The phylogeny and classification of the tribe Halictini, with special reference to the *Halictus* genus-group (Hymenoptera: Halictidae)

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The monophyly of the cosmopolitan tribe Halictini, including over 2300 currently recognized species, is supported by at least a single manifested synapomorphy shared by all members of the tribe: metasomal tergum VII of the male is modified; this forms a transverse ridge giving a false apex beneath which the tergum is strongly reflexed to the morphological posterior margin. On the basis of the present phylogenetic analysis, the tribe Halictini is subdivided into five subtribes: Halictina (comprised of 7 genera: *Echthralictus*, *Glossodialictus*, *Halictus*, *Homalictus*, *Patellapis*, *Seladonia*, and *Thrincohalictus*), Sphecodina (4 genera: *Eupetersia*, *Microsphecodes*, *Ptilocleptis*, and *Sphecodes*), Thrinchostomina (2 genera: *Thrinchostoma* and *Parathrincostoma*), Caenohalictina (9 genera: *Agapostemon*, *Caenohalictus*, *Dinagapostemon*, *Habralictus*, *Mexalictus*, *Paragapostemon*, *Pseudagapostemon*, *Rhinetula*, and *Ruizantheda*), and Gastrohalictina (one large and diverse genus: *Lasioglossum* s. l.). The subtribe Halictina is a paraphyletic group; the remaining four tribes are strictly monophyletic (holophyletic).

The monophyly of the *Halictus* genus-group, comprising the genera *Halictus* and *Seladonia*, is supported by two distinct synapomorphies of the male genitalia: (1) dorsal gonostylus simple (not double), flattened, broad, narrowed proximally, and provided with a clump of very coarse bristles on the inner surface; (2) ventral gonostylus sclerotized, relatively thin and long, directed backward. Only generalized members of the group possess both the character states above. In derived members, the clump of bristles and the ventral gonostylus are often lost independently. The sister group of the *Halictus* genus-group is the genus *Thrincohalictus*. This is supported by the following synapomorphy found among the tribe Halictini only in *Halictus*, *Seladonia*, and *Thrincohalictus*: the ventral gonobasal rim in the male genitalia is forming a right posterolateral angle with a short projection directed laterally. Another feature characterizing these three genera is the presence (except in the parasitic subgenus *Paraseladonia*) of posterior bands of tomentum or dense and much plumose appressed hairs on the metasomal terga. However, this character is shared also with *Patellapis* subgenera *Patellapis* and *Lomatalictus*.

The following subgeneric classification of the genera *Halictus* and *Seladonia* is suggested. The genus *Halictus* includes 12 subgenera: *Acalcaripes* (2 species), *Argalictus* (8), *Halictus* s. str. (4), *Hexataenites* (11), *Lampralictus* (1), *Monilapis* (29), *Nealictus* (2), *Odontalictus* (2), *Platyhalictus* (14), *Protohalictus* (13), *Ramalictus* (2), and *Tytthalictus* (4). The genus *Seladonia* comprises 6 subgenera, including 2 new ones: *Mucoreohalictus* subg. n. (15), *Pachyceble* (22), *Paraseladonia* (1), *Placidohalictus* subg. n. (5), *Seladonia* s. str. (36), and *Vestitohalictus* (16). The subgenera of *Halictus* and *Seladonia* are keyed. The phylogenetic tree of the subgenera of *Halictus* and *Seladonia* is reconstructed with use of 46 morphological characters of adults. All other genera of the tribe Halictini were taken as outgroup. The genus *Halictus* is ascertained as a strictly monophyletic group based upon a single postulated synapomorphy: dorsal gonostylus with a triangular hair patch as a distal appendage on inner side. All the subgenera of this genus appear as strictly monophyletic groups, with the exception of *Monilapis*, which is a paraphyletic one in relation to *Acalcaripes*. The monophyly of the genus *Seladonia* is supported by three synapomorphies, including a novelty (unique synapomorphy): male dorsal gonostylus with a deep cleft. All the subgenera of this genus are strictly monophyletic with the exception of *Placidohalictus*, which is a paraphyletic one in relation to *Vestitohalictus* and *Mucoreohalictus*. A synonymical catalogue of species and species-group names in the genera *Halictus* and *Seladonia*, including 442 names, is provided as an appendix.

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The cosmopolitan tribe Halictini (sweat bees) includes over 2300 currently recognized species belonging to 22-48 genera in classifications of different authors. Hitherto, phylogenetic reconstruction was made only for some restricted groups within Halictini: Pesenko, 1984a (*Halictus* s. str.); McGinley, 1986 (*Lasioglossum* s. str. of the New World); Danforth, 1999 (some *Lasioglossum* s. l. on the basis of molecular data); Danforth et al., 1999 (some *Halictus* and *Seladonia*, including *Vestitohalictus*, on the basis of molecular data); Danforth & Ji, 2001 (*Lasioglossum* s. l. and *Homalictus* on the basis of molecular data); Danforth et al., 2003 ("*Hemihalictus* series" of *Lasioglossum* s. l. on the basis of molecular data); Janjic & Packer, 2003 (*Agapostemon*). The scheme derived by Packer (1998) provided a phylogeny for western Palaearctic species of the *Lasioglossum leucozonium* species-group but his outgroup treatment was not designed to illuminate relationships among the other species of *Lasioglossum* s. str. included. Do-Pham et al. (1984) tried to find the relationships between some species of *Halictus*, *Seladonia*, and *Lasioglossum* on the basis of only the structure of the male genitalia. These authors also did not include any outgroup in their analysis and the results mixed some species of the subgenera *Lasioglossum*, *Dialictus*, and *Evylaeus*. On these reasons, they obtained artificial groupings and wrong general direction as well particular trends in the evolution of the structure of the male genitalia; however, they did bring to light some hitherto ignored aspects of the morphological variation in these structures.

The *Halictus* genus-group is accepted here to be synonymous with the genus *Halictus* as understood by Michener (2000). One of aims of the present paper is the phylogenetic reconstruction and subgeneric classification of *Seladonia*. The main cause for the supraspecific revision of *Seladonia* is an intermediate group including five Central Asian species (*Halictus bulbiceps* Blüthgen, *H. desertorum* Morawitz, *H. fuscicollis* Morawitz, *H. placidulus* Blüthgen, and *H. varentzowi* Morawitz); the majority of those was included in *Halictus* subg. *Vestitohalictus* by Michener (1978b), but in *Halictus* subg. *Seladonia* by Ebmer (1988a).

Phylogenetic relationships among subgenera of *Halictus* and its classification were worked out 20 years ago by me (Pesenko, 1984a). This information is revised here for the following reasons. (1) Ebmer (1984: 315) subsequently described the male of *Halictus modernus* Morawitz, the type species of the monotypic subgenus *Lampralictus*, thereby permitting more precise establishment of the position of this subgenus in the phylogenetic tree of *Halictus*. (2) The phylogenetic reconstruction of *Seladonia* is best understood in relation to that of the subgenera of *Halictus*. (3) The species composition of some subgenera of *Halictus* has changed in accordance with taxonomic publications since 1984 (see Ebmer, 1985, 1988b; Pesenko, 1985, 1986a; Carman & Packer, 1997; Pesenko & Wu, 1997a; Danforth et al., 1998) and my recent study.

All species names listed in the genus *Seladonia* are **new combinations**, except for *S. seladonia* (Fabricius, 1794) (the type species), *S. kudasi* (Ebmer, 1975 (combination by Pesenko, 1986a), *S. confusa* (Smith, 1853), *S. gavarnica* (Pérez, 1903), *S. kessleri* (Bramson, 1879), *S. leucahenea* (Ebmer, 1972), *S. semitecta* (Morawitz, 1874), *S. smaragdula* (Vachal, 1985), *S. subaurata* (Rossi, 1792), and *S. tumulorum* (Linnaeus, 1758) (combinations by Pesenko et al., 2000).

Also in the present paper, a new subtribal classification of the Halictini is suggested and substantiated on the basis of the phylogenetic analysis.

Monophyly of the tribe Halictini

The tribe Halictini is a strictly monophyletic (holophyletic) group (Pesenko, 2000). A single manifested synapomorphy shared by all members of the Halictini is the *modified metasomal tergum VII of the male*: it is provided with a transverse ridge forming a false apex beneath which the tergum is strongly reflexed to the morphological posterior margin (Michener, 1944, 1965, 1978a, 1978b, 2000). Although in some species of the genus *Homalictus*, e.g. *H. dampieri* and *H. fijiensis*, the ventral retrorse part of the tergum VII is very short (narrow), almost all of the topologically dorsal surface of the tergum is occupied by the very large pseudopygidial plate with sharp posterior and lateral margins.

Another possible synapomorphy is the *modified metasomal sternum IV of the male*: shortened, mostly hidden by sternum III, provided with a transverse row of thick bristles on its posterior part, and with strongly produced posterolateral angles. Such a modified sternum IV is possessed by only generalized members of the Halictini. In most of more derived members, this sternum secondarily and sometimes independently has become of normal form and/or has lost the thick bristles. Some members of the tribe Augochlorini, a sister group of Halictini (see Pesenko, 2000), also possess a modified male metasomal sternum IV of similar form (e.g. see Figs. 101, 243, 244, 245, 248, 249, 254, 262, 263, 264 in Eickwort, 1969). However, the possession of such a modification by the nearest common ancestor of Halictini and Augochlorini contradicts to the phylogenetic pattern within the latter tribe: both Eickwort (1969, pp. 506-509, Table 1) and En-

Table 1. Subtribal classification of the tribe Halictini suggested herein and those of other recent authors

Suggested classification	Classifications proposed by			Geographic distribution	Number of genera (species)
	Pesenko, 2000	Engel, 2000a	Michener, 2000		
Halictina	Halictina, partly	Halictina	Not distinguished	Cosmopolitan	7 (~510)
Sphecodina	Sphecodina	Sphecodina	*Sphecodes* group	Cosmopolitan	4 (~495)
Thrinchostomina	Halictina, partly	Halictina, partly	*Thrinchosioma* group	Afrotropical	2 (52)
Caenohalictina	Halictina, partly	Caenohalictina + Agapostemonina	Not distinguished	New World	10 (155)
Gastrohalictina	Gastrohalictina	Gastrohalictini	Genus *Lasioglossum*	Cosmopolitan	1 (~1100)

gel (2000a: 62, Characters 41-45) consider modifications of this sternum to be derived within Augochlorini. Thus, in their opinion, the nearest common ancestor of Augochlorini had an unmodified sternum IV in the male. For this reason, augochlorines having the highly modified male sternum IV appear among the more derived groupings within the Augochlorini in both the phenetic scheme of Eickwort (1969) and the cladogram of Engel (2000a: Fig. 78). Furthermore, the modified sternum IV appears in various places in two of the three main branches of the schemes of both the authors. Eickwort (1969, Table 1) considered only two character states for this feature: "normal" and "modified", but Engel analyzed five separate characters pertaining to this sternum. Below, the augochlorine genera having the shortened (modified) sternum IV of the male are listed with indication of their places in the cladogram derived by Engel (in brackets, states of Characters 41-45 from the matrix by Engel, 2000: Appendix 2): *Thectochlora* (0, 0, 1, 0, 0), *Megalopta* (0, 1, 2, 1, 0), *Augochloropsis* (0, 1, 3, 0, 0), and *Paraugochloropsis* (=*Pseudagochloropsis*) (0, 1, 3, 0, 0) in Clade 2, whereas *Augochlorodes* (0, 1, 0, 0, 0), *Pereirapis* (0, 0, 1, 0, 0), *Megaloptidia* (1, 1, 1, 0, 0), *Megommation* (1, 1, 0, 0, 0), and *Megaloptina* (1, 1, 0, 0, 0) in Clade 3. It is interesting that the states of Characters 41-45 are identical in both *Thectochlora* (0, 0, 1, 0, 0) and *Pereirapis* (0, 0, 1, 0, 0) in the matrix by Engel, though these genera are placed in various main clades. Possibly, Eickwort and Engel incorrectly identified and interpreted the outgroup: the modified sternum IV is rather a synapomorphy for Augochlorini and Halictini combined.

Subtribal classification of the tribe Halictini

Recently, three independent and partly different classifications of the Halictinae were proposed almost simultaneously by Pesenko (2000, January), Engel (2000a, April), and Michener (2000, June)[1]. These, along with the more finely divided classification of the Halictini suggested in this paper are given in Table 1. The main phylogenetic preposition is as follows. The subtribe Halictina is a paraphyletic group. Other four subtribes are separate lineages originated from different members (rather from their ancestors) of the genus *Patellapis* sensu lato.

The number of species and composition of the genera listed below are accepted in accordance with Michener (2000), although it is my opinion that he understands some genera, e.g. *Patellapis* and *Lasioglossum*, too widely. Only the genera *Halictus* and *Seladonia* (including *Vestitohalictus* and *Paraseladonia*) are accepted here differently. The new classification of these two genera, based on the phylogenetic analysis, is given below.

[1] When the present communication has been already sent to press, I received a copy of an important paper by Danforth et al. (2004) published in the end of April 2004 and sent to me by the first author on 20 May. This paper presents results of the phylogenetic analysis of bees of the family Halictidae based on molecular data, a new suprageneric classification of the family and a discussion of their geographical history and the time of the main divergences. In total, three nuclear genes were studied in 51 halictid species belonging to 41 genera and subgenera from 152 ones distinguished by Michener (2000). The pattern of the phylogenetic relationships between subfamilies, derived by Danforth et al., completely coincides with that based on the morphological data (Pesenko, 2000). Also the tree fragment concerning the genera *Thrincohalictus*, *Halictus*, and *Seladonia* (including *Vestitohalictus*), shown in cladograms of Danforth et al. as most related, is topologically identical to that on the scheme of the phylogeny reconstructed here (see figure). The classification of the tribe Halictini sensu lato (as understood by me after Michener, 2000), given by Danforth et al., differs from the classification suggested here in the following items: (1) all the subtribes (with the exception of Gastrohalictina) are considered at the tribal rank; (2) Gastrohalictina are united with Halictina in the tribe Hali ctini sensu stricto; (3) *Mexalictus* , a member of the subtribe Caenohalictina in my classification, is placed in Halictini; (4) *Homalictus* and *Echthralictus*, separate genera belonging to Halictina, are considered by Danforth et al. to be subgenera of *Lasioglossum* (subtribe Gastrohalictina in my classification). Comments on the position of *Mexalictus*, *Homalictus* , and *Echthralictus* are given in the corresponding sections below.

Subtribe HALICTINA Thomson, 1869

This is a paraphyletic group comprising 7 genera:

Echthralictus Perkins & Cheesman, 1928 (cleptoparasitic; Samoa; 2 species);

Glossodialictus Pauly, 1984 (Zaire; 1 species);

Halictus Latreille, 1804 (with 12 subgenera, see below; Holarctic; 90 species);

Homalictus Cockerell, 1919 (with 3 subgenera: *Homalictus* s. str., *Quasilictus* Walker, 1986, and *Papualictus* Michener, 1980; Oriental and Australian; 101 species);

Patellapis Friese, 1909 (with 7 subgenera: *Archihalictus* Pauly, 1984, *Chaetalictus* Michener, 1978, *Dictyohalictus* Michener, 1978, *Lomatalictus* Michener, 1978, *Pachyhalictus* Cockerell, 1929; *Patellapis* s. str., and *Zonalictus* Michener, 1978; Palaeotropical, except for Australia; 176 species);

Seladonia Robertson, 1918 (with 6 subgenera, see below; nearly cosmopolitan, excepting Australia; 95 species);

Thrincohalictus Blüthgen, 1955 (eastern Mediterranean; 1 species).

Subtribe SPHECODINA Schenck, 1869

This is a strictly monophyletic (holophyletic) group comprising 4 genera:

Eupetersia Blüthgen, 1928 (with 2 subgenera: *Eupetersia* s. str. and *Nesoeupetersia* Blüthgen, 1936; Afrotropical and Oriental; 29 species);

Microsphecodes Eickwort & Stage, 1972 (Neotropical; 7 species);

Ptilocleptis Michener, 1978 (Neotropical; 3 species);

Sphecodes Latreille, 1804 (nearly cosmopolitan excepting South America; about 250 species).

This subtribe corresponds to the "*Sphecodes* genus-group" or "the *Sphecodes* clade" of Michener (1978a, 2000). Formally, its monophyly is supported by 10 synapomorphies (in females, except for Character 10): (1) lower lateral part of clypeus nor or gently bent backward; (2) distal median process of labrum short and wide or absent; (3) mandibles simple, without subdistal tooth; (4) hairs on posterior outer surface of hind tibia simple, not dense, not forming a scopa; (5) hairs on inner surface of hind tibia relatively short, sparse, mostly simple; (6) basitibial plate of hind legs defined only partly or entirely absent; (7) penicillus of hind basitarsus absent; (8) prepygidial fimbria of metasomal tergum V entire, not divided by a longitudinal specialized area; (9) pygidial plate of metasomal tergum VI narrow, parallel-sided, rounded distally or a thin slightly upturned apical process; (10) dorsal gonostylus simple, hairy, thick and rounded. However, the majority of the characters above (except for Characters 1 and 10) is evidently connected with cleptoparasitism and shared with other parasitic halictines (*Parathrincostoma*, *Echthralictus*, and *Seladonia* subg. *Paraseladonia*; see Michener, 1978a, 2000), but in each case other characters demonstrate that these are convergences rather than synapomorphies with the parasites in other tribes.

Subtribe THRINCHOSTOMINA Sakagami, 1974

This strictly monophyletic subtribe comprises 2 genera:

Thrinchostoma Saussure, 1890 (with 3 subgenera: *Diagonozus* Enderlein, 1903, *Eothrincostoma* Blüthgen, 1930, and *Thrinchostoma* s. str.; Afrotropical and Oriental; 49 species);

Parathrincostoma Blüthgen, 1933 (cleptoparasitic; Madagascar; 2 species).

