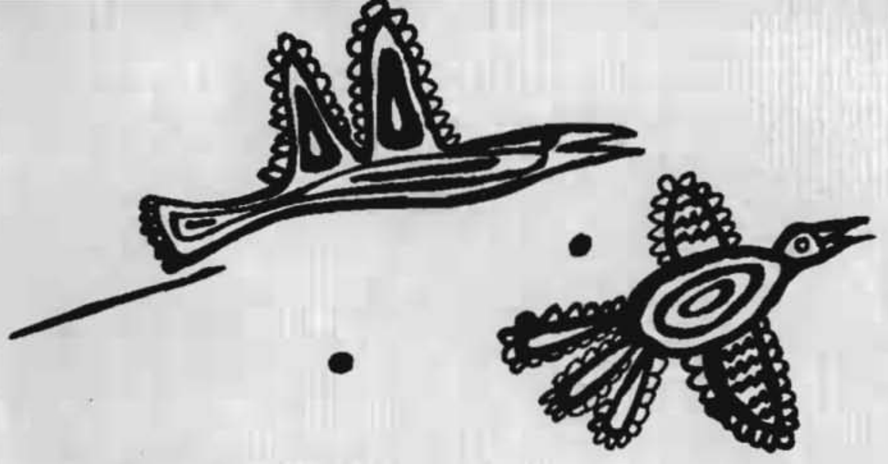
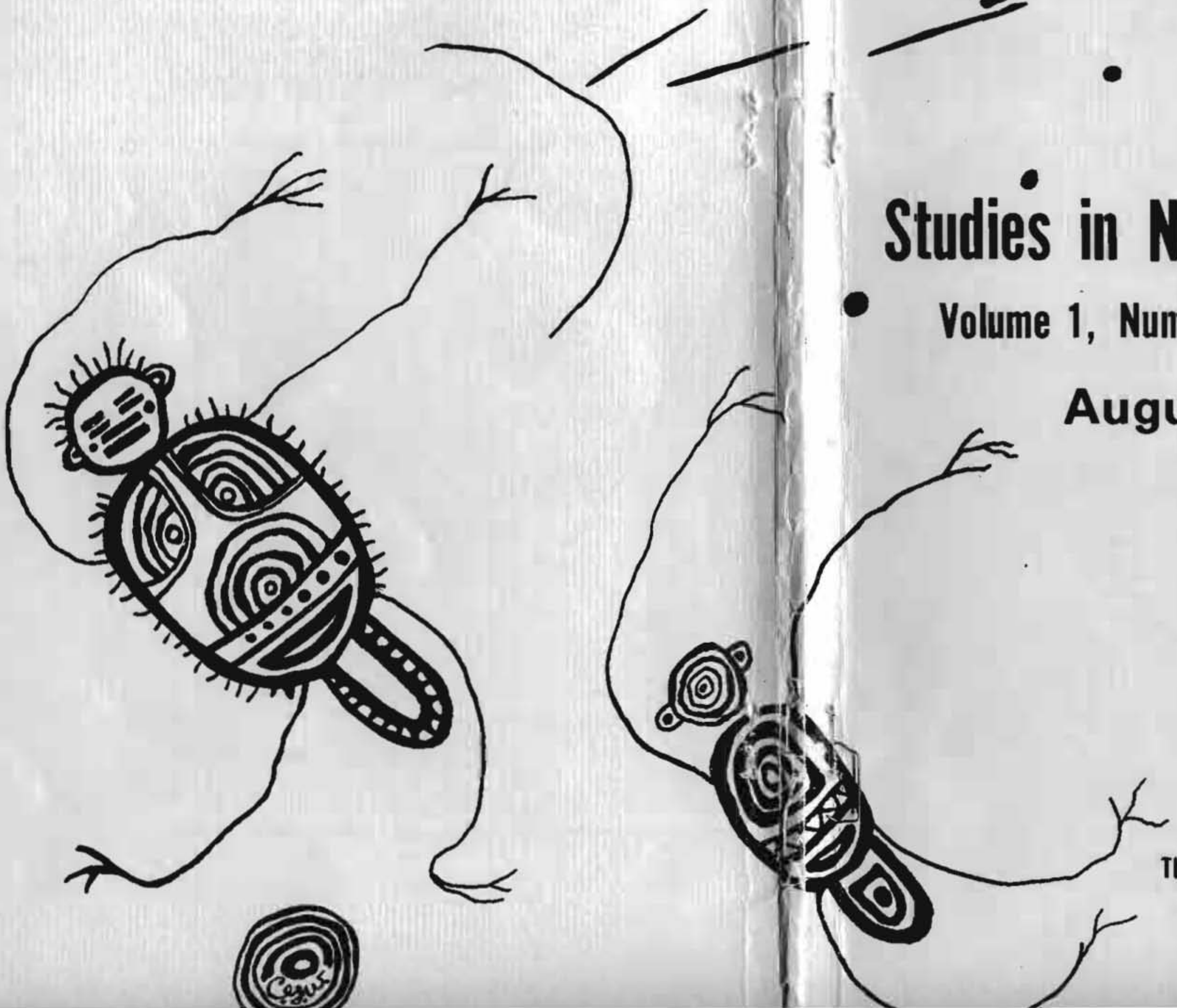


