




Subgeneric classification of the bee genus *Rediviva* Friese (Hymenoptera: Apiformes: Melittidae)



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Abstract

For the first time a subgeneric classification of the oil-collecting bee genus *Rediviva* is presented. Five subgenera comprising 33 species are recognized based on morphological characters. Three of them are described as new: *Deriviva* **subgen. nov.**, *Albiviva* **subgen. nov.** and *Gigaviva* **subgen. nov.**. The genus *Redivivoides* rendered *Rediviva* paraphyletic and is downgraded to subgenus level. A key is provided to enable the identification of subgenera.

Key words: South Africa, oil-collecting bees, new subgenera, *Rediviva*, *Redivivoides*, classification, taxonomy

Introduction

The genus *Rediviva* is an iconic group of bees because females have close evolutionary relationships with their host plants and six species have extremely elongate forelegs (sometimes longer than the bees' body) for collecting oil from floral spurs that is used for larval nourishment (Kuhlmann & Hollens 2015) and for brood cell lining (Kuhlmann 2015). *Rediviva* are ground nesters (Kuhlmann 2015) and females collect floral oil from a range of oil-producing flowers of Iridaceae, Orchidaceae and Scrophulariaceae with *Diascia* (Scrophulariaceae) as the most commonly used floral host exclusively or preferably visited by 19 of the 26 species (summarized in Kuhlmann & Hollens 2015). Lengths of floral spurs and forelegs partly show co-variation at the population level, suggesting co-evolution (Steiner & Whitehead 1990, 1991, Kahnt *et al.* 2017) and making them an ideal model for studying evolutionary and speciation processes (Pauw *et al.* 2017, Kahnt *et al.* 2018, 2019). Thus, this specialised plant-pollinator system might help elucidate the origin of the unusual bee diversity in the Greater Cape Floristic Region (Kuhlmann 2009).

So far 26 *Rediviva* species are known, all of them endemic to South Africa and Lesotho, with 15 species occurring in the winter rainfall region in western South Africa (Whitehead & Steiner 2001) and 11 species in the summer rainfall region of eastern South Africa and Lesotho (Whitehead *et al.* 2008, Kuhlmann 2012a). *Rediviva* belongs to the subfamily Melittinae (Michener 2007) and, as Michez *et al.* (2009) demonstrated based on a molecular phylogenetic study, to the tribe Melittini. Within the Melittini (synapomorphies according to Michener (2007) are: apicolateral lobes of male S7 reduced, reduction/loss of male pygidial plate, gonostylus reduced and broadly fused to gonocoxite), *Rediviva* is characterised by their broadened female hind tibia and basitarsus with the scopa consisting of densely plumose, velvety pubescence for transporting floral oil while the elongate fore tarsi (extreme in some species) are a synapomorphy of *Rediviva* (Michener 1981, 2007). Michez *et al.* (2009) and Dellicour *et al.* (2014) provided the first evidence that *Redivivoides* might not be the sister-group of *Rediviva* but instead that it might render the latter paraphyletic. This was later confirmed by the phylogenetic study of Kahnt *et al.* (2017) (Fig. 1) that was based on a far more comprehensive dataset covering 67 % of the known species (73 % of *Rediviva*, 43 % of *Redivivoides*).

The genus *Redivivoides* is endemic to the winter rainfall region of western South Africa and the biology of its

species is far less understood than in *Rediviva*. Bees of the genus are generally rarely collected and so *Redivivoides* was only described by Michener in 1981 based on a single more common species. Another six species were described by Kuhlmann (2012b) who also provided a detailed redefinition of the genus. Michez *et al.* (2009) suggested *Redivivoides* and *Rediviva* as a key group for understanding the origin of oil-collecting in bees and based on this, Kuhlmann (2012b) discussed in detail potential evolutionary scenarios for the origin of oil-collecting in melittid bees. Results of the molecular phylogeny (Kahnt *et al.* 2017) now strongly support the morphology-based hypothesis of Kuhlmann (2012b) that *Redivivoides* species have lost their oil-collecting structures and stopped collecting floral oil for larval nourishment.

The aim of this paper is to resolve the taxonomic problems caused by *Redivivoides* rendering *Rediviva* paraphyletic (Kahnt *et al.* 2017). By following the recommendations of Vences *et al.* (2013), who argued for minimal classificatory changes so as to provide some nomenclatural stability, we preserve *Rediviva* as a genus name for an iconic group of oil-collecting bees that have been intensively studied as a model for plant-pollinator co-evolution in South Africa (e.g. Steiner & Whitehead 1990, 1991, Pauw *et al.* 2017, Kahnt *et al.* 2017, 2019). As a result *Redivivoides* has to be downgraded to subgenus level and *Rediviva* is divided into monophyletic, morphologically diagnosable groups that are described as subgenera. Based on their morphology *Rediviva* species not represented in the molecular phylogeny of Kahnt *et al.* (2017) are here assigned to the new subgeneric classification.

