INTRODUCTION TO THE CYTOTAXONOMY OF THE ODONATE GENUS *ARGIA* RAMBUR (ZYGOPTERA: COENAGRIONIDAE)*

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In the hitherto studied taxa (12) of the genus the ♂ haploid numbers range from 13 to 19, viz.: n=13: *moesta* (Hag.), *nahuana* Calv., *translata* Hag.; n=14: *fumipennis atra* Gloyd, *f. fumipennis* (Burm.), *f. violacea* (Hag.), *funebris* (Hag.), *immunda* (Hag.), *sedula* (Hag.), *vivida* (Hag.); n=19: *apicalis* (Say), *tibialis* (Ramb.). An additional element occurs in some populations of *f. atra* and *f. violacea* (n=15), but only in the former is its bivalent structure more or less apparent. Save for *translata* and for the n=15 sets of *f. atra* and *f. violacea*, m-chromosomes are lacking. Aside from one case in *Pseudagrion*, this is the only coenagrionide genus in which spp. occur with n lower than the family type number (14); n=19 is the highest chromosome number yet recorded in a dragonfly. The low-n complements are of a secondary origin and are characterized by an increased chiasma frequency. The reduction of n is due to the obligatory fusion of 2 pairs of the primary karyotype. The n=15 complements are not obligatory and are due to fragmentation of one of the original pairs (bivalents). The elements of the n=19 spp. have the usual *Argia* size; the origin of the high-n complements is unknown, and their TCL is significantly higher than that of the n=14 sets. The variation of n does not appear significant on the subgeneric level. The evolutionary significance of the exceptionally high variation in the recombination potentials is discussed and it is concluded that the genus is in the midst of an intense evolutionary process, and is far from having reached its final adaptive level. In this feature *Argia* is unique among the higher taxa of the Order that so far have been studied cytologically.

INTRODUCTION

The New World genus *Argia* is one of the largest in Zygoptera and represents one of the characteristic features of the fauna of the two Americas. Taxonomically, it is among the most difficult and least understood groups in Odonata. While a good number of species, available in collections, still await description, it is certain that many more are to be found in South American habitats. Aside from North America north of Mexico, at least some adequate information is available solely on the fauna of Mexico and Central America (CALVERT, 1908; 35 spp.), Venezuela (RÁCENIS, 1966; 14 spp.) and Peru (RÁCENIS, 1959; 22 spp.), whereas evidence on most of the other regions is greatly incomplete or virtually lacking (cf. PAULSON, 1977). The only significant attempt at a classification and subdivision of the genus is that by KENNEDY (1919, cf. also 1920), based on the morphology of penile characters. A modern arrangement of the natural groups and alliances, if at all possible at the present state of our knowledge, is still lacking.

As follows from the above, the mechanisms governing the processes of speciation and (geographic) variation in the genus are but little understood. Aside from KENNEDY (1919) the only significant contributions in this field are those by BICK & BICK (1965) and JOHNSON (1972a), though both papers deal with the same single species.

In the past years we have gathered some evidence on the chromosome cytology of a number of species from Mexico, United States and Canada, which seems to throw some new light both on the biological properties of and on the evolutionary trends within the group. The sample of the 12 North American taxa recorded in the present paper is far from being representative for the genus, the centre of whose range evidently lies in the neotropical region. Nevertheless, the evidence brought to light is striking, and makes the group peculiar in more than one feature both in Zygoptera and in the Order as a whole.

Most of the material here evidenced has been collected in the southern United States in 1978, and credit for the encouragement goes entirely to our friend and colleague, Professor Dr. Minter J. Westfall, Jr. of Gainesville, Florida.

DESCRIPTIONS OF THE KARYOTYPES

ARGIA APICALIS (SAY, 1839)
Figures 1-7

Material. — United States, Florida: 4 ♂, Branford, Suwannee River, Suwannee Co., 7-VIII-1978; 1 ♂, Ichetucknee River, Columbia Co., 7-VIII-1978; — [106 complements photographed]. — Texas: 1 ♂, Brazos River, 6 mi W of Marlin, Falls Co., 22-VII-1978; 1 ♂,

Marlin (City Lake), Falls Co., 22-VII-1978; 3 ♂, Middle Bosque River nr. Waco, McLennan Co., 23-VII-1978; 1 ♂, Navasota River, Hwy 7, Robertson Co., 25-VII-1978; 2 ♂, Lake Waco, McLennan Co., 27-VII-1978; — [104 complements photographed].
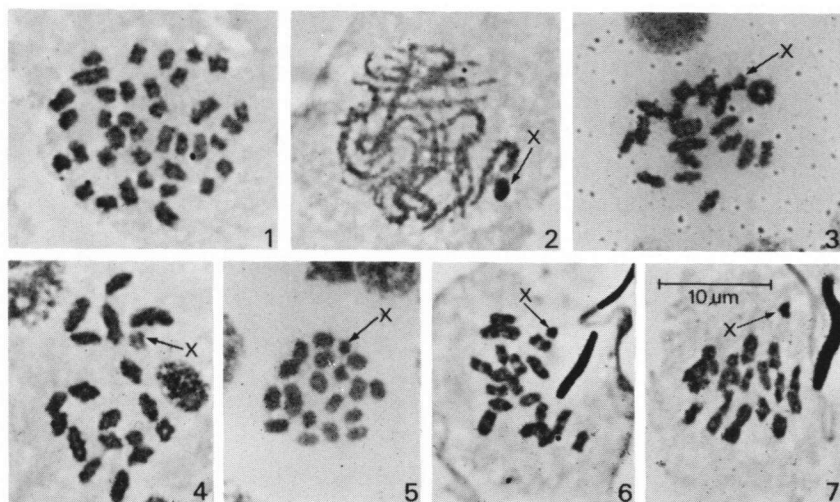
Figs. 1-7. *Argia apicalis* (Say), spermatogenetic cycle (Feulgen squash, 1500×): (1) spermatogonial metaphase (Navasota River, Texas); — (2) pachytene (Middle Bosque River, Texas); — (3) late diakinesis / early metaphase I, note the occurrence of two chiasmata in one of the larger bivalents (ring) (Branford, Florida); — (4) early metaphase I (Middle Bosque River, Texas); — (5) metaphase I (Lake Waco, Texas); — (6) metaphase II, polar view (Middle Bosque River, Texas); — (7) metaphase II / early anaphase II, note the segregating X (Middle Bosque River, Texas).

