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A. Roques & M. Skrzypczyńska

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Seed-infesting chalcids of the genus *Megastigmus* Dalman, 1820 (Hymenoptera: Torymidae) native and introduced to the West Palearctic region: taxonomy, host specificity and distribution

A. ROQUES† and M. SKRZYPCZYŃSKA‡

†*Institut National de la Recherche Agronomique, INRA-CRF Zoologie Forestière, Ardon, F-45160 Olivet, France*
‡*Academy of Agriculture, Al. 29 Listopada 46, 31-425, Kraków, Poland*

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A total of 21 species (including one new to science) of *Megastigmus* seed chalcids are recognized in Europe, North Africa and Asia Minor. From 1977 to 2001, 5260 seed samples were collected from a total of 118 tree and shrub species. *Megastigmus* spp. were found in 29 of the native conifers of genera *Abies*, *Cedrus*, *Cupressus*, *Juniperus*, *Larix* and *Picea*, in 43 of the exotic conifer species introduced to Europe, in 28 species of Rosaceae (*Amelanchier*, *Rosa*, *Sorbus*) and in nine species of Anacardiaceae (*Pistacia*, *Schinus*). Fifteen species develop in seeds of conifers whilst six infest the seeds of Angiosperms. Thirteen of the chalcid species are considered to be native. The other species were probably introduced from North America (seven species) and South Africa (one species) along with seeds. Chalcid specificity and evolutionary relationships with host species are discussed. Illustrated keys to males and females are presented, followed by a detailed description of species morphology, host range and distribution. A list of *Megastigmus* seed chalcids at risk of introduction from other world regions is provided, along with the host plants to be surveyed.

KEYWORDS: *Megastigmus*, taxonomy, distribution, seed damage, conifers, *Rosa*, *Pistacia*, *Sorbus*.

Introduction

World-wide development of tree improvement programmes, especially the establishment of seed orchards to produce genetically improved seeds, focused new attention on insects infesting cones and seeds (Turgeon *et al*., 1994). Among them, seed chalcids of the genus *Megastigmus* Dalman (Chalcidoidea: Torymidae) proved to be serious pests of conifer species (Keen, 1958; Lessmann, 1974a, 1974b; Stadnickii *et al*., 1978; Hedlin *et al*., 1980; Roques, 1983; Jarry *et al*., 1996). Within this genus, four basic feeding types have been recognized: those that feed strictly within tree seeds; facultative parasitoids that require a gall-former but feed on plant tissue within the gall as well; obligate egg-larval or larval parasitoids of gall-forming Hymenoptera; and gall-formers (Grissell, 1999). However, Bouček (1988) suggested that the entomophagous species, which differ noticeably in having a metallic gloss,

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should be transferred to the genus *Bootanomyia* Girault. Also, some of the species considered strictly phytophagous actually induce a gall-like development of the seeds and may be considered as gall-makers (Rouault, 1998).

In his recent catalogue of world Megastigminae, Grissell (1999) recognized 126 species of *Megastigmus* of which 59 are obligate seed feeders. Most of them develop in seeds of the plant families Pinaceae and Rosaceae, but hosts also include conifers of the families Cupressaceae and Taxodiaceae (Yates, 1986) and broad-leaved trees of families Anacardiaceae, Aquifoliaceae, Fabaceae and Hamamelidaceae (Milliron, 1949; Grissell, 1989; Narendran, 1994; Zerova and Seryogina, 1994; Noyes, 1998). However, it is likely that many species still remain to be discovered, especially in Asia where three more species have been recently identified in conifer seeds (Xu *et al*., 1998; Roques and Pan, unpublished data).

In Europe, a large number of works provided keys to species and listings of *Megastigmus* hosts (e.g. Seitner, 1916; Hoffmeyer, 1929, 1931b; Laidlaw, 1931; Escherich, 1938, 1942; Kangas, 1940; (Čermak, 1952; Nikol'skaya, 1952; Lessmann, 1962; Kapuściński, 1966; Nuorteva, 1967; Adamczyk *et al*., 1969; Bouček, 1970b; Nikol'skaya and Zerova, 1978; Schwenke, 1982; Jespersen and Lomholt, 1983; Roques, 1983; Křístek *et al*., 1992; Zerova and Seryogina, 1994; Jensen and Ochsner, 1999). However, many taxonomic uncertainties, regarding either insect species or hosts, have been transmitted over time, severely hindering the analysis of insect–host relationships (Turgeon *et al*., 1994). For example, the Douglas-fir seed chalcid, *M. spermotrophus* Wachtl, has long been recorded to attack seeds of *Abies* spp. (e.g. Čermak, 1952; Lessmann, 1962; Schwenke, 1982; Křístek *et al*., 1992) whilst the species has since been proved to develop only in those of *Pseudotsuga* spp. (Roques, 1988). There existed, therefore, a need to clarify the host range of seed chalcid species. Recently, the development of genetic studies dealing with *Megastigmus* spp. (Roux and Roques, 1996; Carcreff, 1996; Carcreff *et al*., 1998; Roques *et al*., 1999a) provided additional tools for confirming the separation between species as well as for defining the status of conspecific populations developing on different hosts.

Life-cycle features of seed chalcids tend to facilitate insect introduction and establishment in exotic countries. Larval development occurs entirely within a single seed, with a winter diapause that may extend to several additional years (Turgeon *et al*., 1994). Moreover, some species can develop in unfertilized seeds (Niwa and Overhulser; 1992; Rappaport *et al*., 1993; Rouault, 1998). Therefore, the international development of seed trading carries the risk of introduction of exotic chalcids with seed lots (Hussey, 1954a) when ineffective phytosanitary measures are applied at borders. Two newly introduced North American species have thus been recorded in continental Europe recently (Da Ros *et al*., 1993; Ochsner and Jensen, 1998).

The objectives of our study were: (1) to provide an overview of the phytophagous *Megastigmus* species native or introduced to the West Palearctic region, with a revised key including the newly introduced species; (2) to define host ranges and species distribution by carrying out surveys of damage to tree seeds in most countries of Europe and North Africa over the last 17 years; and (3) to identify the seed importations that are potential sources of accidental introduction of exotic seed chalcids that still remain absent from Europe.

Material and methods

Geographical limits of the study and literature review

Biogeographically, the area covered by the study corresponds to the West Palearctic Region; i.e. it includes the whole of Europe and Russia west to the Ural

Mountains, Asia Minor, Africa north of the Sahara and the islands in the Atlantic ocean (Canary Islands, Madeira and Iceland). A total of 345 references dealing with the presence of *Megastigmus* seed chalcids within this area were surveyed. In a few cases, the exact location of the record could not be ascertained within the newly established states resulting from the former Soviet Union, Yugoslavia and Czechoslovakia, respectively, and we only referred to the former Soviet Union, former Yugoslavia and former Czechoslovakia.

A computerized database including author's name, date of publishing, records of species distribution and host plants was compiled. Names of host plants follow Index Kewensis® (Oxford University Press, 1993). Authors names are included in the host plant lists given in tables 1–3 except when the original exotic hosts of introduced chalcids were not introduced or not attacked in the West Palearctic. In this latter case, authors' names are given within the text, in the host range section related to each chalcid species.

Insect collection and rearing

Taking into account the gaps and uncertainties that existed in the published data, an extensive survey was performed from 1977 to 2001. A total of 118 tree and shrub species, including both native and exotic species of conifers, Rosaceae and Anacardiaceae were surveyed. Collection and rearing methods were designed to ascertain the host species. Mature plant female reproductive structures (i.e. seed cones, berries, rose hips and fruits, according to plant species) of native species were collected all over Europe and North Africa. We personally collected samples in Austria (1992–1993), Bulgaria (1994–1996), Croatia (1989), the Czech Republic (1991), France (1978–2000), Germany (1991–1993), Greece (1991–1997), Italy (1991, 1994, 1998), Morocco (1999–2001), The Netherlands (1991–1992), Poland (1977–1997), Portugal (1993–2000), Slovakia (1991), Spain (2000–2001; Canary Islands, 1990), Sweden (2000), Switzerland (1989, 1999) and Tunisia (1986, 1995). At least 100 female reproductive structures were sampled on 10 trees per location whenever possible, cone crop level permitting. After a short drying period, the entire seed content of the cones was extracted manually. Additional cone and seed samples of various conifer species were obtained from 1991 to 2001 from colleagues in Albania, Algeria, Belgium, Bulgaria, Denmark, Finland, France, Greece, Hungary, Italy, Lithuania, Malta, Morocco, Portugal, Switzerland, Spain, Tunisia and Turkey. The French National Forestry Office (ONF) also supplied us with seed samples (1000 seeds per lot at least) from seed orchards and stands used for certified seed collection in France during 1992–1993, 1996 and 1998–2001. To assess the potential of seed chalcids to colonize exotic tree species introduced to Europe, special attention was given to two French arboreta, the 'Les Barres' arboretum and the 'Chèvreloup' arboretum, which are both located in north-central France (47°52′N, 2°48′E and 48°49′N, 2°07′E, respectively). Cone-bearing conifer species at the 'Les Barres' arboretum have been systematically sampled every year since 1982 whilst those at the 'Chèvreloup' arboretum were sampled only in 1992. ONF also provided some seed lots of exotic species before importation to France. Finally, a total of 5260 seed lots, corresponding to *ca* 970 000 seeds, were thus analysed.

All the seed lots were radiographed using a Faxitron-43855® apparatus (15 Kv, 3 mA, 3′30″ to 4′30″ depending on seed species) and X-ray sensitive films (Kodak® 'Industrex M'). The insect-infested seeds were placed in individual rearing boxes stored in an outdoor insectary located at INRA, Orléans, France (107 m elevation).

Adult emergence was recorded over the 5 years following seed maturation because of a possible prolonged diapause. It should be kept in mind that differences in altitude and climatic conditions between native and rearing sites can cause shifts in emergence dates. Most emerging adults were preserved in 70% or 100% alcohol (in view of further genetic analysis) but a few were kept dry in every lot. When no adults emerged at all because of prolonged diapause, we dissected some infested seeds to assess whether larvae were *Megastigmus* spp. or other seed insects, e.g. seed midges or *Eurytoma* seed chalcids. Collecting nets were also used to catch adult chalcids possibly ovipositing on cones.

Preparation and description of adults

Adult morphology was examined using a MZ12 Leica® stereomicroscope equipped with a Leica DC100® Digital Camera. Length of body, head, thorax and abdomen was measured on 50 dry specimens per species and sex (except on *M. nigrovariegatus* because of a low number of specimens) using QWIN® V2.3 image processing and analysis software. The length of the exserted part of the ovipositor and that of ovipositor sheaths was similarly measured on the same 50 females. Then the wings and antenna of both sexes and male genitalia were mounted on glass slides using Euparal®. Male genitalia were cleared in hot 70% potassium solution, then rinsed successively in 30%, 70%, 95% and 100% ethanol prior to mounting. Measurements of forewing stigma characteristics (stigma length, stigma maximal width, uncus length, length of upper part of stigmal vein) and of antenna parts were made as above. Specimens preserved in alcohol were used for scanning microscopy. They were critical-point dried prior to analysis. The head and thorax of at least five specimens per species and sex, and at least five ovipositors per female species were examined. After having been cut from the body, these parts were transferred to metal stubs with a fine brush moistened in water, and were then gold coated to be examined with a Cambridge Stereoscan® 90 scanning electron microscope equipped with Orion® image processing software. The images of head, thorax and ovipositor were stored in TIF format for examination and measurements.

Terms for body sculpture were consistent with those used by Bouček (1988). Terms for morphology follow Grissell (1995) and Gibson (1997). Figures 1–8 present external morphology of both sexes, the abbreviations following Gibson (1997). Terminology used to describe female ovipositors follows Copland and King (1972) and Quicke *et al.* (1994) whilst that used to describe male reproductive systems follows Gibson (1997). Figures 9 and 10 present reproductive systems of both sexes.

Comparison with type material

Whenever possible, type material was obtained using the depository information summarized by Noyes (1998) and Grissell (1999). When the type material was known to be destroyed, we designated a neotype to ensure nomenclature stability. Examination and measurements of body parts were made on dry specimens using the same image processing and analysis software. For the species thought to be introduced, additional specimens from the original areas were obtained for comparison from colleagues of the USA, Canada, Japan and China. The following list, alphabetical according to abbreviations employed, enumerates the depositories of the material examined: AR, collection of A. Roques, INRA-CRF, Olivet, France; BMNH, The Natural History Museum, London, UK; FIUG, Forstzoologischen

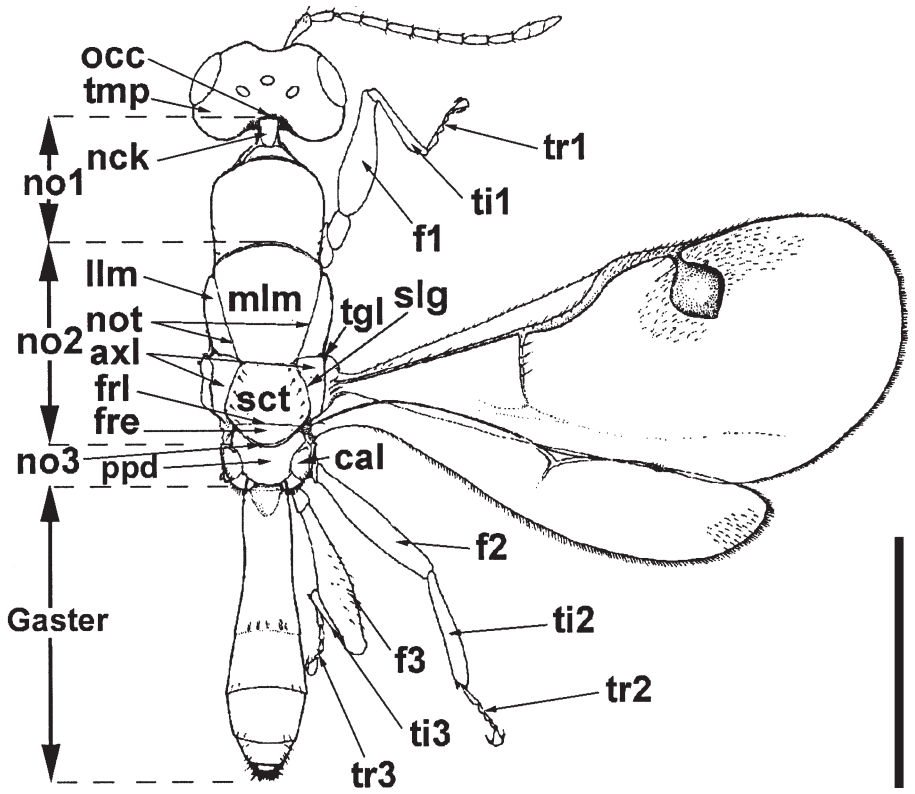


FIG. 1. Dorsal view of body, *Megastigmus amicorum* ♂, ex. *Juniperus phoenicea*, Portugal. axl, axilla; cal, callus; f_n, femur; fre, frenum; frl, frenal line; llm, lateral lobe of mesoscutum; mlm, mid lobe of mesoscutum; mv, marginal vein; nck, neck of pronotum; no_1, pronotum; no_2, mesonotum; no_3, metanotum; not, notaulus; occ, occipital carina; ppd, propodeum; sct, scutellum; slg, sublateral groove; ti_n, tibia; tgl, tegula; tmp, temple; tr_n, tarsi; unc, uncus. Scale bar = 1 mm.

Institutes der Universität Göttingen, Germany; GM, collection of Gordon Miller, Forestry Canada, Victoria, B.C., Canada; JPF, collection of J. P. Fabre, INRA, Avignon, France; MNHN, National Museum of Natural History, Paris; MS, collection of M. Skrzypczyńska, Academy of Agriculture, Kraków, Poland; NHMS, National History Museum Stockholm, Sweden; NHMK, Natural History Museum of Kraków, Poland; USNM, National Museum of Natural History, Washington, DC, USA; NMP, National Museum, Praha, Czech Republic; NMW, Naturhistorisches Museum, Wien, Austria; ZMUC, Zoologisk Museum, University of Copenhagen, Copenhagen, Denmark.

Results

Host–chalcid relationships

Megastigmus seed chalcids were observed in a total of 109 tree and shrub species growing in Europe, North Africa and Asia Minor (tables 1–3). Including literature data, we found 72 conifer hosts of which 29 were native and 43 were exotic species introduced in the West Palearctic region. Most of the surveyed Pinaceae belonging to genera *Abies*, *Picea* and *Larix* were infested by seed chalcids (table 1). In contrast,

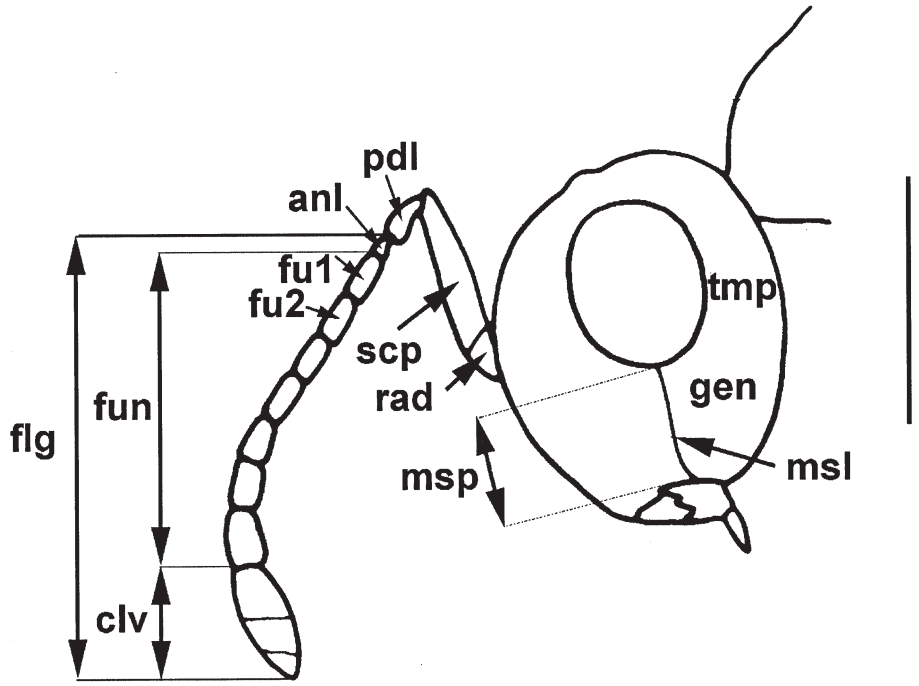


FIG. 2. Lateral view of head, *M. pictus* ♀, ex. *Larix decidua*, Poland. an, anellus; clv, clava; flg, flagellum; fun, funicle; fu_n, *n*th funicular segment; msl, malar sulcus; msp, malar space; pdl, pedicel; rad, radicle; scp, scape. Scale bar = 500 μm.

no native species of genus *Pinus* were attacked although chalcids were observed in the exotic *P. strobus*. Introduced species of genus *Tsuga* did not host any chalcid. Among Cupressaceae, seed chalcids developed in all the native *Cupressus* and *Juniperus*, as well as in a large part of the introduced species of these genera (table 2). No *Megastigmus* were observed in seeds of *Biota*, *Chamaecyparis*, *Cryptomeria* and *Thuja*. Among angiosperms, chalcids were recorded in 28 species of *Rosaceae* belonging to the genera *Rosa*, *Amelanchier* and *Sorbus*, and nine species of *Anacardiaceae* belonging to the genera *Pistacia* and *Schinus* (table 3).

We found a total of 21 *Megastigmus* species of which one, which was observed in the native range of *Cupressus atlantica* Gaussen in Morocco, is new to science (*M. atlanticus* sp. n.). Thirteen of these species were native of the West Palearctic range, the others originating from North America (*M. atedius* Walker, *M. milleri* Milliron, *M. nigrovariegatus* Ashmead, *M. pinus* Parfitt, *M. rafni* Hoffmeyer, *M. specularis* Walley, *M. spermotrophus* Wachtl) and South Africa (*M. transvaalensis* [Hussey]). *M. nigrovariegatus* and *M. transvaalensis* were observed for the first time in the region, on *Rosa* and *Schinus*, respectively. Three additional exotic species were recorded but their establishment needs confirmation. A few specimens of *M. borriesi* Crosby, a far-eastern species attacking firs (Kamijo, 1962), were reared from seeds of *Abies veitchii* Lindley collected in a Danish arboretum but not yet found on firs growing around (Ochsner, 1998; Jensen and Ochsner, 1999). *M. juniperi* Nikol'skaya, a species known to infest junipers in Central Asia (Nikol'skaya, 1966), was identified on *Juniperus excelsa* M. Bieb. in Turkey (Özkazanç, 1982) but it was not possible to check this identification during our study. Finally, individuals

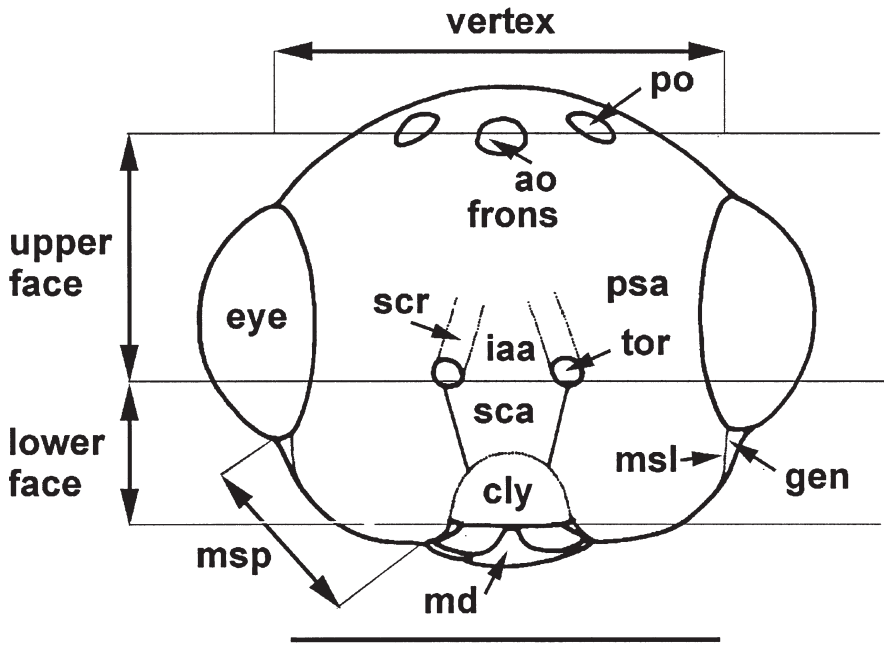


FIG. 3. Front view of head, *M. pictus* ♀, ex. *Larix decidua*, Poland. ao, anterior ocellus; cly, clypeus; gen, gena; iaa, interantennal area; msl, malar sulcus; msp, malar space; po, posterior ocellus; psa, parascrobal area; sca, supraclypeal area; scr, scrobe; tor, torulus. Scale bar = 1 mm.

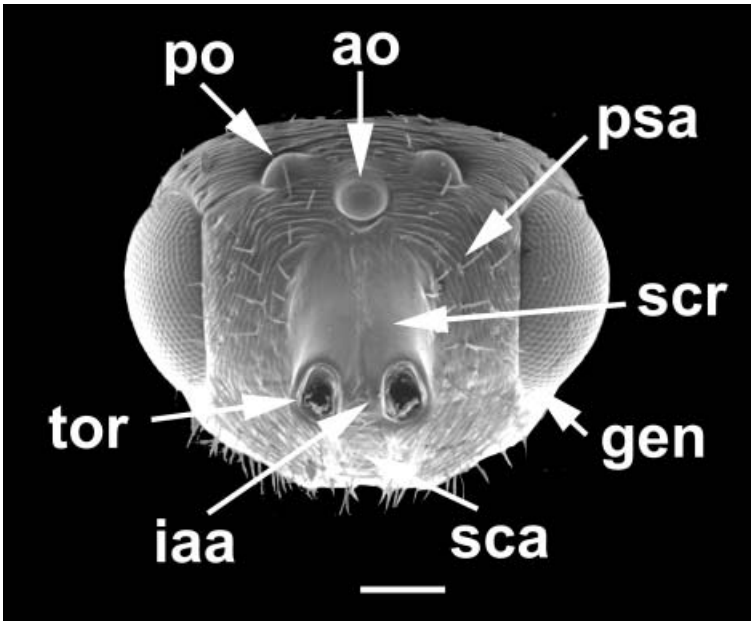


FIG. 4. Electroscan front view of head, *M. bipunctatus* ♀, ex. *Juniperus communis*, France. Same abbreviations as in (2, 3). Scale bar = 100 μm.

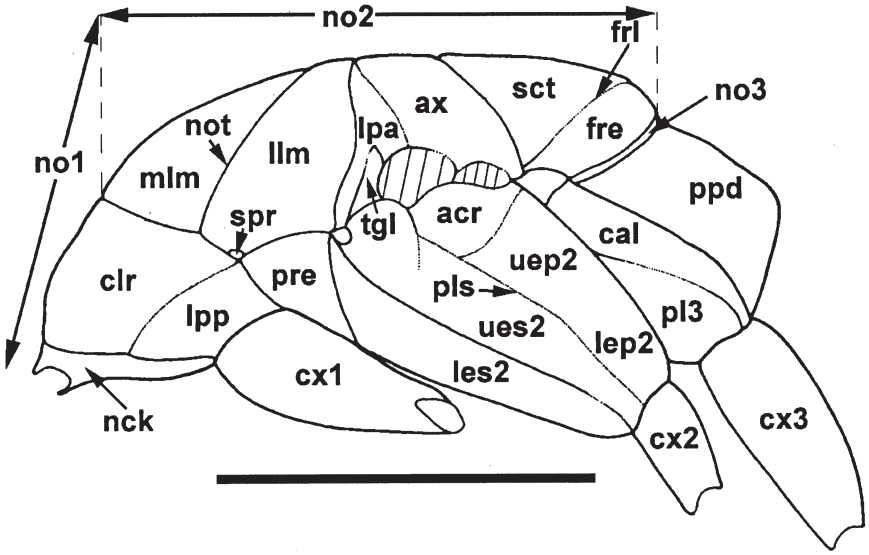
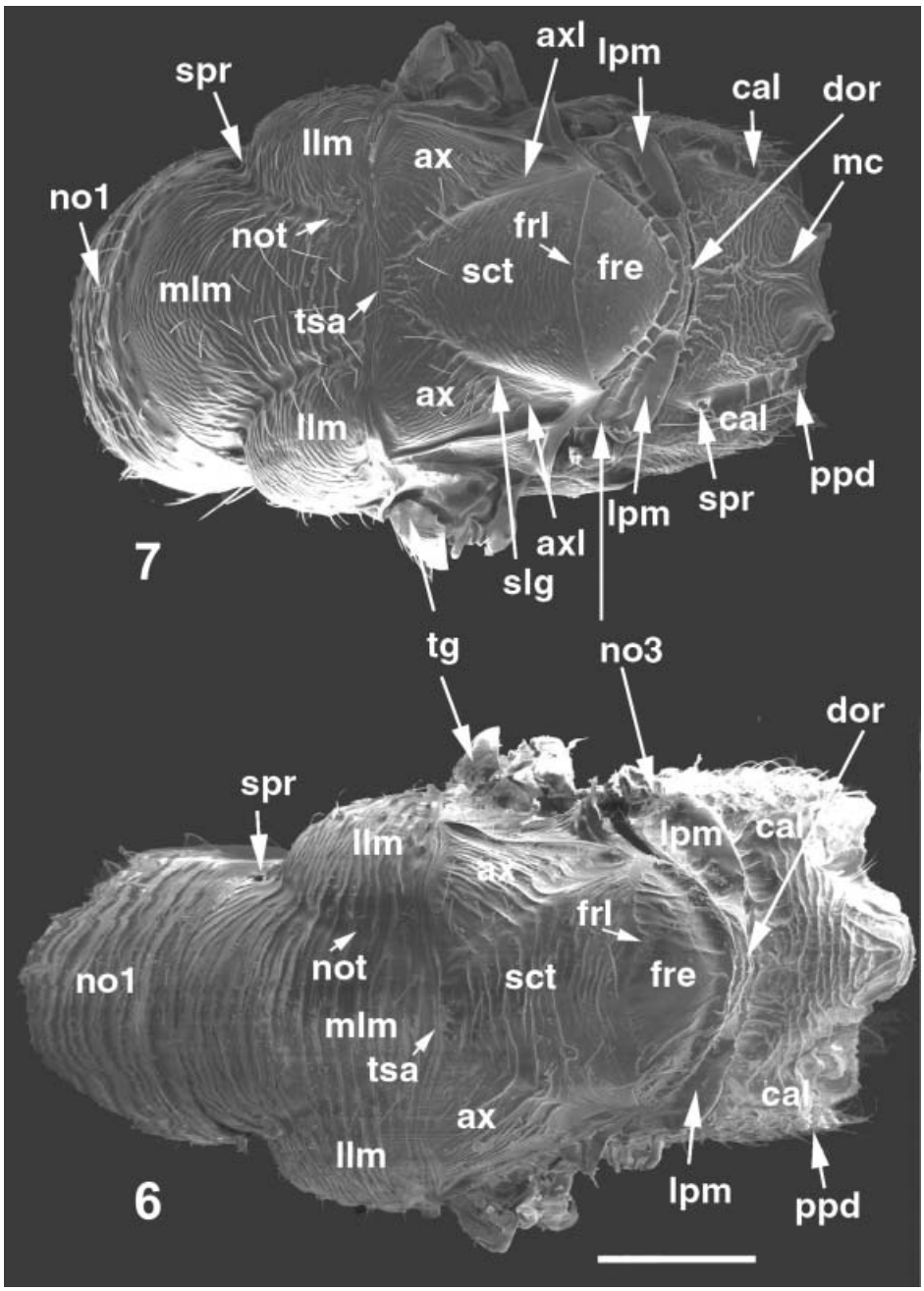


FIG. 5. Lateral view of thorax, *M. suspectus*, ex. *Abies alba*, Poland. acr, acropleuron; ax, axilla; cal, callus; clr, collar; cx_n, coxa; fre, frenum; frl, frenal line; lep_2, lower mesepimeron; les_2, lower mesepisternum; llm, lateral lobe of mesoscutum; lpa, lateral panel of axilla; lpp, lateral panel of pronotum; mlm, mid-lobe of mesoscutum; nck, neck of pronotum; no_1, pronotum; no_2, mesonotum; no_3, metanotum; not, notaulus; pls, pleural suture; pre, prepectus; pl_n, pleuron (pro, meso, meta); ppd, propodeum; sct, scutellum; slg, sublateral groove; spr, spiracle; tgl, tegula; uep_2, upper mesepimeron; ues_2, upper mesepisternum. Scale bar = 1mm.

resembling *M. rhusi* (Hussey), a species developing on Anacardiaceae in South Africa (Hussey, 1956), just emerged from seeds of *Rhus tripartita* (Ucria) Grande we collected during 2000 in the High Atlas Mountains of Morocco (Rykt; Roques and El Alaoui, unpublished observations). However, the taxonomic status of *M. rhusi* seems questionable, and the species may correspond to *M. transvaalensis* (Grissell and Hobbs, 2000).

Most of the introduced seed chalcids have spread to a range larger than that found in previous studies. Today, the Douglas-fir seed chalcid, *M. spermotrophus*, is recorded all over Europe and the European part of Russia, wherever exotic trees of genus *Pseudotsuga* have been planted. Similarly, the range of three north American chalcids attacking *Abies* seeds (*M. milleri*, *M. pinus*, *M. rafni*) now covers all of western Europe, from southern France to Denmark, and probably a large part of central Europe. Introductions also involved some species native to Asia Minor and North Africa, which were introduced to Europe. A cypress seed chalcid, *M. wachtli* Seitner, originating from the south-eastern Mediterranean Basin, is observed all over southern Europe and north Africa, recent genetic studies showing it began to be introduced probably more than two millennia ago since the Ancient Greeks and the Romans established cypress trees in these areas (Roques *et al*., 1999b). More recently (1995), a species attacking *Cedrus* seeds in Asia Minor, *M. schimitscheki* Novitzky, has been found at Mt Ventoux in the southern French Alps (Fabre *et al*., in preparation) whilst another cedar-infesting chalcid probably originating from North Africa, *M. pinsapinis* Hoffmeyer, has colonized most plantations of *Cedrus* spp. in France (Fabre, 1986).



FIGS 6, 7. Compared electroscan dorsal view of thorax of *Megastigmus*. (6) *M. atlanticus* ♀, ex. *Cupressus atlantica*, Morocco. (7) *M. pinsapinis* ♂, ex. *Cedrus atlantica*, France. Same abbreviations as in (5); axl, axillula; dor, dorsellum; lpm, lateral panel of metanotum; mc, median carina; tsa, transscutal articulation. Scale bar = 200 μm.

