HYBRIDIZATION AND AGAMOSPERMY OF BIDENS IN NORTHWESTERN ONTARIO

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Summary

Four weedy taxa of Bidens are common in Thunder Bay: B. cernua, B. connata, B. frondosa and B. vulgata. Since B. connata is intermediate in gross morphology and ecological preference between B. cernua and B. frondosa, and since it is only found in areas where B. cernua and B. frondosa are sympatric, an investigation was undertaken to determine whether B. connata is of hybrid origin (B. cernua × B. frondosa). Representative specimens of the 4 taxa were scored for 23 morphological characters, and these data were analyzed by Principal Coordinates Analysis. Seed germination and pollen viability were determined to be high with no significant differences among the 4 taxa. Morphological and cytological data suggest that B. connata (2n = 48) is the result of either a cross between an unreduced gamete of B. cernua (2n = 24) with a normal gamete of B. frondosa (2n = 48), or a cross between a 2n = 24 of B. frondosa with a typical gamete of B. cernua. Since B. connata shows no decrease in seed viability and apparently produces pollen by mitosis only, Thunder Bay populations of B. connata evidently comprise an agamic complex.

Introduction

Bidens L. (Asteraceae: tribe Heliantheae) is a large and widespread genus; by some accounts (Sherff, 1937) it contains over 240 species concentrated in Africa, the Americas and Polynesia. Of the 7 or 8 species of Bidens found in Ontario (Scoggan, 1979; Gleason and Cronquist, 1963; Argus and White, 1977) five are extensively distributed throughout the province including the district of Thunder Bay. One of these five species, B. beckii Torr. (Megalondonta beckii (Torr.) Greene), is a submersed aquatic annual that is distinct from the others both morphologically and ecologically.

The remaining four Bidens taxa found in the Thunder Bay area are morphologically similar and share many ecological features. These species are adapted to open, disturbed, and often wet habitats. All four are associated with early stages of secondary succession. All are weedy annuals producing barbed awns on their achenes causing them to cling to fur or clothing; it is from this trait that the common name "beggar’s ticks" is derived.

Bidens cernua L. is the most common of the 4 weedy species in the Thunder Bay area; it is found on beaver dams or immediately below them, on river banks, and in wet ditches, usually with its roots submerged. In northern Ontario it is characterized by simple, sessile leaves, retrorsely barbed achenes having 4 equal, retrorsely barbed awns, prominent ray flowers, and usually 8 involucral bracts (Figs. 1 and 2). The second species, B. frondosa L., is common on moist gravel banks of ditches, lakes and streams in the Thunder Bay area. It is characterized by 3- to 5-foliolate, petiolate

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leaves, antrorsely barbed achenes having 2 equal, retrorsely-barbed awns, no ray flowers, and usually 8 involucral bracts. The morphologically similar *B. vulgata* Greene is found on drier sites including packed gravel and the cracks between asphalt roads and cement sidewalks. It is characterized by 3- to 7-foliolate, petiolate leaves, achenes having two retrorsely barbed awns, ephemeral ray flowers, and approximately 13 involucral bracts. However, unlike the other *Bidens* taxa *B. vulgata* has achenes that are retrorsely barbed near their summit and antrorsely barbed in lower regions. The fourth weedy species, *B. connata* Muhl. (*B. tripartita* L. sensu Gleason and Cronquist, 1963) is far less common than the other three species, and was found only on a few sites in Thunder Bay City where *B. cernua* and *B. frondosa* grow together; i.e., on the gravel banks of streams and a wet drainage ditch near Lake Superior. It was characterized by simple, or 1- to 3-basally lobed, petiolate leaves, antrorsely barbed achenes with two long and two short awns, no ray flowers, and usually 8 involucral bracts. However, the awns of this single taxon were generally antrorsely barbed although a few individuals were encountered with retrorsely barbed awns.

