Genetica (1970) **41**: 21–32

A STUDY ON SEX-DETERMINATION AND KARYOTYPIC EVOLUTION IN *TETRANYCHIDAE*

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(*Received Oct. 13, 1969*)

The chromosome complements of 45 species of spider mites (*Tetranychidae*) were studied, making the total number of species now examined in this family 57, approximately 10% of all species known. The chromosome numbers range from $n = 2$ to $n = 7$. The modal number of the family is 3 (found in 44% of the species). It is argued that the ancestral number is $n = 2$ (21% of the species).

In the more primitive subfamily of the *Bryobiinae* both thelytokous and arrhenotokous species occur, whereas the subfamily of the *Tetranychinae* exclusively exhibits arrhenotoky. The karyotype evolution is discussed in connection with arrhenotoky. It is stated that karyotype information is a useful tool for the spider mite taxonomist.

Introduction

All species of spider mites (*Tetranychidae* DONNADIEU) feed on higher plants (Spermatophyta). They form colonies on foliage and some species are serious pests in cultivated crops. There are two subfamilies: *Bryobiinae* BERLESE and *Tetranychinae* BERLESE. Of these two, the former is considered more primitive than the latter (PRITCHARD & BAKER, 1955).

For a long time the *Tetranychidae* attracted the attention mainly of taxonomists and the applied entomologists. But the outstanding ability of spider mites to develop insecticide resistance also evoked interest into their formal genetics. The progress in this field was recently recorded by BALLANTYNE (1969).

As for karyology, a start had been made before with a study of chromosome numbers and sex determination in 13 spider mite species (HELLE & BOLLAND, 1967). This study made clear that arrhenotoky

and thelytoky are the modes of reproduction in the *Tetranychidae*, which was demonstrated by cytological means as well as by rearing experiments. The number of chromosomes in the species investigated was found to be low, ranging from $n = 2$ to $n = 7$. As for the length of the chromosomes of all 13 species values between 1 and 2 μ were found. Constrictions, if present, could not be seen and it could not be decided wether the chromosomes are holokinetic or monocentric. However, because of the presence of V-shaped chromosomes during anaphase it was believed that a localised centromere is present at least in some species.

A somewhat exceptional number of chromosomes ($n = 7$) was found in the arrhenotokous species *Neotetranychus rubi* TRÄGÅRDH. This species is taxonomically related to species having $n = 3$ and $n = 4$. It was therefore suggested that *N. rubi* had originated as a result of allopolyploidy (HELLE & BOLLAND, 1967).

During the last two years the chromosome numbers of more than 40 other spider mite species were determined. The results are given and discussed in the present paper.

Methods and Material

Karyotype determinations were performed on eggs containing young undifferentiated embryonic tissue, using the orcein-squash technique.

For this technique, an egg is placed on a microscope slide and a droplet of 1% sodium citrate is added. Then a cover slip is placed carefully on the object. After this treatment with sodium citrate, which takes about one minute, a droplet of 1% aceto-orcein stain is brought under the cover slip by draining off the sodium citrate with a piece of filtered paper. After a 5 to 15 minutes staining period of the

