Studies in phylogeny and biosystematics of bees: The bee genus *Andrena* (Andrenidae) and the tribe Anthophorini (Apidae) (Insecta: Hymenoptera: Apoidea)

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Andreas Dubitzky
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Erstgutachter:	Prof. Dr. Klaus Schönitzer
Zweitgutachter:	PD Dr. Roland Melzer
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Disclaimer

All nomenclaturically relevant acts in this thesis have to be regarded as unpublished according to Article 8 of the International Code of Zoological Nomenclature, and will become available by separate publications.

This dissertation is dedicated to my parents
Heinz and Christine Dubitzky,
who gave me the opportunity to carry out these studies
and continuously supported me with their love and patience.

Contents

1. Introduction

Natura non facit saltus.
(Carl von Linné, 1707-1778)

Bees have long exercised a strong and fascinating attraction on humankind. At least since the Mesolithic bees have played an important role in human culture, as evidenced by the 8,000 to 12,000 year old rock drawings at Bicorp (Spain), which are the oldest known representations of bees in Europe. Others found in India and South Africa might be even older (Droege, 1993). The first written reports on bees are hieroglyphic inscriptions on 2,000 to 3,000 year old Egyptian papyrus scrolls (Rudnay & Beliczay, 1987). Aristotle (384-322 B.C.) was the first to compile the available knowledge on beekeeping and the biology of bees, for example, with observations on the continuity of flower visiting behaviour and an account of the sex ratio in a colony of bees (Droege, 1993).

However, all early records and studies of bees concentrate exclusively on the honey bee, *Apis mellifera* L. Other groups of bees are never mentioned due to the overwhelming importance of *A. mellifera* as honey maker and its fascinating organization of social life. With the introduction of binominal nomenclature by Linnaeus (1758) and the onset of modern taxonomy, the focus of interest increasingly broadened to include the many different groups of bees. Thus based on the work of systematists, who differentiate and categorize bees into various groups, more and more studies were carried out examining the morphology, behaviour, developmental biology or ecology of each group in great detail. These studies showed that non-domesticated bees were of high economic interest, mainly because they play an important part as pollinators for natural vegetation as well as for many crops. The leafcutter bee, *Megachile rotundata,* for example, is employed worldwide as a pollinator for lucerne (*Medicago varia)* (Dorn & Weber, 1988). Bumblebees (*Bombus)* are relied upon for the pollination of tomatoes in greenhouses (Michener, 2000). Nevertheless the great majority of studies carried out today on bees still concern the honey bee, which, because of its useful products such as honey and wax, is the bee of greatest economic importance. Furthermore in scientific terms of physiology and behaviour, the common honey bee can be called the best-known of all insects (Michener, 2000). Today about 17,000 described species of bees are known, and they are separated into 422 genera (Michener, 2000).

Bees belong to the insect order Hymenoptera. Within the Hymenoptera they are part of the Aculeata, a group, in which the ovipositor of females has been modified to a sting apparatus. Within the aculeate Hymenoptera, crabronid wasps and bees were found in a cladistic study to be sister groups, and together with the remaining sphecoid wasps they constituted a monophyletic group (Melo, 1999). But what are the characteristic features that separate bees from sphecoid wasps? According to Michener (2000) bees are clearly identifiable by two major aspects. The first concerns the dependence of bees on pollen, which is the only protein-source of the larvae. While nearly all bees provision their larvae with

pollen (except bees of the genus *Trigona*, who provide their larvae with carrion), all sphecoid wasps are strictly carnivore. The second aspect concerns two different morphological features of bees, the presence of branched or plumose hairs, which are exclusively found in bees and a hind basitarsus which is distinctly broader than the succeeding tarsal segments. From Kirby (1802) to the present, two informal groups of bees have been distinguished relating to the length of their mouthparts (Michener, 2000): the short tongued (S-T) bees, which are characterized by short and not particularly flattened labial palpi, a short galea and a short truncate or acute glossa. In contrast, the first two segments of labial palpi in the long tongued (L-T) bees are elongated and flattened sheathlike. The elongated galea of L-T bees builds a channel in which the elongated glossa can move back and forth. Seven bee families are currently recognized (Michener, 2000). Of them the Stenotritidae, Colletidae, Andrenidae, Halictidae and Melittidae are designated the S-T bees, and the remaining two families, the Megachilidae and the Apidae, comprise the L-T bees. The systematic position of the Melittidae remains dubious, since recent studies (Alexander & Michener, 1995) regard them either as the sister group to all L-T bees or as a paraphyletic group from which the L-T bees evolved. Although members of the Melittidae show more characters typical for S-T bees than L-T bees, they nonetheless exhibit some characteristic features of latter group (Michener & Greenberg, 1980, Michener, 2000).

Thanks to the strong interest in bees, numerous studies of taxonomy, general biology and phylogeny have been undertaken and many groups have been thoroughly examined. However, due to the great number of existing genera and species, many taxa still require comprehensive study. This especially applies to evolutionary studies on species-rich taxa that are not as “interesting” as the honey bee and its allies or other groups of bees which attract attention by their remarkable behaviour or biology, e.g. the orchid bees (Euglossini) (Bembé, 2004) or the primitive eusocial halictine bees (Danforth, 2002, Danforth & Ji, 2001), which are of special interest because they serve as a model for the evolution of sociality.

The present study therefore focuses on the hitherto neglected and unclarified phylogeny of the following two groups of bees, both of which represent important large taxa within their families: The S-T bee genus *Andrena*, as a member of Andrenidae, it represents the largest genus of bees. Few attempts have been made to trace its phylogeny, and they are either restricted to single subgenera or to distinct geographical regions (LaBerge 1986b, Larkin, 2002, Tadauchi, 1982, 1985a, Warncke, 1968). No previous studies have attempted to tackle this holarctic genus as a whole. The present study thus is an attempt to reconstruct the intrageneric phylogenetic relationships of as many subgenera of *Andrena* as was possible (84 of the 99 currently recognized subgenera were utilized) based on a morphological cladistic analysis. In addition, a molecular analysis was conducted to examine the phylogenetic relationship among several Central European species of the subgenus *Micrandrena*, as well as among 21 different subgenera.

The second part of this study presents a phylogenetic concept for the L-T bee tribe Anthophorini as well as for the Old World species of the anthophorine genus *Habropoda*,

based on a cladistic analysis of adult morphology. Finally a revision is provided of the *Habropoda* species of Taiwan and its corresponding cleptoparasite bee, the Melectine genus *Tetralonioidella*.

2. Material and methods

2.1 Material examined

2.1.1 Morphological studies

In the course of the present work, the following genera, with the total number of specimens in parenthesis, were examined:

Andrenidae: *Andrena* (1985), *Ancylandrena* (4), *Megandrena* (5), *Euherbstia* (2), *Orphana* (2), other Andrenidae except Andreninae (87); Apidae (Anthophorini): *Amegilla* (370), *Anthophora* (500), *Deltoptila* (6), *Elaphropoda* (6), *Habrophorula* (1), *Habropoda* (183), *Pachymelus* (35); Apidae (Melectini): *Tetralonioidella* (18).

Specimens used for coding of morphological characters of the cladistic analyses were labeled with an unique reference number with the format "Referenztier #, Dubitzky, year of examination". Each species was assigned a number, multiple specimens of the same species were lettered "A, B, C, etc." in addition to the species-number. In the analysis of *Andrena* about 260 specimens were marked in this way.

The studied material was obtained from the following collections and institutions (The names of the curators or technical staff members who kindly have put the material at the author's disposal are mentioned in parentheses):

AMNH – American Museum of Natural History, New York, USA (J. G. Rozen)

BMNH – The Natural History Museum (formerly British Museum, Natural History), London, Great Britain (G. Else)

CAD – Private collection of the author, Hebertshausen, Germany

CFG – Private collection of F. Gusenleitner, St. Georgen/Gusen, Austria

CGW – Collection of R. W. Grünwaldt, since 2003 housed in Zoologische Staatssammlung München, Germany

CKW – Collection of K. Warncke, housed in Biologiezentrum des Oberösterreichischen Landesmuseums, Linz, Austria

DEI – Deutsches Entomologisches Institut im ZALF, Müncheberg, Germany (A. Taeger, S. M. Blank)

KUEC – Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan (O. Tadauchi)

NCHUT – National Chung Hsing University, Taichung, Taiwan [Republic of China] (J.-T. Yang)

NML – Nationaal Natuurhistorische Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands (C. van Achterberg)

NMNS – National Museum of Natural Science, Taichung, Taiwan [Republic of China] (K. S. Lin, M. Chan)

OLL – Biologiezentrum des Oberösterreichischen Landesmuseums, Linz, Austria (F. Gusenleitner)

SEMC – Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA (M. S. Engel)

SMF – Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany (J.-P. Kopelke)

SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany (T. Osten)

TARI – Taiwan Agricultural Research Institute, Wufeng (Taichung), Taiwan [Republic of China] (H. T. Shih)

USNM – Smithsonian Institution, National Museum of Natural History (formerly, United States National Museum), Washington D.C., USA (M. Epstein, D. Furth)

ZFMK – Zoologische Forschungsinstitut und Museum "Alexander Koenig", Bonn, Germany (K. H. Lampe)

ZMHB – Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (F. Koch)

ZSM – Zoologische Staatssammlung München, München, Germany (E. Diller, S. Schmidt)

2.1.2 Molecular analysis

In addition to the material listed above fresh material of about 150 specimens was collected and preserved by the author for DNA extraction. A total of 34 taxa were sequenced in the present study of which 28 could be used for final analysis. A list of species used in the molecular analysis with voucher information on each individual specimen is given in Tab. 1.

2.2 Preparation of male genitalia and female head capsule including mouthparts

The study of male genitalia and hidden sterna, as well as female head capsule and mouthparts, nearly always required the dissection of specimens.

First, specimens were softened in a moist chamber gently warmed to about 40 °C. Occasionally specimens resisted the softening treatment and since prolonged treatment in the chamber would increase the risk of mold growth, an alternative method was resorted to. These specimens were fixed to a piece of polystyrene or other floatable material and incubated for about 10 minutes in a tightly shut glass half filled with boiled water. In this manner nearly all specimens could be softened and reused for further preparations. Since the steam and high pressure in the shut glass relax specimens more quickly than in a conventional moist chamber there is no risk of specimens developing mould. To avoid contact of specimens with condensed water from the sides of the glass four pins were inserted diagonally into the piece of polystyrene in each corner to ensure that a distance is maintained between specimens and the sides of the glass.

Male genitalia and hidden sterna were removed from the abdomen of fresh or relaxed specimens using a hooked insect pin and were macerated in 10 % KOH for about 2–6 hours at

Tab. 1: List of voucher specimens sequenced in this study.

voucher code	species	subgenus	sex	coll. date	locality
2033	*Panurgus calcaratus* (Scopoli, 1763)		m	9.7.2002	Trail Hebertshausen/Prittlbach, DAH, Bavaria, Germany
2749	*Andrena aciculata* Morawitz, 1886	*Aciandrena*	f	2.7.2003	Geblingweg, Rohrendorf/Krems, Niederösterreich, Austria
2029	*Andrena praecox* (Scopoli, 1763)	*Andrena*	f	10.3.2002	Former shooting range, Hebertshausen, DAH, Bavaria, Germany
2754	*Andrena hattorfiana* (Fabricius, 1775)	*Charitandrena*	m	7.6.2003	Former shooting range, Hebertshausen, DAH, Bavaria, Germany
2783	*Andrena humilis* Imhoff, 1832	*Chlorandrena*	f	24.5.2003	Gerlesberg, Passau, Bavaria, Germany
2784	*Andrena fulvago* Christ, 1791	*Chrysandrena*	f	24.5.2003	Patriching, Passau, Bavaria, Germany
2028	*Andrena bicolor* Fabricius, 1775	*Euandrena*	f	16.2.2002	Former shooting range, Hebertshausen, DAH, Bavaria, Germany
2747	*Andrena nuptialis* Pérez, 1902	*Hoplandrena*	m	2.7.2003	Geblingweg, Rohrendorf/Krems, Niederösterreich, Austria
2025	*Andrena ventralis* Imhoff, 1832	*Larandrena*	f	10.3.2002	Former shooting range, Hebertshausen, DAH, Bavaria, Germany
2032	*Andrena rufizona* Imhoff, 1834	*Lepidandrena*	m	14.6.2002	Allacher Forest, M, Bavaria, Germany
2030	*Andrena barbilabris* (Kirby, 1802)	*Leucandrena*	f	1.4.2002	Sulzrain, DAH, Bavaria, Germany
2027	*Andrena vaga* Panzer, 1799	*Melandrena*	f	29.3.2002	Trail Hebertshausen/Prittlbach, DAH, Bavaria, Germany
2018	*Andrena alfkenella* Perkins, 1914	*Micrandrena*	f	30.7.2001	Former shooting range, Hebertshausen, DAH, Bavaria, Germany
2748	*Andrena floricola* Eversmann, 1852	*Micrandrena*	f	2.7.2003	Geblingweg, Rohrendorf/Krems, Niederösterreich, Austria
2010	*Andrena minutuloides* Perkins, 1914	*Micrandrena*	f	30.7.2001	Former shooting range, Hebertshausen, DAH, Bavaria, Germany
2752	*Andrena nana* (Kirby, 1802)	*Micrandrena*	f	9.7.2003	Steinmaßlgraben, Rohrendorf/Krems, Niederösterreich, Austria
2016	*Andrena niveata* Friese, 1887	*Micrandrena*	f	1.6.2001	Zicklacke, Illmitz, Neusiedlersee, Burgenland, Austria
2019	*Andrena proxima* (Kirby, 1802)	*Micrandrena*	f	14.5.2001	Trail Hebertshausen/Prittlbach, DAH, Bavaria, Germany
2012	*Andrena subopaca* Nylander, 1848	*Micrandrena*	m	23.4.2001	Allacher Forest, M, Bavaria, Germany
2022	*Andrena chrysosceles* (Kirby, 1802)	*Notandrena*	f	2.6.2002	Leitenberg, DAH, Bavaria, Germany
2751	*Andrena atrata* Friese, 1887	*Parandrenella*	f	4.7.2003	Steinmaßlgraben, Rohrendorf/Krems, Niederösterreich, Austria
2020	*Andrena labiata* Fabricius, 1781	*Poecilandrena*	m	1.5.2001	Eichelberg, Marching, KEH, Bavaria, Germany
2750	*Andrena polita* Smith, 1847	*Poliandrena*	m	3.7.2003	Leimerweg, Rohrendorf/Krems, Niederösterreich, Austria
2745	*Andrena scita* Eversmann, 1852	*Scitandrena*	f	1.7.2003	Steinmaßlgraben, Rohrendorf/Krems, Niederösterreich, Austria
2746	*Andrena propinqua* Schenck, 1851	*Simandrena*	f	1.7.2003	Steinmaßlgraben, Rohrendorf/Krems, Niederösterreich, Austria
2023	*Andrena ovatula* (Kirby, 1802)	*Taeniandrena*	f	14.6.2002	Allacher Forest, M, Bavaria, Germany
2031	*Andrena haemorrhoa* Fabricius, 1781	*Trachandrena*	f	18.5.2002	Garden, Hebertshausen, DAH, Bavaria, Germany
2026	*Andrena flavipes* Panzer, 1799	*Zonandrena*	f	10.3.2002	Former shooting range, Hebertshausen, DAH, Bavaria, Germany

m: male, f: female.

room temperature, depending on the thickness of the cuticle of each structure. Genitalia and hidden sterna cleared this way were stored and examined in 75 % ethanol or glycerin. Ultrasound cleaning of these structures in 75 % ethanol, as used at the beginning of the study, was discontinued since it was not successful, and it often destroyed the structures before a complete cleaning was achieved. After study, male genitalia and hidden sterna were air-dried and stored in a gelatin vial or mounted to a piece of cardboard which then was attached to the pin of the corresponding specimen.

As far as material was available for the preparation of female head capsule including mouthparts, the complete head was removed from the body and put in 10 % KOH for about 2 hours at room temperature. After washing in distilled water the complete proboscis and one mandible each were carefully removed from the head capsule, the latter two were stored and studied in 75 % ethanol. The labium was carefully removed from the maxillary-complex which was divided medially. After transferring to 75 % ethanol, all structures of proboscis were stored in glycerin before being mounted with slides and cover glasses for a complete microscopic examination. After study all parts of the female head were fixed onto cardboard and attached to the corresponding specimen.

2.3 Light microscopy

For general examination of specimens a Leica MZ 6 stereoscopic microscope was utilized.

Wings (removed and fixed on white cardboard) were photographed with a Olympus SZX 12 stereoscopic microscope in combination with a Spot Insight Color 3.2.0 CCD camera (Visitron Systems GmbH) using Spot Advanced Version 4.0.9 (Diagnostic Instruments, Inc.). In addition a polarization filter was used to minimize reflections on the wing-surface. Light microscopic images of preparations of mouthparts were taken with a Spot Insight Color 3.2.0 CCD camera adapted to a Leica (Leitz) DMR compound microscope using Spot Advanced Version 4.0.9 and were subsequently processed with Automontage Version 4.03.0071 (Synoptics Ltd.) to obtain confocal images. All files were processed with Adobe Photoshop 7.0.1 and Adobe Illustrator CS.

2.4 Scanning electron microscopy (SEM)

All SEM examination was conducted with a Philips XL 20 scanning electron microscope.

After their preparation (see 2.2) hidden sterna and genitalia of males as well as female head capsules, mouthparts and legs were transferred to solutions of acetone (75 %, 85 %, 90 %, 95 %, 97 % and 99 % for 10 min each) and subsequently stored in 100 % acetone for 24 h. Nearly all preparations were dried using a BAL-TEC CPD 030 critical point dryer, except for strongly sclerotized structures as some legs, head capsules or large genitalia which were air-dried. Pubescence of air-dried samples were brushed simultaneously while drying to

avoid the sticking together of hairs. The structures were mounted on carbon stickers, sputtered for 120 s with a Polaron SEM coating system and analyzed at 10–15 kV using a conventional high voltage anode (spot 4.5, integrate 1, slow scan 3). At the beginning of the study it was necessary to prepare two pairs of male genitalia and S8 in order to document both the dorsal and ventral aspect, because one side of the structure was attached to the carbon stick. Later a different method was developed. The structures were mounted carefully on either left or right side to a minute insect pin using syndetikon liquid glue before coating with gold. In combination with a conductive plasticine (Leit-C-Plast) this preparation method allows the documentation of different aspects of one and the same sample, achieved by simple rotation of the pin. Another advantage of this method is that it results in a more homogeneous black background caused by the greater distance between the sample and object table.

Pinned and air-dried specimens were cleaned with a small brush and fixed with conductive plasticine on an object table. While most specimens were coated with gold and analyzed at 10–15 kV, rare specimens or type material were left uncoated and studied at about 1.6 kV using a special low voltage anode (spot 4, integrate 1 or 4, slow scan 3).

For detailed information and theoretical background of the advanced methods and techniques of SEM, see Bozzola and Russel (1992) and Schmidt et al. (1994).

2.5 Line drawings

Drawings were made using a drawing tube attached to a Leica MZ 6 stereoscopic microscope. The original pencil drawing was traced onto greaseproof paper with an ink pen. Sculpture and pubescence were omitted in all drawings. Yellowish coloured areas were indicated by dotted lines. Drawings were scanned and digitally processed with Adobe Photoshop 7.0.1 and Adobe Illustrator CS.

2.6 Morphological terminology, abbreviations and measurements

The terminology used in this study follows that of Michener (1944, 2000) and, in special cases regarding the morphology of *Andrena*, the terminology of LaBerge (1986) and Thorp (1969) is relied upon. Different and new morphological terms will be explained in the text.

The following abbreviations are used throughout:

AS: antennal segment (scape = AS 1), **BL:** body length, **DGS:** dorsal gonostylus, **FOV:** facial fovea, **FWL:** length of forewing, **GA:** genal area, **DLP:** dorsal part of lateral propodeum, **LP:** lateral part of propodeum, **LO:** lateral ocellus, **LICD:** lower inter compound eye distance, **L/W:** length/wide, **OD:** diameter of lateral ocellus, **PMX** maxillary palpus, **PLB:** labial palpus, **PLR:** process of labrum, **POA:** paraocular area, **PT:** propodeal triangle,

S: metasomal sternum**, SCA:** supraclypeal area, **T:** metasomal tergum, **UICD:** upper inter compound eye distance, **VGS:** ventral gonostylus.

Character states mentioned in the text are coded as a combination of character number and state, e.g. (15:1) for character number 15, state 1.

Morphological measurements were made using an ocular graticule in a Leica MZ 6 stereoscopic microscope. The following measurements were taken and evaluated in the present study:

BL: Complete body length of specimens was measured in lateral view as a sum of the distances from the front of head (excluding antennae) to the posterior end of the propodeum and from there to the tip of the metasoma. Although measurements taken in this way minimize the differences which are caused by the variable position of the metasoma, the results must be considered as approximations because of the deviations caused by the telescoping of the latter. **Length of head:** Distance from hind margin of vertex to the front (lower) margin of the clypeus in frontal view (Fig. 6A). **Width of head:** Distance between outer margins of compound eyes when seen in frontal view (Fig. 6A). **UICD:** Distance between upper inner margins of compound eyes (Fig. 6A). **LICD:** Distance between lower inner margins of compound eyes (Fig. 6A). **Length of glossa:** Widest distance from the basiglossal sclerite to apical tip of glossa. **Width of glossa:** greatest width of glossa in dorsal or ventral view. **Length of PMX and PLB:** Measurement from basal end of basal segment to distal end of apical segment. **Length of PMX 1 and PMX 2 resp. PLB 3 and PLB 4:** Greatest distance between basal and distal end of these segments. **Length of galea:** Distance between basal insertion of PMX to apical end of galea. **Length of mandible:** Measurement from condyle to distal end of mandible. **Length of clypeus:** Shortest distance between upper (hind) and lower (anterior) margin of clypeus in frontal view (Fig. 6A). **Width of clypeus:** Greatest distance between lateral margins of clypeus in frontal view (Fig. 6A). **Length of PLR:** Greatest distance between basal margin of labrum and apical margin of PLR. **Width of PLR:** Measurement of widest distance between lateral margins of PLR taken basally. **Malar space:** Greatest distance between lower margin of compound eye and insertion of mandible (Fig. 6B). **Width of genal area:** Measurement of widest distance between hind margin of compound eye and hind margin of genal area taken in profile (Fig. 6F). **Width of FOV:** Greatest distance between inner and outer margin of FOV. **Distance between FOV and lateral ocellus:** Shortest distance between inner hind margin of FOV and LO (Fig. 6A). **Width of vertex:** Shortest distance between hind margin of LO and hind margin of vertex in dorsal view. **Length of AS:** Greatest distance between basal and distal end of segment taken along outer surface. **Width of AS:** Greatest width of segment taken on distal end along outer surface. **FWL:** Distance between base of vein R to distal end of wing. **Length of jugal lobe:** Distance from base to distal end of jugal lobe. **Length of vanal lobe:** Measurement from the base of incision between jugal and vanal lobe to distal end of vanal lobe. **Puncture density:** The degree of cuticular surface punctation was measured by the distance between single depressions relative to their diameters. Thus punctation is considered sparse/dense when the

distance between the depressions is as wide or greater/less than the diameter of a single depression.

2.7 Molecular techniques

2.7.1 Collection and preservation of voucher specimens

Nearly all voucher specimens used for the molecular analysis were collected by the author with a hand net. Species that could be easily determined in the field by clear morphological features or by specialized flower visiting behavior were directly put into pure 97 % ethanol for fixation. Fixation in strong ethanol is considered to be one of the best preservation methods for DNA extraction as it effectively minimizes enzymatic breakdown by endonucleases (Quicke et al., 1999). Specimens of species which could not be satisfactorily determined in the field were kept alive until their identification using a stereoscopic microscope. To make identification easier the bees were anesthetized with ethyl acetate for about 5 minutes. Bees immobilized this way could be quickly determined and were subsequently fixated in 97 % ethanol after complete evaporation of ethyl acetate. Treatment of specimens with ethyl acetate as described above caused no negative results in DNA extraction (as mentioned in Quicke et al, 1999) in this study and provided amounts of amplifiable DNA as good as direct fixation in pure ethanol. This result supports one of the arguments of Quicke et al. (1999) that ethyl acetate itself is not responsible for the reduction in the ability to extract amplifiable amounts of DNA, rather it is the lengthy amount of time which elapses between the death of specimens and their fixation. During this phase enzymatic DNA degradation can take place, and that is clearly the reason for degradation of DNA. Transfer of anesthetized specimens or immediate transfer of specimens to the preservation agent are preferable methods.

2.7.2 DNA-extraction, amplification, sequencing and alignment

DNA was extracted exclusively from the thorax of bees, since this is the part of a bee’s body with the most muscular tissue and therefore the highest concentration of mitochondria. After careful dissection of the thorax (remaining parts incl. legs were deposited as voucher references in the collection of the DNA laboratory of the ZSM), it was air-dried and ground with a small glass pestle in individual 1.5 ml Eppendorf tubes. Pincers used for preparation were carefully cleaned after each species to avoid contamination. DNA extraction followed standard protocols. In the presence of 180 µl ATL buffer and 20 µl proteinase K solution the samples were incubated at 55 °C over night and subsequently for 10 minutes after adding 200 µl Al buffer. DNA then was extracted using a DNeasy Tissue Kit (QIAGEN) following the manufacturer`s protocol for animal tissues. Concentration of DNA of each sample was

traced by a fluorescence photometer (BioRad, Versa-Fluor^{TM}) and was subsequently standardized on 50 ng/µl with molecular biology grade water (Eppendorf).

PCR amplification of the mitochondrial cytochrome oxidase I (COI) gene was performed in a total of 25 µl reaction volume using water, 10x PCR buffer, $MgCl_2$, dNTP (2 mM each), primers mtD8 and mtD12 (20 pm/µl each), Taq polymerase and template DNA in a PTC 220 DYAD thermal cycler (MJ Research). Initial amplifications with primer combinations mtD4 + mtD9 and mtD4 + mtD11 were not successful, presumably caused by negative annealing reaction of the mtD4 primer. Sequences of primers used in this study are shown in Tab. 2.

Tab. 2: Primers used in this study for amplifying mitochondrial cytochrome oxidase I

primer	primer sequence	position	direction	PCR success
mtD8	5'–CCA CAT TTA TTT TGA TTT TTT GG–3'	2503	5' → 3'	yes
mtD12	5'–TCC AAT GCA CTA ATC TGC CAT ATT A–3'	3357	3' → 5'	yes
mtD4	5'–TAC AAT TTA TCG CCT AAA CTT CAG CC–3'	–	5' → 3'	no
mtD9	5'–CCC GGT AAA ATT AAA ATA TAA ACT TC–3'	–	3' → 5'	no
mtD11	5'–ACT GTA AAT ATA TGA TGA GCT CA–3'	–	3' → 5'	no

PCR started with an initial denaturation at 94 °C for four minutes followed by 35 cycles of denaturation at 94 °C for 1:30 minutes, annealing at 48 °C for one minute and elongation at 72 °C for 1:30. Final elongation for three minutes at 72 °C followed by cooling at 10 °C. PCR results were visualized using ethdium bromide stained agarose gels under UV light.

Purification of PCR products as well as sequencing was conducted in cooperation with the DNA-TAX-laboratory of the ZSM. Before sequencing, PCR products were purified using the MinElute Purification Kit (QIAGEN) following the manufacturer´s protocols and subsequently were measured and adjusted to a final concentration of 100 ng/µl. Cycle sequencing was conducted using the same primers as in PCR and BigDye V.2 master mix (Applied Biosystems) with 200 ng of PCR product as template in a 10 µl reaction volume. Sequencing was performed on a ABI Prism 377 DNA Sequencer.

Sequence chromatograms were edited and combined using free software package of DNA for Windows version 2.2. Alignment of applicable sequences was conducted using Clustal W (1.83).

The mitochondrial genome of *Apis mellifera* (Crozier & Crozier, 1993) was used as reference to determine the reading frame of the sequences.

2.8 Phylogenetic analysis

2.8.1 Selection of taxa

Species were used exclusively as terminals in all phylogenetic analyses of the present study, since use of higher taxa (esp. for analysis of Anthophorini) would be less

understandable or verifiable and coding of characters more difficult within higher taxa because of an increasing variability which accompanies the integration of lower level taxa into higher level taxa.

As far as possible type species of examined higher taxa (subgenera, genera) were included in the analysis to ensure that generic concepts are stabilized. If type species were not available, species were used which appear quite similar to the type species and therefore they should not be contradictory to the corresponding subgeneric/generic concept. This method proved to be of tremendous important for the analysis of *Andrena*, since many species included in the currently recognized subgenera obviously do not conform with the concept of the corresponding type species. The paraphyly or polyphyly of several groups as revealed by the analysis will be discussed below. In case of obviously heterogeneous subgenera several representatives were included in the analysis to ascertain the monophyly of included taxa within the analysis.

2.8.2 Character selection

The morphological analyses of the present study exclusively concentrate on characters of external morphology. An examination of internal morphology would have been difficult or even impossible as valuable material of rare species or type material would not allow the necessary preparation of specimens. Furthermore, most interesting aspects of inner morphology require fresh material for appropriate examination, which would have strongly narrowed the scope of the analyses as the availability of such material is very limited.

Altogether about 700 species of the examined taxa from the various biogeographical regions were examined in an external morphology study prior to the selection of characters to be used in the analyses.

Autapomorphies were included in each analysis because of their potential value as synapomorphies when more taxa are included in future analyses (Yeates, 1992). Apart from that autapomorphies of the analysis of *Andrena* can be mostly interpreted as (hypothetical) synapomorphies for the corresponding subgenus and may additionally have strong diagnostic value.

2.8.3 Cladistic analysis

2.8.3.1 Morphological data

Character matrices for cladistic analyses were constructed using WinClada (Nixon, 1999–2002) or NEXUS Data Editor. Unknown character states were coded with "?" while inapplicable characters where coded with "–". Polymorphisms (multistate character states) were coded with "$". All characters used in the analyses were equally weighted and all multistate characters were treated as non-additive. Parsimony analysis of the coded data was

performed with NONA 2.0 (Goloboff, 1999). In all analyses the heuristic search procedure was conducted using the following search-parameters: 100–500 random replications, 100–500 starting trees per replication, 2000 maximum trees to keep and multiple TBR + TBR search strategy. Successive character reweighting was applied using PAUP 4.0 beta10 for Windows (Swofford, 2001) according to the rescaled consistency index (*a posteriori* weighting). Common cladogram measures such as the consistency index (CI), the retention index (RI) and the rescaled consistency index (RC) were used to evaluate the fit of the data to the cladogram. Analysis of characters as well as character optimization using fast optimization modus (ACCTRAN) was performed with WinClada.

Bootstrap analysis (Felsenstein, 1985) and jackknife sampling (Lanyon, 1985; Siddall, 1996) were used to assess evidential support for clades of cladograms of Anthophorini and *Habropoda*. Values were calculated based on 100 replicates with 50 random sequence additions per replicate. Presentation of trees as well as character mapping was carried out in WinClada.

2.8.3.2 Molecular data

Phylogenetic analysis of nucleotide sequences was performed with NONA using the heuristic search option (1000 random replications, 100 starting trees per replication, 20000 maximum trees to keep and multiple TBR + TBR search strategy). Bootstrap and jackknife values were calculated based on 100 replicates with 50 random sequence additions per replicate to evaluate nodal support. Presentation of trees was carried out in WinClada.

3. An evolutionary hypothesis for the genus *Andrena* Fabricius

3.1 Introduction

The bees of the genus *Andrena* (Fig. 5), commonly called sandbees, represent the largest genus of bees (cf. Michener, 2000). To date it contains about 1500 valid species and including synonyms about 3001 named taxa (Gusenleitner & Schwarz, 2002). Considering that many species of *Andrena* have yet to be described (especially those from the dry regions of Central Asia and Mesoamerica) and that many described subspecies, in particular those named by Warncke, may be raised to species rank, the real number of species of *Andrena* might be at least around 2000. This bee group rightly deserves to be called one of the largest genera of animals (Mayr & Ashlock, 1991; Minelli, 1993), on par with *Drosophila* (Diptera), *Atheta* or *Onthophagus* (both Coleoptera).

The genus *Andrena* exhibits a widespread holarctic distribution ranging from North America south to Panama, as well as from Western Europe including northern Africa via Asia minor, Central Asia eastward to Korea, Japan and the Kamtschatka region. Except for one species which is found in the tropical lowlands of Panama, the occurrence of *Andrena* in apparently tropical regions, such as the East African highlands south to the Cape province, the southern parts of India, China, Japan and Taiwan, as well as Malaysia (Baker, 1995), is clearly restricted to the mountainous areas within these regions (Michener, 1979, 2000) where the climatic conditions are more temperate than in the tropical lowlands. It should be added that species of *Andrena* occurring in those regions are not as numerous as those in temperate regions. *Andrena* is completely absent in South America, main parts of Central Africa and South East Asia, as well as Australia. Nearly all sandbees undoubtedly prefer dry and warm climatic conditions as found in the Mediterranean region and the steppes of central Asia, where the genus shows its greatest diversity. Of the 99 currently described subgenera of *Andrena*, 17 occur in both hemispheres, while 50 are restricted to the palearctic and 32 to the nearctic realm (Gusenleitner & Schwarz, 2002). Only three species of sandbees, *A. barbilabris* (Kirby, 1802), *A. wilkella* (Kirby, 1802) and *A. clarkella* (Kirby, 1802) are holarctic being distributed in North America, as well as in the Palearctic region.

All species of *Andrena* burrow their nests into the ground, often preferring sunny exposed areas with sparse or bare vegetation and sandy ground – for this reason, the bees are commonly called sandbees. Sandbees are typically solitary, that is, each female constructs its own nest. Some species (e. g. *A. carantonica* Pérez, 1902) show communal nesting behaviour often occurring in large aggregations. Thus, Paxton & Tengö (1996) reported nearly 600 females of *A. carantonica* sharing a single nest entrance. This often facultative communal nesting behaviour may represent a defensive adaptation against predators like cleptoparasitic bees or Bombyliidae (Diptera). Nest cells of *Andrena* are made usually at the ends of lateral

burrows, radiating from the man burrow, sometimes also two or more cells are found in series in a single lateral burrow (Michener, 2000; Radchenko, 1981).

Most species of *Andrena* fly from early spring to early summer (cf. Dubitzky et al., 2005), while only few are typical summer or even autumn species. A remarkable exception is the eastern Mediterranean *A. grossella* Grünwaldt, 1976, which is exclusively active from October to November (Grünwaldt, 1976). Although some species produce two generations per year, most sandbees are univoltine, i.e., produce only one generation. Such species, and especially early spring species, hibernate as adults in their cells with both sexes emerging at more or less the same time of the following year (Michener, 2000).

Regarding flower visitation, many species of *Andrena* are generalists and use pollen from more than a single plant family for the provision of their larvae (polylectic species). In addition, many species are oligolectic, that is, specialized on pollen from a single plant family or even plant genus. These specializations are often associated with morphological adaptations, e.g. the elongation of mouthparts or the development of specialized pollen collecting hairs. Sometimes all species of a subgenus show the same specialization for a distinct plant group, e. g. the nearctic *Onagrandrena*, which is oligolectic on Onagraceae or members of the palearctic *Pallandrena* which exclusively collect pollen of Dipsacaceae.

Considering the large number of species of *Andrena* it is no wonder that the genus has been long subdivided into subgenera or species groups by taxonomists. The first attempt to subdivide *Andrena* was carried out by Nylander in 1851, who combined species described by him into seven different groups, which he called "stirps" (Latin: branch). His subdivision into groups however was largely intended to assist determination than to serve as a taxonomic or systematic classification. Thomson (1872) subdivided the genus *Andrena* into two main groups, which he further subdivided into different subgroups. However, neither Nylander (1851) nor Thomson (1872) established subgeneric names for the groups based on their subdivisions. Thus the introduction of the first formal subgeneric names mainly relies on pre-existing generic or subgeneric names which were given to single species of *Andrena*. These names were not based on ideas of a subdivision of *Andrena* as mentioned above (e. g. Lepeletier, 1841; Guerin-Meneville, 1844; Dours, 1873). Dours (1873) was the first who established subgeneric names based on concrete species groups of *Andrena*. Further subgeneric names based on distinct species groups, which are still valid to date (*Melandrena*, *Holandrena*, *Hoplandrena*, *Chlorandrena* and *Simandrena*) were erected by Pérez (1890). After describing several new species of *Andrena* from Illinois in 1891, Robertson (1902) split *Andrena* into seven distinct genera, most of which later became subgeneric names of nearctic *Andrena*. Viereck (1924) provided a key to the subgenera of *Andrena* known at that time and additionally introduced several new (monotypic) subgenera. Based on the results of the preceding studies of Perkins (1919) and Stöckhert (in Schmiedeknecht, 1930), Hedicke (1933) subdivided all palearctic species of *Andrena*, which were familiar to him, into subgenera and introduced several new names. Furthermore, he was the first to designate type species for each subgenus. He rediscovered the old subgeneric names introduced by Pérez

(1890) and established them in the literature by the designation of type species, although he acknowledged that the species groups described by Pérez (1890) did not represent true phylogenetic groups. Further subgenera including designations of type species were described by Lanham (1949) for the nearctic and by Pittioni (1948) for the palearctic region. In his comprehensive study on the subgenera of the western palearctic region Warncke (1968a) redescribed the known subgenera and introduced 19 new subgenera. Two additional subgenera were erected by him in (1974a). Though his studies represent one of the most comprehensive work dealing with the palearctic subgenera of *Andrena* to date, his descriptions are often insufficient in that they do not clearly distinguish between description and diagnosis. Also, some of the characters listed by him are not typical for most of the included species, sometimes even the type species is different. Several new subgenera were described in detail by Osytshnjuk (1983a, 1984a-b, 1993a-b, 1994a) for central Asia and by Hirashima (1963, 1964), Hirashima & LaBerge (Hirashima, 1965) and Hirashima & Tadauchi (1975) for Japan. Within their comprehensive revisional studies of the North American subgenera of *Andrena* LaBerge (1964, 1971a-b, 1977, 1986a), LaBerge & Hurd (1965), LaBerge & Ribble (1972) and Ribble (1968) presented not only concise descriptions and diagnoses of 20 newly erected subgenera but mostly also provided a well founded phylogenetic study of the included species within each subgenus. In her study of North and Middle European *Andrena*, Dylewska (1987) abandoned subgeneric classification of *Andrena* and introduced discrete species groups and subgroups instead, some of which fused or split up established subgenera.

The taxonomy of *Andrena* has been thoroughly studied as for the western palearctic region by Warncke (1965a-b, 1966, 1967, 1968a-b, 1969a-b, 1972, 1974a-b, 1975a-b, 1976, 1980), for central Asia by Osytshnjuk (1975, 1979, 1982a-c, 1983a-b, 1984a-d, 1985, 1986a-b, 1993a-c, 1994a-b), for the far eastern palearctic region (Japan, China) by Hirashima (1962, 1963, 1964a-b, 1965a-b, 1966), Tadauchi (1985b-c), Tadauchi & Hirashima (1983, 1987, 1988), Tadauchi & Xu (1995, 1998, 1999, 2002), Xu & Tadauchi (1995, 1997a-b, 1998, 2002), and for the nearctic region by LaBerge (1967, 1969, 1971a-b, 1973, 1977, 1980, 1986a, 1987, 1989), LaBerge & Bouseman (1970), LaBerge & Ribble (1972, 1975), Ribble (1968, 1974) and Donovan (1977). Very few studies, however, focus on the phylogenetic relationships of *Andrena*-taxa. For example, in his comprehensive revisions of the nearctic subgenera (see above) LaBerge presented well founded phylogenetic hypotheses for the species in each subgenus he examined. In his paper dealing with the zoogeography of nearctic *Andrena* (LaBerge, 1986b) he also addressed to the phylogenetic relationships of North American *Andrena* on the subgeneric level providing hints on possible relationships to some palearctic subgenera. Warncke (1968) postulated relationships among the palearctic subgenera, but these were based on his subjective opinion, rather than common characters, thus his theory on the phylogeny of palearctic *Andrena* remains obscure and is in large parts incomprehensible. Tadauchi (1982, 1985), inconstant, presented a well founded numerical taxonomic study of Japanese *Andrena* based on the methods of phenetic numerical taxonomy.

Larkin (2002) was the first, to conduct a molecular phylogenetic study of *Andrena*. She focused her analysis on the nearctic subgenus *Callandrena*, and additionally included in nearctic representatives of 25 different subgenera of *Andrena*.

Andrena is clearly a member of the Andrenidae, yet the phylogenetic position of the genus within the family, as well as the relationships of the Andrenidae to remaining families of short-tongued (S-T) bees has not been satisfactory analyzed. The results of the various cladistic analyses on the phylogeny of S-T bees by Alexander & Michener (1995) placed any one of the families of S-T bees (Stenotritidae, Colletidae, Halictidae, Andrenidae, Melittidae) as the most basal member except the Andrenidae. Likewise, concerning the position of *Andrena* within the Andrenidae, their results varied strongly depending on the analysis.

Despite these several attempts to shed light on the evolution of *Andrena* the phylogenetic relationships of its 99 subgenera remain largely in the dark. The main goal of the present study therefore is to present a nearly complete phylogenetic hypothesis for *Andrena* worldwide based on a cladistic analysis of 162 morphological characters including representatives of 84 of its 99 currently recognized subgenera. The first part of this study set out, furthermore, to examine the monophyly of several palearctic and holarctic subgenera, as well as the phylogenetic position of *Andrena* within the Andreninae.

The second part of this study focuses on a molecular analysis of 27 Central European species of *Andrena*, representing 21 different subgenera, by using DNA sequence data of mitochondrial cytochrome oxidase I (COI). COI is a slowly evolving mitochondrial protein-coding gene that has been used in phylogenetic investigations on a wide variety of insects at generic and subgeneric levels (Simon et al., 1994) and which has been found suitable for obtaining good resolution on subgeneric level within bees (Danforth, 1999; Larkin, 2002). In addition to an examination of the phylogenetic relationships among these 21 Central European subgenera, one of the main goals of the present molecular analysis was to focus on the monophyly of the subgenus *Micrandrena*, for which by seven different Central European species were examined.

Finally the results of both analyses, the morphological and the molecular, should be compared to each other and discussed in detail.

3.2 Results and discussion

3.2.1 Phylogenetic analysis of *Andrena* based on morphological data

Selection of taxa and characters

The phylogenetic analysis of *Andrena* sampled 102 ingroup taxa, representing 84 of the 99 currently recognized subgenera of *Andrena*. Contrary to Michener (2000) *Melittoides*, *Opandrena* and *Truncandrena* are regarded as subgenera in the present study. One representative from each of the remaining Andreninae genera (sensu Michener, 2000) was included in the ingroup. A hypothetical ancestor was used as outgroup, because of the vague phylogenetic relationships within the Andreninae. The following taxa were originally integrated into the data but in the final analysis were omitted because they were available in only one sex. This deficiency interfered with or obstructed the analysis because a high number of characters would have to be coded as missing. These taxa include *A. (Avandrena) avara, A. (Belandrena) nemophilae, A. (Carinandrena) carinifrons, A. (Celetandrena) vinnula, A. (Erandrena) principalis, A. (Habromelissa) omogensis, A. (Nemandrena) crudeni, A. (Psammandrena) cercocarpi, A. (Scaphandrena) scurra* and *A. (Xiphandrena) mendica*. No material was available for study from the monotypic subgenera *Malyapis* and *Oxyandrena*.

The cladistic analysis of *Andrena* was based on 162 characters comprising 452 character states. At the beginning of the analysis a total of 193 characters were included of which 31 were omitted since they caused poor resolution due to great homoplasy when running the initial analyses. Of the characters used in the final analysis 83 were coded binary, 49 with three states, 21 with four states, 4 with 5 states, two with 6 states, two with 8 states and one character with seven states.

Characters and character states used for the cladistic analysis of *Andrena*

In the following character list comments are given on the polarization of each character explaining which of the character states is regarded as plesiomorphic in the present analysis. The polarization of many characters is contrary to that of previous studies or must be established for the first time.

Head and mouthparts

1. Posterior part of hypostomal carina: (0) more or less entire (Figs 7D, E); (1) deeply emarginate (Figs 7A-C).
   A deeply emarginated hypostomal area is found only in *Megandrena enceliae* and *Cubiandrena cubiceps*, being more distinct and stronger in the latter. In *A. (Longandrena) dolini* no distinct hypostomal carina is developed, because posterior parts of hypostomal area and postgenal bridge are indistinguishably fused. An entire hypostomal carina, as found in nearly all Andrenidae, is regarded as the plesiomorphic state.
2. Postgenal bridge: (0) distinctly developed, about as wide as antennal flagellum (Figs 7D, E); (1) strongly reduced, hypostomal carina nearly joining postoccipital suture; (2) deeply concave shaped (Figs 7A, B).
   A distinctly developed postgenal bridge as found in most Andrenidae is held to be plesiomorphic. In *A. (Iomelissa) violae* it is strongly reduced and in *Cubiandrena* the postgenal bridge is deeply concave shaped.
3. Hypostomal area: (0) strongly declivous; (1) slightly sloping; (2) strongly sloping to slightly declivous.
   A strongly declivous hypostomal area as developed in most bees is regarded as plesiomorphic.
4. Subgenal coronet: (0) absent; (1) present (Figs 7H-N, P, Q).
   The presence of a subgenal coronet is autapomorphic for the genus *Andrena*. It is absent in all other bees. In a few subgenera of *Andrena* it is strongly reduced (Figs 7N, P, Q), but in the great majority it is clearly well-developed. Strangely enough, this structure defined by Timberlake (1941) for the first time has hardly received mentioned or investigation; few authors have paid attention to it (Lanham, 1949; Thorp, 1969; LaBerge, 1986a; Patiny & Gaspar, 1999). In their comparative study of the subgenal coronet of several central European species, representing eight different subgenera, Patiny & Gaspar (1999) emphasized the taxonomic importance of this structure. Contrary to their terminology, only the bristles along the inner and hind margin of the paramandibular process are regarded as the subgenal coronet in this study. Their "concentric rows of inner teeth" are termed the “bristles of the paramandibular process” herewith, because their size and shape are nearly always completely different from the outer bristles along the margin, which form the coronet in the strict sense. All bristles of the subgenal coronet and those of the paramandibular process (Figs 7H-R) are true cuticular projections since they show no basal circular articulation as do bristle-like formations of hairs (cf. character 112). The bristles found along the toothlike projection of the paramandibular area of *Cubiandrena cubiceps* seem to be homologous to the bristles of the subgenal coronet, but a convergent development of these structures is also possible. Nevertheless it is regarded as a strongly modified subgenal coronet in this study. Nothing concrete is known about the function of the subgenal coronet, although Patiny & Gaspar (1999) assume a possible connection with the modification of the pollen provisions for the larvae, this is hypothetical since no such behaviour has been observed and pollen is seldom found between the bristles.
5. Bristles of subgenal coronet: (0) developed along inner and hind margin of paramandibular process (Figs 7H-N); (1) only developed along inner margin of

paramandibular process (figs 7P, Q); (2) developed along toothlike projection (figs 7F, G).
A fully developed coronet (bristles found along inner and hind margin of paramandibular process) is regarded as plesiomorphic, state (1) may be a secondary reduction and state (2), which is only found in *Cubiandrena cubiceps,* is interpreted as an aberrant specialization of this structure within *Cubiandrena.*

6. Pubescence between single bristles of subgenal coronet: (0) weakly developed, extremely sparse to absent (Figs 7K-M); (1) strongly developed, dense (Figs 7H-J, N, P, Q).
A nearly hairless to naked outer margin of the paramandibular area, which constitutes the bristle bearing area of the subgenal coronet, is plesiomorphic as it is found in all other members of Andrenidae.

7. Bristles of paramandibular process: (0) absent (Figs 7F, G); (1) strongly reduced, minute to indistinct (Figs 7N-P, R); (2) distinctly smaller than bristles of subgenal coronet (Figs 7H-M); (3) as large to slightly smaller than bristles of subgenal coronet.
The smooth and naked paramandibular area of all Andrenidae and other bees is considered plesiomorphic.

8. Cross section of galea: (0) slightly convex shaped (Figs 9C, 10A-C, E-H, 11A-E); (1) strongly flattened, with outer lateral margin strongly angled (Figs 9A, B, 10D).
The genus *Platygalandrena* is characterized by a flattened, angled galea, which is strongly flattened in *A. (Platygalandrena) fedtschenkoi* and only slightly flattened in *A. (Platygalandrena) tecta.* A slightly convex shaped galea as developed in all other Andrenidae and in most other bees is regarded as plesiomorphic.

9. Apex of galea : (0) rounded (Figs 9A-C, 10A-D, F-H, 11A, C-E); (1) pointed (Figs 10E, 11B).
An apically pointed galea is probably derived since it is found in only six subgenera of *Andrena*, in contrast to the broadly rounded galea of most *Andrena* subgenera and all other Andreninae.

10. Apical part of outer margin of galeal blade: (0) straight to slightly rounded (Figs 9A-C, 10A-F, H, 11C-E); (1) distinctly concave shaped (Figs 10G, 11A, B).
A concave shaped outer margin of the galeal blade is considered apomorphic. In most subgenera of *Andrena* and all other Andreninae the margin is straight to slightly convex.

11. Pubescence of galeal blade (hair-type): (0) absent to normal straight hairs (Figs 9A, B, 10A-H, 11A-C); (1) posteriorly bent, strong, hooked hairs (*nasuta*-type, Fig. 9C); (2) anteriorly bent, hooked hairs (*osmioides*-type, Figs 11D, E); (3) slightly anterior bent, stiff, long hairs (*brevipalpis*-type).
Sparse, unmodified hairs of the galeal blade as in most subgenera of *Andrena* and all other Andrenidae are considered plesiomorphic.

12. Length PMX: (0) about as long as galea or slightly longer (Figs 10A, B, D-H, 11A, B); (1) distinctly shorter than galea (Figs 9C, 10E, 11C, D); (2) distinctly longer than galea.
A PMX that is about as long as galea or slightly longer is the most common state in *Andrena* and all other Andrenidae, and therefore is regarded as plesiomorphic.

13. Length of PMX 2: (0) about as long as or longer than PMX 1 (Figs 10A-C, E-H, 11 A-E); (1) distinctly shorter than PMX 1 (Figs 9A, B, 10D).
Despite the fact that nearly all genera of Andreninae, except *Andrena*, exhibit state (1), the plesiomorphic condition of the PMX 2 for the genus *Andrena* is regarded as about as

long as or longer than PMX 1, because this condition is present in all subgenera of *Andrena* (however lacking in the species *A. (Ulandrena) fedtschenkoi*), and it is present in *Euherbstia*, as well as most other Andrenidae.

14. Hairiness of stipes: (0) sparse (Figs 10B, E, 11C, D); (1) medium to dense (Figs 10A, B, D, F-H, 11A, B).
    Since most subgenera of *Andrena*, as well as *Megandrena, Orphana* and most other Andrenidae, show a sparse pubescence of stipes, this state is considered ancestral.
15. L/W-ratio of glossa: (0) short, not longer than 2 times as wide (Figs 9D, 12A, C, E, G, I); (1) medium-long, 2 to nearly 4 times longer than broad (Figs 12D, F); (2) strongly elongate, at least 4 times as long as broad (Figs 9E, 12B, H, J).
    For short-tongued bees state (0) is probably plesiomorphic, as it is also found in *Orphana*, *Ancylandrena* and most subgenera of *Andrena*.
16. Length of PLB: (0) about as long as glossa to slightly longer (Figs 9D, E, 12A, C, E-J); (1) distinctly shorter than glossa (Figs 12B, D); (2) distinctly longer.
    State (0) is found in most Andrenidae and therefore is considered plesiomorphic.
17. Shape of PLB 2: (0) club-like (Figs 9D, 12A-F); (1) slender (Figs 9E, 12H, J).
    Slender PLB are developed in only few subgenera of *Andrena* and nowhere else in Andreninae, thus this state is apomorphic.
18. Length of PLB 4: (0) about as long as or longer than PLB3 (Figs 9D, E, 12A-F, J); (1) distinctly shorter than PLB 3 (Fig. 12H).
    State (1) is autapomorphic for *A. (Didonia) mucida*.
19. Mental plate: (0) distinctly developed (at least as long as interscleritic region); (1) strongly reduced to absent (distinctly shorter than interscleritic region).
    The basal parts of the labium have been comparatively studied in detail by Michener (1985), as well as by Plant and Paulus (1987). While Michener divided the part basal to the glossa into three different sclerites, termed lorum (basally), mentum and prementum (apically), Plant and Paulus (1987) defined only two clearly separated sclerites called postmentum and prementum. Their postmentum represents a single lorum (=submentum)-mentum complex, since it is undivided in most bees except *Apis, Bombus* and others where it is clearly divided into two separate sclerites and only here is it appropriate to speak of a mentum and lorum. Furthermore, Plant and Paulus (1987) considered the interpretation unlikely that the membranous, interscleritic region between the postmentum and prementum is a desclerotized mentum because an interscleritic region is found regularly in various Hymenoptera even in forms with a well developed mentum (e.g. Melittidae). Plant and Paulus (1987) therefore presumed the presence of an interscleritic region as plesiomorphic and not representing a reduced mentum, contrary to Michener (1985) who regarded a sclerotized mentum (= mental plate of postmentum) as primitive for bees. Regarding *Andrena*, a well developed mental plate of the postmentum (=sclerotized part of mentum of Michener 1985) is regarded as ancestral in this study, since it is found in all other Andreninae and most of the remaining Andrenidae (except Oxaeinae).

20. Prementum: (0) rounded without any ridges; (1) rounded, two incomplete ventrolateral ridges developed (ridges distinctly shorter than prementum); (2) rounded, two complete ventrolateral ridges developed (ridges as long as prementum); (3) strongly compressed laterally, with distinct median keel ventrally.
    State (0) is found in all remaining Andrenidae and therefore is regarded as plesiomorphic. The complete ventrolateral ridges of *A. cubiceps* (3) probably evolved independently and cannot be compared with the incomplete ridges defined in state (2).
21. Hairiness on ventral side of prementum: (0) weak to absent; (1) strong, normal hairs; (2) strong, with stiff and forward curving hairs (*osmioides*-type); (3) strong, with stiff and backward curving hairs (*nasuta*-type).
    Weak or absent pubescence on the ventral side of prementum is considered ancestral as it is present in most *Andrena*-species and all other Andreninae.
22. Condylar lamella of female mandible: (0) absent; (1) developed (Fig. 7H).
    This peculiar feature of most subgenera of *Andrena* is not found elsewhere in bees. Amazingly, it has not been mentioned or termed in relevant papers dealing with mandibular morphology of bees (Michener and Fraser, 1978) or the morphological characteristics of *Andrena* (Lanham, 1949; Warncke, 1968a; Thorp, 1969; Michener, 2000). According to the present knowledge of the author only two articles gave a hint to existence of this character. In their paper on the comparative morphology of the postmentum of bees, Plant and Paulus (1987) clearly illustrated this structure in Fig. 1 but neither mentioned nor explained it in the text as it was not relevant to the topic of their study. Patiny and Gaspar (1999) briefly mentioned a "lamella" as basal part of the female mandible in correlation with the possible function of the subgenal coronet, but neither defined nor explained the structure in detail. In this study the condylar lamella is defined as a convex lamellate projection along the lower margin of female mandible distal to the mandibular condyle. A close interaction between these two structures seems likely since the condylar lamella is well developed in subgenera in which the bristles of the subgenal coronet on the hind margin of the paramandibular area are large and distinct, and since the condylar lamella is absent in subgenera with a strongly reduced subgenal coronet. By opening and closing of mandibles the outline of the condylar lamella is found to fit exactly within the outline of the subgenal coronet which is another argument favoring the joint interaction of these structures. The exact function of both the condylar lamella and the subgenal coronet remains unclear. The presence of the condylar lamella is regarded as derived since it strongly correlates with subgenal coronet, furthermore, it occurs in most subgenera of *Andrena* and is unique among bees.
23. Length of mandible (female): (0) normally long not or only slightly crossing over apically in repose (less than ¼ of mandible length); (1) strongly elongate, distinctly crossing over apically in repose (at least ¼ of mandible length), (2) slightly elongate.
    Slender mandibles which do not, or only slightly cross over apically are typical for Andrenidae and most other short-tongued bees and represent the ancestral type of mandibles occurring also in sphecoid wasps (Michener and Fraser, 1978), while elongate mandibles (states (1) and (2)) are derived.

24. Length of male mandible: (0) short, not or hardly crossing over each other in repose; (1) medium-long, slightly crossing over in repose (less than ¼ of mandible length); (2) elongate, strongly crossing over in repose (at least ¼, Fig. 6F).
    A short male mandible as found in most Andrenidae and other primitive short-tongued bees (Colletidae, Halictidae) is regarded as plesiomorphic.
25. Shape of male mandible (lateral view): (0) straight to slightly curved; (1) strongly curved downward (Fig. 6F).
    A strongly curved male mandible is probably derived from a straight to slightly curved one.
26. Anterior view of male mandible: (0) slightly curved; (1) strongly bent inward.
    State (0) is considered ancestral as it is found in most subgenera of *Andrena* and in all other Andreninae.
27. Preapical tooth on male mandible: (0) absent (mandible simple); (1) present.
    Although a preapical tooth of the male mandible is developed in most subgenera of *Andrena*, a simple male mandible is considered ancestral because it is found in all other Andreninae, except *Ancylandrena*, and it is present in most of the remaining Andrenidae.
28. Distance between preapical tooth and apical tooth of male mandible: (0) no more than 1/4 of mandibles total length; (1) at least 1/4 of mandibles total length.
    State (0) represents the groundplan of bidentate male mandible as in most short-tongued bees.
29. Basal process on posterior margin of male mandible: (0) absent; (1) present.
    The basal process along the posterior margin of male mandibles of some *Andrena*-subgenera is clearly a derived feature.
30. L/W-ratio of female head: (0) <1; (1) ≥1.
    State (0) is considered ancestral as it is found in most subgenera of *Andrena* and all other Andreninae.
31. L/W-ratio of male head: (0) 0.7-0.95; (1) <0.7; (2) >0.95.
    State (0) is suggested plesiomorphic as it is found in most subgenera of *Andrena* and all other Andreninae.
32. UICD/LICD-ratio of female: (0) 1; (1) >1; (2) <1.
    State (0) is presumed to be ancestral as it is present in most subgenera of *Andrena* as well as in *Ancylandrena*, although all other Andreninae and many subgenera of *Andrena* show state (2).
33. Shape of PLR (female): (0) rectangular to broadly rounded (Fig. 8M); (1) more or less triangular (Fig. 8N).
    A rectangular to broadly rounded PLR is found in all Andreninae and most *Andrena*-subgenera and therefore is regarded as the plesiomorphic state.
34. Front margin of PLR (female): (0) without emargination in the middle (Fig. 8M, N); (1) with strong emargination in the middle (Fig. 8O).
    The strong median emargination of the front margin of some subgenera of *Andrena* is apomorphic, as it is not found elsewhere in the Andreninae.

35. W/L-ratio of PLR (female): (0) 2-4; (1) <2; (2) >4.
    State (0), as in *Megandrena* and most subgenera of *Andrena*, is regarded as plesiomorphic while states (1) and (2) as derived. State (2) occurs in *Ancylandrena* and *Orphana*.
36. PLR (male): (0) ventrally orientated, apical margin not protruding front margin of clypeus; (1) strongly protuberant, apical margin distinctly protruding front margin of clypeus (Fig. 6F).
    State (1) is developed only in some subgenera of *Andrena* and in *Euherbstia*. This state is apomorphic and probably evolved independently in *Andrena* and *Euherbstia*.
37. L/W-ratio of female clypeus: (0) <0.7; (1) >0.7.
    A clypeus which is distinctly broader than long, as in most species of *Andrena* and all other Andreninae, is ancestral while an elongate clypeus, only found in some subgenera of *Andrena*, is derived.
38. L/W-ratio of male clypeus: (0) 0.4-0.7; (1) <0.4; (2) >0.7.
    State (0), as present in most species of *Andrena* and all other Andreninae, is regarded as plesiomorphic.
39. Profile of front margin of clypeus (female): (0) ventrally orientated, not curled up anteriorly; (1) distinctly curled up anteriorly.
    State (0) is found in most *Andrena*-subgenera and all remaining Andrenidae and therefore is considered plesiomorphic.
40. Profile of front margin of clypeus (male): (0) ventrally orientated, not curled up anteriorly; (1) distinctly curled up anteriorly.
    State (0) is found in most *Andrena*-subgenera and all other Andrenidae and therefore is considered plesiomorphic.
41. Disc of female clypeus: (0) more or less convex shaped; (1) strongly flattened; (2) slightly flattened.
    Most subgenera of *Andrena* and all other Andreninae, except *Ancylandrena*, show a convexly shaped clypeus, which is assigned the plesiomorphic state (also in males cf. character 42 below).
42. Disc of male clypeus: (0) convex shaped; (1) weakly flattened; (2) strongly flattened.
43. Coarse punctation of disc of clypeus (female): (0) absent; (1) present.
    The coarse punctation of clypeus is derived since among the Andreninae it is developed only in some subgenera of *Andrena* and in *Euherbstia*.
44. Punctation of disc of clypeus honeycombed (female): (0) absent; (1) present.
    Honeycombed punctation of the clypeus is developed only in some subgenera of *Andrena* and nowhere else in the Andreninae.
45. Impunctate median line of clypeus (female): (0) indistinct to absent; (1) strongly developed.
    The distinct impunctate median line of the clypeus of several subgenera of *Andrena* is also present in *Orphana* and *Ancylandrena* but never in other Andrenidae, thus it is considered apomorphic.

46. Cuticular surface of disc of clypeus (female): (0) smooth, shiny; (1) more or less tesselate.
    Although a smooth and shiny clypeus is the less common state in *Andrena*, it is regarded as plesiomorphic because it is present in all other Andreninae except *Euherbstia*.
47. Wrinkles of disc of clypeus (female): (0) absent; (1) weakly wrinkled; (2) distinctly transverse wrinkled; (3) distinctly longitudinal wrinkled.
    A more or less wrinkled clypeus is apomorphic as it is found only in a few subgenera of *Andrena* and nowhere else in the Andrenidae. The absence of any wrinkles therefore is regarded as the ancestral state.
48. Coloration of clypeus (female): (0) completely dark; (1) at least partly yellow to ivory colored.
    Yellow clypeal markings in the female are absent in all other Andreninae and most Andrenidae except several tribes of Panurginae (e.g. Melitturgini, Perditini, Calliopsini), where they are more or less strongly developed. A uniformly dark clypeus is considered ancestral.
49. Coloration of clypeus (male): (0) completely dark; (1) at least partly yellow to ivory colored.
    Though most male Andreninae and most remaining Andrenidae have a more or less yellowish clypeus, a dark clypeus is presumed to be ancestral in *Andrena* as it is present in most subgenera of *Andrena* as well as in *Ancylandrena* and Alocandreninae.
50. Malar space of female: (0) short to absent, distinctly narrower than half the length of antennal flagellum; (1) strongly elongate, at least as long as antennal flagellum (Fig. 6B); (2) slightly elongate, 0.6-0.8 times as wide as antennal flagellum.
    A short strongly reduced malar space is typical for most subgenera of *Andrena* and all other Andrenidae is therefore regarded as plesiomorphic.
51. Malar process of male: (0) absent; (1) developed (Fig. 6D).
    A ventrally orientated process of the malar area is only developed in *Andrena (Derandrena) vandykei* and *Andrena (Hoplandrena) trimmerana* and therefore is regarded as apomorphic.
52. Width of female GA (referring to width of compound eye): (0) 1-2; (1) <1; (2) >2.
    State (0) as represented in most subgenera of *Andrena*, as well as in *Euherbstia, Orphana* and most other *Andrenidae*, is plesiomorphic.
53. Punctation of GA of female: (0) indistinct, weak to absent; (1) distinct; (2) coarse, strongly honeycombed; (3) indistinctly honeycombed; (4) coarse.
    The indistinct weak punctation of the female GA which is found in most subgenera of *Andrena*, as well as in *Orphana* and *Megandrena*, is ancestral.
54. Width of male GA (referring to width of compound eye): (0) 1-1.6; (1) <1; (2) >1.6.
    State (0) as developed in most subgenera of *Andrena*, as well as in *Euherbstia, Orphana* and most other *Andrenidae*, is held to be plesiomorphic.
55. Hind margin of GA (male): (0) rounded; (1) edged.
    A distinctly edged hind margin of the male GA is only found in some subgenera of *Andrena*, but nowhere else within the Andrenidae and therefore is considered apomorphic.

56. Genal process of male: (0) absent; (1) present (Fig. 6C).
Only a few subgenera of *Andrena* show a distinct genal process in the male, it is absent in all other Andreninae and the remaining Andrenidae.

57. Subgenal process of male: (0) absent; (1) present (Fig. 6E).
The subgenal process of male is found to be an autapomorphy for *Andrena (Genyandrena) mackieae*, although it is also developed in some members of the palearctic subgenus *Carandrena*, which were however not included in the present analysis.

58. Coloration of POA (female): (0) dark; (1) yellow to ivory.
Dark POA as in the female are most likely to be plesiomorphic as they are typical for nearly all subgenera of *Andrena* and all other Andreninae.

59. Cuticular surface of frons (female): (0) longitudinal ridges indistinct to absent; (1) longitudinal ridges strong, distinct.
The absence of longitudinal ridges on the female frons as found in all other Andrenidae is regarded as ancestral.

60. Punctation of frons: (0) normal, more or less distinct (≥0.5); (1) coarse, strongly honeycombed (<0.5); (2) coarse, weakly honeycombed (<0.5); (3) small, weakly honeycombed (<0.5).
A more or less distinct punctation of frons, as in most subgenera of *Andrena* as well as in *Orphana* and *Euherbstia*, is regarded as plesiomorphic, although in the remaining Andrenidae no clear distinction can be discerned.

61. Velvety FOV: (0) absent; (1) present (Figs 8A-L).
Within the Andreninae, a velvety FOV is found only in the subgenera of *Andrena* as well as *Megandrena* and *Ancylandrena*. It is absent in *Euherbstia* and *Orphana*, as well as all other Andrenidae (except Alocandreninae, which shows a typical velvety FOV) and all remaining bees. In agreement with Schuberth and Schönitzer (1993) and Michener (1986) a velvety pubescence of the FOV is considered apomorphic.

62. Depth of FOV: (0) entire fovea deeply depressed (Figs 8A, C, F, K); (1) only lower or upper part deeply depressed; (2) completely flat, weakly depressed (Fig. 8I).
Schuberth and Schönitzer (1993) regarded a weakly depressed FOV as plesiomorphic for bees. With respect to the Andrenidae the present study concludes that the deeply depressed FOV as in *Ancylandrena* and Alocandreninae is ancestral. This conclusion provides support for one of the theories of Schuberth and Schönitzer (1993) concerning the function of the velvety pubescence of FOV, namely that it prevents dirtying of the cuticular surface of the FOV. Foreign bodies are more likely to be retained in a deep rimed structure than in a flattened one. Therefore a strongly depressed FOV are more likely to have evolved pubescence for protection than flattened foveae. The partially or completely flattened FOV (states 1 and 2) of most *Andrena*-subgenera and *Megandrena* is therefore probably secondarily derived from deeply depressed FOV.

63. Shape of FOV: (0) more or less oval (Figs 8A, I, K); (1) upper part clearly broader (at least 2 times) than lower part, caused by a narrow constriction (Fig. 8C); (2) upper part conspicuously narrower than lower part (Fig. 8F).
A more or less oval FOV, which is typical for most of the subgenera of *Andrena* as well as for *Ancylandrena*, *Megandrena* and *Alocandrena*, is judged to be plesiomorphic.

64. Distance between FOV and LO: (0) developed (1-1.5 times OD), clearly separating FOV and LO (Figs 8A, F); (1) strongly developed (at least 1.6 times OD, Fig. 8K); (2) reduced (>0.5<0.9 OD, Figs 8C, I); (3) absent to strongly reduced (<0.5 OD).
State (0) is regarded as plesiomorphic as it is developed in most subgenera of *Andrena*.

65. Upper (hind) margin of FOV: (0) ending distinctly below upper margin of compound eye (Fig. 8A); (1) reaching upper margin of compound eye (Figs 8F, I, K); (2) ending distinctly behind upper margin of compound eye (Fig. 8C).
State (0) is considered plesiomorphic as it is occurs in most subgenera of *Andrena* as well as in *Megandrena*, *Ancylandrena* and most other Andrenidae, except *Alocandrena* (state (1)).

66. Lower (anterior) margin of FOV: (0) reaching antennal socket; (1) ending distinctly above antennal socket; (2) ending distinctly below antennal socket.
State (0) is regarded as plesiomorphic as it is present in most subgenera of *Andrena* as well as *Megandrena* and most other Andrenidae.

67. Outer margin of FOV: (0) entirely straight to slightly convex (Figs A, F, I, K); (1) with distinct constriction (Fig. 8C).
A more or less straight outer margin of the FOV is ancestral as it is developed in most subgenera of *Andrena* as well as in *Megandrena*, *Ancylandrena* and all other Andrenidae bearing FOV.

68. Inner margin of FOV: (0) entirely straight to slightly concave (Figs A, F, I, K); (1) with distinct constriction (Fig. 8C).
State (0) as found in most subgenera of *Andrena*, as well as in *Megandrena*, *Ancylandrena* and all other Andrenidae bearing FOV, is presumed to be plesiomorphic.

69. Maximum width of FOV (ref. to OD): (0) 1-2 (Figs 8A, C, F); (1) 2-3 (Fig. 8I); (2) <1; (3) >3.
According to Schuberth and Schönitzer (1993) a medium-sized FOV (state (0)), similar to *Colletes* was postulated to be ancestral for *Andrena*.

70. Interspace between inner margin of compound eye and outer margin of FOV: (0) less than 0.8 times OD (Fig. 8A, K); (1) 0.81 times OD to OD (Fig. 8C); (2) more than OD (Fig. 8F); (3) absent (Fig. 8I).
State (0) is suggested to be ancestral as it is found in most subgenera of *Andrena*, though it is absent in *Megandrena* and *Ancylandrena*.

71. Hind margin of female vertex (profile): (0) more or less rounded ; (1) strongly edged; (2) narrowly rounded to slightly edged; (3) broadly rounded.
Despite some subgenera of *Andrena* the female vertex in all remaining Andreninae is more or less rounded which is regarded to be plesiomorphic.

72. Hind margin of male vertex (profile): (0) more or less rounded; (1) sharply edged.
The sharply edged male vertex is apomorphic as most subgenera of *Andrena* and all other Andreninae show a more or less rounded vertex.

73. Width of female vertex (referring to OD): (0) >1; (1) <1.
A female vertex which is at least as wide as OD is considered plesiomorphic as it is developed in most subgenera of *Andrena* and all remaining Andreninae.

74. L/W-ratio of female AS3: (0) 1.1-2.0; (1) 2.1-3.0; (2) <1; (3) >3.
State (0) is deemed the ancestral state, as it is found in most subgenera of *Andrena* as well as in *Euherbstia* and *Ancylandrena*.

75. AS3/AS1-ratio of male: (0) 0.41-0.7; (1) <0.4; (2) >0.7.
State (0) is considered plesiomorphic as it is present in most subgenera of *Andrena* as well as *Ancylandrena*, although all other Andreninae (*Orphana*, *Megandrena*, *Euherbstia*) share state (1).

Thorax

76. Lateral parts of female pronotum below dorsolateral angle: (0) rounded; (1) carinate.
A laterally rounded female pronotum is found in many *Andrena* and all other Andrenidae, except *Euherbstia*, thus it is regarded as ancestral.

77. Lateral parts of male pronotum: (0) rounded; (1) carinate.
Also developed in the male, a laterally rounded pronotum occurs in in many *Andrena*, all other Andreninae and most of the remaining Andrenidae, and is thus plesiomorphic.

78. Pronotal groove (female): (0) indistinct to absent; (1) distinct.
The absence of a pronotal groove in *Euherbstia*, *Orphana* and most of Andrenidae is considered plesiomorphic.

79. Dorsolateral angle (humeral angle) of female pronotum: (0) absent; (1) present.
Although a more or less well developed dorsolateral angle of the pronotum is present in most of the subgenera of *Andrena* and in all other Andreninae, it is postulated to be apomorphic since it is absent in nearly all of the remaining Andrenidae.

80. Dorsolateral angle of pronotum (male): (0) absent; (1) present.
Although about half of all examined subgenera of *Andrena*, as well as all other Andreninae, show a more or less strong dorsolateral angle of the male pronotum, its is regarded as apomorphic since most other Andrenidae lack a distinct dorsolateral angle.

81. Punctation of scutum : (0) distinct; (1) weak, indistinct; (2) extremely coarse.
A distinct punctation of the scutum is found in all other Andreninae, as well as in most Andrenidae, and therefore is presumed to be plesiomorphic.

82. Punctation of scutum: (0) regular to dispersed (>1); (1) honeycombed to dense (<0.75).
State (0) is regarded as ancestral since it occurs in half of all examined subgenera of *Andrena*, in *Euherbstia*, *Orphana* and most other Andrenidae.

83. Pubescence of scutum: (0) medium-long to long branched hairs; (1) extremely short, scale-like, branched hairs; (2) short branched hairs; (3) scale-like, simple hairs (*cubiceps*-type).
Short hairs of the scutum are regarded as apomorphic, medium-long to long hairs as plesiomorphic. The scale-like hairs of states (2) and (3) are not strictly homologous with each other although both are extremely short because the hairs of state (2) are clearly branched while those of state (3) are simple and slightly flattened.

84. Punctation of mesepisternum (female) distinctly honeycombed: (0) absent; (1) present.
A honeycombed punctation of female mesepisterna is not found in Andrenidae other than *Andrena* and therefore is regarded as apomorphic.

85. Cuticular surface of mesepisterna (female): (0) smooth to tesselate/granulate, without wrinkles; (1) tesselate to granulate, weakly wrinkled; (2) strongly wrinkled.
    Wrinkles of the female mesepisterna represent a derived condition because they are absent in most subgenera of *Andrena* as well as in all other Andreninae.
86. Punctation of mesepisternum (female): (0) more or less distinct, weak; (1) distinct, coarse.
    State (0) is considered ancestral as it is found in most subgenera of *Andrena* and all other Andreninae.
87. Ventral part of mesepisterna: (0) similar to lateral part; (1) with small cone-shaped cuticular projection and several stiff bristles.
    The presence of stiff bristles on the ventral part of female mesepisterna constitutes a solid autapomorphy for the palearctic subgenus *Parandrenella*.
88. Punctation of scutellum: (0) regular to dispersed (>1) ; (1) indistinct to absent; (2) honeycombed to dense (<1).
    State (0) is regarded as plesiomorphic as it is developed in most subgenera of *Andrena* as well as all other Andreninae, except *Ancylandrena*.
89. Profile of female propodeum: (0) distinctly separated into a horizontal basal region and a strongly declivous apical region; (1) continuously sloping, without distinct separation into horizontal and declivous regions; (2) weakly declivous to slightly sloping; (3) nearly completely declivous, horizontal basal region strongly reduced to nearly absent.
    A propodeum which is separated into a horizontal basal region and a strongly declivous apical region is found in most subgenera of *Andrena*, in *Megandrena*, *Ancylandrena* and most Andrenidae, therefore this state is accredited to be ancestral.
90. Border between horizontal and vertical surface of female propodeum: (0) rounded; (1) slightly edged; (2) strongly carinate.
    A rounded transition between the horizontal and vertical surfaces of female propodeum as in most subgenera of *Andrena* as well as all remaining Andrenidae, is esteemed to be plesiomorphic.
91. Cuticular surface of PT (female): (0) tesselate to granulate, rarely with few weak wrinkles basally; (1) with coarse wrinkles on basal half, granulate apically; (2) with fine wrinkles on basal half, granulate apically; (3) completely finely wrinkled; (4) completely coarsely wrinkled.
    A weakly structured propodeum (state (0)) as developed in all other Andreninae is regarded as plesiomorphic.
92. Pubescence of DLP (female): (0) well-developed, hairs medium-long to long; (1) indistinct to absent; (2) extremely short, indistinct, weak.
    Medium-long to long pubescence of the female DLP seems to be plesiomorphic as it is occurs in most subgenera of *Andrena* and all other Andreninae.
93. Cuticular surface of LP (female): (0) finely tesselate, without any wrinkles (Figs 13A, E, F); (1) partly irregularly wrinkled; (2) with conspicuous star-shaped wrinkles (Appendix 1, Fig. 2); (3) completely coarsely wrinkled (Figs 13B-D); (4) finely wrinkled.
    A tesselate female LP without any wrinkles is considered ancestral as it is developed in most subgenera of *Andrena* and all other Andreninae.

94. Punctation of LP: (0) indistinct, weak; (1) impunctate; (2) distinct, strong and coarse.
All Andreninae except *Megandrena* and most subgenera of *Andrena* show an indistinct and weak punctation of the LP, which is regarded as the plesiomorphic state.

95. Pubescence of distinct hairs of LP: (0) present (Figs 13A-E); (1) absent, bare (Fig. 13F).
Pubescence of distinct, rather long hairs is found in most subgenera of *Andrena*, *Euherbstia* and *Ancylandrena*. The absence of distinct hairs in some subgenera of *Andrena* as well as *Megandrena* and *Orphana* (only minute hairs developed) is considered apomorphic.

96. Lateral propodeum (kind of pubescence): (0) moderately branched ("normal"-type, Fig. 13A); (1) hairs simple, strong and medium-long to long (Figs 13B-E); (2) simple to slightly branched, weak hairs; (3) bottlebrush-like branching (*cubiceps*-type), intermixed; (4) strongly branched (*plumiscopa*-type); (5) branched (dorsal fringe type) and long; (6) absent, bare (Fig. 13F); (7) strongly branched (*melittoides* type).
Branched hairs similar to those on other parts of propodeum and thorax seem to be the ancestral hair type of pubescence of the LP since they display no specialization.

97. Propodeal corbicula: (0) absent (Figs 13A); (1) present (Figs 13B-F).
In this study, the propodeal corbicula is considered present when at least a distinct dorsoposterior hair fringe is developed. The absence of a propodeal corbicula is presumed to be plesiomorphic as it is absent in *Euherbstia* and most other Andrenidae.

98. Anterior hair fringe of propodeal corbicula: (0) absent (Figs 13B, C); (1) broad (*helvola*-type); (2) narrow (Figs 13E, F); (3) strongly reduced.
An anterior hair fringe of the propodeal corbicula is absent in most subgenera of *Andrena* as well as all other Andrenidae (except *Megandrena*).

99. Length of anterior hair fringe of propodeal corbicula: (0) short to medium-long, straight (Fig. 13E); (1) strongly elongate, distinctly curled (Fig. 13F).
A short to medium-long, straight anterior hair fringe of the propodeal corbicula is considered plesiomorphic in contrast to a strongly elongate and distinctly curled hair fringe.

100. Density of anterior hair fringe of propodeal corbicula: (0) absent (Figs 13b, C); (1) dense (Figs 13E, F); (2) sparse; (3) extremely sparse.
See comment to character 98.

101. Hairs of anterior hair fringe of propodeal corbicula: (0) branched, similar to dorsal fringe (Fig. 13E, F); (1) simple; (2) weakly branched; (3) strongly branched, different from dorsal fringe.
State (0) is considered plesiomorphic as it is developed in most *Andrena*-subgenera which have an anterior hair fringe.

102. Dorsoposterior hair fringe of propodeal corbicula: (0) absent (Fig. 13A); (1) consisting of medium–long, straight to slightly curled hairs; (2) consisting of short, straight hairs (Fig. 13B); (3) consisting of long, dense and strongly curled hairs (Figs 13E, F)
The absence of a distinct dorsoposterior hair fringe is regarded as plesiomorphic (see also comments on character 97).

103. Hairs of dorsoposterior hair fringe of propodeal corbicula: (0) weakly branched (Fig. 13B); (1) strongly branched (Figs 13C, E, F).
The presence of weakly branched hairs of the dorsoposterior hair fringe, for example, in some Andreninae and a few other Andrenidae, is considered ancestral.

104. Density of dorsoposterior hair fringe of propodeal corbicula: (0) sparse; (1) dense (Fig. 13B, C, E, F); (2) extremely sparse.
A sparse dorsoposterior hair fringe of the propodeal corbicula, as opposed to a more dense hair fringe, is presumed to be plesiomorphic.

105. Dorsoposterior part of LP: (0) more or less rounded; (1) distinctly edged.
A more or less rounded dorsoposterior part of the LP is regarded as plesiomorphic as it is found in many subgenera of *Andrena* and all other Andrenidae.

Legs

106. Apex of tibial spur of front legs: (0) pointed; (1) truncate.
Apically truncate tibial spurs of the front legs are coded as apomorphic as they are only developed in a few subgenera of *Andrena* in contrast to the pointed tibial spurs of all other Andrenidae.

107. Apex of mid tibial spur of female: (0) straight to slightly curved, pointed; (1) straight to slightly curved, truncate; (2) strongly curved, hook-shaped (Fig.15F).
The straight to slightly curved mid tibial spur of most subgenera of *Andrena* and all other Andrenidae is considered ancestral.

108. Pubescence on inner side of basitarsus of female mid legs: (0) normal, simple hairs; (1) stiff, apically bent, simple hairs.
Stiff, apically bent hairs on the inner side of the female mid basitarsus are autapomorphic for *A. (Callandrena) accepta*.

109. Hair fringe along anterior side of hind coxa: (0) weakly developed; (1) strongly developed, consisting of long curled hairs forming a dense fringe.
A weakly developed hair fringe along the anterior side of hind coxa is present in most subgenera of *Andrena* and all other Andreninae and is regarded as plesiomorphic.

110. Flocculus of trochanter of hind leg: (0) absent; (1) incomplete, only distal hairs are long and curled (straight basally); (2) complete, all hairs long and strongly curled (Figs 14A, E).
A hind trochanter flocculus in females is lacking in most Andrenidae (except *Megandrena* and *Andrena*) and is thus coded ancestral.

111. Femur of hind leg (female): (0) rounded, without dorsoposterior carina; (1) with distinct dorsoposterior carina.
A rounded hind femur of females is present in most subgenera of *Andrena* and all other Andreninae as well as in most of the remaining Andrenidae, and therefore is considered plesiomorphic.

112. Row of bristles of hind femur (female): (0) absent; (1) long (Fig. 15A); (2) short, cone-shaped to thorn-like (Figs 14C, 15B, C).
Bristles along the female hind femur are absent in most subgenera of *Andrena* as well as all other Andrenidae, thus their occurrence is regarded as apomorphic. These bristles

have to be considered as strongly modified, hair-like formations as they show a distinct circular articulation basally (Figs 15A-C).

113. Posterior side of hind femur of female: (0) more or less convex rounded; (1) more or less concave (at least apically).
A concave rounded posterior side of the female hind femur is found to be derived as it is only developed in some subgenera of *Andrena* but absent in all other Andreninae and most of the remaining Andrenidae.

114. Dorsal carina of female hind femur: (0) absent; strongly developed; (2) (1) weakly developed.
The dorsal carina of the female hind femur of some subgenera of *Andrena* is considered as apomorphic as it is absent in all other Andrenidae.

115. Anterior hair fringe of femur of female hind leg: (0) strongly developed, dense; (1) weakly developed, sparse.
A strongly developed anterior hair fringe of the female hind femur is present in most subgenera of *Andrena*, as well as in *Euherbstia*.

116. Kind of pubescence of anterior hair fringe of female hindfemur: (0) simple; (1) branched, type A (*humilis*-type,); (2) branched, type B (*trevoris*-type); (3) branched, type C (*hattorfiana*-type, similar Fig. 14N); (4) branched, type D (*cubiceps*-type, similar Fig. 14O); (5) short, normal-type (*cochlearicalcar*-type).
The anterior hair fringe of the female hindfemur consisting of simple hairs is presumed to be plesiomorphic as it is found in most subgenera of *Andrena* as well as in all other Andreninae and most of the remaining Andrenidae.

117. Pubescence of scopa of hind tibia (female): (0) simple (Fig. 14H); (1) unilaterally branched (*plumiscopa*-type, Fig. 14J); (2) distinctly bilaterally branched (*humilis*-type, Figs 14K, L); (3) multi-laterally branched, type C (*hattorfiana*-type, Fig. 14N); (4) multi-laterally branched, type D (*cubiceps*-type, Fig. 14O); (5) weakly unilaterally branched (*mackieae*-type, Fig. 14I); (6) distinctly bilaterally branched (*fulvago*-type, Fig. 14M); (7) weakly bilaterally branched (*curvungula*-type).
A tibial scopa consisting of simple hairs seems to be ancestral as it is developed in most subgenera of *Andrena* as well as in all other Andreninae and most of the remaining Andrenidae. Several authors, e.g. Warncke (1968a), Hirashima (1966), Tadauchi (1982), Tadauchi and Hirashima (1988) distinguished only between simple and branched/plumose hairs of the hind tibial scopa, and scarcely paid attention to the different types (states 1-7) of branched scopal-hairs (LaBerge 1986a, Pasteels and Pasteels 1979).

118. Pubescence of inner side of hind tibia: (0) simple (Fig. 14D); (1) branched (*cubiceps*-type, similar Fig. 14O); (2) branched (*mucida*-type); (3) bilateral branched (*fumida*-type) with few simple hairs medially; (4) unilateral branched, with few simple hairs medially.
Simple hairs on the inner side of female hind tibia are found in most subgenera of *Andrena* as well as in all other Andreninae and most of the remaining Andrenidae. The hairs are often keirotrichia-like (Michener, 2000) with an apically spatulate region (Fig. 14O).

119. Inner hind tibial spur (female): (0) finely serrate; (1) strongly pectinate.
Strongly pectinate inner hind tibial spurs are distinctly developed in *Euherbstia* and more weakly in *Orphana*, but absent in all other Andreninae, as well as within *Andrena* and therefore presumed to be apomorphic.

120. Width of inner hind tibial spur of female: (0) basally not distinctly broadened, slender; (1) strongly broadened basally (Figs 15D, E); (2) distinctly broadened on nearly whole length (Fig. 15F).
Slender tibial spurs are regarded as plesiomorphic, as they are found in most subgenera of *Andrena*, as well as all other Andrenidae.

121. Apex of inner hind tibial spur (female): (0) straight to slightly curved, pointed (Fig. 15D); (1) straight to slightly curved, truncate to knob-like thickened (Fig. 15E); (2) strongly curved, hook-shaped (Fig. 15F).
Apically straight to slightly curved inner hind tibial spurs are regarded to be plesiomorphic as they are present in most subgenera of *Andrena* as well as most Andrenidae (except in *Ancylandrena* it is strongly hooked).

122. Inner spur of female hind tibia (dorsal view): (0) more or less straight; (1) strongly curved.
In the dorsal view, the more or less straight female hind tibial spur is present in nearly all Andrenidae and is thus considered ancestral.

123. Pubescence on outer side of basitarsus of hind leg (female): (0) simple (Fig. 14P); (1) unilateral branched (*plumiscopa*-type); (2) bilateral branched (*humilis*-type, Fig. 14Q); (3) bilateral branched (*fulvago*-type, Fig. 14R); (4) multi-sided branched, type D (*cubiceps*-type, Fig. 14S); (5) weakly branched (similar Fig. 14I).
Simple hairs on the outer side of female hind basitarsus represent the plesiomorphic state, as they are developed in most Andrenidae.

124. Claws (female): (0) bidentate (Fig. 14B); (1) inner tooth strongly reduced to absent, unidentate (Fig. 14F).
Only a few subgenera of *Andrena* show simple claws in contrast to the bidentate claws of most subgenera of *Andrena* and the remaining Andrenidae, the latter condition is regarded as plesiomorphic.

Wings

125. Number of submarginal cells: (0) three; (1) two.
The forewings of Andreninae (except four subgenera of *Andrena*) as well as those of Alocandreninae and Oxaeinae show three submarginal cells, however, in several tribes of Panurginae (Protandrenini, Panurgini, Perditini and Calliopsini) only two submarginal cells are quite common. Three submarginal cells are considered to be plesiomorphic as the majority of Andrenidae share this character state.

126. Distance between 1st submarginal crossvein and stigma: (0) more than 3 times as wide as vein; (1) about 3 times as wide as vein; (2) less than 3 times as wide as vein.
State (0) is presumed to be ancestral because it is developed in nearly all Andrenidae.

127. 2nd recurrent vein joining 3rd submarginal cell: (0) distinctly before 3rd submarginal crossvein (about 1/3 of length of 3rd submarginal cell; (1) terminating, joins near or at 3rd submarginal crossvein (less than ¼ of 3rd submarginal cell).
State (1), which is developed only in three subgenera of *Andrena* as well as in *Megandrena* and *Ancylandrena*, is regarded as apomorphic.

128. Vanal lobe: (0) distinctly developed, jugal and vanal lobes distinctly separated; (1) absent, jugal and vanal lobes fused, not distinctly separated.
A distinctly developed vanal lobe is considered plesiomorphic because it is found in all Andrenidae, except *A. (Pallandrena) pallidicincta* and *A. (Ulandrena) schulzi* where it is indistinguishably fused with the jugal lobe (only a very weak incision is recognizable).

129. Jugal lobe of hind wing: (0) hind margin more or less straight, not or only weakly constricted in the middle; (1) hind margin distinctly concave, with strong constriction in the middle.
State (0) is developed in most subgenera of *Andrena*, as well as in *Megandrena*, *Ancylandrena* and most Andrenidae, only *Orphana, Euherbstia* and some subgenera of *Andrena* show a strong concave hind margin of the jugal lobe, which is regarded as apomorphic.

130. Length of vanal lobe: (0) not longer than 0.7 times as long as jugal lobe; (1) 0.71 times to 0.9 times as long as jugal lobe; (2) > 0.9 times as long as jugal lobe.
State (0) represents the ancestral state as it is found in nearly all subgenera of *Andrena* as well as all other Andreninae.

Metasoma

131. Profile of female T1: (0) distinctly separated into a declivous basal region and a horizontal posterior region; (1) strongly sloping, without distinct separation into horizontal and declivous regions; (2) carina separating declivous region from horizontal region; (3) weakly sloping.
State (0) is considered plesiomorphic as it is found in most subgenera of *Andrena* as well as the other Andreninae and most of the remaining Andrenidae.

132. Basal part of female T1: (0) with strong longitudinal rim medially; (1) without distinct longitudinal rim medially.
The longitudinal rim on the basal part of T1 is developed in all Andreninae (except *Poliandrena* and *Lepidandrena*) and most of the remaining Andrenidae and therefore is presumed to be plesiomorphic.

133. Depression of marginal zone of female T: (0) weakly developed to absent; (1) normally developed; (2) strongly developed.
A weakly depressed marginal zone as found in most Andrenidae is regarded as plesiomorphic.

134. Pubescence of disc of female T: (0) minute to short "normally branched" hairs; (1) extremely short scale-like hairs; (2) T with long branched hairs (at least on T 1, 2).
Minute to short branched pubescence of T seems to be ancestral as it is present in most subgenera of *Andrena* as well as the Andreninae (except *Orphana*) and the remaining Andrenidae.

135. Pale apical fasciae of short dense hairs of T1-4 of female: (0) absent to narrow; (1) broad, interrupted; (2) broad, nearly covering complete marginal zone, never interrupted; (3) broad with short, scale-like hairs.
Strong apical fasciae of short dense hairs of female T1-4 are regarded as derived because they are absent in most subgenera of *Andrena* as well as in *Euherbstia*, *Orphana* and most other Andrenidae.

136. Pygidial plate of female: (0) flat to convex rounded, without raised triangular area in the middle; (1) with raised triangular area in the middle and depressed marginal zone (Appendix 1, Fig. 5).
Most Andrenidae (except *Orphana*) have a flat to convex rounded female pygidial plate which is interpreted to be ancestral.

137. Male pygidial plate: (0) absent; (1) weakly developed; (2) strongly developed.
Distinct male pygidial plates are considered derived as they are absent in most subgenera of *Andrena* and in most of the remaining Andrenidae.

138. Sclerite of S 7 of male: (0) homogenously fused, apically undivided (Figs 16B-N); (1) consisting of two separate parts connected by membrane apically (Fig. 16A).
The male S 7 consisting of two separated sclerites is autapomorphic for *A. (Cubiandrena) cubiceps*.

139. Apical lobes of S 7 (male): (0) two distinct lobes developed (Figs 16B, I, J, L, M); (1) absent (Fig. 16A); (2) long single process, ventrally curved apical process developed; (3) single median lobe developed, straight, not ventrally curved (Fig. 16C); (4) two weak lobes developed (broader than long, Figs 16E, F); (5) strongly elongate, nearly completely fused medially; (6) minute, nearly fused (Figs 16D, K).
Two distinct apical lobes of male S 7, as found in most subgenera of *Andrena* and *Ancylandrena*, are ancestral for *Andrena*.

140. Apex of apical lobes of male S7: (0) not truncate; (1) truncate.
State (0) is presumed to be plesiomorphic because it is developed in most subgenera of *Andrena* and all other Andreninae except *Orphana*.

141. Pubescence of male S 7: (0) with conspicuous hair fringe of long hairs medioapically (Figs 16B-F, H-N); (1) without medioapically hair fringe, pubescence short, sparse (Fig. 16 A, G).
A medioapical hair fringe of male S7, which is found in most subgenera of *Andrena,* in *Megandrena* and *Ancylandrena*, is regarded as plesiomorphic.

142. Apical process of S 8 of male: (0) more or less broadened apically (Figs 17A-F, 18B-H, 19A, C); (1) becoming distinctly narrow apically (Fig. 18A).
In most subgenera of *Andrena* and all other Andreninae the male S 8 is more or less broadened apically, this condition is regarded to be ancestral.

143. Deep emargination of apical margin of apical process of male S 8: (0) absent; (1) present.
A deep emargination of the apical process of male S 8, as present in some subgenera of *Andrena* is regarded as apomorphic, since it is not developed in any other Andreninae.

144. Maximum width of apical process of S 8 male: (0) distinctly narrower than basal part (about 0.5 times as wide as basal part, Figs 17A-F, 18A, C-H, 19A-C)); (1) strongly broadened, nearly as wide as basal part (> 0.6 times, Fig. 18B).
Only four subgenera of *Andrena* show a strongly broadened apical process of male S 8, while in most subgenera of *Andrena* and all other Andreninae the apical part is distinctly narrower than the basal part and therefore is considered plesiomorphic.

145. Apical process of male S 8: (0) without distinct toothlike appendages; (1) with strong teeth laterally.
The strong lateral teeth of the apical process of male S 8 constitute an autapomorphic structure for the subgenus *Rufandrena*.

146. Orientation of apical part of S8: (0) not or only slightly bent ventrally; (1) strongly bent ventrally (forming rectangular angle with disc of basal part).
In four subgenera of *Andrena* a ventrally bent apical part of male S 8 is developed, which is bent the strongest in *Holandrena*. The plesiomorphic state (0) is developed in all other subgenera of *Andrena* and all remaining Andreninae.

147. Ventral side of S 8 of male: (0) flat (Figs 17A-F, 18A, C, D, F-H, 19A-C); (1) subapical process strongly developed; (2) subapical process weakly indicated (Fig. 18E); (3) subapical part strongly broadened (Fig. 18B).
A flattened ventral side of male S8 is presumed to be plesiomorphic since it is present in most subgenera of *Andrena* and all other Andreninae (except possibly *Ancylandrena* which could not be positively coded for this character because the S 8 of the single examined male specimen was damaged).

Male genitalia

148. Inner margin of dorsal gonocoxite: (0) nearly completely separated by penis valve (Fig. 20A); (1) joining penis valve for at least half the distance (Figs 20B-D, 21A-D, 22A-F, 23A-D; indicated separations of Figs 21A, C, 22A and 23B have to be regarded as artefacts caused by the treatment of SEM preparation).
Although state (1) is developed in all subgenera of *Andrena* (except *Melittoides*) as well as in *Megandrena* and *Ancylandrena*, it is considered derived because state (0) is found in *Euherbstia*, *Orphana* and most other Andrenidae.

149. Dorsal lobe of gonocoxite: (0) absent (Fig. 20A); (1) developed (Figs 20B-D, 21A-D, 22A, B, E, F, 23A, B, D); (2) strongly developed (distinctly longer than wide basally, Figs 22C, D, 23C).
The presence of a dorsal lobe seems to be typical for *Andrena*, as it is lacking only in some subgenera and is not developed in other Andreninae (except *Megandrena*) or other Andrenidae.

150. Apical margin of dorsal lobe of gonocoxite: (0) broadly rounded (Figs 20B-D, 21A, B, 23A, B, D); (1) truncate (Fig. 21C); (2) narrowly rounded; (3) pointed (Figs 22C, D, 23C).
A broadly rounded dorsal lobe as developed in *Megandrena* and most subgenera of *Andrena* is presumably the plesiomorphic state.

151. Inner margins of dorsal lobes of gonocoxites: (0) more or less parallel sided (Figs 20B-D, 21A-D, 22A, B, E, F, 23A, B, D; indicated divergences of these Figs have to be regarded

as artefacts caused by the treatment of SEM preparation); (1) strongly diverging (Figs 22C, D, 23C).
The inner margins of dorsal lobes being more or less parallel sided is presumed to be ancestral as it is found in most subgenera of *Andrena* as well as in *Megandrena*.

152. Digitus of volsella: (0) large, more distinct than cuspis (Fig. 20A1); (1) small, reduced, often hardly visible behind cuspis (Fig.21C1).
A distinctly chelate, pincer-like volsella with a large digitus belongs to the groundplan of Hymenoptera (Snodgrass, 1941; Schulmeister, 2003) and is considered ancestral for bees. It is present in some Andreninae (however not *Ancylandrena* and not most *Andrena*), the remaining Andrenidae and other short-tongued bees. A strongly reduced volsella with a small digitus is only found in *Ancylandrena* and nearly all subgenera of *Andrena*.

153. Shape of digitus: (0) more or less rounded apically; (1) toothlike (Fig. 20A1); (2) plate-shaped; (3) more or less triangular.
Although most Andreninae exhibit a plate-shaped digitus, within *Andrena* a more or less rounded digitus is regarded as ancestral since it is developed in most subgenera of *Andrena* and in *Ancylandrena*.

154. Width of apical part of gonoforceps: (0) about as broad as dorsal base; (1) distinctly broader than dorsal base (> 1.2 times); (2) distinctly narrower than dorsal base (<1).
A slender gonoforceps which is apically about as wide as basally appears to be plesiomorphic (it is developed in most subgenera of *Andrena*, and in *Euherbstia* and *Ancylandrena*), while states (1) and (2) are considered derived within *Andrena*.

155. Ventral margin of apical part of gonoforceps (profile): (0) distinctly narrower than basal part, not strongly broadened (Figs 20B-D, 21B, 22A-F, 23A-D); (1) slightly broadened, at least basally; (2) strongly broadened, nearly as wide as basal part (Figs 21A, C, D).
A broadened ventral margin of the gonoforceps is absent in most subgenera of *Andrena* as well as all other Andreninae and is regarded as apomorphic within *Andrena*.

156. Inner margin of apical part of gonoforceps: (0) straight to slightly convex without emargination; (1) strongly convex rounded; (2) with distinct emargination.
State (0) is plesiomorphic because it is developed in most subgenera of *Andrena* and all other Andreninae.

157. Shape of penis valve: (0) more or less triangular, continuously becoming more narrow apically (Figs 20A-D, 21A-D, 22A-F, 23A, C, D); (1) completely parallel sided (Fig. 23B); (2) different.
A more or less triangular penis valve is developed in most subgenera of *Andrena* as well as in *Orphana* and *Ancylandrena* and is supposed to be ancestral.

158. Lateral margins of basal penis valve (dorsal view): (0) converging (Figs 20A, B, D, 21B-D, 22A-F, 23A, C, D); (1) parallel sided basally converging apically (Fig. 20C, 21A); (2) more or less parallel sided (Fig. 23B).
Converging lateral margins of the basal penis valve, as present in *Ancylandrena*, *Orphana* and most subgenera of *Andrena*, are considered plesiomorphic.

159. Lateral lamella of penis valve: (0) absent (Figs 20A, C, 21A-D, 22A-F, 23B, C); (1) dorsolateral and ventrolateral lamella present (Figs 20B, D, 23A, D); (2) dorsolateral lamella present, ventrolateral lamella absent.
A lateral lamella of the penis valve is only found in some subgenera of *Andrena*, and is absent in the remaining Andrenidae and therefore is regarded as apomorphic.

160. Lateral view of penis valvae: (0) flat to slightly rounded dorsally (Figs 20A-D, 21A-C, 22A-F, 23A-D); (1) strongly protuberant dorsally (Fig. 21D); (2) different.
Most subgenera of *Andrena* as well as *Ancylandrena* and *Orphana* show a flat to slightly rounded penis valve, which is presumed to be plesiomorphic.

161. Apex of penis valve (dorsal view): (0) rounded (Figs 20D, 21B, 22D, E, F, 23B, C, D); (1) pointed (Figs 20A, C, 21A, C, D, 22A, C, 23A); (2) triangular truncate.
While *Euherbstia*, *Megandrena* and most subgenera of *Andrena* show a rounded apex of the penis valve in dorsal view, it is distinctly pointed in several subgenera as well as in *Orphana* and *Ancylandrena*, and it is triangularly broadened in *Conandrena* and *Nobandrena*. A apically rounded penis valve is presumed to be ancestral.

162. Apex of penis valve (lateral view): (0) more or less rounded (Figs 20B-D, 21A, B, D, 22E, F, 23A-D); (1) pointed (Figs 20A, 21C).
A laterally rounded penis valve as developed in most subgenera of *Andrena* and all other Andreninae except *Ancylandrena* is regarded as plesiomorphic.

Cladograms, tree topology and character state distribution

The analysis of the data matrix (Tab. 4, cf. end of chapter) with NONA using the heuristic search option as described in 2.8.3.1 resulted in six most parsimonious trees (MPTs) with a length of 1875 steps (CI: 0.15, RI: 0.42, RC: 0.06). Characters are mapped onto one cladogram selected from the six MPTs in Fig. 1. The final character sampling included seven autapomorphic characters which were phylogenetically uninformative in the analysis. The strict consensus tree is presented in Fig. 2 with collapsed nodes shown as polytomies. One additional cladogram (1920 steps, CI: 0.15, RI: 0.41, RC: 0.06) was obtained by successive character reweighting (*a posteriori*), based on the RC of each character of the six MPTs of the initial unweighted heuristic analysis (Fig. 3). Identical groups/clades of both analyses are indicated by numbers 1-13 within Figs 2, 3.

Equal weighted analysis (Figs 1, 2)

The strict consensus tree of the six MPTs (Fig. 2) divides the Andreninae into two major clades (node A): One clade comprehends the genera *Euherbstia*, *Orphana* and *Megandrena* (node A1). The other clade contains the genera *Ancylandrena*, *Cubiandrena* and *Andrena* (node A2). Here, *Cubiandrena* is the sister group to *Ancylandrena* (node A3) and therefore it is raised to generic rank, *Cubiandrena* Warncke, 1968 **stat. n.** Retaining *Cubiandrena* at the subgeneric level within *Andrena* would either mean that *Andrena* is paraphyletic or that *Ancylandrena* should be regarded as a subgenus of *Andrena*.

