

THE GENUS *NEHALENNIA* SELYS, ITS SPECIES AND THEIR
PHYLOGENETIC RELATIONSHIPS
(ZYGOPTERA: COENAGRIONIDAE)

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The genus *Nehalennia* Selys is revised and redefined. It is demonstrated that *Argiallagma* Calvert is a synonym of *Nehalennia* Sel. The Brazilian *N. selysi* Kirby is redescribed and assigned to *minuta* Sel., as a subspecies. A lectotype is designated (♂: São João del Rey, Minas Gerais, Brazil; Coll. Selys, Inst. R. Sc. Nat. Belg., Brussels). The genus is closely related to other genera with an angulate frons. It actually includes six species and one subspecies, which are tentatively arranged into a "phylogenetic tree", based on differences and similarities of morphological characters (larval and adult). The penes and the male anal appendages of all species are figured. A new interpretation of the superior appendages is given and a terminology for both the superiors and the inferiors is proposed. Figures of the female prothorax of all species are provided, as well as drawings of other important structures and colour patterns. For the seven taxa a list of synonyms is given. In the case of *N. minuta* and *pallidula* Calv. a more exhaustive bibliography is added. Measures and venational features (males) are presented, as well as a description of the habitat preferences and dates on the distribution.

INTRODUCTION

Doubtless, the genus *Nehalennia* Sel. is not among those coenagrionids most urgently in need of being revised. This was not my purpose, indeed. My aim was simply to describe two supposedly new species of this genus from Venezuela, which have been set apart by the late Dr J. Rácenis many years ago, but apparently were forgotten by him later. — The more I advanced in the study of these two species, the more it became clear that I had to examine as many other species of the genus *Nehalennia* as possible if I wished to arrive at any definite conclusions. A special

need was the reexamination and redescription of the Brazilian *N. selysi* Kirby, and a careful study of the odd *Argiallagma minutum* (Sel.). — It was necessary to relax, with the help of ammonia, the penes and the anal appendages of all species, in order to allow comparisons. This proceeding proved especially useful in the case of the anal appendages, which are very complicated and almost throughout misinterpreted in the literature. However, once relaxed they could be moved around with a pin, and it then became easy to see whether a branch belonged to the superior or to the inferior appendage.

When I finally brought to an end my comparative studies, I had checked virtually all species currently known to -or believed to- belong in the genus *Nehalennia*. As a consequence, the generic name *Argiallagma* Calvert had to be synonymized with *Nehalennia* Sel. Either of the two presumably new species from Venezuela proved to be identic with an already well-known species, while *N. selysi* could be given only a subspecific status.

The realization of the present paper would have been impossible without the help and kind collaboration of the following persons: Dr S. ASAHINA (Tokyo, Japan), Dr D.A.L. DAVIES (Cambridge, United Kingdom), Dr P. DESSART (Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium), Dr T.W. DONNELLY (Binghamton, N.Y., U.S.A.), Dr H.J. DUMONT (Ghent, Belgium), Dr R.W. GARRISON (Azusa, Cal., U.S.A.), Mrs Leonora K. GLOYD (Ann Arbor, Mich., U.S.A.), Dr B. KIAUTA (Utrecht, The Netherlands), Dr J. LEGRAND (Muséum National d'Histoire Naturelle, Paris, France), Dr A.B.M. MACHADO (Belo Horizonte, Brazil), Dr M. MORATORIO (Universidad Nacional Experimental de los Llanos Occidentales "Ezequiel Zamora", Guanare, Venezuela) and Dr M.J. WESTFALL (University of Florida, Gainesville, Fla., U.S.A.).

I wish to express my sincere thanks to these persons and to the institutions they represent, for the loan of material, including type specimens, the furnishing of literature and many valuable comments.

THE GENUS *NEHALENNIA* SELYS

The name *Nehalennia* was established by Selys (SELYS & HAGEN, 1850) for his "1er Groupe" of the genus *Agrion*, with the eurasian *Agrion speciosum* Charpentier as the "type". Later SELYS (1876) enlarged the definition of his now "Sous-Genre 9. — *Nehalennia*", adding new characters.

In view of the results of the present work one may characterize the genus *Nehalennia* as a group of small coenagrionids with a sharply angulate frons and widely separated eyes. Head, thorax and normally the abdomen are more or less extensively marked with brassy black or metallic green. Postocular spots are absent, but a pale occipital line is normally visible. This line may be reduced to a very short mark around the neck, in some species. The second segment of the antenna is marked with a broad central white band. The legs are short with short to fairly long tibial spines. The wings are hyaline with a lozenge-shaped pterostigma, which covers one cell or less. Number of postnodal cross-veins: 7-12 in front wing, 6-11 in hind wing. Number of antenodal cells in the discoidal field 2-3. Origin of R_3 in fore wing between third and sixth postnodals, in most species proximal to the fifth. Origin of R_3 in hind wing between the third and fifth postnodals, normally

proximal to the fourth. IR_2 originates between the sixth and ninth postnodals in front wing as well as in hindwing. Arculus at second antenodal or slightly distally, in both wings. The cubito-anal cross-vein is separated from the posterior border of the wing by a distance of at least its own length. The shape of the quadrangle is variable, even within species. In the front wing the costal side of the quadrangle may be shorter or longer than the proximal side.

The penis has an internal and a terminal fold, but lacks any kind of flagella or spines. Only the lateral lobes of the distal segment do show specific modifications. No vulvar spine is present on the sternite of the eighth segment in the female. At this place an obtuse projecting lamina may be observed. The ovipositor reaches to the end of the abdomen. The dorsum of one or more of the distal abdominal segments display a pale blue colour ("Schlusslicht", see SCHMIDT, 1953). The anal appendages of the male are shorter than or as long as the tenth abdominal segment. The superiors are two or three-branched. The inferiors are variably shaped, but always steep, directed upwards, and with their modified parts in the upper half.

The sharply angulate frons in *Nehalennia* renders it easy to separate its species at a glance from similar species of *Ischnura* Charp., a genus which is characterized by a rounded frons and a compact head with a smaller distance between the compound eyes. Generic differences of the larval stage of the two genera are less obvious, although in *Nehalennia* most species have one principal mental seta and a varying number of small accompanying setae (as have the allied genera *Telebasis* Sel., *Ceriagrion* Sel., etc.), while *Ischnura* larvae have three to five principal mental setae (as has *Enallagma* Charp. and other related genera).

Nehalennia is essentially an American genus distributed from Brazil across northern South America, Central America and the Antilles, up to northwestern Canada. Only one palaeartic species (the generotype) has so far been found. — The genus clearly occupies a specific ecological niche. Its habitat requirements are fulfilled only by lentic habitats with flat water, invaded by emergent, erect, but low and variably dense vegetation in swamps, shores of smaller lakes, as well as around ponds ("Verlandungszonen", cf. DE MARMELS & SCHIESS, 1977).

WHAT IS ARGIALLAGMA?

The bibliography concerning *Nehalennia minuta* (Sel.) shows how one and the same species has been described several times under different names and has continuously been pushed for and back across the genera, but not in a single case attributed under its legal specific name to that genus in which it actually belongs: *Nehalennia* Selys. This in spite of multiple evidence, not only of adult characters, but of larval features as well. — In the following I shall expose the arguments which brought me to the conclusion that *Argiallagma* Calvert (pro *Argiallagma* Selys, nom. nud., see COWLEY, 1934) is nothing else than a synonym of *Nehalennia* Selys.

KENNEDY (1920) thought that the "curious *Argiallagma*" joins characters at once with his "Argia series", "Enallagma — Acanthagrion series" and "Nehalennia — Telebasis series". Still DAVIES (1981) files *Argiallagma* under the Ischnurinae, but *Nehalennia* under the Coenagrioninae and the closely related *Telebasis* under the Pseudagrioninae.

The morphological characters historically and currently used to define the genus *Argiallagma* (type species: *Trichocnemis minuta* Sel.) in its adult stage are: the long tibial spines, the presence of a vulvar spine on the eighth abdominal segment of the female, wing venation, the absence of dorsal processes on the tenth abdominal segment of the male, and colour pattern. Already SELYS (1876, p. 498) says: "Le premier group, composé du seul *Enallagma aduncum* [= *Argiallagma minutum*] est bien notable par la longueur des cils divariqués des tibias, qui le feraient classer parmi les Argias, si l'épine vulvaire de la femelle ne s'y opposait". CALVERT (1907, p. 376) quotes: "This genus [*Argiallagma*] apparently belongs to the same division of the legion Agrion as do *Hyponeura* and *Argia*, since the biserial hairs on the legs are nearly, or quite, twice as long as the intervals separating them. It differs from those genera [. . .] in the presence of an apical ventral spine on the eighth abdominal segment of the female". Later authors followed this diagnosis (BYERS, 1930, p. 168; JOHNSON & WESTFALL, 1970, p. 60), or exposed criticism, but without presenting nomenclatorial alternatives (GEIJSKES, 1943). — I do not think that the length of the tibial spines can serve as a generic character. In *Acanthagrion* Sel. most species have short tibial spines, but *A. rubrifrons* Leonard and *A. longispinosum* Leonard, as well as two yet undescribed species from Venezuela (DE MARMELS, in press), have very long tibial spines. I also have compared a large lot of *Argiallagma minutum* and found that the length of the tibial spines exhibits a considerable individual variability. In some cases it seemed difficult to distinguish a hind tibia of *Argiallagma minutum* from one of *Nehalennia integricollis* Calv., or even of *N. gracilis* Morse, on the basis of the length of the external spines only. GEIJSKES (1943) was the first in criticizing the systematic position of *Argiallagma* near *Argia* Rambur, adducing that the long leg spines are merely a case of convergence.

The so-called vulvar spine in the female of *Argiallagma minutum* (cf. HAGEN, 1861, and other authors, as cited above) has first been questioned by the late Dr J. Rácenis (unpublished manuscript notes). He writes (translated from Spanish): "We have examined a considerable number of females of this species from Cuba, Centralamerica and Venezuela, and we found this spine being of very variable shape. In a relatively small number this organ has the shape of a more or less acute lamina, but never resembles a true vulvar spine. In the overwhelming majority of the specimens, however, the "spine" is merely an obtuse prolongation of the eighth sternite, and in several cases even such a prolongation is entirely absent". — I only can confirm Rácenis' observations. In addition it must be remembered that in the genus *Oxyagrion* Sel. *O. evanescens* Calv. lacks a vulvar spine, while the

remaining species of this genus have it (COSTA, 1978). Similarly, *Acanthagrion rubifrons* and *A. longispinosum* lack the vulvar spine, which is present in all other species of that genus (LEONARD, 1977). In his enumeration of typical characters of the genus *Ischnura*, CALVERT (1913a, p. 316) states: "Females with or without a vulvar spine, in some cases even in the same species". JOHNSON & WESTFALL (1970, p. 80) expose that the females of *Ischnura prognatha* (Hagen) are "inconsistent relative to the presence of a vulvar spine". The presence or absence even of a true vulvar spine should, therefore, not unconditionally be accepted as a diagnostic character to separate genera. In the concrete case it proves to be insufficient for separating *Argiallagma* from *Nehalennia*, the more so since the "spine" is a mere projecting lamina, a morphologically far different structure. I wish to put emphasis on the fact that there is a female *Nehalennia irene* (Hagen) in our collection (No. 12240), which shows a vestige of a vulvar prolongation, too (Fig. 45).

