The chromosome conditions in the spermatogenesis of the caddis-fly *Goera pilosa* (FABRICIUS, 1775) (*Trichoptera, Integripalpia, Limnephiloidea: Goeridae*) from the God dal Fuorn in the Swiss National Park, with considerations on the phylogenetic position of the family

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Résumé

L'auteur a étudié les aspects cytologiques de la spermatogenèse chez le Trichoptère *Goera pilosa* (FABR.), trouvé pour la première fois dans le Parc National Suisse. Contrairement à la situation en d'autres régions de la Suisse (RIS, 1889) l'espèce parait ne produire qu'une seule génération par année dans le Parc.

Chez les mâles, les jeunes nymphes sont le seul stade ou l'on trouve une activité mitotique. *Goera pilosa* est la seule espèce de l'ordre entier à posséder un nombre haploïde de n = 22. Morphologiquement, le caryotype du matériel suisse se distingue nettement de celui décrit par PCHAKADZE (1930) chez une population russe. C'est la premiere fois qu'une variabilité chromosomique au niveau de populations géographiques est signalée.

A la lumière des tendences évolutionnaires caryotypiques des Trichoptères, le caractère «primaire» (*sensu* KIAUTA, 19678, 1968) du complément chromosomique de *Goera pilosa* fait supposer que la famille des *Goeridae* est phylogénétiquement plus primitive que ne l'avait considérée ROSS (1967).

L'auteur a démontré que le nombre n = 30 ne peut être considéré comme nombre typique de l'ordre, parce que ce nombre ne caractérise qu'une seule famille spécialisée. Par conséquent, et contrairement aux opinions courantes (SUOMALAINEN, 1969), la ressemblance entre Trichoptères et Lépidoptères, en ce qui concerne la variation du nombre haploïde, est purement accidentelle et n'a aucune signification phylogénétique.

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Introduction

Goera pilosa (Fabr.) is the only European representative of a large genus, which includes 45 living species: 24 of these have a south Asiatic or southeastern Asiatic distribution, 17 are palearctic and four nearctic. None is holarctic. The genus is completely lacking in Africa, Papua, Australia and South America (cf. Fischer, 1967). A single fossil form has been recovered from the Baltic Amber (Ulmer, 1912).

Our species is common throughout Europe, whereas a single record from Japan (Iwata, 1927), quoted repeatedly in the literature, needs confirmation. Larvae usually inhabit various types of running water biotopes *(Rhithron, Potamon)*, though they are found in stagnant water as well (lakes) (Botosaneanu, 1967).

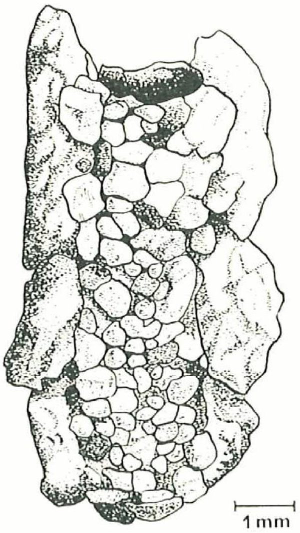
The species has been recorded for the first time from Switzerland by Pictet (1834) and was found since in various Kantons throughout the country. Records from Rhätikon were published by Zschokke (1893a, 1893b). It has hitherto not been listed from the territory of the National Park (cf. Nadig, 1942). At the time of our visit at the God dal Fuorn, however, it was very common there.

Goera pilosa probably has two generations yearly in the surroundings of Oerlikon (Ris, 1889), whereas our observations in June and September, 1969 suggest that it might be univoltine in the National Park.

A brief note on the primary spermatocyte karyotype of a population from the surroundings of Leningrad has been published by Pchakadze (1930). Our observations on the Engadine material deviate from his. So far nothing is known on the chromosome behaviour, nor have any microphotographs been published.

