Koleopterologische Rundschau	62	127 - 135	Wien, Juli 1992

Chromosomal analysis of some European species of the genera *Georissus* LATREILLE, *Spercheus* ILLIGER and *Hydrochus* LEACH

(Coleoptera: Hydrophiloidea)

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Abstract

Karyotypes are illustrated for *Georissus crenulatus* (ROSSI), *Spercheus emarginatus* (SCHALLER) and seven species of *Hydrochus*: *H. angustatus* GERMAR, *flavipennis* KÜSTER, *carinatus* GERMAR, *elongatus* (SCHALLER), *ignicollis* MOTSCHULSKY, *brevis* (HERBST) and *megaphallus* van BERGE HENEGOUWEN. In all cases the sex chromosomes are XY (male), XX (female), and in all except *H. elongatus* the Y-chromosome is dot-like, and forms a parachute association with the X at meiosis. The *H. elongatus* Y-chromosome is larger, but still apears to form a parachute association with the X. The numbers of autosome pairs are: 9 (*Georissus*), 7 (*Spercheus*) and 10 (*Hydrochus*). Chromosomal differences between the various *Hydrochus* species are noted, and a discussion is given of the karyotypes of the more primitive Hydrophiloidea, using the data presented here and published work by the junior author on *Helophorus* FABRICIUS.

Key words: Chromosomes, Hydrophiloidea, *Georissus*, *Spercheus*, *Hydrochus*.

Within the superfamily Hydrophiloidea, as reviewed by HANSEN (1991) five groups, now ranked as families, stand apart from the main family, Hydrophilidae. These are the Georissidae, Spercheidae, Hydrochidae, Helophoridae and Epimetopidae. According to the cladistic analysis of HANSEN (1991) the Spercheidae stand as sister group to the Hydrophilidae, while the remaining four families constitute a Helophorid lineage.

The largest of these families is the Helophoridae, with about 180 species of *Helophorus*, is reasonably well-known chromosomally (ANGUS 1989), but the others are as yet unknown chromosomally. The present work seeks to remedy this as far as is possible - no Epimetopidae are covered as these are a tropical group of which no material has been available for study.

Material & Methods: The species studied, their localities of origin, and the tissues used for chromosome preparation, are given in the Table below. The methods used for preparing chromosomes are given by ANGUS (1982), with information specific to the use of mid-gut given by SHAARAWI & ANGUS (1991). For mid-gut preparations from *Spercheus* and *Hydrochus*, the beetles were injected with colchicine solution, but for *Georissus* preparations the beetles were placed in a watch glass containing colchicine solution, and the abdomens were partially detached.

SPECIES	LOCALITY OF ORIGIN	TISSUES USED
Georissidae:		
G. crenulatus	Denmark: West Jutland, near Esbjerg	Mid-gut, testis

Spercheidae:		
S. emarginatus	Russia: West Siberia, Karasuk	Embryo
	Holland	Mid-gut, testis
Hydrochidae:		
H. angustatus	England: Surrey, Cobham Common	Mid-gut, testis
H. flavipennis	Greece: Corfu	Embryo
H. carinatus	England: Norfolk, East Walton	Embryo
H. elongatus	England: Surrey, Egham	Embryo, mid-gut, testis
H. ignicollis	England: Norfolk, Catfield Fen	Embryo
	Norfolk, Thompson Common	Mid-gut, testis
H. brevis	England: Norfolk, East Walton	Embryo
	Norfolk, Catfield Fen	Embryo, ovary
	Germany: Niedersachsen, 75 km SW of Hamburg	Embryo
H. megaphallus	England: Norfolk, Catfield Fen	Embryo

Georissus crenulatus (Georissidae)

Mitotic chromosomes are shown in Fig. 1a, b. There are nine pairs of autosomes showing an even decrease in relative length, and with the smallest pair acrocentric, similar in appearance to the X-chromosome, but a bit larger. In one male studied chromosome pair 8 shows an inversion polymorphism, with one replicate metacentric, the other acrocentric. In one other male, and in one female, both replicates appeared acrocentric. The Y-chromosome is a very small dot, and at first metaphase of meiosis the XY bivalent appears as the smallest element (Fig. 1c). The Y-chromosome is sometimes visible as a "satellite" of the X (Fig. 1d) - the parachute association.

