EVOLUTIONARY BIOLOGY OF ORTHOPTEROID INSECTS

Editor:
BACCIO M. BACCETTI
Department of Evolutionary Biology
University of Siena, Italy

1987

ELLIS HORWOOD LIMITED
Publishers · Chichester

Halsted Press: a division of
JOHN WILEY & SONS
New York · Chichester · Brisbane · Toronto

29

Evolutionary differentiation of right and left tegmina in crickets

Sinzo Masaki, Mitsuko Kataoka, Kazuya Shirato, & Masahide Nakagahara

The crickets usually fold their tegmina in the right over left position. This positional asymmetry results in functional asymmetry, which in turn may lead to morphological asymmetry. Despite the same evolutionary time since the appearance of the common ancestor, the left tegmen shows highly variable degrees of retrogressive evolution among different species. In some species, the right and left tegmina are almost mirror images of each other, but in others the left tegmen tends to be thinner and less pigmented than the right. Some species have similar numbers of right and left file teeth; others show a slight decrease in the left file teeth; still others retain the number of teeth in the left only less than half that in the right; and a few species do not have even traces of left teeth. These variations are not correlated with the right-tooth number, suggesting that the retrogressive evolution proceeds independently of the modification of tooth number. There are a few lines of evidence for separate origins of the left-file retrogression in different phylogenetic groups.

INTRODUCTION

Most insects are bilaterally symmetrical. This general body plan is highly effective in locomotion, being established by the genetically controlled sequence of morphogenesis. Bilateral symmetry is indeed a functional necessity for any pair of structures performing directional movements. The right and left wings of most insects are thus mirror images of each other owing to both developmental and functional constraints.

As claimed by Sharov (1968), however, the insect wing is a labile structure in terms of evolutionary potential, and there are innumerable cases of its modification. Especially interesting is the disruption of wing symmetry in the Orthopteran families Gryllidae and Tettigoniidae that produce sound signals by rubbing the forewings together. In these insects, the asymmetrical functions and associated morphological differentiation, if any, of the right and left tegmina have evolved in conjunction with the species-specific system of acoustic communication. Study of tegminal asymmetry is therefore highly significant for understanding their evolution.

In this paper we explore the evolutionary tendency in the retrogression of the left stridulating file that leads to the disruption of bilateral symmetry in crickets' tegmina.

OVERLAPPING TEGMINA

The first step for the disruption of bilateral symmetry of the tegmina is overlapping of the right and left structures. This status of folded wings is common among acoustic as well as non-acoustic Orthopterans. In the Gryllidae, the right tegmen usually covers the left (Elliott & Koch 1983, Neville 1976). The same tegminal position, right over left, tends to be retained in both sexes (Fig. 1), although the overlapping area of the tegmina is much narrower in the female than in the male. The inverted position is very rare in the male, and a little more frequent in the female.

In some insects such as grasshoppers that do not make use of the overlapping tegmina for stridulation, the wings can take either one of the two folding positions at random, and right over left and left over right may occur in equal frequencies as exemplified by *Oxya yezoensis* (Fig. 1). Therefore, overlapping itself does not always lead to disruption of the bilateral symmetry of the tegmina. However, right over left is the rule in crickets, while the opposite is the case in katydids (Stärk 1958). I have confirmed these trends by examining about 40 species of crickets and 10 species of katydids, and some examples are given in Fig. 1. The Mogoplistine cricket *Ornebius kanetataki* is a rare exception, showing random overlapping of the right and left tegmina. This probably represents a secondary status and might be related to complete separation of the right and left tegmina in the opening stroke of stridulation. Generally, the right over left position of the tegmina

