

Ber. d. Reinh.-Tüxen-Ges. 30, 149-162. Hannover 2018

## **Wild bees (*Anthophila*) of Macaronesia – biogeographical and evolutionary aspects**

– Anselm Kratochwil, Osnabrück, and Angelika Schwabe, Darmstadt –

### **Abstract**

The Atlantic island groups of Macaronesia are an ideal model for the demonstration of colonisation processes by wild bees and are therefore an excellent example for questions of island biogeography. Azores, Madeira, Canary and Selvagens Islands, as well as Cape Verde, have had different geological histories and show strong modifications of the climatic conditions and biogeographical patterns as well as differences in ages and in distances from mainlands. We summarise the present status of bee-species diversity (partly using unpublished data sources of our own) and compare the different archipelagos with regard to the biogeographical aspects and the colonisation history of selected wild-bee species.

The diversity of native bee species in the Azores is low. The Azores show large distances to mainland sources, and earlier stepping-stone islands were not present. Additionally, dominant west winds and the oceanity combined with relatively low temperatures and the dominance of woody vegetation before human impact did not favour colonisation by wild bees and their long-time establishment. The species of the Azores ( $n = 17$ , from that 1 endemic) are biogeographic elements of the temperate, western Palaearctic region; most of them had been (probably) introduced ( $n = 15$ ).

The islands of the Cape Verde Archipelago ( $n = 14$ , from that 9 endemic) are young. The mainland sources are not suitable because of the tropical character (most of the wild-bee species prefer dry/semi-dry climates and bare soil conditions), but there were probably partial colonisation processes from the Canary Islands.

The Archipelago of Madeira (19 species with 8 endemic species and 1 endemic subspecies) and especially the Canary Islands (124 species with 64 endemic species and 149 taxa with 88 endemic taxa) show conditions that favoured the existence and evolutionary processes of wild-bee species. The relatively high age of some islands, the high habitat diversity, geological barriers that led to separation of populations, sources from the Saharo-Mediterranean high-diversity bee spot in the case of the Canary Islands and former stepping stones in the case of the Madeira Archipelago supported the colonisation and later evolution of endemic bee species. The Canary Islands are a hot spot for bee diversity with many different taxonomical units – this is unique worldwide for an oceanic archipelago. Although Fuerteventura, Lanzarote and Gran Canaria are the oldest islands with the highest bee diversity ( $n = 67$ ,  $n = 62$  and  $n = 66$ , respectively), Tenerife also has remarkable bee diversity ( $n = 63$ ) with many endemic species ( $n = 38$ ). The biogeographical situation with former palaeo islands favoured the development of endemic taxa in Tenerife. The small Selvagens Islands have only one bee species.

In the extreme environments of the Canary Islands and especially Porto Santo (Madeira Archipelago) and Cape Verde, there are nearly no introduced bee species.

Many of the endemic plant species of Macaronesia depend on pollination by wild bees. Therefore, a rich bee fauna plays a key role, especially in the open, dry to semi-dry ecosystems of Macaronesia.

**Key words:** Hymenoptera Apoidea, island biogeography, wild-bee diversity, endemic species, introduced species, bee colonisation, *Micrandrena*, radiation.

## 1. Introduction

Primarily considered as a distinct phytogeographical unit, Macaronesia is today recognised as a zone of varying biogeographical regions. We use ‘Macaronesia’ as a historically based, summarising term for the archipelagos in question. The biogeographical assignments differ among different authors (LOBIN 1982, KUNKEL 1993, LÜPNITZ 1995, POTT et al. 2003). There is a consensus concerning the Azores (Atlantic region, Holarctic; see also SCHÄFER 2003) and Cape Verde (Saharan region, Palaeotropis), but not concerning the affiliation of the Madeira Archipelago and the Canary Islands. According to LOBIN (1982) and BLONDELL & ARONSON (1999), both are part of the Mediterranean region; according to LÜPNITZ (1995), both belong to the Palaeotropis. According to POTT et al. (2003), the Madeira Archipelago is part of the Mediterranean region and the Canary Islands are part of the extratropical Saharan region (southern Holarctic).

The islands emerged from sea level in different time periods: Selvagens Islands 27 Ma ff., Canary Islands 20 Ma ff., Madeira Archipelago 15 Ma ff., the Azores 10 Ma ff. and Cape Verde 8 Ma ff. (WHITTAKER & FERNÁNDEZ-PALACIOS 2007). There is a considerable climatic gradient from temperate-hyperoceanic conditions (Azores) to Mediterranean-oceanic types with strong gradients referring to elevation and tradewind exposure (Madeira Archipelago, Canary Islands) and to tropical dry climate (Cape Verde). The distance from the mainland shows strong differences: 1369 km from the Azores (Sao Miguel) to the western coast of Portugal, 737 km from Madeira Archipelago (Porto Santo) to Cape Sim (Marocco), 570 km from Boa Vista (Cape Verde) to Dakar (Senegal) and 96 km from Fuerteventura (Canary Islands) to Staffors Point (Western Sahara).

Wild bees are key pollinators of many plant species in Macaronesia. HOHMANN et al. (1993) summarised in their impressive monographic study the plant species that were visited by wild bees and (especially in the case of pollen-collecting females) are pollinators. In particular, many endemic Asteraceae, Lamiaceae, Fabaceae and *Echium* species are visited and pollinated by wild bees. The Macaronesian woody *Echium* species are all self-incompatible outbreeders (ALDRIDGE 1981) and show broad spectra of flower-visiting wild bees (HOHMANN et al. l.c.; our own studies also in Madeira and Porto Santo, Fig. 1). For *E. wildpretii* (Tenerife), the wild-bee species *Anthophora a. alluaudi* Pérez, 1902, was identified as the main pollinator (KRAEMER & SCHMITT 1997; Fig. 2).

Brassicaceae play an important role as well, e.g. for the Porto-Santo endemic bee species *Andrena portosanctana* Cockerell, 1922 (main resource plant species: *Cakile maritima*, Fig. 3), or the Porto-Santo endemic bee species *A. dourada* Kratochwil & Scheuchl, 2013, which was observed, e.g. on the Madeira-Archipelago endemic plant species *Crambe fruticosa* (KRATOCHWIL & SCHEUCHL 2013, KRATOCHWIL et al. 2014, KRATOCHWIL & SCHWABE 2018).

The following topics will be introduced and discussed:

(1) We will analyse the wild-bee diversity of the different archipelagos with regard to species/taxa, especially endemic taxa.

(2) The fauna of islands is particularly endangered by the introduction of species; this is also true for wild bees. Therefore, the number of (probably) introduced wild-bee species in contrast to the number of native species will be analysed.



