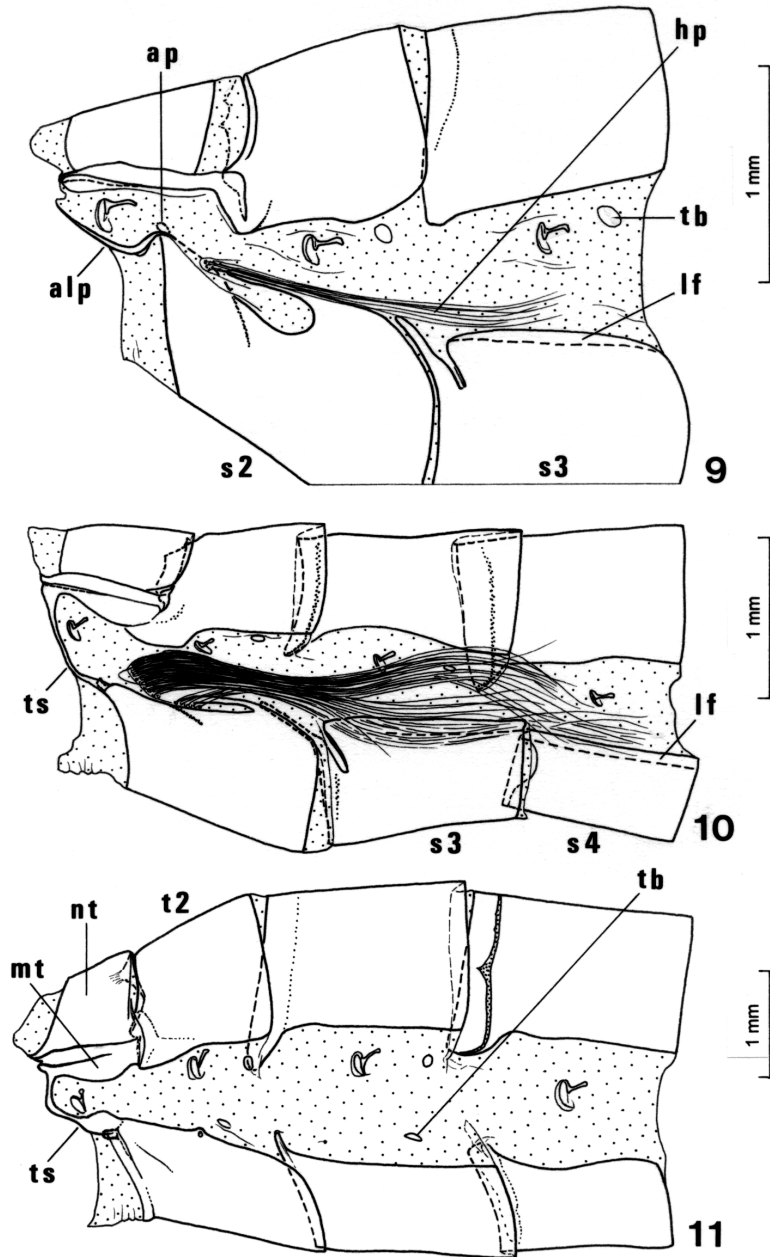
Thoracic exo- and endoskeleton. Patagia and parapatagia not examined (thorax not dissected). Ventral process of the tegula not sharply pointed, distinctly shorter than in *Psychostrophia* and approximately shaped as in *Deuveia* (with an apex apparently slightly less acute than in fig. 29). Mesopleurosternum: anepisternum large; upper sector of the precoxal suture most likely absent or very faintly indicated; marginopleural suture conspicuous, though probably shorter than that of *Deuveia*; meron broad, sharing a long line of junction with the epimeron (in lateral view, the meron is at least twice as broad as the eucoxa);

this line of junction set at right angles to the merocosta. Unscaled posterior area of the metascutellum well developed, vertical, flat to weakly concave (it tends to be concave dorsally). Metascutellar height index: about 0.6. Fenestrae laterales apparently absent; fenestra media present, medium-sized. Metepimeron and metafurca forming a broad furco-epimeral band that is much broader than the coxal membrane: the width of this band equals approx-

imately the height of the metascutellum (the latter being measured along the meson, in posterior view).

Legs. Tibiae and tarsi smooth-scaled; tarsi with a number of ventral spines (basitarsus with about 14 spines, which are not very strong). Epiphysis well developed, arising slightly basad of the fore tibia mid-point and extending to a point situated a little before the apex of the tibia. Tibial spurs fairly well developed,

Figures 9-11
Antero-abdominal region (lateral view: left side) in male epicopeiid moths. − 9, *Deuveia banghaasi* (Hering), segments A1-A3. − 10, *Burmeia leesi* n. sp., A1-A4. − 11, *Parabraxas nigromacularia* (Leech), A1-A4. − *alp*: anterolateral process of sternum A2; *ap*: apodeme; *hp*: hairpencil (or "brush"); *lf*: longitudinal furrow (= pocket for hairpencil); *mt*: marginotergite; *nt*: neotergite; *s2-s4*: sterna A2-A4; *t2*: tergum A2; *tb*: tuberculum; *ts*: tergosternal sclerite.

unspined, with pointed apices. Spur formula: 0-2-4 (the holotype lacks both midlegs but the paratype − a female − shows the usual midleg spur number: 2). Hindleg: distance between the medial spur sockets and the apex of the tibia representing a little more than one-quarter of the tibial length; distal section (more than one-third) of the tibia and median section (less than one-half) of the basitarsus with the integument weakly sclerotized, i.e. turning blue with Chlorazol Black E; basitarsus straight in lateral view, despite its weakly sinuous dorsal edge. Pretarsus: arolium well developed; pulvillus dorsal edge with elongate "outgrowths" that do not form, apparently, a well defined lobe; claws without endodonts.

Wings. Scales mostly lamellar, never deeply cleft (the vesture of the wings is badly preserved in the holotype). A number of piliform scales on forewing under surface and on hindwing upper and under surfaces. Forewing base: spinarea absent; subcostal retinaculum oblique to Sc, longer than broad, with its distal part narrower than its base. Hindwing base: frenulum fairly long, with tapering apex and small, granule-like base. Forewing costa strongly arched just before the apex (fig. 8); termen distinctly concave between the apex and M1, and convex at M2; vein Sc short, ending before middle of costa; R free; stem Rs1 + 2 + 3 rather short and perfectly straight; base of this stem moderately remote from the upper angle of the discal cell; Rs3 running to the costa and stalked with Rs2 for a longer distance than Rs1 with Rs2 + 3; Rs4 stalked with M1; discocellular vein M1-M2 strongly bent basad and much longer than the straight discocellular M2-M3 (hence M2 arises closer to M3 than to M1); CuA1 arising midway between M3 and CuA2; stem of M and vein CuP replaced by folds; "basal fork" of 1A + 2A short, with very thin lower branch. Hindwing: termen angulate at Rs, or just below Rs tip, and between M2 and M3; termen markedly concave between the two "angles" in question and hardly convex between M3 and CuA2; subcosta and upper edge of discal cell strongly bent basally, touching at one point near wing base and then distinctly diverging; Rs and M1 separate, though approximate basad; discocellulars M1-M2 and M2-M3 shaped as in the forewing; M2 arising closer to M3 than to M1; CuA1 remote from M3; CuP and stem of M replaced by folds; 3A present, half as long as 1A + 2A.

Pregenital abdomen (figs. 10, 18, 20, 21). Ventral part of the intersegmental thoraco-abdominal membrane bearing a number of scales, some of which are nearly piliform. Abdomen clothed with appressed lamellar scales on most of its surface but provided with numerous piliform/nearly piliform scales in its anteroventral region. Terga without stiff lanceolate scales posteriorly. Dorsum A1: neotergite well developed and fused, laterally, with the marginotergites; ventral (outer) edge of marginotergite regularly arched (convex) for the posterior three-quarters of its length. Tergum A2 produced anterolaterally, along short posterior sections of the edges of the marginotergites; its antecostal phragma moderately broad; tergal rods absent. Sternum A2: anterolateral angles connected to the anterior lobes of the marginotergites by thin, though complete, prespiracular tergosternal sclerites (*ts*); apodemes minute; venulae absent; sternum lateral edges neither thickened nor heavily pigmented; each lateral edge provided with a free arm, which arises from the posterior half of the edge, extends cephalad, and ends in a concave sclerite bearing a long hairpencil.

Posterior part of the hairpencil lying (when the insect is at rest) in a longitudinal furrow delimited, ventrad, by the infolded lateral edges of sterna A3 and A4. Sternum A3 with elongate anterolateral projections. Most abdominal sterna with parallel or almost parallel lateral edges. Sternum A8 short, with convex lateral edges (fig. 20); its anterior edge provided with a pair of shallow, though well defined, depressions. Tergum A8 entire but constricted near middle (fig. 21); its anterior angles produced antero-laterad. Intersegmental membrane A8-A9 devoid of scales.

Genitalia (figs. 18, 19, 22, 23). Tegumen and vinculum synscleritous; the former separated from the uncus by a well indicated suture. Saccus short, triangular in ventral view. Mesal, posterior region of the vinculum differentiated into a separate, subtrapezoidal, intersaccular sclerite (fig. 19: *is*), which comes very close to the juxta. Valva with concave costa, rounded apex, and densely setose inner surface; costula markedly enlarged, broad and bifid (with a long dorsal arm and a shorter ventral one); dorsal arms of costulae practically adjacent mesally (i.e. only separated by a very narrow strip of membrane); sacculus well defined, ending in a curved, heavily pigmented praesacculus (*ps*). Juxta a free, undivided, medium-sized sclerite. Uncus (*un*) approximately as long as the middorsal region of the tegumen (fig. 22), and regularly arched − concave ventrad − when observed in lateral view (fig. 18); its proximal half subtriangular in dorsal view, its distal half moderately elongate, ending in a pointed apex. Uncus base flanked, ventrally, by a pair of small, wart-like socii (*so*). Gnathos absent. Subscaphium present, though weakly pigmented. Phallus elongate, subcylindrical (fig. 23), with a single cornutus and a medium-sized anteroventral coecum.

Female. *Head.* Approximately as in male, apart from the vestiture of the antennae. Oculo-facial index: 0.91. Supraocular index: 0.255. Antennal flagellum filiform, slightly compressed laterally and distinctly scaled dorsally (the scales form a narrow continuous strip − to the best of my judgment, for the paratype has broken antennae, the longest flagellum having preserved no more than thirteen segments); trichoid sensilla of the flagellum slightly shorter than in male, in particular dorsally. Labial palpus 3-segmented, with segment 1 longer than segment 2; segment 3 short, more or less button-shaped; segments 2 and 3 ascending (rather than porrect).

Thoracic exo- and endoskeleton. Apparently as in male. Mesoscutellum fairly rounded caudad. Dorsal region of the metascutellum convex and narrow. Fenestrae laterales clearly absent.

Legs. Fore tibia as in male. Midleg with two tibial spurs; length of shorter spur exceeding the greatest width of the tibia; longer spur reaching approximately the mid-point of the basitarsus. Hindleg morphology unknown (the paratype lacks both hindlegs).

Wings. Forewing base without subcostal retinaculum (normal female conformation). Hindwing: frenular bristles apparently absent. Venation as in male. Vein M1 is teratological (i.e. cleft) in the right hindwing of the paratype.

Abdomen. Unknown (the paratype has lost it).

Etymology – The generic name refers to the country (Burma) where occurs the type-species.

Gender: feminine.

Burmeia leesi n. sp.

Type-series – Holotype male with four labels: "Htawgaw. N. Burma. 10,000 [feet]. 27-7-[19]27", "Burma. H.C. Tytler. B.M. 1938-678", "*Burmeia leesi* Minet. *Holotype*", "[Uran.] genitalia slide No. 182". Paratype, 1 female with three labels, the first two as above ("Htawgaw …", "Burma …"), the third specifying "*Burmeia leesi* Minet. *Paratype*". Both specimens in BMNH (The Natural History Museum, London).

Diagnostic characters - *Burmeia leesi* (fig. 2) differs from *Deuveia banghaasi* (fig. 1) in lacking three convergent yellow stripes in the forewing, and from those epicopeiids that are usually larger (*Amana*, *Chatamla*, *Parabraxas*, *Schistomitra*, *Nossa* and *Epicopeia*) in retaining, in the forewing venation, a straight stem Rs1 + 2 + 3, which is not approximated to R some distance beyond the discal cell (fig. 8).

