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The phylogeny of the Forficulina, a suborder of the Dermaptera

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Abstract. The phylogeny of the Forficulina (Dermaptera) has been reassessed, examining forty-eight species and thirty characters, of which thirteen characters of the thorax and wings are described or used for phylogenetic purposes for the first time, whereas the remaining seventeen have been extracted from literature. Examination of the thirty characters demonstrates that only twenty-three characters are useful for phylogenetic construction. The characters have been analysed with PAUP 3.1 yielding two equally parsimonious trees. The results suggest an exclusion of the 'Diplatyidae' (themselves paraphyletic) and the Karschiellidae from the Pygidicranidae and support the separation of the Apachyidae from the Labiduridae. A sister-group relationship of Anisolabididae and Spongiphoridae is not supported. The monophyly of the (Spongiphoridae (Forficulidae, Chelisochidae)) is supported.

Introduction

The earwigs (Dermaptera) are a rather uniform, though ancient, group of insects. They are divided into three taxa: the Hermimerina, the Arixeniina, and the Forficulina. The Forficulina are the 'typical' earwigs.

In recent years there have been several proposals concerning the phylogenetics of the Forficulina published by Popham (1985), Sakai (1987) and Steinmann (1986, 1989, 1990, 1993). Unfortunately these systems are not in accord with the principles of phylogenetic systematics. Steinmann (1986, 1989,1990,1993) used the diagnostic approach to the problem, not distinguishing between apomorphic and plesiomorphic character states to define the taxa. The Pygidicranidae, for example, are soly defined by the retention of plesiomophic character states (see Results and Discussion). Popham (1985) and Sakai (1987), respectively, based their systems only on characters which have been well known for a long time.

On the other hand, characters used by the pioneers of Dermapterology – Burr, Verhoeff and Zacher – have not been reassessed by recent workers and new evidence has not been produced.

The present study attempts to fill this gap by reassessing characters already published and by describing new characters – predominantly of the thorax and wings – for phylogenetic purposes. Furthermore, the study applies the principles of phylogenetic systematics to the character set.

A functional interpretation for some of the characters is given.

The Hemimerina and the Arixeniina are epizoic parasites living on bats (Rentz *et al* 1991) and giant rats (Rehn *et al.*, 1935). Since no material has been available, neither group has been included in the present study.

Methods

The characters derived from the literature have been reassessed using the species listed in Table 1. Characters have been excluded from the phylogenetic reconstruction if there are conflicting descriptions in the literature or if my own observations have been in disagreement with the published description.

Original observations concerning the thorax, tegmina and wings of the Forficulina have been made. Hindwing characters were only coded for those species that are known to be able to fly – for example if they have been captured in a light trap – or if the evaluation of the morphology suggested a high probability of flight capability, which has been evaluated according to the criteria given by Kleinow (197 1) and is summarized in Table 1. He has inferred flight-capability from the size of the mesophragma. All other characters of all available species, whether or not flight-capable, have been included. This approach diminished the risk of taking reduced structures for well-developed structures. The venation terminology has been adopted from Giles (1963).

The characters have been equally weighted, non-additively coded and not polarized for phylogenetic reconstruction which has been conducted by using the Heuristic Search command in the search menu of the program PAUP 3.1 (Swofford, 1993). Autapo-morphic characters have not been excluded from the analysis.

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Table 1. The species examined in this study. The column Mesonotum statistics shows the absolute mesonotum length, the mesonotal ratio, the standard deviation and *n*, the number of measured specimens. Flight capability was inferred from Kleinow (1971). '?': flight cabability was not assessable.

Order	Family	Mesonotum statistics	Flight capability
Blattodea			
Blaberidae	*Leucophaea madera* (Fabricius)	5 mm/0.61/0.03/*n* = 5	Yes
Blattellidae	*Periplaneta americana* (Linnaeus)	4 mm/0.69/0.23/*n* = 5	Yes
Polyphagidae	*Polyphaga aegyptica* (Linnaeus)	3.5 mm/0.56/0.01/ *n* = 5	Yes
Dermaptera			
Anisolabididae	*Anisolabis maritima* (Bonelli)	–	Wingless
	Carcinophora americana (Palisot de Beauvois)	1.5 mm/0.54/ — /*n* = 1	Probably yes
	Euborellia moesta (Gene)	–	Wingless
	Gonolabis maxima (Brullé)	–	Wingless
Apachyidae	*Apachyus reichardi* Karsch	2.5 mm/1.54/ — /*n* = 1	No
	Apachyus chartaceus (DeHaan)	2.2 mm/1.43/ — /*n* = 1	?
	Apachyus feae Bormans	2.5 mm/1.6/0.09/ — /*n* = 2	Probably yes
Chelisochidae	*Chelisoches morio* (Fabricius)	0.75 mm/0.52/0.03/*n* = 4	Probably yes
'Diplatyidae'	*Diplatys jacobsoni* Burr	0.8 mm/1/-/n = 1	?
	Diplatys macrocephalus (Palisot de Beauvois)		?
	Haplodiplatys bidentatus (Hincks)		?
	Haplodiplatys orientalis Steinmann	1.2 mm/0.94/ — /*n* = 1	Probably no
	Haplodiplatys rileyi (Hincks)		?
	Haplodiplatys rufescens (Kirby)	–	?
	Haplodiplatys severus (Bormans)	–	?
	Haplodiplatys siva (Burr)	–	?
	Haplodiplatys tibetanus (Hincks)	–	?
	Haplodiplatys tonkinensis (Hincks)	–	?
	Lobodiplatys lamotti (Hincks)	–	?
	Schizodiplatys angustatus (Burr)	–	?
	Schizodiplatys karnyi (Borelli)	–	?
	Schizodiplatys mixtus (Borelli)	–	?
Forficulidae	*Allodahlia scabriuscula* (Serville)	1 mm/0.53/— /*n* = 1	Probably yes
	Anechura bipunctata (Fabricius)	0.9 mm/0.52/0.02/*n* = 10	No
	Apterygida media (Hagenbach)	0.6 mm/0.53/0.02/*n* = 8	Wing remnants
	Chelidurella acanthopygia Gene	–	Wingless
	Chelidura pyrenaica (Bonelli)	–	Wing remnants
	Forficula auricularia Linnaeus	0.67 mm/0.53/0.03/*n* = 10	No
		0.7 mm/0.48/0.02/*n* = 5	Yes
	Forficula pubescens Gene		Wing remnants
	Pseudochelidura sinuata Lafresnaye	–	Wingless
Karschiellidae	*Karschiellia camerunensis* Verhoeff	3 mm/0.85/ — /*n* = 1	Wingless
Labiduridae	*Forcipula trispinosa* (Dohrn)	1.1 mm/0.64/0.01/*n* = 2	No
	Labidura riparia (Pallas)	1 mm/0.63/0.04/*n* = 5	No
	Labidura truncata Kirby	1 mm/0.64/0.03/*n* = 10	Wing remnants
	Nala livipes (Dufour)	0.75 mm/0.63/0.04/*n* = 10	No
Pygidicranidae	*Cranopygia marmoricrura* (Audinet-Serville)	3 mm/1.25/ — /*n* = 1	?
	Cranopygia spec.	1.7 mm/1/ — /*n* = 1	No
	Dacnodes shortridgei (Burr)	2.7 mm/1.31/0.10/*n* = 3	No
	Echinosoma sumatranum (DeHaan)	0.88 mm/0.73/ — /*n* = 1	Yes
	Echinosoma wahlbergi Dohrn	0.8 mm/0.59/ — /*n* = 1	Probably yes
	Pyragra fuscata Audinet-Serville	1.5 mm/0.65/ — /*n* =1	Probably no
	Tagalina erythronota Günther	2.75 mm/1.32/ — /*n* = 1	No
Spongiphoridae	*Labia minor* (Linnaeus)	0.3 mm/0.53/0.03/*n* = 1	Yes
	Marava arachidis (Yersin)	0.5 mm/0.49/0.02/*n* = 5	Yes
	Nesogaster rufipes (Erichson)	1 mm/0.5/0.00/*n* = 2	Wing remnants

Three species of Blattodea (Table 1) have been included in the phylogenetic reconstruction as outgroups to elucidate the evolution of the characters wherever possible. According to Kukalova-Peck & Peck (1993) the Blattodea are closed related to the Dermaptera, which are the sister group to the Dictyoptera [relationships postulated: Dermaptera (Isoptera (Blattodea, Mantodea)].

Character description and Discussion

The following characters are used for the phylogenetic reconstruction.