The monophyly of the subtribe is supported by at least 12 synapomorphies, some of which are uniquely derived (i.e. are not shared with any other members of the Halictini; see Characters 6, 7, 10 and 12): (1) clypeus strongly produced downward and protuberant forward, malar space long, proboscis long and slender (this complex character state is to some extent shared with *Thrincohalictus*, some *Caenohalictus*, and some *Pseudagapostemon* subg. *Pseudagapostemon*); (2) distal median process of labrum in male strong, not keeled (this character state is shared with most species of the *Agapostemon* group and some *Caenohalictus*); (3) first flagellomere of male longer than broad (this character state is shared with most *Halictus*, some *Seladonia*, *Paragapostemon*, *Rhinetula*, and few *Caenohalictus*); (4) transverse carina at anterior (horizontal) part of dorsal surface of pronotum complete or present only medially (this character state is shared with *Ptilocleptis*; (5) anterior extremity of mesoscutum in profile gently convex (this character state is shared with *Microsphecodes*); (6) hind tibia of female slender; (7) pterostigma small, shorter than half length of marginal cell; (8) recurrent veins (1 and 2 *m-cu*) both entering 3rd submarginal cell or 1st recurrent vein interstitial (this character state is shared with *Echthralictus*, *Glossodialictus*, *Eupetersia* subg. *Eupetersia*, and a few *Caenohalictus*); (9) metasoma slender in females, nearly petiolate in males (this character is shared with *Habralictus*, some *Mexalictus*, *Eupetersia*, and some *Caenohalictus*); (10) posterior hair bands on metasomal terga of simple inclined hairs directed laterad; (11) ventral bridge of gonobase incomplete: without ventral bridge (this character is shared with *Pa-*

tellapis subg. *Archihalictus*, most of Caenohalictina, and a few *Homalictus*); (12) ventral gonostylus partly sclerotized, directed downward (ventrad), usually narrow and hook-shaped distally. The apomorphic states of Characters 1-5, 8, 9, and 11 are shared by the Thrinchostomina and some other members of the tribe Halictini but should not be considered as synapomorphies for the larger groups that would result from them (which are in any case generally different for each character). Such character states rather appeared independently in these taxa.

Subtribe CAENOHALICTINA Michener, 1954

This is a strictly monophyletic group including the following 10 genera:

Agapostemon Guйrin-Mйneville, 1844 (with 2 subgenera: *Agapostemon* s. str. and *Notagapostemon* Janjic & Packer, 2003; Western Hemisphere; 42 species);

Agapostemonoides Roberts & Brooks, 1987 (Central and Northern South America; 1 species);

Caenohalictus Cameron, 1903 (Neotropical; 45 species);

Dinagapostemon Moure & Hurd, 1982 (Mesoamerica; 8 species);

Habralictus Moure, 1941 (with 2 subgenera: *Habralictus* s. str. and *Zikaniella* Moure, 1941; Neotropical; 22 species);

Mexalictus Eickwort, 1978 (with 2 subgenera: *Georgealictus* Packer, 1993 and *Mexalictus* s. str.; Mesoamerica; 5 species);

Paragapostemon Vachal, 1903 (Mexico; 1 species);

Pseudagapostemon Schrottky, 1909 (with 3 subgenera: *Brasilagapostemon* Moure & Sakagami, 1984, *Neagapostemon* Cure, 1989, and *Pseudagapostemon* s. str.; Neotropical; 25 species);

Rhinetula Friese, 1922 (Mesoamerica; 1 species);

Ruizantheda Moure, 1964 (with 3 subgenera: *Oragapostemon* Cure, 1989, *Ruizantheda* s. str. and *Rusanthedella* Moure, 1964; Neotropical; 4 species).

In contrast to the case in the Thrinchostomina, the monophyly of this subtribe is not well supported. The present phylogenetic analysis has revealed three possible synapomorphies for the Caenohalictina. However, two of them are not possessed by all Caenohalictina: (1) dull or bright metallic green or blue coloration of the body and (2) long hairs on the compound eyes; i.e. these are postulated synapomorphies which need *ad hoc* assumptions of reversals. The third synapomorphy is shared by Caenohalictina with *Thrincohalictus* and Thrinchostomina: ventral gonostylus partly sclerotized and directed mostly downward. Nevertheless, I consider the subtribe Caenohalictina a natural, strictly monophyletic group including almost all the New World halictines with strong venation (except for few species of the widespread genera *Halictus* and *Seladonia* of the subtribe Halictina).

Danforth et al. (2004) placed the genus *Mexalictus* in their tribe Halictini sensu stricto and united both the subtribes Halictina and Gastrohalictina of my classification. On their cladograms based on molecular data, this genus is shown a basal branch, being a sister group in relation to all other members of Halictini senso stricto. However, the morphological (and geographical) data testify rather to the position of *Mexalictus* within the subtribe Caenohalictina considered a tribe by Danforth et al. In addition to the 1st (not shared by *Mexalictus* subg. *Georgealictus*) and 3rd abovementioned synapomorphies, *Mexalictus* and most of other Caenohalictina share the following characters: (1) the paraocular areas extending into the clypeus as an acute or right angular lobe, (2) elongate first or first and second segments of the labial palps. It is likely that *Mexalictus* is close to *Habralictus*, other member of Caenohalictina. Both these genera are very similar in the following characters: (1) metasoma nearly petiolate in males and very slender in females owing to much elongate tergum I, (2) extensive yellow areas present on the head and mesosoma in most species.

Subtribe GASTROHALICTINA Schrottky, 1911

This is a strictly monophyletic group comprising a single genus, *Lasioglossum* Curtis, 1833 sensu lato (cosmopolitan; containing about 1100 currently recognized species). In my opinion, this enormously large and diverse genus should be divided into at least 17 separate genera, those accepted as subgenera by Michener (2000).

The monophyly of the subtribe is supported by two evident synapomorphies.

(1) The venation of the forewings is "weak": at least the distal transverse "cubital" veins (*2 r-m* and *2 m-cu*) are half or less as thick as the more proximal veins; the character is better demonstrated in females. This character state is shared by *Lasioglossum* sensu lato with *Homalictus* and *Echthralictus* included here in the subtribe Halictina. On the basis of a number of morphological characters shared by *Homalictus* and *Echthralictus* with *Pachyhalictus*, Michener (2000) considered this similarity in the wing venation as a result of parallel changes. I agree with this opinion, in spite of the molecular data showing *Homalictus* and *Echthralictus* to be derived from within

Lasioglossum (Danforth & Ji, 2001; Danforth et al., 2004).

(2) The dorsal gonostylus is relatively small, usually less than one third as long as the gonocoxite. This character state is shared with *Agapostemonoides* (subtribe Caenohalictina), *Homalictus* subg. *Homalictus* (subtribe Halictina), and a few *Sphecodes* (subtribe Sphecodina).

Monophyly of the *Halictus* genus-group and its relationships

The monophyly of the *Halictus* genus-group is supported by distinct, but postulated synapomorphies (for detail, see Characters 40, 41, and 46 below) related to the structure of the male genitalia: (1) upper (dorsal) gonostylus simple (not double), flattened, broad, narrowed proximally, and provided with a clump of very coarse bristles on inner surface; (2) lower (ventral) gonostylus sclerotized, relatively thin and long, directed backward. Only generalized members of the group possess the character states above.

Evidence for a sister-group relationship between the *Halictus* genus-group and genus *Thrincohalictus* is the common possession of the following derived character state, which among the tribe Halictini is found only in *Halictus*, *Seladonia*, and *Thrincohalictus*: *ventral gonobasal rim in male genitalia forming a right posterolateral angle with a short projection directed laterad*. Another feature characterizing these three genera is the *presence* (except for parasitic *Paraseladonia*) *of posterior bands of tomentum or dense and highly plumose appressed hairs on the metasomal terga*. However, this character is shared also with *Patellapis* subgenera *Patellapis* (except for few species) and *Lomatalictus*. Such a common possession of the last character indicates a possible relationship of the common ancestors of *Halictus*, *Seladonia*, and *Thrincohalictus* with both or one of these subgenera of *Patellapis*; alternatively, this could be a homoplasious change in *Patellapis*.

The subgeneric classification of the genera *Halictus* and *Seladonia* (i.e. the *Halictus* genus-group) results from the phylogenetic analysis below. Here I list all subgenera of these genera to facilitate discussion of supraspecific taxa in the text.

The genus *Halictus* includes 12 subgenera: *Acalcaripes*, *Argalictus*, *Halictus* s. str., *Hexataenites*, *Lampralictus*, *Monilapis*, *Nealictus*, *Odontalictus*, *Platyhalictus*, *Protohalictus*, *Ramalictus*, and *Tytthalictus*.

The genus *Seladonia* comprises 6 subgenera, including 2 new ones: *Mucoreohalictus* subg. n., *Pachyceble*, *Paraseladonia*, *Placidohalictus* subg. n., *Seladonia* s. str., and *Vestitohalictus*.

Material for and methods of the phylogenetic analysis

Studied taxa and main literature sources. The phylogenetic analysis was not based upon study of an exemplar of each (or some) of the genera and subgenera of the ingroup (*Halictus* genus-group) and outgroups, but rather on an examination of all available material and taking into account all published information on their morphology. Of course, the main source is the comprehensive book by Michener (2000; it is not indicated below in lists of publications for various taxa). For ascertaining the character polarities, all taxa of the Halictini except for those belonging to the ingroup (genera *Halictus* and *Seladonia*) were taken as outgroups of three levels.

The majority of genera and subgenera of the Halictini belonging to the ingroup and outgroups have been examined from all or most of species. Main published sources on the morphology of the genera of the ingroup and outgroups are as follows.

Ingroup: Blüthgen, 1933a, 1936a, 1936b, 1955, 1961; Sandhouse, 1941; Mitchell, 1960; Sakagami & Wain, 1966; Ebmer, 1969, 1975a, 1984, 1987, 1988a, 1988b; Wille & Michener, 1971; Roberts, 1973b; Warncke, 1975, 1982; Eickwort, 1978; Michener, 1978b, 1979; Pesenko, 1984a, 1984c, 1984d, 1985, 1986a; Sakagami & Ebmer, 1987; Sakagami et al., 1991; Pesenko & Wu, 1997a; Pauly, 1997; Janjic & Packer, 2001.

Outgroup 1 (sister group: genus *Thrincohalictus*): Blüthgen, 1955; Michener, 1978b.

Outgroup 2 (narrower: subtribe Halictina, except for the genera *Halictus* and *Seladonia*): Blüthgen, 1926, 1928a, 1931a; Krombein, 1951; Michener, 1965, 1978b, 1980; Pauly, 1980b, 1984a, 1986, 1989, 1999; Walker, 1986, 1993, 1996, 1997; Pesenko & Wu, 1997b.

Outgroup 3 (wider: all other subtribes of the tribe Halictini):

Thrinchostomina: Blüthgen, 1926, 1928a, 1930, 1931a, 1933b; Michener, 1978a; Sakagami et al., 1991; Pauly, 1999.

Caenohalictina: Michener, 1954, 1979; Mitchell, 1960; Moure, 1941, 1964; Roberts, 1972, 1973a; Eickwort, 1978; Moure & Hurd, 1982; Moure & Sakagami, 1984; Roberts & Brooks, 1987; Cure, 1989; Packer, 1993; Godinez-Garcia, 1997; Rojas & Toro, 2000; Rojas, 2001; Janjic & Packer, 2003.

Sphecodina (cleptoparasitic): Hagens, 1874, 1882; Meyer, 1920; Blüthgen, 1928b, 1928c, 1936b; Љustera, 1959; Mitchell, 1960; Eickwort & Stage, 1972; Baker, 1974; Michener, 1978a; Pauly, 1981b, 1986; Tsuneki, 1983; Warncke, 1992.

Gastrohalictina (halictines with weak venation): Blüthgen, 1926, 1931b, 1934, 1936b;

Michener, 1944, 1965, 1993; Mitchell, 1960; Ebmer, 1970, 1971, 1974, 1975b, 1980, 1984, 1986, 1987, 1988b, 1995, 1997, 1998, 2000, 2002; Bytinski-Salz & Ebmer, 1974; Warncke, 1975, 1982; Svensson et al., 1977; Pauly, 1980a, 1981a, 1984b, 1984c, 1986, 1999, 2001a, 2001b; Moure & Hurd, 1982; Sakagami et al., 1982, 1996, 1998; Do-Pham et al., 1984; Ebmer & Sakagami, 1985a, 1985b, 1990; McGinley, 1986, 1999, 2003; Pesenko, 1986b; Sakagami, 1989, 1991; Sakagami & Tadauchi, 1995; Walker, 1995a, 1995b; Sakagami & Ebmer, 1996; Packer, 1998; Engel, 2000b, 2001; Pesenko et al., 2000; Genaro, 2001; Hinojosa-Diaz, 2003.

Morphological terms. I accept them mostly according to Michener (1944, 1965, 2000) with some changes and comments below.

(1) In accordance with the terminology of the classic anatomy, I use the terms *apex* and *base*, *apical* and *basal* (end, part, etc.) only for description of such structures as protuberances, processes, projections, teeth, tubercles, lobes, etc. The terms *distal* and *proximal* (end, part, etc.) are used for description of articulated structures and appendages, such as antenna, leg, gonostylus, etc., and also their parts: scapus, pedicel, flagellum, flagellomere, labial and maxillary palps, tibia, femur, tarsus, tarsomere, etc. The terms *anterior* and *posterior* (also *median* and *lateral*) are used for characterization of main sclerites of the body: pronotum, mesoscutum, scutellum, metanotum, mesepisterna, propodeum, metasomal terga and sterna, etc., e.g., the posterior margin of the mesoscutum, anterior (not basal) hair bands on the terga, posterior (not apical) areas of the sterna.

(2) Bees are hypognathous insects. So for characterization of the general form of the head in frontal view and its subdivisions such as clypeus, labrum, supraclypeal area, I use the terms *height*, *high* (not *length*, *long*) and also *upper* and *lower* (margin, part, etc.).

(3) In accordance with the current tradition, surfaces and margins of the femora, tibiae and tarsomeres are described in their orientation when legs are directed downward; the antennae considered as directed forward. Natural borders do not mark all margins of some, traditionally distinguished parts of the body surface. For description of these parts, except the frons and vertex, the term *area* is used, e.g., paraocular areas, supraclypeal area, genal areas, posterior areas of the terga, etc. For description of the main, central portion of a sclerite the term *disc* is used, e.g., the punctation on the mesoscutal disc, pubescence on the disc of the tergum II, etc.

Formulation of characters and their states. Below, State 0 means a plesiomorphic state, States 1, 2, etc., apomorphic states. Of them, States coded as 1 and 2 or 1, 2, and 3, are always treated as unordered. States, coded by two or three ciphers divided by points are ordered as follows: $0 \rightarrow 1 \rightarrow 1.1$, or $0 \rightarrow 1 \rightarrow 1.1 \rightarrow 1.1.1$.

I have attempted to formulate characters and their states so they can be interpreted evolutionarily, as well as possible, within the framework of evolutionary systematics (see Pesenko, 1989, 1992) and as well within the framework of classical (Hennigian) cladistics. Patterns of distribution of many character states among halictine taxa show evident homoplasies. Of the two kinds of homoplasy, parallel change and reversal, I prefer to use the latter explanation for those cases when the pattern of a character concerning a morphological novelty may be explained either by independent multiple appearance of the novelty or by secondary loss or losses of the novelty. I consider that the presumption of reversals for such characters is much more probable than the alternative of parallel derivation. For this reason, I bring an additional apomorphic state into many characters. This state means a secondary reversal to an ancestral state and is coded as 1.1, i.e. the transformation series is taken to be $0 \rightarrow 1 \rightarrow 1.1$. If a character, one of states of which is a novelty, varies within a genus or subgenus, I have ascribed usually such an apomorphic state to this taxon as a whole and imply secondary loss of the corresponding novelty by some its members, i.e. in cases where clearly derived members of a genus or subgenus possess a plesiomorphic state for a character, I take this to be a secondary reversal. Thus, I introduce some *postulated synapomorphies* of taxa and their groups. Such synapomorphies should be considered as scientific hypotheses proposed for adequate explanation of patterns of some characters within the ingroup. The postulation of a synapomorphy is accompanied by the suggestion of corresponding *ad hoc* assumptions on reversals in some members of that group for which the synapomorphy was postulated.

I give no comments for those characters for which both the outgroup criterion and the pattern within the ingroup unambiguously indicate their polarity. I indicate in brackets those taxa for which the possession of a derived state in some species is not considered to be synapomorphy with those taxa outside of the brackets. In other words, the bracketed taxa are not considered to be a part of the monophyletic groups to which the unbracketed taxa belong – however, as these bracketed taxa are not monospecific, this would represent another synapomorphic origin of the derived state for the character. Those taxa, for which the common possession of a derived state is hypothesised here as a synapomorphy, are united by the mark "+". In total, 46 characters giving 61 apomorphic states of different levels were considered in the study (Table 2).

Table 2. Matrix <taxa x characters>

Taxon	1	2	3	4	5	6	7	8	8.1	9	10	11	12	12.1	13	14	15	16	17	18	19	20	21	22	23	24	25
Genus ***Halictus***																											
Protohalictus	0	0	0	1	0	0	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lampralictus	0	0	0	0	0	0	0	0	0	1	0	1	(1)	0	0	1	0	2	0	0	0	0	1	0	0	0	0
Halictus s. str.	1	0	0	0	0	0	0	0	0	0	0	2	(1)	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Nealictus	0	0	0	-	0	0	0	0	0	0	1	0	(1)	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ramalictus	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
Platyhalictus	0	0	0	-	0	0	0	1	0	0	0	1	(1)	1	0	0	0	3	0	0	0	0	0	0	0	0	0
Monilapis	0	0	0	-	0	0	0	1	1	0	0	1	(1)	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Acalcaripes	0	0	0	-	0	0	0	1	1	0	0	1	(1)	1	0	0	0	0	0	1	0	2	1	0	0	0	0
Tytthalictus	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
Argalictus	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
Hexataenites	0	0	0	-	0	0	0	0	0	0	0	0	(1)	0	2	0	0	0	1	0	1	1	0	0	0	0	0
Odontalictus	0	0	0	-	0	0	0	0	0	1	1	0	(1)	0	0	0	0	1	1	0	0	0	0	0	0	0	1
Genus ***Seladonia***																											
Seladonia s. str.	0	1	0	-	0	0	0	0	0	0	1	0	(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachyceble	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
Paraseladonia	0	1	0	-	1	0	1	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Placidohalictus	0	1	1	-	0	0	0	0	0	0	0	0	(1)	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Vestitohalictus	0	1	1	-	0	0	0	0	0	0	0	0	(1)	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Mucoreohalictus	0	1	1	-	0	0	0	0	0	0	0	0	(1)	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Genus ***Thrincohalictus***	0	0	0	-	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0
Narrower outgroup	0	0[1	0	-	0[1	0	0[1	0	0	0	0[1	0[1	0	-	0	0[1	0	0/1	0[1	0	0	0	0[1	0[1	0[1	0	0
Wider outgroup	0[1	0[1	0[1	-	0[1	0[1	0[1	0	0	0	0[1	0[1	0[1	-	0	0[1	0	0/1	0[1	0	0	0	0[1	0[1	0[1	0[1	0[1

Table 2. (Continued)

Taxon	26	27	28	29	29.1	30	31	32	32.1	33	34	35	36	37	38	39	40	40.1	41	41.1	42	43	44	45	46	46.1
Genus ***Halictus***																										
Protohalictus	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	0
Lampralictus	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	0
Halictus s. str.	0	1	0	1	0	0	1	0	0	0	0	1	1	0	1	1	1	0	1	0	1	0	0	0	1	0
Nealictus	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	0
Ramalictus	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	(1)	2	(1)	1	1	1	0	0	(1)	1
Platyhalictus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	(1)	1	(1)	1	(1)	0	0	0	(1)	1
Monilapis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	(1)	1	(1)	1	(1)	0	1	0	(1)	1
Acalcaripes	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	(1)	1	(1)	1	(1)	0	1	0	(1)	1
Tytthalictus	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	(1)	1	(1)	1	(1)	0	0	0	(1)	1
Argalictus	0	0	0	1	2	0	0	1	0	0	0	0	0	0	1	1	(1)	1	(1)	1	(1)	0	0	0	(1)	1
Hexataenites	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	(1)	1	(1)	1	(1)	0	0	0	(1)	1
Odontalictus	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	(1)	1	(1)	1	(1)	0	0	0	(1)	1
Genus ***Seladonia***																										
Seladonia s. str.	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0
Pachyceble	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	1	1	0
Paraseladonia	1	0	0	(1)	3	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0
Placidohalictus	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0
Vestitohalictus	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0
Mucoreohalictus	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0
Genus ***Thrincohalictus***	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	1	0	0	0	[1]	0	0	0	0	0	0
Narrower outgroup	0[1	0[1	0[1	0[1	[0	0[1	0[1	0[1	-	0	0	0	0	0[1	0	0	0	0	0	[1]	0[1	0[1	0	0	0	0
Wider outgroup	0[1	0[1	0[1	0[1	[0	0[1	0[1	0[1	-	0	0	0	0	0[1	0[1	0	0[1	0[1	0	[1]	0[1	0[1	0	0	0	0[1

In parentheses, postulated state (for Characters 12, 29, 40, 41, 42, and 46).
"0[1" indicates that both character states occur in the outgroup, but State 1 is possessed by few derived members and considered to be appeared independently from that in the ingroup.

