

Narrow flower specialization in two European bee species of the genus *Colletes* (Hymenoptera: Apoidea: Colletidae)

ANDREAS MÜLLER¹ and MICHAEL KUHLMANN²

¹Institute of Plant Sciences, Applied Entomology, Swiss Federal Institute of Technology (ETH), Clausiusstrasse 25/NW, CH-8092 Zurich, Switzerland; e-mail: andreas.mueller@ipw.agrl.ethz.ch

²University of Münster, Institute of Landscape-Ecology, Robert-Koch-Str. 26, D-48149 Münster, Germany; e-mail: kuhlmmi@uni-muenster.de

Key words. Apoidea, Colletidae, *Colletes*, Boraginaceae, *Cynoglottis*, flower specialization, monolectic, oligolectic, distribution, pollen collection, morphological adaptation

Abstract. *Colletes anchusae* Noskiewicz, 1924 and *C. wolffi* Kuhlmann, 1999 (Colletidae) are closely related bee species with vicariant distributions, the former occurring in east and southeast Europe and Turkey, the latter restricted to the Italian peninsula. Microscopical analysis of scopal pollen revealed that in Europe both species are monolectic collecting pollen exclusively from flowers of *Cynoglottis barrelieri* (All.) Vural & Kit Tan (Boraginaceae). In Turkey, *C. anchusae* possibly visits also *Cynoglottis chetikiana* Vural & Kit Tan. The distributions of the two bee species and of *Cynoglottis* coincide. The females of both *Colletes* species are equipped with stout, curved bristles on their foretarsi used for scraping pollen out of the narrow flower tube of *Cynoglottis*. Compared to other European species of *Colletes* the foretarsi of *C. anchusae* and *C. wolffi* are shortened, presumably an adaptation to the short corolla tube of their host plant.

INTRODUCTION

The closely related bee species *Colletes anchusae* Noskiewicz, 1924 and *Colletes wolffi* Kuhlmann, 1999 are unique among palaearctic *Colletes* in that their females have simple, non bifurcate claws and strongly modified foretibia (Noskiewicz, 1936; Kuhlmann, 1999). In addition to the peculiarly shaped tibia the foretarsi of the females of both species are beset with stout, curved bristles distinctly different from the tarsal hairs of other *Colletes* bees. The females of four North American *Calliopsis* species (Andrenidae), the Australian *Leoproctus macmillani* (Colletidae) and the Eurasian *Colletes nasutus* (Colletidae) have similar tarsal bristles (Shinn, 1967; Houston, 1991; Müller, 1995). In these bee species, the specialized bristles serve to scrape pollen out of the narrow flower tubes of *Verbena* (Verbenaceae), *Astroloma* (Epacridaceae) and *Anchusa* (Boraginaceae), respectively.

There is little doubt that the females of *C. anchusae* and *C. wolffi* use the tarsal bristles to extract pollen from flowers with hidden anthers. Indeed, in Hungary and the Ukraine *C. anchusae* was repeatedly observed on flowers of *Anchusa barrelieri* (All.) Vitman, a member of the Boraginaceae with narrow flower tubes (Noskiewicz, 1924, 1936; Móczár, 1961). *A. barrelieri* differs from other *Anchusa* species in having distinctly smaller pollen grains and a short corolla tube (Vural & Kit Tan, 1983). Because of these differences Vural & Kit Tan (1983) put *A. barrelieri* in its own genus, *Cynoglottis*. Recently, a second *Cynoglottis* species, *C. chetikiana* Vural & Kit Tan, was described from Turkey (Vural & Kit Tan, 1983).

The aim of this study was to examine the host plant spectrum of *C. anchusae* and *C. wolffi*, to compare the distributions of these two bee species with that of their host plants and to analyze potential adaptations of bee morphology to flower structure.

MATERIALS AND METHODS

Pollen sources

To assess the pollen plants of *C. anchusae* and *C. wolffi* we analyzed the scopal contents of females from museum and private collections by light microscopy using the method outlined by Westrich & Schmidt (1986). We identified the pollen grains at a magnification of 400× and 1000× with the aid of Clarke (1980), the literature cited in Westrich & Schmidt (1986) and a reference collection containing the pollen of nearly all European genera of the Boraginaceae, including *Cynoglottis*.

