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A revised description of the larva of *Homilia leucophaea* (Rambur 1842) (Trichoptera: Leptoceridae) and comparisons with the known western European *Athripsodes* larvae

MAXENCE FORCELLINI^{1,4}, BERNHARD STATZNER² & HENRI TACHET³

CNRS-UMR 5023, LEHNA, Biodiversité des Ecosystèmes Lotiques, Université Lyon 1, F-69622 Villeurbanne Cedex, France. IRSTEA, UR-MALY, 5 rue de la Doua, CS 70077, 69626 Villeurbanne Cedex, France. E-mail: ¹forcellini.maxence@gmail.com, ²Bernhard.Statzner@univ-lyon1.fr, ³h.tachet@orange.fr ⁴Corresponding author. E-mail: forcellini.maxence@gmail.com

Abstract

Co-occurrence of mature larvae and male pharate pupae in benthos samples from the Loire River enabled descriptions of the larva of *Homilia leucophaea*. Using characters of the head capsule, the labrum, the meso- and metanotum, and the proand metathoracic legs, we compared *H. leucophaea* with larvae of six western European *Athripsodes* species, including a larval key to these species. The larva of *H. leucophaea* shares characters with some of the six *Athripsodes* species. However, without a phylogenetic analysis including larvae, pupae, and adults of *Homilia* species from the Afrotropical Region, it is currently impossible to decide about a potential synonymy between *Athripsodes* and *Homilia*.

Key words: characters, larval instar V, larval key, synonymy

Introduction

In 1842, Rambur described a new Trichoptera species as *Mystacida leucophaea*, which was caught « le long des rivières, dans les environs de Paris » (i.e., along the rivers around Paris). Three decades later, McLachlan (1877) took into account that the spur formula of this species is 1, 2, 2 instead of 2, 2, 2 and assigned it to the genus *Homilia*. However, *H. leucophaea* (Rambur 1842) is close to species of the genus *Athripsodes*. Therefore, authors such as Botosaneanu & Malicky (1978), Tobias & Tobias (1981), and Malicky (2004) assigned *H. leucophaea* to the genus *Athripsodes*, thus changing its name to *A. leucophaeus*. This change, yet unconfirmed by a phylogenetic analysis, seems premature, however, as Malm & Johanson (2011) emphasize: "The generic difference between *Homilia* and *Athripsodes* has been the absence of one of the foretibial spurs (1,2,2 from 2,2,2), a trait that may have evolved within *Athripsodes*, but more species of both genera are needed to clarify the status of *Homilia*." Accounting for the argument of Malm & Johanson (2011) and following the Trichoptera World Checklist (Morse 2012), we use *H. leucophaea* as the species name here.

The genus *Homilia* occurs in the western Palearctic Region (in particular in France where a species of this genus was discovered for the first time, see above) and in the Afrotropical Region (11 species). In non-French western Europe, the status of *H. leucophaea* varies. It currently occurs in Spain (Gonzalez *et al.* 1992) but is critically endangered in Latvia (Spuris 1989), the Czech Republic (Chvojka & Komzak 2008), and Germany (Klima 1998). Its last records date from 1949 in Belgium (Stroot 1985), 1932 in Italy (Cianficconi *et al.* 2005), 1944 in Switzerland (Lubini-Ferlin & Vicentini 2005), and 1955 in Romania (Botosaneanu 1955). In France, *H. leucophaea* occurs in several large river basins (Garonne, Loire, Rhône, Seine, and Meuse; data from OPIE Benthos: www.opie-benthos.fr/opie/insecte.php).

The first and so far only description of the *H. leucophaea* larva (Botosaneanu 1955) provided no information about the shape of the ventral apotome, which is an essential character to separate the larvae of *Athripsodes* from those of *Ceraclea* (Morse 1975; Morse & Wallace 1976) and may be important for the diagnosis of *Homilia*.

Furthermore, characters such as larval head shape, length of the larval antennae, shape and size of the mesonotal bars and the structure of the setose patches and reinforcing sclerites of the lateral humps on abdominal segment I of the larva are all features that would add additional useful information (Morse & Wallace 1976; De Moor 2002). This suggests that a more-thorough description of the *H. leucophaea* larva may be necessary for confident determination of genera in Athripsodini. The co-occurrence of mature larvae and pharate male pupae in quantitative benthos samples yielding *H. leucophaea* as the only leptocerid species enabled us to complete Botosaneanu's (1955) description and to compare the *H. leucophaea* larva with currently known larvae of western European *Athripsodes* species.