Several factors suggested that the Thunder Bay populations of *B. connata* might be of hybrid origin: 1) it is intermediate in gross morphology to *B. cernua* and *B. frondosa*, or perhaps *B. vulgata* (Figs. 1 and 2); 2) at the few sites where this taxon is found in Thunder Bay, *B. connata* is always closely associated with *B. cernua* and *B. frondosa*; and 3) it always is found growing in an ecologically intermediate zone between *B. cernua* and *B. frondosa*; i.e., very near the water’s edge on disturbed gravel banks in between emerged plants of *B. cernua* and plants of *B. frondosa* found higher up the bank. Also, published distribution information for all of North America (Duncan and Foote, 1975; Kearney et al., 1964; Jepson, 1966; Lakela,
Fig. 2. Comparative achene morphology of *Bidens cernua*, *B. connata*, *B. frondosa* and *B. vulgata*.

1965; Mohlenbrock, 1975; Moss, 1959; Munz, 1968; Roland and Smith, 1969; Scoggan, 1957, 1979; Sherff, 1937; Van Bruggen, 1976), as well as our observations of collection localities of herbarium specimens indicate that *B. connata* apparently occurs only in areas where both *B. cernua* and *B. frondosa* are both present.

The antrorsely barbed awns of *B. connata* may suggest a local, and therefore recent, origin of this morphologically and ecologically intermediate taxon. Since the Thunder Bay area was covered by the Wisconsin ice sheet until approximately 9500 years ago (Zoltai, 1965; Burwasser, 1977), its flora consists of comparatively recent immigrants to the area. However, the antrorsely barbed awns of the Thunder Bay populations of *B. connata* seem to preclude effective dissemination by animal vectors, suggesting that either local populations of this taxon, or at least the trait of antrorse barbing of the awns, likely have been derived following a northern migration in the recent post-glacial period.

The goal of this study was to investigate the possibility that *B. connata* has been derived from a past hybridization between *B. cernua* and *B. frondosa*, and if so, whether hybridization is a recurring process. Since *B. vulgata* is similar morphologically to *B. frondosa*, and could not be excluded as a putative parent, this species was also included in our investigation (Crowe, 1978).

Methods

To investigate relationships of the Thunder Bay populations of *B. connata* to the 3 weedy species, four different experimental methods were employed: 1) a quantitative morphological analysis of the 4 *Bidens* species was carried out to determine whether *B. connata* is phenetically intermediate between *B. cernua* and *B. frondosa*; 2) seed germination tests were carried out to compare levels of seed fertility and to
determine whether any hybrid progeny are being produced in current generations; 3) pollen viability was tested to compare levels of parental sterility; and 4) chromosome counts were made of the 4 species to determine karyotype similarities.

Collections of whole plants and achenes of *B. cernua, B. connata, B. frondosa,* and *B. vulgaris* were made from 6 sites within the Thunder Bay city limits from August to October, 1977. Herbarium specimens were prepared in the usual manner, and voucher specimens were deposited in the Lakehead University Herbarium (LKHD). Fifteen to 20 representative individuals of each species were selected for morphological analysis.

Initially 39 characters of leaves, achenes, involucral bracts, outer chaff and inner chaff were selected to compare a sub-sampling of *B. cernua* and *B. frondosa,* the two suspected parent species. Characters that would not distinguish these two species were eliminated from further analysis with two exceptions; the characters that were not diagnostic for *B. cernua* and *B. frondosa,* but which were believed to have significantly different states for either *B. connata* or *B. vulgaris* were retained. Thus, 23 morphological characters in all were kept for the second stage of analysis. These 23 characters are listed in Table 1.

Specimens of all 4 taxa sampled for this study tended to be variable in size (even within a single plant), although the shapes of many structures (e.g. leaves and achenes) were relatively constant within each taxon. Thus, in an attempt to reduce the effects of size differences on numerical analyses, linear measurements were divided by the length of an associated structure. In this fashion character states of length or width measurements were converted to dimensionless values.

Leaf character states were calculated as the average of measurements from the two largest, undamaged leaves of each specimen. Achen characters were scored and averaged for 3 randomly picked, mature achenes from a single capitulum per specimen.