Materials and methods

For developing a consistent subgeneric classification of *Rediviva* we applied a procedure that is based on recommendations of Vences *et al.* (2013) for naming taxa. In a first step we identified morphological characters that allowed for phenotypic diagnosability of monophyletic groups as defined by Kahnt *et al.* (2017) (i.e. clades A–E and *Redivivoides*). In a second step and as a kind of test for the suitability and validity of our classification, species not represented in the phylogeny of Kahnt *et al.* (2017) were assigned to the newly defined subgenera based only on their morphology. These species are *Rediviva autumnalis* Whitehead & Steiner 2008, *R. pallidula* Whitehead & Steiner 1992, *R. rhodosoma* Whitehead & Steiner 2008, *R. ruficornis* Whitehead & Steiner 2001, *R. rufocincta* (Cockerell 1944), *R. transkeiana* Whitehead & Steiner 2008 and *R. whiteheadi* Kuhlmann 2012; *Redivivoides eardleyi* Kuhlmann 2012, *R. kamieskroonensis* Kuhlmann 2012, *R. karooensis* Kuhlmann 2012 and *R. variabilis* Kuhlmann 2012.

Some species were not available for study so the descriptions and illustrations of Whitehead & Steiner (2001) and Whitehead *et al.* (2008) were consulted to extract relevant morphological information. For males of *Rediviva autumnalis*, *R. brunnea* Whitehead & Steiner 2008, *R. neliana* Cockerell 1931 and *R. rhodosoma* specific structures of genitalia and associated sterna S7 and S8 had not been described in sufficient detail. For these species images of the respective structures were provided by Simon van Noort and Aisha Mayekiso (Iziko South African Museum, Cape Town) and David Notton (Natural History Museum, London).

General morphological terminology follows that of Michener (2007) and Whitehead & Steiner (2001) for *Rediviva* with positions of lateral lobes and median lobes of male metasomal sternum 7 shown in Fig. 4e. Body length was measured from the clypeus to the tip of the metasoma. Images were taken using a Keyence VHX-5000 digital microscope.

Results

Based on the morphological analysis and by applying the recommendations of Vences *et al.* (2013) a consistent subgeneric system was developed that is congruent with the results of the molecular phylogeny (Fig. 1). Overall five subgenera are recognized and described below. Clades B–E of Kahnt *et al.* (2017) are morphologically well defined as one group and are here united in a single subgenus. Nodes defining the suggested subgenera were highly supported by Bayesian analyses (support values 0.96 to 1.0; Fig. 1) (Kahnt *et al.* 2017). Species not represented in the phylogenetic study could be clearly assigned to a subgenus based on the criteria described in the diagnoses. The only exception is *R. transkeiana* that was not included in the phylogeny and whose male is unknown. A checklist of all *Rediviva* species and their subgeneric affiliation is given in Table 1.

