

Faecal case architecture in the *gibbosus* species group of *Neochlamisus* Karren, 1972 (Coleoptera: Chrysomelidae: Cryptocephalinae: Chlamisini)

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Constructions composed of faeces are rare in insects, but occur in certain leaf-beetle clades. Members of the subfamily Cryptocephalinae share a complex behavioural and morphological synapomorphy, involving portable faecal cases that house the immature stages. A maternally initiated egg case is expanded and enlarged through four larval stadia, then sealed to provide a pupal chamber from which adults eventually emerge. We analyse and compare faecal-case architecture in ten taxa of the cryptocephaline genus *Neochlamisus*, and assess structural variation within a life cycle, between different ‘host forms’ of *Neochlamisus bebbianae*, and among species. These cases proved to be comprised primarily of faeces, with plant trichomes representing the only common secondary component. General architectural trends reflected variation in shape, faecal texture, and the incorporation and density of trichomes. Deviations of the *Neochlamisus* case from a simple geometrical gnomon reflect the changing body size of the animal, differential application of faeces, and shifts in the orientation of the carriage of the case. *Neochlamisus* cases are presumably energetically costly to produce, carry, and maintain, and some adaptive hypotheses of case evolution are proposed. Additionally, literature on case morphology in other camptosomates is reviewed. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, **152**, 315–351.

ADDITIONAL KEYWORDS: defence – faeces – host plant – larvae – leaf beetles – trichomes.

INTRODUCTION

Faecal construction is one of the oddest behaviours among certain clades of Chrysomelidae. Adults and immature stages of species in several subfamilies retain faeces as camouflage, clubs, and protective covers. The subfamilies Cryptocephalinae (135 genera; *c.* 3587 species) and Lamprosomatinae (13 genera; *c.* 190 species) (Seeno & Wilcox, 1982; Reid, 1995, 2000; Farrell, 1998) are commonly referred to

as the Camptosomata or ‘case-bearers’, because their species build hard cases of faeces, mixed with anal and oral fluids, around the immature stages (Cockerell, 1891; Lécaillon, 1898; Sharp, 1899; Donisthorpe, 1902; Fiebrig, 1910; Fiori, 1950; Erber, 1968, 1969, 1988; Schmitt, 1988; Reid, 1990, 1991; Olmstead, 1994; Jolivet, 1997; Jolivet & Verma, 2002; Schöller, 2004; Brown & Funk, 2005) (Fig. 1). [We note that the term ‘case-bearers’ is also commonly applied to members of the lepidopteran family Coleophoridae; e.g. Bucheli, Landry & Wenzel (2002) and Falkovitch (2003)].

All case-bearing chrysomelids build their cases in a similar way: cryptocephaline females enclose single eggs in a hardened faecal case. Upon hatching, the

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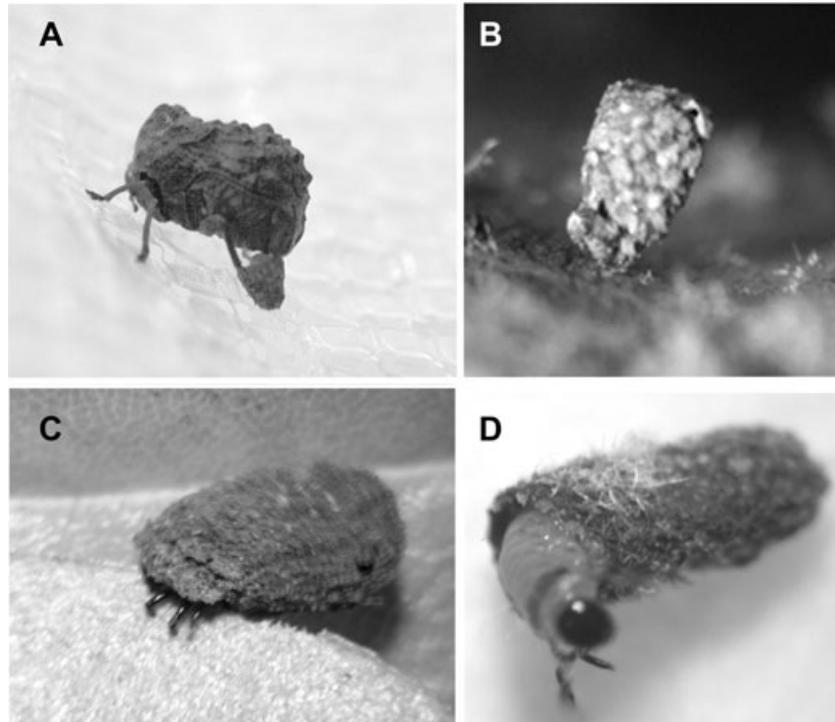


Figure 1. A, *Neochlamisus bebbianae* IV: *Acer* (maple) host form coating her faeces on her eggs. B, egg case of *Neochlamisus platani*. C, third instar of *Neochlamisus chamaedaphnes* walking with its portable case. D, second instar of *Neochlamisus bebbianae*, *Salix* (willow) host form. All photos by CGB.

first larval instar destroys the sealed flattened ‘roof’, turns the egg case upside down, and retains it as a protective home that covers most of the body, with only the legs and head projecting from the base opening, enabling movement and feeding. As the larva grows, it expands the case longitudinally by applying its faeces to extend the basal margins, and laterally by making a longitudinal slit that is forced open and filled in, thus adding to the faecal wall (Erber, 1988; Brown & Funk, 2005). This case is retained, carried, and expanded by all four instars, and is used as a ‘moveable house’ (e.g. Scudder, 1891). The prepupa (late instar IV) fixes the case to the substrate, closes the base opening with its faeces, and so makes a pupal chamber. Finally, the adult exits by cutting away a circular ‘cap’ from the case apex and escaping (e.g. Hislop, 1872). The material comprising these cases appears to be primarily faeces, mixed with salivary and anal secretions, along with inclusions like soil, debris, leaf fragments, wood chips, and leaf trichomes (Fiebrig, 1910; Linsenmaier, 1972; Erber, 1988; Lawson, 1991; Jolivet & Verma, 2002). Cases of the cryptocephaline egg, larva, and pupa are the product of complex and highly integrated morphological and behavioural traits in the adult female and her offspring. In this paper we present the most complete study of case architecture

in the tribe Chlamisini, an unusual example of insect architecture.

The Chlamisini comprise 11 genera and c. 400 species, and occur worldwide with 81% of the known species in the Neotropics (Monrós, 1951; Karren, 1972; Seeno & Wilcox, 1982; Erber, 1988; Reid, 1991). Biological information on immature stages is available for six genera: *Chlamisus* Rafinesque, 1815 (Packard, 1869, 1889; Riley, 1874a, b; Dimmock, 1885; Popenoe & Marlatt, 1889; Scudder, 1891; Wickham, 1896; Briggs, 1905; Fiebrig, 1910; Girault, 1911; Frost, 1942; Brown, 1943; Monrós, 1948, 1951; Peterson, 1951; Morgan & Maxwell, 1952; Wood, 1966; Karren, 1972; Medvedev & Zaitsev, 1979; Zaitsev, 1992; Reu & Del-Claro, 2005), *Exema* Lacordaire, 1848 (Dugès, 1881; Pierce, 1940; Brown, 1943; Karren, 1964; LeSage, 1982; Root & Messina, 1983; Boldt & White, 1992), *Diplacaspis* Jacobson, 1824 (Emden, 1932; Monrós, 1951; Karren, 1972), *Fulcidax* Voet, 1806 (Flinte *et al.*, 2003; Flinte & Macêdo, 2004a, b; Flinte, 2006), *Melitochlamys* Monrós, 1948 (Fiebrig, 1910; Monrós, 1951), and *Neochlamisus* Karren, 1972 (Karren, 1972; LeSage, 1984; Neal, 1989; Brown & Funk, 2005). *Arthrochlamys* Ihering, 1904, *Chlamys* (Knoch, 1801), and some species of *Chlamisus* were synonymized under the *gibbosus* species group of *Neochlamisus* (Karren, 1972), which

is the subject of the present study. Erber (1988) reviewed case structure across the Camptosomates.

The 17 known species of *Neochlamisus* are distributed in the south-western USA and Mexico (five species that constitute the *velutinus* species group), and eastern North America (12 species constituting the *gibbosus* species group) (Karren, 1972). Immature stages (and retention of faecal cases) have been described for a few species of *Neochlamisus*, and a recent paper (Brown & Funk, 2005) provides a highly detailed description of case-associated life history and behaviour, based on the *Neochlamisus gibbosus* group taxa. In the present paper we describe the faecal case architecture of ten North American taxa of *Neochlamisus*. These include seven species of the eastern *gibbosus* group, one of which includes six 'host forms' (Funk, 1998), four of which are studied here. Our treatment of all life-history stages of these ten taxa offers an unprecedented opportunity to examine developmental, individual, and taxonomic variation in cases, to develop a model and terminology for describing its architecture. Recent work is beginning to unveil the intriguing biology of Chlamisini. For example: (1) recent studies on *Neochlamisus* case construction and life history (Brown & Funk, 2005); (2) ecological studies of *Fulcidax monstrosa* Fabricius, 1798 (Flinte *et al.*, 2003; Flinte & Macêdo, 2004a, b; Flinte, 2006); and (3) ecology studies of *Chlamisus minax* Lacordaire, 1848 (Reu & Del-Claro, 2005).

MATERIAL AND METHODS

NATURAL HISTORY (FIG. 1)

Neochlamisus generally appear to be univoltine animals that pass through four larval instars and have an obligate winter diapause that precedes reproduction. Females emerge from this diapause in spring or early summer (depending on latitude and altitude), and proceed to feed, mate, and lay eggs on their host plants. Larval development, pupation, and adult emergence all take place entirely on the host plant as well. Newly emerged adults feed and mate on the host plant until the winter diapause. In the laboratory, development from oviposition through adult emergence lasts *c.* 2 months at 24 °C.

This study included four *Neochlamisus bebbianae* 'host forms', each of which represents the populations natively associated with its namesake plant. For example, the 'maple host form' represents those populations natively associated with *Acer rubrum* trees in nature, whereas the 'willow host form' is associated with *Salix bebbiana*. These host forms are ecologically and evolutionarily differentiated from one another to varying degrees (Funk, 1998; unpubl. data; Funk, Filchak & Feder, 2002; Egan & Funk, 2006).

HOST PLANTS AND HABITATS

The host plants of these species tend to be found in moist and disturbed habitats in eastern North America. Among these, *Chamaedaphnes calyculata* (Ericaceae) is restricted to northern bogs, where it is ecologically dominant and often found in association with *Vaccinium* (Ericaceae). *Betula nigra* (river birch) (Betulaceae) is found along lowland riparian areas in much of the southern two-thirds of the USA, as is *Platanus occidentalis* (Platanaceae), which has a much broader habitat distribution. *Salix bebbiana* (Salicaceae) is a northern species found near moist areas, where it commonly co-occurs with *Alnus* (Betulaceae) and with *Acer rubrum* (Aceraceae). The distribution of *Alnus*, however, extends into the southern USA, as does that of *A. rubrum*, the most widely distributed eastern North American tree. *Acer rubrum* is not restricted to moist areas and occupies a variety of habitats, including upland areas. *Myrica asplenifolia* (Myricaceae) is a northern plant found in areas with sandy soils. *Rubus* (Rosaceae) is found very commonly in a great variety of disturbed habitats across North America. See Karren (1972) for beetle species and distributions.

REARING PROTOCOL

Study animals were collected in the field from their host plants as eggs or larvae, or were obtained from eggs laid in the laboratory by field-collected adults. Larvae were reared in Petri dishes lined with moistened filter paper and host-plant foliage, and these were cleaned and replenished as necessary. Dishes were maintained in sealed plastic boxes in an incubator at 24 °C and a 14-h : 10-h light–dark cycle. As individuals of each species reached successive life history stages, subsets of them were preserved in ethanol for analysis. In this manner, we obtained sufficient material from each life stage for each taxon.

SPECIMENS

Ten study taxa were evaluated. Individuals of the *Neochlamisus* species studied herein were collected from the following host plants and localities.

Neochlamisus bebbianae (Brown, 1943): Alder host form (host = Betulaceae: *Alnus* spp.), White County, GA, USA, and Orleans County, VT, USA; maple host form (host = Aceraceae: *A. rubrum*), Greene County, GA, USA, Rockingham County, NH, USA, and Suffolk County, NY, USA; birch host form (host = Betulaceae: *B. nigra*), White County, GA, USA; willow host form (host = Salicaceae: *S. bebbiana*), Cumberland County, ME, USA, and Caledonia County, VT, USA.

Neochlamisus bimaculatus Karren, 1972 (host = *Rosaceae: Rubus spp.*): White County, GA, USA and Davidson County, TN, USA.

Neochlamisus chamaedaphnes (Brown, 1943) (host = *Ericaceae: Chamaedaphne calyculata L.*): Burnett County, WI, USA.

Neochlamisus comptoniae (Brown, 1943) (host = *Myricaceae: Myrica asplenifolia L.*): Rockingham County, NH, USA.

Neochlamisus cribripennis (LeConte, 1878) (host = *Ericaceae: Vaccinium spp.*): Suffolk County, NY, USA.

Neochlamisus eubati (Brown, 1943) (host = *Rosaceae: Rubus spp.*): Rockingham County, NH, USA.

Neochlamisus platani (Brown, 1952) (host = *Platanaceae: Platanus occidentalis L.*): White County, GA, USA, and Davidson and Williamson Counties, TN, USA.

PRESERVATION

Specimens were collected into and stored in 75% ethanol for photographic analysis, and in 90% ethanol for SEM work. Individuals were removed from their cases and stored in 75% ethanol, whereas their cases were air-dried before imaging.

VOUCHERS

Vouchers of all insect stages and cases have been deposited in four American collections: American Museum of Natural History, D. J. Funk collection (DJFC), University of Kansas Insect Collection, and the US National Museum. Beetle identifications were based on the keys and species descriptions of Karren (1972). Plant taxonomy was checked with the Missouri Botanical Garden W3Tropicos database (Solomon 2006).

EXAMINATION AND PHOTOGRAPHY

Small balls of plasticine were used to stabilize the dried cases in shallow wells of ceramic trays. Cases were stabilized and positioned on a bed of glass beads in a glass dish filled with 75% ethanol for initial examinations, and were then air-dried and examined. They were then cleaved by holding them with fine forceps and gently pressing against the ventral suture. This exposed the internal surface for examination. Exuvial inclusions were determined by tearing apart cases.

Cases were examined with a Zeiss compound microscope with a Type 256576 camera lucida attachment. Measurements were taken with a Lasico digital ocular micrometer. Cases and individuals were photographed with a Nikon D1 Digital camera, Infinity

K2 lenses, and a Microoptics ML1000 fibre optic flash unit. Photos were all taken by the first author, except where noted.

SCANNING ELECTRON MICROSCOPY (SEM)

Air-dried cases were mounted on standard aluminium SEM stubs (diameter, 12 mm; height, 7 mm; Electron Microscopy Sciences) and sputter coated with gold/palladium in a Denton Vacuum Desktop II model. Cases were broken longitudinally and mounted on SEM stubs. Cases were then examined with a Hitachi S4700 Field Emission Scanning Electron Microscope, at the American Museum of Natural History.

IMAGING AND FIGURE PREPARATION

Illustrations were scanned, digitized, and minimally edited in MS-Paint 2000. Images were minimally edited (background removed, some contrast manipulation) in Adobe Photoshop 6.0 and Canvas 9.0.1, and arranged as figures with Adobe Photoshop 6.0. All scanning electron micrographs are indicated; all other images are photomicrographs.

TERMINOLOGY

Cryptocephaline cases have been called 'sac' (Packard, 1869, 1889), 'bag' (Beeson, 1941), 'scatoshells' (Hinton, 1981; Erber, 1988), 'case' (LeSage, 1982), 'mantle' (Erber, 1988), and 'sheath' (Zaitsev, 1992). To avoid inferences about construction materials we eliminated scatoshell, as there may be situations where other materials may be incorporated, as suggested in the literature. Sac and bag suggest a structure that is suspended, so we selected *case* as the more inclusive descriptor.

Major landmarks and terminology for the description of cryptocephalinae cases are illustrated in Figure 2. The egg case is completely sealed and is shaped like an upturned bell, with a stalk at one end and a flattened sealed roof at the other end. The stalk is short and terminates in a flared rounded attachment disc that adheres to the substrate. The sealed roof may have the margin slightly flared, forming a flange (Karren, 1964). It is important to note that the instar-I larva turns the egg case upside down, and this has significant implications for terminology, orientation, and homology concepts. The case is orientated vertically relative to the substrate in young larvae, but is carried almost horizontally in older larvae. The original sealed roof of the egg case is orientated basally and is open in the larvae. We refer to the side walls as dorsal, lateral and ventral surfaces. The ventral surface is easily distinguished in all larval instars (starting with late instar I) and in

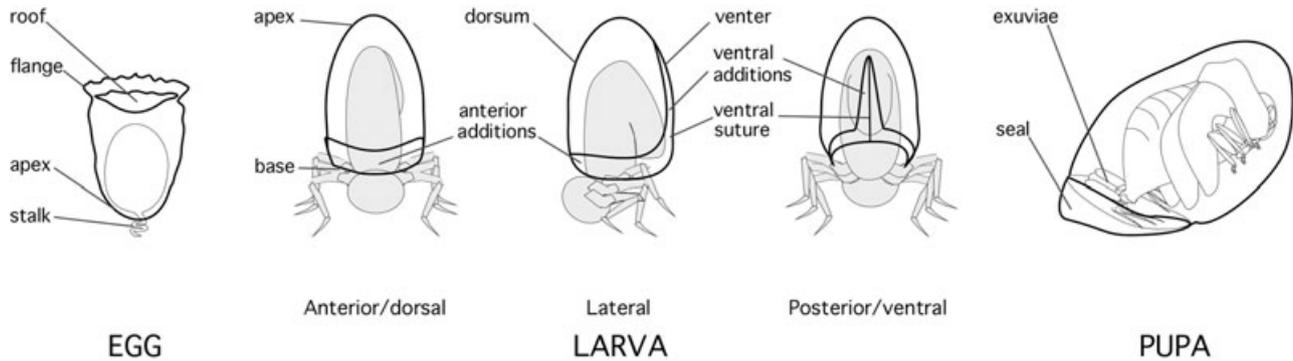


Figure 2. Case-associated terminology for the description of cryptocephalinae cases.

the pupa by a ventral suture, which represents the locus of lateral expansion, as described above. The suture is morphologically variable (flat, convex, or ridge-like) in *Neochlamisus*. This landmark has also been called a 'longitudinal keel' in *Pachybrachis bivittatus* (Say, 1824) (Erber, 1988), where it is protuberant, and a 'seam' (Packard, 1869, 1889; Scudder, 1891). The larva repeatedly creates the ventral suture and inserts faeces into the opening to expand the case; a 'wedge' (Erber, 1988) or field of faeces thus develops in this region with each addition of faecal material to the case.

Various terms for cryptocephaline case material appear in the literature: 'excrement' (Hislop, 1872; Scudder, 1891; Muir & Sharp, 1904; Blatchley, 1924; Flinte *et al.*, 2003), 'excreta' (Wood, 1966; LeSage, 1982), 'faeces' or 'feces' (LeSage, 1982; Erber, 1988; Jolivet & Verma, 2002; Flinte *et al.*, 2003), and 'scat' (Lécaillon, 1898; Hinton, 1981). Frass and fecula are other terms for insect waste materials. Generally, fecula is considered to be the technical term for insects (Frost, 1942); here, we use 'faeces', 'fecula', and the adjectival form 'faecal' where appropriate.