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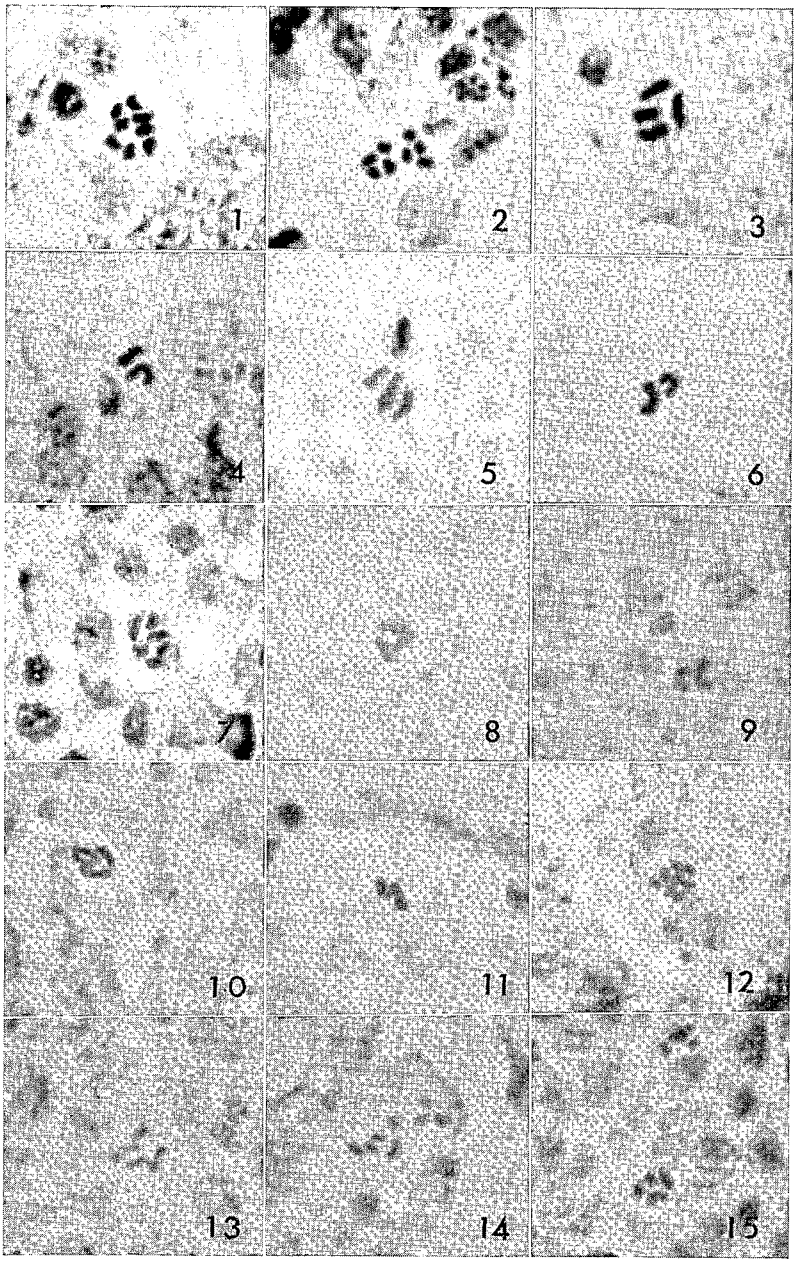
Plate I. Photomicrographs of mitotic stages in egg squashes of different spider mite species. Magnification 1900 ×.

