TAXONOMIC RELATIONSHIPS OF DICERATOBASIS MACROGASTER (SELYS) AND PHYLOLESTES ETHELAE CHRISTIANSEN OF THE WEST INDIES AS REVEALED BY THEIR LARVAE (ZYGOPTERA: COENAGRIONIDAE, SYNLESTIDAE)¹

M.J. WESTFALL, Jr.²

Department of Entomology and Nematology, University of Florida Gainesville, Florida 32611, USA

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Agrion macrogaster Selys from Jamaica has been placed in the genera Nehalennia, Leptobasis, and Telebasis. In 1960 the author reared it from bromeliads in Jamaica and found the larva so unique that the new genus Diceratobasis Kennedy (1920, Ohio J. Sci. 21: 83-88) was accepted for it. Christiansen (1947, Psyche 54: 256-262) described a new genus and species, Phylolestes ethelae, from Haiti and suggested it might belong to the Synlestidae, with its nearest relative in Africa. Larvae which the author collected in 1960 proved him correct. The larvae of both species are herein described.

INTRODUCTION

The reliability of single larval characters in revealing taxonomic relationships is questionable. CORBET (1963) states that the greatest adaptive radiation in functional morphology has taken place in the larval stage. He assumes that this was necessitated by interspecific competition for space and food in the relatively confined aquatic environment. He further emphasizes the idea stressed by LIEFTINCK (1956) that the terminal gills (caudal lamellae) of Zygoptera are to be regarded as highly adaptive organs, and therefore not reliable indicators of phylogenetic relationship. In this paper I am assuming, as did LIEFTINCK in 1939, that if many different larval characters all agree they give good added evidence when combined with adult characters for establishing such relation-

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² Department of Zoology, University of Florida, Gainesville, Florida 32611, USA.

ships. This seems quite well demonstrated by LIEFTINCK (1939) in the case of Lestidae and Synlestidae.

DICERATOBASIS MACROGASTER (SELYS, 1857)

SELYS (1857) described Agrion macrogaster from Jamaica, under his subgenus Nehalennia, and in 1877 with reservation included it in his Leptobasis, along with vacillans Selys. CARPENTER (1897) redescribed this species under Telebasis. KENNEDY (1920) established a new genus Diceratobasis for it with the brief statement, "Type Agrion macrogaster Selys. Characters as in Metaleptobasis, but male without thoracic horns, while a large pair of horns occur on the seminal vesicle." CALVERT (1902) and KLOTS (1932) discussed the generic placement of the species without reaching definite conclusions. Kennedy's genus, like most of the other 42 genera and subgenera of his 1920 paper, was not recognized by most Odonatologists. HAGEN (1861) gave a description of the species as Agrion macrogaster, and GUNDLACH (1888) in his work on the Odonata of Cuba gave a translation of it, but clearly indicated it had not been observed in Cuba.

In my paper on the Odonata of Cuba (WESTFALL, 1964) I discussed macrogaster under Diceratobasis, and stated that I first saw larvae which I supposed to be this species taken from bromeliads in Jamaica in 1952 by Dr. Albert M. Laessle. In 1960 I went to Jamaica for two weeks with an assistant, Peter Drummond. We were welcomed and assisted by Dr. Thomas H. Farr of the Science Museum, Institute of Jamaica. We collected and reared the larvae from bromeliads and gave the definite identification to Dr. LAESSLE for his paper (1961). In my Cuban paper I stated that the larva was so unique that I had no reservations in accepting Kennedy's genus for it and that a description of the larva would appear soon. This is just now materializing. ALAYO (1968) included this species in the Cuban list of his large paper, Las Libelulas de Cuba, despite the fact it has never been collected in Cuba. As far as known this species has never been collected outside of Jamaica, although I have seen it from many localities on this island.

DESCRIPTION OF LARVA

General color light tan with no conspicuous markings; femora each with two obscure bands slightly darker than general body color; eyes black above, gray from side view; caudal gills with darker spots, especially near margins.

Length (including gills) 17.5-20 mm; abdomen (without gills) 11; hind femur 3; hind wing pads 4; caudal gills 4.3-5.