Thorax and tegmina

1. Tegmina. 1: asymmetrical; 0: symmetrical. Own observations (Fig. 1).

2. Metanotum. 0: flat; 1: with median longitudinal groove. Own observations.

3. Spiny crest. 0: absent; 1: present. Verhoeff (1902a); Zacher (1911). Own observations.

4. Tegmina locking device. 0: absent; 1: present. Verhoeff (1902a); Zacher (1911). Own observations (Fig. 1).

These structures have already been described by Giles (1963) and Verhoeff (1902a). Therefore a short description will suffice.

There are, for example, in ***Forficula auricularia*** Linnaeus (Forficulidae) two rows of postero-median directed macrotrichiae which are situated besides a median groove of the metanotum. These two rows are named the tegmina locking device (Fig. 1A) and receive two rows, one on each tegmen, of macrotrichiae which are situated on the ventral side of the tegmina, close to their median margins. These macrotrichiae are situated on a ridge. The row and the ridge together are named the spiny crest. The tegmina overlap each other to improve the protective function (Fig. 1A). In dorsal view there is a undescribed character state with possible phylogenetic relevance. The left tegmen overlaps the right one. Its margin is well sclerotized and the overlapping zone begins right at the anterior margin of the tegmen, just in front of the spiny crest. The overlapping margin of the right tegmen is less sclerotized, almost translucent and begins anteriorly at about half the length of the spiny crest. However, this state is not found in all the examined Forficulina. ***Forficula auricularia*** has been chosen for the description on ground of its general availability.

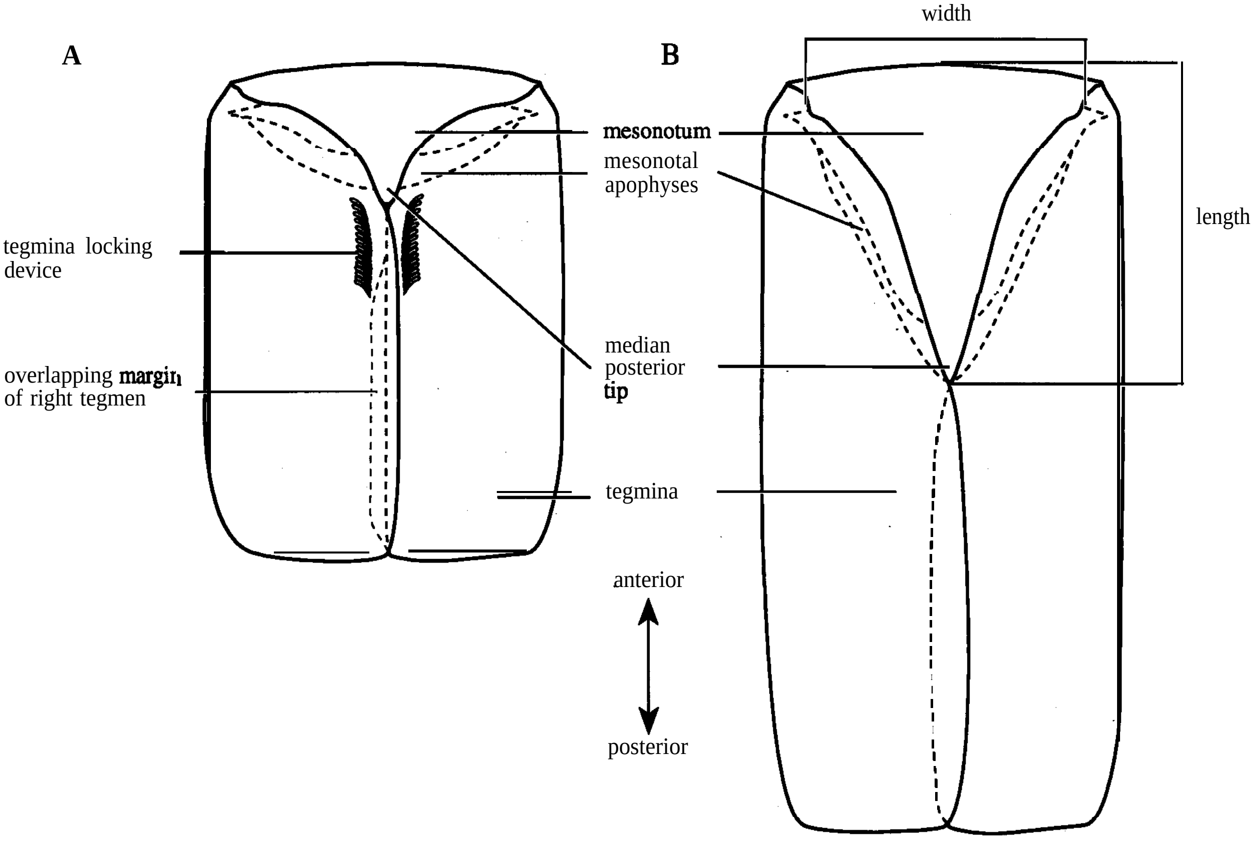

Fig. 1. Schematic dorsal view of the mesonotum with tegmina of different families of the Forficulina. The Chelisochidae, Forficulidae and Spongiphoridae possess a short mesonotum (A); the anterior margin of the tegmina is almost perpendicular to the body axis and the ratio of length divided by width is small. All other families possess a much longer mesonotum, as is shown in (B). The tegmina locking device is situated on the mesonotum (A) and is missing in ***Haplodiplatys*** ('Diplatyidae'), which at the same time possesses symmetrical tegmina that lack the broad and thin overlapping margin found in other families, which extends under the left tegmen. The broken lines indicate structures lying under the tegmina. Not to scale.

The reduced tegmina of *Karschiella camerunensis* Verhoeff (**Karschiellidae**) bear only a few macrotrichiae where one would expect the ridge on which they are normally situated. However, a distinct ridge has not been discernible. The metanotum possesses a few, very thin microtrichiae but they are unevenly distributed and not concentrated into a tegmina locking device. Furthermore, the metanotum is flat and lacks the longitudinal median groove, along which in other species, except for *HapZodipZatys* ***orientalis*** Steinmann ('Diplatyidae'), the tegmina locking device is found.

HapZodipZatys ***orientalis*** differs from all other examined species, including *DipZatys jacobsoni* Burr ('Diplatyidae') in possessing no tegmina locking device (Fig. **1B**). However, its metanotum possesses the longitudinal median groove along which other species bear the tegmina locking device. The tegmina of *Haplodiplatys orientalis* only show a weak spiny crest, and only a few weak macrotrichiae are discernible, situated on a ridge near the lower median margin of the tegmina. In *HapZodipZatys* ***orientalis*** they also overlap, but the shape of one tegmen is the mirror image of the other. There is no translucent overlapping margin, and consequently the situation resembles that found in the Blattodea.

Unfortunately it was not possible to examine more species of the 'Diplatyidae' in detail. However, I have examined the collections of that **taxon** in the BMNH and found some specimens of 'Diplatyidae' with slightly opened tegmina, so that it was possible to assess whether the metanotum was with or without a visible tegmina locking device. The examined species are not included in Fig. 7 because I was not allowed to dissect the specimens. Hence I could not establish the states for all characters and therefore the data matrix is incomplete. The results are rather preliminary and should be reassessed with more and dissectable specimens.

The following species have been found to lack a tegmina locking device: *Haplodiplatys siva* (Burr), *H. tibetanus* (Hinks), *H. bidentatus* (Hinks), ***H.severus*** (Bormans). ***Schizodiplatys angustatus*** (Burr), ***S.mixtus*** (Borelli), ***S.*** *karnyi* (Borelli), *DipZatys macrocephalus* (Palisot de Beauvois), ***D.jacobsoni*** Burr, *Haplodiplatys* ***rileyi*** (Hinks), ***H.rufescens*** (Kirby), *H. tonkinensis* (Hinks) and ***Lobodiplatys*** *Zamotti* (Hinks) have a tegmina locking device.

Little information has been published concerning the presence or absence of a tegmina locking device in the 'Diplatyidae', Karschiellidae and Pygidicranidae (Table 2). Verhoeff (**1902a**) mentioned a weak spiny crest in *DipZatys* ***raffrayi*** Dubrony ('Diplatyidae'). However, he did not explicitly mention the presence or the absence of the tegmina locking device in this species.

