Cytogenetics of chelicerates (Arthropoda: Chelicerata)

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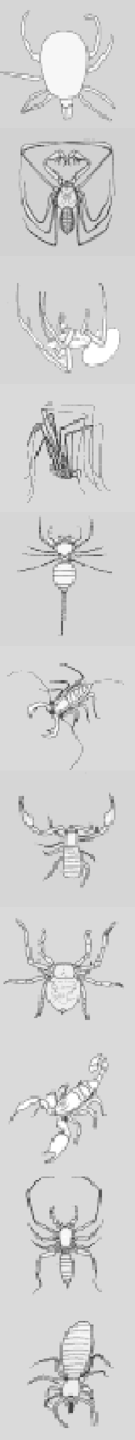
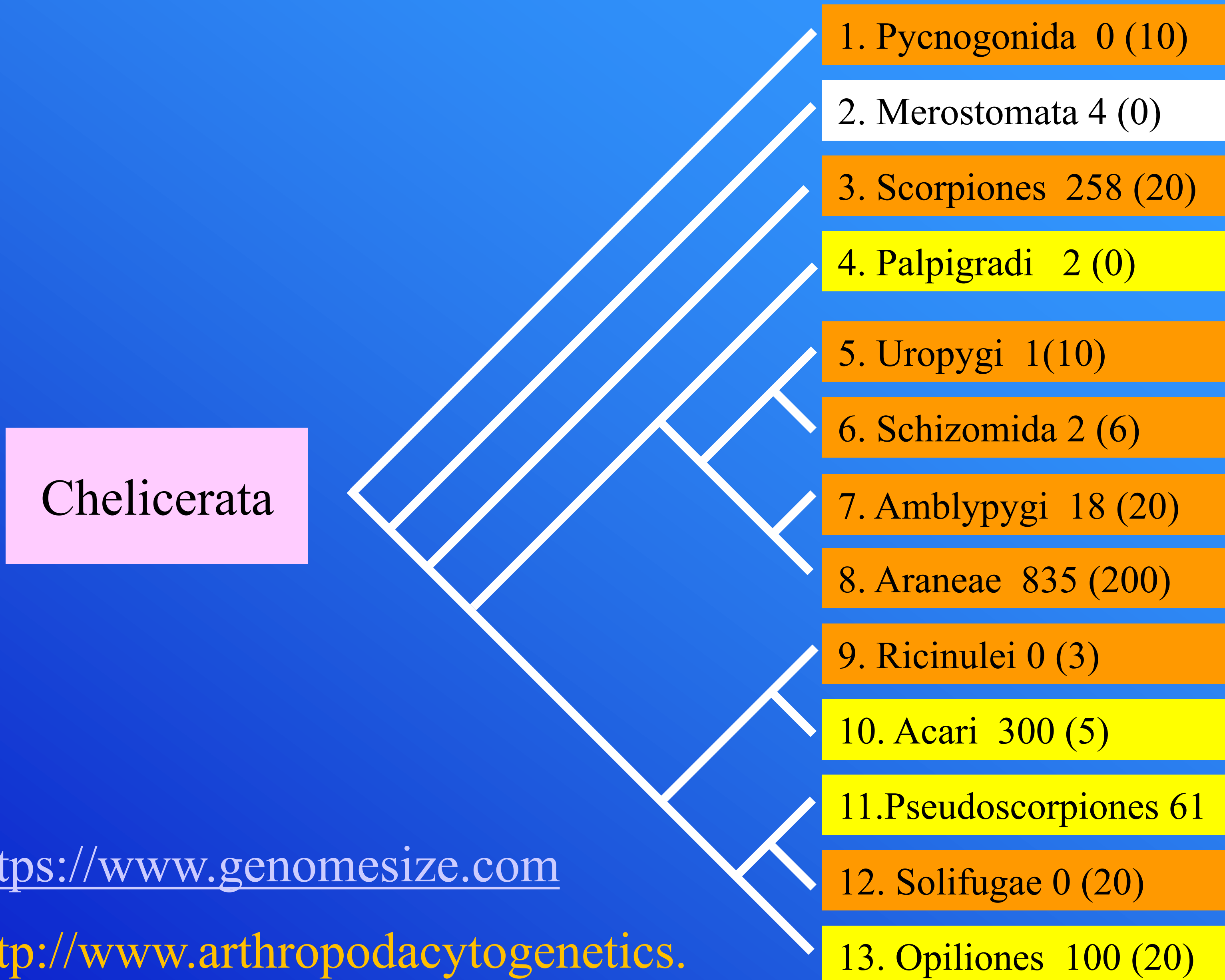


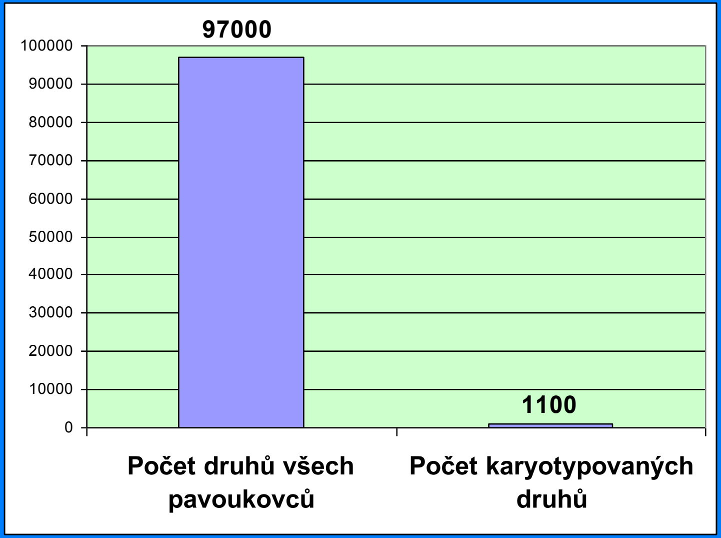


https://www.genomesize.com

http://www.arthropodacytogenetics.bio.br/index.html

Current state of chelicerate cytogenetics

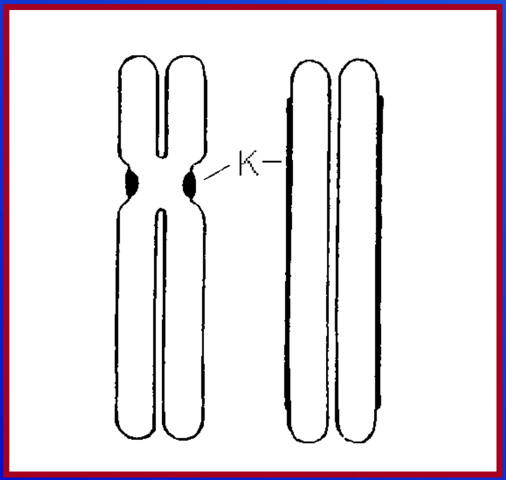
- karyotypes of chelicerates are not satisfactorily understood
- more data on spiders, acariform and parasitiform mites, harvestmen, scorpions and pseudoscorpions; karyotypes of other orders are virtually or completely unknown (in total, karyotypes of nearly 1600 species is described)
- Obtained data do not allow to reconstruct karyotype
- evolution of chelicerates



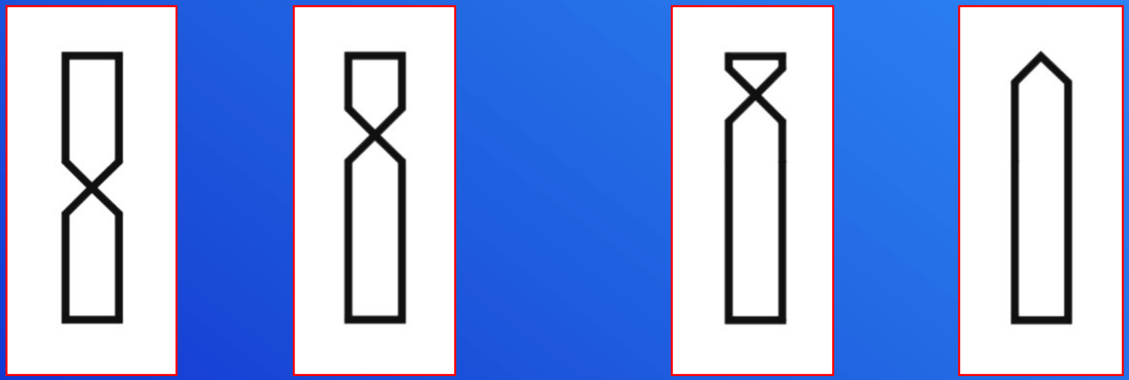
Obtained data show considerable diversity of genome size, diploid numbers, karyotype structure, and number of nucleolus organizer regions

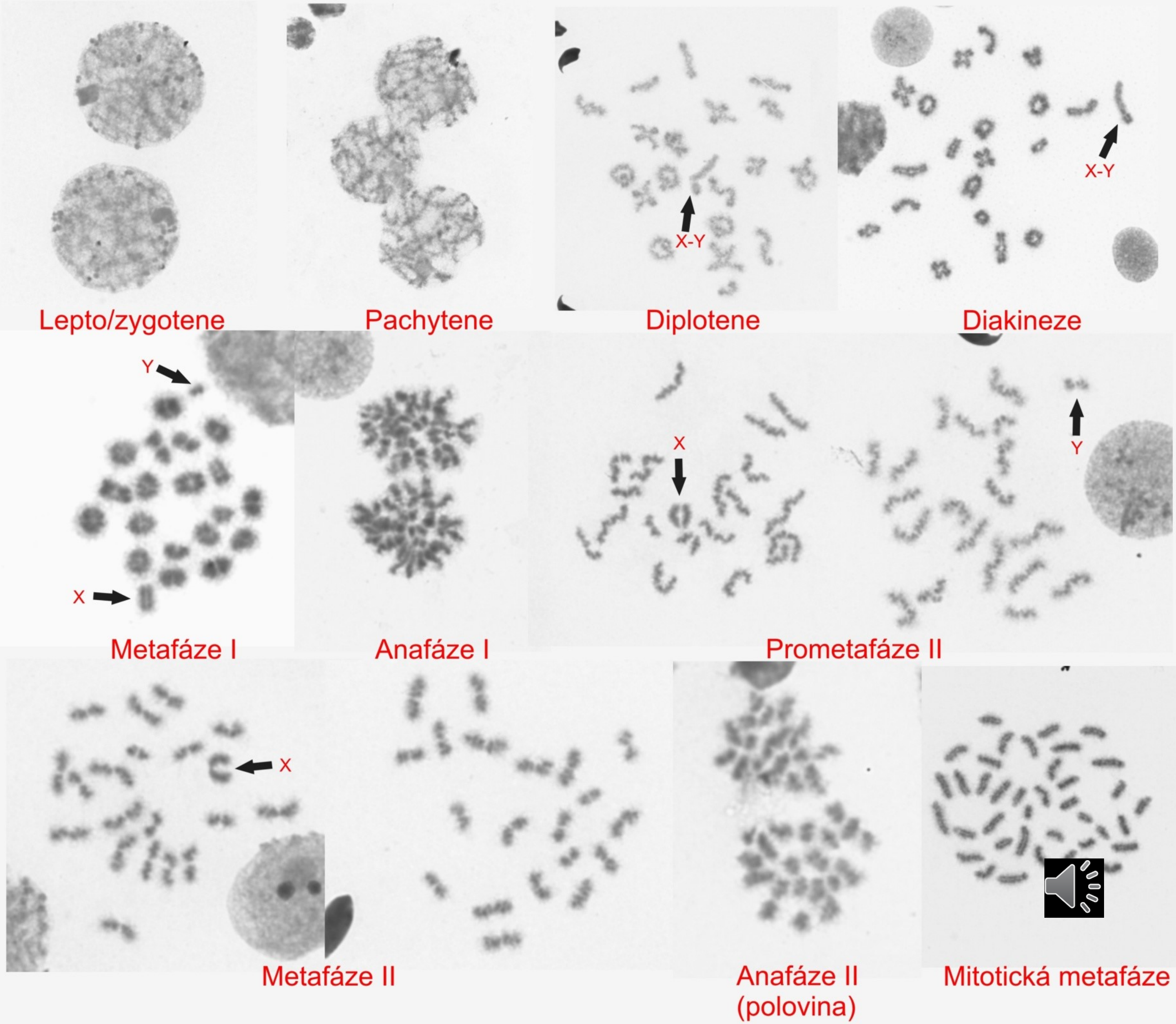
- considerable diversity of genome sizes from 0.08 (*Tetranychus urticae*) to 49 pg (*Caponia hastifera*)
- 2n range from 4 (acariform mites) to 186 (scorpions). Frequent genome duplications
- while some groups exhibit standard (monocentric) chromosomes, other lineages possess holocentric (holokinetic) chromosomes
- enormous diversity of modes of sex chromosome determination ancestral arachnids probably without sex chromosomes (or sex chromosomes homomorphic)
- considerable diversity of number of nucleolar organizer regions (NORs (1-10), ancestral arachnids probably with 1 NOR locus
- insect motive of telomeric repeats except for spiders

Monocentric **Holocentric**



Metacentric **Submetacentric** **Subtelocentric** **Akrocentric**



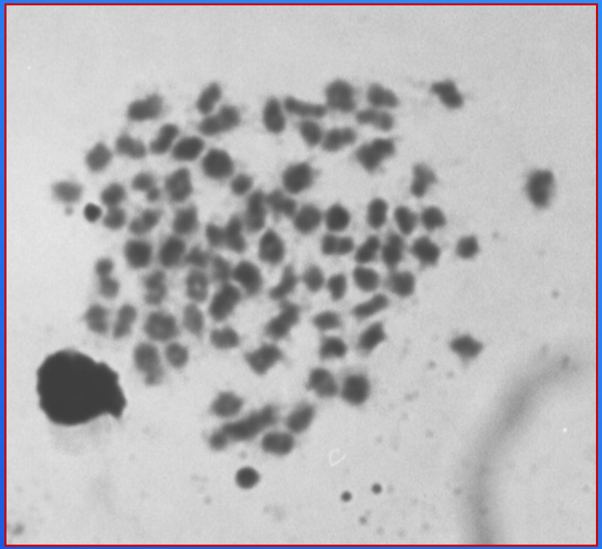


Mus musculus, samec, 2n = 40, XY

Pycnogonida

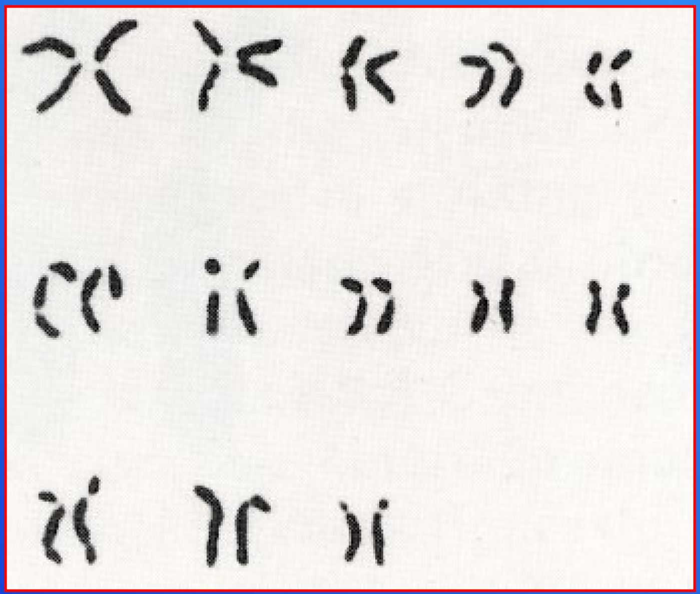
more than 1300 species in 10 families

We studied approx. 10 species belonging to several families at our laboratory; their karyotypes consist of many small chromosomes. No information on NORs. Data are not published yet.



Ammothella biunguiculata (Ammotheidae)

Merostomata 5 species, 1 family



four species studied so far, 2n = 20 - 52

Three rounds of genome duplication in ancestors of Merostomata followed by a reduction of chromosome number. Monocentric chromosomes, usually predomination of biarmed chromosomes. No information on NORs.

sex chromosomes not differentiated morphologically

Solifugae
1100 species, 13 families

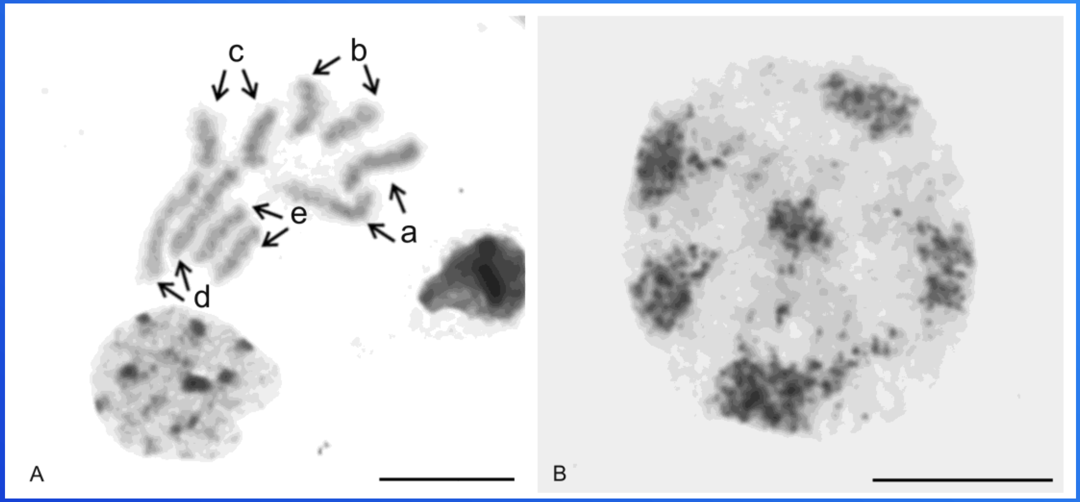
unpublished data on seven families

Ammotrechidae, Daesidae, Eremobatidae, Galeodidae, Gyllippidae, Rhagidiidae, Solpugidae

in total 20 species

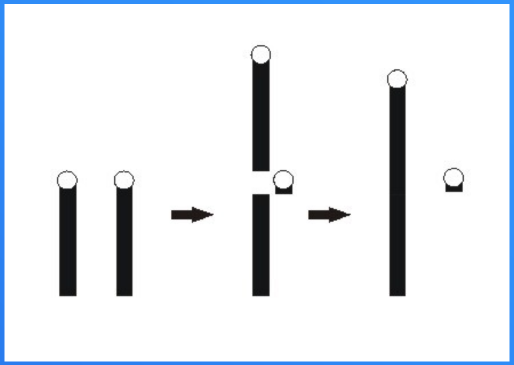
conservative karyotypes
low number of monoarmed chromosomes (8-24)
Sex chromosomes not differentiated morphologically

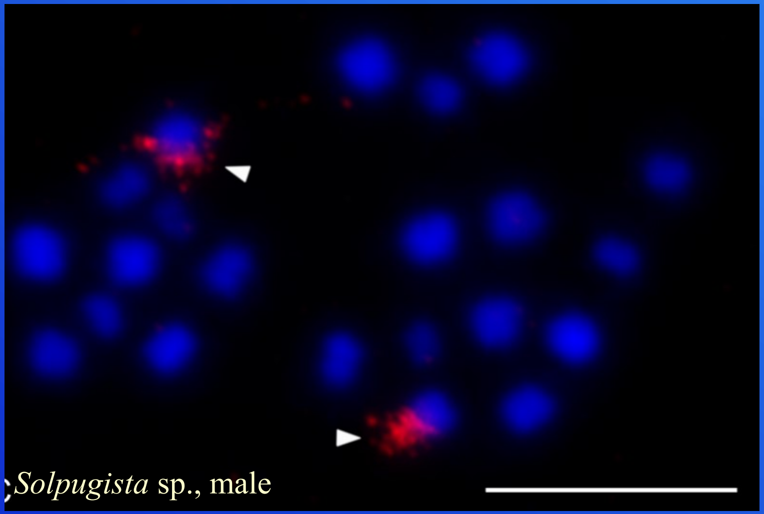
somatic association of homological chromosomes



Ammotrechidae, Daesidae, Eremobatidae, Gyllippidae, Solpugidae
acrocentric chromosomes

ancestral karyotype 2n = 24
decrease of diploid number by tandem fusions





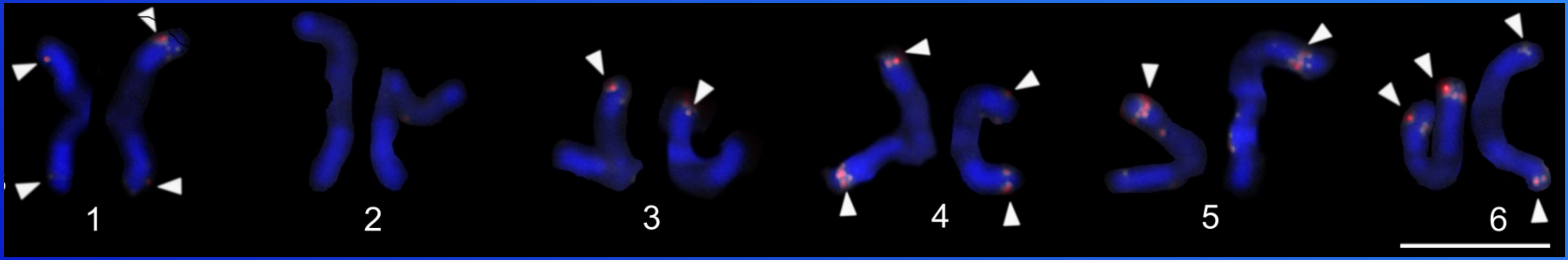
one terminal NOR

Galeodidae and Rhagidiidae

predomination of biarmed pairs

enormous blocks of heterochromatin

***Paragaleodes* sp., male**



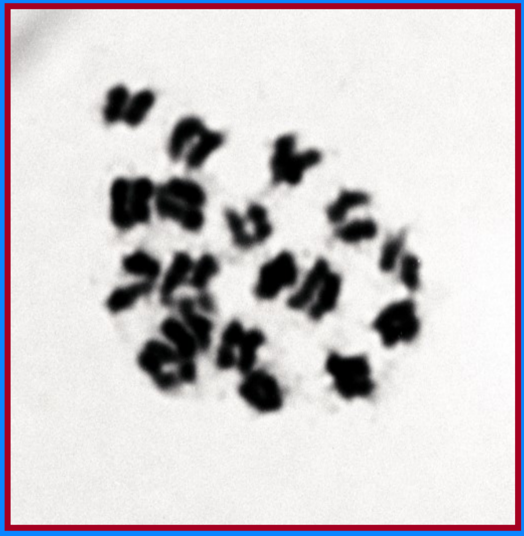
many terminal NORs

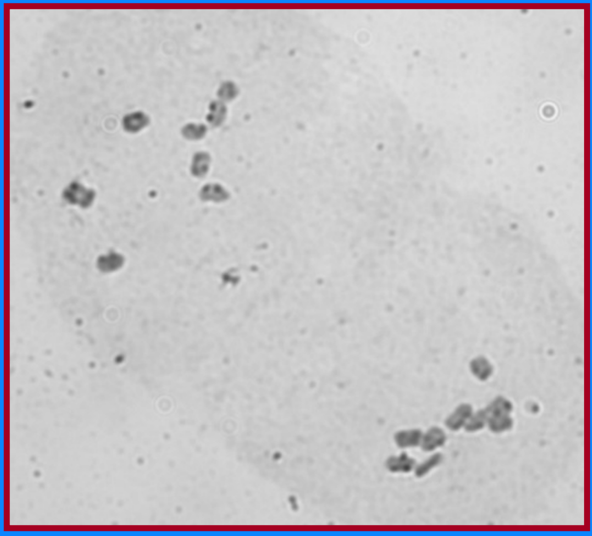
Palpigradi

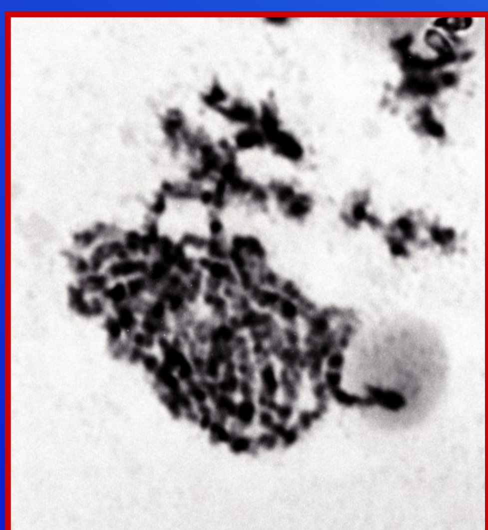
80 species, 2 families

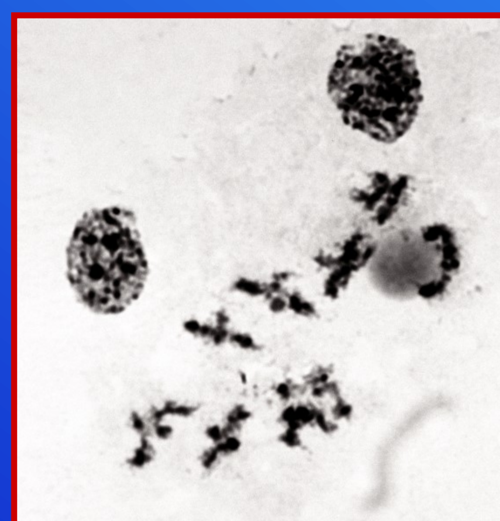
It is difficult to find these arachnids. A dense population of *Eukoenenia spelaea* from Ardovská cave (Slovak Carst) allowed to obtain first data on palpigrade chromosomes

1. karyotype consists of 18 tiny chromosomes of similar size, without visible primary constrictions
2. palpigrade chromosomes probably acrocentric
3. sex chromosomes not differentiated morphologically
4. single terminal NOR



