Entomol Gener | 20(1/2): 043-057 | Stuttgart 1995-09 | ISSN: 0171-8177

EGT-Nr 900 VI

# Morphological Specializations in Central European Bees for the Uptake of Pollen from Flowers with Anthers Hidden in Narrow Corolla Tubes (Hymenoptera: Apoidea)

ANDREAS MÜLLER

Eingang: 1995-05-05 / 1995-08-04 Annahme: 1995-08-06

MÜLLER A [Inst Syst Bot, Univ; CH-8008 Zürich]: **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**(1/2): 043-057; Stuttgart 1995.- [Article]

13 species of the Central European bee fauna belonging to 4 familiae and 5 genera were found to have evolved stout, curved bristles either on the tarsomera of pedes-I [P-I-ta] or on the proboscis which serve to extract pollen from plants having their anthers enclosed in narrow flower tubes, viz representatives of the Boraginaceae and Primulaceae. Pollen from narrow-tubed flowers plays an important role in the larval nourishment of these bees. The development of hooked bristles on the P-I-ta of one bee species is accompanied by a distinct elongation of the pedes-I which is interpreted as an additional adaptation to anthers concealed in deep corolla tubes. A literature survey reveals that morphological specializations enabling female bees to collect pollen efficiently at narrow-tubed flowers are widespread and must have evolved many times during bee evolution. The currently known morphological specializations of bees for the uptake of pollen from flowers are reviewed.

**Keywords:** *Andrena* - *Anthophora* - Boraginaceae - *Colletes* - concealed anthers - *Eucera* - *Osmia* - pollen-collecting apparatus - Primulaceae.

MÜLLER A [Inst Syst Bot, Univ; CH-8008 Zürich]: **Morphologische Spezialisierungen bei mitteleuropäischen Bienen für die Pollenaufnahme auf Blüten mit in engen Kronröhren verborgenen Antheren (Hymenoptera: Apoidea).** - Entomol Gener **20**(1/2): 043-057; Stuttgart 1995.- [Abhandlung]

13 mitteleuropäische Bienenarten aus 4 Familien und 5 Gattungen besitzen auf den Tarsomera der Pedes-I bzw auf den Mundteilen kräftige, hakig gebogene Borsten, mit deren Hilfe Pollen aus engröhrigen Blüten verschiedener Boraginaceae und Primulaceae gewonnen wird. Der Pollen eng-röhriger Blüten spielt eine wichtige Rolle in der Larvennahrung dieser Bienen. Als zusätzliche Anpassung an die versteckte Lage der Antheren in engen Kronröhren sind bei einer Bienenart die mit Hakenhaaren bestandenen Vorderbeine deutlich verlängert. Die Sichtung der Literatur ergibt, daß spezielle morphologische Strukturen für die Pollengewinnung aus engröhrigen Blüten bei Bienen weit verbreitet sind und im Lauf der Evolution bei vielen Verwandtschaftsgruppen konvergent entwickelt wurden. Die bei Bienen bislang bekannten morphologischen Spezialisierungen für die Pollenaufnahme werden besprochen.

**Schlüsselbegriffe:** *Andrena* - *Anthophora* - Boraginaceae - *Colletes* - verborgene Antheren - *Eucera* - *Osmia* - Pollensammelapparat - Primulaceae.

0171-8177/95/0020-0043 $ 3.75

## 1 Introduction

The **FF** of several Central European bee species (Apoidea) and honey wasp species (Vespoidea: Masaridae) are equipped with a pollen-collecting apparatus that consists of a peculiar facial pilosity. It is used as a tool to harvest pollen from nototribic flowers of the Lamiaceae and Scrophulariaceae [SCHREMMER 1959, WESTRICH 1989, MÜLLER in press]. Due to the raised position of the anthers, an efficient collection of pollen at nototribic flowers requires either special morphological devices or specialized behaviours [MÜLLER in press].

Similarly, flowers with anthers hidden in narrow corolla tubes are expected to be difficult for bees to exploit for pollen. It is not easy to imagine how pollen could be harvested efficiently from narrow flower tubes without morphological specializations. Indeed, there are several known examples of bee species outside Central Europe which have developed hooked bristles on the mouth parts or on the forelegs [pedes-I] to extract pollen from concealed anthers [PETERS 1974, MICHENER, WINSTON & JANDER 1978, THORP 1979, WILLE 1979, PARKER & TEPEDINO 1982, EICKWORT, KUKUK & WESLEY 1986].

Several Central European bee species are known to collect pollen exclusively or predominantly from narrow-tubed flowers of the Boraginaceae: *Colletes nasutus* Smith 1853 (Colletidae) and *Andrena nasuta* Giraud 1863 (Andrenidae) are both oligolectic on *Anchusa*, and *Osmia pilicornis* Smith 1846 (Megachilidae) frequently harvests pollen on *Pulmonaria* [WESTRICH 1989]. The examination of these 3 bee species under a dissecting microscope revealed that they actually possess specialized morphological structures either on the tarsomera of pedes-I or on the proboscis which probably aid in the extraction of pollen from flowers of the Boraginaceae.

The aim of this study is to prove that the observed structures are in fact employed in the expected manner and that additional Central European bee species have similar structures equally adapted to concealed anthers.

## 2 Material and methods

The **FF** of the 535 non-parasitic bee species of Central Europe listed by WARNCKE [1986] were checked under a dissecting microscope in order to detect specialized morphological structures on the mouth parts or on the tarsomera of pedes-I which might be used to scrape pollen out of narrow flower tubes.

Morphological structures presumed to play a part in the collection of pollen were examined with a scanning electron microscope.

The relative lengths of the pedes-I and -II of *Colletes nasutus* Smith 1853 were compared with those of 12 further European *Colletes* species - *C cunicularius* (Linnaeus 1761), *C daviesanus* Smith 1846, *C hederae* SCHMIDT & WESTRICH 1993, *C hylaeiformis* Eversmann 1852, *C impunctatus* Nylander 1852, *C marginatus* Smith 1846, *C mlokossewiczi* Radoszkowski 1891, *C nigricans* Gistel 1857, *C sierrensis* Frey-Gessner 1903, *C similis* Schenck 1853, *C spectabilis* Morawitz 1868, *C succinctus* (Linnaeus 1758) - by calculating the ratio of leg length to forewing length. The lengths of femur, tibia, tarsus (up to the insertion of the claws) and of forewing (along the anterior margin) were measured to the nearest 1/20 mm. 3 **FF** of *C nasutus* and 2 **FF** of each of the other *Colletes* species were randomly chosen for the measurements.

Several *Anthophora* and *Eucera* species (both Anthophoridae) were found to have their mouth parts covered with curved bristles which are very similar regarding their localization and their shape. The investigations, therefore, were confined to a single species of each genus, *Anthophora acervorum* (Linnaeus 1758) and *Eucera parvicornis* Mocsary 1878, respectively.

