Mitt. Münch. Ent. Ges.	**100**	137-202	München, 15.10.2010	ISSN 0340-4943

Phylogeny of the bee genus *Andrena* FABRICIUS based on morphology

(Hymenoptera: Andrenidae)

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Abstract

The present study provides the first phylogenetic hypothesis for the largest genus of bees, *Andrena*, at the subgeneric level. A cladistic analysis based on 162 morphological characters was carried out which included representatives from 84 of the nearly 100 currently recognized 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 of other Andreninae. The unweighted heuristic analysis resulted in six most parsimonious trees of 1876 steps. The monophyly of *Andrena* was confirmed by five non-homoplasious apomorphies. The subgenus *Cubiandrena* was not a part of *Andrena* and it is tentatively regarded herein as a separate genus. A second analysis using successive character reweighting (*a posteriori* weighting) resulted in a single cladogram which partly agrees with the results of the unweighted heuristic search. In both analyses 14 clades comprised the same taxa, 11 of which had identical internal topologies. Each of the Holarctic subgenera *Larandrena*, *Micrandrena* and *Ptilandrena* were shown to be polyphyletic in both unweighted and weighted analyses. Although the New World is generally hypothesized as the place of origin of the Andreninae, according to the present study *Andrena* appears to have originated in the Old World, presumably in the Mediterranean region or Central Asia. 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.

The following subgenera of *Andrena* are described as new: *Calcarandrena* DUBITZKY **subgen. nov.**, *Hamandrena* DUBITZKY **subgen. nov.** and *Platygalandrena* DUBITZKY **subgen. nov.** The subgenus, *Cubiandrena* WARNCKE, 1968 **stat. nov.**, was raised to generic rank; the number of *Andrena* subgenera recognized herein amounts to 101 (17 Holarctic, 51 Palearctic, 32 Nearctic and 1 Oriental). Two taxa were raised to specific rank: *A. eburnea* WARNCKE, 1975 **stat. nov.** and *A. impasta* WARNCKE, 1975 **stat. nov.**

Introduction

Andrena FABRICIUS (1775), commonly called sand or solitary mining bees, is the largest genus of bees in numbers of species according to present day classification (MICHENER 2007). To date, *Andrena* contains about 1500 valid species and about as many synonyms (GUSENLEITNER & SCHWARZ 2002, GUSENLEITNER et al. 2005). The actual number of species of *Andrena* may be higher, and we roughly estimate a total of about 2000 species since many have yet to be described, especially from Mesoamerica and the dry regions of Central Asia. The vast number of species is clearly a special challenge for systematists. *Andrena* rightly deserves to be called one of the largest genera of animals (MAYR & ASHLOCK 1991, MINELLI 1993), in the same league as *Drosophila* (Diptera), *Atheta* or *Onthophagus* (both Coleoptera). The diversity in the habitus of the species is exemplified in color plates (Fig. I-III).

Distribution. Sand bees are abundant in the temperate regions of the northern continents of both hemispheres. However, species richness is greatest in the warmer and dryer Mediterranean-like climates, such as occur in the North American southwest, the Mediterranean basin, and the steppes of Central Asia (MICHENER 1979, 2007).

Of the 98 subgenera of *Andrena* recognized by GUSENLEITNER & SCHWARZ (2002), 18 occur in both hemispheres, while 47 are restricted to the Palearctic, 32 to the Nearctic, and one to the Oriental realm (BAKER 1995). Only two species, *A.* (*Leucandrena*) *barbilabris* (KIRBY, 1802) and *A.* (*Andrena*) *clarkella* (KIRBY, 1802), are truly Holarctic, i.e., with a native distribution in the Nearctic and Palearctic regions. A third species, *A.* (*Taeniandrena*) *wilkella* (KIRBY, 1802), is considered to be Holarctic, but was introduced from Europe to North America (LANHAM 1949). No species of *Andrena* occur in South America, Madagascar and surrounding islands, the entire Australian region and neighboring Pacific Ocean islands. Few species are endemic to sub-Saharan Africa and one to Malaysia (MICHENER 2007, BAKER 1995).

History of classification. FABRICIUS (1775) first described *Andrena* and listed 14 species. It was the fourth genus of bees to be proposed after *Apis* LINNAEUS, 1758, *Eucera* SCOPOLI, 1770 and *Nomada* SCOPOLI, 1770. Considering the preponderance of species of *Andrena*, it is no wonder that the genus was early divided into subgenera or species groups by taxonomists. The first attempt to subdivide *Andrena* was carried out by NYLANDER (1852), who combined the species into seven groups called "stirps" (Latin: branch). However, his subdivision was largely intended to assist determination and does not represent a natural classification. THOMSON (1872) split *Andrena* into two main groups and further subdivided each group. However, neither NYLANDER (1852) nor THOMSON (1872) proposed subgeneric names for the groups based on their subdivisions.

DOURS (1873) was the first to establish valid subgeneric names for Andrena that were based on reliable species groups. He split the genus into three subgenera, *Andrena* s.str. (Color plates: Fig. IA,B), *Biareolina* (Fig. ID) and *Campylogaster*. PÉREZ (1890) undertook a broader classification of *Andrena* and provided six additional subgeneric names based on distinct species groups that remain valid to date (i.e., *Melandrena*, Fig. IC, *Holandrena*, *Hoplandrena*, *Notandrena*, *Chlorandrena* and *Simandrena*, Fig. IIIB). The taxa *Didonia* GRIBODO, 1894, *Callandrena* COCKERELL, 1898, *Micrandrena* ASHMEAD, 1899 (Fig. IIID), *Melanapis* CAMERON, 1902 and *Diandrena* COCKERELL, 1903 were proposed initially as separate genera within Panurginae or Andreninae and have been subsequently transferred to *Andrena* as subgenera.

After extensive collection and description of many new species of *Andrena* from Illinois, USA in the years 1891 and 1892, ROBERTSON (1902) reduced the scope of the genus by splitting off six genera: *Parandrena* ROBERTSON, 1897, *Iomelissa* ROBERTSON, 1900, *Opandrena*, *Ptilandrena*, *Trachandrena* and *Pterandrena* ROBERTSON, 1902. All except *Pterandrena*, which is a synonym of *Callandrena*, are currently recognized as Nearctic subgenera of *Andrena*.

VIERECK (1924) provided a key to the subgenera of *Andrena* recognized at that time and introduced several new (and monotypic) subgenera: *Gonandrena* VIERECK, 1917, *Scrapteropsis* VIERECK, 1922, *Conandrena* and *Dactylandrena* VIERECK, 1924. *Melittoides* FRIESE, 1921 was originally proposed as a separate genus for several southern Palearctic species. MICHENER (1944: 254) placed the genus in Melittinae (Melittidae). WARNCKE (1968a) regarded it as a subgenus of *Andrena*. MICHENER (2007: 258) raised *Melittoides* to generic status, while GUSENLEITNER & SCHWARZ (2002) retained *Melittoides* as a subgenus of *Andrena*.

HEDICKE (1933) subdivided all Palearctic species of *Andrena* available to him into subgenera and introduced several new names, the following of which are still considered valid: *Charitandrena*, *Chrysandrena*, *Cnemidandrena*, *Euandrena* (Fig. IIC), *Lepidandrena* (Fig. IE), *Leucandrena*, *Plastandrena*, *Poecilandrena* (Fig. IIIC), *Taeniandrena* (Fig. IIA) and *Zonandrena* HEDICKE, 1933 (Fig. IIIA). His classification was based on studies by PÉREZ (1890), PERKINS (1919) and STOECKHERT (1930), and he designated type species for several previously proposed subgeneric names.

Additional subgenera were described for the Nearctic region by LANHAM (1949) and TIMBERLAKE (in LANHAM 1949). The following subgenera of *Andrena* which they described are still considered valid: *Aporandrena*, *Oligandrena*, *Scaphandrena*, *Scoliandrena*, *Thysandrena* LANHAM, 1949 and *Hesperandrena* TIMBERLAKE, 1949. At about the same time, several new Palearctic subgenera were described by PITTIONI: *Brachyandrena*, *Cryptandrena* and *Hyperandrena* PITTIONI, 1948. Another Palearctic subgenus, *Parandrenella* POPOV, 1958 was added a few years later. Between the 1960s and 1980s numerous new Nearctic and Palearctic subgenera of *Andrena* were introduced. In 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 21 new subgenera but attempted to provide a well-founded phylogeny of the species included within each subgenus: *Chaulandrena*, *Larandrena*, *Tylandrena* LABERGE, 1964, *Celetandrena* LABERGE & HURD, 1965, *Belandrena*, *Derandrena* RIBBLE, 1968, *Nemandrena*, *Rhaphandrena*, *Xiphandrena* LABERGE, 1971, *Geissandrena*, *Pelicandrena* LABERGE

& RIBBLE, 1972, *Dasyandrena* LABERGE, 1974, *Oxyandrena*, *Psammandrena*, *Rhacandrena* LABERGE, 1977, *Anchandrena*, *Archiandrena*, *Augandrena*, *Cremnandrena*, *Erandrena* and *Genyandrena* LABERGE, 1986.

Several subgenera were proposed by HIRASHIMA & LABERGE (in HIRASHIMA, 1963, 1964b, 1965b) and HIRASHIMA & TADAUCHI (1975) for eastern Palearctic species: *Calomelissa* HIRASHIMA & LABERGE, 1963, *Habromelissa* HIRASHIMA & LABERGE, 1964, *Stenomelissa* HIRASHIMA & LABERGE, 1965 and *Oreomelissa* HIRASHIMA & TADAUCHI, 1975.

The western Palearctic subgenera were revised by WARNCKE (1968a) who introduced 19 new subgenera: *Aciandrena*, *Aenandrena*, *Agandrena* (Fig. IIB), *Avandrena*, *Carandrena*, *Cordandrena*, *Cubiandrena*, *Distandrena*, *Graecandrena*, *Margandrena*, *Nobandrena*, *Orandrena*, *Pallandrena*, *Poliandrena*, *Rufandrena*, *Scitandrena*, *Suandrena* (Fig. IID), *Truncandrena* and *Ulandrena*. Two additional subgenera were erected by WARNCKE (1975a): *Fumandrena* and *Troandrena*. WARNCKE's studies represent some of the most comprehensive works dealing with the Palearctic species of *Andrena* to date. Unfortunately his descriptions are often insufficient and do not clearly distinguish between description and diagnosis. Also, some of the characters used to define subgenera are absent in most of the included species, and sometimes even in the type species.

Several new subgenera for central Palearctic species were described by OSYTSHNJUK (1983a, 1984a-b, 1993a, 1994a): *Planiandrena* OSYTSHNJUK, 1983, *Leimelissa*, *Tarsandrena* OSYTSHNJUK, 1984, *Carinandrena*, *Longandrena* OSYTSHNJUK, 1993 and *Fuscandrena* OSYTSHNJUK, 1994. The monotypic subgenus *Malayapis* BAKER, 1995 currently includes the only known species from the Oriental realm.

In a study of North and Middle European species of *Andrena*, DYLEWSKA (1987) abandoned the subgeneric classification and introduced discrete species groups and subgroups, some of which fused or split established subgenera.

MICHENER (2007) listed 95 subgenera of *Andrena*, replaced the preoccupied name *Carinandrena* OSYTSHNJUK, 1993 with *Osychnyukandrena* MICHENER, 2000 and raised the subgenus *Melittoides* to the generic level. GUSENLEITNER & SCHWARZ (2002) recognized 98 subgenera (including *Melittoides*) and synonymized *Truncandrena* WARNCKE, 1968 with *Scaphandrena* LANHAM, 1949. This paper disagrees with the latter synonymy and recognizes *Truncandrena* as a valid subgenus. Lastly, SCHMID-EGGER (2005) removed *Andrena proxima* (KIRBY, 1802) and four closely related species from the subgenus *Micrandrena*, placing them in a new subgenus, *Proxiandrena* SCHMID-EGGER, 2005 (Fig. IF).

Taxonomy. The taxonomy of *Andrena* has been thoroughly studied for the western Palearctic region by WARNCKE (1965a-b, 1966, 1967, 1968a-b, 1969a-b, 1972, 1974a-b, 1975a-b, 1976, 1980) and GUSENLEITNER (1994, 1998); for central Asia by OSYTSHNJUK (1975, 1979, 1982a-c, 1983a-b, 1984a-d, 1985, 1986a-b, 1993a-c, 1994a-b) and TADAUCHI (2006); 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 & MATSUMURA (2007), TADAUCHI & XU (1995, 1998, 1999, 2000, 2002, 2004), XU & TADAUCHI (1995, 1997a-b, 1998, 2002, 2005a-b, 2006), TADAUCHI, MIYANAGA & DAWUT (2005); 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), DONOVAN (1977) and THORP & LABERGE (2005a-b).

Phylogeny. Very few studies have focused on the phylogenetic relationships of *Andrena* species. WARNCKE (1968a) postulated relationships for the species of Palearctic subgenera, but they were based on subjective opinion, rather than character analysis. His ideas on the phylogeny of Palearctic *Andrena* remain obscure and are in large parts incomprehensible due to a lack of data. TADAUCHI (1982, 1985a) presented a phenetic study of species of *Andrena* from Japan. LABERGE presented well founded phylogenetic hypotheses for the species of each subgenus he treated in his comprehensive revisions of the Nearctic subgenera (see references above). In a paper on the zoogeography of Nearctic *Andrena* species, LABERGE (1986b) addressed questions on the phylogenetic relationships of North American species at the subgeneric level, wherein he provided hints for possible relationships for some species of Palearctic subgenera. LARKIN (2002, 2006) was the first to conduct a molecular phylogenetic analysis of *Andrena* species. She focused her analysis on Nearctic species of *Callandrena* and additionally included Nearctic species from 24 subgenera of *Andrena*.

No previous attempts have been made to address the monophyly of *Andrena* by means of phylogenetic analysis. Furthermore, its phylogenetic position within the family, as well as the relationships of the Andrenidae to remaining families of short-tongued (S-T) bees has not been satisfactorily analyzed. The results of the 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 sister group to the remaining S-T bees except the Andrenidae. In that study neither the monophyly of Andreninae nor the placement of *Andrena*, represented by *A*. (*Tylandrena*) *erythrogaster* (ASHMEAD, 1890), in the family could be demonstrated. The results varied depending on the particular design of the analyses, in some the relationship of *Andrena* to the Andreninae, Stenotritidae and Oxaeinae was unresolved; in another analysis, *Andrena* was sister to the remaining Andreninae, Panurginae and Oxaeinae; while in a further analysis, *Andrena* combined with (*Euherbstia* + *Alocandrena*) as sister to *Protoxaea* + (*Megandrena* + Panurginae); and lastly *Andrena* was sister to (*Megandrena* + Panurginae) and more derived than *Euherbstia*, *Protoxaea* and *Alocandrena*.

ASCHER (in ROZEN 2003) presented preliminary results of a cladistic analysis using a molecular data set of 294 parsimony informative sites from two adjacent exons of the nuclear protein-coding gene EF-1α (F2 copy) to determine the position of *Nolanomelissa toroi* (ROZEN, 2003) within the Andrenidae. The analysis included species from a broad sample of genera: 11 Andreninae, one Oxaeinae, 15 Panurginae and 10 outgroup taxa. The results seemed to confirm the monophyly of the Andrenidae with the inclusion of Oxaeinae. Likewise, the monophyly of the Andreninae was demonstrated. The subfamily was divided into the Euherbstiini, containing *Euherbstia* and *Orphana*; and the Andrenini, containing representatives of *Alocandrena*, *Ancylandrena*, *Andrena* and *Megandrena*. The interrelationships of the Andrenini were not discussed in the paper, which focused primarily on the position of *Nolanomelissa* to other Panurginae.

Despite these attempts to shed light on the phylogeny of the Andrenidae, the evolution of *Andrena* and phylogenetic relationships of its nearly 100 subgenera remain largely unknown. In consideration of the extraordinarily large numbers of described species, this study represents an initial investigation focused primarily at the subgeneric level. The main goal is to present a comprehensive phylogenetic hypothesis for species of *Andrena* on a global basis and at the subgeneric level. The paper also entails an examination of the monophyly of selected subgenera and the position of *Andrena* within the Andreninae (*sensu* MICHENER 2007). The systematic position of about 17 species is addressed in consideration of the description of three new subgenera of *Andrena*. Preliminary results of the study were presented in DUBITZKY & SCHÖNITZER (2006).

Material and methods

Material studied

Species of the following genera were morphologically examined (total number of specimens in parenthesis): Andrenidae: *Andrena* (1985), *Ancylandrena* (4), *Megandrena* (5), *Euherbstia* (2), *Orphana* (2), other Andrenidae excepting Andreninae (87). Altogether about 700 species of Andrenidae from diverse biogeographical regions were examined in an external morphological study prior to selection of species and characters to acquire information on morphological variation and character distribution which may assist in estimation of subgeneric concepts and decisions on character polarity (WÄGELE 1999).

The studied material was obtained from the following collections and institutions:

AMNH	American Museum of Natural History, New York, USA
CAD	Private collection of A. DUBITZKY, Hebertshausen, Germany
CFG	Private collection of F. GUSENLEITNER, St. Georgen/Gusen, Austria
CGW	Collection of R. W. GRÜNWALDT, since 2003 housed in ZSM, Munich, Germany
CKW	Collection of K. WARNCKE, housed in Biologiezentrum des Oberösterreichischen Landesmuseums, Linz, Austria
DEI	Deutsches Entomologisches Institut im ZALF, Müncheberg, Germany
KUEC	Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan
NCHUT	National Chung Hsing University, Taichung, Taiwan
NMNS	National Museum of Natural Science, Taichung, Taiwan
OLL	Biologiezentrum des Oberösterreichischen Landesmuseums, Linz, Austria
SEMC	Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
TARI	Taiwan Agricultural Research Institute, Wufeng (Taichung), Taiwan
USNM	Smithsonian Institution, National Museum of Natural History (formerly United States National Museum), Washington D.C., USA
ZFMK	Zoologische Forschungsinstitut und Museum "Alexander Koenig", Bonn, Germany
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
ZSM	Zoologische Staatssammlung München, Munich, Germany

Fig. I. Habitus of *Andrena* 1. **A, B:** Female (A) and male (B) of the early spring species *A. (Andrena) nycthemera* (Bavaria). **C:** Female of the oligolectic *A. (Melandrena) vaga* with pollen loads of *Salix* (Bavaria). **D:** Female of *A. (Biareolina) lagopus* (Bavaria). **E:** Male of the rare species *A. (Lepidandrena) rufizona* (Bavaria). **F:** Female of *A. (Proxiandrena) proxima*, which is oligolegtic on Apiaceae (Bavaria).

Preparation of male genitalia and female head capsule with mouthparts

Specimens were softened using the method in PLANT & DUBITZKY (2008). Preparation of male S7, S8 and genitalia followed the procedure in DUBITZKY (2006). To prepare the female head capsule and 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 were removed from the head capsule and stored in 75 % ethanol. The maxillary-complex was cut medially and the labium removed. For thorough microscopic examination, the structures of the proboscis were mounted onto slides with glycerin. After completion of the morphological examination, the female head and remaining parts were glued to a cardboard label and attached to the pin of the corresponding specimen.

Light and scanning electron (SEM) microscopy

A Leica MZ 6 stereoscopic microscope was utilized for general examination of specimens. 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 deep focus images. All files were processed with Adobe Photoshop 7.0.1 and Adobe Illustrator CS. For detailed information on techniques used for scanning electron microscopy (SEM), see DUBITZKY (2005, 2006).

Morphological terminology, abbreviations and measurements

The terminology in this study follows MICHENER (1944, 2007) and, in special cases regarding the morphology of *Andrena*, LABERGE (1986a) and THORP (1969). Different and new morphological terms are explained in the text.

The following abbreviations are used throughout the work: **AS:** antennal segment (scape = AS 1), **BL:** body length, **FOV:** facial fovea, **GA:** genal area, **DLP:** dorsal part of lateral surface of propodeum, **LP:** lateral part of propodeum, **LO:** lateral ocellus, **LICD:** lower inter compound eye distance, **L/W:** length/width, **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 and **UICD:** upper inter compound eye distance.

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. **BL:** Body length was measured in lateral view as a sum of the distances from the front of the head (excluding antennae) to the posterior end of the propodeum and from there to the apex of the metasoma. Although measurements taken in this way minimize differences caused by the variable position of the metasoma, the results must be considered approximations because of deviations caused by telescoping of the segments. **Length of head:** Distance from hind margin of vertex to front (lower) margin of clypeus in frontal view (Fig. 1A). **Width of head:** Distance between outer margins of compound eyes in frontal view (Fig. 1A). **UICD:** Distance between upper inner margins of compound eyes (Fig. 1A). **LICD:** Distance between lower inner margins of compound eyes (Fig. 1A). **Length of glossa:** Widest distance from 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, PMX 2, 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. 1A). **Width of clypeus:** Greatest distance between lateral margins of clypeus in frontal view (Fig. 1A). **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. 1B). **Width of genal area:** Measurement of widest distance between hind margin of compound eye and hind margin of genal area taken in profile (Fig. 1F). **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. 1A). **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 apical end of segment taken along outer surface. **Width of AS:** Greatest width of segment taken on apical end along outer surface. **Length of jugal lobe:** Distance from base to apex of jugal lobe. **Length of vanal lobe:** Measurement from the base of incision between jugal and vanal lobe to apex of vanal lobe. **Puncture density:** Measured by distance between single depressions relative to their diameters. Punctation is considered sparse or dense when distance between depressions is ≥ or < diameter of a one depression, respectively.

Cladistic analyses

Character matrices for cladistic analyses were constructed using WinClada (NIXON 1999–2002). Parsimony analyses of the coded data were performed with NONA 2.0 (GOLOBOFF 1999). In all analyses the heuristic search procedure was conducted using the following parameters: 100–500 random replications, 100–500 starting trees per replication, 20,000 or more 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 mean value of the rescaled consistency index (*a posteriori* weighting). Analysis of characters, as well as character optimization using fast optimization modus (ACCTRAN), were performed with WinClada.

Bootstrap analysis (FELSENSTEIN 1985) and jackknife sampling (LANYON 1985, SIDDALL 1996) were used to assess support for clades. Values were calculated based on 100 replicates with 50 random sequence additions per replicate. Presentation of trees and character mapping were carried out in WinClada.

Selection of species

The phylogenetic analysis of *Andrena* included 102 ingroup taxa, representing 84 of the 99 subgenera of *Andrena* which we recognized at the outset of the study. Contrary to MICHENER (2007), *Melittoides*, *Opandrena*, *Chaulandrena* and *Truncandrena* are treated as subgenera in the present study. Due to the prevailing vague phylogenetic relationships among the short tongued bees (ALEXANDER & MICHENER 1995, DANFORTH ET AL. 2006a,b, see, also “Characters and character states”), four species from the remaining Andreninae (*sensu* MICHENER 2007) were included in the ingroup: *Euherbstia excellens* FRIESE, 1925, *Orphana inquirenda* VACHAL, 1909, *Megandrena enceliae* (COCKERELL, 1927) and *Ancylandrena atoposoma* (COCKERELL, 1934). To avoid coding autapomorphies of the outgroup as plesiomorphies, a hypothetical null ancestor was used as the primary outgroup in combination with four real taxon outgroups.

When possible the type species of subgenera and genera were included in the analyses to ensure a minimum of stability for the subgeneric concepts. If the type species was not available, one or more species were selected, which were morphologically quite similar to the type species or which closely correspond to the subgeneric concept. This approach was crucial for the analysis of *Andrena*, since numerous species included in the currently recognized subgenera do not conform with the subgeneric concept based on the corresponding type species. Several species of certain clearly heterogeneous subgenera were included in the analyses to rigorously test the monophyly of these subgenera. It must be remembered that many of our statements and conclusions on subgenera are based on the type species or exemplar species included in the analysis as being representative of their respective subgenera. Additional members of subgenera were consulted on numerous occasions (cf. “Material studied”). However, the confirmation of monophyly and definition of the scope of all subgenera are tasks which go beyond the range of the present investigation.

