Phylogeny of the Ensifera (Orthoptera): A Hypothesis Supporting Multiple Origins of Acoustical Signalling, Complex Spermatophores and Maternal Care in Crickets, Katydids, and Weta

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ABSTRACT.—The orthopteran suborder Ensifera is a group of interest to many biologists because members of several families within this group communicate by sounds. The evolutionary history of singing and other social behaviors of crickets, katydids and weta (Gryllidae, Tettigoniidae and Stenopelmatidae, respectively) are unclear because of different published opinions on the relationships among ensiferan subgroups (Ander 1939, Zeuner 1939, Judd 1948, Ragge1955a, Sharov 1968). These opinions were not based on formal quantitative analyses. I undertook a cladistic analysis of ensiferan families using mainly anatomical characters. The single most parsimonious (shortest-length) tree divides the Ensifera into two clades: the 'tettigonioids' which comprise (((((Tettigoniidae & Haglidae) Stenopelmatidae) Cooloolidae) Gryllacrididae) Rhaphidophoridae), and the 'grylloids' ((Schizodactylidae) (Gryllotalpidae & Gryllidae)) (my parentheses enclose separate clades). I used this phylogeny to construct the most parsimonious hypotheses for the origins of certain social behaviours from those present in the ancestor of extant Ensifera (an insect that used a burrow as a retreat). There were two origins of sound communication using tegminal stridulation and foretibial ears, three to four origins of a complex spermatophore that is eaten by the female and about seven origins of maternal care of eggs and/or nymphs, a trait correlated with loss or reduction in the ovipositor. I review support for the hypothesis of dual origins of tegminal stridulation and tibial ears, complex structures that are usually regarded as homologous within the Ensifera.

Crickets, katydids (= long-horned grasshoppers), and weta comprise the Ensifera, one of two suborders of Orthoptera (Table 1). Numerical analyses of orthopteroid insects indicate that the Ensifera is a natural group as taxa in this suborder appear to form a separate clade (monophyletic group) in both cladistic and phenetic analyses (Blackith and Blackith 1968). The group is usually regarded as phylogenetically quite diverged from the other orthopteran suborder, Caelifera, the grasshoppers, locusts, and their allies (Hennig 1981). Kevan (1986) elevates the two suborders to ordinal rank, stating that there are few homologous characters uniting them and that even the enlarged jumping legs, one feature usually coming to mind as typical of most Orthoptera, may not be a shared-derived character (synapomorphy).

Acoustical signalling is another characteristic shared by both Orthopteran suborders. This trait clearly has independent origins as the organs used in both sound production and sound reception involve quite different body parts in the two groups (Alexander 1960, Dumortier 1963). Within Ensifera, however, the most common organs of sound-production, the tegmina (forewings), and sound-reception, the foretibial ears, are found in several families with each organ generally regarded as a homologous, synapomorphic character (Zeuner 1939, Ragge 1955a, Alexander 1962, Otte 1992). Sound communication in Ensifera has been the focus of much biological research, particularly involving the diverse families Gryllidae and Tettigoniidae (Appendix 1) (reviewed in books by Sales and Pye 1974, Ewing 1989, and Bailey 1991). Despite this attention, the evolutionary relationships between these two families and other Ensifera are not clear. For example, what are the relationships between Tettigoniidae, Gryllidae, and a third group showing tegminal stridulation and tibial ears, the Haglidae (Rentz 1979)? Furthermore, how is each of these families related to Stenopelmatidae, a fourth group in which there are taxa with tibial ears but in which acoustical signalling occurs using a tibial-abdominal mechanism (Field 1993a, 1994)?

The answers to these and other historical questions about ensiferans are unclear because there is no consensus on the evolutionary history of the group. The most recent phylogenies of

Ensiferan families—by Ander (1939), Zeuner (1939), Judd (1948), Ragge (1955a) and Sharov (1968)—all differ in topology, even when between-author differences in the taxa considered are taken into account (Fig. 1). Sharov (1968) is the most recent and the one often cited (*e.g.,* Otte 1992). His phylogeny is unique with respect to its conclusion about how the taxa showing tegminal stridulation are related. It is the tegminal stridulation organ and other wing characters (mainly from extinct taxa) that are the basis for Sharov's argument that Haglidae share a more recent common ancestor with Gryllidae than with Tettigoniidae. In reviewing the literature on ensiferan relationships, Hennig (1981) stated that Sharov's views are not well founded (see also Kevan 1977). Hennig reviewed possible synapomorphies other than the stridulatory organ but still confined the examination mainly to certain wing characters and characters related to acoustical communication (those suggested by Zeuner (1939), Ragge (1955a) and Sharov (1968)).

Surprisingly, Hennig's review of Ensiferan relationships did not include the contributions of Judd (1948) or the monograph of Ander (1939), works based on quite different characters than in the other references. Ander (1939), in particular, stressed the importance of a broad range of characters in understanding the systematics of 'Saltatoria' (Orthoptera). Both studies focused mainly on extant taxa, Judd (1948) using characters of the gut and Ander (1939) on a detailed analysis of many anatomical characters. Ander's work is particularly important in that it reviews a large number of taxa within each family and covers a world-wide diversity. The work is surprisingly modern in its phylogenetic conclusions based on shared characters[1]. It was Ander's work that initiated my interest in ensiferan phylogeny. Previous work (Gwynne 1990a) and that of Ander indicated that spermatophore anatomy may contain informative characters; additional informa-
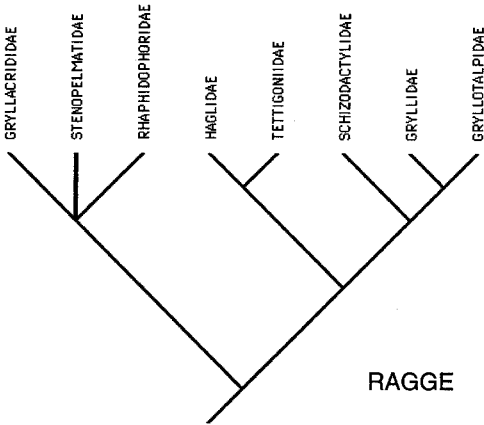
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[1]A draft typescript of an English translation of Ander (1939) by orthopterist, T. H. Hubbell is available from the Insect Division, Museum of Zoology, University of Michigan, Ann Arbor, MI, USA 48109
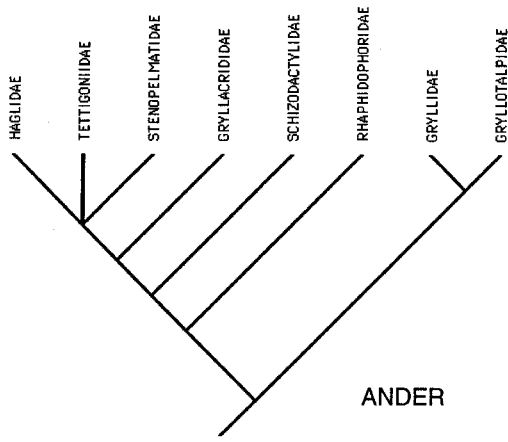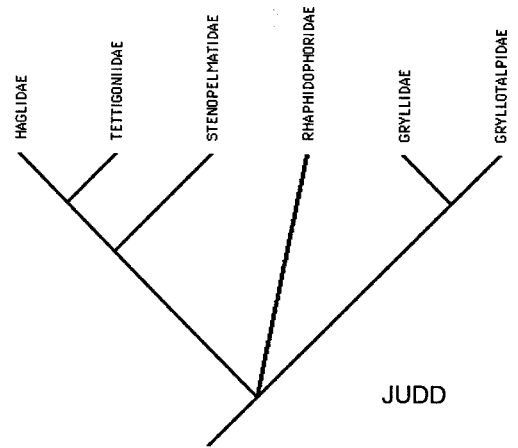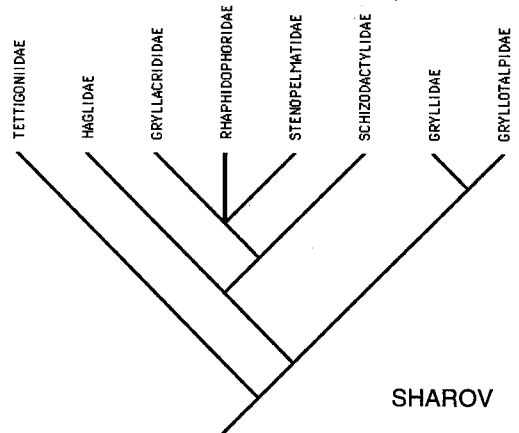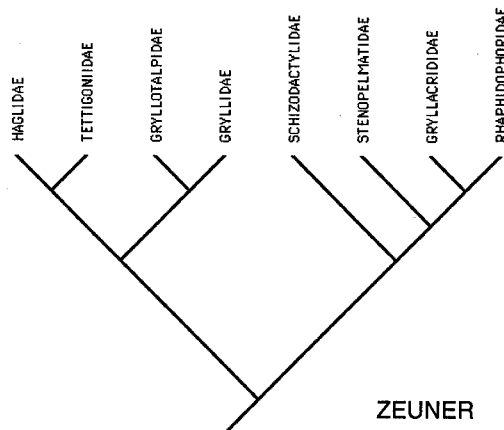
Fig. 1. Previously published phylogenies of Ensifera depicting branching relationships only. The works of Ander (1939), Judd (1948) and Ragge (1955a) based mainly on extant taxa, whereas those of Zeuner (1939) and Sharov (1968) are on fossil taxa. Not included in Sharov's tree are his extinct families Tettavidae and Phasmomimidae. However, these two groups are not in important positions within the tree as they were positioned by Sharov at the tips of branches, i.e., as sister groups to the Tettigoniidae and Haglidae, respectively (Sharov recognizes a further 10 extinct ensiferan families but places these in a sister clade to all the families considered here). There are no extinct families missing from the accompanying depiction of Zeuner's tree. Zeuner (1939) and Sharov (1968) are based mainly on fossil wing and spiracle characters, Ragge (1955a) on the wing venation of extant species, Ander (1939) on detailed anatomical and morphological information, and Judd (1948) on the anatomy of the proventriculus of the ensiferan foregut. For the root of Ander's tree, I used the dotted line he uses to connect the extinct "Oedischioidea" with extant Ensiferan families.

tion on mating and spermatophores that I report here provide further support for this.