Material

Our material originates from a small spring in the little, marshy valley East of the limnokrenic source described by Nadig (1942) as 'God dal Fuornquelle Nr. 1'. The altitude is 1830 m approximately. Water temperature varied in September between 3.0 and 8.3° C at 8 a.m. and 4 p.m. respectively (measured on September 2nd, 10th and 11th, 1969).



Textfigure 1.
Pupal case of *Goera pilosa* (Fabr.) from the God dal Fuorn in the Swiss National Park (September 8th, 1969). Plesiotype.

During the **first** two weeks of September, 1969 there were present **simultaneously** late instar larvae, pupae of different ages and imagines. Preparations were made of all of **these** stages, but the young pupa appeared the only **mitotically** active stage of the male (textfig. 1). In this feature ***Goera pilosa*** resembles the **limnephilidan** ***Glyphotaelius*** pellucidus (RETZ.) (KIAUTA and LANKHORST, 1969).

In all, 41 preparations were made. These yielded 518 microphotographs.

The specimens and preparations will be deposited in the Bündner Naturhistorisches und Nationalparkmuseum (The Graubunden Museum of Natural History and of the National Park) at Chur (Switzerland).

Methods

The **insects** were dissected a few hours after capture. For fixing and staining the lacto-acetic-orcein squash method was used (cf. KIAUTA, **1967a).** The sealed, semipermanent **preparations** were photographed a few days to two weeks after **fixation.**

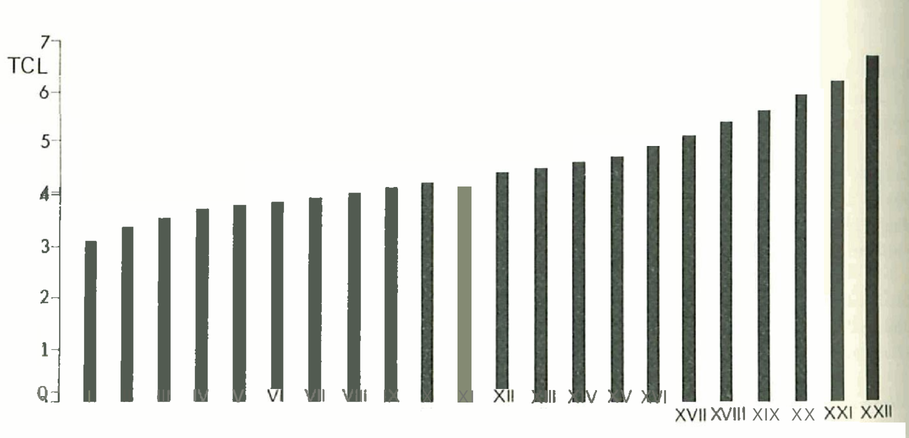
The photographs were taken with a Zeiss photomicroscope (projective 3.2, optovar 1.25, 100× oil immersion, green filter) on Agfa Gevaert copex panchromatic film (magnification on negative 400×). Figures 5, 7 and 9 are made without and the others with phase **contrast optics.** The positives were printed originally at 2250× and are reduced in this report to 1500×.

The measurements for **the** statistical treatment were carried out on **2250×** photographs with the accuracy of **0.5** mm (**1** mm = 0.44 μ). They **values** were rounded to one decimal, square values to **two.**

Morphology of the Primary Spermatocyte Karyotype

The haploid chromosome number, n = 22, is the same as reported earlier by PCHAKADZE (1930) for the population of the surroundings of Leningrad. So far it is unique in the order.

General morphological features of the karyotype are given in **textfig.** 2. The idiogram was calculated from polar views of primary **spermatocyte** metaphase of 34 cells. The bivalents are gradually increasing in magnitude, there are neither extra large nor extra small elements and no size classes can be distinguished in the Swiss material.



Textfigure 2.
Idiogram of the primary spermatocyte karyotype of *Goera pilosa* (FABR.) from the God dal Fuorn, calculated from 34 figures.

