

Phylogenetic and biogeographical remarks on *Thyridates* (Mecoptera: Bittacidae), with the first fossil record of the taxon

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Abstract. Until now, *Thyridates* was considered an American genus. In this work seven African species of *Bittacus* are transferred to *Thyridates*: *T. stanleyi* (BYERS, 1968), *T. erythro stigma* (BYERS, 1975), *T. weelei* (ESBEN-PETERSEN, 1913), *T. nebulosus* (KLUG, 1838), *T. testaceus* (KLUG, 1838), *T. oreinus* (NAVÁS, 1914), and *T. chevalieri* (NAVÁS, 1908). A new species of *Thyridates* from the late Paleocene of Argentina is described. The geographic relationships between species of the genus suggest the idea of a Gondwanan origin of this group before separation of Africa and South America in the Lower Cretaceous.

Key words: Mecoptera, Bittacidae, *Thyridates*, phylogeny, biogeography, Africa, South America, Late Paleocene, new species, new combinations.

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I. INTRODUCTION

Bittacidae is a small family of insects with about half of its genera being known only as fossils, mainly (about 19 genera) from the Mesozoic (ANSORGE 1993, 1996; BECHLY & SCHWEIGERT 2000; BODE 1953; HANDLIRSCH 1906-1908, 1939; NOVOKSCHONOV 1993a, b, 1997a, b, c; MARTYNOV 1927; PETRULEVIČIUS & MARTINS-NETO 2001; PETRULEVIČIUS & JARZEMBOWSKI (submitted); REN 1993, 1994, 1997; SUKAT SHEVA 1990; TILLYARD 1933). Only one of these genera reaches recent times, *Orobittacus* VILLEGAS & BYERS, 1981 (NOVOKSCHONOV 1993a, b). There are few records of Cenozoic fossil hanging flies in the world (late Paleocene of Argentina, Eocene of USA, late Eocene-early Oligocene of England, Oligocene of Baltic and East Asia) (PETRULEVIČIUS 1998, 1999, 2001a, b; CARPENTER 1928, 1954, 1955; JARZEMBOWSKI 1980; NOVOKSCHONOV 1993b; WEITSCHAT & WICHARD 1998). Only one genus is exclusive to the Paleogene, *Palaeobittacus* CARPENTER, 1928. There are about 20 Recent genera, one third of them coming from South America.

In the following study the wing venation nomenclature of KUKALOVÁ-PECK (1991) is applied. The phylogenetic classification of Bittacidae proposed by NOVOKSCHONOV (1993b) is followed. In recent publications, ANSORGE (1996) and BECHLY & SCHWEIGERT (2000) proposed two different phylogenetic classifications of Raptipedia WILLMANN, 1987. I agree with BECHLY & SCHWEIGERT (2000) about the criticism of ANSORGE (1996) phylogeny, and one of the points is the definition of

the Bittacinae with the inclusion of *Orobittacus*. This group sensu ANSORGE (1996) is defined by two synapomorphies: one of them is the base of CuA transverse in forewings; and *Orobittacus* presents an oblique CuA (the plesiomorphic state sensu ANSORGE 1996). I do not use the phylogenetic analysis of Bittacidae conducted by ANSORGE (1996) for the reasons given by BECHLY & SCHWEIGERT (2000); and accordingly to these authors, some characters proposed by ANSORGE (1993, 1996) have to be added to subsequent phylogenetic analysis of Raptipedia. This is in spite of the homoplasies that these characters show in his phylogenetic analysis.

I do not agree with BECHLY & SCHWEIGERT (2000) in some relationships established in their reclassification. The main criticism concerns wrong interpretation of the relationships of some fossil and Recent genera like *Liaobittacus* REN, 1993, *Orobittacus* and *Anabittacus* KIMMINS, 1929. BECHLY and SCHWEIGERT (2000) established that the genera *Asiobittacus* NOVOKSCHONOV, 1993, *Scharabittacus* NOVOKSCHONOV, 1993, *Probittacus* MARTYNOV, 1927, *Sibirobittacus* SUKATCHEVA, 1990, *Cretobittacus* NOVOKSCHONOV, 1993, *Prohylobittacus* NOVOKSCHONOV, 1993, *Palaeobittacus*, and 'crown group Bittacinae' (Recent genera) share the same character state in the stigmal part of RA. However, Recent species of *Orobittacus* have the same state character that fossil ones; also shared with the Recent genus *Anabittacus* and *Liaobittacus* from the Middle Jurassic of China. Thus, the Bittacinae sensu BECHLY & SCHWEIGERT (2000), including *Liaobittacus*, *Palaeobittacus*, *Cretobittacus*, *Bittacus biamensis*, and Bittacini (extant genera, incl. extant *Orobittacus*), seem not to reflect the relationships of these taxa and could be a polyphyletic group.