1. *B. rubrioculus*, $2n = 8$. – 2. *B. praetiosa*, $2n = 8$. – 3. *P. harti*, $2n = 4$. – 4. *P. harti*, $n = 2$. – 5. *E. grewiae*, $2n = 4$. – 6. *E. grandidieri*, $n = 2$. – 7. *E. orientalis*, $2n = 6$. – 8. *E. orientalis*, $n = 3$. – 9. *O. sylvestris*, $n = 2$. – 10. *O. randriamasii*, $n = 2$. – 12. *O. bessardi*, $2n = 8$. – 13. *O. bessardi*, $n = 4$. – 14. *O. monsarrati*, $2n = 8$. – 15. *O. monsarrati*, $n = 4$.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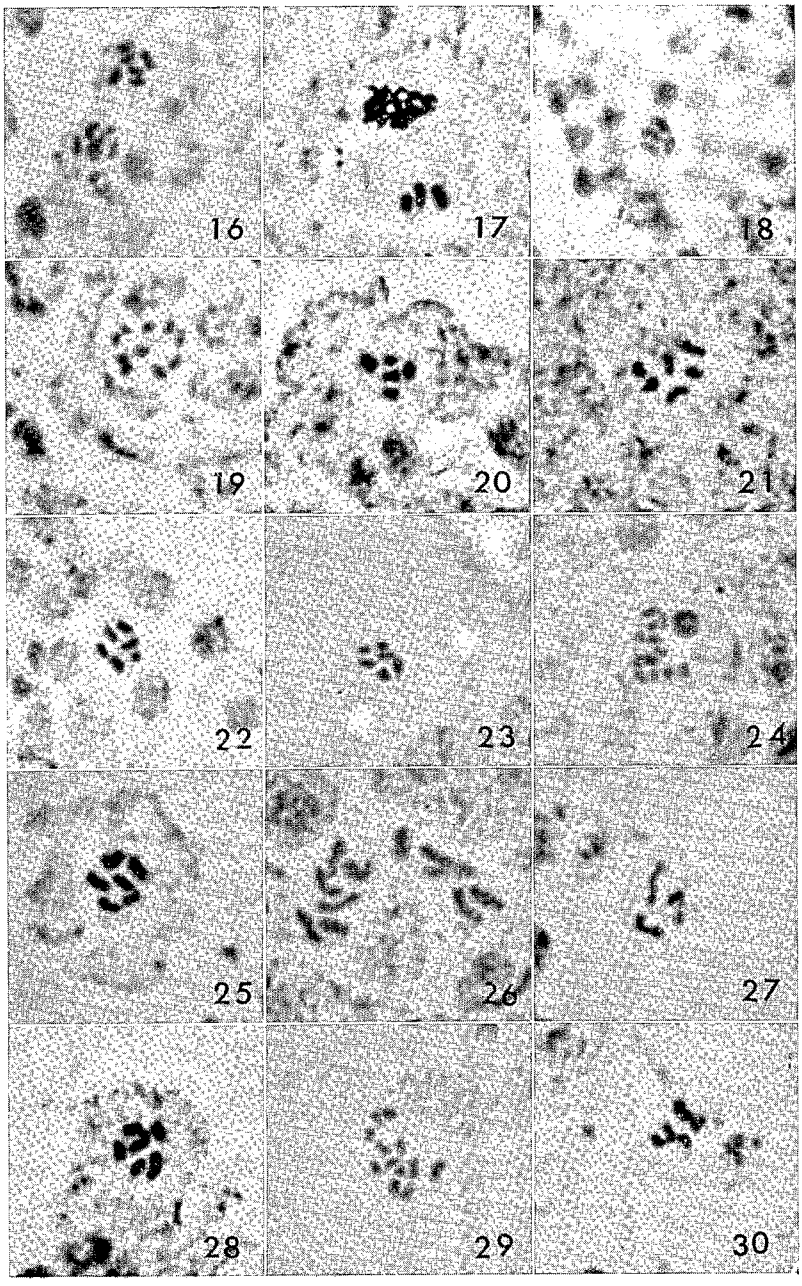
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intact egg, the actual squashing is done. The objects are embedded directly in Euparal.

Preferably, specimens were cultivated in the laboratory. This presented no difficulties with polyphagous species accepting bean (*Phaseolus vulgaris* L.) as hostplant. A detached leafculture (c.f. HELLE, 1965) was then used which made it possible to examine the progeny of mated as well as that of unmated females. The following species were kept in culture on bean: *Eutetranychus banksi, Eu. orientalis, Eu. eliei, Oligonychus bessardi, O. sylvestris, Eotetranychus imerinae, Eo. paracybelus, Eo. ranomafanae, Tetranychus atlanticus, T. ludeni, T. neocaledonicus* and *T. tumidus*. Munger cells (c.f. GUTIERREZ, 1967) were used for those species which could not be reared on beans. For this method we depended on the availibility of the hostplant in the immediate surroundings of the laboratory. In this way the greater part of the species were studied. For some species we had to make do with samples of eggs gathered in the field. The species, localities and hostplants are presented in Table 1.