Spercheus emarginatus (Spercheidae)

Mitotic chromosomes are shown in Fig. 2a. There are seven pairs of autosomes, with the first pair far larger than any of the others, and accounting for nearly half the genome. The X-chromosome is a small acrocentric, and the Y is dot-like. Meiosis (Fig. 2b) shows the XY bivalent as a parachute association and the long autosomes as a ring bivalent, at first metaphase. There is no difference between the chromosomes of Dutch and Siberian specimens.

Hydrochus spp. (Hydrochidae)

Mitotic chromosomes of the seven species studied are shown in Fig. 3. In all cases there are 10 pairs of autosomes, and the sex chromosomes are XY (male), XX (female). The Y-chromosome of *H. elongatus* (Fig. 3d) is quite large, but in all other cases it is small, dot-like or almost so.

The chromosomes of *H. angustatus* (Fig. 3a), *flavipennis* (Fig. 3b) and *carinatus* (Fig. 3c) are very similar, with the autosomes small or medium sized, metacentric or nearly so, and the X-chromosome metacentric, similar in size to the smaller autosomes. In *H. flavipennis* chromosome 7 appears less evenly metacentric than in *angustatus*, while in *H. carinatus* chromosomes 8 and 9 are more evenly metacentric than in either *angustatus* or *flavipennis*.

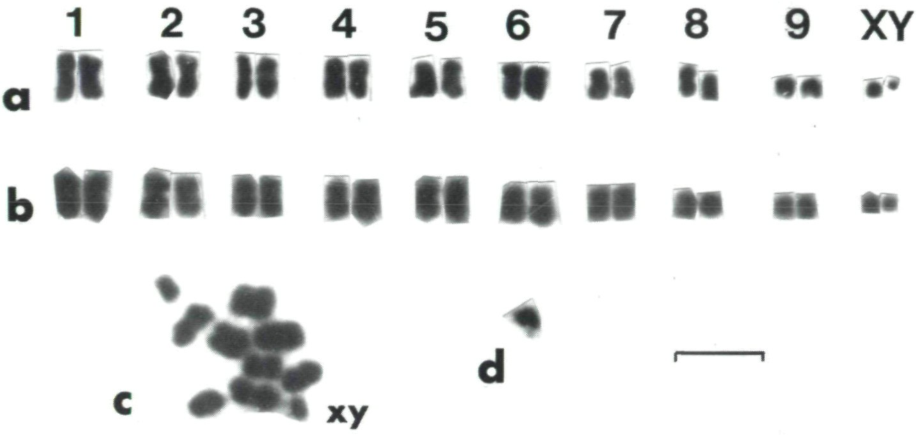


Fig. 1: Chromosomes of *Georissus crenulatus*. a, mitosis, male, mid-gut cell; b, mitosis, female, mid-gut cell; c, meisosis, first metaphase, testis; d, XY bivalent at first metaphase of meiosis, showing the Y-chromosome just below the X. The scale line represents 5 μm.