Fig. 1: Endemic bee subspecies of the Madeira Archipelago: *Amegilla quadrifasciata maderae* (Sichel, 1868), female, average size 15 mm, visiting the Porto-Santo endemic species *Echium portosanctensis* J.A. CARVALHO, PONTES, BATISTA-MARQUES & R. JARDIM, Vereda Pico Branco, 19.03.2012.



Fig. 2: Endemic bee species of the Canary Islands: *Anthophora a. alluaudi*, Pérez, 1902, female, average size 13 mm, visiting *Erysimum scoparium* (WILLD.) WETTST. (endemic species of Tenerife and La Palma), Las Cañadas de Teide, Tenerife, 14.04.1992.



Fig. 3: Endemic bee species of Porto Santo (Madeira Archipelago): *Andrena portosanctana* Cockerell, 1922, female, average size 12 mm, visiting the native plant species *Cakile maritima* SCOP. subsp. *maritima* in a driftline habitat, Campo de Baixo, Porto Santo, 18.03.2012.

(3) We assign the species to different biogeographical regions and correlate the wild-bee fauna of the different archipelagos with age of the archipelago, size and distance to the mainlands.

## 2. Wild-bee diversity of Macaronesia

Currently, about 17,000 bee species have been described worldwide. It can be assumed that more than 20,000 to 25,000 wild-bee species exist on Earth (MICHENER 2007). With the exception of Antarctica and most parts of the Arctic and the nival zone of the mountains, almost all terrestrial habitats (that are populated by vascular plants with suitable pollen and nectar resources) can be colonised by wild bees.

In contrast to vascular plant species and many taxa of animal species, the highest diversity of wild bees is not found in the wet tropics but in semidesert regions, in steppe ecosystems and in areas with Mediterranean-like climates (KRATOCHWIL 2003). In the temperate west-wind zone, the number of species is smaller than in semi-dry regions; Germany currently has 585 species (SCHEUCHL & SCHWENNINGER 2015). Oceanic volcanic islands mostly have small numbers of wild bees. Only three wild-bee species exist on the Galápagos Islands (including two introduced/probably introduced species; GONZALES et al. 2010, RASMUSSEN et al. 2012). An exception are islands with rapid diversification after colonisation (e.g. wild-bee genus *Hylaeus*, Hawai'i, which had an impressive radiation with 63 species from a single ancestor; MAGNACCA & KING 2013).

In the following, we will analyse the wild-bee taxa of Macaronesia. Bee checklists of the Azores are available, e.g. from BORGES et al. (2005), FRANQUINHO DE AGUIAR et al. (2010) and WEISSMANN et al. (2017). The number of wild-bee species in the Madeira Archipelago is based on the updated database of A. Aguiar, J. Smit, and A. Kratochwil (n.p.). A checklist was published by FELLENDORF et al. (1999), which had been corrected and supplemented by KRATOCHWIL et al. (2008), KRATOCHWIL & SCHEUCHL (2013), KRATOCHWIL et al. (2014), KRATOCHWIL et al. (2018). Fundamental to the knowledge of wild bees on the Canary Islands is the monograph of HOHMANN et al. (1993), supplemented, e.g. by data of TKALCU (1993), KUHLMANN (2000), PATINY (2003), PESENKO & PAULY (2005), SMIT (2007), PÉREZ & MACÍAS-HERNÁNDEZ (2012) and SUÁREZ et al. (2017) and data of our own. The wild-bee species of the Cape Verde Islands were summarised, e.g. by PAULY et al. (2002), BÁEZ et al. (2005), PESENKO & PAULY (2005) and STRAKA & ENGEL (2012).

Considering all the Macaronesian Archipelagos, so far, 164 wild-bee species (191 taxa, including subspecies) have been detected. The number of endemic wild bees is high, with 67 species and 104 taxa in general (including subspecies). In comparison, Germany does not claim a single endemic wild-bee species.

The archipelagos differ considerably in their species diversity (Fig. 4). The Canary Islands have by far the highest quantity of species ( $n = 124$ ); this is also true for endemic species (64 species, 88 taxa, including subspecies). The oldest islands, Fuerteventura, Lanzarote and Gran Canaria, are characterised by the highest bee diversity (67, 62 and 66 species, respectively), but Tenerife also has remarkable bee diversity ( $n = 63$ ), with many endemic species ( $n = 38$ ). The Selvagens only have one species. The Azores, Madeira Archipelago and Cape Verde Islands actually have similar numbers of wild-bee species (Azores: 17 species; Madeira Archipelago: 19 species; Cape Verde: 14 species), but in the case of the Azores, all are – with one exception – (probably) introduced (see below). The numbers of endemic species/taxa in the following archipelagos are 9 taxa in Cape Verde, 9 taxa in Madeira Archipelago and 1 species in the Azores.



From a worldwide perspective, the wild-bee fauna of some islands is highly threatened by species that are directly or indirectly introduced by humans. Compared to mainlands, islands have the highest numbers of introduced bees (RUSSO 2016). This is documented, e.g. in the cases of Galápagos (RASMUSSEN et al. 2012); Fiji, Samoa and Vanuatu (GROOM et al. 2014a, 2014b); French Polynesia (GROOM et al. 2016); and Hawai'i (SNELLING 2003, MAGNACCA & KING 2013). In Macaronesia, the Azores hold the highest percentage of introduced species: 15 species (88 %; 10 of them clearly introduced, 5 with high probability). The number of introduced bee species for the Madeira Archipelago is 6 species (32 %; 4 of them clearly introduced, 2 with high probability). In the case of the Canary Islands, 4 species (3 %) are introduced, with only one species (7 %) in Cape Verde. Thus, the northern archipelagos of Macaronesia are more affected by introductions than the climatic more extreme southern ones.