RESULTS

The cases of the studied *Neochlamisus* species share similarities in materials and general shape, and follow a similar ontogenetic trajectory. The egg case is generally bell-shaped, with the apex rounded, a circular cross-section, and a flattened sealed roof. The egg stalk is short and either straight or somewhat coiled (as a result of twisting during case formation). The wall of the egg case is built of small, thin, somewhat flattened units that we call 'plates' (after Karren, 1964 and Hilker, 1994). The degree of overlap between vertically adjacent rows of plates is variable. Overlap is small in most taxa so that most of the plate is exposed, but can range up to almost half a plate length in others. Internally, this pattern of plate arrangement is discernible in some species. Some of

the taxa studied have fine, irregular, longitudinal ridges externally.

Case materials comprise primarily faeces. The faeces are hard and dry, and are packed very densely. Trichomes are a secondary material, and the type varies with host-plant species; both simple and stellate trichomes were found. Soil debris and other plant materials (bark, leaf fragments) were not apparent as they are in some other cryptocephaline cases. Host-derived or self-produced chemicals may also be a component of cases, but this analysis was beyond the scope of this study.

The cases of larval instars I–III are more or less tubiform, circular in cross-section, with a basal opening where the individual projects. The egg stalk may be retained in the case of larval instar I, but is absent in later cases, probably being lost through natural abrasion. During late instar I, the radially symmetrical egg case is split longitudinally and irreversibly when the larva initially creates the ventral suture; the case is thus transformed into an asymmetrical one in lateral aspect, with diagnosable dorsal, lateral, and ventral surfaces. The ventral suture may extend completely from apex to base, or may terminate subapically. In all cases, longitudinal expansion results from the addition of faeces to the basal margin, and lateral expansion results from the insertion of faeces into the ventral surface at the ventral suture (Brown & Funk, 2005). In all species, the wall section deposited by larvae is thicker, darker, more granular, and coarser than the maternally built section. Larval faeces are arranged in fine parallel rows, and are deposited at the edges of the basal margin and along the ventral suture. These faecal rows are continuous around the case, but their orientation varies: longitudinally on the ventral wall, obliquely on the lateral walls, and transversely on the dorsal wall. Case length is doubled during instar I. By the fourth instar, the ventral surface of the larval case is completely scabrous and entirely comprised of longitudinal rows. Between the initiation and conclu-

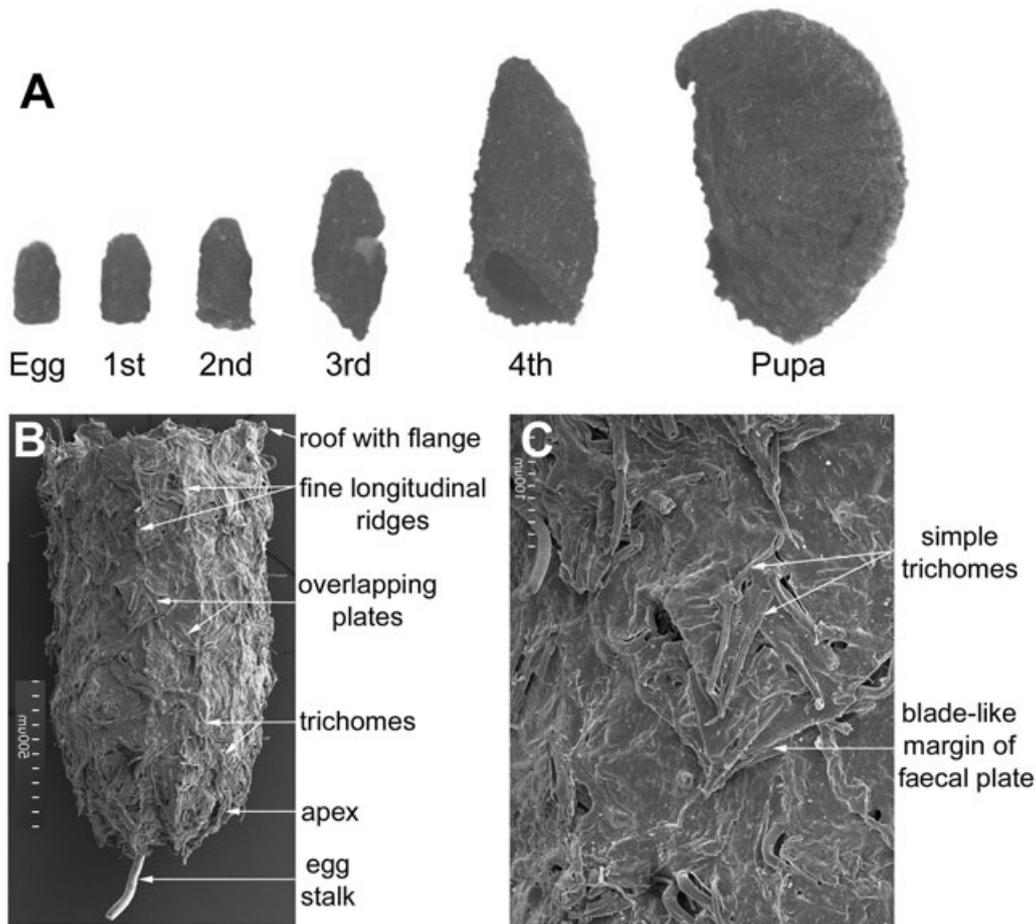


Figure 3. *Neochlamisus bebbianae* I: *Salix bebbianae* (willow) host form. A, case series from egg case (left) to pupal case (right). B, egg case, lateral aspect, scanning electron micrograph. C, egg case, scanning electron micrograph.

sion of stadium IV, there is a striking change in case shape. During this period it is transformed from tubular to ovoid and barrel-like, as a result of uneven faecal deposition, with most material added medially on the ventral wall (rather than the basal margin) during the latter half of the instar (Brown & Funk, 2005). The late instar-IV larva attaches the case opening to the host surface, and seals it completely with faeces and additional secretions to form the pupal case; the seal is very coarse and thick. In the following section, the egg case, larval cases from instars I–III, early and late instar-IV cases, and the pupal cases are described for each taxon studied here.

DESCRIPTIONS OF *NEOCHLAMISUS* CASES

Neochlamisus bebbianae (Brown, 1943) I:
Salix bebbiana host form (Figs 3–5)

Egg case (Fig. 3): Size ($N = 8$): length (L), 1.87–2.68 mm, width (W) at roof, 0.95–1.05 mm. Colour: dark brown with longitudinal ridges lighter brown.

Shape: bell-like, symmetrical in lateral aspect. Apex: conical, transverse in lateral aspect; flange uneven. Egg stalk: present (Fig. 3B), coiled and narrowed, colour translucent white. Roof: slightly convex in lateral view; texture coarse. External surface: texture of walls coarse; faeces arranged as overlapping plates (Fig. 3C). Plates: quadriform, slightly domed medially, with basal edges exposed; longitudinal ridges present, arising from multiple plates of variable lengths, with heights also variable but generally short. Trichomes: present, simple, incorporated deeply into plate matrix; decumbent, some slightly protuberant at surface (Fig. 3C). Internal surface: texture rough, but smoother than external surface, lacking apparent plates and ridges; slight space between case wall and egg.

Larva-I case (Figs 3A, 4A): Size ($N = 9$): L, 1.98–2.12 mm; W at base opening, 0.91–1.09 mm. Colour: unevenly dark-brown–black. Egg case: mostly intact, distinguishable from new larval section by width,

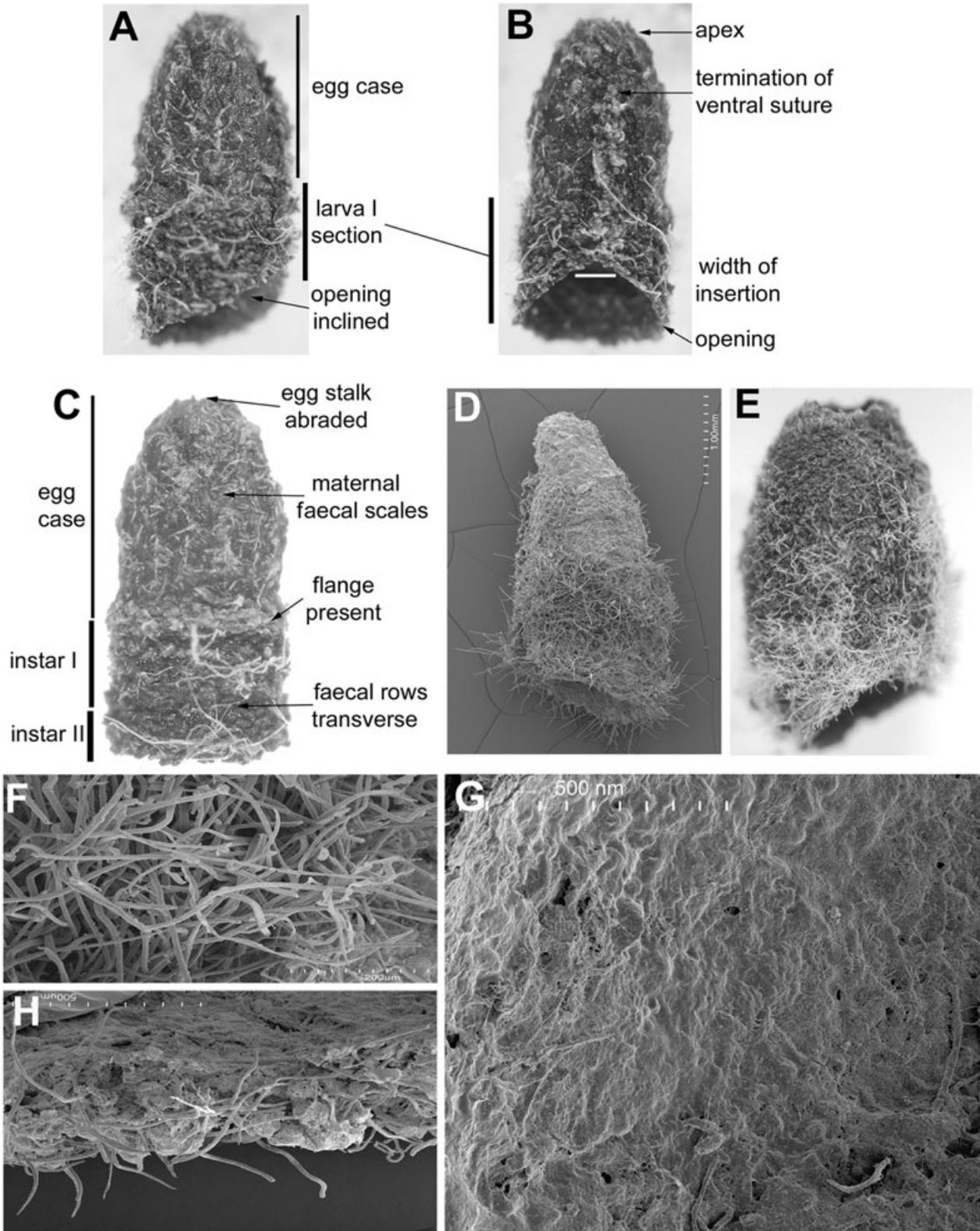


Figure 4. *Neochlamisus bebbianae* I: *Salix bebbianae* (willow) host form. A, instar-I case, lateral aspect. B, instar-I case, ventral aspect. C, instar-II case, dorsal aspect. D, instar-II case, lateral aspect, scanning electron micrograph. E, instar-IV case, lateral aspect. F, instar-IV case, trichomes on external surface. G, instar-IV case, internal surface. H, instar-IV case, wall section showing trichome-faecal matrix.

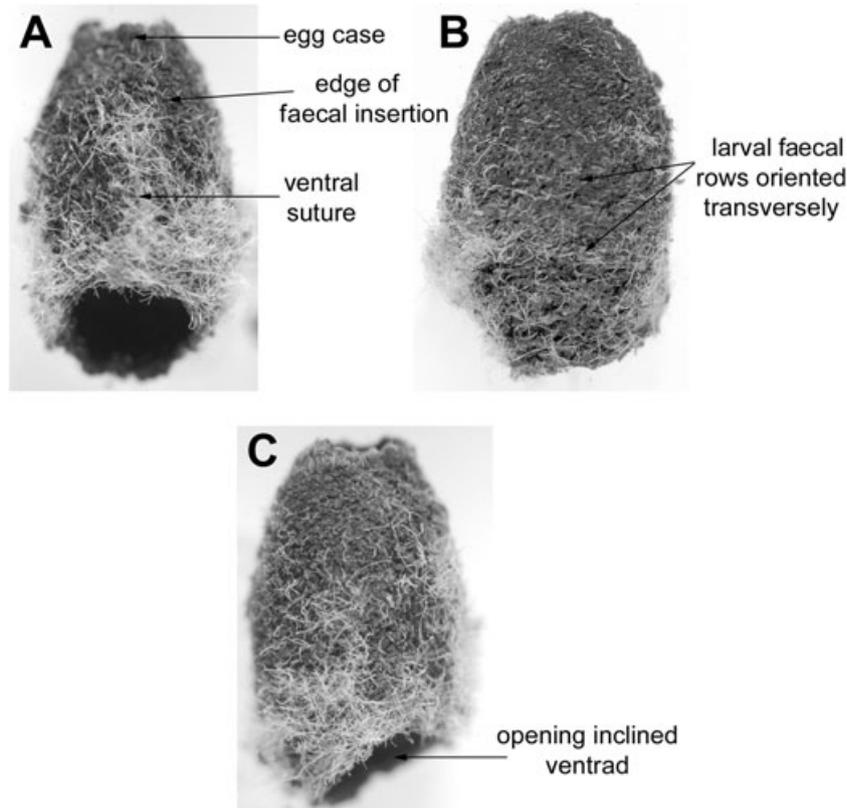


Figure 5. Larval case IV of *Neochlamisus bebbianae* I: *Salix bebbiana* (willow) host form. A, ventral view. B, dorsal view. C, lateral view.

colour, wall thickness texture, trichome placement, and patterning of faecal deposit; egg stalk present or absent. Walls of larval section: slightly wider and thicker than those of egg case. Larval faeces granular: deposited in rows, not in plates. Ventral wall: with suture continuous, extending subapically from egg case through larval section to opening; faecal rows few in number, positioned obliquely; dark triangular wedge spanning ventral suture. Lateral and dorsal walls: with transverse faecal rows. Base opening: slightly oblique in lateral view; basal margin simple. External surface of larval section with trichomes unevenly distributed, protruding as dense fur-like patches in some sections. Internal surface: smooth, lacking apparent plates and ridges.

Larva-II case (Figs 3, 4): Size ($N=8$): L, 2.41–3.48 mm; W at base opening, 1.32–1.58 mm. Shape: tubular, slightly asymmetrical in lateral aspect with dorsal wall longer than ventral wall. Apex: rounded; egg stalk absent. Egg case: generally intact, except for ventral suture; position, shape, colour and other characteristics as above. Larval case additions during phases I and II: not distinguishable; similar in colour and surface texture characteristics. Ventral suture:

extended from apex through egg case to base opening. Trichomes present, as in case of instar I. Internal surface: smooth.

Larva-III case (Fig. 3): Size ($N=10$): L, 3.66–3.91 mm; W at base opening, 1.82–1.91 mm. Colour of larval sections I, II, and III: generally dark, unevenly striate. Shape: tubular; egg case apparent, position inclined ventrad. Trichomes of sections I, II, and III of medium density.

Larva-IV younger case (Figs 3, 4E–G, 5): Size ($N=9$): L, 4.06–6.07 mm; W at base opening, 3.53–3.95 mm. Colour: medium to dark brown, striated appearance, sections deposited by each larval instar not distinguishable. Shape: tubular; apex elongate and cone-like; shape asymmetrical in lateral aspect, ventral wall shorter than dorsal wall and egg case inclined ventrad. External surface texture: coarse, with fine rows of faecal deposits and dense trichomes (Fig. 4D–F). Ventral wall: with large triangular insertion around ventral suture, flattened in lateral view; wall thickened, slightly protuberant from adjacent wall; suture not particularly protuberant; faecal deposit at suture lighter brown than in wall. Lateral

wall: expanded to twice original width as a result of faecal insertion into ventral wall. Dorsal wall: with evenly tapered lateral margins, rounded at apex; surface generally rounded in lateral view, with transverse, even faecal rows. Base opening: oblique, margin simple. Internal surface texture (Fig. 4G): smooth, trichomes not apparent. Larva densely covered in trichomes, evenly distributed.

Larva-IV older case (Fig. 5): Size ($N = 2$): L, 4.60–7.04 mm; W at base opening, 3.59–4.00 mm. Case slightly longer than younger instar-IV case, but two times wider, greatly expanded below egg and instar-I sections. Shape: barrel-like; egg case reduced to a small apical nipple. Trichomes: increasingly dense with age in instar-IV section, eventually with furry appearance; dense trichomes span dorsal and lateral walls, but not ventral wall.

Pupal case (Fig. 3A): Size ($N = 8$): L, 6.07–6.54 mm; W at base opening, 3.53–3.95 mm. Colour: medium to dark brown, striated; seal, lighter brown. Shape: barrel-like; base opening obliquely angled, sealed by flattened circular disc. External surface and basal seal surface: rough, trichomes sparse. Ventral wall: flattened in lateral view, striated longitudinally. Lateral walls: symmetrical, evenly widened below apex and slightly narrowed at basal margins. Dorsal wall: striated transversely. Internal surface: smooth.

Neochlamisus bebbianae (Brown, 1943) II:
Alnus host form (Fig. 6)

Egg case (Fig. 6B–D): Size ($N = 9$): L, 1.37–1.68 mm; W at roof, 0.89–0.94 mm. Colour: brownish black. Shape: bell-like; symmetrical in lateral aspect; ventral, lateral, and dorsal surfaces not apparent. Apex: dome-like; attachment stalk, present, creamy brown, translucent, not coiled. Roof: thin-walled, shallowly convex; internal and external surface textures similarly rough; flange, thin and ragged. External wall: coarse, with faeces arranged as overlapping plates; plates with apical margins exposed and arcuate; shallow uneven longitudinal ridges present; ridges evenly spaced, edges ragged. Trichomes: apparent within matrix, simple, arranged randomly and horizontally. Internal surface: texture lacking apparent plates and ridges; narrow space between case wall and egg.

Larva-I case (Fig. 6E): Size ($N = 5$): L, 1.45–1.70 mm; W at base opening, 1.09–1.7 mm. Colour: unevenly dark brown, with larval addition in basal section and in ventral wall darker, almost blackish. Egg case: generally intact; egg stalk present or absent. External surface of instar-I section: with faeces deposited in

rows. Ventral wall: distinct in late instar I with insertion of ventral suture and faeces; suture extending subapically through egg case to basal margin. Lateral and dorsal walls: as in egg case, basally, with narrow addition of faecal rows; rows arranged transversely. Base opening: transverse, margin simple. Internal surface: relatively smooth; plates and rows not apparent. Wall thickness: evenly thin; apex approximately two times thicker than wall.

Larva-II case (Fig. 6F): Size ($N = 9$): L, 2.75–2.77 mm; W at base opening, 1.23–1.60 mm. Colour: unevenly dark brown. Shape: tubular; apex, dome-like; egg stalk, absent. Egg case: apparent, accounting for half of the total case length; shape, position, and external texture of plates and weak longitudinal ridges, generally intact; flange of original egg case somewhat abraded. Larval-built case section: distinct from maternal section in colour (blackish), surface texture (coarser, in rows), and trichomes (more protuberant). External surface of larval sections: coarse with fine and even faecal rows. Trichomes: present, sparse, deeply embedded into faecal matrix, some more protuberant in larval section. Ventral wall: with suture extending from apex through egg case to base opening; suture and adjacent faecal insertion protuberant. Walls: evenly thick, slightly thicker at base. Base opening: slightly oblique, margin simple. Internal surface: smooth; plates, ridges, and rows not apparent.