Characters involved in the phylogenetic analysis

1. Body size. (0) Relatively small, 5-8 mm, or moderate, 8-12 mm. (1) Very large, over 16 mm: *Halictus* subg. *Halictus*, [*Halictus* (*Hexataenites*) *squamosus* and *H.* (*H.*) *sexcinctus* ssp. *albohispidus*]; wider outgroup: some Oriental species of *Lasioglossum* subg. *Evylaeus* (*L. dybowskii*, *L. melli*, and *L. oncocephalum*). The character widely varies in the ingroup and as well in both the narrower and wider outgroups; therefore I accepted it as only consisting of two states.

2. Main (ground) coloration of body. (0) Black, not metallic. (1) Dully metallic green or blue: *Seladonia* (except for *S.* (*Pachyceble*) *kusdasi*, *S.* (*Vestitohalictus*) *nasica*, and *S.* (*Mucoreohalictus*) *nigricutis*); narrower outgroup: *Homalictus* and *Glossodialictus*; wider outgroup: most of Caenohalictina, *Eupetersia lasurea*, and many Gastrohalictina.

3. Pubescence of body. (0) Moderately long, not unusually dense, plumose, and mostly erect. (1) Unusually short and dense or tomentose on most surfaces of the body (sometimes except for mesoscutum): *Seladonia* subgenera *Placidohalictus* + *Mucoreohalictus* + *Vestitohalictus*, [*Halictus* (*Halictus*) *duplocinctus*, *H.* (*Argalictus*) *senilis*, and *H.* (*Hexataenites*) *squamosus*]; wider outgroup: *Ptilocleptis*, few *Habralictus*, few *Agapostemon*; few *Pseudagapostemon*; few *Dinagapostemon*, and some Gastrohalictina.

4. Head of female in frontal view. (0) As high as wide or higher than wide. (1) Shorter than wide: *Halictus* subg. *Protohalictus*. The character widely varies in the ingroup and as well in both the narrower and wider outgroups. It is introduced only for fixation of the difference of *Halictus* subg. *Protohalictus* from other members of the clade uniting the subgenera *Halictus*, *Lampralictus*, and *Protohalictus*.

5. Clypeus: relative length. (0) As wide as high or somewhat wider than high. (1) Clypeus very short, about 3 times as wide as high: *Seladonia* subg. *Paraseladonia*; narrower outgroup: *Echthralictus*; wider outgroup: many Sphecodina.

6. Lower margin of clypeus in female. (0) Straight. (1) With median tubercle: *Halictus* subg. *Ramalictus*, [*Seladonia* (*Seladonia*) *kessleri* and *S.* (*Vestitohalictus*) *nasica*]; wider outgroup: few *Sphecodes*.

7. Distal median process of labrum in female. (0) Strong, keeled. (1) Short and wide or absent: *Seladonia* subg. *Paraseladonia*; narrower outgroup: *Echthralictus*, few *Homalictus* subg. *Homalictus*; wider outgroup: Sphecodina.

8. Genal area of male. (0) Usual, convex. (1) At least, flattened: *Halictus* subgenera *Platyhalictus* + *Acalcaripes* + *Monilapis* (including the subgenera possessing State 1.1). (1.1) Concave and carinate laterally: *Halictus* subgenera *Acalcaripes* + *Monilapis*. State 1.1 is a unique apomorphy among the Halictidae. The State 1 "genal area flattened" (in males of the subgenus *Platyhalictus*) appears to be a demonstratively intermediate one.

9. Tooth at lower part of genal area of female. (0) Absent. (1) Present: *Halictus* subgenera *Lampralictus* and *Odontalictus* (independently).

10. Antenna of male. (0) Moderately long. (1) Short, almost as short as that in female, at most reaching the scutellum: *Halictus* subgenera *Nealictus* and *Odontalictus* (independently), [*Halictus* (*Hexataenites*) *nadigi*, *H.* (*Platyhalictus*) *graecus*, *H.* (*P.*) *jaramielicus*, *H.* (*P.*) *alfkenellus*, *H.* (*P.*) *rudolphae*], *Seladonia* subg. *Seladonia* (except for *S. semitecta*); narrower outgroup: *Patellapis* subg. *Pachyhalictus* and few *Homalictus* subg. *Homalictus*; wider outgroup: *Mexalictus*, *Rhinetula*; some Sphecodina, and some Gastrohalictina. I believe that the long antenna in *S. semitecta* is a secondary change. In opposite case, this species coincides with the nearest common ancestor hypothesized under the given set of characters. The last preposition, however, contradicts to many other characters (structure of the propodeum, sculpture of the body surface, and details of the male genitalia), which are not included in the present study, but unambiguously show *S. semitecta* as a typical representative of the subgenus *Seladonia*.

11. Antennal flagellum of male. (0) Linear, flagellomeres slightly convex in lower side, with inconspicuous pubescence. (1) Moniliform (with segments convex in lower side), with dense and short pubescence, separated by a glabrous area into proximal and distal bands: *Halictus* subgenera *Lampralictus*, *Acalcaripes* + *Monilapis* (except for *H. aegypticola*, *H. pseudotetrazonius*, *H. pentheri*, *H. nicosiae*, and *H. gruenwaldti*) + *Platyhalictus* (except for *H. albozonatus*, *H. ebmeri*, *H. determinandus*, *H. graecus*, *H. jaramielicus*, *H. alfkenellus*, *H. rudilohae*, *H. holomelaenus*, and *H. minor*), [*Halictus* (*Protohalictus*) *fimbriatus*]; narrower outgroup: *Patellapis* subgenera *Patellapis* and few *Zonalictus*; wider outgroup: *Eupetersia*, most of *Sphecodes*, few *Caenohalictus*, most of *Ruizantheda* (with two glabrous areas on each flagellomere), and *Lasioglossum immunitus*. (2) Flattened, with very long eyelash-like fringe on lower side: *Halictus* subg. *Halictus*. [A fringe of short hairs is present in *Halictus* (*Protohalictus*) *hedini*]. The above exceptions for *Monilapis* and *Platyhalictus* should be considered neither plesiomorphic states, nor merely reversals, because the flagellum in the species listed (1) is covered with much

denser pubescence than that in most of the taxa possessing State 11.0, and (2) is very short (in *H.* (*Platyhalictus*) *graecus*, *H. (P.) jaramielicus*, *H.* (*P.*) *alfkenellus*, and *H.* (*P.*) *rudolphae*; see State 10.1) or moderately shortened (reaching only the propodeum) in other species listed in comparison with that in most of the taxa possessing State 11.0.

12. First flagellomere of male. (0) As broad as long or broader than long. (1) Longer than broad: postulated synapomorphy for the *Halictus* genus-group; wider outgroup: Thrinchostomina, *Paragapostemon* + *Rhinetula*, and few *Caenohalictus*. (1.1) Broader than long (reversal): *Halictus* subgenera *Acalcaripes* + *Monilapis* + *Platyhalictus*. State 12.1.1 should be considered as a reversal within this group, in spite of the common possession of this state by the three subgenera of *Halictus* above with many members of the outgroups. These subgenera of *Halictus* are derived members of the genus as indicated by many other characters. Such an elongation of the first flagellomere of the male in the subgenera above, possibly, has correlated with appearance of the moniliform flagellum.

13. Last flagellomere of male. (0) Normal. (1) Flattened and slightly curved, hockey-stick shaped: *Halictus* subg. *Halictus*. (2) Hook-shaped: *Halictus* subg. *Hexataenites* (except for *H. nadigi* and *H. cochlearitarsis*). The above exception for *H. nadigi* and *H. cochlearitarsis* should be not considered as an indication to the plesiomorphous status of these species. In *H. nadigi*, the male antenna is provided not only with the straight ultimate flagellomere, but it is also very short (see Character 10). *H. cochlearitarsis* possesses a number of unique apomorphies, first of all, in the structure of legs.

14. Sides and posterior surface of mesosoma. (0) Punctate or rugulose. (1) Nearly smooth, polished: *Halictus* subg. *Lampralictus*; narrower outgroup: few *Homalictus*; wider outgroup: *Echthralictis*, few Sphecodina, and few Gastrohalictina.

15. Metapostnotum: relative length. (0) As long as or slightly shorter than scutellum. (1) Very short, shorter than metanotum: *Seladonia* subgenera *Placidohalictus* + *Mucoreohalictus* + *Vestitohalictus*.

16. Metapostnotum: sculpture. (0) Rugose or rugulose. (1) Densely and finely granulate: *Halictus* subgenera *Nealictus* and *Odontalictus* (independently). (2) Mostly smooth, shiny: *Halictus* subg. *Lampralictus*. (3) Obscurely rugulose, silk-shiny: *Halictus* subg. *Platyhalictus*. The sculpture of the dorsal surface of the propodeum widely varies in the outgroups. The polarity of this character is considered to be adequate for assessment of polarity within character in the ingroup.

17. Carina bordering the posterior surface of propodeum in female. (0) Absent. (1) Present and complete laterally and partly across dorsal margin in females: *Halictus* subgenera *Hexataenites* + *Odontalictus*; narrower outgroup: *Pachyhalictus* subg. *Pachyhalictus* and *Homalictus* subg. *Homalictus*; wider outgroup: some *Pseudagapostemon*, *Agapostemon*, many Sphecodina, and some Gastrohalictina.

18. Tarsus of fore legs of male. (0) Normal, slender. (1). Flattened and broadened: *Halictus* subg. *Acalcaripes*; narrower outgroup: *Homalictus latitarsis*.

19. Tarsus of middle legs of male. (0) Normal, poorly pubescent. (1) Modified: flattened and provided with a longitudinal fringe of long dense hairs: *Halictus* subg. *Hexataenites* (in part).

20. Mesotibial spur of male. (0) Normal. (1). Short and thick: *Halictus* subg. *Hexataenites* (in part). (2) Completely lost: *Halictus* subg. *Acalcaripes*.

21. Hind tibia of female. (0) Black. (1) Red or reddish yellow: *Halictus* subgenera *Protohalictus* (except for *H. bagirensis*, *H. funerarius*, *H. hedini*, *H. icarus*, and some individuals of *H. rubicundus*) + *Lampralictus*, *Acalcaripes*, [*Halictus* (*Halictus*) *fulvipes* and *H.* (*Tytthalictus*) *palustris*]; outgroups: few species in various genera. This character is very plastic, so I reasonably consider that the above exceptions are reversals.

22. Pubescence on posterior outer surface of hind tibia in female. (0) Forming a scopa (for carrying pollen) of long dense plumose inclined hairs. (1) Sparse, not forming a scopa: *Seladonia* subg. *Paraseladonia*; narrower outgroup: *Echthralictus*; wider outgroup: *Parathrincostoma* and Sphecodina.

23. Basitibial plate of hind legs in female. (0) Well developed, of moderate size. (1) Defined only partly or absent: *Seladonia* subgenera *Placidohalictus* + *Mucoreohalictus* + *Vestitohalictus*, and *Paraseladonia*, [*Seladonia* (*Pacyceble*) *lanei*]; narrower outgroup: *Patellapis* subg. *Chaetalictus*, *Echthralictus*; wider outgroup: *Parathrincostoma*, Sphecodina, Caenohalictina (except for most of *Caenohalictus*), and some small species of *Lasioglossum* subg. *Evylaeus*. I believe that the basistibial plate in the cleptoparasitic *Paraseladonia* reduced independently. However, State 23.1 is shown to be a synapomorphy for the four subgenera above in the phylogram basing on the formal parsimony consideration.

24. Hind basitarsus of male. (0) Usual, straight. (1) Curved: *Halictus* subg. *Halictus*, [*Halictus* (*Protohalictus*) *atripes* and *H.* (*Tytthalictus*) *constrictus*]; outgroups: few species in various genera.

25. Inner metatibial spur of female. (0) Serrate, with several teeth. (1) With a single distinct

basal tooth: *Halictus* subg. *Odontalictus*; wider outgroup: few *Lasioglossum* (e.g. *L. laticeps*).

26. Penicillus of hind basitarsus in female. (0) Present. (1) Absent: *Seladonia* subg. *Paraseladonia*; narrower outgroup: *Echthralictus*; wider outgroup: Sphecodina.

27. Shape of metasoma in male. (0) Elongate, cylindrical. (1) Widened in posterior part: *Halictus* subgenera *Halictus* + *Lampralictus* + *Protohalictus*; outgroups: few species in various genera

28. Main (ground) coloration of metasoma. (0) Dark (black or metallic green or blue (I also consider those mostly crepuscular species, in which the entire body is of pale coloration, e.g. *Eupetersia*, *Ptilocleptis*, and *Parathrincostoma*, to possess this state, which could be rephrased as dark, or if mesosoma pale, concolorous with mesosoma). (1) Red, at least on terga I-III: *Halictus* subg. *Ramalictus*, [*Halictus* (*Halictus*) *rufipes*, some species of *Seladonia*]; narrower outgroup: few *Patellapis* subg. *Chaetalictus*; wider outgroup: most of *Sphecodes*, few *Thrinchostoma*, few *Ruizantheda*, and some Gastrohalictina. It is a polymorphic character within many species of Halictini and other Aculeata, often depending on the temperature during the prepupa development. On this reason, only those taxa are listed above, in which the red coloration of the metasoma is always present. It should be mentioned also that in all five species of *Seladonia* subg. *Placidohalictus*, some species of the subgenera *Vestitohalictus* (*S. nasica*, females of *S. cupida*, *S. pulverea*, *S. pici* and *S. pseudovestita gobiensis*, males of *S. radoszkowskyi*), and *Mucoreohalictus* (females of *S. kuschkensis*), the metasoma is reddish fuscous to nearly fuscous.

29. Posterior hair bands on metasomal terga. (0) Absent. (1) Present, usually entire, at least, on terga II-IV: *Halictus* + *Seladonia* + *Thrincohalictus*; narrower outgroup: *Patellapis* subgenera *Patellapis* (except for few species) and *Lomatalictus*; wider outgroup: *Pseudagapostemon*. (1.1) Widely interrupted medially: *Halictus* subg. *Tytthalictus*. (1.2) Consisting of coarser hairs: *Halictus* subg. *Argalictus*. (1.3) Much reduced (conspicuous tracks of these bands remaining in female): *Seladonia* subg. *Paraseladonia*. Discussion of this synapomorphy for the *Halictus* genus-group and genus *Thrincohalictus* combined is given in the Section "Monophyly of the *Halictus* genus-group and its relationships".

30. Prepygidial fimbria of metasomal tergum V of female. (0) Divided by a longitudinal median, minutely pilose area. (1) Entire, not divided by a longitudinal specialised area: *Seladonia* subg. *Paraseladonia*; narrow outgroup: *Echthralictus*; wider outgroup: *Parathrincostoma* and Sphecodina.

31. Pubescence of metasomal terga VI and VII of male. (0) Relatively short and sparse. (1) Long and dense: *Halictus* subgenera *Halictus* + *Lampralictus* + *Protohalictus*; outgroups: few species in all subtribes.

32. Metasomal sternum IV of male. (0) Short, widely emarginated. (1) Unmodified: of normal length: *Halictus* subgenera *Nealictus*, *Hexataenites* + *Odontalictus* + *Tytthalictus* (except for *H.* (*Tytthalictus*) *constrictus*) + *Argalictus*, and *Seladonia*; narrower outgroup: *Glossodialictus* and some *Patellapis*; wider outgroup: *Thrinchostoma orchidarum*, *Parathrincostoma*, Sphecodina, many Caenohalictina, and most of Gastrohalictina. (1.1) Of normal length, trapezoidal, narrowed and roundly emarginated in posterior part: *Halictus* subg. *Hexataenites* (except for *H. nadigi*), [some species of *Halictus* subg. *Platyhalictus*: *H. albozonatus*, *H. graecus*, *H. jaramielicus*, and *H. rudolphae*]. The shape of the male metasomal sternum IV widely varies within the subgenera *Platyhalictus* and *Hexataenites*, but most of their representatives possess States 32.0 and 32.1.1 as formulated above, respectively. In addition, differences between the states of this character distinguished by me are indistinct and quantitative (not qualitative), therefore intermediate forms are present. On these reasons, I consider the above exceptions in *Platyhalictus* and *Hexataenites* (also *H. constrictus*) as rather independent apomorphies (formally, reversals) than plesiomorphic states of different levels.

