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Dermapteran life-history evolution and phylogeny with special reference to the Forficulidae family

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ABSTRACT

The order Dermaptera displays a great diversity of life histories from real iteroparity (*n* clutches per year and per female) to strict semelparity (one reproductive cycle per year). Climatic criteria allow a general ordering of these life histories from iteroparous/tropical species to semelparous/cold-adapted taxa. A first molecular phylogeny based on the mitochondrial 16S rRNA partial sequence supports this general trend of evolution. First, the phylogeny confirms the monophyly of Dermaptera, already established on morphological characters. Second, the reduction in the number of reproductive cycles appears to be associated with the invasion of temperate areas, and then of colder regions. Lastly, the phylogeny reveals that the reduction to semelparity is not due to a unique evolutionary event, but occurred at least three times in the Forficulidae family in connection with a colonization of subalpine regions.

Keywords: Dermaptera, reproductive strategies, phylogeny, 16S rRNA.

INTRODUCTION

Within the large class of Insects, the Dermapteran group occupies a singular place. With more than 2000 species described (Sakai, 1982), this order is indubitably monophyletic. The abdominal forceps and the shape of the wings, folded in a complex manner, characterize the order (Beier, 1959). On the physiological and behavioural levels, Dermapteran reproductive behaviour is unique, even if other parental behaviours are observed within non-social insects. Females take care of their eggs from laying until hatching, and then constitute family groups with their newborn larvae. This behaviour, encountered throughout the order, appears to be connected with the special structure of the chorion of the eggs. Indeed, its perviousness to micro-organisms, and the fact that it distends extensively during embryonic development, make the care of eggs a priority. It has been demonstrated that, without female care, the eggs abort (Klostermeyer, 1942; Bhatnagar, 1963). These characteristics of Dermapteran eggs constitute real phylogenetic constraints. This particular reproductive mode, implying complete reorganization of the female behavioural aptitudes, described and analysed for the first time by De Geer (1773) and Weyrauch (1929) respectively, is found

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in every studied species. It therefore constitutes a plesiomorphic character of the species within this order. That is not the case for the constitution of a familial group after hatching that is found in most species, but with greater variability (Vancassel and Forasté, 1980). According to the taxa observed, the end of the parental phase varies from a short contact between the female and the larvae at hatching to a long familial phase covering several larval instars.

The characteristics of the eggs also imply a high level of humidity for embryonic development. The frequent excavation of a burrow before laying can be associated with such humidity. But this construction, which is not found in some species (e.g. *Doru taeniatum*, whose females care for eggs within the leaf sheaths; Jones *et al.*, 1987), appears to be more a consequence than the cause of the maternal behaviour.

Taxa of this group can be classified provisionally depending on whether they show real iteroparity (*n* clutches per year) with a rapid dispersion of the female and/or the larvae, or strict semelparity (one reproductive cycle per year) associated with a very long familial phase (Vancassel and Forasté, 1980). Within this order of tropical origin (Popham and Manly, 1969; Sakai, 1982; Popham, 1996), iteroparity is found in particular in taxa that have kept primitive characters and live in tropical zones, while intermediate forms (two clutches per year) or semelparous species are encountered in the Forficulidae family, essentially distributed in the Palearctic area.

For a more detailed reconstruction of Dermapteran life-history evolution, a reliable phylogeny is required. Indeed, systematicians, whether they argue about numeric or functional taxonomy, still cannot agree on several important points. Here, we present the first elements of a molecular phylogeny based on variation in the mitochondrial 16S rRNA partial sequence, focusing on the Forficulidae family. This could provide a reference to analyse more precisely the physiological and behavioural evolution observed within the life cycles.

MATERIALS AND METHODS

Biological specimens

Our sample consisted of 15 strains from ten Dermapteran species (Table 1). In the Forficulidae family, the taxon *Forficula auricularia* comprises two sibling species, namely A and B (Wirth *et al.*, 1998; Guillet *et al.*, 2000). Two individuals per species were assayed, except for *Labia minor* and *Anechura bipunctata*.

