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GONDWANAN NEPTICULIDAE (LEPIDOPTERA)? SYSTEMATICS AND BIOLOGY OF THE *ECTOEDEMIA* (*FOMORIA*) *VANNIFERA* GROUP

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The *Ectoedemia* (*Fomoria*) *vannifera* species-group is reviewed. Three species are recognized from South Africa (*E. vannifera* (Meyrick), *E. fuscata* (Janse) and *E. hobohmi* (Janse)), one from central Asia (*E. asiatica* (Puplesis)), and one from India (*E. glycystrota* (Meyrick) comb. n., here redescribed); three new species are described and named from Australia (*E. pelops* sp. n., *E. squamibunda* sp. n., and *E. hadronycha* sp. n.). All species share a striking synapomorphy in the male genitalia: a pin-cushion-like lobe at the apex of the valva. Two of the Australian species and one of the South African species have been reared from larvae mining the leaves of Brassicaceae *sensu lato*. A phylogeny of all currently recognized species is presented: this taken together with known distribution suggests either that the group is very ancient and antedates the split between the African and Indian parts of Gondwana (ca. 120 million years ago), or that it has dispersed more recently and has been overlooked in large parts of its range.

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The Nepticulidae constitute one of the more ancient families of Lepidoptera. On the basis of the very wide distribution of many genera and subgenera (e.g. *Stigmella* Schrank, which is known from all continents except Antarctica), and the unlikelihood of successful inter-continental dispersal by moths which show such a high degree of monophagy, Scoble (1983) postulated that the family originated before the break-up of Pangaea into Laurasia and Gondwana, i.e. 150 to 180 million years ago. Although very few lepidopteran, and no nepticulid fossils are known from the Jurassic, such an early date has recently been corroborated by the discovery of leaf-mines from the middle Cretaceous (97 million years BP) of North America (Labandeira et al. 1994). At least one of these mines can be unambiguously assigned to a modern subgenus (*Ectoedemia* Busck subgenus *Ectoedemia*), and even shares the host-plant superfamily of its closest present-day relatives. It is clear that the Nepticulidae had already undergone a considerable period of evolution by this date.

In a group of such age and presumed low dispersal ability, one would expect to be able to detect vicariance patterns among the faunas of different landmasses caused by the break-up of the continents during the late Mesozoic and early Tertiary. The history of the break-up of the great southern continent of Gondwana is now well documented (e.g. Owen 1981, Scotese et al. 1988) and cladistic relationships congruent with this history have been demonstrated in other groups of insects of comparable age (for example Chironomidae (Diptera): Brundin 1966; Ephemeroptera: Edmunds 1975). However, as is true of so many groups, knowledge of the southern hemisphere nepticulid fauna is in its infancy compared to that of the northern hemisphere. Apart from the revision of the New Zealand Nepticulidae by Donner & Wilkinson (1989), the works of Vári (1955, 1963) and Scoble (see references in Hoare et al. 1997) on the South African fauna remain, taken together, the only comprehensive review of a southern hemisphere fauna. Nothing has been published on the South American fauna apart from a few scattered species descriptions (Zeller 1877, Meyrick 1915, 1931, Bourquin 1961) and a very brief review of known host-plant associations (Nielsen 1985). Only 19 species have so far been described from Australia (see Hoare et al. 1997; Hoare in press), and only two from South-east Asia. It is perhaps therefore not surprising that no group of Nepticulidae has been shown to have a classical disjunct 'Gondwanan' type of distribution.

The Australian nepticulid fauna is dominated by numerous (mainly undescribed) species of Pectinivalvinae (mostly belonging to *Pectinivalva* Scoble) and of *Stigmella* Schrank (Nepticulinae: Nepticulini), and these are the only two groups recorded from this country in the literature (Common 1990, Nielsen 1996, Hoare et al. 1997; Hoare in press). During the course of a study of the systematics of Australian Nepticulidae, three genera belonging to the tribe Trifurculini were found to be present in Australia: *Acalyptris* Meyrick, *Trifurcula* Zeller (subgenus *Glaucolepis* Braun) and *Ectoedemia* Busck. In this paper, I define and describe the *Ectoedemia* (*Fomoria*) *vannifera* group, and review it from a phylogenetic perspective. The discovery of this group in Australia, from where three new species are here described, opens up the possibility that this is an ancient Gondwanan group: this is discussed with respect to the phylogenetic hypothesis presented.

Materials and methods

Slides were prepared following the methods described by Hoare (in press). In preparing the male genitalia, one valva was usually removed and mounted dorsum uppermost in order to display the complex structures exhibited in this species group.

Cladistic analysis was performed using the computer program PAUP 3.1.1 (Swofford 1995). The data set was small enough to allow an exhaustive search to be performed; i.e. all possible tree topologies were evaluated. The program MacClade 3.06 (Maddison & Maddison 1996) was used to examine further the most parsimonious trees found by PAUP. The 'Trace Character' option was used to investigate state changes on trees character by character, and to generate the list of apomorphies. Where a character state is equivocal along a branch or part of a branch, this is clearly shown with this option in effect; it is thus possible to distinguish between unambiguous apomorphies, and those which depend on one of two or more possible character state mappings. Where alternative interpretations are possible, I have indicated this in the text.

All material of the three new species described here is deposited in the ANIC (Australian National Insect Collection, CSIRO Entomology, Canberra, A.C.T.). For other material examined (see Appendix), the following abbreviations for institutions have been used:

BMNH	British Museum (Natural History), London, U.K.
RMNH	Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.
NZAC	New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand.
TM	Transvaal Museum, Pretoria, South Africa.

Taxonomy

The *Ectoedemia (Fomoria) vannifera* group

Adults. – Head capsule (figs 2, 3): see under *E.* (*F.*) *squamibunda* sp. n. Frontal tuft either pale ochreous more or less mixed with fuscous, or black. Thorax and forewing pale ochreous with varying pattern of fuscous or blackish scales. Hindwing with or without androconia in male. Underside of male forewing sometimes with hair-pencil and/or patch of androconial scales.

Male genitalia (figs 5-17). – Vinculum with moderately long anterior extension. Tegumen not or only slightly extended into pseuduncus. Uncus inverted Y-shaped or nipple-shaped. Gnathos sometimes enlarged. Valvae widely separated at base, and vinculum extended into a membranous lobe between them. Valva (figs 6, 9, 13, 15) complex: apex with membranous pin-cushion-like lobe, dorsal surface with various projections, each bearing a seta, or with a setose 'ridge', inner (medial) edge often with well-sclerotized projection. Transverse bar of transtilla very long. Aedeagus (figs 7, 11, 16, 17): apex with paired more or less claw-like carinate processes; vesica with numerous cornuti in 1 or 2 rows.

Female genitalia (figs 18, 19). – Vestibulum usually with complex sclerites of irregular shape. Corpus bursae elongate, with well-developed signa reticulata (reticulations modified in *E.* (*F.*) *vannifera*: see Scoble 1983: fig. 117).

Larva (description based on Australian species only). – Head-capsule (figs 20-25) elongate or squarish; labial palpi 2-segmented, segment 2 ca. 2 times as long as segment 1; stipes with 1 seta. Thorax: prothoracic sternite (figs 27, 28) more or less T- or X-shaped; chaetotaxy (fig. 26): prothorax with 12 pairs of setae (one seta in XD-SD group absent, here interpreted as SD2); mesothorax with 9 or 10 pairs of setae (1 D seta present; L3 absent). Abdomen: A1-8 with 6 pairs of setae; A9 with 2 pairs of setae; A10 with 2 pairs of ventral setae, one very short, one long. Anal rods tapered, pointed. Colour yellowish; cuticular spines minute, and reduced in extent.

Pupa (description based on Australian species only). – Head: clypeus transverse; frons without setae; labial palpi slightly longer than maxillae. A2-8 dorsally with 3-4 rows of large spines on each segment; numerous minute spines anterior and posterior to these on each segment, the anterior ones arranged into small pectinations; dorsal abdominal setae absent.

Biology. – Host-plants: *Capparis* L. spp. and *Boscia* Lam. spp. (Brassicaceae). Mine (figs 29, 30): linear;

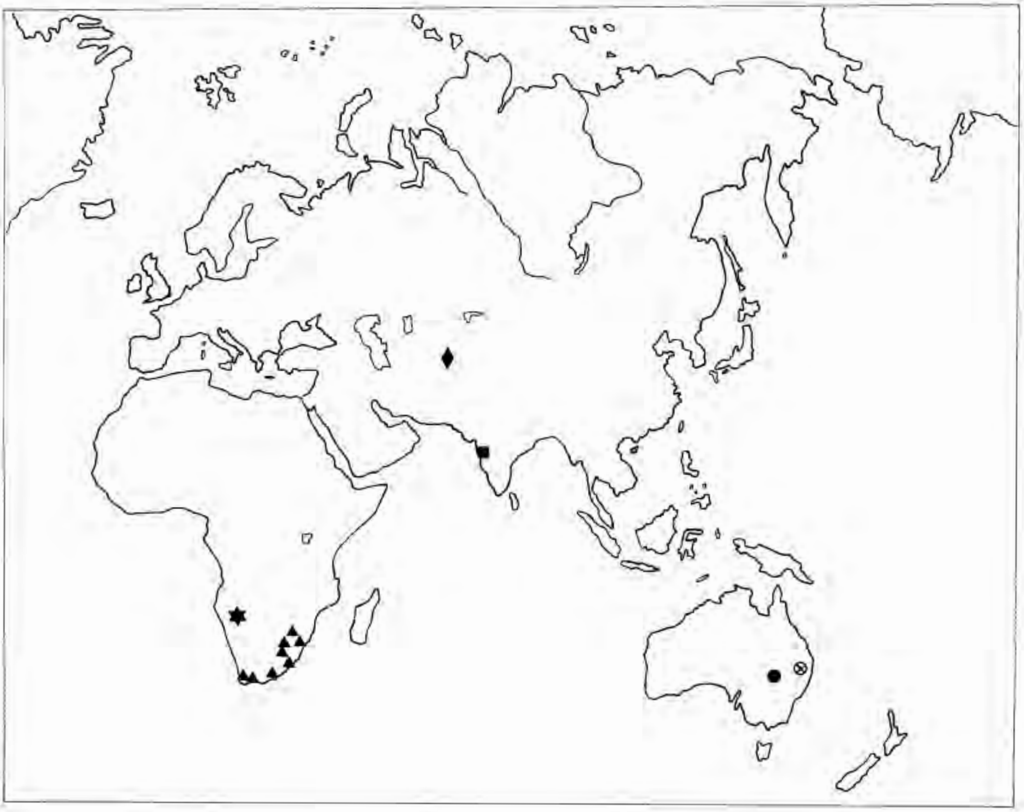


Fig. 1. Known distribution of the *Ectoedemia* (*Fomoria*) *vannifera* group. – Triangles: *E.* (*F.*) *vannifera*; star (Abachaub, Namibia): *E.* (*F.*) *fuscata*, *E.* (*F.*) *hobohmi* and *E.* (*F.*) *vannifera*; diamond: *E.* (*F.*) *asiatica*; square: *E.* (*F.*) *glycystrota*; crossed circle: *E.* (*F.*) *squamibunda* and *E.* (*F.*) *hadronycha*; filled circle: *E.* (*F.*) *pelops.*

exit-hole a semicircular slit.