Head about 1.5 times wider than long; hind margins broadly rounded, with about a dozen setae each side. Antennae about 1/2 width of head; first two segments slightly thicker than remaining five. Relative lengths of antennal

segments about as 5:10:17:15:11:7:4. Prementum of labium 2 mm long and 2 mm wide, extending to hind margin of procoxae; front margin strongly convex, slightly denticulate; premental setae 3, usually with a small fourth; marginal setae 13-16. Palpi long, arcuate, with a strong acute end hook separated by a deep incision from a shorter, broad and blunt tooth; strong movable hook about 5/7 as long as palpus; palpal setae 10 and long.

Wing pads reaching abdominal segment 4, or to middle of segment when contracted. Hind femora not quite extending to tips of wing pads. All femora with two obscure brown bands, the proximal one wider. Tibia equal to femur in length.

Abdomen without lateral spines, the obscure lateral carinae almost devoid of prickles which are very few in number on the dorsum. Ovipositor reaching end of segment 10. Caudal gills approximately 4 times as long as wide. Lateral gill with 4-5 dorsal setae extending to only 1/5-1/4 the gill length; 20-25 small ventral setae extending about 1/3 the length; lateral carina with setae extending as far as the ventral setae. Tracheal branches of gill numerous and oblique to the main axis. Numerous dark spots on gill membrane, larger near the margins; membrane thin and tending to curl, sometimes quite darkened toward apex. Figure 1 is of a female.

Described from three last instar larvae (2 &, 1 ?) and exuviae of a reared female collected from bromeliads near the Bath Fountain Hotel, Bath, St. Thomas Parish, Jamaica, August 17, 1960 by M.J. Westfall, Jr. and Peter Drummond. We also have 5 smaller larvae taken at Bath the same time. Localities in addition to those reported by LAESSLE (1961) are Portland Parish: 3 mi. S. of Fellowship, June 14, 1965, 5 larvae, Coll. by D.A. Jones; John Crow Mts. near Ecclesdown, August 16, 1960, 2 larvae. St. Ann Parish: 2 mi. S. of Moneague, August 19, 1960, adults and 7 larvae. St. Thomas Parish: path to Corn Puss Gap from the south, May 20, 1969, 1 larva, Coll. by Peter Drummond. Trelawney Parish: 5 mi. W. of Troy, August 27, 1965, 1 larva, Coll. by D.A. Jones; Windsor Estate, about 12 mi. S. of Falmouth, August 20, 1960, adults and 7 larvae. Unless otherwise stated all were collected by M.J. Westfall, Jr. and Peter Drummond and all are in the Florida State Collection of Arthropods in Gainesville.

PHYLOLESTES ETHELAE CHRISTIANSEN, 1947

CHRISTIANSEN (1947) described a new genus and species, *Phylolestes ethelae*, from specimens collected by Marston Bates in September, 1934, in the LaSelle Mountains of Southern Haiti, in the vicinity of La Visite, said to be at 4,000 feet elevation. He remarked that external characteristics pointed to a relationship with the family *Synlestidae* of Tillyard, and the penes had a remarkable resemblance to those of the African genus *Chlorolestes*. He further

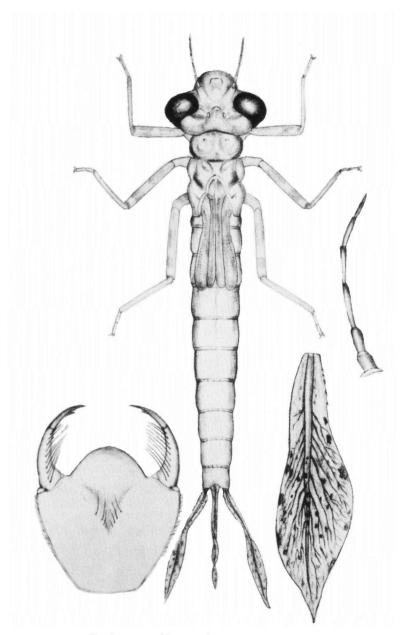


Fig. 1. Larva of Diceratobasis macrogaster (Selys).

added, "however, until the nymph has been uncovered, any family classification must remain a tentative one. Both Tillyard and Lieftinck have shown that the final court of appeal as to members of this family is the nymph." He further stated that if the genus proved to be closest to *Chlorolestes* it would mark another appearance of a new genus in the Neotropics whose closest ally was an African genus. NEEDHAM (1940) had described the new genus *Iridictyon* from British Guiana, indicating its nearest ally as the genus *Phaon* of Africa.