The species belonging to *Psychostrophia* and *Burmeia* have a somewhat similar habitus. They can be easily identified, however, with the help of the following key.

1. Wings pure white with dark brown or black markings; main white area of the forewing reaching most of the inner margin (figs. 2, 4); in male, subscaphium without distinct pilosity (fig. 19) 2
– Wings dark brown or black with light markings, normally yellow or creamy white; main light area(s) of the forewing either separated from the inner margin (fig. 3) or only reaching a relatively short section of this margin (fig. 5); in male, subscaphium distinctly pilose (fig. 24) 3
2. In forewing, vein M2 arising much closer to M3 than to M1 (fig. 8); hindwing termen markedly concave between the apex and a blunt angle situated below M2 (fig. 2) . . . . *Burmeia leesi* n. sp.
– In forewing, vein M2 arising midway between M1 and M3 or slightly closer to M3 than to M1; hindwing termen at most weakly concave between the apex and vein M3 (fig. 4)
. . . . *Psychostrophia nymphidiaria* (Oberthür)
3. Forewing upperside with an entirely black, or blackish, discal cell and without light submarginal spots below M1 (see fig. 1 *in* Inoue 1992); forewing length 16 mm (at least in the holotype) . . . *Psychostrophia endoi* Inoue
– Forewing upperside with a variously developed light area in the discal cell and, typically, two or more light submarginal spots below M1 (these spots may be merged in a continuous band); forewing length often above 17 mm (though occasionally measuring 15 or 16 mm) 4
4. Forewing with two large light – typically yellow – areas, one of which (the proximal one) is subtriangular and longitudinal; hindwing without a transverse, medial, black band (fig. 3) . . *Psychostrophia melanargia* Butler
– Forewing with a single large light area, namely a creamy oblique band that reaches the inner margin; hindwing with a broad, transverse, medial black band (fig. 5)
. . . . *Psychostrophia picaria* Leech

Description – **Male**. Wingspan: 28.5 mm. Forewing length: 17 mm.

Head. In the holotype, the head has lost many scales. Head capsule and antennae with blackish-brown integument. Distance between compound eyes across frontoclypeus: 0.75 mm. Eye "width" when head is observed in frontal view: 0.35 mm. Chaetosema "setae" yellow. Frontoclypeus with a number of brown, appressed scales (possibly also with yellow scales, which may have been lost in the holotype). Interantennal area provided with a few pale yellow, rather long, scales that are directed anteroventrad. Vertex with brown, anteriorly directed scales. On posterior genae, scales either pale yellow or – dorsally, caudad of the eyes – brown. Base of antennal flagellum with a few brown (dorsal) scales. Labial palpus integument yellowish on segments 1 and 2, dark brown on segment 3. Segments 1-3 of this palp measuring, respectively, 0.31 mm, 0.29 mm and 0.20 mm.
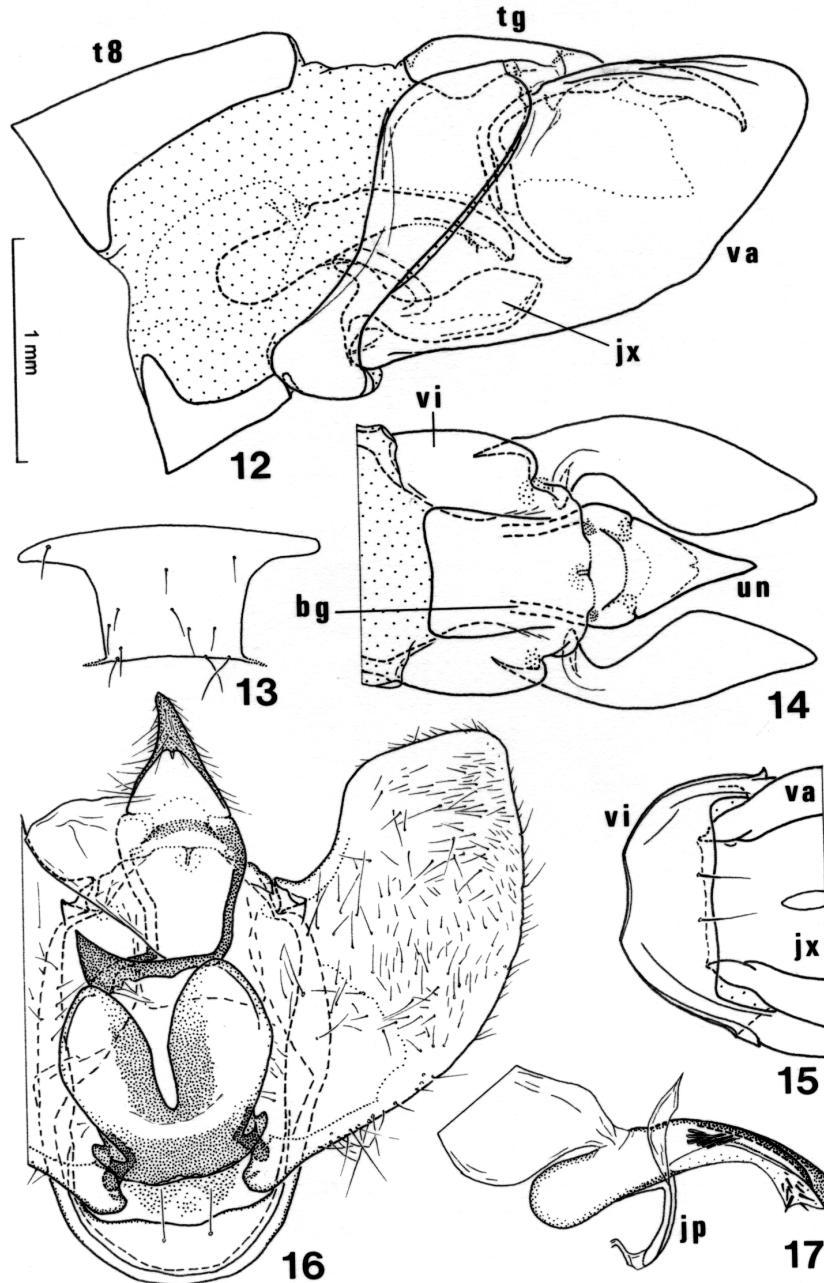
Thorax (wings excepted). Tegulae mainly clothed with brown scales. Dorsal vestiture of thorax essentially composed of brown, appressed scales. Anterodorsal region of thorax with a few yellowish-white scales, some of which are elongate and pointed. Thorax with its lateroventral vestiture badly preserved in the holotype, composed of yellowish-white scales (e.g. anterolaterally) and a number of brown scales. Coxal membranes (of metathorax) clothed with whitish scales, certain of which are piliform. Mesothoracic coxa (in lateral view): eucoxa and meron measuring respectively, in width, 0.30 mm and 0.65 mm (midway between trochanter and epimeron ventral edge). Holotype (without midlegs) having lost many leg scales. Foreleg: coxa and femur yellowish-white, with a few brown scales; tibia and tarsus brown, with a number of pale yellow scales (e.g. near the epiphysis and at the apex of the tibia); femur 2.00 mm in length, tibia 1.50 mm, epiphysis about 0.70 mm, and tarsus 2.25 mm. Hindleg: femur, tibia and tibial spurs with both brown scales and yellowish-white scales; tarsus brown, with a few pale yellow scales; femur 2.00 mm in length, tibia 2.30 mm, each medial spur around 0.40 mm (the inner one is hardly longer than the outer one), inner apical spur 0.75 mm, outer apical spur 0.55 mm, and tarsus 2.15 mm.

Wings. Upperside of forewing dark brown (probably blackish when not faded), with five white areas: a large, proximal, quadrilateral (delimited by the inner margin, a line close to the costa, a line joining a point near discal cell upper angle and another on vein M3, and a line extending from M3 to a point close to the tornus), a fairly large subapical spot (that lies approximately between Rs2 and M1, and three smaller submarginal spots (a medium-sized rounded one, which is adjacent to M2 and crossed by M3, a lunule on CuA1, and an elongate, transverse mark on CuA2). Forewing fringe greatly damaged, apparently dark brown, with a number of white scales between the apex and vein M1. Upperside of hindwing white with a dark brown terminal band, which exhibits four submarginal white spots (a large one between the apex and M1, a medium-sized one on M3, and two small ones on, respectively, CuA1 and CuA2); proximal edge of the dark band bent on M3, and rather indistinct and scalloped between M3 and the tornus; inner margin with a thin dark streak that originates near the middle of 1A + 2A and ends just proximad of the tornus. Hindwing fringe white along a large proximal section (2/3 ?) of the inner margin, dark brown everywhere else, except for a number of

white scales occurring between Sc + R and Rs, and in space M1-M2. Underside of wings (fringes included): as upperside, but with forewing showing white scales scattered over the proximal part of the brown costal area (approximately up to that point where R arises from discal cell), and with hindwing devoid of dark streak along inner margin and exhibiting, between M3 and

the tornus (inwards), a scalloped dark band boundary that is sharper than on the upperside.

Abdomen. Dorsal region uniformly brown. Ventrally and lateroventrally, vesture of abdomen consisting of both brown scales and white scales (the latter do not form any well defined pattern). Anteroventral region of abdomen essentially white,

Figures 12-17
Deuveia banghaasi (Hering), male: genitalia and segment A8. − 12, lateral view of this region after removal of the vesture. − 13, sternum A8 (anterior edge uppermost). − 14, genitalia in dorsal view (vesture removed/omitted). − 15, anterior region of genitalia, ventral view. − 16, genitalia in posterior view, with the valvae spread and the phallus removed. − 17, phallus and "junction piece", lateral view. − *bg*: base of gnathos; *jp*: junction piece; *jx*: juxta; *t8*: tergum A8; *tg*: tegumen; *un*: uncus; *va*: valva (= gonopod); *vi*: vinculum. (Uniform magnification)

being notably provided with long white piliform scales. Anterolateral hairpencils straw-coloured. Valvae with their external surfaces mainly clothed in brown scales. Abdomen exhibiting, ventrad and laterad of the valvae, a number of elongate off-white scales. Genitalia and A8: see figs. 18-23 and the description of the genus.

Female. Wingspan: 31.5 mm. Forewing length: 19 mm.

Head. Chaetosemata represented on head capsule by elongate areas, which are remote from, and parallel to, each other. Each chaetosema composed of slightly above twenty yellowish-white "setae". Head rather smooth-scaled, although provided with erect scales in the posteriormost region of the vertex. Scales of frontoclypeus more or less elongate, either brown or (especially ventrad of antennal sockets) pale yellow. Lower part of frontoclypeus devoid of scales. Vertex scales brown. Vestiture of posterior genae as in male. Antenna: scape with both brown scales and pale yellow scales (the latter lying mostly mesad and ventrad); pedicel and dorsal region of flagellum clothed in brown scales. Pilifer bristles long, pale beige. Proboscis pale chestnut. Labial palpus vestiture mainly pale yellow, with a few brown scales on segment 3; segments 1 and 2 ventrally provided with loose slender scales.

Thorax (wings excepted). Tegulae and dorsal region of thorax brown, with a few yellowish-white scales anteriorly (probably inserted on the patagia). Lateroventral and posterior vestiture of thorax apparently as in male (it is badly preserved in the paratype). Subalar membranes with brown scales. Metathorax: furco-epimeral bands clothed in brown scales; posterior, vertical surface of scutellum about 0.50 mm in height (mesally). Foreleg: coxa off-white; femur and tibia coloured as in male; tarsus brown, with rather numerous yellowish-white scales on its outer lateral surface; each tarsomere with a yellowish-white "fringe" distally; femur about 2.50 mm in length, tibia 1.50 mm, epiphysis 0.75 mm, and tarsus 2.50 mm. Midleg: femur with numerous off-white scales and a few brown scales; tibia and its spurs brown, with a few yellowish-white scales; apex of tibia with a yellowish-white fringe; tarsus brown, with a number of yellowish-white scales, notably on the basitarsus and at the "apex" of each tarsomere; femur 3.00 mm in length, tibia 2.75 mm, inner spur about 0.75 mm, outer spur 0.50 mm, and tarsus 3.00 mm.

Wings. Forewing: apex less produced than in male; termen straight (rather than concave) between the apex and M2. Coloration of wings (upper- and undersides): almost identical to that of the male. Forewing upperside: large white quadrilateral with its upper angle situated midway between the apices of stems Rs1 + 2 + 3 and Rs4 + M1 (the latter stem is short and lies entirely in the white area); lower, elongate, submarginal mark distinctly swollen near the tornus. Hindwing with the spot on M3 reaching vein M2 on the upperside, but not on the underside.

