

# Evolution of the Juan Fernández diving beetle, *Rhantus selkirki* (Coleoptera, Dytiscidae)

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Here we provide evidence that confinement in Robinson Crusoe Island (located about 660 km west of continental Chile) over evolutionary time leads to strong morphological modifications in diving beetle (Dytiscidae) larvae. We analysed a large set of morphological larval characters for all currently recognised genera of Colymbetinae as a framework, to infer phylogenetic relationships within the large genus *Rhantus* Dejean, 1833 and, in particular, of the charismatic Juan Fernández diving beetle, *Rhantus selkirki* Jäch, Balke & Michat, 2015, comparing our results with a recent phylogeny of the Colymbetinae based on DNA sequence data. We suggest that adaptation to the island's particular habitats resulted in the reversal of certain characters of *R. selkirki* back to the plesiomorphic states. This may cause the species to be erroneously interpreted as more 'primitive' if only morphological characters are analysed. Confinement in the particular, shallow and barely vegetated aquatic habitats of Robinson Crusoe Island for a long time seems to have led to this divergent morphology, particularly in characters related to swimming ability such as several leg and urogomphal setae. In this way, *R. selkirki* larvae secondarily resemble those of some earlier diverging dytiscid lineages such as Agabinae and Copelatinae, which typically creep on the bottom of water bodies and do not swim well.

## 1 | INTRODUCTION

The Juan Fernández archipelago, famous for inspiring English writer Daniel Defoe for his fictional novel Robinson Crusoe, is made up of three islands (Robinson Crusoe, Alejandro Selkirk, and Santa Clara) and several small rocky islets that lie at 33° south latitude and between 570 and 720 km west of the Chilean coast in the South Pacific (Haberle, 2009).

The islands are of volcanic origin, forming over a hotspot that underlies the eastward drifting Nazca plate. Radiometric dating of basalts gives ages of approximately four million years for Robinson Crusoe Island and its small western neighbour Santa Clara, which probably were connected at one time, and one to two million years for Alejandro Selkirk Island, which is 150 km farther west (Stuessy, Foland, Sutter, Sanders, & Silva, 1984). These islands have a limited fauna,

with no native mammals, reptiles, or amphibians. Insects, however, are diverse and have evolved extensive adaptations to island ecosystems, reflected in about 70% of endemics, which is comparable to endemism within the flowering plants (Stuessy, Crawford, & Marticorena, 1990). The majority of these species are derived from southern Chile, with some Pacific and Indo-Malaysian elements present (Haberle, 2009).

Diving beetles (Dytiscidae) represent one of the most extensive radiations among aquatic coleopterans (Hunt et al., 2007), inhabiting practically every fresh water environment (Balke & Hendrich, 2016). They are well represented on islands (some of them remote) throughout the world, suggesting that members of this family are good dispersers, either by active flight or, e.g., by wind drift. Juan Fernández Islands, in particular, have been reached at least three times independently by dytiscids, with two reported colonisation events in Robinson Crusoe Island by members of the subfamily Colymbetinae: *Rhantus selkirki* Jäch, Balke & Michat, 2015 and *Rhantus signatus kuscheli* Guignot, 1952 (Morinière et al., 2015), and one in Alejandro Selkirk Island by members of the subfamily Lancetinae: *Lancetes backstromi* Zimmermann, 1920. All three species are endemic giving 100% of endemism for diving beetles, although curiously, and contrary to other groups of insects (see Kuschel, 1952 and derived papers) and to flowering plants (Stuessy, Marticorena, Rodríguez, Crawford, & Silva, 1992), they have not radiated on the islands (assuming there were no extinctions).

Adults of the two dytiscid species inhabiting Robinson Crusoe Island have been known for a long time (Guignot, 1952; Zimmermann, 1924). They are very different from each other morphologically, to such degree that were first described in different tribes within Colymbetinae. One of them, *R. selkirki*, exhibits a disparate morphology with respect to the typical dytiscid body shape, including a cordiform pronotum and less modified legs, thus somewhat resembling a ground beetle (Carabidae) (Michat & Balke, 2013). This species was formerly known as *Anisomeria bistrinata* Brullé, 1835 and included in its own tribe, Anisomeriini, together with the Atlantic Tristán da Cunha endemic *Senilites tristanicola* Brinck, 1948; with no clear affinities within Colymbetinae (Brinck, 1948). Based on molecular data, however, Morinière et al. (2015) suggested that these taxa and *R. signatus kuscheli* are actually more closely related than originally thought, all belonging to the widespread genus *Rhantus* Dejean, 1833, and in particular to the Neotropical *Rhantus signatus* species group.