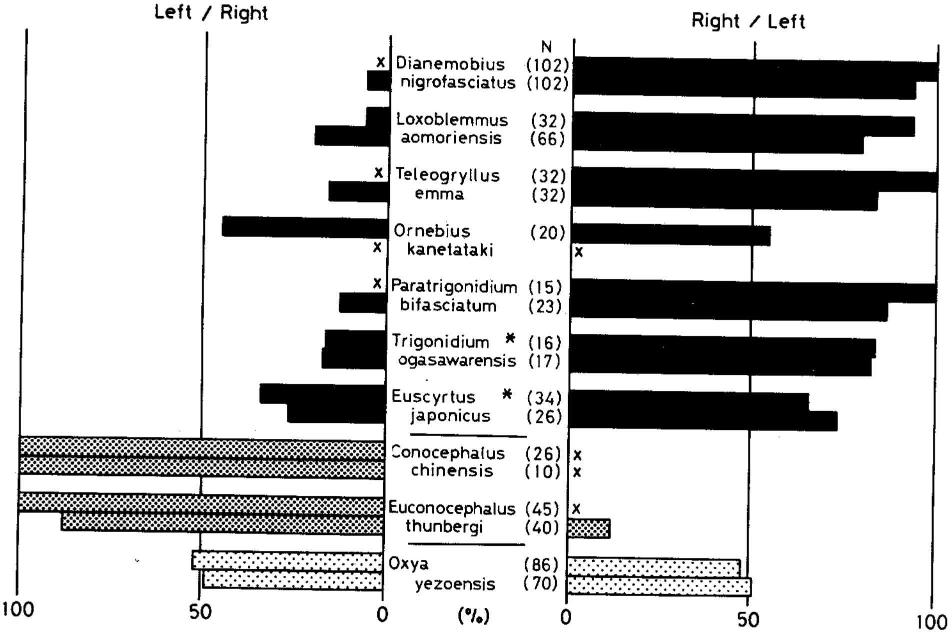

Fig. 1 — Some examples of the folded position of right and left tegmina in several species of Orthoptera. Histograms show percentages of right/left and left/right. Closed-Gryllidae. Densely stippled-Tettigoniidae. Lightly stippled-Acrididae. In each species the upper histogram is the male and the lower the female. Cross stands for zero. Asterisk indicates mute species.

seems to have a genetic basis and not simply sex-linked, because the male and female show similar tendencies (Fig. 1). Furthermore, even in mute species such as *Trigonidium ogsawarensis* and *Euscyrtus japonicus,* the right over left position predominates.

DIFFERENTIATION OF RIGHT AND LEFT TEGMINA

What is intriguing is the big difference in degree of morphological differentiation of the right and left tegmina among various species of crickets. In spite of the strongly biased overlapping position of the right and left tegmina, some species like *Gryllus bimaculatus* as shown in Fig. 2a retain the bilateral symmetry of their tegmina, at least in external appearances such as venation, pigmentation, thickness, etc. In other species, the morphological symmetry is clearly broken and the left tegmen is not a mirror image of the right one.

Thus, in the ground cricket *Pteronemobius nitidus* the left tegmen, which is covered by the right tegmen when folded, is much less pigmented and thinner (Fig. 2b). This may be related to the

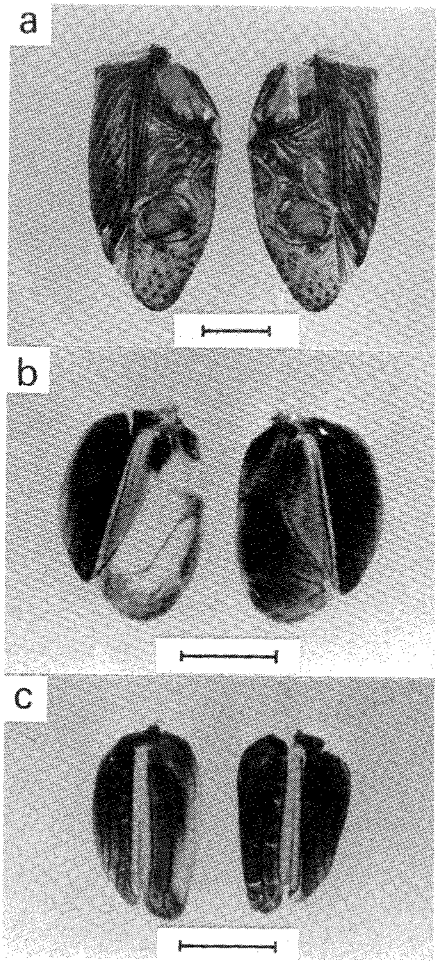

Fig. 2 — Comparison of the right and left tegmina in *Gryllus bimaculatus* (a) and *Pteronemobius nitidus* male (b) and female (c). Note the less pigmented condition in the left tegmen of the latter species. Scale is 5 mm (a) or 2 mm (b, c).

natural selection for a greater efficiency of sound production, but another factor also seems to be involved. A difference in pigmentation and thickness between the right and left tegmina can be seen not only in the male but also in the mute sex, female (Fig. 2c). Although only the narrow area along the inner margin of the female left tegmen is covered by the right tegmen, that portion lacks pigment. A similar status is found in both sexes of the mute species *Trigonidium haani*. These facts suggest that not only the sound production but also the protecting effect of the tegmina covering the dorsal surface of the body exerts selection pressure and disrupts the bilateral symmetry of the tegmina. This assumption is supported by non-acoustic cockroaches. We examined eight species of these animals and found all of them taking tegminal positions strongly biased for left over right. They showed corresponding loss of pigment in the part of the right tegmen covered by the left.