Studies in Natural Sciences

Volume 1, Numbers 10, 11, and 12

August 1974



Published by
The Natural Sciences Research Institute
Eastern New Mexico University
Portales, New Mexico
U.S.A.

Evolutionary Cytology in the Genus *Chironomus* Meigen[1, 2]

by

Jon Martin[3], W. Wülker[4], and J.E. Sublette[5]

INTRODUCTION

The suitability of Chironomidae for studies on the comparative cytology of related species was suggested almost thirty years ago by Bauer (1945), but the group was virtually ignored until the studies of Keyl and various co-workers (Keyl 1957, 1960a, 1960b, 1961a, 1961b; Keyl and Strenzke 1956; Keyl and Keyl 1959) culminating in his major study of 22 European species of the genus *Chironomus* (Keyl 1962). The species which are sometimes put in the separate subgenus *Camptochironomus*, have also been thoroughly investigated, both in Europe (Beermann 1953, 1955; Acton 1957) and in North America (Acton 1958, 1959, 1962, 1965). More recent karyosystematic studies of *Chironomus* species have been undertaken in North America (Wülker, *et al.* 1968; Wülker and Martin 1971), Australia (Martin 1969, 1971a), and Japan (Martin and Sublette 1972). Wülker (1973) and Wülker and Klötzli (1973) added new descriptions of european species.

---

[1] Based on the text of a paper presented at the 14th International Congress of Entomology, Canberra, Australia in August 1972.

[2] Partly supported by Grant No. D71/17815 from the Australian Research Grants Commission; Environmental Protection Agency Grant No. R80/005; and NATO Grant No. 602.

[3] Genetics Department, University of Melbourne, Parkville, Victoria, 3052, Australia.

[4] Biologisches Institut der Universität, (Zoologie) Freiburg i. Br., BRD.

[5] Natural History Museum and Natural Sciences Research Institute, Eastern New Mexico University, Portales, New Mexico 88130, U.S.A.

Species of *Chironomus* in general possess four pairs of chromosomes consisting of three large metacentric chromosomes and a short acrocentric one. Initially these were usually referred to as chromosomes I, II, III, and IV on the basis of their relative length. However, this caused some confusion because chromosomes with the same number were not always homologous in different species. Therefore, Keyl (1962) gave a letter name from A to G to each arm on the basis of homology. His standard species, *Chironomus piger* Strenzke, had the arm combination:

A ∧ B   C ∧ D   E ∧ F | G

However, not all of the species which he studied had this same combination of arms. He found that there were five main groups which differed due to the occurrence of whole arm translocations (Keyl 1962, Fig. 1). The pseudothummi- and the thummi- complexes were the most common.

Subsequent work has disclosed additional complexes also due to whole arm translocations (Krieger-Wolff and Wülker 1971). Figure 1 depicts an updating of the complexes. This figure is based on material from all continents as well as a number of Pacific Islands, although many areas still remain to be collected extensively for cytological studies. As well as the additional complexes this figure has one major alteration as compared to those previously published. The lacunarius-(=commutatus)-complex is no longer shown as a derived group, because two members of this complex have been found which possess the basic four pairs of chromosomes (Wülker and Klötzli 1973).

A total of eight major complexes and three minor complexes have now been identified. The pseudothummi-complex appears to be the most widespread, occurring in all areas studied. The thummi-complex is very common in North America and a single representative has been found in Australia. The maturus-complex (="paralcyon"-complex) is represented by two species in North America (Wülker and Martin 1974). The "calligraphus"-complex[1], which is unique in having arm E as the acrocentric element, is found in South America.