33. Median pencil (narrow flat tassel) consisting of long, dense and not separated hairs directed backward at posterior part of metasomal sternum IV in male. (0) Absent. (1) Present: *Seladonia* subg. *Vestitohalictus*.

34. Median brush of short and very dense hairs directed downward at posterior part of metasomal sterna IV and (or) V in male. (0) Absent. (1) Present: *Seladonia* subg. *Mucoreohalictus*, [*Seladonia* (*Pachyceble*) *lanei*].

35. Metasomal sternum V of male. (0) Straight or broadly and weakly emarginated, relatively inconspicuously pubescent. (1) Strongly emarginated, with a fur-like pubescence: *Halictus* subgenera *Halictus* and *Ramalictus* (independently).

36. Metasomal sternum VI in male. (0) Flattened. (1) With strong median round depression on anterior portion of disc: *Halictus* subg. *Halictus*, *Seladonia* subg. *Pachyceble*.

37. Metasomal sternum VII in male. (0) With a median posterior projection. (1) Without median posterior projection: *Halictus* subg. *Odontalictus*; narrower outgroup: *Patellapis* subg. *Pachyhalictus* and few *Homalictus* subg. *Homalictus*.

38. Median prominence on posterior margin of metasomal sternum VIII in male. (0) Present.

(1) Absent: *Halictus* subgenera *Halictus* + *Lampralictus* + *Nealictus* + *Protohalictus*, *Halictus* subg. *Argalictus* (independently).

39. Ventral gonobasal rim in the male genitalia. (0) Rounded. (1) Forming a right posterolateral angle with short projection directed laterad: *Halictus* + *Seladonia* + *Thrincohalictus*.

40. Upper gonostylus (dorsal gonostylus): general form. (0) Thickened, bifid and composed, not narrowed at base. (1) Simple (not bifid), flattened, broad, narrowed at base: *Halictus* (including subgenera possessing States 1.1 and 1.2) + *Seladonia*. [Simple, but thick and rounded upper gonostylus is possessed by *Homalictus*, *Glossodialictus*, *Thrincohalictus*, Sphecodina, *Parathrincostoma*, *Agapostemonoides*, Gastrohalictina]. (1.1) Elongate, strongly narrowed in proximal half, directed posteromesad: *Halictus* subgenera *Hexataenites* + *Odontalictus* + *Tytthalictus* + *Argalictus* + *Platyhalictus* + *Monilapis* + *Acalcaripes*. (1.2) Narrow, directed backward: *Halictus* subg. *Ramalictus*. The State 1 (in males of *Seladonia* and the clade of *Halictus* subg. *Protohalictus*) appears to be a demonstratively intermediate one.

41. Clump of very coarse bristles on inner surface of upper gonostylus. (0) Absent. (1) Present: *Halictus* (including subgenera possessing State 1.1) + *Seladonia*. (1.1) Secondary loss: *Halictus* subgenera *Ramalictus* + *Hexataenites* + *Odontalictus* + *Tytthalictus* + *Argalictus* + *Platyhalictus* + *Monilapis* + *Acalcaripes*.

42. Hair distal appendage of upper gonostylus. (0) Absent. (1) Present: *Halictus* (including subgenera possessing States 1.1). (1.1) Secondary loss: *Halictus* subgenera *Hexataenites* + *Odontalictus* + *Tytthalictus* + *Argalictus* + *Platyhalictus* + *Monilapis* + *Acalcaripes*. Similar, but rather non-homologous appendages are present in some members of the narrower outgroup.

43. Second distal process of upper gonostylus: slender, projecting downward. (0) Absent. (1) Present: *Halictus* subg. *Ramalictus*. This distal process is considered non-homologous to the median lobe of the upper gonostylus of *Seladonia* (see State 45.1 below), because the latter appearing as the result of a deep cleft in the gonostylus. The distal position of the lobe is not typical of *Seladonia*; it occurs only in some derived species. State 43.1 is the presence of a slender finger-like distal process in *Ramalictus*.

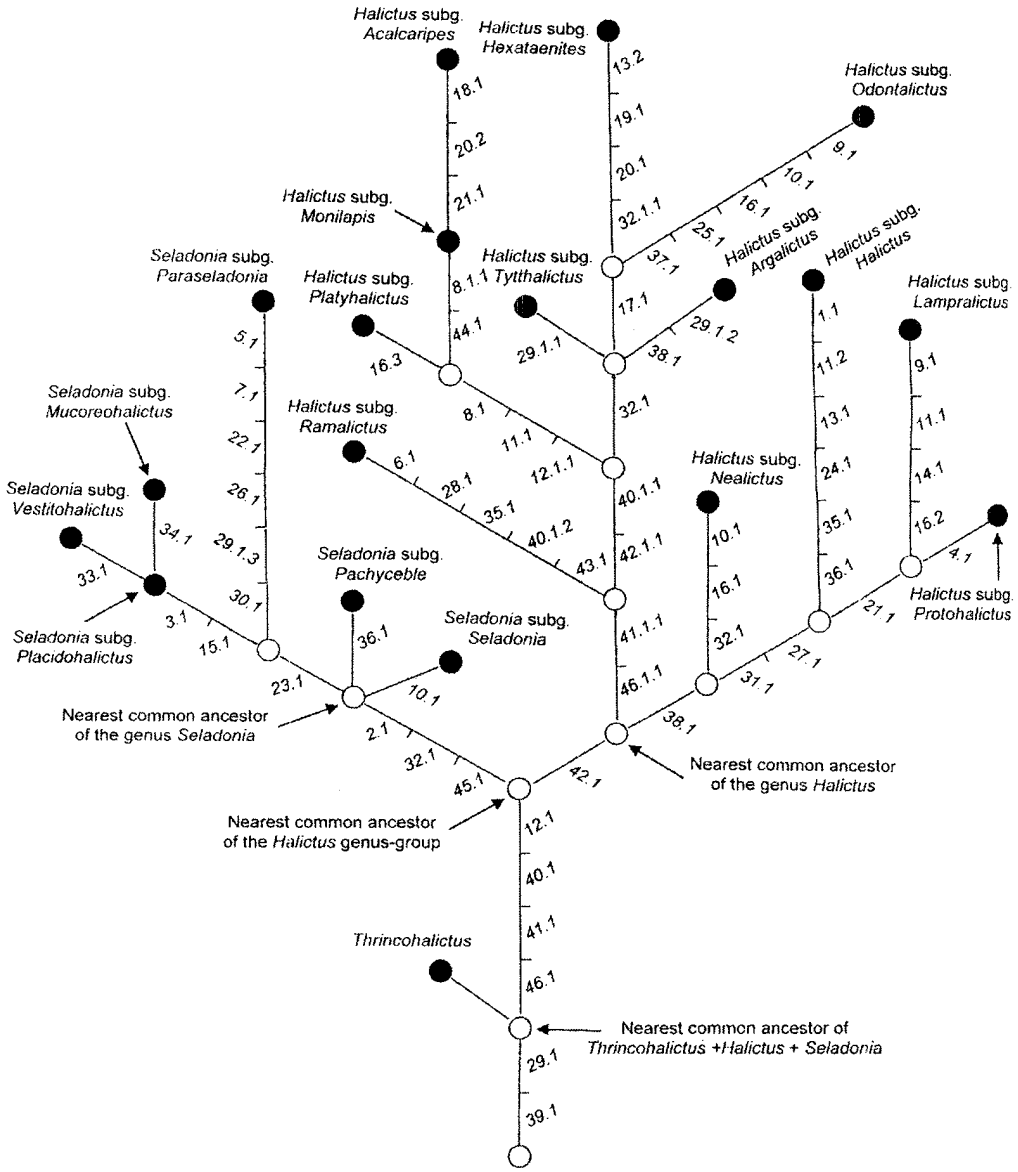
44. Pencil of long hairs directed mesad arising from middle of dorsal surface in the upper gonostylus. (0) Absent. (1) Present: *Halictus* subgenera *Acalcaripes* + *Monilapis* (secondary lost in *H. simplex*).

45. Deep cleft into upper gonostylus forming a narrow inner (median) lobe. (0) Absent. (1) Present: *Seladonia*. This lobe is sometimes (in *Seladonia leucahenea*, *S. nivalis*, *S. harmonia*, *S. hespera*, *S. lanei*, *S. lutescens*, *S. tripartita*, and *S. virgatella*) much longer than the main body of the upper gonostylus. In some members of three subgenera of *Seladonia*, the median lobe was lost; e.g. in *S. radoszkowskii* (subg. *Vestitohalictus*), *S. indefinita*, *S. nigricutis*, and *S. solitudinis* (subg. *Mucoreohalictus*), *S. gemmea* (subg. *Seladonia*). These independent losses of the median lobe of the upper gonostylus in some species of *Seladonia* should be considered evident apomorphies, but not indicators to plesiomorphous status of these species, because, in the whole, the dorsal gonostyli in them are typical of the above subgenera of *Seladonia*.

46. Lower gonostylus (ventral gonostylus, ventral lobe of gonocoxite). (0) Membranous retrorse lobe. (1) Sclerotized, relatively thin, usually long, directed backward: the postulated synapomorphy for *Halictus* + *Seladonia* (including the taxa possessing State 1.1). (1.1) Lost or much reduced: *Halictus* subgenera *Ramalictus* + *Platyhalictus* + *Monilapis* + *Acalcaripes* + *Tytthalictus* + *Argalictus* + *Hexataenites* + *Odontalictus*, [much reduced also in *Halictus* (*Protohalictus*) *rubicundus* and *H.* (*P.*) *hedini*; lost in some species of *Seladonia*, e.g. in the New World species of the subgenus *Pachyceble*: *S. harmonia*, *S. lanei*, *S. lutescens*, *S. hespera* (in some individuals, it is present, but much reduced), *S. tripartita*, *S. virgatella*; most of species of the Palaearctic subgenus *Vestitohalictus*: *S. concinna*, *S. cupida*, *S. microcardia*, *S. persephone*, *S. pici*, *S. pseudovestita*, *S. pulverea*, *S. semitica*, *S. tecta*, and *S. vestita*]; wider outgroup: some Gastrohalictina.

Discussion of the phylogenetic reconstruction

Genus Halictus. The genus *Halictus* is ascertained here as a holophyletic group (see Figure), but despite its apparent monophyly it is supported by only a single postulated synapomorphy (State 42.1). The phylogenetic tree shown in Figure is almost identical to that in the paper by Pesenko (1984a). The only difference is the establishment of an exact position for the subgenus *Lampralictus*. All the subgenera of the genus are holophyletic with the exception of *Monilapis*, which is paraphyletic in relation to *Acalcaripes*. The following four main clades can be distinguished within the genus. Clade 1 is plesiomorphous (for this genus) in relation to the structure of the male genitalia; it includes the subgenera *Halictus* s. str., *Lampralictus*, *Nealictus*, and *Protohalictus*. Clade 2 is formed by the monotypic subgenus *Ramalictus* differing from other members of the genus in five characters including the especial structure of the male genitalia (States 40.1.2 and 43.1). Clade 3 unites the



Phylogram of the *Halictus* genus-group

subgenera *Argalictus*, *Hexataenites*, *Odontalictus*, and *Tytthalictus*, in which only the dorsal gonostylus is present, which is simple (not double) and without appendages (State 40.1.1 and 42.1.1), the metasomal sternum IV of males is not (32.1) or narrowly emarginated (32.1.1). Clade 4 includes the subgenera *Acalcaripes*, *Monilapis*, and *Platyhalictus* characterised by the following morphological peculiarities of males: the genal area flattened (State 8.1) or concave and carinate laterally (8.1.1), flagellum usually moniliform and middle flagellomeres provided with proximal and distal bands of very short dense hairs (11.1), gonostylus simple.

Genus Seladonia. The strict monophyly (holophyly) of the genus *Seladonia* is supported by three synapomorphies, including a novelty expressed by State 45.1 (a deep cleft in the upper gonostylus of the male). In the phylogenetic tree of the genus *Seladonia* based on the present set

of characters, relationships among three of the six subgenera are unresolved. Only relationships among *Mucoreohalictus*, *Placidohalictus*, and *Vestitohalictus* are clear. The common possession of State 23.1 (partly reduced metabasitibial plate in females) by the three subgenera above combined, the subgenus *Paraseladonia* and *Seladonia* (*Pachyceble*) *lanei*, is rather a result of parallel changes, though State 23.1 is shown as a synapomorphy for the four subgenera (*Mucoreohalictus*, *Placidohalictus*, *Vestitohalictus*, and *Paraseladonia*) in the phylogram on the basis of the formal parsimony consideration. All the subgenera of the genus are holophyletic with the exception of *Placidohalictus*. The latter subgenus appears as a paraphyletic group in relation to *Vestitohalictus* and *Mucoreohalictus*. I believe the subgenus *Placidohalictus* (or, at least, a part of it, see below) to be a monophyletic group, but with the current level of analysis have not been able to find any good synapomorphies that prove this. Moreover, this is possibly mixed set of species. Here I have based on the hypothesis on primary absence of specific pubescence on the metasomal terga IV and/or V in the male. However, at least some members of *Placidohalictus* could secondarily loss such a pubescence.

Whole phylogram of the Halictus genus-group. The resulting tree is the most parsimonious phylogram, at least in the evolutionary sense, i.e. with taking into account the significance of a character, which is estimated as the low possibility of its parallel changes. In all, it contains 73 evolutionary steps (for 61 apomorphic states). There are 10 homoplasies: 9.1 (twice), 10.1 (three times), 11.1 (twice), 16.1 (twice), 21.1 (twice), 32.1 (twice), 35.1 (twice), 36.1 (twice), and 38.1 (twice).

The phylogenetic relationships inside and outside of the *Halictus* genus-group derived by me mostly coincide with those published by Danforth et al. (1999) on the basis of molecular data:

(1) The *Halictus* genus-group (genus *Halictus* with three subgenera, *Halictus*, *Seladonia*, and *Vestitohalictus* in the papers by Danforth et al.) appears as a sister group of *Thrincohalictus*.

(2) Both *Halictus* and *Seladonia* are strictly monophyletic.

(3) "*Halictus* subg. *Seladonia* " in understanding of Danforth et al. (after Michener, 1978b; i.e. *Seladonia* subgenera *Paraseladonia*, *Pachyceble*, and *Seladonia* combined in my classification) is a paraphyletic group in relation to "*Halictus* subg. *Vestitohalictus*" in understanding of Danforth et al. (*Seladonia* subgenera *Placidohalictus*, *Vestitohalictus*, and *Mucoreohalictus* combined in my classification).

(4) Main groupings within the genus *Halictus* (Clade 1 and Clades 3 + 4 combined) are strictly monophyletic (*Halictus latisignatus* Cameron, the type species of the monotypic subgenus *Ramalictus*, Clade 2 above was not considered by Danforth et al., 1999).

The main difference between the schemes compared is in the position of *Halictus* subg. *Odontalictus*, which corresponds to the clade uniting *H. ligatus* and *H. poeyi* in the analysis by Danforth et al. (1999). In the tree derived by me, this subgenus is a sister group of the subgenus *Hexataenites*; such a relationship is supported by at least one strong synapomorphy: common possession of the carina bordering the posterior surface of the propodeum along its lateral and partially across its dorsal margins in females (State 17.1). Whereas, in different schemes derived by Danforth et al. (1999), the corresponding clade is either a sister group of the subgenus *Tytthalictus* (*H. maculatus* and *H. pseudomaculatus*; Fig. 1b in their paper) or a sister group of the subgenera *Tytthalictus*, *Monilapis*, and *Hexataenites* combined (see Figs. 3a, 3b, and 4).

Some comments upon the classification. The classification of the *Halictus* genus-group below corresponds well with the phylogenetic pattern. However, I provide here additional argumentation and comments.

(1) On the taxonomic status and volume of *Seladonia*. Michener (2000: 350) disagreed with Pesenko (1984a) on the generic rank of *Halictus*, *Seladonia*, and *Vestitohalictus*, because he found only a single difference between *Halictus* and *Seladonia*: in the coloration of the body, black and dully metallic green, respectively (see Character 2 in the list above). In fact, these genera differ in additional and stronger characters related to the structure on the male metasomal sternum IV (see Character 32) and the male genitalia (see Character 45). I prefer to recognize as separate genera only *Halictus* and *Seladonia* (including *Vestitohalictus* s. l.), so as to avoid the unnecessary appearance of a paraphyletic group (*Seladonia* without *Vestitohalictus*).

(2) On the synonymy of *Halictus* subgenera *Lampralictus* and *Argalictus* by Michener (2000: 252). The first subgenus really belongs to Clade 1 uniting also the subgenera *Halictus* s. str., *Nealictus* and *Protohalictus*, but not to Clade 3 including the subgenus *Argalictus*. This relationship became clear only after the description of the male of *Halictus modernus* Morawitz, the type and only species of this subgenus, by Ebmer (1984: 315) who has also found an additional important diagnostic character of this taxon (see State 11.1 in the list above.

A key to the genera *Halictus* and *Seladonia*

1. *Both sexes*: body black. *Male*: posterior margin of metasomal sternum IV often widely emarginated;

dorsal gonostylus variable, but always entire, without cleft . . . . . **Halictus**

– *Both sexes*: at least, head and mesosoma dully metallic greenish or bluish (except for black *S. kusdasi*, *S. magna*, and some individuals of *S. mondaensis*). *Male*: posterior margin of sternum IV always straight; dorsal gonostylus bifid, divided by a deep longitudinal cleft forming a narrow inner (median) lobe, that sometimes much longer than main body of dorsal gonostylus (in *S. radoszkowskii*, *S. indefinita*, *S. nigricutis*, *S. solitudinis*, and *S. gemmea*, this lobe lost) . . . . . **Seladonia**

Classification of the genus *Halictus*

Subgenus **Protohalictus** Pesenko, 1985

Halictus subg. *Prohalictus* Pesenko, 1984a: 341 (key), 346, junior homonym of *Prohalictus* Armbruster, 1938. Type species: *Apis rubicunda* Christ, 1791, by original designation.

Halictus subg. *Protohalictus* Pesenko, 1986a: 631, replacement name for *Prohalictus* Pesenko, 1984. Type species: *Apis rubicunda* Christ, 1791, autobasic.

Distribution. Palaearctic region; one species, *H. rubicundus*, is Holarctic in occurrence.

Included species (13). *H. atripes* Morawitz, 1893, *H. bagirensis* Blüthgen, 1936, *H. bucharicus* Blüthgen, 1936, *H. fimbriatus* Smith, 1853, *H. funerarius* Morawitz, 1876, *H. georgicus* Blüthgen, 1936, *H. hedini* Blüthgen, 1934, *H. icarus* Ebmer, 1978, *H. rubicundus* (Christ, 1791), *H. stachii* Blüthgen, 1923, *H. takuiricus* Blüthgen, 1936, *H. turanicus* Morawitz, 1893, and *H. turkmenorum* Pesenko, 1984.

