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TAXONOMIC CLARIFICATION OF *NOTOCELIA ROSAECOLANA* (DOUBLEDAY) AND *N. TRIMACULANA* (HAWORTH) (TORTRICIDAE)

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ABSTRACT. The strikingly similar Old World olethreutines *Notocelia rosaecolana* (Doubleday) and *N. trimaculana* (Haworth) have long been differentiated with seven structural and wing-pattern characters. Because these characters are quantitative and difficult to apply, it is unclear whether one or both taxa were accidentally introduced into North America. We evaluate the seven characters by examining each one (y) relative to forewing length (x), a surrogate for body size, in a basic sample of 60 specimens of both taxa from two continents, using the allometric equation $y = a(x^b)$. All seven characters proved to be body-size dependent and to lack discontinuities necessary for discrete states, thus rendering them diagnostically inadequate. Fortunately, a new qualitative diagnostic character emerged from this study: presence or absence of melanic sex scales near the base of the male hindwing hair pencil. These scales were absent in the putative type of *N. trimaculana* but present in those of *N. rosaecolana*, thus clarifying species identities and showing that *N. rosaecolana* is the only member of the pair thus far present in North America.

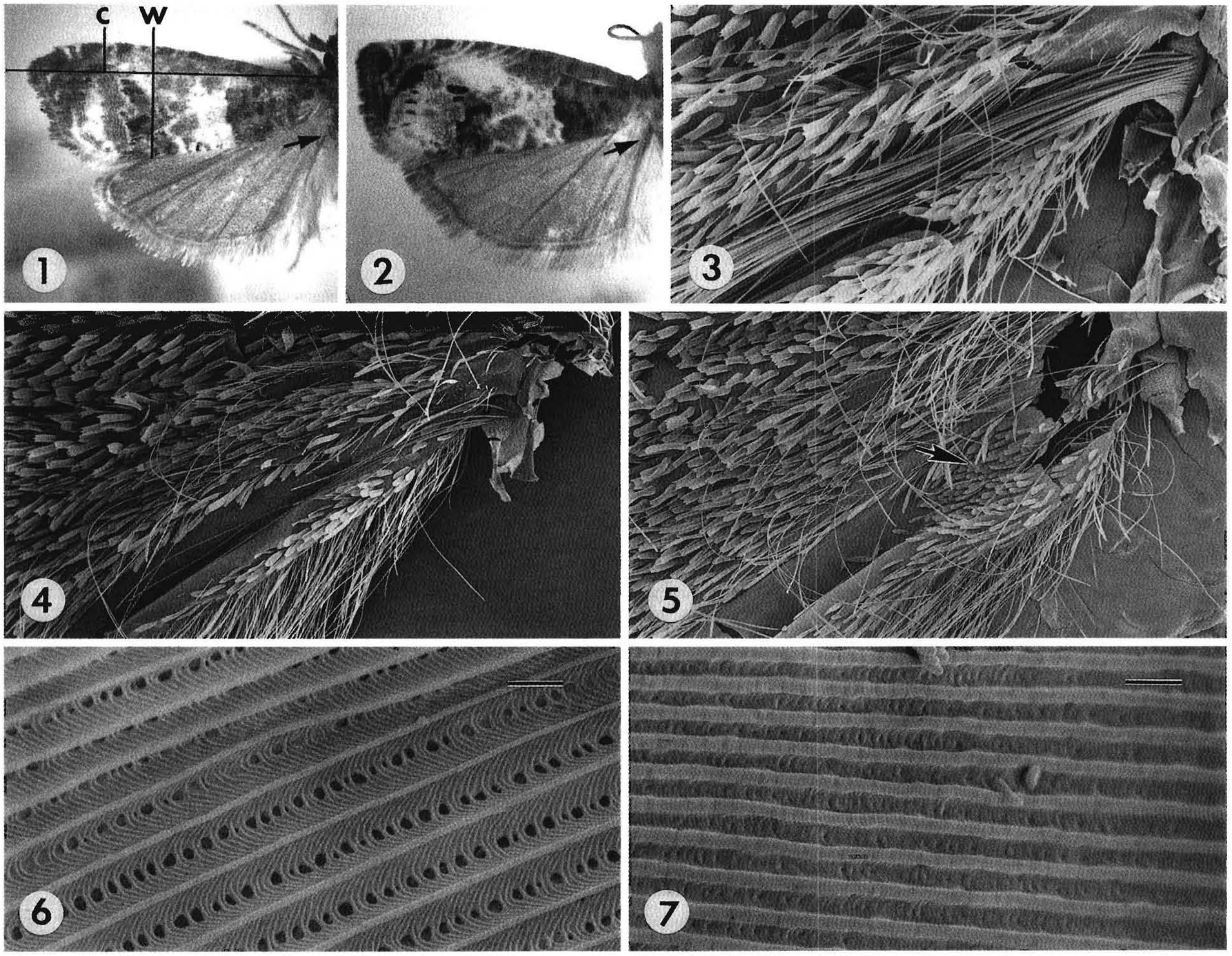
Additional key words: Olethreutinae, allometry, body size, Rosaceae, nitrogen.