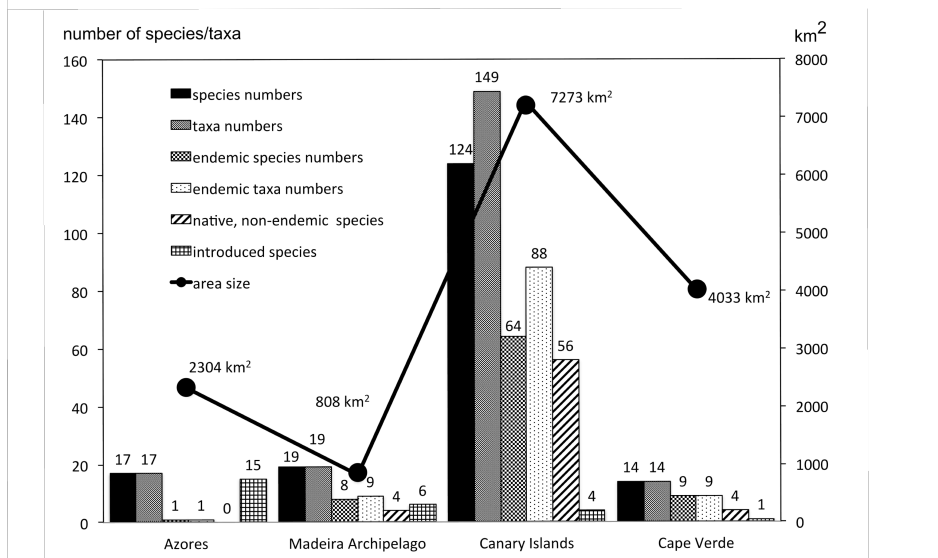


Fig. 4: Number of wild-bee species/taxa of the Archipelagos of Macaronesia (y-axis 1; total species/taxa numbers, endemic, native non-endemic, introduced species/taxa are differentiated. Area sizes (km²) of the specific archipelagos are indicated (y-axis 2).

### 3. Area-type spectra of the wild bees of Macaronesia

An analysis of the area-type spectra of the wild bees of Macaronesia shows great differences between the archipelagos (excluded for this analysis are endemic and introduced species and the Azores with only one probably native, non-endemic species).

The Madeira Archipelago is characterised by species of the Western Palaearctic-Mediterranean region. Western Palaearctic-Mediterranean elements in the Canary Islands are complemented by Holomediterranean and, above all, Sahara-Arabian elements. Cape Verde is dominated by Ethiopian and Sahelo-Sudanese elements. A comparison with the phytogeographic structure of the Macaronesian Islands (POTT et al. 2003) shows a high degree of correspondence with the area-type spectra of wild bees.

## 4. General aspects of wild-bee colonisation

### 4.1 Distance to a mainland source

The distance of the archipelago to a mainland source is significantly and negatively correlated with the number of native and endemic wild-bee species (Fig. 5a). The Canary Islands,

with an actual minimum distance of 96 km to a mainland colonisation source, have many more species than the Azores, with a distance of 1369 km.

It has to be clarified whether the distance between the archipelagos and the mainland was always the same or if there were former ‘stepping stone islands’ (now submerged in the sea as ‘seamounts’).

In the case of the Azores and Cape Verde, there are only seamounts in the direct vicinity of the islands (WHITTAKER & FERNÁNDEZ-PALACIOS 2007, MORATO et al. 2008, EISELE et al. 2015). In the case of the Canary Islands, there are sunken stepping-stone islands, but this does not diminish the already relatively small distance (GELDMACHER et al. 2005, HOERNLE et al. 2009). In the case of the Madeira Archipelago, actually sunken stepping stone islands (Seine 22 Ma, Unicorn 27 Ma, Ampère and Coral Patch 31 Ma, Ormonde 67 Ma) would have shortened the distance to the mainland considerably; GELDMACHER et al. (2005), HOERNLE et al. (2009). These islands represent potential stepping stones from the past (at the earliest, there might have been a bee colonisation in the late Pliocene 3.2-2.6 Ma; see below). Eighteen thousand years ago, the younger ones of the actual seamounts existed as islands (FERNÁNDEZ-PALACIOS et al. 2011). It can be assumed that stepping-stone islands played a role in the wild-bee colonisation process of the Madeira Archipelago.

#### 4.2 Age of the particular archipelago and within the archipelago

The maximum age of an archipelago is significantly and positively correlated with the number of species within the archipelago (Fig. 5b). Within the Canary Islands, the ages of their single islands are also significantly and positively correlated with the number of wild-bee species on those islands (Fig. 5c). This is not true with regard to the age of the islands of the Madeira Archipelago (Desertas, Porto Santo, Madeira Island; Fig. 5d). Porto Santo is an example of the phenomenon of an old, already strongly eroded island. This resulted in loss of altitude, habitats and area size, therefore also a decreasing number of wild-bee species (polynomial curve; see Fig. 5d).

#### 4.3 Size of the particular archipelago and within the archipelago

Different sizes of the archipelagos do not show significant correlations with the number of native bee species in general and endemic wild-bee species. Within the Canary Islands and the Madeira Archipelago, the sizes of the islands are significantly and positively correlated with the number of bee species (Figs 5e, 5f).

### 5. Colonisation of the Madeira Archipelago and the Canary Islands by mining bees (*Andrena*) and their evolution

#### 5.1 Earliest evidence of wild-bee colonisation

There are no wild-bee fossils that determine the time of colonisation, but traces have been discovered in the form of fossilised nest structures in the Canary Islands (EDWARDS & MECO 2000, ALONSO-ZARZA & SILVA 2002, GENISE et al. 2013, LA ROCHE et al. 2014, ZAPATA et al. 2016). Nests of *Anthophora* bees have been detected in Gran Canaria, dated to the late Pliocene 3.2-2.6 Ma (change from tropical wet to semiarid climate, palaeosols); ALONSO-ZARZA & SILVA (2002). Fossil traces of bee nests have also been found in the palaeosols of Fuerteventura and Lanzarote dating from the Quaternary (2.6 Ma ff.). Some nests are similar to those of the recent mining bee *Andrena savignyi* Spinola, 1838; LA ROCHE et al. (2014). Also, some Ichnotaxa have been described as species of the bee genus *Celliforma* (ALONSO-ZARZA & SILVA 2002) and the species *Palmiraichnus castellanosi* (Roselli, 1939); LA ROCHE et al. (2014).

