Entomologische Abhandlungen **62** (2): 99–116

Reproductive Biology and Nymphal Development in the Basal Earwig *Tagalina papua* (Insecta: Dermaptera: Pygidicranidae), with a Comparison of Brood Care in Dermaptera and Embioptera

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Abstract. Based on breeding cultures various behaviours, reproductive biology including maternal brood care, and nymphal development were studied in the basal dermapteran *Tagalina papua* de Bormans, 1903 (Pygidicranidae s.str.). Supplementary observations were made on *T. burri* Hincks, 1955, *Paracranopygia siamensis* (Dohrn, 1863) (Pygidicranidae s.str.), and an unidentified species of Diplatyidae. *T. papua* specimens did not display any courtship behaviour. In egg deposition gonapophyses VIII are used as a guiding device for the proper placement and upright positioning of the eggs. Eggs are fixed to the substrate in *Tagalina*, *Paracranopygia*, and the diplatyid, probably using secretions from the true accessory (colleterial) glands, which have been retained in most basal Dermaptera. Consequently, eggs cannot be transported and piled up, which in other Dermaptera is an important component of brood care. Brood care in *T. papua* consists in the association with and defense of eggs and 1st instar nymphs and the occasional control of the eggs by the mouth parts, but no egg cleaning was observed. Brood care is thus less elaborate than in all examined higher Forficulina. Arguments are provided why this simple pattern is plesiomorphic for Dermaptera. Due to the low complexity of behavioural patterns shared between Embioptera and the basal dermapteran *T. papua*, homology of brood care in Dermaptera and Embioptera is only weakly supported. *T. papua* almost consistently has six nymphal instars, which are here described. This is in contrast to conditions in higher Forficulina, where Anisolabididae and Labiduridae usually have five nymphal instars and Eudermaptera usually have four. However, due to occasional exceptions and intraspecific variation the number of nymphal instars does not yield autapomorphies in support of monophyletic higher Forficulina or Eudermaptera. Problems in the counting of nymphal instars in Dermaptera are discussed, with particular reference to the embryonic cuticle and its egg tooth, but a solution of this issue requires further data.

Key words. Dermaptera, Diplatyidae, Embioptera, *Paracranopygia*, Pygidicranidae, *Tagalina*, behaviour, biology, brood care, development, life history, nymph, reproduction.

Introduction

The Dermaptera comprise nearly 2000 described species (HAAS 2003). Among these the ca. 20 species of Hemimeridae and Arixeniidae are outstanding by their viviparity, epizoic life on Muridae (Rodentia) resp. Molossidae (Chiraptera), and, consequently, a peculiar external appearance. The remaining earwigs, which include the vast majority of species and are often comprised as the Forficulina, show except for the presence or absence of wings a fairly uniform habitus.

The majority of the forficuline species falls into one of the more derived families, the Apachyidae, Anisolabididae, Labiduridae, Forficulidae, Spongiphoridae, and Chelisochidae. These six groups together are here comprised as the 'higher Forficulina' and the three last-mentioned families constitute the Eudermaptera. Both the higher Forficulina and the Eudermaptera are most likely monophyletic – with the restriction that probably the Hemimeridae and Arixeniidae take a subordinate position within the higher Forficulina: Close relationships of Hemimeridae to Apachyidae and of Arixeniidae to Spongiphoridae have been proposed, but the evidence is not strong (POPHAM 1985; HAAS & KUKALOVÁ-PECK 2001; KLASS 2001; HAAS & KLASS 2003).

In addition, the Forficulina include a number of genera that display plesiomorphic states in many characters. They can be informally comprised as the 'basal Dermaptera' and have been classified either into a single family Pygidicranidae (s.l.; e.g., POPHAM 1985) or into three families, Pygidicranidae (s.str.), Karschiellidae, and Diplatyidae (e.g., HAAS & KUKALOVÁ-PECK 2001; herein followed). This assemblage is most likely strongly paraphyletic with regard to the higher Forficulina (HAAS & KLASS 2003), but the phylogenetic relationships among Karschiellidae, Diplatyidae, the nine subfamilies of Pygidicranidae (s.str.), and the higher Forficulina are still essentially unresolved (HAAS & KLASS 2003).

Details on the life history, behaviour, and nymphal development in forficuline earwigs are only known for a handful of species. Furthermore, the available data are almost completely limited to the higher Forficulina, while knowledge on the basal taxa Pygidicranidae, Karschiellidae, and Diplatyidae is extremely scarce. For instance, while Dermaptera are generally well-known for their maternal brood care, this has actually been demonstrated only for species of the higher Forficulina. Life-history, behavioural, and developmental data on the Pygidicranidae, Karschiellidae, and Diplatyidae would therefore be of great interest.

This is particularly true in the light of two recent publications that report an enormous diversity in the structure of the tarsi and the female genitalia in these basal dermapterans, which is likely to reflect a great diversity in the life-history traits and behavioural patterns functionally related to these body parts. The adhesive devices of the tarsi of members of the basal dermapteran families were found to vary greatly

concerning the presence or absence of arolia, widening of tarsomeres, euplantulae, and various types of adhesive setae (HAAS & GORB 2004). This suggests differences in the preferred substrate and related behaviours.

In the female genitalia (KLASS 2003a) structural variations concern the valves and basal sclerites of the ovipositor, the type of genital chamber, the spermatheca(e) (see also KAMIMURA 2004), and the accessory glands. There are plesiomorphic types of female genitalia among the ten selected exemplar species that are hardly changed as compared to the ground plan of Pterygota (e.g., in *Tagalina burri*). On the other hand, there is a variety of highly apomorphic types of female genitalia that show different combinations of reductions and specializations. This is in striking contrast to the strongly simplified or virtually undifferentiated (perhaps paedomorphic) female genitalic region in all examined higher Forficulina, Hemimeridae, and Arixeniidae. The anatomical diversity of the female genitalia probably reflects great differences in reproductive biology among basal Dermaptera. Most likely, many new facets of reproductive behaviour and functionality remain here to be discovered. Differences may also be present in terms of maternal brood care, if this is at all present in all the basal dermapterans.

Maternal brood care is a particularly interesting aspect of dermapteran life history (reviewed in GÜNTHER & HERTER 1974; LAMB 1976). The few higher Forficulina so far examined show a close spatial association of the mother with her eggs within a nest constructed for this purpose (a shallow depression, tunnel, or system of tunnels and chambers; rarely a leaf sheath, BRICEÑO & SCHUCH 1988), an intensive cleaning of the eggs using the mouth parts, an occasional transporting and rearranging of the eggs, an aggressive defense of these, as well as an aggregation of mother and first instar nymphs. In few species the mother helps her young with hatching, she has an intensive contact with the first instar nymphs via her mouth parts, defends them, and provides food for them. Much of the physiological background of maternal care and other reproductive behaviours has been explored in two species, *Labidura riparia* (e.g., VANCASSEL 1973, 1977, 1984) and *Euborellia annulipes* (e.g., RANKIN et al. 1995, 1996). With their behaviour of maternal care, Dermaptera are generally classified as subsocial (based on the definition of MICHENER 1969: 304 – though without the criterion of progressive feeding; EICKWORT 1981; CRESPI & CHOE 1997; see also TALLAMY & WOOD 1986). However, it has remained unknown which of the listed behavioural elements are present in the various groups of basal Dermaptera.

Embioptera is the only other basal pterygote order that is regarded as displaying brood care throughout (e.g., ROSS 2000; EDGERLY 1987, 1988, 1997; not considering here Isoptera, which are likely a subordinate clade of Blattaria; DEITZ et al. 2003; LO 2003; KLASS 2003b). The presence of maternal brood care in both Dermaptera and Embioptera has sometimes been considered as possibly supporting a close relationship between the two taxa (as a potential compound synapomorphy; e.g., KRISTENSEN 1991: 134). Through the lack of data on basal Dermaptera, however, it is presently not possible to tell which elements of the brood care were already present in the ground plan of Dermaptera; this would be a precondition for regarding such elements as potential synapomorphies of Dermaptera and Embioptera.

Just like brood care, the nymphal development of Dermaptera has also only been studied in higher Forficulina. The selection of study species is essentially the same as for brood care, though it is even a bit poorer (compare Tabs. 3 and 4). The papers by HERTER (1943, 1959, 1963, 1964, 1965a,b) provide the fundament for this issue, followed by a few other important contributions (e.g., BHARADWAJ 1966; CAUSSANEL 1966; KNABKE & GRIGARICK 1971). While these studies are altogether limited to five genera (*Forficula*, *Marava*, *Labidura*, *Anisolabis*, *Euborellia*), MATZKE (1997, 2000, 2002a,b) gave brief reports on the nymphal development in genera not considered previously, including tropical ones. While the earlier studies of HERTER and some others suggested a fairly clear pattern of four nymphal instars occurring in Eudermaptera, and five in non-eudermapteran higher Forficulina, the abovementioned later papers revealed a greater plasticity and intraspecific variation depending on environmental parameters. For instance, KNABKE & GRIGARICK (1971) in the anisolabidid *Euborellia cinctipes* found a range of four to eight nymphal instars depending mainly on temperature. This makes a phylogenetic evaluation of nymphal development quite difficult. In addition, data on Pygidicranidae, Karschiellidae, and Diplatyidae are needed to complete our picture of the evolution of nymphal development in Dermaptera.

A problem in counting the nymphal instars in Dermaptera is evident from HERTER's writings (e.g., 1965a,b). While for some species (e.g., *Forficula auricularia*) the hatchlings are stated to have an egg tooth on their head and leave a cuticle behind in the egg shell, both features are considered absent in other species (e.g., *Labidura riparia*). This led HERTER to the interpretation that the first nymphal instar is already completed with hatching in the former taxa and hatchlings represent the second instar; in the latter species the first instar persists until the first moult of the free-living nymphs, which occurs much later. Surprisingly, this issue has not been taken up in later contributions, and the question of the homology of post-hatching instars among different species is thus unresolved and problematic in the attempt to evaluate developmental data.

In this study we provide data on the behaviour, reproductive biology, and nymphal development of *Tagalina papua* (Pygidicranidae s.str.: Pygidicraninae). Some data for the congeneric *T. burri*, for *Paracranopygia siamensis* (Pygidicranidae s.str.: Pygidicraninae), and for an unidentified diplatyid are also included. Observations are based on breeding cultures that were kept over several years in case of the *Tagalina* species but were short-lived in case of *Paracranopygia* and the diplatyid. Our contribution is a first step towards filling the gaps in the knowledge on the life history of basal Dermaptera. We compare our data of *Tagalina* (and partly diplatyids and *Paracranopygia*) with those from higher Forficulina and infer on the dermapteran ground plan. The results are evaluated in terms of their phylogenetic implications, which can legitimately be based on life-history data (for limitations see LUCKOW & BRUNEAU 1997). Based on the discussion of the dermapteran ground plan we critically assess the features of brood care present in Dermaptera and Embioptera and the question of homology of brood care in these taxa. We also address the problems in terms of the interpretation and homologization of the earliest nymphal instars of Dermaptera.

Fig. 1. Adult female of *Tagalina papua*, having caught a cricket.

Materials and Methods

The specimens of *Tagalina papua* de Bormans, 1903 (Pygidicraninae) that served for founding our breeding culture were caught in mountainous rain forest (1400–1500 m asl) near Bokondini (03,7321°S 138,7030°E), West-Papua (Irian Jaya), on expeditions of the Phyllodrom e.V. (Leipzig, Germany) in 1998–2000. The collection included imagines and nymphs of instars V and VI. Some supplementary observations were made for *T. burri* Hincks, 1955 using a breeding culture based on specimens from near Kol (05,7245°S 144,8412°E, 1570 m asl, 24.ii.1997) in Papua New-Guinea. Cultures of both *Tagalina* species could be maintained for several years. Selected *Tagalina* specimens were identified by Fabian Haas. Some selected voucher specimens of different instars were deposited at the Museum für Tierkunde Dresden (Zoological Museum Dresden, MTD).

The single female of *Paracranopygia siamensis* (Dohrn, 1863) (Pygidicraninae) was collected on Sulawesi near Kotamobagu and Mogolingding (00,86308°N 124,44708°E, 820 m asl, 18.i.2001). The nymphs hatching from two egg clutches produced by the female died in their 2nd instar.

The two females of the diplatyid species we observed were also collected on Sulawesi, one near Kotamobagu and Mogolingding (00,86308°N 124,44708°E, 820 m asl, 18.i.2001), and the other near Tomohon (01,30869°N 124,79215°E, 676 m asl, 13–14.i.2001). Both females laid eggs that hatched, but unfortunately the mothers died soon after, and so did the nymphs after their first moult. The females were found quite decayed in their container. Identification to species was not attempted as this is impossible for female Diplatyidae with the available literature.

All species were taken in culture by D. Matzke. The living animals were kept in transparent plastic containers (minimal measures 130×100×70 mm): 1st instar nymphs pairwise, specimens from nymphal instar II onwards single. As a substrate we used coconut powder and clay granulate, usually mixed. Temperature was held at 24–26°C, air humidity at ca. 70–85 %. Food for the imagines of *Tagalina* was provided in form of crickets, which were usually slightly hurt. Leaves and/or pieces of bark were added to provide crevices. Many elements of the behaviour were documented using a video camera (Sony Video 8).