Larva-III case (Fig. 6B): Size ($N = 8$): L, 3.03–3.06 mm; W at base opening, 1.62–1.87 mm. Case III resembles case II, with larval section II similar to larval section I.

Larva-IV case (Fig. 6G): Size ($N = 8$): L, 3.27–3.73 mm; W at base opening, 2.06–3.40 mm. Colour: light brown in egg section, dark brown/black in larval sections. Shape: tubular, asymmetrical in lateral aspect, ventral wall longer than dorsal wall; apex forming elongate dome. Egg and larval sections: distinguishable; external plates of egg case not apparent, longitudinal ridges vague; larval section with fine rows. Ventral wall with suture extended from apex to basal margin; ventral field quadriform, not triangular as in earlier instars. Base opening: transverse, margin simple. Internal surface texture: relatively smooth, instar sections not distinct. Wall thickness of egg case and sections I–III evenly narrow; wall of instar IV approximately twice as thick. Trichomes: present, sparse, deeply embedded in faecal matrix.

Pupal case (Fig. 6H–J): Size ($N = 7$): L, 5.42–5.56 mm; W at base opening, 4.05–4.15 mm. Colour:

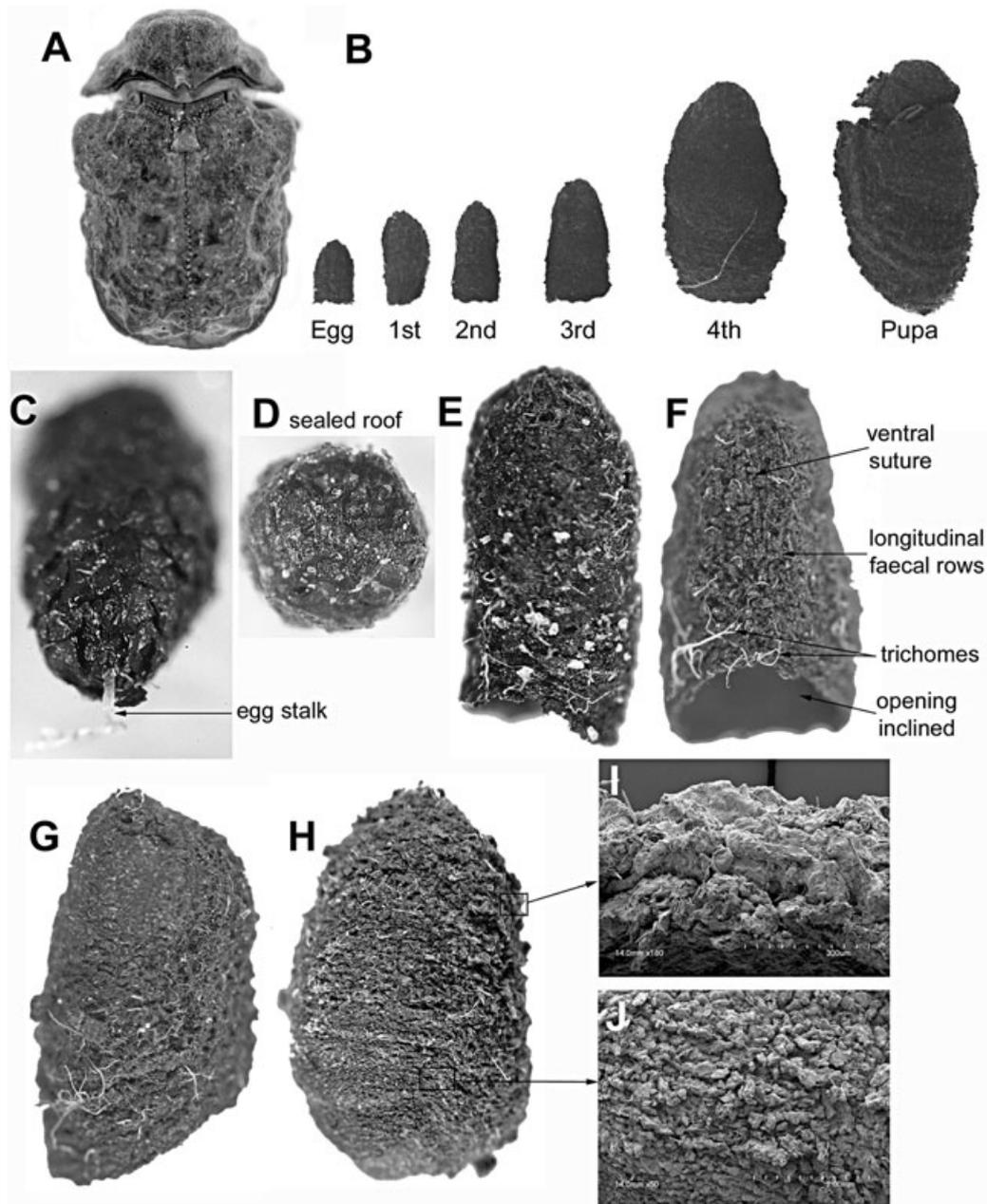


Figure 6. *Neochlamisus bebbianae* II: *Alnus* (alder) host form. A, adult habitus with prothorax unnaturally distended while preserved. B, case series from egg case (left) to pupal case (right). C, egg case apex showing egg stalk. D, egg case, sealed roof. E, instar-I case, lateral aspect. F, instar-II case, ventral aspect. G, instar-IV case, lateral aspect. H, pupal case, dorsolateral aspect. I–J, pupal case, surface textures, scanning electron micrographs.

dark-brown/black, base lighter brown. Shape: barrel-like, asymmetrical in lateral view with ventral wall shorter than dorsal wall. Egg case: occupying c. 1/8th of the total case length, shape completely distorted, split hemispherically and inclined ventrad; surface plates not apparent. External surface: with fine faecal rows arranged longitudinally on ventral wall, obliquely on lateral wall, and transversely on dorsal

wall. Ventral wall: with suture extended from apex to base opening; larval insertions coarse, occupying most of ventral wall. Base opening: oblique, margin simple, completely sealed; seal flattened and discoid, texture rough externally and internally, comprised of faeces and trichomes; exuviae IV positioned internally on top of seal. Trichomes: present, sparse, incorporated deeply into matrix.

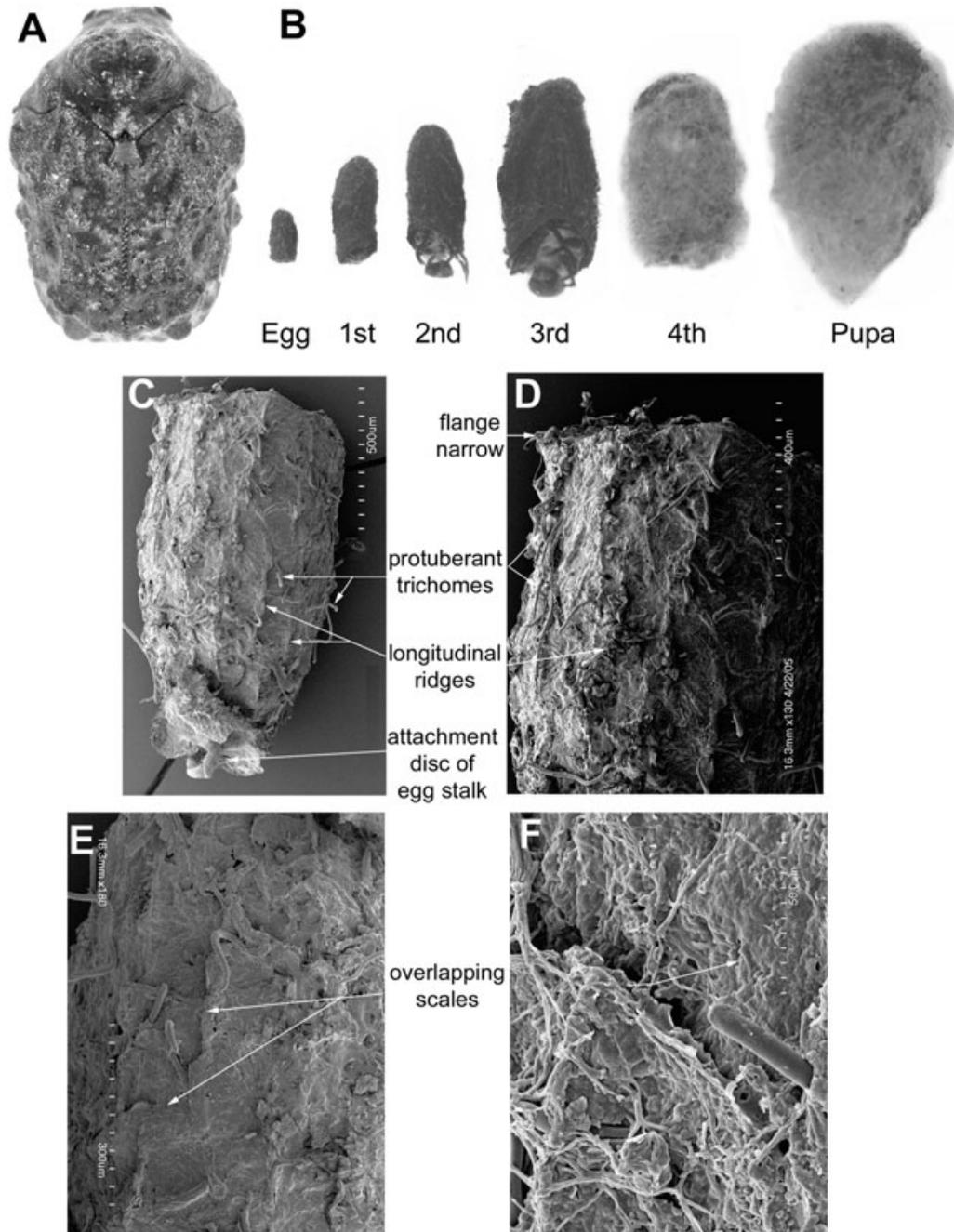


Figure 7. *Neochlamisus bebbianae* III: *Betula* (river birch) host form. A, adult habitus. B, case series from egg case (left) to pupal case (right). C–F, egg case, scanning electron micrographs. C, lateral aspect. E–F, external surface.

Neochlamisus bebbianae (Brown, 1943) III:
Betula nigra host form (Figs 7, 8)

Egg case (Fig. 7B–F): Size ($N = 10$): L, 0.89–1.28 mm; W at roof, 0.79–0.84 mm. Colour: unevenly dark-brown/black. Shape: bell-like, symmetrical in lateral aspect; apex conical. Egg stalk: present basally, short, translucent, slender. Roof: transverse

(Fig. 7C) in lateral aspect, discoid, flattened, not convex; margin simple, not flanged. External surface: coarse with overlapping faecal plates (Fig. 7E, F); plates most apparent apically, their margins exposed apically; short, discontinuous longitudinal ridges present, spanning two or three scales (Fig. 7D). Internal surface: smoother than external surface; slight space between case wall and

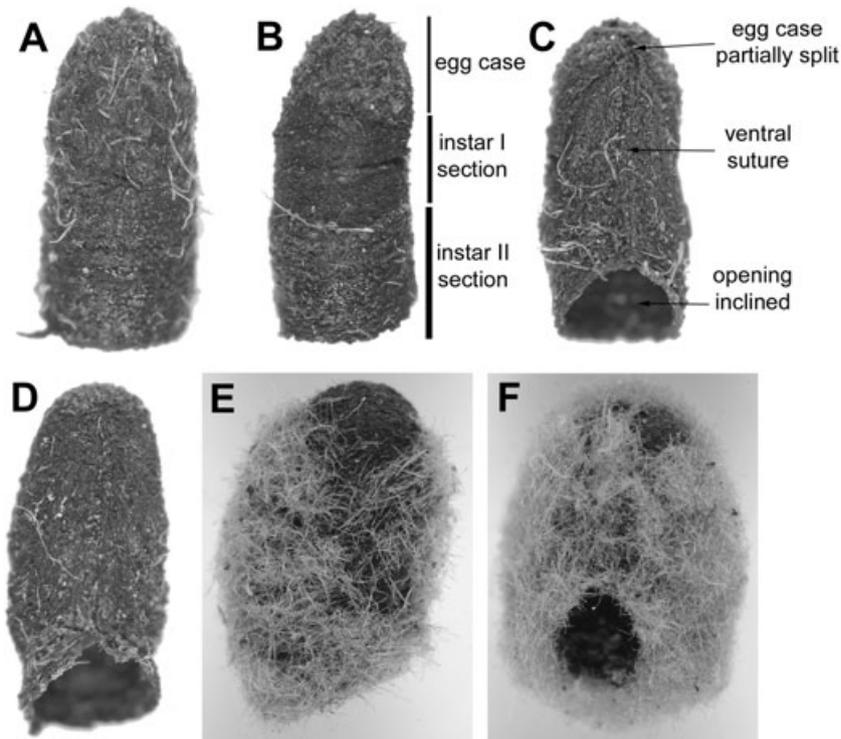


Figure 8. *Neochlamisus bebbianae* III: *Betula* host form. A, instar-I case, lateral aspect. B, instar-II case, lateral aspect. C, instar-II case, ventral aspect. D, instar-III case, ventral aspect. E, instar-IV case, lateral aspect. F, pupal case, ventral aspect.

egg. Trichomes: present, simple, dense, deeply embedded in faecal matrix.

Larva-I case (Fig. 8A): Size ($N = 4$): L, 1.53–1.89 mm; W at base opening, 1.51–2.89 mm. Colour: uneven brownish-black. Shape: asymmetrical in lateral view; egg case distinct, occupying two-thirds of the total case length; apex conical; egg stalk present or absent; base opening slightly transverse. Ventral surface: with suture extending subapically through egg case to basal margin; faecal rows, inserted adjacent to ventral suture, occupy triangular wedge; younger rows of medium brown colour. External surface: rough, faecal rows orientated longitudinally ventrad, transversely lateral, and dorsad. Internal surface: without plates or ridges; texture smoother and darker in larval section than egg section. Case walls: evenly thin, apex slightly thicker. Trichomes: present in larval section, sparse.

Larva-II case (Fig. 8B, C): Size ($N = 7$): L, 3.84–4.02 mm; W at base opening, 1.65–1.87 mm. Colour: uneven dark brown, larval sections appearing striate because of colour tone variation. Shape: tubular; asymmetrical in lateral view; ventral, lateral, and dorsal walls distinguishable by varying orientation

of faecal rows; apex rounded. Egg case: apparent, shape distorted by ventral surface expansion. External surface: coarse, with larval faeces in rows. Ventral surface: with suture extending subapically to basal margin; adjacent triangular field occupying half of the ventral surface area. Base opening: oblique; ventral wall shorter than dorsal wall; margin simple. Internal surface: smooth, boundary between larval instars indistinct. Walls: slightly thicker apically than laterally. Trichomes: at medium density, some protuberant.

Larva-III case (Fig. 8D): Size ($N = 10$): L, 5.12–5.45 mm; W at base opening, 2.5–3.19 mm. Colour: unevenly brownish black with lighter brown striations. Shape: tubular, asymmetrical in lateral view with dorsal wall slightly longer than ventral wall, and egg case inclined ventrad. Egg case: distinguishable by position, surface texture, and colour; general shape distorted, split hemispherically by ventral suture and large ventral insertion of faeces. Ventral surface: with ventral suture extending from apex to base; adjacent longitudinal faecal rows slightly protuberant, occupying three-quarters of the ventral surface. Walls of larval sections: thicker than in egg case. Base opening: transverse, margin simple.

Internal surface: smooth; plates, ridges, and rows, not apparent; larval sections not distinguishable. Trichomes: present, deeply embedded into matrix, with some protuberant.

Larva-IV case (Fig. 8E): Size ($N=4$): L, 4.85–6.51 mm; W at base opening, 3.60–3.88 mm. Colour: uneven dark brownish black. Shape: barrel-like, asymmetrical with distinct ventral, lateral, and dorsal surfaces; egg case hemispherical, inclined ventrad, dissected by ventral suture; apex rounded. External surface: variable; densely covered with trichomes; trichome coat thick dorsally, thinner ventrally. Ventral suture: extending from apex to base; larval faecal insertion occupying most of ventral surface. Base opening: transverse, margin simple. Internal surface texture: smoothed; walls evenly thin, apex wall slightly thicker.

Pupal case (Fig. 8F, G): Size ($N=4$): L, 6.27–7.54 mm; W at base opening, 5.25–6.02 mm. Shape: texture and colour as in late larval case IV; basal seal lacking trichome coat.

Neochlamisus bebbianae (Brown, 1943) IV:
Acer rubrum host form (Figs 9, 10)

Egg case (Fig. 9B–E): Size ($N=6$): L, 1.68–1.87 mm; W at roof, 0.95–1.05 mm. Colour: unevenly brownish-black. Shape: bell-like; symmetrical in lateral aspect; apex rounded; egg stalk present, slender, translucent, one-third of the length of case, lacking coiling. External surface: coarse, with pine cone-like appearance; faeces arranged as overlapping plates, dorsal margin of plates exposed, surface protuberant, producing pine cone-like appearance; plates at apex of case project vertically; longitudinal ridges absent. Roof: transverse, coarse, slightly concave; flange: narrow. Internal surface: smoother than external surface; plates and ridges not apparent. Walls: evenly narrow. Trichomes: present, simple, sparse, deeply embedded into faecal matrix.

Larva-I case (Fig. 9B, F–I): Size ($N=11$): L, 1.47–1.79 mm; W at base opening, 0.94–0.99 mm. Colour: uneven brownish black, larval section grey-black. Shape: bell-like, symmetrical to asymmetrical according to age; egg case generally intact; egg stalk present or absent; base opening transverse. External surface: coarse, larval section with dark fine transverse faecal rows. Internal surface: lacking apparent plates and ridges (Fig. 9G). Walls: evenly narrow (Fig. 9H, I). Trichomes: apparent, deeply

embedded into matrix, not protuberant, lacking furry appearance.

Larva-II case (Figs 9B, 10A, B): Size ($N=8$): L, 2.05–2.21 mm; W at base opening, 1.34–1.36 mm. Colour: uneven dark brownish-black, larval sections greyish-brown, younger sections grey. Shape: tubular, asymmetrical; ventral, lateral, and dorsal surfaces apparent; ventral wall shorter than dorsal wall; apex dome-like. Egg case: apparent; shape, position, and texture generally intact; egg stalk absent. Ventral surface: with ventral suture and triangular insertion extending subapically to margin; insertion protuberant, occupying half of the total ventral surface. External surface: rough; larval sections with fine parallel rows of faecal deposit. Base opening: transverse, margin simple. Walls and apex: generally narrow, slightly thicker in larval section. Internal surface texture of larval section: smoother than external surface; egg section partially papered over with faecal layer. Trichomes: apparent, sparse, deeply embedded into matrix, decumbent.

Larva-III case (Figs 9B, 10C–F): Size ($N=4$): L, 4.45–5.44 mm, W at base opening, 2.6–3.25 mm. Shape: tubular; ventral, lateral, and dorsal walls apparent. Egg case: apparent, position inclined ventrad, shape distorted by ventral insertion of faecal field. External surface: rough, faeces in fine rows (Fig. 10C, D); plates and ridges absent. Anterior surface with transverse faecal rows; lateral surface with obliquely transverse faecal rows; posterior surface with longitudinal faecal rows and medial ventral suture; ventral suture extending from apex through egg case to basal margin. Base opening: transverse, dorsal wall longer than ventral wall; margin simple. Internal surface: smooth; rows, projections, and plates not apparent; walls evenly thick, broader than in egg case. Trichomes: present, sparse, deeply embedded in matrix, decumbent.