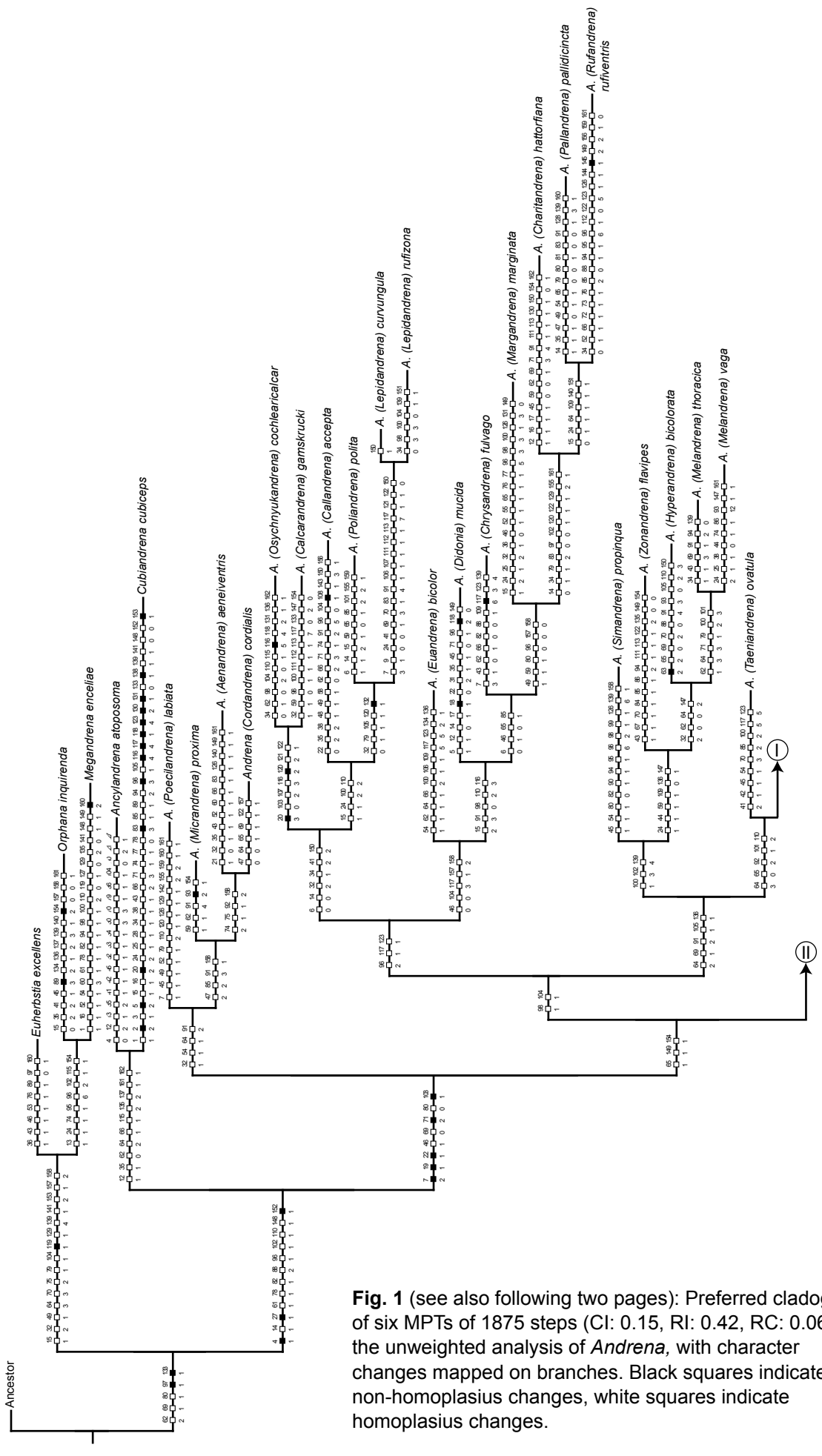

Fig. 1 (see also following two pages): Preferred cladogram of six MPTs of 1875 steps (CI: 0.15, RI: 0.42, RC: 0.06) of the unweighted analysis of *Andrena,* with character changes mapped on branches. Black squares indicate non-homoplasius changes, white squares indicate homoplasius changes.

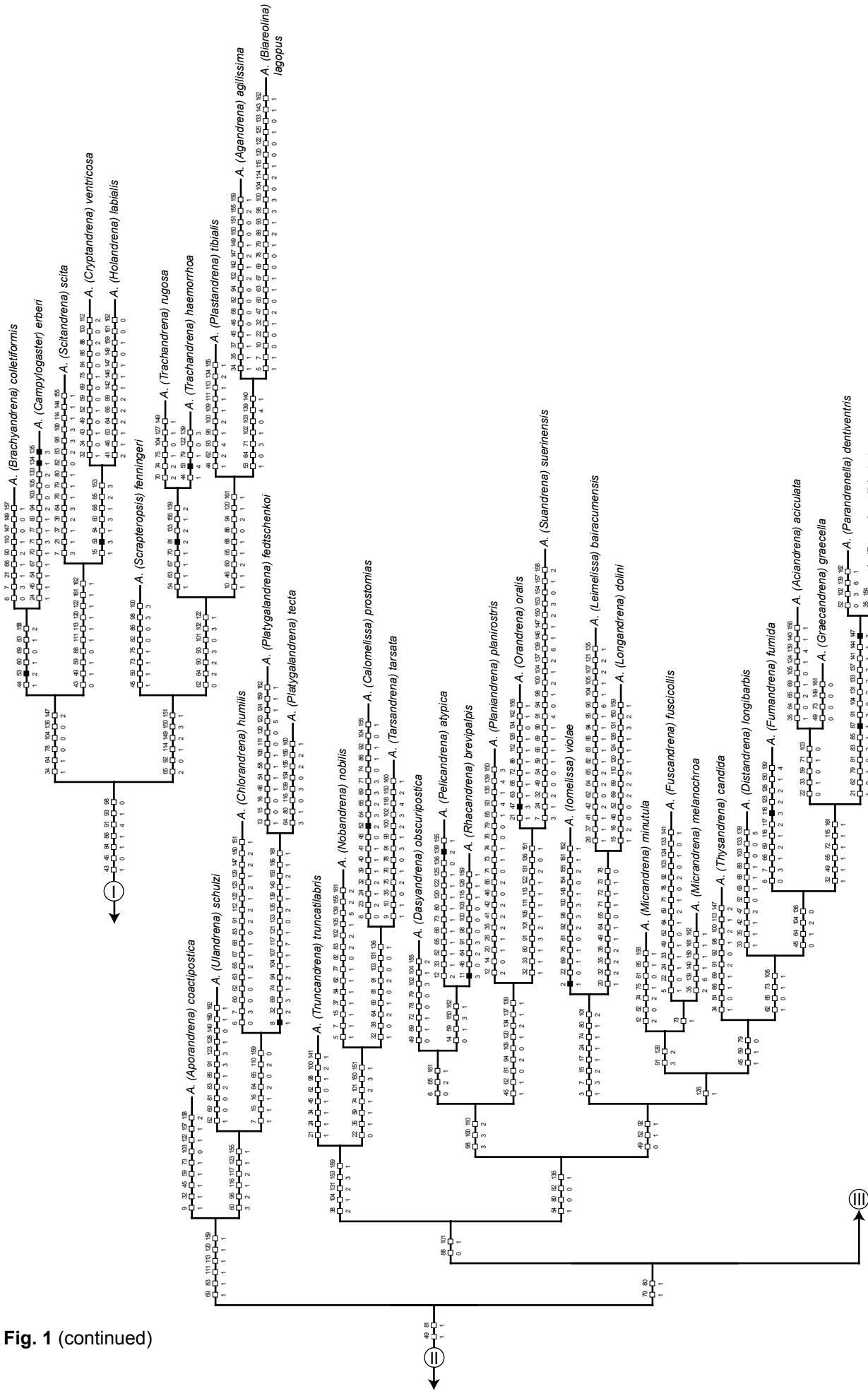

Fig. 1 (continued)

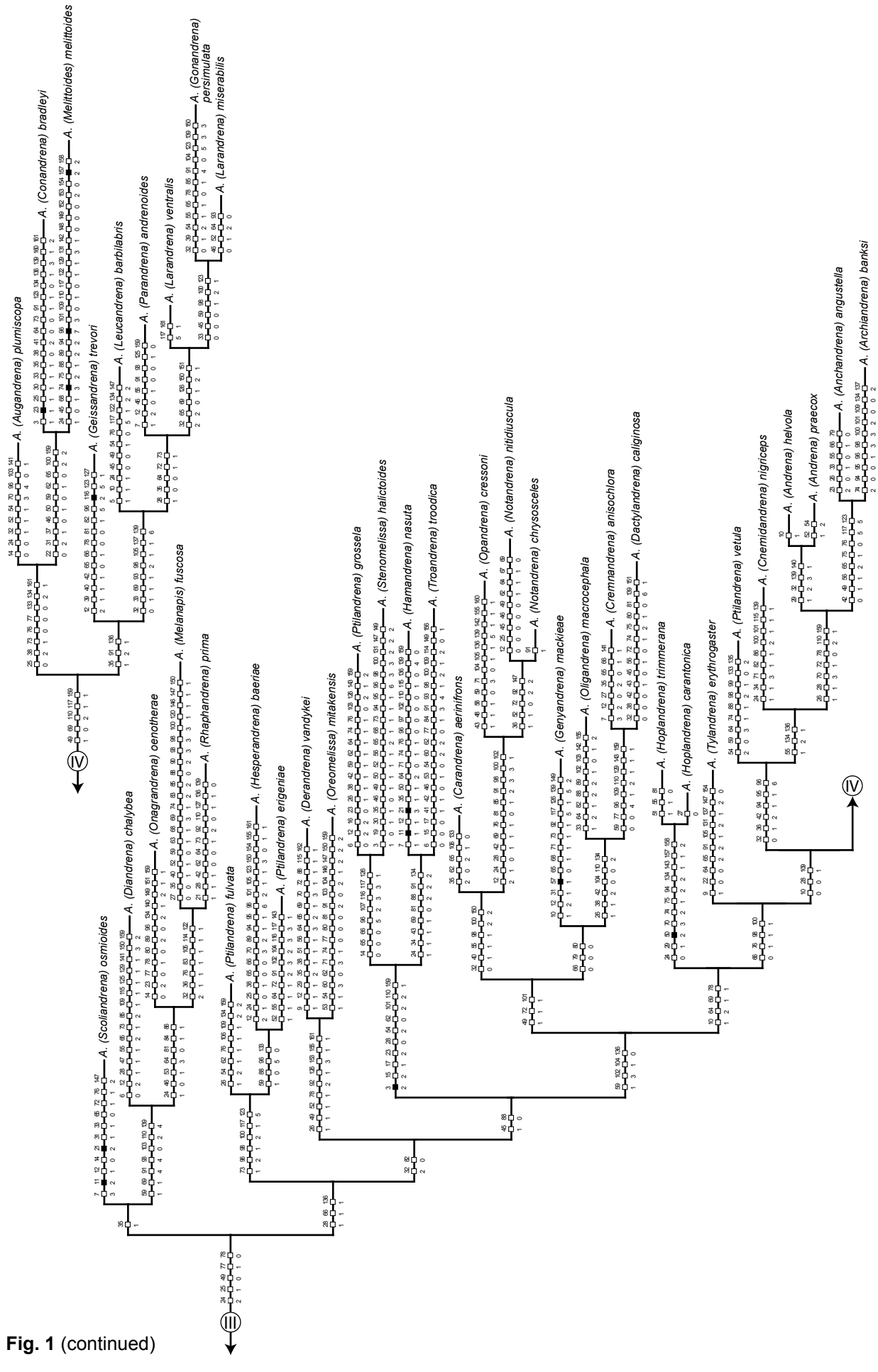

Fig. 1 (continued)

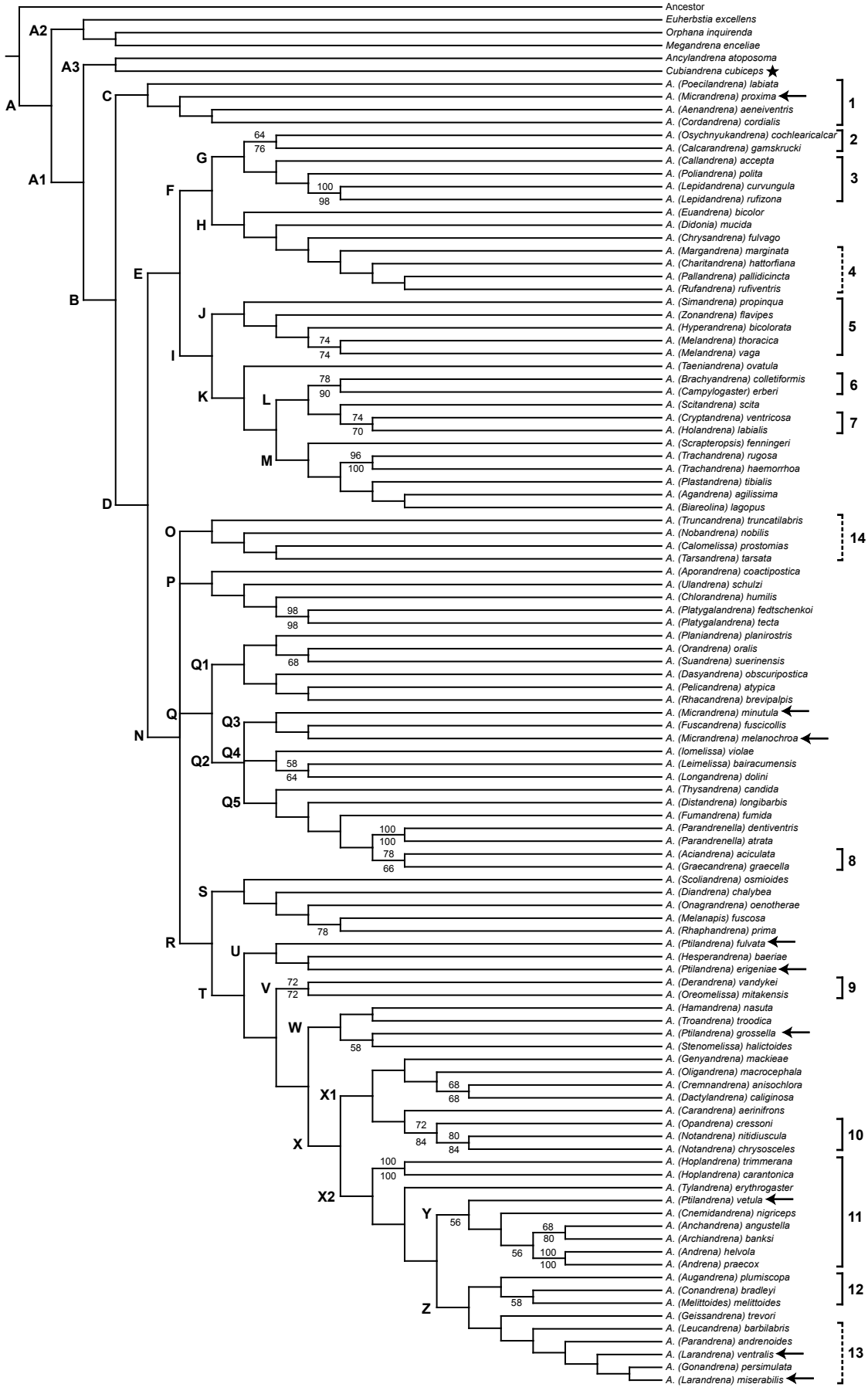

Fig. 2. Strict consensus tree of the six MPTs of 1875 steps ((CI: 0.15, RI: 0.42, RC: 0.06) of the unweighted analysis, with collapsed nodes shown as polytomies. **A-Z:** nodes mentioned in the text; **1-14:** groups of taxa which are also found in the weighted analysis (Fig. 3), with dotted lines indicating groups that combine the same taxa, but show a different tree topology; **arrows:** representatives of polyphyletic groups; **asterisk:** indicating position of *Cubiandrena* **stat. nov.**

The monophyly of the clade *Ancylandrena* and *Cubiandrena* (node A3) is defined by 10 homoplasius synapomorphies (12:1, 35:1, 62:0, 64:2, 66:1, 115:1, 135:2, 137:2, 161:1, 162:1). Of the 12 synapomorphies which establish the monophyly of *Ancylandrena, Cubiandrena* and *Andrena* (node A 2) three are non-homoplasius: (1) Subgenal coronet present (4:1), (2) preapical tooth on male mandible present (27:1) and (3) digitus of volsella small, reduced, often hardly visible behind cuspis (152:1). The latter character however is not found in *Cubiandrena*, whose volsella bears a large, toothlike cuspis.

The genus *Andrena* (node B) is characterized by 8 synapomorphies (7:2, 19:1, 22:1, 46:1, 69:0, 71:2, 80:0, 103:1), five of which are non-homoplasius: (1) bristles of paramandibular process distinctly smaller than bristles of subgenal coronet (7:2), (2) mental plate strongly reduced to absent (19:1), (3) condylar lamella of female mandible developed (22:1), (4) hind margin of female vertex narrowly rounded to slightly edged in profile (71:2) and (5) hairs of dorsoposterior hair fringe of propodeal corbicula strongly branched (103:1). It should be noted that all of the non-homoplasius synapomorphies show reversals and transformations in terminal parts of the tree.

The clade which is the sister group to all other subgenera of *Andrena*, is the *Aenandrena*-group (node C, clade 1). It comprises *Poecilandrena*, *A. (Micrandrena) proxima*, *Aenandrena* and *Cordandrena*, and is is defined by four homoplasius synapomorphies (32:1, 54:1, 64:1, 91:2). The position of *A. (Micrandrena) proxima*, as sister to the common clade of *Aenandrena* and *Cordandrena*, confirms the presumption of Dubitzky & Schönitzer (2001) that *A. proxima* and its allies should be excluded from *Micrandrena* and placed in a new subgenus as postulated by Schmid-Egger (in press).

The remaining subgenera of *Andrena* are again split into two large clades at nodes E and N. Node E, which is supported by only two homoplasius synapomorphies (98:1, 104:1) combines the *Lepidandrena/Charitandrena*-group (node F) with the *Zonandrena/Trachandrena*-group (I).

The *Lepidandrena* /*Charitandrena*-group (node F) splits into the *Lepidandrena*-group (node G), comprising *Osychnjukandrena*, *Calcarandrena*, *Callandrena*, *Poliandrena* and *Lepidandrena*, and the *Charitandrena*-group (node H), comprising *Euandrena*, *Didonia*, *Chrysandrena*, *Margandrena*, *Charitandrena*, *Pallandrena* and *Rufandrena*.

In the *Lepidandrena*-group (node G) the subgenera *Osychnyukandrena* and *Calcarandrena* (clade 2) form a monophyletic group, as well as the subgenera *Callandrena*, *Poliandrena* and *Lepidandrena* (clade 3). The sister-group relationship between *Osychnyukandrena* and *Calcarandrena* is supported by seven synapomorphies of which two are non-homoplasius: (1) A strongly laterally compressed prementum, with distinct median keel ventrally (20:3) and (2) a female tibial spur, which is distinctly broadened for nearly its whole length (120:2). The monophyly of *Poliandrena* + *Lepidandrena* is defined by five synapomorphies, one of which, the basal part of female T1 without distinct longitudinal rim medially (132:1), is non-homoplasius.

In the *Charitandrena*-group, which is characterized by five homoplasius synapomorphies (46:0, 104:0, 117:3, 157:1, 158:2), the subgenera *Charitandrena*, *Pallandrena* and *Rufandrena* build a monophyletic group supported by eleven homoplasius synapomorphies. Apart from this group the absence of a propodeal corbicula (97:0), as well as the absence of an anterior and dorsoposterior hair fringe of the lateral propodeum (129:1) occur only in *A. (Hamandrea) nasuta* and *Euherbstia*.

The *Zonandrena/Trachandrena*-group (node I) combines the *Zonandrena*-group (node J, clade 5), which comprises the subgenera *Simandrena*, *Zonandrena*, *Hyperandrena* and *Melandrena* with the *Trachandena*-group. *Taeniandrena* is located isolated at the base of the *Brachyandrena*/*Trachandrena*-group (node K), which branches into two major clades (nodes L and M).

The *Brachyandrena*-clade (node L) is split into two clades, one comprising *Brachyandrena* and *Campylogaster*, the other *Scitandrena*, *Cryptandrena* and *Holandrena*. The sistergroup relationship between *Brachyandrena* and *Campylogaster* (clade 6) is supported by six synapomorphies, one of which, the coarse and strongly, honeycombed punctation of the female genal area (53:2), is non-homoplasius. The *Scitandrena* + *Cryptandrena* + *Holandrena*-clade is defined by ten homoplasius synapomorphies. *Cryptandrena* and *Holandrena* form a monophyletic group (clade 7) based on seven synapomorphies including one non-homoplasius apomorphy (punctation of female genal area indistinctly honeycombed (53:3)).

The *Trachandrena*-clade (node M) comprising *Scrapteropsis*, *Trachandrena*, *Plastandrena*, *Agandrena* and *Biareolina* is supported by six homoplasius synapomorphies (65:2, 92:0, 114:1, 149:2, 150:3, 151:1). A strong carina on the dorsal side of the female hind femur (114:1), which is also developed in *Scitandrena*, *Melanapis* and *Rhaphandrena*, is characteristic of this group, but only in *Scrapteropsis* is it weakly developed. The monophyly of the holarctic *Trachandrena* seems to be corroborated by the present study since the included nearctic and palearctic representatives form a monophyletic group supported by eight synapomorphies (54:1, 63:1, 67:1, 70:1, 81:2, 133:2, 156:1, 159:2), one of which, the extremely coarse punctation of the scutum (81:2), is non-homoplasius.

The relationships of the basal clades of the second large clade of *Andrena* (node N) are quite variable in each of the six trees, they collapse to a polytomy in the strict consensus tree and therefore remain unresolved. Nevertheless four major groups (nodes O, P, Q, R) can be distinguished in this clade.

The *Truncandrena*-clade (node O), which comprises *Truncandrena*, *Nobandrena*, *Calomelissa* and *Tarsandrena*, is characterized by five homoplasius synapomorphies (38:2, 104:1, 131:2, 153:3, 159:1). Synonymization of the palearctic *Truncandrena* with the nearctic *Scaphandrena* (Ribble, 1974; Michener, 2000; Gusenleitner and Schwarz, 2002) could not be tested by the present analysis as the representative of *Scaphandrena* was excluded from the analysis, due to the lack of data in one sex. A female GA, which is more than twice as wide as

the compound eye (52:2) is autapomorphic for the subgenus *Calomelissa* in the present analysis.

The *Chlorandrena*-clade (node P) combines *Aporandrena*, *Ulandrena*, *Chlorandrena* and *Platygalandrena* and is supported by six homoplasius synapomorphies (69:1, 83:1, 111:1, 113:1, 120:1, 159:1). Based on the results of the present analysis members of *Platygalandrena* were removed from *Ulandrena*, where they were placed originally by Warncke (1968a), otherwise the subgenus *Ulandrena* would be polyphyletic. *Platygalandrena* is characterized by 16 synapomorphies, one of which, a strongly dorsoventrally flattened galea with outer lateral margin strongly angled (8:1), is autapomorphic for this group.

The *Orandrena*/*Micrandrena*-clade (node Q), which combines the *Dasyandrena*/*Orandrena*-group (node Q1) and the *Longandrena*/*Micrandrena/Aciandrena*-group (node Q2) is defined by four homoplasius synapomorphies (54:1, 80:0, 82:0, 136:1).

The *Dasyandrena*/*Orandrena*-clade (node Q1), which is supported by only three homoplasius synapomorphies (98:3, 100:3, 110:2) combines two monophyletic groups, the *Dasyandrena*-clade, comprising the nearctic subgenera *Dasyandrena*, *Pelicandrena* and *Rhacandrena*, and the *Orandrena*-clade comprising the palearctic *Planiandrena*, *Orandrena* and *Suandrena*. While a single, ventrally curved apical process of the male S7 (139:2) is autapomorphic for the subgenus *Pelicandrena*, the slightly anteriorly bent, stiff hairs of the galeal blade (11:3) are typical for the subgenus *Rhacandrena. Orandrena* is characterized by eleven synapomorphies, one of which is autapomorphic for this subgenus: a distinctly longitudinally wrinkled clypeus (47:3).

In the *Longandrena*/*Micrandrena/Aciandrena*-group (node Q2) three clades can be distinguished, which show no clear relationship to each other in the strict consensus tree.

Since the *Micrandrena*-clade (node Q3) comprises palearctic and nearctic representatives of *Micrandrena*, as well as *Fuscandrena*, this clade is polyphyletic or with respect to *Fuscandrena* it is paraphyletic. The clade is supported only by two homoplasius synapomorphies (91:3, 126:2).

The *Longandrena*-clade (node Q4), which is defined by eight homoplasius synapomorphies, comprises the nearctic *Iomelissa*, as well as the palearctic *Leimelissa* and *Longandrena*. A strongly reduced postgenal bridge, with the hypostomal carina nearly joining the postoccipital suture (2:1) is autapomorphic for the subgenus *Iomelissa*.

The *Aciandrena*-clade (node Q5) is supported by three homoplasius synapomorphies (45:1, 59:1, 79:0) and combines the subgenera *Thysandrena*, *Distandrena*, *Fumandrena*, *Aciandrena*, *Graecandrena* and *Parandrenella*. Of these, *Aciandrena* and *Graecandrena* are sister groups (clade 8), and together they are supported by the following homoplasius synapomorphies: (1) Condylar lamella of female mandible absent (22:0), (2) PLR of female more or less triangular (33:1), (3) longitudinal ridges of female frons indistinct to absent (59:0), (4) hind margin of female vertex strongly edged (71:1) and (5) the dorsoposterior hair fringe of propodeal corbicula consisting of weakly branched hairs (103:0). *Parandrenella* is the sister group to the *Aciandrena* + *Graecandrena* clade and clearly characterized by 15

synapomorphies, two of which, the small cone-shaped cuticular projections and stiff bristles on the ventral part of mesepisterna (87:1) and the strongly broadened apical part on ventral side of S 8 of male (147:3), are non-homoplasius. The pubescence of bilateral branched hairs with few simple hairs medially on the inner side of female hind tibia (118:3) is autapomorphic for the subgenus *Fumandrena*, which constitutes the sister group to ((*Aciandrena*, *Graecandrena*) *Parandrenella*).

The large *Scoliandrena*/*Ptilandrena/Hamandrena*/*Carandrena*/*Andrena*-group (node R) is defined by the following homoplasius synapomorphies: Male mandibles distinctly elongate, strongly crossing over in repose (24:2); male mandible strongly curved downward in lateral view (25:1); male clypeus completely dark coloured (49:0); lateral parts of male pronotum carinate (77:1) and an indistinct to absent pronotal groove in females (78:0).

The *Scoliandrena*-clade (node S) comprises the subgenera *Scoliandrena*, *Diandrena*, *Onagrandrena*, *Melanapis* and *Rhaphandrena* and is rather poorly supported by only one homoplasius apomorphy, the W/L-ratio of female PLR <2 (35:1). Except the palearctic *Melanapis*, all members of this group are strictly nearctic in distribution. Two of the eleven synapomorphies characterizing *Scoliandrena*, (1) the anteriorly bent, hooked hairs of the galeal blade (11:2) and (2) the stiff forwardly curved hairs on the ventral side of prementum, are autapomorphic for this subgenus.

The *Ptilandrena*-clade (node U), which is positioned at the base of the sister-clade (node T) of the *Scoliandrena*-group, is supported by six homoplasius synapomorphies (73:1, 96:2, 98:1, 100:2, 117:1, 123:5) and contains a palearctic and a nearctic representative of *Ptilandrena*, as well as the nearctic *Hesperandrena*. However, the holarctic subgenus *Ptilandrena* is paraphyletic since the palearctic (*A. fulvata*) and nearctic representatives (*A. erigeniae*) do not form a monophyletic group. Thus *Hesperandrena* is the sistergroup to *A. (Ptilandrena) erigeniae*, while *A. (Ptilandrena) fulvata* is the sister to *Hesperandrena* + *A. (Ptilandrena) erigeniae*. The position of further palearctic representatives of *Ptilandrena* (*A. vetula*, *A. grossella*, see below) shows that the subgeneric concept of *Ptilandrena* used up to now is no longer valid and needs to be revised because of the polyphyly of this taxon.

The *Oreomelissa*-clade (node V, clade 9) comprises the nearctic *Derandrena* and the palearctic *Oreomelissa* and is defined by nine homoplasius synapomorphies (26:1, 49:1, 52:1, 78:1, 92:2, 126:1, 153:3, 155:1, 161:1).

The *Hamandrena*-group (node W), which is the sister-group to the *Carandrena*/*Andrena*-clade (node X) is characterized by ten synapomorphies, one of which, a strongly sloping to slightly declivous hypostomal area (3:2) is autapomorphic for the group, except *A. (Stenomelissa) halictoides*. The *Hamandrena*-clade combines two sister clades, the *A. (Ptilandrena) grossella* + *Stenomelissa*-clade and the *Hamandrena* + *Troandrena*-clade, each is supported by eight homoplasius synapomorphies. The subgenus *Hamandrena*, the species of which were formerly included in *Didonia*, was erected. The results reveal a polyphyletic *Didonia* s. l. (cf. *A. (Didonia) mucida*, clade H, above). *Hamandrena* is based on 18 synapomorphies in the analysis, two of which, (1) the posteriorly bent, strong, hooked

hairs of the galeal blade (11:2), as well as the (2) stiff and backwardly curved hairs on the ventral surface of prementum (21:3) are autapomorphic for this subgenus.

The *Carandrena/Genyandrena*-clade (node X1), which represents the sister group to the *Hoplandrena*/*Andrena*/*Leucandrena*-clade (node X2) is defined by three homoplasius synapomorphies (49:1, 72:1, 101:1). In this clade two monophyletic groups can be distinguished, the *Carandrena*-group, comprising the palearctic *Carandrena* and *Notandrena* as well as the nearctic *Opandrena*, and the *Genyandrena*-group combining the nearctic subgenera *Genyandrena*, *Oligandrena*, *Cremnandrena* and *Dactylandrena*. The monophyly of the *Carandrena*-group is based on six synapomorphies, and the sistergroup relationship between *Notandrena* and *Opandrena* is supported by twelve homoplasius synapomorphies. The presence of a subgenal process in the male (57:1) is apomorphic for the subgenus *Genyandrena*.

The *Hoplandrena*/*Andrena*/*Leucandrena*-clade (node X2), which is characterized by four homoplasius synapomorphies (10:1, 64:2, 69:1, 78:1) included *Hoplandrena* and *Tylandrena* as well as two large clades, the *Andrena*-clade (node Y) and the *Augandrena*/*Leucandrena*-clade (node Z). While *Hoplandrena* and *Tylandrena* are isolated at the base of the *Hoplandrena*/*Andrena*/*Leucandrena*-clade, the *Andrena*-clade (node Y) and the *Augandrena*/*Leucandrena*-clade (node Z) are apical sister-groups united by three homoplasius synapomorphies (10:0, 28:0, 109:1).

The *Andrena*-clade (node Y), which includes *A. (Ptilandrena) vetula*, *Cnemidandrena*, *Andrena* s. str., *Anchandrena* and *Archiandrena* is supported by six homoplasius synapomorphies (32:0, 36:1, 42:2, 94:1, 95:1, 96:6).

Two large clades can be distinguished in the *Augandrena*/*Leucandrena*-clade (node Z), (1) the *Augandrena*-group and (2) the *Leucandrena*-group.

The *Augandrena*-group (clade 12) is defined by eight homoplasius synapomorphies (25:0, 38:2, 73:1, 76:0, 77:0, 133:0, 134:2, 161:1) and comprises the nearctic subgenera *Augandrena* and *Conandrena* as well as the palearctic *Melittoides*. *Conandrena* and *Melittoides* are sister-groups based on ten homoplasius synapomorphies (22:0, 31:2, 37:1, 46:0, 50:1, 59:0, 62:1, 65:0, 100:2, 159:2). While a strongly elongate mandible in the female (23:1) is autapomorphic for the subgenus *Conandrena*, three autapomorphies (1) a female AS3, which is more than three times as long as wide (74:3), (2) pubescence of LP consisting of strongly branched hairs (96:7) and (3) an abnormally shaped penis valve characterizes the subgenus *Melittoides*.

The *Leucandrena*-group is supported by three homoplasius synapomorphies (35:1, 91:2, 136:1) and combines the nearctic *Geissandrena*, the holarctic *Leucandrena*, *Parandrena* and *Larandrena* and the nearctic *Gonandrena*. The anterior hair fringe of female hindfemur consisting of specially branched hairs (116:2) is autapomorphic for *Geissandrena* which is positioned at the base of the clade. The holarctic *Larandrena* is paraphyletic in the present analysis since the nearctic and palearctic representatives do not form a monophyletic group. Thus the nearctic *A. (Larandrena) miserabilis* constitutes the sister taxon to *Gonandrena*,

while the palearctic *A. (Larandrena) ventralis* represents the sister group to the common clade of *A. (Larandrena) miserabilis* + *Gonandrena*.

Successive weighting (a posteriori weighting, Fig. 3)

The cladogram obtained after applying successive character reweighting (Fig. 3) agrees in some aspects with the results of the heuristic search (Fig. 2) and shows clear differences in tree topology.

In contrast to the results of the heuristic search, *Cubiandrena* is the sistergroup to all other subgenera of *Andrena* (node A1), while *Ancylandrena* represents the sister to *Cubiandrena* + *Andrena*. In the genus *Andrena* (node A2) the subgenus *Hamandrena*, previously a part of the large *Scoliandrena*/*Ptilandrena*/*Hamandrena*/*Carandrena*/*Andrena*-group, now constitutes the sistergroup to all other subgenera of *Andrena* (node B) but is polyphyletic with respect to *Didonia*. The monophyly of *Opandrena* and *Notandrena* (node C) is corroborated, although the clade is positioned at the base of clade B. The sisterclade (node D) to the *Opandrena*/*Notandrena*-group comprises four major lineages (nodes E, G, J, O). The common clade of *Diandrena* + *Scoliandrena* (node E) was removed from *Onagrandrena*, *Melanapis* and *Rhaphandrena*, and is the sister to the large clade (node F), which combines two major clades (nodes G and I).

The first of these clades (node G) largely agrees with the *Scoliandrena*/*Ptilandrena*/*Hamandrena*/*Carandrena*/*Andrena*-group (node R, Fig. 2) of the unweighted heuristic search-analysis, although the *Scoliandrena*-clade (Fig. 2, node S), the *Hamandrena*-clade (Fig. 2, node W) and the common clade of *Opandrena* and *Notandrena* were located outside of this clade. The *Oreomelissa*-clade (clade 9), comprising *Derandrena* and *Oreomelissa*, is the sister group to all other members of this clade. Although *Oligandrena*, *Cremnandrena*, *Dactylandrena* and *Genyandrena* are positioned basally in the sister group to the *Oreomelissa*-clade, they do not constitute a monophyletic group as shown in Fig. 2, only *Cremnandrena* and *Dactylandrena* are sister groups. The subgenus *Carandrena* represents the sister group to the subgenera contained in node H, the subgenera of node H have nearly the same composition of taxa as the *Hoplandrena*/*Andrena*/*Leucandrena*-clade (Fig. 2, node X2) in the unweighted analysis. The basal half of the clade merged to node H (indicated by the non-monophyletic clade 11) comprises the same taxa and shows an identical topology in both analysis, however the *Augandrena*/*Ptilandrena*/*Leucandrena*-group (node H2), which is the sister clade to the *Andrena*-group (node H1) clearly differs. Thus the sister group to the common clade of *Augandrena*, *Conandrena* and *Melittoides* (clade 12), which is identical in both analysis, combines the following two clades: (1) The *Ptilandrena*-group including *Geissandrena*, *A. (Ptilandrena) erigeniae*, *Hesperandrena* and *A. (Ptilandrena) fulvata* and (2) the

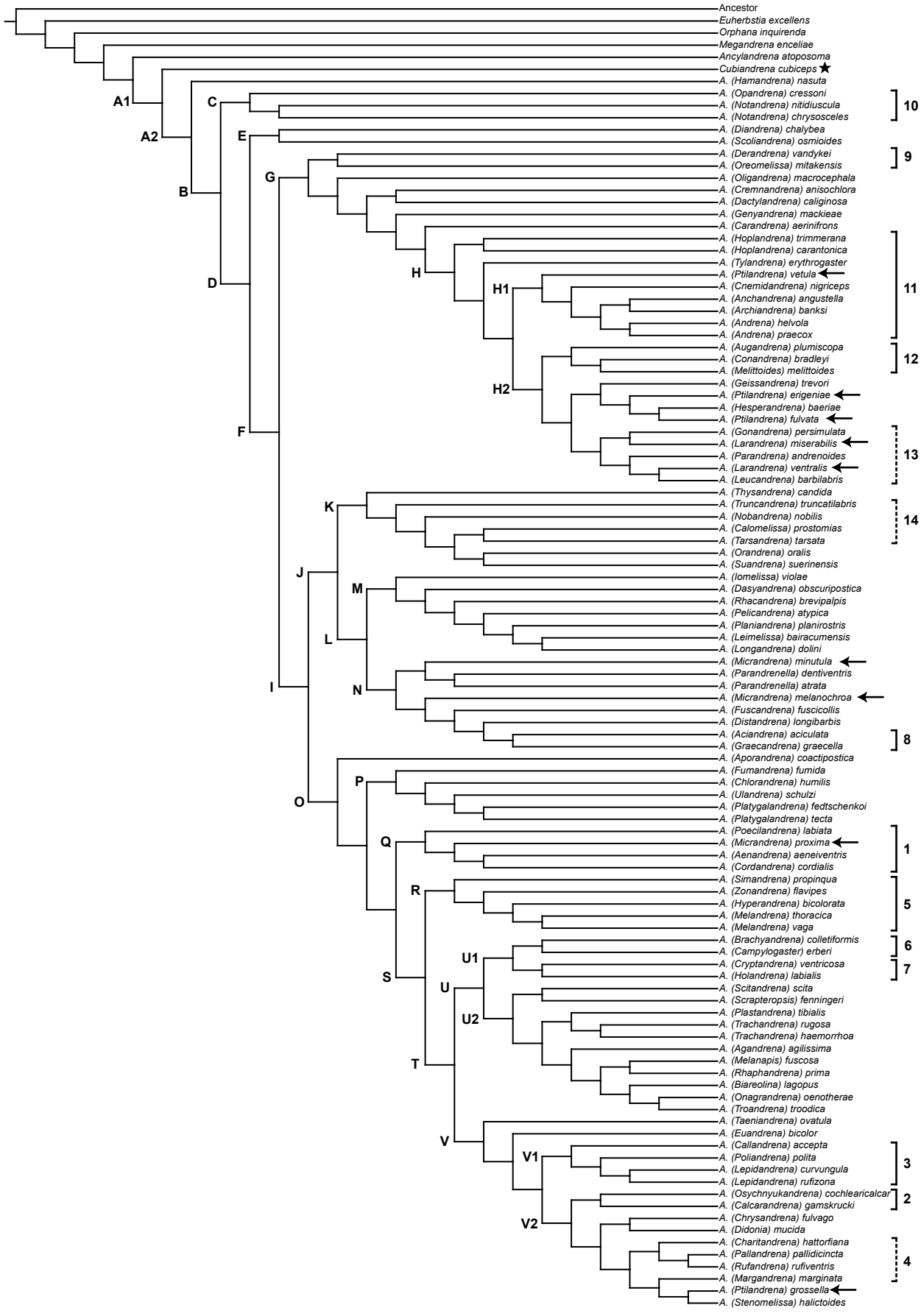

Fig. 3: Single cladogram obtained after successive character reweighting (a posteriori). **A-V2:** nodes mentioned in the text; **1-14:** groups of taxa which are also found in the unweighted analysis (Fig. 2), with dotted lines indicating groups that combine the same taxa, but show a different tree topology; arrows: representatives of polyphyletic groups; **asterisk:** indicating position of *Cubiandrena* **stat. nov.**

Leucandrena-group (clade 13), which unites the same taxa as the *Leucandrena*-group of the unweighted analysis (clade 13, Fig. 2), but the tree topology is different in that *Gonandrena* and *A. (Larandrena) miserabilis* are the sister clade to *Parandrena*, *A. (Larandrena) ventralis* and *Leucandrena*.

The second large clade (node I) combines two major clades indicated by the nodes J and O. The taxa included in node J, the *Truncandrena*/*Longandrena*/*Micrandrena*-clade essentially correspond to a combination of the *Truncandrena*-clade (Fig. 2, node O) with the *Orandrena*/*Micrandrena*-clade (Fig. 2, node Q), except *Fumandrena,* in the unweighted analysis. Within the *Truncandrena*/*Longandrena*/*Micrandrena*-clade the following main lineages can be discerned: (1) The *Truncandrena*-clade (node K), (2) the *Longandrena*-clade (node M) and (3) the *Micrandrena*-clade (node N), the latter two form a monophyletic group (node L), which is the sister group to the *Truncandrena*-clade. The *Truncandrena*-clade (node K) comprises *Thysandrena*, *Truncandrena*, *Nobandrena*, *Calomelissa*, *Tarsandrena*, *Orandrena* and *Suandrena*. *Calomelissa* and *Tarsandrena* as well as *Orandrena* and *Suandrena* are sistergroups, and constitute a common clade well within the *Truncandrena*-group. Despite the subgenera *Thysandrena, Orandrena* and *Suandrena*, which were placed additionally in this group, the clade is identical to the *Truncandrena*-group of the unweighted analysis (Fig. 2, node O). The *Longandrena*-group (node M) includes the nearctic subgenera *Iomelissa*, *Dasyandrena*, *Rhacandrena* and *Pelicandrena*, as well as the palearctic subgenera *Planiandrena*, *Leimelissa* and *Longandrena*. The monophyly of the central Asian subgenera *Planiandrena*, *Leimelissa* and *Longandrena* is a strongly supported by the presence of two incomplete ventrolateral ridges on the ventral side of the prementum (20:1), which is autapomorphic for this group. The *Micrandrena*-clade (node N) comprises two monophyletic groups, one unites the palearctic *A. (Micrandrena) minutula* with the palearctic *Parandrenella*, the other unites the nearctic *A. (Micrandrena) melanochroa* with the palearctic subgenera *Fuscandrena*, *Distandrena*, *Aciandrena* and *Graecandrena*, the latter two being sister taxa. The clade, indicated by node O, mainly comprises the taxa combined in the *Aenandrena*-group (Fig. 2, node C), the *Lepidandrena*/*Charitandrena*/*Zonandrena*/*Trachandrena*-group (Fig. 2, node E) and the *Chlorandrena*-group (Fig. 2, node P) of the equally weighted analysis. Within this large clade six major lineages can be recognized, (1) *Aporandrena*, (2) the *Chlorandrena*-group (node P), (3) the *Aenandrena*-group (node Q), (4) the *Zonandrena*-group (node R), (5) the *Trachandrena*-group (node U) and (6) the *Lepidandrena*/*Charitandrena*-group (node V), of which *Aporandrena* is the sister taxon to all other lineages of this clade. The *Chlorandrena*-group (node P), which comprises the subgenera *Fumandrena*, *Chlorandrena*, *Ulandrena* and *Platygalandrena*, resembles the *Chlorandrena*-group of the unweighted analysis (Fig. 2, node P), except the following changes: *Fumandrena* (instead of *Aporandrena)* constitutes the basal sister taxon to all other subgenera of the group and *Ulandrena* (instead of *Chlorandrena*) is the sistertaxon to *Platygalandrena*. The *Aenandrena*-group (node Q), including *Poecilandrena*, *A. (Micrandrena) proxima*, *Aenandrena* and *Cordandrena* is identical with the *Aenandrena*-group of

the unweighted analysis (Fig. 2, node C), although its position as sister group of the *Zonandrena*/*Trachandrena*/*Charitandrena*-clade (node S) is completely different. Representing the sister group to the common clade of the *Trachandrena*-group and the *Lepidandrena*/*Charitandrena*-group (node T), the *Zonandrena*-clade combines the subgenera *Simandrena*, *Zonandrena*, *Hyperandrena* and *Melandrena* and is identical with the *Zonandrena*-group revealed by the unweighted analysis. The *Brachyandrena*/*Trachandrena*-clade (node U) shows two major lineages basally, the *Brachyandrena*-clade (node U1) and the *Trachandrena*-clade (node U2). The *Brachyandrena*-clade (node U1) is nearly identical to that of the unweighted analysis (Fig. 2, node L), however, it comprises only *Brachyandrena*, *Campylogaster*, *Cryptandrena* and *Holandrena*, with a latter-like topology , but lacking *Scitandrena*. The second major lineage, the *Trachandrena*-clade (node U2), includes all subgenera of the *Trachandrena*-group of the unweighted analysis (Fig. 2, node M), as well as five additional subgenera. Thus *Scitandrena* is the sister taxon to *Scrapteropsis*, and both together constitute the sisterclade to the remaining subgenera in the *Trachandrena*-group. The clade containing the holarctic subgenera *Trachandrena* and *Plastandrena* forms the sister to the clade which unites the palearctic *Agandrena* with the monophyletic group consisting of the following subgenera: *Melanapis*, *Rhaphandrena*, *Biareolina*, *Onagrandrena* and *Troandrena*. The latter group consists of two lineages, one uniting the palearctic *Melanapis* with the nearctic *Rhaphandrena*, and another comprising the palearctic *Biareolina*, the nearctic *Onagrandrena* and the palearctic *Troandrena*. The holarctic subgenera *Taeniandrena* and *Euandrena* are positioned at the base of the *Lepidandrena/Charitandrena*-group (node V). The *Lepidandrena*-clade (node V1, clade 3), which unites the nearctic *Callandrena* with the palearctic *Poliandrena* and *Lepidandrena*, constitutes the sister clade to the clade (node V2) which unites the following four lineages: (1) *Osychnyukandrena* + *Calcarandrena,* (2) *Chrysandrena* + *Didonia*, (3) *Charitandrena* + *Pallandrena* + *Rufandrena* and (4) *Margandrena* + *A. (Ptilandrena) grossella* + *Stenomelissa.* The latter two (3 + 4) constitute a monophyletic group, which is the sister to *Chrysandrena* + *Didonia*.

Monophyly of *Andrena*

Although the genus *Andrena* is considered to be well-characterized (Michener, 2000), it is difficult to find unambiguous autapomorphic characters which would exactly define the genus as a whole. Thus many of the diagnostic characters used to separate bee genera, e.g. the number of submarginal cells in the fore wings, other features of the veins of wings, the presence and size of the inner tooth of the claws, the shape of hidden S 7 and 8 in the males, or the shape of male genitalia, show enormous variability within *Andrena*. Five of the eight synapomorphies defining the genus *Andrena* in the present study are non-homoplasius: (1) bristles of paramandibular process distinctly smaller than bristles of subgenal coronet (7:2), (2) mental plate strongly reduced to absent (19:1), (3) condylar lamella of female mandible developed (22:1), (4) hind margin of female vertex narrowly rounded to slightly

edged in profile (71:2) and (5) hairs of dorsoposterior hair fringe of propodeal corbicula strongly branched (103:1). It should be noted that all of the non-homoplasius synapomorphies show some amount of reversals and transformations in the more terminal parts of the tree. Therefore the presence of a subgenal coronet, is judged to be the most solid character which unequivocally defines the entire genus *Andrena.* It is found in all examined species of *Andrena* (although sometimes strongly reduced) and does not occur else where among bees, except in *Cubiandrena*. The thornlike projection of the paramandibular area of *Cubiandrena*, which bears some bristles and therefore resembles the subgenal coronet of *Andrena* is interpreted as an abnormal modification of this structure, although the possibility of a convergent development cannot be excluded. However, as stated above, the results of the present analysis no longer allow us to treat *Cubiandrena* as a subgenus of *Andrena*, since it would result in a paraphyletic taxon. Apart from that, *Cubiandrena* is characterized by a total of 37 (!) synapomorphies, 13 of which are autapomorphic: postgenal bridge deeply concave rounded (2:2), bristles of subgenal coronet developed along toothlike projection (5:2), prementum rounded, with two complete ventrolateral ridges (ridges as long as prementum) (20:2), pubescence of scutum consisting of scale-like, simple hairs (83:3), LP with bottle-brush-like branched hairs (96:3), anterior hair fringe of female hindfemur composed of peculiar multi-sided branching hairs (116:4), scopa of female hind tibia consisting of peculiar multi-sided branching hairs (117:4), inner side of hind tibia with multi-sided branching hairs (118:1), outer side of female basitarsus of hind legs with specially multi-sided branching hairs (123:4), vanal lobe more than 0.9 times as long as jugal lobe (130:2), female T1 strongly sloping, without distinct separation into horizontal and declivous parts (131:1), S 7 of male consisting of two separate parts connected by membrane apically (138:1) and a toothlike digitus (153:1). These autapomorphies further emphasize the special position of *Cubiandrena* and that it should no longer be considered a subgenus of *Andrena*. In contrast to this are the results regarding *Melittoides*, which was originally described as separate genus by Friese (Fahringer & Friese, 1921), then lowered to subgeneric rank by Warncke (1968a) and recently raised to generic rank by Michener (2000). The results show that *Melittoides* is a clear member of *Andrena* and therefore it is regarded as a valid subgenus of *Andrena*.

In summary, the results of the present cladistic analyses amply demonstrate the monophyly of *Andrena* and the genus can be clearly defined by the characters listed above. Nonetheless, an absolutely unambiguous autapomorphy for the genus is still missing.

Systematic position of *Andrena* within the Andreninae

The results of the unweighted analysis (Figs 1,2) show that *Andrena* is the sister-group to the common clade of the nearctic *Ancylandrena* and palearctic *Cubiandrena*. The monophyly (Fig. 2, node A1) of these three genera is supported by twelve synapomorphies, three of which are non-homoplasius (see above). The clade comprising *Andrena*, *Cubiandrena* and *Ancylandrena* again constitutes the sister-group to a second large clade which combines the

remaining genera, *Euherbstia*, *Orphana* and *Megandrena*, whereby *Megandrena* is the sister-group to *Orphana.* The monophyly of this second large clade within Andreninae is supported by 15 synapomorphies (15:1, 32:2, 49:1, 64:3, 70:3, 75:2, 79:1, 104:1, 119:1, 129:1, 139:4, 141:1, 153: 2, 157:1, 158:2) of which one, the strongly pectinate inner spur of female hind tibia (119:1), is non-homoplasius. However, the feature is not developed in *Megandrena*.

A different tree topology within the Andreninae was revealed by the analysis which applied successive character reweighting (Fig. 3). Thus *Cubiandrena* alone constitutes the sister-group to *Andrena* supported by 15 synapomorphies (4:1, 13:0, 25:1, 34:1, 35:1, 43:1, 52:0, 54:0, 60:0, 70:0, 77:1, 78:0, 104:0, 110:1, 127:0), of which one, the presence of subgenal coronet (4:1) is non-homoplasius. *Ancylandrena* again represents the sister to the common clade of *Cubiandrena* and *Andrena*. The monophyly of (*Ancylandrena* (*Cubiandrena*, *Andrena*)) is defined by 15 synapomorphies (12:1, 14:1, 27:1, 32:0, 49:0, 66:1, 75:0, 88:2, 95:0, 96:1, 102:1, 139:0, 152:1, 153:0, 162:1), two of which are non-homoplasius: the presence of a preapical tooth in the male mandible (27:1) and a small digitus of the volsella (152:1). The latter (152:1), however, is not found in *Cubiandrena*, which instead has a large, toothlike digitus of the volsella. The sister-group of *Megandrena* and the (*Ancylandrena* (*Cubiandrena*, *Andrena*))-clade is supported by twelve synapomorphies (52:1, 54:1, 60:3, 61:1, 78:1, 82:1, 119:0, 127:1, 129:0, 135:2, 141:0, 148:1) of which two characters, the presence of a velvety FOV (61:1) and the inner margins of dorsal gonocoxite joining each other on at least half the length (148:1, not developed in *Cubiandrena*), are non-homoplasius. Twelve synapomorphies (13:1, 24:1, 45:1, 74:1, 95:1, 96:6, 97:1, 102:2, 115:1, 137:2, 154:1, 161:1) support the monophyly of *Orphana* and the lineage combining (*Megandrena* (*Ancylandrena* (*Cubiandrena*, *Andrena*))), one of which, the presence of a propodeal corbicula (97:1), is non-homoplasius. *Euherbstia* is the most basal taxon and the sister to the (*Orphana* (*Megandrena* (*Ancylandrena* (*Cubiandrena*, *Andrena*)))-clade.

To summarized briefly, (Figs 2, 3) *Andrena* is found in both analyses to be one of the most derived taxa within the Andreninae, while *Euherbstia* is most ancestral. This is contrary to the results of Alexander and Michener (1995), which show *Andrena* as more ancestral and as constituting the sister-group to all other Andrenidae. One should be aware that the character sampling of the present analysis was intended to be appropriate for resolving the internal phylogenetic relationships within *Andrena* rather than the relationships within the Andreninae. The results concerning the phylogeny and systematics of Andreninae presented in this study must thus be treated with some degree of caution.

Polyphyletic groups

In the present analyses several subgenera were discovered to be polyphyletic (Figs 1-3). Polyphyletic subgenera, which clearly show distinctive species groups were split resulting in the proposal of new subgenera. New subgenera were not established in cases where the polyphyly was due to the separate position of a single species that did not represent a

previously recognized species group, for example in *Micrandrena*, *Ptilandrena*, and *Larandrena* (indicated by arrows in Figs 2, 3). In other words, the present study abstained from erecting monobasic subgenera.

The newly erected subgenus *Hamandrena* comprises three species which were previously included to the subgenus *Didonia*. The cladistic analyses show that *Hamandrena* is strongly supported by the autapomorphic characters (11:2) and (21:3), and it does not form a monophyletic group with *Didonia*.

A similar situation is found in the subgenus *Ulandrena*. The results of the heuristic search reveal that *Ulandrena* is polyphyletic since *Ulandrena* and the representatives of the newly erected *Platygalandrena*, which were previously included in *Ulandrena* do not constitute a monophyletic group. However, in the successive reweighting analysis *Ulandrena* is the sister to *Platygalandrena* and therefore both taxa form a monophyletic clade. Even so, a new subgenus, *Platygalandrena*, was erected for the species-group in consideration of the results of the unweighted analysis, the strong differences between the two subgenera as well as the presence of a solid autapomorphy (8:1) defining the subgenus. The subgenus that appears to be most closely related to *Platygalandrena* is either *Chlorandrena* (Fig. 2) or *Ulandrena* (Fig. 3).

The species of the newly erected subgenus *Calcarandrena* were formerly included in the subgenus *Lepidandrena* and had to be split off to avoid the polyphyly of *Lepidandrena*. The analyses show that the species of *Calcarandrena* now form the sister group to *Osychnyukandrena*.

The holarctic subgenus *Micrandrena* is also shown to be polyphyletic. The palearctic (*A. minutula*) and nearctic (*A. melanochroa*) representatives of *Micrandrena* included in the present analysis did not form a monophyletic group. Furthermore, *A. (Micrandrena) proxima* is the sister-group to the clade of *Aenandrena* and *Cordandrena* (see above).

The holarctic subgenus *Ptilandrena* appeared to be extremely polyphyletic, as all four taxa of the subgenus included in the analyses occurred in isolated positions throughout the cladograms.

Finally, the palearctic and nearctic representatives of the subgenus *Larandrena* constitute a polyphyletic group, since *Gonandrena* is the sister-group to *A. (Larandrena) miserabilis* rather than to *(Larandrena) ventralis*.

Evaluation and support of trees and clades

The consistency index (ci, CI), which is used as a measure of homoplasy, is considered one of the most important statistics for the evaluation of cladograms and character support (Rieppel, 1999). The CI of the MPTs from the present analysis is rather low (CI: 0.15) and the ci of single characters ranges from 0.04 to 1. This implies a high degree of homoplasy in the data set. One must be aware that in analyses with a high number of taxa the CI is observed to decrease (since the statistically probability of homoplasy rises, the larger the data matrix

becomes) despite no change in information content (Kitching et al., 1998; Rieppel, 1999, Wägele, 2000).

Tracing bootstrap, jackknife or Bremer support (decay index) values are common methods to evaluate the robustness of a cladogram and the support of its nodes (Felsenstein, 1985; Bremer, 1994; Rieppel, 1999). In the present study bootstrap and jackknife procedures, which are methods that involve perturbations of the data, were used for the calculation of branch support. While bootstrapping is based on resampling the characters of a data matrix, jackknifing is based on the deletion of characters. Thus, resampling by the bootstrap procedure creates a new matrix by the omission and duplication of some of the original characters (Bremer, 1994). In a broader sense both methods therefore can be regarded also as a kind of character weighting. Most bootstrap and jackknife values calculated in the present analysis were less than 50 % except a few apical clades (Fig. 2), a tribute paid to the homoplasius support of most clades in the revealed trees. The monophyly of the following subgenera with more than one included representative in the analysis is strongly supported by high to maximum scored bootstrap (first number in parentheses) and jackknife values (second number in parentheses): *Lepidandrena* (100 %, 98 %), *Trachandrena* (96 %, 100 %), *Platygalandrena* (98 %, 98 %), *Parandrenella* (100 %, 100 %), *Hoplandrena* (100 %, 100 %) and *Andrena* (100 %, 100 %). Clades of *Notandrena* (80 %, 84 %) and *Melandrena* (74 %, 74 %) also show clear support, although not as high as the preceding subgenera. Distinct support was also revealed for the sister-group relationship of following subgenera: *Osychnyukandrena* + *Calcarandrena* (64 %, 76 %), *Brachyandrena* + *Campylogaster* (78 %, 90 %), *Cryptandrena* + *Holandrena* (74 %, 70 %), *Orandrena* + *Suandrena* (jackknife: 68 %), *Leimelissa* + *Longandrena* (58 %, 64 %), *Aciandrena* + *Graecandrena* (78 %, 66 %), *Melanapis* + *Rhaphandrena* (jackknife: 78 %), *Derandrena* + *Oreomelissa* (72 %, 72 %), *A. (Ptilandrena) grossella* + *Stenomelissa* (jackknife: 58 %), *Cremnandrena* + *Dactylandrena* (68 %, 68 %), *Opandrena* + *Notandrena* (72 %, 84 %), *Anchandrena* + *Archiandrena* (68 %, 80 %), *Conandrena* + *Melittoides* (jackknife: 58 %). Finally the clade uniting ((*Anchandrena*, *Archiandrena*) *Andrena)*, as well as the complete *Andrena*-clade (node Y) are the only higher-categorized clades which show rather good support by jackknife values (56 % each) in the present analysis.

Although values of branch support are regarded to be one of the most objective ways to evaluate the support of single clades within a tree, their use is not without problems in large data matrices, such as the present one. A higher degree of homoplasy is a compelling statistical result of an increased number of included taxa (see above), this forces not only an decrease in the CI-values but also the branch support values. This problem is aggravated by the limitation of suitable morphological data, especially of external morphology, in contrast to molecular data. Data from internal morphology, histology and larval morphology, as well as behavioural data would be a valuable and interesting adjunct to the present non-molecular data set, which might supply increased support of some clades. Due to the limited available material of several subgenera a character sampling of inner morphology and histology was not

practicable. Comprehensive behavioural data is not available since the biology and ethology of species and groups have been studied only sporadically in detail (Davis & LaBerge, 1975; Gebhard & Röhr, 1987; Grünwaldt & Grünwaldt, 1939; Michener & Rettenmeyer, 1956; Osgood, E. A., 1989; Parker & Griswold, 1982; Schönitzer & Klinksik, 1990).

Unweighted versus weighted analysis

Two forms of character weighting can be distinguished, one, that is conducted before cladogram construction (*a priori*) and the second, which is carried out after cladogram construction (*a posteriori*). Aside from these two methods, character selection itself as one of the first steps in every cladistic analysis represents a kind of character weighting, in that characters omitted from the analysis are in effect weighted with zero weight ("0"), while included characters are weighted with "1" in the simplest case (Haszprunar, 1998). An equal weighting (= nonweighting) procedure therefore can be regarded as the heaviest kind of possible weighting (Neff, 1986).

A priori weighting of morphological data is problematic since it strongly depends on the subjective opinion of each systematist, whether a distinct character (state) is to be regarded as a primary homology or not. Furthermore, generally accepted guidelines, e.g. manifested in the homology criteria as listed by Haszprunar (1998), often cannot be examined in detail since relevant information is missing or hardly understandable. Molecular data, on the other hand, may be more appropriate for *a priori* weighting procedures, because of the degeneracy of the genetic code. Therefore it is a common method to weight differentially the first, second and third positions of the codon relative to particular amino acids (Kitching et al., 1999).

A posteriori weighting, which goes back to the idea of Farris (1969), is based on the degree of homoplasy measured either by ci, ri or rc values (Kitching et al., 1998, Farris, 1989) found in a certain cladogram (yielded by a preceding analysis of unweighted characters). These measures are subsequently used as criterion for "successive weighting" or "implied weighting" procedures. Nevertheless successive weighting and also implied weighting (PeeWee; Goloboff, 1993) reinforces those characters, which show maximum fit to the tree topology of the first cladogram and therefore cannot be regarded as hypotheses independent of tree construction (Wägele, 2000).

In the analysis of the data matrix of *Andrena*, an equally weighted or unweighted analysis (Figs 1, 2), as well as an analysis based on successive character reweighting (Fig. 3) was carried out. Despite the above mentioned problems of the independence of successive reweighting procedures, this method was used as it precisely refers from the degree of homoplasy in the results of the foregoing equally weighted analysis and therefore assumes the role of a touchstone for each clade revealed by the primary analysis. Comparison of results of both analyses shows that 14 groups (clades 1-14, Figs 2, 3) contained the same taxa, 11 of which even showed identical tree topologies. However, especially the more basal parts of each tree show clear differences as described in detail above. Different parts of tree topology

obtained by successive reweighting promised to represent interesting alternative evolutionary scenarios since they seem to promote homologies and apomorphies in a more adequate and objective way than might be possible in the equally weighted analysis.

Comparison to previous studies

In the following the results of the present analyses are compared to those of previous studies dealing with the relationships of subgenera of *Andrena*.

In his work on the western Palearctic subgenera of *Andrena,* Warncke (1968a) postulated vague relationships for the subgenera, which unfortunately were based primarily on subjective opinion rather than objective facts or common characters. Though a complete reconstruction of the relationship between the western Palearctic subgenera of *Andrena* remains obscure and not understandable in main parts of his exposition, Warncke suggested several groupings of subgenera which were confirmed in the present analysis: *Chlorandrena* + *Lepidandrena*, *Pallandrena* + *Charitandrena*, *Nobandrena* + *Truncandrena*, *Plastandrena* + *Agandrena*, *Distandrena* + *Graecandrena* + *Aciandrena*, *Zonandrena* + *Melandrena* + *Hyperandrena*, *Euandrena* + *Didonia*, *Carandrena* + *Notandrena*, *Leucandrena* + *Parandrena* + *Larandrena*, *Cnemidandrena* + *Andrena*. All other relationships mentioned by him could not be corroborated in the present study. Furthermore, he recognized the general common relationship of the following subgenera *Ptilandrena*, *Margandrena*, *Hoplandrena*, *Carandrena*, *Notandrena*, *Leucandrena*, *Parandrena*, *Larandrena*, *Cnemidandrena* and *Andrena,* which he regarded as mostly derived subgenera. The derived position of this group was confirmed by several trees of the equally weighted analysis, although several more nearctic subgenera (*Genyandrena*, *Oligandrena*, *Cremnandrena*, *Dactylandrena*, *Opandrena*, *Tylandrena*, *Anchandrena*, *Archiandrena*, *Augandrena*, *Gonandrena*, *Conandrena*, *Geissandrena* and *Hesperandrena*), as well as a few palearctic (*Melittoides*, members of the polyphyletic *Ptilandrena*) subgenera were included additionally into the group (Fig. 2, node X) in the present analysis. In addition, he postulated that *Avandrena* and *Micrandrena* were among the most ancestral subgenera and that evolved from each other, the latter part of this hypothesis which could be examined in the present analysis, only in part because it was necessary to omit the representative of *Avandrena* from the analysis due to the great degree of missing data in the male sex (see under: Selection of taxa and characters). Nevertheless, *Micrandrena* never occurred in a basal position in the present analyses, and it seems unlikely that *Avandrena* would assume a basal position since subgenera related to *Avandrena*, as listed by Warncke (*Rufandrena*, *Chlorandrena*, *Pallandrena*), did not show up in basal positions in the cladograms of the present study. In summary, only some of the sister groups postulated by Warncke (1968a) were able to be confirmed in the present analyses, whereas the majority was found to be contrary. The inclusion of nearctic subgenera in a broad phylogenetic focus by the present study, however, demonstrates the insufficiency of most of Warncke's hypotheses.

In his computerized numerical taxonomic studies of 85 *Andrena* species of Japan, Tadauchi (1981, 1982, 1985a) examined the position of each species at subgeneric level based on the methods of phenetic numerical taxonomy (Sokal & Sneath, 1963, 1966). Using 130 female morphological characters he obtained different distance phenograms depending on clustering methods (Tadauchi, 1982), as well as which character subsets were used (Tadauchi, 1985a). In the phenogram based on a distance matrix obtained by the group average method (Tadauchi, 1982 and 1985a, Fig. 1) he recognized five major groups. The first group, which comprises *Andrena* s. str., *Larandrena*, *Euandrena*, *Hoplandrena*, *Cnemidandrena*, *Melandrena* and *Simandrena*, resembles the *Hoplandrena*/*Andrena*/*Leucandrena*-clade (Fig. 2, node X2; Fig 3, node H) of the present analyses, despite the presence of *Euandrena*, *Melandrena* and *Simandrena* within this cluster and the absence of *Parandrena* and *Leucandrena*, as well as of several subgenera which do not occur in Japan, of course. Nevertheless the close relationship of *Melandrena* and *Simandrena* was also confirmed by the present investigation, (Fig. 2, node J; Fig. 3, node R), although both subgenera belong to different clades. The second group, combining *Micrandrena*, *Notandrena*, *Leucandrena*, *Poecilandrena*, *Calomelissa* I, *Oreomelissa, Calomelissa* II, *Taeniandrena* and *Habromelissa*, could not be confirmed by the present analyses, except a more or less distinct relationship between *Micrandrena* and *Calomelissa,* the latter being "paraphyletic" in Tadauchi´s phenogram. In the present study *Leucandrena* is found to be a close relative to *Larandrena* and *Parandrena* of the *Augandrena*/*Leucandrena*-clade (Fig 2, node Z) within the *Hoplandrena*/*Andrena*/ *Leucandrena*-group (Fig. 2, node X2; Fig. 3, node H), while *Notandrena* is a member of the sister clade to the *Hoplandrena*/*Andrena*/ *Leucandrena*-group in the unweighted analysis. Furthermore the representative of *Poecilandrena* in the present investigation is a member of the *Aenandrena*-group (Fig. 2, node C; Fig. 3, node Q), *Oreomelissa* is clearly found to be the sister to *Derandrena* and also *Taeniandrena* appears in different positions. *Habromelissa* was not included by the present analysis. The third group within the distance phenogram of Tadauchi includes the subgenera *Chlorandrena* and *Stenomelissa*, whereas the fourth group combines *Plastandrena Trachandrena* and *Holandrena*. The latter is the only group obtained identically in all five different clustering methods (Tadauchi, 1982) and was confirmed, in general, by the present investigation, although several more subgenera were included in the corresponding clade by the present study. The sister group relationship of *Chlorandrena* and *Stenomelissa* was not corroborated in the present analyses. *Parandrena*, which is shown as a close relative of *Leucandrena* and *Larandrena* in the present study, surprisingly represents the fifth major group in the distance phenogram of Tadauchi, where it is the sister to all other taxa. Rather than being restricted to a single geographical region as Tadauchi's studies, the present investigation provides a much more comprehensive phylogenetic study since it embraces the entire genus *Andrena* worldwide. Furthermore, this study presents the first phylogenetic concept of *Andrena* based on morphological data using modern methods of parsimony analysis, in contrast to the methods of phenetic numerical taxonomy.

In a study of the zoogeography of *Andrena*, LaBerge (1986b) summarized his results and those of his colleagues on the taxonomy and phylogeny of North American subgenera of *Andrena*. Their conclusions are not based on the results of a formal parsimony analysis. He regarded the subgenera *Andrena* s. str., *Notandrena*, *Gonandrena* and their relatives as most primitive groups of living subgenera based on previous studies (LaBerge & Ribble, 1972, LaBerge, 1980). This hypothesis could be corroborated only in part by the present analyses. On the one hand some results support the hypothesis. The clade uniting *Opandrena* and *Notandrena* (Fig. 3, node C) represented the most basal branch in the clade which is the sister group to *Hamandrena*. On the other hand several results contradict the hypothesis. The most ancestral subgenera of *Andrena* are the members of the *Aenandrena*-clade in the strict consensus tree of the unweighted analysis (Fig. 2, node C) and *Hamandrena* in the successive weighting analysis (Fig. 3). Furthermore, the subgenera *Andrena* s. str. and *Gonandrena* appeared to be derived, in the present analyses. LaBerge further postulated that *Cnemidandrena* arose from an ancestral lineage of *Andrena* s. str. and that *Geissandrena* and *Gonandrena* arose from the *Notandrena*-line, as well as *Leucandrena*, the latter again forming the ancestral lineage of *Larandrena, Parandrena* and *Pelicandrena*. A close relationship between *Andrena* s. str., *Geissandrena and Gonandrena*, as well as between *Leucandrena Larandrena* and *Parandrena* was confirmed by the present study, however all these genera arose from a common ancestral lineage of the *Hoplandrena*/*Andrena*/*Leucandrena*-clade (Fig. 2, node X2; Fig 3, node H). In the present analyses, *Tylandrena* appeared as more ancestral than *Andrena* s. str., in contrast to LaBerge and Bouseman (1970) where it is represented as a descendant of the *Andrena* s. str. line. Although the present study indicated that *Callandrena*, *Chrysandrena* and *Charitandrena* belong to a common clade (Fig. 2, node F; Fig. 3, node V) it is contrary to the evolutionary scenario postulated for these genera by LaBerge (1967, 1986b). However the close relationship between *Trachandrena*, *Scrapteropsis*, *Biareolina*, *Rhaphandrena*, *Xiphandrena* and *Onagrandrena*, was recognized by LaBerge (1986b) and could be confirmed in general by the successive reweighting analysis except *Xiphandrena*, which was not included in the present analyses (Fig. 3, node U). In the unweighted analysis, only *Trachandrena*, *Scrapteropsis* and *Biareolina* were members of a common clade (Fig. 2, node M), while *Rhaphandrena* and *Onagrandrena* formed a common clade together with *Scoliandrena*, *Diandrena* and *Melanapis* (Fig. 2, node S), which constitutes the sister group to the *Ptilandrena*/*Hamandrena*/*Carandrena*/*Andrena*-group (Fig. 2, node T). The hypothesis of LaBerge (1971b) that *Rhaphandrena* and *Xiphandrena* may be the most primitive of the *Trachandrena*/*Scrapteropsis*/*Biareolina*/*Rhaphandrena*/*Xiphandrena*/*Onagrandrena* group and that they probably are derivatives of the *Andrena* s. str./*Notandrena* stem could not be corroborated by the present study. The close relationship between *Diandrena* and *Rhaphandrena* as postulated by LaBerge could only be confirmed in the unweighted analysis (Fig. 2, node S), whereas in the successive reweighting analysis *Scoliandrena* was the sister of *Diandrena* (Fig. 3, node E) as mentioned above. Both analyses of the present study confirm the hypothesis of LaBerge that *Trachandrena* arose more or less directly from *Scrapteropsis*

and indicate a relationship between *Brachyandrena* and *Scrapteropsis* as suggested by LaBerge (Fig. 2, node K; Fig 3, node U). An *Euandrena-Thysandrena* line, which probably evolved from a *Rhacandrena*-like ancestor (LaBerge & Ribble, 1975; LaBerge, 1977) as well as a *Simandrena-Micrandrena-Scaphandrena* line were not confirmed in the present analyses. Finally a close relationship between *Thysandrena*, *Dasyandrena* and *Psammandrena* as well as between *Euandrena* and *Melandrena* as recognized by LaBerge was not replicated in the present study.

Larkin (2002) was the first to conduct a phylogenetic analysis of *Andrena* based on molecular data; she used sequence data from mitochondrial DNA as well as nuclear DNA. Although the focus of her study was on the members of the subgenus *Callandrena*, she additionally included nearctic representatives from 25 different subgenera in her analyses. In her results from the maximum likelihood analysis of combined data both nuclear and mitochondrial DNA, two large clades can be distinguished (excluding the polyphyletic *Callandrena* in her analyses). Clade A combines *Andrena* s. str., *Cnemidandrena*, *Archiandrena*, *Plastandrena*, *Trachandrena*, *Scrapteropsis*, *Rhaphandrena*, *Onagrandrena*, *Diandrena*, one representative of *Gonandrena* and one representative of *Rhacandrena*. Clade B includes *Larandrena*, a second representative of *Rhacandrena,* a second representative of *Gonandrena, Euandrena, Ptilandrena, Simandrena, Scaphandrena, Micrandrena, Taeniandrena, Holandrena, Tylandrena,* one representative of *Melandrena, Leucandrena,* a second representative of *Melandrena, Belandrena and Parandrena*. Similar to the results of the present study, she recognized the close relationship between *Andrena* s. str., *Cnemidandrena* and *Archiandrena*, between *Plastandrena, Trachandrena*, and *Scrapteropsis*, in part between *Plastandrena, Trachandrena*, *Scrapteropsis* and *Rhaphandrena*, and between *Onagrandrena* and *Diandrena*. The sister group relationship between the *Andrena* s. str./*Cnemidandrena*/*Archiandrena* group and the *Plastandrena*/*Trachandrena*/*Scrapteropsis*/*Rhaphandrena*/*Onagrandrena*/*Diandrena*/*Gonandrena* group as obtained by Larkin within clade A was not confirmed by the present analyses. However, on the one hand, *Tylandrena*, *Parandrena*, *Leucandrena* and *Larandrena*, which all belong to clade B in Larkin´s analysis, are closely related to the *Andrena* s. str./*Cnemidandrena*/*Archiandrena* group in the present analysis. On the other hand, the monophyly of *Parandrena* + *Leucandrena* + *Larandrena* as obtained by the present study was not recognized in Larkin's (except by the mitochondrial data only), wherein only *Parandrena* + *Leucandrena* are monophyletic and *Larandrena* is the sister to all other genera in clade B. The position of *Melandrena*, which appeared as a polyphyletic taxon near *Leucandrena* in clade B of Larkin´s analysis, is completely contrary to that obtained in the present study where *Melandrena* is closely associated with *Simandrena*, *Zonandrena* and *Hyperandrena*, noting that the latter two subgenera were not included in Larkin´s analyses. Finally, the monophyly of *Holandrena* + *Taeniandrena* + *Micrandrena* + *Scaphandrena* + *Simandrena*, *Ptilandrena* + *Euandrena* + a representative of *Gonandrena* + a representative of *Rhacandrena* as recognized by Larkin in her clade B was not confirmed in the present study.

Evolution of *Andrena* and zoogeographical aspects

All members of the Andreninae, except *Cubiandrena* and *Andrena*, are exclusively found in the New World. The North American genera range from the western United States to northern Mexico and include *Ancylandrena* (4 species) and *Megandrena* (2 species) (Zavortink, 1972, 1974). The South American genera, *Orphana* (2 species) and *Euherbstia* (only 1 species), are restricted to Chile (Rozen, 1971). The Old World genus *Cubiandrena* (2 species) ranges from the eastern Mediterranean region to Asia minor. In light of the wide radiation of Andreninae at the generic level in the New World, it is possible that the subfamily originated there. The results of the present analysis as well as the low number of species found in each of the American genera suggest that they may be ancestral within the Andreninae. The genus *Andrena*, which shows the greatest species diversity of all bee genera, however, probably represents the most modern group of the Andreninae, which was derived from the ancestors of *Cubiandrena* or from a common ancestral lineage of *Cubiandrena* + *Ancylandrena*. The latter evolutionary scenario, however, seems more unlikely as it implies that either the ancestor of *Cubiandrena* colonized the Old World independently from *Andrena* or the ancestor of *Ancylandrena* reinvaded the New World from an Old World lineage. Nevertheless, it is more likely, according to the results of this study, that *Andrena* evolved in the Old World, presumably somewhere between the Mediterranean region and Central Asia, since most basal subgenera of *Andrena* are strictly palearctic (*Hamandrena*, Fig. 3; *Poecilandrena*, *A. (Micrandrena) proxima*, *Aenandrena*, Fig. 2). This hypothesis is contrary to LaBerge (1986b), who held that the more ancestral subgenera are in North America and not Eurasia. The earliest fossils of *Andrena* are from Baltic amber and date back to the lower Oligocene (LaBerge, 1986b), thus the genus *Andrena* probably already originated between late Cretaceous and early Tertiary (Eocene), when North America and Europe were still connected in parts. Starting from a palearctic origin *Andrena* could have rapidly dispersed all throughout the holarctic region as fossil records from Colorado Florissant shale (Oligocene or early Miocene) indicate (LaBerge, 1986b). Thus the holarctic distribution of *Andrena* probably is based on dispersal events which could have occurred during the late Cretaceous and early Tertiary. The development of subgenera, which are restricted either to the palearctic or nearctic regions, could be based on vicariance events occurring from the middle Eocene onward that led to the expansion of the Atlantic ocean and the separation of North American and Eurasian landmasses. Several independent migration events of *Andrena*-lineages between western North America and Asia at the time of later Miocene/ early Pliocene, when diverse continental connections between America and Asia existed, can explain the interlocking distribution pattern of nearctic and palearctic subgenera in the cladograms of the present study (Figs 1-3). The existence of 16 holarctic subgenera might be attributed to migration events along land bridges across the Bering Strait during Holocene. Because these migrations took place more recently, palearctic and nearctic representatives of these subgenera still show evidence of their close relationships and have not yet widely diverged from each other.

3.2.2 Molecular evolution of Central European *Andrena*

Selection of taxa

The molecular analysis of Central European *Andrena* comprises 27 ingroup taxa representing 21 different subgenera (which amounts to about half of all subgenera occurring in Central Europe), as well as seven members of the subgenus *Micrandrena*, a subgenus which plays a central role in the present analysis. *Panurgus* was sampled as the outgroup.

DNA sequences

DNA sequencing produced 853 base pairs (bp) of mitochondrial COI. Overall aligned sequences which were used for the analysis totaled 758 bp. Of these, 257 were parsimony informative. Of the 501 uninformative characters, 433 were constant and 68 were variable. The amount of phylogenetically informative characters of the sequenced part of COI was noticeably low (34 %) for *Andrena*. The sequence positions between 2535 and 2786 are rich in parsimony informative characters (86 %), yet the positions between 2787 and 3292 are poorly phylogenetically informative (11 %). The strong A/T bias in base composition agrees in general with that of mitochondrial DNA sequences of most insects (especially holometabolan) (Clary and Wolstenholme, 1985; Simon et al., 1994), as well as with the COI data found in bees (Danforth, 1999, Larkin, 2002). An A/T bias is most dominant at third codon positions and least prevalent at first codon positions. This result is contrary to those of previous studies on bees (Danforth, 1999, Larkin, 2002), in which the A/T bias was least dominant at the second codon position. The base composition of the 28 sequences included in the present study is given in Tab. 3, the complete sequence data is given in Tab. 5 (cf. end of chapter).

Tab. 3. Base composition in COI (758 total nucleotide positions; 28 sequences in total)

	%A	%C	%G	%T	%A/T
First position	34.2	15.0	21.7	29.1	63.3
Second position	22.5	19.6	15.8	42.1	64.6
Third position	49.3	15.2	1.8	33.7	83.0
Overall	35.3	16.6	13.1	35.0	70.3

Cladograms and tree topology

The parsimony analysis of the equally weighted COI data resulted in a single MPT with 1724 steps (CI: 0.28, RI: 0.28, RC: 0.08) and is shown in Fig. 4. Different *a priori* weighting of first, second and third codon positions did not result in a resolution better than the equally weighted analysis and such weighting was discontinued in this study.

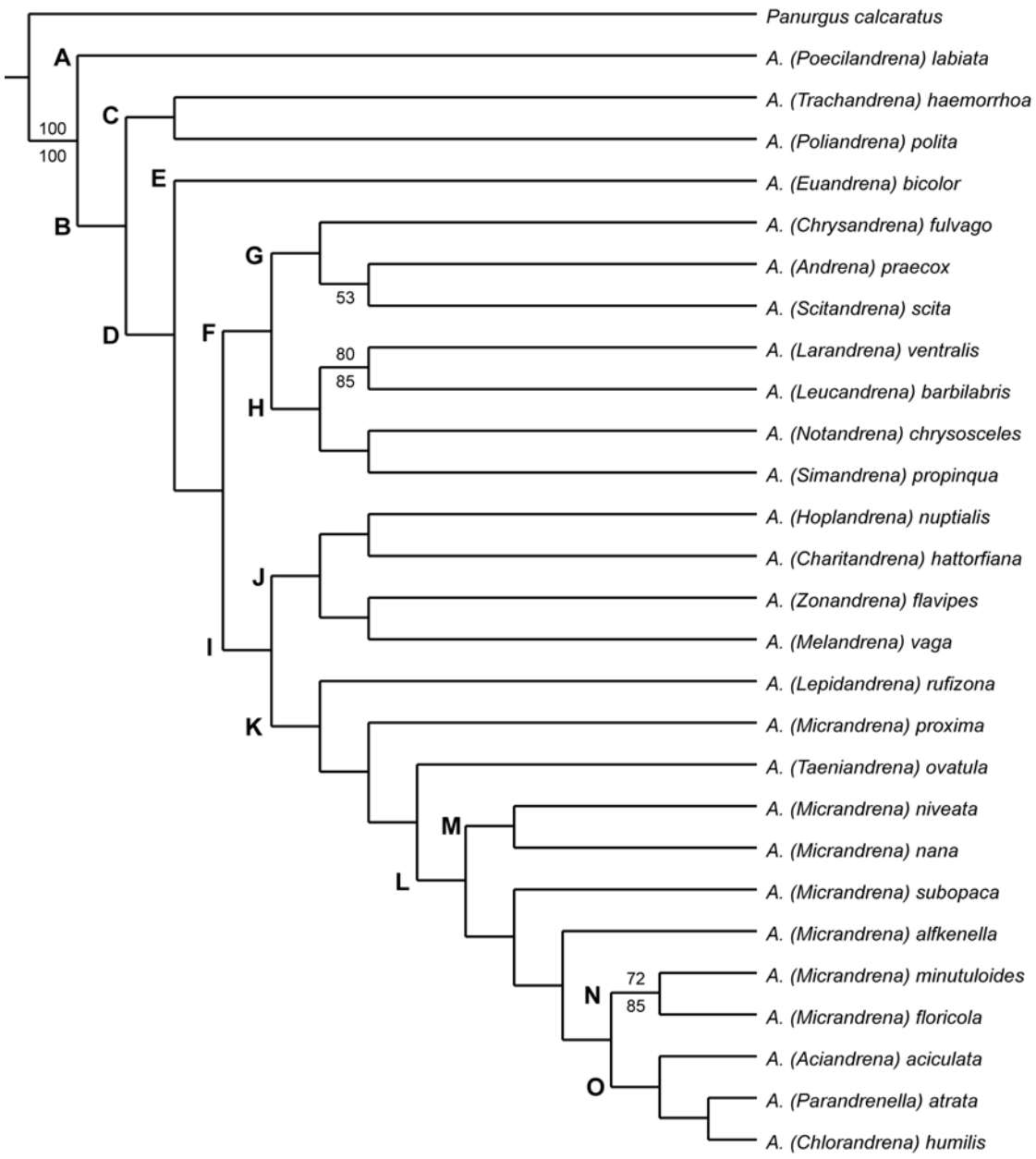

Fig. 4: Single MPT of 1724 steps based on parsimony analysis of unweighted mitochondrial COI data (CI: 0.28, RI: 0.28, RC: 0.08). Bootstrap values are indicated by numbers above, jackknife-values by numbers below branches. **A–O** refer to nodes mentioned in the text.

The cladogram yielded five major lineages: (1) *Poecilandrena*, which is the sister group (node A) to all remaining representatives of subgenera of *Andrena* (node B), (2) a lineage formed by *Trachandrena* and *Poliandrena* (node C) and (3) the *Euandrena* lineage (node E) which shows an isolated position as sister to all remaining subgenera. The latter –again subdivide into the remaining two lineages. (4) A lineage uniting the subgenera *Chrysandrena*, *Andrena* s. str., *Scitandrena*, *Larandrena*, *Leucandrena*, *Notandrena* and *Simandrena* (node F). (5) A lineage combining *Hoplandrena*, *Charitandrena*, *Zonandrena*, *Melandrena*, *Lepidandrena*, *A. (Micrandrena) proxima*, *Taeniandrena*, *Micrandrena*, *Aciandrena*, *Parandrenella* and *Chlorandrena* (node I). Lineage 4 (node F) subdivides into (node G)

Chrysandrena + (*Andrena* s. str. + *Scitandrena*) and (node H) (*Larandrena* + *Leucandrena*) + (*Notandrena* + *Simandrena*). Lineage 5 (node I), however, includes the following two sister clades, nodes J and K. Node J constitutes a monophyletic group uniting (*Andrena* s. str. + *Charitandrena*) + (*Zonandrena* + *Melandrena*). Node K comprises the subgenera *Lepidandrena*, *A. (Micrandrena) proxima*, *Taeniandrena*, six representatives of *Micrandrena*, *Aciandrena*, *Parandrenella* and *Chlorandrena*. This group is made up of three monophyletic groups: *A. (Micrandrena) niveata* + *A. (Micrandrena) nana* (node M), *A. (Micrandrena) minutuloides* + *A. (Micrandrena) floricola* (node N) and *Aciandrena* + *Parandrenella* + *Chlorandrena* (node O).

The following conclusions were made concerning the monophyly of *Micrandrena*, which was one of the main focuses in the present molecular investigation:

The seven representatives of *Micrandrena* (*A. alfkenella, A. floricola, A. minutuloides, A. nana, A. niveata, A. proxima* and *A. subopaca*) included in the present analysis by no means represent a monophyletic group. The separate position of *A. (Micrandrena) proxima* clearly demonstrates the polyphyletic nature of *Micrandrena*. This study clearly supports the thesis of excluding *A. proxima* from *Micrandrena* and regarding it as a member of a different subgenus (Dubitzky & Schönitzer, 2001; Schmid-Egger, in press). Aside from *A. proxima*, all other members of *Micrandrena* are undoubtedly closely related to each other but the group is paraphyletic since it includes representatives from the subgenera *Aciandrena*, *Parandrenella* and *Chlorandrena* (node L).

Support for clades in the MPT using bootstrap and jackknife values was relatively poor (less than 50 %), except the clade defining the monophyly of *Andrena* (100 %), as well as the sister group relationship between *Larandrena* + *Leucandrena* (bootstrap: 69 %, jackknife: 85 %) and *A. (Micrandrena) minutuloides* + *A. (Micrandrena) floricola* (bootstrap: 72 %, jackknife: 85 %). The low support may be attributed to the relatively high degree of homoplasy in the COI data set (CI: 0.28) and to the rather low content of phylogenetically informative characters (34 %) of the sequenced part of COI (see above). Future molecular analyses of *Andrena* therefore should concentrate rather on different DNA fragments, which already have been found suitable for an analysis of bees at the subgeneric level (cf. Danforth, 1999; Larkin, 2002).

Comparison to previous molecular studies

Despite the molecular analysis of nearctic representatives of *Andrena* by Larkin (2002), this study presents the first molecular phylogeny of palearctic representatives of *Andrena*. In her comprehensive molecular study, Larkin analyzed mitochondrial sequence data of COI and COII, as well as nuclear sequence data of the elongation factor 1α. Although her study focused mainly on the nearctic subgenus *Callandrena*, she included representatives from 25 subgenera. Since nine of the 21 subgenera included in the present analysis were also analyzed in Larkin's (2002) study, a comparison between the results is possible to some extent.

Of all analyses conducted by Larkin, her parsimony analysis based exclusively on mitochondrial data shows the greatest similarity to the results of the present molecular study. Thus, on the one hand, the close relationship between *Larandrena*, *Leucandrena* and *Simandrena* as indicated by the present analysis was confirmed in at least one of the 18 MPT yielded by her analysis. On the other hand, in Larkin´s analysis the common clade of subgenera mentioned above also included the subgenera *Melandrena* and *Taeniandrena*, which belong to a different clade in the present analysis. In all analyses of Larkin (see below) *Melandrena* was polyphyletic, even though she only included nearctic representatives of this holarctic subgenus. The monophyly of this group is dubious, especially concerning the combination of nearctic and palearctic species. *Trachandrena* and *Euandrena* were rather isolated with reference to the other seven subgenera in both analyses. The position of *Micrandrena* and *Andrena* s. str., however, clearly differs between Larkin´s study and the present analysis.

Her parsimony analysis based exclusively on nuclear data hardly shows congruence to the present analysis, despite the isolated position of *Trachandrena* with reference to the other eight subgenera and a weak relationship between *Micrandrena* and *Taeniandrena*.

Larkin´s parsimony analysis of combined mitochondrial and nuclear data also supports the relationship of *Larandrena*, *Leucandrena* and *Simandrena*, although again representatives of *Melandrena* are included in the common clade of these subgenera.

Almost no similarities are detectable between the results of Larkin´s maximum likelihood analysis based on combined mitochondrial and nuclear data and results of the MPT in the present analysis. Larkin postulated for example that *Andrena* s. str. is more closely related to *Trachandrena* than to *Leucandrena*, *Larandrena* or *Simandrena*, while the present study shows that *Andrena* s. str. is a member of the sister clade to *Larandrena*, *Leucandrena* and *Simandrena*. Furthermore, the close relationship between *Larandrena* and *Leucandrena* as indicated in the present study was not confirmed by the topology of her maximum likelihood tree, which instead indicate a close relationship between *Leucandrena* and *Melandrena*. *Melandrena*, however, is a member of the sister group to a clade uniting *Micrandrena* and several other strictly palearctic subgenera according to the present analysis. In Larkin´s analysis *Micrandrena* however is more closely related to *Euandrena* than to *Melandrena*. *Euandrena*, again, is considerably isolated in the present cladogram, representing the sister to a large clade combining several strictly palearctic subgenera, as well as *Andrena* s. str., *Larandrena*, *Leucandrena*, *Simandrena*, *Melandrena* and *Micrandrena*. The relative relationship between *Micrandrena* and *Taeniandrena* was the only phylogenetic hypothesis common to both studies.

Comparison to analysis of morphological data

The results of the present molecular analysis are compared in the following to the results of the present cladistic analysis of *Andrena* based on morphological data (chapter 3.2.1). The basal position of *Poecilandrena*, in the molecular analysis, was also observed in the unweighted analysis of morphological data (Figs 1, 2). Yet, the close relationship between *Poecilandrena* and *A. proxima* as postulated in the morphological analyses (Figs 2, 3) was not confirmed in the molecular analysis, where the latter assumes an intermediate position between *Lepidandrena* and *Taeniandrena*, far from *Poecilandrena* (Fig. 4). *Lepidandrena* appeared, however in the morphological analyses, in close association with *Poliandrena* and *Euandrena* (Figs 2, 3). The latter two represent in the molecular analysis either the sister to *Trachandrena* (*Poliandrena*) or the sister to all remaining subgenera except *Poecilandrena*, *Trachandrena* and *Poliandrena (Euandrena)*. *Andrena* s. str., in the morphological analysis, is most closely related to the nearctic subgenera *Archiandrena* and *Anchandrena,* and to the holarctic *Cnemidandrena*, none of which were included into the molecular analysis. Nevertheless in the morphological analysis, *Andrena* s. str. is also relatively closely related to either *Hoplandrena* or *Larandrena* and *Leucandrena* (Figs 2, 3). In the present molecular analysis, however, *Andrena* . str. is most closely related to *Chrysandrena* and *Scitandrena*, while *Hoplandrena* is found to be the sister to *Charitandrena.* On the other hand, *Larandrena* and *Leucandrena*, which comprise a common clade similar to the morphological analysis, constitute the sister group to a common clade of *Notandrena* and *Simandrena*. In the morphological analysis the latter two were closely related to either *Opandrena* (*Notandrena*) or *Zonandrena* (*Simandrena*). The close relationships between *Zonandrena* and *Melandrena*, as well as between *Micrandrena*, *Aciandrena* and *Parandrenella*, however, were obtained in both, the molecular and the morphological, analyses. Surprisingly, *Chlorandrena* is the most derived member of the *Micrandrena*-clade (Fig. 4, node K) in the molecular analysis, while it is closely associated to the subgenera *Ulandrena* and *Platygalandrena* in the morphological analyses (Figs 2, 3), the latter two indeed were not included into the molecular analysis. Nevertheless in the morphological analyses *Chlorandrena* never occurred in the vicinity of *Micrandrena*, *Aciandrena* or *Parandrenella*.

To sum up, a comparison of the results of the molecular and morphological analyses shows that both analyses support the following conclusions: (1) *Poecilandrena* is a rather ancestral subgenus of *Andrena*. (2) The subgenera *Larandrena* + *Leucandrena* as well as (3) *Zonandrena* + *Melandrena* comprise a common clade each and (4) the subgenera *Micrandrena*, *Aciandrena* and *Parandrenella* seem to be closely related to each other.

Despite these similarities, a comparison of the results of the morphological and molecular analyses cannot be made without reservations, since the taxa included are not identical for each analysis. Subsequent analyses may possibly better compare the data sets, for example, by running an additional morphological analysis reduced to the same taxa used in the molecular analysis. Likewise, an analysis combining the molecular and morphological data may be

valuable. A similar procedure could also be applied using the taxa in Larkin's (2002) analyses.

3.2.3 New taxa of the genus *Andrena*

During the course of this investigation on the phylogeny and morphology of *Andrena* numerous species and undescribed specimens were examined, several palearctic species were recognized as new to science. In addition, three new palearctic subgenera of *Andrena* were proposed. In particular, the areas of Central Asia and Asia Minor, as well as the highlands of Taiwan (cf. chapter 4.2.3), have been insufficiently studied, and they harbor not only many new taxa of *Andrena* but also numerous undescribed species from other groups of bees (Dubitzky, 2004a, b; Dubitzky & Kuhlmann, 2004). Descriptions of the following three subgenera and ten species of *Andrena* are given below:

Calcarandrena subgen. n., *Hamandrena* subgen. n., *Platygalandrena* subgen. n.; *A. (Carandrena) planti* sp. n., *A. (Euandrena) yangi* sp. n., *A. (Habromelissa) nantouensis* sp. n., *A. (Larandrena) susanneae* sp. n., *A. (Leucandrena) cheni* sp. n., *A. (Micrandrena) taiwanensis* Dubitzky 2002, *A. (Pallandrena) christineae* sp. n., *A. (Pallandrena) scheuchli* sp. n., *A. (Simandrena) heinzi* sp. n. and *A. lehmanni* Schönitzer & Dubitzky 2002.

Calcarandrena subgen. n.

Type species: *Andrena gamskrucki* Warncke, 1965

Structure. Small to medium-sized bees (BL: 8.5-10.2 mm (female), 8.3-10.1 mm (male)). Mandibles bidentate and of normal length in both sexes. Condylar lamella of female mandible distinctly developed. Galea slightly convex on outer margin. Apex of galea rounded. PMX slightly longer than galea. Glossa short. PLB truncate, about as long as glossa. Prementum strongly flattened laterally, with distinct median keel ventrally. Bristles of subgenal coronet large, developed along inner and hind margin of paramandibular process. Bristles of paramandibular area distinctly developed but smaller than bristles of subgenal coronet. PLR rectangular with distinct median emargination along front margin. Disc of clypeus slightly flattened in females, more or less convex in males. Malar space absent. FOV more or less oval, flat, weakly depressed, about 1 to 2 times as wide as OD. Hind margin of female vertex narrowly rounded to slightly edged. Female vertex slightly wider than OD. Male AS3 about 1.6 times as long as wide and about 2 times as long as AS4. Lateral parts of pronotum rounded. Dorsolateral angle of pronotum absent. Pronotal groove of female distinctly developed. Propodeal triangle tesselate to granulate, rarely with few weak wrinkles basally. DLP granulate similar in structure to propodeal triangle. LP finely tesselate, without wrinkles and indistinct, weak punctation. Apex of mid and hind tibial spurs strongly curved, hook-shaped (similar Fig. 15F). Inner tibial spur of hind legs distinctly broadened for nearly whole length. Femur of hind legs slightly concave on posterior side, with distinct dorsoposterior carina and row of long bristles. Claws of female bidentate, with distinct inner tooth. Forewing

with three submarginal cells and cu-V-vein meeting M+Cu-vein at intersection of M- and Cu-vein to slightly behind M-vein. Basal part of T1 with more or less distinct longitudinal rim medially. Pygidial plate of female flat, without triangular raised area in the middle. Male pygidial plate absent. Male S7 with two distinct lobes medioapically. Male S8 flat in profile, without deep emargination along apical margin. Dorsal lobe of gonocoxite developed, narrowly rounded apically. Inner margins of dorsal lobes more or less parallel sided. Digitus of volsella truncate and small, hardly visible behind cuspis. Gonoforceps about as broad as dorsal base, with ventral margin distinctly narrower than basal part in profile. Penis valve more or less triangular, distinctly shorter than gonoforceps and broadly rounded apex. Lateral lamella of penis valve absent.

Integument colour. Black to blackish brown except a yellowish clypeus in males of *A. eburnea* and *A. impasta*.

Pubescence. Galea, stipes and ventral side of prementum with sparse pubescence of normal simple to weakly branched hairs. Pubescence of thorax medium-long to long. LP with regular pubescence of branched hairs, similar to other parts of thorax. Propodeal corbicula present, with broad and dense anterior hair fringe, consisting of short to medium-long straight hairs and a dense, medium-long to long dorsoposterior hair fringe of weakly branched, straight to slightly curled hairs. Flocculus of trochanter of hind legs incomplete, only distal hairs being long and curled. Anterior hair fringe of hind femur strongly developed, dense, composed of branched hairs of the "*hattorfiana*"-type. Scopa of hind tibia of female dense, with weakly bilateral branched hairs ("*curvungula*"-type). Inner side of hind tibia with pubescence of simple hairs. Disc of T with sparse pubescence of short branched hairs.

Diagnosis. Species belonging to *Calcarandrena* were originally assigned to the subgenus *Lepidandrena* (Warncke, 1968, Gusenleitner & Schwarz, 2002). In the present analyses *Calcarandrena* is the sister taxon to *Osychnyukandrena*. *Calcarandrena* can be clearly distinguished from *Osychnyukandrena* by the presence of a row of long bristles on the female hind femur, the presence of simple hairs on the inner side of female hind tibia and the different shape of male genitalia. From *Lepidandrena* the new subgenus can easily be separated by the different shape and structure of the galea, the strongly hooked tibial spurs of mid and hind legs and the different shape of male genitalia.

Comments. Bees of the subgenus are typical spring species and fly from end of March to end of April.

Etymology. Prefix *Calcar-* from the Latin calcar, which means spur, in combination with *Andrena*, the name of the higher taxon. The name refers to the strongly hooked tibial spurs of mid and hind legs found in the subgenus.

Included species. *A. eburnea* Warncke, 1975 **stat. n.**, *A. gamskrucki* Warncke, 1965, *A. impasta* Warncke, 1975 **stat. n.**.

Hamandrena subgen. n.

Type species: *Andrena nasuta* Giraud, 1863

Structure. Medium-sized to large bees (BL: 10.7-15.5 mm (female), 9.2-13.6 mm (male)). Mandibles slightly elongate in both sexes. Male mandible bidentate, distinctly curved downward in lateral view. Condylar lamella of female mandible slightly developed. Galea slightly convex rounded. PMX distinctly shorter than galea. Glossa strongly elongate (Fig. 9E). PLB slender, about as long as glossa (Fig. 9E). Prementum ventrally rounded. Bristles of subgenal coronet, weak indistinct, developed along inner and hind margin of paramandibular process. Bristles of paramandibular area indistinct, minute. PLR rectangular with distinct transverse wrinkles. Disc of clypeus more or less rounded in both sexes. Malar space distinctly elongate, about as wide as antennal flagellum. FOV more or less oval, completely deeply depressed, about 2 to 3 times as wide as OD. Hind margin of female vertex more or less rounded. Female vertex about twice as wide as OD. Male AS3 about 2 times as long as wide and about 2 times as long as AS4. Lateral parts of pronotum carinate. Dorsolateral angle of pronotum distinctly developed. Pronotal groove of female absent. Propodeal triangle granulate, with fine wrinkles basally. DLP granulate similar in structure to propodeal triangle. LP finely tesselate, without wrinkles and indistinct, weak punctation. Apex of all tibial spurs more or less straight, pointed. Inner tibial spur of hind legs slender and straight, not broadened basally. Femur of hind legs regularly rounded all over, without any carinae or bristles. Claws of female bidentate, with strong and distinct inner tooth. Forewing with three submarginal cells and cu-V-vein meeting M+Cu-vein) at intersection of M- and Cu-vein to slightly before M-vein. Basal part of T1 with distinct longitudinal rim medially. Pygidial plate of female flat, without triangular raised area in the middle. Male pygidial plate absent. Male S7 with two weak lobes medioapically. Male S8 flat in profile, without deep emargination along apical margin. Dorsal lobe of gonocoxite developed, more or less broadly rounded apically. Inner margins of dorsal lobes more or less parallel sided. Digitus of volsella truncate and small, hardly visible behind cuspis. Gonoforceps distinctly broadened apically, with ventral margin being distinctly narrower than basal part in profile. Penis valve more or less triangular, distinctly shorter than gonoforceps and broadly rounded apex. Lateral lamella of penis valve absent.

Integument colour black to blackish brown.

Pubescence. Galea, stipes and ventral side of prementum with posteriorly bent, hooked bristles in female and normal pubescence in male. Pubescence of thorax medium-long to long. LP with regular pubescence of branched hairs, similar to other parts of thorax. Propodeal corbicula absent. Flocculus of trochanter of hind legs absent. Anterior hair fringe of hind femur weakly developed, sparse composed of simple hairs. Scopa of hind tibia of female sparse, with simple hairs. T with medium-long to long sparse branched hairs.

Diagnosis. Species belonging to *Hamandrena* undoubtedly can be recognized by the posteriorly bent, hook-shaped bristles (Fig. 9C) on the galeal blade, stipes and prementum in the females, a feature which is found to be apomorphic for this subgenus.

Comments. *Hamandrena* was found to be closely related to *Troandrena* within the unweighted analysis. Bees of this subgenus are flying from end of April to end of June. *A. nasuta* and *A. teunisseni* seem to be oligolectic on *Anchusa* (Boraginaceae).

Etymology. Prefix *Ham-* from the Latin hamus, which means hook, in combination with *Andrena*, the name of the higher taxon. The name refers to the posteriorly bent, hook-shaped bristles (Fig. 9C) on the galeal blade, stipes and prementum of females within this subgenus.

Included species. *A. nasuta* Giraud, 1863, *A. stepposa* Osytshnjuk, 1985, *A. teunisseni* Gusenleitner, 1998.

Platygalandrena subgen. n.

Type species: *Andrena fedtschenkoi* Morawitz, 1876

Structure. Medium to large-sized bees (BL: 9.8-17.2 mm (female), 8.1-18.9 mm (male)). Mandibles bidentate and of normal length in both sexes. Condylar lamella of female mandible distinctly developed. Galea strongly dorsoventrally flattened, with distinct coarse punctation (Figs 9A, B). Apex of galea rounded. PMX strongly truncate, about as long as galea; PMX 2 distinctly shorter than PMX 1 (Figs 9A, B). Glossa short. PLB truncate, about as long as glossa. Prementum ventrally rounded. Bristles of subgenal coronet large, developed along inner and hind margin of paramandibular process. Bristles of paramandibular strongly reduced, minute to indistinct. PLR rectangular without distinct median emargination along front margin. Disc of clypeus more or less convex rounded in both sexes. Malar space absent. FOV more or less oval, flat, weakly depressed, about 3 times as wide as OD. Hind margin of female vertex narrowly rounded to slightly edged. Female vertex at least two times as wide as OD. Male AS3 about 2 times as long as wide and 2.3 to 2.6 times as long as AS4. Lateral parts of pronotum rounded. Dorsolateral angle of pronotum absent. Pronotal groove of female distinctly developed. Propodeal triangle tesselate to granulate, rarely with few weak wrinkles basally. DLP granulate similar in structure to propodeal triangle. LP finely tesselate, without wrinkles but distinct, coarse punctation. Apex of mid and hind tibial spurs truncate to knoblike. Inner tibial spur of hind legs more or less slender to distinctly broadened basally. Femur of female hind legs more or less concave on posterior side, dorsoposterior carina more or less strongly developed to absent. Bristles on female hind femur absent. Claws of female simple, scarcely with minute inner tooth (*A. tecta*). Forewing with three submarginal cells. Cu-V-vein of forewing meeting M+Cu-vein at or slightly behind intersection of M- and Cu-vein (*A. biguttata*, *A. combaella*, *A. eburneoclypeata*, *A. fedtschenkoi*, *A. leucorhina*, *A. mikhaili*, *A. osychniukae*) to strongly behind M-vein (*A. armeniaca, A. carinata, A. elegans, A. tecta*). Basal part of T1 with more or less distinct longitudinal rim medially. Pygidial plate of female flat to slightly convex, without raised triangular area in the middle.

Male pygidial plate absent. Male S7 without or with weak single lobe medioapically. Male S8 flat in profile, with deep emargination along apical margin. Dorsal lobe of gonocoxite developed, narrowly to broadly rounded apically. Digitus of volsella more or less large and distinct. Ventral margin of gonoforceps more or less broadened basally in profile. Penis valve more or less triangular, distinctly shorter than gonoforceps, flat to strongly protuberant in profile. Lateral lamella of penis valve absent to slightly indicated.

Integument colour. Black or blackish brown to reddish brown (*A. fedtschenkoi).* POA and clypeus of females yellowish to ivory (*A. armeniaca, A. eburneoclypeata, A. fedtschenkoi,*) or dark coloured (*A. biguttata, A. combaella, A. elegans, A. leucorhina, A. mikhaili, A. osychniukae, A. tecta*). POA and clypeus of males yellowish to ivory coloured. Marginal zone of T often brownish transparent.