**Tab 1:** Central European bee species with strong bristles on pedes-I or on mouth parts for extracting pollen from anthers concealed within narrow flower tubes

| Species | Familia | pollen plant preferences | location of the pollen-harvesting bristles | plant species on which the bees were observed to remove pollen by the pollen-harvesting bristles | observation localities |
|---|---|---|---|---|---|
| *Colletes nasutus* Smith 1853 | Colletidae | oligolectic on *Anchusa* (Boraginaceae) | tarsomera-1/ -5 of the pedes-I | *Anchusa officinalis* (Boraginaceae) | Gabow (Mark Brandenburg), Germany |
| *Andrena nasuta* Giraud 1863 | Andrenidae | oligolectic on Boraginaceae | praementum, stipites and galeae of the proboscis | *Anchusa officinalis* (Boraginaceae) | Gabow (Mark Brandenburg), Germany |
| *Osmia pilicornis* Smith 1846 | Megachilidae | polylectic with a preference for Pulmonaria (Boraginaceae) | galeae of the proboscis | *Pulmonaria obscura* (Boraginaceae) | Hemmental (Schaffhausen), Switzerland |
| | | | | *Pulmonaria obscura* (Boraginaceae) | Schaffhausen (Schaffhausen), Switzerland |
| *Anthophora acervorum* (Linnaeus 1758) | Anthophoridae | polylectic, frequently visits *Pulmonaria* (Boraginaceae) and *Pulmonaria obscura* (Boraginaceae) *Primula* (Primulaceae) | galeae of the proboscis | *Nonea lutea* (Boraginaceae) | Zürich (Zürich), Switzerland |
| | | | | *Pulmonaria obscura* (Boraginaceae) | Hemmental (Schaffhausen), Switzerland |
| | | | | *Primula vulgaris* (Primulaceae) | Schaffhausen (Schaffhausen), Switzerland |
| | | | | *Primula vulgaris* (Primulaceae) | Zürich (Zürich), Switzerland |
| *Eucera parvicornis* Mocsary 1878 | Anthophoridae | oligolectic on Boraginaceae | galeae and palpi labiales of the proboscis | ---- | ---- |

The pollen loads of 9 - 26 **FF** from different European localities of the bee species showing putative morphological specializations were analysed by light microscopy. The method outlined by WESTRICH & SCHMIDT [1986] was used for pollen analysis. Prior to removing the pollen from a female bee, the fulness of the scopa was estimated and the amount of pollen assigned to 5 classes: 5 = full load, 1 = scopa 1/5 filled. After removing the surface lipids of the pollen grains by washing them in ether, the pollen was mounted in glycerine jelly on a slide. The different pollen types were determined at a magnification of 400x or 1000x to the family or genus level with the aid of a reference collection and the literature cited in WESTRICH & SCHMIDT [1986]. The %% of the different pollen types were estimated by counting the grains along 4 lines chosen randomly across the cover slip at a magnification of 400x. 100 - 800 pollen grains were counted per sample. Pollen types represented with less than 4% were not considered in order to prevent biases caused by contamination. After assigning different weights to scopae filled to different degrees (full loads were 5 x more strongly weighted than scopae filled to only 1/5), the estimated %% were summed up over all investigated samples of each species.

With the exception of *Eucera parvicornis* not found in the field, the pollen-collecting behaviour of flower-visiting **FF** of the species with specialized morphological structures was recorded in 1993 and 1994 (Tab 1: observation localities) using a 3fold magnifying glass and a video camera.

Workers of *Bombus pascuorum* (Scopoli 1763) (Apidae) and **FF** of *Osmia bicolor* (Schrank 1781) (Megachilidae) were observed at flowers of *Pulmonaria obscura* Dumort. (Boraginaceae) in order to see whether bee species lacking morphological specializations are also able to gather pollen from anthers within narrow tubes.

The nomenclature of the bees follows NOSKIEWICZ [1936] and SCHMIDT & WESTRICH [1993] for the Colletidae, and WARNCKE [1986] for the other bee species. The plants are named according to the Flora Europaea [TUTIN et al 1964-1980].

## 3 Results

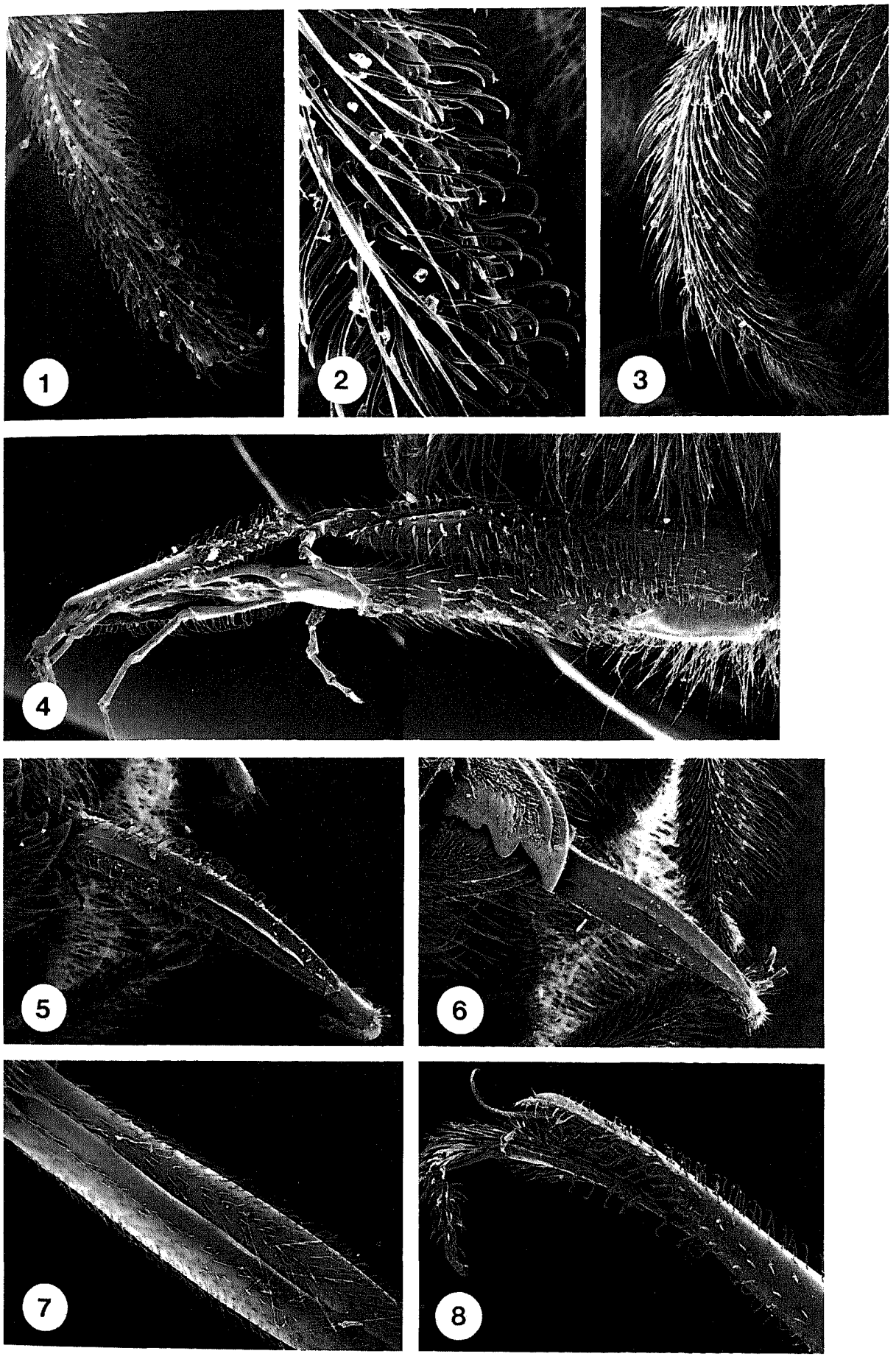
13 Central European bee species were found to possess specialized morphological structures which will be shown to be adaptations for harvesting pollen at flowers with anthers hidden in narrow tubes: *Colletes nasutus* Smith 1853 (Colletidae), *Andrena nasuta* Giraud 1863 (Andrenidae), *Osmia pilicornis* Smith 1846 (Megachilidae), *Anthophora acervorum* (Linnaeus 1758), *A aestivalis* (Panzer 1801), *A crassipes* Lepeletier 1841, *A crinipes* Smith 1854, *A mucida* Gribodo 1873, *A nigrocincta* Lepeletier 1841, *A retusa* (Linnaeus 1758), *Eucera cinerea* Lepeletier 1841, *E parvicornis* Mocsary 1878 and *E seminuda* Brullé 1832 (all Anthophoridae). These specialized morphological structures are developed only in the **FF**.