Thyridates is considered sensu WILLMANN (1983) and rediagnosed in the present work.

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II. THE BITTACIDAE IN SOUTH AMERICA

The family has at present a temperate-tropical world-wide distribution (BYERS 1991), with eight extant genera living in South America: *Bittacus* LATREILLE, 1805; *Thyridates* NAVÁS, 1908; *Anabittacus*; *Neobittacus* PENNY, 1977; *Issikiella* BYERS, 1972; *Kalobittacus* ESBEN-PETERSEN, 1914; *Nannobittacus* ESBEN-PETERSEN, 1927, and *Pazius* NAVÁS, 1913. These last four genera form a monophyletic group (WILLMANN 1983), and the relationships with the other genera are still unknown. Referring to fossil bittacids, there is one described species from Maíz Gordo Formation that could be related to *Thyridates* because of the large pterostigma, but the fragmentary condition of the specimens does not permit a generic attribution (PETRULEVIČIUS 1999). There is, however, another described specimen of Bittacidae from the Lower Cretaceous of Brazil (PETRULEVIČIUS & MARTINS-NETO 2001). This specimen seems to represent a new genus, but in my opinion it should be named as a new species only after deposition in a State repository of Brazil (PETRULEVIČIUS & MARTINS-NETO 2001).

III. PHYLOGENETICAL AND BIOGEOGRAPHICAL REMARKS ON *THYRIDATES*

Thyridates sensu WILLMANN (1983) possesses two autapomorphies that support the monophyly of the group, i.e.:

- 1) RP₁₊₂ forks from RP forming nearly a right angle
- 2) presence of extra crossveins between ScP and wing margin (except the basal one called humeral vein; Fig. 3b).

However, the latter synapomorphy is not sure because some individuals do not possess these crossveins (WILLMANN 1983, 1989). Some Mesozoic genera possess only one crossvein in this area (*Asiobittacus*, *Probittacus*, *Sibirobittacus*, *Cretobittacus*), but the presence of more crossveins is unique among Bittacidae. The last character is present only in some South American species of the genus and therefore was possibly acquired late in the evolution of the taxon. COLLUCCI & AMORIM (2000) added five supposed synapomorphies for *Thyridates*, i.e.

- 3) fork of RP more basally than the apex of Sc
- 4) crossvein sc-r₁ apical
- 5) thyridium evident
- 6) elongate pterostigma
- 7) relatively large size of the species

These characters seem to be not suitable for the definition of the genus. Character 3 could be interpreted as a symplesiomorphy shared with some Mesozoic genera, and shared with some species of *Bittacus* as *B. italicus* (MÜLLER 1776) and *B. henryi* RUST and BYERS 1976. Characters 4 and 5 are present in majority of the genera of the family. Character 6 is not well defined, but an elongate (primarily) sagged distal part of RA₃₊₄ linked with two (one or three) crossveins with RP could be a synapomorphy of *Thyridates* shared with *Harpobittacus*. Character 7 is a rather dubious synapomorphy of the genus since medium and large sized species exist in other genera of the family.

I propose here a new character, i.e.:

8) presence of a forked 'Kreuz der Bittaciden' (sensu NOVOKSCHONOV 1993): bifurcation of MP1-MP2 arising at the same level that both bifurcations: RP3+4-MA, and MP3-MP4+CuA. The bifurcation of MP1-MP2 became more basal reaching the crossveins ma-mp₁₊₂-mp₃₊₄. In this way, one of the sides of the cross is forked (see *T. weelei* in Fig. 3B). This character is present in some species recognised as *Thyridates* by character 1 and other species still considered as *Bittacus*. This character is strictly absent in all other Bittacidae.

A character present in *Palaeobittacus*, some species of *Bittacus*, some of *Thyridates* and some of *Harpobittacus* is:

9) bifurcation of RP clearly basal to that of MP. This character seems to be highly homoplastic but only present in these species.