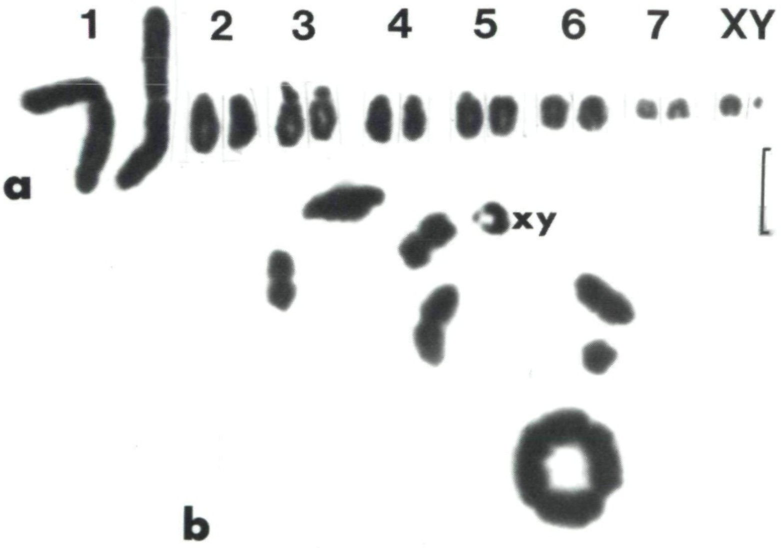


Fig. 2: Chromosomes of *Spercheus emarginatus*, a Dutch male. a, mitosis, mid-gut cell; b, meiosis, first metaphase, testis. The scale line represents 5 μm.

In *H. elongatus* and *ignicollis* (Fig. 3d-h) the X-chromosome is relatively larger, clearly longer than the three smallest pairs of autosomes (nos. 8-10). C-banding (Fig. 3e, f, h) shows dark centromeric C-bands on all chromosomes, and further dark bands, possibly nucleolus organisers, on the long arms of chromosome 1 and the X-chromosome. Chromosomes 1 and 2 are more evenly metacentric in *H. ignicollis* than in *elongatus*. The Y-chromosome of *H. ignicollis* (Fig. 3g, h) is dot-like, though larger than in many Hydrophiloids, but that of *H. elongatus* is much larger (Fig. 3d), and apparently composed of two elements. C-banding (Fig. 3e) shows what appears to be a heavy centromeric band, at first sight difficult to equate with the appearance of the unbanded chromosome (Fig. 3d).The most likely interpretation seems to be that part of the C-band corresponds with a centromere at the proximal end of the larger part of the chromosome, and part corresponds with the constriction separating the two parts.

The karyotype of *H. brevis* (Fig. 3i, j) is very distinctive, with seven pairs of autosomes, and the X-chromosome, acrocentric. The Y-chromosome is small and dot-like. There are no differences between the karyotypes of the populations studied.

H. megaphallus (Fig. 3k) resembles *H. brevis* in the acrocentric X-chromosome, but differs in having only four pairs of autosomes more or less acrocentric - and none has the short arms as short as in the more extreme acrocentrics of H. *brevis*.

In view of the large size of the *H. elongatus* Y-chromosome, and the fact that in some other species (*H. ignicollis* and *carinatus*) the Y-chromosome, though dot-like, is larger than in many hydrophiloids, care has been taken to ascertain whether the XY bivalent at first division of meiosis has a parachute (nucleolar) association. First meiotic metaphases are shown in Fig. 4a-d.

In *H. angustatus* (Fig. 4a) and *carinatus* (Fig. 4b) the Y-chromosome lies slightly away from the X in normal parachute arrangement. However, in *H. elongatus* (Fig. 4c) and *ignicollis* (Fig. 4d) there is no gap between the sex chromosomes. However, the gap is not always clear even in species where it occurs (*Georissus crenulatus*, Fig. 1c, d). Details of the association of the sex chromosomes can sometimes be seen more clearly in zygotene and early pachytene of prophase (JOHN & LEWIS 1960), and a selection of zygotene nuclei with the sex bivalents is shown in Fig. 4e-o. Figure 4e shows *H. elongatus* with the X-chromosome linear and with one end, adjacent to the Y, more condensed. In Fig. 4f the X-chromosome is looped round, with both ends applied to the Y. These arrangements seem comparable with JOHN & LEWIS's figures for *Tenebrio molitor*, for which they demonstrate a parachute association at metaphase. These arrangements are also mirrored by *H. ignicollis* (Fig. 4h, i, j), and, without the looping, *H. carinatus* (Fig. 4k) and *angustatus* (Fig. 4o). Fig. 4n shows the sex bivalent of *H. angustatus* with the X-chromosome looped round more or less as in *H. elongatus* (Fig. 4f) and *ignicollis* (Fig. 4i, j). It therefore seems that the association of the sex chromosomes is the same in all these species, and is a parachute association via a nucleolus.