### 3.1 Description of the specialized morphological structures

The morphological specializations of all bee species consist of stout, curved bristles localized either on the tarsomera of pedes-I (*Colletes nasutus*) or on the mouth parts (remaining species) (Fig 1, 2, 4, 5, 7, 8; Tab 1). Similar bristles are lacking in related species in which the tarsomera of pedes-I bear normal hairs and the mouth parts are provided at most with single fine hairs (Fig 3, 6).

---

**Fig 1-8** [ ⇒ page 47]: Pollen-harvesting bristles on the tarsomera of pedes-I [P-I-ta] and on the mouthparts [M-P] of several species of Apoidea [Hymenoptera].- **1, 2** P-I-ta in *Colletes nasutus* Smith 1853; **4, 5, 7, 8** M-P: **4** *Andrena nasuta* Giraud 1863, **5** *Osmia pilicornis* Smith 1846, **7** *Anthophora acervorum* (Linnaeus 1758) **8** *Eucera parvicornis* Mocsary 1878. By contrast, 3 the normally haired pedes-I in *Colletes succinctus* (Linnaeus 1758), and **6** the naked M-P in *Osmia xanthomelana* (Kirby 1802).- Fig 1, 3: 32x; Fig 2: 88x; Fig 4, 8: 20x; Fig 5, 6: 16x; Fig 7: 14x.


1
2
3
4
5
6
7
8

In *C nasutus*, the bristles are localized at the outside of tarsomera-1 / -4 and of the base of tarsomeron-5. They are hooked and directed towards the tip of the leg (Fig 1, 2). Compared with other *Colletes* species, the P-I but not the P-II of *C nasutus* are distinctly lengthened relative to body size (expressed as wing length). This elongation mainly involves femur and tibia, but not the tarsus which is of equal relative length (Fig 9).

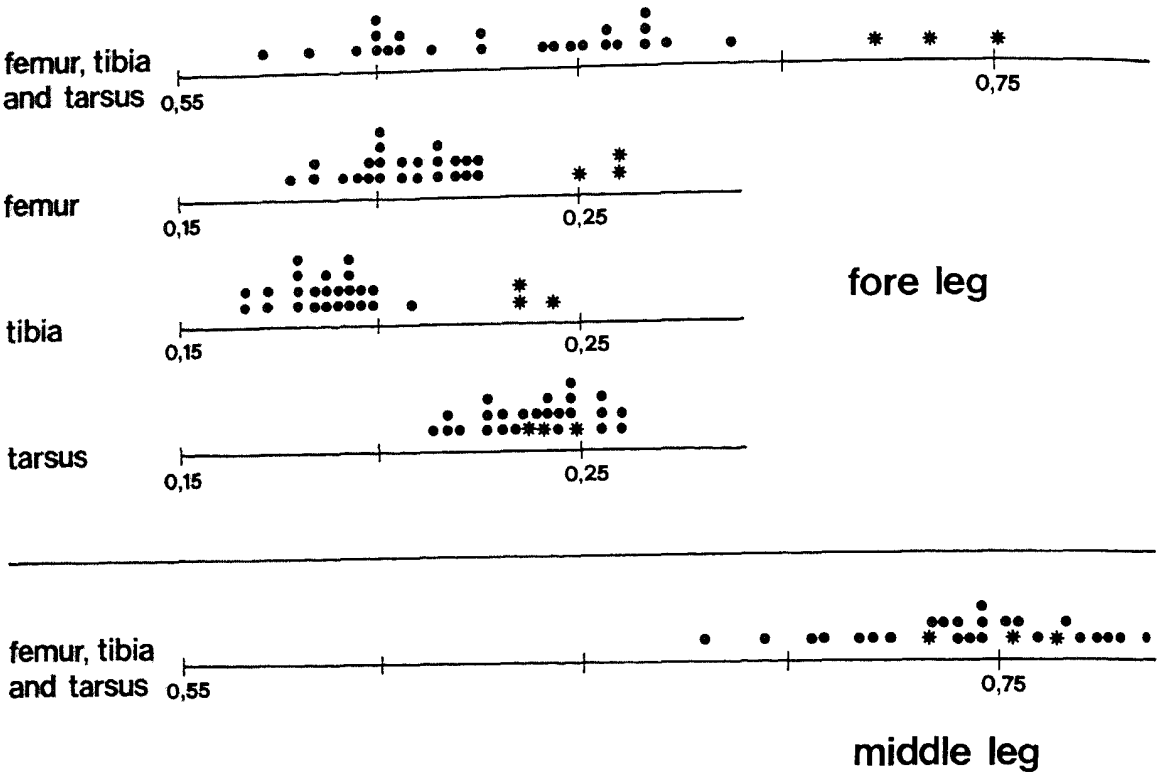



**Fig 9:** The ratio of length of the pedes-I and -II against length of praealae in *Colletes nasutus* Smith 1853 (* 3 individuals) compared with 12 other European *Colletes* species (• 2 individuals).

In *Andrena nasuta,* the bristles densely cover the praementum, the stipites and the galeae of the proboscis (Fig 4). They are mainly straight on praementum and stipites but distinctly hooked on the galeae. In *Osmia pilicornis* as well as in *Anthophora acervorum,* the bristles are confined to the galeae (Fig 5, 7). They are strongly hooked in the former species but only slightly so in the latter. *Eucera parvicornis* possesses strong bristles on the galeae and the outside of the first 2 segments of the palpi labiales (Fig 8). The shape of the bristles varies from distinctly hooked to nearly straight.

### 3.2 Composition of the larval provisions

The **FF** of the bee species examined collect pollen exclusively (*Colletes nasutus, Andrena nasuta, Eucera parvicornis*) or frequently (*Osmia pilicornis, Anthophora acervorum*) on flowers of the Boraginaceae (Fig 10; Tab 1). *C nasutus* appears to be oligolectic at the genus level; the pollen loads analysed consisted solely of *Anchusa* pollen. *Anchusa* is also by far the most important pollen source of *A nasuta* and *E par-*

*vicornis*. *O pilicornis* and *A acervorum* are both polylectic with a distinct preference for *Pulmonaria*. Besides *Pulmonaria* and representatives of the Lamiaceae, *Primula* (Primulaceae) was also found to be an important component in the larval provisions of *A acervorum* (Fig 10).

