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SIXTEEN DRAGONFLY KARYOTYPES FROM THE REPUBLIC OF SOUTH AFRICA AND SWAZILAND, WITH EVIDENCE ON THE POSSIBLE HYBRID NATURE OF *ORTHETRUM JULIA FALSUM* LONGFIELD (ANISOPTERA: LIBELLULIDAE)*

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The ♂ germ-cell complements are described and illustrated of the following spp., 4 of which (asterisked) are new to cytology, while of 10 of the others only the chromosome numbers were previously known: Coenagrionidae: *Coenagrion glabrum* (Burm.) (n=14), *Pseudagrion acaciae* Foerst. (n=14 ?, *m*), *P. kersteni* (Gerst.) (n=14), *P. salisburyense* Ris (n=14, *m*); — Calopterygidae: *Phaon iridipennis* (Burm.) (n=13, *m*); Libellulidae: *Bradinopyga cornuta* Ris (n=13, *m*), *Crocothemis erythraea* (Brullé) (n=13, *m*), *C. sanguinolenta* (Br.)* (n=13, *m*), *Orthetrum abbotti* Calv. (n=13, *m*), *O. chrysostigma* (Burm.) (n=13, *m*), *O. julia falsum* Longf.* (n=13, *m*; in 1 of the 2 specimens regular precocious division of X at diakinesis, some cells with an extra element of unclear structure and unknown provenience; on the basis of these features the possibility of the hybrid nature of the taxon is advanced), *Palpopleura jucunda* Ramb.* (n=13, *m*), *Pantala flavescens* (Fabr.) (n=13, *m* extremely minute), *Trithemis annulata* (P. de Beauv.) (n=13), *T. arteriosa* (Burm.) (n=13, *m*), and *T. dorsalis* (Ramb.)* (n=13, *m*).

INTRODUCTION

This is the final report on the cytological results of the dragonfly collecting trips undertaken by the late Professor Dr. J.W. Boyes, Mrs. B.C. Boyes and the second author, in November 1976, in Swaziland and in the Kruger National Park (Republic of South Africa). A preliminary report has been submitted at the Fourth International Symposium of Odonatology

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(Gainesville, Florida, USA, August 1977) (cf. VAN BRINK & KIAUTA, 1977). Aside from a revised statement on *Trithemis annulata* (P. de Beauv.), however, the present paper also contains observations on four additional taxa, viz. *Crocothemis sanguinolenta* (Brauer), *Orthetrum julia falsum* Longf., *Palpopleura jucunda* Ramb. and *Trithemis dorsalis* (Ramb.), all of which are new to cytology, and were collected and dissected by the late Prof. Boyes at the Usuto Forest Falls, Swaziland, in April, 1977. These are the last dragonfly specimens Dr. Boyes has examined before he has finally settled down in his native Ontario, Canada, where he has suddenly passed away on January 12, 1980 (cf. VAN BRINK, 1980).

We greatly regret that Dr. Boyes did not live to see this note appear in the press, though he has seen the preliminary draft in 1977, and discussed the subject with us again during the Fifth International Symposium of Odonatology, Montreal, August, 1979.

All specimens were dissected and fixed in the field, and the slides photographed in Utrecht. Most of those of 1976 were Feulgen processed, while the 1977 preparations were stained after the lacto-acetic-orcein squash method and photographed in semipermanent condition. All specimens, films and the 1976 slides are in the collection of the third author.

Though small, the collection includes three species, viz. *Bradinopyga cornuta* Ris, *Crocothemis erythraea* (Brullé) and *Pantala flavescens* (Fabr.), that were not listed in BALINSKY's (1965) preliminary list of the Odonata of the Kruger National Park.

DESCRIPTIONS AND DISCUSSIONS OF THE KARYOTYPES

Coenagrionidae

CERIAGRION GLABRUM (BURMEISTER, 1839)
Figures 1-3

Material — 1 ♂, Mkusi Game Reserve, Natal, Republic of South Africa, 13-XI-1976 — [46 complements photographed].

2n = 27, n = 14. Save for one appreciably larger pair, the spermatogonial metaphase elements are only slightly graded in size. The sex element is apparently the smallest of the set and there are no *m*-chromosomes (Fig. 1). At diakinesis, chiasma terminalization occurs nearly simultaneously in all bivalents (Fig. 2), while the large bivalent and the X are the only morphologically distinguishable elements at metaphase I (Fig. 3).