In 1960 after leaving Jamaica, Peter Drummond and I went for two weeks to Haiti with the chief purpose to collect larvae of *Phylolestes ethelae* and determine its family relationship. While in Haiti we stayed with Horace Ashton, an orchid fancier and long-time resident who also served as our guide and interpreter. We searched in several mountainous areas near Port-au-Prince at approximately 4,000 feet elevation, but found no *Phylolestes*. While at Furcy we learned from a Catholic priest who had just walked over the mountains from La Visite that its elevation was 7,000 feet, not 4,000 as stated in Christiansen's paper. We planned to walk from Furcy to La Visite but he told us it was possible with a Jeep to drive there by way of Jacmel and Seguin. September 6, accompanied by Mr. Ashton and the British Ambassador, G. Corley Smith, who was a bird enthusiast, in a Jeep station wagon with a native driver we set out for La Visite before daylight and just after Hurricane Donna had passed the day before. Arrangements had been made for us to sleep in tents that Boy Scouts had erected at La Visite.

Arriving in Seguin about 2:00 p.m. after driving over an extremely rough road, fording and refording swift streams flowing down the precipitous mountainside, we found it quite cold at this elevation. While walking to inspect our campsite on the level plateau on top of the mountain we crossed a clear slow-flowing stream about 8-12 feet wide, with many boulders and quiet pools that were approximately 6 feet deep. The water was freezing cold. Thinking this area was too cold for *Phylolestes* as well as orchids for which he was looking, Mr. Ashton decided we would sleep there and in the morning start back to Port-au-Prince, collecting on the way down the mountain. While the others went to eat a late lunch, I walked a short distance along the stream and soon saw a large damselfly hanging from a dead stick over the water with wings held tightly together over its back. At once I knew it must be Phylolestes and suspected that it would not be in the family Lestidae because members I had collected of that family characteristically perched with wings partially opened. I caught a second male perched just the same as the first and then began looking for larvae. In the cold, clear pools of this spring-fed stream the larvae were easily seen perched on boulders at a depth of about 3 to 4 feet. They were especially conspicuous because of a large white spot on the dorsum of abdominal segment 1, and bold white bands on the legs. In the last instar the wing pads covered the white abdominal spot but the white-banded legs were very evident. When approached

by a water net they were reluctant to move, but when they did they swam upwards and were easily netted. The next morning I collected a third adult male perched as were the two the day before. Also many larvae were collected. I walked about one-fourth mile up the stream and did not come to its source. In some places it flowed between steep banks and I had to wade in water over waist-deep. Just below the campsite it plunged down the steep mountainside. We thought the stream might have been what was shown on the topographic map as Riviere Blanche.

Along with *Phylolestes* at this stream we collected an adult male and many mature larvae of *Aeshna psilus* Calvert. Twice I caught a glimpse of a small red libelluline but did not catch it. In the water were thousands of mayflies, some hydropsychid Trichoptera, water beetles and small Hemiptera. A few mayflies were emerging and were on the surface of the water.

The hurricane-produced rain began at about 10:30 a.m. and we left to join the others who had in the meantime been collecting orchids and observing birds at a lower elevation. The live larvae of Phylolestes were placed in plastic containers and held carefully during the return trip over the unbelievably rough road. As we descended to sea level and it became warmer the larvae began vigorously swinging their abdomens from side to side. One last instar larva with swollen wing pads did not survive the trip to Port-au-Prince. There we put many of the smaller ones in the refrigerator to approximate the temperature at La Visite. During our last two nights in Haiti one of the larvae with swollen wing pads was kept in a Needham pillow cage in a bucket of water in our room. It came up out of the water both nights as if to transform, but each morning it was again in the water. We asked Mr. Ashton to keep it until it emerged, and he reported that it continued for a number of nights to leave the water but finally died. He preserved and sent it to me. The others were removed from the refrigerator and transported safely to Gainesville where we put them in an air-conditioned room but they continued to swing their abdomens back and forth vigorously. A few ate chironomid larvae but most refused to eat and all finally died without transforming.

DESCRIPTION OF LARVA

General color light tan with darker brown markings.

Length (including gills) 30-34 mm; abdomen (without gills) 17-18; hind femur 5.5-6.3; hind wing pad 8; caudal gills 5.4-6.3.

