Revisional notes on *Rhithrodytes* BAMEUL 1989, with the description of a new subspecies and the introduction of *Rhithrodytes dorsoplagiatus* (FAIRMAIRE) as a valid species (Coleoptera, Dytiscidae)

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**Abstract:** *Rhithrodytes agnus* FOSTER has been recollected from in and around the type locality in the Minho region of northern Portugal. Originally described from two females, the male of the species is reported here for the first time, and confirmed as a member of the genus as defined by BAMEUL (1989). The species was also recorded from two localities in the nearby Serra de Arga, the populations from these sites differing sufficiently from those in the locus typicus to justify their recognition as a separate subspecies which is described here. The study of these populations has provided interesting information regarding the biology of *R. agnus*, and this is discussed in the context of the endemic Dytiscidae of the Northwestern Iberia and the differentiation of invertebrate populations in headwater streams. *R. agnus* would appear to be completely flightless, all specimens examined being strongly brachypterous, which is in marked contrast to the situation in the cogeneric *Rhithrodytes bimaculatus* (DUFOUR) and *Rhithrodytes sexguttatus* (AUBÉ). The opportunity is also taken to bring our understanding of the taxonomy of the genus up to date by reporting work which establishes *Rhithrodytes dorsoplagiatus* (FAIRMAIRE) of North Africa as a species distinct from the Pyrenean and North Iberian *R. bimaculatus*. The lectotype for *Hydroporus dorsoplagiatus* FAIRMAIRE is designated.

**Key words:** Coleoptera, Dytiscidae, *Rhithrodytes*, new subspecies, brachypterous species, lectotype.

1. Introduction

BAMEUL (1989) introduced the genus *Rhithrodytes* to include four species of hydrophiline dytiscid which had been referred to *Graptodytes* SEIDLITZ by earlier authors. The fact that these species represented a monophyletic group had been recognised by previous workers, for example ZIMMERMANN (1932), who saw them as closely allied to *Siettitia* ABEILLE de PERRIN, something also clear from BAMEUL'S (1989) phylogenetic analysis. *Rhithrodytes* and *Siettitia* are certainly closely related, showing progressive adaptations to interstitial life. As defined by BAMEUL (1989) *Rhithrodytes* included four species *R. crux* (FABRICIUS), *R. numidicus* (BEDEL), *R. sexguttatus* (AUBÉ) and *R. bimaculatus* (DUFOUR). The genus has a disjunct distribution pattern in upland areas around the West Mediterranean basin, in both Europe and North Africa, which probably resulted from vicariance events due to tectonic activity in the Miocene. Since the work of Bameul, FOSTER (1992) has described a further species...
of the genus, *R. agnus* from northern Portugal. Foster's original description was based on two females, but nonetheless clearly represented an additional taxon.

Visits to the type locality of *R. agnus* and further survey work by both authors has resulted in the discovery of more specimens and an additional three localities for this species, all of which are within about 10 km of each other, in the region between the rivers Minho and Lima. Sites are located in two areas to date, around Ponte de Lima and in the Serra de Arga. Populations from the latter area have been found to be sufficiently distinct to merit their recognition as a new subspecies, *R. agnus argaensis*, which is described here largely to draw attention to the fact that significant interpopulation differentiation is obviously occurring in this headwater species.

The fact that *R. bimaculatus* was apparently distributed in two disjunct areas as far apart as the Pyrenean/Cantabrian mountain systems and the mountains of Algeria has troubled us for some time, particularly since the other species of the genus appear to have rather compact and well-defined geographical ranges. Recently we have had the chance to study the North African material referred to *R. bimaculatus* in the Natural History Museum, Paris. All specimens had been considered to be females, since they lacked the expanded antennal segments characteristic of *R. bimaculatus*. Nevertheless these were dissected and two proved to be male, which in addition to the antennal character, showed significant differences from *R. bimaculatus* in the structure of the penis. We therefore conclude that *Rhithrodytes dorsoplagiatus* (FAIRMAIRE) is another distinct species of the genus, and offer a redescription of this taxon, including the male.