The main purpose of the present paper is to conduct an analysis of extant families of Ensifera using characters from Ander (1939) and other sources in an attempt to resolve the conflict between competing phylogenies of the suborder. Such an exercise is justified because it represents the first formal phylogenetic (cladistic) analysis of the suborder using a broad range of characters. A second justification for this analysis is that there is a need for a phylogeny to fully investigate historical questions about the group. It is now widely acknowledged that phylogenetic analyses are vital for understanding the adaptive origins of traits (as opposed to the adaptive maintenance of traits which can be studied by observing and experimenting with individual species) (Brooks and McLennan 1991; Harvey and Pagel 1991). I use my phylogeny to draw some preliminary conclusions about the origins of some social and communicative behaviors of ensiferans. This includes courtship feeding on specialized spermatophores (known in six families), maternal care of offspring (in five families), and especially the well-known singing behavior of crickets, katydids and weta.

The taxonomy of Ensifera

My analysis uses nine extant families of Ensifera each of which is assumed to be monophyletic. The most diverse families (Table 1), Tettigoniidae and Gryllidae, are very likely to be monophyletic (Hennig 1981). Cladistic analysis supports this assumption for Gryllidae and its sister group Gryllotalpidae (Desutter 1987) (both Hennig and Desutter treated the three taxa as superfamilies). The list of ensiferan families in the systematic treatments of Ander (1939) and Judd (1948) are very similar to the most recent systematic list of Rentz (1991, in *The Insects of Australia*). The only difference among these authors involves the addition by Rentz (1991) of the Myrmecophilidae and the recently-described Cooloolidae. I have not included the Myrmecophilidae, because cladistic analysis places it as the sister group of the gryllid subfamily Mogoplistinae (Desutter 1987) and hence more properly placed within the Gryllidae. I have also ignored Sharov's (1968) recognition of the gryllid subfamily Oecanthinae as a separate family; Desutter's (1987) analysis also places oecanthines (= Desutter's Oecanthidae) within the Gryllidae (= Gryllodea). Thus, the inclusion of either oecanthines or myrmecophilines as taxa equivalent to Gryllidae would make the true crickets paraphyletic.

Ragge (1955a) and Sharov (1968) also differed from other authors in including genera of Stenopelmatidae within the Gryllacrididae.

Phylogenetic analysis

The character matrix (Appendix 2) includes all the characters I could find that varied between ensiferan taxa and the outgroups (mainly anatomy and morphology). The starting point for the matrix was the English translation of Ander (1939) by T.H. Hubbell (1971). Other sources are listed in Appendix 2. Ander's monograph is remarkably broad in its coverage of characters, taxa and biogeography. My data matrix includes 67 characters coded for the nine extant families of Ensifera. As most characters are from the literature (mating characters being the exception), I rely on the judgement of the original authors for their reliability.

I used the family Acrididae (short-horned grasshoppers) and the order Phasmatodea (stick insects) as outgroups to root the trees (see the Fig. 2 legend). Acrididae, a diverse family within the other Orthopteran suborder Caelifera, and Phasmatodea are considered to be groups closely related to Ensifera (Hennig 1981), a contention supported by virtually all numerical analyses of ortho-

pteroid insects in Blackith and Blackith (1968) and Kamp (1973). I used no characters that were polymorphic in outgroups or that appeared to be aspects of the same trait (i.e., were obviously non-independent). For the diverse families Gryllidae and Tettigoniidae, if a character was polymorphic but family-level phylogenetic analysis showed the common state to be ancestral and the other state rare, the taxon was scored as showing only the ancestral state (*e.g.*, ovipositor shape in Gryllidae and tegminal stridulation in Tettigoniidae). All multi-state characters were left unordered so that a change between any two states required only one step. Missing data were coded as "?". I encountered some difficulty in coding certain characters that were not applicable to the taxon (i.e., the character itself is "missing"). These cases mainly involved a number of wing venation characters that were not applicable to the wingless taxon Rhaphidophoridae. Maddison (1993) points out that there are general problems with coding such non-applicable characters as "missing data" ("?"), and specific problems with the alternative—using a third state to denote"character missing." Both coding methods resulted an identical shortest-tree topology as well as similarities in other results. Therefore I present only the analysis in which non-applicable characters are coded as missing data.

I subjected the data matrix (Appendix 2) to an "exhaustive search" (which examines all possible trees) using PAUP 3.1 (licensed to M. Laurin, University of Toronto)(Swofford 1991). This search produced a frequency distribution of lengths of all possible trees. I also determined 50% majority-rule consensus tree of the single shortest tree and trees with one additional step. A bootstrap analysis (500 runs) of the shortest-length tree was also done to determine the robustness of the nodes in the cladogram (a 50% majority-rule tree) (PAUP 3.1).

I used MacClade 3.1 (licensed to M. Laurin, University of Toronto)(Maddison and Maddison 1992) to compare my results with previous phylogenies of Ensifera by examining how many extra steps are required for each phylogeny using my character matrix. In each comparison I deleted any families (*e.g.*, the recently named Cooloolidae) from the analysis that were not considered in each previously published phylogeny in order to make tree length comparisons appropriate.

Character examination

The reconstruction of character evolution was conducted using MacClade. I examined synapomorphies for each clade as well as the origin and evolution of the reproductive traits of interest. In certain cases, these latter traits had been included as characters in the original data matrix (Appendix 2). In these cases phylogenetic analysis of Ensiferan families was repeated with characters of the traits of interest removed (details below).

In order to provide more details of certain lower taxonomic levels, such as subfamilies and tribes, on the tree when tracing the evolution of biological traits of interest, I incorporated the separate phylogenies of Tettigoniidae (Gorochov 1988) and Gryllidae (Desutter 1987). Gorochov used a number of morphological characters. Although his work is not based on a formal analysis, it is the only phylogeny available for this group. It is supplemented by additional information on the suggested relationships among tettigoniid subfamilies from Rentz (1979, 1993 and pers. comm.). Desutter's (1987) analysis of Gryllidae is based on cladistic analysis of genitalic characters. I further expanded the gryllid subfamily Gryllinae by using the taxonomic groupings of Randell (1964) as a proxy for phylogeny. Randell (1964) is also based on male genitalic characters. I also used taxonomy as a proxy for Gryllotalpidae by splitting it into two subfamilies, and in Stenopelmatidae, by placing two New Zealand Deinacridinae (*Deinacrida* and *Hemideina*) in one clade, the New Zealand and

Australian Henicinae in another, and Stenopelmatinae in a third.

An hypothesis of ensiferan relationships

With both Phasmatodea and Acrididae as outgroups the search produced a single most parsimonious tree of 130 steps, with a consistency index of 0.63 (excluding uninformative characters) and a retention index of 0.77. The phylogeny divides into two clades, the "tettigonioids" and "grylloids" (Appendix 3 lists synapomorphies defining each clade). The same topology of shortest-length tree was obtained when Acrididae or Phasmatodea alone were designated as outgroups; and, when sound communication and spermatophore characters were excluded in two separate analyses (see below and in Figure legends). The character matrix has a reasonably strong phylogenetic signal as in the distribution of all possible trees my shortest-length tree is on the opposite tail of a distribution skewed toward the longest tree-lengths (see Stewart 1993) (Fig. 2).

Three trees require one additional step than the shortest. Two of these differ only in the positioning of cooloolids and gryllacridids as the outgroups to the haglid-tettigoniid-stenopelmatid clade. The third tree moves Schizodactylidae from the grylloid clade (in the shortest-length tree) to the base of the tettigonioid clade. As a result, both the bootstrap 50% majority-rule consensus tree and a 50% majority-rule consensus (of the four shortest trees) show a trichotomy of the tettigonoids, Schizodactylidae, and the gryllid-gryllotalpid clade. Characters supporting the inclusion of Schizodactylidae in the tettigonioid clade are those this family shares with the six tettigonioid families: complex teeth in the gut's proventriculus (see Judd 1948), and four tarsal segments. Ander (1939) placed Schizodactylidae in the tettigonioid clade (Fig. 1) (see Fig. 1 legend for the rooting of Ander's tree). The taxonomies of Ragge (1977) and Kevan (1989) also placed this family with the tettigonioids.

