Some remarks on the evolution of the centromere, based upon the distribution of centromere types in insects[1]

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SCHRADER (1947) was the first to start the discussion on the evolution of the centromere. The subject was widened by LIMA DE FARIA (1949) (whose original ideas are of principal importance for the understanding of the centromere development), whereas CAMARA (1953) reviewed the problem in detail. The most comprehensive considerations on centromere evolution were given by VAARAMA (1954). His studies resulted in the proposal of a tentative hypothesis on the possible paths of the phylogeny of the centromere. The most primitive chromosome is represented by a "single block with a diffuse centromere", from which the compound chromosome with multiple centromeres is thought to be derived on one hand, and the chromosome with localised kinetochore on the other. VAARAMA's theory has not been generally accepted. The main argument brought against it was the sporadic occurrence of diffuse centromeres in widely separated groups of organisms, which "obviously stem from more primitive forms with localised centromeres", and the observation that in such species as maize and rye other regions of the chromosomes (knobs in maize and the chromosome ends in rye) may secondarily acquire the properties of typical centromeres. If such properties were acquired by all chromomeres, a diffuse centromere condition would evolve (SWANSON, 1957).

We are of opinion that this criticism does not affect VAARAMA's hypothesis but only demonstrates the complexity of the problem.

Lists of organisms possessing diffuse kinetochores have been given by BATTAGLIA & BOYES (1955) and BAUER (1967) and include representatives of the following orders other than insects:

Scutigeromorpha (Chilopoda), Scorpionida and Acarina (Arachnida), Conjugales (Chlorophyceae), Plasmodiophorales (Myxomycetes), Jungermanniales (Hepaticae) and Graminales (Monocotyledonae).

In the present note the discussion is limited to the insects, but some general considerations are also added.

In Fig. 1 the information on the distribution of various types of kinetochore in insects is combined with the phylogenetic tree of the class as constructed by MARTYNOV (1938) and revised by JEANNEL (1965). It is a matter of course that the information on the nature of the centromere concerns the living representatives only. However, since the centromere condition does not vary within an order (save probably in the Coleoptera) and for the sake of convenience, the condition found in the living members was marked in the figure throughout the time-range of the order concerned. It should be stressed that for some of the

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orders plotted the cytological information is very fragmentary and the condition of the centromere could only be determined on the basis of descriptions and figures published (e.g. Thysanoptera; BOURNIER, 1956). In the cases where even such information is too scanty or uncertain (e.g. Collembola; TUZET & MANIER, 1956; SAITOH & CHIBA, 1959; NUNEZ, 1962) the indication of the character of the centromere was altogether omitted. It is also necessary to point out that the phylogenetic affinities between some super-orders are arbitrary, those between Ephemeropteroida and Odonatopteroida perhaps most of all.

The first problem to be considered is the phylogenetic level at which the split took place between the lines that led to the diffuse condition of the centromere in living insects on one hand, and to what is called a localised kinetochore on the other. The evidence on the phylogenetic branching of the oligoneopteran orders demonstrates clearly that this event occurred at the primitive insect stage and not in a preinsectan ancestor.

The answer to the question whether the diffuse and localised condition of the kinetochore (both or one of them), as seen in the living orders, are of monophyletic or of polyphyletic origin must be given with a necessary reservation. Nevertheless, it is sure that one of the two conditions is certainly monophyletic in general, but some of its forms might be of secondary origin, being analogous rather than homologous to the original situation. The other is then polyphyletic.

Before the discussion of the above mentioned points can be conducted further, it is necessary to consider briefly the primitiveness (specialisation) of the two centromere conditions. For the time being we see at least two tentative paths of approach to this problem. The first of these considers the functional and the other the phylogenetic aspect of the problem.

There is no doubt that, in case of fragmentations, fusions or translocations the chances of survival of diffuse kinetochore chromosomes are much greater than those of elements with localised centromeres. The former kind of kinetochore thus gives a kind of priority to those primitive (unspecialised) organisms that are destined to evolve new forms and can, therefore, be expected to have been present in ancient unspecialised organisms. It seems to us very significant, when the phylogenetic tree of insects is considered from this point of view, that in most superorders which have supposedly branched off from the common stem already during the early history of the class (prior to the Late Devonian), diffuse kinetochores are found. Among the superorders thus far studied cytologically, there are only two exceptions viz. Ephemeropteroida and Orthopteroida, but, for different reasons, the situation in neither of these is really clear. Thus, this evidence, coupled with the biological and evolutionary plasticity of the diffuse kinetochore, greatly supports the idea of the phylogenetic primitivity of the latter. This being so, the localised centromere represents a specialised situation.