Results

It was possible to determine the number of chromosomes in all species under investigation. Often, several dozens of metaphase plates were found in the embryonic tissue of one egg. Therefore, also of species where the sample of eggs studied was small, the number of chromosomes could be determined.

The chromosome numbers of the species reported here are given in Table 1; photomicrographs of the karyotypes are presented in Plates I and II.

Plate II. Photomicrographs of mitotic stages in egg squashes of different spider mite species. Magnification 1900 ×.

16. *O. coffeae*, $2n = 6$. – 17. *A. tephrosiae*, $n = 3$. – 18. *E. befandrianae*, $n = 4$. – 19. *E. ranomafanae*, $2n = 10$. – 20. *E. ranomafanae*, $n = 5$. – 21. *E. imerinae*, $2n = 6$. – 22. *E. paracybelus*, $2n = 6$. – 23. *E. roedereri*, $2n = 6$. – 24. *S. australis*, $2n = 12$. – 25. *T. kaliphorae*, $2n = 6$. – 26. *T. atlanticus*, $2n = 6$. – 27. *T. atlanticus*, $n = 3$. – 28. *T. neocaledonicus*, $2n = 6$. – 29. *T. tumidus*, $2n = 12$. – 30. *T. tumidus*, $n = 6$.

TABLE 1

CHROMOSOME NUMBERS IN 45 DIFFERENT SPIDER MITE SPECIES. EGG NUMBER IN PARENTHESES. N = THE NETHERLANDS, M = MADAGASCAR

Species	Location	Hostplant	Number of chromosomes	
			in randomly taken eggs	in eggs obtained from unfertilized females
Subfamily *Bryobiinae* BERLESE				
Bryobia rubrioculus (SCHEUTEN)	Amsterdam (N.)	*Malus* sp.	8(43)	
Bryobia praetiosa KOCH	Amsterdam (N.)	*Gramineae*	8(14)	
Porcupinychus insularis (GUT.)	Ihosy (M.)	*Sida rhombifolia* L.	8(10) and 4(7)	4(2)
Petrobia harti (EWING)	Tananarive (M.)	*Oxalis corniculata* L.	4(23) and 2(49)	2(14)
Petrobia latens (MÜLLER)	Amsterdam (N.)	*Gramineae*	8(14)	
Subfamily *Tetranychinae* BERLESE				
Eonychus curtisetosus GUT.	Betioky (M.)	*Grewia lavanalensis* H.BN.	4(3) and 2(1)	
Eonychus grewiae GUT.	Maevatanana (M.)	*Grewia flavicans* H.BN.	4(1) and 2(6)	
Eurytetranychus madagascariensis GUT.	Tuléar (M.)	*Nerium oleander* L.	6(4) and 3(3)	
Eutetranychus grandidieri GUT.	Ihosy (M.)	*Phragmites mauritianus* KURTH.	4(5) and 2(6)	2(9)
Eutetranychus eliei GUT. et HELLE	Tuléar (M.)	*Plumeria alba* L.	8(4) and 4(3)	
Eutetranychus ranjatoi GUT.	Befandriana-Sud (M.)	*Rinorea greveana* H.BN.	6(7) and 3(1)	
Eutetranychus orientalis KLEIN	Israel	*Citrus* spec.	6(5) and 3(4)	3(3)
Eutetranychus banksi (MCGREGOR)	Florida (U.S.A.)	*Citrus* spec.	6(16) and 3(12)	3(4)
Oligonychus sylvestris GUT.	Tananarive (M.)	*Sida rhombifolia* L.	4(3) and 2(3)	2(7)
Oligonychus andrei GUT.	Ihosy (M.)	*Grewia lavanalensis* H.BN.	4(3) and 2(3)	
Oligonychus randriamasii GUT.	Ampanihy (M.)	*Croton* sp.	4(9) and 2(4)	
Oligonychus gossypii (ZACHER)	Majunga (M.)	*Grangeria* sp.	4(5) and 2(5)	
Oligonychus hassani GUT.	Tananarive (M.)	*Oxalis corniculata* L.	8(4) and 4(3)	4(14)