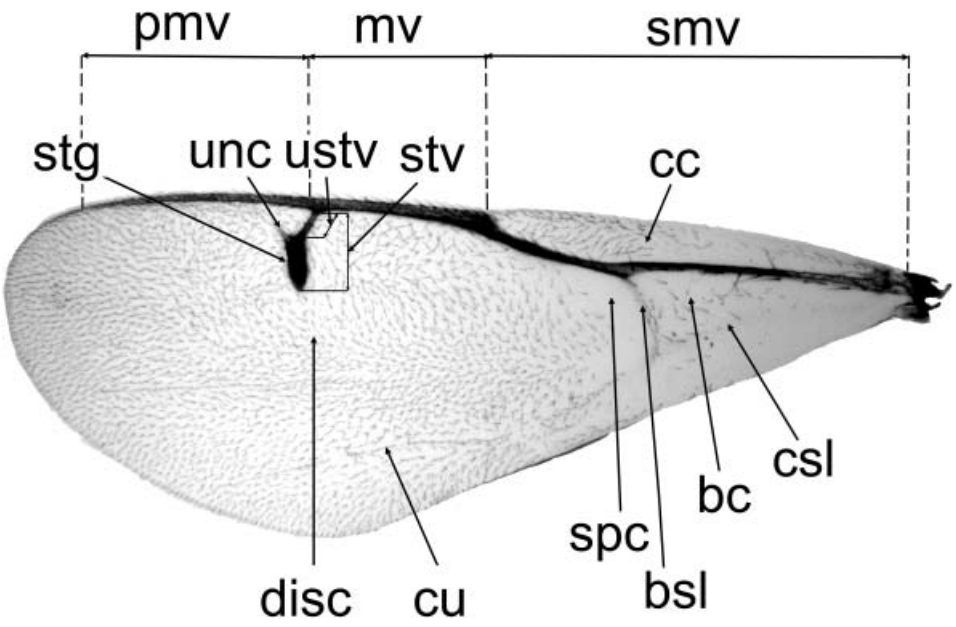


FIG. 8. Forewing of *M. suspectus* ♀, ex. *Abies alba*, Denmark. bc, basal cell; bsl, basal setal line; cc, costal cell; cu, cubital vein; pmv, postmarginal vein; smv, submarginal vein; spc, speculum; stg, stigma; stv, stigmal vein; ustv, upper part of stigmal vein.

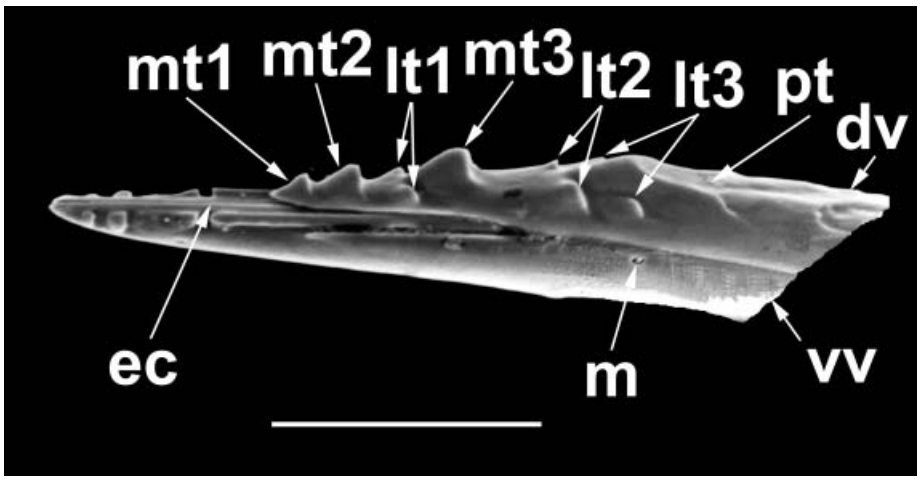


FIG. 9. Electroscan view of exserted part of ovipositor, *M. pistaciae* ♀, ex. *Pistacia lentiscus*, France. dv, dorsal valve; ec, egg canal; mt_1, first median tooth; mt_2, second median tooth; mt_3, third median tooth; lt_1, first pair of lateral teeth; lt_2, second pair of lateral teeth; pt, dorsal plate with reticulate sculpture; vv, ventral valve. Scale bar = 50 μm.

The host specificity lies at the genus level; i.e. most of the *Megastigmus* species are specialized in the exploitation of the seeds of a given genus. The native chalcids were shown to shift on to most of the exotic tree species congeneric to the original host whilst the introduced chalcids attacked most of the native tree species congeneric to the hosts observed in the country from which they originate (tables 1–3). In

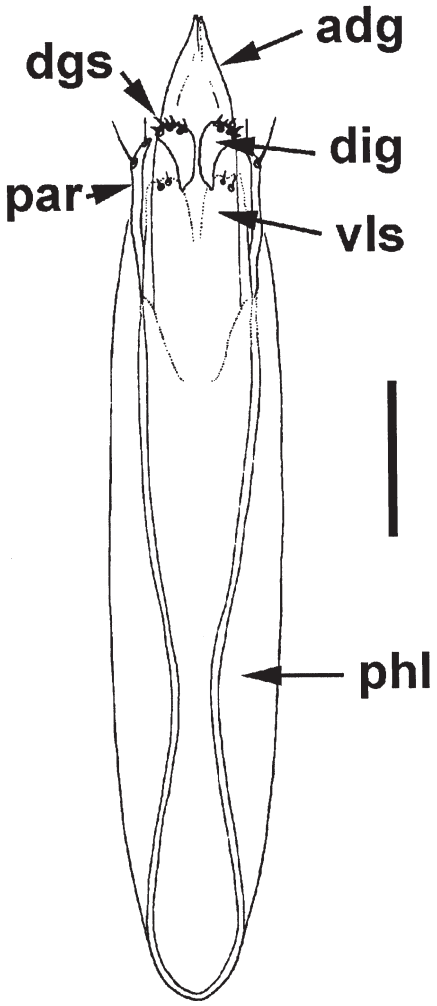


FIG. 10. Male genitalia, *M. wachtli* ♀, ex. *Cupressus sempervirens*, Greece. adg, aedeagus; dgs, digital spine; dig, digitus; par, paramere; phl, phallobase; vls, volsella. Scale bar = 100 μm.

conifers, only five species were capable of attacking more than one genus. Three of the cases involved hosts of the closely related genera *Cedrus* and *Abies* (tables 1, 2). The North African *M. pinsapinis* attacking *Cedrus* shifted on to native *Abies* spp. in Europe. Similarly, *M. schimitscheki* from Minor Asia shifted from *C. libani* to *Abies pinsapo* when introduced to southern France. In contrast, the native *M. suspectus* attacking *Abies* was observed, but scarcely, to shift on to *Cedrus brevifolia* and *C. atlantica* introduced to France. The native *M. amicorum* Bouček originally infesting seeds of the Mediterranean junipers shifted on to two cypress species introduced from California, *Cupressus arizonica* Greene and *C. goveniana* Gord. The exotic *M. atedius* Walker was observed in seeds of both the oriental spruce, *Picea orientalis* (L.) Link. and the eastern white pine, *Pinus strobus* L., in the range of introduction of these conifers in Europe. Similar relationships exist for angiosperms (table 3). Only *M. brevicaudis* Ratzeburg was found to develop in seeds of two genera of Rosaceae, *Sorbus* and *Amelanchier*.

Table 1. Host range of *Megastigmus* seed chalcids in the West Palearctic Region. Species infesting conifers of the family Pinaceae.

Host species	***M. atedius***	***M. milleri***	*M. pictus*	*M. pinsapinis*	***M. pinus***	***M. rafni***	*M. schimitscheki*	***M. specularis***	***M. spermotrophus***	*M. strobilobius*	*M. suspectus*
Abies alba Mill.		▲		▲	■	▲		▲			▲
***Abies amabilis* (Dougl.) Forbes**								●			
***Abies balsamea* (L.) Mill.**		●						●			
Abies borisii-regis Mattf.											■
Abies bornmülleriana Mattf		■			■	■		■			▲
Abies cephalonica Loud.						■					▲
Abies cilicica (Ant. et Kotschy) Carr.					■	■					■
***Abies concolor* (Gord.) Engelm.**		●			●	●		●			●
Abies equi-trojani Asch. et Sint.						■					▲
***Abies grandis* Lindl.**		●			●	●					●
***Abies holophylla* Maxim.**								●			
***Abies homolepis* Sieb. et Zucc.**		●				●		●			●
***Abies koreana* Wils.**						●		●			
***Abies lasiocarpa* (Hook.) Nutt.**					●			●			
***Abies magnifica* A. Murr.**		●									
Abies marocana Trabut.						■					
Abies nebrodensis (Lojac.) Mattei						■					■
***Abies nephrolepis* Maxim.**								●			●
Abies nordmanniana (Steven) Spach		■		■	■	■		■			▲
Abies numidica Carr.					■	■					▲
Abies pinsapo Boissier		■		▲	■	■	■	■			■
***Abies pindrow* Royle**						●					
***Abies procera* Rheder (=*nobilis* Lindl.)**					●	●					
***Abies sachalinensis* (Schmidt) Mast.**								●			
Abies sibirica Ledeb.								▲			●
***Abies veitchii* Lindl.**					●	●		●			
Cedrus atlantica (Endl.) Manetti				▲			■				■
Cedrus brevifolia (Hook. f.) Henry				■			▲				■
***Cedrus deodara* (D. Don.) G. Don.**				●							
Cedrus libani Loud.				■			▲				
Larix decidua Mill. (=*europaea* DC.)			▲								
Larix decidua polonica (Racib. ex. Woyicki) Dom.			▲								
***Larix gmelinii* (Rupr. Litvin.) (=*dahurica* Turcz.)**			●								
***Larix gmelinii olgensis* (Henry) Ostenf. et Larsen**			●								
***Larix gmelinii principis-ruprechtii* (Mayr.) Pilg.**			●								
***Larix leptolepis* (Sieb et Zucc.) Gord.**			●								
***Larix sibirica* Ledeb.**			●								
***Larix sukaczewii* Dylis**			●								
***Larix* × *czekanowskii* Szafer**			●								
***Larix* × *eurolepis* Henry**			●								
Picea abies (L.) Karst.	+									▲	
***Picea asperata* Mast.**										●	
***Picea engelmannii* (Parry) Engelm.**	●										

Table 1. (*Continued*).

Host species	***M. atedius***	***M. milleri***	*M. pictus*	*M. pinsapinis*	***M. pinus***	***M. rafni***	*M. schimitscheki*	***M. specularis***	***M. spermotrophus***	*M. strobilobius*	*M. suspectus*
***Picea ghlenii* (Fr. Schmidt) Mast.**										●	
***Picea montigena* Mast.**										●	
Picea obovata Ledeb										▲	
Picea omorica (Panč) Purkyne	■									+	
Picea orientalis (L.) Link.	■									■	
***Picea pungens* Engelm.**										●	
***Picea sitchensis* (Bong.) Carr.**	●										
***Pinus contorta murrayana* (Balf.) Critch.**	●										
***Pinus strobus* L.**	●										
***Pseudotsuga guinieri* Flous**									●		
***Pseudotsuga japonica* (Shir.) Beissn.**									●		
***Pseudotsuga macrocarpa* (Vasey) Mayr.**									●		
***Pseudotsuga menziesii* (Mirb.) Franco**									●		
***Pseudotsuga rehderi* Flous**									●		

In bold: chalcids and tree species introduced to the West Palearctic Region. (▲): Chalcid species recorded in the native range of a native tree species; (■): chalcid species recorded in plantations of a native tree species outside its natural range; (●): chalcid species recorded in plantations of an exotic tree species; (+): probably present but not confirmed yet.

Table 2. Host range of *Megastigmus* seed chalcids in the West Palearctic Region. Species infesting conifers of the family Cupressaceae.

Host species	*M. amicorum*	*M.atlanticus*	*M. bipunctatus*	*M.wachtli*
***Cupressus abramsiana* C. B. Wolf**				●
***Cupressus arizonica* Greene**	●			●
Cupressus atlantica Gaussen		▲		■
***Cupressus bakeri* Jeps.**				●
Cupressus dupreziana Camus		+		■
***Cupressus goveniana* Gord. ex. Lindl.**	●			●
***Cupressus lusitanica* Mill.**				●
***Cupressus macrocarpa* Hartw.**				●
Cupressus sempervirens L.		■		▲
Juniperus communis L. (=*J. nana* Willd.)			▲	
Juniperus excelsa Bieb.	+			
Juniperus oxycedrus L.	▲			
Juniperus phoenicea L.	▲			
Juniperus sabina L.			▲	
Juniperus thurifera L.	▲[†]		▲[‡]	

In bold: tree species introduced to the West Palearctic Region. (▲): Chalcid species recorded in the native range of a native tree species; (■): chalcid species recorded in plantations of a native tree species outside its natural range; (●): chalcid species recorded in plantations of an exotic tree species; (+): probably present but not confirmed yet.

[†]In Corsica. [‡]In Morocco, Spain and continental France.

Table 3. Host range of *Megastigmus* seed chalcids in the West Palearctic Region. Species infesting Angiosperms of families Anacardiaceae and Rosaceae.

Family	Host species	*M. aculeatus*	*M. brevicaudis*	***M. nigrovariegatus***	*M. pistaciae*	*M. rosae*	***M. transvaalensis***
Anacardiaceae	*Pistacia atlantica* Desf.				▲		
Anacardiaceae	***Pistacia chinensis* Bunge**				●		
Anacardiaceae	*Pistacia integerrima* Stewart				▲		
Anacardiaceae	*Pistacia lentiscus* L.				▲		
Anacardiaceae	*Pistacia mutica* Fisch et Mey				▲		
Anacardiaceae	*Pistacia terebinthus* Scop.				▲		
Anacardiaceae	*Pistacia vera* L.				▲		
Anacardiaceae	***Schinus molle* L.**						●
Anacardiaceae	***Schinus terebinthifolius* Raddi**						●
Rosaceae	*Amelanchier ovalis* Medikus		▲				
Rosaceae	*Amelanchier spicata* C. Koch.		▲				
Rosaceae	*Rosa alpina* L.	▲					
Rosaceae	***Rosa andreae* Lange**	●					
Rosaceae	*Rosa arvensis* Huds.	▲				▲	
Rosaceae	*Rosa beggeriana* Schrenk.	▲					
Rosaceae	*Rosa blanda* Pursh.	▲					
Rosaceae	*Rosa canina* L. (=*monticola* Rappin)	▲				▲	
Rosaceae	*Rosa cinnamomea* L.	▲					
Rosaceae	*Rosa collina* Jacquin	▲					
Rosaceae	*Rosa davurica* Pallas (=*dahurica* Auct.)	▲					
Rosaceae	*Rosa ferruginea* Vill. (=*glauca* Pourret; =*mayerii* Braun; =*rubrifolia* Vill.)	▲				▲	
Rosaceae	*Rosa gallica* L.	▲					
Rosaceae	*Rosa glutinosa* Sibth et Sm.	▲					
Rosaceae	*Rosa jundzillii* Besser	▲					
Rosaceae	*Rosa mollissima* Willd. (=*mollis* Smith)	▲					
Rosaceae	*Rosa montana* Chaix	▲					
Rosaceae	***Rosa multiflora* Thunb.**	●					
Rosaceae	*Rosa pendulina* L.	▲		▲		▲	
Rosaceae	*Rosa pouzini* Trat.	▲					
Rosaceae	*Rosa rubiginosa* L. (=*eglanteria* L.)	▲				▲	
Rosaceae	*Rosa rugosa* Thunb. (=*kamtschatika* Regel)	▲					
Rosaceae	*Rosa spinosissima* L. (=*pimpinellifolia* L.)	▲					
Rosaceae	*Rosa tschatyrdagi* Chrshan.					▲	
Rosaceae	*Rosa turkestanica* Regel	▲				▲	
Rosaceae	*Rosa villosa* L.	▲					
Rosaceae	*Sorbus aria* L.		▲				
Rosaceae	*Sorbus aucuparia* L.		▲				

In bold: chalcids and tree species introduced to the West Palearctic Region. (▲): Chalcid species recorded in the native range of a native tree species; (●): chalcid species recorded in plantations of an exotic tree species.

In parallel, each of the native conifers seems to host only one native chalcid in the original range (tables 1–2). With two native chalcid species, the incense juniper, *Juniperus thurifera* L., seems to constitute an exception but the chalcids actually share the host range (table 2). However, when additional *Megastigmus* species were introduced, we observed that the native conifer might host several chalcid species (e.g. up to six in *Abies alba* Mill.; table 1). In contrast, in angiosperms some *Rosa* spp. host two native chalcid species, *M. aculeatus* Swederus and *M. rosae* Bouček (table 3).

Keys to adult species of Megastigmus

The following keys present diagnostic, dichotomic characters allowing separation of females and males of the *Megastigmus* species present in tree seeds within the West Palearctic region. Although probably belonging to the genus *Bootanomyia* (Bouček, 1988), five additional species still considered as *Megastigmus* are known to develop within plant galls in this region: *M. almusiensis* Doğanlar (Doğanlar, 1989), *M. dorsalis* (Fabricius) (Askew, 1966; Bouček, 1977; Narendran, 1994), *M. dumicola* Bouček (Bouček, 1982), *M. stigmatizans* (Fabricius) (Milliron, 1949; Sellenschlo, 1984a, 1984b) and *M. synophri* Mayr (Mayr, 1874; Wall, 1984). For more convenience, these species are included in the keys.

Key to females of *Megastigmus* native and introduced to the West Palearctic region (measurements done on dry specimens)

1 Thoracic dorsum metallic-coloured (green, bluish or violet) at least partly; antenna inserted just above lower ocular line; species living within galls 2
– Thoracic dorsum yellow and/or brown to black, without any metallic-coloured part; antenna inserted distinctively well above lower ocular line; species living within seeds 6

2 Gaster with a very conspicuous petiole, nearly half as long as propodeum length . . . . . *M. dumicola* Bouček
– Gaster not petiolate 3

3 Ovipositor sheaths longer than body (min.: 1.1 × body) . *M. stigmatizans* (Fabricius)
– Ovipositor sheaths smaller than body (max.: 0.9 × body) 4

4 Frenal area sculptured; thoracic pleurae entirely yellow 5
– Frenal area smooth; thoracic pleurae partly metallic-coloured . *M. synophri* Mayr

5 Mid-lobe of mesoscutum finely rugulose; pronotum with eight rows of hairs . . . . . *M. dorsalis* (Fabricius)
– Mid-lobe of mesoscutum with dense transverse striae; pronotum with 16 rows of hairs or more . . . . . *M. almusiensis* Doğanlar

6 Forewing stigma surrounded by a distinct infuscated area (figure 55) . . . . . *M. nigrovariegatus* Ashmead
– Forewing stigma not surrounded by a distinct infuscated area 7

7 Ovipositor sheaths never longer than 0.9 × gaster 8
– Ovipositor sheaths much longer than 0.9 × gaster (min.: 1.1 × gaster) 9

8 Thoracic dorsum mostly yellow (pale to brownish); flagellum of antenna longer (1.2–1.4 ×) than head width, with elongate funicular segments (figure 15); pronotum only 1.1–1.2 × wider than long; pronotum and mesoscutum with strong transverse carinae; frenal area with strong longitudinal carinae (figure 128); forewing stigma roughly ovoid, more than 1.5 × as long as broad, with a short uncus equal to about one-fifth of stigma length (figure 52); distal part of ovipositor with a third median tooth much larger than others (figure 91) . . . . . *M. bipunctatus* Swederus

– Thorax mostly brownish black, except pronotum more or less yellowish; flagellum of antenna as long as head width or smaller (0.9–1.0 ×), with median funicular segments subquadrate (figure 16); pronotum more than 2.0 × wider than long; pronotum and mesoscutum with fine arcuate cross-striae; frenal area smooth, without longitudinal carinae (figure 129); forewing stigma oblong, 1.4 × as long as broad, with a very long uncus about half as long as stigma length (figure 53); distal part of ovipositor with median teeth of equal size (figure 92) . . . . . *M. brevicaudis* Ratzeburg

9 Exserted part of ovipositor less than 1.2 × as long as gaster (max.: 1.1 ×) . . . . . *M. pistaciae* Walker
– Exserted part of ovipositor 1.2 × as long as gaster or more 10

10 Exserted part of ovipositor smaller than 0.8 × body, never longer than thorax and gaster combined 11
– Exserted part of ovipositor longer than 0.8 × body (min.: 0.9 ×), clearly longer than thorax and gaster combined 15

11 Thoracic dorsum testaceous; frenal area with strong longitudinal carinae . . . 12
– Thoracic dorsum showing some brown or black areas; frenal area smooth . . . 13

12 Pilosity on thoracic dorsum black; longitudinal carinae on the middle part of the frenal area (figure 125); forewing stigma roughly oblong, less than 1.8 × as long as wide (figure 49) . . . . . *M. amicorum* Bouček
– Pale pilosity on thoracic dorsum; longitudinal carinae only on the lateral parts of the frenal area (figures 6, 127); forewing stigma elongate, more than 1.8 × as long as wide (figure 51) . . . . . *M. atlanticus* sp.n.

13 Propodeum with a distinct, simple or double, median carina 14
– Propodeum without median carina but with oblique carinae (figure 143) . . . . . *M. transvaalensis* (Hussey)

14 Body mostly yellowish; head in dorsal view slightly narrowed behind the eyes, with barely protruding eyes; frenal area with short, interrupted, longitudinal carinae (figure 137); forewing stigma rounded, 1.4–1.5 × as long as broad, with upper part of stigmal vein about as long as one-third of stigma length (figures 61, 62) . . . . . *M. rosae* Bouček
– Body mostly brownish to black; head in dorsal view strongly narrowed behind the eyes, with distinctly protruding eyes (figure 3); frenal area entirely smooth (figure 132); forewing stigma elongate, more than 1.7 × as long as broad, with upper part of stigmal vein longer than half of stigma length (figure 56) . . . *M. pictus* (Förster)

15 Scape of antenna less than 1.2 × (max: 1.1 ×) as long as pedicel, anellus and first funicular segment combined (figures 17, 21, 26, 29) 16
– Scape of antenna 1.2 × as long as pedicel, anellus and first funicular segment combined, or more (figures 13, 23, 27, 31) 21

16 Pilosity on thoracic dorsum mostly pale, even on yellow maculae . . *M. pinus* Parfitt
– Pilosity on thoracic dorsum mostly black 17

17 Pilosity on lower face (below antenna) mostly dark; forewing stigma elongate, more than 1.6 × as long as wide (figures 57, 62, 66); body mostly black 18
– Pilosity on lower face (below antenna) mostly pale; forewing stigma oval, less than 1.6 × as long as wide (max: 1.5 ×) (figures 54, 63); body black and yellow . . . 20

18 Frenal area wrinkled (figure 142); face partially yellow at least; thorax with lateral yellow spots; stigma very elongate, 1.8–2.2 × as long as broad (figure 57, 66) . . 19
– Frenal area smooth with a few short carinae extending longitudinally from the frenal line (figure 138); face entirely black except oral area orange-brown to brown; thorax entirely black; stigma oval-elongate, less than 1.8 × as long as broad (max. 1.7 ×) (figure 62). . . . . *M. schimitscheki* Novitzky

19 Face yellow but always with more or less extended black markings; temple with a black-brown patch extending to gena; prepectus, tegula and acropleuron black; coxae mostly black with the distal parts of fore- and mid-coxa yellow . *M. suspectus* Borries

– Face entirely yellow; temple with a limited black patch, extending to occipital carina but not reaching gena; prepectus, tegula and acropleuron yellow to light brown; coxae mostly yellow except mid-coxa sometimes with black markings and hind coxa brownish to black with yellow markings ventrally . . . . *M. pinsapinis* Hoffmeyer

20 Pronotum yellow, except for two isolated dorsal black spots; mesonotum yellow with black bands; forewing stigma oval, 1.5–1.6 × as long as broad, with upper part of stigmal vein comparatively short, 0.4 × as long as stigma length or less (figure 54) . . . . . *M. milleri* Milliron
– Pronotum black, except for two small transverse yellow (or brownish) spots above the posterior margin and sides yellow; mesonotum black; forewing stigma rounded, less than 1.5 × as long as broad, with upper part of stigmal vein comparatively elongate, 0.6 × as long as stigma length or more (figure 63) . . *M. specularis* Walley

21 Exserted part of ovipositor longer than 1.1 × body length (min: 1.2 ×) 22
– Exserted part of ovipositor never longer than 1.1 × body length (max.: 1.1 ×) . . 24

22 Forewing stigma with upper part of stigmal vein 0.3 × as long as stigma length at more (figures 48, 68) 23
– Forewing stigma with upper part of stigmal vein longer than 0.3 × stigma length (min: 0.4 ×) (figure 60) . . . . . *M. rafni* Hoffmeyer

23 Propodeum at least anteriorly black; head with vertex partly black; thorax with anterior part of mesoscutum and axilla partly black; head about 1.4 × as broad as long in dorsal view; stigma roughly oval, less than 1.5 × as long as broad (figure 48) . . . . . *M. aculeatus* Swederus
– Propodeum wholly yellow or brownish yellow; head entirely light yellow; thorax entirely dirty yellow with pronotum lighter and a brownish stripe at pronotum base; head 1.2 × as broad as long in dorsal view; stigma elongate, more than 1.5 × as long as broad (min.: 1.7 ×) (figure 68) . . . . . *M. wachtli* Seitner

24 Body predominantly dark yellow . . . . . *M. spermotrophus* Wachtl
– Body predominantly black 25

25 Pronotum with two transverse light yellowish spots, separated from each other by about their own width; hind part of mid-lobe of mesoscutum with transverse cross-striae; forewing with basal cell showing few hairs (four to eight) on disc . . . . . *M. atedius* Walker
– Pronotum with a pale translucent cross-band in front of hind margin, this band possibly interrupted, but very narrowly, in the middle; hind part of mid-lobe of mesoscutum with very arcuate cross-striae; forewing with basal cell showing 10–18 hairs on disc . . . . . *M. strobilobius* Ratzeburg

Key to males of *Megastigmus* native and introduced to the West Palearctic region

1 Thoracic dorsum metallic-coloured (green, bluish or violet) at least partly; antenna inserted just above lower ocular line; species living within galls 2
– Thoracic dorsum yellow and/or brown to black, without any metallic-coloured part; antenna inserted distinctly well above lower ocular line; species living within seeds . 4

2 Forewing stigma elongate; body 5–7 mm long . . . . *M. stigmatizans* (Fabricius)
– Forewing stigma rounded or short-oval; body less than 5 mm long (max.: 4 mm) . 3

3 Mid-lobe of mesoscutum finely rugulose; pronotum with eight rows of hairs . . . . . *M. dorsalis* (Fabricius)
– Mid-lobe of mesoscutum with dense transverse striae; pronotum with 16 rows of hairs or more . . . . . *M. almusiensis* Doğanlar

4 Forewing stigma surrounded by a distinct infuscated area (figure 74) . . . . . *M. nigrovariegatus* Ashmead
– Stigma not surrounded by a distinct infuscated area 5

5 Frenal area strongly impressed (figure 153) or with numerous rounded carinae (figures 149, 154, 160) 6

– Frenal area mostly smooth (figure 151) or with only a few longitudinal carinae (e.g. figure 146). 11

6 Thorax usually entirely yellow . . . . . *M. pistaciae* Walker
– Thorax with some black parts at least 7

7 Pilosity on thoracic dorsum mostly pale, even on yellow maculae; frenal area strongly impressed but without distinct carinae (figure 153) . . . . . *M. pinus* Parfitt
– Pilosity on thoracic dorsum mostly black; frenal area with distinct carinae (figures 149, 160) 8

8 Pilosity on lower face (below antenna) mostly pale; thoracic dorsum not entirely black; stigma broadly oval, less than 1.5× as long as broad (max: 1.4×) (figure 73) 9
– Pilosity on lower face (below antenna) mostly dark; thoracic dorsum entirely black; stigma elongate, more than 1.5× as long as broad (min.: 1.6×) (figures 76, 84) . . 10

9 Thorax black with more or less extended yellow spots on sides and posterior margin of pronotum, outer surface of mesoscutum, tegula, prepectus and mid-part of metanotum; propodeum entirely black, with a distinct median carina . . *M. milleri* Milliron
– Thorax orange yellow except black sutures along prepectus, tegula, acropleuron and lateral panel of metanotum; propodeum orange yellow with a triangular black patch in the middle, without central but with lateral carinae (figure 161) . . . . . *M. transvaalensis* (Hussey)

10 Hind coxa black; frenal area with coarse longitudinal carinae (figure 160); aedeagus smaller than digitus (figure 122) . . . . . *M. suspectus* Borries
– Hind coxa yellow with black markings; frenal area without coarse longitudinal carinae but rounded wrinkles (figure 145); aedeagus longer than digitus (figure 114) . . . . . *M. pinsapinis* Hoffmeyer

11 Mesoscutum and/or scutellum predominantly yellow or brownish yellow 12
– Mesoscutum and/or scutellum predominantly black 19

12 Forewing stigma with upper part of stigmal vein 0.3× as long as stigma length at more (figures 70, 86) 13
– Forewing stigma with upper part of stigmal vein longer than 0.3× stigma length (min.: 0.4×) (figures 75, 82) 17

13 Thoracic dorsum mostly brownish black, only pronotum more or less yellowish . . 14
– Thoracic dorsum mostly yellow (pale to brownish) 15

14 Propodeum without distinct median longitudinal carina; forewing stigma ovoid, with a short uncus, 2× shorter than upper part of stigmal vein (figure 72) . . . . . *M. bipunctatus* Swederus
– Propodeum with a median longitudinal carina; forewing stigma with a long uncus, about as long as upper part of stigmal vein . . . . . *M. rosae* Bouček

15 Forewing stigma with uncus smaller than upper part of stigmal vein (figure 70) . . . . . *M. amicorum* Bouček
– Forewing stigma with uncus as long as upper part of stigmal vein or longer (figures 69, 86). 16

16 Body entirely dirty yellow; frenal area with distinct longitudinal carinae (figure 162); upper part of stigmal vein very short, more than 10× smaller than stigma length (figure 86); aedeagus elongate, digitus with six teeth (figure 8) . *M. wachtli* Seitner
– Body brownish yellow with a few brown to black markings on axilla, mesoscutum and propodeum; frenal area without distinct carinae (figure 145); upper part of stigmal vein only 4–5× smaller than stigma length (figure 69); aedeagus short and conical, digitus with three teeth (figure 107) . . . . . *M. aculeatus* (Swederus)

17 Thoracic dorsum mostly brownish black, only pronotum more or less yellowish . . . . . *M. pictus* (Förster)
– Thoracic dorsum mostly yellow (pale to brownish) 18

18 Proximal funicular segments similarly elongate, twice as long as wide (figure 40); frenal area nearly smooth with a limited reticulation below the frenal line (figure 155); body colour highly variable, from golden yellow to brownish but always with dark spots on thorax (on outer axilla and anterior margin of acropleuron at least); propodeum usually brown to black anteriorly; dorsum of gaster dark brown to black . . . . . *M. rafni* Hoffmeyer

– Only the first funicular segment twice as long as wide, slightly longer than the following segments (figure 43); frenal area with short longitudinal carinae extending from the posterior margin (figure 158); body colour varying from dark lemon-yellow to orange-reddish yellow, but without dark spots on thorax; propodeum wholly yellow or brownish yellow; dorsum of gaster reddish yellow, with a dark patch at base of terga . . . . . *M. spermotrophus* Wachtl

19 Pedicel as long as anellus and first funicular segment combined or less (figure 41) . 20

– Pedicel clearly longer than anellus and first funicular segment combined (min. 1.1 ×) (figure 44). 21

20 Pilosity on lower face mostly dark; stigma rounded, less than 1.4 × as long as broad (max.: 1.3 ×), with a short uncus, about half as long as upper part of stigmal vein (figure 80); pronotum entirely black; coxae black . . . *M. schimitscheki* Novitzky

– Pilosity on lower face mostly pale; stigma oblong, more than 1.4 × as long as broad (min.: 1.6 ×), with an elongate uncus, 0.7 × as long as upper part of stigmal vein or more (figure 81); pronotum with lateral panel and two large transverse spots on posterior margin yellow; coxae mostly yellow . . . . . *M. specularis* Walley

21 Pronotum with two large transverse light yellowish spots, separated from each other by about their own width; hind part of mid-lobe of mesoscutum with transverse cross-striae . . . . . *M. atedius* Walker

– Pronotum with a pale translucent cross-band in front of hind margin, this band interrupted but very narrowly in the middle in some specimens; hind part of mid-lobe of mesoscutum with very arcuate cross-striae . . . *M. strobilobius* Ratzeburg

Treatment of species

Megastigmus aculeatus (Swederus)
(figures 11, 32, 48, 69, 87, 107, 124, 145)

Pteromalus aculeatus Swederus, 1795: 221–222. Lectotype ♀, Sweden (?NHMS [not examined]).

Megastigmus transversus Walker, 1833: 117. Syntype ♀, England (BMNH [not examined]). Synonymy with *collaris* by Mayr, 1874: 137.

Torymus (*Megastigmus*) *collaris* Boheman, 1834: 332. Syntypes ♀ and ♂, 'Westrogothia, Smolandia and Scandia', Sweden (NHMS [6♀, 3♂ examined]). Synonymy with *aculeatus* by Milliron, 1949: 289.