---

[1] Identity of South American species not clearly defined.

The carus-complex contains only *Chironomus carus* Townes which has a distribution from central America into southern U.S.A. The arms of this species are difficult to identify, possibly because it is more distantly related to the other species. This species may open the way to relating the banding patterns in genera near *Chironomus*, because the larvae of *C. carus* show indications of relationships to *Goeldichironomus* and *Einfeldia*. It is difficult to determine if *C. carus* has three or four pairs of chromosomes. Arm G is always associated with arm E (Fig. 2); the connection often appearing as a nucleolus, but often being rather tenuous. Unfortunately, there was no opportunity to investigate mitotic or meiotic chromosomes because all material available was slide mounted.

In three, or possibly four, complexes there has been a reduction to three pairs of chromosomes (Fig. 1). In one North American species there is a reduction to two pairs of chromosomes. This species does not appear to be derived from the known three chromosome species (at least not in any simple way) because it appears to have the arm combination GAB, FEDC, although the arms cannot be recognized with any certainty.

There are many other possible combinations of chromosome arms (Wülker *et al.* 1968); but while we may expect other combinations to be found in species from other areas not yet studied, it seems unlikely that all theoretical combinations do occur. Certain translocation combinations must be favored over others and are therefore more likely to survive. This is demonstrated by species with a reduction to three pairs of chromosomes, inasmuch as this must have occurred on at least four occasions (if *C. carus* has in fact three pairs of chromosomes). On each occasion arm G has become fused to arm E by a tandem fusion. The combination GA, which occurs in *C. cf. calligraphus* and in the North American two chromosome species, would also be the result of independent occurrences. These combinations apparently have some selective advantage compared with the other four possible combinations of arm G and another arm.

The multiple occurrences of fusions or translocations involving G raise the question: Are each of the complexes the result of a single reciprocal translocation or the result of several independent events, each giving a similar result? This question is particularly applicable to the pseudothummi-complex which has such a wide distribution. Keyl (1962) suggests that the thummi-complex in Europe is the result of two separate translocations. He based this on the fact, that arms A and E of *Chironomus riparius* Meigen (=*Chironomus thummi* Kieffer) can be related directly to species in the pseudothummi-complex but are only related to the other species in the thummi-complex via these pseudothummi-complex species. It appears that *C. riparius* evolved separately to the other species of the thummi-complex.

The situation in the other complexes is not clear. Spontaneous whole arm translocations are still occurring. Keyl (1962) reported a translocation in *Chironomus annularius* Meigen which converted the thummi-complex CD, EF to Camptochironomus-complex DE, CF. A translocation in *Chironomus cloacalis* (Fig. 3) converts pseudothummi- AE, BF to thummi-complex AB, EF. An unidentified North American thummi-complex species showed a translocation from AB, EF to maturus-complex combination AF, BE, although not strictly a whole arm translocation; the BE product is dicentric and the AF product acentric (Fig. 4).

However, Australian pseudothummi-complex species show a definite relationship to European species in the arm A, E, and F sequences. For instance, the sequence in arm A of *C. cloacalis* (Fig. 3 and Martin 1971b) is apparently identical with that in *Chironomus holomelas* Keyl and *Chironomus melanescens* Keyl in Europe (Keyl 1962) and *Chironomus yoshimatsui* Martin and Sublette in Japan (Martin and Sublette 1972). This supports the hypothesis that this complex is a true phylogenetic entity over a large part of its range.

