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Evolutionary relationships within *Monoxia* (Coleoptera: Chrysomelidae: Galerucinae): chromosomal evidence for its intrageneric classification

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SUMMARY — Chromosome numbers for six species of *Monoxia* (Coleoptera: Chrysomelidae: Galerucinae) fall in two main groups: species with 9 or 10 bivalents and species with 16 or 19 bivalents. The sex determination system is Xy, (possibly neoXY). The intrageneric classification of *Monoxia* is now based on congruent cytological, morphological, and host plant feeding information.

INTRODUCTION

*Monoxia* LeConte (1865) contains some of the most common yet little known North American galerucine chrysomelids. Although adults are quite drab externally, the biology of this genus is fascinating. First, as larvae, all species have been reported, or are believed to be, leaf miners or flower/fruit borers, both largely unexploited life modes in chrysomelids, particularly among galerucines (SANTIAGO-BLAY, unpl. data) Larvae of *Monoxia* have been found pupating in silken cocoons located inside leaves (SANTIAGO-BLAY, unpl. data). Second, most of the 19 described species of *Monoxia* feed, both as larvae and adults, either on members of the Asteraceae (= Compositae) or on members of the Chenopodiaceae, two phylogenetically distant families (CRONQUIST 1988).

The chromosomes of *Monoxia* are little known. PETITPIERRE et al. (1988) list only two meioformulæ: 8 + neoXY for an unidentified species living in British Columbia, which we suspect is either *M. grisea* Blake (1939) or *M. angularis* (LeConte 1859), and 17 + XY for *M. batisia* Blatchley (1917) (or near *M. batisia*). The latter meioformula was depicted by PETITPIERRE et al. (1990) who, referring to then unpublished data by Futuyma and McCafferty, consider *Monoxia* to be closely related to *Erynephala* both chromosomally and protein-electrophoretically (FUNK et al. 1995; FUTUYMA and McCAFFERTY 1990).
Pursuant to an ongoing integrated, multidisciplinary revision of the genus, we have examined six species of *Monoxia*, including one apparently undescribed species. Their meioformae are congruent with the main morphological and ecological subdivision of the genus, thus shedding additional light on the intrageneric classification of *Monoxia*. We report and discuss those finds herein.

**MATERIALS AND METHODS**

Table 1 summarizes the collection data for the specimens studied. Methods follow Virkki (1983, schedule 5); nomenclature according Virkki et al. (1992). A Zeiss Photomicroscope II and Kodak Plus-X Pan 35mm film were used throughout. Scanning electron micrographs were prepared by glueing specimens unto metal cylinders, coating them with a 30-60 μm layer of gold-palladium, and examining the specimens with an ISI-DS 130 scanning electron microscope.

**RESULTS**

*Monoxia guttulata* (LeConte 1857) \(8+X_y\). A nearly complete meiotic series is shown. The heteropycnotic sex bivalent is already visible in early diplotene (Fig. 1). Later, in diplotene (Fig. 2), its structure resembles a question mark figure of the end-to-end association of the early parachute (Xyp) bivalent (cf. Fig. 3 in Virkki et al. 1991). The autosomes form unichiasmate bivalents (Fig. 2) that in diakinesis may appear as open crosses (Fig. 3). Although the sex bivalent seems to retain its end-to-end association (Figs. 3 and 4), it does not show the typical parachute shape. Also, the y chromosome is larger than in the typical Xyp's. Consequently, the sex bivalent is best classified as the rod-type sex bivalent, Xyr. The segregation at A I is regular, to \(8+X\) and \(8+y\) (Fig. 5).

*Monoxia species 1, nr. M. inornata* Blake 1939, \(8+X_y\). We have found only diakinesis approximating PM I (Fig. 6). There is a smaller size difference between the X and y, than in the previous species; we tentatively consider the sex chromosomes as Xyr. This is the same taxon discussed by Santiago-Blay (1990).

*Monoxia sp., possibly M. puberula* Blake 1939, \(9+X_y\). A prometaphase I showing the above meioformula (Fig. 7).

*Monoxia obesula* Blake 1939, \(18+X_y\). A metaphase I showing the above mentioned meioformula (Fig. 8). As in *M. guttulata*, the y chromosome is conspicuous. Two to five of the autosomal bivalents could be bichiasmatic rings.