This is the fifth *Ceriagrion* species we had the opportunity to examine cytologically. In *C. azureum* (Sel.) and *C. (fallax) cerinomelas* Lieft., both from Nepal, the *m*-pair is definitely lacking, in the Nepalese *C. coromandelianum* (Fabr.) the X and the smallest bivalent are rather large and

equal in size (all KIAUTA, 1975), while *C. t. tenellum* (de Vill.) is the only one of our taxa possessing a clearly distinct *m*-bivalent (KIAUTA, 1971b). At variance with our observations on *C. coromandelianum*, RAY CHAUDHIRI & DAS GUPTA (1949), SRIVASTAVA & DAS (1953) and DAS (1956) have reported and figured very distinct *m*-chromosomes in various Indian populations of this species. In the three *Ceriagrion* taxa examined by earlier workers, viz. *C. cerinorubellum* (Br.), *C. fallax* Ris (both DASGUPTA, 1957) and *C. rubiae* Laidl. (ASANA & MAKINO, 1935), an *m*-pair is also present. It seems that on the geographic population level a certain amount of variation in the size of the *m*-element occurs at least in *C. coromandelianum* and in the *C. fallax* complex. In all other features the karyotypic morphology of the eight hitherto examined taxa appears similar, and, at present, we are unable to detect any tentative parallels between the structurally defined species groups (cf. ASAHINA, 1967) on one hand, and the available cytological evidence on the other, though Asahina's classification will certainly have to serve as a working hypothesis in future cytotaxonomic studies of the genus.

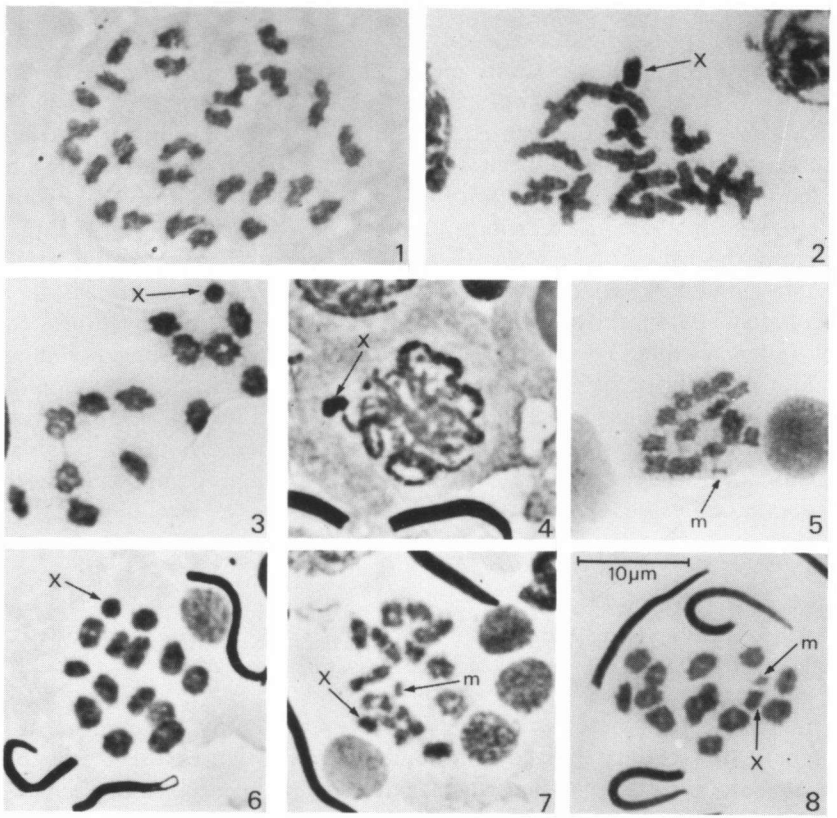
PSEUDAGRION ACACIAE FOERSTER, 1906
Figures 4-5

Material. — 1 ♂, Mkusi Game Reserve, Natal, Republic of South Africa, 13-XI-1976 — [11 complements photographed].

n = 14; *m*. Our material is too poor to even identify the chromosome number with certainty. Judged from some pachytene figures, the X probably has a medium size (Fig. 4), hence the small element appearing at metaphase-I is likely to represent an *m*-bivalent (Fig. 5). Based on a preliminary abstract (chromosome number only) by VAN BRINK & KIAUTA (1977), KIAUTA & BOON VON OCHSSÉE (1979) have regarded the *acaciae* complement as a "normal" *Pseudagrion* karyotype. It is possible that a different interpretation of the karyotype would result from the examination of fresh and more abundant material.