Other character present in all species of *Thyridates*, *Palaeobittacus* and some of *Bittacus* is:

- 10) in hind wings RP+MA do not change its direction at fork of RP₁₊₂.

Character 1 is present in all species of the genus sensu WILLMANN (1983), the species considered by COLLUCCI & AMORIM (2000), and other African species of *Bittacus* (PETRULEVIČIUS 2001a): *B. stanleyi* BYERS 1968; *B. erythro stigma* BYERS 1975; *B. weelei* ESBEN-PETERSEN 1913; *B. nebulosus* KLUG 1838; and *B. testaceous* KLUG 1838. Character 6 seems to be present in all species of *Thyridates* and in *Harpobittacus*. In some species of *Thyridates*, and *Bittacus* from Africa the RP₃₊₄ is greatly elongated and lost its sagged condition to follow the wing margin shape (Fig. 3a), i.e. *B. stanleyi*, *B. erythro stigma*, *B. weelei*, *B. nebulosus*, *B. testaceous*, *T. femoralis*, *T. panamensis*, *T. angrensis*, *T. nebulosus*, *T. maculosus*; *T. latreillei*; and *T. brunipennis*.

Thus, it is possible that there is a series of transformation states in character 6 between the plesiomorphic condition: RP₃₊₄ short (pterostigma short) of other bittacid genera to the ordered apomorphic conditions: RP₃₊₄ elongate (pterostigma elongate) (state 1; see Figs 2, 3B) and RP₃₊₄ greatly elongated (pterostigma greatly elongated) losing its sagged condition to follow the wing margin shape (state 2; see Fig. 3A). The African species listed above possess characters 1 and 2, which allows including them into *Thyridates*. Character 8 is present in: *B. erythro stigma*, *B. weelei*, *B. testaceous*, *B. oreinus* NAVÁS 1914, *B. chevalieri* NAVÁS 1908, *T. maculosus*, *T. flavescens*, *T. boraceiensis*, *T. andinus*, *T. angrensis*, *T. froehlichii*, *T. brunnipennis*, *T. stanleyi*, *T. erythro stigma*. In *B. indicus* WALKER the bifurcation of RP1 and RP2 is close to the crossveins ma-mp₁₊₂-mp₃₊₄ and not exactly touching them. Same situation is present in species of *Harpobittacus*. These simi-

larities could represent a retained intermediate situation of a series of transformation states. Characters 1 and 8 seem to have been acquired in different times of the evolution of the taxon, to be reversed or even be due by convergence. With the most parsimonious approach, these characters are considered as (respectively, more and less inclusive) synapomorphies of the group, and the homoplasies found could be explained as reversals.

Until now, *Thyridates* was considered to be an American genus. Nevertheless, COLLUCCI & AMORIM (2000) taking into account some points remarked by WILLMANN (1983), considered the possibility of finding some *Bittacus* in Asia and Africa 'with closer phylogenetic relationships with the tropical group of *Thyridates*'. Here some African species of *Bittacus* are transferred into the genus. All species transferred except *B. chevalieri* and *B. oreinus* share the main synapomorphy of the genus 'RP₁₊₂ forking from RP forming nearly a right angle' and the pterostigma greatly elongated (Table I). *T. chevalieri* and *T. oreinus* present the forked cross and a pterostigma elongate, and seem to belong to the group.

In this way, a Gondwanan origin of this group is suggested. Additionally, the possible close relationship of *B. indicus* with *Thyridates* agrees with its inferred Gondwanan origin. On the other hand, the absence of *Thyridates* in Australia has to be taken into account, and could be related to the presence of *Harpobittacus*.

Until now, no representatives of *Thyridates* have been recorded as fossil. A specimen representing a new species was recovered from the Paleogene of Argentina and is described below.

IV. SYSTEMATIC PALEONTOLOGY

MECOPTERA PACKARD, 1886

Bittacidae HANDLIRSCH, 1906

Genus *Thyridates* NAVÁS, 1908

Seven African species of *Bittacus* are transferred to *Thyridates* in accordance with the presence of synapomorphies of *Thyridates* (see above and Table I). *Thyridates stanleyi* (BYERS, 1968), comb. nov.; *Thyridates erythro stigma* (BYERS, 1975), comb. nov.; *Thyridates weelei* (ESBEN-PETERSEN, 1913), comb. nov.; *Thyridates nebulosus* (KLUG, 1838), comb. nov.; *Thyridates testaceus* (KLUG, 1838), comb. nov.; *Thyridates oreinus* (NAVÁS 1914), comb. nov.; *Thyridates chevalieri* (NAVÁS 1908), comb. nov.