*Monoxia apicalis* Blake 1939, \(15+X_y\). A late diplotene (Fig. 9), most probably showing the above meioformula.
Fig. 1. to 6. — Eight autosomal bivalents plus Xy, sex bivalent of Monoxia guttulata (Figs. 1 to 5) and Monoxia, near M. inornata (Fig. 6) under phase contrast optics. Sex bivalent or sex chromosomes indicated with arrows. Fig. 1. Diplotene. 1187×. Fig. 2. Later diplotene. 1187×. Fig. 3. Diakinesis. 2045×. Fig. 4. M.I. Fig. 5. A.I. Fig. 6. Diakinesis near to PM I. 2313×.
### Table 1 - Collection and host plant data for the species of *Monoxia* included in this study.

<table>
<thead>
<tr>
<th>Species, Author year</th>
<th>Collection data</th>
<th>Host plant</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Monoxia</em> sp. (possibly <em>M. puberula</em> Blake 1939)</td>
<td>AZ: Cochise Co., near Southwestern Research Station, June 1992</td>
<td><em>Gutierrezia</em> sp. (Asteraceae)</td>
</tr>
<tr>
<td><em>M. obesula</em> Blake 1939</td>
<td>MD: Balto Co., Dundalk 1992</td>
<td><em>Atriplex</em> sp. (Chenopodiaceae)</td>
</tr>
</tbody>
</table>

*Monoxia sordida* (LeConte 1858), n = 16. A metaphase II (Fig. 10). The sex chromosomes were non recognizable in these metaphases, but we suggest the meioformula is $15 + Xy$.

The mode of association of the sex chromosomes in *Monoxia* is somewhat obscure. The bivalents could be neoXY's, as Smith (in Smith and Virkki 1978) has given for *Monoxia* sp. (probably *M. grisea*). Because there seems to be an early end-to-end association of X and y instead of an interstitial chiasma, the genesis of these Xyr's also resembles that of the Xyp's (Virkki et al. 1991). The difference resides in the lack of the interchromosomal substance typical of the Xyp. However in side views, the *Monoxia* sex bivalents do not look like Xyp's either.

**DISCUSSION**

Phylogenies with good congruence between different groups of characters seem uncommon in the Chrysomelidae, except for the chrysomelines *Chrysolina* and *Timarcha*, the alticine *Psylliodes* (Petitpierre 1990; Petitpierre et al. 1991), and the galerucines *Galerucella nymphaeae* complex (summed up by Nokkala 1989, and references therein), *Phyllobrotica* (Farrell and Mitter 1990) and *Ophraella* (Futuyma and McCafferty 1990; Petitpierre et al. 1990). Nevertheless, there are also examples where the cytological, morphological, and host plant data are incongruent, such as the *Timarcha goettingensis*
Figs. 7 to 10. — Meiosis in four species of Monoxia. Sex bivalent indicated with arrow.

Fig. 7. Monoxia sp., possibly M. puberula. PM I. 9 + Xy, 2045 x. Fig. 8. M. obesula. M I. 18 + Xy. A precociously divided autosomal bivalent between arrowheads. 1300 x. Fig. 9. M. apicalis. Diplotene suggesting 15 + Xy, 2415 x. Fig. 10. M. sordida M. II. 16 chromosomes; sex chromosome not recognizable. 2313 x.

complex, the alticine Longitarsus (Petitpierre 1990; Petitpierre et al. 1991), and several genera of Scolytidae [e.g. many of Hopkins' species of Dendroctonus and Ips (Smith and Virkki 1978)].

Blake's (1939) review of Monoxia sheds little light on the formal basis of her classification. It seems that Blake, like her predecessors (Crotch 1873; Jacoby 1887; Horn 1893; Boving 1927; Beller and Hatch 1932) and a successors (Hatch 1971), shared a rather informal view based mostly on a few external morphological characters. The cytogenetic data are congruent with the major subdivision in Blake's classification. Monoxia seems to consist of one well defined group (which we informally call Group I) generally diagnosed polythetically by the following characters: 1) small size (≤ 3.5 mm long), 2)
Figs. 11 to 12. - Monoxia from Group I. Fig. 11. Pronotum. Fig. 12. Elytron setation.