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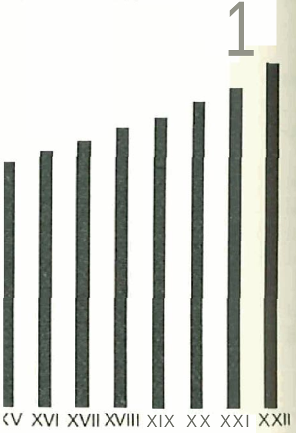

FABR.) from the God dal Fuorn,

The total length of the complement (TCL) measured in the same figures amounts to 60.0±20.4 μ. In table I the mean percentage values are given for the 22 elements. The confidence intervals account for 95 per cent of cases.

Table I

Length (in % of TCL) of the metaphase elements in the polar view of the primary spermatocytes

Bivalent No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Mean	3.1	3.4	3.5	3.7	3.8	3.9	4.0	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.9	5.1	5.4	5.6	5.9	6.2	6.7
Confidence limits	0.6	0.5	0.5	0.4	0.4	0.4	0.4	0.4	0.3	0.4	0.4	0.4	0.4	0.4	0.4	0.5	0.5	0.7	0.7	0.7	0.7	1.2

If the above observations are compared with the hitherto published trichopteran karyotypes, two important conclusions can be drawn:

(1) The TCL of *Goera pilosa* is essentially inferior to that of the limnephilidan species, regardless of their chromosome numbers, whereas it is superior to the complements of the primitive families *(Annulipalpia, Hydroptilidae)*, consequently:

(2) The karyotype of *Goera pilosa* represents a true primary complement; the relatively low chromosome number thus does not originate in secondary fusions of the elements of an 'ancestral' high-n. set. It might be assumed, therefore, that the numeric situation is solely reflecting the degree of advancement and specialisation reached by this form. (For theoretical considerations cf. KIAUTA, 1967b, 1968).

The karyotypic morphology of the Swiss population studied, differs essentially from that described by PCHAKADZE (1930: 231, 315, pl. 3, f. 15–16) for the material from the surroundings of Leningrad. In polar views of the primary and secondary spermatocyte metaphase of the Russian population, 4 big, 16 medium and 2 smaller elements can clearly be recognized, whereas no size classes appear in our material. Though several trichopteran species have been so far studied from geographically widely distant localities, this is the first record of a well pronounced cytotaxonomic variation on the geographic population level hitherto reported for a caddis-fly.

Behaviour of the Spermatocyte Chromosomes

The cysts contain cells of approximately the same divisional stage.

At prophase stages the chromosomes are uniformly despiralised and no element appears heteropycnotic. At diakinesis most elements have a single chiasma per bivalent.

Table I shows that the variation of the degree of contraction of most of the bivalents is fairly uniform at primary metaphase (Pl. I, figs. 1–3), but it increases from the 18th bivalent onwards and is greatest in the longest element. In lateral views of this stage the bivalents are lined up in the equatorial plane. At anaphase I they divide equationally and nearly simultaneously, though one of the biggest bivalents enters anaphase earlier than the others (Pl. I, fig. 4). In all figures of late anaphase I and telophase I one element is lagging (Pl. I, figs. 5–6). It is not likely that it represents the sex element.