In terms of nomenclature on the species and generic level we follow STEINMANN (1989).

Results

Field observations

The specimens of *Tagalina papua* were found during daytime in mountainous rain forest between 1400 and 1500 m elevation, predominantly in leaf sheaths of *Musa* sp. (Zingiberales: Musaceae, banana plants) and cultivated *Freycinetia* sp. (Pandanales: Pandanaceae). In spite of intensive search, usually only a single specimen was found on each plant. When two specimens were found, these were usually male and female. The situation was the same for *T. burri*, except for rare cases where three specimens were observed on a single plant; these were always young nymphs (instars II or III). The specimen of *Paracranopygia siamensis* was also collected from a *Musa* leaf sheath. There are no field observations on the diplatyid species.

Some general observations from breeding cultures

The specimens of *T. papua* usually sit motionless in their crevices or tunnels, the head directed towards the entrance, from which the antennae slightly project. No differences between day and night were obvious with regard to the reactivity (e.g., contact with potential prey). If no material is offered to provide crevices, nymphs up to instar III dig a tunnel into the ground, with an inclination of ca. 30–40° and a depth approximately corresponding to body length. Animals of all instars clean themselves frequently and intensively. This includes dragging the antennae through the mouth parts and bending the anterior part of the body horizontally back towards the abdomen. Specimens of all instars are able to move vertically over smooth surfaces (plastic walls of containers; see also HAAS & GORB 2004). While young nymphs are usually agile, the animals become increasingly less mobile in later instars. Nymphs after instar I (i.e., after having left the nest shared with mother and siblings) are very aggressive against conspecifics. When two animals approach each other too closely, they attack each other, back to back with straight bodies, using the cerci and making rapid movements. At least in breeding cultures this can culminate in cannibalism, one specimen grasping the other with the cerci and devouring it. Since older nymphs usually stay in their locations, such aggression may be an aspect of territoriality. This agrees with field observations: there were never found more than three specimens per plant.

Feeding and diet

T. papua is exclusively zoophagous, any vegetal substances are rejected. The animals are essentially ambush predators. Potential prey is attacked when it reaches a minimum distance, about antenna length. *Tagalina* first contacts the prey with its mouth parts, perhaps testing the suitability of the prey, and then rapidly bends over its abdomen and grasps the prey with the cerci (Fig. 1). It remained unclear whether contacting the prey with the antennae is required or whether visual recognition is sufficient for triggering the attack. When the prey manages to escape the grip of the cerci, the earwig follows it, intensively moving its antennae, and then again contacts it with the mouth parts and grasps it with the cerci. An imago can subdue prey that is slightly more massive than itself (such as crickets). Nymphs of instars I–III were observed to catch and eat psocopterans. The acceptance of dead insects (sliced larvae of *Tenebrio molitor*, Coleoptera: Tenebrionidae) was limited.

Mating

Males and females of *T. papua* are approximately of the same size. Any kind of courtship behaviour was never observed. Our observations suggest that mating can be initiated either by the male or the female. Provided that both partners are in the mood for mating, the male pushes its cerci beneath the subgenital plate of the female, and the genitalia come into contact. If one partner is not inclined to mate, it aggressively rejects the other, beating with its cerci. In one case mating occurred between a male and a female that had viable eggs 1–2 weeks old (hatching of nymphs observed). Copulation lasts 14–20 h, with partners back to back in straight posture. When disturbed, they do not separate but try to move away jointly, one partner dragging the other behind it. Occasionally joint movements are made without disturbance. In the breeding cultures males survived mating for 4–26 days.

Oviposition, hatching, and young nymphs

For laying eggs, female *T. papua* search a crevice or dig a trough of about body length; small stones were removed using the mandibles. The whitish, smooth, ellipsoid eggs (Figs. 2, 3) are initially ca. 1.5 mm long and 1.3 mm wide; we did not measure the increased size (compare KNABKE & GRIGARICK 1971: 171ff; HERTER 1964: 8) of the older eggs. The eggs are usually attached singly onto smooth surface (stone, container wall) near the margins of the trough. Their arrangement is mostly irregular, though sometimes partly in rows. The usual distance between the eggs is 0.2–2 × the width of an egg (Fig. 3), but some eggs can be quite remote from the main cluster. It takes 4–11 days until all 40–80 eggs are laid. 2–4 eggs are laid in a sequence, following each other closely. We observed that the two gonapophyses VIII of the ovipositor (1st valves; gp8 in KLASS 2003a: figs. 27, 28), which project far from the vestibulum (= space above the subgenital plate, coxosternum VII), act jointly as a guiding device for the eggs. The eggs approach their attachment site along the dorsomesal face of the gonapophyses. Gonapophyses VIII also serve for the upright positioning of the eggs upon the substrate. The function of the short and hidden gonapophyses IX (2nd valves) and gonoplacs (3rd valves) was not observed.

Shortly after the deposition of an egg, a collar-like brownish structure is seen around the base of the egg (Fig. 4, sec in Fig. 13; also seen in *T. burri*, Fig. 5), which fixes the egg to the substrate. It is thus probable that together with the egg some adhesive secretion is deposited, which makes the egg stick to the substrate and soon hardens. We assume that this secretion comes from the accessory glands of abdominal segment IX (ag in KLASS 2003a: fig. 28), whose orifice in the dorsal wall of the vestibulum must be passed by each egg when laid, and which is present in both *Tagalina* species. Eggs attached to the substrate are difficult to remove without destroying them. Occasionally the mother ate single eggs; possibly these had no viable embryo.

In our diplatyid species and in *Paracranopygia siamensis* we could not observe oviposition but we found the laid eggs (Figs. 6–10). These also have a basal collar formed from some hardened secretion and fixing the egg to the substrate. The collar in *P. siamensis* (Fig. 8) resembles that in the *Tagalina* species. In the diplatyid, however, this collar is additionally extended into a short stalk (Fig. 10). The presence of accessory glands has not yet been examined for *P. siamensis*. From Diplatyidae two species have so far been examined in this respect: *Diplatys macrocephalus* (Palisot de Beauvois, 1805) and *Haplodiplatys orientalis* Steinmann, 1974 in KLASS (2003a: figs. 36–45). While in the latter species the accessory glands are well developed, they are vestigial, though perhaps still functional, in the former. It appears plausible that the secretion for the egg stalk comes from the accessory glands, though we do not know the degree of development of the glands in our species of Diplatyidae.

Nymphs of *T. papua* hatched 12–33 days after egg deposition. Near the end of embryonic development the eggs

Figs. 2–4. Eggs of *Tagalina papua*. **2**: Egg clutch and some 1st instar nymphs; the mother has died. **3**: Part of egg clutch; dark spots on eggs are compound eyes of embryo. **4**: Mature egg, dark spots are compound eyes (lateral) and cerci (mesal; dark setae) of embryo; dark secretions for attachment visible at base of egg; brown patches beside the egg are secretions of eggs already hatched and shells eaten. **Fig. 5.** Eggs of *Tagalina burri*; eggs on left and right sides attacked by fungus; secretions for attachment visible at base of all eggs. **Figs. 6–8.** Eggs of *Paracranopygia siamensis*. **6**, **7**: Mother with part of egg clutch. **8**: Part of egg clutch, dark secretions for attachment visible at base of some eggs. **Figs. 9–10.** Eggs of the diplatyid here studied. **9**: Mother with part of egg clutch. **10**: Some eggs with stalk-like dark secretions for attachment visible at base.

Tab. 1. Measurements and antennomere number in *Tagalina papua* specimens of different instars, all from breeding cultures. Measurements taken from living or freshly died specimens.

	I	II	III	IV	V	VI	Imago
no. of specimens	24	13	8	12	10	10	15
head width HW [mm]	1.1	1.2–1.3	1.7–1.9	2.1–2.5	2.8–3.1	3.2–3.6	3.8–4.3
body length BL [mm]	8–9	9.5–10	13–15	16–19	20–25	26–29	29–36
no. antennomeres AM	8	15	17–20	22–24	25–26	26–28	28–30

slightly enlarge and change their shape, as the embryo becomes increasingly pressed against the egg shell. About 4–6 days before hatching, outline and segmentation of the whitish embryo as well as the dark pigmented eyes are recognizable through the almost transparent egg shell (Figs. 11, 12). Somewhat later the one-segmented, clasper-shaped cerci, which bear dark setae, become visible (Figs. 13, 14). The embryo takes the same position as is known for *Labidura riparia* (CAUSSANEL 1966: figs. 3, 4): curved, with the head and tip of abdomen pointing into the same direction (away from the point of attachment in *T. papua*, Figs. 11–14). The presence of an egg tooth on the frons of the head was vaguely indicated in some photographs (et? in Fig. 11), but further confirmation is required. During hatching the egg shell ruptures irregularly in its upper part (i.e., opposite to the point of attachment). It remained unclear whether or not the embryo moults during hatching, but we noted that the freshly hatched nymphs lack an egg tooth. The nymphs of the whole egg clutch sequentially hatch within several days, surmisedly in correspondence with the sequence the eggs had been laid.

After ca. 1 h the hatched, still very pale nymphs (Fig. 2) have become quite agile and eat the egg shell. For ca. 6–7 days they remain aggregated around the former egg clutch. Like older animals they rest almost motionless most of the time, but in contrast to these they occasionally start running around or conduct quick movements. The situation is the same irrespective of whether the mother is present or not (in some cases the mother had died prior to the hatching of the nymphs). When disturbed, the nymphs run away and disperse; after 5–10 min all have reassembled in the same place. Only shortly before their first moult they disperse permanently. Then, from the 2nd instar onwards, the animals usually react aggressively (see above) when meeting each other.

Maternal care of eggs and young nymphs

In *T. papua* the mother usually remains few centimetres beside the egg cluster or aggregated 1st instar nymphs, and she does not go foraging. Once or twice per day she rapidly whisks her mouth parts over the eggs. This can hardly include a cleaning of the eggs or an application of secretions to them, but more likely serves for detecting non-viable eggs or for controlling the clutch after disturbance. A more intensive treatment of the eggs with the mouth parts did not occur. Since the eggs are firmly attached to the substrate, the mother cannot transport or rearrange them or pile them up more densely as other earwigs do; eggs always remained at their initial point of deposition. The mother did not show any particular interest in the hatching of her nymphs, nor did she help the hatching nymphs in any way. Neither do the 1st instar nymphs experience any special attention or care by their mother. There is no physical contact through any body part, such as the mouth parts, and no nourishment for the nymphs is provided. The most essential aspect of brood care in *T. papua* likely consists in the guarding of the egg clutch and aggregated 1st instar nymphs. An artificial threatening of the eggs or nymphs occasionally remained unnoticed by the mother, but in other cases she attacked using her cerci.

Eggs and 1st instar nymphs developed normally if located far from the main cluster and mother (maximum distance observed: ca. 20 cm) and even if the mother had died after egg deposition. Consequently, in *T. papua* care by the mother is not indispensable for the brood as reported for other Dermaptera (see GÜNTHER & HERTER 1974: 123).

Based on a single copulation preceding the production of the first egg clutch, three of the *T. papua* females produced a second egg clutch when the nymphs from the first had reached the 2nd or 3rd instar (2–3 months after production of first egg clutch). One female produced a third clutch, but no nymphs hatched. Thus, with a single copulation sufficient sperm is present in the spermatheca (KLASS 2003a: fig. 28 for *T. burri*) for at least two egg clutches. However, the number of eggs per clutch was consistently decreasing in all three females (70/58; 48/30; 56/50/45).

Nymphal development

Our counts of nymphal instars are based on two sources of evidence: (1) The exuviae of freshly moulted nymphs could be secured in most cases, and from the 2nd instar onwards they could be ascribed to a certain individual because these were kept singly. Nymphs usually eat their exuviae, but with some delay because first the new cuticle of the mandibles must harden. (2) In the nymphs we regularly measured head width (HW: maximal width of head including compound eyes) and body length (BL: from tip of labrum to tip of cerci) and counted antennomeres (AM) (Tab. 1). We note that body length gradually increases within a given instar, because the abdominal intersegmental membranes expand with increasing body mass. In addition, variation in antennomere number may partly reflect damaging of antennae and subsequent regeneration (see HERTER 1960: 219, 1964: 16, 1965b: 435ff for these problems). In the three parameters we used we found almost no overlap between the values for the different instars (Tab. 1), but we note that more overlap may be revealed with a greater number of specimens examined (as, e.g., in BHARADWAJ's 1966 study of *Euborellia annulipes*, tabs. 5–7 therein).

Based on both methods (1) and (2) we consistently counted 6 nymphal instars for both *T. papua* and *T. burri* (instars I–VI) – with the sole exception of 7 nymphal instars in a single specimen of *T. papua* (with all exuviae secured). Specimens that correspond with the two final instars as described below were also caught in the field.