Material and methods

Larvae and pupae of *H. leucophaea* were found in the Loire River (near the village of Chambilly, Saône et Loire department, France: $004^{\circ}00'53"$ E and $46^{\circ}16'42"$ N) in June 2005. The species identification was easy because fifth instar larvae, prepupae, and pharate adults co-occurred in quantitative benthos samples (area sampled: $0.3 \text{ m} \times 0.2 \text{ m}$; sample size: 50) from cobble substrates of one riffle (for details see Statzner 2011). Moreover, *H. leucophaea* was the only leptocerid species present in these samples. Thus, larvae were associated with pharate adults using the metamorphotype method (Milne 1938), which relies on the collection of pharate males within the pupal case. Given that the molted larval sclerites of leptocerids are typically ejected through the posterior opening of the pupal case (Wallace *et al.* 2003), we associated larvae with pharate males via the unique case type in the samples.

Seven Athripsodes species are known in France: A. albifrons (Linnaeus 1758), A. aterrimus (Stephens 1836), A. bilineatus (Linnaeus 1758), A. braueri (E. Pictet 1865), A. cinereus (Curtis 1834), A. commutatus (Rostock 1874), and A. genei (Rambur 1842). For A. albifrons, A. aterrimus, A. cinereus, and A. bilineatus, we have many recent records from France (see data at www.opie-benthos.fr/opie/insecte.php). Athripsodes braueri is a common species in the western part of the Iberian Peninsula (Gonzalez et al. 1992), but there is only one old record for France (Rhône department). Athripsodes commutatus is a widespread, but very local species in eastern Europe, Scandinavia, and Great Britain; there are only four old records for France. Athripsodes genei is endemic to Corsica and Sardinia but its larva is unknown. Finally, an eighth species, A. rieli (Navas 1918), has been recorded for France ("St. Rambert le Barbe (Rh.) sur la Saônt Quai de le Sauvagerie, 31 août 1912"), but its holotype and paratype ("en la colección Riel") have disappeared (Tachet, personal communication 2012). Furthermore, this species has not been recognized in the Rhône department (its type locality) since its original description (Usseglio-Polatera 1985). In Navas' (1918) description, the species is said to resemble the Iberian A. inaequalis (McLachlan 1884) and the text and figures confirm that similarity. Nevertheless, the description is insufficient for identification; its actual identity remains unknown and the name is therefore inapplicable to any known species, so that A. rieli is a nomen dubium, a dubious species name.

To compare the larva of *H. leucophaea* with the known, common western European *Athripsodes* larvae, we used our collected French material of *A. albifrons*, *A. aterrimus*, and *A. cinereus*. Based on larval descriptions by others, we re-drew characters illustrated for *A. braueri* by Vieira-Lanero (2000) and for *A. bilineatus* and *A. commutatus* by Wallace *et al.* (2003) and Waringer & Graf (1997, 2011).

Description of the larvae of Athripsodini genera

The genus *Homilia* belongs to the tribe Athripsodini that has two other European genera, *Athripsodes* and *Ceraclea* (Morse 1981; Malm & Johanson 2011). Typically, Athripsodini larvae are characterized by a mesonotum with a pair of dark posterolateral bars that converge anteriorly and by multibranched abdominal gills (Morse & Wallace 1976; De Moor 2002).

Morse & Wallace (1976) provided a description of the typical characters of *Athripsodes* larvae. Their ventral apotome is triangular; the head is longer than broad and parafrontal lines are never present; the mesonotal bars in the final instar are short and straight; the reinforcing sclerites (lateral case-holding plates) of lateral humps on abdominal segment I are each strongly bent in the distal anterior part or are slightly forked or with a large clear

space in the anterior half; abdominal gills are present on no more than abdominal segments I–III; no posterolateral projections are evident on the abdominal tergum IX and a definite tergite is present; each anal claw has a single strong dorsal accessory hook; and the larval case is long and tapering and slightly curved but never with the anterodorsal lip overhanging the anteroventral edge (Morse & Wallace 1976). In contrast, several Afrotropical *Athripsodes* species may have an almost rectangular ventral apotome, long mesonotal bars, or no gills (De Moor 2002).