DNA sequencing

A portion of the 16S rRNA gene was amplified using primers and the polymerase chain reaction conditions described previously (Guillet *et al.*, 2000). Double-stranded DNA products were purified with five units of exonuclease I and two units of shrimp alkaline phosphatase (Amersham Pharmacia Biotech). Sequencing reactions were conducted according to the protocol outlined in the ABI Prism Dye Terminator cycle sequencing ready reaction kit (Perkin Elmer). Cycle sequencing was performed on a Hybaid thermal cycler at 96°C for 30 s, 50°C for 30 s and 60°C for 4 min for 30 cycles. Sequencing products were precipitated with 95% ethanol, washed with 70% ethanol, and then dried and resuspended in 25 μl of template suppression reagent. Denatured samples were loaded

Table 1. Origin of the Dermapteran specimens sequenced for the 16S mitochondrial region

Family	Species	Location
Forficulidae	*Forficula auricularia* A (Linnaeus, 1758)	France (Mijanes 1500 m, Fos)
	Forficula auricularia B	France (Rennes, St Brévin), the Azores
	Forficula decipiens (Gené, 1832)	France (Fos)
	Forficula pubescens (Serville, 1839)	France (Fos)
	Forficula lesnei (Finot, 1887)	France (Rennes)
	Anechura bipunctata (Fabricius, 1781)	France (Alpes)
	Doru taeniatum (Dohrn, 1862)	Mexico
	Chelidura pyrenaica (Gené, 1832)	Spain (Pyrénées)
Labiduridae	*Labidura riparia* (Pallas, 1773)	France (Fos), Portugal
Carcinophoridae	*Euborellia moesta* (Gené, 1837)	France (Châteauneuf du Pape)
Labiidae	*Labia minor* (Linnaeus, 1758)	France (Rennes)

on an ABI Prism 310 sequencer (Applied Biosystems) following the instructions of the manufacturer.

Sequence alignment and secondary structure

DNA sequences were read from chromatograms and automated sequencer output. Ambiguities were resolved by comparing light and heavy strand sequences using Sequencher. Alignment was accomplished with the help of Clustal W 1.7 and was corrected visually using Seqpup. The ribosomal genes produce a single strand of RNA that is folded to pair with itself to form helices (regions of consecutive hydrogen bonds between two strands) and loops (single-stranded regions). These two regions are thought to evolve under different selective constraints, and a secondary structure may be useful to ensure the homology of aligned sequences. So, the secondary structure of the earwigs' 16S rRNA was assessed manually by comparison with the proposed structure of *Drosophila yakuba* large subunit rRNA (Gutell and Fox, 1988). (The alignments and secondary structure are available on request.)

Phylogenetic analysis

Phylogenetic relationships among taxa were analysed using maximum parsimony (Paup 4.0b2a) on two separate data sets: (1) the total number of variable sites regardless of secondary structure, and (2) variable sites aligned according to the secondary structure, ambiguously aligned regions being excluded. In both cases, the most parsimonious tree was obtained with a heuristic search; stepwise addition of taxa was done randomly with 100 replicates. One thousand bootstrap replicates were performed to establish the stability of internal nodes. Two Orthopteran species whose 16S sequences were obtained from Genbank, *Locusta migratoria* (X05287) and *Schistocerca gregaria* (AF145492), were used as outgroups. The evolution of reproductive characters within the Dermaptera was assessed by tracing the reproductive modes on the optimal phylogeny using MacClade.

RESULTS

We obtained sequences up to 546 bp for this 16S rRNA region, but only 482 bp were available for all species (Genbank Accession Numbers AF290371 to AF290385).

From a total of 482 bases aligned in the first data set, 290 sites were variable and 226 were parsimony-informative. Due to ambiguous alignment, gaps were treated as missing data. A unique tree was obtained (Fig. 1a) that confirmed the monophyly of the Dermaptera and the existence of two sibling species in *F. auricularia*. Low resolution was observed for two Forficulidae, *C. pyrenaica* and *D. taeniatum*, and for *L. minor*.

In the second data set, secondary structure was considered. Loop regions were extremely variable and difficult to align. Nucleotides from positions 232 to 304 were omitted from the analysis. Indeed, the loop contained in this region was 54 nucleotides long in *C. pyrenaica* and was absent in *E. moesta*. Of 411 bases aligned, 240 sites were variable and 174 were parsimony-informative. Gaps were treated as a fifth base. A unique tree was obtained (Fig. 1b) with a higher resolution for the Forficulidae family. The transition : transversion ratio was estimated as 2 : 1 using maximum likelihood. Using this evaluation, the same tree was obtained. As nucleotide changes in helices are not always independent, they were down-weighted to 50% and once again the same tree was obtained.

Evolution of reproductive mode

The reproductive modes of each species, as well as the climatic conditions, were added to the optimal phylogenetic tree (Fig. 2). Reduction from iteroparity to strict semelparity occurred several times, and at least three times within the Forficulidae family where species invaded subalpine regions.

DISCUSSION

The monophyly of the Dermaptera, already established on morphological characters, is confirmed by this molecular phylogeny (Fig. 1). Our sample focused on the Forficulidae family, which presents many apomorphic characters and which constitutes most of the European Dermapteran fauna. But monophyly of this family is not well sustained. Due to the small number of sequenced taxa, phylogenetic relationships between Dermapteran species from other families have yet to be resolved.