Although strikingly similar, the olethreutines *Notocelia rosaecolana* (Doubleday 1850) and *N. trimaculana* (Haworth 1811) are considered separate entities in the Old World (Benander 1950, Bentinck & Diakonoff 1968, Bradley et al. 1979, Hannemann 1961, Kuznetsov 1987, Nasu 1980, Obraztsov 1965, Razowski 1987, Van Deurs 1956). The similarity, which encompasses genitalia as well as wing pattern, is acknowledged by most authors, with Hannemann (1961) adding that the taxa cannot be separated with certainty. Wing patterns (Figs. 1, 2) demonstrate the diagnostic difficulty, the illustrated specimens having been reliably identified by a newly discovered qualitative structural character introduced later in this paper.

The close similarity of these taxa has posed a problem in North America because it is unclear whether one or both are invading immigrants. The first American record is Kearfott's (1910) report from New Jersey of what he called *Eucosma suffusana* ([Lienig &] Zeller), a junior synonym of *Notocelia trimaculana.* This and subsequent specimen records were verified or reported by Brown (1973), Heinrich (1923), and Procter (1946). Later, Bradley et al. (1979) asserted that *N. rosaecolana* is the correct name for the taxon in North America. Their claim presumably rests on the fact that the reported larval foodplant in North America is *Rosa* (Rosaceae) (Ferguson 1975, Heinrich 1923, Kearfott 1910), which is the foodplant of putative *N. rosaecolana* in Eurasia. Doubleday (1850) described this species from specimens that developed on *Rosa,* probably the same specimens Douglas (1849) reared shortly before. In announcing the discovery of putative *N. rosaecolana* in Quebec, Landry (1995) used the nomenclature of Bradley et al. (1979), but suggested that both taxa might be present in North America.

The adult characters purported in the past to differentiate the two taxa are quantitative, and hence potentially ambiguous. These traditional characters consist of four structural and three wing-pattern traits. The states of these characters diagnosing *N. rosaecolana* and *N. trimaculana,* respectively, are: (1) strong vs. weak forewing costal curvature; (2) more vs. less obliqueness of forewing costal strigulae; (3) more (5–7) vs. fewer (4–5) pairs of forewing costal strigulae; (4) male forewing costal fold two-fifths of forewing length vs. one-half; (5) wide vs. narrow forewing width; (6) lighter vs. darker forewing coloration; (7) long and narrow vs. short and broad male socii (Benander 1950, Bentinck & Diakonoff 1968, Bradley et al. 1979, Hannemann 1961, Kuznetsov 1987, Nasu 1980, Razowski 1987, Van Deurs 1956). The *N. rosaecolana* states of characters (1), (2), and (6) were noted in the original description (Doubleday 1850). States of an eighth quantitative structural character mentioned by Bentinck and Diakonoff (1968)—thickness of male valval neck—contradict their illustrations, so this character is not considered further here.

The above sources give range of wing span or forewing length for both taxa as body size indicators.