Concerning ***Karschiella***, Verhoeff (**1902a:** p. 92) has written: '.. .nur die Gattung *Karschiella* Verh. **(...)** nimmt eine gewisse Mittelstellung ein, indem **Doppelbürste** und Stachelleisten zwar vorhanded aber schwach **sind, . . .**'. 'Nahtrippe vorhanden, aber nur mit **dünnen** Borsten. . . . Metanotum klein, **durch** die Elytren vollkommen verdeckt, zu Seiten der Mitterlrinne mit **verkümmerter**, nur **durch** kleine Borsten angedeuteter **Bürste.**' (Verhoeff, **1902b:** p. 183).

['...only the genus ***Karschiella*** Verh. **(...)** assumes a certain transitional position because tegmina locking device and spiny crests are only weakly developed, . ..'. 'Spiny crest present, but only with thin bristles. . . . metanotum small, completely covered by the elytra, alongside the median groove with reduced, only indicated by small bristles, tegmina locking device.' Translation by the author].

Verhoeff (**1902a,** b) has obviously found macrotrichiae on the metanotum and on the lower side of the tegmina. He has interpreted the findings as a reduction of the once well-developed tegmina locking device and spiny crest **accompaying** the reduction of the wings. However, in my view, the following observations suggest that these two structures have never been developed in *Karschiella camerunensis.*

First, the metanotum of *Karschiella camerunensis* is flat and possesses no longitudinal median groove, whereas the metanota in other Forficulina have a well-developed groove. Its shape shape shows great similarity to the shape of the flat metanota of those Blattodea, which I have been able to examine.

Second, I regard a secondary reduction of the tegmina locking device to be improbable because in many species, e.g. *Apterygida media* (Hagenbach) **(Forficulidae)** and ***Forficula pubescens*** Gene **(Forficulidae)** the tegmina locking device and the tegmina are well developed but'wings are reduced or absent. The same is true for *Dacnodes* ***shortridgei*** (Burr) (Pygidicranidae), ***Cranopygia*** sp. (Pygidicranidae), *Labidura* ***truncata*** Kirby (Labiduridae) and ***Nesogaster rufipes*** (Erichson) (Spongiphoridae). In *Pseudochelidura sinuata* Lafresnaye **(Forficulidae)** the tegmina are reduced to flap-like protrusions but the tegmina locking device and the spiny crest are still well developed. The wings are completely reduced.

Obviously the tegmina locking device and the spiny crest are reduced very late in phylogeny, much later than the wings, as in ***Gonolobis*** *maxima* **(Brullé)** (Anisolabididae). In this species even the tegmina are reduced. *HapZodipZatys* ***orientalis***, however, is fully winged and possesses a well-developed spiny crest. *Karschiella camerunensis,* on the other hand, is wingless with well-developed tegmina. Yet there is not trace of a tegmina locking device and spiny crests, and so it strongly resembling species within the Blattodea.

Both the great similarity to the metanotum of the Blattodea and the improbable secondary reduction of the tegmina locking device and spiny crest suggest that these structure have never been developed in *Karschiella camerunensis.*

How useful is a spiny crest without the tegmina locking device on the metanotum? The metanotum of *HapZodipZatys* ***orientalis*** does not form a flat plate but has a more or less pronounced median longitudinal groove. A weak spiny crest, as it is found in the *HapZodipZatys orientalis,* could interfere with this groove, thus preventing the sliding apart of the tegmina even without a tegmina locking device. Thus, a spiny. crest without tegmina locking device is functional and possibly a 'stage' or **pre**-adaptation in the evolution of a complete spiny crest-tegmina locking device system. It would be interesting to examine whether there are any differences, which are correlated to tegmina opening, in the thorax musculature of the Forficulina.

Besides this, I cannot imagine any reason why a tegmina locking device should be reduced at all. As verified by experiments, the tegmina locking device, together with the spiny crest, locks the tegmina very well to the metanotum and prevents the sliding apart of the tegmina. They not only protect the wings but the whole metanotum and, more important, the third thoracic stigma. Therefore there is more than one reason -just protection of the wings **–** why a tegmina locking device is useful for species which move in crevices of all kind, so a secondary reduction of this structure seems unlikely.

The three examined outgroup Blattodea possess symmetrical tegmina, a flat metanotum without median groove, no spiny crest and no tegmina locking devices. My own observations and the literature on characters 1-4 lead me to the conclusion that the possession of asymmetric tegmina, a spiny crest, the longitudinal median groove of the metanotum and a tegmina locking device are all synapomorphies.

5. Mesonotal ratio. 0: high (over 0.55); 1: low (under 0.54). Own observations.

6. Median posterior tip. 0: lightly sclerotized, not pronounced; 1: heavily sclerotized, well marked. Own observations.

7. Cranial margin of tegmen. 0: curved; 1: straight. Own observations.

The mesonotal ratio described here for the first time is calculated by dividing the length of the mesonotum by its width (Fig. 1 B). The measurements demonstrate that the Anisolabididae, Spongiphoridae, Forficulidae and Chelisochidae are distinct from the remaining families in having a low value. The ratio of all other species measured is high (Table 1). In those species with a low ratio the cranial margin of the tegmen is almost straight and nearly perpendicular to the longitudinal body axis. The median posterior tip of the mesonotum is pronounced and heavily sclerotized.

In species with a high ratio, the cranial margin of the tegmen is curved and has a small angle to the longitudinal body axis (Fig. 1B). The median posterior tip of the mesonotum of these Forficulina is not well marked and only lightly sclerotized. High ratios (0.59-1.40) are found in Apachyidae, ‘Diplatyidae’, Karschiellidae, Labiduridae and Pygidicranidae.

Table 1 also demonstrates that the ratio is independent of the length of the mesonotum and therefore of the body size of the species investigated.

Leucophaea madera (Fabricius) (Blaberidae), *Periplaneta americana* (Linnaeus) (Blattellidae) and *Polyphaga aegyptica* (Linnaeus) (Polyphagidae) have high ratios (Table 1), a lightly sclerotized median posterior tip of the mesonotum, and a curved cranial margin of the tegmina. Hence, I consider a low ratio, a strongly sclerotized tip and a straight margin of the tegmina as a synapomorphy for Anisolabididae, Spongiphoridae, Forficulidae and Chelisochidae.

The functional significance of a short mesothorax is not understood. The centre of gravity if shifted cranially by a compression of the mesothorax which may have implications for flight ability. A short mesothorax might be confined to species that fly well, so it could be convergent. This question could be elucidated by data on flight capabilities of different species of Forficulina. However, these data are lacking. On the other hand, the ratio of 0.53 (Table 1) for *Apterygida media,* which possesses only small wing remnants, demonstrates that this ratio is to a certain extent independent of the flight capability and wing reduction.

In *Forficula auricularia* and *Labia minor* (Linnaeus) (Spongiphoridae) Kleinow (1966) has found that the groove in the mesonotum serves as a hinge for the tegmina. Evidently this is only possible when the grooves are nearly perpendicular to the longitudinal body axis. If species with a long curved cranial margin used this groove, the tegmina would collide there. How species with curved tegmina margins open their tegmina is unknown.

Hindwing

8. Marginal area. 0: absent; 1: present. Verhoeff (1917). Own observations.

The marginal area is situated in front of the squama and is about half the length of the squama in *Forficula auricularia* (Fig. 2). It differs from the squama in being less sclerotized; its distal end meets the squama at an angle (Fig. 2).

A distinct marginal area of this specific kind has not been found in the Blattodea, ‘Diplatyidae’, Pygidicranidae and Apachyidae. Therefore it is considered to be synapomorphic for the other families.

The functional significance of the marginal area in the Forficulina is completely unknown and it remains uncertain whether or not it lies pre-costal.

9. Cross vein. 0: in front of bend; 1: behind the bend. Own observations.

10. Cu2. 0: indistinct. 1: distinct. Giles (1963). Own observations.

11. Concave longitudinal fold. 0: median; 1. lateral. Kleinow (1966). Own observations.

The concave longitudinal fold (Fig. 3) runs anteriorly (in the folded wing, dorsal view) from about the middle of the median margin of the squama and ends at the height of a cross vein which arises from the first anal. This cross vein does not reach Cu2 (Fig. 3) and it marks the anterior end of the concave longitudinal fold. Hence the concave longitudinal fold is well defined by sclerotized areas (Fig. 3) and a cross vein. It counteracts the bending forces between squama and ulnar area in the unfolded wing (Kleinow, 1966).

As I am not dealing with the homology of veins and folds in this article, I adopt the nomenclature of Giles (1963) and Kleinow (1966) for this description. In the nomenclature introduced by Wootton (1979), the Cu2 probably corresponds to the CuP and the concave longitudinal fold would be called a flexion line.

