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A CYTOGENETIC LOOK AT THE HAGLIDAE THROUGH STUDY OF THE CHROMOSOMES OF TWO OF ITS FOUR RELICT SPECIES: *CYPHODERRIS MONSTROSA* AND *C. STREPITANS* (ORTHOPTERA: ENSIFERA)

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INTRODUCTION

During the Mesozoic Era there flourished a group of species of saltatorial Orthoptera of the suborder Ensifera that are included in the family Haglidae, of which fossils representing more than 30 genera are known. The Haglidae comprise the subfamilies Haglinae, Isfaropterinae, Cyrtophyllitinae, and Prophalangopsinae. During the upper Jurassic, according to Sharov (1971), species of the last-named subfamily were the most numerous, not only among the Haglidae, but perhaps among all the saltatorial Orthoptera. Today the Haglidae are represented only by *Prophalangopsis obscura* (F. Walker) (Prophalangopsinae), known by a single male specimen collected over 100 years ago in "Hindostan" [India], and by the genus *Cyphoderris* Uhler (Cyrtophyllitinae), with three species (*monstrosa* Uhler, *buckelli* Hebard, and *strepitans* Morris and Gwynne) in the northwestern United States and southwestern Canada. The genus was recently revised by Morris and Gwynne (1978).

The phylogenetic relationships of Haglidae with other taxa of Ensifera, as inferred from morphological and fossil evidence, are still a

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matter of debate. No cytogenetic information bearing on this subject has hitherto been presented. In this paper the chromosomes of *Cyphoderris monstrosa* and *C. strepitans* are described, and their significance in relation to other ensiferan karyotypes is discussed.

MATERIALS AND METHODS

Males of *C. strepitans* and *C. monstrosa* were collected at a number of localities and their testes were fixed in the field in a mixture of 3 parts 100% ethyl alcohol and 1 part acetic acid. Permanent slides were made after softening the tissues in 45% acetic acid, drying, and staining with 1% lactoacetic orcein. The specimens were collected during the summer of 1979 at the following localities:

C. strepitans: WYOMING: Yellowstone National Park; Washburn Mountain, 8,800 ft., 27 July, 4 ♂; 4.1 mi. SW of Tower Junction, 7,200 ft., 27 July, 1 ♂; 1.1 mi. SW of Lake [city], 7,750 ft., 29 July, 3 ♂. Of these specimens, a single one from the last-named locality proved to have a few meiotic divisions.

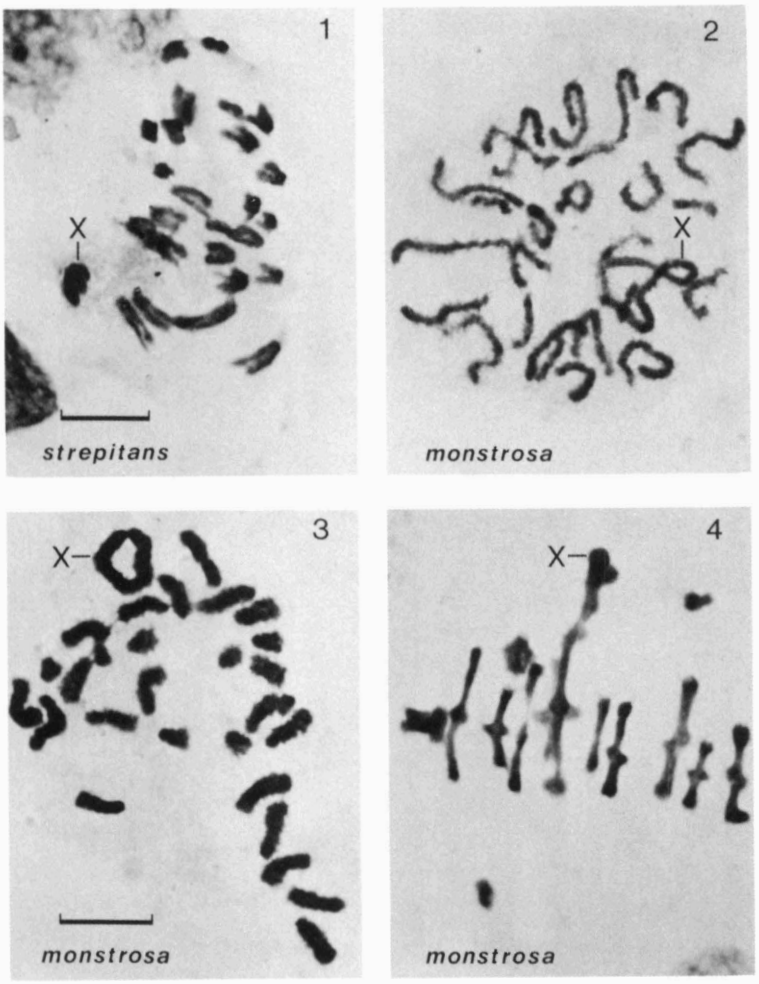
C. monstrosa: IDAHO: Lemhi Co.; Lemhi Pass, 12.4 mi. E of Tendoy, 31 July, 8 ♂; Custer Co.; Stanley Lake, 10 mi. NW of Stanley, 5 Aug., 1 ♂; Adams Co.; Goose Lake, 16.5 mi. N of McCall, 6 Aug., 2 ♂. OREGON: Linn Co.; 25 mi. NW of Sisters, 12 Aug., 3 adults, 2 juv. ♂.