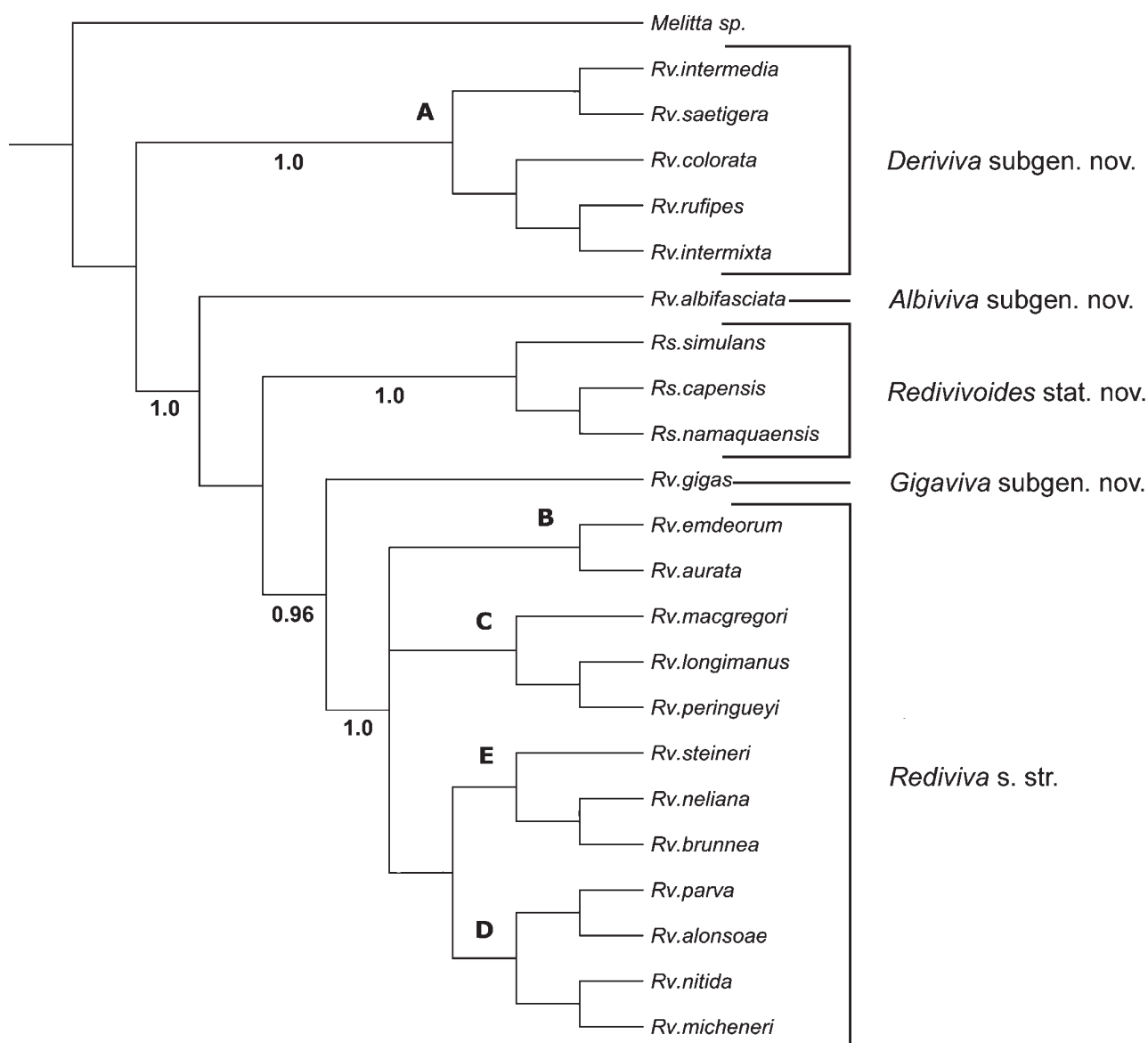


FIGURE 1. New subgenera assigned to the phylogeny of *Rediviva* (Rv.) and *Redivivoides* (Rs.) based on the molecular phylogeny and clades A–E as defined by Kahnt *et al.* (2017). Support values of Bayesian analyses provided by Kahnt *et al.* (2017) are added to nodes defining subgenera.

Subgenera of *Rediviva* Friese 1911

Rediviva (*Deriviva*) subgen. nov.

Type species: *Notomelitta intermixta* Cockerell 1934: 450; designated here.

Rediviva intermixta (Cockerell 1934): Transferred to *Rediviva* by Michener (1981: 47).

The five species placed in this subgenus (clade A of Kahnt *et al.* 2017) are listed in table 1.

Diagnosis. Males of *Deriviva* have a unique combination of lateral lobes of S7 either smooth (not striate) or completely reduced (striate in *Rediviva* s.str.), and median lobes either short and hardly longer than their basal width (much broader than long in *Gigaviva*) or if longer forming jointly \pm a right angle (acute-angled or parallel in *Rediviva* s.str.); median lobes not distinctly apically broadened (Figs 2a–b, d–e) (spatulate in *Albiviva*). Apical plate of S8 distally notched (Fig. 2c) (strait, deeply cleft, emarginate or semi-circular in other subgenera), except in *R. intermedia* where it is evenly rounded (Fig. 2f). Males of *Redivivoides* species fit this diagnosis and are currently indistinguishable from *Deriviva* so can only be assigned to a subgenus through the associated female.

Females of three of the five species (Table 1) in this subgenus (*R. intermedia*, *R. intermixta*, *R. rufipes*) can be identified by a broadened hind tibia and basitarsus with the scopa consisting of densely plumose pubescence for transporting floral oil (Fig. 3f) (in *Redivivoides* hind tibia not broadened and without plumose pubescence), bidentate mandible (tridentate in *Gigaviva*) and inconspicuous yellowish apical tergal hair bands (Fig. 3b) (distinct white apical hair bands in *Albiviva*) in combination with a small shiny scale-like projection on the distal-dorsal angle of the hind basitarsus (Fig. 3e). In *R. intermedia* and *R. rufipes* this projection is in combination with an apical hairy spine on the front coxa (Fig. 3d). The remaining two species, *R. colorata* and *R. saetigera*, lack this projection and cannot be distinguished from females of *Rediviva* s. str.

