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DETECTION AND IDENTIFICATION OF TWO NEW NATIVE HYMENOPTERAN PARASITOIDS ASSOCIATED WITH THE EXOTIC SIREX NOCTILIO IN NORTH AMERICA

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Abstract.—Rhyssa crevieri (Provancher), a primary parasitoid of Siricidae wasps, and the Holarctic poemeniine ichneumonid, Pseudorhyssa nigricornis (Ratzeburg), a cleptoparasitoid of Siricidae via its parasitoids (Ichneumonidae: Rhyssinae), were reared from two stands of Scots pine (Pinus sylvestris L.) and red pine (P. resinosa Ait.) infested with the exotic siricid Sirex noctilio F. near Tully (Onondaga Co.), New York, in 2010. Previously, P. nigricornis has been recorded from the primary siricid parasitoids Rhyssa persuasoria (in Europe and North America) and R. howdenorum Townes and Townes and R. lineolata (Kirby) (in North America). Peak emergence of P. nigricornis occurred in early May concurrently with R. persuasoria and R. crevieri. A second peak occurred in late May, which overlapped peak emergence of R. lineolata and Megarhyssa nortoni (Cresson). Although 14 individuals of two native siricids, Sirex nigricornis F. and S. edwardsii Brullé, emerged from sampled trees, the number of S. noctilio recovered was far higher (372), suggesting cleptoparasitism of the exotic woodwasp rather than native siricids. Approximately 26% of rhyssine parasitoids in pine stands were cleptoparasitized by P. nigricornis. This study marks the first association of R. crevieri and P. nigricornis with S. noctilio in North America. A diagnosis, color images of characters, and a key are provided to aid in the identification of all parasitoids in this study.

Key Words: cleptoparasitism, Rhyssa persuasoria, Rhyssa lineolata, Rhyssa crevieri, Megarhyssa nortoni, morphological characters, identification key, rearing data

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*Sirex noctilio* F. (Hymenoptera: Siricidae) is a relatively large wood-boring wasp native to Eurasia and North Africa (Borchert et al. 2007). Its primary hosts are stressed trees within the genus *Pinus* (Spradbery and Kirk 1978). However, under outbreak population levels, *S. noctilio* possesses the ability to attack relatively healthy trees (Spradbery 1973), disperse rapidly...
(Neumann et al. 1987, Tribe and Cillié 2004, Corley and Villacide 2009), and cause great economic damage (Haugen 1990, Hurley et al. 2007). Previous invasions have been documented throughout the southern hemisphere (Hurley et al. 2007). In 2004, a single adult female was captured in Fulton, NY, eliciting concerns for native North American pine forests (Hoebeke et al. 2005).

In areas where *S. noctilio* has become an economically important invasive, *Rhyssa*, *Megarhyssa* (Ichneumonidae: Rhyssinae), and *Ibalia* (Cynipoidea: Ibaliidae) parasitoids have been introduced for biological control (Miller and Clark 1935, 1937; Rawlings 1951; Zondag 1959; Zondag and Nuttall 1961; Cameron 1965; Nuttall 1972; Taylor 1976, 1978; Murphy 1998). Species of *Rhyssa* and *Megarhyssa* attack late-instar larvae (Murphy 1998) by drilling into wood after hosts ( Chrystal and Myers 1928a, b). Ibaliid wasps attack eggs and early-instar siricid larvae (Murphy 1998) using drill shafts left by ovipositing siricids.

The parasitoid guild of native siricid woodborers in eastern North American conifers (Taylor 1976, Murphy 1998) includes primary parasitoids of the ichneumonid genera *Rhyssa* [*R. crevieri* (Provancher), *R. lineolata* (Kirby), *R. howdenorum* Townes and Townes, and *R. persuasoria* (L.)] and *Megarhyssa* [*M. nortoni* (Cresson)], and the ibaliid genus *Ibalia* [*I. leucospoides ensiger* (Norton)]. This parasitoid community also includes a secondary parasitoid or cleptoparasitoid, the Holarctic poemeniine ichneumonid *Pseudorhyssa nigricornis* (Ratzeburg). Two recently published studies (Long et al. 2009, Eager et al. 2011) have documented the hymenopteran parasitoids associated with *S. noctilio*-infested pine trees in North America as *Ibalia l. ensiger*, *Rhyssa persuasoria*, *R. lineolata*, and *Megarhyssa nortoni*.