In the figures, the length of each bar indicating enlargement corresponds to 10 μm.

OBSERVATIONS

Cyphoderris monstrosa.—Of the 16 specimens studied, only two proved to have useful cytological material—an adult male from Goose Lake, Idaho, and a last-instar nymph from Linn Co., Oregon. In the adult male several first metaphase plates were analyzed, and in the nymph many gonadial prometaphases and late prophases were also studied. The scarcity of meiotic divisions observed in the adult male probably means that meiosis takes place very soon after the final moult or even in last instar male nymphs during the spring. In middle-aged or old males collected in the summer, meiotic divisions are rare or entirely absent.

In this species, the first metaphases show 2n ♂ = 27, with an XO ♂ sex mechanism. The X is a large metacentric element (see Figs. 2–6) and the autosomes form a group of 13 pairs. In decreasing order of size, the pairs four and twelve are metacentric and the pairs six, nine, ten and thirteen are acrocentric; while the remaining pairs are either submetacentric or subacrocentric, their detailed morphology being impossible to establish accurately. During the first metaphase most of the bivalents show a single chiasma, either interstitial, subterminal, or



FIGS. 1–4. Chromosomes of *Cyphoderris*: 1, *Cyphoderris strepitans*: First anaphase. 2–4, *Cyphoderris monstrosa*: 2, Late spermatogonial prophase; 3, Spermatogonial prometaphase; 4, First metaphase with pair twelve asynaptic. Scale bar = 10 μm.

terminal; a few bivalents present two chiasmata. In the single adult male studied, the pair "twelve" frequently appears asynaptic at first metaphase, as seen in figures 4 and 6.

Cyphoderris strepitans.—From the eight specimens studied, a single first anaphase was the only analyzable nucleus observed in an adult male collected in Yellowstone Park, Wyoming. A photograph of this