Tab. 2. Duration of nymphal instars and entire nymphal development (hatching from egg until imaginal moult) in some *Tagalina papua* specimens from breeding cultures. All entries in days. Temperature 24–26 °C, air humidity 70–85 %.

Specimen	I	II	III	IV	V	VI	Sum
#1 female	19	24	23	17	69	41	193
#3 female	19	23	50	19	25	29	165
#6 female	18	19	24	49	29	45	184
#7 male	23	30	11	33	29	39	165
#8 male	20	45	21	30	30	52	198
#9 male	22	20	37	21	31	49	180
#17 female	27	38	26	29	65	37	222

Development from hatching to the imaginal moult takes about half a year (Tab. 2). By keeping nymphs singly we could observe individual differences in the duration of nymphal instars. These were partly striking in spite of all nymphs being kept under uniform conditions. Sexes did not noticably differ in the time needed for development. Nymphs of all instars lack pretarsal arolia, which are present in the adult, but all have ventroterminal euplantulae on the 1st and 2nd tarsomeres.

Instar I. BL 8–9 mm, HW 1.1 mm, AM 8 (Fig. 15). Dark grey to black, but the following parts yellowish to greyish white: palps, hind margin of pro- and metanotum, posteromedian part of abdominal terga 3–5, basal and distal 1/4 of cerci, legs except for basal 1/2 and tips of femora. Antennae whitish basally, increasingly darkened greyish distally.

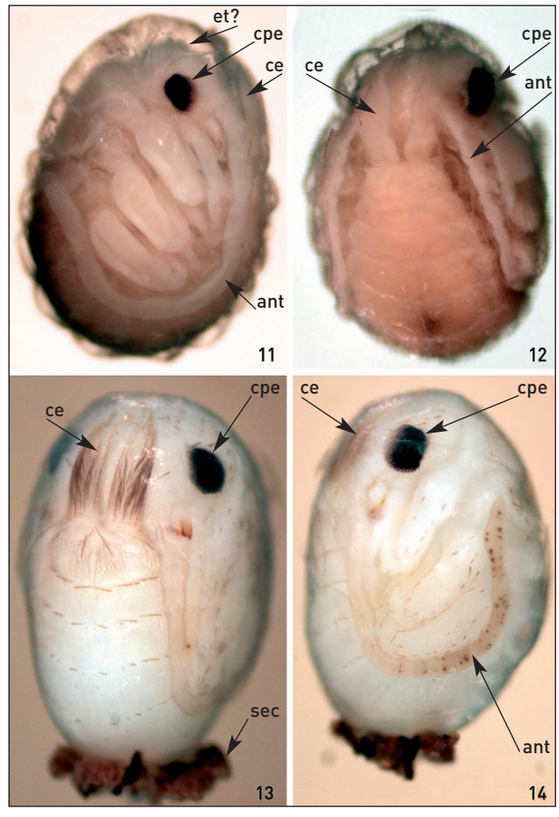
Instar II. BL 9.5–10 mm, HW 1.2–1.3 mm, AM 15 (Fig. 16). Colouration as in preceding instar, but antennae yellowish brown basally and darker grey distally, mouth parts yellowish brown, legs more strongly darkened, and tips of cerci brown beyond white distal 1/4.

Instar III. BL 13–15 mm, HW 1.7–1.9 mm, AM 17–20 (Fig. 17). Colouration as in preceding instar.

Instar IV. BL 16–19 mm, HW 2.1–2.5 mm, AM 22–24 (Fig. 18). Colouration as in preceding instar, but hind margins of abdominal terga 3–5 yellowish only around middle (particularly narrow on tergum 5), distal 1/4 of cerci reddish to brownish (no whitish colouration in distal part of cerci).

Instar V. BL 20–25 mm, HW 2.8–3.1 mm, AM 25–26 (Fig. 19). Colouration as in preceding instar, but antennae not darkened distally, posteromedian part of head whitish to brownish, on pronotum brighter colouration expanded anteriorly in median part; dorsal side of abdomen with continuous bright colouration from posterior part of tergum 2 to tergum 8, this colouration changing in anteroposterior direction from yellowish brown to reddish brown; basal 1/4 of cerci yellowish brown, tips of cerci darker.

Instar VI. BL 26–29 mm, HW 3.2–3.6 mm, AM 26–28 (Fig. 20). As compared to preceding instar entire posterior half of head yellowish brown, on pronotum only a pair of far lateral, irregular longitudinal ribbons as well as anterior margin dark, mesonotum yellowish brown, only two narrow oblique ribbons near middle and the lateral margins dark brown, metanotum yellowish brown, only the rudiments of the hind wings and the lateral margins dark brown; in addition, a narrow dark median stripe extends along the entire thorax; bright dorsal colouration of abdomen expanded anteriorly to 1st segment, joining bright colouration of thorax; cerci uniformly dark brown or with reddish-brownish basal 1/4.



Figs. 11–14. Embryos of *Tagalina papua* in mature eggs in lateral view (11, 14) and oblique ventral view (12, 13); the embryo in Figs. 13, 14 likely represents a somewhat later stage than that in Figs. 11, 12, visible by the dark setation of the cerci in the latter; ant = antenna; ce = cercus; cpe = compound eye; et? = egg tooth (doubtful identification); sec = dark secretions for attachment at base of egg. Photos by Fabian Haas (Staatliches Museum für Naturkunde Stuttgart).

Imago. BL 29–36 mm, HW 3.8–4.3 mm, AM 28–30 (Fig. 21, male). As compared to the last nymphal instar femora not darker basally than distally; dorsal side of abdomen (almost) as dark as lateral and ventral sides; cerci uniformly dark brown; see Fig. 21 for colouration of fore wings.

Discussion

General aspects of reproductive biology

Our observation that in *Tagalina papua* mating can be initiated by either sex complies with reports for other Dermaptera (e.g., *Forficula auricularia*; Günther & Herter 1974: 115). Dermaptera usually display some courtship behaviour, which includes, e.g., mutual contact via antennae and mouth parts or more complex behaviours (mainly) of the male. These can differ strongly among the studied species. Examples are slow side-to-side movements of the abdomen, vibration of the entire body, and nipping the female's cerci or legs using the cerci (e.g., Günther & Herter 1974: 115ff; Briceño & Eberhard 1995: 45ff; Matzke 1997; Bharadwaj 1966). In *T. papua*, however, we

Figs. 15–21. Nymphal instars and adult male of *Tagalina papua*. **15**: 1st nymphal instar. **16**: 2nd nymphal instar. **17**: 3rd nymphal instar. **18**: 4th nymphal instar. **19**: 5th nymphal instar. **20**: 6th nymphal instar. **21**: Adult male.

could not observe any courtship behaviour at all. In the way copulation is initiated after contact between the postabdomina as well as in the posture taken during copulation (back to back, with straight bodies) *T. papua* conforms with other Dermaptera (see, e.g., KNABKE & GRIGARICK 1971: fig. 11).

The duration of copulation varies widely in Dermaptera. The maximum was reported for *Forficula auricularia* (up to 14 h; HERTER 1965b: tab. 2). The shortest known durations were observed in *Euborellia plebeja* (1–8 min; KAMIMURA 2000), *E. annulipes*, and *Anisolabis maritima* (15 resp. 20 min, GÜNTHER & HERTER 1974: 117). It appears unlikely that the "few seconds" reported by KNABKE & GRIGARICK (1971: 167) for part of their *E. cincticollis* specimens can concern successful copulations. For some species considerable variation has been reported, e.g., 6 min to almost 9 h in *Diplatys flavicollis* (KAMIMURA 2004), and 9 min to 7 h in *Marava arachidis* (HERTER 1943). In *T. papua* (14–20 h) copulation is very long for a dermapteran.

According to (HERTER 1943: 165) it is quite unusual for Dermaptera that a copulating pair moves away jointly when disturbed as observed in *T. papua*. In other Dermaptera partners mostly separate immediately (various papers by HERTER), but joint movements have also been reported for, e.g., *Euborellia cincticollis* (KNABKE & GRIGARICK 1971). Copulations during brood care, observed once in *T. papua*, have also been reported for various other Dermaptera.

With 40–80 eggs the size of a single egg clutch in *T. papua* is about the same as in most higher Forficulina (GÜNTHER & HERTER 1974: 120). In the ovoviviparous *Marava arachidis* (15–27 eggs; GÜNTHER & HERTER 1974: 120) as well as in *Hamaxas nigrorufus* (20–25 eggs; MATZKE 2000), *Apterygida media* (10–30 eggs; MATZKE 2002b), and *Auchenomus javanus* (10–20 eggs; MATZKE 2002a), however, egg number is constantly lower (at least in the respective breeding cultures). The potential of a single adult female to produce several egg clutches over a longer period of time is normal for Dermaptera (e.g., HERTER 1965a; LAMB 1976; KNABKE & GRIGARICK 1971). However, exceptions occur in regions with short vegetation periods (GÜNTHER & HERTER 1974; GUPPY 1950) and are correlated with a different structure of the ovaries (details in VANCASSEL 1984). It has also been reported that several clutches can be produced from a single copulation (e.g., KLOSTERMEYER 1942). Nonetheless, especially in such cases the number of eggs per clutch can decline in later clutches. Multiple mating is generally common, and KAMIMURA (2003) has shown for *Euborellia plebeja* that it increases the number of egg clutches produced by a female as well as the proportion of viable eggs. We did not examine this aspect for *Tagalina*. We also note that breeding conditions can affect the egg number per clutch (KNABKE & GRIGARICK 1971: 168).

The whitish, smooth, ellipsoid appearance of the eggs, their transparence near the end of their development, the very dark compound eyes contrasting the pale remainder of the embryo (or near-to-hatch nymph), and the lack of a discrete mechanism for the opening of the egg shell (such as an operculum) complies with conditions reported for other oviparous Dermaptera (e.g. GÜNTHER & HERTER 1974).

The variable duration of egg development that we found in *T. papua* (12–33 days) corresponds with the results of KNABKE & GRIGARICK (1971) for *Euborellia cincticollis*. These authors found considerable differences in the time of development (7–15 days) with relatively minor changes in temparature. HERTER (1965a) hypothesized that a species specific amount of temperature over time is needed for the completion of embryonic development, and he presented a mathematical correlation between temperature and the duration of embryonic development. According to his graphs, small changes in the mean temperature can strongly change the duration of development if temperature is close to the minimum (i.e., the temparature below which no development can occur; also species specific). We thus assume that the temparature we used in our cultures was close to the minimum temperature for *T. papua*.

Prior to reproduction females of all examined Forficulina species construct a nest, which either consists of a low trough, or of a short tunnel, or of a system of tunnels and chambers. In our breeding cultures *T. papua* consistently formed a low trough, but the structure of the substrate we provided did not permit the construction of some tunnel, so that the natural condition of the nest remains unclear. Aspects of nest building in Dermaptera are surveyed in LAMB (1976) and not further considered here.

Comparative aspects of brood care

Comparison among different Dermaptera. Brood care has so far been described only for members of the higher Forficulina – with a single notable exception: A female of *Syndiplatys greeni* (Burr, 1904) (Diplatyidae) from Ceylon has been reported to stay with its freshly laid eggs. However, no further information is provided (data from Green in BURR 1910: 13f; likely the basis for the often-repeated statement in CHOPARD 1949: 761 of brood care occurring in a "*Diplatys* de Ceylan").

In the previously studied higher Forficulina maternal brood care includes the following components (survey and references in Tab. 3; construction of nest not considered): (1) Association of mother with her eggs: The mother usually sits above the eggs, more rarely closely beside the eggs. This nearly always includes a reduced nourishment (LAMB 1976); only rarely the eggs are left for foraging, or food is stored at the nest prior to egg deposition. (2) Cleaning of eggs: The single eggs are subjected to extensive licking with the mouth parts, which probably includes the application of secretions (SHEPARD et al. 1973). This probably serves for both humidification and desinfection, mainly against fungus (KNABKE & GRIGARICK 1971; GÜNTHER & HERTER 1974: 123; BUXTON & MADGE 1974). In *Labidura riparia* the fore tarsi are also involved in egg cleaning (CAUSSANEL 1970: 606). (3) Transport of eggs: The laid eggs are taken up using the mandibles and palps (LAMB 1976) and are transported to a suitable place within the nest, where they are piled up. Under unfavourable circumstances (e.g., drought) several species have been observed to move the eggs to a more suitable (e.g., more humid) part of the nest, or into another nest. *Forficula auricularia* was observed to rearrange the eggs of a pile into a single layer prior to hatching (LAMB 1976). (4) Defense of eggs: When the eggs are threatened the mother usually reacts with an attack using her cerci. (5) Association of mother with her aggregated 1st instar nymphs and (6) their defense: The relationships of the mother to her young nymphs are of varied intensity and include several aspects. Frequently the mother sits immediately above her nymphs, more rarely at some distance beside them. The mother either hardly cares about the nymphs (e.g., *Apterygida media*, *Guanchia pubescens*), or (7) she actively keeps the nymphs together, grasps and transports them, and, if escaped, returns them into the group (e.g., *Anechura bipunctata*, *Chelisoches morio*, *Labidura riparia*, *Euborellia annulipes*).