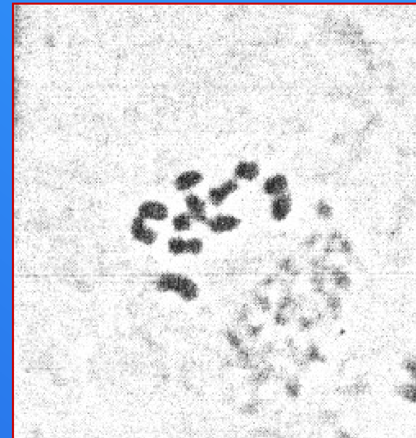






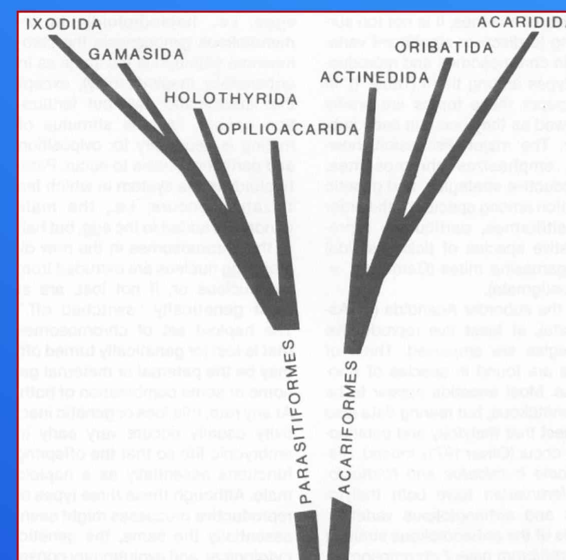
Acariformes

32 000 species



karyotypes described in approx. 200 species,
2n = 4 až 28

holocentric chromosomes



A considerable diversity of modes of sex determination

sex chromosomes are usually not differentiated morphologically (except for Acarididae, Glyciphagidae - X0 a XY systems)

haplodiploidy, parahaploidy (Phytoseiidae), thelytoky, ? deuterotoky in Listrophoridae

Parasitiformes

more than 12000 species

approx. 100 druhů species karyotyped
2n = 6 - 36

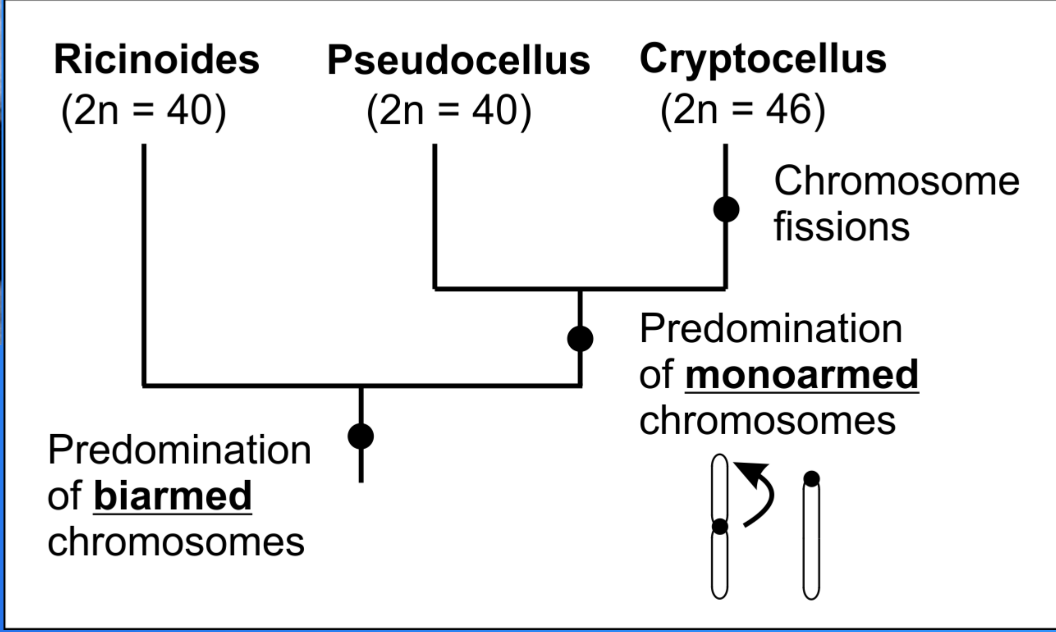
monocentric chromosomes
predomination of biarmed chromosomes: Argasidae
predomination of monoarmed chromosomes: Ixodidae, Opilioacarida

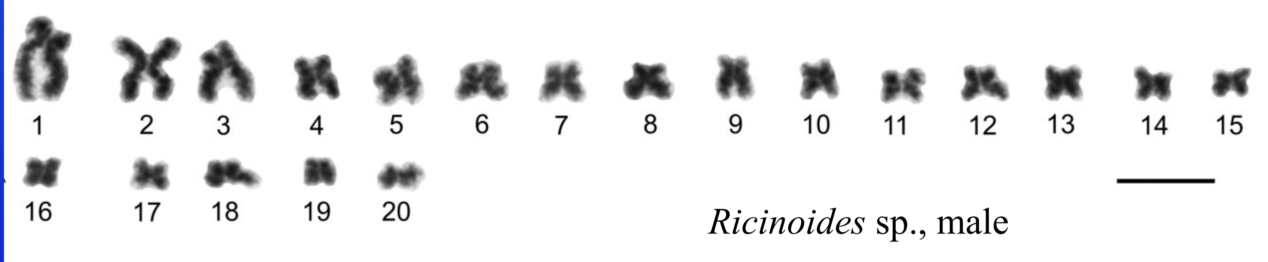
considerable diversity of sex determination
frequently differentiated sex chromosomes
XY (Argasidae, prostriate Ixodidae), X0 (metastriate Ixodidae)
haplodiploidy + parahaploidy (Gamasida), thelytoky
some thelytokous ixodids polyploid

Ricinulei

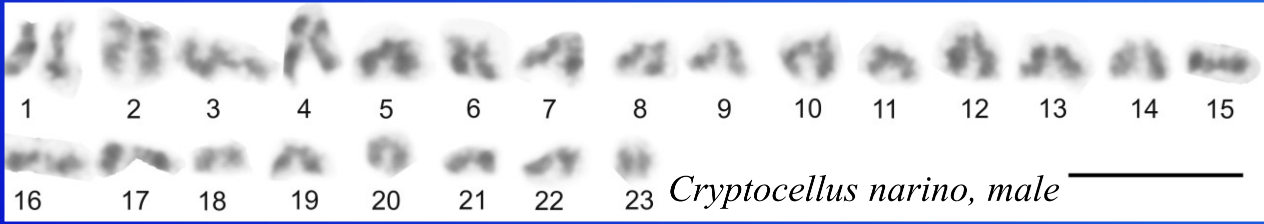
nearly 100 species
extant genera
***Ricinoides*,**
Pseudocellus*, *Cryptocellus

40-46 monoarmed chromosomes
sex chromosomes not differentiated morphologically
1 terminal NOR
slow evolution of karyotypes

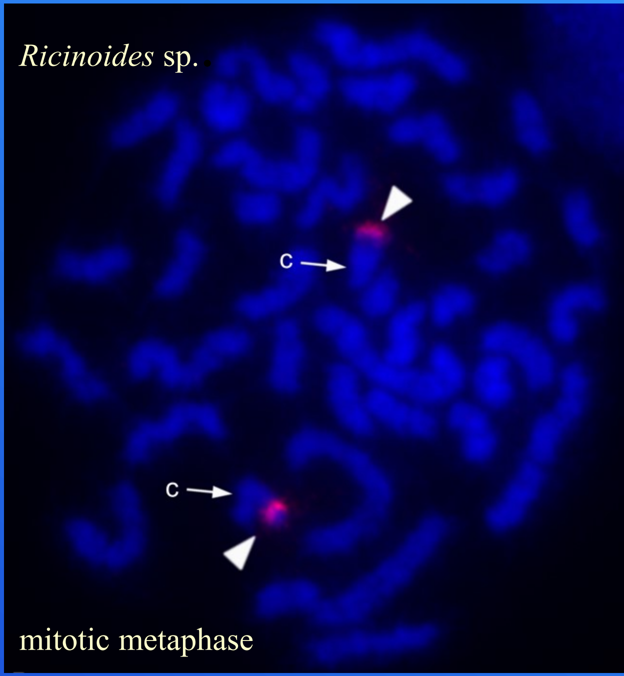




Ricinoides sp., male



Cryptocellus narino, male



Opiliones

more than
6500 species

100 karyotyped species, 2n = 10 - 109, ancestral 2n = 30 (Laniatores 25-109, Cyphopthalmi 24-52, Dyspnoi 10-28, Eupnoi 10-36). Laniatores polyploid?

monocentric chromosomes, usually predomination of biarmed chromosomes
considerable intraspecific and interspecific variability of karyotypes
B chromosomes in some species (*Psathyropus* – up to 18 elements)
Karyotype changes: fusions, fissions, pericentric inversions
Number of NORs ranges from 1 to 7

Sex chromosomes are not differentiated morphologically or exhibit a low morphological differentiation
Most species: XY system
some Phalangiidae: probably ♂ZZ/♀ZW (*Abraxas*) sex chromosomes including NORs
In some harvestmen found thelytoky. Thelytokous taxa frequently polyploid

Pseudoscorpiones

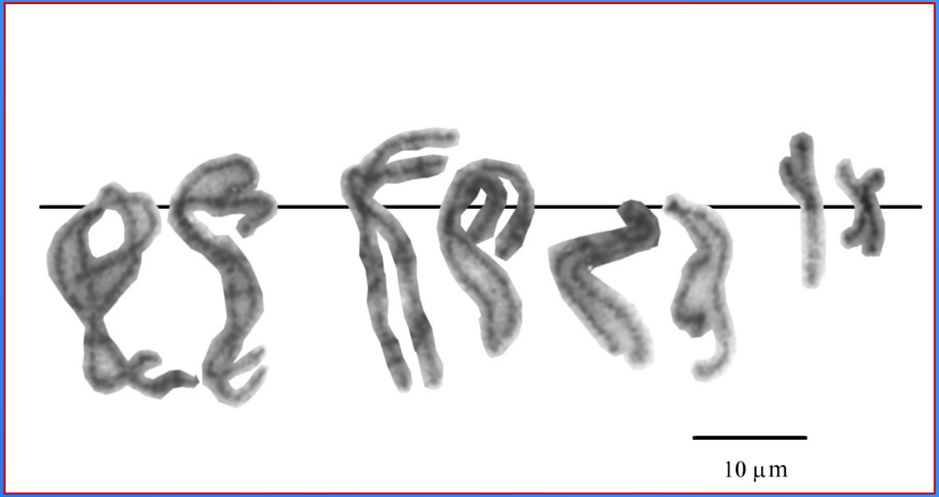
3000 species, 27 families

Published data on 61 species. Male diploid number 2n♂ = 7 (Olpiidae) – 143 (Atemnidae). Monocentric chromosomes.

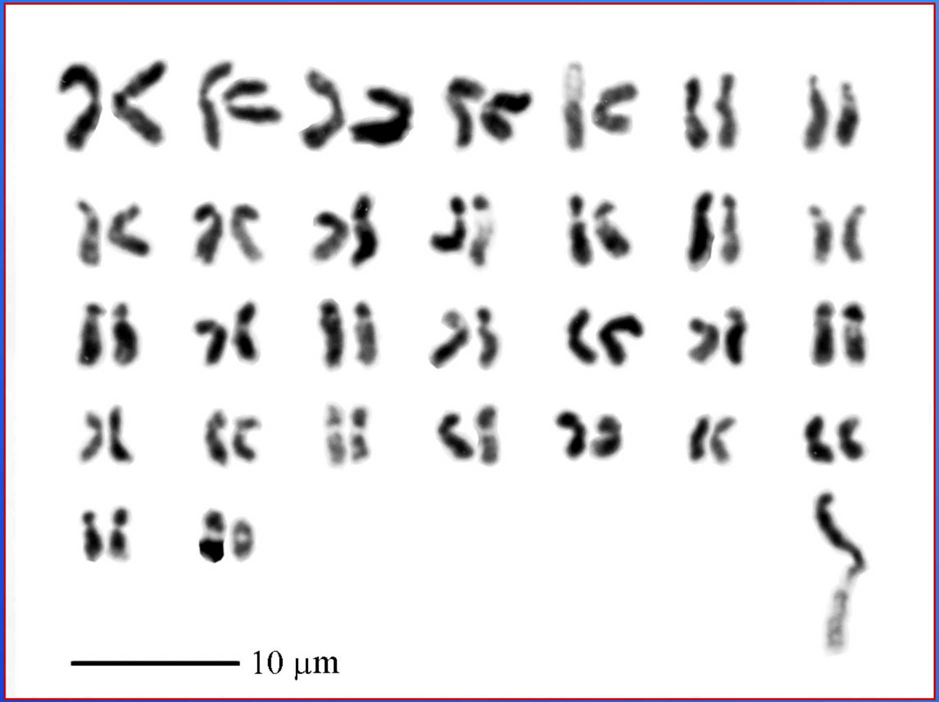
Considerable diversity of number and morphology of chromosomes. Predominatly biarmed chromosomes (except for most Chthoniidae)

Differentiated sex chromosomes: ancestral X0 system (X large metacentric chromosome), neo-sex chromosome systems XY (Neobisiidae, Larcidae)

Olpium palipes
2n♀ = 8, XX

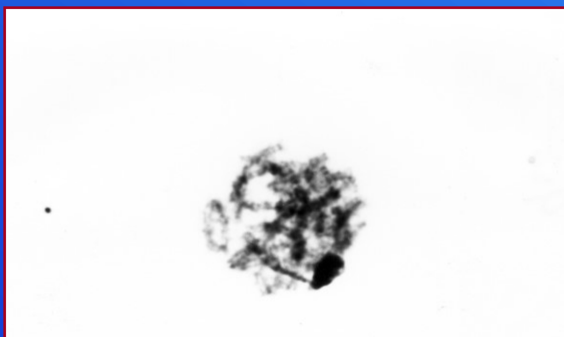


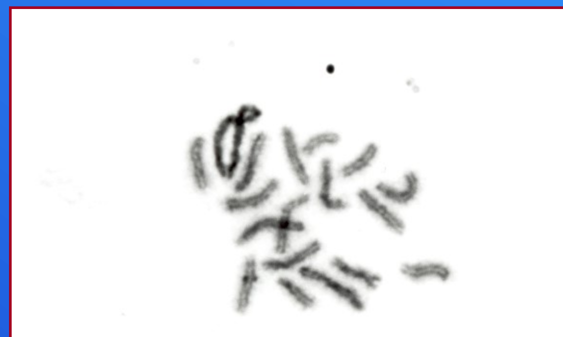
Lasiochernes pilosus
2n♂ = 61, X0



Chthoniidae – achiasmatic meiosis in males

Chthonius litoralis (2n♂ = 35, X0)


pachytene

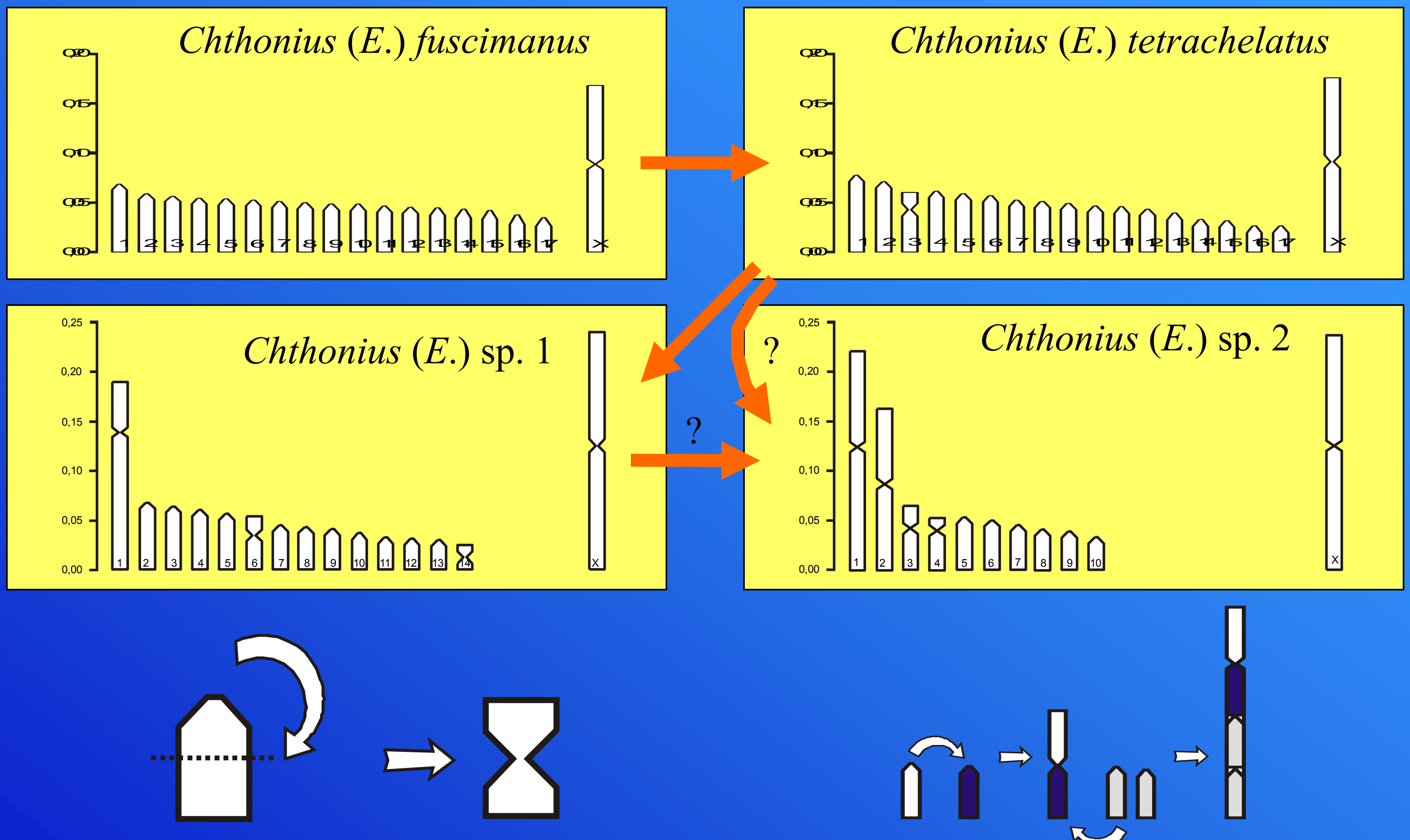

postpachytene


metaphase I


metaphase II


anaphase II

Hypothesis on karyotype evolution of European chthoniids

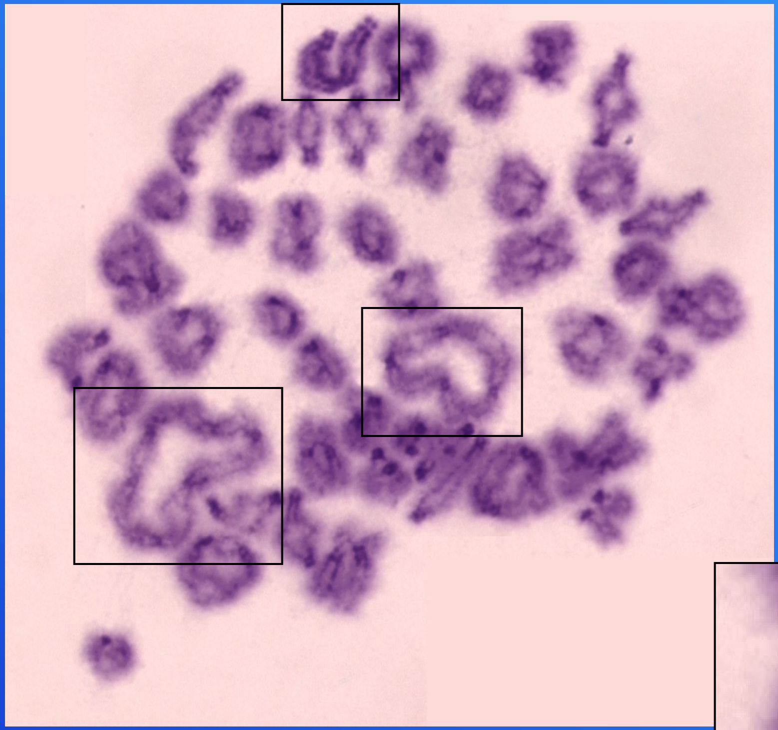


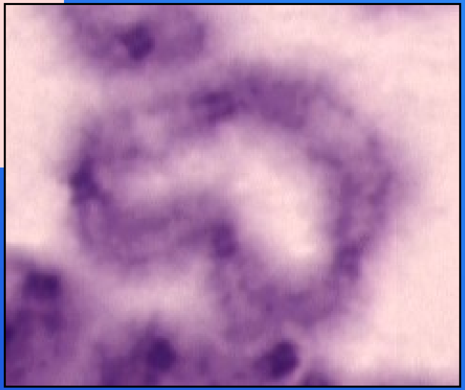
Neobisiidae: *Roncus* – centric fusions. *Neobisium* – multiple fusions (macrochromosomes)

Atemnus politus (Atemnidae): 2n = 95, X0

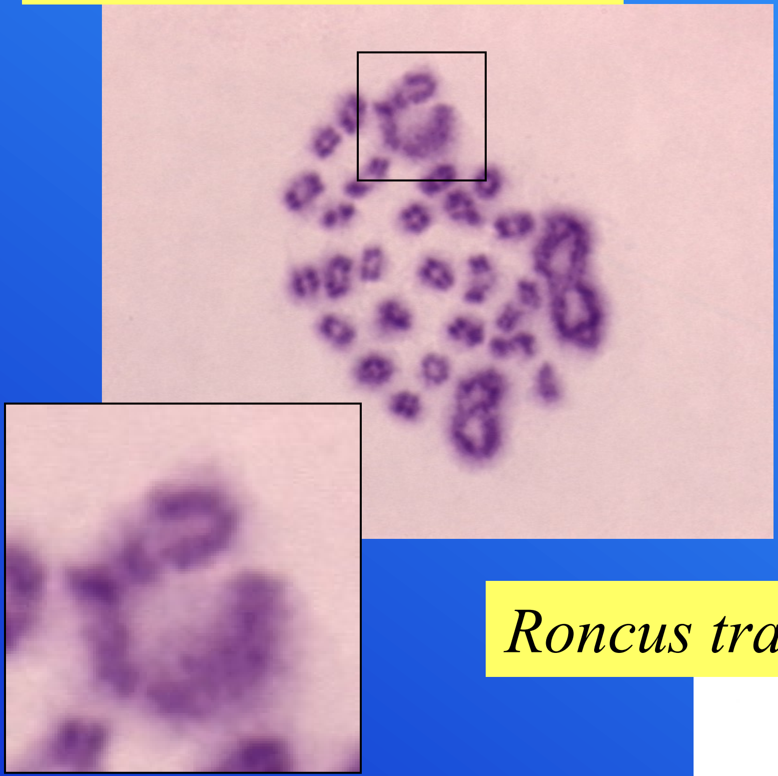
Heterozygotes for reciprocal translocations

prophase I - 42 bivalents, X chromosome
1 tetravalent, 1 hexavalent

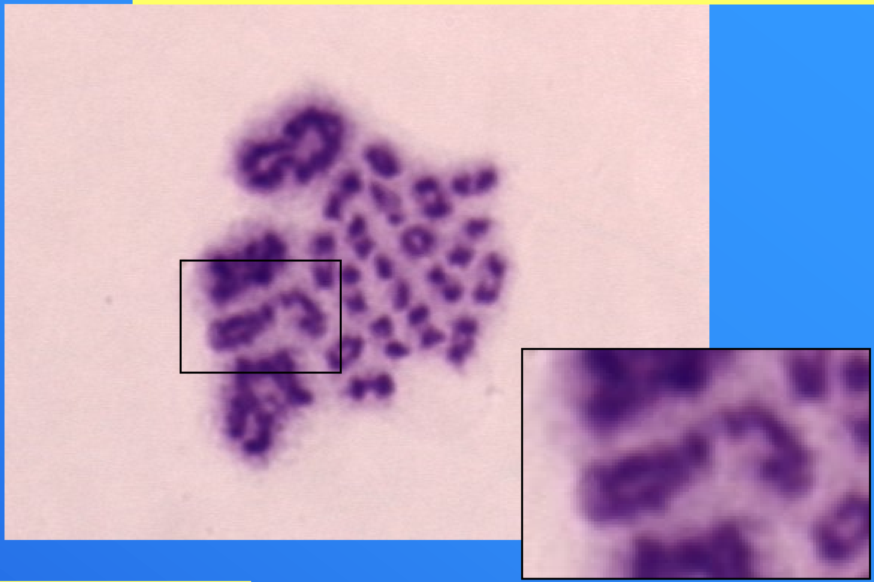




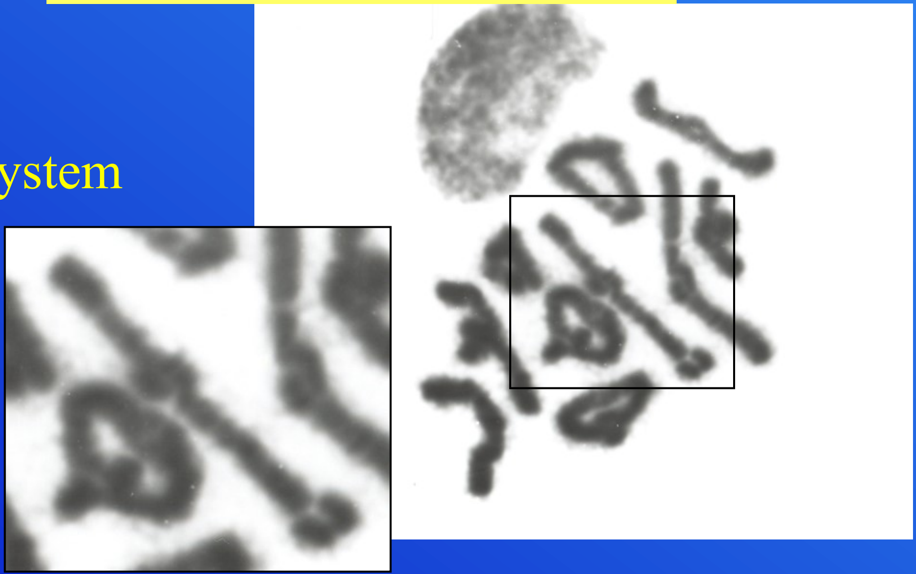
Neobisium sylvaticum



Neobisium erythrodactylum



Roncus transsilvanicus



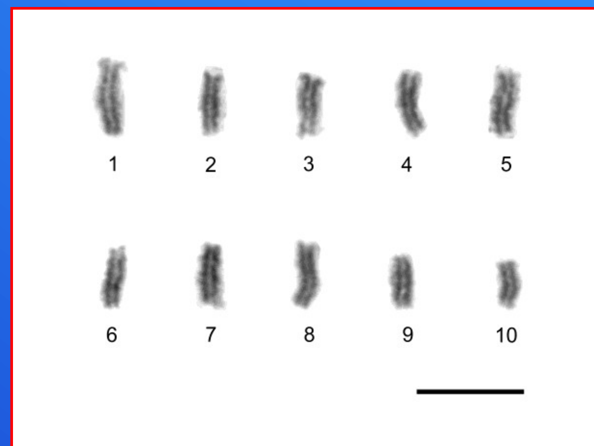
Species with XY system

Scorpiones

more than 2100 species
up to 22 families

Opisthacanthus asper (Liochelidae)