The type species of ten additional subgenera were examined and originally integrated into the data matrix but omitted from the final analyses since they were available in one sex only.

Character selection

The parsimony analyses of the present study are based exclusively on characters of external morphology, care was taken to select as many potentially informative characters as possible (RIEPPEL 1999, POE & WIENS 2000). An examination of internal morphology would have been difficult or even impossible as valuable material of rare species or type specimens would not allow the necessary preparation of specimens. Furthermore, most interesting aspects of internal morphology require fresh specimens for appropriate examination, which would have dramatically narrowed the scope of the analyses as the availability of such material is heavily limited.

Occasionally, autapomorphies were incorporated in the analysis because of their potential value as synapomorphies when more taxa are included in future studies (YEATES 1992). Indeed, some of the autapomorphies in the analysis of *Andrena* may be interpreted as synapomorphies for the corresponding subgenus and have strong diagnostic value for recognizing subgenera, as well.

During the process of preparation of the material many measurements were taken and ratios calculated, but only those ratios were included in the analyses for which the values reflected discrete groups of data which could be coded as definite character states (e.g., characters 15, 16, 30 to 32, 35, 37, 38, 74 and 75; cf. ZELDITSCH ET AL. 2000).

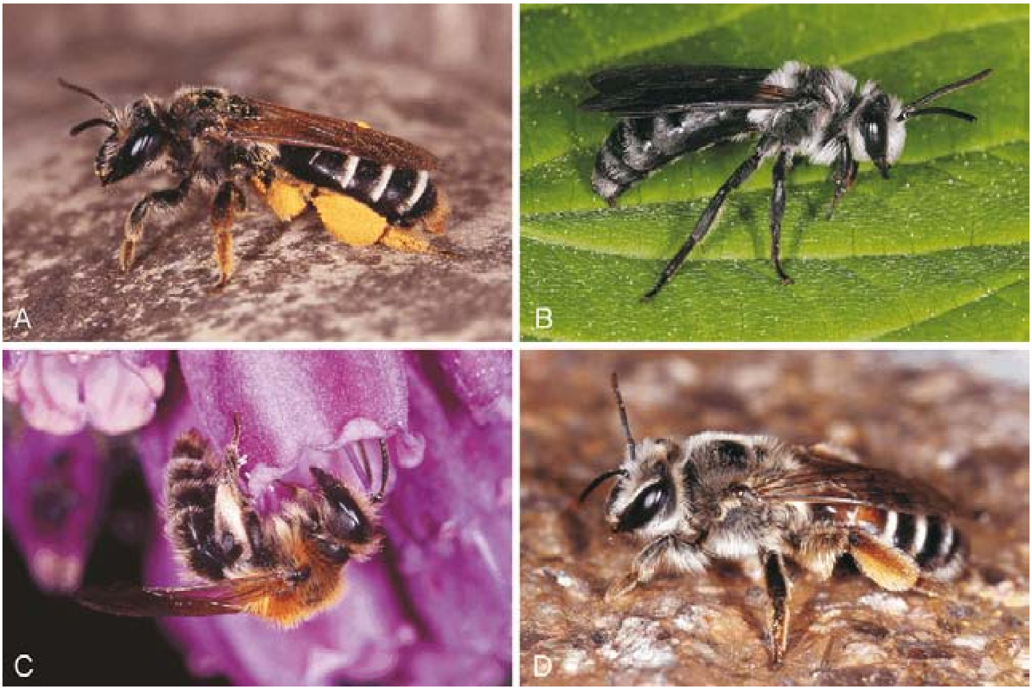


Fig. II. Habitus of *Andrena* 2. **A:** Female of *A. (Taeniandrena) aberrans* which is oligolectic on (Fabaceae) (Bavaria). **B:** Male of the oligolectic (Brassicaceae) *A. (Agandrena) agilissima* (Bavaria). **C:** Female of the oligolectic *A. (Euandrena) symphyti* collecting pollen from flowers of *Symphytum* (Bavaria). **D:** Female of *A. (Suandrena) savignyi* (La Gomera, Canary Islands).

Species included in analysis:

Ancylandrena atoposoma (COCKERELL, 1934)
Cubiandrena cubiceps (FRIESE, 1914)
Euherbstia excellens FRIESE, 1925
Megandrena enceliae (COCKERELL, 1927)
Orphana inquirenda VACHAL, 1909

Andrena (Callandrena) accepta VIERECK, 1916
Andrena (*Aciandrena*) *aciculata* MORAWITZ, 1886
Andrena (*Aenandrena*) *aeneiventris* MORAWITZ, 1872
Andrena (*Carandrena*) *aerinifrons* DOURS, 1873
Andrena (*Agandrena*) *agilissima* (SCOPOLI, 1770) (Fig. IIB)
Andrena (*Parandrena*) *andrenoides* (CRESSON, 1878)
Andrena (*Anchandrena*) *angustella* COCKERELL, 1936
Andrena (*Cremnandrena*) *anisochlora* COCKERELL, 1936
Andrena (*Parandrenella*) *atrata* FRIESE, 1887
Andrena (*Pelicandrena*) *atypica* (COCKERELL, 1941)
Andrena (*Hesperandrena*) *baeriae* TIMBERLAKE, 1941
Andrena (*Leimelissa*) *bairacumensis* MORAWITZ, 1876
Andrena (*Archiandrena*) *banksi* MALLOCH, 1917
Andrena (*Leucandrena*) *barbilabris* (KIRBY, 1802)
Andrena (*Euandrena*) *bicolor* FABRICIUS, 1775
Andrena (*Hyperandrena*) *bicolorata* (ROSSI, 1790)
Andrena (*Conandrena*) *bradleyi* VIERECK, 1907
Andrena (*Rhacandrena*) *brevipalpis* COCKERELL, 1930
Andrena (*Dactylandrena*) *caliginosa* VIERECK, 1917
Andrena (*Thysandrena*) *candida* SMITH, 1879
Andrena (*Hoplandrena*) *carantonica* PÉREZ, 1902
Andrena (*Diandrena*) *chalybaea* (CRESSON, 1878)
Andrena (*Notandrena*) *chrysosceles* (KIRBY, 1802)
Andrena (*Aporandrena*) *coactipostica* VIERECK, 1917
Andrena (*Osychnyukandrena*) *cochlearicalcar* LEBEDEV, 1933
Andrena (*Brachyandrena*) *colletiformis* MORAWITZ, 1874
Andrena (*Cordandrena*) *cordialis* MORAWITZ, 1877
Andrena (*Opandrena*) *cressonii* ROBERTSON, 1891
Andrena (*Lepidandrena*) *curvungula* THOMSON, 1870
Andrena (*Parandrenella*) *dentiventris* MORAWITZ, 1874
Andrena (*Longandrena*) *dolini* OSYTSHNJUK, 1979
Andrena (*Campylogaster*) *erberi* MORAWITZ, 1871
Andrena (*Ptilandrena*) *erigeniae* ROBERTSON, 1891
Andrena (*Tylandrena*) *erythrogaster* (ASHMEAD, 1890)
Andrena (*Platygalandrena*) *fedtschenkoi* MORAWITZ, 1876
Andrena (*Scrapteropsis*) *fenningeri* VIERECK, 1922
Andrena (*Zonandrena*) *flavipes* PANZER, 1799
Andrena (*Chrysandrena*) *fulvago* (CHRIST, 1791)
Andrena (*Ptilandrena*) *fulvata* STOECKHERT, 1930
Andrena (*Fumandrena*) *fumida* PÉREZ, 1895
Andrena (*Fuscandrena*) *fuscicollis* MORAWITZ, 1876
Andrena (*Melanapis*) *fuscosa* ERICHSON, 1835
Andrena (*Calcarandrena*) *gamskrucki* WARNCKE, 1965
Andrena (*Graecandrena*) *graecella* WARNCKE, 1965
Andrena (*Ptilandrena*) *grossella* GRÜNWALDT, 1976
Andrena (*Trachandrena*) *haemorrhoa* (FABRICIUS, 1781)
Andrena (*Stenomelissa*) *halictoides* SMITH, 1869
Andrena (*Charitandrena*) *hattorfiana* (FABRICIUS, 1775)

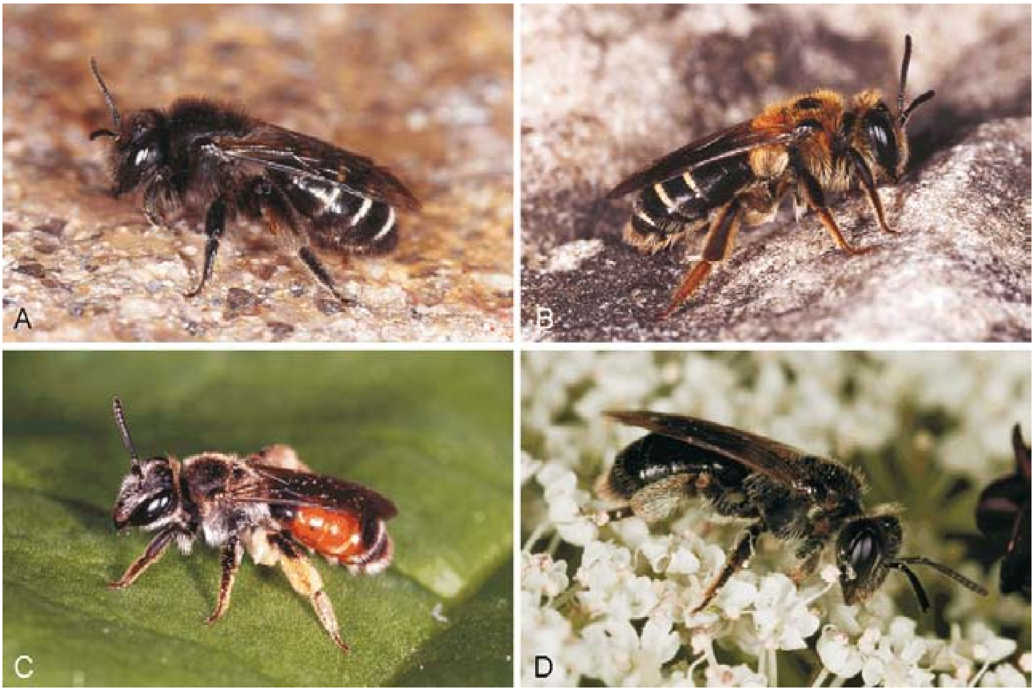


Fig. III. Habitus of *Andrena* 3. **A:** Female of the endemic *A. (Zonandrena) vulcana nyroca* (La Gomera, Canary Islands). **B:** Female of *A. (Simandrena) dorsata* (Bavaria). **C:** Female of *A. (Poecilandrena) labiata* (Bavaria). **D:** Female of *A. (Micrandrena) minutuloides* (Bavaria).

Andrena (*Andrena*) *helvola* (LINNAEUS, 1758)
Andrena (*Chlorandrena*) *humilis* IMHOFF, 1832
Andrena (*Holandrena*) *labialis* (KIRBY, 1802)
Andrena (*Poecilandrena*) *labiata* FABRICIUS, 1781 (Fig. IIIC)
Andrena (*Biareolina*) *lagopus* LATREILLE, 1809 (Fig. ID)
Andrena (*Distandrena*) *longibarbis* PÉREZ, 1895
Andrena (*Genyandrena*) *mackieae* COCKERELL, 1937
Andrena (*Oligandrena*) *macrocephala* COCKERELL, 1916
Andrena (*Margandrena*) *marginata* FABRICIUS, 1776
Andrena (*Micrandrena*) *melanochroa* COCKERELL, 1898
Andrena (*Melittoides*) *melittoides* FRIESE, 1899
Andrena (*Micrandrena*) *minutula* (KIRBY, 1802)
Andrena (*Larandrena*) *miserabilis* CRESSON, 1872
Andrena (*Oreomelissa*) *mitakensis* HIRASHIMA, 1963
Andrena (*Didonia*) *mucida* KRIECHBAUMER, 1873
Andrena (*Hamandrena*) *nasuta* GIRAUD, 1863
Andrena (*Cnemidandrena*) *nigriceps* (KIRBY, 1802)
Andrena (*Notandrena*) *nitidiuscula* SCHENCK, 1853
Andrena (*Nobandrena*) *nobilis* MORAWITZ, 1874
Andrena (*Dasyandrena*) *obscuripostica* VIERECK, 1916
Andrena (*Onagrandrena*) *oenotherae* TIMBERLAKE, 1937
Andrena (*Orandrena*) *oralis* MORAWITZ, 1876
Andrena (*Scoliandrena*) *osmioides* COCKERELL, 1916
Andrena (*Taeniandrena*) *ovatula* (KIRBY, 1802)
Andrena (*Pallandrena*) *pallidicincta* BRULLÉ, 1832
Andrena (*Gonandrena*) *persimulata* VIERECK, 1917
Andrena (*Planiandrena*) *planirostris* MORAWITZ, 1876
Andrena (*Augandrena*) *plumiscopa* TIMBERLAKE, 1951
Andrena (*Poliandrena*) *polita* SMITH, 1847
Andrena (*Andrena*) *praecox* (SCOPOLI, 1763)
Andrena (*Rhaphandrena*) *prima* CASAD & COCKERELL, 1896
Andrena (*Simandrena*) *propinqua* SCHENCK 1853
Andrena (*Calomelissa*) *prostomias* PÉREZ, 1905
Andrena (*Proxiandrena*) *proxima* (KIRBY, 1802) (Fig. IIIC)
Andrena (*Rufandrena*) *rufiventris* LEPELETIER, 1841
Andrena (*Lepidandrena*) *rufizona* IMHOFF, 1834 (Fig. IE)
Andrena (*Trachandrena*) *rugosa* ROBERTSON, 1891
Andrena (*Ulandrena*) *schulzi* STRAND, 1921
Andrena (*Scitandrena*) *scita* EVERSMANN, 1852
Andrena (*Suandrena*) *suerinensis* FRIESE, 1884
Andrena (*Tarsandrena*) *tarsata* NYLANDER, 1848
Andrena (*Platygalandrena*) *tecta* RADOSZKOWSKI, 1876
Andrena (*Melandrena*) *thoracica* (FABRICIUS, 1775)
Andrena (*Plastandrena*) *tibialis* (KIRBY, 1802)
Andrena (*Geissandrena*) *trevoris* COCKERELL, 1897
Andrena (*Hoplandrena*) *trimmerana* (KIRBY, 1802)
Andrena (*Troandrena*) *troodica* WARNCKE, 1975
Andrena (*Truncandrena*) *truncatilabris* MORAWITZ, 1877
Andrena (*Melandrena*) *vaga* PANZER, 1799 (Fig. IC)
Andrena (*Derandrena*) *vandykei* COCKERELL, 1936
Andrena (*Larandrena*) *ventralis* IMHOFF, 1832
Andrena (*Cryptandrena*) *ventricosa* DOURS, 1873
Andrena (*Ptilandrena*) *vetula* LEPELETIER, 1841
Andrena (*Iomelissa*) *violae* ROBERTSON, 1891

Characters and character states

The cladistic analysis of *Andrena* was based on 162 characters comprising 452 character states (Table 1). Except for the successive approximations procedure, which weights characters according to their level of homoplasy, all characters used in the analyses were equally weighted (*a priori* character weighting *sensu* WÄGELE 2004), and all multistate characters were treated as non-additive (unordered); 83 characters were coded binary, 49 with 3 states, 21 with 4 states, 4 with 5 states, 2 with 6 states, 2 with 8 states and 1 character with 7 states.

The following list of characters and their character states provides comments on the polarization of each character explaining which character states are treated as plesiomorphic in the present analysis. Decisions on character polarity were based on evaluation of the condition in *Andrena* compared to the remaining Andreninae and other short-tongued bees. For example, if a character state was common among short-tongued bees, it would be considered likely to be plesiomorphic for Andrenidae, in the absence of contradictory information. An all plesiomorphic hypothetical outgroup is appropriate for morphological cladistic analyses, in particular when choice of a real outgroup is difficult and when *a priori* decisions are postulated about polarity and character transformation. These character hypotheses are subjected to test in the parsimony analysis.

Since the phylogenetics of the allies of *Andrena* remains unclear (ALEXANDER & MICHENER 1995, DANFORTH 2006a,b,), the best working hypotheses on character polarity are those based on the principle of parsimony.

The character matrix in Table 1 corrects minor errors of the version presented in DUBITZKY (2005).

Head and mouthparts

1. Posterior part of hypostomal carina: (0) more or less entire (Fig 2a, D, E); (1) deeply emarginate (Fig 2a, A-C). A deeply emarginate hypostomal area is found only in *Megandrena enceliae* (COCKERELL, 1927) and *Cubiandrena cubiceps* (FRIESE, 1914), being more distinct and stronger in the latter. No distinct hypostomal carina is developed in *A*. (*Longandrena*) *dolini* OSYTSHNJUK, 1979, because posterior parts of the hypostomal area and postgenal bridge are indistinguishably fused. An entire hypostomal carina, as found in nearly all andrenids, is very likely to be the plesiomorphic state.
2. Postgenal bridge: (0) distinctly developed, about as wide as antennal flagellum (Fig 2a, D, E); (1) strongly reduced, hypostomal carina nearly joining postoccipital suture; (2) deeply concave (Fig 2a, A, B).
   A distinctly developed postgenal bridge, as found in most andrenids is held to be plesiomorphic. In *A*. (*Iomelissa*) *violae* ROBERTSON, it is strongly reduced, and in *Cubiandrena* the postgenal bridge is deeply concave.
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 most likely plesiomorphic.
4. Subgenal coronet: (0) absent; (1) present (Fig 2a, H-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 (Fig 2a, N, P, Q), but in the great majority it is clearly well-developed. Strangely enough, since the structure was first defined by TIMBERLAKE (1941), it has hardly received mention or investigation; only the following authors have studied 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 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 (Fig 2a, H-R), are true cuticular projections since they show no basal circular articulation as do bristle like formations of setae (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. PATINY & GASPAR (1999) supposed that it is associated with the modification of the pollen provisions. This supposition remains 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 (Fig 2a H-N); (1) developed only along inner margin of paramandibular process (Fig 2a P, Q); (2) developed along toothlike projection (Fig 2a F, G).
   A fully developed coronet (bristles along inner and hind margin of paramandibular process) is regarded as plesiomorphic for *Andrena* as a genus, state (1) may be a secondary reduction, and state (2), which occurs only 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 (Fig 2a K-M); (1) strongly developed, dense (Fig 2a H-J, N, P, Q).
   A sparsely setiferous to glabrous 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 Andrenidae.
7. Bristles of paramandibular process: (0) absent (Fig 2a F, G); (1) strongly reduced, minute to indistinct (Fig 2a N-P, R); (2) distinctly smaller than bristles of subgenal coronet (Fig 2a H-M); (3) as large to slightly smaller than bristles of subgenal coronet.
   The smooth and glabrous paramandibular area of all Andrenidae and other bees is very likely to be plesiomorphic.
8. Cross section of galea: (0) slightly convex (Figs 3C, 4A-C, E-H); (1) strongly flattened, with outer lateral margin strongly angled (Figs 3A, B, 4D).
   The subgenus *Platygalandrena* is characterized by a flattened, angled galea, which is strongly flattened in *A*. (*Platygalandrena*) *fedtschenkoi* MORAWITZ, 1876 and only slightly flattened in *A*. (*Platygalandrena*) *tecta* RADOSZKOWSKI, 1876. A slightly convex galea, as developed in all other andrenids and in most other bees, is most likely plesiomorphic.
9. Apex of galea: (0) rounded (Figs 3A-C, 4A-D, F-H); (1) pointed (Fig 4E).
   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 3A-C, 4A-F, H); (1) distinctly concave (Fig 4G).
    A concave outer margin of the galeal blade is probably apomorphic. In most subgenera of *Andrena* and all other Andreninae the margin is straight to slightly convex.
11. Pubescence of galeal blade (setation-type): (0) absent to normal straight setae (Figs 3A, B, 4A-H); (1) posteriorly bent, strong, hooked setae (*nasuta*-type, Fig. 3C); (2) anteriorly bent, hooked setae (*osmioides*-type, DUBITZKY 2005: Fig 11D, E); (3) slightly anterior bent, stiff, long setae (*brevipalpis*-type).
    Sparse, unmodified setae of the galeal blade, as in most subgenera of *Andrena* and all other andrenids, are very likely to be plesiomorphic.
12. Length PMX: (0) about as long as galea or slightly longer (Fig 4A, B, D-H); (1) distinctly shorter than galea (Figs 3C, 4E); (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 we therefore regard it as plesiomorphic.
13. Length of PMX 2: (0) about as long as or longer than PMX 1 (Fig 4A-C, E-H); (1) distinctly shorter than PMX 1 (Figs 3A, B, 4D).
    Despite the fact that nearly all genera of Andreninae except *Andrena*, exhibit state (1), the presumably plesiomorphic condition for the genus *Andrena* is regarded to be as about as long as or longer than PMX 1 (state 0), because this condition is present in all subgenera of *Andrena* (except in *A*. (*Platygalandrena*) *fedtschenkoi*), in *Euherbstia* and most other andrenids.
14. Setation of stipes: (0) sparse (Fig 4C, E); (1) medium to dense (Fig 4A, B, D, F-H).
    Since most subgenera of *Andrena*, as well as *Megandrena*, *Orphana* and most other andrenids, show a sparse pubescence of stipes, this state is likely to be ancestral.
15. L/W ratio of glossa: (0) short, not longer than 2 times as wide (Figs 3D, 5A, C, E, G, I); (1) medium-long, 2 to nearly 4 times longer than broad (Fig 5D, F); (2) strongly elongate, at least 4 times as long as broad (Figs 3E, 5B, H, J).
    For short-tongued bees state (0) is most 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 3D, E, 5A, C, E-J); (1) distinctly shorter than glossa (Fig 12B, D); (2) distinctly longer.
State (0) is found in most andrenids and therefore is likely to be plesiomorphic.
17. Shape of PLB 2: (0) club like (Figs 3D, 5A-F); (1) slender (Figs 3E, 5H, J).
Slender PLB are developed in only few subgenera of *Andrena* and nowhere else in Andreninae, thus this state is clearly apomorphic.
18. Length of PLB 4: (0) about as long as or longer than PLB3 (Figs 3D, E, 5A-F, J); (1) distinctly shorter than PLB 3 (Fig. 15H).
State (1) is clearly autapomorphic for *A.* (*Didonia*) *mucida* KRIECHBAUMER, 1873 and was included in the matrix because of its potential value for the subgeneric concept. Autapomorphies cannot effect tree topology.
19. Mental plate: (0) well 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) and PLANT & PAULUS (1987). While MICHENER divided the part basal to the glossa into three different sclerites from basal to apical, lorum, mentum and prementum, PLANT & PAULUS (1987) defined only two clearly separated sclerites: the postmentum and prementum. According to their concept the postmentum, although being simple in some taxa, such as *Hylaeus*, in many groups it is a complex structure which is differentiated apically into the lorum (= submentum) and basally into the mentum. In most bees the two parts are not clearly divided from each other except in *Apis*, *Bombus* and others where it is appropriate to speak of a mentum and lorum as separate sclerites. Furthermore, PLANT & PAULUS (1987) considered it 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). Therefore, PLANT & PAULUS (1987) presumed that the presence of an interscleritic region was plesiomorphic and that it does not represent a reduced mentum; contrary to MICHENER (1985) who regarded a sclerotized mentum (= mental plate of postmentum) as ancestral for bees. With respect to *Andrena*, a well developed mental plate of the postmentum (= sclerotized part of mentum of MICHENER 1985) is likely to be plesiomorphic since it is occurs in all other Andreninae and most of the remaining andrenids (except Oxaeinae).
20. Prementum: (0) rounded without 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 andrenids and therefore is likely to be plesiomorphic. The complete ventrolateral ridges of *Cubiandrena cubiceps* (3) probably evolved independently and cannot be compared with the incomplete ridges defined in state (2).
21. Setation on ventral side of prementum: (0) weak to absent; (1) strong, normal setae; (2) strong, with stiff and forward curving setae (*osmioides*-type); (3) strong, with stiff and backward curving setae (*nasuta*-type).
Weak or absent pubescence on the ventral side of prementum is probably ancestral as it is present in most *Andrena* species and all other Andreninae.
22. Condylar lamella of mandible (female): (0) absent; (1) developed (Fig. 2H).
This peculiar feature of most subgenera of *Andrena* is not found elsewhere in bees. Amazingly, it has never been mentioned in relevant papers dealing with mandibular morphology of bees (MICHENER & FRASER 1978) or the morphological characteristics of *Andrena* (LANHAM 1949, WARNCKE 1968a, THORP 1969, MICHENER 2007). According to the present knowledge of the authors, only two articles gave a hint to the existence of this character. In their paper on the comparative morphology of the postmentum of bees, PLANT & PAULUS (1987: fig. 1) clearly illustrated this structure but neither mentioned nor explained it in the text, as it was not relevant to the topic of their study. PATINY & 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 the 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; also, 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, yet 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 clearly derived since it strongly correlates with the subgenal coronet. Furthermore, it occurs in most subgenera of *Andrena* and is unique among bees.

