Maternal care in Australian oncomerine shield bugs (Insecta, Heteroptera, Tessaratomidae)[1]

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Abstract: Maternal care of eggs and nymphs is described in *Bromocoris* (Pentatomidae) and in five genera of Tessaratomidae (*Cumare*, *Garceus*, *Lyramorpha*, *Peltocopta* and *Stilida*) in Australia and new information is given on distribution and foodplants. Three of the genera (*Cumare*, *Garceus* and *Peltocopta*) show nymphal phoresy where the nymphs are carried on the modified body of the female for a period after hatching. It is proposed that maternal care in the Oncomerinae is partly a device to protect the vulnerable first instar nymphs before they moult to second instars which have morphological protection derived from their extremely flattened form.

Key words: Australia, Heteroptera, maternal care, nymphal phoresy, Oncomerinae, Queensland, Tessaratomidae.

Introduction

Several groups of shield bugs (pentatomoid Heteroptera) exhibit an unusual behaviour where the gravid female deposits her eggs in a close-packed group, usually glueing them to a plant surface such as the bark or a leaf, and then rests with her body over the top of the eggs in a protective manner until they hatch. The female does not feed during this period. In some species the female also remains with the newly hatched nymphs for a period after they hatch, and this may extend, in extreme cases, right up to the time that the mature nymphs are ready to moult to adults themselves. This protective, sub-social behaviour is generally termed "maternal care", "maternal solicitude" or simply "brooding" and there is a considerable literature on the phenomenon in pentatomoids and other Hemiptera which has been reviewed in works such as BEQUAERT (1935), MELBER & SCHMITT (1977) and TALLAMY & SCHAEFER (1997). Within the Pentatomoidea, this simple egg-guarding maternal care has been noted in several families including Acanthosomatidae, Cydnidae, Dinidoridae, Pentatomidae, Phloeidae, Plataspidae, Scutelleridae and Tessaratomidae.

One of the earliest detailed observations is that by the Australian pioneer naturalist, F.P. DODD (1904), who described females of the scutellerid, *Tectocoris diophthalmus* (THUNBERG), brooding batches of up to 60 eggs (Fig. 1). He noted that they turned their body towards an attacker when threatened and his observations were deemed so interesting at that time that a special colour plate was arranged by his wealthy patrons in London to illustrate his paper (MONTEITH 1991). Despite some earlier disbelief that this brooding behaviour by female bugs could have any functional benefit for their progeny (e.g., MILLER 1956), it is now well established, largely due to the elegant, experimental observations of EBERHARD (1975) on the pentatomid, *Antiteuchus tripterus limbativentris* RUCKES, that the female bugs actively defend their eggs against the attacks of parasitic wasps and other enemies. TALLAMY & SCHAEFER (1997) discuss the evolutionary significance of hemipteran

[1]Dedicated to Ernst Heiss on his 70th birthday, in fond appreciation of his contribution to hemipteran studies as scientist, collector, illustrator and gentleman.

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Fig. 1: *Tectocoris diophthalmus* (THUNBERG). Female brooding an egg mass laid around the petiole of a natural host, *Hibiscus tiliaceus* L. (Malvaceae). (Photo: J. Wright).

maternal care. They argue that it is an inherently inefficient system because of both the excess time investment of the female and the vulnerable nature of eggs being deposited in groups. They put forward the view that egg-guarding is a plesiomorphic behaviour retained in only a few unrelated taxa, and that most groups of modern Hemiptera have advanced to more efficient methods of egg protection, usually involving deposition of single eggs, often in concealed situations.

Some pentatomoids take the egg-guarding stage of maternal care a step further and the female carries the young nymphs on her body for some time after they hatch. This is referred to in this discussion by the convenient term "nymphal phoresy" which, although usually used for separate species, has been used previously in this context by MONTEITH (1998) and SINCLAIR (2002b). Nymphal phoresy is well-documented in the peculiar family Phloeidae, which has three large Neotropical species in the genera *Phloea* LEPELETIER & SERVILLE and *Phloeophana* KIRKALDY (LENT & JURBERG 1965). The adults are depressed in form and have the perimeter of the head, tegmina, thorax and abdomen remarkably expanded into flattened lobes which are inclined somewhat downwards, so that a broad, concave cavity is enclosed beneath the body. They are camouflaged in appearance and live on the trunks of certain trees where they suck sap from the bark. Females stand over batches of eggs laid on the bark surface. When the eggs hatch, the first instar nymphs climb onto the under surface of the female's abdomen where they cling upside-down with their dorsal surface towards the bark. When they moult to second instar, they leave the female permanently and feed independently on sap sucked from the bark, although the female remains near the family groups of nymphs. These large bugs are common in Brazil and have attracted attention from early times. Unfortunately, the fact that the phoretic nymphs face away from the bark has caused unsubstantiated speculation that the young nymphs must feed by piercing the body of the female (BRIEN 1930), or by feeding on sap being sucked by the mother (MARGALHÃES 1909), or even by feeding on secretions emitted from the female (POISSON 1951). Despite these suggestions being ridiculed by LESTON (1953) and not being supported by the observations of LENT & JURBERG (1966), the idea of phloeid nymphs feeding on their mother's body fluids was still being repeated as recently as TALLAMY & SCHAEFER (1997). However, the careful recent observations of GUILBERT (2003) failed to find evidence of any feeding by the first instars of *Phloea subquadrata* SPINOLA. Therefore it can be assumed that these phoretic first instar phloeids are non-feeding, as is the case with first instars of many other pentatomoids (MCDONALD 1963; EBERHARD 1975; CANT et al. 1996; this paper), and this is also the view of SCHUH & SLATER (1995).

Until very recently it has been assumed that, among pentatomoid bugs, nymphal phoresy was a Neotropical syndrome unique to the Phloeidae. However we now know that it also occurs in several taxa of the Tessaratomidae in the Indo-Australian region. The few records for the subfamily Tessaratominae pertain to the genus *Pygoplatys* DALLAS. GOGALA (1994) illustrates a female of an unidentified *Pygoplatys* species from Thailand carrying about 30 first instar nymphs on its abdomen. It was collected by beating and was kept alive briefly, during which it walked and flew while carrying the nymphs. GOGALA et al. (1998) provide photographs of another species, tentatively identified as *Pygoplatys acutus* DALLAS, guarding eggs in Peninsular Malaysia and carrying nymphs in Sabah. Egg-guarding

and subsequent nymphal phoresy have been observed for both *Pygoplatys minax* VOLLENHOVEN and a new species in Sumatra (Koen Smets pers. comm. 2002). From the photographs, it appears that *Pygoplatys* lays egg clusters of at least 30, rather small eggs. Unfortunately no information apart from the bare observations of these SE Asian records is available. In Australia, several instances of nymphal phoresy in the tessaratomid subfamily Oncomerinae have been referred to, but without supporting observations, by DODD (1904, 1916), MONTEITH (1998) and SINCLAIR (2002b). The purpose of this paper is to summarise these Australian records of extreme maternal care and to present available details and photographs.

Maternal care in the Oncomerinae

The Tessaratomidae is a family of 51 genera and about 240 species of medium to large, robust shield bugs (ROLSTON et al. 1993; SINCLAIR 2002a). Three subfamilies are recognised (SCHUH & SLATER 1995): the Natalicolinae are principally Ethiopian with one genus in India, the Tessaratominae occur in Asia-Indonesia with a few genera in Africa and Madagascar, while the Oncomerinae are mainly Australian. SINCLAIR (2002b) has recently reviewed the genera of Oncomerinae, their distribution and their food plants. Of the 15 genera and 57 species known, fully 12 genera occur in Australia with 6 of them restricted to this continent. Outside Australia, species of Oncomerinae are also diverse in New Guinea (7 genera) with a few taxa extending through the Indonesian archipelago to S.E. Asia. The only oncomerine genus occurring outside the Indo-Australian region is *Piezosternum* AMYOT & SERVILLE with species in Africa, Madagascar and South America. The subfamily includes some of the largest pentatomoids in the world, with species of *Oncomeris* LAPORTE reaching 44 mm in length (SINCLAIR 2002b).