The following elements of brood care have been observed in few higher Forficulina but are surely absent in some others: (8) By feeding part of the egg shell, the mother helps the nymphs when hatching. This was observed in *Labidura riparia* (CAUSSANEL 1966: 473) and the ovoviviparous *Marava arachidis* (HERTER 1943: 171); surely absent in *Forficula auricularia* (LAMB 1976). (9) A frequent contact between 1st instar nymphs and the mother's mouth parts is found in *Marava arachidis* (HERTER 1943: 172), *Chelisoches morio* (MATZKE 1997), *Forficula auricularia* (LAMB 1976), and *Labidura riparia*. It is unresolved whether this is only social contact or includes the transfer of nutrients; the demonstrated transfer of radioactive markers (^{32}P) in *L. riparia* (SHEPARD et al. 1973) suggests the second alternative at least for this species. It has been reported for few species that (10) the mother provides 1st instar nymphs with food (*Anechura bipunctata*, *Anisolabis maritima*, *Forficula auricularia*) or guides them to food

sources (*Chelidura pyrenaica*). (11) Young nymphs of *E. annulipes* have been reported to sit occasionally on the mother's back (THIAGARAJAN 1939).

In cases of strong disturbance mothers have frequently been reported to eat their eggs (e.g., KLOSTERMEYER 1942; SHEPARD et al. 1973; KNABKE & GRIGARICK 1971). The duration of the period the nymphs stay with their mother varies: Nymphs may leave already few days after hatching, or they may stay until shortly before their moult into the 2nd instar. In few species the association between mother and nymphs extends into the 2nd nymphal instar (*Euborellia annulipes*, *Forficula auricularia*: LAMB 1976); this also includes species that produce only a single clutch of eggs (e.g., *Anechura bipunctata*; VANCASSEL 1984: 59). In non-gregarious species older nymphs are attacked and eaten by the mother (e.g., CAUSSANEL 1966).

With regard to brood care *Tagalina papua* differs in two aspects (2 and 3 above) fundamentally from all examined higher Forficulina: (3) Because in *T. papua* the eggs become firmly attached to the substrate immediately after their deposition, they cannot be transported, piled up, or rearranged by the mother. This is surely the most substantial difference. *T. burri*, *Paracranopygia siamensis*, and the diplatyid species we examined also fix their eggs to the substrate, and no transport of eggs was ever observed. (2) The cleaning of the eggs is at least much less extensive or, more likely, is entirely absent: The mother only occasionally and briefly touches the eggs with her mouth parts; this is unlikely to effect cleaning but rather seems to be a control, which is also known from higher Forficulina (recognition of non-viable eggs by means of olfactory sensilla located on palps, see GÜNTHER & HERTER 1974: 124). Explicit cleaning behaviour was neither observed in *T. burri*, *Paracranopygia siamensis*, and the diplatyid. However, since we did not watch these as carefully as *T. papua*, such behaviour may have been overlooked. The behavioural elements listed under (7)–(11), which mostly only occur in few higher Forficulina, are also missing in *T. papua*. In terms of the components (1), (4), (5), and (6), i.e., the association of the mother with the eggs and 1st instar nymphs as well as their defense, *T. papua* is within the behavioural range found in the examined higher Forficulina; the intensity of these elements is rather low (position of mother beside eggs or nymphs, no consistent reaction to threats). In the dissociation of the nymphs near the end of the 1st instar *T. papua* also corresponds with most higher Forficulina.

The attachment of the eggs to the substrate in *Tagalina*, *Paracranopygia siamensis*, and our diplatyid is probably correlated with the plesiomorphic presence of an accessory gland in abdominal segment IX of the female (groundplan element of Dicondylia; KLASS 2003a: 215), which was found in most examined Pygidicranidae s.str. – including *T. burri* (KLASS 2003a: ag in fig. 28) and *T. papua* – as well as in Karschiellidae and some (but not all) Diplatyidae (KLASS 2003a; conditions unknown in *P. siamensis*). We assume that, as in many other insects, the accessory gland yields the secretion for the attachment of the eggs – though an experimental demonstration is still missing. The accessory gland has never been reported for any species of higher Forficulina, and its absence has been shown for *Forficula auricularia* (KLASS 2001, 2003a), *Anisolabis maritima* (GILES 1961a: 294), *Labidura riparia* (BHATNAGAR & SINGH 1965b), and *Hemimerus vosseleri* Rehn & Rehn, 1935 (KLASS 2001). The gland has probably become lost at the basis of the higher Forficulina (compare phylogenetic tree of this group in HAAS & KLASS 2003: fig. 1; condition in Apachyidae unknown).

When eggs are firmly attached to the substrate, their targeted deposition is much more important than in cases where a later transport of the eggs is possible. Therefore we suggest a further correlation between the fixation of the eggs and the retention of a plesiomorphic ovipositor in the *Tagalina* species (KLASS 2003a: figs. 27–31 for *T. burri*; similar in *T. papua*). The ovipositor consists of long gonapophyses VIII, short gonapophyses IX, and stout gonoplacs IX. This configuration is also to be assumed for the dermapteran ground plan (KLASS 2003a; see therein for ovipositors of other Pygidicranidae). We could directly observe gonapophyses VIII as they guided and directed the eggs. Gonapophyses IX, which in the ground plan of Dicondylia extend all along gonapophyses VIII and form an egg channel together with these, bridge in *Tagalina* the area where the accessory glands open. They may have the function to prevent the eggs from slipping away laterally and to secure a proper distribution of the secretions over the eggs. Ovipositor structure in an unidentified species of *Paracranopygia* was found to closely resemble that in *Tagalina* (Klass, unpublished results). However, *P. siamensis* was not studied in this regard.

The Diplatyidae studied by KLASS (2003a: figs. 36, 41) also have a complete ovipositor, but all three valve pairs (gonapophyses VIII and IX, gonoplacs IX) are fairly short and end within the vestibulum. Still, the valves may well be capable of specifically directing the egg in order to position it properly. Furthermore, in these diplatyids the gonapophyses IX, which have their bases immediately beside the orifice of the accessory glands and project posteriorly from there, have a peculiar lobe-like shape. These structures appear suitable to shape, within the vestibulum, an egg stalk from the still viscuous, glutinous gland secretions, as present in the species we studied.

The lack in *Tagalina papua* (and perhaps in the other pygidicranids and diplatyids we studied) of an extensive treatment of the eggs with the mouth parts might also be correlated with the presence of accessory glands. Egg "cleaning" in higher Forficulina likely plays a role in the desinfection of the eggs (see above), and eggs isolated from their mother are frequently destroyed by fungus. In some other insects it has been shown that structures produced (mainly?) from the secretions of the accessory glands include defensive chemicals (e.g., egg stalks in Neuroptera, see DETTNER & PETERS eds. 1999: 591, produced by accessory/colleterial glands – see NEW 1989: 67 – homologous to those in basal Dermaptera). Thus, it appears possible that in basal Forficulina chemicals limiting the attack by fungus are added to the egg by the accessory glands, but after the loss of these a "cleaning" behaviour evolved to replace this kind of defense. This, however, is rather speculative in view of the lack of biochemical analyses of the egg surface or stalk in basal and higher Forficulina, and eggs were also occasionally attacked by fungus in our *Tagalina* breeding cultures (Fig. 5). We also note that most Pygidicranidae (s.l.) (including *Tagalina burri* and one of the studied diplatyid species) have paired internal tubes (tl in KLASS 2003a: figs. 24, 28, 33, 43, 47) that are closely associated with the accessory glands and whose function is unknown. They may well be glandular and are thus another possible source of defensive secretions.

Species	Family	AE	FE	CE	TE	DE	HH	AN	DN	GN	CN	FN	Sources
Tagalina papua (de Bormans, 1903)	Pygidicranidae	++	++	—	—	++	—	++	++	––	—	––	this paper
Tagalina burri Hincks, 1955	Pygidicranidae	++	++	?	—	?	?	++	?	?	?	?	this paper
Paracranopygia siamensis (Dohrn, 1863)	Pygidicranidae	++	++	?	—	++	?	++	?	?	?	?	this paper
Diplatyidae sp.	Diplatyidae	++	++	?	—	?	?	++	?	?	?	?	this paper
Anisolabis maritima (Bonelli, 1832)	Anisolabididae	++	—	++	++	++	—	++	++*	++	—^{0}	++	G&H, RJL, HERTER (1959), GUPPY (1950), MUP
Anisolabis littorea (White, 1846)	Anisolabididae	++	—	?	++	++	?	++	?	++	?	?	G&H, RJL, GILES (1953)
Euborellia annulipes (Lucas, 1847)	Anisolabididae	++	—	++	++	++	?	++	?	++	?	?	G&H, RJL, THIAGARAJAN (1939), BHARADWAJ (1966), KLOSTERMEYER (1942), RANKIN et al. (1996)
Euborellia cincticollis (Gerstaecker, 1883)	Anisolabididae	++	—	++	++	++	—	++	?	++	?	?	RJL, KNABKE & GRIGARICK (1971)
Euborellia plebeja (Dohrn, 1863)	Anisolabididae	++	—	?	++	++	?	++	?	?	?	?	BAIJAL & SRIVASTAVA (1974)
Nala lividipes (Dufour, 1820)	Labiduridae	++	—	++	++	?	?	++	?	?	?	?	SITUMORANG & GABRIEL (1988)
Labidura riparia (Pallas, 1773)	Labiduridae	++	—	++^{1}	++	++	++	++	––^{0}	++	++	++	G&H, RJL, HERTER (1963), CAUSSANEL (1966, 1970), RADL & LINSENMAIR (1991), SHEPARD et al. (1973), TAWFIK et al. (1972), VANCASSEL (1973, 1977)
Allostethus celebense Burr, 1911	Labiduridae	++*	—*	++*	++*	++*	—*	++*	++*	––*	—*	––*	MUP
Marava arachidis (Yersin, 1860)	Spongiphoridae	++	—	x	x	x	++	++	++	++	++	++	G&H, HERTER (1943)
Auchenomus javanus (de Bormans, 1883)	Spongiphoridae	++	––*	++*	++*	++*	––*	++*	++*	––*	—*	—*	MATZKE (2002a), MUP
Hamaxas nigrorufus (Burr, 1902)	Spongiphoridae	++	—*	++?	++	++	—*	++	++*	++*	—*	––*	MATZKE (2000), MUP
Labia minor (Linnaeus, 1758)	Spongiphoridae	++	—	++	++	++	?	++	?	++	?	?	MOURIER (1986)
Chelisoches morio (Fabricius, 1775)	Chelisochidae	++	—*	++	++	++	—	++	++	++	++	––	MATZKE (1997), MUP
Apterygida media (Hagenbach, 1822)	Forficulidae	++	—*	++*	++*	++*	—*	++*	++*	––*	—*	––*	MATZKE (2002b), MUP
Chelidurella guentheri (Galvagni, 1994)	Forficulidae	++	—	++	++	++*	—*	++	?	++	?	?	VERHOEFF (1912), HARZ (1958, 1960), MUP
Forficula auricularia Linnaeus, 1758	Forficulidae	++	—	++	++	++	—	++	++	++	++	++	G&H, RJL, HERTER (1965a,b), VERHOEFF (1912), WEYRAUCH (1929)
Forficula tomis (Kolenati, 1846)	Forficulidae	++	?	++	?	?	?	++	?	?	?	?	PESOTSKAJA (1927) fide RJL and G&H
Forficula lesnei Finot, 1887	Forficulidae	++	—	++	++	++	—	++	++	?	++	?	TIMMINS (1995)
Forficula senegalensis Serville, 1839	Forficulidae	++	?	?	?	?	?	++	?	?	?	?	BAOUA BOUKARY et al. (1996)
Guanchia pubescens (Géné, 1837)	Forficulidae	++	—	++	++	++	—	++	––^{0}	––^{0}	—^{0}	––^{0}	HERTER (1964, 1965a)
Doru taeniatum (Dohrn, 1862)	Forficulidae	++	—	++	++	++	++	++	?	?	?	?	BRICEÑO & SCHUCH (1988), RANKIN et al. (1996)
Anechura bipunctata (Fabricius, 1781)	Forficulidae	++	—	++	++	++	?	++	?	++	?	++	G&H, HARZ (1960), STÄGER (1930)
Pseudochelidura sinuata (Lafresnaye, 1828)	Forficulidae	++	?	?	?	?	?	++	?	?	?	?	GADEAU DE KERVILLE (1931)
Chelidura pyrenaica (Bonelli, 1832)	Forficulidae	++	?	?	?	?	?	++	?	?	?	++	G&H, GADEAU DE KERVILLE (1907), XAMBEU (1903)

Tab. 3. Components of brood care in species of Dermaptera. AE = association of mother with eggs; FE = fixation of eggs on substrate; CE = intensive cleaning of eggs with mouth parts (and fore tarsi in addition[1]); TE = transport or rearrangement of eggs; DE = defense of eggs; HH = helping nymphs in hatching by feeding part of egg shell; AN = association of mother with young 1st instar nymphs; DN = defense of young 1st instar nymphs; GN = grasping of young 1st instar nymphs with mouth parts, including retrieval of escaped ones; CN = contact with mouth parts between mother and young (feeding of nymphs with body secretion or social contact?); FN = supply of nymphs with food, or guiding nymphs to food source; ++ = present; — = absent; x = not applicable (ovoviviparous species); ? = no data available. Many data were extracted from the summary descriptions in GÜNTHER & HERTER (1974) = G&H and LAMB (1976) = RJL (see therein for further references); a further source of data are unpublished observations by D. Matzke = MUP (entries marked with *); data from PESOTSKAJA (1927) were adopted fide G&H and RJL. HERTER (various papers) reports absence of any maternal care conducted upon 1st instar nymphs (HH, DN, GN, CN, FN) in *Anisolabis maritima*, *Labidura riparia*, *Forficula auricularia*, and *Guanchia pubescens*; this has been revised for some of these species by later authors; untested absence data from HERTER are marked[0]. *Chelidurella guentheri* (Galvagni, 1994) = *Chelidura acanthopygia* (Géné, 1832); *Euborellia annulipes* (Lucas, 1847) = *Euborellia stali* (Dohrn, 1864); *Chelidura pyrenaica* (Bonelli, 1832) = *Chelidura dilatata* (Burmeister, 1838). The paper by SITUMORANG (1978) on *Nala lividipes* is not accessible to us.