Tityus magnimanus (Buthidae)

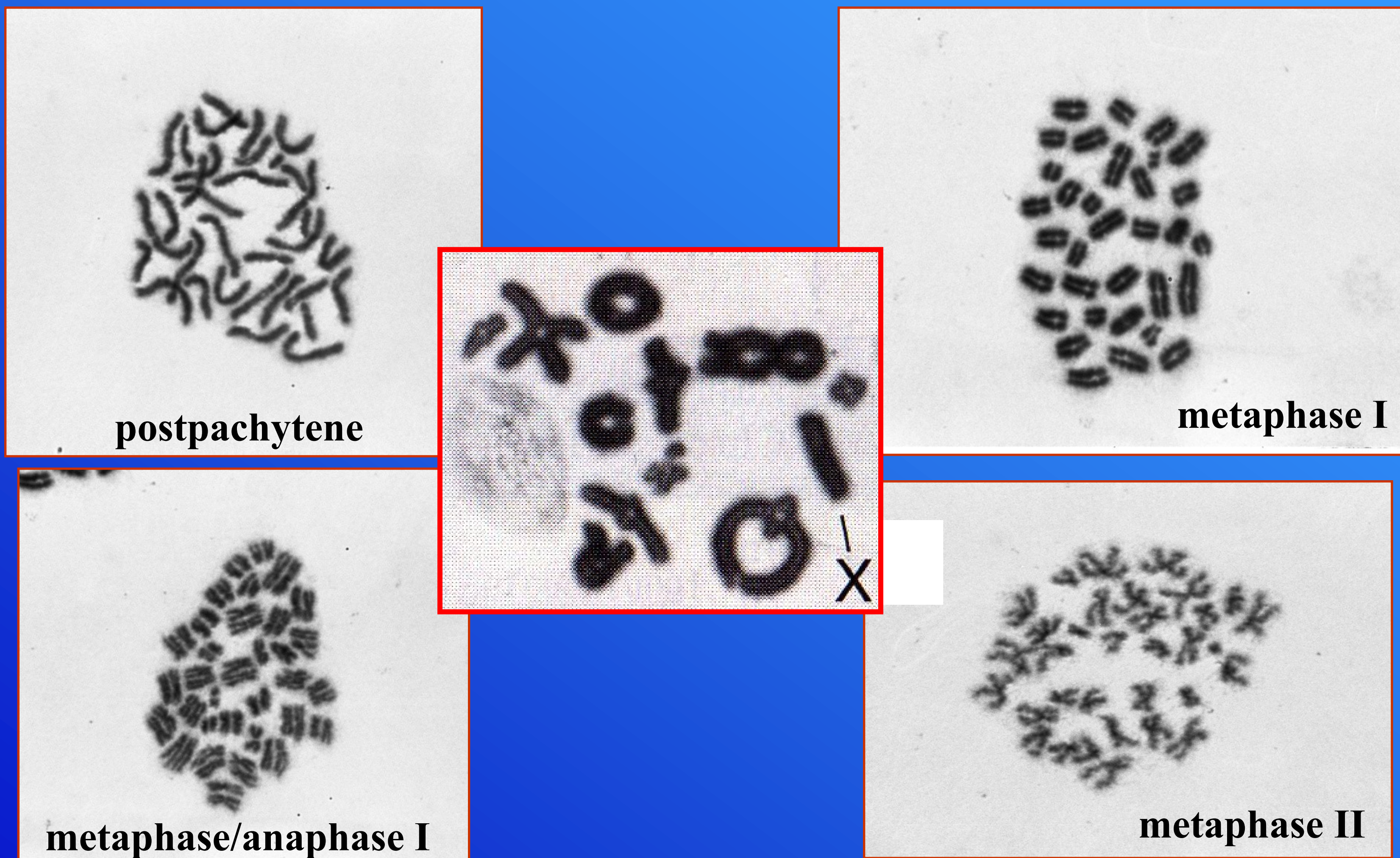


more than 250 species from 11 families studied so far, 2n = 5 – 186, usually one terminal NOR.

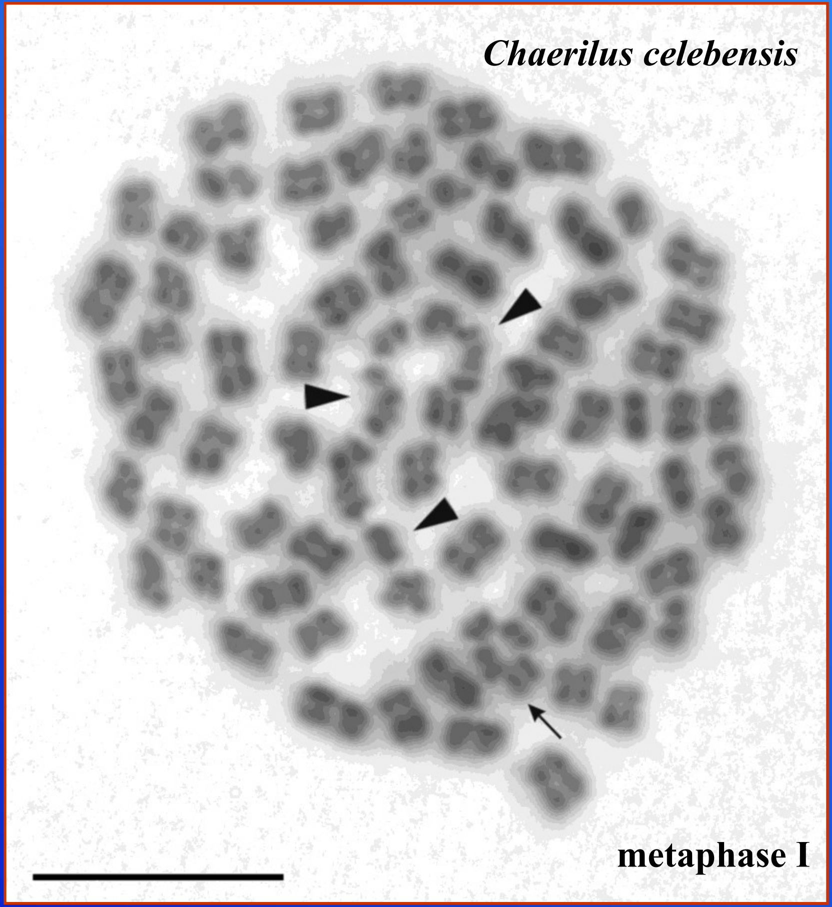
Buthidae: holocentric chromosomes (2n = 5 – 56)
Other scorpions: monocentric chromosomes (2n = 28 – 186), usually predomination of biarmed chromosomes,

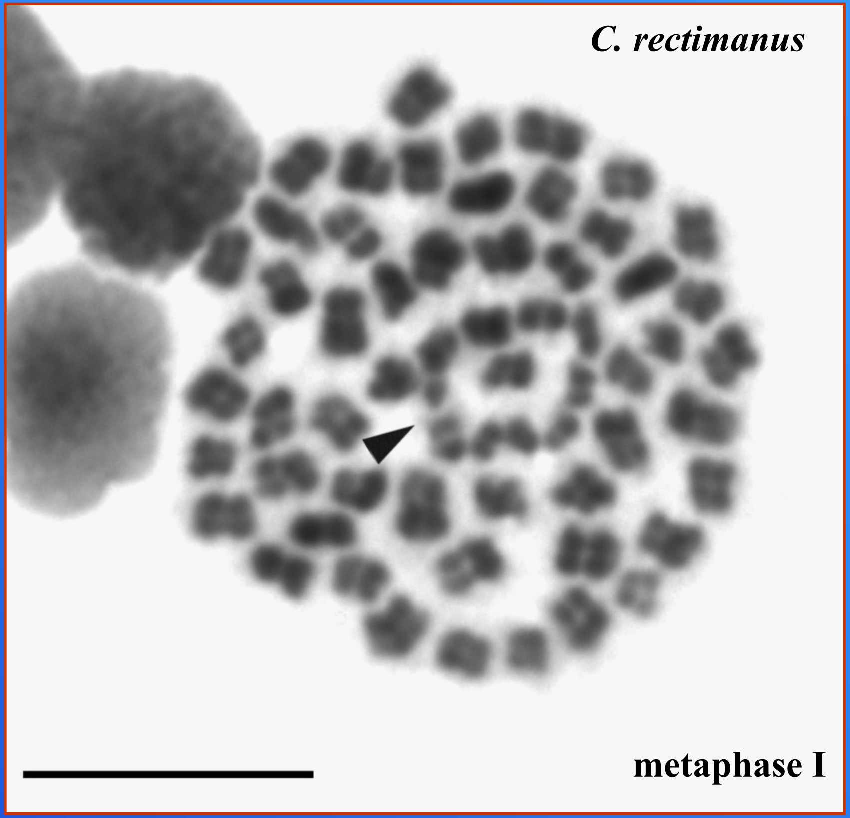
Sex chromosomes not differentiated morphologically

male meiosis achiasmatic, female meiosis ?



A considerable interspecific and intraspecific diversity o karyotypes, a frequent occurrence of multiple reciprocal translocations in populations





In heterozygotes, chromosomes involving translocations form chains or circles during meiotic division

Pedipalpi: Amblypygi, Uropygi a Schizomida

Amblypygi 220, Thelyphonida 124, Schizomida approx. 300 species

Published data include 18 amblypygids,1 thelyphonid, and 2 schizomids. We dispose unpublished data on approx. other 40 species.

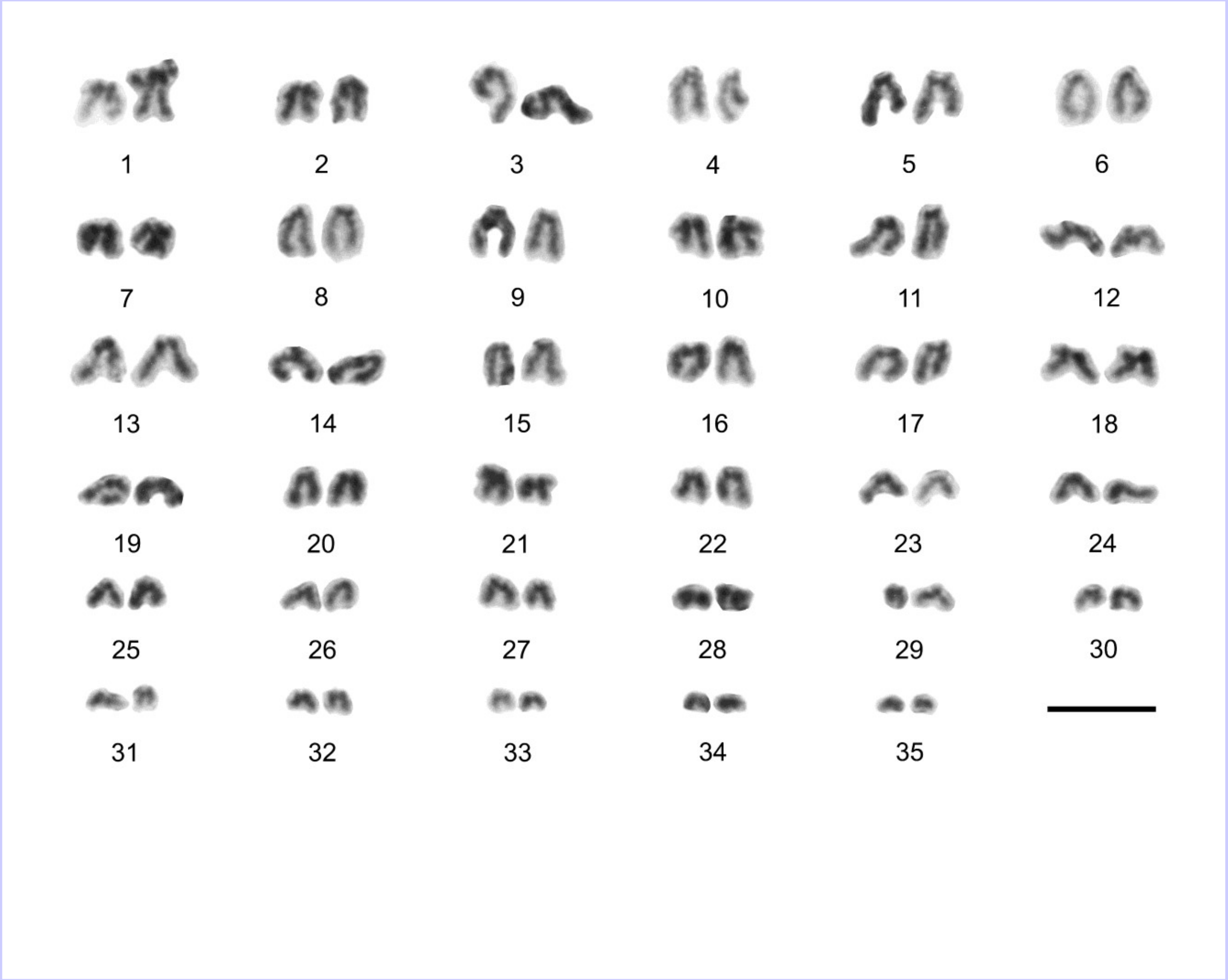
Monocentric chromosomes.

Amblypygi and Thelyphonida: considerable interspecific diversity of karyotypes (Amblypygi 2n = 22-86, Uropygi 28-78), in most species 2n > 50.

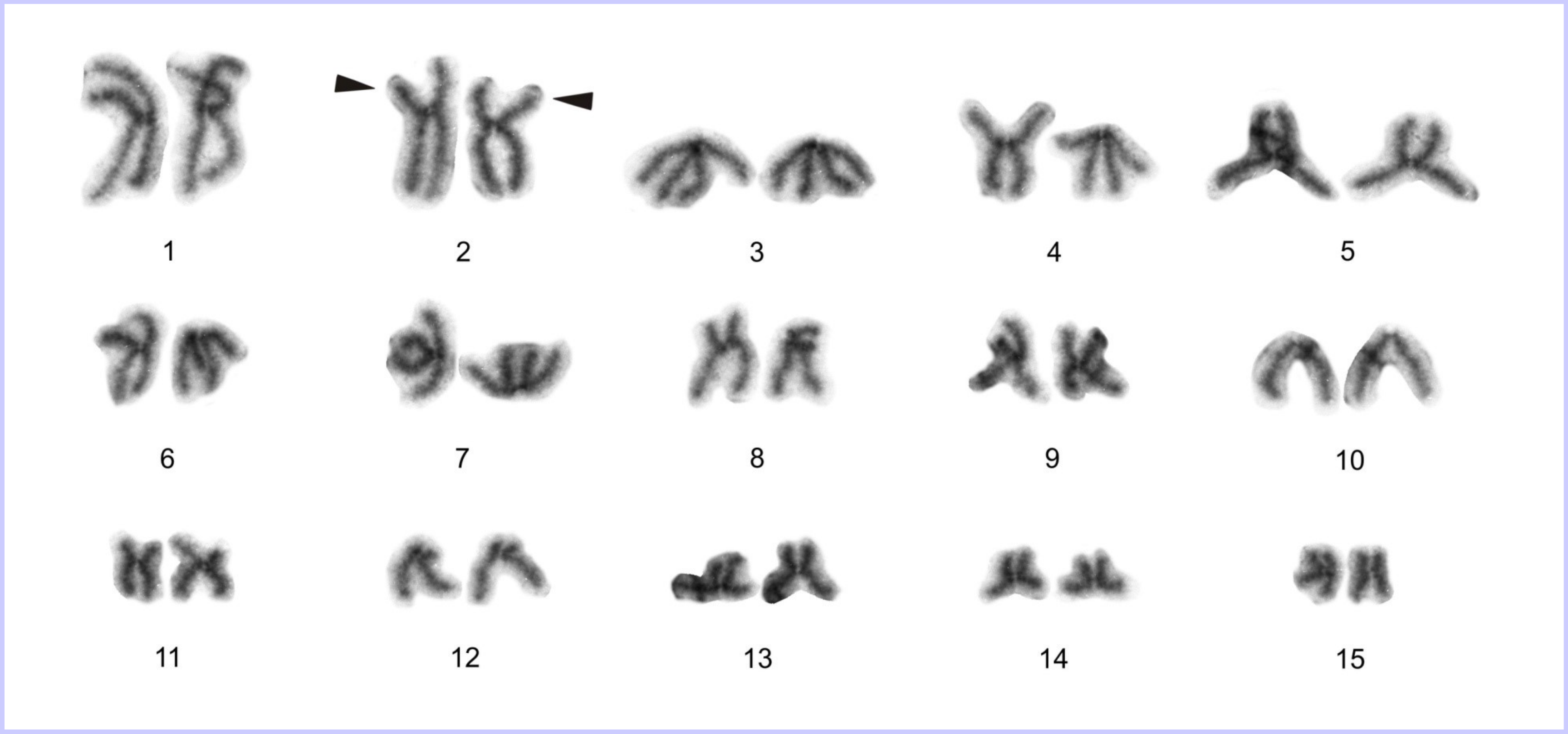
Low number of terminal NORs (1-3)

Amblypygids and uropygids with a high diploid numbers: Predomination of monoarmed chromosomes

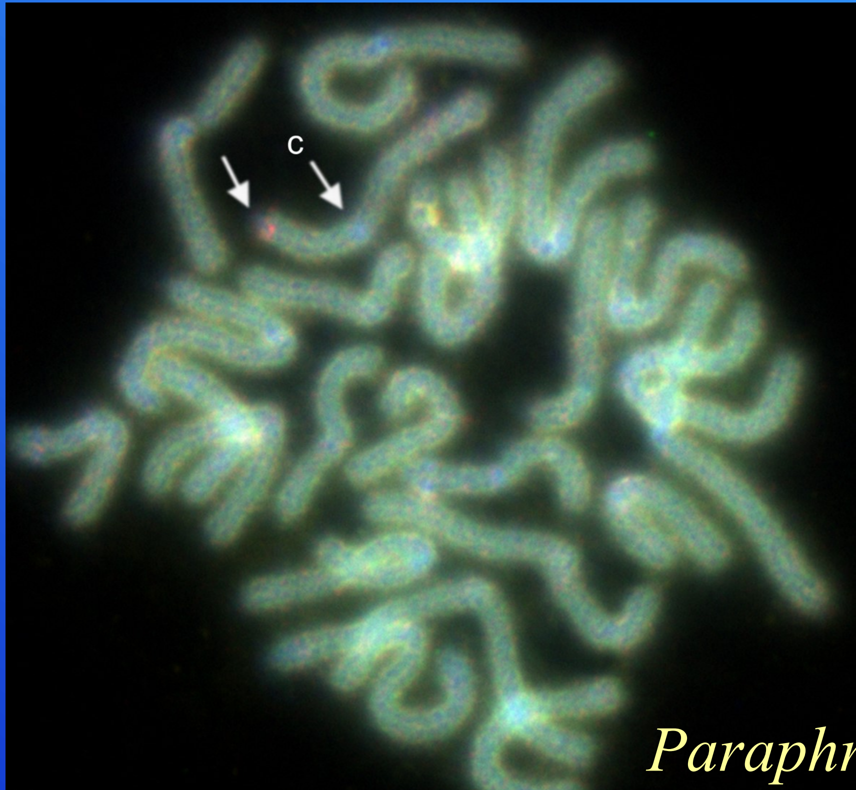
Charon grayi, ♂
(Charontidae,
Amblypygi)
2n = 70
metaphase II

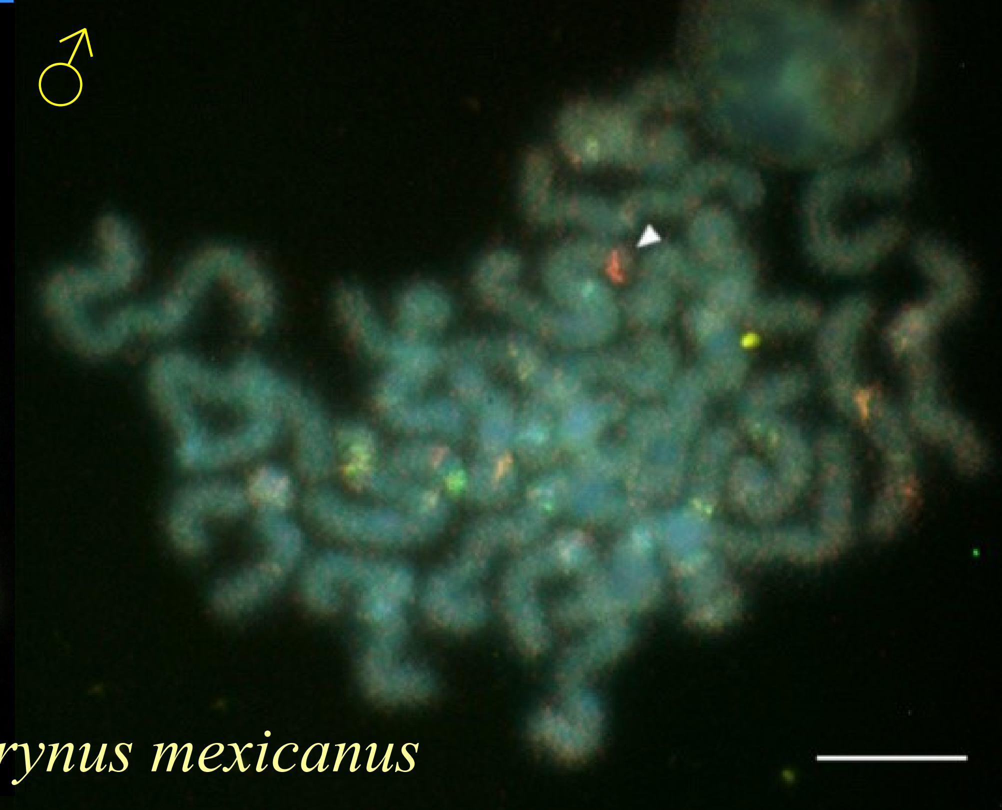


Decrease of diploid number in many lineages
Accompanied by increase of number of biarmed pairs: centric fusions
Total number of chromosome arms changed during decrease of 2n: involvement of pericentric inversions