Head about 1.5 times wider than long. Antennae about equal in length to maximum head width; first and second segments thicker than remaining ones, first one thickest. Relative lengths of antennal segments about as 60:88:45:48: 32:20:10. Prementum of labium 4.2 mm long and 3.1 mm wide, extending to middle of mesocoxae. Slender proximal part of prementum only slightly longer

than the expanded distal part, and its minimum width 1/2 the maximum width. Front margin of prementum convex, denticulate, and incised deeply and narrowly to a point below the articulation of the palpi which are narrow and straight, ending in two simple, unequal, sharply pointed teeth, the median one larger; each lobe of prementum formed by the deep median incision bearing on its inner surface an isolated denticle much larger than the marginal ones; movable hook long and slender. No premental or palpal setae.

Thorax with a few brown streaks each side. Wing pads extending almost to apex of abdominal segment 4, each with a dark streak on front margin proximal to nodus. Legs long; hind femora extending to end of abdominal segment 3; all femora with a lateral brown streak almost full length, and a brown band near apex; tibiae a little longer than femora.

Abdomen with lateral spines on segments 5-9. Segment 10 without a lateral carina, but with a sharp middorsal ridge bearing numerous small spines or denticles. Segment 1 dorsally, and between the wing pad bases, white. Each of the middle segments with a pair of brown parallel streaks, one each side of the median line. Lateral to these on each side another streak, these diverging posteriorly; laterally a large brown basal spot; on segments 2 and 9 dorsal streaks tend to fuse; segment 10 mostly brown on lateral surface. Venter of abdomen without conspicuous markings. Ovipositor about 3 mm long, extending almost to ventral apex of segment 10. Caudal gills short and broad, narrowed somewhat at their bases, apices broadly rounded; lateral gills about twice, the median gill less than twice as long as wide; minute teeth on margins for about 4/5 of gill length. Obscure dark band across gills near middle, proximally more sharply defined than distally where dark band gradually becomes lighter, the apex quite colorless; secondary tracheae oblique to main axis. Pedicel of gills distinct, flattened, forming a part of the gill lamella and separated from this by a "breaking joint". Gills not caducous. Cercoids acute, conspicuous, longer and more acute in male (1.3 mm) than female (.9 mm). Figure 2 is of a female.

Described from three last instar larvae (2 \, 1 \, 3) collected September 7, 1960 at La Visite, near Seguin, in the LaSelle Mountains, Dept. de L'Ouest, Haiti by M.J. Westfall, Jr. and Peter Drummond. In addition we have 40 smaller larvae collected at the same time, the smallest 16 mm long. Ten of these shed their skins once in the laboratory in Gainesville before dying and we have these casts also. All are in the Florida State Collection of Arthropods at Gainesville.

Dr. Oliver S. Flint, Jr. of the U.S. Museum of Natural History visited the Santo Domingo side of Hispaniola in 1969 and collected more adults which he sent to me for study. They were collected in high mountains of the Dominican Republic, 15 kms south of Constanza, June 3, 1969, 1 d, and 20 kms south of Constanza, June 7, 1969, 9 d, 1 9, all by Flint and J. Gomez. In all essentials they are like those from the LaSelle Mountains of Haiti, although showing some variations possibly due to long isolation of this population.

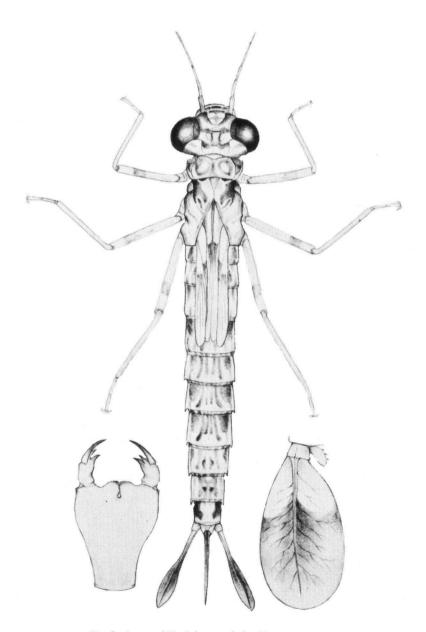


Fig. 2. Larva of Phylolestes ethelae Christiansen.

