

# World revision of the oil-collecting bee genus *Macropis* Panzer 1809 (Hymenoptera: Apoidea: Melittidae) with a description of a new species from Laos

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**Abstract.** The genus *Macropis* Panzer 1809 includes 16 species, with the new taxon described here: *M. (Sinomacropis) orientalis* n. sp. The present paper is the first global revision of the genus. The authors propose a comprehensive catalogue, a key to the species and maps of some species. On the basis of an extensive morphological revision, the subgenera earlier proposed by Michener are further discussed and assessed. Moreover, several notable range expansions are reported and discussed. The species floral choices are discussed: all the species are oligolectic on various *Lysimachia* species.

**Résumé.** Le genre *Macropis* Panzer 1809 comprend 16 espèces, avec le nouveau taxon décrit ici : *M. (Sinomacropis) orientalis* n. sp. Cette étude est la première révision complète de ce genre. Les auteurs proposent un catalogue détaillé, une clé des espèces ainsi que des cartes de répartition de quelques espèces. Sur la base d'une révision morphologique approfondie, le sous-genre précédemment proposé par Michener est amplement discuté et évalué. De plus, des extensions de répartitions notables sont données et discutées. Le choix floral des espèces est discuté : toutes les espèces sont oligolectiques sur différentes espèces de *Lysimachia*.

*Macropis* Panzer 1809 is one of the 14 genera included in Melittidae (Michener 2000). Among the taxa of this family, the genus *Macropis* is characterised notably by the males yellow facial markings, the two submarginal cells (while most Melittidae have three) and the well-developed pygidial plate in both sexes (Michener 1981). The floral choices of the females and their morphological adaptations for the oil foraging on *Lysimachia* L. are also unique.

*Macropis* includes 16 species (*M. orientalis* n. sp. included), subdivided into three subgenera: *Macropis* s.str., *Paramacropis* Popov & Guiglia 1936 and *Sinomacropis* Michener 1981. The nominal subgenus is Holarctic (Michener 1981; Popov 1958), while the two others subgenera and most species are restricted to East-Palaearctic. Based on the literature, the distribution can be summarized as follows. Two species are distributed in the West-Palaearctic (Warncke 1973): *M. europaea*

Warncke 1973 and *M. frivaldszkyi* Mocsary 1878. *M. fulvipes* (Fabricius 1805) is a transpalaeartic species, distributed from Europe to Russian Far East (Pekkarinen *et al.* 2003). In North America, Snelling & Stage (1995) recorded four species: *M. ciliata* Patton 1880, *M. nuda* (Provancher 1882), *M. patellata* Patton 1880 and *M. steiromacropis* Robertson 1891. From East-Palaearctic, Yasumatsu & Hirashima (1956) described two species in Japan: *M. tibialis* Yasumatsu & Hirashima 1956, *M. dimidiata* Yasumatsu & Hirashima 1956, while Wu (2000), reviewing the Chinese fauna, recorded seven species: *M. dimidiata*, *M. hedinii* Alfken 1936, *M. immaculata* Wu 1965, *M. kiangsuensis* Wu 1978, *M. micheneri* Wu 1992, *M. omeiensis* Wu 1965 and *M. ussuriensis* (Popov 1936). The genus is absent from the tropical region and Central-Asia.

*Macropis* are tightly associated with *Lysimachia* (Primulaceae) (Cane *et al.* 1983; Popov 1958; Rozen & Jacobson 1980; Vogel 1976). The females of all the species collect oil in these flowers' eliaophores (at the base of the stamen). They display morphological adaptations to oil collecting (such as typical hairs on legs) suggest-

**Table 1.** Origin of the studied material (BDFGM = Banque de Données fauniques de Gembloux et Mons).

Specimen origin	Number of specimens	
	Original data	BDFGM
<b>Private collections</b>		
Collection S.P.M. Roberts	0	93
Collection V. Lefeber	0	87
Others	20	33
<b>Institutions</b>		
AMNH (American Museum of Natural History)	64	–
CUI (Cornell University, Department of Entomology, Ithaca, USA)	2	0
ELKU (Entomological laboratory, Kyushu University, Fukuoka, Japon)	3	0
FUSAGx (Faculté universitaire des Sciences agronomiques de Gembloux, Belgium)	64	19
IRSNB (Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium)	32	22
MHNG (Muséum d'Histoire naturelle, Genève, Suisse)	3	0
IZUL (Université de Liège, Institut de Zoologie, Belgium)	0	22
MCZ (Musée cantonal de Zoologie, Lausanne, Switzerland)	65	0
MNHN (Musée national d'Histoire naturelle, Paris, France)	334	0
MZL (Zoologiska Museet, Lunds Universitet, Sweden)	45	0
MZS (Muséum zoologique de Strasbourg, France)	82	0
NHM (Natural History Museum, Londres, United Kingdom)	178	0
NMW (Naturhistorisches Museum Wien, Austria)	92	0
OÖLL (Oberösterreichisches Landesmuseums Linz, Austria)	202	0
RNHL (Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands)	152	0
UMH (Université de Mons-Hainaut, Mons, Belgium)	5	2
UZMC (Zoologisk Museum, Københavns Universitet, Copenhagen, Denmark)	13	0
ZMA (Zoologisch Museum van Amsterdam, Netherlands)	56	39
ZSM (Zoologische Staatssammlung München, Germany)	109	0
Sums	1 521	317

ing a very tight insect-plant association (Michener, 1981). Cane *et al.* (1983) hypothesized the females use the oil to coat their cell walls, but oil is also mixed with the pollen for larval provisions.

The genus *Lysimachia* L. includes 180 species ranging mainly in temperate and subtropical areas of the Northern Hemisphere (but also present in the Neotropical region). Following Peng & Hu (1999), 138 among these latter 180 species occur in China. *Lysimachia* is usually subdivided into five subgenera: *Lysimachia* L. s. str., *Naumbergia* (Mönch) Klatt.,

*Palladia* (Moench) Hand.-Mzt., *Seleucia* Bigel and *Theopyxis* (Gris.) Pax (Handel-Mazzetti 1928; Simpson *et al.* 1983). *Palladia* and *Naumbergia* contain non oil-producing species (Vogel 1976). *Theopyxis* is endemic of South America (Simpson *et al.* 1983) and consequently non sympatric with *Macropis*. On the contrary, *Seleucia* is endemic of New World and includes 7 species, all producing oil (Coffey & Jones 1980), while *Lysimachia* s.str. is Holarctic and includes 85 species (of which most are oil-producing). So, from the biogeographical point of view, the *Macropis* could only visit

only the oil-producing species of two subgenera: *Lysimachia* s. str. and *Seleucia*.

In the present paper the authors propose the first comprehensive catalogue and a key to the species. The taxon ranges are mapped and discussed with a particular attention to new distributional data from North Africa (Algeria), Europe (Corsica) and South-Eastern Asia (Laos). Finally, we synthesise and discuss briefly the available data on floral associations.

### Material and method

#### Systematic

The reviewed material is conserved in the collections and institutions listed in table 1.

In the following catalogue, one quotes, for each taxon, the description reference, the described sex(es), the exhaustive synonymy and the distribution limits.

The partial (regional) keys of Wu (2000) and Snelling & Stage (1995) were adapted to complete the comprehensive one presented hereafter. The following abbreviations are used in this key:

Bt = Basitarsus	F = Femur
Fe = Female	S = Sternum
M = Male	T = Tergum
Pp = Pygidial plate	Tb = Tibia

We use the terminology of Michener (2000) and Warncke (1973). The pictures are made with a scanning electron microscope JEOL JSM-6100 associated to the software SEMAFOR (JEOL, Sollentuna, Sweden).