Larvae of these two colymbetine species remained unknown until Michat and Balke (2013) reported their finding in an expedition to Robinson Crusoe Island performed few years ago. Larval morphology, however, remained

unexplored as that paper focused on ecological and conservation aspects of the species. Study of these larvae, in particular of those of *R. selkirki*, would be of the utmost interest to explore an additional signal for clarifying the taxonomic position of this taxon, given the deviating morphology exhibited by adults. This would also allow to test previous phylogenetic hypotheses on the position of these taxa based on molecular and adult morphological characters.

Here we present a comprehensive phylogenetic analysis of the Colymbetinae based on larval characters, aimed to (i) test monophyly of the subfamily and of its largest genus, *Rhantus*; (ii) evaluate previous phylogenetic hypotheses on intergeneric relationships; and (iii) place the Juan Fernández diving beetles, in particular the enigmatic species *R. selkirki*, and document its remarkable morphology.

## 2 | MATERIAL AND METHODS

### 2.1 | Taxon sampling

The phylogenetic analysis provided here is mainly devoted to study the relationships of the Juan Fernández endemic diving beetles *R. signatus kuscheli* and *R. selkirki*. This was accomplished by using a cladistic approach and considering the character set provided by the larval morphology and chaetotaxy. Forty-four dytiscid species were included in the analysis. The ingroup consisted of 26 species of Colymbetinae in all currently recognised genera except the South Africa endemic *Caperhantus* Balke, Hájek, & Hendrich, 2017; which represents a comprehensive sampling, considering that larvae of many species of this subfamily are still unknown. An extensive sampling of outgroup taxa was included, consisting of 18 species in eight of the remaining 10 subfamilies, with the purpose of allowing the target taxa to move freely, thus testing relationships in a broadest possible context. Hydrodytinae could not be included because their larvae are unknown, and Cybistrinae was excluded because, although recent studies based on molecular data (Miller & Bergsten, 2014; Ribera, Vogler, & Balke, 2008) suggested subfamily status, morphological evidence strongly suggests its subordinate position as a tribe of the subfamily Dytiscinae (Michat, Alarie, & Miller, 2017; Miller, 2000, 2001). Previous papers have suggested that the subfamily Matinae represents the sister group of the remaining Dytiscidae (Miller, 2001). Therefore, *Matus bicarinatus* (Say, 1823) was selected to root the tree. Data for most species were scored directly from the observation of the specimens, whereas data for *Melanodytes pustulatus* (Rossi, 1792) were scored from the literature (De Marzo, 1974; Nilsson, 1988; Nilsson & Hilsenhoff, 1991). All instars of each species were observed for character coding,

except *Bunites distigma* (Brullé, 1837) and *Carabdytes upin* Balke, Hendrich & Wewalka, 1992 of which only the first and third instars were available, respectively.

## 2.2 | Methods

The specimens were cleared in lactic acid, dissected, and mounted on glass slides in polyvinyl-lacto-glycerol. Microscopic examination at magnifications up to 1,000× and drawings were made using an Olympus CX31 (Olympus Corporation, Tokyo, Japan) compound microscope equipped with a camera lucida. Drawings were scanned and digitally inked using a Genius PenSketch tablet (KYE Corporation, Taipei, Taiwan). Voucher specimens are deposited in the collection of the Laboratory of Entomology (Buenos Aires University, Argentina).

The methods and terms used in the morphometric and chaetotaxic analyses follow those employed in previous papers dealing with the larval morphology and chaetotaxy of members of Colymbetini. The reader is referred to Michat (2005), Alarie and Hughes (2006) and Alarie, Michat, Nilsson, Archangelsky, and Hendrich (2009) for a complete list and additional explanations of the terms used in the present study. Setae and pores present in first-instar larvae were labelled using the ground plan of chaetotaxy of the genus *Rhantus* (Alarie et al., 2009). Homologies were determined by using the criterion of similarity of position (Wiley, 1981). Setae located on the apices of the maxillary and labial palpi were extremely difficult to distinguish due to their position and small size, and, therefore, they are not well represented in the drawings.

## 2.3 | Phylogenetic procedure

All characters were treated as equally weighted. Multistate characters were treated as non-additive. The data matrix was analysed using the program TNT (Goloboff, Farris, & Nixon, 2008). Three search strategies were implemented to find the most parsimonious trees: (i) a common heuristic search under 'Analyze/Traditional search', using 'tree bisection reconnection' (TBR) as algorithm, with 200 replicates and saving 100 trees per replication, previously setting 'hold 20000'; (ii) a search involving additional heuristics, with 100 random addition sequences and TBR followed by 'tree drifting', using the commands 'hold 20000' and 'mult 100 =tbr drift ;'; and (iii) 100 random addition sequences and TBR followed by 'ratchet', using the commands 'hold 20000' and 'mult 100 =tbr ratchet ;'. Bremer support values were calculated using the commands 'hold 20000', 'sub n', and 'bsupport', where 'n' is the number of extra steps allowed. The process was repeated increasing the length of the suboptimal cladograms by one step until 10 (Kitching, Forey, Humphries, & Williams, 1998). Bremer support values higher than 10 are

indicated by the symbol '>10'. Bootstrap values were calculated using the following parameters: 'standard (sample with replacement)'; 1,000 replicates.