Subgenus **Lampralictus** Pesenko, 1984

Halictus subg. *Lampralictus* Pesenko, 1984a: 345 (key), 348. Type species: *Halictus modernus* Morawitz, 1876, by original designation.

Distribution. Central Asia.

Included species (1). *Halictus modernus* Morawitz, 1876.

Subgenus **Halictus** Latreille, 1804

Halictus Latreille, 1804: 182. Type species: *Apis quadricincta* Fabricius, 1776, by subsequent designation (Richards, 1935: 170).

Distribution. Palaearctic region.

Included species (4). *H. brunnescens* (Eversmann, 1852), *H. duplocinctus* Vachal, 1902, *H. quadricinctus* (Fabricius, 1776), and *H. rufipes* (Fabricius, 1793).

Subgenus **Nealictus** Pesenko, 1984

Halictus subg. *Nealictus* Pesenko, 1984a: 341 (key), 346. Type species *Halictus parallelus* Say, 1837, by original designation.

Distribution: Nearctic region.

Included species (2): *H. farinosus* Smith, 1853, and *H. parallelus* Say, 1837.

Subgenus **Ramalictus** Pesenko, 1984

Halictus subg. *Ramalictus* Pesenko, 1984a: 343, 345 (keys), 347. Type species: *Halictus latisignatus* Cameron, 1908, by original designation.

Distribution. India, Pakistan.

Included species (2). *H. latisignatus* Cameron, 1908; ?*H. acrocephalus* Blüthgen, 1926 (see discussion in Ebmer, 1988a: 358-359).

Subgenus **Platyhalictus** Pesenko, 1984

Halictus subg. *Platyhalictus* Pesenko, 1984a: 344, 345 (keys), 347. Type species: *Halictus minor* Morawitz, 1876, by original designation.

Distribution. Southern Palaearctic region.

Included species (14). *H. albozonatus* Dours, 1872, *H. alfkenellus* Strand, 1909, *H. asperatus* Bingham, 1898, *H. constantinensis* Strand, 1910, *H. determinandus* Dalla Torre, 1896, *H. ebmeri* Pesenko, 1984, *H. fumatipennis* Blüthgen, 1923, *H. graecus* Blüthgen, 1933, *H. holomelaenus* Blüthgen, 1936, *H. lussinicus* Blüthgen, 1936, *H. mediterranellus* Strand, 1909, *H. minor* Morawitz, 1876, *H. rudolphae* Pesenko, 1984, and *H. tridivisus* Blüthgen, 1923.

Subgenus **Monilapis** Cockerell, 1931

Halictus subg. *Monilapis* Cockerell, 1931: 529. Type species: "*Hylaeus tomentosus* Eversmann, 1852" = *Apis flavipes* Panzer, 1798 (junior homonym of *Apis flavipes* Fuesslin, 1775, and *Apis flavipes* Fabricius, 1787) = *Andrena compressa* Walckenaer, 1802 (nom. n. for *A. flavipes* Panzer, 1798) = *Hylaeus tomentosus* Herrich-Schäffer, 1840 (nom. n. for *A. flavipes* Panzer, 1798), by original designation. Hence, the valid name of the type species is *Andrena compressa* Walckenaer, 1802; this name is a senior, not pre-occupied objective synonym in the series of names above. After designation of the neotype of *A. flavipes* Panzer, 1798 by Pesenko (1985: 94), additional synonymy appeared as follows: *H. senex* Förster, 1860; *Halictus eurygnathus* Blüthgen, 1931; *H. eurygnathopsis* Blüthgen, 1936; *H. veneticus* Ebmer, 1969.

Comments on the type species (after Pesenko, 1985: 78-80). Cockerell (1931: 529) designated "*Hylaeus tomentosus* Eversmann, 1852" as the type species of his new subgenus *Monilapis*. However, such a species does not exist. In fact, Eversmann (1852: 37) only used the name *Hylaeus tomentosus* proposed by Herrich-Schäffer (1840a: 141) for replacement of the pre-occupied name *Apis flavipes* Panzer, 1798. It follows unambiguously from the brief description and colour figure given by Panzer

(1798, H. 56, Taf. 17) that the female described by him as a new species *Apis flavipes* belongs to the subgenus *Monilapis*. This conclusion conforms to the opinion by Peets (1912: 50; see also: Ebmer, 1974: 123; 1988b: 693) on the species as a member of the "*Halictus tetrazonius*-group" and contradicts to the synonymy of *A. flavipes* Panzer with *Halictus rubicundus* (Christ, 1791), which was traditionally accepted after Kirby (1802: 53) by many authors (e.g. Dalla Torre, 1896: 80; Warncke, 1973a: 24). The name *Apis flavipes* Panzer was pre-occupied by *A. flavipes* Fuesslin, 1775 and *A. flavipes* Fabricius, 1787. For replacement of *Apis flavipes* Panzer, Walckenaer (1802: 105) proposed the new name *Andrena compressa* with a direct indication of the replaced name and with a shortened reference to the paper by Panzer; three pages below he recorded the senior homonym of Panzer's name (Walckenaer, 1802: 108). Although Walckenaer, judging from his brief diagnosis of *A. flavipes* Panzer, treated this species differently from Panzer (rather as *H. rubicundus*), the new replacement name by Walckenaer should be accepted as an appropriate objective synonym of *A. flavipes* Panzer (Code, Arts. 23.3.5, 60.3, 61.3). However, the name *Andrena compressa* Walckenaer was taken no notice by entomologists and was missed in all catalogues. Only 170 years later the name was mentioned by Warncke (1973b: 281) in the synonymy of *H. rubicundus* (the synonymy is wrong, see above). Herrich-Schäffer, who probably oevrlooked the paper by Walckenaer, proposed for replacement of *Apis flavipes* Panzer another new name, *Hylaeus tomentosus*, in two his monographs published in the same year: "*Nomenclator entomologicus ...*" (Herrich-Schäffer, 1840a: 141) and "*Fauna Ratisbonensis ...*" (Herrich-Schäffer, 1840b: 279). The new name was proposed with a direct indication of the replaced name, a shortened reference to the paper by Panzer (its complete bibliographic reference was given in the introduction to "*Nomenclator entomologicus ...*", p. viii) and also citation of the senior homonym (Herrich-Schäffer, 1840a: 140). I do not know exact dates of publication of these works, and, according to current tradition (e.g. Dalla Torre, 1896: 86), accept "*Nomenclator entomologicus ...*" as that paper in which the name *H. tomentosus* was established. After establishing, the name *H. tomentosus* Herrich-Schäffer was used for the first time by Eversmann (1852: 37). Eversmann gave brief descriptions of female and male (for the first time) and noticed that males of this species, inhabiting foothills of the Ural Mts., are almost indistinguishable from those of *H. rubicundus*. All later authors (Smith, 1854: 23; Morawitz, 1866: 22; Blüthgen, 1923: 77, 125, 130; 1924: 487; 1931c: 209; Cockerell, 1931: 529; Michener, 1978b: 534) erroneously ascribed the authorship of the name *H. tomentosus* to Eversmann, while "*Hylaeus tomentosus* Herrich-Schäffer" was considered to be a nomen nudum, probably on the reason of absence of a description (Herrich-Schäffer's indication that it is a replacement name was not taken into account). After Morawitz (1866: 22), subsequent authors (e.g. Dalla Torre, 1896: 86; Blüthgen, 1923: 77, 125, 130) treated the name as follows: *Halictus tomentosus* (Eversmann, 1852) = *Melitta quadricincta* sensu Kirby, 1802: 51 = *Halictus qadricinctus* Morawitz, 1866: 22; etc., nec Fabricius, 1776 = *H.* aff. *tetrazonius* (Klug, 1817), i.e. as a species of the *H. tetrazonius*-group with broadened mandibles of male. Later, Blüthgen (1931c: 209) examined a male ("cotypus") and female ("holotypus") of "*H. tomentosus* Eversmann" sent to him by V. Popov in 1929. I examined all material of this species in Eversmann's collection (4 males and 7 females; see: Pesenko, 1985: 80). It includes males of *H. rubicundus* and females belonging to two species of *Monilapis* and one species of *Platyhalictus*. However, this bears no direct relation to the problem of the type species. There is no reason to consider that Cockerell understood this species differently from a species of the *H. tetrazonius*-group, when he established *Monilapis*, a new subgenus of the genus *Halictus*, with "*Hylaeus tomentosus* Eversmann" as type species. Hence, *Andrena compressa* Walckenaer, 1802, should be accepted as the valid name of the type species (see its synonymy above). However, the nomenclatural status of the name *Monilapis* was vague until its type species remained a nomen dubium.

Comments on the neotype designation for the type species. The type of *A. flavipes* Panzer was lost long ago (Peets, 1912: 50; see also: Warncke, 1973a; Ebmer, 1974; Pesenko, 1984b). From the brief description and figure by Panzer (see above), it can be only concluded that the species belongs to the subgenus *Monilapis* ("*H. tetrazonius*-group"), which includes over two dozens of species. Therefore, for validation of the name *Monilapis*, it was necessary to designate the neotype of *A. flavipes* Panzer. In the type locality of *A. flavipes* (Nürnberg), three species of *Monilapis* occur, all agreeing with the description and figure by Panzer: *H. simplex* Blüthgen, 1923, *H. eurygnathus* Blüthgen, 1931, and *H. langobardicus* Blüthgen, 1944. When Cockerell (1931: 529) designated "*Hylaeus tomentosus* Eversmann, 1852"(= *H. quadricinctus* auct. nec Fabricius) as the type species of his new subgenus *Monilapis*, he rather meant one of species with broadened mandibles of male. Such species, of the three listed above, are *H. langobardicus* and *H. eurygnathus*. The latter species is much more common than *H. langobardicus*. Therefore, I designated (Pesenko, 1985: 94) as the neotype of *Apis flavipes* Panzer, 1798 a male of *H. eurygnathus* (from Regensburg, near the type locality) kindly sent to me by Mr. Ebmer. The designation was made for purpose of stabilization of the generic (first of all) and specific names. It meets all requirements of the Code (Art. 75). Ebmer (1988b) has rejected the designation. He wrote: "Demgegenüber muβ ich feststellen, daβ die Festlegung eines Neotypus fьr Nomen dubium [i.e. *A. flavipes* Panzer] nach ICZN Art. 75 (b) ungültig ist, weil sich dieser Name nicht im allgemeinen Gebrauch befinden" (p. 693). His criticism is incorrect, as the validity of *A. flavipes* Panzer, as the name of the type species of a genus-group taxon, does not depend on the frequency of using this specific name. Further, Ebmer wrote that it is not clear which species, at least of the two ones, *H. langobardicus* or *H. eurygnathus*, was meant by Cockerell when he designated the type species of his *Monilapis*. This consideration is correct (see above), but just elimination of such an uncertainty is the purpose of the neotype designation. In an analogous case, Ebmer (1988a) also designated the neotype of *Apis subaurata* Rossi "zur Stabilisierung". He wrote: "Weil nach Beschreibung und dem Locus typicus diese Art. [*A. subaurata*] auch als *H. seladonius*, unter Umständen auch als *H. gemmeus* oder *H. smaragdulus* gedeutet werden kann, lege ich zur Stabilisierung der bisherigen Deutung in Übereinstimmung mit Art. 75 des ICZN einen Neotypus [von *A. subaurata*] fest…" (p. 342).

Distribution. Palaearctic region.

Included species (29). *H. adjikenticus* Blüthgen, 1923, *H. aegypticola* Strand, 1909, *H. beytueschebapensis* Warncke, 1984, *H. carinthiacus* Blüthgen, 1936, *H. centaurea* Ebmer, 1985, *H. compressus* (Walckenaer, 1802) (= *H. eurygnathus* Blüthgen, 1931), *H. consobrinus* Pérez, 1895, *H. crenicornis* Blüthgen, 1923, *H. gordi-*

us Warncke, 1975, *H. grossellus* Ebmer, 1978, *H. gruenwaldti* Ebmer, 1975, *H. hermon* Ebmer, 1975, *H. langobardicus* Blüthgen, 1944, *H. lobatus* Ebmer, 1978, *H. nicosiae* Blüthgen, 1923, *H. pentheri* Blüthgen, 1923, *H. ponticus* Blüthgen, 1934, *H. pseudotetrazonius* Strand, 1921, *H. pyrenaeus* Pérez, 1903, *H. quadricinctoides* Blüthgen, 1936, *H. quadripartitus* Blüthgen, 1923, *H. rossicus* Ebmer, 1978, *H. sajoi* Blüthgen, 1923, *H. simplex* Blüthgen, 1923, *H. tetrazonianellus* Strand, 1909, *H. tetrazonius* (Klug, 1817), *H. tsingtauensis* Strand, 1910, *H. wjernicus* Blüthgen, 1936, and *H. xanthoprymnus* Warncke, 1984.

H. quadripartitus Blüthgen, 1923, *H. rossicus* Ebmer, 1978, *H. sajoi* Blüthgen, 1923, *H. simplex* Blüthgen, 1923, *H. tetrazonianellus* Strand, 1909, *H. tetrazonius* (Klug, 1817), *H. tsingtauensis* Strand, 1910, *H. wjernicus* Blüthgen, 1936, and *H. xanthoprymnus* Warncke, 1984.

Subgenus **Acalcaripes** Pesenko, 1984

Halictus subg. *Acalcaripes* Pesenko, 1984a: 344, 346 (keys), 347. Type species: *Halictus patellatus* Morawitz, 1874, by original designation.

Distribution. Mediterranean basin in wider understanding.

Included species (2). *H. falcinellus* Warncke, 1982, and *H. patellatus* Morawitz, 1874.

Subgenus **Tytthalictus** Pesenko, 1984

Halictus subg. *Tytthalictus* Pesenko, 1984a: 344, 345 (keys), 348. Type species: *Halictus maculatus* Smith, 1848, by original designation.

Distribution. Palaearctic region.

Included species (4). *H. asperulus* Pérez, 1895, *H. constrictus* Smith, 1853, *H. maculatus* Smith, 1848, and *H. palustris* Morawitz, 1876 (= *H. pseudomaculatus* Blüthgen, 1925; *H. marikovskayae* Pesenko, 1986, **syn. n**.; *H. frostus* Fan, 1990).

Subgenus **Argalictus** Pesenko, 1984

Halictus subg. *Argalictus* Pesenko, 1984a: 344, 345 (keys), 348. Type species: *Hylaeus senilis* Eversmann, 1852, by original designation.

Distribution. Southern Palaearctic region.

Included species (8). *H. dschulfensis* Blüthgen, 1936, *H. fatsensis* Blüthgen, 1936, *H. humkalensis* Blüthgen, 1936, *H. luganicus* Blüthgen, 1936, *H. senilis* (Eversmann, 1852), *H. submodernus* Blüthgen, 1936[2], *H. subsenilis* Blüthgen, 1955, and *H. tibialis* (Walker, 1871).

Subgenus **Hexataenites** Pesenko, 1984

Halictus subg. *Hexataenites* Pesenko, 1984a: 344, 345 (keys), 348. Type species: *Apis sexcincta* Fabricius, 1775, by original designation.

Distribution. Palaearctic region.

Included species (11). *H. berlandi* Blüthgen, 1936, *H. cochleariatarsis* (Dours, 1872), *H. cyrenaicus* Blüthgen, 1930, *H. frontalis* Smith, 1853, *H. fulvipes* (Klug, 1817), *H. intumescens* Pérez, 1895, *H. nadigi* Blüthgen, 1934, *H. resurgens* Nurse, 1903, *H. scabiosae* (Rossi, 1790), *H. sexcinctus* (Fabricius, 1775), and *H. squamosus* Lebedev, 1910.

Subgenus **Odontalictus** Robertson, 1918

Odontalictus Robertson, 1918: 91. Type species: *Halictus ligatus* Say, 1837, by original designation.

Distribution. North and Central America.

Included species (2). *H. ligatus* Say, 1837, and *H. poeyi* Lepeletier, 1841.

A key to subgenera of the genus *Halictus*

1. *Both sexes*: metasoma red at least on terga I-III. *Male*: metasomal sternum V strongly emarginated, provided with a fur-like pubescence; upper gonostylus bearing a finger-like distal process and thin rectangular plate. *Female*: clypeus with median tubercle on lower margin . . . . . **Ramalictus**
– *Both sexes*: metasoma black, except for *H.* (*Halictus*) *rufipes* and some individuals of *H.* (*Argalictus*) *senilis*. *Male*: sternum V straight or broadly and weakly emarginated, relatively inconspicuously pubescent, except for subg. *Halictus*; upper gonostylus of other form. *Female*: clypeus straight along lower margin 2
2. *Male*: metasomal sternum VIII without median prominence on posterior margin; upper gonostylus broad, with clump of very coarse bristles on inner surface; lower gonostylus a slender process (much reduced in *H.* (*Protohalictus*) *rubicundus* and *H.* (*P.*) *hedini*) 3
– *Male*: sternum VIII with median prominence on posterior margin, except for subg. *Argalictus*; upper gonostylus elongate, strongly narrowed in proximal half, without clump of very coarse bristles on inner surface; lower gonostylus absent 6
3. *Both sexes*: very large, body length over 16 mm. *Male*: antennal flagellum flattened, with very long eyelash-like fringe on lower side; last flagellomere flattened and slightly curved, hockey-stick shaped; hind basitarsus curved; metasomal sternum V strongly emar-

[2] The male of "*H. modernus*" described by Ebmer (1984: 314) belongs to a species of the subgenus *Protohalictus* (Pesenko, in preparation).

ginated, with a fur-like pubescence; metasomal sternum VI with strong median round depression on anterior portion of disc. *Female*: mesoscutum sparsely punctate . . . . . **Halictus** s. str.