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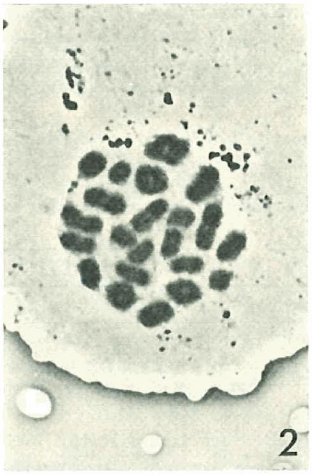
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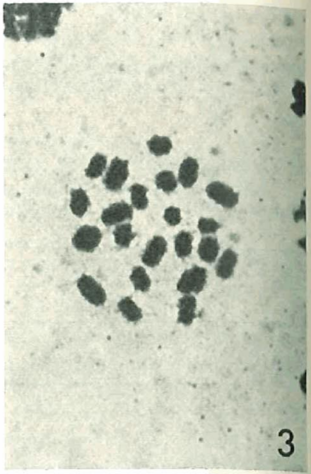
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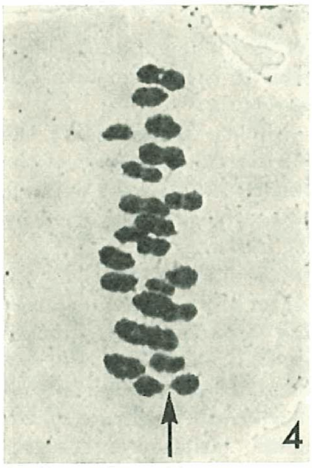
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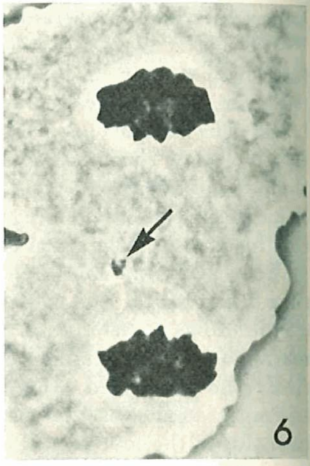
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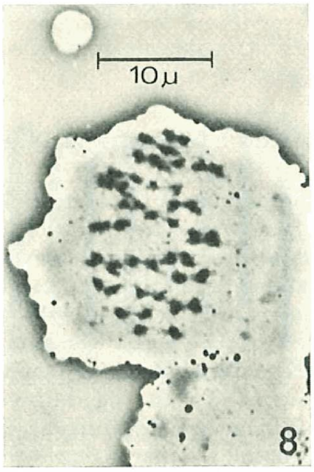

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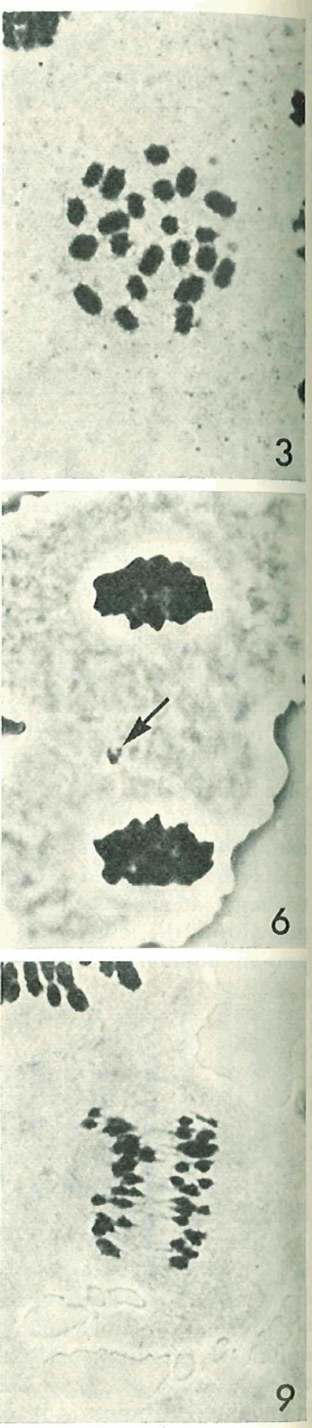


The dumbbell shaped elements are characteristic of polar views of the secondary metaphase (Pl. *I*, fig. 7). They divide simultaneously at anaphase II (Pl. *I*, fig. *8)* and no lagging or bridges were ever observed at secondary telophase (Pl. I, fig. 9).

There are no m-chromosomes in this species and the paired sex element can be recognized neither by heteropycnotic nor by heterokinetic behaviour at any stage of the maturation division in the male.

The general uniformity of the chromosome behaviour is similar to that described for *Glyphotaelius pellucidus* (RETZ.) (KIAUTA and *LANKHORST*, 1969).