COMPARISON OF LARVAE OF P. ETHELAE AND CHLOROLESTES CONSPICUA SELYS

The only Synlestid larvae which I have to compare with P. ethelae are four specimens, three last instar with swollen wing pads and one half grown, of Chlorolestes conspicua Selys from Table Mt., Cape Town, South Africa collected March 26, 1938 and sent by K.H. Barnard to J.G. Needham who gave them to me. These four larvae are so similar to P. ethelae that it is difficult to see possible generic differences. In conspicua the first and third antennal segments are about equal in length, but in ethelae the third is only about 3/4 as long as the first. In conspicua the abdominal color pattern is not conspicuous as it is in ethelae, and the wing pads do not possess the longitudinal dark streak near the front margin. The isolated denticle each side of the median incision of the prementum is nearer the front margin in ethelae than in conspicua. Perhaps the best difference is in the terminal teeth of the palpi. In conspicua the lateral tooth ends bluntly, almost truncately, but is sharply pointed in ethelae. Also the median tooth is uniformly tapered to a point, whereas in conspicua there is a very distinct notch on the inner margin with a sudden narrowing of the tooth near the end. In these respects the end of the palpus resembles more TILLYARD's figure (1917) of Synlestes weversi Selvs from Australia. I can find no other significant differences.

DISCUSSION OF THE RELATIONSHIPS OF PHYLOLESTES

When the larvae were first compared with the lists of characters given by LIEFTINCK (1939) for *Synlestidae* and *Lestidae* they fit all of the characters checked for the first family. The gizzard was not examined.

When I wrote to Dr. F.C. Fraser of the collecting of this Synlestid in Haiti he replied in a letter September 23, 1961 that he considered the finding of *Phylolestes* in Haiti nothing less than fantastic, and that it "pointed more than ever to the great antiquity of this group, whose distribution is now as widely spaced as the Petaluras." TILLYARD (1917) treated the *Synlestinae* as one of his five paleogenic groups, remains of an ancient fauna that was once far more widely spread. The others were *Petalurinae*, *Chlorogomphinae*, *Petaliini*, and *Epiophlebiinae*. Fraser pointed out that the figure published by CHRISTIAN-SEN (1947) of the quadrangular area of *Megalestes major* is incorrect as it shows the arculus distal to the antenodal whereas it is always in the same line. He further questioned the drawing of the wings of *P. ethelae*. He stated that if the vein descending from the nodus arises distal to the end of the subcosta as shown it would be a very archaic structure for in *Megalestes* and *Chlorolestes* this vein arises distinctly from the subcosta. Figure 3 is a photograph of the wings of one of the males of *ethelae* which I collected in the LaSelle Mountains. It clarifies

this point, as that vein is shown to arise from the subcosta, but very close to the subnodus. It shows the origin of vein R_{iv} of Tillyard and Fraser (M₃ of Comstock and Needham, R₄₊₅ of Pinhey) to be proximal to the subnodus. This is the character used to separate *Ecchlorolestes* Barnard from *Chlorolestes* Selys which has this vein arising at the subnodus. In *Ecchlorolestes*, BARNARD (1937) and PINHEY (1951) included *peringueyi* Ris and *nylephtha* Barnard, both taken only in mountain ranges of South Africa. BARNARD (1937) considered *Ecchlorolestes* a subgenus of *Chlorolestes* but Pinhey gave it full generic status as did FRASER (1957). Barnard would probably consider *Phylolestes* worthy of sub-generic status only.

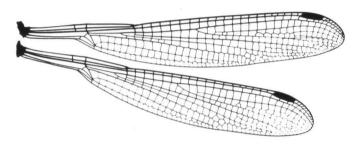


Fig. 3. Wings of Phylolestes ethelae Christiansen, male.

With regard to habits BARNARD (1937) has some interesting notes. He says that females of *Chlorolestes conspicua* Selys and *C. umbrata* Selys in Africa oviposit by puncturing twigs on trees overhanging streams and then hold the wings horizontally at right angles to the body. He further says of these two species that they settle on bushes and rushes, never far from the stream. Of *C. peringueyi* Ris, Barnard writes that they inhabit open stream-beds, where they settle on rocks with their wings spread out flat and closely adpressed to the surface of the rock. Only rarely did he observe the males to settle on bushes, although he says females were often seen in such situations probably with the view to ovipositing.