Diagnosis. – Species can only with certainty be recognized as belonging to this group on the basis of the male genitalia. The presence of the pin-cushion lobe at the apex of the valva is diagnostic; all known species also have a ridge or projection on the dorsal surface of the valva which usually bears more or less conspicuous setae.

Distribution (fig. 1). – South Africa (3 or 4 species), India (1 species), central Asia (1 species), Australia (4 species).

Included species. – The known described species belonging to the *E.* (*F.*) *vannifera* group are as follows: *Ectoedemia* (*Fomoria*) *vannifera* (Meyrick), South Africa; *E.* (*F.*) *fuscata* (Janse), South Africa; *E.* (*F.*) *hobohmi* (Janse), South Africa; *E.* (*F.*) *asiatica* (Puplesis), Central Asia; *E.* (*F.*) *glycystrota* (Meyrick), comb. n., India; *E.* (*F.*) *pelops* sp. n., Australia; *E.* (*F.*) *squamibunda* sp. n., Australia; *E.* (*F.*) *hadronycha* sp. n., Australia.

In addition, one undescribed species is known from South Africa, and one from Australia, as follows: Scoble (1983: 38) mentions a male paralectotype of *E.* (*F.*) *hobohmi*, which shows characters intermediate between that species and *E.* (*F.*) *vannifera*, and probably represents an undescribed species. The undescribed Australian species is dealt with under *E.* (*F.*) *pelops*, q.v.

The South African species were redescribed by Scoble (1983), and *E.* (*F.*) *asiatica* has been recently redescribed and illustrated by Puplesis (1994). *E.* (*F.*) *glycystrota* is here redescribed, and the adult and male genitalia are illustrated for the first time. The new Australian species are described and illustrated.

It should be noted that Puplesis et al. (1996) erected a '*Fomoria asiatica* group': apart from *E.* (*F.*) *asiatica*, all species included in this group by these authors lack the pin-cushion lobe, and the group was not defined. Although it is undesirable to create a confusion of overlapping species-group concepts in the literature, I propose that the clearly monophyletic *vannifera* group as defined here is a biologically more meaningful entity than the *asiatica* group of Puplesis et al. (1996) and should be adopted in preference.

Ectoedemia (Fomoria) glycystrota comb. n.

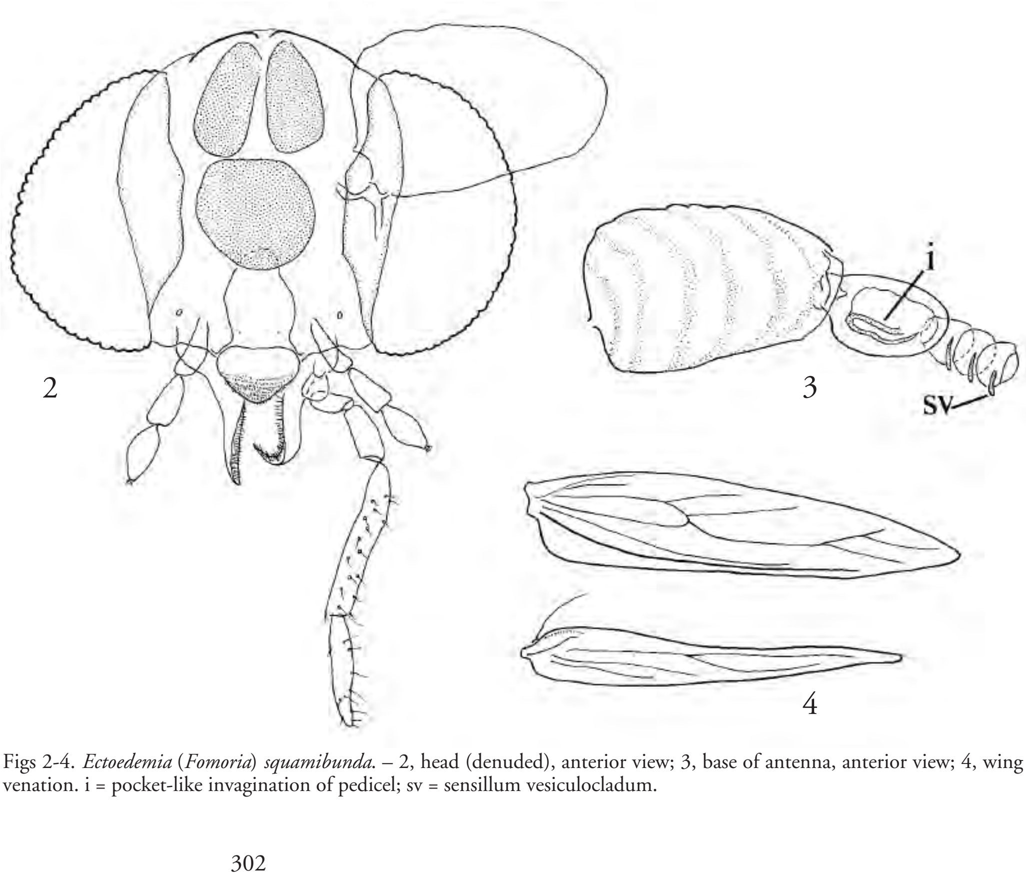
Nepticula glycystrota Meyrick, 1928: 462.

Material examined. – Lectotype (here designated) ♂, INDIA: Bombay, Kaira, 19 Mar 1925, R. Maxwell. Genitalia slide 24108 (BMNH).

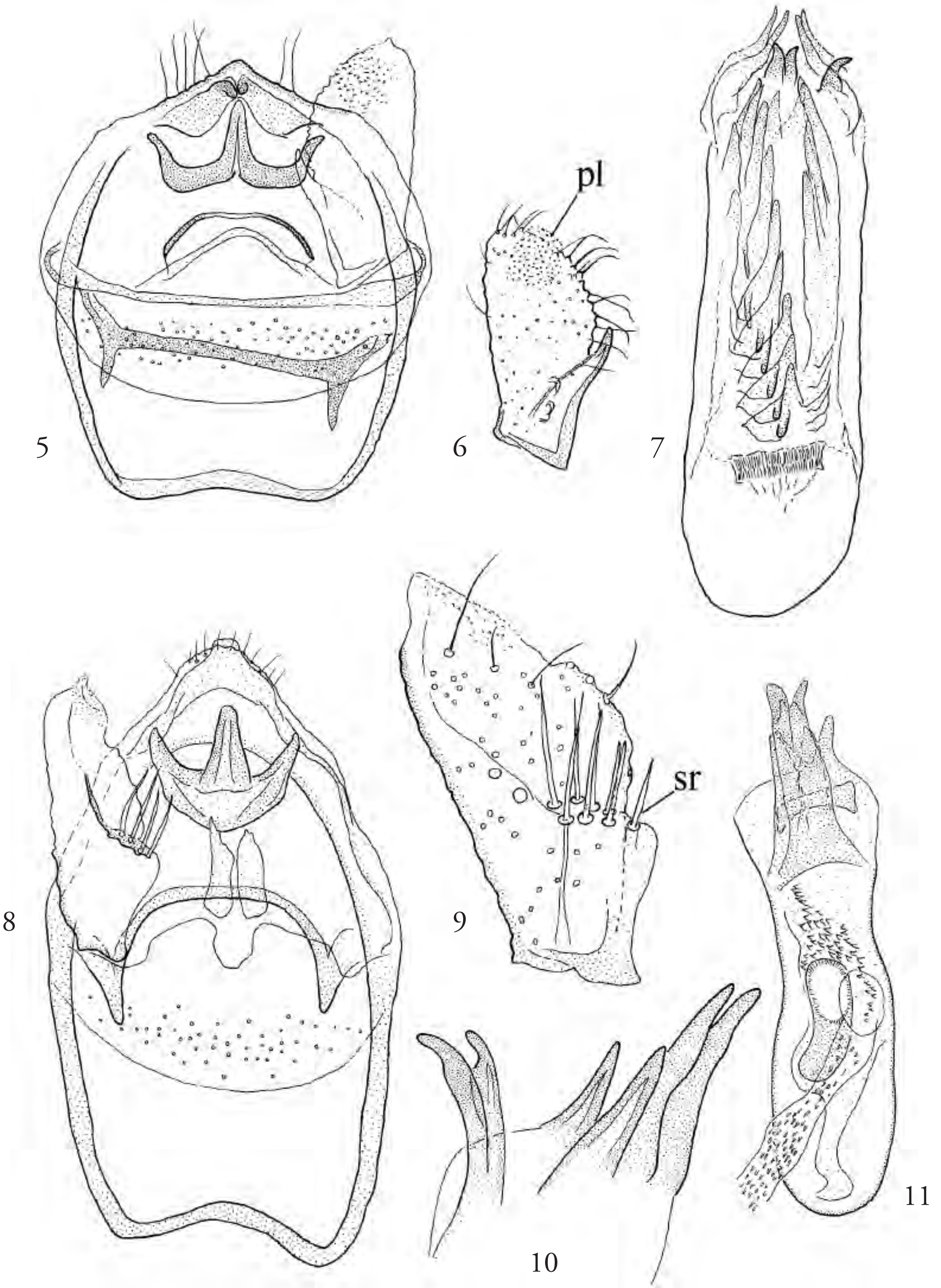
Male (fig. 31). – Wingspan 4.8 mm. Head: Frontal tuft whitish ochreous, with admixture of fuscous scales; collar whitish; eyecaps whitish ochreous with a few fuscous scales towards base; antennae light grey, 52 segments. Thorax and forewing pale ochreous, irrorated with fuscous scales, except for a narrow whitish ochreous strip along dorsum; cilia whitish ochreous. Hindwing whitish; cilia whitish. Underside: forewing shining greyish ochreous, with patch of white granular androconial scales in basal 1/2 in centre; overlapping this patch a row of long shining pale grey scales arising from base of hindwing costa; rest of hindwing and cilia shining whitish.