Torymus punctum Förster, 1840: 31. Syntype ♀, Germany (NMW [not examined]). Synonymy with *collaris* by Mayr, 1874: 137.

Megastigmus vexillum Ratzeburg, 1848: 182. Syntypes ♀ and ♂, Germany (destroyed). Synonymy with *collaris* by Mayr 1874: 137.

Megastigmus flavus Förster, 1859: 109–110. Syntypes ♀ and ♂, Tyrol, Austria (female) and Aachen, Germany (male) (NMW [1♀ examined]). Synonymy with *collaris* by Mayr, 1874: 137.

Megastigmus collaris flavus Förster: Mayr, 1874: 138 [subspecies]

Megastigmus cynorrhodi Perris, 1876: 222. Syntypes, France (MNHN [lost, not examined]). Synonymy with *aculeatus* by Milliron, 1949: 289.

Female

Body length (without ovipositor) 3.4 mm. Colour predominantly brownish yellow with brown to black markings. Head light brownish yellow except ocelli and occipital

carina partly surrounded with black. Pilosity pale on lower face, dark on dorsum of head. Antenna dark brown. Thorax mostly brown except anterior part of pronotum light brown, and posterior part of mid-lobe of mesoscutum, scutellum and dorsellum orange-yellow. Pilosity on thorax black. Legs tawny to brownish yellow, except front tarsus and distal segments of other tarsi brown. Wings subhyaline; forewing stigma light brown without any infuscation. Propodeum dark brown to black except latero-posterior margin brownish yellow. Gaster dark amber on the dorsum and brownish yellow laterally. Ovipositor sheaths black.

Head about 1.4 × as broad as long in dorsal view. Antennal scape much longer (about 1.8 ×) than pedicel, anellus and first funicular segment combined. Funicular segments 1–6 about 1.5 × as long as wide (figure 11). Pronotum and mid-lobe of mesoscutum with coarse cross-striation. Scutellum 1.1–1.2 × as long as broad, with coarse, arcuate cross-striae on the anterior part, the frenal area nearly smooth with a few weak longitudinal furrows on the sides (figure 124). Forewing stigma roughly oval, less than 1.5 × as long as broad; upper part of stigmal vein comparatively short, smaller than one-third of stigma length (figure 48). Propodeum with a double median carina and distinct sublateral carinae. Ovipositor sheaths about 1.2 × as long as body. Distal end of the dorsal valve of ovipositor bearing small cutting teeth, the first median tooth lanceolate (figure 87).

Male

Body length 2.9 mm. Body light brownish to brownish yellow, with some brown to black markings. Head brownish yellow except ocelli surrounded with black. Pilosity pale on lower face, black on remainder of head. Antenna orange-yellow with scape and pedicel lighter. Thoracic dorsum mostly light brownish with some dark brown patterns: a narrow band along anterior margin of pronotum, mid-lobe, anterior part of lateral lobes and transscutal articulations of mesoscutum, a patch on outer part and lower internal part of axilla, and a patch on lateral panel of metanotum. Lateral parts of thorax light brownish except mesepisternum, mesepimeron and metapleuron dark brown. Pilosity on thoracic dorsum black. Legs light brownish except hind coxa at base and claws dark brown. Wings subhyaline; forewing stigma light brown without any infuscation. Middle part of propodeum black, callus yellowish. Gaster with the terga black on dorsum and the sides orange-yellow except the two last terga entirely orange-yellow.

Head about 1.5 × as broad as long in dorsal view. Antennal scape slightly longer (about 1.1 ×) than pedicel, anellus and first funicular segment combined (figure 32); funicular segments more elongate than in female, about 1.8 × as long as broad. Pronotum and mid-lobe of mesoscutum with dense cross-striae. Scutellum nearly 1.3 × as long as wide, the anterior part densely striate-reticulate, and the frenal area nearly smooth with sparse areolae (figure 145). Forewing stigma broadly oval, about 1.5 × as long as broad; upper part of stigmal vein comparatively short, about 4 × as small as length of stigma; uncus comparatively long, 1.1–1.2 × as long as upper part of stigmal vein (figure 69). Aedeagus short and conical, digitus with three teeth (figure 107).

Variation

The above description is based on the type material of *M. collaris*. In the other specimens we examined, body length varied from 2.6 to 4.0 mm in females, from 2.5

to 3.2 mm in males. Large variations in female colour were observed. The type material of *M. flavus* as well as female specimens from western and central Europe presented lighter colour patterns, with a thorax mostly brownish yellow to yellow and dark brown patterns limited to outer surface of axilla and anterior margin of mesoscutum. By contrast, females originating from south-central (Italy, Switzerland) and southeastern Europe (Bulgaria, Croatia, Greece) were usually darker with the following parts coloured in black: a spot on the anterior margin of pronotum, a more or less extended band covering the anterior half of the mid-lobe of mesoscutum, the outer surface of axilla, and the frenal line.

Males showed only little variations in colour. The dark patterns on thorax varied from brown to black. Some specimens from the French Alps were lighter with no dark brown band on anterior margin of pronotum, the dark brown colour on mid-lobe of the mesoscutum reduced to two small spots on anterior part, and lateral parts of thorax and legs (excpet claws) entirely light brownish.

Sex ratio

Strongly skewed in favour of females because of thelytokous parthenogenesis. Males usually constituted less than 7% of the populations sampled in western and central Europe: 0% (Lessmann, 1974b) in Germany; 1.1% (Eichhorn, 1967) and 2.3% (Kurir, 1975) in Austria; 0–7% in France (AR).

Hosts

Develops exclusively in seeds of *Rosa* spp. (Rosaceae), earlier records from other plant species having not been confirmed (Milliron, 1949). Seed damage has been observed in most of the native and naturalized species of *Rosa* growing in Europe and Eurasia: *R. alpina* (Milliron, 1949; Bouček, 1977; USNM), *R. andreae* (USNM), *R. arvensis* (AR), *R. beggeriana* (Zerova and Seryogina, 1994), *R. blanda* (USNM), *R. canina* (=*R. monticola*; Kapuściński, 1948; Eichhorn, 1967; Lessmann, 1974b; Kurir, 1975; Křístek *et al*., 1992; Xu and He, 1995; Ochsner, 1998; Jensen and Ochsner, 1999; AR; USNM), *R. cinnamomea* (Nikol'skaya, 1934; Kapuściński, 1948; Zerova and Seryogina, 1994; Skrzypczyńska, 2000), *R. collina* (Eichhorn, 1967; AR), *R. davurica* (=*R. dahurica*; Milliron, 1949; Zerova and Seryogina, 1994; USNM), *R. ferruginea* (=*R. glauca*, =*R. mayeri*, =*R. rubrifolia*; Kapuściński, 1948; AR; USNM), *R. gallica* L. (Milliron, 1949), *R. glutinosa* (Kapuściński, 1948; AR), *R. jundzilli* (Kapuściński, 1948; Milliron, 1949), *R. mollissima* (=*R. mollis*; Milliron, 1949; USNM), *R. montana* (AR), *R. multiflora* (Kamijo, 1962; USNM), *R. pendulina* (Kurir, 1975; AR), *R. pouzini* (AR), *R. rubiginosa* (=*R. eglanteria*; Balduf, 1957; Eichhorn, 1967; Syrett, 1990; Xu and He, 1995; AR), *R. rugosa* (=*R. kamtschatika*; Kapuściński, 1948; Milliron, 1949, Kamijo, 1962; Valentine in Bouček, 1988; Xu and He, 1995; USNM), *R. spinosissima* (=*R. pimpinellifolia*; Kapuściński, 1948; Křístek *et al*., 1992; AR), *R. turkestanica* (Zerova and Seryogina, 1994) and *R. villosa* (Eichhorn, 1967). Additional *Rosa* species are likely to be attacked, records often having noted only *Rosa* sp. as host (Seitner, 1916; Hoffmeyer, 1931b; Zacher, 1932; Escherich, 1938, 1942; Kangas, 1940; Prisiazhniuk, 1949; Pavlovskii and Bei-Bienko, 1950; Čermak, 1952; Sorauer, 1953; Bouček, 1954, 1970a, 1977; Novitzky, 1954; Györfi, 1962; Lozovoi, 1965; Vikberg, 1966; Nikol'skaya and Zerova, 1978; Schwenke, 1982; Jespersen and Lomholdt, 1983).

Distribution

Widely distributed in the Holartic and Australasian region. Recorded from the eastern part of North America (Milliron, 1949; Balduf, 1957; Peck, 1963; Grissell, 1979), Ethiopia (Milliron, 1949; USNM), South Africa (AR), Iran (Milliron, 1949; USNM), Iraqi (USNM), China (Milliron, 1949; Xu and He, 1995; USNM), Japan (Milliron, 1949; Kamijo, 1962) and Australasia including New Zealand (Bouček, 1988; Syrett, 1990). In Europe, known from Austria (Eichhorn, 1967; Kurir, 1975); Bulgaria (AR); Czech Republic (Čermak, 1952; Bouček, 1954; Křístek *et al*., 1992); Denmark (Hoffmeyer, 1931b; Jespersen and Lomholt, 1983; Ochsner, 1998; Jensen and Ochsner, 1999); France (Vayssières, 1931; AR; USNM); Finland (Hellén, 1933; Vikberg, 1966); Germany (Milliron, 1949; Eichhorn, 1967; Lessmann, 1974b); Great Britain (Laidlaw, 1931; Bouček, 1970b); Greece (AR); Hungary (Györfi, 1962; AR); Italy (AR); The Netherlands (AR); Poland (Kapuściński, 1948); Russia: from the European part to the Caucasus, Ural, Siberia and Far East (Kniazheckii, 1949; Milliron, 1949; Prisiazhniuk,1949; Pavlovskii and Bei-Bienko, 1950; Nikol'skaya, 1952; Nikol'skaya and Zerova, 1978; USNM); Spain (AR); Sweden (Swederus, 1795; Hansson, 1991; AR, USNM); Switzerland (Milliron, 1949; MS; USNM); former Yugoslavia: Croatia, Serbia; Morocco (Bouček, 1977; AR).

Comments

Two other species of *Megastigmus*, *M. nigrovariegatus* and *M. rosae*, develop in *Rosa* seeds in the West Palearctic region. Females of *M. aculeatus* can be easily distinguished by the relative size of the ovipositor sheaths, which are 1.2 × as long as body length whilst they are only 0.7–0.8 × as long as body length in the two other species, and by the absence of infuscation around the forewing stigma (wide infuscation in *M. nigrovariegatus* and slight infuscation in some specimens of *M. rosae*). Males of *M. aculeatus* differ from those of *M. nigrovariegatus* by the absence of infuscation around the forewing stigma, and from those of *M. rosae* by the lighter colour of thorax (mostly brownish yellow versus mostly brownish black).

A third species, *M. aculeatus nigroflavus* Hoffmeyer, was recognized in Japan (Kamijo, 1962) and Russia (Milliron, 1949). It was also observed in North America (Milliron, 1949; Balduf, 1957; Peck, 1963; Grissell, 1979; Nalepa and Grissell, 1993) but suspected to be introduced with *Rosa* seeds imported from Eurasia and Japan (Milliron, 1949). It was first considered as a variety (Hoffmeyer, 1929; Peck, 1963) but recent genetic studies confirmed that the North American populations of *M. aculeatus nigroflavus* correspond to a valid separate species (Roques and Roux, unpublished). Although the species has not been recorded from Europe yet, one specimen was found emerging from *Rosa* seeds imported from Germany to the USA (Hoboken Poe, 16 May 1966, USNM). We examined the type specimens that emerged from *Rosa multiflora* (1♀, 1♂, Japan, 1928, Hoffmeyer [ZMUC]; 4♀ paratypes, same data as holotype [USNM]). The female is smaller in size than that of *M. aculeatus*, with brown and amber pattern of gaster more intensified dorsally, and ovipositor sheaths are only 0.8–0.9 × as long as body length (as long as body length according to Nalepa and Grissell, 1993). Two specimens which emerged from hips of *R. rubiginosa* in the southern French Alps (Saint Crépin, June 1990) fitted that description but the record needs to be confirmed by a larger series. Male is lighter than that of *aculeatus* and more sharply sculptured, with a stigma surrounded by a narrow, inconspiscuous infuscation as noted by Milliron (1949). Sex ratio seems

different from that usually observed in *M. aculeatus*, with a larger proportion of males (33♀:1♂; Balduf, 1957; Kamijo, 1962; Mays and Kok, 1988).

Material examined

Austria: 1♀ syntype *M. flavus*, Tyrol, Mayr coll. (NMW). **Bulgaria**: 22♀, 2♂, ex. *Rosa canina*, Saranci, June 1996, D. Pilarska (AR). **China**: 1♀ Tien Tsin, 8 September 1929, Cagswell coll. (USNM). **Croatia**: 6♀, ex. *Rosa* sp., Gruda, June 1990 (AR). **Ethiopia**: 1♀, French Somaliland, PQ US quarantine inspection (USNM). **France**: 2♀, ex. *R. alpina*, 5 July 1935, D. P. Limber (USNM); 26♀, 2♂, ex. *R. arvensis*, Marcillac (12†), elev. 400 m, June 1986 (AR); 10♀, ex. *R. canina*, Fontainebleau (77), May 1991 (AR); 12♀, ex. *R. canina*, Six-Fours (83), June 1993 (AR); 35♀, 1♂, ex. *R. ferruginea*, Saint Crépin (05), elev. 990 m, June 1990 (AR); 15♀, 1♂, ex. *R. montana*, Névache (05), elev. 1550 m, June 1987 (AR); 1♂, ex. *R. pendulina*, 30 April 1995, Salles La Source (12), AR (MNHN); 15♀, ex. *R. pendulina*, Briançon (05), elev. 1600 m, June 1987 (AR); 12♀, ex. *R. rubiginosa*, Saint Crépin, elev. 950 m, June 1990 (AR); 25♀, 1♂, ex. *R. spinosissima*, Briançon, elev. 1850 m, July 1990 (AR); 1♀, Dijon (21), 22 June 1973, J. Barbier (MNHN). **Greece**: 2♀, ex. *R. glutinosa*, Parnon Mt, July 1988 (AR). **Hungary**: 5♀, ex. *Rosa* sp., Hortobágy, February 2001, G. Csóka (AR); 4♀, ex. *Rosa* sp., Balatonfürfö, February 2001, G. Csóka (AR). **Iran**: 1♀, ex. 'rose seeds', Washington, DC, US quarantine inspection (USNM). **Iraq**: 1♀, ex. 'rose seeds', 1 May 1953, D. C. Poe, N. Y. Gouldman (USNM). **Italy**: 3♀, ex. *R. pouzini*, San Marcello (Pistoia), 15 June 1992 (AR); 45♀, 2♂, ex. *R. canina*, Barbarano (Vicenza), June 1998 (AR). **The Netherlands**: 2♀, ex. *Rosa* sp., Cadzand-Bad, June 1991 (AR). **Poland**: 15♀, ex. *R. canina*, Ojców Natl. Park, 14 June 1989 (MS). **Russia**: 1♀, ex. *R. dahurica*; 1♀, ex. *R. kamtschatika*; 1♀, ex. *R. mollis*; 1♀, ex. *R. rugosa*, Moscow, US quarantine inspection (USNM). **South Africa**: 1♀, ex. *Rosa* sp, Barkley East, 1994, G. Hemm (AR). **Spain**: 5♀, ex. *R. canina*, Sierra de Guadarrama, nr San Ildefonso la Granja, January 2001 (AR). **Sweden**: 5♀, 2♂ syntypes of *M. collaris*, Westrogothia (1♀), Smolandia (3♂, 3♀), Scandia (2♀) (NHMS); 1♀ ex. *R. andreae*, 1♀ ex. *R. blanda*, 1♀ ex. *R. mayerii*; 1♀ ex. *R. monticola*; 1941, Hoboken Poe, US quarantine inspection (USNM); 2♀, ex. *Rosa* sp., Bogesund, July 2000 (AR). **Switzerland**: 1♀, ex. *R. alpina*, Genève, US quarantine inspection (USNM); 5♀, ex. *Rosa* sp., Sion (Valais), 22 April 1999 (MS).

Megastigmus amicorum Bouček

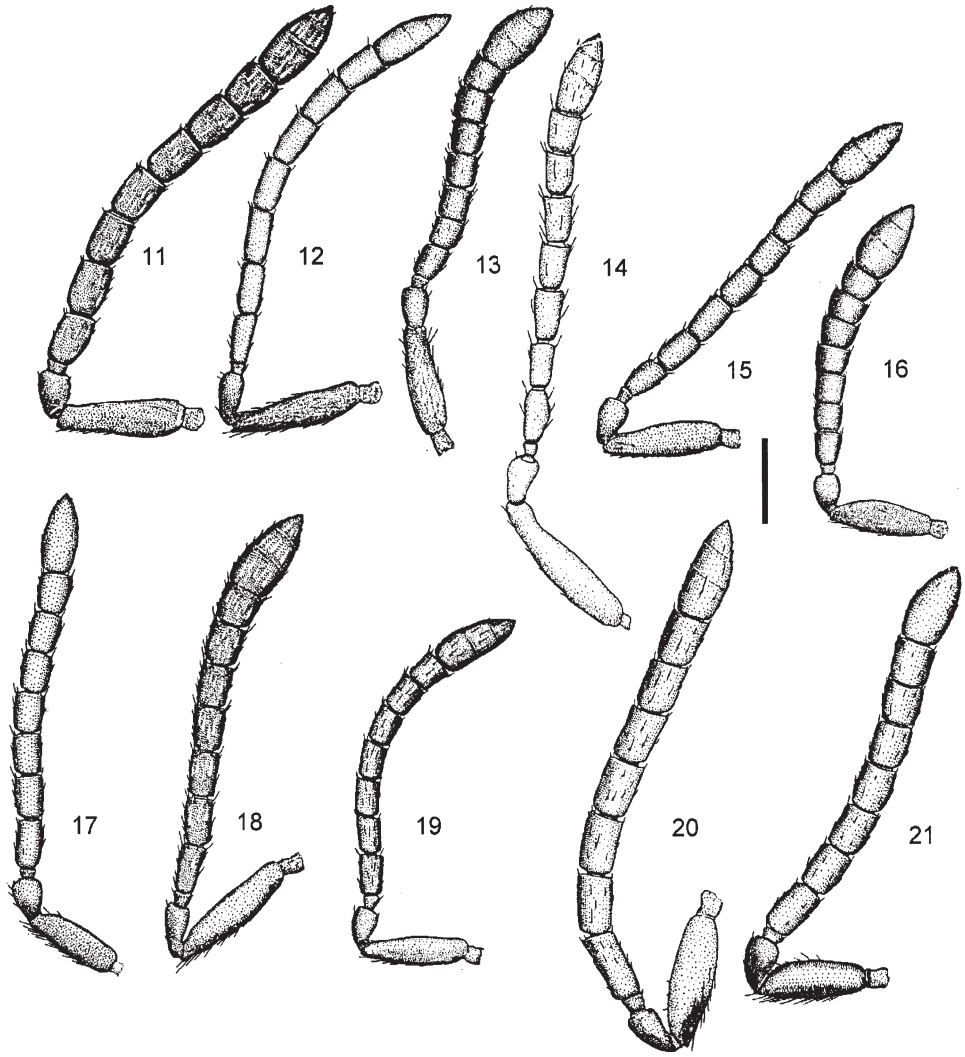
(figures 1, 12, 33, 49, 70, 88, 108, 125, 146)

Megastigmus amicorum Bouček, 1970a: 37–39. Holotype ♀, Biograd na Moru, Dalmatia (NMP [not examined]. 2♀, 1♂ paratypes, same data as holotype (MNHN [1♀ examined]). 1♂ paratype, Cmorg, Sutomore (NMP [1♂ examined]).

Female

Body length (without ovipositor) 3.7 mm. Body orange yellow to dark brown. Head dark testaceous, darker than thorax, except supraclypeal and clypeal area yellowish. Pilosity pale on face, dark on remainder of head. Funicular segments of antenna dark brown but scape, pedicel and anellus yellow. Thoracic dorsum, including the sutures, uniformly orange yellow. Pilosity black on thoracic dorsum, pale on lateral parts. Legs orange yellow, distal part of tarsi black. Wings very setose;

†For France, numbers in brackets correspond to administrative departments.



Figs 11–21. Female antenna of *Megastigmus*. (11) *M. aculeatus*, France; (12) *M. amicorum*, Portugal; (13) *M. atedius*, France; (14) *M. atlanticus*, Morocco; (15) *M. bipunctatus*, France; (16) *M. brevicaudis*, Poland; (17) *M. milleri*, the Netherlands; (18) *M. nigrovariegatus*, France; (19) *M. pictus*, China; (20) *M. pinsapinis*, France; (21) *M. pinus*, Belgium. Scale bar = 200 μm.

forewing stigma dark brown. Propodeum orange. Pilosity on callus and legs whitish, arising from black dots. Gaster dark brown. Ovipositor sheaths black.

Head about 1.5 × as broad as long in dorsal view. Antennal scape elongate, about 4 × as long as broad, 1.2 × longer than pedicel, anellus and first funicular segment combined; pedicel relatively long, as long as first funicular segment; funicular segments 1–4 elongate, about 2.5 × as long as wide (figure 12). Pronotum and mid-lobe of mesoscutum with coarse cross-striation. Anterior part of scutellum with fine transverse rugae, the frenal area with strong longitudinal carinae (figure 125). Forewing stigma roughly oblong, 1.6 × as long as wide; upper part of stigmal vein comparatively short, about 4 × as small as stigma length; uncus short, 0.7 × as long

as upper part of stigmal vein (figure 49). Propodeum without central carina. Ovipositor sheaths distinctly shorter (0.6 ×) than body, only 0.8 × as long as thorax and gaster combined, 1.4 × as long as gaster. Distal end of dorsal valve of ovipositor with strong teeth, the third median tooth broader than others (figure 88).

Male

Body length 3.8 mm. Body darker than in female. Face dark brown except clypeus light brown, temple and gena dark brown, frons and occiput yellow-orange to orange-brown. Antenna light brown except scape dark brown above. Pilosity pale on face, dark on remainder of head. Thoracic dorsum yellow to orange-brown but lateral parts (prepectus, mesopleuron, metapleuron) dark brown to black except lower mesepisternum brownish apically. Pilosity black on thoracic dorsum, pale on lateral parts. Anterior part of fore coxa dark brown, mid- and hind coxa entirely dark brown; middle part of femurs brown; remainder of legs yellowish. Wings very setose, forewing stigma little infuscated, dark brown. Propodeum black. Gaster black with small orange-yellow patch on both extremities.

Head about 1.3 × as broad as long in dorsal view (figure 1). Antennal scape elongate, 1.3 × as long as pedicel, anellus and first funicular segment combined; funicular segments 1–5 elongate, 2.2 × as long as broad, about 1.2 × longer than pedicel (figure 33). Anterior part of scutellum with fine transverse rugae, the frenal area with strong longitudinal carinae (figure 146). Forewing stigma quite circular, 1.2–1.3 × as long as broad; upper part of stigmal vein comparatively very short, about 5.2 × as small as stigma length; uncus short, 0.75 × as long as upper part of stigmal vein (figure 70). Aedeagus elongate, with a narrow aedeagus, digitus with three teeth (figure 108).

Variation

In specimens other than type material, body length varied from 2.5 to 4.0 mm in females, from 2.5 to 4.5 mm in males. The relative length of the exserted part of female ovipositor varied from 0.6 × to 0.7 × the body length. Some male specimens, especially from *Juniperus phoenicea* (e.g. from Ericeira, Portugal) were lighter than the typical form, with the thorax entirely orange-yellow, and the stigma not infuscated at all.

Sex ratio

Generally balanced (Roques, 1983).

Hosts

Develops in seeds of Mediterranean junipers (*Juniperus* spp., Cupressaceae). Observed in *J. oxycedrus* (Bouček, 1970a, 1977; Nikol'skaya and Zerova, 1978; Roques, 1983 as *Megastigmus* sp.; Roques *et al*., 1984; El Hassani and Messaoudi, 1986 as *Megastigmus* sp.; Bouaziz, 1993; Zerova and Seryogina, 1994; Bouaziz and Chakali, 1998; El Alaoui El Fels, 1998), *J. phoenicea* (Roques, 1983; Roques *et al*., 1984; El Alaoui El Fels, 1998) and likely to occur in *J. excelsa* in the eastern Mediterranean basin. Damage to seeds of *J. thurifera* were recorded in Corsica (Roques *et al*., 1984), but not in continental France where these seeds were attacked by *M. bipunctatus*. *M. amicorum* was not observed in seeds of common juniper (*J. communis*) in the areas where common juniper co-exists with Mediterranean junipers, e.g. in southern France (Roques *et al*., 1984). Limited shifts of *M. amicorum*

on to two exotic species of cypress, *Cupressus arizonica* and *C. goveniana*, were recently observed in cypress seed orchards of southeastern France (Roques *et al*., 1999b).

Distribution

Widely distributed in the Mediterranean basin within the range of Mediterranean junipers, i.e. coastal, Mediterranean and sub-Mediterranean vegetation levels. Observed in Bulgaria (Bouček, 1970a; Nikol'skaya and Zerova, 1978); southern France, including Corsica (Bouček, 1977; Roques *et al.*, 1984; Sellenschlo, 1984b); Greece, including Crete (Roques *et al*., 1984; AR); Italy, including Sardinia (Bouček, 1977; Roques *et al*., 1984; AR); Portugal (AR); Spain (AR) but not observed in the Canary Islands although we reared large numbers of juniper cones from that area; Ukraine: Crimea (Nikol'skaya and Zerova, 1978); former Yugoslavia: Croatia, Bosnia, Montenegro, Serbia (Bouček, 1970a, 1977; AR). Present in North Africa: Morocco (High and Middle Atlas; El Hassani and Messaoudi, 1986; El Alaoui El Fels, 1998; AR); Algeria (Bouaziz, 1993; Bouaziz and Chakali, 1998; AR); Tunisia (AR).

Comments

Another species, *M. bipunctatus*, develops in seeds of junipers in the West Palearctic region. Females of *M. amicorum* are easily distinguished by comparing the relative size of the ovipositor sheaths (1.2 × longer than gaster versus 0.9 × as long as gaster or less in *M. bipunctatus*). The males of *M. amicorum*, even of dark form, show a lighter thoracic dorsum, entirely orange-yellow to orange-brown, than most specimens of *M. bipunctatus* whose mesoscutum is olive-brown. Light forms of *M. bipunctatus* with a thoracic dorsum entirely yellowish can be confusing but the stigma shape, quite circular in *M. amicorum* (figure 70) versus oval-elongate (figure 72) in *M. bipunctatus*, allows one to differentiate between the two species. In addition, the aedeagus of *M. amicorum* is narrow and elongate (figure 108) whilst that of *M. bipunctatus* is short and rounded (figure 110).

Two other species, *M. wachtli* and *M. atlanticus*, attack cypress seeds within the region. Diagnostic characters allowing separation of the females are given in the chapter concerning *M. atlanticus.* For males, the upper part of the stigmal vein is comparatively longer in *M. amicorum* (1.5–2 × as long as uncus; figure 70) than in *M. wachtli* (2.0x smaller than uncus; figure 86). The two species also differ by the genital apparatus, digitus bearing six teeth in *M. wachtli* (figure 8) and only three in *M. amicorum* (figure 108). Males of *M. atlanticus* are not yet known.

Material examined

Algeria: 1♀, 2♂, ex. *J. oxycedrus*, Meurdja Arboretum, June 1993, K. Bouaziz (AR). **Croatia**: 2♀, 1♂ paratype, Biograd na Moru, 12 July 1969, Z. Bouček (MNHN); 7♀, 8♂, ex. *J. oxycedrus*, Dubrovnik, July 1990 (AR). **France**: 8♀, 5♂, ex. *Juniperus oxycedrus*, Ponte Leccia (Corsica), June 1981 (AR); 11♀, 12♂, ex. *J. oxycedrus*, Cassis (13), June 1983 (AR); 6♀, 5♂, ex. *J. oxycedrus*, Sigean (11), June 1983 (AR); 4♀, 6♂, ex. *J. phoenicea*, Rondinara (Corsica), June 1982 (AR); 10♀, 8♂, ex. *J. phoenicea*, Lubéron Mt (84), July 1983, J. P. Fabre (AR); 5♀, 8♂, ex. *J. thurifera*, Cuccia (Corsica), June 1982 (AR); 1♀, 2♂, ex. *Cupressus arizonica*, Le Rouet seed orchard (83), August 1996, (AR); 4♀, 2♂, ex. *C. goveniana*, Le Rouet seed orchard (83), August 1995 (AR). **Greece**: 6♀, 7♂, ex. *J. phoenicea*, Kalogria

(Peloponnesis), June 1991 (AR); 9♀, 8♂, ex. *J. phoenicea*, Romanu (Peloponnesis), June 1991 (AR). **Italy**: 8♀, 4♂, ex. *J. oxycedrus*, Bari, July 1990 (AR). **Morroco**: 4♀, 4♂, ex. *J. phoenicea*, Asni, Marrakech, 27 June 1989, A. El Hassani (AR); 6♀, 5♂, ex. *J. oxycedrus,* Tizrag, July 1999 (AR); 3♀, 2♂, ex. *J. thurifera*, Tizrag, July 1999 (AR). **Portugal**: 2♀, 1♂, ex. *J. phoenicea*, Cabo Espichel, July 1993 (AR); 2♀, 1♂, ex. *J. phoenicea*, Corveiro (Algarve), July 1993 (AR); 10♀, 8♂, ex. *J. phoenicea*, Ericeira, July 1994 (AR). **Spain**: 3♀, 5♂, ex. *J. phoenicea*, Pueblo San Miguel (Valencia), July 2001, P. García-Fayos (AR). **Tunisia**: 2♀, 3♂, ex. *J. oxycedrus*, Tabarka, June 1987 (AR). **Yugoslavia**: 1♀ paratype, Cmorg, Sutomore (Montenegro), 6 July 1968, Z. Bouček (NMP); 5♀, 4♂, ex. *J. oxycedrus*, Boka Kotorska (Montenegro), June 1990 (AR).

Megastigmus atedius Walker

(figures 13, 34, 50, 71, 89, 109, 126, 147)

Megastigmus atedius Walker, 1851: 214. Holotype ♀, England (Oxford University Museum [not examined]).

Megastigmus piceae Rohwer, 1915: 97–98. Holotype ♀, Crescent City, California, USA (USNM [examined]). Synonymy by Bouček, 1970b: 265.

Megastigmus zwoelferi Scheffer-Immel, 1957: 53–56. Syntypes ♀ and ♂, Odenwald, Germany (FIUG [1♀, 2♂ examined]). Synonymy by Bouček, 1970b: 265.

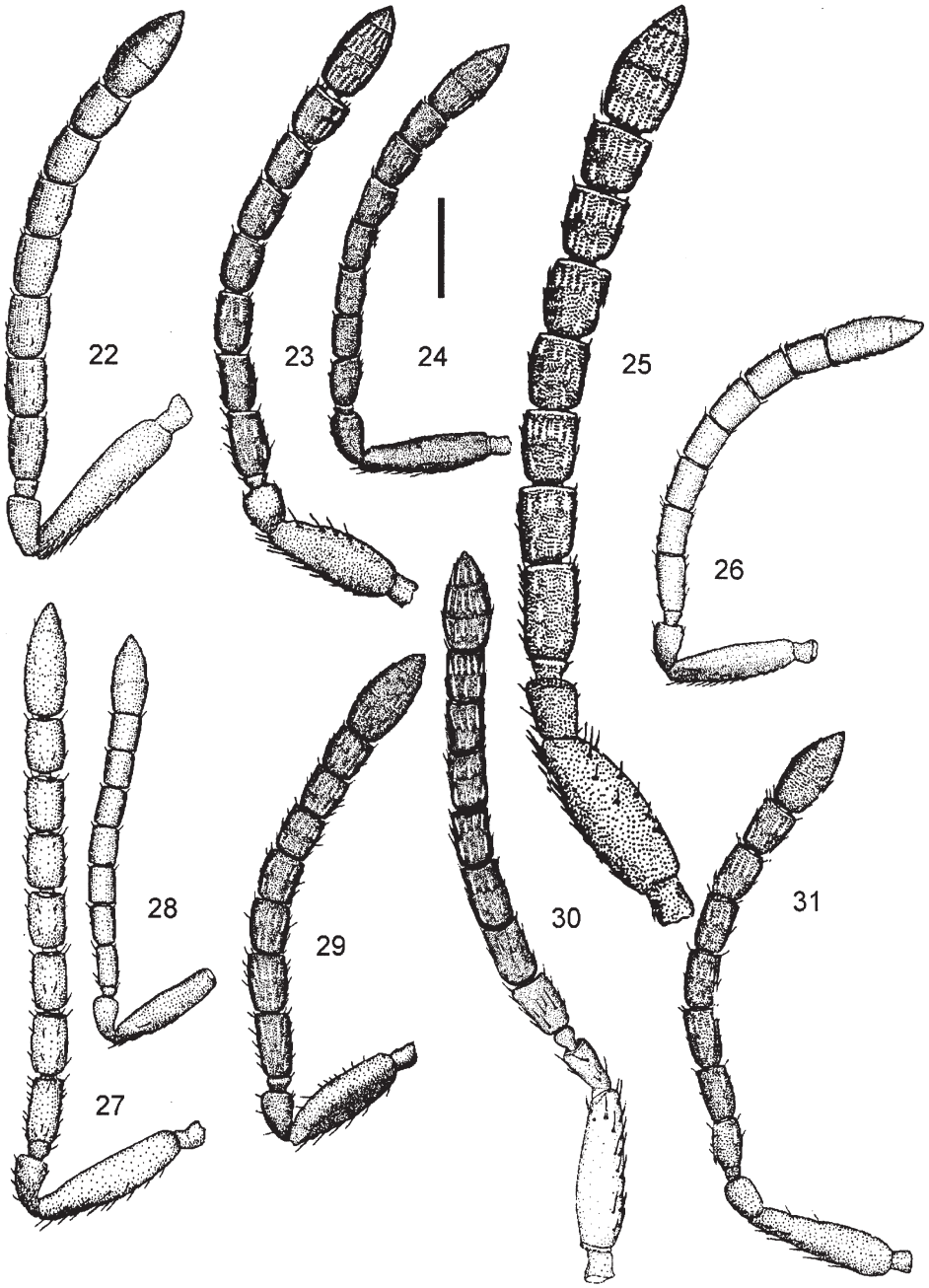
Female

Body length (without ovipositor) 2.7 mm. Body colour mostly black with yellow markings. Lower face yellow to brownish yellow except a median brown to black spot extending on to supraclypeal area; lower gena and temple light brownish; remainder of the head black except a small, triangular yellow spot above eye. Pilosity pale on lower face, black on remainder of head. Antenna light brown with scape and pedicel yellowish beneath. Thorax entirely black except two slightly transverse dark yellowish spots on posterior part of pronotum, the spots being separated from each other by about their own width at least, and tegula yellowish. Pilosity black on thoracic dorsum. Legs mostly brownish yellow except mid- and hind coxa black. Wings subhyaline; disc of basal cell of forewing bearing eight hairs. Propodeum black with numerous pale bristles on callus. Gaster dark brown to black, with lighter sterna. Ovipositor sheaths dark brown to black.