The genus *Pseudorhyssa* contains four species: the Eurasian *P. alpestris* (Holmgren) (northwest and central Europe and Japan), *P. acutidentata* Kusigemati (Japan), and *P. maculiventris* Sheng and Sun (China), as well as the Holarctic *P. nigricornis* (Fitton et al. 1988, http://www.taxapad.com/global.php). Species of *Pseudorhyssa* cleptoparasitize rhyssine Ichneumonidae, consuming the primary parasitoid larvae and feeding on the siricid larvae paralyzed by the primary parasitoid (Kerrich 1966, Spradbery 1969). Although most of the literature dealing with *P. nigricornis* uses the name *P. maculicoxis* (Kreichbaumer), Horstmann (1999) concluded *P. maculicoxis* should be synonymized with *P. nigricornis*.

Several studies indicate *P. nigricornis* is associated exclusively with conifer-feeding siricid larvae via their rhyssine parasitoids (Spradbery 1969, Schimitschek 1974, Kusigemati 1984). In Europe, *P. nigricornis* (cited as *P. maculicoxis*) is well documented as a cleptoparasitoid of the siricids *Sirex juvencus* L., *S. cyaneus* F., and *S. noctilio* F. via the Holarctic *R. persuasoria* (L.) (Spradbery 1969, 1970). The North American range of *P. nigricornis* includes Quebec south to western North Carolina, west to Alberta and California and southwest to northern Arizona (Townes and Townes 1960; Kirk 1974, 1975; Carlson 1979). Kirk (1974, 1975) documented the association of *P. nigricornis* with *R. persuasoria* in Arizona and with *R. persuasoria*, *R. lineolata*, and *R. howdenorum* in western North Carolina. Porter (2001) noted an abundance of *R. howdenorum* and *P. nigricornis* (cited as *P. maculicoxis*) on loblolly pine (*Pinus taeda* L.) on the Eastern Shore of Maryland; the siricids *Urocerus cressoni* Norton, *S. nigricornis* F., and *S. edwardsii* Brullé on the same trees were the likely hosts of *R. howdenorum*. 
Female *P. nigricornis* are receptive to males two or three days post emergence (Spradbery 1969). Gravid females observe *R. persuasoria* drilling for siricid larvae and, following completion of drilling, use the drill shafts to access and cleptoparasitize hosts (Spradbery 1969, Townes 1969). Females of *P. nigricornis*, however, do not necessarily have to observe drilling by the primary parasitoid, as they can locate drill shafts several days after their completion (Spradbery 1969). The ovipositor of *P. nigricornis* is smaller in cross-section and less sclerotized than primary rhyssine attackers, which facilitates successful access to drill shafts and siricid hosts (Spradbery 1969).

Oviposition by *P. nigricornis* occurs close to primary parasitoid eggs and, following eclosion, a battle ensues between larvae of *P. nigricornis* and those of the primary parasitoid (Spradbery 1969, 1970). First-instar larvae of *P. nigricornis* are heavily armored and larger than rhyssine larvae, with exaggerated, sickle-shaped mandibles, and paired caudal appendages that aid in defeating primary species (Spradbery 1969, 1970). During the initial interaction, *P. nigricornis* larvae rear on their hind, paired appendages to kill rhyssine larvae with their large mandibles (Spradbery 1969). No rhyssine larvae, irrespective of instar, prevailed against attacking first instars of *P. nigricornis*. After consuming the rhyssine larva, *P. nigricornis* consumes the siricid host paralyzed by the adult rhyssine before emerging the following spring (Spradbery 1969).

Methods and Materials

In April 2010, pine trees in two pure stands of *P. resinosa* Ait. and *P. sylvestris* L. near Tully, NY, were examined thoroughly for the diagnostic resin beads associated with *S. noctilio* oviposition drills along the bole. Within each stand, five *P. resinosa* and five *P. sylvestris* trees with clear signs of infestation were felled. Trees ranged from 14.5 to 23.0 cm diameter at breast height (dbh), with crown conditions ranging from recently dead with a few brown needles to dying with sparse green needles.