Wing venation has been used to show the distinctness of *Argiallagma* from *Argia* (CALVERT, 1907), but nobody has ever compared the wings of *Argiallagma* with those of *Nehalennia*. It is true that the first antenodal (costal) space is only slightly shorter than, or almost as long as, the third one in *Argiallagma minutum*, but very much shorter in *Nehalennia speciosa*. However, *N. gracilis*, *N. irene* and, especially, *N. integricollis* can perfectly be considered intermediates relative to this feature. It is rather *N. integricollis* which differs considerably more from the remaining species of the genus than does *Argiallagma minutum*, by its narrow wings and in having only two antenodal cells in the discoidal field instead of three as in the case in its congeners. — The wing venation of *Argiallagma minutum* agrees in all respects perfectly with that of other *Nehalennias*.

The distal margin of the tenth abdominal segment shows exactly the same incision and lack of protuberances in *Argiallagma minutum* as is known from the northamerican species of *Nehalennia*. — The only striking difference between *Argiallagma* and *Nehalennia* appears, therefore, to be the colour pattern of the pterothorax. In *Argiallagma* the brassy black or metallic green median stripe does not reach to the humeral suture but for the distal sixth, while in all northern species traditionally comprised in the genus *Nehalennia* the strongly metallic green colour not only covers almost the entire mesepisternum and mesepimeron, but invades the upper metepisternum as well. — Colour, however, never has been a good character to separate genera. As examples I mention the case of *Argiallagma* / *Oxyagrion*, or that of *Aeolagrion* Williamson / *Telebasis*. Melanistic specimens of *Argiallagma minutum* are marked on the mesepimeron with conspicuous brassy black stripes or dots. These specimens may be considered intermediates in coloration between *Argiallagma* and the remaining *Nehalennias* (especially *N. gracilis*, cf. Fig. 52). It is further noteworthy that neither SELYS (1876) in the case of *N. sophia* (= *selysi* Kirby), nor CALVERT (1913b) when describing *N. pallidula* hesitated in attributing their respective species to the genus *Nehalennia*, even if the brassy black

median stripe of the thorax did not reach to the humeral suture. The genus *Argiallagma* did not even come to their mind. Had it, I would not write this paper now, for they would have recognized immediately that *Argiallagma* and *Nehalennia* are one and the same thing. The expansion of the pale colour in *Argiallagma minutum*, *N. selysi* and *N. pallidula* may speculatively be interpreted as an adaptation to the tropical climate; likewise the abundant dark colour of the boreal species would be an adaptation to the colder climate in the north.

I would like, however, to add further evidence to the proposed synonymy. The penes of all species of *Nehalennia* — including *Argiallagma minutum* — have a well-developed terminal and internal fold. They show comparatively weak interspecific differences in the shape of the terminal lobes of the apical segment, while in ventral view the aspect can vary considerably, depending on the degree of back-bending of these terminal lobes. There is absolutely no difference which could be considered generic between the penis of *Argiallagma minutum* and those of the remaining species of *Nehalennia*.

The configuration of the anal appendages of *Argiallagma minutum*, and of *Nehalennia* in general, has often been misinterpreted: *Argiallagma minutum*: [as *Agrion aduncum*] "appendages very short, the superior ones biparted..." (HAGEN, 1861, p. 79); [as *Enallagma? aduncum*] "Appendices anals très-courts. Les supérieurs [...] à branche supérieure externe cylindrique, obtuse, droite, la branche interne plus grêle, courbée en bas". (SELYS, 1876, p. 499/500). — *Nehalennia selysi*: [as *N. sophia*] "Appendices anals [...] supérieurs coniques [...] paraissant munis à leur base d'une branche interne, les inférieurs plus courts, bifides [...]" (SELYS, 1876, p. 1242). — *Nehalennia irene*: "Appendices supérieurs extrêmement courts, obtus, divisés en deux branches dont l'inférieure est la plus longue" (SELYS, 1876, p. 1240). — The figure of the appendages of *N. integricollis* in JOHNSON & WESTFALL (1977, p. 72, fig. 13F) reveal a similar error of interpretation, showing the ventral branch of the superior appendage as a part of the inferior one.

Actually, the superior anal appendages in the genus *Nehalennia* are originally (this is my guess) three-branched, consisting of a dorsal, a ventral and an internal branch! This archaic, fully developed three-branched type is still present in *Argiallagma minutum* and in *Nehalennia pallidula* while partial or total reduction of single branches can be observed in the remaining species. This phenomenon will be discussed in a later chapter.

One of the most important characters of the "Nehalennia — Telebasis series" (KENNEDY, 1920; ST. QUENTIN, 1960) is the angulate frons in the adult stage. *Argiallagma minutum* would never have been placed near *Enallagma*, *Argia*, *Leptobasis* Sel. or whatever, if these authors had observed the frons of this species, which is extremely angled, exactly as in *Nehalennia*. In fact, a head of *Argiallagma minutum* can be distinguished from one of a boreal species of *Nehalennia* only by the colour, especially the pale colour of the lower head in the former.

GELJSKES (1943) made the very important observation, that the larva of *Argiallagma minutum* shares more morphological characters with those of *Telebasis* and *Aeolagrion* than with larvae of *Argia*. This, again, agrees perfectly with KENNEDY's (1920) "Nehalennia — Telebasis series". The comparison of the larva of *Argiallagma minutum* with the same stage of the other Nehalennias apports further evidence for the generic identity of *Argiallagma* with *Nehalennia*. The whole structure, and even pigmentation of the caudal lamellae in *Argiallagma minutum* is overwhelmingly similar to that in *N. integricollis* and also in *N. irene*. In *N. gracilis* the gills are narrower, the apex is less acute and even blunt in some specimens. In *N. speciosa* a blunt apex is the rule. The variations in the number of setae of the larval labium between *Argiallagma minutum* and all other species of *Nehalennia* are small, all patterns being clearly deducible from each other. GELJSKES (1943) describes the apical border of the labial palpe of *Argiallagma minutum* as "straight and not toothed but denticulated with five or six small spines". I did not personally see the larva of this species, but an examination of larvae of *Nehalennia integricollis* and *N. speciosa* revealed that also in these species the denticles -or "spines"- are present, especially towards the movable hook, while near the apical hook, at the other end of the palpe, one or two "jags" of the border itself can be seen. The denticles are distinguishable through a microscope only.

Considering all those features compared above, larval and adult, it becomes obvious that *Argiallagma* Calv. is a mere synonym of *Nehalennia* Sel.

THE SPECIES OF THE GENUS *NEHALENNIA*

The genus *Nehalennia* comprises currently six species and one subspecies. In the following list a reasonably complete bibliography is given only in the case of the less-known subtropical and tropical species. For the taxa inhabiting the temperate and boreal zones a list of synonyms is presented.

NEHALENNIA MINUTA MINUTA (SELYS, 1857), NEW STATUS, NEW COMBINATION

Figures 1-3, 10, 11, 18, 24, 31-33, 40-43, 47, 48, 53, 56, 59, 62

1857 *Trichocnemis minuta* SELYS (Cuba: Calisco); — 1861 *Trichocnemis minuta* HAGEN (Cuba: Calisco); *ibid.* *Agrion aduncum* (Cuba); — 1867 *Leptobasis adunca* HAGEN (Cuba); — 1876 *Enallagma? aduncum* SELYS (Cuba: Calisco); — 1888 *Agrion (Enallagma) aduncum*; — GUNDLACH (Cuba: "parte occidental"); *ibid.*, *Trichocnemis minuta* [♀] (Cuba: "toda la Isla"); — 1890 *Enallagma minutum* KIRBY (Cuba); — 1907 *Argiallagma minutum* CALVERT (Cuba: Calisco; Guatemala: Los Amates); — 1919 *Agrion (Enallagma) aduncum*, *Argiallagma minutum*, *Trichocnemis minuta* [♀], *Enallagma? aduncum* CALVERT (citing GUNDLACH, 1888); — 1920 *Argiallagma [minutum]* KENNEDY (in part: Cuba); — 1930 *Argiallagma minutum* BYERS (in part: Cuba, Guatemala); — 1932 *Argiallagma minutum* KLOTS (in part: Centralamerica: Cuba; Isle of Pines); — 1934 *Enallagma aduncum*, *Trichocnemis minuta*, *Argiallagma [minutum]* COWLEY (discussing

authorship of the generic name *Argiallagma*); — 1938 *Argiallagma minutum* GARCIA DIAZ (Puerto Rico: Lake Tortuguero); — 1943 *Argiallagma minutum* GELJSKES (Surinam); — 1959 *Argiallagma minutum* KORMONDY (Guatemala: Tikal); — 1960 *Argiallagma minutum* WESTFALL (in part: Mexico; Cuba; Jamaica; Guatemala south to Surinam; Bahamas: Eleuthera Is., San Salvador Is.); — 1966 *Argiallagma minutum* PAULSON (Bahamas: Cat Is., San Salvador Is., Andros Is.); — 1966 *Argiallagma minutum* RÁCENIS (Venezuela); *ibid.* *Nehalennia pusilla* (nomen nudum) (Venezuela); *ibid.* *Nehalennia scorzai* (nomen nudum) (Venezuela); — 1977 *Nehalennia pusilla*, *Nehalennia scorzai* BELYSHV & KHARITONOV (Venezuela); — 1981 *Argiallagma* [*minutum*], *Trichocnemis minuta* DAVIES (Central and South America); — 1981 *Argiallagma minuta* [sic!] SANTOS (South America).