The 18 known species of Australian Oncomerinae are catalogued by CASSIS & GROSS (2002). All are confined to the warm tropical/subtropical parts of Queensland and New South Wales and most species are rather rare in collections. An exception is the so-called Bronze Orange Bug, *Musgraveia sulciventris* (STÅL) (Fig. 2), which naturally feeds on native limes (*Citrus australis* (A.CUNN. ex MUDIE) PLANCH., *C. australasica* F. MUELL. and *C. glauca* (LINDL.) BURKILL). It has become a pest of cultivated citrus and on that host has extended its natural range considerably within Australia. It is the only species for which the biology is well studied and the extensive literature is summarised by CANT et al. (1996a, 1996b). Pairs mate in late summer, remaining in tail-to-tail copulation for about 4 days (Fig. 3). The abdomen is very deep in cross section and shows no flattening (Fig. 33a). Females lay clusters of 14 eggs (usually in regular rows of 3, 4, 4, 3, Fig. 4) on leaf surfaces in late summer/early autumn and there is no maternal care. Eggs hatch to stout, non-

Fig. 2: *Musgraveia sulciventris* (STÅL). Male on one of its natural hosts, *Citrus australasica* (Rutaceae). (Photo: J. Wright).

Fig. 3: *Musgraveia sulciventris* (STÅL). Mating pair with male to the left. (Photo: G. Monteith).

Fig. 4: *Musgraveia sulciventris* (Stål). Egg clutch of 14 eggs in standard rows of 3, 4, 4, 3. (Photo: A. Outteridge)

feeding first instars (Fig. 5) which cluster on or near the raft of eggs shells. They moult to thin, flat, green, semi-transparent, second instars which disperse among the leaves and go into camouflaged winter diapause. In spring they become active, feed and develop through to adults.

The first observer to publish records of maternal care in the Oncomerinae, including nymphal phoresy, was Frederick Parkhurst Dodd, the same observer who made the seminal observations on egg brooding in the scutellerid *Tectocoris diophthalmus* mentioned above (Dodd 1904). During his long residence in tropical north Queensland between 1899 and 1937, Dodd published several pertinant comments on other brooding pentatomoids, but usually the names of the species were unknown to him. For this reason they have been overlooked by most subsequent reviewers. However, with modern knowledge we can interpret some of these species. In the introduction to his 1904 paper Dodd writes: "*…about the month of June, 1901*, [Dodd lived at Townsville in 1901] *I took a large oval, flat, and pale-green bug upon one of our 'Bitter Barks'* , Petalostigma quadriloculare. *Adhering to her abdomen underneath were three or four young ones, certainly several days old; these dropped off several hours later, when placed in the killing bottle*". In 1916, then resident at Kuranda, Dodd sent specimens of various insects to London for exhibition on his behalf at a meeting of the Entomological Society of London by his correspondent, E.B. Poulton. Part of the text of the record of that meeting (Dodd 1916) is: "*4. Two pentatomid bugs which stay with their ova and larvae until they have grown considerably. The larvae of the larger species* (*Garceus fidelis* Dist.) *shelter upon the underside of the abdomen of their parent. I have not often met with this bug, but when I did come across a mother with young, they were never on the leaf, though I suppose they came down to feed.*" Later, in an unpublished handwritten manuscript of insect reminiscences (Dodd, undated) he writes (p. 90): "*We know half a dozen bugs which guard their eggs, staying with their young for days, two species allowing the young to crawl on to the body underneath for shelter.*" As shown below, we can now confirm on the basis of modern observations, that the two species he saw carrying nymphs are the oncomerines, *Cumare pallida* Blöte and *Garceus fidelis* Distant. Sinclair (2002b) confirms Dodd's observation of phoresy in *G. fidelis* by recording that "*four large nymphs were found adhered to the basal, ventral surface of a dead, pinned female from the NMNH* [Smithsonian] *collected in the early 1900s by J.F. Illingworth at Babinda in N. Queensland.*" Monteith (1998) briefly mentions, without details, records of nymphal phoresy in the oncomerines *Cumare pallida* and *Peltocopta crassiventris* (Bergroth) in the abstract of an oral conference paper. This abstract is cited by Sinclair (2002b) and Guilbert (2003). The foodplant of *Cumare* is

Fig. 5: *Musgraveia sulciventris* (Stål). Simultaneous hatching of ungarded egg clutch. (Photo: A. Outteridge)

Petalostigma (see below), confirming that this is the bug seen carrying its young by DODD (1904).

KUMAR (1969), in an important paper on Oncomerinae, describes the nymphs and gives brief life history observations for the following six species, mostly from the Brisbane district in SE Queensland: *Agapophyta bipunctata* GUERIN (no breeding information); *Erga longitudinalis* (WESTWOOD) (eggs laid in batches of 24-26); *Lyramorpha rosea* WESTWOOD (female guards eggs in batches of up to 42); *Musgraveia sulciventris* (no new information); *Peltocopta crassiventris* (eggs laid in batches of 16-23); *Stilida indecora* STÅL (female guards eggs and the first instars in batches of about 40; when disturbed, the brooding female "jumps forward" and discharges repugnatorial fluid). Kumar also records that the number of ovarioles per ovary is seven for all Oncomerinae studied. He also points out that the marked difference in body form between the stout first and highly flattened second instars is peculiar to the Oncomerinae. Kumar predates the views of TALLAMY & SCHAEFER (1997) in regarding maternal care and the laying of eggs in clusters as being plesiomorphic, and his 1969 paper is overlooked by them.

Observations

The following observations have been made on Australian species on a casual basis over a number of years. Most are simply field observations with some species having been kept alive for short periods in the laboratory. Taxonomic and distributional background for each species is given, as well as new maternal care observations. Observations are by the author unless stated otherwise. Voucher specimens are in the Queensland Museum, Brisbane.

1. *Bromocoris souefi* (DISTANT 1910) (Pentatomidae: Halyinae)

This tropical species is known from eastern Indonesia, New Guinea, Bismarck Archipelago and northern Queensland where its type locality is Cooktown (CASSIS & GROSS 2002). During April 2006 the species was found breeding in numbers on the tree *Brachychiton acerifolius* (A. CUNN. ex G. DON) MACARTHUR (Sterculiaceae) in Brisbane by Ms Katie Schuler, this being a new southern record for the species and the first recorded food plant. Observations were made on the trees and several brooding females were brought into the laboratory by the author for monitoring. Females guarded batches of usually 14 eggs laid in the 3, 4, 4, 3 pattern on the undersides of leaves (Fig. 6); egg batches were sometimes less but never more. During hatching, nymphs sometimes emerged on to the body of the female (Fig. 7). When all had hatched, the first instar nymphs remained as a tight group clustered on or beside the empty eggs, and the female continued to guard (Fig. 8). The female was very active in moving position to cover the eggs or nymphs when threatened

Fig. 6: *Bromocoris souefi* (DISTANT). Egg clutch of 14 eggs in standard rows of 3, 4, 4, 3, on the verge of hatching. Brooding female has been removed. (Photo: J. Wright).

Fig. 7: *Bromocoris souefi* (DISTANT). Female guarding egg clutch in the process of hatching. The first emerging nymph is temporarily on the body of the female. (Photo: J. Wright).