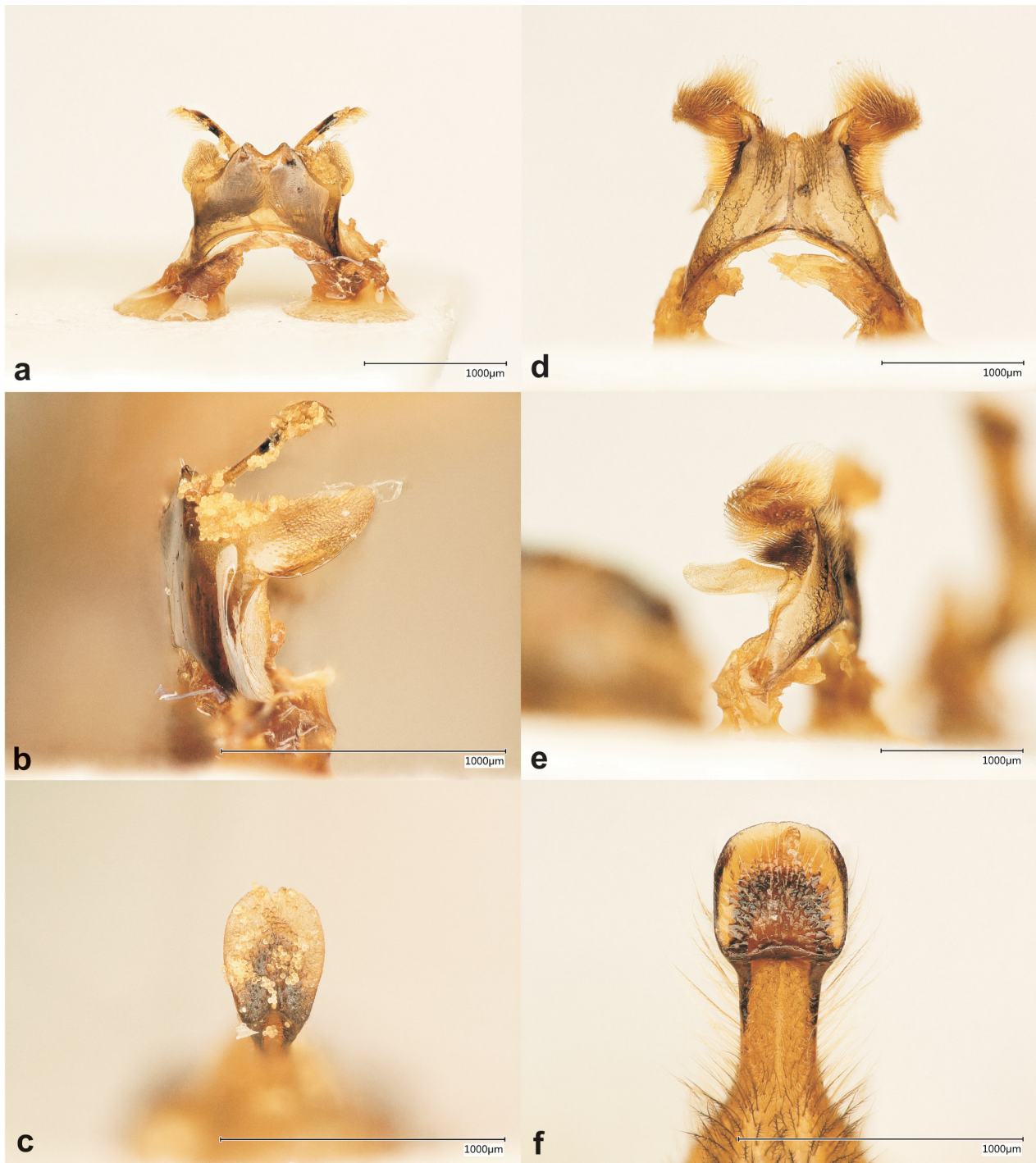


FIGURE 2. *Rediviva (Deriviva) intermixta* Cockerell ♂: a. metasomal sternum 7, dorsal view; b. metasomal sternum 7, lateral view; c. metasomal sternum 8, apical plate. *R. (Deriviva) intermedia* Whitehead & Steiner ♂: d. metasomal sternum 7, dorsal view; e. metasomal sternum 7, lateral view; f. metasomal sternum 8, apical plate.

Etymology. The new subgeneric name is an anagram of the generic name *Rediviva*. The gender of the name is feminine.

Distribution. Species of *Deriviva* occur in most parts of the range of the genus (Whitehead & Steiner 2001, Whitehead *et al.* 2008).

***Rediviva (Albiviva)* subgen. nov.**

Type species: *Rediviva (Albiviva) albifasciata* Whitehead & Steiner 1994, designated here.

The only species in this subgenus is *R. albifasciata*.

Diagnosis. The subgenus is monotypic and just contains *R. albifasciata* which is the smallest species of the genus (8–10 mm). Males can be recognized by a combination of the following characters: median lobes of S7 spatulate (Fig. 4b) (not apically broadened in other subgenera); lateral lobes large and smooth, papillate on basal third (in *Gigaviva* lateral lobes missing; not papillate in other subgenera); apical plate of S8 distally straight (Fig. 4a) (apical margin deeply cleft in *Gigaviva*; apically notched, emarginate or semi-circular in other subgenera).

Females show a unique combination of a broadened hind tibia and basitarsus with the scopa consisting of densely plumose pubescence (Fig. 3f) (in *Redivivoides* hind tibia not broadened and without plumose pubescence), bidentate mandible (tridentate in *Gigaviva*) and small shiny scale-like projection on the distal-dorsal angle of the hind basitarsus (smaller than in Fig. 3e) (projection distinctly larger in *R. intermedia*, *R. intermixta* and *R. rufipes* of subgenus *Deriviva*, missing in all other species) in combination with the small size and distinct white apical tergal hair bands (Fig. 3a) (less conspicuous yellowish or missing in all other subgenera) that only occur in this species. This is the only *Rediviva* species that collects oil in flowers of *Colpias mollis* (Scrophulariaceae) (Steiner & Whitehead 2002, Kuhlmann & Hollens 2015).

Etymology. The new subgeneric name is a combination of the first part of the specific epithet of the type species *R. albifasciata* and the last part of the generic name *Rediviva*. The gender of the name is feminine.

Distribution. The species is only known from the western part of the winter rainfall region (Whitehead & Steiner 2001).

***Rediviva (Redivivoides)* Michener 1981, stat. nov.**

Redivivoides Michener, 1981: 42. Type species: *Redivivoides simulans* Michener 1981, by original designation.

The seven species placed in this subgenus are listed in table 1.