<table>
<thead>
<tr>
<th>Table 1. Morphological characters of <em>Bidens</em> used for comparative analysis.</th>
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<tbody>
<tr>
<td>1 = Length of petiole/Length of leaf (The petiole was defined as that part of the leaf between the stem and the lamina that was less than 2.5 mm wide).</td>
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<tr>
<td>2 = Width of leaf/Length of leaf.</td>
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<tr>
<td>3 = Shape of leaf (1) Simple, 2) 1-lobed, 3) 2-lobed, 4) 3-foliolate, 5) 5-foliolate).</td>
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<tr>
<td>4 = Number of serrations on 20 mm of leaf margin, near middle.</td>
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<td>5 = Height of widest point of achene/Length of achene body.</td>
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<td>6 = Length of lateral awns/Length of achene body.</td>
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<tr>
<td>7 = Length of front and back awns/Length of achene body.</td>
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<tr>
<td>8 = Fraction of body barbs that were antrorse.</td>
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<tr>
<td>9 = Fraction of awn barbs that were antrorse.</td>
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<tr>
<td>10 = Number of trichomes on summit of achene between two lateral awns.</td>
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<tr>
<td>11 = Number of barbs in top 1 mm of achene face between two angles.</td>
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<tr>
<td>12 = Number of barbs on outer two rows of lateral awns.</td>
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<tr>
<td>13 = Number of barbs on outer two rows of front and back awns.</td>
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<tr>
<td>14 = Number of barbs on central row of lateral awns.</td>
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<tr>
<td>15 = Number of barbs on central row of front and back awns.</td>
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<tr>
<td>16 = Number of hairs in top 1 mm of body angles.</td>
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<tr>
<td>17 = Number of awns longer than 1 mm.</td>
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<tr>
<td>18 = Width of involucral bract/Length of bract.</td>
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<tr>
<td>19 = Height of widest point of involucral bract/Length of bract.</td>
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<tr>
<td>20 = Number of involucral bracts.</td>
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<tr>
<td>21 = Number of cilia on edge of outer chaff between 1 and 2 mm from tip.</td>
</tr>
<tr>
<td>22 = Number of outer chaff on one capitulum.</td>
</tr>
<tr>
<td>23 = Height of widest point of inner chaff/Length of inner chaff.</td>
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</table>
Three types of bracts were present on each head. There were usually 8 (except for *B. vulgarata*) green involucral bracts subtending the receptacle. Within the circle of involucral bracts were 8 or fewer yellow, chartaceous bracts with radial black stripes, each subtending a sterile achene or ray flower; these were the outer chaff. Subtending all fertile achenes and any sterile inner achenes were narrower bracts designated inner chaff. All involucral bract and chaff characters were scored and averaged for 4 bracts from the same capitulum used for achene measurements.

The morphological data were analyzed in two ways. First, diagrams (Hubbs and Hubbs, 1953) presenting mean, standard deviation and range data for each character were constructed comparing 5 groups: all individuals of *B. cernua*, *B. frondosa* and *B. vulgarata*, and 2 groups of individuals of *B. connata* representing 2 collection sites. *B. connata* was treated as 2 separate groups to determine whether any differences existed between plants from the two sites.

The data were also analyzed by Principal Coordinates Analysis (Sneath and Sokal, 1972; Gower, 1966; Wilkinson and Reinsch, 1971; Strang, 1976) using a program written by the senior author. Our objective in using this technique was to objectively demonstrate intermediacy of *B. connata* considering all 23 characters simultaneously. To this end the results of the Principal Coordinates Analysis were used to construct a three-dimensional ordination of individual plants summarizing relationships among the 4 *Bidens* taxa. Since *B. frondosa* and *B. vulgarata* were very similar, a separate Principal Coordinates Analysis including only these two species was run to determine whether they are consistently, morphologically distinct taxa.

Seed germination trials were conducted for *B. connata*, *B. cernua*, *B. frondosa* and *B. vulgarata* at 20°C and 16 hour daylength following clipping the achenes distally.
7. Number of Trichomes in Top 1 mm of Achene Face

8. Petiole Length/Leaf Length

9. Height of Widest Point of Achene/Achene Length

10. Leaf Width/Leaf Length

Figs. 7–10. Means, ranges and standard deviations of 4 characters for 5 populations of Bidens. The vertical lines indicate mean values; the horizontal lines indicate the range of observed values; the broad bars represent one standard deviation on each side of the mean.