The flowers of *Anchusa*, *Pulmonaria* and *Primula* are all characterized by narrow corolla tubes with enclosed anthers. Pollen from flowers with hidden anthers, therefore, plays an important role in the larval nourishment of all examined bee species.

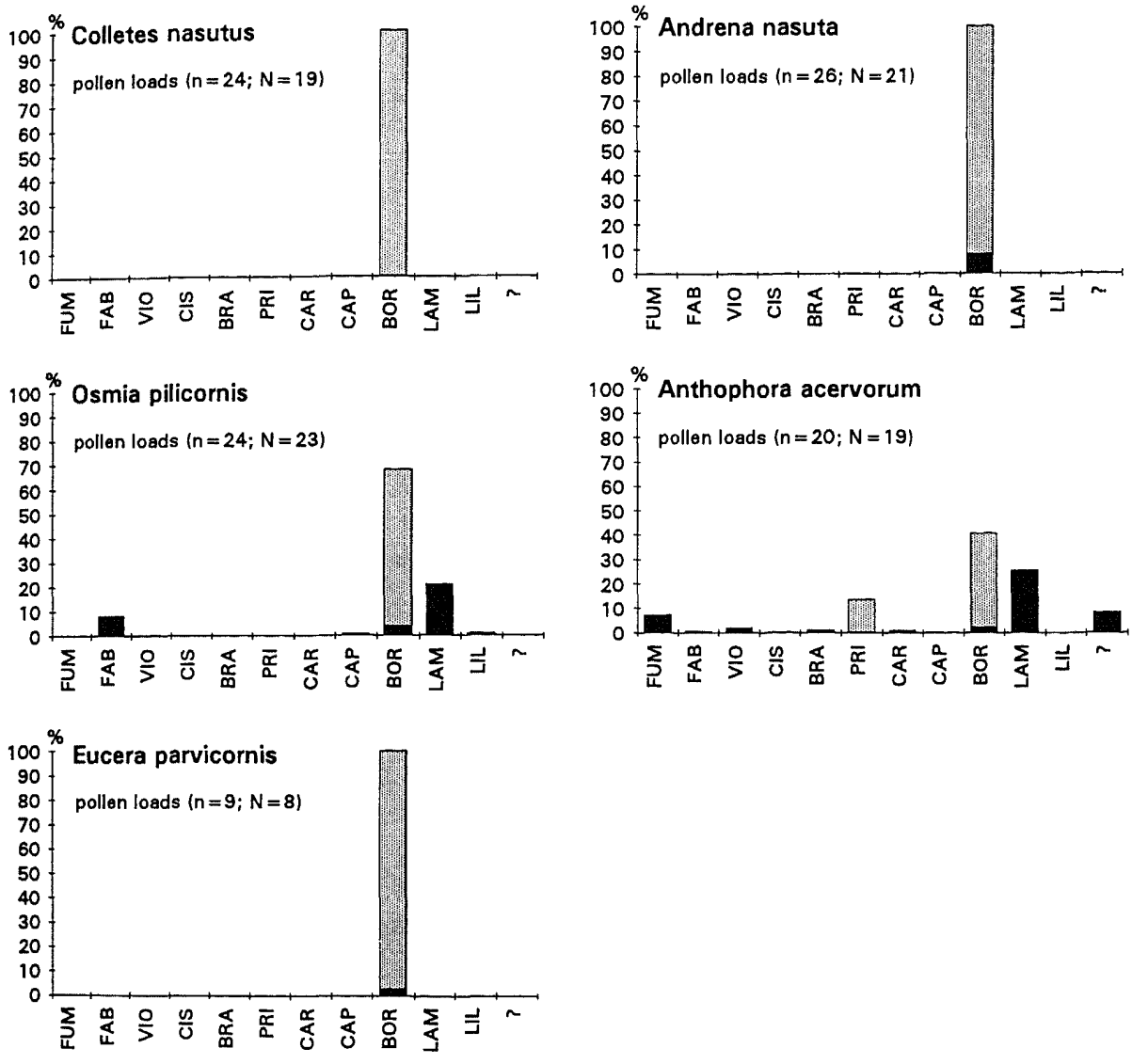



**Fig 10:** Composition of pollen loads in several European species of Apoidea [Hymenoptera].- **n** total number of examined loads; **N** number of different localities. **FUM** Fumariaceae; **FAB** Fabaceae; **VIO** Violaceae; **CIS** Cistaceae; **BRA** Brassicaceae; **PRI** Primulaceae; **CAR** Caryophyllaceae; **CAP** Caprifoliaceae; **BOR** Boraginaceae; **LAM** Lamiaceae; **LIL** Liliaceae; **?** unidentified pollen .- The stippled areas specify the part of amount of *Anchusa* pollen in the examined pollen loads of *Colletes nasutus* Smith 1853, *Andrena nasuta* Giraud 1863, and *Eucera parvicornis* Mocsary 1878, or the part of amount of *Pulmonaria* pollen in the investigated scopae of *Osmia pilicornis* Smith 1846, or the part of amount of *Pulmonaria* and *Primula* pollen in the analysed samples of *Anthophora acervorum* (Linnaeus 1758), respectively.

### 3.3 Flower-visiting behaviour

The observation of flower-visiting **FF** of *Colletes nasutus*, *Andrena nasuta*, *Osmia pilicornis* and *Anthophora acervorum* revealed that the strong bristles on the tarsomera of pedes-I and on the mouth parts, respectively, are indeed used to scrape pollen out of narrow flower tubes (Tab 1). *Eucera parvicornis* could not be observed in the field but the occurrence of the same type of bristles on the proboscis (Fig 8) in combination with a distinct preference for pollen of narrow-tubed flowers of the Boraginaceae (Fig 10) indicates that this species, too, makes use of the specialized morphological structures for removing pollen from hidden anthers.

After landing on a flower of *Anchusa officinalis*, **FF** of *C nasutus* were first observed to force the head between the throat scales and drink nectar which is located at the bottom of the flowers. The **FF** then withdraw their heads, insert both P-I into the flower tube and extract pollen out of the hidden anthers by repeatedly moving their lengthened (see above) pedes-I up and down. The legs are moved simultaneously but in an alternate manner inside the flower tube.

Pollen-collecting **FF** of *A nasuta* insert their extended proboscis into the flower tube of *Anchusa officinalis* and pick up pollen with the bristles by violently moving the proboscis several times up and down. Pollen grains adhering to the proboscis are removed by rapid stroking movements of the P-I immediately before leaving the flower. For that purpose, the bees lean back on the flower petals. The same up and down brushing movements of the extended proboscis were observed in the **FF** of *A acervorum* harvesting pollen at flowers of *Pulmonaria obscura*, *Nonea lutea* (Desr) DC (Boraginaceae) and *Primula vulgaris* Hudson, respectively. This bee species picks up the pollen grains sticking to the bristled galeae in flight with the tarsomera of pedes-I immediately after leaving the flower. The supposed function of the hooked bristles on the proboscis of *O pilicornis* could be ascertained only in an indirect way. Because **FF** visiting the flowers of *Pulmonaria obscura* press their head tightly against the small tube entrance, the action of the mouth parts cannot be seen. But the conspicuous white-coloured pollen grains of *Pulmonaria*, which were always seen sticking to the black mouthparts after the **FF** had withdrawn them from the flower tube, confirmed that pollen is harvested with the aid of the bristled proboscis in this species, too. As in *A acervorum*, the pollen grains are removed from the proboscis in flight with the pedes-I immediately after leaving the *Pulmonaria* flowers.