There is no doubt that both Ephemeropteroida and Orthopteroida have a very ancient origin, but it is unfortunate that very fragmentary information is available on the cytology of the former (cf. KATAYAMA, 1929; WOLF, 1946) and no details are known on the nature of the localised kinetochore in mayflies. Due to their morphologically and structurally very clear chromosomes, some of the

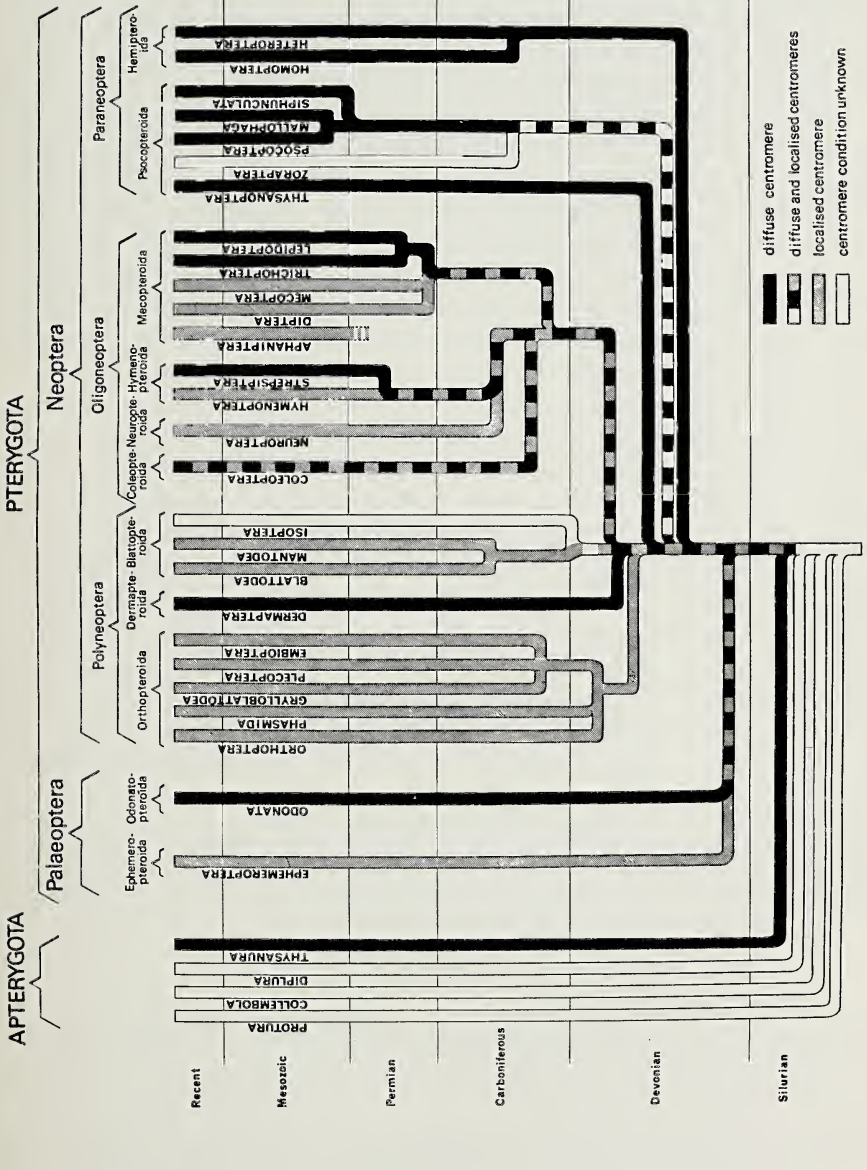

Fig. 1. MARTYNOV's phylogenetic tree of insects. Colours of branches indicate nature of centromere in living groups.

orthopteroidan orders, on the other hand, belong to the cytologically most studied groups of insects. If the centromere shift as observed in Orthoptera could really be regarded as representing a primitive, not yet fully stabilised condition (VAARAMA, 1956) and thus a step in the evolution from diffuse to localised kinetochore, the ancient origin of the group would certainly support such a suggestion. (The other possibility, of course, remains that the shift was recorded only because of the extraordinary clear chromosome pictures found usually in the orthopteroid insects and the great amount of material studied cytologically, whereas any details in most of the other groups are very hard to observe).