#### Biogeography

The data used for the species distributions are derived from 3 sources. One part is constituted by the 1521 specimens reviewed in the collections and institutions previously listed (table 1). In addition, 317 specimens from the Gembloux-Mons databank (BDFGM) were also considered (main contributors are B.V. Lefeber, 125 specimens and Prof. J. Leclercq, 113 specimens). Finally, 481 distributional data points come from varied literature reports: Alfken (1913), Baldovski (1983), Banaszak (1982a,b,c), Dylewska & Noskiewicz (1963), Elfving (1968), Erlandsson *et al.* (1988), Gogala (1991, 1994), Jacob-Remacle & Jacob (1988), Litt (1998), Malyshev (1929), Moczar (1957), Möschler (1938), Ornosa & Ortiz-Sánchez (1998), Pagliano (1992), Peeters *et al.* (1999), Pekkarinen *et al.* (2003), Phipps (1948), Popov (1936, 1958), Saunders (1882, 1896), Tkalcu (1974), Warncke (1973, 1981), Wu (1965), Wu & Michener (1986), Yasumatsu & Hirashima (1956).

The maps are consequently based on more than 2300 records.

Data were managed using Data Fauna Flora (DFF) 2.0 (Barbier *et al.* 2000). The geographical position of the specimens caught was searched on the basis of the labelled localities using the-gazetteer included in this software (CFFGazet). Maps were realized using Carto Fauna Flora (CFF) 2.0 (Barbier & Rasmont 2000). All are displayed on a Gall geographical projection.

#### Floral choices

The floral choices data are from the same origin. We use the following additional literature: Elfving (1968), Erlandsson (1960), Gogala (1994), Litt (1998), Patton (1880), Phipps (1948), Rozen & Jacobson (1980), Simpson *et al.* (1983), Snelling & Stage (1995), Wu & Michener (1986), Wu (1965) and Yasumatsu & Hirashima (1956).

## RESULTS

### Commented catalogue

#### Macropis *Panzer* 1809

Type species: *Megilla labiata* Fabricius 1805 (see MICHENER, 1983, 1984).  
*Megilla* Fabricius 1805 (*partim*): 328.  
*Macropis* Panzer 1809: 107.

#### Subgenus *Macropis* Panzer 1809 s. str.

*Megilla* Fabricius 1805 (*partim*): 328.  
*Macropis* Panzer 1809: 107.

**Diagnosis.** Table 2.

**Distribution** (Fig. 29). Holarctic.

#### *Macropis (Macropis) ciliata* Patton 1880

*Macropis ciliata* Patton 1880: 31-33 (♂/♀). *Locus typicus*: "Waterbury, New Haven" (USA).  
*Macropis longilingua* Provancher 1888: 424 (♀). *Locus typicus*: "Canada".

**Distribution.** Canada (Quebec), USA (North Carolina, Connecticut, Maine, South Georgia, Wisconsin).

#### *Macropis (Macropis) dimidiata* Yasumatsu & Hirashima 1956

*Macropis dimidiata* Yasumatsu & Hirashima 1956: 250 (♂/♀). *Locus typicus*: "Nishiashoro" (Japan).

**Distribution.** China, Japan.

#### *Macropis (Macropis) europaea* Warncke 1973

*Macropis europaea* Warncke 1973: 112 (♂). *Locus typicus*: "Erlangen" (Germany).  
*Macropis labiata* auct., *nee* Fabricius 1805.

**Distribution** (Fig. 31). *M. europaea* has a medio-european distribution reaching 65° N in the North and extending in Spain, Italy and Greece in the South. The species is the only one distributed in the British Islands. To the East, *M. europaea* is recorded to Barnoul (Russia, [WGS: 53° 24' N 83° 42' E]; Popov, 1958).

**Table 2.** Comparative diagnosis of the *Macropis* subgenera.

Characters	Subgenus <i>Macropis</i>	Subgenus <i>Sinomacropis</i>	Subgenus <i>Paramacropis</i>
<b>Both sexes</b>			
Propodeal triangle	Hairless (Fig. 24)	Hairy	Hairless
Basal veins	Interstitial with or basal to nervulus	Distal or basal to nervulus	Interstitial to nervulus
<b>Female</b>			
Labrum	With a median or subapical crest (Fig. 23)	Without crest	With a subapical crest
Metabasitarsus	Less than half as long as tibia Less than four times as long as broad	Less than half as long as tibia Less than four times as long as broad	About half as long as tibia Over four times as long as broad
<b>Male</b>			
Clypeus apical margin	Convex (Fig. 1)	Truncated (Fig. 2)	Truncated
Eyes inner margin	Converging (Fig. 1)	Subparallel	Converging
Metabasitarsus	With comb of stiff bristles on underside extending the full length of the segment	With comb of stiff bristles on underside of base only	Without comb of stiff bristles
Pygidial plate	Longer than T6 proximal part (Figs. 7-10)	Shorter than T6 proximal part (Fig. 4)	Shorter than T6 proximal part
Sterna 3-4	With apical fringe	With apical fringe	Without apical fringe
Sternum 6	Not narrowed preapically Apex acute and curved outwards	Not narrowed preapically Apex acute and curved outwards	Narrowed preapically Apex enlarged truncated and straight
Sternum 8	Not constricted just behind middle (Fig. 13) With 2 circular median structures (Fig. 13) Apex spiny prolonged (Figs. 15 and 16)	Not constricted just behind middle (Fig. 14) Without median structures (Fig. 14) Apex not prolonged	Strongly constricted just behind middle Without median structure Apex not prolonged
Gonocoxite apex	Generally weakly hairy (Fig. 17-22) Pointed (Figs. 17-22)	Usually hairy Truncated	Hairless Truncated
Gonostylus	Bilobated (Figs. 20-22)	Bilobated	Simple

***Macropis (Macropis) frivaldszkyi* Mocsary 1878**

*Macropis frivaldszkyi* Mocsáry 1878: 119-120 (♂/♀). *Locus typicus*: "Hungaria meridionali" (Hungary).

**Distribution** (Fig. 32). *M. frivaldszkyi* ranges from Balkans to Anatolia and Syria.

***Macropis (Macropis) fulvipes* (Fabricius 1805)**

*Megilla fulvipes* Fabricius 1805: 332 (♀). *Locus typicus*: "Austria, Dom. De Mergele" (Austria).

*Megilla labiata* Fabricius 1805: 333 (♀). *Locus typicus*: "Austria, Dom. De Mergele" (Austria).

**Distribution** (Fig. 30). In Europe, *M. fulvipes* has a distribution close to *M. europaea* though not so wide than in this latter species. The authors recorded recently several data from Algeria (Oran, 1 ♂, leg. Handl, det. D. Michez, OÖLL; Biskra, 1 ♂, 27/05/1891, leg. Handl, det. D. Michez, OÖLL). Eastern, *M. fulvipes* is recorded to Ussuriysk (Russia, [WGS: 43° 48' N 131° 59' E]) (Pekkarinen *et al.* 2003).

***Macropis (Macropis) kiangsuensis* Wu 1978**

*Macropis kiangsuensis* Wu 1978: 426-427 (♀). *Locus typicus*: Zhengjiang (China).

**Distribution.** China.

***Macropis (Macropis) nuda* (Provancher 1882)**

*Eucera nuda* Provancher 1882: 174 (♀). *Locus typicus*: "Canada".  
*Macropis (Macropis) morsei* Robertson 1897: 338-339 (♂/♀). *Locus typicus*: "Mass., N.Y., Mich." (USA).  
*Macropis clypeata* Swenk 1907: 293 (♂). *Locus typicus*: "Warbonnet Canon, Sioux County, Nebraska" (USA).

**Distribution.** Canada, USA (Colorado, Idaho, Maine, Montana, New Jersey, New York).

***Macropis (Macropis) patellata* Patton 1880**

*Macropis patellata* Patton 1880: 33 (♂). *Locus typicus*: "Plymouth, New Haven" (USA).