None of the bee species mentioned above was observed to vibrate its indirect flight muscles during pollen collection. Thus, buzzing is not involved in pollen uptake from concealed anthers in these bees.

At the same 2 localities where the pollen-collecting behaviour of *O pilicornis* and *A acervorum* was observed (Tab 1), numerous workers of *Bombus pascuorum* (Apidae) and several **FF** of *Osmia bicolor* (Megachilidae) also visited the flowers of *Pulmonaria obscura*. Both bee species lack a specialized pollen-collecting apparatus. Their tarsomera of pedes-I bear normal hairs and their mouth parts are naked. All bumblebee workers only collected nectar at *Pulmonaria*. Their corbiculae were devoid of pollen without exception. No *Pulmonaria* pollen grains were detected in the examined pollen loads of 2 *O bicolor* **FF** captured at *Pulmonaria*. Bee species lacking specialized morphological devices, therefore, may be unable to gather pollen efficiently from anthers located within narrow tubes unless the floral openings are wide enough allowing pollen gathering by buzzing.

# 4 Discussion

## 4.1 Adaptive morphological convergence for pollen removal from narrow-tubed flowers

The **FF** of 13 Central European bee species belonging to 4 familiae and 5 genera were found to have developed a pollen-collecting apparatus that is used for harvesting pollen at plants which have their anthers concealed in narrow corolla tubes, viz representatives of the Boraginaceae and Primulaceae. It consists of stout, hooked or straight bristles localized either on the tarsomera of pedes-I or on different parts of the proboscis.

Similar morphological specializations are also known to exist in the **FF** of several bee species from outside Central Europe where they likewise serve as a tool for removing pollen from narrow flower tubes.

The tarsomera of pedes-I of 4 North American *Calliopsis* species (Andrenidae) are provided with curled bristles which are used to scrape pollen out of the slender flower tubes of *Verbena* (Verbenaceae) [ROBERTSON 1914, 1925, SHINN 1967]. The praementum and galeae of the proboscis of 2 North American *Andrena* species (Andrenidae) which are both oligolectic on narrow-tubed *Cryptantha* species (Boraginaceae) are covered with numerous hooked setae [MICHENER 1944, LABERGE 1964]. The **FF** of 7 *Perdita* species (Andrenidae) occurring in North and Central America are equipped with a pollen-collecting apparatus composed of long, coarse hairs on the inner margins of the cheeks next to the proboscideal cavity which serve to pull pollen out of the slender corolla tubes of *Heliotropium* and *Coldenia* flowers (Boraginaceae) [TIMBERLAKE 1954, THORP 1979].

*Coldenia* is also the main or exclusive pollen source of 3 North American *Hesperapis* species (Melittidae) which likewise possess specialized morphological devices for harvesting *Coldenia* pollen: the mandibula, the proboscis and the cheeks adjacent to the proboscideal cavity are covered with long, apically wavy hairs [STAGE 1966, MICHENER 1981]. In the North American *Dufourea novaeangliae* (Halictidae), strong setae on praementum, galeae and palpi labiales are thought to be an adaptation for collecting pollen from the short anthers hidden in the corolla of the tristylous *Pontederia cordata* (Pontederiaceae), a plant species on which this bee is completely dependent [EICKWORT, KUKUK & WESLEY 1986].

The galeae and/or the palpi labiales of 4 North American *Osmia* species (Megachilidae) belonging to 3 different subgenera are beset with hooked bristles. **FF** of these species visit, among other plants, the narrow-tubed flowers of *Lithospermum*, *Amsinckia* and *Cryptantha* which all belong to the Boraginaceae [SANDHOUSE 1939, MICHENER 1944, 1949, PARKER & TEPEDINO 1982]. 3 *Osmia* species living in Asia and the Canary Islands, respectively, possess long and apically thickened bristles on their palpi labiales which are probably employed when gathering pollen at flowers of *Heliotropium* [PETERS 1974]. Most of the 32 described North American *Proteriades* species (Megachilidae) exclusively or preferentially collect pollen on *Cryptantha*. Stiff, curved bristles on the galeae and the palpi labiales help these bees extract the pollen from the slender *Cryptantha* tubes [MICHENER 1944, TIMBERLAKE & MICHENER 1950, PARKER 1978, THORP 1979].

Hairs on the basal part of the proboscis of a South American *Euglossa* species (Apidae) were observed by MICHENER, WINSTON & JANDER [1978] to be responsible for the extraction of pollen out of the small tubular flowers of *Sabicea* (Rubiaceae). Several South American and African stingless bee species of the genera *Trigona* and *Dactylurina* (Apidae) have a few very long bristles on galeae and palpi labiales which are either sinuate or hooked. These are believed to assist the mouth parts in pulling pollen from flowers with small tubular corollae, from poricidal anthers or from anthers the bees have perforated or chewed open [MICHENER 1944, WILLE 1979, RENNER 1983, ROUBIK 1989].

The above-mentioned bee species belong to many different taxonomical groups and live in many different parts of the world. Thus, specialized morphological structures enabling female bees to harvest pollen efficiently at flowers with concealed anthers have evolved independently many times during bee evolution.

In another pollen-collecting Hymenoptera group, the honey wasps (Vespoidea: Masaridae), no similar adaptations to pollen harvesting at flowers with concealed anthers are currently recognized [RICHARDS 1962, GESS & GESS 1989, GESS 1992]. The tarsomera of pedes-I of the **FF** of the South American Masaridae species *Trimeria monrosi*, however, are beset with "an outstanding bristle-like pubescence of which the tips are in part recurved", and the **FF** of the Australian *Rolandia maculata* have a "marked fringe of bristles on the periphery of the lower side of the head around the oral fossa making a sort of basket" [RICHARDS 1962].

It may be assumed that these peculiar structures also have evolved for extracting pollen from hidden anthers, especially since the latter species was observed to visit flowers of *Lippia nodiflora* (*Verbena*ceae), a plant species which keeps its stamina enclosed in a flower tube.

## 4.2 The pollen-collecting apparatus of *Colletes nasutus*

The specialized bristles for pollen uptake are localized on different parts of the head and the mouth parts in the majority of the bee species discussed above. Only in the Eurasian *Colletes nasutus* and the above-mentioned North American *Calliopsis* species, they cover the tarsomera of pedes-I. The question arises why these species did not evolve hooked bristles on the mouth parts, too. At least in the case of *C nasutus,* a tentative answer can be given. The glossa of the Colletidae is thought to be a highly derived structure that is employed for lining the walls of the brood cells with glandular secretions [BATRA 1980, MICHENER 1992]. It may be postulated that the colletid proboscis cannot be easily modified because the glossa plays an important role in cell lining.