Male genitalia (figs 5-7). – Genital capsule ca. 435 µm long. Anterior extension of vinculum about 1/2 length of capsule, squared off; posterior edge with juxta-like lobe short and broad, sclerotized along each side. Tegumen produced into bluntly pointed pseuduncus, a row of ca. 8 setae on each side. Uncus inverted V-shaped, weakly divided medially. Gnathos simple, W-shaped. Valva (fig. 6) reaching just beyond uncus, more or less rounded, terminating in a small blunt projection; inner (medial) edge with short spine-like process arising from about 1/2 way up and projecting slightly dorsally into capsule; dorsal surface with 2 or 3 small projections near base (no setae observed, but these may have been detached); pin-cushion lobe large but not projecting as far from body of valva as in other members of the group. Aedeagus (fig. 7) ca. 600 µm long, with 2 pairs of lateral carinate processes, one pair of central carinae, and a single curved carina on right in ventral view; vesica with 2 parallel fields of strong cornuti.

Remarks. – A superficial examination of a female paralectotype of *E.* (*F.*) *glycystrota* showed that it had a collar consisting of lamellate scales, and was therefore referable to the genus *Stigmella* Schrank or possibly *Acalyptris* Meyrick, but certainly not to *Ectoedemia.* The third specimen in the type series has not been examined by me, but it is a male (K. R. Tuck, pers. comm.). The



Figs 2-4. *Ectoedemia* (*Fomoria*) *squamibunda.* – 2, head (denuded), anterior view; 3, base of antenna, anterior view; 4, wing venation. i = pocket-like invagination of pedicel; sv = sensillum vesiculocladum.



Figs 5-11. *Ectoedemia* (*Fomoria*) spp., male genitalia. – 5-7, *E.* (*F.*) *glycystrota*: 5, genital capsule, ventral view; 6, left valva, ventral view; 7, aedeagus, ventral view. 8-11, *E.* (*F.*) *pelops*: 8, genital capsule, ventral view; 9, right valva, dorsal view; 10, tip of aedeagus, lateral view, with ventral carinae to right; 11, aedeagus, ventral view. pl = pin-cushion lobe; sr = setose ridge of valva.

larva and biology of *E. glycystrota* are unknown.

Ectoedemia (Fomoria) pelops sp. nov.

Material examined. – Holotype, ♂, AUSTRALIA: New South Wales, 70 miles [113 km] N. of Bourke, 24 Oct 1957, I. F. B. Common. Genitalia slide 11532 (ANIC). – Paratypes, 3♂, same data as holotype. Genitalia slides 12092, 12098, 12099 (ANIC).

Male (fig. 32). – Wingspan 4.4-5.2 mm. Head: frontal tuft black; collar lead-grey; eyecaps white with a few fuscous scales; antennae grey, ca. 42 segments. Thorax and tegulae whitish ochreous. Forewing whitish ochreous, more or less heavily irrorated with fuscous; basal 1/3 of wing blackish towards costa; a conspicuous patch of raised blackish and whitish ochreous scales at base of costa; cilia whitish grey. Hindwing whitish grey; cilia whitish grey. Underside: forewing greyish, yellowish around base of cilia; hindwing pale greyish with a few blackish scales in basal 1/3. Abdomen pale silvery grey, with a patch of blackish scales on each side at base.

Female. – Not positively associated (see under Remarks).

Male genitalia (figs 8-11). – Genital capsule ca. 400 µm long. Anterior extension of vinculum long, with slight medial excavation. Tegumen rounded, with ca. 5 setae on each side. Uncus more or less teat-shaped, reaching just beyond tegumen. Gnathos not enlarged, basal plate relatively broad, central element a narrow triangle. Valva (fig. 9) with base of inner (mesal) edge thickened, extended laterally into a ridge, approximately 1/2 way up dorsal surface of valva; the ridge surmounted by 8 strong spine-like setae in two parallel rows; main body of valva rounded, pin-cushion lobe prominent. Aedeagus (figs 10, 11) ca. 420 µm long, relatively broad, somewhat constricted medially; one pair of dorsal, one pair of medial and one pair of ventral carinae. Vesica with numerous very small cornuti near base of ejaculatory duct, and a transverse subrectangular sclerite near apex of aedeagus.

Larva and biology unknown. The host-plant is likely to be *Capparis mitchellii* Lindley (Brassicaceae), which is common in the area where the moths were taken.

Diagnosis. – Easily distinguished from the other known Australian species by the smaller size and the absence of the black costal patch on the forewing at 1/2. In the genitalia, the strong setae arising from the dorsal surface of the valva, and the relatively small gnathos are also characteristic.

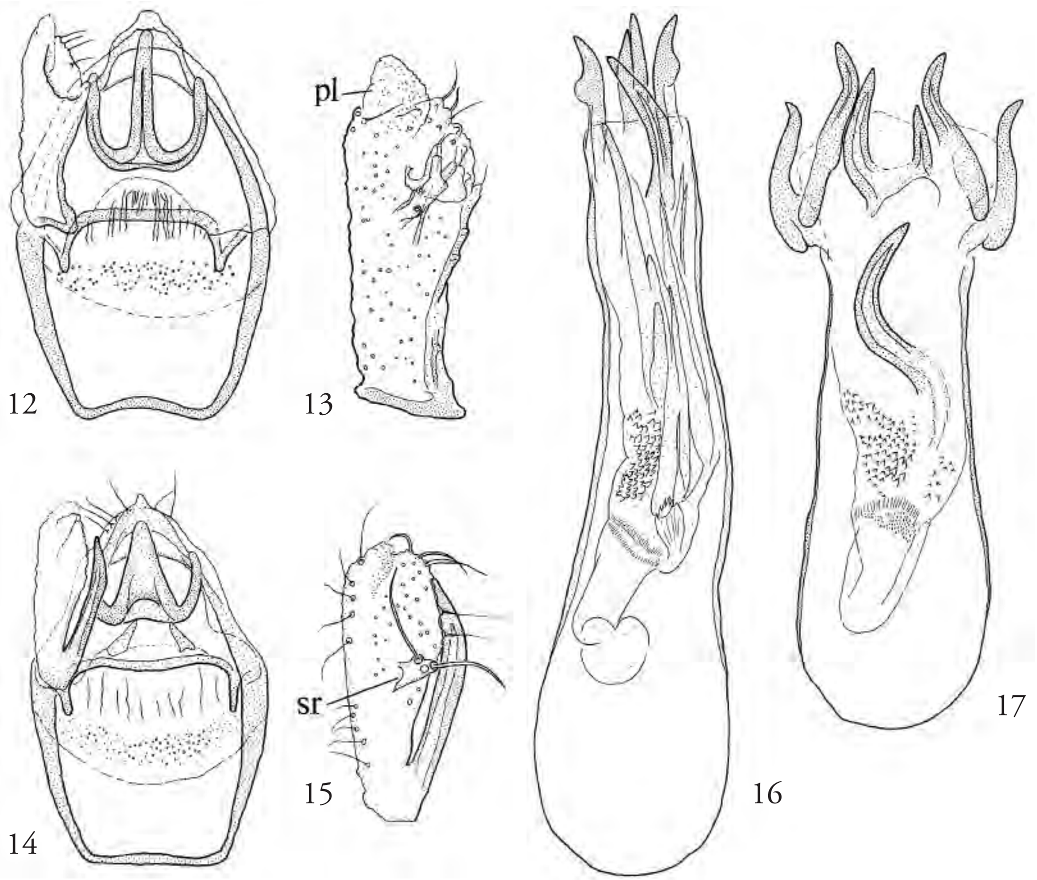
Derivation. – The species is named after Pelops, a character in Greek mythology. His father Tantalus cut him up and served his flesh to the gods to test them. The goddess Demeter ate part of Pelops' shoulder, but soon realized her mistake. Pelops was then reassembled and given a new shoulder made of ivory. (Tantalus was suitably, and eternally, punished). The name was suggested by the conspicuous patch of raised white scales at the base of the moth's forewing.

Remarks. – Three female specimens collected in the same locality and on the same date as the males of *E.* (*F.*) *pelops* are present in ANIC. The genitalia show that they belong to *Ectoedemia*, so they are presumed on circumstantial evidence to be referable to the *vannifera* group. They closely resemble the males of *E.* (*F.*) *pelops* apart from lacking the androconial scales on the wings and abdomen. Although no superficial differences have been observed between these specimens, the genitalia indicate that they belong to two species, i.e. presumably *E.* (*F.*) *pelops* and an undescribed species. The females are therefore excluded from the type series of *E.* (*F.*) *pelops*.

Ectoedemia (Fomoria) squamibunda sp. n.

Material examined. – Holotype, ♂, AUSTRALIA: Queensland, 27.34S 152.01E, Toowoomba, Redwood Park, emerged 22-23 Jan 1996, R. J. B. Hoare & I. F. B. Common. Genitalia slide 12095 (ANIC). – Paratypes, 2♂, 3♀, same data as holotype, emerged 4-27 Jan 1996; 1♂, Queensland, 27.34S 152.01E, 5km E of Toowoomba, 340m, emerged 10 Nov 1985, I. F. B. Common; 1♂, 1♀, Queensland, Toowoomba, 30 Nov 1983, E. S. Nielsen. Slides 10176, 11259, 11298 (ANIC). 1♂, Queensland, 28.11S 153.11E, Lamington Nat. Pk, Binna Burra, 700m, 27 Nov 1989, I. F. B. Common. Slides 10197, 11272 (ANIC).