Likewise, Morse & Wallace (1976) provided a description of the typical characters of *Ceraclea* larvae. Their ventral apotome is quadrangular or polygonal; the head is generally broader; parafrontal regions are usually present in the final instar; final instar mesonotal bars are long and bent about midway; reinforcing sclerites on lateral humps of abdominal segment I are straight or slightly curved anteriorly; gills are present on at least abdominal segments II–VI, sometimes also on I, VII, and VIII; a pair of gill-like, filamentous, posterolateral projections are present on tergum IX of all instars and no distinct tergite is present (only a weak, pigmented patch in some species); each anal claw has one or two small dorsal accessory hooks; and the larval case typically is cornucopia-shaped, with a definite overhanging anterodorsal lip on cases of later instars (Morse & Wallace 1976). In contrast, the mesonotal bars of the Afrotropical *C. schoutedeni* (Navas 1930) are relatively short and straight (De Moor 2002).

The head capsule of the larva of *H. leucophaea* (Figs 1 & 2) is yellow and the antennae are extremely short. The dorsal (character mentioned by Botosaneanu 1955) and ventral muscle scars are ill-defined. The ventral apotome is triangular, its posterior apex is pointed, and it has a thickened anterior margin forming a roll. The ventral apotome is yellow like the ventral head surface. The anterior part of the labrum has a dark anteromedian crescentic mark connecting setae 4 and anteromedian pit P1, not invaginated around P1 (nomenclature of Williams & Wiggins 1981) (Fig. 3).



FIGURES 1–7. *Homilia leucophaea*, larval instar V and its case. (1) Head, dorsal view; (2) head, ventral view; (3) labrum, dorsal view, the arrow indicating the anteromedian pit P1; (4) mesonotum; (5) metanotum, the arrows indicating the four posteromedian (*sa*2) setae; (6) tibia of left prothoracic leg, interior view, the arrow indicating the additional short, pointed spur on the ventral edge of the tibia; (7) larval case, left lateral view.

The muscle scars of the mesonotum are ill-defined. The dark mesonotal bars converge slightly anteriorly and have sharp contours (Fig. 4). The four posteromedian (*sa*2) setae on the metanotum are of equal length (Fig. 5). The tibia of each prothoracic leg has a spur at the distal end and its ventral margin has another short, pointed spur (Fig. 6). The interior face of the trochanter and the distal section of the femur of each metathoracic leg have no short, dagger-shaped setae, their dorsal and ventral margins have only long setae. The reinforcing sclerites of the lateral humps on abdominal segment I are almost rectangularly bent in the distal anterior part, thus resembling an inverse "L-shape" (similarly to Fig. 4g in De Moor 2002). The larval case, composed of sand grains forming an irregularly paved surface, is slightly curved and tapered posteriorly (Fig. 7). In our material, it had no overhanging dorsal lip, but the case described by Botosaneanu (1955) and Waringer & Graf (2011) had such a lip.

Comparing larvae of H. leucophaea and Athripsodes

Wallace (1981), Wallace *et al.* (2003), and Waringer & Graf (2011) carefully defined a set of discriminating characters to identify the different British and central European *Athripsodes* species. Here, we primarily use "macroscopic" characters that are visible with a stereo microscope. Among these, the general shape of the body, the antennal length, the shape of the mandibles, the setose patch and sclerotized bars on the lateral abdominal hump, the relative size of the thoracic legs, the shape of the foretrochantin, the gills, the dorsal sclerite of abdominal segment IX, the anal claws, and the larval case are very similar across *H. leucophaea* and the different *Athripsodes* species. In contrast, the head capsule and meso- and metanota provide the most relevant characters to discriminate among the species.

In addition to these macroscopic characters, we also use "microscopic" characters that have to be examined with a compound microscope. Among these are the shape of the mark in the middle of the anterior part of the labrum and its relationship with the anteromedian pit P1, which are two useful, discriminating characters. More useful microscopic characters are found on the tibia of each prothoracic leg and trochanter and femur of each metathoracic leg.

The head capsule has the same shape in the different species (Figs 1 & 2 and 8–19). The main discriminating characters are color patterns on dorsal and ventral head surface and shape and color of the ventral apotome.