P. whellani Pinhey is the only other cytologically examined member of PINHEY's (1964) species-group B of the genus. The group is characterized by a considerable colour variation and melanistic tendency in many of its species, and by the structure of the 10th male abdominal segment. In *P. whellani* the original chromosome number is reduced by fusion of two autosomal pairs of the primary n = 14 set, resulting in an n = 13 complement, characterized by an extra large bivalent, and by a slight reduction of the TCL (cf. KIAUTA & BOON VON OCHSSÉE, 1979).

Save for *P. acaciae*, all n = 14 *Pseudagrion* taxa are referable to the widely spread species-group A of Pinhey (with Australian, Oriental and African



Figs. 1-8. Male germ cell chromosomes of Coenagrionidae (Feulgen squash, 1500X): (1-3) *Ceriagrion glabrum* (Burm.): (1) spermatogonial metaphase, (2) diakinesis, (3) early metaphase-I; — (4-5) *Pseudagrion acaciae* Foerst.: (4) pachytene, (5) metaphase-I; — (6) *P. kersteni* (Gerst.), metaphase-I; — (7-8) *P. salisburyense* Ris, metaphase-I.

distribution), while the members of group B, save for one species, have a strictly African continental range. If in more taxa of the latter group similar variation in chromosome numbers, TCL and recombination potential will be found, this could indicate that the species of group B are phylogenetically younger than those of group A, and that the recombination index of the group has not yet been stabilized at the usual *Pseudagrion* level. This idea would be tentatively supported also by the circumstance that in the allied Hawaiian *Megalagrion oahuense* (Blackburn), which certainly represents a derivate of the Oriental *Pseudagrion* stock, the karyotypic morphology ($n = 14$) already is of the usual *Pseudagrion* type, and the recombination potential is stabilized (cf. KIAUTA, 1969).

PSEUDAGRION KERSTENI (GERSTAECKER, 1869)
Figure 6

Material. — 1 ♂, Manzini, Swaziland, 20-XI-1976 — [28 complements photographed].

n = 14. At primary spermatocyte metaphase one bivalent is distinctly large and one is distinctly small, while the others are of decreasing magnitude. The medium-sized X is the smallest of the set at this stage; it is only slightly inferior in size to the smallest bivalent. Neither for its size nor for its behaviour could the latter be called an *m*.

Leaving aside *P. whellani*, the identity of the smallest element of which is uncertain (KIAUTA & BOON VON OCHSSÉE, 1979), *P. kersteni* is the only one of the nine cytologically examined members of the genus (for the others cf. DASGUPTA, 1957) in which an *m*-pair is lacking.

PSEUDAGRION SALISBURYENSE RIS, 1921
Figures 7-8

Material. — 1 ♂, Malkerns, Swaziland, 18-XI-1976 — [15 complements photographed].

n = 14; *m*. The metaphase-I karyotype is characterized by a very large bivalent and by a minute *m*. The sex chromosome is the second smallest of the set at this stage, though it is several times larger than the *m*-bivalent.

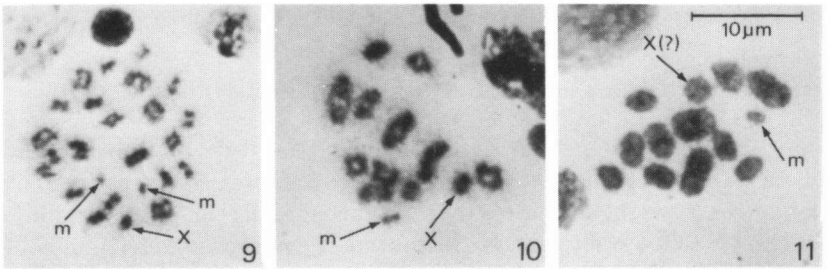
This is, after the New World *Argia* (cf. KIAUTA & KIAUTA, 1980), the only coenagrionide genus so far in which complements occur with chromosome numbers lower than the family type number (*P. whellani*). On the other hand, in the n = 14 complements, the interspecific variation in TCL is perhaps smaller than in most other coenagrionide genera.

Calopterygidae

PHAON IRIDIPENNIS (BURMEISTER, 1839)
Figures 9-11

Material. — 1 ♂, Mkusi Game Reserve, 13-XI-1976 — [76 complements photographed].