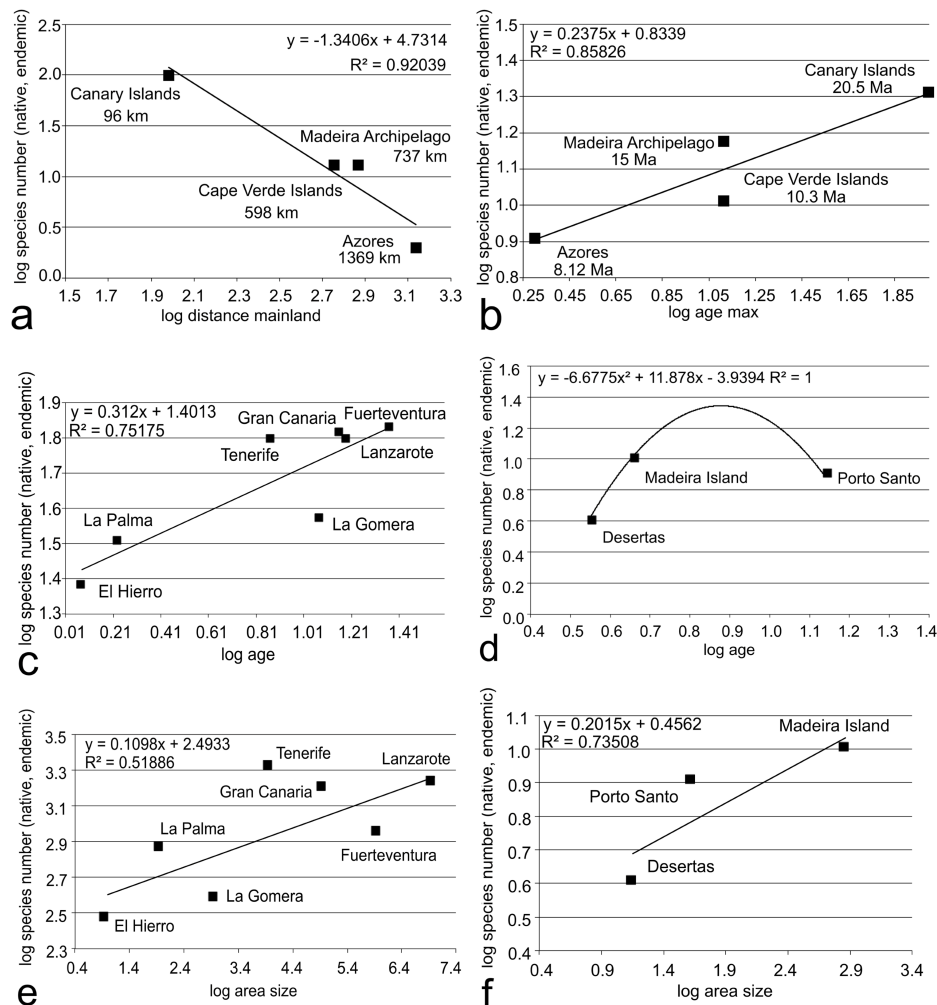


Fig. 5: Correlation (log-log) between the number of native and endemic wild-bee species and a) distance of a colonisation source of the different archipelagos; b) maximum age of the different archipelagos; c) age of the different islands of the Canary Islands; d) age of the different islands of the Madeira Archipelago; e) area size of the different islands of the Canary Islands; and f) area size of the different islands of the Madeira Archipelago.

## 5.2 The mining bee *Andrena tiaretta* or its ancestor as a hypothetical coloniser of the Madeira Archipelago and the Canary Islands

The most important source for colonisation of the Madeira Archipelago and the Canary Islands by mining bee species of the subgenus *Micrandrena* is the North African semiarid and Mediterranean region (KRATOCHWIL & SCHEUCHL 2013, KRATOCHWIL 2014). According to our knowledge, the mining bee *Andrena tiaretta* Warncke, 1974 (named after mount Tiaret in Algeria), played a key role. For this species, a large Mediterranean and Saharo-Arabian distribution area was assumed with localities from southern Spain via Morocco to Syria. The question of whether the populations differ within such a large distribution area arose. Meanwhile, it had been described that there are three distinct species within the *A. tiaretta* aggregate: *A. tiaretta* Warncke, 1974, is restricted to Southern Spain, Morocco, Algeria and Tunisia;

*A. cyrenaica* Kratochwil, 2015, exists in Libya; and *A. orientalis* Kratochwil, 2015, is in Israel (KRATOCHWIL 2015). Between the three species with Saharo-Arabian distribution, a morphological and morphometric feature gradient (in east-west direction) could be identified with the phylogenetically more basal features of the easternly distributed *A. orientalis* and higher evolved features of the western *A. tiaretta*. With high probability, the latter was the coloniser of the Madeira Archipelago and the Canary Islands (KRATOCHWIL 2015).

### 5.3 Radiation of the subgenus *Micrandrena* of the Madeira Archipelago and the Canary Islands

#### 5.3.1 Madeira Archipelago

Theodore Dru Allison Cockerell (1866-1948), an American entomologist and malacologist, described *Andrena wollastoni*, a *Micrandrena* species. According to the knowledge at that time, this species was designated as endemic to Madeira Island and Porto Santo (KRATOCHWIL 2018).

COCKERELL (1922) mentioned the following in his publication: ‘A single female, collected by my wife in Porto Santo, is described as being *A. wollastoni*, although it is distinctly smaller and otherwise slightly different’. KRATOCHWIL & SCHEUCHL (2013) demonstrated that this is a new species and described *Andrena dourada* from Porto Santo, which differs in numerous morphological and morphometric characteristics compared to *A. wollastoni* from Madeira Island (Fig. 6). Based on several morphological features, *A. dourada* shows a close relation to *A. tiaretta*. Our hypothesis is that *A. tiaretta* first colonised Porto Santo (or its former stepping-stone islands) from the North African mainland and evolved to the endemic *A. dourada* (Fig. 7) Porto Santo (14 Ma) was with high probability earlier colonised by wild-bee species than Madeira Island (5 Ma); GELDMACHER et al. (2000). Our hypothesis is that *Andrena dourada* colonised Madeira Island from Porto Santo and developed into the endemic *A. wollastoni* (Fig. 7).



Fig. 6: First published photo of a living individual of the species *Andrena dourada* Kratochwil & Scheuchl, 2013, female, average size 7 mm, endemic to Porto Santo, Pico de Ana Ferreira (flower resource of this individual: *Crambe fruticosa* L.f.: Madeira-Archipelago endemic species), 30.03.2017.

#### 5.3.2 Canary Islands

The German entomologist Klaus Warncke (1937-1993) described the *Micrandrena* taxa of the Canary Islands (which are morphologically similar to *A. wollastoni*) as three endemic subspecies of *A. wollastoni*: *A. wollastoni acuta* Warncke, 1968 (Tenerife, La Palma); *A. wollas-*

*toni catula* Warncke, 1968 (Gran Canaria); and *A. wollastoni gomerensis* Warncke, 1993 (La Gomera). A detailed morphological and morphometric analysis of these three subspecies revealed that they should be upgraded to species and their distribution range should be revised: '*A. catula*' (Gran Canaria), '*A. gomerensis*' (La Gomera, La Palma) and '*A. acuta*' (Tenerife); KRATOCHWIL (2014, detailed descriptions of 'indicated species' in prep.; taxa with quotation marks are not described until yet, KRATOCHWIL in prep.); see also Fig. 7.