In the Pygidicranidae, *Haplodiplatys orientalis* and *Diplatys jacobsoni,* this fold makes a small angle with the median margin of the squama. This cross vein lies just in front of the lateral bend of the first anal, being far from the median plate. The complete Cu2 is visible as a distinct vein, obviously forming an articulation with the next anterior vein.

In all other taxa this folding line has a less acute angle to the median margin of the squama. The end of the fold is still marked by the short cross vein arising from the first anal. This cross vein lies behind the lateral bend of the first anal, just in front of the median plate. Cu2 has disappeared as a distinct vein, only its base being visible, forming an articulation with the next vein. The concave longitudinal fold is accompanied by a large, more sclerotized area on the right of the fold in Fig. 3 and a smaller one on the left side of the fold. These areas are well marked in *Chelisoches morio* (Fabricius) (Chelisochidae) but less well marked in other species. These areas are not visible in the Pygidicranidae, *Haplodiplatys orientalis* and *Diplatys jacobsoni.* Giles (1963) noted the absence of Cu2 in *Forficula auricularia.* My observations demonstrate its presence in all familes examined. The observation leading Giles to his conclusion was the lateral shift of the concave longitudinal fold (in the folded wing; Fig. 3), which is seemingly incompatible with a distinct Cu2 vein. However, in all specimens examined the articulation of Cu2 with

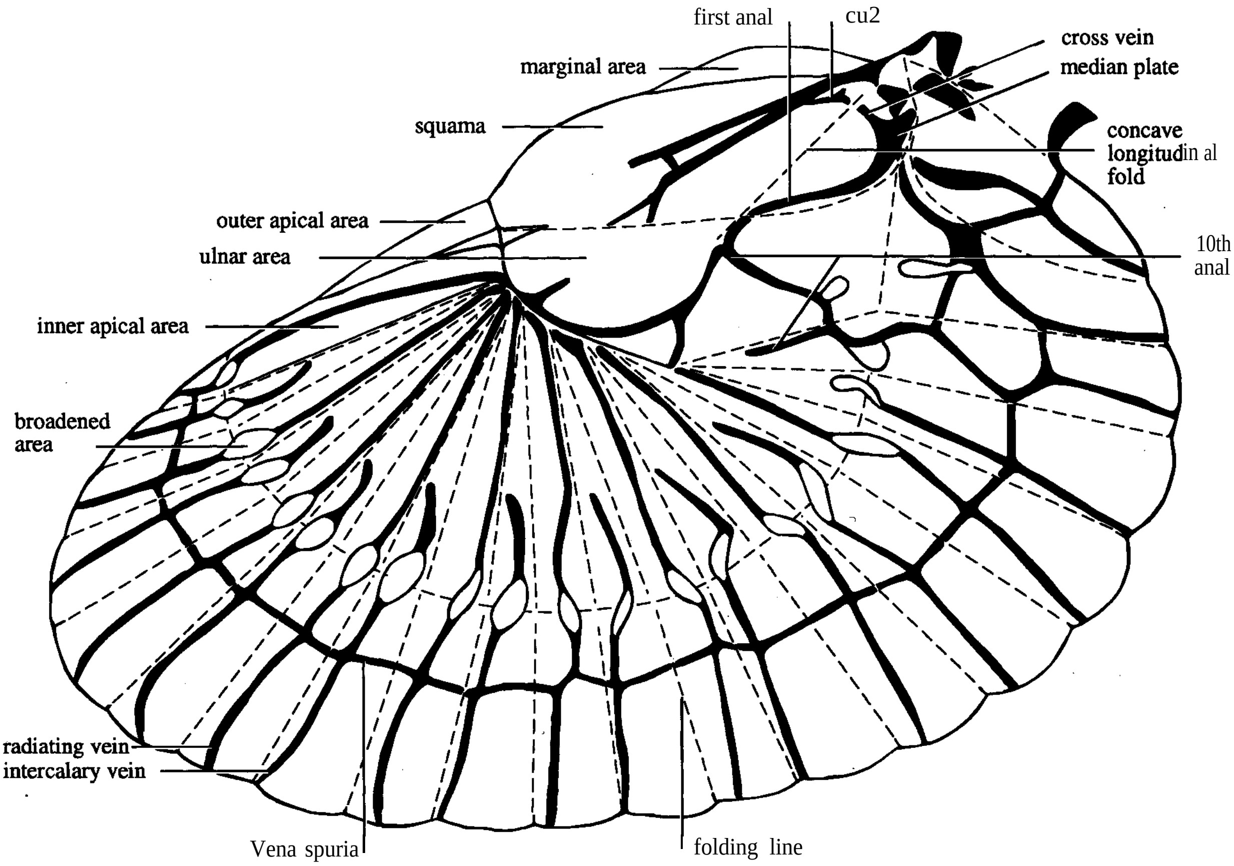

Fig. 2. Left hindwing of *Forficula auricularia* (Forficulidae). Note that the tenth analis '4'-shaped (cf. Fig. 4). Modified from Kleinow (1966).

the next anterior vein is clearly visible.

In the three species of Blattodea the Cu2 is distinct and this condition is therefore considered to be plesiomorphic. Characters 9 and 11 are closely related to the special wing folding pattern of the Dermaptera and are therefore not found in the Blattodea. A small cross vein in front of the lateral bend of first anal and a medially lying concave longitudinal fold are probably plesiomorphies. The state found in Apachyidae, Labiduridae, Anisolabididae, Spongiphoridae, Chelisochidae and Forficulidae (small cross vein just behind median plate; Cu2 indistinct, only its base visible; sclerotized areas accompany concave longitudinal fold) is considered to be a synapomorphy for these families.

12. Tenth anal. 0: 'Y'-shaped; 1: '4'-shaped. Beier (1959); Burr (1914); Zacher (1911). Own observations.

This character has been described by Zacher (19 11) and has been used in the key for the identification of Dermapteran subfamilies by Beier (1959). In the Labiduridae, Anisolabididae, Spongiphoridae, Forficulidae and Chelisochidae the shape of the tenth anal resembles the number 4 (Fig.2), whereas in all other families the shape is more Y-like (Fig. 4). This has been confirmed by my own observations.

The venation pattern of the wings of *Leucophaea madera*, *Periplaneta americana* and *Polyphaga aegyptica* is completely different from that of the Dermaptera. Hence, they do not show which character state is the plesiomorphic one. The tree suggests that the state found in Anisolabididae, Chelisochidae, Forficulidae, Labiduridae and Spongiphoridae is a synapomorphy.

13. Broadened areas of radiating and intercalary veins. 0: connected, 1: separated. Giles (1963). Own observation.

Both radiating and intercalary veins have broadened areas about the ring fold (Fig. 2).

In all taxa except the Spongiphoridae, Forficulidae and Chelisochidae the broadened area of each radiating vein is extended, across the adjacent radiating folding line, to meet an extension of the broadened area of the intercalary vein which lies behind the radiating vein (Fig. 5).

Giles (1963) noticed the fusion of the broadened areas of radial and intercalary vein in *Echinosoma afrum* (Palisot de Beauvois) (Pygidicranidae); however, he did not discern that the areas are seperate in the higher Forficulina.

The wings of the examined Blattodea do not possess broadened areas or similar structures. The tree suggests that the situation found in the Spongiphoridae, Forficulidae and Che'lisochidae is a synapomorphy for those families.