The disruption of bilateral symmetry poses a challenging problem for both evolutionary and developmental biologists. Morphogenetic process is apparently canalized to keep bilateral organs symmetrical and thereby the balance between the right and left sides of the body. If this canalization is to be modified in response to natural selection, there should be some system conveying the positional information to distinguish between the right and left sides of the body.

RETROGRESSION OF LEFT STRIDULATING FILE

Different species of crickets show different degrees of differentiation of the right and left tegmina not only in pigmentation but also in stridulating file and associated structures. This was noticed by Ohmachi & Ashida (1940) for the Gryllidae and by Stärk (1958) for the Tettigoniidae.

A stridulating file consists of a row of fine teeth arranged on the lower branch of cubitus (Fig. 3).

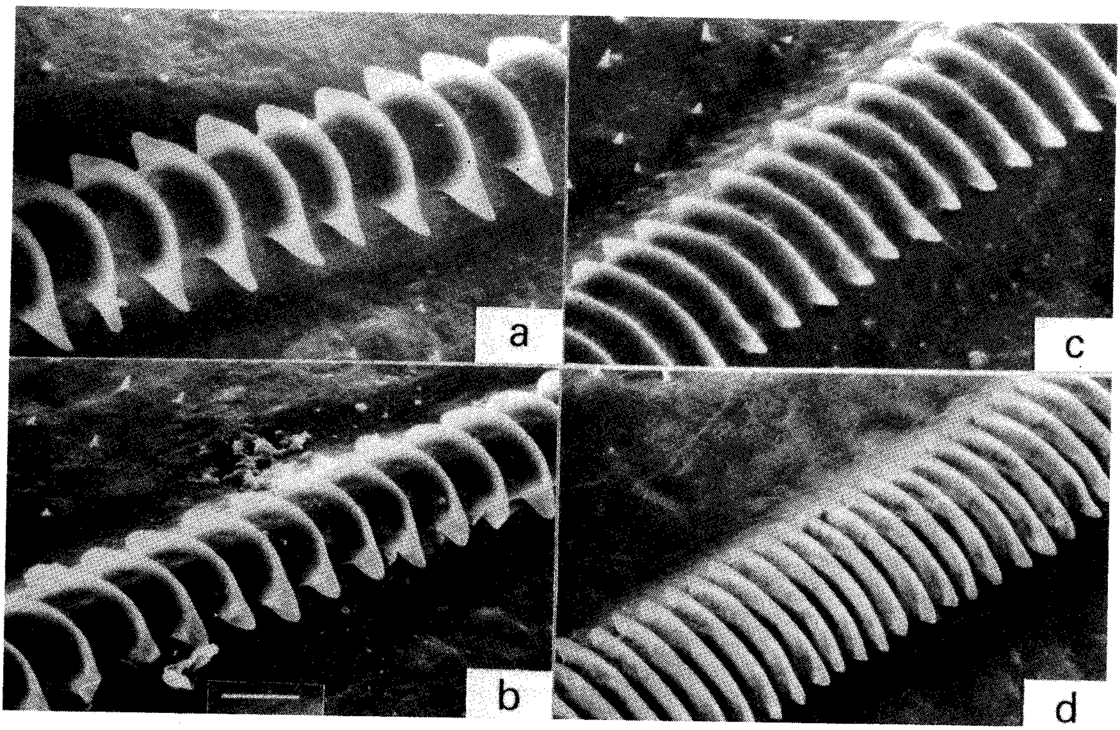

Fig. 3 — Some examples of cricket file teeth. (a) *Pteronemobius nitidus*. (b) *Dianemobius fascipes*. (c) *D. flavoantennalis*. (d) *D. furumagiensis*. Scale is 10 μm.

The number of teeth is highly variable among different species. In some cases, it can be used as a diagnostic character to distinguish closely related species (e.g., McIntyre 1977, Otte & Alexander 1983, Walker & Carlysle 1975), although there is a certain amount of size-dependent variation in each species. In Fig. 4 is shown a wide range of interspecific variation from about 50 in *Oecanthus longicaudus* to 340 in *Schleropterus coriaceus*. Otte (1983) observed an enormous range of interspecific variation in tooth number, ranging from 38 to 1308 within the single genus *Afrogryllopsis!*