The circumstance that a single chiasma occurs per bivalent is supporting our suggestion (cf. above) of the primary nature of the karyotype of ***Goera pilosa.*** In species possessing diffuse kinetochores in which the chromosome number has been reduced by means of secondary fusions of some elements of the original set, the original recombination index is usually maintained by an increase in chiasma frequency (cf. KIAUTA, 1969).

Considerations on the Phylogenetic Position of the Family Goeridae in View of the Evolutionary Trends in the Trichopteran Karyotype

There is some controversy as to the taxonomic status and/or structural affinities of the family ***Goeridae.*** The group is considered by some workers (e.g. HICKIN, 1967) as a subfamily in the ***Sericostomatidae,*** whereas it is assigned a family rank by other students (e.g. ROSS, 1967). Though only a single goeridan species has been studied cytologically, and nothing is known on the cytology of the 'true' ***Sericostomatidae,*** it seems worth while to briefly consider the problem in the light of general cytotaxonomic evidence.

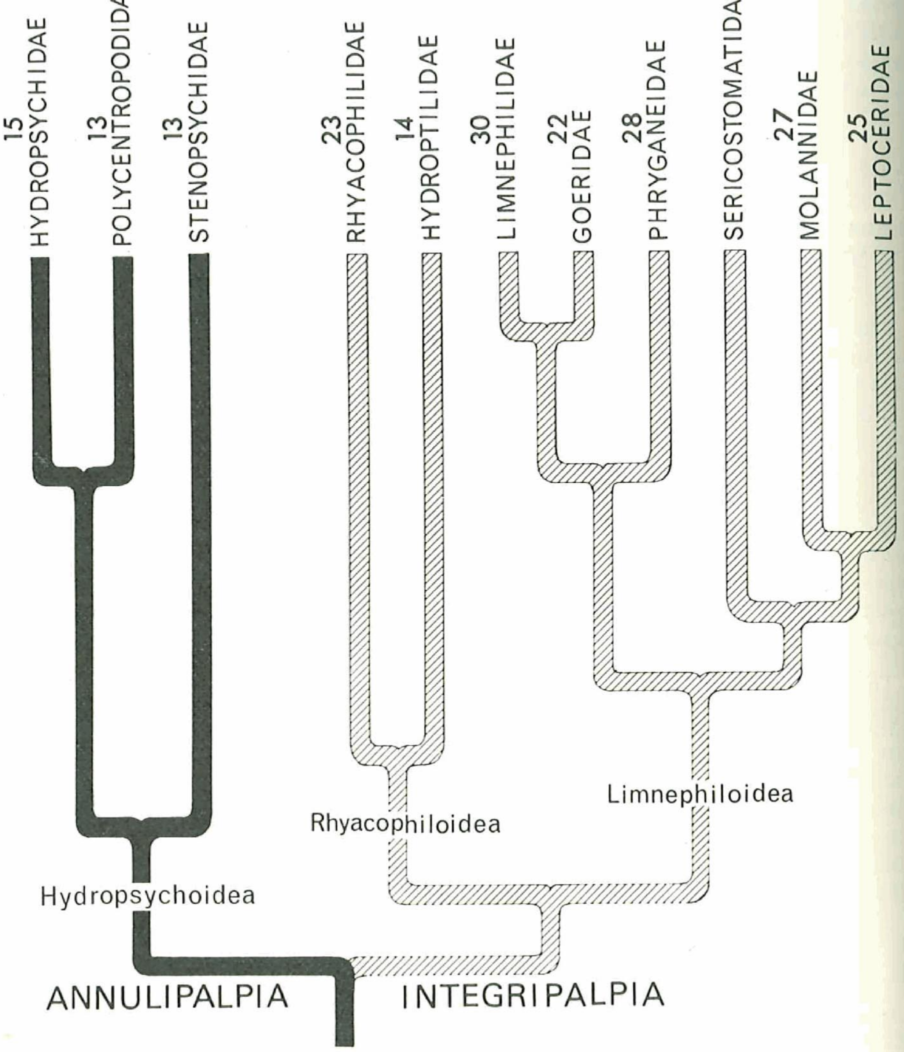
Much has been written on the classification, origin and affinities of the order, but ROSS' scheme of phylogenetic affinities of the trichopterous families seems to offer the best interpretation of the inner relationships and evolution of the order so far at our disposal (ROSS, 1967). It is based on comparative morphological analysis, whereas aspects of the functional evolution (viz. adaptations of ontogenetic stages) are also taken into account.