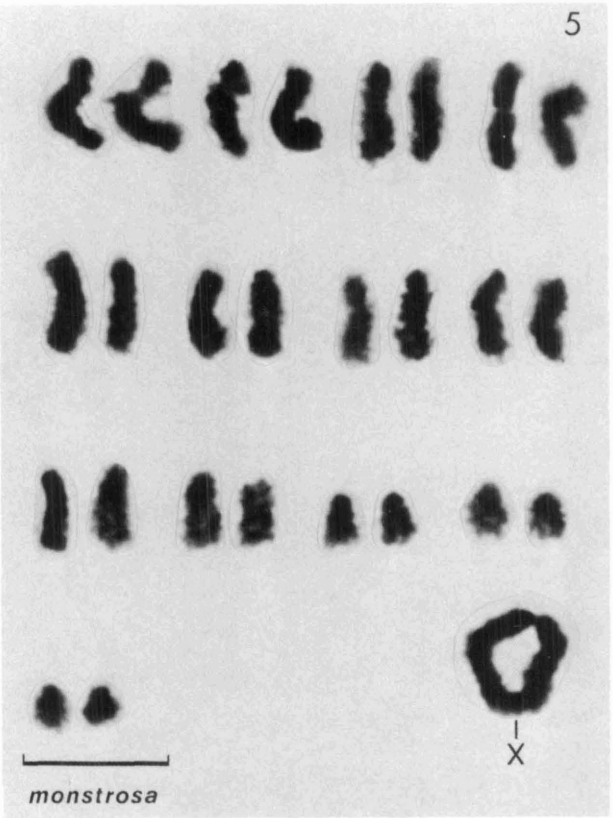
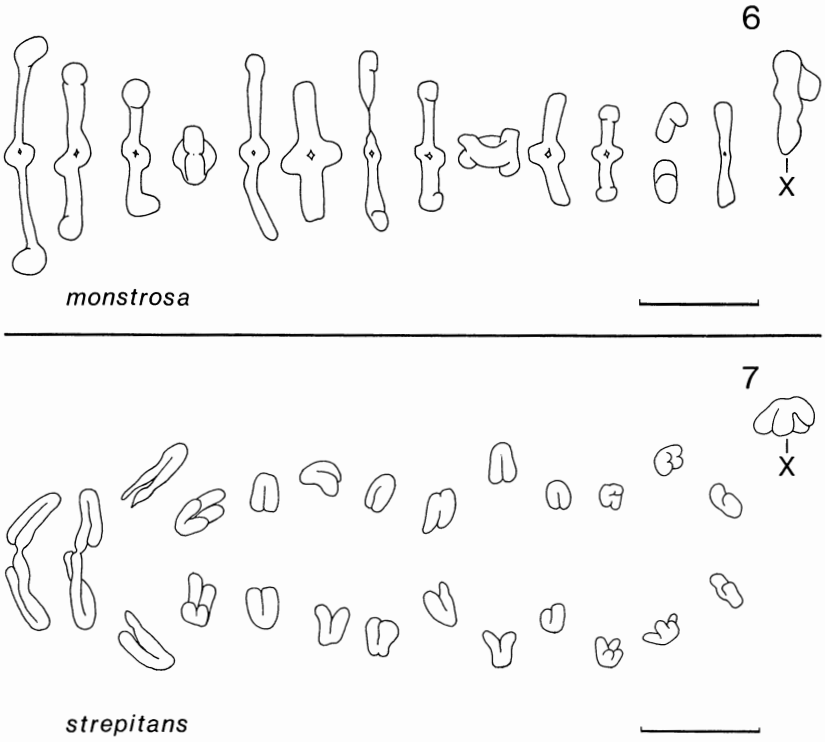


FIG. 5. Chromosomes of *Cyphoderris monstrosa*: The spermatogonial prometaphase shown in fig. 3, with the autosomes arranged in decreasing order of size and the X-chromosome at the lower right. Scale bar = 10 μm.

anaphase is shown in figure 1, and its interpretation, with the pairs ordered in decreasing size, is given in figure 7. As determined from this anaphase, the chromosome number is 2n ♂ = 27, with an XO ♂ sex mechanism and the X metacentric. Among the 13 chromosome pairs observed, numbers four, eleven, and twelve seem to be metacentric. The remaining pairs look to be acrocentric or at most subacrocentric, though it was impossible to be certain of their true morphology.



FIGS. 6–7. 6, Chromosomes of *Cyphoderris monstrosa*: The first metaphase shown in fig. 4 with the autosomal bivalents arranged in decreasing order of size and the X-chromosome at the right; 7, Chromosomes of *Cyphoderris strepitans*: The first anaphase shown in fig. 1 with the autosomal bivalents arranged in decreasing order of size and the X-chromosome at the right. Scale bar = 10 μm.

DISCUSSION

Although the first ideas about phylogenetic relationships within the Ensifera were put forth toward the end of the last century, only during the present one have various authors made serious attempts to explain the origin and evolution of this group of Orthoptera. These attempts have been based primarily on morphological and paleontological arguments; none of them considers cytological evidence. This is understandable, since karyological data for ensiferan taxa were at best fragmentary and generally nonexistent until about the middle of

the century. Over the last decades, however, the available information has slowly increased, and even though it is still scarce for some taxa, we now have an idea of what modal chromosome numbers are at the family level.

It is widely accepted that primitive karyotypes are generally characterized by a high number of acrocentric chromosomes, while more advanced ones have fewer chromosomes and mediocentric elements. This becomes quite clear, at least in relation to chromosome number, if the modal numbers of modern Ensifera (a group already present in the Mesozoic) are compared with those of the more recently arisen Caelifera (the most characteristic of which, Acrididae, first appear in the Tertiary) (Sharov, 1971).