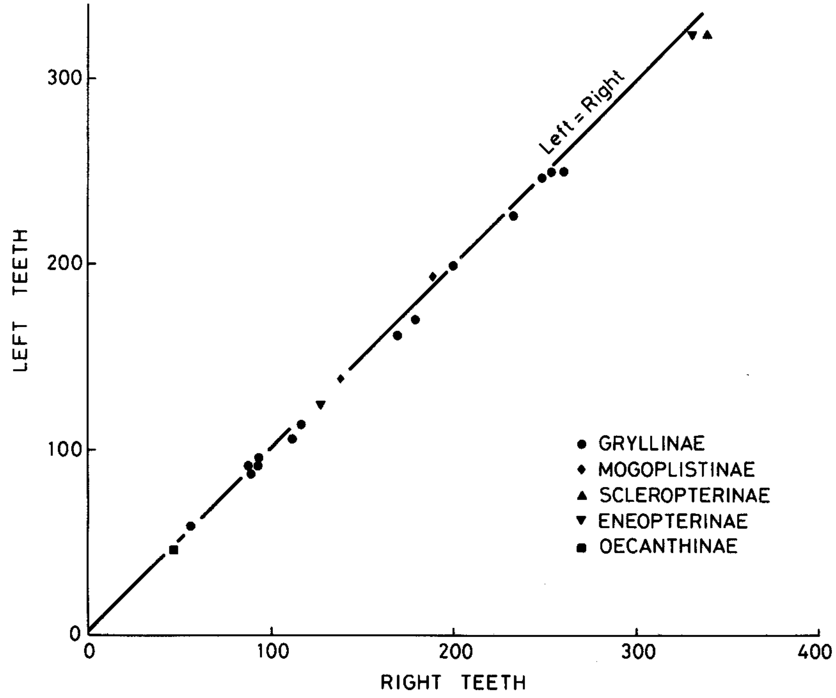

Fig. 4 — Examples of cricket species showing similar numbers of file teeth on the right and left tegmina. Each point represents mean of 5 to 20 specimens.

Many species — about 20 among 40 species we have examined — retain an approximately symmetrical relation between the right and left files so far as the tooth number is concerned. The plots of tooth numbers for these species representing five subfamilies are distributed very close to the line, indicating equal numbers of right and left teeth. Needless to say, the left teeth are useless for stridulation so far as the right over left folding of the tegmina is maintained. If this tegminal position represents a synplesiomorphic status in the Gryllidae, the left file teeth would have never been used throughout the entire evolutionary history of the crickets. In fact, Elliott & Koch (1983) found that in *Gryllus campestris* the sound intensity is reduced to 100 times less if the wing orientation is inverted, and also that the normal right over left orientation is restored by a special wing-spreading behaviour. The formation of the useless teeth on the left file should be due to the bilaterally symmetrical body plan.

As we have already noticed in the pigmentation, certain species of crickets have lost the bilateral symmetry of the tegmina. A close inspection of Fig. 4 reveals uneven distribution of the plotted points in the two sides of the line indicating the same tooth numbers on the left and right stridulating veins. There are more points in the lower side than in the upper side of the line. This means that the left file tends to have a smaller number of teeth than the right.

A much clearer trend to retrogression of the left file can be seen in Fig. 5, which shows the correlation between the right and left tooth numbers for 12 other species of crickets. The left numbers are consistently smaller than the right. Only one subfamily, the Nemobiinae, is represented in this graph. Even in this single subfamily, there is a great interspecific variation in tooth number, ranging from about 55 to 260, but the plots for these Japanese species are distributed all around the same line denoting (left number)=0.75 (right number). This may suggest that the retrogression of the left file is associated with neither increase nor decrease in tooth number of the right file. Similar degrees of retrogression may occur when the tooth number is either small or large.