$2n = 37$, $n = 19$. — The spermatogonial metaphase elements are of gradually decreasing magnitude, save for the largest two pairs which are clearly distinct. There are no *m*-elements and the sex chromosome can not be distinguished at this stage (Fig. 1). The pachytene bouquet configuration is normal, including the occurrence of the positively heteropycnotic X (Fig. 2). At diakinesis one of the large bivalents often has two chiasmata (Figs. 3-4); the X is apparently the smallest of the set (Figs. 3-5) and can be particularly clearly distinguished at metaphase II (Fig. 6). The secondary anaphase is normal, the undivided sex element preceding the dividing autosomes (Fig. 7).

The absolute size (volume) of the chromosomes does not appear unusually small at any stage, hence the DNA content of the complement must be exceptionally high. Due to the exceptionally high chromosome number the recombination index is high, and is further increased by a slight increase of the chiasma frequency.

There is no evidence on any karyotypic variation on the geographic population level in our material.

<div align="center">

ARGIA FUMIPENNIS ATRA GLOYD, 1968

Figures 8-15

</div>

Material. — United States, Florida: 6 ♂, Ichetucknee River, Columbia Co., 2/7-VIII-1978; 4 ♂ (incl. 2 subadult), Hatchet Creek, Hwy 225, N of Gainesville, Alachua Co., 4-VIII-1978; — [190 complements photographed].

2n = 27, n = 14 (Hatchet Creek), 14, 15 (*m*) (Ichetucknee River). — The spermatogonial metaphase elements are nearly uniform in size and the *m* pair is lacking (Fig. 8). At diakinesis a single chiasma occurs per bivalent in the
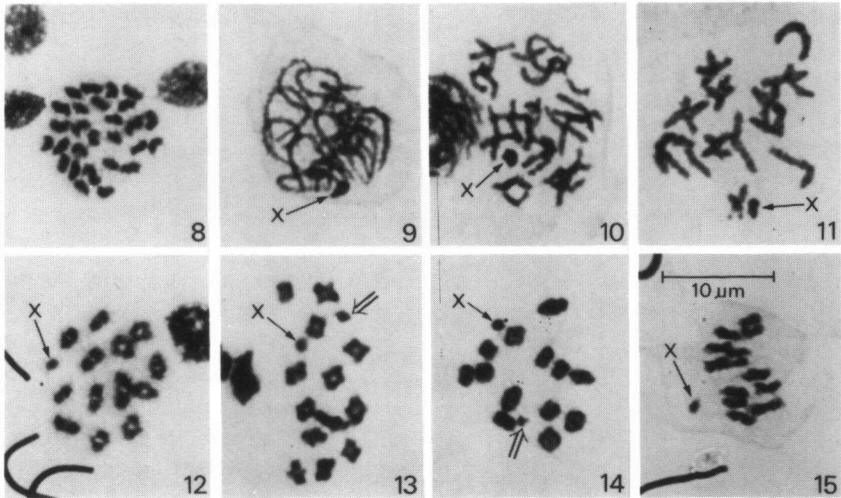
Figs. 8-15. *Argia fumipennis atra* Gloyd, spermatogenetic cycle (Feulgen squash, 1500×): (8) spermatogonial metaphase (Gainesville, Florida); — (9) pachytene (Ichetucknee River, Florida); — (10) early diakinesis (Ichetucknee River, Florida); — (11) early diakinesis (Gainesville, Florida); — (12) metaphase I, the usual n = 14 complement (Gainesville, Florida); — (13-14) metaphase I, note the additional small element, having apparently a bivalent structure (arrow) (Ichetucknee River, Florida); — (15) early anaphase II (Ichetucknee River, Florida).

Hatchet Creek specimens (Fig. 11), but the frequency might be slightly higher in the Ichetucknee River population (cf. Fig. 10). The two populations appear distinct also with respect to the metaphase I complement. Although 13 bivalents of gradually decreasing magnitude are usually present in the primary spermatocyte metaphase, in addition to the small X (Fig. 12), in some figures of the Ichetucknee material there are 15 elements at metaphase I (Figs.

13-14). The additional element is similar in size to X and, in some figures, seems to have a bivalent structure (Fig. 14).

ARGIA FUMIPENNIS FUMIPENNIS (BURMEISTER, 1839)
Figure 16

Material. — United States, Alabama: 1 ♂, Fish River nr. Loxley, Baldwin Co., 31-VII-1978; — [7 complements photographed].
KIAUTA & VAN BRINK, 1978: 16-17, fig. 1 (Blackwater River, Holt, Okaloosa — Santa Rosa Co., NW Florida).

n = 14. — The metaphase I elements are of varying size. The volume of the one considered to represent the sex element hardly amounts to one third of the smallest bivalent.