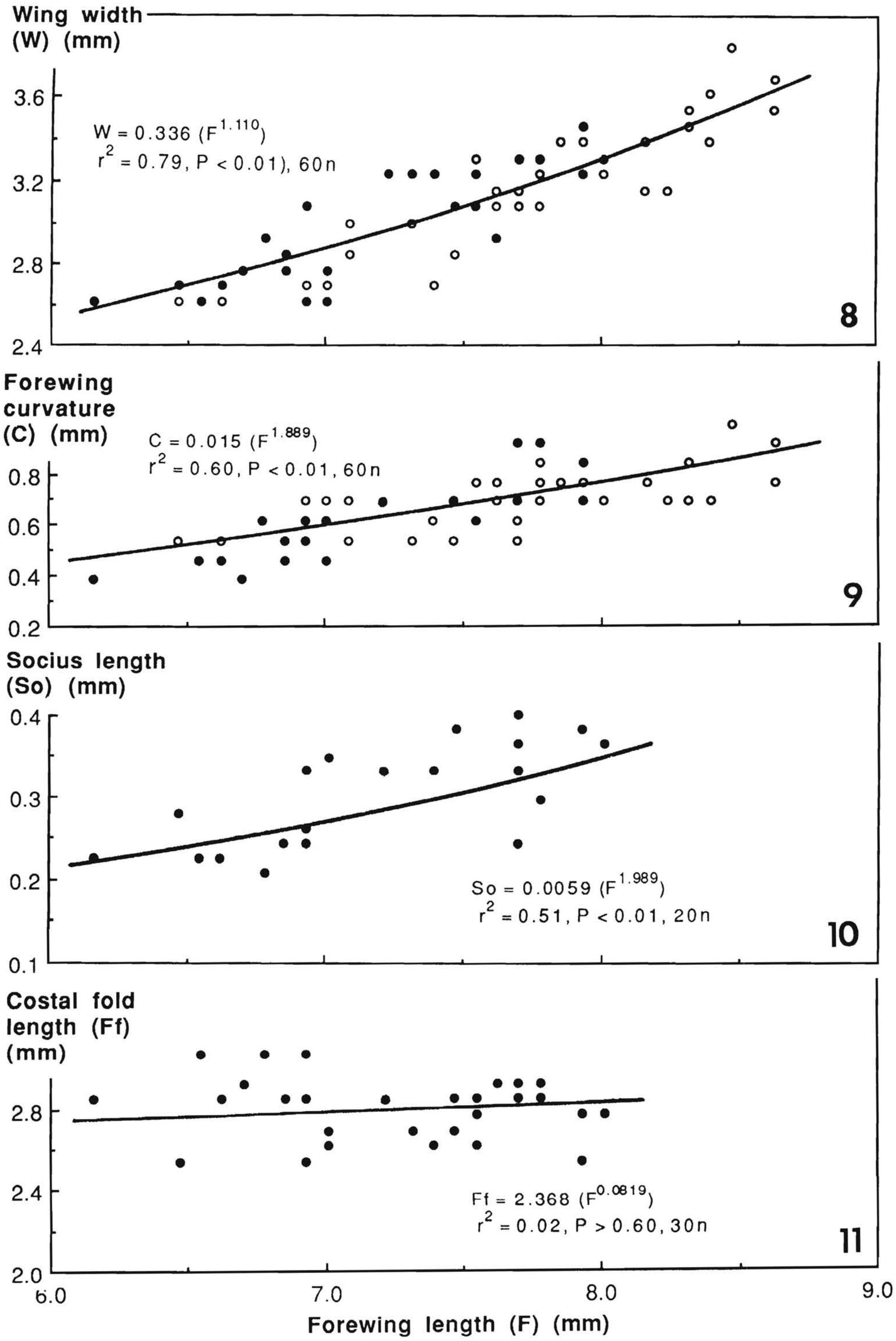
FIGS. 1–7 *Notocelia* wings and wing details. 1, *N. rosaecolana* male from St. Johns, Newfoundland (CNC) showing where forewing width (W) and curvature (C) were measured. Arrow points to barely visible hindwing anal fold containing hair pencil. Melanic sex scales, not visible, are present near base of the hair pencil. Forewing length 7.7 mm. 2, *N. trimaculana* male from "England" (Hodgkinson Coll., No. 54698) (BMNH). Arrow points to barely visible hindwing anal fold containing hair pencil. Melanic sex scales are absent near base of the hair pencil. Forewing length 6.9 mm. 3, Hair pencil in hindwing anal fold of male *N. trimaculana* from "Germany" (MEM), with melanic sex scales absent near the base of the hair pencil. 4, Hindwing anal fold of male *N. trimaculana* from "Germany" (MEM) with hair pencil removed to show absence of melanic sex scales. 5, Hindwing anal fold of male *N. rosaecolana* from Ithaca, NY (MEM) with hair pencil removed to show presence of melanic sex scales (arrow). Blackness of melanic sex scales is not evident in scanning electron micrographs. 6, Surface of normal scale adjacent to hindwing anal fold and hair pencil of male *N. rosaecolana* from Ithaca, NY (MEM). Bar = 2 microns. 7, Surface of melanic sex scale in anal fold beneath hair pencil of male *N. rosaecolana* from Ithaca, NY (MEM). Bar = 2 microns.