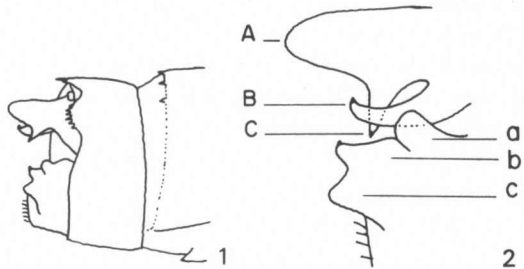
Material examined (40 ♂, 25 ♀). — Cuba, Costa Rica, Surinam and Venezuela: Amazonas Federal Territory and the States of Apure, Aragua, Barinas, Bolívar, Guárico and Portuguesa. The specimens were collected in all months of the year.

I did not examine the type, a female from Cuba. In the collection of the Instituto de Zoología Agrícola, Facultad de Agronomía, Maracay, there is a pair taken at Soledad, Las Villas, Cuba, by "Needham" (supposedly Dr J.G.Needham). These specimens do not differ from examples collected in Costa Rica, Venezuela and Surinam. — The colour pattern of *N. m. minuta* is basically the same as that of *N. m. selysi* and *N. pallidula*. The extension of black on the head is very variable in the Venezuelan specimens and is normally less than in the one figured from Cuba. Several males taken in the Savannah ("llanos") of Apure and Guárico States in Venezuela show a conspicuous black dot on each mesepimeron. On two such specimens (from Espino, Guárico) which are also very small (total length 24.5 mm), but do not exhibit any structural differences, the specific name *pusilla* Racenis (nomen nudum) is based.

Venation. — Postnodals in front wing 9-12 (normally 10), hind wing 7-11 (9); antenodal cells of discoidal field 3 (rarely 2 in one wing); origin of R_3 in front wing normally proximad to the fifth postnodal, in hind wing proximad to the fourth. Origin of IR_2 in front and hind wing between sixth and eighth postnodal.

Measurements (males). — Total length 24.5-29 mm; abdomen 20-24 mm; hind wing 11.5-15 mm.

The larva is characterized by its moderately broad caudal gills, each with a long



Figs 1-2. *Nehalennia m. minuta*: (1) Male anal appendages, right lateral view (right superior and left inferior appendage removed); — (2) Position of the right superior and inferior anal appendages, right lateral view, schematized. [Superior appendage: (A) dorsal branch, (B) ventral branch, (C) internal branch; — inferior appendage: (a) proximal lobe, (b) hooked lobe, (c) distal lobe].

pointed tip. The labium bears four mental setae on each side, three of them being long, the internal one short; palpus with seven setae (after GEIJSKES, 1943).

Distribution. — Mexico and Central America south to Surinam, the Antilles. According to a personal communication of Prof. A.B.M. Machado (September 1982) *N. m. minuta* does not occur in Brazil where it is replaced by *N. m. selysi*, *N. minuta* is also absent from the United States. All Florida specimens appear to belong in *N. pallidula*.

Habitat. — Cat Island (Bahamas): "Larvae, exuviae and teneralis were numerous at shallow marshes with abundant sedge (*Eleocharis*) growth [. . .]" (PAULSON, 1966, p. 99). — Surinam: "The specimen [a larva] was collected [. . .] in a flat pool on the savannah [. . .]" GEIJSKES, 1943, p. 176). — Venezuela: After unpublished manuscript notes of the late Dr J. Rácenis he had collected adult specimens at swampy stretches in the savannah of Guayaraca, Bolivar State. Further adults were caught recently by myself in the States of Apure and Portuguesa, on the savannah. The water level oscillated between 5 and 20 cm, but rarely exceeded 8 cm. The place may dry out completely during the dry season. The grassy vegetation, which included only few Cyperaceae, was 30-80 cm high and moderately to fairly dense (coverage 40-90%). *N. m. minuta* flies among the vegetation near the ground, avoiding open water.

NEHALENNIA MINUTA SELYSI KIRBY, 1890, NEW STATUS

Figures 4, 12, 25, 34, 49, 50, 54, 57, 60, 62

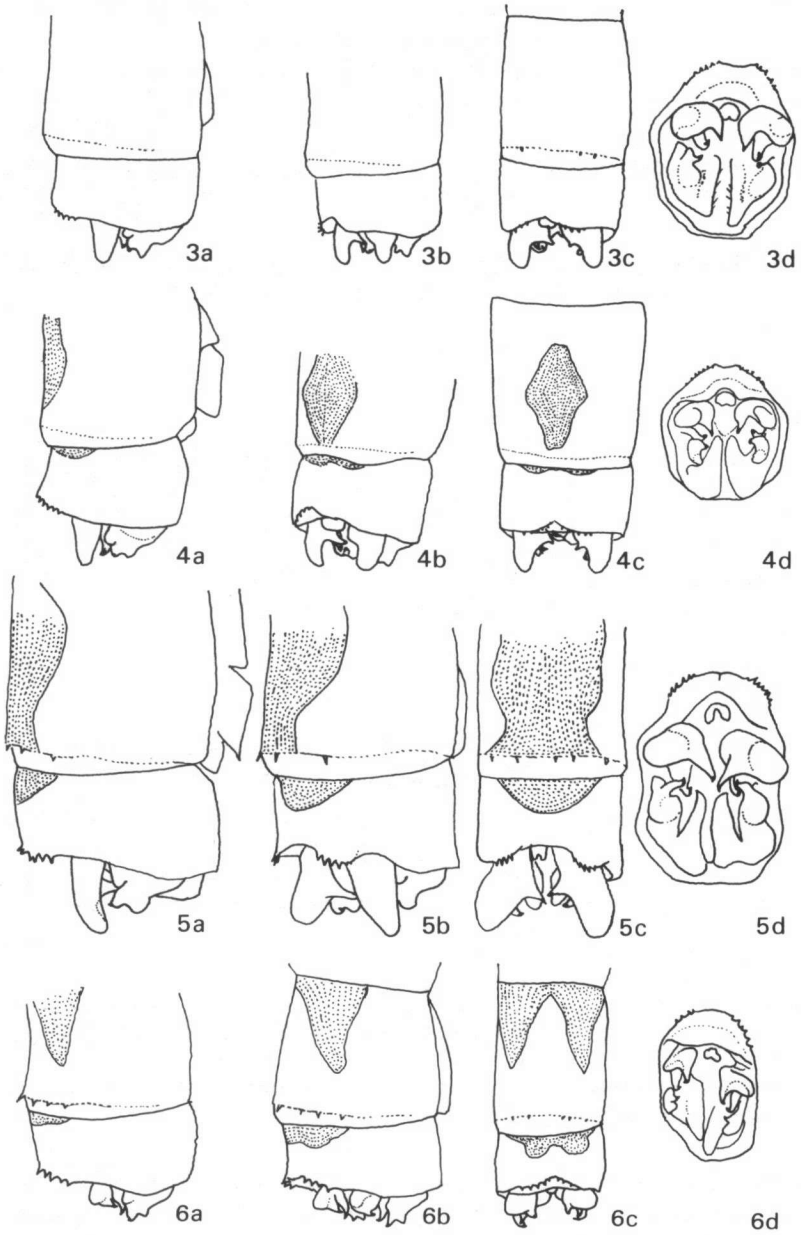
1876 *Nehalennia sophia* SELYS (Brazil: Minas Gerais, São João del Rey); — 1890 *Nehalennia selysi* KIRBY (nomen novum; cf. below); — 1913 *Nehalennia selysii* CALVERT ("From de Selys' description"); — *Nehalennia selysi* ST. QUENTIN (questioning the presence of the genus in South America); — 1978 *Nehalennia selysii* BELYSHEV & KHARITONOV (zoogeography and phylogeny).

Material examined (3 ♂, including the lectotype and the paralectotype, both with the same data). The third male, kindly sent to me by Dr A.B.M. Machado, is also from São João del Rey, Minas Gerais, Brazil, and was collected by himself in December 1955.

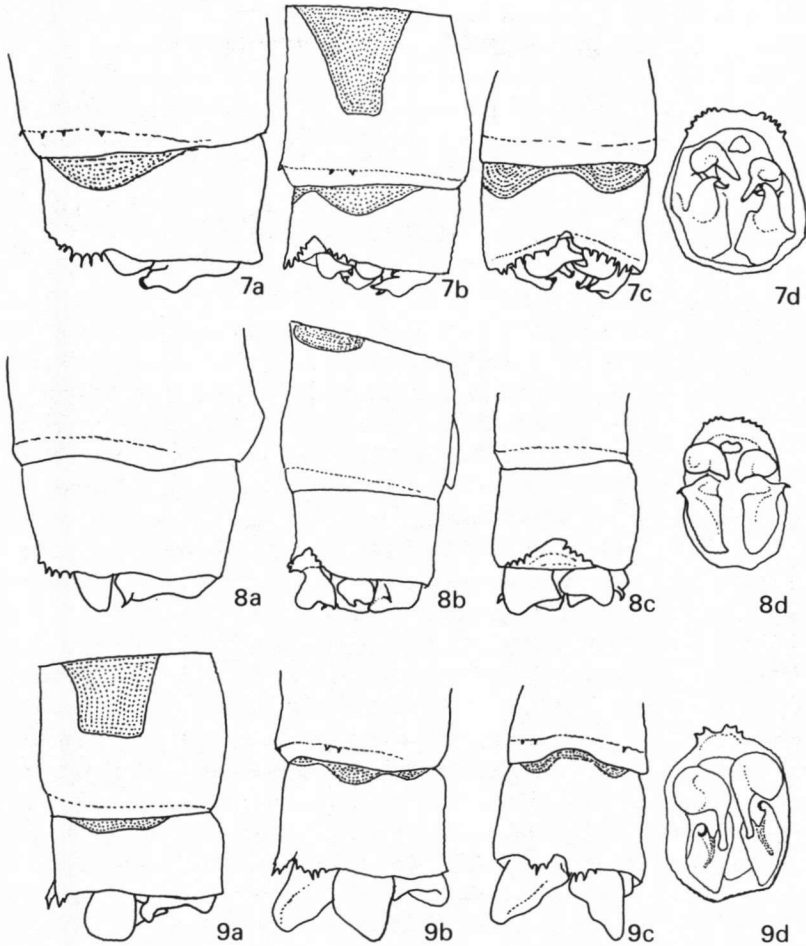
The specific name *selysi* was established by KIRBY (1890) as nomen novum for *sophia* Selys, 1876, which is a homonym of (*Agrion*) *sophia* Selys, 1840, for its part a synonym of *Agrion speciosum* Charpentier, 1840 (= *Nehalennia speciosa*).

Designation lectotype (male): Brazil, Minas Gerais, São João del Rey; deposited in the Institut Royal des Sciences Naturelles de Belgique, Brussels. — The following labels are attached to the specimen: one in Selys' handwriting, quoting "N. sophia de Selys ♂"; a second label states, in printed letters: "Sn — João d'el Rey"; on the third one is written: "dessiné par Sanos, 5.X.1964". — The specimen is completely eaten out by museum pests and, especially the abdomen, covered with their excrements.