23. Length of mandible (female): (0) usually not long, or only slightly crossing over apically when at rest (less than ¼ of mandible length); (1) strongly elongate, distinctly crossing over apically (at least ¼ of mandible length), (2) slightly elongate, slightly crossing over (less than ¼ of mandible length).
    Slender mandibles which do not, or only slightly, cross over apically are typical for andrenids and most other short-tongued bees and clearly represent the ancestral type of mandibles occurring also in apoid wasps (MICHENER & FRASER 1978), while elongate mandibles (states 1 and 2) are apomorphic.
24. Length of mandible (male): (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. 1F).
    A short male mandible as found in most andrenids and other alleged ancestral short-tongued bees (Colletidae, Halictidae) is clearly plesiomorphic.
25. Profile of mandible (lateral view, male): (0) straight to slightly curved; (1) strongly curved downward (Fig. 1F).
    A strongly curved male mandible is probably derived from a straight to slightly curved one since the latter is found in other andrenids.
26. Curvature of mandible (frontal view, male): (0) slightly bent inward, not angled; (1) strongly bent inward (median), forming a strong angle.
    State (0) is likely to be ancestral as it is found in most subgenera of *Andrena* and in all other Andreninae.
27. Preapical tooth on mandible (male): (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 probably ancestral because it is found in all other Andreninae except *Ancylandrena*, and it is present in most of the remaining andrenids.
28. Distance between preapical tooth and apical tooth of mandible (male): (0) no more than 1/4 of mandible length; (1) at least 1/4 of mandible length.
    State (0) probably represents the groundplan of bidentate male mandible as it occurs in most short-tongued bees.
29. Basal process on posterior margin of mandible (male): (0) absent; (1) present.
    The basal process along the posterior margin of the male mandible of some *Andrena* subgenera is clearly a derived feature.
30. L/W ratio of head (female) (frontal view, Fig. 1A): (0) <1; (1) ≥1.
    State (0) is likely ancestral as it is found in most subgenera of *Andrena* and all other Andreninae.
31. L/W ratio of head (male) (frontal view, Fig. 1A): (0) 0.7-0.95; (1) <0.7; (2) >0.95.
    State (0) is probably 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* exhibit state (2).
33. Shape of PLR (female): (0) rectangular to broadly rounded (Fig. 2b M); (1) more or less triangular (Fig. 2b N).
    A rectangular to broadly rounded PLR is found in all Andreninae and most *Andrena*-subgenera and therefore probably represents the plesiomorphic state.
34. Front margin of PLR (female): (0) without emargination in middle (Fig. 2b M,N); (1) with strong emargination in middle (Fig. 2b O).
    The strong median emargination of the front margin of some subgenera of *Andrena* is clearly apomorphic, as it is not found elsewhere in 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 likely to be plesiomorphic while states (1) and (2) are probably derived. State (2) occurs in *Ancylandrena* and *Orphana*.
36. PLR (male): (0) ventrally orientated, apical margin not protruding beyond margin of clypeus; (1) strongly protuberant, apical margin distinctly protruding beyond margin of clypeus (Fig. 1F).
    State (1) is developed only in some subgenera of *Andrena* and in *Euherbstia*. It is probably apomorphic and must have evolved independently in *Andrena* and *Euherbstia*.

37. L/W ratio of clypeus (female): (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 very likely to be ancestral while an elongate clypeus, only found in some subgenera of *Andrena*, is derived.
38. L/W ratio of clypeus (male): (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 likely to be plesiomorphic.
39. Profile of front margin of clypeus (female): (0) ventrally orientated, not curved upwards anteriorly; (1) distinctly curved upwards anteriorly.
State (0) is found in most subgenera of *Andrena* and all remaining andrenids, it is therefore probably plesiomorphic.
40. Profile of front margin of clypeus (male): (0) ventrally oriented, not curved upwards anteriorly; (1) distinctly curved upwards anteriorly.
State (0) is found in most subgenera of *Andrena* and all other andrenids, it is therefore probably plesiomorphic.
41. Disc of clypeus (female): (0) more or less convex (SCHÖNITZER et al. 1995: fig. 5b); (1) strongly flattened; (2) slightly flattened.
Most subgenera of *Andrena* and all other Andreninae except *Ancylandrena*, show a convex clypeus, which is likely to be the plesiomorphic state (also in males cf. character 42 below).
42. Disc of clypeus (male): (0) convex; (1) weakly flattened; (2) strongly flattened.
State 0 is presumably plesiomorphic because it is found in the majority of species of *Andrena* and most other andrenids.
43. Coarse punctation of disc of clypeus (female): (0) absent; (1) present.
The coarse punctation of clypeus is probably 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, thus it is clearly derived.
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 andrenids, thus it is probably 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 probably plesiomorphic because it is present in all other Andreninae except *Euherbstia*.
47. Wrinkles of disc of clypeus (female): (0) absent; (1) weak; (2) transverse; (3) longitudinal.
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 wrinkles therefore is most likely to be the ancestral state.
48. Coloration of clypeus (female): (0) completely dark; (1) at least partly yellow to ivory.
Yellow or ivory clypeal markings in the female are absent in all other Andreninae and most andrenids except several tribes of Panurginae (e.g. Melitturgini, Perditini, Calliopsini), where they are more or less strongly developed. A uniformly dark clypeus is probably ancestral. The yellow to white colorings should not be separated into different states because of intrapecific variation and intermediate stages.
49. Coloration of clypeus (male): (0) completely dark; (1) at least partly yellow to ivory.
Though most male Andreninae and most remaining andrenids have a more or less yellowish clypeus, a dark clypeus is presumably ancestral in *Andrena* as it is present in most subgenera of *Andrena*, as well as in *Ancylandrena* and Alocandreninae.
50. Malar space (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. 1B); (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 andrenids is therefore probably plesiomorphic.
51. Malar process (male): (0) absent; (1) developed (Fig. 1D).
A ventrally orientated process of the malar area is only developed in *Andrena* (*Derandrena*) *vandykei* COCKERELL, 1936 and *Andrena* (*Hoplandrena*) *trimmerana* (KIRBY, 1802) and is therefore clearly apomorphic.

52. Width of GA (female) (compared 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*, and *Orphana* and most other andrenids, is probably plesiomorphic.
53. Punctation of GA (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 probably ancestral.
54. Width of GA compared to width of compound eye (male): (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 andrenids, is probably 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. Therefore it is clearly apomorphic.
56. Genal process (male): (0) absent; (1) present (Fig. 1C).
Only a few subgenera of *Andrena* show a distinct genal process in the male, which is likely to be apomorphic since it is absent in all other Andreninae and the remaining andrenids.
57. Subgenal process (male): (0) absent; (1) present (Fig. 1E).
The subgenal process of the male is an autapomorphy for *Andrena* (*Genyandrena*) *mackieae* COCKERELL, 1937, although. This structure was included in this analysis because it is also developed in some members of the Palearctic subgenus *Carandrena*, which were not included in the present analysis. This character does not effect the tree topology.
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 andrenids is likely to be 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 probably plesiomorphic, although in the remaining andrenids no clear distinction can be discerned.
61. Velvety FOV: (0) absent; (1) present (Figs 1A, 2b A-L).
Within the Andreninae, a velvety FOV is found only in the subgenera of *Andrena* and in *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 & SCHÖNITZER (1993) and MICHENER (1986), a velvety pubescence of the FOV is considered apomorphic.
62. Depth of FOV: (0) entire fovea deeply depressed (Figs 2b A, C, F, K); (1) only lower or upper part deeply depressed; (2) completely flat, weakly depressed (Fig. 2b I).
Although SCHUBERTH & SCHÖNITZER (1993) regarded a weakly depressed FOV as plesiomorphic for bees as a whole, we presume that the deeply depressed FOV, as in *Ancylandrena* and Alocandreninae, is plesiomorphic for the Andrenidae. The partially or completely flattened FOV (states 1 and 2) of most *Andrena*-subgenera and *Megandrena* are therefore probably secondarily derived from deeply depressed FOV of the hypothetical ancestor.
63. Shape of FOV: (0) more or less oval (Figs 2b A, I, K); (1) upper part clearly broader (at least 2 times) than lower part, caused by narrow constriction (Fig. 2b C); (2) upper part conspicuously narrower than lower part (Fig. 2b F).
A more or less oval FOV, which is typical for most of the subgenera of *Andrena* and in *Ancylandrena*, *Megandrena* and *Alocandrena*, is judged likely to be plesiomorphic.
64. Distance between FOV and LO: (0) developed (1-1.5 times OD), clearly separating FOV and LO (Figs 2b A, F); (1) strongly developed (≥ 1.6 times OD, Fig. 2b K); (2) reduced (0.5-0.9 OD, Figs 2b C, I); (3) absent to strongly reduced (<0.5 OD).
State (0) is probably plesiomorphic as it is developed in most subgenera of *Andrena*.

65. Upper hind margin of FOV: (0) terminating distinctly below upper margin of compound eye , Fig. 2b A); (1) reaching upper margin of compound eye (Fig 1A, 2b F, I, K); (2) terminating distinctly behind upper margin of compound eye (Fig. 2b C).
    State (0) is probably plesiomorphic, as it is occurs in most subgenera of *Andrena*, as well as in *Megandrena*, *Ancylandrena* and most other andrenids except *Alocandrena*, which exhibit 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 presumably plesiomorphic as it is present in most subgenera of *Andrena*, as well as *Megandrena* and most other andrenids.
67. Outer margin of FOV: (0) entirely straight to slightly convex (Figs 2b A, F, I, K); (1) with distinct constriction.
    A more or less straight outer margin of the FOV is likely to be ancestral as it is developed in most subgenera of *Andrena*, as well as in *Megandrena*, *Ancylandrena* and all other andrenids bearing FOV.
68. Inner margin of FOV: (0) entirely straight to slightly concave (Fig. 1A); (1) with distinct constriction (Fig. 2b C).
    State (0) as found in most subgenera of *Andrena*, as well as in *Megandrena*, *Ancylandrena* and all other andrenids bearing FOV, is presumably plesiomorphic.
69. Maximum width of FOV (ref. to OD): (0) 1-2 (Figs 2b A, C, F); (1) 2-3 (Fig. 2b I); (2) <1; (3) >3.
    According to SCHUBERTH & SCHÖNITZER (1993) a medium-sized FOV (state 0), similar to *Colletes*, is likely to be ancestral for *Andrena*.
70. Interspace between inner margin of compound eye and outer margin of FOV: (0) <0.8 times OD (Figs 1A, 2b A, K); (1) 0.81 times OD to OD (Fig. 2b C); (2) > OD (Fig. 2b F); (3) absent (Fig. 2b I).
    State (0) is probably ancestral as it is found in most subgenera of *Andrena*, however it is absent in *Megandrena* and *Ancylandrena*.
71. Hind margin of vertex (profile) (female): (0) more or less rounded; (1) strongly edged; (2) narrowly rounded to slightly edged; (3) broadly rounded.
    Aside from some subgenera of *Andrena*, the female vertex in all remaining Andreninae is more or less rounded which is probably plesiomorphic.
72. Hind margin of vertex (profile) (male): (0) more or less rounded; (1) sharply edged.
    The sharply edged male vertex is probably apomorphic, as most subgenera of *Andrena* and all other Andreninae show a more or less rounded vertex.
73. Width of vertex compared to OD (female): (0) >1; (1) <1.
    A female vertex which is at least as wide as OD is probably plesiomorphic as it is developed in most subgenera of *Andrena* and all remaining Andreninae.
74. L/W ratio of AS3 (female): (0) 1.1-2.0; (1) 2.1-3.0; (2) <1; (3) >3.
    State (0) is probably the ancestral state, as it is found in most subgenera of *Andrena*, as well as in *Euherbstia* and *Ancylandrena*.
75. AS3/AS1 ratio (male): (0) 0.41-0.7; (1) <0.4; (2) >0.7.
    State (0) is probably plesiomorphic, as it is present in most subgenera of *Andrena* and in *Ancylandrena*, although all other Andreninae (*Orphana*, *Megandrena*, *Euherbstia*) share state (1).

Mesosoma

76. Lateral parts of pronotum below dorsolateral angle (female): (0) rounded; (1) carinate.
    A laterally rounded pronotum is found in many female *Andrena* and all other andrenids except *Euherbstia*, thus it is probably plesiomorphic.
77. Lateral parts of pronotum (male): (0) rounded; (1) carinate.
    A laterally rounded pronotum occurs in many male *Andrena*, all other Andreninae and most of the remaining andrenids, and is thus probably plesiomorphic.
78. Pronotal groove (female): (0) indistinct to absent; (1) distinct.
    The absence of a pronotal groove in *Euherbstia*, *Orphana* and most andrenids is probably plesiomorphic.

79. Dorsolateral angle (humeral angle) of pronotum (female): (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 hypothesized to be apomorphic since it is absent in nearly all of the remaining andrenids.

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, it is coded as apomorphic since most other andrenids, as well as several other short-tongued bees, 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 andrenids, and therefore is probably plesiomorphic.

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

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

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

85. Cuticular surface of mesepisterna (female): (0) smooth to tesselate or granulate, without wrinkles; (1) tesselate to granulate, weakly wrinkled; (2) strongly wrinkled.
Wrinkles of the female mesepisterna likely 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 probably 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*, of which two species were included in the analysis.

88. Punctation of scutellum: (0) regular to dispersed (>1); (1) indistinct to absent; (2) honeycombed to dense (<1).
State (0) is probably plesiomorphic as it is developed in most subgenera of *Andrena*, as well as all other Andreninae except *Ancylandrena*.

89. Profile of propodeum (female): (0) distinctly separated into a horizontal basal region and 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 andrenids. Therefore, this state is hypothesized to be ancestral.

90. Border between horizontal and vertical surface of propodeum (female): (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 andrenids, is very likely 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 probably plesiomorphic.

92. Pubescence of DLP (female): (0) well-developed, setae 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 occurs in most subgenera of *Andrena* and all other Andreninae.
93. Cuticular surface of LP (female): (0) finely tesselate, without wrinkles (Figs 6A, E, F); (1) partly irregularly wrinkled; (2) with conspicuous star shaped wrinkles (DUBITZKY & SCHÖNITZER 2001: Fig. 2); (3) completely coarsely wrinkled (Fig 6B-D); (4) finely wrinkled.
    A tesselate female LP without wrinkles is very likely to be 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 probably the plesiomorphic state.
95. Pubescence of distinct setae of LP: (0) present (Fig 6A-E); (1) absent, bare (Fig. 6F).
    Pubescence of distinct, rather long setae is found in most subgenera of *Andrena*, *Euherbstia* and *Ancylandrena*. The absence of distinct setae in some subgenera of *Andrena*, as well as *Megandrena* and *Orphana* (only minute setae developed), is probably apomorphic.
96. Pubescence of lateral propodeum: (0) moderately branched ("normal"-type, Fig. 6A); (1) setae simple, strong and medium-long to long (Fig 6B-E); (2) simple to slightly branched, weak setae; (3) bottlebrush like branching (*cubiceps*-type), intermixed; (4) strongly branched (*plumiscopa*-type); (5) branched (dorsal fringe type) and long; (6) absent, glabrous (Fig. 6F); (7) strongly branched (*melittoides* type).
    Branched setae similar to those on other parts of propodeum and thorax are probably the ancestral type of pubescence of the LP since they display no specialization.
97. Propodeal corbicula: (0) absent (Fig 6A); (1) present (Fig 6B-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 presumably plesiomorphic as it is absent in *Euherbstia* and most other andrenids.
98. Anterior hair fringe of propodeal corbicula: (0) absent (Fig 6B, C); (1) broad (*helvola*-type); (2) narrow (Fig 6E, F); (3) strongly reduced.
    An anterior hair fringe of the propodeal corbicula is absent in most subgenera of *Andrena*, as well as all other andrenids except *Megandrena* and is therefore probably apomorphic.
99. Length of anterior hair fringe of propodeal corbicula: (0) short to medium-long, straight (Fig. 6E); (1) strongly elongate, distinctly curled (Fig. 6F).
    A short to medium-long, straight anterior hair fringe of the propodeal corbicula is very probably plesiomorphic in contrast to a strongly elongate and distinctly curled hair fringe.
100. Density of anterior hair fringe of propodeal corbicula: (0) absent (Fig 6B, C); (1) dense (Fig 6E, F); (2) sparse; (3) consisting only of single scattered hairs. See also comment to character 98.
101. Setae of anterior hair fringe of propodeal corbicula: (0) branched, similar to dorsal fringe (Fig. 6E, F); (1) simple; (2) weakly branched; (3) strongly branched, different from dorsal fringe.
    State (0) is considered plesiomorphic, as it is developed in most subgenera of *Andrena* which have an anterior hair fringe.
102. Dorsoposterior hair fringe of propodeal corbicula: (0) absent (Fig. 6A); (1) consisting of medium–long, straight to slightly curled setae; (2) consisting of short, straight setae (Fig. 6B); (3) consisting of long, dense and strongly curled setae (Fig 6E, F).
    The absence of a distinct dorsoposterior hair fringe is probably plesiomorphic (see also comment to character 97).
103. Branching of setae on dorsoposterior hair fringe of propodeal corbicula: (0) weakly branched (Fig. 6B); (1) strongly branched (Fig 6C, E, F).
    The presence of weakly branched setae of the dorsoposterior hair fringe, for example, in some Andreninae and a few other andrenids, is probably ancestral.
104. Dorsoposterior hair fringe of propodeal corbicula: (0) sparse; (1) dense (Fig. 6B, C, E, F); (2) consisting only of single scattered hairs.

A sparse dorsoposterior hair fringe of the propodeal corbicula, as opposed to a more dense hair fringe, is probably 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 probably plesiomorphic, as it is found in many subgenera of *Andrena* and all other andrenids.

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 andrenids.

107. Apex of middle tibial spur (female): (0) straight to slightly curved, pointed; (1) straight to slightly curved, truncate; (2) strongly curved, hook shaped (Fig.8F).
The straight to slightly curved middle tibial spur of most subgenera of *Andrena* and all other andrenids is probably ancestral.

108. Pubescence on inner side of basitarsus of female middle legs: (0) consisting of normal and simple setae; (1) stiff, apically bent, simple setae.
Stiff, apically bent setae on the inner side of the middle basitarsus are autapomorphic for females of *A*. (*Callandrena*) *accepta* VIERECK, 1916. The character was included because of its potential value for the subgeneric concept; it does not effect tree topology.

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

110. Flocculus of trochanter of hind leg: (0) absent; (1) incomplete, only distal setae long and curled (straight basally); (2) complete, all setae long and strongly curled (Fig 7A, E).
A hind trochanter flocculus in females is lacking in most andrenids (except *Megandrena* and *Andrena*) and is thus probably 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 andrenids, and therefore is probably plesiomorphic.

112. Row of bristles of hind femur (female): (0) absent; (1) long (Fig. 8A); (2) short, cone shaped to thorn like (Figs 7C, 8B, C).
Bristles along the female hind femur are absent in most subgenera of *Andrena*, as well as all other andrenids; thus, their occurrence is probably apomorphic. The bristles are most likely strongly modified, hair like formations since they reveal a distinct circular articulation basally (Fig 8A-C).

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

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

115. Anterior hair fringe of hind femur (female): (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*, and is therefore probably plesiomorphic.

116. Pubescence of anterior hair fringe of hind femur (female): (0) simple; (1) branched, type A (*humilis*-type,); (2) branched, type B (*trevoris*-type); (3) branched, type C (*hattorfiana*-type, similar Fig. 7N); (4) branched, type D (*cubiceps*-type, similar Fig. 7O); (5) short, normal-type (*cochlearicalcar*-type).
The anterior hair fringe of the female hind femur consisting of simple setae is presumably plesiomorphic as it is present in most subgenera of *Andrena*, as well as in all other Andreninae and most of the remaining andrenids.

117. Pubescence of scopa of hind tibia (female): (0) simple (Fig. 7H); (1) unilaterally branched (*plumiscopa*-type, Fig. 7J); (2) distinctly bilaterally branched (*humilis*-type, Fig 7K, L); (3) multi-laterally branched, type C (*hattorfiana*-type, Fig. 7N); (4) multi-laterally branched, type D (*cubiceps*-type, Fig. 7O); (5) weakly unilaterally branched (*mackieae*-type, Fig. 7I); (6) distinctly bilaterally branched (*fulvago*-type, Fig. 7M); (7) weakly bilaterally branched (*curvungula*-type).
A tibial scopa consisting of simple setae 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 andrenids. Several authors, e.g. WARNCKE (1968a), HIRASHIMA (1966), TADAUCHI (1982), TADAUCHI & HIRASHIMA (1988) distinguished only between simple and branched/plumose setae of the hind tibial scopa, and scarcely paid attention to the different types (states 1-7) of branched scopal-setae (LABERGE 1986a, PASTEELS & PASTEELS 1979).

118. Pubescence of inner side of hind tibia: (0) simple (Fig. 7D); (1) branched (*cubiceps*-type, similar Fig. 7O); (2) branched (*mucida*-type); (3) bilateral branched (*fumida*-type) with few simple setae medially; (4) unilateral branched, with few simple setae medially.
Simple setae on the inner side of female hind tibia are found in most subgenera of *Andrena*, as well as all other Andreninae and most of the remaining andrenids, and therefore are probably plesiomorphic. The setae are often keirotrichia like (MICHENER 2007) with an apically spatulate region (Fig. 7O).

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. Therefore, the condition is presumably apomorphic.

120. Width of inner hind tibial spur (female): (0) basally not distinctly broadened, slender; (1) strongly broadened basally (Fig 8D, E); (2) distinctly broadened on nearly whole length (Fig. 8F).
Slender tibial spurs are probably plesiomorphic as they are found in most subgenera of *Andrena* and in all other andrenids.

121. Apex of inner hind tibial spur (female): (0) straight to slightly curved, pointed (Fig. 8D); (1) straight to slightly curved, truncate to knob like and thickened (Fig. 8E); (2) strongly curved, hook shaped (Fig. 8F).
Apically straight to slightly curved inner hind tibial spurs are probably plesiomorphic as they are present in most subgenera of *Andrena*, as well as most andrenids (except it is strongly hooked in *Ancylandrena*).

122. Inner spur of hind tibia in dorsal view (female): (0) more or less straight; (1) strongly curved.
The more or less straight female hind tibial spur is present in nearly all andrenids and is thus probably ancestral.

123. Pubescence on outer side of basitarsus of hind leg (female): (0) simple (Fig. 7P); (1) unilateral branched (*plumiscopa*-type); (2) bilateral branched (*humilis*-type, Fig. 7Q); (3) bilateral branched (*fulvago*-type, Fig. 7R); (4) multiple branched, type D (*cubiceps*-type, Fig. 7S); (5) weakly branched (similar to Fig. 7I).
Simple setae on the outer side of the female hind basitarsus probably represent the plesiomorphic state, as they are developed in most andrenids.

124. Claws (female): (0) bidentate (Fig. 7B); (1) inner tooth strongly reduced to absent, unidentate (Fig. 7F).
Only few subgenera of *Andrena* exhibit simple claws in contrast to the bidentate claws of most subgenera of *Andrena* and the remaining andrenids. Thus, the latter condition is probably plesiomorphic.