**Distribution.** USA (North Carolina, Iowa, Maryland, Nebraska, Vermont)

***Macropis (Macropis) steironematis* Robertson 1891**

*Macropis steironematis* Robertson 1891: 63 (♂/♀). *Locus typicus*: "Carlinville, Illinois" (USA).

**Distribution.** USA (North Carolina, Georgia, Illinois, Iowa, Kansas, Missouri, Nebraska, Virginia, Washington).

***Macropis (Macropis) tibialis* Yasumatsu & Hirashima 1956**

*Macropis tibialis* Yasumatsu & Hirashima 1956: 248-249 (♂/♀). *Locus typicus*: "Higashikawa" (Japan).

**Distribution.** Japan.

Subgenus ***Paramacropis*** Popov & Guiglia 1936

**Type species.** *Ctenoplectra ussuriana* Popov 1936.

*Paramacropis* Popov & Guiglia 1936: 287.

**Diagnosis.** Table 2.

**Distribution** (Fig. 33). The range of this subgenus seems to be restricted to the North-East of China (Jilin) and the Siberian Pacific coasts.

***Macropis (Paramacropis) ussuriana* (Popov 1936)**

*Ctenoplectra ussuriana* Popov 1936: 78-80 (♂). *Locus typicus*: Krivoj Kljuch (Russia).

*Macropis ussuriana*; Wu & Michener, 1986: 46-47 (♀).

**Distribution.** Ussuria and Manchuria (Fig. 33).

**Subgenus *Sinomacropis*** Michener 1981

**Type species.** *Macropis hedini* Alfken 1936.

*Macropis (Sinomacropis)* Michener 1981: 51.

**Diagnosis.** Table 2.

**Distribution** (Fig. 33). Most species are endemic to China, *M. orientalis* sp. nov. is the only one recorded in Laos.

***Macropis (Sinomacropis) hedini* Alfken 1936**

*Macropis hedini* Alfken 1936: 16-17 (♀). *Locus typicus*: "N. O. Szeschuan" (China).

*Macropis hedini*; Wu, 1965: 592-594 (♂).

**Distribution** (Fig. 33). China (Hubei, Sanghai, Shaanxi, Sichuan, Zhejiang).

***Macropis (Sinomacropis) immaculata* Wu 1965**

*Macropis hedini*; Popov, 1958: 502-504, description of male but use a wrong name.

*Macropis immaculata* Wu 1965: 594-596 (♀). *Locus typicus*: Omeishan (China).

**Distribution** (Fig. 33). China (Sichuan, Yunnan, Zhejiang).

***Macropis (Sinomacropis) orientalis* n. sp.**

**Holotype.** ♀, Laos N, Louang Phrabang province, Ban Song Cha ngbd. [WGS: 20°34'N 102°15'E], 1,200 m, V.1999, leg. V. Kubañ.

**Etymology.** The name *orientalis* is chosen in regard of the *locus typicus* geographical position.

**Diagnosis. Females.** Labrum smooth. Supraclypeal area dark. Fore legs with brownish pilosity. Bt3 inner face with brownish pilosity; outer with an apical fringe of black hairs. Propodeal triangle punctured, hairy, with a small smooth (shiny and hairless) medio-basal area. T2 margin medially longer than the proximal part. T2-4 with short and sparse pilosity. T3-4 margin with brown hairs. **Males.** Unknown.

**Table 3.** Comparative diagnosis of *Sinomacropis*.

Characters	<i>M. immaculata</i>	<i>M. orientalis</i>	<i>M. bedini</i>
Supraclypeal area	Dark	Dark	Yellow spotted
Legs 1	With yellow hairs	With brown hairs	With yellow hairs
Tibia 1	Partly orange	Dark	Partly orange
Metabasitarsus	With pale hairs	With brownish hairs on inner face and the outer face with black apical fringe	With brownish hairs on inner face and the outer face with black apical fringe
Propodeal triangle	Unpunctured smooth, shiny and hairless (on a medio basal area)	Unpunctured smooth, shiny and hairless (on a medio basal area)	With an unpunctured smooth and shiny median stripe
T2 median part	Margin shorter than the proximal part	Margin longer than the proximal part	Margin shorter than the proximal part
Anal fringe	Yellowish	Medially brown and laterally whitish	Yellowish

**Comparative diagnosis. Females.** *M. orientalis* is morphologically close to *M. bedini* and *M. immaculata* (see diagnosis table 3). It differs of the two other *Sinomacropis*, *M. micheneri* and *M. omeiensis*, by the short and sparse hairs on T2-4 while the latter species have the terga densely covered with yellowish laying pilosity. **Males.** Unknown.

**Description. Females.** *Length:* 10 mm. *Head:* Cuticle dark. Flagellum ventral face reddish. Labrum smooth. Malar space very short. Clypeus densely punctured, space between punctures smaller than one diameter; the surface convex, shiny (though lightly chagrinated); apex truncated. Face and vertex densely punctured, smooth and shiny between punctures. Inner eye margins subparallel. Face and vertex with pale hairs. Clypeus and genae with dark hairs. Vertex posterior margin with a fringe of dark hairs. *Mesosoma:* Cuticle dark, punctured and shiny. Propodeal triangle with a small smooth medio-basal part. Scutum, scutellum, Tb1 and Bt2 outer face, as well as Bt3 inner face with brown pilosity. Margins of the scutum and lateral margins of the scutellum, postscutellum (=metanotum), propodeum and Tb3 with whitish pilosity. Mesosoma ventral face with yellowish hairs, as well as Tb2 outer face and 2sd tarsus. Bt3 outer face with an apical black hairs fringe. Tb2 with a row of strong yellow bristles on inner face. F1-3 and Tb1-2 inner faces hairless. **Metasoma:** Sterna and T1-2 orangish, the other segments black. T1 unpunctured. Proximal part of T2-5 finely punctured. T2 margin medially as long as the proximal part. Pilosity scarce. T1-2 margins hairless. T3-4 margins with brown hairs. Anal fringe medially brown, laterally whitish. S2-4 with an apical fringe of yellowish hairs. S5 with brownish pilosity. **Males.** unknown.

**Distribution** (Fig. 33). Laos.

***Macropis (Sinomacropis) micheneri* Wu 1992**

*Macropis (Sinomacropis) micheneri* Wu 1992: 1387-1388 (♂/♀). *Locus typicus:* Yongshenludai (China)