Abdomen. Unknown, probably brown dorsally.

Distribution and bionomics – The only specimens that I was able to find in BMNH collections are the holotype and paratype, both from Htawgaw (26°00'N, 98°20'E) in eastern Kachin (extreme N.-E. of Burma). They were caught at an elevation of about 3000 m. This moth flies by day in all probability. Indeed the two spec-

imens from Htawgaw were taken by Major-General Harry C. Tytler, who was a collector of butterflies (Talbot 1939). Moreover, their date of capture – 27.vii.1927 – is also mentioned by Tytler (1940: 116) for a butterfly of the genus *Euthalia* Hübner (with a slightly different spelling of the locality in question: Hthawgaw).

Etymology – I have chosen to name this species after Dr David C. Lees (BMNH). Indeed I would like to thank him for his invaluable help with my exploration of certain collections kept in the BMNH.
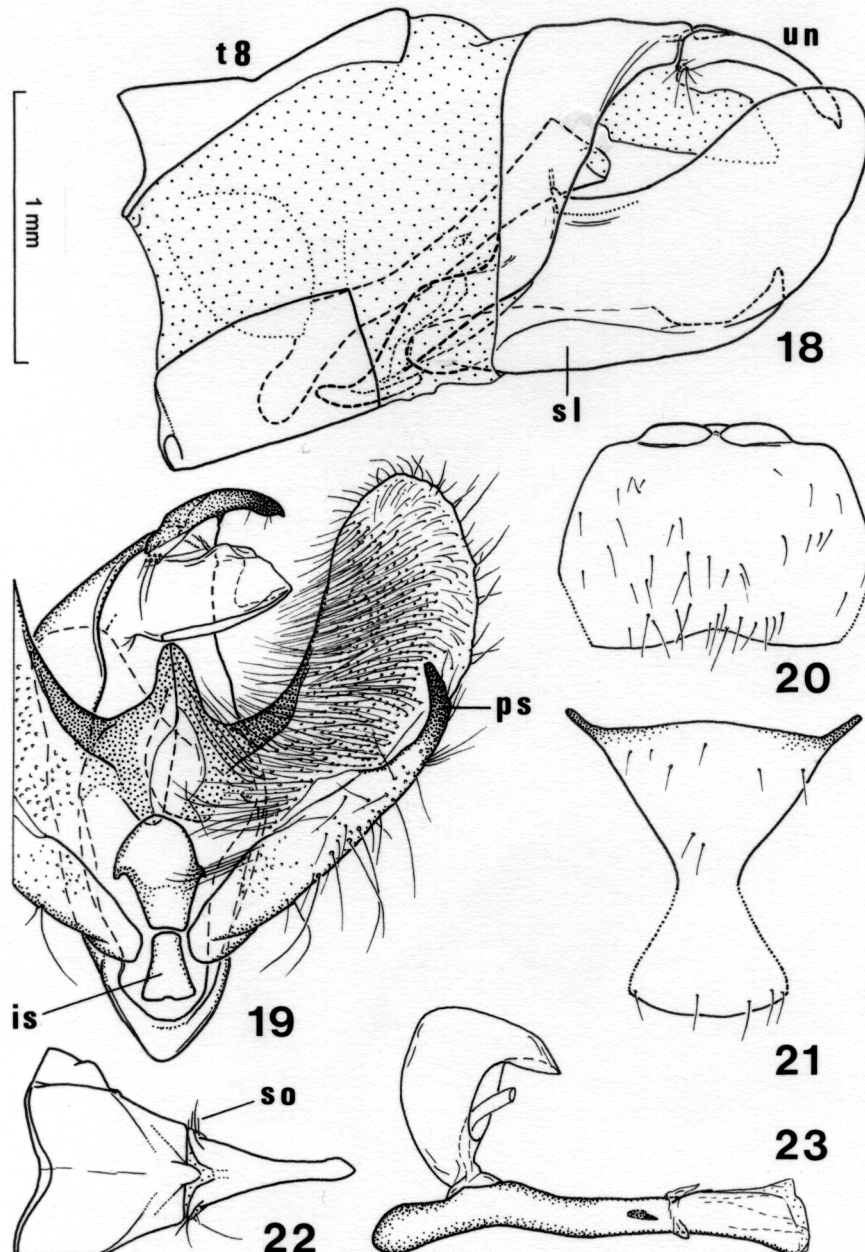
II. THE DREPANOIDEA: PHYLOGENY AND SUBFAMILY-LEVEL CLASSIFICATION

As recently redefined (Minet 1991), the superfamily Drepanoidea includes only two families, namely the Epicopeiidae and Drepanidae. Since the former is composed of a limited number of genera (9), it is probably advisable to avoid dividing it into subfamilies. However, as proposed in section III, its basic dichotomy lies, fairly clearly, between *Deuveia* and the other epicopeiid genera. Within the Drepanidae, the first dichotomy is likely to lie between the Cyclidiinae and the Thyatirinae + Drepaninae. Indeed, the latter lineage differs from the former (subfamily Cyclidiinae) in possessing, in the imaginal ground plan, the following three apomorphies: a male frenulum with clubbed apex (e.g. fig. 17 *in* Scoble & Edwards 1988), a small tympanal chamber provided with a fairly broad dorsal sclerotized wall (e.g. Gohrbandt 1937: fig. 14, HW ["Hinterwand"]), and a large tympanal chamber that is distinctly fused with sternum A2 mesad of the apodemal protrusion (e.g. Minet 1983: fig. 95). Unlike that of many Thyatirinae and Drepaninae, the small tympanal chamber of the Cyclidiinae has a dorsal sclerotized wall which varies from extremely narrow to entirely absent.

These assumptions about the phylogeny of the Epicopeiidae and Drepanidae are essential for defining the ground plan of the Drepanoidea and its possible autapomorphies. It should be noted that the Thyatirinae now include, among their "primitive" members, the genus *Hypsidia* Rothschild, which was previously regarded as "*incertae sedis*" within the Drepanidae (Scoble & Edwards 1988; see Holloway 1998: 73). *Hypsidia* indeed has a number of derived traits that I interpret as thyatirine autapomorphies: segment A2 without androconial brush-organs (a loss also occurring, through homoplasy, in most Drepaninae and a few Epicopeiidae); sternum A8 of male with concave, V-shaped posterior edge; tergum A8 (of male) unsclerotized or weakly scle-

rotized, except for its anterior "arms", a narrow medio-longitudinal strip and, sometimes, variously developed posterolateral areas (the anterior arms and mesal strip form a T- or Y-shaped structure); etc. From a comparison between the basalmost Epicopeiidae (*Deuveia*; *Burmeia* and *Psychostrophia*) and several "primitive"

Drepanidae (Cyclidiinae, *Hypsidia*, *Chaeopsestis*, *Spica* [three thyatirine genera], etc.) I now consider five autapomorphies for the definition of the Drepanoidea, namely an imaginal abdomen base (α) with complete or nearly complete (*Deuveia*) tergosternal sclerites and (β) whose neotergite is distinctly fused with the marginotergites

Figures 18-23
Burmeia leesi n. sp., male: genitalia and A8. − 18, this region in lateral view (scales removed). − 19, genitalia, posterior view (valvae spread; phallus removed). − 20, sternum A8 (anterior edge uppermost). − 21, tergum A8. − 22, tegumen and uncus in dorsal view. − 23, phallus, lateral view. − *is*: intersaccular sclerite; *ps*: praesacculus; *sl*: sacculus; *so*: socius; *t8*: tergum A8; *un*: uncus.(Uniform magnification)

(unlike many Geometroidea: cf., e.g., *Archiearis*), a larva (γ) whose mandible shows a large, flat, lateral area, which is delimited ventrally by a well defined carina (Minet 1991; Minet & Scoble [1998]), and (δ) whose most abdominal segments have at least one secondary seta cephalad of L3 (*ibid.*), lastly a pupa (ε) that never exhibits a conspicuous portion of the fore femur (Minet 1991: 87). However, apomorphies γ-ε are only proposed tentatively since the early stages remain unknown in the genera *Deuveia* and *Burmeia*.

For the time being, only the imaginal morphology can disclose synapomorphies shared by the nine epicopeiid genera (i.e. autapomorphies of the Epicopeiidae). I regard the 12 following traits as such apomorphies: (a) compound eyes reduced in size, their posterior margins never really extending − backwards − beyond the posterior parts of the antennal sockets (for that reason, the posterior gena is broad: primarily, e.g. as in *Deuveia*, it is broader than the postgena), (b) posterior part of the ocular ridge unpigmented (unlike the anterior part), (c) head without ocelli (while these occur in certain Drepanidae: Minet & Scoble [1998]: 303), (d) proximal outer surface of the labial palpus clothed with yellow scales (which are replaced by red scales in *Epicopeia*, by dark scales in *Schistomitra* and certain *Nossa*), (e) ventral process of the tegula ending in a fairly sharp point (that is not necessarily elongated: cf. the ground plan condition found in two genera, viz. *Deuveia* − fig. 29 − and *Burmeia*), (f) in mesothorax, basisternal mesal suture and its ridge not exactly reaching the anterodorsal margin of the basisternum (by contrast, the suture distinctly reaches this margin in the drepanid ground plan), (g) in metathorax, furco-epimeral band very broad, primarily much broader than the coxal membrane lying below it, (h) metacoxa with its merocosta ending, ventrally, close to the sagittal plane and well above the coxotrochanteral articulation, (i) pretarsal claws without endodonts (unlike the condition occurring in many Drepanidae), (j) forewing without an areole, (k) in the forewing ground plan, vein Rs4 stalked with M1 and separated from Rs1 + 2 + 3 (figs. 7, 8), (l) spinarea absent (whereas it is present in most Thyatirinae: e.g. fig. 17.1 B *in* Minet & Scoble [1998]). For many of these apomorphies, the corresponding plesiomorphic states can be easily inferred from the above descriptions. In the case of d, the plesiomorphic coloration of the labial palpus is characterized by a wholly brownish or greyish outer surface: it is commonplace in (e.g.) the Drepanidae and can be regarded as part of the ground plan of this family. Instances of reversal or secondary modification must be considered for a few of the epicopeiid autapomorphies, in particular for d and k. In the latter case, for example, vein Rs4 is

secondarily free in certain species of the genera *Nossa* (Elwes 1890: pl. 34, figs. 2, 3) and *Epicopeia* (e.g. Janet & Wytsman 1903: pl. 1, fig. 2); occasionally it may also be free, or almost free, in *Amana angulifera* Walker (sometimes in one forewing only). Many of the 12 above-mentioned apomorphies also occur, through parallel evolution, in a number of groups standing in the vicinity of the Epicopeiidae: i occurs notably in nearly all Geometroidea (not in *Eumelea* Duncan, however), k in various Uraniidae, l in many Drepanidae and all Geometroidea, etc.

The monophyly of the Drepanidae is clearly supported by a type of hearing organ, which is unique in the Lepidoptera (e.g. Scoble 1992: 139). A derived trait of the male genitalia can be regarded as an additional autapomorphy of the Drepanidae: in the family ground plan, the costula emits an elongate, tapering, ventral arm that comes into a lateral notch of the juxta. Outwards and ventrad, this notch is delimited by a setose lobe, which belongs to the juxta and may be flat or raised ("Juxtalappen" of Werny 1966; "clavus" *sensu* Forbes 1940). The long ventral arm of the costula is easily observable in *Cyclidia* Guenée (Cyclidiinae) and the Thyatirinae, but never occurs in the Epicopeiidae.