There is fairly close agreement in forewing length among the sources after spans are converted to lengths by an empirically derived equation (Miller 1977). The resulting ranges for putative *N. trimaculana* and putative *N. rosaecolana* are, respectively, 6.8–8.3 mm, and 7.3–9.1 mm. The larger body size of *N. rosaecolana* was noted in its original description (Doubleday 1850).

None of the seven traditional characters has been shown to be independent of body size. If characters are body-size dependent without discontinuities, they may erroneously appear to assume dichotomous states at different ends of the body-size spectrum, more so if they are positively allometric relative to body size. We examine the seven characters with respect to body size to decide whether they are sufficient for differentiating *N. rosaecolana* and *N. trimaculana.* Also, we introduce and elucidate a new qualitative structural character that for the first time clearly differentiates the taxa.

MATERIALS AND METHODS

We gathered data on the seven traditional characters from 60 pinned specimens of combined *N. rosaecolana* and *N. trimaculana,* half male and half female, which are referred to as the basic sample. To



FIGS. 8–11. Relations of structural character measurements to forewing length in 30 females and 19–30 males of combined *N. trimaculana*-*N. rosaecolana*. 8, Wing width. 9, Forewing curvature. 10, Socius length. 11, Costal fold length. Solid circles are males, hollow circles females. Some points represent more than one observation.

avoid accidentally including closely related taxa such as *N. roborana* (Denis & Schiffermüller), we used only pristine specimens with well preserved wing patterns. Using standard procedures, we made genitalia preparations of nearly half of the basic sample. To count presence and absence of melanic scaling associated with the male hindwing hair pencil—the new character—and to measure respective forewing lengths, we more than quadrupled the number of males in the basic sample, creating what is referred to as the augmented sample. Specimens of the basic sample originated in the U.K., France, Germany, the U.S. (Connecticut, Maryland, Massachusetts, Michigan, New Jersey, New York, Pennsylvania, Vermont), and Canada (Newfoundland, Ontario, Quebec); specimens of the augmented sample had the same origins plus Japan. We labeled each specimen of the basic sample "Voucher, Miller-Brown-Tuck 2001."

To gather character data from specimens, we measured dimensions, and categorized wing patterns, as follows: (1) Forewing width of both sexes in mm at W in Fig. 1; (2) Forewing curvature of both sexes measured in mm from costal edge at C in Fig. 1 to the perpendicular reference line; (3) Male socius length in mm from tip to cleft at the uncus; (4) Male forewing costal fold length in mm; (5) Number of pairs of strigulae in one forewing of females only, as the costal fold interfered with counting such strigulae in males; (6) Maximum slant of female forewing costal strigulae scored subjectively from 1 for slight to 4 for extreme; (7) Proportion of white or near white in the forewings of both sexes estimated subjectively to the nearest 10%.

We measured maximum length of one forewing as a surrogate for body size, including fringe and excluding tegula. Forewing length is a sensitive and reliable index of body size, with body mass in olethreutine adults increasing approximately as the cube of forewing length (Miller 1977). In the basic sample, using an ocular micrometer, we measured wing variables to the nearest 0.08 mm at nominal 10.5× magnification, and socius length to the nearest 0.02 mm at nominal 45× magnification. In the augmented sample, we measured wing length to the nearest 0.5 mm with a ruler.