7. Number of trichomes in top 1 mm of achene face. 8. Petiole length/leaf length. 9. Height of widest point of achene/achene length. 10. Leaf width/leaf length.

such that their seed coats were broken (Hogue, 1976). All seedlings were allowed to develop until their identity could be determined from their leaf morphology.

The percentage of pollen viability of B. cernua, B. connata, B. frondosa, and B. vulgata was estimated using the "cotton-blue lactophenol" staining method described by Radford et al. (1974). Fresh pollen from plants grown in the seed germination trials was used for these estimations.

Chromosome counts were made of the 4 Bidens species using basic Feulgen's stain technique of root tips and aceto-carmine stain (Snow, 1963) of pollen mother cells. Root tips and anthers were taken from plants grown to maturity in a greenhouse following the seed germination trials.

Results

Although diagrams comparing mean, range and standard deviation data were constructed for all 23 characters that were retained for statistical analysis, only 8 of these diagrams are presented here (Figs. 3–10); these 8 diagrams were selected to be generally representative of the other 15, unpictured diagrams as well. In all diagrams B. cernua and B. frondosa are seen as separated entities since the ability to distinguish these 2 taxa was a major criterion for character retention. Significantly, B. connata has character states between those of B. cernua and B. frondosa for all but one of the 8 characters, relative awn length (Fig. 5); however, for most characters (Figs. 3, 4, 8, 9, and 10) B. connata is not exactly intermediate, but instead is more similar to either one taxon or the other.
Although the plants of *B. connata* from the 2 sites gave a somewhat different impression overall, the 8 diagrams depicting mean, range, and standard deviation data show no substantial differences between sites except for the single character, relative awn length (Fig. 5). This is the same character for which *B. connata* lies outside the range of variation determined by *B. cernua* and *B. frondosa*.

In Figs. 3–10 *B. vulgata* is seen to be similar to *B. frondosa* in most respects (Figs. 4, 6, 8, 9, and 10), yet distinct in other respects (Figs. 3 and 7). The character that most clearly distinguishes *B. vulgata* from the other 3 taxa is number of involucral bracts (results not shown); *B. vulgata* normally has 13 such bracts, while the others usually have 8. The paler-yellow color of the disc corollas of *B. vulgata* also separates this species consistently from the others. However, this character was not included in our analysis due to the difficulty of quantifying its character states.

The ordination of plants based on Principal Coordinates Analysis (Fig. 11) shows patterns of variation among the 4 *Bidens* taxa similar to those indicated by the single-character comparisons; however, the overall affinities of each plant are easier to assess. In Fig. 11 each taxon is drawn as a different shaped glyph, and collection site numbers are indicated within each glyph. On the main axis of variation accounting for 48% of the total variance, *B. connata* is clearly intermediate between *B. cernua* and *B. frondosa*. On the second axis *B. connata* is distinct from the other 3 taxa while it overlaps them on the third axis. However, the second and third axes account for only 26% and 7% of the residual sums of squares respectively.

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### Fig. 11. Three-dimensional ordination of individuals of *Bidens cernua*, *B. connata*, *B. frondosa* and *B. vulgata* based on Principal Coordinates Analysis of 23 morphological characters.

<table>
<thead>
<tr>
<th>TAXON</th>
<th>SITE</th>
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<tbody>
<tr>
<td><em>BIDENS CERNUA</em></td>
<td>1,3</td>
</tr>
<tr>
<td><em>BIDENS CONNATA</em></td>
<td>1,3</td>
</tr>
<tr>
<td><em>BIDENS FRONDOSA</em></td>
<td>1,3,4,14</td>
</tr>
<tr>
<td><em>BIDENS VULGATA</em></td>
<td>8,10</td>
</tr>
</tbody>
</table>

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**TAXON**

- *BIDENS CERNUA* 1,3
- *BIDENS CONNATA* 1,3
- *BIDENS FRONDOSA* 1,3,4,14
- *BIDENS VULGATA* 8,10
In Fig. 11 plants of *B. connata* from the two sites form 1 cluster in the ordination, but with minimal overlap between sites. But, whether this difference arises from phenotypic plasticity rather than from genetic differences cannot be determined for the present since the microclimatic conditions associated with the two sites were somewhat dissimilar.