Phrynichus deflersi arabicus (Phrynichidae, Amblypygi), ♂, 2n = 30, metaphase II

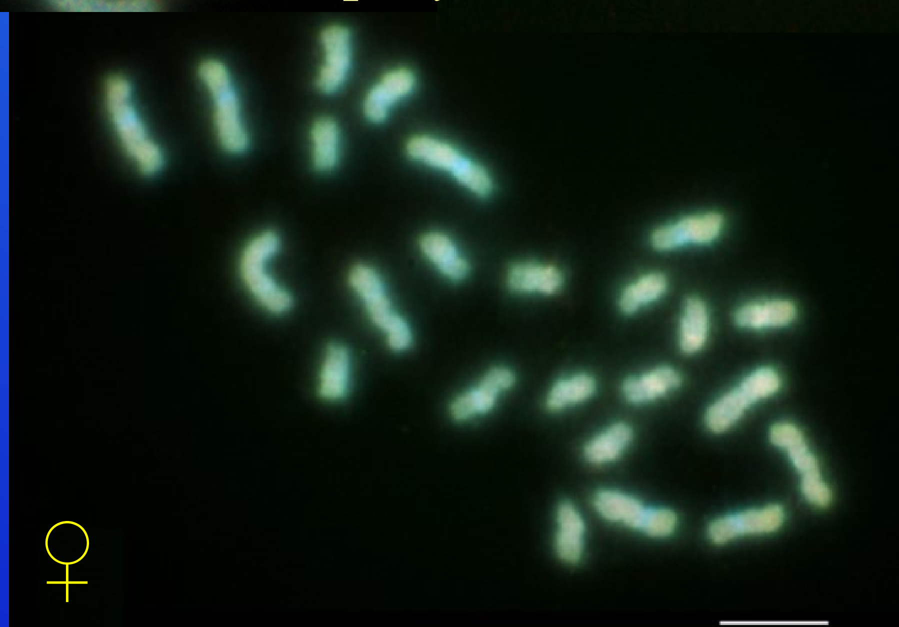




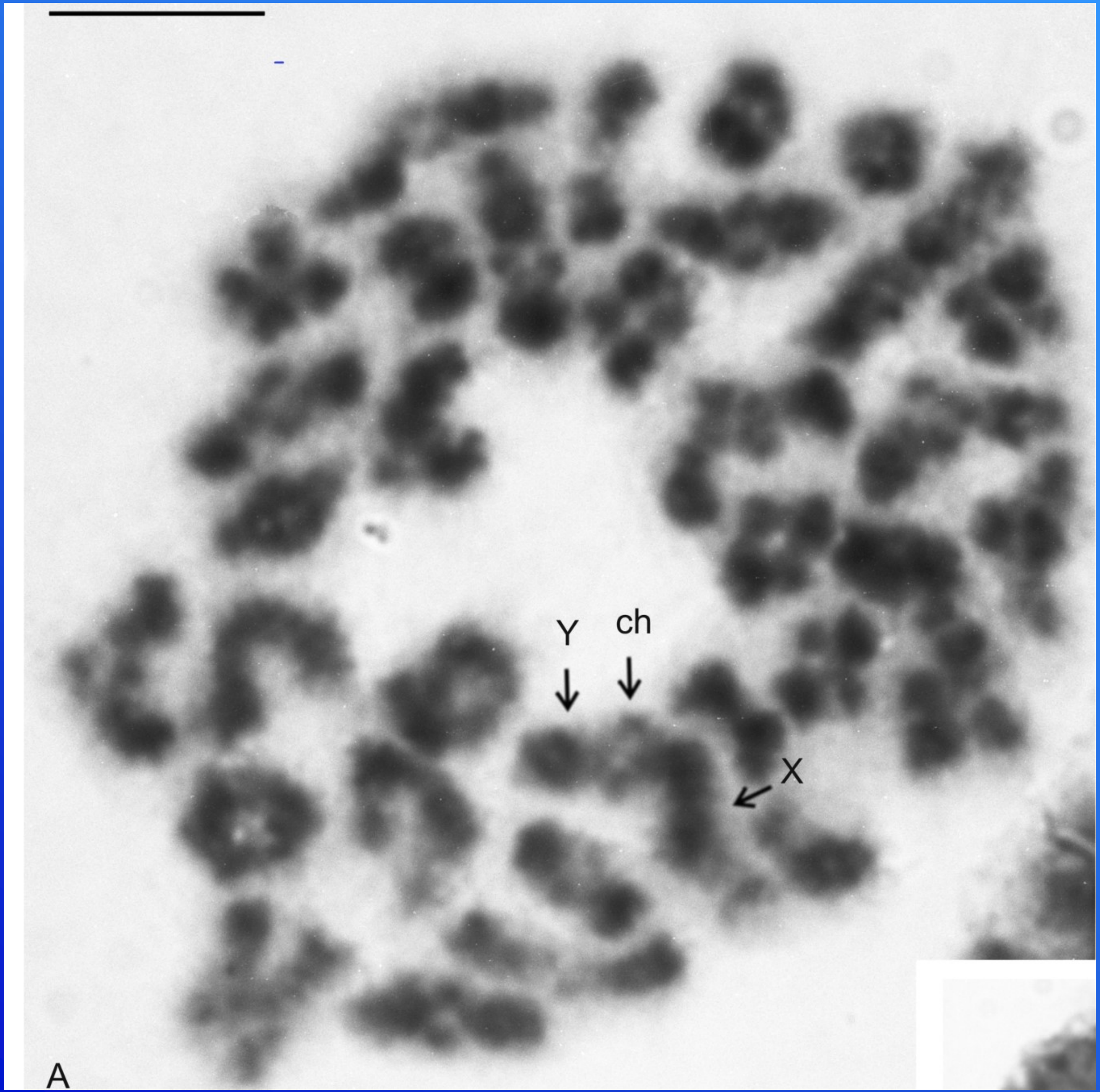
Paraphrynus mexicanus

sex chromosome detection

Comparative genomic hybridization



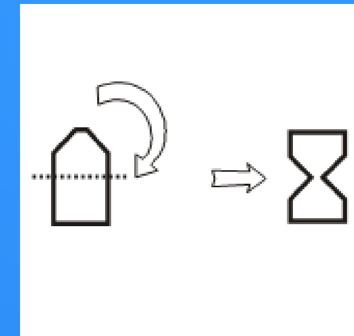
sex chromosome system ♂XY/♀XX



Thelyphonus cf. *linganus*
male metaphase I

note hetetomorphic
bivalent XY

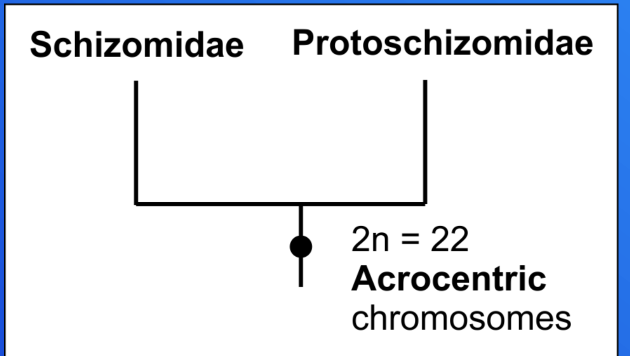
Damon medius, male

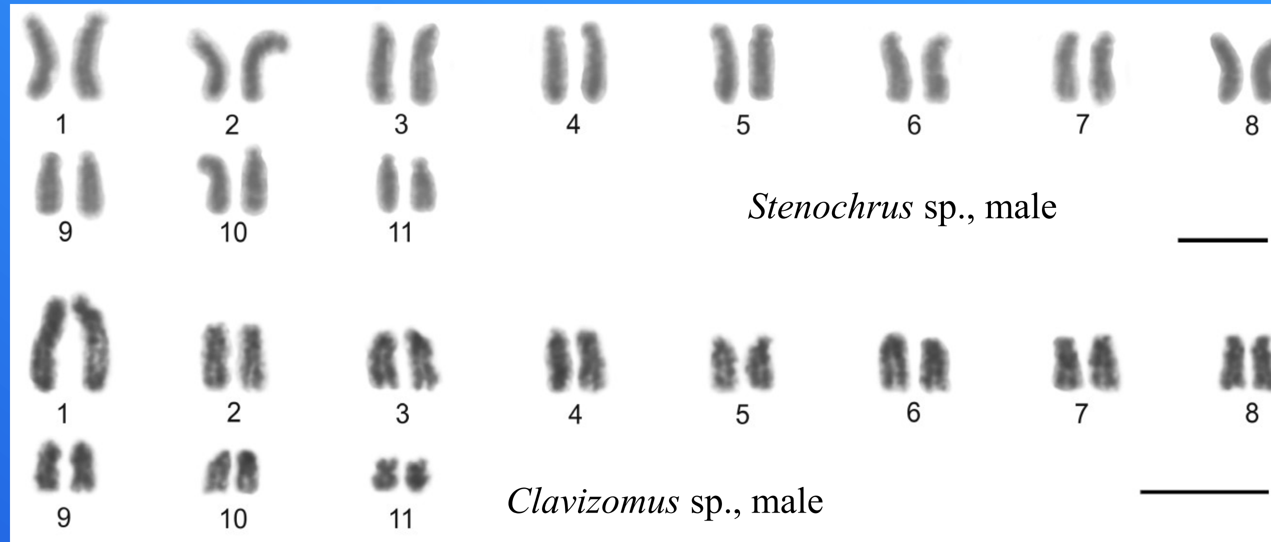


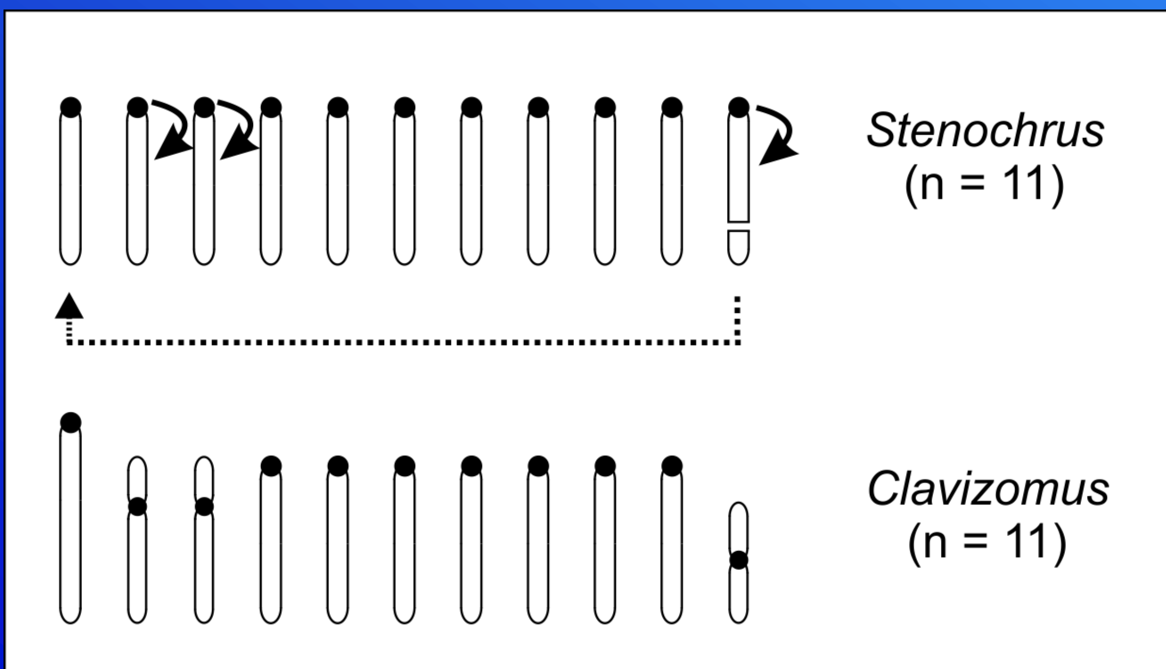
Togo: 2n = 72

Senegal: 2n = 70

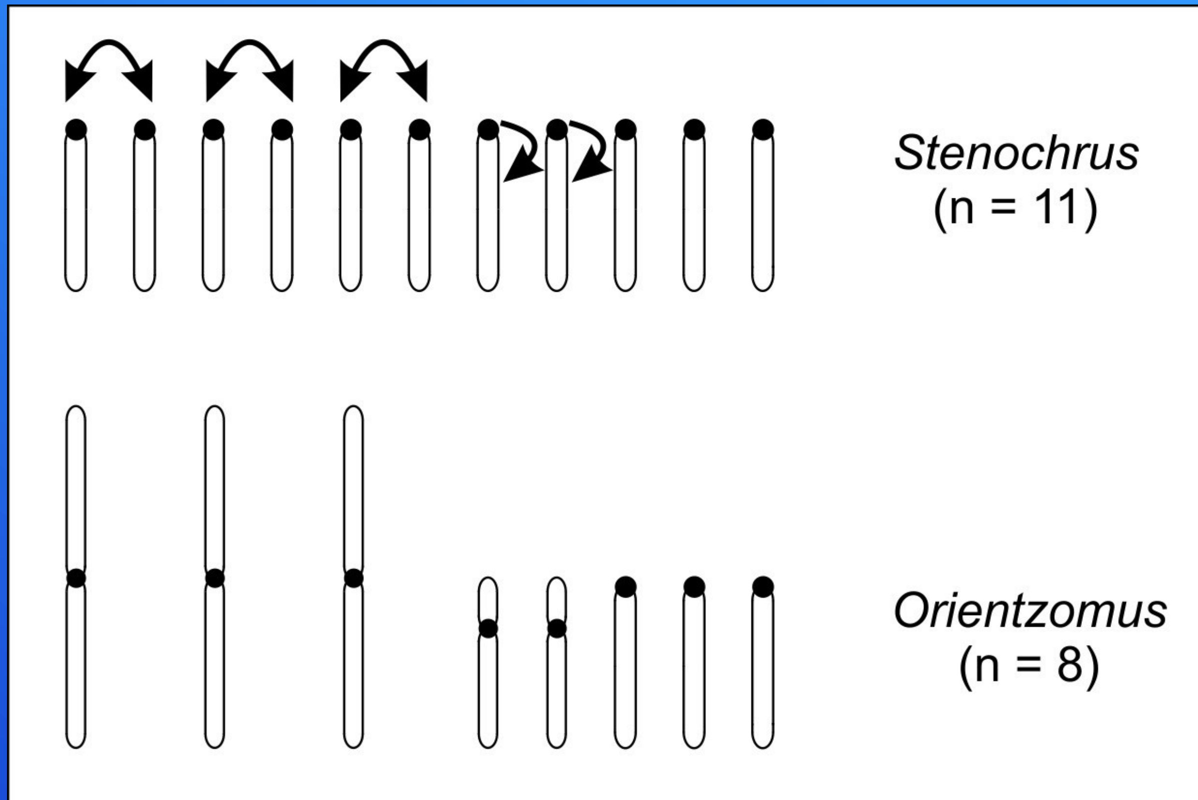
Schizomida

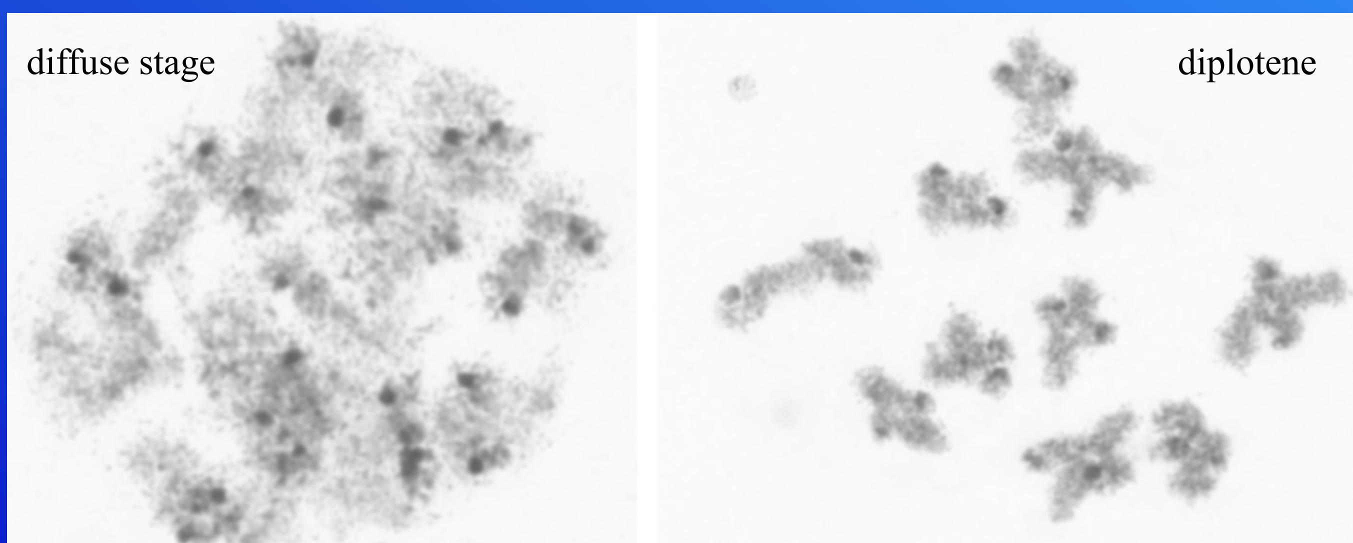


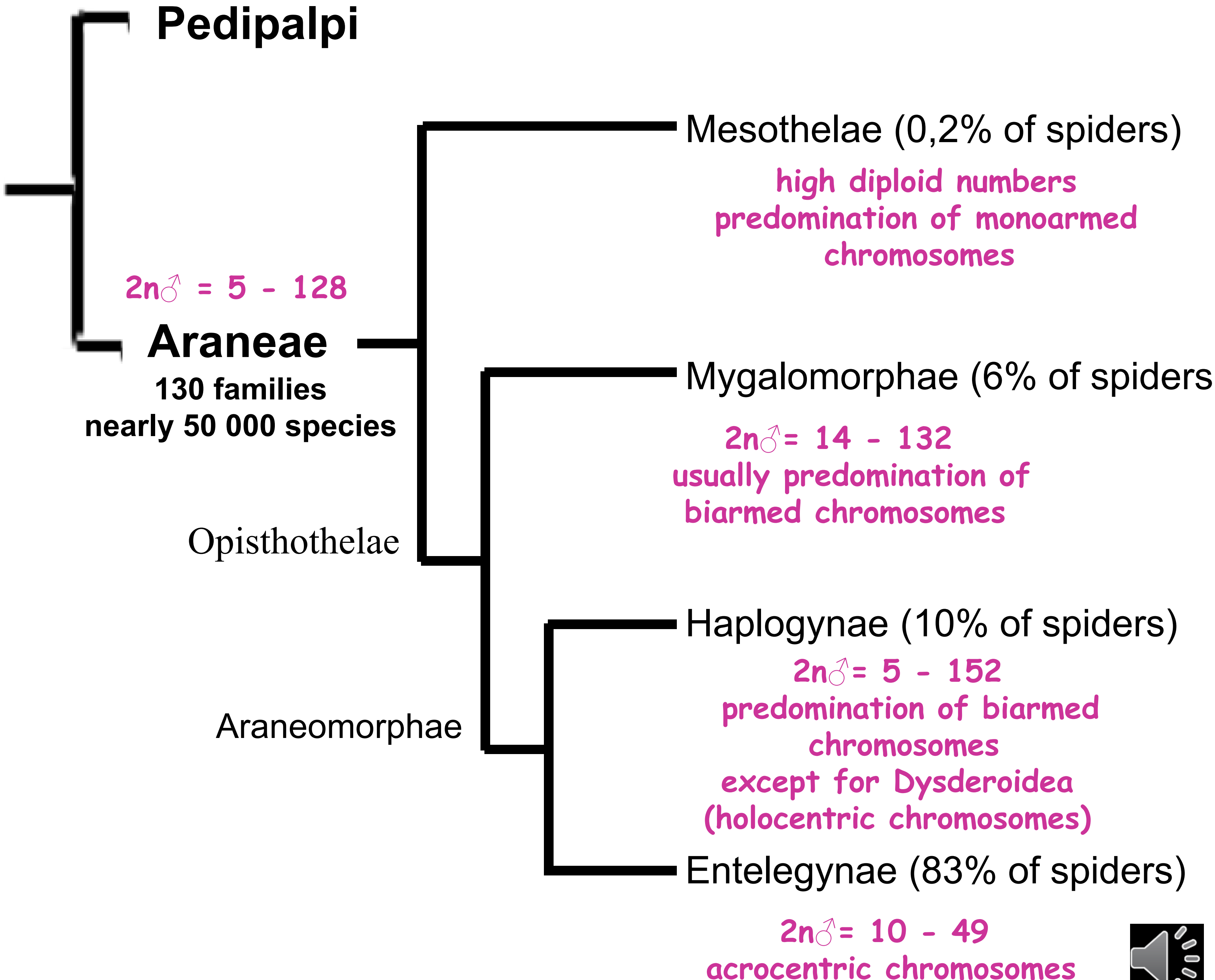




very low chromosome numbers
(2n = 16 – 22)
usually predomination of acrocentric chromosomes

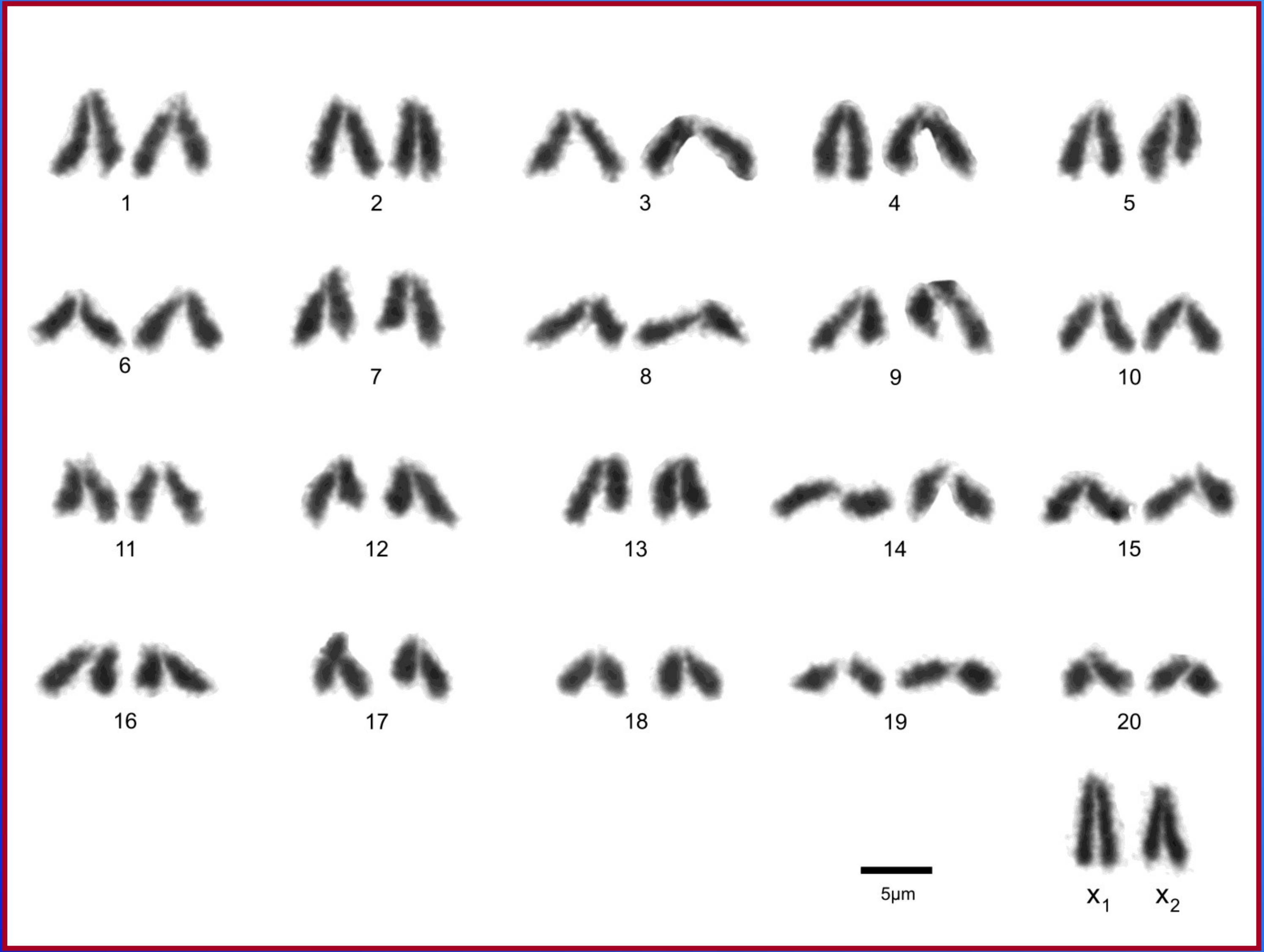

Stenochrus
(n = 11)
Orientzomus
(n = 8)


diffuse stage
diplotene



Pedipalpi
2n♂ = 5 - 128
Araneae
130 families
nearly 50 000 species
Mesothelae (0,2% of spiders)
high diploid numbers
predomination of monoarmed chromosomes
Opisthothelae
Mygalomorphae (6% of spiders)
2n♂= 14 - 132
usually predomination of biarmed chromosomes
Araneomorphae
Haplogynae (10% of spiders)
2n♂= 5 - 152
predomination of biarmed chromosomes
except for Dysderoidea (holocentric chromosomes)
Entelegynae (83% of spiders)
2n♂= 10 - 49
acrocentric chromosomes

Ancestral karyotype of entelegyne spiders

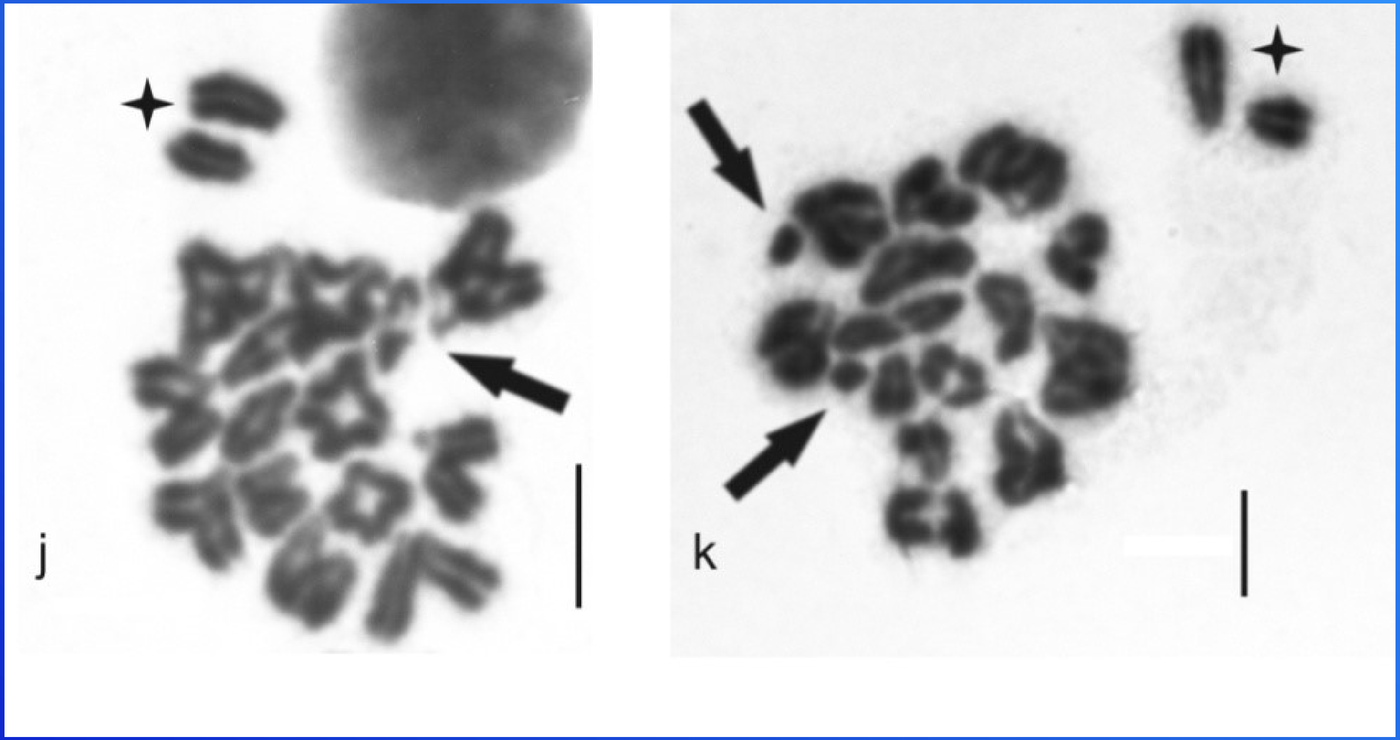


Paracoelotes birulai (Agelenidae): 2n♂ = 42 (metaphase II)

Decrease of diploid numbers by cycles of centric fusions and pericentric inversions or tandem fusions

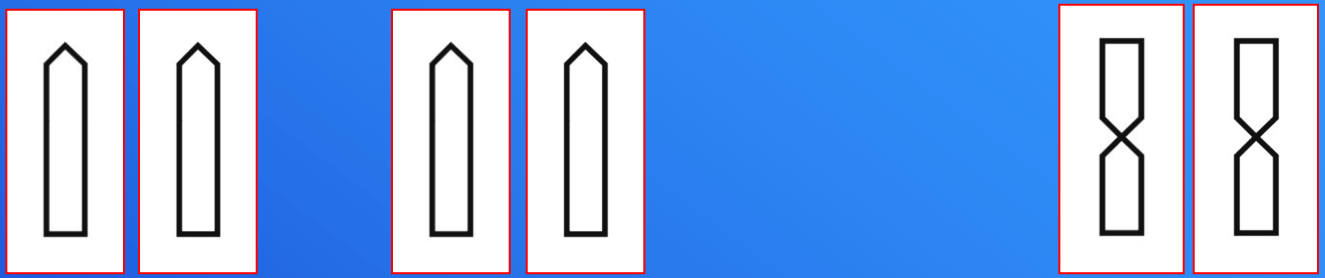
these rearrangements do not change acrocentric morphology