2. Material and acknowledgements

Collections from which we cite material are referred to in the text by the following abbreviations: coll. R. B. Angus, Egham (RA), coll. D. T. Bilton, Plymouth (DB), coll. H. Fery, Berlin (HF), coll. G. N. Foster, Ayr (GF), coll. J. Fresneda, Llesp, Lleida, Spain (JF), Muséum National d'Histoire Naturelle (Dr H. Perrin, Paris) (MNHN), Naturhistorisches Museum (Dr M. Jäch, Wien) (NHMW). Measurements are as follows: TL - total body length; MW - maximum body width. Unless otherwise stated the handwriting on museum labels is unknown.

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3. Systematics

The new subspecies and *R. dorsoplagiatus* both conform to the genus as defined by BAMEUL (1989), having pronotal striae that run almost the full length of the pronotum, and a downcurved tip to the penis.
Rhithrodytes agnus agnus FOSTER

Rhithrodytes agnus FOSTER 1992: 249.

Holotype: ♂, collected 5.1.1991, deposited in the Naturhistorisches Museum, Basel (Switzerland). Single paratype: ♀, with same dates in GF.

Type locality: Portugal, Viana do Castelo, Rio Labruja, 6 km N Ponte de Lima, ca. 275 m.


Descriptive notes: Habitus and coloration as described and figured by FOSTER (1992). Most of the specimens we have collected are considerably darker than figured by Foster. It should be noted, however, that Foster illustrated the elytral patterning of his specimen using transmitted light, and the appearance of the insect is considerably darker than in his figure. Dark specimens have the head more or less darkened, with two triangular pale spots between the eyes. If the elytra have a pale sutural stripe then the suture itself is darkened. In our darker specimens the whole elytra, including the area near the suture, are dark brown, except for a diffuse pale area near the apex and a pale marginal stripe, which can only be seen clearly in lateral view.

♂: Penis as in fig. 1; paramere fig. 2. Antennae simple, not expanded as in R. bimaculatus, the only species of the genus to show such a feature.

♀: Lacking significant structural differences.

Measurements: TL 2.35-2.7 mm, MW 1.2-1.3 mm, ratio of TL/MW 1.98-2.08. We have not studied the paratype, but according to FOSTER (1992) this is very large, with a TL of 2.95 mm and MW 1.39 mm, giving a TL/MW ratio of 2.12.

Distribution: Portugal, Minho; at present known only from the locus typicus and one nearby locality, both in the headwaters of the Rio Labruja.

Rhithrodytes agnus argaensis n. ssp.

Holotype: ♂, Portugal, Minho, NE Viana do Castelo, Serra de Arga, stream at 700 m. 17.3.1993, Bilton leg. (NHMW).

Paratypes: 2 ind., with same dates as the holotype; 6 ind., idem, 18.3.1993; 38 ind., idem. 5.5.1993; 1 ind., Portugal, Minho, NE Viana do Castelo, Serra de Arga, above Montario, stream at 400 m, Bilton leg.; 239 ind., idem, 30.1.1994; 12 ind., idem, 1.2.1994, Fery leg. (RA, DB, HF, JF).

Type locality: Portugal, Minho, NE Viana do Castelo, Serra de Arga. Small granite headwater stream at 700 m, flowing through scrub of Ulex, Cistus and Ericaceae.