In Fig. 11 *B. vulgata* is seen to form a cluster in close proximity to, but not overlapping with, *B. frondosa*. This separation depends on components of variation expressed on the second and third axes. This result indicates that the characters with the greatest contribution to the main axis of variation (i.e., those for which *B. connata* is intermediate to *B. cernua* and *B. frondosa*) have little or no diagnostic ability for *B. vulgata* and *B. frondosa*. The results of a second Principal Coordinates Analysis using the same data as the first, but considering only *B. frondosa* and *B. vulgata* are presented in Fig. 12. In this analysis the two species are clearly shown as morphologically discrete groups.

The results of seed germination trials showed that most achenes were viable with no significant differences observed for any of the 4 *Bidens* taxa. Furthermore, all achenes produced progeny obviously belonging to the same taxon as the maternal plant, even when achenes were collected from sites where more than one taxon were growing in close proximity. This result indicates that if hybridization does occur among the 4 taxa, it does not commonly recur in the Thunder Bay area.

All 4 *Bidens* taxa had 90–95% stainable pollen by the cotton-blue lactophenol method. These results suggest that pollen viability is high for all species with no significant differences among them.

The chromosome numbers of *B. cernua*, *B. connata*, *B. frondosa*, and *B. vulgata* are given in Table 2. The previously published numbers for these taxa indicate considerable polyploidy, more than is known for any other group of *Bidens*. Our counts of Thunder Bay specimens indicate somatic numbers of 2n = 24 for *B. cernua*, and 2n = 48 for *B. connata*, *B. frondosa*, and *B. vulgata*.

Squashes of anthers revealed normal meiosis in pollen mother cells (PMCs) of *B. cernua* with n = 12. However, although considerable efforts were taken to observe meiosis in developing PMCs of the other 3 taxa, no meiotic divisions could be found in any of several series of developing anthers. Since each PMC of these plants eventually gave rise to pollen-forming daughter cells, this process was apparently accomplished by mitosis only. Pollen development of this sort is known in certain agamosperous plants (Gustafsson, 1947), and the presence of this pattern of pollen development in *B. connata*, *B. frondosa*, and *B. vulgata* suggest that all 3 taxa are reproducing agamosperously in Thunder Bay.

**Discussion**

Ecological preferences, distributional data, and gross morphology all suggest that Thunder Bay populations of *B. connata* are of hybrid origin being derived from a cross of *B. frondosa* with *B. cernua*. However, the experimental results presented here indicate that although *B. connata* may be a hybrid derivative, other evolutionary processes have also probably played a role in determining the present status of this taxon, including polyploidy and agamospermy.

The Principal Coordinates Analysis of the morphological data indicates that *B. connata* is intermediate between *B. frondosa* and *B. cernua* in some but not all respects. However, the lack of intermediacy on the second and third axes does not necessarily run counter to the hybrid origin hypothesis for two reasons: 1) other researchers have found known hybrid progeny to be non-intermediate in at least one dimension in ordinations based on multivariate statistical methods (Whitehouse, 1970); and 2) some of the 23 characters selected for analysis in this study may be controlled by one, or a very few genes with dominant and recessive alleles, rather than by several genes with additive effects. For such traits, intermediate character
TAXON  SITE

- BIDENS FRONDOSA  ALL
- BIDENS VULGATA  ALL

Fig. 12. Three-dimensional ordination of individuals of Bidens frondosa and B. vulgata based on Principal Coordinates Analysis of 23 morphological characters.

states would not be expected in hybrid progeny. For example, the characteristic of antrorse barbs on achene awns appears in scattered locales for many species of Bidens (Sherff, 1937) including the Thunder Bay population of B. connata, and usually this trait is associated with varietal status (Scoggan, 1979). Our observations indicate that the direction of an achene barb is either antrorse or retrorse with no intermediate condition, thus suggesting that this trait is inherited in simple Mendelian fashion. If so, this hypothesis could explain why B. connata in the Thunder Bay area differs from both putative parent species in this regard; a normally masked, recessive allele(s) has been exposed by hybridization.