Considering these correlations with plesiomorphic morphological conditions (presence of accessory glands and complete ovipositor), the lack of any transport and piling-up of eggs and possibly the lack of extensive egg cleaning appear as conditions plesiomorphic for Dermaptera. Egg transport and perhaps the cleaning of eggs are brood care elements having evolved within Dermaptera. We assume that the attachment of the eggs was given up and the accessory glands reduced in favour of an intensified brood care including transport of eggs to more favourable conditions (ability to react upon changes in environmental parameters such as humidity). An ovipositor was then no longer required because (1) the proper positioning of the eggs was done after their initial deposition, and (2) there was no gland secretion any more that needed to be distributed properly over the egg surface.

Comparison between Dermaptera and Embioptera. Besides the Dermaptera, the Embioptera are another insect taxon whose representatives display maternal brood care throughout. Occasionally the presence of brood care was tentatively proposed as a potential synapomorphy of these two taxa (e.g., KRISTENSEN 1981: 145, 1991: 134). Further characters could be added in support of this relationship, whereas other important characters suggested different ordinal relationships (see KRISTENSEN 1991) and thus contradicted the assumption of brood care being homologous in Embioptera and Dermaptera. The characters obtained as synapomorphies of Embioptera and Dermaptera in the cladistic analysis of BEUTEL & GORB (2001) (lack of ocelli; hairy adhesive soles of tarsomeres; oblique implantation fossa of spermatozoon nucleus) were refuted or considered doubtful in KLASS (2003a: 218). The question has remained whether or not, or to what extent brood care is a compound synapomorphy of Embioptera and Dermaptera.

In Embioptera maternal brood care also comprises several elements. EDGERLY's (1987, 1988, 1997) descriptions of brood care in *Antipaluria urichi* (Saussure, 1896) (= *Clothodes urichi* [Saussure, 1896]) are particularly valuable: They concern a member of Clothodidae, which is usually considered the sister group of the remaining Embioptera (SZUMIK 1996; SZUMIK et al. 2003), and they are the most elaborate studies of brood care in Embioptera to date. In *A. urichi* (1) each single egg, which initially remains unattached, is immediately coated with chewed plant material or fecal pellets using the mouth parts. The coating is possibly supplemented by salivary secretions. Finally, silk is added. (2) Afterwards the egg is placed next to the foregoing ones, which altogether form a dense cluster upon the substrate. (3) The cluster is additionally provided with a cover of debris and silk. (4) The mother sits above or shortly beside the egg cluster for most of the time, (5) actively defends eggs against some natural enemies (Hymenoptera: Scelionidae) but not against others (Hymenoptera: Formicidae, Sclerogibbidae), and (6) her feeding is reduced. (7) The cover of the egg cluster is removed using the mandibles just before the nymphs are going to hatch, so the mother actively helps in hatching (which is additionally facilitated by the operculum, or lid, of the egg shell). (8) The mother tends to remain close to her young nymphs, but without feeding them and apparently without defending them against enemies. (9) Living conditions of nymphs are much improved through silk production by the mother (protection from certain predators and rain), which is intensified when nymphs are present in the galleries and can thus be regarded as an element of brood care. (10) A repeated treatment of the eggs using the mouth parts (probably cleaning) has been reported in some older literature for species other than *A. urichi*.

How does this compare with Dermaptera? (1) The coating of eggs by debris and silk is unique to Embioptera, as are (3) the covering of the egg cluster and (9) silk spinning in favour of the nymphs. (2) The eggs are not attached to the substrate immediately after laying, but are secondarily arranged into a cluster. This resembles the conditions in higher Dermaptera. However, it is likely homoplastic, since *Tagalina* species, *Paracranopygia siamensis*, and the diplatyid we examined glue eggs to the substrate when depositing them and do not rearrange them thereafter, this likely being plesiomorphic for Dermaptera. In this context one should note that the ovipositor in embiopterans is at most vestigial, and the presence of a true female accessory gland of segment IX is unclear (ROSS 2000: 39, figs. 37, 38). (10) The extensive treatment of eggs with the mouth parts is also found in many Dermaptera, but this behaviour does not occur in *Tagalina* species (and possibly in *P. siamensis* and our diplatyid) and its presence in the dermapteran ground plan appears unlikely. (7) Helping nymphs in hatching occurs among Dermaptera only in a few higher Forficulina and has surely developed within the order, thus not being homologous with the helping behaviour found in the embiopteran. In addition, the latter removes the debris and silk from the egg cluster and in all Embioptera the operculum is the tool to facilitate the hatching of the nymph from the egg shell. In contrast, the respective Dermaptera open and feed the egg shell. Consequently, the helping activities in the two taxa are not comparable anyway.

Only (4) the close association of the mother with the eggs, (5) their (partial) defense, (6) reduced feeding of the mother during this period, and (8) the tendency to maintain a spatial association with the young nymphs are common to the ground plans of Embioptera and Dermaptera. These shared features are quite unspecific and partly highly interdependent. In addition, the same set of exclusively maternal brood care elements (frequently supplemented by additional ones) is found in insects from many orders and has frequently developed independently (examples and evolutionary considerations in, e.g., TALLAMY & WOOD 1986).

There are additional data for a few other Embioptera, but these are mostly anecdotal (surveyed in ROSS 2000; EDGERLY 1987, 1988, 1997; CHOE 1994): In some species eggs are placed singly into the silken gallery walls and either covered with silk (*Anisembia texana* [Melander, 1902]) or not (*Oligotoma humbertiana* [Saussure, 1896]). *Oligotoma ceylonica* Enderlein, 1912 lays a single egg per day over a period of several weeks, assembling eggs altogether in a row. In other webspinners an egg mass is attached to the gallery walls using silk (*Embia major* Imms, 1913), or irregularly clustered eggs lying on the ground are covered with silk (*Dinembia* sp.). In *Embia ramburi* Rimsky-Korsakov, 1905 eggs are transported using the mandibles in case of threat, and young nymphs depend on feeding by the mother (chewed plant material). For webspinners from several families it is reported that females stay with their eggs and nymphs, and maternal brood care can thus be assumed to be present throughout the order. This all does not add any additional ground plan features of brood care shared with Dermaptera: transporting of eggs and feeding of nymphs in Dermaptera are most likely apomorphic conditions, and all activities involving silk are peculiar to Embioptera.

Tab. 4. Number of nymphal instars in species of Dermaptera. The second column gives the systematic assignation (HF = higher Forficulina; EU = Eudermaptera; see HAAS & KLASS 2003). The third column gives the number of nymphal instars; occasionally observed lower or higher numbers are given in brackets before or behind the usual number, e.g., (6)5(4); "1+" means that a strongly reduced first instar has explicitly been assumed by HERTER (various papers); * only for these taxa we found explicit statements in the literature whether or not a cuticle is shed with hatching and remains in the egg shell (unknown for the remaining taxa). Many data were extracted from the summary description in GÜNTHER & HERTER (1974) = G&H (see therein for further references); data from PESOTSKAJA (1927) were adopted fide G&H. For synonymy of species names see legend Tab. 3.

Species	Systematic assignation	Instars	Sources
Tagalina papua (de Bormans, 1903)	Pygidicranidae	(7)6	this paper
Tagalina burri Hincks, 1955	Pygidicranidae	6	this paper
Anisolabis maritima (Bonelli, 1832)	Anisolabididae HF	(6)5(4)*	G&H, HERTER (1959, 1965a), GUPPY (1950)
Anisolabis littorea (White, 1846)	Anisolabididae HF	5	G&H, GILES (1953)
Euborellia annulipes (Lucas, 1847)	Anisolabididae HF	(6)5	G&H, BHARADWAJ (1966)
Euborellia cincticollis (Gerstaecker, 1883)	Anisolabididae HF	(8)7–5	G&H, KNABKE & GRIGARICK (1971)
Euborellia plebeja (Dohrn, 1863)	Anisolabididae HF	4	BAIJAL & SRIVASTAVA (1974)
Nala lividipes (Dufour, 1820)	Labiduridae HF	4	SITUMORANG & GABRIEL (1988)
Labidura riparia (Pallas, 1773)	Labiduridae HF	(6)5*	G&H, HERTER (1963), CAUSSANEL (1970), SHEPARD et al. (1973), TAWFIK et al. (1972)
Marava arachidis (Yersin, 1860)	Spongiphoridae HF EU	4*	G&H, HERTER (1943)
Auchenomus javanus (de Bormans, 1883)	Spongiphoridae HF EU	4	MATZKE (2002a)
Hamaxas nigrorufus (Burr, 1902)	Spongiphoridae HF EU	4	MATZKE (2000)
Chelisoches morio (Fabricius, 1775)	Chelisochidae HF EU	4	MATZKE (1997)
Doru taeniatum (Dohrn, 1862)	Forficulidae HF EU	5–6	BRICEÑO & SCHUCH (1988)
Apterygida media (Hagenbach, 1822)	Forficulidae HF EU	4	MATZKE (2002b)
Chelidurella guentheri (Galvagni, 1994)	Forficulidae HF EU	4	FRANKE (1985)
Forficula auricularia Linnaeus, 1758	Forficulidae HF EU	1+4*	HERTER (1965a,b)
Forficula tomis (Kolenati, 1846)	Forficulidae HF EU	4	PESOTSKAJA (1927) fide G&H
Forficula senegalensis Serville, 1839	Forficulidae HF EU	4	BAOUA BOUKARY et al. (1996)
Guanchia pubescens (Géné, 1837)	Forficulidae HF EU	1+4*	HERTER (1964, 1965a)

In sum, the ground plans of Dermaptera and Embioptera do not share any complex pattern of maternal brood care; rather, the shared elements only include few quite unspecific and partly interdependent elements ((4), (5), (6), and (8) above). Consequently, the homology of maternal brood care in Dermaptera and Embioptera is still possible, but due to a low complexity of the behavioural pattern it is only weakly supported. This complies with the low and conflicting support of dermapteran-embiopteran relationships by morphological characters (see above) and with the absence of a dermapteran-embiopteran clade in the trees obtained in molecular analyses (WHEELER et al. 2001: 18S + 28S rDNA tree fig. 12 left; KJER 2004: fig. 1).

Comparative aspects of nymphal development

An overall view of current knowledge gives the impression that within the higher Forficulina members of the more basal groups have usually 5 nymphal instars (Anisolabididae and Labiduridae; Apachyidae not examined), while those of the more advanced groups have 4 (Eudermaptera: Forficulidae, Chelisochidae, Spongiphoridae). The 6 nymphal instars in *Tagalina* species would thus appear unique within the Forficulina (and Dermaptera as a whole) and in agreement with the basal position of this genus. However, there are two important complications that must be considered in this issue: intraspecific variation and the correct identification of the 1st instar.

Intraspecific variation in the number of nymphal instars. The taxa usually having 5 nymphal instars (most Anisolabididae and Labiduridae) actually show much variation, and this partly occurred within the same breeding cultures (Tab. 4; see GÜNTHER & HERTER 1974: 133ff). Thus, 6 rather than 5 nymphal instars were found in a considerable proportion of *Anisolabis maritima* (males 14 %; females 33 %) and in large males of *Labidura riparia* (SHEPARD et al. 1973; CAUSSANEL 1966; OZEKI 1958 fide GÜNTHER & HERTER 1974: 133). For *Euborellia cincticollis*, KNABKE & GRIGARICK (1971) reported the frequent occurrence of 6 or 7 and even a single case of 8 nymphal instars with relatively high temperatures, while with lower temperatures 5 instars were most common. Thus, the occurrence of 6 nymphal instars in *Tagalina* is not so exceptional. On the other hand, in *A. maritima* there was also a high (males) or low (females) percentage of specimens with only 4 instars (OZEKI 1958), and a single case of 4 nymphal instars was also found in *E. cincticollis* by KNABKE & GRIGARICK (1971). The latter authors demonstrated for *E. cincticollis* that, by and large, with increasing temperature the duration of nymphal development is altogether shorter but the number of instars is higher.