Wings

125. Number of submarginal cells: (0) three; (1) two.
The forewings of Andreninae (except for four subgenera of *Andrena*), as well as those of Alocandreninae and Oxaeinae, show three submarginal cells. However, two submarginal cells are quite common in species of Protandrenini, Panurgini, Perditini and Calliopsini. The presence of three submarginal cells is clearly 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 very probably ancestral because it is developed in nearly all andrenids.

127. 2nd recurrent vein joining 3rd submarginal cell: (0) distinctly before 3rd submarginal crossvein (about ⅓ 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 probably 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 probably plesiomorphic because it is found in all andrenids except *A*. (*Pallandrena*) *pallidicincta* BRULLÉ, 1832 and *A*. (*Ulandrena*) *schulzi* STRAND, 1921 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 andrenids. Only *Orphana*, *Euherbstia* and some subgenera of *Andrena* show a strong concave hind margin of the jugal lobe, which is probably 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) probably represents the ancestral state as it is found in nearly all subgenera of *Andrena*, as well as all other Andreninae.

Metasoma

131. Profile of T1 (female): (0) distinctly separated into declivous basal region and horizontal posterior region; (1) strongly sloping, without distinct separation into horizontal and declivous regions; (2) sharply angled by carina separating declivous region from horizontal region; (3) basal region weakly sloping.
   State (0) is very likely plesiomorphic as it is found in most subgenera of *Andrena*, as well as the other Andreninae and most of the remaining andrenids.
132. Basal part of T1 (female): (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 andrenids and therefore is presumably plesiomorphic.
133. Depression of marginal zone of T (female): (0) weakly developed to absent; (1) slightly steep; (2) strongly developed.
   A weakly depressed marginal zone, as found in most andrenids, is regarded as probably plesiomorphic.
134. Pubescence of disc of T (female): (0) minute to short "normally branched" setae; (1) extremely short scale like setae; (2) T with long and branched setae (at least on T 1, 2).
   Minute to short branched pubescence of T is most probably ancestral as it is present in most subgenera of *Andrena*, as well as the Andreninae (except *Orphana*) and the remaining andrenids.
135. Pale apical fasciae of short dense setae of T1-4 (female): (0) absent to narrow; (1) broad, interrupted; (2) broad, nearly covering complete marginal zone, never interrupted; (3) broad with short, scale like setae.
   Strong apical fasciae of short dense setae of female T1-4 are probably derived because they are absent in most subgenera of *Andrena*, as well as in *Euherbstia*, *Orphana* and most other andrenids.
136. Pygidial plate (female): (0) flat to convex, without raised triangular area mesally; (1) with raised triangular area mesally and depressed marginal zone (DUBITZKY 2002: fig. 5, SCHÖNITZER & DUBITZKY 2002: fig. 7d).
   Most andrenids (except *Orphana*) have a flat to convex female pygidial plate which is probably ancestral.
137. Male pygidial plate: (0) absent; (1) weakly developed; (2) strongly developed.
   Distinct male pygidial plates are probably derived, as they are absent in most subgenera of *Andrena* and in most of the remaining andrenids.
138. Sclerite of S7 (male): (0) homogenously fused, undivided apically (Fig 9B-F); (1) consisting of two separate parts connected by membrane apically (Fig. 9A).
   The male S 7 consisting of two separated sclerites is autapomorphic for *Cubiandrena cubiceps*. The character was included because of its potential value for subgeneric/generic concepts, and it does not effect tree topology.
139. Apical lobes of S7 (male): (0) two distinct lobes developed (Fig 9B, F); (1) absent (Fig. 9A); (2) long single process, ventrally curved apical process developed; (3) single median lobe developed, straight, not ventrally curved (Fig. 9C); (4) two weak lobes developed (broader than long, Fig. 9E); (5) strongly elongate, nearly completely fused medially; (6) minute, nearly fused (Fig. 9D).

Two distinct apical lobes of male S7, as found in most subgenera of *Andrena* and *Ancylandrena*, are probably ancestral for *Andrena*.

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

141. Pubescence of S7 (male): (0) with conspicuous hair fringe of long setae medioapically (Fig 9B-F); (1) without medioapically hair fringe, pubescence short, sparse (Fig. 9A).
A medioapical hair fringe of male S7, which is found in most subgenera of *Andrena*, as well as *Megandrena* and *Ancylandrena*, is probably plesiomorphic.

142. Apical process of S8 (male): (0) more or less broadened apically (Figs 10a A-D, 10b B-E); (1) becoming distinctly narrow apically (Fig. 10b A).
In most subgenera of *Andrena* and all other Andreninae, the male S8 is more or less broadened apically. This condition is probably ancestral.

143. Deep emargination of apical margin of apical process of S8 (male): (0) absent; (1) present.
A deep emargination of the apical process of male S8, as present in some subgenera of *Andrena*, is presumably apomorphic since it is not developed in other Andreninae.

144. Maximum width of apical process of S8 (male): (0) distinctly narrower than basal part (about 0.5 times as wide as basal part, Figs 10a A-D, 10b A, C, D, E; (1) strongly broadened, nearly as wide as basal part (> 0.6 times, Fig. 10b B).
Only four subgenera of *Andrena* show a strongly broadened apical process of male S8; in most subgenera of *Andrena* and all other Andreninae the apical part is distinctly narrower than the basal part and therefore is probably plesiomorphic.

145. Apical process of S8 (male): (0) without distinct toothlike appendages; (1) with strong teeth laterally.
The strong lateral teeth of the apical process of male S8 constitute an autapomorphic structure for the subgenus *Rufandrena*. The character was included because of its potential value for the subgeneric concept, and it does not effect tree topology.

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 S8 is developed, which is bent the strongest in *Holandrena*. The presumed plesiomorphic state (0) is developed in all other subgenera of *Andrena* and all remaining Andreninae.

147. Ventral side of S8 (male): (0) flat (Figs 10a A-D, 10b A, C, D); (1) subapical process strongly developed; (2) subapical process weakly indicated (Fig. 10b E); (3) subapical part strongly broadened (Fig. 10b B).
A flattened ventral side of male S8 is presumably 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 S8 of the single examined male specimen was damaged).

Male genitalia

148. Inner margin of dorsal gonocoxite: (0) nearly completely separated by penis valve (Fig. 11A); (1) joining penis valve for at least half the distance (Fig 11B-E; although the separation is shown as nearly complete in Fig 11C, D, it must be regarded as an artifact caused by SEM preparation).
Although state (1) is developed in all subgenera of *Andrena* (except *Melittoides*), as well as in *Megandrena* and *Ancylandrena*, it is likely to be derived because state (0) is found in *Euherbstia*, *Orphana* and most other andrenids.

149. Dorsal lobe of gonocoxite: (0) absent (Fig. 11A); (1) developed (Fig 11B-D); (2) strongly developed (distinctly longer than wide basally, Fig. 11E).
The presence of a dorsal lobe seems to be apomorphic for *Andrena*, as it is lacking only in some subgenera and is not developed in other Andreninae (except *Megandrena*) or other andrenids.

150. Apical margin of dorsal lobe of gonocoxite: (0) broadly rounded (Fig. 11B); (1) truncate (Fig. 11C); (2) narrowly rounded; (3) pointed (Fig. 11E).
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 (Fig 11B, C, D; in the latter two figures, distortion caused by SEM preparation makes this less apparent); (1) strongly diverging (Fig. 11E).
The inner margins of dorsal lobes being more or less parallel sided is presumably 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. 11A1); (1) small, reduced, often hardly visible behind cuspis (Fig.11C1).
A distinctly chelate, pincer like volsella with a large digitus belongs to the groundplan of Hymenoptera (SNODGRASS 1941, SCHULMEISTER 2003) and is probably ancestral for bees. It is present in some Andreninae (however not *Ancylandrena* and not most *Andrena*), the remaining andrenids and other short-tongued bees. A strongly reduced volsella with a small digitus is found only in *Ancylandrena* and nearly all subgenera of *Andrena*.
153. Shape of digitus: (0) more or less rounded apically; (1) toothlike (Fig. 11A1); (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 probably 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 (0.9 to 1.2 times); (1) distinctly broader than dorsal base (>1.2 times); (2) distinctly narrower than dorsal base (<0.9).
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 probably derived within *Andrena*.
155. Ventral margin of apical part of gonoforceps (profile): (0) distinctly narrower than basal part, not strongly broadened (Fig 11B, D, E); (1) slightly broadened, at least basally; (2) strongly broadened, nearly as wide as basal part (Fig. 11C).
A broadened ventral margin of the gonoforceps is absent in most subgenera of *Andrena*, as well as all other Andreninae, and is probably apomorphic within *Andrena*.
156. Inner margin of apical part of gonoforceps: (0) straight to slightly convex without emargination; (1) strongly convex; (2) with distinct emargination.
State (0) is probably 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 (Fig 11A-E); (1) completely parallel sided (DUBITZKY 2006: Fig. 5A); (2) uniquely shaped (*A. melittoides*).
A more or less triangular penis valve is developed in most subgenera of *Andrena*, as well as in *Orphana* and *Ancylandrena*, and is likely to be ancestral.
158. Lateral margins of basal penis valve (dorsal view): (0) converging (Fig 11A-E); (1) parallel sided basally, converging apically; (2) more or less parallel sided (DUBITZKY 2006: Fig. 5A).
Converging lateral margins of the basal penis valve, as present in *Ancylandrena*, *Orphana* and most subgenera of *Andrena*, are probably plesiomorphic.
159. Lateral lamella of penis valve: (0) absent (Fig 11A, C-E); (1) dorsolateral and ventrolateral lamella present (Fig. 11B); (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 andrenids. Therefore, it is probably apomorphic.
160. Lateral view of penis valvae: (0) flat to slightly rounded dorsally (Fig 11A-E); (1) strongly protuberant dorsally; (2) uniquely shaped (*Megandrena*).
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 (DUBITZKY 2005: Figs 20D, 21B, 22D, E, F, 23B, C, D); (1) pointed (Fig 11A, C-E); (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*. It is triangularly broadened in *Conandrena* and *Nobandrena*. An apically rounded penis valve is presumably ancestral.
162. Apex of penis valve (lateral view): (0) more or less rounded (Fig. 11B); (1) pointed (Fig 11A, C, D).
A laterally rounded penis valve, as developed in most subgenera of *Andrena* and all other Andreninae except *Ancylandrena*, is probably plesiomorphic.

Results

Cladograms, tree topology and character state distribution

The analysis of the data matrix (Tab. 1) with NONA employing the heuristic search options described above resulted in a total of six most parsimonious trees (MPTs) with a length of 1876 steps (CI: 0.15, RI: 0.42, RC: 0.06). The MPTs were recovered in two sets of three trees each.

No single analysis in NONA produced all six trees. The MPTs, obtained by repeated analysis of the same data-set sometimes using identical search parameters and sometimes different parameters, were pooled together and compared. Duplicate and suboptimal trees were rejected, resulting in a total of six different MPTs.

Characters were mapped onto one of the MPTs (Fig.14, exemplary cladogram) to display their distribution. The final character sampling included seven autapomorphic characters which were phylogenetically uninformative in the analysis. The strict consensus tree is presented in Fig. 12 with three collapsed nodes shown as polytomies. One cladogram (1920 steps, CI: 0.15, RI: 0.41, RC: 0.06) was obtained by successive character reweighting (*a posteriori* weighting) (Fig. 13), based on the RC of each character from the initial unweighted heuristic analysis. Identical location of groups and clades in both analyses are indicated by numbers 1-13 in Figs 12, 13.

Equal weighted analysis (Figs 12, 14)

The strict consensus tree of the six MPTs contains few polytomies (Fig. 12). It divides the Andreninae (node A) into two major clades: One clade subtends the genera *Euherbstia*, *Orphana* and *Megandrena* (node A2). The other clade contains the genera *Ancylandrena*, *Cubiandrena* and *Andrena* (node A1). 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 mean that either *Andrena* is paraphyletic or that *Ancylandrena* should be regarded as a subgenus of *Andrena*.

The monophyly of the clade *Ancylandrena* and *Cubiandrena* (node A3) is defined by 10 homoplasious synapomorphies (12:1, 35:1, 62:0, 64:2, 66:1, 115:1, 135:2, 137:2, 161:1, 162:1) (for character distribution in the following sections, see Fig. 14). Of the 12 synapomorphies that establish the monophyly of *Ancylandrena*, *Cubiandrena* and *Andrena* (node A2), three are non-homoplasious: (1) Subgenal coronet present (except *Ancylandrena*) (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). However, the latter character 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-homoplasious: (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) setae of dorsoposterior hair fringe of propodeal corbicula strongly branched (103:1).

The clade which is the sister group to all other subgenera of *Andrena* is the *Aenandrena*-group (node C, clade 1). It comprises *Poecilandrena*, *Proxiandrena*, *Aenandrena* and *Cordandrena* and is supported by four homoplasious synapomorphies (32:1, 54:1, 64:1, 91:2). The position of *Proxiandrena* as sister to the common clade of *Aenandrena* and *Cordandrena*, confirms the presumption of DUBITZKY & SCHÖNITZER (2001) that *A. proxima* and closely related species should be removed from *Micrandrena* and placed in a new subgenus as carried out by SCHMID-EGGER (2005).

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 homoplasious synapomorphies (98:1, 104:1), combines node F with the *Zonandrena/Trachandrena*-group (I).

The *Lepidandrena*/*Charitandrena*-group (node F) splits into the *Lepidandrena*-group (node G), comprising *Osychnyukandrena*, *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-homoplasious: (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-homoplasious.

In the *Charitandrena*-group (clade 4), which is characterized by five homoplasious synapomorphies (46:0, 104:0, 117:3, 157:1, 158:2), the subgenera *Charitandrena*, *Pallandrena* and *Rufandrena* build a monophyletic group supported by eleven homoplasious 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*. (*Hamandrena*) *nasuta* GIRAUD, 1863 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 *Trachandrena*-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 contains *Scitandrena*, *Cryptandrena* and *Holandrena*. The sister group 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-homoplasious. The *Scitandrena* + *Cryptandrena* + *Holandrena*-clade is defined by ten homoplasious synapomorphies. *Cryptandrena* and *Holandrena* form a monophyletic group (clade 7) based on seven synapomorphies, including one non-homoplasious 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 homoplasious 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 a notable feature of this group. Only in *Scrapteropsis* is it weakly developed. The monophyly of the Holarctic *Trachandrena* is well founded in 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-homoplasious.

The relationships of the basal clades of the second large clade of *Andrena* (node N) are quite variable in each of the six trees. Thus, they collapse to a polytomy in the strict consensus tree. Nevertheless four major groups (nodes O, P, Q, R) were recovered in this clade although support for each is modest.

The *Truncandrena*-clade (node O), which comprises *Truncandrena*, *Nobandrena*, *Calomelissa* and *Tarsandrena*, is characterized by five homoplasious synapomorphies (38:2, 104:1, 131:2, 153:3, 159:1). Synonymization of the Palearctic *Truncandrena* with the Nearctic *Scaphandrena* (RIBBLE 1974, MICHENER 2007, GUSENLEITNER & 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 for one sex. Autapomorphic for the subgenus *Calomelissa* in the present analysis is a female genal area that is more than twice as wide as the compound eye (52:2).

The *Chlorandrena*-clade (node P) combines *Aporandrena*, *Ulandrena*, *Chlorandrena* and *Platygalandrena* and is supported by six homoplasious 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.

The *Orandrena*/*Micrandrena*-clade (node Q), which includes nodes Q1 and Q2, is defined by four homoplasious synapomorphies (54:1, 80:0, 82:0, 136:1).

The *Dasyandrena*/*Orandrena*-clade (node Q1), which is supported by only three homoplasious 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 setae of the galeal blade (11:3) are typical for the subgenus *Rhacandrena*. *Orandrena* is characterized by 11 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 (nodes Q3-5) can be distinguished. However, relationships among the lineages are unresolved 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 homoplasious synapomorphies (91:3, 126:2).

The *Longandrena*-clade (node Q4), which is defined by eight homoplasious 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 homoplasious 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 homoplasious 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) dorsoposterior hair fringe of propodeal corbicula consisting of weakly branched setae (103:0). *Parandrenella* is the sister group to the *Aciandrena* + *Graecandrena* clade and clearly characterized by 15 synapomorphies, two of which are non-homoplasious: 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 S8 of male (147:3). The condition of the pubescence consisting of bilateral branched setae with few simple setae medially on the inner side of the female hind tibia (118:3) is autapomorphic for the subgenus *Fumandrena*, which constitutes the sister group to ((*Aciandrena*, *Graecandrena*) *Parandrenella*). A rather close relationship of *Graecandrena* and *Fumandrena* was discussed previously (SCHÖNITZER & DUBITZKY 2002).

The large *Scoliandrena*/*Ptilandrena/Hamandrena*/*Carandrena*/*Andrena*-group (node R) is defined by the following homoplasious 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 colored (49:0); lateral parts of male pronotum carinate (77:1) and 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 homoplasious apomorphy (35:1).

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 homoplasious 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* STOECKHERT, 1930) and Nearctic representatives (*A. erigeniae* Robertson, 1891) do not form a monophyletic group. Thus, *Hesperandrena* is the sister group 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* LEPELETIER, 1841, *A. grossella* GRÜNWALDT, 1976, see below) shows that the subgeneric concept of *Ptilandrena* used up to now is no longer valid and needs to be revised due to the polyphyly of this assemblage.

The *Oreomelissa*-clade (node V, clade 9) comprises the Nearctic *Derandrena* and the Palearctic *Oreomelissa* and is defined by nine homoplasious 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* SMITH, 1869. The *Hamandrena*-clade combines two sister clades, the *A*. (*Ptilandrena*) *grossella* + *Stenomelissa*-clade and the *Hamandrena* + *Troandrena*-clade, each is supported by eight homoplasious synapomorphies The subgenus *Hamandrena*, the species of which were formerly included in *Didonia*, was erected herein. 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) posteriorly bent, strong, hooked setae of the galeal blade (11:2), and (2) stiff and backwardly curved setae on the ventral surface of prementum (21:3), are autapomorphic for the subgenus.

The *Carandrena/Genyandrena*-clade (node X1), which represents the sister group to node X2, is defined by three homoplasious synapomorphies (49:1, 72:1, 101:1). In this clade two monophyletic groups can be distinguished: *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 sister group relationship between *Notandrena* and *Opandrena* is supported by twelve homoplasious synapomorphies. The presence of a subgenal process in the male (57:1) is apomorphic for *Andrena* (*Genyandrena*) *mackieae*.

The *Hoplandrena*/*Andrena*/*Leucandrena*-clade (node X2), characterized by four homoplasious synapomorphies (10:1, 64:2, 69:1, 78:1), included *Hoplandrena*, *Tylandrena*, the *Andrena*-clade (node Y) and the *Augandrena*/*Leucandrena*-clade (node Z). While *Hoplandrena* and *Tylandrena* are isolated at the base of node X2, nodes Y and Z form apical sister groups united by three homoplasious 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 homoplasious 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 homoplasious 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 homoplasious 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 setae (96:7) and (3) an abnormally shaped penis valve, characterize the subgenus *Melittoides*.

The *Leucandrena*-group is supported by three homoplasious 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 hind femur consisting of specially branched setae (116:2) is autapomorphic for *Geissandrena*, which is sister to the rest 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* CRESSON, 1872 constitutes the sister taxon to *Gonandrena*, while the Palearctic *A*. (*Larandrena*) *ventralis* IMHOFF, 1832 represents the sister group to the clade of *A*. (*Larandrena*) *miserabilis* + *Gonandrena*.

Successive weighting (*a posteriori* weighting, Fig. 13)

The cladogram obtained after applying successive character reweighting (Fig. 13) agrees in some aspects with the results of the heuristic search (Fig. 12) and shows clear differences in tree topology.

In contrast to the results of the heuristic search, *Cubiandrena* is the sister group to all other subgenera of *Andrena* (node A1), while *Ancylandrena* represents the sister to *Cubiandrena* + *Andrena*. Regarding *Andrena* (node A2), the subgenus *Hamandrena*, previously a part of the large group contained by node R, now constitutes the sister group to all other subgenera of *Andrena* (node B). The sister clade (node D) to the monophyletic *Opandrena*/*Notandrena*-group (node C) 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 subtends two major clades (nodes G and I).

The first of these clades (node G) largely agrees with node R (Fig. 12) of the unweighted heuristic search-analysis, although the *Scoliandrena*-clade (node S, Fig. 12), the *Hamandrena*-clade (Fig. 12, node W) and the 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. 12, as 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 in the *Hoplandrena*/*Andrena*/*Leucandrena*-clade (Fig. 12, node X2) of the unweighted analysis. The basal half of the clade merged to node H (indicated by the non-monophyletic group 11) subtends the same taxa and shows an identical topology in both analyses. 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 *Leucandrena*-group (clade 13), which unites the same taxa as the *Leucandrena*-group of the unweighted analysis (clade 13, Fig. 12) but differs in that *Gonandrena* + *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. 12, node O) with the *Orandrena*/*Micrandrena*-clade (Fig. 12, node Q) except *Fumandrena*, in the unweighted analysis. In node J, 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 clades 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 sister groups and constitute a common clade well within the *Truncandrena*-group. Despite the subgenera *Thysandrena*, *Orandrena* and *Suandrena*, which were placed additionally in this group, this clade is identical to the *Truncandrena*-group of the unweighted analysis (Fig. 12, 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 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 uniting the Palearctic *A*. (*Micrandrena*) *minutula* (KIRBY, 1802) with the Palearctic *Parandrenella*; the other uniting the Nearctic *A*. (*Micrandrena*) *melanochroa* COCKERELL, 1898 with the Palearctic subgenera *Fuscandrena*, *Distandrena*, *Aciandrena* and *Graecandrena*. The latter two subgenera are sister taxa.

The large clade, indicated by node O, mainly comprises the nodes C, E and P (Fig. 12) of the equally weighted analysis. Within it 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. The *Chlorandrena*-group (node P), which comprises the subgenera *Fumandrena*, *Chlorandrena*, *Ulandrena* and *Platygalandrena*, resembles the *Chlorandrena*-group of the unweighted analysis (Fig. 12, node P) except the following changes: *Fumandrena* (instead of *Aporandrena*) constitutes the sister taxon to all other subgenera of the group and *Ulandrena* (instead of *Chlorandrena*) is the sister taxon to *Platygalandrena*. The *Aenandrena*-group (node Q), including *Poecilandrena*, *Proxiandrena*, *Aenandrena* and *Cordandrena*, is identical with the *Aenandrena*-group of the unweighted analysis (Fig. 12, 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) splits into two major lineages: 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. 12, 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. 12, node M), as well as five additional subgenera. Thus, *Scitandrena* is the sister taxon to *Scrapteropsis*, and together constitute the sister clade to the remaining subgenera in the *Trachandrena*-group. The clade containing the Holarctic subgenera *Trachandrena* and *Plastandrena* is the sister to the clade uniting 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 the other 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 lineages (3 + 4) constitute a monophyletic group which is the sister to *Chrysandrena* + *Didonia*.

New subgenera of palearctic *Andrena*

The results of the cladistic analyses revealed three lineages of Palearctic *Andrena*, which were found to be clearly polyphyletic regarding to their previous subgeneric concept: *Larandrena*, *Micrandrena*, and *Ptilandrena*. Resolving the polyphyly entailed splitting off of distinct groups of species and placing them in independent and monophyletic subgenera. New subgenera are described in the following section.

Calcarandrena DUBITZKY subgen. nov.

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 middle and hind tibial spurs strongly curved, hook shaped (similar Fig. 8F). 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 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 color. Black to blackish brown except 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 setae. Pubescence of thorax medium-long to long. LP with regular pubescence of branched setae, similar to other parts of thorax. Propodeal corbicula present, with broad and dense anterior hair fringe, consisting of short to medium-long straight setae and dense, medium-long to long dorsoposterior hair fringe of weakly branched, straight to slightly curled setae. Flocculus of trochanter of hind legs incomplete, only distal setae being long and curled. Anterior hair fringe of hind femur strongly developed, dense, composed of branched setae of "*hattorfiana*"-type. Scopa of hind tibia of female dense, with weakly bilateral branched setae ("*curvungula*"-type). Inner side of hind tibia with pubescence of simple setae. Disc of T with sparse pubescence of short branched setae.