Neck and legs

14. Neck. 0: blattoid-type; 1: forficuloid-type. Popham (1959, 1985); Steinmann (1986).

The structure of the neck has been used for phylogenetic purposes in the Forficulina and is well founded. All taxa except

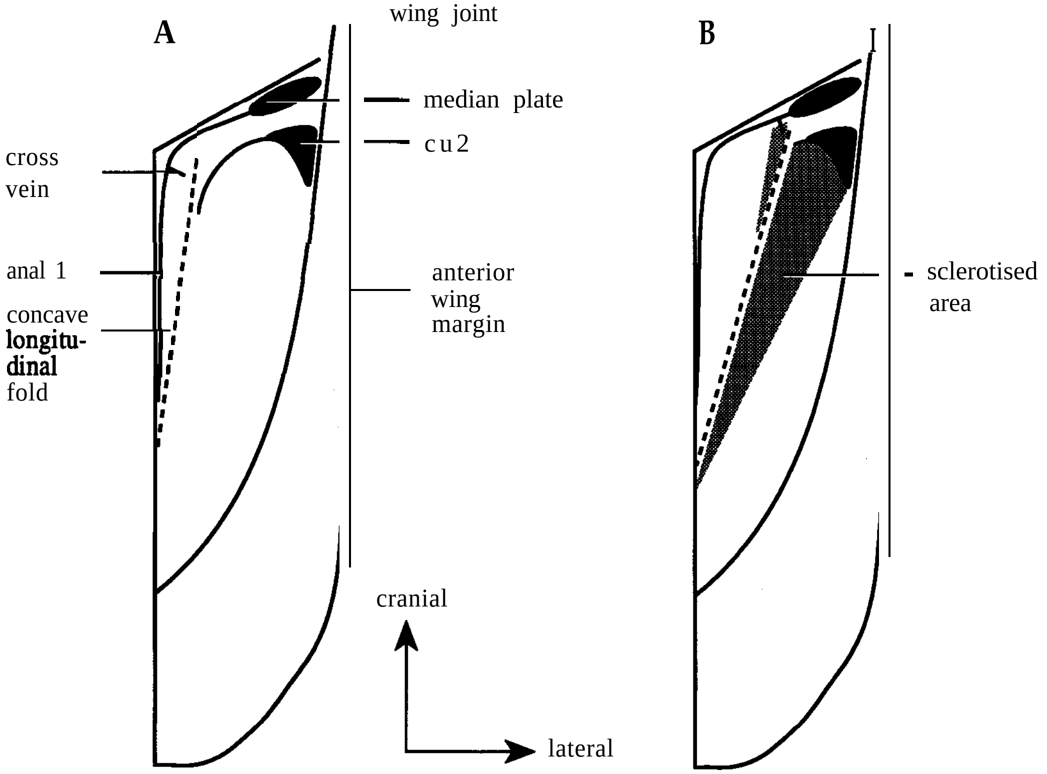

Fig. 3. Right wing-packages of different genera of Forficulina showing concave longitudinal fold, cross vein and Cu2; dorsal view. (A) Situation found in ***Haplodiplatys*** ('Diplatyidae'), ***Diplatys*** ('Diplatyidae') and Pygidicranidae. (B) Situation found in Apachyidae, Labiduridae, Anisolabididae, Spongiphoridae and Forficulidae. Not to scale. The nomeclature is adopted from Giles (1963).

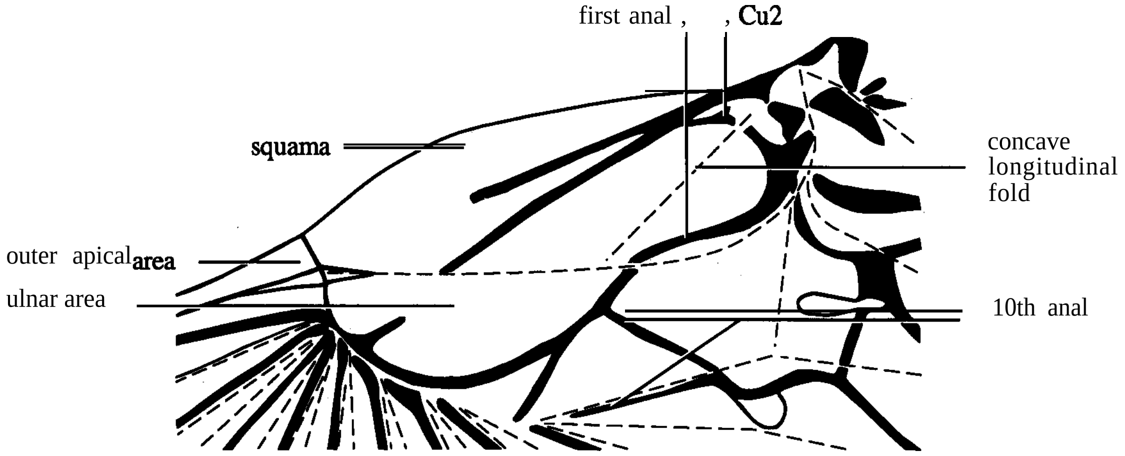

Fig. 4. Schematic view of a left hindwing which demonstrates a 'Y'-shaped tenth anal (cf. Fig. 2).

Karschiellidae, 'Diplatyidae' and the Pygidicranidae possess a 'forficuloid-type' neck which is considered to be a synapomorphy for these taxa (Popham, 1985).

The examined Blattodea resemble the blattoid-type and it is therefore assumed that this is plesiomorphic.

15. Femur. 0: carinate; 1: 'round'. Burr(19 10). Own observations.

The femurs of the 'Diplatyidae', Karschiellidae and Pygidicranidae posses on their ventral side two very distinct keels and are therefore called carinate. In the other taxa the femur is much more rounded; no distinct keel is visible. The Apachyidae occupy a more or less intermediate or transitional position in this respect, possessing rounded keels. Nonetheless they are considered to be plesiomorphic in this character (a different assignment would not influence the reconstruction).

The carinate condition is considered to be plesiomorphic because *Leucophaea madera* and *Periplaneta americana* possess

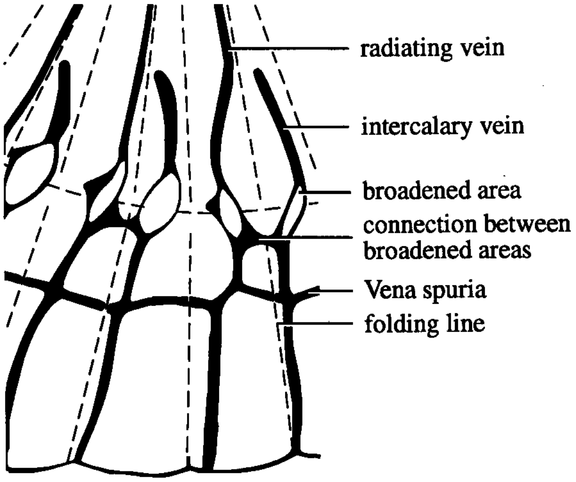

Fig. 5. Schematic view of a right hindwing of *Echinosoma sumatranum* (Pygidicranidae) showing the connection between the broadened areas of adjacent radiating and intercalary veins, which is also found in 'Diplatyidae', Apachyidae, Labiduridae and Anisolabididae.

carinate femora, although they are rounded in *Polyphaga aegyptica*. This is thought to be a secondary development. A rounded femur is considered to be apomorphic in the Forficulina.

16. Number of tarsomeres. 0: five; 1: three. Gunther & Herter (1974). Own observations.

All examined taxa of the Forficulina possess tarsi with three tarsomeres, which is considered to be apomorphic, because the examined outgroup Blattodea possess tarsi with five tarsomeres.

17. Tenth abdominal segment. 0: normal; 1: dilated. Steinmann (1986, 1989, 1990, 1993).

A dilation of the tenth abdominal segment is exclusively found in the Apachyidae and is considered to be an autapomorphy. The examined Blattodea as well as all other Forficulina (Steinmann, 1986, 1989, 1990, 1993) show no such dilation.

18. Larval cerci. 0: unsegmented; 1: segmented. Green (1896); Steinmann (1986, 1989, 1990, 1993); Verhoeff (1902b); Vishnyakova (1980).

There are only two reports of taxa with larvae which possess setgmented cerci: Verhoeff (1902b) on Karschiellidae and Green (1896) on *Diplatys* (Table 2). All other taxa obviously possess unsegmented cerci (Steinmann, 1986, 1989, 1990, 1993). Inferring from the fossil record (Vishnyakova, 1980) segmented cerci is a symplesiomorphy for Karschiellidae, *Diplatys* and probably *Haplodiplatys*. Furthermore, the larvae of the Blattodea possess segmented cerci. Unsegmented larval cerci are considered to be a synapomorphy of all other families.

19. Adult cerci. 0: segmented; 1: unsegmented. Steinmann (1986, 1989, 1990, 1993). Own observations.

A survey of the data given by Steinmann demonstrates that all Recent adult Forficulina possess unsegmented cerci. This is considered to be apomorphic because the three examined species of Blattodea possess segmented cerci.

20. Segmentation of telson. 0: fused; 1: segmented Popham (1985); Verhoeff (1903).

The telson or pygidium consists of three parts which are fused in the Anisolabididae, Apachyidae, Chelisochidae, Forficulidae, Labiduridae and Spongiphoridae.

In accord with Popham (1985), I regard the segmented condition to be a plesiomorphic character state and the fused one an apomorphy.

Male genitalia

21. Number and direction of penes. 0: two penis lobes unidirected; 1: two penis lobes bidirected; 2: one penis lobe; 3: karschellid-type. Hincks (1955, 1959); Steinmann (1986, 1989, 1990, 1993).