Head only 1.2 × as broad as long in dorsal view. Antennal scape 1.2 × as long as pedicel, anellus and first funicular segment combined; funicular segments 2–7 nearly as broad as long (figure 13). Mid-lobe of mesoscutum and anterior part of scutellum finely cross-striated, the frenal area quite entirely smooth with a few short longitudinal grooves extending from the hind margin (figure 126). Scutellum 1.2 × as long as broad. Forewing stigma nearly oval, 1.3 × as long as broad; upper part of stigmal vein comparatively elongate, 0.8 × as long as stigma length; uncus about 0.6 × as long as upper part of stigmal vein (figure 50). Propodeum with an irregular median carina (figure 126). Exserted part of ovipositor 0.8 × as long as body, nearly equal to combined length of thorax and gaster. Distal part of dorsal valve of ovipositor bearing small, elongate teeth (figure 89).

Male

Body length 2.8 mm. Body colour mostly black with yellow markings. Lower face yellow to brownish-yellow, without brown spots; remainder of head black



FIGS 22–31. Female antenna of *Megastigmus*. (22) *M. pistaciae*, Croatia; (23) *M. rafni*, France; (24) *M. rosae*, France; (25) *M. schimitscheki*, Lebanon; (26) *M. specularis*, Finland; (27) *M. spermotrophus*, France; (28) *M. strobilobius*, Poland; (29) *M. suspectus*, France; (30) *M. transvaalensis*, Morocco; (31) *M. wachtli*, Greece. Scale bar = 200 μm.

except a yellow patch extending on gena and temple adjacent to eye margin. Pilosity pale on lower face, black on remainder of head. Thorax black except two yellow rounded spots on posterior part of pronotum. Pilosity black on thoracic dorsum, pale laterally. Legs mostly brownish yellow except mid- and hind coxa black. Wings subhyaline; disc of basal cell of forewing bearing only six hairs. Propodeum black, with numerous pale bristles on callus. Gaster dark brown with yellowish brown spots on sides, expanding on the last terga.

Head 1.3 × as broad as long in dorsal view. Antennal scape 1.2 × as long as pedicel, anellus and first funicular segment (figure 34). Thorax and propodeum sculpture as in female (figure 147). Forewing stigma wider than that of female, nearly as long as broad; upper part of stigmal vein comparatively elongate, about 0.7 × as long as stigma length; uncus very elongate, as long as upper part of stigmal vein (figure 71). Aedeagus short, digitus with four teeth (figure 109).

Variation

The above description is based on the type material of *M. piceae* for female and *M. zwoelferi* for male. In the other specimens we examined, body length varied from 1.9 to 4.0 mm in females, from 1.9 to 3.4 mm in males. Females emerging from seeds of *Picea* spp. were usually smaller (1.9–3.0 mm) than these emerging from *Pinus* spp. According to Hussey (1967), body length of females from *Pinus contorta* is longer than that of females from *P. strobus* (4.0 versus 3.3–3.5 mm). Very few colour variations were recorded. The transverse yellowish spots on pronotum were absent in the darkest female specimens (Bouček, 1970b). The basal cell of forewing bore from four to eight hairs in both sexes. Hussey (1967) also noticed a difference in the number of stout bristles on the posterior two-thirds of submarginal vein according to host species (10–12 in females from *P. strobus* vs eight to nine in these from *P. contorta*). However, this number varied from 8 to 12 in our specimens, which emerged from *P. strobus* and *Picea orientalis*, and we did not find any definite pattern related to host. In the same specimens, the relative length of the exserted part of female ovipositor varied from 0.8 to 0.9 × the body length. Hussey (1967) observed a male specimen with four teeth on the left digitus but five on the right one.

Sex ratio

Quite balanced in most of the European records (Scheffer-Immel, 1957; Lessmann, 1974b). According to Ostermeyer (1990) and Da Ros *et al.* (1993), male proportion differed with host species in France: 19.2% in *Picea orientalis* vs 66.6% in *Pinus strobus*.

Hosts

In the native North American areas, hosts consist of several spruce species [*Picea* spp., Pinaceae: *P. engelmannii*, *P. glauca* Moench. (Boss.), *P. mariana* (Mill.) B.S.P., *P. pungens* and *P. sitchensis*; Milliron, 1949; Grissell, 1979; Hedlin *et al.*, 1980; Ruth *et al.*, 1980; Turgeon and de Groot, 1992; Turgeon, 1994] and the eastern white pine (*Pinus strobus*; Speers, 1974; Turgeon, 1994). In addition, Hussey (1967) recorded emergence from seeds of lodgepole pine (*Pinus contorta* Loud. subsp. *murrayana*) imported from USA (Washington State) to Great Britain although this tree species was not mentioned as a host in the insect native range (Hedlin *et al.*, 1980). According to Bouček (1970b), an earlier record of Hoffmeyer (1931a) in seeds of *Abies lasiocarpa* var. *arizonica* Merriam sent from the USA to Denmark is very

doubtful. We examined the corresponding slides (forewing, antenna and genitalia of ♀ and ♂) of the Hoffmeyer collection. Without any doubt, the stigmas, antenna and genitalia are similar to these of *M. atedius*. Therefore, it is possible that the host seeds were not correctly identified.

Once introduced into Europe, *M. atedius* was found in the seeds of the introduced *Pinus strobus* (Gäbler, 1954, 1958; Scheffer-Immel, 1957; Kapuściński, 1966; Bouček, 1970b; Lessmann, 1974b; Bekreneva and Tropin, 1975; Nikol'skaya and Zerova, 1978; Ostermeyer, 1990; Da Ros *et al*., 1993). Infestation was also recorded on two American spruce species introduced to Europe, *Picea sitchensis* (Hussey, 1954b; Ochsner, 1998; Jensen and Ochsner, 1999) and *P. engelmannii* (Hussey, 1954b). However, we did not find this insect in seeds of any of the original American spruce hosts during the extensive survey performed at the Les Barres arboretum in France. The very limited number of filled seeds in these species may, however, have prevented successful chalcid attacks (Da Ros *et al*., 1993). In western Europe, *M. atedius* also shifted to oriental spruce, *Picea orientalis* (Bouček, 1970b; Lessmann, 1974b; Křístek *et al*., 1992; Da Ros *et al*., 1993; Ochsner, 1998; Jensen and Ochsner, 1999) and Serbian spruce, *P. omorica* (Ochsner, 1998; Jensen and Ochsner, 1999; AR), but it is not yet recorded from the natural range of these two spruce species in Asia Minor and Yugoslavia, respectively (Çanakçioglü, 1959, 1969; Mihajlović and Glavendekić, 1986). No attack was ever observed on the native Norway spruce, *Picea abies*, except one infested seed (!) recorded by Lessmann (1974b).

Distribution

Originates from North America, the native range covering northern and western USA (Milliron, 1949; Keen, 1958; Speers, 1974; Grissell, 1979; Hedlin *et al*., 1980) and Canada (Ruth *et al*., 1980; Turgeon and de Groot, 1992). Introduced to Europe where it is presently recorded from the western, central and eastern parts: Czech Republic (Křístek *et al*., 1992); Denmark (Ochsner, 1998; Jensen and Ochsner, 1999); France (Ostermeyer, 1990; Da Ros *et al*., 1993; AR); Germany (Scheffer-Immel, 1957; Lessmann, 1974b; Bouček, 1970b); Great Britain (Hussey, 1954b, 1967; Bouček, 1970b); Poland (Kapuściński, 1966); Russia: Northwest (Bekreneva and Tropin, 1975; Nikol'skaya and Zerova, 1978).

Comments

In Europe, spruce seeds are also attacked by a native species, *M. strobilobius*. Both sexes of *M. atedius* differ from *M. strobilobius* by the pilosity on disc of the forewing basal cell (four to eight hairs versus 10–18 hairs), and the sculpture of hind part of mid-lobe of mesoscutum (fine transverse cross-striae vs very arcuate cross-striae). The yellowish patterns on the posterior margin of pronotum (two tranverse spots in *M. atedius* versus a cross-band very narrowly interrupted in the middle in *M. strobilobius*) appear more variable and difficult to be used with certainty, especially for separating males. Forewing stigma is usually more elongate in *M. strobilobius* (1.8 vs. 1.3 × as long as broad in females; 1.3 × versus about as long as broad in males).

No other chalcid species has been observed in pine seeds in Europe for the moment.

Material examined

France: 2♀, ex. *P. omorica*, Arboretum des Barres (45), June 1996 (AR); 1♀, 2♂, ex. *Picea orientalis*, Amance Arboretum (54), June 1978; 12♀, 13♂, ex. *Picea orientalis*, Arboretum des Barres (45), June 1991, R. Ostermeyer (AR); 3♀, 5♂, ex. *Pinus strobus*, Arboretum des Barres (45), June 1990, R. Ostermeyer (AR); 3♀, 1♂, ex. *P. strobus*, Dampierre en Burly (45), June 1993 (AR); 2♀, 2♂, ex. *P. strobus*, Treffor Forest (01), June 1993, J. Castille (AR). **Germany**: 1♀, 2♂, ex. *Pinus strobus*, Hessen, Berfelden Odenwald, 2–17 January 1956, H. Münden (FIUG); 1♀, ex. *P. orientalis*, Halzminden Oktib, D. Lessman (MNHN). **USA**: 1♀ holotype *M. piceae*, Crescent City, CA, USA (USNM); one slide with wing and antenna of ♀, wing, antenna and penis of ♂, ex. '*Abies arizonica*', Amazona, 6 June 1929, seeds sent to Rafn and Søn (Denmark), Hoffmeyer coll. (ZMUC); one slide with four wings ♀, four wings ♂, January 1929; seeds sent to Rafn and Søn (Denmark), Hoffmeyer coll. (ZMUC).

Megastigmus atlanticus Roques and Skrzypczyńska, sp. nov.
(figures 6, 14, 51, 90, 127)

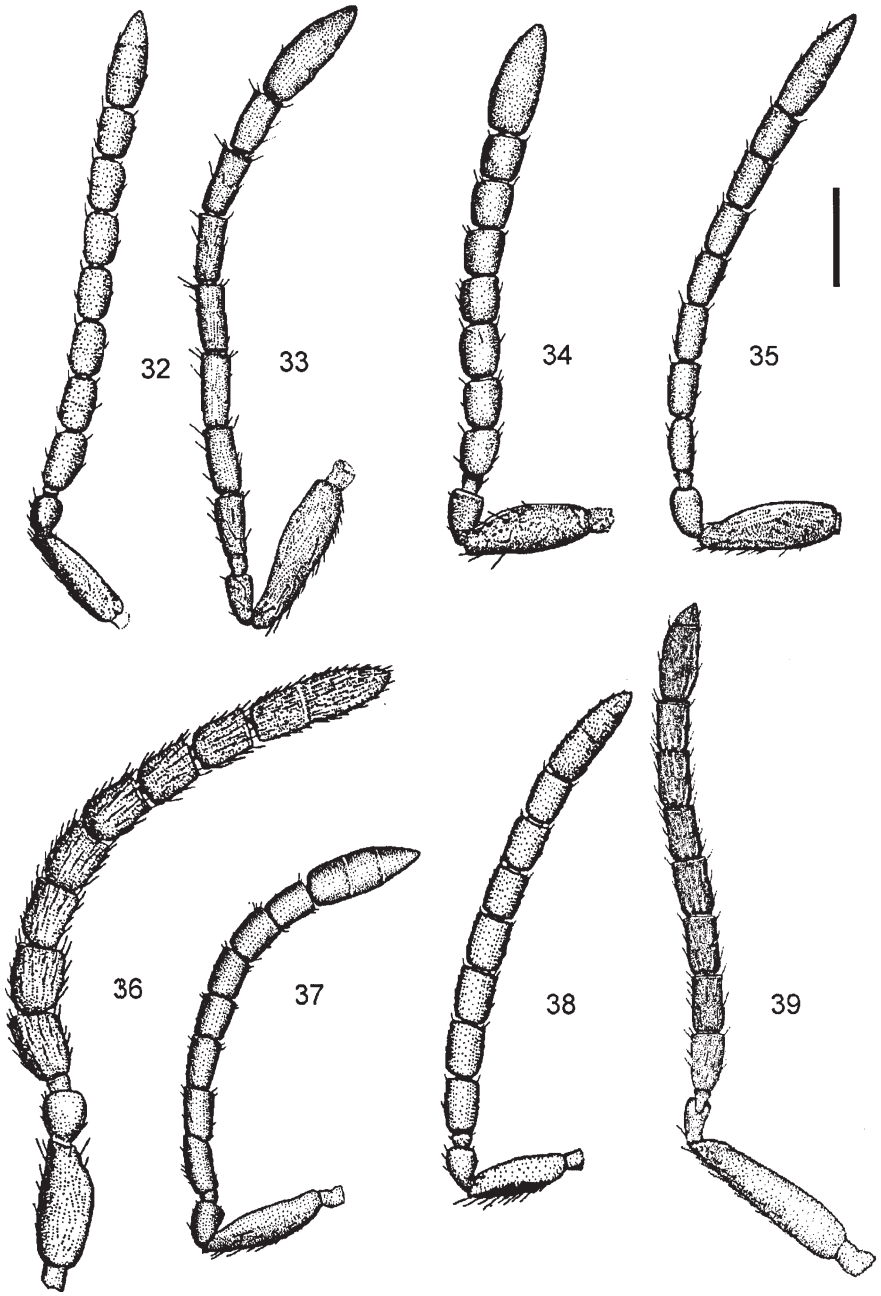
Holotype female

Body length (without ovipositor) 2.5 mm; length of exserted part of ovipositor 1.6 mm. Body colour dark orange. Head light orange except occelli and occipital carina surrounded with black. Pilosity mostly pale on head. Antenna with scape, pedicel and anellus yellowish, the funicular segments brownish yellow. Pronotum light orange; remainder of thorax quite entirely dark orange except transscutal articulation, suture of prepectus, and sublateral grooves black, anterior suture of mid-lobe of mesoscutum brownish, and an elongate black spot on lateral panel of metanotum. Pilosity pale on thoracic dorsum. Legs yellowish orange, with claws darker. Wings subhyaline; forewing stigma light brown. Propodeum dark brown in the middle part, the anterior suture black; callus yellowish with pale hairs extending from conspicuous black dots. First apparent segment of gaster blackish; remainder of gaster mostly yellowish brown with darker bands on distal part of terga, which extend laterally. Ovipositor sheaths black.

Head about 1.2 × as broad as long in dorsal view. Eyes little protruding. Scape elongate, reaching level of clypeus, 0.9 × as long as combined length of pedicel, anellus, first and second funicular segments (figure 14); pedicel elongate, nearly twice as long as wide; anellus subquadrate; first funicular segment 1.3 × as long as pedicel, nearly twice as long as wide, the following funicular segments progressively tending to subquadrate. Thorax about 1.6 × as long as width of mesoscutum. Pronotum, mid- and lateral lobes of mesoscutum, and axilla with strong cross-striae (figure 6). Scutellum 1.2 × as long as wide, with coarse transverse carinae on the anterior part; frenal area mostly smooth with a few longitudinal carinae on the lateral parts (figure 127). Stigma elongate, about 2 × as long as wide; upper part of stigmal vein comparatively short, *ca* 4 × as small as stigma length; uncus 0.8 × as long upper part of stigmal vein (figure 51). Propodeum without median carina (figure 6). Ovipositor sheaths 0.7 × as long as body, nearly (0.8 ×) as long as thorax and gaster combined, 2.1 × as long as gaster. Distal end of dorsal valve of ovipositor bearing strong first and second median teeth (figure 90).

Male

Not known.



FIGS 32–39. Male antenna of *Megastigmus*. (32) *M. aculeatus*, France; (33) *M. amicorum*, Portugal; (34) *M. atedius*, France; (35) *M. bipunctatus*, France; (36) *M. milleri*, the Netherlands; (37) *M. pictus*, Poland; (38) *M. pinus*, France; (39) *M. pistaciae*, Italy. Scale bar = 200 μm.

Variation

Females ranged in length from 2.4 to 2.8 mm, with length of exserted part of ovipositor varying from 1.6 to 1.8 mm. Body colour was little variable, except head which could be dark orange and propodeum light brown with a black anterior suture.

Material examined

Type material. HOLOTYPE ♀, Amizmiz, Morocco, ex. 20 September 1995 from seeds of *Cupressus atlantica* (Cupressaceae) collected in summer 1995 (A. El Hassani), deposited at MNHN. PARATYPES: 3♀, with same rearing data as holotype, deposited at MNHN; 5♀, Marakkech, Morocco, ex. 14 October 1998 from seeds of *C. atlantica* collected August 1998 (A. El Alaoui El Fels), deposited at Faculty of Sciences Semlalia, Marrakech, Morocco; 8♀, Idni, Morocco, ex. 5 October 1999 from seeds of *C. atlantica* (A. El Alaoui El Fels) deposited in AR collection.

Non-type material. **Algeria**: 1♀, Chréa, ex. 12 April 1993 from seeds of *Cupressus macrocarpa*, K. Bouaziz leg. (AR). **Morroco**: 2♀, Marakkech, ex. 10 October 1998 from seeds of *C. sempervirens*, A. El Alaoui El Fels leg. (AR).

Etymology

Named from the host species, *Cupressus atlantica*.

Hosts

Develops specifically in seeds of cypresses, *Cupressus* spp. (Cupressaceae). It probably originates from *C. atlantica* in Morocco but it has shifted on some exotic species of cypress introduced to north Africa: the East Mediterannean *C. sempervirens* and the American *C. macrocarpa*. *Megastigmus* emergence holes were observed on another cypress species native of Algeria, *C. dupreziana* (Bouaziz, 1993), but the species could not be ascertained yet.

Distribution

North Africa: Algeria, Morocco.

Comments

Two other species, *M. amicorum* and *M. wachtli*, attack seeds of cypresses within the Mediterranean range. The relative length of the exserted part of female ovipositor allows an easy differentiation of *M. wachtli*. In that species, the ovipositor sheaths are nearly 3.0× longer than gaster and 1.2–1.3× longer than body whereas they are smaller than gaster and thorax combined in *M. atlanticus* and *M. amicorum*. Females of *M. atlanticus* differ from these of *M. amicorum* (as well as from these of *M. wachtli*) by the pale pilosity of the thoracic dorsum.

Megastigmus bipunctatus (Swederus)
(figures 4, 15, 35, 52, 72, 91, 110, 128, 148)

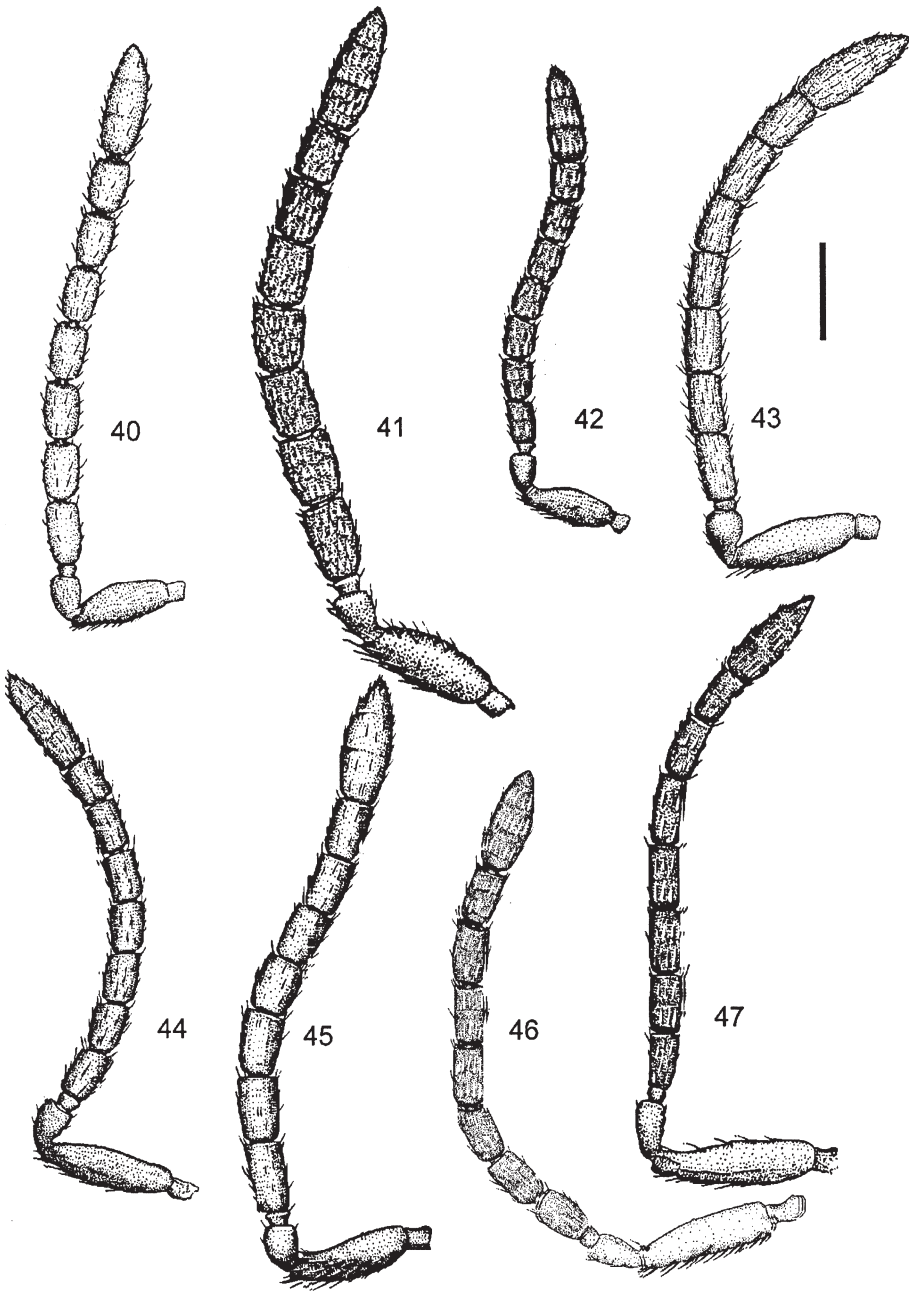
Pteromalus bipunctatus Swederus, 1795: 205. Sex and number unknown, Sweden (depository unknown).

Torymus erythrothorax Nees, 1834: 65. Syntypes ♂, locality unknown (destroyed; Grissell, 1999). Synonymy by Dalla Torre, 1898: 286.

Megastigmus microspilus Thomson, 1876: 62. Syntype ♀, Sweden (Museum of Zoology, Lund [not examined]. Synonymy by Hoffmeyer, 1931b: 266.

Megastigmus microphilus Thomson, Dalla Torre, 1898: 287 [misspelling].

Megastigmus kuntzei Kapuściński, 1946: 12–19, 120–129. Holotype ♀, Myslenice, Poland (NHMK [not examined]); 1♀ paratype, same data as holotype (NHMK [examined]); 1♂ paratype, Wąbrzeżno, Poland (NHMK [examined]). Synonymy by Nuorteva 1967: 123.



FIGS 40–47. Male antenna of *Megastigmus*. (40) *M. rafni*, the Netherlands; (41) *M. schimitscheki*, Lebanon; (42) *M. specularis*, Finland; (43) *M. spermotrophus,* France; (44) *M. strobilobius*, France; (45) *M. suspectus*, France; (46) *M. transvaalensis* Morocco; (47) *M. wachtli*, Greece. Scale bar = 200 μm.

Female

Body length (without ovipositor) 2.7 mm. Body colour predominantly brownish olive-grey and black. Head olive to grey brownish except vertex, gena and lower

face brownish black, and occipital area black. Pilosity pale on lower face, black on remainder of head. Antenna grey brownish with scape, pedicel and anellus brownish yellow. Pronotum light olive brown. Mesoscutum brownish with anterior parts of mid-lobe and lateral lobes darker; notuli black. Scutellum and axilla brownish yellow except anterior part of axilla dark brown. Remaining parts of thorax black. Pilosity black on thoracic dorsum. Fore coxa brown at basis, remainder yellowish brown; mid- and hind coxa brown; remainder of legs yellowish brown except hind femur brown on dorsal side. Wings slightly blackened, very setose; forewing stigma brown. Propodeum black except callus brown. Gaster brownish yellow to black, with the last tergum grey. Ovipositor sheaths black.

Head about 1.3 × as broad as long in dorsal view (figure 4). Eyes hardly protruding, large and wide-oval; temple in dorsal view about 0.4 × length of eye. Postocellar distance about 2 × as long as ocellocular distance. Relative measurements: eye 17:15, malar space 5, width of head 22, width of frons 14. Antenna scape slightly longer (1.1 ×) than combined length of pedicel, anellus and first funicular segment; pedicel about 2 × as long as broad, slightly longer (1.1 ×) than first funicular segment; funicular segments about 2 × as long as wide (figure 15). Pronotum and mid-lobe of mesocutum with strong transverse carinae. Scutellum about 1.1 × as long as broad, the anterior part with arcuate, coarse rugae; frenal area smooth with a few strong longitudinal carinae (figure 128). Propodeum with central carina (figure 128). Forewing stigma roughly ovoid, about 1.3 × as long as broad; upper part of stigmal vein half as long as width of stigma; uncus very short, 0.4 × as long as upper part of stigmal vein (figure 52). Ovipositor sheaths much shorter (0.4 ×) than body, slightly shorter than gaster (0.9 ×). Distal part of the dorsal valve of ovipositor with a very large third median tooth (figure 91).

Male

Body length 3.0 mm. Body colour predominantly brownish olive-grey and black. Head black except parascrobal area and clypeus olive-brown. Pilosity pale on lower face, black on remainder of head. Antenna grey brownish with scape, pedicel and anellus brownish yellow. Pronotum light olive-brown. Mesoscutum brownish with anterior parts of mid-lobe and lateral lobes darker; notuli black. Scutellum and axilla brownish yellow except anterior part of axilla dark brown. Metanotum with dorsellum yellowish and lateral panel dark brown. Lateral parts of thorax mostly dark brown except prepectus, tegula and acropleuron brownish. Pilosity black on thoracic dorsum. Anterior part of fore coxa light brown, mid-and hind coxa dark brown, remainder of legs yellow. Wings slightly blackened, very setose; forewing stigma dark brown. Propodeum shining black. Gaster mostly brownish black with a few lighter stripes on sides.

Head about 1.3 × as broad as long. Antenna scape slightly longer (1.1 ×) than combined length of pedicel, anellus and first funicular segment; pedicel slightly smaller (0.9 ×) than first funicular segment; funicular segments 1–6 twice as long as broad (figure 35). Pronotum and mid-lobe of mesocutum with strong transverse carinae. Scutellum more elongate than in female, about 1.3 × as long as broad, the anterior part with arcuate, coarse rugae; frenal area smooth with a few strong longitudinal carinae (figure 148). Forewing stigma oval-elongate, about 1.4 × as long as broad; upper part of stigmal vein comparatively short, about as long as one-third of stigma width; uncus short, 0.6 × as long as upper part of stigmal vein

(figure 72). Propodeum without median carina. Aedeagus rounded, digitus with three teeth (figure 110).

Variation

The above description is based on the type material of *M. kuntzei*. In the other specimens we examined, body length varied from 1.8 to 3.1 mm in females, from 1.8 to 3.2 mm in males. Little variation was observed in female colour all over Europe. In specimens originating from the French Alps, the olive-grey colour of pronotum was replaced by dark orange-yellow. Most males of the same origin emerging from *Juniperus communis* were much darker than the type material, with the dorsum and lateral parts of thorax entirely dark brown except the pronotum orange-yellow, the coxae mostly black except distal end of fore coxa and a conspicuous black patch on femurs. In contrast, the Alpine specimens emerged from *J. sabina* showed a thoracic dorsum predominantly orange-yellow except indefinite small brownish spots on anterior parts of mesoscutum. However, the propodeum was always partly black at least, with a brownish callus, and the gaster quite entirely black with a few small, lateral brownish spots at the apical extremity. A few individuals from both sexes presented a central carina on propodeum.

Moroccan specimens of both sexes emerged from *Juniperus thurifera* appeared to differ largely from the type material. Both male and female presented a predominant dark yellow colour on head and thorax, with a pronotum pale yellow, and black markings limited to notuli, suture of axilla and a line on lateral panel of metanotum. In female, gaster was predominantly orange-yellow with a dark brown patch on dorsum of terga III–V. In male, gaster presented a dark brown petiole and four dark brown lateral stripes alternating with dark yellow lateral stripes. Genetic tests are presently carried out to understand whether these Moroccan specimens correspond to a different species.

Sex ratio

Balanced in most cases (Vikberg, 1966; Lessmann, 1974b; Roques, 1983).

Hosts

Specialized in seeds of alpine junipers (*Juniperus* spp., Cupressaceae). Many records from *J. communis* (=*J. nana*; among others, Kapuściński, 1946; Vikberg, 1966; Nuorteva, 1967; Lessmann, 1974a; Göttsche, 1976; Stadnickii *et al*., 1978; Roques, 1983; Voolma, 1986; Křístek *et al*., 1992; Dolgin, 1994; García, 1997, 1998), and *J. sabina* (Roques, 1983; García *et al*., 1997). The submediterranean species, *J. thurifera*, was attacked in the Alps (Roques *et al*., 1984) and Morocco (El Hassani and Messaoudi, 1986 as *Megastigmus* sp.; El Alaoui El Fels *et al*., 1999 as *Megastigmus* sp.; AR). Records from *J. excelsa* Bieb. (Seitner in Wall, 1984) may refer to *M. amicorum*.

Distribution

Widely distributed all over Europe. Extends to western Siberia at least. Recorded from Austria (Milliron in Lessmann, 1974b; Wall, 1984); former Czechoslovakia (Čermak, 1952; Bouček, 1954; Křístek *et al*., 1992); Denmark (Hoffmeyer, 1931b; Jespersen and Lomholdt, 1983; Ochsner, 1998; Jensen and Ochsner, 1999); Estonia (Voolma, 1986; Luik and Voolma, 1988); Finland (Vikberg, 1966; Nuorteva, 1967); France including Corsica (Roques, 1983; Roques *et al*., 1984); Germany (Gäbler,

1962; Lessmann, 1974a, 1974b; Göttsche, 1976; Schneider, 1985); Great Britain (Laidlaw, 1931; Bouček, 1970b); Hungary (Györfi, 1962); Italy (Lessmann, 1974b; AR); Morocco (El Hassani and Messaoudi, 1986 as *Megastigmus* sp.; El Alaoui El Fels *et al*., 1999 as *Megastigmus* sp.; AR); Poland (Kapuściński, 1946; Borusiewicz and Kapuściński, 1948); Romania (Kapuściński, 1946); Russia from Kola peninsula and Karelia to Komi Republic, Transcaucasia, Uzbekistan, Khazakhstan and western Siberia (Nikol'skaya, 1952, 1966; Vikberg, 1966; Nikol'skaya and Zerova, 1978; Stadnickii *et al*., 1978; Dolgin, 1994); Sweden (Wall, 1984; AR); Spain (García, 1997, 1998; García *et al*., 1997; AR); Switzerland (Wall, 1984; Hanson, 1991); Ukraine (Zacher, 1932); former Yugoslavia: Montenegro, Serbia, Slovenia (Bouček, 1977).