Fig. 8: *Bromocoris souefi* (DISTANT). Female guarding non-dispersing first instars after they have hatched. (Photo: J. Wright).

from any side, and she discharged repugnatorial secretion if threat continued. Neither she nor the first instar nymphs were seen to feed. As soon as the nymphs moulted to second instars the female left the group. The group of second instars remained around the eggs shells for a few hours (Fig. 9), then dispersed and began to feed on terminal stems of the plant. Dissection of a female taken in copulation showed seven well-developed eggs in each of the two ovaries. Each egg is in a separate ovariole. This species is not a tessaratomid but gives further evidence of the brooding of non-feeding first instars.

Fig. 9: *Bromocoris souefi* (DISTANT). Second instar nymphs abandoned by female after their moult and prior to dispersing away from the hatched egg shells. (Photo: J. Wright).

2. *Cumare pallida* BLÖTE 1945 (Tessaratomidae: Oncomerinae)

This species was described from a single male from Gayndah, in southern Queensland, by BLÖTE (1945) and its apparent rareness was commented on by LESTON & SCUDDER (1957) when they recorded a pair from Carnarvon Gorge, which is 300 km inland from Gayndah. In 1974, the author collected it on *Petalostigma pubescens* DOMIN (Euphorbiaceae) at Coen (13°57'S, 143°11'E), 1300 km further north. With the knowledge of its foodplant, *Cumare pallida* has since been collected at many sites over most of the eastern half of Queensland from the tip of Cape York to as far south as Noosa (26°24'S, 153°07'E). Near Mareeba and Kuranda, where F.P. Dodd lived from 1904, it occurs on both *P. pubescens* and *P. quadriloculare* F. MUELL.

Petalostigma is an Australian genus of seven species of shrubs and small trees of which *P. pubescens* also occurs in the region of the lower Fly River in southern New Guinea. They are known as "quinine trees" or "bitter barks" because of their extremely bitter sap. In the Queensland Museum there is a single female specimen of an undescribed, much larger species of *Cumare* from Kiunga on the Fly River in NG. Its food plant is expected to be *P. pubescens*.

Nymphal phoresy was first noted in *C. pallida* when a female was netted in flight in April 1987 at Auburn River National Park (25°43'S, 151°07'E), 50 km west of the Gayndah type locality. She had three first instar nymphs clinging to the underside of her abdomen. The species was found to be common on groves of *P. pubescens* at that locality and further observations were made then, at the same locality in April 1989, and at Granite Gorge (17°02'S, 145°21'E), near Mareeba, in February 1996. All observations are summarised in the next paragraph, illustrated by monochrome photographs taken in the field at Auburn River in April 1989.

Cumare pallida is oval in shape and uniformly pale green (Fig. 11). The leaves of *Petalostigma* are dark green on the upper side and pale on the underside. The bugs always rest on the pale underside of the leaves, pressed closely against the surface, and in

Fig. 10: The coccinellid beetle, *Synona seminigra* (WEISE), which predates on the early nymphs of *Cumare pallida* (Photo: G. Thompson).

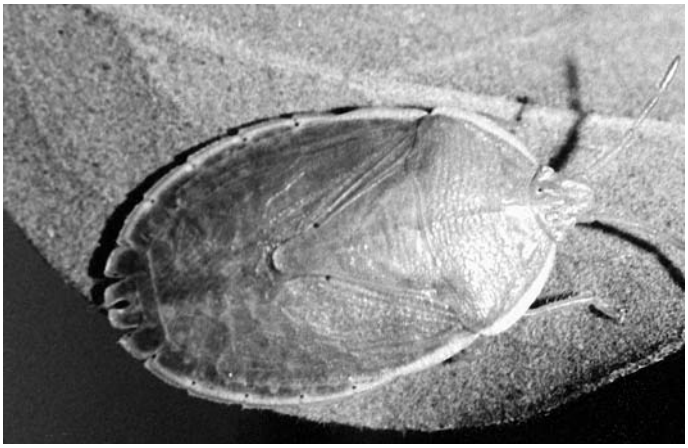

Fig. 11: *Cumare pallida* BLÖTE. Female on underside of leaf of its native foodplant, *Petalostigma pubescens* (Euphorbiaceae) (Photo: G. Monteith).

Fig. 12: *Cumare pallida* BLÖTE. Mating pair with male to right (Photo: G. Monteith).

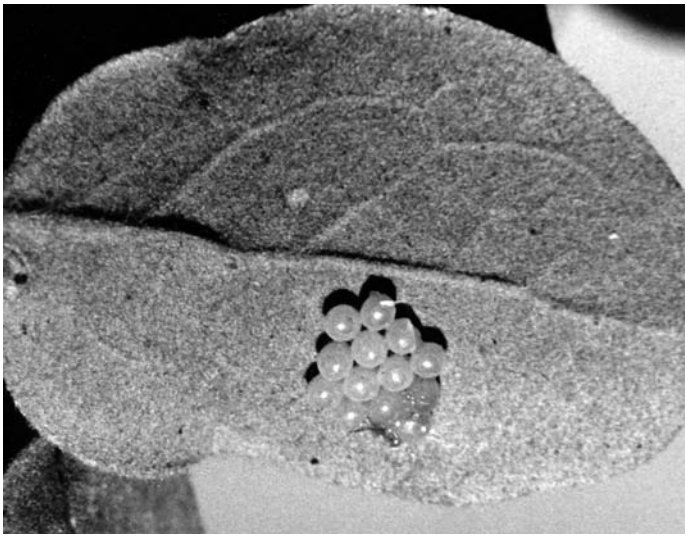

Fig. 13: *Cumare pallida* BLÖTE. Egg clutch of 14 eggs on underside of leaf. Brooding female removed (Photo: G. Monteith).

this situation they are very inconspicuous. They discharge their metapleural scent glands at the slightest disturbance and the strong odour often indicates their presence when searching foliage. The abdomens of both sexes are flattened, with that of the female underside being concave on either side of the slightly raised midline (Fig. 33c). Copulation takes place in the tail-to-tail position with the tip of the male's abdomen beneath the female (Fig. 12). Females lay batches of eggs on the underside of leaves. These are usually 14 in number and arranged in rows of 3, 4, 4, 3 (Fig. 13). Occasionally there are less than 14 and one cluster was seen with two rows of 5. Females brood the eggs until they hatch, the eggs being almost completely concealed from view by the body of the female. Males have been seen in copulation with egg-brooding females. When disturbed, the male separates from the female and flies off, but the female remains in the egg brooding position. The eggs hatch to sub-globular first instar nymphs which cluster on the underside of the female's abdomen (Figs 14, 15), sometimes in layers. She leaves the hatched eggs and roams freely with the first instars. Females carrying first instars have been seen to feed, to fly and to copulate with males. First instars do not leave the female and are apparently non-feeding. The first instars moult to second instars which remain on the body of the mother and are extremely flattened and thin (Figs 16, 17). They are sometimes in three layers on the female. The second instars have been seen to temporarily leave the female and disperse on the surface of the

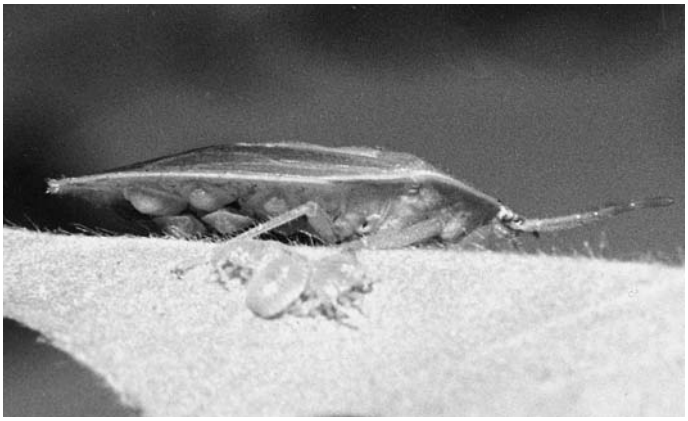

Fig. 14: *Cumare pallida* Blöte. Side view of female carrying batch of first instar nymphs under abdomen. Displaced nymphs on leaf in foreground (Photo: G. Monteith).