One further point of interest is provided by a triploid female embryo found among the material of *H. elongatus* (Fig. 5). There is no record of triploid *H. elongatus*, nor are there any known cases of populations with a preponderance of females, which would suggest parthenogenesis. There is also no evidence that this embryo could have completed its development. A similar state of affairs was once encountered by the junior author who found a triploid female embryo among a sample of French *Helophorus aequalis* THOMSON. It is possible that such occasional triploids may give rise to parthenogenetic races among hydrophiloids. Thus ANGUS (1992) has found triploid female *Helophorus brevipalpis* BEDEL in Spain, in populations which consist mainly of triploid females, but have small numbers of diploid individuals of both sexes. The parthenogenesis of *Anacaena lutescens* STEPHENS is different, however, as here the basic arrangement is of diploid parthenogenetic females, with some populations subsequently acquiring triploids (SHAARAWI & ANGUS 1991).

Discussion

The three genera dealt with in this paper show distinctive and completely dissimilar karyotypes. If, as is suggested by SMITH (1950) and PETITPIERRE (1987) the basic karyotype of Polyphagan beetles is 9 pairs of autosomes plus XYp sex chromosomes, then at a first glance the Georissidae, at least in the species studied, appear to retain this primitive arrangement. The Georissidae are of worldwide distribution, with 72 species, all in the genus *Georissus* (HANSEN 1991), and it is possible that other species have different numbers of chromosomes as, for instance, happens in *Helophorus* (ANGUS 1989). HANSEN's cladogram (HANSEN 1991) shows the Georissidae to be a part of the Helophorid lineage, and to have branched off from the stem of that lineage after both the Helophoridae and the Epimetopidae, and to be the sister group of the Hydrochidae. Angus (1989) showed that most of the *Helophorus* studied have 10 pairs of autosomes plus XYp sex chromosomes, with some species showing a reduction to 8 pairs plus XYp. No species is known with 9 pairs of autosomes. The Hydrochidae, also a family of worldwide distribution, have 87 described species, all in the genus *Hydrochus* (HANSEN 1991), so that the present data, which show 10 pairs of autosomes plus XYp sex chromosomes in all cases, cannot be taken as implying that this is the case for all *Hydrochus*. Nevertheless, the fact that this karyotype has been found in a majority of *Helophorus* as well as all *Hydrochus* studied does suggest that this may be the primitive arrangement for the Helophorid lineage. If this is the case then *Georissus crenulatus* has lost one pair of autosomes and its chromosome number is secondarily acquired, not primitive.

The single species of *Spercheus* studied has a very distinctive and unusual karyotype, with the longest pair of autosomes about four times the length of the next longest pair, and accounting nearly half the genome. The Spercheidae comprise 16 species of Spercheus, distributed worldwide with the exception of the Nearctic region. Information on additional species would be very interesting, to see whether this unusual karyotype is typical of the family. HANSEN's preferred cladogram (HANSEN 1991) places Spercheidae as the sister group of the Hydrophilidae, but other versions place them as the sister group of the Helophorid lineage. The karyotypes of a handful of species cannot be used as evidence in such a major question, but it is perhaps worth noting that the smallest autosome pair, and the X-chromosome, have similar appearances in *Spercheus emarginatus* and *Georissus crenulatus*.