Pubescence. Galea and stipes with sparse pubescence of normal simple to weakly branched hairs. Ventral side of prementum with dense brush of weakly branched hairs. PMX (esp. PMX 1-3) with conspicuous, more less dense pubescence of strong, simple hairs. Scutum, scutellum and metanotum with short to scale-like, branched hairs. LP with regular pubescence of long, simple to slightly branched hairs. Propodeal corbicula present, without anterior hair fringe consisting of short to medium-long straight hairs and a dense, medium-long to long Dorsoposterior hair fringe of propodeal corbicula medium-long, dense, with straight to slightly curled, strongly branched hairs. Flocculus of trochanter of hind legs complete, all hairs long and curled. Anterior hair fringe of hind femur strongly developed, dense, composed of simple to branched hairs of the "*humilis*"-type. Scopa of hind tibia of female long and rather dense, consisting of weakly bilateral branched hairs ("*curvungula*"-type). Inner side of hind tibia with pubescence of simple hairs. T with dense pubescence of short branched hairs, forming pale and distinct apical hair bands on marginal zone.

Diagnosis. Species belonging to *Platygalandrena* originally were placed in the subgenus *Ulandrena* (Warncke, 1968, Gusenleitner & Schwarz, 2002). In the present analyses *Platygalandrena* is the sister taxon either to *Chlorandrena* or *Ulandrena. Platygalandrena* can be most clearly distinguished from *Chlorandrena* and *Ulandrena* by the strongly dorsoventrally flattened and somewhat coarsely punctured galea, the more or less truncate PMX and PLB and the conspicuous, strong pubescence of PMX.

Comments. Adult bees of this subgenus are active from end of March to July.

Etymology. Prefix *Platy-* from the Greek πλατύ, which means flattened, in combination with gal- for galea and *Andrena*, the name of the higher taxon. The name refers to the distinctly dorsoventrally flattened galea of this subgenus.

Included species. *A. armeniaca* Popov, 1940, *A. biguttata* Friese, 1923, *A. carinata* Morawitz, 1877, *A. combaella* Warncke, 1966, *A. eburneoclypeata* Lebedev, 1929, *A. elegans* Giraud, 1863, *A. fedtschenkoi* Morawitz, 1876, *A. leucorhina* Morawitz, 1876, *A. mikhaili* Osytshnjuk, 1982, *A. osychniukae* Osytshnjuk, 1977, *A. tecta* Radoszkowski, 1876.

***Andrena (Carandrena) planti* sp. n.**

Male. BL: 6.8 mm - 7.4 mm. FWL: 5.3 mm.

Structure. Head nearly round, 1.1 times broader than long in frontal view. Galea truncate, tesselate and dull, without distinct punctation. PMX 3-6 distinctly protruding apex of galea. Mandibles extremely long, falcate, without preapical tooth. PLR small, trapezoid, smooth and shiny. Clypeus smooth and shiny, about 1.3 times as broad as long with distinct punctation being dense along margins (<1) and more dispersed on disc (>1.5). Apical part of clypeus strongly elongate, protruding ventrally. Front margin of clypeus slightly curled up, concave, only 0.3 times as wide as maximum width of clypeus. POA smooth and shiny, with distinct, dense punctation (<1) except area along inner margin of compound eye which has minute and dispersed punctation. SCA distinctly tesselate, dull to weakly shiny, with indistinct punctation. Frons weakly shiny, with weak longitudinal ridges and indistinct punctation (≥1) between. GA slightly tesselate, shiny, with indistinct weak punctation (1), about as wide as compound eye in lateral view. GA distinctly concave when seen dorsally. GA with strong, broad triangular projections ventrally. Vertex slightly tesselate, weakly shiny, with indistinct dispersed punctation (≥1). Distance from hind margin of lateral ocellus to hind margin of vertex 1.4 times as wide as diameter of lateral ocellus. Hind margin of vertex strongly concave in dorsal view, weakly carinate in the middle. AS 3 about 2 times as long as broad, as long as following two AS together. AS 4 truncate, slightly broader (1.2 times) than long. AS 5-12 slightly longer than broad (AS 5-7: 1.2 times; AS 8-12: 1.3 times), AS 13 1.6 times longer than broad. Pronotum strongly tesselate, dull to weakly shiny, with two distinct humps dorsolaterally. Scutum and scutellum smooth and shiny with dispersed minute punctation (>1) on disc. Metanotum strongly tesselate, dull. PT strongly tesselate to granulate all over. DLP, LP and declivous part of propodeum strongly tesselate, dull to weakly shiny. Mesepisterna tesselate weakly shiny, with indistinct punctation. Claws bidentate. T polished, shiny, with minute and dispersed punctation (> 2) on disc. S weakly tesselate, shiny, with indistinct minute punctation. Apical margin of S 6 strongly curled ventrally. Structure of S7, S8 and genitalia as in Figs 16J, 18F, and 22E.

Integument colour. Mandibles black, apically reddened. Clypeus ivory except black area along front margin and blackish C-shaped maculation along basal margin. POA with small ivory maculation apically. AS blackish brown except AS 5-13 bright orange on underside. Other parts of head, as well as thorax, dark green to blue metallic. Coxa to femur of all legs dark brownish, tibia and tarsal segments bright yellowish brown. Spurs bright yellowish grey transparent. Claws yellowish grey basally, brownish apically. Veining of wings, as well as stigma bright brownish. T blackish brown on disc, bright brownish transparent on marginal zone. S uniformly brownish.

Pubescence. Head and thorax with medium-long to long greyish white to yellowish white hairs. Legs with sparse greyish white pubescence of varying length. T with greyish white pubescence of short hairs forming weak incomplete hairbands along apical margin. S 2-5 with

pale, extremely short and weak pubescence on disc and complete whitish hairbands along apical margin. Apical margin of S 6 with dense brush of short, bright yellowish hairs.

Female. BL: 7.0 mm. FWL: 5.7 mm.

Structure. Head round similar to male in frontal view. Proboscis and PLR similar to male. Clypeus 1.6 times as broad as long, distinctly tesselate, shiny. Punctation of clypeus more regular than in male (>1). Front margin of clypeus similar to male, 0.5 times as wide as maximum width of clypeus. FOV nearly parallel sided, becoming slightly more narrow at lower margin, reaching from hind margin of compound eye to middle of antennal socket. Maximum width of FOV 1.5 times OD. Vertex weakly rounded, distance from hind margin of lateral ocellus to hind margin of vertex similar to male. GA as wide as compound eye in lateral view, weakly tesselate with indistinct minute punctation. AS 3 about 2.2 times as long as broad, slightly longer (1.2 times) than following two AS together. AS 4-11 about as long as broad, AS 12 1.4 times longer than broad. Pronotum similar to male but dorsolateral humps only weakly developed, forming indistinct broadly rounded carina. Scutum shiny, distinctly tesselate anteriorly, polished on disc, with more dense and distinct punctation (1) than in male. Scutellum similar to male but with more dense and distinct punctation (1). Metanotum, PT, DLP, LP and declivous part of propodeum, as well as mesepisterna similar to male. Claws with minute inner tooth, inconspicuously bidentate. T similar to male, pygidial plate shiny, with elevated triangular area in the middle. S weakly tesselate, shiny, with indistinct punctation.

Integument colour. Head and thorax dark green metallic except following structures: Mandibles black, apically reddened. Upper part of clypeus with reddish to yellowish oily shimmer. AS blackish brown except AS 6-12 bright orange on underside, bright brownish dorsally. Coxa to femur of all legs dark brownish. Tibia of front and mid legs brownish, hind tibia brownish with bright yellowish brown maculation apically. Tarsal segments of all legs conspicuously yellow. Spurs bright yellowish grey transparent. Claws yellowish basally, reddish brown apically. Basitibial plate reddish brown. Tegulae yellowish brown transparent. Veins of wings, as well as stigma, bright yellowish brown, distinctly paler than in male. T blackish brown with weak metallic gleam on disc, bright brownish transparent on marginal zone. Pygidial plate bright reddish brown basally, blackish brown apically. S uniformly blackish brown.

Pubescence. Head and thorax with pubescence similar to male but distinctly shorter, esp. scutum and scutellum with conspicuously short hairs. LP with few long and simple hairs intermixed with extremely short ones. Femoral, tibial and basitarsal scopa of hind legs consisting of simple hairs. Pubescence of T similar to male but distinctly longer and more dense. Prepygidial, as well as pygidial fimbria, with bright yellowish grey hairs. S with inconspicuous short (disc) to medium-long (apical margin) greyish pubescence.

Diagnosis. *Andrena* (*Carandrena*) *planti* sp.n. is most similar to *A.* (*Carandrena*) *deserta* Warncke, 1974 from which it can be distinguished by the following characters (character states of *A. deserta* in brackets): Mandible of males without preapical tooth (with minute

preapical tooth); clypeus elongate, 1.6 times (female) and 1.3 times (male) as broad as long (clypeus normally long, 1.8 (female) and 1.7 times (male) as broad as long); GA of male with strong, broad triangular projection ventrally (without projection ventrally); POA of male with ivory maculation apically (POA without ivory maculation); AS 3 slender, about 2 times as long as broad, 0.72 times as long as scape (AS 3 truncate, only 1.3 times as long as broad, 0.38 times as long as scape); distance from hind margin of lateral ocellus to hind margin of vertex 1.4 times as wide as diameter of lateral ocellus (only 0.83 times as wide as diameter of lateral ocellus); FOV of females hardly narrowed below (strongly narrowed below); claws of female with minute, hardly visible inner tooth (claws distinctly bidentate); T of females with weak metallic gleam (T with distinct metallic gleam); T smooth (distinctly tesselate); pygidial plate of female with elevated triangular area in the middle (pygidial plate flat, without elevated area in the middle).

Etymology. This species is named in honor of my dear friend John Plant for his great knowledge and contributions to bee systematics and morphology. His valuable assistance has been enormously helpful in particular for my understanding of bee systematics and cladistic work.

Type material. Holotype: ♂, Turkmenistan, Umg. Aschghabat, 22.IV.1996, ex coll. Grünwaldt (ZSM). Paratypes: 1♂, 1♀, same data as Holotype (ZSM, CAD).

Andrena (Euandrena) yangi sp. n.

Female. BL: 7.9-9.1 mm (8.4 mm). FWL: 6.8-7.3 mm (7.0 mm).

Structure. Head nearly round, only 1.14 times broader than long in frontal view. Galea shiny to weakly dull, densely tesselate, without distinct punctation. Mandibles bidentate. PLR large, trapezoid, smooth and shiny, about 2 times broader than long. Apical margin of PLR about half as wide as basal margin, straight to weakly emarginate in the middle. Clypeus about 1.5 times broader than long, with regular (1) large punctation on disc. Basal part of clypeus densely tesselate, dull becoming more and more smooth and shiny apically. POA tesselate, dull to weakly shiny with dense punctation (<1). SCA tesselate, dull with extremely dense, inconspicuous small punctation. Frons dull to weakly shiny with distinct longitudinal notches between dense punctation. Vertex finely tesselate, dull to weakly shiny except a smooth and shiny area behind upper margin of compound eyes. FOV especially upper part extremely broadened, nearly reaching LO along inner margin. Extension of FOV reaching from hind margin of LO to lower margin of antennal insertion. GA broad, slightly broader than compound eye in lateral view, tesselate, shiny with indistinct punctation. Scape distinctly longer than following three segments together, densely tesselate on ventral side. AS 3 about 2 times as long as broad, distinctly longer than AS 4 and 5 together. AS 4 and 5 broader than long, AS 6-9 about as long as broad, AS 10 and 11 slightly longer than broad. AS 12 about 2 times as long as broad. Pronotum strongly tesselate, dull to weakly shiny, with inconspicuous weak punctation. Scutum strongly tesselate, dull (anterior part) to weakly shiny (posterior

part) with distinct, large punctation (≤1). Anterior part of scutum with distinct smooth and shiny median line. Scutellum tesselate, dull to weakly shiny with indistinct dispersed punctation (≥1). Metanotum strongly tesselate to granulate, dull. PT granulate, dull to weakly shiny, with few weak wrinkles basally. DLP distinctly more shiny than PT, weakly granulate, with inconspicuous punctation (1). LP weakly tesselate, shiny with dispersed punctation. Mesepisterna tesselate, dull to weakly shiny, with indistinct punctation. Tegulae weakly tesselate, distinctly shiny. Claws of all legs distinctly bidentate. T tesselate, with indistinct flat punctation (1). Dorsolateral convexity of T weakly developed. Pygidial plate with distinctly elevated, apically pointed triangular area in the middle. S densely tesselate shiny to weakly dull. S 2 with completely distinct punctation (1), S 3-5 with impunctate basal zone on disc and distinct punctation (1) laterally. S 6 triangular, with large punctation apically.

Integument colour. Proboscis dark brownish. Mandibles apically dark reddened. AS 5-12 black dorsally, dark brownish on underside. Other parts of head, as well as thorax blackish. Tegulae brownish transparent. Veins of wings yellowish brown to dark brownish, stigma brownish. Front and middle legs black to blackish brown. Coxa to femur of hind legs black to blackish brown, tibia and basitarsus bright yellowish brown to orange. Distal tarsal segments brownish. Claws of all legs yellowish brown basally, dark reddish apically. T 1-5 black, except yellowish brown transparent marginal zone. Elevated triangular area of pygidial plate reddish brown, except blackish brown tip. Marginal zone of pygidial plate apically blackish brown, basally slightly reddish brown. S blackish except yellowish brown transparent marginal zone.

Pubescence. Labrum with medium-long yellowish brown hairs. Clypeus along front margin with medium-long to long yellowish brown hairs, on disc nearly bare, area along lateral and basal margin with yellowish grey pubescence of medium-long to long branched hairs. POA, SCA, dorsal side of scape, as well as main parts of vertex and GA with yellowish grey, long hairs. Pubescence along inner margin of FOV, main parts of frons and area along upper and hind margin of compound eyes consisting of dark brownish to blackish brown hairs. FOV reddish brown, when seen from above. Thorax with bright yellowish grey pubescence, especially long on scutellum and metanotum. PT bare, DLP with yellowish grey hairs. Dorsal fringe of propodeal corbicula with long, branched yellowish grey hairs. LP with few simple, yellowish grey hairs. Pubescence of legs mainly yellowish grey. Flocculus of trochanter of hind legs rather short, sparse. T 1 with long, sparse pubescence of greyish hairs. T 2-4 with greyish hairs, hairs longest and most dense on marginal zone, forming distinct apical hair fringes. Prepygidial (T 5) and pygidial (T 6) fimbria brownish. S 2-6 with sparse yellowish grey pubescence forming weak fringe along apical margin.

Male. BL: 6.8-9.0 mm (7.8 mm). FWL: 5.7-6.6 mm (6.2 mm).

Structure. Head oval, 1.2 times broader than long in frontal view. Proboscis similar to female. Mandibles long, falciform, distinctly bidentate. PLR large and shiny, 1.2 times broader than long. Front margin of PLR with weak emargination in the middle. Clypeus

similar to female, but distinctly more shiny especially in lower part. POA similar to female but more shiny. GA about 1.3 times as wide as compound eye seen in profile. Vertex slightly longer than in female, distance from hind margin of LO to hind margin of vertex distinctly wider than OD. Other parts of head similar to female. Scape nearly as long as following three segments together. AS 3 nearly 2 times as long as broad, as long as AS 4 and 5 together. AS 4 slightly shorter than broad, AS 5 as long as broad. AS 6-12 distinctly longer than broad, AS 13 about 2 times as long as broad. Thorax similar to female. T less tesselate than in female, therefore more smooth and shiny, with minute punctation. S tesselate, shiny with large distinct punctation. S 7 and 8 as shown in Figs 16M and 19A. Male genitalia as in Fig. 23B.

Integument colour. Mandibles apically reddened. Antenna completely black. Apical part of tibia and basitarsus of hind legs mostly bright yellowish brown. All other parts of body black to blackish brown.

Pubescence. Head with long greyish to yellowish grey pubescence except row of brown to blackish brown hairs around compound eye. Pubescence of thorax less colourful than in female, more greyish. Pubescence of T greyish, more sparse and shorter than in female, only fresh animals with indication of apical hairbands. S with sparse, short to medium-long greyish hairs forming weak apical fringes in the middle.

Diagnosis. The new species is most similar to *A. (Euandrena) takachioi* Hirashima, 1964 from which it can be distinguished by following characters (characters of *A. takachioi* given in brackets): Female. FOV extremely broad, distance between LO and FOV ≤ 0.5 times OD (FOV distinctly narrower). Vertex strongly tesselate, dull to weakly shiny (weakly tesselate, distinctly shiny). Structure of DLP as fine or even finer than those of PT, without rugous punctation (structure of DLP distinctly stronger than PT, with strong rugous punctation). Propodeal triangle granulate, with short and distinct wrinkles basally (granulate, partly extremely fine rugously structured). T strongly tesselate with inconspicuous, weak punctation (weakly tesselate, more shiny, with distinct punctation). Hind tibia bright yellowish brown to orange (blackish brown). Frons and POA with distinct brown pubescence (pubescence yellowish grey). Pubescence of scutum, scutellum and metanotum extremely pale, bright yellowish grey to grey (pubescence distinctly yellowish). Male gonostylus long (short).

Etymology. This species is named in honor of Prof. Dr. Jeng-tze Yang for his valuable contributions to the insect taxonomy of Taiwan and his generous support during two collecting trips of the author on Taiwan.

Type material. Holotype: ♀, Central Taiwan (ROC), Hualien Hsien, Tayuling, 2560 m, 12.-15.IX.1980, leg. K. S. Lin & C. H. Wang (TARI). Paratypes: 1 ♂, same data as holotype; 1 ♀, Central Taiwan (ROC), Nantou Hsien, Tsuifeng, 2300 m, VIII.1984, Malaise trap, leg. K. S. Lin & K. C. Chou (TARI); 1 ♂ Central Taiwan (ROC), Nantou Hsien, Tsuifeng, 2300 m, 27.VIII.1981, leg. L. Y. Chou & S. C. Lin (TARI); 1 ♂ Central Taiwan (ROC), Nantou Hsien, Tsuifeng, 2300 m, 1.-3.VIII.1981, leg. T. Lin & W. S. Tang (TARI); 1 ♀, Central Taiwan (ROC), Nantou Hsien, Tsuifeng, 2300 m, IX.1984, Malaise trap, leg. K. S. Lin & K.

C. Chou (TARI); 1 ♀, Central Taiwan (ROC), Nantou Hsien, Tsuifeng, 2300 m, XI.1984, Malaise trap, leg. K. S. Lin & K. C. Chou (TARI); 1 ♀, Central Taiwan (ROC), Nantou Hsien, Tsuifeng, 2300 m, IX.1985, Malaise trap, leg. K. S. Lin & K. C. Chou (TARI); 1 ♂ Central Taiwan (ROC), Nantou Hsien, Tsuifeng, 2300 m, 12.-14.IX.1984, leg. K. S. Lin & S. C. Lin (TARI); 1 ♀, Central Taiwan (ROC), Nantou Hsien, Tungpu, 1200 m, IX.1985, Malaise trap, leg. K. S. Lin (TARI); 1 ♂, Central Taiwan (ROC), Nantou Hsien, Meifeng, 2150 m, XI.1984, Malaise trap, leg. K. S. Lin & K. C. Chou (TARI).

***Andrena (Habromelissa) nantouensis* sp. n.**

Male. BL: 8.6mm. FWL: 5.9 mm.

Structure. Head oval, about 1.3 times broader than long in frontal view. Mandibles long, falcate with distinct preapical tooth. PLR rectangular, smooth and shiny, distinctly protruding front margin of clypeus (Fig. 6F). Clypeus shiny, about 2 times as broad as long with distinct punctation (>1). Disc of clypeus strongly flattened to slightly concave, weakly tesselate. POA on lower part smooth and shiny, with distinct, dense punctation (<1) and oblique honeycombed punctation (<0.3) on tesselate and dull upper part. SCA dull, tesselate to slightly wrinkled with indistinct weak punctation. Frons dull to weakly shiny, with strong longitudinal notches and large honeycombed punctation. GA smooth and shiny, with weak dispersed punctation (>1), about 1.4 times broader than compound eye in lateral view (Fig. 6F). Lower part of hind margin of GA nearly rectangular arcuate, forming a weak lamella apically. Vertex behind ocelli rugously tesselate, dull, with inconspicuous weak punctation. Lateral parts of vertex becoming more and more smooth and shiny, similar to GA. Hind margin of vertex strongly concave, weakly carinate in the middle. AS 3 extremely short, only 1.3 times as long as broad and only 1.1 times longer than AS 4. AS 4-AS 12 about 1.4 times longer than broad, AS 13 about 2 times as long as broad. Pronotum strongly tesselate, dull, laterally distinctly carinate. Scutum with large distinct punctation (<1), weakly tesselate near front margin, smooth and shiny on disc. Scutellum smooth and shiny, with irregular strong punctation. Metanotum slightly tesselate, weakly dull to shiny. PT strongly wrinkled basally, nearly smooth and shiny apically. DLP, LP and declivous part of propodeum tesselate, dull to weakly shiny. Mesepisterna with distinct large punctation, strongly tesselate and dull on upper part, nearly smooth on lower part. Tegulae smooth and shiny. Veins 1m-cu and 2m-cu respectively joining 2nd and 3rd submarginal cell at distal apex. Legs, especially hind legs extremely slender. Basitarsus of hind legs about 0.8 times as long as tibia. Claws bidentate. T polished, shiny, disc with distinct punctation (≤ 1), more dispersed (≥1) on T 1. Marginal zone nearly impunctate. S weakly tesselate, shiny, with inconspicuous punctation, punctation most dense apically. Structure of S 8 and genitaliaas in Figs 19B, 23C.

Integument colour. Mandibles black, apically reddened. Clypeus ivory except black front margin and two triangular brownish maculations. Antenna blackish brown on both sides. Other parts of head, as well as thorax black to blackish brown. Legs dark brownish, spurs

yellowish grey transparent. Claws yellowish grey basally, reddish brown apically. Tegulae dark brownish transparent, wings bright brownish transparent. Veins of wings and stigma brownish. T uniformly blackish brown, S dark brownish.

Pubescence. Head with mainly short to medium-long blackish brown hairs, except bright yellowish grey hairs on GA and hind margin of vertex. Thorax with medium-long to long rather sparse pubescence of bright yellowish grey hairs except blackish brown hairs on scutellum and small region below insertion of wings. Legs with yellowish grey hairs basally (coxa to femur) and brownish hairs apically (apical part of femur to tarsi). T 1-4 with inconspicuous sparse pubescence of mainly short brownish hairs. T 5 and 6 with rather dense pubescence of medium-long brown hairs. S with sparse, yellowish grey to bright brownish hairs.

Female. Unknown.

Diagnosis. *A. nantouensis* sp. n. is most similar to *A. (Habromelissa) omogensis* Hirashima, 1953 from which it can be distinguished by the following characters (characters of *A. omogensis* given in brackets): Clypeus smooth and shiny (tesselate, weakly dull), with more dense and stronger punctation. Disc of clypeus flattened to slightly concave (weakly convex). GA distinctly broader than compound eye in lateral view, smooth and shiny (distinctly shorter than compound eye, distinctly tesselate, weakly dull). Hind margin of vertex strongly concave (slightly concave). Scutum nearly smooth, shiny with distinct, dense punctation (<1) (tesselate, with indistinct, more dispersed punctation (≥ 1)). Scutellum smooth and shiny, with distinct strong punctation (weakly tesselate, with indistinct, small punctation). PT with strong, coarse wrinkles basally (strongly granulate to extremely fine wrinkled basally). Punctation of T esp. T 1 strong and distinct (small indistinct, on T 1 nearly absent). Pubescence of face including clypeus and lower parts of vertex, as well as disc of scutum and scutellum blackish brown (pubescence yellowish grey). Pubescence of T bright brownish (whitish grey).

Etymology. The name of the species refers to the Nantou county district of Taiwan, where it was collected.

Type material. Holotype: ♂, Central Taiwan (ROC), Nantou Hsien, Meifeng, 2150 m, 28.-29.VIII.1981, leg. L. Y. Chou & S. C. Lin (TARI).

Andrena (Larandrena) susanneae sp. n.

Female. BL: 9.1 – 10 mm (9.7 mm); FWL: 7.3-7.8 mm (7.6 mm).

Structure. Head oval, about 1.4 times broader than long in frontal view. Mandibles normally long, apically bidentate. Process of labrum triangular, apically rounded, weakly dull to shiny. Clypeus 1.6 times broader than long, weakly tesselate except broad smooth and shiny area in the middle. Punctation of clypeus strong and distinct (≥1) except broad impunctate median area. Lower part of supraclypeal area smooth and shiny, upper part strongly tesselate, dull. Frons densely tesselate, dull with distinct, dense longitudinal notches. Genal area slightly

broader (1.2 times) than compound eye in lateral view, tesselate, weakly dull to shiny. Vertex 0.9 times as wide as lateral ocellus, tesselate to weakly granulate, dull. Hind margin of vertex weakly carinate in the middle. FOV long, parallel sided, reaching from upper margin of compound eye down to the level of anterior tentorial pit. Maximum width of FOV 1.7 times OD. Nearly no free space between inner margin of compound eye and FOV, only thin and smooth bare line on upper part developed. AS 3 about 1.8 times longer than broad, 1.2 times longer than following two segments together. AS 4-AS 6 slightly broader than long, AS 7-AS 11 about as long to slightly longer than broad. AS 12 about 1.4 times as long as broad. Pronotum tesselate, weakly dull to shiny, with indistinct punctation. Dorsolateral angle of propodeum distinctly carinate. Scutum strongly tesselate, dull except a smooth and shiny area on posterior part of disc, with large flat punctation (≥1). Scutellum completely smooth and shiny except tesselate and dull area along hind margin. Punctation of scutellum similar to scutum. Metanotum densely granulate to finely wrinkled, dull, with indistinct punctation. PT granulate (apically) to indistinct finely wrinkled (basally). DLP and LP strongly tesselate to finely granulate, dull with indistinct weak punctation. Claws apically bidentate. T 1-5 completely weakly tesselate, weakly dull to shiny with very indistinct, minute punctation. T therefore nearly impunctate. Marginal zone of T 2 and 3 about 1/3 of total length of T, marginal zone of T 4 nearly half as long as total length of T. Dorsolateral convexity of T weakly developed. Pygidial plate apically truncate, weakly dull to shiny with strongly elevated triangular area in the middle. Marginal zone of pygidial plate slightly concave with fine wrinkles arising from elevated triangular area. S tesselate, dull with indistinct dense punctation (1).

Integument colour. Mandibles black, apically reddened. Antennal flagellum blackish brown. All other parts of head and thorax black. Tegulae yellowish brown transparent. Legs blackish brown to brownish. Distal tarsal segments brownish. Claws pale yellowish brown basally, reddish brown apically. Spurs bright yellowish grey. Veins of wings and stigma bright yellowish brown. T black to blackish brown, with yellowish brown transparent marginal zone. T 1 and 2 sometimes with weak yellowish brown maculations lateroventrally. Pygidial plate blackish brown. S black to blackish brown.

Pubescence. Clypeus with sparse yellowish grey hairs, except bare median line. POA, SCA, dorsal side of scape, as well as main parts of vertex and GA with yellowish grey to whitish, long hairs. FOV bright brownish (upper part) to whitish (lower part), when seen from above. Thorax with long yellowish grey to white pubescence, hairs of scutellum and metanotum especially long and dense. PT bare, DLP with bright yellowish grey hairs. Dorsal and anterior fringe of propodeal corbicula distinctly developed, consisting of long and dense, bright yellowish grey hairs. LP with few branched, yellowish grey hairs. Pubescence of legs mainly bright yellowish grey. Flocculus of trochanter of hind legs distinctly developed, with long and dense branched, yellowish white hairs. Tibial scopa of hind legs with long and dense yellowish brown hairs, except few branched hairs ventrally. T 1 with medium-long, dispersed pubescence of greyish white hairs except short white apical fringes laterally. T 2-4 with short

dispersed white hairs on disc and dense white hair fringes apically (distinctly interrupted on T 2 and 3, complete on T 4). Prepygidial and pygidial fimbria yellowish grey. S 2-6 with sparse and short whitish grey hairs forming weak fringe along apical margin.

Male. BL: 8.6 mm; FWL: 6.8 mm

Structure. Head oval, 1.5 times broader than long in frontal view. Proboscis similar to female. Mandibles medium-long, weakly falciform, bidentate. PLR triangular, apically rounded, shiny. Clypeus 2.2 times broader than long, weakly tesselate with distinct punctation (≥1). GA broad, 1.1 times as wide as compound eye in profile, strongly tesselate, dull. Vertex granulate, dull, distance from hind margin of LO to hind margin of vertex about as wide as OD. Scape nearly as long as following three segments together. AS 3 1.3 times longer than broad, 1.2 times longer than AS 4. AS 4 -12 about 1.2 times longer than broad, AS 13 nearly 1.6 times as long as broad. Pronotum tesselate, dull, laterally strongly carinate, with several longitudinal wrinkles. Other parts of thorax including wings similar to female. Legs slender, weakly tesselate. T and S similar to female. S 7 and 8 as shown in Figs 16K, 18H. Male genitalia as in Fig. 23A.

Integument colour. Mandibles black, apically reddened. Clypeus completely bright yellowish, except two inconspicuous dark spots. Antenna blackish brown. Legs completely blackish brown. Metasoma blackish brown to brownish. Other parts of body black to blackish brown.

Pubescence. Head with long whitish grey pubescence, hairs most dense and distinct on clypeus. Pubescence of thorax less colourful, whitish grey, much more sparse than in female. Pubescence of T extremely sparse, consisting of medium-long (T 1) to short (T 2-5) whitish hairs, weakly indicating apical fringes laterally on T 2-4. Pubescence of T 6 and T 7 yellowish grey. S with sparse, short to medium-long whitish hairs forming weak apical fringes in the middle.

Diagnosis. *Andrena susanneae* sp. n. is most similar to *Andrena* (*Larandrena*) *echizenia* Hirashima & Haneda, 1973 from which it can be distinguished by the following characters (character states of *A. echizenia* in brackets): FOV broad, about 2 times as wide as diameter of lateral ocellus (narrow, about 1.4 times OD); no interspace between FOV and inner margin of compound eye developed (FOV and inner margin of compound eye separated by distinct smooth interspace); scutum on disc partly smooth and shiny, with distinct strong punctation (tesselate all over, punctation weak, indistinct); apical hair fringes of T 2-4 strongly developed, nearly complete on T 2 and 3 (weakly developed, broadly interrupted on T 2 and 3); prepygidial and pygidial fimbria bright yellowish grey (prepygidial and pygidial fimbria brownish); clypeus of male completely yellow (black with irregular yellow maculation in the middle); pubescence of head in the male uniformly bright grey (lateral parts of face, as well as dorsal parts of genal area with dark brownish pubescence); AS 3 of male about as long as AS 4 (AS 3 about 1.3 times longer than AS 4).

Etymology. This species is named in honor of my beloved partner Susanne Szczepanek for her tremendous support throughout the duration of the study and for her valuable assistance in the molecular analysis.

Type material. Holotype: ♀, China, Mandschurei, Charbin, 29.IV.1954, leg. V. Alin, Eing. Nr. 22, 1954 (ZFMK). Paratypes: 1 ♀, 1 ♂, same data as holotype (ZFMK); 2 ♀♀, same data as holotype but Eing. Nr. 29, 1954 (ZFMK); 1 ♀, China, Mandschurei, Charbin, 22.IV.1954, leg. V. Alin, Eing. Nr. 22, 1954 (ZFMK); 1 ♀, China, Mandschurei, Charbin, 25.-30..IV.1953, leg. V. Alin, Eing. Nr. 25, 1953 (CD).

Andrena (Leucandrena) cheni sp. n.

Male. BL: 7.9 mm. FWL: 6.6 mm.

Structure. Head oval, 1.3 times broader than long. Mandibles normally long, bidentate. PLR weakly tesselate, shiny, trapezoid, basally about 0.7 times as broad as front margin of clypeus. Clypeus nearly 2 times as broad as long, tesselate (area along margins) to nearly smooth (disc). Disc of clypeus flattened, with distinct punctation (≥1) being more dispersed in the middle. SCA strongly tesselate, dull with indistinct, dispersed punctation. POA tesselate, dull to weakly shiny with distinct, dense punctation on lower part and dense but more oblique punctation on upper part, similar to frons. Vertex strongly tesselate to granulate, dull to weakly shiny with inconspicuous punctation (1) behind ocelli. Distance from hind margin of LO to hind margin of vertex about 1.3 times OD. Hind margin of vertex rounded to weakly carinate in the middle. GA 1.4 times as broad as compound eye in lateral view, strongly tesselate, dull to weakly shiny. AS 3 distinctly shorter than AS 4 and AS 5 together, 1.3 times as long as broad. AS 4 as long as broad, AS 5-12 slightly longer than broad, AS 13 about 1.5 times as long as broad. Pronotum rugously tesselate with distinct wrinkles laterally, dull to weakly shiny. Scutum dull, strong and densely tesselate with distinct, flat punctation (≥1). Scutellum weakly tesselate nearly smooth and shiny anteriorly, strongly tesselate and dull with indistinct punctation posteriorly. Metanotum dull to weakly shiny, rugously tesselate, basally weakly wrinkled. PT basally coarsely wrinkled, apically granulate, dull. DLP, LP, as well as declivous part of propodeum rugously tesselate to granulate, shiny. Mesepisterna rugously tesselate dull to weakly shiny with distinct honeycombed wrinkles. Legs slender, claws bidentate. T 1 smooth and shiny with inconspicuous small, dispersed punctation (>2). T 2-6 weakly tesselate to nearly smooth, shiny, with distinct dense punctation (≤1). Marginal zone of T 2-6 more than half as long as T. Pygidial plate distinctly developed, concave, basally slightly wrinkled, apically truncate. S 1-6 finely tesselate, shiny with dispersed (>1) punctation. S 6 with broad emargination in the middle of posterior margin. S7, S8 and male genitalia as shown in Figs 16N, 19C and 23D.

Integument colour. Mandibles black basally, reddened apically. Antenna blackish brown on both sides. Legs mainly blackish brown, distal tarsal segments brownish. Claws yellowish brown basally, reddish brown apically. Tegulae dark brownish. Veins of wings and stigma

dark brownish. Spurs yellowish grey, transparent. S dark reddish brown, marginal zone yellowish brown transparent. Other parts of body black.

Pubescence. Head with rather sparse pubescence of silvery white medium-long to long hairs, hairs of clypeus most dense at lateral parts. Ventral side of scape, frons and anterior parts of vertex with brownish hairs. Scutum and scutellum with medium-long to long yellowish to brownish grey hairs. Other parts of thorax with medium-long to long yellowish white (DLP) to white hairs. Legs with sparse pubescence of long to medium-long, white hairs. T 2-4 with short brownish transparent hairs on disc and distinct white hair fringes apically, which are distinctly interrupted medially. T 5-7 with sparse pubescence of medium-long yellowish grey hairs. S with mainly medium-long yellowish grey hairs.

Diagnosis. *A. cheni* sp. n. is most similar to *A. (Leucandrena) richardsi* Hirashima, 1957 from which it is clearly separated by the following characters (characters of *A. richardsi* given in brackets): AS 3 nearly 1.2 times as long as broad (1.5 times), 0.6 times as long as AS 4 and AS 5 together (AS 3 little shorter, 0.8 times than AS 4 and AS 5 together); scutum strongly tesselate, dull (scutum nearly smooth, distinctly shiny); disc of scutum with rather dense (1) punctation (punctation on disc more dispersed (>1.5)); PT only basally coarsely wrinkled, apically granulate (completely wrinkled all over); DLP weakly wrinkled (strongly wrinkled).

Etymology. This species is named in honor of Mr. Keh-miin Chen for his great contributions to dung beetle taxonomy and for his enthusiasm and warm hospitality during two collecting trips of the author on Taiwan.

Type material. Holotype: ♂, Central Taiwan (ROC), Nantou Hsien, Meifeng, 2150 m, 24.-26.VI.1981, leg. K. S. Lin & W. S. Tang (TARI).

Andrena (Micrandrena) taiwanella Dubitzky 2002

For description of this species see Appendix 2.

Andrena (Pallandrena) christineae sp. n.

Female. BL: 9.6 - 11.2 mm (10.6 mm). FWL: 7.4 mm - 8.0 mm (7.8 mm)

Structure. Head oval, about 1.3 times broader than long in frontal view. Mandibles normally, apically bidentate. PLR large, trapezoid with distinct triangular emargination apically in the middle, as commonly found in *Pallandrena*. Surface of process of labrum finely wrinkled, dull to weakly shiny. Clypeus nearly two times as broad as long, dull, with extremely dense punctation. Structure of supraclypeal area and paraocular area similar to clypeus. Frons slightly shiny with clear longitudinal notches and honeycombed punctation between. Vertex densely tesselate to granulate, dull. Area behind median ocelli with inconspicuous, weak wrinkles. Distance from hind margin of LO to hind margin of vertex 1.8 times OD. Hind margin of vertex rounded. Genal area tesselate, weakly dull to shiny, about 2.5 times as broad as compound eye in lateral view. FOV parallel sided, reaching from lower margin of antennal insertion to nearly hind margin of lateral ocelli. Width of FOV nearly twice (1.8 times) OD.

Smooth area between inner margin of compound eye and FOV about 1/4 maximum width of FOV. Scape ventrally densely tesselate, dull with strong punctation. AS 3 about 2.3 times longer than broad, nearly as long as following three segments together. AS 4 and 5 slightly broader than long, AS 6-AS 12 about as long as to slightly longer than broad. AS 12 nearly 2 times as long as broad. Pronotum tesselate, weakly dull to shiny, with scant punctation. Scutum strongly tesselate to granulate, dull, with indistinct large punctation (≤1), punctation most dense near front and hind margin. Scutellum similar to scutum but with weaker punctation. Metanotum finely wrinkled, dull, with indistinct punctation. Propodeal triangle weakly shiny with fine wrinkles, wrinkles most dense basally. DLP, as well as declivous part of propodeum strongly tesselate, with weakly wrinkled punctation. LP tesselate, shiny, with strong and dense punctation (<1). Claws apically bidentate. Tibia and basitarsus of hind legs slender, the latter about 4 times as long as broad and half as long as tibia. Inner spur of hind tibia basally velum-like broadened. T 1 nearly smooth, shiny with distinct punctation (1) on disc. Marginal zone of T 1 with only few single punctures. T 2-4 strongly tesselate, slightly dull with more dispersed (>1) and indistinct punctation on disc. Marginal zone of T 2-4 with dense weak punctation (≤1). T 5 strongly tesselate, dull with clear punctation (1). Marginal zone of T 2-4 nearly half as long as total length of T. Dorsolateral convexity of T distinctly developed. Pygidial plate strongly tesselate, dull, apically truncate. S tesselate, dull to weakly shiny, with large and distinct punctation (≤1).

Integument colour. Mandibles black, apically reddened. Antennal flagellum blackish brown on both sides. All other parts of head, as well as thorax steel-grey. Tegulae brownish transparent. Legs black to blackish brown. Distal tarsal segments brownish. Claws pale yellowish brown basally, reddish brown apically. Spurs bright yellowish. T 1 black with exception of bright reddish marginal zone and small reddish maculations laterally (sometimes also reddish maculations on declivous basal part of T 1). T 2 and 3 bright reddish except a large black coloured maculation in the middle of disc. T 4 mainly blackish except two laterobasal reddish maculations and the reddish transparent marginal zone. Disc of T 5 completely black, marginal zone brownish transparent. Pygidial plate with bright reddish triangular area in the middle and blackish brown margin. S 1 mainly blackish. S 2-4 bright reddish with black round maculation in the middle. S 5 with large black maculation along front margin and reddish areas laterobasally. S 6 reddish, with large black maculation apically.

Pubescence. Main parts of head as well as scape with rather dense, medium-long to long silvery white pubescence of branched hairs. FOV whitish brown when seen from above. Thorax with medium-long to long silvery white pubescence. Propodeal corbicula absent, LP with regularly sparse pubescence of long whitish branched hairs. T1 with sparse short to medium-long branched hairs. T 2-4 nearly bare with few dispersed short hairs on disc and sparse ciliate apical fringes on marginal zone. Prepygidial and pygidial fimbria consisting of greyish brown pubescence. Pubescence of front and middle legs whitish to bright yellowish white. Flocculus of long silvery white pubescence. Femoral and tibial scopa silvery white,

consisting of long curly-branched hairs. S 2-5 with inconspicuous short, sparse hairs on disc and medium-long to long white hair fringe along apical margin.

Male. Unknown.

Diagnosis. *Andrena christineae* sp. n. is most similar to *Andrena (Pallandrena) pallidicincta* Brullé, 1832 from which it can be distinguished by the following characters (character states of *A. pallidicincta* given in brackets): T 1-4 bright reddish with blackish brown maculations (completely blackish brown); integument colour of head and thorax steel-grey (head and thorax blackish brown); dorsolateral convexity of T 2-4 protuberant swollen, apically smooth and shiny (dorsolateral convexity of T 2-4 flattened, apically tesselate, dull); T 1-4 weakly tesselate, strongly shiny (distinctly tesselate, weakly shiny to dull); PT finely wrinkled (PT granulate all over, no wrinkles developed); distance from hind margin of lateral ocellus to hind margin of vertex 1.8 times OD (1.3 times OD); head 1.3 times as long as broad (1.2 times).

Etymology. This species is named in honor of my beloved mother Christine Dubitzky, for her curiosity and great interest in biology, she is also an excellent bee collector.

Type material. Holotype: ♀, Turkey, Hakkari: Pass E, Uludere, 6.VI.1977, leg. Klaus Warncke, ex Coll. Warncke (OLL). Paratypes: 1 ♀, same data as holotype (OLL); 1 ♀, Turkey, Hakkari: Mt. sat, 2050-2450 m, 10.VI.1981, leg. Klaus Warncke, ex Coll. Warncke (OLL); 2 ♀♀, Turkey, Hakkari: Tanin-Tanin-Pass, 2.VI.1980, leg. Klaus Warncke, ex Coll. Warncke (OLL); 1 ♀, Turkey, Agri: 10 kmN Tutak, 1600 m, 28.V.1980, leg. Klaus Warncke, ex Coll. Warncke (OLL, CAD); 1 ♀, Iran, Kermanshahan, 80 km SE Kermanshaha, Buchan, 1900-2000 m, 19.5.1975, leg. Holzschuh & Ressl, ex Coll. Grünwaldt (ZSM).

Andrena (Pallandrena) scheuchli sp. n.

Female. BL: 9.5 - 9.9 mm (9.7 mm). FWL: 7.0 – 7.1 mm (7.05 mm).

Structure. Head oval, about 1.3 times broader than long in frontal view. Mandibles apically bidentate. PLR smooth and shiny, trapezoid with median triangular emargination apically. Clypeus dull to weakly shiny, about 2 times broader than long, strongly tesselate to finely wrinkled with distinct punctation (1). Supraclypeal area and paraocular area similar to clypeus. Frons shiny with distinct longitudinal notches between honeycomb-like punctation. Vertex shiny, smooth to finely wrinkled. Hind margin of vertex rounded, strongly tesselate, dull to weakly shiny with indistinct large punctation. Distance from hind margin of lateral ocellus to hind margin of vertex about 1.5 times as wide as diameter of lateral ocellus. Genal area slightly broader (1.2 times) than compound eye in lateral view, with large dense punctation (<1). FOV teardrop-shaped, extremely broad at least 2.5 times OD, reaching from lower margin of antennal insertion to front margin of LO. Almost no free space between inner margin of compound eye and FOV. AS 3 about 1.6 times longer than broad, distinctly longer than AS 4 and 5 together. AS 4 about half as long as broad, AS 5 slightly longer than half width. AS 6-11 slightly shorter than broad, AS 12 about 1.3 times longer than broad.

Pronotum weakly tesselate, dull to slightly shiny with inconspicuous punctation (1). Scutum smooth and shiny on disc, area near front and hind margin weakly tesselate, with distinct strong punctation (max. 1). Structure of scutellum similar to scutum but more strongly tesselate. Metanotum finely wrinkled, dull to weakly shiny with inconspicuous dense (<1) punctation. Propodeal triangle shiny with fine coarse wrinkles. DLP tesselate, upper parts granulate to slightly wrinkled, mainly dull, with indistinct punctation. Mesepisterna tesselate, with dense (<1) wrinkled punctation. Legs slender, with bidentate claws and basally broadened inner spur of hind tibia. T 1-4 smooth to weakly tesselate, shiny. T 1 with distinct punctation (>1), T 2-4 with more dense (max. 1) distinct punctation on disc as well as marginal zone. T 5 densely tesselate, dull, with large dense (1) punctation. Marginal zone of T 2 distinctly shorter than half length of T, marginal zone of T 3-4 about half as long as T. Dorsolateral convexity of T 2-4 strongly developed, distinctly stepped. Pygidial plate strongly tesselate, dull, apically truncate. S weakly tesselate, shiny, with distinct large punctation (max. 1).

Integument colour. Head and thorax black with lead-like metallic shimmer. Mandibles apically reddened. Antennal flagellum (AS 4-12) yellowish brown on underside. Legs black to blackish brown. Distal tarsal segments dark brownish. Claws yellowish grey basally, reddish brown apically. Spurs bright yellowish grey. Tegulae brownish transparent. Veins of wings dark brownish grey, stigma bright brownish with dark brownish grey margins. T 1 completely black except bright reddish marginal zone. T 2 bright reddish except black median maculation on disc. T 3 bright reddish with large broad black maculation on disc. T 4 nearly completely black with two reddish maculations laterobasally and yellowish transparent marginal zone. T 5 completely black except brownish transparent marginal zone. Pygidial plate black with indistinct dark reddish brown maculation in the middle. S 1 completely blackish brown S 2 and 3 blackish brown except bright reddish brown maculations laterobasally. S 4-6 mainly blackish brown.

Pubescence. Pubescence of head and thorax of medium-long to long silvery white hairs similar to *A. christineae*. FOV bright brownish if seen from above. Propodeal corbicula absent, regularly pubescence of branched white hairs instead. T 1-4 with short to medium-long white hairs like in *A. christineae*. Prepygidial and pygidial fimbria bright greyish brown. Flocculus of trochanter as well as femoral and tibial scopa of hind legs with silvery white, long, curly-branched hairs. S 2-5 with inconspicuously short sparse hairs on disc and medium-long to long hair fringes along apical margin.

Male. Unknown.

Diagnosis. *Andrena (Pallandrena) scheuchli* sp. n. is most similar to *Andrena (Pallandrena) christineae* sp. n., from which it can be distinguished by the following characters (character states of *A. christineae* given in brackets): FOV extremely broad, at least 2.5 times as broad as OD (FOV distinctly narrower, only 1.8 times OD); vertex partly smooth and shiny (vertex completely granulate, dull); scutum and scutellum weakly tesselate to smooth, strongly shiny, with distinct punctation (strongly tesselate, dull, punctation indistinct) T nearly smooth,

strongly shiny, with distinct coarse punctation (tesselate, weakly shiny, with indistinct fine punctation); T 3 on disc with transverse extended black maculation nearly as broad as T (disc of T 3 with black maculation only medially).

Etymology. This species is named in honor of Erwin Scheuchl for his important contributions to bee taxonomy of central Europe and for his excellent taxonomic knowledge of palearctic *Andrena*.

Type material. Holotype: ♀, Turkmenistan, Kugitang-Mts., Hodschapil (1400-1500 m), 3.V.1995, leg. K. Schönitzer (ZSM); Paratype: ♀, same data as holotype.

Andrena (Simandrena) heinzi sp. n.

Female. BL: 8.0 – 9.1 mm (8.4 mm). FWL: 5.8 – 6.6 mm (6.2 mm).

Structure. Head 1.2 times broader than long in frontal view. Galea shiny, finely tesselate, without distinct punctation. Mandibles bidentate. PLR nearly 2.5 times broader than long, trapezoid, smooth and shiny. Apical margin of PLR about 0.6 times as wide as basal margin, with broad emargination in the middle. Clypeus weakly shiny, about 1.5 times as broad as long, distinctly tesselate with indistinct punctation (≤1). POA slightly tesselate, weakly shiny with dense coarse punctation (<1). SCA dull, minutely wrinkled, with indistinct punctation. Frons dull with irregular longitudinal ridges between indistinct punctation. Vertex tesselate to finely wrinkled, dull to weakly shiny with indistinct punctation. Hind margin of vertex rounded. Distance from hind margin of LO to hind margin of vertex about 1.5 times OD. FOV especially upper part extremely broadened, maximum width about 2.7 times OD, reaching from hind margin of LO below upper margin of clypeus. GA tesselate, shiny with indistinct punctation, about as wide as compound eye in lateral view. AS 3 about 1.7 times as long as broad, as long as AS 4 and 5 together. AS 4 and 5 distinctly broader than long (1.2 and 1.3 times as broad as long respectively), AS 6-11 about as long as broad, AS 12 about 1.6 times as long as broad. Pronotum strongly tesselate, dull to weakly shiny, with inconspicuous punctation (≤1). Scutum anteriorly as well as along hind margin, strongly tesselate, dull. Disc of scutum weakly tesselate to nearly smooth, shiny with coarse and distinct punctation (1). Scutellum nearly smooth on disc, strongly tesselate along margins, with irregular, coarse punctation. Metanotum strongly tesselate to granulate, dull. PT dull, finely wrinkled, strongly granulate between. DLP coarsely wrinkled, dull. LP finely tesselate, weakly shiny, impunctate. Mesepisterna finely tesselate, weakly shiny, with indistinct coarse punctation (<1). Claws of all legs distinctly bidentate. T finely tesselate, shiny, with dense punctation (<0.5), punctation most dispersed on T 1 (≤1). Dorsolateral convexity of T weakly developed apically smooth and shiny. Pygidial plate tesselate, dull with weakly elevated area in the middle. S 2-5 strongly tesselate dull to weakly shiny with coarse dense punctation (<0.7). S6 tesselate dull, with indistinct punctation.

Integument colour. Black to blackish brown except the following: Proboscis dark brownish. Mandibles dark reddish apically. AS 3 and 4 apically on underside with small yellowish

brown maculation, AS 5-12 completely yellowish brown on underside. Tegulae dark brownish transparent. Stigma bright yellowish brown transparent, with dark brownish hind margin. Legs dark brownish except for bright yellowish brown on distal tarsal segments of front legs, apical part of tibia and tarsus of mid legs as well as tibia and tarsi of hind legs. Claws of all legs yellowish grey basally, bright brownish apically. Spurs yellowish grey. Marginal zone of T 1-5 brownish transparent. Pygidial plate dark reddish basally, blackish apically.

Pubescence. Head as well as lateral parts of thorax with yellowish grey pubescence of varying length. FOV bright yellowish grey all over. Scutum, scutellum and metanotum of fresh animals with yellowish brown pubescence of medium-long (about as long as metanotum), strong hairs. PT bare, DLP with long yellowish grey hairs. Propodeal corbicula complete, anterior and dorsal fringe consisting of long and dense yellowish grey hairs. LP bare. Pubescence of legs bright yellowish grey. Flocculus of trochanter of hind legs of long and dense silvery white hairs. T 1 with two short yellowish white hair patches lateroapically and few dispersed yellowish grey hairs basally. T 2 with broadly interrupted yellowish white apical hair fringe. T 3 and 4 each with complete yellowish white hair fringe apically, short and dispersed brownish hairs basally. Prepygidial as well as pygidial fimbria with bright yellowish brown pubescence. S 2-6 with sparse yellowish grey pubescence forming weak hair fringes along apical margin. Disc of S 2 with sparse brush of medium-long hairs.

Male. BL: 7.1 – 7.5 mm (7.2 mm). FWL: 5.1 – 5.6 mm (5.4 mm).

Structure. Head oval, 1.3 times broader than long in frontal view. Proboscis similar to female. Mandibles rather short distinctly bidentate. PLR shiny, rectangular, nearly 2 times broader than long. Front margin of PLR with weak emargination in the middle. Clypeus similar to female about 1.6 times broader than long. GA similar to female 1.2 times as wide as compound eye in lateral view. Frons with stronger longitudinal ridges than in female. Vertex more rugose than in female, distance from hind margin of LO to hind margin of vertex similar to female. Other parts of head similar to female. AS 3 1.4 times as long as broad, about as long as AS 4. AS 4 and 5 of equal length, nearly 1.3 times as long as broad. AS 6-12 nearly 1.4 times as long as broad, AS 13 nearly 2 times as long as broad. Thorax similar to female, but disc of scutellum stronger tesselate, punctation therefore more indistinct. PT stronger wrinkled than in female. Claws distinctly bidentate. T less tesselate than in female, with more dispersed punctation (1). S 2-6 tesselate, shiny with more dispersed punctation than in female (≥1). S 7 and 8 as shown in Figs 16L and 18G. Male genitalia as in Fig.22F.

Integument colour. Black to blackish brown except the following: Proboscis dark brownish. Mandibles apically reddened. AS 4-13 dark brownish on underside. Legs dark brownish, except for bright yellowish brown distal tarsal segments of front legs and tarsi of mid and hind legs . Often also distal part of mid and hind tibia with yellowish brown maculation of varying size. Spurs yellowish grey. Marginal zone of T 1-5 brownish transparent. S brownish.

Pubescence. Head with long yellowish brown pubescence, distinctly more colourful than in female. Scutum, scutellum and metanotum with yellowish brown pubescences of rather long

hairs. Lateral parts of thorax, as well as legs, with yellowish grey pubescence similar to female. T 1 with sparse pubescence of medium-long yellowish grey hairs. Apical hair fringes of T 2-4 similar to female but more sparse and indistinct. T 5 and 6 with dense yellowish brown pubescence of long stiff hairs. S with sparse, short to long yellowish grey pubescence.

Diagnosis. The new species is most similar to the species *A. (Simandrena) sarta* Morawitz, 1876, *A. (Simandrena) mehelyi* Alfken, 1936 and *A. (Simandrena) combinata* (Christ, 1791). It can be distinguished from *A. sarta* by the following characters (character states of *A. sarta* given in brackets; all characters listed below refer to females only, because no males of *A. sarta* were available for comparison): clypeus strongly tessellated on disc, dull (smooth and shiny on disc); hind margin of vertex rounded (carinate); distance from hind margin of lateral ocellus to hind margin of vertex about 1.5 times as wide as lateral ocellus (nearly as wide (0.8 times) as lateral ocellus); scutum and scutellum distinctly tesselate, weakly shiny on disc (weakly tesselate to smooth, strongly shiny); punctation on T more fine and dispersed (punctation more coarse and dense); pubescence of head, lateral parts of thorax and apical hair fringes of metasoma yellowish grey (whitish); pubescence of scutum, scutellum and metanotum bright yellowish brown of medium-length (whitish, short); only apical hair fringes of T 3 and 4 complete, apical fringe of T 2 broadly interrupted (apical hair fringes complete on T 2-4); distal tarsal segments of front legs, apical part of tibia and tarsus of mid legs, as well as tibia and tarsi of hind legs, bright yellowish brown (blackish brown); AS 5-12 bright yellowish brown on underside (dark brownish). The new species can be separated from *A. mehelyi* and *A. combinata* as follows (character states of *A. mehelyi* and *A. combinata* given in parentheses): AS 5-12 of female yellowish brown on underside (blackish brown); male AS 3 about 1.2 times as long as broad, distinctly longer (1.4 times) than AS 4 (AS 3 as long as broad, slightly shorter (0.9 times) than AS 4); clypeus with impunctate median line (female), transverse wrinkles absent in both sexes (impuctate median line absent, strong transverse wrinkles developed); FOV broad, about 2.9 times OD (distinctly narrower, 2.6 times OD); PT of female with few wrinkles basally, mainly granulate (nearly completely coarsely wrinkled, only apically granulate); tarsi of all legs and hind tibia yellowish in female (blackish); lateroapical hair fringes of T1 and laterobasal hair fringes of T 2 absent in female (distinctly developed); prepygidial, as well as pygidial fimbria, bright yellowish grey (greyish brown); punctation on T minute, dense in both sexes (coarse, honeycombed); dorsal lobe of gonocoxite weakly developed (absent).

Etymology. This species is named in honor of my beloved father Heinz Dubitzky for his wonderful support during the duration of my studies and for his broad interest in the natural world.

Type material. Holotype, ♀, Southern Kazakhstan , Karatau, 16 km NO Kentau, Biresek-Tal, auf Ferula, 5.V.1994, leg. W. Dolin, ex coll. Grünwaldt (ZSM). Paratypes: 5 ♀♀, 2 ♂♂, same data as holotype (ZSM); 2 ♀♀, 4 ♂♂, same data as holotype except 7.V.1994 (ZSM); 1 ♀, same data as holotype except 12.V.1994 (ZSM); 1 ♀, Kirgistan, Tschatkal, G. K., Kanysch-Kija, 1700 m, 4.VI.1998, leg. W. Dolin, ex coll. Grünwaldt (ZSM).

Andrena (*Graecandrena*) *lehmanni* Schönitzer & Dubitzky 2002

For description of this species see Appendix 3.

Tab. 4. Data matrix for the cladistic analysis of *Andrena*.

	1 2 3 4 5 6 7 8 9 10	1 2 3 4 5 6 7 8 9 20	1 2 3 4 5 6 7 8 9 30	1 2 3 4 5 6 7 8 9 40	1 2 3 4 5 6 7 8 9 50	1 2 3 4 5 6 7 8 9 60	1 2 3 4 5 6 7 8 9 70	1 2 3 4 5 6 7 8 9 80
Ancestor	0 0 0 0 - - 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
Ancylandrena atoposoma	0 0 0 0 - - 0 0 0 0	0 2 1 1 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 2 0 0 0 0 0	1 1 0 0 1 0 0 0 0 0	0 1 1 1 0 0 0 0 0 3	1 0 0 2 0 1 0 0 1 3	0 0 0 0 0 0 0 1 1 1
Cubiandrena cubiceps	1 2 1 1 2 - 0 0 0 0	0 1 0 1 1 1 0 0 0 2	0 0 0 2 1 0 1 1 0 0	0 0 0 1 1 0 0 1 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	1 0 0 2 0 2 0 0 1 0	3 0 0 1 0 0 1 0 0 1
Euherbstia excellens	0 0 0 0 - - 0 0 0 0	0 0 0 ? 1 0 0 0 0 0	? 0 0 0 0 0 0 - 0 0	0 2 0 ? ? 1 0 0 0 0	0 0 1 0 0 1 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 - - - - - - - - -	0 0 0 0 2 1 0 0 1 1
Megandrena enceliae	1 0 0 0 - - 0 0 0 0	0 0 1 0 1 1 0 0 0 0	0 0 0 1 0 0 0 - 0 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 1 0 1 0 0 0 0 0 3	1 2 0 3 0 0 0 0 1 3	0 0 0 1 2 0 0 1 1 1
Orphana inquirenda	0 0 0 0 - - 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 - 0 0	0 2 0 0 2 0 0 0 0 0	2 0 0 0 1 0 0 0 1 0	0 0 0 0 0 0 0 0 0 0	0 - - - - - - - - -	0 0 0 1 2 0 0 0 1 1
Andrena (Aciandrena) aciculata	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 0 0 0 0 0 1 0 0 0	0 1 1 0 1 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 1 0 1 0 0 0 0 0 0	1 1 0 0 2 0 0 0 1 0	1 1 1 0 0 0 0 1 0 0
Andrena (Aenandrena) aeneiventris	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 0 0 0 1 0 0 0	0 0 0 0 1 0 0 0 0 0	0 0 1 0 0 1 2 0 0 0	0 1 0 1 0 0 0 0 0 1	1 2 0 1 0 1 0 0 0 0	2 0 0 2 1 0 0 1 0 0
Andrena (Agandrena) agilissima	0 0 0 1 0 1 2 0 0 1	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 1 1 0 1 0 0 0	0 0 1 0 1 0 0 0 0 0	0 0 1 0 0 0 0 0 0 2	1 0 0 0 1 0 0 0 1 0	3 0 0 0 0 0 0 1 0 0
Andrena (Anchandrena) angustella	0 0 0 1 0 1 ? 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 2 2 1 0 1 1 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 1 1 0 0 1 0	0 0 0 0 0 1 0 0 1 0	1 2 0 2 2 1 0 0 1 3	2 1 0 0 1 0 1 0 0 1
Andrena (Andrena) helvola	0 0 0 1 0 1 2 0 0 1	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 1 1 1 1 0	0 2 0 0 0 1 0 0 0 0	0 2 0 0 1 1 0 0 0 0	0 0 0 0 1 0 0 0 1 0	1 2 0 2 1 0 0 0 1 3	2 1 0 0 0 1 1 0 1 1
Andrena (Andrena) praecox	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 1 1 1 1 0	0 2 0 0 0 1 0 0 0 0	0 2 0 0 1 1 0 0 0 0	0 1 0 2 1 0 0 0 1 0	1 2 0 2 1 0 0 0 1 3	2 1 0 0 0 1 1 0 1 1
Andrena (Aporandrena) coactipostica	0 0 0 1 0 1 2 0 1 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 1 0	0 0 0 0 0 0 0 0 1 0	1 2 0 0 1 0 0 0 1 0	2 0 1 0 0 0 0 1 0 0
Andrena (Archiandrena) banksi	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 1 1 1 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 1 1 0 0 1 0	0 0 0 0 1 1 0 0 1 0	1 2 0 2 2 0 0 0 1 3	2 1 0 2 1 0 1 0 1 1
Andrena (Augandrena) plumiscopa	0 0 0 1 0 1 2 0 0 0	0 0 0 0 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 2 0 0	0 0 0 0 1 1 0 0 1 0	0 1 0 1 0 0 0 0 1 0	1 2 0 2 1 0 0 0 0 3	2 0 1 0 0 0 0 1 1 1
Andrena (Biareolina) lagopus	0 0 0 1 1 1 1 0 0 0	0 0 0 1 0 0 0 0 1 0	0 0 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 1 2 0 0 0	0 0 1 0 0 0 0 0 0 0	1 0 1 0 1 0 1 1 0 0	3 0 0 0 0 0 0 0 1 0
Andrena (Brachyandrena) colletiformis	0 0 0 1 0 0 3 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 0 0 0 1 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 1 1 0 0 0 0 0 0	0 0 2 0 0 0 0 0 0 1	1 2 0 1 0 1 0 0 0 0	2 0 0 0 0 0 0 0 0 0
Andrena (Calcarandrena) gamskrucki	0 0 0 1 0 0 2 0 0 0	0 0 0 0 0 0 0 0 1 3	0 1 0 0 0 0 1 0 0 0	0 1 0 1 0 0 0 0 0 0	2 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 2 0 0 1 0 0 0 0 0	2 0 0 0 0 0 0 1 0 0
Andrena (Callandrena) accepta	0 0 0 1 0 0 2 0 0 0	0 0 0 0 1 0 0 0 1 0	0 0 0 1 0 0 1 0 0 0	0 2 0 1 2 0 0 2 0 0	2 0 0 0 0 1 0 1 1 0	0 0 0 0 0 0 0 1 0 0	1 0 0 0 1 2 0 0 0 0	3 0 0 1 0 0 0 1 0 0
Andrena (Calomelissa) prostomias	0 0 0 1 0 0 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 0 2 1 0 0 1 0 0 0	0 2 0 0 1 0 0 0 1 1	1 0 0 0 0 0 0 0 1 0	0 2 0 0 0 0 0 0 1 0	1 2 0 3 2 0 0 0 3 0	3 0 0 0 0 0 0 1 1 1
Andrena (Campylogaster) erberi	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 1 1 1 0 0 0 0 0	0 0 2 1 0 0 0 0 0 1	1 2 0 1 0 0 1 0 0 1	3 0 0 0 0 0 1 0 0 1
Andrena (Carandrena) aerinifrons	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 1 0 0	0 0 0 0 2 0 0 0 0 1	0 0 0 0 1 1 0 0 1 0	0 0 0 0 1 0 0 0 1 0	1 0 0 0 2 1 0 0 0 0	2 1 0 0 0 0 1 0 1 1
Andrena (Charitandrena) hattorfiana	0 0 0 1 0 0 2 0 0 0	0 1 0 0 2 1 1 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 1 1 0 0 1 0	0 0 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 1 0	3 0 0 0 0 0 0 1 1 1
Andrena (Chlorandrena) humilis	0 0 0 1 0 0 3 0 0 0	0 0 0 1 1 1 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 0 0 0 0 0 0 0 0 0	1 0 1 2 2 0 1 1 1 0	2 0 0 0 0 0 0 1 0 0
Andrena (Chrysandrena) fulvago	0 0 0 1 0 0 3 0 0 0	0 0 0 1 2 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	1 0 0 0 0 1 0 0 0 0	2 0 0 0 0 0 0 1 0 0
Andrena (Cnemidandrena) nigriceps	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 1 0 1 0 0 0	0 0 0 1 0 1 0 0 0 0	0 2 0 0 1 1 0 0 0 0	0 0 0 0 1 0 0 0 1 0	1 2 0 2 1 0 0 0 1 0	3 0 0 0 0 1 1 1 1 1
Andrena (Conandrena) bradleyi	0 0 1 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 0 1 2 1 0 1 0 0 1	2 2 1 0 1 0 1 0 0 0	2 0 0 0 1 0 0 0 1 1	0 0 0 0 0 0 0 0 0 0	1 1 0 0 0 0 0 0 0 0	2 0 0 0 0 0 0 1 1 1
Andrena (Cordandrena) cordialis	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	1 2 0 0 1 0 0 0 1 0	2 0 0 2 1 0 0 1 0 0
Andrena (Cremnandrena) anisochlora	0 0 0 1 0 1 3 0 0 0	0 2 0 1 0 0 0 0 1 0	0 1 0 2 1 1 0 - 0 0	0 2 0 0 2 0 0 1 0 0	0 2 0 - 1 1 0 0 1 0	0 0 0 0 0 0 0 0 0 0	1 2 0 0 0 1 0 0 0 0	2 1 0 0 0 0 0 0 0 0
Andrena (Cryptandrena) ventricosa	0 0 0 1 $ 1 2 0 0 0	0 0 0 1 1 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 1 3 1 0 0 0 0 0 3	1 2 0 1 0 0 0 1 0 0	2 0 0 0 1 0 0 0 0 0
Andrena (Dactylandrena) caliginosa	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 1 1 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 1 0	0 0 0 0 0 1 0 0 0 0	1 2 0 0 1 0 0 0 0 0	2 0 0 1 2 0 0 0 0 1
Andrena (Dasyandrena) obscuripostica	0 0 0 1 0 0 ? 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	1 2 0 0 2 0 0 0 1 0	2 1 0 0 0 0 0 0 0 0
Andrena (Derandrena) vandykei	0 0 0 1 0 1 ? 0 1 0	0 1 0 1 0 0 0 0 1 0	0 1 0 2 1 1 1 1 1 0	0 2 0 0 2 0 0 1 0 0	0 0 0 0 0 1 0 0 1 0	1 1 0 0 0 1 0 0 0 0	1 2 0 3 2 1 0 0 1 3	2 1 0 0 0 0 1 1 1 1
Andrena (Diandrena) chalybea	0 0 0 1 0 0 2 0 0 0	0 2 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 1 0 0	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 1 1 0 0 0	0 0 0 0 1 0 0 0 1 0	1 2 0 0 2 0 0 0 1 0	2 0 1 0 0 0 1 0 1 1
Andrena (Didonia) mucida	0 0 0 1 1 1 2 0 0 0	0 1 0 0 2 0 1 1 1 0	0 0 0 0 0 0 1 0 0 0	2 0 0 0 1 0 0 0 0 0	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	1 2 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 1 0 0
Andrena (Distandrena) longibarbis	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 1 - 1 0 0 0 0 0	0 1 0 0 1 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 1 0 0 0 0 1 0 0	? 0 1 0 0 0 0 1 0 0
Andrena (Euandrena) bicolor	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	1 1 0 1 1 1 0 0 0 0	2 0 0 0 0 0 0 1 0 0
Andrena (Fumandrena) fumida	0 0 0 1 0 0 3 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 1 0 1 0 0 0 0 1 0	1 1 0 1 0 1 0 0 2 0	2 0 1 0 0 0 0 1 0 0
Andrena (Fuscandrena) fuscicollis	0 0 0 1 1 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 0 0 1 0 0 1 0 0 0	0 0 1 - 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 1 0 1 0 0 0 0 0 0	1 0 0 1 1 0 0 0 2 0	1 0 1 0 0 0 0 0 1 0
Andrena (Geissandrena) trevori	0 0 0 1 0 ? ? 0 0 0	0 2 0 1 0 0 0 0 1 0	0 ? 0 2 1 0 1 0 0 0	0 2 0 0 1 0 0 0 1 1	0 1 0 0 - 1 0 0 1 0	0 0 0 0 0 0 0 0 1 0	1 2 0 2 0 1 0 0 0 0	2 0 0 0 0 1 1 0 1 1
Andrena (Genyandrena) mackieae	0 0 0 1 0 1 2 0 0 1	0 2 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 1 0 0	1 2 0 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 1 0	0 0 0 0 0 0 1 0 1 0	1 2 0 0 0 0 0 1 0 0	1 1 1 0 0 0 1 0 0 0
Andrena (Gonandrena) persimulata	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 ? ? ? 1 ? 0 0	? 0 0 0 0 ? 0 ? 1 ?	0 ? 0 0 0 1 0 0 ? 0	0 0 0 2 1 0 0 0 0 0	1 2 0 0 1 0 0 0 0 0	2 ? 1 ? ? 1 ? 0 1 ?
Andrena (Graecandrena) graecella	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 0 0 0 0 0 1 0 0 0	0 1 1 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 1 0 1 0 0 0 0 0 0	1 1 0 1 1 0 0 0 0 0	1 1 0 0 0 0 0 1 0 0
Andrena (Hamandrena) nasuta	0 0 2 1 0 1 1 0 0 0	1 1 0 1 2 0 1 0 1 0	3 1 2 1 1 0 1 0 0 0	0 2 0 1 1 0 0 0 0 0	0 0 1 0 1 1 0 0 0 1	0 0 0 2 0 0 0 0 0 0	1 0 0 2 1 1 0 0 1 0	0 0 0 1 0 1 1 0 1 1
Andrena (Hesperandrena) baeriae	0 0 0 1 0 1 2 0 0 0	0 2 0 1 0 0 0 0 1 0	0 1 0 1 0 0 1 1 0 0	0 0 0 0 0 0 0 1 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 2 0 0 0 0 0 0 0 3	2 0 1 0 0 0 1 0 1 1
Andrena (Holandrena) labialis	0 0 0 1 0 1 2 0 0 0	0 0 0 1 1 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 1 0 0 0 0 0 0	2 0 0 0 0 1 0 0 1 0	0 0 3 1 0 0 0 0 1 3	1 2 1 2 0 2 0 1 1 0	2 0 0 0 0 0 0 0 0 0
Andrena (Hoplandrena) carantonica	0 0 0 1 0 1 2 0 0 1	0 0 0 1 0 0 0 0 1 0	0 1 0 ? 1 0 0 ? 1 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 0 2	0 0 0 0 0 0 0 0 1 0	1 2 0 2 1 1 0 0 1 3	2 0 0 2 1 0 ? 1 1 ?
Andrena (Hoplandrena) trimmerana	0 0 0 1 0 1 2 0 0 1	0 0 0 1 0 0 0 0 1 0	0 1 0 0 1 0 1 - 1 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 0 2	1 0 0 0 1 0 0 0 1 0	1 2 0 2 1 1 0 0 1 3	2 0 0 2 1 0 1 1 1 1
Andrena (Hyperandrena) bicolorata	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 2 0 0 0 0 0 0 0 0	0 0 0 1 0 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 0 2 0 2 0 0 0 0 2	2 0 0 0 0 0 0 1 0 0
Andrena (Iomelissa) violae	0 1 1 1 0 1 3 0 0 0	0 0 0 1 2 0 1 0 1 0	0 0 0 1 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 1 0 1 0 0 0 0 0 0	1 2 0 0 1 0 0 0 1 0	2 0 0 1 0 1 0 1 1 1
Andrena (Larandrena) miserabilis	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 1 0 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 1 0 0 0 0 0 0 0 0	1 2 0 2 2 0 0 0 0 0	2 1 1 0 0 1 1 1 1 1
Andrena (Larandrena) ventralis	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 1 0 0	0 2 1 - 0 0 0 0 0 0	0 0 0 0 1 1 0 0 1 0	0 0 0 0 0 0 0 0 1 0	1 2 0 0 2 0 0 0 0 0	2 1 1 0 0 1 1 1 1 1
Andrena (Leimelissa) bairacumensis	0 0 1 1 0 ? ? 0 0 0	0 0 0 1 2 0 1 0 1 1	0 1 0 1 0 1 1 0 0 0	0 2 0 0 2 0 1 2 0 0	1 2 0 0 0 1 0 0 1 0	0 1 0 1 0 0 0 0 0 0	1 0 0 2 2 0 0 0 0 0	1 1 1 1 0 0 0 0 1 1
Andrena (Lepidandrena) curvungula	0 0 0 1 0 0 3 0 1 0	0 0 0 0 1 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	1 2 0 0 1 0 0 0 1 3	2 0 0 0 0 0 0 1 1 0
Andrena (Lepidandrena) rufizona	0 0 0 1 0 0 3 0 1 0	0 0 0 0 1 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	1 2 0 0 1 0 0 0 1 3	2 0 0 0 0 0 0 1 1 0
Andrena (Leucandrena) barbilabris	0 0 0 1 1 1 2 0 0 1	0 0 0 1 0 0 0 0 1 0	0 1 0 1 1 0 1 0 0 0	0 0 1 - 1 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 1 0 0 0 0 1 0	1 2 0 2 1 0 0 0 1 0	2 0 0 0 0 0 1 1 1 1

Unknown character states are coded with "?", not applicable ones with "–", and multistate ones with "$".

Tab. 4. Data matrix for the cladistic analysis of *Andrena* (continued).

	81–90	91–100	101–110	111–120	121–130	131–140	141–150	151–160	161–162
Ancestor	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 - 0	- 0 - - 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0
Ancylandrena atoposoma	0 1 0 0 0 1 0 2 0 0	0 0 0 0 0 1 1 0 - 0	- 1 0 1 0 0 0 0 0 0	0 0 0 0 1 0 0 0 0 0	2 0 0 0 0 0 1 0 0 0	0 0 1 0 2 0 2 0 0 0	0 0 0 0 0 0 ? 1 0 -	- 1 0 0 0 0 0 0 0 0	1 1
Cubiandrena cubiceps	0 1 3 0 1 0 0 2 1 -	0 0 0 2 0 3 1 0 - 0	- 1 0 0 1 0 0 0 0 1	0 0 0 0 1 4 4 1 0 0	0 0 4 0 0 0 0 0 0 2	1 0 0 0 2 0 2 1 1 -	1 0 0 0 0 0 0 0 0 -	- 0 1 - - 0 0 0 0 0	1 1
Euherbstia excellens	0 0 0 0 0 0 0 0 1 -	0 0 0 0 0 0 0 0 - 0	- 0 - - 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 0 0 0 0 0 0 0 1 0	0 0 1 0 0 0 0 0 4 0	1 0 0 0 0 0 0 0 0 -	- 0 2 0 0 0 1 2 0 1	0 0
Megandrena enceliae	0 1 0 0 0 0 0 0 0 0	0 0 0 1 1 6 1 1 ? 1	- 2 0 1 0 0 0 0 0 2	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0	0 0 1 0 2 0 0 0 4 0	0 0 0 0 0 0 0 1 1 0	0 0 2 1 0 0 1 2 0 2	0 0
Orphana inquirenda	0 0 0 0 0 0 0 0 3 -	0 0 0 0 1 6 1 0 - 0	- 2 0 1 0 0 0 0 0 0	0 0 0 0 1 0 0 0 1 0	0 0 0 0 0 0 0 0 1 0	0 0 1 2 0 1 2 0 3 1	1 0 0 0 0 0 0 0 0 -	- 0 2 2 0 0 0 0 0 0	1 0
Andrena (Aciandrena) aciculata	1 0 0 0 0 0 0 0 0 0	0 1 0 0 0 1 1 0 - 0	- 1 0 2 0 0 0 0 0 1	0 0 0 0 1 0 0 0 0 0	0 0 0 1 0 1 0 0 0 0	0 0 1 0 0 0 0 0 4 1	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 1 0 0 0 0	1 0
Andrena (Aenandrena) aeneiventris	0 1 1 0 2 0 0 2 0 0	3 1 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 0 0 0 0 1	0 0 0 0 0 0 0 1 1 0	0 1 0 0 0 0 0 2 0 0	1 0
Andrena (Agandrena) agilissima	0 0 0 1 - 1 0 0 0 2	4 0 3 0 0 1 1 0 - 0	- 2 0 1 1 0 0 0 0 2	0 0 0 1 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 4 1	0 1 0 0 0 0 2 1 1 0	0 1 0 1 2 0 0 0 1 0	1 0
Andrena (Anchandrena) angustella	1 0 0 0 0 0 0 0 0 0	0 0 0 1 1 6 1 1 0 1	0 3 1 1 0 0 0 0 1 2	0 0 0 0 0 0 5 0 0 0	0 0 5 0 0 0 0 0 0 0	0 0 1 2 $ 1 0 0 0 0	? 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 1 0	0 0
Andrena (Andrena) helvola	1 0 0 0 0 0 0 0 0 0	0 0 0 1 1 6 1 1 0 1	0 3 1 1 0 0 0 0 1 2	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 1 0 0 3 1	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 1 0	0 0
Andrena (Andrena) praecox	1 0 0 0 0 0 0 0 0 0	0 0 0 1 1 6 1 1 0 1	0 3 1 1 0 0 0 0 1 2	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 1 0 0 3 1	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 1 0	0 0
Andrena (Aporandrena) coactipostica	1 1 1 0 0 0 0 2 0 0	0 0 0 0 0 1 1 0 0 0	- 1 0 0 0 0 0 0 0 1	1 0 1 0 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 1 2 1 0	0 0
Andrena (Archiandrena) banksi	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 1 3 0 3	2 3 1 1 0 0 0 0 0 2	0 0 0 0 0 0 5 0 0 0	0 0 5 0 0 0 0 0 0 0	0 0 1 0 0 1 2 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 1 0	0 -
Andrena (Augandrena) plumiscopa	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 4 1 1 0 1	0 3 0 1 0 0 0 0 1 2	0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 2 0 0 0 0 0 0	1 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 1 0	1 0
Andrena (Biareolina) lagopus	0 1 0 1 0 1 0 2 0 2	4 0 1 2 0 1 1 3 0 3	0 1 0 0 1 0 0 0 0 2	0 0 0 2 1 0 0 0 0 0	0 0 0 0 1 0 - 0 0 0	0 0 0 0 0 1 0 0 4 1	0 0 1 0 0 0 0 1 2 3	1 1 0 1 0 0 0 0 0 0	1 1
Andrena (Brachyandrena) colletiformis	0 1 1 1 0 1 0 2 0 2	4 2 1 0 0 1 1 0 - 0	- 1 1 0 1 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 -	- 1 0 1 0 0 1 2 0 0	0 0
Andrena (Calcarandrena) gamskrucki	0 1 0 0 0 0 0 2 0 0	0 0 0 0 0 0 1 1 0 1	0 1 0 1 0 0 2 0 * 1	1 1 1 0 0 3 7 0 0 2	2 1 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 2 1 1 2	0 1 0 0 0 0 0 0 0 0	0 0
Andrena (Callandrena) accepta	0 1 0 0 0 0 0 2 0 0	2 0 0 0 0 5 1 1 0 2	0 1 1 0 0 0 0 1 0 2	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 1 0 0 0 0 1 1 3	0 1 0 1 0 1 0 0 0 0	0 0
Andrena (Calomelissa) prostomias	0 1 0 0 0 1 0 0 0 0	2 1 0 0 0 1 1 0 - 0	- 1 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 3	1 1 3 1 1 0 0 0 1 0	0 0
Andrena (Campylogaster) erberi	0 1 1 1 0 1 0 2 0 0	4 2 1 2 0 1 1 0 - 0	- 1 0 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 2 1 3 0 0 0 0 0	0 0 0 0 0 0 2 1 1 0	0 1 0 1 0 0 0 2 0 0	0 0
Andrena (Carandrena) aerinifrons	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 1 1 0 2	1 3 1 1 0 1 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 1 2	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Charitandrena) hattorfiana	0 1 2 0 1 0 0 2 0 0	4 0 0 0 0 0 0 0 - 0	- 0 - - 0 0 0 0 0 2	1 0 1 0 0 3 3 0 0 1	0 1 1 0 0 0 0 0 1 1	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 1 1	0 1 $ 0 2 0 0 0 0 0	1 1
Andrena (Chlorandrena) humilis	1 1 0 0 0 0 0 2 0 0	2 0 0 0 0 2 1 0 - 0	- 1 1 0 0 0 0 0 0 2	1 2 1 0 0 1 2 0 0 1	0 1 2 0 0 0 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 2 1 1 2	1 1 0 1 1 0 0 0 0 0	0 0
Andrena (Chrysandrena) fulvago	0 0 0 0 1 0 0 0 0 0	3 0 0 0 0 2 1 0 - 0	- 1 1 0 0 0 0 0 1 2	0 0 0 0 0 3 6 0 0 0	0 0 3 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 4 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 1 2 0 0	0 0
Andrena (Cnemidandrena) nigriceps	1 1 0 0 0 1 0 0 0 0	0 0 0 1 1 6 1 1 0 2	1 3 1 1 0 0 0 0 1 1	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 1 0 0 1 -	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Conandrena) bradleyi	1 0 0 0 0 0 0 0 0 0	1 0 0 0 0 1 1 1 0 2	0 3 1 1 0 0 0 0 1 2	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 3 -	0 0 0 0 0 0 0 0 1 1 -	- 1 0 1 0 0 0 0 2 1	2 0
Andrena (Cordandrena) cordialis	0 1 0 0 2 0 0 2 0 0	3 1 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 -	- 1 0 0 0 0 1 2 0 0	0 0
Andrena (Cremnandrena) anisochlora	1 0 0 0 0 0 0 - 0 0	0 0 0 0 0 4 1 0 - 0	- 3 1 0 0 0 0 0 1 2	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 0 1 2 0 0 0 0 0 0	1 0 1 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 1 0	0 0
Andrena (Cryptandrena) ventricosa	0 1 0 0 2 0 0 2 0 0	4 2 1 0 0 1 1 0 - 0	- 1 0 0 1 0 0 0 0 2	1 2 1 0 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 2 1 1 -	- 1 3 1 0 0 0 0 0 0	1 1
Andrena (Dactylandrena) caliginosa	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 4 1 0 - 0	- 3 1 0 0 0 0 0 1 2	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 0 1 2 0 0 0 0 6 0	0 0 1 0 0 0 0 1 1 0	1 1 0 1 0 0 0 0 1 0	0 0
Andrena (Dasyandrena) obscuripostica	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 1 3 0 3	1 3 1 1 0 0 0 0 ? 2	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 ? 1 0 0 ? 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 2 0 0 0 0 0	1 0
Andrena (Derandrena) vandykei	1 0 0 0 0 0 0 1 0 0	0 2 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 1	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 ? 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 3 1 1 0 0 0 0 0	1 1
Andrena (Diandrena) chalybea	1 1 0 0 2 0 0 2 0 0	4 0 4 0 0 1 1 0 - 0	- 1 0 0 0 0 0 0 1 2	0 0 0 0 1 0 0 0 0 0	0 0 0 0 1 0 - 0 1 0	0 0 1 0 0 0 0 0 4 0	1 0 0 0 0 0 0 1 1 3	0 1 $ 1 0 0 0 0 2 0	0 0
Andrena (Didonia) mucida	0 1 0 0 0 0 0 2 0 0	3 0 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 2	0 0 0 0 0 3 3 2 0 0	0 0 1 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 -	- 1 0 1 0 0 1 2 0 0	0 0
Andrena (Distandrena) longibarbis	1 - 0 0 0 0 0 1 0 0	0 1 0 0 0 1 1 0 - 0	- 1 0 0 1 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 1 0 0 5 0	0 0 0 0 0 0 0 1 1 0	0 1 $ 1 0 0 0 0 0 0	0 0
Andrena (Euandrena) bicolor	0 1 0 0 0 0 0 2 0 0	0 0 0 0 0 2 1 1 0 2	0 1 1 0 0 1 0 0 1 1	0 0 0 0 0 0 5 0 0 0	0 0 5 0 0 0 0 0 0 0	0 0 1 2 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 1 2 0 0	0 0
Andrena (Fumandrena) fumida	1 0 0 0 0 0 0 0 0 0	0 1 0 0 0 1 1 0 - 0	- 1 1 2 1 0 0 0 0 1	0 0 0 0 0 1 2 3 0 0	0 0 2 0 0 2 0 0 0 1	0 0 1 0 0 0 0 0 4 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Fuscandrena) fuscicollis	1 0 0 0 0 0 0 0 0 0	3 2 0 0 0 1 1 0 - 0	- 1 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 2 0 0 0 0	0 0 0 0 0 1 0 0 0 0	1 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Geissandrena) trevori	0 1 0 0 0 0 0 0 0 0	2 0 0 0 0 5 1 1 0 1	0 3 1 1 0 0 0 0 1 2	0 0 0 0 0 2 1 0 0 0	0 0 5 0 0 0 1 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 1 0	0 0
Andrena (Genyandrena) mackieae	1 0 0 0 0 0 0 0 0 0	0 1 0 0 0 1 1 0 - 0	- 3 1 1 0 0 0 0 0 1	0 0 0 0 0 0 5 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 0 0 0 5 0	0 0 0 0 0 0 0 1 2 0	0 1 $ 1 0 0 0 0 0 0	0 0
Andrena (Gonandrena) persimulata	1 0 0 0 1 0 0 0 0 0	4 0 1 0 0 1 1 1 0 2	0 3 1 0 1 0 0 0 1 2	0 0 0 0 0 0 1 0 0 0	0 0 5 0 0 1 0 0 0 0	0 0 1 0 0 1 ? 0 3 -	0 0 0 0 0 0 0 1 1 3	1 ? 0 1 ? 0 0 0 ? ?	? ?
Andrena (Graecandrena) graecella	1 0 0 0 0 0 0 0 0 0	0 1 0 0 0 1 1 0 - 0	- 1 0 2 1 0 0 0 0 1	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 -	- 1 0 1 0 0 0 0 0 0	0 0
Andrena (Hamandrena) nasuta	0 0 0 0 0 0 0 2 0 0	2 0 0 0 0 0 0 0 - 0	- 0 - - 0 0 0 0 0 0	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 0 0 0 4 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Hesperandrena) baeriae	1 1 0 0 0 0 0 0 2 0	0 0 0 1 1 6 1 1 0 2	2 1 1 0 1 0 0 0 0 1	0 0 0 0 0 0 1 0 0 $	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 ? 0 0 0 0	0 0 0 0 0 0 0 1 1 3	0 1 0 0 1 0 0 0 0 0	1 0
Andrena (Holandrena) labialis	0 1 0 1 - 1 0 0 2 0	4 2 $ 0 0 1 1 0 - 0	- 1 1 0 1 0 0 0 0 2	1 0 1 0 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 1 0 0 0 1 1 1 0 -	- 1 3 1 0 0 0 0 1 0	0 0
Andrena (Hoplandrena) carantonica	1 0 0 0 0 0 0 0 0 0	0 0 0 2 0 1 1 0 - 0	- 3 1 1 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 0 0 0 0 0	0 0 1 0 0 0 0 1 1 0	0 1 0 1 0 0 1 2 0 0	0 0
Andrena (Hoplandrena) trimmerana	0 0 0 0 0 0 0 0 0 0	0 0 0 2 0 1 1 0 - 0	- 3 1 1 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 0 0 0 0 0	0 0 1 0 0 0 0 1 1 0	0 1 0 1 0 0 1 2 0 0	0 0
Andrena (Hyperandrena) bicolorata	0 1 0 0 0 0 0 0 0 0	4 0 3 0 0 1 1 1 0 1	0 3 1 1 0 0 0 0 1 2	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 4 0	0 0 0 0 0 0 2 1 1 3	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Iomelissa) violae	0 0 0 0 0 0 0 0 0 0	0 2 0 0 0 1 1 3 0 3	2 1 1 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 1 0 0 0 0 1 1 -	- 1 0 0 2 - 0 0 0 0	1 1
Andrena (Larandrena) miserabilis	1 0 0 0 0 0 0 0 0 0	2 0 0 0 0 1 1 1 0 2	0 3 1 1 1 0 0 0 1 2	0 0 0 0 0 0 1 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 1 0 0 1 1 0 6 0	0 0 0 0 0 0 0 1 1 2	1 1 0 1 0 0 0 0 1 0	0 0
Andrena (Larandrena) ventralis	1 0 0 0 0 0 0 0 0 0	2 0 1 0 0 1 1 2 0 1	0 3 1 1 1 0 0 0 1 2	0 0 0 0 0 0 5 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 1 1 0 6 0	0 0 0 0 0 0 0 1 1 2	1 1 0 1 0 0 0 0 1 0	1 0
Andrena (Leimelissa) bairacumensis	1 1 1 0 0 1 0 0 0 0	0 1 0 1 1 6 1 0 - 0	- 1 1 1 1 0 2 0 0 1	0 0 0 0 0 0 0 0 0 0	2 0 0 0 0 0 0 0 0 0	0 0 1 0 1 1 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	? 0
Andrena (Lepidandrena) curvungula	0 1 1 0 0 0 0 2 0 0	4 0 0 0 0 2 1 1 0 2	0 1 1 1 1 1 1 0 0 2	1 1 1 0 0 0 7 0 0 1	1 1 1 0 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 1 1	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Lepidandrena) rufizona	0 1 1 0 0 0 0 2 0 0	4 0 0 0 0 2 1 3 0 3	0 1 1 0 1 1 1 0 0 2	1 1 1 0 0 0 7 0 0 1	1 1 1 0 0 0 0 0 0 0	0 1 1 0 0 0 0 0 1 -	0 0 0 0 0 0 0 1 1 0	1 1 0 1 0 0 0 0 0 0	0 0
Andrena (Leucandrena) barbilabris	1 0 0 0 0 0 0 0 0 0	2 0 1 0 0 1 1 2 0 1	0 3 1 1 1 0 0 0 1 2	0 0 0 0 0 0 5 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 1 2 0 1 1 0 6 0	0 0 0 0 0 0 2 1 1 0	0 1 0 1 0 0 0 0 1 0	0 0

Unknown character states are coded with "?", not applicable ones with "–", and multistate ones with "$".

Tab. 4. Data matrix for the cladistic analysis of *Andrena* (continued).

	1 2 3 4 5 6 7 8 9 10	1 2 3 4 5 6 7 8 9 20	1 2 3 4 5 6 7 8 9 30	1 2 3 4 5 6 7 8 9 40	1 2 3 4 5 6 7 8 9 50	1 2 3 4 5 6 7 8 9 60	1 2 3 4 5 6 7 8 9 70	1 2 3 4 5 6 7 8 9 80
Andrena (Longandrena) dolini	- 0 1 1 0 1 3 0 0 0	0 0 0 1 1 2 1 0 1 1	0 1 0 1 0 0 ? ? 0 0	0 2 0 0 2 0 0 2 0 0	0 0 0 0 0 0 0 0 1 0	0 0 0 1 0 0 0 0 0 0	1 2 0 1 0 0 0 0 2 0	1 ? 1 1 0 0 0 0 1 1
Andrena (Margandrena) marginata	0 0 0 1 0 0 2 0 0 0	0 0 0 1 1 0 0 0 1 0	0 1 0 2 1 0 1 0 0 0	0 2 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 1 0 0 1 0 0 0 1 0	1 2 0 0 1 0 0 0 0 0	2 0 0 0 0 1 1 1 0 1
Andrena (Melanapis) fuscosa	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 1 0 0 0 0 0	0 2 0 0 0 1 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 0	1 2 1 3 1 0 0 1 3 0	2 0 0 1 0 1 1 0 1 1
Andrena (Melandrena) thoracica	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 2 0 1 0 0 0 0 0 0	0 0 1 1 0 - - 0 0 0	0 0 0 0 0 0 0 0 1 0	1 1 0 3 1 0 0 0 3 0	3 0 0 0 0 0 0 1 1 0
Andrena (Melandrena) vaga	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 0 0 0	0 2 0 0 0 0 0 1 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 1 0 3 1 0 0 0 1 0	3 0 0 1 0 0 0 1 1 0
Andrena (Melittoides) melittoides	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 0 0 1 0 0 1 0 0 0	2 2 0 0 0 0 1 2 0 0	0 0 0 0 0 0 0 0 1 1	0 0 0 0 0 0 0 0 0 0	1 1 0 2 0 0 0 1 0 0	2 0 1 3 2 0 0 1 1 1
Andrena (Micrandrena) melanochroa	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 2 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 1 0 1 0 0 0 0 0 0	1 2 0 0 1 0 0 0 0 0	2 0 1 0 0 0 0 1 1 0
Andrena (Micrandrena) minutula	0 0 0 1 0 1 2 0 0 0	0 2 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	1 2 0 0 1 0 0 0 0 0	2 0 0 2 1 0 0 1 1 0
Andrena (Micrandrena) proxima	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 0 0 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 1 0 0 0 0 0 0	2 0 0 0 0 0 0 1 0 0
Andrena (Nobandrena) nobilis	0 0 0 1 1 1 1 0 0 0	0 0 0 1 1 0 0 0 1 0	0 0 0 0 0 0 1 0 0 0	0 0 0 0 1 0 1 2 0 0	0 0 0 0 0 1 0 0 1 0	0 0 0 1 0 0 0 0 1 0	1 1 0 0 1 0 0 0 0 0	2 0 0 1 0 0 1 1 1 1
Andrena (Notandrena) chrysosceles	0 0 0 1 0 1 2 0 0 0	0 2 0 1 0 0 0 0 1 0	0 1 0 1 1 0 1 0 0 0	0 0 0 0 0 1 0 0 0 1	0 1 0 0 1 1 0 0 1 0	0 1 0 0 1 0 0 0 1 0	1 2 0 0 1 1 0 0 1 0	2 0 0 0 0 1 1 0 1 1
Andrena (Notandrena) nitidiuscula	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 0 0 0 0 1 0 0 0 1	0 1 0 0 0 0 0 0 0 0	0 1 0 0 1 0 0 0 1 0	1 1 0 1 1 1 1 0 0 0	2 0 0 0 0 1 1 0 1 1
Andrena (Oligandrena) macrocephala	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 1 1 - 0 0	0 2 1 0 0 0 0 1 0 0	0 2 0 0 1 1 0 0 1 0	0 0 0 0 0 0 0 0 1 0	1 2 0 2 1 0 0 0 0 0	2 1 0 0 0 0 1 0 0 0
Andrena (Onagrandrena) oenotherae	0 0 0 1 0 1 2 0 0 0	0 0 0 0 0 0 0 0 1 0	0 1 2 1 1 0 1 0 0 0	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 1 0	1 2 0 3 1 0 0 0 1 0	2 0 0 0 0 0 0 1 1 0
Andrena (Opandrena) cressoni	0 0 0 1 0 1 ? 0 0 0	0 2 0 1 0 0 0 0 1 0	0 1 0 1 1 0 1 0 0 0	0 0 0 0 0 0 0 0 0 *	0 1 1 0 1 1 0 1 1 0	0 0 0 0 1 0 0 1 0 0	1 2 0 0 1 1 0 0 1 0	3 1 0 0 0 1 1 0 1 1
Andrena (Orandrena) oralis	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 0 0 0 1 0 0 0	0 1 1 0 0 0 0 0 0 0	0 0 0 0 1 1 3 0 1 0	0 0 0 1 0 0 0 0 0 0	1 1 1 0 1 0 0 1 0 0	2 1 0 0 0 0 0 1 1 1
Andrena (Oreomelissa) mitakensis	0 0 0 1 0 1 ? 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 1 1 1 0 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 1 1 1 0 0 0 0 0 3	1 0 0 0 1 1 0 0 0 0	3 0 0 1 0 0 0 1 1 0
Andrena (Osychnyukandrena) cochlearicalcar	0 0 0 1 0 0 ? 0 0 0	0 0 0 0 0 0 0 0 1 3	0 1 0 0 0 0 1 0 0 0	0 2 0 0 0 0 0 0 0 0	2 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	1 1 0 0 1 0 0 0 0 0	2 0 0 0 0 0 0 1 0 0
Andrena (Pallandrena) pallidicincta	0 0 0 1 0 0 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 0 0 1 1 0 0 0 0 0	0 0 0 0 0 1 1 0 0 0	0 0 0 1 0 0 0 0 1 0	1 2 0 1 1 0 0 0 0 0	2 0 0 0 0 0 0 1 0 0
Andrena (Parandrena) andrenoides	0 0 0 1 0 1 1 0 0 0	0 2 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 1 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 1 0 0 0 1 0	0 0 0 0 1 0 0 0 1 0	1 2 0 0 1 0 0 0 1 0	2 1 1 0 0 1 1 1 1 1
Andrena (Parandrenella) atrata	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 0 0 0 1 0 0 0	0 1 0 0 1 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 1 0 1 0 0 0 0 1 0	1 0 0 1 1 0 0 0 0 0	2 1 1 0 0 0 0 1 1 0
Andrena (Parandrenella) dentiventris	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 0 0 1 0 0 0 0 1 0	1 0 0 1 1 0 0 0 0 0	2 1 1 0 0 0 0 1 1 0
Andrena (Pelicandrena) atypica	0 0 0 1 0 0 2 0 0 0	0 2 0 0 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 1 0 1 0 0 0 0 1 0	1 2 0 0 1 1 0 0 0 0	2 0 1 0 0 0 0 1 1 1
Andrena (Planiandrena) planirostris	0 0 $ 1 0 1 2 0 0 0	0 2 0 0 0 0 0 0 1 1	0 1 0 0 0 1 1 0 0 0	0 0 0 0 2 0 0 0 0 0	2 2 0 0 1 0 0 0 1 0	0 0 0 1 0 0 0 0 0 0	1 1 0 0 1 2 0 0 0 0	0 0 1 1 0 0 0 0 0 0
Andrena (Plastandrena) tibialis	0 0 0 1 0 1 2 0 0 1	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 1 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 2	1 2 0 2 1 0 0 1 1 0	2 0 0 0 0 0 0 1 0 0
Andrena (Platygalandrena) fedtschenkoi	0 0 0 1 0 1 1 1 0 0	0 0 1 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 1 1 0	0 0 0 1 0 0 0 1 0 3	1 2 0 2 0 0 0 0 3 0	2 0 0 1 0 0 0 1 0 0
Andrena (Platygalandrena) tecta	0 0 0 1 0 1 1 1 0 0	0 0 0 1 1 1 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 0 0 0 0 0 0 0 0 3	1 2 0 3 0 0 0 0 3 0	2 0 0 1 0 0 0 1 0 1
Andrena (Poecilandrena) labiata	0 0 0 1 0 1 1 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 1 0	0 1 0 1 0 0 0 0 0 0	1 2 0 1 0 0 0 0 0 0	2 0 0 0 0 0 0 1 1 0
Andrena (Poliandrena) polita	0 0 0 1 0 1 2 0 0 0	0 0 0 1 2 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 0 0 1 0 0 0 0 0 0	2 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 2 0 0 0 0 0 0 0 0	2 0 0 0 0 0 0 1 1 0
Andrena (Ptilandrena) erigeniae	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 1 0 0 1 0 0 0 1 0	1 2 0 1 1 1 0 0 0 0	2 1 1 0 0 0 1 0 1 1
Andrena (Ptilandrena) fulvata	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 1 1 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 2 0 0 0 0 0 0	1 1 0 0 1 1 0 0 0 0	2 0 1 0 0 1 1 0 1 1
Andrena (Ptilandrena) grossella	0 0 2 1 0 0 2 0 0 0	0 2 0 0 2 2 1 - 1 0	0 1 0 2 1 1 1 0 0 0	0 2 0 0 0 0 0 1 0 0	0 1 0 0 1 1 0 0 0 0	0 0 0 2 0 0 0 0 1 0	1 1 0 1 0 0 0 0 0 0	2 0 0 1 0 1 1 0 1 1
Andrena (Ptilandrena) vetula	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 2 1 0 1 - 0 0	0 0 0 0 0 1 0 0 0 0	0 2 0 0 1 1 0 0 0 0	0 0 0 2 0 0 0 0 0 0	1 2 0 3 1 0 0 0 1 0	2 0 0 1 0 1 1 1 1 1
Andrena (Rhacandrena) brevipalpis	0 0 0 1 0 0 ? 0 0 0	3 0 0 0 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 0 0 1 0 0 0 0 1 0	1 2 0 2 2 0 0 0 0 0	2 0 0 0 0 0 0 1 1 0
Andrena (Rhaphandrena) prima	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 1 1 0 1 1 0 0	0 2 0 0 1 1 0 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 1 0	1 0 0 0 1 0 0 0 1 0	2 0 1 0 0 1 1 0 1 1
Andrena (Rufandrena) rufiventris	0 0 0 1 0 0 2 0 0 0	0 0 0 0 0 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 1 0 0 0 0 0 0 1 0	1 2 0 1 0 1 0 0 0 0	2 1 1 0 0 1 0 1 1 1
Andrena (Scitandrena) scita	0 0 0 1 0 1 3 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 0 0 0 1 0 0 0	0 0 0 1 0 0 1 2 0 0	0 0 0 0 0 0 0 0 1 0	0 0 0 0 0 0 0 0 1 0	1 2 0 3 0 0 0 0 1 0	2 0 0 0 0 1 0 0 1 1
Andrena (Scoliandrena) osmioides	0 0 0 1 0 1 3 0 0 0	2 1 0 0 0 0 0 0 1 0	2 1 0 2 1 0 1 0 0 0	1 0 1 0 1 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	1 2 0 0 0 0 0 0 0 0	2 1 0 0 0 1 1 0 1 1
Andrena (Scrapteropsis) fenningeri	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 2 0 3 2 0 0 0 1 0	2 0 1 0 1 0 0 1 0 0
Andrena (Simandrena) propinqua	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	1 2 0 2 1 0 0 0 1 0	2 0 0 0 0 0 0 1 0 1
Andrena (Stenomelissa) halictoides	0 0 1 1 0 1 2 0 0 0	0 0 0 0 2 0 1 0 0 0	0 1 2 2 1 0 1 - 0 1	0 2 0 0 1 0 0 0 0 0	0 0 0 0 1 0 0 0 1 1	0 1 0 2 0 1 0 0 0 0	1 0 0 0 2 0 0 1 0 0	? 0 1 0 0 0 1 ? 1 1
Andrena (Suandrena) suerinensis	0 0 0 1 0 1 3 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 2 1 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 1 0 0 1 1 0 0 1 0	2 0 0 0 0 0 0 1 1 1
Andrena (Taeniandrena) ovatula	0 0 0 1 0 1 $ 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	2 1 0 0 1 1 0 0 0 0	0 0 0 1 0 0 0 0 0 0	1 2 0 3 0 0 0 0 1 3	2 0 0 0 0 0 0 1 0 0
Andrena (Tarsandrena) tarsata	0 0 0 1 0 1 2 0 1 1	0 0 0 1 0 0 0 0 1 0	0 0 0 0 0 0 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 0 0 0 0 0 0 0 1 0	1 2 0 2 1 0 0 0 1 0	2 0 0 1 2 1 0 0 1 1
Andrena (Thysandrena) candida	0 0 0 1 0 1 $ 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 1 1 0 0 0 0	0 1 0 0 0 0 0 0 1 0	1 2 0 0 1 1 0 0 1 0	2 0 0 0 0 0 0 1 0 0
Andrena (Trachandrena) haemorrhoa	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 1 0 0 0 0 0 0	0 0 4 1 0 0 0 0 0 0	1 0 1 2 2 0 1 0 1 1	2 0 0 0 0 0 0 1 1 0
Andrena (Trachandrena) rugosa	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	1 0 1 2 2 0 1 0 1 2	2 0 0 2 1 0 0 1 0 0
Andrena (Troandrena) troodica	0 0 2 1 0 0 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 2 1 1 0 1 0 0 0	0 2 0 1 0 0 0 0 0 0	1 1 1 0 1 0 0 0 0 0	0 0 1 0 0 0 0 0 0 2	1 2 0 0 1 1 0 0 1 0	2 0 0 0 0 0 0 0 1 1
Andrena (Truncandrena) truncatilabris	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	1 1 0 1 0 0 1 0 0 0	0 0 0 1 0 0 0 2 0 0	0 0 0 0 1 1 0 0 1 0	0 0 0 0 0 0 0 0 0 0	1 0 0 0 1 0 0 0 0 0	2 0 0 0 0 0 0 1 1 1
Andrena (Tylandrena) erythrogaster	0 0 0 1 0 1 2 0 1 1	0 0 0 1 0 0 0 0 1 0	0 0 0 2 1 0 1 1 0 0	0 2 0 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 2 0 0 2 0 0 0 1 0	2 0 0 0 0 1 1 1 1 1
Andrena (Ulandrena) schulzi	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 1 0	0 0 0 0 0 0 0 0 0 3	1 1 0 0 1 0 0 0 0 0	2 0 0 0 0 0 0 1 0 0
Andrena (Zonandrena) flavipes	0 0 0 1 0 1 2 0 0 0	0 0 0 1 0 0 0 0 1 0	0 1 0 1 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 1 0 1 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 2 0 2 1 0 1 0 1 1	2 0 0 0 0 0 0 1 0 0

Unknown character states are coded with "?", not applicable ones with "–", and multistate ones with "$".