**Distribution.** China (Sichuan, Zhejiang).

***Macropis (Sinomacropis) omeiensis* Wu 1965**

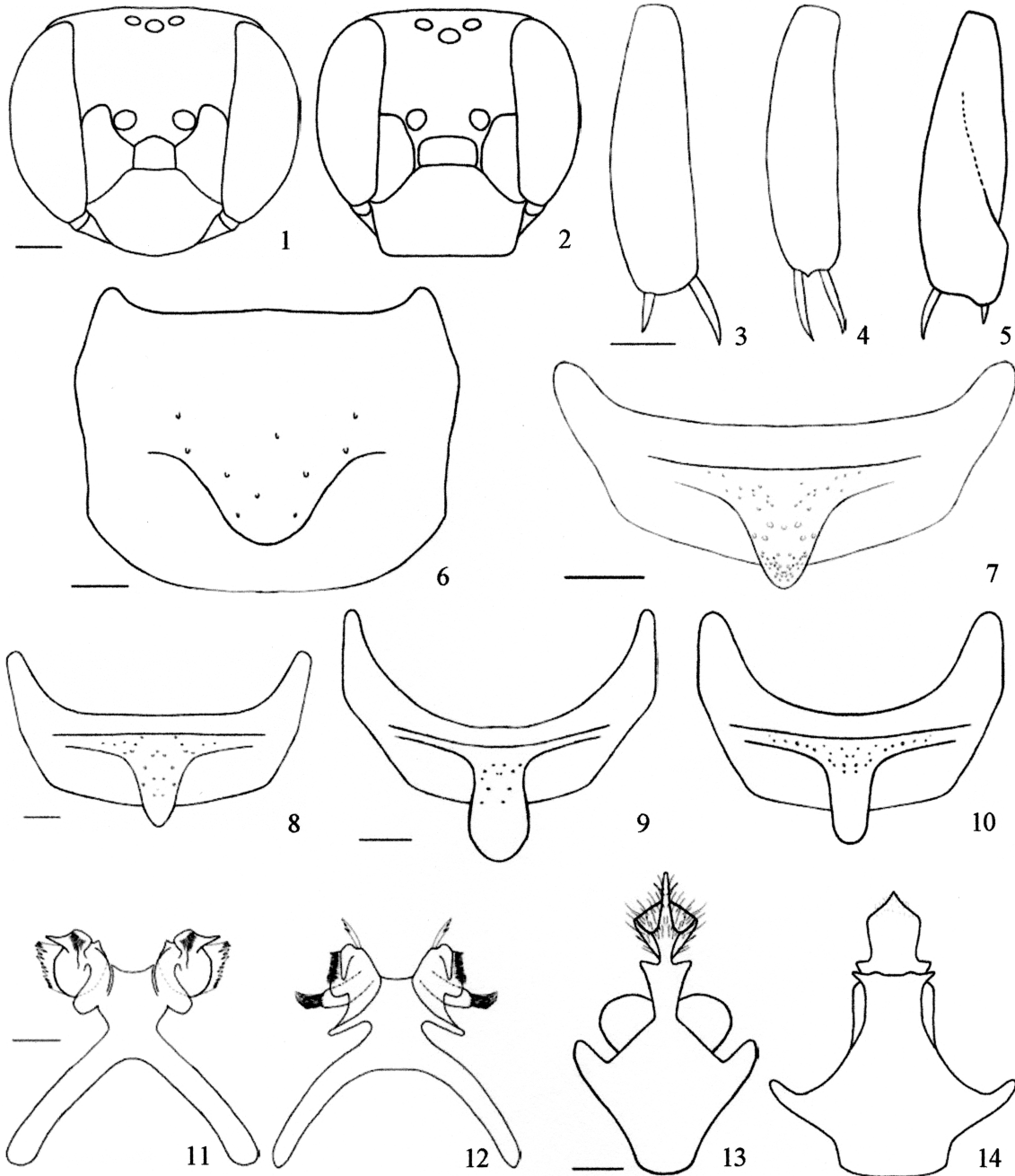
*Macropis (Sinomacropis) omeiensis* Wu 1965: 596-597 (♂/♀). *Locus typicus:* "Mt. Omei" (China).

**Distribution** (Fig. 33). China (Sichuan, Zhejiang).

**Key to species**

1. Female vertex enlarged behind the ocelli, with a terminal pre-occipital angular carina. Male S6 apical process truncated. S8 apical process wider than the base; densely covered with long hairs. Gonostylus simple and slender. China, Russia . . . ***M. (Paramacropis) ussuriana* (Popov)**
  - Female vertex narrow, without carina. Male S6 apical process reduced. S8 apical process narrower than the base; tapered and less hairy (Figs. 13-14). Gonostylus apex enlarged and bilobate (Figs. 17-22). Holarctic . . . **2**
2. Propodeal triangle punctured, hairy, except a small median part. Females T4 margin with a continuous fringe of brownish hairs. Clypeus margin of male slightly truncated or emarginated (Fig. 2). Male eyes with inner margins sub-parallel (Fig. 2). Male Pp shorter than the T6 anterior part (Fig. 6). S8 without apical tooth and median circular structure (Fig. 14). Gonocoxites apically truncated. China . . . ***M. (Sinomacropis): 3***
  - Propodeal triangle unpunctured, smooth or rough, hairless (Fig. 24). Females T4 margin with a continuous fringe of whitish hairs. Clypeus apical margin of the male convex (Fig. 1). Inner margins of eyes in male converging dorsally (Fig. 1). Males Pp longer than the T6 anterior part (Figs. 7-10). S8 with 2 median circular structures; ending in an apical tooth (Figs. 13, 15 and 16). Apex of gonocoxite acute (Figs. 6 and 17-22). Holarctic . . . ***M. (Macropis): 11***
3. Antennae 13-segmented. Scopae absent. Clypeus at least partly yellow . . . **Males: 4**

- Antennae 12-segmented. Scopae well developed. Clypeus dark ..... **Females:** 7
- 4. Mesotarsus of normal length; the 4th article as long as wide. 8-9 mm ..... **5**
- Mesotarsus elongated; the 4th article longer than wide. 9-10 mm ..... **6**
- 5. Clypeus apical margin straight. Supraclypeus and face lateral marks contiguous. Bt3 narrow and lightly hollow. China ..... ***M. bedini* Alfken**



**Figures 1-14**

Males faces (scale: 1 mm). 1, *Macropis (Macropis) fulvipes*. 2, *M. (Sinomacropis) immaculata*.

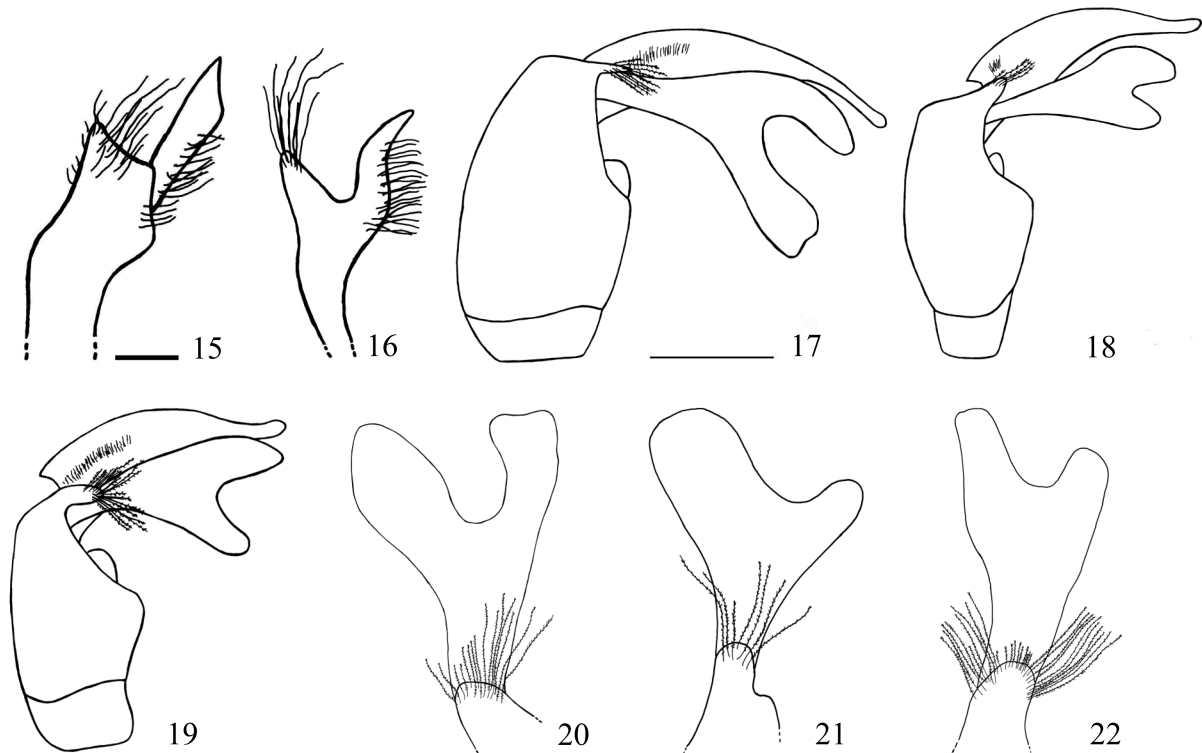
Males Tb3 (scale: 0,5 mm). 3, *M. (Macropis) europaea*. 4, *M. (Macropis) frivaldszkyi*. 5, *M. (Macropis) fulvipes*.