Each tree was subsampled using methods developed by Eager et al. (2011). Nine 0.5 m bolts were removed systematically from each of the ten felled trees. If trees were < 10 m tall, the whole tree was taken. All sample bolts were transported to a rearing facility at the State University of New York, College of Environmental Science and Forestry (SUNY ESF), Syracuse, NY. Ends of bolts were sealed with Waxon™ end sealant (Willamette Valley Company) to prevent desiccation and placed in cardboard emergence tubes. Tubes were held at ambient environmental conditions in an outdoor insectary. All emerging insects were collected and recorded multiple times per day. To reduce noise when reporting emergence phenologies, daily data were summed over weekly time periods.

Identity of all rhyssine Ichneumonidae and *Pseudorhyssa* reared in this study was confirmed morphologically using keys in Townes and Townes (1960) and in Kerrich (1966) and Wahl (1993),
respectively, and/or by comparison with identified research specimens housed in the Cornell University Insect Collection (Ithaca, NY) and the United States National Museum of Natural History (Washington, DC). Reared specimens of S. noctilio, its ichneumonid parasitoids, and P. nigricornis, are deposited in the SUNY ESF Entomology Museum Collection (Syracuse, NY), Cornell University Insect Collection (Ithaca, NY), and the University of Georgia Museum of Natural History Collection of Arthropods (Athens, GA).

Percent cleptoparasitism by P. nigricornis was calculated as the number of P. nigricornis divided by the total number of rhyssines plus P. nigricornis.

**Results**

**Diagnosis**

Species of the Rhyssinae and the genus Pseudorhyssa are easily recognized by the presence of strong transverse ridges on the mesoscutum (Fig. 11). No other Nearctic ichneumonid has this unique and distinctive feature. The following morphological characters differentiate P. nigricornis from any species of Rhyssa. Conspicuous yellow or cream markings on the head, thorax, propodeum, and hind margins of the gastral segments (Figs. 1, 2) characterize species of Rhyssa, whereas the head, thorax, propodeum, and gaster in P. nigricornis lack any yellow or cream markings (Fig. 3). Pseudorhyssa nigricornis is further distinguished by the fore wing with vein cu-a joining at the bifurcation of M and Cu (Fig. 5), the occipital carina is incomplete mediodorsally (Fig. 9), the last visible tergite of the female gaster is extended into a polished, truncate horn (Fig. 7), and tergite 2 of the gaster lacks defined anterolateral grooves. Also, gastral segment 1 in Pseudorhyssa has a sharp lateral longitudinal carina extending from the spiracle to the posterior margin, while in species of Rhyssa gastral segment 1 lacks this distinct lateral longitudinal carina (Wahl 1993).

The Palearctic Pseudorhyssa alpestris, also reared from S. noctilio in Europe (Schimitschek 1974), has not been detected in North America. It differs from P. nigricornis by dorsal segments 1-3 of the gaster usually with a distinct reddish-brown mark near the posterior margin and by the face of the female often with obscure brownish marks (Fitton et al. 1988). In contrast, the gaster and face of the female of P. nigricornis are black without any brownish markings.

Among the species of Rhyssa reared in this study, R. persuasoria is readily recognized by the flagellum of the antenna being entirely black (Fig. 2). In both R. crevieri and R. lineolata, the flagellum of the antenna has a broad white band (Fig. 1), except in occasional small males (Townes and Townes 1960). Coloration distinguishes these two latter species. In R. crevieri, the white mark on the metapleuron is subtriangular (Fig. 12), prolonged forward along the upper margin. This subtriangular mark varies substantially in females and is often absent or much reduced in some males. The hind coxa has no white mark dorsobasally (Fig. 12) or sometimes a very small white mark limited to its constricted base. In contrast, the white mark on the metapleuron in R. lineolata is rounded.
(Fig. 13), constricted next to the upper margin. This mark is absent or reduced in some males. The hind coxa of *R. lineolata* has a white mark dorsobasally (Fig. 13), usually in the form of a small dash but in larger females often enlarged and irregular in shape or covering the entire upper surface of the coxa. Although both species...
are recognized currently as valid, a footnote in the “Catalog of Hymenoptera North of Mexico” (Carlson 1979) states: “It remains to be proven that crevieri is distinct from lineolata.”