Table I

List of African species of *Bittacus* transferred to *Thyridates* and the states for characters '1', '6', and '8'

Taxa/characters	1	6	8
<i>Thyridates stanleyi</i> (BYERS, 1968)	1	2	0
<i>Thyridates erythro stigma</i> (BYERS, 1975)	1	2	1
<i>Thyridates weelei</i> (ESBEN-PETERSEN, 1913)	1	2	1
<i>Thyridates nebulosus</i> (KLUG, 1838)	1	2	0
<i>Thyridates testaceus</i> (KLUG, 1838)	1	2	1
<i>Thyridates oreinus</i> (NAVÁS, 1914)	0	1	1
<i>Thyridates chevalieri</i> (NAVÁS, 1908)	0	1	1

Thyridates novokschonovi sp. nov.

Figs 1, 2

Differential diagnosis. The main characters of venation in this species are as follows: (1) RA₃₊₄ curves posteriorly forming a deep hemi-hexagonal sag; (2) two cross-veins from RA₃₊₄ to RP, (3) in hind wings RP+MA do not change its direction at fork of RP₁₊₂; (4) elongate (primarily) sagged distal part of RA₃₊₄ linked with two (one or three) crossveins with RP (pterostigma long); (5) RP₁₊₂ bends from RP at a nearly right angle; (6) ScP ending basal to CuP apex; (7) 'Kreuz' not modified; (8) wide space between RA and anterior wing margin; (9) smooth venation.

Character 3 is highly homoplastic and present in *Palaeobittacus*, *Thyridates*, and some species of *Harpobittacus* and *Bittacus*. Character 4 is a synapomorphy (?) of *Thyridates* and *Harpobittacus*. Character 5 is a synapomorphy of the species of *Thyridates*. Character 7 seems to be a plesiomorphy of some species of *Thyridates*. Characters 8, and 9 are autapomorphies of the new species.

Holotype. Specimen No. MLP 29017, in the Departamento Científico Paleozoología Invertebrados, Museo de La Plata, Argentina. Type locality and stratum: La Mendieta, province of Jujuy, Northwest Argentina, at latitude 24° 21' S, longitude 64° 59' W (PETRULEVIČIUS, 2001). Maíz Gordo Formation, late Palaeocene (MARSHALL et al. 1997, QUATTROCCHIO et al. 1997, VOLKHEIMER et al., 1984).

Etyymology. After the paleoentomologist and specialist on Mecoptera, Victor Grigorievich NOVOKSCHONOV. Even with his unexpected lost the 29 of January of this year; he is still alive in his ideas and in the memory of his friends.

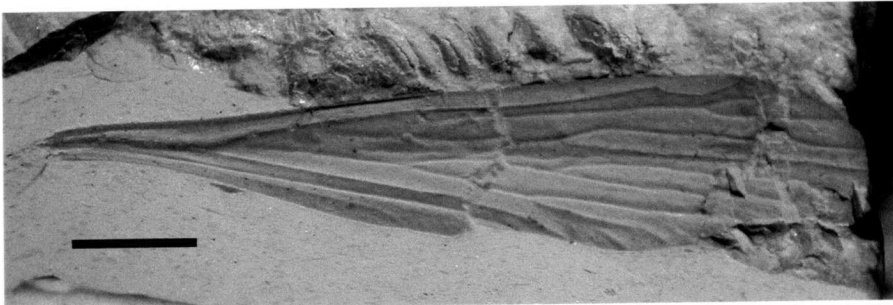


Fig. 1. *Thyridates novokschonovi* sp. nov., wing, holotype MLP 29017; La Mendieta, Province of Jujuy, Northwest Argentina, lat. 24° 21' S, long. 64° 59' W; Maíz Gordo Formation, late Paleocene. Scale bar 2 mm.