III. PHYLOGENY OF THE EPICOPEIIDAE

As specified in the introductory section, the composition of the Epicopeiidae has long been restricted to one or two genera. Henceforth this family includes as many as nine genera.
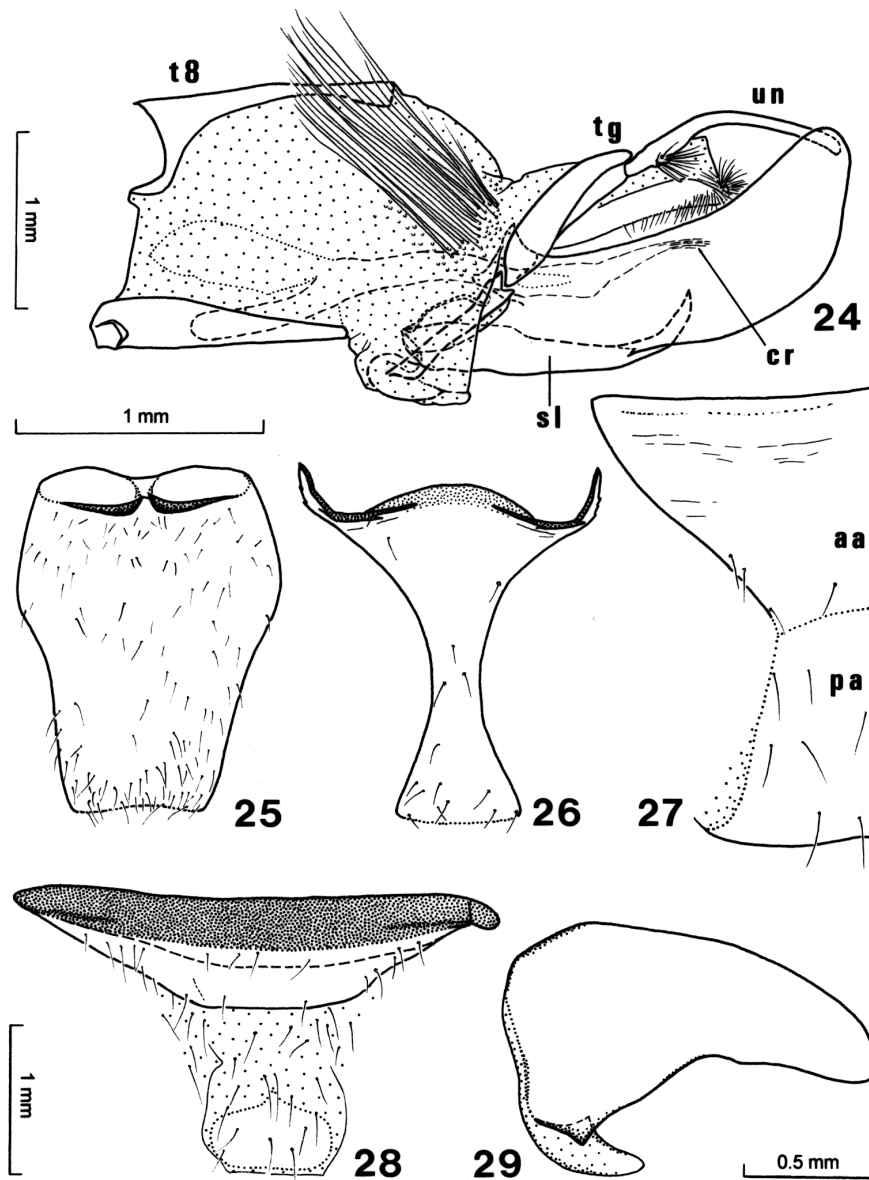
Preliminary remarks about the monophyletic nature of the nine considered genera

In the cladistic analysis proposed below, the epicopeiid genera have been selected as terminal taxa, which implies that they can all be regarded as monophyletic units. This is indeed the case, although the monophyly of *Nossa* is less obvious than that of the other genera, being supported by two, rather commonplace, apomorphies (sacculus truncate distally; gnathos apex bifid, i.e. gnathos consisting of a pair of independent "arms", which are connected only by a mesal membrane). A limited number of apomorphies that may characterize genera have been indicated on the cladogram of fig. 30: in fact, they correspond to features already used for defining one or more suprageneric groups, that is to characters whose interpretation is not unquestionable (see next section). However, for each genus, further apomorphies turn out to support its monophyly. They are listed hereafter, although not exhaustively for five

genera currently regarded as monotypic (viz. *Deuveia*, *Burmeia*, *Amana*, *Chatamla* and *Schistomitra*).

Deuveia: labial palpi 2-segmented; anterior edge of the mesobasisternum concave mesally, between the arms of the mesoclidium (while it is convex or slightly produced dorsad/cephalad (mesally) in *Psychostrophia*, *Cyclidia* and most other Drepanoidea); veins Rs and M1 stalked in the hindwing; in the male, sterna A4-A6 with lateral edges that are markedly convergent cephalad; tegumen small, much less extensive than the vinculum in lateral view; valva without a praesacculus (while the latter pertains to the drepanoid ground plan: cf. *Mimozethes*, many Thyatirinae, *Burmeia*, *Psychostrophia*, etc.); juxta specialized, provided with a pair of conspicuous, posteriorly projecting, lobes.

Figures 24-29

Epicopeiidae: male segment A8, male genitalia and tegula. − 24, *Psychostrophia picaria* Leech, A8 and genitalia, lateral view (after removal of most scales). − 25, ditto, sternum A8. − 26, ditto, tergum A8. − 27, *Parabraxas nigromacularia* (Leech), left half of tergum A8. − 28, *Nossa moorei* (Elwes), tergum A8. − 29, *Deuveia banghaasi* (Hering), tegula (vestiture removed). − *aa*: anterior (weakly sclerotized) area; *cr*: cornuti; *pa*: posterior (well sclerotized) area; *sl*: sacculus; *t8*: tergum A8; *tg*: tegumen; *un*: uncus. − Anterior edges uppermost in figs 25-28. (Uniform magnification for figs 25-27)

Burmeia: antennal flagellum of the male without scales, except in its basalmost section (dorsally); in both pairs of wings, M2 arising closer to M3 than to M1; hindwing termen markedly concave below apex; tegumen and vinculum synscleritous (i.e. neither articulated nor separated by a furrow or distinct suture).

Psychostrophia: presence of a pigmented line – with narrow internal ridge – along each lateral edge of sternum A2 (apomorphy relating to the male sex, like the next four ones); sternum A8 longer than in the other epicopeiid genera (approximately as long as broad in *P. nymphidiaria*; longer than broad in the other three species: fig. 25); anterolateral projections of tergum A8 distinctly arched, that is to say with convex posterolateral margins (fig. 26; by contrast, these margins are straight in *Burmeia*: fig. 21); intersegmental membrane A8-A9 provided with piliform scales close to the genitalia (fig. 24); uncus elongate, thin (tubular) for most of its length (only the distal half of the uncus is thin and tubular in *Burmeia*).

Amana: compound eyes with long interommatidial sensilla; in male genitalia, intersaccular sclerite very narrow.

Chatamla: forewing with several translucent spots, which are covered – dorsally and ventrally – with erect, translucent scales; hindwing termen more or less concave below the apex of M1 (e.g. Hampson 1895: fig. 63); in male genitalia, costula ventrally provided with an elongate, caudally projecting, heavily sclerotized, free arm.

Parabraxas: costal area of the forewing yellow or orange with dark spotting (secondarily black in "*P. erebina* (Oberthür)", a taxon here regarded as a melanic form – stat. rev. – of *P. davidi*); ventral surface of the abdomen with a mediolongitudinal row of black spots (cf. discussion about character 23); sacculus without a praesacculus (as in *Deuveia* [parallel evolution]); uncus bifid.

Schistomitra: labial palpi entirely blackish-brown (therefore not coloured as in most Epicopeiidae: cf. section II, apomorphy d); free (i.e. distal) region of the gnathos represented by a pair of fairly short, independent arms, which are finely dentate dorsally.

Epicopeia: labial palpi with red scales, at least proximally; male retinaculum vestigial (*E. mencia*) to absent (other species); forewing dorsal surface without distinct transverse markings (notably without any transverse series of spots); hindwing termen concave below the apex (almost straight, however, in certain specimens of *E. mencia*: e.g. p. 83, fig. 3, *in* Endo & Kishida 1999).

Searching for the relationships among epicopeiid genera

In 1982, Inoue created the subfamily Schistomitrinae for *Schistomitra* and *Psychostrophia*, two genera occurring in Japan and maintained by him in the "Epiplemidae" (currently Uraniidae: Epipleminae). However, these genera belong to the Epicopeiidae and, according to the present study, *Schistomitra* turns out to be more closely related to *Nossa* and *Epicopeia* than to *Psychostrophia*. The "Schistomitrinae" should thus be regarded just as a synonym of the Epicopeiidae. To date the phylogeny of this family has not been really investigated. Only one publication proposes, tentatively and without justification, to divide the Epicopeiidae into "at least three major lineages", namely *Epicopeia*, *Nossa* + *Parabraxas* and *Schistomi[t]ra* + *Psychostrophia* (Yen *et al.* 1995: 183). Except for the genus *Epicopeia*, these groups cannot be considered monophyletic if one takes into account the two cladograms (figs. 30, 31), which result from the analysis of the following 34 characters. Before discussing these diagrams, I shall describe the characters in question, mentioning for each of them, first the apomorphic state (= [1]) and then, in brackets, the corresponding plesiomorphy (= [0]). In the four sections hereafter, all characters are informative (i.e. neither restricted to one genus nor invariably present throughout the Epicopeiidae) and stem from the imaginal – mostly male – morphology.

Head of the male imago

1. [1]: *antennae heavily "ciliated", each flagellomere bearing a crown of long sensilla trichodea, which are arranged – laterally – in a horseshoe-shaped row* ([0]: antennae with short to moderately long sensilla trichodea, which primarily are densely and regularly distributed over the lateroventral sides of the flagellum).

   In my opinion, this is a clear synapomorphy of *Chatamla* and *Parabraxas*. In these genera, the lateral sensilla appear distinctly longer than the width of the flagellum when the latter is observed in dorsal view; they are arranged as in typical Sphingidae (Eaton 1988: fig. 4.7), which represents a case of parallel evolution. *Deuveia*, *Burmeia*, *Psychostrophia* and *Amana* have lamellate or "prismatic" antennae that bear short or fairly short, close-set, sensilla trichodea. A similar conformation occurs in primitive Drepanidae (e.g. in *Cyclidia*) and can be ascribed to the ground plan of the Drepanoidea. In those Epicopeiidae provided with bipectinate antennae, the sensilla trichodea situated along the rami may be moderately long, but remain less conspicuous than in *Chatamla* and *Parabraxas*.

2. [1]: *antennae bipectinate* ([0]: antennae simple, primarily lamellate).

Within the Epicopeiidae, bipectinate antennae occur only in *Schistomitra*, *Nossa* and *Epicopeia*. Furthermore these three genera have the antennal rami always more or less flattened (compressed, actually).

3. [1]: *ramus dorsal region entirely unscaled, but with sensilla trichodea in (at least) its distal half* ([0]: this region scaled, at least for most of the length of the ramus).

This character and the next one can be considered only for those epicopeiids whose antennae are bipectinate (hence a number of question marks inserted in the data matrix : see Appendix). The presence of sensilla trichodea on the dorsal edge of a ramus is quite unusual in lepidopterans, even when this edge is devoid of scales. Accordingly, I regard as apomorphic the ramus vesti-ture shared by *Nossa* and *Epicopeia*: here the rami lack scales but are dorsally provided with sensilla trichodea, either for their whole length or, less often, approximately in their distal half. By contrast, in *Schistomitra*, the dorsal region of a ramus bears scales, except for its distal third where occur a few sensilla trichodea.

4. [1]: *ventral edges of the rami irregularly denticulate* ([0]: every ramus with a relatively regular ventral edge that lacks conspicuous teeth or notches).

A synapomorphy of *Nossa* and *Epicopeia*. In these genera, adjacent rami may differ markedly in shape. It should be noted that character 4 has been polarized like character 3, basically on similar grounds (rarity of one state in non-epicopeiid families).

Imaginal thorax

5. [1]: *tegula with elongate ventral process* (fig. 51 *in* Minet 1991) ([0]: process short, though rather acute apically: fig. 29).

In *Deuveia* and *Burmeia*, the process of the tegula has a shape that probably corresponds to the ground plan of the Epicopeiidae (if one disregards a slight difference in the sharpness of the process apex). As mentioned in section II, this shape can be considered autapomorphic at the epicopeiid level, since the process apex is comparatively obtuse in "primitive" Drepanidae (*Cyclidia*, *Hypsidia*, *Thyatira*, etc.). However, it is plesiomorphic in rela-tion to the elongated shape which characterizes the clade *Amana + Chatamla + Parabraxas + Schistomitra + Nossa + Epicopeia*, as well as the genus *Psychostrophia* (sister to *Burmeia*).

6. [1]: *mesothorax with enlarged anepisternum* ([0]: anepisternum medium-sized, i.e. approximately as in *Cyclidia substigmaria* (Hübner): fig. 43 *a in* Brock 1971).