Male (fig. 33). – Wingspan 5.2-5.8 mm. Head capsule (fig. 2): labial palpi moderate, slightly longer than galeae; maxillary palpi with ratio of segments from base approximately 0.3: 0.3: 0.6: 1.3: 1; eyes very large, interocular index 1.15; scape (fig. 3) large, with scale-sockets grouped into 6 parallel rows; pedicel modified, with complex pocket-like invagination; flagellar segments with sensillum vesiculocladum unbranched and bordered by long microtrichia. Frontal tuft black; collar blackish; eyecaps whitish ochreous; antennae whitish ochreous, 45-48 segments. Thorax and tegulae whitish ochreous. Basal 1/2 of forewing with blackish scales overlain by whitish ochreous scales, giving grey appearance; base of costa, small basal spot just dorsad of fold, and small spot near wing apex black; a black, slightly outwardly oblique streak from costa just beyond 1/2 reaching 1/2 way across wing; rest of wing whitish ochreous with a few fuscous-tipped scales; cilia whitish ochreous. Hindwing translucent whitish; basal 1/2 overlain with elongate black androconial scales, extending into fringe on dorsum; these in turn overlain by a few whitish ochreous



Figs 12-17. *Ectoedemia* (*Fomoria*) spp., male genitalia. – 12, 13, 16, *E.* (*F.*) *squamibunda*: 12, genital capsule, ventral view; 13, right valva, dorsal view; 16, aedeagus, ventral view; 14, 15, 17, *E.* (*F.*) *hadronycha*: 14, genital capsule, ventral view; 15, right valva, dorsal view; 17, aedeagus, ventral view. pl = pin-cushion lobe; sr = setose ridge of valva.

scales; cilia whitish ochreous. Underside: forewing with basal 1/2 silver-grey, blackish towards costa; a broad band of blackish scales from costa at about 1/2 reaching 1/2 way across wing, rest of wing ochreous-fuscous; hindwing silver-grey with long black androconial scales at base of cilia in basal 1/2. Wing venation as in fig. 4; typical of the subgenus. Abdomen: dorsum of basal segment overlain by black androconial scales; rest of abdomen shining pale grey.

Female (fig. 34). – Wingspan 5.8-6.2 mm. Similar to male, but eyecap smaller; antenna with 42 segments; forewing broader, whitish ochreous without underlying black scales, basal dot absent, but additional black dot on fold at 1/4 present. Hindwing and abdomen pale shining greyish without androconial scales. Underside: forewing ochreous fuscous, unmarked; hindwing pale grey.

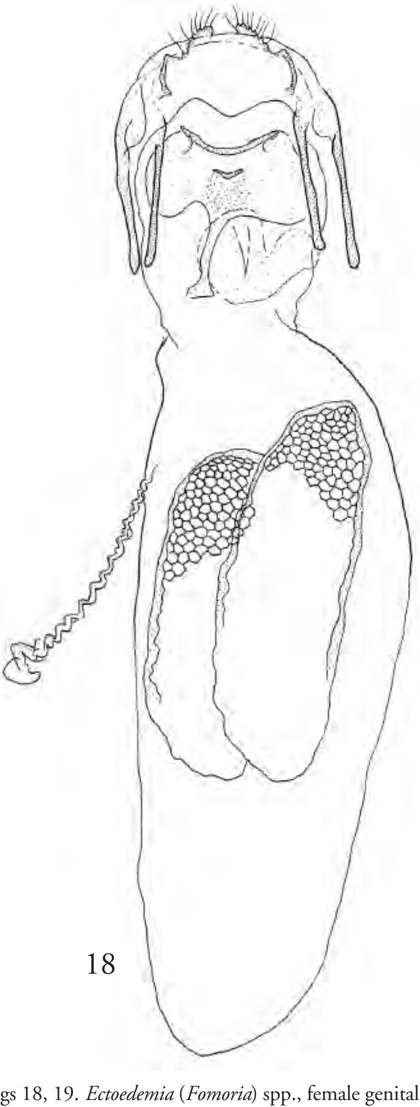
Male genitalia (figs 12, 13, 16). – Genital capsule ca. 455 µm long. Vinculum anteriorly squared off. Tegumen rounded, slightly produced posteriorly, with 4 setae on each side. Uncus teat-shaped, reaching beyond tegumen. Gnathos enlarged, with long narrow central element. Valva (fig. 13) ca. 250 µm long, squarish, inner (medial) margin nearly perpendicular; inner 1/2 of apex with 2-3 rows of small blunt projections, each bearing a seta; a row of 4-5 elongate papillae, each bearing a seta, projecting from just below apex of valva dorsally into genital capsule; pin-cushion lobe prominent, projecting beyond rest of valva. Aedeagus (fig. 16) ca. 590 µm, narrow; a large ventral carina, apically with 2 points, one slightly longer than the other; 2 small lateral claw-like carinae. Vesica with central field of very long narrow cornuti; apex with a long, curved cornutus projecting between carinae.

Female genitalia (fig. 19). – Total length ca. 1080-

1120 µm. Abdomen bluntly rounded. T9 with ca. 15 setae on each side. Apophyses narrow, posteriores and anteriores about equal in length. Vestibulum with complex sclerotizations. Ductus spermathecae with 151/2 convolutions. Corpus bursae oblong; signa reticulata ca. 415-430 µm long, borders of reticulations relatively broad.

Larva. – Yellowish. Head-capsule (figs 20-22) rather elongate; length ca. 615 µm; width ca. 510 µm; frontoclypeus (fig. 20) stirrup-shaped; anterior tentorial arms ca. 2 times as long as posterior. Thorax: mesothorax with 10 pairs of setae (4 setae ventral to SV1). Spines distributed as follows: meso- and metathorax and A1-5 with 2 small patches on anterior margin of venter, each side of the mid-line; A6-9 with a single larger patch; A5-9 with an additional patch on anterior edge of dorsum, larger on A7-8.

Biology. – Host-plant: *Capparis arborea* (F. Muell.) Maiden (Brassicaceae). Egg: usually on the upperside of the leaf, near or adjacent to the midrib. Mine (fig. 29): a more or less contorted gallery with linear frass leaving very narrow clear margins; exit-hole on upperside of leaf. Cocoon: reddish brown. Occupied mines were collected on 17 July 1995.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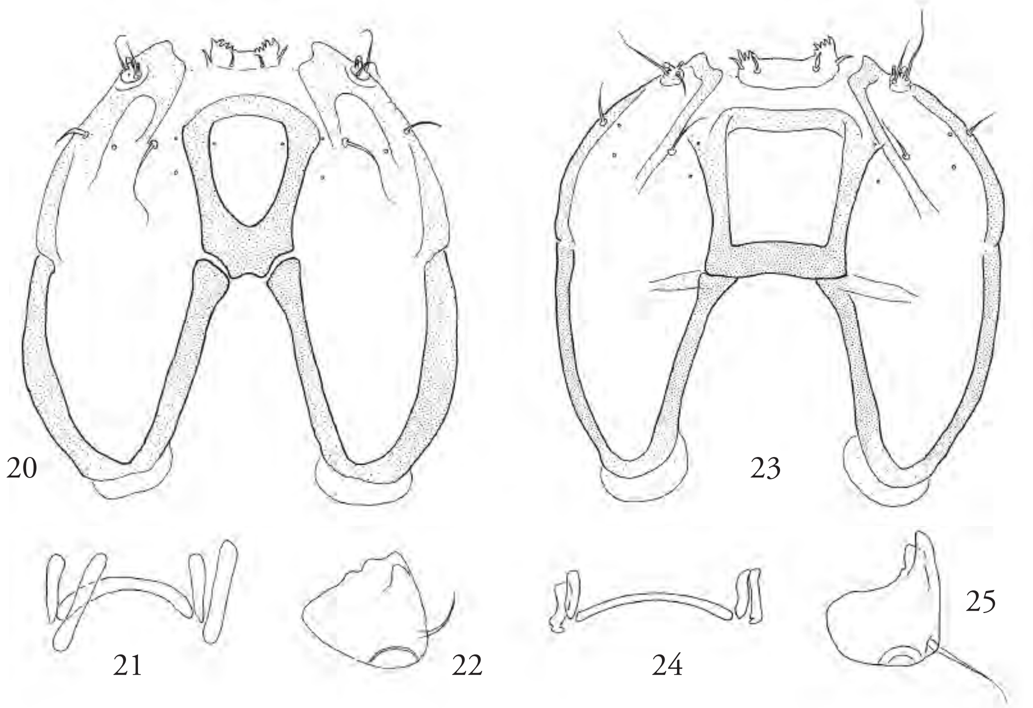
Figs 18, 19. *Ectoedemia* (*Fomoria*) spp., female genitalia (reticulations of signa only partly indicated). – 18, *E.* (*F.*) *hadronycha*; 19, *E.* (*F.*) *squamibunda*.



Figs 20-25. *Ectoedemia* (*Fomoria*) spp., larval heads (final instar). – 20-22, *E.* (*F.*) *squamibunda*: 20, head capsule, dorsal view; 21, tentorium; 22, right mandible; 23- 25, *E.* (*F.*) *hadronycha*: 23, head capsule, dorsal view; 24, tentorium; 25, right mandible.

Diagnosis. – Superficially similar to *E.* (*F.*) *hadronycha* sp. n.; the differences are listed under that species.

Derivation. – The specific name means 'very scaly' and is derived from the Latin *squama* (a scale) and the suffix *-bundus* (denoting augmentation). It refers to the many black androconial scales at the base of the forewing and hindwing in the male, which give the moth a roughened appearance.

Remarks. – Specimens reared in a cool room in Canberra did not emerge until January; however as the three wild-caught specimens were all taken in November (and the male paratype reared in Toowoomba also emerged during this month), the latter is more likely to represent the normal time of flight.