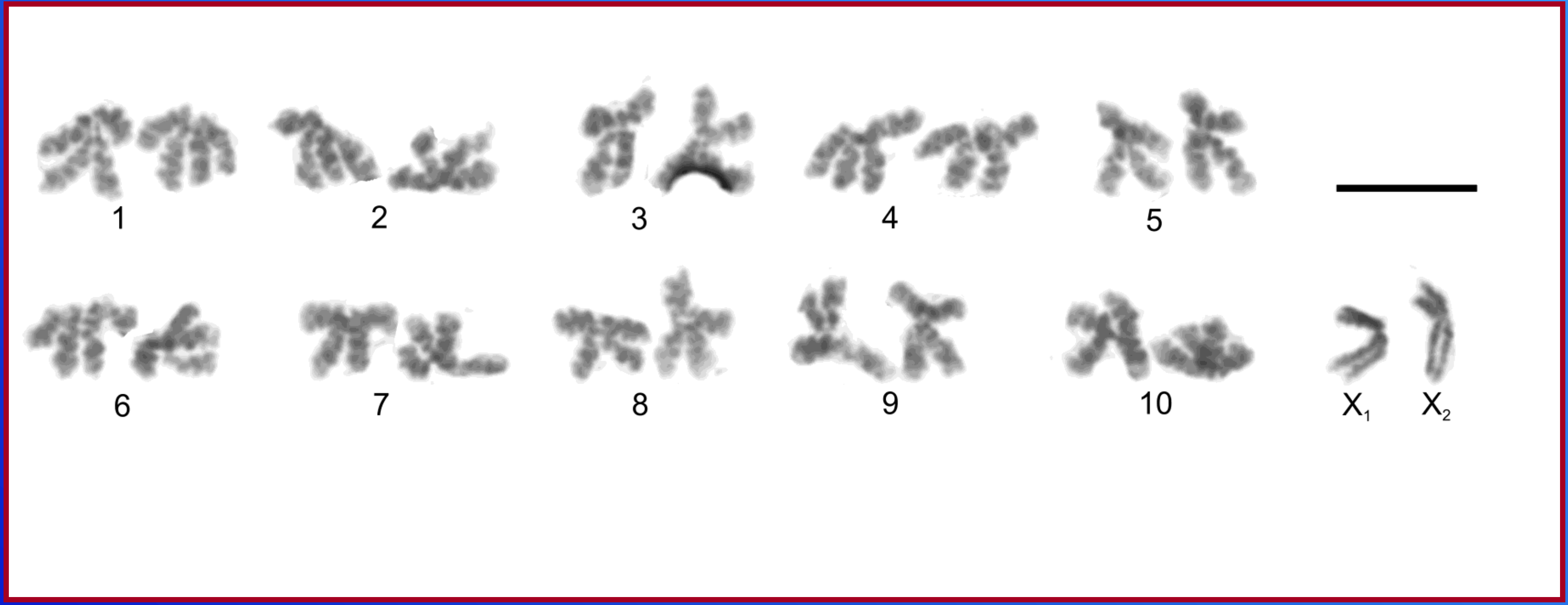
- centric fragments – remnants of tandem fusions



Stegodyphus africanus (Eresidae)

Karyotype saturated by biarmed chromosomes pericentric inversions or centric fusions

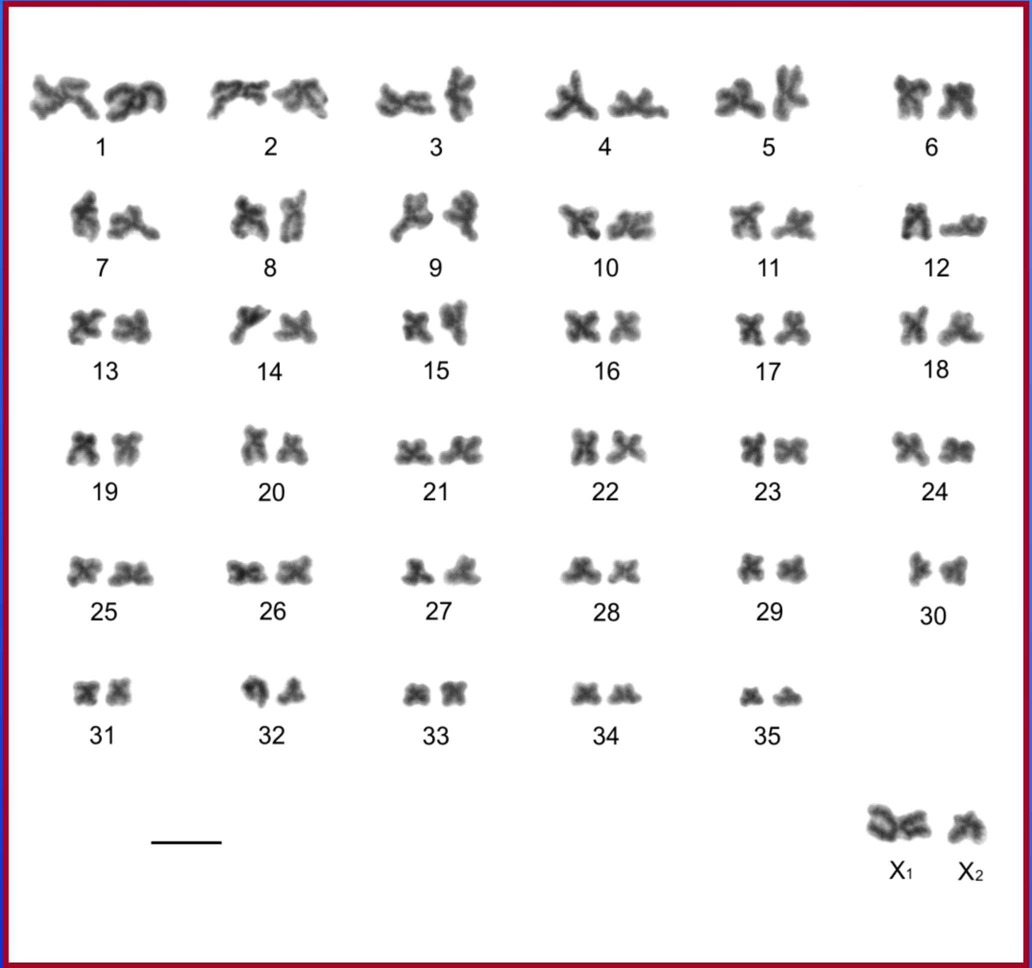




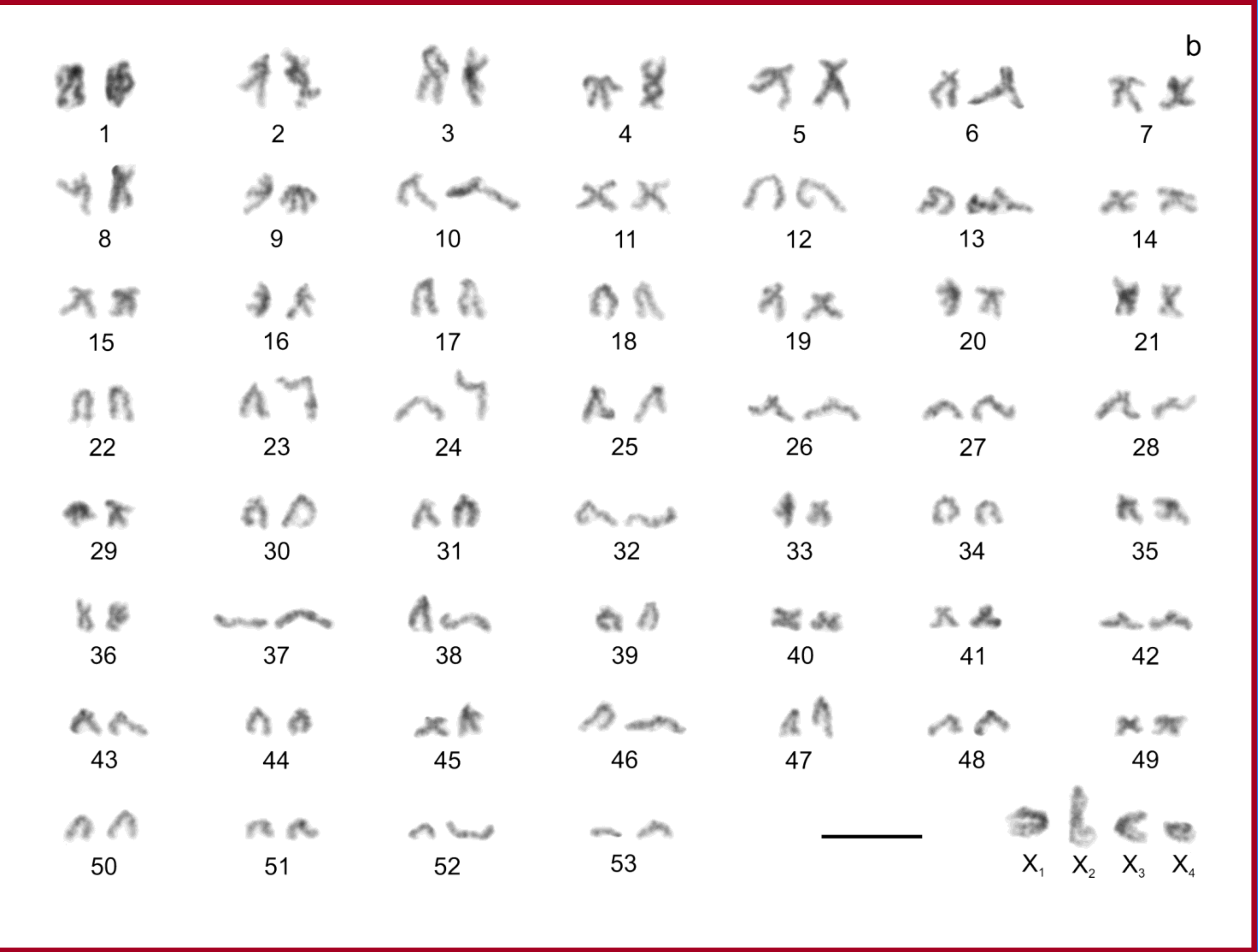
Tegenaria fuesslini (Agelenidae), 2n♂ = 22 (metaphase II)

Mygalomorphs

- usually high diploid numbers (14-132)
- predomination of biarmed chromosomes
- considerable interspecific diversity of karyotypes

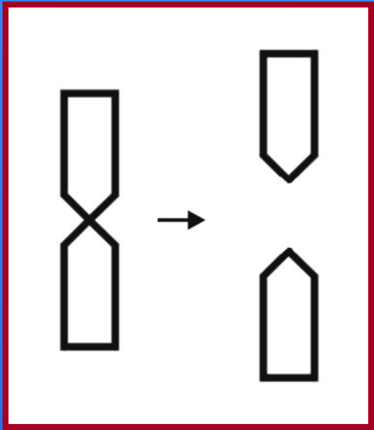


Grammostola rosea (Theraphosidae)
2n♂ = 72, mephase II



Poecilotheria formosa
(Theraphosidae)
2n♂ = 110

metaphase II



A high proportion of acrocentric autosomal pairs in mygalomorphs with highest diploid numbers

Probably reflect frequent centric fissions of biarmed chromosomes

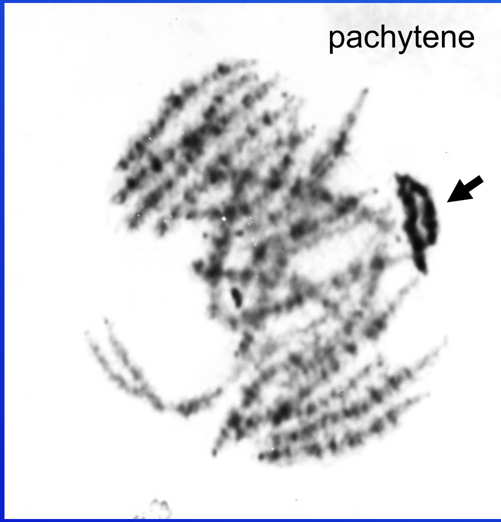
Most spiders exhibit multiple X chromosome systems

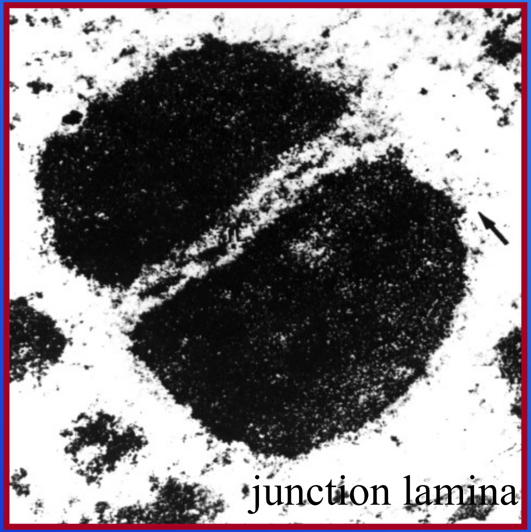
Entelegyne spiders

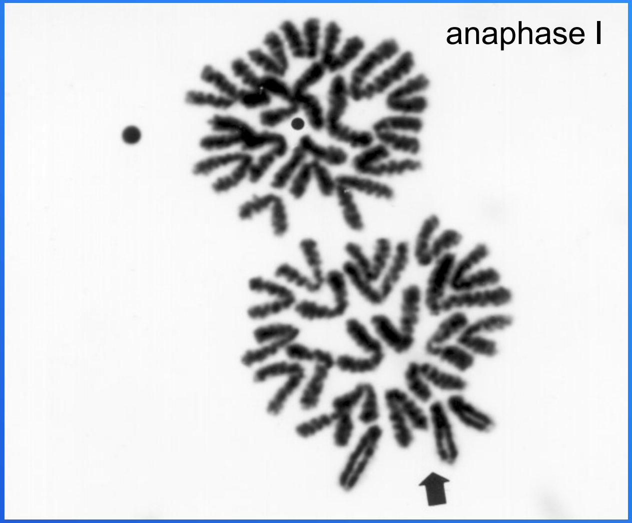
Systems ♂X_1X_2/♀$X_1X_1X_2X_2$ (X_1X_20), ♂$X_1X_2X_3$/♀$X_1X_1X_2X_2X_3X_3$ ($X_1X_2X_30$), ♂$X_1X_2X_3X_4$/♀$X_1X_1X_2X_2X_3X_3X_4X_4$ ($X_1X_2X_3X_40$)

most frequent X_1X_20 system

specific behaviour during male meiosis



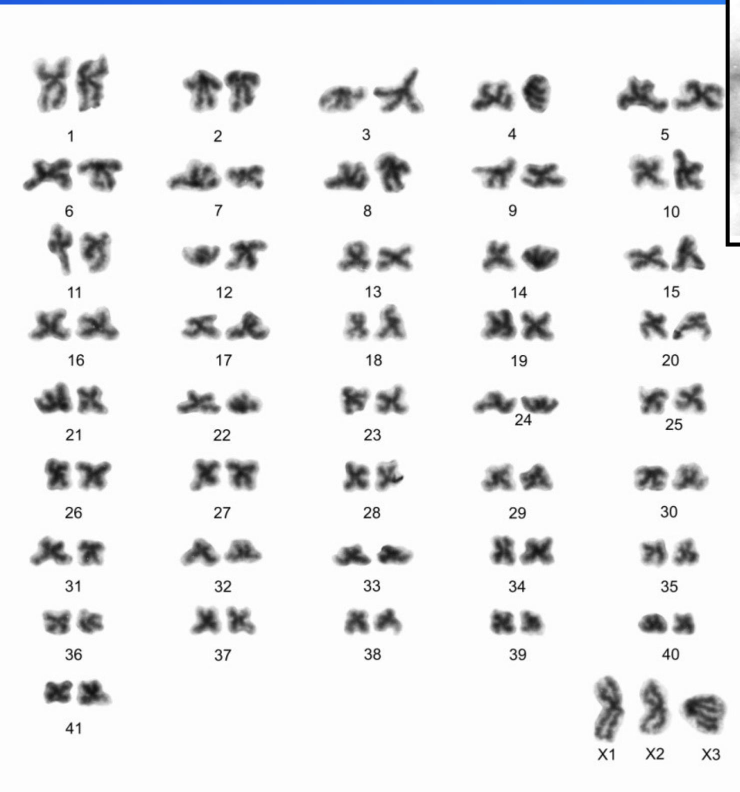




inactivation, pairing in parallel, without recombinations

segregation to the same po
association of sister chromat

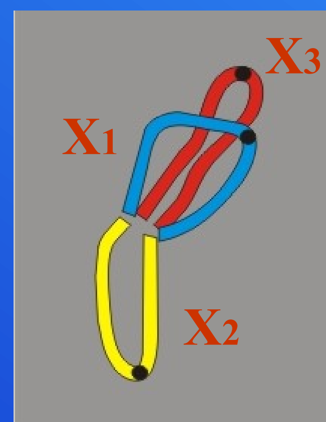
Ischnocolus jickelii (Theraphosidae)



$2n♂ = 85, X_1X_2X_30$

metaphase II

metaphase I



Avicularia minatrix (Theraphosidae)

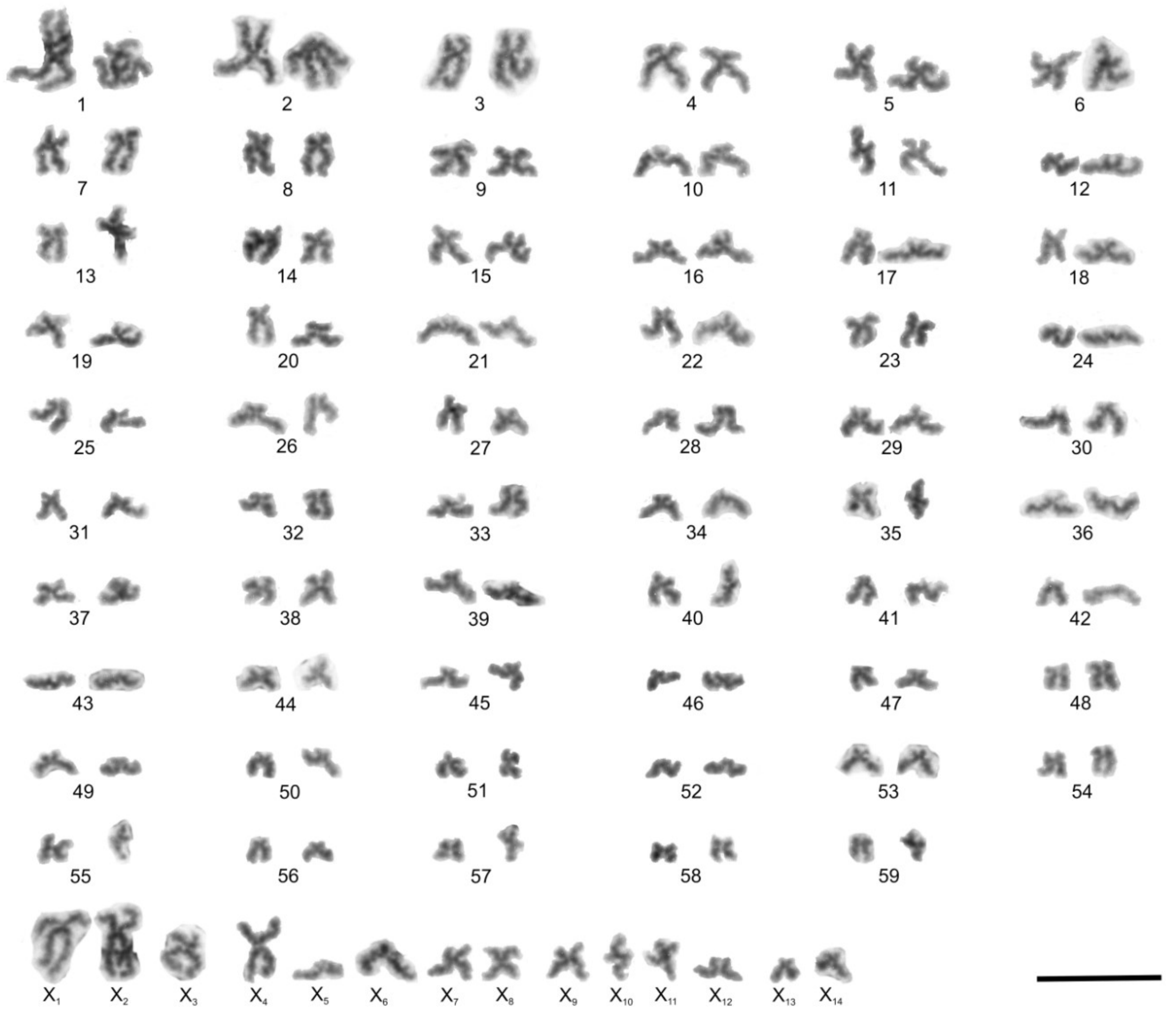
$2n♂ = 78, X_1X_2X_3X_40$

metaphase II

Macrothele (Macrothelidae)

Macrothele calpeiana, male

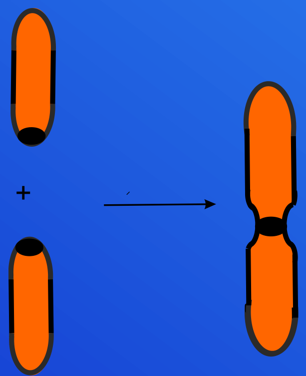
$118 + X_1X_2X_3X_4X_5X_6X_7X_8X_9X_{10}X_{11}X_{12}X_{13}X_{14}0$

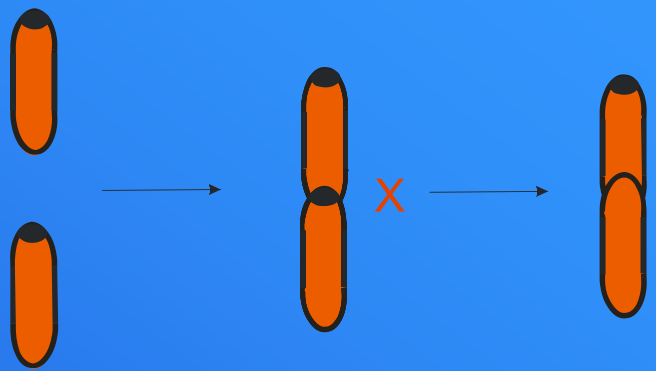


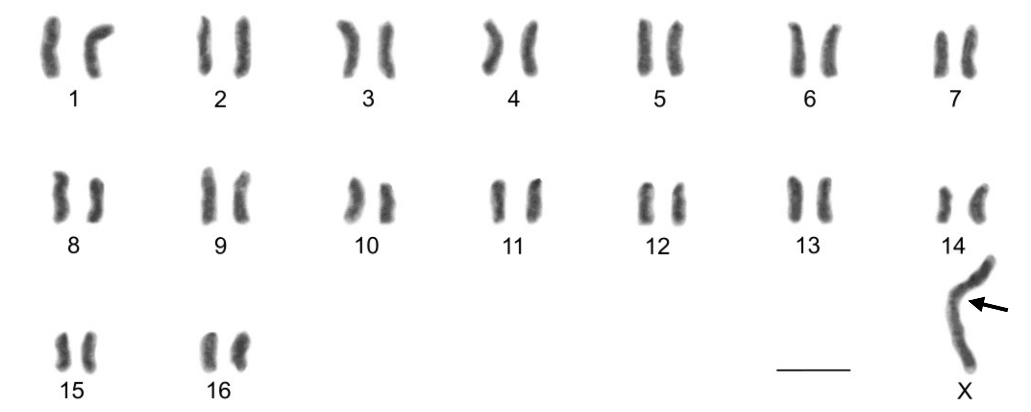
metaphase I

System X0

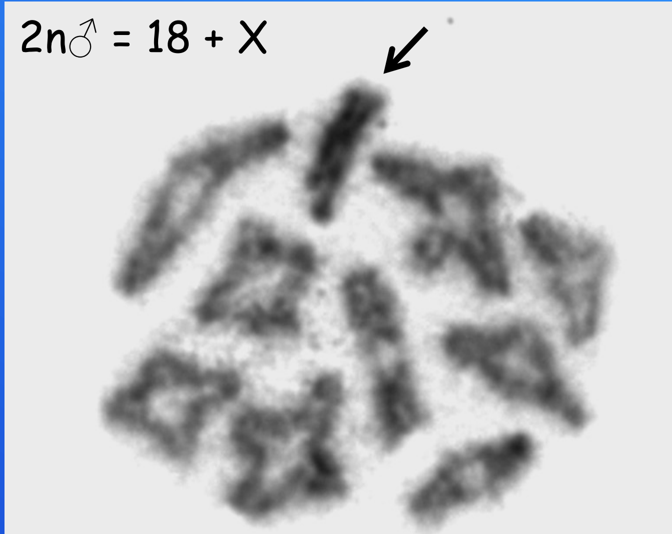
- found at all major spider clades
- arose independently many times by centric or tandem fusions between X chromosomes







Poecilomigas sp., male karyotype (32 + X)

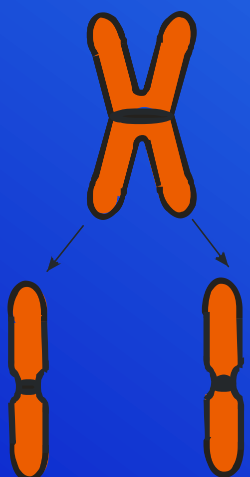


Oecobius navus metaphase I

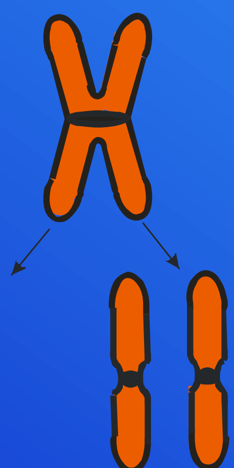
Origin of multiple X chromosomes in spiders