ARGIA FUMIPENNIS VIOLACEA (HAGEN, 1861)
Figures 17-20

Material. — Canada, Ontario: 1 ♂, Credit River, E of Georgetown, Hwy 7, 13-VIII-1979; 3 ♂, Medway River, London, 15/19-VIII-1979; 2 ♂, Moira River nr. Marmora, Hwy 7, 13-VIII-1979; 1 ♂, North Thames River, London, 16-VIII-1979; — [34 complements photographed]. — United States, Texas: 1 ♂, Little Creek, Dead End Rd 218, Sam Houston National Forest, San Jacinto Co., 24-VII-1978; — [29 complements photographed].
CRUDEN, 1968: 209 (Vilas Co., Wisconsin).

2n = 27, n = 14. — The spermatogonial (Fig. 17) and the spermatocyte I elements are gradually decreasing in magnitude, there are no *m* chromosomes, and the karyotypic morphology of the metaphase I complement appears similar throughout the range (cf. Figs. 18-19), except for a more or less regular appearance of an additional minute fragment in the Medway specimens (Fig. 20). Its structure is unclear and its provenience is unknown, since it is too small to cause any detectable reduction in size of the bivalent of which it may be a fragment.

ARGIA FUNEBRIS (HAGEN, 1861)

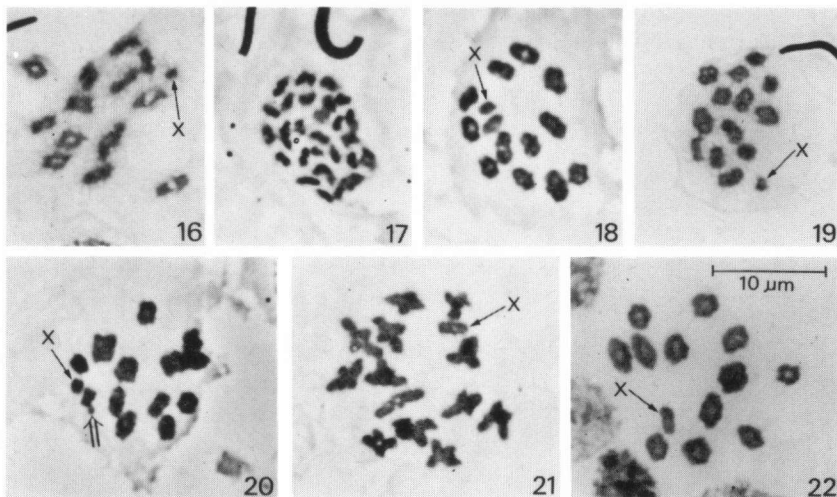KIAUTA, 1972a: 24-25, fig. 1 (San Cristobal de las Casas, Mexico).

2 n ♀ = 28, no *m*.

ARGIA IMMUNDA (HAGEN, 1861)
Figures 21-22

Material. — United States, Texas: 1 ♂, Lake Creek Reservoir, 17 mi NW of Marlin, McLennan Co., 28-VII-1978: — [34 complements photographed].

n = 14. — The metaphase I elements show but little variation in size, save

Figs. 16-22. Male germ cell chromosomes of *Argia fumipennis fumipennis* (Burm.) (Fig. 16), *A. fumipennis violacea* (Hag.) (Figs. 17-20), and *A. immunda* (Hag.) (Figs. 21-22) (Feulgen squash, 1500×): (16) early metaphase I (Loxley, Alabama); — (17) spermatogonial metaphase (Marmora, Ontario); — (18) metaphase I (London, Ontario); — (19) metaphase I (Sam Houston National Forest, Texas); — (20) metaphase I, note the additional minute, weakly stained element of unclear structure (arrow) (London, Ontario; the same locality as Fig. 18); — (21) late diakinesis (Marlin, Texas); — (22) metaphase I (Marlin, Texas).

for two smaller bivalents and the X, which is the smallest of the set at this stage (Fig. 22). The largest bivalent is also discernible; at diakinesis it despiralizes ahead of the other bivalents, in which the chiasma terminalization occurs nearly simultaneously (Fig. 21).

ARGIA MOESTA (HAGEN, 1861)
Figures 23-28

Material. — United States, Florida: 2 ♂, Branford, Suwannee River, Suwannee Co., 7-VIII-1978; — [65 complements photographed]. — Texas: 1 ♂, Middle Bosque River nr. Waco, McLennan Co., 23-VII-1978; 3 ♂, Big Creek, Rd 217, Sam Houston National Forest, San Jacinto Co., 24-VII-1978; 1 ♂, Robbins, Hwy 7, Leon Co., 25-VII-1978; 1 ♂, Lake Waco, McLennan Co., 27-VII-1978. — [66 complements photographed].

Additional material (preliminarily recorded by KIAUTA, 1978): 1 ♂, Thames River, London, Ontario, Canada, 11-VIII-1978; — [39 complements photographed].

$2n = 25$, $n = 13$. — The karyotype is characterized by the presence of an exceptionally large pair (bivalent). The other elements are graded in size, save for a relatively small X, recognizable at all stages. At diakinesis the huge bivalent often appears as a ring, probably possessing two chiasmata (Figs. 25-

26).

The karyotype morphology seems identic in the southern- and southeastern United States and in Canadian material. The pale form, *putrida* (Hag.), to which some of our material may be referable, can not be defined cytotaxonomically (cf. WILLIAMSON, 1912; BYERS, 1930; JOHNSON, 1973).

Due to the large size of one of the pairs, the TCL of *A. moesta* does not deviate significantly from that of the n=14 members of the genus. Since the chiasma frequency is apparently increased, the recombination index is also probably stabilized at a similar level as in most of the n=14 congeners.