My tree is congruent with the topology of the only three Ensiferan families in both a phenetic and a cladistic analysis of higher taxa of orthopteroids; Blackith and Blackith (1968) placed Tettigoniidae and Gryllidae together with this clade as the sister group of Rhaphidophoridae. Comparisons of my tree with extensive (but non-formal) treatments of Ensifera (Fig. 1) were made by determining how many extra steps were required for each of the previous trees using the present character matrix. The greatest congruence of the new tree is with conclusions based mainly on extant taxa. A scheme based on interpretation of characters of the gut proventriculus by Judd (1948) shows almost perfect congruence with my tree (both = 112 steps for the 6 families Judd considered). Although Judd's (1948) figure left as unresolved the trichotomy of grylloids (minus Schizodactylidae), rhaphidophorids and the clade of Tettigoniidae + Haglidae + Stenopelmatidae (Fig. 1), he appeared to support the inclusion of Rhaphidophoridae with the latter three groups by placing it in the superfamily Tettigonioidea. Ander's (1939) phylogeny differs from mine only in the placement of Schizodactylidae (in the tettigonioid clade above Rhaphidophoridae). His topology (132 steps) requires only 3 more steps than the most parsimonious tree of 129. Ragge (1955a) requires 9 extra steps (138, compared to 129) (Vickery (1989) shows a similar topology).

The greatest conflicts between the present results and previous work are those phylogenies that include extinct (fossil) representatives of extant ensiferan families; Zeuner (1939) (150 steps) requires 21 more steps than the most parsimonious tree (129) and Sharov (1968) 38 extra steps (167 compared to 129). Although Zeuner and Sharov include extinct families that are not scored here, their placement by the authors would not have affected tree topologies in a major way because they were placed either in a group as a sister taxon to the extant Ensifera or they are at the tips
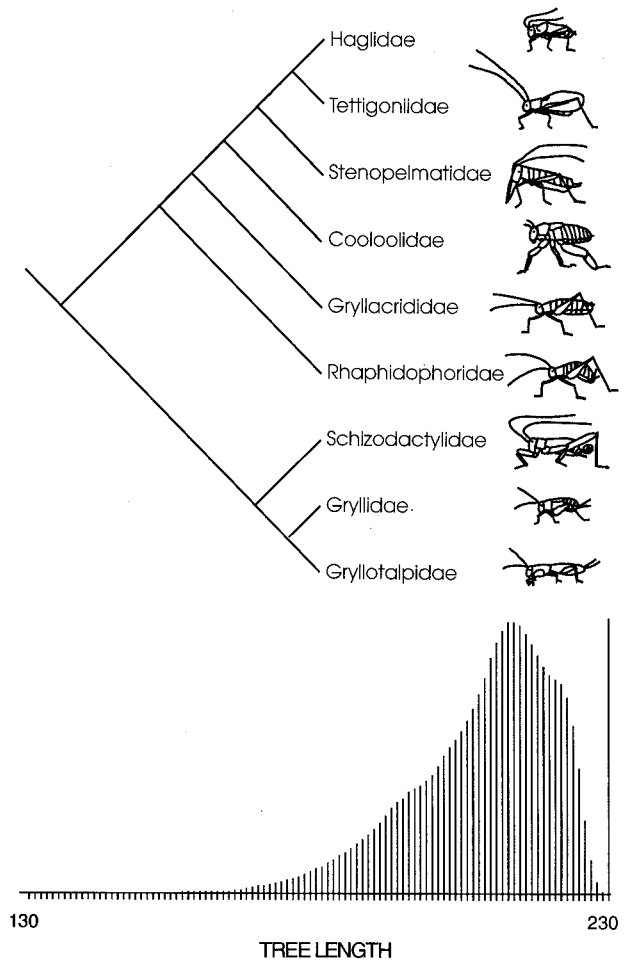
Fig. 2. Hypothesis for relationships among extant Ensifera families. Only one shortest length tree was found. Two outgroups were used, Phasmatodea and Acrididae (see text). The histogram below the tree is the distribution of all possible tree lengths (from an exhaustive search using PAUP). The distribution is highly skewed away from the shortest tree (g1 = -0.97, g2 = 0.79).

of tree branches (details in the Fig. 1 legend).

Finally, Kukalova-Peck and Rentz (personal communication 1994) have used wing veins and the morphology of the wing base of extinct and extant taxa to determine the relationships among orthopteroid insects and related groups such as Plecoptera (stoneflies). The Ensifera part of their tree shows the gryllid-gryllotalpid clade as a sister group of Haglidae. This clade and the Tettigoniidae form a clade distinct from that of Schizodactylidae and the "gryllacridoids" (Gryllacrididae, Cooloolidae, and Gryllacrididae). Using my character matrix such a topology requires at least 34 additional steps.

The new phylogenetic hypothesis (Fig. 2) has implications for both the taxonomy of Ensifera and the origin and evolution of communication and other aspects of life histories in the group. The following conclusions and discussion assume that the diagrammed hypothesis is true. The conclusions are relatively unchanged if Schizodactylidae is moved to the base of the tettigonioid clade.

Taxonomic groupings

The phylogeny supports a natural taxonomic grouping of Ensifera into two main subgroups that I have labelled the tettigonioids and grylloids. Except for the position of Schizodactylidae, this is consistent with the taxonomies suggested by Ander (1939), Judd (1948), and Ragge (1977)—who recognized only the superfamilies Tettigoniodea and Grylloidea and Kevan (1977), Vickery and Kevan (1986), and Vickery (1989) who split Ensifera, as an order—Grylloptera—into the suborders Tettigonioidea and Gryllodea. The phylogeny does not support as natural (monophyletic) groups either the three superfamilies (Beier 1972, Rentz 1979, 1991; see Appendix 1) or the scheme of four infraorders within Ensifera proposed by Kevan (1982); the superfamily Gryllacridoidea (Beier, Rentz) and the infraorder Stenopelmatidea (Kevan) become paraphyletic groups. In fact, in previous phylogenies, only Ragge (1955a) and Zeuner (1939) support the three ensiferan superfamilies and four infraorders as distinct clades.

The phylogeny also supports multiple origins of traits associated with acoustical signalling, mating and offspring production. I now discuss these in detail.

A dual origin of tegminal stridulation and tibial ears?

In Gryllidae, Gryllotalpidae, Haglidae, and Tettigoniidae, males produce sounds to call or court mates, or in inter-male aggression (Alexander 1960; and see Snedden and Irazuzta (1994) and Mason (in press) for Haglidae). The sounds result from tegminal stridulation and are detected by tibial tympana (ears). Tegminal stridulation is never present in a taxon without tibial tympana although the reverse can be true (Ander 1939, Otte 1990,

1992). I traced the evolution of tibial ears and tegminal stridulation on the Ensifera phylogeny (the same single shortest length tree is obtained when the character matrix is analysed with all characters related to acoustical behaviour removed; see legend to Fig. 3). Figure 3 traces only the evolution of tegminal stridulation. Results for tibial ears were very similar so, for ears, only the character states are presented in the figure (top row of boxes). The most parsimonious explanation is a dual origin of these traits (see also Ander 1939). Tegminal stridulatory organs on males evolved once in the ancestor of grylloids (Gryllidae + Gryllotalpidae) and once within the tettigonioids, in the ancestor to Tettigoniidae + Haglidae (Fig. 3). Figure 3 shows the grylloid origin to be equivocal because tegminal stridulation is polymorphic in Gryllotalpidae and in virtually all the gryllid subfamilies. However, absence of these traits are probably losses (Otte 1992) and a more detailed gryllid phylogeny will probably show a single origin in grylloids. The origins of tibial ears also occurred ancestrally to Gryllidae + Gryllotalpidae and to Tettigoniidae + Haglidae but in the latter case it is equivocal whether tibial ears originated before or after the Stenopelmatidae branched off as ear presence is polymorphic in this family. In eared stenopelmatids (at least in the New Zealand taxa, the tree (Hemideina) and giant weta (Deinacrida)) the sexes communicate using femoro-abdominal, not tegminal stridulation (Field 1993a, 1994) (Fig. 3).

The frequency of losses of tegminal stridulation and tibial tympana within the singing taxa of the tettigonioid and grylloid clades is markedly different (Fig. 3). Of the approximately 5,000 extant species in the haglid-tettigoniid clade (Table 1) the tegminal stridulatory organ has been lost only four times, all in the Tettigoniidae: Phasmodinae (three species) (Lakes-Harlan et al. 1991), Phyllophorinae (60 species) (Ander 1939, Dumortier 1963, Lloyd 1976), Meconema (other members of the Meconematinae
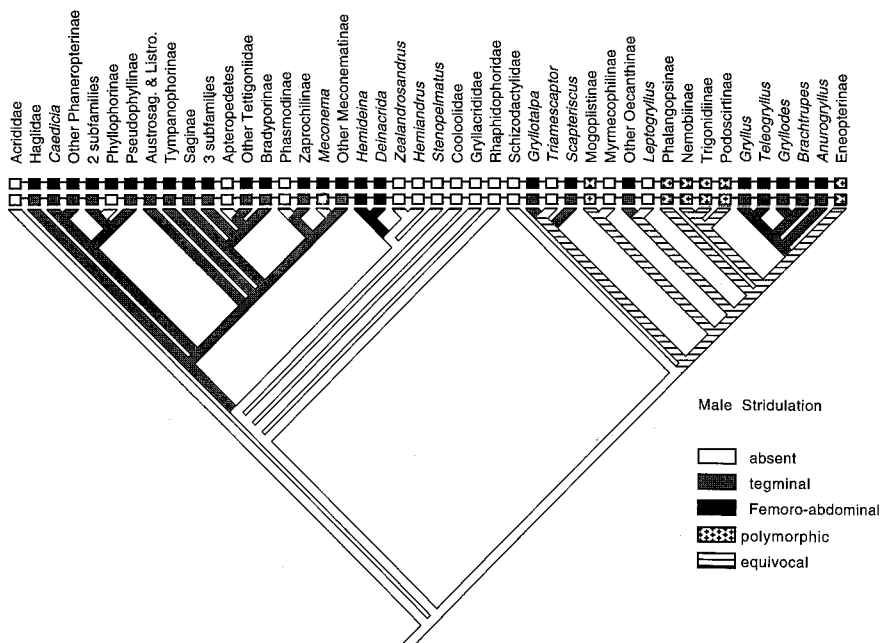
Fig. 3. The origin and evolution of male stridulation mechanisms and fore-tibial 'ears' in Ensifera. The stippled areas of cladogram (and character boxes in the bottom row = calling by tegminal stridulation; black areas = "calling" by hindfemoral-abdominal stridulation; hatched = character evolution is equivocal. The bottom row of boxes are the character states for stridulation (dots = tegminal stridulation both absent and present, i.e., polymorphic). The top row of boxes shows the character states for foretibial ears in each taxon (black = present, dots = polymorphism). Austrosag. and Listro. = tettigoniid subfamilies Austrosaginae and Listroscelidinae. Five characters associated with sound-producing and sound-receiving organs were included in the original data matrix. In order to remove the influence of the characters of interest on the tree topology I reanalysed the matrix with these characters deleted. The single shortest-length tree has the same topology as Fig. 2.