Larva-IV case (Fig. 9B): Size ($N=4$): L, 6.49–6.81 mm; W at base opening, 4.40–4.64 mm. Colour: brownish-black. Shape: tubular, asymmetrical in lateral view, ventral surface somewhat flattened. Egg case: apparent, distorted with ventral insertion of faeces, position inclined ventrad. External surface: rough, striated appearance with faecal rows orientated longitudinally on ventral surface, obliquely transverse laterally and transverse dorsally. Base opening: transverse, margin simple. Internal surface: smooth, walls evenly thick; rows, ridges, and plates not apparent. Trichomes: present, deeply embedded in faecal matrix.

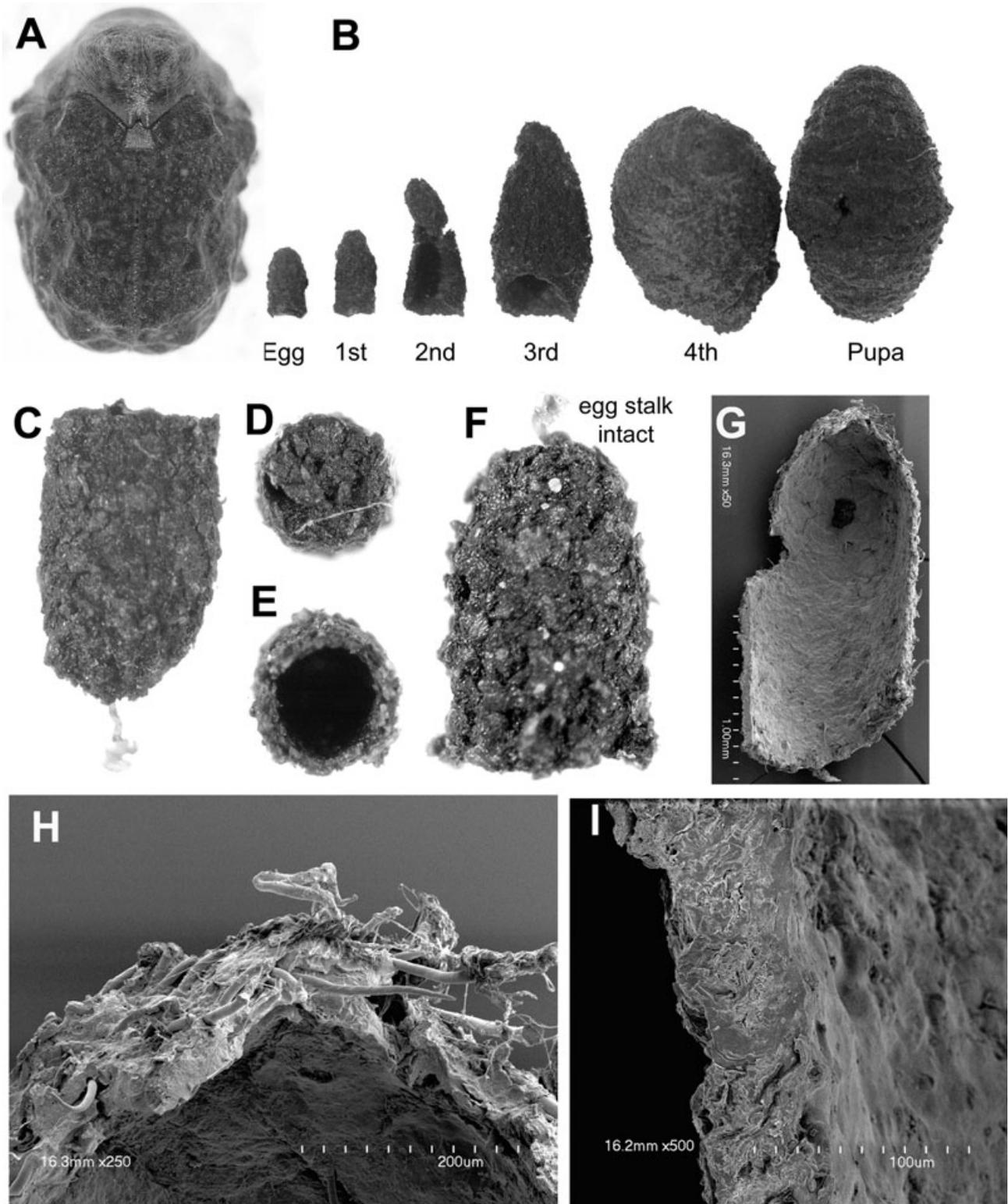


Figure 9. *Neochlamisus bebbianae* IV: *Acer* (maple) host form. A, adult habitus. B, case series from egg case (left) to pupal case (right). Instar-II case: broken. C, egg case, with twisted egg stalk. D, egg-case roof sealed. E, egg-case roof unsealed by instar-I larva. F, instar-I case, egg stalk intact. G–I, scanning electron micrographs. G, instar-I case, internal aspect. H, instar-I case, cross-section of apex showing faecal matrix. I, instar-I case, cross-section of wall showing dense faecal matrix.

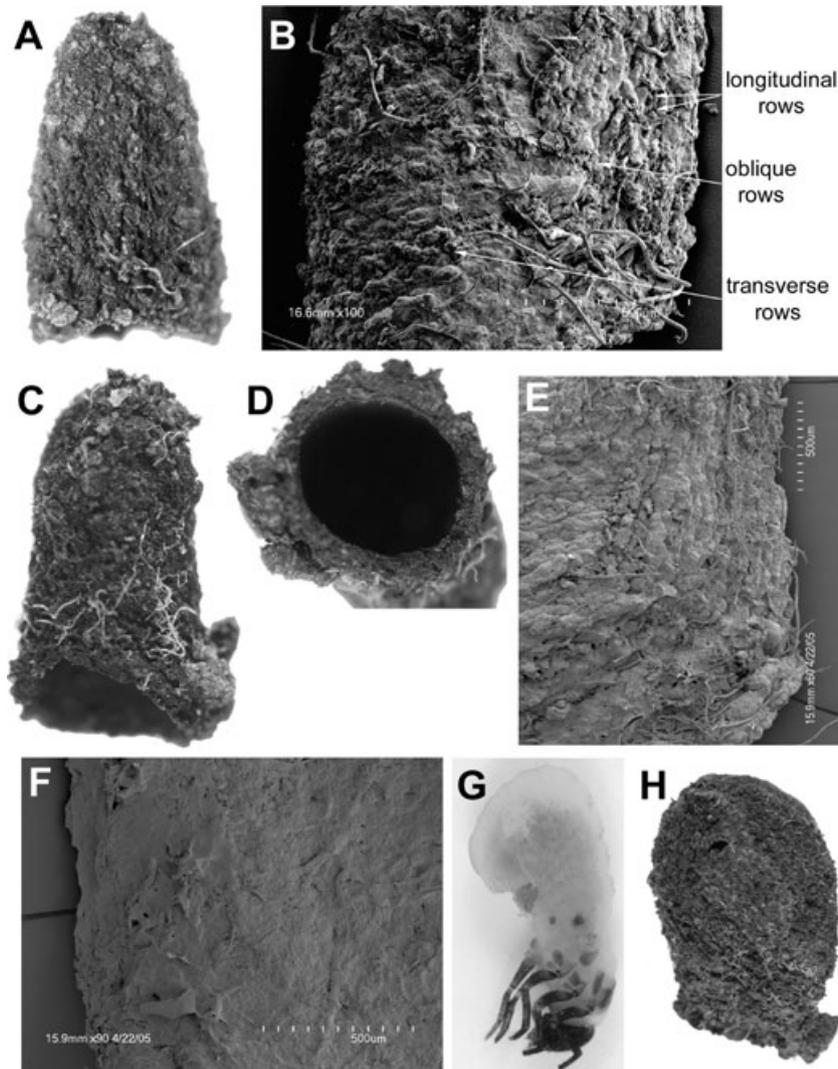


Figure 10. *Neochlamisus bebbianae* IV: *Acer* (maple) host form. A, instar-II case, ventral aspect. B, instar-II case, lateral aspect, orientation of faecal rows, scanning electron micrograph. C, Instar-III case, lateral aspect. D, instar-III case, base opening. E, instar-III case, ventral faecal wedge at base, scanning electron micrograph. F, instar-III case, internal surface, scanning electron micrograph. G, larval instar-IV, lateral aspect. H, Pupal case, lateral aspect.

Pupal case (Figs 9B, 10H): Size ($N=9$): L, 6.98–7.23 mm; W at base opening, 4.74–5.20 mm. Colour: brownish-black. Shape: bean-shaped, asymmetrical in lateral view; ventral, lateral, and dorsal walls apparent. Egg case: not easily discernible, split hemispherically by ventral suture and faecal insertions, each hemisphere shifted laterad and ventrad. Ventral wall: somewhat flattened, texture coarse with fine faecal rows; faecal rows orientated longitudinally, faecal insertion occupying most of wall; ventral suture extending medially from apex to base. Lateral walls: bulging medially, tapering centrad apically and basally. Base: transverse, margin simple. Internal surface: smooth; plates, rows, and ridges absent.

Trichomes: present, deeply embedded in faecal matrix, not forming furry surface.

Neochlamisus bimaculatus Karren, 1972:
host plant *Rubus* spp. (Fig. 11)

Egg case (Fig. 11B–E): Size ($N=10$): L, 1.27–1.61; W at roof, 0.97–1.18 mm. Colour: unevenly brownish black. Shape: bell-like; symmetrical in lateral aspect; flange narrow. Egg stalk: present, short, not coiled. External surface: coarse; faeces arranged as flattened plates; plates rounded to quadriform, some slightly protuberant medially, overlapping basally with apical margin exposed; longitudinal ridges absent. Roof:

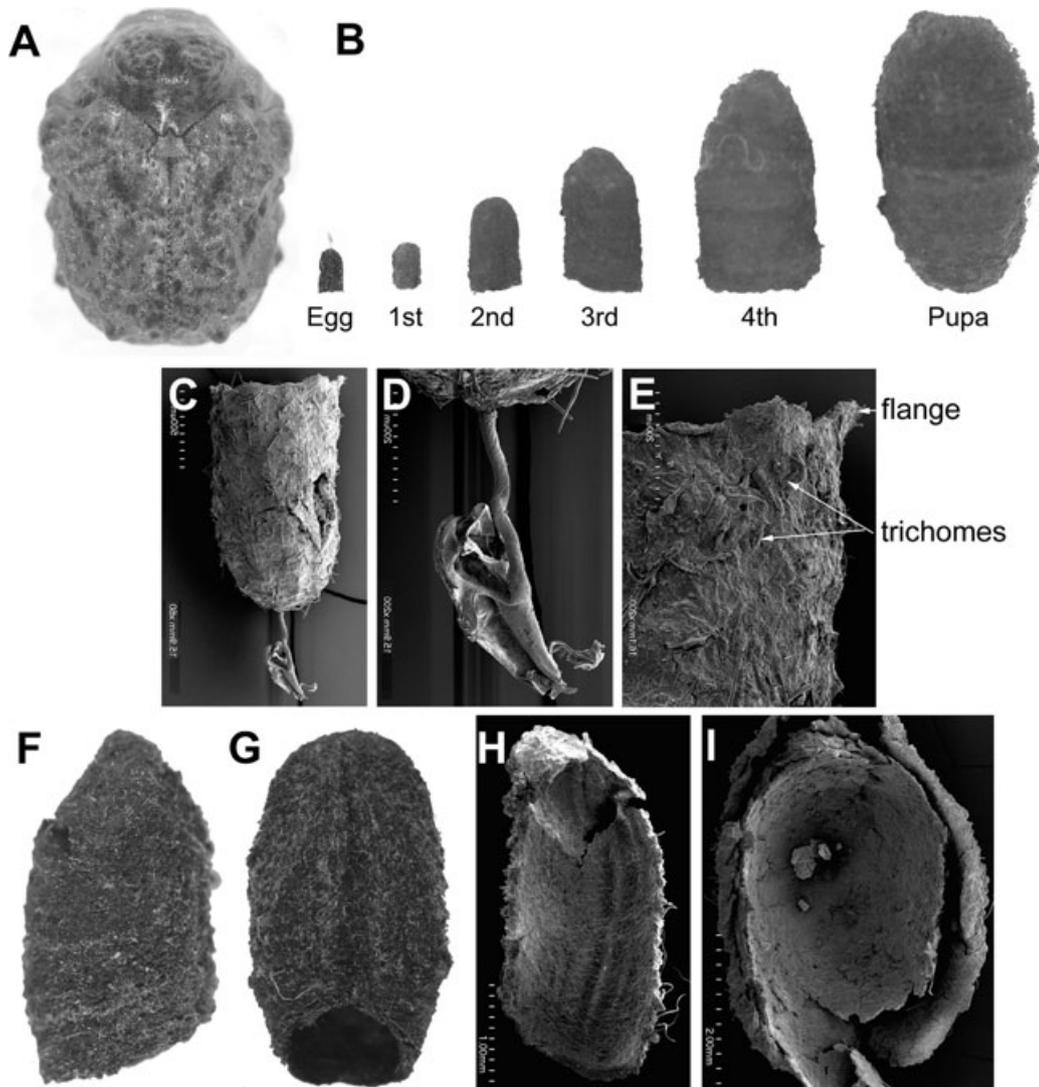


Figure 11. *Neochlamisus bimaculatus*. A, adult habitus. B, case series from egg case (left) to pupal case (right). C–E, scanning electron micrographs. C, egg case, lateral aspect, broken medially. D, egg case, egg stalk. E, egg case, flange. F, instar-II case, lateral aspect. G–I, instar-IV case. G, ventral aspect. H, internal aspect with forewall removed. I, internal aspect, faecal layers of wall.

transverse; surface shallowly concave and texture coarse. Internal surface: smooth, scale outline sometimes apparent. Trichomes: present, sparse, deeply embedded in faecal matrix.

Larva-I case (Fig. 11B): Size ($N = 8$): L, 2.37–3.37 mm; W at base opening, 1.46–1.62 mm. Young cases: shape, colour, and texture the same as in egg case. Older cases: asymmetrical in lateral view; dorsal, ventral, and lateral surfaces distinct; egg section occupying half of the total case length; apex rounded; egg stalk present or absent. Larval section: with fine faecal rows extending longitudinally on ventral surface and transversely on other surfaces. Ventral suture: slightly

protuberant, extending subapically to base. Base opening: transverse, basal margin continuous with lateral walls; flange of egg case slightly discernible. Internal surface: smooth, internal surface of egg case as original, larval surface lacking discernible patterns of plates, rows, or ridges. Wall thickness: evenly narrow. Trichomes: present, very sparse.

Larva-II case (Fig. 11B, F): Size ($N = 8$): L, 3.47–5.06 mm; W at base opening, 1.7–2.40 mm. Colour: unevenly dark brownish-black. Shape: asymmetrical in lateral view; egg case apparent, inclined ventrad; apex rounded; attachment stalk absent. External surface: coarse; dorsal surface with faeces in

transverse rows; ventral surface with larval section roughly triangular, occupying half of the total surface area, and comprising longitudinal rows; ventral suture extending subapically to base. Base opening: slightly transverse. Internal surface: smooth; rows, plates, or ridges absent. Walls: evenly thin. Trichomes: present, sparse, deeply embedded in faecal matrix.

Larva-III case (Fig. 11B): Size ($N = 9$): L, 5.12–5.99 mm; W at base opening, 2.43–3.62 mm. Colour: uneven brownish-black, with striated appearance. Shape: asymmetrical; dorsal, lateral, and ventral surfaces apparent; apex rounded, apical margin continuous with lateral walls; diameter widest in basal third. Egg case: apparent, shape distorted, split into two hemispheres by larval insertion; inclined ventrad, appearing as nipple-like dome. External surface: coarse; longitudinal ridges absent. Ventral surface: with larval insertion occupying more than half of the total surface area; ventral suture extending from apex to base, dissecting egg case. Base opening: transverse. Internal surface: smoothened. Wall: thickness, surface, and trichome density as in case II.

Larva-IV case (Fig. 11B, G–I): Size ($N = 9$): L, 7.27–7.78 mm; W at base opening, 4.96–5.12 mm. Shape, colour, surface texture, and trichome density and distribution, as in case III. Older cases: barrel-shaped, being widest in basal third; egg case distorted, inclined ventrad; base opening transverse. Internal surface (Fig. 11H): smoothened. Walls: with layers of faeces (Fig. 11I).

Pupal case (Fig. 11B): Size ($N = 7$): L, 7.98–785 mm; W at base, 4.96–5.12 mm. Shape, colour, texture, trichome pattern as in case IV; ventral wall shorter than dorsal wall.

Neochlamisus chamaedaphnes (Brown, 1943)
(Figs 12, 13): host plant *Chamaedaphnae calyculata*

Egg case (Fig. 12B–D): Size ($N = 18$): L, 1.55–2.35 mm; W at roof, 0.84–1.24 mm. Colour: uneven, medium to dark brown. Shape: elongate bell-shape; symmetrical in lateral aspect; apex rounded; flange narrow. Egg stalk: slender, translucent, broadly coiled. External surface: coarse, wall comprised of faecal plates; plates somewhat flattened, triangular to quadriform, overlapping basally, apical margin exposed; apical plates project vertically; plate surface slightly protuberant medially, projections forming overall effect of slight, irregular longitudinal rows. Roof: surface rough, shallowly concave; flange narrow, thin, unevenly flared. Trichomes: present, sparse.

Internal surface: smooth; plate outline slightly discernible; space between egg and wall narrow.

Larva-I case (Fig. 12E–G): Size ($N = 9$): L, 1.46–2.00 mm; W at base opening, 0.81–0.87 mm. Colour: unevenly dark brown, larval section darker. Shape: bell-like, similar to egg case; apex rounded; apical faecal plates projecting slightly; egg stalk absent. External surface of larval section: rough, faeces arranged as fine horizontal rows, not pellets. Base opening: transverse; margin slightly flared. Ventral surface: apparent in older cases; ventral suture terminating subapically. Internal surface: smooth; wall of larval section slightly thicker than wall of egg case. Trichomes: present, sparse.

Larva-II case (Fig. 13A–C): Size ($N = 4$): L, 2.34–2.91 mm; W at base opening, 1.39–1.72 mm. Shape: elongate tube, twice as long as base width; slightly asymmetrical in lateral view with anterior margin slightly longer than posterior margin. Apex: rounded; egg stalk absent. Egg case: generally intact, distorted ventrally by insertion of ventral suture and faecal wedge. Larval sections: darker brown than egg case; boundary between instar-I section and instar-II section marked by light-brown colour; surface texture scabrous. Ventral surface: with triangular faecal wedge occupying half the surface; surface slightly projecting, lateral margins with irregular projections. Ventral suture: terminating subapically. Base opening: slightly oblique in lateral view; margin simple, not flared. Internal surface: smooth, egg case surface intact, larval sections with rows not apparent. Wall of larval section: slightly thicker than in egg case.

Larva-III case: Size ($N = 4$): L, 3.84–4.09 mm; W at base opening, 1.84–1.87 mm. Shape: elongate tube, widest medially and slightly narrowed basally; asymmetrical in lateral view with dorsal wall longer than ventral wall; apex rounded. Egg case: split hemispherically by ventral suture, hemispheres connected apically; egg stalk absent. Larval section-III surface texture: coarser and lighter brown than previous sections. Base opening and margin: as in case II. Internal surface: smooth, external pattern of plates and rows not apparent; wall, evenly narrow. Trichomes: present, sparse, unevenly distributed, decumbent.