FIGURES 8–19. Heads of *Athripsodes* spp. larvae, instar V, dorsal and ventral views, respectively. (8 & 9) *Athripsodes albifrons*; (10 & 11) *A. aterrimus*; (12 & 13) *A. bilineatus*; (14 & 15) *A. braueri*; (16 & 17) *A. cinereus*; (18 & 19) *A. commutatus*.



FIGURES 20–22. Labra of Athripsodes spp. larvae, instar V, dorsal views. (20) A. aterrimus; (21) A. bilineatus; (22) A. cinereus.



FIGURES 23–26. Mesonota of *Athripsodes* spp. larvae, instar V, dorsal views. (23) *A. albifrons*; (24) *A. aterrimus*; (25) *A. braueri*; (26) *A. cinereus*.



FIGURES 27–30. Metanota of *Athripsodes* spp. larvae, instar V, dorsal views. (27) A. albifrons; (28) A. aterrimus; (29) A. bilineatus, A. cinereus, A. braueri; (30) A. commutatus.



FIGURES 31–34. Left prothoracic legs of *Athripsodes* spp. larvae, instar V, interior views. (31) *A. albifrons*; (32) *A. aterrimus*; (33) *A. braueri*, the arrows indicating short, pointed spurs; (34) *A. cinereus*, the arrows indicating short, pointed spurs.

In *Athripsodes* and *Homilia*, the frontoclypeal apotome is elongated with a constriction in the anterior half. It is separated from the parietal sclerites by the frontoclypeal sutures. Posteriorly, the parietal sclerites are separated by the coronal suture. In addition, there are two subocular ecdysial lines joining the frontoclypeal sutures anterolaterally in front of the eyes and terminating posterolaterally in the occipital foramen.

In *A. albifrons*, the head capsule is dorsally pale yellow (Fig. 8). The muscle scars are generally ill-defined, especially on the frontoclypeus. In this species, the muscle scars are darker patches with irregular outlines on either side of the frontoclypeal sutures; but even the transverse muscle scars just behind the constriction of the frontoclypeal apotome are ill-defined. In *A. aterrimus*, the head capsule is dorsally beige and has two darkly colored stripes along the frontoclypeal sutures (Fig. 10). All muscle scars are dark and well-defined. The anterior part of the frontoclypeal apotome has three pairs of small muscle scars and, just behind the constriction, it has four or five transversely arranged median muscle scars. Furthermore, several muscle scars are found posterolaterally on the parietal sclerites behind the eyes and along the coronal suture. In *A. bilineatus*, the dorsal surface of the head capsule (Fig. 12) is dark. The two stripes along the frontoclypeal sutures and the muscle scars are less visible on this darkly pigmented background than in *A. aterrimus*, *A. braueri*, and *A. cinereus*.

Dorsally, the head capsule of *A. braueri* (Fig. 14) is yellow or orange. According to the photographs of Vieira-Lanero (2000), colored stripes along the frontoclypeal sutures are lacking. As in *A. aterrimus* and *A. cinereus*, four or five median muscle scars are transversely arranged on the frontoclypeal apotome just behind its constriction. *Athripsodes braueri* has four muscle scars on the parietal sclerites along the frontoclypeal sutures and several posterolateral muscle scars on the parietal sclerites behind the eyes and along the coronal suture. In *A. cinereus*, the dorsal head capsule (Fig. 16) is pale beige. As in *A. braueri*, well-defined colored stripes along the frontoclypeal sutures are lacking. Instead, only a slightly darkened area is found close to the constriction zone of the frontoclypeal apotome. Only two pairs of small muscle scars are visible on the anterior third of the frontoclypeal apotome, and just behind its constriction, five muscle scars are transversally arranged. On the parietal sclerites, along the frontoclypeal sutures, there are four muscle scars on each side, the first one being smaller than the other three. Lightly pigmented muscle scars are found laterally on the parietal sclerites, behind the eyes, and along the coronal suture. Finally, the dorsal head capsule of *A. commutatus* (Fig. 18) most closely resembles that of *H. leucophaea* (Fig. 1), as both are yellow and pigmented patches or well-defined muscle scars are lacking.