In terms of reproductive mode, each transition from iteroparity to strict semelparity is encountered in the Forficulidae family, which regroups tropical taxa (*D. taeniatum*) and Paleartic species living in the coldest regions reached by this group. Organization of the reproductive characters and of the life-cycle structure, in relation to climatic conditions, is globally reinforced. The iteroparous taxon *Labia minor* (Labiidae), the only non-tropical primitive species, is known to live in dung heaps between 18 and 25°C in Atlantic Europe (Mourier, 1986). The reduction in the number of reproductive cycles from iteroparity to semelparity appears to be associated with the invasion of temperate areas and then of subalpine regions. The distribution of these life cycles on the phylogenetic tree (Fig. 2) illustrates that this transition occurred at least three times within the Forficulidae, in the genera *Chelidura*, *Anechura* and *Forficula*.

However, iteroparity is not simply associated with climatic conditions. The species *Forficula tomis*, which lives in the cold Siberian climate, presents a reproductive strategy with two annual clutches. In the same way, strict iteroparity can be lost in a tropical climate

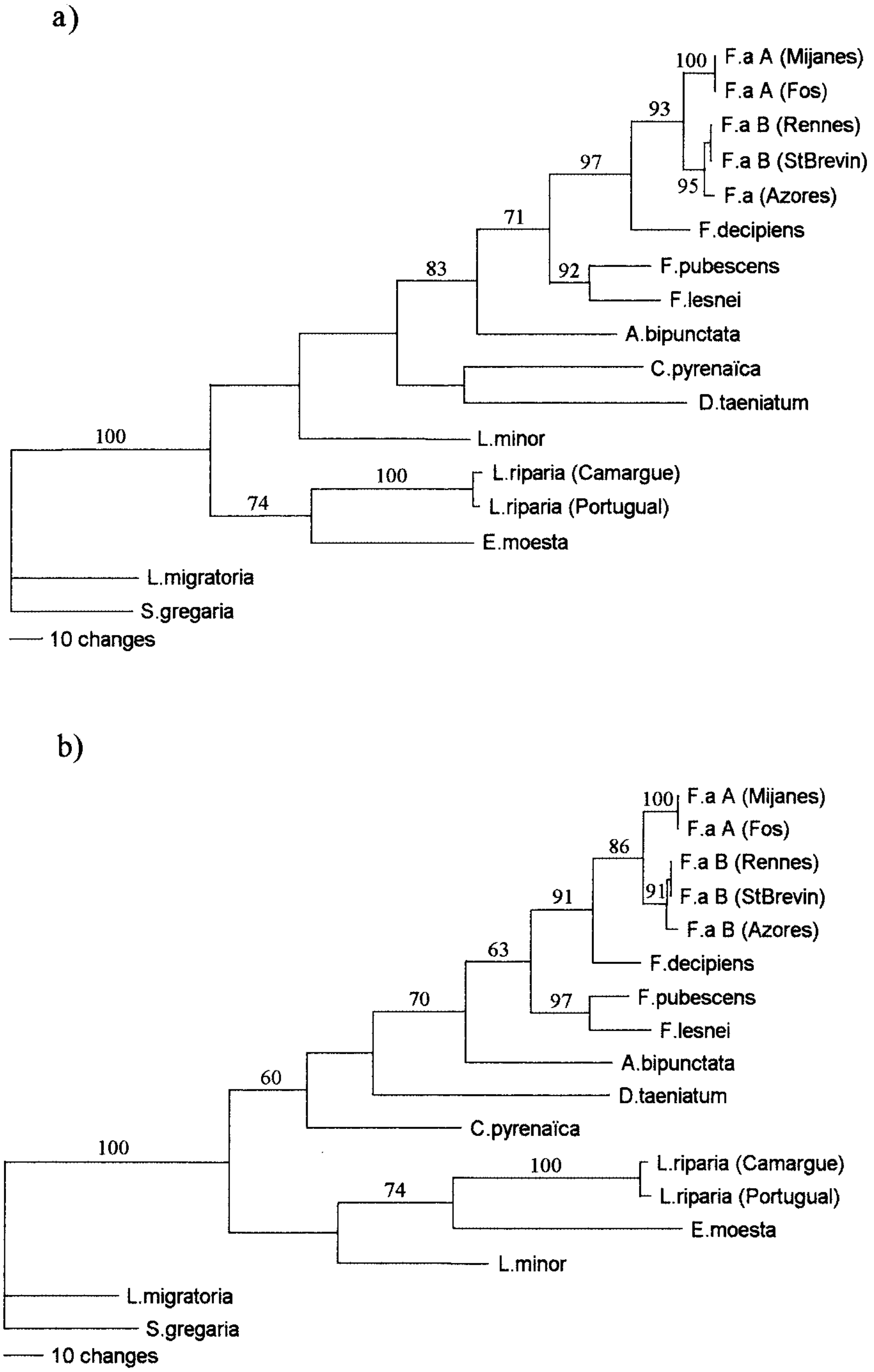

Fig. 1. Phylogenetic trees obtained with maximum-parsimony analysis (Paup 4.0b2a) on the 16S rRNA region, with two different data sets: (a) all variable sites; (b) variable sites considering secondary structure. Bootstrap values exceeding 60% are presented above the branches.

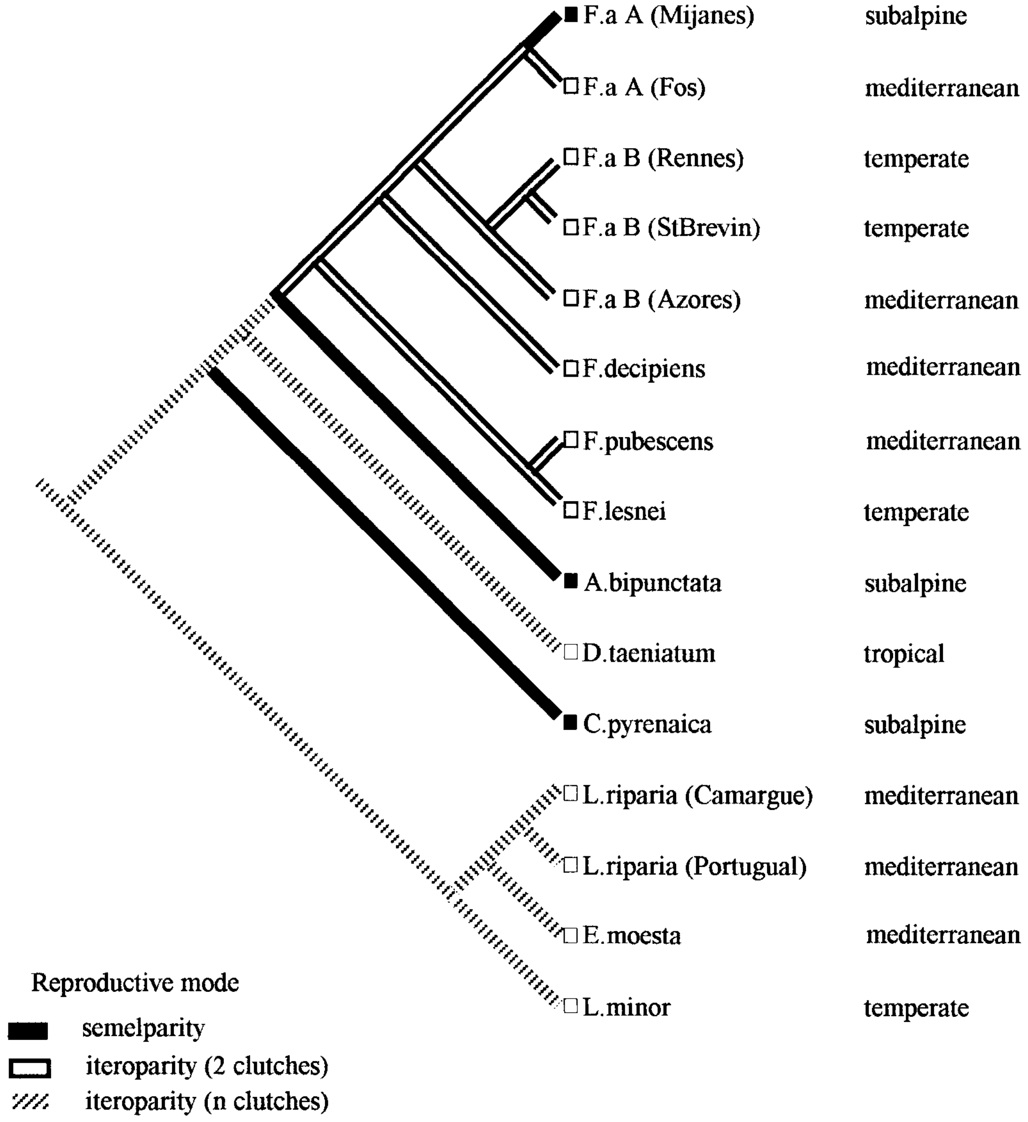

Fig. 2. Evolution of the reproductive modes from iteroparity to semelparity in the Dermaptera. The climatic conditions, observed for each species studied, are indicated to the right of the tree.

but with a very pronounced dry season, as observed in *Forficula senegalensis*, whose females produce only two clutches a year. In a coherent way with multiple and independent access to semelparity, the alternative behaviours observed (essentially the length of the familial phase) are adaptations of individual species to particular conditions in their environment. For example, although strictly semelparous, the species *C. pyrenaica* does not form durable family groups, in contrast with *F. auficularia* (Mijanes 1500 m) and *A. bipunctata*.