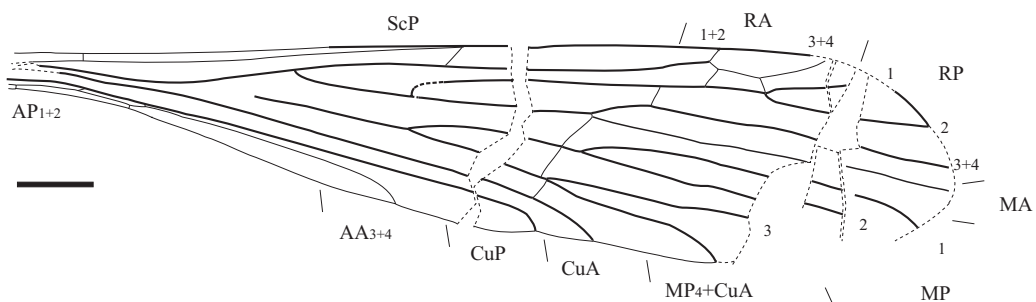
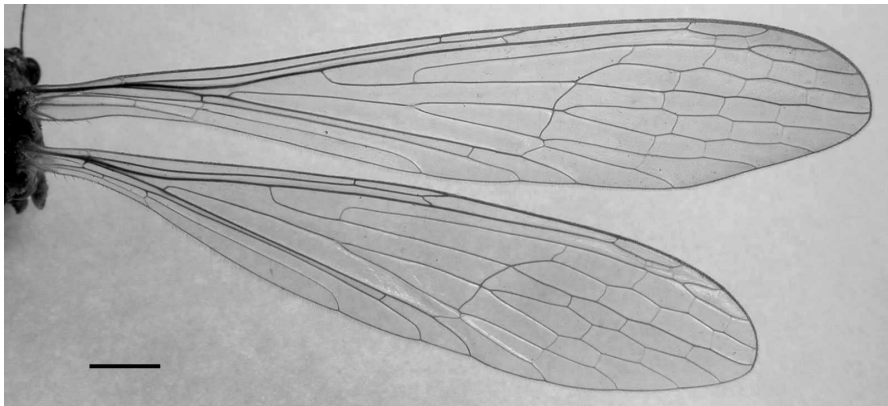
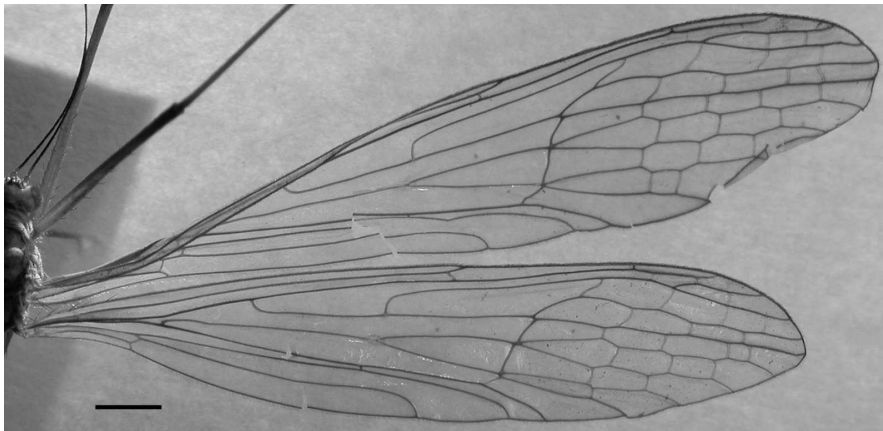


Fig. 2. *Thyridates novokschonovi* sp. nov., wing reconstruction from part and counter-part, holotype MLP 29017; La Mendieta, Province of Jujuy, Northwest Argentina, lat. 24° 21' S, long. 64° 59' W; Maíz Gordo Formation, late Paleocene. Scale bar 1 mm.



A



B

Fig. 3. A, *Thyridates weelei*, fore- and hindwing. Photograph of type specimen of *Bittacus negus* NAVÁS, 1915 (syn. of *T. weelei*), stored at the Muséum national d'Histoire naturelle, Paris, France; B, *T. fritzi*, fore and hindwing. Specimen of the paratype series, stored at the Instituto Miguel Lillo, Tucumán, Argentina. Scale bars 2 mm.