The ventral apotome of *A. albifrons* (Fig. 9) is dark and has a rounded posterior apex. Ventrally, the parietal sclerites are darkly pigmented except for some less pigmented spots in the posterior part. In *A. aterrimus*, the ventral apotome (Fig. 11) is pale, except for a narrow dark anterior marginal stripe. It has a weakly rounded posterior apex. Ventrally, the parietal sclerites are beige with several dark muscle scars. *Athripsodes bilineatus* has a darkly pigmented ventral apotome with a clearly pointed apex (Fig. 13) that is most similar to that of *H. leucophaea* (Fig. 2). In contrast, the ventral parietal sclerites of *A. bilineatus* are also darkly pigmented and not yellow as in *H. leucophaea*. In *A. braueri*, the ventral apotome (Fig. 15) has a narrow dark anterior marginal stripe and the most rounded posterior apex of all seven species. The ventral parietal sclerites have a few posterior muscles scars. In *A. cinereus*, the ventral apotome is dark, forming an obtuse to rounded posterior apex (Fig. 17). Ventrally, the parietal sclerites are beige with weakly pigmented and elongated muscle scars. In *A. commutatus*, the ventral apotome is posteriorly rounded (Fig. 19) and it and the parietal sclerites are weakly pigmented. In comparison, *H. leucophaea* differs from all six Athripsodes species by the presence of a thickened anterior margin forming a roll on the ventral apotome and its acutely pointed posterior apex, making the ventral apotome look somewhat like a nail (Fig. 2).

All seven species have a small dark mark in the middle of the anterior part of the labrum. This mark is rounded and has no contact with pit P1 as seen in *A. aterrimus* (Fig. 20). In *A. bilineatus*, it is bean-shaped, either separated from (Fig. 21) or just abutting P1. In *A. albifrons*, *A. braueri*, *A. cinereus*, and *A. commutatus*, this mark is subtriangular and its posterior margin is invaginated around P1 (e.g., Fig. 22). This combination of features in the six *Athripsodes* species is not found in *H. leucophaea*, for which the labral mark is crescent-shaped and its posterior margin is not invaginated around P1 (Fig. 3).

Two discriminating features are found on the mesonotum: the pair of dark bars near the posterolateral projections of the mesonotum and the overall pigmentation pattern of the mesonotal sclerites. In *H. leucophaea*, *A. albifrons*, *A. braueri*, and *A. cinereus*, the dark bars have sharp contours (Figs 4, 23, 25, 26) and have anteriorly more or less curved diverging pale marks. In contrast, the dark mesonotal bars of *A. aterrimus* have a blurred contour and no anterior diverging pale marks (Fig. 24). Corresponding information is currently unavailable for *A. bilineatus* and *A. commutatus*. Overall, the mesonotal sclerites are weakly pigmented. They are orange and lightly pigmented anteriorly in *A. albifrons* (Fig. 23). *Athripsodes aterrimus*, *A. braueri and A. cinereus* have several muscle scars (Figs 24–26), whereas the sclerites are yellow and with no further underlying pigmentation in *H. leucophaea* (as shown in Fig. 4). Again, the overall mesonotal pigmentation is currently unknown for *A. bilineatus* and *A. commutatus*.

As in other leptocerids, the metanotum is membranous. In the posteromedian area, all but one of the discussed species have four setae projecting forward [indicated by arrows in Fig. 5 and termed *setal area* 2 (*sa*2) by Williams & Wiggins 1981]. In *A. albifrons*, the outer setae are less than half the length of the inner ones (Fig. 27). These outer setae are lacking in *A. aterrimus* (Fig. 28). The four setae have the same length in *H. leucophaea* (Fig. 5) as well as in *A. bilineatus*, *A. braueri*, *and A. cinereus* (Fig. 29). Finally, *A. commutatus* has outer setae more than half as long as the inner ones (Fig. 30).

All seven species have a longer spur at the distal apex on the tibia of each prothoracic leg (e.g., Figs 6, 31–34). Furthermore, *A. braueri* has four additional shorter spurs along the ventral margin of the tibia (Fig. 33) and both *A. cinereus* and *H. leucophaea* have one (sometimes two in *A. cinereus*) additional shorter spur on the ventral tibial margin (Figs 6, 34). On the interior surface of the trochanter and the distal section of the femur of the metathoracic leg, two or three irregular rows of short, dagger-shaped setae are found in *A. aterrimus* (Fig. 36). Such setae are lacking in the other six species (Fig. 35).