Throughout the Dermapteran order, the reduction in iteroparity sees the loss of an active germarium in adult females, and evolution to semelparity through a reduction in the number of ovocytes per ovariole (Vancassel and Forasté, 1989). The diversity of observed situations shows that, apart from ovarian anatomy, different controls on laying (more or less marked diapause) or on maternal care (parental activity more or less linked to ovarian activity) have evolved in each strain. The diversity of observed life histories could not be explained without integrating multiple factors. This point justifies more precise studies, like the one we are currently conducting at the intraspecific level on the taxon *F. auricularia* (sibling species A), which presents a reproductive bimodality.

The small number of taxa used in this study, and the analysis of a unique gene, do not allow us to contribute to the discussion of systematicians (Sakai, 1982; Popham, 1996) on the position of the Labiduridae family. That the American genus *Doru* is considered within the European group of Forficulidae, in spite of a weak bootstrap, supports Popham's view that the principal Forficulidae families differentiated before the separation of Gondwanaland. Utilization of different molecular markers and the sequencing of more taxa might allow a more detailed phylogenetic analysis.

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REFERENCES

Beier, M. 1959. *Klassen und Ordnungen des Tierreichs*, *Ordnung Dermaptera*, pp. 455–585. Leipzig: Gest & Portig.

Bhatnagar, R.D.S. 1963. The life-history, growth and transformation in the earwig *Labidura riparia* (Pallas) (Dermaptera) (Labiduridae). *Res. Bull. Panjab Univ. Sci.*, **14**: 225–229.

De Geer, C. 1773. *Mémoires pour servir à l'histoire des insectes*, Vol. 3, p. 548.

Guillet, S., Josselin, N. and Vancassel, M. 2000. Multiple introduction of the *Forficula auricularia* species complex (Dermaptera: Forficulidae) in eastern North America. *Can. Entomol.*, **132**: 49–57.

Gutell, R.R. and Fox, G.E. 1988. A compilation of large subunit RNA sequences presented in a structural format. *Nucl. Acids Res.*, **16**: 175–269.

Jones, R.W., Gilstrap, F.E. and Andrews, K.L. 1987. Activities and plant associations of the earwig, *Doru taeniatum*, in a crop-weed habitat. *Southwest. Entomol.*, **12**: 107–118.

Klostermeyer, E.C. 1942. The life history and habits of the ring-legged earwig, *Euborellia annulipes* (Lucas) (Order Dermaptera). *J. Kansas Entomol. Soc.*, **15**: 13–18.

Mourier, H. 1986. Notes on the lift history of *Labia minor* (L.) (Dermaptera), a potential predator of housefly eggs and larvae (Diptera, *Musca domestica* L.). *Ent. Meddr.*, **53**: 143–148.

Popham, E.J. 1996. The geographical distribution of Dermaptera with reference to their classification. In *Proceedings of the XX International Congress of Entomology*, *Phylogeny of the Dermaptera* (S. Sakai, ed.), pp. 196–214. Tokyo: Ochiai Printing Company.

Popham, E.J. and Manly, B.F.J. 1969. Geographical distribution of the Dermaptera and the continental drift hypothesis. *Nature*, **222**: 981–982.

Sakai, S. 1982. A new proposed classification of the Dermaptera with special reference to the check list of Dermaptera of the world. *Bull. Daito Bunka Univ.*, **20**: 1–108.

Vancassel, M. and Forasté, M. 1980. Le comportement parental des Dermaptères. *Reprod. Nutr. Dev.*, **20**: 759–770.

Weyrauch, W.K. 1929. Experimentelle analyse der Brutpflege des Ohrwurmes *Forficula auricularia* L. *Biol. Zbl.*, **49**: 543–558.

Wirth, T., Le Guellec, R., Vancassel, M. and Veuille, M. 1998. Molecular and reproductive characterization of sibling species in the European earwig (*Forficula auricularia*). *Evolution*, **52**: 260–265.