C. anchusae and *C. wolffi* are among the rarest *Colletes* species in Europe. Though all available material was examined only 13 females each of *C. anchusae* and *C. wolffi* had pollen in their scopa. These 26 bee specimens were collected at 15 different localities. The pollen samples from *C. anchusae* originate from Macedonia (1 sample), Bulgaria (1) and the Turkish provinces of Antalya (1), Konya (2), Adana (1), Nevsehir (2) and Erzincan (5), the samples from *C. wolffi* from the Italian provinces of Piemonte (8), Toscana (1), Umbria (2) and Abruzzo (2).

Distribution

The distribution of the genus *Cynoglottis* was clarified with the aid of regional, national and European floras. For details regarding habitat and flowering time Davis (1978, 1988), Pignatti (1982), Shishkin (1974), Strid & Kit Tan (1991) and Vural & Kit Tan (1983) were consulted.

Information on the distribution and flight period of *C. anchusae* and *C. wolffi* were extracted from Noskiewicz (1924, 1936) and the *Colletes* data bank of M. Kuhlmann (unpublished).

Bee morphology and flower structure

To examine the structure of the flowers of *C. barrelieri* herbarium specimens were soaked in water.

To estimate the fit between leg length and corolla depth the relative length of the foreleg of *C. anchusae* and *C. wolffi* was compared with that of 16 other European and North African



Fig. 1. Distribution of *Cynoglottis* (shaded) and localities for *Colletes anchusae* (squares) and *C. wolfi* (triangles) in Europe and Asia Minor.

Colletes species, each belonging to another species group (see Kuhlmann, 2000), by calculating the ratio of leg length to forewing length. Forewing length was used as a measure of body size. The lengths of femur, tibia and tarsus (up to the insertion of the claws), and forewing (along the anterior margin) were measured under a dissecting microscope to the nearest 1/20 mm. For this nine females of *C. anchusae*, ten females of *C. wolfi* and two females each of *C. albomaculatus* (Lucas, 1849), *C. cunicularius* (Linnaeus, 1761), *C. daviesanus* Smith, 1846, *C. formosus* Pérez, 1895, *C. gallicus* Radoszkowski, 1891, *C. hederæ* Schmidt & Westrich, 1993, *C. hylaeiformis* Eversmann, 1852, *C. impunctatus* Nylander, 1852, *C. lacunatus* Dours, 1872, *C. maidli* Noskiewicz, 1936, *C. marginatus* Smith, 1846, *C. meyeri* Noskiewicz, 1936, *C. mlokoszewicz* Radoszkowski, 1891, *C. moricei* Saunders, 1904, *C. nasutus* Smith, 1853 and *C. nigricans* Gistel, 1857 were selected.

RESULTS

Pollen sources

The pollen samples from both *C. anchusae* and *C. wolfi* consisted of exactly the same pollen type. At a magnification of 1000×, the pollen grains in the 26 samples could not be distinguished from a reference pollen sample of *C. barrelieri*.

Distribution

C. barrelieri occurs from Italy eastwards to Turkey and Syria, and northwards to the Ukraine and Russia (Fig. 1). The distribu-

tion is split into two parts, a western part covering Italy and an eastern part ranging from Slovenia eastwards. *C. chetikiana*, the second species of the genus, is endemic to north, central and south Anatolia. In Turkey, the distributions of the two *Cynoglottis* species partially overlap. Both species grow on dry rocky slopes, stony pastures, fallow fields and open coniferous forest, mostly on limestone. Depending on the altitude the flowering time is May to July.

C. wolfi and *C. anchusae* show a vicariant distribution (Fig. 1). *C. wolfi* is confined to Italy whereas *C. anchusae* is found in east and southeast Europe and Turkey. All known localities of the two *Colletes* species fall within the distribution area of *Cynoglottis*. Collection records date from 7 May to 28 July (n = 24) for *C. anchusae* and from 27 May to 19 July (n = 25) for *C. wolfi*.