In the phylogenetic chart (Fig. 1) no directional arrows were shown, except in the case of the three chromosome complexes. It is much more likely that they have arisen as a result of a number of independent tandem fusions, rather than the four chromosome species arising from them following a dissociation. For the other complexes the situation is not clear. The large number of species in the pseudothummi- and thummi-complexes, together with the fact that all of the other complexes except the carus-complex, can be derived from one or other of them suggests that one of these may be the ancestral complex. However, a wide distribution at the present time is not evidence of a wide distribution in the past, or vice versa. The banding sequence of species in different complexes suggests that the distribution of these complexes was different than the present. For example, because the two species of the maturus-complex have been closely investigated (Wülker and Martin 1974) it would seem that it should be possible to determine whether or not this complex is related to the thummi- or the pseudothummi-complex. However, a comparison of these complexes reveals an interesting situation. Although arm F can be related directly to *C. piger*, arms A and E are related to sequences found in both the thummi- and pseudothummi-complexes. The maturus-complex is related at the region of differentiation of the thummi- and pseudothummi-complexes. If this region is investigated more closely in Keyl's Fig. 24 (1962), we find that the relationship is at the point where the parathummi-complex also connects. Therefore these complexes may have arisen at about the same evolutionary period or from some common ancestor. Keyl (1962) suggested the sequences which a common ancestor must have carried in arms A, E, and F. No alterations of the sequences are necessary with the more recent addition of maturus-complex. This ancestor would have arm F of *C. piger*; arm A of *Chironomus pseudothummi* Strenzke and *C. holomelas* (i.e., two sequences); and arm E as in *C. piger*. *Chironomus crassimanus* Strenzke and *Chironomus plumosus* Linnaeus (i.e., three sequences). This ancestral species must have had either a holarctic distribution, to have descendents in both Europe and North America, or the present parathummi- and maturus-complexes previously occurred in the same geographical region. Keyl (1962) has suggested that the pseudothummi-complex may be older than the thummi-complex, or at least that section not including *C. riparius* and *C. piger*. He bases this on the fact that the inversions which occur as interspecific differences in these thummi-complex species are still present as intraspecific differences in some of them, but in the pseudothummi-complex all such inversions have become fixed. If this interpretation is correct, then the lacunarius-complex must also be a derived complex because of its relationship to these thummi-complex species. Insufficient data exist to allow any speculation on the relative phylogenetic age of the other complexes.

LITERATURE CITED

Acton, A B. 1957. Chromosome inversions in natural populations of *Chironomus tentans*. J. Genet. 55: 61-94

———. 1958. A cytological comparison of Nearctic and Palaearctic representatives of *Chironomus tentans* (Diptera). Proc. Linn. Soc. Lond. 169: 129-131.

———. 1959. A study of the differences between widely separated populations of *Chironomus (Tendipes) tentans* (Diptera). Proc. R. Soc. Lond. Ser. B. 151: 277-296.

———. 1962. Incipient taxonomic divergence in *Chironomus* (Diptera). Evolution 16: 330-337.

———. 1965. *Chironomus tentans* (Diptera) the giant chromosomes and taxonomic divergence. Proc. XIIth Int. Congr. Entomol. (Lond), p. 245.

Bauer, H. 1945. Chromosomen und Systematik bei Chironomiden. Arch. Hydrobiol. 40: 994-1008.

Beermann, W. 1953. Chromosomenpolymorphismus und Bastardierung zweier *Chironomus* - Arten. Zool. Anz. Supplement 17: 290-295.

———. 1955. Cytologische Analyse eines *Camptochironomus*-Artbastards. I. Kreuzungsergebnisse und die Evolution des Karyotypus. Chromosoma 7: 198-259.

Keyl, H.G. 1957. Untersuchungen am Karyotypus von *Chironomus thummi*. I. Karte der Speicheldrüsenchromosomen von *Chironomus thummi thummi* und die cytologische Differenzierung der Subspecies *Ch. th. thummi* und *Ch. th. piger*. Chromosoma 8: 739-756.

———. 1960a. Die cytologische Diagnostik der Chironomiden. II. Diagnosen der Geschwisterarten *Chironomus acidophilus* n.sp. and *Ch. uliginosus* n.sp. Arch. Hydrobiol. 57: 187-195.

———. 1960b. Chromosomenumbau und Evolution in der Gattung *Chironomus*. Zool. Anz. Suppl. 24: 280-283.

———. 1961a. Die cytologische Diagnostik der Chironomiden. III. Diagnose von *Chironomus parathummi* n.sp. und Ergänzungen zur Bestimmungstabelle. Arch. Hydrobiol. 58: 1-6.

———. 1961b. Chromosomenevolution bei *Chironomus* I. Strukturabwandlungen an Speicheldrüsen-Chromosomen. Chromosoma 12: 26-47.

———. 1962. Chromosomenevolution bei *Chironomus*. II. Chromosomenumbauten und phylogenetische Beziehungen der Arten. Chromosoma 13: 464-514.

Keyl, H.G., and I. Keyl. 1959. Die cytologische Diagnostik der Chironomiden. Arch. Hydrobiol. 56: 43-57.