Tab. 4. Data matrix for the cladistic analysis of *Andrena* (continued).

	1 2 3 4 5 6 7 8 9	10 1 2 3 4 5 6 7 8 9 0	11 1 2 3 4 5 6 7 8 9 0	12 1 2 3 4 5 6 7 8 9 0	13 1 2 3 4 5 6 7 8 9 0	14 1 2 3 4 5 6 7 8 9 0	15 1 2 3 4 5 6 7 8 9 0	16 1 2 3 4 5 6 7 8 9 0	1 2
Andrena (Longandrena) dolini	1 0 0 0 0 0 0 0 2 0	0 1 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 0 0 1	0 0 0 1 0 1 0 0 0 0	3 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 1 1 2	0 1 0 1 0 0 0 0 1 0	0 0
Andrena (Margandrena) marginata	0 1 0 0 1 0 0 2 0 0	3 0 0 0 0 5 1 3 0 3	0 1 1 0 0 0 0 0 0 0 2	0 0 0 0 0 3 3 0 0 0	0 0 1 0 0 1 0 0 0 0	3 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0 -	- 1 0 1 0 0 0 0 0 0	0 0
Andrena (Melanapis) fuscosa	0 1 2 1 2 1 0 0 0 2	4 0 3 - 0 1 1 3 0 3	0 1 0 0 1 0 0 0 0 2	0 0 0 1 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 4 0	0 0 0 0 0 0 1 1 1 1	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Melandrena) thoracica	0 1 0 0 0 0 0 2 0 0	1 0 0 2 0 1 1 1 0 2	3 3 1 1 1 0 0 0 1 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 2 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Melandrena) vaga	0 1 0 0 0 1 0 2 0 0	2 0 $ 0 0 1 1 1 0 2	3 3 1 1 1 0 0 0 1 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 4 0	0 0 0 0 0 0 1 1 1 0	0 1 0 1 0 0 0 0 0 0	1 0
Andrena (Melittoides) melittoides	1 - 0 0 0 0 0 1 2 0	0 0 0 2 0 7 1 1 0 2	3 3 1 1 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 1 0	3 0 0 2 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 -	- 0 2 0 - 0 2 2 2 0	1 0
Andrena (Micrandrena) melanochroa	1 - 0 0 0 0 0 - 0 0	3 1 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 2 0 0 0 0	0 0 1 0 0 1 0 0 6 1	0 0 0 0 0 0 0 1 1 1	0 1 0 1 0 0 0 0 0 0	1 1
Andrena (Micrandrena) minutula	0 0 0 0 1 0 0 0 0 0	3 1 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 2 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 1 0 0	0 0
Andrena (Micrandrena) proxima	0 1 0 0 2 0 0 2 0 0	4 0 2 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 -	- 1 0 1 0 0 0 1 0 0	0 0
Andrena (Nobandrena) nobilis	1 0 2 0 0 0 0 0 0 0	0 0 0 0 0 1 1 0 - 0	- 2 1 1 1 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	2 0 1 0 0 0 0 0 5 0	0 0 0 0 0 0 0 1 1 3	1 1 3 1 2 0 0 0 1 0	2 0
Andrena (Notandrena) chrysosceles	0 0 0 0 1 0 0 0 0 0	1 2 0 0 0 1 1 3 0 3	1 1 1 1 * 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 2 1 1 -	- 1 0 1 0 0 0 0 0 0	0 0
Andrena (Notandrena) nitidiuscula	0 0 0 0 1 0 0 0 0 0	2 2 0 0 0 1 1 3 0 3	1 1 1 1 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 2 1 1 -	- 1 0 1 0 0 0 0 0 0	0 0
Andrena (Oligandrena) macrocephala	1 1 0 0 0 0 0 2 2 0	0 0 0 0 0 1 1 0 - 0	- 1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 0 0 0 0 0	0 1 0 0 0 0 0 1 1 0	0 1 0 1 2 0 0 0 0 0	0 0
Andrena (Onagrandrena) oenotherae	0 1 0 1 0 1 0 2 2 0	4 0 4 0 0 0 1 0 - 0	- 1 0 0 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 0 0 0 4 1	0 0 0 0 0 0 0 1 2 0	1 1 0 1 0 0 0 0 1 0	0 0
Andrena (Opandrena) cressoni	0 0 0 0 1 0 0 0 0 0	2 0 0 0 0 1 1 3 0 3	1 1 1 0 1 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 5 0	0 1 0 0 0 0 0 1 1 -	- 1 0 1 1 0 0 0 0 1	0 0
Andrena (Orandrena) oralis	0 0 0 0 0 1 0 0 0 0	3 0 0 2 0 1 1 3 - 3	2 1 0 0 1 0 0 0 0 2	1 1 1 0 0 0 0 0 0 1	0 1 0 0 0 1 0 0 0 0	2 0 1 0 0 0 1 0 1 -	0 1 0 - 0 0 0 1 1 0	1 1 0 1 0 1 0 0 0 0	0 0
Andrena (Oreomelissa) mitakensis	0 0 0 0 0 0 0 2 0 0	2 2 0 0 0 0 1 1 0 - 0	- 1 0 2 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 1 ? 0 0 0	0 0 0 0 0 0 1 2 1 1 2	0 1 3 1 1 0 0 0 2 0	1 0
Andrena (Osychnyukandrena) cochlearicalcar	0 1 0 0 0 0 0 2 0 0	0 0 0 0 0 2 1 0 - 0	- 1 0 2 0 0 2 0 0 0	0 0 0 0 1 5 1 4 0 2	2 1 1 0 0 0 0 0 0 0	2 0 1 0 0 1 0 ? ? ?	? 0 0 0 0 0 0 1 1 -	- 1 0 1 0 0 0 0 0 0	0 1
Andrena (Pallandrena) pallidicincta	1 1 0 0 1 0 0 2 0 0	0 0 0 0 0 0 0 - - -	- 0 - - 0 0 0 0 1 2	0 0 0 0 0 3 3 0 0 1	0 1 1 0 0 0 0 1 1 -	0 0 1 0 0 0 0 0 3 1	0 0 0 0 0 0 0 1 1 -	- 1 0 1 2 0 0 0 0 1	1 0
Andrena (Parandrena) andrenoides	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 1 2 0 1	0 3 1 1 1 0 0 0 1 2	0 0 0 0 0 0 1 0 0 0	0 0 0 0 1 0 - 0 0 0	0 0 1 0 0 1 1 1 0 6 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Parandrenella) atrata	0 0 2 0 1 0 1 0 0 0	3 1 0 0 0 1 1 0 - 0	- 1 1 0 1 0 0 0 0 1	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	2 0 2 0 0 0 2 0 0 0	1 0 0 1 0 0 3 1 1 0	0 1 0 0 0 0 0 0 0 0	1 0
Andrena (Parandrenella) dentiventris	0 0 2 0 1 0 1 0 0 0	3 1 0 0 0 1 1 0 - 0	- 3 1 0 1 0 0 0 0 1	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	2 0 2 0 0 0 2 0 6 0	1 0 0 1 0 0 3 1 1 0	0 1 0 1 0 0 0 0 0 0	1 1
Andrena (Pelicandrena) atypica	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 1 3 0 3	1 1 1 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 0 1	0 1 0 0 1 0 - 0 0 0	0 0 1 0 0 0 0 0 2 -	0 0 0 0 0 0 0 1 1 3	0 1 0 1 1 0 0 0 0 0	1 1
Andrena (Planiandrena) planirostris	0 0 0 0 1 0 0 0 0 0	0 0 4 2 0 1 1 3 0 3	1 1 0 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 1 2 1 1 1 0 4 0	0 0 0 0 0 0 0 1 1 3	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Plastandrena) tibialis	0 1 0 1 0 1 0 0 0 2	4 0 4 2 0 1 1 1 0 2	0 3 1 1 1 0 0 0 1 2	1 0 1 1 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 0	0 0 1 2 0 1 0 0 0 0	0 0 0 0 0 0 0 1 2 3	1 1 0 1 1 0 0 0 0 0	1 0
Andrena (Platygalandrena) fedtschenkoi	1 1 1 0 0 0 0 2 0 0	0 0 0 2 0 2 1 0 - 0	- 1 1 1 0 1 1 0 0 2	0 0 1 0 0 1 7 0 0 0	1 0 5 1 0 0 0 0 0 0	0 0 0 0 2 0 0 0 1 -	0 0 1 0 0 0 0 1 1 0	0 * 2 1 1 1 0 0 1 0	1 1
Andrena (Platygalandrena) tecta	1 1 1 0 0 0 0 2 0 0	0 0 0 2 0 2 1 0 - 0	- 1 1 1 0 0 1 0 0 2	1 0 1 0 0 0 7 0 0 1	1 0 1 0 0 0 0 0 0 -	0 0 0 0 2 0 0 0 3 0	0 0 1 0 0 0 0 1 1 0	0 1 2 0 2 2 0 0 0 1	1 0
Andrena (Poecilandrena) labiata	0 1 0 0 0 0 0 2 0 0	2 0 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 0 1	0 0 0 0 0 1 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 1 0 0 0 0 0 1 0 -	- 1 0 0 2 0 0 0 2 1	1 0
Andrena (Poliandrena) polita	0 1 0 0 1 0 0 2 0 0	0 0 0 0 0 2 1 1 0 2	2 1 1 1 1 0 0 0 0 2	0 0 0 0 0 0 1 0 0 1	0 0 1 0 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 1 2	0 1 0 1 2 0 0 0 1 0	0 0
Andrena (Ptilandrena) erigeniae	1 1 0 0 0 0 0 0 0 0	2 0 0 0 0 5 1 1 0 2	0 3 1 2 0 0 0 0 0 1	0 0 0 0 0 3 3 0 0 0	0 0 5 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Ptilandrena) fulvata	1 1 0 0 0 0 0 2 0 0	0 0 0 0 0 2 1 1 0 2	0 1 1 0 0 1 0 0 1 1	0 0 0 0 0 0 1 0 0 0	0 0 5 0 0 0 0 0 0 0	0 0 1 2 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 2 0	0 0
Andrena (Ptilandrena) grossella	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 5 1 0 - 0	- 1 0 0 0 0 2 0 0 2	0 0 0 0 0 3 3 0 0 0	0 0 0 0 0 2 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 1 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 2 0	0 0
Andrena (Ptilandrena) vetula	1 0 0 0 0 0 0 1 0 0	0 0 0 1 1 6 1 2 1 1	0 3 1 1 0 0 0 0 1 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 ?	0 0 0 0 2 0 0 0 0 0	0 0 0 0 0 0 0 1 1 -	- 1 0 1 0 0 0 0 0 0	0 0
Andrena (Rhacandrena) brevipalpis	1 0 0 0 0 0 0 0 0 0	3 0 0 0 0 1 1 0 - 0	- 1 0 0 0 0 0 0 0 2	0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 3	0 1 0 1 0 0 0 0 1 0	1 1
Andrena (Rhaphandrena) prima	0 1 1 1 0 1 0 2 0 0	4 2 4 0 0 1 1 0 - 0	- 1 0 0 1 0 0 0 0 0 0	0 0 0 1 0 0 0 0 0 0	0 1 0 0 0 0 1 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Rufandrena) rufiventris	0 1 2 0 2 0 0 0 0 0	3 0 0 1 1 6 0 0 - 0	- 0 - - 0 0 0 0 1 2	0 1 0 0 0 3 3 0 0 1	0 0 5 0 0 1 0 0 1 0	0 0 1 0 0 0 0 0 0 1	0 0 0 1 1 0 0 1 2 0	1 1 0 1 2 2 0 0 1 0	0 0
Andrena (Scitandrena) scita	0 0 2 1 0 1 0 0 0 0	4 2 1 0 0 1 1 3 0 3	1 1 1 0 1 0 0 0 0 2	1 0 1 1 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 1 0 0 2 1 1 0	0 1 0 1 1 0 0 0 0 0	1 1
Andrena (Scoliandrena) osmioides	1 1 0 0 0 0 0 2 0 0	0 0 0 0 0 1 1 0 - 0	- 1 1 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 2 1 1 0	0 1 0 1 0 0 0 0 0 0	? 0
Andrena (Scrapteropsis) fenningeri	0 0 0 1 0 0 0 2 0 0	4 0 1 0 0 1 1 3 0 3	1 1 1 1 1 0 0 0 0 2	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 1 2 3	1 1 0 1 0 0 0 0 0 0	0 0
Andrena (Simandrena) propinqua	0 0 0 0 0 0 0 2 0 1	2 0 0 1 1 6 1 2 1 1	0 3 1 1 1 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 1 0 0 6 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 1 0 0	0 0
Andrena (Stenomelissa) halictoides	1 0 0 0 0 0 0 0 0 0	0 0 0 1 1 6 1 3 0 3	2 1 1 0 0 0 2 0 0 2	0 0 0 0 0 3 3 0 0 0	0 0 0 0 0 1 0 0 0 0	2 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 2 1 2 0	0 1 0 1 0 0 0 0 1 0	0 0
Andrena (Suandrena) suerinensis	0 0 0 0 0 0 0 0 0 1	4 0 0 0 0 1 1 1 0 2	2 1 0 1 1 0 0 0 0 2	1 0 1 0 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 0	2 0 1 2 0 0 2 0 6 0	0 0 0 0 0 1 1 1 1 2	1 1 3 0 0 0 1 2 0 0	0 0
Andrena (Taeniandrena) ovatula	0 1 0 0 2 0 0 2 0 0	2 2 0 0 0 1 1 1 0 2	1 1 1 1 1 0 0 0 0 2	0 0 0 0 0 0 5 0 0 0	0 0 5 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Tarsandrena) tarsata	0 1 0 0 0 0 0 0 0 0	3 0 0 0 0 1 1 1 0 2	2 3 0 1 0 0 0 0 0 1	0 0 0 0 0 0 4 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 1 1 2	1 1 3 1 0 0 0 0 1 1	0 0
Andrena (Thysandrena) candida	1 0 0 0 0 0 0 0 0 0	2 0 0 0 0 1 1 1 0 2	1 1 1 0 0 0 0 0 0 1	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 2 1 1 0	0 1 0 1 0 0 0 0 0 0	0 0
Andrena (Trachandrena) haemorrhoa	2 1 0 1 - 1 0 2 0 2	4 0 3 0 0 1 1 0 - 0	- 3 1 1 1 0 0 0 0 2	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 2 0 0 1 0 0 3 0	0 0 0 0 0 0 0 1 2 3	1 1 0 1 0 1 0 0 2 0	0 0
Andrena (Trachandrena) rugosa	2 1 0 1 - 1 0 2 0 2	4 0 3 0 0 1 1 0 - 0	- 3 1 0 1 0 0 0 0 2	0 0 0 1 0 0 0 0 0 0	0 1 0 0 0 0 1 0 0 0	0 0 2 0 0 1 0 0 0 0	0 0 0 0 0 0 0 1 1 3	1 1 0 1 0 1 0 0 2 0	0 0
Andrena (Troandrena) troodica	0 0 0 1 0 0 0 2 0 0	3 0 4 0 0 1 1 1 0 2	2 1 1 0 0 0 0 0 1 2	0 0 0 2 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 2 0 1 0 0 0 0	0 0 0 0 0 0 0 1 0 -	- 1 0 1 0 1 0 0 1 0	0 0
Andrena (Truncandrena) truncatilabris	1 1 0 0 0 0 0 0 0 0	0 0 0 0 0 1 1 1 0 2	1 1 1 1 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	2 0 1 0 0 0 0 0 0 0	1 0 0 0 0 0 0 1 1 0	0 1 3 1 0 0 0 0 1 0	0 0
Andrena (Tylandrena) erythrogaster	1 0 0 0 0 0 0 0 0 0	2 0 0 0 0 1 1 1 0 1	0 3 1 1 1 0 0 0 0 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	2 0 1 0 0 0 1 0 0 0	0 0 0 0 0 0 2 1 1 0	0 1 0 0 0 0 0 0 0 0	0 0
Andrena (Ulandrena) schulzi	0 1 2 0 1 0 0 2 0 0	3 0 0 0 0 2 1 0 - 0	- 1 1 0 0 0 0 0 0 1	1 0 1 0 0 1 2 0 0 1	0 0 3 0 0 0 0 1 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 -	- 1 0 1 1 0 0 0 1 1	0 1
Andrena (Zonandrena) flavipes	0 1 0 1 1 1 0 2 0 0	2 0 0 2 0 1 1 1 0 1	0 3 1 1 1 0 0 0 1 1	1 0 1 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0	0 0 1 0 2 0 0 0 4 0	0 0 0 0 0 0 1 1 0 -	- 1 0 0 0 0 0 0 0 0	0 0

Unknown character states are coded with "?", not applicable ones with "–", and multistate ones with "$".

Tab. 5. Complete sequence data

		1 2 3 4 5 6
		123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890
02033	*Panurgus calcaratus*	GGA TTT GGT TTA ATT TCT CAT ACA ATT TTT AAT GAA AGA GGA AAA AAA GAA ATT TTT GGA
02749	*Andrena (Aciandrena) aciculata*	GGA TTC GGA TTA ATT TCN CAC ANT ATC TTC AAC GAA AGA GGG AAA AAA GAA ACA TTT GGT
02029	*Andrena (Andrena) praecox*	GGA TTT GGG CTA ATT TCT CAT ATT ATT TAC AAT GAA AGT GGT AAA AAA GAA ACA TTT GGT
02754	*Andrena (Charitandrena) hattorfiana*	GGA TTC GGA TTA ATC TCC CAT ATC ATT TTC AAT GAG AGT GGA AAA AAA GAA ACG TTC GGA
02783	*Andrena (Chlorandrena) humilis*	GGA TTT GGC CTA ATC TCC CAT ATC ATT TTT AAT GAA AGA GGA AAA AAA GAA ACT TTT GGA
02784	*Andrena (Chrysandrena) fulvago*	GGA TTC GGA TTA ATT TCA CAT ATT ATT TAT AAT GAA AGT GGA AAA AAA GAA ACT TTT GGA
02028	*Andrena (Euandrena) bicolor*	GGA TTT GGA CTA ATT TCC CAT ATT ATT TAC AAT GAA AGA GGT AAA AAA GAA ACC TTT GGT
02747	*Andrena (Hoplandrena) nuptialis*	GGA TTC GGA TTA ATT TCT CAT ATC ATC TTT AAT GAA AGA GGA AAA AAA GAA ACA TTT GGT
02025	*Andrena (Larandrena) ventralis*	GGA TTT GGT CTA ATC TCC CAC ATT ATT TAT AAT GAA AGA GGA AAA AAA GAA ACA TTT GGT
02032	*Andrena (Lepidandrena) rufizona*	GGA TTT GGA CTA ATC TCT CAT ATC ATC TAT AAC GAA AGA GGA AAA AAA GAA ACA TTT GGA
02030	*Andrena (Leucandrena) barbilabris*	GGA TTT GGT CTA ATT TCC CAC ATT ATT TAT AAT GAA AGA GGG AAA AAA GAA ACA TTT GGT
02027	*Andrena (Melandrena) vaga*	GGA TTT GGA TTA ATT TCA CAT ATT ATC TAT AAT GAA AGA GGA AAA AAA GAA ACA TTT GGT
02018	*Andrena (Micrandrena) alfkenella*	GGA TTT GGT TTA ATT TCA CAT ATT ATT TTC AAT GAA AGA GGG AAG AAA GAA ACA TTT GGA
02748	*Andrena (Micrandrena) floricola*	GGA TTT GGT TTA ATT TCT CAT ATT ATT TTC AAT GAA AGA GGG AAA AAA GAA ACA TTT GGT
02010	*Andrena (Micrandrena) minutuloides*	GGA TTT GGA TTA ATT TCT CAT ATC ATT TTC AAC GAA AGA GGG AAA AAA GAA ACA TTC GGT
02752	*Andrena (Micrandrena) nana*	GGG TTT GGT TTA ATT TCC CAT ATC ATT TTT AAT GAA AGA GGA AAA AAA GAG ACA TTT GGT
02016	*Andrena (Micrandrena) niveata*	GGA TTT GGA TTA ATT TCA CAT ATC ATC TTT AAC GAA AGA GGA AAG AAA GAA ACC TTC GGA
02019	*Andrena (Micrandrena) proxima*	GGA TTT GGG TTA ATT TCC CAT ATC ATT TTT AAC GAA AGA GGT AAA AAA GAA ACA TTT GGT
02012	*Andrena (Micrandrena) subopaca*	GGA TTT GGT CTA ATT TCA CAC ATC ATT TTC AAT GAA AGA GGA AAG AAA GAA ACT TTT GGA
02022	*Andrena (Notandrena) chrysosceles*	GGA TTC GGA TTA ATT TCT CAT ATT ATC TAT AAT GAA AGA GGT AAA AAA GAA ACA TTT GGT
02751	*Andrena (Parandrenella) atrata*	GGA TTC GGA TTA ATT TCT CAT ATC ATT TTC AAC GAA AGA GGA AAA AAA GAA ACA TTT GGT
02020	*Andrena (Poecilandrena) labiata*	GGA TTT GGA TTA ATT TCC CAT ATT ATT TAT AAT GAA AGA GGT AAA AAA GAA ACA TTT GGT
02750	*Andrena (Poliandrena) polita*	GGA TTT GGT TTA ATT TCC CAT ATT ATT TAC AAT GAG AGA GGA AAA AAA GAA ACA TTT GGA
02745	*Andrena (Scitandrena) scita*	GGA TTT GGA TTA ATT TCC CAT ATC ATT TAC AAC GAA AGA GGT AAA AAA GAA ACA TTT GGT
02746	*Andrena (Simandrena) propinqua*	GGA TTT GGA TTA ATC TCC CAT ATT ATC TAT AAC GAA AGA GGT AAA AAA GAA ACA TTT GGA
02023	*Andrena (Taeniandrena) ovatula*	GGG TTT GGA TTA ATT TCA CAC ATC ATC TTT AAT GAA AGA GGA AAA AAA GAA ACA TTT GGT
02031	*Andrena (Trachandrena) haemorrhoa*	GGA TTT GGT TTA ATT TCA CAT ATT ATT TAT AAT GAA AGA GGT AAA AAA GAG ACA TTT GGA
02026	*Andrena (Zonandrena) flavipes*	GGA TTT GGT TTA ATT TCA CAC ATC ATT TAT AAT GAA AGA GGT AAA AAA GAA ACA TTT GGT
		** ** ** **** ** * * ** ** ** ** ** ** ** * ** **
		1 1 1
		7 8 9 0 1 2
		123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890
02033	*Panurgus calcaratus*	AAT TTA GGA ATA ATT TAT GCA ATA ATA GGA ATT GGT TTC TTA GGT TTT ATT GTA TGG GCT
02749	*Andrena (Aciandrena) aciculata*	AAT ATT GGT ATA ATT TAC GCC ATA TTA GGA ATC GGA TTT TTA GGA TTT ATT GTT TGA GCT
02029	*Andrena (Andrena) praecox*	AAT ATC GGC ATA GTA TAC GCT ATA TTA GGA ATT GGA TTT CTA GGA TTT ATT GTA TGA GCA
02754	*Andrena (Charitandrena) hattorfiana*	AAT ATT GGT ATA ATC TAT GCT ATA TTA GGA ATT GGT TTT CTA GGG TTT ATC GTT TGA GCC
02783	*Andrena (Chlorandrena) humilis*	AAT ATC GGA ATA ATT TAT GCC ATA CTA GGA ATT GGA TTT CTA GGA TTT ATC GTG TGA GCT
02784	*Andrena (Chrysandrena) fulvago*	AAT ATT GGT ATA ATC TAC GCT ATA TTA GGT ATT GGA TTT CTA GGA TTC ATT GTA TGG GCC
02028	*Andrena (Euandrena) bicolor*	AAT ATT GGA ATA ATT TAC GCC ATA TTA GGA ATT GGA TTT TTA GGA TTT ATC GTA TGA GCC
02747	*Andrena (Hoplandrena) nuptialis*	AAT ATT AGT ATA ATT TAT GCT ATA TTA GGA ATT GGA TTT CTA GGA TTT ATC GTA TGA GCA
02025	*Andrena (Larandrena) ventralis*	AAT ATT GGA ATA ATT TAC GCT ATA CTA GGT ATT GGA TTT CTA GGA TTT ATT GTA TGA GCT
02032	*Andrena (Lepidandrena) rufizona*	AAT ATT GGT ATA ATC TAC GCA ATA TTA GGT ATT GGA TTT TTA GGA TTC ATT GTA TGA GCA
02030	*Andrena (Leucandrena) barbilabris*	AAT ATT GGA ATA ATT TAC GCT ATA CTA GGC ATT GGA TTT CTA GGA TTC ATC GTA TGA GCC
02027	*Andrena (Melandrena) vaga*	AAT ATT GGA ATA ATT TAC GCT ATA CTA GGT ATT GGA TTT TTA GGA TTC ATT GTA TGA GCT
02018	*Andrena (Micrandrena) alfkenella*	AAC ATT GGT ATA ATT TAT GCA ATA CTA GGA ATT GGA TTT CTA GGG TTC ATT GTT TGA GCC
02748	*Andrena (Micrandrena) floricola*	AAC ATT GGT ATA ATT TAC GCA ATA TTA GGA ATT GGG TTT CTA GGA TTC ATT GTA TGA GCT
02010	*Andrena (Micrandrena) minutuloides*	AAT ATC GGT ATA ATT TAC GCA ATA CTA GGA ATT GGA TTC CTA GGG TTC ATT GTA TGA GCC
02752	*Andrena (Micrandrena) nana*	AAT ATC GGT ATA ATC TAT GCC ATA CTA GGA ATT GGA TTT CTA GGA TTC ATT GTA TGA GCT
02016	*Andrena (Micrandrena) niveata*	AAT ATT GGT ATA ATT TAC GCA ATA CTA GGA ATT GGA TTT TTA GGA TTC ATT GTA TGG GCA
02019	*Andrena (Micrandrena) proxima*	AAT ATT GGT ATA ATC TAC GCA ATA TTA GGA ATT GGA TTT TTA GGA TTC ATC GTA TGA GCA
02012	*Andrena (Micrandrena) subopaca*	AAT ATT GGT ATA ATC TAC GCA ATA CTA GGA ATT GGA TTT TTA GGA TTC ATT GTT TGA GCT
02022	*Andrena (Notandrena) chrysosceles*	AAT ATT GGA ATA ATC TAC GCC ATA CTA GGT ATT GGA TTT CTT GGA TTT ATT GTA TGG GCA
02751	*Andrena (Parandrenella) atrata*	AAT ATT GGT ATA ATC TAC GCC ATA CTA GGA ATT GGA TTT CTA GGA TTC ATC GTT TGA GCT
02020	*Andrena (Poecilandrena) labiata*	AAT ATC GGA ATA ATC TAC GCT ATA TTA GGA ATT GGT TTC CTA GGA TTT ATT GTA TGA GCA
02750	*Andrena (Poliandrena) polita*	AAT ATC GGA ATA ATT TAC GCT ATA TTA GGA ATC GGA TTT CTA GGA TTT ATT GTA TGA GCA
02745	*Andrena (Scitandrena) scita*	AAT ATT GGA ATA ATT TAC GCT ATG TTA GGA ATT GGA TTT CTT GGA TTC ATT GTA TGA GCC
02746	*Andrena (Simandrena) propinqua*	AAT ATT GGA ATA ATT TAT GCT ATA CTA GGG ATT GGA TTC CTA GGA TTT ATC GTA TGA GCC
02023	*Andrena (Taeniandrena) ovatula*	AAT ATT GGA ATA ATT TAC GCT ATA CTA GGT ATT GGA TTT TTA GGA TTT ATT GTA TGA GCT
02031	*Andrena (Trachandrena) haemorrhoa*	AAT ATT GGA ATA ATT TAT GCC ATA CTA GGA ATT GGA TTT TTA GGA TTT ATT GTA TGA GCC
02026	*Andrena (Zonandrena) flavipes*	AAT ATT GGA ATA ATT TAC GCT ATA CTA GGA ATT GGT TTC CTT GGA TTT ATT GTT TGA GCC
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02033	*Panurgus calcaratus*	CAT CAC ATA TTT ACT GTT GGA ATA GAT GTA GAT ACC CGA GCT TAT TTT ACT TCA GCA ACT
02749	*Andrena (Aciandrena) aciculata*	CAT CAT ATA TTC ACA GTC GGN ATG GAT GTA GAT ACA CGA GCN TAC TTC ACT TCA GCT ACT
02029	*Andrena (Andrena) praecox*	CAT CAC ATA TTC ACT GTA GGT CTT GAT GTT GAT ACT CGA GCC TAC TTT ACT TCT GCA ACC
02754	*Andrena (Charitandrena) hattorfiana*	CAT CAT ATG TTT ACA GTA GGT CTT GAT GTA GAC ACA CGA GCA TAT TTC ACC TCA GCT ACA
02783	*Andrena (Chlorandrena) humilis*	CAT CAC ATA TTT ACA GTA GGT CTA GAT GTT GAT ACA CGA GCT TAC TTT ACA TCA GCT ACT
02784	*Andrena (Chrysandrena) fulvago*	CAT CAT ATA TTC ACA GTT GGG CTA GAT GTT GAT ACA CGA GCT TAC TTC ACC TCA GCA ACC
02028	*Andrena (Euandrena) bicolor*	CAT CAT ATA TTC ACA GTT GGA TTA GAT GTT GAT ACA CGG GCA TAT TTT ACT TCA GCT ACT
02747	*Andrena (Hoplandrena) nuptialis*	CAT CAT ATA TTT ACA GTA GGA TTA GAT GTA GAC ACA CGA GCC TAT TTC ACT TCA GCT ACA
02025	*Andrena (Larandrena) ventralis*	CAT CAT ATA TTT ACA GTA GGA TTA GAT GTA GAT ACA CGA GCC TAT TTC ACC TCA GCT ACC
02032	*Andrena (Lepidandrena) rufizona*	CAT CAT ATA TTT ACA GTT GGA CTA GAT GTC GAT ACT CGA GCA TAC TTC ACA TCA GCT ACA
02030	*Andrena (Leucandrena) barbilabris*	CAT CAC ATA TTC ACC GTA GGA TTA GAT GTA GAT ACA CGA GCT TAT TTT ACT TCA GCC ACA
02027	*Andrena (Melandrena) vaga*	CAT CAT ATA TTT ACA GTA GGA TTA GAC GTA GAT ACT CGA GCT TAC TTT ACC TCA GCT ACA
02018	*Andrena (Micrandrena) alfkenella*	CAT CAT ATA TTC ACT GTA GGA CTA GAT GTA GAT ACA CGA GCC TAC TTC ACA TCA GCT ACA
02748	*Andrena (Micrandrena) floricola*	CAC CAT ATA TTC ACC GTA GGG CTA GAT GTA GAT ACA CGA GCC TAC TTT ACC TCA GCT ACC
02010	*Andrena (Micrandrena) minutuloides*	CAT CAT ATA TTT ACA GTA GGT CTA GAC GTA GAT ACA CGA GCC TAC TTT ACC TCG GCC ACC
02752	*Andrena (Micrandrena) nana*	CAC CAT ATA TTC ACT GTA GGA CTA GAT GTA GAT ACA CGA GCC TAC TTT ACA TCA GCT ACC
02016	*Andrena (Micrandrena) niveata*	CAT CAT ATA TTT ACC GTA GGA TTA GAT GTA GAT ACA CGA GCC TAC TTT ACA TCC GCT ACT
02019	*Andrena (Micrandrena) proxima*	CAT CAT ATA TTC ACA GTT GGA CTA GAT GTA GAT ACA CGT GCC TAC TTC ACT TCA GCA ACC
02012	*Andrena (Micrandrena) subopaca*	CAT CAC ATA TTT ACT GTA GGT CTA GAT GTA GAC ACA CGA GCA TAC TTC ACC TCT GCT ACT
02022	*Andrena (Notandrena) chrysosceles*	CAT CAT ATA TTT ACA GTA GGA TTA GAT GTA GAT ACT CGA GCC TAC TTT ACC TCA GCA ACC
02751	*Andrena (Parandrenella) atrata*	CAT CAC ATA TTT ACT GTT GGT ATA GAT GTA GAT ACA CGT GCA TAT TTC ACA TCA GCT ACT
02020	*Andrena (Poecilandrena) labiata*	CAT CAC ATA TTT ACA GTA GGT ATA GAT GTA GAT ACA CGA GCA TAT TTT ACC TCA GCT ACA
02750	*Andrena (Poliandrena) polita*	CAC CAC ATA TTC ACA GTA GGT CTA GAT GTT GAT ACT CGA GCC TAC TTC ACT TCA GCT ACT
02745	*Andrena (Scitandrena) scita*	CAC CAC ATA TTT ACT GTT GGG CTA GAT GTT GAT ACA CGA GCA TAC TTC ACC TCA GCA ACA
02746	*Andrena (Simandrena) propinqua*	CAC CAC ATA TTT ACA GTA GGT CTA GAT GTC GAT ACA CGA GCC TAT TTC ACC TCT GCA ACT
02023	*Andrena (Taeniandrena) ovatula*	CAT CAC ATA TTC ACC GTT GGA TTA GAT GTA GAT ACT CGA GCT TAC TTC ACA TCA GCA ACA
02031	*Andrena (Trachandrena) haemorrhoa*	CAC CAT ATA TTT ACA GTA GGA CTA GAT GTT GAT ACA CGA GCA TAC TTT ACC TCA GCA ACA
02026	*Andrena (Zonandrena) flavipes*	CAC CAT ATA TTC ACA GTA GGA TTA GAT GTT GAC ACT CGA GCC TAT TTT ACT TCA GCT ACA
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Tab. 5. Complete sequence data (continued)

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		1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
02033	*Panurgus calcaratus*	A T A A T T A T T G C A A T T C C A A C T G G A A T T A A A G T A T T T A G A T G A T T A G C T A C A T A T T A T G G A
02749	*Andrena (Aciandrena) aciculata*	A T A A T T A T T G C A A T T C C A A C A G G A A T T A A A G T A T T T A G A T G A T T A G C A A C A T A T C A C G G A
02029	*Andrena (Andrena) praecox*	A T A A T C A T T G C T A T T C C T A C T G G A A T T A A A G T A T T T A G A T G A C T A G C C A C C T A T C A T G G A
02754	*Andrena (Charitandrena) hattorfiana*	A T A A T C A T T G C A A T T C C A A C A G G A A T T A A A G T A T T T A G A T G A C T A G C A A C A T A T C A C G G A
02783	*Andrena (Chlorandrena) humilis*	A T A A T C A T T G C A G T A C C A A C T G G A A T T A A A G T T T T C A G A T G A A T A G C T A C A T A T C A T G G A
02784	*Andrena (Chrysandrena) fulvago*	A T A A T T A T C G C C A T T C C T A C A G G A A T C A A A G T A T T T A G A T G A T T A G C A A C A T A C C A T G G T
02028	*Andrena (Euandrena) bicolor*	A T A A T C A T T G C T A T T C C A A C A G G A A T T A A A G T A T T T A G A T G A C T A G C A A C A T A T C A T G G T
02747	*Andrena (Hoplandrena) nuptialis*	A T A A T C A T T G C A A T T C C A A C A G G A A T C A A A G T A T T T A G A T G A T T A G C C A C A T A T C A T G G A
02025	*Andrena (Larandrena) ventralis*	A T A A T T A T C G C C A T C C C C A C A G G A A T C A A G G T A T T T A G A T G A T T A G C T A C G T A C C A C G G C
02032	*Andrena (Lepidandrena) rufizona*	A T A A T T A T T G C A A T T C C T A C G G G A A T T A A A G T A T T T A G A T G A T T A G C A A C A T A T C A T G G A
02030	*Andrena (Leucandrena) barbilabris*	A T A A T T A T C G C C A T T C C T A C A G G A A T T A A A G T A T T T A G A T G A T T A G C C A C A T A C C A C G G A
02027	*Andrena (Melandrena) vaga*	A T A A T C A T T G C T A T C C C C A C A G G A A T C A A A G T A T T T A G A T G A T T A G C A A C A T A T C A T G G A
02018	*Andrena (Micrandrena) alfkenella*	A T A A T T A T T G C A A T T C C A A C C G G A A T T A A A G T A T T T A G A T G A T T A G C A A C A T A T C A T G G A
02748	*Andrena (Micrandrena) floricola*	A T A A T C A T C G C C A T C C C A A C A G G A A T T A A A G T T T T T A G A T G A C T A G C A A C A T A C C A C G G A
02010	*Andrena (Micrandrena) minutuloides*	A T A A T C A T C G C T A T T C C A A C A G G A A T T A A A G T A T T C A G A T G A T T A G C A A C A T A C C A C G G C
02752	*Andrena (Micrandrena) nana*	A T A A T T A T T G C C A T C C C A A C A G G T A T T A A A G T A T T T A G A T G A C T A G C A A C A T A T C A T G G A
02016	*Andrena (Micrandrena) niveata*	A T A A T T A T T G C A A T C C C A A C A G G A A T T A A A G T A T T T A G A T G A T T A G C A A C A T A T C A T G G A
02019	*Andrena (Micrandrena) proxima*	A T A A T T A T T G C T A T C C C C A C A G G A A T C A A A G T A T T T A G A T G A C T A G C C A C A T A T C A T G G A
02012	*Andrena (Micrandrena) subopaca*	A T A A T C A T T G C T A T T C C A A C A G G A A T T A A A G T A T T T A G A T G A T T A G C A A C A T A T C A T G G A
02022	*Andrena (Notandrena) chrysosceles*	A T A A T C A T C G C T A T T C C C A C A G G A A T T A A A G T A T T C A G A T G A C T A G C A A C A T A T C A C G G A
02751	*Andrena (Parandrenella) atrata*	A T A A T T A T C G C C A T T C C A A C G G G A A T T A A A G T C T T T A G A T G A A T A G C A A C C T A T C A T G G G
02020	*Andrena (Poecilandrena) labiata*	A T A A T C A T C G C T A T T C C C A C A G G A A T T A A A G T T T T C A G A T G A T T A G C A A C T A T C A T G G A
02750	*Andrena (Poliandrena) polita*	A T A A T T A T T G C T A T C C C A A C A G G A A T C A A A G T A T T T A G A T G A T T A G C A A C A T A T C A C G G A
02745	*Andrena (Scitandrena) scita*	A T A A T C A T C G C A A T C C C C A C A G G G A T T A A A G T A T T T A G A T G A T T A G C A A C C T A T C A T G G A
02746	*Andrena (Simandrena) propinqua*	A T A A T T A T T G C T A T T C C T A C G G G A A T T A A A G T A T T T A G A T G A T T A G C T A C A T A T C A C G G A
02023	*Andrena (Taeniandrena) ovatula*	A T A A T C A T T G C A A T T C C A A C A G G A A T T A A A G T T T T T A G A T G A C T C G C C A C A T A T C A T G G T
02031	*Andrena (Trachandrena) haemorrhoa*	A T A A T T A T T G C C A T C C C A A C A G G A A T T A A A G T A T T T A G A T G A T T A G C C A C A T A T C A T G G A
02026	*Andrena (Zonandrena) flavipes*	A T A A T C A T T G C A A T T C C A A C A G G A A T T A A A G T A T T T A G A T G A T T A G C T A C T T A T C A T G G A
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		1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
02033	*Panurgus calcaratus*	A T A A A A T A T A T A A T A A A C C A T C T A T A T T A T G A A C A A T A G G A T T T A T T T T T A T T T A C T
02749	*Andrena (Aciandrena) aciculata*	A C A A A A T A T T T A T A A A C C C A C A A T T A T A T G A T C C T T A G G A T T C A T C T T C C T A T T T A C T
02029	*Andrena (Andrena) praecox*	A C A A A A T A A T C T T A A A T C C T C A A A T C T T A T G A T C A T T G G G A T T C A T C T T C T T A T T T A C A
02754	*Andrena (Charitandrena) hattorfiana*	A C A A A A T T T A A A T T A A A T C C T C A A A T C T T A T G A T C C C T A G G A T T C A T T T T C C T A T T T A C A
02783	*Andrena (Chlorandrena) humilis*	A C A A A A T A A C A A T A A A C C C A C A A T C C T A T G A T C A C T T G G A T T T A T C T T C C T A T T T A C A
02784	*Andrena (Chrysandrena) fulvago*	A C T A A A A T A A T A A T A A A T C C T C A A A T A T T A T G A T C A T T A G G G T T T A T T T T T C T A T T T A C A
02028	*Andrena (Euandrena) bicolor*	A C T A A A A T A A T A A T A A A T C C T C A G A T C C T A T G A T C A T T A G G G T T T A T T T T T C T A T T C A C T
02747	*Andrena (Hoplandrena) nuptialis*	A C A A A A T A A T A A T A A T A A T C C A C A A A T T C T T T G A T C A T T A G G A T T T A T T T T C C T A T T C A C C
02025	*Andrena (Larandrena) ventralis*	A C T A A A A T A G T A A T A A A T C C T C A A A T C A T A T G A T C A T T A G G A T T C A T T T T C T A T T C A C T
02032	*Andrena (Lepidandrena) rufizona*	A C T A A A C T A A C A T T A A A T C C A C A A A T T C T T T G A T C A T T A G G A T T T A T T T C C T A T T T A C T
02030	*Andrena (Leucandrena) barbilabris*	A C A A A A T A A T T A T C A A C C C A C A G A T T A T A T G A T C A C T A G G A T T C A T T T T C T A T T T A C C
02027	*Andrena (Melandrena) vaga*	A C A A A A T A A T A A T A A A T C C A C A A A T A T T A T G A T C T T T A G G A T T T A T T T T C C T A T T C A C T
02018	*Andrena (Micrandrena) alfkenella*	A C A A A A T A T C A A T A A A T C C T C A A A T C T T A T G G T C C C T T G G A T T T A T C T T T T T A T T C A C T
02748	*Andrena (Micrandrena) floricola*	A C A A A A T A T C A A T A A A T C C A C A A A T C C T A T G A T C C T T A G G A T T C A T T T T C C T A T T C A C C
02010	*Andrena (Micrandrena) minutuloides*	A C A A A A T A T C A A T A A A T C C A C A A A T C C T A T G A T C A C T T G G A T T T A T C T T C C T A T T C A C C
02752	*Andrena (Micrandrena) nana*	A C A A A A T A T C A A T T A A A T C C A C A A A T T T T A T G A T C T C T A G G A T T T A T C T T C C T A T T C A C C
02016	*Andrena (Micrandrena) niveata*	A C A A A A T A T C A A T A A A T C C A C A A A T T T T A T G A T C T A T T G G A T T T A T T T T C T C T T C A C C
02019	*Andrena (Micrandrena) proxima*	A C A A A A T A A A A T A A A T C C A C A A A T C C T A T G A T C C T T A G G C T T T A T T T T C T A T T C A C C
02012	*Andrena (Micrandrena) subopaca*	A C A A A A T A T C A A T A A A T C C A C A A A T T T T A T G A T C C T T A G G A T T C A T C T T T C T A T T C A C C
02022	*Andrena (Notandrena) chrysosceles*	A C A A A A T A A T A A T A A A T C C C C A A A T C C T A T G A T C A C T A G G A T T C A T C T T C T T A T T T A C T
02751	*Andrena (Parandrenella) atrata*	A C A A A A T A T C A T T T A A T C C C C A A A T T T T A T G A T C T T T A G G A T T C A T T T T C T G T T T A C A
02020	*Andrena (Poecilandrena) labiata*	A C A A A A T A T C A T A T T T A A T C C T C A A A T T C T A T G A T C A T A G G G T T C A T T T T C C T A T T T A C A
02750	*Andrena (Poliandrena) polita*	A C A A A A T T T A T T A T A A A T C C A C A A A T A T T A T G A T C T A T T G G A T T T A T T T T C T C T T C A C C
02745	*Andrena (Scitandrena) scita*	G C A A A A T A A A A T A A A T A A C C C T C A A A T T T G T G A T C A T T A G G A T T T A T C T T C T T A T T C A C A
02746	*Andrena (Simandrena) propinqua*	G C T A A A T A T A A T T A T A A C C C T C A A A T C C T T G A T C A T T A G G G T T T A T T T T C T A T T T A C C
02023	*Andrena (Taeniandrena) ovatula*	A C A A A A T A T A C T A T A A A T C C T C A A A T C T T A T G A T C T T T A G G A T T C A T T T T C T A T T C A C C
02031	*Andrena (Trachandrena) haemorrhoa*	G C A A A A T A T A A T T T A A A T C C T C A A A T T C T T T G A T C T C T T G G A T T C A T C T T T T A T T C A C C
02026	*Andrena (Zonandrena) flavipes*	A C G A A A T A T A A T A A A T C C A C A A A T T C T C T G A T C A T T A G G A T T T A T T T T C C T A T T C A C T
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		1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
02033	*Panurgus calcaratus*	G T T G G A G G A T T A A C A G G T A T T A T A C T A T C T A A T T C T T C A A T T G A T A T T A T T T C T A C A T G A T
02749	*Andrena (Aciandrena) aciculata*	G T A G G A G G A T T A A C A G G A A T T A T A C T A T C A A A T T C A T C A A T T G A T A T T A T T C T T C A C G A T
02029	*Andrena (Andrena) praecox*	G T T G G A G G T C T T A C T G G T A T T A T A C T A T C A A C T C T T C A A T T G A T A T T A T T T T A C A T G A T
02754	*Andrena (Charitandrena) hattorfiana*	A T A G G A G G A T T A A C T G G A A T C A T A T T A T C A A A T T C A T C A A T T G A T A T C A T T T T A C A C G A C
02783	*Andrena (Chlorandrena) humilis*	G T A G G A G G A T T A A C A G G A A T C A T A T T A T C A A A T T C A T C T A T T G A T A T T A T T C T C C A T G A C
02784	*Andrena (Chrysandrena) fulvago*	G T A G G A G G A T T A A C A G G A A T T A T A C T A T C A A T T C A T C A A T T G A T A T T A T C C T T C A C G A C
02028	*Andrena (Euandrena) bicolor*	G T A G G T G G A T T A A C A G G A A T T A T A T T A T C A A T T C T T C A A T T G A T A T T A T T C T T C A T G A T
02747	*Andrena (Hoplandrena) nuptialis*	G T T G G A G G T T T A A C C G G A A T C A T A T T A T C A A T T C A T C A A T T G A T A T T A T T C T T C A T G A T
02025	*Andrena (Larandrena) ventralis*	G T A G G A G G A C T T A C A G G A A T T A T A T T A T C T A A C T C A T C A A T T G A T A T T A T C C T T C A T G A T
02032	*Andrena (Lepidandrena) rufizona*	G T T G G A G G A T T A A C T G G A A T T A T A C T T T C A A A C T C A T C A A T T G A T A T T A T T T T A C A T G A T
02030	*Andrena (Leucandrena) barbilabris*	G T A G G A G G A C T A A C A G G A A T T A T A T T A T C A A A T T C T T C T A T T G A T A T T A T T C T A C A C G A C
02027	*Andrena (Melandrena) vaga*	G T A G G A G G A T T A A C T G G A A T T A T A T T G T C A A A T T C A T C A A T T G A T A T T A T T T T A C A T G A C
02018	*Andrena (Micrandrena) alfkenella*	G T A G G G G G G T T A A C A G G G A T T A T A C T G T C C A A T T C A T C A A T T G A T A T C A T T C T T C A T G A T
02748	*Andrena (Micrandrena) floricola*	G T A G G A G G A C T A A C A G G A A T T A T A C T A T C C A A T T C A T C A A T T G A T A T T A T C C T A C A C G A T
02010	*Andrena (Micrandrena) minutuloides*	G T A G G G G G A C T G A C A G G A A T T A T A T T A T C C A A T T C A T C A A T T G A T A T T A T T C T T C A T G A C
02752	*Andrena (Micrandrena) nana*	G T A G G A G G A T T A A C A G G A A T T A T A T T A T C A A A T T C A T C A A T C G A T A T T A T T C T G C A T G A C
02016	*Andrena (Micrandrena) niveata*	G T A G G A G G G T T G A C A G G A A T T A T A C T A T C A A T T C A T C A A T C G A T A T T A T T C T A C A C G A T
02019	*Andrena (Micrandrena) proxima*	G T A G G A G G G N T A A C A G G A A T T A T A T T A T C A A C T C A T C A A T T G A T A T T A T C T T A C A T G A T
02012	*Andrena (Micrandrena) subopaca*	G T A G G G G G A T T A A C A G G A A T T A T A T T A T C C A A T T C A T C A A T T G A T A T T A T C T T A C A T G A C
02022	*Andrena (Notandrena) chrysosceles*	G T A G G G G G A C T A A C A G G A A T C A T A T T A T C A A T T C T T C A A T T G A T A T T A T T C T T C A T G A C
02751	*Andrena (Parandrenella) atrata*	A T T G G A G G T C T G A C A G G A A T T A T A C T A T C A A C T C A T C A A T T G A T A T T A T T C T T C A T G A C
02020	*Andrena (Poecilandrena) labiata*	G T A G G T G G A T T A A C A G G A A T T A T A C T A T C C A A C T C A T C G A T T G A T A T T A T C T T A C A T G A T
02750	*Andrena (Poliandrena) polita*	G T T G G A G G T T T A A C T G G A A T T A T A C T A T C A A T T C A T C A A T T G A T A T T A T C C T T C A T G A T
02745	*Andrena (Scitandrena) scita*	G T T G G G G G T C T A A C T G G A A T T A T A C T A T C A A A T T C A T C A A T T G A T A T C A T T C T G C A T G A T
02746	*Andrena (Simandrena) propinqua*	G T T G G T G G G T T A A C A G G A A T T A T A T T A T C A A A T T C C T C A A T T G A T A T T A T T C T T C A C G A T
02023	*Andrena (Taeniandrena) ovatula*	G T A G G T G G A T T A A C A G G A A T T A T A T T A T C A A T T C A T C A A T T G A T A T T A T T C T T C A T G A C
02031	*Andrena (Trachandrena) haemorrhoa*	G T T G G A G G A T T A A C T G G T A T T A T A T T A T C A A T T C A T C A A T T G A T A T T A T T C T T C A T G A T
02026	*Andrena (Zonandrena) flavipes*	G T A G G A G G A T T A A C T G G A A T T A T A T T A T C A A T T C A T C A A T T G A T A T T A T T T T A C A C G A T
		* *

Tab. 5. Complete sequence data (continued)

		123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890
02033	*Panurgus calcaratus*	ACT TAT TAT GTA GTA GGA CAT TTC CAT TAT GTT TTA TCT ATA GGA GCA GTA TTT GCA ATT
02749	*Andrena (Aciandrena) aciculata*	ACT TAC TAT GTA GTG GGT CAT TTT CAC TAT GTA CTA TCT ATA GGA GCA GTA TTC TCA ATC
02029	*Andrena (Andrena) praecox*	ACA TAC TAC GTC GTA GGT CAT TTT CAC TAT GTT CTA TCA ATA GGA GCT GTA TTC TCA ATT
02754	*Andrena (Charitandrena) hattorfiana*	ACA TAT TAC GTT GTT GGT CAT TTC CAC TAC GTT TTA TCC ATA GGT GCA GTA TTC TCA ATT
02783	*Andrena (Chlorandrena) humilis*	ACA TAC TAC GTA GTA GGT CAT TTC CAC TAT GTA CTA TCA ATA GGA GCA GTA TTT TCA ATT
02784	*Andrena (Chrysandrena) fulvago*	ACC TAC TAT GTA GTA GGT CAT TTT CAT TAT GTT CTA TCA ATA GGA GCA GTT TTC TCA ATC
02028	*Andrena (Euandrena) bicolor*	ACA TAT TAT GTA GTA GGA CAT TTT CAC TAT GTT CTA TCT ATA GGT GCA GTA TTC TCA ATC
02747	*Andrena (Hoplandrena) nuptialis*	ACA TAC TAT GTT GTT GGT CAT TTT CAC TAC GTA TTA TCA ATA GGA GCA GTA TTC TCA ATT
02025	*Andrena (Larandrena) ventralis*	ACA TAC TAT GTA GTA GGT CAT TTC CAC TAT GTA TTA TCT ATA GGA GCT GTA TTC TCA ATT
02032	*Andrena (Lepidandrena) rufizona*	ACA TAT TAT GTA GTA GGT CAT TTT CAT TAT GTT TTA TCA ATA GGA GCA GTA TTT TCA ATT
02030	*Andrena (Leucandrena) barbilabris*	ACA TAC TAT GTA GTA GGT CAT TTC CAC TAC GTT CTA TCA ATA GGG GCC GTA TTC TCA ATC
02027	*Andrena (Melandrena) vaga*	ACA TAC TAC GTT GTA GGA CAC TTT CAC TAT GTA TTA TCA ATA GGA GCA GTA TTT TCA ATT
02018	*Andrena (Micrandrena) alfkenella*	ACA TAC TAT GTA GTA GGA CAT TTC CAT TAT GTA CTA TCT ATA GGA GCA GTA TTC TCA ATT
02748	*Andrena (Micrandrena) floricola*	ACA TAT TAC GTT GTA GGA CAC TTT CAC TAT GTT TTA TCA ATA GGG GCC GTA TTT TCA ATT
02010	*Andrena (Micrandrena) minutuloides*	ACA TAC TAC GTC GTA GGG CAC TTC CAC TAT GTC CTA TCT ATA GGG GCC GTA TTT TCA ATC
02752	*Andrena (Micrandrena) nana*	ACA TAC TAC GTT GTA GGT CAT TTT CAT TAT GTT TTA TCA ATA GGA GCT GTA TTC TCG ATT
02016	*Andrena (Micrandrena) niveata*	ACA TAT TAC GTT GTA GGA CAT TTT CAT TAT GTT TTA TCT ATA GGA GCA GTA TTT TCA ATT
02019	*Andrena (Micrandrena) proxima*	ACA TAT TAT GTA GTA GGT CAT TTC CAC TAT GTT CTA TCA ATA GGA GCT GTA TTC TCA ATC
02012	*Andrena (Micrandrena) subopaca*	ACA TAC TAT GTA GTA GGA CAT TTT CAC TAT GTT CTG TCT ATA GGA GCT GTA TTT TCA ATT
02022	*Andrena (Notandrena) chrysosceles*	ACA TAC TAT GTT GTG GGC CAT TTC CAC TAT GTT CTA TCA ATA GGA GCA GTA TTC TCA ATT
02751	*Andrena (Parandrenella) atrata*	ACT TAC TAC GTA GTA GGT CAC TTC CAT TAT GTT CTT TCT ATA GGA GCA GTA TTT TCA ATC
02020	*Andrena (Poecilandrena) labiata*	ACC TAT TAT GTA GTT GGT CAT TTC CAT TAT GTT TTA TCA ATG GGG GCA GTA TTT TCA ATT
02750	*Andrena (Poliandrena) polita*	ACA TAT TAT GTT GTA GGT CAC TTT CAT TAC GTT TTA TCA ATA GGA GCA GTA TTT TCA ATT
02745	*Andrena (Scitandrena) scita*	ACA TAC TAC GTA GTT GGT CAT TTT CAC TAC GTA CTA TCT ATG GGT GCA GTA TTC TCA ATC
02746	*Andrena (Simandrena) propinqua*	ACA TAT TAT GTT GCA GGT CAT TTC CAT TAT GTA CTA TCA ATA GGA GCA GTA TTC TCA ATT
02023	*Andrena (Taeniandrena) ovatula*	ACA TAT TAT GTT GTT GGA CAT TTT CAC TAC GTG CTT TCA ATA GGA GCT GTA TTT TCA ATT
02031	*Andrena (Trachandrena) haemorrhoa*	ACA TAT TAT GTA GTA GGT CAC TTT CAC TAT GTT TTA TCA ATA GGA GCA GTA TTT TCA ATT
02026	*Andrena (Zonandrena) flavipes*	ACA TAT TAT GAA GTT GGT CAT TTC CAC TAC GTA CTA TCT ATA GGA GCA GTA TTC TCA ATT
		** ** ** * * ** ** ** ** ** ** * ** ** ** ** ** ** ** * **

		123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890
02033	*Panurgus calcaratus*	ATT AGA AGA TTA ATT CAT TGA TAT CCT TTA ATT ACT GGT TTA TTA TTA AAC AAT AAA TTA
02749	*Andrena (Aciandrena) aciculata*	ATC GCA AGT ATT ATT CAT TGA TTC CCA TCA ATT ACA GGA GTA TCA ATA AAT ACA AAA TGA
02029	*Andrena (Andrena) praecox*	ATT GCA AGA ATT GTT CAC TGA TTT CCT GCA GTA ACT GGA TTT TCA ATA AAT AAC AAA TGA
02754	*Andrena (Charitandrena) hattorfiana*	ATT GCA AGT ATT ATT CAC TGA TTT CCA GCA ATT ACT GGT CTA TCA ATA AAT AAA AAA TGA
02783	*Andrena (Chlorandrena) humilis*	ATC GCA AGA ATC GTA CAC TGA TTC CCT GCA ATT ACA GGA GTA TCA ATA AAT AAA AAA TGA
02784	*Andrena (Chrysandrena) fulvago*	ATT GCT AGA ATT GTT CAT TGA TTC CCA GCA GTA ACT GGC CTA TCA ATA AAT AAA AAA TGG
02028	*Andrena (Euandrena) bicolor*	ATC GCA AGT ATT GTT CAC TGA TTT CCA GCA GTA ACT GGT CTA TCA TTA AAT AAA AAA TGA
02747	*Andrena (Hoplandrena) nuptialis*	ATT GCA AGT ATT GTT CAT TGA TTT CCA GCA ATT ACT GGA TTA TCA TTA AAT AAA AAA TGA
02025	*Andrena (Larandrena) ventralis*	ATT GCA AGA ATT ATT CAT TGA TTC CCA GCA ATT ACA GGT CTA TCA TTA AAT AAA AAA TGA
02032	*Andrena (Lepidandrena) rufizona*	ATT GCA AGA ATT ATC CAC TGA TTT CCA GCA ATT ACC GGA CTA TCA TTA AAT AGA AAA TGA
02030	*Andrena (Leucandrena) barbilabris*	ATC GCA AGA ATC ATT CAT TGA TTT CCA GCA GTA ACA GGT TTA TCA CTT AAT AAT AAA TGA
02027	*Andrena (Melandrena) vaga*	ATT GCT AGA ATT GTA CAC TGA TTT CCA GCA ATT ACT GGT TTA TCA ATA AAT AGT AAA TGA
02018	*Andrena (Micrandrena) alfkenella*	ATT GCA AGA ATC GTG CAC TGA TTC CCA GCA ATT ACA GGA GTA TCA ATA AAT AAA AAA TGA
02748	*Andrena (Micrandrena) floricola*	ATC GCA AGA ATT GTT CAT TGA TTC CCA GCA ATT ACA GGA GTA TCA ATA AAC AAA AAA TGA
02010	*Andrena (Micrandrena) minutuloides*	ATC GCA AGA ATC GTA CAC TGA TTC CCA GCA ATT ACA GGA GTA TCA ATA AAT AAA AAA TGA
02752	*Andrena (Micrandrena) nana*	ATT GCA AGA ATT ATT CAT TGA TTC CCA GCT ATT ACA GGT ACA TCA ATA AAT AAA AAG TGA
02016	*Andrena (Micrandrena) niveata*	ATT GCA AGA ATT GTA CAT TGA TTC CCA GCA ATT ACA GGA ACA TCA ATA AAT AAA AAA TGA
02019	*Andrena (Micrandrena) proxima*	ATT GCA AGC ATC GTA CAC TGA TTC CCA GCA ATC ACA GGA GTT TCA ATA AAT AAT AAA TGA
02012	*Andrena (Micrandrena) subopaca*	ATC GCA AGA ATT GTA CAC TGA TTC CCA GCA ATC ACG GGA GTA TCA ATA AAT AAA AAA TGA
02022	*Andrena (Notandrena) chrysosceles*	ATT GCA AGT ATT GTT CAC TGA TTC CCA ACA ATC ACT GGG CTA ACA ATA AAT AAA AAT TGA
02751	*Andrena (Parandrenella) atrata*	ATC GCA AGA ATC GTT CAT TGA TTC CCA GCA ATT ACT GGT CTA TCT TTA AAT AAT AAA TGA
02020	*Andrena (Poecilandrena) labiata*	ATC GCA AGT ATT GTC CAT TGA TTT CCA GCA ATT ACA GGA TTA TCA TTA AAT AAT AAA TGA
02750	*Andrena (Poliandrena) polita*	ATT GCA AGT ATT GTC CAC TGA TTC TCA ACA ATC ACT GGA TTA ACA ATA AAT AAC AAA TGA
02745	*Andrena (Scitandrena) scita*	ATC GCA AGA ATC GTA CAC TGA TTC CCT GCA GTA ACA GGA TTA TCA ATA AAT AAC AAA TGA
02746	*Andrena (Simandrena) propinqua*	ATT GCA AGT ATT GTC CAC TGA TTC CCA GCA GTT ACT GGA CTA TCA ATA AAT AAA AAA TGA
02023	*Andrena (Taeniandrena) ovatula*	ATC GCA AGA ATC GTA CAC TGA TTC CCC GCA ATT ACC GGT ATA TCA ATA AAT AAC AAA TGA
02031	*Andrena (Trachandrena) haemorrhoa*	ATT GCA AGA ATT GTA CAC TGA TTC CCA GCA ATT ACT GGA TTT TCA ATA AAT AAT AAA TGA
02026	*Andrena (Zonandrena) flavipes*	ATT GCA AGA ATT GTA CAC TGA TTT CCA GCA GTT ACC GGT CTA ACT ATA AAT AGT AAA TGA
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		123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890
02033	*Panurgus calcaratus*	TTA AAA ATT CAA TTT TAT TTA ATG TTT TTA GGG GTT AAT TTA ACA TTT TTC CCC CAA CAT
02749	*Andrena (Aciandrena) aciculata*	CTA AAA ATT CAA TTC TTC ATA ATA TTT ATT GGA GTA AAT TTA ACA TTC TTC CCA CAA CAC
02029	*Andrena (Andrena) praecox*	CTA AAA ATC CAA TTC TAC ATA ATA TTT ATC GGA GTA AAC TTA ACA TTC TTT CCC CAA CAT
02754	*Andrena (Charitandrena) hattorfiana*	TTA AAA ATT CAA TTT TAT ATA ATA TTT ACT GGA GTA AAC TTA ACA TTC TTT CCA CAG CAT
02783	*Andrena (Chlorandrena) humilis*	TTA AAA ATT CAA TTC ATT ATA ATA TTT ATT GGA GTA AAT CTA ACC TTC TTC CCA CAA CAT
02784	*Andrena (Chrysandrena) fulvago*	TTA AAA ATT CAA TTC CTT ATA ATA TTT GTA GGT GTA AAT TTA ACA TTC TTC CCA CAA CAT
02028	*Andrena (Euandrena) bicolor*	TTA AAA ATT CAA TTT ACT ATA ATA TTT GTA GGA GTA AAT TTA ACT TTC TTC CCG CAA CAC
02747	*Andrena (Hoplandrena) nuptialis*	TTA AAA ATT CAA TTT TCC ATA ATA TTT ATT GGA GTA AAT TTA ACA TTC TTT CCA CAA CAC
02025	*Andrena (Larandrena) ventralis*	CTA AAA ATT CAA TTC ATT ATA ATA TTT ACA GGA GTA AAT TTA ACT TTT TTT CCA CAA CAT
02032	*Andrena (Lepidandrena) rufizona*	TTA AAA ATT CAA TTC TAT ATA ATA TTT ATT GGA GTA AAT TTT ACA TTC TTT CCA CAA CAC
02030	*Andrena (Leucandrena) barbilabris*	TTA AAA ATT CAA TTC ATA ATA ATA TTT ACA GGA GTA AAT TTA ACA TTT TTC CCC CAA CAC
02027	*Andrena (Melandrena) vaga*	TTA AAA ACC CAA TTC TAT ATA ATA TTT ATT GGA GTA AAT TTA ACA TTC TTC CCC CAG CAC
02018	*Andrena (Micrandrena) alfkenella*	CTA AAA ATT CAA TTC TTT ATA ATA TTT ATT GGA GTA AAT TTA ACA TTC TTC CCC CAA CAT
02748	*Andrena (Micrandrena) floricola*	CTA AAA ATT CAA TTT TTT ATA ATA TTT ATT GGG GTA AAT TTA ACT TTC TTC CCT CAG CAC
02010	*Andrena (Micrandrena) minutuloides*	CTA AAA ATT CAA TTC TCT ATA ATA TTC ATT GGA GTA AAT ATA ACA TTC TTC CCA CAA CAC
02752	*Andrena (Micrandrena) nana*	TTA AAA ATT CAA TTC TTC ATA ATA TTT ATT GGA GTA AAC TTA ACA TTC TTC CCC CAA CAT
02016	*Andrena (Micrandrena) niveata*	CTA AAA ATT CAA TTC TTT ATA ATA TTC ATT GGA GTA AAT TTA ACA TTC TTC CCA CAA CAT
02019	*Andrena (Micrandrena) proxima*	CTA AAA ATT CAA TTC TCC ATA ATA TTT ATT GGA GTA AAC TTA ACA TTC TTT CCG CAG CAT
02012	*Andrena (Micrandrena) subopaca*	TTA AAA ATT CAA TTC TTC ATA ATA TTT ATT GGA GTA AAT TTA ACA TTC TTT CCA CAA CAC
02022	*Andrena (Notandrena) chrysosceles*	TTA AAA ATC CAA TTC TTT ATA ATA TTT ATT GGT GTA AAT CTA ACA TTC TTT CCA CAA CAT
02751	*Andrena (Parandrenella) atrata*	TTA AAA ATT CAA TTC ACT ATA ATA TTT ATT GGA GTA AAT TTA ACG TTC TTC CCC CAA CAC
02020	*Andrena (Poecilandrena) labiata*	TTA AAA ATT CAA TTC TAC ATA ATA TTC ATC GGA GTT AAT TTG ACA TTT TTT CCT CAA CAC
02750	*Andrena (Poliandrena) polita*	CTA AAA ATC CAA TTC TAT ATA ATA TTT ATT GGA GTA AAT CTA ACA TTT TTC CCC CAA CAC
02745	*Andrena (Scitandrena) scita*	TTA AAA ATC CAA TTC TAC TTA ATA TTT ACT GGA GTA AAT TTA ACA TTT TTC CCA CAA CAC
02746	*Andrena (Simandrena) propinqua*	TTA AAA ATT CAA TTC CTT ATA ATA TTT ATT GGA GTA AAC TTA ACA TTC TTC CCC CAA CAT
02023	*Andrena (Taeniandrena) ovatula*	TTA AAA ATT CAA TTT TAT ATA ATA TTC ATT GGA GTA AAT ATA ACA TTT TTC CCC CAA CAT
02031	*Andrena (Trachandrena) haemorrhoa*	CTA AAA ATT CAA TTT TAT ATA ATA TTT ACA GGC GTA AAC TTA ACA TTT TTC CCA CAA CAT
02026	*Andrena (Zonandrena) flavipes*	TTA AAA ATT CAA TTC TAT ATA ATA TTT ATT GGA GTA AAT CTT ACA TTC TTT CCC CAA CAT
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Tab. 5. Complete sequence data (continued)

		1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
02033	*Panurgus calcaratus*	T T T T T A G G A T T A A T A G G A A T A C C A C G A C G A T A T T C T G A T T A T C C A G A T T C A T A T T A T T G T
02749	*Andrena (Aciandrena) aciculata*	T T T T T A G G A C T T A T A G G A A T A C C T C G T C G A T A T T C A G A A T A C C C T G A T G C A T A T T A C T G T
02029	*Andrena (Andrena) praecox*	T T T C T A G G A C T A A T A G G A A T A C C A C G T C G A T A C T C T G A A T A T C C A G A T G C C T T C T A T T G C
02754	*Andrena (Charitandrena) hattorfiana*	T T T C T A G G A T T A A T A A G A A T A C C A C G A C G A T A C T C A G A A T A T C C A G A T G C C T A C T A T T G T
02783	*Andrena (Chlorandrena) humilis*	T T C C T T G G A C T T A T A G G A A T A C C C C G A C G G T A T T C A G A A T A T C C A G A T G C A T A C T A C T G T
02784	*Andrena (Chrysandrena) fulvago*	T T T T T A G G A C T T A T A G G T A T A C C T C G C C G A T A C T C T G A A T A T C C A G A C T C T A T T A C T G C
02028	*Andrena (Euandrena) bicolor*	T T T T T A G G A T T A A T A G G A A T A C C T C G A C G A T A T T C T G A A T A T C C A G A T G C C T A T T A T T G C
02747	*Andrena (Hoplandrena) nuptialis*	T T T T T A G G A C T T A T A G G A A T A C C T C G A C G A T A T T C C G A A T A T C C A G A T G C T T A T T A T T G T
02025	*Andrena (Larandrena) ventralis*	T T T C T A G G C C T A A T A G G A A T A C C A C G A C G A T A T T C T G A A T A T C C A G A T G C T T A T T A T T G C
02032	*Andrena (Lepidandrena) rufizona*	T T C C T A G G T C T A A T A G G A A T A C C A C G A C G A T A T T C A G A A T A T C C A G A C G C A T A T T A T T G C
02030	*Andrena (Leucandrena) barbilabris*	T T C T T A G G T C T T A T A G G A A T A C C A C G A C G A T A T T C C G A A T A T C C A G A T G C T T A T T A T T G C
02027	*Andrena (Melandrena) vaga*	T T T C T A G G C C T A A T A G G A A T A C C A C G A C G A T A T T C A G A A T A C C C A G A T A C A T A T T A T T G T
02018	*Andrena (Micrandrena) alfkenella*	T T C T T A G G A T T A A T A G G G A T A C C A C G T C G C T A C T C T G A A T A C C C A G A T G C C T A C T A C T G T
02748	*Andrena (Micrandrena) floricola*	T T T C T A G G C C T A A T A G G A A T G C C A C G T C G A T A C T C C G A A T A C C C A G A T G C A T A C T A T T G C
02010	*Andrena (Micrandrena) minutuloides*	T T T C T A G G A C T A A T A G G A A T A C C A C G T C G A T A C T C C G A A T A T C C A G A T G C C T A C T A C T G C
02752	*Andrena (Micrandrena) nana*	T T C T T A G G A T T A A T A G G A A T A C C T C G C C G A T A C T C T G A A T A T C C A G A T G C C T A C T A C T G T
02016	*Andrena (Micrandrena) niveata*	T T C C T A G G A T T A A T A G G A A T A C C A C G A C G A T A T T C T G A A T A T C C A G A T G C C T A T T A C T G T
02019	*Andrena (Micrandrena) proxima*	T T C C T A G G T C T A A T A G G A A T A C C A C G C C G A T A C T C T G A A T A T C C A G A T G C C T A C T A C T G C
02012	*Andrena (Micrandrena) subopaca*	T T C C T A G G A T T A A T A G G A A T A C C A C G C C G A T A T T C T G A A T A T C C A G A T G C C T A C T A T T G T
02022	*Andrena (Notandrena) chrysosceles*	T T C C T A G G T C T T A T A G G C A T A C C A C G A C G A T A T T C A G A A T A T C C A G A T C T T A C T A T T G T
02751	*Andrena (Parandrenella) atrata*	T T C C T A G G A T T A A T A G G C A T A C C T C G A C G T T A C T C A G A A T A C C C G G A T G C G T A C T A T T G C
02020	*Andrena (Poecilandrena) labiata*	T T C T T A G G A T T A A T A G G A A T A C C A C G A C G A T A T T C C G A A T A T C C A G A T G C A T A T T A T T G C
02750	*Andrena (Poliandrena) polita*	T T T C T A G G A C T A A T A G G A A T A C C A C G T C G T T A T T C T G A A T A T C C A G A T G C A T A C T A T T G C
02745	*Andrena (Scitandrena) scita*	T T C C T A G G A C T T A T A G G T A T A C C A C G T C G A T A C T C T G A A T A C C C T G A C A C T T A C T A C T G T
02746	*Andrena (Simandrena) propinqua*	T T C C T A G G T C T T A T A G G A A T A C C A C G A C G T T A C T C A G A A T A T C C A G A T G C C T A T T A C T G T
02023	*Andrena (Taeniandrena) ovatula*	T T C C T A G G T C T A A T A G G A A T A C C A C G A C G A T A C T C T G A A T A T C C T G A C G T A T A T T A C T G T
02031	*Andrena (Trachandrena) haemorrhoa*	T T T T T A G G A T T A A T A G G A A T A C C A C G C C G A T A T T C A G A A T A T C C A G A C A C T T A C T A C T G T
02026	*Andrena (Zonandrena) flavipes*	T T T T T A G G C C T T A T A G G A A T A C C A C G C C G A T A C T C A G A A T A T C C A G A T A C A T A T T A C T G T

		1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
02033	*Panurgus calcaratus*	T G A A A T C T T T T T C T C T T A G G T T C A A T T A T C T C A A T T A A T A G A A T A G T T T T T T A A T T
02749	*Andrena (Aciandrena) aciculata*	T G A A A T T T A T T A T C A T C C A T A G G A G C C A T C A T T T C T C T T A A C A G A A C A A T T C T A T T C A T T
02029	*Andrena (Andrena) praecox*	T G A A A T A C A C T A T C T T C A A T A G G A G C A A T T A T T T C A T T A A T A G A A T A A T T C T A T T T A T T
02754	*Andrena (Charitandrena) hattorfiana*	T G A A A T T T A T T A T C A T C A A T A G G A G C A A T T A T C T C A A T A A A C A G A A C A A T T T T A T T T A T T
02783	*Andrena (Chlorandrena) humilis*	T G A A A T C T A T T A T C T T C A A T T G G T G C A A T C A T T T C C C T T A A C A G A A C A A T C C T A T T C A T T
02784	*Andrena (Chrysandrena) fulvago*	T G A A A T T T A C T T T C A T C A A T A G G G G C A A T T A T C T C T C T T A A T A G A A T A A T T A T A T T C A T C
02028	*Andrena (Euandrena) bicolor*	T G A A A T T T A T T A T C C T C T A T A G G T G C T A T T A T T T C A T T A A T A G A A T A A T T A T A T T C A T T
02747	*Andrena (Hoplandrena) nuptialis*	T G A A A T T T A T T A T C C T C A T A G G T G C A A T T A T T T C C T A A A T A G A A C A A T T T T A T T C A T T
02025	*Andrena (Larandrena) ventralis*	T G A A A T A T T T T A T C C T C A A T A G G A G C A A T T A T C T C T C A A T A G T A C A A T C T T A T T T A T T
02032	*Andrena (Lepidandrena) rufizona*	T G A A A T C T A T T A T C C T C A A T A G G A T C A A T T A T C T C A T T A A T A G A A C A A T T T T A T T C A T C
02030	*Andrena (Leucandrena) barbilabris*	T G A A A T C T T T T A T C C T C A A T A G G A G C A A T T A T T T C T C T T A A T A G A A C A A T T C T A T T C A T T
02027	*Andrena (Melandrena) vaga*	T G A A A T C T A T T A T C T T C A A T A G G A G C A A T T A T T T C A T C T C A A C A G T A T A A T T T T A T T T A T T
02018	*Andrena (Micrandrena) alfkenella*	T G A A A T C T C C T G T C T T C A A T A G G A G C A A T T A T C T C A C T A A A C A G A A C A A T T A T A T T C A T T
02748	*Andrena (Micrandrena) floricola*	T G A A A C C T C C T A T C A T C A A T A G G A G C A A T T A T T T C C C T T A A C A G T A C T A T C A T A T T T A T T
02010	*Andrena (Micrandrena) minutuloides*	T G A A A C C T C T T A T C A T C A A T A G G A G C A A T C A T T T C A C T T A A C A G A A C A A T T A T A T T C A T T
02752	*Andrena (Micrandrena) nana*	T G A A A T C T T C T A T C A T C A A T A G G A G C T A T C A T T T C A C T T A A T A G A A C A A T T A T A T T C A T T
02016	*Andrena (Micrandrena) niveata*	T G A A A T C T T T T A T C A T C T A T A G G A G C A A T C A T C T C A C T C A A C A G A A C A A T T A T A T T C A T C
02019	*Andrena (Micrandrena) proxima*	T G A A A T C T A C T A T C A T C A A T A G G A G C A A T T A T T T C A C T A A A T A G T A C A A T T A T A T T T A T T
02012	*Andrena (Micrandrena) subopaca*	T G A A A T C T T T T A T C A T C A A T A G G A G C A A T T A T T T C C C T C A A C A G A A C A A T T A T A T T T A T T
02022	*Andrena (Notandrena) chrysosceles*	T G A A A T C T T C T A T C A T C A A T G G G A G C A A T T A T T T C A T T A A T A G A A C A A T C T T A T T T A T C
02751	*Andrena (Parandrenella) atrata*	T G A A A C T T A C T A T C C T C G T T A G G A G C T A T T A T C T C A T T A A T A G A A C A A T C C T A T T T A T T
02020	*Andrena (Poecilandrena) labiata*	T G A A A T T T A T T A T C A T C T A T A G G A G C A A T T A T C T C T C T T A A T A G A A C A A T T T T A T T T A T T
02750	*Andrena (Poliandrena) polita*	T G A A A T C T A C T A T C A T C T A T A G G A G C A A T T A T T T C T C T T A A T A G A A T A A T C T T A T T C A T T
02745	*Andrena (Scitandrena) scita*	T G A A A T T T A T T A T C T T C C A T A G G A G C A A T T A T C T C A T T A A T A G A A C A A T T A T A T T C A T C
02746	*Andrena (Simandrena) propinqua*	T G A A A T C T T T T A T C A T C A T T A G G G G C T A T T A T C T C A T T A A A C A G A A T A A T T T T A T T T A T T
02023	*Andrena (Taeniandrena) ovatula*	T G A A A T C T T T T A T C C T C A A T A G G A G C A A T T A T T T C C T T A A T A G A A T A A T T C T A T T T A T T
02031	*Andrena (Trachandrena) haemorrhoa*	T G A A A T T T A T T A T C A T C T A T A G G A G C A A T C A T T T C A T T A A T A G A A T A A T C T T A T T T A T T
02026	*Andrena (Zonandrena) flavipes*	T G A A A T T T A C T A T C A T C A A T A G G A G C A A T T A T T T C A T C T C A A T A G A A C A A T T T T A T T T A T C

		1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
02033	*Panurgus calcaratus*	T A T A T T A T A T T A G A A A G A T T A A T A T C T A A A C G A T T A A T T T T A T T T A A G T T T T T C A A T C A
02749	*Andrena (Aciandrena) aciculata*	T T C A T T A T A C T A G A A A G A T T A A T A G C T A A A C G A A T A G T T A T A T T T A A A T T T T A T C A A G G A
02029	*Andrena (Andrena) praecox*	T T T A T C A T A A T A G A A A G A T T T A T A G C T A A A C G A T T A G T T A T A T T C A A A T T C A A T C A A G G A
02754	*Andrena (Charitandrena) hattorfiana*	T T T A T T A T A T T A G A A A G A C T A A T A T C A A A A C G G C T A A T T T T A T A A T A A A T T C A A T C A G A G A
02783	*Andrena (Chlorandrena) humilis*	T T T A T T A T A A T A G A A A G A C T T A T A A C A A A C G A C T A G T A A T A T T T A A A T T C A A C C A A A G G
02784	*Andrena (Chrysandrena) fulvago*	T T C A T T A T A T T A G A A A G A T T T A T A T C T A A A C G A T T A A T T A T A T T T A A A T T T A A T C A A G G A
02028	*Andrena (Euandrena) bicolor*	T T T A T T A T A T T A G A A A G A T T T A T A T C A A A C G A T T A A T T A T A T T T A A A T T T A A T C A A G G G
02747	*Andrena (Hoplandrena) nuptialis*	T T C A T T A T A T T A G A A A G A T T C A T A T C A A A C G A C T A A T T A T A T T T A A A T T T T A T C A A A G A
02025	*Andrena (Larandrena) ventralis*	T T C A T C A T A T T A G A A A G A T T T A T A T C T A A A C G A C T A A T A A T A T T T A A A T T C A A T C A A G G A
02032	*Andrena (Lepidandrena) rufizona*	T T C A T T A T A T T A G A A A G A T T T A T A T C T A A A C G A T T A A C T A T A T T T A A A T T T A A T C A A G G A
02030	*Andrena (Leucandrena) barbilabris*	T T C A T T A T A T T A G A A A G A T T T A T A T C T A A A C G A T T A G T A A T A T T T A A A T T C A A T C A A G G A
02027	*Andrena (Melandrena) vaga*	T T C A T T A T A C T A G A A A G A T T T A T A T C T A A A C G A C T A A T T A T A T T C A A A T T C A A T C A A G G A
02018	*Andrena (Micrandrena) alfkenella*	T T C A T C A T A C T A G A A A G A T T T A T A T C A A A C G T A T A A T T A T A T T C A A A T T T A A T C A A G G C
02748	*Andrena (Micrandrena) floricola*	T T C A T T A T G T T A G A A A G A T T C A T A T C T A A A C G T C T A A T T A T A T T C A A A T T T T A T C A A G G T
02010	*Andrena (Micrandrena) minutuloides*	T T T A T T A T A C T A G A A A G T T T C A T A T C A A A C G G T T A A T T A T A T T T A A A T T T A A T C A A G G C
02752	*Andrena (Micrandrena) nana*	T T C A T T A T A T T A G A A A G T T T A T A T C T A A A C G T C T A A T T A T A T T C A A A T T T A A T C A A G G T
02016	*Andrena (Micrandrena) niveata*	T T C A T T A T A T T A G A A A G A T T T A T A T C T A A A C G T A T A A T T A T A T T T A A A T T T A A T C A A G G A
02019	*Andrena (Micrandrena) proxima*	T T C A T T A T A T T A G A A A G T T T C A T A T C C A A A C G A T T A A T T A T A T T T A A A T T T A A C C A A G G A
02012	*Andrena (Micrandrena) subopaca*	T T C A T T A T A C T A G A A A G T T T A T A T C T A A A C G C C T A A T T A T A T T C A A A T T C A A T C A A G G T
02022	*Andrena (Notandrena) chrysosceles*	T T C A T T A T A C T A G A A A G A T T T A T A G C T A A A C G A C T A A T T A T A T T C A A A T T T A A T C T A G G A
02751	*Andrena (Parandrenella) atrata*	T T T A T T A T A C T A G A A A G A C T T A T A T C T A A A C G A C T A A T T A T A C A A A T T T A A C C A A A G C
02020	*Andrena (Poecilandrena) labiata*	T T T A T T A T A T T A G A A A G A T T A A T A T C A A A C G A T T A A T T A T A T A A A T T T A A T C A A A G T
02750	*Andrena (Poliandrena) polita*	T T T A T T A T A C T A G A A A G A T T A A T A T C A A A C G A T T A A T T A T T A T A A A T T C A A T C A A G G T
02745	*Andrena (Scitandrena) scita*	T T C A T T A T A C T A G A A A G A T T T A T A T C T A A A C G C T T A A T T A T A T T T A A A T T T A A T C A A G G T
02746	*Andrena (Simandrena) propinqua*	T T T A T T A T A T T A G A A A G A T T A A T A T C T A A A C G A T T A G T T A T A T T T A A A T T T T A T C A A G G G
02023	*Andrena (Taeniandrena) ovatula*	T T T A T T A T A C T A G A A A G T C T T A T T T C T A A A C G A C T A A T T A T A T T T A A A T T T T A T C A A G G A
02031	*Andrena (Trachandrena) haemorrhoa*	T T T A T T A T A T T A G A A A G A T T T A T A T C T A A A C G A T T A A T T A T G T T A A A T T T A A T C A A A G A
02026	*Andrena (Zonandrena) flavipes*	T T C A T C A T A T T A G A A A G A T T T A T A T C T A A A C G A C T A A T T A T A C A A A T T T A A T C A A G G G

Tab. 5. Complete sequence data (continued)

		7 3	7 4	7 5	7 5
		1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8
02033	*Panurgus calcaratus*	T C A T T A G A A T G A T T A C A A A T A T C A C C T C C T T T G A A T C A
02749	*Andrena (Aciandrena) aciculata*	T C T C T A G A A T G A T C A C A A A A T T A T C C C C C A T T A A A C C A
02029	*Andrena (Andrena) praecox*	T C A T T A G A A T G A T C C C A A A A T T A C C C A C C A T T C A A T C A
02754	*Andrena (Charitandrena) hattorfiana*	T C A C T A G A A T G A T C A C A G A A T T A C C C C C A A T T A A T C A
02783	*Andrena (Chlorandrena) humilis*	T C A C T A G A A T G A T C A C A A A A T T A C C C A C C A T T T A A T C A
02784	*Andrena (Chrysandrena) fulvago*	T C C C T A G A A T G A T C A C A A A A T T T A C C A C C A T T T A A T C A
02028	*Andrena (Euandrena) bicolor*	T C A T T A G A A T G A T C A C A G A A T T A C C C C C C C T T A A A T C A
02747	*Andrena (Hoplandrena) nuptialis*	T C A C T T G A A T G A T C A C A A A A T T A T C C A C C C T T T A A T C A
02025	*Andrena (Larandrena) ventralis*	T C A C T A G A A T G A T C A C A A A A T T A C C C A C C C T T T A A C C A
02032	*Andrena (Lepidandrena) rufizona*	T C T C T A G A A T G A T C A C A A A A T T A T C C C C C T T T C A A T C A
02030	*Andrena (Leucandrena) barbilabris*	T C A C T A G A A T G A T C A C A A A A T T A T C C A C C T T T C A A T C A
02027	*Andrena (Melandrena) vaga*	T C A C T A G A A T G A T C A C A A A A T T A C C C A C C T T T T A A A C A
02018	*Andrena (Micrandrena) alfkenella*	T C T T T A G A G T G A T C A C A A A A T T A T C C C C C A T T T A A T C A
02748	*Andrena (Micrandrena) floricola*	T C A T T A G A A T G G T C A C A A A A T T A C C C A C C C T T T A A C C A
02010	*Andrena (Micrandrena) minutuloides*	T C A T T A G A A T G G T C A C A A A A T T A C C C C C C C T T C A A C C A
02752	*Andrena (Micrandrena) nana*	T C A T T A G A A T G A T C A C A A A A T T A C C C C C C T T T A A T C A
02016	*Andrena (Micrandrena) niveata*	T C A C T A G A A T G A T C A C A A A A T T A T C C A C C T T T T A A T C A
02019	*Andrena (Micrandrena) proxima*	T C A C T A G A A T G A T C A C A A A A T T T T C C T C C T C T A A A T C A
02012	*Andrena (Micrandrena) subopaca*	T C A T T A G A A T G A T C A C A A A A T T A T C C A C C A T T C A A T C A
02022	*Andrena (Notandrena) chrysosceles*	T C A T T A G A A T G G T C A C A A A A T T A C C C A C C C T T T A A T C A
02751	*Andrena (Parandrenella) atrata*	T C T C T A G A A T G A T C A C A A A A C T A C C C T C C C T A T A A T C A
02020	*Andrena (Poecilandrena) labiata*	T C A T T A G A A T G A A C A C A A A A T T A T C C C C C C T T T A A T C A
02750	*Andrena (Poliandrena) polita*	T C C C T A G A A T G A T C A C A A A A T T T T C C T C C C T T T A A T C A
02745	*Andrena (Scitandrena) scita*	T C A C T C G A A T G A T C A C A A A A T T T A C C C C C A T T C A A T C A
02746	*Andrena (Simandrena) propinqua*	T C G T T A G A A T G G T C A C A A A A T T A T C C A C C C T T T A A T C A
02023	*Andrena (Taeniandrena) ovatula*	T C A T T A G A A T G A T C A C A A A A T T A T C C C C C T T T C A A T C A
02031	*Andrena (Trachandrena) haemorrhoa*	T C A C T T G A A T G A T C A C A A A A T T A C C C C C A T T T A A T C A
02026	*Andrena (Zonandrena) flavipes*	T C A C T A G A A T G A T C A C A A A A T T A C C C T C C C T T C A A T C A
		* *

Fig. 5. Habitus of *Andrena*. **A, B:** Female (A) and male (B) of the early spring species *A. (Andrena) nycthemera.* **C:** Female of the oligolectic *A. (Melandrena) vaga* with pollen loads of *Salix.* **D:** Female of *A. (Biareolina) lagopus.* **E:** Male of the rare species *A. (Lepidandrena) rufizona.* **F:** Female of *A. (Micrandrena) proxima,* which is oligolegtic on Apiaceae.

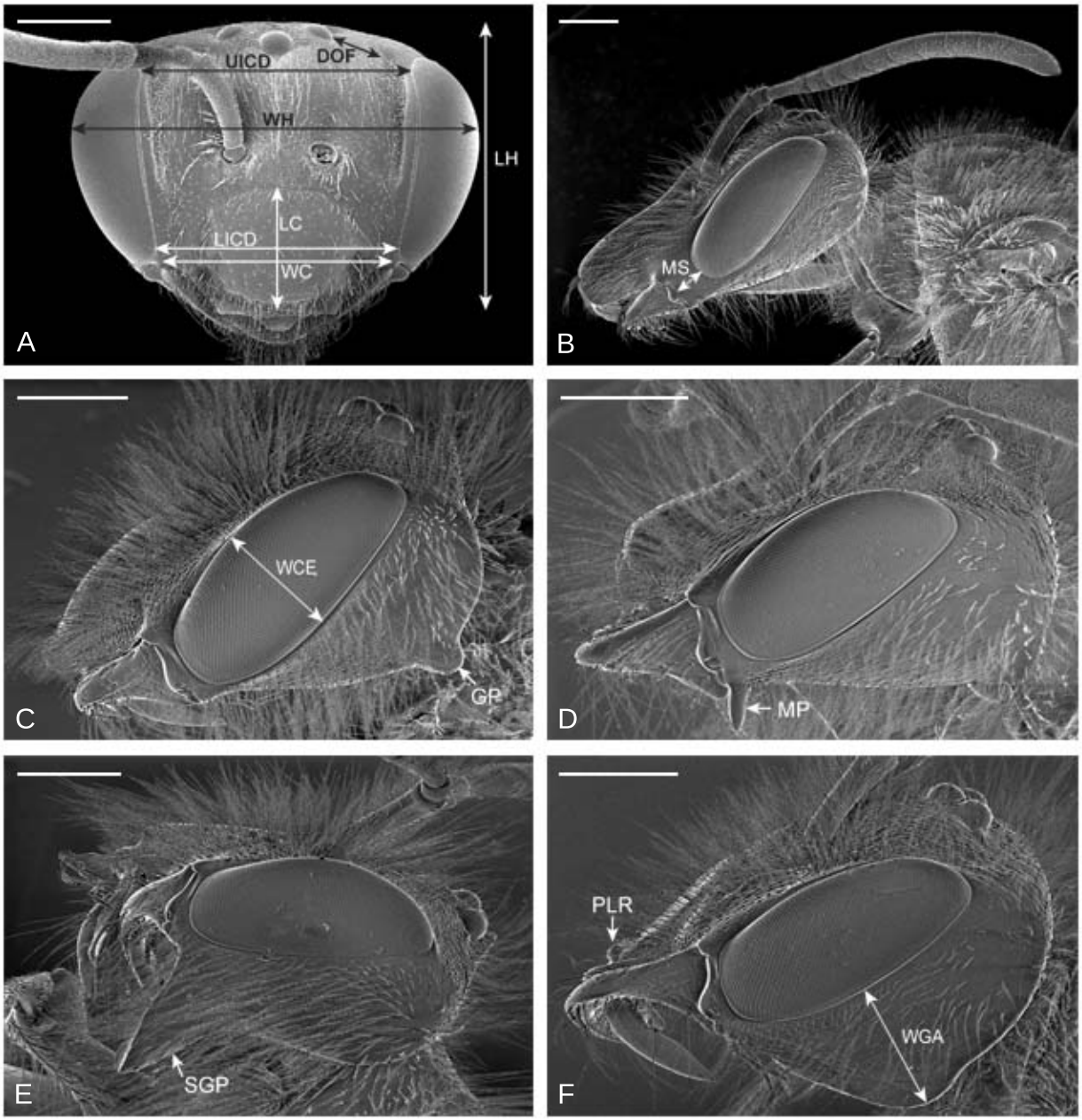

Fig. 6. Head structures of *Andrena* with indicated morphometric measurements. **A:** Portrait of female of *A. (Parandrenella) dentiventris,* **B:** Profile of female *A. (Stenomelissa) halictoides.* **C-F:** Profile of male *A. (Archiandrena) banksi* **(C),** *A. (Derandrena) vandykei* **(D),** *A. (Genyandrena) mackieae* **(E),** *A. (Habromelissa) nantouensis* **(F).** DOF: distance between OD and FOV, GP: genal process, LC: length of clypeus, LH: length of head, MP: malar process, MS: malar space, WC: width of clypeus, WCE: width of compound eye, WGA: width of genal area, WH: width of head, SGP: subgenal process. Scale bars: 500 µm.

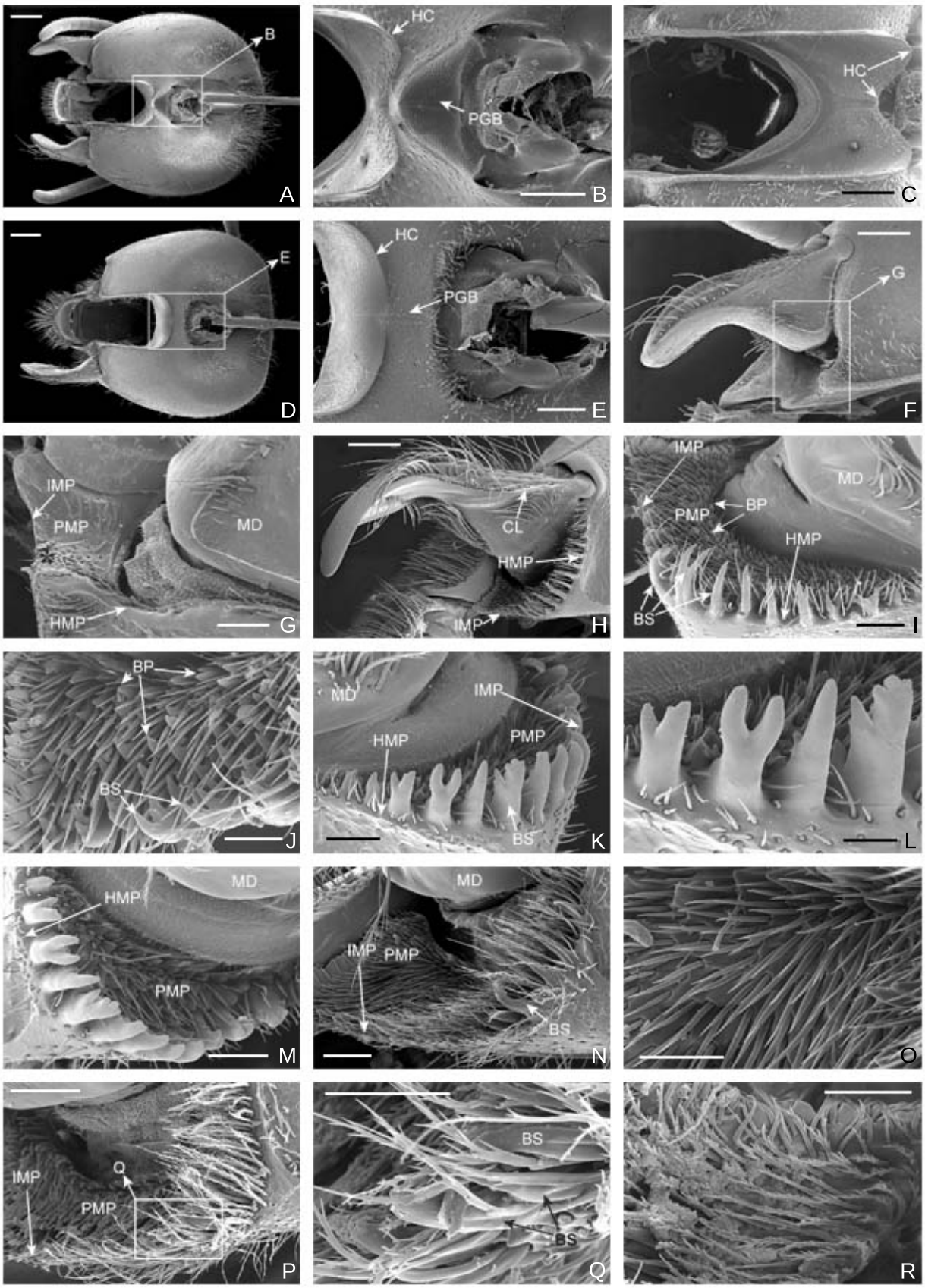

Fig. 7. Head and mandibular structures of female *Cubiandrena* and *Andrena.* A, D: Underside of head of *Cubiandrena cubiceps* (A) and *A. (Nobandrena) nobilis* (D). B, C, E: Hypostomal carina and postgenal bridge of *Cubiandrena cubiceps* (B, C) and *A. (Nobandrena) nobilis* (E). F-R: Mandible and paramandibular structures of *Cubiandrena cubiceps* (F, G), *A. (Zonandrena) flavipes* (H-J), *A. (Charitandrena) hattorfiana* (K-M), *A. (Hamandrena) nasuta* (N, O) and *A. (Nobandrena) nobilis* (P-R). BP: bristles of paramandibular process, BS: bristles of subgenal coronet, CL: condylar lamella of mandible, HC: hypostomal carina, HMP: hind margin of paramandibular process, IMP: inner margin of paramandibular process, MD: mandible, PGB: postgenal bridge, PMP: paramandibular process. Black asterisk in G indicates the position of toothlike projection of the paramandibular process of *Cubiandrena cubiceps,* which was damaged in the shown picture. Scale bars: 500 µm (A, D), 250 µm (B, C, E, F, H), 100 µm (G, I, K, M, N, P) and 50 µm (J, L, O, Q, R).

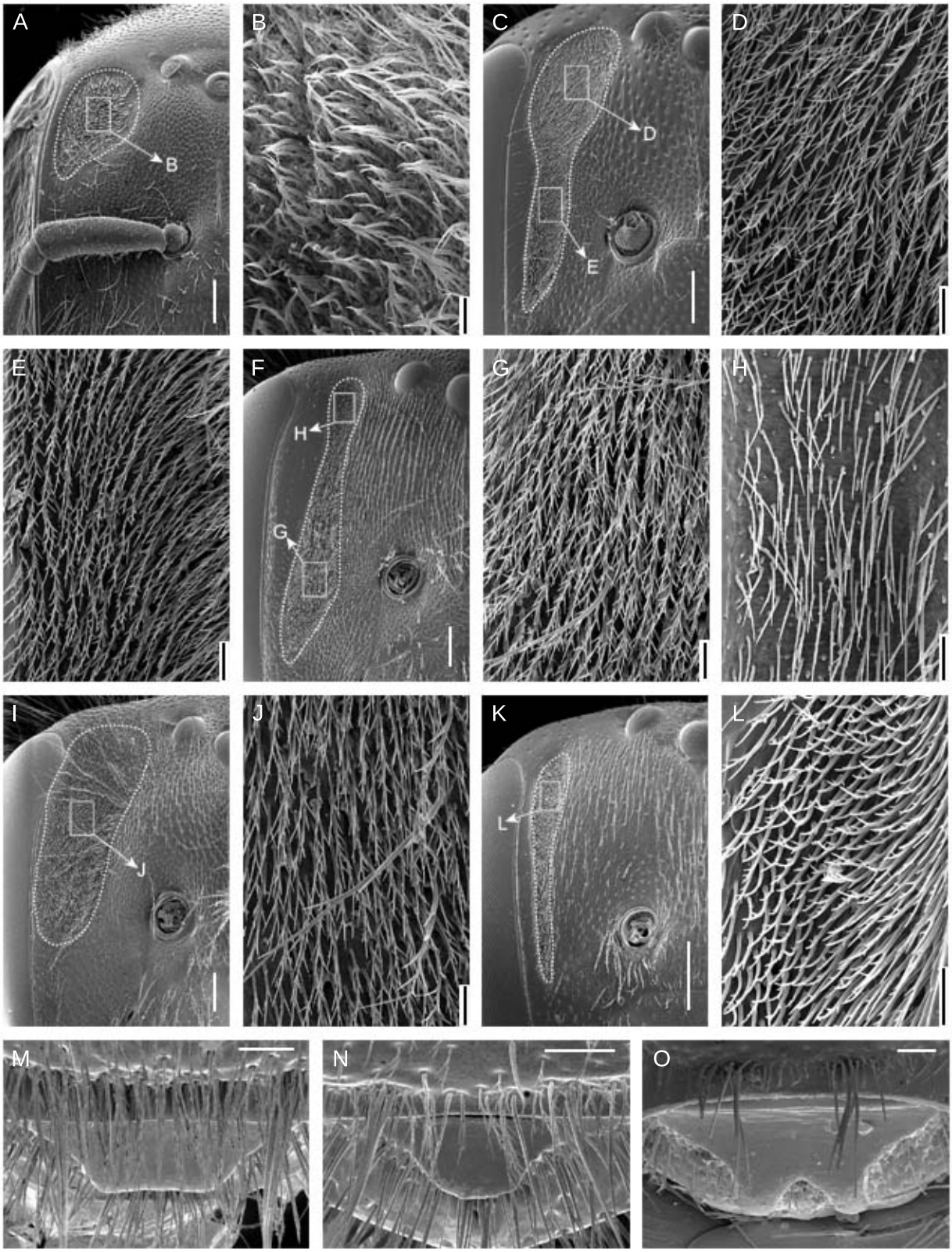

Fig. 8. FOV **(A-L)** and PLR **(M-O)** of female *Andrena* and *Cubiandrena* (only FOV): **A, B:** *Cubiandrena cubiceps.* **C-E:** *A. (Trachandrena) haemorrhoa.* **F-H:** *A. (Hyperandrena) bicolorata.* **I, J:** *A. (Hoplandrena) carantonica.* **K, L:** *A. (Parandrenella) dentiventris.* **M:** *A. (Zonandrena) flavipes.* **N:** *A. (Larandrena) ventralis.* **O:** *A. (Charitandrena) hattorfiana.* Scale bars: 250 µm (A, C, F, I, K), 100 µm (P-R), 25 µ (B, D, E, G, H, J, L). Dotted lines indicate the shape of FOV.