## 3 | RESULTS

### 3.1 | List of characters

In total, 144 characters derived from larval morphology and chaetotaxy were included, of which 112 were coded as binary and 32 as multistate. They are listed in Table S1.

### 3.2 | Results of the parsimony analysis

The resulting data matrix is shown in Table S2. The searches with TNT using different parameters (see Material and methods) converged to 12 equally most parsimonious trees of 421 steps (CI = 0.44; RI = 0.73). The trees differed in the relative positions of some Agabinae taxa and in the relative positions of *Carabdytes* Balke, Hendrich & Wewalka, 1992, *Colymbetes* Clairville, 1806 and some *Meridiorhantus* Balke et al., 2017 species (*M. calidus* (Fabricius, 1792), *M. orbignyi* (Balke, 1992), *M. antarcticus nahueli* (Trémouilles, 1984), *M. validus* (Sharp, 1882)). The strict consensus (of similar topology in the three analyses) was calculated, in which both *R. selkirki* and *R. signatus kuscheli* are resolved in a derived position within Colymbetinae, closely related to other species of *Rhantus* (Figure 1). The support was generally weak for the ingroup, although Colymbetinae and some internal clades showed somewhat increased values. Characters were mapped in one of the most parsimonious cladograms (Figure 2).

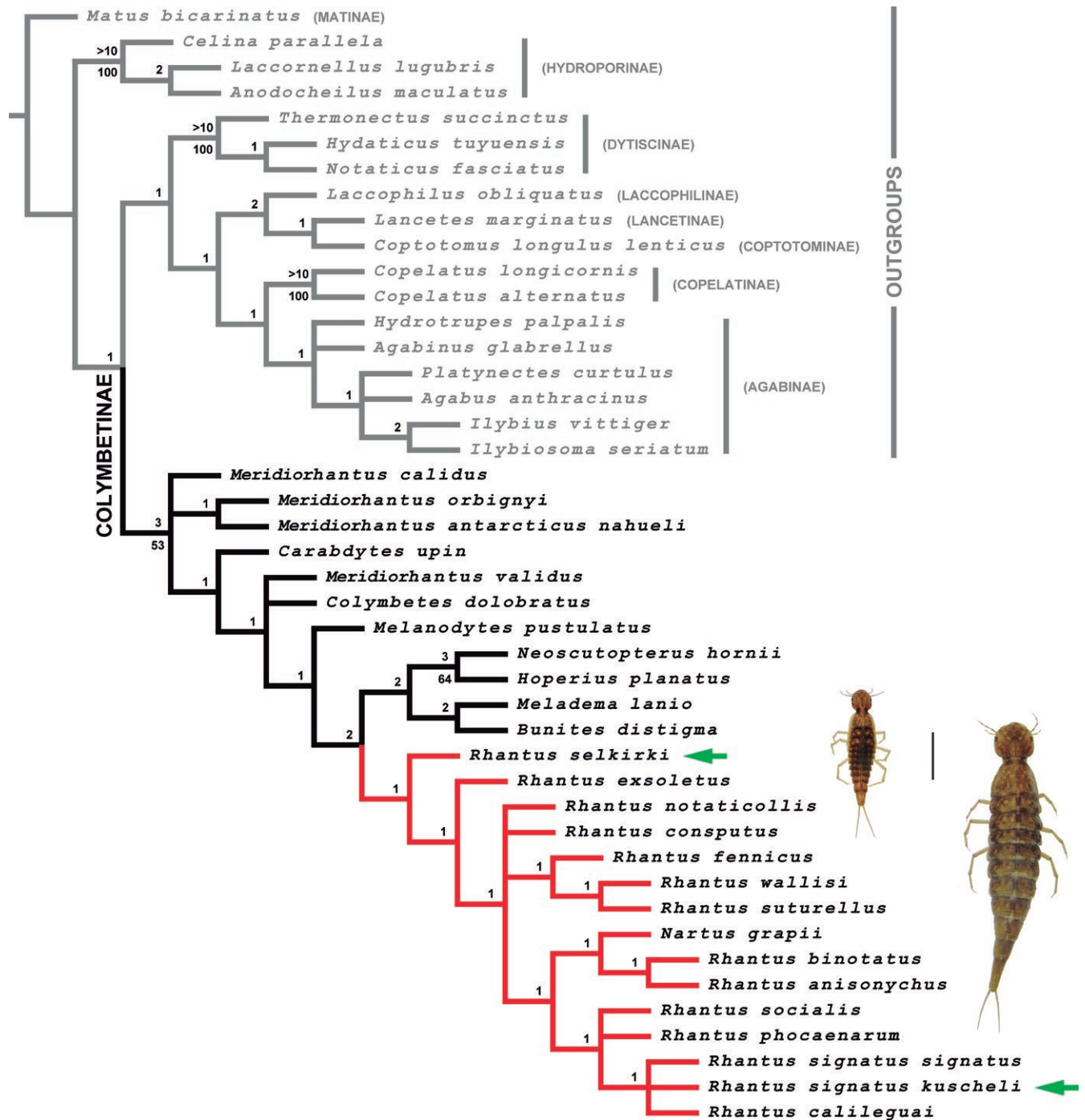
### 3.3 | Diagnoses of diving beetle larvae of Robinson Crusoe Island