Diagnosis. The subgenus *Redivivoides* comprises seven species (Table 1). Males are morphologically diverse and no apomorphies are known that distinguish them from those of other subgenera (see detailed discussion in Kuhlmann 2012b). Some can easily be mistaken for males of the subgenus *Deriviva* so they can only be assigned to a subgenus through the associated female.

Females lack the broadened hind tibia and basitarsus and the scopa does not consist of densely plumose pubescence for transporting floral oil that females of all other subgenera have. Instead the hind leg is narrow with the hind basitarsus only slightly broadened and the scopa consists of sparse simple bristles (Fig. 3c) (branched in other subgenera). Within the genus *Rediviva*, species of *Redivivoides* are unique because they do not collect floral oil for larval nourishment. Detailed descriptions of species including a discussion of morphology and biology were provided by Kuhlmann (2012b) and are not repeated here.

Distribution. *Redivivoides* species are known only from the winter rainfall region of western South Africa (Kuhlmann 2012b).

***Rediviva (Gigaviva)* subgen. nov.**

Type species: *Rediviva (Gigaviva) gigas* Whitehead & Steiner 1993, designated here.

The only species in this subgenus is *R. gigas*.

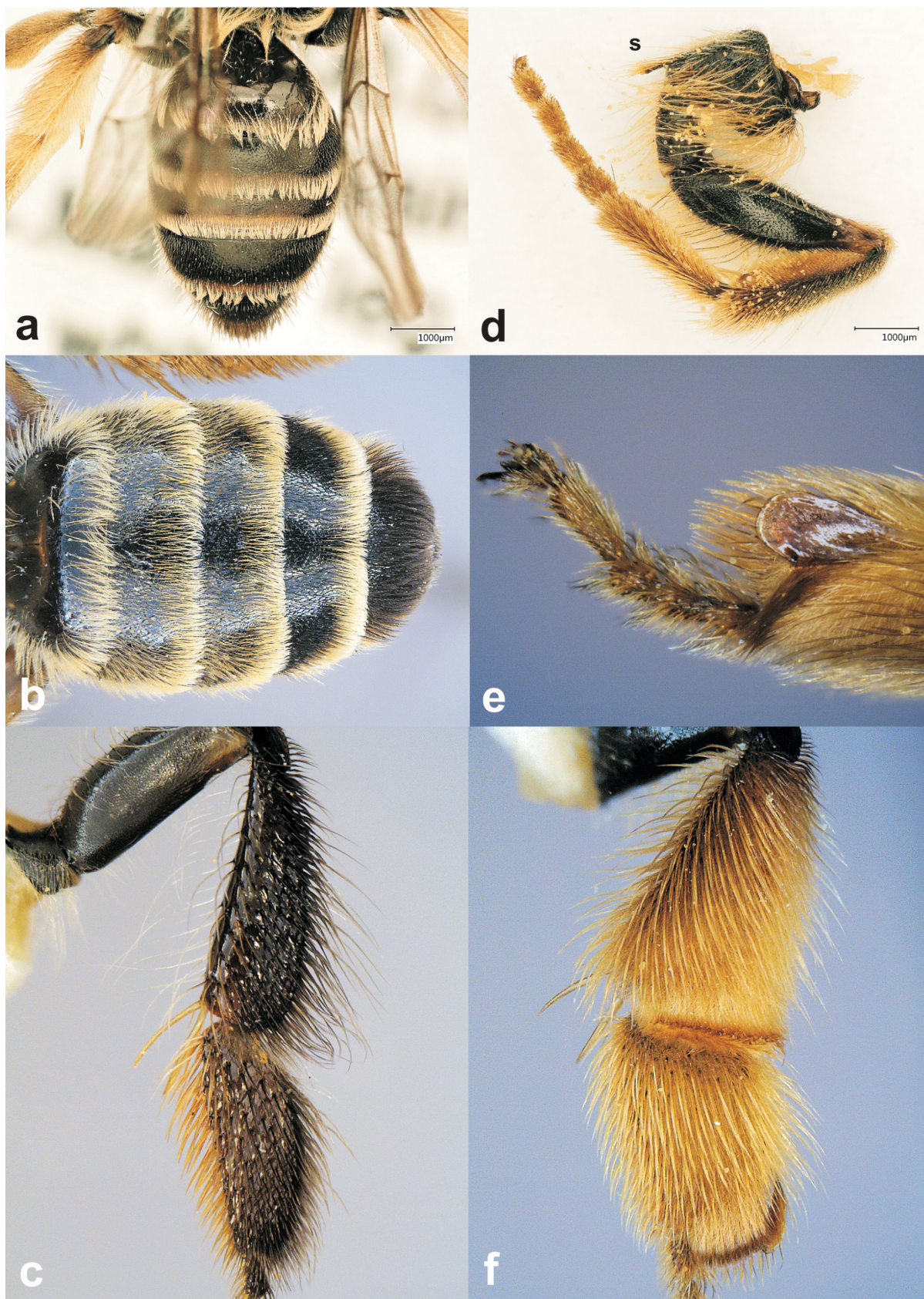


FIGURE 3. *Rediviva* (*Albiviva*) *albifasciata* Whitehead & Steiner ♀: a. metasoma with distinct white apical hair bands. *R.* (s. str.) *whiteheadi* Kuhlmann ♀: b. metasoma with indistinct yellowish apical hair bands. *R. (Redivivoides) capensis* (Kuhlmann) ♀: c. hind leg. *R. (Deriviva) intermedia* Whitehead & Steiner ♀: d. front leg, coxa with apical hairy spine (s). *R. (Deriviva) intermixta* Cockerell ♀: e. hind basitarsus with shiny scale-like projection; f. hind leg.