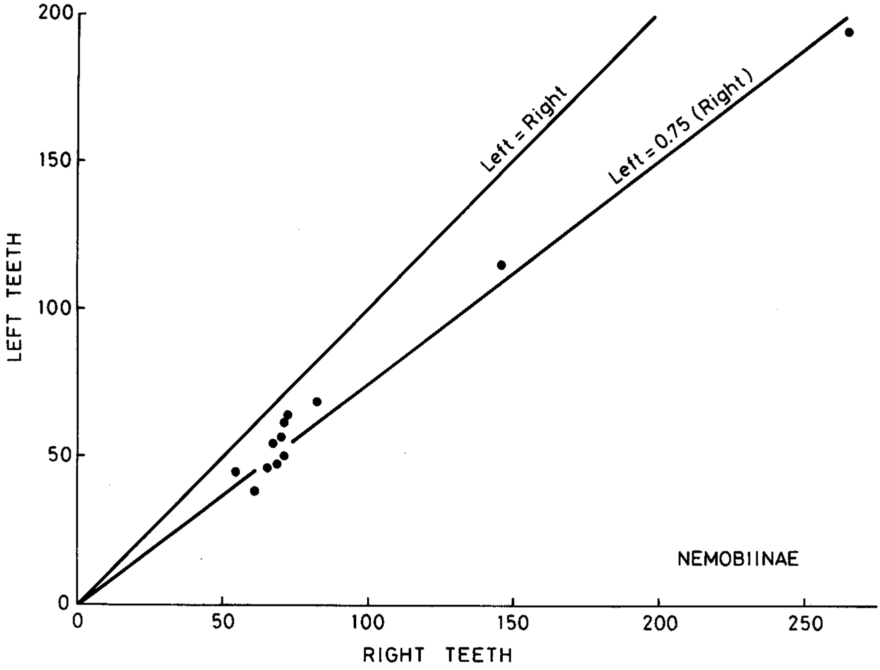

Fig. 5 — Examples of cricket species showing the tooth number on the left file reduced to about 75% of that on the right file. Each point represents mean of 10 to 20 specimens.

These crickets show another aspect of retrogressive evolution of the left tegmen. Near the inner end (plectrum side) of the stridulating file, there is a conspicuous group of long sensory hairs that may take part in keeping the tegmina in the right position at rest and in motion (Elliott & Koch 1983). Fig. 6 compares the corresponding portions of the right and left tegmina. In the latter, there is nothing where there should be a group of sensory hairs.

Retrogressive evolution has proceeded a step further in certain other species, as shown in Fig. 7. Here there is again a great interspecific variation in file-tooth number, ranging from about 80 to 470. The plots for the left-right relationship in six species are distributed around the line showing the left file teeth being reduced in number to only about 20% of the right. Once again, therefore,

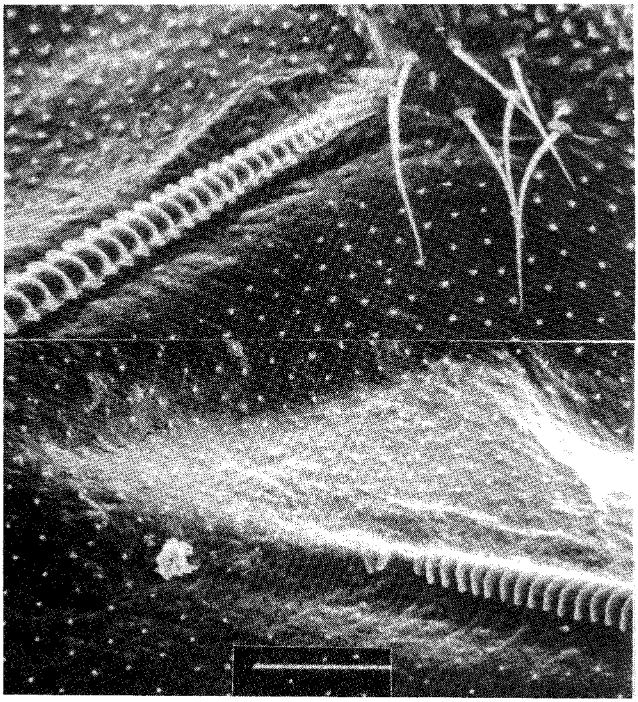

Fig. 6 — Comparison of the right (upper) and left (lower) tegmina of *Dianemobius fascipes* at the inner (plectrum) end of the stridulating vein. Note the presence or absence of a group of sensory hairs. Scale is 50 μm.