Males pygidial plate (scale: 0,5 mm). 6, *M. (Sinomacropis) immaculata*. 7, *M. (Macropis) ciliata*. 8, *M. (Macropis) europaea*. 9, *M. (Macropis) frivaldszkyi*. 10, *M. (Macropis) fulvipes*.

Males S7 (scale: 0,4 mm). 11, *M. (Macropis) fulvipes*. 12, *M. (Sinomacropis) immaculata*.

Males S8 (scale: 0,3 mm). 13, *M. (Macropis) frivaldszkyi*. 14, *M. (Sinomacropis) immaculata*.

- Clypeus apical margin lightly emarginated. Supraclypeus and face lateral marks not contiguous. Bt3 wide and widened along its inner face. China . . . *M. micheneri* Wu
- 6. Bt3 nearly 3 times longer than wide, apex narrowed. Terga deeply punctured. T2-4 basally and distally strongly depressed. S7 with 2 discoidal apico-lateral process. China . . . . . *M. omeiensis* Wu
- Bt3 2 times longer than wide, apex truncated. Terga finely and sparsely punctured. Terga not depressed basally or apically. S7 with 2 spiny 2 narrow apico-lateral process (Fig. 12). China . . . . . *M. immaculata* Wu
- 7. T2-4 densely covered of semi-erected yellowish hairs . . . 8
- T2-4 with short and sparse pilosity; the apical margin with dense whitish pilosity covering partially the T3-4 basis . . . . . 9
- 8. Hind legs with white pilosity. T5 partly (less than half of its length) reddish-yellow. T6 black. 9-11 mm. China . . . . . *M. omeiensis* Wu
- Hind legs with yellow hairs (hairs tip black). One half of T5 reddish yellow. T6 reddish yellow. 9-11 mm. China . . . . . *M. micheneri* Wu
- 9. Supraclypeal area with a yellow mark. Propodeal dorsal area with a median smooth, unpunctured, shiny and hairless stripe. 8 mm. China . . . . . *M. hedini* Alfken
- Supraclypeal area dark. Only one small medio-basal area of the propodeal dorsal area unpunctured, smooth, shiny and hairless. 9-10 mm. China . . . . . 10
- 10. Bt1 with yellowish pilosity. Bt3 with pale hairs. F1 cuticle partly orange. Anal fringe yellowish. T2 margin, medially shorter than the tergum proximal part. China. . . . . *M. immaculata* Wu
- Bt1 with brownish pilosity. Bt3 inner face with brownish pilosity; the outer with a black hairs fringe. F1 cuticle dark. Anal fringe brown medially; the lateral parts whitish. T2 margin medially as long as the tergum proximal part. Laos . . . . . *M. orientalis* sp. nov.
- 11. Antennae 13-segmented. Scopa absent. Clypeus at least partly yellow . . . . . **Males: 12**
- Antennae 12-segmented. Scopa well developed. Clypeus dark . . . . . **Females: 20**
- 12. Pp at least 4 times longer than the proximal part of T6 (Figs. 8-10). Propodeal triangle rough, charginated and wrinkled (excepted in *M. frivaldszkyi*). Usually large species, 9-11 mm (excepted *M. dimidiata*, 8-9 mm). Palaearctic . . . . . 13
- Pp mostly 3 times longer than the proximal part of T6 (Fig. 7). Propodeal triangle smooth and shiny. Usually smaller species, 7-9 mm. Nearctic . . . . . 17



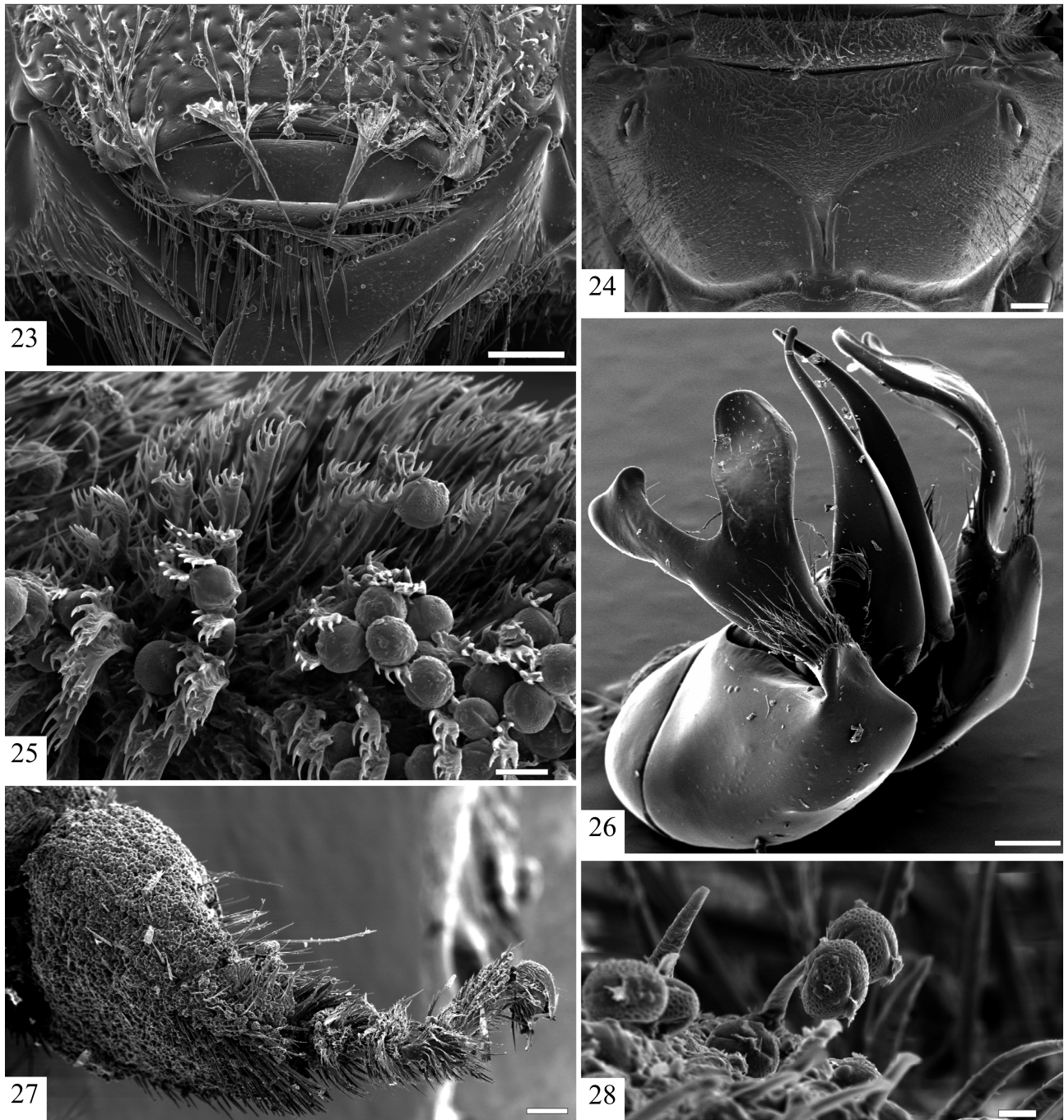
**Figures 15-22**

Male S8 apex (scale: 0,5 mm). 15, *Macropis (Macropis) frivaldszkyi*. 16, *M. (Macropis) fulvipes*.