Male (lectotype). — Frons sharply angulate; antennae dark brown, the second segment broadly pale in the middle. Top of head with a transverse black band with



Figs 3-6. For caption cf. p. 511.



Figs 3-9. Male anal appendages in *Nehalennia*, right lateral (a), right laterodorsal (b), dorsal (c) and posterior (d) views: (3) *N. m. minuta* (Venezuela, Guárico); — (4) *N. m. selysi* (a: lectotype, b-d: paralectotype); — (5) *N. pallidula* (U.S., Florida); — (6) *N. integricollis* (U.S., New Jersey); — (7) *N. irene* (U.S., Pennsylvania); — (8) *N. gracilis* (U.S., Pennsylvania); — (9) *N. speciosa* (Japan, Ozeegahara). — For Figs 3-6 cf. p. 510.

metallic reflections; this band covers the area between the base of antennae and the posterior border of the vertex. A continuous pale occipital band is present and separated from the pale underparts of the head by a diffuse brown line, largely interrupted around the neck. Labium pale, labrum blue with a dark centrobasal spot and basal line; clypeus pale, black on its anterior margin and with a very fine

dark basal line. — Prothorax broadly dark brown above, with weak metallic reflections, laterally pale; posterior margin almost straight, without any incision in the middle, and low-lying. Pterothorax with a brassy black median stripe covering almost three fourths of the mesepisternum, and touching the humeral suture for the last sixth of its length. The humeral suture black lined; a dark spot is present at the upper end of the metapleural suture; sides and ventral parts of thorax pale. Legs pale; femora black lined externally; tibial spines black, those six of the hind tibiae larger than the intervening spaces, apically shorter. Apex of all and tarsi and claws dark brown; tooth of tarsal claws well-developed, at four fifths of the length of the claws. — Apex of wings somewhat acute; petiolation does not reach to Ac. The origin of IA as much proximad to Ac as Ac is long. In fore and hind wings Ac lies definitely distal to the middle between first and second antenodals. Venation reddish in costal and basal parts, darker distally; pterostigma hardly covering one cell, yellowish, darker in center, its proximal side with a weak tendency to be more oblique than the distal side. Third antenodal space little longer than the first, and two times as long as the second. Discoidal cell of front wing with its proximal and costal sides about equally long; in the hind wing the costal side less than three times the length of the proximal side. Arculus slightly distally of the second antenodal. 11 postnodals in front wing, 9 in hind wing. Origin of R_3 proximal to the fifth postnodal in front wing, at fourth postnodal in hind wing; IR_2 at eighth and seventh postnodal, respectively. Discoidal field of all wings with three antenodal cells; three cells after the stigma. — Abdominal segment 1 pale with a black apical twin-spot; segments 2-7 dorsally dark, but extreme base of segments 3-7 blue. Dorsum of segment 8 with a black triangular spot; segment 9 with an elliptic black centrodorsal mark; segment 10 blue with an ill-defined black basal line. Distal margin of segment 10 broadly incised dorsally, this part furnished with black spinules. Superior anal appendages pale, trifid, the dorsal branch long and conical, the internal and the ventral branch each ending in a strongly chitinized hook. Inferior appendages shorter than superiors, trilobate, the middle lobe armed with a chitinized mesally directed hook ("hooked lobe"). Penis with well-developed internal and terminal fold.

Measurements. — Total length 30.8 mm; abdomen 25.3 mm; hind wing 16 mm.

The paralectotype male is similar to the lectotype, but has 10 postnodals in one hind wing, and R_3 originates somewhat proximad to the fourth postnodal in both hind wings.

Measurements. — Total length 29.6 mm; abdomen 24.1 mm; hind wing 15.5 mm.

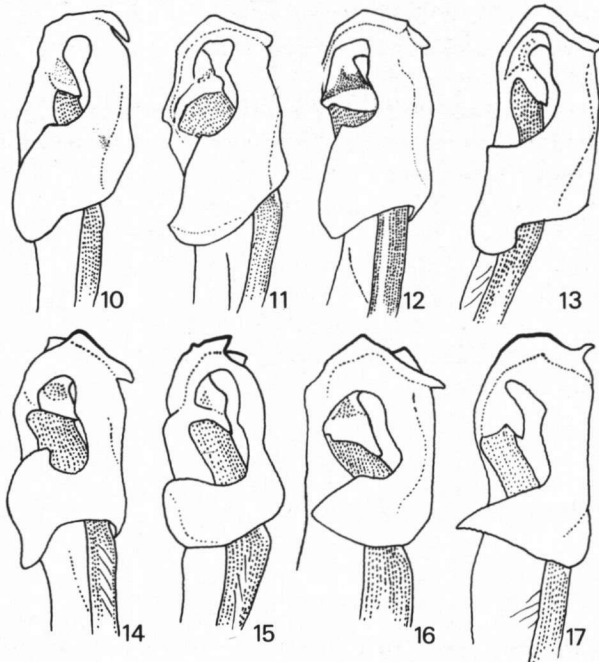
The third male examined differs from the type series by the considerable extension of black on upper head and thorax (Fig. 50). The wings have rather rounded tips, and there are only two cells after the stigma.

Measurements. — Total length 29 mm; abdomen 23.5 mm; hind wing 15 mm.

Distribution. — Brazil, State of Minas Gerais. Perhaps also Bahia (Alcobaça) and Maranhão (Imperatriz). — The two male specimens from Bahia and

Maranhão respectively (both in A.B.M. Machado's collection) differ, however, from the type series in lacking precisely the black rhomboidal spot on segment 9. The same is true for one of Dr Machado's males from Minas Gerais (Dr A.B.M. Machado, pers. comm., September 1983). This throws some doubt even on a subspecific distinctness of *selysi* from *minuta*. It must be remembered that *minuta* is recorded from Surinam. Neither the penis nor the anal appendages of *selysi* differ in any way from the same structures in *minuta*. On the other hand, the female sex as well as the larval stage of *selysi* are still unknown. This, together with the slightly larger size of *selysi* and the repeated presence of a black dorsomedian spot on segment 9 make me think that at least the populations from South Eastern Brazil (Minas Gerais) — a known zoogeographical province — may indeed be subspecifically different from the typical northern *minuta*.

Habitat. — Brazil, Minas Gerais, Parque Estadual do Rio Doce: "[...] collected flying on the grass at the border of a small lake, as written on the envelope by the collector. I know the lake and it is probable that the specimen was collected in its shallow area where it is continuous with a marshy grassy region, but one cannot be sure" (Dr A.B.M. Machado, pers. comm., September 1982).



Figs 10-17. Penes in *Nehalennia*, left lateral view: (10) *N. m. minuta* (Cuba, Las Villas); — (11) the same (Venezuela, Guárico); — (12) *N. m. selysi* (paralectotype); — (13) *N. pallidula* (U.S., Florida); — (14) *N. integricollis* (U.S., New Jersey); — (15) *N. irene* (U.S., Pennsylvania); — (16) *N. gracilis* (U.S., Pennsylvania); — (17) *N. speciosa* (Japan, Ozeegahara).

NEHALENNIA PALLIDULA CALVERT, 1913

Figures 5, 13, 19, 26, 35, 44, 51, 55, 58, 62

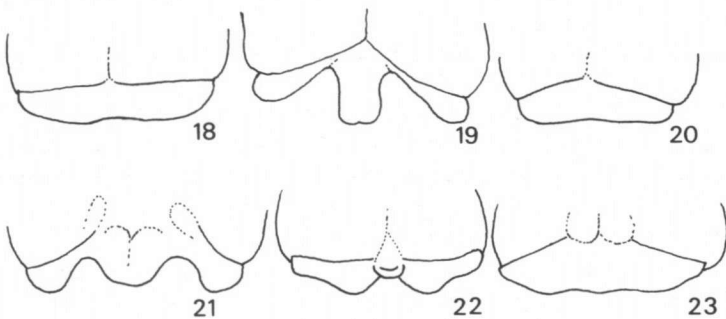
1913a *Nehalennia integricollis* CALVERT, in part [♂] (United States: Florida); — 1913b *Nehalennia pallidula* CALVERT (nomen novum); — 1920 *Argiallagma [pallidulum]* KENNEDY (in part: United States: Florida); — 1930 *Argiallagma minutum* BYERS (in part: U.S.: Florida); *ibid.* *Nehalennia pallidula* (Florida); — 1932 *Argiallagma minutum* KLOTS (in part: U.S.: "southeast"); — 1960 *Argiallagma minutum* WESTFALL (in part: U.S.: Florida); — 1970 *Argiallagma pallidulum* JOHNSON & WESTFALL (U.S.: "endemic to Florida"); — 1977 *Nehalennia pallidula* BELYSHEV & KHARITONOV; *ibid.* *Nehalennia integricollis* (U.S.); — 1981 *Argiallagma [pallidulum]*: implicitly in "J2" DAVIES (genus: "Central and South America").

Material examined (4♂, 4♀). — United States, Florida, Glades County, Palmdale, U.S. Highway 27, at Fisheating Creek, 1.IV.1961, M.J. Westfall leg.

This species is closely related to *N. minuta* from which it differs in the male sex by the distally abruptly extended apex of the terminal lobes of the penis, the broad and upright posterior margin of prothorax, and the mostly black coloured dorsum of segment 9. Also the apex of the ventral branch of the superior anal appendage is not visible in lateral view in *N. pallidula*, but clearly discernible in *minuta*. The female of *pallidula* differs from that of *minuta* chiefly by the highly modified distal border of prothorax.

Venation. — Postnodals in front wing (males) 9-10, hind wing 8. Origin of R₃ in front wing slightly proximad to the fifth postnodal, to the fourth in hind wing. IR₂ at seventh postnodal, in both wing pairs.

Measurements (males). — Total length 27-29 mm; abdomen 22-23 mm; hind wing 14-14.5 mm.



Figs 18-23. Hind border of the female prothorax in *Nehalennia*, dorsal view: (18) *N. m. minuta* (Surinam, Landerij); — (19) *N. pallidula* (U.S., Florida); — (20) *N. integricollis* (U.S., Florida); — (21) *N. irene* (U.S., Michigan); — (22) *N. gracilis* (U.S., Pennsylvania); — (23) *N. speciosa* (Japan, Ozeegahara).

Larva. — "We [. . .] had a couple larvae from the Everglades that were very similar to *minutum* [. . .]" (M.J. Westfall, pers. comm., August 3, 1983).

Distribution. — Endemic to Florida (U.S.), here especially in the South.