Figs. 13 to 14. - Monoxia from Group II. Fig. 13. Pronotum. Fig. 14. Elytron setation.
relatively broad pronotum (length/width ratio ≤ 0.5, Fig. 11), about as wide as head, 3) adults of both sexes with toothed claws, 4) significant hirsutism (Fig. 12), 5) host plants belonging mostly to the Chenopodiaceae, and 6) a haploid autosomal number \( n = 15 \). On the other hand, most but not all, other species of *Monoxia* (informally placed by us in «Group II») are or have: 1) larger (> 3.5 mm), 2) relatively narrower pronotum (l/w ratio > 0.5, Fig. 13), wider than head, 3) only males with toothed claws, 4) less hirsutism (Fig. 14), and 5) a haploid autosomal number, \( n \leq 10 \). The first group includes *M. apicalis* and *M. sordida*; we predict cytological data will place *M. brisleyi* Blake 1939 there as well. The relationships between the species in the second group, a difficult to define aggregate with host plants in several families, including most in the Asteraceae, clearly need more study. *Monoxia batisia* (or near *M. batisia*, PETITPIERRE et al. 1990) as well as the unidentified species of *Monoxia* from British Columbia reported earlier (SMITH and VIRKKI 1978; PETITPIERRE et al. 1988), also seem to belong in the second group by most characters listed [*M. batisia* feeds on *Lycium* (Solanaceae)].

Like *M. obesula*, several putatively related genera of the galerucine section Schematizites (Galerucini) (SEENO and WILCOX 1982) have high chromosome numbers. For instance, in the Puerto Rican taxon *Yingaresca varicornis* Weise, the chromosome number is \( 2n = 42; 20 + neoXY \) and in *Erynephala* near *E. maritima* it is \( 2n = 30; 14 + neoXY \) (VIRKKI and SANTIAGO-BLAY, unpubl. data). *Erynephala maritima* LeConte from New York State is reported to have \( 17 + XY \) (PETITPIERRE et al. 1990). Except for the Diabroticites, many sections in the Galerucinae also tend to have high chromosome numbers. Indeed, the Galerucinae shows the most diversified chromosome numbers among all chromosomelids studied, except for the Donaciinae (PETITPIERRE 1989). A broad chromosome number range within a genus is relatively common (PETITPIERRE et al. 1988). Apparently, Robertsonian translocations have occurred many times and independently in many genera of Galerucinae. However, the prevalence of high numbers in the Galerucini suggests \( 2n = 34 \) or 36 as the fundamental number for this tribe (PETITPIERRE et al. 1990). The Asian species of *Aulacophora* (Luperini) show chromosome numbers even as high as \( 2n = 59 \) (\( \delta \)) (PETITPIERRE et al. 1988). Thus, ancestors of extant Galerucinae, excluding Diabroticites, may have evolved with a tendency for high autosome numbers, with a subsequent trend to lower their number through centric fusions. This view is supported by the high frequency of the neoXY, as well as the XY or Xy systems, most of which may be masked neoXY's as reported in Galerucini (PETITPIERRE et al. 1988, 1990). Thus, our «Group II» of *Monoxia*, with lower chromosome number, may represent a higher degree of relative cytogenetic derivation than Group I.

Cytological evolutionary scenarios pose many challenges for evolutionary biologists. Especially in Coleoptera, the Robertsonian translocations are supposed to be responsible for most changes in chromosome number (SMITH and
Apparently, they become established under disruptive selection pressures favoring either a few or many genetic recombination patterns. Why the supposed fission chromosomes are almost always metacentric in Coleoptera remains uncertain. Perhaps the fission acro- and telocentrics experience pericentric inversions in order to improve their chances of becoming established (CHARLESWORTH 1985, G. Foster in BORSTEL 1988). Also, the formation of second chromosomal arms by accretion is possible because the increased chromosomal number has been found to be positively correlated with an increasing genome size in some chrysomelids (PETITPIERRE et al. 1993, 1994).

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EVOLUTIONARY RELATIONSHIP WITHIN MONOXIA


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