Keyl, H.G., and K. Strenzke. 1956. Taxonomie und Cytologie von zwei Subspecies der Art *Chironomus thummi*. Z. Naturforsch. 11b: 727-735.

Krieger-Wolff, E., and W. Wülker. 1971. Chironomiden (Diptera) aus der Umgebung von Freiburg i.Br. (mit besonderer Berücksichtigung der Gattung *Chironomus*). Beitr. Naturkd. Forsch. Suedwestdtsch. 30: 133-145.

Martin, J. 1969. The salivary gland chromosomes of *Chironomus oppositus* Walker (Diptera: Nematocera). Aust. J. Zool. 12: 473-486.

———. 1971a. A review of the genus *Chironomus* (Diptera, Chironomidae). IV. The karyosystematics of the *australis* group in Australia. Chromosoma 35: 418-430.

———. 1971b. A review of the genus *Chironomus* (Diptera, Chironomidae). II. Added descriptions of *Chironomus cloacalis* Atchley and Martin from Australia. Stud. Nat. Sci. (Portales, N.M.) 1(2): 1-21.

Martin, J., and J.E. Sublette. 1972. A review of the genus *Chironomus* (Diptera, Chironomidae). III. *Chironomus yoshimatsui* new species from Japan. Stud. Nat. Sci. (Portales, N.M.) 1(3): 1-59.

Wülker, W. 1973. Revision der Gattung *Chironomus* Meig. III. Europäische Arten des *thummi*-Komplexes. Arch. Hydrobiol. 72: 356-374.

Wülker, W. and A.M. Klötzli. 1973. Revision des Gattung *Chironomus* Meig. IV. Arten des lacunarius-(-commutatus-) komplexes. Arch. Hydrobiol. 72: 474-489.

Wülker, W.F., J.E. Sublette, M.F. Sublette and J. Martin. 1971. A review of the genus *Chironomus* (Diptera, Chironomidae). I. The *staegeri* group. Stud. Nat. Sci. (Portales, N.M.) 1(1): 1-89.

Wülker, W., and J. Martin. 1974. A review of the genus *Chironomus* (Diptera, Chironomidae). VI. Cytology of the *Chironomus maturus* complex. Stud. Nat. Sci. (Portales, N.M.) 1(9): 1-17.

Wülker, W., J.E. Sublette, and J. Martin. 1968. Zur Cytotaxionomie nordamerikanischer *Chironomus*-Arten. Ann. Zool. Fenn. 5: 155-158.