Habitat. — "Habitats with dense emergent vegetation appear to be favored" (JOHNSON & WESTFALL, 1970, p. 84).

NEHALENNIA INTEGRICOLLIS CALVERT, 1913

Figures 6, 14, 20, 27, 36, 62

1913a *Nehalennia integricollis* CALVERT (U.S.: Florida, Georgia, New Jersey); —
1913b *Nehalennia integricollis* CALVERT (U.S.: New Jersey).

Material examined (3 ♂, 5 ♀). — United States, New Jersey, Burlington Co., Red Lion, 2 ♂, 22.VIII. 1946, Beatty leg.; Florida, Seminole Co., Sml Lake at jct. US. 17 & S. 436, 1 ♂ (ex larva), 21.II.1959, M.J. Westfall leg.; Highlands Co., Highlands Hammock State Park, 2 ♀, 1-IV-1960, W.H. Cross & L. Bottimer leg.; Alachua Co., San Felasco Hammock, Fox Pond, 2 ♀, 15 and 17-V-1969, M.J. Westfall leg.; Walculla Co., Panacea, 1 ♀, 7-X-1971, M.K. Borden leg. — Larvae: Florida, exuvia of the male "ex larva", as above; Gadsden Co., Dam Lake, 3 larvae (ultimate instar), 19.IV.1957; Seminole Co., Prairie Lake, 3 larvae (ult. inst.), 25.II.1956, all M.J. Westfall leg.

This species is similar to the boreal species in having extended metallic green areas on head, thorax and abdomen. However, the penis, the anal appendages, the rounded hind margin of the prothorax in the female, the rather long tibial spines, as well as number and distribution of the larval labial setae and the structure of the caudal gills place *N. integricollis* equally close to the tropical *N. minuta*. *N. integricollis* is the smallest *Nehalennia*, and is further characterized by having only two (occasionally one) antenodal cells in all wings.

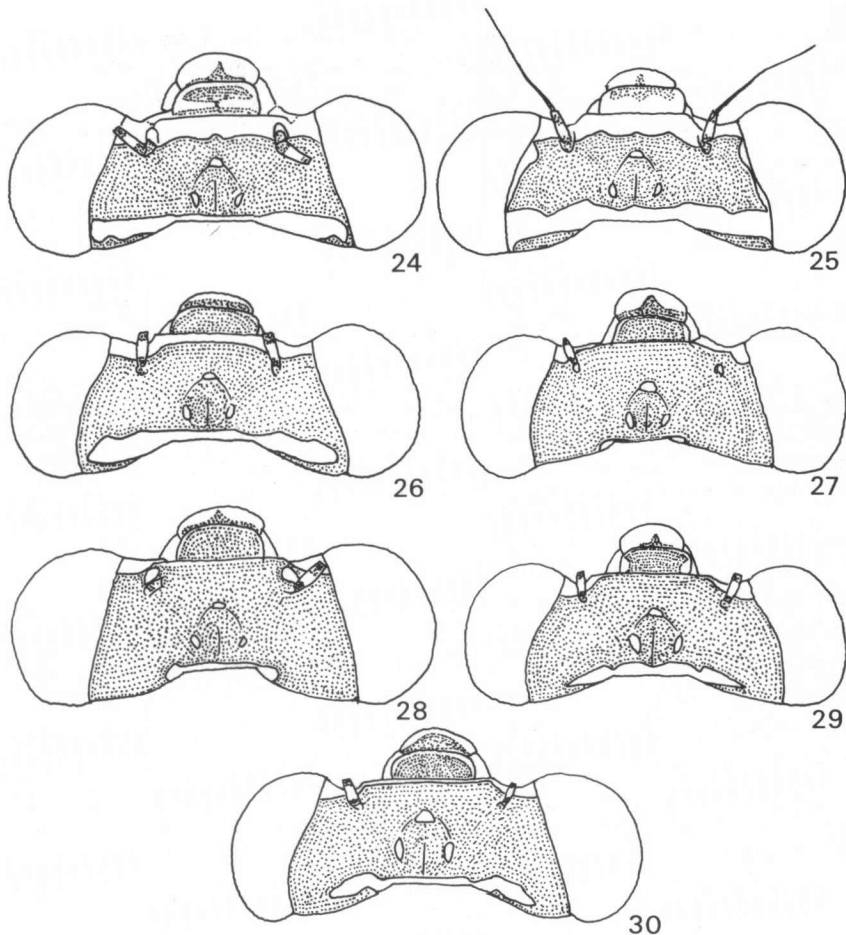
Venation. — Postnodals in front wing 7-9, hind wing 6-7. Origin of R_3 proximad to the fourth postnodal in fore wing, around the third in hind wing. IR_2 at the sixth postnodal, in all wings.

Measurements (males). — Total length 23-24 mm; abdomen 18.5-19.5 mm; hind wing 11-12.5 mm.

Larva. — The larva "comes closest to *minutum* in structure of the gills and markings of the *Nehalennia* species" (Dr M.J. Westfall, pers. comm., February 1983). The labium is armed on each side with four mental setae of whom the external seta is the only long one; palpus with six setae.

Distribution. — United States: New Jersey to Florida.

Habitat. — The larvae "are usually taken in sand-bottomed lakes of Central Florida in rather thick vegetation near the edge" (Westfall, pers. comm., February 1983). — Adults were "flying among the abundant pickerel weeds (*Pontederia cordata*, var. *angustifolia*) and white water lilies (*Castalia*) [. . .]" (CALVERT, 1913b, p. 374).



Figs 24-30. Colour pattern of head in *Nehalennia* (males), dorsal view: (24) *N. m. minuta* (Cuba, Las Villas); — (25) *N. m. selysi* (lectotype); — (26) *N. pallidula* (U.S., Florida); — (27) *N. integricollis* (U.S., New Jersey); — (28) *N. irene* (U.S., Pennsylvania); — (29) *N. gracilis* (U.S., Pennsylvania); — (30) *N. speciosa* (Japan, Ozegahara).

***NEHALENNIA IRENE* (HAGEN, 1861)**

Figures 7, 15, 21, 28, 37, 45, 62

1861 *Agrion* (*Nehalennia*) *irene* HAGEN (U.S.: Chicago, Florida, Wisconsin, Illinois, New Jersey, Maine); — 1914 *Nehalennia carlotta* BUTLER (U.S.: New York, Saranac Inn).

Material examined (4 ♂, 2 ♀). — United States, Michigan, Schoolcraft Co., 1 ♀, 4.VIII.1947, R. Dreisbach leg.; New York, Ithaca, 1 ♂, 14.VIII.1946, without collector; Pennsylvania, Bucks Co.,

Plumsteadville, 3 ♂, 1 ♀, 17.VI.1947, Beatty leg. — Larvae: Minnesota, Clearwater Co., Nicollet Cr., Itasca St. Pk., 9 larvae (ultimate instar), 22.VI.1960, K.C. Kim leg.

The shape of the superior and inferior anal appendages, reveals a close relationship of *N. irene* with *N. integricollis*. The modified hind margin of the female prothorax, the shorter tibial spines, the reduced number of mental setae of the larval labium place *irene* near *gracilis*.

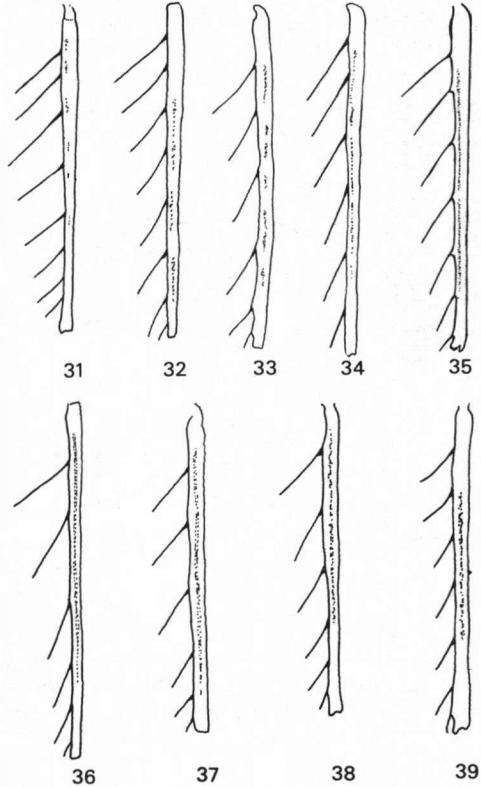
Venation. — Postnodals in front wing 9-12, hind wing 8-11. Origin of R_3 in fore wing proximad to the fourth, or between fourth and fifth postnodal, in hind wing between third and fifth postnodal. IR_2 originates between the sixth and the ninth postnodal in the front wing and between the sixth and the eighth in the hind wing. Individuals with only two antenodal cells in one wing can be found.

Measurements (males). — Total length 24.4-27.5 mm; abdomen 20-22 mm; hind wing 14.5-15 mm.

Larva. — The larva is similar to that of *N. integricollis*. The labium is armed with one long principal mental seta and one or two accompanying small setae (rarely none), on each side; palpus with six setae.

Distribution: Canada and United States (south to Illinois, Maryland, etc.).

Habitat: "It inhabits almost all still waters that support a stand of emergent vegetation, e.g. [...] ponds among cat-tails; shallow clay-bottomed sloughs amidst rushes, sedges and horse-tails; oxbow ponds with any or all these types of standing aquatic plants [...], flying close to the water among the rushes or other emergent plants, and in the grass and sedge along the shore [...]" (WALKER, 1953, p. 169).



Figs 31-39. Left hind tibia with outer row of spines in *Nehalennia* (males): (31) *N. m. minuta* (Cuba, Las Villas); — (32) the same (Venezuela, Guárico); — (33) the same (Venezuela, Amazonas); — (34) *N. m. selysi* (paralectotype); — (35) *N. pallidula* (U.S., Florida); — (36) *N. integricollis* (U.S., New Jersey); — (37) *N. irene* (U.S., New York); — (38) *N. gracilis* (U.S., Pennsylvania); — (39) *N. speciosa* (Japan, Ozegahara).

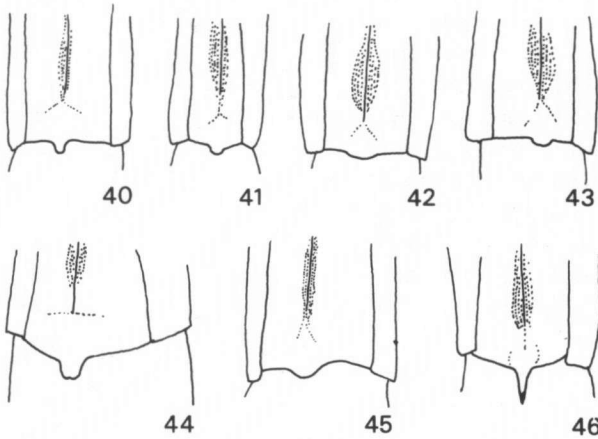
NEHALENNIA GRACILIS MORSE, 1895

Figures 8, 16, 22, 29, 38, 52, 61, 62

1895 *Nehalennia gracilis* MORSE (U.S.: Massachusetts, Sherborn).