Oligonychus pratensis (BANKS)	Tuléar (M.)	*Dactylocteniuм capitatum* A.CAMUS	8(3)	
Oligonychus chazeaui GUT.	Majunga (M.)	*Hyphaene shatan* BOJ.	8(6) and 4(1)	
Oligonychus coffeae (NIETNER)	Tuléar (M.)	*Vitis vinifera* L.	6(6) and 3(3)	
Oligonychus quercinus HIRST	Amsterdam (N.)	*Quercus robur* L.	6(6) and 3(7)	
Anatetranychus tephrosiae (GUT.)	Tuléar (M.)	*Mundulea pungens* VIGU.	6(9) and 3(4)	
Eotetranychus befandrianae GUT.	Ampanihy (M.)	*Croton* sp.	4(3) and 2(2)	
Eotetranychus sakalavensis GUT.	Befandriana-Sud (M.)	*Phyllánthus* sp.	4(7) and 2(4)	
Eotetranychus tulearensis GUT.	Befandriana-Sud (M.)	*Bauhinia* sp.	4(13) and 2(6)	
Eotetranychus ranomafanae GUT.	Ranomafana (M.)	*Rosa* sp.	10(8) and 5(10)	5(5)
Eotetranychus rinoreae GUT.	Befandriana-Sud (M.)	*Rinorea greveana* H.BN.	6(3) and 3(2)	
Eotetranychus friedmanni GUT.	Tananarive (M.)	*Solanum auriculatum* AIT.	6(4) and 3(3)	
Eotetranychus imerinae GUT.	Tananarive (M.)	*Erythrina macrophylla* D.C.	6(11) and 3(5)	3(14)
Eotetranychus paracybelus GUT.	Ivato (M.)	*Tephrosia vogelii* HOOK.	6(5) and 3(3)	3(6)
Eotetranychus roedereri GUT.	Ankazobe (M.)	*Cephalostachyum* sp.	6(2) and 3(2)	
Eotetranychus grandis GUT.	Majunga (M.)	*Hippocratea* sp.	6(6) and 3(2)	
Schizotetranychus australis GUT.	Tuléar (M.)	*Mundulea pungens* VIGU.	12(9) and 6(3)	
Tetranychus roseus GUT.	Majunga (M.)	*Medemia nobilis* GALL.	8(15) and 4(10)	
Tetranychus viennensis ZACHER	Goes (N.)	*Prunus avium* L.	6(17) and 3(3)	
Tetranychus panici GUT.	Ankazobe (M.)	*Panicum uvulatum* STAPF.	8(3) and 4(2)	
Tetranychus ludeni ZACHER	Tananarive (M.)	*Thunbergia alata* BOJ.	6(10) and 3(4)	3(8)
Tetranychus kaliphorae GUT.	Ankazobe (M.)	*Kaliphora madagascariensis* HOOK	6(3) and 3(1)	
Tetranychus atlanticus MCGREGOR	Bosnia (Yugoslavia)	*Humulus lupulus* L.	6(12) and 3(11)	3(8)
Tetranychus neocaledonicus ANDRÉ	Louisiana (U.S.A.)	Unknown	6(29) and 3(2)	3(15)
Tetranychus neocaledonicus ANDRÉ	Ihosy (M.)	*Gossypium hirsutum* L.	6(1) and 3(1)	3(9)
Tetranychus tumidus BANKS	Louisiana (U.S.A.)	*Gossypium hirsutum* L.	12(36) and 6(20)	6(192)

With the exception of *Oligonychus pratensis*, in all bisexual species two classes of eggs were found, apparently having the haploid and