22. Total number of virgae. 0: one; 1: two; 2: four. Hincks (1955, 1959); Steinmann (1986, 1989, 1990, 1993).

23. Basal vesicle. 0: absent; 1: present. Hincks (1955, 1959); Popham (1965a, b, 1985); Steinmann (1986, 1989, 1990, 1993).

The Pygidicranidae and the 'Diplatyidae' possess male genitalia with two penis lobes, which are pointing in one direction (unidirected). However, the 'Diplatyidae', Pyragrinae and Esphalmeninae possess two virgae, which are the ejaculatory ducts in the Dermaptera, in each lobe, whereas the remaining subfamilies of the Pygidicranidae possess only one virgae in each lobe.

The Anisolabididae, Apachyidae and Labiduridae posses genitalia with two penis lobes; however, they are pointing in different directions (bidirected). Each of the lobes possesses one virga. In the Chelisochidae, Forficulidae and Spongiphoridae one penis lobe is reduced so only one lobe is left, which has one virga.

The Karschiellidae also posses male genitalia with only one penis lobe; however, the second lobe is still visible as a vestige. The single virga is surrounded by several twisted sclerites. The structure is clearly different from that found in the Chelisochidae, Forficulidae and Spongiphoridae and is therefore regarded as a separate character state. The basal vesicle is a small vesicle at the base of the virga of unknown function. It is found in the Apachyidae, Chelisochidae, Labiduridae and Forficulidae.

Discussions of relationships within the Dermaptera have generally been focused on the male genitalia. It was Burr (1915a, b, 1916) who. first realized their usefulness, founded on the work of Verhoeff (1902b) and Zacher (1911). The genitalia proved to be highly useful for the identification of taxa at any level and are therefore extensively used for diagnostic purpose. The male genitalia of the Dermaptera are highly derived, therefore outgroup comparison has not been possible.

The published descriptions are consistent for characters 21, 22 and 23 and so they are included in the reconstruction. The tree suggests that the last common ancestor possessed male genitalia with two unidirected penis lobes, four virgae and no basal vesicle. It also suggests that the genitalia with one penis lobe found in the Chelisochidae, Forficulidae and Spongiphoridae is an apomorphy.

Characters not used in the reconstruction

The following characters are not used in the reconstruction because the published descriptions proved to be inconsistent or in disagreement with my observations. They are listed here because the characters have been used by previous workers and a reassessment seems useful. They are not listed in Table 3.

Table 2. The occurrence of spiny crest, tegmina locking device and segmented larval cerci in the genera of 'Diplatyidae' and Karschiellidae. All other genera of the Forficulina possess a spiny crest, a tegmina locking device and unsegmented larval cerci, hence they are not listed here. It has not been possible to dissect the museum specimens, so the presence or absence of the spiny crest could not always be established. '–': data not available.

Family Genus	Spiny crest	Tegmina locking device	Remark/structure of larval cerci	Literature
'Diplatyidae'				
Circodiplatys	–	–	Tegmina and wings present.	Steinmann (1986)
Diplatys jacobsoni	yes	yes	Tegmina present; wings more or less developed; spiny crest only weakly developed. Larval cerci segmented. Verhoeff (1902a) has not mentioned a tegmina locking device.	Own observations; Green (1896); Steinmann (1986); Verhoeff (1902a)
D. macrocephalus	–	yes	Wings present; museum specimen, not dissectable.	Own observations
Haplodiplatys bidentatus	–	no	Wings present; museum specimen, not dissectable.	Own observations
H. orienatlis	yes	no	Wings present; museum specimen, not dissectable.	Own observations
H. rileyi	–	yes	Wings present; museum specimen, not dissectable.	Own observations
H. rufescens	–	yes	Wings present; museum specimen, not dissectable.	Own observations
H. severus	–	no	Wings present; museum specimen, not dissectable.	Own observations
H. siva	–	no	Wings present; museum specimen, not dissectable.	Own observations
H. tibetanus	–	no	Wings present; museum specimen, not dissectable.	Own observations
H. tonkinensis	–	yes	Wings present; museum specimen, not dissectable.	Own observations
Lobodiplatys lamotti	–	yes	Wings present; museum specimen, not dissectable.	Own observations
Schizodiplatys angustatus	–	yes	Wings present; museum specimen, not dissectable.	Own observations
S. karnyi	–	yes	Wings present; museum specimen, not dissectable.	Own observations
S. mixtus	–	yes	Wings present; museum specimen, not dissectable.	Own observations
Karschiellidae				
Karschiella	no	no	Tegmina more or less developed, wings absent. Tegmina locking device and spiny crest only weakly developed or not developed (see text). Larval cerci segmented.	Own observations; Steinmann (1986); Steinmann (1986);
Bormansia	no	no	Tegmina and wings absent. Larval cerci segmented.	Verhoeff (1902a, b)

Characters not used in the reconstruction

The following characters are not used in the reconstruction because the published descriptions proved to be inconsistent or in disagreement with my observations. They are listed here because the characters have been used by previous workers and a reassessment seems useful. They are not listed in Table 3.

24. Veins of squama. 0: without cross-connection; 1: with cross-connection. Burr (1914); Zacher (1911). Own observations.

25. Third vein of squama. 0: without sector; 1: with sector. Burr (1914); Zacher (1911). Own observations.

The venation was used early in the literature (Zacher, 1911) for systematic purposes. My reassessment of these two characters demonstrates, however, that they are not readily established. Their perception depends on the illumination – incident or transmitted light – and on the microscope used – with or without stereo-microscope. Moreover, examination of *Nala Zivipes* (Dufour) (Labiduridae) and *Marava arachidis* (Yersin) (Spongiphoridae) yields results that contradict those published by Zacher (19 11) and Burr (1914). It has not been possible to establish which character state is the plesiomorphic and which is the apomorphic because the examined Blattodea have a completely different venation pattern. Therefore these characters are not used in the phylogenetic reconstruction.

26. Second tarsomere. 0: normal; 1: forficuloid-type lobed; 2: chelisochoid-type lobed. Popham (1965a, b, 1985). Own observations.

Table 3. Character distribution for the examined taxa. '–': character not applicable.

Character	12345678901234567890123
Blattodea	
Leucophaea madera	*oooooooo*- 1---0000101---
Periplaneta americana	*oooooooo*-1---0000101---
Polyphaga aegyptica	*oooooooo*-1---0100101---
Dermaptera	
Karschiellidae	0000000 -----0010111300
Haplodiplatys orientalis	*01100000010000010111020*
Diplatys jacobsoni	*11110000010000010111020*
Pygidicranidae	11110000010000010011010
Apachyidae	11110000101001011010111
Labiduridae	11110001101101110010111
Anisolabididae	11111111101101110010110
Spongiphoridae	11111111101111110010200
Chelisochidae	11111111101111'110010201
Forficulidae	11111111101111110010201

According to Popham (1965a, b, 1985) the Labiduridae (including the Apachyidae), Forficulidae and Chelisochidae share a similar morphology of the second tarsal segment: it is more or less prolonged so that the third tarsal segment inserts somewhat dorsally and not terminally. The Chelisochidae and Forficulidae, then, evolved a prolonged tarsal segment which is bilobed. The

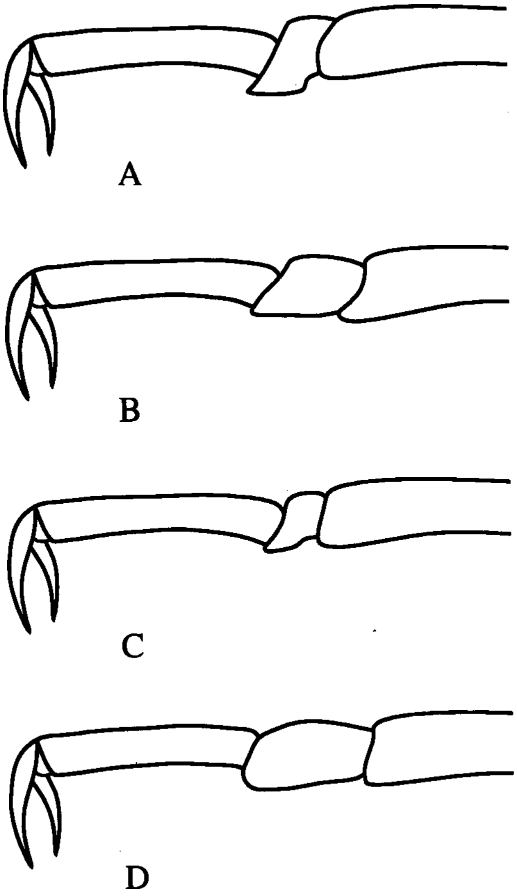

Fig. 6 . Tarsal segments of (A) ***Euborellia** moesta* (Anisolabididae), (B) ***Marava arachidis*** (Spongiphoridae), (C) ***Nala** Zivipes* (Labiduridae), and (D) ***Labidura riparia*** (Labiduridae). There is no marked difference in the morphology of the second tarsal segment of the Anisolabididae and Spongiphoridae on one hand and the Labiduridae on the other. For further explanation see text. Not to scale.