Comments

Another species, *M. amicorum*, may infest seeds of incense cedar, *J. thurifera*, in some parts of the range. Diagnostic characters for separating the two species are given in the chapter concerning *M. amicorum.*

Material examined

France: 2♀, 3♂, ex. *Juniperus communis*, Fontainebleau (45), May 1979 (AR); 8♀, 5♂, ex. *J. communis*, Marcillac (12), elev. 400 m, July 1991 (AR); 6♀, 8♂, ex. *J. communis*, Névache (05), elev. 1600 m, August 1988 (AR); 5♀, 10♂, ex. *J. communis* (*J. nana*), Névache, elev. 1850 m, August 1988 (AR); 22♀, 25♂, ex. *Juniperus communis*, Briançon (05), elev. 1550 m, July 1983 (AR); 6♀, 4♂, ex. *J. sabina*, Saint Crépin (05), elev. 990 m, July 1990 (AR); 4♀, 3♂, ex. *J. thurifera*, Saint Crépin, July 1990 (AR). **Italy**: 6♀, 5♂, ex. *J. communis*,Vittignano (BO), May 1992 (AR). **Morroco**: 3♀, 2♂, ex. *J. thurifera,* Tizrag, July 1999 (AR); 4♀, 5♂, ex. *J. thurifera,* Lazaden, July 1999 (AR); 3♀, 2♂, ex. *J. thurifera,* Tizrag, July 2000, M. A. El Alaoui El Fels (AR). **Poland**: 1♂, ex. *J. communis,* Wąbrzeżno, forest district Leśno, 15 June 1946, T. Wiśniewski (coll. S. Kapuściński, Kraków, MS); 4♀, 4♂, ex. *J. communis*, Karpaty, Pochyba (Kraków), 9 August 1957, S. Kapuściński (MNHN). **Sweden**: 2♀, 1♂, ex. *J. communis*, Bogesund, July 2000 (AR). **Spain**: 10♀, 10♂, ex. *J. communis*, Sierra Nevada, 1997, D. García (AR); 10♀, 10♂, ex. *J. sabina*, Sierra Nevada, 1997, D. García (AR).

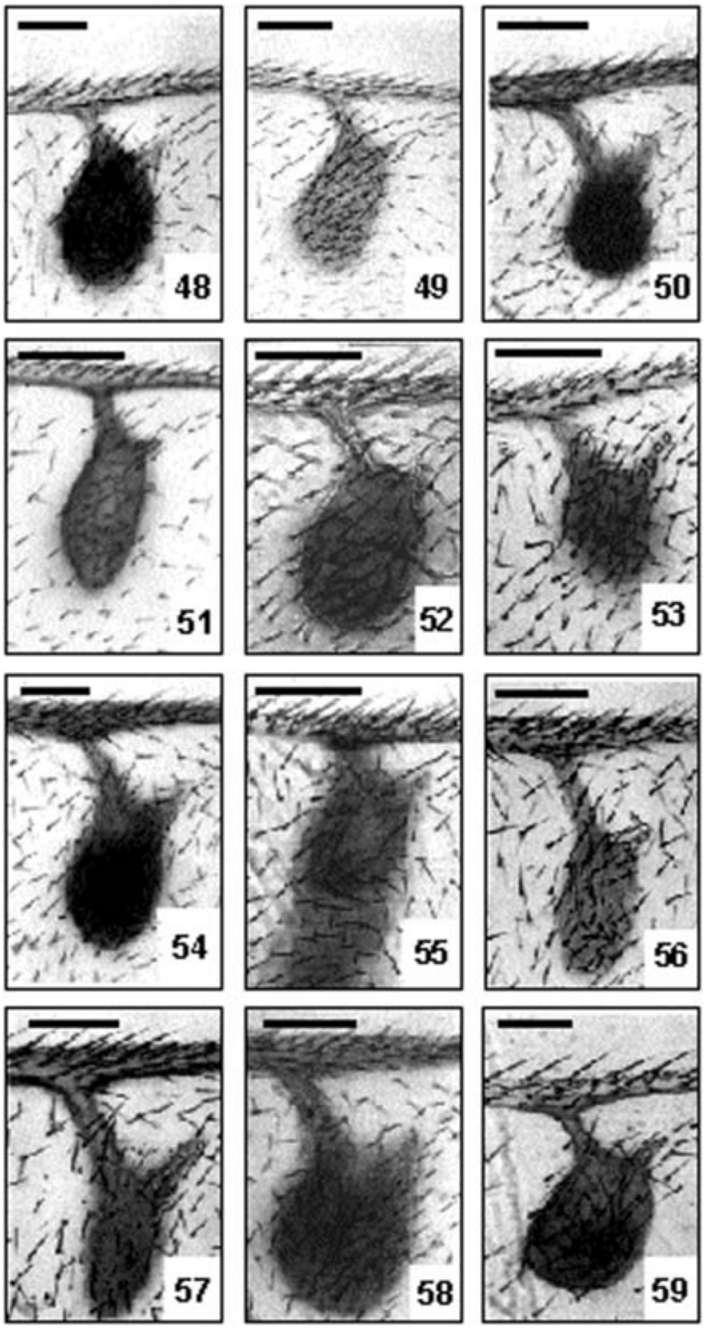
Megastigmus brevicaudis Ratzeburg
(figures 16, 53, 92, 129)

Megastigmus brevicaudis Ratzeburg, 1852: 225. Holotype ♀, Germany (destroyed probably in World War II; Grissell, 1999).

Neotype ♀ *here designated*, ex. *Sorbus aucuparia*, 4 May 1995, Ojców, Poland, M. Skrzypczyńska leg., deposited at NHMK.

Female

Body length (without ovipositor) 1.8 mm. Colour mainly brownish yellow and black. Face brownish yellow, vertex including ocelli and occiput dark brown to black; eye surrounded with yellowish; temple mainly dark brown. Antenna brownish yellow, scape yellowish beneath. Pilosity pale on lower face, dark on remainder of head. Pronotum mainly yellow with dark brown spots on the middle and a dark band on the posterior margin. Remainder of the thorax black, including mesoscutum, scutellum, axilla, metanotum, mesopleuron and metapleuron. Pilosity on thorax pale. Legs brownish yellow except hind coxa black. Wings subhyaline, with a narrow



FIGS 48–59. Female stigma of *Megastigmus* seed chalcids. (48) *M. aculeatus*; (49) *M. amicorum*; (50) *M. atedius*; (51) *M. atlanticus*, ex. *Cupressus atlantica*, Morocco; (52) *M. bipunctatus*; (53) *M. brevicaudis*; (54) *M. milleri*; (55) *M. nigrovariegatus*; (56) *M. pictus*; (57) *M. pinsapinis*; (58) *M. pinus*; (59) *M. pistaciae*. Same origins as in (11–22). Scale bars = 100 μm, except for (58) = 50 μm.

infuscation around the forewing stigma; venation brown. Propodeum black. Gaster dark dorsally dark brown with weakly marked band on the anterior part. Ovipositor sheaths black.

Head about 1.2 × as broad as long in dorsal view. Eye hardly protruding. Postocellar distance about 2 × as long as ocellocular distance. Relative measurements: eye 11:8, malar space about 5, width of head 20, width of frons 12. Scape much longer (1.2 ×) than combined length of pedicel, anellus and first funicular segment, but nearly equal (0.9 ×) to combined length of pedicel, anellus and the first two funicular segments; funicular segments 2–6 progressively becoming wider than long (figure 16). Flagellum about as long as head width. Pronotum 2.3 × wider than long. Pronotum and mesoscutum with fine arcuate cross-striae. Scutellum 1.2 × as long as broad, the anterior part striate-reticulate, the frenal area smooth with a few short longitudinal carinae extending from the anterior margin (figure 129). Forewing stigma densely hairy; basal cell closed by complete cubital and basal setal lines; marginal vein about half as long as costal cell; postmarginal vein not clearly defined apically but slightly longer than marginal vein; stigma oblong, 1.4 × as long as broad; uncus elongate, as long as upper part of stigmal vein, about half as long as stigma length (figure 53). Propodeum irregularly reticulate in the middle, with a more or less distinct median carina in the anterior part. Ovipositor sheaths much smaller (0.3 ×) than body, about 0.9 × as long as gaster. Distal part of dorsal valve of ovipositor with blunt teeth, the second median tooth being a bit larger than others (figure 92).

Male

No specimen observed during the study. Zerova and Seryogina (1994) described it as follows. Body length: 2 mm; thorax brighter than in female, sternum, head and abdomen darker; legs including coxae yellow; stigma wider than in female. The description given by Crosby (1913) refers to another species attacking *Sorbus* seeds in North America, *M. americanus* Mill. (Milliron, 1949).

Variation

Females other than type ranged in length from 1.7 to 2.7 mm. Body colour was stable. Vikberg (1966) noticed that the length of upper part of stigmal vein is highly variable.

Sex ratio

Most studies revealed only females (Vikberg, 1966; AR) but Lessmann (1974b) reared 1♂ for 127♀.

Hosts

Seeds of *Sorbus* spp. and *Amelanchier* spp. (Rosaceae): *Sorbus aucuparia* (Seitner, 1916; Hoffmeyer, 1931a; Laidlaw, 1931; Kapuściński, 1948, 1966; Vikberg, 1966; Lessmann, 1974b; Nikol'skaya and Zerova, 1978; Křístek *et al*., 1992; Zerova and Seryogina, 1994; Ochsner, 1998; Jensen and Ochsner, 1999; AR), *S. aria* (Crantz) (AR), *Sorbus* sp. (Hoffmeyer, 1931a; Čermak, 1952; Bouček, 1954), *Amelanchier ovalis* (Seitner, 1916; Zacher, 1932), *Amelanchier spicata* (Vikberg, 1966) and *Amelanchier* sp. (Hoffmeyer, 1931a). However, we did not find any chalcid on *Amelanchier ovalis* although we reared a large number of seeds from the Southern French Alps.

Distribution

Observed in western, central and northern Europe, extending eastwards to Siberia (Komi, Irkustk, Zerova and Seryogina, 1994). Recorded from the Czech Republic (Čermak, 1952; Bouček, 1954; Křístek *et al*., 1992); Denmark (Hoffmeyer, 1931b; Jespersen and Lomholdt, 1983; Ochsner, 1998; Jensen and Ochsner, 1999); Finland (Vikberg, 1966); France (AR); Germany (Milliron, 1949; Lessmann, 1974b); Great Britain (Askew and Shaw, 1979); Poland (Kapuściński, 1948, 1966; MS); Sweden (Lessmann, 1974b); Russia (Kniazheckii, 1949; Nikol'skaya, 1952; Shtakel'berg, 1955; Vikberg, 1966; Nikol'skaya and Zerova, 1978; Zerova and Seryogina, 1994); Ukraine (Zacher, 1932).

Comments

It is the only species infesting seeds of *Sorbus* and *Amelanchier* in the West Palearctic.

Material examined

France: 11♀, ex. *Sorbus aria*, Briançon (05) elev. 1200 m, July 1992 (AR); 18♀, ex. *S. aucuparia*, Marcillac (12), elev. 400 m, July 1991 (AR). **Poland**: 5♀, ex. *S. aucuparia*, Las Wolski, 27 July 1972 (MS); 1♀ neotype, 3♀, ex. *S. aucuparia*, Ojców National Park, 4 May 1995 (MS).

Megastigmus milleri Milliron

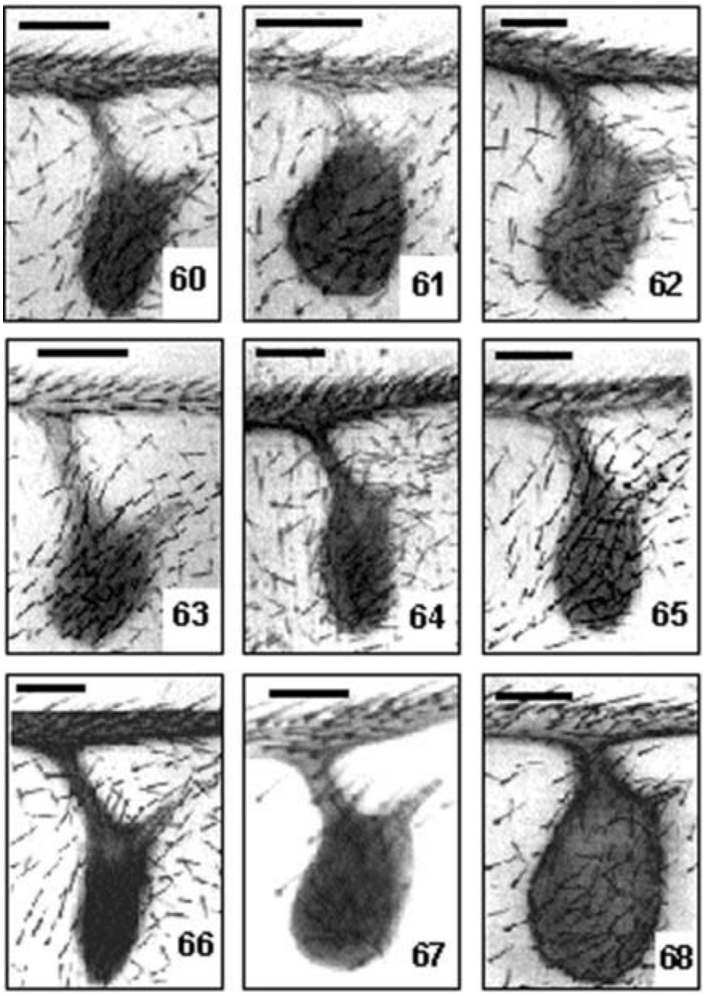
(figures 17, 36, 54, 73, 93, 111, 130, 149)

Megastigmus pinus Parfitt of Crosby, 1913: 162, 168 (in part according to Milliron, 1949) [misidentification].

Megastigmus milleri Milliron, 1949: 323–326. Holotype ♀, ex. *Abies grandis*, Crescent City, CA, USA (USNM [examined]); 39♀, 22♂ paratypes, same data as holotype (USNM [3♀, 2♂ examined]).

Female

Body length (without ovipositor) 4.2 mm. Body colour black and golden yellow. Head colour as follows according to Milliron (1949; no more head at present on holotype): face mostly yellow except the sides of clypeus with a more or less distinct black circular spot and the antennal scrobes black; frons yellow with a narrow black line extending from the scrobe extremity to the eye; vertex and occiput black but temple and gena mostly yellow. Pilosity pale on lower face, black on remainder of head. Antenna brownish yellow except scape, pedicel and anellus yellow beneath. Thoracic dorsum predominantly yellow with black patterns as follows: two oblique lateral stripes on middle part of pronotum, a transverse band covering anterior part of mid-lobe of mesoscutum, a longitudinal median band on lateral lobe of mesoscutum which extends to axilla (leaving yellow only on outer surface and posterior inner angle of mid-lobe of mesosctum and on inner angle of axilla), and lateral panel of metanotum. Scutellum with a small, lighter (dark brown) spot on middle of anterior margin. Mesopleuron and metapleuron entirely black. Pilosity on thoracic dorsum black. Fore coxa yellow, mid-coxa and hind coxa black with yellow distally, remainder of legs yellowish except hind femur infuscated dorsally. Propodeum black except a longitudinal yellow spot on callus. Gaster with first apparent tergum black; the following terga with transverse, rectangular black bands alternating with similar



FIGS 60–68. Female stigma of *Megastigmus* seed chalcids. (60) *M. rafni*; (61) *M. rosae*, Poland; (62) *M. schimitscheki*; (63) *M. specularis*; (64) *M. spermotrophus*; (65) *M. strobilobius*; (66) *M. suspectus*; (67) *M. transvaalensis*; (68) *M. wachtli*. Same origins as in (23–31). Scale bars = 100 μm.

transverse yellow bands which are broadening progressively; last tergum black; gaster sides and sterna mostly yellowish. Ovipositor sheaths black.

Head about 1.5 × as broad as long in dorsal view. Scape slightly shorter (0.97 ×) than pedicel, anellus and first funicular segment combined (figure 17); pedicel 0.9 × as long as first funicular segment. Pronotum and mesoscutum with strong cross-striae. Posterior margin of mid-lobe of mesoscutum at least twice as wide as anterior margin of scutellum (figure 130). Scutellum 1.2 × as long as broad, the anterior part striate-reticulate, the frenal area with longitudinal, irregular wrinkles (figure 130). Forewing stigma oval-elongate, 1.5 × as long as wide; upper part of stigmal vein about half as long as stigma length; uncus half as long as upper part of stigmal vein (figure 54). Propodeum with a sharp median carina. Ovipositor sheaths 1.2 × longer than gaster and thorax combined, 0.9 × as long as body. Distal part of dorsal valve

of ovipositor with blunt teeth, the second median tooth larger than the others (figure 93).

Male

Body length 3.3 mm. Colour black and yellow. Head black except face, lower part of temple, gena and a small spot above eye, yellow. Pilosity pale on lower face, black on the remainder of head. Antenna brownish yellow. Pronotum predominantly black with the sides, the lateral panel and a transverse bilobed band on posterior margin yellow. Remainder of thorax mostly black except outer surface of lateral lobe of mesoscutum, tegula and dorsellum yellow, and prepectus brownish. Pilosity on thoracic dorsum black. Fore coxa yellow, mid-coxa brown, hind coxa mostly black except at distal extremity; remainder of legs yellow. Propodeum black. Gaster with first apparent tergum black, the following terga black on dorsum with the sides orange-yellow except the last tergum entirely orange-yellow.

Head about 1.4× as broad as long in dorsal view. Antennal scape short and medially expanded, only 0.9× as long as pedicel, anellus and first funicular segment combined; pedicel 0.7× as long as first funicular segment (figure 36). Anterior margin of scutellum much shorter than posterior margin of mid-lobe of mesoscutum; scutellum 1.2× as long as broad, the anterior part transversely striate-reticulate, the frenal area with longitudinal, irregular wrinkles (figure 149). Forewing stigma broadly oval, nearly 1.4× as long as wide; upper part of stigmal vein comparatively, 0.3× as long as stigma length; uncus shorter (0.7×) than upper part of stigmal vein (figure 73). Propodeum with a sharp median carina. Aedeagus narrow and elongate, digitus with four teeth (figure 111).

Variation

The above description is based on the type material from North America. In Europe, body length varied from 2.7 to 4.3 mm in females, from 3.0 to 3.5 mm in males, the smallest examined individuals originating from Denmark (ex. *Abies grandis*). The relative length of the exserted part of female ovipositor varied from 0.9 to 1× the body length. Most of the female specimens examined from Europe fitted the type description. A few variations in colour were observed as follows: oblique black stripes on pronotum reduced to small spots, mesopleuron and metapleuron extensively yellow, anterior part of scutellum black, yellow patch on central part of propodeum. In males, most French specimens differed from the type in having two rounded yellow spots on posterior margin of pronotum and the scutellum with two longitudinal yellow bands. In both sexes, the median carina on propodeum was sometimes bifid, especially in the posterior part.

Sex ratio

Apparently balanced in the areas of introduction in Europe (AR).

Hosts

Specific to fir seeds (*Abies* spp., Pinaceae). Recorded in native American areas from *A. grandis*, *A. procera* (=*A. nobilis*) and *A. magnifica shastensis* Lemmon (Milliron, 1949; Peck, 1963; Grissell, 1979; Hedlin *et al*., 1980). In Europe, found in seeds of firs introduced from North America, *Abies balsamea* (Ochsner and Jensen, 1998), *A. concolor* (Ochsner and Jensen, 1998), *A. grandis* (Hussey, 1952, 1954a; Ochsner and Jensen, 1998; AR) and *A. magnifica* (Hussey, 1954b) but not on

A. procera in Denmark (Ochsner, 1998; Jensen and Ochsner, 1999). It also shifted on to seeds of the native *A. alba* (Ochsner and Jensen, 1998; AR) and of some other Eurasian firs introduced to Denmark (*A. bornmülleriana*, *A. homolepis*, *A. nordmanniana* and *A. pinsapo*; Ochsner and Jensen, 1998).

Distribution

Originates from the western North America, the native range extending from California to British Columbia (Milliron, 1949; Peck, 1963; Grissell, 1979; Hedlin *et al*., 1980). Introduced to Europe, but apparently limited to the western part: Denmark (Ochsner and Jensen, 1998; Jensen and Ochsner, 1999); France (Da Ros *et al*., 1993; AR); Great Britain (Hussey, 1952, 1954a, 1954b; Hussey and Klingler, 1954); The Netherlands (AR). The important seed damage observed during 1999–2000 in several native stands of eastern France (Auger-Rozenberg, unpublished observations) suggests that the species is more widespread than present data indicate, in connection with continuous importations of *A. grandis* seeds which may be chalcid-infested (Hussey, 1954a).

Comments

Until today, six other species of seed chalcids were regularly observed in seeds of *Abies* spp. in the West Palearctic region: *M. pinus*, *M. pinsapinis*, *M. rafni*, *M. schimitscheki*, *M. specularis* and *M. suspectus* (an additional species, *M. borriesi*, has just been recorded from Denmark—see the chapter concerning *M. suspectus* for diagnosis). Females of *M. pinus* easily differentiate from these of the other species by the pale pilosity on thoracic dorsum. The thoracic dorsum is entirely or quite entirely black in females of *M. pinsapinis*, *M. schimitscheki* and *M. suspectus* whereas more or less extended light parts are observed on that of *M. milleri*, *M. rafni* and *M. specularis*. The females of *M. rafni* differ by the relative size of the exserted part of ovipositor, which is much more important than that of the two other species (1.2 versus 0.9–1.0 body length). The females of *M. milleri* can be differentiated from these of *M. specularis* by the colour of pronotum. Pronotum is mostly black in *M. specularis* except two yellow spots on posterior margin of pronotum whereas that of *M. milleri* is predominantly yellow, even in dark forms, except two isolated stripes or spots on middle. They also differ by the shape of stigma (1.5–1.6 × as long as broad in *M. milleri* versus less than 1.5 × in *M. specularis*). The females of *M. schimitscheki* can be easily recognized from these of *M. pinsapinis* and *M. suspectus* by the thorax and the face entirely black except oral area, and by the stigma shape (1.6 versus 1.9–2.2 × as long as wide). *M. pinsapinis* differs from *M. suspectus* by the colour of face (entirely yellow versus yellow with more or less extended black markings), temple (with a limited black patch not reaching gena versus a black-brown patch extending to gena), prepectus, tegula, acropleuron (yellow to light brown versus black) and coxae (fore and mid-coxa yellow versus only distal part yellow; hind coxa brownish to black with yellow markings versus entirely black).

Males of fir seed chalcids are less easy to separate, except these of *M. pinus* which present a pale pilosity on thoracic dorsum whereas this vestiture is mostly dark in other species. Males of *M. pinsapinis*, *M. schimitscheki* and *M. suspectus* can be separated from others by the colour of the thoracic dorsum, which is entirely black whereas it presents more or less extended light parts in the other species. In males of *M. schimitscheki*, the three pairs of coxa are entirely black whereas they are mostly yellow in *M. pinsapinis* and *M. suspectus*. *M. pinsapinis* differs from

M. suspectus by the colour of hind coxa (yellow with black markings versus black), the sculpture of the frenal area (rounded wrinkles versus coarse longitudinal carinae) and the shape of aedeagus. Male of *M. specularis* can be separated from that of *M. milleri* and *M. rafni* by the scutellum entirely black whereas it always presents some light patterns in the two other species, even in dark forms. *M. milleri* differs from *M. rafni* by the colour of pronotum (black with yellow sides and a yellow transverse bilobed band on posterior margin versus brownish yellow with a triangular black spot on anterior part which can extend to posterior margin in dark forms).

Material examined

Canada: 9♀, 8♂, ex. *Abies grandis*, Vancouver, B.C., 1993, G. R. Hopping (GM). **Denmark**: 10♀, ex. *A. grandis*, Skramsø, East Jutland, May 1994, T. Jensen (AR). **France**: 3♀, 2♂, ex. *A. alba*, Les Barres (45), May 1981 (AR); 50♀, 50♂, ex. *A. alba*, Forest of Lafage (15), June 2000, M. Auger-Rozenberg (AR). **The Netherlands**: 10♀, 10♂, ex. *A. grandis*, Sleenerzand, April–May 1990, P. Grijpma (AR). **USA**: 1♀ holotype, 3♀, 2♂, paratypes, ex. *A. grandis*, Crescent City, CA, 26 April 1915, J. M. Miller (USNM).

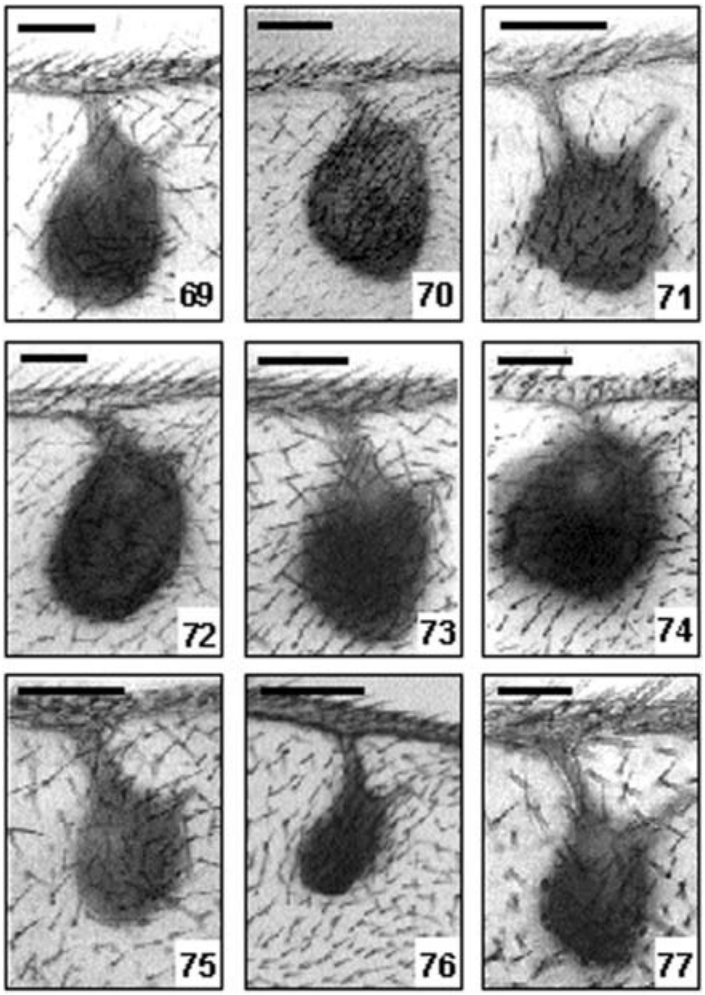
Megastigmus nigrovariegatus Ashmead
(figures 18, 55, 74, 94, 112, 131, 150)

Megastigmus nigrovariegatus Ashmead, 1890: 26. Lectotype ♀ (Milliron, 1949: 295), Greeley, CO, USA (USNM [examined]); Neoallotype ♂ (Milliron, 1949: 296), Minneapolis, USA (University of Minnesota [not examined]).

Female

Body length (without ovipositor) 3.2 mm. Body brownish yellow with black, brown and yellow markings. Head mostly brownish yellow except supraclypeal area, ocellar area, temple, gena and occipital area dark brown. Pilosity pale on lower face, black on remainder of head. Antenna dark brown except scape and pedicel yellowish beneath. Pronotum yellow, contrasting with the much darker head. Thoracic dorsum brownish yellow except anterior part of mid-lobe of mesoscutum, outer surface of axilla and lateral panel of metanotum black; mesopleuron and metapleuron dark brown. Pilosity on thoracic dorsum mostly dark. Fore and mid-coxa light brownish, hind coxa dark brown; remainder of legs yellow. Wings subhyaline; forewing stigma dark brown, distinctly surrounded by a clouded area. Propodeum black. Dorsum of the first two apparent gastral terga mostly brown, then becoming yellowish brown. Ovipositor sheaths black.

Head about 1.3 × as wide as long in dorsal view. Antennal scape elongate, 1.1 × longer than pedicel, anellus and two first funicular segment combined; pedicel elongate, about twice as long as broad, funicular segments 1–3 slender, 2.4 × as long as broad (figure 18). Pronotum and mesoscutum with cross-striae. Scutellum about 1.2 × as long as wide, the anterior part reticulate and the frenal area with longitudinal carinae (figure 131). Forewing stigma oblong, 1.3 × as long as broad,; upper part of stigmal vein comparatively short, 0.3 × as long as stigma length; uncus as long as upper part of stigmal vein (figure 55). Propodeum without median carina. Ovipositor sheaths much shorter (0.8 ×) than body, nearly as long as gaster and thorax combined. Distal part of dorsal valve of ovipositor with blunt teeth, the second median tooth a bit larger than others (figure 94).



FIGS 69–77. Male stigma of *Megastigmus* seed chalcids. (69) *M. aculeatus*; (70) *M. amicorum*; (71) *M. atedius*; (72) *M. bipunctatus*; (73) *M. milleri*; (74) *M. nigrovariegatus*, France; (75) *M. pictus*; (76) *M. pinsapinis*, Mt Ventoux, France; (77) *M. pinus*. Same origins as in (32–38). Scale bars = 100 μm, except for (70) = 200 μm.

Male (according to Milliron, 1949)

Body length 2.9 mm. Body brownish yellow with black and yellow markings. Head mostly dark brown with brownish yellow on lateral area of lower face and on parascrobal area, then extending along dorsal eye margin to gena. Pilosity pale on lower face, black on remainder of head. Antenna dark brown. Thorax mostly brownish yellow with a wedge-shaped brown spot extending on dorsum of pronotum from middle of anterior margin towards posterior margin; metapleuron dark brown with distal part lighter. Coxae dark brown except fore coxa posteriorly and anterior half of mid-coxa light brown; remainder of legs light brown. Wings subhyaline; forewing stigma darker than in female, surrounded by a broad clouded area. Propodeum dark brown except posterior margin lighter. Gaster with first apparent tergum blackish brown on dorsum and brownish yellow at side; following terga

brownish black except some yellowish infuscation at side, and last two terga brownish yellow.

Head about 1.3 × as wide as long in dorsal view. Funicular segment of antenna more elongate than in female, about twice as long as wide. Pronotum and mesoscutum with cross-striae; scutellum about 1.3 × as long as broad, the anterior part reticulate and the frenal area with curved longitudinal carinae (figure 150). Stigma large, rounded, 1.1 × as long as broad; upper part of stigmal vein comparatively very short, about 6.5 × as small as stigma length; uncus much longer (1.7 ×) than upper part of stigmal vein (figure 74). Propodeum without median carina. Aedeagus very elongate, much more than in other *Megastigmus* spp., digitus with six teeth (figure 112).

Variation

The above description is based on the type material from North America. In other specimens from America, body length varied from 3 to 3.4 mm in females, from 2.9 to 3.3 mm in males. Body colour, especially of thorax, was highly variable in the native areas. Female colour ranged from dark forms where black extended to the anterior part of pronotum, anterior part of lateral lobes of mesoscutum and axilla to light forms almost entirely flame red, orange or light brownish yellow, black being limited to a small band on the anterior margin of mid-lobe of mesoscutum (Milliron, 1949; Balduf, 1957). The few female specimens yet found in Europe corresponded to dark forms.

Extreme colour variations occurred at a higher degree in males (see Balduf, 1957 for figures). The lightest specimens observed in North America were almost wholly flame red or yellow, black being confined to the limits of the ocellar triangle on head. In darker specimens, black was invading most of the dorsum including propodeum and gaster, yellow being confined to a small patch on the vertex adjacent to the inner edge of eye, two squared patches on the posterior half of pronotum, an elongate spot along notula on lateral lobe of mesoscutum, a small spot at inner angle of axilla, two rounded spots on anterior half of scutellum, tegula and dorsellum. The few male specimens found in Europe were of dark type, with the following yellow patterns: a triangular patch on vertex near eye, a large band covering the posterior half of pronotum, a triangular patch on posterior margin of mid-lobe of mesoscutum and inner angle of axilla, two large bands on the sides of scutellum extending to the frenal line, and dorsellum. The scutellum sculpture also appeared highly variable in both sexes (Milliron, 1949).

Sex ratio

Balanced in the USA (0.69 to 1.65; Balduf, 1945, 1957), the ratio of females to males is in favour of females in Nova Scotia (1.43 to 2.57; Gillan and Richardson, 1997). Sex ratio presently unknown in the countries of introduction.

Hosts

Develops specifically in seeds of *Rosa* spp. (Rosaceae). Recorded in the native areas from numerous wild and cultivated species: *R. acicularis* Lindl., *R. arkansana* Port. and Coult., *R. blanda* Ait., *R. californica* Cham. and Schlecht., *R. canina*, *R. carolina* L. (= *R. palustris* Marsh., = *R. virginiana* Mill.), *R. engelmanni* Wats., *R. lunellii* Greene, *R. macounii* Greene, *R. spinosissima*, *R. pyrifera* Rybd., *R. rubiginosa*, *R. rugosa*, *R. setigera* Michx., *R. suffulta* Greene, *R. ultramontana* Hell., *R. woodsii*

A. Goory, *R. xanthina* Lindl. (Balduf, 1945, 1957; Milliron, 1949; Peck, 1963; Grissell, 1979; Mays and Kok, 1988; Gillan and Richardson, 1997). For the moment, only observed on *R. pendulina* in France.