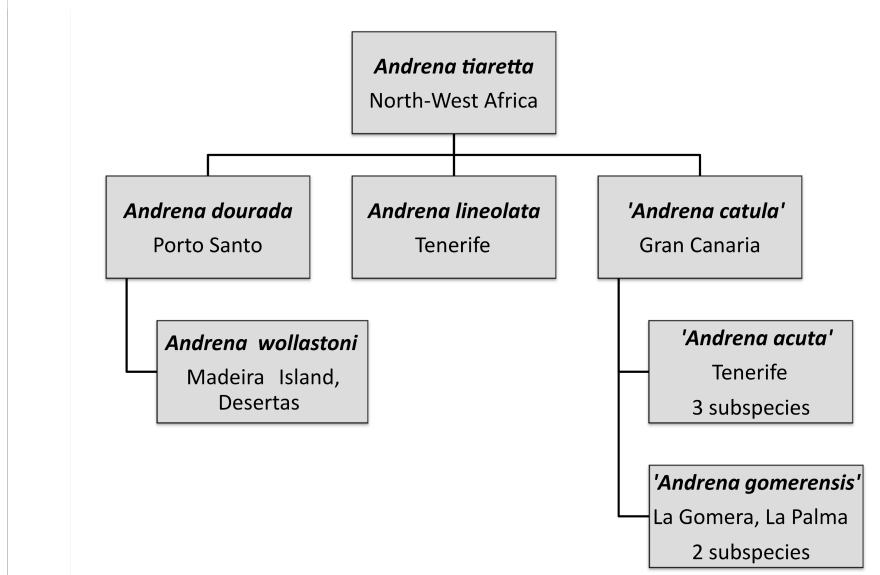


Fig. 7: Radiation of mining bees of the subgenus *Micrandrena*: The Madeira Archipelago and the Canary Islands. Quotation marks: indicate species descriptions in preparation.

In the Canary Islands, there are two other *Micrandrena* species: *A. lineolata* Warncke, 1968, endemic to Tenerife, is also morphologically very close to '*A. catula*' and *A. tiaretta*, and *A. spreata* Pérez, 1895 (Fuerteventura, Lanzarote), which is not related to the other *Micrandrena* species of Canary Islands or to *A. tiaretta*. *A. spreata* is a Mediterranean Saharo-Arabian element and also occurs in North Africa (GUSENLEITNER & SCHWARZ 2000).

The results of the analysis of the *Micrandrena* species of the Canary Islands are summarised in Fig. 7: *A. tiaretta* is the ancestor of all endemic *Micrandrena* species of the Canary Islands. *A. lineolata* shares most morphological features with *A. tiaretta* and '*A. catula*'. There is no doubt that *A. lineolata* was an early endemic *Micrandrena* species originating from the colonisation of *A. tiaretta*/*A. catula*' specimens or their ancestors. Colonisation of the Canary Islands by wild bees occurred at the earliest in the Pliocene (5.3-2.6 Ma); see also comments in CARRACEDO & PÉREZ-TORRADO (2013).

*A. lineolata* exists mainly in Las Cañadas del Teide (altitudes of about 2000 m a.s.l.). It is not known whether a colonisation of Tenerife by *A. tiaretta* or its ancestor took place via Lanzarote and Fuerteventura (age 20.2 Ma, today not populated by a *Micrandrena* species of this taxonomic group) or via Gran Canaria (age 14.6 Ma, where *A. tiaretta* developed into a new endemic species: '*A. catula*'). '*A. catula*' and *A. lineolata* are well-separated species.

'*A. acuta*' is the second *Micrandrena* species of Tenerife and shows numerous more highly evolved features compared to *A. lineolata*. According to morphological and morphometric characteristics, *A. lineolata* and '*A. acuta*' are also distinct species.

The palaeo island Anaga (4.89-3.95 Ma) was with high probability the colonisation area of the ancestors of '*A. acuta*' and *A. lineolata*. ANCOCHEA et al. (1990) hypothesised that Tenerife was built up by the integration of three old massifs. The Anaga and Teno palaeo islands were separated four million years ago. An alternative hypothesis, which was introduced by GUILLOU et al. (2004), is that a large Central Miocene shield (age 11.6-8.9 Ma) extended towards the Anaga massif (4.89-3.95 Ma). According to the latter hypothesis, the Teno volcano (6.11-5.15 Ma) grew attached to the central part.

Morphological and morphometric analyses indicated that '*A. acuta*' exists in Tenerife with three subspecies: one restricted to the Anaga region and another restricted to the Teno region, separated by the formation of barriers of lava flows. From the '*A. acuta*' subspecies in the Anaga area, another subspecies developed, which is distributed in the Dorsal Rift Zone east of the Cañadas up to 2000 m a.s.l. (KRATOCHWIL in prep.).

'*A. catula*' or its ancestors had also colonised La Gomera and developed there into a new species, '*A. gomerensis*', which then colonised La Palma and developed a subspecies of its own. In El Hierro, there is no evidence for the existence of a *Micrandrena* species.

With high probability, similar colonisation processes can also be described for other species groups, e.g. the subgenus *Suandrena* (KRATOCHWIL 2014, KRATOCHWIL et al. 2014). *Andrena fratella* Warncke, 1968, from Morocco is closely related to *A. mirna* Warncke, 1969, from Israel, which is the ancestor. *A. fratella* or its ancestor colonised Fuerteventura and Lanzarote and developed into the endemic species *A. notata* Warncke, 1968. *A. fratella* or its ancestor later colonised Porto Santo or one of the volcanic islands that are today seamounts. In Porto Santo, the endemic species *A. portosanctana* evolved, which then colonised Madeira Island and evolved into the endemic *A. maderensis* Cockerell, 1922.

## 6. Outlook

It has been demonstrated that there were exciting colonisation processes by wild bees mainly in the Canary Islands and the Madeira Archipelago. The colonisation took place not only via mainlands but also via other islands, and in the case of the Madeira Archipelago, also probably via former 'stepping stones', now seamounts. Especially in the case of the Canary Islands, with small distances to the wild-bee 'hot spots' of the Saharo-Mediterranean zone, there had been different colonisation events of different species and genera similar to plant taxa, where different genera show a broad radiation, as in the case of the Crassulaceae genus *Aeonium* or the woody *Echium* species. In contrast, only one bee species of the genus *Hylaeus* colonised Hawai'i, and 63 species were developed by adaptive radiation. The Galápagos Islands are characterised by only one endemic wild-bee species. No other native species exists.

There had been very strong evolutionary processes, which were shown mainly for the small *Andrena* species (subgenus *Micrandrena*), in the Madeira Archipelago and Canary Islands. In order to obtain further evidences of species structures, molecular genetic analyses are being conducted.