sing; Ander 1939), and *Apteropedetes* (other members of the Tettigoniinae sing (Rentz (1979) and pers. comm.)) (Fig. 3). Only two of these taxa, Phasmodinae (Lakes-Harlan *et al.* 1991) and *Apteropedetes* (Rentz 1979), have lost tympana possibly because the other two make sounds; *Meconema* males drum on the substrate (Bailey 1991) and phyllophorines have a coxal-sternal mechanism (Carl 1906, Dumortier 1963, Lloyd 1976). Alternatively, both eared species retain tympana bacause both fly and may have evolved to hear echolocating bats. Many other Tettigoniidae have lost their wings, in that females are apterous, yet males retain short forewings that function only in stridulation (*e.g., Kawanaphila* Rentz 1993). In contrast to tettigonioids, the approximately 2,000 species of singing grylloids have lost tegminal and tibial organs many times and this is true of the two families as well as virtually all subfamilies within Gryllidae (Fig. 3). Otte (1990, 1992) estimates at least 27 and 17 losses, respectively, of tegminal stridulation in the Australian and African Gryllidae alone.

The alternative to a dual-origin hypothesis for tegminal stridulation and tibial tympana in Ensifera is that instead of two gains of both these adaptations, there was a single gain in the ancestral ensiferan and five subsequent losses of the tegminal organ at the family level and at least four losses of tibial ears. This would have occurred once in the grylloid clade and four (ear) or five (tegminal organ) times in the tettigonioid clade. Based on just the number of evolutionary changes (six for tegminal organs), this alternative is less parsimonious than one of dual origins. However, if losses of sound communication have occurred more easily in evolutionary time than gains, the single-origin hypothesis may be a reasonable alternative under parsimony. But there is no evidence for Ensifera in general that losses of these traits are easy; as stated above, loss of tegminal organs and tibial ears have been frequent in singing grylloids but very rare in singing tettigonioids (and, with the single-origin hypothesis, most of the losses would have occurred in tettigonioids). Finally, the most parsimonious tree for a single gain and a single loss of singing is Ragge (1955a), a phylogeny of Ensifera requiring nine additional steps (see above).

Students of ensiferan communication and behavior usually regard the tibial tympana and tegminal stridulation in Ensiferans as too similar and too complex to have evolved more than once (Alexander 1962, Otte 1992, Michelsen 1992, Field 1993b). However, some discussions of ensiferan phylogeny have argued for multiple origins. Handlirsch (1929, cited in Ander 1939), Zeuner (1934,1939), Ragge (1955a) and Sharov (1968) all supported a single-origin hypothesis with Zeuner and Ragge viewing the tegminal singing as a synapomorphic character for a single clade within the Ensifera (Fig. 1). However, Ander (1939), Karny (several papers cited in Ander 1939) and Graber ((1876, cited in Zeuner 1939) argued for independent origins of these acoustic devices.

Is there any anatomical evidence that the ears and/or tegminal organs of tettigonioids and grylloids are different? Furthermore why should these organs be expected to evolve in exactly the same locations in different groups? Ander (1939) emphasized the latter point, particularly for the tibial ears. I will deal with these organs first.

Evidence that tibial ears may have independent origins

First, there is clear evidence from another group of insects that ears of similar structure can evolve more than once on the same part of the body. Such an evolutionary event has occurred twice in parasitoid Diptera that locate their hosts using song. Ormiine tachinids (hunters of calling male Ensifera (Cade 1975)) and certain sarcophagids (hunters of calling cicadas (Soper *et al.*1976)) are phylogenetically quite different yet have very similar ears positioned on the front of the thorax (Robert *et al.* 1992 and personal communication).

The grylloid and tettigonioid 'ear' consists of single or paired tympana on the proximal part of each prothoracic tibia. In Tettigoniidae, tympana can be simple, exposed strucures or associated with cuticular modifications (Bailey 1993). Receptor cells associated with the tympana include an auditory organ that functions as the main sensor of airborne sounds and in frequency discrimination (Oldfield 1982, Oldfield et. al 1986), and a subgenual organ that detects substrate vibrations (Rossler 1992). The tympanum is backed by an auditory trachea that exits to a (usually modified) mesothoracic spiracle (Ander 1939 and references therein).

There are some distinct differences between tettigonioid and grylloid ears. Ander (1939) stated that Tettigoniidae, Haglidae and Stenopelmatidae resemble each other in the possession of enlarged trachea (vesicula acoustica) in the thorax. Recently, Mason (1991) added that unlike Gryllidae, the ears of the three singing tettigonioid families have both tympana (on each tibia) as functional structures and also have a tympanal membrane with two morphologically distinct regions (see also Schumacher 1978). The mechanism of hearing in Gryllidae may also function differently from the three tettigonioid families because in field crickets (Gryllinae) a tracheal connection between the tracheae leading to left and right mesothoracic spiracles appears to be important in directional hearing (Ewing 1989, Mason 1991, Michelsen et al 1994a,b).

Finally, the structure of the receptors per se of Tettigoniidae, Haglidae and Stenopelmatidae is very similar and contrasts greatly with that of Gryllidae (Ball and Field 1981, Mason 1991 (see Michelsen and Larsen (1985) for a comparison of gryllid and tettigoniid ears)). This includes the number of sensillae in the auditory and subgenual organs (the only exception being that the number of cells in the haglid and gryllid subgenual organ are most similar), the three-dimensional arrangement of the auditory organ relative to the tympana, and the arrangement of the subgenual organ with respect to the wall of the leg (Ball and Field1981, Mason 1991). In fact, even the terminology used differs for the grylloid and tettigonioid ear. The substrate-vibration detecting (likely ancestral; Zeuner 1939) subgenual organ is found in both groups but only in the Tettigoniidae, Haglidae and Stenopelmatidae is there both a crista acustica as an auditory organ and an "intermediate organ" positioned between the crista and subgenual organ (Eibl 1978, Michel 1979, Ball and Field 1981, Oldfield 1982, Oldfield *et al.* 1986, Mason 1991).

The prothoracic tibiae of acoustical Ensifera were probably preadapted to evolve ears because receptor cells were almost certainly present in the tibiae before the origin of tympana. This is evidenced first by the fact that a rhaphidophorid, the basal family in the tettigonioid clade (Fig. 2), possesses prothoracic tibial receptor organs. Jeram *et al.* (in press) described these "tibial organs" for *Trogophilus neglectans* as having a subgenual organ but no crista acustica. The tibial organ of this species shows some affinity with that of the three singing families in the same clade (tettigonioids) as it has an intermediate organ and the structure of the trachae associated with the organ is similar to that of Tettigoniidae.

Tibial sensory organs also occur in the middle and hind legs. Embryological evidence for Tettigoniidae (Maier and Reichert 1990) reveals that these organs are homologous with the hearing organ in the front leg. The middle and hind tibial organs of Gryllidae (Eibl 1978), Haglidae (Mason 1991) and Tettigoniidae (Friedrich 1929, cited in Ander 1939), Rossler 1992) all have organs homologous with the 'eared' foretibiae. In tettigoniids and haglids these include a crista acustica, intermediate and subgenual organs with the two latter organs detecting airborne sounds of very low frequency (but only at, possibly unnaturally, high intensities (see Yack and Fullard 1993)). Mason (1991) shows not only an anatomi-

cal but also a physiological match between the front leg's auditory sensory structures and those of other legs; in a haglid (*Cyphoderris*) the mesothoracic tibial organ is most sensitive to approximately the same sound frequencies as the prothoracic tibial ear.

As to the reason why ears have evolved only on front legs and not others, Ander (1939) points to another apparent preadaptation. Unlike the other thoracic spiracles, the anterior (mesothoracic) spiracles in orthopteroids (even in Blattodea) have three outer lips and certain other structures that represent a "precondition for isolation of the leg trachea (for an acoustic function)." There may also be other adaptive advantages to placing ears anteriorly such as reducing interference of other body parts with arriving sound waves (Mason, personal communication 1994).