ARGIA NAHUANA CALVERT, 1902
Figure 29

Material. — United States, Texas: 1 ♂, Marlin (Municipal Park), Falls Co., 28-VII-1978; — [33 complements photographed].

n = 13. — The metaphase I karyotype is similar to that of the preceding species. The large bivalent is significantly larger than the others, though it is
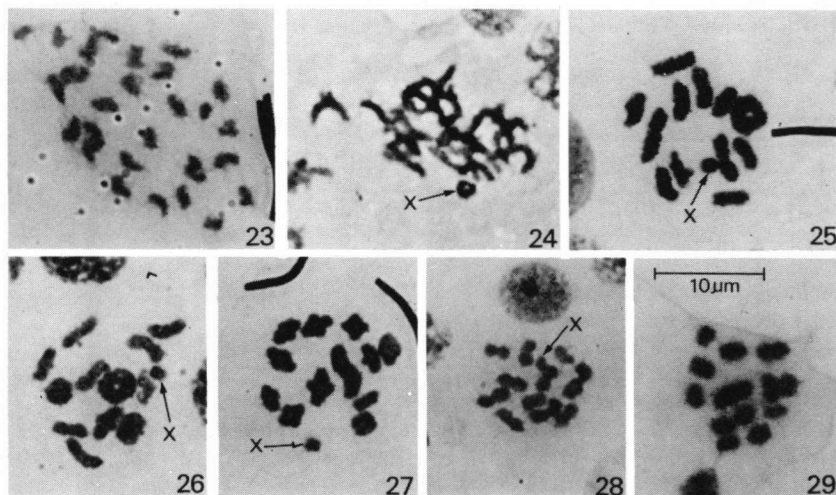
Figs. 23-29. Male germ cell chromosomes of *Argia moesta* (Hag.) (Figs. 23-28) and *A. nahuana* Calv. (Fig. 29) (Feulgen squash, 1500×): (23) spermatogonial metaphase (Branford, Florida); — (24) pachytene / early diakinesis (Middle Bosque River, Texas); — (25-26) early metaphase I, note the occurrence of two chiasmata in the largest bivalent (ring) (Branford, Florida); — (27) metaphase I, the two chiasmata of the largest bivalent are terminalized slightly ahead of the other bivalents (Sam Houston National Forest, Texas); — (28) metaphase II (Lake Waco, Texas); — (29) metaphase I (Marlin, Texas).

relatively smaller than in *moesta*. The smallest element at this stage is a bivalent, but could be hardly called an *m*. In some figures it appears considerably smaller than the other autosomes; in the others the size difference is less significant. In some figures the terminalization of its chiasma occurs somewhat later than that of the other autosomes. The medium-sized sex element is the second smallest of the set.

There is no evidence of any increase in chiasma frequency, hence, the recombination index of *nahuana* is lower than in any other *Argia* species so far examined, with the sole exception of *translata*.
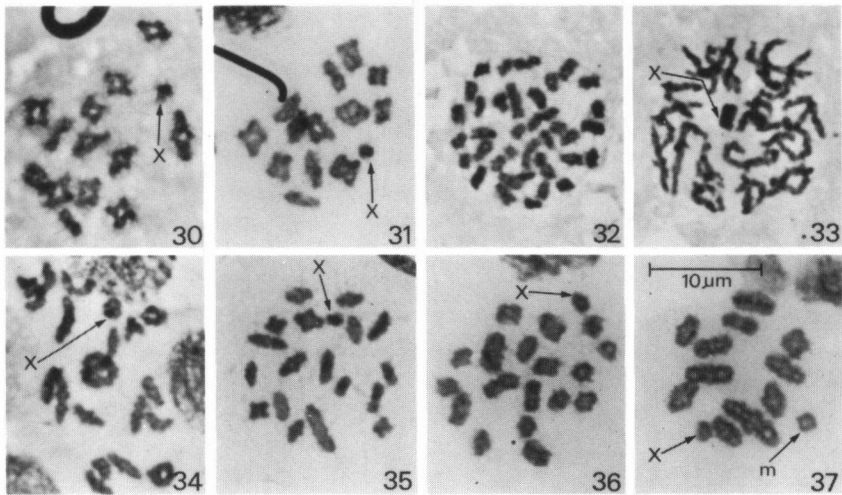
ARGIA SEDULA (HAGEN, 1861)
Figures 30-31

Material. — United States, Florida: 4 ♂, Sneads, Hwy 90 E, Gadsden Co., 1-VIII-1978; 2 ♂, Rocky Creek, Gainesville, Alachua Co., 5-VIII-1978; 2 ♂, Ichetucknee River, Columbia Co., 7-VIII-1978; — [33 complements photographed]. — Texas: 2 ♂, Lake Creek Reservoir, 17 mi NW of Marlin, McLennan Co., 28-VII-1978; — [67 complements photographed].
CUMMING, 1964: 62, 73 (Florida).

$2n = 27$, $n = 14$. — The spermatogonial metaphase elements are uniform in

Figs. 30-37. Male germ cell chromosomes of *Argia sedula* (Hag.) (Figs. 30-31), *A. tibialis* (Ramb.) (Figs. 32-36) and *A. translata* Hag. (Fig. 37) (Feulgen squash, 1500×): (30-31) early metaphase I (Ichetucknee River, Florida and Gainesville, Florida respectively); — (32) spermatogonial metaphase (Gainesville, Florida); — (33) early diakinesis (Gainesville, Florida); — (34) diakinesis (Sam Houston National Forest, Texas); — (35) early metaphase I (Sam Houston National Forest, Texas); — (36) metaphase I (Gainesville, Florida); — (37) metaphase I (Coro Bayou River, Texas).

size and shape, those of metaphase I are graded, without *m*, and the X is the smallest of the set.

ARGIA TIBIALIS (RAMBUR, 1842)
Figures 32-36

Material. — United States, Florida: 1 ♂, Little River, Tallahassee, Leon Co., 1-VIII-1978; 3 ♂, Blues Creek and Fox Pond, Rd 232, NW of Gainesville, 5-VIII-1978; — [43 complements photographed]. — Texas: 6 ♂, Big Creek, Sam Houston National Forest, San Jacinto Co., 24/25-VII-1978; — [50 complements photographed].