Natural selection, therefore, might have favoured the development of hooked bristles on the tarsomera of pedes-I instead. Similarly, the conspicuous elongation of the palpi labiales or the palpi maxillares, but not of the glossa which enables several Australian Colletidae to reach nectar even in long-tubed flowers is explained by the important function of the glossa in nesting behaviour of Colletidae species [HOUSTON 1983].

The development of hooked bristles on the tarsomera of pedes-I of *C nasutus* is accompanied by a distinct elongation of femur and tibia of the pedes-I. This lengthening may facilitate the pollen-collecting process by improving the reach and versatility of the P-I. The elongated P-I of *C nasutus*, therefore, appear to be an additional adaptation to pollen harvesting at the deep tubular *Anchusa* flowers. A similar, though much more distinct prolongation of the P-I is known from several bee species of the South African genus *Rediviva* (Melittidae). Here, the extraordinarily lengthened P-I are simultaneously inserted into the 2 long spurs of *Diascia* flowers (Scrophulariaceae) in order to harvest the floral oils [VOGEL 1984, STEINER & WHITEHEAD 1990]. A noticeable prolongation of the P-I was also found in the South American bee species *Centris hyptidis* (Anthophoridae) where it has apparently evolved to facilitate the handling of the divergent deep pouches of the oil flowers of *Angelonia pubescens* (Scrophulariaceae) [VOGEL & MACHADO 1991].

## 4.3 Frequency and kinds of morphological specializations for pollen harvesting

In contrast to both nectar and oil which can be hidden deep inside the flower and which are actually used to place nectar-sucking or oil-harvesting insects in a position favourable for pollination [VOGEL 1974, WESTERKAMP 1987, STEINER & WHITEHEAD 1990], the concealing of anthers within flowers is constrained by their own function, viz pollen export. Morphological adaptations for harvesting nectar or oil are thus expected to be much more frequent than for pollen uptake. Indeed, while there are many known morphological adaptations in bees for extracting nectar and harvesting flower oils, respectively [STEPHEN, BOHART & TORCHIO 1969, VOGEL 1974, NEFF & SIMPSON 1981, BUCHMANN 1987, WESTERKAMP 1987, CANE & EICKWORT unpublished manuscript], female bees obviously have only exceptionally developed specialized morphological structures for the uptake of pollen from the flowers [THORP 1979, WESTERKAMP 1987, WESTRICH 1989, CANE & EICKWORT unpubl manuscr). Bees usually harvest pollen with the basitarsal brushes of the (pro)pedes [GRINFEL'D 1962, MICHENER, WINSTON & JANDER 1978, WESTERKAMP 1987, WESTRICH 1989]. Basitarsal brushes are widespread among aculeate Hymenoptera where they primarily serve as grooming structures. In bees, they are additionally employed as pollen-harvesting tools. Basitarsal brushes are thus believed to have been a preadaptation to pollen collection in the precursors of the bees [GRINFEL'D 1962, JANDER 1976]. Apart from leg basitarsal brushes, both mandibula and scopal brushes (particularly the abdominal scopa) are also involved in pollen uptake in many bees [STEPHEN, BOHART & TORCHIO 1969, WESTERKAMP 1987, WESTRICH 1989]. They too, however, were not specially developed as pollen-harvesting devices, the scopal brushes being primarily pollen transport structures [WESTERKAMP 1987].

Other morphological devices especially developed for pollen uptake are expected to have evolved only as a response to pollen collection at plants with complicated flower structures or with dense inflorescences composed of small flowers where an efficient pollen removal either with the (pro)pedes, the mandibula or the scopal brushes proves difficult. As the following short synopsis shows, bees dependent on such plants actually have developed specialized morphological structures for pollen gathering.

Bees gaining pollen at flowers which have their anthers enclosed in narrow flower tubes are provided with strong, curved bristles either on the P-I or on the mouth parts (present publ). The **FF** of several European bee and honey wasp species are equipped with a pollen-collecting apparatus that consists of a peculiar facial pilosity. It is used to harvest pollen from nototribic flowers of the Lamiaceae and Scrophulariaceae where the raised position of the anthers obviously renders it difficult to collect pollen in an efficient manner [SCHREMMER 1959, WESTRICH 1989, MÜLLER in press]. The tarsomera of P-I in the **FF** of the North American bee species *Megandrena mentzeliae* (Andrenidae) bear long, flexible and wavy bristles. By pulling the tarsomera of P-I through the compact multistaminate androecium of *Mentzelia tricuspis* (Loasaceae), the bristles comb the pollen from spaces between the filaments where it has fallen after anther dehiscence [ZAVORTINK 1972].

The oral vestiture of the **FF** of 2 North American *Xeralictoides* species (Melittidae) which are associated with *Eucnide urens* and *Mentzelia* spp. (Loasaceae) is modified: the mandibula, the stipites of the proboscis, and the inner margins of the cheeks next to the proboscideal cavity are densely covered with unusually long and minutely barbed hairs [STAGE 1966, MICHENER 1981]. Judging from the flower-visiting behaviour described by ZAVORTINK [1972], this oral brush may assist the bees in wiping the pollen masses from a basal pollen chamber that in both, *Eucnide* and *Mentze-*

*lia,* is formed around the base of the style by the incurvature of the filaments [THOMPSON & ERNST 1967].

Specialized arrays of branched or sinuous setae on the underside of the abdomen or thorax in various species of *Svastra, Xenoglossodes, Tetralonia* (all Anthophoridae) and *Anthidium* (Megachilidae) associated with the Asteraceae are thought to be directly involved in pollen removal from the floral heads [NEFF 1984, WESTERKAMP 1987, personal observation]. Similarly, several Paracolletini (Colletidae) which harvest pollen on the dense inflorescences of *Prosopis* (Mimosaceae) are provided with a special metasomal pilosity which probably aids in pollen uptake [NEFF 1984].

Stingless bee species of the subgenus *Scaura* of *Trigona* (Apidae) are specialized pollen gleaners which visit inflorescences consisting of relatively broad surfaces from which fallen pollen is swept up by dragging the extraordinarily flattened and hairy hind basitarsus across the flower parts [MICHENER, WINSTON & JANDER 1978, ROUBIK 1989].

The peculiarly shaped clypeus of several Eurasian *Osmia* species (Megachilidae) may prove to be a further example of a specialized pollen-harvesting device. The clypeus of the FF of these bees bears laterally 2 projecting horns enclosing a hairless, smooth and impressed area that is bordered by a dense fringe of hairs towards the insertions of the antennae [PETERS 1978]. The function of this conspicuous clypeus structure remains obscure. It is interpreted either as a tool to tamp down and smooth mud during nest building [O'TOOLE & RAW 1991], as a basket to catch pollen from hanging anthers [WESTRICH 1989] or as a short-term reservoir for pollen that the bees have picked up from small flowers with the aid of the tarsomera of pedes-I and mandibula [PETERS 1978]. Other examples of morphological specializations for pollen removal in bees are not known at present [MICHENER 1944, STEPHEN, BOHART & TORCHIO 1969, THORP 1979, EICKWORT & GINSBERG 1980, WESTERKAMP 1987, ROUBIK 1989, WESTRICH 1989, CANE & EICKWORT unpubl manuscr].

In summary, specialized morphological structures evolved to facilitate the uptake of pollen are more widely spread in bees than hitherto thought. Nevertheless, they are rare and restricted to bees associated with plants the flowers of which are difficult to exploit efficiently by usual methods.