Problems in counting nymphal instars. Counting nymphal instars in Dermaptera is generally problematic due to doubtful identification of early instars around hatching and homologization of these instars among species. The core of this problem is HERTER's report of the 1st nymphal instar being long-lived in some Dermaptera, vestigial (extremely short) in others, and absent in still others – combined with the lack of clear data on this issue in the remaining species.

For the Eudermaptera *Forficula auricularia* and *Guanchia pubescens* HERTER (1964, 1965a,b; the latter species as *Forficula pubescens*) found that, when hatching from the egg, the nymph at the same time sheds a cuticle, which remains in the egg shell. He interprets this moult done with hatching as that between the 1st and 2nd instars, and the freshly hatched nymph as the 2nd instar rather than the 1st. He consequently revises earlier counts of 4 nymphal instars in *Forficula* and states a number of 5, with the 1st instar being extremely reduced (see also GÜNTHER & HERTER

1974: 129, 135f; this condition is represented as "1+4" in Tab. 4). For the eudermapteran *Marava arachidis* HERTER (1943, 1965a) and GÜNTHER & HERTER (1974: 135f) report the true presence of only 4 instars, with the early moult of *Forficula* lacking; this may, in HERTER's sense, be interpreted as a complete loss of the 'true' 1st instar. In the non-eudermapterans *Labidura riparia* and *Anisolabis maritima* HERTER (1963: 312, 1965a) also considers the early moult within the egg to be absent. However, since these taxa usually have 5 nymphal instars, they are assumed to have long-lived 1st instar nymphs that correspond to the 1st instar as identified by other authors in these species. Consequently, the freshly hatched nymphs in *Forficula auricularia* and *Guanchia pubescens* (and probably *M. arachidis*) on the one hand and in *L. riparia* and *A. maritima* on the other would not represent corresponding instars, and maternal care would be extended by one instar in *Forficula* as compared to the other two species.

Unfortunately, in none of the publications – including our own – on the development of other dermapteran species clear data are provided on the presence or absence of a moult co-occurring with the hatching from the egg. In all the remaining species it is thus unclear whether there is, in HERTER's sense, a reduced early instar or not (i.e., whether or not "1+" should be placed in front of the number in Tab. 4). Nonetheless, a reduced or absent 1st instar may in the framework of HERTER's proposal also be suspected for the remaining Dermaptera having 4 nymphal instars. These are nearly all examined Eudermaptera, *Euborellia plebeja*, *Nala lividipes* (see Tab. 4), and the Arixeniidae and Hemimeridae (probably with 4 nymphal instars: GILES 1961b; GÜNTHER & HERTER 1974: 136; NAKATA & MAA 1974: 316, 340; DAVIES 1966; see below).

There are two problems in HERTER's revised counting for *Forficula auricularia* and *Guanchia pubescens* (or Eudermaptera as a whole) and the resulting homologization of nymphal instars with those in non-Eudermaptera:

(1) In the studied Eudermaptera (1+4 instars) a number of 8 antennomeres is then retained for one more instar than in other Forficulina (1st plus 2nd rather than 1st only; see GÜNTHER & HERTER 1974: 137, tab. 3). This may be attributed to the usually lower final number of antennomeres in the imagines of Eudermaptera (11–13) as compared to other Forficulina (more than 16) and a resulting delayed development of antennae. However, this explanation would not apply to *Chelisoches morio* (20 antennomeres).

(2) More importantly, the issue of counting nymphal instars is intimately correlated with the embryonic cuticles produced in the egg and the presence of an egg tooth on the frons of the head. Generally in insects there are up to three embryonic cuticles that precede the cuticle of the 1st instar nymph/larva: the serosal, first embryonic, and second embryonic (HEMING 2003: 229). Insects can variously shed the latest embryonic cuticle when hatching from the egg (e.g., some Odonata, ANDO 1962: 70; some Plecoptera, MILLER 1940: 447; examined Blattaria, BEIER 1974: 92; Orthoptera: Gryllidae, BEIER 1972: 165), while others retain this cuticle for a shorter or longer time after hatching (e.g., Mantodea, see below; Orthoptera: Acrididae, BEIER 1972: 165; Zygentoma, HEYMONS 1897: 597, SAHRHAGE 1953: 110–116, and SCHMIDT 1957: 360). In the latter case the free-living animal bearing the latest embryonic cuticle is best considered a pronymph/prolarva (often a "vermiform nymph", see HEMING 2003: 235), the 1st instar nymph emerging with the following moult. Unfortunately, the full set of embryonic cuticles has not been studied in Dermaptera.

The egg tooth occurs in various Dicondylia (e.g., HEYMONS 1897: 597 for Zygentoma; ANDO 1962: 65, fig. 67-4 for Odonata; ZWICK 1980: 86 and MILLER 1940: 447f for Plecoptera; NEW 1989: 90 for Neuroptera) and is potentially autapomorphic for this taxon (STURM & MACHIDA 2001: 173). The cuticle bearing it is generally regarded as the (latest) embryonic cuticle (= cuticle of pronymph; see same references and HEMING 2003: 235), which can also form other specialized structures such as the hatching threads originating from the cerci in Mantodea (e.g., HEVERS & LISKE 1991: figs. 22, 23; on second embryonic cuticle, see HEMING 2003: 235). This egg tooth can perhaps be used as a landmark for homologizing cuticles around the time of hatching. In Dermaptera an egg tooth has been claimed to be absent in *Anisolabis maritima* and *Labidura riparia* (HERTER 1959, 1963), but it is clearly present in *Forficula auricularia* and *Guanchia pubescens* (HERTER 1964) and possibly present in *Tagalina papua* (see above and Fig. 11) – located on the frons of the abovementioned cuticle shed with hatching. We also note that HEYMONS (1912: 178), in contrast to HERTER (1959: 217), reports an egg tooth for a species of *Anisolabis* (*A. littorea*). This dermapteran cuticle bearing the egg tooth is best considered the latest embryonic (pronymphal) cuticle, and only the instar emerging from it is the 1st nymphal instar. This is in contrast to the counting of HERTER, i.e., HERTER's 2nd instar in *Forficula* is better considered the 1st, as in the traditional counting. Still the question remains how nymphal instars should be homologized among the various Dermaptera: is the long-lived 1st instar of, e.g., *Labidura riparia* perhaps a pronymph? This appears unlikely to us. Alternatively, *Labidura riparia* and *Anisolabis maritima* may also possess an eggtooth bearing cuticle left behind in the egg shell and overlooked in HERTER's contributions, as actually indicated by HEYMONS' (1912) note on *A. littorea*. On the other hand, CAUSSANEL (1966), whose studies are fairly detailed, neither reports an egg tooth for *L. riparia*; this appears plausible since in this species the mother helps her nymphs in hatching (Tab. 4). This issue remains thus quite confused.

There may be an additional problem of counting nymphal instars in the Hemimeridae. In *Hemimerus talpoides* Walker, 1871 the instar bearing an egg tooth (here surely not with the function to break the egg shell, which is absent; HEYMONS 1912) is considered the 1st instar nymph by GÜNTHER & HERTER (1974: 133) – in accord with HERTER's interpretation for *Forficula* and *Guanchia*. DAVIES (1966) reports 4 nymphal instars for *Hemimerus vicinus* Rehn & Rehn, 1936 based on a reconstruction from dead material, the 1st instar having been dissected from the mother's body. This 1st instar thus corresponds to the abovementioned instar described by HEYMONS (1912). Both this 1st and the 2nd instar are claimed to have 8 antennomeres. This agrees with the data in HEYMONS (1912; instars 'completed embryo–ny1–ny2–ny3' in HEYMONS corresponding to instars 'ny1–ny2–ny3–ny4' in DAVIES). However, DAVIES (1966) in his detailed account on head structure in the various nymphal instars does not mention an egg tooth for this 1st instar, nor do NAKATA & MAA (1974) in their revision of Hemimeridae (1st instar nymphs occasionally considered therein). Nonetheless, the eggtooth bearing instar in HEYMONS (1912) and, if actually identical with it, the 1st nymphal instar in DAVIES (1966) are best considered a pronymph rather than the 1st nymph, and there is no indi-

cation how long-lived this instar is. The number of nymphal instars in Hemimeridae would then be 3.

In sum, the identification and homologization of particular instars and their cuticles around hatching and, consequently, the counting of nymphal instars is very confused in Dermaptera. We suggest that in future studies on dermapteran development it should be examined whether a cuticle is left behind in the egg shell or not and on which cuticle an egg tooth is present. Preferably the entire series of embryonic cuticles should be included in such studies.

Phylogenetic implications from nymphal instars. The figures so far known for nymphal instars in Dermaptera agree only roughly with current hypotheses on phylogenetic relationships (see HAAS & KLASS 2003: fig. 1). The interpretation of stepwise reductions as autapomorphies of dermapteran subgroups is difficult (Tab. 4) due to the low number of species studied, the great amount of intraspecific variation, and the existence of species with exceptional numbers of nymphal instars.

The constant occurrence of at least 6 full nymphal instars in *Tagalina papua* and *T. burri* is so far unique for Dermaptera, and a reduction to 5 instars may tentatively be viewed as an autapomorphy of the higher Forficulina. This interpretation, however, is strongly limited by the observation of up to 8 instars in *Euborellia cincticollis*. Nonetheless, our breeding cultures were likely kept near the minimum temparature for development (see above), while *E. cincticollis* has only 5 instars at low temperatures (KNABKE & GRIGARICK 1971); this may be seen as increasing the value of this character.

The Eudermaptera by and large differ from the more basal Forficulina by the occurrence of only 4 nymphal instars (due to a strong reduction of the 1st instar in the framework of HERTER's hypotheses). However, there are some important exceptions: (1) the eudermapteran (forficulid) *Doru taeniatum* has 5 or 6 nymphal instars; (2) for the non-eudermapterans *Euborellia plebeja* (an anisolabidid) and *Nala lividipes* (a labidurid) there are only reports of 4 nymphal instars (see Tab. 4). Case (1) suggests that the reduction to 4 instars occurred several times in Eudermaptera, and the cases under (2) suggest that, in addition, at least two homoplastic reductions occurred outside the Eudermaptera.

For the Arixeniidae and Hemimeridae weak support exists for a placement within the higher Forficulina, and Arixeniidae may be nested within the Eudermaptera (related to Spongiphoridae; HAAS & KLASS 2003). The low number of nymphal instars in both epizoic taxa may support the position of these within the Eudermaptera, but this is only a weak argument.

The assumption that in Dermaptera a high number of nymphal instars is plesiomorphic is supported by outgroup comparison, although not unambiguously. The great number of immature moults in Archaeognatha, Zygentoma, and Ephemeroptera (STURM & MACHIDA 2001: 175ff, 185; DUNGER 2003; BAUERNFEIND 2003) and the range of 7–15 nymphal instars in Odonata (XYLANDER & GÜNTHER 2003) clearly suggest this polarity. According to the data in BEIER (1968, 1972: 166, 1974: 92) and ZWICK (1980: 90), in some – but not all – orders of lower Neoptera there occur significantly higher numbers of instars than in Dermaptera (e.g., Plecoptera up to ca. 23, Blattaria up to ca. 13, Orthoptera up to 16), but in some of these taxa there also occur lower numbers (e.g., Blattaria minimum 3, Orthoptera minimum 4). In Blattaria and Orthoptera low and high numbers are partly found in different members of the same subgroup. Consequently, the number of instars has been reduced several times independently within each of these two orders (e.g., Blattaria males: *Eurycotis floridana* 6–7 versus *Periplaneta americana* 10–13 in Blattidae, and *Blaberus craniifer* 10–11 versus *Diploptera punctata* 3–4 in Blaberidae; situation similar in various subgroups of Orthoptera). Intraspecific variation in the number of nymphal instars, probably in correlation with environmental parameters such as temperature (as reported for *Euborellia cinctipes*), is not unusual and is also found in taxa with a low number of instars. Thus, as compared to, e.g., Blattaria and Orthoptera, the number of nymphal instars in Dermaptera appears relatively stable with respect to phylogeny.

In Dermaptera only the Karschiellidae and Diplatyidae have long, multi-annulated, filiform cerci in the nymphal instars; the basal cercomere alone then develops into the claspers of the adults (GÜNTHER & HERTER 1974: 136). In *Tagalina papua* the cerci are already quite short, non-annulated, and clasper-shaped in freshly hatched nymphs (Fig. 15), and the same condition is visible in late embryos through egg shell (Figs. 12, 13). In this character *Tagalina* is thus more derived than Karschiellidae and Diplatyidae and complies with higher Forficulina such as *Labidura riparia* (CAUSSANEL 1966: pl. 1 fig. 3; BHATNAGAR & SINGH 1965a: fig. 39). This character supports that *Tagalina* is more closely related to higher Forficulina than Karschiellidae and Diplatyidae (compare HAAS & KLASS 2003: fig. 1).