Acknowledgements

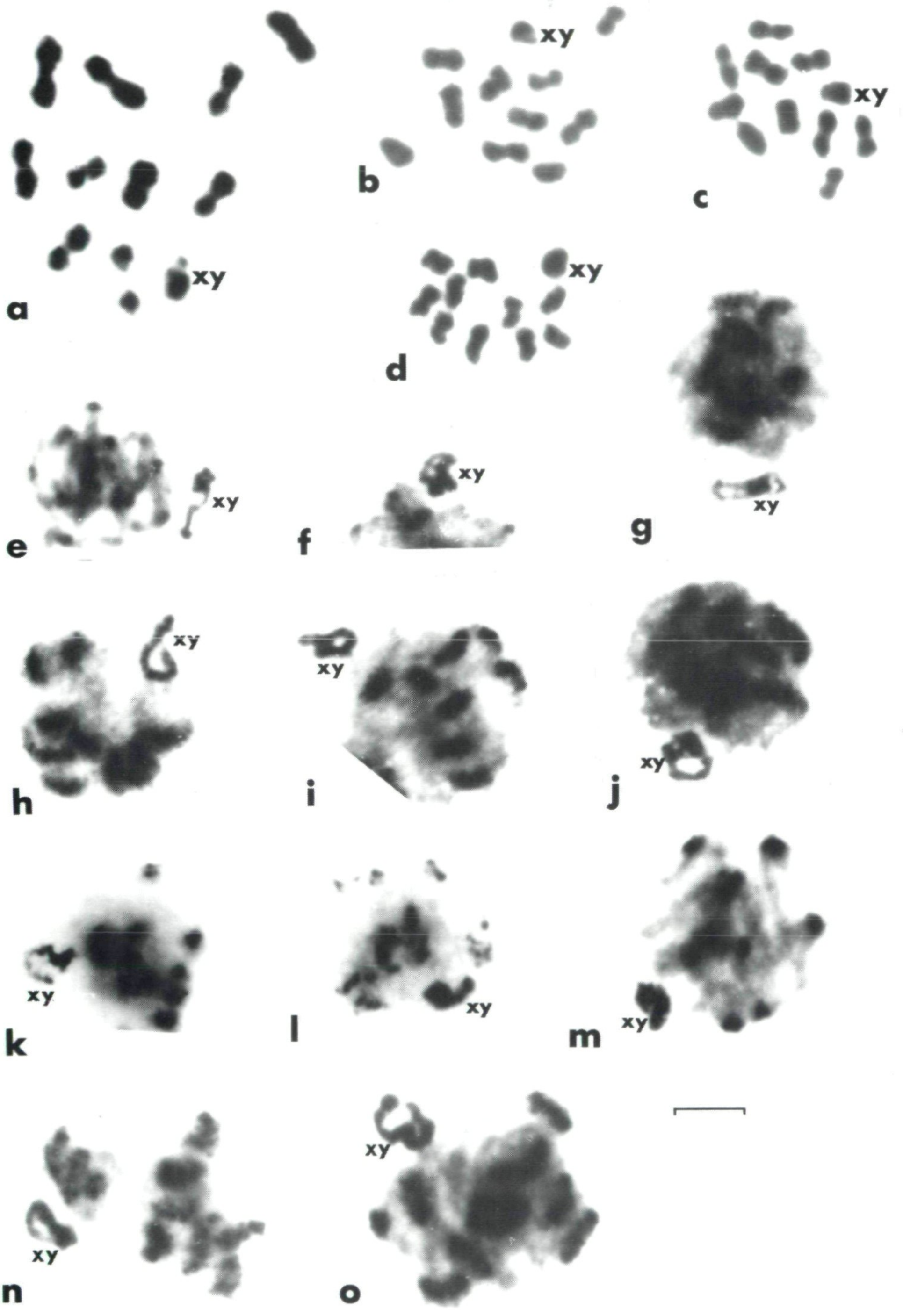
This paper is based on work done by F.A.I. Shaarawi for a Ph.D. thesis, supervised by R.B. Angus, in the Department of Biology (formerly Department of Zoology), Royal Holloway & Bedford New College, University of London. We thank Prof. C.T. Lewis and R.P. Dales for the facilities to carry out this work, and the Egyptian government for financial support. The main additional work, by the junior author, is the addition of *Georissus crenulatus* to the study. We thank the Linnaean Society of London for a grant to Dr. Angus for a visit to Denmark in May 1991, during which the material was collected. The junior author further thanks the Royal Society and the Soviet Academy of Sciences for the opportunity to work at Karasuk, west Siberia, in 1982, Dr. A. van Berge Henegouwen for sending live Dutch *Spercheus*, Captain H. Birkbeck for permission to collect on his land at East Walton, Mr. D.S. McDougall for permission to collect on his land at Catfield Fen, and the National Trust for permission to collect on its Runnymede reserve near Egham.