2n = 25, n = 13; *m*. At spermatogonial metaphase there are 3 pairs of distinctly large autosomes, 8 pairs of medium-sized elements, a pair of minute *m*-chromosomes, and a medium-sized X (Fig. 9). At primary spermatocyte metaphase the 3 large bivalents and the minute *m* are readily discerned. The other elements are of decreasing magnitude. The smallest two of them are usually almost identic in size; one of these is a bivalent, the other represents the unpaired sex chromosome (Fig. 10). At least in the two smallest of the medium-class bivalents chiasma terminalization occurs during late



Figs. 9-11. Male germ cell chromosomes of *Phaon iridipennis* (Burm.) (Feulgen squash, 1500X): (9) spermatogonial metaphase, (10-11) early and late metaphase-I respectively.

diakinesis, therefore the sex element is almost indistinguishable from the smallest bivalent from late diakinesis onwards (Fig. 11).

This is the first member of this endemic African genus the chromosome complement of which has become known. The more or less clearly cut size classes of the metaphase-I elements do occasionally occur in some other calopterygide genera (or species) as well. Neither in this feature nor in the chromosome number does *P. iridipennis* seem to show any peculiarities.

Libellulidae

BRADINOPYGA CORNUTA RIS, 1911
Figure 12

Material. — 1 ♂, Memorial Tablets, Kruger National Park, Republic of South Africa, 27-XI-1976 — [5 complements photographed].

n = 13; *m*. The spermatocyte metaphase-I elements are of gradually decreasing magnitude, save for a small X and a smaller *m*. The relative size of the latter two elements, as compared to those of the Indian *B. geminata* (Ramb.), is considerably larger (cf. DASGUPTA, 1957, fig. 31 C-E).

CROCOTHEMIS ERYTHRAEA (BRULLÉ, 1832)
Figures 13-14

Material. — 1 ♂, Tshokwane, Kruger National Park, Republic of South Africa, 27-XI-1976 — [11 complements photographed]; — 1 ♂, Hgw M 13, W of junction M 92/M 13, Swaziland, 11-XII-1976 — [15 complements photographed].

n = 13; *m*. While in the Kruger National Park specimen the metaphase-I elements are of more or less gradually decreasing magnitude, with the volume of X and *m* about half that of the second smallest bivalent (Fig. 13), in the Swaziland individual the absolute size of the two elements at this stage is

essentially smaller (Fig. 14). In both populations, however, the *m*-bivalent and the sex chromosome are similar in size at primary spermatocyte metaphase.

YADAV (1979) has summarized the evidence on the appreciable variation of cytotaxonomic characters in different geographic populations of *C. erythraea* and *C. servilia* (Drury), and has pointed out that the two taxa cannot be discerned on the basis of karyotypic morphology. Recently, on structural grounds, PINHEY (1979) has advanced the opinion that the two taxa are only subspecifically distinct. It is interesting, therefore, that in our case the karyotypic distinctions are considerable, even if compared to the whole of the *erythraea-servilia* complex. The only so far cytologically well-characterized geographic population seems to be that of the Japanese *servilia*, in which a secondary reduction of the chromosome number has taken place, involving the fusion of the original X, and resulting in a male haploid number of 12 and a neo-XY sex determination (cf. OMURA, 1955). If, upon the examination of more Japanese material, this condition would turn out to be general, a specific rank for the Japanese *servilia* could be considered.

CROCOTHEMIS SANGUINOLENTA (BRAUER, 1839)
Figures 15-16

Material. — 1 ♂, Usutu Forest Falls, Swaziland, 24-IV-1977 — [33 complements photographed].

2n = 25, n = 13; *m*. The metaphase-I morphology of this cytologically new species is similar to that of *C. erythraea*, except for the considerable size difference between the X and the *m*-bivalent. In most micrographs the latter is by far the smallest of the set and its volume is hardly half that of the univalent sex chromosome (Fig. 16). Another, even more striking peculiarity of *sanguinolenta* is its apparently exceptionally high recombination potential. While in both *erythraea* and *servilia* (with the sole exception of the Japanese form of the latter) the recombination index is stabilized at the usual libellulide level, at diakinesis of *sanguinolenta* often up to four bivalents appear as rings, having thus at least two chiasmata (Fig. 15). Our personal field experience with the African taxa concerned is too small to enable us to detect any significant ecological distinction between them, but the general geographic range of *erythraea* is, of course, immensely larger than that of *sanguinolenta*. In Southern Africa, according to PINHEY (1951) *sanguinolenta* is less common than *erythraea*, thus by no means scarce, and very often found in the same habitats, though probably preferring the warmer localities. These features definitely do not seem to be reflected in the very substantial differences in recombination potential between the two species.