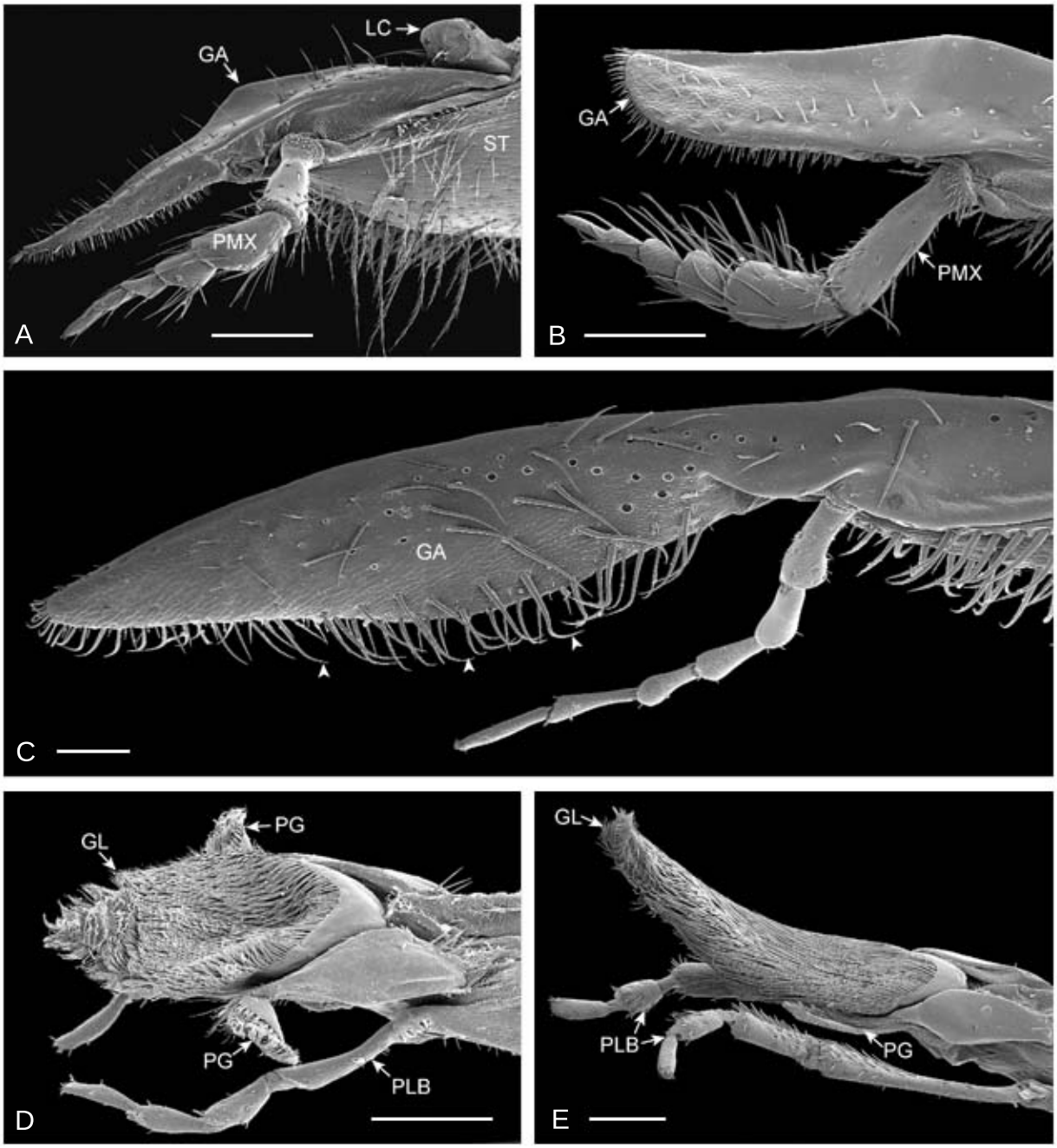

Fig. 9. Galea **(A-C)** and glossa **(D-E)** of female *Andrena.* **A, B:** *A. (Platygalandrena) fedtschenkoi,* lateral view **(A)** dorsal view **(B). C:** *A. (Hamandrena) nasuta,* lateral view, with arrowheads indicating posteriorly bent, stiff hairs. **D:** *A. (Zonandrena) flavipes.* **E:** *A. (Hamandrena) nasuta.* GA: galea, GL: glossa, LC: lacinia, PG: paraglossa, ST: stipes. Scale bars: 200 µm.

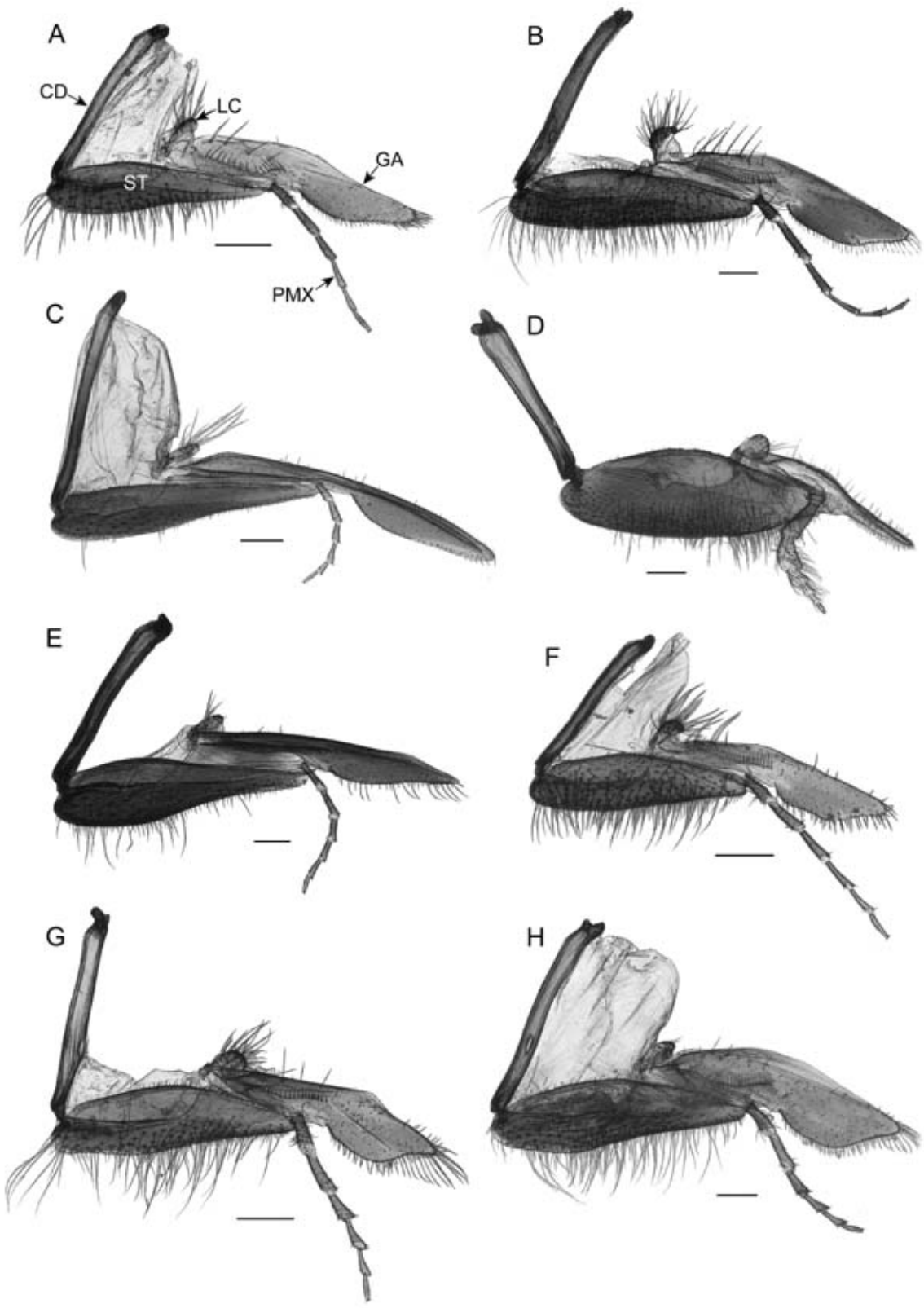

Fig. 10. Maxilla of female *Andrena*, part 1. **A:** *A. (Fumandrena) fumida*, **B:** *A. (Carandrena) aerinifrons*, **C:** *A. (Charitandrena) hattorfiana*. **D:** *A. (Platygalandrena) fedtschenkoi*. **E:** *A. (Lepidandrena) curvungula*. **F:** *A. (Aciandrena) aciculata*. **G:** *A. (Andrena) helvola*. **H:** *A. (Cnemidandrena) nigriceps*. CD: cardo, GA: galea, LC: lacinia, ST: stipes. Scale bars: 250 µm.

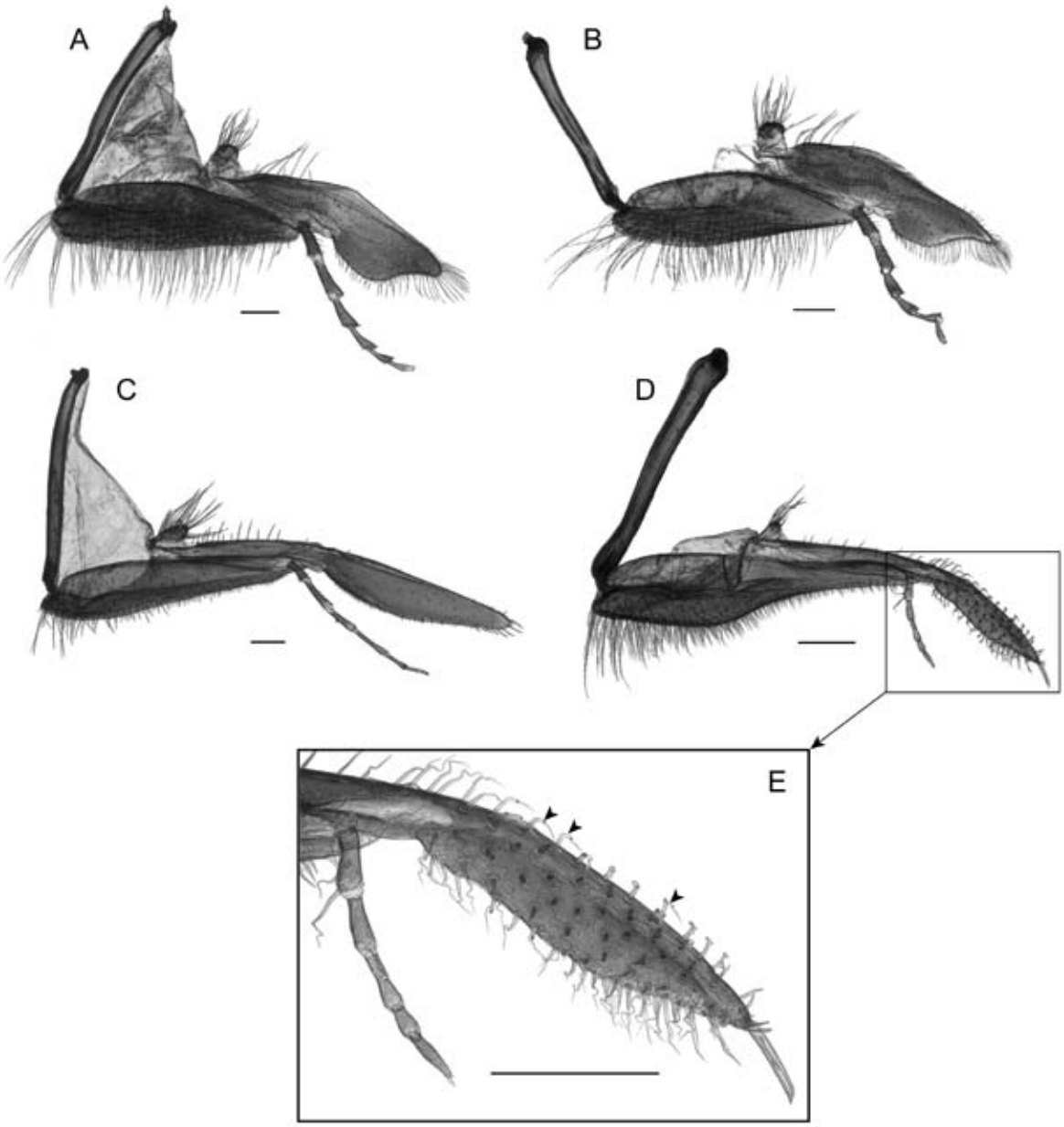

Fig. 11. Maxilla of female *Andrena*, part 2. **A:** *A. (Hoplandrena) carantonica*, **B:** *A. (Tylandrena) erythrogaster*, **C:** *A. (Didonia) mucida*. **D, E:** *A. (Scoliandrena) osmioides*, with close-up of anteriorly bent hairs of galea **(E,** arrowheads). Scale bars: 250 µm.

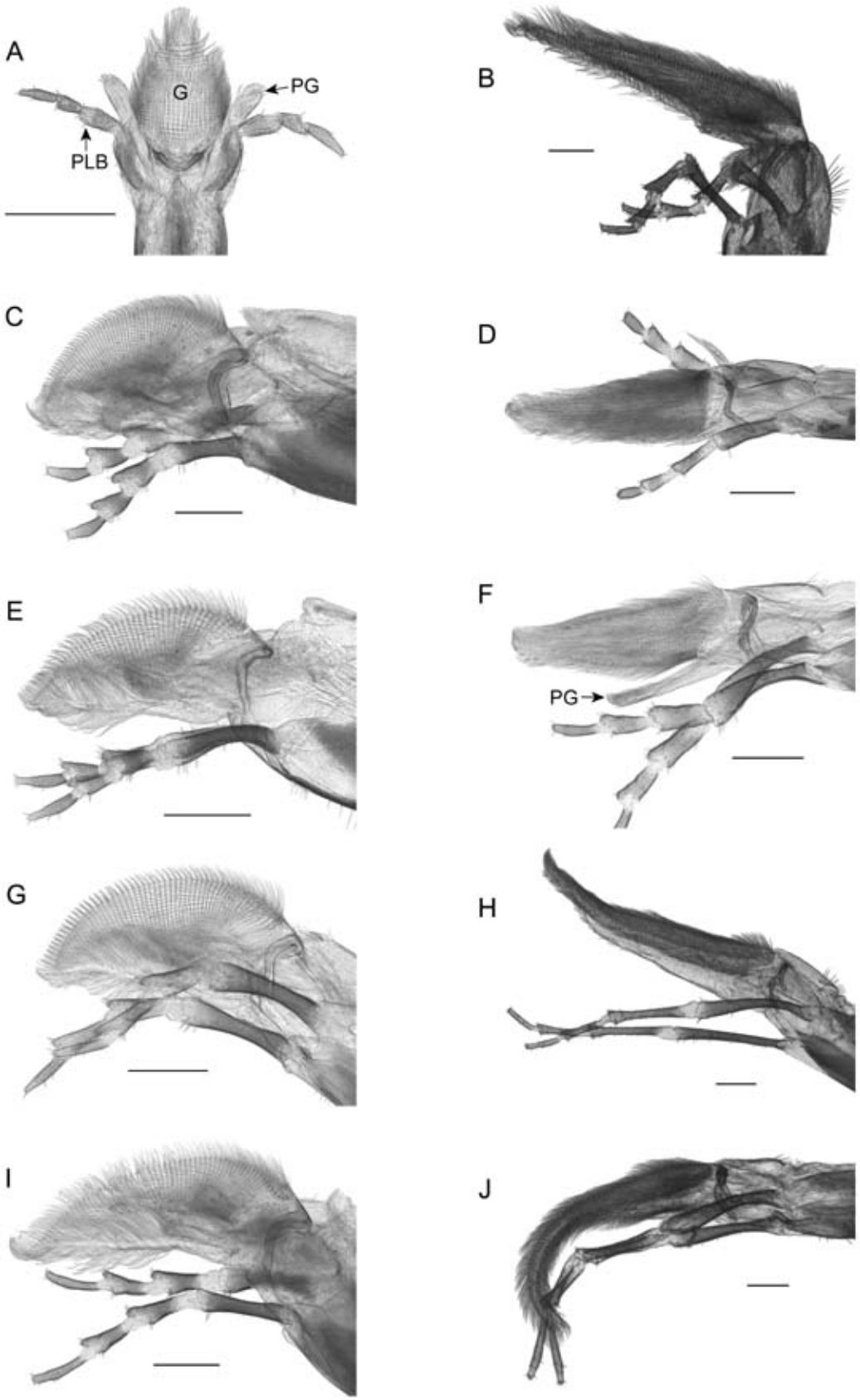

Fig. 12. Glossa of female *Andrena*. **A:** *A. (Rufandrena) rufiventris,* dorsal view. **B:** *A. (Melittoides) curiosa,* lateral view. **C:** *A. (Hoplandrena) carantonica,* lateral view. **D:** *Cubiandrena cubiceps,* lateral view. **E:** *A. (Truncandrena) truncatilabris,* lateral view. **F:** *A. (Margandrena) marginata,* lateral view. **G:** *A. (Suandrena) suerinensis,* lateral view. **H:** *A. (Didonia) mucida,* lateral view. **I:** *A. (Holandrena) labialis,* lateral view. **J:** *A. (Hamandrena) nasuta,* lateral view. G: glossa, PG: paraglossa. Scale bars: 250 µm.

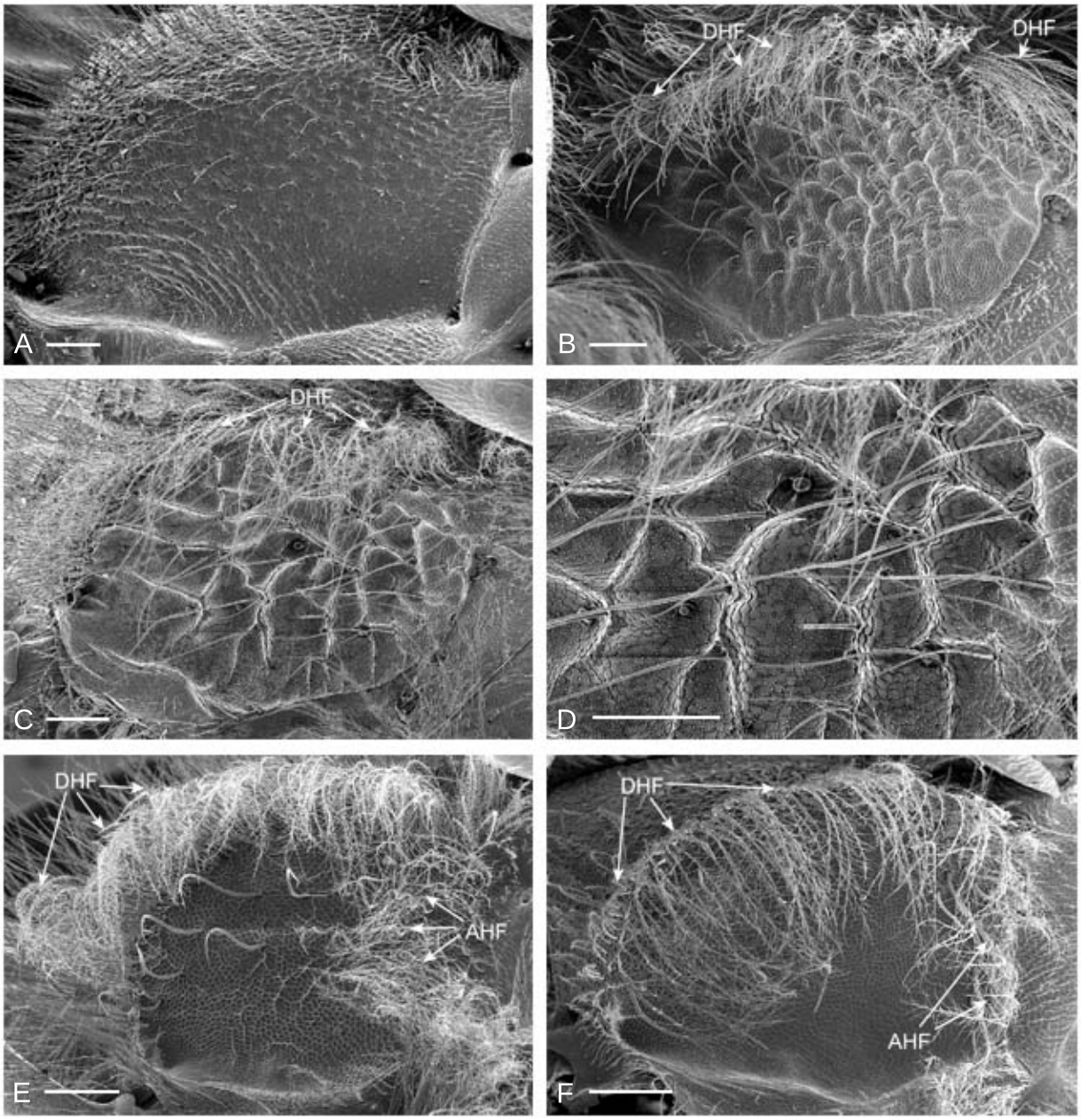

Fig. 13. Lateral propodeum of female *Andrena.* **A:** *A. (Charitandrena) hattorfiana.* **B:** *A. (Agandrena) agilissima.* **C, D:** *A. (Trachandrena) haemorrhoa.* **E:** *A. (Larandrena) ventralis.* **F:** *A. (Simandrena) dorsata.* AHF: anterior hair fringe, DHF: dorsoposterior hair fringe. Scale bars: 200 µm.

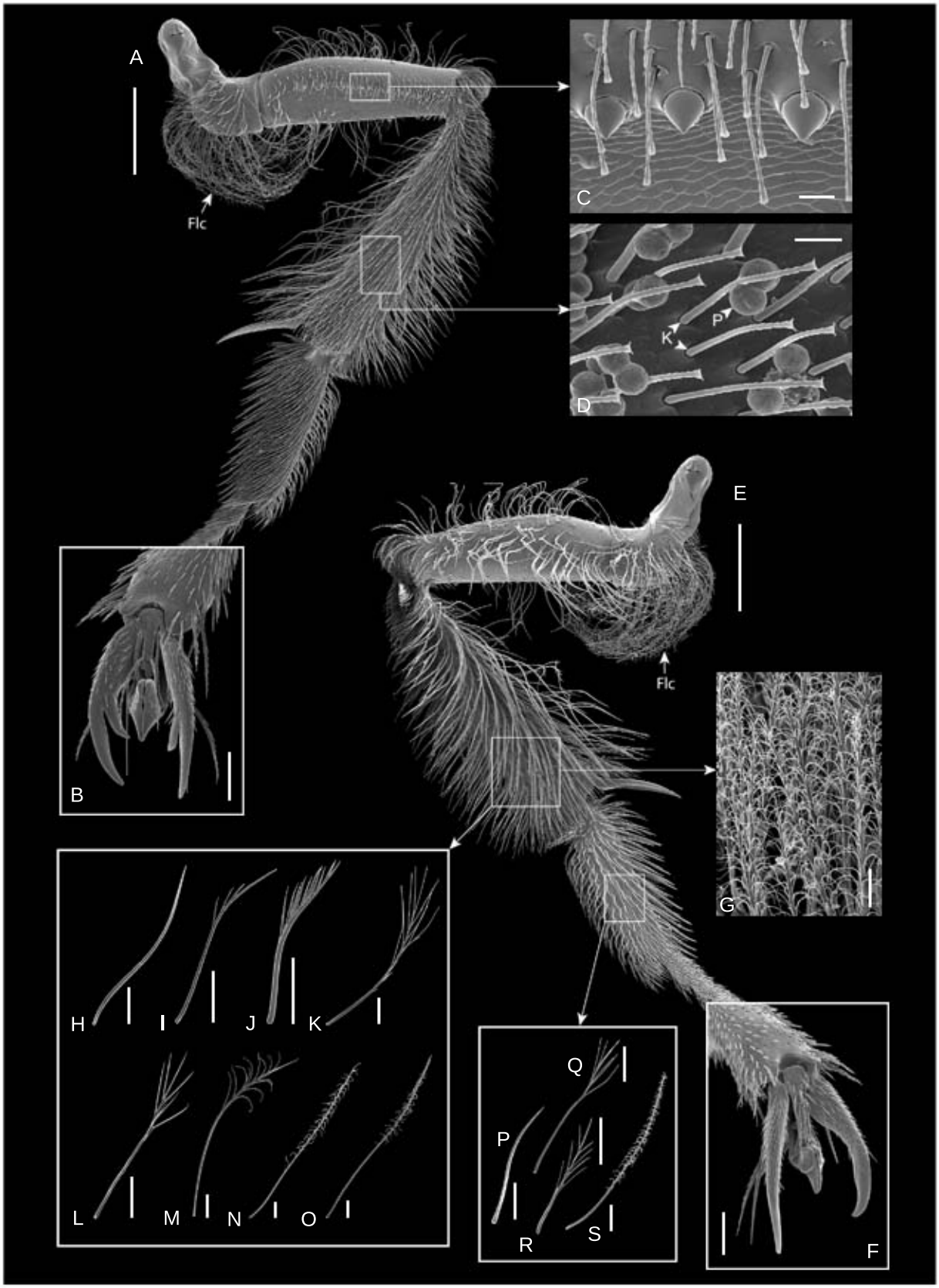

Fig. 14. Hind leg and associate structures of female *Andrena.* **A:** Inner side of hind leg of *A. (Cryptandrena) ventricosa.* **B:** Bidentate claws of *A. (Zonandrena) flavipes.* **C:** Close-up of row of bristles on inner side of hind femur of *A. (Cryptandrena) ventricosa.* **D:** Close-up of inner side of hind tibia of *A. (Aciandrena) aciculata.* **E:** Outer side of hind leg of *A. (Cryptandrena) ventricosa.* **F:** Simple claws of *A. (Platygalandrena) fedtschenkoi.* **G:** Close-up of tibial scopa of *A. (Charitandrena) hattorfiana.* **H-O:** Hairs of tibial scopa, of *A. (Zonandrena) flavipes* **(H),** *A. (Genyandrena) mackieae* **(I),** *A. (Augandrena) plumiscopa* **(J),** *A. (Chlorandrena) humilis* **(K),** *A. (Fumandrena) fumida* **(L),** *A. (Chrysandrena) fulvago* **(M),** *A. (Charitandrena) hattorfiana* **(N),** *Cubiandrena cubiceps* **(O). P-S:** Hairs of outer side of basitarsus of *A. (Zonandrena) flavipes* **(P),** *A. (Chlorandrena) humilis* **(Q),** *A. (Chrysandrena) fulvago* **(R),** *Cubiandrena cubiceps* **(S).** Flc: flocculus of hind trochanter, K: keirotricha-like hairs, P: pollen. Scale bars: 500 µm (A, E), 100 µm (B, F, H-S) 50 µm (D, G), 25 µm (C).

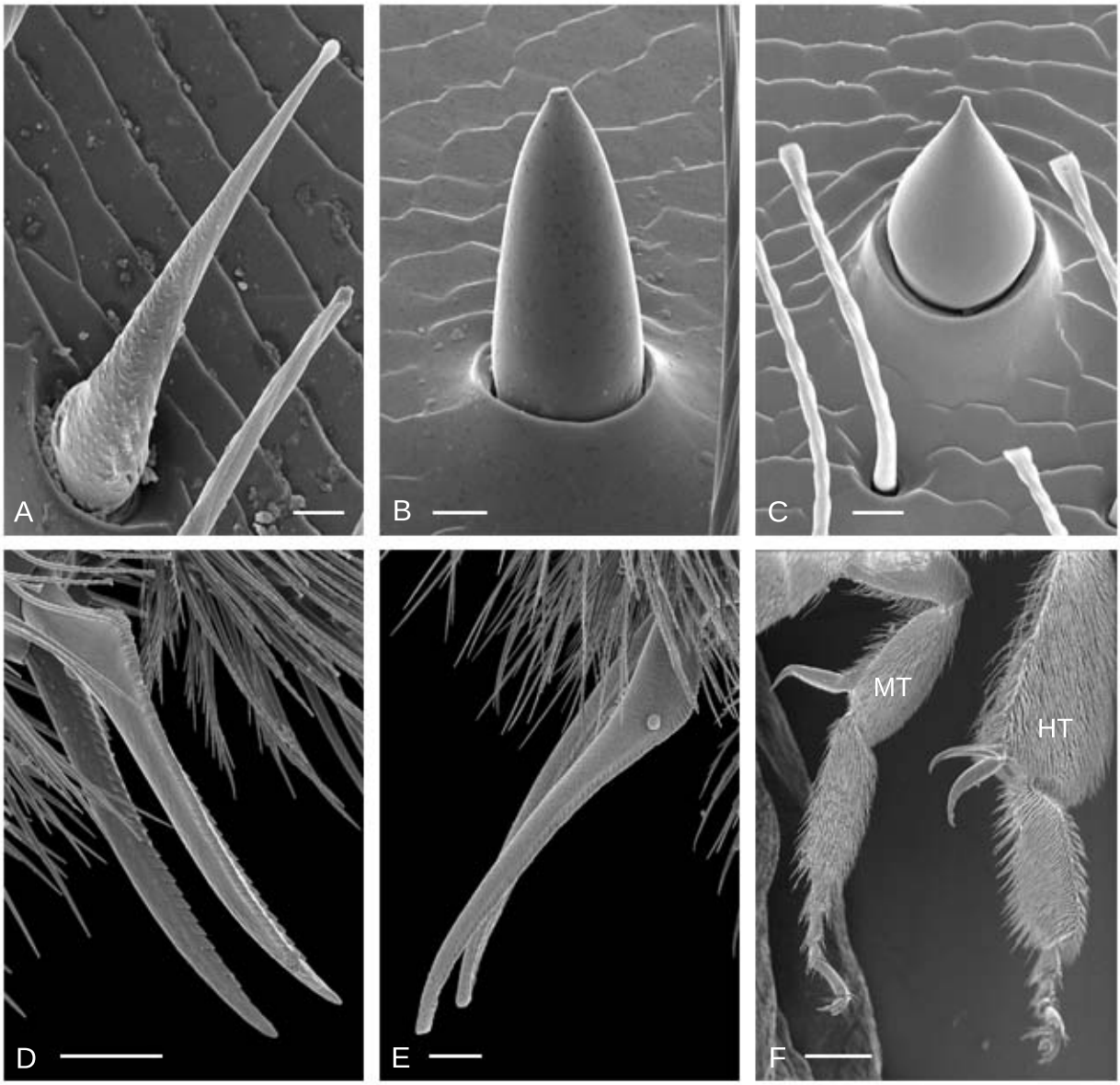

Fig. 15. Bristles of hind femur **(A-C)** and inner spurs of hind tibia **(D-E)** of female *Andrena.* **A, D:** *A. (Lepidandrena) curvungula.* **B:** *A. (Chlorandrena) humilis.* **C, D:** *A. (Cryptandrena) ventricosa.* **E:** *A. (Osychnyukandrena) cochlearicalcar.* Scale bars: 500 µm (F), 100 µm (D, E), 10 µm (A-C).

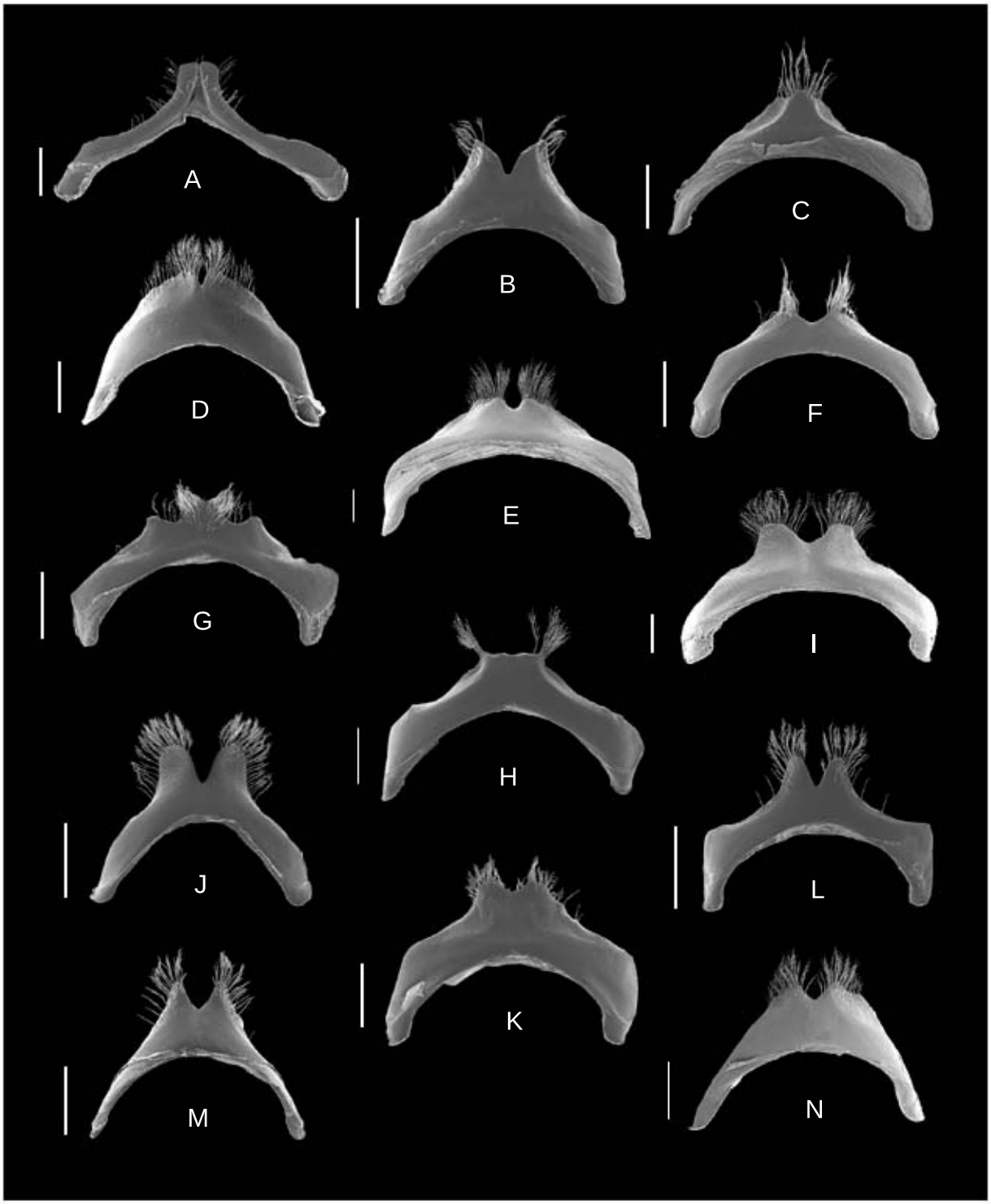

Fig. 16. Ventral side of male S 7 of *Cubiandrena* **(A)** and *Andrena* **(B-N): A:** *Cubiandrena cubiceps.* **B:** *A. (Aenandrena) aeneiventris,* **C:** *A. (Andrena) helvola.* **D:** *A. (Leucandrena) barbilabris.* **E:** *A. (Agandrena) agilissima.* **F:** *A. (Zonandrena) flavipes.* **G:** *A. (Parandrenella) dentiventris.* **H:** *A. (Pallandrena) pallidicincta.* **I:** *A. (Chlorandrena) humilis.* **J:** *A. (Carandrena) planti.* **K:** *A. (Larandrena) susanneae.* **L:** *A. (Simandrena) heinzi.* **M:** *A. (Euandrena) yangi.* **N:** *A. (Leucandrena) cheni.* Scale bars: 250 µm.

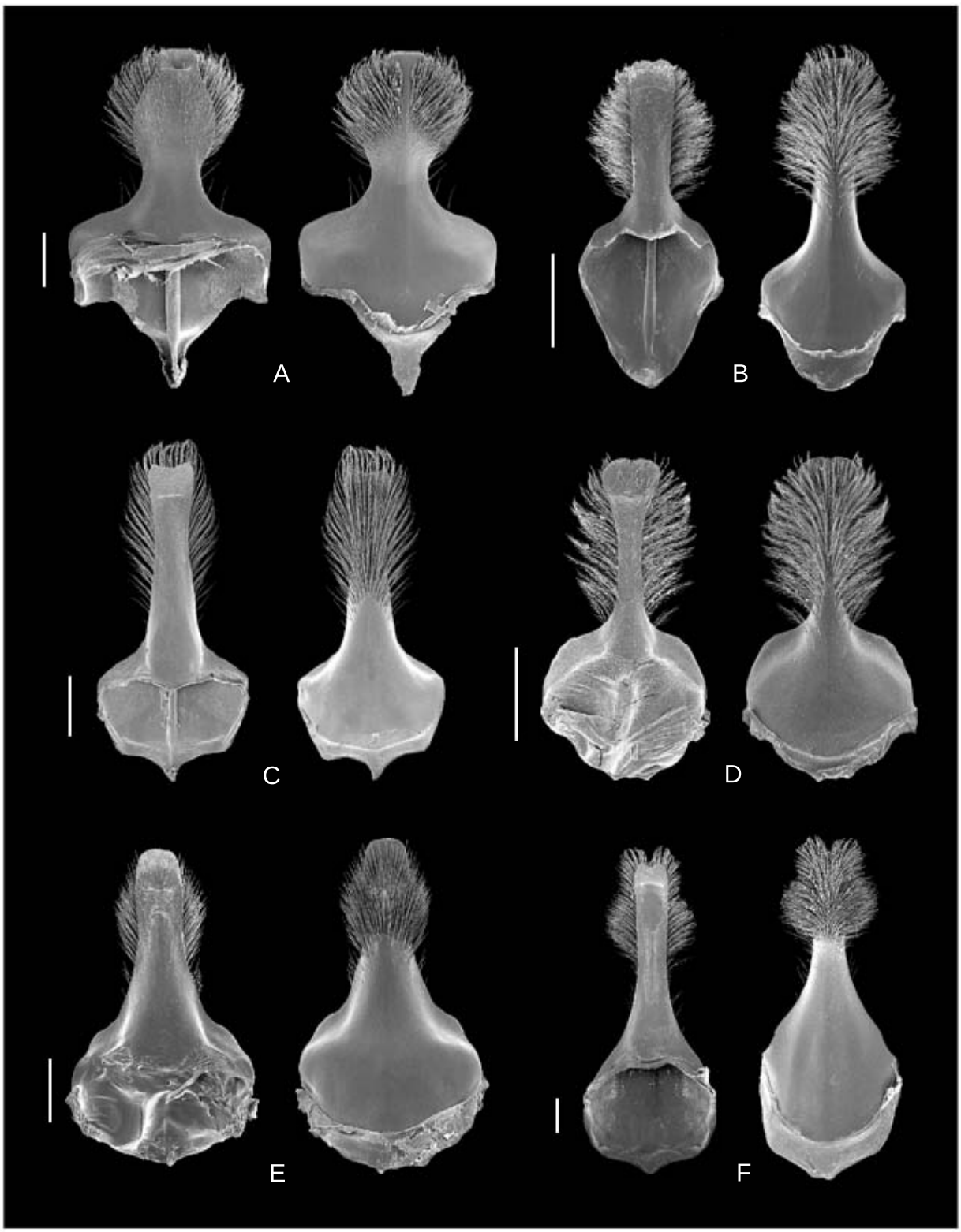

Fig. 17. S8 of male *Cubiandrena* **(A)** and *Andrena* **(B-F),** left dorsal, right ventral view. **A:** *Cubiandrena cubiceps.* **B:** *A. (Aenandrena) aeneiventris,* **C:** *A. (Andrena) helvola.* **D:** *A. (Fuscandrena) fuscicollis.* **E:** *A. (Leucandrena) barbilabris.* **F:** *A. (Charitandrena) hattorfiana.* Scale bars: 250 µm.

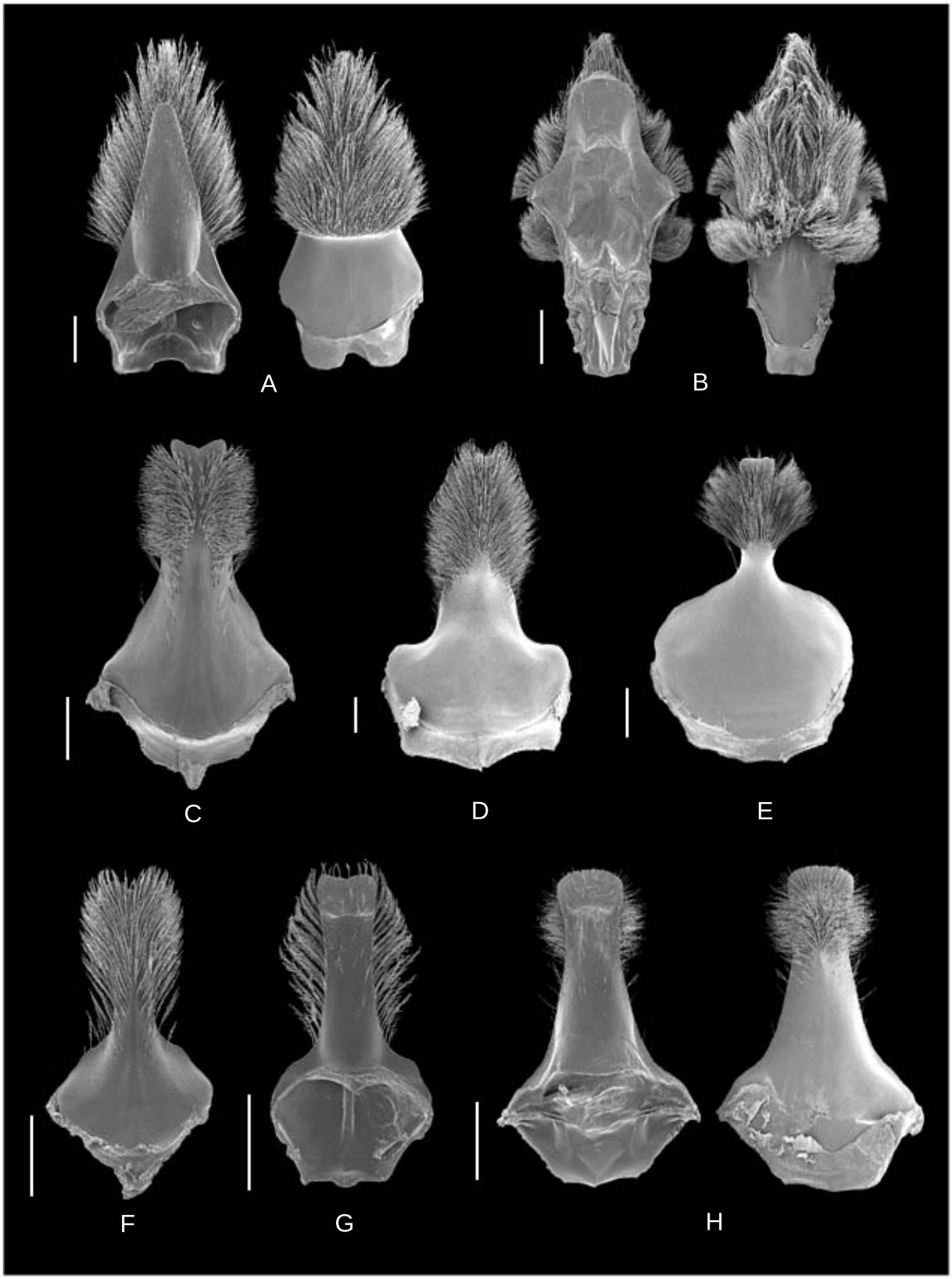

Fig. 18. S8 of male *Andrena,* left dorsal, right ventral view. **A:** *A. (Orandrena) oralis.* **B:** *A. (Parandrenella) dentiventris.* **C:** *A. (Pallandrena) pallidicincta.* **D:** *A. (Agandrena) agilissima.* **E:** *A. (Chlorandrena) humilis.* **F:** *A. (Carandrena) planti.* **G:** *A. (Simandrena) heinzi.* **H:** *A. (Larandrena) susanneae.* Scale bars: 250 µm.

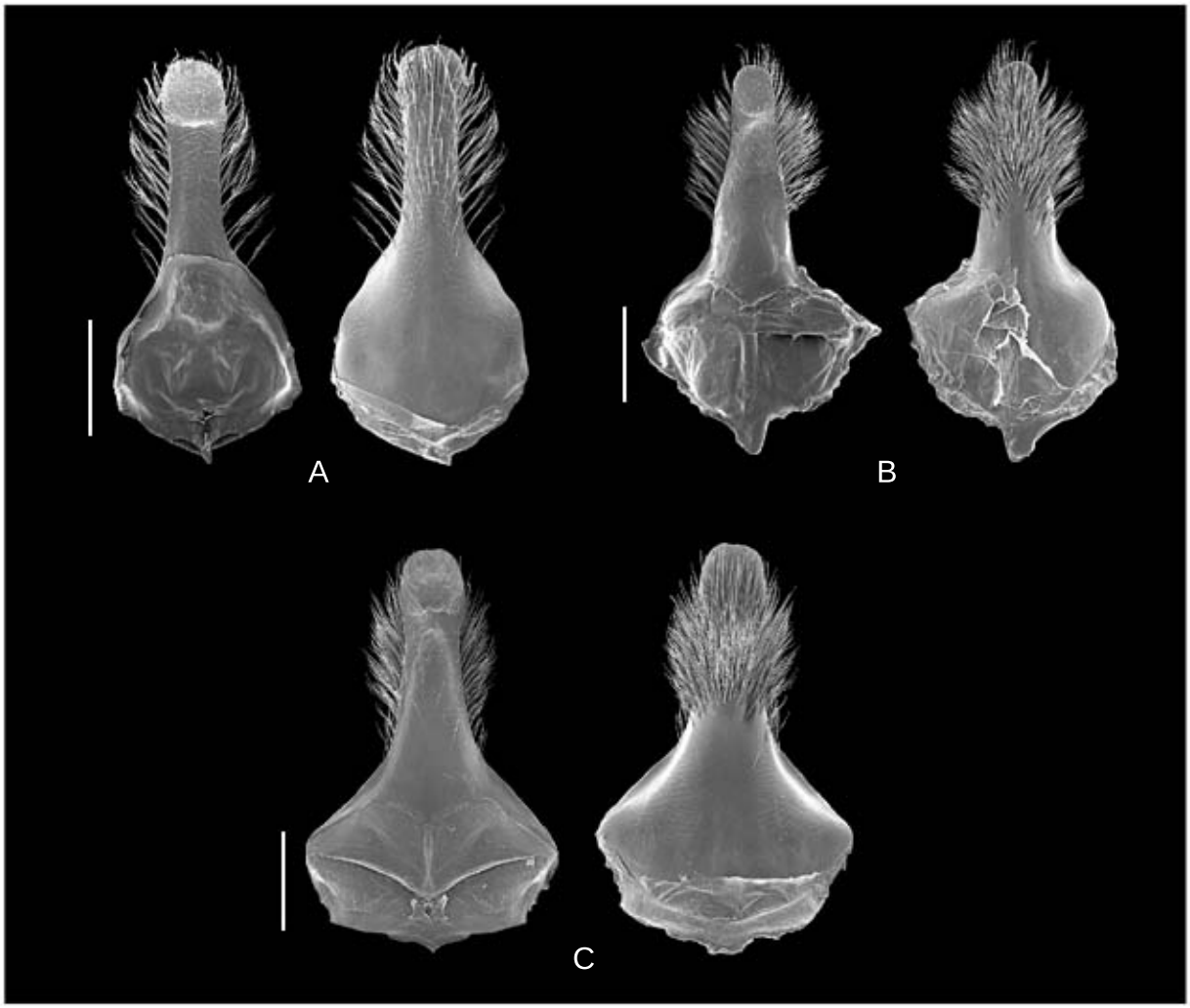

Fig. 19. S8 of male *Andrena,* left dorsal, right ventral view. **A:** *A. (Euandrena) yangi.* **B:** *A. (Habromelissa) nantouensis.* **C:** *A. (Leucandrena) cheni.* Scale bars: 250 µm.

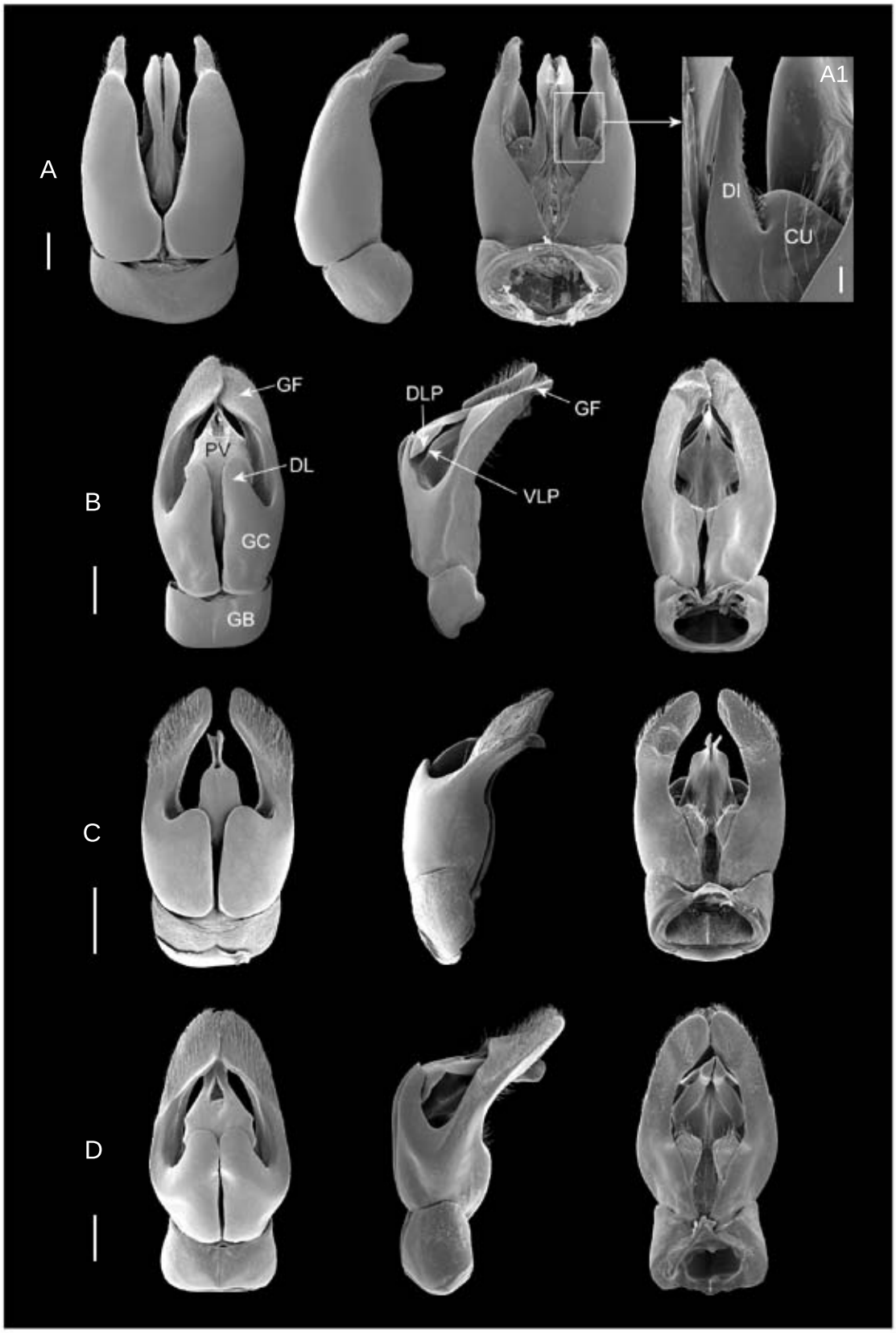

Fig. 20. Male genitalia of *Cubiandrena* **(A)** and *Andrena* **(B-D),** left dorsal, middle lateral and right ventral view. **A:** *Cubiandrena cubiceps.* **A1:** Close-up of volsella of *Cubiandrena cubiceps.* **B:** *A. (Andrena) helvola.* **C:** *A. (Aenandrena) aeneiventris.* **D:** *A. (Leucandrena) barbilabris.* CU: cuspis, DI: digitus, DL: dorsal lobe of gonocoxite, DLP: dorsolateral lamella of penis valve, GB: gonobase, GC: gonocoxite, GF: gonoforceps, PV: penis valve, VLP: ventrolateral lamella of penis valve. Scale bars: 250 µm (A-D), 50 µm (A1).

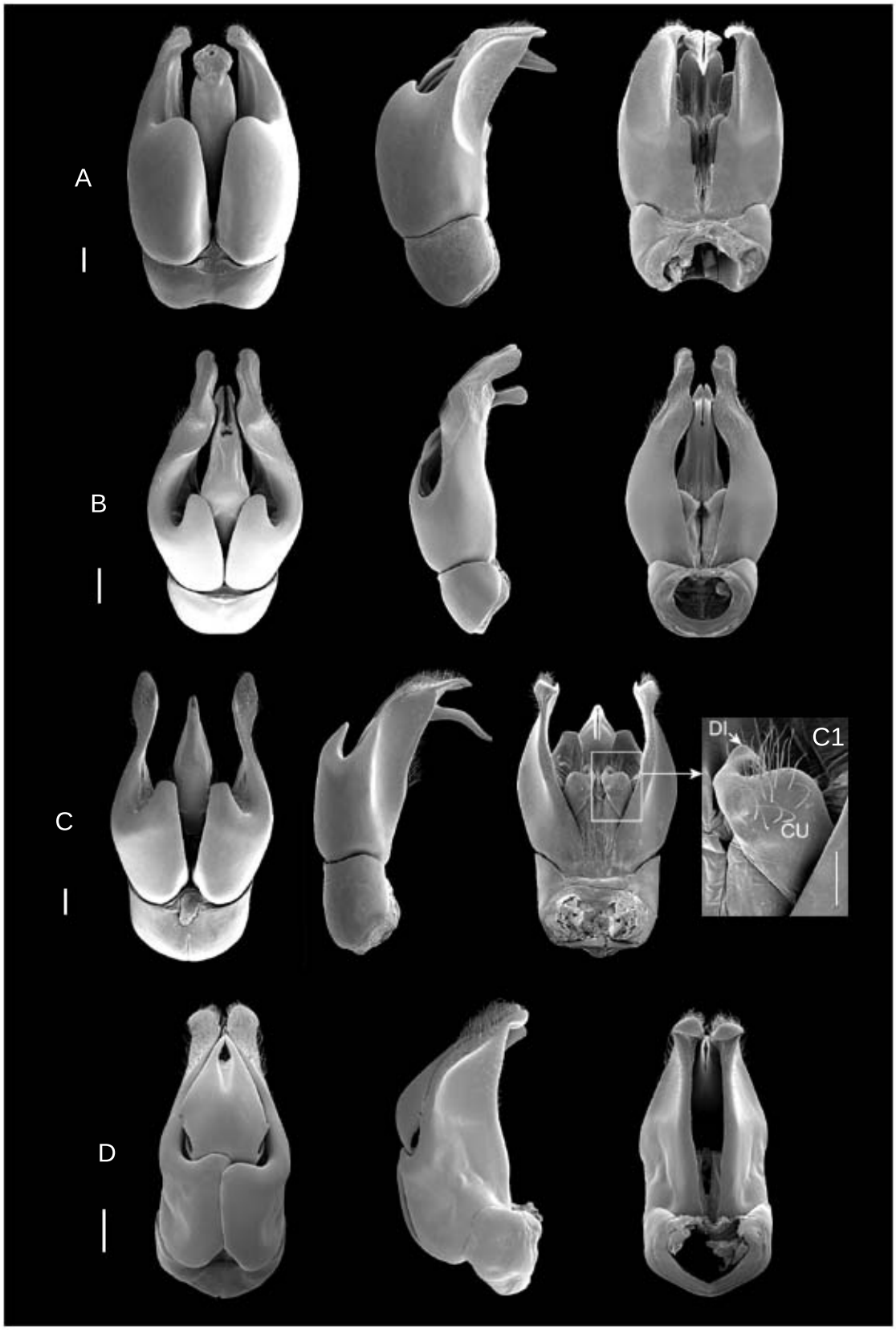

Fig. 21. Male genitalia of *Andrena,* left dorsal, middle lateral and right ventral view. **A:** *A. (Agandrena) agilissima.* **B:** *A. (Orandrena) oralis.* **C:** *A. (Charitandrena) hattorfiana.* **C1:** Close-up of volsella of *A. (Charitandrena) hattorfiana.* **D:** *A. (Pallandrena) pallidicincta.* CU: cuspis, DI: digitus. Scale bars: 250 µm.

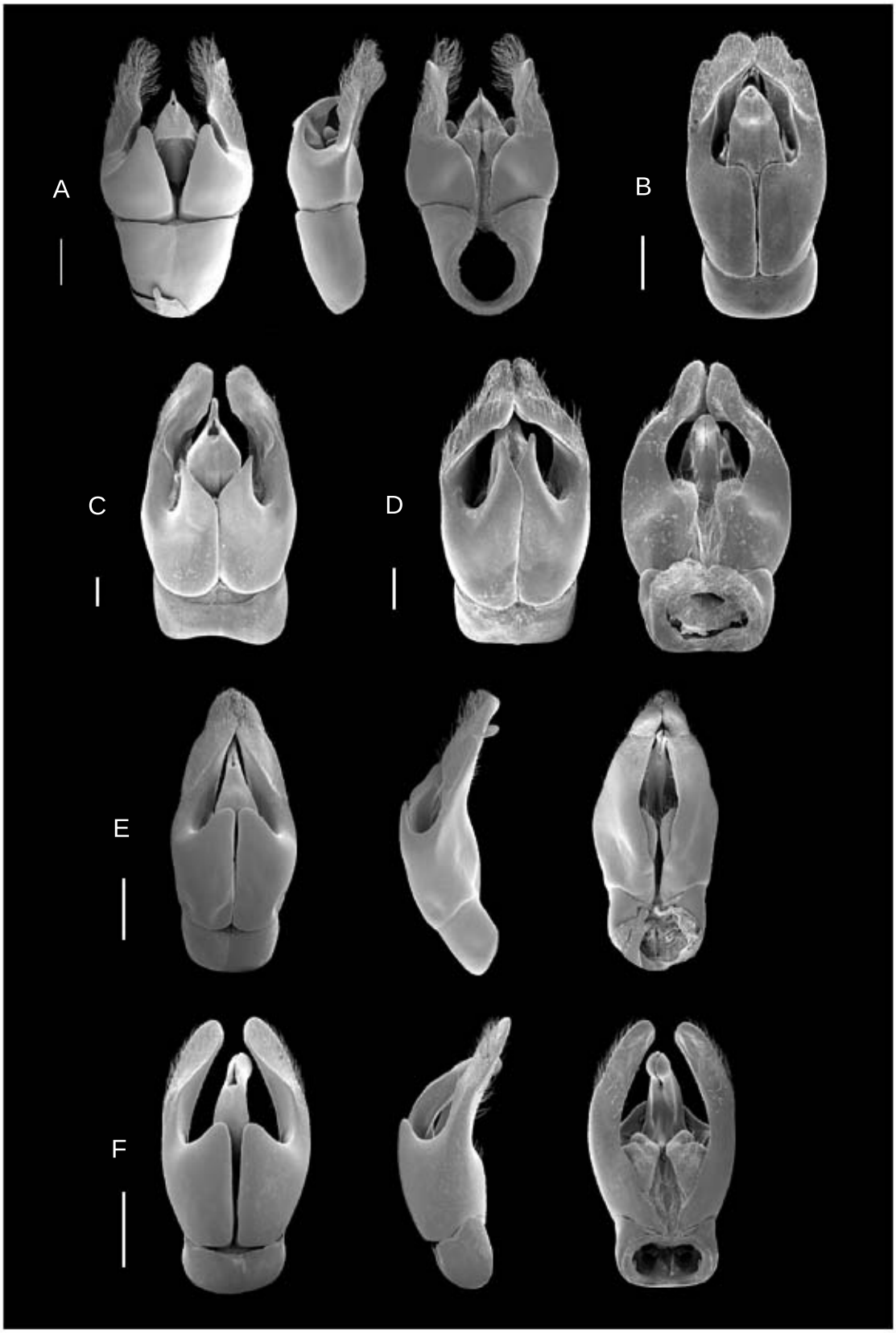

Fig. 22. Male genitalia of *Andrena,* left dorsal, middle lateral and right ventral view. **A:** *A. (Parandrenella) dentiventris.* **B:** *A. (Zonandrena) flavipes* (dorsal view only). **C:** *A. (Plastandrena) tibialis (dorsal view only).* **D:** *A. (Trachandrena) haemorrhoa* (dorsal and ventral view only). **E:** *A. (Carandrena) planti.* **F:** *A. (Simandrena) heinzi.* Scale bars: 250 µm.

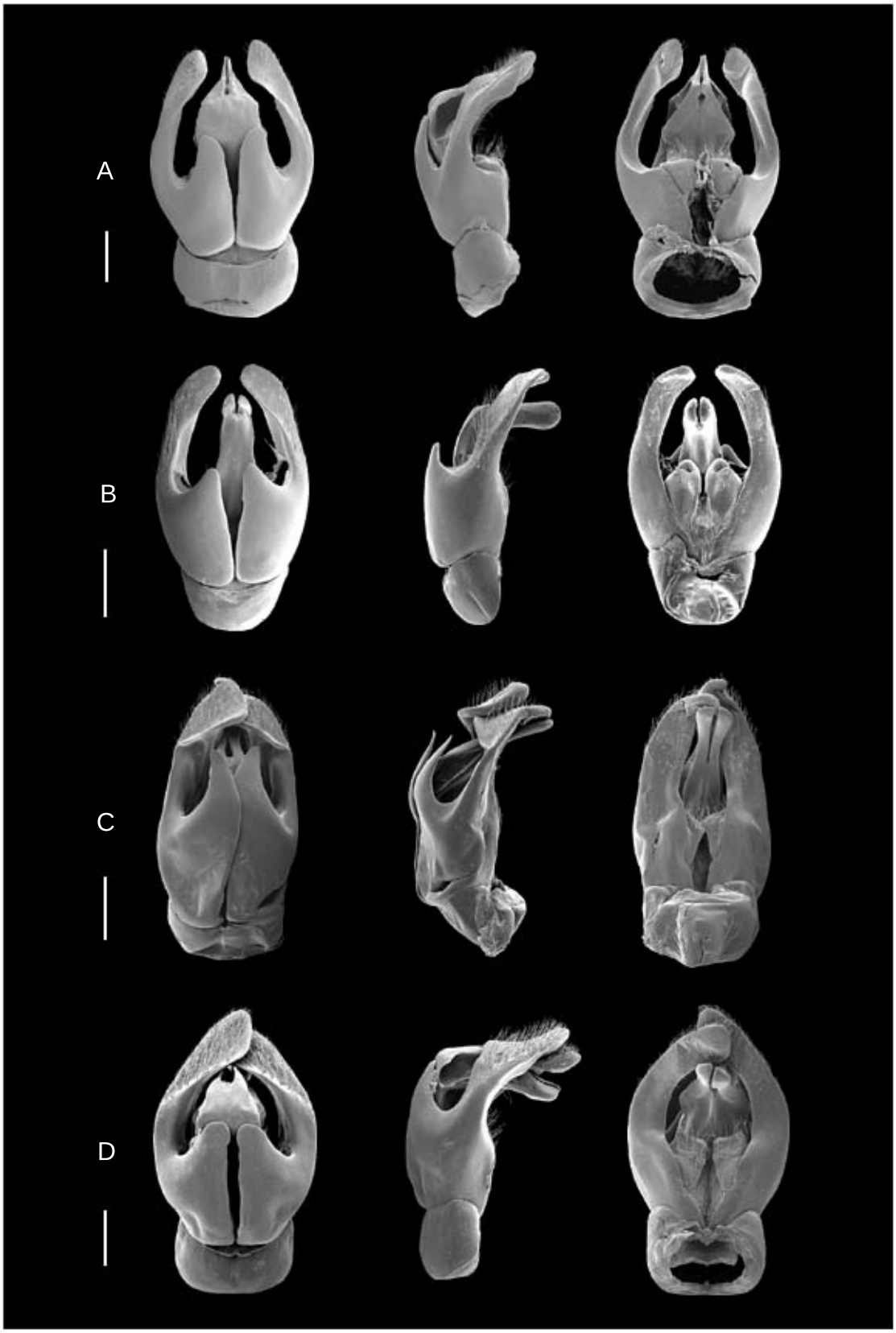

Fig. 23. Male genitalia of Andrena, left dorsal, middle lateral and right ventral view. **A:** *A. (Larandrena) susanneae.* **B:** *A. (Euandrena) yangi.* **C:** *A. (Habromelissa) nantouensis.* **D:** *A. (Leucandrena) cheni.* Scale bars: 250 µm.

4. Phylogeny of the world Anthophorini, in particular the genus *Habropoda*

4.1 Introduction

Latreille (1802a) proposed the group Podalirii based on the genus *Podalirius,* which he described in the same year (1802b). One year later, after learning that the latter name was preoccupied among the plants, he suggested *Anthophora* as a replacement (Latreille, 1803). In 1835 Dahlbom designated *Anthophora* as the type genus of his newly erected tribe, the Anthophorini. Since *Podalirius* was suppressed by the International Commission on Zoological Nomenclature (Hemming, 1944), the name *Podalirius* was no longer available as the type genus for a higher categorical name and Anthophorini as the tribal name of Dahlbom became valid (Brooks, 1988). For further details see the historical review of the classification of this tribe from the time of Linnaeus onward by Brooks (1988).

The Anthophorini (*sensu* Michener 2000) with about 710 species in seven genera constitute one of the largest tribes of medium to large-sized, nest-building bees within the Apinae. The type genus ***Anthophora*** (Figs 33A-C), which is the largest genus of the tribe, comprises about 350 species and is subdivided into 14 subgenera (Brooks, 1988). Seven of these are Holarctic to worldwide in distribution, six are exclusively found in the Old World and one is endemic to North America. Species of *Anthophora* were listed by Brooks (1988), Eardley & Brooks (1989) and Wu (2000). The genus ***Amegilla*** Friese, 1897 (Figs 33D, E), with more than 250 species, represents the second largest group within the Anthophorini. Brooks (1988) recognized 11 subgenera of *Amegilla*, however Michener (2000) declined to subdivide the genus. *Amegilla* is strictly Old World in distribution, ranging throughout the Palearctic region, Africa (including Madagascar), the Oriental region and Australia, but is absent from America. Three of the subgenera are strictly African, three are African to Palearctic and one subgenus is African and Oriental in distribution. Finally, three of the 11 subgenera are restricted to the Oriental region and Australia and one subgenus is endemic to Australia. Species of *Amegilla* were listed by Brooks (1988), Eardley (1994), Pauly et al. (2001) and Wu (2000). The Mesoamerican genus ***Deltoptila*** LaBerge & Michener, 1963, with ten species, which were revised by LaBerge & Michener (1963), is known from moderate to high altitudes from Central Mexico to Costa Rica. The genera ***Elaphropoda*** Lieftinck, 1966, with 11 species ranging from the Himalayan region to southeast Asia and Indonesia and ***Habrophorula*** Lieftinck, 1974 with three species from southeast China are endemic to the Oriental region. Species of these two genera were revised by Lieftinck (1944, 1966, 1972, 1974) and Wu (1979, 1985, 1991, 2000). The genus ***Habropoda*** Smith, 1854 includes about 60 species, in the Old World ranging from the Mediterranean region via Asia minor to North India, the Himalayan region, Vietnam and China (including Taiwan) and in the New World from North to Middle America. Krombein et al. (1979) listed 21 American species of

Habropoda, while about 39 species are known from the Old World (Lieftinck, 1966, 1974; Schwarz & Gusenleitner, 2001; Wu, 2000). The genus ***Pachymelus*** contains about 20 species and is subdivided into two subgenera, ***Pachymelus* s. str.** Smith, 1879 (15 species), which is endemic to Madagascar and includes the largest representatives of Anthophorini, and ***Pachymelopsis*** Cockerell, 1905 (5 species), which is restricted to Southern Africa. Species of *Pachymelus* s. str. were revised by Pauly et al. (2001), those of *Pachymelopsis* by Eardley (1993).

The phylogenetic position of the Anthophorini within the Apinae, as examined by Roig-Alsina and Michener (1993) in their cladistic analysis of long-tongued (LT) bees based on adult and larval morphology, depended on the particular analysis. Using all adult morphological characters (analysis A, cladogram 1a) the Centridini emerged as most probable sister-group of the Anthophorini (Fig. 24A). The monophyly of Anthophorini + Centridini was supported by three homoplasious synapomorphies: (1) apophyseal arms of prosternum separate from one another, (2) a double gonostylus with two nearly independent gonostylar structures arising from gonocoxite and (3) vestiture of wings being partly bare. In another analysis (analysis C, cladograms 2a and 2b), in which characters were excluded that seemed related to cleptoparasitism, the common clade of Melectini and Ericrocidini emerged as the sister of Anthophorini (Fig.24B). In contrast, analyses which omitted all cleptoparasitic taxa (cladogram 3a, b) or which were based exclusively on larval characters (cladogram 4) resulted in a paraphyletic Centridini with either *Centris* or *Epicharis* as the sister group of the Anthophorini.

The phylogenetic relationship of another group within the Apinae, the corbiculate bees, has been repeatedly studied by cladistic analysis using morphological, ethological and most recently molecular data (e.g., Cameron, 2004; Cameron & Mardulyn, 2001; Lockhart & Cameron, 2001; Noll, 2002; Prentice, 1991; Schultz et al., 1999, 2001), however, the phylogeny of Anthophorini still remains dubious and unresolved (Michener, 2000). To date there are no published cladistic analyses on this tribe as a whole.

Noteworthy are the solid cladistic analyses conducted by Brooks (1988), which however were restricted to the genera *Anthophora* and *Amegilla*, respectively. Earlier taxonomic studies (including evolutionary hypothesis) have been conducted only for specific groups, e.g. *Amegilla* (Popov, 1950), *Clisodon* (Popov, 1951) and *Habropoda* (Popov, 1948) but seldom concerned the tribe as a whole. Michener (1944) included *Anthophora, Amegilla* (as a subgenus of *Anthophora*), *Habropoda* (as well as *Emphoropsis*) and *Pachymelus* in the Anthophorini. The scope of the Anthophorini was extended by LaBerge & Michener (1963) with the discovery of *Deltoptila* as a new genus of this tribe. Subsequently, Lieftinck (1966, 1974) described two additional genera from the Oriental region (*Elaphropoda* and *Habrophorula*).

Based mainly on the morphology of male genitalia and male S7 and S8, Marikovskaya (1976) split the Anthophorini into two tribes, the Anthophorini s. str. with three genera, *Anthophora*, *Amegilla* and *Pachymelus*, and a new tribe, the Habropodini, comprising

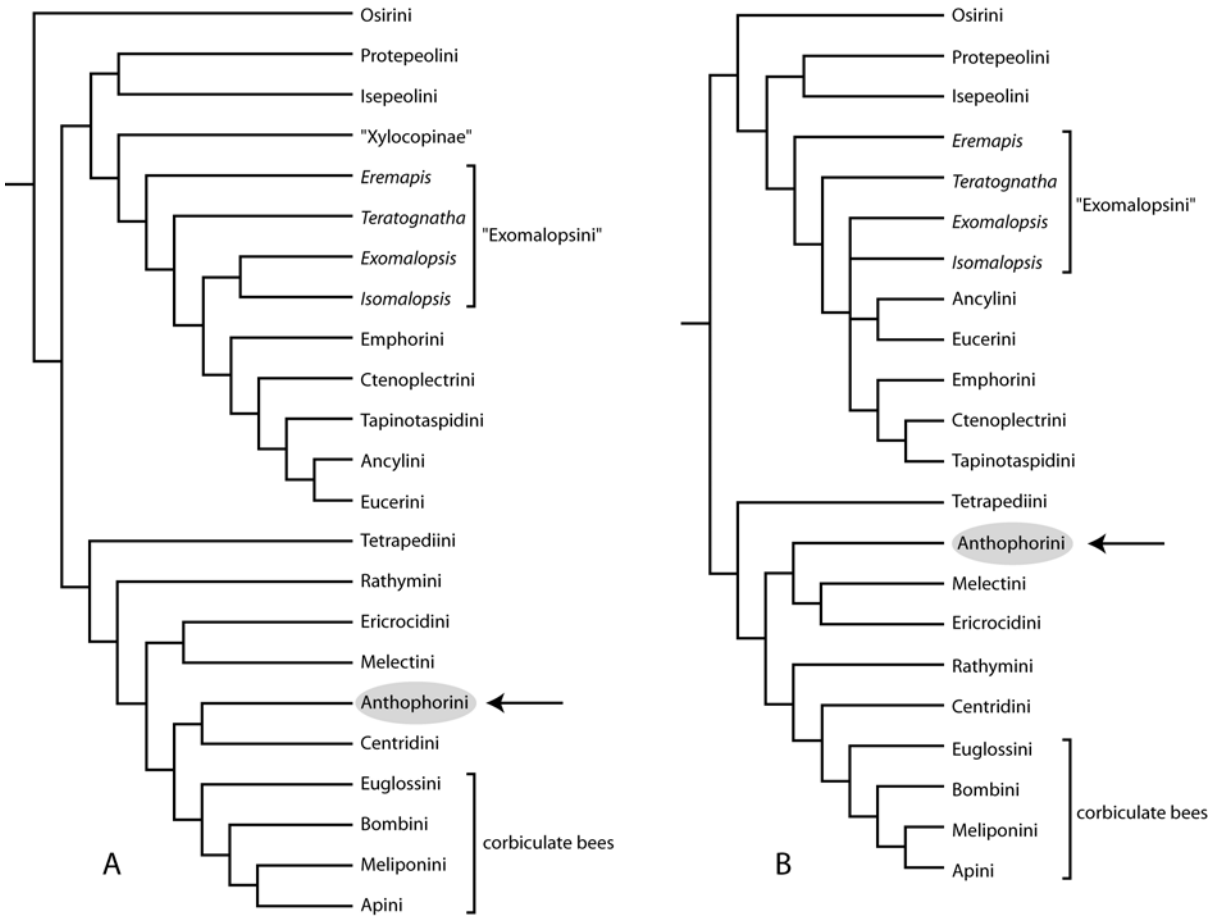

Fig. 24. Phylogeny of Apinae, redrawn from Roig-Alsina and Michener (1993). **A:** Cladogram based on analysis of all adult morphological characters. **B:** Cladogram based on analysis with characters omitted which are related to cleptoparasitism.

Habropoda, *Elaphropoda* and *Deltoptila*. In a comprehensive study of the systematics and phylogeny of the anthophorine bees, Brooks (1988) adopted Marikovskaya's differentiation between Anthophorini and Habropodini and transferred the genera *Pachymelus* and *Habrophorula* to the Habropodini, leaving the Anthophorini s. str. with two genera, *Anthophora* and *Amegilla*. Michener (2000) however chose not to recognize Habropodini as a separate tribe and emphasized the importance of showing the relationship of *Habropoda* and its allies to *Anthophora* by classification.

The Old World species of *Habropoda* have been extensively studied (Lieftinck, 1966, 1969, 1972, 1974; Popov, 1948; Schwarz & Gusenleitner, 2001; Wu, 1979, 1983, 2000). Nonetheless, no phylogenetic concepts or higher taxonomic grouping have been developed except for some interspecific relationships indicated by Popov (1948) and some informal species groups mentioned by Lieftinck (1966, 1974). This is surprising since the differences between, e.g., the western palearctic and oriental members of this genus are striking. It was thus conceivable that a resolution of phylogenetic relationships within this genus would be made possible by a cladistic analysis based on morphological characters.

In the following a phylogenetic concept is presented for the Anthophorini based on a cladistic analysis of adult morphology and a likely evolutionary scenario of the tribe is discussed. In addition, a detailed cladistic analysis of Old World *Habropoda* was conducted, accompanied by a revision of the *Habropoda* species of Taiwan and its cleptoparasite bee, *Tetralonioidella* Strand, 1914 (Melectini, Apinae).

4.2 Results and Discussion

4.2.1 Cladistic analysis of World Anthophorini

Selection of taxa and characters

To analyse the Anthophorini, 26 ingroup taxa were selected representing all known genera as well as the most important subgenera. *Centris* was chosen as the outgroup according to the results of the analysis of Roig-Alsina & Michener (1993).

A total of 51 adult characters consisting of 123 character states were used in the present analysis. 33 characters were coded as binary, 16 characters have three states and one character has four and another five states.

Definition of characters and character states used in the cladistic analysis of Anthophorini

In the following character list for the tribe, as well as for *Habropoda* (4.2.2), it was not necessary to present hypotheses about character polarisation or transformation since the morphological conditions are relatively clear-cut and the polarity could be derived by comparison with the outgroups. State (0) therefore always represents the plesiomorphic condition for each character.

Head and mouthparts

1. Length of proboscis: (0) normal, distinctly shorter than 2 times length of head; (1) elongate, about 2 times as long as head.
2. Flabellum: (0) oval, only slightly longer than broad, apically rounded; (1) distinctly longer than broad, apically rounded (Figs 34G, H); (2) distinctly longer than broad, apically pointed (Figs 34A, B); (3) medium to large-sized, with distinct apical finger-shaped projections (Figs 34C, D); (4) absent (Figs 34E, F).
3. Ventral surface of flabellum: (0) with cobblestone pattern (Fig. 34H); (1) smooth (Figs 34B, D).
4. Pubescence of PMX 2: (0) with sparse long hairs mainly along posterior margin, anterior margin bare or with few short hairs (Fig. 34I); (1) nearly bare, with few inconspicuous minute hairs; (2) with distinct comb-like hair fringe along anterior margin and medium long sparse hairs along posterior margin (Fig. 34J).

5. PMX 2: (0) straight to weakly curved (Fig. 34I); (1) distinctly curved, with concave anterior margin and convex posterior margin (Fig. 34J).
6. Cross section of PMX 2: (0) rounded to weakly flattened (Fig. 34I); (1) strongly flattened (Fig. 34J).
7. Length of PMX 3: (0) about as long, to slightly longer as half the length of PMX 2 (at least 0.45x as long as PMX 2, Fig. 34I); (1) shorter than half the length of PMX 2 (Fig. 34J); (2) about as long as PMX 2 (at least 0.8x as long as PMX 2).
8. Mandibles (female): (0) with one preapical tooth on upper margin, bidentate; (1) with two preapical teeth on upper margin, tridentate; (2) with more than two preapical teeth on upper margin.
9. Labrum: (0) distinctly broader than long (> 1.2x); (1) about as long as broad.
10. Clypeus (female): (0) normally rounded; (1) extremely convex, protuberant; (2) more or less flattened.
11. Thorn-like bristles on female clypeus: (0) absent; (1) present.
12. Front margin of clypeus: (0) extending to or slightly beyond base of mandibles; (1) extending distinctly beyond base of mandibles.
13. Malar space (female): (0) absent to strongly reduced, nearly no free space between mandible and compound eye; (1) distinctly present, at least as long as width of antennal flagellum.
14. Colour of paraocular area (female): (0) dark; (1) with bright yellowish to ivory maculations.
15. AS 3 (female): (0) distinctly shorter than scape; (1) about as long as scape; (2) elongate, distinctly longer than scape.

Wings

16. 2nd submarginal cell: (0) distinctly shorter than 1st and 3rd submarginal cell (Figs 37E, G, I); (1) shorter than 1st submarginal cell, about as long as 3rd submarginal cell (Figs 37A, C, K, M); (2) longer than 1st and 3rd submarginal cell.
17. 1st recurrent vein (1 m-cu) joining 2nd submarginal cell: (0) near middle (Figs 37A, C); (1) terminating near apex (Figs 37E, G, I, K, M).
18. Front margin of 2nd submarginal cell: (0) about half as long as hind margin or shorter (Figs 37A, C); (1) distinctly longer than half the length of hind margin (Figs 37E, G, I, K, M).
19. 3rd submarginal cell: (0) front margin distinctly shorter than hind margin (Figs 37C, E, G, I, K, M); (1) front margin about as long as hind margin(Figs 37A,); (2) front margin distinctly longer than hind margin.
20. Cu-V-vein meeting M+Cu-vein: (0) behind M-vein (Fig. 37E); (1) at intersection of M- and Cu-vein (Figs 37A, G, I, K, M); (2) before M-vein (Fig. 37C).
21. Marginal cell: (0) short, about 4 times as long as broad (Figs 37A, C); (1) medium long, about 5 times as long as broad (Figs 37E, G, I, M); (2) long, nearly 7 times as long as broad (Fig. 37K).

22. Distance from apex of marginal cell to wing tip: (0) about as long to slightly longer than marginal cell (Figs 37 E, M; (1) distinctly longer (ca. 1.4x) than marginal cell (Fig. 37A) (2) distinctly shorter (ca. 0.5x) than marginal cell (Figs 37G, I, K).
23. Stigma: (0) well-developed, at least as long as broad (Figs 37A, C, E, G, I, M); (1) nearly absent, minute, broader than long (Fig. 37K).
24. Vein cu-v of hind wing: (0) distinctly shorter (about half as long) than second abscissa of M+Cu-vein (37B, H, J, N); (1) about as long as second abscissa of M+Cu-vein (Figs 37D, F); (2) distinctly longer than second abscissa of M+Cu-vein (Fig. 37L).
25. Jugal lobe of hind wing: (0) large, nearly as long as vannal lobe or longer (≥ 0.7x); (1) small, about half as long as vannal lobe or shorter (<0.65x, Fig. 37N)).
26. Incision between jugal and vannal lobe: (0) long, deep (Fig. 37N); (1) short.
27. Apex of jugal lobe: (0) narrowly rounded to slightly pointed; (1) broadly rounded.

Legs

28. Arolia: (0) distinctly developed (Figs 35C, 36C, D); (1) strongly reduced, minute; (2) absent (Fig. 36E).
29. Foretrochanter of female with row of hooked bristles: (0) absent; (1) present (Fig. 35A).
30. Basitibial plate (female): (0) about as long as broad; (1) elongate, distinctly longer than broad.
31. Apical margin of basitibial plate (female): (0) rounded; (1) pointed.
32. Tibial scopa: (0) consisting exclusively of simple hairs; (1) lower area near ventral margin consisting mainly of branched hairs; (2) consisting exclusively of branched hairs.
33. Hind femur (male): (0) slender to symmetrically swollen; (1) dorsal side strongly protuberant or swollen, ventral side flattened.

Metasoma

34. Shape of S 6 (male): (0) variable, never triangular at apex; (1) distinctly triangular at apex.
35. Apical region of S 6 (male): (0) without dense brush of short hairs; (1) with dense brush of short hairs.
36. Apical part of S 7 (male): (0) absent, S 7 not divided in apical and basal parts (Fig. 38E); (1) apical part distinctly narrower than basal apodemal region, Figs 38A, C, F-L (less than 0.6x as wide as apodemal region); (2) apical part nearly as wide as basal apodemal region, Fig. 38B, D (at least 0.7x as wide as apodemal region).
37. Median disc-region of S 7 (male): (0) absent, apical and basal apodemal region joining each other without an interspace (Figs 38A, D, E); (1) elongate, broadly separating apical and apodemal parts (Figs 38C, F-L).
38. Transverse collar-like ridge of S 7 (male): (0) absent (Figs 38A-E, J, K); (1) present, distinctly separating basal and apical parts of S 7 (Figs 38F-I, L).
39. S 8 (male): (0) as long as broad to broader than long (Figs 39A, C, D, F-L); (1) distinctly longer than broad, Figs 39B, E (at least 1.2x longer than broad).

Male genitalia

40. Apical part of ventral side of gonocoxite: (0) bare (Figs 40D-F, 41A-F); (1) with distinct brush of hairs (Figs 40A-C).
41. Gonostylus: (0) distinctly divided in dorsal and ventral gonostylus (Figs 40D-F, 41A-F); (1) simple, not divided in dorsal and ventral gonostylus (Figs 40A, C); (2) fused to gonocoxite or absent (Fig. 40B).
42. Apex of gonostylus: (0) distinctly protruding beyond apex of penis valvae (Figs 40E, F, 41A-F); (1) not or only slightly protruding beyond apex of penis valvae.
43. Width of lateral sclerite of penis valvae: (0) thin (Figs 40F, 41A-F); (1) more or less broadened (Figs 40A-E).
44. Orientation of lateral sclerites of penis valve (dorsal aspect): (0) parallel sided or nearly so (Figs 40A-D, F, 41A-F); (1) claw-shaped, curved inwardly (Fig. 40E).
45. Lateral sclerites of penis valve: 0) joining each other along inner margin (Figs 40A-D); (1) joining each other only apically (Fig. 40E); (2) broadly separated, not joining each other (Figs 40F, 41A-F); (3) joining each other medially.
46. Apex of penis valve: (0) without distinct tooth or bristles (Figs 40A-C, E, F, 41A-F); (1) with distinct tooth-like bristles ventrally (Fig. 40D).
47. Gonocoxite: (0) nearly joining each other basally, with only narrow interspace between (Figs 40A, B, D, E); (1) clearly separated from each other basally with distinct an interspace, Figs 40C, F, 41A-F (at least half as broad as single gonocoxite).
48. Ventral lobe of gonocoxite: (0) absent (Figs 40D, E); (1) distinctly developed (Figs 40A-C, F, 41A-F).
49. Gonobase: (0) large, distinctly protruding beyond basal margin of gonocoxites (Figs 40C-F, 41A-F); (1) small, reduced to triangular area between basal parts of gonocoxites (Figs 40A, B).
50. Shape of DGS: (0) slender, strongly spatulate (Figs 40F, 41A-F); (1) oval (Fig. 40D); (2) truncate, weakly spatulate to slightly oval (Fig. 40E).
51. Shape of VGS: (0) slender, finger-shaped (Figs 40D, E); (1) truncate flattened, oval to ear-shaped (Figs 40F, 41A-F).

Cladograms and tree topology

The analysis of the data matrix (Tab. 6) with NONA using the heuristic search option as described in 2.8.3.1 resulted in two most parsimonious trees (MPTs) of 132 steps (CI: 0.54, RI: 0.81, RC: 0.44). Two characters (11 and 25) were phylogenetically uninformative as they constitute autapomorphies. The strict consensus tree, with bootstrap and jackknife values is presented in Fig. 26. Collapsed nodes are shown as polytomies. Characters are mapped onto one cladogram selected from the MPTs in Fig. 25 with unsupported nodes shown as polytomies.

Tab. 6. Data matrix for the cladistic analysis of Anthophorini.

	1										2										3										4										5	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
Centris decolorata	0	1	0	0	0	1	1	2	1	2	0	0	0	1	0	2	0	1	0	2	0	1	0	0	0	0	0	2	0	0	0	2	0	0	0	1	0	0	1	0	0
Amegilla (Amegilla) quadrifasciata	0	3	1	2	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	2	0	0	0	1	1	1	1	2	1	0	0	0	0	0	2	1	0	1	1	2	–
Amegilla (Glossamegilla) urens	0	3	1	2	1	1	0	0	1	0	0	0	0	1	1	1	0	0	0	2	0	0	0	1	1	1	1	2	1	0	0	0	0	0	2	1	0	1	1	2	–
Amegilla (Micramegilla) byssina	0	3	1	2	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	2	0	0	0	1	1	1	1	2	0	0	0	0	0	0	2	1	0	1	1	2	–
Amegilla (Zebramegilla) albigena	0	3	1	2	1	1	0	0	1	0	0	0	0	1	1	1	0	0	0	2	0	0	0	1	1	1	1	2	1	0	0	0	0	0	2	1	0	0	1	2	–
Amegilla (Zonamegilla) zonata	0	3	1	2	1	1	0	0	1	0	0	0	0	1	1	1	0	0	0	2	0	0	0	0	1	1	1	2	1	0	0	0	0	0	2	1	0	1	1	2	–
Anthophora (Anthophora) plumipes	0	2	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	–
Anthophora (Caranthophora) dufourii	0	3	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	–
Anthophora (Clisodon) furcata	0	2	1	0	0	0	1	0	1	0	0	0	0	0	2	1	0	0	1	1	0	1	0	0	1	1	1	0	0	1	1	0	0	0	0	2	1	0	0	0	–
Anthophora (Dasymegilla) quadrimaculata	0	3	1	0	0	0	1	0	0	0	0	0	0	0	2	1	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	1	1	1	–
Anthophora (Heliophila) bimaculata	0	3	1	0	0	0	1	0	1	0	0	0	0	0	2	1	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	–
Anthophora (Lophanthophora) dispar	0	3	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	–
Anthophora (Mystacanthophora) borealis	0	3	1	0	0	0	2	0	1	0	0	0	0	0	2	1	0	0	1	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	–
Anthophora (Petalosternon) crassipes	0	3	1	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	2	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	–
Anthophora (Pyganthophora) retusa	0	3	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	–
Deltoptila elefas	1	0	0	1	0	0	2	0	1	2	1	1	1	0	1	1	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
Deltoptila montezumia	1	0	0	1	0	0	2	0	1	?	?	1	1	?	?	1	1	1	0	1	1	0	0	0	1	0	0	0	?	0	0	0	0	0	1	1	0	0	0	1	0
Elaphropoda moelleri	1	0	0	0	0	1	2	1	1	?	0	0	?	?	?	0	1	1	0	1	1	2	0	0	1	0	0	0	?	?	?	0	1	1	0	2	0	0	1	0	0
Elaphropda percarinata	1	0	0	0	0	1	2	1	1	1	0	0	0	1	0	0	1	1	0	1	1	2	0	0	1	0	0	0	1	1	1	0	1	1	0	2	0	0	0	0	0
Elaphropoda sp.	1	0	0	0	0	1	?	1	1	1	0	0	0	1	0	0	1	1	0	1	1	2	0	0	1	0	0	0	?	1	1	0	1	1	0	2	0	0	0	0	0
Habrophorula nubilipennis	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	1	1	2	0	0	1	0	0	0	1	0	1	0	0	1	0	3	0	0	0	?	2
Habropoda (Fulvohabropoda) radoszkowskii	0	4	–	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	2	1	0	0	0	1	0	0	1	0	1	1	1	1	1	0	0	0
Habropoda (Habropoda) tarsata	0	4	–	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	1	1	1	1	1	0	0	0
Habropoda (Zonhabropoda) zonatula	0	4	–	0	0	0	1	0	1	0	0	0	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	1	1	1	1	0	0	0
Habropoda cineraria	0	4	–	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	1	1	1	1	1	0	0	0
Pachymelopsis (Pachymelopsis) conspicuus	0	1	0	0	0	0	2	0	1	0	0	0	0	0	2	0	1	0	0	1	1	0	1	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0
Pachymelus (Pachymelus) radovae	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	2	2	1	2	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0

Unknown character states are coded with "?", not applicable ones with "–".

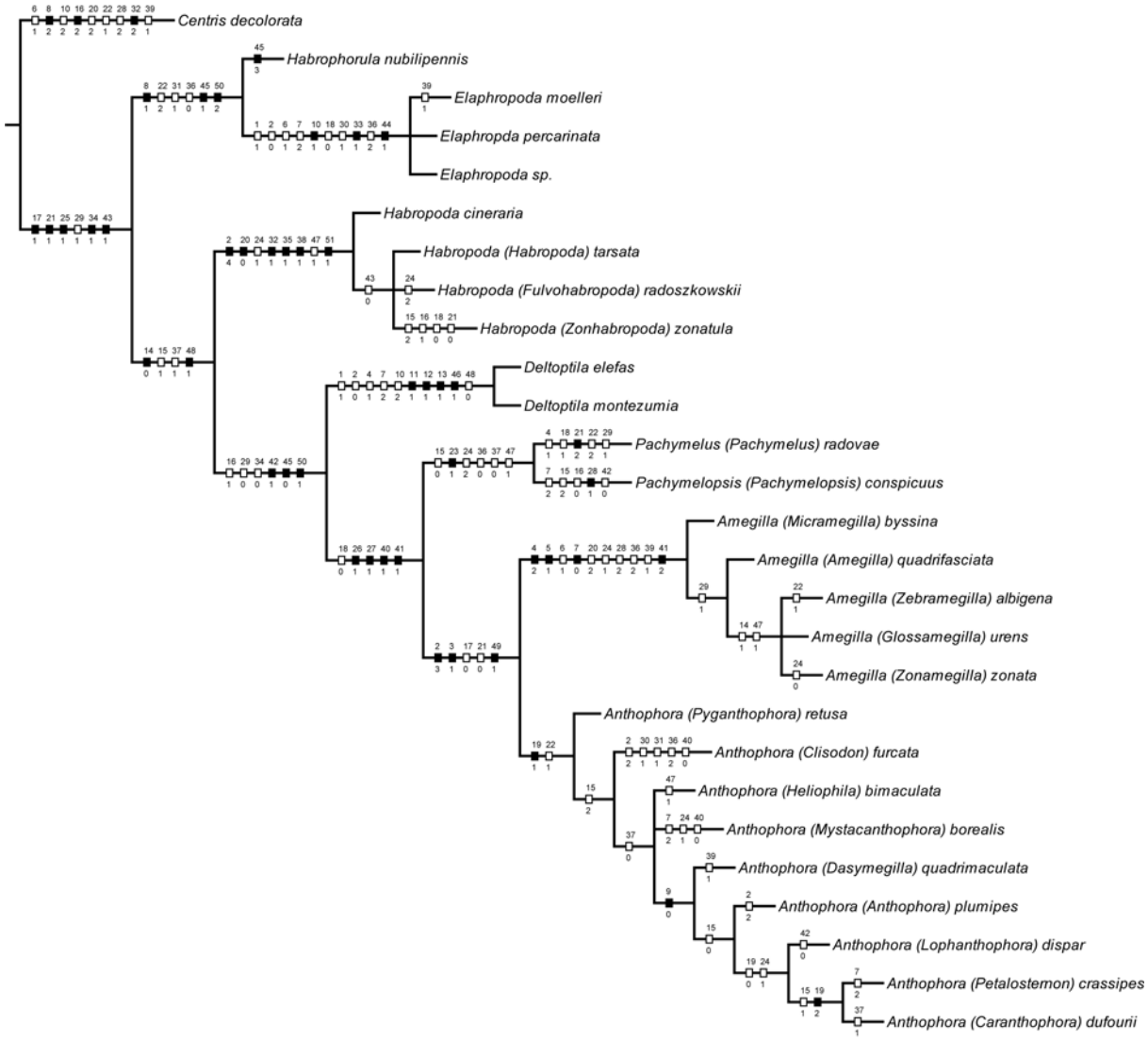

Fig. 25. Selected cladogram of the two MPTs of 132 steps (CI: 0.54, RI: 0.81, RC: 0.44) of analysis of Anthophorini, with characters mapped on branches. Unsupported nodes are shown as polytomies. Black squares indicate non-homoplasius changes, white squares indicate homoplasius changes.

In all analyses the following tree topology was obtained at the genus level (Fig. 26): ((*Habrophorula*, *Elaphropoda*) (*Habropoda* (*Deltoptila* (*Pachymelus* (*Amegilla*, *Anthophora*))))).

Two observations regarding the cladistic results are worth mentioning here. First, there is no support for a clear separation of the Anthophorini into two tribes (Habropodini and Anthophorini s. str.) as contended by Marikovskaya (1976) and Brooks (1988). Second, each genus of the Anthophorini appears to be well-supported. The polytomies of the strict consensus tree (Fig. 26) are found exclusively in the apical lineages of the genera, while the basal clades, which define the genera and genera-groups, never collapse in the analyses. This is attributed to the character sampling which was intended to resolve the genera but not necessarily the subgenera. The strict consensus tree reveals two major clades: a basal clade composed of *Habrophorula* + *Elaphropoda* (Fig. 26, node B) and a large second clade

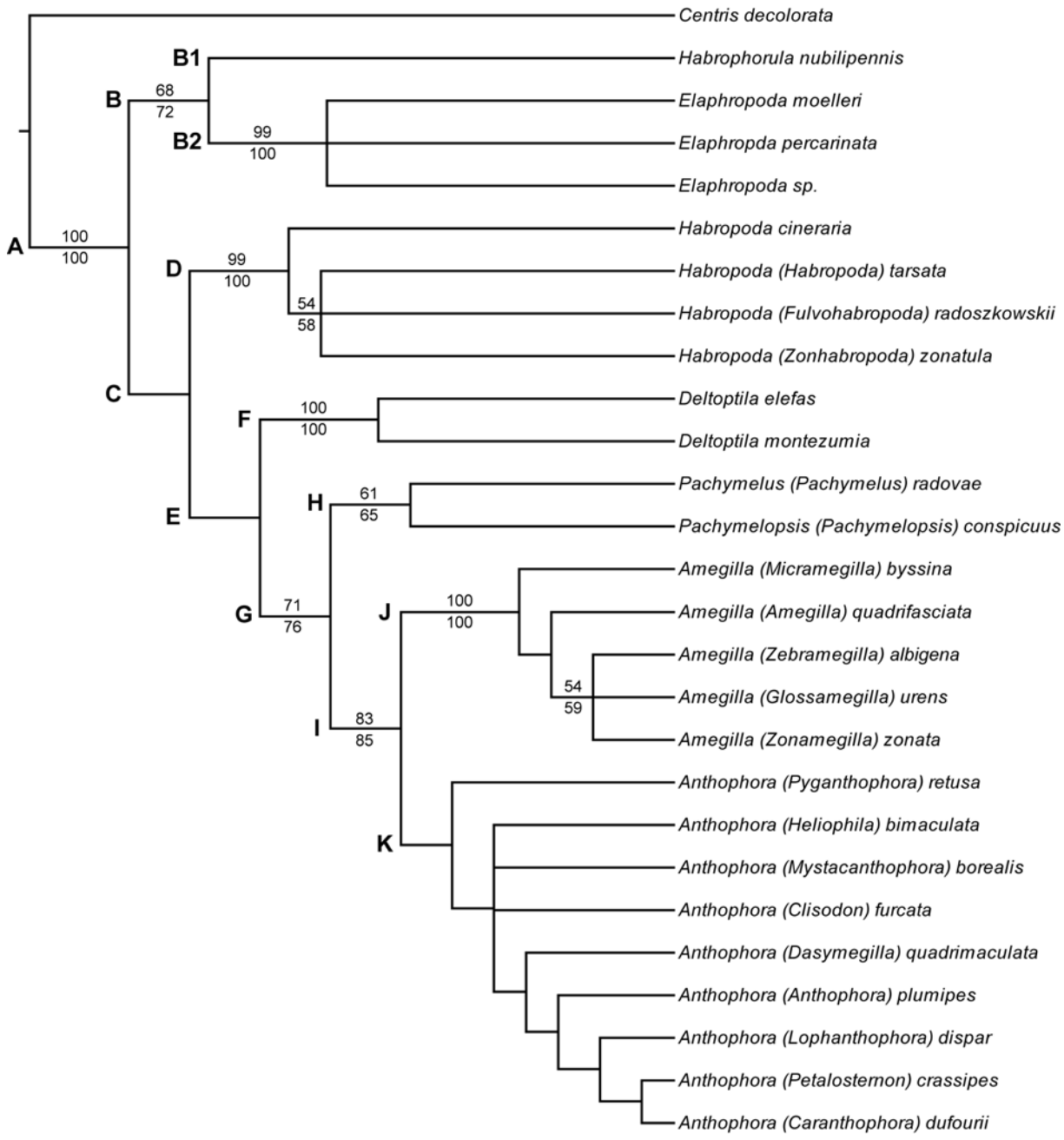

Fig. 26. Cladistic analysis of World Anthophorini. Strict consensus tree of two most parsimonious trees of 132 steps (CI: 0.54, RI: 0.81, RC: 0.44). Collapsed nodes are shown as polytomies, bootstrap values are indicated by numbers above, jacknife-values by numbers below branches. A-K referring to nodes mentioned in the text.

containing the remaining genera (*Habropoda* (*Deltoptila* (*Pachymelus* (*Amegilla*, *Anthophora*)))) (Fig. 26, node C). Based on branch length, as well as bootstrap and jackknife values, both of which are less than 50 %, *Anthophora* is the most weakly supported genus (Figs 25, 26).

Monophyly of Anthophorini – Paraphyly of Habropodini

The Habropodini-Anthophorini concept, established by Marikovskaya (1976), was based mainly on similar structures of the male genitalia and male S7 and S8 of *Habropoda*, *Elaphropoda* and *Deltoptila* which differ from those of other Anthophorini. Brooks (1988) regarded the Habropodini (including *Habrophorula* and, additionally, *Pachymelus*) as distinct from the Anthophorini as the Emphorini are from the Eucerini. His "Anthophorini" included only two genera, *Anthophora* and *Amegilla*, which share three synapomorphies, (1) 1st recurrent vein meeting the posterior margin of 2nd submarginal cell near its middle (17:0), (2) the second abscissa of vein M + Cu of the hind wing being subequal in length to the cu-v crossvein (24:1) and (3) an elongate, narrow gonostylus, which is never flattened and paddle-shaped.

The monophyly of the *Anthophora* + *Amegilla* was also confirmed in the present study. This clade (Fig. 26, node I) is supported by five synapomorphic characters, three of which are non-homoplasious. Nevertheless, there is no clade combining the remaining genera despite the basal *Elaphropoda* + *Habrophorula* clade (node B) which is distinct from all other Anthophorini by (1) presence of two preapical teeth along the upper margin of the female mandible (8:1), (2) the lateral sclerites of the penis valve joining each other only apically (45:1) and (3) the presence of a truncate, spatulate to slightly oval DGS (50:2). Therefore, the Habropodini *sensu* Marikovskaya (1976) and Brooks (1988) represents a paraphyletic group and should not be used as a taxon name. The present study thus follows Michener (2000) in recognizing only a single tribe, the Anthophorini.

The Anthophorini of the present study (Fig. 26, node A) clearly constitute a monophyletic group. It is supported by six apomorphies, five of which are non-homoplasious: (1) 1st recurrent vein of forewing (1 m-cu) joining 2nd submarginal cell terminating near apex (17:1), (2) marginal cell of forewing medium long (21:1), (3) jugal lobe of hind wing small, about half as long as vannal lobe or shorter (25:1), (4) male S 6 distinctly triangular apically (34:1) and (5) the lateral sclerite of penis valve more or less broadened (43:1). Characters (1), (2) and (4) show reversals in higher tree topology and therefore do not strictly characterize the Anthophorini as a whole. Character (5) is unambiguous except within Old World *Habropoda* and character (3) is completely unambiguous for all Anthophorini.

Because the present study focuses on the relationships of the genera within the Anthophorini and not on the phylogenetic position of the Anthophorini within the Apidae, the present character sampling does not reveal any new unambiguous synapomorphies which define the tribe Anthophorini. Autapomorphic characters of the Anthophorini, which emphasize its monophyly, are (6) a strongly concave, rather short stipital comb (cf. Brooks, 1988; Roig-Alsina and Michener, 1993), as well as (7) articulation of propodeum with T1 accompanied by two teeth at each side of articulation orifice instead of only one, as in all other long-tongued bees (Roig-Alsina and Michener, 1993). Since these characters are

uninformative for resolving the generic relationships within the Anthophorini, they were not included in the present analysis and are only mentioned here for the sake of completeness.

Evaluation of clades and monophyly of genera

The Anthophorini-clade (node A) is clearly supported by several unambiguous apomorphies (as stated above), and by maximum bootstrap and jackknife values (Fig. 26).

The *Elaphropoda* + *Habrophorula*-clade (Fig. 26, node B) constitutes the sister-group of the remaining genera in the present analysis and is supported by two non-homoplasius apomorphies: (1) the presence of two preapical teeth in the female mandible (8:1) and (2) a distinctly oval-shaped DGS (50:2). A strong synapomorphy for the clade is the presence of two preapical teeth along the upper margin of the female mandible. This feature has gone unnoticed in the past, and even Lieftinck (1974), who described the genus, made no mention of it. The tridentate mandible of *Elaphropoda* and *Habrophorula* is not homologous to the tridentate mandible in *Clisodon*, a subgenus of *Anthophora*, as the latter is composed of an apical and a preapical tooth on the upper and also the lower margins of the mandible. Bootstrap and jackknife values (68 % and 72 %) indicate strong support for the clade. Besides the clear support based on morphological data, the monophyly is also confirmed by biogeographical data, since both genera are exclusively Oriental.

The genus *Habrophorula* (Fig. 26, node B1) is characterized by the lateral sclerites of penis valve joining each other medially (45:1), which is autapomorphic for the genus.

The clade containing all members of the genus *Elaphropoda* (Fig. 26, node B2) shows high bootstrap and jackknife support (99%, 100%). They are united by the following non-homoplasius apomorphies: (1) clypeus of female extremely convex, protuberant (10:1), (2) hind femur of male dorsal side strongly protuberant dorsally, distinctly flattened ventrally (33:1) and (3) lateral sclerites of penis valve claw-shaped in dorsal aspect (44:1).

The clade of (*Habropoda* (*Deltoptila* (*Pachymelus* (*Amegilla*, *Anthophora*)))) is supported by a small number of apomorphies (Fig. 26, node C; 14:0, 15:1, 37:1, 48:1), only two of which, the dark paraocular area of females (14:0) and the lateral sclerites of penis valve joining each other only apically (48:1), represent non-homoplasious apomorphies. Nevertheless they must be regarded as ambiguous since they show reversals within the clade. Bootstrap and jackknife analyses revealed values of less than 50% at this node, which indicates a weak support.

The genus *Habropoda* (Fig. 26, node D), however, scored high bootstrap and jackknife values (99%, 100%) and is strongly supported by several autapomorphies: (1) the absence of a flabellum at the tip of glossa (2:4), (2) cu-V-vein meeting M+Cu-vein behind M-vein (20:0), (3) lower part of tibial scopa (area near ventral margin of hind tibia) consisting mainly of branched hairs (32:1), (4) apical region of male S 6 with dense brush of short hairs (35:1), (5) S 7 of male with distinct transverse collar-like ridge (38:1) and (6) a truncate and flattened, oval to ear-shaped VGS (51:1). The present cladistic analysis also confirmed the

synonymization of Nearctic *Emphoropsis* with Old World *Habropoda* established by Brooks (1988), since the Nearctic *Habropoda cineraria* (formerly *Emphoropsis cineraria*) was shown to be a true member of the *Habropoda* clade, even if it stands in opposition to the Old World representatives (Fig.26; node D).

Clade E is composed of (*Deltoptila* (*Pachymelus* (*Amegilla*, *Anthophora*))) and is characterized by six apomorphies, including three non-homoplasious synapomorphies related to male genitalia: (1) apex of gonostylus not or only slightly protruding beyond apex of penis valve (42:1), (2) lateral sclerites of penis valve joining each other nearly completely along inner margin (45:0), and (3) an oval to ear-shaped DGS (50:1). Since (1) shows reversals within *Pachymelopsis* and *Lophanthophora* and (3) is inapplicable for *Pachymelus*, *Amegilla* and *Anthophora*, only (2) seems to be a solid apomorphy for this clade. The weak support of node E becomes obvious in consideration that synapomorphy (2) represents an ancestral state and not a derived character state. The bootstrap and jackknife values (both less than 50%) also show little support of this clade.