Independent origins of tegminal stridulation

There have been several independent origins of communicative stridulation in Ensifera. Hindfemur-abdominal stridulation has evolved in weta (Stenopelmatidae; Deinacridinae) (Field 1993a); and a simple tegminal mechanism, used by females of certain phaneropterine Tettigoniidae to answer male song, involves tegminal spines that are not homologous with the male tegminal organ (Nickle and Carlysle 1975, Robinson 1990).

The most common structure, however, is the elaborate "tegminal organ" (Ander 1939) of gryllids, gryllotalpids, haglids and tettigoniids. In males in all of these groups this organ is a raised toothed vein (the file) on the underside of one tegmen that, during wing movement, contacts the scraper, on the other tegmen (Sales and Pye 1974, Ewing 1979, Bailey 1991). In virtually all Tettigoniidae the functional file is on the left wing and the scraper on the right whereas for most grylloids (Gryllidae and Gryllotalpidae) the locations of file and scraper are reversed (Bennet-Clark 1970, Morris and Gwynne 1978, Rentz 1991). The opposite tegmen has a vestigial file. The other family of tegminal singers, Haglidae, cannot be allied to other groups using tegmen overlap; male Haglids (*Cyphoderris*) have two functional files and an individual can use both sorts of wing orientation (Spooner 1973, Morris and Gwynne 1978). A tegminal organ apparently homologous with that of males is found in females of certain species in the tettigoniid subfamily Ephippigerinae. It is used to answer males and, unlike males, the file vein is toothed on its dorsal surface. As this is on the right tegmen females still show the typical katydid "left over right" tegmen overlap (Hartley *et al.* 1974, Nickle and Carlysle 1975).

The several different mechanisms of "social stridulation" attest to its multiple origins in Ensifera. However, the differences of opinion in previous work focus on whether the tegminal organ *per se* had one or more origins. An elaborate tegminal file can evolve more than once: males of certain Tridactylidae (pygmy mole grasshoppers, members of the suborder Caelifera), have a stridulatory file on the dorsum of the tegmen that bears a striking resemblance to that of certain ensiferans (see Fig. 24-5E in Rentz 1991) even though the "scraper" is not a tegminal structure but is on the leg (Günther 1978).

A different male stridulatory vein (file) in grylloids and tettigonioids would constitute evidence for a dual origin of this structure within the Ensifera, but there is disagreement in the literature over whether the male stridulatory vein is in fact homologous within Ensifera. Ander (1939) stated that male grylloids have a modified 2nd cubital vein (Cu2) and that in the haglid, *Cyphoderris*, the file vein is similar in structure to that of the Tettigoniidae and might also involve both Cu2 and the first anal vein (1A). Zeuner (1939) argued for 1A in all three groups although Ragge (1955a) corrected this by stating that it was the Cu2 not the 1A that Zeuner had observed. Ragge's (1955a) view agreed more with Ander in stating that gryllids used the Cu2 but that in

haglids and most tettigoniids 1A has a strong downward bend where it fuses with Cu2 to form the stridulatory vein. Sharov (1968) was the only dissenter from the view that the stridulatory vein was either homologous in all three groups or showed differences between tettigonioids and grylloids. His proposal was that grylloids and haglids used Cu2 but Tettigoniidae used 1A. Hennig (1981), in reviewing Zeuner, Ragge and Sharov, favors a homologous ensiferan stridulatory vein and is critical of Sharov's view, stating that it lacks justification. It is somewhat contradictory that Sharov argues for a male stridulatory vein as ancestral in the Ensifera while at the same time disputing the homology of this organ within the suborder.

Even if the male stridulatory vein is the same one in all Ensifera, multiple origins of this organ could still have occurred if there were preadaptations for stridulation evolving in a specific region of the wing. The ancestral state of the tegmina in the grylloid and tettigonioid clades (in Fig. 2) was similar in that the forewings "wrapped around the abdomen" (see below). Given a similarity in tegminal positioning, it seems possible that some ancestral courtship wing movements of males could have resulted, more than once, in a single prominent vein on one tegmen contacting the other. The origin of male tegminal calling is thought to lie in the lifting and fluttering the forewings, a male courtship display in a number of orthopteroids (Alexander 1962, Otte 1992) (males of at least one non-singing gryllid appear to court females using the pulsed air from male tegminal movement; Heinzel and Dambach 1987).

The Ancestral Function of Ensiferan Ears

Acoustical Ensifera, especially Gryllidae, are known to hear and avoid high frequency sounds such as those produced by echolocating bats (reviewed in Doherty and Hoy 1985). Further evidence that ensiferan ears may serve in predator detection is the fact that ears have never been lost in fully-winged species that have lost tegminal stridulation (Otte 1992 and the taxa *Meconema* and Phyllophorinae in Fig. 3). Bat detection appears to be a derived function of the ensiferan ear, however (Fullard and Yack 1993; Pollack 1994); in fact, tympanate ears evolved before bats and other mammals did (Otte 1992). My analysis (Fig. 3) strongly supports this hypothesis. The origin of the gryllid ear was coincident with the origin of tegminal stridulation. The origin of the tettigonioid ear also appears to have occurred only when communicative stridulation evolved. Interestingly, this origin may well have involved the hind femoral-abdominal mechanism found in several ensiferan families and used by eared Stenoplematidae to communicate (Field 1993b). As a femur-abdominal mechanism is a disturbance (anti-predator) sound in earless Ensifera, this may have been its original function. Flying ensiferans such as Gryllacrididae have not evolved tibial ears despite the fact that they are probably preadapted by possessing tibial sensory organs.

Adaptations for Singing and Other Characters

The dual origin of tegminal organs and tibial ears that is consistent with the phylogeny proposed here calls into question the assumption of homology of associated characters previously considered to be of phylogenetic importance. A character clearly linked to acoustic signalling, and one that Zeuner (1939) considered informative, is the structure of the mesothoracic spiracle (see Hennig 1981). As we have seen, this spiracle is an opening to the tibial-thoracic sound-receiving organ. Zeuner (1939, who termed it the prothoracic spiracle) argued that a primitive spiracle with a single opening is found in the non-singing ensiferan families but that a divided spiracle is a derived character for Gryllodea and Tettigonioidea (evolving into two separate spiracular openings in

Tettigoniidae). Ander (1939) is, however, critical of this and points out that Zeuner missed some important anatomical details (and some key references!). According to Ander not all Stenopelmatidae have a single opening. He suggests that the simple ancestral mesothoracic spiracle has been modified in acoustical Ensifera. He thus argues that similarities between haglid and grylloid spiracles are a result of convergence. Ander points out the more detailed similarities among tettigonioids- in the auditory spiracles of *Cyphoderris* (Haglidae) and those of acoustically-signalling stenopelmatids, as well as the large auditory spiracle opening common to both Tettigoniidae and another extant haglid genus, *Prophalangopsis*.

Zeuner (1939) considered that tegmina that 'wrap' around the body is a character common to grylloids and his "Gryllacrididae" (a taxon that included the Schizodactylidae, Gryllacrididae, Rhaphidophoridae and Stenopelmatidae of the present work) (see also Hennig 1981). This appears to be a plesiomorphic trait in Ensifera, lost in the tettigoniid-haglid clade (Fig. 2). Again, the origin of sound communication in this clade may have been the cause of the large change in the positions of the tegmina (as well as the modifications of the "wrapping tegmina" in Gryllidae and Gryllotalpidae (Zeuner 1939)).

A informative character from previous work discussed by Hennig (1981) may be in error. He states that an abdominal pseudo-tympanal organ is found in Stenopelmatidae as well as Gryllidae and Gryllotalpidae. However, according to Ander (1939) it is not Stenopelmatidae but Rhaphidophoridae that have this character.

The origins of elaborate, edible spermatophores

Males of many Ensifera produce an elaborate spermatophore in which the sperm-containing part of this structure, the ampulla, is surrounded by a spermatophylax. The spermatophylax is a sperm-free mass that is eaten by the female after copulation. Studies of certain Tettigoniidae show that the spermatophylax meal supplies important nutrients affecting offspring fitness (e.g., Gwynne 1988) and can be a very costly male investment (Gwynne 1990b) that influences sexual selection and the courtship roles of the sexes (in mate choice and sexual competition) (Gwynne 1993, Gwynne and Simmons 1990). Gwynne (1995) discusses the selection pressures that probably led to the origin of the spermatophylax and other forms of "courtship feeding" within the Ensifera. Another elaboration of the spermatophore in several ensiferan families is the presence of two sperm chambers within the sperm ampulla.

I traced spermatophore characters onto a tree from a data matrix in which these characters had been removed. This removal did not affect the topology of the shortest length tree (Fig. 2). Parsimony analysis reveals that the ancestral ensiferan spermatophore consisted of a sperm-containing ampulla with a single sperm cavity and no spermatophylax and that the spermatophylax had several origins (Fig. 4). One origin was in the ancestor of the tettigonioid clade; the spermatophylax is found in all of the families within this clade. In addition it appears to have evolved three times within the family Gryllidae, in *Gryllodes*, *Teleogryllus* and possibly another origin in *Gryllomorpha* (Gwynne 1995; not shown in Fig. 4). *Gryllomorpha* is in a separate tribe within the Gryllinae (Otte and Alexander 1983). Within the tettigonioid clade there has been a loss of the spermatophylax in one genus of tettigoniids (*Tympanophora* (Gwynne, unpublished) (Fig. 4)) and a very large reduction in its size (to a barely visible structure and recorded as a "loss" in Fig. 4) in two other tettigoniid subgroups (Phasmodinae and certain Copiphorini; Boldyrev 1915, Gwynne 1995). A fourth reduction or loss of the spermatophylax in Tettigoniidae is in the tettigoniine genus *Decticita* (Rentz 1963). Based on two observations of mating by Schmidt (1990) there may be a further loss of the spermatophylax in the heterodine katydid

Fig. 4. The evolution of a spermatophylax "courtship meal" in Ensifera. Black =spermatophylax present, hatched bars = character evolution equivocal. Dots in boxes indicate taxa polymorphic for this character.