ORTHETRUM ABBOTTI CALVERT, 1892
Figure 17

Material. — 1 ♂, Kwaluseni, Swaziland, 11-XI-1976 — [75 complements photographed].

n = 13; *m*. At metaphase-I one bivalent is distinctly larger than the other, which are of decreasing magnitude. The small X is more than twice as large as the *m*-bivalent.

ORTHETRUM CHRYSOSTIGMA (BURMEISTER, 1839)
Figures 18-20

Material. — 2 ♂, 1 ♀, Kwaluseni, Swaziland, 20/21-XI-1976 — [46 complements photographed].

2n ♂ = 25, 2n ♀ = 26, n = 13; *m*. Except for a minute *m*-pair, in spermatogonial metaphase the size gradation is moderate (Fig. 18). The spermatocyte-I elements are gradually decreasing, save for the small X and *m*, the latter of which is appreciably smaller than the former (Fig. 20).

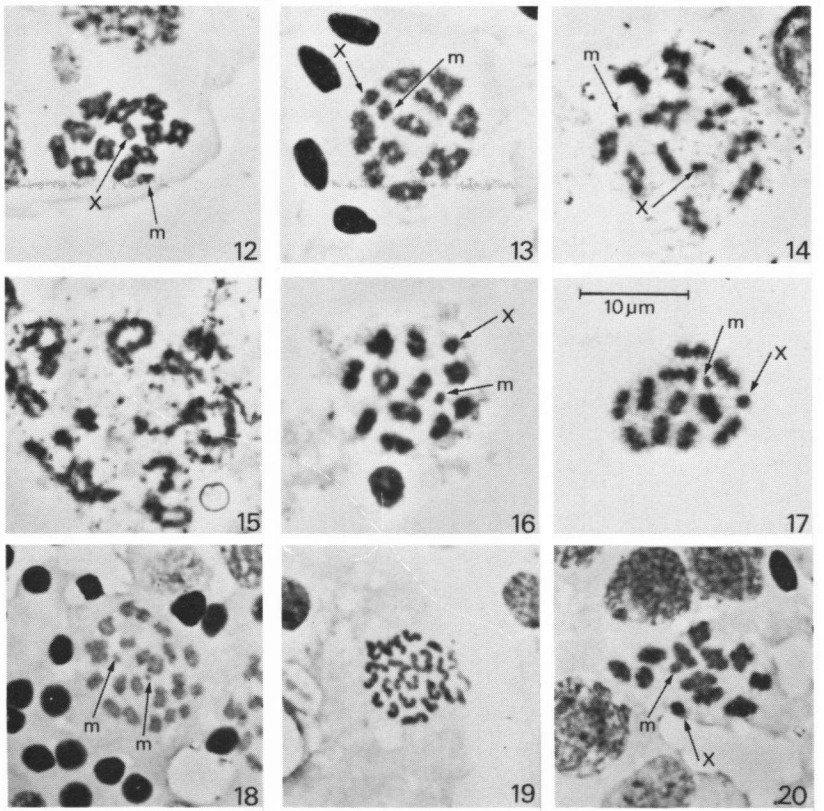
The karyotypic morphology of the Swaziland material is essentially in agreement with that recorded in a specimen from the Upper Volta (KIAUTA & BOON VON OCHSSÉE, 1979).

ORTHETRUM JULIA FALSUM LONGFIELD, 1955
Figures 21-28

Material. — 2 ♂, Usutu Forest Falls, Swaziland, 24-IV-1977 — [109 complements photographed].

n = 13; *m*. The morphology of the metaphase-I karyotype of the two individuals examined shows amazing differences. While no peculiarities occur in the specimen Coll. No. DS-3 (82 micrographs), which is characterized by bivalents gradually decreasing in size, a relatively large X and a somewhat smaller *m* (Figs. 21-23), in the specimen Coll. No. DS-4 (27 micrographs) 14 elements usually appear at diakinesis (Figs. 24-25) and metaphase-I (Figs. 26-27).