#### 3.3.1 | *Rhantus selkirki* Jäch, Balke & Michat, 2015 (Figures 3a,c, 4a,c, S1a,c, S2a,b,c,d,e,f, S3a,b, S4a,b,e, S5a,c)

Diagnosis and full description of this species are provided in File S1 and Tables S3 and S4.

#### 3.3.2 | *Rhantus signatus kuscheli* Guignot, 1952; (Figures 3b,d, 4b,d, S1b,d, S2g,h,i,j,k, S3c,d, S4c,d,f, S5b,d)

Diagnosis of this species is provided in File S2 and Tables S3 and S4. As larvae of *R. signatus kuscheli* are morphologically very similar to those of *R. signatus signatus* (described in detail by Alarie et al., 2009), no full description is provided here.



**FIGURE 1** Strict consensus cladogram obtained from the cladistic analysis, with Bremer support values indicated above branches and Bootstrap values higher than 50 indicated below branches. Green arrows indicate position of species endemic to Robinson Crusoe Island (pictures). Scale bar = 1.5 mm

### 3.4 | Key to diving beetle larvae of the Juan Fernández archipelago

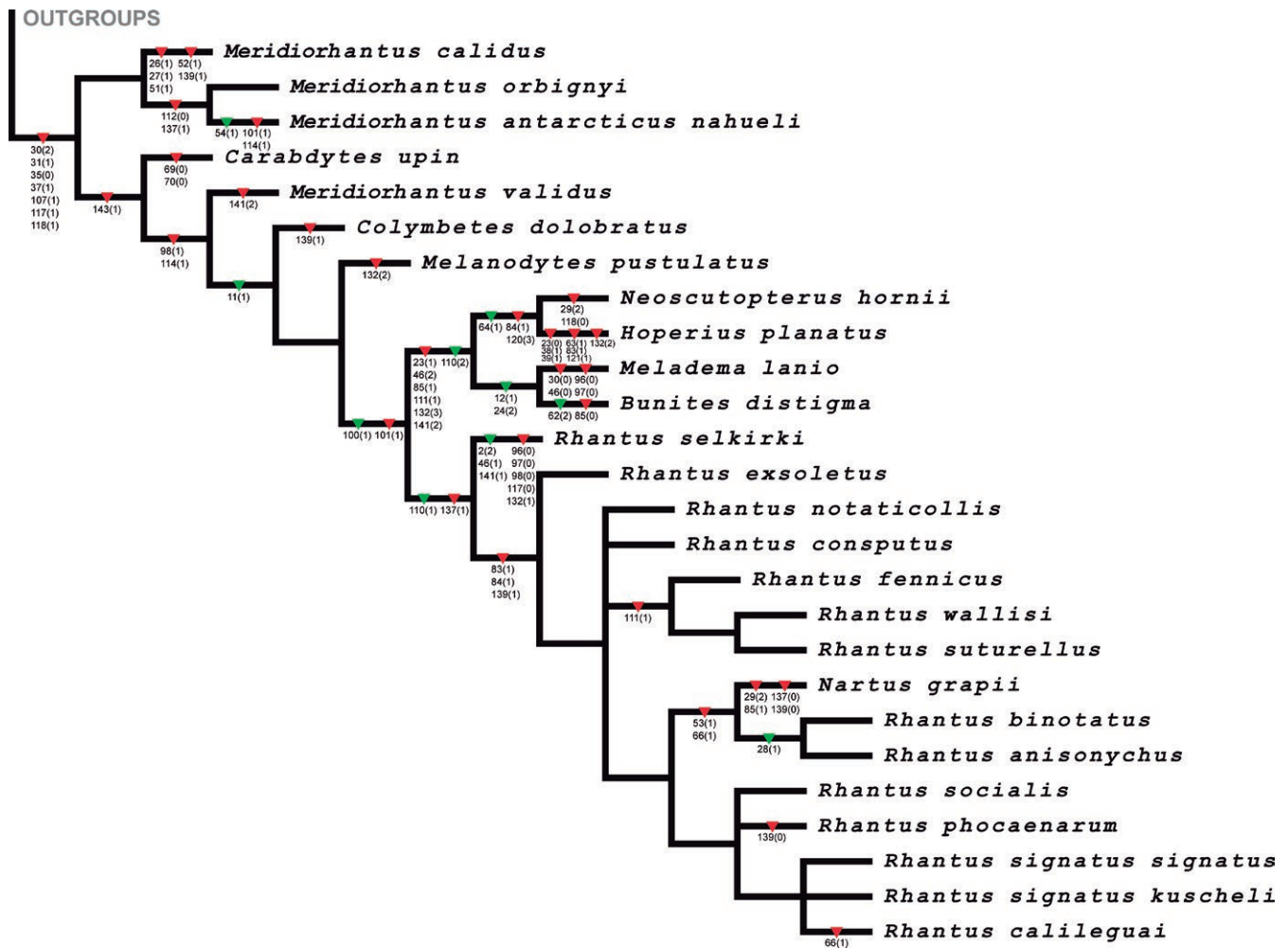
The key (File S3) applies to all instars. As larvae of *Lancetes backstromi* were not studied, it is assumed that they lack an occipital suture, similarly to all other known *Lancetes* Sharp, 1882 larvae. Geographic information can also be used with confidence to identify this species, as it is the only known dytiscid inhabiting Alejandro Selkirk Island.