Material examined (3 ♂, 3 ♀). — United States, Pennsylvania, Centre Co., Bear Meadows, 1 ♂, 1 ♀, 22.VI.1951, C. Cook leg.; 2 ♂, 2 ♀, 13.VII.1953, Beatty leg. — Larvae: North Carolina, Highlands, 9 larvae (ultimate instar), 15-16. VI.1953, M.J. Westfall leg.

Although *N. gracilis* has many characteristics in common with *irene*, the shape of the penis and superior anal appendages shows a closer relationship with *N. speciosa*.



Figs 40-46. Eight sternite with vulvar prolongation in some females of *Nehalennia* compared with a "true" vulvar spine in a female of *Enallagma* Charp., ventral view: (40) *N. m. minuta* (Cuba, Las Villas); — (41) (Venezuela, Aragua); — (42) (Venezuela, Guárico); — (43) (Surinam, Landerij); — (44) *N. pallidula* (U.S., Florida); — (45) *N. irene* (U.S., Michigan); — (46) *Enallagma basidens* (U.S., Texas).

Venation. — Postnodals in front wing 9-11, in hind wing 7-10. Origin of R_3 in fore wing between fourth and fifth postnodals, around the fourth in hind wing. Origin of IR_2 in both wing pairs between sixth and ninth postnodal.

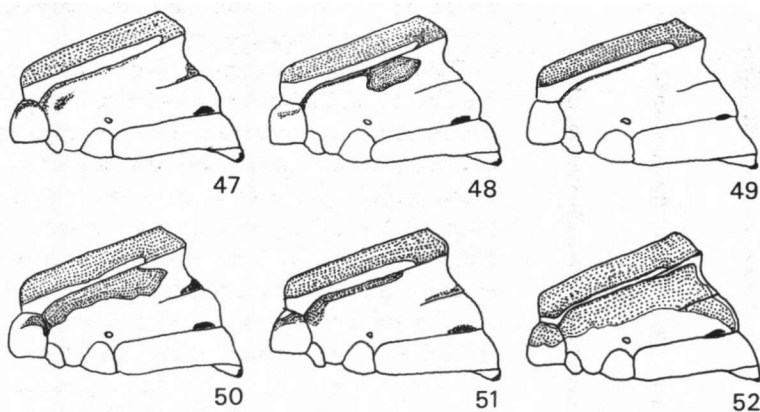
Measurements (males). — Total length 25-27.5 mm; abdomen 19.5-23 mm; hind wing 12-15 mm.

Larva. — The larva is characterized by its fairly narrow caudal gills, which normally have acute tips, but occasionally may be blunt. Besides one long principal mental seta there is a group of one or two small accompanying setae, on each side of the labium; palpus with only five setae.

Distribution. — Canada and United States (south to Florida).

Habitat. — "Sphagnum-bog ponds". "[...] occasionally found in open marshes among low sedges and grasses, but these occurrences [...] may be

regarded as probably transient. [...] flies close to the bog over the wet *Sphagnum* moss and among the slender branches of cranberry and other bog plants. They skirt the edge of the floating marginal plants of such ponds, but avoid the open water". (WALKER, 1953, p. 172).



Figs 47-52. Colour pattern of thorax in some species of *Nehalennia* (47-51 males, 52 female), schematic left lateral view: (47) *N. m. minuta* (Cuba, Las Villas); — (48) *N. "pusilla" Rácenis (= m. minuta Sel.)* (Venezuela, Guárico); — (49) *N. m. selysi* (lectotype); — (50) the same (Brazil, Minas Gerais); — (51) *N. pallidula* (U.S., Florida); — (52) *N. gracilis* (U.S., Pennsylvania).

NEHALENNIA SPECIOSA (CHARPENTIER, 1840)

Figures 9, 17, 23, 30, 39, 62

1840 *Agrion speciosum* CHARPENTIER; — 1840 *Agrion sophia* SELYS; — 1850 *Agrion speciosum* SELYS & HAGEN (Type of the "group" *Nehalennia*); — 1964 *Nehalennia speciosa sibirica* BELYSHEV (Siberia).

Material examined (2 ♂, 2 ♀). — German Federal Republic, Bavaria, Tutzing, 1 ♀, 1.VII.1953, Bilek leg.; Japan, Ozegahara, 1 ♂, 1 ♀, 21.VII.1949, S. Asahina leg.; Switzerland, Ct. of Zurich, Lützelsee, 1 ♂, 25.VI.1976, J. De Marmels and H. Schiess leg. — Larvae: — Switzerland, 3 exuviae, dates as above.

This only eurasiatic *Nehalennia* is fairly closely related only to *N. gracilis*. Both species lack a ventral branch on the superior anal appendage, while the lateral lobes of the terminal penis segment are tapering, especially in *speciosa*. Apparent similarities between *speciosa* and *minuta* such as the well-developed dorsal branch of the superior appendage, the rounded posterior lobe of the female prothorax and the tendency to increasing the number of mental and palpal setae of the larval labium are rather due to secondary convergence than to close relationship.

Venation. — Postnodals in fore wing 8-9, in hind wing 7-8. Origin of R_3 at

fourth or between fourth and fifth postnodal in front wing, between third and fourth in hind wing. IR₂ at seventh postnodal in both wings.

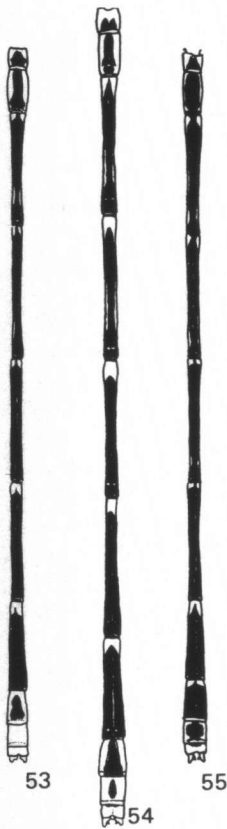
Measurements (males). — Total length 24–25.8 mm; abdomen 19–21 mm; hind wing 12–12.5 mm.

Larva. — *N. speciosa* is the only species whose larva has obtusely rounded caudal gills. However, as has been pointed out above, in *N. gracilis* specimens with almost or completely blunt lamellae exist.

The instability concerning number and size of the larval labial setae is noticeable in this species. The three Swiss exuviae have all seven palpal setae and one principal mental seta, on each side, each accompanied by one to three minute additional setae. CARCHINI (1983) figures a labium of an Italian specimen with six palpal setae and one principal mental seta, accompanied by three to four additional small setae. In a Japanese larva ASAHINA (1939) observed also six palpal setae and one principal mental seta, but only one to two additional small setae. SCHMIDT (1965) figures a specimen from Germany which shows five to six palpal setae and four (!) principal mental setae, accompanied by one additional short seta.

Distribution. — Japan, northern Asia to western Europe.

Habitat. — Phytosociological analyses in nine Swiss localities with surviving populations of *N. speciosa* revealed that this species is restricted to six vegetational associations, with a strong preference for the Scorpidio-Caricetum elatae comaretosum. All vegetational types found develop under meso- or oligotrophic conditions. The level of the stagnant water in these swamps oscillates around 10 cm. The growth and distribution of the sedges (*Carex*) is even, meadow-like, without forming "eyries". The vegetation is normally 30–40 cm high and covers an average of 70% of the ground. *N. speciosa* is absent from open water (DE MARMELS & SCHIESS, 1977).



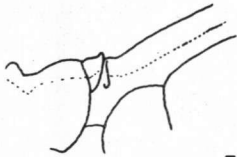
Figs 53–55. Colour pattern of abdomen in two species of *Ne-halennia*: (53) *N. m. minuta* (Cuba, Las Villas); — (54) *N. m. selysi* (lectotype); — (55) *N. pallidula* (U.S., Florida).

THE CASES OF "*NEHALENNIA*" *ATRINUCHALIS* SELYS, 1876
AND "*NEHALENNIA*" *ARAKAWAI* MATSUMURA, 1931

In order to clear up the identity of the Chinese "*Nehalennia*" *atrinuchalis*, I borrowed a male of the type series from the Paris Museum. Attached to the pin of this specimen, a male, I found among other labels, one with the following handwritten appointments: "*Cercion calamorum* Ris, det. Asahina, 1953". I then wrote to Dr S. Asahina, Tokyo, whose reply I cite here (dated 1 April, 1983): "When I examined the type series of '*N. atrinuchalis* Selys 1876' at Paris Museum in 1953 there were badly damaged three males, of which two were '*Cercion calamorum* Ris 1916' but the third male was

Cercion hieroglyphicum (Brauer 1865)'. So, in order to keep stability I decided myself to suppress '*atrinuchalis*' by selecting, as the first reviser, the third male to be the lectotype of '*atrinuchalis*'. This rescues '*calamorum*' which name has been used very commonly in general since 1916, whereas '*atrinuchalis*' has been forgotten, until today, for more than hundred years. [...]"

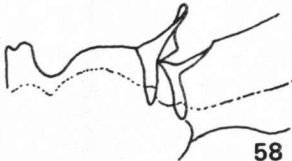
In the same letter Dr Asahina clears the identity of "*Nehalennia*" *arakawai*, saying: "*N. arakawai* Matsumura 1931 is nothing but *Aciagrion migratum* (Selys, 1876). This fact was verified by me already in 1938 by checking the types, but I did not [...] [publish that] yet. This is because Matsumura's works on Odonata are not valued at all here, so this name is always being neglected by our colleagues".