Nondisjunctional hypothesis

White 1940, Postiglioni and Brum-Zorrilla 1981



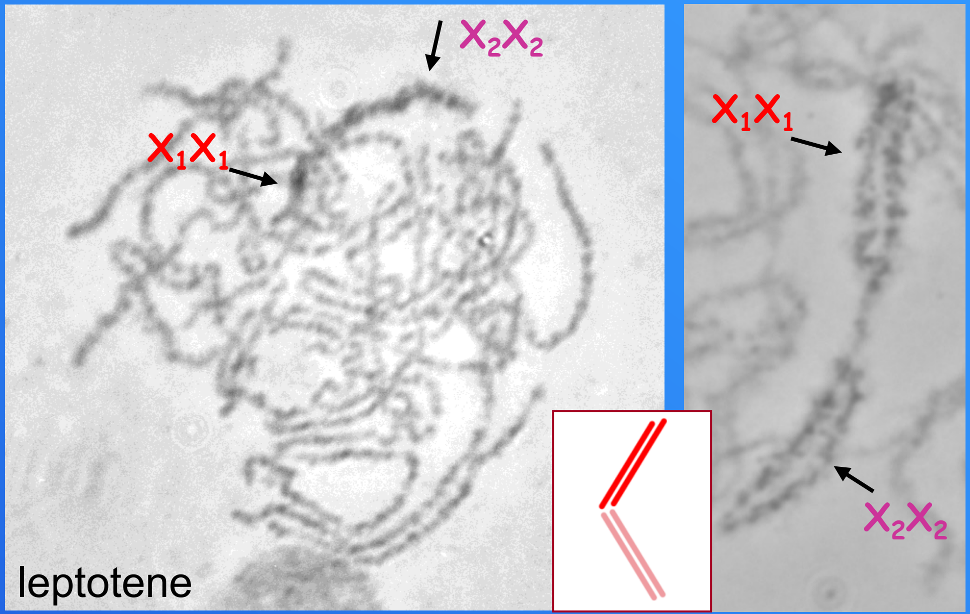
standard segregation

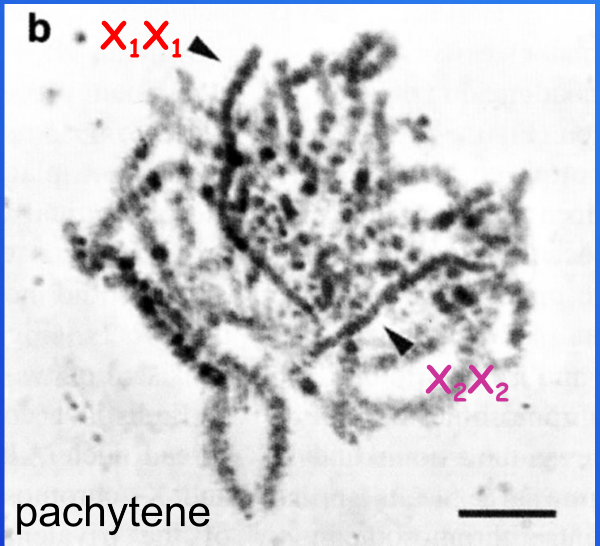


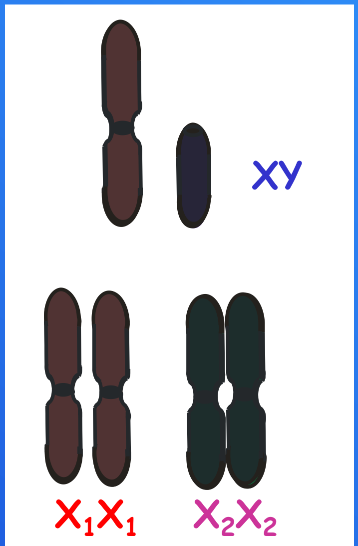
nondisjunctions

mitosis
second meiotic division

unique behaviour of multiple X chromosomes in female germline

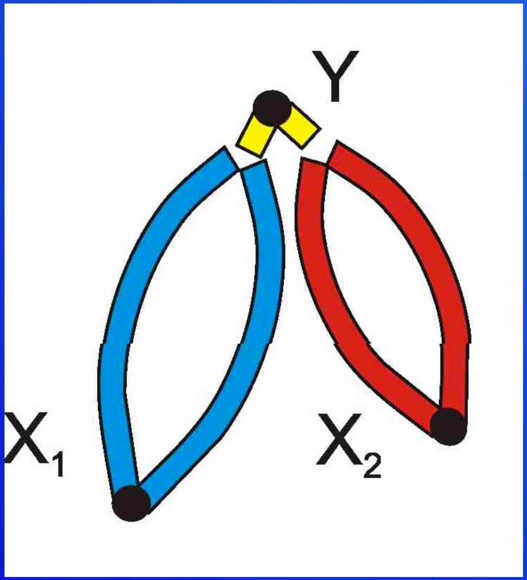


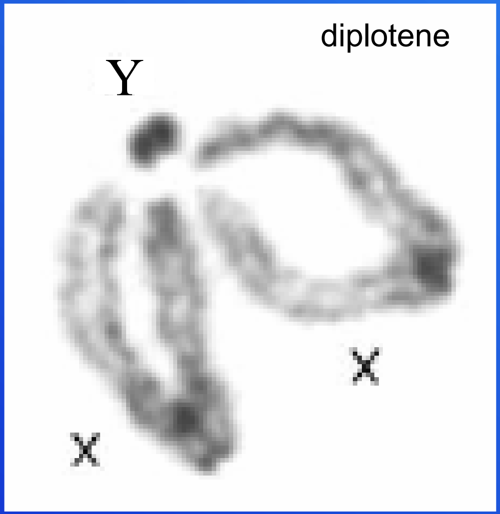


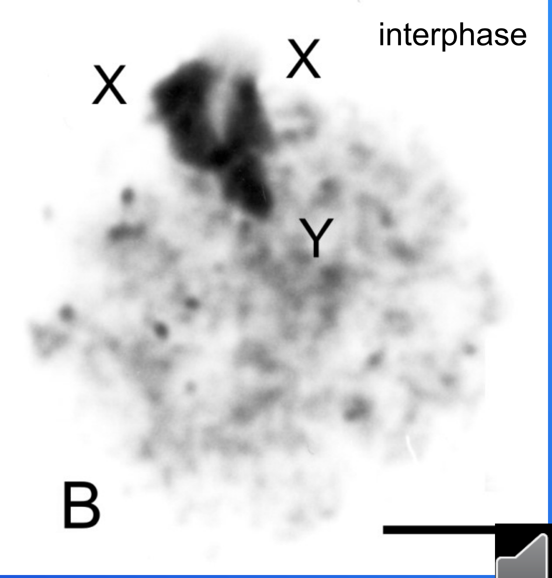


X_1X_2Y system

- probably ancestral for araneomorph spiders
- found in seven families of haplogyne spiders
- specific chromosome structure and meiotic pairing
- ancestral X_1X_2Y system formed by two large metacentric X chromosomes and metacentric Y microchromosome
- specific end-to-end pairing during male meiosis

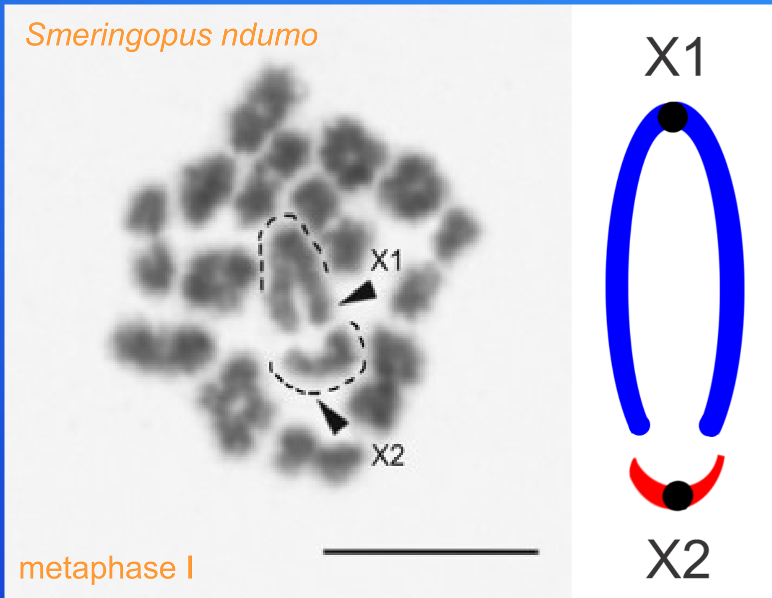




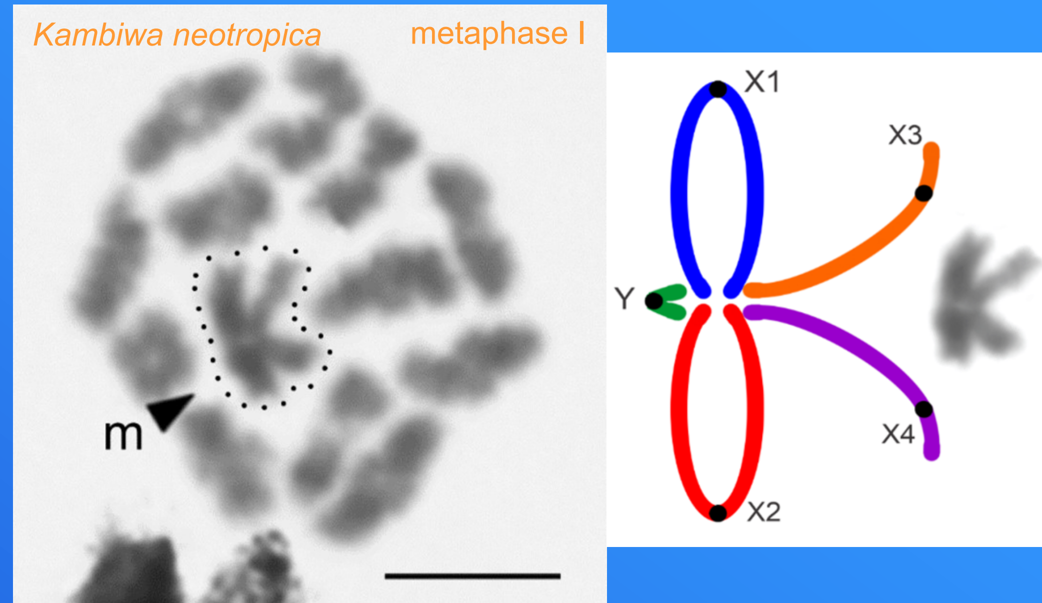


Loxosceles spinulosa

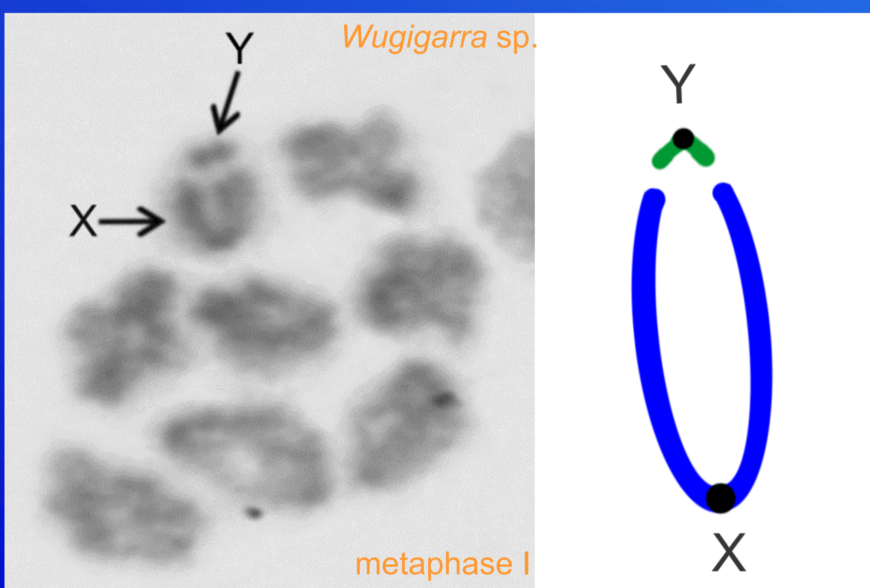
X_1X_20



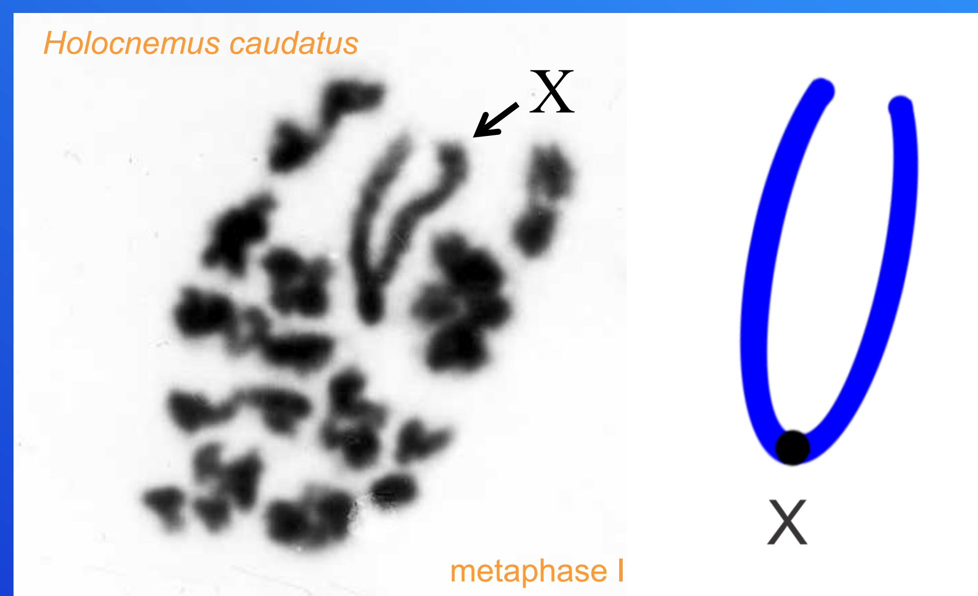
$X_1X_2X_3X_4Y$



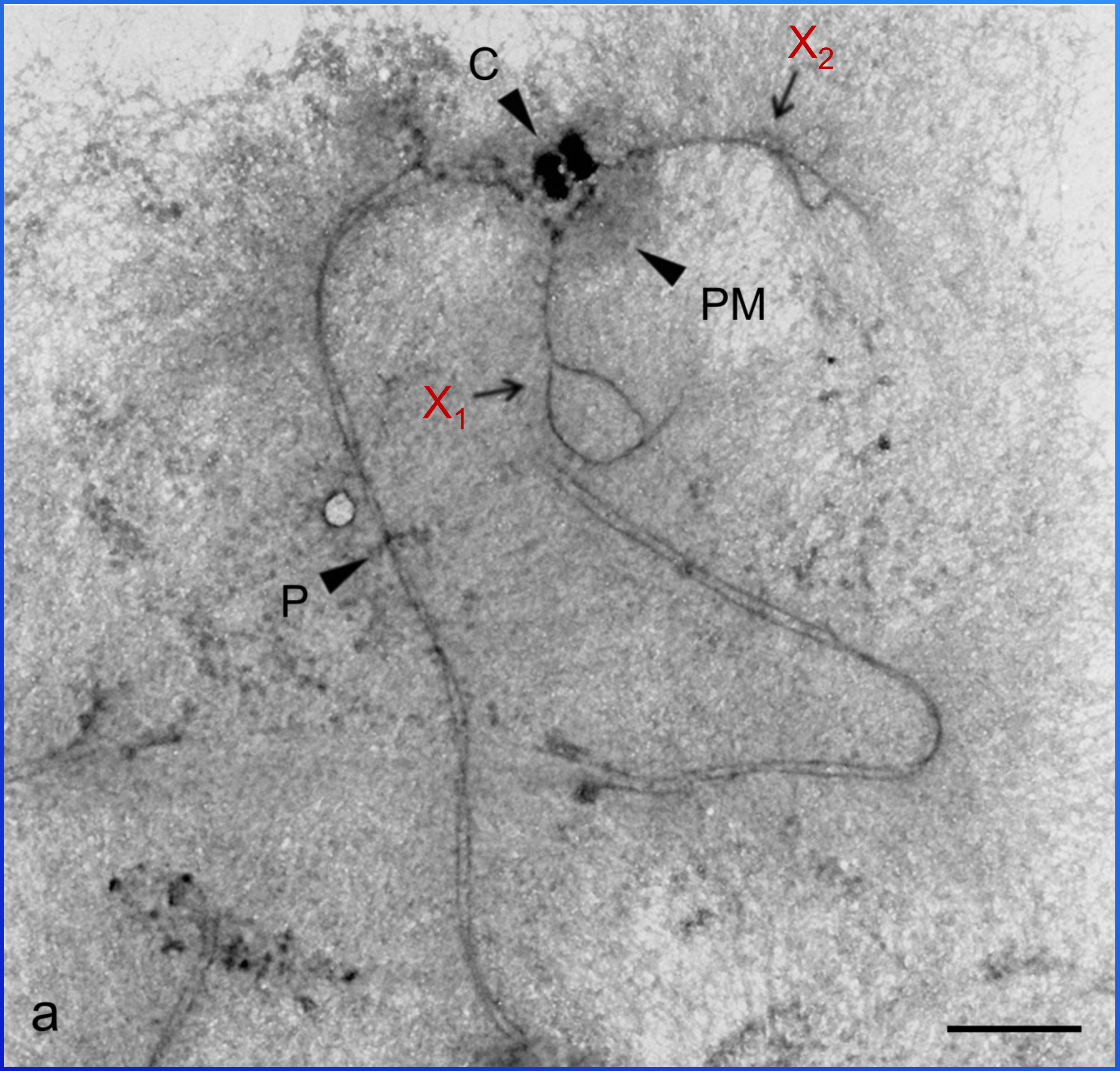
XY

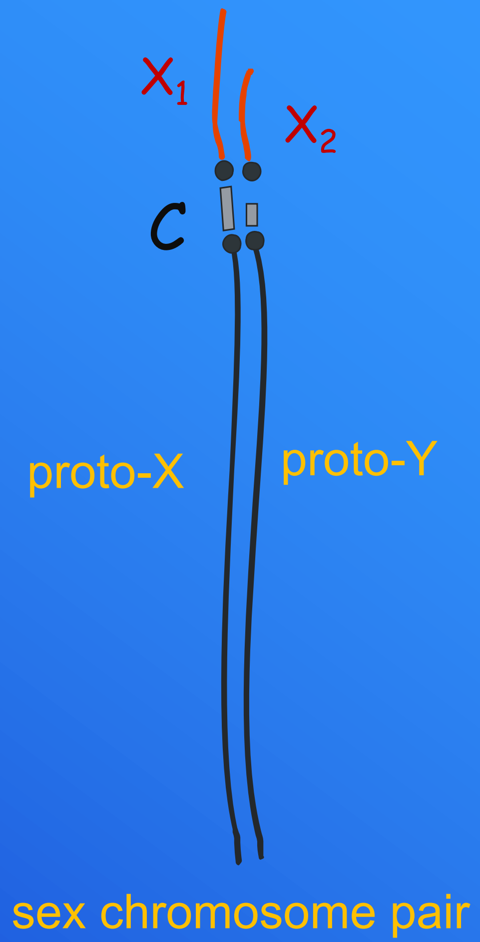


X0

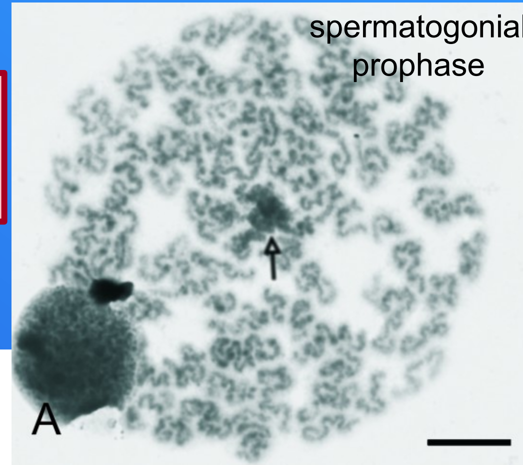


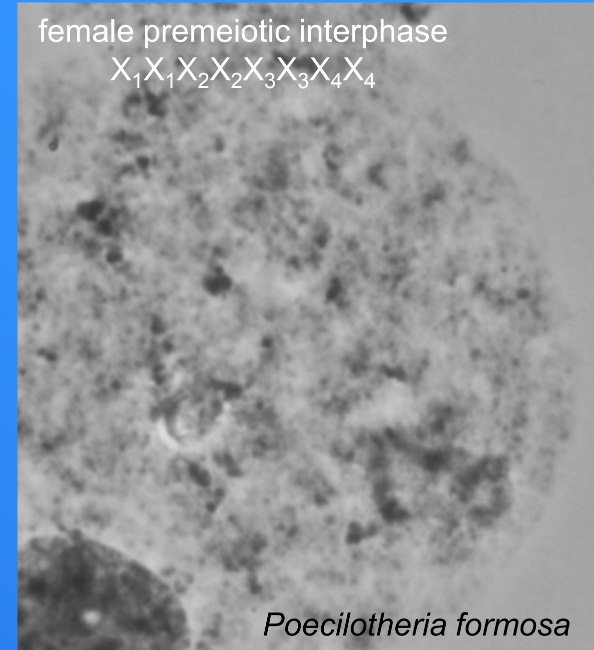
pair of homomorphic sex chromosomes associated with multiple X chromosomes or X_1X_2Y system