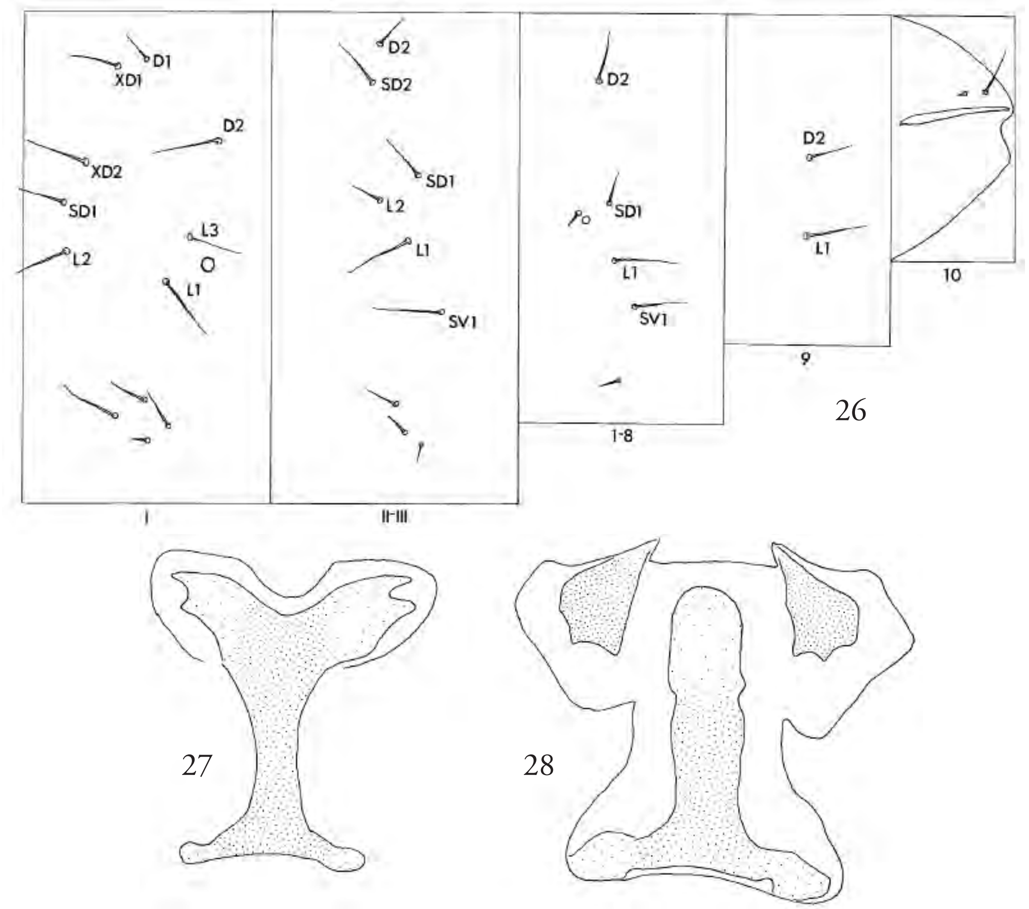
Ectoedemia (Fomoria) hadronycha sp. n.

Material examined. – Holotype ♂, AUSTRALIA: Queensland, 26.57S, 151.52E, 6km NNE of Cooyar, emerged 29 Sep 1995, R. J. B. Hoare & I. F. B. Common. Genitalia slide 12094 (ANIC). – Paratypes, 3♂, 2♀, same data as holotype, emerged 22-29 Sep 1995. Genitalia slides 11268, 11319 (ANIC).

Male (fig. 35). – Wingspan 6.2-6.6 mm. Head: frontal tuft black; collar black; eyecaps whitish ochreous with a few fuscous-tipped scales; antennae dark lead-grey, 51-53 segments. Thorax, tegulae and forewing whitish ochreous irrorated with fuscous; base of costa blackish; a tuft of raised elongate whitish ochreous to fuscous scales just below costa near base; a blackish streak from costa just beyond 1/2 reaching 1/2 way across wing; a blackish dot near apex; cilia at apex concolorous with forewing, shining yellowish grey on tornus and dorsum. Hindwing pale grey; cilia shining yellowish grey. Underside: forewing fuscous, darker towards costa; hindwing pale grey. Abdomen shining grey.

Female (fig. 36). – Wingspan 6.5-7.1 mm. Similar to male, but antenna with 42 segments; eyecaps without fuscous-tipped scales; forewing broader, more yellowish, with sparser irrorations and no subcostal patch of raised scales.

Male genitalia (figs 14, 15, 17). – Genital capsule ca. 410-425 µm long. Vinculum with anterior extension relatively long, squared off. Tegumen rounded, with ca. 4-5 setae on each side. Uncus teat-shaped, reaching beyond tegumen. Gnathos enlarged, with broad triangular central element. Valva (fig. 15) ca. 190-215 µm, deeply cleft from near base; inner (medial) part consist-



Figs 26-28. *Ectoedemia* (*Fomoria*) spp., larval cuticle. – 26, *E.* (*F.*) *hadronycha*, chaetotaxy; 27, *E.* (*F.*) *squamibunda*, prothoracic sternite; 28, *E.* (*F.*) *hadronycha*, prothoracic sternite.

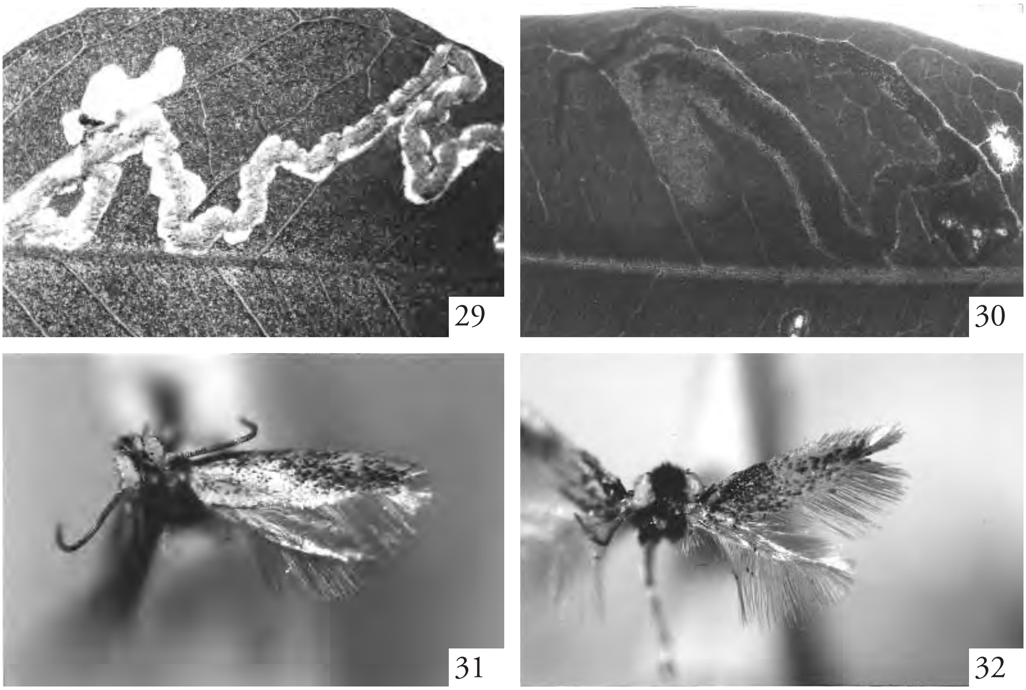
ing of a narrow, strongly sclerotized, curved spine, 4/5 length of valva; main (exterior) part rounded, with moderately large pin-cushion lobe and a complex setose process arising on dorsal surface and projecting into genital capsule. Aedeagus (fig. 17) ca. 465 µm long, broad, fused to posterior membranous part of vinculum by 2 very small sclerotized tooth-like processes; 2 pairs of curved lateral carinae, one pair situated dorsally, one pair ventrally; 2 central, ventral carinae. Vesica with one very large curved cornutus, and a field of small, leaf-like cornuti near base of ejaculatory duct.

Female genitalia (fig. 18). – Total length ca. 1170 µm. T9 with ca. 14 setae on each side. Apophyses narrow, anteriores slightly longer than posteriores. Vestibulum with large ventral dumbbell-shaped sclerotization, produced antero-dorsally into a narrow process; a second irregular sclerite to the right of this process in dorsal view. Ductus spermathecae with 111/2 convolutions. Corpus bursae oblong; signa reticulata broad, ca. 440 µm long, borders of reticulations narrow.

Larva. – Yellowish, gut green. Head capsule (figs 23-25) rather broad; length ca. 600 µm; width ca. 520 µm; frontoclypeus (fig. 23) squarish, only slightly narrowed posteriorly; anterior and posterior tentorial arms short and roughly equal in length. Thorax: chaetotaxy as in fig. 26; mesothorax with 9 pairs of setae (3 setae ventral to SV1). Spinosity: ventral spines as described for *E.* (*F.*) *squamibunda*; dorsal spines absent.

Biology. – Host-plant: *Capparis arborea* (Brassicaceae). Egg: on leaf upperside. Mine (fig. 30): similar to that of *E.* (*F.*) *squamibunda*, but distinctly broader in its later stages. Cocoon: reddish brown. Occupied mines were collected on 18 July 1995.

Diagnosis. – Both male and female are larger than those of *E.* (*F.*) *squamibunda*. The male of *E.* (*F.*)



Figs 29-32. *Ectoedemia* (*Fomoria*) spp., larval mines and adults. – 29, *E.* (*F.*) *squamibunda* sp. n., larval mine on *Capparis arborea*; 30, *E.* (*F.*) *hadronycha* sp. n., larval mine on *Capparis arborea*. 31, *E.* (*F.*) *glycystrota*, ♂ lectotype; 32, *E.* (*F.*) *pelops* sp. n., ♂ holotype.

hadronycha lacks the black androconial scales on forewing and hindwing, and the female has the forewing more extensively irrorated with fuscous than that of *E.* (*F.*) *squamibunda*, and lacks the conspicuous black dot on the fold. In the male genitalia, the broad gnathos, the large valval spine and the broad aedeagus of *E.* (*F.*) *hadronycha* distinguish it from *E.* (*F.*) *squamibunda*. In the female genitalia, *E.* (*F.*) *hadronycha* is distinguished by the narrow borders to the reticulations of the signa, and by the smaller number of convolutions in the ductus spermathecae.