In the ground plan of the Geometromorpha, the anepister-num is moderately developed: if one terms M the midpoint of an imaginary line drawn between the anterior angle of the anepis-ternum and the ventral extremity of the pleural suture, M is then situated on the anapleural cleft (e.g. as in *Deuveia*) or even ventrad of this suture. In all Epicopeiidae but *Deuveia*, M is situated on the anepisternum as a result of a decided enlargement of this sclerite.

7. [1]: *in mesothorax, meron and epimeron broadly conti-guous* ([0]: meron and epimeron with a fairly short line of junction).

A synapomorphy of *Burmeia*, *Psychostrophia*, *Amana*, *Chatamla*, *Parabraxas*, *Schistomitra*, *Nossa*, and *Epicopeia*. In these taxa, meron and epimeron have a line of junction that clearly exceeds, in length, one-half of the greatest breadth of the meron.

8. [1]: *ventralmost region of the metathoracic meron flat or hardly convex in lateral view* ([0]: this region distinctly convex).

The convex shape can be ascribed to the epicopeiid ground plan since it occurs in the primitive genus *Deuveia*, as well as in a number of more "advanced" taxa: at least *Psychostrophia*, *Amana* and *Parabraxas* (for this character, *Burmeia* and *Chatamla* were unsatisfactorily studied). There is apparently a connection between this shape and the unusual course of the merocosta, which I interpret as an autapomorphy (h) of the Epicopeiidae. Secondarily, the lower region of the meron has become relatively flat in *Schistomitra + Nossa + Epicopeia*.

9. [1]: *in the male, epiphysis long (i.e. arising from proxi-mal half of fore tibia and reaching distal extremity of tibia)* ([0]: epiphysis shorter: it arises from, or beyond, tibia midpoint if it really reaches the distal extremity of the tibia).

Again a synapomorphy of *Schistomitra*, *Nossa* and *Epicopeia*.

10. [1]: *presence of spines on the tibial spurs* ([0]: spurs unarmed).

A remarkable synapomorphy of *Chatamla* and *Parabraxas*. I have not found it in any other genus or family. This peculiar conformation shows that tibial spurs and spines cannot be regarded as homologous structures.

11. [1]: *large wingspan (forewing length above 28 mm)* ([0]: forewing length 28 mm or less).

A synapomorphy of *Nossa* and *Epicopeia*. Forewing length is around 25 mm in *Schistomitra*, between 15 and 20 mm in *Deuveia*, *Burmeia* and *Psychostrophia*, and around 22 mm in the smallest species of *Parabraxas*, namely *P. nigromacularia* (Leech) (whose size probably corresponds to the ground plan of *Parabraxas*). In the monotypic genera *Amana* and *Chatamla*, the wingspan is quite variable but the smallest specimens have a forewing length of 27-28 mm (here tentatively regarded as the ground-plan size for these taxa).

12. [1]: *in the forewing, stem Rs1 + 2 + 3 more or less arched, distinctly approximated to the median region of vein R* ([0]: stem Rs1 + 2 + 3 straight or hardly arched, some-times close to the base of R but not approximated to the median region of this vein: figs. 7, 8).

The apomorphic state occurs in *Amana*, *Chatamla*, *Parabraxas*, *Schistomitra*, *Nossa* and *Epicopeia*. It can also be described in this way: the space between R and Rs1 + 2 + 3 is clearly constricted some distance beyond the point of origin of Rs1 + 2 + 3.

13. [1]: *in the forewing, Rs3 running to the apex or to the termen* ([0]: Rs3 running to the costa: figs. 7, 8).

Considering the cladograms of figs. 30 and 31, one could interpret this as an autapomorphy of the main epicopeiid line-age (*Amana* to *Epicopeia*), which would have been lost in *Parabraxas* (reversal). However, I tend to prefer a slightly less parsimonious hypothesis (involving three steps instead of two):

the apomorphy might have appeared independently in three clades, namely *Amana*, *Chatamla* and *Schistomitra + Nossa + Epicopeia*. Indeed, the course of Rs3 may be genuinely plesiomorphic in *Parabraxas*, a genus which also retains, in its ground plan, a relatively small wingspan (see character 11), in other words a size nearing that of the most "primitive" Epicopeiidae.

14. [1]: *on forewing dorsal surface, stem of M, CuP and other veins tinged with dark scales* ([0]: veins, or at least certain veins, not contrasting with the background colour(s)).

A prominent synapomorphy of *Nossa* and *Epicopeia* (e.g. pl. 34, *left*, *in* Elwes 1890, and figs. *in* Endo & Kishida 1999). In *Parabraxas flavomarginaria* (Leech) and *Parabraxas davidi* (Oberthür), the lower region of the forewing exhibits darkened, or partly darkened, veins. By contrast, *Parabraxas nigromacularia* lacks this apomorphic pattern.

15. [1]: *forewing and hindwing fringes black or dark brown, with − at least − a few white scales between Rs4 and M1 (in forewing) or M1 and M2 (in hindwing)* ([0]: hindwing fringe without white scales in space M1-M2 if white or whitish scales occur below the apex in the forewing fringe).

This apomorphy is restricted to *Burmeia* and *Psychostrophia*, though apparently only conspicuous in the latter (figs. 3-5). The white sections of the fringes vary in length. In the hindwings of *Psychostrophia*, they tend to reach vein M3.

16. [1]: *in male hindwing, distance between wing base and apex of Rs more or less increased (i.e. primarily greater than the distance separating, in the forewing, the wing base from the apex of CuA2)* ([0]: the distance in question approximately equal to, or even less than, the distance (wing base – CuA2 apex) measurable in the forewing).

Despite differences in hindwing shape, this trait can be regarded as a synapomorphy of *Nossa* and *Epicopeia*. It has been lost in *Epicopeia battaka* Dohrn, owing to a modified shape of the male hindwing. However, it is usually clearly present in *Epicopeia*, including in the most primitive member of this genus, namely *Epicopeia hainesii* Holland (see wing venation *in* Grünberg 1908: 108). Incidentally, I regard this species as sister to the other *Epicopeia* taxa insofar as the latter share at least three synapomorphies, viz. a hypertrophy of the tibial spurs (which become very acute distally), the loss of stem Rs4 + M1 in the forewing, and the presence of dark intervenous stripes on the dorsal surface of the forewing (these vary from inconspicuous to quite noticeable).

Male pregenital abdomen

17. [1]: *base of abdomen with complete tergosternal sclerites* (figs. 10, 11, *ts*) ([0]: sternum A2 with anterolateral processes that do not reach the marginotergites: fig. 9).

In 1991 (p. 87), I regarded these complete tergosternal sclerites as an autapomorphy of the Drepanoidea (= Epicopeiidae + Drepanidae). In fact they occur in all epicopeiid genera but one:

Deuveia. Nevertheless the anterolateral processes of sternum 2 are distinctly longer in *Deuveia* than in the geometroid ground plan (cf. diagnosis of Sematuridae: Minet & Scoble [1998], p. 307).

18. [1]: *antero-abdominal, lateroventral pockets (that shelter androconial hairpencils) long, reaching the posterior region of segment A4* (fig. 10; Inoue 1992: fig. 5) ([0]: these slit-like pockets shorter, not extending, caudad, beyond the posterior edge of sternum A3: fig. 9).

Brush-organs of the "noctuid type" occur in different groups of Macrolepidoptera (Minet & Scoble [1998]; Lemaire & Minet [1998]; Kitching & Rawlins [1998]: fig. 19.12 A). Actually such organs can be ascribed to the macrolepidopteran ground plan (Minet 1998) and their most characteristic elements are usually present in the Epicopeiidae, in particular a rod-like "lever" arising from the posterolateral area of sternum 2, an elongate hairpencil attached to the anterior end of the lever, and a longitudinal, lateroventral, pocket where the hairpencil lies in ordinary circumstances. The posterior part of this slit-like pocket is formed by the infolded lateral edge of sternum 3 in several taxa, for example *Oxytenis* Hübner (primitive Saturniidae), many Sphingidae (e.g. figs. 4.32 and 4.33 *in* Eaton 1988) and four epicopeiid genera (*Deuveia*, *Schistomitra*, *Nossa* and *Epicopeia*). A longer pocket, which reaches the posterior region of sternum 4, may be ascribed to the noctuid ground plan (e.g. fig. 2 *in* Zilli 1995) and also occurs in *Burmeia* and *Psychostrophia* (synapomorphy of these genera; parallel evolution with Noctuidae). Of course nothing can be said about character 18 when anteroabdominal brush-organs have been lost or have turned out vestigial (see below).

19. [1]: *base of abdomen without lateral pencils of hairscales* ([0]: base of abdomen with such brushes).

A probable, or possible, synapomorphy of *Amana*, *Chatamla* and *Parabraxas*.

20. [1]: *sternum A2 without lateral, anteriorly directed arms, that is without levers* (fig. 11) ([0]: sternum A2 with a pair of levers: figs. 9, 10).

A synapomorphy of *Chatamla* and *Parabraxas*. Sternum 2 retains short, inconspicuous levers in *Amana*, although this taxon is devoid of antero-abdominal hairpencils.

21. [1]: *tergum A2 with a prominent anterolateral lobe, which extends − ventrad − beyond the imaginary straight line joining the ventralmost points of the A1 and A2 spiracles* ([0]: anterolateral lobe absent or rather small, sometimes reaching the imaginary line in question, but never produced ventrad of it: figs. 9-11).

A synapomorphy of *Schistomitra*, *Nossa* and *Epicopeia*.

22. [1]: *dorsal tubercula of A2 on the tergum or adjacent to its lateral edges* ([0]: dorsal tubercula separated from tergum 2: figs. 9-11).

In most lepidopterans, these dorsal tubercula lie in the pleural membranes, near the lateral edges of the tergum and caudad of the spiracles of the considered segment (e.g. figs. 2 and 8 *in* Kristensen 1984). Within the Epicopeiidae, the apomorphic state of character 22 is restricted to three genera, namely

Schistomitra, *Nossa* and *Epicopeia*. However, it is sometimes difficult to distinguish from the plesiomorphic state. The tubercula may indeed come very close to the tergum (e.g. as in *Amana*).

23. [1]: *most abdominal sterna clothed laterally, or anterolaterally, with dark scales, which form well defined patches (these patches may join mesally)* ([0]: sterna laterally without well delimited dark patches).

In the most "primitive" Epicopeiidae (*Deuveia*, *Burmeia*, *Psychostrophia*, *Amana*), the ventral surface of the abdomen is more or less one-coloured, relatively light, or at least not distinctly patterned. In *Parabraxas*, the abdomen is ventrally bicoloured, but with the dark areas represented by a mediolongitudinal row of black spots, that is not homologous with the above-mentioned dark patches. The latter, which occur in *Chatamla*, *Schistomitra*, *Nossa* and *Epicopeia*, may have appeared independently in *Chatamla* and the clade composed of the other three genera (fig. 30). Alternatively, they may be viewed as an autapomorphy of a hypothetical larger clade (*Chatamla* to *Epicopeia* in fig. 31), imagining a possible "reversal" or secondary modification in the case of *Parabraxas*.

24. [1]: *anterior edge of tergum A8 with concave lateral sections* (figs. 21, 26) ([0]: this edge laterally straight or convex: figs. 12, 27, 28).

Clearly a synapomorphy of *Burmeia* and *Psychostrophia*.

25. [1]: *tergum A8 markedly narrow midway between its anterior and posterior edges (width at this level measuring less than one-third length of anterior edge)* ([0]: width in question above one-third length of anterior edge).

An apomorphy present in *Burmeia* + *Psychostrophia* but also, due to parallel evolution, in *Amana* and *Chatamla*. The question mark corresponding to *Nossa* in the data matrix (Appendix 1) alludes to the fact that this genus has a modified tergum 8 (fig. 28), which tends to be ill-delimited in its median region.

26. [1]: *tergum A8 composed of two distinct sclerites, an elongate anterior one, which is transversely arranged, and a posterior one, which ends cephalad in an unpaired — pointed or very narrow — process (a membranous, or almost membranous, region separates these two sclerites, at least each side of the median process:* fig. 28*)* ([0]: tergum 8 undivided, though sometimes showing — as in fig. 27 — a differentiated (less sclerotized or less pigmented) anterior region).

A striking synapomorphy of *Nossa* and *Epicopeia*.