Left lateral view of male genitalia (scale: 1 mm). 17, *M. (Macropis) europaea*. 18, *M. (Macropis) frivaldszkyi*. 19, *M. (Macropis) fulvipes*.

Left gonostylus, dorsal view of male genitalia (scale: 1 mm). 20, *M. (Macropis) europaea*. 21, *M. (Macropis) frivaldszkyi*. 22, *M. (Macropis) fulvipes*.





Figures 23-26

*Macropis europaea*. 23, labrum ♀ (scale = 200 µm). 24, propodeum ♀ (scale = 100 µm). 25, setae of protarsus ♀ with pollen of *Lysimachia vulgaris* (scale = 10 µm).

26, genitalia ♂ (scale = 200 µm).

*Macropis frivaldszkyi*. 27, metabasisarsus ♀ (scale = 200 µm). 28, setae of metabasisarsus with pollen of *Lysimachia* sp. (scale = 10 µm).

13. F3 and Tb3 with apical yellow markings. 9-10 mm.  
 Japan . . . . . *M. tibialis* Yasumatsu & Hirashima  
 – F3 and Tb3 dark. 8-11 mm. China, Japan and W-Palae-  
 arctic . . . . . 14

14. A smooth, well-defined, subtriangular area in front of  
 mid ocellus. Posterior margin of vertex with a sharp edge.  
 8-9 mm. China and Japan . . . . .  
 . . . . . *M. dimidiata* Yasumatsu & Hirashima

Table 4 – Floral choices of the *Macropis* ♀. The number of specimens is indicated in brackets, + = qualitative data (number of specimens undefined in references)

<i>Macropis</i>	Distribution	<i>Lysimachia</i> visited	Others floral choice	References
<b>Subgenera <i>Macropis</i></b>				
<i>M. ciliata</i>	Nearctic	<i>L. (Selenacia) ciliata</i> L. (+); <i>L. (S.) quadrifolia</i> L. (+)	Anacardiaceae: <i>Rhus glabra</i> L. (+); <i>Rhus typhina</i> L. (+). Apiaceae: <i>Archangelica hirsuta</i> Torr. & Gray (+). Apocynaceae: <i>Apocynum</i> sp. (+). Hydrangeaceae: <i>Hydrangea</i> sp. (+); Rhamnaceae: <i>Ceanothus americanus</i> L. (+); Rubiaceae: <i>Houstonia</i> sp. (+)	Patton (1880), Snelling & Stage (1995)
<i>M. nuda</i>	Nearctic	<i>L. (S.) ciliata</i> (+)	Apocynaceae: <i>Apocynum androsaemifolium</i> L. (+). Araliaceae: <i>Aralia hispida</i> Vent. (+). Asteraceae: <i>Lactuca pulchella</i> (Pursh) DC (+). Ericaceae: <i>Vaccinium</i> sp. (+). Geraniaceae: <i>Geranium</i> sp. (+). Rosaceae: <i>Rubus</i> sp. (+). Rhamnaceae: <i>Ceanothus americanus</i> (+)	Rozen & Jacobson (1980), Snelling & Stage (1995)
<i>M. patellata</i>	Nearctic	<i>L. (S.) ciliata</i> (+)	–	Patton (1880)
<i>M. steironematis</i>	Nearctic	<i>L. (S.) ciliata</i> (+); <i>L. (S.) lanceolata</i> (+); <i>L. (S.) quadriflora</i> (+)	Apocynaceae: <i>Apocynum cannabinum</i> L. (+). Asteraceae: <i>Seriocarpus</i> sp. (+). Fabaceae: <i>Melilotus alba</i> Medicus (+). Rhamnaceae: <i>Ceanothus americanus</i> (+)	Simpson et al. (1983), Snelling & Stage (1995)
<i>M. dimidiata</i>	East-Palaearctic	<i>L. (Lysimachia) vulgaris</i> <i>sp. danuvica</i> (5)	–	Yasumatsu & Hirashima (1956)
<i>M. tibialis</i>	East-Palaearctic	–	Polygonaceae: <i>Reynoutria</i> sp. (1)	Yasumatsu & Hirashima (1956)
<i>M. europaea</i>	West-Palaearctic	<i>L. (L.) vulgaris</i> L. (72)	Apiaceae: <i>Angelica sylvestris</i> L. (+). Asteraceae: <i>Aster tripolium</i> L. (1); <i>Bidens tripartita</i> L. (1); <i>Cirsium arvense</i> (L.) Scop. (2); <i>Eupatorium cannabinum</i> L. (1); <i>Lactuca sibirica</i> (L.) Maxim. (+); <i>Taraxacum</i> sp. (+). Caryophyllaceae: <i>Stellaria graminea</i> L. (+). Euphorbiaceae: <i>Euphorbia</i> sp. (1). Fabaceae: <i>Lotus</i> sp. (1); <i>Melilotus</i> sp. (1). Geraniaceae: <i>Geranium palustre</i> L. (+). Lamiaceae: <i>Lycopus</i> sp. (10); <i>Lycopus europaeus</i> L. (+); <i>Meniba</i> sp. (4); <i>Mentha arvensis</i> L. (+); <i>Stachys sylvatica</i> L. (+); <i>Thymus pulegioides</i> L. (+). Onagraceae: <i>Epilobium</i> sp. (1). Ranunculaceae: <i>Ranunculus repens</i> L. (+). Rhamnaceae: <i>Frangula alnus</i> Miller (1). Rosaceae: <i>Filipendula ulmaria</i> (L.) Maxim. (+); <i>Potentilla palustris</i> (L.) Scop. (+); <i>Rubus</i> sp. (1). Scrophulariaceae: <i>Scrophularia nodosa</i> L. (+)	Cavro (1950), Elfving (1968), Erdanson (1960), Litt (1998), Petit (1977), Phipps (1948), Original data
<i>M. fulvipes</i>	West-Palaearctic	<i>L. (L.) vulgaris</i> (+, 61); <i>L. (L.) nummularia</i> L. (+, 3); <i>L. (L.) punctata</i> L. (+)	Asteraceae: <i>Cirsium arvense</i> (L.) Scop. (1). Boraginaceae: <i>Myosotis</i> sp. (+). Geraniaceae: <i>Geranium</i> sp. (+). Lamiaceae: <i>Lycopus europaeus</i> L. (+). Lythraceae: <i>Lythrum</i> sp. (3). Malvaceae: <i>Malva moschata</i> L. (1). Rosaceae: <i>Potentilla palustris</i> (L.) Scop. (+). Scrophulariaceae: <i>Scrophularia nodosa</i> L. (+)	Elfving (1968), Gogala (1994), Litt (1998), Simpson et al. (1983), Original data
<b>Subgenera <i>Paramacropis</i></b>				
<i>M. ussuriana</i>	East-Palaearctic	–	Fabaceae (3)	Wu & Michener (1986)
<b>Subgenera <i>Sinomacropis</i></b>				
<i>M. bredini</i>	East-Palaearctic	<i>L. (L.) congestiflora</i> Hemsley (6); <i>L. (L.) triantuboides</i> Hemsley (6)	Caryophyllaceae: <i>Stellaria</i> sp. (1)	Wu (1965)
<i>M. immaculata</i>	East-Palaearctic	<i>L. (L.) congestiflora</i> Hemsley (14); <i>L. (L.) triantuboides</i> Hemsley (35)	Rosaceae: <i>Rubus</i> sp. (34)	Wu (1965)