The following key, based on characters given in the diagnosis above, allows for the separation of all rhyssine ichneumonids and Pseudorhyssa reared from Sirex noctilio-infested trees in the northeastern U.S.

Key to Species of Ichneumonidae With a Strongly Transversely Rugose Mesoscutum (Fig. 11)
(Adapted from Fitton et al. 1988 and Townes and Townes 1960)

1. Occipital carina complete mediadorsally (Fig. 8). Female: last visible tergite of gaster not extended as horn (Fig. 6). Gastral tergite 2 with deep anterolateral grooves (Fig. 10) ................
   . . . Pseudorhyssa nigricornis (Ratzeburg) [synonyms: Pseudorhyssa maculicostis (Kreichbaumer 1889), Pseudorhyssa sternata Merrill 1915, and Pseudorhyssa prealpina (Gyorfi 1946)]
   – Occipital carina incomplete mediadorsally (Fig. 9). Female: last visible tergite of gaster extended into a polished, truncate horn (Fig. 7). Gastral tergite 2 without anterolateral grooves ....................... 2.

2. Clypeus with median tooth or projection. Female: sternite 2 of gaster with 2 median tubercles near middle ................... Rhyssa spp. ................... 3.
   – Clypeus truncate. Female: sternite 2 of gaster with 2 median tubercles near base .... . . . . . Megarhyssa nortoni (Cresson) [wings unicolorous, subhyaline; stigma yellowish; female: tergites 4–6 with conspicuous, yellow, round, lateral spots on each side; thorax and gaster light brown to blackish, with conspicuous yellow markings]

3. First 4 tergites of gaster with narrow whitish apical margin, of even width, and continuous
across middle, or slightly narrower or interrupted medially. 

- First 4 tergites of gaster with white apical spots, not forming a continuous band across middle. 

4. Flagellum of antenna with broad white band (Fig. 1). 

- Flagellum of antenna entirely black (Fig. 2). 

5. Metapleuron with subtriangular white spot, prolonged forward along upper margin (Fig. 12); hind coxa without white spot dorsobasally (Fig. 12), but sometimes with small white spot at base. 

- Metapleuron with rounded white spot, constricted next to upper margin (Fig. 13); hind coxa with white spot dorsobasally (Fig. 13), often enlarged and irregular in shape. 

Emergence phenology.—Twenty adult R. crevieri (9 males, 11 females) and fifty-one adult P. nigricornis (30 males, 21 females) emerged from sample bolts taken from five of the ten felled pine trees (Table 1). Peak emergence of P. nigricornis overlapped with its previously recorded host, R. persuasoria, and with R. crevieri, a previously unrecorded host (Fig. 14). A second peak in P. nigricornis emergence (Fig. 14) overlapped with two other native rhyssines, R. lineolata and Megarhyssa nortoni. Cleptoparasitism of rhyssines by P. nigricornis was ~ 26%. The introduced S. noctilio was by far the dominant siricid with 372 individuals emerging from the infested bolts and only 14 native S. nigricornis and S. edwardsii, < 4% of the total siricid emergence from sampled trees (Table 2, Fig. 15).

**Discussion**

The rearing and identification of R. crevieri as well as P. nigricornis from Sirex noctilio-infested trees at our study site in central New York marks the first association of both this primary parasitoid and the cleptoparasitoid with S. noctilio in North America. Previous studies in this region (Long et al. 2009, Eager et al. 2011) recorded only the rhyssines R. persuasoria and R. lineolata. However, morphological similarity between R. crevieri and R. lineolata may explain why R. crevieri went unnoticed in both studies. Both species contain broad, white bands on the antennae, except for some small males (Townes and Townes 1960), and similar white highlights on the rest of the body. Despite these similarities, differences in emergence phenologies of these parasitoids (Fig. 14) provide further support for their separate species status.