## 5 References

BATRA S W T [1980]: Ecology behavior pheromones parasites and management of the sympatric vernal bees Colletes inaequalis, C thoracicus and C validus.- J Kans Entomol Soc **53**: 509-538; Manhattan / USA.

BUCHMANN S L [1987]: The ecology of oil flowers and their bees.- Annu Rev Ecol Syst **18**: 343-369; Palo Alto / USA.

CANE J H & EICKWORT G C [unpublished manuscript]: Oligolecty oligophily and the role of specialization in bee-flower coevolution.

EICKWORT G C & GINSBERG H S [1980]: Foraging and mating behavior in Apoidea.- Ann Rev Entomol **25**: 421-446; Palo Alto / USA.

EICKWORT G C, KUKUK P F & WESLEY F R [1986]: The nesting biology of Dufourea novaeangliae (Hymenoptera: Halictidae) and the systematic position of the Dufoureinae based on behavior and development.- J Kans Entomol Soc **59**: 103-120; Manhattan / USA.

GESS S K [1992]: Biogeography of the masarine wasps (Hymenoptera: Vespidae: Masarinae) with particular emphasis on the southern African taxa and on correlations between masarine and forage plant distributions.- J Biogeogr **19**: 491-503; Oxford / Britain.

GESS S K & GESS F W [1989]: Flower visiting by masarid wasps in southern Africa (Hymenoptera: Vespoidea: Masaridae).- Ann Cape Prov Mus Nat Hist **18**: 95-134; Grahamstown / South Africa.

GRINFEL'D E K [1962]: Origin and development of the apparatus for pollen collection in bees (Hymenoptera: Apoidea).- Entomol Rev **41**: 37-42; Washington / USA.

HOUSTON T F [1983] An extraordinary new bee and adaptation of palpi for nectar-feeding in some Australian Colletidae and Pergidae (Hymenoptera).- J Aust Entomol Soc **22**: 263-270; Brisbane / Australia.

JANDER R [1976]: Grooming and pollen manipulation in bees (Apoidea): the nature and evolution of movements involving the foreleg.- Physiol Entomol **1**: 179-194; Oxford / Britain.

LABERGE W E [1964]: Prodromus of American bees of the genus Andrena (Hymenoptera Apoidea).- Bull Univ Nebraska State Mus **4**: 297-316; Lincoln / USA.

MICHENER *C* D [1944]: Comparative external morphology phylogeny and a classification of the bees (Hymenoptera).- Bull Am Mus Nat Hist **82**: 151-326; New York / USA.

MICHENER *C* D [1949]: Records and descriptions of American megachilid bees (Hymenoptera).- J Kans Entomol Soc **22**: 41-59; Manhattan / USA.

MICHENER *C* D [1981]: Classification of the bee family Melittidae with a review of species of Meganomiinae.- Contrib Am Entomol Inst **18**: 001-135; Ann Arbor / USA.

MICHENER *C* D [1992]: Sexual dimorphism in the glossa of Colletidae (Hymenoptera Apoidea).- J Kans Entomol Soc **65**: 1-9; Manhattan / USA.

MICHENER *C* D, WINSTON M L & JANDER R [1978]: Pollen manipulation and related activities and structures in bees of the familiy Apidae.- Univ Kans Sci Bull **51**: 575-601; Lawrence / USA.

MÜLLER A [in press]: Convergent evolution of morphological specializations in Central European bee and honey wasp species as an adaptation to the uptake of pollen from nototribic flowers (Hymenoptera Apoidea and Masaridae).- Biol J Linn Soc; London / Britain.

NEFF J L [1984]: Observations on the biology of Eremapis parvula Ogloblin an anthophorid bee with a metasomal scopa (Hymenoptera: Anthophoridae).- Pan-Pac Entomol **60**: 155-162; San Francisco / USA.

NEFF J L & SIMPSON B B [1981]: Oil-collecting structures in the Anthophoridae (Hymenoptera): morphology function and use in systematics.- J Kans Entomol Soc **54**: 95-123; Manhattan / USA..

NOSKIEWICZ J [1936]: Die palearktischen Colletes-Arten.- Prace Naukowe Wydawnictwo Towarzystwo Naukowego We Lwowie **3**: 001-532; Lwowie / Polska.

O'TOOLE *C* & RAW A [1991]: Bees of the World.- Blandford London / Britain.

PARKER F D [1978]: Biology of the bee genus Proteriades Titus.- J Kans Entomol Soc **51**: 145-173; Manhattan / USA.

PARKER F D & TEPEDINO V J [1982]: A nest and pollen-collection records of Osmia sculleni Sandhouse a bee with hooked hairs on the mouthparts (Hymenoptera: Megachilidae).- J Kans Entomol Soc **55**: 329-334; Manhattan / USA.

PETERS D S [1974]: Über die Untergattung Haetosmia Popov 1952 (Insecta: Hymenoptera: Megachilidae: Osmia).- Senckenb Biol **55**: 293-309; Frankfurt a M / Deutschland.

PETERS D S [1978]: Systematik und Zoogeographie der west-paläarktischen Arten von Osmia Panzer 1806 s str Monosmia Tkalcu 1974 und Orientosmia n subgen (Insecta: Hymenoptera: Megachilidae).- Senckenb Biol **58**: 287-346; Frankfurt a M / Deutschland.

RENNER S [1983]: The widespread occurrence of anther destruction by Trigona bees in Melastomataceae.- Biotropica **15**: 251-256; Washington / USA.

RICHARDS O W [1962]: A revisional study of the masarid wasps (Hymenoptera Vespoidea).- British Museum (Natural History) London / Britain.

ROBERTSON *C* [1914]: Origin of oligotropy in bees.- Entomol News **25**: 67-73; Philadelp / USA.

ROBERTSON *C* [1925]: Heterotropic bees.- Ecology **6**: 412-436; New York / USA.

ROUBIK D W [1989]: Ecology and natural history of tropical bees.- Cambridge Tropical Biological Series Cambridge University Press Cambridge / Britain.

SANDHOUSE G A [1939]: The north American bees of the genus Osmia (Hymenoptera: Apoidea).- Mem Entomol Soc Wash **1**: 001-167; Washington / USA.

SCHMIDT K & WESTRICH P [1993]: Colletes hederae n sp eine bisher unerkannte auf Efeu (Hedera) spezialisierte Bienenart (Hymenoptera: Apoidea).- Entomol Z **103**: 89-93; Essen / Deutschland.

SCHREMMER F [1959]: Der bisher unbekannte Pollensammelapparat der Honigwespe Celonites abbreviatus (Vespidae Masarinae).- Z Morph Ökol Tiere **48**: 424-438; Berlin / Deutschland.

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; Lawrence /USA

STAGE G I [1966]: Biology and systematics of the American species of the genus Hesperapis Cockerell.- Ph D thesis University of California Berkeley / USA.

STEINER K E & WHITEHEAD V B [1990]: Pollinator adaptation to oil-secreting flowers.- Rediviva and Diascia.- Evolution **44**: 1701-1707; Lawrence / USA.

STEPHEN W P, BOHART G E & TORCHIO P F [1969]: The biology and external morphology of bees.- Oregon State University Press; Corvallis / USA.