- Face entirely punctured. Posterior margin of vertex somewhat rounded. 9-11 mm. West-Palaeartic . . . . . 15
15. Propodeal triangle smooth and shiny. Mandible dark. Supraclypeal area dark. Legs 2-3 outer sides with dense yellow pilosity. Margin of T3 continuously hairy. Pp reddish, enlarged medio-apically (Fig. 9). Bt3 inner face with a stripe of strong yellowish hairs; with a small hairless area. Tb3 apex medially toothed; spurs of equal lengths (Fig. 4). Penis valves with a small patch of yellow pilosity (Fig. 18). 9-10 mm. Central and Eastern-Europe . . . . . *M. frivaldszkyi* Mocsary
- Propodeal triangle mat, chagrinated and wrinkled. Mandibles with at least a basal yellow spot, at most half of basal part yellow. Supraclypeal area yellow. Legs 2-3 outer sides hairless. Margin of T3 discontinuously hairy. Pp dark, not enlarged medio-apically (Figs. 8-10). Bt3 inner face with a strong black hairs stripe, hairless elsewhere. Tb3 apex without tooth; spurs of different lengths (Figs. 3 and 5). Penis valves with a stripe of yellow hairs at least on the first third (Figs. 17 and 19). 10-11 mm. Central and Eastern Europe . . . . . 16
16. Base of mandible yellow. Labrum yellow. Tb3 apex with a subtriangular flattened tooth; spurs of varied lengths (Fig. 5). Pp narrow (Fig. 10). Basitibial plate sometimes yellow. Bt3 untoothed. S8 apex with a well-developed outer tooth (Fig. 16). Gonostylus emargination shorter than 1/3 of the length (Fig. 22). Palaeartic . . . . . *M. fulvipes* (Fabricius)
- Base of mandible with only a small yellow spot. Labrum dark, sometimes with a little median yellow spot. Tb3 apex untoothed; spurs of nearly equal length (Fig. 3). Pp basally enlarged (Fig. 8). Basitibial plate dark. Bt3 with a flattened inner tooth. S8 apex with a weak outer tooth. Gonostylus emargination longer than 1/3 of its length (Fig. 20). Europe . . . . . *M. europaea* Warncke
17. Terga dull; punctures coarse and distinct, separated by less than the diameter of one puncture. 9 mm. USA . . . . . *M. steiromacropis* Robertson
- Terga smooth; punctures minute and scattered, separated by more than one puncture diameter. 7 mm . . . . 18
18. Surpaclypeal and lateral face marks reduced or absent. Metatibia without distal tooth-like processes on inner surface and both apical spurs normally developed. Gonocoxite apex mostly 3 times longer than wide. Canada and USA . . . . . *M. nuda* (Provancher)
- Face mostly yellow below level of antennal sockets. Metatibia with one or two distal tooth-like processes on its inner side at the base of apical spurs; one or both apical spurs reduced. Gonocoxite apex more than 4 times longer than wide . . . . . 19
19. Metatibia with two tooth-like distal processes and both spurs reduced. Labrum dark. Gonocoxite apex hairless. Canada and USA . . . . . *M. ciliata* Patton
- Metatibia with one tooth-like distal process and only outer spur reduced. Labrum pale. Gonocoxite apex hairy. USA . . . . . *M. patellata* Patton
20. Propodeal triangle chagrinated, wrinkled, mat (excepted by *M. frivaldszkyi*). Palaeartic . . . . . 21
- Propodeal triangle smooth and shiny. Nearctic . . . . . 25
21. Anal fringe yellow. Propodeal triangle smooth and shiny. T3 margin entirely covered of whitish pilosity. Cuticle smooth and shiny between the antennal sockets. Central and Eastern-Europe . . . . . *M. frivaldszkyi* Mocsary
- Anal Fringe brownish with some white hairs laterally. Propodeal triangle chagrinated and wrinkled, mat. T3 margin covered with whitish pilosity; medially hairless. Cuticle punctured between antennal sockets. Palaeartic . . . . . 22
22. A smooth, well-defined, sub-triangular space in front of mid-ocellus. Anal fringe whitish. Tb3 apex with black hairs. Clypeus sparsely hairy. 9 mm. China and Japan . . . . . *M. dimidiata* Yasumatsu & Hirashima
- Area in front of mid-ocellus punctured. Anal fringe black with white lateral hairs. Tb3 with apical white pilosity. Clypeus densely hairy. 10-11 mm. Japan and W-Palaeartic . . . . . 23
23. Propodeal triangle with transverse wrinkles. Clypeus flat. Japan . . . . . *M. tibialis* Yasumatsu & Hirashima
- Propodeal triangle with irregular rugae. Clypeus convex. West-Palaeartic . . . . . 24
24. Tb2 with brown pilosity. Tb3 with white hairs. Bt3 inner face with black pilosity. T4 densely punctured. Post-scutellum with brown pilosity on apical margin. Europe . . . . . *M. europaea* Warncke
- Tb2, Tb3 and Bt3 inner face with yellow pilosity. T4 lesser punctured. Postscutellum pilosity usually whitish. Palaeartic . . . . . *M. fulvipes* (Fabricius)
25. Terga dull; punctures coarse and distinct, separated by less than the diameter of one puncture. 9 mm. USA . . . . . *M. steiromacropis* Robertson
- Terga smooth; punctures minute and scattered, separated by more than one puncture diameter. 7 mm . . . . . 26
27. Clypeus densely punctured; punctures separated by less than one diameter; cuticle not strongly shiny between punctures. Propodeum posterior face with punctures deep and distinct mostly separated by one puncture diameter or less. Process of labrum low, inconspicuous and weakly carinate. USA . . . . . *M. patellata* Patton
- Clypeus shiny between the distinctly separated punctures; some interspaces as large as, or larger than, one puncture diameter. Posterior face of propodeum mostly smooth and shiny, with sparse, obscure, fine punctures. Process of labrum high, conspicuous, convex and strongly carinate . . . . . 27
27. Bt2-3 outer face with brownish pilosity. Anterior rim of propodeal triangle roughened and with fine, oblique rugules. Canada and USA . . . . . *M. nuda* (Provancher)
- Bt2-3 outer face with whitish pilosity. Anterior rim of propodeal triangle smooth and shiny, at least across middle one-third. Canada and USA . . . . . *M. ciliata* Patton

## DISCUSSION

### Systematic

The present revision, based on the morphological study of 2 200 specimens, validates the subdivision of the genus *Macropis* into three subgenera: *Macropis*, *Para-*

*macropis* and *Sinomacropis*, as proposed by Michener (1981). Numerous male characters support this classification (table 2). The females are usually less distinct. Nevertheless, they can easily be included to their respective subgenera on the basis of such characters as the sculpture of the propodeum, the basal vein shape, the metabasitarsus and the labrum (table 2).

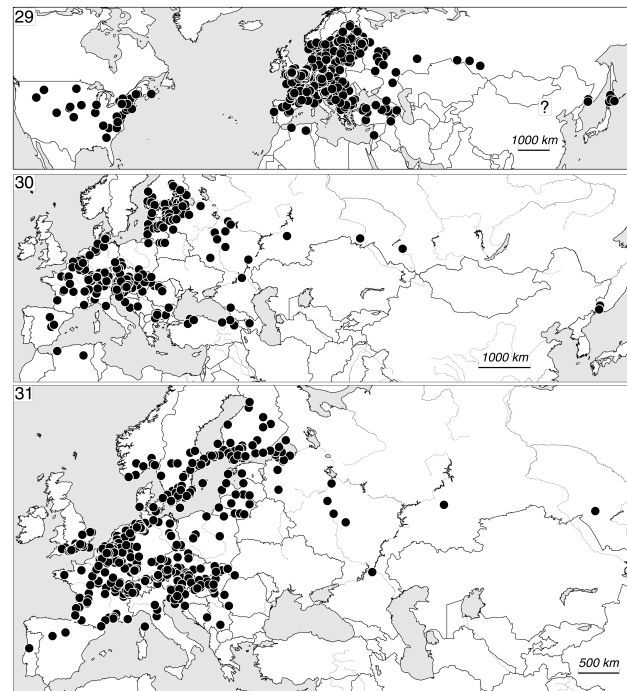
On the basis of the same characters, *M. orientalis* sp. nov. can easily be placed in *M. (Sinomacropis)* with the four other species previously described. Like indicated in tables 2, 3 and the *M. orientalis* description, this latter species displays most of the diagnostic characters for the subgenus. *M. orientalis* differs mainly of the other *M. (Sinomacropis)* by the legs pilosity development and cuticle coloration (see description).