## 4 | DISCUSSION

### 4.1 | Phylogeny of Colymbetinae

The subfamily Colymbetinae is monophyletic in our analysis, in agreement with previous studies based on various data sets (Beutel, Ribera, & Bininda-Emons, 2008; Burmeister, 1990; Michat et al., 2017; Miller, 2001; Miller & Bergsten, 2014; Morinière et al., 2016; Ribera, Hogan,





**FIGURE 2** Portion of one of the 12 most parsimonious cladograms obtained from the cladistic analysis, with selected character state changes mapped for each clade (using ACCTRAN optimisation). Green triangles indicate unique character state transformations; red triangles indicate homoplasious character state transformations

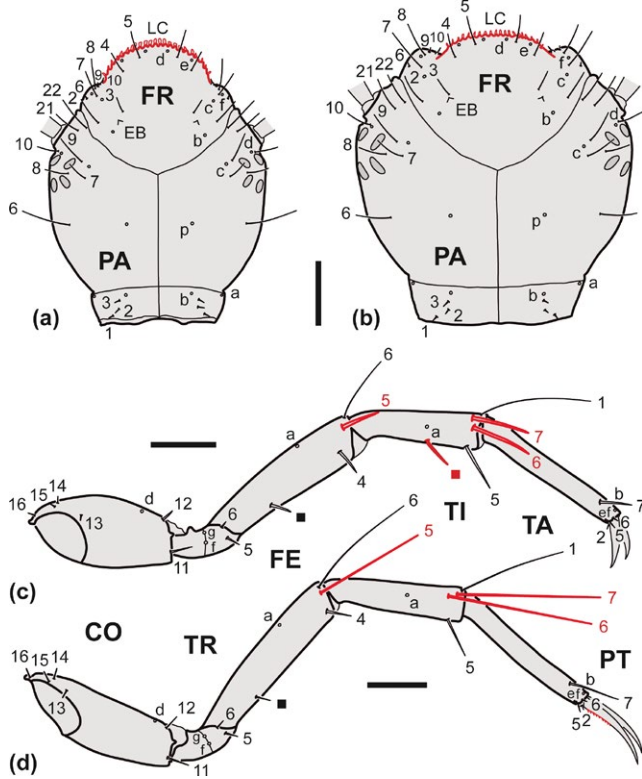
& Vogler, 2002; Ribera et al., 2008). The support obtained was moderate (Figure 1), and no unambiguous synapomorphies were discovered (Figure 2). The group, however, is well supported by several characters including: apical lateroventral process of antennomere 3 not protruding (Figure S2c,h; ch. 30.2); antennomere 4 subequal or somewhat longer than antennomere 3 (Figure S2b,c,g,h; ch. 31.1); pore ANg inserted submedially on antennomere 4 (Figure S2b,g; ch. 35.0); basoventral spinulae on claws present (Figures 3d, S1d; chs. 117.1, 118.1).

Our study supports the exclusion of several species from *Rhantus*, as recently proposed based on molecular data (Balke et al., 2017; see also Morinière et al., 2016). According to our results, the genus *Rhantus* as conceived previously to Balke et al. (2017) was paraphyletic with respect to all other colymbetine genera, with species currently in *Meridiorhantus* resolved at the base of the Colymbetinae. Larvae of *Meridiorhantus* exhibit several distinctive features

within Colymbetinae (Alarie et al., 2009; Michat, 2005; Nilsson & Hilsenhoff, 1991), but these features optimise as plesiomorphic in our study, confirming their primitive nature. The clade Colymbetinae exclusive of these species plus *Carabdytes upin* is defined by one unambiguous synapomorphy: the presence of the pore FRe on the frontoclypeus (Figure 3a,b; ch. 11.1).