The main features of ROSS' genealogical tree could be summarised as follows:

(1) The existing caddis-fly families form two fairly homogeneous large groups with three families left over: the retreat-makers ***(Annulipalpia)***, the tube-case-makers ***(Integripalpia s. str. = Limnephiloidea)***, and the free living ***Rhyacophilidae***, the saddle-case-making ***Glossosomatidae,*** and the purse-case-making ***Hydroptilidae.*** These are related to ***Integripalpia***, but the similarities of the adult structural characters in the primitive genera of all three families suggest that the three are extremely closely related ***(Rhyacophiloidea)***.

Pl. I
Spermatocyte stages of ***Goera pilosa*** (FABR.) from the God dal Fuorn (1500 ×). Figs. 1–3. **Metaphase I** (polar view). – Fig. 4. Metaphase **I** (lateral view). The arrow indicates a bivalent that has already divided. – Fig. 5. Late anaphase **I.** – Fig. **6.** Telophase **I** (note the lagging element indicated by the arrow). – Fig. 7. Metaphase **II** (polar view). – Fig. 8. Anaphase **II.** – Fig. **9. Anaphase-telophase II.**

(2) The seven families constituting the suborder *Annulipalpia* (three of these were studied cytologically) are arranged into phylogenetic sequence on the basis of a successive loss of primitive characters, combined with the acquisition of a few specialised ones. The most primitive branch includes *Stenopsychidae* and *Philopotamidae*, whereas among the more specialised families the *Polycentropodidae* are more primitive than the *Hydropsychidae*.



Textfigure 3.
Ross' phylogenetic tree of Trichoptera, reduced to the cytologically examined families and the *Sericostomatidae*. Figures indicate the tentative type numbers.

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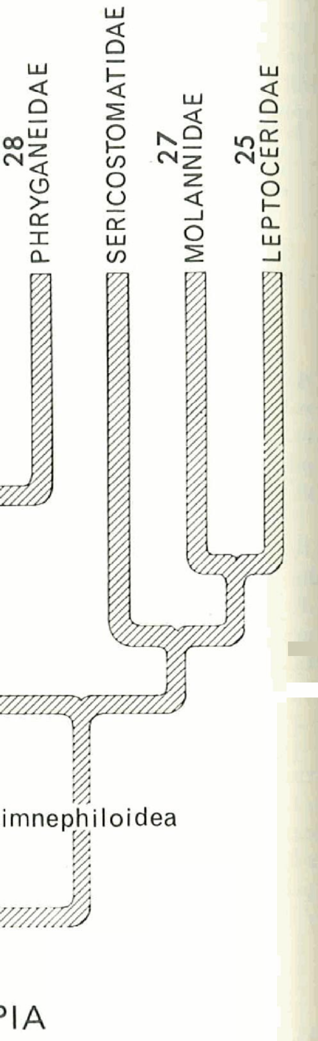

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(3) The three families of the Rhyacophiloidea (two of these were studied cytologically) represent side branches of the rest of the suborder Integripalpia. ***Rhyacophilidae*** are more archaic than *Glos*sosomatidae, but the phylogenetic character of Hydroptilidae seems rather obscure.

(4) The ***Integripalpia*** **s.** str. (Limnephiloidea) fall into two branches. The **limnephilid** branch includes the cytologically studied families ***Phryganeidae,*** Limnephilidae and *Goeridae*, whereas the leptocerid branch is composed of ***Sericostomatidae, Molannidae,*** *Leptoceridae* etc. The direct phylogenetic lines (branching off from the common ancestor) are shorter in the limnephilid families mentioned than they are in the leptocerid groups.