Comments

Two other species, *M. aculeatus* and *M. rosae*, co-exist with *M. nigrovariegatus* in *Rosa* seeds in the West Palearctic. Diagnostic characters for separating the three species are given in the chapter concerning *M. aculeatus*.

Distribution

Originates from North America. Widely distributed in the USA and Canada, from California to Alaska and from Nova Scotia to Vancouver Island (Balduf, 1945, 1957; Milliron, 1949; Peck, 1963; Grissell, 1979; Mays and Kok, 1988; Gillan and Richardson, 1997). A few specimens recently recorded from south-central and southeastern France (AR).

Material examined

France: 1♀, ex. *Rosa* sp., Briançon (05), elev. 1200 m, 6 June 1987 (AR); 1♀, 1♂, ex. *Rosa pendulina*, Briançon (05), elev. 1200 m, 23 June 1990 (AR); 1♀, flying, Sousceyrac (46), June 1993, G. Bour (AR); 1♀, beating of *Rosa* sp., Brouis (06), 19 July 1990, J. Y. Rasplus (AR). **USA**: Lectotype ♀, Greeley, CO (USNM); 1♀, ex. *Rosa* sp., Washington, DC, 4 March 1940, E. L. King (USNM); 2♀, ex. *Rosa* sp., Jenkinson Lake, CA, 15 June 1994, N. Rappaport (AR); 1♂, ex. *R. rugosa*, Kingston, G. A. Thomson (USNM).

Megastigmus pictus (Förster)

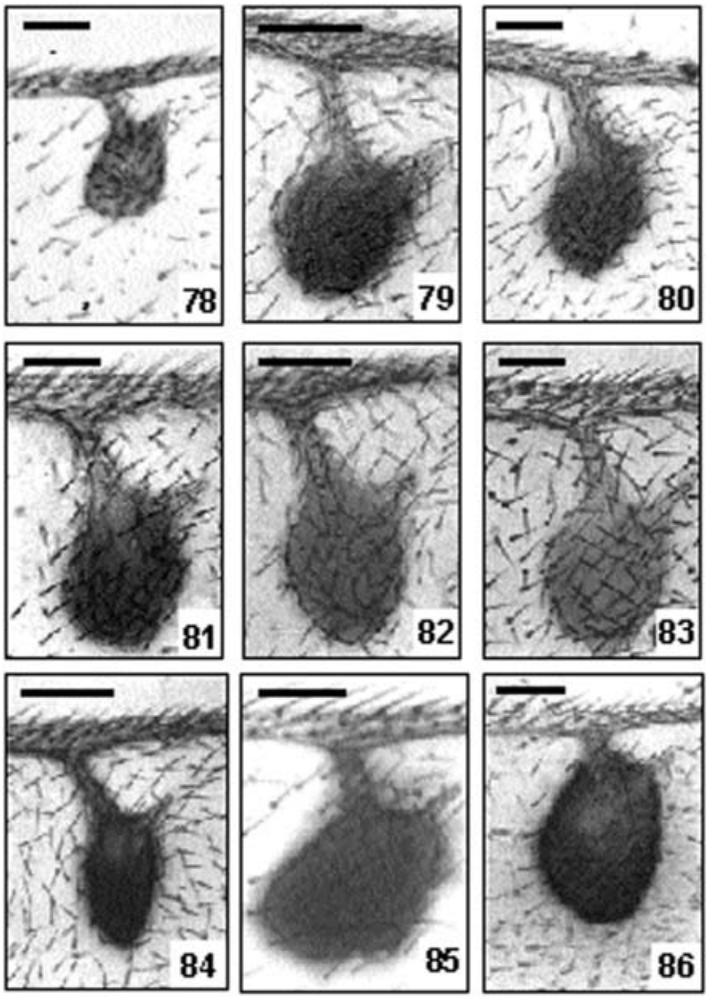
(figures 2, 3, 19, 37, 56, 75, 95, 113, 132, 151)

Torymus pictus Förster, 1840: 31. Lectotype ♀ (Bouček, 1970b: 268), Germany, coll. Mayr (NMW [examined]); 5♀ paralectotypes (NMW [examined]).

Megastigmus seitneri Hoffmeyer, 1929: 327. Holotype ♀ (mounted on slide), 5♀ paratypes, Lellinge Skov, Denmark (ZMUC [examined]); Allotype ♂ (Hussey, 1962: 39–40), Great Britain (Hussey collection [not examined]). Synonymy by Bouček, 1970b: 268.

Female

Body length (without ovipositor) 3.0 mm. Body colour black with yellow-brown patterns. Head yellowish except a brown patch extending from scrobes to ocellar area and occipital area. Pilosity pale on clypeal and supraclypeal area, black on remainder of head. Antenna brownish. Pronotum mostly orange-yellow, with a large dark brown spot on the middle of anterior margin which continues in a dark median band narrowing towards the posterior margin; mesoscutum with mid-lobe and notuli brownish black to black, and lateral lobe yellow with indefinite light brown markings; axilla yellowish with a large brown spot on the outer part; scutellum brownish black with two lateral yellow spots on anterior margin; lateral panel of metanotum black but dorsellum yellow; mesopleuron mostly light brown except upper mesepimeron and pleural suture dark brown; metapleuron dark brown. Pilosity black on thoracic dorsum. Legs mostly yellowish except hind coxa brown at basis. Wings subhyaline but extremely setose. Propodeum black except callus yellowish. Dorsum of gaster black, extending laterally in large bands in the proximal part and in narrow bands in the distal part; remainder of gaster orange-yellow. Ovipositor sheaths black.



FIGS 78–86. Male stigma of *Megastigmus* seed chalcids. (78) *M. pistaciae*; (79) *M. rafni*; (80) *M. schimitscheki*; (81) *M. specularis*; (82) *M. spermotrophus*; (83) *M. strobilobius*; (84) *M. suspectus*; (85) *M. transvaalensis*; (86) *M. wachtli*. Same origins as in (39–47). Scale bars = 100 μm, except for (81, 83) = 50 μm.

Head about 1.5× as broad as long in dorsal view, with distinctly protruding eyes (figures 2, 3). Scape elongate, slightly longer (1.1×) than pedicel, anellus and first funicular segment combined; following funicular segments about twice as long as broad (figure 19). Pronotum and mesoscutum strongly cross-striated. Scutellum elongate, nearly 1.4× as long as broad, striate-reticulate in the anterior part, the frenal area smooth (figure 132). Forewing stigma elongate-oval, 1.6× as long as wide; upper part of stigmal vein comparatively elongate, slightly longer (1.1×) than stigma width; uncus short, 0.3× as long as upper part of stigmal vein (figure 56). Propodeum with a median carina (figure 132). Ovipositor sheaths much shorter (0.7×) than body, nearly (0.9×) as long as thorax and gaster combined. Distal part of dorsal valve of ovipositor with the third median tooth enlarged (figure 95).

Male

Body length 2.4 mm. Head yellow except a T-shaped black area on vertex around ocelli. Pilosity pale on lower face below antenna, black on remainder of head. Antenna brown, with scape and pedicel yellowish beneath. Pronotom yellowish with a triangular, light brown spot on middle of anterior margin; mid-lobe of mesoscutum dark brown with two large lateral yellow lunules along notuli, lateral lobes yellow; scutellum mostly yellow with a brown patch resembling a four-branched star, which extends longitudinally from above the frenal line to the posterior margin and laterally along the frenal line; axilla yellow with a light brown spot along anterior suture; mesopleuron and metapleuron yellow. Pilosity black on thoracic dorsum, with four pairs of hairs on scutellum. Legs yellow, including coxae. Propodeum black with two small, lateral yellow spots on the posterior part. Gaster mostly yellow with a black dorsum, extending laterally in three distinct large, triangular stripes in the mid-part; last segment entirely yellow.

Head rounded, nearly 1.3 × as broad as long in dorsal view. Scape elongate, slightly longer (1.1 ×) than pedicel, anellus and first funicular segment combined; following funicular segments about twice as long as broad (figure 19). Thoracic sculpture similar to that of female with cross-striae on pronotum and mesoscutum, the anterior part of scutellum striate-reticulate, and the frenal area smooth (figure 151). Forewing stigma elliptical, 1.2 × as long as wide; upper part of stigmal vein comparatively short, about 0.4 × as long as stigma length; uncus 0.6 × as long as upper part of stigmal vein (figure 75); basal cell of forewing with 30 hairs including hairs on basal and cubital setal lines. Propodeum with a distinct median carina (figure 151). Aedeagus short, rounded, digitus with three teeth (figure 113).

Variation

The above description is based on the type material of *M. pictus*. In the other examined specimens, body length varied from 1.9 to 3.3 mm in females, from 2.4 to 2.9 mm in males. Female colour was highly variable. The dark median band on pronotum was absent in the lightest specimens (e.g. from Poland, MS). Scutellum colour varied from black with two anterior lateral yellow spots to yellowish with a median longitudinal brown band crossed by a transverse brown band on the posterior part. Both forms were observed in the Alps (AR). Darker specimens (e.g. emerged from *Larix gmelinii*, Les Barres arboretum, France, AR) showed a thoracic dorsum quite entirely black (mid-lobe of mesoscutum, scutellum except two small yellow spots, metanotum except dorsellum yellow, and propodeum). The median carina on propodeum was often double posteriorly.

Male colour was not very variable but the dark parts often turned from brown to black. The specimens observed by Hussey (1962) in Great Britain presented a pronotum entirely yellow and a mid-lobe of mesoscutum with black areas limited to spots on anterior margin. In a few individuals from Southern Poland, the longitudinal brown band on scutellum extended to the anterior margin (MS). Hussey (1962) did not notice a distinct carina on propodeum but observed four teeth on digitus.

Sex ratio

The species usually reproduces by thelytokous parthenogenesis, males being very scarce (16♂:2123♀, i.e. 0.74%, in Poland; Skrzypczyńska, 1981a).

Hosts

Specific to seeds of Eurasian species of larch (*Larix* spp., Pinaceae). Observed to damage seeds in the natural range of *L. decidua* (=*L. europaea*; among others, Skrzypczyńska, 1973, 1974, 1977, 1984a; Roques, 1983; Křístek *et al*., 1992; Da Ros and Battisti, in press), *L. decidua* var. *polonica* (Kapuściński, 1966; Karpiński, 1967; Skrzypczyńska, 1974, 1977, 1984a), *L. gmelinii* (=*L. dahurica*; Stadnickii *et al*., 1978; Zhang and Zhou, 1990; Xu and He, 1995; AR), *L. gmelinii olgensis* (Xu and He, 1995), *L. gmelinii principis-ruprechtii* (Xu and He, 1995), *L. sibirica* (Stadnickii and Grebenshchikova, 1977; Stadnickii *et al*., 1978), *L. sukaczewii* (Stadnickii *et al*., 1978). The species has extensively colonized seeds of the same larch species planted outside their natural range, additionally attacking *L.* × *czekanowski* (Ostermeyer, 1990), the Japanese larch *L. leptolepis* (Hussey, 1962; Ostermeyer, 1990; Grijpma and van de Weerd, 1991; Xu and He, 1995) and *L.* × *eurolepis* (Hussey, 1952, 1962). However, no attack was noticed on larch species introduced from North America to France (Ostermeyer, 1990). Records on spruce (e.g. Stadnickii, 1971) probably referred to *M. strobilobius* while earlier records on *Rosa* spp. (e.g. Zacher, 1932; Čermak, 1952; Sorauer, 1953) corresponded to *M. rosae* (Bouček, 1971).

Distribution

Palearctic, probably originating from the native range of Eurasian larch species. Has largely colonized larch plantations and forests from Great Britain to far-eastern Asia (northeastern China; Zhang and Zhou, 1990; Roques *et al*., 1995; Xu and He, 1995; AR). In Europe, recorded from Austria (Vikberg and Valkeila, 1977); former Czechoslovakia (Čermak, 1952; Bouček, 1954; Hrubík, 1973; Křístek *et al*., 1976, 1992); Denmark (Hoffmeyer, 1929, 1931b; Jespersen and Lomholdt, 1983; Ochsner, 1998; Jensen and Ochsner, 1999); Estonia (Luik and Voolma, 1988); Finland (Hellén, 1933; Vikberg and Valkeila, 1977); France (Roques, 1983; Ostermeyer, 1990); Germany (Zacher, 1932; Escherich, 1938; Bouček, 1970b; Lessmann, 1974b; Schwenke, 1982); Great Britain (Laidlaw, 1931; Hanson, 1952; Hussey, 1952, 1954a, 1962; Bouček, 1970b); Ireland (Bouček, 1970b); Italy (Da Ros, 1997; Da Ros and Battisti, in press); The Netherlands (Sorauer, 1953; Grijpma and van de Weerd, 1991); Poland (Adamczyk *et al*., 1969; Banaszak and Szmidt, 1987; Kapuściński, 1966; Karpiński, 1967; Skrzypczyńska, 1973, 1974, 1977, 1981a, 1984a, 1996; Szmidt, 1986); probably in Romania (Olenici, 1990); Russia from the European part to Siberia (Irkutsk), at least (Okunev, 1958; Golutvina *et al*., 1972; Bekreneva and Tropin, 1975; Smetanin, 1977; Nikol'skaya and Zerova, 1978; Stadnickii *et al*., 1978; Gusev, 1984; Zerova and Seryogina, 1994); Sweden (Hansson, 1991); Ukraine (Padii, 1952; Jurchenko, 1973); former Yugoslavia (Bouček, 1977). In the Alpine range, the insect seems limited to low altitude stands (Roques, 1983; Da Ros and Battisti, in press).

Comments

No other chalcid species has yet been observed to attack larch seeds in the West Palearctic. However, an additional species, *M. inamurae* Yano, exists in the Far East (Yano and Koyama, 1918). Because some specimens have been observed in the 1950s in seeds of Japanese larch imported from Japan to Great Britain (Hussey, 1954a), the species may have been introduced to Europe. Based on Yano's original description, Hussey (1962) stated that females of *M. inamurae* differ by a more limited black margin on the anterior part of pronotum. However, this black margin

is sometimes absent in the European specimens of *M. pictus.* We examined females of larch seed chalcids from far-eastern Asia, both Japanese specimens identified as *M. inamurae* (1♀, Shikotan, Kuriles Islands, Russia, 12 June 1944, K. Kamijo; 1♀, ex. *L. leptolepis*, Usuda, Nagano Pref., Honshu, J, April 1964, K. Kobayashi) and Chinese specimens identified as *M. pictus* (Heilongjiang, northeastern China; AR). Both exhibited highly variable colour patterns for thorax, ranging from the typical pattern of *pictus* to forms with an extended brownish coloration on mesoscutum, scutellum and axilla, yellow stripes being limited to a transverse band on scutellum and an oblique one at inner margin of axilla. No reliable difference thus appeared between females of *M. pictus* and *M. inamurae*. Hussey (1962) separated the males of the two species by the colour of pronotum, considered as entirely yellow in *M. pictus* whilst black anteriorly in *M. inamurae*. Similarly as for female, the variation in thorax colour observed in males of *M. pictus* did not allow Hussey's key for separating the two species to be used.

Material examined

China: 2♀, ex. *Larix gmelinii*, Jagedaqi (Heilongjiang), 28 July 1987, Zhang Xu-dong (AR); 12♀, ex. *L. gmelinii*, Daï-ling (Heilongjiang), June 1994 (AR); 22♀, ex. *L. gmelinii*, Xin-lin (Heilongjiang), June 1994 (AR). **Denmark**: 1♀ holotype of *M. seitneri* and 5♀ paratypes, Lellinge Wald, 1928 (ZMUC). **France**: 3♀, ex. *L. decidua*, Briançon (05), elev. 1200 m, July 1983 (AR); 4♀, ex. *L. decidua*, St Sernin/Rance (12), June 1991 (AR); 6♀, ex. *L. decidua*, Les Barres, May 1991, R. Ostermeyer (AR); 5♀, Les Barres, ex. *L. sibirica*, June 1980 (AR); 4♀, ex. *L. x czekanowskii,* Les Barres, June 1991, R. Ostermeyer (AR); 5♀, ex. *L. gmelinii*, Les Barres (45), May 1993 (AR); 3♀, ex. *L. leptolepis*, Les Barres, June 1991, R. Ostermeyer (AR); 3♀, ex. *L. leptolepis*, Argonne Forest (51), June 1993 (AR). **Germany**: 1♀ lectotype and 5♀ paralectotypes of *M. pictus*, Mayr coll. (NMW). **Italy**: 2♀, ex. *L. decidua*, Cavedine (TN), elev. 650 m, June 1993, N. Da Ros (AR). **The Netherlands**: 1♂, ex. *L. leptolepis,* Vaals seed orchard (Limburg), 14 July 1990, P. Grijpma (AR). **Poland**: 1♂, ex. *L. decidua* var. *polonica*, Rudy Raciborskie, Kotlarnia Forest, 24 April 1970 (MS); 1♂, ex. *L. decidua* var. *polonica*, Skarżysko, Dalejów Forest, 30 March 1976 (MS); 1♂, ex. *L. decidua* var. *polonica*, Skarżysko, Jastrzębie Forest, 6 April 1976 (MS); 1♂, ex. *L. decidua* var. *polonica*, Odrowążek Forest (Swiętokrzyskie Mts.), 21 April 1976 (MS); 25♀, ex. *L. decidua* var. *polonica*, Forest Wojkowa (Beskid Sądecki), 27 May 1990 (MS).

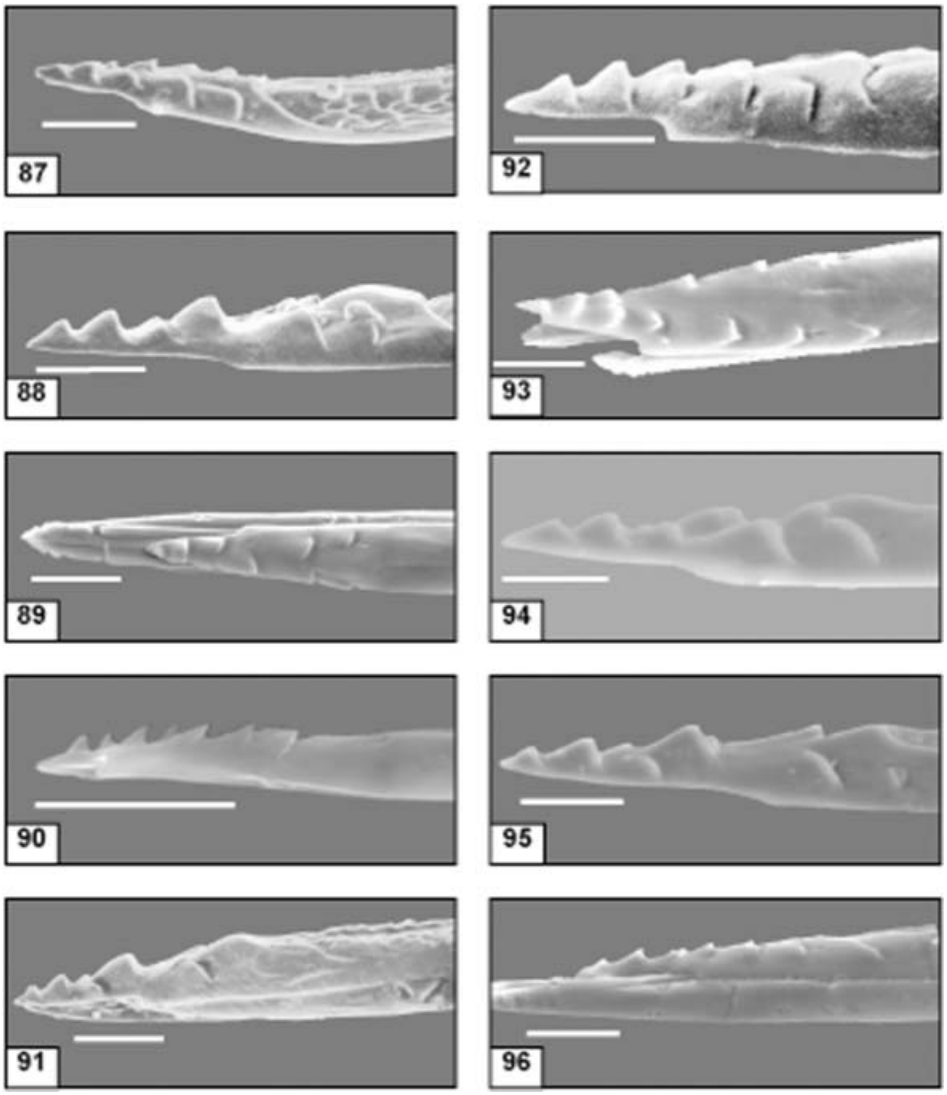
Megastigmus pinsapinis Hoffmeyer

(figures 7, 20, 57, 76, 96, 114, 133, 152)

Megastigmus pinsapinis Hoffmeyer, 1931b: 264. Holotype ♀, Spain, 29 May 1930 (depository unknown).

Female

Body length (without ovipositor) 4.2 mm. Body colour black and yellow. Face, parascrobal area, circumorbital area and gena bright yellow, temple yellow with outer eye margin black; frons, vertex and occiput black. Pilosity on head mostly dark, with conspicuous pale bristles. Antenna brownish with scape and pedicel yellow with black markings. Thorax predominantly black except lateral panel of pronotum yellow, suture of prepectus and tegula light brown, mesopleuron dark brown with acropleuron and upper mesepimeron lighter. Pilosity black on thorax



FIGS 87–96. Female ovipositor of *Megastigmus* seed chalcids. (87) *M. aculeatus*; (88) *M. amicorum*; (89) *M. atedius*; (90) *M. atlanticus*; (91) *M. bipunctatus*; (92) *M. brevicaudis*; (93) *M. milleri*; (94) *M. nigrovariegatus*; (95) *M. pictus*; (96) *M. pinsapinis.* Same origins as in (11–20). Scale bar = 20 μm.

even on yellow parts. Legs yellow except hind coxa black, front and mid-tarsi brownish yellow. Propodeum black except callus brown, with pale pilosity. Dorsum of gaster black with limited lateral infuscations, remainder orange-yellow. Ovipositor sheaths black.

Head rounded in dorsal view, 1.2 × as broad as long. Antennal scape 0.9 × as long as pedicel, anellus and first funicular segment combined; first funicular segment elongate, 1.2 × longer than the following segments (figure 20). Pronotum and mesoscutum with strong arched cross-striae. Scutellum 1.3 × as long as broad, the anterior part with transverse cross-striae tending to reticulation, the frenal area weakly

wrinkled (figure 133). Forewing stigma very elongate, 2.1 × as long as broad; upper part of stigmal vein comparatively elongate, 0.9 × as long as stigma length; uncus elongate, 1.2 × longer than stigma width (figure 57). Propodeum with a curved median carina. Ovipositor sheaths 1.2 × as long as body. Distal part of dorsal valve of ovipositor with blunt teeth (figure 96).

Male

Body length 3.9 mm. Body colour black and yellow. Face, parascrobal area and gena bright yellow, temple yellow with outer eye margin black; frons, vertex and occiput black. Head pilosity mostly black, even on lower face. Scape and pedicel shining black above, yellowish beneath; remainder of antenna brown. Thorax with dorsum entirely black but lateral and ventral parts mostly bright yellow, including lateral panel of pronotum, prepectus, tegula, acropleuron and mesopleuron; metapleuron black. Pilosity mostly black on thoracic dorsum but pale on callus. Legs mostly yellow except hind coxa with longitudinal black patches on outer surface and conspicuous black dots at base of bristles on inner surface; pilosity pale on coxa. Propodeum black except callus yellow with conspicuous black dots at base of bristles. Gaster mostly bright yellow with a black dorsum extending laterally in three distinct, large, triangular stripes.

Head about 1.1 × as broad as long in dorsal view. Antennal scape 0.9 × as long as pedicel, anellus and first funicular segment; first funicular segment elongate, about 2 × as long as wide, the following segments tending to subquadrate (not figured—see Pintureau *et al*., 1991). Pronotum and mesoscutum with strong cross-striae. Scutellum 1.3 × as long as broad, the anterior part with coarse cross-striae and the frenal area with weak irregular wrinkles (figures 7, 152). Forewing stigma elongate-oval, 1.6 × as long as broad; upper part of stigmal vein comparatively elongate, 0.5 × as long as stigma length; uncus short, 0.5 × as long as upper part of stigmal vein (figure 76); basal cell closed with 35 bristles. Propodeum with a median carina interrupted in the middle (figure 7). Aedeagus small, rounded, digitus with four small teeth (figure 114).

Variation

The above description is based for female on a specimen emerged from *Abies pinsapo* (June 1858, coll. Sichel) and for male on a specimen emerged from *Cedrus atlantica* (Barjac, France, 25 May 1997, J. P. Fabre leg.) both deposited at MNHN. In the other examined specimens, body length varied from 4.0 to 5.6 mm in females, from 3.9 to 4.2 mm in males. Only the colour of lateral parts of thorax was variable in females, prepectus, acropleuron and upper mesepimeron being entirely yellow in some specimens from southern France. Mid-coxa could show black patches and hind coxa could be entirely yellow beneath. Specimens from southern France observed by Hussey (1957) also presented distinct longitudinal carinae across the frenal area.

No variation in male colour was observed but a few French specimens showed an asymmetrical morphology: presence of five teeth on the left digitus versus four teeth on the right one (Pintureau *et al*., 1991), presence of a female-like stigma (2 × as long as broad) on the right forewing versus a male-like stigma (1.6 × as long as broad) on the left one (Marcelly Forest, AR).

Sex ratio

Mostly reproducing by thelytokous parthenogenesis (Pintureau *et al*., 1991). Males are very scarce, about 1♂:4000♀ (Fabre *et al*., 1994).

Hosts

Develops in seeds of both cedars (*Cedrus* spp.) and some European firs (*Abies* spp.) (Pinaceae). Observed in the natural range of *Cedrus atlantica* (Milliron, 1949; El Hassani and Messaoudi, 1986; Pintureau *et al*., 1991; Bouaziz, 1993; Bouaziz and Chakali, 1998) and *Abies pinsapo* (Hoffmeyer, 1931b). It has extensively colonized the plantations of *C. atlantica* and *A. pinsapo* in southern France (Berland, 1950; Hussey, 1957; Roques, 1983; Fabre, 1986, 1989; Pintureau *et al*., 1991; AR) and Italy (USNM). In French arboreta, it also attacked other exotic cedars (*C. brevifolia*, *C. deodara* and *C. libani*), the introduced Caucasian fir, *A. nordmanniana* and the native *A. alba* (Roques, 1983; Ostermeyer, 1990; AR).

Distribution

Originating from North Africa and/or Spain; probably introduced to France with cedar seeds (Pintureau *et al*., 1991). The present range covers the major part of the western Mediterranean basin, but the species is also present in more northern locations (e.g. north-central France; Roques, 1983). Recorded from Algeria (Pintureau *et al*., 1991; Bouaziz, 1993; Bouaziz and Chakali, 1998); France (Berland, 1950; Hussey, 1957; Roques, 1983; Fabre, 1986, 1989; Pintureau *et al*., 1991); Italy (USNM); Morocco (Roques, 1983; El Hassani and Messaoudi, 1986; El Hassani *et al*., 1994) and Spain (Hoffmeyer, 1931b).

Comments

Two other species, *M. schimitscheki* and more scarcely *M. suspectus*, are capable of attacking seeds of *Cedrus* spp. in the West Palearctic. The face colour allows the females of the three species to be differentiated. It is entirely yellow in *M. pinsapinis* whereas that of *M. suspectus* always shows more or less extended black markings, and that of *M. schimitscheki* is entirely black except the oral area orange-brown. *M. schimitscheki* also differentiates from the two others by the thorax colour (entirely black versus presence of lateral yellow spots in the two others), the sculpture of the frenal area (mostly smooth with a few short longitudinal carinae versus wrinkled), and a less elongated forewing stigma (1.6 × as long as broad versus 1.7–2.2 ×). The female of *M. pinsapinis* differs from that of *M. suspectus* by a shorter black spot on temple, which never reaches gena (versus extending to gena in the other species), the colour of some lateral parts of thorax (prepectus, tegula and acropleuron yellow to light brown versus black), and the colour of coxae (fore-coxa yellow; mid-coxa yellow sometimes with black markings; hind coxa brownish to black with yellow markings versus all coxae black with the distal parts of fore- and mid-coxa yellow).

Males of *M. schimitscheki* differ by the thorax and coxae entirely black whereas lateral parts of thorax and coxae are partly yellow in the two other species. Males of *M. pinsapinis* always present a yellow hind coxa whereas this coxa is black in *M. suspectus.*

A total of six other species compete for fir seeds. Diagnostic characters are given in the chapter regarding *M. milleri.*

Material examined

Algeria: 2♀, ex. *Cedrus atlantica*, Chréa, May 1993, K. Bouaziz (AR). **France**: 4♀, ex. *A. alba*, Les Barres (45), May 1981 (AR); 5♀, ex. *Abies nordmanniana*, Amance arboretum (54), June 1982 (AR); 1♀, ex. *A. pinsapo*, June 1858, Sichel (MNHN); 15♀, ex. *A. pinsapo*, Catus (46), May 1982 (AR); 1♂, ex. *C. atlantica*, Barjac (30), 25 May 1997 (JPF); 1♂, ex. *C. atlantica*, Marcelly (11), 30 April 1999 (JPF); 9♀, ex. *C. atlantica*, Les Barres, May 1981 (AR); 62♀, ex. *C. atlantica*, Mt Ventoux, 15 May 1980 (JPF); 12♀, ex. *C. atlantica*, Mt Ventoux (84), 15 May 1993, French National Forestry Office (AR); 3♀, ex. *C. brevifolia*, Les Barres, May 1990, R. Ostermeyer (AR); 3♀, ex. *C. deodara*, Les Barres, June 1989 (AR); 2♀, ex. *C. libani*, Les Barres, May 1981 (AR); 10♀, ex. *Cedrus* sp., Apt (84), J. Gobert, 1947 (MNHN). **Italy**: 1♀, ex. *C. atlantica*, PQ, US quarantine (USNM). **Morocco**: 2♀, ex. *C. atlantica*, Azrou, May 1985, A. El Hassani (AR).

Megastigmus pinus Parffit

(figures 21, 38, 58, 77, 97, 115, 134, 153)

Megastigmus pinus Parfitt, 1857a: 5543–5544 (and 5629–5630). Holotype ♀, California, USA (BMNH [examined]).

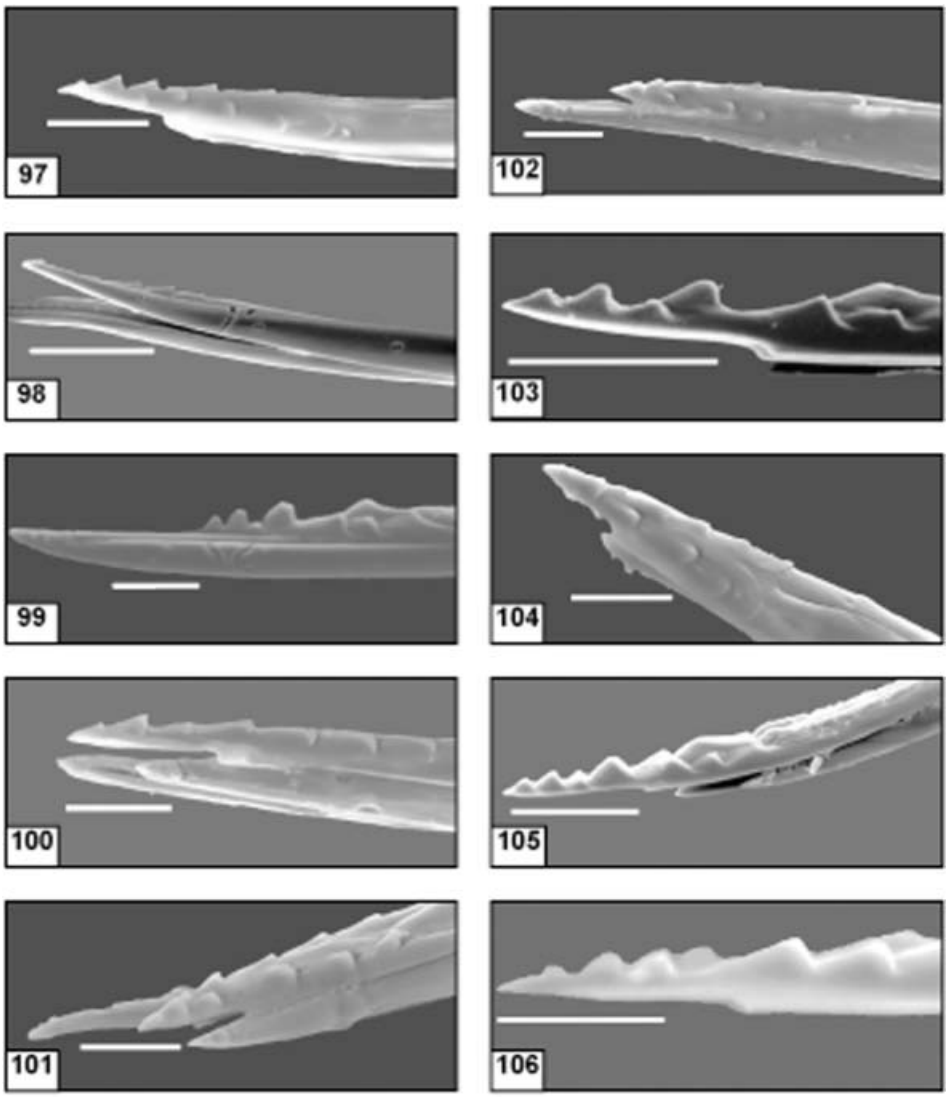
Megastigmus pinus crosbyi Hoffmeyer, 1931a: 215. Holotype ♀, *Abies concolor*, Colorado, USA (ZMUC [examined]).