Larva-IV case (Fig. 13D): Size ($N = 5$): younger cases, L, 4.20–4.68 mm, W at base opening, 2.26–2.74 mm; older cases, L, 4.65–4.91 mm, W, 3.39 mm. Colour: light to dark brown, striated appearance, thick coloured bands marking some instar sections. Shape:

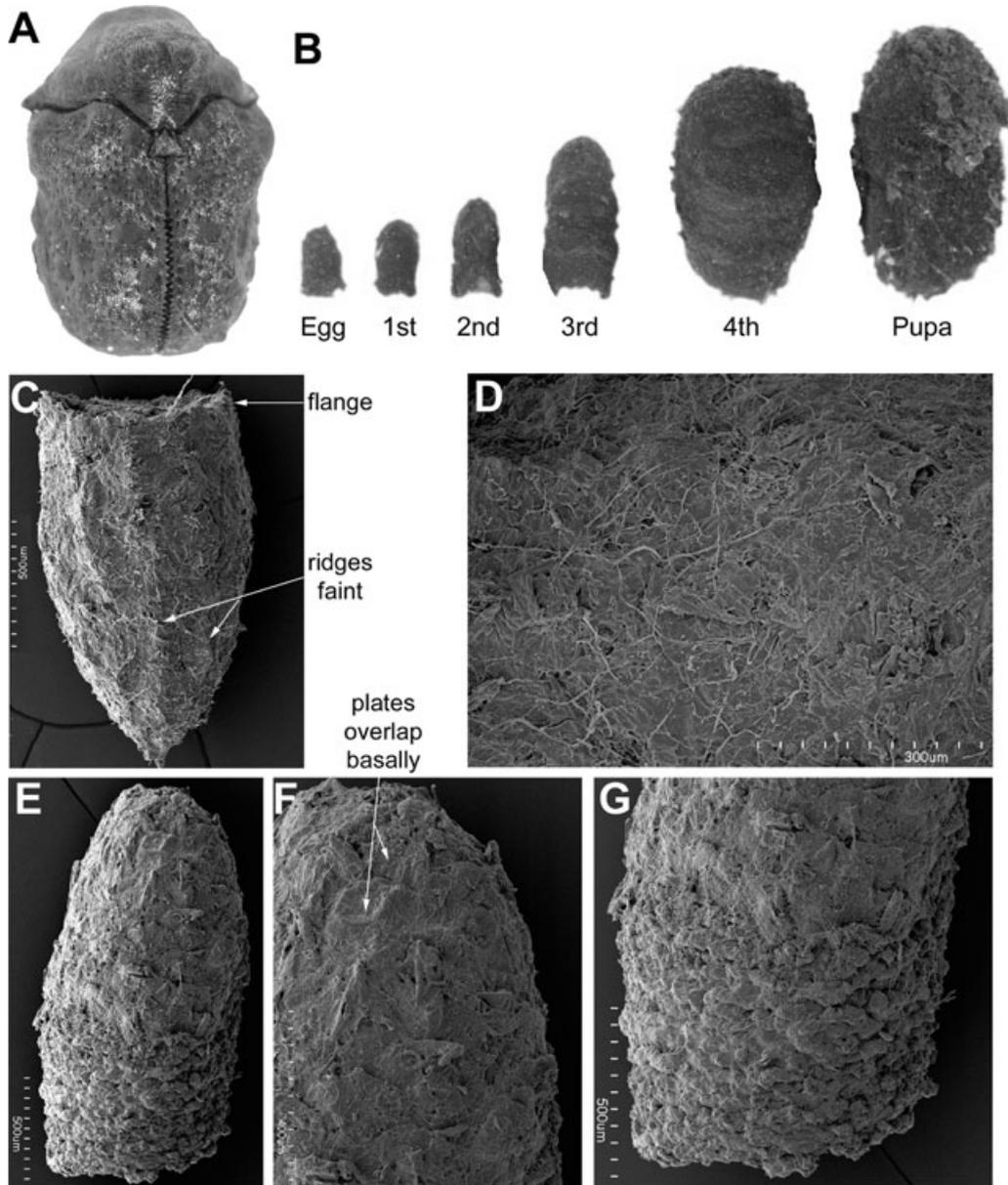


Figure 12. *Neochlamisus chamaedaphnes*. A, adult habitus. B, case series from egg case (left) to pupal case (right). C–G, scanning electron micrographs. C, egg case, lateral aspect. D, egg case surface with trichomes. E, instar-I case, lateral aspect. F, instar-I case, egg section showing faecal plates. G, instar-I case, larval section with faecal rows.

ovoid to conical, widest in apical half, narrowed by half at base; apex rounded. External surface: granulose; section IV and posterior wall scabrous. Ventral surface: entirely comprised of longitudinal rows and suture; ventral suture slightly protuberant, extending from apex to base opening. Base opening and margin: as in case III. Trichomes: absent. Internal surface: smooth, without apparent patterns (no subunits, ridges, or rows); striated colour patterning apparent.

Pupal case (Fig. 13E–G): Size ($N = 1$): L, 5.82 mm; W at base, 3.37 mm. Colour: striated, medium to light brown. Shape: ovoid, asymmetrical lateral views, dorsal surface longer than ventral surface; egg case forming nipple-like projection at apex. Case: as in larval instar IV, similar in colour, striation, and faecal arrangement; diameter widest in basal section. Egg case: distorted, protuberant, and inclined ventrad. Base: circular in apical view, transverse in lateral view, margin thickened; disc-like seal, coarse.

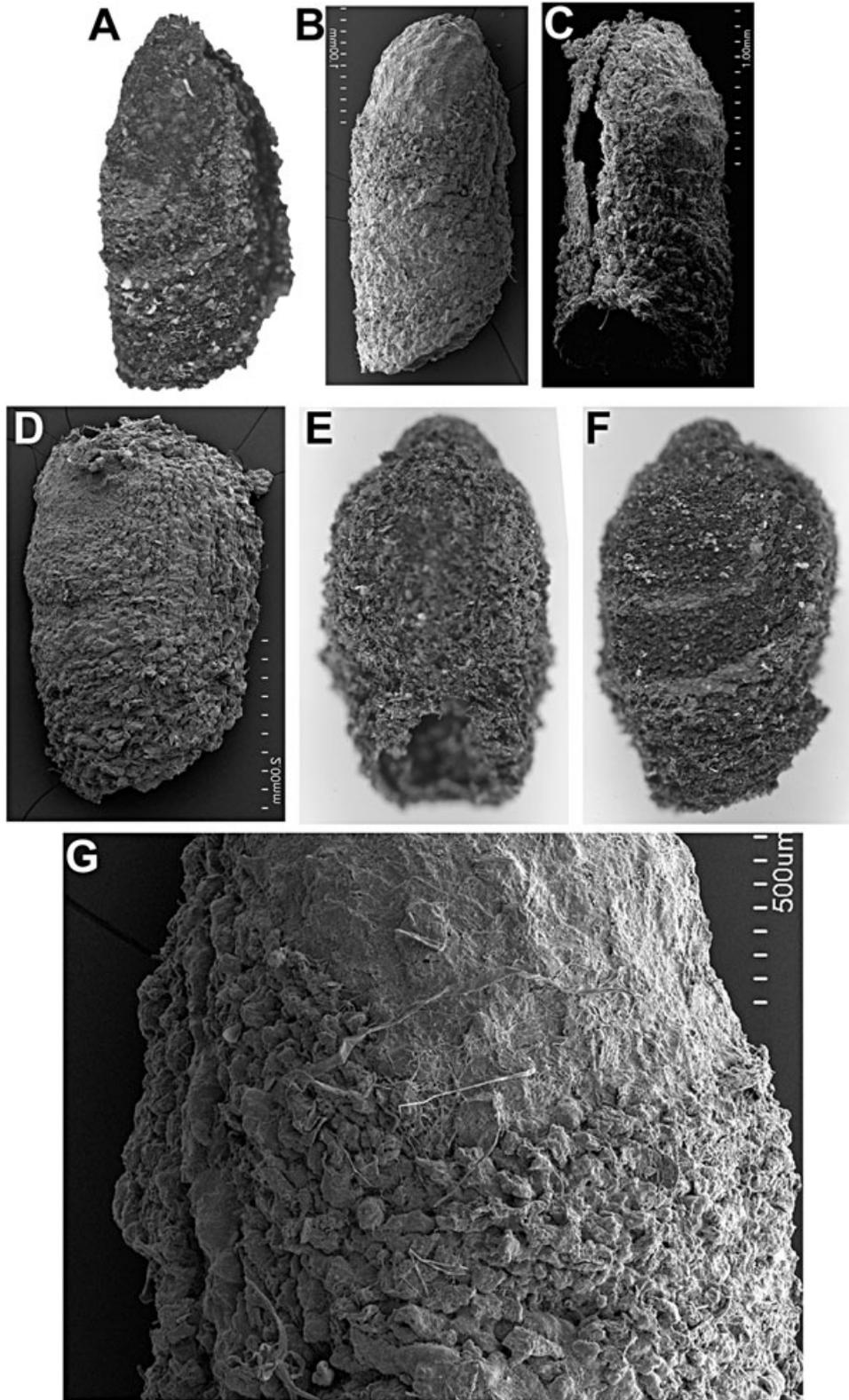


Figure 13. *Neochlamisus chamaedaphnes*. A, instar-II case, lateral aspect, with striations that vary in colour. B–D, G, scanning electron micrographs. B, instar-II case, lateral aspect. C, instar-II case, ventral suture split open. D, instar-IV case, lateral aspect. E, pupal case, ventral aspect. F, pupal case, lateral aspect. G, pupal case, boundary between egg case and larva-I sections.

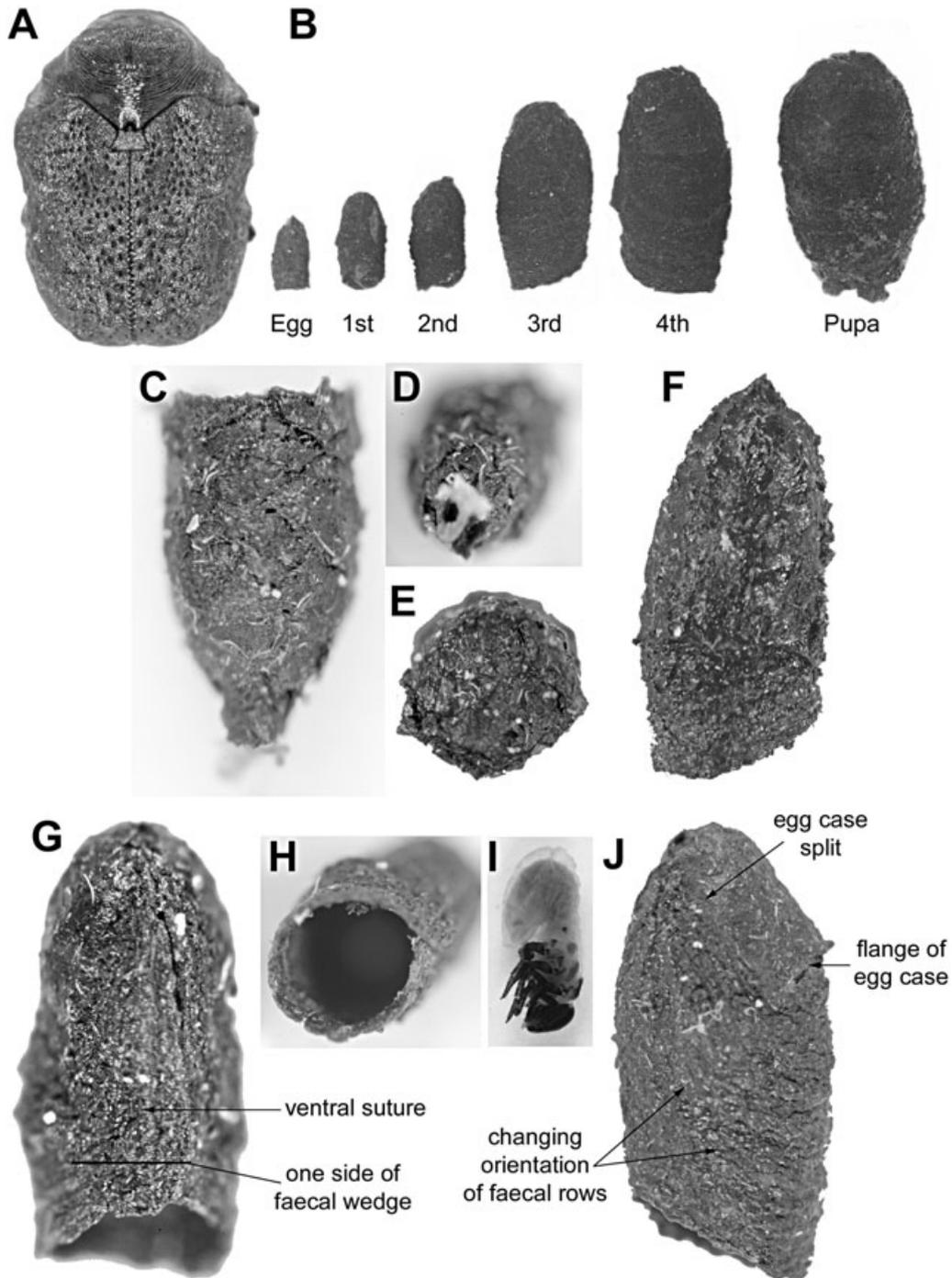


Figure 14. *Neochlamisus comptoniae*. A, adult habitus. B, case series from egg case (left) to pupal case (right). C–E, egg case. C, lateral aspect. D, apex with egg stalk. E, roof. F, instar-I case, lateral view. G, instar-I case, ventrolateral view. H, larval instar-II case, opening. I, larval instar III. J, instar-III case, lateral view.

Neochlamisus comptoniae (Brown, 1943) (Fig. 14):
host plant *Myrica asplenifolia*

Egg case (Fig. 14B–E): Size ($N = 10$): L, 1.4–1.53 mm;
W at roof, 0.89–0.92 mm. Colour: unevenly brownish-

black. Shape: bell-like; symmetrical in lateral aspect;
apex rounded or pointed; flange present, narrow;
dorsal, ventral, and lateral walls not distinguishable;
egg stalk present, short, not coiled, forming flattened
disc at substrate. Roof: transverse, external texture

coarse. External surface of walls: rough, faeces arranged in plates; plates rounded to quadriform, fitted together apically, overlapping with basal margin exposed; longitudinal ridges very weakly developed. Internal surface: smoothed; case walls evenly thin, external plate pattern not distinct. Trichomes: not apparent.

Larva-I case (Fig. 14F, G): Size ($N = 7$): L, 0.99–1.35 mm; W at base opening, 1.65–2.46 mm. Young phase of case with shape, colour, texture, and symmetry as in egg case. Apex: rounded; lateral margins subparallel; base opening transverse. Flange of egg case: apparent. Larval case section: darker than egg case, with fine faecal rows. Older case: with insertion of ventral suture and development of dorsal, lateral, and ventral walls; suture terminating subapically. Internal surface: as in egg case, larval section darker and wall thicker. Trichomes: present, very sparse, deeply embedded in faecal matrix, evenly distributed.

Larva-II case (Fig. 14H, I): Size ($N = 7$): L, 2.54–2.57 mm; W at base opening, 1.39–1.50 mm. Colour: uneven, egg case dark brown; sections of instars I–II darker, boundary between I and II marked by fine light-brown line. Shape: tubular, asymmetrical in lateral aspect, margins subparallel. Apex: rounded; egg case split ventrally by ventral suture and faecal insertion; flange of egg case apparent in some cases; egg stalk absent. External surface: coarse; larva I–II sections with faeces arranged in fine rows. Ventral surface: with protuberant triangular wedge, longitudinal faecal rows occupying half surface; ventral suture slightly protuberant, terminating subapically. Base opening: transverse, margin simple. Internal surface: rough, lacking any plates, ridges, or row patterns; colour and texture of egg case intact; larval section evenly darker; wall thickness evenly narrow. Trichomes: sparse, evenly distributed, and deeply embedded in faecal matrix.

Larva-III case (Fig. 14B, J): Size ($N = 10$): L, 4.15–4.58 mm; W at base opening, 1.88–2.00 mm. Colour of larval sections: dark-brown/black. Shape: tubular, asymmetrical in lateral aspect. Egg case: occupying 1/8th of case length, split into two hemispheres, forming basal cap, position not markedly inclined ventrad. Ventral wall: with triangular wedge occupying two-thirds of the surface; ventral suture terminating subapically; walls with faeces arranged in rows. Internal surface: smooth, external patterning not apparent. Trichomes: apparent, sparse, evenly distributed, deeply embedded into faecal matrix.

Larva-IV case (Fig. 14B): Size ($N = 9$): L, 5.17–5.18 mm; W at base opening, 2.86–3.00 mm. Shape: tubular, ovoid, widest in basal half. Egg case: distinguishable by lighter brown coloration, granular texture, and lack of colour striations; larval section darker, blackish, striated in appearance; surface texture granular in early stages, coarser in later phases; faecal rows unevenly ridged and coarse. Boundaries between subsequent larval phases distinguishable by texture changes, indentations, and sometimes coloration; indentation especially apparent on anterior wall between the instar I–II boundary. Base opening: transverse in lateral aspect, ventral wall shorter than dorsal wall; basal margin simple. Ventral surface: with broad faecal insertion occupying most of wall; ventral suture protuberant, terminating subapically. Internal surface: smooth; plates, ridges, and rows not apparent; wall evenly narrow. Trichome: density and distribution as in younger cases.

Pupal case (Fig. 14B): Size ($N = 12$): L, 5.40–5.42 mm; W at base opening, 3.26–3.32 mm. Colour, texture, and trichomes: as in larval case IV. Shape: somewhat barrel-shaped, apex and base inclined ventrad; ventral wall flattened. Egg case: split into two hemispheres, inclined ventrad. Base: obliquely transverse in lateral aspect; coarse seal texture, margin sometimes with irregular projections.

Neochlamisus cribripennis (LeConte, 1878)
(Figs 15, 16): host plant *Vaccinium spp.*

Egg case (Fig. 15B–D): Size ($N = 9$): L, 1.48–1.56 mm; W at roof, 0.99–1.04 mm. Colour: unevenly dark brown. Shape: bell-like, symmetrical in lateral aspect; apex arcuate; egg stalk present, short, not coiled; flange slight. External surface: with faeces arranged in rounded plates; plates: protuberant medially, giving uneven surface texture, contiguous, not overlapping; longitudinal ridges absent. Trichomes: not apparent.

Larva-I case (Fig. 15B): Size ($N = 5$): L, 1.57–1.73 mm; W at base opening, 1.08–1.36 mm. Colour: background dark brown. Shape: conical, symmetrical in lateral view; apex arcuate; egg stalk present; flange of egg case distinct. External surface: flattened and rough; egg case with faecal plates fitted together, not overlapping; section I with faeces in horizontal rows, not in plates. Faecal rows arranged horizontally on ventral, lateral, and dorsal surfaces; ventral suture apparent in older cases. Base opening: slightly oblique; margin simple, not flared or thickened. Trichomes: not apparent.