Description. Imprinting of an almost complete hind wing, three-dimensionally preserved, without trace of coloration. Total length: 13.1 mm, maximum width: 2.8 mm. Wing elongated, slender in basal third, broadened distally, with few cross-veins. Smooth venation (not zig-zagged). ScP ending basal than CuP apex. Cross-vein between costal margin, ScP and R in basal part of wing. One cross-vein between end of ScP and RA. R curved posteriorly in basal third. RA forks in RA₁₊₂ and RA₃₊₄; the former reaches wing margin near fork, and the latter curves posteriorly forming a deep and elongate hemi-hexagonal sag ('elongate pterostigma'). RP₁₊₂ bends from RP vein at nearly right angle. RP+MA does not change its direction at fork of RP₁₊₂. Wide space between RA and anterior wing margin. Two cross-veins from RA₃₊₄ to RP, one to RP₁₊₂ and the other just to the bifurcation of RP₁-RP₂ (that forks at half of RA₃₊₄). Fork of RP basal to end of ScP. Cross-vein between RP₁₊₂ and RP₃₊₄. One cross-vein from RP₃₊₄ to RP₂, and three to MA. Fork of RP₁₊₂ beneath the 'pterostigma'. MA, MP₁₊₂, and MP₃₊₄ linked by two cross-veins ('Kreuz der Bittaciden' present). 'Kreuz' not modified. MP₄ fused with CuA₁₊₂. Distal part of MP₁ and MP₄+CuA curved to posterior margin. MA nearly straight. One preserved cross-vein between MP₁ and MP₂; other between MP₄+CuA and MP₃. CuA reaches the wing margin at 45°. Incision on wing margin at end of CuP, that reaches the margin at 3/5 of wing length. Cross-veins between CuP and AA, AA₃₊₄ and

AP₁₊₂. AA₃₊₄ reduced like a cross-vein. Distal half of the wing becomes narrower (posterior from CuP end).

D i s c u s s i o n. Presence of the apomorphic state (RA₃₊₄ deeply sagged) in *Thyridates novokschonovi* sp. nov. excludes genera *Jichoristella* REN, 1995, *Orobittacus*, *Preanabittacus* NOVOKSCHONOV, 1993, *Microbittacus* NOVOKSCHONOV, 1993, and *Anabittacus*. Likewise, the presence of the apomorphic state: two (or more) crossveins between RA₃₊₄ and RP (against a plesiomorphic state: one crossvein between RA₃₊₄ and RP) excludes the genera *Asiobittacus*, *Scharabittacus*, *Karattacus* NOVOKSCHONOV, 1997 (?), *Baissobittacus* NOVOKSCHONOV, 1997, *Sibirobittacus*, *Probittacus*, *Cretobittacus* (?), *Prohylobittacus* and *Hylobittacus* BYERS, 1971, and places the specimen into the monophyletic (?) group formed by: *Palaeobittacus* (North America), *Austrobittacus* RIEK, 1954 (Australia), *Edriobittacus* BYERS, 1974 (Australia), *Tytthobittacus* SMITHERS, 1973 (Australia), *Symbittacus* BYERS, 1986 (Australia), *Harpobittacus* ESBEN-PETERSEN, 1915 (Australia), *Anomalobittacus* (?) KIMMINS, 1928 (Africa), *Eremobittacus* BYERS, 1997 (Mexico), *Bittacus* (Africa, Europe, Asia and America), *Afrobittacus* LONDT, 1994, *Thyridates*, *Kalobittacus*, *Pazius*, *Nannobittacus*, and *Issikiella*. The latter synapomorphy may be insecure for NOVOKSCHONOV (1993b), since two genera, *Nannobittacus* and *Issikiella*, have only one crossvein between RA₃₊₄ and RP. These genera form a monophyletic group together with *Kalobittacus* and *Pazius* (WILLMANN 1983, 1989) in Central and South America. The reduction of distal crossvein (WILLMANN 1983) in these two genera is an apomorphic state. *Kalobittacus*, *Pazius*, *Nannobittacus*, and *Issikiella* form a monophyletic group with *Afrobittacus*, *Austrobittacus*, *Edriobittacus*, *Tytthobittacus*, and *Symbittacus* with a Gondwanian origin (Gondwanoraptoria nom. nov.). This group has to be excluded because they present the apomorphic state: 'AA₂₊₃ (A₁) of the hindwing arising from CuP at a long distance from AP₁₊₂ (A₂); and there is no crossvein between them'. *Palaeobittacus* has to be excluded because of the presence of a partially fused MP₄ with CuA ('MP₄ gegabelt' sensu WILLMANN 1989), and a crossvein between RP and MP, both autapomorphies not present in *T. novokschonovi* sp. nov. Presence in the new species of a RP₁₊₂ bending from RP at a nearly right angle excludes *Harpobittacus*. The new species is not related to Bittacidae sp. 1 PETRULEVIČIUS (1999) from the same locality because of its broadest wing, similar to *T. chilensis*.