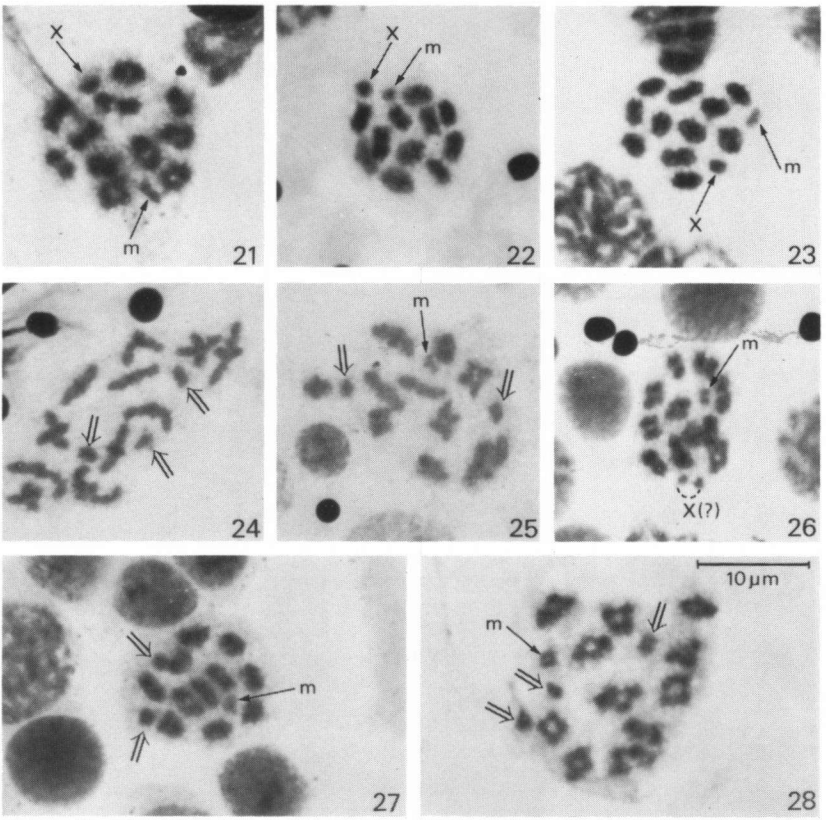
In most of the "n = 14" figures the identity of the *m*-bivalent seems certain and its morphology normal. This is also true for the appearance of the other bivalents as compared to the n = 13 set of the No. DS-3 specimen. As is apparent from Figure 26, all autosomes clearly show a bivalent structure, while the unpaired X is precociously divided. This interpretation could be also applied to the diakinesis and metaphase Figures 24, 25 and 27, where the bivalent structure of 12 elements, including the *m*, is clear, if it were not for the absolute size of the two remaining univalent chromosomes which are identic



Figs. 12-20. Male germ cell chromosomes (if not stated otherwise) of: (12) *Bradinopyga cornuta* Ris, early metaphase-I; — (13-14) *Crocothemis erythraea* (Brullé), early metaphase-I: (13) Kruger National Park, (14) Swaziland; — (15-16) *C. sanguinolenta* (Brauer), diakinesis and metaphase-I, respectively (note the high chiasma frequency in Fig. 15); — (17) *Orthetrum abbotti* Calv., metaphase-I; — (18-20) *O. chrysostigma* (Burm.) oogonial and primary spermatocyte metaphase, respectively. — (1500X; Figs. 14-16 lacto-acetic-orcein squash, all others Feulgen squash).

in size but which appear too big to represent the two halves of the original X. In spite of this difficulty, we are not in the position to offer any other tentative interpretation, and are inclined to consider our Figure 26 as the clue for the interpretation. It should be noted that the precocious behaviour of X sets in at a relatively early stage of diakinesis.

In some figures of late diakinesis and early metaphase-I of the specimen Coll. No. DS-4, there are four small elements, in addition to the 11 normal-size bivalents (cf. Fig. 28). Though, occasionally, some of these seem to have a bivalent structure, the others do not, therefore neither the nature nor the



Figs. 21-28. The chromosomal evidence on the possible hybrid nature of the Swaziland population of *Orthetrum julia falsum* Longf. (♂; lacto-acetic-orcein squash, 1500X). (21-23) specimen Coll. No. DS-3, metaphase-I of the normal n = 13 karyotype; — (24-28) specimen Coll. No. DS-4, showing various morphological and behavioural deviations in the karyotype, viz. the precocious division of X (Fig. 26; probably also Figs. 24-25, 27) and the occurrence of extra elements of unclear structure and origin (Fig. 28): (24-25) late diakinesis, (26-27) metaphase-I, (28) early metaphase-I. — (Further comments in text).

origin of the "n = 15" complement can be ascertained.