Description: Habitus in general broader, more parallel and less tapering towards the apex than in the nominotypical subspecies. Colour generally dark brown, shining, with even microreticulation of small round or ovoid meshes. Head dark between the eyes, with two distinct dark spots. Between these is a pale triangular area which reaches to the anterior margin of the clypeus. Antennae yellow with the last three or four articles darkened distally. Pronotum yellow outside the longitudinal
striae; inside the striae dark brown with some diffuse paler areas near the striae and around the anterior and posterior margins. A row of larger punctures present behind the anterior margin. Area between the striae and lateral margin, and in front of the posterior margin (except centrally) also with some larger punctures. Rest of pronotum with fewer finer punctures which are almost absent on the disk. Elytra without any yellow patterning, almost totally dark brown, except for a yellow lateral margin, visible in lateral view only. This yellow margin narrowed near the shoulders and enlarged in the posterior two thirds. Sometimes indistinctly paler before the apex, especially near the suture. Microreticulation more impressed than on the head and pronotum. Each elytron with a single row of larger punctures on the disk, and a second row closer to the margin which is poorly distinct. The rest of the elytra more or less evenly punctured; punctures larger than on the disk of pronotum and head, generally less distinct and dense than in *R. agnus agnus*. Each puncture supplied with a short pale hair.

Ventral surface more shiny than dorsal. Underside of head yellowish brown; prosternum, metasternum, metacoxae and abdomen distinctly darker. Metacoxal process, first and last visible abdominal sternites slightly paler. Epipleura yellow. Metasternum (except on the middle), metacoxae and sternites microreticulate, the meshes being larger than those on the dorsum, and more transverse on the last visible abdominal sternite and more longitudinal on the first and second visible abdominal sternites and metacoxae. Metasternum with large punctures, metacoxae and abdomen less distinctly punctured. Pale hairs of punctures much longer than those on the elytra. Legs yellowish with the metafemora slightly darkened in some specimens.

♂: Penis as in fig. 3; paramere fig. 4. Outline of penis somewhat variable, as in *R. agnus agnus*, but with the tip consistently less deflexed.

♀: Lacking significant structural differentiation.

**Measurements:** TL 2.45-2.7 mm, MW 1.15-1.3 mm, ratio of TL/MW 2.04-2.17.

**Distribution:** So far recorded from two headwater streams in the Serra de Arga, between at 400 and 700 m. Interestingly these flow into different drainages, one being, like the Rio Labruja, a headwater of one of the northern tributaries of the Lima, the other flowing west into the Rio Ancora.

**Note:** Preliminary karyological investigations by R.B. Angus have failed to demonstrate significant differences between the two subspecies of *R. agnus* recognised here. This is quite expected for such a pair of taxa, however, which are obviously very recently separated, and more detailed genetic analysis would almost certainly demonstrate a clear separation of the two subspecies.

**Rhithrodytes dorsoplagiatus** (FAIRMAIRE) n. stat.

Hydroporus (Graptodytes) dorsoplagiatus Fairmaire, Seidlitz 1887: 61.
Hydroporus jucundus Perris, Régimbart 1895: 22.
Graptodytes numidicus Bedel, Zimmermann 1919: 183.
Rhithrodytes bimaculatus (Dufour), Bameul 1989: 489.

Lectotype (present designation): ♀, "212" [handwriting illegible], "dorsoplagiatus Fairm Alg" [handwriting Fairmaire], "Type" [red], "Muséum Paris, 1906, Coll. Léon Fairmaire" and our red lectotype label (MNHN).

Type locality: "Algérie" - Algeria.


Description: Habitus smaller and more parallel than R. bimaculatus, maximum width around the middle, whereas in R. bimaculatus this is before the middle. Less tapering towards the end of the elytra than R. bimaculatus (fig. 1 in Bameul 1989). Whole upper surface reddish yellow with a limited and diffuse weakly darker pattern which in principle resembles that of R. bimaculatus. Microreticulation much less impressed than in R. bimaculatus, making the surface appear more shining. Distinctly flatter in lateral view than R. bimaculatus. Head with fine punctures; darkened near the eyes and on the frons. Articles of antennae not darkened. Pronotum weakly darkened between the longitudinal striae. A row of larger punctures present behind the anterior margin, and another before the posterior margin, these being absent from the middle. Outside the longitudinal striae with some additional large punctures; the rest of the pronotum almost impunctate. Each elytron with two distinct rows of punctures which appear much more prominent than in R. bimaculatus, largely due to the less impressed microsculpture of R. dorsoplagiatus. Punctures between the rows are sparse but visible; whereas in R. bimaculatus these are hidden by the microsculpture. Elytral pattern very diffuse, similar to that of R. bimaculatus, with a broad discal band which is extended in a stripe backwards beside the suture and another parallel to the margin. These stripes are posteriorly extended, almost flowing together, and thus forming a paler spot behind the discal band. In this respect the pattern resembles that of R. numidicus and R. sexguttatus. A paler stripe close to the suture is always recognisable, however, as in R. bimaculatus and lighter specimens of R. agnus agnus.