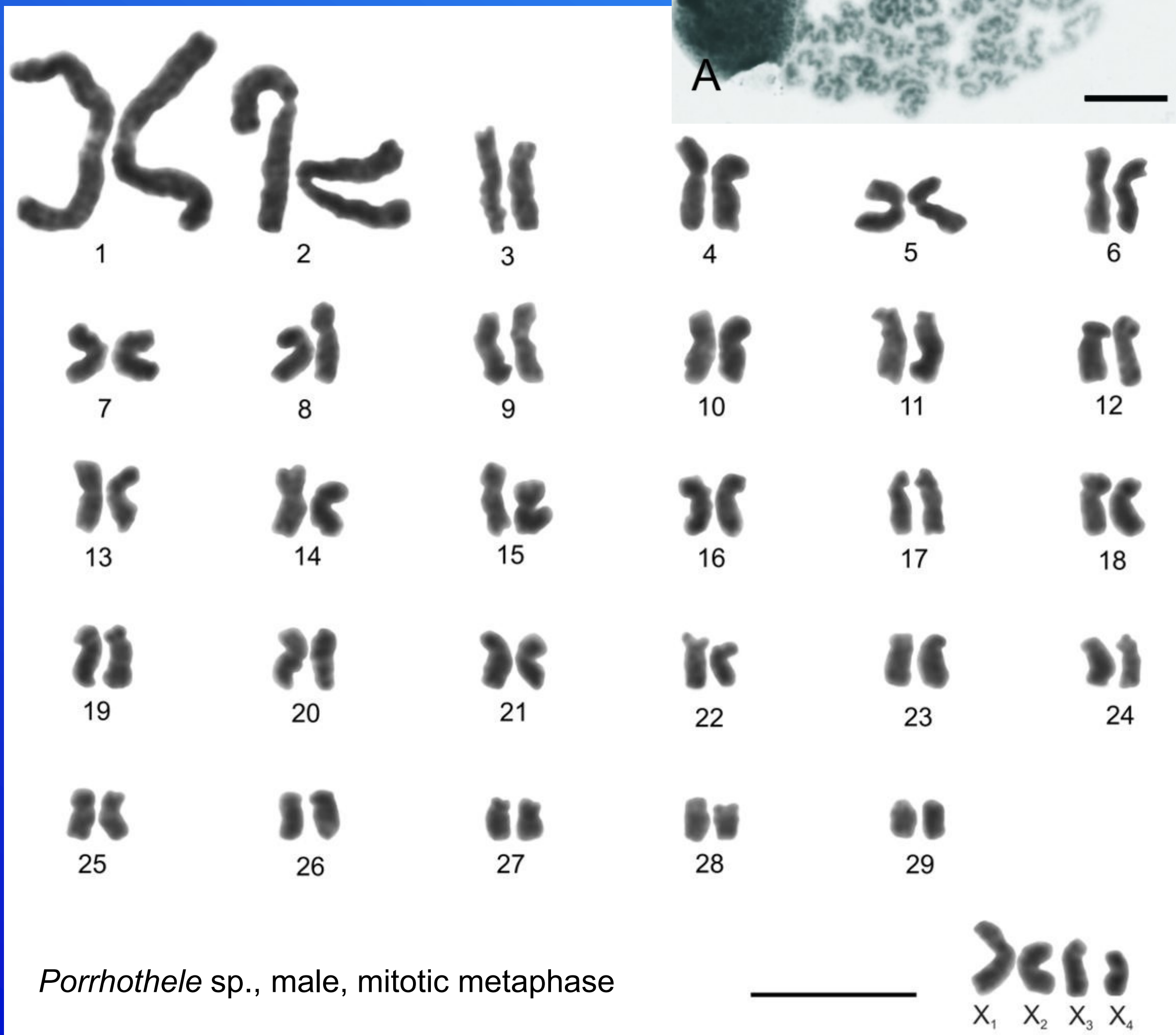


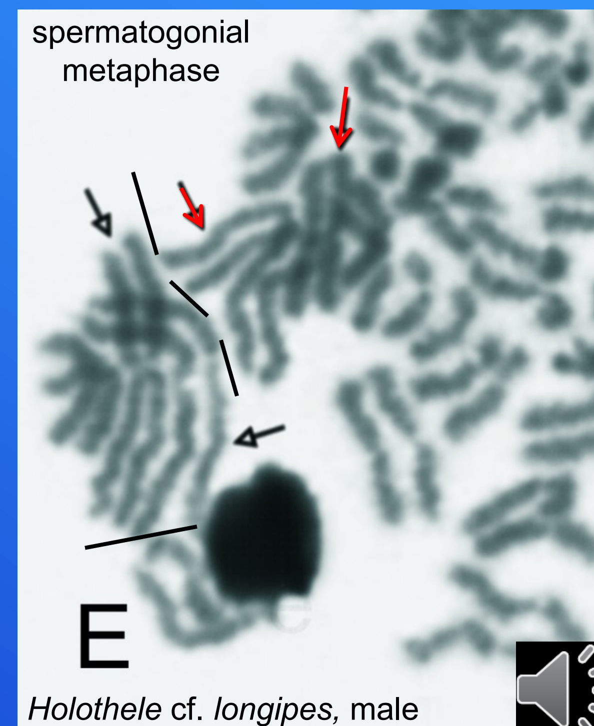


Sex chromosomes of avicularioid mygalomorphs

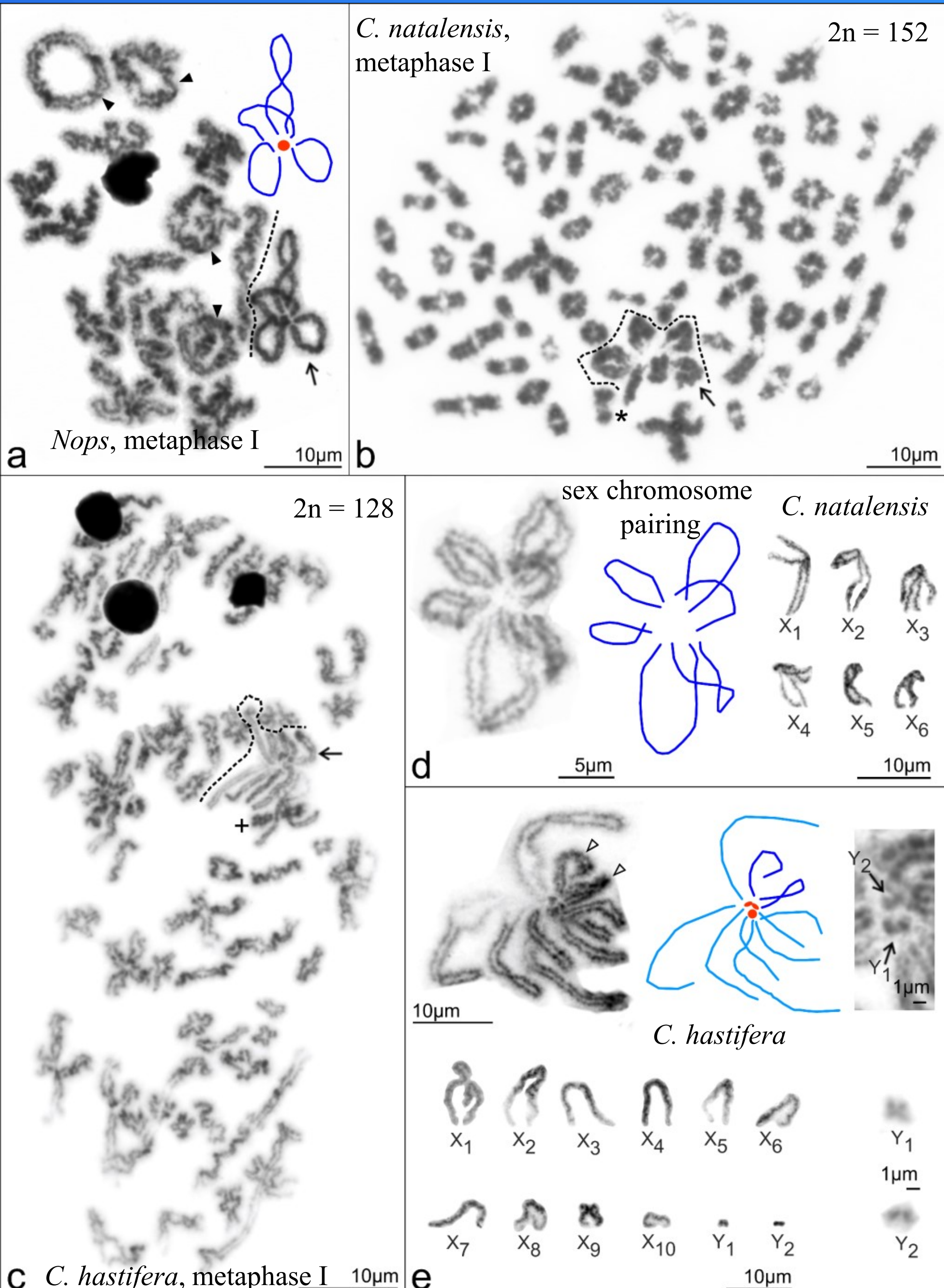


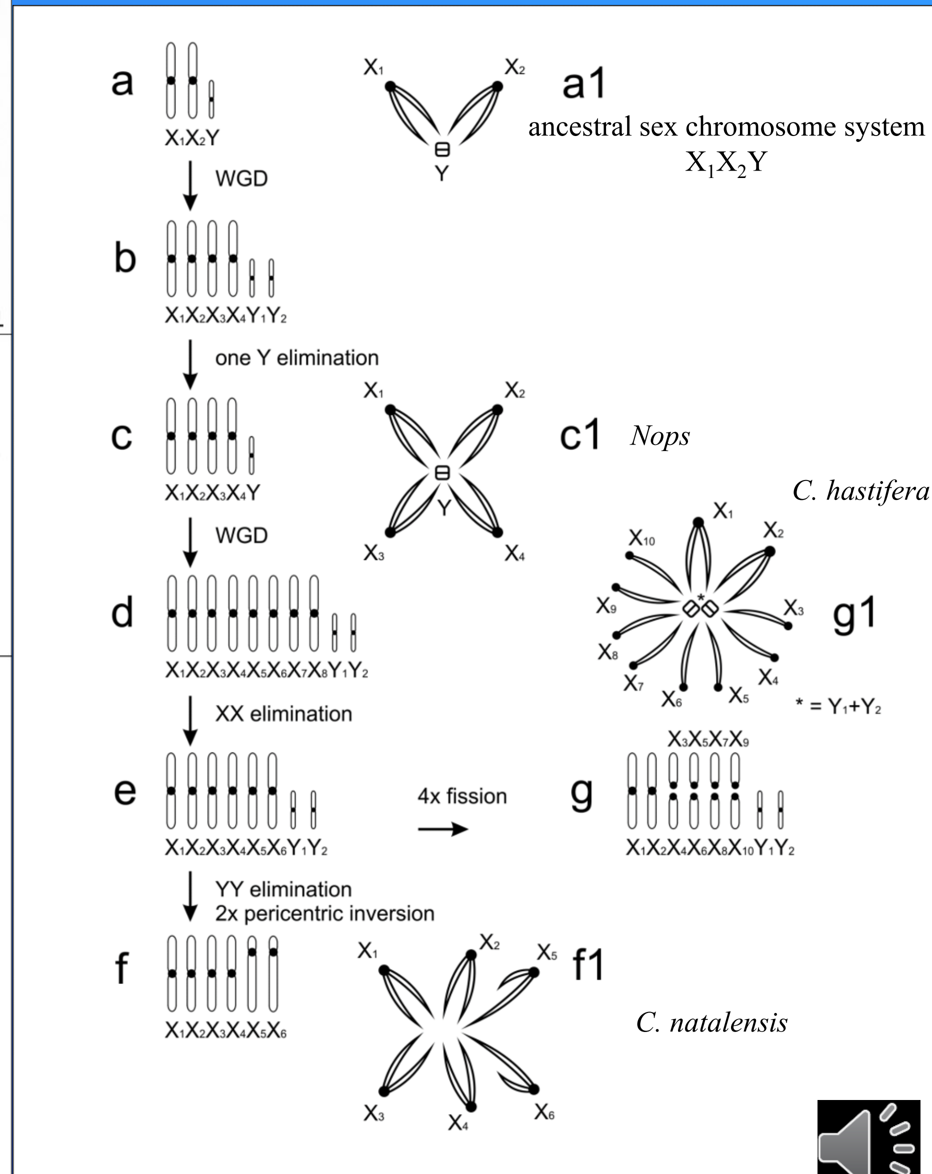






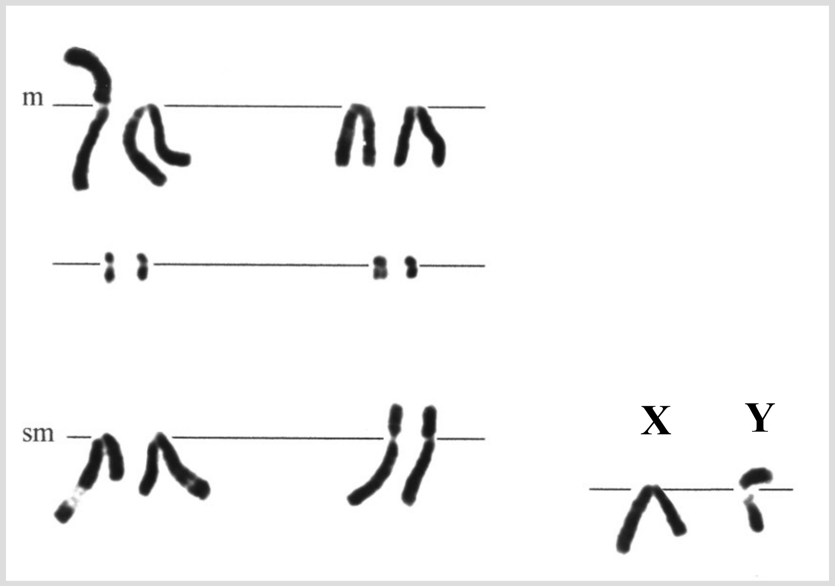
genome duplication in caponiids including sex chromosomes





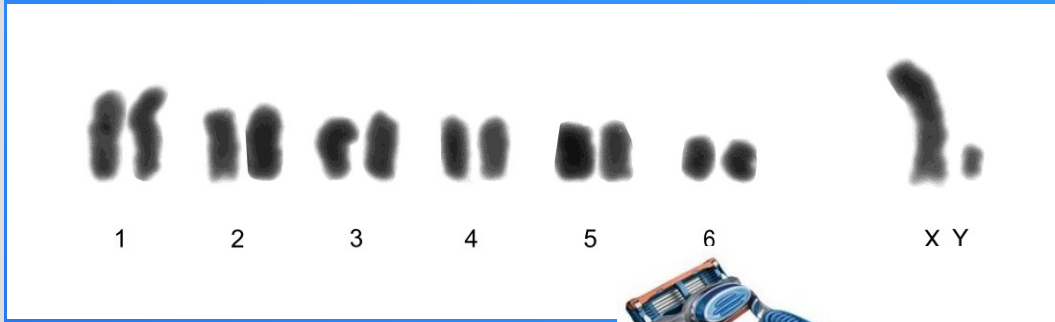
Atypus affinis

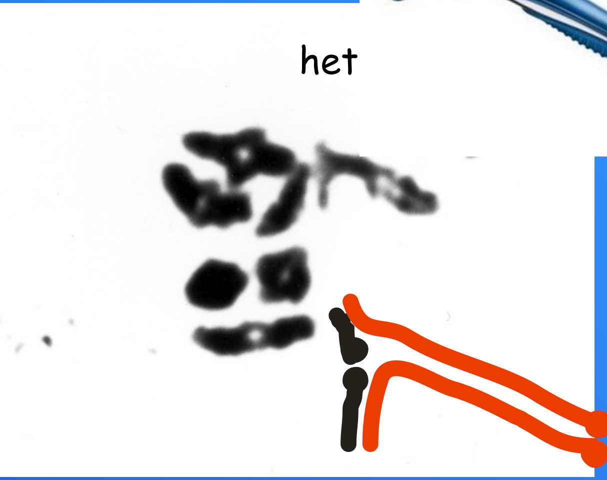
male karyotype: 14 + XY

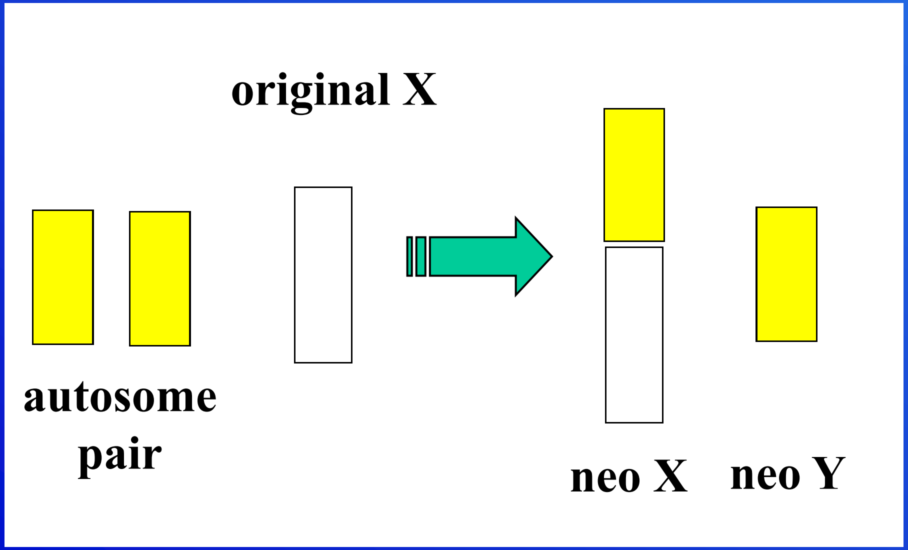


Leptoneta infuscata

male karyotype: 12 + XY



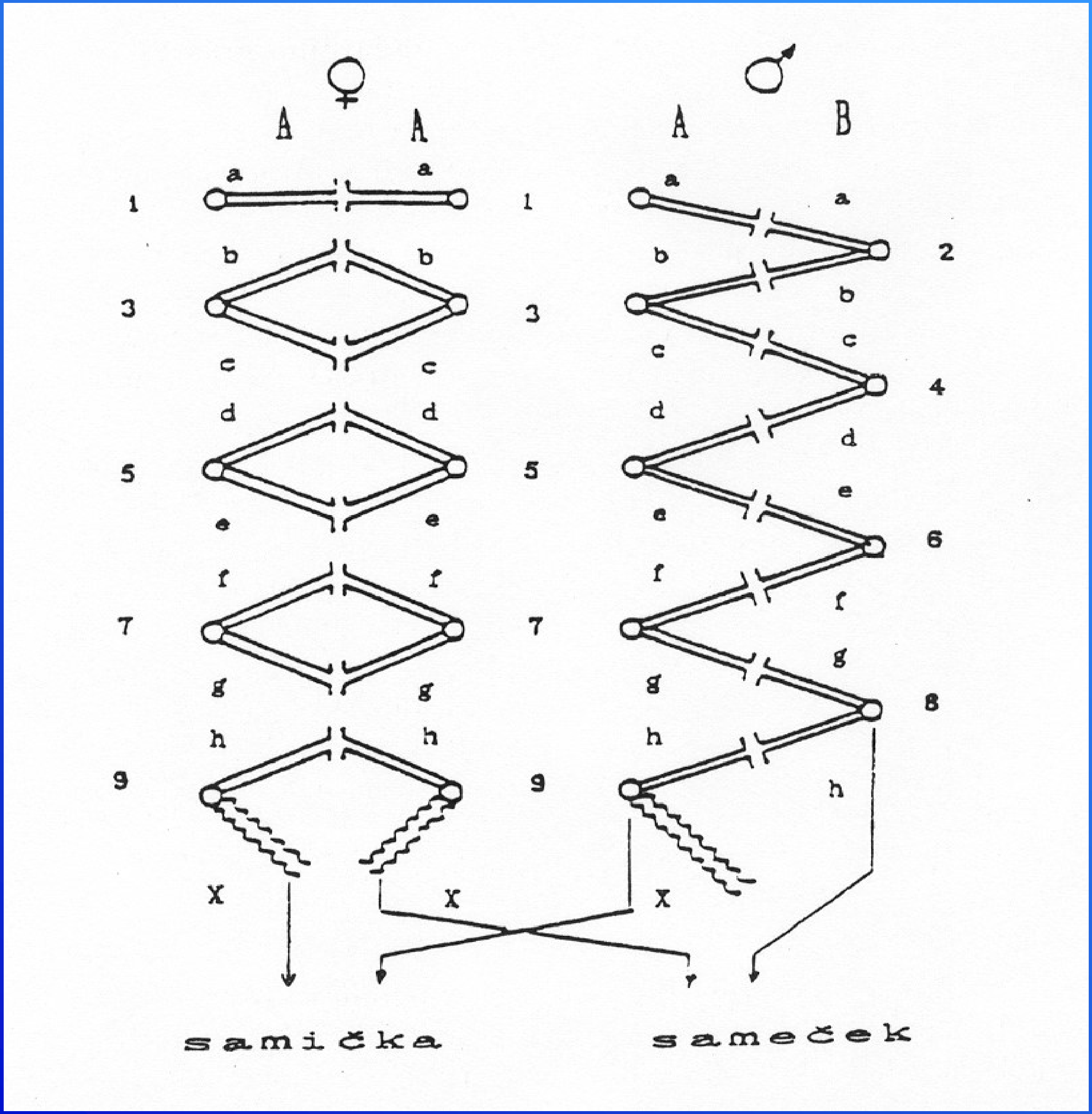




Spider systems including Y chromosome:

fusion of X chromosome and an autosome

found at all primary spider clades



Delena cancerides
(Sparassidae)
$X_1X_2X_3X_4X_5Y_1Y_2Y_3Y_4$ system

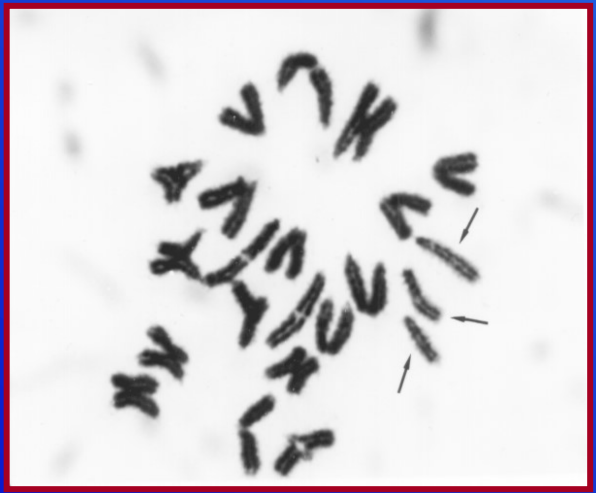
Analysis of neo-sex chromosome system in *Tegenaria ferruginea* (Agelenidae)

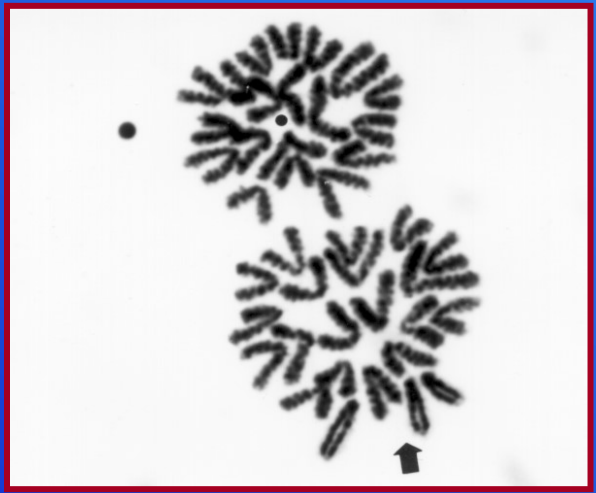
An odd metacentric chromosome at mitotic metaphases of male indicates a complex sex chromosome system including Y Chromosome. Karyotype analysis revealed $X_1X_2X_3X_4X_5Y$ system.

1. Male karyotype consists of 39 acrocentric and one large metacentric chromosome, female karyotype comprises 44 acrocentrics

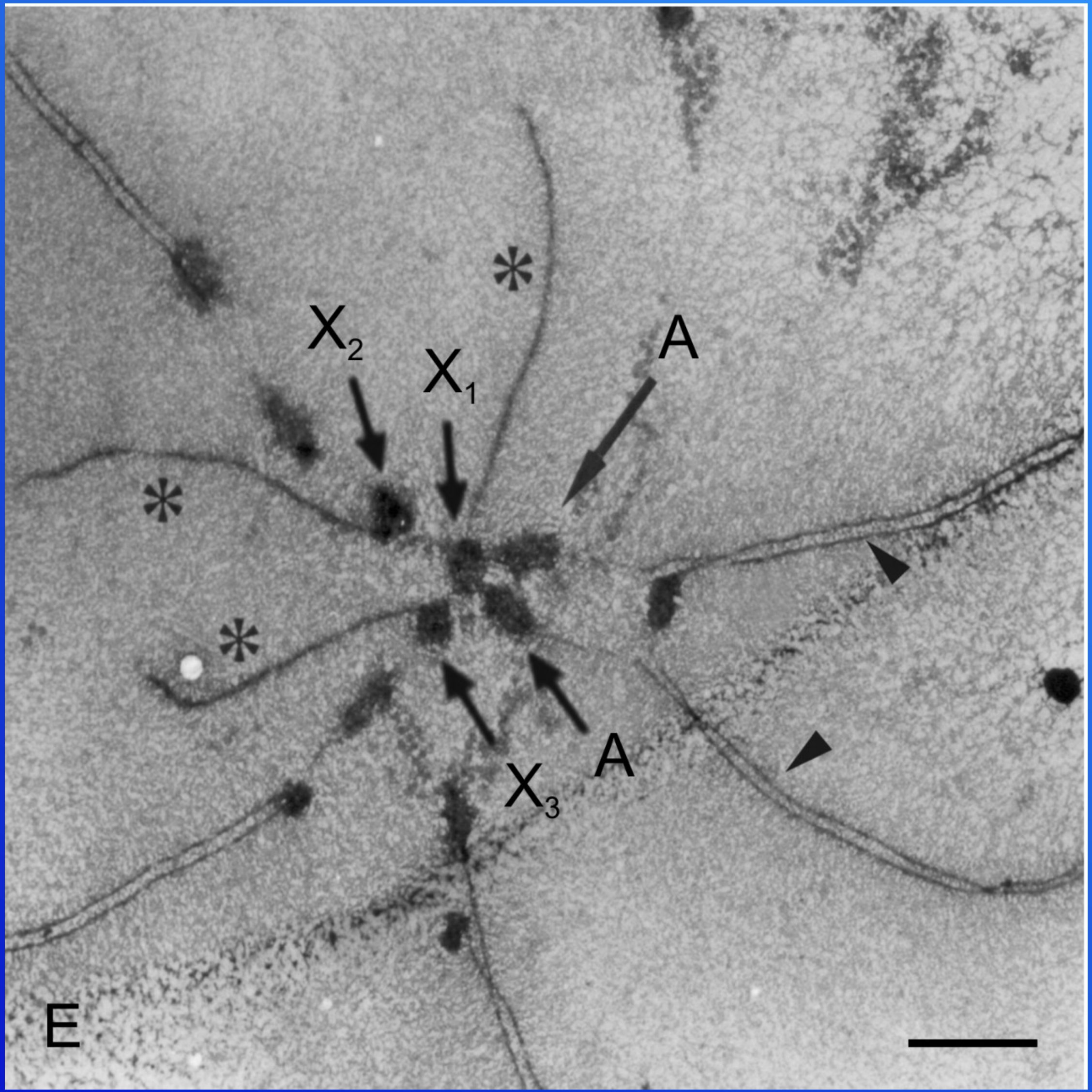
2. Analysis of the metaphase I:
chromosomes X_1, X_2 a X_3 are original multiple X chromosomes. Their meiotic behaviour is the same as behaviour of multiple X chromosomes in closely related species.

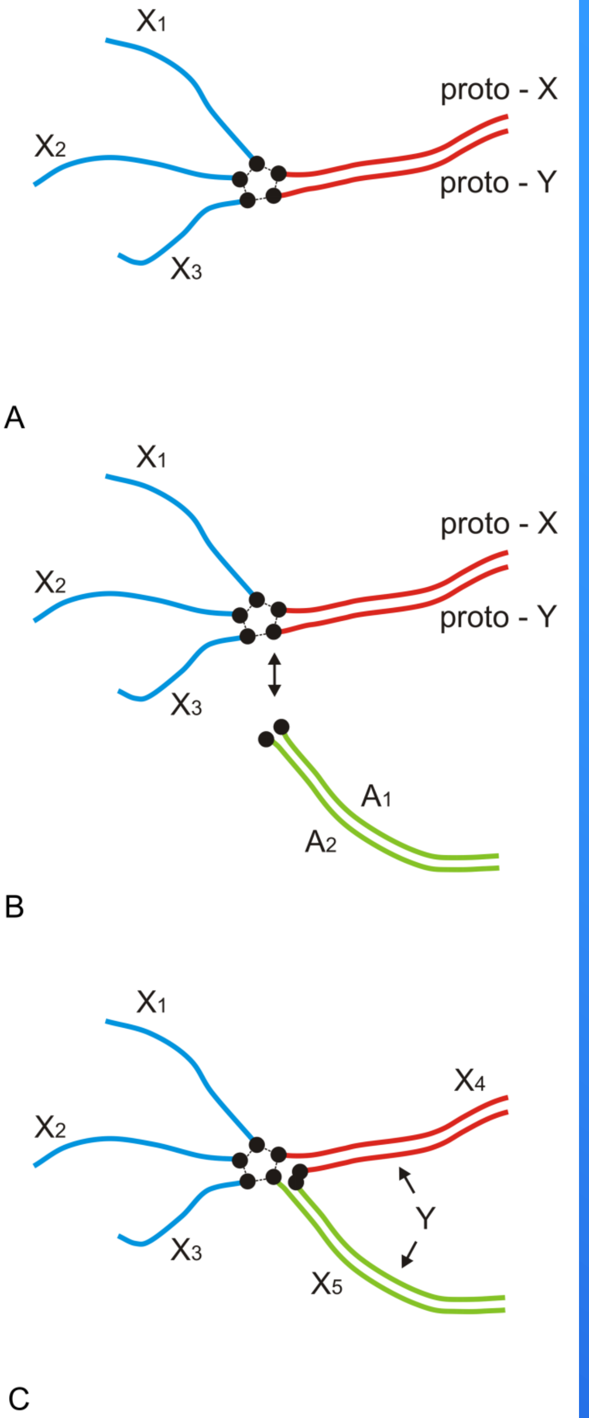
3. Analysis of anaphase I:
segregation of 22 acrocentrics (including chromosomes X_1,X_2 and X_3) to one pole and 17acrocentrics and metacentric chromosome to another pole.