Labiduridae (including Apachyidae), Forficulidae and Chelisochidae are, with reference to this character thus more closely related to each other than to the Anisolabididae and the Spongiphoridae, in which the third tarsal segment is inserted terminally on the second tarsal segment. The latter two families retain the plesiomorphic character state in this respect **(Popham, 1985).** However, with the material available it has not been possible to establish a clear distinction between both groups.In contrast, the transition from a ventrally and distally prolonged second tarsal segment to a simple second tarsal segment is rather gradual (Fig. 6). My view is supported by Rentz **& Kevan** (1991) who, in a key to Australian Dermaptera, state that the third tarsal segment arises more or less dorsally or terminally.

Because of this discrepancy, this character is not included in the phylogenetic reconstruction. Nonetheless, the particular morphology of the second tarsal segment of Forficulidae and Chelisochidae is believed to be a synapomorphy for these two families. Inferring from outgroup comparison, the tarsal morphology found in the Pygidicranidae, which is virtually identical to that found in the Blattodea, is considered to be plesiomorphic.

27. Gut. 0: straight, 1: coiled to the left; 2: coiled to the right. **Popham (1965a,** 1985). Own observation.

According to **Popham (1965a)** the gut of the Forficulidae and Chelisochidae is coiled to the left side of the specimen, thus the transverse loop of the mid-gut lies ventrally of the hind-gut, whereas in the Spongiphoridae the gut is coiled to the right. The Labiduridae have been found to have a straight gut **(Popham, 1965a).** In 1985 **Popham** took the coiling to the left as a synapomorphy for Labiduridae, Forficulidae and Chelisochidae although the Labiduridae have, according to his results **(Popham, 1965a),** a straight gut. Furthermore, he has used the character of gut-coiling twice (as characters **8** and 13; **Popham** 1985) at two different levels in his **clade.** This procedure is questionable. My observations have shown that, in contrast to **Popham's** results, the gut of ***Forficula auricularia*** coils to the right and the mid-gut crosses the hind-gut dorsally. In *Labia minor* the same situation has been encountered, besides two situations, in which the gut has no loop but is 'S' **-** or 'Z-shaped, respectively. ***Nala** Zivipes,* a species of the Labiduridae, has been found to have a straight gut in some specimens, but a gut which is coiled to the left side in other specimens. Species of other families have not been available in adequate numbers and states of preservation to establish character states.

Obviously there are discrepancies, therefore this character has not been used for phylogenetic reconstruction. Seemingly, a straight gut is a symplesiomorphy for the Forficulina; however, this must be confirmed or rejected by further research.

28. Gonapophyses. 0: absent; 1: present. Giles (1963); Hinks (1955, 1959); **Popham (1965a,** 1985); Steinmann (1986).

Hincks (1955, **1959),** as well as **Popham (1985),** report that the Pygidicranidae (including Karschiellidae and 'Diplatyidae' but excluding the Pyragrinae) still possess the gonapophyses, whereas all other families have lost them. However, **Popham (1965a)** notes that there are vestigial structures which he regards as gonapophyses in ***Labidura riparia* (Pallas)** (Labiduridae). There seems to be a rather gradual reduction of the gonapophyses. Furthermore, material has not been available for my own observations, so the character is not used for phylogenetic reconstruction. The possession of gonapophyses is regarded to be the plesiomorphic character state **(Popham, 1965a).** The Blattodea posses gonapophyses.

29. Auxillary sclerites at the base of virgae. 0: absent; 1: present. Brindle (1965); Hincks (1955, 1959); **Popham (1965a,** 1985); **Popham &** Brindle **(1966);** Steinmann **(1986, 1989,** 1990, 1993).

30. Preputial sac sclerites. 0: absent. 1: present, Hincks (1955, 1959); **Popham (1965a,** 1985); Steinmann (1986, 1989, 1990, 1993).

Popham (1985), using evidence from the auxiliary and preputial sac sclerites, argues for a sister-group relationship between the Anisolabididae and Spongiphoridae. However, my survey of the data given by Steinmann demonstrates that not all Anisolabididae and Spongiphoridae possess sclerites at the base of the virga, and even more important these sclerites are not confined to these families. There are members of the Apachyidae and Labiduridae which possess auxiliary sclerites as well. The presence or absence of the preputial sac sclerite cannot be confirmed with the data given by Steinmann. Brindle(1965) notes for ***Gonolabidura*** (Labiduridae): 'The prominence of the sclerites associated with the virgae varies in different mounts of the same species, as does their orientation.' Popham & Brindle (1966) note concerning ***Brachylabis*** (Anisolabididae): 'the male genitalia have a virga without any additional sclerite'. The descriptions and opinions on these sclerites are obviously contradictory.

The genitalia of the examined Blattodea are completely different and do not help in the interpretation of these problems.

Results and Discussion

Analysing the twenty-three used characters (1-23) with PAUP 3.1 results in two, equally parsimonious, phylogenetic trees (tree length = 30; CI = 0.87) which are shown in Fig. 7. The branching order of the tree does not change with a change of the outgroup. It remains the same if two or all species of the examined Blattodea are chosen as outgroup.

An ideal phylogenetic system should be founded exclusively on monophyletic groups. Obviously the taxa at family level treated here are not well defined by autapomorphic characters, which are known for only four out of eight families. The Karschiellidae posses a distinct morphology of the male genitalia, the Apachyidae are well marked by a dilated tenth abdominal segment and the Forficulidae and Chelisochidae are well characterized by their respective tarsal morphology. It has been beyond the scope of this paper and beyond the available material to find new autapomorphic characters for the families. Therefore the monophyletic status of these families has not in general been questioned.

As the tree demonstrates however, the Pygidicranidae, *sensu* Popham and Steinmann (including Anataelinae, Blandicinae, Challinae, Cylindrogastrinae, 'Diplatyidae', Echinosomatinae, Esphalmeninae, Karschiellidae, Pygidicraninae and Pyragrmae) constitute a paraphyletic group. The Karschiellidae and the 'Diplatyidae' (the latter themselves paraphyletic), have to be excluded from the Pygidicranidae, as proposed by Sakai (1987). The remaining subfamilies probably do not constitute a monophyletic taxon because the Espahalmeninae and Pyragrinae have four virgae in total (Hincks, 1955, 1959), which is considered to be the plesiomorphic character state (see below). Hence, the other subfamilies share a synapomorphy – only two virgae – with the higher Forficulina. However, this point has not been investigated in detail due to a lack of material.

There is no synapomorphy which would define Pygidicranidae as a monophyletic taxon; indeed, there are synapomorphies which suggest other relationships. Previously (Popham, 1985; Steinmann, 1986), they have been placed in one family apparently by symplesiomorphic characters.

Surprisingly, the phylogenetic reconstruction does not support the monophyly of the 'Diplatyidae'. This is due to the retention of plesiomorphic character states in *Haplodiplatys orientalis,* which possesses symmetrical tegmina and lacks the tegmina locking device. These structures are found in *Diplatys jacobsoni.*

The lack of a tegmina locking device obviously splits the family 'Diplatyidae' and the genus *Haplodiplatys*. The 'Diplatyidae' and *Haplodiplatys* have been assumed to be monophyletic due to the morphology of the male genitalia (Sakai, 1987; Steinmann, 1986). However, at least some species of the genus *Haplodiplatys* and all examined species of the genera *Schizodiplatys*, *Diplatys* and *Lobodiplatys* share two apomorphies with the other Forficulina (except Karschiellidae): the possession of asymmetrical tegmina and a tegmina locking device. Hence, they are more closely related to these Forficulina than to the remaining species of *Haplodiplatys* and so the 'Diplatyidae' are considered to be paraphyletic.

Concerning the evolution of the male genitalia, the tree suggests that the last common ancestor of all Recent Forficulina had two unidirected penis lobes and four virgae in total. This situation is still found in the 'Diplatyidae', Esphalmeninae and Pyragrinae. The 'Diplatyidae' have been thought to constitute a monophyletic group due to the peculiar morphology of the male genitalia (possession of four virgae). However, no conclusive argument has been given to reject the view that genitalia with two penis lobes directed in one direction and four virgae are symplesiomorphic. On the other hand, there are characters, as pointed out above, which suggest the paraphyly of the 'Diplatyidae'. That view is adopted here.