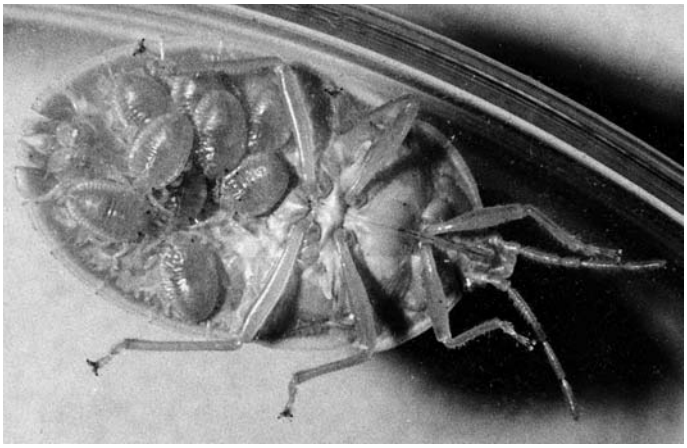

Fig. 15: *Cumare pallida* Blöte. Ventral view of female carrying first instar nymphs (Photo: G. Monteith).

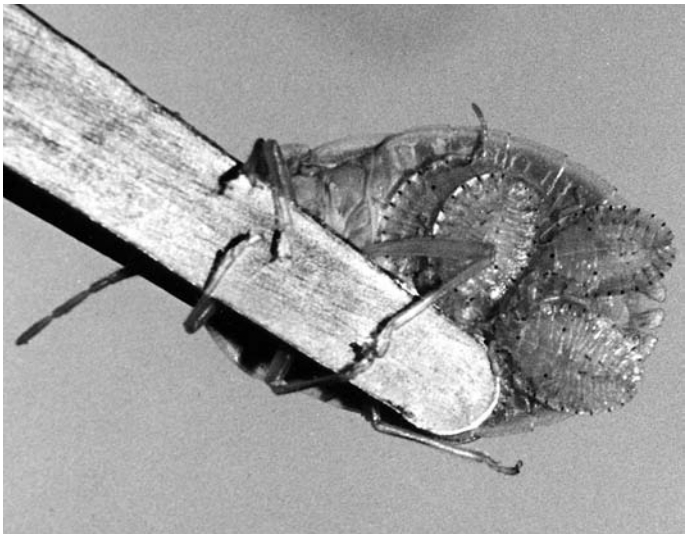

Fig. 16: *Cumare pallida* Blöte. Ventral view of female carrying second instar nymphs (Photo: G. Monteith).

Fig. 17: *Cumare pallida* Blöte. Female with second instar nymphs (Photo: G. Monteith).

Fig. 18: *Cumare pallida* Blöte. Free living fifth instar nymph (Photo: G. Monteith).

leaf near the mother, and then later return to the mother's body. On one occasion a male and female were seen together on a leaf together with 13 second instar nymphs. The female carried some of the nymphs on her body and others were dispersed over the leaf surface. When approached, the male flew away but the female remained with the nymphs. The leaf with the bugs on was picked and placed in a dry specimen vial. When examined at the end of the day, all nymphs (13) were clustered on the female's abdomen. All nymphs older than second instar live solitarily on the foliage, independent of the female (Fig. 18).

Two predators were seen eating *Cumare* nymphs at Auburn River. One was the large black coccinellid, *Synona seminigra* (Weise) (Fig. 10), a species known to feed on other pentatomoids (nymphs of Plataspidae) (Pope 1989), as does its congenor, *S. melanaria* in India (Iablokoff-Khnzorian 1982). The other was the mantid, *Archimantis latistyla* (Serville).

Fig. 19: *Garceus fidelis* DISTANT. Male (Photo: G. Thompson).

Fig. 20: *Garceus fidelis* DISTANT. Female (Photo: G. Thompson).

3. *Garceus fidelis* DISTANT 1893 (Tessaratomidae: Oncomerinae)

This species was originally described from "Peak Downs" (23°S, 148°E), which is an early-settled part of inland Queensland where vegetation is dry, sparse open woodlands. All subsequent localities recorded (DODD 1916; LESTON & SCUDDER 1957; KUMAR 1969; SINCLAIR 2002b; CASSIS & GROSS 2002) are wet rainforest localities on the lowland tropical coast between Cooktown (15°S) and Townsville (19°S). This suggests that the label data for the type material may be erroneus.

Garceus fidelis is uniformly pale greenish brown in life and ovate in shape (Figs 19, 20). Both sexes are moderately flattened but the female is not more so than the male (Fig. 33d). Incomplete records of nymphal phoresy in this species by DODD (1916) and SINCLAIR (2002b) have recently been substantiated by Mr. J. Hasenpusch who has discovered the species breeding on the "quandong tree", *Elaeocarpus grandis* F. MUELL. (Elaeocarpaceae), on his property at the western base of the Seymour Range (17°28'S, 146°01'E). Mr. Hasenpusch's notes with a specimen collected on 7 April, 1998 read: "*Female leaves the foodplant quandong, lays her eggs in a clutch on a nearby tree. Once emerged from the ova, they gather on the underside of female and are transported back to the female's foodplant.*" Clearly the female broods the egg clutch, but no information is available about clutch size or whether the nymphs stay on the female until the second instar.

Fig. 21: *Peltocopta crassiventris* (BERGROTH). Adult male on underside of leaf of its food plant, *Mallotus discolor* (Euphorbiaceae) (Photo: J. Wright).

Fig. 22: *Peltocopta crassiventris* (BERGROTH). Adult female (Photo: S. Wilson).

Fig. 23: *Peltocopta crassiventris* (BERGROTH). Two first instar nymphs beside hatched egg mass (Photo: J. Wright).

Fig. 24: *Peltocopta crassiventris* (BERGROTH). Nine second instar nymphs on underside of leaf (Photo: J. Wright).

4. *Lyramorpha (Lyrodes) parens* BREDDIN 1900 (Tessaratomidae: Oncomerinae)

This species is restricted to tropical north Queensland from the tip of Cape York south to Koumala (21°35'S, 149°11'E), whereas the more widespread smaller species studied by KUMAR (1969), *Lyramorpha rosea*, occurs along the southeastern coast from Victoria north to Mt Woowoonga (25°27'S, 152°06'E) in southern Queensland. The record for Adelaide given by (CASSIS & GROSS 2002) needs confirmation. Kumar cites *L. rosea* females brooding clutches of up to 42 eggs, but gives no other details of maternal care. I record here a female of *L. parens* collected on 1 November 1995 at the Seymour Range (17°28'S, 146°01'E) brooding 40 eggs. The egg mass was arranged in rows of 6, 6, 7, 8, 7, 6. No other information was obtained. Species of *Lyramorpha* show no flattening of the body to enhance brooding behaviour.