Diagnosis. In the present analyses *Calcarandrena* is the sister taxon to *Osychnyukandrena*. *Calcarandrena* can be clearly distinguished from *Osychnyukandrena* by possessing a row of long bristles on female hind femur, the presence of simple setae on inner side of female hind tibia and differently shape of male genitalia. *Calcarandrena* can easily be separated from *Lepidandrena* by its strongly hooked tibial spurs of middle and hind legs and the different shape of galea and 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 middle and hind legs found in the subgenus.

Included species. *A. eburnea* WARNCKE, 1975, *A. gamskrucki* WARNCKE, 1965, *A. impasta* WARNCKE, 1975. Species belonging to *Calcarandrena* were originally assigned to the subgenus *Lepidandrena* (WARNCKE, 1968a, GUSENLEITNER & SCHWARZ 2002).

The taxa *A. eburnea* WARNCKE, 1975 **stat. n.** and *A. impasta* WARNCKE, 1975 **stat. n.** were regarded as subspecies of *A. gamskrucki* WARNCKE, 1965 in his original descriptions. The extensive study of these two taxa during this investigation showed that both are clearly distinct from each other, as well as from *A. gamskrucki* WARNCKE. Therefore, they have been elevated to specific rank.

Hamandrena DUBITZKY subgen. nov.

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, curved downward in lateral view. Condylar lamella of female mandible slightly developed. Galea slightly convex. PMX shorter than galea. Glossa strongly elongate (Fig. 3E). PLB slender, about as long as glossa (Fig. 3E). 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 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 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 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 broadened apically, ventral margin narrower than basal part in profile. Penis valve more or less triangular, shorter than gonoforceps and broadly rounded apex. Lateral lamella of penis valve absent.

Integument color. 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 setae, similar to other parts of thorax. Propodeal corbicula absent. Flocculus of trochanter of hind legs absent. Anterior hair fringe of hind femur weakly developed with individual simple setae. Scopa of hind tibia of female sparsely developed, setae simple. T with medium-long to long sparse branched setae.

Diagnosis. Species belonging to *Hamandrena* can be recognized by the posteriorly bent, hook shaped bristles (Fig. 3C) on the galeal blade, stipes and prementum in females, a feature which is apomorphic for the subgenus.

Comments. *Hamandrena* is closely related to *Troandrena* according to the unweighted cladistic analysis. Bees of this subgenus fly from end of April to end of June. The species *Andrena nasuta*, *A. grozdanici* 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. 3C) on the galeal blade, stipes and prementum of females within the subgenus.

Included species. *A. nasuta* GIRAUD, 1863, *A. grozdanici* OSYTSHNJUK, 1975, *A. stepposa* OSYTSHNJUK, 1977, *A. teunisseni* GUSENLEITNER, 1998. The included species were previously placed in the subgenus *Didonia* (e.g. GUSENLEITNER & SCHWARZ 2002) except *A. grozdanici* which has been assigned to Hoplandrena by Osytshnjuk (1975).

Platygalandrena DUBITZKY subgen. nov.

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 well developed. Galea strongly dorsoventrally flattened, with distinct coarse punctation (Fig 3A, B). Apex of galea rounded. PMX strongly truncate, about as long as galea; PMX 2 shorter than PMX 1 (Fig 3A, 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 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 well 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 middle and hind tibial spurs truncate to knoblike. Inner tibial spur of hind legs more or less slender to basally broadened. 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 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, shorter than gonoforceps, flat to strongly protuberant in profile. Lateral lamella of penis valve absent to slightly indicated.

Integument color. 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 colored (*A. biguttata*, *A. combaella*, *A. elegans*, *A. leucorhina*, *A. mikhaili*, *A. osychniukae*, *A. tecta*). POA and clypeus of males yellowish to ivory. Marginal zone of T often brownish transparent.

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

Diagnosis. In the present analyses, *Platygalandrena* emerged as the sister taxon either to *Chlorandrena* or *Ulandrena*. *Platygalandrena* can be most clearly distinguished from *Chlorandrena* and *Ulandrena* by its 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 the end of March to July.

Etymology. Prefix *Platy*- from the Greek πλατύς, 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. Species belonging to *Platygalandrena* originally were placed in the subgenus *Ulandrena* (WARNCKE 1968a, GUSENLEITNER & SCHWARZ 2002).

Discussion

Monophyly of *Andrena*

Although the genus *Andrena* has been considered as well characterized (MICHENER 2007), in actuality it is difficult to find unambiguous autapomorphic characters which precisely define the genus as a whole. Thus, many of the diagnostic characters used to separate bee genera show enormous variability within *Andrena*, e.g. the number of submarginal cells in the forewings, 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 and the shape of male genitalia. Five of the eight synapomorphies defining the genus *Andrena* in the present study are non-homoplasious: (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) setae of dorsoposterior hair fringe of propodeal corbicula strongly branched (103:1). The presence of 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 elsewhere among bees except in *Cubiandrena*. The thornlike projection of the paramandibular area with bristles in *Cubiandrena*, which resemblances to the subgenal coronet of *Andrena*. However, it is interpreted as an unusual modification of the area, yet the possibility of a convergent development cannot be fully discounted.

Nonetheless, 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 (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 setae (83:3), LP with bottle-brush like branched setae (96:3), anterior hair fringe of female hind femur composed of peculiar multiple branching setae (116:4), scopa of female hind tibia consisting of peculiar multiple branching setae (117:4), inner side of hind tibia with multiple branching setae (118:1), outer side of female basitarsus of hind legs with specially multiple branching setae (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), S7 of male consisting of two separate parts connected by membrane apically (138:1) and toothlike digitus (153:1). These autapomorphies further emphasize the unique position of *Cubiandrena* and indicate that it should no longer be treated as a subgenus of *Andrena*. In contrast, the results regarding *Melittoides* show that it is a clear member of *Andrena*, therefore we retain it at the subgeneric level within *Andrena* in accord with the classification of GUSENLEITNER & SCHWARZ (2002).

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 Andreninae

The results of the unweighted analysis (Figs 12, 14) show that *Andrena* is the sister group to the common clade of the Nearctic *Ancylandrena* and Palearctic *Cubiandrena*. The monophyly (Fig. 12, node A1) of these three genera is supported by twelve synapomorphies, three of which are non-homoplasious (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-homoplasious. 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. 13). According to this *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-homoplasious. *Ancylandrena* again represents the sister to the common clade of *Cubiandrena* and *Andrena*. The monophyly of the clade formed by (*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-homoplasious: 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 12 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-homoplasious. 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 the clade (*Megandrena* (*Ancylandrena* (*Cubiandrena*, *Andrena*))), one of which, the presence of a propodeal corbicula (97:1), is non-homoplasious. *Euherbstia* is sister to the clade formed by (*Orphana* (*Megandrena* (*Ancylandrena* (*Cubiandrena*, *Andrena*)))).

Polyphyletic groups

As previously discussed the subgenera *Didonia*, *Ulandrena* and *Lepidandrena*, discovered to be polyphyletic (Figs 12, 14), were each split resulting in the proposal of three new subgenera, *Hamandrena*, *Platygalandrena* and *Calcarandrena*, respectively. The cladistic analyses showed that *Hamandrena* is strongly supported by the autapomorphic characters (11:2) and (21:3), and that it did not form a monophyletic group with *Didonia*; that the subgenus *Platygalandrena* was well defined by the presence of a solid autapomorphy (8:1); and that *Calcarandrena* was supported by numerous characters.

Several Holarctic subgenera were also demonstrated to be polyphyletic (e.g. *Micrandrena*, *Ptilandrena* and *Larandrena*). Regarding the large subgenus *Micrandrena*, the Palearctic (*A. minutula*) and Nearctic (*A. melanochroa*) representatives included in the present analysis failed to form a monophyletic group. Further, this study confirms the recent removal and transfer by SCHMID-EGGER (2005) of a small group of *Micrandrena* species revolving around (*A. proxima*) to a new subgenus, *Proxiandrena*, which according to the results of the study is the sister group to the clade of *Aenandrena* and *Cordandrena* (see above).

The Palearctic and Nearctic representatives of *Larandrena* appear unrelated to each other, since *Gonandrena* is the sister group to *A.* (*Larandrena*) *miserabilis* rather than to *A.* (*Larandrena*) *ventralis*. Furthermore, *Ptilandrena* appeared to be exceedingly polyphyletic, all four members of the subgenus included in the analyses occurred in isolated positions throughout the cladograms.

However, 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, (e.g., *Micrandrena*, *Ptilandrena*, and *Larandrena*, indicated by arrows in Figs 12, 13), i.e., the present study refrained from erecting monobasic subgenera.

Evaluation and support of trees and clades

The consistency index 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 despite no change in information content, since the statistical probability of homoplasy rises as the data matrix becomes larger (KITCHING ET AL. 1998, RIEPPEL 1999, WÄGELE 2001).

Most bootstrap and jackknife values calculated in the present analysis were less than 50 % except for several apical clades (Fig. 12), a tribute paid to the homoplasious 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 following sister group relationships: *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 more than 50 % support by jackknife values in the present analysis (56 % each).

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 a decrease in the CI-values but also in branch support values, both of which are also 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 possible. Comprehensive behavioral data are 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 1989, PARKER & GRISWOLD 1982, SCHÖNITZER & KLINKSIK 1990).

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. A complete reconstruction of the relationships of the western Palearctic subgenera of *Andrena* according to Warncke remains obscure, and main parts of his exposition are not understandable. WARNCKE (1968a) 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 grouped together the following as mostly derived subgenera: *Ptilandrena*, *Margandrena*, *Hoplandrena*, *Carandrena*, *Notandrena*, *Leucandrena*, *Parandrena*, *Larandrena*, *Cnemidandrena* and *Andrena*. 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 in the group (Fig. 12, node X) by the present analysis. In addition, WARNCKE (1968a) held that *Avandrena* and *Micrandrena* were among the most ancestral subgenera of *Andrena* and that they were closely related. This hypothesis could not be properly examined in the present analysis, since it was necessary to omit the representative of *Avandrena* from the analysis due to the great degree of missing data in the male sex. Nevertheless, *Micrandrena* never occurred in basally in the present analyses, and it seems unlikely that *Avandrena* would neither since subgenera related to *Avandrena*, as listed by WARNCKE (*Rufandrena*, *Chlorandrena*, *Pallandrena*), failed to show up in basal positions in the cladograms of the present study. In summary, only some of the sister groups postulated by WARNCKE (1968a) could be confirmed in the present analyses, whereas the majority were not different. The inclusion of Nearctic subgenera in a broad phylogenetic focus by the present study demonstrates an insufficiency in most of WARNCKE's hypotheses.

In computerized phenetic analyses of 85 *Andrena* species from Japan, TADAUCHI (1981, 1982, 1985a) examined the subgeneric position of each species based on methods explained in SOKAL & SNEATH (1963, 1966). The studies employed 130 female morphological characters, and different distance phenograms were obtained depending on clustering methods (TADAUCHI 1982) and which character subsets were used (TADAUCHI 1985a). In the phenogram based on a distance matrix obtained by the group average method, Tadauchi (1982, 1985a) recognized five major groups. The first group comprises *Andrena* s. str., *Larandrena*, *Euandrena*, *Hoplandrena*, *Cnemidandrena*, *Melandrena* and *Simandrena*. It resembles the *Hoplandrena*/*Andrena*/*Leucandrena*-clade (Fig. 12, node X2; Fig. 13, node H) of the present analyses, aside from the presence of *Euandrena*, *Melandrena* and *Simandrena* within the cluster and the absence of *Parandrena*, *Leucandrena* and several subgenera which do not occur in Japan. Nevertheless, the close relationship of *Melandrena* and *Simandrena* was also confirmed by the present investigation, (Fig. 12, node J; Fig. 13, 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 for a more or less distinct relationship between *Micrandrena* and *Calomelissa*, the latter being "paraphyletic" in Tadauchi's phenogram. In the present study *Leucandrena* is a close relative to *Larandrena* and *Parandrena* of the *Augandrena*/*Leucandrena*-clade (Fig 12, node Z) within the *Hoplandrena*/*Andrena*/*Leucandrena*-group (Fig. 12, node X2; Fig. 13, 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. 12, node C; Fig. 13, node Q), *Oreomelissa* is clearly found to be the sister to *Derandrena* and *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, 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*. His conclusions were not based on the results of a formal parsimony analysis. He regarded the subgenera *Andrena* s. str., *Notandrena*, *Gonandrena* and their relatives as the most "primitive" groups of extant subgenera based on previous studies (LABERGE & RIBBLE

1972, LaBerge 1980). This hypothesis could be corroborated only in part by the present analyses. Supporting the hypothesis is the result that the clade uniting *Opandrena* and *Notandrena* (Fig. 13, node C) was the sister group to *Hamandrena*, while several other results contradict the hypothesis. Among the most ancestral subgenera of *Andrena* are the members of the *Aenandrena*-clade in the strict consensus tree of the unweighted analysis (Fig. 12, node C) and *Hamandrena* in the successive weighting analysis (Fig. 13). A close relationship between *Andrena* s. str., *Geissandrena and Gonandrena*, as well as between *Leucandrena Larandrena* and *Parandrena*, as postulated by LaBerge, was confirmed by the present study. However, all these genera arose from a common ancestral lineage of the *Hoplandrena*/*Andrena*/*Leucandrena*-clade (Fig. 12, node X2; Fig. 13, node H). Although the present study indicated that *Callandrena*, *Chrysandrena* and *Charitandrena* belong to a common clade (Fig. 12, node F; Fig. 13, 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 was confirmed in general by the successive reweighting analysis except *Xiphandrena*, which was not included in the present analyses (Fig. 13, node U). In the unweighted analysis, only *Trachandrena*, *Scrapteropsis* and *Biareolina* were members of a common clade (Fig. 12, node M), while *Rhaphandrena* and *Onagrandrena* formed a common clade together with *Scoliandrena*, *Diandrena* and *Melanapis* (Fig. 12, node S), which constitutes the sister group to the *Ptilandrena*/*Hamandrena*/*Carandrena*/*Andrena*-group (Fig. 12, node T). The close relationship between *Diandrena* and *Rhaphandrena*, as postulated by LaBerge (1971b), was confirmed only in the unweighted analysis (Fig. 12, node S), whereas in the successive reweighting analysis *Scoliandrena* was the sister of *Diandrena* (Fig. 13, node E) as mentioned above. Both analyses of the present study confirm 1) the hypothesis of LaBerge that *Trachandrena* arose more or less directly from *Scrapteropsis* and 2) the relationship between *Brachyandrena* and *Scrapteropsis* as suggested by LaBerge (Fig. 12, node K; Fig. 13, 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 (1986b) was not replicated in the present study.

Larkin (2002, 2006) 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 members of the subgenus *Callandrena*, she additionally included Nearctic representatives from 24 subgenera in the analyses. In her results from the maximum likelihood analysis of a combined nuclear and mitochondrial DNA data matrix (Larkin 2002), two large clades were distinguished (excluding the polyphyletic *Callandrena* in her analyses). Clade A combined *Andrena* s. str., *Cnemidandrena*, *Archiandrena*, *Plastandrena*, *Trachandrena*, *Scrapteropsis*, *Rhaphandrena*, *Onagrandrena*, *Diandrena*, one representative of *Gonandrena* and one representative of *Rhacandrena*. Clade B included *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 (2002) 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 (2002) (except by the mitochondrial data only), wherein only *Parandrena* + *Leucandrena* is monophyletic and *Larandrena* is 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 (2002), 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*, of Larkin (2002) in clade B, was not confirmed in the present study. The results of maximum parsimony analysis of the combined data in Larkin (2006) were similar to those of the maximum likelihood analysis, although most of the internal nodes were unresolved. Nevertheless, close relationships observed in this study between *Andrena* s. str., *Cnemidandrena* and *Archiandrena*, between *Plastandrena*, *Trachandrena* and *Scrapteropsis* and between *Parandrena* and *Leucandrena* were also found through maximum parsimonious analysis in Larkin (2006).

Evolution of *Andrena* and zoogeographical aspects

Despite certain very large genera of bees (e.g., *Megachile*, *Lasioglossum*) being more widespread than *Andrena* and some social bees (*Apis*) more numerous in individuals, in terms of species richness, *Andrena* exceeds all. The overwhelming majority of its species are concentrated in the Holarctic region; only a few occur in sub-Saharan Africa, the lowlands of India, southeast Asia and Central America. Other than *Andrena* and *Cubiandrena*, which contains two species from the eastern Mediterranean region to Anatolia, the other four genera of the Andreninae are restricted to the New World. The North American genera, *Ancylandrena* (four species) and *Megandrena* (two species), range from the western United States to northern Mexico (Zavortink 1972, 1974); the South American genera, *Orphana* (two species) and *Euherbstia* (one species), are restricted to Chile (Rozen 1971). Additionally, there is the monotypic *Alocandrena* of Peru which appears to be closely related to other Andreninae but was removed and placed in its own subfamily (Alocandreninae) by Michener (2007).

The small American genera are ancestral within the Andreninae according to the results of the cladistic study. Likewise, their biogeography suggests a relictual appearance (Michener 1979) (i.e., low number of species for each genus, disjunct distribution and great diversity of genera). The subfamily may have had its origin in the New World. In contrast, the genus *Andrena*, with its immense diversity of species, probably represents the most modern group of Andreninae and most likely evolved in the Old World (presumably somewhere between the Mediterranean region and Central Asia), since most basal subgenera of *Andrena* are strictly Palearctic. *Andrena* appears to be derived from the ancestors of *Cubiandrena* or the common ancestral lineage of *Cubiandrena* + *Ancylandrena*. The former evolutionary scenario seems more likely since the latter would imply that the splitting off of *Andrena* occurred in the New World and that both *Andrena* and the ancestor of *Cubiandrena* colonized the Old World independently or that the ancestor of *Ancylandrena* reinvaded the New World from an Old World lineage.

Estimating the age of the *Andrena* split from the *Cubiandrena*-lineage is difficult. The oldest fossils attributed to *Andrena* were previously believed to be from Baltic amber (Eocene) (Zeuner & Manning 1976, LaBerge 1986b). One specimen was originally described as *Andrena wrisleyi* Salt, 1931, but based on the original figures and description, Alexander & Michener (1995) and Michener & Poinar (1996) stated that it is not an *Andrena* but possibly a melittid. Engel (2001) suggested that it may actually be an *Electrapis*, an extinct group belonging to the corbiculate Apinae. The remaining Baltic amber specimens originally attributed to andrenids were merely recorded to be *Andrena* and neither described nor illustrated (Zeuner & Manning 1976). Although the diversity of extinct bees in Baltic amber is extraordinary, reinvestigations have revealed that none of the bee specimens can be reliably considered an andrenid.

Compression fossils originally ascribed to andrenids are those from Florissant shale in Colorado (Oligocene, 30-38 Myr) and Oeningen in Germany (Miocene, 15-20 Myr).

The remaining fossils alleged to belong to the Andrenidae are primarily compression fossils from Florissant shale in Colorado (Oligocene, 30-38 Myr) and Oeningen in Germany (Miocene, 15-20 Myr). These are five species of *Andrena* from Florissant: *A. clavula* Cockerell, 1906, *A. sepulta* Cockerell, 1906, *A. hypolitha* Cockerell, 1908, *A. grandipes* Cockerell, 1911 and *A. percontusa* Cockerell, 1914. Two other species of Andreninae, considered to be allied to *Andrena*, are also from Florissant shale: *Lithandrena saxorum* Cockerell, 1906 and *Pelandrena reducta* Cockerell, 1909. Cockerell described the oldest known Panurginae fossils, two species of *Libellulapis* (*L. antiquorum* Cockerell, 1906 and *L. wilmattae* Cockerell, 1913) from Florissant (Zeuner & Manning 1976). A lost fossil specimen of *Andrena*, "probably" from Florissant, was reported by Zeuner & Manning (1976) to have been identified as *Andrena lagopus* Latreille, 1809, a recent species occurring today in western Europe and northern Africa. After visiting the Oeningen site in Germany, Cockerell described *Andrena primaeva* Cockerell, 1909. In consideration of the lack of revisionary work on these compression fossils we decline to comment on them.

The only inclusion specimen of the Andrenidae is a male Panurginae, *Protandrena* (*Heterosarus*) *eichworti* (Rozen, 1996), from Dominican amber (Miocene, 15-20 Myr) (Michener & Poinar 1996, Camargo et al. 2000), which belongs to a present day subgenus from North to South America.

The fossil record for *Andrena* is meager, and we hesitate to speculate on the antiquity of the genus. Yet based on considerations from zoogeography it is conceivable that *Andrena* originated in the Oligocene or early Eocene when North America and Europe were still partially connected. Starting from an Old World origin, the genus could have rapidly radiated throughout the northern continents. The development of subgenera exclusive to either the Palearctic or Nearctic region could be based on vicariance events occurring from the middle Eocene onward that led to the expansion and separation of the Atlantic Ocean between the North American and Eurasian landmasses. In a second wave of dispersal events, it can be postulated that various lineages of *Andrena* migrated between western North America and Asia during the Miocene and early Pliocene, when diverse continental connections existed between America and Asia. This would explain the interlocking pattern of Nearctic and Palearctic subgenera in the cladograms of the present study (Figs 12-13). The existence of 17 Holarctic subgenera might be attributed to a third set of migration events along land bridges of the Bering Strait during the Holocene. Since 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. The recolonization of Central Europe (north of the Alps) after the last glacial period, which took place from southern parts of Europe via routes to the east or west of the Alps (GRÜNWALDT 1979), is an even more recent set of migration events and had certainly no effect on the evolution of subgenera of *Andrena*.

Acknowledgements

We would like to thank the following persons who generously placed material of their museums and institutions at our disposal: Stephan M. BLANK (DEI), Meiling CHAN (NMNS), Michael S. ENGEL (SEMC), Marc EPSTEIN (USNM), Fritz GUSENLEITNER (CFG, CKW, OLL), Frank KOCH (ZMHB), Karl-Heinz LAMPE (ZFMK), Cheng-Shing LIN (NMNS), Jerome G. ROZEN, Jr. (AMNH), Stefan SCHMIDT (ZSM), Hsien TZUNG SHIH (TARI), Andreas TAEGER (DEI), Osamu TADAUCHI (KUEC) and Jeng-Tze YANG (NCHUT). Roland MELZER, Frank RECKEL and Heidemarie GENSLER (all Munich) generously enabled the use of the SEM facility at the Zoological Institute of the Ludwig-Maximilians-Universität Munich. Fritz GUSENLEITNER (Linz) and Erwin SCHEUCHL (Velden) kindly provided valuable information and literature on taxonomy and morphology of Palearctic *Andrena*. We appreciate the helpful comments of two anonymous reviewers of an earlier version of the manuscript. Finally our special thanks go to Johannes SCHUBERTH (ZSM) for his effort on editing the manuscript. This study was supported in part by a PhD scholarship awarded to the first author by the Ludwig-Maximilians-Universität of Munich.

Zusammenfassung

Die vorliegende Arbeit präsentiert das erste umfassende Konzept zur Phylogenie der weltweit artenreichsten Bienengattung *Andrena* auf Untergattungsebene, basierend auf morphologischen Daten. Für die 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 wird diskutiert. Insgesamt wurden 107 Taxa kodiert, von denen fünf je einen Vertreter aller anderen Gattungen der Unterfamilie Andreninae representierten.