If Ross' scheme is combined with cytological findings (textfig. 3), the following features can be pointed out that are of importance for the consideration of the **phylogenetic** position of *Goeridae* (for other parallels and considerations cf. Kiauta, 1968):

(1) The chromosome numbers in ***Annulipalpia*** and in the two groups of ***Limnephiloidea*** generally show clear patterns. The extent of the numeric variation appears peculiar to each group. The great variation in Rhyacophiloidea, on the other hand, could tentatively be explained by the extraordinary long phylogenetic lines of each of the two families studied cytologically.

(2) In all of the most advanced (modern) and specialised families the high chromosome numbers prevail. A high chromosome number is considered, therefore, as an **indication** of advancement and specialisation (Kiauta, 1968).

(3) The sole exception to this rule are the *Goeridae*, which are considered by **Ross** (1967) as a late derivative of an ancestor common also to Limnephilidae, to which family they are thought to be closely related.

(4) If, on the other hand, the Goeridae were to be maintained as a subfamily in the *Sericostomatidae*, as it has indeed been done by Hickin **(1967),** the relatively **low** chromosome number would be in perfect agreement with the primitive origin of the family.

Although the small material studied cytologically does not permit any far reaching conclusions, it should nevertheless be stressed, in the light of the general evolutionary trend in the trichopteran **karyotype,** that the **cytotaxonomic** evidence does not support the phylogenetic position of Goeridae as it has been outlined, on the basis of structural characters, by **Ross** (1967). Since the Goeridae stand structurally **well** apart from the Sericostomatidae. the cytological evidence would suggest that the origin of the former **should** be looked for at a more primitive level than it has been done by Ross. This statement does not imply a **criticism** of the outstanding work of the lattkr author, **but it** is meant rather as a suggestion for reevaluation of non-cytological characters that could lead to a reconsideration of the phylogenetic status of the family.

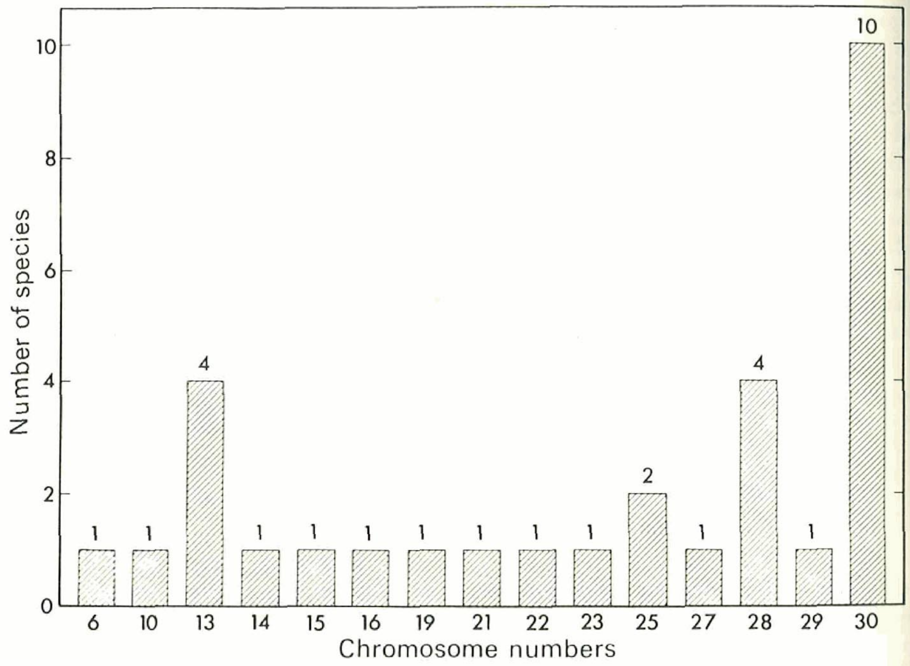
A Note on the seeming Affinity between the Trichopteran and Lepidopteran Type Numbers

Although a discussion on the general aspects of the trichopteran cytology falls well outside the scope of the present report, the author can not dismiss the subject without a brief marginal note, the less so in view of the repeatedly stressed affinity between the lepidopteran and trichopteran type numbers.