The new species could be included into *Thyridates* because of it RP₁₊₂ bending from RP at a nearly right angle. The new species is different from all other species of *Thyridates*. Among these, *T. maculosus*, *T. flavescens*, *T. boraceiensis*, *T. andinus*, *T. angrensis*, *T. froehlichii*, *T. brunnipennis*, *T. stanleyi*, *T. erythro stigma*, *T. weelei*, *T. testaceous*, *T. oreinus*, *T. chevalieri*, and *T. testaceous*, have to be excluded because they share the presence of the forked cross. Presence of a RA₃₊₄ ('pterostigma' greatly elongated) that lost its sagged condition to follow the wing margin shape, excludes the species: *T. stanleyi*, *T. femoralis*, *T. angrensis*, *T. erythro stigma*, *T. weelei*, *T. nebulosus*, *T. testaceous*, *T. maculosus*, *T. latreillei*, and *T. brunnipennis*. *Thyridates chilensis* has to be excluded because of its wide wings and large size. *T. pintoii* has to be excluded because its RP₁₊₂ in hindwing forks near the wing margin, and not beneath the 'pterostigma' (as in *T. novokschonovi*). *T. diversinervis* has to be excluded because of the presence of a long ScP (reaching height of CuP) and presence of two distal crossveins between ScP and wing margin. *T. omega* has to be excluded because of the presence of one crossvein beneath the pterostigma. *T. flavescens*, *T. boraceiensis*, *T. brunneus*, *T. froehlichii*, *T. golbachii*, *T. fritzi*, *T. geniculatus*, *T. chlorostigma*, and *T. mexicanus* has to be excluded because of the presence in the new species of a wide space between RA and anterior wing margin, and a smooth venation.

V. LIST OF SPECIES OF *THYRIDATES*

Thyridates NAVÁS, 1908 was monospecific until WILLMANN (1983) made a rediagnosis of the genus and transferred 11 South American species from *Bittacus*: *Thyridates andinus* (LONDT & BYERS, 1974); *Thyridates chilensis* (KLUG, 1838); *Thyridates pintoii* (DE SOUZA LOPES & MANGABEIRA, 1942); *Thyridates diversinervis* (DE SOUZA LOPES & MANGABEIRA, 1942); *Thyridates an-*

grensis (DE SOUZA LOPES & MANGABEIRA 1942); *Thyridates flavescens* (KLUG, 1836); *Thyridates femoralis* (KLUG, 1836); *Thyridates maculosus* (BYERS, 1965); *Thyridates brunneus* (ESBEN-PETERSEN, 1927); *Thyridates boraceiensis* (MORGANTE, 1967); and *Thyridates omega* (MORGANTE, 1967). After that, three new species were described by COLLUCCI & AMORIM (2000): *T. froehlichii* COLLUCCI & AMORIM 2000; *T. brunnipenis* COLLUCCI & AMORIM 2000; and *T. latreillei* COLLUCCI & AMORIM 2000. They transferred three South American and two North American species of *Bittacus* to *Thyridates*: *T. golbachii* (WILLINER, 1990); *T. fritzi* (WILLINER, 1990); *T. geniculatus* (ERICHSON, 1848); *T. chlorostigma* (MACLACHLAN, 1881); and *T. mexicanus* (KLUG, 1838). The African species transferred here are *T. weelei*, *T. nebulosus*, *T. testaceous*, *T. chevalieri*, *T. oreinus*, *T. stanleyi* and *T. erythrostroma*.

CONCLUSION

Thyridates was considered until now an American genus. Seven African species of *Bittacus* are transferred to *Thyridates*: *T. stanleyi*, *T. erythrostroma*, *T. weelei*, *T. nebulosus*, *T. testaceous*, *T. oreinus*, and *T. chevalieri*. A new South American species coming from the late Paleocene of Argentina is considered the first fossil species of *Thyridates*. Because of the presence of South American and African species, the genus has to be older than their separation in the earliest Cretaceous, suggesting the idea of a Gondwanan origin of the group. In spite of all these considerations, a wider review of *Thyridates* and *Bittacus* has to be made to conclude their relationships, and to prove their monophyly.

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