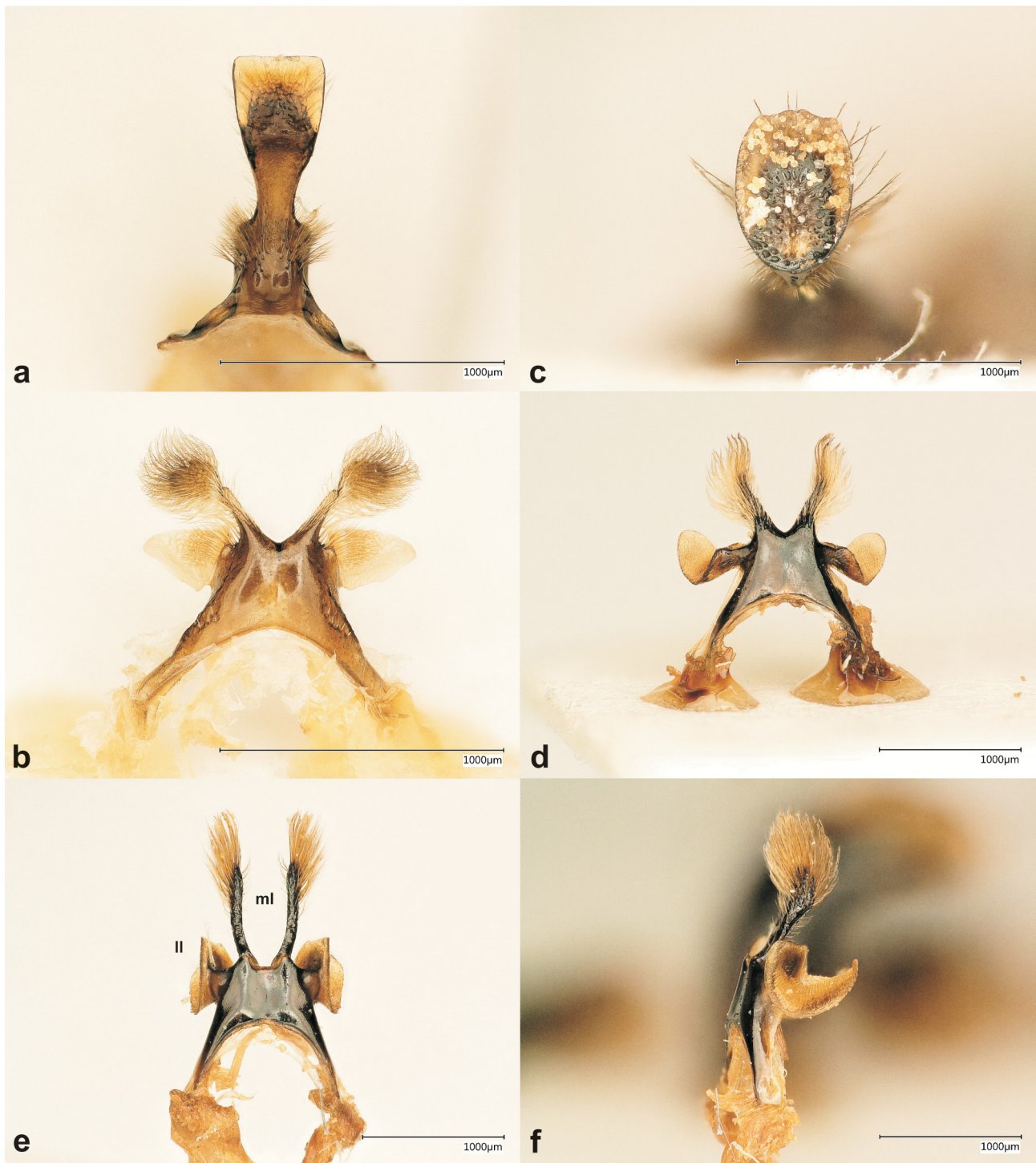


FIGURE 4. *Rediviva* (*Albiviva*) *albifasciata* Whitehead & Steiner ♂: a. metasomal sternum 8, apical plate; b. metasomal sternum 7, dorsal view. *R.* (s. str.) *macgregori* Whitehead & Steiner ♂: c. metasomal sternum 8, apical plate; d. metasomal sternum 7, dorsal view. *R.* (s. str.) *longimanus* Michener ♂: e. metasomal sternum 7, dorsal view (ll: lateral lobe; ml: median lobe); f. metasomal sternum 7, lateral view.

Diagnosis. The subgenus is monotypic and contains only *R. gigas* which is the largest species of the genus (15–18 mm). Males are characterised by a combination of S7 without lateral lobes (with lateral lobes in all other species except *Redivivoides karoensis* and *R. namaquaensis*), median lobes basally twice as broad as long (Whitehead & Steiner 2001: Figs 5B–C) (as broad as long or longer in other subgenera) and S8 apically broadened with margin deeply cleft (strait, notched, emarginate or semi-circular in other subgenera) (Whitehead & Steiner 2001: Figs 5D, 64G).