5. *Peltocopta crassiventris* (BERGROTH 1895) (Tessaratomidae: Oncomerinae)

This strange, rare species is truly enigmatic. Though its foodplant, the small tree *Mallotus discolor* F. MUELL. ex BENTH. (Euphorbiaceae), is common over a 1000 km range along the eastern Australian coast from Grafton in New South Wales to Proserpine in Queensland, *Peltocopta crassiventris* occurs in a narrow coastal strip of only 140

km at the southern end of that range, and has the smallest range of any Australian Oncomerinae. The region where it occurs is densely populated, the focus of much outdoor tourist activity, and has been extensively explored scientifically since the late 1800s. However, even though *P. crassiventris* is large and brightly coloured, it has been found at only four documented localities and collections have averaged only once every 30 years. Despite this apparent rarity, one occurrence was of large numbers in an urban hotel beer garden and persisted for several years. It's history of collection is worth recording.

The species was initially described as a new genus and species by BERGROTH (1895) from a single female sent to him by the then Victorian Government Entomologist, Charles French, and labelled simply "Queensland". Sixty years later, LESTON (1955) found a male labelled "N.E.Aust." in the British Museum from the Buchanan White Collection and, not recognising it, described it again under the name, *Chinatessa natalicoloides* LESTON. Buchanan White died in 1894, so that specimen was also collected in the 1800s. Anthony Musgrave, an hemipterist at the Australian Museum in Sydney, advised Leston of the probable synonymy with Bergroth's taxon and this was published by LESTON & SCUDDER (1957). Examination of the Australian Museum collection shows that Musgrave would probably have recognised the synonymy because that collection has a female specimen labelled "Wardell, Richmond River, NSW, Jan 1936, M.J.Geraghty"(28°59'S, 153°26'E) and identified by Musgrave. This is the first confirmed locality for the species. The species was not seen again for 35 years until 1961 when Ian Cunningham, then an entomology student at the University of Queensland in Brisbane (as was then the author), had a live one fall on his table while in the beer garden of the Chevron Hotel at Surfers Paradise (28°02'S, 153°26'E), a popular beach resort SE of Brisbane. Cunningham collected the specimen and submitted it to the university as part of his student collection. Fortuitously, his course lecturer was noted hemipterist, T.E.Woodward, who had been a colleague of Leston's in London, and was familar with the rarity and taxonomic uniqueness of *Peltocopta*. Woodward revisited the beer garden with Ray Kumar, then a doctoral student studying pentatomoid morphology, and they found a thriving colony of *P. crassiventris* on a native shade tree of *Mallotus discolor* overhanging the table, thus establishing the bug's food plant. Kumar revisited several times and later published studies on the morphology of adults and nymphs (KUMAR 1964, 1969) though, curiously, he mentions neither egg brooding nor nymphal phoresy. That colony persisted on that isolated tree in an urban area for several years and numerous specimens were collected, including more than 50 in November 1966 by T.G. Campbell of the Australian National Insect Collection. Most specimens in Australian and overseas museums are from that tree. Some, including the Campbell series, were collected from adjacent plants of *Eugenia* and *Cupaniopsis* and bear these labels as erroneous host records (KUMAR 1969). In the early 1970s the hotel (and the tree) were demolished for redevelopment and the whole area is now an urban cityscape. During that period a single specimen from another site was collected, a female in the Australian Museum labelled "Iluka, Clarence R., NSW, 22 Feb 1965, D.K.McAlpine" (29°24'S, 153°22'E). This locality is at the southern limit of distribution of the food plant.

Another 40 years passed before the species was found again in 1996 by D.J.Cook in the Upper Tallebudgera Valley (28°12'S, 153°20'E), a rural locality only 25 km SW of the Surfers Paradise site. Several *Mallotus* trees in semi-cleared habitats were found to have colonies. As expected, considering the highly modified morphology, they were found to be egg-brooders with phoretic nymphs. The following paragraphs summarise observation made by Mr Cook and the author during February 1996.

The sexes are highly dimorphic in colour, males having bright red tibiae on all legs and red blotches on the connexiva (Fig. 21); females are much more sombre, and lack red colour (Fig. 22). Much of their colour fades in pinned specimens. Adults and nymphs spend most of their time on the underside of the leaves which are pale and pilose. Females tend to rest quietly most of

Fig. 25: *Peltocopta crassiventris* (Bergroth). Ventral view of female carrying first instar nymphs (Photo: J. Wright).

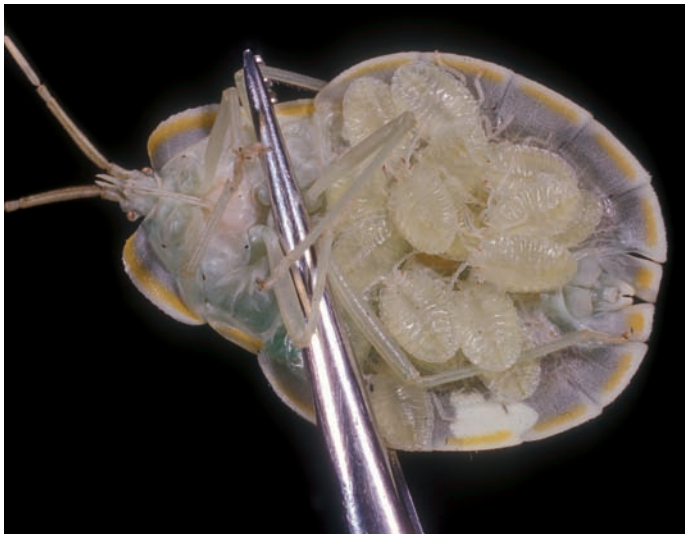

Fig. 26: *Peltocopta crassiventris* (Bergroth). Ventral view of female carrying first instar nymphs (Photo: J. Wright).

Fig. 27: *Peltocopta crassiventris* (Bergroth). Lateral view of female carrying first instar nymphs (Photo: J. Wright).

Fig. 28: *Peltocopta crassiventris* (Bergroth). Female carrying second instar nymphs (Photo: J. Wright).

the time, and are quite inconspicuous, while males are much more active and move from leaf to leaf frequently. Both sexes have the abdomen strongly expanded laterally, more prominently so in the female. The edges of the abdomen slope downwards so that the underside, particularly of the female, forms a large cavity (Fig. 33b).

The marginal explanation of the abdomen is so pronounced that the genitalia are displaced from the margin of the body (Figs 29, 30) with the male pygophore almost completely enclosed by incurved projections of segment VIII. This has the effect of making it difficult for male and female to oppose genitalia during mating (observed twice). It is achieved in an ungainly manner by both sexes elevating the abdominal apex high off the surface of the leaf (Fig. 31).

During a visit to the Upper Tallebudgera site on 18 February 1996, many specimens were noted on a low tree in a semi-open situation. These included a female brooding an egg batch, females carrying phoretic nymphs, a mating pair and several groups of hatched eggs (Fig. 23). Counts of five egg clutches were as follows: 39 in rows of 6, 7, 8, 7, 6, 5; 30 (4, 4, 5, 6, 6, 5); 24 (3, 4, 4, 5, 4, 4); 24 (3, 4, 4, 5, 4, 4); 28 (3, 4, 6, 6, 5, 4). A female brooding a clutch of eggs, which were in the process of hatching, was collected during the morning. Some stout, ovate first instars were already on her body. By the end of the day all eggs had hatched

Fig. 29: *Peltocopta crassiventris* (BERGROTH). Ventral apex of female abdomen (Photo: G. Thompson).