Ventral surface shining, coloured as the dorsum, with the sides of the metasternum and first visible abdominal sternite weakly darkened. Microreticulation very weak, totally absent on the centre of the metasternum, metacoxae and metacoxal process. Puncturation of the metasternum and the first two visible abdominal sternites strong, weaker on the metacoxae and the rest of the abdomen.
Penis as in fig. 5; paramere as in fig. 6. Penis and paramere of *R. bimaculatus* shown for comparison (figs. 7-8). Antennae simple, unlike those of *R. bimaculatus* (see BAMEUL 1989). Elytra with additional rows of punctures beside the suture.

Additional rows of punctures beside the suture of elytra being absent in the females studied.

**Measurements:** Lectotype (♀): TL 2.85 mm, MW 1.35 mm; ♂: TL 2.7 mm, MW 1.35 mm; 2 ♀ measured: TL 2.7 mm, MW 1.3 mm.

**Distribution:** Known only from Algeria. The specimen labelled „Pyrénnées“ as *R. bimaculatus* in the Peschet collection is undoubtedly a case of mislabelling. The exact locality of the lectotype is unknown. One of the males and two females are from one locality, with another female from a separate site. The remaining two females and single male (mentioned above) either have illegible or incorrect locality data. It is therefore not possible to give precise information regarding the extent of the species' distribution in North Africa, and further collecting is urgently required in the region.

**Note:** It is interesting that *R. dorsoplagiatus* appears to be the sister species of *R. bimaculatus*, despite the wide geographical separation of these taxa. This situation is mirrored in the genus *Graptodytes*, *G. castilianus* FERY of northern Spain being the closest relative of the Tunisian and Algerian *G. pietrii* NORMAND (FERY 1995). These observations obviously point to a vicariance event between the Iberian and North African faunas during the evolution of the Mediterranean basin.

**Additional records of Rhithrodytes bimaculatus (DUFOUR)**

From the work conducted in the Paris museum we are able to add the following records to those in BAMEUL (1989). The species is, like the others of the genus, endemic to a limited region in southern Europe: the west Pyrenees and the Cantabrian mountains of northern Spain. Further collecting in the north of Spain would, we suspect, reveal a continuous pattern of distribution in mountain massifs from the Pyrenees to the Cantabrian chain.


**4. Observations on the biology of Rhithrodytes and its taxonomic status**

We have recently had the opportunity to make a number of interesting observations on the ecology and biology of members of the genus, particularly in the case of *R. agnus*. BAMEUL (1989) stated that the species of the genus were apparently re-
stricted to headwater streams and torrents in mountains, being characteristic of the rhithron, or upper reaches of rivers. He also pointed out based on observations in the French Pyrenees that *R. bimaculatus* appeared to have colonised the spring region at the very head of such torrents.

Whilst we would largely agree with such observations we would like to reemphasise that our knowledge of the ecology of the two north African species of the genus is practically non-existent. Additionally it should be noted that the Tyrrhenian endemic *R. sexguttatus*, is, on Corsica at least, widely distributed in gravelly streams and rivers from high mountain passes to sea level. The remaining European species do, on present evidence, appear to be headwater taxa, and all species appear to live interstitially in river gravels, especially where underflow from the hyporheic zone enters the stream along its banks.

The rather weak pigmentation and flattened appearance of most *Rhithrodytes* species does immediately suggest an adaptation to such a „semisubterranean“ existence. Such adaptations are paralleled by at least one species of the related genus *Graptodytes*, *G. fractus* SHARP, a species which also lives interstitially in the gravel of swift-flowing streams and rivers.