2n = 37, n = 19. — The spermatogonial metaphase elements are gradually decreasing in magnitude, but a large pair (bivalent) is discernible at this stage (Fig. 32) and at spermatocyte metaphase I and II. There are no *m*-chromosomes and the X is distinct from the pachytene (Fig. 33) onwards. At metaphase I (Figs. 35-36) the largest bivalent is relatively smaller than in *apicalis*. The X is the smallest of the set at this stage.

Since the absolute size of the elements is not inferior to that in the n = 14 *Argia* species, the TCL is high and, due to a considerable increase of chiasma frequency, the recombination index is even higher than in *apicalis*.

The karyotypic morphology is identic in all populations examined.

ARGIA TRANSLATA HAGEN, 1865
Figure 37

Material. — United States, Texas: 1 ♂, Coro Bayou River, Falls Co., 23-VII-1978; — [33 complements photographed].

n = 13 (*m*). — This is the only member of the genus possessing a true *m*-element. The complement is characterized by the presence of a large bivalent, while the other autosomal elements are of decreasing magnitude. At metaphase I the X is slightly smaller than *m*. Diakinetic figures are not available in our material, hence nothing can be said on the chiasma frequency.

ARGIA VIVIDA HAGEN, 1865

CRUDEN, 1968: 203, 209, fig. 11 (Alameda Co., California).

n = 14, no *m*. — From the published camera lucida drawing of early metaphase I, the autosome bivalents appear graded in size and the X is the smallest of the set.

GENERAL FEATURES OF THE CHROMOSOME CYTOLOGY OF *ARGIA*

The *Argia* chromosome cytology, though still known inadequately, is peculiar in a number of features, some of which are unique in the Order. The most noteworthy of these are: (1) the exceptionally high chromosome numbers in some taxa, (2) frequent occurrence of secondary low-n complements, (3) broad intrageneric range of chromosome numbers, (4) pronounced variation in chiasma frequency and, hence, in the recombination potentials, and (5) the amazing parallels that exist between the karyotypic morphology, on one hand, and some other properties of the involved taxa, such as autecology, pattern of geographic distribution, and structural morphology, on the other.

The nearly general absence of *m*-chromosomes in the genus resembles the situation in the Ischnurinae, but is unusual in the other coenagrionide groups of which representative samples have been examined (cf. KIAUTA, 1972c).

The occurrence of any numbers other than the family type numbers is also known, as far as the Coenagrionidae are concerned, (and save for one case in Pseudagrioninae), in the Ischnurinae only.

Unlike in many anisopterans, the original XX/XO sex determining mechanism remained unaffected in *Argia* secondary (low-n) complements.

In Table I a review is given of the main cytotaxonomic features of the examined taxa.

CHROMOSOME NUMBER AND TCL

The male haploid chromosome numbers in the genus range between 13 and 19, with less than half of the examined taxa having obligatorily the coenagrionide family type number of 14 (cf. Tab. I). The haploid number of 19 is by far the highest chromosome number ever reported in a dragonfly.

Aside from *Ischnura pumilio* (Charp.) (KIAUTA, 1979), *Leptagrion macrurum* (Burm.) (KIAUTA, 1972b) and some populations of *Enallagma cyathigerum* (Charp.) (CRUDEN, 1968, KIAUTA, 1969b), this is the first case in Coenagrionidae where the chromosome number exceeds the family type number. The n = 15 complements in *fumipennis atra* and *f. violacea* are apparently of secondary origin and are not always found (not even in one individual), though the occurrence of the n = 15 complements seems to be restricted to marginal populations. A similar situation has been found in *Calopteryx meridionalis* Sel. (KIAUTA, 1971). In *Enallagma cyathigerum* (Charp.) the high-n karyotypes are either restricted to some populations (cf. CRUDEN, 1968) or to some cells of some individuals in certain populations (KIAUTA, 1969b), while in *Hetaerina rosea* Sel. a normal-n and a high-n

geographic population were brought on record (cf. CUMMING, 1964; FERREIRA et al., 1979).

The n=19 complements are obligatory in all populations of *apicalis* and *tibialis*.

No coenagrionide species, save for *Argia*, and *Pseudagrion whellani* Pinhey (KIAUTA & BOON VON OCHSSÉE, 1979), have ever been reported with chromosome numbers lower than the family type number. This phenomenon is extremely rare in Zygoptera, and was recorded so far only in a *Mecistogaster* sp. (Pseudostigmatidae; CUMMING, 1964), *Lestes forcipatus* Ramb. (Lestidae; CRUDEN, 1968) and in *Hypolestes clara* (Calv.) (Pseudolestidae; CUMMING, 1964). The low-n numbers (n=13) of *moesta*, *nahuana* and *translata* are found in all specimens examined. As is apparent from the presence of an exceptionally large pair (bivalent) in the karyotypes of these species, their complements originate in a secondary fusion of two autosomal pairs of the primary coenagrionide karyotype.

Table I

Main cytotaxonomic features of *Argia* taxa examined

Taxa	n	m	Other autosomes	Increase/decrease of the "usual" family TCL	Male autosomal recombination index
apicalis	19	—		increase	>36
fumipennis atra	14, 15	+ (n=15)	extra small bivalent in n=15	increase in n=15	>26, 27
f. fumipennis	14	—			26
f. violacea	14, 15	+ (n=15)	minute fragment of unclear structure and unknown origin in n=15	increase in n=15 not detectable	26, 27 (?)
funebris	14	—			27
immunda	14	—			27
moesta	13	—	I pair extra large	no decrease	>24
nahuana	13	—	I pair extra large	no decrease	24
sedula	14	—			27
tibialis	19	—		increase	>36
translata	13	+	I pair extra large	no decrease	24
vivida	14	—			26

An *m*-pair occurs only in *translata*. The additional *m*-element (bivalent?) in the n=15 sets of *violacea* is certainly a minute fragment of one of the original pairs of the n=14 complement, and this is most likely also the origin of the *m* of the n=15 sets of *atra*, though in this case its size is larger and its bivalent structure at metaphase I is often clear.