Fig. 30: *Peltocopta crassiventris* (BERGROTH). Ventral apex of male abdomen (Photo: G. Thompson).

and 22 nymphs were clinging to her abdomen in an overlapping cluster (Figs 25-27). This brooding female was returned to the laboratory and placed on a potted food plant for monitoring and photography. During the following week the female rested closely against the underside of a leaf. The first instar nymphs were seen to periodically leave the female and feed on the leaf, then return to the female's body. This feeding always took place beneath the shelter of the female's broad body and nymphs were seen to inflate to almost spherical shape during feeding. On the night of 27 February every nymph moulted to second instar. It was not seen if this took place on the leaf or on the female, but when first noticed all were on the female body. The second instars were highly flattened, semi-transparent and were in three layers on the female (Fig. 28). Two days after the moult, the first second instar was seen feeding on the leaf beneath the female's body. However such feeding was infrequent and the nymphs remained rather quiescent on the female. During handling for photographs on 15 March the female discharged her metapleural scent glands and all nymphs fell off. All specimens were returned to the plant but the nymphs never returned to the female which died on 14 April. The nymphs formed into immobile, non-feeding groups on the leaf undersides and, with the onset of winter, appeared to be going into diapause (Fig. 24). Observations were terminated about this time.

6. *Stilida indecora* STÅL 1863 (Tessaratomidae: Oncomerinae)

This species was originally described from the Brisbane area ("Moreton Bay") and occurs commonly in dry inland rainforest habitats from near Grafton (30°S) in northern NSW north to the Mareeba district (17°S) in northern Queensland. Records much further north (Torres Strait and Cape York) given by KUMAR (1969) and CASSIS & GROSS (2002) probably refer to the related species, *S. sinuata* STÅL, which has its type locality at Cape York. The Queensland Museum holds specimens of *S. sinuata* from Andoom (12°2'S, 141°51'E) and Iron Range (12°45'S, 143°15'E), both in central Cape York Peninsula well south of the type locality, but still 450 km distant from the known northern records of *S. indecora*.

Fig. 31: *Peltocopta crassiventris* (BERGROTH). Pair in copulation on foodplant in the field, male to the right (Photo: G. Monteith).

Fig. 32: *Stilida indecora* STÅL. Female brooding a mass of newly-hatched nymphs above an egg mass laid on the leaf of a natural host, *Arytera foveolata* (Sapindaceae) (Photo: J. Wright).

Recorded foodplants of *S. indecora* are trees and shrubs of the family Sapindaceae in the genera *Cupaniopsis*, *Arytera* and *Guioa* (KUMAR 1969; SINCLAIR 2002b). New sapindaceous foodplant records by the author are *Arytera foveolata* F. MUELL., *Alectryon connatus* (F. MUELL.) RADLK. (see below) and *Alectryon diversifolius* (F.MUELL.) S.T.REYNOLDS. There are records on cultivated *Citrus* in the early literature (FROGGATT 1901, 1907; TILLYARD 1926) which have been repeated in the modern catalogue of CASSIS & GROSS (2002). However as pointed out by CANT et al (1996a) these citrus records for *Stilida* are based on misidentification of the superficially similar citrus pest, *Musgraveia sulcipennis*, by FROGGATT (1901) and should be ignored.

Stilida indecora shows no body flattening in cross section as seen in other egg brooding species and is very similar in body proportions to *Musgraveia* (Fig. 33a). A female was found brooding a cluster of 42 eggs (in rows of 6, 7, 8, 8, 5) on a leaf of *Arytera foveolata* at Canungra Creek (28°03'S, 153°07'E) on December 27, 1995. When undisturbed she crouched low on top of the eggs. When threatened, she raised the body high on the legs and tilted away from the threat so that the metapleural scent gland on the threat side was directed upwards towards the threat. The glands were discharged if threat continued. She also buzzed her wings loudly, as if to take flight, while clinging firmly to the leaf. This created sudden noise, movement, display of the bright orange abdominal dorsum and a strong air current over the eggs. The leaf bearing the egg cluster and steadfast female was picked, taken to Brisbane and pinned to a garden *Cupaniopsis* shrub. She maintained her stance for seven days until all 42 eggs hatched overnight on January 3 to sub-globular first instars. Initially the first instars clustered on top of the eggs and beneath the female (Fig. 32). Over the next day or two all the first instar nymphs gradually dispersed away and the female remained guarding the empty eggs until January 9. There is a possibility that the first instars dispersed prior to moulting to second instars because the leaf on which they hatched was by then dry and withered. An indication that perhaps first instars do not normally disperse is given by a recent observation at Mt Pollux (22°28'S, 147°52'E) where large numbers of adults and nymphs were feeding on *Alectryon connatus*. However, although second instars were numerous feeding on shoots, no first instars were found dispersed independently on the plants.

Discussion

This paper, and those cited in the introduction, provide breeding information, sometimes fragmentary, for 7 of the 18 recorded species of Australian Oncomerinae. This limited sample shows a remarkable range of complexity, from those which simply lay eggs and abandon them (*Musgraveia sulciventris*), to those which lay eggs and brood them until they hatch (*Lyramorpha* and *Stilida*), to those which brood the eggs and then carry the hatching nymphs on their bodies for a time (*Garceus*, *Cumare* and *Peltocopta*). The females of those that carry their nymphs all have their bodies modified for the purpose. This involves flattening of the abdomen and extension of the connexival area outwards and downward to provide a concave surface beneath (Fig. 33). This concavity fits over the egg mass during brooding, and is the surface where the nymphs cluster after hatching. This abdominal modification is weakly expressed in *Garceus*, moderately so in *Cumare* and strongly so in the bizarrely-shaped *Peltocopta*. In *Cumare* and *Peltocopta*, the eggs or phoretic nymphs are completely enclosed and concealed from view when the female is adpressed against the leaf surface. The mod-