The species has not been previously examined cytologically. The cytogenetic features encountered in our material certainly indicate that *O. julia falsum* is genetically not a stabilized taxon. Similar precocious segregation behaviour of a varying number of elements (bivalents) has been recorded in marginal and/or hybrid populations of *Calopteryx meridionalis* Sel. (KIAUTA, 1971a) and *Argia fumipennis atra* Gloyd (KIAUTA & KIAUTA, 1980), therefore it is not unlikely that LONGFIELD (1955) is

correct in assuming the hybrid nature of *O. falsum* (cf. also PINHEY, 1970; PARR, 1980).

PALPOPLEURA JUCUNDA RAMBUR, 1842
Figure 29

Material. — 2 ♂, Usutu Forest Falls, Swaziland, 24-IV-1977 — [69 complements photographed].

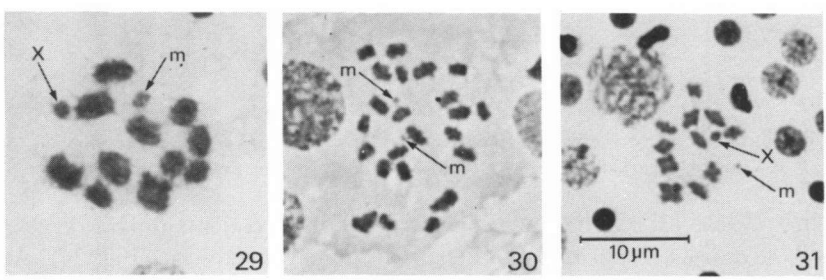
n = 13; *m*. The metaphase-I elements fall into three size-classes: 6 bivalents are large, 5 bivalents are medium-sized, and the X and the *m* are moderately small, but similar in size. Three of the large bivalents are particularly distinct in most figures. In this size gradation, our species, the chromosome complement of which is here recorded for the first time, essentially deviates from its congeners, *P. lucia portia* (Drury) (KIAUTA & BOON VON OCHSSEE, 1979) and *P. sexmaculata* (Fabr.) (KIAUTA, 1975).

As is now apparent, the *Palpopleura* species show considerable interspecific variation in karyotypic morphology, which is very characteristic also of the allied New World *Perithemis*, though, contrary to the situation in the latter, no low-n species have so far been found in *Palpopleura*.

PANTALA FLAVESCENS (FABRICIUS, 1798)
Figures 30-31

Material. — 1 ♂, Memorial Tablets, Kruger National Park, Republic of South Africa, 27-XI-1976 — [9 complements photographed]; — 2 ♂, Kwaluseni, Swaziland, 23/29-XI-1976 — [119 complements photographed].

2n = 25, n = 13; *m*. At spermatogonial and at primary spermatocyte metaphase (Figs. 30, 31 resp.) one pair (bivalent) is distinctly superior to the



Figs. 29-30. Male germ cell chromosomes (1500X) of: (29) *Palpopleura jucunda* Ramb. (lacto-acetic-orcein squash), metaphase-I; — (30-31) *Pantala flavescens* (Fabr.) (Feulgen squash), spermatogonial and spermatocyte-I metaphase respectively; both from a Kwaluseni specimen.

others in size, while the *m*-pair (bivalent) is extremely minute. The sex chromosome in spermatogonial metaphase is similar in size to the second smallest autosome pair, but it is appreciably smaller than this bivalent at metaphase-I, though very much bigger than the tiny *m* at this stage. Due to the minuteness and weak absorption of stain the *m* often can hardly be traced in the micrographs, particularly in those of the spermatocyte stages. These features are essentially identic in the two South African populations.

As suggested by KIAUTA (1975) and stressed by VAN BRINK & KIAUTA (1977), the relative magnitude of the *m* in *P. flavescens* is often peculiar on the geographic population level. A true geographic gradient, however, seems to be lacking. Thus, a minute to extremely minute *m*-bivalent occurs in Bolivia (CUMMING, 1964), West Bengal, Orissa (DASGUPTA, 1957) and Nepal (KIAUTA, 1975), while it appears significantly larger in material from Bombay (ASANA & MAKINO, 1935) and Brazil (FERREIRA et al., 1979). On the other hand, the occurrence of a distinctly large pair (bivalent) has been evidenced for all populations on which data are available.