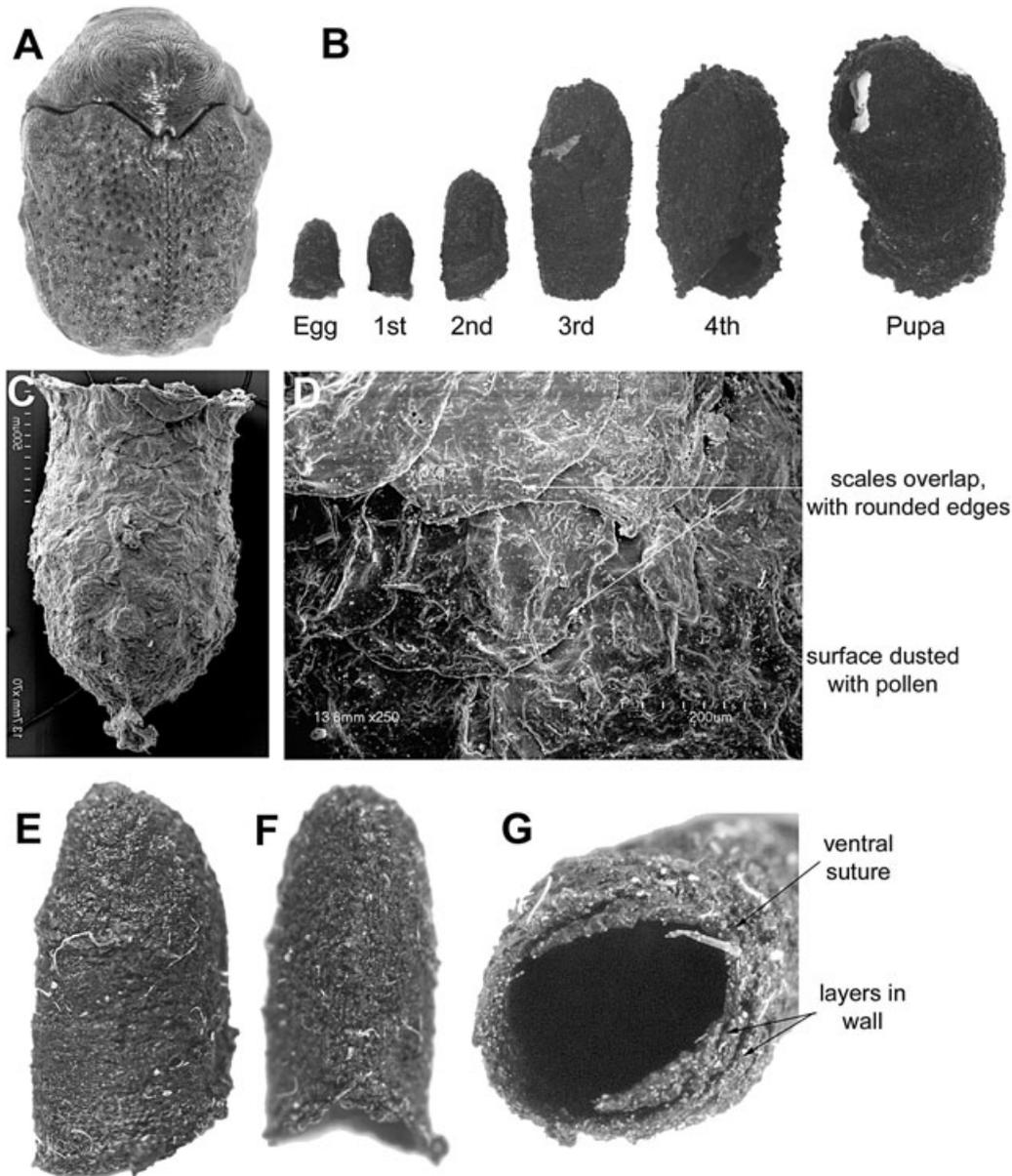


Figure 15. *Neochlamisus cribipennis*. A, adult habitus. B, case series from egg case (left) to pupal case (right); instar-III and pupal cases are broken, exposing stage inside. C, egg case, scanning electron micrograph. D, egg case, lateral wall, scanning electron micrograph. E–G, instar-III case. E, lateral aspect. F, ventral aspect. G, base opening.

Larva-II case (Fig. 15B): Size ($N = 5$): L, 2.53–3.78 mm; W at base opening, 1.36–2.00 mm. Colour: unevenly dark brown; lighter brown marking boundaries between egg case and section I, and between sections I and II. Shape: generally conical, symmetrical in lateral view; apex rounded; egg stalk absent. Diameter of sections I and II similar, slightly wider than diameter of egg case at apical margin; remnants of flange of egg case apparent. External surface texture: scabrous with faecal rows. Ventral suture: present, terminating subapically, dissecting egg case.

Base opening: oblique, basal margin simple, not thickened. Trichomes: present, sparse, irregularly arranged, deeply incorporated into wall matrix, some emergent and decumbent.

Larva-III case (Figs 15E–G, 16A): Size ($N = 4$): L, 4.31–4.36 mm; W at base opening, 1.63–2.23 mm. Colour: uneven dark brown, boundaries between egg case and section I, sections I–II and sections II–III marked by slightly lighter-brown coloration. Shape: conical, symmetrical in lateral view; apex rounded.

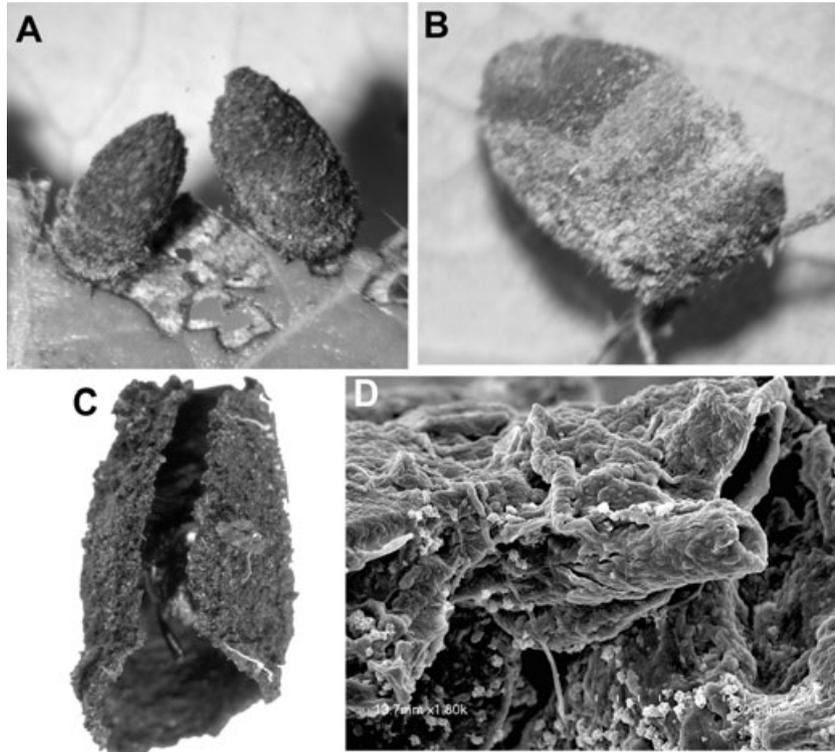


Figure 16. *Neochlamisus cribipennis*. A, larval instar III, live feeding on host plant leaf (photo by CGB). B, pupa attached to host leaf petiole (photo by CGB). C, instar-IV case, ventral suture split open. D, instar-IV case, wall cross-section showing trichome in faecal matrix, scanning electron micrograph.

External surface: rough. Ventral suture: extending from apex to base, dissecting egg case. Base opening: oblique; margin simple, uneven, not flared or thickened. Trichomes: as in case II.

Larva-IV case (Figs 15B, 16C, D): Size ($N=3$): L, 4.31–4.86 mm; W at base opening, 2.61–2.8 mm. Colour: uneven dark brown; boundaries of sections distinct. Shape: barrel-like, symmetrical in lateral view; apex rounded. External surface: rough. Ventral suture: extended from apex to base, dissecting egg case. Base opening and margin: as in case III. Trichomes: as in cases II and III.

Pupal case (Figs 15B, 16B): Size ($N=1$): L, 5.47 mm; W at base opening, 3.28 mm. Shape, colour, texture, and trichomes as in instar IV. Apex: somewhat flattened; egg case discernible, inclined ventrad. Base opening: inclined at 45° to ventral wall, margins flared.

Neochlamisus eubati (Brown, 1943) (Fig. 17):
host plant *Rubus* spp.

Egg case (Fig. 17B, C): Size ($N=10$): L, 1.62–1.76 mm; W at roof, 1.00–1.12 mm. Colour: dark

brown. Shape: bell-like, approximately twice as long as wide; symmetrical in lateral aspect; flange very slight. Apex: rounded; egg stalk present, short, narrow, tan-coloured. Faeces shaped into flattened triangular plates; plates overlap basally, apical margins free; scale pattern indistinct near apex. External surface: uneven with inclusions of trichomes; longitudinal ridges not apparent; wall thickness very narrow; internal surface smooth. Base opening: rounded; disc seal concave, texture uneven, rough. Trichomes: sparse, evenly distributed, and deeply incorporated into faecal material, some trichomes occasionally protuberant.

Larva-I case (Fig. 17B): Size ($N=14$): L, 1.58–2.29 mm; W at base opening, 0.94–1.02 mm. Colour of larval addition: brownish-black. Shape, symmetry, texture, and colour of young cases: as in egg case. Older cases: double the length of egg case; ventral suture terminating subapically; lateral margins subparallel, evenly tapered. Egg case: intact except for ventral suture; egg stalk present or absent; flange of egg case sometimes apparent. Base opening: transverse in lateral aspect. Internal surface: smooth, thicker in larval section, external patterns of plates and rows not apparent internally.

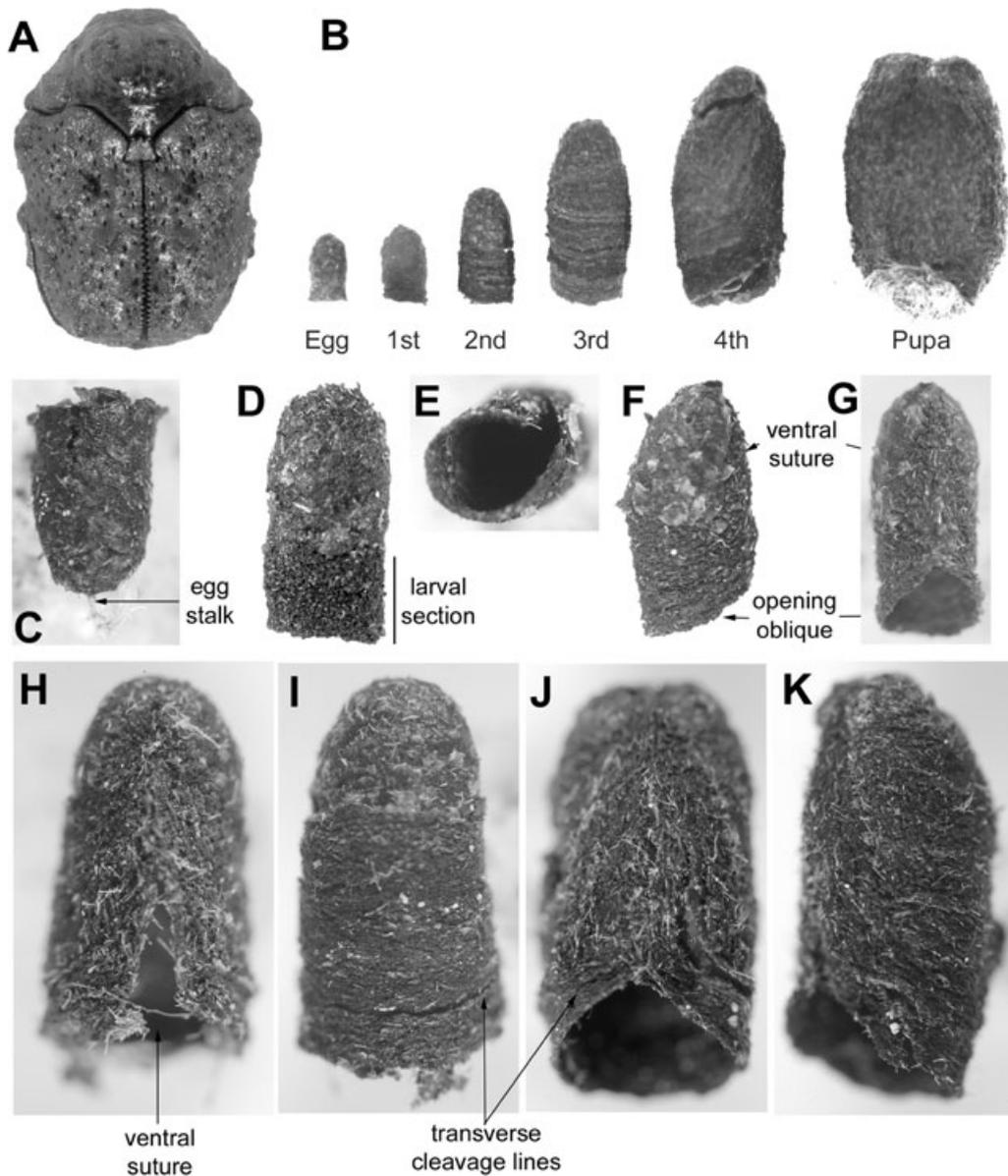


Figure 17. *Neochlamisus eubati*. A, adult habitus. B, case series from egg case (left) to pupal case (right). C, egg case, lateral aspect. D, instar-I case. E, instar-I case, base opening. F, instar-II case, lateral aspect. G, ventral aspect, with suture. H, instar-III case, ventral aspect. I, instar-III case, dorsal aspect. J, instar-IV case, ventral aspect. K, instar-IV case, lateral aspect.

Larva-II case (Fig. 17F, G): Size ($N = 10$): L, 2.18–2.6 mm; W at base opening, 1.16–1.39 mm. Shape, colour, symmetry, and texture: as in late larva case I. Ventral surface: with triangular wedge, inserted by larvae I–II; ventral suture not protuberant, terminating subapically, dissecting egg case. Wedge: distinguishable from adjacent case material by inclusion of trichomes and coarse surface texture. Case-II section: with trichome inclusions more dense than in case I. Case diameter evenly enlarged basad. Base opening:

rounded, obliquely transverse in lateral aspect; margin not flared. Internal surface: texture smooth.

Larva-III case (Fig. 17H, I): Size ($N = 10$): L, 3.22–3.67 mm; W at base opening, 1.88–2.17 mm. Shape: tubular, as in case II. Egg case: completely split by ventral suture into two slightly protuberant lobes, and separated by triangular faecal wedge, inclined slightly ventrad. Larval insertions: with dense trichomes. Base opening: obliquely transverse in lateral

view; lateral walls evenly tapered, widening basad. Internal surface: as in case II.

Larva-IV case (Fig. 17J, K): Size ($N = 8$): L, 5.37–6.52 mm; W at base opening, 2.80–3.89 mm. Colour, texture, and orientation of faecal rows: as in case III. Shape of young cases: tubular, as in case III. Older cases: ovoid or barrel-shaped, widest near base opening; egg case distorted, as in case III. Ventral wall: slightly protuberant near base. Base opening: strongly obliquely transverse in lateral view, margin simple.

Pupal case (Fig. 17B): Size ($N = 5$): L, 5.76–6.82 mm; W at base, 4.13–4.67 mm. Shape: barrel-shaped, dorsal wall longer than ventral wall; apex somewhat flattened. Egg case: not easily discernible. Base: obliquely transverse; coarse seal texture. Internal surface: smooth, evenly thickened, multi-layered, layers parchment-like; apex thick, comprising many layers.

Neochlamisus platani (Brown, 1952) (Figs 18, 19):
host plant *Platanus occidentalis*

Egg case (Fig. 18B–E): Size ($N = 11$): L, 1.32–1.56 mm; W at roof, 0.91–0.95 mm. Colour: unevenly dark brown. Shape: bell-like, symmetrical in lateral aspect; apex rounded; roof margin simple, flange absent; egg stalk present. Walls composed of faecal plates; plates faintly pentagonal, fitted together basally, and overlapping apically, some projecting vertically at case apex; plate surface protuberant centrally. Wall with fine longitudinal ridges, extending from apex to base, spanning multiple plates; ridges evenly spaced and slightly radially arranged. Trichomes: present, filamentous type, medium density, evenly distributed, deeply embedded in matrix. Internal surface: rough, external plates and ridges not apparent; wall evenly thin. Roof: transverse, seal unevenly flattened.

Larva-I case (Fig. 18G, H): Size ($N = 9$): L, 2.13–2.30 mm; W at base opening, 1.04–1.14 mm. Shape, colour, and symmetry of young case: as in egg case; larval section brownish-black; egg stalk sometimes present. Older cases: conical, asymmetrical in lateral aspect; dorsal, ventral, and lateral surfaces apparent. Ventral suture: terminating subapically; triangular faecal insertion not protuberant. Trichomes: present, stellate type, light to medium density. Internal surface: smooth. Wall of larval section: slightly thicker than in egg case. Base opening: obliquely transverse.

Larva-II case (Figs 18B, F, 19A): Size ($N = 9$): L, 3.94–4.27 mm; W at base opening, 1.46–1.72 mm. Colour: uneven brown-black. Shape: tubular; egg case shape, position, and texture intact; ventral suture present ventrally, terminating subapically; apex evenly rounded; egg stalk lacking. Larval section with faeces as in instar I. Boundaries between egg case and larval-I case well demarcated; boundary between larval sections I and II obscured by trichomes. Internal surface: smooth. Base opening: obliquely transverse, anterior wall slightly longer than ventral wall. Trichomes: more dense than in case I, obscuring surface.

Larva-III case (Figs 18B, 19B): Size ($N = 12$): L, 4.97–5.08 mm; W at base opening, 2.38–2.85 mm. Shape, colour, texture, and trichome arrangement: as in case II. Egg case: apparent, position inclined ventrad.

Larva-IV case (Figs 18B, 19G, H): Size ($N = 8$): L, 7.26–8.86 mm; W at base opening, 3.95–4.46 mm. Shape: tubular in young phase; barrel-like in older stage, widest in apical section. Asymmetry, colour, and trichome pattern: as in case III. Egg case: somewhat distorted, split into two hemispheres, inclined ventrad, diagnosable by lack of stellate trichomes.

Pupal case (Figs 18B, 19I, J): Size ($N = 15$): L, 7.33–8.75 mm; W at base, 4.24–4.42 mm. Shape, colour, asymmetry, and trichome type and density: as in late case IV. Egg case: inclined ventrad, protuberant, overhanging ventral suture. Base: rough seal surface; trichomes present, medium density, incorporated into faecal matrix, not forming fuzz.

DISCUSSION

In this study of *Neochlamisus* cases, we found that the underlying patterns in form and ontogeny indicate highly repetitive construction behaviour. The conservative nature of the architecture and attachment of the egg case suggests a stereotypical behaviour in case construction. The patterns of architecture described here are consistent with the tempo and mode of case construction presented by Brown & Funk (2005), and these patterns may hold generally for most camptosomates (Cryptocephalinae and Lamprosomatinae). Interestingly, the *Neochlamisus* cases share certain traits with caddisfly cases (Trichoptera) (e.g. Hansell, 1974), for example, wall asymmetry, the pupal seal, and smaller subunit composition. Perhaps that better-studied system can provide models for future research on camptosomate cases.