Aside from structural affinities, palaeontological evidence and several important common cytogenetic features (heterogamety of female, achiasmatic oogenesis, elimination of chromatin in the primary oocyte division in the egg and formation of apyrene sperms), which indeed clearly indicate the common origin of the two orders, the holokinetic nature of the centromere and the similar type numbers (*Trichoptera:* n = 30, *Lepidoptera:* n = 31) were also repeatedly brought up in this connection (cf. Suomalainen, 1969, with references to earlier literature).

Since in another paper we have already argued that the condition of the centromere does not indicate, *eo ipso*, any phylogenetic affinities between the insect orders (Kiauta, 1970) (though in the case of *Trichoptera-Lepidoptera* it might well furnish additional evidence in view of numerous other common features), the nature of the 'type' number of *Trichoptera* should be briefly considered here.

So far the chromosome numbers of 32 representatives of ten of the 34 trichopteran families have become known (Lutman, 1910; Pchakadze, 1928, 1930; Klingstedt, 1928, 1931; Gresson, 1933, 1935; Makino and Kichijo, 1934; Suomalainen, 1966; Kiauta and Lankhorst, 1969; Higler, 1969). The haploid chromosome numbers vary between n = 6 and n = 30. A histogram of the order is given in textfig. 4. It is evident, from the histogram, that the haploid number, n = 30, is the most common in the order (10 species), nevertheless we are of the opinion that it can not be regarded as the true type number of *Trichoptera*. The problem becomes apparent, when the numeric variation is reviewed from the point of view of the distribution within the families. This has been done in table II.



Textfigure 4.
Histogram of the order *Trichoptera*.

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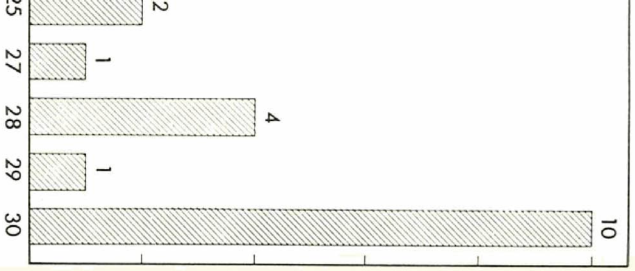

Table II

Distribution within families of the haploid chromosome numbers and tentative family type numbers in *Trichoptera* (figures marked with an asterisk (*) refer to secondary karyotypes sensu KIAUTA, 1967b, 1968)

Family	Number of species studied	Number of species with haploid chromosome number															(Tentative) family type number
		6	10	13	14	15	16	19	21	22	23	25	27	28	29	30	
Hydropsychidae	1					1											15
Polycentropodidae	1			1													13
Stenopsychidae	1			1													13
Rhyacophilidae	1										1						23 (?)
Hydroptilidae	1				1												14
Molannidae	1												1				27
Leptoceridae	2											2					25
Phryganeidae	5							1*						4			28
Goeridae	1									1							22
Limnephilidae	17	1*	1*	2*			1*		1						1	10	30

Although, in view of the small material studied, the family type numbers can in most cases not be identified with certainty, it is apparent, from table **II**, that the haploid number, n = 30, is peculiar to the ***Limnephilidae.*** Considering that most species studied belong to this most advanced family, it becomes clear, that the n = 30 complement is not characteristic of the order and, therefore, can not be regarded as the type number of caddis-flies.

The distribution of the chromosome numbers in Trichoptera thus suggests that the numeric variation in the caddis-fly karyotype evolved independently of that of the Lepidoptera, and has reached a 'similarity with the latter order only in the most advanced family. The similarity is therefore incidental and does not indicate any phylogenetic affinities. Until more material will have been examined the type number of Trichoptera can not be identified.

Acknowledgements

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