27. [1]: *sternum A8 anteriorly provided with a pair of conspicuous, approximate depressions* (figs. 20, 25) ([0]: sternum 8 without such depressions: fig. 13).

Paired depressions along the anterior margin of sternum 8 are rather uncommon outside the Epicopeiidae. Within this family, they occur in *Burmeia* and *Psychostrophia* (synapomorphy), as well as in one species of *Nossa* (viz. *N. moorei* (Elwes)) and certain species of *Epicopeia*, but not in the most "primitive" members of the latter genus (i.e. neither in *E. hainesii* nor in *E. mencia* Moore — see character 16 for a discussion of the systematic position of *E. hainesii*). The states of character 27 mentioned

for *Nossa* and *Epicopeia* in the data matrix correspond, in my opinion, to the ground-plan conditions of these two genera (see Appendix).

Male genitalia

28. [1]: *presence of an intersaccular sclerite between the valvae and ventrad of the juxta* (fig. 19, *is*; Kuznetzov & Stekolnikov 1993: fig. 5) ([0]: intersaccular sclerite absent, the integument being more or less membranous ventrad of the juxta and mesad of the sacculi: fig. 16).

The intersaccular sclerite may or may not be separated from the vinculum by a narrow membrane. It is very rare in non-epicopeiid Macrolepidoptera, although present (and usually spinulose) in the Sematuridae (Geometroidea). Within the Epicopeiidae, it occurs in all genera, excepting *Deuveia* (primary absence) and *Schistomitra* (most likely owing to a loss).

29. [1]: *base of uncus without typical socii* (fig. 16) ([0]: uncus with typical socii: figs. 18, 19, 22, 24).

Typical socii (*so*) can be defined as well delimited setose areas that are somewhat convex and lie along the anteroventral edges of the uncus, near the tegumen-uncus joint. Such structures are present in three epicopeiid genera, namely *Burmeia*, *Psychostrophia* and *Amana*. In the other Epicopeiidae, a number of sensilla chaetica may be homologous with those of the socii in question, but either they are situated — lateroventrally — in the median region of the uncus (i.e. far from the tegumen, e.g. as in *Chatamla*) or they merge into long ventral rows of sensilla, sometimes observable for about the whole length of the uncus (Kuznetzov & Stekolnikov 1993: fig. 4). Within the Drepanidae, the socii are usually modified into conspicuous, elongated projections (Thyatirinae, Drepaninae) but turn out to be variously shaped in the Cyclidiinae.

30. [1]: *gnathos absent* (figs. 18, 19, 24) ([0]: gnathos present, either divided or entire: figs. 12, 16).

A synapomorphy of *Burmeia* and *Psychostrophia*.

31. [1]: *"arms" of the gnathos broadly fused with the tegumen* ([0]: tegumen only connected to the very base of the gnathos: fig. 14; Kuznetzov & Stekolnikov 1993: fig. 4).

This character cannot be studied in *Burmeia* and *Psychostrophia*, two genera secondarily devoid of a gnathos (as mentioned above). The plesiomorphic condition occurs in *Deuveia* and several species of *Nossa*. Tentatively, I ascribe the free gnathos found in these *Nossa* to the ground plan of the genus, and consider a phenomenon of parallel evolution to explain the gnathos conformation observed in *Nossa moorei* (Elwes): here, as in *Epicopeia* and four other genera, the proximal region of the gnathos merges with the tegumen, so that the gnathos appears to arise from the posteroventral areas of the tegumen (near the costulae). In these taxa showing the apomorphic state of character 31, the distal region of the gnathos is occasionally strongly modified, hence not easily recognizable: for example, it is represented by a pair of long sickle-shaped processes in *Epicopeia hainesii* (Okano 1973: pl. 3, fig. 3; Kuznetzov & Stekolnikov 1988: fig. 2).

32. [1]: *distal half of the gnathos divided into three strong projections* ([0]: gnathos never trifid distally).

A synapomorphy of *Chatamla* and *Parabraxas*.

33. [1]: *coecum penis markedly reduced, that is shorter than the phallus width measured just caudad of the bulbus ejaculatorius (the phallus being observed in lateral view)* (Okano 1973: pl. 3, figs. 1, 3; Kuznetzov & Stekolnikov 1993: fig. 4) ([0]: coecum penis as long as, or longer than, the width in question: figs. 17, 23).

The apomorphic condition occurs in *Schistomitra + Nossa + Epicopeia* and, as instances of parallel evolution, in *Chatamla* and certain *Parabraxas*. The ground plan of the latter genus apparently includes a moderately developed coecum, like that of *Parabraxas nigromacularia*. In this species, the coecum length approximately equals the greatest width of the phallus region where ends the bulbus ejaculatorius.

34. [1]: *vesica with a single cornutus* (fig. 23) ([0]: vesica with several cornuti: fig. 17).

The plesiomorphic state is retained in two epicopeiid genera (*Deuveia*, *Psychostrophia*), several Thyatirinae and Drepaninae (Werny 1966; Watson 1968), at least certain Sematuridae (e.g. *Apoprogones hesperistis* Hampson), many Geometridae, etc. In Epicopeiidae the cornutus, where single, is usually strong. However its size is moderate in *Burmeia* (fig. 23), a genus whose sister-group has the vesica ornamented with a cluster of minute cornuti (fig. 24, *cr*).

Phylogenetic analysis

The cladogram shown in fig. 30 represents a "manually" derived tree, which I regard as the best hypothesis on the basis of the above-mentioned characters 1-34. Although none of these is connected with the (poorly known) morphology of the early stages, the branches of this cladogram can be considered rather robust — that is supported by some convincing apomorphies — except for one however, namely *Amana + Chatamla + Parabraxas*. As a matter of fact, this possible clade is here proposed on account of characters 19 and 31: the apomorphic state of the former corresponds to a loss and is commonplace in the Macrolepidoptera, while the evolution of the latter is difficult to interpret owing to the apparent preservation of its plesiomorphic state in several species of *Nossa* (see discussion about character 31). In my opinion, apomorphy 31 may have appeared independently in four epicopeiid lineages (viz. *Amana + Chatamla + Parabraxas*, *Schistomitra*, *Nossa moorei*, and *Epicopeia*). Admittedly, this assumption is less "parsimonious" (four steps) than another possible scenario involving two steps: the appearance of apomorphy 31 in a large group of epicopeiids (*Amana … Epicopeia*) and its loss (i.e. a reversal) in one group within *Nossa*. However, I think hardly conceivable such a rever-

sal, which would imply that a divided, initially immovable, gnathos could recover mobility while remaining somewhat reduced (all *Nossa* species having lost the apical, unpaired region of the gnathos).

The number and nature of the apomorphies characterizing a given clade provide clues for a rough estimate of its "robustness". In fact one of the most significant criteria to take into account is the relative rarity of the apomorphies in question. Accordingly any "manual" phylogenetic reconstruction represents, in a way, an approach based on character weighting (in which weights are not precisely assessed). Fig. 30 shows a cladogram built according to such a method. For comparative purposes, the above-mentioned 34 characters were also analysed with the computer programs Hennig86, version 1.5 (Farris 1988), and PAUP, version 4 (Swofford 1998), in both cases under the standard protocol relying on a uniform treatment of the data (all characters being given equal weight).
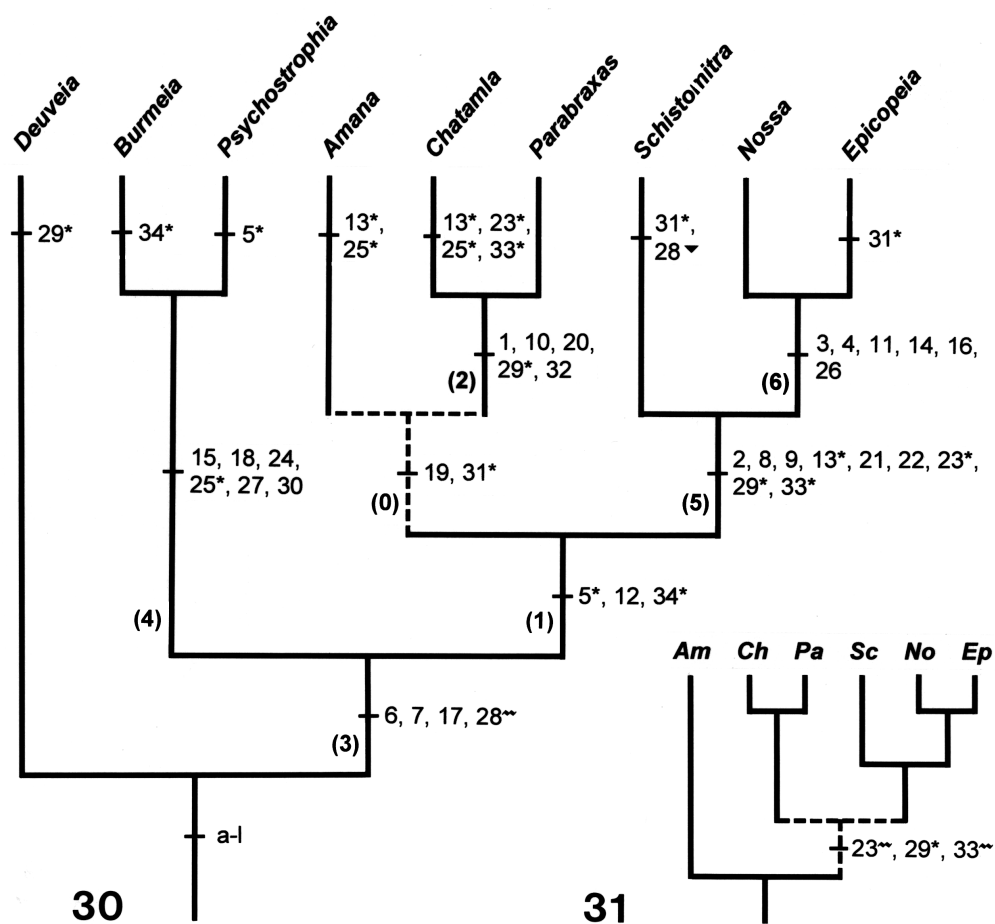
In the data matrix used for these analyses (Appendix), the first line corresponds to a hypothetical ancestor (ANCES) that would be plesiomorphic (0) for every character. As defined above, all characters are binary (states: 0; 1) and have been polarized by outgroup comparison. With Hennig86, the "implicit enumeration" option (ie) gives two most parsimonious trees (length: 45), which satisfactorily describe the considered data set (CI = 0.75, RI = 0.80; for a definition of these indices, see e.g. Forey *et al.*, 1992: section 5.1.2). Interestingly, one of these trees is structurally identical with the manually derived cladogram of fig. 30, while the other one differs from it only in the position of *Amana*, which becomes sister to *Chatamla + Parabraxas + Schistomitra + Nossa + Epicopeia* (fig. 31). Actually three synapomorphies tend to support the possible monophyly of this group of five genera, namely apomorphies 23, 29 and 33. However, none of them is homoplasy-free within the Epicopeiidae: apomorphies 23 and 33 are absent in *Parabraxas* (reversals ?), and apomorphy 29 also occurs in *Deuveia* (parallel evolution). By contrast, of the two traits that may be synapomorphic for *Amana* and *Chatamla + Parabraxas* (fig. 30), one (19) does not exhibit homoplasy within the limits of the Epicopeiidae, assuming that *Amana + Chatamla + Parabraxas* is indeed a monophylum. For that reason but rather tentatively, I prefer the tree represented in fig. 30 to that partly shown in fig. 31.

Naturally the same two trees were also proposed by PAUP (branch-and-bound search) as the most parsimonious reconstructions resulting from the analysis of the above-mentioned data matrix (ANCES having been selected as the only "outgroup"). Their length is still of 45 steps, while their consistency index (CI) and reten-

tion index (RI) can be calculated more precisely with PAUP than with Hennig86: CI = 0.7556 and RI = 0.8070. It should be noted however that, with an option such as ACCTRAN ("accelerated transformation", the procedure selected by default for character-state optimization), the transformation process considered by PAUP for a given character may differ from my interpretation, which is summarized by the distribution of the apomorphies shown in fig. 30 (preferred tree). For example, under ACCTRAN, PAUP assigns apomorphies 5 and 34 to the sister-group of *Deuveia* and envisages a loss (reversal) of the former in *Burmeia*, of the latter in *Psychostrophia*. Actually it is not less "parsimo-

nious" to view the distribution of each of these apomorphies as the result of one event of parallel evolution (my hypothesis; see fig. 30).