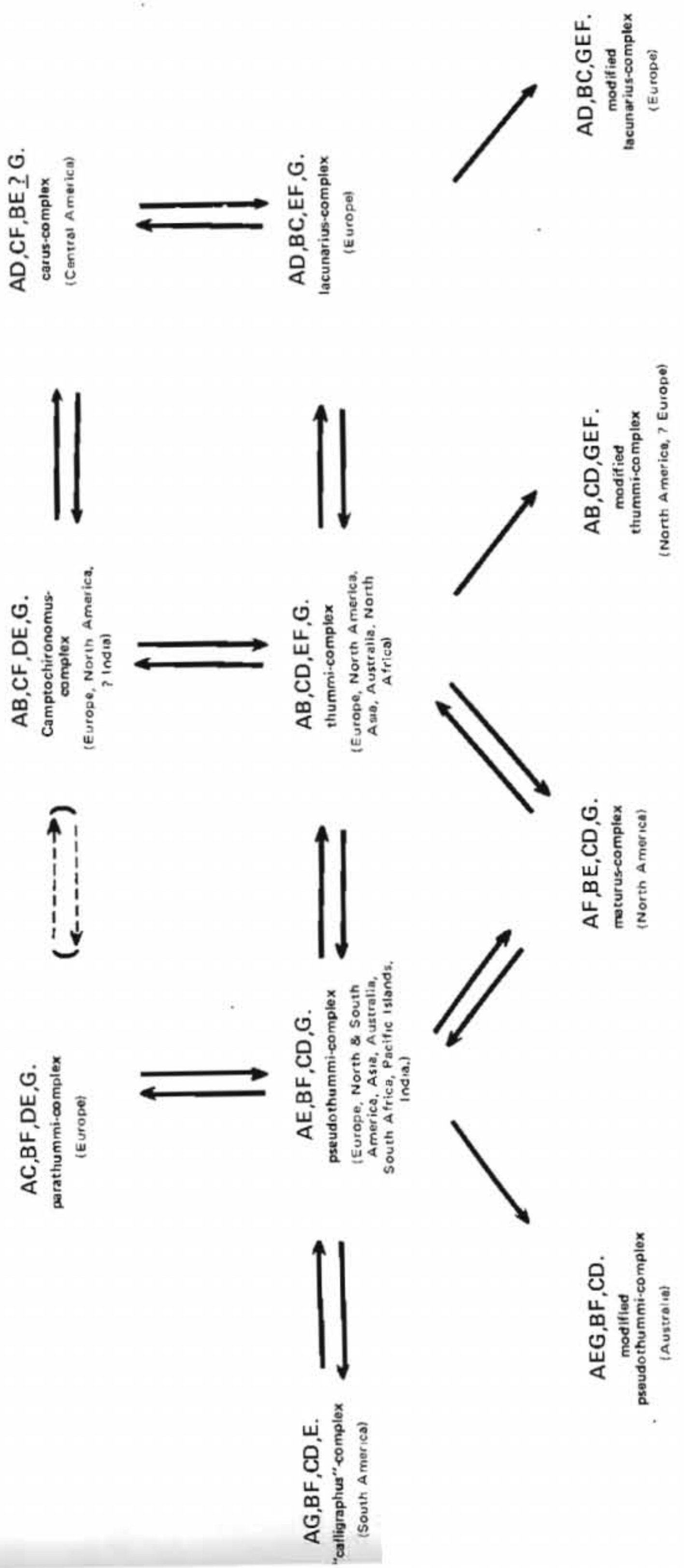


Fig. 1. Chart of the phylogenetic relationships of different chromosome arm combination complexes in the genus *Chironomus* and areas in which they are known to occur.

Fig. 2. Arms G and E of *Chironomus carus* showing the nucleolus-like connection between them.

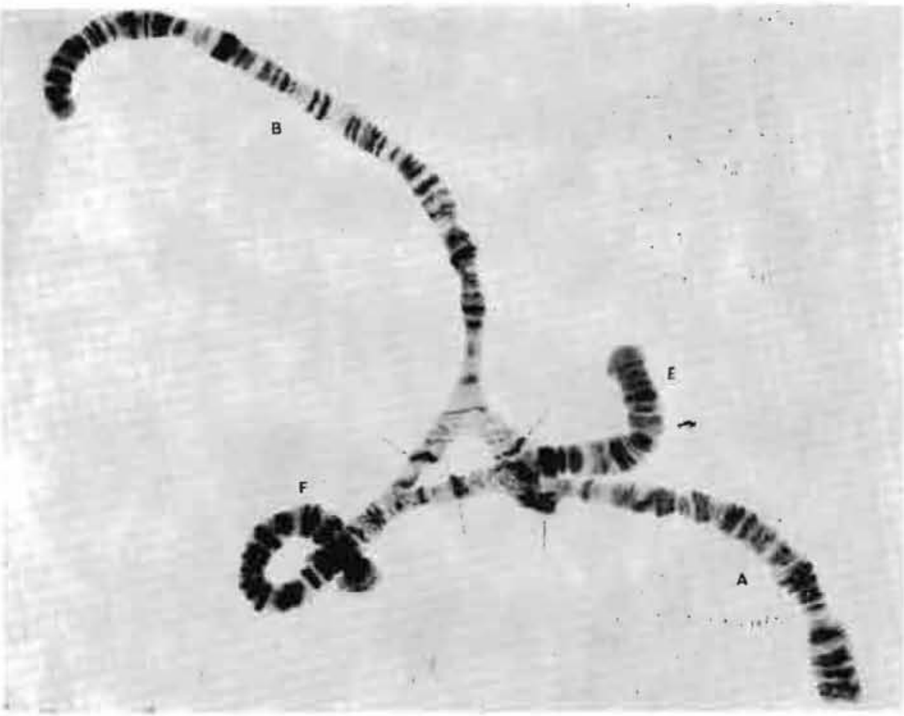


Fig. 3. Spontaneous translocation heterozygote in *Chironomus cloacalis* involving AE and BF chromosomes. The translocated chromosomes become AB and EF. Arrows indicate the position of the centromeres.

Fig. 4. Spontaneous translocation heterozygote in an unidentified thummi-complex species from Yankton, South Dakota. AB and EF chromosomes are translocated to become AF and BE.