The similarity of the basic architecture across *Neochlamisus* cases suggests that construction does not vary in significant ways. In fact, case growth does

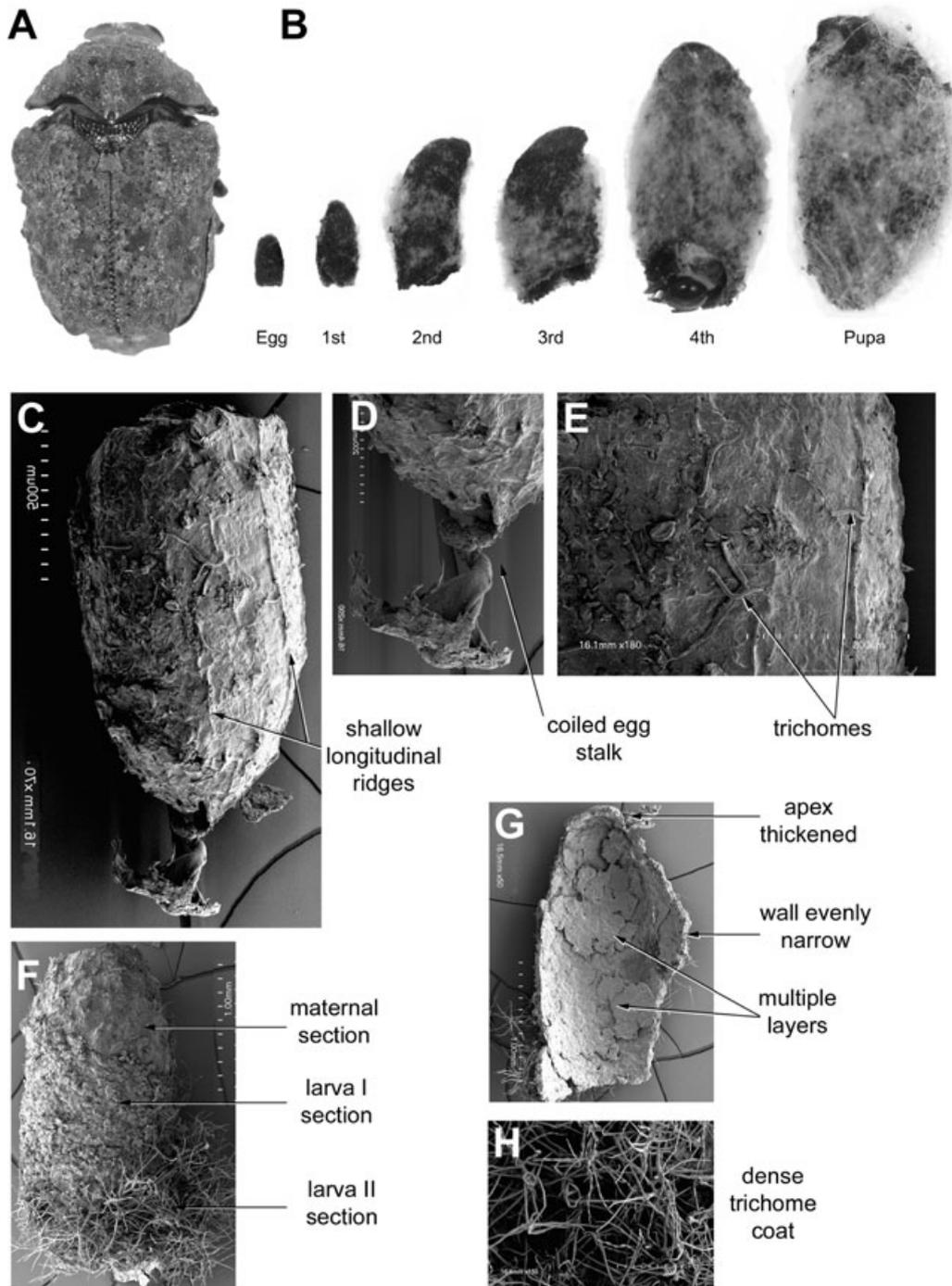


Figure 18. *Neochlamisus platani*. A, adult habitus, with prothorax distended as a result of preservation. B, case series from egg case (left) to pupal case (right). C–H, scanning electron micrographs. C, egg case, lateral aspect. D, egg stalk. E, egg case surface. F, instar-II case, showing external texture variation between maternal and larval sections. G, instar-I case, forewall removed, internal aspect. H, instar-I case, exterior trichome coat of larval section.

seem to follow a logarithmic growth pattern (A.E. Aldridge, pers. comm.). However, unlike other natural gnomons (e.g. claws, sunflowers, and seashells) that grow in mathematically predictable self-repeating

patterns, the chlamisine case shape is more ontogenetically dynamic, and several different shapes may be exhibited within a single life history (see Aldridge, 1999). The addition of material to the anterior

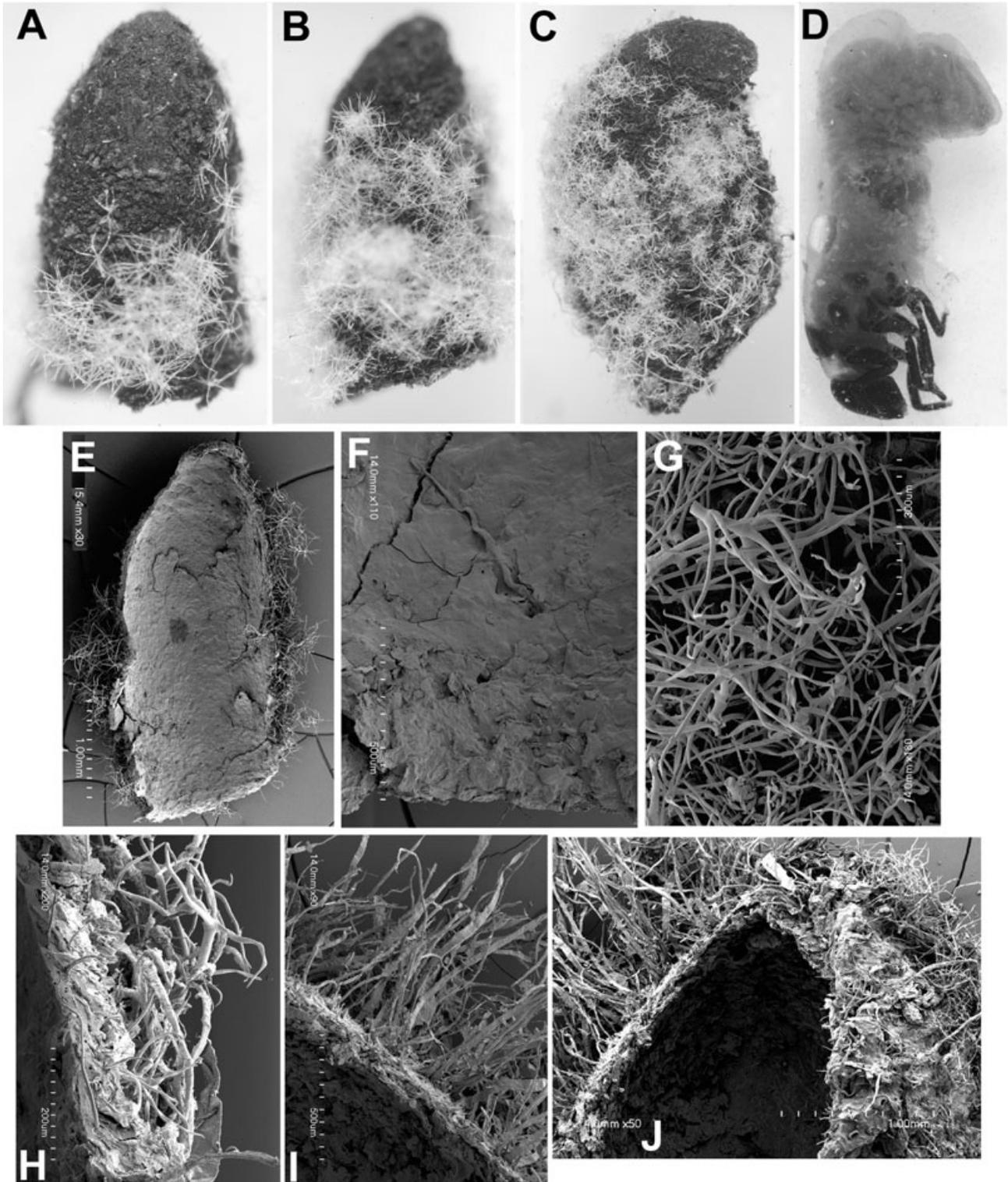


Figure 19. *Neochlamisus platani*. A, instar-II case, dorsal aspect. B, instar-III case, lateral aspect. C, instar-IV case, lateral aspect. D, larva, instar IV, lateral aspect. E–J, Scanning electron micrographs. E, instar-III case, forewall removed, internal aspect. F, instar-III case, forewall removed, internal surface with trichome. G, instar-IV case, external surface with stellate trichomes. H, instar-IV case, cross-section of wall showing trichome–faecal matrix. I, pupal case, cross-section of wall. J, Pupal case, cross-section near apex.

dorsum and the ventral seam in different orientations and at different rates (see Brown & Funk, 2005) contributes to these patterns. The case is initially maintained as a tube by larval additions only to the apical opening. It is then widened and turned into a barrel-shape by also adding material to the ventral suture. Case growth then follows an interesting trajectory, with the dorsal wall curving such that the case is held ever more closely to the substrate, while the case is expanded by increased faecal additions to the ventral suture.

MODEL DESCRIPTION AND TERMINOLOGY FOR CASE ARCHITECTURE

The case can be described by the following characters: length-to-width ratio, symmetry, apex shape (rounded or arcuate), colour (striated or banded; black-brown to light brown), regions (apex, base, or opening), wall (internal versus external), and inclusions (e.g. trichomes, soil, etc.). Ultimately, our description of the states of these characters should facilitate phylogenetic analyses that will elucidate the evolution of these unusual examples of insect architecture. Below, we discuss the nature and hypothetical functions of various case stages and characters that were the subject of our study.

Egg stalk: *Neochlamisus* eggs are attached to the host plant via an initially pliable string of unknown substance, known as the 'egg stalk'. The substance of the stalk and morphological site of its production has not been determined. It is probably a glandular product in all species (Hilker, 1994). The stalk may provide leverage that helps the female pull the egg from her abdomen (Karren, 1964), or serve to elevate the egg from the substrate away from predators. In larval cases, the stalk may be chewed away, abraded, or obscured. The egg stalk is not present in all camp-tosomates, and its presence/absence may reflect the differing requirements of strictly phytophagous species versus the omnivorous, detritivorous, and myrmecophilic taxa that generally lack them.

Plates: The egg cases of all *Neochlamisus* species appear to be comprised of smaller subunits. Scudder (1891) first described the egg case surface appearance as resembling 'papier mâché', an effect arising from the layers of individual plates. Plates have also been termed 'scales' (Karren, 1964; Lawson, 1976) or 'platelets' (Lawson, 1976; Neal, 1989; LeSage & Stiefel, 1996). Maternal faeces are flattened and shaped as discrete plates, which form the basic building blocks. A new row of plates is added when the preceding one is complete, yet in the completed egg case there is no indication of initiation or termination

points. Across the taxa examined, plates are similarly sized, but vary in being triangular, quadrate, or pentagonal in shape, and have adjoined or overlapping arrangements. The use of plates as basic building units is common in cryptocephaline cases, but this is not universal.

Egg case ridges: Often, a longitudinal ridge exists along the median of each plate. In *Neochlamisus* egg cases, these ridges were generally fine, and did not project greatly from the surface. They extended from the roof margin across multiple plates, but terminated subapically, never extending fully to the attachment stalk. Plate convexity, shape, and external longitudinal ridges may reflect the individual peculiarities in the female rectal morphology of each species (see Erber, 1988). For example, they may be formed by a depression in the rectal sclerites used by the mother to construct the plates (see Erber, 1988).

Flange: Karren (1964) coined this term for the flared margin of the roof of the egg case. The flange, also called 'shoulder' in *Pachybrachis bivittatus* (Lawson, 1976), is characteristic to the overall bell shape consistently observed in *Neochlamisus* egg cases. This shape has also been described as a 'bell-flower' (Karren, 1964) or 'flask-shape' (Packard, 1869, 1889), and appears to be common throughout Cryptocephalinae (Erber, 1968, 1988). It is very broad and curving in cases of *Fulcidax* (Flinte *et al.*, 2003). The flange may be an inadvertent consequence of the female's anatomy pressing down on the longitudinally extended case wall when she seals the roof of the egg case. No specific function has been suggested.

Anterior additions: Case surface texture varies greatly between the egg section and the larval section as a result of differences in faecal arrangement, building units (plates versus rows), and trichome density. Unlike the maternal production of plates, larvae add rows of moistened faecal material to the case. The larva starts applying faeces horizontally along the edge of the flared margin of the case. In all cases compared, the larval sections comprised fine faecal rows arranged radially, but with changing orientation. This is similar to patterns described for *Pachybrachis* (LeSage, 1985) and *Anomoea* (LeSage & Stiefel, 1996) cases, and suggests a taxonomically widespread approach to larval faecal application. By the end of stadium I, the larva has applied numerous horizontal rows and the bell-shaped egg case has been transformed into a tube.

Ventral suture: This is common to all instars of *Neochlamisus* and provides a useful descriptive landmark. This cleavage line is initiated during instar I,

as the larva cuts through the case longitudinally in order to spread the case walls apart and fill in the resulting triangular space with faecal material (the wedge), thus widening the case. A new suture is formed exactly in the centre of the wedge in order to widen the case further, and this process is repeated many times during development. The ventral position of the suture relative to the substrate is maintained, even if the case is removed from the larva and then replaced on the larva in reverse orientation; this is because the larva will spin the case until the suture is ventrally aligned again (DJF & CGB, pers. observ.).

The cutting of the suture has not been observed, but is presumably performed with the mandibles. The ventral suture is typically the weakest point in the case, and the place in which it will most likely break if pressure is applied to the case. Nonetheless, other cleavage lines can form under pressure, running transversely between the larval constructed faecal rows, especially between the egg case and the larval sections.

Surface texture: The internal surface appears quite smooth, and much smoother than the external surface, although SEM analysis reveals irregularities. It is not known if the smooth internal texture is achieved by passive rubbing of the walls by the larva, or by the active smoothing of internal layers of faeces. Only in the rougher, external surface are the individual layers of faecal additions apparent. Unlike the internal surface, the external surface is, to varying degrees, covered by trichomes in certain taxa.

Ecdysis fixation ring: Just before moulting, larval *Neochlamisus* attach their cases to the substrate along the rim of the opening with a new ring of faecal material. Only the perimeter of the case is attached to the substrate, and the larva often leaves a ring of faeces on the substrate when its moult is complete and it frees itself again (see Brown & Funk, 2005).

Nipple: Some camptostomate taxa, such as *N. platani* and the *Salix* host form of *N. bebbianae*, may not completely split the egg case via construction of the ventral suture during larval development. In such situations, the egg case remains mostly intact and appears as a short narrowed extension of the case apex in older stages. Such a structure has been termed a 'nipple' (e.g. Brown & Funk, 2005).

Trichome attic: Brown & Funk (2005) found that older *N. platani* cases contained a package of plant trichomes in the inside of a small chamber, inside the apex of the case that is sealed off from the main larval chamber with an extra internal wall of faeces. They called this structure a 'trichome attic'. This may be

similar to chambers in *Exema* cases that contain larval exuviae (LeSage, 1982) or empty pockets in a *Lamprosoma* species (Monrós, 1948). Brown & Funk (2005), however, found no exuviae in this attic or in any other portion of any *Neochlamisus* case, except for the final larval exuvium that is left on top of the seal inside the pupal case. Under our SEM analysis, no exuviae were found to be otherwise incorporated into cases.

Pupal seal: Just before pupation, the prepupa once again attaches the case to the substrate, and completely seals the entry with faecal material. In *Neochlamisus*, the pupal seal is constructed from the basal case edge inwards, and the seal is often thicker than the walls of the case. This seal helps prevent the case from being dislodged from the host plant during metamorphosis. As the seal is created by the fourth instar larvae (pupae do not excrete faecal material), sealed 'pupal' cases may be found to house a still-active larva if opened within a few days of attachment.

Pupal cap: Once the cuticle hardens, recently eclosed adult *Neochlamisus* use their mandibles to cut a complete circular cap at the case apex, push this open (if still connected by a small hinge), or entirely off, and crawl out. Caps are similar across *Neochlamisus* taxa, but show variation in structure (and perhaps associated behaviour) in some other camptostomates, such as *Fulcidax* and *Chlamisus* (Flinte & Macêdo, 2004a, b; Reu & Del-Claro, 2005).

FAECAL-CASE-ASSOCIATED ANATOMY

The Camptostomata show several morphological adaptations associated with constructing and living within their constructions, and which provide strong synapomorphic support for their status as a distinct lineage within Chrysomelidae.

Adult: Erber (1968, 1988) presented beautifully detailed studies of the 'kotpresse', the adult female rectal apparatus, and the abdominal fovea or dimple involved in case construction. Rectal structures may compress faecal pellets to form the plates; the dimple serves to stabilize the egg while it is being rotated during case construction. Additional potentially adaptive features are several rows of fine hairs that may help guide the female during egg-case construction (Brown & Funk, 2005). Adult mandibles might be especially robust or sharp for cutting through the case after eclosion. Similarly, the unusual humped pronota of *Neochlamisus* could conceivably play a role in pushing away the case 'cap'. Such possibilities deserve further investigation.

Larva: Morphological features of larvae associated with case carriage have not been well studied. All cryptocephaline larvae have an enlarged abdomen that is bent forward into a U shape. This shape positions the anus close to the mouth, legs, and case opening, facilitating the application of faeces. The enlarged size of the abdomen might retain the case more securely, reducing the chance of the larva being dislodged from its case through the comparatively narrower case opening. The especially long legs (Root & Messina, 1983) of these larvae easily extend beyond the margins of the case, allowing for movement. In nonherbivorous camptostomates, the head is often heavily sclerotized and flattened, forming a plug that can seal the narrow case opening, and presumably serves in predator defence. The head of a *Neochlamisus* larva, by contrast, is not of this type, and is much smaller than the case opening. Like some burrowing animals, case-bearing larvae and especially sealed-in pupae could have special respiratory adaptations and sensory structures (Hansell, 2005), although these possibilities have not been evaluated.

CONSTRUCTION MATERIALS

An ideal case would have strength and durability, yet be sufficiently lightweight to minimize the energetic cost of carriage. It would also be pliable enough to allow cleavage and expansion at the ventral suture. The composition of such a case would allow aeration, minimize desiccation and radiation, and perhaps have antibacterial and antifungal properties. Understanding the composition of construction materials is therefore fundamental to understanding the potential functions of the cryptocephaline case.

Faeces: The use of faeces as a building material appears in some species of termites, moths, and flies (Weiss, 2006), as well as several lineages of Chrysomelidae (Morton & Vencl, 1998; Chaboo & Nguyen, 2004; Chaboo, 2007; Chaboo, Grobbelaar & Larsen, 2007). Faeces are advantageous in being readily available (given regular food supply), lightweight when dry, and potentially distasteful to predators (Olmstead, 1994; Weiss, 2006). We know that not all larval faeces are added to the case in *Neochlamisus*, as additional free faecal material is regularly observed in containers in which larvae are reared (DJF & CGB, pers. observ.). The varying shades of faecal layers seen in cases probably reflects variation in the parts and composition of the host consumed at different times, as the larva wanders and feeds during development.

Wax: Spruyt (1925) suggested that the attachment stalk and egg case of *Saxinis saucia* Leconte, 1857 (Clytrini) was composed of colleterial material and

wax, respectively. A wax component was not obvious in *Neochlamisus* cases, but may require additional methods for detection.

Glues and wetting agents: The female appears to mix her faeces with other fluids before applying plates to the case, and the chemical identity of these liquid agents and their effects are not known. Candidate roles are as glues, wetting or hardening agents, or sources of antimicrobial/fungal protection. Cryptocephaline cases, including those of *Neochlamisus*, are remarkably durable and retain their integrity after long periods of preservation in alcohol. Empty cases are used as homes for ants and spiders long after the original builder departed (Schöller, 1999), and persist for a year or more in the field in areas with harsh winters (DJF, pers. observ.). Although neither adult nor larval exudates have been evaluated chemically, both dry into solid substances.