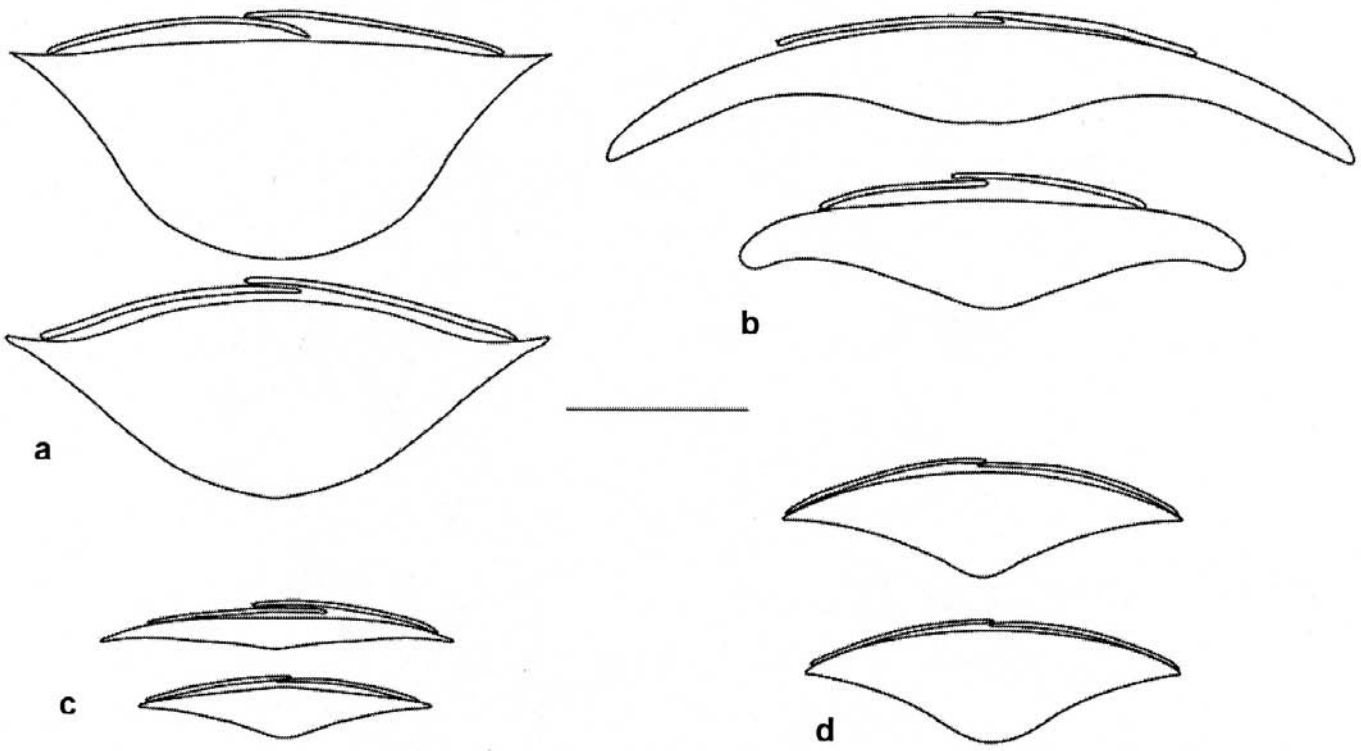

Fig. 33: Diagrammatic cross sections of abdomen and wings at mid length, female above, male below. Scale line is 5 mm. (a) *Musgraveia sulciventris* (STÅL) (b) *Peltocopta crassiventris* (BERGROTH) (c) *Cumare pallida* BLÖTE (d) *Garceus fidelis* DISTANT.

ification of the abdomen of *Peltocopta* resembles that of neotropical Phloeidae (LENT & JURBERG 1966; GUILBERT 2003). By contrast, the SE Asian phoretic species of *Pygoplatys* in the Tessaratominae show no abdominal modification and the phoretic nymphs are fully exposed on a convex abdominal surface (GOGALA et al. 1998).

All tessaratomids and most pentatomids have barrel-shaped eggs laid in groups. The clutch size of these egg depositions is important in discussions of reproductive success. KUMAR (1969) showed that all seven oncomerines he studied (including *Peltocopta*, *Musgraveia* and *Lyramorpha* from the present study), have 14 ovarioles and this seems to control the primary egg clutch number of 14 (i.e. one egg formed simultaneously by each ovariole). These are almost always laid in a regular group of four rows having 3, 4, 4, 3 eggs. This is seen in both *Musgraveia* (Fig. 4) and *Cumare* (Fig. 13) and MILLER (1956) reports the same for the Asian tessaratomine, *Pycanum ponderosum* STÅL. The pentatomid included in the present study, *Bromocoris souefi*, also laid the same arrangement (Fig. 6) but the brooding species of *Antiteuchus* studied by EBERHARD (1975) regularly laid 28 eggs per clutch, or two eggs per ovariole. For the well-studied, non-brooding oncomerine, *Musgraveia sulciventris*, it is known that females go on to lay 4-5 egg clutches per season, each of 14 eggs (CANT et al. 1996a, 1996b). TALLAMY & SCHAEFER (1997) argue that a major drawback regarding maternal care is the large time-investment of the female brooding when she could be feeding, mating and maturing more eggs. Therefore it can be argued that species showing maternal care need to lay larger clutches to justify the time spent by the female in brooding. This idea is supported by the fact that brooding oncomerines such as *Stilida* and *Lyramorpha* have clutch sizes of 40-42 (i.e. 3 eggs from each of the 14 ovarioles). The spectacular defence behaviour shown by *Stilida* females (wing buzzing, aposematic colour display, irritant spray) indicates the effort expended on protecting that large egg investment, which may be the female's total output of eggs.

A controlling factor for egg clutch number in the phoretic species is the area available on the female's body to accommodate the nymphs. In the small, moderately explanate species, *Cumare pallida*, the clutch size is the basic minimum of 14 and photographs show that the 14 nymphs need to rest

in several layers to fit on the female (Figs 15-17). However, the brooding female is not as inhibited from non-brooding activity as some evolutionary theoreticians might assume, e.g. TALLAMY & SCHAEFER (1997). Females of *Cumare* brooding eggs have been seen in copulation, and, once the eggs have hatched and the nymphs are on her body, feeding, flight and mating have been observed. Clearly, females have considerable "multi-tasking" capacity, and may well be able to produce subsequent egg clutches soon after shedding the current family of phoretic nymphs. The large phoretic species, *Peltocopta crassiventris*, produces clutches of 24-39 eggs and the greatly explanate body gives room to accommodate these (Figs 25-28).

A striking feature of oncomerine immature stages is the extremely flattened form of the intermediate stage nymphs, starting with instar 2 and lasting to instar 3-4. They are wafer-thin, almost transparent, and spend their time adpressed against the leaf surface with their vulnerable legs largely concealed beneath the expanded flat body (Fig. 24). In the centre of their dorsum are two powerful paired scent glands which produce pungent liquid if the nymph is disturbed. These nymphs are highly protected, and in this stage some species pass long periods of diapause. They contrast strongly with the first instars which emerge from the barrel-shaped eggs as soft, semi-globular, slow-moving forms which have a high profile above the leaf surface and often do not feed (Fig. 23). These first instars are very vulnerable. KUMAR (1969) points out that this remarkable metamorphosis of form from first to second instars is characteristic of the Oncomerinae. I suggest that the great range of maternal care in the Oncomerinae is a device, which has largely arisen to protect those vulnerable first instars before they moult to protected second instars. Nymphal phoresy provides the first instars with a protected refuge completely removed from the leaf surface. In many species the relatively immobile first instars are not sap-feeding. However, in the most advanced example of nymphal phoresy (*Peltocopta*), both first and second instars leave the female's body temporarily to feed, an advantage clearly facilitated by the extreme protection provided by the female's expanded body.

Acknowledgements

I am especially grateful to several excellent observers. Doug Cook discovered populations of the long lost *Peltocopta crassiventris* on his property at Tallebudgera Creek, and confirmed our suspicion that it would exhibit nymphal phoresy. Jack Hasenpusch found the host plant of *Garceus fidelis* on his property at Garradunga and saw that its early nymphs were also phoretic. Katie Schuler found *Bromocoris souefi* brooding nymphs in Brisbane when the final draft of this paper was being written. Jeff Wright, Steve Wilson and Adele Outteridge took excellent photographs of living insects. Geoff Thompson provided much graphic assistance with image editing and drawings. David Hanger donated potted plants of *Mallotus discolor* on which to maintain live *Peltocopta*.

Zusammenfassung

Das Brutpflegeverhalten der Weibchen von *Bromocoris* (Pentatomidae) und fünf Gattungen der Tessaratomidae (*Cumare*, *Garceus*, *Lyramorpha*, *Peltocopta* und *Stilida*) aus Australien wird beschrieben und neue Informationen zur Verbreitung und Nahrungspflanzen gegeben. Drei der Gattungen (*Cumare*, *Garceus* und *Peltocopta*) zeigen "Larven-Phoresie", bei der die Larven nach dem Schlüpfen eine gewisse Zeit vom Weibchen getragen werden. Es wird vorgeschlagen, dass dieses Brutpflegeverhalten der Oncomerinae einen Teil des Schutzes für die empfindlichen ersten Larvenstadien darstellt, bevor diese sich zum zweiten Larvenstadium häuten, in dem sie durch die stark abgeflachte Körperform einen morphologischen Schutz genießen.

References

Bequaert J. (1935): Presocial behavior among the Hemiptera. — Bull. Brooklyn Entomol. Soc. **30**: 177-191.

Bergroth E. (1895): Contributions to a knowledge of the Rhynchota of Australia. — Proc. R. Soc. Victoria (n.s.) **7**: 287-302.

Brien P. (1930): Notes sur *Phloea paradoxa* Burm. — Mission biologique belge au Brésil (1922-1923) **2**: 207-212.