The genus *Deltoptila* (Fig. 26, node F) is strongly supported by bootstrap and jackknife values (100%, 100%) and is characterized by the following autapomorphies: (1) presence of thorn-like bristles on the female clypeus (11:1), (2) front margin of clypeus extending distinctly beyond base of mandibles (12:1), (3) malar space of females distinctly developed, at least as long as width of antennal flagellum (13:1) and (4) apex of penis valve bearing distinct tooth-like bristles on ventral side (46:1). It is still unclear whether the thorn-like bristles on the female clypeus of *D. elefas* are typical for all female *Deltoptila* or only for this species, as this feature was not mentioned by LaBerge & Michener (1963). Probably, they are adaptations for collecting pollen, similar to the convergent bristles on the frons of *Rophites* species, which are used in connection with buzzing to remove pollen from flowers (Müller, 1996).

The clade comprising (*Pachymelus* (*Amegilla*, *Anthophora*)) is characterized by five apomorphies (node G; 18:0, 26:1, 27:1, 40:1, 41:1), four of which are non-homoplasious: (1) short incision between jugal and vannal lobe (26:1), (2) apex of jugal lobe broadly rounded (27:1), (3) apical part of ventral side of gonocoxite with distinct brush of hairs (40:1) and (4) simple gonostylus (41:1). Of these apomorphies two (26:1, 27:1) proved to be unambiguous, as they show no reversals or changes within the higher topology of the clade and therefore contribute significantly to the moderately strong support of this node (bootstrap value: 71%, jackknife value: 76%).

Pachymelus (Fig. 26, node H) is supported by only one non-homoplasious apomorphy: strongly reduced stigma of the forewing (23:1). On the one hand, the character state is unambiguous and thus represents a valuable autapomorphy, a fact which is confirmed by the monophyly of this genus and solid bootstrap and jackknife values (61%, 65%). On the other hand, this apomorphy represents the reduction of a character state (stigma of forewing) and therefore might be considered less valuable than an apomorphy which represents the development of a new character state. There can be no doubt that both subgenera of

Pachymelus (*Pachymelopsis* and *Pachymelus* s. str.), are closely related to each other and constitute a monophyletic group (node H). Furthermore, each subgenera occurs with its own autapomorphy (*Pachymelus* (21:2), *Pachymelopsis* (28:1), which support the monophyly of each.

The genera *Amegilla* and *Anthophora* comprise the most apical clade (Fig. 26, node I) at the generic level, which is supported by five apomorphies (2:3, 3:1, 17:0, 21:0 and 49:1). Three of these are non-homoplasious: (1) medium to large-sized flabellum, with distinct apical finger-shaped projections (2:3), (2) ventral surface of flabellum smooth, without a cobblestone pattern (3:1), and (3) a small gonobase reduced to a triangular area between the basal parts of gonocoxites (49:1). While (1) includes changes in *Clisodon* as well as in *Anthophora* s. str., (2) and (3) represent solid autapomorphies for this clade, which are supported by strong bootstrap and jackknife values (83%, 85%).

The genus *Amegilla* (Fig. 26, node J) is characterized by several autapomorphies: (1) PMX 2 with distinct comb-like hair fringe along anterior margin and medium long sparse hairs along posterior margin (4:2), (2) PMX 2 distinctly curved, with concave anterior margin and convex posterior margin (5:1), (3) PMX about as long, to slightly longer than half the length of PMX 2 (7:0) and (4) gonostylus fused to gonocoxite or absent (41:2). Bootstrap and jackknife values reveal maximum support for this clade (100% each).

The genus *Anthophora* is supported by only two apomorphies (Fig. 26, node K; 19:1, 22:1), one of which (front margin of 3rd submarginal cell about as long as hind margin, 19:1) is non-homoplasious. Since the character state is clearly ambiguous with reversals (*Lophanthophora*) and changes (*Petalosternon*, *Caranthophora*), there is only weak support for the genus *Anthophora*, which is also confirmed by bootstrap and jackknife values less than 50%. The monophyly of *Anthophora*, which was weakly confirmed in the present analysis, may be uncertain, especially in light of the strength of support which the remaining genera of Anthophorini receive. The bilobed basistipital process, referred to by Brooks (1988) as an autapomorphy for *Anthophora,* could not be recognized in the present study and no significant differences in the basistipital process in *Anthophora* and the other genera of Anthophorini were observed. It is noteworthy that a strong autapomorphy, which supports the monophyly of *Anthophora*, is still missing.

Evolution and biogeography of Anthophorini

Based on the results of the present analysis (Figs 25, 26), two main lineages of Anthophorini are distinguished. One, a relatively small clade (Fig. 26, node B) comprising the exclusively Oriental genera *Habrophorula* and *Elaphropoda* and, two, a distinctly larger clade (Fig. 26, node C) containing the remaining genera of Anthophorini with a limited geographical distribution (*Deltoptila*: Mesoamerica, *Pachymelus*: Southern Africa/Madagascar) and those with a relatively extensive distribution (*Habropoda, Amegilla* and *Anthophora*).

Data on the fossil record of the anthophorine bees is too insufficient to draw conclusions on evolution of the lineage, there being only two doubtful records from the Oligocene (Brooks, 1988). To obtain more information about probable evolutionary processes and vicariance events which may have taken place within the Anthophorini, the foregoing results of the cladistic analysis were associated with the biogeographical data for the tribe (Fig. 27).

The Oriental region exhibits the highest diversity of Anthophorini at the generic level, harbouring five of the seven genera (*Habrophorula*, *Elaphropoda*, *Habropoda*, *Amegilla* and *Anthophora*). Furthermore, the genera *Habrophorula* and *Elaphropoda,* both of which are restricted to this area, show the lowest species richness within the Anthophorini (*Habrophorula* with four species, *Elaphropoda* with eleven), a trait which is typical for basal taxa. High diversity at the generic level and relict-like occurrence of basal groups are indications that the origin and centre of radiation for the Anthophorini may have been in the northern part of South East Asia (India to South East China).

The oldest known fossil bee, *Cretotrigona prisca* (Meliponini, Apinae) (Michener and Grimaldi, 1988) shows us that the diversification of bees and the evolution of derived families and tribes probably took place in the late Cretaceous (Maastrichion) (Engel, 2000; Michener and Grimaldi, 1988). It is thus probable to assume that the basal lineages of Anthophorini (*Habrophorula*, *Elaphropoda* and at least *Habropoda*) also arose by the late Cretaceous, a period during which the continental connection of America and Eurasia still existed and climatic conditions were more or less tropical without polar caps (Sedlag, 1995). Whether *Habrophorula* and *Elaphropoda* showed a more extensive distribution at that time and became restricted to their place of origin in younger periods remains unclear.

Habropoda is mainly subtropical to tropical in distribution and clearly must have entered North America by the late Cretaceous while the continental connection between Western Europe and Eastern North America still existed. However, it is puzzling that many New World *Habropoda* display a greater resemblance to the basal lineages of Old World *Habropoda*, which today occur in Asia, than to the more modern groups of the Mediterranean region (cf. chapter 4.2.2). These facts are contrary to the supposed vicariance events at that time. An alternative scenario for the colonization of North America by *Habropoda* suggests that it could have taken place much later, during the late Miocene or early Pliocene, when diverse continental connections between America and Asia existed. This would also explain the close resemblance between American and East Asian *Habropoda,* although the climatic conditions at that time with the beginning of polar freezing were distinctly colder than in the upper Cretaceous and therefore would have made a successful introduction of *Habropoda* more difficult.

A second and independent migration to North America by the probable ancestors of *Deltoptila* is conceivable. This lineage may have become isolated on the string of islands between North and South America during the Tertiary (Futuyma, 1990) and subsequently led to *Deltoptila,* at least before the Pliocene when the land bridge was formed between North and South America creating today's Mesoamerica. Because of the low support for nodes C

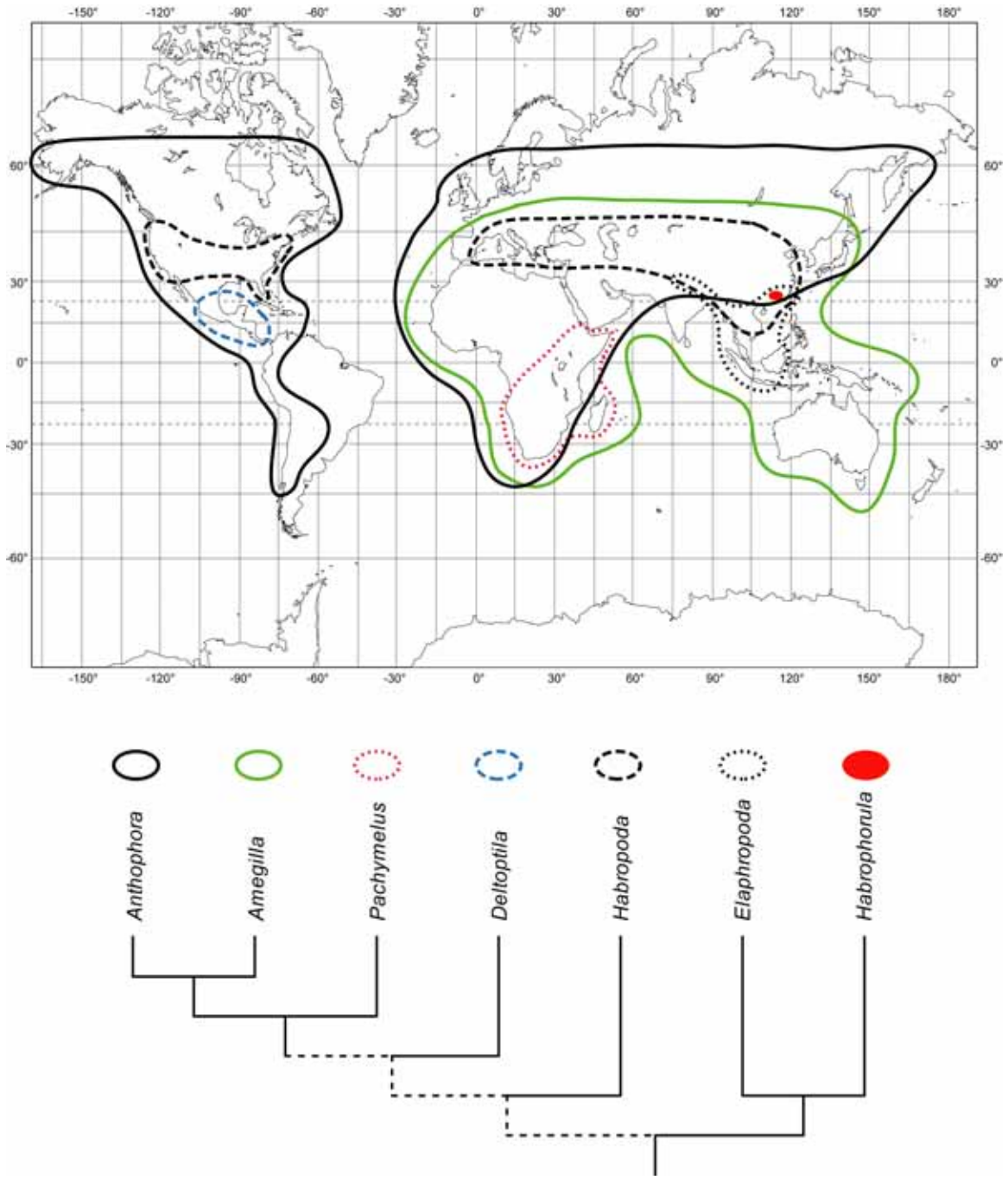

Fig. 27: Phylogeny of Anthophorini within their biogeographical context
Broken lines within the cladogram indicate clades of low support (cf. Evaluation of clades and monophyly of genera). Biogeographical data referred to the following sources: all genera: Michener (1979, 2000); *Amegilla:* Brooks (1988), Eardley (1994), Lieftinck (1944), Pauly et al (2001), Wu (2000); *Anthophora:* Brooks (1988), Eardley & Brooks (1989), Popov (1951), Wu (2000); *Deltoptila:* LaBerge & Michener (1963); *Elaphropoda:* Lieftinck (1944, 1966, 1972), Wu (1979, 1985, 2000); *Habrophorula:* Lieftinck (1974), Wu (2000); *Habropoda:* Krombein et al. (1979), Lieftinck (1966, 1969, 1972, 1974), Popov (1948), Schwarz & Gusenleitner (2001), Wu (1979, 1983, 2000); *Pachymelus:* Eardley (1993), Pauly et al (2001).

and E in the cladogram (Figs 26, 27), it cannot be excluded that *Deltoptila* may also be derived from Nearctic members of *Habropoda*, which reached the Tertiary string of islands, became isolated and led to *Deltoptila*.

The Old World ancestral lineage of *Deltoptila*, however, must have split into two groups, one forming the genus *Pachymelus* in southern Africa, the other evolving into the genera *Amegilla* and *Anthophora*. In light of the present cladistic analysis, the ancestral lineages of the Ethiopian *Pachymelus*, as well as the American *Deltoptila* may have arisen in late Cretaceous by vicariance events. Since *Pachymelus* has two distinct subgenera, one occurring in the southern part of Africa (*Pachymelopsis*) and the other in Madagascar (*Pachymelus* s. str.) and since the last connection between Madagascar and Southern Africa occurred in the Cretaceous, it is likely that the ancestral lineage of *Pachymelus* had already existed at that time and the subgenera developed after Madagascar separated from Africa.

Anthophora, with about 350 species, and *Amegilla*, with about 250 species, show the greatest diversity of species of all Anthophorini genera, and their range of distribution is the widest. These are indications that their radiation may have taken place more recently than that of the other genera. A derived position for both genera within the Anthophorini is also upheld by the cladograms of the present phylogenetic analysis. *Anthophora* has a nearly worldwide distribution, ranging from the northern Holarctic to Neotropical and Afrotropical regions (but absent from Paleotropics and Australia). *Amegilla* is most abundant in the Paleotropics (including Ethiopian and Australian regions) and Mediterranean region eastward to the steppes of Central Asia. Evidently, tropical regions present a barrier for the dispersal of *Anthophora*, while *Amegilla* appears to be restricted by its weak tolerance for lower temperatures (Brooks, 1988). It is thus probable to assume that the main vicariance events and the radiation of both genera took place, by the earliest, in the Miocene with the beginning of polar freezing. The lower temperatures after the Miocene would have prevented a colonization of America by *Amegilla*, yet the more tolerant, boreal forms of *Anthophora*, such as *Pyganthophora*, would have been able to reach North America, especially in Holocene, via land bridges, such as the Bering Strait, which was postulated by Brooks (1988) to be the most likely route taken to enter America.

Conclusions on the evolution of the Anthophorini in a biogeographical context are summarized as follows.

- Except for *Amegilla* and *Anthophora*, which might have originated during the Oligocene, the remaining genera of Anthophorini probably evolved by the late Cretaceous.
- The northern part of South East Asia (India to South East China) is regarded as the most probable place of origin and centre of radiation for the Anthophorini, since most genera including the most basal lineages of the tribe occur in this region.
- America was probably colonized on three separate occasions, by *Habropoda* in the upper Cretaceous to Tertiary, by the ancestral lineage to *Deltoptila* in upper Cretaceous to Tertiary, and by *Anthophora* in the Tertiary to Quaternary.
- The present distribution of *Deltoptila* and *Pachymelus* reflects an evolution connected with vicariance events, while the distribution of the other genera seems to be based on simple dispersal processes such as expansion (*Habropoda*, *Anthophora*, *Amegilla*) or isolation (*Elaphropoda, Habrophorula*) based on ecological or abiotic (climatic) factors.

4.2.2 Cladistic analysis of Old World *Habropoda*

Selection of taxa and characters

The cladistic analysis sampled 25 representatives of Palearctic and Oriental species of *Habropoda*, reflecting all major lineages of the genus. Based on the results of the analysis of which included all Anthophorini genera, *Elaphropoda* was selected as the outgroup.

The data set encompassed 41 characters with 96 character states; 31 of these characters were coded as binary, nine characters have three states and one character has seven states.

Characters and character states used in the cladistic analysis of *Habropoda*

Head and mouthparts

1. Length of retracted proboscis: (0) medium long, clearly reaching beyond hind margin of forecoxa; (1) extremely short, just reaching front margin of forecoxa; (2) long, reaching coxa of middle legs.
2. Flabellum: (0) present (Figs 34A-D, G, H); (1) absent (Figs 34E, F).
3. Structure of galea: (0) tesselate, dull; (1) smooth, shiny.
4. Cross section of PMX 3-6: (0) rounded to weakly flattened; (1) strongly flattened.
5. Length of PMX 3: (0) distinctly shorter than PMX 2 (Fig. 34I); (1) as long as PMX 2 to slightly longer.
6. Length of PMX 6: (0) distinctly shorter than PMX 5 (Fig. 34I); (1) as long to slightly longer than PMX 5.
7. Pubescence of PMX: (0) short and weak, sparse (Fig. 34I); (1) long and strong, somewhat dense.
8. Colour of mandibles (male): (0) completely dark; (1) yellowish to ivory basally.
9. Colour of clypeus (female): (0) completely dark; (1) dark with yellowish to ivory maculations.
10. Colour of clypeus (male): (0) completely or mainly yellow to ivory, Figs 44C, E, G (if black maculations present, then only along lateral margins, never isolated in the centre); (1) mainly yellowish with dark maculations in the centre; (2) mainly dark, with yellowish to ivory I-shaped maculation (Fig. 44A).
11. Colour of POA (male): (0) dark (Figs 44E, G); (1) yellowish to ivory (Figs 44A, C).
12. Colour of supraclypeal area (male): (0) completely dark (Fig. 44A); (1) with yellowish to ivory marking along front margin (Figs 44C, E, G).
13. Length of male AS 3: (0) about as long as AS 4 (Figs 44E-H); (1) distinctly longer than AS 4 (Figs 44A-D).
14. Colour of ventral side of scape (male): (0) completely dark (Figs 44E-H); (1) with yellowish to ivory maculation (Figs 44A-D).

15. Distal AS (male): (0) weakly flattened to rounded; (1) strongly dorsoventrally flattened.
16. Compound eyes (male): (0) normal, not enlarged, shortest distance between compound eyes at least 1.6 times as broad as single compound eye in frontal view; (1) distinctly enlarged, shortest distance between compound eyes only slightly broader than single compound eye in frontal view (ca. 1.2x).

Legs

17. Forecoxa (male): (0) rounded, without ventral thorn-like projection; (1) with long, ventral thorn-like projection (Fig. 35B).
18. Foretrochanter with row of hooked bristles (female): (0) absent; (1) present (Fig. 35A).
19. Forefemur (male): (0) normal, slender; (1) ventral side basally lobe-like
20. Foretarsi (female): (0) normal in structure and pubescence (Fig. 35F); (1) truncate, with bottlebrush-like, dense pubescence of apically hooked hairs (Figs 36A, B).
21. Forebasitarsi (male): (0) not broadened, unmodified; (1) broadened, with row of thorn-like bristles on ventral side (Fig. 35C-E).
22. Middle coxa (male): (0) unarmed, without thorn-like projection; (1) with thorn-like projection (similar to Fig. 35B).
23. Branched hairs on lower part of tibial scopa: (0) absent; (1) present.
24. Basitarsi of hind legs (male): (0) normal, slender; (1) with bulbous ventral projection apically; (2) extremely broadened.
25. Lower margin of basitarsus of hind legs (male): (0) similar in structure to other parts of basitarsus, no smooth, bare area developed; (1) with smooth and hairless area.

Wings

26. Front margin of 2nd submarginal cell: (0) distinctly longer than half the length of hind margin (about 0.6–0.7x as long as hind margin); (1) nearly as long as hind margin (at least 0.8x as long as hind margin); (2) half as long as hind margin or shorter.

Metasoma

27. Pubescence of T: (0) bombiform, long and dense; (1) with distinct hair bands of short dense hairs apically and dispersed medium long hairs basally; (2) long, rather dense, with inconspicuous apical hair bands that are interrupted in the middle; (3) inconspicuous, short and sparse.
28. Pygidial plate (male): (0) absent; (1) weakly indicated; (2) distinctly developed.
29. Pygidial plate (female): (0) slender, weakly triangular, apically broadly rounded; (1) broad, distinctly triangular, apically narrowly rounded to slightly pointed.
30. Median hair tuft of S 3-4 (male): (0) absent; (1) present.
31. Apical region of S 6 (male): (0) without dense brush of short hairs; (1) with dense brush of short hairs.
32. Apical part of male S 7: (0) differently shaped than listed below; (1) medium-sized, triangular, with two distinct lateral tooth-like projections and a broad hair fringe apically

(Fig. 38G); (2) medium-sized, triangular, with a more or less tridentate apical projection bearing small apical hair fringe in the middle (Fig. 38H); (3) medium to large-sized, triangularly rounded, apically with distinct median projection, similar to (Fig. 38I); (4) distinctly smaller than basal part, simple, with distinct lateral hair fringes (Fig. 38F); (5) large, broadly concave along apical margin, with distinct medium long hairs on ventral side (Fig. 38L); (6) large, broadly convex along apical margin, with short inconspicuous hairs on ventral side similar to Figs 38J, K.

33. Transverse collar-like ridge of S 7 (male): (0) absent; (1) distinctly developed (Fig. 38F-I, L); (2) strongly reduced (Figs 38J, K).
34. S 8 (male): (0) bilobed to rounded apically, without distinct projections (Fig. 39H-L); (1) with two median and two lateral lobe-like projections along apical margin (Fig. 39G); (2) with three distinct tooth-like projections apically (Fig. 39F).

Male genitalia

35. Gonostyli: (0) DGS distinctly longer than VGS (> 1.3x) (Figs 40F, 41A, D-F); (1) DGS short, as long as to slightly longer than VGS (≤1.3x) (Figs 41B, C).
36. Shape of DGS: (0) apically distinctly broadened (Figs 41A, C-F); (1) apically weakly broadened (Fig. 40F); (2) slender, apically not broadened (Fig. 41B).
37. Pubescence of DGS: (0) distinctly shorter than half the length of DGS (Figs 40F, 41B, D, F); (1) about half as long as DGS (Figs 41A, C).
38. Apical hair fringe of DGS: (0) sparse (Figs 41B, C, F); (1) dense (Figs 40F, 41A, D, E).
39. Shape of VGS: (0) slender; (1) more or less oval to ear-shaped (Figs 40F, 41A-F)).
40. Pubescence of VGS: (0) distinct, long (Figs 40F, 41A, E); (1) indistinct, dispersed minute setae (Figs 41C, D, F).
41. Penis valve: (0) slender (Figs 41B, E, F); (1) apically broadened (Figs 40F, 41A, C, D).

Cladograms and tree topology

Analysis of the data matrix shown in Tab. 7 using the heuristic search option in NONA as described in 2.8.3.1 produced three MPTs of 96 steps (CI: 0.58, RI: 0.82, RC: 0.48). Characters 2, 8, 23, 31 and 39 were phylogenetically uninformative. The strict consensus tree including bootstrap and jackknife values is given in Fig. 29. Collapsed nodes are shown as polytomies. Character distribution of the MPTs is displayed in Fig. 28 with unsupported nodes shown as polytomies.

Tab. 7. Data matrix for the cladistic analysis of *Habropoda.*

	1									1 0	2									2 0	3									3 0	4									4 0	1
Elaphropoda	2	0	1	1	0	0	0	1	1	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
Habropoda annae	2	1	0	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	0	0	0	0	1	2	1	0	0	1	0	1	1	4	1	2	0	1	0	1	1	0	1
Habropoda bucconis	0	1	0	0	0	1	0	1	1	2	1	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	2	1	1	0	1	2	1	0	1	0	1	0	1	1	1
Habropoda christineae	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	6	2	0	0	0	0	1	1	0
Habropoda deiopea	1	1	0	?	?	?	?	1	0	0	1	0	1	0	0	0	0	?	0	?	0	0	?	0	1	0	2	1	1	0	1	2	1	0	1	0	1	0	1	1	1
Habropoda hakkariensis	2	1	0	0	0	0	0	1	?	1	1	1	0	1	1	0	0	1	0	0	0	0	1	2	1	2	$	1	0	1	1	4	1	2	1	0	1	1	1	0	1
Habropoda imitatrix	0	1	0	0	0	1	0	1	1	2	1	0	1	1	0	0	0	1	0	?	0	0	1	0	1	1	2	1	1	0	1	2	1	0	1	0	1	0	1	1	1
Habropoda krishna	1	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	1	1	2	1	1	0	1	2	1	0	1	0	1	0	1	1	1
Habropoda mimetica	1	1	1	0	0	0	1	0	0	0	0	1	1	0	0	1	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	3	1	0	1	2	0	0	1	0	0
Habropoda omeiensis	?	1	?	?	?	?	?	?	0	0	0	1	?	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	0	1	3	1	0	1	2	0	0	1	0	0
Habropoda oraniensis	2	1	0	0	0	1	0	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	2	1	2	0	0	1	1	1	0	0	1	1	1	0	1
Habropoda pekinensis	2	1	0	0	0	0	0	?	0	1	1	1	1	?	0	1	1	?	0	1	1	1	1	?	0	1	2	0	0	1	1	1	1	0	0	1	1	1	0	1
Habropoda pelmata	0	1	0	?	?	?	?	1	?	2	1	1	?	1	?	0	0	?	0	?	0	0	?	0	1	1	2	0	?	0	1	2	1	0	1	0	1	0	1	1	1
Habropoda plantifera	1	1	0	0	0	1	0	1	?	2	1	0	1	1	0	0	0	?	0	?	0	0	1	1	1	0	2	0	?	0	1	2	1	0	1	0	1	0	1	1	1
Habropoda radoszkowskii	0	1	0	0	0	1	0	1	1	2	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	2	1	1	0	1	2	1	0	1	0	1	0	1	1	1
Habropoda rowlandi	2	1	1	0	0	1	0	1	?	0	1	1	1	0	0	0	0	?	0	?	0	0	1	0	1	0	2	0	0	0	1	2	1	0	1	1	1	0	1	1	1
Habropoda schafelneri	2	1	0	0	0	0	0	1	?	1	1	1	1	1	1	0	1	?	1	?	1	1	?	1	1	2	1	2	?	0	1	1	1	1	0	0	0	1	1	0	1
Habropoda sinensis sinensis	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1	0	1	6	2	0	0	0	0	0	1	1	0
Habropoda sinensis taiwana	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1	0	1	6	2	0	0	0	0	0	1	1	0
Habropoda sutepensis	2	1	0	?	?	?	?	1	1	0	1	0	1	1	0	0	0	?	0	?	0	0	?	0	0	1	2	0	?	0	1	2	1	0	1	?	1	0	1	1	?
Habropoda tadzhica	?	1	?	?	?	?	?	?	1	0	1	1	?	1	?	0	1	?	?	0	0	?	2	1	?	0	?	0	1	1	4	1	2	0	0	0	1	1	0	?
Habropoda tainanicola maaiella	2	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	5	1	0	0	0	0	1	1	1
Habropoda tainanicola tainanicola	2	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	5	1	0	0	0	0	1	1	1
Habropoda tarsata	2	1	0	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	0	0	0	0	1	2	1	0	0	1	0	1	1	4	1	2	0	1	0	1	1	0	1
Habropoda turneri	2	1	1	0	0	1	0	1	0	0	1	1	1	1	?	0	0	1	0	0	0	0	1	0	0	0	?	0	0	1	0	1	0	1	0	1	1	0	1	1	1
Habropoda zonatula	2	1	1	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	1	0	1	1	1	1	2	1	2	0	0	1	1	1	1	0	0	1	1	1	0	1

Unknown character states are coded with "?", not applicable ones with "–", and multistate ones with "$".

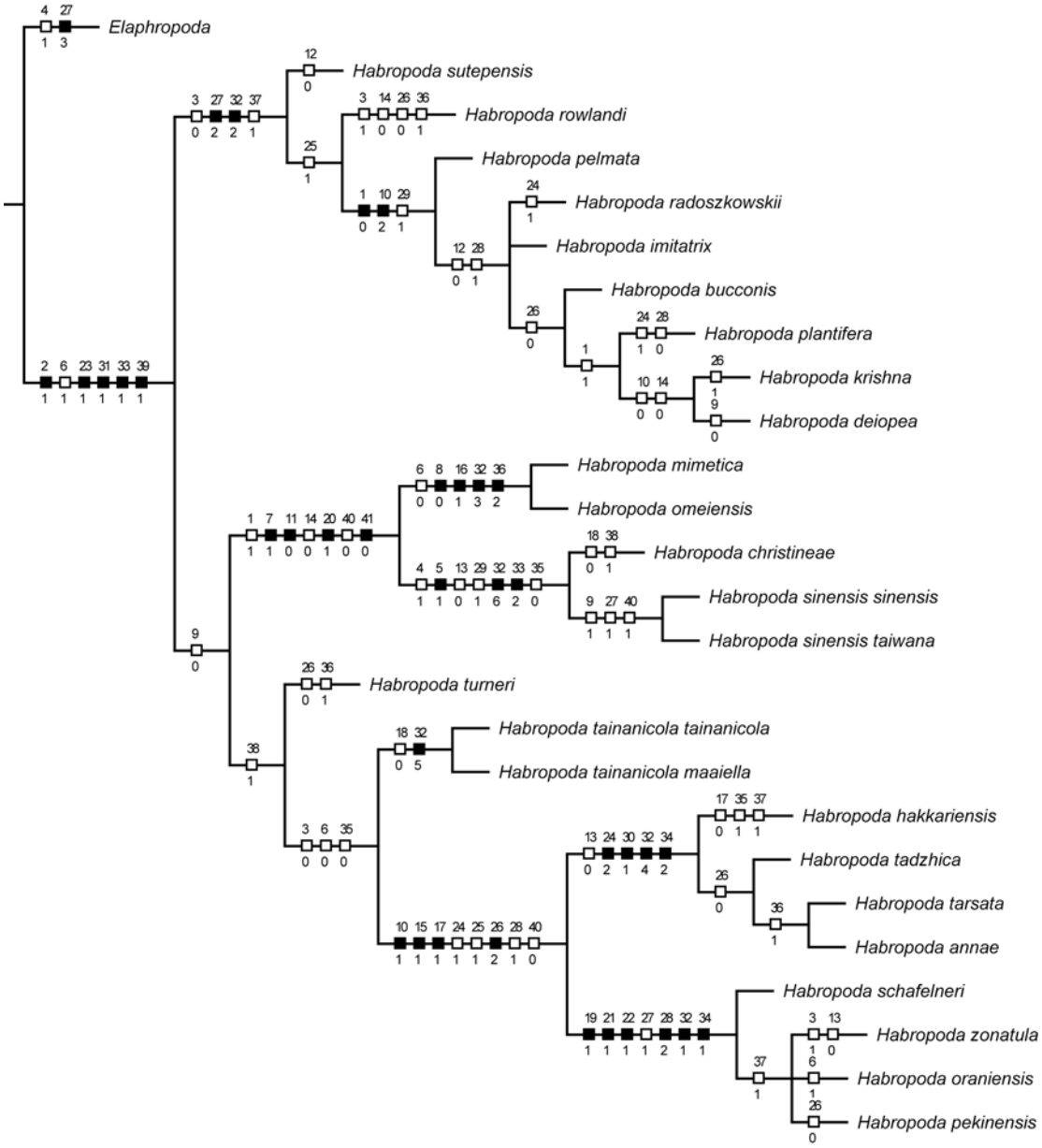

Fig. 28. Prefered cladogram of the three MPTs of 96 steps (CI: 0.58, RI: 0.82, RC: 0.48) of the analysis of Old World *Habropoda*, with characters mapped on branches. Unsupported nodes are shown as polytomies. Black squares indicate non-homoplasius changes, white squares indicate homoplasius changes.

The strict consensus tree (Fig. 29) revealed five major clades, each representing a subgenus, summarized as follows: (*Fulvohabropoda* ((*Oculhabropoda, Phyllohabropoda)* (*Zonhabropoda, Habropoda* s. str.))).

Fulvohabropoda constitutes a major clade (node B) and is the sister group to the remaining groups. *Oculhabropoda* (node E) and *Phyllohabropoda* (node F), as well as *Habropoda* s. str. (node J) and *Zonhabropoda* (node K), represent two very closely related subgenera each stemming from a common clade (nodes J and K, respectively). Two species, however, *H. turneri* and *H. tainanicola*, are located in isolated positions between the clades C

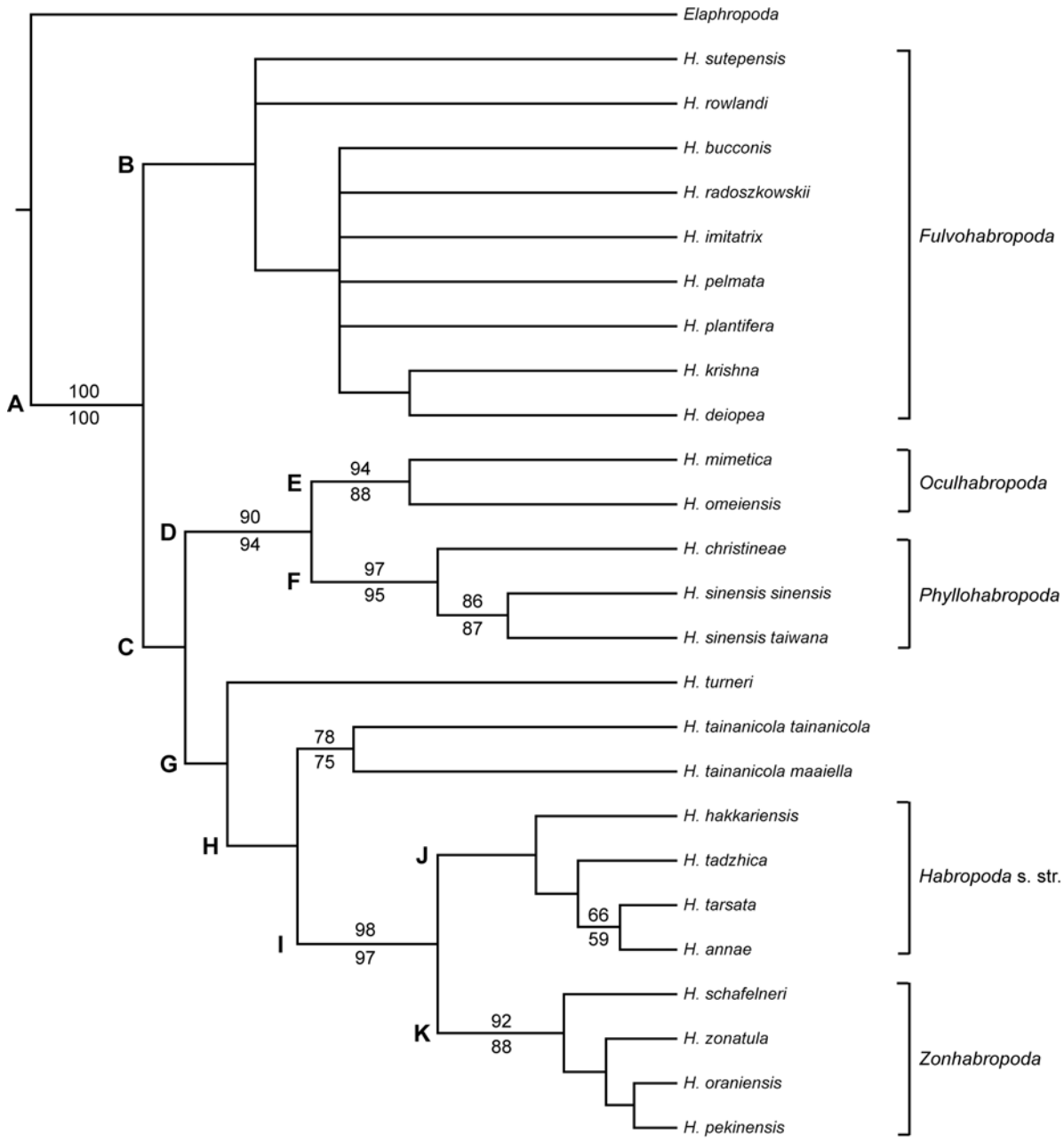

Fig. 29. Cladistic analysis of Old World *Habropoda*. Strict consensus tree of three most parsimonious trees of 96 steps (CI: 0.58, RI: 0.82, RC: 0.48). Collapsed nodes are shown as polytomies, bootstrap values are indicated by numbers above, jacknife-values by numbers below branches. **A-K** referring to nodes mentioned in the text.

and I. Their systematic position as indicated by the present analysis remains uncertain, as reflected by the weak support (bootstrap values < 50%) of the corresponding clades (nodes G, H).

Subgenera of Old World *Habropoda*

The results of the cladistic analysis revealed five distinct species groups of Old World *Habropoda*. In the following these groups are described and, for the first time, recognized as subgenera.

Subgenus *Habropoda* Smith s. str. (Fig. 29, node J)

Type species: *Habropoda tarsata* (Spinola).

Structure. Proboscis long in repose, reaching coxa of middle legs. Galea tesselate, dull. PMX 3-6 rounded to weakly flattened. PMX 3 distinctly shorter than PMX 2. PMX 6 distinctly shorter than PMX 5. Male AS 3 about as long as AS 4. Distal AS of male strongly dorsoventral flattened. Compound eyes of male not distinctly enlarged, shortest distance between compound eyes at least 1.6 times as broad as single compound eye in frontal view. Forecoxa of male with long, ventral thorn-like projection (similar Fig. 35B). Foretrochanter of female with row of hooked bristles (similar Fig. 35A). Forefemur of male normal, slender. Foretarsi of female slender. Forebasitarsi of male not broadened, unmodified. Middle coxa of male unarmed, without thorn-like projection. Hindbasitarsi of male extremely broadened. Lower margin of hindbasitarsus of male with smooth and hairless area. Front margin of 2nd submarginal cell distinctly longer than half the length of hind margin (about 0.6-0.7x as long as hind margin). Pygidial plate of male weakly indicated. Pygidial plate of female slender, weakly triangular, apically broadly rounded. S 7 of male with apical part distinctly smaller than basal part, with distinct lateral hair fringes (Fig. 38F). Transverse collar-like ridge of male S 7 distinctly developed (Fig. 38F). S 8 of male with three apical tooth-like projections (Fig. 39F). DGS (Fig. 40F) clearly longer than VGS (except *H. hakkariensis*: DGS short, as long to slightly longer than VGS), apically weakly broadened (except *H. hakkariensis*, *H. tadzhica*: apically strongly broadened). Pubescence of DGS distinctly shorter than half length of DGS (*H. hakkariensis*: about half as long as DGS), forming dense apical hair fringe (Fig. 40F). Pubescence of VGS distinct, long (Fig. 40F). Penis valve apically broadened (Fig. 40F).

Integumental colour. Mandibles of male yellowish to ivory basally. Clypeus of female completely dark. Clypeus of male mainly yellowish with dark maculations in the centre. POA of male yellowish to ivory. Supraclypeal area of male with yellowish to ivory marking along front margin. Ventral side of male scape with yellowish to ivory maculation.

Pubescence. PMX with sparse pubescence of rather short and weak hairs. Foretarsi of female with normal, unmodified hairs. Vestiture of T bombiform, with long dense hairs. Median hair tuft of male S 3-4 distinctly developed.

Diagnosis. *Habropoda* s. str. is characterized by the following (autapomorphic) characters by which it can be distinguished from other subgenera of *Habropoda*:

- basitarsi of male hind legs extremely broadened
- presence of median hair tufts of male S 3–4

- characteristic shape of S 7 of male, as in Fig. 38F, with distinct lateral hair fringes
- S8 of male with three apical tooth-like projections, as in Fig. 39F

Comments. All members of *Habropoda* s. str. show a distinct Mediterranean to Central Asian distribution ranging from France through Italy, Greece, Turkey, Syria and Israel eastward to Tadzhikistan (Lieftinck, 1966; Schwarz & Gusenleitner, 2001). Species of this subgenus are active in spring and summer with adults flying from March to July. Members of *Habropoda* s. str. superficially resemble species of *Bombus*, probably due to Müllerian mimicry.

Habropoda s. str. is most closely related to *Zonhabropoda*, from which it can be easily distinguished by the characters given above and in the diagnosis of *Zonhabropoda*. Both subgenera show similar Mediterranean to Central Asian distributions.

Included species. *Habropoda annae* Schwarz & Gusenleitner, 2001, *H. hakkariensis* Schwarz & Gusenleitner, 2001, *H. tadzhica* Popov, 1948 and *H. tarsata* (Spinola, 1838). *H. moesta* Popov, 1952 might also be included in this subgenus based on the similarity of this species to the members of *Habropoda* s. str. as indicated by Lieftinck (1966).

Fulvohabropoda subgen. n. (Fig. 29, node B)

Type species: *Habropoda bucconis* (Friese, 1911).

Structure. Proboscis short (in repose reaching front margin of forecoxa) to long (reaching coxa of middle legs). Galea tesselate, dull (except *H. rowlandi*: smooth and shiny). PMX 3–6 rounded to weakly flattened. PMX 3 distinctly shorter than PMX 2. PMX 6 as long as to slightly longer than PMX 5. Male AS 3 distinctly longer than AS 4. Distal AS of male weakly flattened to rounded. Compound eyes of male not distinctly enlarged, shortest distance between compound eyes at least 1.6 times as broad as single compound eye in frontal view. Forecoxa of male ventrally rounded, without thorn-like projection. Foretrochanter of female with row of hooked bristles (similar Fig. 35A). Forefemur of male normal, slender. Foretarsi of female slender. Forebasitarsi of male not broadened, unmodified. Middle coxa of male unarmed, without thorn-like projection. Hindbasitarsi of male slender, sometimes with ventral bulbous projection. Lower margin of hindbasitarsus of male with smooth and hairless area (except *H. sutepensis*: similar to other parts of basitarsus, no smooth and hairless area developed). Front margin of 2nd submarginal cell distinctly longer than half the length of hind margin (about 0.6-0.7x as long as hind margin) to nearly as long as hind margin (at least 0.8x as long as hind margin). Pygidial plate of male absent to weakly indicated. Pygidial plate of female broad, distinctly triangular, apically narrowly rounded to slightly pointed (except *H. rowlandi*: slender, weakly triangular, apically broadly rounded). S 7 of male with apical part of medium-sized, triangular, with a more or less tridentate apical projection bearing a small apical hair fringe in the middle (Fig. 38H). Transverse collar-like ridge of male S 7 distinctly developed (Fig. 38H). S 8 of male bilobed to rounded apically, without distinct projections (Fig. 39L). DGS (Fig. 41C) short, as long as to slightly longer than VGS (≤1.3x), apically distinctly broadened (except *H. rowlandi*: weakly broadened). Pubescence of DGS

about half as long as DGS, forming a sparse apical hair fringe (Fig. 41C). Pubescence of VGS indistinct and composed of dispersed minute setae (Fig. 41C). Penis valve apically broadened (Fig. 41C).

Integumental colour. Mandibles of male yellowish to ivory basally. Clypeus of female dark with yellowish to ivory maculations (except *H. deiopea*: completely dark). Clypeus of male mainly yellowish with dark maculations in the centre (*H. rowlandi*, *H. sutepensis*, *H. deiopea* and *H. krishna*) to mainly dark, with yellowish to ivory I-shaped maculation (*H. pelmata*, *H. imitatrix*, *H. bucconis*, *H. radoszkowskii* and *H. plantifera,* Fig. 44A). POA of male yellowish to ivory. Supraclypeal area of male mainly completely dark, sometimes (*H. rowlandi*, *H. pelmata*) also with yellowish to ivory marking along front margin. Ventral side of male scape with yellowish to ivory maculation (Figs 44A, B), sometimes also completely dark (*H. rowlandi*, *H. krishna* and *H. deiopea*).

Pubescence. PMX with sparse pubescence of rather short and weak hairs. Foretarsi of female with normal, unmodified hairs. Vestiture of T yellowish to brownish grey with long, rather dense hairs and inconspicuous apical hair bands with short hairs, interrupted in the middle. Median hair tuft of male S 3-4 absent. Apical region of male S 6 without brush of short hairs.

Diagnosis. *Fulvohabropoda* s. str. is adequately characterized by the following (autapomorphic) characters, from which it clearly can be distinguished from other subgenera of *Habropoda*:

- the yellowish brown to yellowish grey pubescence of long dense hairs; on T between long pubescence with inconspicuous, medially interrupted apical hair bands
- the characteristic shape of S 7 of male, as in Fig. 38H, with a medium-sized, triangular apical part, being more or less tridentate apically, often with small apical hair fringe in the middle

Comments. The species of *Fulvohabropoda* show an exclusive Oriental distribution, ranging from North-West India and Nepal through the Himalayan region eastward to mainland China and southward to South-East China, Taiwan and Thailand. The adults of this subgenus are typical autumn and winter species, active from September to January.

Fulvohabropoda stands aside from the other groups of *Habropoda* (Figs 28, 29), and thus it is difficult to speculate on its closest ally. However, a close relationship to *Uncinhabropoda* is quite probable, as indicated in the cladogram and by the isolated position of *H. turneri* and *H. tainanicola*.

Etymology. Prefix *Fulvo-* from the Latin *fulvus*, which means yellowish brown, in combination with *Habropoda*, the name of the higher taxon. The name refers to the characteristic appearance of yellowish brown to yellowish grey pubescence of most species in this subgenus.

Included species. *H. apostasia* Lieftinck, 1974, *H. bucconis* (Friese, 1911), *H. bucconoides* Wu, 1991, *H. deiopeia* (Cameron, 1897), *H. imitatrix* Lieftinck, 1974, *H. krishna* Bingham, 1909, *H. medogensis* Wu, 1988, *H. plantifera* Lieftinck, 1974, *H. pelmata* Lieftinck, 1974,

H. radoszkowskii (Dalla Torre, 1896), *H. rowlandi* Meade-Waldo, 1914, *H. sutepensis* Cockerell, 1929, *H. ventiscopula* Wu, 1984 and *H. yunnanensis* Wu, 1983.

Oculhabropoda subgen. n. (Fig. 29, node E)

Type species: *Habropoda mimetica* Cockerell, 1927

Structure. Proboscis extremely short in repose, just reaching front margin of forecoxa. Galea smooth and shiny. PMX 3-6 more or less rounded. PMX 3 distinctly shorter than PMX 2. PMX 6 distinctly shorter than PMX 5. Male AS 3 about as long as AS 4. Distal AS of male rounded. Compound eyes of male distinctly enlarged (shortest distance between compound eyes about 1.2x broader than single compound eye in frontal view). Forecoxa of male ventrally rounded, without thorn-like projection. Foretrochanter of female with row of hooked bristles (similar Fig. 35A). Forefemur of male normal, slender. Foretarsi of female truncate. Forebasitarsi of male not broadened, unmodified. Middle coxa of male unarmed, without thorn-like projection. Hindbasitarsi of male slender. Lower margin of hindbasitarsus of male similar to other parts of basitarsus, without smooth and hairless area. Front margin of 2nd submarginal cell nearly as long as hind margin (at least 0.8x as long as hind margin). Pygidial plate of male absent. Pygidial plate of female slender, weakly triangular, apically broadly rounded. Apical part of male S 7 medium to large-sized, triangularly rounded with distinct apical median projection, as in Fig. 38I. Transverse collar-like ridge of male S 7 distinctly developed (Fig. 38I). S 8 of male bilobed to rounded apically, without distinct projections (Fig. 39I). DGS as long as to slightly longer than VGS (≤1.3x), slender, apically not broadened (Fig. 41B. Pubescence of DGS (Fig. 41B) distinctly shorter than half the length of DGS, forming a sparse apical hair fringe. Pubescence of VGS distinct, long. Penis valve slender, not distinctly broadened apically (Fig. 41B).

Integumental colour. Mandibles of male completely dark. Clypeus of female completely dark. Clypeus of male completely or mainly yellow to ivory. POA of male dark. Supraclypeal area of male with yellowish to ivory marking along front margin. Ventral side of male scape completely dark.

Pubescence. PMX with dense pubescence of long and strong hairs. Foretarsi of female with bottlebrush-like, dense pubescence of apically hooked hairs (similar Figs 36A, B). Vestiture of T bombiform, long and dense. Median hair tuft of male S 3–4 absent.

Diagnosis. *Oculhabropoda* is characterized by the following (autapomorphic) features, from which it can be distinguished from other subgenera of *Habropoda*:

- mandibles of males completely dark
- compound eyes of males distinctly enlarged (shortest distance between compound about 1.2x broader than single compound eye in frontal view)
- characteristic shape of S 7, as in Fig. 38I, with apical part medium to large-sized, triangularly rounded, bearing a distinct apical median projection
- DGS slender, apically not broadened (Fig. 41B)

Comments. All species of *Oculhabropoda* are exclusively Oriental in distribution, ranging from North Vietnam to mainland China. The bees of this subgenus fly from August to November.

Oculhabropoda is most closely related to *Phyllohabropoda,* from which it can be clearly distinguished by the characters given in the diagnosis for the subgenus, as well as in the diagnosis for *Phyllohabropoda.*

Etymology. Prefix *Ocul-* from the Latin *oculus*, which means eye, in combination with *Habropoda*, the name of the higher taxon. The name refers to the enlarged compound eyes of the males within this subgenus.

Included species. *Habropoda disconota* Lieftinck, 1974, *H. mimetica* Cockerell, 1927 and *H. omeiensis* Wu, 1979.

Phyllohabropoda subgen. n. (Fig. 29, node F)

Type species: *Habropoda sinensis* Alfken, 1937

Structure. Proboscis extremely short in repose, just reaching front margin of forecoxa. Galea smooth and shiny. PMX 3-6 strongly flattened. PMX 3 as long as PMX 2 to slightly longer. PMX 6 as long as to slightly longer than PMX 5. Male AS 3 distinctly longer than AS 4. Distal AS of male weakly rounded. Compound eyes of male not distinctly enlarged (shortest distance between compound eyes at least 1.6 times as broad as single compound eye in frontal view). Forecoxa of male ventrally rounded, without thorn-like projection. Foretrochanter of female with row of hooked bristles (Fig. 35A), except *H. christineae*, where bristles are absent. Forefemur of male normal, slender. Foretarsi of female truncate (Fig. 36A). Hindbasitarsi of male not broadened, unmodified. Middle coxa of male unarmed, without thorn-like projection. Hindbasitarsi of male slender. Lower margin of hindbasitarsus of male similar to other parts of basitarsus, without smooth and hairless area. Front margin of 2nd submarginal cell nearly as long as hind margin (at least 0.8x as long as hind margin). Pygidial plate of male absent. Pygidial plate of female broad, distinctly triangular, apically narrowly rounded to slightly pointed. Apical part of S 7 of male strongly convex (Figs 38J, K). Transverse collar-like ridge of male S 7 absent. S 8 of male bilobed to rounded apically, without distinct projections (Figs 39J, K). DGS longer than VGS (>1.3x), distinctly broadened apically. Pubescence of DGS (Figs 41E, F) distinctly shorter than half the length of DGS, forming sparse apical hair fringe (except *H. christineae*: forming dense apical hair fringe). Pubescence of VGS (Figs 41E, F) distinct, long (except *H. sinensis*: indistinct, composed of dispersed minute setae). Penis valve slender, not distinctly broadened apically (Figs 41E, F).

Integumental colour. Mandibles of male yellowish to ivory basally. Clypeus of female dark with yellowish to ivory maculations or completely dark (*H. christineae*). Clypeus of male completely or mainly yellow to ivory (Figs 44E, G). POA of male dark (Figs 44E, G).

Supraclypeal area of male with yellowish to ivory marking along front margin. Ventral side of male scape completely dark (Figs 44E-H).

Pubescence. PMX with dense pubescence of long and strong hairs. Foretarsi of female with bottlebrush-like, dense pubescence of apically hooked hairs (Figs 36A, B). Vestiture of T bombiform, long and dense, in *H. sinensis* with distinct hair bands of short dense hairs apically and dispersed medium long hairs basally. Median hair tuft of male S 3-4 absent.

Diagnosis. *Phyllohabropoda* is clearly distinguished from other subgenera of *Habropoda* by the following (autapomorphic) characters:

- PMX 3-6 strongly flattened, leaf-like
- PMX 3 as long as PMX 2 to slightly longer
- transverse collar-like ridge of male S 7 absent
- characteristic shape of S 7, as in Figs 38J, K, with funnel-shaped, convex apical part

Comments. Members of *Phyllohabropoda* show an exclusively Oriental distribution ranging from North-West Thailand to South Vietnam, China and Taiwan. Bees of this subgenus seem to be summer to autumn species, adults fly from June to the beginning of October.

Phyllohabropoda is very closely related to *Oculhabropoda* with which it is clearly sympatric. For characteristics common to both subgenera, see comments given in discussion of the cladograms below.

Etymology. Prefix *Phyllo-* from the Greek τὸ φύλλ·ον, which means leaf, in combination with *Habropoda*, the name of the higher taxon. The name refers to the leaf- or sheet-like flattened PMX of the species in this subgenus.

Included species. *Habropoda christineae* sp. n., *H. orbifrons* Lieftinck, 1974, *H. sinensis* Alfken, 1937 and *H. tumidifrons* Lieftinck, 1974.

Zonhabropoda subgen. n. (Fig. 29, node K)

Type species: *Habropoda zonatula* Smith, 1854.

Structure. Proboscis long in repose, reaching to coxa of middle legs. Galea tesselate, dull (except *H. zonatula*: smooth, shiny). PMX 3-6 rounded to weakly flattened. PMX 3 distinctly shorter than PMX 2. PMX 6 distinctly shorter than PMX 5 (except *H. zonatula*: as long as to slightly longer than PMX 5). Male AS 3 distinctly longer than AS 4 (except *H. zonatula*: about as long as AS 4). Distal AS of male strongly dorsoventrally flattened. Compound eyes of male not distinctly enlarged, shortest distance between compound eyes at least 1.6 times as broad as single compound eye in frontal view). Forecoxa of male with long, ventral thorn-like projection (Fig. 35B). Foretrochanter of female with row of hooked bristles (similar Fig. 35A). Ventral side of forefemur of male basally lobe-like. Foretarsi of female slender. Forebasitarsi of male broadened, with row of thorn-like bristles on ventral side (Figs 35C, D). Middle coxa of male with thorn-like projection. Hindbasitarsi of male with bulbous ventral projection apically. Lower margin of hindbasitarsus of male with smooth and hairless area. Front margin of 2nd submarginal cell nearly as long as hind margin (except *H. pekinensis*:

distinctly longer than half length of hind margin). Pygidial plate of male well-developed. Pygidial plate of female slender, weakly triangular, apically broadly rounded. Apical part of male S 7 medium-sized, triangular, with two strong, lateral tooth-like projections and broad hair fringe apically (Fig. 38G). Transverse collar-like ridge of male S 7 distinctly developed (Fig. 38G). S 8 with two median and two lateral lobe-like projections along apical margin (Fig. 39G). DGS distinctly longer than VGS (> 1.4x), apically strongly broadened (Fig. 41A). Pubescence of DGS about half as long as DGS (*H. schafelneri*: clearly shorter than half the length of DGS), forming dense apical hair fringe (Fig. 41A). Pubescence of VGS distinct, long (Fig. 41A). Penis valve apically broadened (Fig. 41A).

Integumental colour. Mandibles of male yellowish to ivory basally. Clypeus of female completely dark. Clypeus of male mainly yellowish with dark maculations in the centre. POA of male yellowish to ivory. Supraclypeal area of male with yellowish to ivory marking along front margin. Ventral side of male scape with yellowish to ivory maculation.

Pubescence. PMX with sparse pubescence of rather short and weak hairs. Foretarsi of female with normal, unmodified hairs. Vestiture with distinct hair bands of short dense hairs apically and dispersed short to medium long hairs basally. Median hair tuft of male S 3-4 absent.

Diagnosis. *Zonhabropoda* undoubtedly can be recognized by the following (autapomorphic) characters:

- basitarsus of male front legs broadened, with row of thorn-like bristles on ventral side (Figs 35C, D)
- coxa of male middle legs with thorn-like projection
- pygidial plate strongly developed in males
- characteristic shape of male S7 similar Fig. 38G, with medium-sized, triangular apical part, bearing two strong, tooth-like projections laterally and a broad hair fringe apically

Comments. *Zonhabropoda* shows a distribution similar to that of *Habropoda* s. str., however, it is extends much further to the south and east ranging from France and Northern Africa (Algeria, Tunisia) eastward through the Mediterranean region and Asia Minor to China (Beijing). Adult bees of this subgenus fly from April to July.

This subgenus is very closely related to *Habropoda* s. str. as indicated in the diagnosis of that subgenus and by the characters given in the following discussion of the cladistic analysis.

Etymology. Prefix *Zon-* from the Latin *zona*, which means zone, in combination with *Habropoda*, the name of the higher taxon. The name refers to the distinct hair bands on the apical zone of T of the species of this subgenus.

Included species. *Habropoda oraniensis* (Lepeletier, 1841), *H. pekinensis* Cockerell, 1911, *H. schafelneri* Schwarz & Gusenleitner, 2001 and *H. zonatula* Smith, 1854.

Habropoda of uncertain status

The following species of *Habropoda* could not be assigned with certainty to a subgenus for several reasons, either they appeared distinctly isolated from other subgenera in the

cladogram (it was abstained in this study from erecting monobasic subgenera), the males were unknown, descriptions were insufficient, or types and relevant material was not recoverable or has not yet been studied:

Habropoda eurycephala Wu, 1991, *H. hainanensis* Wu, 1991, *H. hookeri* Cockerell, 1920, *H. moesta* Popov, 1952, *H. rufipes* Wu, 1983, *H. sichuanensis* Wu, 1986, *H. tainanicola* Strand, 1913, *H. turneri* Cockerell, 1909 and *H. xizangensis* Wu, 1979.

Evaluation of clades and character states

The monophyly of the genus *Habropoda* (Figs 28, 29, node A), which was previously demonstrated in the cladistic analysis of the Anthophorini as a tribe in 4.2.1, is strongly supported by maximum bootstrap and jackknife values (100% each), as well as by six synapomorphies (2:1, 6:1, 23:1, 31:1, 33:1, 39:1). The following non-homoplasious characters were regarded as autapomorphic for *Habropoda* (cf. 4.2.1) and therefore constitute the generic concept of the genus: (1) absence of a flabellum on the glossa (2:1), (2) presence of branched hairs on lower part of tibial scopa (23:1), (3) apical region of male S 6 with dense brush of short hairs (31:1), (4) the presence of a collar-like ridge on male S 7, separating the basal part from the apical (33:1) and (5) a more or less oval to ear-shaped VGS (39:1).

The species constituting the subgenus *Fulvohabropoda* (Fig. 29, node B) share four synapomorphies (3:0, 27:2, 32:2 and 37:1) of which the following two are non-homoplasious: (1) pubescence of T long, rather dense, with inconspicuous apical hair bands (27:2) and (2) shape of male S 7 similar Fig. 38H, with a medium-sized, triangular apical part, bearing a more or less tridentate apical projection with a small apical hair fringe in the middle (32:2). Although the subgenus is well supported, at least, by the shape of male S 7 (32:2), which is an autapomorphic character for the subgenus, this support is not confirmed by bootstrap and jackknife values (both less than 50%). In the strict consensus tree (Fig. 29), two taxa (*H. sutepensis, H. rowlandi*) form a polytomy basal to all remaining species of *Fulvohabropoda*, which themselves constitute an unresolved but monophyletic group (node B1). The latter group is supported by three synapomorphies (1:0, 10:2, 29:1). Two of these characters are non-homoplasious and not well-supported by bootstrap and jackknife values (both less than 50%): (1) proboscis of medium length (1:0) and (2) male clypeus with yellowish to ivory coloured I-shaped maculation (10:2).

The sister clade to *Fulvohabropoda* (Fig. 29, node C) contains ((*Oculhabropoda*, *Phyllohabropoda*) (*H. turneri* (*H. tainanicola* (*Habropoda* s. str., *Zonhabropoda*)) and is weakly supported by a single homoplasious apomorphy, the completely darkly coloured clypeus in the female (9:0). The monophyly of the clade is therefore uncertain. The bootstrap and jackknife values also show no support for the group.

Clade D, which is the sister group to clade G (*H. turneri* (*H. tainanicola* (*Habropoda* s. str., *Zonhabropoda*))), combines the subgenera *Oculhabropoda* (Fig. 29, node E) and *Phyllohabropoda* (Fig. 29, node F). *Oculhabropoda* + *Phyllohabropoda* constitute a

monophyletic group which is strongly supported by the seven apomorphies at node D (1:1, 7:1, 11:0, 14:0, 20:1, 40:0, 41:0). Four of these are non-homoplasious characters: (1) PMX with long, strong and rather dense pubescence (7:1), (2) POA of male being darkly coloured (11:0), (3) foretarsi of female truncate, with bottlebrush-like, dense pubescence of apically hooked hairs (20:1, Fig. 36A, B) and (4) a slender penis valve (41:0). Especially (1), (3) and (4) are solid structural synapomorphies, which strongly support the sister-group relationship between *Oculhabropoda* and *Phyllohabropoda*, as indicated by high bootstrap (90%) and jackknife (94%) values.

Oculhabropoda (node E) is supported by several apomorphies (6:0, 8:0, 16:1, 32:2, 36:2), four of these are non-homoplasious characters: (1) male mandibles completely darkly coloured (8:0), (2) male compound eyes distinctly enlarged (16:1), (3) characteristic shape of male S 7, as in Fig. 38I, apical part medium to large-sized, triangularly rounded , bearing a distinct median projection apically (32:2) and (4) a slender, apically not broadened DGS (36:2). The monophyly of this subgenus is also confirmed by bootstrap (94%) and jackknife (88%) values.

Phyllohabropoda (Fig. 29, node F), the sister-group of *Oculhabropoda*, is characterized by seven apomorphies (4:1, 5:1, 13:0, 29:1, 32:6, 33:2, 35:0), several of which are autapomorphic for the subgenus: (1) PMX 3 as long as to slightly longer than PMX 2 (5:1), (2) the shape of male S 7 as in Figs 38J, K (32:6) and (3) transverse, collar-like ridge of male S 7 strongly reduced (33:2, Figs 38J, K). The strongly flattened leaf- or sheet-like PMX 3-6 (4:1) also occur in the outgroup (and therefore contains some amount of homoplasy), nonetheless in the present study it is regarded as a strong character uniting clade F, as it does not occur elsewhere in the genus *Habropoda*. The monophyly of *Phyllohabropoda* is also reflected in the high bootstrap (97%) and jackknife (95%) values.

Clade G combines (*H. turneri* (*H. tainanicola* (*Habropoda* s. str., *Zonhabropoda*))) and is supported by a single homoplasious apomorphy, the presence of a dense apical hair fringe on DGS (38:1). The weak support for this clade is confirmed by low bootstrap and jackknife values (both less than 50 %); the monophyly of this clade is therefore dubious.

Clade H (*H. tainanicola* (*Habropoda* s. str., *Zonhabropoda*)) is united by the following homoplasious apomorphies: (1) galea tesselate, dull (3:0), (2) PMX 6 distinctly shorter than PMX 5 (6:0) and (3) DGS distinctly longer than VGS (35:0). Due to the degree of homoplasy of these characters (ci: 0,25 (3); 0,25 (6); 0,33 (35)), no distinct support, based on bootstrap and jackknife values (both less than 50%), was obtained for this clade.

The sister group relationship between *Habropoda* s. str. and *Zonhabropoda* is strongly confirmed by a common clade (Fig. 29, node I), which is supported by eight apomorphies (10:1, 15:1, 17:1, 24:1, 25:1, 26:2, 28:1, 40:0), four of which are non-homoplasious: (1) male clypeus mainly yellowish, with dark maculations in the centre (10:1), (2) distal AS of male strongly dorsoventral flattened (15:1), (3) forecoxa of male with long, spine-like projection (17:1) and (4) front margin of 2nd submarginal cell half as long as hind margin or shorter

(26:2). High bootstrap (98%) and jackknife (97%) values additionally support for the monophyly of the common clade of *Habropoda* s. str. and *Zonhabropoda*.

The monophyly of *Habropoda* s. str. (Fig. 29, node J) is supported by five apomorphies (13:0, 24:2, 30:1, 32:4, 34:2), some of which are non-homoplasious: (1) forebasitarsi of male extremely broadened (24:1), (2) presence of a median hair tuft on male S 3-4 (30:1), (3) shape of male S 7 as in Fig. 38F, with small apical part, distinct lateral hair fringes (32:4) and (4) male S 8 with three tooth-like projections apically, as in Fig. 39F (34:2). Bootstrap and jackknife values, however, show little support of the clade (less than 50 %).

Zonhabropoda (Fig. 29, node K), the sister clade of *Habropoda* s. str., is characterized by seven apomorphic characters (19:1, 21:1, 22:1, 27:1, 28:2, 32:1, 34:1), six of which are non-homoplasious: (1) ventral side of forefemur of male protuberant basally (19:1), (2) forebasitarsi of male broadened, with row of thorn-like bristles on ventral side (21:1), (3) middle coxa of males with thorn-like projection ventrally (22:1), (4) pygidial plate strongly developed in males (28:2), (5) shape of male S 7, as in Fig. 38G, apical part medium-sized, triangular , bearing two tooth-like projections laterally and a broad hair fringe apically (32:1) and male S 8 with two median and two lateral lobe-like projections along apical margin, as in Fig. 39G (34:1). High bootstrap (92%) and jackknife (88%) values reflect high support for the monophyly of the clade.

Evolution of Old World *Habropoda* within the biogeographical context

The phylogenetic results of the cladistic analysis are correlated with the biogeographical data of *Habropoda* for the Old World in Fig. 30. Similar to the Anthophorini (4.2.1), East Asia is the most probable place of origin for the genus, as the greatest diversity of species and subgenera is found there. It is likely that *Habropoda* had already arisen in upper Cretaceous together with the other basal lineages of Anthophorini (cf. 4.2.1). Based on the results of the cladistic analysis, two major clades (Figs 29, 30) can be distinguished on the species-level. One, the strictly Oriental subgenus *Fulvohabropoda* (node B), which constitutes the largest subgenus within *Habropoda*, and second, a clade comprising all other subgenera as well as isolated species (node C). Although *Fulvohabropoda* exhibits the greatest species richness, it possibly represents the most ancestral lineage within *Habropoda* because it has almost no distinct morphological peculiarities as found in other subgenera, and is the most widespread group in the Oriental region. All basal groups within clade C show a strictly Oriental distribution, while the most apical lineage (node I), which combines *Habropoda* s. str. and *Zonhabropoda* is widespread only in the Palearctic region, being most diverse and abundant in the Mediterranean region and Asia Minor.

The collision of India with the Eurasian continent and the resulting upfolding of the Himalayan mountain range at the time of Eocene (Cox & Moore, 1987) is one of the most important events which effected the evolution of Old World *Habropoda*. As evident in Fig. 30, the Himalayans form an effective geological barrier separating the Palearctic groups

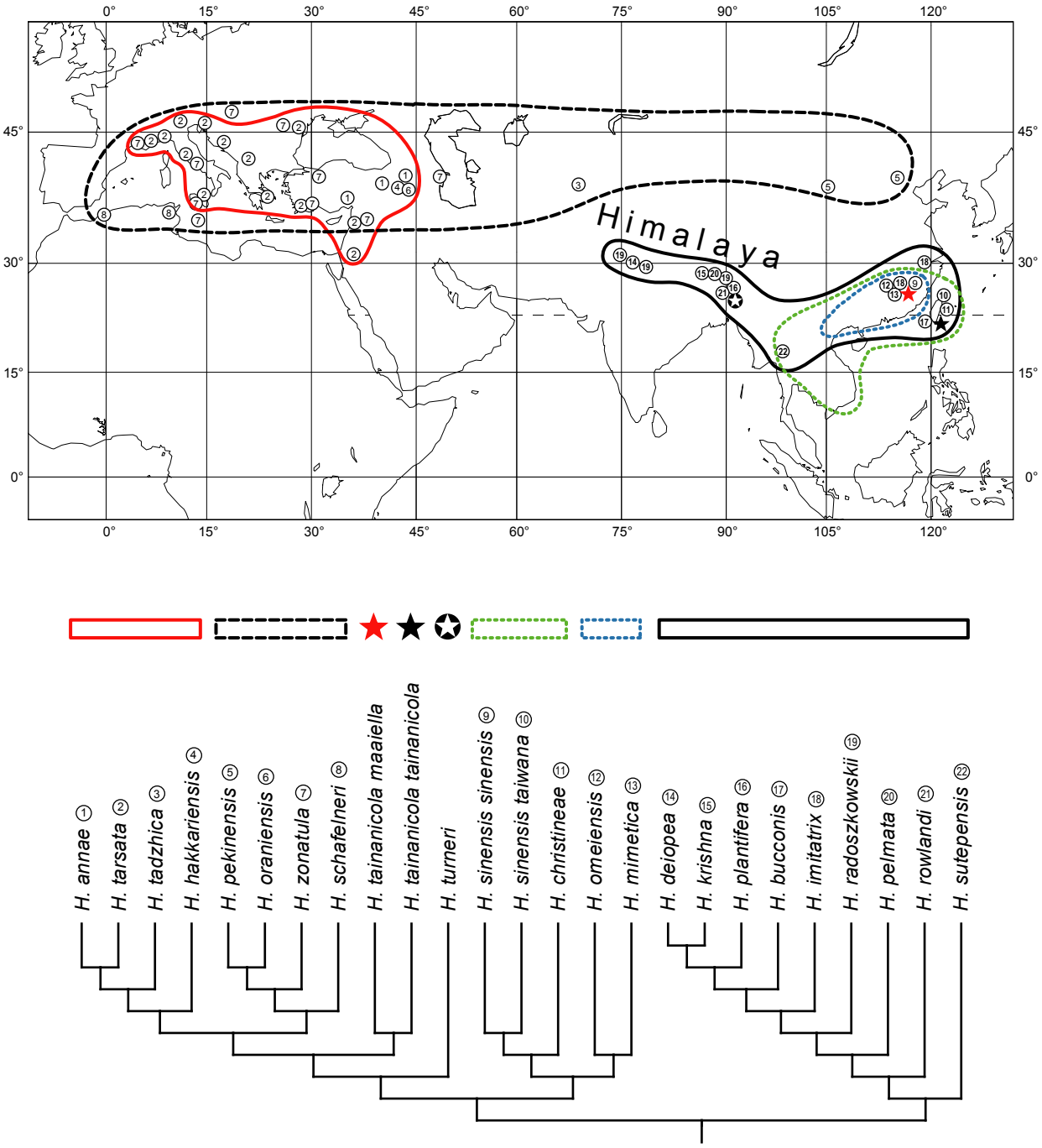

Fig. 30: Phylogeny of Old World *Habropoda* within its biogeographical context.
To make clear the evolutive scenario of the main lineages within Old World *Habropoda,* the distribution of subgenera, as additive ranges of all their included taxa each, was illustrated by corresponding outlines in the map. These subgeneric distribution also considers data of taxa which have not been included in the present analysis, but are clearly designated as members of a certain subgenus. Distribution of each species included in the cladistic analysis is indicated additionally by its corresponding number (1-22). Biogeographical data were obtained from the following sources: Lieftinck (1966, 1969, 1972, 1974), Michener (1979, 2000), Popov (1948), Schwarz & Gusenleitner (2001), Wu (1979, 1983, 2000).

(*Habropoda* s. str., *Zonhabropoda*) from the Oriental groups (*Fulvohabropoda, Phyllo–habropoda, Oculhabropoda* and isolated species) of *Habropoda.* An early radiation of the basal lineages of *Habropoda* may have taken place at the time of upper Cretaceous, however the main radiation at the species level, as well as, the separation of Palearctic and Oriental groups may be more recent, occurring together with the origin of the Himalayan region. Especially the radiation of the subgenus *Fulvohabropoda*, which is most diverse along the southern slope of the Himalayans, leads to the assumption that these diversification processes were caused by the presence of the Himalayan mountain ranges, as shown for other insects, e.g. Sericini beetles (Ahrens, 2004). Furthermore, it is probable that the initial formation of the Himalayans split the originally sympatric distribution of *Habropoda* and consequently produced an isolated Palearctic lineage (*Habropoda* s. str., *Zonhabropoda*), which seems to be the most derived group of *Habropoda*, based on the results of the cladistic analysis. However, the occurrence of *H. (Zonhabropoda) pekinensis* in East Asia as a representative of the Palearctic lineage may be secondary resulting from dispersal events eastward along the steppes of the "Central Asian-corridor" north of the Himalayas. The fact that the subgenus is not found in the more southern parts of East Asia might be attributed to its adaptation to arid or semi-arid climatic conditions which would have developed during its time of isolation in the West Palearctic region. These conditions contrast strongly with the high humidity of South East Asia. The development of the Palearctic lineage was thus probably caused by vicariance events of spatial segregation, while climatic adaptations seem to have prevented a recolonization of the genus during more recent dispersal events. The Oriental region may have served as a refugium for the main lineages of the early radiation of *Habropoda*, since it harbours three different subgenera (*Fulvohabropoda*, *Oculhabropoda*, *Phyllohabropoda*) and two isolated species (*H. tainanicola*, *H. turneri*).

Probably North America was colonised by ancestral *Habropoda*. In particular, the Oriental lineages (*Fulvohabropoda, Phyllohabropoda*) may have reached the New World by the late Miocene or early Pliocene *via* a land bridge between America and Asia. North American and East Asian *Habropoda* show strong similarities in the male genitalia and hidden sterna (cf. 4.2.1).

Regarding the evolution of Old World *Habropoda*, the following main events are postulated:

- The main lineages of *Habropoda* evolved in the upper Cretaceous in South East Asia.
- *Fulvohabropoda* represents one of the most basal lineages.
- Two major events occurred which were caused by the origin of the Himalayan mountain range in the Eocene:
  a) *Habropoda* was split into a Palearctic (with *Habropoda* s str., *Zonhabropoda*) and a Oriental lineage (with the remaining subgenera and isolated species), and
  b) the initial radiation of *Fulvohabropoda* began.

- The occurrence of *Zonhabropoda* in East Asia is secondary probably caused by recent dispersal events along the Asian steppes north of the Himalayans.
- Climatic adaptations prevented *Zonhabropoda* from recolonising the Oriental region.

4.2.3 Host-parasitoid coevolution: Revision of the species of *Habropoda* (Anthophorini) and *Tetralonioidella* (Melectini) of Taiwan

During the course of two expeditions to Taiwan in the years 2000 and 2002, the author had the opportunity to collect bees at various sites on the island and to study the bee material housed in local institutions and collections.

Taiwan, which is located on the tropic of cancer, is separated from mainland China by the Taiwan strait, which is about 140 km wide. Almost two thirds of its total area of 36000 km² are mountainous, reaching up to 3997 m above sea level (Mount Yushan), including the highest mountain peak in East Asia east of the Himalayans. The central mountain range, with 62 mountains over 3000 m above sea level, forms the dominant geological structure of the island of about 350 km length in north-south extension. The climatic conditions of high mountain regions (over 2000 m above sea level) are temperate, with snow in winter months, while in the lowlands of Taiwan the conditions are subtropical to tropical. Although the fauna of Taiwan is mostly assigned to the Oriental region, that of the higher mountainous parts resembles more greatly the Eastern Palearctic region.

The bee fauna of Taiwan was studied intensively in the first half of last century (Cockerell 1911a, b, c, 1912, 1927; Friese, 1911, 1914; Hedicke, 1925; Strand 1913, 1914a, b) and was based in large part on the extensive material collected by Hans Sauter between 1902 and 1914 (Chen, 2002). Subsequent study of the bees of Taiwan has been sporadic (Shiokawa, 1999, 2002; Yasumatsu & Hirashima, 1965). First results of the author`s expeditions to Taiwan (Dubitzky, 2002; Dubitzky & Kuhlmann, 2004) show how insufficiently the bee fauna of Taiwan had been investigated up to now. In particular, the higher mountain regions were poorly collected by Sauter, mainly because of the danger of local headhunting rituals still practiced at that time. Expeditions to the mountain regions therefore provided valuable material and furnished interesting results for example the first record of the genus *Colletes* on Taiwan (Dubitzky & Kuhlmann, 2004).

In the following a revision is presented of the Taiwanese species of *Habropoda* and its corresponding cleptoparasite *Tetralonioidella*. Both genera of bees were extensively observed and collected by the author in the field. Additional interesting material of both genera was examined from several insect-collections on Taiwan. The following study attempts to contribute to a better understanding of these bee genera on Taiwan by bringing together information on their ecology and coevolution.

Genus *Habropoda* F. Smith, 1854

Habrophora Smith, 1854: 318. Type species: *Habrophora ezonata* Smith, 1854 = *Tetralonia tarsata* Spinola, 1838, by designation of Patton, 1879.

Habropoda Smith, 1854: 320, replacement for *Habrophora* Smith, 1854. Type species: *Habrophora ezonata* Smith = *Tetralonia tarsata* Spinola, 1838, by designation of Patton, 1879.

Emphoropsis Ashmead, 1899: 60. Type species: *Anthophora floridana* Smith, 1854 = *Bombus laboriosus* Fabricius, 1804, by designation of Cockerell & Cockerell, 1901.

Meliturgopsis Ashmead, 1899: 62, no included species; Cockerell, 1909: 414 included a species while synonymizing *Meliturgopsis* under *Emphoropsis*. Type species: *Emphoropsis murihirta murina* Cockerell, 1909, first included species. (See also Michener, 1997)

Psithyrus (Laboriopsithyrus) Frison, 1927: 69. Type species: *Bombus laboriosus* Fabricius, 1804, by original designation.

For a description of this genus, see chapters 4.2.1 and 4.2.2. Old World *Habropoda* is most diverse in the Oriental region and with 17 species on mainland China. On Taiwan, *Habropoda* comprises four species, of which one species and one subspecies are new to science.

Determination key to the *Habropoda* species of Taiwan

Females (12 AS):

1. Pubescence of body mainly black, except hairs orange on apical terga of metasoma; clypeus without distinct yellow to ivory maculations 2

– Pubescence of body brown to yellowish grey; clypeus with distinct yellow to ivory maculations 3

2. Galea tesselate, dull; AS 3 distinctly (1.3 times) longer than AS 4 and 5 together, about 3 times as long as broad apically; pubescence of POA yellowish grey; ventral part of GA, occiput and mesepisterna with bright yellowish grey pubescence; foretarsi with unmodified, simple hairs (Fig. 35F); T black only basally, apical half (marginal zone) transparent, amber coloured ..... ***H. tainanicola tainanicola* Strand**

– Galea smooth, shiny; AS 3 about as long as AS 4 and 5 together, about 2 times as long as broad apically; pubescence of POA black; ventral part of GA, occiput and mesepisterna with dark brown pubescence; foretarsi with bottlebrush-like pubescence of modified, apically hooked hairs (Figs 36A, B); T completely black ..... ***H. christineae* sp. n.**

3. Clypeus with single triangular yellow spot along middle of apical margin; AS 3 long, nearly as long as following three AS together, about 3.5 times as long as broad apically; foretarsi with unmodified, simple hairs; pubescence of T long, intermixed with short hairs, distinct apical hair bands absent; punctation of T flat, inconspicuous ..... ***H. bucconis* Friese**

– Clypeus with yellow, inverted T-shaped marking along apical margin; AS 3 short, about as long as AS 4 and 5 together, about 2.5 times as long as broad apically; foretarsi with

bottlebrush-like pubescence of modified, apically hooked hairs; pubescence of T medium long (except T 1 with long hairs instead), with distinct, fox-red to dark ochreous coloured apical hair bands; punctation of T strong, dense ..... ***H. sinensis taiwana* ssp. n.**

Males (13 AS):

1. POA and ventral side of scape black coloured (Figs 44E-G) 2
– POA and ventral side of scape yellowish coloured (Figs 44A-D)..... 3
2. Pubescence of body blackish brown except orange coloured hairs of apical terga of metasoma; mandibles only basally with small ivory coloured spot; galea in repose medium long, reaching middle coxae; genitalia and hidden S as in Figs 38K, 39K, 41E.. ..... ***H. christineae* sp. n.**
– Pubescence of head and thorax mainly brownish grey (dorsally) to bright greyish white (ventrally), pubescence of T 2-4 with bright ochreous coloured hair bands apically and dispersed short black hairs basally, pubescence of apical T black; mandibles at least on basal half ivory coloured; galea extremely short in repose almost reaching forecoxae; genitalia and hidden S as in Figs 38J, 39J, 41F ..... ***H. sinensis taiwana* ssp. n.**
3. Clypeus except two small lateral blackish brown spots completely yellow (Fig.44C); galea long in repose, almost reaching hind coxae, AS 3 distinctly shorter than AS 4 and 5 together, about 1.8 times longer than broad apically (Figs 44C, D); marginal zone of T transparent amber coloured; genitalia and hidden S as in Figs 38L, 39H, 41D..... ..... ***H. tainanicola tainanicola* Strand**
– Clypeus with I-shaped ivory mark along median line and broad blackish brown maculations laterally (Fig. 44A); galea short in repose, reaching forecoxae; AS 3 about as long as AS 4 and 5 together, about 2.4 times longer than broad apically (Figs 44A, B); depressions of T black, densely covered with bright beige, short hairs forming broad hair bands between long pubescence of terga; genitalia and hidden S as in Figs 38H, 39L, 41C ..... ***H. bucconis* Friese**

***Habropoda (Fulvohabropoda) bucconis* (Friese, 1911)** (Figs 38H, 39L, 41C, 44A, B)

Anthophora bucconis Friese, 1911: 127. Type locality: Tainan (Formosa). Types ♂, ♀ SMF (examined)

Habropoda bucconis (Friese): Lieftinck, 1974: 201-202.

Female. BL: 14.7 mm. FWL: 10.2 mm.

Structure. Head triangular, about 1.4 times broader than long. Proboscis short to medium long in repose, extending to the forecoxae. Galea tesselate, weakly shiny (basally) to dull (apically), with large, flat punctation. Mandibles bidentate. Labrum shiny, about 1.4 times broader than long, with irregular strong wrinkles on disc between prominent lateral humps. Area before front margin with four tooth-like projections in the middle. Clypeus shiny, with very dense punctation (<<1), disc flattened in profile. SCA protuberant, with fine dense punctation and impunctate median line becoming distinctly broader from hind to front margin. All other parts of head strongly tesselate with inconspicuous tiny punctation. Scape slightly shorter than AS 3, with inconspicuous, dispersed punctation ventrally. AS 3 nearly as

long as following three AS together, about 3 times as long as broad apically. Scutum weakly shiny, with dense (≤1) punctation. Scutellum tesselate, dull with dense small punctation. Propodeum weakly tesselate, shiny with inconspicuous, dispersed punctation laterally. Mesepisterna weakly shiny, tesselate, with dense flat punctation. T weakly shiny tesselate, with dense inconspicuous punctation on disc and nearly impunctate marginal zone. Pygidial plate tesselate, dull. S tesselate, shiny to weakly dull with large dense (≤1) punctation.

Integumental colour. Body black to dark brown. Glossa and galea transparent brown. Mandibles yellow transparent basally, blackish brown apically. All parts of head black to blackish brown except triangular ivory maculation along the middle of front margin of clypeus. Antenna blackish brown except AS 4–12 reddish brown beneath. Thorax blackish brown. Legs brown to yellowish brown. Veins of wings blackish brown, tegulae bright yellowish brown, transparent. T blackish brown except marginal zone being transparently amber. Pygidial plate black. S reddish brown with broad blackish brown maculations in the middle of disc of S 2–4.

Pubescence. Ventral margin of mandibles with long white hairs. Labrum and clypeus with medium long, yellowish grey pubescence except long blackish brown hairs along lateral margins of clypeus. POA, SCA as well as main parts of frons with dense, short, whitish grey pubescence, intermixed with long blackish brown hairs. Area around ocelli and vertex with long yellowish grey to dark brown hairs. Genal area with long silvery white hairs. Dorsal and dorso-lateral parts of thorax with dense pubescence of long, yellowish grey hairs, intermixed with long dark brown hairs. Ventral and ventro-lateral parts of thorax with bright yellowish grey to silvery white long hairs. Ventral side of forefemur with long greyish white to brownish grey hairs. Foretibia with brownish grey hairs. Foretarsi with dense brush of simple, yellowish brown hairs on ventral side. Pubescence of other parts of middle legs greyish brown except dense brush of reddish brown hairs on ventral side of tarsi. Tibial scopa of hind legs with yellowish brown to brown long, mainly branched hairs. Basitarsus of hind legs with long, dark brown pubescence. T 1–4 with long, yellowish grey, apically often dark brown coloured, hairs. Marginal zone of T 1–4 with dense, short, yellowish white hairs, apically forming inconspicuous hair bands between long pubescence. Prepygidial fimbria yellowish grey to yellowish brown. Pygidial fimbria dark brown. S 2–4 with long yellowish to greyish white hairs apically and short, bright reddish brown hairs in the middle. S 5 with dense brush of reddish brown hairs on disc and long dark brown hairs apically.

Male. BL 11.1–13.2 mm (12.1 mm). FWL: 8.8–9.9 mm (9.3 mm).

General appearance of structures, integumental colour and pubescence similar to female except in following characters: AS 3 about as long as following two AS together (Figs 44A, B); colouration of head as in Fig. 44A; mandibles ivory coloured except brown region apically; clypeus with T-shaped, ivory maculation along median line (Fig. 44A); SCA and ventral side of scape ivory coloured; long pubescence of T 3-5 with distinctly fewer dark brown hairs than on T 1 and 2; apical hair bands of short, yellowish white hairs on T 1-5 extended on whole marginal zone (on T 4 and 5 nearly completely covering each T), therefore

much more broad and distinctive than in female; apical part of S 7 (Fig. 38H) broad, triangular, with distinct incision on top, the latter bearing a distinct hair fringe in the middle; ventral side of apical part of S 7 with strong short hairs along apical margin; apical margin of S 8 nearly oval, except flat incision in the middle (Fig. 39L).

Male genitalia (Fig. 41C). DGS short, about as long as VGS, slightly spatulate apically. Apical margin of DGS with long hairs. VGS ear-shaped, about 1.8 times longer than broad, with regularly spaced microtricha on ventral surface.

Diagnosis. *H. bucconis* is very similar to *H. imitatrix* Lieftinck, 1974, which occurs in SE China. The present observations are based on males of the latter species only, almost no significant differences were found between *H. bucconis* and *H. imitatrix* in structural characters. The differences are predominantly in colouration of integument and pubescence (clypeal spot of *H. imitatrix* more slender, I-shaped, pubescence of hind basitarsus blackish brown, darker than in *H. bucconis*). Both characters are variable within each species. Weak structural differences are only found in AS 3, which is slightly shorter than the scape in *H. imitatrix* and slightly longer than the scape in *H. bucconis*, also the apical incision in S 7 is more concave in *H. bucconis* than in *H. imitatrix* and the lateral parts of the triangular apical part is more acutely angled in *H. imitatrix*.

Distribution. Records of *H. bucconis* are based mainly on old collection data from the low hill countryside and areas near the coast line of Taiwan, e.g. Fengshan, Taitung, Puli, Tainan, Taipei, Tailin and Kaohsiung (Lieftinck, 1974). Recently this species was recorded from Kukung (Yunlin Hsien) and from the surroundings of the TESRI-Station Tengchi (Kaohsiung Hsien). For seasonal and altitudinal distribution of this species, see Fig. 31.

Biology. All male specimens collected by the author in Tengchi were found exclusively at flowers of *Teucrium viscidum* Bl. (Lamiaceae).

Comments. Based on the weak distinctive features listed above for *H. bucconis* and *H. imitatrix*, it is conceivable that *H. imitatrix* is a continental subspecies of *H. bucconis*. However, no females of *H. imitatrix* were available for examination in the present study, thus the two taxa must be regarded as separate species by the differences listed above for the males and those for the females given by Lieftinck (1974).

Material examined. Type material. 1 ♂, 1 ♀, Formosa, Tainan, collection A. Weis (SMF). Other material. 1 ♂, Taiwan, Yunlin, Ku-kung Shih-pi, 29.X.1992, W.T. Yang, Sweeping Net, NMNS ENT 1426-777 (NMNS); 1 ♂, Taiwan, Tengchi (1600m), N 23°04'/ E 120°46', 17.IX.2002, leg. Dubitzky & Szczepanek (CAD); 4 ♂♂, Taiwan, Tengchi (1600 m), N 23°05'/ E 120°47', 19.IX.2002, leg. Dubitzky & Szczepanek (CAD, NCHUT).

***Habropoda tainanicola tainanicola* Strand, 1913** (Figs 35F, 38L, 39H, 41D, 44C, D)

Anthophora (Habropoda) tainanicola tainanicola Strand, 1913: 51-52. Type locality: Tainan & Hoozan (Taiwan). Syntypes 5 ♀♀ DEI (examined)

Female. BL: 12.9–14.4 mm (13.5 mm). FWL: 9.7–10.4 mm (10.1 mm).

Structure. Head about 1.4 times as broad as long. Proboscis long in repose, reaching coxa of middle legs. Galea fine and densely tesselate, dull, with dispersed, flat punctation. Labrum about 1.5 times broader than long, with dense punctation on disc. Area before front margin of labrum with two tooth-like erections in the middle. Front margin of clypeus with distinct incision in the middle. Clypeus tesselate, dull except shiny triangular flattened area along front margin. Punctation of clypeus dense to very dense (<<1), flat. SCA dull, with fine and dense punctation. Other parts of head smooth to weakly tesselate, with small and dense punctation (≤1). Scape about as long as AS 3 and 4 together, with large dispersed punctation on ventral side. AS 3 mainly cylindrical, only apically conically broadened, about 1.3 times as long as AS 4 and 5 together. Scutum tesselate, dull to weakly shiny, with large dense (<1) punctation. Punctation of scutellum distinctly smaller, denser (<<1) than on scutum. Metanotum tesselate, shiny, with similar but more dispersed punctation than on scutellum. Propodeum tesselate, shiny, with large dispersed punctation laterally and impunctate median line forming trapezoid impunctate area in the middle. Structure of mesepisterna similar to scutum. T tesselate, dull, with dense, inconspicuous punctation except impunctate marginal zone. S tesselate, weakly shiny, with dense punctation.

Integumental colour. Colour of body black to blackish brown. Mandibles yellowish to reddish brown basally, black apically. Labrum yellowish brown. Clypeus dark brown, sometimes with yellowish brown to yellow maculation apically. Antenna blackish brown except apical part of AS 3–11 bright yellowish brown beneath. Legs chestnut brown (coxae to basal part of tibia) to yellowish brown (apical part of tibia to tarsi). T black except amber, transparent marginal zone. S blackish brown with bright yellowish brown maculations, mainly apically.

Pubescence. Ventral margin of mandibles with long, brown hairs. Labrum with long, distinct hairbrush of dense, yellowish grey hairs. Lateral parts of clypeus, POA, SCA and main parts of frons, with short and dense, yellowish white pubescence, intermixed with long blackish brown hairs. Vertex with long, blackish brown hairs. Ventral part of GA and occiput with bright, yellowish grey pubescence. Thorax with long, blackish brown pubescence, except ventral part of mesepisterna with long yellowish grey hairs. Forefemur with long blackish brown hairs, intermixed with long yellowish grey hairs. Pubescence of foretibia brown (basally) to yellowish brown (apically). Foretarsi with simple, bright orange-grey hairs (Fig. 35F). Middle and hind legs from coxa to femur with mainly blackish brown pubescence. Pubescence of middle tibia and tarsi similar to forelegs. Tibial scopa of hind legs bright orange, with branched hairs along dorsal and ventral margin. Inner side of hind tibia with short and dense, mainly brown hairs. T with variably coloured pubescence, tergum 1 mainly

with long blackish brown hairs, T 2-3 with black hairs, often intermixed with orange pubescence and T 4-6 with bright orange pubescence. S 1-4 with long, brown to orange hair fringe apically and inconspicuous, short, yellowish grey hairs basally. S 5 with dense brush of reddish brown to orange hairs on apical half.

Male. BL: 11.9-13.1 mm (12.6 mm). FWL: 8.8-9.7 mm (9.26 mm).

General appearance of structures, integumental colour and pubescence similar to female except following characters: AS 3 distinctly shorter than in female, about 1/3 shorter than AS 4 and 5 together (Fig. 44D); AS 4 and 5 (Fig. 44D) distinctly longer than broad; mandibles ivory transparent with black apical region; clypeus ivory with two teardrop-shaped black maculations laterally (Fig. 44C); labrum bright yellowish brown to yellowish transparent; apical part of SCA, POA and ventral side of scape ivory (Fig. 44C); tegulae brown, paler than in female; pubescence of head mainly bright yellowish grey except few single blackish brown hairs on lateral parts of clypeus, SCA and vertex; thorax with long dense, yellowish grey hairs, on scutum intermixed with dispersed long blackish brown hairs; coxa to femur of all legs with long yellowish grey hairs ventrally; tibia and tarsi of fore and middle legs with bright orange, long pubescence; distal tarsal segments of hind legs with short yellow to orange hairs; T with medium long yellowish orange pubescence; S 1-3 with long fringe of yellowish grey hairs apically; S 4 and 5 with inconspicuous short, yellowish grey hairs in the middle and dense brush of yellowish orange hairs laterally; S 6 nearly bare, except brush of short dense hairs apically; S 7 (Fig. 38L) apically with concave incision, ventral side with strong, dense hairs apically; S 8 (Fig. 39H) with very slight incision apically.

Male genitalia (Fig. 41D). DGS long, nearly 2 times as long as VGS, spatulate apically. Inner margin of apical spatulate part of DGS with long hairs, about as long as basal part. VGS longer than broad, with inconspicuous short hairs on ventral side.

All other characters in structure, integumental colour and pubescence similar to female.

Diagnosis. This species resembles very closely *H. christineae* sp. n., from which it can be distinguished by the characters given for the diagnosis for *H. christineae* sp. n.

Distribution. The species is mainly known from the low land to low hill countryside of Taiwan, such as Neihu (Taipei Hsien), Fushan (Taipei Hsien), Shihting (Taipei Hsien), Hokuto (Taipei Hsien), Tainan (Tainan Hsien) and Tungpu (Nantou Hsien). For seasonal and altitudinal distribution of this species, see Fig. 31.

Material examined. Type material. 1 ♀, Syntype, Formosa, Tainan, 7.IV.1911, leg. H. Sauter, herewith designated as Lectotype to ensure the stability of the species status (DEI); 4 ♀♀, Syntypes, Formosa, Tainan, 7.IV.1911, leg. H. Sauter (DEI); 1 ♀, Syntype, Formosa, Hoozan, IV.1910, leg. Sauter (DEI). Other material. 1 ♀, Taiwan, Fushan, Hsueshan Shanmo, ca. 650 m, 7.V.2001, leg. Schönitzer (ZSM); 1 ♀, Central Taiwan, Tungpu, 1200 m, Nantou Hsien, 28.IV.-2.V.1981, T. Lin & C.J. Lee (TARI); 1 ♀, Taiwan, Taipei, Neihu, 250 m, IV-V.1972, leg. Maa (NML); 2 ♀♀, N-Taiwan, Shihting, at nest, 2.V.1976, leg. Lieftinck (NML); 2 ♂♂, Taiwan, Taipei, Neihu, 11.IV.1973, leg. Maa (NML); 2 ♂♂, Taiwan, Taipei, Neihu, ex colony, 28.III.-18.V.1974, leg. Maa (NML); 1 ♂, Taiwan, Taipei, Neihu, 20.-

25.III.1973, leg. Maa (NML); 2 ♂♂, Formosa, Hokuto, 7.III.1912, H. Sauter, erroneously determined as *Anthophora bucconis* Friese by Strand (DEI); 4 ♂♂, Taiwan, Taipei Hsien, Chu-Tze Lake, 570 m (locality name written in Chinese), 20.IV.1956, col. K.S. Lin (TARI, ZSM).

***Habropoda (Phyllohabropoda) christineae*, sp. n.** (Figs 36A, B, 38K, 39K, 41E, 44E, F)

Female. BL: 11.2-13.4 mm (12.3 mm). FWL: 8.9-9.2 mm (9.0 mm).

Structure. Head triangular, about 1.3 times broader than long. Proboscis medium long in repose, extending beyond the forecoxae. Galea smooth and shiny with dispersed, flat punctures. Stipites smooth and shiny. PMX 5-segmented, PMX 4 and 5 equal in length. Mandibles strongly punctured basally. Labrum nearly 2 times broader than long, irregularly punctured, with two lateral humps basally. Area near front margin of labrum with two small tooth-like projections. Clypeus smooth and shiny with dispersed irregular punctation which is smallest and most dense basally. Basal half of clypeus protuberantly rounded, apical half with flattened, triangular area. SCA protuberant apically, with large, dense punctation and two lateral humps before each antennal insertion. Median ridge of SCA indistinct, flattened. Other parts of head as POA, face, vertex and GA shiny with small, dense punctation. Scape about as long as following three AS together, with large and dense punctation on ventral side. AS 3 conical, becoming increasing broader from base to apex, nearly as long as AS 4 and 5 together. AS 4 slightly broader than long. AS 5 nearly as broad as long, AS 6–11 distinctly longer than broad. Apical AS two times as long as broad. Scutum smooth and shiny, with very dense and distinct punctation. Scutellum rounded, weakly tessellated, punctation similar to scutum with slightly notched median line. Metanotum with dull area in the middle, lateral parts with large, distinct punctation, more shiny. Propodeum strongly tesselate, dull, with indistinct and small but dense punctation, except impunctate, smooth to weakly tesselate, triangular area in the middle. Structure of pronotal lobes and mesepisterna similar to scutum and scutellum. Tegulae shiny, with indistinct small punctation. Veins of wings typical for *Habropoda*. Tarsal segments of forelegs conspicuously truncate (Fig. 36A), especially segments 2–4 distinctly broader than long, heart-shaped. T shiny, with small, dense punctation (<1), also on marginal zone. Marginal zone of T 2–3 about one third of total length of T. Dorsolateral convexity of T distinctly developed. Pygidial plate triangular, strongly tesselate, dull. Apical half of pygidial plate distinctly narrower, apically pointed. S tesselate, dull with more coarse punctation than on T. Apical margin of S 2 and 3 impunctate, shiny.

Integumental colour. Colour of body black. Proboscis reddish brown. Mandibles brown basally, nearly black apically. Labrum and clypeus chestnut brown. Clypeus sometimes with weak yellowish white marking along front margin (one female with additional marking along median line). Antenna black, from AS 4 onwards chestnut brown beneath. Fore and middle legs black to chestnut brown. Basitarsi of middle legs reddish brown. Hind legs brown (femur) to yellowish brown (tibia, tarsus). Claws of all legs yellowish brown basally, dark

reddish brown apically. Spurs yellowish brown. T 1-4 black, T 5 and 6 orange. Pygidial plate yellowish brown basally to black coloured apically. S dark brown basally to transparent yellowish brown apically.

Pubescence. Labrum regularly covered with medium long, golden brown hairs. Disc of clypeus with dispersed inconspicuous short, golden brown hairs. Lateral parts of clypeus with scant, long black hairs. Posterior margin of mandible with yellowish brown hairs apically and long, blackish brown hairs basally. Upper parts of GA covered with long black hairs, lower parts near mandibles with long greyish brown hairs. Pubescence of other parts of head black. Scapus with medium long black hairs mainly on ventral side. Thorax densely covered with long black hairs. Ventral side of thorax and LP covered with long, dark grey hairs. Propodeum covered with short, dark grey hairs except area along median line. Tarsal segments of forelegs conspicuously covered with dense, bottlebrush-like yellowish grey pubescence mostly with the characteristically hooked tips of the hairs (Figs 36A, B). Pubescence of other parts of forelegs black except small spot of short golden brown hairs on apical part of tibia. Hairs of femur and tibia of middle legs similar to forelegs. Tarsi of middle legs with simple, dispersed, yellowish brown hairs, except inner side of basitarsi with dense brush of short orange-brown hairs. Hind legs with relatively long black hairs on coxa and trochanter but short dark grey hairs on ventral side of femur. Outer side of hind tibia with long and bright orange hairs, in contrast to the relatively short (dorsally) to long (ventrally), dense and simple brown hairs on inner side. Tibial scopa with feathered hairs along ventral (brown) and dorsal margin (dark orange). Basitarsi of hind legs with orange brown hairs about 2 times longer on outer than on inner side. Hind basitarsus with dense orange hairbrush along apical margin. Other segments of hind tarsi with dispersed brown hairs. T 1 and 2 with regular pubescence of black hairs being longest on basal part of T 1. Pubescence of T 3 black except an inconspicuous spot of dispersed orange hairs in the middle. T 4 with dense pubescence of short orange hairs, intermixed with single long black hairs on disc and black hairs laterally. Prepygidial as well as pygidial fimbria of bright orange hairs. S 2-4 with apical hair fringe of long blackish brown hairs, S 5 with golden brown hairs and S 6 nearly bare with few golden brown hairs apically.

Male. BL: 10.4-12.9 mm (11.5 mm). FWL: 8.0-8.9 mm (8.5 mm).

Structure. Head triangular, similar to female (Fig. 44E). Proboscis and other mouthparts similar to female. Clypeus with more dispersed punctation on triangular flattened area than in female. Other parts of head similar to female. Scape as long as following three AS together (Figs 44E, F). AS 3 conical, distinctly shorter than in female about as long as AS 4 (Figs 44E, F). AS 4-12 longer than broad, AS 13 about two times longer than broad. Thorax in all parts similar to female. Tarsal segments of forelegs longer than broad, not truncate as in female. T as female except pygidial plate absent. S not as intensively tesselate as in female, more shiny. Punctation of S similar to those of T, but more dispersed (≥1). S 7 (Fig. 38K) strongly convex apically. Apical part of S 7 funnel-shaped in dorsal view. S 8 (Fig. 39K) with distinct, broad incision apically, apical margin bilobed.

Integumental colour. Body mainly black. Proboscis bright reddish brown. Mandibles similar to female except small ivory spot basally. Clypeus ivory except chestnut line along front margin and black areas along lateral margins (Fig. 44E). Triangular ivory maculation along front margin of SCA with distinct incision medially (Fig. 44E). Labrum chestnut brown. Antenna black, AS 3-13 dark brown beneath. Other parts of head black. Forelegs dark brown to chestnut brown. Femur of all legs dark brown except inner side reddish brown. Tibia and tarsi of middle legs brown except pale yellowish brown maculation at tibia apically. Tibia and tarsi of hind legs yellowish brown to orange. Claws of all legs yellowish brown basally, dark brown to nearly black apically. Spurs of all legs yellowish brown. Basal part of T 1 chestnut brown, apical part (disc) black. T 2-4 black, except chestnut coloured maculations laterally. T 5 brown except large, dark brown to black maculation in the middle. T 6 and 7 bright yellowish brown to orange. S 1-5 chestnut brown basally to yellowish brown apically. S 6-8 transparent amber.

Pubescence. Labrum with medium long yellowish grey hairs. Disc of clypeus almost bare, with few yellowish grey to black short hairs. Lateral parts of clypeus with scant long black hairs, similar to female. Ventral part of occiput (area around proboscis insertion) and GA with long, greyish white to brownish grey hairs. Pubescence of other parts of head similar to female. Pubescence of thorax similar to female but slightly more pale (blackish brown) dorsally. Foretarsi with simple, yellowish brown hairs (not hooked apically as in female) short and dense ventrally, long and sparse dorsally. Pubescence of other parts of forelegs as in female. Femora of middle and hind legs with sparse medium long black hairs. Dorsal side of tibia of middle and hind legs with short yellowish grey hairs intermixed with single black hairs apically. Ventral side of tibia of middle and hind legs with sparse, long, black hairs especially along front and hind margins. Tarsi of middle legs with yellowish grey to orange pubescence forming a dense brush of strong hairs ventrally. Pubescence of hind tarsi similar to those of middle tarsi, except row of long sparse hairs along hind margin of basitarsus. T 1 and 2 with long blackish brown hairs similar to pubescence of scutum, longest on basal half of T 1. Pubescence of T 3 similar to T 2 but intermixed with few single yellowish grey hairs. T 4 with black hairs basally and yellowish grey hairs on marginal zone. Pubescence of T 5 short, yellowish grey except few black hairs intermixed basally. T 6 with yellow pubescence except row of strong black hairs along each lateral margin. Pubescence of T 7 completely yellowish orange. Disc of S 1-5 with sparse pubescence of short, simple, yellowish grey hairs. Apical margin of S 1-5 with row of long, feathered, yellow to dark brown hairs. S 6 with inconspicuous sparse pubescence of short yellow hairs except strong, dense brush of dark orange coloured hairs in the middle of apical margin. Ventral side of S 7 (Fig. 39K) densely covered with microtricha apically, dorsal side only along apical margin. Ventral side of S 8 (Fig. 39K) with single microtricha only along apical margin.