Gymnoproctus. In Stenopelmatidae the spermatophylax has been greatly reduced in tree weta *Hemideina maori*, and probably other species in this genus (Gwynne, unpublished), and lost in species of giant weta (another deinacridine, *Deinacrida*) (Ramsey 1955, Richards 1973) (Fig. 4). Giant weta have other very specialized (derived) mating characters compared to other tettigonioids (including the other New Zealand deinacridine *Hemideina*): they have only a single sperm cavity in the spermatophore (ampulla) (but with a ridge suggesting the loss of the dividing wall) (Ramsey 1955) and pass multiple spermatophores in a single, often full-day mating (Ramsey 1955, Richards 1973).

The origin of two sperm chambers in the ampulla is coincident with the origin of the spermatophylax in tettigonioids. Except for *Deinacrida*, all tettigonioids in the clade above the Rhaphidophoridae have a sperm ampulla that is divided into two sperm cavities. Rhaphidophorids have either a single sperm cavity or have the beginnings of a dividing wall (Boldyrev 1915). The grylloid spermatophore differs from tettigonioids in having one sperm cavity in the ampulla and also a long ejaculatory duct.

Origins of maternal care

Females of several ensiferan Orthoptera show some level of care for eggs and/or hatched offspring. This behavior may be a result of the habit of many species of digging, or at least occupying, a burrow (probably as a refuge from low humidity or to escape predation (Hubbell 1936, Kevan 1989)). The habit of using a burrow, at least as a retreat from other activities, appears to be ancestral to the extant Ensifera (Fig. 5). Although common in Ensifera such use of a burrow is rarely found in the outgroups

(other Orthoptera and Phasmatodea) (Kevan 1989). Most katydids (Tettigoniidae) and some Gryllidae (*e.g.,* many tree crickets, Oecanthinae) rely on crypsis for protection; these habits appear to be derived (Fig. 5). The use of a burrow may well preadapt Ensifera to maternal care.

Eggs of most Ensifera are simply injected into the substrate. However, females of ten groups of burrow-using taxa in five families appear to show some degree of care for offspring. In two genera of gryllids (West and Alexander 1963, Walker 1973) and *Schizodactylus* (Choudhuri and Bagh 1974), females care for eggs and nymphs in the burrow by protecting and feeding them, and this includes the provision of specialized eggs as food in the gryllid *Anurogryllus* (West and Alexander 1963). In mole crickets (Gryllotalpidae) care varies from construction of a brood chamber in which eggs are laid (*Gryllotalpa, Scapteriscus,* and *Neocurtilla* (Yueh-Liang 1975, Forrest 1984)) to protecting the hatched nymphs through several instars (*Triamescaptor* (Gutterson 1988)). A caeliferan version of mole crickets—a pygmy mole grasshopper (*Tridactylis apicalis*)—also shows protection of eggs in a brood cell (Urquart 1937)). In Stenopelmatidae, female ground weta *Hemiandrus* stay with eggs and nymphs (Salmon 1950, Gibbs 1994, Gwynne unpublished). Jerusalem cricket females (*Stenopelmatus*) appear to construct a brood chamber but it is unknown whether the female tends the offspring (the evidence is a photograph of spherical eggs in an apparent brood chamber in Essig (1926)). Females of a sand treader camel cricket (*Daihinibaenetes giganteus*: Rhaphidophoridae) may also stay with eggs; young nymphs have been found in adult burrows (M.J. Weissmann pers. comm.). However, it remains a possibility that eggs are not placed in a brood cell but are laid directly in burrow walls as in another camel

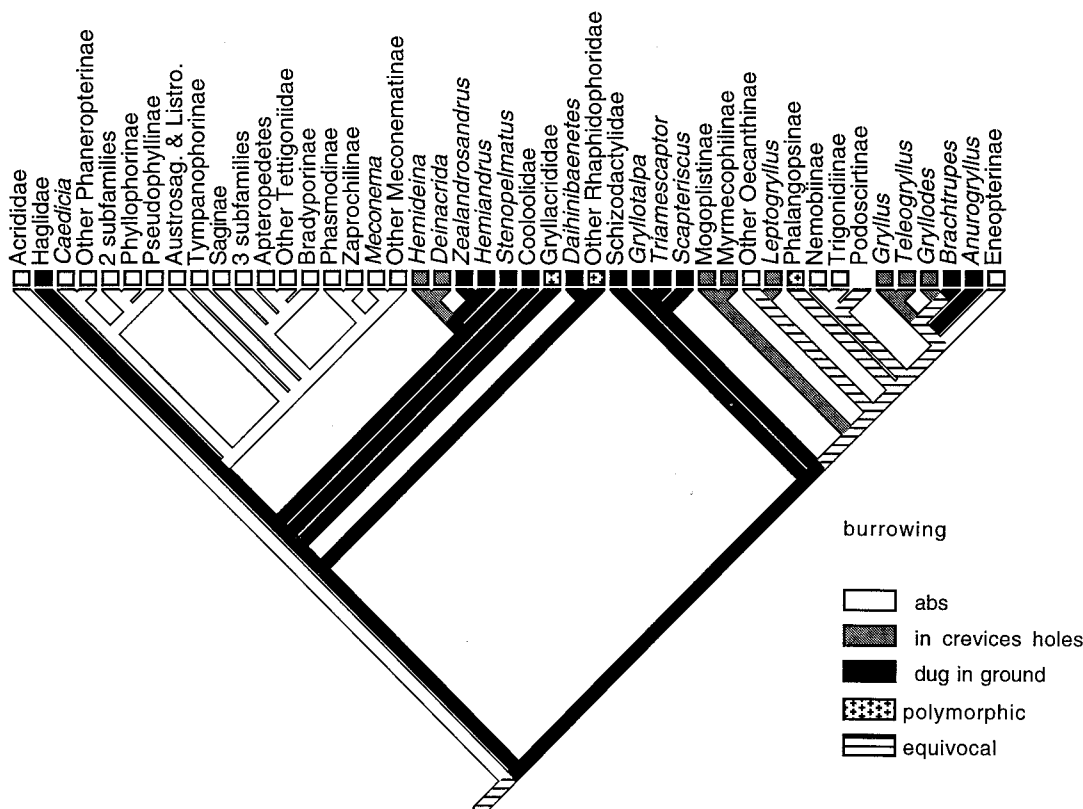Fig. 5. Microhabitat use by Ensifera (a character not included in the original matrix). Tracing this character on the tree suggests that use of a burrow is the ancestral microhabitat state for Ensifera. Black = use of a burrow in ground, stippled = use of crevices and holes, white = lives on vegetation, using crypsis etc for defence, hatch = equivocal character evolution, dots (in character boxes) = taxon polymorphic.
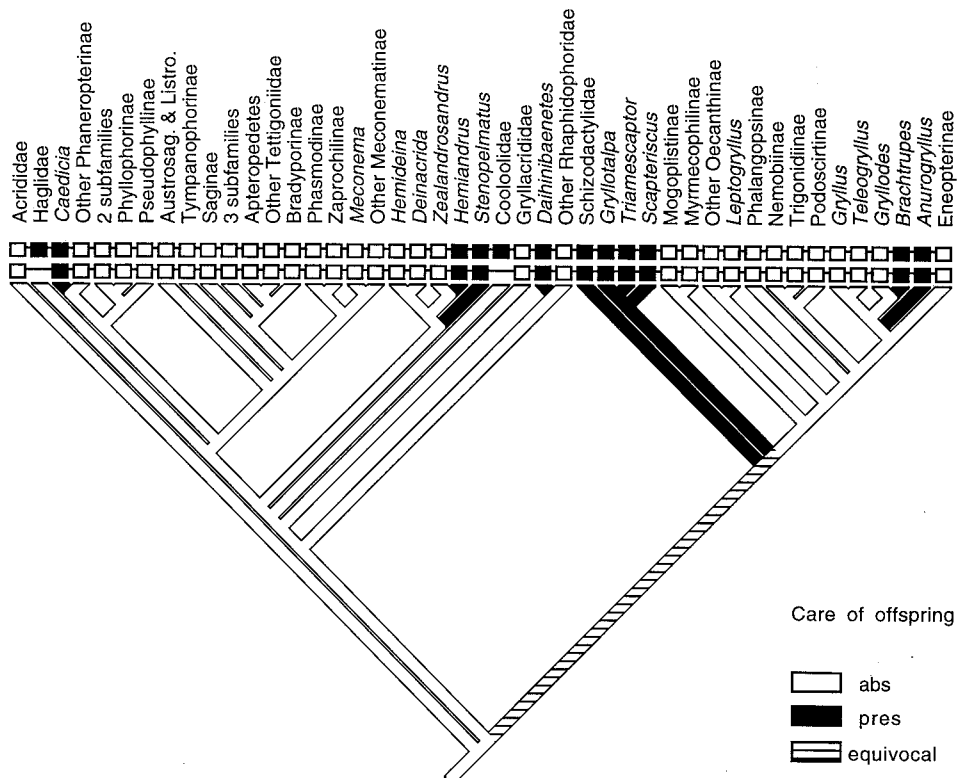
Fig. 6. The evolution of maternal care and reduced ovipositors in Ensifera. Black = maternal care present, hatched = character evolution equivocal. The row of boxes above the tree represents the character states in the taxa. The top row of boxes represents either a loss or great reduction in the ovipositor (black). Boxes with dots indicate taxa polymorphic for each character. Maternal care was not included as a character in the original data matrix.

cricket *Daihina brevipes* (Whitehead and Miner 1944). Finally, two Australasian tettigoniids, *Caedicia* and *Polichne* (Phaneropterinae) show a simple form of care in which females place their eggs in a specialized nest (on plant tissue) by covering the eggs with mud (Lysaght 1931, T. Houston pers. comm.).