The ordination of all 4 Bidens species (Fig. 11) shows some differences between individuals of B. connata from the two collection sites. One of the individuals in the ordination tends toward B. cernua and might be the result of one or more back-crosses (B. cernua × B. connata). However, the distinctness of all 4 taxa in the Principal Coordinates Analyses indicates that introgression is not important as an evolutionary process in determining the present genetic status of these plants.

Observations of progeny type derived from achenes collected from sites where B.
Table 2. Chromosome numbers of Thunder Bay area *Bidens* taxa.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Thunder Bay</th>
<th>Other reports</th>
<th>Source</th>
</tr>
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<tbody>
<tr>
<td><em>B. connata</em></td>
<td>2n = 48</td>
<td>n = 24; 2n = 48, n = 36; 2n = 72</td>
<td>Weedon, Butler, 1976.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>n = 24; 2n = 48</td>
<td>Weedon &amp; Butler, 1976.</td>
</tr>
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</table>

**connata, B. cernua and B. frondosa** were all growing in close proximity indicated that no hybrid individuals had been produced. Furthermore, *B. connata* (2n = 48) cannot be a simple F₁ hybrid of *B. cernua* (2n = 24) and *B. frondosa* (2n = 48), nor an allopolyploid resulting from such a cross, since its chromosome number is inappropriate for either condition. However, *B. connata* from other areas has been counted at 2n = 72 (Weedon and Butler, 1976) and could be of allopolyploid origin.

The chromosome number of 2n = 48 of Thunder Bay populations of *B. connata* could result from either a cross between an unreduced gamete of *B. cernua* with a normal gamete of *B. frondosa* or a cross between a 2n = 24 race of *B. frondosa* with a typical (2n = 24) plant of *B. cernua*. The published chromosome numbers for these two species (Table 2) indicate that either of these two alternatives is feasible. However, a hybrid produced by either mechanism probably would show some loss of sexual fertility (Stebbins, 1950).

Seed viability and pollen fertility of Thunder Bay populations of *B. connata* are high, matching the levels of the other 3 taxa. These results do not conflict with the hybrid origin hypothesis for *B. connata*, however, if this taxon is reproducing agamospermy as our observations of PMC divisions suggest.

Weedon (Weedon and Butler, 1976) apparently was able to make meiotic chromosome counts of *B. frondosa* and *B. connata*, a result that we could not duplicate with Thunder Bay representatives of these 2 taxa. Although no other studies have reported agamospermy in *Bidens*, this method of reproduction is well known in many Compositae genera including certain widespread members of the Heliantheae (Grant, 1971). In fact, the very large number of poorly demarcated species and varieties of *Bidens* (Sherff, 1937) typify the characteristic pattern of an agamic complex (Stebbins, 1950); i.e., reproduction of highly heterozygous hybrids, in conjunction with a few sexual species, by a combination of agamospermy and intermittent sexual means. At any rate, regardless of how widespread this reproductive method is, it is probable that agamospermy has played a central role in the success of 3 of the 4 weedy taxa of *Bidens* found in the Thunder Bay area.

If a hybrid of *B. cernua* and *B. frondosa* could be produced by controlled cross pollination, it could be compared directly to *B. connata* to prove or disprove the hybrid origin hypothesis. However, we made preliminary attempts to cross *B. cernua* and *B. frondosa* that were unsuccessful, perhaps partly due to problems encountered in emasculation attempts, although we also suspect that normal fertilizations in *B. frondosa* are very rare.

In conclusion, it is probable that in the Thunder Bay area *B. connata* is the agamospermosously reproducing hybrid of *B. cernua* and *B. frondosa*. However, al-
ternate hypotheses to its origin cannot be eliminated for the present, nor is this conclusion necessarily valid for other more southern regions where B. connata is found. Nonetheless, certain other Bidens taxa that are poorly differentiated from B. connata, including B. tripartita L., B. comosa (A. Gray) Wieg., B. radiata Thuill., B. heterodoxa Fern., and B. eatonii Fern., may likely be elements of a widespread agamic complex. Possibly each of these poorly differentiated taxa consists of one or a few clones that have become fixed by agamospermy following sporadic hybridization with sexually reproducing members of the complex such as B. cernua. Developmental studies of embryo sac formation and observations of PMC divisions in these taxa are required to test this hypothesis.

Acknowledgments

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Literature Cited