To examine character measurements (y) relative to forewing length (x), we used the power or nonlinear form of the allometric equation, $y = a(x^b)$, where a and b are parameters (Smith 1980). We obtained parameter values using the Quasi-Newton method of estimation for nonlinear models (SYSTAT 1992). Because r^2 values in SYSTAT nonlinear output are rounded to one decimal place (nearest 10%), we obtained more precise r^2 values with the exponential regression option of StatWorks (Rafferty et al. 1985), which produced trend lines virtually identical to those of the allometric equation. We used absolute male forewing costal-fold length in the analysis rather than fold/wing length ratio to avoid the statistical complication of fold length appearing on both sides of the equation.

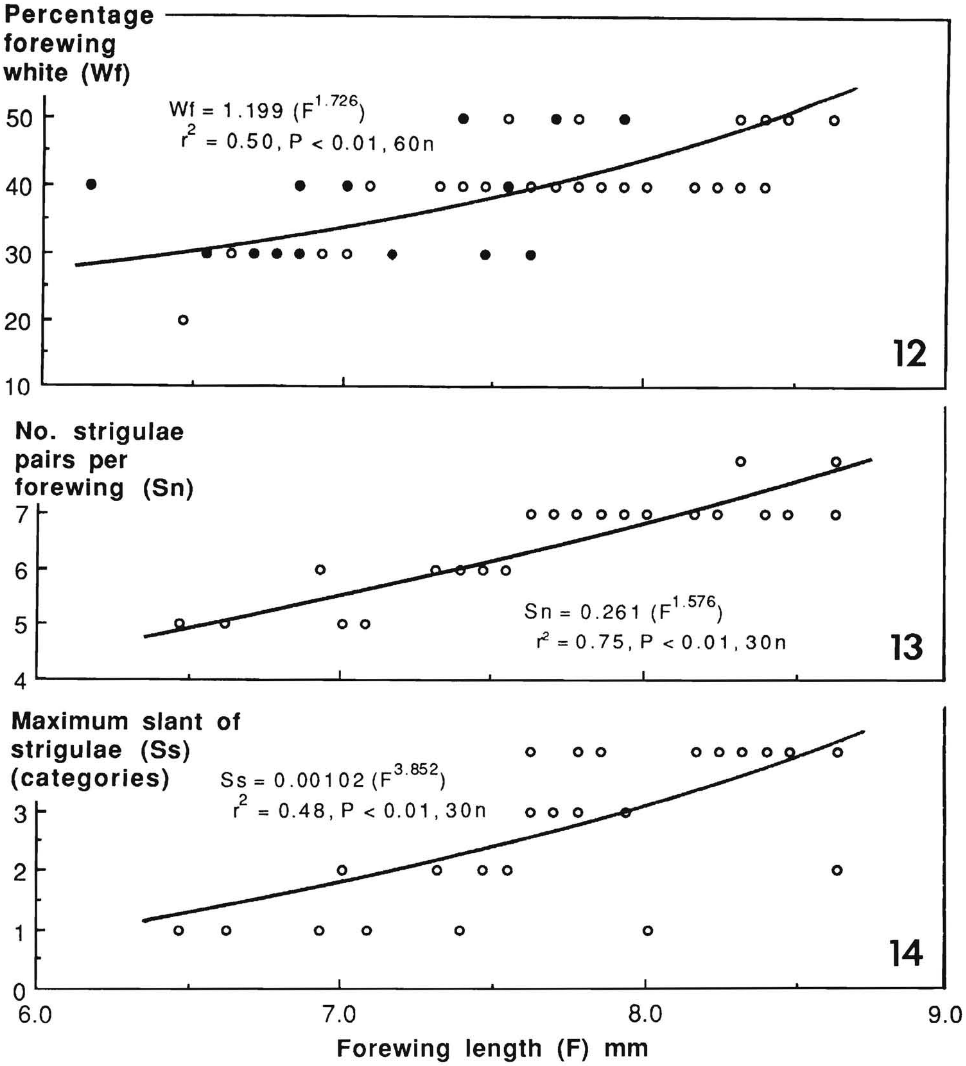
Male hindwing anal folds and associated structures were photographed with a LEO S 360 scanning electron microscope at an acceleration voltage of 15.0 kV. Specimen preparation for scanning electron microscopy followed Adamski and Brown (1987).