Bee morphology and flower structure

The corolla of *C. barrelieri* is blue to bluish-violet. The limb is almost flat, 6–9 mm across, with rounded lobes (Fig. 2). The narrowly campanulate tube is short, measuring 1.0 to 1.5 mm in depth and 2.0 mm in diameter. At its apex the tube is narrowed by five whitish faucal scales, which protrude slightly from the tube. The anthers are hidden under the hairy scales and reach the base of the scales. The style is included and about half as long as the tube.

The forelegs of both *C. anchusae* and *C. wolfi* are modified in two ways. The slightly curved tibia is on its outer surface distinctly concave and hairless (Fig. 3) and the basitarsus is beset

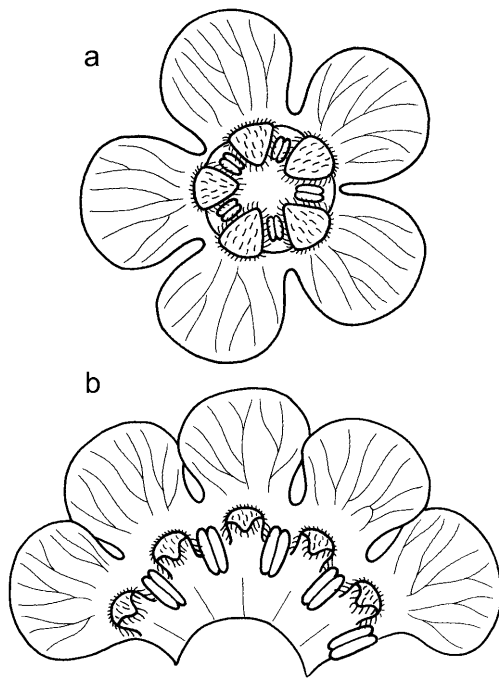


Fig. 2. *Cynoglottis barrelieri*: corolla from above (a) and dissected (b). 7× natural size.

with stout, curved bristles on its outside and along its longitudinal borders (Figs 4–5). The same type of curved bristles are found on tarsal segments 2 to 4. The total length of the foretarsus (without claws) is 1.3 to 1.4 mm, the bristle bearing part is about 1 mm long.

The tarsus of the foreleg of *C. anchusae* and *C. wolfi* is significantly shorter relative to body size (mean = 0.191, $s = 0.005$, $t = -13.854$, $p < 0.0001$, $n = 19$) compared to the other *Colletes* species (mean = 0.224, $s = 0.010$, $n = 32$). In contrast, the total relative length of the foreleg, comprising tarsus, tibia and femur, does not significantly differ between *C. anchusae* and *C. wolfi* (mean = 0.600, $s = 0.010$, $t = -1.970$, $p = 0.055$, $n = 19$) and the other *Colletes* species (mean = 0.616, $s = 0.033$, $n = 32$).

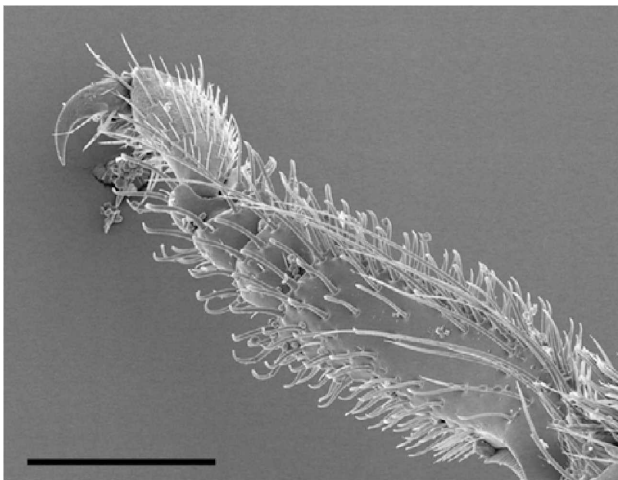


Fig. 4. *Colletes wolfi*: female left foretarsus seen from the outside. (Scale bar = 300 μm)