Zusammenfassung

Die Karyotypen von *Georissus crenulatus* (ROSSI), *Spercheus emarginatus* (SCHALLER) und sieben *Hydrochus*-Arten (*H. angustatus* GERMAR, *flavipennis* KÜSTER, *carinatus* GERMAR, *elongatus* (SCHALLER), *ignicollis* MOTSCHULSKY, *brevis* (HERBST) und *megaphallus* van BERGE HENEGOUWEN) werden abgebildet. In allen Fällen sind die Geschlechtschromosomen XY (Männchen) und XX (Weibchen), und bei allen (außer *H. elongatus*, bei dem es größer ist) ist das Y-Chromosom punktförmig klein und verbindet sich während der Meiosis mit dem X-Chromosom. Die Anzahl der Autosomen-Paare beträgt 9 (*Georissus*), 7 (*Spercheus*) oder 10 (*Hydrochus*). Die chromosomalen Unterschiede zwischen den verschiedenen *Hydrochus*-Arten werden dargelegt. Auf Grundlage der hier präsentierten Befunde sowie der bereits erschienenen Arbeiten des zweiten Autors über *Helophorus* FABRICIUS werden die Karyotypen der primitiveren Hydrophiloidea verglichen.

Fig. 3: Mitotic chromosomes of *Hydrochus* spp. The scale line represents 5 μm. a, *H. angustatus*, male, mid-gut, Chobham, Surrey; b, *H. flavipennis*, male embryo, Corfu; c, *H. carinatus*, male, embryo, East Walton, Norfolk; d, *H. elongatus*, male, mid-gut, Egham, Surrey; e, *H. elongatus*, male, embryo, C-banded, Egham, Surrey; f, *H. elongatus*, female, embryo, C-banded, Egham, Surrey; g, *H. ignicollis*, male, embryo, Catfield Fen, Norfolk; h, *H. ignicollis*, male, embryo, C-banded, Thompson Common, Norfolk; i, *H. brevis*, male, embryo, East Walton, Norfolk; j, *H. brevis*, male, embryo, Niedersachsen, Germany; k, *H. megaphallus*, male, embryo, Catfield Fen, Norfolk.