Many of the endemic plant species of Macaronesia depend on pollination by wild bees, especially the woody *Echium* species. Other pollinators (mainly not as effective in pollen transfer compared to wild bees) are also present: e.g. butterflies and other insect groups, lizards and birds.

In actuality, there is still rich bee life in many areas despite the high anthropogenic impact. National parks and other protected areas as well as difficult relief situations with no possibil-

ity for construction projects and without intensive agricultural use that included pesticides help to protect the rich bee fauna, which is characteristic especially for the Canary Islands. The two endemic bee species (*Andrena dourada* and *A. portosanctana*) of the anthropogenically highly influenced Island of Porto Santo (Madeira Archipelago) are threatened, and their survival is not guaranteed.

### Acknowledgements

We thank cordially for cooperation: Antonio M.F. Aguiar (Laboratório Agrícola, Camacha, Madeira, Portugal), Jan Smit (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands), Pater Andreas Werner Ebmer (Puchenau, Austria), Holger Dathe (German Entomological Institute, Müncheberg, Germany), Patricia Gentili-Poole and Brian Harris (Department of Entomology Smithsonian Institution, Washington DC, USA), Ysabel Gonçalves (Museu de História Natural do Funchal, Madeira, Portugal), Fritz Gusenleitner (Biology Centre Museum Linz, Austria), James Hogan (Hope Entomological Collections, Oxford University, United Kingdom), Michael Kuhlmann (Kiel University, Zoological Museum, Germany), Vincent F. Lee (Department of Entomology, California Academy of Sciences, San Francisco, CA, USA), Volker Lohrmann and Herbert Hohmann (Übersee-Museum Bremen, Germany), David Nott (Natural History Museum, London, United Kingdom), Hans-Richard Schwenninger (Stuttgart, Germany), Erwin Scheuchl (Ergolding, Germany), Special thanks go to the facilities and authorities in the Madeira Archipelago and the Canary Islands for access and collection permits.

### References

- ALDRIDGE, A.E. (1981): Anatomy and evolution in Macaronesian *Echium* (Boraginaceae). – Plant Syst. Evol. **138**: 9-22.
- ALONSO-ZARZA, A.M. & P.G. SILVA (2002): Quaternary laminar calcretes with bee nests: evidences of small-scale climatic fluctuations, Eastern Canary Islands, Spain. – Palaeogeography, Palaeoclimatology, Palaeoecology **178**: 119-135.
- ANCOCHEA, E., J. FÜSTER, E. IBARROLA, A. CENDRERO, J. COELLO, F. HERNAN, J.M. CANTAGREL & C. JAMOND (1990): Volcanic evolution of the island of Tenerife (Canary Islands) in the light of new K-Ar data. – J. Volcanol. Geotherm Res **44**: 231-249.
- BÁEZ, M., A. GARCÍA & M. KOPONEN (2005): Hymenoptera. – In: ARECHAULETA, M., N. ZURITA, M.C. MARRERO & J.L. MARTÍN (eds.): Lista Preliminar de Especies Silvestres de Cabo Verde (Hongos, Plantas y Animales Terrestres). – Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias, Santa Cruz de Tenerife, Islas Canarias: 96-100.
- BLONDELL, J. & J. ARONSON (1999): Biology and Wildlife of the Mediterranean Region. 350 pp. – Oxford University Press, Oxford.
- BORGES, P.A.V., K. VAN ACHTERBERG, R.R. ASKEW, K. ZWAKHALS, O. OLIVEIRA & A.M.C. SANTOS (2005): Apidae (Hymenoptera). – In: BORGES, P.A.V., R. CUNHA, R. GABRIEL, A.F. MARTINS, L. SILVA & V. VIEIRA (eds.): A list of the terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores. 218 pp. – Direcção Regional do Ambiente and Universidade dos Açores, Horta, Angra do Heroísmo and Ponta Delgada.
- CARRACEDO, J.C. & F.J. PÉREZ-TORRADO (2013): Geological and Geodynamic Context of the Teide Volcanic Complex. – In: CARRACEDO, J.C. & V.R. TROLL (eds.): Teide Volcano. Geology and Eruptions of a Highly Differentiated Oceanic Stratovolcano, 279 pp. – Springer, Berlin, Heidelberg.
- COCKERELL, T.D.A. (1922): New bees from Madeira islands. – Proc. Ent. Soc. Wash. **24** (1): 31-32.
- EDWARDS, N. & J. MECO (2000): Morphology and palaeoenvironment of brood cells of Quaternary ground-nesting solitary bees (Hymenoptera, Apidae) from Fuerteventura, Canary Islands, Spain. – Proceedings of the Geologists' Association **111**: 173-183.
- EISELE, S., A. FREUNDT, R.S. RAMALHO, T. KWASNITSCHKA, K.-L. WANG & S.R. HEMMING (2015): Stratigraphy of the Pleistocene, phonolitic Cão Grande Formation on Santo Antão, Cap Verde. – J. Volcanol. Geoth. Res. **301**: 204-220.