Male genitalia (Fig. 41E). DGS long, about twice as long as VGS, slightly broadened apically. DGS with distinct brush of long hairs (about half length of ventral process) along apical and inner margin. Inner margin of apical part of DGS straight, without concave

incision. VGS ear-shaped, distinctly broader than long, with dense brush of distinct hairs (length about 1/4 of lateral extension of VGS) along inner margin.

Diagnosis. *H. christineae* sp. n. is very similar to *H. tainanicola* Strand, 1913, which occurs in two subspecies, the nominotypical *H. t. tainanicola* Strand from Taiwan and *H. t. maiella* Lieftinck from mainland China (Fukien). Superficially the new species could be confused with these two subspecies but it is clearly differentiated by the following characters (character states of the two subspecies of *H. tainanicola* Strand in parenthesis).

Both sexes: Structure of galea smooth and shiny (structure of galea tesselate, dull); pubescence of labrum shorter, more dispersed (pubescence of labrum longer, dense); apical tooth-like projections of labrum short, inconspicuous (apical tooth-like projections of labrum long, distinct); T completely black (T black only basally, marginal zone amber transparent); T polished, shiny with strong, distinct punctation (dull between flat, indistinct punctation). Females: Pubescence of POA black (yellowish grey); AS 3 continuously becoming broader, two times as long as broad apically, about as long as AS 4 and 5 together (AS 3 cylindrical, only apically conically broadened, about three times as long as broad apically, distinctly longer (1.3 times) than AS 4 and 5 together); ventral part of GA, occiput and mesepisterna with dark brown pubescence (with bright yellowish grey pubescence); foretarsi truncate, with bottlebrush-like pubescence of apically hooked hairs (foretarsi truncate with normal pubescence of apically straight hairs). Males: Clypeus (Fig. 44E) ivory, along lateral margins distinctly black (clypeus (Fig. 44C) completely yellow, without black along lateral margins); POA and ventral side of scape (Figs 44E) completely black (POA and ventral side of scape with yellow maculation (Figs 44C)); AS 3 (Fig. 44F) about as long as AS 4 (AS 3 (Fig. 44D) distinctly longer than AS 4); pubescence of body mainly blackish brown (pubescence of body mainly yellowish brown: *H. t. tainanicola* Strand; pubescence dark greyish brown: *H. t. maiella* Lieftinck, see also Lieftinck 1974); S 7 (Fig. 38K) convex rounded apically, ventral side apically with inconspicuous microtricha (S 7 (Fig. 38L) apically concave, ventral side with distinct, strong and dense hairs apically). S 8 (Fig. 39K) with strong and distinct incision apically (S 8 (Fig. 38H) with weak, indistinct incision apically); male genitalia as in Fig. 41E, lateral sclerites of PV slender, hardly broadened apically (male genitalia as in Fig. 41D, lateral sclerites of PV distinctly broadened apically); inner margin of apical spatulate part of DGS (Fig. 44E) about half as long as basal part (inner margin of apical spatulate part of DGS (Fig. 44D) about as long as basal part); VGS (Fig. 44E) distinctly broader than long, with strong, dense hairbrush along inner margin (VGS (Fig. 44D) distinctly longer than broad, without distinct hairbrush along inner margin).

Etymology. This species is named *christineae* in honour of my beloved mother Christine Dubitzky in gratitude of her tremendous support for me and my studies. She has always encouraged my biological interests and showed great sympathy and tolerance for the diverse zoological pursuits of my youth.

Distribution. *H. christineae* sp. n. is known from the surroundings of the mountain range near the medium altitude TESRI station Tengchi (1600 m), Kaoshiung Hsien, from Meifeng

(2150 m), Tsuifeng (2700 m), Sungkang (2100 m) in Nantou Hsien, Central Taiwan and from Tapinshan (1950 m), Ilan Hsien, North Taiwan. Strangely enough two males were also collected in the low land area of Taiwan: Taichung, Tong-hai University (ca. 310m), Taichung Hsien and in the area of the Taiwan provincial council (ca. 100 m), Nantou Hsien. The collection localities of these males show a strong discrepancy according to the altitudinal data of all other specimens of this species. The data from these two male specimens was excluded from the seasonal and altitudinal distribution table (Fig. 31) of the species. As yet, they are only records for lowland Taiwan, an area has been more intensively collected than the mountainous regions. It is possible that mislabelling or drifting of specimens by typhoon winds from mountainous to lowland regions of Taiwan may be the reason for their appearance.

Biology. All specimens were collected by the author in Tengchi and taken on *Rubus formosensis* (Rosaceae), where females gathered pollen and males patrolled for females.

Type material. Holotype. ♂ (NCHUT), Central Taiwan (Republic of China, ROC), Tengchi, near Taiwan Endemic Species Research Institute (TESRI), 1600 m, 23°07'N/ 120°47'E, 6.7.2000, leg. A. Dubitzky. Paratypes. 9 ♂♂ (CAD, NCHUT), same data as holotype (5 ♂♂ collected on 7.7.2000); 7 ♂♂(CAD, NCHUT), same collecting locality as holotype, 6 ♂♂ collected on 6.7.2000, 1 ♂ on 7.7.2000, all leg. S. Szczepanek; 4 ♀♀, same data as holotype (3 ♀♀ collected on 7.7.2000, 1 ♀ on 6.7.2000); 1 ♀, same collecting locality as holotype, 7.7.2000, leg. S. Szczepanek; 15 ♂♂, 4 ♀♀ (TARI, ZSM), Central Taiwan, Meifeng (2150 m), Nantou Hsien, Malaise trap, VIII. 1984, leg. K.S. Lin & K.C. Chou (1 ♂ and ♀ collected in IX.1984); 1 ♂ (TARI), Central Taiwan, Sungkang (2100 m), Nantou Hsien, 6.8.1984, leg. K.S. Lin; 1 ♂ (TARI), North Taiwan, Tapinshan (1950 m), Ilan Hsien, 26.-28.VII.1983, leg. L.Y. Chou; 1 ♂ (NCHUT), Taichung, Tong-hai University, 27.7.1976, leg. Chi-ping Lin; 1 ♂ (NCHUT), Nantou, Taiwan provincial council, 13.8.1976, leg. Chi-ping Lin; 2 ♀♀ (TARI), Central Taiwan, Tsuifeng (2300 m), Nantou Hsien, Malaise trap, VIII.1984, leg. K.S. Lin & K.C. Chou.

***Habropoda (Phyllohabropoda) sinensis taiwana,* ssp. n.** (Figs 38J, 39J, 41F, 44G, H)

Male. BL: 11.4-11.9 mm (11.7 mm). FWL: 8.4-8.6 mm (8.5 mm).

Structure. Head triangular, broader than long (Fig. 44G). Proboscis in repose short, just reaching front margin of forecoxae. Galea smooth with flat dispersed punctures. Labrum about 1.7 times broader than long, with large dense punctation basally except impunctate lateral humps. Front margin of labrum convex with a small incision in the middle. Clypeus smooth with regular, large punctation (≤1). SCA protuberant, with small honeycombed punctation and distinct median ridge on basal half. Area around ocelli with dense small punctation. Vertex, GA, SCA and area between ocelli and compound eyes with dense medium-sized punctation. Frons tesselate, with medium-sized dispersed punctation. Scape almost as long as following three AS together (Figs 44G, H), with dense distinct punctation

ventrally. AS 3 conical, short, about as long as AS 4, only 1.2 times longer than broad apically (Figs 44G, H). AS 4-13 distinctly longer than broad (AS 4-AS 5 about 1.6 times, AS 6 to AS 12 about 1.8 times and AS 13 about 2 times longer than broad). Scutum with honeycombed punctation of variable diameters. Metanotum tesselate, dull, with large and regular punctation except small area in the middle. Scutellum, mesepisterna and pronotal lobe similar to scutum. Tegulae smooth and shiny with inconspicuous weak punctation. Veins of wings as typical for *Habropoda*. T shiny, weakly tesselate, with very dense (<<1) honeycombed punctation of coarse, distinct punctures, sometimes of varying diameters. S shiny, with large dense punctation which becomes smaller from base to apex . Area near apical margin of S impunctate. Apical part of S 7 (Fig. 38J) convex , separated from basal part by a narrow constriction. S8 as shown in Fig. 39J.

Integumental colour. Body black. Galea and glossa reddish brown. Mandibles yellow, except apical part as well as dorsal and ventral margins being blackish brown. Clypeus yellow except blackish brown line along front margin, two lateral teardrop-shaped maculations and a black area latero-ventrally (Fig. 44G). SCA black with yellowish line along front margin (Fig. 44G). All other parts of head black. Antenna black, AS 4-13 chestnut beneath. All legs mainly black (coxae to tibiae) to blackish brown (apical tarsal segments). Claws reddish brown basally to black apically. Spurs of all legs bright greyish brown. Tegulae transparent, amber. T as well as S black, except brown transparent line along apical margin of S 1-4.

Pubescence. Mandibles with short to medium long white hairs basally and long white hairs along ventral margin. Labrum with medium long dispersed white hairs. Clypeus mainly bare on disc and dispersed long brown hairs laterally. Lateroapical corner of clypeus as well as lower part of SCA with short white hairs. Upper part of POA and SCA as well as face and vertex covered with dark brown hairs. Main parts of GA and occiput with long and dense, yellowish white to white hairs. Scape with long blackish brown hairs on ventral side. Scutum densely covered with long yellowish brown pubescence, intermixed with dark brown to black hairs. Pronotal lobe with long, blackish brown hairs. Pubescence of mesepisterna yellowish brown dorsally to white ventrally. Ventral side of forefemur ventrally with long white pubescence intermixed with blackish brown hairs. Foretibia with brown to blackish brown long hairs ventrally and short yellowish white hairs dorsally. Foretarsi with brown to black pubescence of dense short hairs ventrally and long dispersed hairs dorsally. Coxa and trochanter of middle and hind legs with long white pubescence. Femur of middle and hind legs with long white hairs. Pubescence of tibia and tarsus of middle and hind legs brown to blackish brown. T 1 regularly covered with long yellowish white hairs. T 2-4 with short blackish brown hairs on disc and bright ochreous hair bands apically. T 5-7 regularly covered with short blackish brown hairs. S 2-4 with row of long greyish white hairs along apical margin. S 5 and 6 covered with short blackish brown hairs. Apical margin and ventral surface of apical part of S 7 with inconspicuous sparse microtricha (Fig. 38J). S 8 with sparse microtricha ventrally and along apical margin (Fig. 39J).

Male genitalia (Fig. 41F). DGS about 1.3 times as long as VGS, slightly spatulate apically. Hairbrush of DGS sparse, about 1/3 as long as DGS. VGS about 1.5 times longer than broad, with brush of dense hairs (length about 1/3 of lateral extension of VGS) along corner of apical to basal inner margin of VGS. Apical part of inner margin of VGS with only few sparse hairs.

Female. BL: 12.6-13.8 mm (13.2 mm). FWL: 8.8 mm.

Structure. Head triangular, about 1.5 times broader than long. Proboscis extremely short in repose, just reaching front margin of forecoxa. Galea shiny, with flat dispersed punctation. Mandibles as in male. Labrum similar to male, with two tooth-like projections medially near front margin. Clypeus and SCA protuberant, the first is strongly convex in profile. Structure of clypeus weakly shiny, with irregular strong punctation, punctures largest and most dispersed on disc and apical half. Basal half of clypeus as well as POA with smaller, dense punctation. Other parts of head as in male. Scape more slender and longer than in male, about as long as following three AS together, with distinct punctation on ventral side. AS 3 twice as long as broad apically and about 2 times as long as AS 4. Structure of thorax similar to male. Legs stronger and more truncate than in male. Tarsal segments 2-4 of forelegs truncate, flattened, distinctly broader than long. Forebasitarsus distinctly longer than broad, flattened, slightly concave ventrally. Structure of T and S similar to male but S duller and with more dense punctation than male. Pygidial plate dull, broadly triangular, apically pointed, with weakly elevated area in the middle.

Integumental colour. Body as in male. Mandibles only on basal third yellow. Clypeus blackish brown except inverted T-shaped yellow maculation along front margin. SCA completely black, sometimes with indication of yellow maculation along front margin.

Pubescence. Mandibles with greyish brown to white pubescence. Labrum with dense, medium long greyish brown hairs. Pubescence of proboscis and clypeus as male. SCA with dense, short ochreous hairs. Pubescence of other parts of head and thorax as in male. Foretarsi with bottlebrush-like pubescence of dense, apically hooked, greyish brown hairs. Pubescence of other parts of forelegs as male. Pubescence of trochanter and femur of middle legs greyish brown to brown, with brush of dense and short dark brown hairs on ventral side of apical trochanter and basal femur. Tibia and tarsus of middle legs with brown pubescence, ventral side of metatarsus with brush of dense dark brown hairs. Pubescence of trochanter and femur of hind legs dark brown. Tibial scopa brown to dark yellowish brown. Pubescence of inner side of hind tibia dark brown, consisting of dense, short hairs. Basitarsus of hind legs with dark brown pubescence on outer side and dark reddish brown pubescence on inner side. Pubescence of T 1 similar to male but being more yellowish ochreous. T 2-4 with short, yellow to orange coloured hairs on disc and dense ochreous hair bands along apical margin. T 4 with dispersed, dark brown hairs laterally. Disc and lateral parts of T 5 with dispersed dark brown hairs. Prepygidial fimbria dark brown, only basally with inconspicuous yellowish brown spot. Pygidial fimbria dark brown. S 2-4 with rows of long yellowish grey hairs apically. S 5 with apical hairbrush of brown to dark brown pubescence.

Diagnosis. *H. sinensis taiwana* ssp. n. is differentiated from the nominotypical form as follows (character states of *H. sinensis sinensis* Alfken, 1937 in parentheses):

Pubescence of middle and hind legs dark brown, especially on trochanter, femur and basitarsus of female hind leg (pubescence of middle and hind legs yellowish grey); prepygidial fimbria of female dark brown to black except small yellowish brown spot basally (completely bright yellowish grey); pubescence on disc of female T dark yellowish brown (T 1-3) to dark brown (T 4-5) (pubescence on disc of all T yellowish grey); apical hair bands of female T 1-4 dark yellow to fox-red coloured (bright ochreous to yellowish white coloured); mark of SCA of male more or less linear (distinctly triangular); male AS 3 as long as AS 4 (AS 3 slightly longer than AS 4); male antenna from AS 4 onwards dark brown beneath (completely reddish brown beneath).

Since the distinctive features exclusively concern colouration of integument and pubescence and not structural characters, both taxa are treated on the subspecies level herewith.

Etymology. This subspecies is named after its occurrence on Taiwan.

Distribution. *H. sinensis taiwana* ssp. n. is currently known only from the surroundings of the experimental forest Hueisun on Taiwan. For seasonal and altitudinal distribution of the species, see Fig. 31.

Type material. Holotype. ♂ (NCHUT), Taiwan (ROC), Hueisun, experimental forest, ca. 600 m, 24°07'N/ 121°03'E, 27.VI.2000, leg. A. Dubitzky. Paratypes. 1 ♂, 2 ♀♀ (CAD), same data as holotype.

Genus *Tetralonioidella* Strand, 1914

Tetralonioidella Strand, 1914 (April/May): 140. Type species: *Tetralonia ? hoozana* Strand, 1914, monobasic.

Protomelissa Friese, 1914 (June): 322. Type species: *Protomelissa iridescens* Friese, 1914, by designation of Sandhouse, 1943: 592.

Callomelecta Cockerell, 1926: 621. Type species: *Callomelecta pendleburyi* Cockerell, 1926, by original designation.

The genus *Tetralonioidella* was conditionally erected by Strand (1914) in his original description of *Tetralonia (?) hoozana* (=*Tetralonioidella hoozana*) from Taiwan. The "description" and designation of *T. hoozana* as type species (being the first included in the genus) was rediscovered by Lieftinck (1983) and has nomenclatorical priority over *Protomelissa* Friese, 1914, which was published one month later. *Tetralonioidella* is an exclusively Oriental bee genus and contains 10 species. It ranges from northern India and Nepal along the Himalayans through southeast China and Taiwan, as well as Thailand and Malaysia and as far south as Sumatra and Java. The genus comprises rather slender, melectine bees, which differ from other Melectini in the following characters:

- Marginal cell distinctly longer than distance from its apex to wing tip, exceeding third submarginal cell, usually slightly shorter than three submarginal cells together;

- Scutellum convex, with distinct longitudinal carina in the middle and two ventrally curved spines laterally;
- Metasoma uniformly covered with feathered appressed hairs, typical lateral hair patches of pale short pubescence on metasoma absent (sometimes conspicuous hair bands of yellowish to reddish brown hairs developed).

The long marginal cell as well as the uniform pubescence of the metasoma are plesiomorphic among bees and therefore emphasise a basal position of *Tetralonioidella* within Melectini. Perhaps *Tetralonioidella* even represents the most primitive melectine genus at all.

With three species, *Tetralonioidella* is most diverse on Taiwan. Two species have been recorded from India, and except for Taiwan, only a single species is known from each of the remaining localities (Tab. 8). This is remarkable considering the small area of Taiwan, in contrast to the large size of the other areas listed in Tab. 8. Furthermore, only 4 species of *Habropoda* and one species of *Elaphropoda* (Wu, 2000), which is the main host of *Tetralonioidella*, have been recorded from Taiwan, so far. Yet, both anthophorine genera show their greatest diversity in mainland China. It is entirely possibly that several more species of *Tetralonioidella* will be discovered there.

Tab. 8. Distribution of *Tetralonioidella*-species in the Oriental region

Species	Taiwan	India	China	Nepal	Malaysia	Thailand	Sumatra	Java
T. hoozana	●							
T. heinzi	●							
T. himalayana formosana	●							
T. himalayana himalayana		●						
T. tricolor		●						
T. fukienensis			●					
T. nepalensis				●				
T. pendleburyi					●			
T. habropodae						●		
T. vulpecula							●	
T. insidiosa								●

Determination key to the *Tetralonioidella* species of Taiwan

1. Fore wings with numerous short dark setae apically, distinct papillae absent; inner spur of hind tibia strongly curved in male (Fig. 42B); apical part of male S 7 (Fig. 43A) with short, strong setae on ventral side; S 8 and genitalia of male as in Figs 43B, G .... ***T. heinzi* sp. n.**

– Fore wings with distinct numerous papillae apically; inner spur of hind tibia straight to slightly curved in male; apical part of male S 7 with rather long, fine hairs on ventral side (Figs 43C, E) 2

2. Antenna of male long, reaching behind tegulae, distal part of AS 4-13 strongly nodiform in dorsal view (Fig. 45A); pubescence of scutum in both sexes with dark brown hair band between tegulae; genitalia and hidden S of male as in Figs 43E, F, I..... ..... ***T. himalayana formosana*** **Cockerell**

– Antenna of male short, reaching front margin of tegulae, AS 4-13 straight to weakly nodiform in dorsal view (Fig. 45C); pubescence of scutum uniformly fox-red coloured, without dark hair band between tegulae in either sexes; genitalia and hidden S of male as in Figs 43C, D, H..... ***T. hoozana*** **Strand**

Tetralonioidella himalayana formosana **(Cockerell, 1911) stat. n.** (Figs 43E, F, I, 45A)

Melecta himalayana Bingham, 1897: 516, fig. 172. Type locality: Kumaon (5000 ft.), Himalaya.

Melecta formosana Cockerell, 1911: 227, 228. Type locality: Kosempo (today: Kaohsiung), Formosa. Type ♀ ZMHB (examined).

Anthophora sauteri Friese, 1911: 127, 128. Type locality: Tainan, Formosa. Type ZMHB.

Protomelissa sauteri Friese, 1914: 323, 324. ♂, ♀, Tainan & Takao, Formosa.

Protomelissa formosana Lieftinck, 1972: 273-277.

Protomelissa himalayana Lieftinck, 1972: 273, 274, figs. 3,7,8 .

Tetralonioidella formosana Lieftinck, 1983: 270-271(key), 276.

Tetralonioidella himalayana Lieftinck, 1983: 270-271(key), 277, figs. 13, 14.

Male. BL: 14.5 mm. FWL: 9.2 mm.

Structure. Head oval, about 1.3 times broader than long. Face rectangular, space between compound eyes dorsally nearly as broad as ventrally. Proboscis in repose reaching front margin of trochanter of forelegs. Galea shiny, smooth to weakly tesselate, with minute, dispersed punctation. Labrum about 1.3 times broader than long, apically with deep median incision. Frons with distinct, large punctation. Punctation of vertex indistinct, smaller than on frons. Frons and vertex tesselate, dull to weakly shiny, except smooth and shiny area around ocelli. Antenna (Fig. 45A) long, reaching behind tegulae. Scape conically broadened, about as long as following two AS together, with dense punctation ventrally. AS 3 segment slightly broader than long. AS 4 long, nearly 2 times longer than broad, 2 times longer than AS 3. AS 5 to 8 distinctly longer than broad, AS 9-12 only slightly longer as broad and AS 13 segment about 2 times as long as broad. AS 5 to 13 with strong concave posterior margin, therefore distinctly nodiform in dorsal view (Fig. 45A). Scutellum shiny, with large honeycombed punctation anteriorly, coarse wrinkles posteriorly. Posterior margin of scutellum straight to slightly concave, without broad incision in the middle. Scutellum with distinct median keel. Scutellar spines long, distinctly visible between pubescence. Propodeum smooth and shiny, only basally slightly tesselate to minutely wrinkled. Mesepisterna as well as LP shiny with wrinkle-like, irregular punctation. Fore and hind wings distinctly papillate distally. Femur and tibia of middle and hind legs slender, not thickened. Middle tibia apically with long tooth-like, curved projection. Inner spur of hind tibia slightly curved. Basitarsus of hind legs straight, without ventral groove. T shiny, with large, flat and dense punctation, also on

marginal zone. Apical margin of T 1-6 straight to slightly concave in the middle. T 7 with weak, triangular incision apically. S 1-5 shiny, with distinct, dense punctation basally and more dispersed, indistinct punctation on marginal zone. S 6 triangular, with regular, dense punctation. Apical margin of S 1 and 2 straight, of S 3-5 slightly concave in the middle.

Integumental colour. Proboscis brown. Mandibles brown except dark reddish brown at apex. Labrum yellowish brown transparent. Antenna blackish brown on top, AS 4-13 bright brown beneath. Pronotal lobe brown, tegulae bright brownish transparent. All legs completely brown. Scutellar spines black with brown tips apically. Tibial spurs all dark brown. T 1 dark brown basally, bright brownish transparent apically. T 2 blackish brown basally in contrast to bright brownish transparent marginal zone. Following T dark brown to black. S 1 and 2 bright yellowish brown, transparent; S 3-5 dark reddish brown basally and yellowish transparent apically. S 6 brownish transparent. S 7 (Fig. 43E) , with broad incision apically. S 8 as in Fig. 43F. Male genitalia as in Fig. 43I.

Pubescence. Mandibles with silvery long hairs along ventral margin and short silvery hairs basally. Labrum with short, feathered, grey hairs, intermixed with numerous long yellowish grey hairs. Clypeus extremely densely covered with short, feathered, white pubescence, intermixed with few long, simple hairs. POA with white pubescence, intermixed with few dark brown hairs laterally. Frons with long white pubescence of branched hairs except tufts of long blackish brown hairs beside median keel of frons. Vertex around ocelli with blackish brown short to long, branched hairs. Area along hind margin of vertex, occiput and GA with long, white hairs. Scutum with long, yellowish white pubescence except blackish brown hair band between tegulae. Scutellum with yellowish white pubescence similar to scutum, except two dark brown hair tufts around base of scutellar spines. Other parts of thorax with long, branched yellowish white to white pubescence except areas ventral of tegulae and around pronotal lobes, which bear tufts of apically dark brown hairs. Femur of all legs with long pubescence of greyish brown to white hairs except pubescence of forefemur being intermixed with single dark brown hairs. Pubescence of tibia and tarsi of all legs brown. S regularly covered with short feathered yellowish brown hairs. S with short, feathered, yellowish transparent hairs, intermixed with longer, simple hairs of the same colour. Ventral side of S 7 with thin, inconspicuous pubescence along apical margin (Fig. 43E). S 8 with distinct median hair fringe apically (Fig. 43F).

Female. BL: 13.1-14.5 mm (13.8 mm). FWL: 9.3-9.5 mm (9.4 mm).

General appearance as in male except the following features: galea with more distinct punctation. Clypeus tesselate, shiny to weakly tesselate, with dense wrinkle-like punctation; length of AS similar to male, except AS 9-11 being distinctly longer than broad, similar AS 4-8; AS 5-12 straight along posterior margin, not nodiform in dorsal view; pygidial plate apically pointed, dull, with only small apical region elevated; pubescence of clypeus similar male, but more sparse; scape with more sparse pubescence than in male; pubescence of forefemora uniformly grey on ventral side, without dark brown hairs; pygidial plate dark reddish brown (apically) to black (basally) coloured.

Diagnosis. From the nominotypical subspecies, *T. himalayana himalayana* Smith, *T. himalayana formosana* Cockerell can be separated in both sexes by the following characters (character states of *T. himalayana himalayana* in parentheses): Yellowish grey pubescence of scutellum with two lateral tufts of dark brown hairs around scutellar spines (pubescence of scutellum uniformly yellowish grey). Small tufts of dark brown tipped hairs ventrally of tegulae and around pronotal lobe (without tufts of dark tipped hairs around these structures). Propodeal triangle shiny, smooth to slightly wrinkled laterally (propodeal triangle distinctly wrinkled laterally, dull to weakly shiny).

Distribution. For seasonal and altitudinal distribution of the species, see Fig. 32.

Comments. Lieftinck (1972, p. 274) treated *T. himalayana* and *T. formosana* as two separate species although he found no solid characters to justify the separation, after comparison with the type material he wrote: "As a matter of fact, *P. himalayana* and *formosana* are undoubtedly very nearly related and so closely similar to one another that they may be only geographical representatives of but one species". The structural differences between the two forms listed in Lieftinck´s determination key (Lieftinck, 1972) are negligible, therefore only differences in the colouration of pubescence remain (see diagnosis). Also the structural differences of the propodeal triangular mentioned by him are insufficient , because only a single male of *T. himalayana himalayana* Smith was studied and the variation of this character remains unknown. Regarding the male genitalia and hidden S, as well as the flight season, these two forms are identical. The only distinctive features are the different colour patterns of thoracic pubescence, which do not justify a separation of the two taxa at a species level, but rather indicate that they should be treated as geographical subspecies.

Material examined. Type material. Holotype, ♀ (ZMHB), Formosa, Kosempo, II.1908, S. V. Sauter, *Melecta formosana* Cockerell, type, *Protomelissa formosana* Ckll., holotype, det. M.A. Lieftinck, 1972. Other material. 1 ♀ (DEI), Formosa, Taihorin, XII.1911, H. Sauter; 1 ♀ (TARI), C-Taiwan, Tungpu (1200 m), Nantou Hsien, X.1985, Malaise trap, leg. K.S. Lin; ♂ (ZMHB), Formosa, Takao, XII.1908, Sauter.

***Tetralonioidella hoozana* Strand, 1914** (Figs 43C, D, H, 45C)

Tetralonioidella (Tetralonia?) hoozana Strand, 1914: 139-141. Type locality: Hoozan (Fengshan today), Formosa. Type, ♂ (DEI, examined).

Male. BL: 12.7-13.6 mm (13.2 mm). FWL: 9.2-9.4 mm (9.3 mm).

Structure. Head about 1.4 times broader than long. Face trapezoid, space between compound eyes dorsally broader than ventrally. Proboscis in repose reaching front margin of foretrochanter. Galea shiny, with dense, small punctation. Labrum shiny, about 1.5 times broader than long, with dense punctation of large punctures. Apical margin of labrum convex, with broad incision in the middle. Clypeus shiny, with dense, honeycombed punctation. SCA distinctly keeled in the middle. Other parts of head shiny to dull, lateral parts of vertex and frons with irregular punctation. Antenna rather short, reaching front margin of tegulae

(Fig. 45C). Scape with dense punctation ventrally, about as long as following 3 AS together. AS 3 slightly longer than broad. AS 4 segment short, nearly 1.5 times longer than broad, distinctly longer than AS 3 and about 1.4 times longer than AS 5 in ventral view. Following AS about as long as broad except AS 13 is about 1.9 times as long as broad. AS 5-12 weakly concave along posterior margin, distally only slightly convex, not distinctly nodiform dorsally (Fig. 45C). Scutum smooth and shiny, with large and dense punctation. Scutellum weakly shiny, with dense, honeycombed punctation, no median keel developed. Posterior margin of scutellum with broad incision in the middle. Scutellar spines short, truncate, barely visible between pubescence. Mesepisterna smooth and shiny, with large and dense punctation. Fore and hind wings distinctly papillate distally. Femur and tibia of middle and hind legs thickened. Inner spur of hind tibia straight, distinctly longer than outer spur. Basitarsus of hind legs ventrally flattened, without groove, therefore straight in profile. T distinctly tesselate, dull to weakly shiny, with inconspicuous, small and dense punctation. Apical margin of T 1-6 straight to slightly convex in the middle. T 7 with a triangular, apically pointed incision. S 1-5 weakly tesselate, shiny, with small punctation that is most dense basally. Apical margins of S convex (S 1) to straight (S 2) respectively slightly concave (S 3-5) in the middle. S 6 triangular, with small dense punctation. S 7 S as in Fig. 43C, apically rounded. S 8 as in Fig. 43D, apically truncate. Male genitalia as in Fig. 43I.

Integumental colour. Colour of body mainly black. Proboscis brown, mandibles reddish brown in the middle. AS 3-13 yellowish to reddish brown beneath, dark brown coloured dorsally. Tarsi blackish brown (basitarsi) to yellowish brown (distitarsi). Tegulae amber coloured, transparent. Apical 2/3 of T 1-6 bright amber coloured, transparent in contrast to the black coloured basal third, T therefore conspicuously banded. T 1-6 mainly apically with distinct metallic gloss (difficult to see between dense pubescence). S 1 and 2 yellowish brown, S 2 with large, blackish brown maculations laterally. Other S blackish brown basally to dark brown transparent apically.

Pubescence. Mandibles with few, long grey hairs along ventral margin and short grey hairs basally. Labrum and clypeus with short grey pubescence of feathered hairs, intermixed with long, branched hairs. POA as well as SCA with dense, short pubescence of grey, feathered hairs, on POA intermixed with long yellowish grey hairs. Frons as well as vertex with long, bright yellowish brown pubescence of feathered hairs, area around ocelli with short, branched yellow hairs. Genal area with short branched hairs along hind margin of compound eye, becoming longer to occiput. Pubescence of thorax fox-red to yellowish orange of long, branched hairs. Lateral parts of thorax with yellowish grey to grey, long, branched hairs. T with dense fox-red pubescence of short feathered hairs, which are most dense on lateral parts of T 1 and apical parts of T 2-6, forming apical hair bands which emphasize the banding of integumental colour on the latter. S with inconspicuous, short to medium long yellowish grey, transparent pubescence. S 7 (Fig. 43C) with thin hairs on ventral side along apical margin. S 8 (Fig. 43D) bare.

Female. BL: 12.0 mm. FWL: 9.2 mm.

Structure. Head oval, as in male about 1.4 times broader than long. Face same as male, distinctly trapezoid. Proboscis and mandibles same as in male. Labrum about 1.4 times broader than long, shiny, with large and distinct punctation. Front margin of labrum weakly concave, with small tooth-like projection in the middle. Clypeus shiny to weakly dull, with honeycombed punctation. SCA and lower part of frons distinctly keeled in the middle. Other parts of head mainly shiny, with more or less distinct, irregular punctation. Antenna rather short, reaching front margin of tegulae. Scape similar to male, about as long as following three AS together. Length of AS 3 and AS 4 similar to male. AS 5-11 distinctly longer than broad (1.2 to 1.3 times). AS 12 nearly twice as long as broad. Posterior margin of AS 5-11 straight, not concave as in male. Scutum same as in male but with distinct median groove, nearly reaching hind margin. Scutellum similar to male, with very short, truncate scutellar spines. Basal half of scutellum in contrast to male with weak and flat median keel. Mesepisterna similar to male. Apical parts of fore and hind wings distinctly papillate. Femur and hind tibia of middle and hind legs only weakly thickened, distinctly more slender than in male. Inner spur of hind tibia straight, distinctly longer than outer spur. Basitarsus of hind legs rounded, only weakly flattened ventrally. T1-5 similar to male. Triangular pygidial plate of T 6 tesselate, slightly elevated in the middle. Structure of S 1-6 similar to male, marginal zone apically shiny, nearly impunctate. S 5 with shiny elevated triangular flattened area apically.

Integumental colour. Head and thorax mainly black. Proboscis brown, mandibles mainly reddish brown. Labrum brownish transparent. Clypeus blackish brown with two small bright brown spots laterally. Antenna dark blackish brown except AS 3-12 yellowish to reddish brown beneath. Legs black to blackish brown, tarsi blackish brown to bright brown. Tegulae amber transparent. T 1-5 coloured similar to male, with distinct metallic gloss. Basal parts of S dark brown to blackish brown, marginal zone transparent amber. Basal parts of pygidial plate reddish brown, apical part black.

Pubescence. Similar to male.

Diagnosis. *T. hoozana* is similar to *T. heinzi* n. sp., from which it can be separated by the diagnostic features given for *T. heinzi* n. sp.

Distribution. Beside the type locality near Hoozan, which today is known as Fengshan (Kaohsiung Hsien, South-West Taiwan), this species also occurs in Lienhuachih (Nantou Hsien, Central Taiwan) and Raisha, now known as Sungkang (Nantou Hsien, Central Taiwan). For seasonal and altitudinal distribution of this species, see Fig. 32.

Material examined. Type material. Type, ♂ (DEI), Formosa, Hoozan (= Fengshan today), IX.1910, leg. Sauter. Other material. 1 ♂ (TARI), Raisha (= Sungkang today), 30.VIII.1927, J. Sonan, K. Shibata; 1 ♀ (TARI), Central Taiwan, Lienhuachih (650 m), Nantou Hsien, IX.1984, Malaise trap, leg. K.S. Lin & K.C. Chou.

***Tetralonioidella heinzi* sp. n.** (Figs 42A-D, 43A, B, G)

Male. BL: 9.9-14.3 mm (11.3 mm). FWL: 8.6-10.3 mm (9.3 mm).

Structure. Head (Fig. 42A) oval, about 1.3 times broader than long. Inner margin of compound eyes divergent (space between compound eyes dorsally about 1.2 times as broad as ventrally), face therefore trapezoid in frontal view. Proboscis in repose reaching coxa of forelegs. Galea lanceolate in lateral view, apically pointed. Surface of galea shiny, smooth to very weakly tesselate, with small but distinct punctation. Labrum nearly rectangular, about 1.5 times broader than long, shiny, with large and dense punctation except for the slender impunctate median line. Apical margin of labrum convexly rounded, with a broad incision in the middle. Clypeus with dense punctation, about 1.5 times broader than long. SCA shiny, with distinct, dense punctation and a strong lamellate keel in the middle. All other parts of head smooth to weakly tesselate, shiny with irregular, dense punctation. Lateral region of vertex flattened. Ocelli arranged in a straight line, distance to hind margin of vertex about 2 times OD. Antenna long, reaching behind hind margin of tegulae (Fig. 45B). Scape tesselate, dull, nearly as long as following three AS together, with dense punctation on ventral side. AS 3 short, about as long as broad. AS 4 nearly twice as long as broad, 1.5 times longer than AS 3. Further AS distinctly longer than broad. Margins of AS 4-13 convex anteriorly, concave posteriorly in dorsal view, AS 4-12 therefore distally nodiform along posterior margin (Fig. 45B). Scutum shiny, with large and dense punctation. Scutellum wrinkled, caused by honeycombed and coarse punctation, with a broad lamellate, longitudinal keel in the middle. Lateral parts of scutellum with two long backward curving spines. Propodeum strongly tesselate, dull with coarse wrinkles basally and two smooth oval maculations in the middle. Mesepisterna strongly tesselate, dull, with large and dense punctation. LP tesselate, dull with coarse wrinkle-like punctation. Forewings not papillate, hind wings with only few weak papillae distally. Claws typical for Melectini with a long and apically pointed outer claw, inner claw short and plate-like (Fig. 42D). Arolia present. Femur of middle and hind legs thickened, convex on outer side, slightly concave on inner side. Hind tibia thickened, apically broadened. Inner spur of hind tibia distinctly curved, apex truncate, ventrally curved (Fig. 42B). Basitarsus of hind legs slightly concave to flattened dorsally and with a broad distinct groove ventrally, therefore concave in profile (Figs 42B, C). T shiny to weakly dull, with small punctation (≥1). Apical margin of T 1-4 straight to slightly convex, apical margin of T 5 and 6 broadly concave in the middle. T 7 with distinct, triangular incision apically, apex therefore two-cornered. S 1-5 smooth and shiny, with dense punctation on disc and dispersed punctation on marginal zone. Apical margin of S 1-5 with broad, concave incision in the middle. S 6 triangular, weakly dull, with dense, small punctation. Apical part of S 7 triangular, with small incision on apex (Fig. 43A). S 8 with distinct incision apically (Fig. 43B).

Integumental colour. Galea chestnut brown with dark blackish brown region in the middle. Glossa and PLB yellowish brown. Mandibles dark reddish brown to black. All other parts of

head including both sides of antenna black. Thorax black, except tegulae (brownish transparent) and distal parts of tarsi (blackish brown). claws bright yellowish brown basally to dark reddish brown apically. Spurs dark brown to black. T 1-6 black basally, dark amber transparent on marginal zone. T 7 black to blackish brown. S 1-5 black basally, amber transparent apically. S 6 dark brown to amber transparent. S 7 and 8 transparently amber.

Pubescence. Galea bare, with only few, tiny hairs basally. Mandibles with row of long yellowish grey hairs along ventral margin and short feathered hairs basally on outer surface. Labrum with dense pubescence of short, feathered grey hairs, intermixed with long, simple, yellowish grey hairs. Clypeus and POA, as well as, SCA with yellowish grey pubescence of short, feathered hairs, intermixed with long, simple to branched hairs. Frons, vertex, occiput and GA with long, branched, yellowish orange pubescence, sometimes intermixed with short feathered hairs. Scape and pedicel with short, yellowish grey pubescence, AS 3 with very short and dense hairs apically. Other segments nearly bare. Surface of compound eyes with single dispersed microtricha. Scutum and scutellum with yellowish orange to fox-red coloured pubescence of long, branched hairs. Mesepisterna and LP with yellowish grey to bright grey pubescence of long branched hairs. Tegulae with short yellowish grey hairs. Dorsal and ventral surface of forewings with short, blackish brown setae, being most dense distally. Femur of fore to middle legs with medium long, grey to yellowish grey, branched hairs. Tibia of all legs as well as hindfemur with short, yellow, feathered hairs. tarsi with thin yellow pubescence of simple hairs dorsally and dense strong, brown hairs ventrally (especially basitarsi). T usually covered with short, fox-red, feathered hairs, intermixed with few long to short simple hairs in the same colour basally and laterally. S 1-5 with thin yellow transparent pubescence of long simple hairs basally and single short, branched hairs on marginal zone. Ventral side of apical part of S 7 with stiff, short setae laterally (Fig. 43A). S 8 completely bare (Fig. 43B).

Male genitalia (Fig. 43G). Apical part of gonostylus with short hairs on inner side and apex. Basal part of gonostylus with a dense brush of short hairs on inner side and rectangular process dorsally. Rectangular process with long hairs along dorsal and apical margins. PV with two rectangular processes laterally.

Female. BL: 10.5 mm. FWL: 8.2 mm.

Structure. Head oval, about 1.3 times broader than long. Inner margin of compound eyes divergent as in male. Proboscis short, similar to male. Galea in repose reaching coxa of forelegs . Clypeus broad, about 1.7 times broader than long. Bidentate mandibles and labrum as in male. Other parts of head similar to male. Antenna rather long, reaching middle of tegulae. Length and structure of AS similar to male, except AS 4-12 is straight along posterior margin in dorsal view, not nodiform as in male. Structure of thorax similar to male but spines of scutellum distinctly shorter. Fore wings apically not papillate, with numerous setae instead, hind wings with only few weak papillae distally. Claws same as male. Middle and hind legs more slender, especially femur and tibia not thickened as in male. Inner hind tibial spur straight, not curved as in male. Basitarsus of hind legs regularly rounded, without distinct

groove ventrally like male. T similar to male but apical margin of T 5 convex. Pygidial plate retracted, therefore not visible. S similar to male. Apical margin of S 2-4 medially concave, S 5 convex. S 6 triangular.

Integumental colour. Colour of proboscis, mandibles and head similar to male. Scape and pedicel chestnut brown beneath. AS 3-12 dark brown ventrally, blackish brown dorsally. Thorax black. Tegulae brownish transparent. Legs chestnut brown to dark brown. Claws bright yellowish brown basally, blackish brown apically. Spurs dark brown. Colouration of metasoma similar to male.

Pubescence. Pubescence of body as in male, but no microtricha on compound eyes visible.

Diagnosis. *T. heinzi* n. sp. is similar to *T. hoozana* Strand and *T. nepalensis* Lieftinck, from which it easily can be distinguished by the following characters (character states of *T. hoozana* and *T. nepalensis* in parentheses): absence of numerous distinct papillae on the apical part of forewings in both sexes, with dark setae instead (forewings strongly papillate, setae absent); male antenna long, reaching behind hind margin of tegulae, AS as in Fig. 45B (short, reaching only front margin of tegulae, AS as in Fig. 45C); inner spur of male hind tibia distinctly curved, as in Fig. 42B (more or less straight); distinct ventral groove (Figs 42C, D) on basal part of male basitarsus of hind legs developed (basitarsus of male hind leg entire, without ventral groove); S 7 (Fig. 43A) of male, with strong lateral setae on its ventral surface (S 7 (*T. hoozana*: Fig. 43C) with long, thin lateral setae ventrally); male genital capsule as in Fig. 43G (as in Fig. 43H, *T. hoozana* only).

The absence of papillae on fore wings as well as the bristle-like setae on the ventral surface of S 7 are unique features within this genus. The non-papillate forewings is a unique feature within the Melectini.

Etymology. This species is named *heinzi* in honour of my beloved father, Heinz Dubitzky, to whom I am forever grateful for his wonderful support of me and my studies, as well as for inspiring my interests in biology and the beauty of nature, in general.

Distribution. *T. heinzi* sp. n. is currently known only from the surroundings of the medium altitude TESRI station near Tengchi (Kaohsiung Hsien), Meifeng (Nantou Hsien) and Taipingshan (Ilan Hsien). The seasonal/altitudinal distribution of this species is illustrated in Fig. 32.

Biology. The males of *T. heinzi* sp. n. collected by the author were exclusively found at flowers of *Torenia concolor* in close association with *Habropoda christineae* sp. n.. The fact that this was the only species of *Habropoda* and *Tetralonioidella* each, which was found by the author at the same time and the same locality undoubtedly indicates a host-cleptoparasite relationship of these two species. This is also supported by the convergent seasonal and altitudinal distribution pattern (Figs 31, 32) of both species.

Type material. Holotype, ♂ (NCHUT), Central Taiwan (Republic of China, ROC), Tengchi, near Taiwan Endemic Species Research Institute (TESRI), ca. 1600 m, 23°07`N/120°47`E, 6.7.2000, leg. A. Dubitzky. Paratypes. 1 ♂ (CAD), same data as holotype; 2 ♂♂ (TARI), Central Taiwan, Meifeng, ca. 2150 m, Nantou Hsien, Malaise trap, VIII. 1984, leg. K.S. Lin

& K.C. Chou; 1 ♂, 1 ♀ (TARI), Northeast Taiwan, Taiheizan (=Taipingshan today), 30.VII.1935 (♂), 13.VIII.1935 (♀).

Species of uncertain status: *Tetralonioidella iridescens* (Friese, 1914)

Protomelissa iridescens Friese, 1914: 322. Type locality Takao (Kaoshiung today), Formosa.

The unique male type of this species could not be located in any museum or collection. Possibly, it is lost or destroyed (see also Lieftinck 1972, 1983). Presently, Friese's very short original description is the only available record for the existence of the species. Based on this original description, Lieftinck (1983) synonymized *T. iridescens* Friese with *T. hoozana* Strand. Both species were described in the same year (*T. hoozana*: IV/V. 1914, *T. iridescens*: VI. 1914), and neither author knew of the existence of the other species. Several morphological and ecological characters are very similar between the two, e.g. length and colouration of antenna. In both species the antenna reaches the tegulae; in *T. hoozana* the ventral side of antenna is yellowish to reddish brown, however, in *T. iridescens*, Friese (1914) merely stated "antenna reddish". In addition, the length of single ASs is quite similar between the species. The weak metallic shimmer of the T mentioned for *T. iridescens* by Friese (1914) is also typical of *T. hoozana*. This attribute was not remarked upon by Lieftinck (1983), possibly because of the dense metasomal pubescence of the male holotype of *T. hoozana* he studied. Additional material of this species, studied in the course of the present investigation, clearly shows a metallic gloss on the bare parts of T. Furthermore, both species were largely collected in September (*T. hoozana*: 30.VIII., IX; *T. iridescens*: IX) and in the lowlands of Taiwan (*T. hoozana:* Hoozan = Fengshan, Lienhuachih, 650 m; *T. iridescens*: Takao = Kaoshiung).

In contrast to *T. hoozana* Strand, *T. heinzi* sp. n. is clearly distinguishable from *T. iridescens* by several characters, e.g. the completely black antenna (as opposed to reddish in *T. iridescens*), and the lack of metallic shimmer on the tegulae (distinctly metallic in *T. iridenscens*). Additionally, the flight season of *T. heinzi* sp. n. is much earlier (beginning of July to middle of August), and it is found exclusively in medium to high altitude mountainous areas of Taiwan.

The characters listed above indicate that *T. iridescens* Friese might actually to be a synonym of *T. hoozana* Strand. The different shape of T 7 ("apically truncate" in *T. iridescens*; with distinct incision apically in *T. hoozana*), however, remains unclear and can only be clarified by rediscovery of the type of *T. iridescens* which therefore is treated here as species *incerte sedis*.

Host parasitoid coevolution based on seasonal and altitudinal distribution patterns

Seasonal and altitudinal distribution

An examination of the seasonal and altitudinal distribution patterns of *Habropoda* and *Tetralonioidella* species on Taiwan (Figs 31, 32) shows that the species of each genus are clearly separated from each other either by a disjunct distribution with regard to altitude or by different flight seasons. In this manner, sympatric species-pairs, such as *H. tainanicola*/ *H. bucconis* and *H. bucconis*/*H. christineae*, are seasonally separated, and species flying at the same time (*H. christineae/H. sinensis taiwana*) are isolated from each other by different altitudes (Fig. 31). Temporal and altitudinal forms of specialization ensure segregation of all *Habropoda* species from each other and therefore no real "sympatric" distribution can be observed. The Taiwanese species of *Habropoda* must be regarded as "allopatric" with regard to their seasonal and spatial separation.

Host-parasitoid relationships

Lieftinck (1972) reported *Habropoda* and *Elaphropoda* as the hosts of *Tetralonioidella* in Thailand, Malaysia, Sumatra and Java based on the close spatial correlation of the three genera. However, he was not able to provide details for the Taiwanese species. A comparison of the seasonal and altitudinal distribution patterns of *Habropoda* and *Tetralonioidella* on Taiwan (Figs 31, 32) leads to several conclusions.

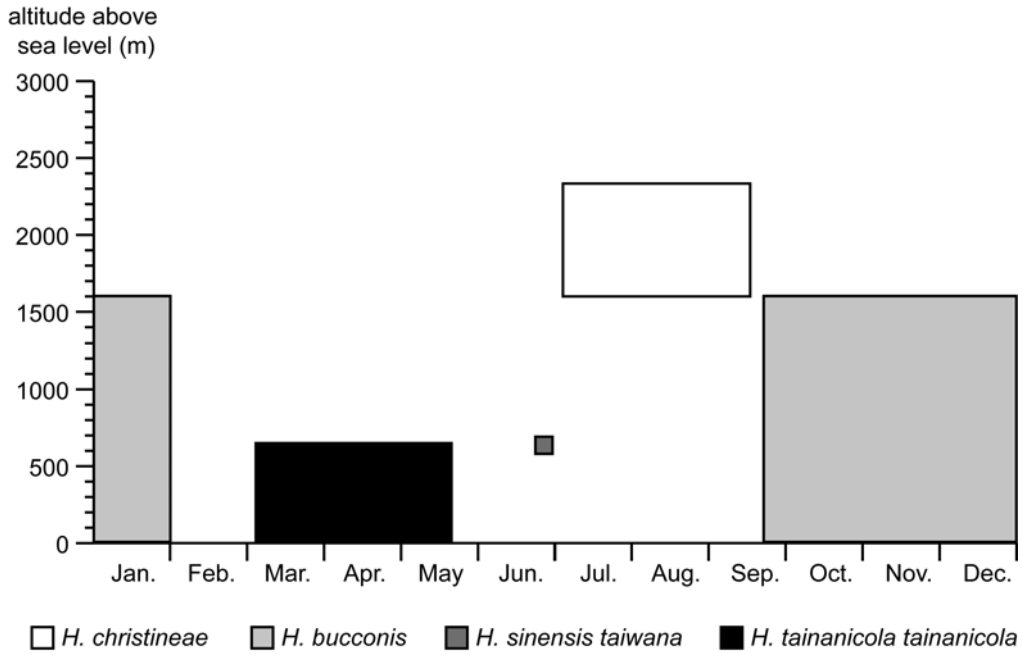

Fig. 31. Seasonal-altitudinal distribution pattern of *Habropoda* on Taiwan

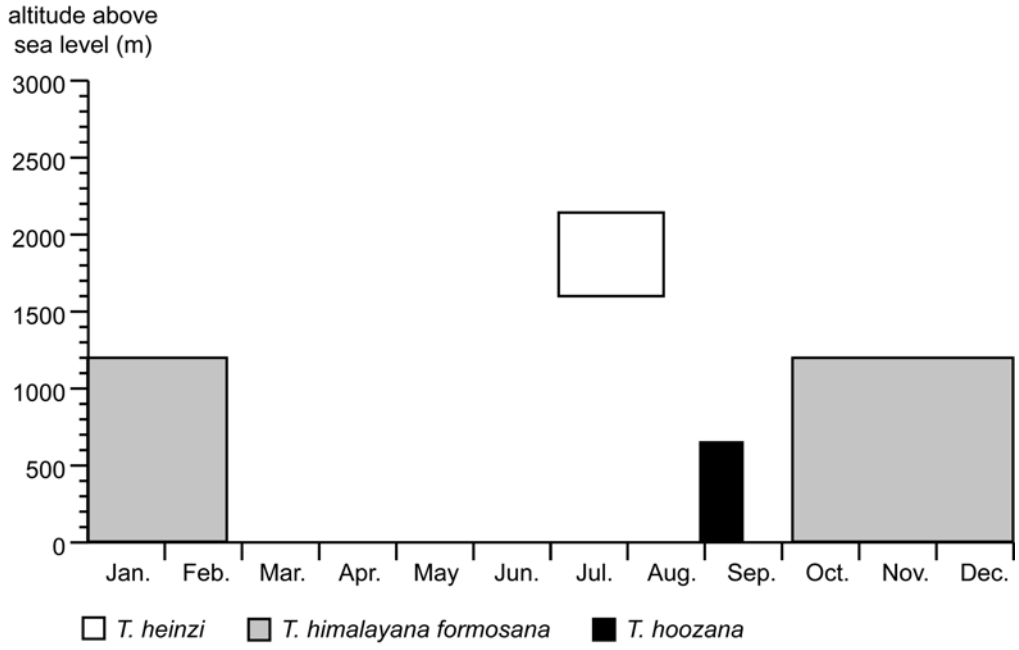

Fig. 32. Seasonal-altitudinal distribution pattern of *Tetralonioidella* on Taiwan

First, the distribution of *T. heinzi* is clearly correlated with that of *H. christineae*, which suggests a host-parasitoid relationship between the two taxa (see also comments on *T. heinzi*). Second, *T. himalayana formosana* and *H. bucconis* show partial congruence in their distribution, so that a host-parasitoid relationship between them is likely. Third, *T. hoozana* appears to be isolated without any apparent corresponding host-species of *Habropoda*. Fourth, *H. tainanicola tainanicola* and *H. sinensis taiwana* show no distinct association to any species of *Tetralonioidella*. Likewise, the distribution data for *Elaphropoda taiwanica* (Taipei, 17.VI.) (Wu, 2000) cannot be brought into line with any species of *Tetralonioidella*. Therefore, the host of *T. hoozana* and the parasitoides of *H. tainanicola tainanicola* and *H. sinensis taiwana* remain unknown.

The highly specialized seasonal and altitudinal distribution patterns of *Habropoda* species on Taiwan may be an important factor for the occurrence of the numerous species of *Tetralonioidella* on the island, since parasitoides, if they are to survive, must become specialized in ways similar to their hosts.

Fig. 33. Habitus of Anthophorini. **A, B:** Male **(A)** and female **(B)** of *Anthophora (Anthophora) plumipes.* **C:** Male of *Anthophora (Dasymegilla) quadrimaculata.* **D:** Sleeping aggregation of male *Amegilla (Glossamegilla) urens.* **F:** Close-up of sleeping male of *Amegilla (Glossamegilla) urens.*

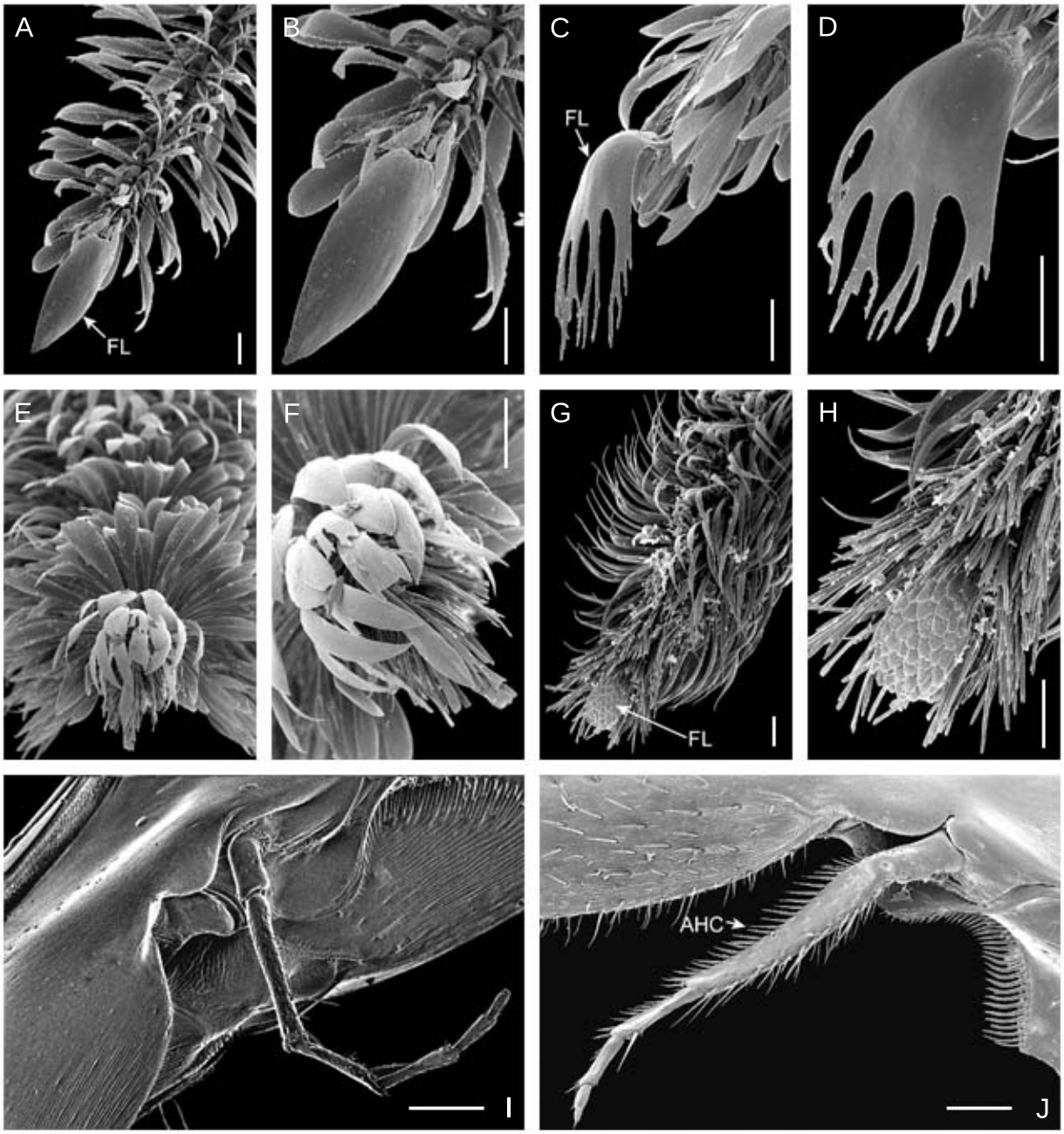

Fig. 34. Apical part of glossa **(A-H)** and PMX **(I, J)** of female Anthophorini. **A, B:** *Anthophora plumipes.* **C, D, J:** *Amegilla quadrifasciata.* **E, F:** *Habropoda tarsata.* **G, H:** *Pachymelus radovae.* **I:** *Habropoda tainanicola*. **B, D, H:** Close-up of ventral side of flabellum. AHC: comb-like hair fringe along anterior margin of PMX 2, FL: flabellum. Scale bars: 200 µm (I, K), 50 µm (A-H).

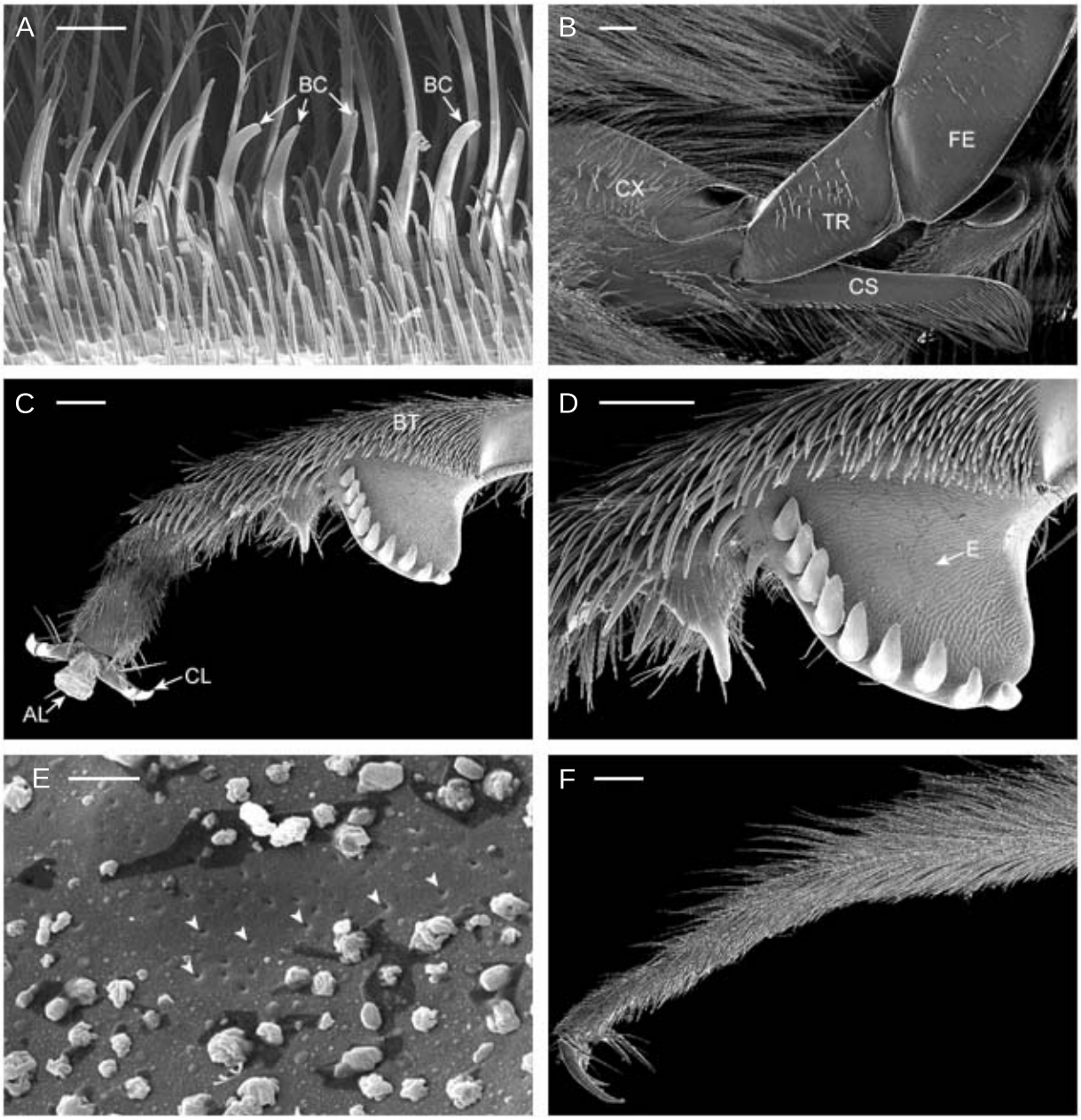

Fig. 35. Structures of legs of Anthophorini, part 1. **A:** Bristles on ventral side of forecoxa of female *Amegilla (Amegilla) quadrifasciata.* **B:** Basal parts of foreleg of male *Habropoda (Habropoda) tarsata* with thorn- or spine-like projection of coxa. **C, D:** Foretarsus of male *Habropoda (Zonhabropoda) zonatula* with enlarged structure of basitarsus **(D). E:** Ventral surface of broadened basitarsus of male *Habropoda (Zonhabropoda) zonatula,* showing minute pores (indicated by white arrowheads). **F:** Tarsus of female of *Habropoda tainanicola tainanicola.* AL: arolium, BC: bristles of forecoxa, BT: basitarsus, CL: claw, CS: spinelike projection of coxa, CX: coxa, FE: femur, TR: trochanter. Scale bars: 250 µm (B, C, D, F), 50 µm (A), 2 µm (E).

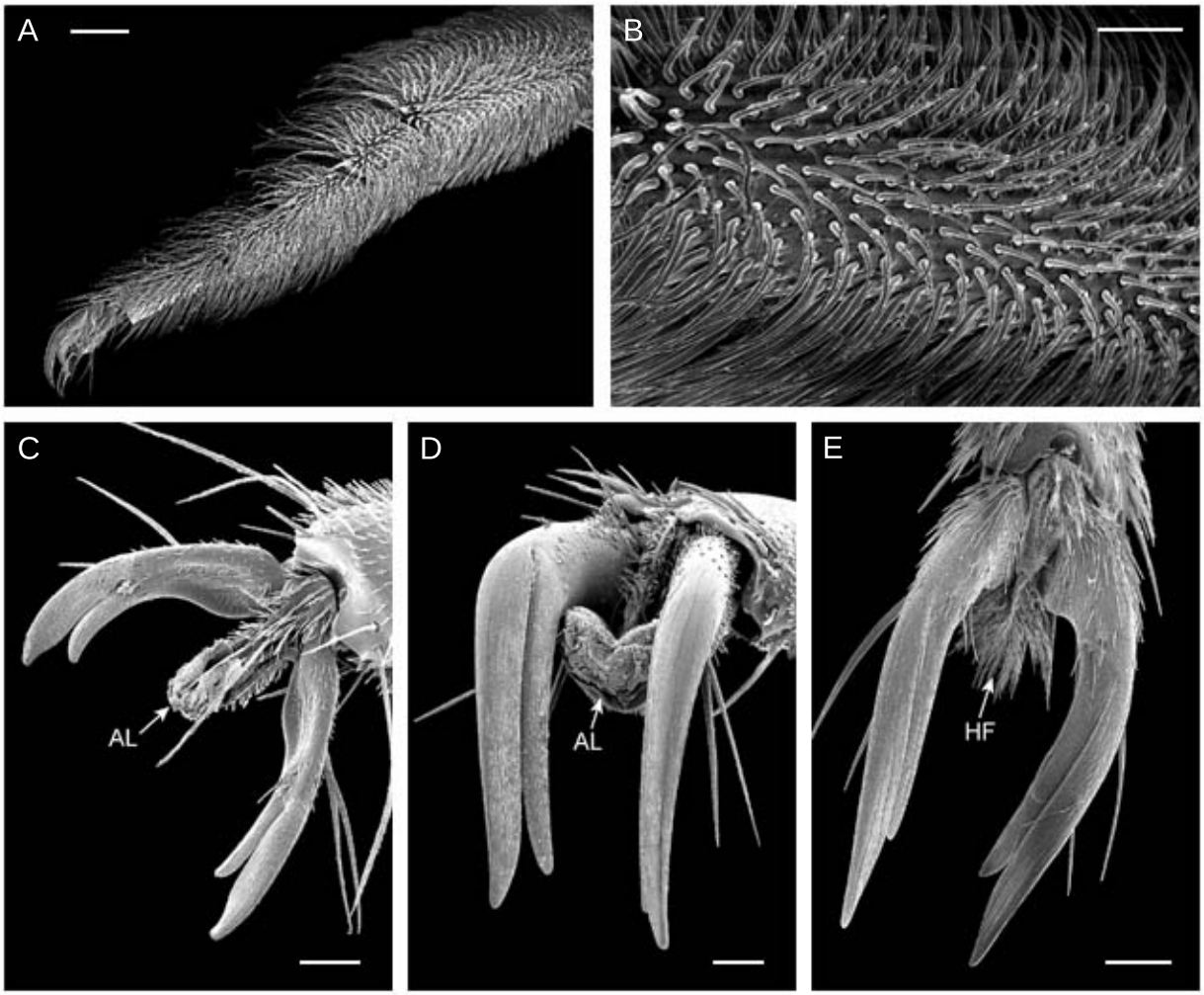

Fig. 36. Structures of legs of Anthophorini, part 2. **A:** Foretarsus of *Habropoda (Phyllohabropoda) christineae* with bottlebrush-like pubescence of apically hooked hairs. **B:** Close-up of ventral side of forebasitarsus of female *Habropoda (Phyllohabropoda) christineae,* showing apically bent hairs. **C-E:** female claws of *Anthophora (Anthophora) plumipes* **(C),** *Pachymelus (Pachymelus) hova* **(D)** and *Amegilla (Amegilla) quadrifasciata* **(E).** AL: arolium, HF: median hair fringe. Scale bars: 250 µm (A), 100 µm (B-E).

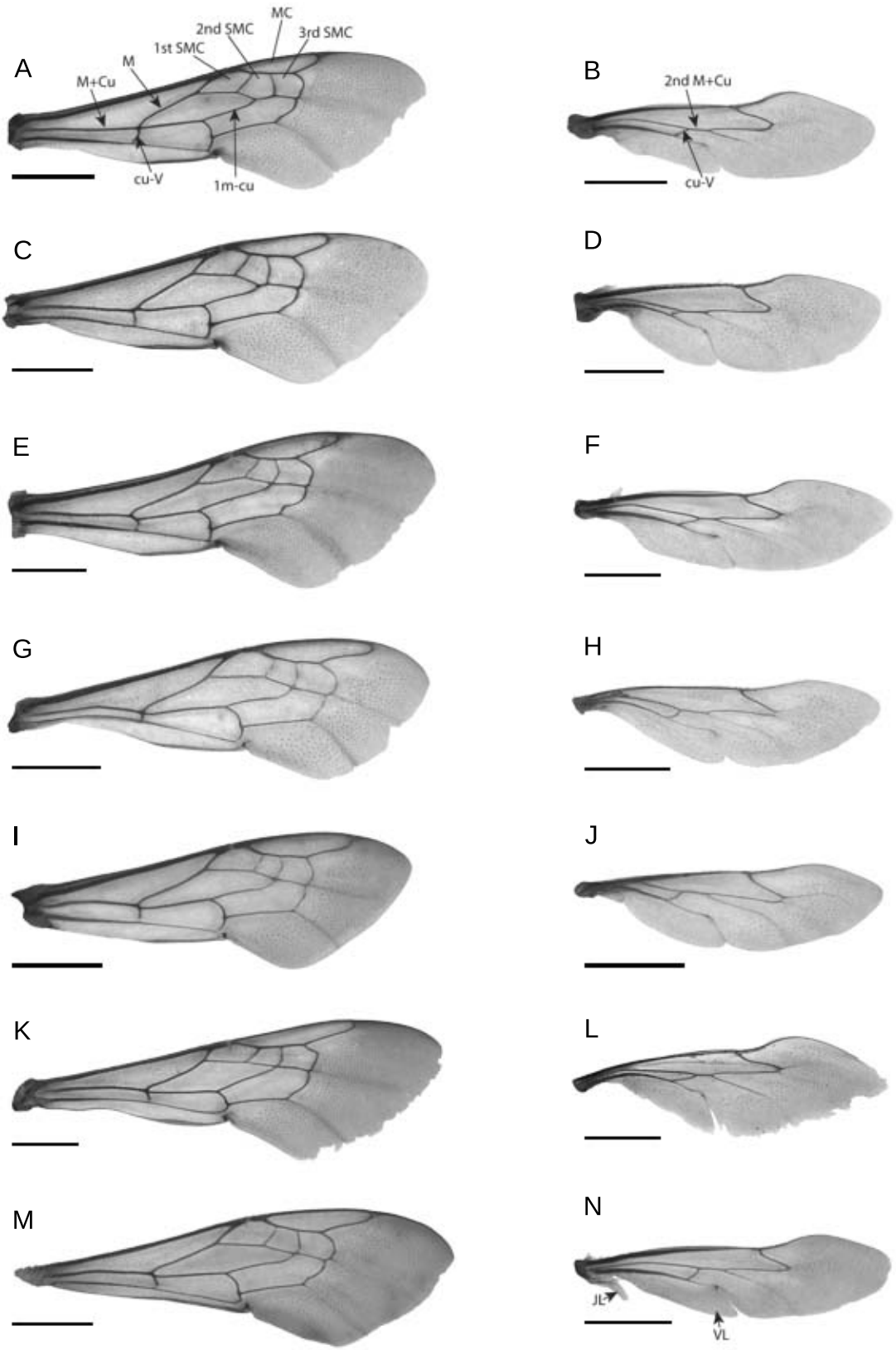

Fig. 37. Wings of Anthophorini. **A, C, E, G, I, K, M:** forewings; **B, D, F, H, J, L, N:** hindwings. **A, B:** *Anthophora (Anthophora) plumipes.* **C, D:** *Amegilla (Amegilla) quadrifasciata.* **E, F:** *Habropoda (Habropoda) tarsata.* **G, H:** *Elaphropoda moelleri.* **I, J:** *Habrophorula nubilipennis.* **K, L:** *Pachymelus (Pachymelus) radovae.* **M, N:** *Deltoptila elefas.* JL: jugal lobe MC: marginal cell, SMC: submarginal cell, VL: vanal lobe. Scale bars: 2 mm.

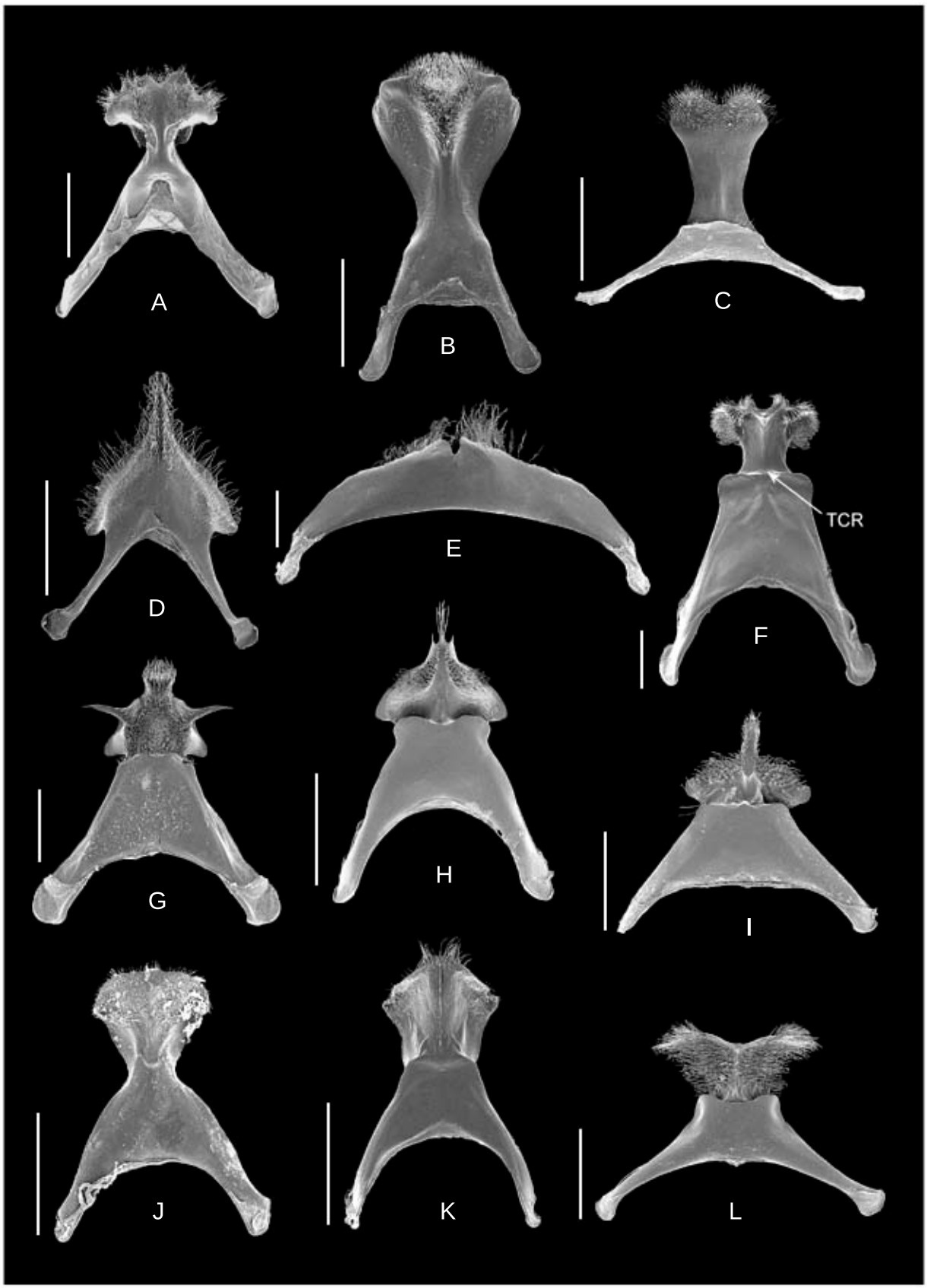

Fig. 38. S7 of male Anthophorini (ventral side): **A:** *Anthophora (Anthophora) plumipes.* **B:** *Amegilla (Amegilla) quadrifasciata.* **C:** *Deltoptila elefas.* **D:** *Elaphropoda moelleri.* **E:** *Pachymelus (Pachymelus) radovae.* **F:** *Habropoda (Habropoda) tarsata.* **G:** *Habropoda (Zonhabropoda) zonatula.* **H:** *Habropoda (Fulvohabropoda) bucconis.* **I:** *Habropoda (Oculhabropoda) mimetica.* **J:** *Habropoda (Phyllohabropoda) sinensis taiwana.* **K:** *Habropoda (Phyllohabropoda) christineae.* **L:** *Habropoda tainanicola tainanicola.*TCR: transverse collar-like ridge of S7. Scale bars: 500 µm.

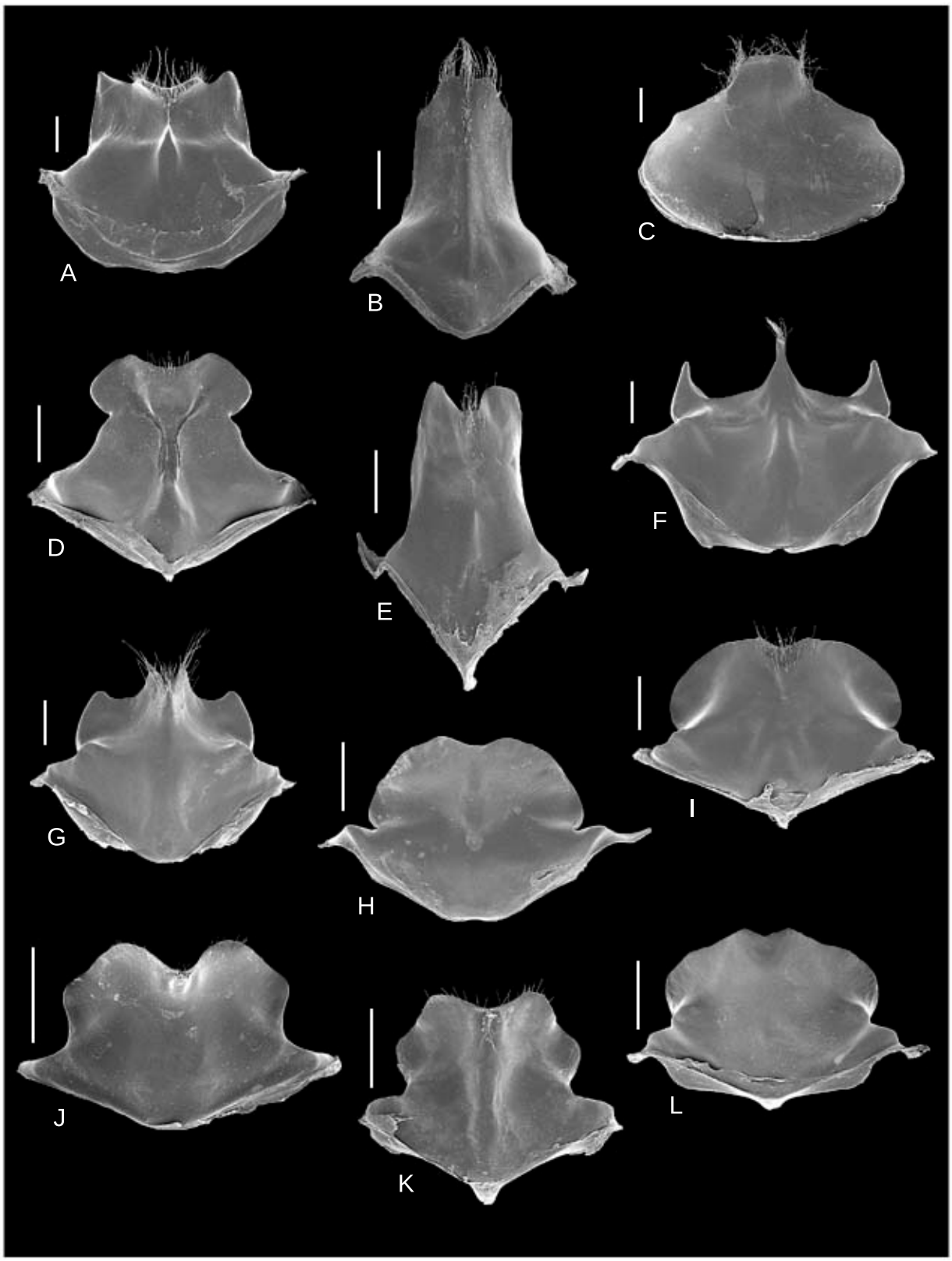

Fig. 39. S8 of male Anthophorini (ventral side): **A:** *Anthophora (Anthophora) plumipes.* **B:** *Amegilla (Amegilla) quadrifasciata.* **C:** *Pachymelus (Pachymelus) radovae.* **D:** *Deltoptila elefas.* **E:** *Elaphropoda moelleri.* **F:** *Habropoda (Habropoda) tarsata.* **G:** *Habropoda (Zonhabropoda) zonatula.* **H:** *Habropoda tainanicola tainanicola.* **I:** *Habropoda (Oculhabropoda) mimetica.* **J:** *Habropoda (Phyllohabropoda) sinensis taiwana.* **K:** *Habropoda (Phyllohabropoda) christineae.* **L:** *Habropoda (Fulvohabropoda) bucconis.* Scale bars: 250 µm.

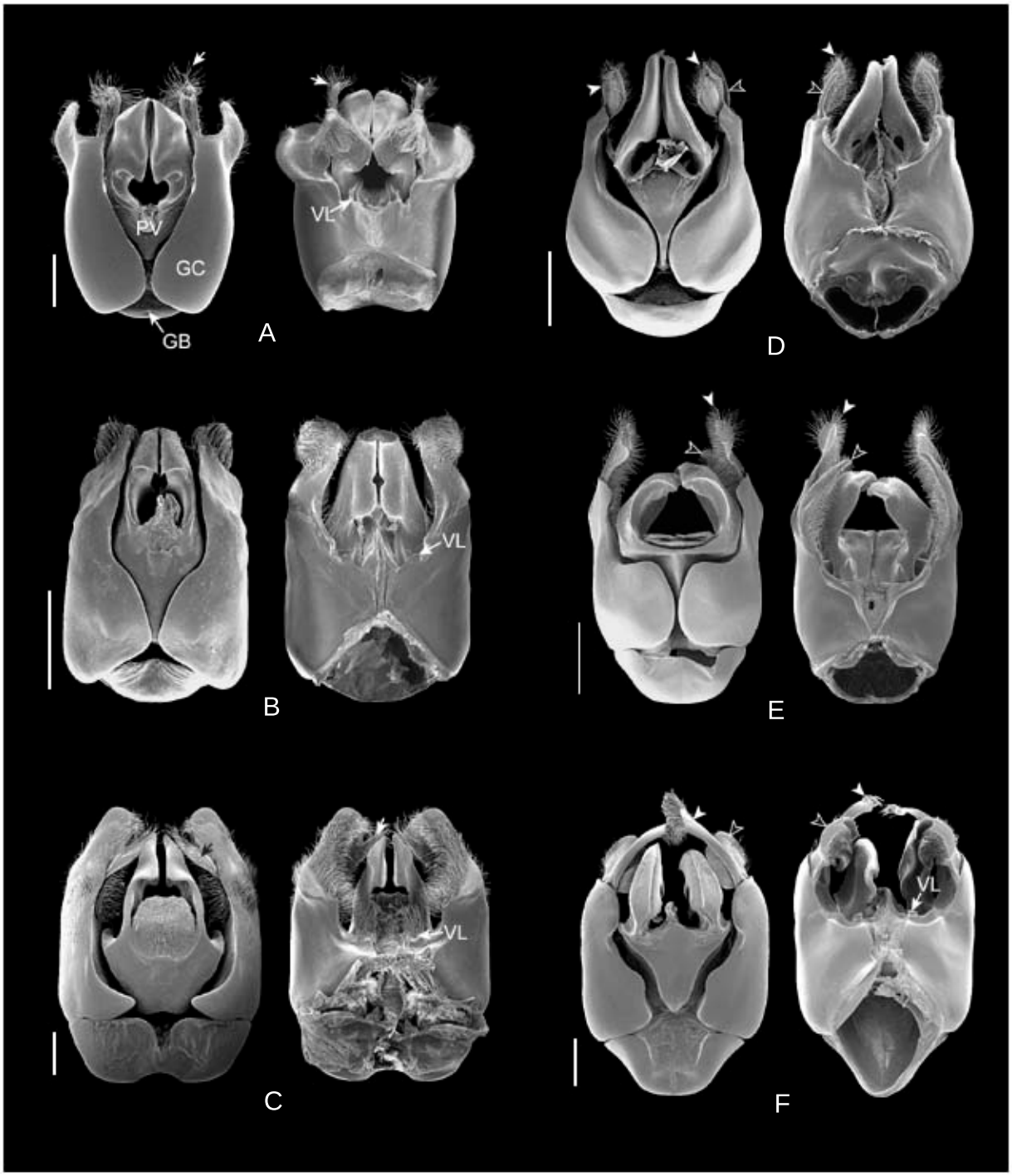

Fig. 40. Genitalia of male Anthophorini (left dorsal, right ventral view). **A:** *Anthophora (Anthophora) plumipes.* **B:** *Amegilla (Amegilla) quadrifasciata.* **C:** *Pachymelus (Pachymelus) radovae.* **D:** *Deltoptila elefas.* **E:** *Elaphropoda moelleri.* **F:** *Habropoda (Habropoda) tarsata.* GB: gonobase, GC: gonocoxite, PV: penis valve, VL: ventral lobe of gonocoxite. White arrows: simple gonostylus, white arrowheads: dorsal part of divided gonostylus, white rimmed arrowheads: ventral part of divided gonostylus. Scale bars: 500 µm.

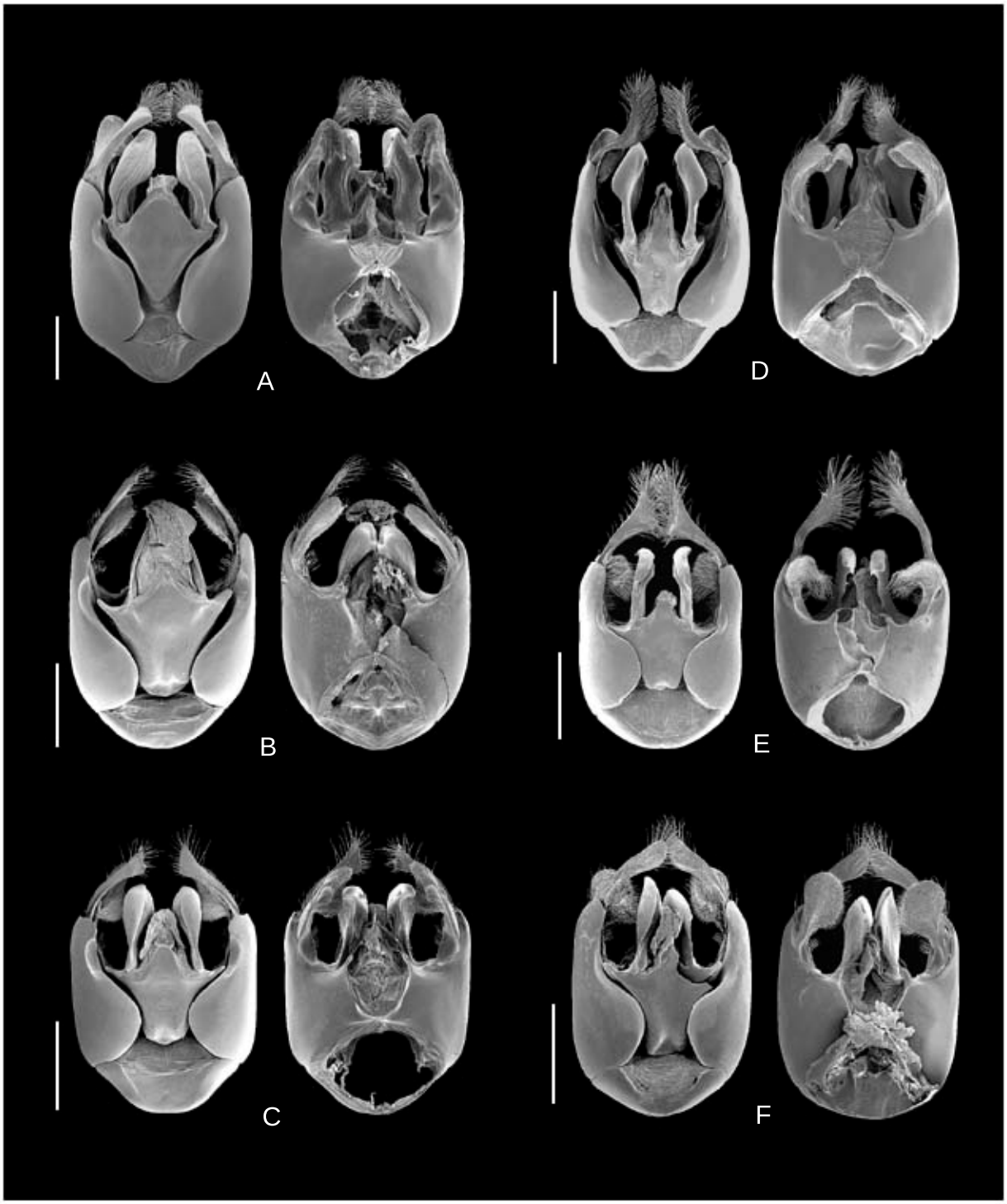

Fig. 41. Genitalia of male *Habropoda* (left dorsal, right ventral view). **A:** *Habropoda (Zonhabropoda) zonatula.* **B:** *Habropoda (Oculhabropoda) mimetica.* **C:** *Habropoda (Fulvohabropoda) bucconis.* **D:** *Habropoda tainanicola tainanicola.* **E:** *Habropoda (Phyllohabropoda) christineae.* **F:** *Habropoda (Phyllohabropoda) sinensis taiwana.* Scale bars: 500 µm.

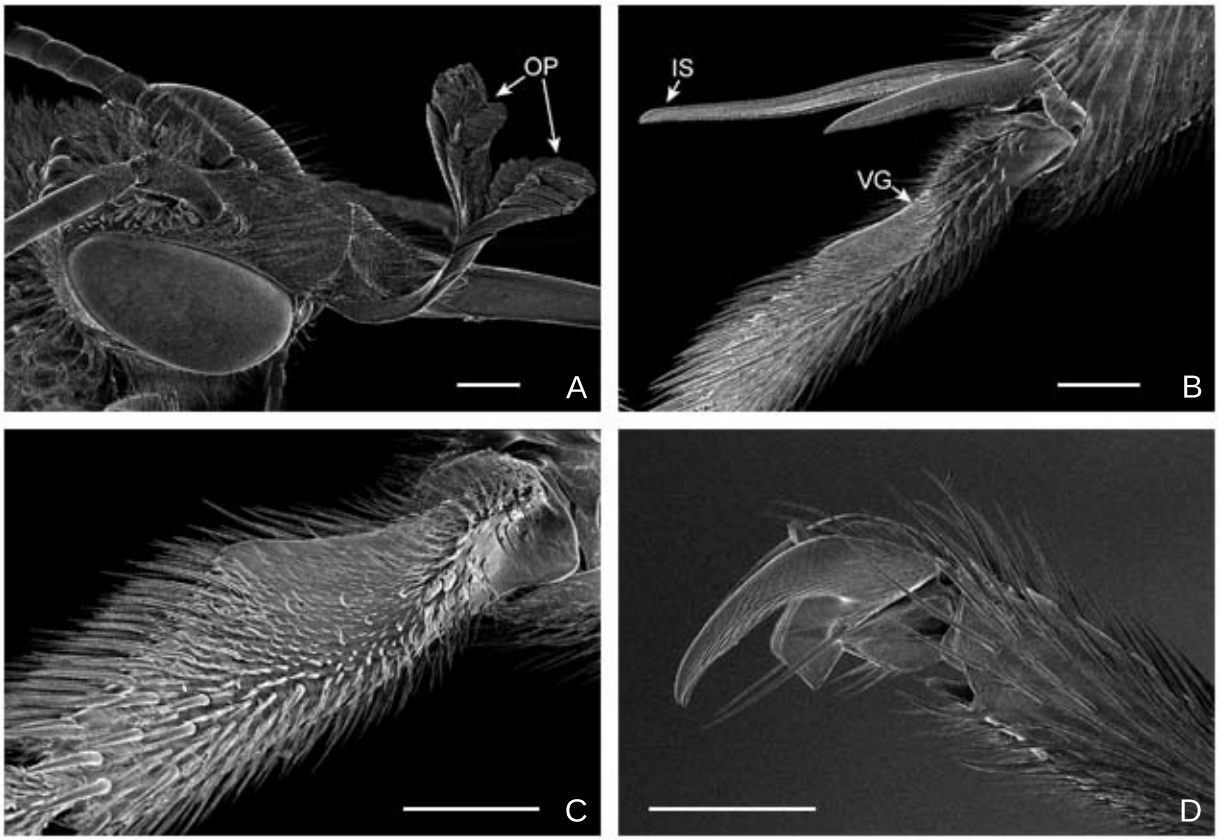

Fig. 42. Male of *Tetralonioidella heinzi.* **A:** Portrait with orchid pollinium. **B:** Spurs and basitarsus of hind leg. **C:** Ventral aspect of basitarsus of hind leg. **D:** Claws of hind leg. IS: inner spur of hind leg, OP: orchid pollinium, VG: ventral groove of hind basitarsus. Scale bars: 500 µm (A, B), 250 µm (C, D).

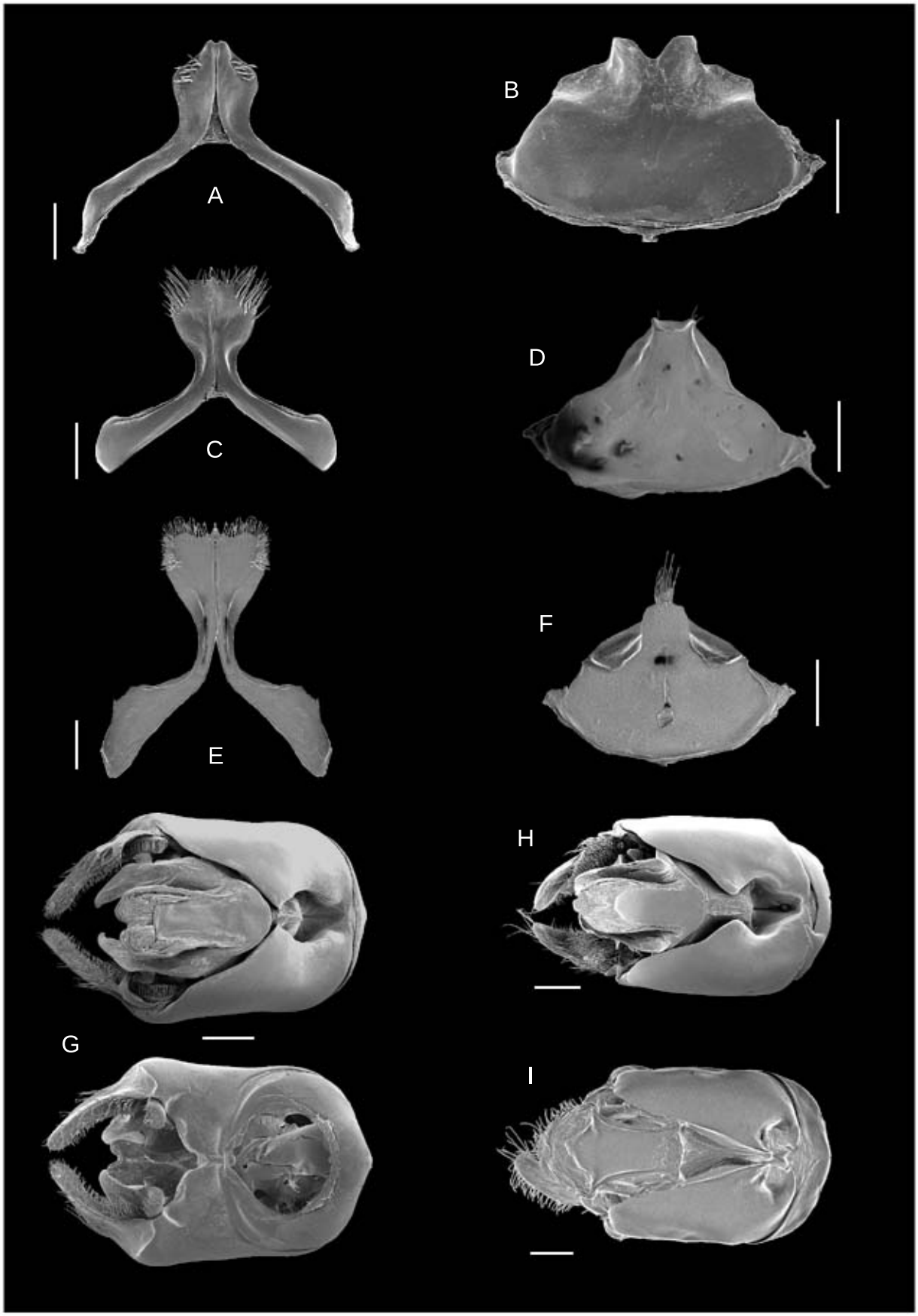

Fig. 43. Male S7, S8 and genitalia of *Tetralonioidella* of Taiwan. **A, C, E:** S7, ventral view. **B, D, F:** S8, ventral view. **G-I:** genitalia, dorsal view, except G below, showing ventral aspect. **A, B, G:** *Tetralonioidella heinzi.* **C, D, H:** *Tetralonioidella hoozana.* **E, F, I:** *Tetralonioidella himalayana formosana.* Scale bars: 250 µm.

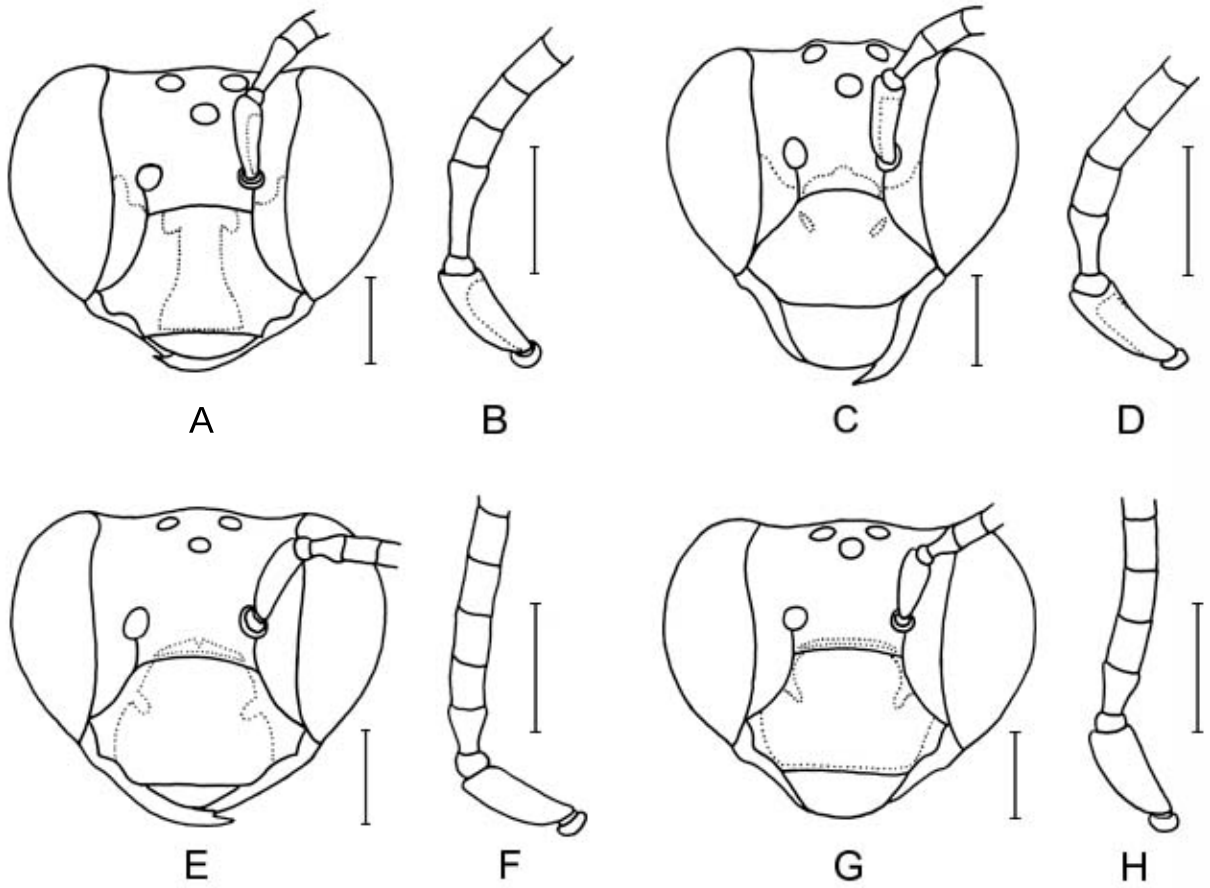

Fig. 44. Colour pattern of head (A, C, E, G) and basal AS (B, D, F, H) of male *Habropoda* of Taiwan. **A, B:** *Habropoda (Fulvohabropoda) bucconis.* **C, D:** *Habropoda tainanicola tainanicola.* **E, F:** *Habropoda (Phyllohabropoda) christineae.* **G, H:** *Habropoda (Phyllohabropoda) sinensis taiwana.* Dotted lines indicate yellow to ivory coloured areas (except on clypeus of *H. tainanicola* (C): dark maculations). Scale bars: 1 mm.

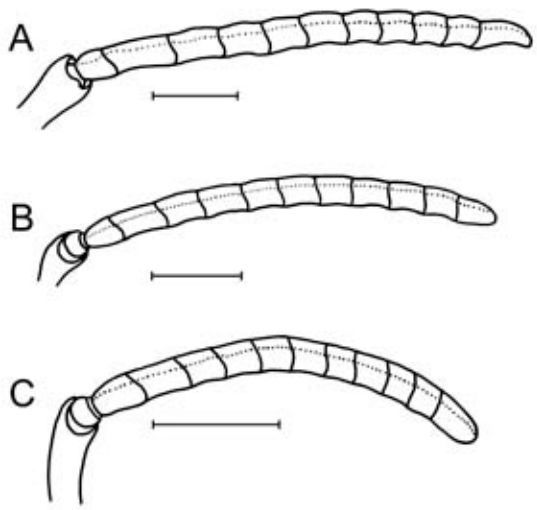

Fig. 45. Antenna of male *Tetralonioidella* of Taiwan. **A:** *Tetralonioidella himalayana formosana.* **B:** *Tetralonioidella heinzi.* **C:** *Tetralonioidella hoozana.* Scale bars: 1 mm.

5. Conclusions and outlook

The main goal of the present study was to provide the first comprehensive phylogenetic analysis for the entire genus of *Andrena* – the largest genus of bees – on the subgeneric level. Furthermore, a phylogenetic concept for the tribe Anthophorini and the genus *Habropoda* was elaborated.

Comparing the results of the cladistic analysis based on morphology of *Andrena* with those of the Anthophorini and *Habropoda,* it becomes clear that the successful use of morphological data in a cladistic analysis strongly depends on the particular group under study. Thus in the analyses of Anthophorini and *Habropoda* the morphological data set provided well supported results, however the results from the analysis of *Andrena* were less well supported. This may be due to two major reasons. First, an almost complete analysis of the genus *Andrena*, with nearly 100 described subgenera, would require an extraordinarily large data set. In addition, the larger a data set becomes, the higher is the probability of encountering homoplasy, which again results in a decrease of support. The second reason concerns the great difficulty of finding enough suitable morphological characters to apply within *Andrena*, a problem which was not present in *Habropoda*. *Andrena*, as indicated by its enormous number of species, represents a rather "young" genus, these often show only subtle morphological differences between the single subgenera. Thus due to their great similarity, many subgenera are only characterized by the distinct combination of different characters rather than by discrete autapomorphies as for the subgenera of *Habropoda*.

A similar situation, however, was observed in the molecular analysis of *Andrena*, where support for the resulting cladogram was rather low, due to the great degree of uninformative characters in the sequenced part of COI. Use of molecular data does not automatically guarantee results with a better level of support, so it seems to be most important to pay special attention to the selection of suitable DNA regions. Future molecular investigations of *Andrena* therefore should either concentrate on mitochondrial sequence data of other regions of COI, e.g. the region which was successfully used by Danforth (1999) in the analysis of the halictine genus *Lasioglossum*, or use sequence data of COII, which has proved well suited for good resolution in *Andrena* (Larkin, 2002). Also the use of nuclear molecular data, e.g. a region of the elongation factor 1-alpha (EF-1α) as used by Larkin (2002), yielded good resolution within *Andrena*.

The results of the present morphological cladistic analysis represent a search to reconstruct the phylogeny of *Andrena* on a worldwide basis which certainly cannot yet be regarded as attained. The present results rather may serve as a fundamental base for further morphological as well as for molecular analyses. The next step for future investigations would be to fill in the missing data in the morphological analysis by including representatives of the subgenera which were not available for study. Further primarily morphological studies should concentrate on discrete subgenera, mainly holarctic and palearctic ones, to examine their monophyly as well as their internal phylogenetic relationships since the present results

indicate a dubious monophyletic status for several subgenera (e.g. *Ptilandrena*, *Micrandrena*, *Larandrena*). Results of the present study could also provide helpful information for future analyses to select the most suitable outgroup. Another interesting aspect for future work would be a more extensive molecular analysis of *Andrena* including taxa represented in the present morphological study. This would enable a comparison of the results of the morphological analyses with those of the molecular based analysis. Also, a combination of morphological and molecular data may yield interesting results and should be the aim of future projects.