Females show a unique combination of a broadened hind tibia and basitarsus with the scopa consisting of densely plumose pubescence for transporting floral oil (Fig. 3f) (in *Redivivoides* hind tibia not broadened and without plumose pubescence) and a tridentate mandible (bidentate in other subgenera). The species has an isolated position within the genus and, among others, collects oil on flowers of *Tritoniopsis parviflora* (Iridaceae) (Manning & Goldblatt 2002, 2005) and *Ixianthes retzioides* (Scrophulariaceae) (Whitehead & Steiner 1993, Steiner & Whitehead 1996) that are not used by any other *Rediviva* species (Kuhlmann & Hollens 2015).

Etymology. The new subgeneric name is a combination of the first part of the specific epithet of the type species *R. gigas* and the last part of the generic name *Rediviva*. The gender of the name is feminine.

Distribution. The species is only known from the southwestern part of the winter rainfall region (Whitehead & Steiner 2001).

TABLE 1. Checklist of the 33 *Rediviva*-species.

Subgenus	Species
<i>Deriviva</i>	<i>R. colorata</i> Michener 1981
	<i>R. intermedia</i> Whitehead & Steiner 2001
	<i>R. intermixta</i> (Cockerell 1934)
	<i>R. rufipes</i> (Friesse 1913)
	<i>R. saetigera</i> Whitehead & Steiner 1992
<i>Albiviva</i>	<i>R. albifasciata</i> Whitehead & Steiner 1994
<i>Redivivoides</i>	<i>R. capensis</i> (Kuhlmann 2012)
	<i>R. eardleyi</i> (Kuhlmann 2012)
	<i>R. kamieskroonensis</i> (Kuhlmann 2012)
	<i>R. karooensis</i> (Kuhlmann 2012)
	<i>R. namaquaensis</i> (Kuhlmann 2012)
	<i>R. simulans</i> (Michener 1981)
	<i>R. variabilis</i> (Kuhlmann 2012)
<i>Gigaviva</i>	<i>R. gigas</i> Whitehead & Steiner 1993
<i>Rediviva</i> s. str.	<i>R. alonsoae</i> Whitehead & Steiner 2001
	<i>R. aurata</i> Whitehead & Steiner 2001
	<i>R. autumnalis</i> Whitehead & Steiner 2008
	<i>R. brunnea</i> Whitehead & Steiner 2008
	<i>R. emdeorum</i> Vogel & Michener 1984
	<i>R. longimanus</i> Michener 1981
	<i>R. macgregori</i> Whitehead & Steiner 2001
	<i>R. micheneri</i> Whitehead & Steiner 2001
	<i>R. neliana</i> Cockerell 1931
	<i>R. nitida</i> Whitehead & Steiner 2001
	<i>R. pallidula</i> Whitehead & Steiner 1992
	<i>R. parva</i> Whitehead & Steiner 2001
	<i>R. peringueyi</i> (Friesse 1911)
	<i>R. rhodosoma</i> Whitehead & Steiner 2008
	<i>R. ruficornis</i> Whitehead & Steiner 2001
	<i>R. rufocincta</i> (Cockerell 1944)
	<i>R. steineri</i> Kuhlmann 2012
	<i>R. whiteheadi</i> Kuhlmann 2012
	<i>R. transkeiana</i> Whitehead & Steiner 2008 (♂ unknown)

***Rediviva* (s. str.) Friese 1911**

Andrena (*Rediviva*) Friese, 1911: 671. Type species: *Andrena peringueyi* Friese 1911, by designation of Cockerell, 1931: 402 (transferred to *Rediviva*).

Notomelitta Cockerell, 1933: 128. Type species: *Rediviva neliana* Cockerell 1931, by original designation, monobasic.

The 18 species placed in this subgenus (clades B–E of Kahnt *et al.* 2017) are listed in table 1.

Diagnosis. This is the most speciose subgenus comprising 18 species (Table 1); *R. transkeiana* likely belongs here, too.

Males combine the following characters: S7 with usually large strigate translucent lateral lobes (lateral lobes either missing or smooth in other subgenera); median lobes long and narrow lanceolate to spatulate with pilosity mostly restricted to the apical third, longest hairs about half as long as length of median lobe (Figs 4e–f) (in other subgenera median lobes much shorter, of different form and hairs shorter). In *R. emdeorum* and *R. aurata* median lobes are shorter (Whitehead & Steiner 2001: Figs 25B–C) and both have a vestigial pygidial plate (Whitehead & Steiner 2001: Fig. 44F) that is absent in all other species. Males of *R. macgregori* are divergent in that the median lobes are relatively short and completely covered with hair (Fig. 4d).

Females can be identified by a combination of the following character states: broadened hind tibia and basitarsus with the scopa consisting of densely plumose pubescence for transporting floral oil (Fig. 3f) (in *Redivivoides* hind tibia not broadened and without plumose pubescence), bidentate mandible (tridentate in *Gigaviva*) and inconspicuous yellowish apical tergal hair bands (Fig. 3b) (distinctly white in *Albiviva*) in combination with the absence of a scale-like projection on the distal-dorsal angle of the hind basitarsus (present in *Albiviva* and three species of *Deriviva*; *R. intermedia*, *R. intermixta* and *R. rufipes*). This set of characters also applies to females of two species in the subgenus *Deriviva*, namely *R. colorata* and *R. saetigera*, that cannot be distinguished from those of *Rediviva* s. str.. They can only be assigned to a subgenus through the associated male.