Megastigmus pinus marginatus Hoffmeyer, 1931a: 215. Holotype ♂, *Abies grandis,* Oregon, USA (ZMUC [examined]).

Female

Body length (without ovipositor) 5.1 mm. Body colour combining black, yellow and orange. Face yellow with a black spot at side of clypeus extending to antennal base; remainder of the head mostly black, with a more or less discontinuous yellow ring around eye. Pilosity pale on lower face, black on remainder of head. Antenna mostly dark brown to black; scape yellow beneath; pedicel and anellus partly brownish yellow beneath. Thoracic dorsum mostly black except a trilobed, orange-yellow transverse band on the posterior margin of pronotum, and a large orange-reddish patch covering posterior margin of mid-lobe of mesoscutum, inner angles of both lateral lobe of mesoscutum and axilla, and scutellum; lateral parts of thorax black except lateral panel of pronotum, a spot on prepectus and tegula orange-yellow. Pilosity on thoracic dorsum pale, even on yellow maculae. Fore and mid-coxa black basally, the latter also on outer surface, hind coxa entirely black; fore femur yellow, mid-femur yellow with limited basal infuscation, hind femur with black patch on anterior and ventral surface; tarsi brownish yellow. Propodeum black. First apparent tergum of gaster black; second tergum with dorsum anteriorly black, posteriorly brownish, and with lateral parts alternating black and yellow spots; yellow colour progressively becoming predominant on the following terga. Ovipositor sheaths black.

Head about 1.5× as broad as long in dorsal view. Scape as long as pedicel, anellus and first funicular segment combined; pedicel oval, 0.9× as long as first funicular segment; first funicular segment twice as long as wide, the rest of funicular segments progressively decreasing in length (figure 21). Pronotum and mesoscutum coarsely cross-striated. Scutellum 1.3× as long as broad, the anterior part with dense cross-striae, the frenal area deeply wrinkled (figure 134). Forewing stigma nearly circular, only 1.1 as long as broad, with a comparatively elongate upper part



FIGS 97–106. Female ovipositor of *Megastigmus* seed chalcids. (97) *M. pinus*; (98) *M. rafni*; (99) *M. rosae*, France; (100) *M. schimitscheki*; (101) *M. specularis*; (102) *M. spermotrophus*; (103) *M. strobilobius*; (104) *M. suspectus*; (105) *M. transvaalensis*; (106) *M. wachtli*. Same origins as in (21–31). Scale bar = 20 μm.

of stigmal vein, about 0.6 × as long as stigma length; uncus short, 0.4 × as long as upper part of stigmal vein (figure 58). Propodeum with a more or less distinct median carina (figure 134). Ovipositor sheaths 2.1 × longer than gaster, little longer (1.1 ×) than body. Distal part of the dorsal valve of ovipositor with small teeth, but the second median tooth larger than the others (figure 97).

Male

Body length 4.4 mm. Body colour combining black and yellow. Face yellow, dorsum of head black with a yellow spot extending along outer margin of eye to

gena. Pilosity pale on lower face. Thoracic dorsum black except two lateral, irregular spots on posterior margin of pronotum and dorsellum yellow; lateral parts of thorax mostly black except lateral panel of pronotum, tegula, a spot at base of wing. Pilosity on thoracic dorsum mostly pale. Legs mostly yellowish except hind coxa black and a brown patch on dorsum of hind femur. Propodeum black. First apparent tergum of gaster black; next terga black on dorsum with hind margin brown and lateral margin light brown; the lateral margins progressively extend on the following terga, the last tergum being mostly light brown except distal end black.

Head about 1.5 × as broad as long in dorsal view. Antennal scape nearly equal (0.98 ×) to combined length of pedicel, anellus and first funicular segment; funicular segments more elongate than in female (figure 38). Pronotum and mesoscutum coarsely cross-striated. Scutellum nearly 1.3 × as long as broad, the anterior part with dense cross-striation, the frenal area deeply wrinkled with distinct fovea (figure 153). Forewing stigma oval, 1.3 × as long as broad, with a comparatively elongate upper part of stigmal vein, about 0.6 × as long as stigma length; uncus long, 0.9 × as long as upper part of stigmal vein (figure 77). Propodeum with a weak median carina and two lateral carinae. First apparent segment of gaster very elongate. Aedeagus conical, medium-sized, larger than that of *M. suspectus*; digitus with four teeth (figure 115).

Variation

The above description is based on the type material from North America. In the European specimens, body length varied from 2.8 to 5.6 mm in females, from 2.6 to 4.5 mm in males. The colour pattern was highly variable, especially in females (Hussey and Klingler, 1954), but about half of the examined European specimens fitted the type description. The darkest female specimens showed a thoracic dorsum quite entirely black, with yellow reduced to a narrow band on both posterior margin of pronotum and posterior margin of mid-lobe of mesoscutum, and to a tiny spot at inner angle of axilla. Such specimens were observed on *A. procera* in Great Britain (Hussey and Klingler, 1954) and on *A. grandis* in France. The lightest specimens presented a quite continuous circumorbital yellow ring, a pronotum quite entirely orange-yellow with black colour reduced to a narrow band on anterior margin and sides, the mid-lobe of mesoscutum being black only in its proximal third (variety *crosbyi* described by Hoffmeyer, 1931a). Such specimens were frequently observed on *A. nordmanianna* in France and on *A. grandis* in Belgium. Many intermediary forms were observed, the colour of light parts of thorax varying from greenish yellow (e.g. Laidlaw, 1931, in Scotland) to bright orange (e.g. McNeill, 1946, in Scotland) and orange-reddish (some specimens from France). The relative length of the exserted part of ovipositor female varied from 0.9 to 1.1 × the body length. The propodeum carina was often double.

Colour variation was more limited in males. About 20% of the specimens found on *A. grandis* in Belgium had the pronotum entirely black, without any yellow spot. The lightest males showed a continuous circumorbital yellow ring, large yellow spots on pronotum, and lateral parts of thorax quite entirely yellow except metapleuron black (observed in France on *A. alba*). A few (10%) also showed a yellow dorsellum. The colour of light parts of thorax varied from lemon yellow to orange-yellow. Gaster colour was also variable, but usually the terga were black with yellow spots on sides which progressively extended, the last tergum being mostly orange-yellow except distal end black. The light brown colour noticed above on gaster of the

examined type material (known as variety *marginatus*; Hoffmeyer, 1931a) was not observed in our European specimens as already stated by Hussey and Klingler (1954). The shape of the stigma was also very variable, from nearly circular to oval (1.1–1.3 × as long as wide).

Sex ratio

Quite balanced in areas of introduction (45♀:52♂, Ostermeyer, 1990; 135♀:107♀, Tombuyses, 1993; Jensen, in press).

Hosts

Specific to fir seeds (*Abies* spp., Pinaceae). In native countries, develops in *Abies amabilis*, *A. bracteata*, *A. concolor*, *A. grandis*, *A. lasiocarpa*, *A. magnifica*, *A. magnifica shastensis* and *A. procera* (= *A. nobilis*) (Keen, 1958; Hedlin, 1974; Hedlin *et al*., 1980). Usually recorded in Europe from plantations of some of these introduced North American firs: *A. concolor* (Ostermeyer, 1990; Ochsner and Jensen, 1998), *A. grandis* (Escherich, 1938; Hussey, 1954a; Jespersen and Lomholdt, 1983; Roques, 1983; Ostermeyer, 1990; Ochsner and Jensen, 1998), *A. lasiocarpa* (Ochsner and Jensen, 1998), *A. procera* (Laidlaw, 1931; McNeill, 1946; Hussey, 1954a; Jespersen and Lomholdt, 1983; Tombuyses, 1993; Iversen and Jensen, 1998; Jensen and Larsen, 1998; Ochsner, 1998; Ochsner and Jensen, 1998; Jensen and Ochsner, 1999; USNM). However, the species was observed to shift on to seeds of *A. alba* in Denmark (Ochsner and Jensen, 1998), and on to some Mediterranean firs introduced to France and Denmark such as *A. cilicica* (Roques, 1983), *A. bornmülleriana* (Roques, 1983; Ochsner and Jensen, 1998), *A. nordmanianna* (Ochsner and Jensen, 1998), *A. numidica* (Roques, 1983; Ostermeyer, 1990; AR) and *A. pinsapo* (Roques, 1983; Ostermeyer, 1990; Ochsner and Jensen, 1998; AR). It also shifted on to seeds of an Asian fir introduced to France (*A. veitchii* Lindl.; AR). Biotypes living on *A. alba* and *A. procera* were distinguished on the basis of behavioural responses to cone volatiles but cone odours of *A. grandis* seemed to repel females of *M. pinus* (Luik *et al*., 1999). Records on *Picea* and *Pinus* species (e.g. Lessmann, 1962) probably represented misidentifications.

Distribution

Originates from western North America, from British Columbia (Hedlin, 1974) to California (Milliron, 1949; Keen, 1958; Peck, 1963; Grissell, 1979; Hedlin *et al*., 1980). Introduced to Europe and presently recorded in most of western Europe: Belgium (Tombuyses, 1993); former Czechoslovakia (Wall, 1984); Denmark (Jespersen and Lomholdt, 1983; Iversen and Jensen, 1998; Jensen and Larsen, 1998; Ochsner, 1998; Ochsner and Jensen, 1998; Jensen and Ochsner, 1999); France (Roques, 1983; Ostermeyer, 1990); Germany (Escherich, 1938; Wall, 1984); Great Britain (Laidlaw, 1931; McNeill, 1946; Hussey, 1954a, 1954b; Hussey and Klingler, 1954; Bouček, 1970b; USNM); Ireland (O'Connor and O'Connor, 1984); The Netherlands (Oudemans, 1933; AR); Sweden (Hansson, 1991).

Comments

To date, six other species of seed chalcids were observed in fir seeds in the region: *M. milleri*, *M. pinsapinis*, *M. rafni*, *M. schimitscheki*, *M. specularis* and *M. suspectus*. Adults of both sexes of *M. pinus* are easily differentiated by the pale pilosity dominant on thoracic dorsum, even on the light parts, whereas that of other fir seed chalcids

is predominantly dark. For separating the other species, see the chapter concerning *M. milleri*.

Material examined

Belgium: 8♀, 9♂, ex. *Abies procera*, Vielsalm arboretum, 1993, F. Tombuyses (AR). **Canada**: 15♀, 5♂, ex. *A. grandis*, Cowichan Lake, B.C., 1958, A. Hedlin (GM). **France**: 7♀, 5♂, ex. *A. bornmülleriana,* Les Barres (45), May 1981 (AR); 6♀, 3♂, ex. *A. cilicica*, Les Barres, May 1981, (AR); 6♀, 6♂, ex. *A. concolor*, Les Barres, May 1990, R. Ostermeyer (AR); 11♀, 12♂, ex. *A. grandis*, Les Barres, May 1981, R. Ostermeyer (AR); 1♀, 1♂, ex. *A. numidica*, Les Barres, May 1997 (AR); 4♀, 5♂, ex. *A. pinsapo*, Les Barres, May 1981 (AR); 1♂, ex. *A. veitchii*, Les Barres, May 2000, M. Auger-Rozenberg (AR). **Great Britain**: 1♀, ex. *A. nobilis*, Scotland (USNM). **USA**: 1♀, ex. *A. concolor*, 8 January 1929, Colorado, Hoffmeyer collection (ZMUC); 1♂, ex. *A. grandis,* Oregon, 26 December 1928, Hoffmeyer collection (ZMUC).

Megastigmus pistaciae Walker

(figures 9, 22, 39, 59, 78, 116, 135, 154)

Megastigmus pistaciae Haliday, Walker, 1869: 313 [*nomen nudum*].

Megastigmus pistaciae Walker, 1871: 35. 2 Syntypes ♀, 'South of France, on *Pistacia terebinthus*, M. Joudras coll.' and 'Tuscany on *Pistacia lentiscus*' (BMNH [examined]).

Trogocarpus ballestrerii Rondani, 1877: 35. Lectotype ♀ (Bouček, 1974: 245), Italy (La Specola, Firenze [not examined]). Synonymy by Masi, 1934: 210.

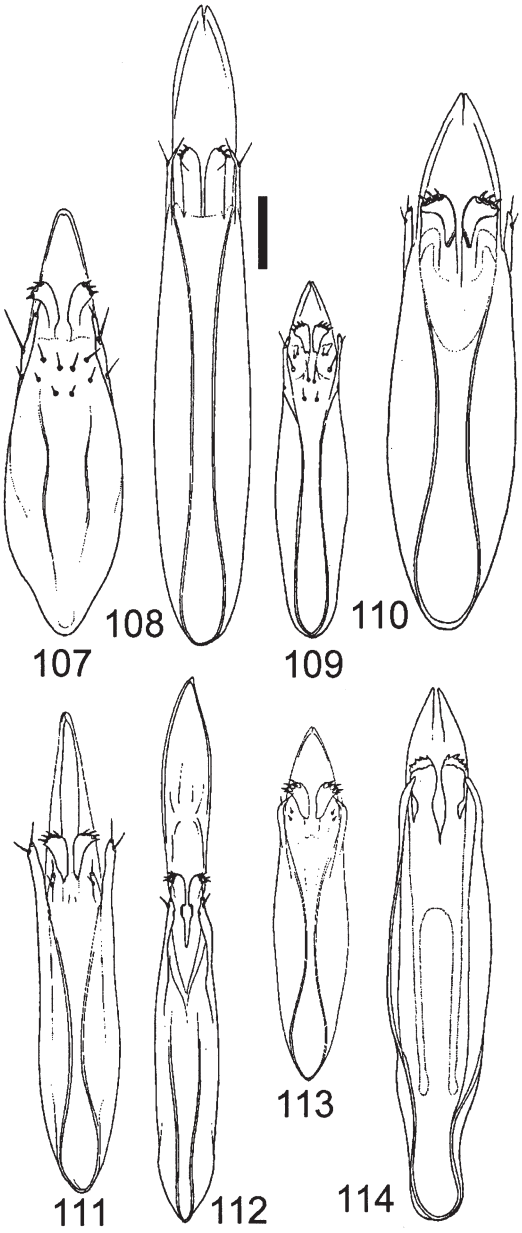
Female

Body length (without ovipositor) 3.4 and 3.5 mm. Body colour predominantly pale yellow. Head entirely pale yellow. Pilosity pale on lower face, black on remainder of head. Antenna mostly brownish; scape and pedicel yellowish. Thorax mostly pale yellow; pronotum and mesonotum pale yellow with longitudinal, somewhat indistinct red-brownish stripes; metanotum and scutellum darker, orange to red-brownish. Pilosity black on thoracic dorsum. Legs yellowish. Forewing stigma light brown. Propodeum dark orange. Gaster mostly orange-yellow. Ovipositor sheaths black.

Head about 1.1 × as broad as long in dorsal view. Antennal scape elongate, as long as the combined length of pedicel, anellus, first funicular segment and one-half of second funicular segment; funicular segments 1–3 about 1.6 × as long as wide, then tending to subquadrate (figure 22). Pronotum and mesoscutum with regular cross-striae. Scutellum elongate, 1.4 × as long as broad, the anterior part with cross-striae tending to reticulation, the frenal area with longitudinal carinae (figure 135). Forewing stigma oval-oblique, 1.2 × as long as wide; upper part of stigmal vein comparatively short, 0.2 × as long as stigma length; uncus as long as upper part of stigmal vein (figure 59). Propodeum without median carina. Ovipositor sheaths much shorter (0.5 ×) than body, nearly 0.6 × as long as gaster and thorax combined, 1.1 × as long as gaster. Distal part of the dorsal valve of the ovipositor with the third median tooth enlarged (figure 9).

Male

Body length 3.3mm. Body predominantly yellow with a few dark parts. Head entirely yellow. Pilosity pale on lower face, but black on parascrobal area and vertex. Antenna mostly brownish with scape yellowish. Thorax entirely yellow with long,



FIGS 107–114. Male genitalia of *Megastigmus* seed chalcids. (107) *M. aculeatus*; (108) *M. amicorum*; (109) *M. atedius*; (110) *M. bipunctatus*; (111) *M. milleri*; (112) *M. nigrovariegatus*; (113) *M. pictus*; (114) *M. pinsapinis*. Same origins as in (32–37, 76). Scale bar = 100 μm.

black bristles; four bristles in arched rows along lateral margins of scutellum. Legs yellowish. Wings subhyaline; forewing stigma dark brown, darker than in female. Propodeum yellow. Gaster quite entirely black with yellow spots on first apparent and last tergum.

Head rounded, nearly 1.2× as wide as long in dorsal view. Antennal scape

elongate, 1.2 × as long as the combined length of pedicel, anellus and the first two funicular segments; funicular segments more elongate than in female, about twice as long as wide (figure 39). Mid-lobe of mesoscutum very elongate, about 1.8 × as long as broad, more than 2 × longer than the transcutal line; pronotum and mesoscutum with regular cross-striae; scutellum 1.3 × as long as broad, the anterior part with coarse cross-striation tending to reticulation, the frenal area with arcuate wrinkles (figure 154). Stigma oval-oblique, about 1.4 × as long as wide; upper part of stigmal vein about 0.3 × as long as stigma length; uncus as long as upper part of stigmal vein (figure 78). Propodeum without median carina. Aedeagus truncated, digitus with three teeth (figure 116).

Variation

The above description is based on the type material of *M. pistaciae* for female and, for male, on a specimen from Ceriale nr Albenga, Italy (3 September 1972, Z. Bouček leg., MNHN). In the other examined specimens, body length varied from 2.6 to 3.5 mm in females, from 2.0 to 3.5 mm in males. Female colour ranged from whitish in pale specimens to rust-yellow in darker ones. Males were more variable in colour than females, with forms much darker than the type material. In these forms, head, margins of mesoscutum, propodeum and coxae were black. Gaster could be yellow to brownish yellow with a dorsal black line more or less extending laterally on the first four terga (Zerova and Seryogina, 1994).

Sex ratio

Reproducing by thelythokous parthenogenesis. Males were very scarce (less than 1♂:1000♀) in rearings of pistaccio nuts from Europe, North Africa and Iran but De Stefani (1917) noticed ratios of 6♂:760♀ in *Pistacia vera* and 1♂:37♀ in *P. terebinthus* in Italy. Males seemed more common in the USA (58♀:1356♀, i.e. 4.1% of males, caught in yellow traps at Chico, CA, Rice and Michailides, 1988; 3♂:50♀ emerged from pistaccio nuts, Placerville, CA, AR).

Hosts

Develops in seeds of *Pistacia* spp. (Anacardiaceae). In the native areas, recorded from *P. atlantica* (Davatchi, 1958; AR), *P. integerrima* (Rice and Michailides, 1988), *P. lentiscus* (Agnostopoulos, 1938; AR), *P. mutica* (Nikol'skaya, 1935, 1952; Davatchi, 1956, 1958; Lozovoi, 1965; Zerova and Seryogina, 1994), *P. terebinthus* (De Stefani, 1908, 1917, 1918; Agnostopoulos, 1938; Davatchi, 1956; AR) and *P. vera* (De Stefani, 1917, 1918; Nikol'skaya, 1934, 1935, 1952; Davatchi, 1956, 1958; Jarraya and Bernard, 1971; Çanakçioglü, 1993; Zerova and Seryogina, 1994; USNM). It shifted on exotic *P. chinensis* introduced to California (Rice and Michailides, 1988). The pinkpepper tree, *Schinus molle*, was also listed as a host (Furth, 1985 in Grissell, 1999; Rice and Michalides, 1988) but confusion with a peppertree seed chalcid, *M. transvaalensis*, may have occurred. Previous records on *Eucalyptus* (e.g. Escherich, 1938, 1942) are probably erroneous.

Distribution

Coastal Mediterranean areas to Afghanistan (USNM), Iran (Davatchi, 1956, 1958; Abai and Adeli, 1984) and China (USNM). Introduced to California (Rice and Michailides, 1988; AR) and Mexico (USNM). In Europe, known from Bulgaria (Bouček, 1977); Cyprus (Rice and Michailides, 1988); France: southern part

including Corsica (Davatchi, 1956, 1958; AR); Greece (Agnostopoulos, 1938; AR); Italy including Sicily (De Stefani, 1908, 1917, 1918; Greco and Nucifora, 1999; AR); Israel (Furth, 1985 in Grissell, 1999; USNM); Portugal (AR); former Soviet Union: from Crimea and Transcaucasia to Turkmenia and Uzbekistan (Nikol'skaya, 1934, 1935, 1952; Lozovoi, 1965; Nikol'skaya and Zerova, 1978; Zerova and Seryogina, 1994; USNM); Turkey (Schimitschek, 1944; Özkazanç, 1982; Çanakçioglü, 1993); Ukraine (Lozovoi, 1965); former Yugoslavia: Croatia, Montenegro (Bouček, 1977; AR). Also observed in North Africa: Algeria (USNM); Morocco (Davatchi, 1958); Tunisia (Jarraya and Bernard, 1971; AR).

Comments

No other *Megastigmus* species is yet known to develop in *Pistacia* seeds in the West Palearctic but two species of Eurytomidae (*Eurytoma pistaciae* Rondani and *E. plotnikovi* Nikol'skaya) compete for the resource in the major part of the distribution area (Davatchi, 1956, 1958; Jarraya and Bernard, 1971; Bouček, 1974, 1977). *M. pistaciae* can be easily recognized by the large stigma on forewing.

Material examined

Afghanistan: 1♀, PQ, US quarantine service (USNM). **Algeria**: 1♀, ex. *P. lentiscus*, US quarantine service Miami (USNM). **China**: 1♀, 1♂, ex. 'seeds of *Pistacia*', EQ# 059182, 3 June 1938, US quarantine service (USNM). **Croatia**: 43♀, ex. *P. terebinthus*, Gruda, August 1989 (AR). **France**: 1♀ syntype, ex. *P. terebinthus*, south of France, M. Joudras (BMNH); 15♀, ex. *Pistacia lentiscus*, Rognes (13), August 1990, (AR); 15♀, ex. *P. terebinthus*, Saint-Chinian (34), July 1990, (AR); 20♀, ex. *P. terebinthus*, Menton (06), August 1992 (AR); 1♀, ex. *P. lentiscus*, December 1950, J. Ghesquière (MNHN); 15♀, ex. *P. terebinthus*, La Ciotat (13), August 1993, (AR); 13♀, ex. *P. terebinthus*, Fréjus (83), August 1992 (AR); 22♀, ex. *P. terebinthus*, Rondinara (Corsica), July 1987 (AR). **Greece**: 39♀, ex. *P. terebinthus*, Pylos, August 1991 (AR). **Israel**: 1♀, ex. *P. terebinthus*, 'Palestine', PQ, US quarantine service (USNM). **Italy**: 1♀ syntype, ex. *P. lentiscus*, Tuscany (BMNH); 1♂, Ceriale nr Albenga, 3 September 1972, Z. Bouček (MNHN); 2♀, Sicily, 1911, De Stefani (MNHN). **Mexico**: 1♀, ex. seed *Pistacia*, Saltillo, May 1987, V. Carapia (USNM). **Portugal**: 81♀, ex. *P. terebinthus*, Corveiro, 23–25 August 1993 (AR); 44♀, ex. *P. terebinthus*, Cabo Espichel, 20–25 August 1993 (AR). **Tunisia**: 10♀, ex. *P. atlantica*, Sidi Khedr, 15 July 1995 (AR); 10♀, ex. *Pistacia lentiscus*, Semeche, 25 July 1995 (AR); 13♀, ex. *P. terebinthus*, Tabarka, 13 August 1987 (AR); **USA**: 65♀, 3♂, ex. *Pistacia* sp., Placerville, CA, 24 February 1994, N. Rappaport (AR); 30♀, 1♂, ex. *Pistacia chinensis*, Placerville, CA, 15 April 2000 (AR). **Uzbekistan**: 1♀, ex. *P. vera*, Taschkent, PQ US quarantine service (USNM). **Yugoslavia**: 15♀, ex. *P. terebinthus*, Kotor (Crna Gora), August 1989 (AR).

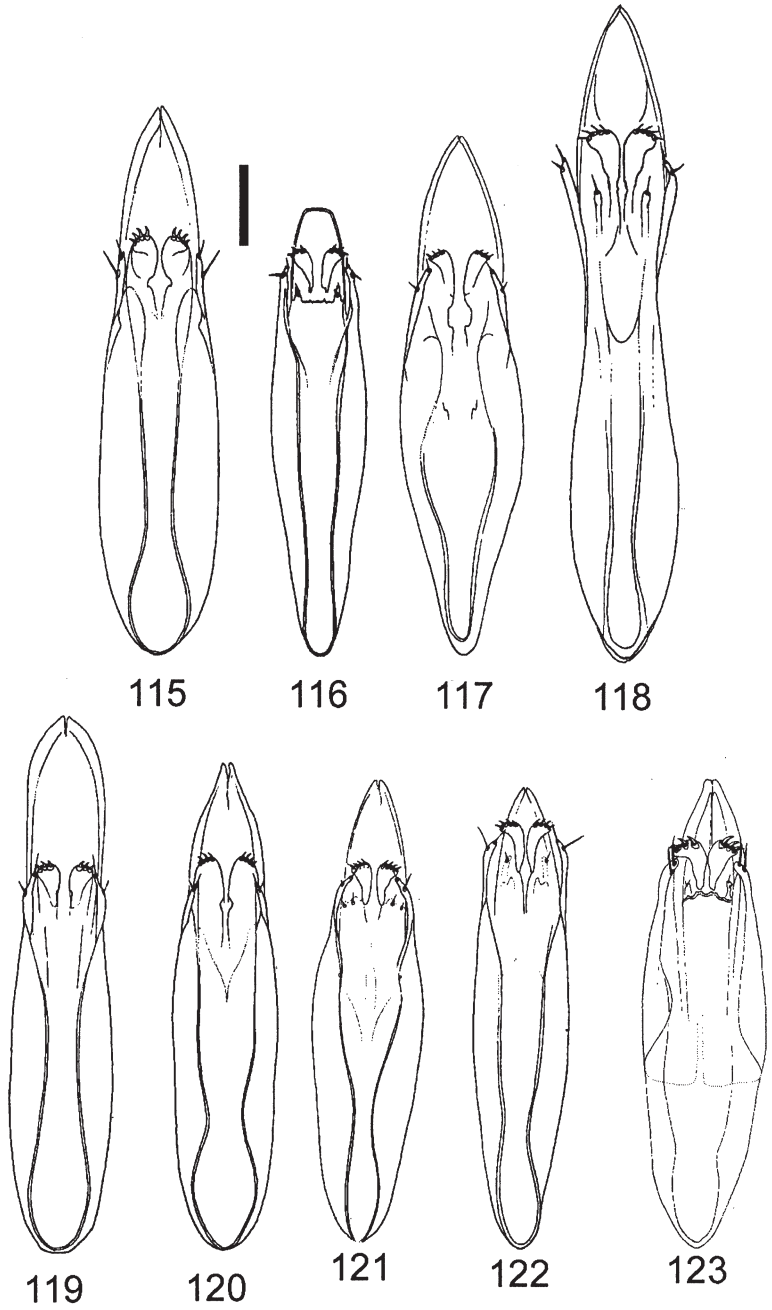
Megastigmus rafni Hoffmeyer

(figures 23, 40, 60, 79, 99, 117, 136, 155)

Megastigmus pinus Parfitt, 1857b: 5721 (subsequent description of ♂, *nec* ♀ 1857a).

Megastigmus spermotrophus of Crosby, 1913: 163 and authors (misidentifications in part).

Megastigmus rafni Hoffmeyer, 1929: 331–332. Holotype ♀, Colorado, *Abies concolor*, USA (ZMUC [examined]). 1♀ paratype, same data as holotype (USNM [examined]). Allotype ♂ (Hoffmeyer, 1931a: 216–217), Colorado, USA (?ZMUC [not examined]).



FIGS 115–123. Male genitalia of *Megastigmus* seed chalcids. (115) *M. pinus*; (116) *M. pistaciae*; (117) *M. rafni*; (118) *M. schimitscheki*; (119) *M. specularis*; (120) *M. spermotrophus*; (121) *M. strobilobius*; (122) *M. suspectus*; (123) *M. transvaalensis*. Same origins as in (38–46). Scale bar = 100 μm.

Female

Body length (without ovipositor) 4.0 mm. Body colour mostly brownish yellow with a few brown markings. Head tawny yellow with a brownish triangular spot

extending from side of clypeus to malar sulcus, and occiput brown. Pilosity pale on lower face, black on remainder of head. Antennal scape yellow, except distal end, remainder of antenna dark brown to black. Thoracic dorsum predominantly brownish yellow, with pronotum lighter than other parts, except anterior part of mid-lobe of mesoscutum and outer part of axilla dark brown; lateral parts of thorax brownish yellow except tegula and upper mesepisternum darker; metanotum with lateral panel brown, and dorsellum brownish yellow. Pilosity black on thoracic dorsum. Legs mostly brownish yellow except hind coxa dark orange-brown on the ventral side. Propodeum black anteriorly, then brownish yellow. First apparent gastral tergum brown, following terga brownish yellow with lateral oblique dark brown stripes, that are successively narrowing; distal terga mostly brownish yellow. Ovipositor sheaths black.

Head about 1.5 × as wide as long in dorsal view. Antennal scape enlarged, 1.1 × as long as pedicel, anellus and first funicular segment combined; proximal funicular segments about twice as long as wide but length of funicular segments successively decreasing, the distal ones quite subquadrate (figure 23). Pronotum and mesoscutum irregularly but strongly cross-striated, the striae being very arcuate in the distal part of the mid-lobe of mesoscutum. Scutellum 1.2 × as long as broad, the anterior part coarsely cross-striate and the frenal area quite smooth with a shallow reticulation below the frenal line and a few weak wrinkles on the lateral parts (figure 136). Forewing stigma elongate-oval, 1.7 × as long as broad, with the upper part of stigmal vein comparatively elongate, about 1.2 × as long as stigma width; uncus nearly 0.5 × as long as upper part of stigmal vein (figure 60). Propodeum with a weak irregular median carina. Ovipositor sheaths about 1.2 × longer than body. Distal part of dorsal valve of ovipositor with a large second median tooth (figure 98).

Male (from Milliron redescription, 1949)

Body length 3.0 mm. Body colour mostly brownish yellow with a few brown to black markings. Head entirely yellow except a narrow circumocellar black line. Pilosity pale on lower face, black on remainder of head. Antenna brownish yellow with scape yellowish. Thoracic dorsum mostly brownish yellow except the following dark brown to black parts: triangular black spot on anterior part of pronotum, large band on anterior margin of mid-lobe of mesoscutum prolongated by light brown infuscation extending towards posterior margin, outer part of axilla, narrow band along frenal line, and lateral panel of metanotum. Lateral parts of thorax entirely yellowish. Pilosity on thoracic dorsum black. Legs yellowish. Propodeum black anteriorly. First apparent tergum of gaster dark brown, the three following terga dark brown on dorsum, orange-yellow laterally, and the last ones entirely orange-yellow.

Head about 1.6 × as broad as long in dorsal view. Antennal scape shorter than in female, only 0.8 × as long as combined length of pedicel, anellus and first funicular segment; proximal funicular segments about twice as long as wide (figure 40). Pronotum and mesoscutum strongly cross-striated, the striae being very arcuate in the distal part of the mid-lobe of mesoscutum. Scutellum 1.3 × as long as broad, the anterior part coarsely cross-striated and the frenal area quite smooth with a limited reticulation below the frenal line (figure 155). Forewing stigma rounded, only 1.1 × as long as broad, with a comparatively elongate upper part of stigmal vein, 0.8 × as long as stigma width; uncus elongate, 0.6 × as long as upper part of

stigmal vein (figure 79). Propodeum with an irregular median carina. Aedeagus large, rounded, digitus with three teeth (figure 117).