Due to the general lack of the *m*-chromosomes, the TCL in *Argia* is mostly above the coenagrionide average. The increase of the chromosome number caused its further increase as compared to what is considered the usual

coenagrionide TCL of the n=14 complements. In the secondary, n=13, karyotypes the TCL remained basically unchanged, though it is higher in *moesta* and lowest in *translata*.

Summarizing the above, the chromosome number in *Argia* is far from being stabilized at the family type number level, and the DNA content is probably higher than that of other Coenagrionidae.

RECOMBINATION INDEX

With a single chiasma per bivalent, the autosomal recombination index in the overwhelming majority of male dragonflies is stabilized at the 2n-1 level, i.e. at the 26 mark in Coenagrionidae. The relatively small variation in recombination indices is one of the principal features of the odonate genetic system.

This, however, is not the case in *Argia*. Due to the increased chromosome numbers, partly coupled with an increased chiasma frequency, the recombination indices in some taxa greatly exceed any values so far known in the Order, and the variation is considerable (cf. Tab. I).

The lowest values (24), are found in *nahuana* and *translata*, followed closely by *moesta* (close to 25). The coenagrionide index of 26 is peculiar only to five out of 12 taxa, though it is but little exceeded by *fumipennis violacea* and slightly more so by *f. atra*. The list is topped by *apicalis* (slightly above 36) and *tibialis*. In the latter species the recombination index may approach the value of 40.

CYTOLOGICAL FEATURES IN THE LIGHT OF STRUCTURAL CHARACTERS

In his unpublished PhD thesis, KENNEDY (1919), mostly on the basis of penile characters, classified the genus into six subgenera, and subdivided these further into 14 groups of species. Members of his subgenera, *Argia*, *Chalcargia* and *Heliargia*, referable to his species groups V, VII, IX, X and XIV, are represented in our material and are shown in Table II along with their chromosome numbers.

As stated earlier (KIAUTA, 1969b), only the primary karyotypes, i.e. those (obligatory or non-obligatory) complements in which the chromosomes cannot be considered as direct products of one or more fusions of the elements of an original set, give information on the phyletic affiliations of the taxa involved, therefore they only should be considered in phylogenetic speculations. Fragmentations are about the only way in which the recombination index in Odonata is raised, which is in good agreement with the circumstance that they occur, as a rule, only in some specialized forms.

Table II

Kennedy's subgeneric and species-group classification of the cytologically
examined *Argia* taxa

Group	HELIARGIA	n ♂	Group	ARGIA	n ♂	Group	CHALCARGIA	n ♂
V	*funebris*	14	VII	*fumipennis*	14 (15)	XIV	*sedula*	14
V	*immunda*	14	VII	*nahuana*	13	XIV	*translata*	13
V	*vivida*	14	IX	*moesta*	13			
			X	*apicalis*	19			
			X	*tibialis*	19			

This would mean that structurally specialized dragonflies are capable of retaining their genetic flexibility by increasing their recombination index. As to the secondary complements, the tendency to secondary fusion may be characteristic, to a certain extent, of some groups; however, its results (decreased number of chromosomes and/or modified mode of sex determination) do not bear any phylogenetic implications (cf. also KIAUTA, 1969a). Since fusions are often coupled with an increase of chiasma frequency, they usually do not cause a significant decrease of the recombination potential.

In the case of *Argia* only the haploid numbers of 14, 15 and 19 are considered "primary" in the above sense. The $n = 13$ complements are secondarily derived from the original $n = 14$ set, hence their TCL is not significantly different. It is not clear whether or not the $n = 15$ complement of *atra* originates in a direct fragmentation of an element (pair, bivalent) of the primary set. It is likely that it does, and this is certainly the case in *violacea*. The former species, and even more those with the $n = 19$ sets, possess a significantly larger TCL than the $n = 14$ taxa.

Since the coenagrionide family type number is 14, the occurrence of $n = 14$ sets would be of little interest on lower taxonomic levels, if it were not for the fact that there are relatively few members of the genus *Argia* possessing this complement. It is interesting that, save for one, all are pertaining to *Heliargia*, giving the impression that this subgenus is the only one in our material that is uniformly genetically stabilized at the coenagrionide "type" level.

Similar uniformity, though on greatly elevated level, is apparent in the group X of *Argia* s.str. (*apicalis, tibialis*). In Professor Westfall's manuscript "Manual", in the keys to males, females and larvae, the two are also separated in the same couplet. The enormous increase of the recombination index, however, cannot be conditioned by structural affinities only; the general biological properties of the two species, therefore, are examined elsewhere in this paper (cf. below).

Although the similarity in the chromosome numbers of the primary

karyotypes, on the lower taxonomic levels, may reflect some structural affinities between the taxa concerned, often it may not. The chromosome number in dragonflies is responsible for most of the variation of the recombination index. The latter, in its turn, represents one of the most important features of the genetic system of a species, conditioning its ecological and evolutionary patterns.

RECOMBINATION INDEX AND GENERAL BIOLOGICAL FEATURES OF THE EXAMINED TAXA

The recombination index is defined as the sum of the number of bivalents and the average number of chiasmata per nucleus. A high recombination index promotes flexibility, i.e. the ability of a genotype to vary and adapt to changing conditions. A low recombination index, on the other hand, promotes fitness, i.e. the survival value and the reproductive capability of a genotype. In stabilized conditions a balance is achieved between genetic variability and biological efficiency and stability. Under conditions of ecological stress and evolutionary pressure, however, the balance may be shifted in favour of one or the other of these aspects. In other words, high recombination is often associated with wider ecological diversity, and a lower recombination potential with less diversity.