Host plant derivatives: Host plants probably influence case construction and function in many ways. The sequestration of plant defensive chemicals in faeces, as described in faecal shields of other chrysomelids (Gómez, 1997; Morton & Vencl, 1998; Gómez, Witte & Hartmann, 1999; Vencl *et al.*, 2005), is one relevant hypothesis. Boldt & White (1992) previously suggested this possibility in noting that *Baccharis halmifolia* L., the host of *Exema elliptica* Karren, 1966, contains a cardio-toxic glucoside. In the future, comparative chemical profiling of host plants, beetles, and their cases could explore the contributions of host chemicals.

Trichomes are the only plant parts we found incorporated into the *Neochlamisus* faecal case. Trichome inclusions in cryptocephaline cases have been noted in *Exema pennsylvanica* Pierce, 1940 (Karren, 1964), and in some *Clytra* ('hairy cases' in Hislop, 1872), and have possibly been illustrated in the case of *Chlamisus melochiae* (Monrós, 1952). Chewed plant fragments were described from the case of the clytrine *Coscinoptera dominicana* (Fabricius, 1801) (Riley, 1874b; Wickham, 1896). Interestingly, these have also been described for *Chlamys plicata* Olivier, 1808 (Packard, 1869, 1889), a name that historically included some *Neochlamisus* species. Trichome cutting (mowing, shaving, or plucking) has been reported in chrysomelid larvae (Jolivet, 1988; Jolivet & Verma, 2002; Medeiros, Bolignon & Moreira, 2004), including *Neochlamisus* (Brown & Funk, 2005).

Trichome additions to cases may simply represent an inadvertent by-product of larval feeding, adhering to the case after being removed by the larva to grant it better access to host foliage (Brown & Funk, 2005). Alternatively, the incorporation of trichomes as a building material could be adaptive. Their mesh-like

arrangement within the faecal matrix and externally may increase case durability. Smith (1922) indicated that plant fibers, along with spider silk, are used to hold trash packets together in chrysopid larvae. A similar structural role may be conceived for plant trichomes in *Neochlamisus* cases, providing a network or mesh that holds wet faeces together until dried into a sturdy case. Additionally, toxic or sticky glandular exudates from trichomes could enhance predator deterrence or increase handling time. Trichome-covered cases may also more closely resemble plant structures such as buds, thus increasing cryptic concealment from potential predators (Hansell, 1996). Or they might provide insulation, moderating temperature and humidity within cases. The potential benefits of trichome inclusions versus their possible disadvantages (e.g. increasing case weight; time and energy spent in active incorporation) require further study.

LIFE HISTORY AND TAXONOMIC VARIATION

Instar variation within Neochlamisus species: As the individual grows, the shape of the case changes completely from an initial bell-shaped maternal case, to a conical case in early instars, and finally to the increasingly ovoid shape of the late fourth instar and pupa. Early instar cases are cylindrical to conical, with a fairly longitudinally consistent diameter, except at the narrowed apex, and with the basal margin slightly angular in lateral view. In late instar IV and in the pupal case, the case is widest medially, acquiring a barrel-shaped or ovoid form similar to that noted for *E. canadensis* (LeSage, 1982). This pattern may anticipate the space needed for the broadly block-shaped adult (Brown & Funk, 2005). Cases of late-instar larvae also tended to exhibit the highest density of trichomes.

The case widens and lengthens in each subsequent larval instar. In later instars, the egg case has usually been completely, or mostly, dissected by the ventral suture into two hemispherical portions, which have by then become incorporated into the rounded case apex. The progressive shift in the position of the egg case and its eventual ventral inclination appears in other published illustrations of cryptocephaline cases (Dugès, 1881; Hinton, 1981; Erber, 1988). In all studied taxa, the angle of carriage of the case, relative to the substrate, declines from close to 90° in the first instar larvae to approximately 45° in pupae. This is a result of the uneven deposition of faeces along the rim of the opening, in a manner that lengthens the dorsal wall at a greater rate than the ventral wall. It is not obvious what, if any, function this change in case angle serves, although it may be promoted by the constraints of carrying an increasingly heavy case.

The differential shape changes (viewed in lateral aspect) observed between the dorsal and ventral walls suggest asymmetrical growth. In the ventral wall, the pattern of incorporation of faeces results in a large triangular field of longitudinal rows. This field is somewhat flattened in some taxa, so that the ventral case margin is in one plane in lateral view. This flattened surface may ease carriage over the substrate or represent a means of better balancing the increased case weight. By contrast, the dorsal wall remains rounded and hemispherical.

Variation among host forms of N. bebbianae: The egg cases of all four *N. bebbianae* host forms studied here have overlapping plates and simple trichomes. Differences in elongation and width were minute, and the degree of flaring of the basal margins varied slightly among individuals. Egg cases of the *Alnus* host form varied in the depth of the convex roof. The *Betula* host form had a flattened roof and simple margin, whereas other forms had a concave roof and a slightly flared margin. The *Betula* host form also had external ridges that varied in length, spanning the entire case or terminating subapically, whereas the *Salix* host forms had more developed longitudinal ridges. The *Salix* host form case had the lightest brown coloration (and sometimes appears reddish in nature; DJF, pers. observ.), in contrast to the blackish colour of various other host forms. The *Acer* host form egg cases had faecal plates that were slightly protuberant medially, producing a resemblance to pinecones.

The larval case of the *Salix* host form differed somewhat from those of the other three host forms, which were quite similar to each other. *Salix* host form cases had more trichome inclusions and were more elongate. Cases of the *Betula* host form showed the widest variation in trichome density, ranging from naked to densely pubescent. Instar IV of the *Salix* host form tended to have trichomes arranged in a very dense row, forming an incomplete collar at the base in larval sections III–IV. Within an instar, considerable variation in case size was observed. Trichome density varied most, from a complete lack of trichomes to complete coverage with trichomes for case IV.

Pupae in all forms of *N. bebbianae* are somewhat similar: flattened ventrally, with the opening deeply oblique in lateral aspect. Pupae in the *Salix* and certain individuals of the *Acer* host forms exhibited a slightly protuberant apical nipple.

Interspecific variation within Neochlamisus: All study taxa had generally similar egg cases, with some exceptions: the egg case of *N. platani* was notably more elongate, with the length almost twice the width. Individual faecal plates were less discernible in *N. bimaculatus*, and appeared to be absent in *N. eubati*. In

N. cribripennis, plates overlapped by half their length. The shapes of individual plates ranged from flattened, as in *N. cribripennis*, to protuberant, as described above for the *Acer* host form of *N. bebbianae*.

Although the vertical ridges on the plates of some taxa were laid parallel to the longitudinal axis of the egg case, in others they were orientated diagonally so as to appear to spiral around the case from the apex to the roof. The egg cases of *N. cribripennis* showed the widest variation in length, some being at least a third longer than others. Trichomes were incorporated into the faecal wall of all egg cases, but were most dense in that of the willow host form of *N. bebbianae*. The flange on the edge of the case roof also varied across *Neochlamisus* taxa. In *N. eubati*, the edge curved outwards yielding a very flared flange. In *N. platani*, by contrast, the flange was completely vertical, so that the roof of the case was recessed by comparison. The greatest degree of interspecific variation in the observed *Neochlamisus* larval cases was in coloration and trichome incorporation and density. Larval cases of all species included trichomes in the case-wall matrix, but *N. platani* and the *Salix* host form of *N. bebbianae* had the most externally pubescent pupal cases, with the *Betula* and *Acer* host forms also including some highly pubescent individuals.

Among the taxa we studied, the pupal cases of *N. bimaculatus* and *N. platani* were the largest, whereas those of *N. comptoniae* were the smallest. *Neochlamisus chamaedaphnes* had the most obvious colour variations, varying from light brown to blackish within and between cases. *Neochlamisus bimaculatus* appears to have the most barrel-shaped form, and has a somewhat flattened apex. The shape of the case in *N. chamaedaphnes* is peculiar, being widest apically, rather than medially as in other taxa.

Generic variation in cases of Chlamisini: Insights from the comparison of *Neochlamisus* cases with published descriptions and illustrations of cases from other camptostomates falls short of those allowed by comparing actual specimens. Nonetheless, these comparisons are useful for initiating discussion on generic and tribal-level variations in case architecture.

The cases of *Neochlamisus* appear to be quite similar in structure and form to those of *Exema*, but differ from particular species of two other genera of Chlamisini that have been studied, i.e. *Fulcidax* (Flinte & Macêdo 2004b) and *Chlamisus* (Reu & Del-Claro, 2005). *Fulcidax monstrosa* differs from these other taxa in producing egg cases that are not composed of individual plates, but instead cover eggs in 'a long strip of accumulated feces' (Flinte & Macêdo, 2004b: 460). The ventral suture receives no mention in the description of cases of some other chlamisines (Erber, 1988; Flinte & Macêdo, 2004b;

Reu & Del-Claro, 2005). Rather, *C. minax* is said to add new layers in a ring around the opening for most of the larval stadia (Reu & Del-Claro, 2005), whereas *Fulcidax* constructs two anterior lobes as part of its case (Erber, 1988).

The final position of material from the original egg case within the pupal case varies among chlamisine genera. As described here, in *Neochlamisus* taxa, the egg case is split, and tends to become gradually flattened by faecal insertion and shifting, with its outline becoming less clear (Brown & Funk, 2005). Monrós (1951) illustrated a very tapered case for *Chlamisus melochiae* Monrós, 1952, in which the maternal section is distinguishable only by texture and position. On the other hand, the egg case remains distinctive in a few *Neochlamisus* taxa, as described above, and also in some *Exema* cases (LeSage, 1982). The egg case in *C. minax* is obvious as a round ball atop the larval case, and is lost before pupation (Reu & Del-Claro, 2005). Flinte & Macêdo (2004a) show that the egg case remains intact until pupation in *F. monstrosa*. Ellis & LeRoux (1964) were the first to point out variations between *N. cribripennis* and *E. canadensis* in the shape and protrusion of the egg case section of the pupal case. This variation could be explored further for diagnostic and phylogenetic utility.

Brown & Funk (2005) found exuvial skins inside the pupal case. We also found the last larval exuviae in some pupal cases, where it was crumpled and sitting on the inside wall of the pupal case seal. LeSage (1982) found exuviae I–II, and possibly III, packed into the apex of the case, and exuviae IV packed next to the sealed pupal base opening in *E. canadensis*. We did not find exuviae of other instars inside the larval or pupal cases examined here.

Tribal variation in cases of Cryptocephalini: Longitudinal ridges appear in many cryptocephaline egg cases, but vary widely in form. In *Neochlamisus* these are slender and short, and are orientated longitudinally. In the egg cases of the cryptocephalines *Pachybrachis pecans* Suffrian, 1852 and *P. bivittatus* (LeSage, 1985), and *Cryptocephalus moraei* (Linnaeus, 1758), these ridges have a radial arrangement and are broken into regular short thick sections (Schöller, 1999). In an unidentified *Cryptocephalus* species illustrated in Emden (1932), completely parallel ridges extend from apex to base. In contrast, such ridges are absent altogether in the egg cases of the chlamisine *E. canadensis* (LeSage, 1982). The case of *S. saucia* (Clytrini) was described as having the arrangement of a double faecal envelope, with an internal wall of small plates and an external wall of long strands (Erber, 1988).

The various tribes of Camptostomata may differ most in the presence of an egg stalk. Many Chlamisini

are completely phytophagous and require fresh leaves to live. In this tribe, eggs are attached to the host plant substrate with an egg stalk. Egg stalks are also present in some species of Lamprosomatinae (Erber, 1988). Although they are phytophagous as adults, many clytrine larvae are detritivores and myrmecophiles. Their eggs have the egg stalk, and rather are often dropped to the ground to await discovery by ants, which take them to live in their nests.

Older instar cases of *Neochlamisus* are generally similar in texture to earlier instars. This does not appear to be the same in some other cryptocephalines. The last instar larval cases of *Anomoea laticlava* (Forster, 1771) (Clytrini) have a band of short, parallel, horizontally orientated, crescent-shaped ridges that are not present in earlier instars (LeSage & Stiefel, 1996). The radial arrangement of faecal rows around the case, with their changing orientation, is discernible in many illustrations of cryptocephaline cases (e.g. Dugès, 1881; Hinton, 1981), and suggests a universal pattern in the way larvae add faecal material.

COSTS AND BENEFITS OF CASES

It seems implausible that cryptocephaline species have invested so many morphological features, time, and energetic costs towards the construction, carriage, and maintenance of their faecal cases by chance alone. There may indeed be costs involved in producing and carrying these cases, such as the time involved in construction and repair, and the energy required to carry a structure that may weigh considerably more than the larva itself. Additionally, most animals avoid faeces generally as a source of disease, and to avoid attracting enemies through chemical cues, as in the example of faeces-orienting parasitoid wasps (Weiss, 2006). Yet the evolutionary persistence of these cases despite these costs argues that they are likely to present some functional utility, and represent evolutionary adaptations.

Several explanations have been proposed for the utility of cryptocephaline cases. These include mimicry of buds and other host-plant structures (Briggs, 1905; Karren, 1964; LeSage, 1984), and of plant debris (LeSage, 1982) or insect faeces (especially caterpillar frass) (Popenoe & Marlatt, 1889; Karren, 1964; LeSage, 1982; Verma & Vyas, 1987; Jolivet & Verma, 2002), hypotheses that remain untested. The case may also provide a physical or chemical barrier against various predators and parasitoids (Cockerell, 1891; Karren, 1964; Wallace, 1970; Root & Messina, 1983; Hilker, 1994).

The interactions between larval chlamisines and their predator and parasitoid enemies have not been studied in great detail (but see observations below). Predation of immatures has not been observed in the

field (except for a handful of observations by DJF), and it is unclear what the range of natural predators might be (Cox, 1996). Cases may increase the predator search and handling times or be distasteful. Cockerell (1891) speculated that case manufacture could have originated as protection from ants, birds, lizards, and other predator enemies. Protection from ants is a well-supported hypothesis for certain taxa (Wallace, 1970; Jolivet & Verma, 2002; Flinte *et al.*, 2003; Flinte & Macêdo, 2004a; Vencl *et al.*, 2005), although ants have never been observed to attack *Neochlamisus* specifically (despite abundant field observation by DJF). Predator deterrence through incorporation of host-plant chemicals into faeces is highly possible, as there is growing evidence demonstrating this in other Chrysomelidae (Pasteels *et al.*, 1984; Olmstead & Denno, 1992; Olmstead, 1994, 1996; Gómez, 1997, 2004; Morton & Vencl, 1998; Gómez *et al.*, 1999; Müller & Hilker, 1999, 2001, 2003, 2004; Nogueira-de-Sá & Trigo, 2002).

Chalcid parasitoids have been reared from immatures of *Neochlamisus* (Packard, 1869, 1889) and *N. chamaedaphnes* (Haardstad 2001). Eulophid and eupelmid parasites were also reared from larvae and pupae of *E. elliptica* (Boldt & White, 1992), *N. platani* (Neal, 1989), and *N. cribripennis* (Ellis & LeRoux, 1964; Wood, 1966). A considerable variety of parasitoid taxa have been reared from eggs, larvae, and pupae of *Neochlamisus* (D. Funk, unpubl. data). A few instances of parasitoids circumventing the case, by drilling through it and by successfully inserting the ovipositor through the case opening, have been observed in the field (DJF, pers. observ.). A need to avoid parasitism may thus influence when the case is to be sealed to the substrate.

Cases could also play some role in humidity control (minimizing water loss) (Karren, 1964) or thermoregulation (minimizing heat loss or gain). Cryptocephaline immatures have a light-coloured, soft abdomen that is largely lacking in sclerotization. The reduction in sclerotization may be an evolutionary consequence of case carriage – either as a result of relaxed selection on the maintenance of heavily sclerotized bodies, or perhaps via selection against the maintenance of energetically costly structures. In turn, however, such reduced sclerotization may result in increased vulnerability to ambient changes. It has been observed that humidity is important for hatching (Karren, 1972), that larvae quickly die once removed from cases (Karren, 1964), and that adult emergence is reduced under low humidity (Ellis & LeRoux, 1964).

Each of these hypotheses about the potential abiotic and biotic functional roles of cryptocephaline cases, and their relative importance, remain to be tested and evaluated. The role of these cases in governing the dynamics of interactions between *Neochlamisus*

host plants, the herbivorous beetles themselves, and their natural enemies would present one interesting path for future studies. Some of these hypotheses have been tested in other faecal-using chrysomelids, especially in Cassidinae, which employ faecal shields. Perhaps general patterns exist for the retention of faeces in several clades of Chrysomelidae, and for the particular structures that characterize each lineage.

PHYLOGENETICS OF CASE CONSTRUCTION AND ARCHITECTURE IN CHLAMISINI

The case-associated traits evaluated may offer phylogenetic character information that will be useful to further resolve *Neochlamisus* phylogeny (Funk, 1999; D. J. Funk, unpubl. data), and to study the evolution of case-associated biology in this group. Dominican amber fossils (C.S. Chaboo, unpubl. data) indicate that this complex camptostomate behaviour/construction dates at least to the Miocene (25 Mya). However, additional case-associated life history, behavioural, and morphological studies of comparable detail with those presented here and in Brown & Funk (2005) are needed in order to more generally evaluate the evolution of case-associated biology across camptostomates. Additionally, work is needed on the degree to which variation in case morphology represents genetically based differences in their inhabitants, rather than environmental circumstance. Although Chlamisini have been reviewed, with species keys, for particular regions (Gressitt, 1946; Monrós, 1951; Gressitt & Kimoto, 1961; Karren, 1966, 1972; Medvedev, 1989; Reid, 1991), and phylogenetic work on *Neochlamisus* is actively continuing, explicitly phylogenetic higher-level studies are lacking. Reid's (1990) cryptocephaline study is a useful point for initiating such work.

In comparing cases of *Neochlamisus*, Brown (1943: 121) stated 'larval cases may offer little in the way of characters'. However, the present paper highlights potentially informative camptostomate characters: such as presence, type, and arrangements of inclusions; case microstructure; plate arrangements and shape; construction behaviours; case-associated features of the adult female (kotpresse, glands, egg dimple, and sensory hairs) and larvae (head, leg, and anus morphology; abdominal shape and sclerotization); and host-associated chemistry in cases and beetles. A key factor in future comparative studies of these characters will be the accumulation and maintenance of a specimen collection. Fortunately, Chlamisini cases appear to be easily preserved and maintained in alcohol, although this affects the appearance of trichomes, which become matted. Nonetheless, the cases are remarkably durable, as demonstrated by museum specimens and the fossil record.

Fundamental questions that might be evaluated via the phylogenetic analysis of characters provided by this specimen collection include the following. How did such a complex structure, with its morphological, physiological, behavioural, and ecological aspects, originate? How has its function evolved through time? What role has been played by evolutionary cost-benefit trade-offs? It is difficult to imagine the sequence of evolutionary novelties that were necessary to transform a non-case-bearing phenotype into the ancestors of the cryptocephaline and lamprosomatine lineages, and thenceforth to the varied case-associated strategies we see today, but phylogenetic trait reconstructions might provide such insights.

LeSage (1982) pointed out that descriptions of chlamisine immature stages have been either too brief, too general, or included errors, and do not yet allow discrimination among chlamisine species. This could also be said for their cases. We hope that the detailed descriptions of the present study provide a model for further descriptions and additional avenues of research in Chlamisini and Cryptocephalinae. The faecal cases of the camptostomates are a marvel of integrated insect behaviour, and they offer a rich and exciting area for further research.

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