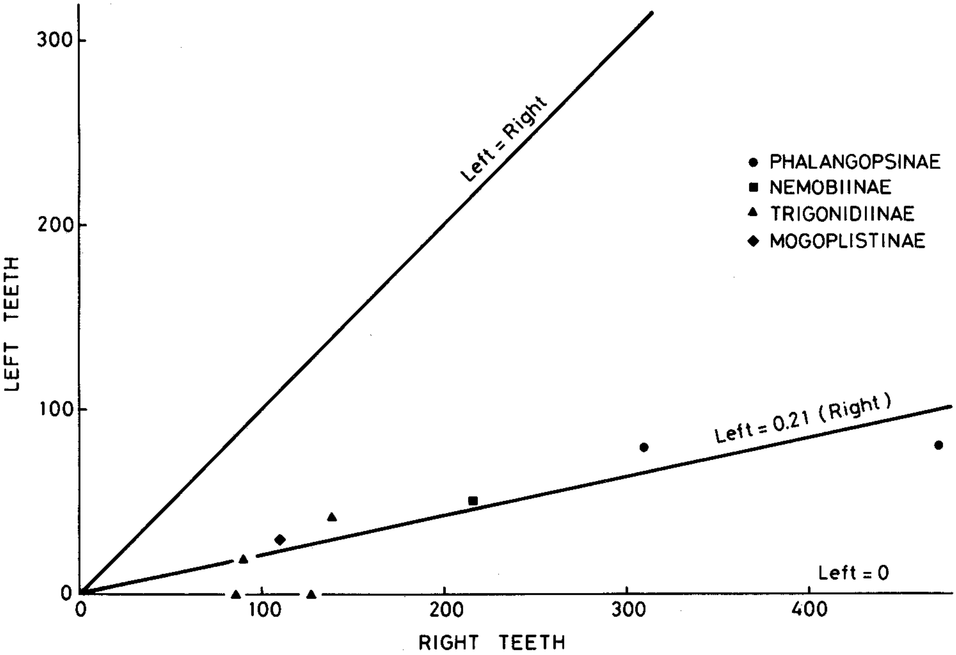

Fig. 7 — Examples of cricket species showing the tooth number on the left file reduced to about 20% of that on the right file, or to zero. Diamond is based on a single individual examined by Ohmachi & Ashida (1940).

the variation in tooth number is nothing to do with the retrogression of the left file. In other words, the tooth number on the right file is not increased at the expense of that on the left file. Or the tooth number on the left file can decrease without associated decrease on the right file. Therefore, the retrogression of the left file and the modification of tooth number are evolutionary phenomena independent of each other. Theoretically, natural selection against the useless structure should culminate in a complete disappearance of teeth from the left vein. Two species plotted on the horizontal axis of this graph represent such a situation.

We have thus graded series of retrogression of the left file. In one extreme any sign of retrogression is hardly seen. In the other extreme the left teeth have been completely lost. Between them there are various intermediate situations.

INVOLVEMENT OF PHYLOGENETIC FACTORS

As the rate of retrogression of the left file is not correlated with the variation in tooth number, we may ask next if a phylogenetic factor is involved. The data given in Figs 4, 5, and 7 can be re-examined from this view point.

All of the 15 species of the Gryllinae we have examined are included in Fig. 4; that is, they have without exception similar numbers of teeth on the left and right files. It might be inferred that crickets of this subfamily are conservative in modifying the left tegmen. A phylogenetic factor thus seems to be somehow involved in determining the speed of the retrogressive evolution. It cannot be determined whether or not the same tendency prevails in each of the other subfamilies plotted in the same graph because only a few species are available.

All the Japanese species of the Nemobiinae show similar rates of decrease in the left-tooth number (Fig. 5), the fact again suggesting a phylogenetic factor. However, there is a remarkable deviation from this general subfamily trend. Namely, the left-file retrogression has gone much further in the New Zealand cricket, *Pteronemobius (? Bobilla) nigrovus* (Fig. 7).

A similar diversity in the degree of retrogression occurs in the Mogoplistinae, though only three Japanese species are available. Two of them belonging to *Ornebius* (Chopard 1968) have similar numbers of right and left teeth, but a remarkable retrogression of the left file is found in *Ectatoderus annulipedus* (Figs 4, 7). If this classification is accepted, the susceptibility to the retrogression of file teeth would be highly variable even in the same subfamily.

In the Trigonidiinae, two species have arrived at the final stage of retrogressive evolution and completely lost the left teeth. The other two species still retain left teeth, though much reduced in number. This subfamily in general may be at advanced stages of left retrogression.

We may deduce that some phylogenetic factor is involved in the retrogression of the left file, because different subfamilies, the Gryllinae and the Nemobiinae for example, show clearly different degrees of retrogression. At the same time, however, conspicuous deviations from the general subfamily trend can occur, which means that the retrogressive evolution originates in various subfamilies independently of one another.

PATTERNS OF RETROGRESSION

Independent origins of retrogression of the left file can be inferred also from morphological features. Fig. 8 compares the right and left stridulating files of *Pteronemobius (? Bobilla) nigrovus* by means of simple replica preparations (Ragge 1969). The toothed portion of the left file is diminished from both ends to about only one-fourth in length of that of the right file. At the same time, the tooth density decreases and spacing becomes less regular towards both ends.