Museum and collection abbreviations are as follows: AMNH, American Museum of Natural History, New York, NY; BL, collection of B. Landry, Ottawa, ON; BMNH, Natural History Museum, London, UK; CAES, Connecticut Agricultural Experiment Station, New Haven, CT; CMP, Carnegie Museum, Pittsburgh, PA; CNC, Canadian National Collection, Ottawa, ON; JDG collection of J. D. Glaser, Baltimore, MD; LDG, collection of L. D. Gibson, Florence, KY; MEM, Mississippi Entomological Museum, Mississippi State, MS; MNHP, Muséum National d'Histoire Naturelle, Paris, France; UMC, University of Missouri, Columbia, MO; UMSP, University of Minnesota Entomology Museum, St. Paul, MN; USNM, National Museum of Natural History, Washington, DC; WDA, Washington State Dept. of Agriculture, Olympia, WA.

RESULTS

All seven traditional characters proved to be body-size dependent in their expressions, and to lack discontinuities necessary for discrete character states (Figs. 8–14). The size dependency of three structural characters—forewing width, forewing curvature, and male socius length—is direct, with forewing length explaining from 51 to 79% of character variability (Figs. 8–10). The size dependency of the remaining structural character, length of male forewing costal fold, is indirect; fold length is stable at a mean 2.8 mm regardless of forewing length (Fig. 11). Thus relative fold length is greater at shorter forewing lengths, and less at longer forewing lengths. Toward the shorter end at 6.5 mm of forewing length, the costal fold/wing length ratio is 0.43 (2.8 / 6.5 = 0.43)—near that for putative *N. trimaculana*—whereas toward the longer end at 8.0 mm of forewing length, the ratio is 0.35 (2.8 / 8.0 = 0.35)—near that for putative *N. rosaecolana*. In all the wing pattern characters, body-size dependency is direct, with forewing length explaining from 48 to 75% of character variability (Figs. 12–14). There were no pronounced sexual differences in characters measured on both sexes (Figs. 8, 9, 12).

Allometry is evident in several characters. Allometry refers to the numerical change in one body part or



FIGS. 12–14. Relations of scale pattern character measurements to forewing length in 30 females and 30 males of combined *N. trimaculana-N. rosaecolana*. 12, Percentage forewing white. 13, No. strigulae pairs per forewing. 14, Maximum slant of strigulae. Solid circles are males, hollow circles females. Some points represent more than one observation.

character relative to that in overall body size or in another body part or character (Smith 1980). If the exponent b in the allometric equation is >1, positive allometry is indicated; if it is <1, negative allometry is indicated; and if it is ≈1, isometry is indicated. Thus wing width, with a rounded exponent of 1.1, is essentially isometric (Fig. 8). Forewing curvature, male socius length, and number of pairs of forewing strigulae, with rounded exponents of 1.9, 2.0, and 1.6, respectively, are positively allometric (Figs. 9, 10, 13). Length of male costal fold, with a rounded exponent of 0.08, is negatively allometric (Fig. 11). Percentage forewing white (Fig. 12) and maximum slant of forewing strigulae (Fig. 14) may also exhibit positive allometry, but less definitely so because these variables were arbitrarily scaled. Allometry increases the apparent contrast in character states at opposite ends of the body-size spectrum. Incidentally, the visual impact of some of these relations is reduced because their vertical axes were compressed for economy of reproduction.

In contrast to the traditional characters, all seven of which are quantitative, the new diagnostic character discovered during this study is qualitative. It consists of melanic scales which are possessed by one taxon but not the other. When present, these scales occur in a fold between hindwing vein 3A and the anal wing margin near the base of a hair pencil lying in the fold (Figs. 3–5). The scales are assumed to have a sexual function.

The hair pencils of both species are similar except for their bases, the base appearing thicker and darker when the melanic scales are present. Hair pencil coloration ranges from brown to black in each species, perhaps depending on degree of exposure to light and fading. In the basic sample, the melanic sex scales were present in 10 males, and absent in the remaining 20.