THOMPSON H J & ERNST W R [1967]: Floral biology and systematics of Eucnide (Loasaceae).- J Arnold Arbor Harv Univ **48**: 56-88; Lancaster / USA.

THORP R W [1979]: Structural behavioral and physiological adaptations of bees (Apoidea) for collecting pollen.- Ann Mo Bot Gard **66**: 788-812; St Louis / USA.

TIMBERLAKE P H [1954]: A revisional study of the bees of the genus Perdita F Smith with special reference to the fauna of the Pacific Coast (Hymenoptera Apoidea) Part 1.- Univ Calif Publ Entomol **9**: 345-432; Berkeley / USA.

TIMBERLAKE P H & MICHENER C D [1950]: The bees of the genus Proteriades (Hymenoptera Megachilidae).- Univ Kans Sci Bull **33**: 387-439; Lawrence / USA.

TUTIN T G, HEYWOOD V H, BURGES N A, VALENTINE D H, WALTERS S M & WEBB D A [1964-1980]: Flora Europaea Vol 1-5.- Cambridge University Press Cambridge / Britain.

VOGEL S [1974]: Ölblumen und ölsammelnde Bienen.- Tropische und subtropische Pflanzenwelt **7**: 1-267; Wiesbaden / Deutschland.

VOGEL S [1984]: The Diascia flower and its bee - an oil-based symbiosis in southern Africa.- Acta Bot Neerl **33**: 509-518; Amsterdam / Nederland

VOGEL S & MACHADO I C [1991]: Pollination of 4 sympatric species of Angelonia (Scrophulariaceae) by oil-collecting bees in NE Brazil.- Plant Syst Evol **178**: 153-178; Wien / Österreich.

WARNCKE K [1986]: Die Wildbienen Mitteleuropas ihre gültigen Namen und ihre Verbreitung (Insecta: Hymenoptera).- Entomofauna Supplement **3**: 001-128; Linz / Österreich.

WESTERKAMP C [1987]: Das Pollensammeln der sozialen Bienen in Bezug auf die Anpassungen der Blüten.- Ph D Thesis Universität Mainz / Deutschland.

WESTRICH P [1989]: Die Wildbienen Baden-Württembergs. Vol 1-2.- Eugen Ulmer Vlg Stuttgart / Deutschland.

WESTRICH P & SCHMIDT K [1986]: Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hymenoptera Apoidea).- Linzer Biol Beitr **18**: 341-360; Linz / Österreich.

WILLE A [1979]: Phylogeny and relationships among the genera and subgenera of stingless bees (Meliponinae) of the world.- Rev Biol Trop **27**: 241-277; San José / Costa Rica

ZAVORTINK T J [1972]: A new subgenus and species of Meg*andrena* from Nevada with notes on its foraging and mating behavior.- Proc Entomol Soc Wash **74**: 61-75; Washington / USA.

**Acknowledgements:** I am grateful to C U Kramer (†), C Westerkamp and P Westrich for discussions, encouragement and comments on the manuscript; to D Dürrenfeld and C Saure for showing me a suitable locality for the observation of *Colletes nasutus* and *Andrena nasuta*; to F Amiet, M Bernasconi, J Gusenleitner, S Risch, M Schwarz, K Warncke (†) and the conservators of the entomological collections of the following institutions for allowing me to remove pollen samples from insects in their collections: Eidgenössische Technische

Hochschule Zürich, Oberösterreichisches Landesmuseum Linz, Zoologische Staatssammlung München, Zoologisches Museum der Alexander-Humboldt-Universität Berlin, Forschungsinstitut und Naturmuseum Senckenberg; to I Bisang and T Hotz for commenting on earlier drafts of the manuscript, to U Jauch for help with the scanning electron microscope, to A Zuppiger for skilful photographic work, and to P K Endress and K Reiser for linguistic help.

**Author's address:** Andreas MÜLLER, Institut für Systematische Botanik der Universität, Zollikerstrasse 107, CH-8008 Zürich; Schweiz

***

DÖRFLER E & DÖRFLER M: **Neue Lebensräume.** Mehr Artenvielfalt in Landschaft und Garten. -- [200 Pp, 49 Zweifarb-Fig, 42 Farbfot, 7 Tab, 130 x 220mm, Balacr-Hartkart-Ug].- **Publ:** Harri Deutsch Vlg, Frankfurt/M-Thun 1990; **ISBN:** 3-8171-1175-4; **Pr:** DM 26,30. --- [EGR-Nr 1938].

"Artenschwund durch Landschaftswandel", "Bedarf an Lebensräumen", "Vernetzung statt Verinselung" -- das sind nur drei von zahlreichen Themen, die in diesem Büchlein behandelt werden. Von einer Erörterung der historischen Entwicklung des mitteleuropäischen Landschaftsbildes, seinen Lebensgemeinschaften, seiner Flora und Fauna bis zur praktischen Anleitung zwecks Erhaltung letzter Naturreservate und zur Wiedereinrichtung naturnaher Landschaftsgemeinschaften, im großen wie im kleinen, auch im eigenen Hausgarten, bietet es eine Fülle von Wissen und Ideen. Ökologen und Entomologen, Schüler und Studenten, die sich dem Natur- und Landschaftsschutz widmen möchten, aber auch Behörden, Vereine, Verbände sowie Architekten und Landschaftspfleger sollten es gewinnbringend zu Rate ziehen.

***

NULTSCH W: **Mikroskopisch-Botanisches Praktikum für Anfänger.** 9. durchgesehene Aufl unter Mitarbeit von U RÜFFER. [VIII + 207 S, 101 Abb in 315 Einzeldarst, 120 x 190 mm, Balacr Weichkart Ebd].- **Publ:** Georg Thieme Verlag, Stuttgart-New York 1993; **ISBN:** 3-13440309-9; **Pr:** DM 19,80. --- [EGR-Nr 2220].

Given the large number of botanical textbooks, one might wonder why a guide for basical microscopical practica is necessary. The book by W Nultsch has a long tradition in giving essential information about usually studied botanical subjects of general interest. Basic practica in botany deal with cellular and histological details of representative plant material to gain insight into principles of plant life. This book reveals an overview about all important subjects covering the usual contents of botanical practica for beginners. The text is concisely written and reduces all facts on certain objects in a manner that the reader will be informed in detail without being confused by minor matters. In order to focus on practical application, detailed descriptions of instructive light microscopic images are completed by paragraphs about several techniques concerning the proof of a variety of cellular and cell wall ingredients. The microscopic images improve and fasten the re-cognition and location of certain structures and tissues in the preparation slide studied. Throughout the concept of this book, the relation between structure and function is emphasized and demonstrated with the help of selected subjects, thus revealing a principle of general importance. The 9th edition does not contain new objects compared to the previous edition, keeping the tradition of a concise practical guide. The text has been checked over again and linguistically improved. Following the development in the field, the form of expression is scientifically even more exact than in the 8th edition, but still remains comprehensible for the student. The mode of expression and the use of scientific terms is in agreement with that of most botany textbooks used at universities. Resulting from permanent use in practica by a vast range of biology students, this book really contains information about the practical approach it promises. The thorough testing by generations of students made the 9th edition of this book what it should be: a clear-written practical guide through the basic botanical practica for students and supervisors.

Dr Gabriele Wolff, Ruhr-Universität Bochum.