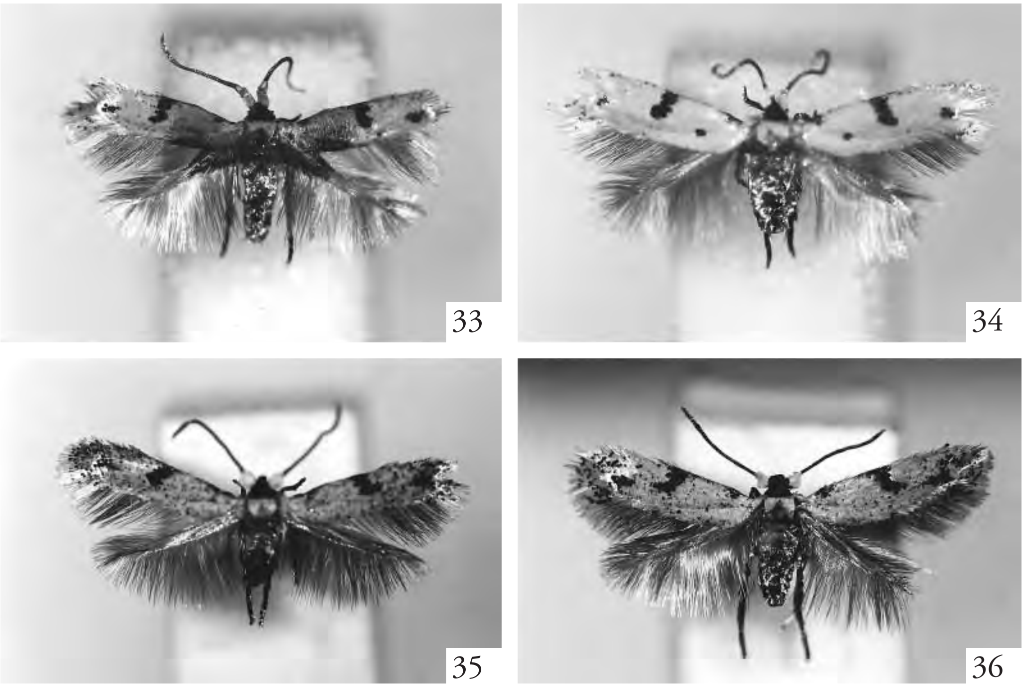
Derivation. – The specific name is derived from the Greek *hadros* (stout or thick) and *onyx* (a claw), and refers to the large spine-like process on the medial edge of the valva.

Remarks. – This species has only been collected from a single tree in a narrow belt of dry rainforest along a roadside. Much of the original vegetation in the area has been cleared; therefore it is possible that the species is under threat.

Phylogenetic analysis

Choice of terminal taxa

All named (including newly described) species known to have the pin-cushion lobe of the valva in the male genitalia were included as ingroup taxa in the analysis. Apart from the *Ectoedemia* (*Fomoria*) *vannifera* group, the *E.* (*F.*) *weaveri* group is the only other recognized species group within *Fomoria* (see van Nieukerken 1986). The monophyly of the *E.* (*F.*) *weaveri* group has been asserted by van Nieukerken (1986) and by Johansson et al. (1990), but these authors did not list any defining apomorphies. I believe that the monophyly of the *weaveri* group is confirmed by the following apomorphies shared by all species: lateral arms of gnathos straight, more or less horizontal; lateral arms of vinculum strongly expanded medially and meeting anterior to gnathos. The following may represent apomorphies of the *weaveri* group as a whole, but are not shared by all species: host-plant *Hypericum* (Clusiaceae); pupation inside mine; valva with sharp dorsal spine (this spine differs in position and shape from the blunt spine on the medial edge of the valva in some species of the *E.* (*F.*) *vannifera* group (see below), although it may be homologous). On this basis, I regard the following described species as belonging to the *weaveri* group (cf. van Nieukerken 1986): *E.* (*F.*) *septembrella* (Stainton), Palaearctic; *E.* (*F.*) *weaveri* (Stainton), Palaearctic; *E.* (*F.*) *luisae* (Klimesch), Turkey; *E.* (*F.*) *deschkai* (Klimesch), Greece; *E.* (*F.*) *variicapitella* (Chrétien), Morocco, Canary Islands; *E.* (*F.*) *hyperi-*



Figs 33-36. *Ectoedemia* (*Fomoria*) spp., adults. – 33, 34, *E.* (*F.*) *squamibunda* sp. n.: 33, ♂ holotype, 34, ♀ paratype; 35, 36, *E.* (*F.*) *hadronycha* sp. n., paratypes: 35, ♂, 36, ♀.

cifoliella (Kuroko), Asia; *E.* (*F.*) *permira* (Puplesis), Asia; *E.* (*F.*) *hypericella* (Braun), North America; *E.* (*F.*) *pteliaeella* (Chambers), North America.

The *E.* (*F.*) *weaveri* group is considered to be closely related to the *E.* (*F.*) *vannifera* group. In a cladistic analysis of the Nepticulidae (Hoare unpublished) based on 23 ingroup taxa (including one member of each of these groups) and 56 characters, a sister-group relationship between the two groups was recovered on the basis of the following apomorphies in the male genitalia: valvae widely separated at base; vinculum produced posteriorly into a membranous juxta-like lobe between the valvae. These apomorphies are shared by all members of both groups. The species of the *E.* (*F.*) *weaveri* group are mostly very similar in morphology, and it would make little difference which species was chosen as an outgroup exemplar for the phylogenetic analysis of the *vannifera* group. Because of availability of material, *E.* (*F.*) *septembrella* was used as the outgroup taxon in the current analysis.

Characters

The three multi-state characters were treated as unordered.

1. Colour of head-tuft: (0) orange; (1) whitish to ochreous (may be mixed with fuscous scales); (2) black.
2. Ground colour of forewing: (0) greyish; (1) ochreous.
3. Forewing – black streak from costa at 1/2: (0) absent; (1) present.
4. Knob of raised scales at base of male forewing: (0) absent; (1) present.
5. Underside of male forewing: (0) without specialized scales; (1) with black androconial scales; (2) with white androconial scales.
6. Underside of male forewing – hair pencil: (0) absent; (1) present.
7. Base of male hindwing: (0) normal; (1) expanded

Table 1. Data matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
E. septembrella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E. vannifera	1	1	0	0	1	1	1	1	0	0	1	1	1	0	1
E. fuscata	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0
E. hobohmi	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1
E. glycystrota	1	1	0	0	2	0	0	0	0	0	1	1	1	0	1
E. asiatica	1	1	0	0	1	1	1	1	0	0	1	1	1	0	1
E. pelops	2	1	0	1	0	0	0	2	1	0	1	0	1	1	0
E. squamibunda	2	1	1	0	0	0	0	2	0	1	1	0	1	1	0
E. hadronycha	2	1	1	1	0	0	0	0	1	1	1	1	1	1	0

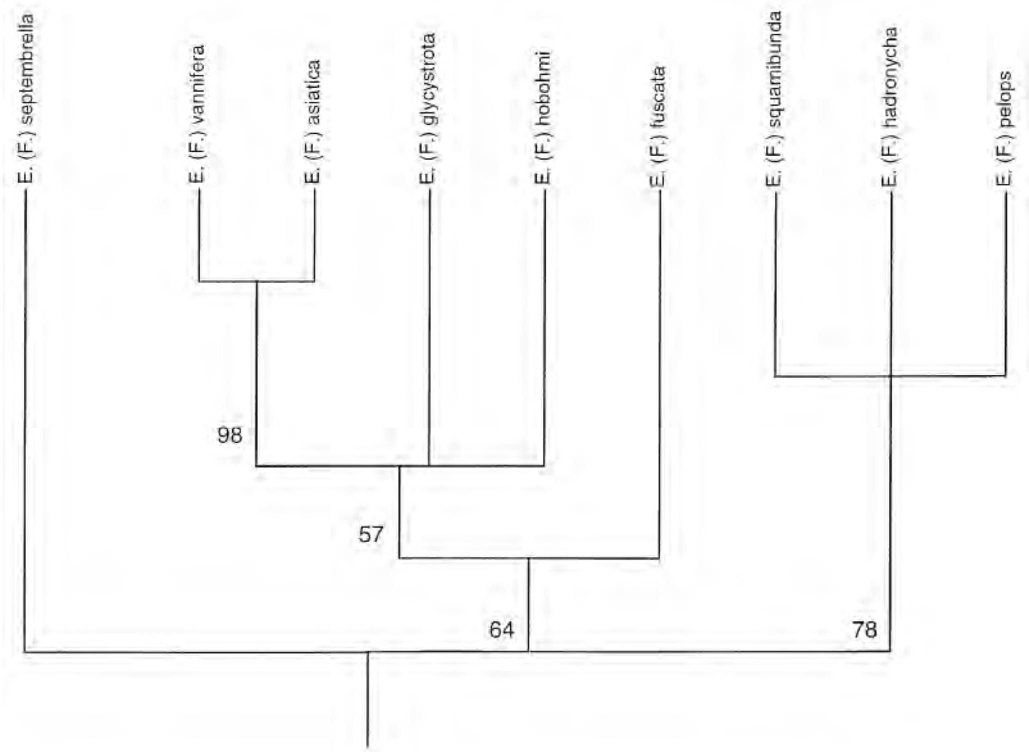


Fig. 37. Strict consensus tree of 4 equally most parsimonious trees from data set of *Ectoedemia* (*Fomoria*) *vannifera* group, with bootstrap support for clades (1000 bootstrap replicates, branch and bound search).

(Scoble 1983: fig. 49).

8. Base of male hindwing: (0) without specialized scales; (1) with a patch of black scales in anterior half ; (2) with black scales across whole depth of wing.
9. Male genitalia – posterior extension of vinculum: (0) without sclerotized juxta-like processes; (1) with paired sclerotized processes (figs 8, 14).
10. Male genitalia – gnathos: (0) normal; (1) enlarged (figs 12, 14).
11. Male genitalia – pin-cushion lobe of valva: (0) absent; (1) present (figs 6, 9, 13, 15).
12. Male genitalia – mesal spine of valva: (0) absent; (1) present (fig. 15).
13. Male genitalia – ridge or projection on dorsal surface of valva: (0) absent; (1) present (figs 6, 9, 13, 15). The form of this ridge varies considerably between species; it usually bears more or less conspicuous setae.
14. Male genitalia – shape of uncus: (0) inverted V or Y, shorter than tegumen (fig. 5; Scoble 1983: fig. 100); (1) nipple-like, reaching beyond tegumen (figs 8, 12, 14).
15. Male genitalia – aedeagus: (0) with 1 field of cornuti (figs 11, 16, 17); (1) with 2 parallel fields (fig. 7).

The data matrix is presented in table 1.