The present study indicates that several palearctic and holarctic subgenera are not monophyletic since they represent paraphyletic or even polyphyletic groups. The erection of three new subgenera in this study is deemed useful: *Calcarandrena* subgen. n., *Hamandrena* subgen. n. and *Platygalandrena* subgen. n. Likewise the introduction of subgenera to subdivide the genus *Habropoda* is justified based on the results of the present cladistic analysis. The objection against establishing additional subgenera as propagated by Mayr et al. (1991) because it burdens the literature with too many names, is not appropriate for bees. Already a high number of subgenera of bees exist, and the differences between the definitions of genus versus subgenus are not standardized and often depend on the subjective view of the specialist. Therefore in dealing with a large genus the question is not whether to recognize informal species-group names or subgenera (the former need not be nomenclatorical mentioned in literature) but whether to recognize subgenera or genera (Michener, 2000). Furthermore, species-group names have generally not been used for *Andrena* despite Dylewska's (1987) attempt to substitute species-group names for some palearctic subgenera. The use of species-group names in *Andrena* would cause considerable confusion when used along side with or instead of subgeneric names. An additional advantage of preferring subgenera is that they do not need to be cited in the literature since they represent optional parts of zoological nomenclature (Michener, 2000).

In addition to the phylogenetic aspects presented in this study, suggestions are formulated for future functional-morphological and behavioural investigations. For example, the function of the subgenal coronet of female *Andrena*, or of the condylar lamella on the female mandible. It is still not known if there is a functional connection between these structures. Future behavioural and ultrastructural investigations might provide answers to these questions. Other puzzling structures are the conspicuously broadened front tarsi in males of *Zonhabropoda* and the spine-like projections on the male front coxae of this subgenus and *Habropoda* s. str. These are most likely adaptations used during mating, since they strongly resemble structures found in several male *Megachile* bees and certain sphecoid wasps, of which the function is known (Wittmann & Blochtein, 1995). Future behavioural studies as well as ultrastructural investigations should provide valuable results concerning these questions.

The results of the present cladistic analyses, both morphological and molecular, whether strongly supported or not, clearly represent a hypothetic evolutionary scenario that is based on

the ideas of parsimony analysis. One should not forget that evolution certainly does not always follow the rules of parsimony which itself is but a theory. The results must be regarded for what they really are, namely a set of verifiable evolutionary hypotheses based on the ideas of parsimony for the particular taxa and characters (morphological or molecular) used.

6. Summary – Zusammenfassung

Summary

The present investigation focused on the phylogeny of the short-tongued bee genus *Andrena* as well as on the phylogeny of the long-tongued bee tribe Anthophorini, in particular the anthophorine genus *Habropoda*.

The holarctic bee genus *Andrena* (sandbees) with about 1,500 validly described species represents the largest genus of bees. The phylogeny of *Andrena* has been insufficiently studied, earlier investigations were restricted to few discrete subgenera or regional elements of *Andrena*, and did not engage the genus as a whole with all its subgenera. A cladistic analysis based on 162 morphological characters was carried out in the present study which included representatives of 84 of the 99 currently known subgenera of *Andrena*. The possible evolution of characters with respect to the used character polarity was discussed. Altogether 107 taxa were sampled, five of which were representatives from other Andreninae. A hypothetical ancestor was used as outgroup due to the unclear phylogenetic relationships within the Andreninae.

An unweighted heuristic analysis resulted in six most parsimonious trees (MPTs) of 1875 steps. Seven major clades of *Andrena* were recognized in the strict consensus tree. The monophyly of *Andrena* was confirmed by five non-homoplasius apomorphies. *Cubiandrena* was not a part of *Andrena* and it is regarded as separate genus. A second analysis using successive character reweighting (*a posteriori* weighting) resulted in a single cladogram which agrees in some aspects with the results of the heuristic search but also shows clear differences in tree topology. In both analyses 14 groups combined the same taxa, 11 of which had identical tree topologies. *Andrena* was found in both analyses to be one of the most derived taxa of the Andreninae, and *Euherbstia* the most ancestral. The holarctic subgenera *Larandrena*, *Micrandrena* and *Ptilandrena* were each polyphyletic in unweighted and the weighted analyses.

The New World is regarded as the place of origin of the Andreninae, however according to the present study *Andrena* appears to have originated in the Old World, presumably in the Mediterranean region or Central Asia, since most basal subgenera of *Andrena* are strictly palearctic. The holarctic distribution of *Andrena* probably is based on dispersal events which occurred during the late Cretaceous and early Tertiary, while the development of subgenera restricted either to the palearctic or nearctic regions may be based on vicariance events caused by the expansion of the Atlantic ocean and the separation of North American and Eurasian landmasses from the middle Eocene onward.

This study also included a molecular study analysing a 758 base pair DNA fragment obtained from the mitochondrial cytochrome oxidase I (COI) in 27 Central European species

of *Andrena*. The species sampled represent 21 different subgenera as well as seven members of the subgenus *Micrandrena*. *Panurgus* was sampled as the outgroup. The parsimony analysis of the equally weighted COI data resulted in a single MPT of 1724 steps. Five major lineages of *Andrena* were recognized in the cladogram. The subgenus *Micrandrena*, a main focus of this analysis, was clearly polyphyletic.

The following taxa belonging to the genus Andrena were described as new for science: *Calcarandrena* **subgen. n.**, *Hamandrena* **subgen. n.**, *Platygalandrena* **subgen. n.**; *A. (Carandrena) planti* **sp. n.**, *A. (Euandrena) yangi* **sp. n.**, *A. (Habromelissa) nantouensis* **sp. n.**, *A. (Larandrena) susanneae* **sp. n.**, *A. (Leucandrena) cheni* **sp. n.**, *A. (Micrandrena) taiwanensis* Dubitzky 2002, *A. (Pallandrena) christineae* **sp. n.**, *A. (Pallandrena) scheuchli* **sp. n.**, *A. (Simandrena) heinzi* **sp. n.** and *A. lehmanni* Schönitzer & Dubitzky 2002. The following two taxa were raised to specific rank: *A. eburnea* Warncke, 1975 **stat. n.** and *A. impasta* Warncke, 1975 **stat. n.** The following subgenus was raised to generic rank: *Cubiandrena* Warncke, 1968 **stat. n.**

In another part of this study the phylogenetic relationships of the Anthophorini were investigated. This is one of the largest tribes of medium to large-sized, nest-building bees of the subfamily Apinae, and it comprises about 710 species placed into seven genera. The cladistic analysis of Anthophorini was based on 51 morphological characters and included 26 ingroup taxa, representing all known genera and the most important subgenera of the tribe. *Centris* was used as the outgroup. The analysis obtained two MPTs of 132 steps, yielding the following tree topology at the generic level: ((*Habrophorula*, *Elaphropoda*) (*Habropoda* (*Deltoptila* (*Pachymelus* (*Amegilla*, *Anthophora*))))). A second tribe, Habropodini, as postulated by some authors, was not recognized since it would represent a paraphyletic taxon. The monophyly of the Anthophorini and each of its genera was confirmed. Based on the present cladistic results and the biogeographic data of Anthophorini the following evolutionary scenario was postulated in which all genera of Anthophorini probably evolved at the time in the late Cretaceous, except *Amegilla* and *Anthophora*, which might have been originated in Oligocene. The northern part of Southeast Asia (India to Southeast China) is regarded as the most probable place of origin and radiation of Anthophorini since most of its genera as well as the most basal lineages of the tribe occur in this region. The New World was probably colonized three times independently by *Habropoda* (upper Cretaceous to Tertiary), by the ancestral lineage of *Deltoptila* (upper Cretaceous to Tertiary) and by *Anthophora* (Tertiary to Quaternary). The present distribution of *Deltoptila* and *Pachymelus* indicates that the evolution of these genera may be based on vicariance events, while the distribution of all other genera seems to be based on simple dispersal processes, such as expansion (*Habropoda, Anthophora, Amegilla*) or isolation (*Elaphropoda, Habrophorula*) due to ecological or abiotic (climatic) factors.

Finally, the genus *Habropoda* was subjected to a phylogenetic analysis. This genus includes about 60 species in the New and Old Worlds. A cladistic analysis using 25 palearctic

and oriental species of *Habropoda,* reflecting all major lineages of this genus, was conducted based on 41 morphological characters. Three MPTs trees resulted each of 96 steps. The strict consensus tree revealed the following topology: (*Fulvohabropoda* ((*Oculhabropoda, Phyllohabropoda)* (*Zonhabropoda, Habropoda s. str.*))). The main lineages of *Habropoda* probably evolved in upper Cretaceous in South East Asia. The origin of the Himalayan mountain range in Eocene may have caused a separation of *Habropoda* into a palearctic (*Habropoda* s. str., *Zonhabropoda*) and an oriental lineage (remaining subgenera and isolated species) as well as the initial stages of radiation processes occurring in *Fulvohabropoda.* That *Zonhabropoda* inhabits East Asia seems to be secondary and caused by recent dispersal events along the Asian steppes north of the Himalayas. Climatic adaptations during its separation probably prevented *Zonhabropoda* from reaching the origin place of *Habropoda.*

The Taiwanese species of *Habropoda* and the corresponding cleptoparasite *Tetralonioidella* are revised and the coevolution between the species of these two genera is discussed in consideration of their seasonal and altitudinal distribution patterns.

The following taxa of *Habropoda* and *Tetralonioidella* were described as new for science: *Fulvohabropoda* **subgen. n.**, *Oculhabropoda* **subgen. n.**, *Phyllohabropoda* **subgen. n.**, *Zonhabropoda* **subgen. n.**; *Habropoda (Phyllohabropoda) christineae* **sp. n.**, *Habropoda (Phyllohabropoda) sinensis taiwana* **ssp. n.** and *Tetralonioidella heinzi* **sp. n.**. *Tetralonioidella himalayana formosana* **stat. n.** was transferred to subspecific rank and a lectotype for *Habropoda tainanicola tainanicola* Strand, 1913 was designated.

Zusammenfassung

In der vorliegenden Arbeit wurde die Phylogenie der kurzzungigen Bienengattung *Andrena,* sowie die der langzungigen Bienentribus Anthophorini unter besonderer Berücksichtigung der Gattung *Habropoda* untersucht.

Mit ca. 1500 gültig beschriebenen Arten weltweit stellt die holarktische Bienengattung *Andrena* (Sandbienen) die größte Bienengattung überhaupt dar. Die Phylogenie dieser Gattung ist bislang nur unzureichend erforscht worden. So beschränkten sich frühere Untersuchungen nur auf einige wenige Untergattungen oder bestimmte regionale Vertreter von *Andrena,* aber berücksichtigten niemals die gesamte Gattung und all ihre verschiedenen Untergattungen. Im Rahmen dieser Untersuchung, welche 84 Vertreter der 99 gegenwärtig bekannten *Andrena*-Untergattungen einschließt, wurde eine kladistische Analyse, basierend auf 162 morphologischen Merkmalen durchgeführt. Eine mögliche Merkmalsentwicklung im Hinblick auf die verwendete Polarität wurde diskutiert. Insgesamt wurden 107 Taxa kodiert, von denen fünf je einen Verterter aller anderen Gattungen der Unterfamilie Andreninae representierten. Aufgrund der ebenfalls ungeklärten Verwandschaftsverhältnisse innerhalb der Andreninae wurde ein hypothetischer Vorfahre als Außengruppe verwendet.

Eine heuristische Analyse ohne Merkmalsgewichtung ergab insgesamt sechs maximal sparsame Kladogramme (MPTs) mit einer Länge von 1875 Schritten. Das strikte Konsensus-Kladogramm dieser sechs Bäume ließ sieben Großgruppen innerhalb der Gattung *Andrena* erkennen. Die Monophylie von *Andrena* wurde durch fünf, nicht-homoplastische Synapomorphien begründet. *Cubiandrena* stellte sich als nicht zu *Andrena* gehörig heraus und wird als eigene Gattung betrachtet. Eine zweite Analyse unter Verwendung iterativer Mermalsgewichtung (*a posteriori* Gewichtung) resultierte in einem einzigen Kladogramm. Dieses stimmte in einigen Teilen mit den Ergebnissen der ungewichteten Analyse überein, zeigte aber auch deutliche Unterschiede zu diesen. In beiden Analysen wurden 14 Gruppen festgestellt, die die gleichen Taxa zusammenfassten, elf davon wiesen eine identische Topologie auf. In beiden Analysen erwies sich *Andrena* als die am stärksten abgeleitete Gattung innerhalb der Andreninae, während *Euherbstia* den ursprünglichsten Vertreter darstellte. Die holarktisch verbreiteten Untergattungen *Larandrena, Micrandrena* und *Ptilandrena* erwiesen sich sowohl in der ungewichteten als auch in der gewichteten Analyse als polyphyletische Taxa.

Amerika wird als Ursprungsort der Andreninae angesehen, während die Gattung *Andrena*, wahrscheinlich altweltlichen Ursprungs (Mittelmeergebiet oder Zentralasien) ist, da die meisten ursprünglichen Untergattungen eine ausschließlich paläarktische Verbreitung aufweisen. Während sich die holarktische Verbreitung von *Andrena* wahrscheinlich auf Ausbreitungsvorgänge am Ende der Kreidezeit und im frühen Tertiär zurückführen läßt, scheint die Entstehung rein nearktischer und paläarktischer Untergattungen auf Vikarianzereignissen, verursacht durch die beginnende Ausdehnung des Atlantiks und die damit einhergehende Trennung der nordamerikanischen und europäischen Landmassen seit dem mittleren Eozän, zu beruhen.

Die vorliegende Studie beinhaltet außerdem eine molekulare Analyse eines 758 basenpaarlangen DNA Abschnittes der mitochondrialen Cytochrom Oxidase I für 27 zentraleuropäische *Andrena*-Arten. Die untersuchten Arten repräsentieren 21 verschiedene Untergattungen, sowie sieben Vertreter der Untergattung *Micrandrena*. Als Außengruppe wurde *Panurgus* verwendet. Die Parsimonie-Analyse der ungewichteten COI-Daten ergab ein einzelnes MPT mit einer Länge von 1724 Schritten, in welchem fünf Großgruppen unterschieden wurden. Die Untergattung *Micrandrena*, welche einen Schwerpunkt der Analyse bildete, erwies sich als eindeutig polyphyletisch.

Folgende Taxa der Gattung Andrena wurden als neu für die Wissenschaft beschrieben: *Calcarandrena* **subgen. n.**, *Hamandrena* **subgen. n.**, *Platygalandrena* **subgen. n.**; *A. (Carandrena) planti* **sp. n.**, *A. (Euandrena) yangi* **sp. n.**, *A. (Habromelissa) nantouensis* **sp. n.**, *A. (Larandrena) susanneae* **sp. n.**, *A. (Leucandrena) cheni* **sp. n.**, *A. (Micrandrena) taiwanensis* Dubitzky 2002, *A. (Pallandrena) christineae* **sp. n.**, *A. (Pallandrena) scheuchli* **sp. n.**, *A. (Simandrena) heinzi* **sp. n.** and *A. lehmanni* Schönitzer & Dubitzky 2002. Die folgenden zwei Taxa wurden in den Status einer Art erhoben: *A. eburnea* Warncke, 1975

stat. n. and *A. impasta* Warncke, 1975 **stat. n.** Die folgende Untergattung wurde zur Gattung erhoben: *Cubiandrena* Warncke, 1968 **stat. n.**

Im zweiten Teil dieser Arbeit wurde die Phylogenie der Anthophorini untersucht. Die Anthophorini stellen eine der größten Triben von mittelgroßen bis großen, nestbauenden Bienen der Unterfamilie Apinae dar, und umfassen etwa 710 Arten aus sieben Gattungen. Die kladistische Analyse der Anthophorini basierte auf 51 morphologischen Merkmalen und umfasste 26 Innengruppen-Taxa, welche alle bekannten Gattungen und die wichtigsten Untergattungen der Tribus repräsentierten. Als Außengruppe wurde *Centris* verwendet. Die Analyse resultierte in zwei MPTs mit einer Länge von 132 Schritten. Die folgende Baumtopologie auf Gattungsebene konnte festgestellt werden: ((*Habrophorula*, *Elaphropoda*) (*Habropoda* (*Deltoptila* (*Pachymelus* (*Amegilla*, *Anthophora*))))). Eine zweite, von manchen Autoren vertretene Tribus, die Habropodini, konnte nicht bestätigt werden, da diese ein paraphyletisches Taxon bildet. Die Monophylie der Anthophorini sowie all ihrer Gattungen wurde bestätigt. Basierend auf den Ergebnissen der kladistischen Analyse und den biogeographischen Daten der Anthophorini wurde eine mögliche Hypothese zur Evolution der Anthophorini entwickelt. Demnach entwickelten sich alle Anthophorini-Gattungen, abgesehen von *Anthophora* und *Amegilla*, die frühestens im Oligozän entstanden sein dürften, wahrscheinlich bereits in der späten Kreidezeit. Der nördliche Teil Südostasiens (Indien bis Südost China) kann als wahrscheinlichster Ursprungsort und als Radiationszentrum der Anthophorini angesehen werden, da in dieser Region die meisten Gattungen sowie die ursprünglichsten Vertreter dieser Tribus vorkommen. Amerika wurde wahrscheinlich dreimal unabhängig von Vertretern der Anthophorini besiedelt: Von *Habropoda* (Obere Kreide bis Tertiär), von einem *Deltoptila*-ähnlichen Vorfahren (Obere Kreide bis Tertiär) und von *Anthophora* (Tertiär bis Quartär). Die rezente Verbreitung von *Deltoptila* und *Pachymelus* impliziert, daß die Evolution dieser Gattungen höchstwahrscheinlich auf Vikarianzereignisse zurückzuführen ist, während die Verbreitung aller anderen Gattungen auf einfachen verbreitungsdynamischen Prozessen wie Ausbreitung (*Habropoda*, *Anthophora*, *Amegilla*) oder Isolation (*Elaphropoda*, *Habrophorula*) aufgrund ökologischer oder abiotischer (klimatischer) Faktoren beruhen dürfte.

Darüber hinaus wurde die Phylogenie der Gattung *Habropoda*, welche weltweit etwa 60 Arten umfasst, näher untersucht. Eine durchgeführte kladistische Analyse 25 paläarktischer und orientalischer *Habropoda*-Arten, welche alle wichtigen altweltlichen Gruppen dieser Gattung repräsentieren, basierte auf 41 morphologischen Merkmalen und ergab 3 MPTs mit einer Länge von 96 Schritten. Basierend auf dem Konsensus-Baum ergab sich folgende Baumtopologie auf Untergattungsebene: (*Fulvohabropoda* ((*Oculhabropoda, Phyllohabropoda)* (*Zonhabropoda*, *Habropoda s. str.*))). Wahrscheinlich entwickelten sich die Hauptlinien von *Habropoda* bereits in der Oberen Kreide im nördlichen Teil Südostasiens. Die beginnende Auffaltung des Himalayas im Eozän hat dann möglicherweise eine Trennung der Gattung in eine paläarktische (*Habropoda* s. str., *Zonhabropoda*) und eine

orientalische (alle anderen Untergattungen sowie isoliert stehende Arten) Entwicklungslinie bewirkt und wahrscheinlich eine verstärkte Radiation innerhalb der Untergattung *Fulvohabropoda* ausgelöst. Das Vorkommen von *Zonhabropoda* in Ostasien scheint sekundär zu sein und ist höchstwahrscheinlich auf jüngere Ausbreitungsprozesse entlang der asiatischen Steppen nördlich des Himalayas zurückzuführen. Während der Isolation entstandene klimatische Anpassungen verhinderten möglicherweise die Ausbreitung von *Zonhabropoda* in Richtung Südostasien.

Im Rahmen einer Revision der taiwanesischen *Habropoda*-Arten und ihrer parasitoiden Kuckucksbienen aus der Gattung *Tetralonioidella* wurde außerdem die Koevolution zwischen den Vertretern dieser beiden Bienengattungen anhand ihrer jahreszeitlichen und höhenabhängigen Verbreitungsmuster untersucht.

Die folgenden Taxa aus den Gattungen *Habropoda* und *Tetralonioidella* wurden als neu für die Wissenschaft beschrieben: *Fulvohabropoda* **subgen. n.**, *Oculhabropoda* **subgen. n.**, *Phyllohabropoda* **subgen. n.**, *Zonhabropoda* **subgen. n.**; *Habropoda (Phyllohabropoda) christineae* **sp. n.**, *Habropoda (Phyllohabropoda) sinensis taiwana* **ssp. n.** and *Tetralonioidella heinzi* **sp. n.**. *Tetralonioidella himalayana formosana* **stat. n.** wurde in den Rang einer Unterart gestuft und für *Habropoda tainanicola tainanicola* Strand, 1913 wurde ein Lectotypus designiert.

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Appendix 1

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The propodeal corbicula of *Andrena proxima* and allied species (Hymenoptera, Andrenidae)

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Original article

The propodeal corbicula of *Andrena proxima* and allied species (Hymenoptera, Andrenidae)

Andreas DUBITZKY, Klaus SCHÖNITZER*

Zoologische Staatssammlung München, Münchhausenstr. 21, 81247 München, Germany

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Abstract – In the present study the external morphology of the lateral surface of the propodeum of females of *Andrena proxima* and *A. alutacea* – which is possibly a synonym of the former – is investigated by light- and scanning electron microscopy. Two different hair types and characteristic star-shaped structures of the cuticle at the bases of hairs in the central region of the lateral surface of the propodeum are described. Between the two taxonomic forms no differences could be found. Both, the different hair types as well as the star-shaped structures of the cuticle are possibly used for retention of the collected pollen. The described structures are probably autapomorphic characters which justify *A. proxima*-group as a separate species group not included in the subgenus *Micrandrena* as Warncke did.

propodeum / pollen collecting / taxonomy / *Andrena proxima* / *Andrena alutacea*

1. INTRODUCTION

The univoltine sandbee *Andrena proxima* may be observed in Central Europe from May to July. This species is oligolectic on Apiaceae and can be recognized in the field because of its floral relationship as well as by its obvious white tergal hair bands and its small size, 8 to 10 mm (Müller et al., 1997; Westrich, 1989).

Like in other species of *Andrena*, in *A. proxima* the sides of the propodeum are functional corbiculae for transporting pollen. These serve for the transport of pollen (Fig. 1) and are additional to the hairs of the tibia and the flocculus of the trochanter, both on the posterior legs. In several species with the propodeal corbiculae more pollen is transported there than on the posterior legs. The pollen collecting facilities of several species of sandbees were investigated by scanning electron microscopy (SEM) by Pasteels and Pasteels (1977). These authors, however, did not investigate the propodeum

* Correspondence and reprints
E-mail: andreas_dubitzky@yahoo.de; schoenitzer@zsm.mwn.de

Figure 1. Female of *Andrena proxima* on the flower of *Aegopodium podagraria*. White arrows indicate the filled corbicula of the propodeum.

of *A. proxima* although it is characterized by special structures. They predominantly described the propodeal corbicula of several species of the subgenus *Andrena* and some reductions within the genus, for example in the American subgenus *Diandrena* and in *Andrena humilis* [1].

In the present communication the lateral propodeal surface of *Andrena proxima* is investigated by SEM and the function of its structures is discussed. This is also of interest from the taxonomic view. Although this species can be recognized in the field rather easily, its taxonomic status is not yet clear. Some authors suggest that *Andrena proxima* is actually two species (i.e. *Andrena proxima* (Kirby, 1802) and *A. alutacea*: Stöckhert, 1942; Schmid-Egger and Scheuchl, 1997), whereas others state that *A. alutacea* is a synonym of *A. proxima* (e.g. Dylewska, 1987; Westrich, 1989; Schwarz et al., 1996). At any case *A. proxima* is a polymorphic species and some subspecies have been described (*A. proxima ampla* Warncke, 1967; *A. p. aspericollis* Peréz, 1895; *A. p. bernicla* Warncke, 1975).

2. MATERIALS AND METHODS

Although it is not clear whether they are synonyms, in the present paper the two forms are treated like two species: *A. proxima* and *A. alutacea* Stoeckhert, 1942. The two taxa can be differentiated by the diagnosis of Schmid-Egger and Scheuchl (1997).

Three specimens of each, *A. alutacea* and *A. proxima*, were investigated by SEM. They were conventionally sputtered (*A. proxima*) or investigated unsputtered (*A. alutacea*). The pinned specimens were fixed on a conventional stubb by Leit-C-Plast (a plastic conductive carbon cement) and investigated with a Phillips XL-20 or LEO 1430 VP. Unsputtered material was examined with a special low voltage anode at 1.6 kV (XL-20) or with a variable pressure device (20–30 Pa, BSE detector, 15 kV, 1430 VP).

Furthermore, for comparison with light microscopy (LM) we investigated several specimens of the above mentioned species as well as material of the following species: *Andrena subproximana* Strand, 1913 (holotype, DEI Eberswalde); the *Andrena labialis*-group (subgen. *Holandrena*): *A. variabilis* Smith, 1853; *A. labialis* (Kirby, 1802); *A. forsterella* Osytshnjuk, 1978; *A. decipiens* Schenk, 1861; the *A. dorsata*-group (subgen. *Simandrena*): *A. dorsata* (Kirby, 1802); *A. propinqua* Schenk, 1853; and other species of the genus *Andrena*. Most specimens of *A. alutacea* investigated were either paratypes or determined by Stöckhert, we also investigated the holotype of *A. alutacea*. If not stated else, the investigated bees are from the stocks of the Zoological State Collection (= Zoologische Staatssammlung München).

[1] For the sake of correctness it should be mentioned that in their Figure 17 unbranched hairs are shown as scopal hairs of *Andrena humilis*, although this species is characterized by clearly branched hairs of the scopa.

3. RESULTS AND DISCUSSION

The sides (= corbiculae) of the propodeum of *A. proxima* and *A. alutacea* respectively, are shown in Figures 2a and 2e. The long hairs of the edge of the side of the propodeum constitute a fringe along the upper and posterior borders of the corbicula. The anterior side of the corbicula is open. This corresponds to the general observation that pollen is transfered from anterior to posterior before it is deposited in any corbicula (Jander, 1976). In contrast to this, the species of the *A. dorsata*-group bear an additional fringe of hairs at the anterior end of the side of the propodeum (cf. Schmid-Egger and Scheuchl,

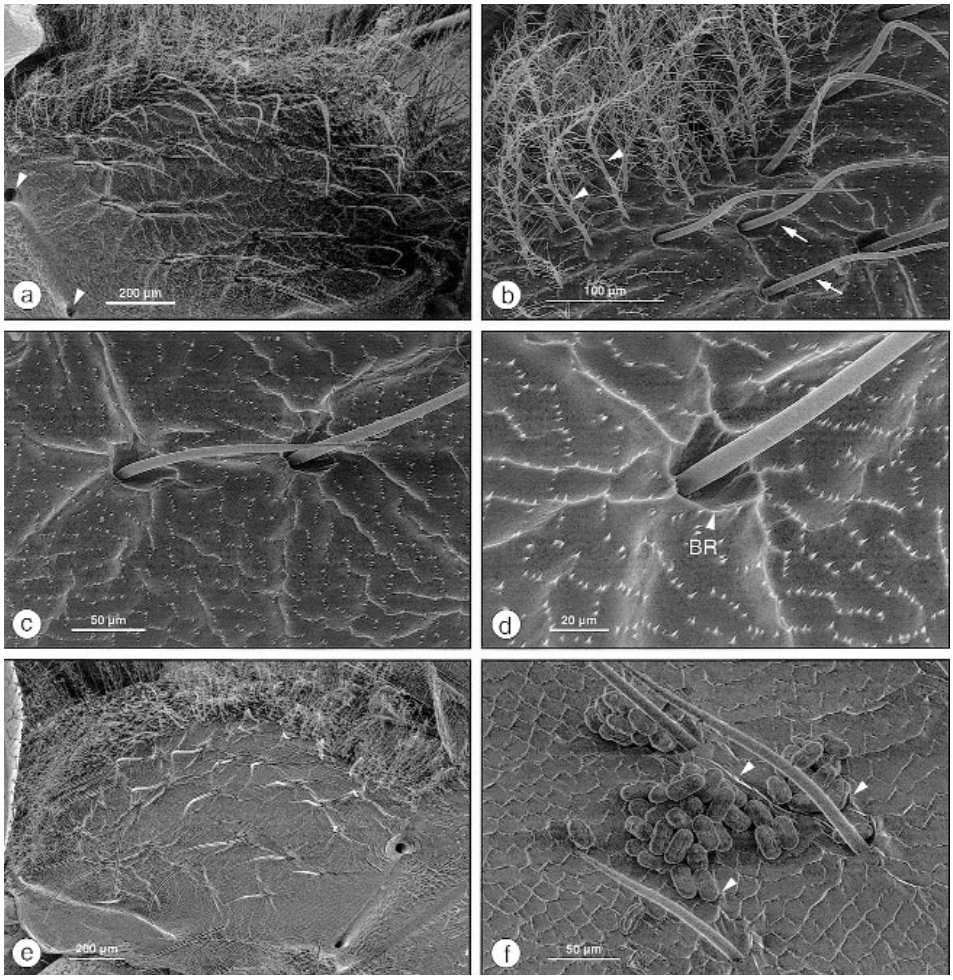

Figure 2. Corbiculua of the propodeum (= lateral side of the propodeum) of *A. proxima* (a–d) and of *A. alutacea* (e–f) respectively. (**a**) Overall view. Orientation: top: dorsal, left: anterior; (**b**) Detail of the dorsal part of the corbicula with setae (arrows) and branched hairs outside the corbicula (arrowheads); (**c**) Setae arising from the surface of the corbicula with starlike keels; (**d**) Base of a seta in the corbicula with starlike keels and rows of cuticular spicules (microtrichia). BR: basal ring of seta; (**e**) Overall view. orientation: top: dorsal, right: anterior; (**f**) Surface of propodeal corbicula with pollen. Arrowheads: cuticular keels.

1997). Furthermore in the species of the *A. dorsata*-group, the surface of the corbicula is completely bare. At the anterior edge of the corbicula in *A. proxima* and *A. alutacea* there are two apodemal holes (Figs. 2a and 2e) as in most but not all species of the genus.

A most remarkable feature are the numerous starlike wrinkles of the cuticle on the surface of the corbilula which may be seen by LM as well as by SEM. The centre of each of these starlike structures is formed by an elevated, irregularly round, basal ring of a hair or seta (Fig. 2). From each basal ring, stellate cuticular keels radiate with reducing height (Figs. 2c, 2d), like the root-stock of a tree. Altogether about 30 to 35 setae are inserted on the surface of each corbicula. As compared to the branched hairs of the fringe on the upper margin of the corbicula, the hairs of the surface of the corbicula are unbranched and two to three times as thick (Fig. 2b). Most, especially the longest of the setae of the surface of the corbicula are bent posteriorly nearly rectangularily at an altitude of about 100 µm (Figs. 2a, 2b and 2e). On the posterior part of the corbicula surface the setae are somewhat longer and not bent. Another special feature of the cuticle of the corbicula are rows of acute triangular spicules (microtricha) standing in zig-zag rows (Figs. 2c, 2d). These rows of microtricha probably correspond to epidermal cell borders. They can not be seen by LM and should be investigated by SEM if they are to be found in other species of *Andrena*. No significant difference in the morphology of the propodeal corbicula was found between *A. proxima* and *A. alutacea*.

Surprisingly the starlike cuticular structures were not observed by various previous authors (Dylewska, 1987; Stöckhert, 1942) who investigated *Andrena proxima* and *A. alutacea*. On the other hand these are clear features for the recognition of the group of *A. proxima/alutacea* (cf. Schmid-Egger and Scheuchl, 1997).

Andrena proxima (and *A. alutacea*) was integrated into the subgenus *Micrandrena* (= *A. minutula*-group) by Warncke (1968, see also later publications of Warncke). Dylewska (1987), however, transferred the species into a separate species group of its own (*Andrena proxima*-group) mainly because of the dense punctation of the mesopleura (= mesepisterna). The structures described in the present communication are possibly autapomorphic and justify considering the *Andrena proxima*-group as a separate species group. Furthermore the distinct tergal bands as well as the longer distance between the stigma and the ending of the cubital vein into the radial cell support separation of *A. proxima* and its allies from the subgenus *Micrandrena*.

In contrast to other species of *Andrena*, similar starlike structures are also found in species of the *A. labialis*-group (subgen. *Holandrena*): the starlike structures are quite clear in *A. variabilis* and *A. forsterella*, less clear in *A. labialis*, and not found in *A. decipiens*; they have not been mentioned previously (Schönitzer et al., 1995). They are, however, never spread over the whole surface of the propodeum and are much less clear than those of *A. proxima/A. alutacea*. Nevertheless they might be a hint (a putative synapomorphy) for a closer relationship of these two taxa; possibly the *A. labialis*-group and the *A. proxima*-group are sistergroups.

On the other hand the propodeum of *A. subproximana* is clearly different from that of *A. proxima*. Its floor is bare of any hairs and wrinkles; it is chagreened and surrounded by branched hairs which are similar to those of the *A. dorsata*-group. In contrast to its description (Strand, 1913), *A. subproximana* is unequivocally not related to *A. proxima*. By a distinct hair fringe at the anterior side of the propodeal corbicula, a clear keel between the middle and lateral part of the propodeum, a rather broad fovea facialis and the postscutellum with rather long hairs, *A. subproximana* is clearly characterized as a member of the *A. dorsata*-group (subgen. *Simandrena*).

The star shaped structures of the cuticle as well as the bent setae of the propodeal

corbicula are possibly an adaptation for the retention of pollen grains in the corbicula. These structures possibly cause an enlargement of the surface area and permit better adhesion of the pollen grains to the cuticular surface. This idea is supported by the observation of pollen grains lined up at the starlike wrinkles and keels in those cases with only small amounts of pollen in the corbicula (cf. Fig. 2f). Westrich and Schmidt (1989) show pollen grains of Apiaceae on the tibia of *A. proxima* in an SEM photo, they are similar to the pollen found in the present investigation which is obviously also from Apiaceae (see also Müller et al., 1997).

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We thank Dr. W. Grünwaldt and Mr. J. Schuberth for most valuable hints on the literature. Mr. S.M. Blank lent us the holotype of *Andrena subproximana* from the Deutsches Entomologisches Institut, Eberswalde. Dr. R. Melzer enabled us to use the SEM of the Zoological Instiute of the Ludwig-Maximilians-Universität, Munich. To all those involved we want to express our sincere thanks.

Résumé – Les corbicules propodéales d'*Andrena maxima* et espèces voisines (Hymenoptera, Andrenidae). La morphologie externe de la surface latérale du propodeum des femelles d'*Andrena maxima* et d'*A. alutacea* – synonyme éventuel de l'espèce précédente – a été étudiée en microscopie optique et microscopie électronique à balayage. On décrit deux types différents de soies et des structures caractéristiques en forme d'étoile situées sur la cuticule à la base des soies dans la région centrale de la surface latérale du propodeum. Les différents types de soies comme les structures étoilées sont susceptibles d'être utilisés pour retenir le pollen récolté. Aucune différence n'a été trouvée entre les deux formes taxonomiques. Les structures décrites sont probablement des caractères autapomorphiques qui justifient que le groupe *A. proxima* soit un groupe d'espèces séparé non inclus dans le sous-genre *Micandrena*. On a trouvé des structures semblables de la surface du propodeum latéral chez les espèces du groupe *A. labialis* (sous-genre *Holandrena*), qui est peut-être un groupe sœur de *A. proxima/ A. alutacea*. Contrairement à sa description originelle, *A. subproxima* n'est pas reliée à *A. proxima* mais est nettement caractérisée comme un membre du groupe *A. dorsata* (sous-genre *Simandrena*).

***Andrena proxima* / *Andrena alutacea* / taxonomie / propodeum / corbicule**

Zusammenfassung – Das Körbchen am Propodeum von *Andrena proxima* und verwandten Arten (Hymenoptera, Andrenidae). Von *Andrena proxima* und *A. alutacea,* wobei von letzterer nicht klar ist, ob es sich um ein Synonym der erstgenannten Art handelt, wurde die äußere Morphologie des Sammel-Körbchens an der Propodeumseite der Weibchen licht- und rasterelektronenmikroskopisch untersucht. Dabei konnten neben zwei verschiedenen Haartypen an Oberkante und Körbchenboden des Sammelkörbchens charakteristische, sternförmige Cuticula-Runzeln an der Basis der Körbchenbodenhaare dokumentiert werden. Sowohl die verschiedenen Haartypen als auch die sternförmigen Runzeln des Körbchenbodens dürften das Fixieren der Pollenkörner im Körbchen unterstützen. Zwischen den beiden Formen konnte kein Unterschied gefunden werden. An Hand dieser und anderer morphologischer Merkmale wurde diskutiert, dass *A. proxima/A. alutacea* als eigenständige Artengruppe anzusehen sind und nicht in die Untergattung *Micrandrena* gehören. Ähnliche Strukturen am Propodeumkörbchen wurden bei Arten der *A. labialis* Gruppe (subgen. *Holandrena*) festgestellt, die möglicherweise die Schwestergruppe von *A. proxima/A. alutacea* ist. *A. subproximana,* die gemäß ihrer Originalbeschreibung mit *A. proxima* verwandt sein sollte, ist der *A. dorsata*-Gruppe (subgen. *Simandrena*) zuzuordnen.

Propodeum / Pollen sammeln / Taxonomie / *Andrena proxima* / *Andrena alutacea*

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Appendix 2

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A new sandbee from the mountain region of central Taiwan: *Andrena taiwanella* spec. nov. (Insecta, Hymenoptera, Andrenidae)

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A new sandbee from the mountain region of central Taiwan: *Andrena taiwanella*, spec. nov.

(Insecta, Hymenoptera, Andrenidae)

Andreas Dubitzky

Dubitzky, A. (2002): A new sandbee from the mountain region of central Taiwan: *Andrena taiwanella*, spec. nov. (Insecta, Hymenoptera, Andrenidae). – Spixiana **25/1:** 69-77

A new sandbee *Andrena (Micrandrena) taiwanella*, spec. nov. from Taiwan is described. It was caught at the beginning of July in the mountain region of central Taiwan at 1600-2500 m altitude. The new species is similar to *Andrena hirashimai* Tadauchi, 1985 and *Andrena sublevigata* Hirashima, 1966, both from Japan. From *A. hirashimai* Tadauchi *Andrena taiwanella* can be differentiated by the broader process of the labrum, the less tesselate structure of the scutum and the enclosure of propodeum wrinkled much more finer and being granulated in larger extension. By the more tesselate structure and the distinct punctation of the hairy scutum and scutellum the new species can be distinguished easily from *A. sublevigata* Hirashima. Up to now apart from *Andrena formosana* Cockerell, 1911 this sandbee is the second species of *Andrena* and the first species of the subgenus *Micrandrena* which is recorded from the main island of Taiwan.

Andreas Dubitzky, Zoologische Staatssammlung München, Münchhausenstr. 21, D-81247 München, Germany; e-mail: andreas_dubitzky@yahoo.de

Introduction

Taiwan, with an total area of about 36,000 km², is located ca. 140 km east of the mainland of China on the Tropic of Cancer. The central mountain range from Keelung in the north to Kenting in the south (about 350 km in extension) is the dominant geological structure of the island with almost two third of its total area. It is characterised by 62 mountains over 3000 m altitude, with the 3997 m high Yushan (Jade Mountain) being the highest mountain of East Asia, east of the Himalaya. The climatic conditions of the higher mountain regions (over 2000 mts altitude) are temperate, even with snow in winter months, in contrast to the subtropical and tropical regions of Taiwan. Although the fauna of Taiwan is assigned to the Oriental region, parts of it (especially the fauna of the higher mountain regions) are very similar to the Eastern Palearctic region.

In June / July 2000 Miss Susanne Szczepanek and I had the possibility of joining Mr Wolfgang Schacht from the Munich Zoological Museum (Zoologische Staatssammlung München = ZSM) on a five weeks visit (15.6.-18.7. 2000) to Taiwan. By the great effort of Mr Keh Miin Chen (Taipei) and Prof. Jeng-Tze Yang (Department of Entomology, Chung-Hsing University, Taichung) we were able to collect insects in many interesting parts of Taiwan. At the beginning of July we visited the Rei En Shi region (at 2200-2500 m altitude) in the central mountain range about 40 km north east of Puli, where the new species of sandbee was collected. Further specimens of the new species were

found near the TESRI-Station Ternge (at 1600 m altitude) and in the collection of the National Museum of Natural Science, Taichung.

The bee-fauna of Taiwan was studied mainly by Cockerell (1911a,b, 1912, 1927) and Strand (1913a, 1914a,b), who examined the extensive material of Sauter (Sauter's Formosa-Ausbeute) in the first half of last century. The bee fauna of mainland China was examined by Strand (1913b) Yasumatsu & Narisada (1935) and Yasumatsu (1946). The latter also studied the Far Eastern species of *Andrena* (Yasumatsu 1941). Wu (1982), Kim (1980) and Kim & Kim (1989) described species of *Andrena* of China (Xizang) and Korea. Detailed descriptions and records of the genus *Andrena* of Eastern Asia were given by Tadauchi & Lee (1992), Xu & Tadauchi (1995, 1996, 1997a,b, 2000) and Tadauchi & Xu (2000). Systematic studies on the species of *Andrena* of Japan were mainly done by Hirashima (1964, 1965a,b, 1966), Tadauchi (1985a,b) and Tadauchi et al. (1987a,b). The Japanese species of the subgenus *Micrandrena* were studied and described by Hirashima (1965b, 1966) and Tadauchi (1985a,b), both with keys to the species.

The collected females of *Micrandrena* from the Rei En Shi region of Taiwan are similar to the two Japanese species *Andrena hirashimai* Tadauchi, 1985 and *Andrena sublevigata* Hirashima, 1966, from which they can be distinguished by the characters given in the following description.

Methods and material

The material was studied by lightmicroscopy with a Leica MZ 6 binocular. The morphological documentation of the species by SEM was made with a Philips XL 20 SEM. For this the pinned specimens were fixed with Leit-C-Plast on the object table and were analysed with a low voltage anode by 1,6 kV (spot 4, integrate 4, slow scan 3).

Examined species:

Andrena hirashimai: 1♀, Amami-Ohshima Islands, Japan, 2.4.1958, leg. O. Takahashi, det. O. Tadauchi, ex coll. Tadauchi

Andrena sublevigata: 2♀♀, Moya, Aomori (Honshu), Japan/Mt. Daisen, Masumizu (Honshu), Japan, 30.5.1975/26.4.1975, leg. O. Tadauchi, det. O. Tadauchi, ex coll. Gusenleitner/Tadauchi

Andrena kaguya: 1♀, Chikuho-machi, Kuroubaru (Kyushu), Fukuoka Pref., Japan, 9.4.1975, leg. O. Tadauchi, det. O. Tadauchi, ex coll. Gusenleitner

Andrena hanedai: 1♀, Suwara, Ohno, Fukui, Japan, 9.9.1973, leg. Y. Haneda, det. O. Tadauchi, ex coll. Tadauchi

Andrena brassicae: 1♀, Miyano, Hiroshima (Honshu), Japan, 15.4.1975, leg. O. Tadauchi, det. O. Tadauchi, ex coll. Gusenleitner

Andrena komachi: 1♀, Shimohanda, Ôita (Kyushu), Japan, 4.4.1975, leg. O. Tadauchi, det. O. Tadauchi, ex coll. Gusenleitner

Nearly all Central European species of *Micrandrena* were investigated with the material of the ZSM. Furthermore *Andrena alfkenella, A. minutula, A. minutuloides* and *A. subopaca* were studied by SEM during earlier investigations (Dubitzky 2000).

The used morphological terminology is according to Michener (2000).

Andrena taiwanella, spec. nov.

Figs 1-6, 9, 11, 14

Types. Holotype: ♀, Central Taiwan (Republic of China, R.O.C.), Rei En Shi region, Road No. 14, 40 km North East of Puli, ca. 4 km East of Tsuifeng, 2300-2500 m, 24°08'N/121°12'E, 1.7.2000, leg. Andreas Dubitzky. The Holotype is deposited at the collection of the Department of Entomology, Chung-Hsing University, Taichung, Taiwan. – Paratypes: 4♀♀, same data as Holotype, leg. Andreas Dubitzky; 1♀, same data as Holotype leg. Susanne Szczepanek; 1♀, Central Taiwan, Kaoshiung County, TESRI-Station Ternge, 1600 m, 23°07'N/120°47'E, 6.7.2001, leg. Andreas Dubitzky; 1♀, Taiwan, Kaoshiung, Yushan National Park, yellow pan trap, 24.-28.10.1990, leg. C. K. Starr. Two Paratypes are deposited at the Zoologische Staatssammlung München, the others are deposited at the National Museum of Natural Science, Taichung (1♀) and the private collections of the author (3♀♀) and Miss Susanne Szczepanek (1♀).

Floral record: The Holotype and all Paratypes from Tsuifeng were found on *Filipendula* spec. (Rosaceae), where they were collecting pollen of the flowers.

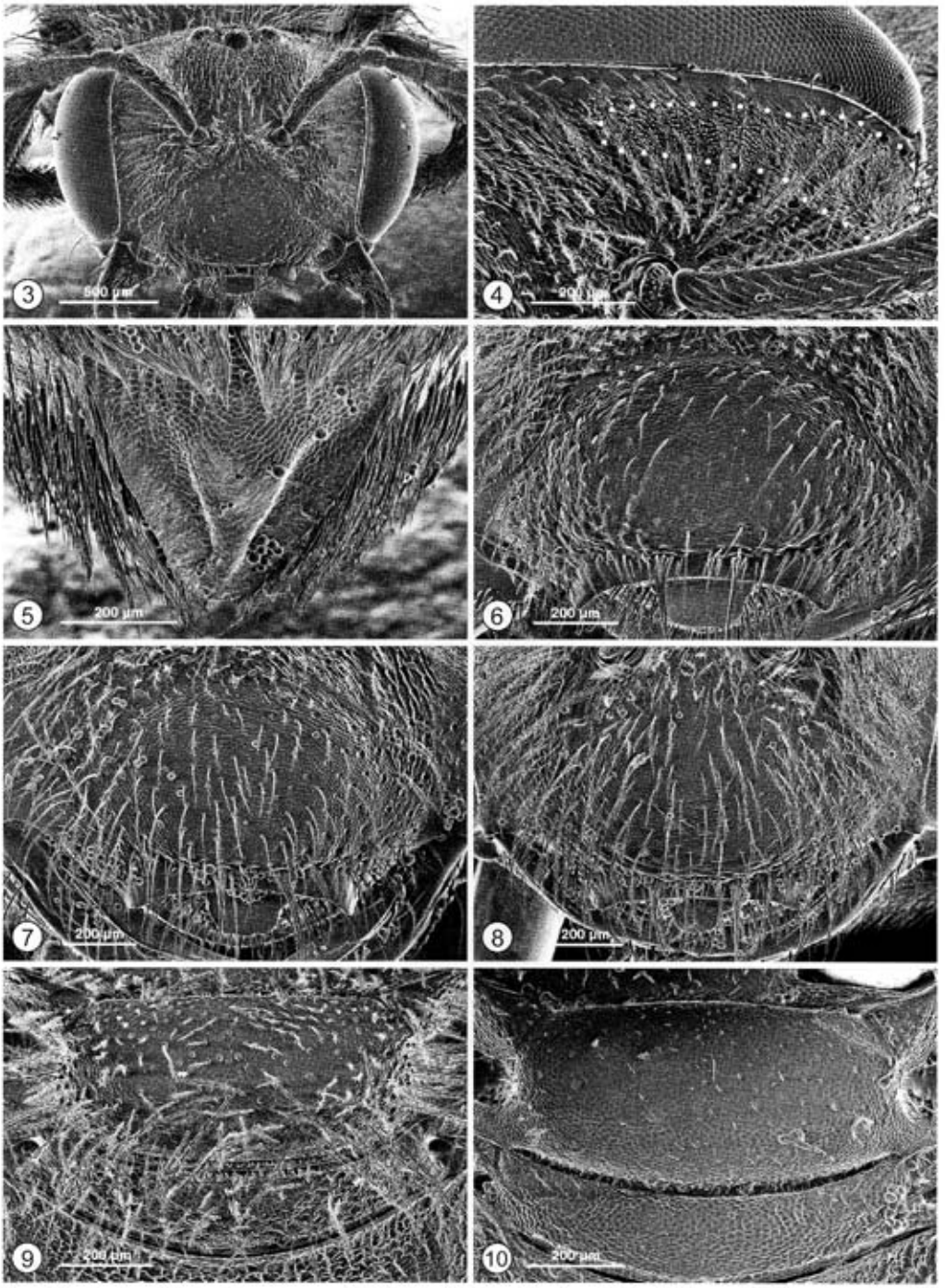
Description

Female. Length 6.8-7.1 mm ($\bar{x}$ = 6,95). Habitus see Figs 1 and 2.

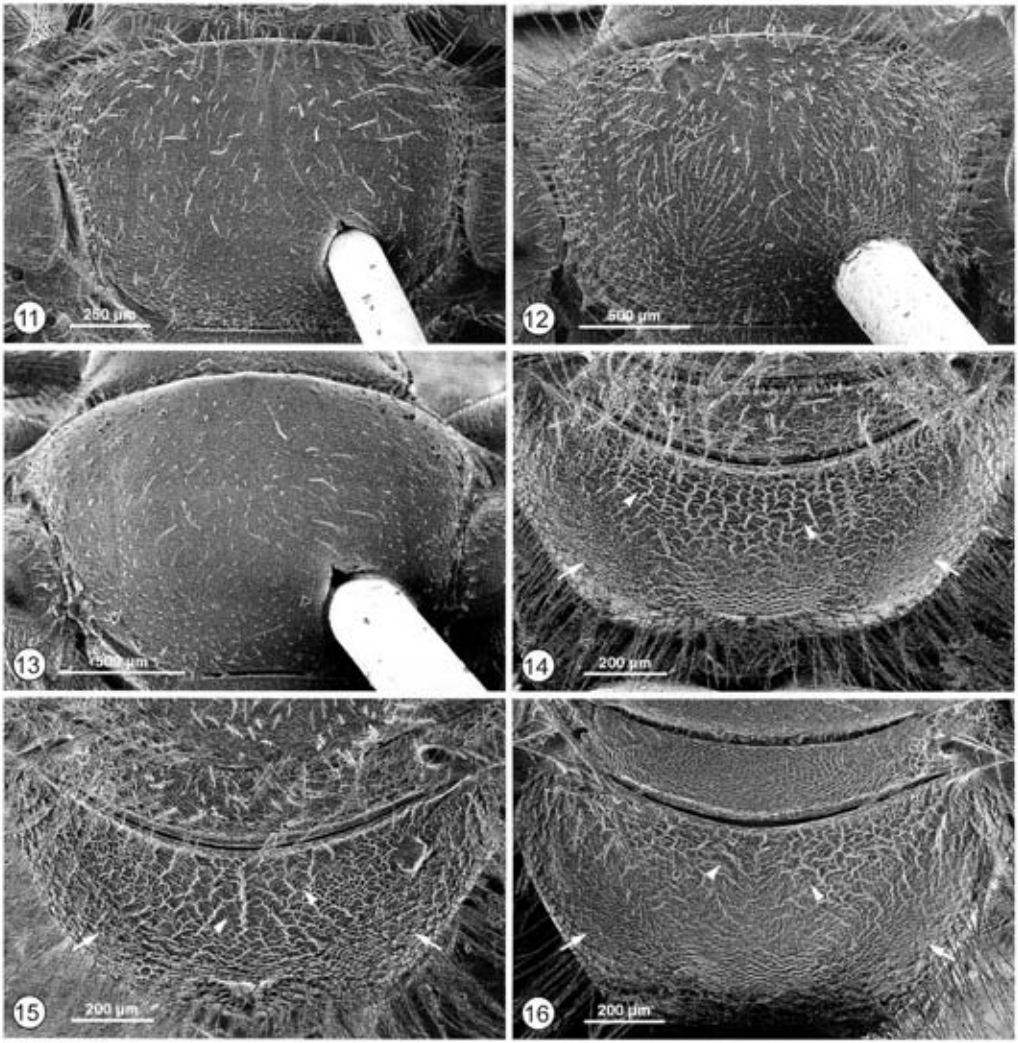
Structure. Head ca. 1.2 times broader than long in frontal view (Figs 2, 3). Process of labrum rectangular, about two times broader than long, with convex apical margin (Figs 3, 6). Tip of mandibles with two teeth, inner margin of

Figs 1, 2. Habitus of *Andrena taiwanella*, spec nov., ♀. **1**. Lateral view of holotype. **2.** Dorsal view of paratype.

mandibles angeled at ca. 100° (Fig. 2). Clypeus convex, weakly flattened in the middle. Cuticula of clypeus weakly tesselated, sometimes shiny, with dispersed large punctures (Fig. 6). Distance between the single punctures of the disc of clypeus ≥1 (about the diameter of one puncture or more), distance of punctures of the lateral front margin of clypeus <1. Disc of clypeus with impunctate median line. Facial fovea (FOV) with the upper end reaching the basal margin of lateral ocelli and with the lower end nearly reaching the upper margin of the clypeus (Fig. 3). Upper third of FOV almost twice as broad as in its lower two third (Fig. 4).



Figs 3-5. *Andrena taiwanella*, spec nov., ♀. **3**. Head in frontal view. **4**. Facial fovea (FOV), orientation: left side – anterior, right side – posterior, dotted line: outline of FOV. **5**. Pygidial plate.
Figs 6-10. Comparison of *Andrena taiwanella*, spec nov., ♀ (Figs 6, 9) with *Andrena hirashimai* Tadauchi, ♀ (Fig. 7) and *Andrena sublevigata* Hirashima, ♀ (Figs 8, 10). **6-8**. Clypeus and process of labrum. **9, 10**. Scutellum (top) and metanotum (bottom).



Figs 11-16. Comparison of *Andrena taiwanella*, spec nov., ♀ (Figs 11, 14) with *Andrena hirashimai* Tadauchi, ♀ (Figs 12, 15) and *Andrena sublevigata* Hirashima, ♀ (Figs 13, 16). **6-8**. Clypeus and process of labrum. **9, 10**. Scutellum (top) and metanotum (bottom). **11-13**. Scutum, orientation: anterior – top, posterior – bottom. **14-16**. Dorsal propodeum with propodeal enclosure (arrowheads) and lateral parts (arrows), orientation: anterior – top, posterior – bottom. The arrowheads indicate the space between the wrinkles of the propodeal enclosure.

Almost no free space between the upper third of the FOV and the compound eye, between the lower two third of the FOV and the compound eye free space of nearly half of the lateral extension of the lower FOV. Frons with clear, longitudinal grooves from the ocelli down to the upper margin of the clypeus (Fig. 3). Distinct keel between the basis of antennae. Cuticula between ocelli and the compound eyes dull to weakly shiny. Distance between lateral ocelli and the upper margin of the vertex only a little bit shorter than the diameter of lateral ocellus (ca. 0.8×∅). Scape short, not reaching lower margin of the median ocellus. Third antennal segment as long as fourth and fifth together (Fig. 2). Segments 4 and 5 broader than long, 6-10 as long as broad, 11 to 12 longer than broad (in frontal view). Genal area tesselate, in lateral

view as broad as compound eye. Pronotum dull, the apical transverse groove not notched in middle. Scutum weakly tesselate, dull (area along posterior margin) to shiny (disc area), with indistinct dense punctation (Fig. 11). Distance of the small weak punctures <1. Scutellum weakly tesselate with two flat, smooth and shiny lateral humps (Fig. 9). Punctation of scutellum dispersed and indistinct (distance >1). Metanotum tesselate to granulate, dull (Fig. 9). Propodeal enclosure with fine, dense wrinkles only in basal half, apical half totally granulated (Fig. 14). Lateral parts of dorsal propodeum smooth to weakly granulated, shiny (Fig. 14). Lateral propodeum weakly tesselate, shiny. Metasomal terga 1-4 tesselate and impunctate. Metasomal tergum 5 with irregular, basal punctation. Depressions of metasomal terga weakly (1-3) to clearly (4) indicated. Depression of metasomal tergum 2 less than the half of the tergums length in extension (ca. 0.4), depressions 2-4 over the half of the length of their terga (ca.0.6). Metasomal sternits weakly tesselate, shiny, with distinct, dense punctation (>1). Pygidial plate triangular, weakly tesselated, dull (Fig. 5). Elevated triangular centre surrounded by lower edge of ca. ¼ of basal pygidial plate's extension.

Tab. 1. Abbreviations: d: distance, l/w: length extension/wide extension, ldp: lateral parts of dorsal propodeum, pe: propodeal enclosure.

character	*A. taiwanella*, spec nov.	*A. hirashimai* Tadauchi	*A. sublevigata* Hirashima
process of labrum	broad, rectangular l/w = 0.47 (Fig. 6)	narrower, l/w = 0.67 (Fig. 7)	small triangular, l/w = 0.71 (Fig. 8)
clypeus	punctation big, distinct; impunctate median line; sparse, indistinct, scanty hairs only along lateral and lower margin; disc without any hairs (Fig. 6)	punctation small, indistinct, regular without impunctate median line; distinct, dense hairs regularly spread all over the clypeus (Fig.7)	punctation distinct; impunctate median line; dense distinct hairs regularly spread all over the clypeus (Fig. 8)
facial fovea (FOV)	upper third of FOV ca.2 times broader than lower ⅔ of FOV; pubescence brownish to yellowish (Fig. 4)	FOV scarcely getting narrower from up to down; pubescence whitish	FOV continuously getting narrower to ⅓ of maximum wide from up to down; pubescence yellowish white
genal area	sparse hairs	dense hairs	sparse short hairs
scutum	weakly tesselate, disc shiny to dull, dense punctation (d >1), disc less hairy (Fig. 11)	tesselate, disc dull, very dense punctation (d<1), disc more hairy (Fig. 12)	smooth to weakly tesselate disc shiny, indistinct dispersed punctation (d>1) of very small punctures, disc nearly bare (Fig. 13)
scutellum	weakly tesselate, with shiny lateral parts, dispersed punctation and scanty long hairs (Fig. 9)	tesselate, dull all over, punctation and hairs more distinct and dense than by *A. taiwanella*	smooth and shiny all over small, indistinct, dispersed punctation, completely bare (Fig. 10)
metanotum	dispersed hairs, dull (Fig. 9)	dispersed hairs, dull	completely bare, dull (Fig. 10)
propodeum	fine, dense wrinkles with almost no space between only in basal half of pe; apical half granulated; ldp granulate to smooth, shiny, without any hairs (Fig. 14)	pe with strong, wide wrinkles, extended nearly to apical end of pe, with dull, granulated space between; ldp granulate to slightly wrinkled, dull, with single sparse hairs (Fig. 15)	pe with fine, wide wrinkles only in basal half of pe, with smooth, shiny space between; at least apical half granulated; ldp granulate to smooth, without hairs (Fig. 16)

Integumental colour. Colour of body black. Mandibles black, reddened apically. All segments of antennae black, also beneath. Legs and basitarsi black, tarsi and claws brownish, spurs pale yellowish brown. Tegulae dark brown anteriorly to semihyaline posteriorly. Wings slightly brownish to transparent, stigma dark brownish, veins paler brown. Pygidial plate black, sometimes dark reddened apically.

Pubescence. Hairs on head pale yellowish grey. Clypeus with sparse, pale hairs only at the ventral and lateral margins. Labrum and posterior margin of mandibles with long, yellowish brown hairs. Frons with scanty, sparse hairs and long, distinct hairs between FOV and basis of antennae. FOV brownish above, yellowish brown below. Genal area with dispersed, whitish-transparent, short to medium-long hairs. Vertex with scanty, long and sparse greyish hairs. Occiput with distinct, long and dense yellowish grey, strong hairs. Scape anteriorly with yellowish grey hairs (length: ca. ∅ scape). Apical part of scutum with strong, long, yellowish grey hairs; lateral and posterior parts of scutum with strong, short, yellowish grey hairs. Disc of scutum with very short, indistinct, sparse hairs and few, scanty long hairs (Fig. 11). Lateral and posterior parts of scutellum and metanotum with long, distinct, strong yellowish grey hairs (Fig. 9). Lateral parts of thorax with long, yellowish grey to whitish hairs. Propodeum broadly bare dorsally. Dorsal fringe of propodeal corbicula of long yellowish grey, branched hairs, bottom of propodeal corbicula with single, dispersed, simple, transparent hairs. Hairs on legs short, pale yellowish brown; inner side of basitarsi with brownish hairs. Flocculus of long, branched, silvery whitish hairs. Tibial scopa with yellowish to brownish grey, simple hairs; along upper and lower margin with single dispersed feathered hairs. First metasomal tergum almost naked, with only few dispersed, small, whitish hairs laterally. Metasomal terga 2 and 3 with poorly developed lateral white hair fringes with an extension of only ⅛ of the tergas wide on each side (Figs 1,2). Tergum 4 with sparse, dispersed, whitish transparent hairs on disc and long, strong hairs along lateral and posterior margins. Tergum 5 and 6 with strong, feathered, brownish grey hairs. Metasomal sternits 2-4 with indistinct, sparse, short (basal half) and long (posterior ending of sternits), whitish hairs. Sternites 5 and 6 with distinct yellowish grey hairs.

Male. unknown.

Diagnosis: By the first transverse cubital vein ending very close to the pterostigma, the rather large enclosure of dorsal propodeum, the incomplete propodeal corbicula and the lack of prominent hair bands at the end of metasomal terga the new species of *Andrena* is clearly characterised as a member of the subgenus *Micrandrena*.

The new species is similar to *Andrena hirashimai* Tadauchi, 1985 and *Andrena sublevigata* Hirashima, 1966, both from Japan. From *A. hirashimai* the new species is separated mainly by the broader process of labrum, the shape of FOV, the less tesselated structure of the scutum and the propodeal enclosure wrinkled much more finer and closer and granulated in larger extension. The more hairy, tesselate and punctate scutum and scutellum as well as the closer wrinkled propodeal enclosure are the main characters of which *A. taiwanella* can easily be distinguished from *A. sublevigata*.

In Table 1 the differences between *Andrena taiwanella*, spec. nov. and the closely resembled species *A. hirashimai* Tadauchi and *A. sublevigata* Hirashima are shown.

Determination key

For recognition of *A. taiwanella*, spec. nov. the new species has been integrated in the key of Japanese *Micrandrena* (Tadauchi 1985b), which therefore should be modified as follows:

4. Propodeal enclosure finely wrinkled only in basal half, at least half of its total length widely granulate apically ..... 5.
– Propodeal enclosure strongly wrinkled at least ⅔ in extension, only about ⅓ of its total length apically granulate ..... 6.

5. Propodeal enclosure densely wrinkled, with almost no free space between single wrinkles; mesoscutum hairy, with distinct, dense punctation; scutellum with distinct, long, yellowish grey hairs, punctate ..... *taiwanella*, spec. nov.
– Propodeal enclosure dispersed wrinkled, with smooth distinct space between the

weak wrinkles; mesoscutum nearly bare, with small, indistinct, dispersed punctuation; scutellum totally bare, impunctate ..... *sublevigata*

6.(5) Mesepisternum smooth to weakly tesselate, shiny; mesoscutum nearly smooth to weakly tessellate ..... *brassicae*

– Mesepisternum densely tesselate .... 7(6).

Numbers in brackets: corresponding numbers in Tadauchi 1985b. For continuation see Tadauchi 1985b No. 6!

Discussion

A. taiwanella, spec. nov. is the 13th species of *Micrandrena* which is recorded from East Asia (Tadauchi 1985, Tadauchi & Lee 1992).

Apart from *Andrena formosana* Cockerell, 1911, *Andrena taiwanella*, spec. nov. is the second species of *Andrena* and the first record of the subgenus *Micrandrena* recorded from the main island of Taiwan. Tadauchi recorded another species of *Micrandrena* from the Nansei Islands near Taiwan (Tadauchi, pers. com.). Possibly the new sandbee is an endemic species of the higher mountain regions (>2000 m) of central Taiwan. Because of the palearctic character of this region certainly some more species of *Andrena* can be expected there. For the distribution of *Andrena taiwanella* further investigations and data of other parts of the central mountain range of Taiwan would be necessary. Perhaps the new species also occurs in other, higher mountain regions of Asia, especially the Himalaya as it is known for other insects e.g. the Ichneumon-fly *Stenodontus regieri* (Diller et al. 1996).

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Chinese Abstract

本文描述臺灣地花蜂科 *Micrandrena* 亞屬一新種 *Andrena taiwanella* spec. nov.。此新種於七月上旬採自台灣中部瑞岩溪海拔 2300 至 2500 公尺處。本新種與日本產 *A. hirashimai* TADAUCHI 1985 和 *A. sublevigata* HIRASHIMA 1966 相似。*A. taiwanella* 與 *A. hirashimai* TADAUCHI 之差異在於具較寬廣上唇突起，盾片花紋較少以及環繞前伸腹節之鏃折較細微且大部分區域具有粒狀突起；與 *A. sublevigata* HIRASHIMA 1966 之不同在於本種具毛的盾片及小盾片上有較多花紋及明顯的斑點。至目前爲止，在台灣除原有之記錄之 *A. formosana* COCKERELL 1911 外，本種爲臺灣 *Andrena* 屬中被發現的第二個種類，而所屬 *Micrandrena* 亞屬則是首度記錄於台灣。

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Appendix 3

SCHÖNITZER, K. & DUBITZKY, A. 2002

Sandbienen des Kugitang Gebirges in Turkmenistan und Beschreibung einer neuen Art: *Andrena lehmanni* spec. nov. (Hymenoptera Apoidea, Andrenidae)

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Sandbienen des Kugitang-Gebirges in Turkmenistan und Beschreibung einer neuen Art: *Andrena lehmanni* sp. nov. (Hymenoptera: Apoidea, Andrenidae)

● Klaus Schönitzer & Andreas Dubitzky

Abstract. 27 species of *Andrena* sand bees have been recorded from the Kugitang Mountains in the far eastern part of the Central Asian Republic of Turkmenistan during a 10-day field trip. *Andrena lehmanni* sp. nov., is described and compared to *Andrena hyemala* Warncke, 1973, and *Andrena ebneri* Alfken, 1924. It is not clear whether *A. lehmanni* sp. nov. belongs to one of the subgenera *Graecandrena* Warncke, 1968, *Micrandrena* Ashmead, 1899, or *Fumandrena* Warncke, 1975. The new species is characterized by the lack of hair bands at the end of the abdominal terga. The latter are shiny, hardly tesselate, and finely punctured.

Zusammenfassung. Im Kugitang-Gebirge im äußersten Osten der zentralasiatischen Republik Turkmenistan wurden während einer 10-tägigen Exkursion 27 Sandbienenarten nachgewiesen. Eine Art, *Andrena lehmanni* sp. nov., wird neu beschrieben und mit *Andrena hyemala* Warncke, 1973, und *Andrena ebneri* Alfken, 1924, verglichen. Die mögliche Zugehörigkeit von *A. lehmanni* sp. nov. zu einer der Untergattungen *Graecandrena* Warncke, 1968, *Micrandrena* Ashmead, 1899, oder *Fumandrena* Warncke, 1975, wird diskutiert. Die neue Art fällt insbesondere durch das Fehlen von Tergit-Binden und die glänzenden, kaum chagrinierten und fein punktierten Tergite auf.

Key words. Hymenoptera, Apoidea, Andrenidae, *Andrena*, Turkmenistan, Kugitang Mountains, fauna.

Einleitung

Das Kugitang-Gebirge (= Kugitangtau) im äußersten Osten der zentralasiatischen Republik Turkmenistan und dem benachbarten Usbekistan ist ein Kalkgebirge mit verschiedenen Karstphänomenen, das von tiefen Schluchten durchzogen ist (Babaev 1994). Der höchste Gipfel ist der Airibaba mit 3.137 m Höhe (Abb. 1). Die längste Schlucht heißt Dareidare und ist etwa 10 km lang (Abb. 2). Vorherrschend in dem insgesamt sehr niederschlagsarmen Gebiet ist eine typische artenarme Wüstenvegetation, lediglich in den etwas feuchteren Tälern befindet sich eine reichhaltigere Flora und jeweils eine eigene charakteristische Fauna. Dieses interessante Gebiet ist entomologisch noch kaum erschlossen, da es nur sehr schwer zugänglich ist. Relativ gut untersucht sind vor allem die Käfer (Kryzhanovsky & Atamuradov 1994). Durch die freundliche Unterstützung von Herrn Dr. K. Atamuradov (Aščhabad) und Prof. V. Dolin (Kiev) konnte der Erstautor diese interessante Gegend bereisen und dort Bienen sammeln. Turkmenistan leidet in großen Bereichen unter dem weit verbreiteten Problem der Überweidung, das seit dem Ende der Sowjetunion zunimmt. Aber gerade in den Schluchten und unzugänglichen Gebirgsgegenden des Kugitang-Gebirges ist viel von der Ursprünglichkeit der Natur erhalten. Im Jahre 1986 hat die Turkmenische Regierung ein Naturschutzreservat (Natural reserve = zapovednik) im Kugitang-Gebirge mit 27.000 ha Größe sowie zwei Schutzgebiete (Karlyuk und Khodzhapil, natural refuge = zakaznik) ausgewiesen (Rustamov & Sopyev 1994).

Eine besondere Attraktion sind eindrucksvolle Dinosaurierspuren, die in der Gegend von Hodschapil (= Khodzheipil), nur wenige Kilometer von der usbekischen Grenze in einer herrlichen Landschaft gelegen sind (Abb. 3, 4). Im Unteren und Mittleren Jura bildete sich im Gebiet des heutigen Kugitang-Gebirges und in den östlich benachbarten Teilen von Usbekistan und Tadzhikistan eine große Lagune, die bis zur Kreide bestand und an deren Küste die Fußabdrücke entstanden sind.

Bei den bis zu etwa 60 cm langen Fußabdrücken, welche aus dem oberen Jura (Oxford-Periode, Atamuradov pers. com.) stammen, dürfte es sich um „*Iguanodon*"-Fährten handeln (Lockley 1993). Vielfach sind auch für einen Laien komplette Fährten zu erkennen (Abb. 4). Manche Fährten sind in Gruppen angeordnet, so dass man vermuten kann, dass es sich bei den Tieren um Gruppen oder Familien gehandelt haben könnte (Atamuradov 1994 und pers. com.). Man kann deutlich drei „Arten" von Fußabdrücken unterscheiden, die möglicherweise auch drei Arten von Dinosauriern zuzuordnen sind.

In der vorliegenden Arbeit werden die Sandbienen, die im Kugitang-Gebirge gefangen wurden, zusammengestellt. Außerdem wurde noch eine neue Art der Gattung *Andrena* Fabricius, 1775, identifiziert. Diese ist im Habitus der erst vor wenigen Jahren beschriebenen *Andrena ledermanni* Schönitzer, 1997, relativ ähnlich, gehört aber, im Gegensatz zu dieser, eindeutig nicht in die Untergattung *Carandrena* Warncke, 1968 (Schönitzer 1997). Sie soll hiermit beschrieben werden und mit den beiden ähnlichen Arten *Andrena ebneri* Alfken, 1924, und *Andrena hyemala* Warncke, 1973, aus der Untergattung *Graecandrena* Warncke, 1968, verglichen werden.

Material und Methoden

Um Strukturmerkmale der Cuticula wie Chagrinierung oder Punktierung besser zu erkennen und hervorzuheben, wurde bei der lichtmikroskopischen Untersuchung das diffuse Licht einer Energiesparlampe verwendet und auf die konventionelle, stärker fokussierte Binokularbeleuchtung weitgehend verzichtet.

Für die rasterelektronenmikroskopische Dokumentation von *A. lehmanni* sp. nov. wurde ausschließlich unbesputtertes, genadeltes Material verwendet, welches mittels Leit-C-Plast auf dem Objekttisch fixiert wurde. Die anschließende Untersuchung im Philips XL-20 REM erfolgte bei ca. 1,6 kV unter Verwendung einer low-voltage-Anode (integrate 1, slow scan 3). Teilweise wurde auch ein LEO 1430 VP Gerät verwendet.

Die Bestimmung der Sandbienen erfolgte größtenteils durch Vergleich mit sicher bestimmtem Material, wobei uns Frau ANNA Z. OSYTŠNJUK (Kiew) in vielfältiger Weise behilflich war. Zu einer Reihe von zentralasiatischen Arten gibt es neuere morphologische Beschreibungen auf Deutsch von GUSENLEITNER & SCHWARZ (2000, 2001). Die Arbeiten von Frau OSYTŠNJUK sind in SCHEUCHL *et al.* (2000) aufgelistet.

Verglichene Arten. Da nicht sicher geklärt werden konnte, zu welcher Untergattung die in dieser Arbeit neu beschriebene Art gehört, wurde sie mit allen zur Verfügung stehenden Arten der relevanten Untergattungen verglichen. Soweit keine Sammlung genannt ist, stammen die Bienen aus der Zoologischen Staatssammlung München (ZSM).

Subgenus *Fumandrena* WARNCKE, 1975

Andrena (Fumandrena) fumida PEREZ, 1895, coll. WARNCKE (OÖLM, Oberösterreichisches Landesmuseum, Linz); *A. (F.) kurda* WARNCKE, 1975, Holotypus, coll. WARNCKE (OÖLM).

Subgenus *Graecandrena* WARNCKE, 1968

Andrena (Graecandrena) argyreofasciata SCHNIEDEKNECHT, 1900, coll. WARNCKE (OÖLM); *A. (G.) amicula* WARNCKE, 1967, coll. WARNCKE (OÖLM); *A. (G.) arsinoe* SCHMIEDEKNECHT, 1900, coll. WARNCKE (OÖLM); *A. (G.) butea* WARNCKE, 1966, coll. WARNCKE (OÖLM), *A. (G.) ebneri* ALFKEN, 1924, coll. WARNCKE (OÖLM); *A. (G.) graecella* WARNCKE, 1965, coll. WARNCKE (OÖLM) und coll. GRÜNWALDT(München); *A. (G.) hyemala* WARNCKE, 1973, coll. GRÜNWALDT, *A. (G.) hyemala repressa* WARNCKE, 1975, Paratype, coll. GRÜNWALDT, *A. (G.) ketupa* WARNCKE, 1975, coll. WARNCKE (OÖLM); *A. (G.) impunctata contusa* PE-

Tabelle 1. Liste der im Kugitang-Gebirge in Turkmenistan gefundenen Sandbienen.

		Nummer der Fundorte							
Art	**Untergattung**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
A. acutilabris MORAWITZ, 1876	*Nobandrena*		1♂						
A. albopunctata (ROSSI, 1792)	*Melandrena*		5♀♀ , 1♂	6♀♀					
A. combinata (CHRIST, 1791)	*Simandrena*		1 ♀	1 ♀					
A. cordialis MORAWITZ, 1877	*Corandrena*		1 ♀						
A. dolini OSYTSNJUK, 1979	*Langandrena*		7♀♀	2♀♀					
A. eversmanni RADOSZKOWSKI, 1867	*Plastandrena*	1 ♀							
A. fedtschenkoi MORAWITZ, 1876	*Ulandrena*								33♀♀ , 9♂♂
A. ferghanica MORAWITZ, 1876	*Plastandrena*						1♂	9♀♀ , 1♂	
A. flavipes PANZER, 1799	*Zonandrena*			5♀♀		2♀♀		8♀♀ , 1♂	
A. fuscosa ERICHSON, 1835	*Melanapis*	1♂	5♀♀	4♀♀					
A. gloriosa OSYTSNJUK, 1993	*Chlorandrena*		1♀	36 ♀♀		8 ♀♀		14 ♀♀	
A. ledermanni SCHÖNITZER, 1997	*Carandrena*			17 ♀♀		3♀♀			
A. maculipes MORAWITZ, 1876	*Chrysandrena*			3 ♀♀					
A. mikhaili OSYTSNJUK, 1982	*Ulandrena*					3♀♀			
A. nesteroviella OSYTSNJUK, 1993	*Micrandrena*		6 ♀♀	5♀♀	1♀				
A. pilipes FABRICIUS, 1781	*Plastandrena*					1 ♂		1♀, 3♂♂	
A. splendidicollis MORAWITZ, 1895	*Carandrena*	12♀♀							
A. subsmaragdina OSYTSNJUK, 1984	*Carandrena*						1 ♀		
A. thoracica (FABRICIUS, 1775)	*Melandrena*			1♀					
A. transiloria MORAWITZ, 1871	*Simandrena*							2♀, 1♂	
A. tringoides OSYTSNJUK, 1993	*Mircrandrena*		1♀	4♀♀, 2♂♂					2 ♀♀
A. tuberculiventris MORAWITZ, 1871	*Parandrenella*		2♀♀	1♀		1♀			
A. turanica OSYTSNJUK, 1993	*Chlorandrena*			1♀					
A. vetula LEPELETIER, 1841	*Ptilandrena*							2♂♂	
A. viridigastra MORAWITZ, 1876	*Melandrena*		1 ♀						

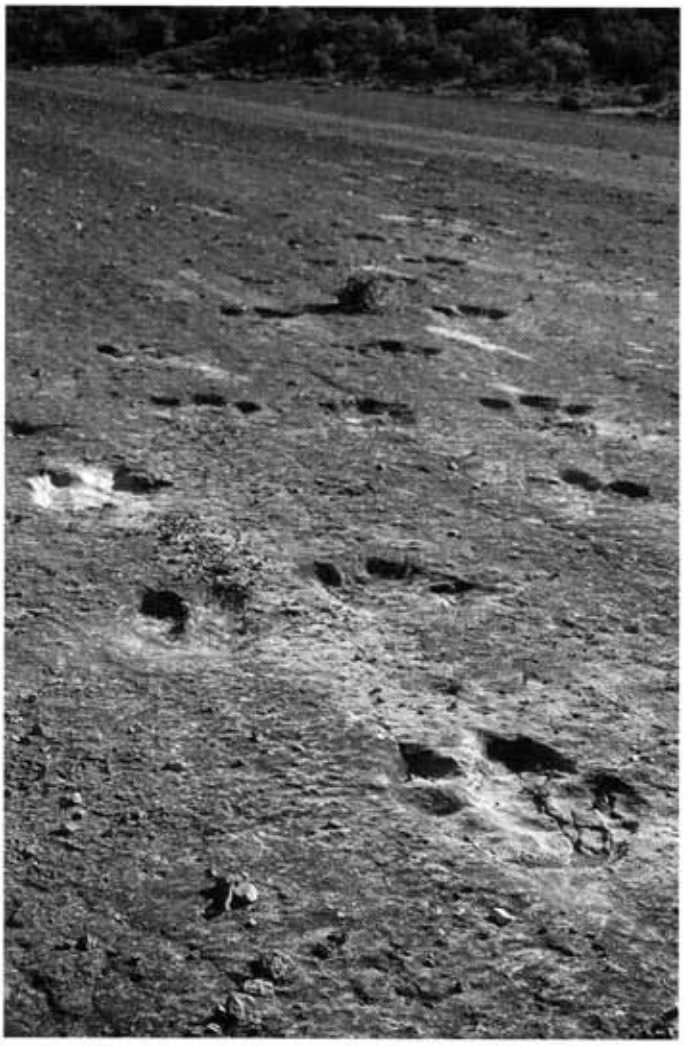

Abb. 1–4. Landschaften im Kugitang-Gebirge, Turkmenistan. **1:** ca. 1.600m, mit Blick auf den Airibaba (3.137m), etwas über dem Fundort Nr. 3 der Fundortliste; **2:** Blick in eine der Schluchten (Dareidare); **3:** Hodschapil, Plateau der Dinosaurierspuren aus dem oberen Jura, Fundort Nr. 6 der Fundortliste; **4:** Versteinerte Fußspuren von Dinosauriern (*Iguanodon*) im Kugitang-Gebirge (Fotos: Verfasser).

REZ, 1895, coll. WARNCKE (OÖLM); *A. (G.) montarca* WARNCKE, 1975, Paratypus, coll. WARNCKE (OÖLM), *A. (G.) nebularia* WARNCKE 1975, coll. GRÜNWALDT; *A. (G.) totana* WARNCKE, 1974, Paratypus, coll. WARNCKE (OÖLM); *A. (G.) verticalis* PEREZ,1895, coll. GRÜNWALDT und coll. WARNCKE (OÖLM); *A. (G.) zarkolia* OSYTSNJUK, 1994, Paratypus, coll. GRÜNWALDT.

Subgenus *Carandrena* WARNCKE, 1968

Andrena (Carandrena) aerinifrons DOURS, 1873; *A. (C.) cara* NURSE, 1904, coll. GRÜNWALDT; *A. (C.) ledermanni* SCHÖNITZER, 1997, Holotypus und Paratypen, Turkmenistan, Kugitang-Gebirge; *A. (C.) subsmaragdina* OSYTSNJUK 1984, Paratypen und Material aus Turkmenistan.

Subgenus *Micrandrena* ASHMEAD, 1899

Andrena (Micrandrena) minutula KIRBY, 1802; *A. minutoloides* PERKINS, 1914; *A. (M.) alfkenella* PERKINS, 1914; *A. (M.) pusilla* PEREZ, 1903; *A. (M.) subopaca* NYLANDER, 1848.

Ergebnisse

Der vorliegende Beitrag ist der erste zusammenhängende Bericht über die Sandbienenfauna des Kugitang-Gebirges und insofern natürlich nur von vorläufigem Charakter. Es konnten im Verlauf von nur zehn Tagen 27 *Andrena*-Arten nachgewiesen werden. Die einzelnen Arten und die jeweiligen Funddaten sind in Tabelle 1 zusammengestellt. Der Nachweis von *A. eversmanni* RADOSZKOWSKI, 1867, sowie ein Teil der Tiere von *A. nesteroviella* OSYTŠNJUK, 1993, und *A. tringoides* OSYTŠNJUK, 1993, wurden von V. DOLIN gefangen (coll. GRÜNWALDT), alle anderen wurden vom Erstautor gesammelt (ZSM).

Die geographischen Koordinaten des Kugitang-Gebirges sind etwa 37°30' bis 37°38' Nord und 66°15' bis 66°40' Ost.

Fundorte:

1. Umgebung von Čaršanga (Charshanga), Kainababa (350 m), 27.iv.95
2. Daraidare (Schlucht, 600–800 m); 28../29.IV.95
3. Plateau südl. von Daraidare (1.100–1.500 m); 30.iv./1.v.95 (Abb. 1)
4. Eingang zur Daraidare; 2.v.95
5. Hodschapil (= Khodzhapil) (1.150m); 2./3.v.95
6. Hodschapil (ca. 1.400 m); 2./3.v.95 (Abb.3)
7. Hodschapil (ca. 1.000 m), Krkgisata; an *Tamarix*; 4.v.95
8. Tutlidara (Schlucht, südlich von Daraidare, 600 m); 5.v.95
9. Umgebung Karlyuk; 6.v.95

Andrena lehmanni sp. nov.

Holotypus. ♀, Turkmenistan, Kugitang-Gebirge, Plateau neben Dareidare (ca. 1.500 m), leg. K. SCHÖNITZER, 30.IV.1995; Zoologische Staatssammlung München (ZSM).

Paratypen. 8 ♀: Turkmenistan, Kugitang-Gebirge, Plateau neben Dareidare (ca. 1.500 m), leg. K. SCHÖNITZER, 30.IV.1995 (ZSM); 1 ♀, Turkmenistan, Kugitang-Gebirge, Hodschapil, leg. K. SCHÖNITZER, 3.v.1995 (ZSM); 3 ♀, Turkmenistan, Kugitang-Gebirge, Plateau neben Dareidare (ca. 1100–1200 m), leg. W. DOLIN, 29.–30.IV.1995, coll. W. GRÜNWALDT (München).

Derivatio nominis. Die neue Art ist Herrn MICHAEL LEHMANN (Frankfurt am Main) gewidmet, der die biosystematische Forschung großzügig finanziell unterstützt hat[1].

Beschreibung. ♀, 7–8 mm. Habitus siehe Abb. 5.

Kopf. Kopf relativ breit (Abb. 6a). Clypeus nur wenig gewölbt, mit rauher Oberflächenskulptur, undeutlich und flach punktiert (Abb. 7b). Labrumanhang breit, flach trapezförmig, am Vorderrand bei manchen Tieren leicht eingebuchtet (Abb. 6c). Galea chagriniert, unpunktiert. Breite der Fovea facialis (FOV) im oberen Drittel ca. 0,31 bis 0,32 der Gesichtshälfte (gemessen nach SCHMID-EGGER & SCHEUCHL 1997), nach unten zu um knapp die Hälfte verschmälert. FOV oben relativ klar begrenzt. Sie reicht nach unten nur bis zur Höhe der Antennenbasis und erreicht nicht die Höhe des Oberrandes der Komplexaugen (Abb. 6a, b, 7a). Zwischen FOV und Komplexauge ein glänzender glatter, fein punktierter Kutikulastreifen. Stirn längsgerieft, Mittellinie undeutlich. Abstand der seitlichen Ocellen vom Scheitelrand etwas kleiner als ihr Durchmesser. Schläfen deutlich breiter als das Komplexauge, rauh chagriniert, undeutlich punktiert.

Antennen. Relativ kurz, breit, leicht gekeult, Scapus reicht nicht bis zur Mittelocelle. 3. Antennenglied deutlich kürzer als die drei folgenden zusammen, 4. und 5. Antennenglied deutlich kürzer als breit, 5. Antennenglied meist kürzer als das vierte. 6. und 7. Antennenglied etwas kürzer als breit (Abb. 6d).

Thorax. Mesonotum chagriniert, zerstreut punktiert, Punktierung hinten dichter. Scutellum chagriniert, aber rauher als Mesonotum, punktiert. Postscutellum noch rauher strukturiert (Abb. 7c). Mesopleura chagriniert, vor allem vorne mit Kraterpunkten, Metapleura unpunktiert. Mittelfeld des Propodeums feinrunzelig, ohne gratige Erhebungen (Abb. 7c). Seitenteile des Propodeums (Körbchen des Propodeums) wabig chagriniert, zerstreut punktiert. Flügel: Nervulus antefurcal oder intermedial. Discoidalader mündet i. d. R. vor der Mitte in die 2. Cubitalzelle.

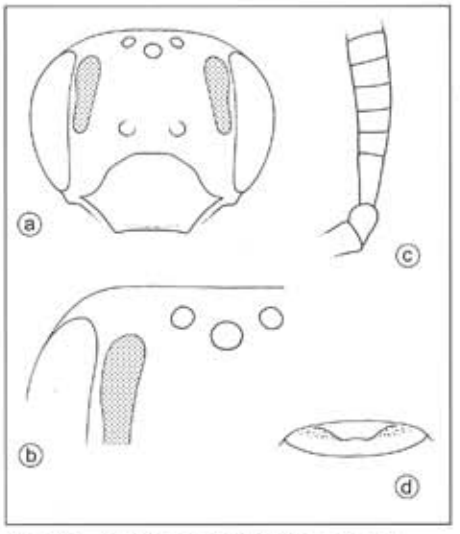

Abb. 6. *Andrena lehmanni* sp. nov. **a:** Gesicht von vorne, gepunkteter Bereich = Fovea facialis; **b:** oberer Teil des Gesichtes mit Ocellen und oberem Teil der Fovea facialis; **c:** Labrumanhang; **d:** Basale Glieder der Antennengeißel (Zeichnungen: E. SCHEUCHL).

Abdomen. Gesamtform nach hinten zu relativ breit. Tergite auffällig glänzend, glatt, praktisch nicht chagriniert, sehr fein punktiert. Tergite bei zwei Paratypen schwach chagriniert, weniger glänzend. Depressionen relativ breit, mehr als ein Drittel des sichtbaren Teils der Tergite einnehmend, apical fast vollständig hyalin. Seitlich an den Tergiten leichte, praktisch unpunktierte Erhebungen. Pygidialplatte mit deutlich erhöhtem dreieckigem Mittelfeld sowie abgesenktem Rand (Abb. 7d).

Behaarung und Färbung. Insgesamt sehr schwach behaart, weißlich oder gelblich (Abb. 5). Sammelfranse des Körbchens schwach ausgebildet. Scopa relativ schwach entwickelt, hellbraun mit deutlich

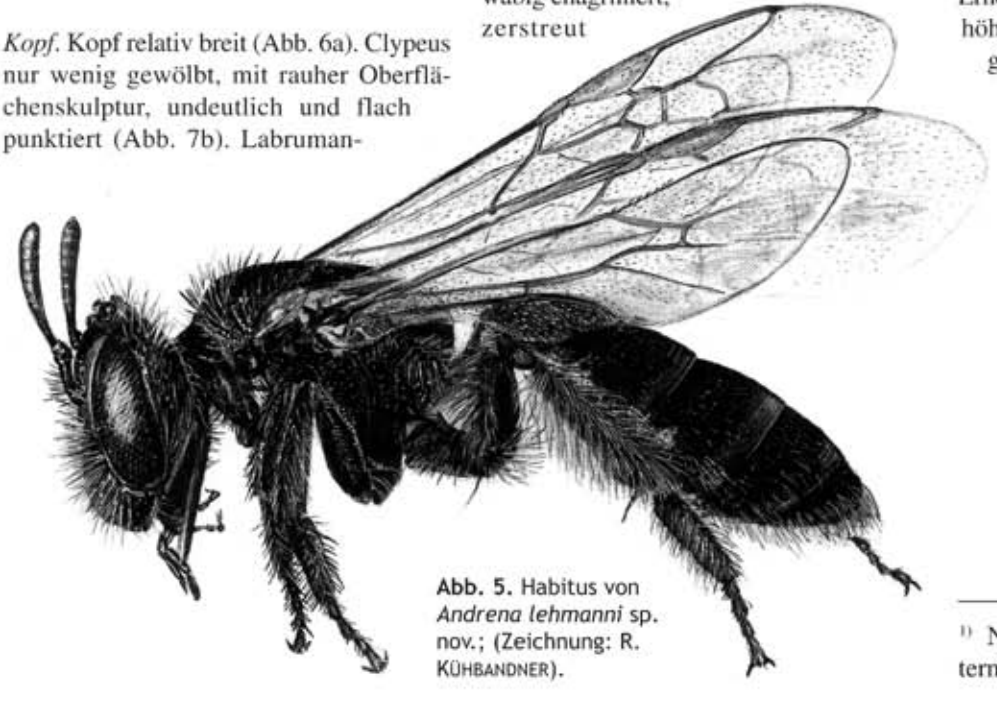

Abb. 5. Habitus von *Andrena lehmanni* sp. nov.; (Zeichnung: R. KÜHBANDNER).

[1] Näheres hierzu ist zum Beispiel im Internet unter www.biopat.de zu finden.

verzweigten Haaren, die seitlichen Verzweigungen sehr zart. Flocculus schwach entwickelt, weiß. Keine Binden auf den Tergiten, praktisch haarlos, lediglich Wimpernreihe am 4. Tergitende. Sternite kurz behaart, nur am Ende länger, gelblich. Endfranse gelb bis braun. Kutikula dunkel, lediglich Antennengeißel ab dem 2. oder 3. Glied gelblich, Mittel- und Hintertarsen etwas aufgehellt. Stigma und Flügelgeäder gelblich. Bei zwei Exemplaren (vom gleichen Fundort wie der Holotypus) Behaarung und Kutikula etwas heller, z.B. praktisch gelbe, unpigmentierte Fühlergeißel.

Differentialdiagnose. *Andrena lehmanni* sp. nov. ist den Arten *Andrena (Graecandrena) ebneri* und *A. (G.) hyemala* am ähnlichsten. Vor allem mit *A. ebneri* verbindet die neue Art zahlreiche gemeinsame Merkmale wie Habitus, Größe und Behaarung sowie die Struktur des Propodeum-Mittelfeldes. Letzteres weist bei beiden Arten keinerlei Runzelung auf und ist, wie die angrenzenden Seitenflächen, lediglich punktartig skulptiert. Von den beiden oben genannten Arten lässt sich die neue Art jedoch eindeutig durch die folgenden Merkmale unterschieden:

Von *A. (G.) ebneri* kann die neue Art durch die deutlicher abgegrenzte und etwas schmälere FOV, die insgesamt kürzere Fühlergeißel, das Fehlen von Haarbinden am Ende der Abdominaltergite, den viel stärkeren und breiteren Depressionen auf diesen sowie das deutlich erhöhte Mittelfeld der Pygidialplatte unterschieden werden. Während bei *A. (G.) ebneri* das 2. Antennenglied mehr oder weniger quadratisch ist, ist es bei *A. (G.) lehmanni* deutlich kürzer als breit. Ebenso verhält es sich mit dem 4. und 5. Antennenglied. Zudem ist bei der neuen Art das Mesonotum und Scutellum zwischen den Punkten deutlich chagriniert, im Gegensatz zu den glatten Punktzwischenräumen bei *A. (G.) ebneri.* Ein weiteres sehr auffälliges Unterscheidungsmerkmal stellt die lange verzweigte Scopabehaarung auf der gesamten Außenseite der Hintertibien bei *A. lehmanni* sp. nov. dar. Bei *A. (G.) ebneri* befindet sich lediglich entlang der Hinterkante eine schmale Reihe dieses Haartyps, auf der Tibienaußenseite hingegen besteht die Behaarung aus einfachen, unverzweigten Haaren.

An Hand der Scopabehaarung kann *Andrena lehmanni* sp. nov. auch eindeutig von *A. (G.) hyemala* (mit einfacher Scopabehaarung) abgegrenzt werden. Als weitere Unterscheidungsmerkmale zwischen diesen beiden Arten wären der deutlich breitere Kopf, die deutlich flachere und insgesamt breitere und kürzere FOV bei *A. (G.) lehmanni* sp. nov., sowie die flache Pygidialplatte bei *A. (G.) hyemala* anzuführen. Während die Stirn bei *A. lehmanni* sp. nov. eine auffällige, sehr feine Längsriefung aufweist, ist bei *A. (G.) hyemala* der Abstand zwischen den hinteren Ocellen und dem Scheitelrand deutlich kleiner als die Hälfte eines Ocellendurchmessers, bei *A. lehmanni* sp. nov. entspricht er dagegen fast einem Ocellendurchmesser. Die bei *A. lehmanni* sp. nov. deutlich punktierten und schwach chagrinierten Abdominaltergite 1 und 2 sind bei *A. (G.) hyemala* vollkommen punktlos, aber viel stärker chagriniert. Gemeinsam ist beiden Arten die Fühlerform und -farbe sowie die Länge der Geißelglieder.

Diskussion

Obwohl schon FEDTSCHENKO in den Jahren 1886 bis 1871 Bienen in Zentralasien („Turkestan") gesammelt hatte, die von MORAWITZ bearbeitet wurden (MORAWITZ, 1876; WARNCKE, 1989), wurde vom Kugitang-Gebirge bisher noch keine faunistische Arbeit über Bienen publiziert. Die vorgelegte Artenliste stellt auch nur einen ersten Beitrag zur Faunistik der Sandbienen im Kugitang-Gebirge dar und stellt sicher nur einen kleinen Ausschnitt aus dem insgesamt wohl viel höheren Artenspektrum dieser Region dar. *A. (Longandrena) dolini* wurde bisher lediglich von der Typuslokalität in anderen Gebieten Turkmenistans (dem Badghiz) bekannt. *A. (Chlorandrena) gloriosa, A. (Micrandrena) nesteroviella, A. (Micrandrena) tringoides* und *A. (Chlorandrena) turanica* wurden von OSYTŠNJUK (1993a, b) aus dem Kugitang-Gebirge und anderen Teilen Zentralasiens beschrieben. Über die tatsächliche Verbreitung dieser Arten kann man nur spekulieren, es ist aber anzunehmen, dass es sich um rein zentralasialische Arten handelt. Andere Arten sind sehr weit verbreitet, wie *A. (Plastandrena) pilipes* und *A. (Simandrena) combinata*, die von der Ostpalaearktis bis Europa vorkommen. Auf jeden Fall ist das Gebiet noch unzureichend untersucht und sicher sind noch etliche weitere Arten zu erwarten.

Eine weitere Sandbienenart für das Kugitang-Gebirge wurde von Frau OSYTŠNJUK bereits 1986 nachgewiesen (*Andrena (Euandrena) zaaminensis* OSYTŠNJUK, 1986). Damit sind insgesamt 28 *Andrena*-Arten aus dem Kugitang-Gebirge bekannt.

Die in der vorliegenden Arbeit beschriebene Art *Andrena lehmanni* sp. nov. kann nicht eindeutig einer der bestehenden Untergattungen zugeordnet werden, da die Abgrenzung der Untergattungen nicht geklärt ist. Aus den Beschreibungen der einzelnen Untergattungen geht oft nicht klar genug hervor, an welchen Merkmalen man die einzelnen Untergattungen eindeutig erkennen kann. Nach der Bestimmungstabelle von WARNCKE 1968 gehört die neue Art in die Untergattung *Graecandrena*. Auch ihre Ähnlichkeit mit den Arten *A. (G.) ebneri* und *A. (G.) hyemala* weist darauf hin, dass sie eventuell in diese Untergattung gehört. Das deutlich erhabene Mittelfeld der Pygidialplatte legt andererseits ein verwandtschaftliches Verhältnis zur Untergattung *Micrandrena* nahe. Die kaum gerunzelte Skulptur des Mittelfeldes des Propodeums sowie die verzweigten Haare der Tibialscopa weisen jedoch auf eine mögliche Verwandtschaft mit der Untergattung *Fumandrena* hin. An Hand der oben genannten Arten wurden deshalb Übereinstimmungen bzw. Unterschiede von *A. lehmanni* sp. nov. zu den drei ähnlichen Untergattungen *Graecandrena, Micrandrena* und *Fumandrena* charakterisiert und tabellarisch zusammengestellt (Tab. 2). Aufgrund der bei *A. lehmanni* sp. nov. gefundenen Merkmalskombinationen ist somit die Einordnung in eine neue Untergattung denkbar, jedoch ohne Kenntnis des Männchens allein auf der Morphologie des Weibchens basierend nach jetzigem Kenntnisstand nicht sinnvoll. Leider liegen keine Männchen der neuen Art vor, offensichtlich war die Flugzeit während der Aufsammlung bereits weit fortgeschritten. Dafür spricht auch, dass ein Großteil der gefangenen Weibchen stark abgeflogen waren.

Ebenso ist die Zuordnung von *Andrena semiaenea* MORAWITZ, 1876, in eine der bestehenden Untergattungen unklar. Nach GUSENLEITNER & SCHWARZ (2001) gehört sie zur Untergattung *Poecilandrena* HEDICKE, 1933, jedoch nach XU & TADAUCHI (1997) in die Untergattung *Lepidandrena* HEDICKE, 1933. Nach unserer Ansicht ist diese Art jedoch auf Grund verschiedener Merkmale (Dornen an den Hinterfemora, Innensporn der Hintertibien basal nicht verbreitert, Pygidialplatte

mit dreieckig erhöhtem Mittelfeld) in keine der beiden Untergattungen problemlos einzugliedern.

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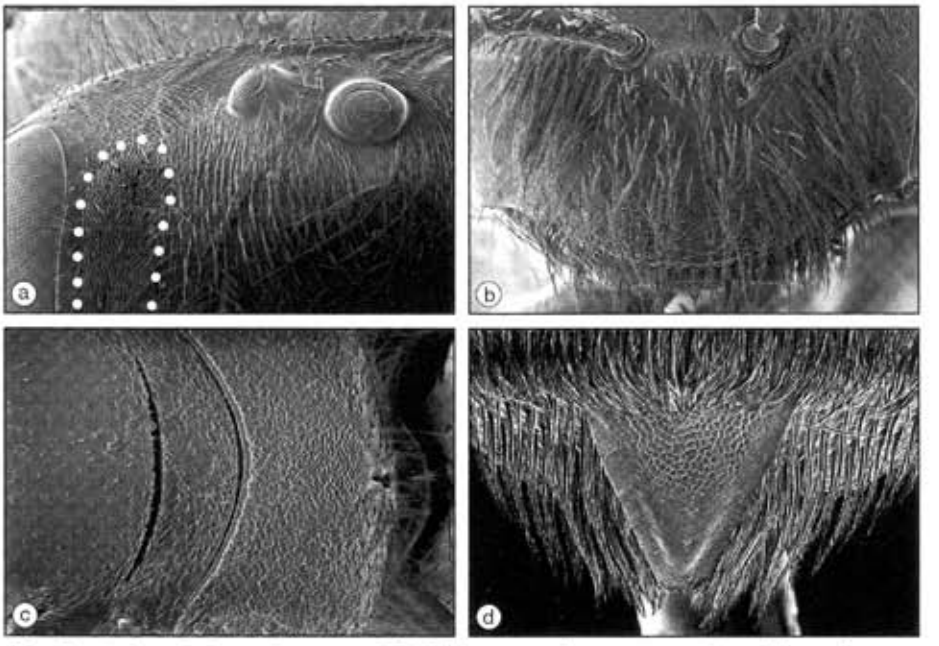

Abb. 7. *Andrena lehmanni* sp. nov., REM-Bilder von unbesputtertem Material. **a:** oberer Teil des Gesichtes mit Ocellen und oberem Teil der Fovea facialis (Außenrand gepunktet); **b:** Clypeus; **c:** Scutellum, Postsutellum und Mittelsegment des Propodeums (links = anterior); **d:** Pygidium. (Aufnahmen: A. DUBITZKY & K. SCHÖNITZER).

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Tabelle 2. Gemeinsamkeiten und Unterschiede von *Andrena lehmanni* spec. nov. und den nah verwandten Untergattungen *Graecandrena* WARNCKE, 1968, *Micrandrena* ASHMEAD, 1899, und *Fumandrena* WARNCKE, 1975 (die angeführten Merkmalszustände beziehen sich auf *Andrena lehmanni* spec. nov.).

Untergattung	Übereinstimmungen	Unterschiede
Graecandrena WARNCKE, 1968	- Struktur von Mesonotum und Scutellum - relativ kurze keulenförmige, gelbliche Antennen - spärlich behaarte Tergite	- dreieckig erhöhtes Mittelfeld der Pygidialplatte - Tibialscopa aus verzweigten Haaren - stark eingedrückte, hyaline Depressionen der Tergite
Micrandrena ASHMEAD, 1899	- dreieckig erhöhtes Mittelfeld der Pygidialplatte - Form der FOV	- Tibialscopa aus verzweigten Haaren - stark eingedrückte, hyaline Depressionen der Tergite - Mittelfeld des Propodeums ohne jede Runzelung, wie Seiten strukturiert - relativ kurze keulenförmige, gelbliche Antennen - Stigma und Flügeladerung gelblich
Fumandrena WARNCKE, 1975	- Mittelfeld des Propodeums kaum gerunzelt, wie Seiten strukturiert - Tibialscopa aus verzweigten Haaren - spärlich behaarte Tergite	- dreieckig erhöhtes Mittelfeld der Pygidialplatte -Kopf breiter - flacher Labrumanhang - stark eingedrückte, hyaline Depressionen der Tergite

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● Prof. Dr. KLAUS SCHÖNITZER & Dipl.-Biol. ANDREAS DUBITZKY, Zoologische Staatssammlung München, Münchhausenstr. 21, D-81247 München, Germany; E-Mail: schoenitzer@zsm.mwn.de

Curriculum vitae

Personal Details

Dipl.-Biol. Andreas Dubitzky
Birkenweg 5
85241 Hebertshausen
phone: 08131/279572
e-mail: andreas_dubitzky@yahoo.de

8.10.1972 — Born in Dachau
Status: single
Nationality: German

Schooling

1979-1983 — Primary school in Hebertshausen

1983-1992 — Josef-Effner-Gymnasium in Dachau
Final examination: Abitur

Alternative Service

09/1992-11/1993 — Landesbund für Vogelschutz in Bayern e.V., Office Munich

Academic Education

11/1993-03/2000 — Study of Biology at the Ludwig-Maximilians-Universität München (LMU). Main subject: Zoology; minor subjects: Ecology, Systematic Botany, Paleontology.

Diploma thesis: "Faunistisch-ökologische Untersuchung der Insektenfauna (Schwerpunkt Hymenoptera, Orthoptera) im Dachauer Norden"
Award of the academic degree "Diplom-Biologe"
General mark: 1.1

since 02/2001 — Doctoral dissertation: "Studies in phylogeny and biosystematics of bees: The bee genus *Andrena* (Andrenidae) and the tribe Anthophorini (Apidae) (Insecta: Hymenoptera: Apoidea)"
Supervisor: Prof. Klaus Schönitzer, LMU

Scholarships

10/2001-10/2003 — Scholarship of the LMU (Graduiertenförderung)

8-9/2002 — Scholarship by the DAAD-NSC joint Research Collaboration (DAAD, PPP D/0039914) supporting field work on Taiwan

Relevant positions

1996-2000 — Teaching assistent for the course "determination and diversity in zoology" at the Zooological Institute of the LMU and during several university field trips

1996-2000 — Student assistant at the Zoologischen Staatssammlung München, sections Herpetology and Hymenoptera

04/2000-04/2001 — Scientific assistant at the Zoologische Staatssammlung München, section Hymenoptera

9-11/2005 — Expertise within a landscape managment project of the Bayerisches Landesamt für Umwelt (LfU)