While recombination can be readily ascertained cytologically, this is not the case with genetic position effects, occurring inevitably as a consequence of fragmentations and fusions. These too are of fundamental importance in the process of speciation and ecological adaptation. Position effects certainly play an important role even in those cases where fragmentations and fusions did not cause any significant change of the original recombination potential. The character of such effects, however, is neither predictable nor definable in terms other than those of selection.

THE n = 13 SPECIES

The recombination potential in *moesta, nahuana* and *translata* is significantly lower than in the n = 14 taxa, stabilized at the usual coenagrionide level, though in *moesta* the index is slightly higher than in the other two. It follows, from the above, that the aspect of survival and reproductive capability, is emphasized in these species, as compared to the other genotypes in the population. This makes them fit to settle down over a wide geographic range, but restricts their ability of adaptation to a substantial ecological diversity of habitats.

At least as far as the geographic range is concerned, this does not hold entirely true in the case of *nahuana*, but it is in perfect agreement with the

Fig. 38. Some of the cytologically examined *Argia* taxa. T o p, left: *A. apicalis* (Say), ♂; Brazos River, Falls Co., Texas; Sept. 18, 1975; — right: *A. fumipennis fumipennis* (Burm.), ♂; Juniper Creek, Rt 20; Calhoun Co., Florida; Aug. 6, 1977; — M i d d l e, left: *A. moesta* (Hag.), ovipositing; Lake Creek Reservoir, 17 mi NW of Marlin, McLennan Co., Texas; Nov. 3, 1971; — right: *A. sedula* (Hag.), ♂; Marlin (City Park), Falls Co., Texas; Sept. 3, 1979; — B o t t o m, left: *A. tibialis* (Ramb.), ovipositing; Big Creek, Sam Houston National Forest, San Jacinto Co., Texas; May 25, 1977; — right: *A. translata* Hag., ovipositing; Cow House Creek, Coryell Co., Texas; Aug. 31, 1979. — (All photographs by Curtis E. WILLIAMS, Marlin, Texas, save for *A. fumipennis*, by Dr. Rainer RUDOLPH, Münster, German Federal Republic).

situation in *moesta* and *translata*, both of which have an appreciably wide geographic range. The latter species has the widest distribution (from Maine to Brazil) of all *Argia* taxa.

THE n = 19 SPECIES

The very high recombination potential in *tibialis* and *apicalis* enables them to meet successfully an appreciable range of ecological conditions. According to a personal communication from Dr. Clifford Johnson, Gainesville, Florida (Nov. 25, 1978), the two occur in a wider range of habitats, if the whole geographic range is considered, than any other North American *Argia* species.

Geographic dispersal, by favouring outbreeding, enhances the genetic variability and flexibility of a species. If dispersal is relatively limited, the compensation provided by a higher recombination potential is likely to achieve the same effect, as recently demonstrated in Trichoptera (KIAUTA & KIAUTA, 1979b).

It could be argued that the pronounced geographic variation in *apicalis* (cf. JOHNSON, 1972a) is also caused by the high recombination.

Whether or not the high recombination potential also promotes the survival ability in certain polluted environments, as vaguely noted by Mrs Leonora K. Gloyd, Ann Arbor, Michigan (pers. comm., Nov. 22, 1978), for a population of *tibialis*, remains a subject for a future systematic examination.

CYTOTAXONOMY OF THE *FUMIPENNIS* COMPLEX

GLOYD (1968) has suggested, on morphological grounds, that *A. fumipennis* and *A. violacea* should be understood as infraspecific forms of one and the same species. In addition, she described a third subspecies, *atra*, from central and northern Florida. The three taxa are only distinct in the intensity of wing coloration, but do show well defined geographic patterns, though transitional forms occur near the meeting of the ranges, and there is no significant distinction in their ecological requirements. We are not acquainted with the subspecies *pallens* Calv., recorded from South Carolina and Alabama to Arizona, Mexico and Guatemala (cf. CALVERT, 1908; MUTTKOWSKI, 1910; WALKER, 1953).

On the basis of morphological and geographical features it can be tentatively assumed that *violacea* is phylogenetically the oldest and *atra* the youngest of the three cytologically examined taxa. The evidence derived from the chromosome cytology is in agreement with this assumption and largely supports it.

The cytology of the *fumipennis* complex is characterized by the following

three principal features: (1) the apparent stability of the nominate form karyotype, stabilized at the usual coenagrionide level with regards to both the complement morphology and TCL, and the recombination potential; (2) a small, but not unusual karyotypic variation close to the northernmost range limit in *violacea*, evidenced by the occurrence of an extra, minute element, certainly a fragment, in some cells of the Ontario individuals; and (3) by the considerable karyotypic variation and instability in the Ichetucknee River population of *atra*, close to its contact zone with the nominate form, caused by the increase of TCL and recombination index due to the increase in chromosome numbers and chiasma frequency.

The occurrence of karyotypic variation in some, often marginal populations is a rather wide-spread phenomenon in dragonflies, certainly more so than would seem apparent from the available record, as only relatively few taxa have been examined systematically from more than a single population. Since in most, though not in all cases the variation occurs among the cells of the same individual, this indicates that the "search" for a new adaptive level of the recombination potential is an "experimental" evolutionary process and not a sudden event. If this were not so, only individuals with successful karyotypic rearrangements of this kind would survive for record and no transitional stages would ever be found in nature.