- FELLENDORF, M., C. MOHRA, S. ROBERTS, P. WIRTZ & G. van der ZANDEN (1999): The bees of Madeira (Hymenoptera, Apoidea). – *Bocagiana. Museu Municipal do Funchal (História Natural)* **197**: 1-17.
- FERNÁNDEZ-PALACIOS, J.M., L. DE NASCIMENTO, R. OTTO, J.D. DELGADO, E. GARCÍA-DEL-REY, J.R. ARÉVALO & R.J. WHITTAKER (2011): A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. – *J. Biogeogr.* **38**: 226-246.
- FRANQUINHO DE AGUIAR, A., K. VAN ACHTERBERG, R.R. ASKEW, K. ZWAKHALS, A.M.C. SANTOS & P.A.V. BORGES (2010): Apidae (Hymenoptera). – In: BORGES, P.A.V., A. COSTA, A. CUNHA, R. GABRIEL, V. GONÇALVES, A.F. MARTINS, I. MELO, M. PARENTE, P. RAPOSEIRO, P. RODRIGUES, R.S. SANTOS, L. SILVA, P. VIEIRA & V. VIEIRA (eds.): A list of the terrestrial and marine biota from the Azores, 244 pp. – *Principia, Cascais*.
- GELDMACHER, J., P. VAN DEN BOGAARD & H.-U. SCHMINCKE (2000): The  $^{40}\text{Ar}/^{39}\text{Ar}$  age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). – *Geochim. Geophys. Geosyst.* **1** (1): 1008.
- GELDMACHER, J., K. HOERNLE, P.V.D. BOGAARD, S. DUGGEN & R. WERNER (2005): New  $^{40}\text{Ar}/^{39}\text{Ar}$  age and geochemical data from seamounts in the Canary and Madeira Volcanic Provinces: A contribution to the ‘Great Plume Debate’. – *Earth and Planetary Science Letters* **237**: 85-101.
- GENISE, J.F., A.M. ALONSO-ZARZA, M. VERDE & A. MELÉNDEZ (2013): Insect trace fossils in aeolian deposits and calcretes from the Canary Islands: Their ichnotaxonomy, producers, and palaeoenvironmental significance. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **377**: 110-124.
- GONZALEZ, V. H., J.B. KOCH & T. GRISWOLD (2010): *Anthidium vigintiduopunctatum* Friese (Hymenoptera: Megachilidae): the elusive ‘dwarf bee’ of the Galápagos Archipelago? – *Biol. Invasions* **12**: 2381-2383.
- GROOM, S., S. HAYES, H. NGO, M. STEVENS & M. SCHWARZ (2014a): Recipe for disruption: Multiple recent arrivals of megachilid bees in Pacific archipelagos. – *J. Insect Conserv.* **18**: 613-622.
- GROOM, S., H. NGO, S. REHAN & P. SKELTON (2014b): Multiple recent introductions of apid bees into Pacific archipelagos signify potentially large consequences for both agriculture and indigenous ecosystems. – *Biol. Invasions* **16**: 2293-2302.
- GROOM, S., M. STEVENS, T. RAMAGE & M. SCHWARZ (2016): Origins and implications of apid bees (Hymenoptera: Apidae) in French Polynesia. – *Entomol. Sci.* **20** (1): 65-75
- GUILLOU, H., J.C. CARRACEDO, R. PARIS & F.J. PÉREZ-TORRADO (2004): Implications for the early shield-stage evolution of Tenerife from K/Ar ages and magnetic stratigraphy. – *Earth Planet Sc. Lett.* **222**: 599-614
- GUSENLEITNER, F. & M. SCHWARZ (2002): Weltweite Checkliste der Bienengattung *Andrena* mit Bemerkungen und Ergänzungen zu paläarktischen Arten (Hymenoptera, Apidae, Andreninae, Andrena). – *Entomofauna, Suppl.* **12**: 1-1280.
- HOERNLE, K. & J.-C. CARRACEDO (2009): Canary Islands, Geology. – In: GILLESPIE, R.D. & D.A. CLAGUE (eds.): *Encyclopedia of Islands*: 133-143. University of California Press, Berkeley, California, USA.
- HOHMANN, H., F. LA ROCHE, G. ORTEGA & J. BARQUIN (1993): Bienen, Wespen und Ameisen der Kanarischen Inseln (Insecta: Hymenoptera: Aculeata). – *Veröff. Überseemus. Bremen, Naturw.* **12** (1): 14-465, (col.) pls. I-XII; **12** (2): 493-712.
- KRAEMER M & U. SCHMITT (1997): Nectar production patterns and pollination of the Canarian endemic *Echium wildpretii* Pearson ex Hook. fil. – *Flora* **192**: 217-221.
- KRATOCHWIL, A. (2003): Bees (Hymenoptera: Apoidea) as keystone species: specifics of resource and requisite utilisation in different habitat types. – *Berichte der Reinhold-Tüxen-Gesellschaft* **15**: 59-77.
- KRATOCHWIL, A. (2014): *Suandrena* and *Micrandrena* species of the Canary Islands and the Madeira Archipelago – new taxonomic, phylogenetic and biogeographical aspects. – *Mitt. Entomol. Ver. Stuttgart* **49** (1): 18-19.
- KRATOCHWIL, A. (2015): Revision of the *Andrena* (*Micrandrena*) *tiaretta* group: redescription of *A. tiaretta* Warncke (1974) and description of two new species (*A. cyrenaica* nov.sp. and *A. orientalis* nov.sp.) demarcating the central and eastern part of the range (Libya, Israel, Syria). – *Linzer biologische Beiträge* **47** (2): 1403-1437.
- KRATOCHWIL, A. (2018): Type specimens of *Andrena wollastoni* COCKERELL, 1922 (Hymenoptera, Anthophila): Deposition, evaluation and designation of a lectotype. – *Linzer biologische Beiträge* **50** (1): 1-14.