Several procedures have been proposed for assessing the robustness of the branches composing a cladogram. Those relying on some sort of perturbation of the data matrix should be avoided for theoretical reasons (Carpenter 1992; Bremer 1994). Accordingly, instead of bootstrap percentages, Bremer's support indices have been chosen to compare the branches of the preferred cladogram (numbers in brackets in fig. 30). These support values reflect the faculty of persistence of these branches when less and less parsimonious trees are

Figures 30-31
Two hypotheses for the phylogeny of the Epicopeiidae. − 30, manually derived (preferred) cladogram, whose structure is identical with that of one of the two most parsimonious trees found with both Hennig86 and PAUP (options as specified in text). − 31, part of the other most parsimonious tree proposed by the above-named computer programs (generic names abbreviated; relationships not shown for *Deuveia*, *Burmeia* and *Psychostrophia*, but as in fig. 30). − (3), (4), etc.: Bremer's support indices (calculated with PAUP); a-l: autapomorphies of the Epicopeiidae; 1-34: apomorphic states of characters 1-34; 28−: an autapomorphy for which a case of "reversal" (or secondary loss: 28▼) should be considered; 29⁻,: an apomorphy characteristic of more than one clade within the Epicopeiidae (i.e. involving parallel evolution − infrageneric variability here not taken into account). Apomorphies not mentioned at generic level, except for a number of homoplastic characters.

successively examined (Källersjö *et al.* 1992: 284). For the cladogram under consideration (fig. 30), they have been calculated by going through the consensus trees corresponding to the trees of lengths 46 (= 45 + 1), 47, 48, 49, 50, and 51 (trees easily found with PAUP, though not obtainable with Hennig86). Of course, Bremer's indices cannot take into account the nature of the studied characters, nor their variability in the groups not included in the data matrix. Accordingly, they are sometimes misleading. For example, if the monophyly of *Nossa + Epicopeia* seems relatively indisputable (support index = 6), that of *Chatamla + Parabraxas* should not be regarded as less obvious, despite the rather low support index (= 2) assigned to this branch: indeed, among the synapomorphies of *Chatamla* and *Parabraxas*, one (apomorphy 10) is apparently unique within the Lepidoptera and another one (32) turns out to be quite rare in the Ditrysia.

In conclusion, although characters from the early stages and female genitalia remain to be discovered and/or analysed, all the branches of the preferred cladogram can be considered well, or fairly well, established, except for that represented by a pecked line in fig. 30. Concerning the tree generated by PAUP or Hennig86 which is 45 steps long and whose structure matches this cladogram, one finds a relatively high value (TI = 0.47) for the total support index proposed by Bremer (1994). This phylogenetic reconstruction already permits a hypothesis about the evolution of the larval hostplants.

Although poorly known, these have been recorded for four epicopeiid genera (Sugi *et al.* 1987; Kuznetzov & Stekolnikov 1993: 14). *Psychostrophia*, *Schistomitra* and *Nossa* are associated with, respectively, the Clethraceae, Theaceae and Cornaceae; the hostplants of *Epicopeia* belong to the Cornaceae (for *E. hainesii*), Ericaceae and Ulmaceae. Since *E. hainesii* can be regarded as the basalmost member of *Epicopeia*, feeding on Cornaceae may constitute an ecological synapomorphy of *Nossa* and *Epicopeia*, and is likely to have disappeared secondarily in most species of the latter genus. It should also be noted that all these plant families belong to the Asteridae (Cornales − Cornaceae − and Ericales: Clethraceae, Ericaceae, Theaceae) except for the Ulmaceae, which are currently placed in the Rosidae (Rosales − see e.g. Bremer *et al.* 1998).

REFERENCES

BARRIEL V., TASSY P. 1993 − Characters, observations and steps: comment on Lipscomb's "Parsimony, homology and the analysis of multistate characters". − *Cladistics*, **9**: 223-232.

BIRCH M.C. 1972 − Male abdominal brush-organs in British noctuid moths and their value as a taxonomic character. Part I. − *The Entomologist*, **105**: 185-205.

BREMER K. 1994 − Branch support and tree stability. − *Cladistics*, **10**: 295-304.

BREMER K. *et al.* (The Angiosperm Phylogeny Group) 1998 − An ordinal classification for the families of flowering plants. − *Annals of the Missouri botanical Garden*, **85**: 531-553.

BROCK J.P. 1971 − A contribution towards an understanding of the morphology and phylogeny of the ditrysian Lepidoptera. − *Journal of natural History*, **5**: 29-102.

CARPENTER J.M. 1992 − Random cladistics. − *Cladistics*, **8**: 147-153.

CLENCH H.K. 1955 − Revised classification of the butterfly family Lycaenidae and its allies. − *Annals of the Carnegie Museum*, **33**: 261-274.

DALLA TORRE K.W. von 1924 − Fam. Epiplemidae. − *Lepidopterorum Catalogus*, **30**: 1-38.

DAVIS D.R. 1975 − A review of the West Indian moths of the family Psychidae with descriptions of new taxa and immature stages. − *Smithsonian Contributions to Zoology*, **188**: i-iii, 1-66.

EASSA Y.E.E. 1963a − The musculature of the head appendages and the cephalic stomodaeum of *Pieris brassicae* (Lepidoptera: Pieridae). − *Annals of the entomological Society of America*, **56**: 500-510.

EASSA Y.E.E. 1963b − Metamorphosis of the cranial capsule and its appendages in the cabbage butterfly, *Pieris brassicae*. − *Annals of the entomological Society of America*, **56**: 510-521.

EATON J.L. 1988 − *Lepidopteran anatomy*. New York: John Wiley & Sons, xiii + 257 p.

ELWES H.J. 1890 − On some new moths from India. − *Proceedings of the zoological Society of London*, 1890: 378-401 + 3 pls.

ENDO T., KISHIDA Y. 1999 − *Day-flying moths: Chalcosiinae; Epicopeia* (Endless Collection Series, 8). Tokyo: Endless Science Information, 120 p.

FÄNGER H. 1999 − Comparative morphology of tergal phragmata occurring in the dorsal thoraco-abdominal junction of ditrysian Lepidoptera (Insecta). − *Zoomorphology*, **119**: 163-183.

FARRIS J.S. 1988 − *Hennig86, version 1.5* (computer program distributed by J.S. Farris). New York.

FAUCHEUX M.J. 1999 − Biodiversité et unité des organes sensoriels des insectes lépidoptères [Biodiversity and unity of sensory organs in lepidopteran insects]. − *Bulletin de la Société des Sciences naturelles de l'Ouest de la France,* Nantes, suppl. hors série 1999: 1-296.

FERRIS G.F. 1940 − The morphology of *Plega signata* (Hagen) (Neuroptera: Mantispidae). − *Microentomology*, **5**: 33-56.

FLETCHER D.S. 1979 − Geometroidea: Apoprogonidae, Axiidae, Callidulidae, Cyclidiidae, Drepanidae, Epicopeiidae, Epiplemidae, Geometridae, Pterothysanidae, Sematuridae, Thyatiridae, Uraniidae. *In*: Nye I.W.B. (ed.), *The generic names of moths of the world*, 3: i-xx, 1-243 + 2 pls. London: Trustees of the British Museum (Natural History).

FORBES W.T.M. 1923 − The Lepidoptera of New York and neighboring states. [Part I]: primitive forms, microlepidoptera, pyraloids, bombyces. −

Memoirs of the Cornell University agricultural Experiment Station, **68**: 1-729.

FORBES W.T.M. 1940 − The genus Plusinia (Lepidoptera, Thyatiridae). − *Annals of the entomological Society of America*, **33**: 588-589.

FOREY P.L., HUMPHRIES C.J., KITCHING I.J., SCOTLAND R.W., SIEBERT D.J., WILLIAMS D.M. 1992 − *Cladistics: a practical course in systematics* (The Systematics Association Publication No. 10). Oxford: Clarendon Press, xi + 191 p.

GOHRBANDT I. 1937 − Das Tympanalorgan der Drepaniden und der Cymatophoriden zugleich ein Beitrag zur vergleichenden Morphologie und Histologie der Lepidopteren). − *Zeitschrift für wissenschaftliche Zoologie*, **149**: 537-600.

GOYLE S. 1990 − *Anatomy of the common lemon butterfly,* Papilio demoleus demoleus *(L).* New Delhi: Today & Tomorrow's Printers and Publishers, [xiii] + 151 p.

GRÜNBERG K. 1908 − Zur systematischen Stellung der Epicopiiden. (Lep.). *Epicopiopsis* nov. gen. − *Deutsche entomologische Zeitschrift*, 1908: 107-110.

HAMPSON G.F. 1895 − Moths, vol III. *In*: Blanford W.T. (ed.), *The fauna of British India, including Ceylon and Burma.* London: Taylor and Francis, xxviii + 546 p.

HANDLIRSCH A. 1925 − Ordnung: Lepidoptera (Schmetterlinge). *In*: Schröder C. (ed.), *Handbuch der Entomologie*, **3**: 852-941. Jena: Verlag von Gustav Fischer.

HERING M. 1932 − Zwei neue paläarktische Heteroceren. (Lep.). − *Mitteilungen der deutschen entomologischen Gesellschaft*, **3**: 28-29.

FORBES W.T.M. 1966 − A preliminary comparative anatomical study of the mesothoracic aorta of the Lepidoptera. − *Annals of the entomological Society of America*, **59**: 1217-1227.

FORBES W.T.M. 1969 − The comparative morphology of the dorsal vessel and accessory structures of the Lepidoptera and its phylogenetic implications. − *Annals of the entomological Society of America*, **62**: 353-370.

HESSEL J.H. 1998 − The moths of Borneo [part 8]: families Castniidae, Callidulidae, Drepanidae and Uraniidae. − *The Malayan Nature Journal*, **52**: 1-155 + 58 pls.

HESSEL J.H. BRADLEY J.D., CARTER D.J. 1987 − Lepidoptera. *In*: Betts C.R. (ed.), *CIE guides to insects of importance to man*, 1: [i-iv], 1-262. London: CAB International Institute of Entomology & British Museum (Natural History).

INOUE H. 1978 − Genus *Epicopeia* Westwood from Japan, Korea and Taiwan (Lepidoptera: Epicopeidae). − *Tyô to Ga*, **29**: 69-75.

INOUE H. 1982 − Geometroidea. *In*: Inoue H. *et al.*, *Moths of Japan*, 1 (text): 412-579; 2 (plates and synonymic catalogue): 257-312, 455-459 + 97 pls. Tokyo: Kodansha.

INOUE H. 1992 − A new species of *Psychostrophia* Butler from Laos (Epiplemidae). − *Tyô to Ga*, **43**: 149-150.

JANET A., WYTSMAN P. 1903 − Lepidoptera Heterocera. Fam. Epicopiidae. − *Genera Insectorum*, **16**: 1-5 + 2 pls.

JAROŠ J., SPITZER K. 1999 − Notes on the ecology and distribution of two species of the genus *Epicopeia* in Korea and Vietnam (Epicopeiidae). − *Nota lepidopterologica*, **22**: 183-189.

JORDAN K. 1902 − Das Mesosternit der Tagfalter. − *Verhandlungen des V. internationalen Zoologen-Congresses*, Berlin, 1902: 816-830.

KÄLLERSJÖ M., FARRIS J.S., KLUGE A.G., BULT C. 1992 − Skewness and permutation. − *Cladistics*, **8**: 275-287.

KITCHING I.J., FOREY P.L., HUMPHRIES C.J., WILLIAMS D.M. 1998 − *Cladistics (second edition): the theory and practice of parsimony analysis* (The Systematics Association Publication No. 11). Oxford: University Press, xiii + 228 p.

KITCHING I.J., RAWLINS J.E. [1998] − The Noctuoidea. *In*: Kristensen N.P. (ed.), *Lepidoptera, moths and butterflies*, 1 (evolution, systematics, and biogeography): 355-401 (Handbuch der Zoologie [founded by Willy Kükenthal; ed.: Fischer M.], Band 4, Teilband 35). Berlin: Walter de Gruyter.

KLOTS A.B. 1970 − Lepidoptera. *In*: Tuxen S.L. (ed.), *Taxonomist's glossary of genitalia in insects* (second edition), p. 115-130. Copenhagen: Munksgaard.

KRISTENSEN N.P. 1968 − The skeletal anatomy of the heads of adult Mnesarchaeidae and Neopseustidae (Lep., Dacnonypha). − *Entomologiske Meddelelser*, **36**: 137-151.