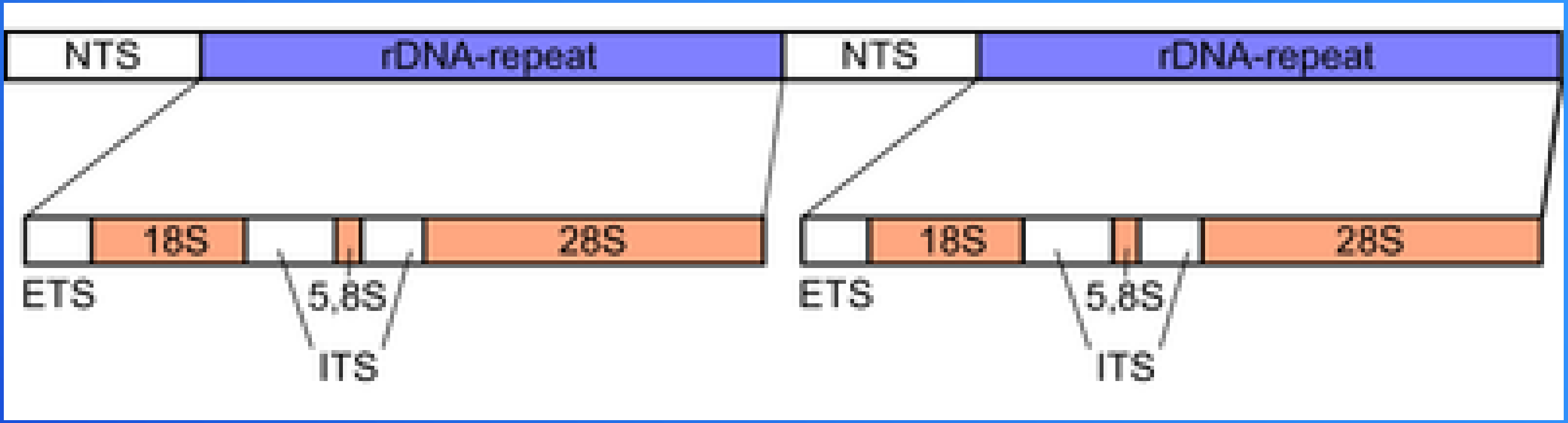


Transmission electron microscopy

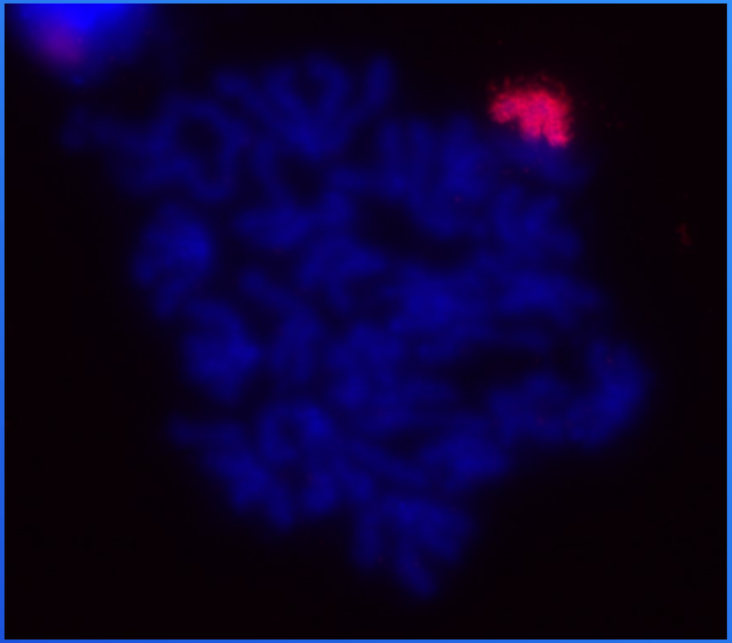


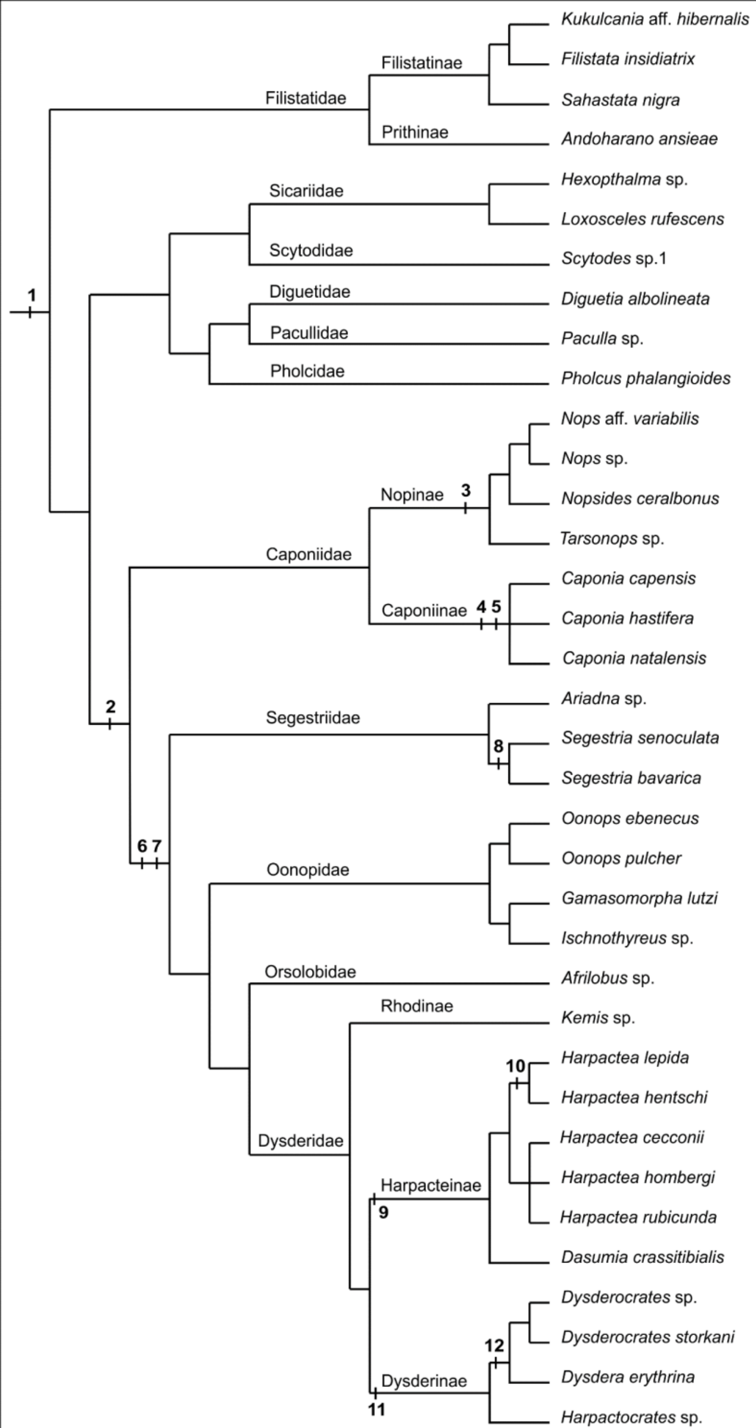


Evolution of nucleolar organizing regions



- ancestral pattern 1 terminal NOR locus
- NORs usually terminal, placed on autosomes
- in haplogynes frequently on sex chromosomes (involvement into sex chromosome pairing)
- enormous NORs of mygalomorphs



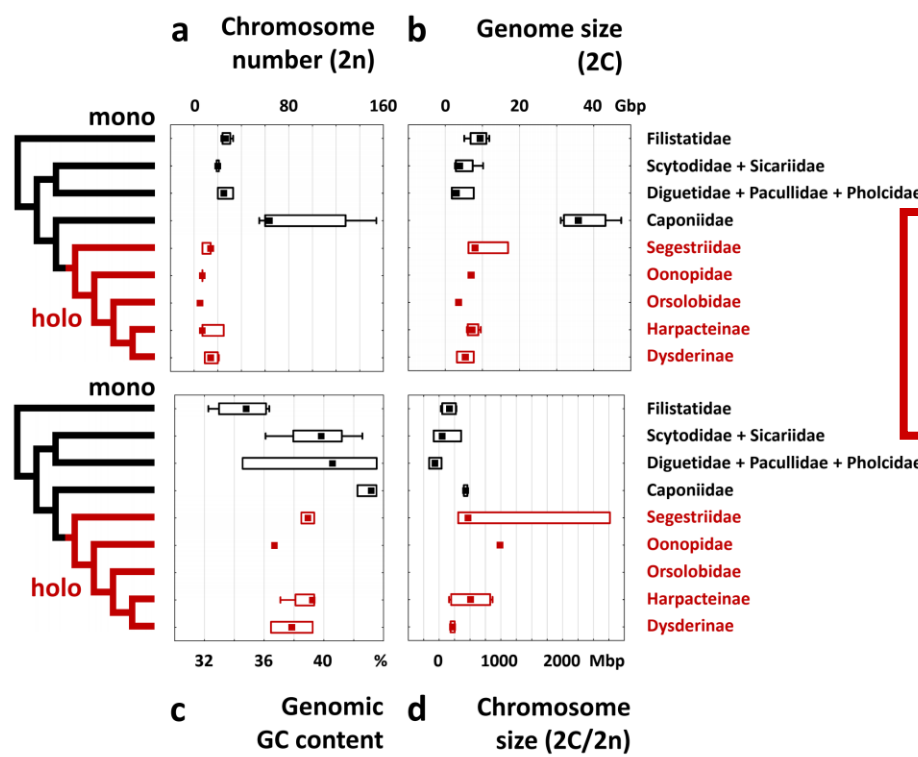


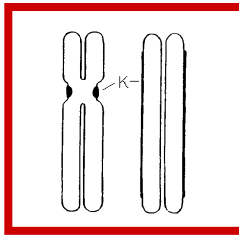
Holokinetic chromosomes

in spiders discovered first in *Dysdera crocata* (Dysderidae) (Díaz and Sáez 1966)

synapomorphy of the haplogyne superfamily Dysderoidea

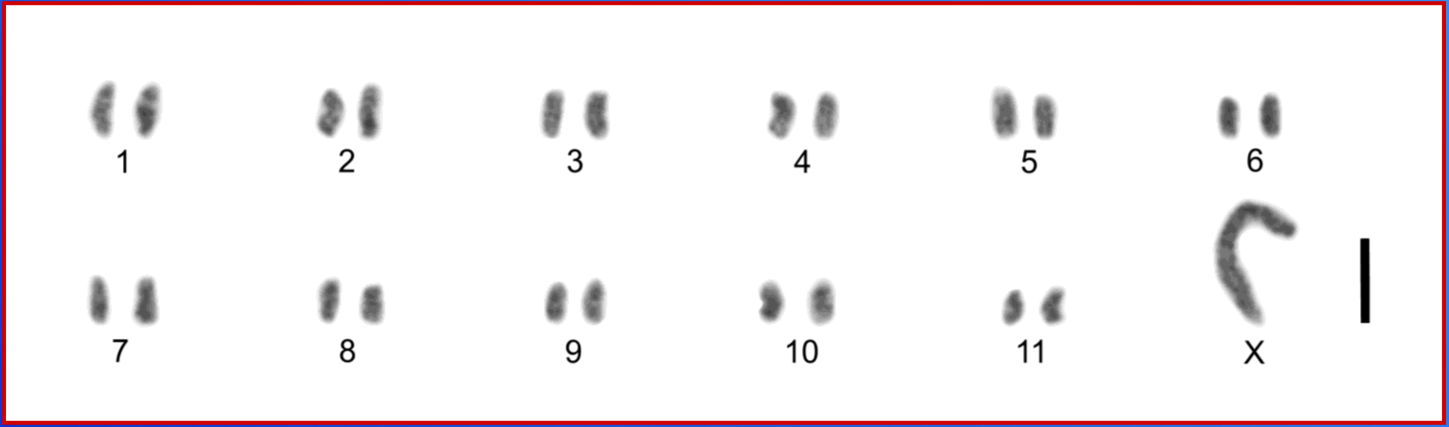
Ancestral male karyotype of Dysderoidea:
2n♂ = 7, X0



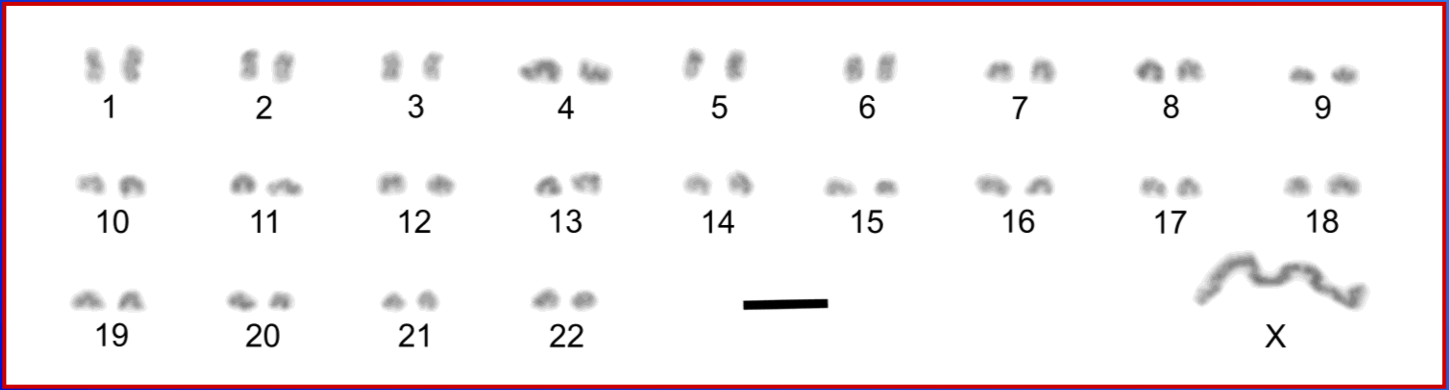



Segestria senoculata (female)
Foto: Glenn Halvor Morka ©

- autosomes: frequent fusions and fissions of chromosomes
- in some species number of autosomes doubled in comparison with closely related species
- comparison of genome size: concerted fission of all chromosomes (agmatoploidy)



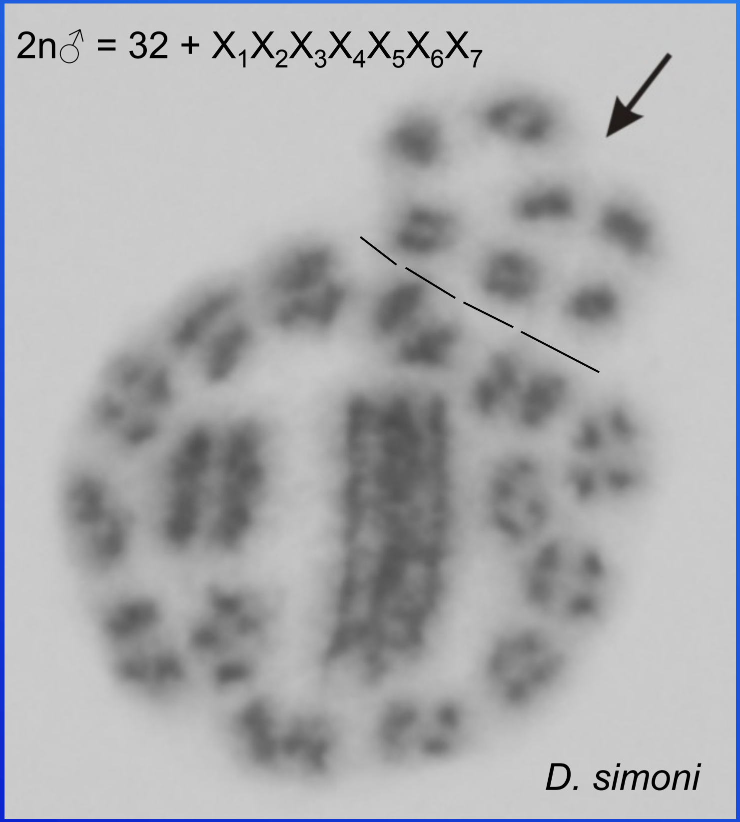
Dysdera spinicrus
2n♂ = 23, X0

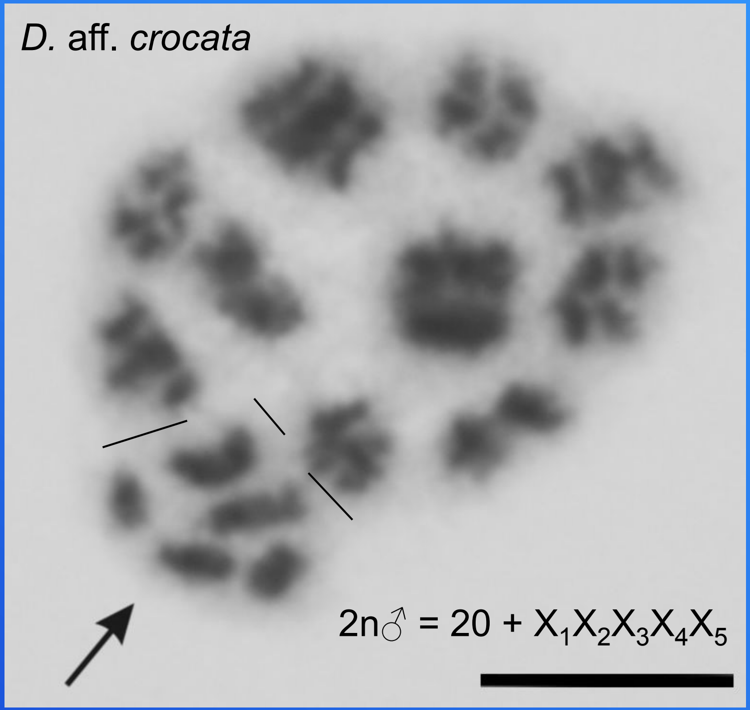


Dysdera westringi
2n♂ = 45, X0

Sex chromosome fissions

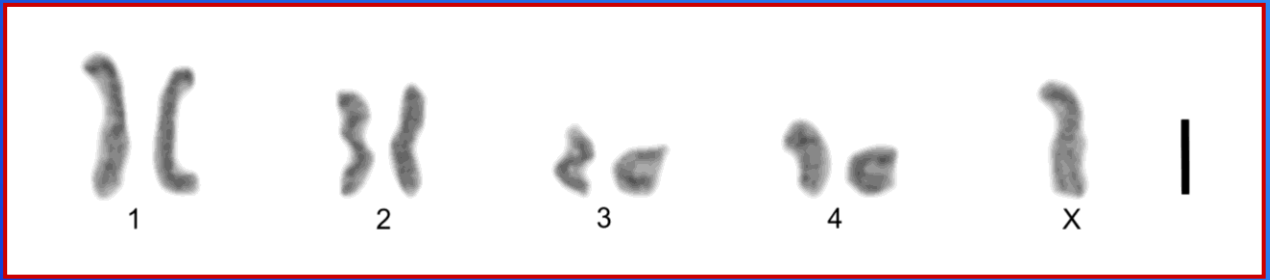
frequent event in spiders with holokinetic chromosomes



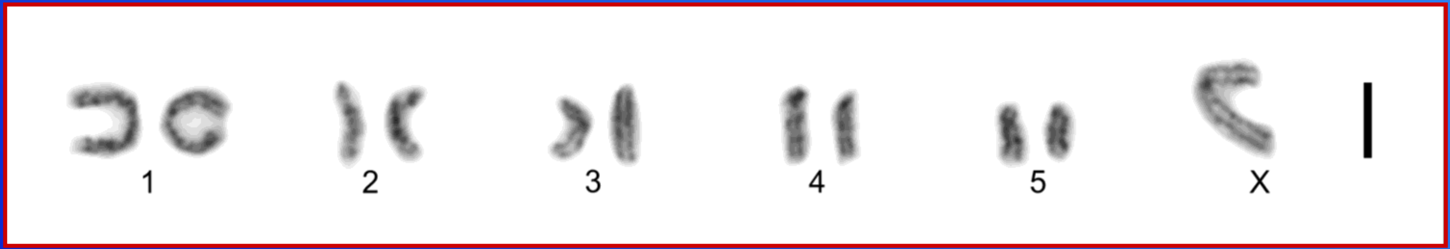


Some clades of Dysderoidea exhibit a considerable karyotype diversity. Closely related species shows frequently very different karyotypes

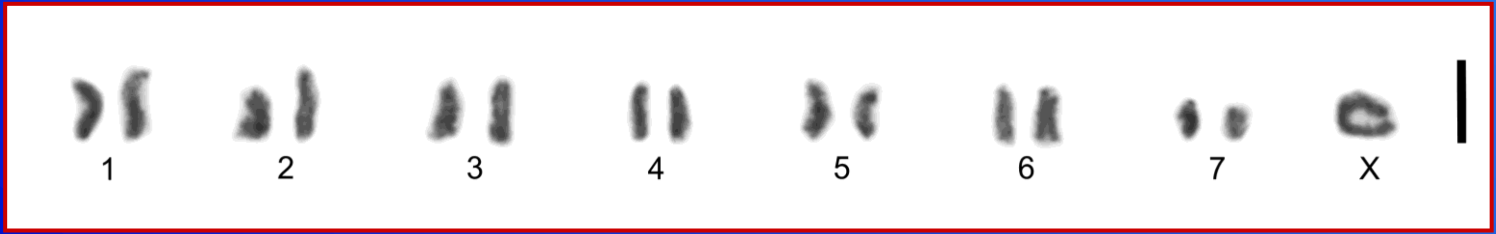
Enormous diversity in *Dysdera* (2n♂ = 7 – 42): detection of cryptic species, suitable model to study role of chromosome changes in speciation



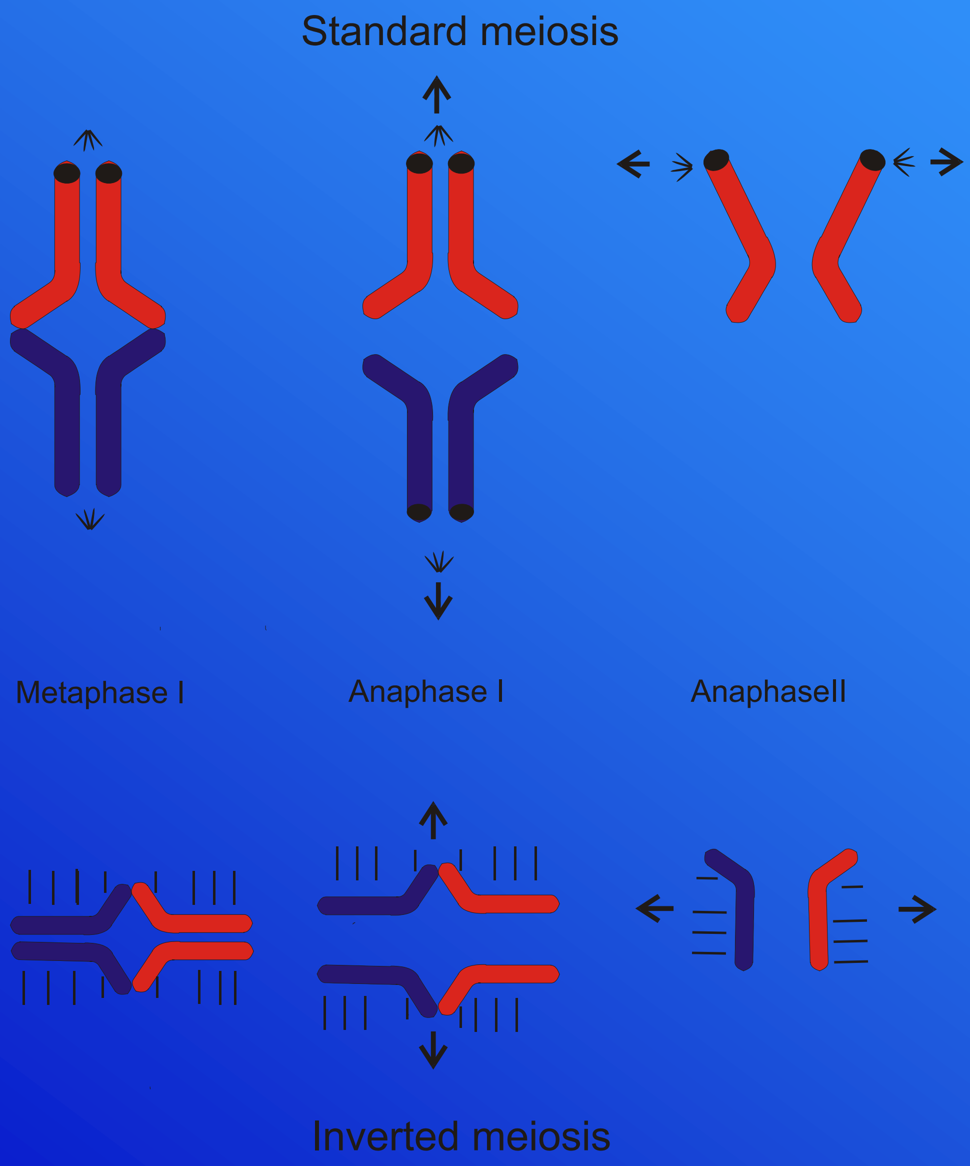
Dysdera catalonica
2n♂ = 9, X0

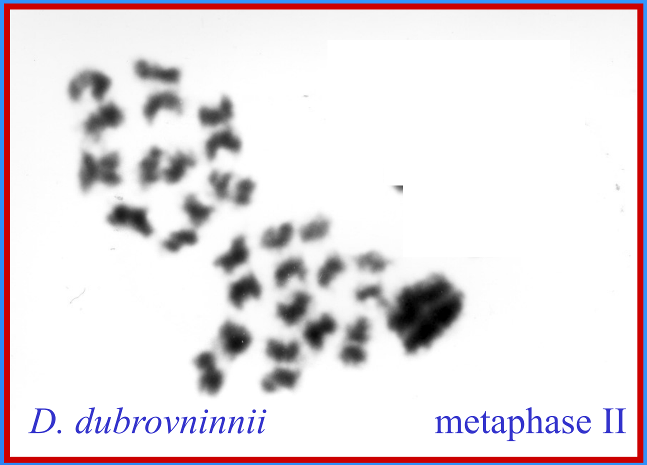


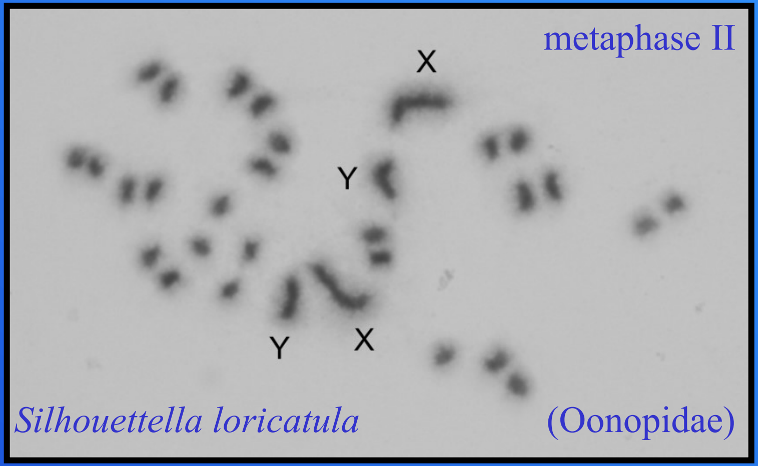
D. undecima
2n♂ = 11, X0



D. quindecima
2n♂ = 15, X0


Standard meiosis
Metaphase I
Anaphase I
AnaphaseII
Inverted meiosis


D. dubrovninnii
metaphase II


metaphase II
X
Y
Y
X
Silhouettella loricatula
(Oonopidae)