- KRATOCHWIL, A., A.M.F. AGUIAR & J. SMIT (2008): Hymenoptera - Apoidea. – In: BORGES, P.A.V., C. ABREU, A.M.F. AGUIAR, P. CARVALHO, R. JARDIM, I. MELO, P. OLIVEIRA, C. SÉRGIO, A.R.M. SERRANO & P. VIEIRA (eds.): A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos. – Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo: 346. Funchal, Madeira.
- KRATOCHWIL, A. & E. SCHEUCHL (2013): *Andrena (Micrandrena) dourada* nov.sp. from Porto Santo, Madeira Archipelago, Portugal. – Linzer biologische Beiträge **45** (1): 755-774.
- KRATOCHWIL, A. & A. SCHWABE (2018): The bee fauna of Porto Santo: distribution pattern and pollinator network. – Linzer biologische Beiträge **50** (2).
- KRATOCHWIL, A., A. SCHWABE & E. SCHEUCHL (2014): *Andrena (Suandrena) portosanctana* Cockerell, 1922 and *A. (Suandrena) maderensis* Cockerell, 1922 – new taxonomical and ecological data for two closely related endemic bee species of the Madeira Archipelago, Portugal. – Linzer biologische Beiträge **46** (2): 1535-1567.
- KRATOCHWIL, A., SMIT, J. & A.F. AGUIAR (2018): Updated checklist of the wild bees of the Madeira Archipelago (Hymenoptera: Apoidea: Anthophila). – Linzer biologische Beiträge **50** (2).
- KUHLMANN, M. (2000): Katalog der paläarktischen Arten der Bienengattung *Colletes* Latr., mit Lectotypenfestlegungen, neuer Synonymie und der Beschreibung von zwei neuen Arten (Hymenoptera: Apidae: Colletinae). – Linzer biologische Beiträge **32**: 155-193.
- KUNKEL, G. (1993): Die Kanarischen Inseln und ihre Pflanzenwelt. 3. Aufl., 239 S. – Gustav Fischer, Stuttgart.
- LOBIN, W. (1982): Untersuchungen über Flora, Vegetation, und biogeographische Beziehungen der kapverdischen Inseln. – Cour. Forsch.-Inst. Senckenberg **53**: 1-112, Frankfurt.
- LA ROCHE, F., J.F. GENISE, C. CASTILLO, M.L. QUESADA, C.M. GARCÍA-GOTERA & J. DE LA NUEZ (2014): Fossil bee cells from the Canary Islands. Ichnotaxonomy, palaeobiology and palaeoenvironments of *Palmiraichnus castellanosi*. – Palaeogeography, Palaeoclimatology, Palaeoecology **409**: 249-264.
- LÜPNITZ, D. (1995): Beitrag zur phytogeographischen Stellung der Kanarischen Inseln. – Mainzer naturwiss. Archiv **33**: 83-93.
- MAGNACCA, K. & C. KING (2013): Assessing the Presence and Distribution of 23 Hawaiian Yellow-Faced Bee Species on Lands Adjacent to Military Installations on O’ahu and Hawai’i Island. 26 pp. and appendix. – Pacific Cooperative Studies Unit, University of Hawaii at Manoa: Honolulu, HI, USA.
- MICHENER, C.D. (2007): The Bees of the World. 2nd ed., 992 pp. – John Hopkins University Press, Baltimore & London.
- MORATO, T., D.A. VARKEY, C. DAMASO, M. MACHETE, M. SANTOS, R. PRIETO, R.S. SANTOS & T. J. PITCHER (2008): Evidence of a seamount effect on aggregating visitors. – Marine Ecology Progress **357**: 23-32.
- PATINY, S. (2003): Contemporary distributions of *Panurginus* species and subspecies in Europe (Apoidea: Andrenidae: Panurginae). – Proc. 13th Int. Coll. EIS, September 2001: 115-121. Leiden.
- PAULY, A., PESENKO, Y.A. & F. LA ROCHE (2002): The Halictidae of the Cape Verde Islands (Hymenoptera Apoidea). – Bulletin de l’Institut Royal des Sciences Naturelles de Belgique. Entomologie **72**: 201-211.
- PÉREZ, A.J. & N. MACÍAS-HERNÁNDEZ (2012): Presencia de *Bombus (Megabombus) ruderatus* en Canarias. – Rev. Acad. Canar. Cienc. **24**: 103-114.
- PESENKO, Y. A. & A. PAULY (2005): Monograph of the bees of the subfamily Nomiodinae (Hymenoptera: Halictidae) of Africa (excluding Madagascar). – Ann. soc. entomol. Fr. (n.s.) **41** (2): 129-236.
- POTT, R., J. HÜPPE & W. WILDPRETT DE LA TORRE (2003): Die Kanarischen Inseln. Natur- und Kulturlandschaften, 320 S. – Ulmer, 320 S., Stuttgart.
- RASMUSSEN, C., A.L. CARRION, R. CASTRO-URGAL, S. CHAMORRO, V.H. GONZÁLEZ, T.L. GRISWOLD, H.W. HERRERA, C.K. MCMULLEN, J.M. OLESEN & A. TRAVESET (2012): *Megachile timberlakei* Cockerell (Hymenoptera: Megachilidae): Yet another adventive bee species to the Galápagos Archipelago. – The Pan-Pacific Entomologist **88** (1): 98–102.
- RUSSO, L. (2016): Positive and negative impacts of non-native bee species around the World. – Insects **7**: 1-22.
- SCHÄFER, H. (2003): Chorology and Diversity of the Azorean Flora. – Diss. Bot. **374**: 1-130; 1 CD-Rom.

- SCHEUCHL, E. & H.R. SCHWENNINGER (2015): Kritisches Verzeichnis und aktuelle Checkliste der Wildbienen Deutschlands (Hymenoptera, Anthophila) sowie Anmerkungen zur Gefährdung. – Mitt. Ent. Ver. Stuttgart, **50** (1): 3-225.
- SMIT, J. (2007): New wasps and bees for the fauna of the Canary Islands (Hymenoptera, Aculeata). – Linzer biol. Beitr. **39** (1): 651-656.
- SNELLING, R. (2003): Bees of the Hawaiian Islands, exclusive of *Hylaeus* (*Nesoprotopis*) (Hymenoptera: Apoidea). – J. Kansas Entomol. Soc. **76**: 342-356.
- SUÁREZ, D., D. HERNÁNDEZ-TEIXIDOR, A.J. PÉREZ, E. FERRERA-LEÓN, J.J. ARECHAVALETA & P. OROMI (2017): New chorological data on arthropod biodiversity in the Canary Islands (Spain). – Boletim de la Sociedad Entomológica Aragonesa (S.E.A.) **60**: 349-351.
- TKALCU, B. (1993): Neue Taxa der Bienen von den Kanarischen Inseln. Mit Bemerkungen zu einigen bereits bekannten Arten. – Veröff. Überseemus. Bremen, Naturw. **12**: 791-858.
- STRAKA, J. & M.S. ENGEL (2012): The apid cuckoo bees of the Cape Verde Islands (Hymenoptera, Apidae). – ZooKeys **218**: 77-109.
- WEISSMAN, J.A., A. PICANÇO, P.A.V. BORGES & H. SCHAEFER (2017): Bees of the Azores: an annotated checklist (Apidae, Hymenoptera). – ZooKeys. **642**: 63-95.
- WHITTAKER, R.J. & J.M. FERNÁNDEZ-PALACIOS (2007): Island Biogeography. Ecology, Evolution, and Conservation. 2nd ed., 416 pp. – Oxford University Press.
- ZAPATA, L., V. KRAPOVICKAS, M.S. RAIGEMBOM & S.D. MATHEOS (2016): Bee cell trace fossils associations on paleosols from the Santa Cruz Formation: Palaeoenvironmental and palaeobiological implications. – Palaeogeography, Palaeoclimatology, Palaeoecology **459**: 153-169.

#### Addresses of the authors:

Prof. Dr. Anselm KRATOCHWIL, Department of Biology/Chemistry, Ecology Section, University of Osnabrück, Barbarastraße 13, D-49069 Osnabrück, Germany

Corresponding author: E-Mail: [anselm.kratochwil@biologie.uni-osnabrueck.de](mailto:anselm.kratochwil@biologie.uni-osnabrueck.de)

Prof. Dr. Angelika SCHWABE, Department of Biology, Technische Universität Darmstadt, Schnittspahnstraße 4, D-64287 Darmstadt, Germany

Fotos von den Autoren

# ZOBODAT - [www.zobodat.at](http://www.zobodat.at)

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Berichte der Reinhold-Tüxen-Gesellschaft](#)

Jahr/Year: 2018

Band/Volume: [30](#)

Autor(en)/Author(s): Kratochwil Anselm, Schwabe [Kratochwil] Angelika

Artikel/Article: [Wild bees \(Anthophila\) of Macaronesia – biogeographical and evolutionary aspects 149-162](#)