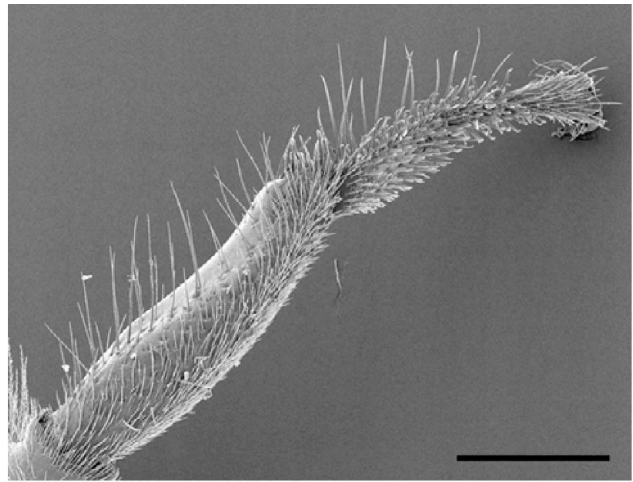


Fig. 3. *Colletes wolfi*: female left foreleg seen from above. (Scale bar = 500 μm)

DISCUSSION

Pollen sources

All scopal pollen from both *C. anchusae* and *C. wolfi* consisted only of *Cynoglottis* pollen suggesting an exclusive preference for this boraginaceous plant. The 26 pollen samples originated from 15 different localities scattered over most of the distribution areas of the two *Colletes* species. This strong specialization is corroborated by observations made in the Ukraine where *C. anchusae* is quite common and collects pollen exclusively from *Cynoglottis barrelieri* (Noskiewicz, 1924, 1936). In Hungary, *C. anchusae* is also believed to be a specialist of this plant species (Móczár, 1961). The close match in the distributions of the bees and *Cynoglottis* is a further indication of this intimate relationship as is the coincidence of the flowering time of *Cynoglottis* with the flight period of the bees.

C. barrelieri is the only *Cynoglottis* species in Europe. In Turkey, a second *Cynoglottis* species occurs. *C. chetikiana* differs from *C. barrelieri* in its distinctly longer corolla tube (Vural & Kit Tan, 1983). Whether *C. anchusae* also visits flowers of *C. chetikiana* in Turkey is an open question.

C. anchusae and *C. wolfi* are not the only European species of *Colletes* with very restricted flower preferences. *C. nasutus* seems to visit only *Anchusa officinalis* (Boraginaceae), *C. sier-*

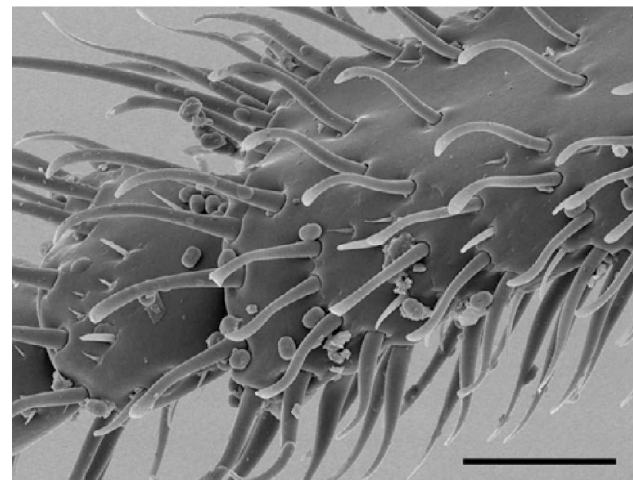


Fig. 5. *Colletes wolfi*: Apex of basitarsus and second tarsal segment seen from the outside. (Scale bar = 90 μm)

rensis is a likely monolege of *Odontites viscosa* (Scrophulariaceae), *Colletes hederæ* restricts pollen harvesting to *Hedera helix* (Araliaceae), *C. punctatus* is presumed to collect pollen exclusively from *Nigella* (Ranunculaceae), *C. graeffei* probably visits only *Allium* (Liliaceae) and *C. hylaeiformis* is specialized to *Eryngium* (Apiaceae) (Noskiewicz, 1936; Westrich, 1990; Schmidt & Westrich, 1993; Westrich & Amiet, 1996; Mader, 1999; own observations). Though the percentage of oligolectic species might be higher in the genus *Colletes* than in other bee genera in Europe (Westrich, 1990; Westrich, 2001) not all European *Colletes* species are narrow pollen specialists. *C. floralis* is highly polylectic (Westrich, 2001) and the microscopical analysis of several hundred pollen samples from many western palaearctic *Colletes* species revealed that in several species groups polylectic species occur (Müller & Kuhlmann, unpublished).