The remaining species of *Rhantus* and *Nartus grapii* (Gyllenhal, 1808) are a monophyletic unit. However, we consistently recovered *Rhantus* paraphyletic by *Nartus* Zaitzev, 1907, contradicting Balke et al. (2017) who recovered both taxa as sister groups.

We found some evidence for a clade comprising the genera *Neoscutopterus* J. Balfour-Browne, 1943, *Hoperius* Fall, 1927, *Meladema* Laporte, 1835, *Bunites* Spangler, 1972, *Nartus* and *Rhantus*, in agreement with Michat et al. (2017). The support obtained for this grouping, as well as for its internal nodes, was weak, with the possible exception of a moderately supported



**FIGURE 3** *Rhantus* spp., cephalic capsule and leg of first-instar larva. (a) *R. selkirki*, cephalic capsule, dorsal aspect; (b) *R. signatus kuscheli*, cephalic capsule, dorsal aspect; (c) *R. selkirki*, right metathoracic leg, posterior aspect; (d) *R. signatus kuscheli*, right metathoracic leg, posterior aspect. Numbers and lowercase letters indicate primary setae and pores, respectively. Solid squares indicate additional setae. Remarkable differences between species are represented in red. Scale bars = 0.20 mm. CO, coxa; EB, egg burster; FE, femur; FR, frontoclypeus; LC, lamellae clypeales; PA, parietal; PT, pretarsus; TA, tarsus; TI, tibia; TP, tentorial pit; TR, trochanter

clade *Neoscutopterus* + *Hoperius*. The clade *Rhantus* + *Nartus* is recovered as sister to the other genera, but relationships within this group are not fully resolved and in general weakly supported, suggesting that a more comprehensive taxon and character sampling are required.

## 4.2 | Phylogenetic placement of Robinson Crusoe Island diving beetles

Both molecular (Morinière et al., 2015, 2016) and morphological datasets agree that *R. selkirki* belongs to *Rhantus*, although arguably our analysis posits this species as sister to all other species in this clade, thus giving room for exclusion. The *Rhantus* clade (including *Nartus*) is supported by one unambiguous synapomorphy: the presence of a single additional anteroventral seta on the meso- and metatarsus in instar I (Figure 2; ch. 110.1). The presence of a basal suture on the urogomphus (ch. 137.1) gives some support to this group, although it is also

present in some basal colymbetine lineages and absent in *Nartus gapii*.

Molecular results support the inclusion of *R. selkirki* in the Neotropical *R. signatus* group (Morinière et al., 2015, 2016). Our analysis contradicts this assertion, although arguably our result is weakly supported compared to the robust *R. signatus* clade obtained based on molecules. The hypothesis suggested by DNA sequence data, therefore, is considered more plausible.

*Rhantus selkirki* is characterised by the following larval autapomorphies: anterior margin of the frontoclypeus projected forward into short nasale (Figures 3a, S5a; ch. 2.2); presence of a single additional seta on mandible, contiguous to pore MNc (Figure S2f; ch. 46.1); and presence of a single additional seta on the basal half of urogomphus (Figure S4e; ch. 141.1). The presence of a short nasale is noteworthy and reminds, although with differences in shape, that found in the Hydroporinae, highlighting the strongly modified morphology of this taxon (see below). Another interesting feature of *R. selkirki* larvae is the presence of a single additional seta on the dorsolateral surface of abdominal segment VIII (Figure S4a; ch. 132.1), unique within Colymbetinae, but convergent with *Platynectes curtulus* (Régimbart, 1899) (Agabinae).

Larvae of *R. signatus kuscheli* are morphologically very similar to those of the continental subspecies, *R. signatus signatus*, at the point that we were unable to find reliable morphological differences between them. Both taxa are resolved as sisters in our analysis (Figure 1), in agreement with molecular data (Morinière et al., 2015, 2016).