Within the Ensifera, the Gryllacridoidea are thought by some authors to be very old, since they apparently preserve more primitive characters than any other group of living saltatorial Orthoptera. Zeuner (1939) considered the Haglidae (his Prophalangopsidae) more advanced than the gryllacridoids (his Gryllacrididae) because they have tegminal stridulatory organs, unknown in the others. The presence in the Jurassic of haglid fossils as well as that of a presumed gryllacridoid, *Jurassobatea*, led him to conclude that the Gryllacridoidea probably arose in the Triassic. Karny (1929), Ander (1939), and Hubbell (in Hubbell and Norton, 1978) also regard the gryllacridoids as having originated in early Mesozoic or even Permian times; their grounds for this conclusion are morphological and zoogeographic, with present distributions interpreted in terms of continental drift and the break-up of Pangaea.

Sharov (1971) doubts the great antiquity of the gryllacridoids because with his assignment of the Mesozoic *Jurassobatea* to the Haglidae there are left no fossil gryllacridoids prior to Tertiary. He rejects Zeuner's arguments based on the stridulatory apparatus, and believes that the loss of the tegminal sound-producing organ in those gryllacridoids that retain wings was a relatively recent event. This, in Sharov's view, explains why the fore tibial tympanum for sound reception (generally believed to have developed along with tegminal sound producing organs) is present in some species of quite distantly related groups of gryllacridoids including apterous ones. On the other hand, the fact that among the scores of genera and hundreds of species of gryllacridoids not a single instance is known of retention of tegminal stridulatory organs strongly suggests that loss of these organs occurred early in the history of the group. Gryllacridoid fossils are not common even in Cenozoic strata, and failure to find them in older rocks may be the result of rarity caused by low population densities or

by adaptation to life in humid environments where decomposition is rapid and preservation unlikely.

If cytological arguments are considered, the gryllacridoids indeed seem to be the most primitive group of Orthoptera Saltatoria, or at least the most conservative, since they show the highest chromosome number within the order. In Stenopelmatidae, two species of *Stenopelmatus* studied by Stevens (1905, 1909) have 2n ♂ = 47. Among the Rhaphidophoridae, the circum-antarctic Macropathinae (considered to be the most primitive subfamily) has a basic karyotype of 2n ♂ = 45 (Mesa, 1970; Mesa and Mesa, 1971). But the highest chromosome number, not only in the Gryllacridoidea but in the entire order Orthoptera Saltatoria, was found in the Rhaphidophoridae, in *Diestrammena japonica* (Makino, 1931) and *Tachycines asynamorus* (Mohr and Eker, 1934), both of which have 2n ♂ = 57. Other gryllacridoids have secondarily lowered the chromosome number, as in the Henicidae, in which *Lutosa brasiliensis* has 2n ♂ = 15 (Piza, 1947). In the divergent, highly modified family Schizodactylidae, McClung (1924) found that *Schizodactylus monstrosus* has 2n ♂ = 14, a notably low number; and in the Gryllacrididae (s.s.) the numbers are quite divergent, ranging from 2n ♂ = 11 in *Gryllacris signifera* (Heberer, 1937) to 2n ♂ = 31 in *Hadrogryllacris* sp. (White, 1973).

Thus, among the seven recognized families of gryllacridoids, the Rhaphidophoridae and Stenopelmatidae include species with what are interpreted as the most archaic karyotypes, while the Gryllacrididae, Schizodactylidae, and Henicidae have evolved toward lower chromosome numbers. Nothing is known of the chromosomes of Lezinidae and Deinacrididae.

The Tettigonioidea are undoubtedly very old, since their fossils are known from the early Triassic. Using arguments based on wing venation, Zeuner (1939) considered the Pseudophyllidae and Mecopodidae the most primitive of living tettigoniids. Sharov (1971) does not agree; he regards the Decticidae, Sagidae, and Tettigoniidae as the most primitive, resting his conclusion partly on the carnivorous habits of those three families, which resemble those inferred for the extinct Oedischiidae from which they apparently descended.