The form *violacea* has by far the widest distribution, and its appearance (hyaline wings) is of the usual *Argia* type. Cytologically it appears uniform and well stabilized throughout the range, save at the northernmost edge of its distribution. All odonate species, whether zygopterans or anisopterans, in which a similar instability (whether or not obligatorily) occurs in the karyotypes of different geographic populations, are characterized by their wide or exceptionally wide geographic range, coupled with the lack of any significant structural variation within the entire area of the taxon involved. The centre of origin and dispersal of *violacea* probably lies somewhere in the northern or central parts of the United States.

In the course of its southward penetration *violacea* developed several infraspecific forms. Leaving aside the cytologically unknown *pallens*, the smoky-winged *fumipennis* has a certain overlap in distribution with *violacea* but, unfortunately, no transitional populations were examined cytologically. In northwestern Florida it shows an absolutely stabilized karyotype. The geological age of *fumipennis*, is, thus, younger than that of *violacea* in the central parts of its range, but it is older than the northern populations of the latter; a circumstance easily understood in terms of the quarternary history and paleogeography of the Northamerican Continent.

The dark *atra* of central and northern Florida has the smallest range of the three and seems to have originated in the North, though we are unable to

explain the occurrence of an allopatric population (in the midst of the *fumipennis* range) in the northwestern part of the State. Morphologically, *atra* is clearly related to *fumipennis* and intermediates are known from northeasternmost Florida. Its geological age is similar to that of the northern populations of *violacea*. The Suwannee River represents about the borderline between *atra* and *fumipennis* and, while no karyological peculiarities were noticed in the *atra* population east of the river, in the vicinity of the borderline the karyotypes are greatly unstabilized and the recombination index is increased, enhancing the ecological potential of the genotype. A very similar situation has been recorded in the case of a population of *Calopteryx meridionalis* in northern Spain (KIAUTA, 1971).

The *Argia-fumipennis*-complex of taxa tentatively radiates from the North, its principal expansion being in the southward direction. The original *violacea* n = 14 karyotype tends to alteration of the original adaptive level in the peripheral areas of the range (*atra*, northern *violacea*), where the altering ecological conditions are apparently necessitating the modification of the recombination potential. The increase in the intensity of coloration (wing pigmentation) in the southward direction is not uncommon in dragonflies in general.

No systematic study has ever been carried out on material from the intergradation zones of the three taxa. Nevertheless, from the little evidence available, coupled with the morphology of the territory, the zones of intergradation of both *violacea-fumipennis* and *fumipennis-atra* seem to be zones of primary intergradation in most cases, and the populations involved appear to be in continuous contact, certainly so in the case of *violacea-fumipennis*, where the gradients of phenotypic characters (wing coloration) develop very gradually. Judging from the map published by GLOYD (1968), the *fumipennis-atra* intergradation zone, along the Suwannee River, could represent a true hybrid zone of introgression (secondary intergradation), if it were not for a low degree of individual variation, unusual in the hybrid belts between populations which have become differentiated during the preceding period of isolation.

The above way of reasoning poses, among others, two interesting problems, viz. (1) the ancestry of the *fumipennis* complex, and (2) the degree of infraspeciation reached by various geographic populations.

The direct ancestor of *A. fumipennis* was most certainly a species with 14 elements in the haploid set. Out of the five cytologically examined members of Kennedy's subgenus *Argia* s.str., however, *fumipennis* is the only species with this chromosome number (cf. Tab. II), though this is also the original number of *nahuana* and *moesta*, i.e. groups VII and IX respectively. At the present state of our knowledge of the *Argia* taxonomy and cytotaxonomy, nothing can be said on this problem.

WALKER (1913) has expressed the opinion, based on observations of *A. moesta*, that "the mutual adaptation [of the secondary copulatory organs] in the two sexes [...] is so precise that it seems improbable that copulation could take place between different species of *Argia*, even though very closely related". As is apparent from the occurrence of transitional forms, *violacea-fumipennis* and *fumipennis-atra*, (cf. GLOYD, 1968), interbreeding between these may occur and, considering the holokinetic nature of the odonate kinetochore, it is technically easily achieved (cf. KIAUTA, 1967). Though geographically more or less isolated, the three infraspecific forms did not achieve the grade of speciation and specific adaptation of the sexes that would, in the sense of Walker, technically prevent a successful interbreeding. For cytogenetical reasons the interbreeding on the intrageneric level is relatively common in dragonflies (for reviews cf. KIAUTA, 1967; ASAHINA, 1974).

THE EVOLUTIONARY CHARACTERIZATION OF *ARGIA* AS REVEALED FROM ITS CYTOGENETIC FEATURES

Six decades have elapsed since the appearance of KENNEDY's (1919) PhD thesis, whose section on *Argia* still remains the only work on the genus as a whole. What is more, our cytogenetic observations are to a great extent in agreement with Kennedy's view, arrived at by the methods of comparative anatomy and morphology. The small sample of cytologically examined taxa could not be considered representative, if it were not for the unique picture revealed by it and which has not been so far encountered in any other odonate group, viz.:

(1) The Coenagrionidae is the only zygopteran family with the number exceeding the type number of the Order; in *Argia* even the coenagrionide family type number of 14 is surpassed. The exceptionally high chromosome numbers and TCL values indicate the young phylogenetic age of the genus. Phylogenetically, *Argia* should definitely be counted among the most recent and advanced groups in Zygoptera and in the Order in general.

(2) The extraordinary amount of variation in recombination potentials suggests that *Argia*, as a genus, is today in the midst of an intense evolutionary process, and it is far from having reached its final adaptive level, hence, as a whole, the genus is not a "specialized" group in the evolutionary sense.

(3) The average recombination index value, considerably above the family mean, associates *Argia* with ecological diversity, reflected probably in the rheophilous character of the habitats of its members. The sample of taxa examined is too small to reveal with any certainty any tentative affinities

between the subgenera and species groups.

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