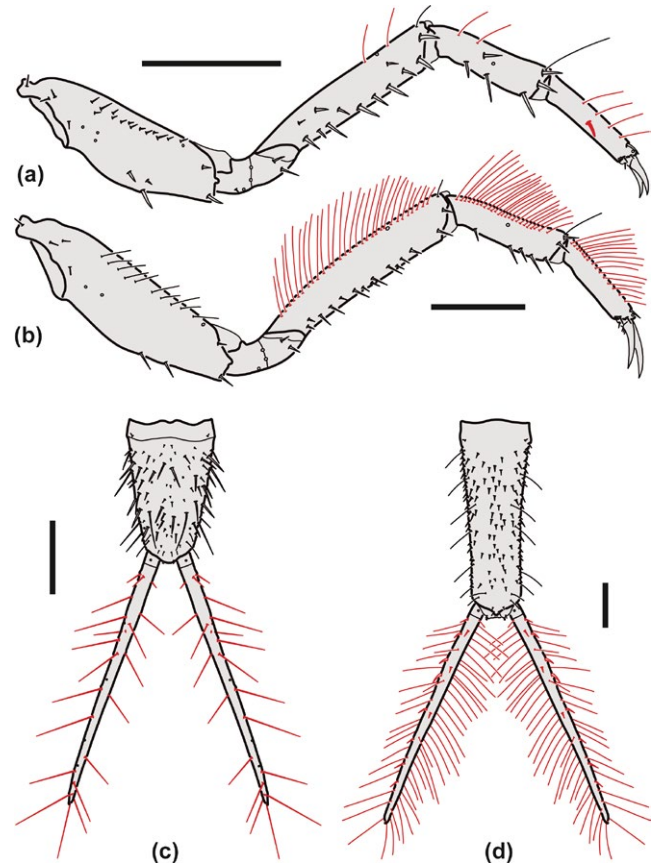
## 4.3 | Morphological evolution vs. molecular evidence

Above we favoured the molecular estimate over the morphology-based estimate regarding the position of *R. selkirki*. It would be interesting, however, to address the question why morphological and molecular analyses are incongruent in the position of this taxon. One possible reason is our limited taxon sampling within *Rhantus* compared to Morinière et al. (2015, 2016). Even though we are providing a comprehensive sampling for the genus, larvae of many species are still unknown, which may have a negative impact on the results. Undersampling of taxa, and its consequent decrease in support measures, is a common cause of incongruence between molecular and morphological phylogenies (Hillis & Wiens, 2000).

Another, more interesting explanation for the incongruence in the position of *R. selkirki* is morphological divergence from the generic larval ground plan. Morphological differences of this species with other *Rhantus* are remarkable, the most obvious at first sight being size of larva and consequently adult (Figure 1). Whereas most *Rhantus*

species (and colymbetines in general) have a medium to large size, *R. selkirki* (c. 6.5 mm as adult beetle) apparently undergone a process of reduction, to the point that it is among the smallest members of the subfamily, along with few South Pacific island species. Other larval features of *R. selkirki* seem to have experienced a reversal to the plesiomorphic condition found in putatively more primitive dytiscid lineages such as Copelatinae, Agabinae, and Hydroporinae (Michat et al., 2017). The tibial setae TI6 and TI7 (Figure 3c; chs. 96.0, 97.0, 98.0) have recovered a short and spine-like condition, and the claws of the first instar have lost the basoventral spinulae typical of the Colymbetinae (Figures 3c, S1c; ch. 117.0). Second and third instars have strongly reduced spinulae on the claws, although not completely absent. Also, if *R. selkirki* is considered part of the *R. signatus* clade, the meso- and metafemoral seta FE5 has also adopted a short and spine-like (ancestral) condition (Figure 3c; chs. 83.0, 84.0). Another interesting character worth to discuss here are the natatory setae. Dense fringes of natatory setae on the posterodorsal surface of femora, tibiae, and tarsi of instars II and III are widespread within Colymbetinae (Figure 4b). Larvae of *R. selkirki*, however, bear a much reduced number of these setae compared to other *Rhantus* species (Figure 4a; Table S4). Although we have coded these characters (90, 106, and 115) as apomorphic for *R. selkirki*, they are likely in a process of reversal to the plesiomorphic condition (i.e., absence of natatory setae) found in earlier diverging lineages. A similar argument can be applied to the secondary setae on the urogomphus of later instars. A considerable reduction in the number of these setae took place in *R. selkirki* with respect to other *Rhantus* species (compare Figures 4c and 4d).

All these reversals, and the consequent evolutionary convergence with several outgroup taxa, may cause *R. selkirki* to drift towards the root in our tree. To test this hypothesis, we reanalysed our data matrix coding characters 83, 84, 96, 97, 98, and 117 as apomorphic (i.e., state 1) for *R. selkirki*. As a result, the number of equally most parsimonious trees increased from 12 to 20, with 12 of these trees showing *R. selkirki* in the same position as above (i.e., sister to the remaining *Rhantus* plus *Nartus*, Figure 1) and the remaining eight trees recovering this taxon deeply nested within a paraphyletic *Rhantus* with respect to the genera *Neoscutopterus*, *Hoperius*, *Meladema*, *Bunites* and *Nartus*. The resulting strict consensus is therefore highly polytomous, with half of the *Rhantus* species (including *R. selkirki*) forming a basal polytomy within the clade mentioned above. This indicates, although not conclusively, that the reversal of several characters to the plesiomorphic condition may cause *R. selkirki* to drift backward in the tree, and to be erroneously interpreted as more primitive, thus obscuring its true phylogenetic position.