Distribution

C. wolffi and *C. anchusae* differ morphologically only slightly (Kuhlmann, 1999) indicating a recent separation of these two species. This is compatible with the hypothesis that populations of the ancestor of the two species survived the ice age in at least two refuges, one in Italy and another in southeast Europe or Turkey, from where they spread northwards after the end of the last glacial period. The gap in the distribution area of their host plant might then have prevented the two populations from coming into contact again.

Both *C. anchusae* and *C. wolffi* are considered to be very rare. However, their flower specialization might account for why these bees are so rarely collected in the field. We expect them to be much more widespread occurring wherever *Cynoglossis* grows.

Bee morphology and flower structure

Thirteen Central European species of bees belonging to four families and five genera are known to have evolved stout, curved bristles either on the forelegs or on the proboscis (Müller, 1995). In all these species the specialized bristles serve to extract pollen from the flowers of plants whose anthers are hidden in narrow tubes. Similar morphological specializations are also known in bees from outside Europe (Shinn, 1967; Thorp, 1979, 2000; Houston, 1991). Here too, the modified hairs are a tool for removing pollen from narrow flower tubes. Though field observations are still lacking both *C. anchusae* and *C. wolffi* are thought to use the specialized bristles on their foretarsi to harvest pollen from *Cynoglossis*. Females of *C. nasutus* are known to insert both forelegs simultaneously into a flower tube of *Anchusa officinalis* before extracting pollen from the hidden anthers with repeated upward and downward movements of their forelegs (Müller, 1995). Females of *C. anchusae* and *C. wolffi* probably collect pollen in much the same way.

The function of the modified female tibia in *C. anchusae* and *C. wolffi* is obscure. The tibial curvature might enable the bees to bring the tarsi of their forelegs closer together and in a parallel position before they are simultaneously inserted into the narrow entrance of a flower.

In both *C. anchusae* and *C. wolffi* the development of hooked bristles on the foretarsus is accompanied by a shortening of the foretarsus. The tarsal length is similar to the tube length of *C. barrelieri*. Consequently, the shortening of the foretarsus might be an adaptation to the short corolla tube of the host plant allowing the bees to use the total length of their tarsi to scrape pollen out of the flower. In contrast to *C. anchusae* and *C. wolffi* forelegs, head and proboscis of *C. nasutus* are distinctly lengthened compared to other European *Colletes* species, doubtless an adaptation for collecting pollen and nectar from the deep tubular

flowers of *Anchusa officinalis*, which are 7 to 10 mm long (Müller, 1995).

ACKNOWLEDGEMENTS. We thank Slavica Katulic for compiling information on the distribution of *Cynoglossis*, Dr. Reto Nyffeler (Institute for Systematic Botany, University of Zurich) for the permission to work in the herbarium, Urs Jauch (Institute for Botany, University of Zurich) for help with the scanning electron microscope, Fritz Gusenleitner (Oberösterreichisches Landesmuseum, Linz) and Guido Pagliano (Museo Regionale di Scienze Naturali, Torino) for loan of specimens from collections under their curatorship, Dr. Kathrin Tschudi-Rein (ETH Zurich) for correcting the English and Prof. Dr. Silvia Dorn (ETH Zurich), Dr. Jörg Samietz (ETH Zurich) and three reviewers for helpful comments on earlier drafts of the manuscript.