Assuming that the diffuse kinetochore represents the original, primitive condition, and that the localised kinetochores in insects are polyphyletic (arising independently in different branches of the phylogenetic tree and in different time-sections of the phylogenetic history of the class), the question arises whether or not at least the diffuse centromeres of living insect orders can be regarded as h o m o l o g o u s. Generally, there is no evidence against this suggestion (nor in favor of it), but observations on some Coleoptera might indicate that a kind of multiple (if not diffuse) centromere has (probably) secondarily developed in some representatives of this order (cf. VON BORSTEL, 1963).

From the narrated evidence the conclusion may be safely drawn that the condition of the centromere does not indicate, *eo ipso,* any phylogenetic affinities between the insect orders.

The argument of the "sporadic occurrence of diffuse centromeres in widely separated groups of organisms which obviously stem from more primitive forms with localised centromeres" as brought against the hypothesis of the originality of the diffuse kinetochore (SWANSON, 1957; cf. above) has no grounds, since (1) the evolution of at least one kind of centromere is polyphyletic and (2) there are no methods to determine the centromere condition in the ancestral lines of living organisms, though, as far as the insects are concerned, in which the type of the centromere does not vary within the order (save for the isolated case of Coleoptera), it can be assumed that it did not in the course of the phyletic history of the order either.

The case of the Coleoptera, though different from that of rye and maize, demonstrates that the specialised chromosomes (with localised centromere) may secondarily acquire the properties of the original diffuse-kinetochore condition.

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Curtis, William, A short history of the Brown-tail Moth, [1782], Facsimile uitgave 1969 met een inleiding van W. T. STEARN en entomologische aantekeningen van D. S. FLETCHER. Curwen Press. Uitgever: E. W. Classey Ltd., 353, Hanworth Road, Hampton, Middlesex, England, 6 pag. plus 16 pag. facsimile met gekleurde plaat. Prijs gebonden £ 3.15.0 (£. 3.75).

Het boek is het eerste van een serie herdrukken getiteld „Classica Entomologia", een facsimile uitgave van een nu zeer zeldzame publicatie, die William CURTIS in 1782 het licht deed zien na een ernstige plaag van de basterdsatijnvlinder. In een inleiding bespreekt W. T. STEARN het leven van de oorspronkelijke auteur (1746—1799), die in zijn tijd een expert was op het gebied van de botanie en de entomologe. Zijn voornaamste publicaties zijn van botanische aard (Flora Londinensis, Curtis 's Botanical Magazine). Zijn „Short History" kan men beschouwen als een voorloper van de talloze publicaties, die later over schadelijke insekten het licht zouden zien.

FLETCHER geeft een overzicht van de schade, die vooral in Noord-Amerika door *Porthesia chrysorrhoea* is veroorzaakt en de maatregelen, die daartegen genomen zijn.

Zeer fraai is de eigenlijke facsimile uitgave met de gekleurde plaat, waarop alle stadia van de soort met de parasieten zijn afgebeeld en die in kwaliteit zeker met de goede platen van onze beroemde J. C. SEPP kan wedijveren. Het geheel is een luxueuse uitgave van een zeldzame achttiende-eeuwse Engelse verhandeling, in zijn tijd ongetwijfeld een voortreffelijk stuk werk. — LPK.

Benno, P., De Nederlandse bijen. Wetenschappelijke Mededeling no. 18 van de K.N.N.V. Tweede druk, september 1969. 32 pag., 30 tekstfiguren. Prijs voor leden van K.N.N.V. en N.E.V. f 3,—, voor anderen f 3,50, te voldoen door storting op postrekening 13028 ten name van Bureau K.N.N.V. te Hoogwoud-N.H.

De eerste druk van deze W. M. verscheen in 1955. Eveneens als bij alle andere herdrukken is ook deze tweede druk een aanmerkelijke uitbreiding van de eerste: van 24 pagina's op 32! De nomenclatuur is bijgewerkt, de systematiek zoveel mogelijk aangepast aan moderne inzichten en bij alle geslachten zijn lijsten gegeven van de uit ons land bekende soorten. Het nummer bevat bovendien een blad met aanvullingen en correcties op W. M. 67, 1967, De Nederlandse Wespen. — LPK.