Fig. 9 compares the central one-fifth of the right file and the entire left file of *Homoeogryllus venosus,* a phalangopsine cricket from Uganda. This picture illustrates how spectacular a result of

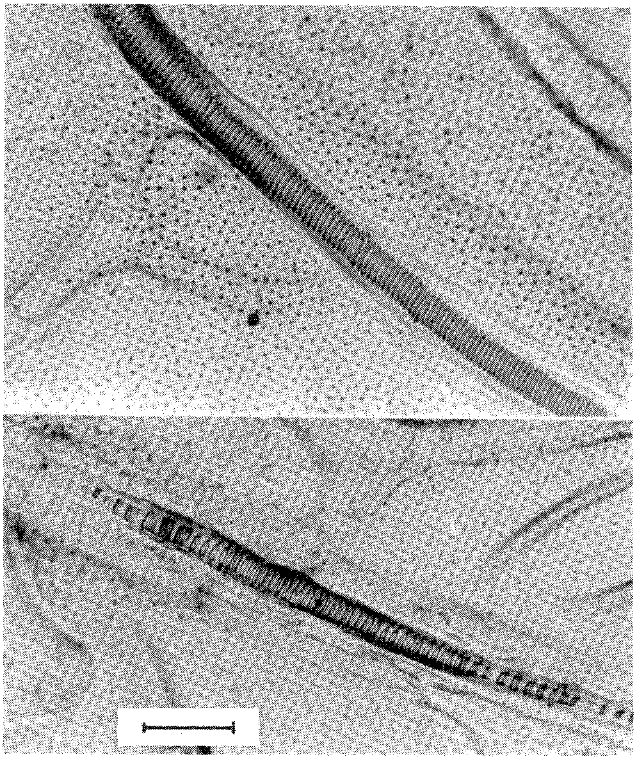

Fig. 8 — Comparison of the right (central part, upper) and left (lower) rows of file teeth in *Pteronemobius* (? *Bobilla*) *nigrovus*. Scale is 0.1 mm.

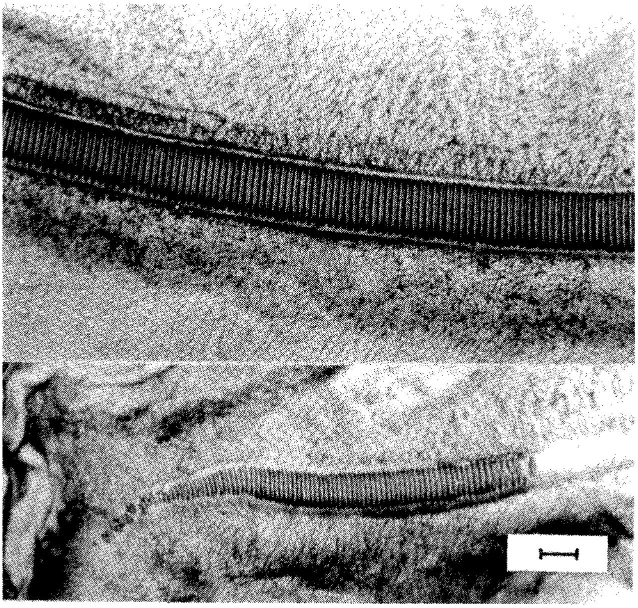

Fig. 9 — Comparison of the right (central part, upper) and left (lower) rows of file teeth in *Homoeogryllus venosus*. Scale is 0.1 mm.

retrogessive evolution can be. What is more important here is the pattern of retrogression clearly different from the previous example. The left file is diminutive, only one-eighth of the right file in length, and yet the teeth are densely arranged in a regular fashion. As a matter of fact, this diminutive left file is situated close to the inner (plectrum) margin of the left tegmen, and almost a mirror image of the corresponding part of the right file. In Fig. 10, the upper picture shows the inner terminal portion of the right file, and the lower picture that of the left file. So far as only these portions are compared, there is little morphological retrogression in the left file. We infer therefore that in this species the left retrogression occurs as elimination of teeth from the central major part of the file. In some individuals, a few deformed teeth grow on the file vein near the outer (costal) end. This pattern of retrogression is quite distinct from that in *Pteronemobius (? Bobilla) nigrovus*. Therefore, retrogression of the left file in various groups of crickets can be a result of convergent evolution.