There appear to be seven independent origins of maternal care in Ensifera (if *Daihinibaenetes* is included). Care by schizodactylids and gryllotalpids may not be independent (Fig. 6). There is a strong association between maternal care and loss or extreme shortening of the ovipositor, an occurrence in all seven origins of care (ovipositor character states shown in the upper row of boxes in Fig. 6). An ovipositor is apparently no longer required for its "hypodermic" function of inserting eggs into soil or plant tissue. There are only two other ensiferans that possess a reduced ovipositor, the families Haglidae and Cooloolidae. Oviposition behavior is unknown in these groups. Both show some degree of burrowing (Table 1) and the present analysis predicts maternal care in both the humped-backed crickets and Cooloola 'monsters.'

Conclusions

Phylogenies are hypotheses about relationships. The hypothesis I propose here and the subsequent interpretations of the origins of acoustical, mating and parental behaviors may change if there are changes to the subgroup taxa or to the character matrix itself. However, phylogenetic hypotheses are important for a number of reasons. First, they can be tested for congruence with other character sets. It will be particularly interesting to see how the addition of molecular characters will affect our understanding and interpretation of the evolutionary relationships in this ortho-

pteran suborder. Finally, phylogenetic hypotheses can be helpful in directing the course of future research even in areas not obviously related to evolutionary biology. For example, it would be useful for biologists interested in ensiferan hearing to study "non-singing" families of Ensifera. The conclusion that ears have evolved twice in the suborder predicts that there should be no trace of of auditory structures in the tibial organs of these families. However, if acoustical communication has a single ancestral origin in Ensifera (*e.g.*, Sharov 1968) there should be vestigial auditory structures in non-singing taxa such as in phasmodine Tettigoniidae (Lakes-Harlan et al 1991), one of the few cases of ear and song loss in the katydid-weta lineage.

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Appendix 1. Nine extant families of Ensifera in the three superfamilies recognized by Rentz (1991) (other details from Kevan. 1982).

GRYLLACRIDOIDEA

Cooloolidae—Cooloola 'monsters,' a group of burrowing insects that spend virtually the complete life cycle below ground (Four species: Southeastern Queensland, Australia).

Gryllacrididae—Locust-crickets and leaf-rolling crickets. Gryllacridids dig burrows, or use rolled leaves and other refuges in vegetation (over 500 species: Indo-Malaysia, America and Australia).

Stenopelmatidae—Jerusalem crickets, sand crickets, ground, giant and tree weta. These insects live in burrows, tree holes or rock crevices. The giant (*Deinacrida*) and tree weta (*Hemideina*) possess tympana and males communicate by sound using femoral-abdominal stridulation. (About 200 species: New Zealand, Australia, America, Africa).

Rhaphidophoridae—Camel and cave crickets, cave weta. A group of wingless Ensiferans that live in caves, dig burrows, or live in crevices. (About 300 species: Europe to Japan, America, Australia, and Africa).

Schizodactylidae—The splay-footed crickets. Burrowing insects (7 species: India, Asia, South Africa).

TETTIGONIOIDEA

Haglidae (= Prophalangopsidae)—Hump-winged and sagebrush crickets. Individuals burrow under leaf litter and into soil but at night climb into vegetation to feed and mate. Males will ascend tree trunks to produce calling songs using tegminal stridulation. (Five species: Northwestern America, India, and Russia).

Tettigoniidae—Katydids, long-horned grasshoppers, and bush-crickets. A very diverse family of mostly nocturnal species that hide in vegetation during the day. Males call using tegminal stridulation. (Over 5000 species found worldwide in habitats as diverse as peat bogs, mountain tops, and tropical rain forests).

GRYLLOIDEA

Gryllidae: True crickets (containing tree, ground, field, and house crickets). Another diverse family. Individuals usually live in burrows but some, such as tree crickets, hide in vegetation during the day. Males of most species call using tegminal stridulation. (Over 2000 species found worldwide in diverse habitats).

Gryllotalpidae—Mole crickets. Individuals live in burrows and have characteristic "molelike" front legs adapted for digging. Males of most species call from burrows using tegminal stridulation. (About 50 species in the Neotropics, southern US, Europe, Australia, and New Zealand).

Appendix 2. Character Matrix.

Taxa: Phasmatodea (PH), Acrididae (AC), Haglidae (HG), Tettigoniidae (TE), Stenopelmatidae (ST) Cooloolidae (CO), Gryllacrididae (GC), Rhaphidophoridae (RH), Schizodactylidae (SC), Gryllidae (GR), and Gryllotalpidae (GT). 0 = character absent, 1 = character present unless otherwise indicated. Two character states indicates the character is polymorphic in that taxon. "?" = "character missing".

	PH	AC	HG	TE	ST	CO	GC	RH	SC	GR	GT
Antennae much longer than body	0	0	1	1	1	1	1	1	1	1	1
Fastigium verticalis	0	1	1	1	0,1	0	1	0,1	1	0	0
Double fastigium verticalis	?	0	0	0	0	?	0	0,1	1	?	?
Pronotum with lateral lobes	0	1	1	1	1	1	1	1	1	1	1
Prothorax with cryptopleuron	0	1	1	1	1	1	1	1	1	1	1
Meso and metasternum with sclerotized space	0	0	0	0	0,1	0	0	1	1	0	0
1st spiracle single (0) divided (1) or dual (2)	0	0	1,2	2	0,1	?	0	0	0	1	1
Forecoxae shorter than broad	0	0	0,1	1	1	0	0	0	0	0	0
Tibial tympana present	0	0	1	1	0,1	0	0	0	0	0,1	0,1
Tympana with thick and thin parts	?	?	1	1	1	?	?	?	?	0	0
Tympanal vesicles present	0	0	1	1	0	0	0	0	0	1	?
Hind tibiae with alternate spine sizes	0	0	0	0	0	0	0	0,1	0	1	1
4 tarsal segments in middle leg	0	0	1	1	1	1	1	1	1	0	0
Tarsal segments 1 -3 with pulvillae	0	1	1	1	1	1	1	0,1	1	0	0
Pulvillae lobed and broad	0	1	0	1	0	0	1	0	1	?	?
Pulvillae with tubules	0	0	1	1	1	0	0	0	0	?	?
Femoral-abdominal stridulation	0	0	0	0	0,1	0	1	0,1	1	0	0
Male tegminal stridulation	0	0	1	1	0	0	0	0	0	0,1	0,1
Tegmen with harp	0	0	0	0	0	0	0	?	0	1	1
Tegmina folded at base of R, M, Cu	0	0	0	0	0	0	0	?	1	1	1
Tegmen Sm1, R, M, Cu run close together	0	0	0	0	0	0	0	?	0	1	1
Cu1/MP fused especially in tegmina	0	0	1	1	1	1	0	?	0	0	0
Costa reduced or absent	1	0	0	0	0	0	0	?	1	1	1
Archedictyon present	1	1	0	1	0	0	0	?	1	0,1	1
Numerous tegminal anal veins	0	0	0	0	1	0	1	?	0	0	0
Tegmina wrap around body	0	0	0	0	1	?	1	?	1	1	1
Tegmen with mirror and subcostal branching	0	0	1	1	0	0	0	?	0	0	0
Tegmina held roof-like over abdomen	0	0	1	1	0	0	0	?	0	0	0
Hindwing (HW) fusion of Rs and M	0	0	1	1	0	?	0	?	0	0	0