The description of the male of *R. agnus* further strengthens the separation of *Rhithrodytes* as a genus distinct from *Graptodytes*, since this species is confirmed to share the hooked tip of the penis present in all other species of the genus. *Rhithrodytes* and *Siettitia* are further separated from *Graptodytes* by the longitudinal striae of the pronotum, which run for its entire length in these two genera. On present evidence these two genera would appear to be sister groups, since in addition to the pronotal striae character they share the bent tip to the penis (BAMEUL 1989; RICHOUX 1978). What taxonomic status should be given to these groups appears to be unclear, however. BAMEUL (1989) in his cladistic analysis separates *Siettitia* from *Rhithrodytes* on the basis of a number of supposed synapomorphies: reduced pigmentation, reduced eyes, phreatobiotic ecology and the shape of the metacoxae in the latter, and the presence of transverse elytral pigment bands and an epigean lotic ecology in the former. In the case of the supposed synapomorphies of *Siettitia*, the first two characters result from the greater adaptation to subterranean life in the genus, which could therefore be seen simply as derived *Rhithrodytes* species which have penetrated further into endogean freshwater environments. Use of an ecological character (phreatic) in cladistic analysis is best avoided, since there is no way of telling whether this is a synapomorphic or homoplasic feature. The two supposed synapomorphies of *Rhithrodytes* also do not really stand up to closer scrutiny. The statement on their ecology is covered by the remarks given above, and the elytral patterning can now be seen to be variable in the genus, *R. agnus argaensis* often being almost black! Their darker pigmentation with respect to *Siettitia* is again a consequence of their „semisubterranean“ as opposed to endogean existence.

This all leaves the significance of the incised metacoxae of *Siettitia* (simple in *Graptodytes* and *Rhithrodytes*), which remains unresolved, however, meaning that, for the
moment we prefer to retain this as a genus separate from *Rhithrodytes*, despite the difficulties pointed out above.

*Rhithrodytes agnus* is known from two adjacent areas of northern Portugal. At all locations the beetles were collected from granitic gravel in small pools in headwater streams. *R. agnus* was found to be most abundant at the edges of pools, where hyporheic water apparently entered the stream bed. In the Serra de Arga the species was taken in numbers by disturbing the bank sides with the net, specimens apparently originating from interstitial spaces between stones and gravel in the bank face, as well as in the edges of the pools themselves. The single specimen from above Montaria was found in gravel in a small pool on a watercourse which earlier in the year had been observed to be completely dry, meaning that the species is obviously capable of retreating into interstitial water remaining below intermittent watercourses.

It is interesting, and surprising, that *R. agnus* occurs as two morphologically distinct forms in such close proximity to each other. This situation can largely be explained when one considers the dispersal abilities of the species, however. Three specimens of *R. agnus agnus* and 15 of *R. agnus argaensis* were examined for wing development and all were found to be extremely brachypterous, the wings lacking clear venation, and being strongly reduced beyond the carpal cell and intercubital plate (fig. 9). Such strong wing reduction means that the species is obviously incapable of dispersal by flight. For comparison the situation was investigated in ten specimens of *R. sexguttatus* from Corsica and two of *R. bimaculatus* from the Pyrenees, all of which possessed fully developed wings showing the normal hydroporine venation pattern (figs. 10-11). In addition the basalar and subalar wing discs which receive the large direct flight muscles are considerably smaller in *R. agnus*, a feature which is associated with the loss of capacity for flight (SPENCER SMITH 1964). Such wing reduction is rather rare in dytiscids, and is most often associated with endogean and interstitial lotic taxa (e.g. JACKSON 1956, 1958; LARSON & STOREY 1994; ORDISH 1976; WATTS 1982). With such reduced powers of dispersal it is not surprising that separate populations of *R. agnus* demonstrate morphological differences, since for such an immobile species each headwater system contains isolated populations between which there will be severely limited gene flow. ZERA (1981) in an analysis of genetic differentiation of gerrid populations showed that marked allozyme differentiation occurred over distances as short as 8 km in a largely flightless species, whereas such substructuring was not observed in a fully winged relative. In the case of stenotopic headwater taxa, such as *R. agnus* genetic drift in small isolated populations is likely to lead to continued accumulation of genetic differences over time, and may eventually lead to allopatric speciation. The situation is apparently similar to that reported for hydrobiid molluscs in drainages in SE Australia (PONDER et al. 1994), where different drainage systems were found to contain genetically distinct taxa which in many cases probably represent separate allopatric species.
Figs. 5-8 Penis in dorsal and lateral views, and the point in a view indicated by the arrow: 5: *Rhithrodytes dorsoplagiatus* (FAIRMAIRE); 7: *Rhithrodytes bimaculatus* (DUFOUR); left paramere: 6: *Rhithrodytes dorsoplagiatus* (FAIRMAIRE); 8: *Rhithrodytes bimaculatus* (DUFOUR).
Fig. 9: Hind wing and metatergum of *Rhithrodytes agnus argaensis* n. ssp. Note the reduced wing and very small pleural wing discs. Wing length is 1.5 mm.