Later the number of virgae was reduced to two, a condition which is (phylogenetically) found in the Pygidicranidae (see above).

After this one penis lobe changed its direction, resulting in genitalia in which the two penis lobes point in different directions. The Apachyidae, Labiduridae and the Anisolabididae represent this 'stage' in the evolution. However, as the tree shows, this is not a synapomorphy for these families as presently constituted. The Apachyidae, which are well defined by the morphology of their tenth abdominal segment, have to be excluded from the Labiduridae, as has been proposed by Verhoeff (1902b), Zacher (1911) and, more recently, by Steinmann (1989). There is no synapomorphy which would justify their inclusion in the Labiduridae, which has been based on the common morphology of the male genitalia.

As a last 'step' in the evolution, one penis lobe was reduced leading to genitalia with only one penis lobe, as is found in the Chelisochidae, Forficulidae and the Spongiphoridae. This is considered to be apomorphic for these families. Also, the genitalia of the Karschiellidae possess only one lobe. However, the structure of the penis is clearly different from the one found in the Chelisochidae, Forficulidae and the Spongiphoridae and the Karschiellidae are marked by many primitive character states. Therefore the structure of the genitalia of this family probably constitutes an autapomorphy.

The data given do not support the sister-group relationship of Anisolabididae and Spongiphoridae as proposed by Popham (1985). However, they confirm that both taxa are closely related to each other (Fig. 7), which could account for the similarities – especially the structures of the male genitalia, in which some taxa of the Anisolabididae and Spongiphoridae show an intermediate state between these families.

My view of the evolution of the male genitalia is in disagreement with Popham (1965a, 1985) who assumed that the last common ancestor had two unidirected penis lobes and two virgae in total. He also assumed that the condition found in the 'Diplatyidae' is a apomorphy and not a symplesiomorphy. The tree shown here does not support his view that Anisolabididae and the Spongiphoridae constitute a monophyletic group due to the possession of auxiliary sclerites. As discussed above, the descriptions of the auxiliary sclerites have been found to be

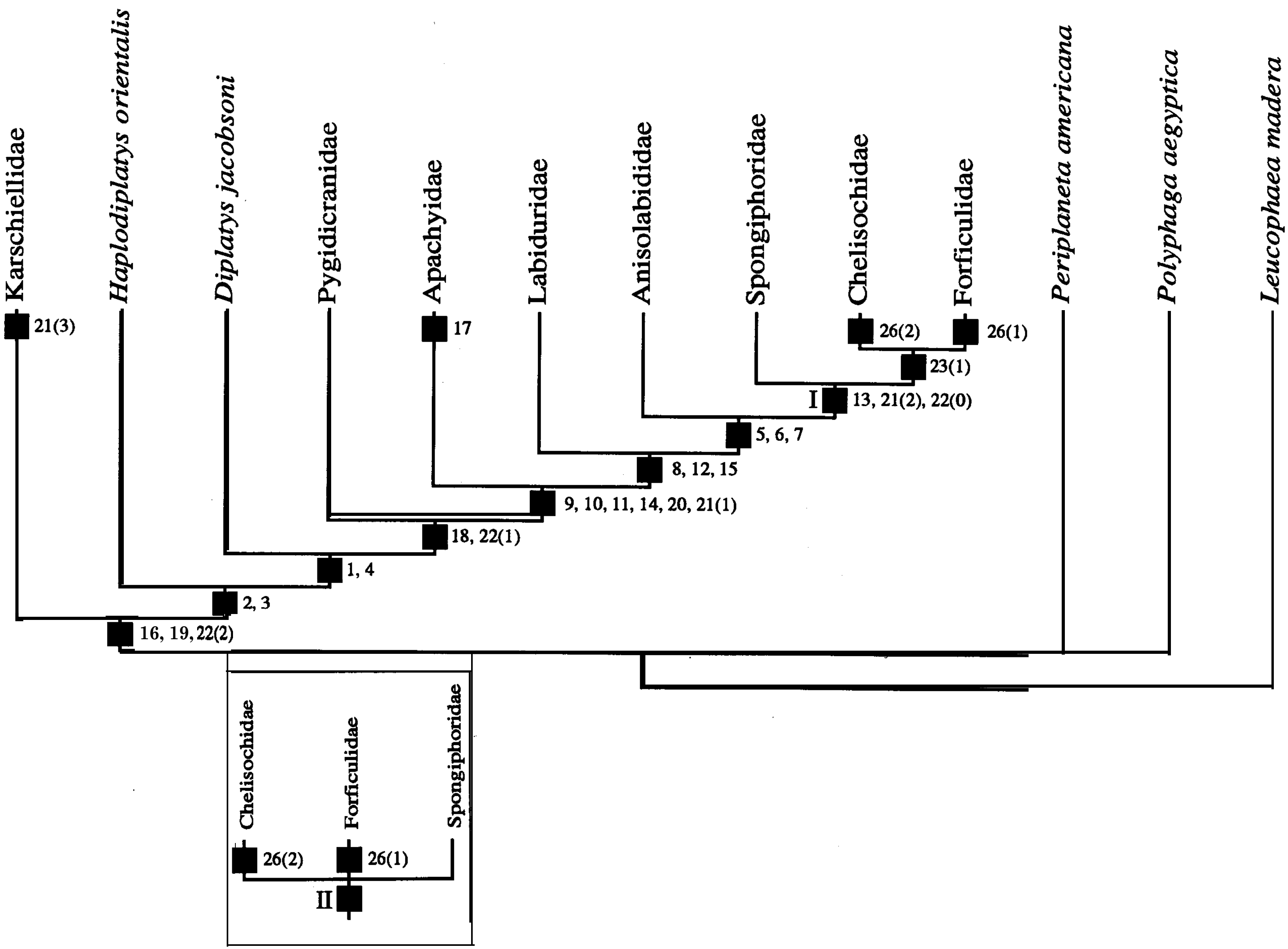

Fig. 7. The two equally parsimonious phylogenetic trees showing the apomorphies for the taxa. They result from the analyses of characters 1-23 with PAUP 3.1 (tree length = 30; CI = 0.87). At (I) the state of character 23 is equivocal, whereas at (II) the state of characters 13, 21, 22 and 23 are equivocal. Character 26 has not been used in the reconstruction but has been added afterwards. The inset shows that part of the second tree which differs from the first tree, all other parts are identical. The numbers in parentheses refer to the character states.

inconsistent and have therefore not been used here. Also, the reconstruction does not support **Popham's** (1985) view that the basal vesicle is a apomorphy for the Forficulidae, Chelisochidae and the Labiduridae (including Apachyidae). However, it does suggest that the basal vesicle is a synapomorphy for the Chelisochidae and Forficulidae.

This research has also shown that many of the **taxa** used by Steinmann **(1986, 1989, 1990, 1993)** and **Popham** (1985) are not monophyletic, for instance the term Mesodermaptera used by Steinmann (1989) refers to Labiduridae and Anisolabididae, which do not, together, form a monophyletic group. The **taxon** Laboidea, used by **Popham (1985),** refers to the Anisolabididae and Spongiphoridae, which do not constitute a monophyletic group either. I have not introduced new terms for monophyletic **taxa** found in this study, in order to prevent an explosion of the number of taxonomic groupings.

It should be a major task for further research to find autapomorphic characters for the **taxa** at every level. In my opinion, it would be no surprise to find that the Anisolabididae or Pygidicranidae (in the sense used here) are not monophyletic.

Conclusions

Previous phylogenetic research in the Forficulina has been almost completely confined to male genitalia, tarsal-structure and **neck**-structure. This originated in the work of Burr, Verhoeff and Zacher from 1900 to 1920. They considered the structures mentioned to be most reliable and later workers rejected the use of other characters, assuming a high degree of convergence, which is certainly true of characters such as forceps form and **wing**-reduction.

I have shown that other structures may indeed provide phylogenetic information, even the wings, which are very often reduced. However, by evaluating the degree of reduction it is possible to use wing-characters for phylogenetic reconstruction. I can do no better than repeat the words of Burr **(1909),** which are quoted in Zacher (1911): 'I shall eagerly welcome all criticisms, however severe, all notes, observations and suggestions, and I earnestly beg all Dermapterists to come to the rescue and give me the benefit of their opinions and their suggestions, both on the details and the general scheme outlined in the following [above, FH] notes.'

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