Character											
Extension of fanlike folding in HW	0	0	0	0	0	?	0	?	1	1	1
HW: no demarcation of vannus	1	0	1	1	1	1	1	?	1	1	1
HW: Cu1 forks onto 2 branches	0	0	0	0	0	0	0	?	1	1	1
HW: Cu1a developed fused with mp	0	0	1	1	0	0	0	?	0	0	0
Anal fan with anterior and posterior cubital areas	0	0	1	1	1	1	1	1	1	1	1
Pinch on anal veins 3 and 4	1	0	0	0	?	?	1	?	?	0	0
Pseudotympanum on abdomen	0	0	0	0	0	0	0	1	0	1	1
Two kinds of cercal hairs	0	0	0	0	0	0	0	0	0	1	1
Male 10th abdom segment with paired organ	0	0	1	0	1	1	1	0	0	0	0
Male paraproct with grasping projection	0	0	1	0,1	1	1	1	0	0	0	0
Male subgenital plate with styles	0	0	1	0,1	1	1	0,1	0,1	1	0	0
Blade-like ovipositor	0	0	1	1	1	1	1	1	?	0	0
Ovipositor absent	0	0	0	0	0	0	0	0	1	0	1
Ovipositor united with fold	0	0	1	1	1	?	0	0	0	0	0
Proventricular teeth complex (1) simple (2)	0	0	1	1	1	1	1	1	1	2	2
Proventricular tooth tip sclerotised	0	?	0	0	0	0	0	1	1	0	0
One outlet for malpighian tubes	1	1	0	0	0	0	0	0	0	1	1
Dorsal space in male genitalia	0	0	1	1	1	?	0	0	0	0	0
Abdominal ganglia 2 +3 fused	0	0	1	1	1	1	1	1	0	0	0
Abdominal ganglia 7-10 fused	0	0	0	0	0	0	0	0,1	1	1	1
Additional abdominal sternal plates	1	1	1	1	1	1	1	1	?	0	0
Ovaries fascicle-shaped	0	0	1	1	1	?	0	0,1	1	1	?
Ovary with both comb and fascicle-shaped parts	0	0	1	1	0	?	0	0	0	0	0
Testis with suspensory ligament	0	0	0	0	0	0	0	0	0	1	1
Long ejaculatory duct	0	0	0	0	0	0	0	1	0	1	1
Very short seminal duct	0	0	1	1	1	?	1	1	0	0	0
Genital sacs in male	0	0	2	2	1	?	2	2	1	0	0
Spermatophylax present	0	0	1	1	0,1	?	1	0,1	0	0,1	0
Ventral median vesicle in tracheae	?	0	1	1	1	?	1	0	1	0	0
Large ventral tracheae	?	0	1	1	1	?	0	0	0	0	0
Thorax trach with lg cephal stem	?	0	0	0	0	0	0	1	0	1	1
Trach: separated cephalic stem	?	0	1	1	1	1	1	0	1	1	1
Trach: strong transverse in prothorax	?	0	1	1	1	?	1	0	0	0	0
Sperm heads not filiform	0	0	?	1	?	1	?	0,1	?	0	0
Flat sperm head + nucleus	0	0	?	1	?	1	?	0	?	0	0
Spermat cavities 1 (0) 2 (2) intermed (1)	0	0	2	2	0,2	?	2	1	0	0	0
Male on top in copulation	1	1	0	0	0	0	0	0	0	0	0
M behind F faces same way in copulation	0	?	1	1	0,1	?	1	0,1	?	0	0,1

Some character information on outgroups came from Ander (1939); most, however, is from other sources. For Phasmatodea general characters, Beier (1968) and Key (1991); for wing venation, Ragge (1955b); for spermatophores, LeFeuvre (1939), Clark (1974), Carlberg (1981), and Bragg (1991). I could not locate information on tracheal system characters for Phasmatodea. For general information on acridid characters I used Uvarov (1977) and Rentz (1991); for wing venation, Ragge (1955a); for spermatophores, the review by Pickford and Padgham (1973) and C. Gillott (pers. comm. 1993). For tracheal information, I had to rely mainly on characters for one species, *Locusta migratoria* (Albrecht 1953). Alexander and Otte (1967) was used for information on mating position in both outgroups.

General information on Ensifera (ingroup families) came from Ander (1939), Kevan (1982, 1986) and Rentz (1980, 1991); cooloolid characters from Rentz (1980, 1986); schizodactylid characters from Ragge (1957), Khattar (1959, 1966, 1972a,b); some additional information on Tettigoniidae from D.C. Rentz (pers. comm.); wing venation characters, Ragge (1955a, 1957) (wing venation character "pinch on anal veins 3 and 4" from Kukalova-Peck (pers. comm., 1993)); rhaphidophorid and stenopelmatid stridulatory structures from Field (1993a); formating characters in Ensifera generally, Alexander and Otte (1967), but also Gwynne (pers. obs.) and Richards (1956) for additional information on Rhaphidophoridae; for Stenopelmatidae, Ramsey (1955), and Richards (1973) (*Deinacrida*), Sandlant (1981), Field and Sandlant (1983), Moller (1985), Field (1993c) and Gwynne (unpublished) (*Hemideina*), Cary (1981) and Butts (1983) (*Zealandosandrus*), Monteith and Gwynne (unpub) (*Penalva* and *Transaevum* (Henicinae)), Gwynne (unpublished) (*Hemiandrus* (Henicinae)), and Tinkham and Rentz (1969) and (Weissman (MS) (*Stenopelmatus*)); for Gryllotalpidae, Alexander and Otte (1967) and Forrest (1984); for spermatophore characters of Tettigoniidae, Gryllidae and Rhaphidophoridae, Boldyrev (1915), Alexander and Otte (1967), Sakaluk (1984) and Gwynne (1990a, and pers. obs.); for Stenopelmatidae, Tinkham and Rentz (1969) and Weissmann (MS) (*Stenopelmatus*), Monteith and Gwynne, (unpub.) (*Penalva* and *Transaevum* (Henicinae)), Gwynne (unpublished) (*Hemiandrus* and *Hemideina* (Henicinae)), Ramsey (1955) (*Deinacrida*); for Gryllacrididae, Rentz and John (1990), Gwynne (pers. obs.) and Heller (pers comm.); for gut characters, Judd (1948), and Rentz (1980); for spermatozoa, Baccetti (1987); for microhabitat information in general, Alexander and Otte (1967), Kevan (1982) and Rentz (1991); for Rhaphidophoridae, Hubbell (1936), Whitehead and Miner (1944), Richards (1956); for maternal care and oviposition information in gryllids, West and Alexander (1963), and Walker (1973); *Schizodactylus*, Chouri and Bagh (1974); in Gryllotalpidae, Weiss and Dickerson (1918), Thomas (1928), Hayslip (1943), Yeuh-Liang (1975), Forrest (1984) and Gutterson (1988); for Stenopelmatidae, Salmon (1950), and Gwynne (pers. obs.) (*Hemiandrus*), Cary (1981), Butts (1983), and Gwynne (unpublished) (*Zealandosandrus*), Tettigoniidae (*Caedicia*) Lysaght (1931); *Daihinibaenetes* ovipositor structure from Tinkham (1962); for tegminal and tympanal organs in Gryllidae, Kevan (1982) and Otte (1992), Haglidae, Mason (1991) and Stenopelmatidae (*Hemideina*), Ball and Field (1981).

Tettigonioid Clade (six families)
  (65% of bootstrap replications):
—Spermatophylax present (although it is equivocal whether this is ancestral to the Rhaphidophoridae as it is polymorphic in this family)
—A very short seminal duct in the male
—2nd abdominal ganglion fused with the 3rd but not with the thoracic ganglion
—A blade-like ovipositor (a blade-like ovipositor also occurs in the Gryllid subfamily Trigonidiinae but Desutter's (1987) phylogeny argues for an independent origin of this trait within Gryllidae).

Haglid-Tettigoniid-Stenopelmatid-Cooloolid-Gryllacridid Clade
  (93% of bootstrap replications):
—Two sperm chambers in the sperm ampulla
—A "kama-sutra" position at the end of copulation in which the male is behind the female, facing up, or in the same direction as her (a character polymorphic in Rhaphidophoridae, Gryllidae and Gryllotalpidae)
—Strong transverse tracheae in the prothorax
—Ventral median vesicle-like abdominal tracheae
—Male paraprocts with a projection, and a male 10th abdominal segment with projections that form paired "clasping" organs (functioning as a mate-grasping "gin trap" in Haglidae (Morris 1979) and a character that is lost in the Tettigoniidae).

Haglid-Tettigoniid-Stenopelmatid-Cooloolid Clade
  (75% of replications):
—Fusion of Cu1 and MP veins, especially in forewings.

Haglid-Tettigoniid-Stenopelmatid Clade
  (90% of replications):
—Anterior and posterior parts of the ovipositor united by a fold
—A large ventral longitudinal stem in the thoracic tracheae
—Fore coxae shorter than broad
—Chitinous tubes in the tarsal pulvillae
—A dorsal space in the male genitalia
—Tibial tympana that have both a thick and a thin region (as the presence of tympana is polymorphic in Stenopelmatidae, it is equivocal whether this trait is ancestral to the clade). Also shared by the three taxa are certain characters of the fore-"tibial organ" receptor cells (characters not included in the data matrix but discussed in the text).

Haglid-Tettigoniid Clade
  (100% of all bootstrap replications):
—Tympanal tracheal vesicles
—Ovary structure is partly comb-like and partly fascicle-like
—Development of the Cu1a vein in the hind wing that fuses with MP
—Fusion of Rs and M veins in hind wing
—Fore wings are "roof-like" over the abdomen
—Male forewing having a mirror and many accessory subcostal branches, an adaptation to tegminal stridulation.

Grylloid Clade (three families)
  (less than 50% of bootstrap replications):
—Development of a median fan in the forewing
—Fusion of abdominal ganglia 8, 9 and 10 with 7
—Wing costa reduced or absent
—Extension of fan-like folding along Rm and Cu of the hind wing
—Male tegmen is bent downward at an angle

Gryllidae-Gryllotalpidae Clade
  (100% of bootstrap replications):
—1st spiracle divided
—Hindtibiae with alternating sized spines
—Male tegmen with a harp
—Tegminal veins Sm1, R, M, and Cu run close together
—Pseudotympanum on abdomen
—Two kinds of cercal sense hairs
—Simple proventricular teeth
—Testis with suspensory ligament
—Long ejaculatory duct
—Thoracic trachea with large cephalic stem