Results

An exhaustive search in PAUP 3.1.1 resulted in 4 most parsimonious trees (length 23; C.I. = 0.83, R.I. = 0.83), differing only in the position of *E.* (*F.*) *hobohmi* with respect to *E.* (*F.*) *glycystrota* and the clade formed by *E.* (*F.*) *vannifera* + *E.* (*F.*) *asiatica*, and in the inter-relationships of the three Australian species. A strict consensus tree is presented in fig. 37, together with bootstrap support for the nodes recovered (1000 bootstrap replicates, branch and bound search). The species-group falls into two monophyletic sub-groups: one comprising the Australian species, and one comprising all the remaining species from South Africa, India and central Asia. The biogeographical implications are discussed below.

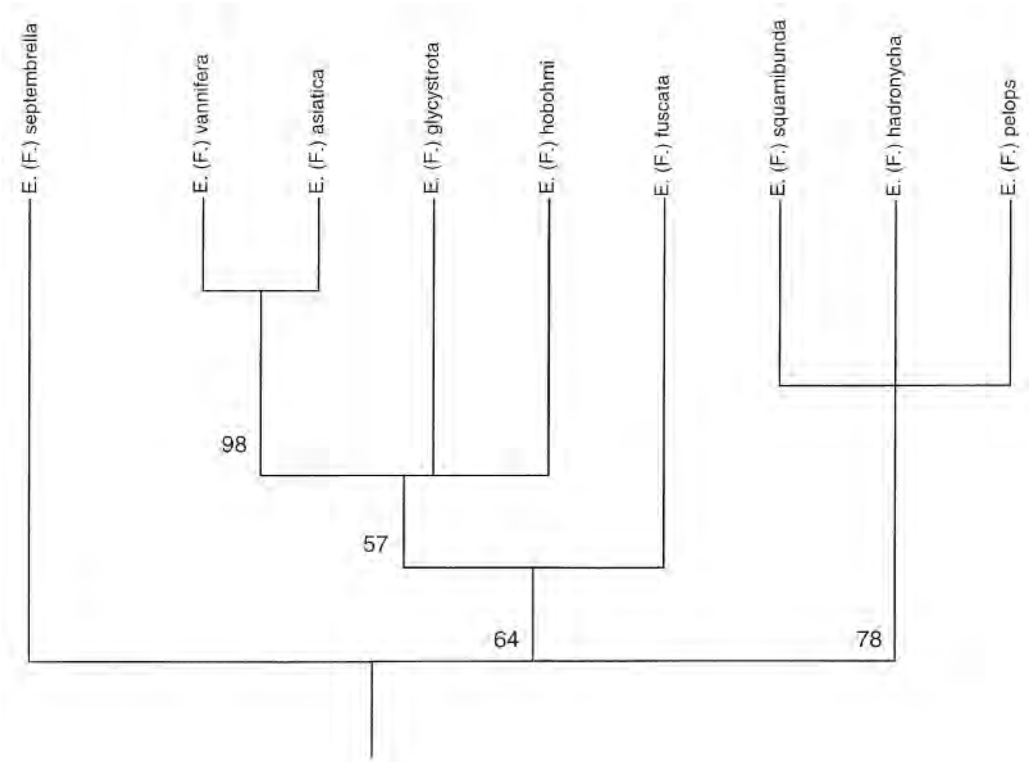


Fig. 38. Preferred fully resolved estimate of phylogeny of *E.* (*F.*) *vannifera* group, with apomorphies of clades.

The apomorphies for groups that are constant in all most parsimonious trees are listed here; the character number followed by state are given in parentheses. As only a single outgroup was used, the monophyly of the *E.* (*F.*) *vannifera* group was not strictly tested in the current analysis. However, its monophyly is strongly supported by the following three apomorphies (there is little doubt about the polarity of the characters concerned): male valva with pin-cushion lobe (11-1; present in all species, and unique to the group); male valva with dorsal projection or sclerotized ridge (usually setose) (13-1; present in all species and unique to the group); forewing ground colour ochreous (2-1; most species of *Ectoedemia*, including all described species in the *E.* (*F.*) *weaveri* group, have the forewing ground colour greyish fuscous to black).

The monophyly of the group containing all the South African and both the Asian species is supported by the following two apomorphies: head colour whitish to ochreous, more or less mixed with fuscous scales (1-1; in most species of *Ectoedemia*, including members of the *E.* (*F.*) *weaveri* group, the frontal tuft of the head is orange); valva with spine on medial edge (12-1; in these species the spine is short and blunt, and it is most parsimonious to assume that the very large spine on the valva of the Australian *E.* (*F.*) *hadronycha* has evolved independently: otherwise, the spine has been lost independently by *E.* (*F.*) *squamibunda* and *E.* (*F.*) *pelops*).

The monophyly of the group comprising the Australian species is supported by seven apomorphies. Two are unambiguous, viz.: head colour black (1-2); uncus nipple-like (14-1; in the other members of the *vannifera* group and in the members of the *weaveri* group, the uncus is in the form of an inverted V or Y). The following five apomorphies are present in only two of the three species: forewing with a black streak from the costa at 1/2 (3-1; absent from *E.* (*F.*) *pelops*); base of male forewing with a knob of raised scales (4-1; absent from *E.* (*F.*) *squamibunda*); base of male hindwing with black androconial scales from costa to dorsum (8-2; absent from *E.* (*F.*) *hadronycha*); membranous posterior extension of vinculum with a pair of sclerotized juxta-like processes (9-1; absent from *E.* (*F.*) *squamibunda*); gnathos enlarged (10-1; paralleled in *E.* (*F.*) *hobohmi*: the gnathos is normal in *E.* (*F.*) *pelops*). I assume that a gain of a structure followed by a loss is a more parsimonious explanation of the data than two independent gains. Then, if *E.* (*F.*) *hadronycha* and *E.* (*F.*) *pelops* are sister-species, character states

3-1, 8-2 and 10-1 are apomorphies of the entire clade of three species. If, however, *E.* (*F.*) *squamibunda* and *E.* (*F.*) *hadronycha* are considered sister-species, it is most parsimonious to assume that character states 4-1, 8-2 and 9-1 are apomorphies of the Australian clade as a whole. I tentatively prefer this latter hypothesis, as these two species share the same host-plant (*Capparis arborea*) (host-plant data are missing for most species in the analysis, so this was not coded as a character).

Within the African / Asian clade, *E.* (*F.*) *fuscata* is sister to the remaining species, which all share the following apomorphy: aedeagus with two parallel fields of cornuti (15-1). The sister-species relationship between *E.* (*F.*) *asiatica* and *E.* (*F.*) *vannifera* is supported by the following four apomorphies: male forewing underside with a patch of black androconial scales (5-1); male forewing underside with a hair-pencil (6-1); base of male hindwing expanded (7-1); base of male hindwing with black androconial scales in anterior half (8-1).

It is very probable that the white androconial scales on the underside of the male forewing in *E.* (*F.*) *glycystrota* are homologous with the black scales in *E.* (*F.*) *asiatica* and *E.* (*F.*) *vannifera*, and have not been developed independently. I therefore suggest that *glycystrota* is sister-species to *asiatica* + *vannifera*.

The preferred fully resolved phylogenetic hypothesis is presented in fig. 38.

Discussion

Some caution is needed in interpreting the results of the cladistic analysis presented here. Most of the characters used are derived from the males, and a number of them are secondary sexual characters such as presence or absence of androconial scales and associated modifications. As such structures are presumably subject to strong sexual selection, and hence are liable to evolve quickly, they may be expected to show a relatively high level of homoplasy. Moreover, separate structures associated with the dispersal of pheromones may not always evolve independently; i.e. it may be incorrect to treat them as independent characters for the purpose of cladistic analysis. For example, in *Trifurcula* Zeller, the tufts of hair-scales on T6-7 of the male abdomen, together with the patch of raised scales on the underside of the hindwing and the third branch of Rs+M in the hindwing are probably a complex scent-dispersal structure, rather than three independent characters (cf. Johansson et al. 1990: 260). The same may be true of the androconial structures of *Ectoedemia* (*Fomoria*) *vannifera* and *E.* (*F.*) *asiatica*. However, other species in the group show some of the same androconial structures, but not all: for example, a male paralectotype of *E.* (*F.*) *hobohmi* (which probably represents an undescribed species) has a hair-pencil on the underside of the forewing similar to that found in *E.* (*F.*) *vannifera*, but lacks the black specialized scales of the latter species (Scoble 1983: 38). There is therefore some justification for treating the characters as independent.

The monophyly of the subgenus *Fomoria*

Fomoria was named by Beirne (1945) after a race of demonic and malevolent beings who ruled Ireland in the mythical past (Emmet 1991). This is perhaps appropriate from a systematist's point of view, given that it remains the only subgenus in the Nepticulidae for whose monophyly no evidence has been found. However, some monophyletic groups can be recognized within the subgenus; these are discussed below.

The monophyly of the *E.* (*F.*) *vannifera* group has been argued for above. The monophyly of the *E.* (*F.*) *weaveri* group has also been argued for here (see above, under Phylogenetic analysis). In addition to the material of the *E.* (*F.*) *vannifera* group, there is a single male *Ectoedemia* specimen in ANIC from Lamington National Park, Queensland, collected on 14 Nov 1990. It differs strikingly from most members of the genus, and indeed most nepticulids, in the predominantly silver coloration of its forewings. However, it shares both the apomorphies (lateral arms of gnathos horizontal; lateral arms of vinculum expanded) here used to define the *E.* (*F.*) *weaveri* group. It also shares the possible apomorphy: valva with sharp dorsal spine. This represents the first record of the *weaveri* group from the southern hemisphere, and has potentially interesting implications for the origin and age of the group. Unfortunately, the males of the *weaveri* group show less morphological variation than those of the *vannifera* group. Therefore, until more material of the Australian species becomes available, including females and larvae, it is probably premature to speculate on the phylogeny and biogeography of the group.

I tentatively propose here that a third species-group can be recognized within *Fomoria*. This group includes at least three species: *E.* (*F.*) *groschkei* (Skala) from southern Europe, *E.* (*F.*) *thermae* Scoble from South Africa, and an undescribed species from Japan (van Nieukerken 1986). I have not examined these species in detail, and am unable to suggest any morphological apomorphies defining this group, but all three species share an unusual choice of host-plant family, the Verbenaceae: *E.* (*F.*) *groschkei* and *E.* (*F.*) *thermae* have larvae mining in *Vitex* L. spp., and the undescribed species mines in *Callicarpa* L. The recently described *E.* (*F.*) *aegaeica* Z. & A. Laštuvka from Greece and Crete is also suspected to feed on *Vitex* (Laštuvka & Laštuvka 1998), and so possibly also belongs here. The group is referred to below as the *groschkei* group.