Blöte H.C (1945): Catalogue of the Pentatomidae in the Rijksmuseum van Natuurlijke Historie. Part 1: Tessaratominae, Urolabidinae. — Zool. Meded. **25**: 285-316.

Cant R.G., Spooner-Hart R.N., Beattie G.A.C. & A. Meats (1996a): The biology and ecology of the Bronze Orange Bug, *Musgraveia sulciventris* (Stål) – A literature review. Part I. – Description, biology, host species and distribution. — Gen. Appl. Entomol. **27**: 19-29.

Cant R.G., Spooner-Hart R.N., Beattie G.A.C. & A. Meats (1996b): The biology and ecology of the Bronze Orange Bug, *Musgraveia sulciventris* (Stål) – A literature review. Part II. – Feeding, control, defensive secretions, pheromones, reproduction and aggregation. — Gen. Appl. Entomol. **27**: 30-42.

Cassis G. & G.F. Gross (2002): Hemiptera: Heteroptera (Pentatomomorpha). — In: Houston W.W.K. & A. Wells (Eds), Zoological Catalogue of Australia Vol **27**. 3B. CSIRO Publishing, Australia: xiv + 1-737.

Distant W.L. (1893): On new and little known Tessaratominae of the Order Rhynchota. — Ann. Mag. Nat. Hist. (6) **11**: 430-435.

Dodd F.P. (1904): Notes on maternal instinct in Rhynchota. — Trans. Entomol. Soc. London **1904**, part iii: 483-486, Plate 28.

Dodd F.P. (1916): Observations on various insects in N. Queensland. 4. Two pentatomid bugs which stay with their ova and larvae until they have grown considerably. — Trans. Entomol. Soc. London **1916**, part i: xxvii.

Dodd F.P. (undated): The Wonders of Entomology. — Unpublished, handwritten manuscript in Queensland Museum, 135 pp.

Eberhard W.G. (1975): The ecology and behavior of a subsocial pentatomid bug and two scelionid wasps: strategy and counter-strategy in a host and its parasites. — Smithsonian Contribut. Zool. **205**: 1-39.

Froggatt W.W. (1901): Notes on Australian Hemiptera. — New South Wales Agricultural Gazette **12**: 1596-1607.

Froggatt W.W. (1907): Australian Insects. — William Brooks & Co, Sydney: ix + 1-449.

Gogala M. (1994): Skrb za zarod pri stenicah iz družine Tessaratomidae. — Proteus **56**: 266-267.

Gogala M., Yong H.-S. & C. Brühl (1998): Maternal care in *Pygoplatys* bugs (Heteroptera: Tessaratomidae). — Eur. J. Entomol. **95**: 311-315.

Guilbert E. (2003): Habitat use and maternal care of *Phloea quadrata* (Hemiptera: Phloeidae) in the Brazilian Atlantic forest (Espirito Santo). — Eur. J. Entomol. **100**: 61-63.

Iablokoff-Khnzorian S.M. (1982): Les Coccinelles Coléoptères – Coccinellidae. — Société nouvelles des Editions Boubée, Paris: 1-568.

Kumar R. (1964): On the structure and function of the so called ejaculatory reservoir in Pentatomoidea (Hemiptera: Heteroptera). — Proc. R. Soc. Queensland **75**: 51-63.

Kumar R. (1969): Morphology and relationships of the Pentatomoidea (Heteroptera) IV. Oncomerinae (Tessaratomidae). — Aust. J. Zool. **17**: 553-606.

Lent H. & J. Jurberg (1965): Contribuição ao conhecimento do Phloeidae Dallas 1851, com um estudo sôbre genitalia (Hemiptera, Pentatomoidea). — Rev. Bras. Biol. **25**: 123-144.

Lent H. & J. Jurberg (1966): Os estádios larvares de *Phloeophana longirostris* (Spinola 1837). — Rev. Bras. Biol. **26**: 1-4.

Leston D. (1953): Phloeidae Dallas: Systematics and morphology, with remarks on the phylogeny of Pentatomoidea Leach and upon the position *Serbana* Distant (Hemiptera). — Rev. Bras. Biol. **13**: 121-140.

Leston D. (1955): A key to the genera of Oncomerini Stål (Heteroptera: Pentatomidae, Tessaratominae), with the description of a new genus and species from Australia and new synonymy. —Proc. R. Entomol. Soc. Lond. (B) **24**: 62-68.

Leston D. & G.G.E. Scudder (1957): The taxonomy of the bronze orange-bug and related Australian Oncomerinae (Hemiptera: Tessaratomidae). — Ann. Mag. Nat. Hist. **12**: 439-448.

Margalhães P.S. de (1909): Contribution a l'histoire naturelle des Phlées. — Mem. Soc. Zool. Fr. **22**: 234-260.

Melber A. & G.H. Schmidt (1977): Sozialphänomene bei Heteropteren. — Zoologica **127**: 19-53.

Miller N.C.E. (1956): The Biology of the Heteroptera. — Leonard Hill Limited, London: xii + 1-162.

Monteith G.B. (1991): The Butterfly Man of Kuranda - Frederick Parkhurst Dodd. — Queensland Museum, Brisbane: 1-32.

Monteith G.B. (1998): Bug bubs aboard! Nymphal phoresy in two genera of Australian Tessaratomidae (Hemiptera). — Australian Entomological Society 29th Annual General Meeting and Scientific Conference, University of Queensland, Brisbane. Abstracts and program, p. 25.

Poisson R.A. (1951): Ordre des Hétéroptères. — In: Grassé P.P. (Ed.), Traité de Zoologie **10**: 1657-1803.

Fig. 34: Female of *Agapophyta bipunctata* brooding eggs (Photo: J. Deckert).

Appendix

At the time of writing this chapter there were no records of egg-brooding in the oncomerine genus *Agapophyta*, though nymphs of *A. bipunctata* GUERIN were described by KUMAR (1969) who records its host as *Cassia fistula* L (Caesalpiniaceae). After this chapter was accepted, I received photographs of females of *A. bipunctata* on the same food plant taken by Dr. Jürgen Deckert, Museum of Natural History Berlin, near Daintree, northern Queensland, in February 2005. These show that this species does brood its eggs which are laid in the basic group of 14 in rows of 3,4,4,3 as seen in several other genera recorded in this chapter. I am most grateful to Dr. Deckert for permission to cite this information and to reproduce one of his photographs (Fig. 34).

POPE R.D. (1989): A revision of the Australian Coccinellidae. I. Subfamily Coccinellinae. — Invertebrate Taxonomy **2**: 633-735.

ROLSTON L.H., AALBU R.L., MURRAY M.J. & D.A. RIDER (1993): A catalogue of the Tessaratomidae of the world. — Papua New Guinea Journal of Agriculture, Forestry and Fisheries **36** (2): 36-108.

SCHUH R.T. & J.A. SLATER (1995): True Bugs of the World (Hemiptera: Heteroptera). Classification and Natural History. — Cornell University Press, Ithaca, New York: xii + 1-336.

SINCLAIR D.P. (2002a): Two new genera of Tessaratomidae (Hemiptera: Heteroptera: Pentatomoidea). — Mem. Queensl. Mus. **46** (1): 299-305.

SINCLAIR D.P. (2002b): A generic revision of the Oncomerinae (Hemiptera: Heteroptera: Tessaratomidae). — Mem. Queensl. Mus. **46** (1): 307-329.

TALLAMY D.W. & C.W. SCHAEFER (1997): Maternal care in the Hemiptera: ancestry, alternatives, and current adaptive value. — In: CHOE J.C. & B.J. CRESPI (Eds), The evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge, United Kingdom: 94-115.

TILLYARD R.J. (1926): The Insects of Australia and New Zealand. — Angus & Robertson, Sydney, Australia: xi + 1-560.

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