Eine heuristische Analyse ohne Merkmalsgewichtung ergab insgesamt sechs maximal sparsame Kladogramme (MPTs) mit einer Länge von 1875 Schritten. Die Monophylie von *Andrena* wurde durch fünf, nicht-homoplastische Synapomorphien begründet. *Cubiandrena* stellte sich als nicht zu *Andrena* gehörig heraus. Eine zweite Analyse unter Verwendung iterativer Merkmalsgewichtung (*a posteriori* Gewichtung) resultierte in einem einzigen Kladogramm, welches teilweise mit den Ergebnissen der ungewichteten Analyse übereinstimmt. In beiden Analysen wurden 14 Gruppen festgestellt, die die gleichen Taxa zusammenfassten, elf davon wiesen eine identische Topologie auf. Die holarktisch verbreiteten Untergattungen *Larandrena*, *Micrandrena* und *Ptilandrena* erwiesen sich sowohl in der ungewichteten als auch in der gewichteten Analyse als polyphyletische Taxa.

Obwohl allgemein Amerika als Ursprungsort der Andreninae angesehen wird, scheint die Gattung *Andrena* altweltlichen Ursprungs zu sein (Mittelmeergebiet oder Zentralasien). 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.

Folgende Taxa der Gattung Andrena wurden als neu für die Wissenschaft beschrieben: *Calcarandrena* **subgen. n.**, *Hamandrena* **subgen. n.**, *Platygalandrena* **subgen. n.** Die Untergattung *A. (Cubiandrena)* WARNCKE, 1968 wurde zur Gattung erhoben: *Cubiandrena* WARNCKE, 1968 **stat. n.;** Aktuell gibt es weltweit 101 gültige *Andrena*-Untergattungen (17 holarktische, 51 paläarktische, 32 nearktische und 1 orientalische). Zwei Taxa wurden in den Status einer Art erhoben: *A. eburnea* WARNCKE, 1975 **stat. n.** und *A. impasta* WARNCKE, 1975 **stat. n.**

Tab. 1. Data matrix for the cladistic analysis of *Andrena*.

	1	2	3	4	5	6	7	8
	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	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
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 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 1 0 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) chalybaea	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) trevoris	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) 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 (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 (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 with "-". Multistate codings in single taxa are denoted by following symbols $: (0,1), #: (0,2), %: (0,3),*:(1,2), +: (2,3)

Tab. 1. Data matrix for the cladistic analysis of *Andrena* (continued).

	1	2	3	4	5	6	7	8
	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	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
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 (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) 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 (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 (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) cressonii	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) 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 (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 (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 (Proxiandrena) 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 (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) 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 (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 (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 with "-". Multistate codings in single taxa are denoted by following symbols $: (0,1), #: (0,2), %: (0,3),*:(1,2), +: (2,3)

Tab. 1. Data matrix for the cladistic analysis of *Andrena* (continued).

	9 1 2 3 4 5 6 7 8 9 0	1 0 1 2 3 4 5 6 7 8 9 0	1 1 1 2 3 4 5 6 7 8 9 0	1 2 1 2 3 4 5 6 7 8 9 0	1 3 1 2 3 4 5 6 7 8 9 0	1 4 1 2 3 4 5 6 7 8 9 0	1 5 1 2 3 4 5 6 7 8 9 0	1 6 1 2 3 4 5 6 7 8 9 0	1 2
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 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 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) chalybaea	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) trevoris	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) 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 (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 (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 with "-". Multistate codings in single taxa are denoted by following symbols $: (0,1), #: (0,2), %: (0,3),*:(1,2), +: (2,3)

Tab. 1. Data matrix for the cladistic analysis of *Andrena* (continued).

		1	1	1	1	1	1	1	
	9	0	1	2	3	4	5	6	
	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	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
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 2	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 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 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 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 1 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 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 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 (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) 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 (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 (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 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 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) cressonii	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 1 1 0 - 0	- 1 0 2 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 1 ? 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 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) 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 (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 (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 (Proxiandrena) 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 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 (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 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 0 4 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 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) 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 (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 (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 with "-". Multistate codings in single taxa are denoted by following symbols $: (0,1), #: (0,2), %: (0,3),*:(1,2), +: (2,3)

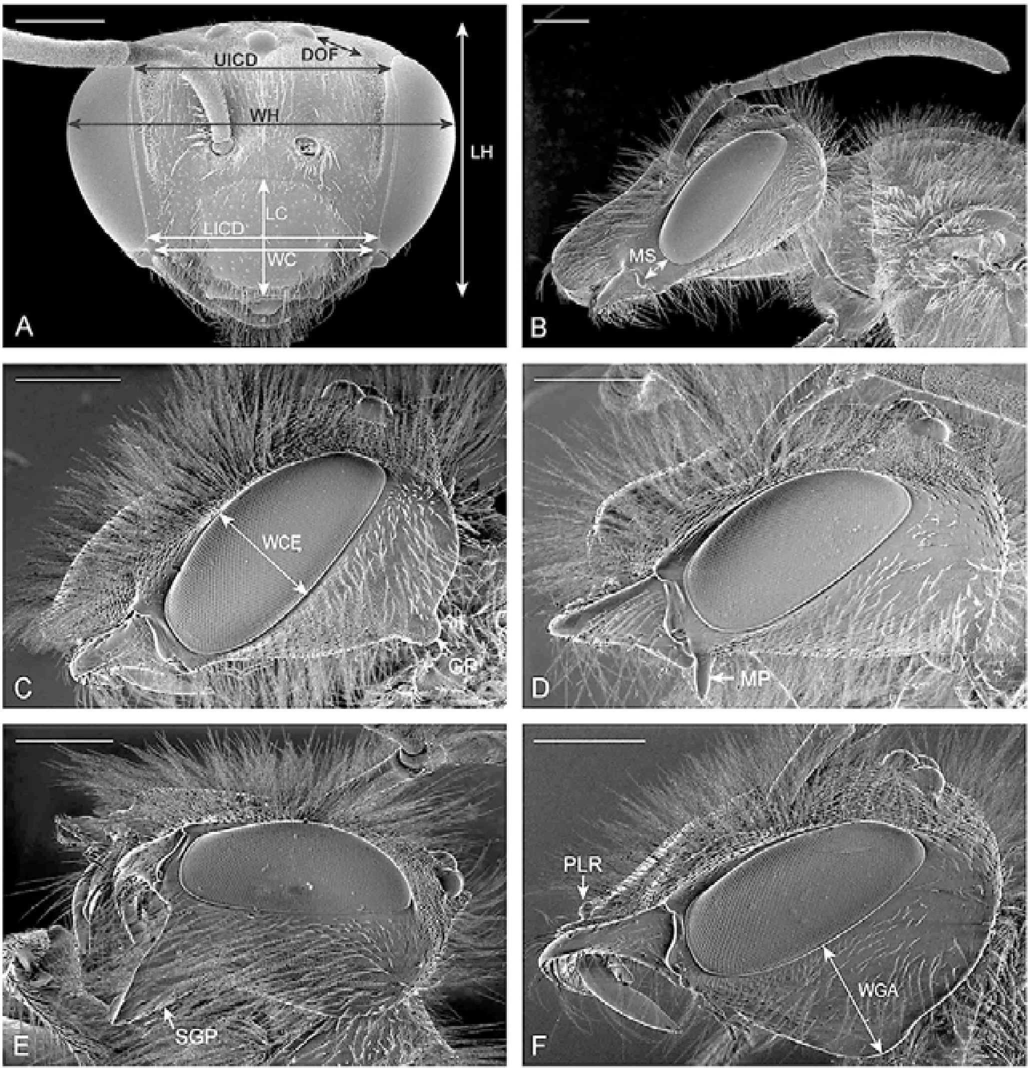


Fig. 1. Head and head structures of *Andrena* with indicated morphometric measurements. **A:** Frontal view of female of *A. (Parandrenella) dentiventris* MORAWITZ, 1874, **B:** Lateral view of female *A. (Stenomelissa) halictoides* SMITH, 1869. **C-F:** Lateral view of male *A. (Archiandrena) banksi* MALLOCH, 1917 (C), *A. (Derandrena) vandykei* COCKERELL, 1936 (D), *A. (Genyandrena) mackieae* COCKERELL, 1937 (E), *A. (Habromelissa) nantouensis* DUBITZKY, 2006 (F).
DOF: distance between lateral ocellus and facial fovea, GP: genal process, LC: length of clypeus, LH: length of head, LICD: lower inter compound eye distance, MP: malar process, MS: malar space, SGP: subgenal process, UICD: upper inter compound eye distance, WC: width of clypeus, WCE: width of compound eye, WGA: width of genal area, WH: width of head. Scale bars: 500 µm.

Fig. 2a (*next page*). Head and mandibular structures of female *Cubiandrena* and *Andrena*. **A, D:** Underside of head of *Cubiandrena cubiceps* FRIESE, 1914 (A) and *A. (Nobandrena) nobilis* MORAWITZ, 1874 (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* PANZER, 1799 (H-J), *A. (Charitandrena) hattorfiana* (FABRICIUS, 1775) (K-M), *A. (Hamandrena) nasuta* GIRAUD, 1863 (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 photographed specimen. 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).

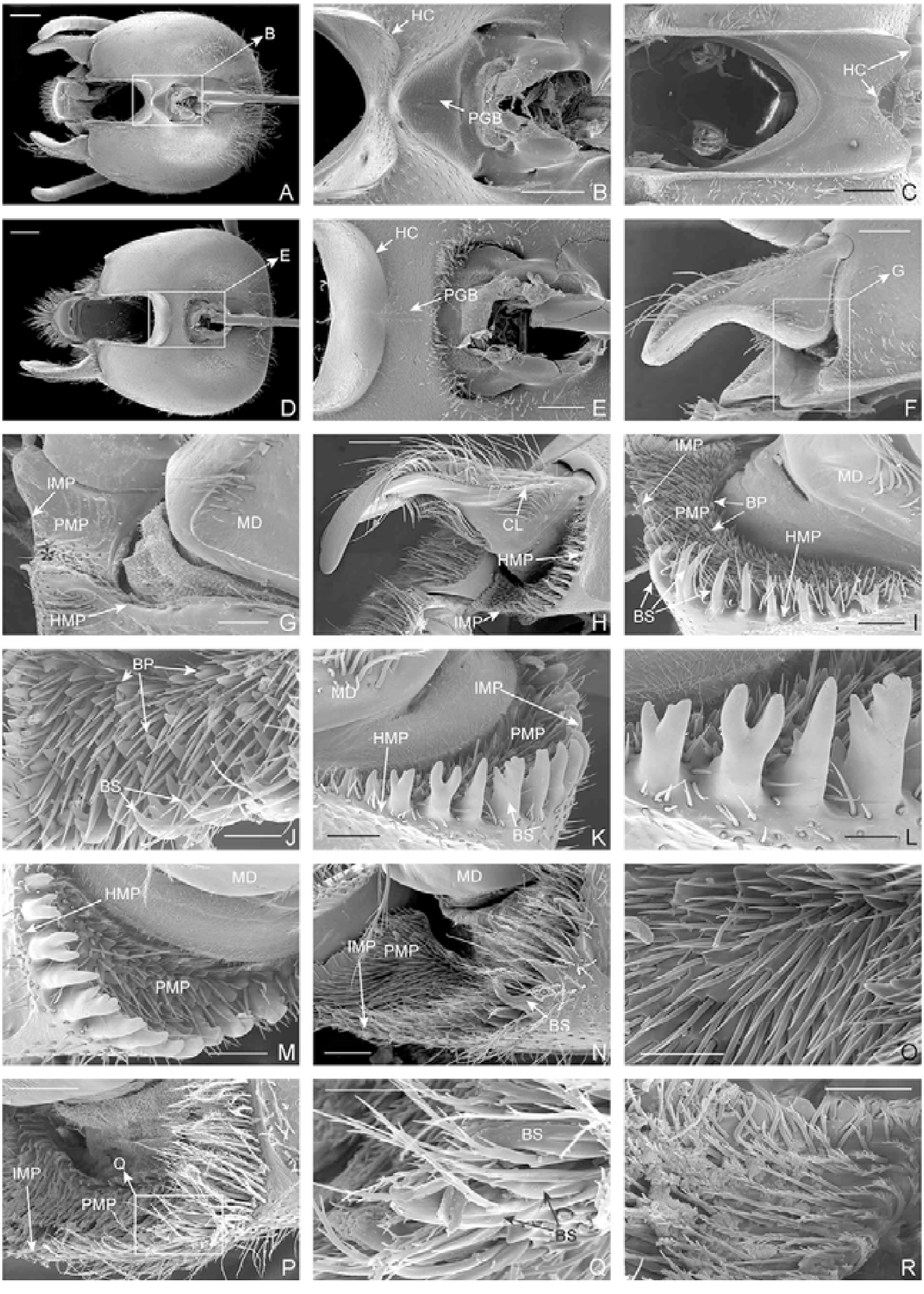


Fig. 2a (Figure legend see left).

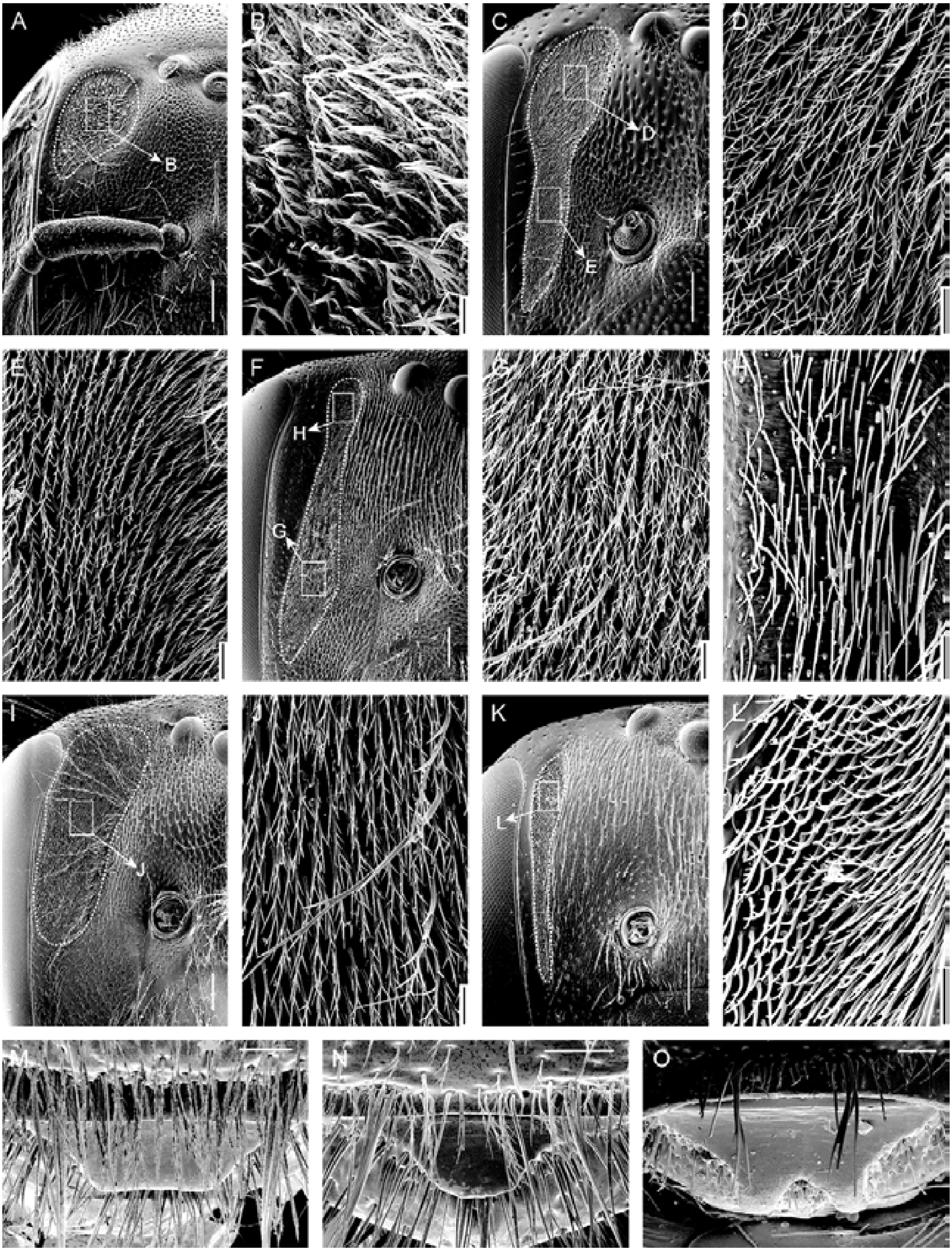


Fig. 2b. FOV (A-L) and PLR (M-O) of female *Andrena* and *Cubiandrena* (only FOV): **A, B:** *Cubiandrena cubiceps*. **C-E:** *A. (Trachandrena) haemorrhoa*. **F-H:** *A. (Hyperandrena) bicolorata*. **I, J:** *A. (Hoplandrena) carantonica*. **K, L:** *A. (Parandrenella) dentiventris*. **M:** *A. (Zonandrena) 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.

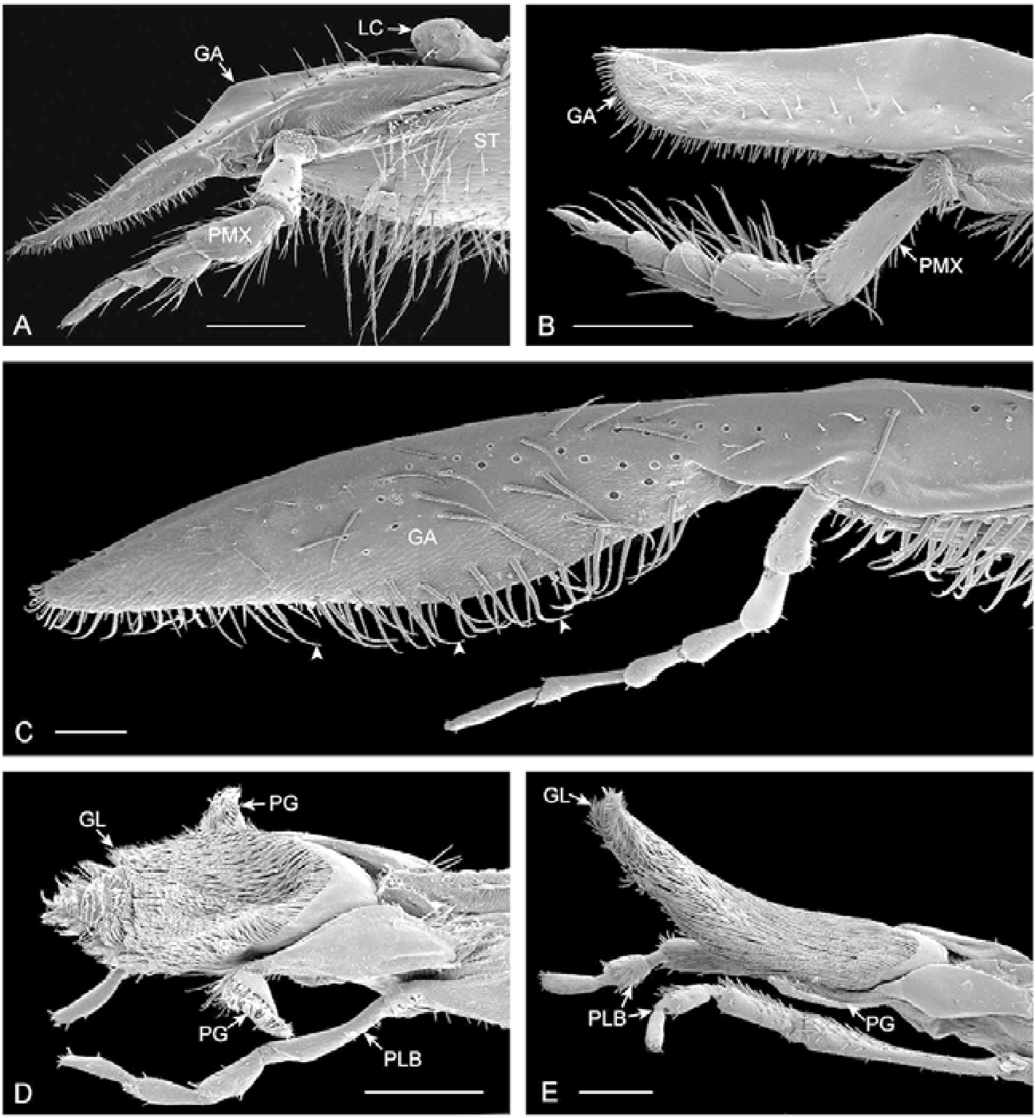


Fig. 3. Galea (A-C) and glossa (D-E) of female *Andrena*. **A, B:** *A. (Platygalandrena) fedtschenkoi* MORAWITZ, 1876, lateral view (A) dorsal view (B). **C:** *A. (Hamandrena) nasuta*, lateral view, with arrowheads indicating posteriorly bent, stiff hairs. **D:** *A. (Zonandrena) flavipes*. **E:** *A. (Hamandrena) nasuta*.
GA: galea, GL: glossa, LC: lacinia, PG: paraglossa, PLB: labial palpus, PMX: maxillary palpus, ST: stipes. Scale bars: 200 µm.

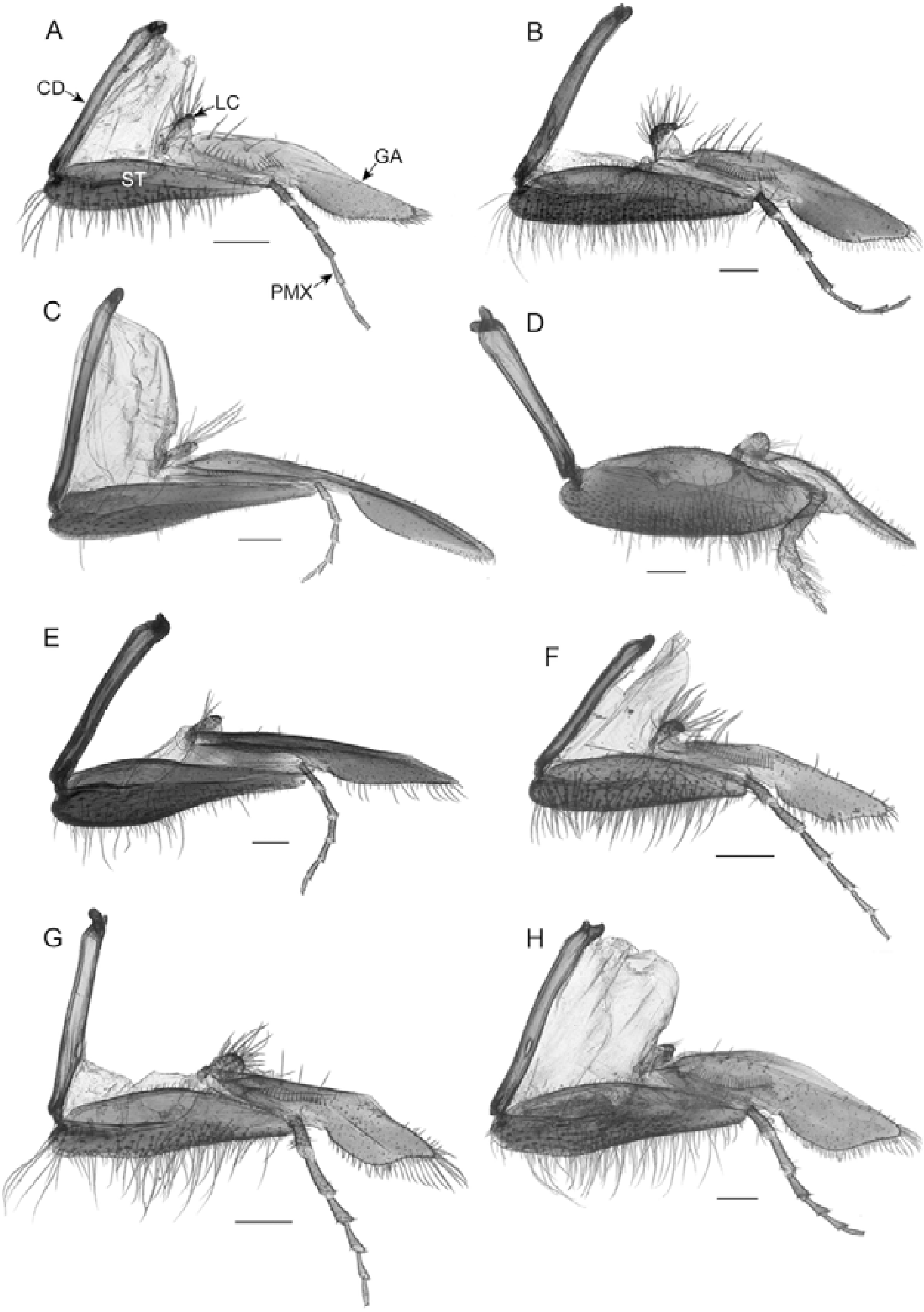


Fig. 4. Maxilla of female *Andrena*. **A:** *A. (Fumandrena) fumida* PÉREZ, 1895, **B:** *A. (Carandrena) aerinifrons* DOURS, 1873, **C:** *A. (Charitandrena) hattorfiana*. **D:** *A. (Platygalandrena) fedtschenkoi*. **E:** *A. (Lepidandrena) curvungula* THOMSON, 1870. **F:** *A. (Aciandrena) aciculata* MORAWITZ, 1886. **G:** *A. (Andrena) helvola* (LINNAEUS, 1758). **H:** *A. (Cnemidandrena) nigriceps* (KIRBY, 1802). CD: cardo, GA: galea, LC: lacinia, PMX: maxillary palpus, ST: stipes. Scale bars: 250 µm.