REFERENCES

- CLARKE G.C.S. 1980: Boraginaceae. In: Punt W. & Clarke G.C.S. (eds): *The Northwest European Pollen Flora*. Vol. 2. Elsevier, Amsterdam, pp. 59–102.
- DAVIS P.H. 1978: *Flora of Turkey and the East Aegean Islands*. Vol. 6. University Press, Edinburgh, 825 pp.
- DAVIS P.H. 1988: *Flora of Turkey and the East Aegean Islands*. Vol. 10. University Press, Edinburgh, 590 pp.
- HOUSTON T.F. 1991: Two new and unusual species of the bee genus *Leioproctus* Smith (Hymenoptera: Colletidae), with notes on their behaviour. *Rec. West. Austral. Mus.* **15**: 83–96.
- KUHLMANN M. 1999: *Colletes wolffi* spec. nova from Italy, and lectotype designation for palaearctic bees of the genus *Colletes* Latr., with notes on new homonymies and synonymies (Hymenoptera: Apidae: Colletinae). *Linz. Biol. Beiträge* **31**: 71–81.
- 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). *Linz. Biol. Beiträge* **32**: 155–193.
- MADER D. 1999: *Geologische und Biologische Entomöökologie der Rezenten Seidenbiene Colletes*. Band 1. Logabook, Köln, 807 pp.
- MÖCZÁR M. 1961: Revision, Faunakatalog und ethologische Angaben über die Arten der Gattung *Colletes* Latr. (Fam. Colletidae II., Cat. Hym. XIX). *Folia Entomol. Hungar., N.S.* **14**: 403–412. [in Hungarian, German abstr.]
- MÜLLER A. 1995: Morphological specializations in Central European bees for the uptake of pollen from flowers with anthers hidden in narrow corolla tubes (Hymenoptera: Apoidea). *Entomol. Gener.* **20**: 43–57.
- NOSKIEWICZ J. 1924: Zwei neue Bienenarten aus Polen. *Kosmos* **49**: 118–127. [in Polish, German abstr.]
- NOSKIEWICZ J. 1936: Die palaarktischen *Colletes*-Arten. *Pr. Nauk. Wyd. Tow. Nauk, Lwow* **3**: 1–531.
- PIGNATTI S. 1982: *Flora d'Italia*. Vol. 2. Edagricole, Bologna, 732 pp.
- SCHMIDT K. & WESTRICH P. 1993: *Colletes hederæ* n. sp., eine bisher unerkannte, auf Efeu (*Hedera*) spezialisierte Bienenart (Hymenoptera: Apoidea). *Entomol. Zeitschr.* **103**: 89–112.
- SHINN A.F. 1967: A revision of the bee genus *Calliopsis* and the biology and ecology of *C. andreniformis* (Hymenoptera: Andrenidae). *Kans. Univ. Sci. Bull.* **46**: 876–891.
- SHISHKIN B.K. 1974: *Flora of the U.S.S.R.* Vol. 19 (Tubiflorae). Israel Program for Scientific Translations, Jerusalem, 556 pp.
- STRID A. & KIT TAN 1991: *Mountain Flora of Greece*. Vol. 2. University Press, Edinburgh, 974 pp.

- THORP R.W. 1979: Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. *Ann. Miss. Bot. Garden* **66**: 788–812.
- THORP R.W. 2000: The collection of pollen by bees. *Plant Syst. Evol.* **222**: 211–223.
- VURAL M. & KIT TAN 1983: New taxa and records from Turkey. *Notes RBG Edinb.* **41**: 65–76.
- WESTRICH P. 1990: *Die Wildbienen Baden-Württembergs*. Vol. 1 and 2. Ulmer Verlag, Stuttgart, 972 pp.
- WESTRICH P. 2001: Zum Pollensammelverhalten der Seidenbiene *Colletes floralis* Eversmann 1852 (Hymenoptera: Apidae). *Linz. Biol. Beiträge* **33**: 519–525.
- WESTRICH P. & AMIET F. 1996: Der taxonomische Status von *Colletes sierrensis* Frey-Gessner 1901 mit Beschreibung des noch unbekannten Männchens (Hymenoptera, Apidae). *Linz. Biol. Beiträge* **28**: 1161–1167.
- WESTRICH P. & SCHMIDT K. 1986: Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hymenoptera Apoidea). *Linz. Biol. Beiträge* **18**: 341–360.

Received February 12, 2003; revised May 7, 2003; accepted June 9, 2003