56



57



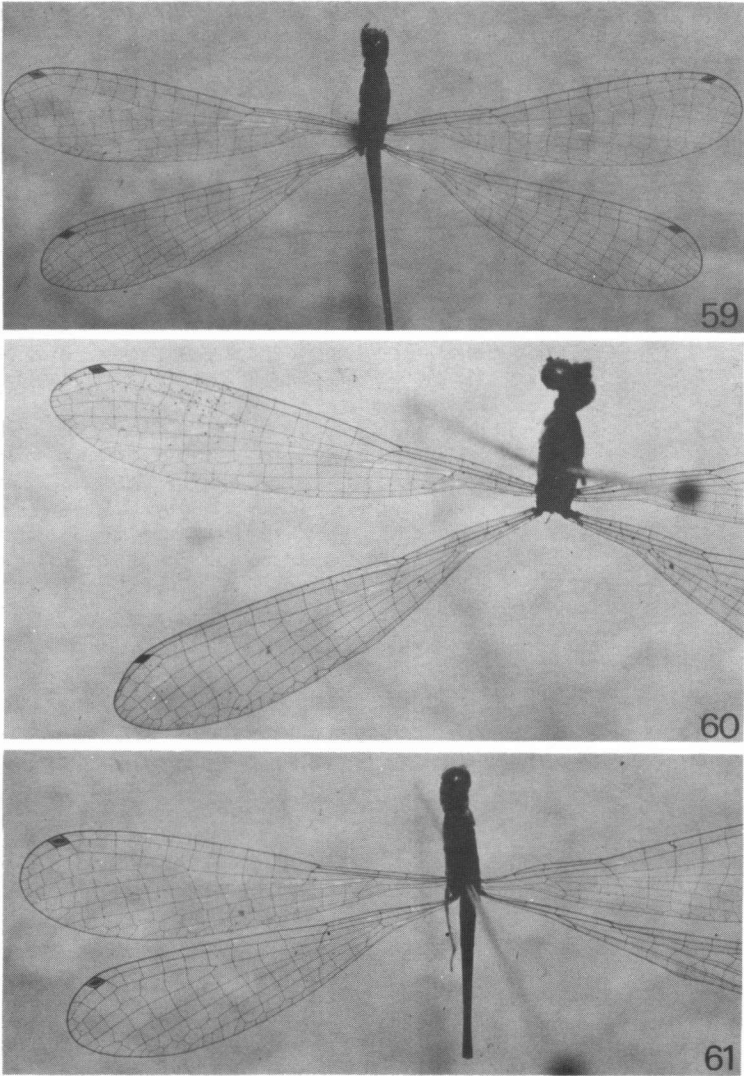
58

Figs 56-58. Shape of the hind margin of the male prothorax in two species of *Nehalennia*, left lateral view: (56) *N. m. minuta* (Cuba, Las Villas); — (57) *N. m. selysi* (lectotype); — (58) *N. pallidula* (U.S., Florida).

PHYLOGENETIC RELATIONSHIPS

It has been pointed out that the genus *Nehalennia* is closely related to other genera with an angulate frons. This was recognized by KENNEDY (1920), who established for them his "*Nehalennia* — *Telebasis* Series", an entity which may well deserve subfamily status ("*Nehalenninae*"), as proposed by the late Dr J. Rácenis (DE MARMELS, 1984a) This subfamily would include genera such as *Helveciagrion* Machado, *Ceriagrion* Selys, *Telebasis* Sel., *Aeolagrion* Williamson, *Hylaeonympha* Rácenis, *Diceratobasis* Kennedy, *Metaleptobasis* Calvert, *Mina-grion* Santos, *Nehalennia* Sel., *Leptagrion* Sel., and presumably other Old and New World genera.

Some features shared partly or universally by these genera are, beside of the angulate frons: the lack of postocular spots; the absence of a vulvar spine in the female; a comparatively large distance between the compound eyes; the rearwards not enlarged lateral lobes of head; the presence of metallic colour on head and thorax; one principal mental seta with a varying number of accompanying small setae, in the larval labium (on each side); the



Figs 59-61. Left wing pair in two species of *Nehalennia* (males): (59) *N. m. minuta* (Venezuela, Guárico); — (60) *N. m. selysi* (lectotype); — (61) *N. gracilis* (U.S., Pennsylvania).

southern origin.

The six species of the genus *Nehalennia* can be arranged into a "phylogenetic tree", on the base of similarities and differences in their morphological characters, including larval features. This "tree" is shown in Figure 62. — The only tropical

american representative (*minuta*) is thought to be closest to the ancestral species, which must have been South American, for the subfamily Nehalenniinae is of southern origin (see above). Hence the mere fact that there are more nearctic than South American species does not by itself imply a North American origin of the genus.

Maps presenting the supposed geography in upper cretaceous times (cf., for example ROSS, 1968, p. 433) clearly show that the nowadays peninsular Florida

was then separated from the North American continent by an interior sea and was, therefore, an island. The exact geohistorical events concerning the American hemisphere are unknown to me, but the mentioned fact may explain the presence of *N. pallidula* in Florida, where it is endemic. This species must have evolved from a *minuta*-like ancestor in about that period, while the caribbean islands were colonized by *minuta* much later. These populations do not seem subspecifically different from continental (Central and South American) *minuta*. That the tiny *N. minuta* must be an occasional wanderer becomes apparent not only when considering its wide distribution, but specimens may actually be caught on well-known migration routes, such as Portachuelo Pass (Rancho Grande, 1100 mts), on the Venezuelan Coastal Cordillera. Such a specimen, a female, is indeed represented in the collection of the Instituto de Zoología Agrícola (Maracay). It was collected by the late Dr J. Rácenis on January 12, 1958. If *N. minuta* has failed to colonize Florida this could well be due to com-

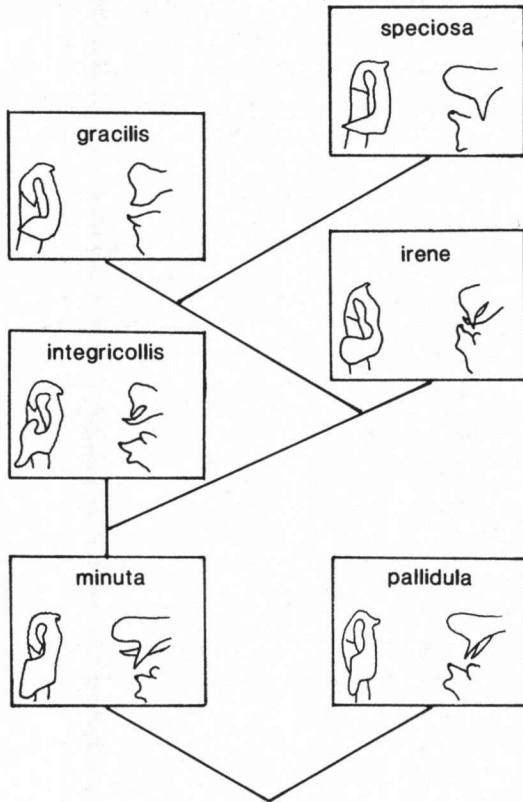


Fig. 62. The phylogenetic tree of the genus *Nehalennia* Selys. For each species a schematized figure of the penis (left lateral view) and of the left superior and right inferior appendages (right lateral view) is presented.

men, a female, is indeed represented in the collection of the Instituto de Zoología Agrícola (Maracay). It was collected by the late Dr J. Rácenis on January 12, 1958. If *N. minuta* has failed to colonize Florida this could well be due to com-

petitive exclusion by the resident *N. pallidula*, its closest relative. On the other hand, *N. integricollis* and *N. gracilis* successfully established themselves in Florida, immigrating into the peninsula from the North, that is, over continuous land.

Following BELY SHEV & KHARITONOV (1977), the immigration of the (doubtless *gracilis*-like) ancestral species of *N. speciosa* from North America into Eurasia took place in the Oligocene, when there was still no atlantic hiatus in the North, but the single land mass of Laurasia. — In passing, it must be kept in mind that these authors when mentioning "*N. integricollis*" are effectively meaning *N. pallidula*.

A series of evolutionary changes observed on the way from *N. minuta* to *N. speciosa* are enumerated here step by step by comparing some morphological features. This does, of course, not mean that -for instance- *N. speciosa* "descends" from *N. gracilis*. It just indicates tendencies.

- *N. minuta* → *N. integricollis*. Adult: Expansion of the dark (metallic) colour; expansion of the lateral lobes of the distal penis segment; reduction of the dorsal branch of the male superior anal appendage and of the projecting lamina on the eighth sternite of the female. Larva: Reduction in size of some mental setae, and in number of palpal setae.
- *N. integricollis* → *N. irene*. Adult: Reduction of the lateral lobes of the distal penis segment; modification of the hind lobe of the female prothorax towards a trilobate type. Larva: Reduction in number of the (small) mental setae.
- *N. irene* → *N. gracilis*. Adult: Tapering of the lateral lobes of the distal penis segment; partial reduction of the internal, and loss of the ventral branch of the male superior anal appendage; reduction of the proximal and the distal lobe of the inferior anal appendage, and -partly- of the middle lobe of the trilobate hind margin of the female prothorax. Larva: narrowing of the caudal gills and individual tendency towards blunt apices; reduction in number of the palpal setae.
- *N. gracilis* → *N. speciosa*. Adult: Further tapering of the lateral lobes of the distal penis segment; increasing in size of the internal branch of the male superior anal appendage; reduction of the trilobate hind margin of the female prothorax. Larva: Broadening of the (always blunt) caudal gills, and tendency for increasing the number of palpal setae, individually also number and size of the mental setae.

It is interesting to observe how the shape of the male superior and inferior anal appendages does not undergo any essential change on the way from *N. minuta* to *N. integricollis* and *N. irene*. The first antenodal costal space and the tibial spines are, however, suffering a slight, but continuous shortening between *minuta* and *speciosa*.

Table I

Indices of similarity in all possible species combinations in the genus *Nehalennia* (except *pallidula*). In brackets figures of any species compared with itself (cf. text for further explanations)

	<i>minuta</i>	<i>integricollis</i>	<i>irene</i>	<i>gracilis</i>	<i>speciosa</i>
<i>minuta</i>	(12)	8	6	3	5
<i>integricollis</i>	8	(12)	8	3	5
<i>irene</i>	6	8	(12)	7	6
<i>gracilis</i>	3	3	7	(13)	11
<i>speciosa</i>	5	5	6	11	(14)

Table I shows how many morphological characters are shared by any one species with any other. Twelve features with two alternatives each were compared. These alternatives are mutually exclusive. In larval *N. gracilis*, however, some individuals have rounded caudal gills while others show pointed ones. In this case the species as a whole fits in both alternatives of this specific character. Similarly, larval *N. speciosa* differ individually regarding the number of mental and also of palpal setae. Hence the species as a whole fits in both possible alternatives of each of these features.