Homilia leucophaea would key with *A. cinereus* in the works by Wallace *et al.* (2003) and Waringer & Graf (2011) except that the head is yellow and the dorsal and ventral muscle scars are ill-defined in *H. leucophaea*, whereas the muscle scars are dark and well-defined in *A. cinereus*. Those works do not consider *A. braueri*. The following key will distinguish final instar larvae of *H. leucophaea* and the six *Athripsodes* species of France.



FIGURES 35–36. Left metathoracic legs of *Athripsodes* spp., larval instar V, interior views. (35) complete leg of typical *Athripsodes* spp., tr: trochanter; fe: femur; (36) trochanter of *Athripsodes aterrimus*.

Key to last instar larvae of H. leucophaea and the six Athripsodes species of France

1	Dorsal head surface with many dark round or oval spots (muscle scars) (Figs 10, 12, 14, 16)
-	Dorsal head surface either without dark round or oval spots or with ill-defined dark spots (Figs 1, 8, 18)
2	Ventral apotome pale, except near its anterior margin (Figs 11, 15)
-	Ventral apotome dark (Figs 13, 17)
3	Two posteromedian (sa2) setae on metanotum (Fig. 28) A. aterrimus
-	Four posteromedian (sa2) setae on metanotum (Fig. 29)
4	Posterior apex of ventral apotome clearly pointed (Fig. 13)
-	Posterior apex of ventral apotome rounded (Fig. 17) A. cinereus
5	Ventral apotome dark, with rounded posterior apex (Fig. 9) A. albifrons
-	Ventral apotome pale, with rounded or acute posterior apex (Figs 2, 19)
6	Prothoracic tibiae each with apical spur, but no additional spurs on ventral margin (e.g., Fig. 31); ventral apotome with rounded
	posterior apex (Fig. 19)
-	Prothoracic tibiae each with one short spur on ventral margin in addition to apical spur (Fig. 6); ventral apotome with acute
	posterior apex (Fig. 2)

Conclusions

With one exception, the species distribution of *H. leucophaea* was so far entirely based on records of adults. The present description of its larva increases the chance to rediscover *H. leucophaea* in countries where it is considered as extinct or critically endangered. For example, the recent rediscovery of larvae of *Calamoceras marsupus* Brauer 1865 in France after a last previous record in 1963 (Coppa & Tachet 2010) suggests that the situation for *H. leucophaea* also may be less critical than indicated by surveys of adult caddisflies.

The yellow head, the lack of pigmented muscle scars on the dorsal head surface, the yellow ventral apotome having a thickened anterior margin forming a roll and an acute posterior apex, the crescent-shaped anteromedian mark of the labrum not indented at P1, the one short spur on the ventral margin of each prothoracic tibia in addition to the apical spur, the two pairs of equally long *sa*² metanotal setae, and the absence of numerous short and orange setae interiorly on the hind trochanters and femora constitute a set of characters that is sufficient to identify the larva of *H. leucophaea*. Although some of these characters are found also in certain species of *Athripsodes*, their combination is found only in *H. leucophaea*.

Whereas the *H. leucophaea* larva shares several characters with the other species of *Athripsodes* larvae, *A. aterrimus* has several characters that are unique among French *Athripsodes* species. These are (1) the small, rounded anteromedian labral mark that is larger and differently shaped in the other French species; (2) the blurred contours of the posterolateral dark bars on the mesonotum that have sharp contours in the other species for which this character is known; (3) the lack of an outer pair of the posteromedian (*sa*2) metanotal setae that are present in

the other French species; and (4) the two or three irregular rows of short dagger-shaped setae on the interior surface of the trochanter and the distal section of the femur of each metathoracic leg that are lacking in the other French species. Thus, considering only the larva, *H. leucophaea* more closely resembles the other French *Athripsodes* species than does *A. aterrimus*.

So far, the discussion about the status of *Homilia* versus *Athripsodes* has considered only adults (e.g., Gibon 1991; Malm & Johanson 2011). Our revised description of the larva of *H. leucophaea* suggests a close relationship between *Homilia* and *Athripsodes*. However, we agree with the claim by Malm & Johanson (2011) that more species of both genera are needed to clarify the status of *Homilia*, to which we would add that not only adults of the Afrotropical Region, but also larvae and pupae of more species of both genera should be studied. This latter statement is clearly supported by disagreements and anomalies in larval characters of Afrotropical *Athripsodes* and *Homilia* species (De Moor 2002).

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