Conclusions

Our studies of the reproductive behaviour and nymphal development in species of *Tagalina* and our observations on the eggs of *Paracranopygia siamensis* and a diplatyid have expanded previous knowledge in three important aspects:

(1) *Tagalina* is the first dermapteran taxon reported to have consistently (at least) 6 nymphal instars. This is likely plesiomorphic for Dermaptera. A predominant reduction to 5 (higher Forficulina) and, later, 4 nymphal instars (Eudermaptera) agrees roughly with current hypotheses on dermapteran phylogeny. However, the strong variation and dependence on external parameters of the number of nymphal instars in non-eudermapterans as well as the report of 5 nymphal instars in one eudermapteran constitute problems in the phylogenetic interpretation. Counting nymphal instars and homologizing early nymphal instars in Dermaptera remain problems whose resolution requires a careful comparative study of cuticles formed before and around hatching and of the occurrence of an egg tooth on these.

(2) Through the absence of egg cleaning and rearrangement, brood care in *Tagalina* is simpler than in the previously examined Dermaptera. Since the lack of egg transport correlates with the firm attachment of the eggs to the substrate, which, in turn, plausibly correlates with the plesiomorphic presence of IXth-segmental accessory glands and of a complete ovipositor with long gonapophyses VIII, this lack in *Tagalina* is probably plesiomorphic for Dermaptera. This view is strengthened by the fact that *P. siamensis* and our diplatyid, two other basal dermapterans, also attached their eggs to the substrate. The absence of the cleaning behaviour might also correlate with the presence of the accessory glands, then being plesiomorphic.

(3) A comparison of broodcare behaviour in Dermaptera and Embioptera, based on our new data, indicates that only some unspecific and partly intercorrelated elements of brood care are shared between the ground plans of the two taxa. Homology of brood care in Dermaptera and Embioptera is thus only weakly supported. Furthermore, the view that other characters shared between the two taxa may be synapomorphies (BEUTEL & GORB 2001) must be seen critically (KLASS 2003a). Thus, the morphological-behavioural support for a sistergroup relationship between Dermaptera and Embioptera appears now very weak, which is consistent with the lacking support of such a relationship in molecular analyses (WHEELER et al. 2001; KJER 2004).

As demonstrated by our new evidence from a single genus of the morphologically highly diverse Pygidicranidae (see KLASS 2003a for female genitalia; HAAS & GORB 2004 for tarsi), supplemented by glimpses on egg structure in another pygidicranid genus and in Diplatyidae, studies of reproductive biology and development in further species of Pygidicranidae as well as Karschiellidae and Diplatyidae could be highly rewarding. Such studies could not only discover further interesting aspects of life history – reproductive biology in particular – but also contribute to resolving basal phylogenetic relationships in Dermaptera.

Acknowledgements

A. Michalczik and M. Hoffmann (both Leipzig, Germany) kindly provided the *Tagalina* specimens that they brought from Irian Jaya and on which our breeding culture was based. For a critical review of our manuscript we thank Fabian Haas (Staatliches Museum für Naturkunde Stuttgart), who is also acknowledged for identification of some *Tagalina* specimens and for providing photographs of *Tagalina* embryos (Figs. 11–14). His database (http://www.earwigs-online.de) greatly facilitated the literature search for this study. For the processing of photographs we thank Markward Fischer (Museum für Tierkunde Dresden).

References

ANDO, H. 1962. The Comparative Embryology of Odonata with Special Reference to a Relic Dragonfly *Epiophlebia superstes* Selys. – The Japan Society for the Promotion of Science, Tokyo.

BAIJAL, H.N. & G.K. SRIVASTAVA 1974. Notes on the biology of *Euborellia plebeja* (Dohrn). – Indian Journal of Entomology **36**: 23–27.

BAOUA BOUKARY, I., J.-C. TOURNEUR & J. GINGRAS 1996. Life cycle of *Forficula senegalensis* Serv. (Dermaptera: Forficulidae) and its relationship to the development of bulrush millet in the Sudanese-Sahelian zone of Niger. – The Canadian Entomologist **128**: 831–838.

BAUERNFEIND, E. 2003. 6. Ordnung Ephemeroptera, Eintagsfliegen. Pp. 108–120 *in*: H.H. DATHE (ed.), Lehrbuch der Speziellen Zoologie, Band I: Wirbellose Tiere, 5. Teil: Insecta, 2nd edn. – Spektrum Akademischer Verlag, Heidelberg, Berlin.

BEIER, M. 1968. 10. Ordnung Phasmida (Stab- oder Gespenstheuschrecken). Pp. 1–56 *in*: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie 4 (2) 2/10. – De Gruyter, Berlin.

BEIER, M. 1972. 9. Ordnung Saltatoria (Grillen und Heuschrecken). Pp. 1–217 *in*: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie 4 (2) 2/9. – De Gruyter, Berlin.

BEIER, M. 1974. Blattariae (Schaben). Pp. 1–127 *in*: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie 4 (2) 2/13. – De Gruyter, Berlin.

BEUTEL, R.G. & S.N. GORB 2001. Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. – Journal of Zoological Systematics and Evolutionary Research **39**: 177–207.

BHARADWAJ, R.K. 1966. Observations on the bionomics of *Euborellia annulipes* (Dermaptera: Labiduridae). – Annals of the Entomological Society of America **59**: 441–450.

BHATNAGAR, R.D.S. & K.I. SINGH 1965a. Studies on the embryonic development of the earwig *Labidura riparia* (Pallas) (Labiduridae: Dermaptera). – Research Bulletin of the Panjab University **16**: 19–30.

BHATNAGAR, R.D.S. & K.I. SINGH 1965b. Anatomy of the male and female reproductive system of the earwig *Labidura riparia* (Pallas); (Labiduridae: Dermaptera). – Research Bulletin of the Panjab University **16**: 327–332.

BRICEÑO, R.D. & W.G. EBERHARD 1995. The functional morphology of male cerci and associated characters in 13 species of tropical earwigs (Dermaptera: Forficulidae, Labiidae, Carcinophoridae, Pygidicranidae). – Smithsonian Contributions to Zoology **555**: i–iii, 1–63.

BRICEÑO, R.D. & W. SCHUCH 1988. Reproductive biology and behavior of *Doru taeniatum* (Forficulidae). – Revista de Biologia Tropical **36**: 437–440.

BURR, M. 1910. Dermaptera (Earwigs). *In*: A.E. SHIPLEY (ed.), The Fauna of British India Including Ceylon and Burma. – Taylor & Francis, London.

BUXTON, J.H. & D.S. MADGE 1974. Artificial incubation of eggs of the common earwig, *Forficula auricularia* (L.). – Entomologist's Monthly Magazine **110**: 55–57.

CAUSSANEL, C. 1966. Étude du développement larvaire de *Labidura riparia* (Derm. Labiduridae). – Annales de la Société Entomologique de France NS **2**: 469–498.

CAUSSANEL, C. 1970. Principales exigences écophysiologiques du forficule des sables, *Labidura riparia* (Derm. Labiduridae). – Annales de la Société Entomologique de France NS **6**: 589–612.

CHOE, J.C. 1994. Communal nesting and subsociality in a webspinner, *Anisembia texana* (Insecta: Embiidina: Anisembiidae). – Animal Behaviour **47**: 971–973.

CHOPARD, L. 1949. Dermaptera. Pp. 745–770 *in*: P.P. GRASSÉ (ed.), Traité de Zoologie, vol. 9. – Masson, Paris.

CRESPI, B.J. & J.C. CHOE 1997. Introduction. Pp. 1–7 *in*: J.C. CHOE & B.J. CRESPI (eds.), The Evolution of Social Behavior in Insects and Arachnids. – Cambridge University Press.

DAVIES, R.G. 1966. The postembryonic development of *Hemimerus vicinus* Rehn & Rehn (Dermaptera: Hemimeridae). – Proceedings of the Royal Entomological Society, London, A **41**: 66–77.

DEITZ, L.L., C.A. NALEPA & K.-D. KLASS 2003. Phylogeny of the Dictyoptera re-examined. – Entomologische Abhandlungen **61**: 69–91.

DETTNER, K. & W. PETERS (eds.) 1999. Lehrbuch der Entomologie. – Gustav Fischer, Stuttgart, Jena, etc.

DUNGER, W. 2003. 5. Ordnung Zygentoma, Silberfischchen. Pp. 102–107 *in*: H.H. DATHE (ed.), Lehrbuch der Speziellen Zoologie, Band I: Wirbellose Tiere, 5. Teil: Insecta, 2nd edn. – Spektrum Akademischer Verlag, Heidelberg, Berlin.

EDGERLY, J.S. 1987. Maternal behaviour of a webspinner (Order Embiidina). – Ecological Entomology **12**: 1–11.

EDGERLY, J.S. 1988. Maternal behaviour of a webspinner (Order Embiidina): mother-nymph associations. – Ecological Entomology **13**: 263–272.

EDGERLY, J.S. 1997. Life beneath silk walls: a review of the primitively social Embiidina. Pp. 14–25 *in*: J.C. CHOE & B.J. CRESPI (eds.), The Evolution of Social Behavior in Insects and Arachnids. – Cambridge University Press.

EICKWORT, G.C. 1981. Presocial insects. Pp. 199–268 *in*: H.R. HERMANN (ed.), Social Insects, vol. 2. – Academic Press, New York.

FRANKE, U. 1985. Zur Biologie eines Buchenwaldbodens. 7. Der Waldohrwurm *Chelidurella acanthopygia*. – Carolinea **43**: 105–112.

GADEAU DE KERVILLE, H. 1907. Accouplement, œufs, et amour maternal des Forficulides. – Rouen, 31 pp.

GADEAU DE KERVILLE, H. 1931. Sur les œufs et l'instinct maternel du *Pseudochelidura sinuata* Germ. [Dermaptera]. – Bulletin de la Société Entomologique de France **1931**: 119–120.

GILES, E.T. 1953. The biology of *Anisolabis littorea* (White) (Dermaptera: Labiduridae) – Transactions of the Royal Society of New Zealand **80**: 383–398.

GILES, E.T. 1961a. The female reproductive organs and genital segments of *Anisolabis littorea* (White) (Dermaptera, Labiduridae). – Transactions of the Royal Society of New Zealand (Zoology) **1**: 293–302.

GILES, E.T. 1961b. Further studies on the growth stages of *Arixenia esau* Jordan and *Arixenia jacobsoni* Burr (Dermaptera Arixeniidae), with a note on the first instar antennae of *Hemimerus talpoides* Walker (Derm. Hemimeridae). – Proceedings of the Royal Entomological Society, London, A **36**: 21–26.

GÜNTHER, K. & K. HERTER 1974. 11. Ordnung Dermaptera (Ohrwürmer). Pp. 1–158 *in*: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie 4 (2) 2/11. – De Gruyter, Berlin.

GUPPY, R. 1950 [1949]. Biology of *Anisolabis maritima* (Gene) the seaside earwig, on Vancouver Island (Dermaptera, Labiduridae). – Proceedings of the Royal Entomological Society of British Columbia **46**: 14–18.

HAAS, F. 2003. 12. Ordnung Dermaptera, Ohrwürmer. Pp. 173–180 *in*: H.H. DATHE (ed.), Lehrbuch der Speziellen Zoologie, Band I: Wirbellose Tiere, 5. Teil: Insecta, 2nd edn. – Spektrum Akademischer Verlag, Heidelberg, Berlin.

HAAS, F. & S. GORB 2004. Evolution of locomotory attachment pads in the Dermaptera (Insecta). – Arthropod Structure & Development **33**: 45–66.

HAAS, F. & K.-D. KLASS 2003. The basal phylogenetic relationships in the Dermaptera. *In*: K.-D. KLASS (ed.), Proceedings of the 1st Dresden meeting on insect phylogeny: "Phylogenetic Relationships within the Insect Orders" (Dresden, September 19–21, 2003). – Entomologische Abhandlungen **61**: 138–142.

HAAS, F. & J. KUKALOVÁ-PECK 2001. Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). – European Journal of Entomology **98**: 445–509.

HARZ, K. 1958. Orthopterologische Beiträge. – Nachrichtenblatt der Bayerischen Entomologen (München) **7**: 47–48.

HARZ, K. 1960. Geradflügler oder Orthopteren (Blattodea, Mantodea, Saltatoria, Dermaptera). – Die Tierwelt Deutschlands und der angrenzenden Meeresteile 46. Teil. Gustav Fischer, Jena.

HEMING, B. 2003. Insect Development and Evolution. – Cornell University Press, Ithaca and London.

HERTER, K. 1943. Zur Fortpflanzungsbiologie eines lebendgebärenden Ohrwurmes. – Zeitschrift für Morphologie und Ökologie der Tiere **40**: 158–180.

HERTER, K. 1959. Zur Fortpflanzungsbiologie des Meeresstrand-Ohrwurmes *Anisolabis maritima* Bor. – Zoologische Beiträge **5**: 199–239.