Distribution. Species of *Rediviva* (s. str.) occur throughout the range of the genus (Whitehead & Steiner 2001, Whitehead *et al.* 2008).

Key to subgenera of *Rediviva*

Using the keys provided here, it is currently impossible to assign females of *R. transkeiana*, *R. colorata* and *R. saetigera* and males of *Redivivoides* to one of the proposed subgenera. If in doubt about the identity of a specimen the well illustrated keys published by Whitehead *et al.* (2008) and Kuhlmann (2012b) should be used for species identification.

Males

Males of subgenus *Redivivoides* are excluded from the key because they show no morphological characters that make them diagnosable as a group.

- | | | |
|---|--|-------------------------------------|
| 1 | S7 without lateral lobes (Whitehead & Steiner 2001: Figs 5B–C); S8 with apical margin deeply cleft (Whitehead & Steiner 2001: Figs 5D, 64G) | <i>Gigaviva</i> subgen. nov. |
| - | S7 with distinctly developed lateral lobes (Figs 2a–b, 4b, d–e); S8 with apical margin either evenly rounded, notched or crenulate (Figs 2c, f, 4a, c) | 2 |
| 2 | Median lobes of S7 formed like a spoon, apically broadened like a disc (Fig. 4b) | <i>Albiviva</i> subgen. nov. |
| - | Median lobes of S7 not spoon-like and not distinctly apically broadened (Figs 2a–b, 4d–e) | 3 |
| 3 | Lateral lobes large and striate (Figs 4d, e–f) | <i>Rediviva</i> s. str. |
| - | Lateral lobes either reduced or not striate, with smooth surface (Figs 2a–b, d–e) | <i>Deriviva</i> subgen. nov. |

Females

- | | | |
|---|---|---------------------------------------|
| 1 | Hind tibia and basitarsus narrow with scopa consisting of sparse simple bristles (Fig. 3c); front tarsi without dense plumose oil-collecting hairs | <i>Redivivoides</i> stat. nov. |
| - | Hind tibia and basitarsus broadened with scopa consisting of densely plumose pubescence for transporting floral oil (Fig. 3f); front tarsi with dense plumose oil-collecting hairs. | 2 |
| 2 | Mandible tridentate; largest <i>Rediviva</i> species (15–18 mm) | <i>Gigaviva</i> subgen. nov. |
| - | Mandible bidentate; smaller (at most 14 mm) | 3 |
| 3 | Hind basitarsus without scale-like projection on distal dorsal edge. | <i>Rediviva</i> s. str. |

NOTE: Females of *R. colorata* and *R. saetigera* also run here but belong to *Deriviva* **subgen. nov.**

Rediviva transkeiana also runs here but because the male is unknown it is not clear if this species belongs to *Rediviva* s.str. or perhaps *Deriviva* **subgen. nov.**

- Hind basitarsus with scale-like projection on distal dorsal edge (Fig. 3e or similar) 4
- 4 T1–T4 with distinct white apical hair bands (Fig. 3a); smallest *Rediviva* species (8–10 mm) ***Albiviva* subgen. nov.**
- T1–T4 with less conspicuous, more yellowish apical hair bands (Fig. 3b or similar); larger species ***Deriviva* subgen. nov.**

Discussion

For the first time a consistent subgeneric classification of *Rediviva* is suggested. This classification is based on a molecular phylogeny of 22 (67 %) out of 33 species (Kahnt *et al.* 2017) and a morphological analysis that resulted in the description of five subgenera. Diagnostic morphological characters are mainly associated with the shape of the male sterna S7 and S8 and the female scopa. These characters are also used to diagnose subgenera in other melittid genera like *Melitta* (e.g. shape of the latero-apical processes of S7; Dellicour *et al.* 2014) and *Dasypoda* (e.g. shape of the basal area of S8; Michez *et al.* 2004).

There are still a few open taxonomic questions that need to be solved. First, in the morphologically quite heterogeneous subgenus *Deriviva* no common character could be found that allowed for the identification of all females. So currently females of *R. colorata* and *R. saetigera* cannot be separated from those of *Rediviva* s. str.. Second, as already discussed by Kuhlmann (2012b) males of *Redivivoides* are indistinguishable from those of the other subgenera, in particular from those of *Deriviva*, so they can only be assigned to a subgenus through the associated female. Third, the subgeneric affiliation of *R. transkeiana* is unresolved because this rare species was neither included in the molecular phylogenetic study (Kahnt *et al.* 2017) nor is the male known. Solving these problems will also be a test for the robustness of the classification we present here.

Acknowledgements

We are very grateful for the support of Simon van Noort and Aisha Mayekiso (Iziko South African Museum, Cape Town) and David Notton (Natural History Museum, London) who kindly imaged male terminalia of *Rediviva* species for us that otherwise would not have been available for study. The comments of two anonymous reviewers helped to improve the quality of the manuscript.

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