Considering now the karyotypes, the highest chromosome numbers are lower in the tettigonioids than among the stenopelmatid-rhaphidophorid gryllacridoids. The commonest chromosome numbers in the tettigonioids are 2n ♂ = 33, 31, and 29, and the highest diploid number was reported by Mesa and Ferreira (1977) in the South American *Platydecticus angustifrons* (Decticidae), with 2n ♂ = 37. Other Decticidae possess 2n ♂ = 33, 32, 31, 29, 27, 25,

23, and 22, with the modal number 29 (Hewitt, 1979). The Pseudophyllidae also present relatively high chromosome numbers; four of its species have 2n ♂ = 35, and one, *Meroncidius intermedius*, has 31, owing to two centric fusions (Piza, 1950).

The Grylloidea (used as including the modern Gryllidae, Gryllotalpidae, and Myrmecophilidae) comprise an estimated 2800 known species, including several hundred described in the Gryllidae since the appearance of Chopard's catalogue (1967, 1968). In the Gryllidae, chromosome numbers are relatively low, with the highest number in Gryllini; most of the species assigned to *Gryllus* and *Acheta* that have been studied have 2n ♂ = 29. Many gryllids have fewer than 20 chromosomes, and the lowest numbers recorded in the family are 2n ♂ = 9 in *Eneoptera surinamensis* (Piza, 1946; Claus, 1956; Mesa and Bran, 1964), and 2n ♂ = 8 in the North American species of *Nemobius,* subgenera *Allonemobius* and *Neonemobius* (Davenport, 1960).

Fossils of cricket-like insects are found from the beginning of the Triassic. According to Sharov (1971) species of Gryllidae from the Lower Triassic deposits of Maydygen (Isfaha, Kirghizia) show clear evidence of relationship with the subfamily Cyrtophyllitinae of the family Haglidae. Since fossil cyrtophyllitines also occurring in the Lower Triassic are evidently related to the Oedischiidae, it seems probable that both Cyrtophyllitinae and Gryllidae had a common ancestor within the Oedischiidae, and that in that ancestor the chromosome number had already been lowered to 29. According to this hypothesis the presence of a karyotype with a relatively low chromosome number in the Cyrtophyllitinae (in *Cyphoderris* 27), comparable to that found in the Gryllini, is at least compatible with Sharov's conclusion that these groups had a common ancestor, although not proof of close relationship between them.

The Prophalangopsinae, Sharov believes, were derived from Cyrtophyllitinae. If this is correct, and if in the future the species *Prophalangopsis obscura* is rediscovered, we should expect it to have the same chromosome number as its more primitive relative, *Cyphoderris*, 2n ♂ = 27 or most probably lower.

Inclusion of the gryllacridoids, Haglidae, and Gryllidae in a single group, as Sharov (1971) has done with his superfamily Gryllidea (essentially the same as Karny's earlier Grylloidea), has no cytological support. Since the gryllacridoids include species with the highest (and hence by hypothesis the most primitive) chromosome numbers found in the Orthoptera, and if they are a monophyletic group, they should have branched off from the ancestral Oedischiidae independently from and earlier than the tettigonioids. If they did not originate ear-

lier, and again assuming monophyly, they must have come from a group of Oedischiidae that retained a relatively high number of chromosomes, and in some families such as the Stenopelmatidae and Rhaphidophoridae the primitive karyotypes were retained with few modifications. But if, as seems probable, the "gryllacridoids" are not a monophyletic assemblage, their various stocks are most likely to have branched off from the Oedischiidae at different times, with the Rhaphidophoridae and Stenopelmatidae arising earlier than the others and from more primitive oedischiids.

Obviously the karyology of the extinct Oedischiidae can only be inferred from that of their presumed modern descendants. The species of that family were probably cytologically heterogeneous, but it is likely that in general they had relatively high chromosome numbers and a preponderance of acrocentric elements.

The opinions and arguments here advanced are admittedly in large part speculative, and the discovery of new fossils, comparative morphological studies, or the results of further cytological investigations could substantially modify these views.

SUMMARY

The karyotypes of two of the three described species of the haglid genus *Cyphoderris* (*monstrosa* and *strepitans*) are reported here. Both have the chromosome number 2n ♂ = 27, with an XO ♂ –XX ♀ sex determination mechanism. The sex chromosomes are metacentric and the largest elements of each set. The majority of the bivalents have a single unlocalized chiasma.

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