Fig. 10: Hind wing and metatergum of *Rhithrodytes sexguttatus* (AUBÉ). Wing length is 2.55 mm.
Fig. 11: Close-up of wing base of Rhithrodytes sexguttatus (AUBÉ). Note the large pleural wing discs, indicated by the arrow.

The true status of R. agnus agnus and R. agnus argaensis could only be revealed by genetic investigations, but it would appear that these represent taxa on their way to speciation. Should populations of the species be found in other, separate headwater systems it is almost certain that they will represent yet other genetically and morphologically distinct forms.

It is important to consider this intraspecific biodiversity in such taxa, particularly from the point of view of conserving future biodiversity at the species level. Two other species of dytiscid have been described from adjacent areas of northern Portugal in recent years. One of these, Hydroporus brancoi ROCCHI (ROCCHI 1981) is now known from the Serra da Estrêla in central Portugal (FERY & HENDRICH 1988) through Galicia to the Picos de Europa in northern Spain. The species is characteristic of springs and boggy seepages at high altitude, and is abundant on the plateaux of the Serra de Arga, where the streams containing R. agnus argaensis originate. Hydroporus brancuccii FERY (FERY 1987) was, like H. brancoi, described from the Serra de Soajo, and has to date only been reported from a handful of localities between the rivers Minho and Lima (FOSTER 1989), to which we can add the following record: Spain, province Pontevedra, near Estancas, small streamlet on meadow, 12.8.1989 and 4.11.1989, Fery leg. Again this is a springwater species, being found in sites with silt substrates. Whether R. agnus occurs outside the area of northern
Portugal from which it is so far recorded can only be demonstrated by further survey work, especially early in the season. It is worth noting however that extensive collecting by DB in adjacent areas of Portugal and southern Galicia has failed to reveal this species, even in apparently suitable habitats, and it is possible that this beetle is endemic to a very limited region.

5. Zusammenfassung


Die Hinterflügel beider Subspezies weisen eine starke Reduktion auf, so daß diese als flugunfähig anzusehen sind. Dies läßt die Entwicklung beider Unterarten in zwei eng benachbarten Arealen verständlich erscheinen und ist Anlaß, die Biologie dieser und anderer für den Nordwesten der Iberischen Halbinsel endemischer Dytisciden im Rahmen der Differenzierung von wasserbewohnenden Invertebrata zu diskutieren.

Der Lectotypus für Hydroporus dorsoplagiatus FAIRMAIRE (Algerien) wird festgelegt, und es wird nachgewiesen, daß dieses Taxon nicht wie bisher üblich als Synonym des Rhithrodytes bimaculatus (DUFOUR) (Pyrenäen, Cantabrien) angesehen werden kann, sondern eine weitere valide Art der Gattung Rhithrodytes darstellt.

6. References


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