– *Both sexes*: smaller, length less than 14 mm. *Male*: flagellum not flattened, without eyelash-like fringe, except for *H.* (*Protohalictus*) *hedini*, the flagellum of which is provided with a fringe of short hairs; last flagellomere of normal form; hind basitarsus straight, except for *H.* (*Protohalictus*) *atripes*; sternum V straight or broadly and weakly emarginated, relatively inconspicuously pubescent; sternum VI flattened. *Female*: mesoscutum densely punctate 4

4. *Both sexes*: metapostnotum densely and finely granulate. *Male*: antenna short, almost as short as that in female, at most reaching the scutellum; metasoma elongate, cylindrical; metasomal sternum IV of normal length, nearly straight along posterior margin; pubescence of metasomal terga VI and VII relatively short and sparse. *Female*: hind tibia black . . . . . **Nealictus**

– *Both sexes*: metapostnotum rugose or rugulose. *Male*: antenna moderately long; metasoma widened in posterior part; metasomal sternum IV short, widely emarginated; pubescence of metasomal terga VI and VII long and dense. *Female*: hind tibia red or reddish yellow, except for some members of subg. *Protohalictus* (*H. bagirensis*, *H. funerarius*, *H. hedini*, *H. icarus*, and some individuals of *H. rubicundus*) 5

5. *Both sexes*: sides and posterior surface of mesosoma nearly smooth, polished. *Male*: antennal flagellum with dense and short pubescence, separated by glabrous area into proximal and distal bands. *Female*: head in frontal view as high as wide; genal area with large tooth at lower part . . . . . **Lampralictus**

– *Both sexes*: sides and posterior surface of mesosoma densely granulate or rugulose, mat. *Male*: flagellum with inconspicuous pubescence. *Female*: head in frontal view shorter than wide; genal area without tooth . . . . . **Protohalictus**

6. *Male*: genal area flattened or concave and carinate laterally; antennal flagellum usually moniliform (with segments convex on lower side); flagellomeres with dense and short pubescence, often separated by a glabrous area into proximal and distal bands; first flagellomere broader than long; metasomal sternum IV shortened, widely emarginated 7

– *Male*: genal area usual, convex; flagellum linear; flagellomeres slightly convex on lower side, with inconspicuous pubescence; first flagellomere as broad as long or broader than long; metasomal sternum IV of normal length and straight along posterior margin, except for *H.* (*Tytthalictus*) *constrictus*, in subg. *Hexataenites* trapezoidal, narrowed and roundly emarginated in posterior part 9

7. *Both sexes*: metapostnotum obscurely rugulose, silkshiny. *Male*: genal area flattened; upper gonostylus without pencil of long hairs . . . . . **Platyhalictus**

– *Both sexes*: metapostnotum with distinct wrinkles, shiny. *Male*: genal area concave and carinate laterally; upper gonostylus with pencil of long hairs directed mesad arising from middle of dorsal surface, except for *H. simplex* 8

8. *Male*: tarsus of fore leg flattened and broadened; mesotibial spur completely reduced. *Female*: hind tibia reddish . . . . . **Acalcaripes**

– *Male*: tarsus of fore leg normal, slender; mesotibial spur normal. *Female*: hind tibia black . . . **Monilapis**

9. *Both sexes*: metapostnotum densely and finely granulate. *Male*: antenna short, almost as short as that in female, at most reaching the scutellum; sternum VII without median posterior projection. *Female*: genal area with tooth at lower part; inner metatibial spur with a single distinct basal tooth . . . . . **Odontalictus**

– *Both sexes*: metapostnotum rugose or rugulose. *Male*: antenna moderately long, except for *H.* (*Hexataenites*) *nadigi*; metasomal sternum VII with median posterior projection. *Female*: genal area without tooth; inner metatibial spur serrate, with several teeth 10

10. *Male*: last flagellomere hook-shaped, except for *H. nadigi* and *H. cochlearitarsis*; metasomal sternum IV trapezoidal, narrowed in posterior part, emarginate on posterior margin. *Female*: propodeum with carina bordering its posterior surface . . . . **Hexataenites**

– *Male*: last flagellomere of normal form; sternum IV not narrowed in posterior part, straight along posterior margin, except for *H.* (*Tytthalictus*) *constrictus*. *Female*: propodeum ecarinate 11

11. *Both sexes*: propodeum and metasomal terga distinctly punctate, with shiny interspaces; posterior hair bands on terga consisting of finer hairs, widely interrupted medially. *Male*: metasomal sternum VIII with median prominence on posterior margin . . . . . **Tytthalictus**

– *Both sexes*: propodeum and terga obscurely punctate; posterior hair bands on metasomal terga consisting of coarser hairs, not interrupted medially. *Male*: sternum VIII without median prominence on posterior margin . . . . . **Argalictus**

Classification of the genus *Seladonia*

Subgenus **Seladonia** Robertson, 1918

Seladonia Robertson, 1918: 91. Type species: *Apis seladonia* Fabricius, 1794, by original designation.

The subgenus corresponds to the *Halictus* (*Seladonia*) *seladonius*, *H.* (*S.*) *smaragdulus*, and *H.* (*S.*) *gemmeus* species-groups of Ebmer (1988a) combined.

Distribution. Old World, absent in Australia.

Included Palaearctic and Oriental species (23). *S. aeneobrunnea* (Pérez, 1895), *S. aeraria* (Smith, 1873), *S. caelestis* (Ebmer, 1976), *S. cephalica* (Morawitz, 1874), *S. gemmea* (Dours, 1872), *S. kessleri* (Bramson, 1879), *S. laticephala* (Warncke, 1984), *S. lucidipennis* (Smith, 1853), *S. magna* (Ebmer, 1980), *S. mongolica* (Morawitz, 1880), *S. mugodjarica* (Blüthgen, 1933), *S. paropamisos* (Ebmer, 1978), *S. pjalmensis* (Strand, 1909), *S. propingua* (Smith, 1853), *S. secunda* (Dalla Torre, 1896), *S. seladonia* (Fabricius, 1794), *S. semitecta* (Morawitz, 1874), *S. smaragdula* (Vachal, 1895), *S. subaurata* (Rossi, 1792), *S. subauratoides* (Blüthgen, 1926), *S. verticalis* (Blüthgen, 1931), *S. vicina* (Vachal, 1894), and *S. wollmanni* (Blüthgen, 1933).

Included Afrotropical species (13; their subgenric position from information by A. Pauly). *S. atroviridis* (Cameron, 1906), *S. centrosa* (Vachal, 1910), *S. diducta* (Cockerell, 1932), *S. experta* (Cockerell, 1916), *S. foana* (Vachal,

1899), *S. hotoni* (Vachal. 1903), ?*S. iridicolor* (Cameron, 1905), *S. jucunda* (Smith, 1853), *S. niveocinctula* (Cockerell, 1940); *S. opulenta* (Benoist, 1950); *S. orientalis* (Lepeletier, 1841*); S. pruinescens* (Cockerell, 1937), and *S. vansoni* (Cockerell, 1935).

Subgenus **Pachyceble** Moure, 1940

Pachyceble Moure, 1940: 54. Type species: *Pachyceble lanei* Moure, 1940, by original designation.

The subgenus corresponds to the *Halictus* (*Seladonia*) *tumulorum* and *H.* (*S.*) *leucaheneus* species-groups of Ebmer (1988a) combined.

Distribution. Nearly cosmopolitan, absent in Australia.

Included species from the Old World (15). *S. clandula* (Warncke, 1984), *S. confusa* (Smith, 1853) (Holarctic species), *S. dissidens* (Pérez, 1903), *S. dorni* (Ebmer, 1982), *S. gavarnica* (Pérez, 1903), *S. kusdasi* (Ebmer, 1975), *S. leucahenea* (Ebmer, 1972), *S. mondaensis* (Blüthgen, 1923), *S. nivalis* (Ebmer, 1985), *S. petraea* (Blüthgen, 1933), *S. subpetraea* (Blüthgen, 1933), *S. tibetana* (Blüthgen, 1926), *S. transbaikalensis* (Blüthgen, 1933), *S. tumulorum* (Linnaeus, 1758), and *S. yunnanica* (Pesenko & Wu, 1997).

Included species from the New World (7). *S. harmonia* (Sandhouse, 1941), *S. hespera* (Smith, 1862), *S. lanei* (Moure, 1940), *S. lutescens* (Friese, 1921), *S. pinguismenta* (Janjic & Packer, 2001), *S. tripartita* (Cockerell, 1895), and *S. virgatella* (Cockerell, 1901).

This taxon comprises diverse forms and can be easily subdivided into the following species groups: *S. tumulorum* group (including most of Old World species), *S. leucahenea* group (including also *S. nivalis*; differing from other groups in the structure of the upper gonostylus in males and the structure of the head in females), *S. lanei* group (including also *S. hespera* and *S. lutescens*), and *S. tripartita* group (including also *S. harmonia* and *S. pinguismenta*, differing in the structure of the upper gonostylus in males and the sculpture of metapostnotum in both sexes). Both the two last groups are also characterized by the absence of the lower gonostylus in male.

Subgenus **Paraseladonia** Pauly, 1997

Paraseladonia Pauly, 1997: 92. Type species: *Halictus chalybeatus* Friese, 1909, by original designation.

Distribution. Afrotropical region.

Included species (1). *S. chalybeata* (Friese, 1909).

Subgenus **Placidohalictus** subg. n.

Type species: *Halictus placidus* Blüthgen, 1923.

Diagnosis. See the key.

The subgenus partly corresponds to the *Halictus* (*Seladonia*) *varentzowi* species-group of Ebmer (1988a). It includes also *S. desertorum*, which was not included by the last author in any group of *Seladonia*, *S. bulbiceps* and *S. fuscicollis*, which were considered by Michener (1978b) as members of the *Halictus* subg. *Vestitohalictus*.

Distribution. Central Asia.

Included species (5). *S. bulbiceps* (Blüthgen, 1929), *S. desertorum* (Morawitz, 1876), *S. fuscicollis* (Morawitz, 1876), *S. placidula* (Blüthgen, 1923), and *S. varentzowi* (Morawitz, 1894).

Subgenus **Vestitohalictus** Blüthgen, 1961

Halictus subg. *Vestitohalictus* Blüthgen, 1961: 287. Type species: *Halictus tectus* Radoszkowski, 1876, **fixed here** (under Article 70.3 of the Code), misidentified as *Halictus vestitus* Lepeletier, 1841 in the original designation by Blüthgen (1961). See comment below.

Comment on the type species. Blüthgen (1961: 287) established a new subgenus *Vestitohalictus* of the genus *Halictus*, and designated *Halictus vestitus* Lepeletier, 1841, as the type species. Ebmer designated the lectotypes of *H. vestitus* (Ebmer, 1976: 398) and *H. tectus* Radoszkowski, 1876 (Ebmer, 1988b: 573) and has shown that Blüthgen, when he designated the type species of *Vestitohalictus,* actually had *H. tectus*, a closely related species belonging to the same subgenus.

The subgenus corresponds to the *Halictus* (*Vestitohalictus*) *vestitus* species-group of Blüthgen (1955, 1961) and Ebmer (1975a).

Distribution. Southern Palaearctic region.

Included species (16). *S. concinna* (Brullé, 1840), *S. cupida* (Vachal, 1902), *S. ferreota* (Fan, 1991), *S. inpilosa* (Ebmer, 1975), *S. microcardia* (Pérez, 1895), *S. mordacella* (Blüthgen, 1929), *S. mordax* (Blüthgen, 1923), *S. nasica* (Morawitz, 1876), *S. persephone* (Ebmer, 1976), *S. pici* (Pérez, 1895), *S. pseudovestita* (Blüthgen, 1925), *S. pulverea* (Morawitz, 1874), *S. radoszkowskii* (Vachal, 1902), *S. semitica* (Blüthgen, 1955), *S. tecta* (Radoszkowski, 1876), and *S. vestita* (Lepeletier, 1841).

Subgenus **Mucoreohalictus** subg. n.

Type species: *Hylaeus mucoreus* Eversmann, 1852.

Diagnosis. See the key.

The subgenus corresponds to the *Halictus* (*Ves-*

titohalictus) *mucoreus* and *H.* (*V.*) *radoszkowskii* species-groups of Blüthgen (1955, 1961) and Ebmer (1975a) combined.

Distribution. Southern Palaearctic region.

Included species (15). *S. aestuans* (Ebmer, 1978), *S. balearica* (Pérez, 1903), *S. cyprica* (Blüthgen, 1937), *S. indefinita* (Blüthgen, 1923), *S. kuschkensis* (Ebmer, 1975), *S. morawitzi* (Vachal, 1902), *S. mucida* (Blüthgen, 1923), *S. mucorea* (Eversmann, 1852), *S. nigricutis* (Warncke, 1975), *S. ochropus* (Blüthgen, 1923), *S. pollinosa* (Sichel, 1860), *S. pseudomucorea* (Ebmer, 1975), *S. solitudinis* (Ebmer, 1975), *S. surabadensis* (Ebmer, 1975), and *S. tuberculata* (Blüthgen, 1925).

A key to subgenera of the genus *Seladonia*

1. *Both sexes*: pubescence of body moderately long, dense and plumose, with areas covered with very short and dense hairs, metasomal terga with distinct posterior and sometimes anterior bands of white short plumose appressed hairs directed backward, without tomentum; dorsal surface of propodeum relatively long, subequal to scutellum; metapostnotum of normal length, reaching the posterior vertical surface of propodeum, hairless. *Female*: basitibial plate of hind legs usually well developed 2
– *Both sexes*: pubescence of body tomentose on most surfaces, including metasoma; dorsal surface of propodeum short, subequal to metanotum; metapostnotum very short, not reaching the posterior vertical surface of propodeum, at least partly covered with tomentum as well as other surfaces of propodeum. *Female*: basitibial plate of hind legs defined only partly 4
2. *Female*: distal median process of labrum broad and rounded, with scarcely defined keel; mandible simple, without subapical tooth; pubescence on outer surface of hind tibia sparse, not forming a scopa; basitibial plate of hind legs defined only partly; penicillus of hind basitarsus absent; posterior hair bands of metasomal terga almost completely absent; prepygidial fimbria of metasomal tergum V entire, not divided by a longitudinal specialized area; pygidial plate of tergum VI united with suprapygidial plate, tergal gradulus weak . . . . **Paraseladonia** (cleptoparasitic)
– *Female*: distal median process of labrum well developed, narrow and long, with strong keel; mandible with subdistal tooth; pubescence on outer surface of hind tibia forming a scopa (for carrying pollen) of long dense plumose inclined hairs; basitibial plate of hind legs well developed (except in *S. lanei* from South America), of normal size; penicillus of hind basitarsus present, usual; posterior hair bands of terga well developed, occasionally narrowed medially; prepygidial fimbria of tergum V divided by a longitudinal median, minutely pilose area; pygidial plate of tergum VI well defined, tergal gradulus distinct 3
3. *Male*: antenna relatively short, reaching only the scutellum (except for *S. semitecta*); 2nd flagellomere 1.2-1.4 times as long as wide; metasomal sternum VI flattened or with a slight longitudinal median depression . . . . . **Seladonia** s. str.
– *Male*: antenna long, usually reaching the metasoma; 2nd flagellomere 1.7-2.0 times as long as wide; sternum VI with a deep triangular depression behind gradulus . . . . . **Pachyceble**
4. *Male*: metasomal sterna IV and V weakly pubescent, without hair tassels, brushes or areas with other specific pubescence . . . . . **Placidohalictus**
– *Male*: sternum IV at posterior margin with median narrow flat hair tassel or sterna IV and/or V with median brushes of short and very dense hairs 5
5. *Male*: metasomal sternum IV at posterior margin with narrow flat tassel consisted of long dense and not separated hairs directed backward; sternum V without hair tassels, brushes, bristles or other special pubescence. *Female*: inner metatibial spur armed with 3-5 roundly triangular broadened and flattened teeth which join at their bases (except for *S. radoszkowskii*); clypeus and antefrons (supraclypeal area) usually more convex and sparsely punctate (except for *S. mordax*) . . . . . **Vestitohalictus**
– *Male*: sternum IV, or sternum V, or both sterna on their posterior areas with median brushes formed with short and very dense hairs directed downward. *Female*: inner metatibial spur dentate or pectinate, armed with 4-8 separate sharp or elongate cylindrical teeth; clypeus and antefrons usually less convex and denser punctate (except for *S. farabensis*) . . . . . **Mucoreohalictus**

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Appendix. Synonymical catalogue of species-group names of the genera *Halictus* and *Seladonia*

Valid names of species are given in **bold** font; valid names of subspecies, in normal; junior synonyms or junior homonyms, in *italics*; nomina dubia, in s p a c i n g. Original genus or combination is given in parentheses.