HERTER, K. 1963. Zur Fortpflanzungsbiologie des Sand- oder Uferohrwurmes *Labidura riparia* Pall. – Zoologische Beiträge **8**: 297–329.

HERTER, K. 1964. Zur Fortpflanzungsbiologie des Ohrwurmes *Forficula pubescens* (Géné). – Zoologische Beiträge **10**: 1–28.

HERTER, K. 1965a. Vergleichende Beobachtungen und Betrachtungen über die Fortpflanzungsbiologie der Ohrwürmer. – Zeitschrift für Naturforschung **20b**: 365–375.

HERTER, K. 1965b. Die Fortpflanzungsbiologie des Ohrwurmes *Forficula auricularia* L. – Zoologische Jahrbücher Jena, Abteilung für Systematik, Ökologie und Geographie der Tiere **92**: 405–466.

HEVERS, J. & E. LISKE 1991. Die Lauernde Gefahr. Das Leben der Gottesanbeterinnen. – Staatliches Naturhistorisches Museum Braunschweig.

HEYMONS, R. 1897. Entwicklungsgeschichtliche Untersuchungen an *Lepisma saccharina* L. – Zeitschrift für Wissenschaftliche Zoologie **62**: 583–631.

HEYMONS, R. 1912. Über den Genitalapparat und die Entwicklung von *Hemimerus talpoides* Walk. – Zoologische Jahrbücher Supplementum **15**: 141–184.

KAMIMURA, Y. 2000. Possible removal of rival sperm by the elongated genitalia of the earwig, *Euborellia plebeja*. – Zoological Science **17**: 667–672.

KAMIMURA, Y. 2003. Effects of repeated mating and polyandry on the fecundity, fertility and maternal behaviour of female earwigs, *Euborellia plebeja*. – Animal Behaviour **65**: 205–214.

KAMIMURA, Y. 2004. Mating behaviour and insemination in *Diplatys flavicollis*, an earwig with double-barrelled penises and a variable number of female sperm-storage organs. – Journal of Zoology **262**: 37–46.

KJER, K.M. 2004. Aligned 18S and insect phylogeny. – Systematic Biology **53**: 506–514.

KLASS, K.-D. 2001. The female abdomen of the viviparous earwig *Hemimerus vosseleri* (Insecta: Dermaptera: Hemimeridae), with a discussion of the postgenital abdomen of Insecta. – Zoological Journal of the Linnean Society **131**: 251–307.

KLASS, K.-D. 2003a. The female genitalic region in basal earwigs (Insecta: Dermaptera: Pygidicranidae s.l.). – Entomologische Abhandlungen **61**: 173–225.

KLASS, K.-D. 2003b. Relationships among the principal lineages of Dictyoptera inferred from morphological data. *In*: K.-D. KLASS (ed.), Proceedings of the 1st Dresden meeting on insect phylogeny: "Phylogenetic Relationships within the Insect Orders" (Dresden, September 19–21, 2003). – Entomologische Abhandlungen **61**: 134–137.

KLOSTERMEYER, E.C. 1942. The life history and habits of the ring-legged earwig, *Euborellia annulipes* (Lucus <sic>) (Order Dermaptera). – Journal of the Kansas Entomological Society **15**: 13–18.

KNABKE, J.J. & A.A. GRIGARICK 1971. Biology of the African earwig, *Euborellia cincticollis* (Gerstaecker) in California and comparative notes on *Euborellia annulipes* (Lucas). – Hilgardia **41**: 157–194.

KRISTENSEN, N.P. 1981. Phylogeny of insect orders. – Annual Review of Entomology **26**: 135–157.

KRISTENSEN, N.P. 1991. Phylogeny of extant hexapods. Pp. 125–140 *in*: CSIRO (ed.), The Insects of Australia: a Textbook for Students and Research Workers, 2nd edn., vol. 1. – Melbourne University Press, Carlton, Victoria.

LAMB, R.J. 1976. Parental behaviour in the Dermaptera with special reference to *Forficula auricularia* (Dermaptera: Forficulidae). – Canadian Entomologist **108**: 609–619.

LO, N. 2003. Molecular phylogenetics of Dictyoptera: insights into the evolution of termite eusociality and bacterial endosymbiosis in cockroaches. *In*: K.-D. KLASS (ed.), Proceedings of the 1st Dresden meeting on insect phylogeny: "Phylogenetic Relationships within the Insect Orders" (Dresden, September 19–21, 2003). – Entomologische Abhandlungen **61**: 137–138.

LUCKOW, M. & A. BRUNEAU 1997. Circularity and independence in phylogenetic tests of ecological hypotheses. – Cladistics **13**: 145–151.

MATZKE, D. 1997. Beobachtungen bei der Zucht des Ohrwurmes *Chelisoches morio* (FABRICIUS, 1775) (Dermaptera, Insecta). – Arthropoda **5**(4): 4–8.

MATZKE, D. 2000. Zur Entwicklungsbiologie des Ohrwurmes *Hamaxas nigrorufus* (BURR 1902) (Dermaptera: Chelisochidae). – Arthropoda **8**(3): 2–5.

MATZKE, D. 2002a. Zur Entwicklungsbiologie des Ohrwurmes *Auchenomus javanus* (DE BURMANS, 1883) (Dermaptera: Spongiphoridae). – Arthropoda **10**(2): 9–12.

MATZKE, D. 2002b. Zur Biologie und Phänologie des Gebüschohrwurmes *Apterygida media* (HAGENBACH, 1822) (Dermaptera, Forficulidae). – Articulata **17**(2): 1–11.

MICHENER, C.D. 1969. Comparative social behavior of bees. – Annual Review of Entomology **14**: 299–342.

MILLER, A. 1940. Embryonic membranes, yolk cells, and morphogenesis of the stonefly *Pteronarcys proteus* Newman (Plecoptera: Pteronarcidae). – Annals of the Entomological Society of America **33**: 437–477.

MOURIER, H. 1986. Notes on the life history of *Labia minor* (L.) (Dermaptera), a potential predator of housefly eggs and larvae (Diptera, *Musca domestica* L.). – Entomologiske Meddelelser **53**: 143–148.

NAKATA, S & T.C. MAA 1974. A review of the parasitic earwigs. – Pacific Insects **16**: 307–374.

NEW, T.R. 1989. Planipennia (Lacewings). Pp. 1–132 *in*: M. FISCHER (ed.), Handbuch der Zoologie / Handbook of Zoology vol. IV part 30. – De Gruyter, Berlin.

OZEKI, K. 1958. Effect of corpus allatum hormone on development of male genital organs of the earwig, *Anisolabis maritima*. – Scientific Papers of the College of General Education, University of Tokyo **8**: 69–75.

PESOTSKAJA, E. [PESSOZKAJA, F.S.] 1927. Zur Biologie der Ohrwürmer *Forficula tomis* Kol. und *Labidura riparia* Pall. – Bulletin de l'Institut Lesshaft **12**: 51–62. [in Russian]

POPHAM, E.J. 1985. The mutual affinities of the major earwig taxa (Insecta, Dermaptera). – Zeitschrift für Zoologische Systematik und Evolutionsforschung **23**: 199–214.

RADL, R.C. & K.E. LINSENMAIR 1991. Maternal behaviour and nest recognition in the subsocial earwig *Labidura riparia* Pallas (Dermaptera: Labiduridae). – Ethology **89**: 287–296.

RANKIN, M.S., K.M. FOX & C.E. STOTSKY 1995. Physiological correlates to courtship, mating, ovarian development and maternal behaviour in the ring-legged earwig. – Physiological Entomology **20**: 257–265.

RANKIN, M.S., S.K. STORM, D.L. PIETO & A.L. RISSER 1996. Maternal behaviour and clutch manipulation in the ring-legged earwig (Dermaptera: Carcinophoridae). – Journal of Insect Behaviour **9**: 85–103.

ROSS, E.S. 2000. EMBIA. Contributions to the biosystematics of the insect order Embiidina, part I. – Occasional Papers of the California Academy of Sciences **149**: 1–43.

SAHRHAGE, D. 1953. Ökologische Untersuchungen an *Thermobia domestica* (Packard) und *Lepisma saccharina* L. – Zeitschrift für Wissenschaftliche Zoologie **157**: 77–168.

SCHMIDT, E.M. 1957. Untersuchungen zur Cytologie des Wachstums in der postembryonalen Entwicklung von *Lepisma saccharina* L. – Zoologische Jahrbücher Jena, Abteilung für Anatomie und Ontogenie der Tiere **77**: 357–410.

SHEPARD, M., V. WADDILL & W. KLOFT 1973. Biology of the predaceous earwig *Labidura riparia* (Dermaptera: Labiduridae). – Annals of the Entomological Society of America **66**: 837–841.

SITUMORANG, J. 1978. The biology of three species of earwig, *Labidura riparia* (Pallas), *Nala lividipes* (Dufour), *Euborellia* sp., and their role as predators of corn borer. – Thesis M. Sci., Univ. Philippines Los Banos, 104 pp.

SITUMORANG, J. & B.P. GABRIEL 1988. Biology of two species of predatory earwigs, *Nala lividipes* (Dufour) (Dermaptera: Labiduridae) and *Euborellia (Euborellia) annulata* (Fabricius) (Dermaptera: Carcinophoridae). – The Philippine Entomologist **7**: 215–238.

STÄGER, R. 1930. Einige Notizen über *Anechura bipunctata* (Dermatopt.). – Entomologische Zeitschrift, Frankfurt am Main **43**: 271–273.

STEINMANN, H. 1989. World Catalogue of Dermaptera. – Ser. Entomol. **43**. Kluwer Academic Publishers, The Hague, 934 pp.

STURM, H. & R. MACHIDA 2001. Archaeognatha. Pp. 1–213 *in*: N.P. KRISTENSEN & R.G. BEUTEL (eds.), Handbuch der Zoologie / Handbook of Zoology vol. IV part 37. – De Gruyter, Berlin, New York.

SZUMIK, C. 1996. The higher classification of the order Embioptera: a cladistic analysis. – Cladistics **12**: 41–64.

SZUMIK, C., J. EDGERLY-ROOKS & C.Y. HAYASHI 2003. Phylogenetics of Embioptera (= Embiidina). *In*: K.-D. KLASS (ed.), Proceedings of the 1st Dresden meeting on insect phylogeny: "Phylogenetic Relationships within the Insect Orders" (Dresden, September 19–21, 2003). – Entomologische Abhandlungen **61**: 131.

TALLAMY, D.W. & T.K. WOOD 1986. Convergence patterns in subsocial insects. – Annual Review of Entomology **31**: 369–390.

TAWFIK, M.F.S., S. ABUL-NASR & M.M. EL-HUSSEINI 1972. The biology of *Labidura riparia* Pallas (Dermaptera: Labiduridae). – Bulletin de la Société Entomologique d'Egypte **56**: 75–92.

THIAGARAJAN, K.B. 1939. The habits of the common earwig of Annamalainagar, *Euborellia stali* (Dohrn). – Journal of the Bombay Natural History Society **40**: 721–723.

TIMMINS, C.J. 1995. Parental behaviour and early development of Lesnei's earwig *Forficula lesnei* (Finot). – The Entomologist **114**: 123–127.

VANCASSEL, M. 1973. La fin du cycle parental de *Labidura riparia* (Dermaptère, Labiduridae). – Terre et Vie **27**: 481–490.

VANCASSEL, M. 1977. Le développement du cycle parental de *Labidura riparia*. – Biology of Behaviour **2**: 51–64.

VANCASSEL, M. 1984. Plasticity and adaptive radiation of dermapteran parental behaviour: results and perspectives. – Advances in the Study of Behavior **14**: 51–80.

VERHOEFF, K.W. 1912. Ueber Dermapteren: Zur Kenntnis der Brutpflege unserer Ohrwürmer. – Zeitschrift für Wissenschaftliche Insektenbiologie **8**: 381–385, **9**: 21–24, 55–58.

WEYRAUCH, W.K. 1929. Experimentelle Analyse der Brutpflege des Ohrwurms *Forficula auricularia* L. – Biologisches Zentralblatt **49**: 543–558.

WHEELER, W.C., M. WHITING, Q.D. WHEELER & J.M. CARPENTER 2001. The phylogeny of the extant hexapod orders. – Cladistics **17**: 113–169.

XAMBEU, V. 1903. Instinct de la maternité chez le *Chelidura dilatata*, Lafrenaye, Orthoptère du groupe des Forficuliens. – Le Naturaliste **25**: 143–144.

XYLANDER, W.E.R. & K.K. GÜNTHER 2003. 7. Ordnung Odonata, Libellen. Pp. 121–142 *in*: H.H. DATHE (ed.), Lehrbuch der Speziellen Zoologie, Band I: Wirbellose Tiere, 5. Teil: Insecta, 2nd edn. – Spektrum Akademischer Verlag, Heidelberg, Berlin.

ZWICK, P. 1980. 7. Ordnung Plecoptera (Steinfliegen). Pp. 1–115 *in*: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie 4 (2) 2/7. – De Gruyter, Berlin.