BARNARD (1937) remarks of *Chlorolestes longicauda* Burmeister and *C. nylephtha* Barnard that there is a blue spot between the bases of the hind wings of at least the males. In the second species he speaks of it as "a bright cobalt-blue metanotal spot between bases of hind-wings", and again he says that in *nylephtha*, "the blue metanotal spot in d", is distinctive in separating it from *peringueyi*. In mature males and females of *ethelae* from Hispaniola, this spot is very prominent and appears to be due to pruinosity.

The great similarity between P. ethelae of the mountains of Hispaniola and

species of *Ecchlorolestes* from the mountains of South Africa would seem to be further evidence to support the now widely accepted theory of continental drift. DONNELLY (1974) discussed this with reference to Australian and South American Odonata, which land masses he states were broadly connected until the Eocene. He cited several examples of species placed in different genera solely on the basis of geography which he thought might better be placed in the same genus.

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REFERENCES

- ALAYO, P.D., 1968. Las Libelulas de Cuba, Parts 1 & 2. Torreia (New Ser.) (2 & 3): 1-102, 1-54
- BARNARD, K.H., 1937. Notes on dragonflies of the S.W. Cape with descriptions of the nymphs and of new species. *Ann. S. Afr. Mus.* 32 (3): 169-260.
- CALVERT, P.P., 1902. Neuroptera. Odonata. Biologia cent.-am. Porter & Dulau, London. p. 120.
- CARPENTER, G.H., 1897. On some dragonflies in the Dublin Museum of Science and Art. Proc. R. Dubl. Soc. 8 (5): 434-438.
- CHRISTIANSEN, K.A., 1947. A new genus and species of damselfly from southern Haiti (Odonata). *Psyche* 54 (4): 256-262.
- CORBET, P.S., 1963. A biology of dragonflies. Quadrangle Books, Chicago. 247 pp.
- DONNELLY, T.W., 1974. Odonata collecting "Down Under". Selysia 6 (2): 1-7.
- FRASER, F.C., 1957. A reclassification of the order Odonata. R. zool. Soc. N.S.W., Sydney. 133 pp.
- GUNDLACH, J., 1888-1890. Contribucion a la entomologia Cubana, Vol. 2, pt. 3, Neuropteros Havana, pp. 189-281.
- HAGEN, H., 1861. Synopsis of the Neuroptera of North America. Smithson. misc. Collns., Washington. XX + 347 pp.
- KENNEDY, C.H., 1920. Forty-two hitherto unrecognized genera and subgenera of Zygoptera. Ohio J. Sci. 21: 83-88.
- KLOTS, E.B., 1932. Insects of Porto Rico and the Virgin Islands, Odonata or Dragon Flies. Scient. Surv. P. Rico 14 (1): 1-107.
- LAESSLE, A.M., 1961. A micro-limnological study of Jamaican bromeliads. *Ecology* 42 (3): 499-517.
- LIEFTINCK, M.A., 1939. On the true position of the genus Orolestes McLach., with notes on O. wallacei (Kirby), its habits and life-history (Odon., Lestid.). Treubia 17 (1): 45-61.
- LIEFTINCK, M.A., 1956. Revision of the genus Argiolestes Selys (Odonata) in New Guinea and the Moluccas, with notes on the larval forms of the family Megapodagrionidae. *Nova Guinea* (n.s.) 7: 59-121.

- NEEDHAM, J.G., 1940. Two neotropical Agrionine damselflies (Odonata) from Mts. Duida and Roraima. Am. Mus. Novit. 1081: 1-3.
- PINHEY, E.C.G., 1951. The dragonflies of southern Africa. Transv. Mus. Mem. 5: 1-335.
- SELYS-LONGCHAMPS, E. de, 1857. Odonates de Cuba. In: R. de la Sagra, Histoire physique, politique et naturelle de l'Ile de Cuba. Paris, pp. 436-472.
- SELYS-LONGCHAMPS, E. de, 1877. Synopsis des Agrionines. Bull. Ac. r. Belg. (II), 43 (2): 102 (reprint p. 8).
- TILLYARD, R.J., 1917. The Biology of the Dragonflies, Cambridge University Press, London. XII + 396 pp.
- WESTFALL, M.J. Jr., 1964. Notes on the Odonata of Cuba. Q. Jl Fla Acad. Sci. 27 (1): 67-85.