TABLE 2

RANGE IN SIZE IN MICRONS OF DIFFERENT ADULTS OF *Tetranychus* SPECIES

	female		male	
	length	width	length	width
T. urticae	490–515	290–305	310–325	165–195
T. pacificus	490–530	280–295	325–340	165–180
T. atlanticus	500–530	290–310	295–325	170–185
T. neocaledonicus	490–530	300–325	295–340	170–185
T. tumidus	610–630	390–415	375–400	210–230
T. tumidus (uniparental giant males)			520–570	270–310

TABLE 3

CHROMOSOME COMPLEMENTS IN DIFFERENT GENERA OF THE *Tetranychidae*

Genus	Species examined	Number of species with haploid complement (n)					
		2	3	4	5	6	7
Bryobia	3			3			
Tetranycopsis	1	1					
Porcupinychus	1			1			
Petrobia	2	1		1			
Subfamily Bryobiinae	7	2		5			
Eonychus	2	2					
Eurytetranychus	2		1		1		
Eutetranychus	5	1	3	1			
Oligonychus	12	4	3	5			
Panonychus	1		1				
Anatetranychus	1		1				
Neotetranychus	1						1
Eotetranychus	12	3	6	2	1		
Schizotetranychus	2		1			1	
Tetranychus	12		9	2		1	
Subfamily Tetranychinae	50	10	25	10	2	2	1
Family Tetranychidae	57	12	25	15	2	2	1

diploid numbers. In those species in which eggs from virgin females were studied, the haploid number occurred. Also was found that eggs deposited by unmated females, resulted in males only. These two facts reflect the haplo-diploid sex determination of the bisexual species.

As for *O. pratensis*, only three eggs were examined and the 8 chromosomes found presumably represent the diploid number. The sex ratio in *O. pratensis* is such that the females outnumber the males by far.

In the populations of *Bryobia praetiosa*, *B. rubrioculus* and *Petrobia latens*, no males were observed. For these particular species only one class of eggs was found with a number of 8 chromosomes, presumably representing the diploid number.

Tetranychus tumidus is a species which exhibits the for the genus rather unusual numbers of 6 and 12 chromosomes. An interesting point, still under study, about this species is noteworthy. It was observed that in the particular population sex aberrants occurred which had a male appearance but which were extremely large in size. Closer examination of these giant males learned that they were actually intersexes, however, with male characteristics predominating. The frequency of these giant males was very low: among 1490 individuals 2 giant males were found. Giant males also occurred regularly in progenies of unfertilized females. Since it has up till now been impossible to determine the chromosome number in adult spider mites, one can only speculate about their cytogenetic basis. The 192 examined eggs obtained from unmated females of *T. tumidus* only showed the normal haploid number of 6. In Table 2 a review is given of the sizes of various *Tetranychus* species, measured on 10 living adults of each species, to give an impression of the deviating size of *T. tumidus*, and of the giant males. A survey of the variation in chromosome numbers within the various genera examined (including those mentioned in HELLE & BOLLAND, 1967) is presented in Table 3.

Discussion

Three subjects for discussion come to the fore: sex-determination, karyotype-evolution and the usefullness of karyotype information for taxonomic purposes.

We can be short about sex-determination, as the results presented

here do not open new view points. All bisexual species clearly exhibit an arrhenotokous parthenogenesis. This has been demonstrated in a number of arbitrarily chosen species, by cytological and by rearing means both. The fact that virgin females do produce eggs, facilitates the evidence for arrhenotoky. It should be mentioned, however, that most species of which unmated ♀♀ were isolated had a lower fecundity than those of which ♀♀ had been impregnated. This phenomenon was demonstrated before in *T. neocaledonicus* by GUTIERREZ (1967).

Thelytokous species are found in the *Bryobiinae* and not in the *Tetranychinae*. It is interesting to point out here that several times a number of *Tetranychus* species in the laboratory switched over to thelytokous reproduction. In all cases known, such thelytokous strains could only be maintained for a limited number of generations.

It needs no argument that arrhenotoky is the ancestral type of reproduction of the *Tetranychidae*. The few data about other families of the *Prostigmata* sensu stricta (suborder *Trombidiformes*), to which belong the *Tetranychidae*, indicate that arrhenotoky is the predominant type of reproduction.