The synapomorphies given above to link the *vannifera* and *weaveri* groups (valvae widely separated at base; vinculum with posterior extension) may be evidence of the monophyly of a subsection of *Fomoria*

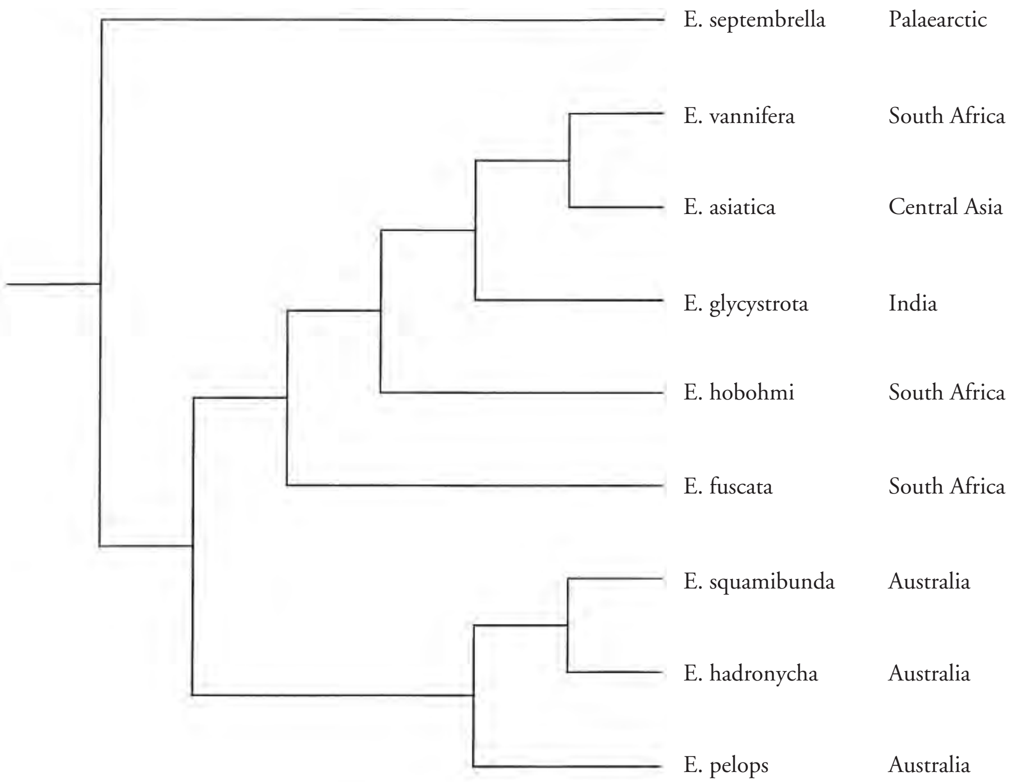


Fig. 39. Phylogeny of *E.* (*F.*) *vannifera* group, with geographical origin of each species.

comprising the *weaveri* group, the *vannifera* group and the *groschkei* group. However, the degree of separation of the valvae at their bases is a rather variable character, and perhaps should not be accorded too much weight: widely separate valvae are also found elsewhere in *Ectoedemia*, for example in *E.* (*Laqueus*) *crispae* Scoble. Even if one accepts the monophyly of this 'core group' within *Fomoria*, there remains a substantial residue, comprising at least 12 described species from South Africa, *E.* (*F.*) *flavimacula* (Puplesis & Diškus) and *E.* (*F.*) *lacrimulae* (Puplesis & Diškus) from Central Asia and the European *E.* (*F.*) *viridissimella* (Caradja).

Some preliminary studies of larval morphology indicate a possible sister-group relationship between the subgenera *Fomoria* and *Laqueus* (Hoare unpublished). The two most convincing synapomorphies supporting this relationship are: loss of seta D1 on larval mesothorax, and loss of one SD seta on larval prothorax. It would be interesting to see whether these synapomorphies applied to the many South African species of *Laqueus* and *Fomoria* whose larvae have not been examined. The monophyly of *Laqueus* is not in serious doubt: all species have veins 1A and 2A separate at the base of the forewing, forming a so-called 'anal loop' (Scoble 1983; van Nieukerken 1986). The European species at least also have a bisetose larval stipes (van Nieukerken 1986) (a character state not otherwise found in the Nepticulinae, although at least some pectinivalvine larvae have a bisetose stipes (Hoare in press)). However, the possibility cannot be ruled out that *Laqueus* was derived from within *Fomoria*: if so, the latter subgenus is paraphyletic as it stands, and *Laqueus* should be synonymized with *Fomoria*. It is obviously premature to make this synonymy at this stage, but it is perhaps increasingly unlikely that any apomorphic features unique to *Fomoria* and not shared by *Laqueus* will be found.

Host-plant relationships and biogeography of the *Ectoedemia (Fomoria) vannifera* group

The preferred phylogeny of the *E.* (*F.*) *vannifera* group from the current analysis is reproduced in fig. 39, annotated with the region in which each species occurs. The nesting of *E.* (*F.*) *glycystrota* (Meyrick) from India and *E.* (*F.*) *asiatica* (Puplesis) from central Asia within the clade formed by the South African species, together with the strongly supported sister-species relationship between *E.* (*F.*) *asiatica* and *E.* (*F.*) *vannifera*, indicate a complex biogeography for the group. Clearly, the group has dispersed widely at some stage in its history: the question is whether this dispersal preceded the break-up of the continents in the Mesozoic, in which case the group is very old, or whether it has spread more recently.

India, Australia and South Africa are well known to have been joined as part of the southern supercontinent Gondwana until the early Cretaceous (e.g. Scotese et al. 1988). If the *vannifera* group originated before Gondwana began to fragment, it is possible that its current distribution is a reflection of that continental break-up. If so, the group perhaps shows a 'northern Gondwanan' distribution of the type described by Edmunds (1975) for leptophlebiid mayflies, and by Cranston & Hare (1995) for *Conochironomus* Freeman (Diptera: Chironomidae), although the presence of a species in central Asia, not usually considered a part of Gondwana, remains anomalous. The paraphyly of the South African species with respect to those from India and central Asia could then indicate that speciation within the *vannifera* group had already begun before Africa and India separated ca. 130-120 million years B.P. However, one should probably not make too much of the relationships within the major clades in arguing about biogeography, given the relatively limited nature of the data set. If vicariance is the true explanation for the current distribution of the group, further field-work should reveal its presence in Madagascar, which was contiguous with both India and southern Africa in Gondwanan times.

Unfortunately, the host-plant relationships of the *vannifera* group are not conclusive in deciding whether its apparently disjunct distribution is indeed a result of vicariance. Only three species of the group have been reared: *E.* (*F.*) *squamibunda* and *E.* (*F.*) *hadronycha* from Australia both feed on *Capparis arborea*, and the South African *E.* (*F.*) *vannifera* feeds on *Boscia oleoides* (Burch. ex DC.) Tölken (Scoble 1983: 38). *Capparis* L. and *Boscia* Lam. are closely related genera which have long been included in the Capparaceae, but there is now strong evidence that this family is paraphyletic with respect to Brassicaceae (Judd et al. 1994), and the latter family has been expanded to include it (Angiosperm Phylogeny Group 1998). As *E.* (*F.*) *squamibunda* and *E.* (*F.*) *hadronycha* are relatively distant from *E.* (*F.*) *vannifera* in the phylogeny, it seems fair to assume that all species in the group will be found to feed on *Capparis* or related brassicaceous plants. The genus *Capparis* itself is worldwide in the tropics and in warm temperate regions, occurring both in rainforest and in semi-arid or arid habitats, and does not share the apparently disjunct distribution of the *vannifera* group. 'Capparaceae' have never been considered to be an ancient Gondwanan group of plants, although it should be noted that little biogeographic work has been done on the group. It seems possible that relatively recent dispersal has played at least some part in the current distribution of these plants, and that *Capparis* may not have reached Australia until the late Tertiary. As Nepticulidae are unlikely to be able to disperse effectively over very long distances, their ranges should track contiguous parts of their host-plants' ranges fairly closely. It is important to note that very few Nepticulidae have been sampled from large areas of tropical Africa and Asia. Thus, if a hypothesis of relatively recent dispersal is correct, further collecting should reveal new species of the *vannifera* group in other areas where the host-plants occur, for example northern Africa, the Middle East and South-East Asia. A very different picture of the distribution and phylogenetic relationships of the group may then emerge.

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APPENDIX

Material examined for cladistic analysis

Material examined of the three Australian species and of *Ectoedemia* (*Fomoria*) *glycystrota* is listed in the main text.

Ectoedemia (Fomoria) septembrella (Stainton)

2♂, UK: Hants, Winchester, emg. Apr 1990, R. J. B. Hoare (ANIC slide 11269), ex larvae / pupae in leaves of *Hypericum* sp., Dec 1989 (ANIC, NZAC).

Larvae: Beekhuizen, NETHERLANDS, 24 Jun 1979, E.J. van Nieukerken, mining leaves of *Hypericum maculatum* (VU no. 79065; RMNH).

E. (*F.*) *asiatica* (Puplesis)

Paratype ♂, TADZHIKISTAN: 30 km N of Dushanbe, 21 Aug 1986, R.K. Puplesis (VU slide 2911; RMNH).

E. (*F.*) *vannifera* (Meyrick)

1♂, SOUTH AFRICA: Worcester, Fairy Glen, 15 or 19 Oct 1966, L. Vári, J.H. Potgieter (TM).

External characters of the following two species wer e scored from Janse (1948) and Scoble (1983): I have only personally examined the genitalia slides cited.

E. (*F.*) *fuscata* (Janse)

Lectotype ♂, NAMIBIA: Abachaub, Oct 1945, G. Hobohm (slide 4971; TM).

E. (*F.*) *hobohmi* (Janse)

Paralectotype ♂, NAMIBIA: Abachaub, Sep 1944,