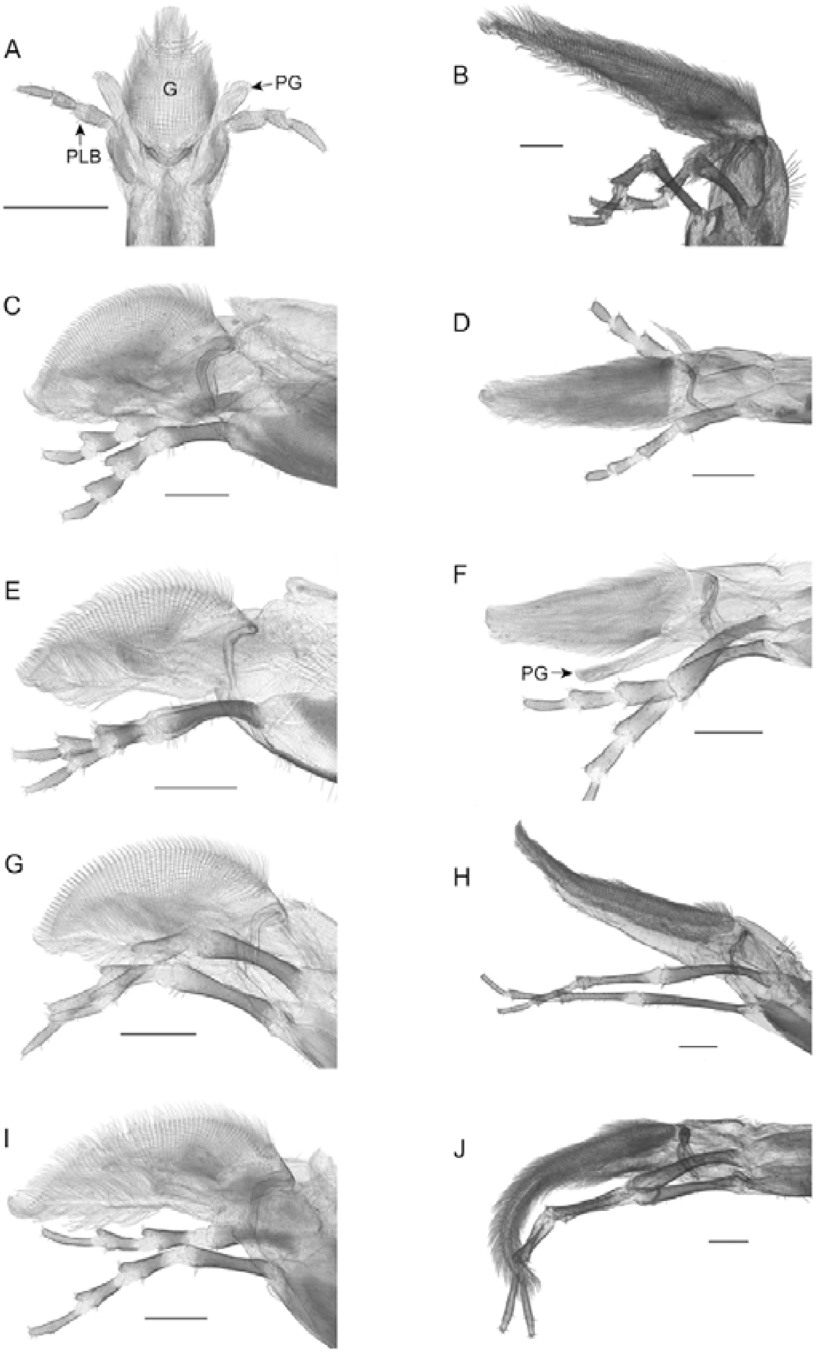


Fig. 5. Glossa of female *Andrena*. **A:** *A. (Rufandrena) rufiventris* LEPELETIER, 1841, dorsal view. **B:** *A. (Melittoides) curiosa* FRIESE, 1899, lateral view. **C:** *A. (Hoplandrena) carantonica* PÉREZ,1902, lateral view. **D:** *Cubiandrena cubiceps*, lateral view. **E:** *A. (Truncandrena) truncatilabris* MORAWITZ, 1877, lateral view. **F:** *A. (Margandrena) marginata* FABRICIUS, 1776, lateral view. **G:** *A. (Suandrena) suerinensis* FRIESE, 1884, lateral view. **H:** *A. (Didonia) mucida* KRIECHBAUMER, 1873, lateral view. **I:** *A. (Holandrena) labialis* (KIRBY, 1802), lateral view. **J:** *A. (Hamandrena) nasuta*, lateral view.
G: glossa, PG: paraglossa, PLB: labial palpus. Scale bars: 250 µm.

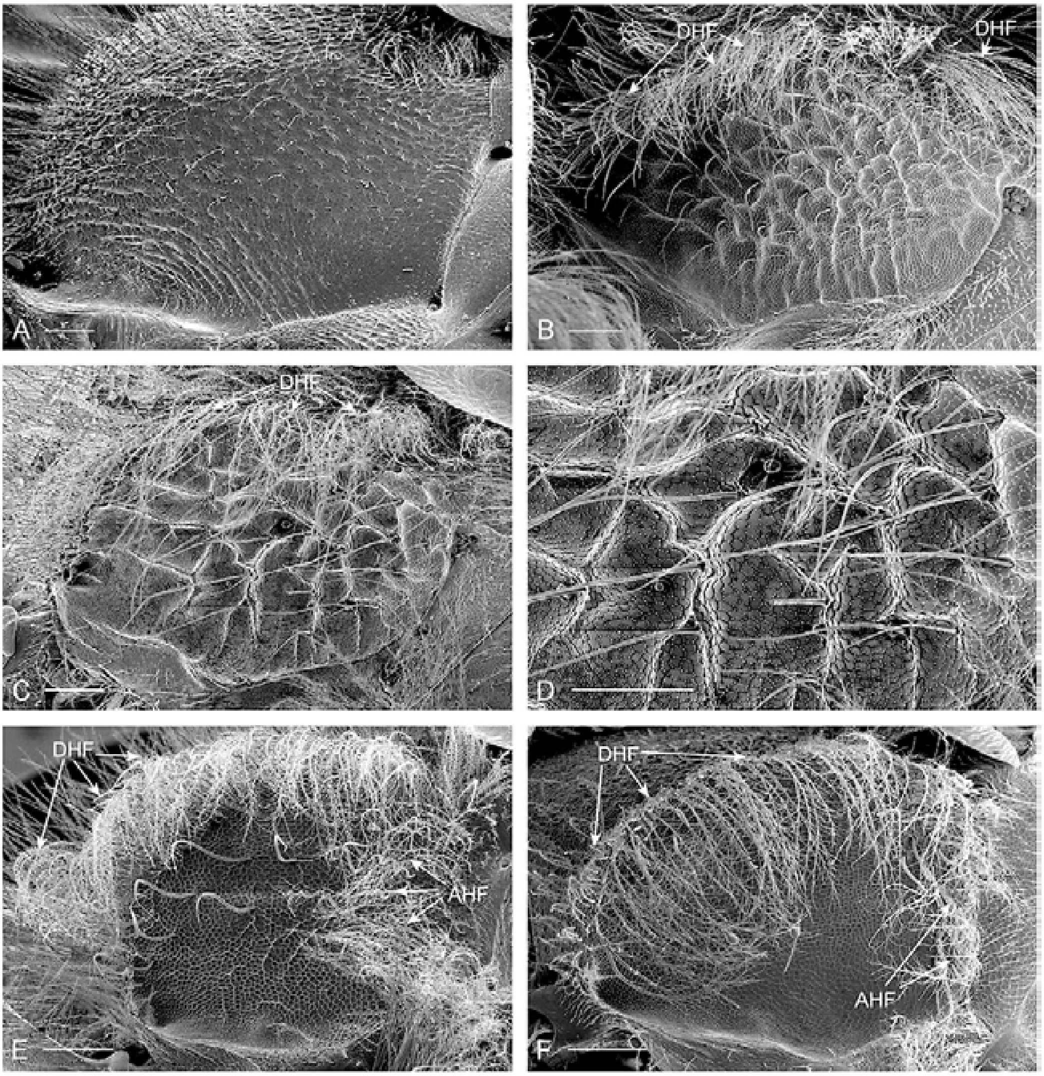


Fig. 6. Lateral propodeum of female *Andrena*. **A:** *A. (Charitandrena) hattorfiana*. **B:** *A. (Agandrena) agilissima* (Scopoli, 1770). **C, D:** *A. (Trachandrena) haemorrhoa* (Fabricius, 1775. **E:** *A. (Larandrena) ventralis* Imhoff, 1832. **F:** *A. (Simandrena) dorsata* (Kirby, 1802).
AHF: anterior hair fringe, DHF: dorsoposterior hair fringe. Scale bars: 200 µm.

Fig. 7 (*next page*). Hind leg and associate structures of female *Andrena*. **A:** Inner side of hind leg of *A. (Cryptandrena) ventricosa* Dours, 1873. **B:** Bidentate claws of *A. (Zonandrena) flavipes*. **C:** Detail of row of bristles on inner side of hind femur of *A. (Cryptandrena) ventricosa*. **D:** Detail of inner side of hind tibia of *A. (Aciandrena) aciculata* Morawitz, 1886. **E:** Outer side of hind leg of *A. (Cryptandrena) ventricosa*. **F:** Simple claws of *A. (Platygalandrena) fedtschenkoi*. **G:** Detail 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* Timberlake, 1951 (J), *A. (Chlorandrena) humilis* Imhoff, 1832 (K), *A. (Fumandrena) fumida* (L), *A. (Chrysandrena) fulvago* (Christ, 1791) (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: keirotrichia like hairs, P: pollen. Scale bars: 500 µm (A, E), 100 µm (B, F, H-S) 50 µm (D, G), 25 µm (C).

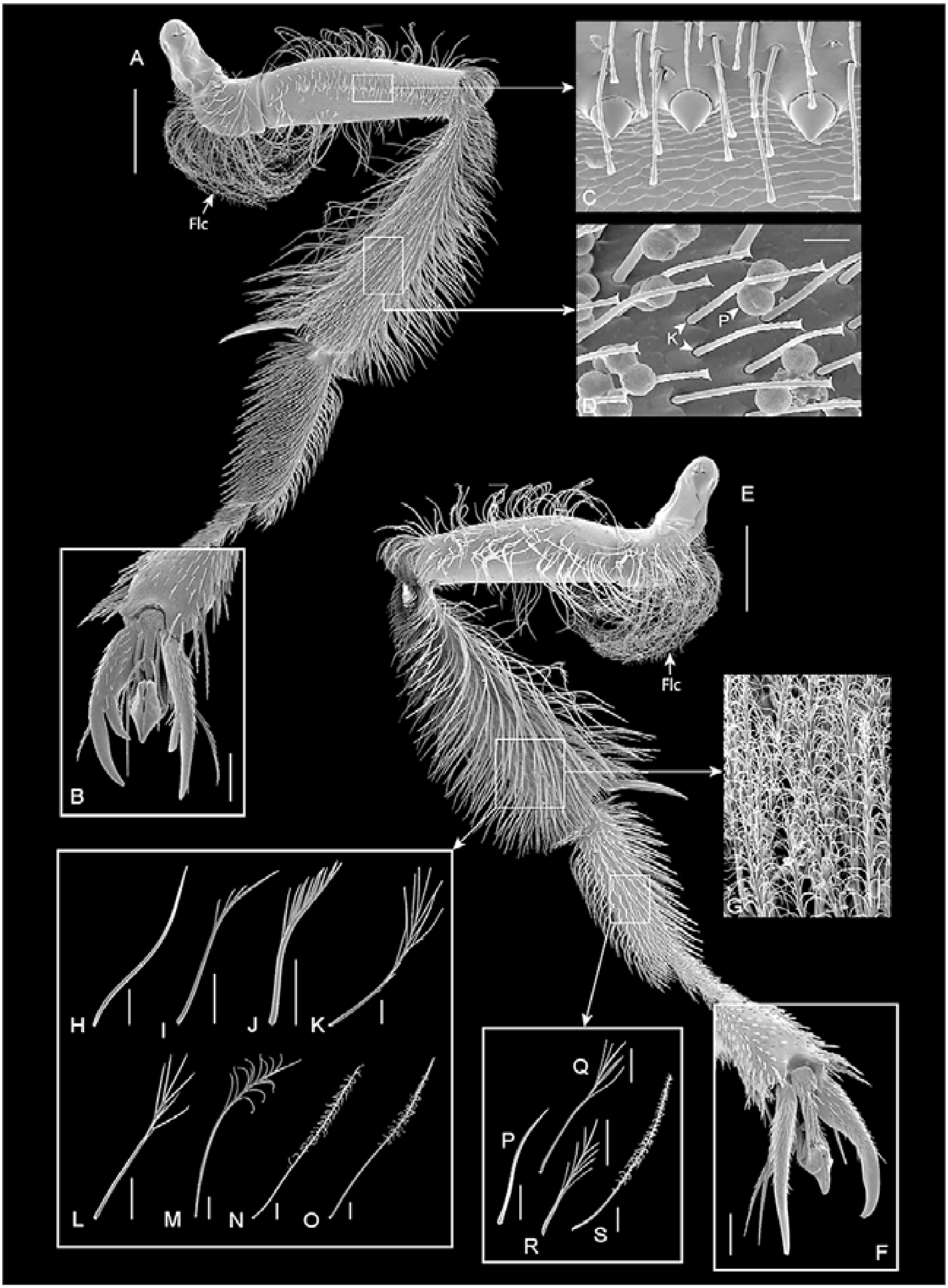


Fig. 7 (Figure legend see left).

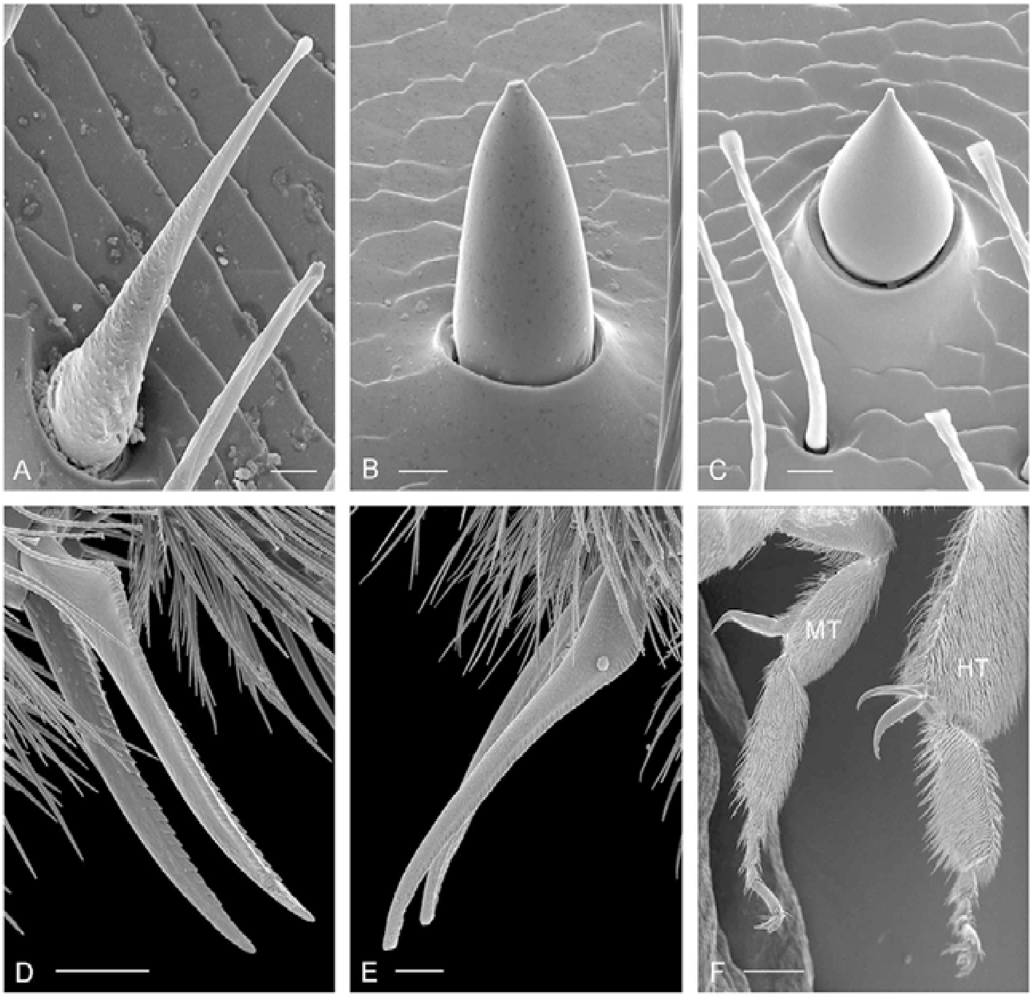
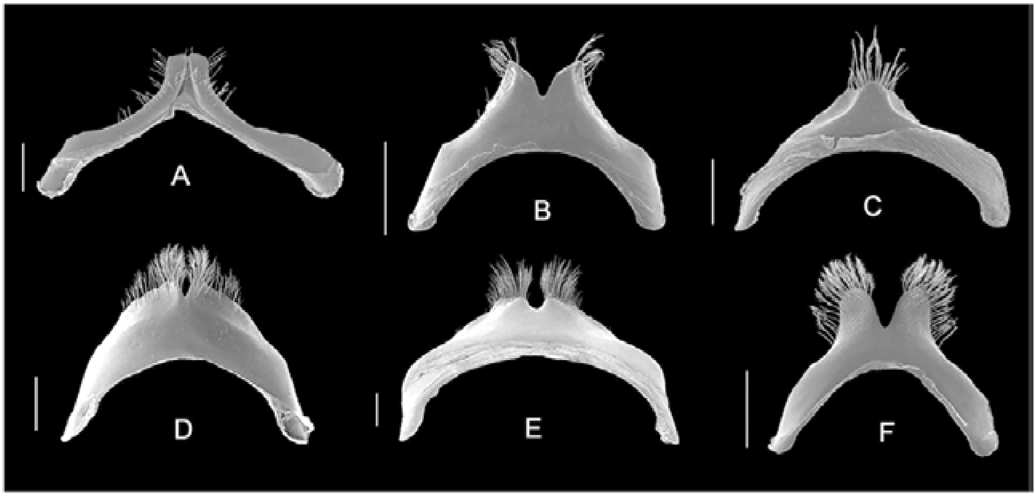


Fig. 8. Bristles of hind femur (A-C) and inner spurs of hind tibia (D-F) of female *Andrena*. Inner spur in foreground, outer spur behind it. **A, D, E:** *A. (Lepidandrena) curvungula*. **B:** *A. (Chlorandrena) humilis*. **C, D:** *A. (Cryptandrena) ventricosa*. **F:** *A. (Osychnyukandrena) cochlearicalcar* LEBEDEV, 1933.
MT: middle tibia, HT: hind tibia. Scale bars: 500 µm (F), 100 µm (D, E), 10 µm (A-C).

Fig. 9 (***next page***). Ventral side of male S7 of *Cubiandrena* (A) and *Andrena* (B-F): **A:** *Cubiandrena cubiceps*. **B:** *A. (Aenandrena) aeneiventris*, **C:** *A. (Andrena) helvola*. **D:** *A. (Leucandrena) barbilabris* (KIRBY, 1802). **E:** *A. (Agandrena) agilissima*. **F:** *A. (Carandrena) planti* DUBITZKY, 2006.
Scale bars: 250 µm.

Fig. 10a (*next page*). 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.*
Scale bars: 250 µm.



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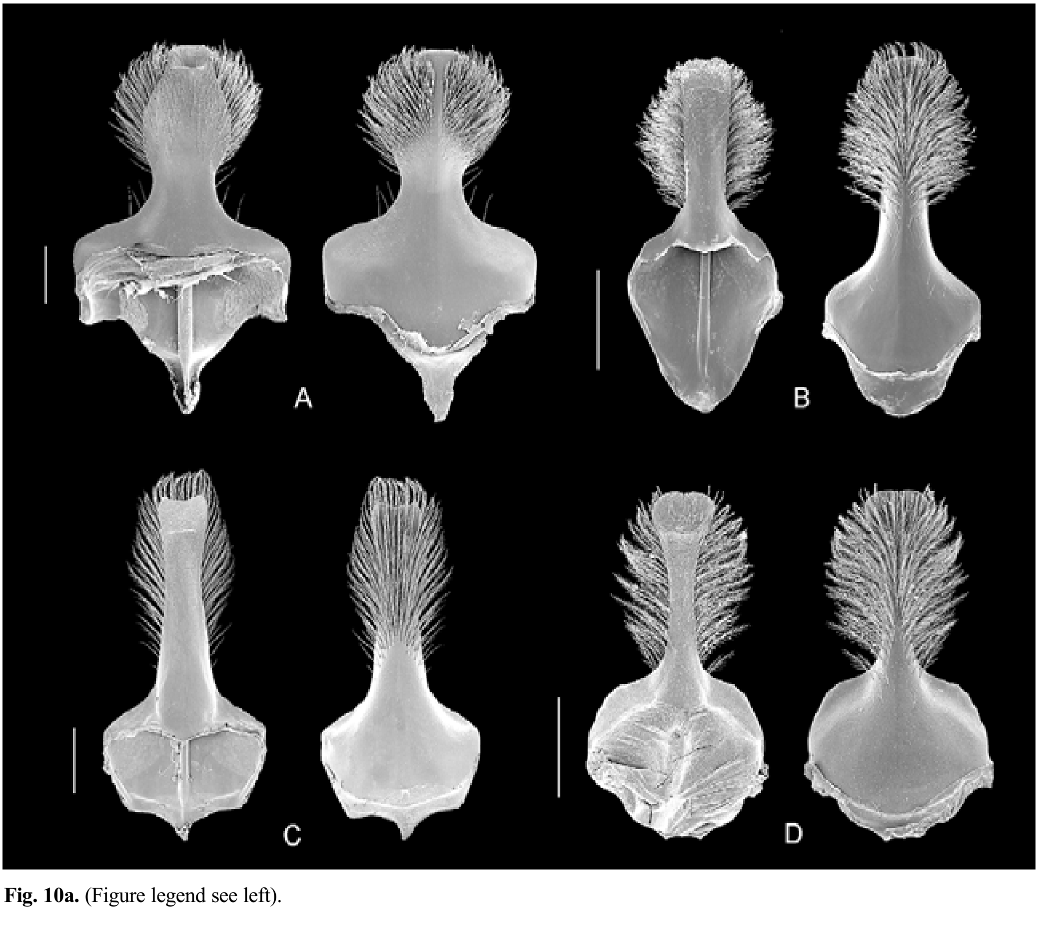

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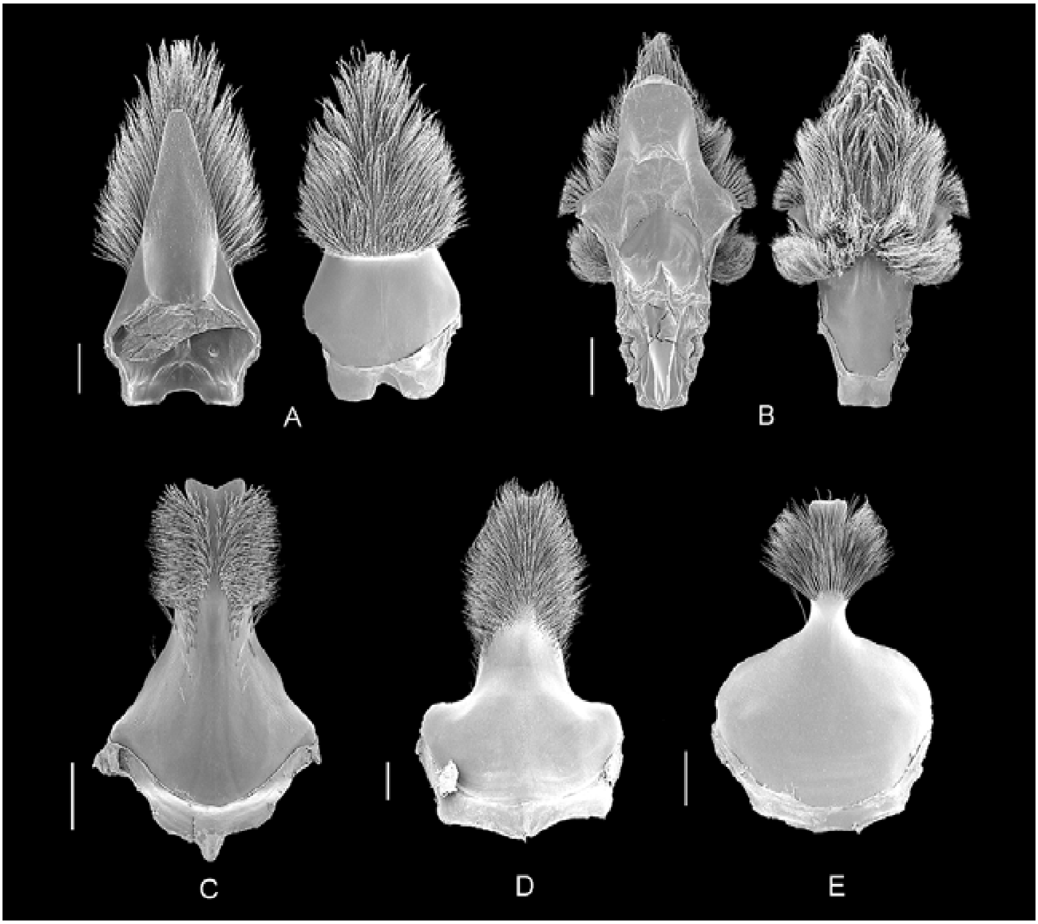

Fig. 10b. S8 of male *Andrena,* left dorsal, right ventral view. **A:** *A. (Orandrena) oralis.* **B:** *A. (Parandrenella) dentiventris.* **C:** *A. (Pallandrena) pallidicincta.* **D:** *A. (Agandrena) agilissima.* **E:** *A. (Chlorandrena) humilis.*
Scale bars: 250 µm.