In both species, ordinary scales on either side of the fold in which the hair pencil lies exhibit definable fenestrae, cross ribs, and scutes on longitudinal ridges (Fig. 6) and are similar to ordinary wing scales in the anal and cubital regions of other olethreutines (Brown & Miller 1983). In contrast, the melanic sex scales are coated with a substance that can be seen extruding from some fenestrae (Fig. 7). Similar coatings on melanic sex scales in males of the olethreutine *Cydia caryana* (Fitch) are removable by solvents, and have been postulated to be accreted glandular scent components (Brown & Miller 1983). The melanic sex scales reported here could be important in isolating males of one *Notocelia* species from females of the other.

The ability to separate males based on the new character enabled us to verify more subtle differences between the two taxa. We believe the following character states apply more often than not, and that they may be useful for separating females until a qualitative diagnostic character emerges for them: The forewing pattern is more precisely defined in *N. trimaculana*, with the dark markings having more definite boundaries than in *N. rosaecolana;* the forewing apex is more acute in *N. trimaculana*, and the apical scales more reddish brown than in *N. rosaecolana;* and the transverse silvery bars of the forewing ocellus are closer together in *N. trimaculana* than in *N. rosaecolana.*

Based on the augmented sample, the mean, computed standard deviation, and range of forewing lengths of males with and without melanic sex scales are, respectively, 7.9 ± 0.5 mm (6.5–9 mm) (n = 76) and 7.3 ± 0.5 mm (6–8.5 mm) (n = 59). Despite a broad overlap, the mean difference, 0.6 mm, is highly significant ($P < 0.001$, Student *t*-test).

In the basic sample, range in forewing length (6.1–8.6 mm) (n = 60) is similar to that published for the combined taxa (6.8–9.1 mm). Range interval of forewing length (higher range limit minus lower range limit) in the basic sample (8.6 – 6.1 = 2.5 mm) is likewise similar to that published for the combined taxa (9.1 – 6.8 = 2.3 mm). In the augmented sample, forewing length range (6–9 mm) and range interval (9 – 6 = 3 mm) (n = 135) are similar to the corresponding published values for the combined taxa (6.8–9.1 mm and 2.3 mm).

The new diagnostic character begs a review of names currently used for the two species. Presence or absence of melanic sex scales should enable species identities to be clearly established from the respective male primary type specimens. Besides *trimaculana* Haworth, 1811, and *rosaecolana* Doubleday, 1850, the name *suffusana* Duponchel (1843) is used instead of *trimaculana* by some modern authors apparently because Obraztsov (1965) considered *trimaculana* of Haworth to be a misidentification. Further complicating matters, the name *suffusana* was known for many years in collections as "*suffusana* Kuhlwein." Kuhlwein never published the name even though credited as the author by [Lienig &] Zeller (1846) who also reported *Crataegus* as its foodplant. The name *suffusana* [Lienig &] Zeller was originally used for the taxon introduced into North America, but *suffusana* [Lienig &] Zeller is a junior homonym of *suffusana* Duponchel. In addition, *suffusana* [Lienig &] Zeller is inferred to be a junior synonym of *trimaculana* Haworth because of the *Crataegus* rather than *Rosa* foodplant, and the liklihood that Duponchel also used Kuhlwein's name for his *suffusana.*

According to Horn et al. (1935–37), the collections of Haworth and Doubleday are in BMNH, and that of Duponchel in MNHP. Searches of those collections did indeed reveal male examples presumably used in describing the three taxa. Specimens of such vintage are usually considered types, in the present case a holotype each for *trimaculana* Haworth and *suffusana* Duponchel, and several syntypes of *rosaecolana* Doubleday. These examples of *trimaculana* and *suffusana* were found to lack melanic sex scales, while those of *rosaecolana* had them.

The present known North American distribution by states and provinces of the taxon possessing the melanic sex scales—*N. rosaecolana*—is Alabama, Connecticut, Delaware, Kentucky, Maine, Maryland, Massachusetts, Michigan, Missouri, New Jersey, New York, Newfoundland, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, Tennessee, Vermont, Virginia, Washington state, and West Virginia (AMNH, BL, CAES, CMP, CNC, JDG, LDG, MEM, UMC, UMSP, USNM, WDA). None of our North American male specimens lacked the melanic sex scales (n = 49).