TRITHEMIS ANNULATA (PALISOT DE BEAUVOIS, 1805)
Figures 32-33

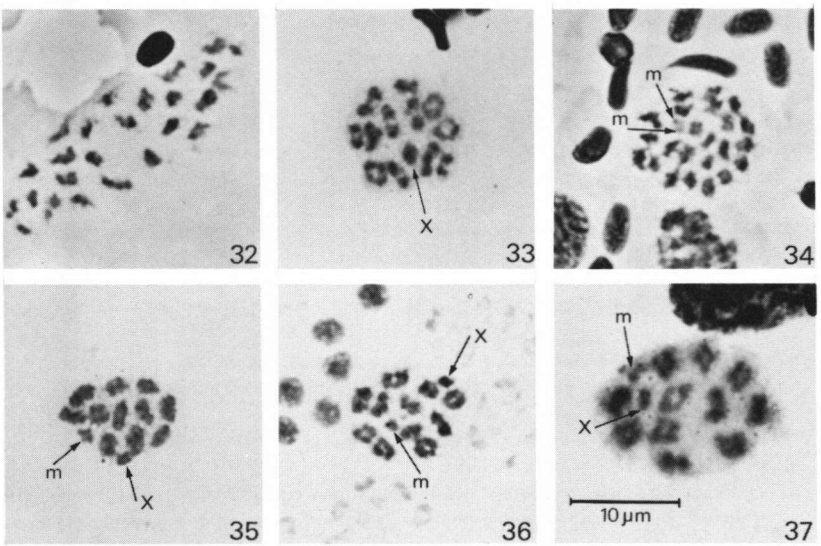
Material. — 2 ♂, Mkusi Game Reserve, Natal, Republic of South Africa, 13-XI-1976 [106 complements photographed].

2n = 25, n = 13. Contrary to the preliminary statement in the abstract by VAN BRINK & KIAUTA (1977), based on the same material, the smallest metaphase-I bivalent could not be called an *m*. All elements at this stage are gradually decreasing in size, including the unpaired sex chromosome. The latter is of medium magnitude, being similar in size to or slightly larger than the smallest bivalent (Fig. 33). Our spermatogonial figures are hardly analyzable (Fig. 32).

TRITHEMIS ARTERIOSA (BURMEISTER, 1839)
Figures 34-36

Material. — 3 ♂, Malkerns, Swaziland, 18-XI-1976 — [49 complements photographed]; — — 2 ♂, Kwaluseni, Swaziland, 21/30-XI-1976 — [73 complements photographed].

2n = 25, n = 13; *m*. The gradation in size of both univalents and bivalents is small, save for a small *m*-pair in spermatogonial metaphase (Fig. 34). At metaphase-I the X and *m* are of medium magnitude and of similar size (Figs. 35-36). In some figures there occurs an extremely minute additional element of unknown provenience and unclear structure (Fig. 36).



Figs. 32-37. Male germ cell chromosomes of (32-33) *Trithemis annulata* (P. de Beauv.), spermatogonial and spermatocyte-I metaphase respectively; — (34-36) *T. arteriosa* (Burm.): (34) spermatogonial metaphase, (35-36) metaphase-I, note the additional minute element (arrow) in Fig. 36; — (37) *T. dorsalis* (Ramb.), early metaphase-I. — (1500X, Fig. 37 lacto-acetic-orcein squash, all others Feulgen squash).

TRITHEMIS DORSALIS (RAMBUR, 1842)
Figure 37

Material. — 1 ♂, Usutu Forest Falls, Swaziland, 27-IV-1977 — [42 complements photographed].

n = 13; *m*. There is only a small gradation in size of the metaphase-I elements, save for the X and *m*, which are medium-sized and of similar magnitude.

The chromosome complement has not been previously recorded.

ACKNOWLEDGEMENTS

The help of Dr. M.A. LIEFTINCK (Rhenen, The Netherlands) and Dr. M.J. PARR (Salford, England), who have checked and/or identified the 1976 and 1977 specimens respectively, is gratefully acknowledged. Mrs. M.A.J.E. KIAUTA has taken care of the Feulgen processing and microphotography.

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