**FIGURE 4** *Rhantus* spp., leg and terminalia of third-instar larva. (a) *R. selkirki*, right prothoracic leg, posterior aspect; (b) *R. signatus kuscheli*, right prothoracic leg, posterior aspect; (c) *R. selkirki*, abdominal segment VIII and urogomphi, dorsal aspect; (d) *R. signatus kuscheli*, abdominal segment VIII and urogomphi, dorsal aspect. Remarkable differences between species are represented in red. Scale bars = 0.50 mm

#### 4.4 | Possible causes for the morphological divergence of *Rhantus selkirki*

Interestingly, none of the morphological reversals mentioned above for larvae of *R. selkirki* are observed in the other inhabitant of Robinson Crusoe Island and putatively closely related (Morinière et al., 2015, 2016) *R. signatus kuscheli*, raising the question what are the underlying causes for these notable morphological differences. According to Morinière et al. (2015), both taxa derived from mainland South American ancestors belonging to the *R. signatus* group. Therefore, both likely were very similar morphologically when they arrived to the island. The colonisation event leading to *R. selkirki*, however, took place much earlier than the colonisation event derived in *R. signatus kuscheli* (Morinière et al., 2016). Under this scenario, we suggest that the divergent morphology currently observed in larvae of this species is due to longer-term confinement (and consequent adaptation) in the particular habitats of Robinson Crusoe Island.



This hypothesis, however, requires that aquatic habitats exploited by the island population differ from those typically used by the continental ancestors, thus leading to the selection pressure required for evolution. Currently, aquatic habitats on the island are rather homogeneous, consisting mainly of small shallow creeks (Michat & Balke, 2013). Extant members of mainland South American *Rhantus*, however, seem to be mainly inhabitants of lentic water bodies, more profound and with more abundant aquatic vegetation than the island environments. *Rhantus signatus signatus*, for example, is characteristic of such habitats all throughout Southern South American plains up to moderate altitudes (Fontanarrosa, Torres, & Michat, 2004; Torres, Mazzucconi, & Michat, 2007; Torres, Mazzucconi, Michat, & Bachmann, 2008; M.C. Michat, pers. obs.), whereas *Rhantus calileguai* Trémouilles, 1984 is commonly collected from lentic or very slowly flowing, vegetated habitats at altitudes over 1,500 masl in the Argentinean Yungas (M.C. Michat, pers. obs.). We were unable to find such 'typical' lentic habitats in Robinson Crusoe Island in a one-week sampling performed few years ago (Michat & Balke, 2013). The only 'lentic' environments we detected were slow current zones along the creeks, and artificial, man-made containers. In both kinds of habitats, we were able to collect adults and larvae of *R. selkirki*, confirming Zimmermann's (1924) note that the species inhabited still water zones along the creeks.

It is therefore likely that confinement in the particular aquatic habitats of Robinson Crusoe Island for a long time led to the evolution of the divergent morphology of *R. selkirki*. Interestingly, most characters showing reversals to the putatively plesiomorphic conditions are related to swimming ability. Long setal fringes on the legs, abdomen, and urogomphi are commonly associated with an increased performance in swimming and are characteristic of several dytiscid groups (Galewski, 1971; Michat et al., 2017). The shortening of several leg setae and the disappearance of most natatory setae on the legs and urogomphi can therefore be associated with the loss of swimming ability by larvae of *R. selkirki*, likely driven by the particular, shallow and barely vegetated aquatic habitats of the island. In this way, *R. selkirki* larvae secondarily resemble those of the subfamilies Agabinae and Copelatinae, which typically creep on the bottom of water bodies and have reduced, if any, swimming ability (Galewski, 1971). Additionally, as mentioned above, the considerable reduction in body size currently observed in *R. selkirki* makes it comparable to an Agabinae or Copelatinae, and was also likely canalised by niche requirements.

*Rhantus signatus kuscheli*, on the other hand, seems to be a relatively recent coloniser, and its morphology was still not affected by the selection pressure imposed by the aquatic habitats of the island. Alternatively, this species

may exploit a different ecological niche than *R. selkirki*, as both species were collected together in only one of seven visited sites (Michat & Balke, 2013), which may have been incidental.

## 5 | CONCLUSIONS

Here we provide empirical evidence that confinement in Robinson Crusoe Island over evolutionary time led to strong morphological modifications in diving beetle larvae. Adaptation to the island's particular habitats may have resulted in evolution of certain characters back to the plesiomorphic states. This may cause the taxon in question (*R. selkirki*) to be erroneously interpreted as more primitive if only morphological characters are analysed. Although not implemented in the present paper, our results highlight the importance of molecular methods in the phylogenetic reconstruction of groups with morphologically highly divergent lineages.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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