KRISTENSEN N.P. 1978a − Ridge dimorphism and second-order ridges on wing scales in Lepidoptera: Exoporia. − *International Journal of Insect Morphology & Embryology*, **7**: 297-299.

KRISTENSEN N.P. 1978b − A new familia of Hepialoidea from South America, with remarks on the phylogeny of the subordo Exoporia (Lepidoptera). − *Entomologica germanica*, **4**: 272-294.

KRISTENSEN N.P. 1984 − The pregenital abdomen of the Zeugloptera (Lepidoptera). − *Steenstrupia*, **10**: 113-136.

KRISTENSEN N.P. [1998] − The homoneurous Glossata. *In*: Kristensen N.P. (ed.), *Lepidoptera, moths and butterflies*, 1 (evolution, systematics, and biogeography): 51-63 (Handbuch der Zoologie [founded by Willy Kükenthal; ed.: Fischer M.], Band 4, Teilband 35). Berlin: Walter de Gruyter.

KRISTENSEN N.P., NIELSEN E.S. 1979 − A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). − *Steenstrupia*, **5**: 69-147.

KUZNETZOV V.I., STEKOLNIKOV A.A. 1988 − Functional morphology of the male genitalia and phylogenetic relationships of some families of geometroid moths and butterflies (Lepidoptera: Epicopeiidae, Uraniidae, Papilionidae, Nymphalidae, Danaidae) from the fauna of Vietnam. − *Trudy zoologicheskogo Instituta*, Leningrad, **176**: 14-51.

KUZNETZOV V.I., STEKOLNIKOV A.A. 1993 − Comparative morphology of the male genitalia and systematic status of some little-known lepidopterous families (Lepidoptera: Pterolonchidae, Ochsenheimeriidae, Carposinidae, Callidulidae, Epicopeiidae) from the fauna of Russia. − *Trudy zoologicheskogo Instituta*, Saint-Petersburg, **255**: 3-21.

KYRKI J. [1984] − Adult abdominal sternum II in ditrysian tineoid superfamilies − morphology and phylogenetic significance (Lepidoptera). − *Annales entomologici fennici*, **49** (1983): 89-94.

LAITHWAITE E., WATSON A., WHALLEY P.E.S. 1975 − *The dictionary of butterflies and moths in colour.* London: Michael Joseph, xlvi + 296 p.

LEMAIRE C., MINET J. [1998] − The Bombycoidea and their relatives. *In*: Kristensen N.P. (ed.), *Lepidoptera, moths and butterflies*, 1 (evolution, systematics, and biogeography): 321-353 (Handbuch der Zoologie [founded by Willy Kükenthal; ed.: Fischer M.], Band 4, Teilband 35). Berlin: Walter de Gruyter.

MATSUDA R. 1970 − Morphology and evolution of the insect thorax. − *Memoirs of the entomological Society of Canada*, **76**: 1-431.

MINET J. 1982 − Les Pyraloidea et leurs principales divisions systématiques [Lep. Ditrysia]. − *Bulletin de la Société entomologique de France*, **86** (1981): 262-280.

MINET J. 1983 − Etude morphologique et phylogénétique des organes tympaniques des *Pyraloidea*. 1 − généralités et homologies. (*Lep. Glossata*). − *Annales de la Société entomologique de France* (N.S.), **19**: 175-207.

MINET J. 1984 − Contribution à l'analyse phylogénétique des Néolépidoptères (*Lepidoptera, Glossata*). − *Nouvelle Revue d'Entomologie* (N.S.), **1**: 139-149.

MINET J. 1985 − Etude morphologique et phylogénétique des organes tympaniques des *Pyraloidea*. 2 − *Pyralidae*; *Crambidae*, première partie. (Lepidoptera Glossata). − *Annales de la Société entomologique de France* (N.S.), **21**: 69-86.

MINET J. 1986 − Ebauche d'une classification moderne de l'ordre des Lépidoptères. − *Alexanor*, **14**: 291-313.

MINET J. 1990 − Nouvelles frontières, géographiques et taxonomiques, pour la famille des Callidulidae (Lepidoptera, Calliduloidea). − *Nouvelle Revue d'Entomologie* (N.S.), **6**: 351-368.

MINET J. 1991 − Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). − *Entomologica scandinavica*, **22**: 69-95.

MINET J. 1994 − The Bombycoidea: phylogeny and higher classification (Lepidoptera: Glossata). − *Entomologica scandinavica*, **25**: 63-88.

MINET J. 1998 − Some topical issues in Macrolepidoptera phylogenetic systematics. − *Programme & Abstracts of the XIth European Congress of Lepidopterology*, Malle (Belgium), 1998: 72-73.

MINET J., SCOBLE M.J. [1998] − The drepanoid/geometroid assemblage. *In*: Kristensen N.P. (ed.), *Lepidoptera, moths and butterflies*, 1 (evolution, systematics, and biogeography): 301-320 (Handbuch der Zoologie [founded by Willy Kükenthal; ed.: Fischer M.], Band 4, Teilband 35). Berlin: Walter de Gruyter.

NAKAMURA M. 1972 – What is the suitable family for *Schistomitra funeralis* Butler ? – *The entomological Review of Japan*, **24**: 56.

NICHOLS S.W. *et al.* 1989 – *The Torre-Bueno glossary of entomology.* New York: New York Entomological Society (& American Museum of Natural History), xvii + 840 p.

NIELSEN E.S., KRISTENSEN N.P. 1989 – Primitive ghost moths. Morphology and taxonomy of the Australian genus *Fraus* Walker (Lepidoptera: Hepialidae *s. lat.*). – *Monographs on Australian Lepidoptera*, **1**: i-xii, 1-206.

NIELSEN E.S., KRISTENSEN N.P. 1996 – The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera–Glossata. – *Invertebrate Taxonomy*, **10**: 1199-1302.

OKANO M. 1964 – On the Formosan species of the family Epicopeidae (Lepidoptera). – *Tohoku Konchu Kenkyu*, Morioka, **1**: 25-26.

OKANO M. 1973 – A revision of the Formosan species of the family Epicopeidae (Lepidoptera). – *Artes Liberales*, Iwate Univ., **13**: 81-84 + 3 pls.

ROUCHY R. 1964 – Squelette et musculature céphaliques de deux types d'imagos de Lépidoptères hétéroneures. – *Travaux du Laboratoire de Zoologie et de la Station aquicole Grimaldi de la Faculté des Sciences de Dijon*, **61**: 1-59 + 29 figs.

SCOBLE M.J. 1992 – *The Lepidoptera. Form, function and diversity.* Oxford: Oxford University Press, xi + 404 p. + 4 pls.

SCOBLE M.J., EDWARDS E.D. 1988 – *Hypsidia* Rothschild: a review and a reassessment Lepidoptera: Drepanoidea, Drepanidae). – *Entomologica scandinavica*, **18**: 333-353.

SEITZ A. 1911 – Familie: Callidulidae. *In*: Seitz A. (ed.), *Die Gross-Schmetterlinge der Erde*, **2**: 207-208. Stuttgart: Alfred Kernen.

SHARPLIN J. 1963a – Wing base structure in Lepidoptera. I. Fore wing base. – *The Canadian Entomologist*, **95**: 1024-1050.

SHARPLIN J. 1963b – Wing base structure in Lepidoptera. II. Hind wing base. – *The Canadian Entomologist*, **95**: 1121-1145.

SHORT J.R.T. 1951 – Some aspects of the morphology of the insect head as seen in the Lepidoptera. – *Proceedings of the Royal entomological Society of London* (A), **26**: 77-88.

SIBATANI A., OGATA M., OKADA Y., OKAGAKI H. 1954 – Male genitalia of Lepidoptera: morphology and nomenclature. I. Divisions of the valvae in Rhopalocera, Phalaenidae (= Noctuidae) and Geometridae. – *Annals of the entomological Society of America*, **47**: 93-106.

STRONG E.E., LIPSCOMB D. 1999 – Character coding and inapplicable data. – *Cladistics*, **15**: 363-371.

SUGI S. (ed.), YAMAMOTO M., NAKATOMI K., SATO R., NAKAJIMA H., OWADA M. 1987 – *Larvae of larger moths in Japan.* Tokyo: Kodansha, 455 p.

SWOFFORD D.L. 1998 – *PAUP: Phylogenetic Analysis Using Parsimony (and other methods), version 4.0* (computer program). Sunderland, Massachusetts: Sinauer Associates.

TALBOT G. 1939 – Obituary. Major-General Sir H. C. Tytler, K.C.B., C.M.G., C.I.E., D.S.O. – *Journal of the Bombay natural History Society*, **41**: 409.

TYTLER H. 1940 – Notes on some new and interesting butterflies chiefly from Burma. – *Journal of the Bombay natural History Society*, **42**: 109-123.

WATSON A. 1968 – The taxonomy of the Drepaninae represented in China, with an account of their world distribution (Lepidoptera: Drepanidae). – *Bulletin of the British Museum (natural History)* (Entomology), suppl. **12**: 1-151 + 14 pls.

WEBER H. 1928 – Die Gliederung der Sternopleuralregion des Lepidopterenthorax. Eine vergleichend morphologische Studie zur Subcoxaltheorie. – *Zeitschrift für wissenschaftliche Zoologie*, **131**: 181-254.

WELLER S.J. 1990 – Revision of the *Nystalea aequipars* Walker species complex with notes on nystaleine genitalia (Lepidoptera: Notodontidae). – *Journal of the New York entomological Society*, **98**: 35-49.

WERNY K. 1966 – *Untersuchungen über die Systematik der Tribus Thyatirini, Macrothyatirini, Habrosynini und Tetheini (Lepidoptera: Thyatiridae).* Saarbrücken: Universität des Saarlandes, [iv] + 464 p. + 433 figs.

WOOTTON R.J. 1979 – Function, homology and terminology in insect wings. – *Systematic Entomology*, **4**: 81-93.

YACK J.E., FULLARD J.H. 1993 – Proprioceptive activity of the wing-hinge stretch receptor in *Manduca sexta* and other atympanate moths: a study of the noctuoid moth ear B cell homologue. – *Journal of comparative Physiology* (A), **173**: 301-307.

YEN S.-H., MU J.-H., JEAN J.-L. 1995 – The life histories and biology of Epicopeiidae of Taiwan. – *Transactions of the lepidopterological Society of Japan*, **46**: 175-184.

ZILLI A. 1995 – On the systematic position of *Pseudeustrotia candidula* ([Denis & Schiffermüller, 1775]). – *Bollettino della Societá entomologica italiana*, **127**: 142-146.

APPENDIX

Data matrix used for software-based cladistic analyses

This table summarizes character state distribution – for 34 binary characters – in 9 genera and a hypothetical ancestor (of family Epicopeiidae). The question marks correspond to character states that either remain unknown (character 8) or cannot be specified for conceptual reasons (characters 3, 4, 18, 25, 31 and 32).

```
                        1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3
Taxa \ Characters   1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4

Ancestor            0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Deuveia             0 0 ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0
Burmeia             0 0 ? ? 0 1 1 ? 0 0 0 0 0 1 0 1 1 0 0 0 0 0 1 1 0 1 1 0 1 ? ? 0 1
Psychostrophia      0 0 ? ? 1 1 1 0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 1 1 0 1 1 0 1 ? ? 0 0
Amana               0 0 ? ? 1 1 1 0 0 0 0 1 1 0 0 0 1 ? 1 0 0 0 0 0 1 0 0 1 0 0 1 0 0 1
Chatamla            1 0 ? ? 1 1 1 ? 0 1 0 1 1 0 0 0 1 ? 1 1 1 0 0 1 0 1 0 0 1 1 0 1 1 1
Parabraxas          1 0 ? ? 1 1 1 0 0 1 0 0 0 0 1 0 0 ? 1 1 1 0 0 0 0 1 0 0 1 1 0 1 1 0 1
Schistomitra        0 1 0 0 1 1 1 1 1 0 0 1 0 0 0 1 0 0 0 1 0 0 0 1 1 1 0 0 0 0 1 0 1 1
Nossa               0 1 1 1 1 1 1 1 1 0 1 1 1 1 0 1 1 0 0 0 1 1 1 0 ? 1 0 1 1 0 0 0 1 1
Epicopeia           0 1 1 1 1 1 1 1 1 0 1 1 1 1 0 1 1 0 0 0 1 1 1 0 0 1 0 1 1 0 1 0 1 1
```