It is less likely that P. nigricornis would be misidentified as a species of Rhyssa based on distinguishing morphological characteristics as noted in the key. Timing of sampling may account for the absence of this species in one of the prior studies. Long et al. (2009) collected samples from Sirex-infested trees in late June, which, according to our emergence phenology (see Fig. 14), is late for recovery of Rhyssa and the associated cleptoparasitoid. In

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Height (m)</th>
<th>DBH (cm)</th>
<th>Crown condition</th>
<th>No. R. crevieri</th>
<th>No. P. nigricornis</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. resinosa</td>
<td>11.3</td>
<td>17.5</td>
<td>sparse green needles</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>P. resinosa</td>
<td>16.2</td>
<td>18.5</td>
<td>needles all brown</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>P. resinosa</td>
<td>12.7</td>
<td>23</td>
<td>few brown needles</td>
<td>13</td>
<td>19</td>
</tr>
<tr>
<td>P. sylvestris</td>
<td>9.0</td>
<td>13</td>
<td>sparse green needles</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>P. sylvestris</td>
<td>8.9</td>
<td>17</td>
<td>sparse green needles</td>
<td>5</td>
<td>24</td>
</tr>
</tbody>
</table>
another study (Eager et al. 2011), collections from the same field site used in our study (Heiberg Forest) did not yield $P. nigricornis$, perhaps because it focused exclusively on larval sampling. Characteristics distinguishing $P. nigricornis$ larvae from rhyssine larvae are not obvious (Spradbery 1970) and individuals of this species could have been easily overlooked. Alternatively, $P. nigricornis$ may exhibit a density dependent relationship with its rhyssine hosts as Eager (2010) recorded relatively low numbers of rhyssines in 2009. In 2011, sampled trees at Heiberg Forest also had low numbers of rhyssines and failed to yield any $P. nigricornis$ (C. Standley, unpublished).

Table 2. Number of emerged Pseudorhyssa nigricornis, rhyssine Ichneumonidae, and species of Siricidae during the 2010 flight season from 0.5 meter logs removed from four trees near Tully, NY.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. emerged</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudorhyssa nigricornis</td>
<td>51</td>
</tr>
<tr>
<td>Rhysa lineolata</td>
<td>70</td>
</tr>
<tr>
<td>Rhysa crevieri</td>
<td>20</td>
</tr>
<tr>
<td>Rhysa persuasoria</td>
<td>31</td>
</tr>
<tr>
<td>Megarhyssa nortoni</td>
<td>27</td>
</tr>
<tr>
<td>Sirex noctilio</td>
<td>372</td>
</tr>
<tr>
<td>Sirex nigricornis</td>
<td>8</td>
</tr>
<tr>
<td>Sirex edwardsii</td>
<td>6</td>
</tr>
</tbody>
</table>

In North America, $P. nigricornis$ has been associated with primary parasitoids of the native siricids Sirex abbottii Kirby (= cyaneus F.), $S. nigricornis$ F., and $S. cyaneus$ in the southeastern U.S. (Kirk 1974) and of $S. cyaneus$, S. californicus (Ashmead), and S. longicauda Middlekauff in the southwestern U.S. (Kirk 1975). The strong overlap in emergence phenology of $P. nigricornis$ with the four rhyssine species suggests that all ($R. persuasoria$, $R. lineolata$, $R. crevieri$, and possibly $M. nortoni$) may be suitable hosts. Initial peak emergence of $P. nigricornis$ (early May in 2010) was concurrent with both $R. persuasoria$ and $R. crevieri$, while the later peak coincided with $R. lineolata$ and $M. nortoni$ (Fig. 14). Emergence phenologies of $P. nigricornis$ supports utilization of $R. persuasoria$ and $R. lineolata$ as reported by Spradbery (1969) and Kirk (1974). Phenologies also indicate $R. crevieri$ is likely being exploited and it is possible $P. nigricornis$ is utilizing $M. nortoni$. When $M. nortoni$ is excluded from calculations, percent cleptoparasitism of the remaining rhyssines increases from 26 to 30%.

Our data suggest $P. nigricornis$ may be a significant source of mortality for $R. persuasoria$, $R. lineolata$, and $R.
crevieri (Table 2). As each *P. nigricornis* uses only a single rhyssine host, emergence of equivalent numbers of adults of each species indicate that mortality of rhyssines from *P. nigricornis* is not trivial and that the ability of *R. persuasoria* to check the growth of *S. noctilio* populations (see Taylor 1978) could be compromised. The importance of cleptoparasitism in the population dynamics of *S. noctilio* in North America was not previously known and research toward a more comprehensive understanding of the host-parasitoid relationships in this system is warranted.

**ACKNOWLEDGMENTS**

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