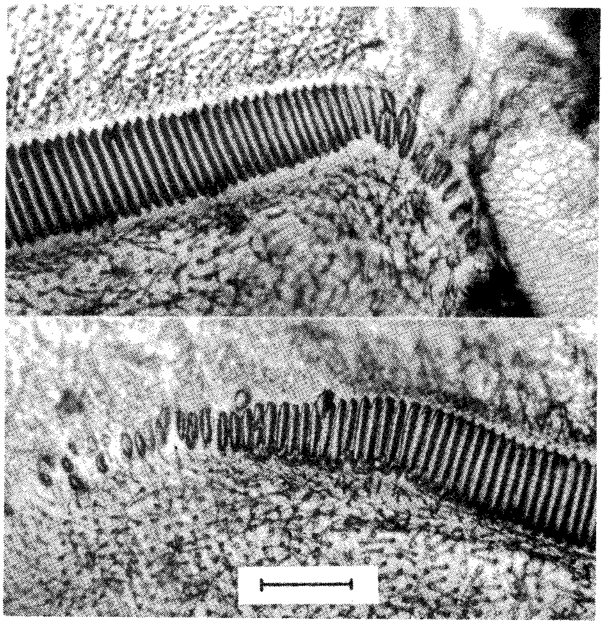

Fig. 10 — Comparison of the inner terminal portions of the right (upper) and left (lower) stridulating files in *Homoeogryllus venosus*. Scale is 0.1 mm.

CONCLUDING REMARKS

The retrogressive evolution of the left stridulating file in crickets is a fascinating phenomenon, posing a problem of basic biological importance. Why is there so big a difference between different species in the extent of left retrogression? To answer this question is to explore the factor determining the speed of evolution — one of the most challenging riddles in biology. Different degrees of retrogression are indeed due to different speeds of evolution, because the left file lost its utility when the cricket ancestor with the right over left tegmina appeared. All the existing species of crickets have had the same evolutionary time since the Jurassic (Sharov 1968, Alexander 1968), and thus have as a rule never been using the left file for more than 150 million years.

ACKNOWLEDGEMENTS

This paper is contribution no. 102 from the Laboratory of Entomology, Hirosaki University. We are gratefully indebted to Ichiro Matsuura, Shozo Jakahashi, and Tetsuo Arai for offering interesting specimens, Takashi Fujita for help in SEM work, Nobuko Sasaki for drawing figures, and Mitsuko Sasaki for typing the manuscript. Our thanks are also due to Professor B. Baccetti who has given impetus to publish this article by inviting S. M. to the symposium at Siena.

REFERENCES

Alexander, R. D. (1968) Life cycle origins, speciation, and related phenomena in crickets. *The Quartery Review of Biology* **43** 1–41.

Chopard, L. (1968) *Orthopterorum Catalogus*. Pars 12, Gryllides: 215–500. Uitgeverij Dr W. Junk N. V., Gravenhage.

Elliott, C. J. H. & Koch, U. T. (1983) Sensory feedback stabilizing reliable stridulation in the field cricket *Gryllus campestris* L. *Animal Behaviour* **31** 887–901.

McIntyre, M. E. (1977) Acoustical communication in the field crickets *Pteronemobius nigrovus* and *P. bigelowi* (Orthoptera: Gryllidae). *New Zealand Journal of Zoology* **4** 63–72.

Neville, A. C. (1976) *Animal asymmetry*. 60 pp. Edward Arnold, London.

Ohmachi, F. & Ashida, H. (1940) On the tooth number in stridulating files of crickets. *Oyo-Dobutsugaku Zasshi* **12** 139–142. (In Japanese)

Otte, D. (1983) African crickets (Gryllidae). 2. *Afrogryllopsis* Randell and *Neogryllopsis* n. gen. of eastern and southern Africa (Gryllinae, Brachytrupini). *Procedings of the Academy of Natural Sciences of Philadelphia* **135** 218–235.

Otte, D. & Alexander, R. D. (1983) *The Australian crickets (Orthoptera: Gryllidae)*. 447pp. The Academy of Natural Sciences of Philadelphia, Philadelphia.

Ragge, D. R. (1969) A revision of the African species of *Pseudorhynchus* Serville (Orthoptera: Tettigoniidae). *Bulletin of the British Museum (Natural History) Entomology* **23** 169–190.

Sharov, A. G. (1968) Phylogeny of the Orthopteroidea. *Transactions of the Institute of Paleontology* **118**. Izdatel'stvo Nauka, Moscow. (English translation, 251 pp. Israel Program for Scientific Translations, Jerusalem.)

Stärk, A. A. (1958) Untersuchungen am Lautorgan einiger Grillen-und Laubheuschrecken-Arten, zugleich ein Beitrag zum Rechts-Links-Problem. *Zoologische Jahrbucher Abteilung für Anatomie und Ontogenie der Tiere* **77** 9–50.

Walker, T. J. & Carlysle, T. C. (1975) Stridulatory file teeth in crickets: taxonomic and acoustic implications (Orthoptera: Gryllidae). *International Journal of Insect Morphology & Embryology* **4** 151–158.