DISCUSSION

The demonstration that all seven traditional characters used to distinguish *N. rosaecolana* and *N. trimaculana* are governed by body size, and that they lack discontinuities with change in body size, renders them inadequate for diagnostic use. Analogous situations have been demonstrated in other olethreutine genera, such as *Endothenia* (Miller 1983) and *Epiblema* (Miller & Pogue 1984). As for the larvae, Swatschek (1958) does not explicitly differentiate *N. rosaecolana* and *N. trimaculana,* but his key separates them by head color. MacKay (1959), however, considered head color a dubious diagnostic character for olethreutine larvae. Comparisons of forewing length range and range interval of study specimens with published values for the two taxa show that body size in the study specimens is representative.

Were it not for the new qualitative diagnostic character discovered during this study, results of the analysis of the seven traditional characters would cast doubt on whether *N. rosaecolana* and *N. trimaculana* are in fact different species. Although the new character distinguishes males only, it is sufficient to confirm that the two taxa are indeed separate entities. Females thus far cannot be reliably diagnosed, but certain wing characters verified in males enable tentative separation of some females.

The difference in mean body size between the taxa may be explainable by foodplant differences. Larvae of both are said to feed on terminal foliage of their respective foodplants: *N. rosaecolana* on the shrub genus *Rosa,* and *N. trimaculana* on the arboreal genera *Crataegus, Prunus,* and *Pyrus* (Rosaceae) (Benander 1950, Bradley et al. 1979, Hannemann 1961, Kuznetsov 1987, Nasu 1980, Razowski 1987, Swatschek 1958, Van Deurs 1956). These four plant genera differ in foliar nutrient quality. Nitrogen concentration in foodplant tissues is positively linked to growth in phytophagous insects (Mattson & Scriber 1987). Concentrations of foliar nitrogen in the three arboreal genera range from 1.7 to 2.9%, with one high outlier at 3.4% (Blinn & Buckner 1989, Cannon et al. 1960, Chase & Young 1978, Gerloff et al. 1964, Henry 1972, Vang-Petersen 1973). In contrast, concentrations of foliar nitrogen in the shrub genus *Rosa* under regimes of cultivation and fertilization range from about 3.0 to 5.6%, with one low outlier at 2.2% (Armitage & Tsujita 1979, Di Benedetto et al. 1995, Johansson 1979a, 1979b). Thus the foliage of cultivated *Rosa* can often be a third or more richer in nitrogen than the foliage of the arboreal foodplant genera. Significantly, Bradley et al. (1979) state that in the U.K., the larger bodied *N. rosaecolana* occurs especially on cultivated roses. Interestingly, elevated foliar nitrogen in *Rosa* may be an artifact of cultivation because foliar nitrogen reported for wild *Rosa* ranges from 1.5 to 2.2% (Henry 1972)—essentially the same as for the arboreal genera. Thus the body size difference between the two *Notocelia* taxa could also be an artifact.

Five reared adults available to us approximated body size expectations. All North American in origin, two males and two females developed on *Rosa* (CAES, USNM). These range in forewing length from 7.0 to 8.2 mm, which places them among the largest two-thirds of the basic sample. Both males possess the melanic sex scales of *N. rosaecolana.* The fifth specimen developed on *Robinia pseudoacacia* L. (Leguminosae) (CAES), which constitutes a new foodplant record for the *N. rosaecolana-trimaculana* group. This adult, which cannot be identified with certainty because it is a female, measures 7.4 mm in forewing length, and thus also falls among the largest two-thirds of the basic sample. Foliar nitrogen values for *Robinia* range from 3.1 to 4.0% (Blinn & Buckner 1989, Day & Monk 1977), which is in the foliar nitrogen range of cultivated *Rosa.*

Results of examining the putative types for melanic sex scales confirm the currently prevailing nomenclature of the two species, while clearly making *suffusana* Duponchel a junior synonym of *trimaculana* Haworth. The results also show that males of the invading species in North America are *N. rosaecolana* rather than *N. trimaculana.* Of course, the absence thus far of *N. trimaculana* males in North America makes it likely that North American females of the complex are also *N. rosaecolana.*

In conclusion, we would underscore that invalidating traditional but unreliable diagnostic characters can have the positive effect of fostering fruitful searches for new and strong diagnostic characters.

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