Fig. 11 (*next page*). Male genitalia of *Cubiandrena* (A) and *Andrena* (B-E), left dorsal, middle lateral and right ventral views. **A:** *Cubiandrena cubiceps*. A1: Detail of volsella. **B:** *A. (Andrena) helvola*. **C:** *A. (Charitandrena) hattorfiana*. C1: Detail of volsella. **D:** *A. (Parandrenella) dentiventris*. **E:** *A. (Plastandrena) tibialis* (Kirby, 1802), dorsal view only.
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).

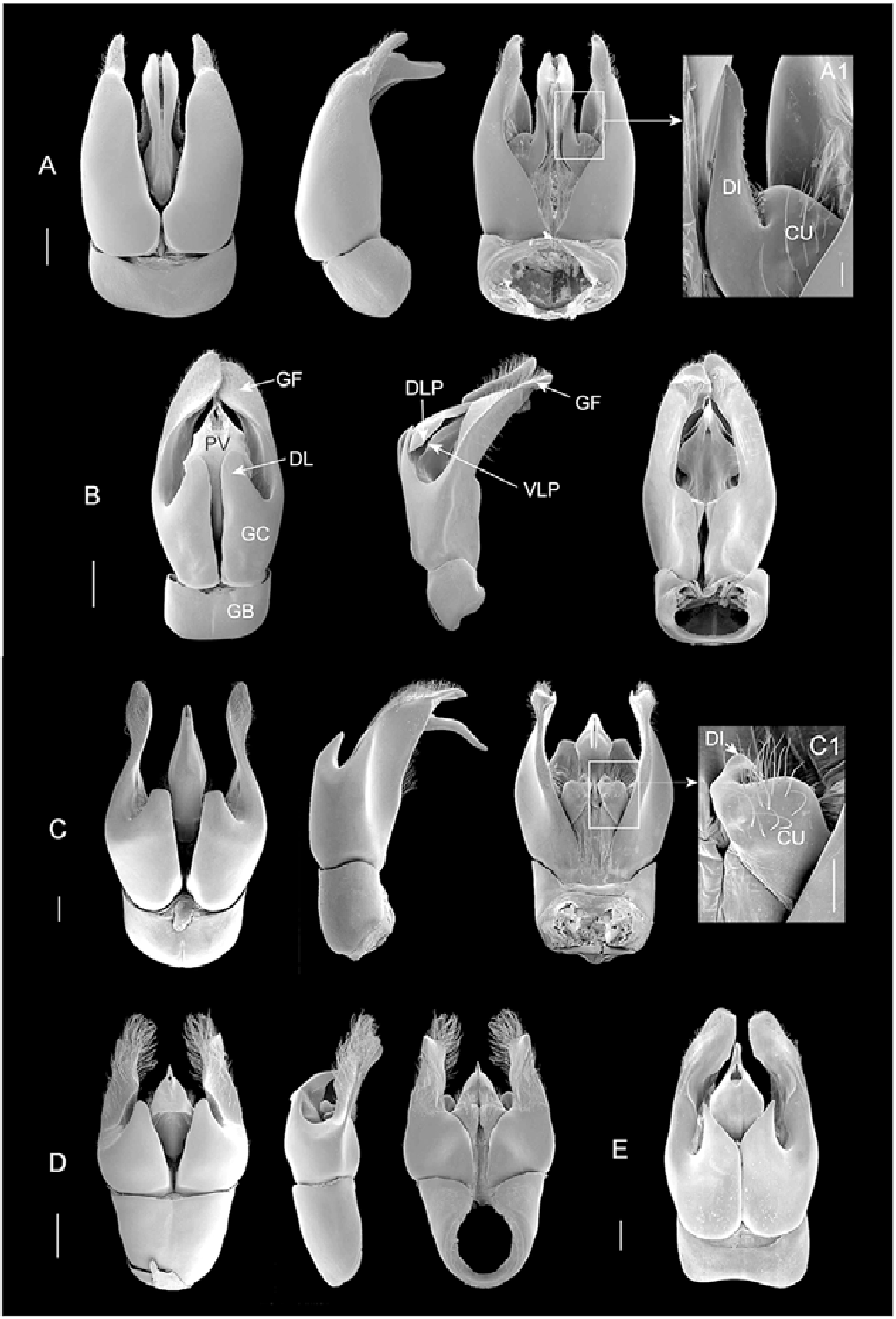

Fig. 11 (Figure legend see left).

Fig. 12. Strict consensus tree of the six MPTs of 1879 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. 13), with dotted lines indicating groups that combine the same taxa, but show a different tree topol-ogy; **arrows:** representatives of polyphyletic groups; **asterisk:** indicating position of *Cubiandrena* **stat. nov.**

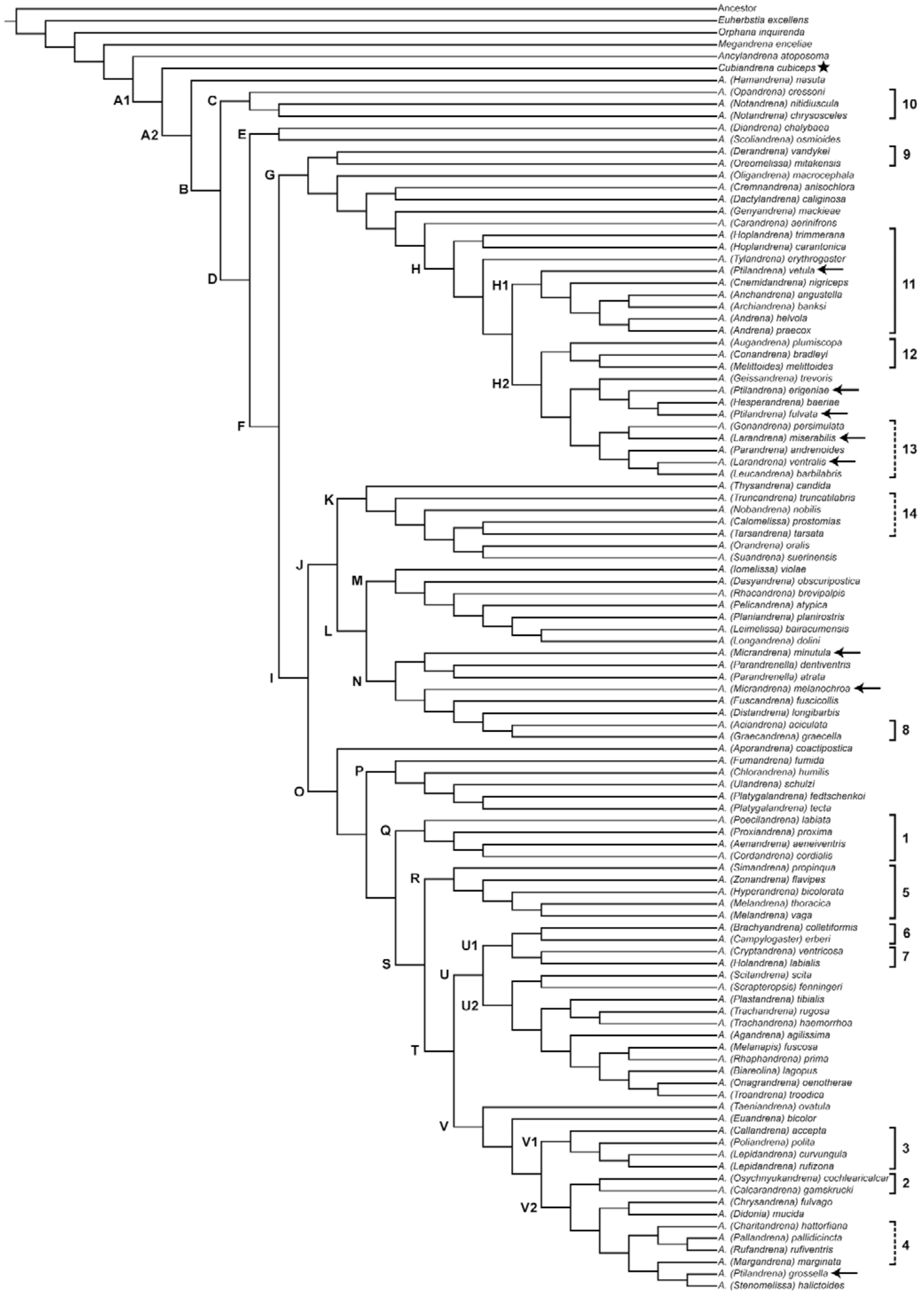

Fig. 13. Single cladogram obtained after successive character reweighting (a posteriori). **A-V2:** nodes mentioned in the text; **1-14:** groups of taxa which are also found in the unweighted analysis (Fig. 12), with dotted lines indicating groups that combine the same taxa, but show a different tree topology; **arrows:** representatives of polyphyletic groups; **asterisk:** indicating position of *Cubiandrena* **stat. nov**.

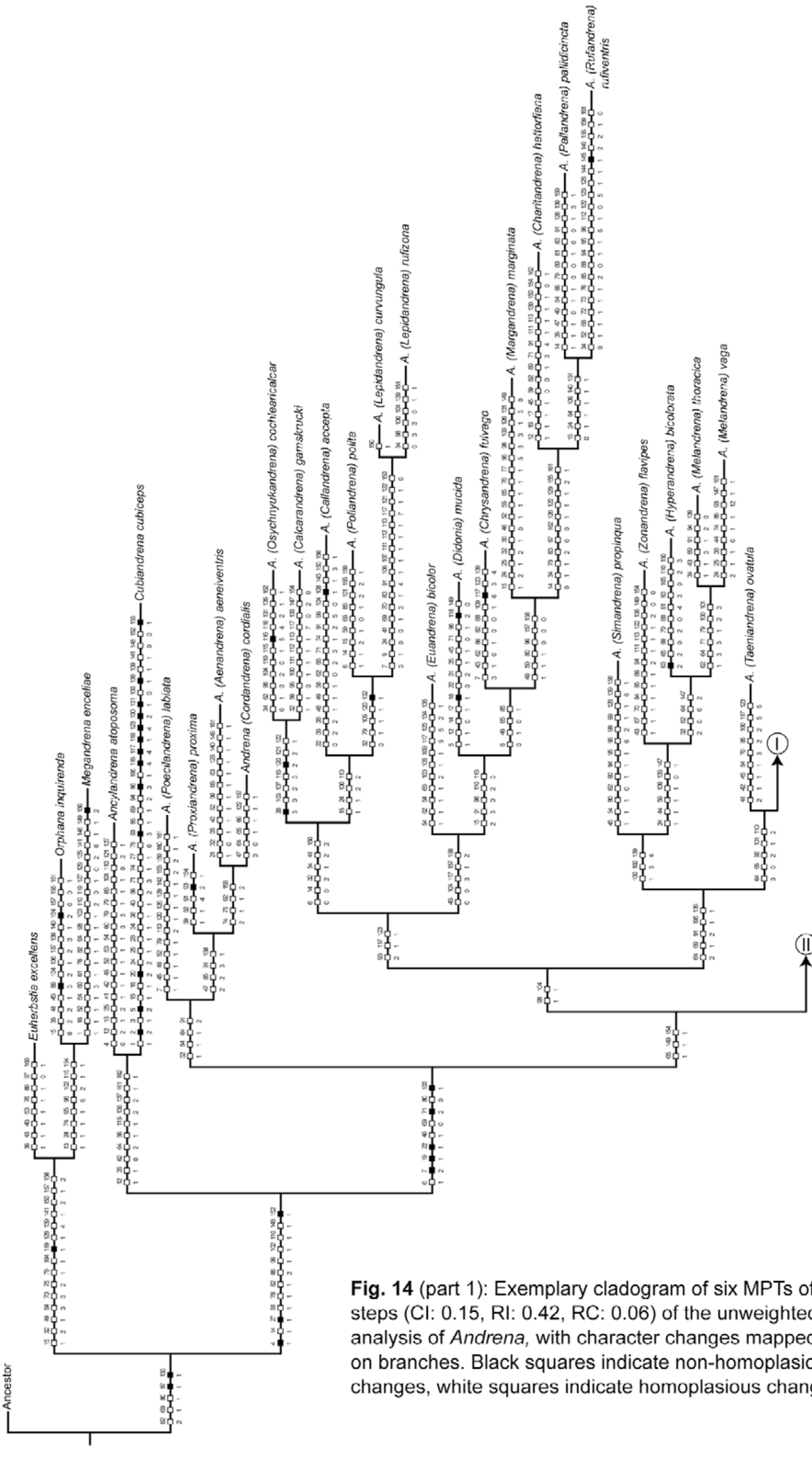

Fig. 14 (part 1): Exemplary cladogram of six MPTs of 1876 steps (CI: 0.15, RI: 0.42, RC: 0.06) of the unweighted analysis of *Andrena,* with character changes mapped on branches. Black squares indicate non-homoplasious changes, white squares indicate homoplasious changes.

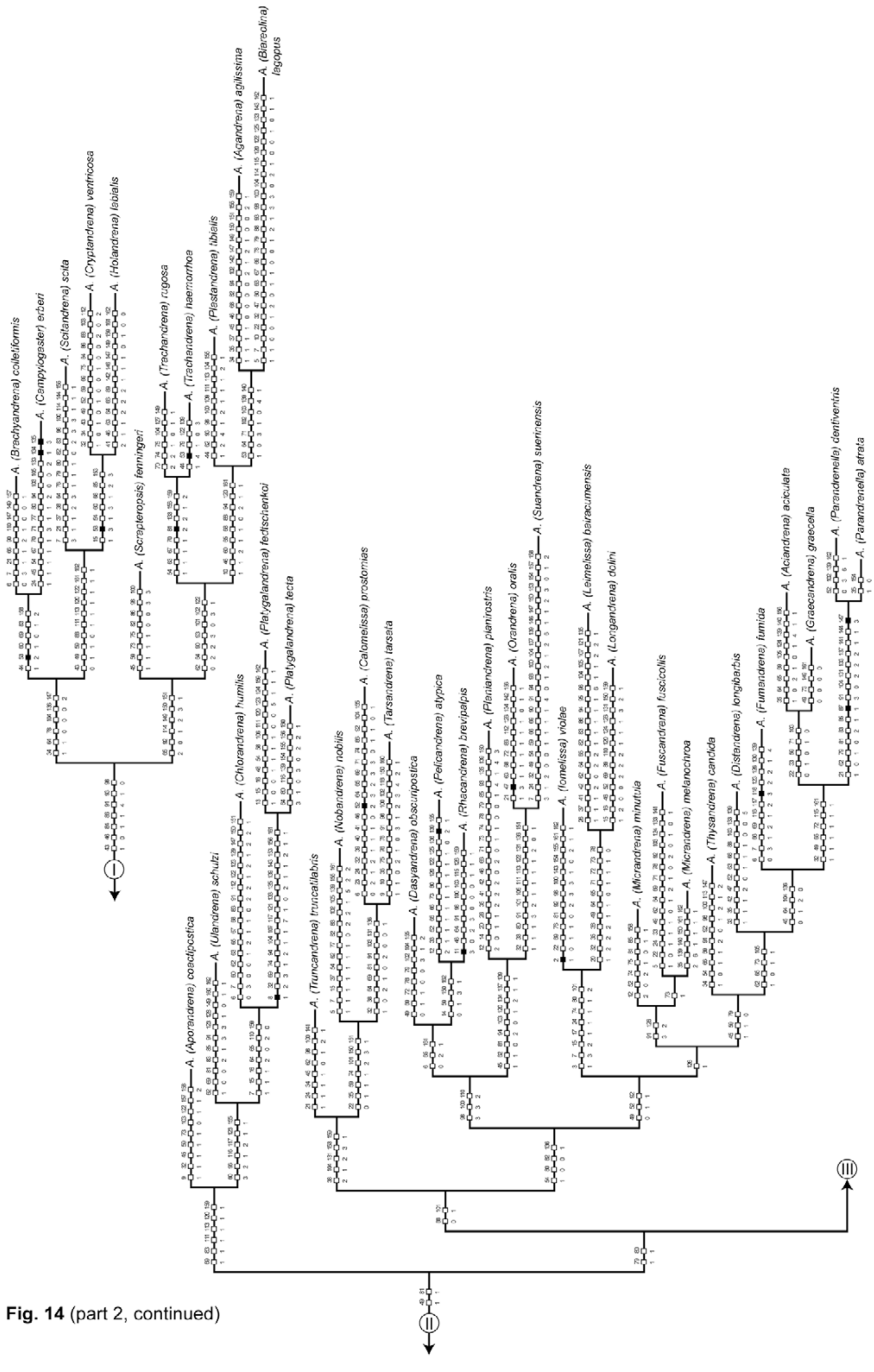

Fig. 14 (part 2, continued)

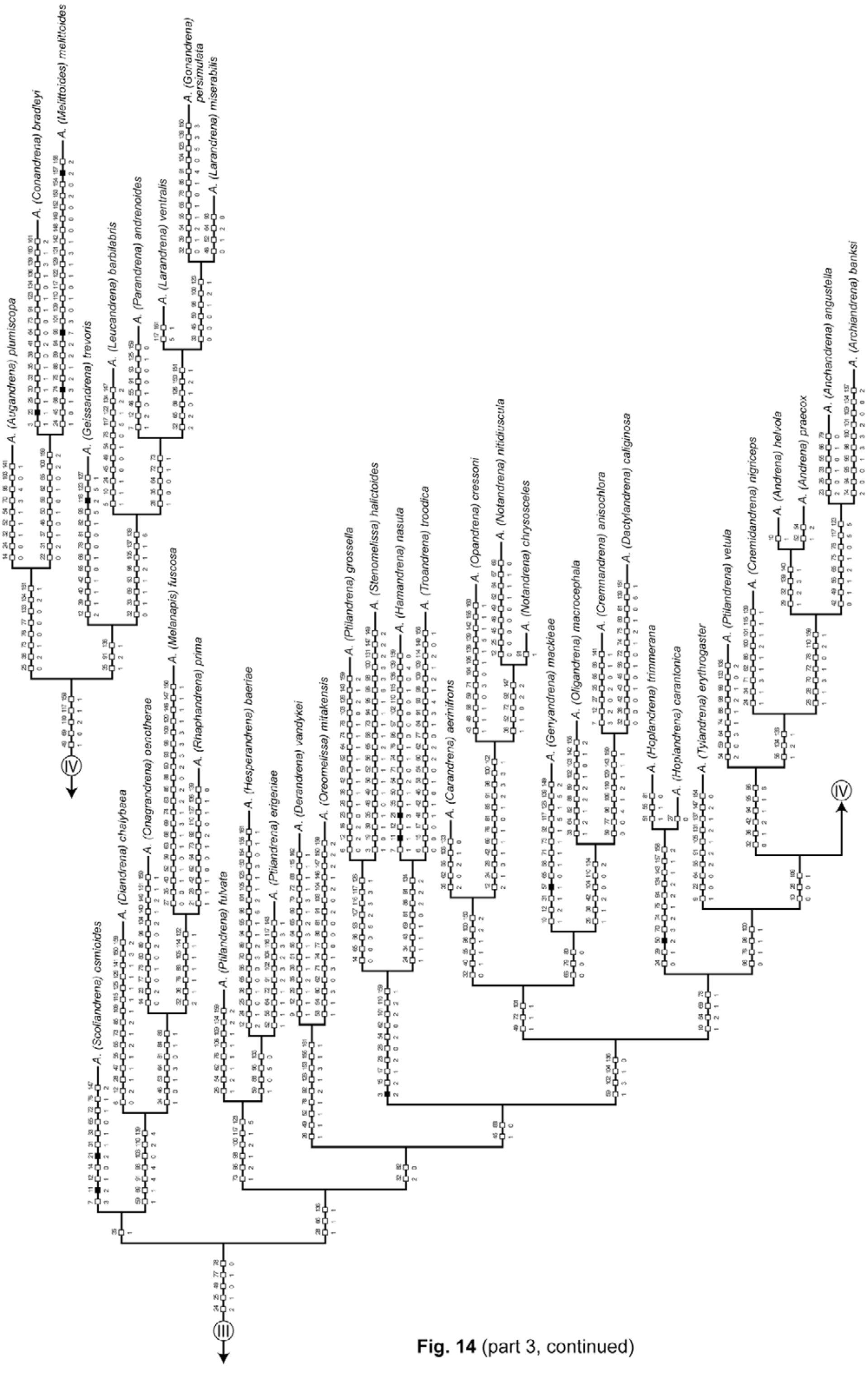

Fig. 14 (part 3, continued)

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Zeitschrift/Journal: Mitteilungen der Münchner Entomologischen Gesellschaft

Jahr/Year: 2010

Band/Volume: 100

Autor(en)/Author(s): Dubitzky Andreas, Plant John, Schönitzer Klaus

Artikel/Article: Phylogeny of the bee genus Andrena FABRICIUS based on morphology (Hymenoptera: Andrenidae). 137-202