abuensis Cameron, 1908 (Halictus) = Seladonia vicina
acrocephalus Blüthgen, 1926 (Halictus), ?Halictus subg. Ramalictus
adjikenticus Blüthgen, 1923 (Halictus), Halictus subg. Monilapis
adolphifrederici Strand, 1911 (Halictus) = Seladonia foana
aegyptiacus Friese, 1916 (Halictus quadricinctus var.) = Halictus brunnescens
aegypticola Strand, 1909 (Halictus), Halictus subg. Monilapis
aeneobrunnea Pérez, 1895 (Halictus), Seladonia subg. Seladonia
aenescens Radoszkowski, 1893 (Nomioides) = Seladonia pulverea
aeraria Smith, 1873 (Halictus), Seladonia subg. Seladonia
aestuans Ebmer, 1978 (Halictus), Seladonia subg. Mucoreohalictus
africana Friese, 1909 (Halictus virescens var.) = Seladonia jucunda ssp.
agilis Smith, 1879 (Halictus) = Seladonia hespera
albarius Pérez, 1895 (Halictus) = Halictus senilis
albohispidus Blüthgen, 1923 (Halictus sexcinctus var.), Halictus sexcinctus ssp.
albozonatus Dours, 1872 (Halictus), Halictus subg. Platyhalictus
alexis Cameron, 1897 (Halictus) = Seladonia propingua
alexoides Strand, 1910 (Halictus) = Seladonia aeraria
alfkenellus Strand, 1909 (Halictus), Halictus subg. Platyhalictus
alpina Alfken, 1907 (Halictus), Seladonia confusa ssp.
altaicus Pérez, 1903 (Halictus) = Halictus minor
alternans Fabricius, 1793 (Hylaeus) = Halictus scabiosae
anomalipes Lebedev, 1910 (Halictus) = Halictus cochleariatarsis
apatellatus Strand, 1921 (Halictus) = Halictus tetrazonianellus
arapahonum Cockerell, 1906 (Halictus), Seladonia confusa ssp.
arbustorum Panzer, 1797 (Hylaeus) = Halictus sexcinctus
arenosa Ebmer, 1976 (Halictus), Seladonia leucahenea ssp.
armaticeps Cresson, 1872 (Halictus) = Halictus ligatus
asiaeminoris Strand, 1921 (Halictus) = Halictus resurgens
asperatus Bingham, 1898 (Halictus), Halictus subg. Platyhalictus (?= Halictus fimbriatus)
asperulus Pérez, 1895 (Halictus), nom. n. pro Halictus rugosulus Pérez, 1895, Halictus subg. Tytthalictus
asunicus Strand, 1921 (Halictus) = Halictus fulvipes
atripes Morawitz, 1893 (Halictus), Halictus subg. Protohalictus
atroviridis Cameron, 1906 (Halictus), Seladonia subg. Seladonia
a u r e i p e s Dours, 1872 (Halictus), nomen dubium in genus Halictus
austrovagans Cockerell, 1932 (Halictus) = Seladonia atroviridis
bagirensis Blüthgen, 1936 (Halictus), Halictus subg. Protohalictus
balearica Pérez, 1903 (Halictus), Seladonia subg. Mucoreohalictus
banaliana Strand, 1911 (Halictus), Seladonia jucunda ssp.
barcelonicus Pérez, 1903 (Halictus) = Seladonia smaragdula
benguellensis Cockerell, 1908 (Halictus jucundus ssp.), Seladonia jucunda ssp.
berlandi Blüthgen, 1936 (Halictus), Halictus subg. Hexataenites
beytueschebapensis Warncke, 1984 (Halictus senex spp.), Halictus subg. Monilapis
bifidus Warncke, 1975 (Halictus) = Halictus sajoi
bivinctus Vachal, 1902 (Halictus) = Halictus senilis
brachyceros Blüthgen, 1923 (Halictus), non Vachal, 1903, = Halictus carinthiacus
brunnescens Eversmann, 1852 (Hylaeus), Halictus subg. Protohalictus
bulbiceps Blüthgen, 1929 (Halictus), Seladonia subg. Placidohalictus
buteus Warncke, 1975 (Halictus) = Seladonia smaragdula
caelestis Ebmer, 1976 (Halictus), Seladonia subg. Seladonia
candescens Cockerell, 1945 (Halictus) = Seladonia hotoni
capensis Friese, 1909 (Halictus) = Seladonia atroviridis
capitosus Smith, 1853 (Halictus) = Halictus poeyi
carinaeventris Fahringer & Friese, 1921 (Halictus), unjustified emendation of Halictus cariniventris Morawitz, 1876, = Seladonia pollinosa ssp. cariniventris
cariniventris Morawitz, 1876 (Halictus), Seladonia pollinosa ssp.
carinthiacus Blüthgen, 1936 (Halictus), nom. n. pro Halictus brachyceros Blüthgen, 1923, Halictus subg. Monilapis
catalinensis Cockerell, 1903 (Halictus) = Seladonia tripartita
cedens Blüthgen, 1931 (Halictus), nom. n. pro Halictus posthumus Blüthgen, 1925, = Halictus alfkenellus
centaurea Ebmer, 1985 (Halictus), Halictus subg. Monilapis
centrosa Vachal, 1910 (Halictus), Seladonia subg. Seladonia
cephalica Morawitz, 1874 (Halictus), Seladonia subg. Seladonia
chaharensis Yasumatsu, 1940 (Halictus) = Halictus quadricinctus
chalybaea Friese, 1925 (Halictus), non Friese, 1909 = Seladonia niveocinctula
chalybeata Friese, 1909 (Halictus), Seladonia subg. Paraseladonia
chloropina Cockerell, 1946 (Halictus) = Seladonia niveocinctula
c i n c t u s Desmarest, 1860 (Halictus), nomen dubium in genus Halictus.
clandula Warncke, 1984 (Halictus), Seladonia subg. Pachyceble
cochleareitarsis Dalla Torre, 1896 (Halictus), unjustified emendation of Halictus cochleariatarsis Dours, 1872, = Halictus cochleariatarsis
cochleariatarsis Dours, 1872 (Lucasius), Halictus subg. Hexataenites
colliciatus Blüthgen, 1923 (Halictus) = Halictus pseudotetrazonius
compressus Walckenaer, 1802 (Andrena), nom. n. pro Apis flavipes Panzer, 1798, Halictus subg. Monilapis
concinna Brullé, 1840 (Halictus), Seladonia subg. Vestitohalictus
confluens Morawitz, 1890 (Halictus) = Seladonia aeraria
confusa Smith, 1853 (Halictus), Seladonia subg. Pachyceble
conjungens Blüthgen, 1921 (Halictus) = Seladonia cephalica
consobrinus Pérez, 1895 (Halictus), Halictus subg. Monilapis
constantinensis Strand, 1910 (Halictus tetrazonius var.), Halictus subg. Platyhalictus
constrictus Provancher, 1882 (Halictus), non Smith, 1853, = Seladonia confusa ssp. confusa

constrictus Smith, 1853 (Halictus), Halictus subg. Tythalictus
corsa Blüthgen, 1933 (Halictus subauratus var.), Seladonia subaurata ssp.
crenicornis Blüthgen, 1923 (Halictus), Halictus subg. Monilapis
creticola Strand, 1921 (Halictus cariniventris var.) = Seladonia pollinosa ssp. cariniventris
c r o c e i p e s Dalla Torre, 1896 (Apis), unjustified emendation of Apis crocipes Geoffroy, 1785, nomen dubium in genus Seladonia
c r o c i p e s Geoffroy, 1785 (Apis), nomen dubium in genus Seladonia
cupida Vachal, 1902 (Halictus), Seladonia subg. Vestitohalictus
c u p r e a Geoffroy, 1785 (Apis), nomen dubium in genus Seladonia
cyprica Blüthgen, 1937 (Halictus), Seladonia subg. Mucoreohalictus
cyrenaicus Blüthgen, 1930 (Halictus), Halictus subg. Hexataenites
dampfi Alfken, 1927 (Halictus), justified emendation of Halictus dampti Alfken, 1927, by Blüthgen, 1930; = Halictus tibialis
dampti Alfken, 1927 (Halictus), lapsus calami for Halictus dampfi, = Halictus tibialis
daturae Cockerell, 1929 (Halictus) = Seladonia vicina
delphinalis Blüthgen, 1935 (Halictus gavarnicus var.) = Seladonia gavarnica ssp. tatarica
denticulus Vachal, 1904 (Halictus) = Halictus farinosus
desertorum Morawitz, 1876 (Halictus), Seladonia subg. Placidohalictus
determinandus Dalla Torre, 1896 (Halictus), nom. n. pro Halictus determinatus Morawitz, 1876, Halictus subg. Platyhalictus
determinatus Morawitz, 1876 (Halictus), non Walker, 1871, = Halictus determinandus
d e t e r m i n a t u s Walker, 1871 (Halictus), nomen dubium in genus Halictus
deviridata Strand, 1910 (Halictus tumulorum var.) = Seladonia tumulorum ssp. tumulorum
diducta Cockerell, 1932 (Halictus), Seladonia subg. Seladonia
dissensis Cockerell, 1945 (Halictus) = Seladonia lucidipennis
dissidens Pérez, 1903 (Halictus), Seladonia subg. Pachyceble
distinctus Walker, 1871 (Halictus), non Schenck, 1869, = Halictus tibialis
dives Pérez, 1895 (Halictus) = Seladonia lucidipennis
dorni Ebmer, 1982 (Halictus), Seladonia subg. Pachyceble
dschulfensis Blüthgen, 1936 (Halictus), Halictus subg. Argalictus
dunganicus Blüthgen, 1936 (Halictus) = Halictus takuiricus
duplocinctula Cockerell, 1940 (Halictus) = Seladonia jucunda ssp. benguellensis
duplocinctus Vachal, 1902 (Halictus), Halictus subg. Halictus
ebmeri Pesenko, 1984 (Halictus), Halictus subg. Platyhalictus
ecaphosus Walckenaer, 1817 (Halictus) = Halictus quadricinctus
errans Ritsema, 1880 (Halictus), nom. n. pro Halictus vagans Smith, 1879 = Seladonia hespera
erudita Cockerell, 1924 (Halictus) = Seladonia aeraria
eurygnathopsis Blüthgen, 1936 (Halictus) = Halictus compressus
eurygnathus Blüthgen, 1931 (Halictus), nom. n. pro Halictus tomentosus auct., = Halictus compressus
experta Cockerell, 1916 (Halictus), Seladonia subg. Seladonia
exquisita Warncke, 1975 (Halictus) = Seladonia mugodjarica
extorris Vachal, 1902 (Halictus) = Seladonia pici
falcinellus Warncke, 1982 (Halictus), Halictus subg. Acalcaripes (?= Halictus patellatus)
farinosus Smith, 1853 (Halictus), Halictus subg. Nealictus
fasciata Nylander, 1848 (Halictus), non auct., = Seladonia tumulorum ssp. tumulorum
fatsensis Blüthgen, 1936 (Halictus), Halictus subg. Argalictus
ferreota Fan, 1991 (Halictus), Seladonia subg. Vestitohalictus
ferripennis Cockerell, 1929 (Halictus) = Seladonia tumulorum ssp. tumulorum
ferrugineizonatus Dalla Torre, 1896 (Halictus), unjustified emendation of Halictus ferrugineozonatus Dours, 1872; = Halictus rufipes
ferrugineozonatus Dours, 1872 (Halictus) = Halictus rufipes
festae Gribodo, 1921 (Nomioides) = Seladonia cupida
fimbriatus Smith, 1853 (Halictus), Halictus subg. Protohalictus
f l a v i c o r n i s Gmelin, 1790 (Apis), nomen dubium in genus Halictus
flavipes Fabricius, 1787 (Apis), non Fuesslyn, 1775 (Apis) = Seladonia tumulorum ssp. tumulorum
f l a v i p e s Fuesslyn, 1775 (Apis); nomen dubium in genus Halictus
flavipes Panzer, 1798 (Apis), non Fuesslyn, 1775, non Fabricius, 1787, = Halictus compressus
flavocallosa Morawitz, 1894 (Halictus) = Seladonia fuscicollis
flavotecta Cockerell, 1922 (Halictus cariniventris ssp.) = Seladonia pollinosa ssp. cariniventris
foana Vachal, 1899 (Halictus), Seladonia subg. Seladonia
formosus Dours, 1872 (Halictus) = Halictus rufipes
fraserae Cockerell, 1916 (Halictus) = Seladonia virgatella
frater Pesenko, 1984 (Halictus) = Halictus rubicundus
frontalis Smith, 1853 (Halictus), Halictus subg. Hexataenites
frostus Fan, 1990 (Halictus) = Halictus palustris
fucosus Morawitz, 1876 (Halictus) = Halictus senilis
fulvipes Klug, 1817 (Hylaeus), Halictus subg. Hexataenites
fumatipennis Blüthgen, 1923 (Halictus), Halictus subg. Platyhalictus
funerarius Morawitz, 1876 (Halictus), Halictus subg. Protohalictus
furcatus Blüthgen, 1925 (Halictus) = Halictus tetrazonius
fuscicollis Morawitz, 1876 (Halictus), Seladonia subg. Placidohalictus
galilaeus Ebmer, 1969 (Halictus), unjustified emendation of Halictus galileus Blüthgen, 1955, = Halictus tetrazonius
galileus Blüthgen, 1955 (Halictus) = Halictus tetrazonius
gaschunica Blüthgen, 1935 (Halictus pjalmensis ssp.), Seladonia pjalmensis ssp.
gavarnica Pérez, 1903 (Halictus), Seladonia subg. Pachyceble
geminata Pérez, 1903 (Halictus) = Seladonia seladonia
gemmea Dours, 1872 (Halictus), Seladonia subg. Seladonia
g e n e r o s a Harris, 1776 (Apis); nomen dubium in genus Halictus
georgicus Blüthgen, 1936 (Halictus), Halictus subg. Protohalictus

gissaricus Pesenko, 1985 (Halictus compressus ssp.), Halictus compressus ssp.
glacialis Ebmer 1979 (Halictus confusus ssp), Seladonia confusa ssp.
gobiensis Ebmer, 1982 (Halictus), Seladonia pseudovestita ssp.
gordius Warncke, 1975 (Halictus), Halictus subg. Monilapis
graecus Blüthgen, 1933 (Halictus), Halictus subg. Platyhalictus
graminea Smith, 1849 (Halictus) = Seladonia subaurata ssp. subaurata
grandiceps Cameron, 1897 (Halictus) = Seladonia propingua
griseozonatus Dours, 1872 (Halictus) = Halictus scabiosae
grossellus Ebmer, 1978 (Halictus), Halictus subg. Monilapis
gruenwaldti Ebmer, 1975 (Halictus), Halictus subg. Monilapis
gusenleitneri Ebmer, 1973 (Halictus) = Halictus tetrazonianellus
hakkaria Warncke, 1984 (Halictus kessleri ssp.) = Seladonia kessleri
harmonia Sandhouse, 1941 (Halictus), Seladonia subg. Pachyceble
hebeiensis Pesenko & Wu, 1997 (Halictus hedini ssp.), Halictus hedini ssp.
hedini Blüthgen, 1934 (Halictus), Halictus subg. Protohalictus
hermon Ebmer, 1975 (Halictus), Halictus subg. Monilapis
hespera Smith, 1862 (Halictus), Seladonia subg. Pachyceble
higashi Sakagami & Ebmer, 1979 (Halictus tumulorum ssp.), Seladonia tumulorum ssp.
holomelaenus Blüthgen, 1936 (Halictus), Halictus subg. Platyhalictus
holtzi Schulz, 1906 (Halictus) = Halictus resurgens
hondurasica Cockerell, 1949 (Halictus) = Seladonia hespera
hortensis Geoffroy in Fourcroy, 1785 (Apis) = Halictus quadricinctus
hotoni Vachal, 1903 (Halictus), Seladonia subg. Seladonia
humkalensis Blüthgen, 1936 (Halictus), Halictus subg. Argalictus
hybridopsis Blüthgen, 1923 (Halictus sexcinctus var.) = Halictus sexcinctus ssp. albohispidus
hyemala Warncke, 1982 (Halictus morinellus ssp.) = Seladonia lucidipennis
ibex Warncke, 1973 (Halictus), nom. n. pro Halictus simplex Blüthgen, 1923 non Paralictus simplex Robertson, 1901, = Halictus simplex
icarus Ebmer, 1978 (Halictus), Halictus subg. Protohalictus
ichneumonea Christ, 1791 (Apis) = Halictus sexcinctus
ifranensis Cockerell, 1931 (Halictus) = Halictus intumescens
ifranicola Cockerell, 1937 (Halictus) = Halictus patellatus ssp. taorminicus
indefinita Blüthgen, 1923 (Halictus), Seladonia subg. Mucoreohalictus
inpilosa Ebmer, 1975 (Halictus), Seladonia subg. Vestitohalictus
interruptus Lepeletier, 1841 (Halictus), non Panzer, 1798, = Halictus maculatus
intumescens Pérez, 1895 (Halictus), Halictus subg. Hexataenites
i n v i c t a Harris, 1776 (Apis), nomen dubium in genus Halictus
iridicolor Cameron, 1905 (Halictus), Seladonia subg. ?Seladonia
jaramielicus Blüthgen, 1923 (Halictus), Halictus subg. Platyhalictus
jarkandensis Strand, 1909 (Halictus) = Halictus minor
jucunda Smith, 1853 (Halictus), Seladonia subg. Seladonia
jucundiformis Cockerell, 1940 Halictus) = Seladonia jucunda ssp. jucunda
kerkiensis Friese, 1916 (Halictus nasica var.) = Seladonia nasica
kessleri Bramson, 1879 (Halictus), Seladonia subg. Seladonia
komensis Cockerell, 1939 (Halictus jucundus ssp.) = Seladonia jucunda ssp. africana
koptica Blüthgen, 1933 (Halictus varipes var.) = Seladonia lucidipennis
kurdica Warncke, 1984 (Halictus verticalis ssp.), Seladonia verticalis ssp.
kuschkensis Ebmer, 1975 (Halictus), Seladonia subg. Mucoreohalictus
kusdasi Ebmer, 1975 (Halictus), Seladonia subg. Pachyceble
kyrnos Ebmer, 1988 (Halictus tumulorum ssp.), Seladonia tumulorum ssp.
lanei Moure, 1940 (Pachyceble), Seladonia subg. Pachyceble
langobardicus Blüthgen, 1944 (Halictus), Halictus subg. Monilapis
laosina Cockerell, 1929 (Halictus daturae var.) = Seladonia vicina
laticephala Warncke, 1984 (Halictus), Seladonia subg. Seladonia
laticinctula Cockerell, 1946 (Halictus) = Seladonia foana
laticinctus Blüthgen, 1923 (Halictus rubicundus var.) = Halictus rubicundus
latisignatus Cameron, 1908 (Halictus), Halictus subg. Ramalictus
lerouxii Lepeletier, 1841 (Halictus), Halictus rubicundus ssp.
leucahenea Ebmer, 1972 (Halictus), Seladonia subg. Pachyceble
leucognathus Morice, 1921 (Halictus) = Halictus tetrazonianellus
leucopogon Strand, 1914 (Halictus) = Seladonia aeraria
libanensis Pérez, 1911 (Halictus) = Halictus aegypticola
ligatus Say, 1837 (Halictus), Halictus subg. Odontalictus
limissica Blüthgen, 1937 (Halictus pollinosus ssp.) = Seladonia pollinosa ssp. cariniventris
lobatus Ebmer, 1978 (Halictus), Halictus subg. Monilapis
longigenae Warncke, 1988 (Halictus) = Seladonia gavarnica ssp. gavarnica
lucidipennis Smith, 1853 (Halictus), Seladonia subg. Seladonia
luganicus Blüthgen, 1936 (Halictus), Halictus subg. Argalictus
lunatus Warncke, 1975 (Halictus senex ssp.), Halictus compressus ssp.
lupinelli Cockerell, 1939 (Halictus) = Halictus rubicundus
lussinicus Blьthgen, 1936 (Halictus), Halictus subg. Platyhalictus
lutescens Friese, 1921 (Halictus schmidti var.), Seladonia subg. Pachyceble
maculatus Smith, 1848 (Halictus), Halictus subg. Tythalictus
madecassa Pauly, 1984 (Halictus jucundus ssp.), Seladonia jucunda ssp.