### Biogeography

The genus *Macropis* is distributed in the Holarctic region. It includes two large disjunctions: one centred on the Yellow Sea and the second on the Atlantic. In East-Palaearctic, *M. (Paramacropis)* are distributed Northern the Yellow Sea and *M. (Sinomacropis)* Southern (Fig. 33). This disjunction and taxonomical divergence looks like the consequence of a possible allopatry due to ancient changes in local climates. This biogeographical scheme fits well to the description of the Asian diversity centres and refugia by varied authors (De Lattin 1967). Regarding the Atlantic disjunction, it was recently displayed that *Macropis* evolved early during the Tertiary period (Engel 2001; Michez *et al.*, *submitted*). At that time, there were opportunities for transatlantic migrations and population exchanges between the Western and Eastern Hemisphere. Migrations were most likely through the Bering strait or across the Atlantic. Other bee groups show similar interchanges between North America and Eurasia including the andrenid and halictid genera *Panurginus* Nylander 1848, *Halictus* Latreille 1804 and *Lasioglossum* CURTIS, 1833 e.g. (Michener 2000; Patiny 2003)

The subgenus *Macropis* is also exclusively Holarctic (Fig. 29). One can consider three well-distinct species groups. First, the Western Old-World group distributed in West-Palaearctic and extending Eastern since Altaj (Russia), Northern Kazakhstan. This latter species-group includes 3 species. Second, the Asian group, which includes the 3 Chinese, East-Siberian and Japanese species. Third, the Nearctic group includes 4 species mainly distributed along the eastern portions of the USA and Canada. The new records of *M. fulvipes* specimens caught in two Algerian localities shows that the subgenus also exists in North-Africa (Fig. 30).

The subgenus *Sinomacropis* is East-Palaearctic (Fig. 33). The *M. orientalis* locus typicus is one of the



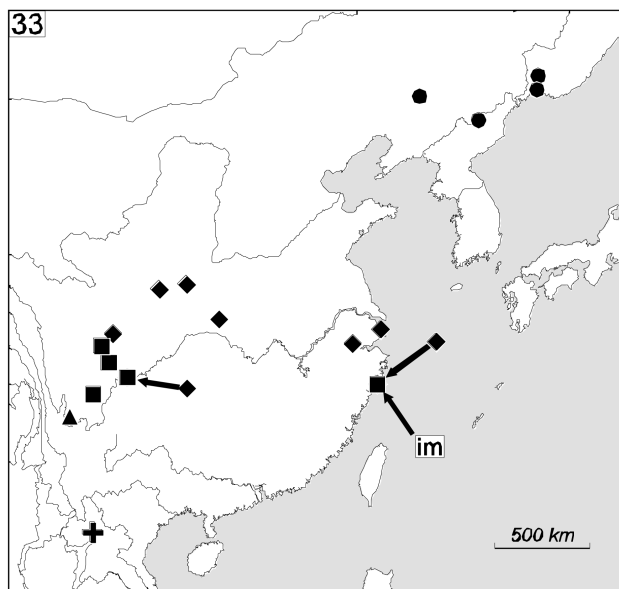
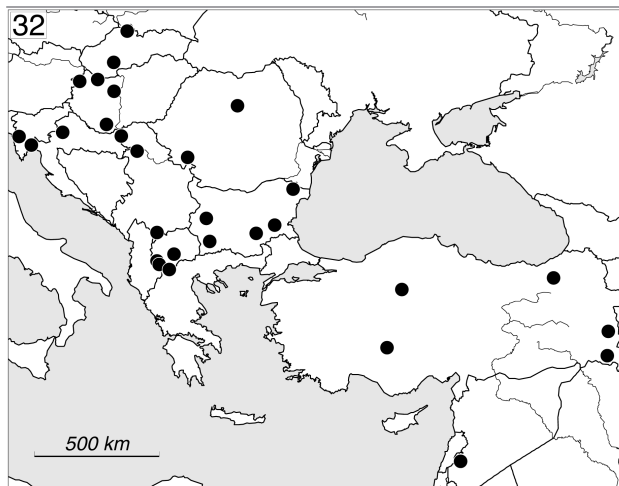
**Figures 29-31**  
Distribution. 29, subgenus *Macropis*. 30, *M. (Macropis) fulvipes*. 31, *M. (Macropis) europaea*.

most Southern locations of the known distribution of the genus. Others *Sinomacropis* are mostly distributed to the North of the Yangtze river (25°N) and the subgenus was previously not known from South-East Asia.

### Floral choices

The literature overview and our study of the pollen confirm that *Macropis* is oligolectic on *Lysimachia* (table 4; Figs 25, 27 and 28). In any part of their distribution, *Macropis* forage on *Lysimachia* for pollen and oils (one can see the tricolpored pollen of *Lysimachia* on Figs 25, 27 and 28). *Macropis* females appear to collect nectar from a wide variety of host plants (Pekkarinen *et al.* 2003; table 4).

Moreover, the data points out the vicariance in the floral choices of bees between the Western and Eastern Hemisphere populations (table 4). In the Eastern Hemisphere, the bees are seemingly monolectic on *Lysimachia* s. str., while they are exclusive on the subgenus *Seleucia* in North America (although the two plant subgenera are sympatric in this latter area). This behavioural divergence can actually not be explained on the basis of the available informations.



- *Macropis (Paramacropis) ussuriana*
- ◆ *Macropis (Sinomacropis) hedini*
- ▲ *Macropis (Sinomacropis) micheneri*
- *Macropis (Sinomacropis) omeiensis*
- + *Macropis (Sinomacropis) orientalis*
- im *Macropis (Sinomacropis) immaculata*

Figures 32-33

Distribution. 32, *M. (Macropis) frivaldszkyi*. 33, subgenera *Paramacropis* and *Sinomacropis*.

**Acknowledgements.** The authors want to thank the numerous peoples who give them a free access to the studied collections: Dr R. Danielsson (Lund, Sweden), Mme A. Freitag (Lausanne, Switzerland), Dr G. Else (London, UK), Dr P. Grootaert (Brussel, Belgium), Prof C. Gaspar (Gembloux, Belgium), Mag F. Gusenleitner (Linz, Austria), Dr W. Hogenes (Amsterdam, Netherlands), Mme G. Lachaise (Paris, France); Mr. J. Matter (Strasbourg, France), Dr. B. Merz (Genève, Switzerland), Prof P. Rasmont (Mons, Belgium), M. Roberts (Salisbury, UK), M. S. Schmidt (Munich, Germany), Dr S. Schoedl (Vienne, Austria),

Dr. O. Tadauchi (Fukuoka, Japon), Dr C. van Achterberg (Leiden, Netherlands), Dr L. Vilhelmsen (Copenhagen, Denmark), Dr C. Villeman (Paris, France). Sincerely thanks to Prof. B.N. Danforth (Ithaca, USA) for kindly proofreading the English and his remarks on the final text. Thanks to Prof. C. D. Michener for this help to find locus typicus. Thanks also to Prof. P. Rasmont and Dr. M. Terzo for their second reading. Thanks to S. Iserbyt for the management of the Gembloux-Mons databank. During first year of this research preparation D. Michez was granted by FRIA (Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture). S. Patiny is a FNRS (Fonds national de la Recherche Scientifique) scientific collaborator.

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