So far, the chromosome complements of 57 species of Tetranychids are known. After this important extension of karyotype information, the first thing noticeable is the numerical variation in chromosome numbers in most genera, like *Eutetranychus*, *Oligonychus*, *Eotetranychus*, *Schizotetranychus* and *Tetranychus*. It is clear that an earlier suggestion that a reduction in chromosome number accompanies the evolutionary development in the *Tetranychinae*, is too simplistic (HELLE & BOLLAND, 1967).

In the following discussion on karyotype evolution, it must be postulated that our knowledge is inadequate on two points. Notwithstanding the great number of metaphase-plates of the various species examined, we are still uncertain about the condition of the centromere. This implies that in case of diffuse-centricity, processes like fragmentation may be involved in the increase in chromosome number. The second gap in our knowledge is the relatively low number of species examined the subfamily *Bryobiinae*.

As can be seen in Table 3, $n = 3$ is the modal number of the family. It occurs in 44% of the species investigated. The numbers $n = 2$ and $n = 4$ represent 21% and 26% respectively, of the species concerned.

In the random sample of seven species, analysed sofar, of the

Bryobiinae (c.f. HELLE & BOLLAND, 1967, and Table 3), the number $n = 3$ is not found: all species of this primitive subfamily exhibit haploid complements with either 2 or 4 chromosomes. This may be an indication that the ancestral chromosome number of the family is not 3 but probably 2.

The number $n = 2$ is also found in the phylogenetically important genus *Eonychus*. Owing to the number of anal setae and the absence of tenent hairs on the empodium, this genus, endemic for Madagascar, undoubtedly belongs to the *Tetranychinae*. The genus does, however, show an abundance of primitive characteristics, such as the form of the empodium, the peritremata, the aedeagus and the reticulation of the propodosoma, indicating a close relationship with the *Bryobiinae*. Obviously, of the genera of the *Tetranychinae* studied, *Eonychus* is the least specialized genus. Apart from these morphological criteria, *Eonychus* can also be considered as unspecialized in other biological aspects, since this genus, like the *Bryobiinae*, lacks the ability to produce silk.

The production of silk-structures is an important evolutionistic step for the *Tetranychinae*. It offers protection against rain and many predator mites. This type of specialization can be followed step by step in the genus *Eotetranychus*. The species *E. befandrianae*, *E. sakalavensis* and *E. tulearensis* (with $n = 2$) belong to the less specialized group within this genus. They produce only a few threads to cover an egg mass. In the other species (with $n = 3$, 4 or 5) within the genus *Eotetranychus*, the production of silk-structures is further developed (GUTIERREZ, HELLE & BOLLAND, 1970).

On the basis of these data, we are inclined to presume that $n = 2$ is the primary chromosome number. Unfortunately, there is little information about chromosome numbers in other families of the *Prostigmata* sensu stricto. The only data existing concern the family *Harpyrhynchidae*, two species of which were examined by OLIVER & NELSON (1967). Both species have $n = 2$ and $2n = 4$ and are arrhenotokous.

With respect to changes in chromosome numbers, it is tempting to hypothesize that polyploidy contributed to speciation in spider mites. The case of *Neotetranychus rubi* TRÄGÅRD with $n = 7$ (whereas related species show $n = 3$ and $n = 4$) has already been mentioned before (HELLE & BOLLAND, 1967). The present investigations offer new material for this supposition. We want to draw the attention to the

genus *Schizotetranychus*, of which the species *S. schizopus* (Table 3) shows a haploid complement with $n = 3$, whereas *S. australis* has $n = 6$. We further mention *Tetranychus tumidus* with $n = 6$, which belongs to the more advanced species of *Tetranychus*, all with $n = 3$. The big size of *T. tumidus*, as compared to related species (see Table 2) together with the occurrence of sex-aberrants, are phenomena that can be connected with a recent speciation of *T. tumidus* by doubling of the chromosome complement. One could continue this view by conceiving the species with $n = 5$ (like for instance *Eotetranychus ranomafanae*) as allopolyploids. And to return to the *Bryobiinae*, the situation in *Petrobia* can also be seen in the same light.