Fig. 4 (page 133): Meiotic chromosomes of male *Hydrochus* spp., from testis. a - d, first metaphase; e - o, zygotene of first prophase, showing the XY bivalent. The scale line represents 5 μm. a, *H. angustatus*, Chobham, Surrey; b, *H. carinatus*, East Walton, Norfolk; c, *H. elongatus*, Egham, Surrey; d, *H. ignicollis*, Thompson Common, Norfolk; e,f, *H. elongatus*, Egham, Surrey; g - j, *H. ignicollis*, Thompson Common, Norfolk; k - m, *H. carinatus*, East Walton, Norfolk; n, o, *H. angustatus*, Chobham, Surrey. The scale line represents 5 μm.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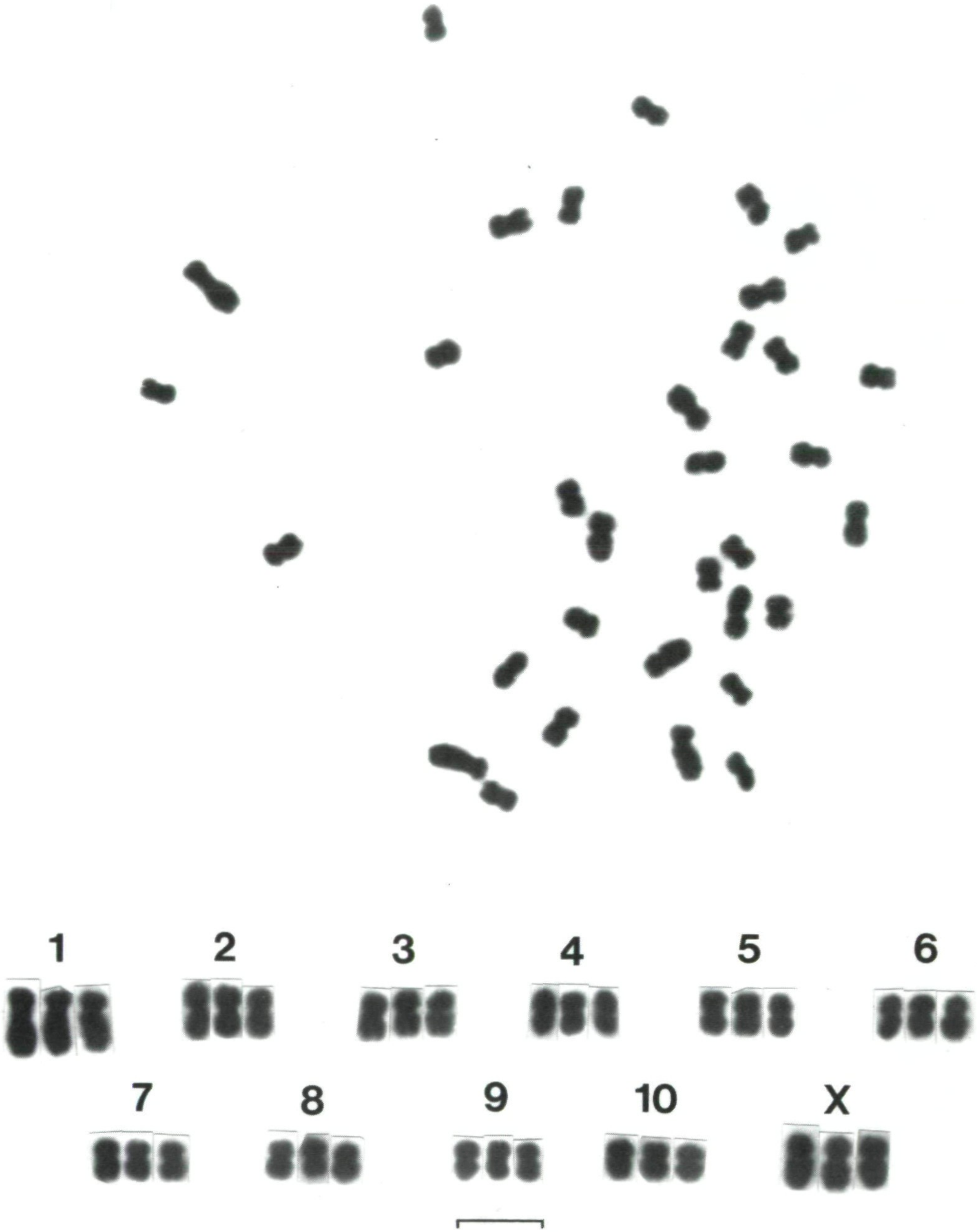

Fig. 5: Triploid female embryo of *H. elongatus* from Egham, Surrey. The scale line represents 5 μm.

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Zeitschrift/Journal: Koleopterologische Rundschau

Jahr/Year: 1992

Band/Volume: 62_1992

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Artikel/Article: Chromosomal analysis of the genera Georissus LATREILLE, Spercheus ILLIGER and Hydrochus LEACH (Hydrophiloidea). 127-135