magna Ebmer, 1980 (Halictus), Seladonia subg. Seladonia
magnificus Nurse, 1903 (Halictus) = Halictus duplocinctus
magretti Vachal, 1892 (Halictus) = Seladonia lucidipennis
m a r c h a l i Vachal, 1891 (Halictus), nomen dubium in Halictus subg. Monilapis
marikovskayae Pesenko, 1986 (Halictus) = Halictus palustris
maroccanus Blüthgen, 1933 (Halictus) = Halictus consobrinus
maximus Friese, 1916 (Halictus quadricinctus var.) = Halictus brunnescens
medanica Cockerell, 1945 (Halictus) = Seladonia lucidipennis
medaniella Cockerell, 1945 (Halictus) = Seladonia lucidipennis
mediterranellus Strand, 1909 (Halictus), Halictus subg. Platyhalictus
meliloti Cockerell, 1895 (Halictus) = Seladonia tripartita
meridionalis Morawitz, 1874 (Halictus) = Seladonia subaurata ssp. subaurata
microcardia Pérez, 1895 (Halictus), Seladonia subg. Vestitohalictus
minor Morawitz, 1876 (Halictus), Halictus subg. Platyhalictus
modernus Morawitz, 1876 (Halictus), Halictus subg. Lampralictus
mogrensis Cockerell, 1945 (Halictus) = Seladonia lucidipennis
mondaensis Blüthgen, 1923 (Halictus), Seladonia subg. Pachyceble
mongolensis Blüthgen, 1936 (Halictus rubicundus var.) = Halictus rubicundus
mongolica Morawitz, 1880 (Halictus), Seladonia subg. Seladonia
montanus Crawford, 1902 (Halictus) = Halictus farinosus
morawitzi Vachal, 1902 (Halictus), Seladonia subg. Mucoreohalictus
mordacella Blüthgen, 1929 (Halictus), Seladonia subg. Vestitohalictus
mordax Blьthgen, 1923 (Halictus), Seladonia subg. Vestitohalictus
morinella Warncke, 1975 (Halictus) = Seladonia smaragdula
mucida Blьthgen, 1923 (Halictus), Seladonia subg. Mucoreohalictus
mucorea Eversmann, 1852 (Hylaeus), Seladonia subg. Mucoreohalictus
mugodjarica Blüthgen, 1933 (Halictus), Seladonia subg. Seladonia
muruticus Friese, 1916 (Halictus quadricinctus var.) = Halictus squamosus
nadigi Blüthgen, 1934 (Halictus), Halictus subg. Hexataenites
nasica Morawitz, 1876 (Halictus), Seladonia subg. Vestitohalictus
nearctica Cockerell, 1911 (Halictus provancheri ssp.), non Vachal, 1904, = Seladonia confusa ssp. arapahonum
nearctica Vachal, 1904 (Halictus) = Seladonia confusa ssp. confusa
nebulosa Warncke, 1975 (Halictus kessleri ssp.) = Seladonia kessleri
nesiotis Perkins, 1922 (Halictus rubicundus var.), non Crawford, 1918, = Halictus rubicundus
neutra Blüthgen, 1923 (Halictus) = Seladonia cephalica
nicosiae Blüthgen, 1923 (Halictus), Halictus subg. Monilapis
nidulans Walckenaer, 1817 (Halictus) = Halictus rubicundus
n i g r i c a n s Gmelin, 1790 (Apis), nomen dubium in genus Halictus
nigricutis Warncke, 1975 (Halictus cypricus ssp.), Seladonia subg. Mucoreohalictus
nikkoensis Cockerell, 1911 (Halictus) = Seladonia aeraria
nilotica Smith, 1879 (Halictus) = Seladonia lucidipennis
nisoria Warncke, 1975 (Halictus sogdianus ssp.) = Seladonia semitica
n i t e n s Dalla Torre, 1877 (Halictus tetrazonius var.), nomen dubium in Halictus subg. Monilapis
nivalis Ebmer, 1985 (Halictus), Seladonia subg. Pachyceble
niveocinctula Cockerell, 1940 (Halictus), Seladonia subg. Seladonia
occidentalis Cresson, 1872 (Halictus) = Halictus parallelus
occipitalis Ebmer, 1972 (Halictus), Seladonia leucahenea ssp.
o c h r a c e o v i t t a t u s Dours, 1872 (Halictus), nomen dubium in Halictus subg. Hexataenites
o c h r o c e p h a l a Gmelin, 1790 (Apis), nomen dubium in genus Halictus
ochropus Blüthgen, 1923 (Halictus), Seladonia subg. Mucoreohalictus
olivaria Sandhouse, 1924 (Halictus) = Seladonia confusa ssp. arapahonum
omanica Pérez, 1907 (Halictus) = Seladonia lucidipennis
opulenta Benoist, 1950 (Halictus), Seladonia subg. Seladonia
o r d i n a r i u s Smith, 1853 (Halictus), nomen dubium in genus Halictus
orientalis Lepeletier, 1841Halictus), Seladonia subg. Seladonia
ornaticeps Cresson, 1872 (Halictus) = Halictus ligatus
ororyctes Cockerell, 1933 (Halictus) = Seladonia virgatella
oros Ebmer, 1988: 364 (Halictus tumulorum ssp.), Seladonia tumulorum ssp.
palustris Morawitz, 1876 (Halictus), Halictus subg. Tythalictus
pannonica Zilahi-Kiss, 1915 (Osmia) = Seladonia kessleri
pannonicus Ebmer, 1969 (Halictus) = Halictus tetrazonius
parallelus Say, 1837 (Halictus), Halictus subg. Nealictus
paris Bingham, 1908 (Halictus) = Halictus constrictus
paropamisos Ebmer, 1978 (Halictus), Seladonia subg. Seladonia
parumpunctata Morawitz, 1893 (Halictus), non Schenck, 1869, = Seladonia secunda
patellatus Morawitz, 1874 (Halictus), Halictus subg. Acalcaripes
pelagia Ebmer 1996 (Halictus confusus ssp),. Seladonia confusa ssp.
pentheri Blüthgen, 1923 (Halictus), Halictus subg. Monilapis
perkinsi Blüthgen, 1926 (Halictus), nom. n. pro Halictus flavipes auct. non Apis flavipes Fabricius, 1787, Seladonia confusa ssp.
persephone Ebmer, 1976 (Halictus), Seladonia subg. Vestitohalictus
pervirens Cockerell, 1940 (Halictus) = Seladonia hotoni
petraea Blüthgen, 1933 (Halictus), Seladonia subg. Pachyceble
pici Pérez, 1895 (Halictus), Seladonia subg. Vestitohalictus

pinguis Vachal, 1902 (Halictus) = Seladonia propingua
pinguismenta (Janjic & Packer, 2001), Seladonia subg. Pachyceble
pjalmensis Strand, 1909 (Halictus), Seladonia subg. Seladonia
placidula Blüthgen, 1923 (Halictus), Seladonia subg. Placidohalictus
poeyi Lepeletier, 1841 (Halictus), Halictus subg. Odontalictus
pollinosa Sichel, 1860 (Halictus), Seladonia subg. Mucoreohalictus
ponticus Blüthgen, 1934 (Halictus), Halictus subg. Monilapis
pontifica Cockerell, 1940 (Halictus) = Seladonia hotoni
posthumus Blüthgen, 1925 (Halictus), non Halictus postumus Vachal, 1903, = Halictus alfkenellus
powelli Cockerell, 1931 (Halictus scabiosae ssp.) = Halictus scabiosae
priesneri Ebmer, 1975 (Halictus), Halictus maculatus ssp.
procerus Vachal, 1904 (Halictus) = Halictus farinosus
propingua Smith, 1853 (Halictus), Seladonia subg. Seladonia
provancheri Dalla Torre, 1896 (Halictus), nom. n. pro Halictus constrictus Provancher, 1882, = Seladonia confusa ssp. confusa
pruinescens Cockerell, 1937 (Halictus), Seladonia subg. Seladonia
pseudoaraxana Blüthgen, 1929 (Halictus) = Seladonia varentzowi
pseudoconfluens Strand, 1910 (Halictus) = Seladonia aeraria
pseudomaculatus Blüthgen, 1925 (Halictus) = Halictus palustris
pseudomucorea Ebmer, 1975 (Halictus), Seladonia subg. Mucoreohalictus
pseudotakuiricus Fan, 1990 (Halictus) = Halictus takuiricus
pseudotetrazonius Strand, 1921 (Halictus), Halictus subg. Monilapis
pseudovagans Cockerell, 1949 (Halictus)) = Seladonia hespera
pseudovestita Blüthgen, 1925 (Halictus), Seladonia subg. Vestitohalictus
pulverea Morawitz, 1874 (Halictus), Seladonia subg. Vestitohalictus
pyrenaeus Pérez, 1903 (Halictus), Halictus subg. Monilapis
quadricinctoides Blüthgen, 1936 (Halictus), Halictus subg. Monilapis
quadricinctus Fabricius, 1776 (Apis), Halictus subg. Halictus
quadrifasciatus Smith, 1870 (Halictus) = Halictus rubicundus
quadripartitus Blüthgen, 1923 (Halictus), Halictus subg. Monilapis
quadristrigatus Latreille, 1805 (Halictus) = Halictus quadricinctus
radoszkowskii Vachal, 1902 (Halictus), Seladonia subg. Vestitohalictus
rejectus Cockerell, 1937 (Halictus) = Halictus consobrinus
resurgens Nurse, 1903 (Halictus), Halictus subg. Hexataenites
reunioni Pauly, 1984 (Halictus) = Seladonia orientalis
rossicus Ebmer, 1978 (Halictus), nom. n. pro Halictus samarensis Blьthgen, 1936, Halictus subg. Monilapis
ruae Cockerell, 1949 Halictus) = Seladonia lutescens
rubicundus Christ, 1791 (Apis), Halictus subg. Protohalictus
ruborum Cockerell, 1898 (Halictus lerouxii var.) = Halictus rubicundus
rubripes Friese, 1916 (Halictus quadricinctus var.) = Halictus rufipes
rudolphae Pesenko, 1984 (Halictus), Halictus subg. Platyhalictus
rufa Friese, 1916 (Halictus) = Seladonia radoszkowskii
rufipes Fabricius, 1793 (Andrena), Halictus subg. Halictus
rufipes Spinola, 1806 (Andrena), non Fabricius, 1793, = Halictus sexcinctus
rugosulus Pérez, 1895 (Halictus), non Hylaeus rugosulus Schenck, 1853, = Halictus asperulus
sajoi Blüthgen, 1923 (Halictus), Halictus subg. Monilapis
samarensis Blüthgen, 1936 (Halictus), non Blьthgen, 1926, = Halictus rossicus
sansoni Cockerell, 1911 (Halictus) = Seladonia virgatella
scabiosae Rossi, 1790 (Apis), Halictus subg. Hexataenites
scardicus Blüthgen, 1936 (Halictus) = Halictus adjikenticus
schmidti Friese, 1921 (Halictus) = Seladonia hespera
secunda Dalla Torre, 1896 (Halictus), nom. n. pro Halictus parumpunctatus Morawitz, 1893, Seladonia subg. Seladonia
sefidicus Blüthgen, 1936 (Halictus takuiricus ssp.) = Halictus takuiricus
seladonia Fabricius, 1794 (Apis), Seladonia subg. Seladonia
seminigra Cockerell, 1937 (Halictus) = Seladonia centrosa
semitecta Morawitz, 1874 (Halictus), Seladonia subg. Seladonia
semitica Blüthgen, 1955 (Halictus), Seladonia subg. Vestitohalictus
senex Förster, 1860 (Hylaeus) = Halictus compressus
senilis Eversmann, 1852 (Hylaeus), Halictus subg. Argalictus
sepositus Cockerell, 1921 (Halictus) = Halictus frontalis
sexcinctellus Dours, 1872 (Halictus) = Halictus fulvipes
sexcinctus Fabricius, 1775 (Apis), Halictus subg. Hexataenites
shevestensis Blüthgen, 1933: 59 (Halictus), lapsus calami for Halictus thevestensis Pérez, 1903, = Seladonia pollinosa ssp. thevestensis
siculus Blüthgen, 1923 (Halictus) = Halictus mediterranellus
silvatica Blüthgen, 1926 (Halictus propinguus var.) = Seladonia vicina
simplex Blüthgen, 1923 (Halictus), Halictus subg. Monilapis
smaragdula Vachal, 1895 (Halictus), Seladonia subg. Seladonia
sogdiana Morawitz, 1876 (Halictus) = Seladonia pulverea
solitudinis Ebmer, 1975 (Halictus); Seladonia subg. Mucoreohalictus
speculifera Cockerell, 1929 (Halictus) = Seladonia vicina
squamosus Lebedev, 1910 (Halictus), Halictus subg. Hexataenites
stachii Blьthgen, 1923 (Halictus), Halictus subg. Protohalictus
subalfkenellus Blüthgen,1936 (Halictus) = Halictus alfkenellus
subaurata Rossi, 1792 (Apis), Seladonia subg. Seladonia
subauratoides Blüthgen, 1926 (Halictus), Seladonia subg. Seladonia

subauratovestitus Blüthgen, 1929 (Halictus) = Seladonia pjalmensis ssp. pjalmensis
subincerta Cockerell, 1940 (Halictus) = Seladonia foana
submodernus Blüthgen, 1936 (Halictus), Halictus subg. Argalictus
subpetraea Blüthgen, 1933 (Halictus), Seladonia subg. Pachyceble
subsenilis Blüthgen, 1955 (Halictus), Halictus subg. Argalictus
sudanica Cockerell, 1945 (Halictus) = Seladonia lucidipennis
surabadensis Ebmer, 1975 (Halictus), Seladonia subg. Mucoreohalictus
syria Blüthgen, 1933 (Halictus subauratus ssp.) = Seladonia subaurata ssp. subaurata
syrica Warncke 1975 (Halictus), unjustified emendation of Halictus syrius Blüthgen, 1933, = Seladonia subaurata ssp. subaurata
takuiricus Blüthgen, 1936 (Halictus), Halictus subg. Protohalictus
taorminicus Strand, 1921 (Halictus), Halictus patellatus ssp.
tatarica Blüthgen, 1933 (Halictus), Seladonia gavarnica ssp.
tecta Radoszkowski, 1876 (Halictus), Seladonia subg. Vestitohalictus
tetrazonianellus Strand, 1909 (Halictus), Halictus subg. Monilapis
tetrazonius Klug, 1817 (Hylaeus), Halictus subg. Monilapis
texanus Cresson, 1872 (Halictus) = Halictus ligatus
thesea Ebmer, 1975 (Halictus morawitzi ssp.), Seladonia morawitzi ssp.
thevestensis Pérez, 1903 (Halictus), Seladonia pollinosa ssp.
tibetana Blüthgen, 1926F (Halictus), Seladonia subg. Pachyceble
tibialis Walker, 1871 (Hylaeus), Halictus subg. Argalictus
tinicus Strand, 1921 (Halictus) = Halictus fulvipes
tokarensis Cockerell 1945 (Halictus) = Seladonia lucidipennis
tokariella Cockerell 1945 (Halictus) = Seladonia lucidipennis
tomentosus Herrich-Schäffer, 1840 (Hylaeus), nom. n. pro Apis flavipes Panzer, 1798, = Halictus compressus
townsendi Cockerell, 1896 (Halictus) = Halictus ligatus
transbaikalensis Blьthgen, 1933 (Halictus), Seladonia subg. Pachyceble
transcaspica Blüthgen, 1923 (Halictus) = Seladonia fuscicollis
transvolgensis Pesenko, 1985 (Halictus compressus ssp.), Halictus compressus ssp.
trichiura Cockerell, 1940 (Halictus) = Seladonia hotoni
tridivisus Blьthgen, 1923 (Halictus), Halictus subg. Platyhalictus
tripartita Cockerell, 1895 (Halictus), Seladonia subg. Pachyceble
tsingtauensis Strand, 1910 (Halictus), justified emendation for Halictus tsingtouensis by Blüthgen, 1923, Halictus subg. Monilapis
tsingtouensis Strand, 1910 (Halictus tetrazonius var.); lapsus calami for Halictus tsingtauensis, = Halictus tsingtauensis
tsushimae Friese, 1916 (Halictus) = Seladonia aeraria
tuberculata Blüthgen, 1925 (Halictus), Seladonia subg. Mucoreohalictus
tumulorum Linnaeus, 1758 (Apis), Seladonia subg. Pachyceble
turanicola Dalla Torre, 1896 (Halictus), nom. n. pro Halictus turanicus Morawitz, 1893; = Halictus turanicus
turanicus Morawitz, 1893 (Halictus), non Nomioides turanica Morawitz, 1876, Halictus subg. Protohalictus
turkmenorum Pesenko, 1984 (Halictus), Halictus subg. Protohalictus
turkomannus Pérez, 1903 (Halictus) = Halictus resurgens
typographica Cockerell, 1918 (Halictus) = Seladonia virgatella
umbrosa Cockerell, 1929 (Halictus) = Seladonia vicina
vagans Smith, 1879 (Halictus), non Smith, 1857, = Seladonia hespera
valligensis Cockerell, 1937 (Halictus) = Seladonia centrosa
vansoni Cockerell, 1935 (Halictus), *Seladonia* subg. Seladonia
varentzowi Morawitz, 1894 (Halictus), Seladonia subg. Placidohalictus
variipes Dalla Torre, 1896 (Halictus), unjustified emendation of Halictus varipes Morawitz, 1876, = Seladonia lucidipennis
varipes Morawitz, 1876 (Halictus) = Seladonia lucidipennis
vaulogeri Pérez, 1895 (Halictus) = Halictus albozonatus
velatus Pérez, 1895 (Halictus) = Seladonia vestita
venablesii Ashmead, 1903 (Halictus) = Halictus farinosus
veneticus Ebmer, 1969 (Halictus), non Móczár, 1967, = Halictus compressus
veneticus Móczár, 1967 (Halictus) = Halictus sajoi
vernalis Smith, 1879 (Halictus) = Seladonia lucidipennis
verticalis Blüthgen, 1931 (Halictus), Seladonia subg. Seladonia
vestita Lepeletier, 1841 (Halictus), Seladonia subg. Vestitohalictus
vicina Vachal, 1894 (Halictus), Seladonia subg. Seladonia
vinula Blüthgen, 1923 (Halictus smaragdulus f.) = Seladonia smaragdula
virescens Lepeletier, 1841 (Halictus) = Seladonia subaurata ssp. subaurata
virgatella Cockerell, 1901 (Halictus), Seladonia subg. Pachyceble
viridibasis Cockerell, 1946 (Halictus) = Seladonia atroviridis
wagneri Blьthgen, 1937 (Halictus) = Halictus patellatus ssp. patellatus
wjernicus Blüthgen, 1936 (Halictus), Halictus subg. Monilapis
wollmanni Blüthgen, 1933 (Halictus), Seladonia subg. Seladonia
xanthoprymnus Warncke, 1984 (Halictus), Halictus subg. Monilapis
yarkandensis Michener, 1978 (Halictus), lapsus calami for Halictus jarkandensis Strand, 1909, = Halictus minor
yunnanica Pesenko & Wu, 1997 (Halictus), Seladonia subg. Pachyceble
zadaensis Fan, 1990 (Halictus) = Halictus takuiricus
zebrus Walckenaer, 1817 (Halictus) = Halictus scabiosae

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