Polyploidy as a factor for speciation in bisexual animals is rather unpalatable for many cytologists (cf. WHITE, 1961; SUOMALAINEN, 1958). However, it is relevant to consider the peculiarities of arrhenotoky, since the evolutionary possibilities resulting from arrhenotoky seem different from those of animals with diploid sexes.

Establishment of genome mutations in zygogenetic bisexual animals meets with serious difficulties. These difficulties result from the fact that for propagation the mutant depends on a sexual partner of the wild-type. It may be that the mutation is expressed in some phenotypical change which causes an instantaneous reproductive isolation of the mutant. In case of polyploidy, for instance, an increase in size can result in physical non-correspondance of the genitalia, or in lack of mutual attraction. But even if the mutant is fully compatible with normal, numerous hindrances can prevent establishment. If sex is balanced by a chromosomal mechanism, the upset in balance may cause sterility amongst the descendants (cf. MULLER, 1925).

In animals with an arrhenotokous reproduction the chance of establishment of genome mutations seems more favourable, for this reproductive type offers an escape to the mutation, as the mutant female can mate with her partheno-genetically produced sons. This would be an opportunistic way in which instantaneous differentiation can occur resembling the possibilities of monoecious organisms. Arrhenotoky can be considered in this respect as a kind of "monoecy in time". However, it is difficult to appraise the evolutionistic value of this possibility inherent to arrhenotoky. Especially with respect to polyploidy, the question arises whether tetraploid females can produce diploid sons.

The genetic basis of the haplo-diploid sex-determination, however, is still obscure. In a study on the occurrence of giant males and intersexes in an inbred line of *Tetranychus urticae* KOCH it was shown that the giant males in this inbred line were diploid and produced viable spermatids (HELLE, unpublished). We mention these facts to illustrate that diploidy is not per se female-determining.

Our sceptical attitude towards polyploidy is due to our conviction that a more detailed study is needed for the cases mentioned. More common processes, like dissociations or fragmentations can result in similar chromosome numbers.

Remains an evaluation of karyotypic information for taxonomic purposes. It is beyond doubt that karyotypic information is a useful tool for the acarologist. In a heterogeneous genus like *Oligonychus* the chromosome numbers are indicative for a division into a number of subunits. An integration of the karyotypic information, with morphological and biological disciplines, will be presented in a separate paper (GUTIERREZ, HELLE & BOLLAND, 1970).

This study was financially supported by the Netherlands Foundation for the Advancement of Tropical Research (W.O.T.R.O.) and the Uyttenboogaart-Eliasen Foundation. The authors are indebted to the Director of the I.R.C.T.-Station at Tuléar for the laboratory facilities. They are grateful for the material supplied by Prof. Z. AVIDOV, Rehovot, Israël; Prof. H. B. BOUDREAUX, Baton Rouge, U.S.A.; Ing. M. KAC, Ljubljana, Yugoslavia; Prof. J. G. RODRIQUEZ, Lexington, U.S.A.; Dr. F. F. SMITH, Beltsville, U.S.A. and Mr. M. v. d. VRIE, Goes, the Netherlands.

The senior author wishes to express his special gratitude to Mr. ROEDERER, Director O.R.S.T.O.M. at Tananarive, for various facilities. It is also a pleasure to express his gratitude to Mr. Jean-Elie RANDRIAMASY for his technical assistance in so many ways.

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Vol. 41 No. 1 1970

genetica

netherlands journal of genetics

[HELLE (W.)] GUTIERREZ (J.) [BOLLAND (H.R.)]
A study on sex-determination and karyotypic evolution in tetranychidae.

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