Following the figures given in Table I. *N. integricollis* appears to be exactly as closely related to the tropical *N. minuta* as to the boreal *N. irene*. This species is less related to its neighbour stem upwards on the phylogenetic tree than to that stem downwards. *N. gracilis* has much more in common with *N. speciosa* than with *irene*. The peripheral *N. minuta* and *N. speciosa* clearly show closest relations to their direct neighbour. — It is noteworthy how the "index of similarity" decreases continuously from the couple *minuta/integricollis* towards that of *minuta/gracilis*, but shows a renewed augment in the couple *minuta/speciosa*. The higher index is due to two shared characters, viz. the straight posterior border of the female prothorax, and the higher number of mental setae in the larva (in *speciosa* at least as a tendency, in single specimens; see above). *N. pallidula* has not been included in Table I, because the exact larval characteristics are unknown. This species is, however, intimately related to *N. minuta* and may be considered an "offshoot" of it, rather than a link between *minuta* and any of the remaining species. Intriguing is the presence in the female *pallidula* of a trilobate hindlobe of prothorax, a pattern observed also in *N. irene*, and -to a lesser extent- in *N. gracilis*.

The morphological characters used for the determination of the "index of similarity" in all possible species combinations (except *pallidula*) are quoted here:

- (1) Mesepimeron entirely metallic green (*integracollis, irene, gracilis, speciosa*)
- (1a) Mesepimeron partly or entirely pale (*minuta*)
- (2) Postocular stripe well-developed (*minuta, gracilis, speciosa*)
- (2a) Postocular stripe reduced to an inconspicuous ring around the neck (*integracollis, irene*)
- (3) Females with a more or less projecting lamina on the distal margin of the eighth sternite (*minuta*)
- (3a) Females normally without such a lamina (*integracollis, irene, gracilis, speciosa*)
- (4) Three antenodal cells (*minuta, irene, gracilis, speciosa*)
- (4a) Two or less antenodal cells (*integracollis*)
- (5) Tibial spines slightly to considerably longer than the intervening spaces (*minuta, integracollis*)
- (5a) Tibial spines generally shorter (*irene, gracilis, speciosa*)
- (6) Hind margin of female prothorax straight (*minuta, integracollis, speciosa*)
- (6a) Hind margin of female prothorax trilobate (*irene, gracilis*)
- (7) A proximal lobe visible on the inferior anal appendages of the male (*minuta, integracollis, irene*)
- (7a) No proximal lobe visible (*gracilis, speciosa*)
- (8) Superior anal appendages of the male with a ventral branch (*minuta, integracollis, irene*)
- (8a) Superior anal appendages without a ventral branch (*gracilis, speciosa*)
- (9) Caudal gills of larva pointed (*minuta, integracollis, irene, gracilis* — in part)

- (9a) Caudal gills blunt (*gracilis* — in part, *speciosa*)
 (10) Four to five mental setae on the larval labium, on each side (*minuta*, *integricollis*, *speciosa* — in part)
 (10a) One to three mental setae (*irene*, *gracilis*, *speciosa* — in part)
 (11) Six to seven palpal setae (*minuta*, *integricollis*, *irene*, *speciosa* — in part)
 (11a) Five palpal setae (*gracilis*, *speciosa* — in part)
 (12) Lateral lobes of terminal penis segment tapering (*gracilis*, *speciosa*)
 (12a) Lateral lobes not tapering (*minuta*, *integricollis*, *irene*).

REFERENCES

- ASAHINA, S., 1939. Notulae odonatorum japonicorum, I. *Zool. Mag., Tokyo* 51(1): 33-38.
 BELYSHEV, B.F., 1964. Odonatologicheskaya fauna Verhnogo Priob'ya. *Trudy vost.-sib. Fil. Akad. Nauk SSSR* 40: 4-70. (Russian).
 BELYSHEV, B.F., 1973. *The dragonflies of Siberia (Odonata)*, vol. 1, part 2. Nauka, Novosibirsk.
 BELYSHEV, B.F. & A.Y. KHARITONOV, 1977. On the history of the boreal dragonfly species *Nehalennia speciosa* Charp., 1840, and the center of origin of the genus *Nehalennia* Selys, 1850 (Odonata, Coenagrionidae). *Ent. Rev.* 56(4): 46-49.
 BUTLER, H., 1914. Three new species of Odonata. *Can. Ent.* 46(10): 346-348.
 BYERS, C.F., 1930. A contribution to the knowledge of Florida Odonata. *Univ. Fla. Publ.* (Biol. Sci.) 1(1): 1-327.
 CALVERT, P.P., 1907. Neuroptera. *Biologia cent. am.*, pp. 309-404.
 CALVERT, P.P., 1913a. The species of *Nehalennia* (Odonata), including one from the eastern United States hitherto undescribed. *Ent. News* 24: 310-316.
 CALVERT, P.P., 1913b. The true male of *Nehalennia integricollis* and *N. pallidula*, n. sp. (Odon.). *Ent. News* 24: 373-374.
 CALVERT, P.P., 1919. Gundlach's work on the Odonata of Cuba: a critical study. *Trans. Am. ent. Soc.* 45(797): 335-396.
 CARCHINI, G., 1983. A key to the Italian odonate larvae. *Soc. int. odonatol. rapid Comm.* (Suppl.) 1: 1-101.
 CHARPENTIER, T. de, 1940. *Libellulinae europaeae descriptae ac depictae*. Voss, Lipsiae.
 COSTA, J.M., 1978. Revisão do gênero *Oxyagrion* Selys, 1876 (Odonata, Coenagrionidae). *Publções avuls. Mus. nac. Rio de J.* 61: 1-213, pls 1-39 excl.
 COWLEY, J., 1934. Notes on some generic names of Odonata. *Ent. mon. Mag.* 70: 240-247.
 DAVIES, D.A.L., 1981. A synopsis of the extant genera of the Odonata. *Soc. int. odonatol. rapid Comm.* 3: 1-59.
 DE MARMELS, J., 1984a. La náyade de *Leptagrion fernandezianum* Rácenis, especie bromelícola (Odonata: Coenagrionidae), y consideraciones sobre la posible relación filogenética del género *Leptagrion* Selys. *Boln. Ent. venez.* (N.S.). (In press).
 DE MARMELS, J., 1984b. *Acanthagrion dichrostigma* sp. n. y *Acanthagrion tepuiense* sp. n. de Venezuela (Odonata: Coenagrionidae). *Boln. Ent. venez.* (N.S.). (In press).
 DE MARMELS, J. & H. SCHIESS, 1977. Zum Vorkommen der Zwerglibelle *Nehalennia speciosa* (Charp. 1840) in der Schweiz (Odonata: Coenagrionidae). *Vjschr. naturf. Ges. Zürich* 122(3): 339-348.
 GARCIA DIAZ, J., 1938. Insectae borinquenses. Odonata. *J. Agr. Univ. Puerto Rico* 22: 56-60.
 GEIJSKES, D.C., 1943. Notes on Odonata of Surinam. IV. Nine new or little-known zygopterous nymphs from the inland waters. *Annls ent. Soc. Am.* 36(2): 165-184.
 GUNDLACH, J., 1888. *Contribución a la entomología cubana*, vol. 2, pp. 225-232, Alvarez, Habana.
 HAGEN, H., 1861. Synopsis of the Neuroptera of North America, with a list of the South American species. *Smithson misc. Collns* 4: 1-347.

- HAGEN, H., 1867. The odonate-fauna of the Island of Cuba. *Proc. Boston Soc. nat. Hist.* 11: 289-294.
- JOHNSON, C. & M.J. WESTFALL, 1970. Diagnostic keys and notes on the damselflies (Zygoptera) of Florida. *Bull. Fla St. Mus.* (Biol. Sci.) 15(2): 45-89.
- KENNEDY, C.H., 1920. The phylogeny of the zygopterous dragonflies as based on the evidence of the penes. *Ohio J. Sci.* 21(1): 19-29.
- KIRBY, W.F., 1890. *A synonymic catalogue of Neuroptera Odonata, or dragonflies.* Gurney & Jackson, London.
- KLOTS, E.B., 1932. Insects of Porto Rico and the virgin Islands. Odonata or dragonflies. *Sci. Surv. Porto Rico virgin Isl.* 14(1): 3-107.
- KORMONDY, E.J., 1959. *Lestes tikalus* n. sp. and other Odonata from Guatamala. *Ohio J. Sci.* 59(5): 305-312.
- LEONARD, J.W., 1977. A revisionary study of the genus *Acanthagrion* (Odonata: Zygoptera). *Misc. Publs Mus. Zool. Univ. Mich.* 153: 1-173.
- MORSE, A.P., 1895. New North American Odonata. II. *Psyche* 1895: 274-275.
- PAULSON, D.R., 1966. New records of Bahamian Odonata. *Quart. J. Fla Acad. Sci.* 29(2): 97-110.
- RACENIS, J., 1966. *Preliminary list of Venezuelan Odonata.* Inst. Zool. Trop. Univ. Centr. Venezuela, Caracas.
- ROSS, H.H., 1968. *Introducción a la entomología general y a aplicada.* [Translated from the second American edition]. Omega, Barcelona.
- ST QUENTIN, D., 1960. Zur Kenntnis der Agrioninae (Coenagrioninae) Südamerikas (Odonata). *Beitr. neotrop. Fauna* 2(1): 45-64.
- SANTOS, N.D. dos, 1981. Odonata. In: S.H. Hurlbert, G. Rodríguez & N.D. dos Santos, Aquatic biota of tropical South America, Part 1 (Arthropoda pp. 64-85.), San Diego St. Univ., San Diego, California.
- SCHMIDT, E., 1953. Über das "Schlusslicht" am Abdomenende von Libellen. *Naturwissenschaften* 12: 335.
- SCHMIDT, E., 1965. Über die Auffindung der letzten Larvenhaut von *Nehalennia speciosa* (Charpentier) (Odonata, Zygoptera). *Ent. Z., Frankf. a. M.* 75(15): 169-172.
- SELYS LONGCHAMPS, E. de, 1840. Sur trois espèces nouvelles européennes du genre *Agrion*. *Revue zool.* 3: 213-215.
- SELYS LONGCHAMPS, E. de, 1857. Odonata de Cuba. In: R. de la Sagra, *Hist. phys. polit. nat. Ile Cuba* 8: 436-472.
- SELYS LONGCHAMPS, E. de, 1876. Synopsis des Agrionines, 5me légion: *Agrion* (suite). *Bull. Acad. Belg.* 41(2-3): 3-282 (reprint).
- SELYS LONGCHAMPS, E. de & H. HAGEN, 1850. *Revue des Odonates ou libellules d'Europe.* Muquardt, Bruxelles — Leipzig & Roret, Paris.
- WALKER, E.M., 1953. *The Odonata of Canada and Alaska*, Vol. 1. Univ. Toronto Press, Toronto.
- WESTFALL, M.J., 1960. The Odonata of the Bahama Islands, the West Indies. *Am. Mus. Nov.* 2020: 1-12.