Variation

The above description is based on the type material from North America. In Europe, body length varied from 2.3 to 5.5 mm in females, from 2.3 to 3.7 mm in males. Body colour was highly variable, especially in females. In light specimens, head and thorax were quite entirely orange to golden-yellow except small brown spots on anterior margin of acropleuron and at base of hind wing. Such specimens were found in France on *Abies alba* and *A. nordmanianna*. Darker specimens showed a conspicuous dark brown triangular patch on face, and a dark brown coloration extending on anterior margin and suture of lateral panel of pronotum, anterior margin of mid- and lateral lobes of mesoscutum, lower and upper mesepisternum, outer and inner margin of axilla, acropleuron and metanotum. Such specimens were found in France on *Abies numidica* and *A. pinsapo*. The median carina on propodeum could be interrupted in the middle.

Body colour was also highly variable in males. The darkest specimens observed in Europe (e.g. on *Abies bornmülleriana* introduced to France) showed a thoracic dorsum mostly dark brown to black, with the spot on pronotum nearly extending to the posterior margin, the mid-lobe of mesoscutum with only limited oval brownish yellow spots on sides of the posterior half, the axilla with only a small yellowish spot on inner angle, and the band on frenal line of scutellum extending from the centre in the direction of both the anterior and posterior margin of scutellum. In lighter specimens (e.g. from *A. alba* in France), brown was limited to a narrow band on the anterior margin of mid-lobe of mesoscutum and on the anterior central part of propodeum. Many intermediate forms were observed but the lateral parts of the thorax remained yellow in any case. No strict relationships between colour forms and hosts could be established.

Sex ratio

Apparently balanced in areas of introduction (16♀:14♂ in France; Ostermeyer, 1990; cf. above).

Hosts

Specific to fir seeds (*Abies* spp., Pinaceae). In native areas, recorded from *Abies concolor*, *A. magnifica*, *A. magnifica shastensis*, *A. grandis* and probably other *Abies* species (Peck, 1963; Grissell, 1979; Hedlin *et al*., 1980). Recorded in Europe from three of these introduced American species, *A. concolor* (Ostermeyer, 1990; Ochsner and Jensen, 1998; AR; USNM), *A. grandis* (Hussey, 1954a; Ostermeyer, 1990; Ochsner and Jensen, 1998; AR) and *A. procera* (Hussey, 1952). It shifted on to the native *A. alba* in natural stands all other southern France (Mt Ventoux to Pyrénées, AR). It also attacked most of the Mediterranean firs growing in aboreta and plantations of Denmark and France: *A. alba* (Ochsner and Jensen, 1998), *A. bornmülleriana* (Ochsner and Jensen, 1998), *A. cephalonica* (Ostermeyer, 1990; AR), *A. cilicica* (Ostermeyer, 1990; AR), *A. equi-trojani* (Ochsner and Jensen, 1998), *A. marocana* (Ostermeyer, 1990; AR), *A. nordmanniana* (Ochsner and Jensen, 1998), *A. nebrodensis* (AR), *A. numidica* (Ostermeyer, 1990; AR) and *A. pinsapo* (Ostermeyer, 1990; Ochsner and Jensen, 1998; AR). It was also observed on Asian firs introduced to France and Denmark: *A. homolepis* (Ochsner and Jensen, 1998;

AR), *A. koreana* (AR), *A. pindrow* (AR), *A. veitchii* (AR) but not on *A. procera* (Ochsner, 1998; Jensen and Ochsner, 1999). Records referring to *M. spermotrophus* in seeds of North American firs introduced to Europe (e.g. Čermak, 1952; Lessmann, 1962) are likely to represent misidentifications of light specimens of *M. rafni* (such as in Hussey, 1955b).

Distribution

Originates from North America, where its range covers Canada (British Columbia; Hedlin, 1974), western and southwestern USA, from Oregon and Idaho to California and New Mexico (Hedlin *et al*., 1980). Introduced to Europe where it was recorded with certainty only from the western part: Belgium (USNM); Denmark (Ochsner, 1998; Ochsner and Jensen, 1998; Jensen and Ochsner, 1999); France (Ostermeyer, 1990, as *Megastigmus* aff. *suspectus*; Da Ros *et al*., 1993; AR); Great Britain (Hussey, 1952, 1954a); The Netherlands (AR). However, recent investigations carried out in France showed that the species is now present in most fir stands of the country, especially in the eastern and southern range (M. Auger-Rozenberg and J. P. Fabre, unpublished), and it may soon extend to central Europe if not already done.

Comments

To date, six other species of seed chalcids were observed in fir seeds in the West Palearctic region: *M. milleri*, *M. pinsapinis*, *M. pinus*, *M. schimitscheki*, *M. specularis* and *M. suspectus*. Both sexes of *M. rafni* are easily differentiated by the light colour predominant on thorax and abdomen, even in the darkest specimens. For separating the other species, see the chapter concerning *M. milleri*. For lighter specimens, confusion may occur with the Douglas-fir seed chalcid, *M. spermotrophus*, but the exserted part of female ovipositor is 1.2 × longer than body in *M. rafni* whereas it is never longer than 1.1 × body in *M. spermotrophus*. Stigma shape, especially the relative length of uncus, also allows both sexes of the two species to be differentiated (see chapter concerning *M. spermotrophus*).

Material examined

Belgium: 1♀, ex. *Abies concolor* (USNM). **Canada**: 5♀, 6♂, ex. *A. grandis*, Cowichan Lake, British Columbia, 1958, A. F. Hedlin (GM). **France**: 11♀, 2♂, ex. *A. alba*, Mt Ventoux (84), May to June 1998 (JPF); 13♀, 8♂, ex. *A. alba*, Saint André les Alpes (04), June 1998 (JPF); 12♀, 5♂, ex. *A. alba*, Rialsesse (11), June 1998 (JPF); 5♀, 5♂, ex. *A. alba*, Gérardmer (88), May 1999, M. Auger-Rozenberg (AR); 5♀, 5♂, ex. *A. alba*, Le Frézillon (57), May 1999, M. Auger-Rozenberg (AR); 3♀, 1♂, ex. *A. alba* Freissinières (05), June 2000 (AR); 50♀, 50♂, ex. *A. alba*, Forest of Lafage (15), June 2000, M. Auger-Rozenberg (AR); 1♀, ex. *A. bornmülleriana*, Les Barres (45), May 1981 (AR); 2♀, 2♂, ex. *A. cephalonica*, Les Barres, May 1990, R. Ostermeyer (AR); 12♀, 6♂, ex. *A. cephalonica,* Marcelly (11), June 1998 (JPF); 3♀, ex. *A. cilicica*, Les Barres, May 1990, R. Ostermeyer (AR); 12♀, 14♂, ex. *A. concolor*, Les Barres, May 1990, R. Ostermeyer (AR); 1♀, 1♂, ex. *A. grandis*, Les Barres, May 1990, R. Ostermeyer (AR); 3♀, 3♂, ex. *A. grandis*, Forest of Der (52), June 2000, M. Auger-Rozenberg (AR); 1♀, ex. *A. homolepis*, Les Barres, May to June 1999, M. Auger-Rozenberg (AR); 1♀, ex. *A. koreana*, Les Barres, May 2000, M. Auger-Rozenberg (AR); 2♀, 2♂, ex. *A. marocana*, Les Barres, May 1990, R. Ostermeyer (AR); 4♀, 3♂, ex. *A. nebrodensis*, Les Barres, May to June 1999,

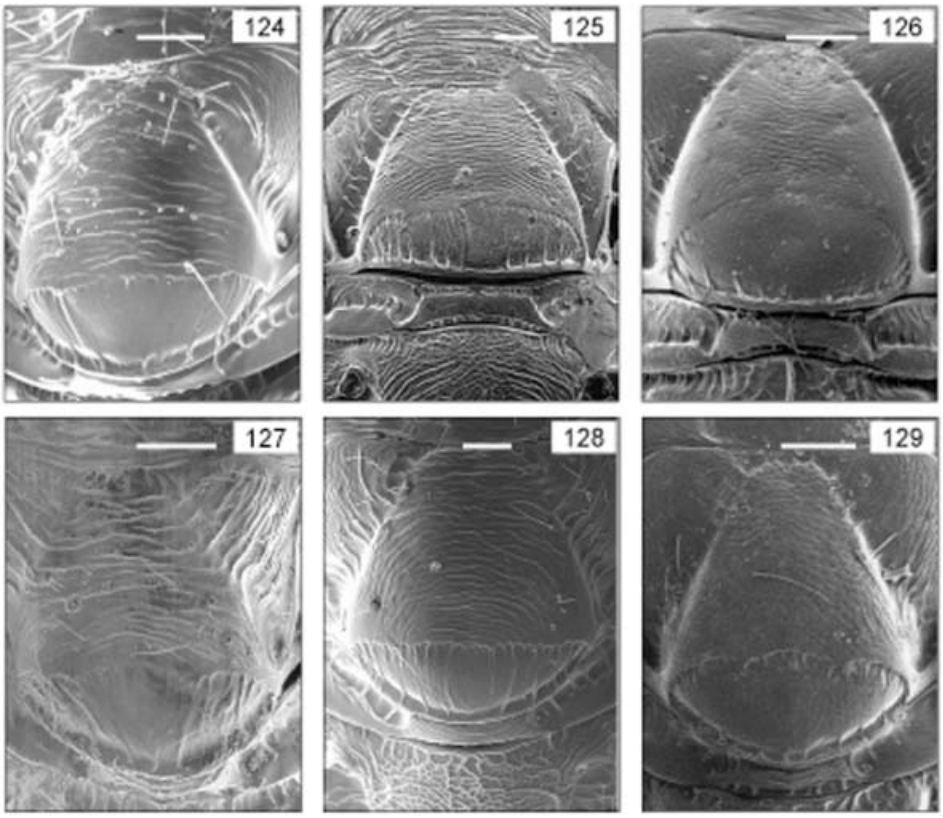
M. Auger-Rozenberg (AR); 6♀, 4♂, ex. *A. nordmanniana*, Les Barres, May 1990, R. Ostermeyer (AR); 3♀, ex. *A. numidica*, Les Barres, May 1995 (AR); 1♀, ex. *A. pindrow*, Les Barres, May 2000, M. Auger-Rozenberg (AR); 9♀, 8♂, ex. *A. pinsapo*, Les Barres, May 1990, R. Ostermeyer (AR); 54♀, 22♂, ex. *A. pinsapo*, Rialsesse (11), June 1998 (JPF); 1♂, ex. *A. veitchii*, Les Barres, May 2000, M. Auger-Rozenberg (AR). **The Netherlands**: 7♀, 10♂, ex. *A. grandis*, Sleenerzand, May 1989, P. Grijpma (AR). **USA**: 12♀, holotype and paratypes, ex. *A. concolor*, Colorado, 12–21 July 1928, Hoffmeyer collection (ZMUC, USNM).

Megastigmus rosae Bouček
(figures 24, 61, 99, 137)

Megastigmus pictus of Wachtl, 1884: 214 (according to Bouček, 1970b) [misidentification].
Megastigmus pictus of Hoffmeyer, 1931b: 265 (according to Bouček, 1970b) [misidentification].
Megastigmus rosae Bouček, 1971: 43–44. Holotype ♀, Botanical Garden, Wien, A, Novitzky leg. (BMNH [examined]).

Female

Body length (without ovipositor) 2.4 mm. Colour mainly yellowish with brownish black markings. Head yellowish with a broad dark brown spot extending on vertex



Figs 124–129. Electroscan photographs of scutellum of female *Megastigmus*. (124) *M. aculeatus*; (125) *M. amicorum*; (126) *M. atedius*; (127) *M. atlanticus*; (128) *M. bipunctatus*; (129) *M. brevicaudis*. Same origins as in (11–16). Scale bars = 100 μm.

including the ocelli, and connected with extensively dark occiput. Pilosity pale on lower face, black on head dorsum. Antenna brown with scape yellowish beneath. Pronotum mainly yellow; whole mid-lobe and anterior part of lateral lobes of mesoscutum, whole scutellum, axilla (except a spot at inner corner), metanotum, mesopleuron, metapleuron and propodeum dark brown to black. Pilosity dark on thoracic dorsum. Legs mainly yellowish, with hind coxa black basally. Propodeum brown with a black band on anterior margin. Gaster dorsally brownish with faintly indicated cross-bands but sides mainly yellowish. Ovipositor sheaths black.

Head 1.5 × as broad as long in dorsal view, with the eyes hardly protruding. Antennal scape elongate, 1.3 × as long as pedicel, anellus and first funicular segment combined; pedicel 1.8–1.9 × as long as broad, longer (1.2 ×) than first funicular segment (figure 24). Pronotum and mesoscutum with fine cross-striae. Scutellum fewly elongate, 1.1 × as long as broad, the anterior part reticulate-striate, the frenal area nearly smooth with short carinae extending longitudinally from both the frenal line and the hind margin (figure 137). Forewing stigma rounded, about 1.2 × as long as broad, with an upper part of stigmal vein longer (1.4 ×) than uncus (figure 61); basal cell with disc bearing 7–10 hairs. Propodeum with a rather straight, double median carina. Ovipositor sheaths distinctly smaller (0.7 ×) than body, 0.9 × as long as gaster and thorax combined. Distal part of dorsal valve of ovipositor with strong median teeth, the third one being larger than others (figure 99).

Male

Not observed. According to Bouček (1971): body length 2.7 mm; very similar to female in body colour and structure; head and antenna hardly different, pedicel slightly longer (1.2 ×) than first funicular segment; stigma hardly broader than in female.

Variation

The above description is based on the type material of *M. rosae*. In the other female specimens we examined, body length varied from 2.1 to 3.2 mm. The specimens from southern Europe (Bulgaria, Croatia, France) were highly variable but usually showed a thorax colour lighter than that of the type, mostly dirty yellowish with variable black to brown patches on dorsum. Lighter specimens (e.g. from the French Alps) presented a black band on anterior margin of mid-lobe of mesoscutum, a black patch on outer axilla, two black lines on metanotum, prepectus and mesepimeron being dark brown. In darker specimens (e.g. from Bulgaria), black covered anterior part of mid-lobe of mesoscutum, notula, axilla, metanotum, mesopleuron, metapleuron and propodeum. In specimens from southern Europe, forewing stigma was slightly infuscate and more elongate (1.5 × as long as broad) than in type, with uncus as long as upper part of stigmal vein. The median carina on propodeum was often simple in specimens from southern Europe.

Sex ratio

Bouček (1971) estimated it as 31:1. There were no males in our samplings.

Hosts

Develops exclusively in seeds of *Rosa* spp. (Rosaceae). Recorded from *R. arvensis* (AR), *R. canina* (Zerova and Seryogina, 1994; AR), *R. ferruginea* (AR), *R. pendulina* (AR), *R. rubiginosa* (AR), *R. tschatyrdagi* and *R. turkestanica* (Zerova and

Seryogina, 1994), and *Rosa* sp. (Bouček, 1971; Nikol'skaya and Zerova, 1978). In Bulgaria, we observed emergences of both *M. aculeatus* and *M. rosae* from the same rose hips as did Zerova and Seryogina (1994) in Russia.

Distribution

From the southern Alps to central and southern Europe, Caucasus and Siberia: Austria (Bouček, 1971), Bulgaria (AR); Croatia (AR); former Czechoslovakia (Čermak, 1952, as *M. pictus*; Bouček, 1971); France (AR); Poland (MS); Russia (Siberia, AR; Crimea, the Caucasus, Tadjikistan, Turkmenistan; Nikol'skaya and Zerova, 1978; Zerova and Seryogina, 1994); Switzerland (MS).

Comments

Two other species, *M. aculeatus* and *M. nigrovariegatus*, co-exist with *M. rosae* in *Rosa* seeds of the West Palearctic. Diagnostic characters for separating the three species are given in the chapter concerning *M. aculeatus*.

M. rosae kondaricus Zerova and Seryogina, was identified on *Rosa kokanica* Regel in the Pamir Altaï mountains of Tadjikistan (Zerova and Seryogina, 1994). According to the original description, the female differs from *M. rosae* by a longer body (2.6–3.5mm), a wider stigma surrounded by a limited infuscated area and the absence of carina on propodeum. The male has a longer body (2.8–3.5 mm), predominantly black except light spots on vertex, around the eyes, on pronotum, on the basis of scutellum, and on axilla. Its forewing stigma is surrounded by a limited infuscated area. Sex ratio (1:1) highly differed from the one usually observed in *M. rosae*.

Material examined

Austria: 1♀, Wien, 1957, S. Novitzky (BMNH). **Bulgaria**: 30♀, ex. *Rosa canina*, Sofia, June 1994 (AR); 12♀, ex. *R. arvensis*, Dolno Kamarci, June 1996, D. Pilarska (AR); 15♀, ex. *R. canina*, Saranci, June 1996, D. Pilarska (AR). **Croatia**: 6♀, ex. *Rosa* sp., Gruda, 24 April 1990 (AR). **Czech Republic**: 2♀, ex. *R. canina*, Kromeřiz, July 1992 (AR); 1♀, ex. *Rosa* sp., Třebič, June 1992 (AR). **France**: 9♀, ex. *R. canina*, Briançon (05), elev. 1200 m, 3 April 1996 (20°C), (AR); 2♀, ex. *R. ferruginea*, Briançon, elev. 1200 m, July 1990, (AR); 8♀, ex. *R. pendulina*, Névache (05), elev. 1600 m, July 1994, (AR); 7♀, ex. *R. rubiginosa*, Briançon, elev. 1200 m, 20 April 1996 (20°C) (AR); 1♀, beating *Rosa* sp., Brouis Pass (06), 19 July 1992, J. Y. Rasplus (AR). **Poland**: 1♀, ex. *R. canina*, Ojców Natl. Park, 25 May 1990 (MS); **Russia**: 5♀, ex. *Rosa* sp., Bratsk (Siberia), June 1989, A. Chavagnat (AR). **Switzerland**: 1♀, ex. *Rosa* sp., Sion, April 1999 (MS).

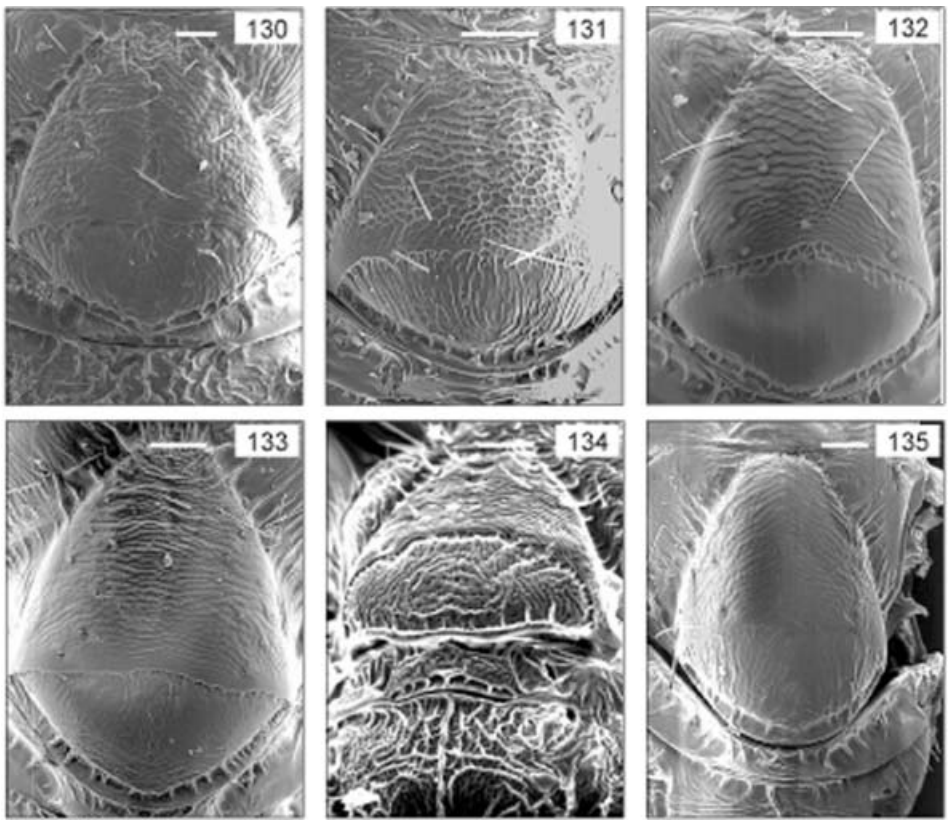
Megastigmus schimitscheki Novitzky

(figures 25, 41, 62, 80, 100, 118, 138, 156)

Megastigmus schimitscheki Novitzky, 1954: 220–224. 10♀, 10♂ syntypes, Alanya-Ayandere, Turkey (depository unknown: 'Novitzky collection' and 'Schimitschek collection' according to Grissell, 1999 [not examined]).

Female

Body length (without ovipositor) 5.0 mm. Body predominantly shining black except a few parts coloured in orange-brown to brown. Head mostly black with the following parts coloured in orange-brown: oral area, a small triangular spot below



FIGS 130–135. Electroscan photographs of scutellum of female *Megastigmus*. (130) *M. milleri*; (131) *M. nigrovariegatus*; (132) *M. pictus*; (133) *M. pinsapinis*; (134) *M. pinus*; (135) *M. pistaciae.* Same origins as in (17–22). Scale bars = 100 μm.

eye extending along malar sulcus, and a narrow, semi-continuous circumorbital line interrupted by irregular black patches. Antenna brown except scape and pedicel orange beneath. Pilosity black on head, even on lower face. Thorax almost entirely black with a dark orange, quite indistinct spot along posterior margin of lateral panel of pronotum and at basis of forewing. Pilosity black on thorax. Coxae black; femurs mostly dark brown except the distal part orange; remainder of legs orange. Forewing stigma brown, without surrounding infuscation. Propodeum black. First apparent tergum of gaster brown, the following ones brown with a narrow, orange-yellow transverse band posteriorly; lateral parts and sterna orange-yellow except first apparent sternite brown. Ovipositor sheaths black.

Head 1.3 × as broad as long in dorsal view. Antennal scape as long as pedicel, anellus and first funicular segment combined; first funicular segment 1.2 × longer than the following segments (figure 25). Pronotum and mesoscutum with coarse cross-striae. Scutellum about 1.3 × as long as broad, the anterior part reticulate-striate, the frenal area smooth or with only a few short wrinkles extending longitudinally from the frenal line (figure 138). Forewing stigma oval-elongate, about 1.6 × as long as wide (figure 62). Propodeum with a median carina. Exserted part of ovipositor 1.1 × as long as body. Distal part of dorsal valve of ovipositor with small, blunt teeth, the second median tooth being larger than others (figure 100).

Male

Body length 3.9 mm. Body colour very similar to that of female, predominantly shining black except a few parts coloured in orange-brown to brown. Head with lower face orange, circumorbital area and temple orange-brown, a narrow black line interrupting circumorbital area between gena and temple; remainder of head black. Antenna brown except scape and pedicel orange beneath. Pilosity black on head, even on lower face. Thorax almost entirely black with a dark orange, quite indistinct spot along posterior margin of lateral panel of pronotum and at basis of fore wing. Pilosity black on thorax with five pairs of conspicuous bristles on scutellum. Coxae black; femurs mostly dark brown except the distal part orange; remainder of legs orange. Forewing stigma brown, without surrounding infuscation. Propodeum black. First apparent tergum of gaster brown, the following ones brown with a narrow, orange-yellow transverse band posteriorly; lateral parts and sterna orange-yellow except first apparent sternite brown.

Head about 1.5 × as broad as long in dorsal view. Antennal scape smaller than in female, 0.9 × as long as pedicel, anellus and first funicular segment combined; first funicular segment slightly longer (1.1 ×) than the following ones (figure 41). Pronotum and mesoscutum with very coarse cross-striae. Scutellum 1.4 × as long as broad, the anterior part reticulate-striate, the frenal area smooth with only a few short carinae extending longitudinally from the frenal line (figure 156). Forewing stigma more rounded than that of female, about 1.5 × as long as broad, with a small uncus (figure 80). Propodeum with a median carina, interrupted in the middle in some specimens. Aedeagus conical, medium-sized; phallobase compressed in its medium; digitus with four teeth (figure 118).

Variation

The above description is based on a female and a male emerged from *Cedrus libani*, Sultandagi, Turkey (May 1997, Turkey, J. P. Fabre leg.) deposited at MNHN. In other specimens we examined, body length varied from 4.8 to 5.3 mm in females, from 3.0 to 4.2 mm in males. Very little variation in colour was observed. The dark orange spots on lateral panel of pronotum and at wing base were absent in about 30% of the examined specimens, and were not observed on the material used by Novitzky (1954) for the original description, nor on that described by Hussey (1957). The circumorbital line could also disappear, especially in females. The carina on propodeum was frequently interrupted in the middle.

Sex ratio

Novitzky (1954) assumed the sex ratio to be balanced in native countries. Fabre *et al.* (1994) measured a ratio of 730♂:825♀ when summing emergences from 18 locations in Turkey, but the sex ratio largely varied between locations. In south-eastern France, the introduced populations showed a ratio of 433♂:602♀ at Mt Ventoux.

Hosts

Observed in seeds of the cedar species (*Cedrus* spp., Pinaceae) originating from the eastern part of the Mediterranean Basin: *C. libani* (Novitzky, 1954; Schimitschek, 1955; Çanakçioglü, 1959, 1969, 1990; Lessmann, 1962; Ozkazanç, 1979; Fabre *et al.*, 1994; AR; USNM) and *C. brevifolia* (Hussey, 1957; USNM). In France, it shifted on to another introduced cedar, *C. atlantica*, and a Spanish fir, *Abies pinsapo* (Fabre

et al., in preparation). Records on cypress (Schimitschek in Schwenke, 1982) probably represented misidentifications.

Distribution

Originates from southeastern Europe and Asia Minor. Present in Cyprus (Hussey, 1957); Greece: Crete and islands of the eastern Aegean Sea (Schimitschek, 1955); Lebanon (Novitzky, 1954; Fabre *et al*., 1994; AR); Syria (Novitzky, 1954; USNM); and Turkey (Acatay, 1961; Novitzky, 1954; Çanakçioglü, 1959, 1969, 1990, 1993; Lessmann, 1962; Ozkazanç, 1979; Fabre *et al*., 1994; AR). Recently introduced to Mt Ventoux, southeastern France (probably in 1994 with seed lots of *C. libani* from Turkey; J. P. Fabre, personal communication), where it is gradually invading the naturalized stands of cedars and Spanish fir.

Comments

Two other chalcid species were observed to attack seeds of *Cedrus* spp. in the West Palearctic, *M. pinsapinis*, and more scarcely *M. suspectus*. Females are easily differentiated by the face coulour, which is entirely yellow in *M. pinsapinis* and yellow with black markings in most specimens of *M. suspectus*. Confusion may exist with the darkest specimens of *M. suspectus,* whose face can show extended black markings, but *M. schimitscheki* differs by the three pairs of coxae being entirely black. Similarly, males of *M. schimitscheki* can be recognized from those of the two other species by the coxae being entirely black. A total of six other species compete for seeds of *Abies pinsapo*. Diagnostic characters are given in the chapter regarding *M. milleri*.

Material examined

France: 602♀, 433♂, ex. *Cedrus atlantica*, Mt Ventoux (84), May to June 1998 (JPF); 54♀, ex. *Abies pinsapo*, Mt Ventoux (84), April 1995 (JPF); 1♂, ex. *A. pinsapo*, Mt Ventoux (84), April 1997 (JPF). **Lebanon**: 2♀, 2♂, ex. *C. libani*, Barouk Forest, 1981, G. Riom (AR). **Syria**: 1♀, ex. *C. libani* (USNM). **Turkey**: 1♀, ex. *C. libani,* Y. Gokdere, 3 June 1998 (JPF); 12♀, 15♂, ex. *C. libani*, seed lot to be introduced in France from Yenice (37°30′N, 35°00′E), 1994 (AR); 33♀, 55♂, ex. *C. libani*, Sultandagi, May to June 1997 (JPF); 13♀, 12♂, ex. *C. libani*, Aykiriçay, May to June 1997 (JPF).

Megastigmus specularis Walley

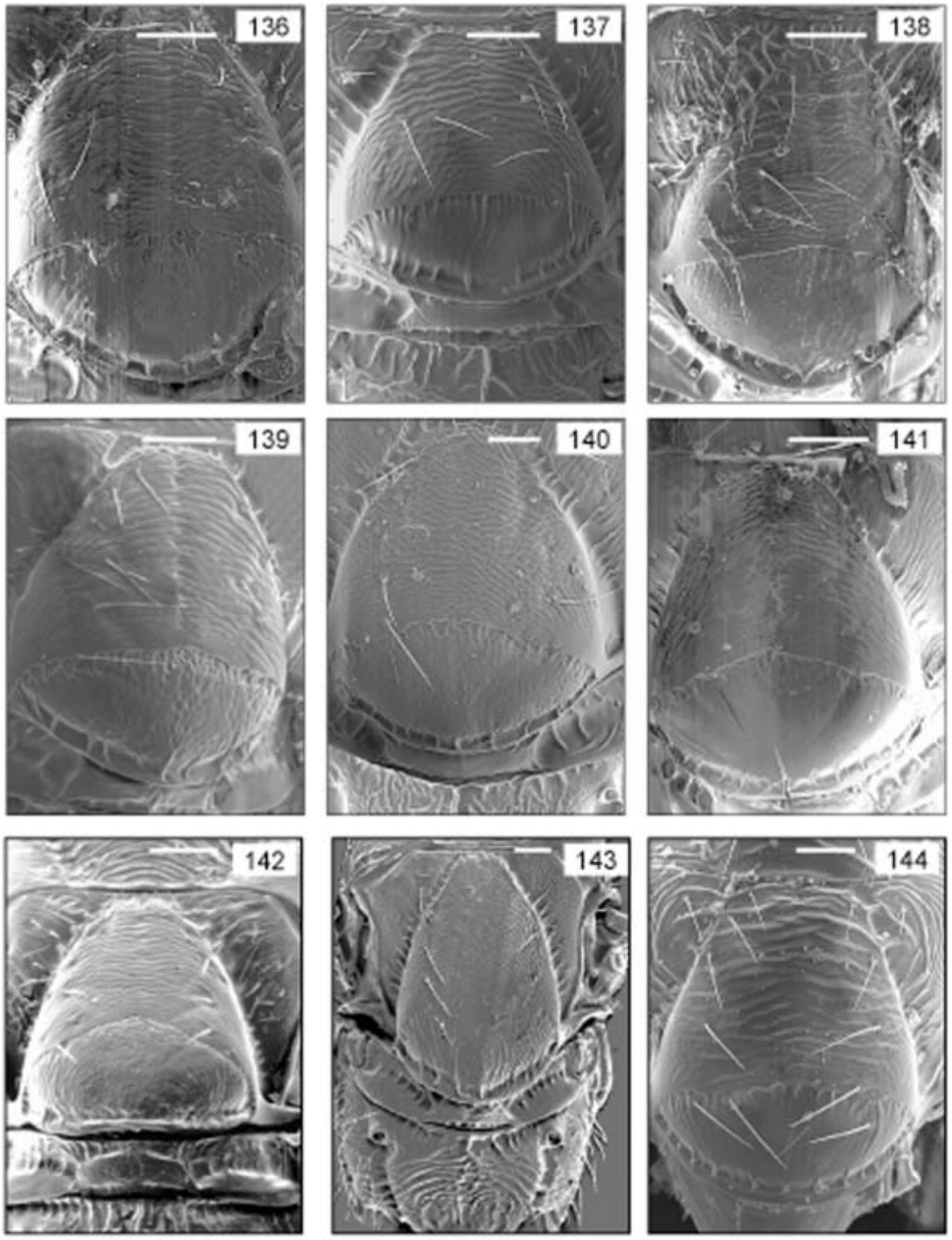
(figures 26, 42, 63, 81, 101, 119, 139, 157)

Megastigmus specularis Walley, 1932: 187–188. Holotype ♀, New Brunswick, Canada (Canadian National Collection, Ottawa [not examined]).

Megastigmus gronblomi Kangas, 1945: 177–180. Syntypes ♀ and ♂, Tampere, Finland (Museum Zoologicum Universitatis Helsinki, according to Hussey, 1954 [not examined]). Synonymy by Bouček, 1970b: 267.

Female

Body length (without ovipositor) 2.8 mm. Body colour black and tawny yellow. Face, parascrobal area and a circumorbital band interrupted on the middle of inner margin of eye, yellow; remainder of head black. Pilosity pale on lower face, black on remainder of head. Antenna brown except scape and pedicel yellow beneath. Dorsum of thorax mostly black except two transverse, broadly separated yellow



FIGS 136–144. Electroscan photographs of scutellum of female *Megastigmus*. (136) *M. rafni*; (137) *M. rosae*, Bulgaria; (138) *M. schimitscheki*; (139) *M. specularis*; (140) *M. spermotrophus*; (141) *M. strobilobius*; (142) *M. suspectus*; (143) *M. transvaalensis*; (144) *M. wachtli*. Same origins as in (23–31). Scale bars = 100 μm, except for (138, 142). Scale bars = 200 μm.

spots at posterior margin of pronotum, and a yellow spot on outer surface of lateral lobe of mesoscutum; lateral parts of thorax lighter: lateral panel of pronotum and tegula tawny-yellow; prepectus and upper mesepisternum light brown; acropleuron and mesepimeron dark brown. Pilosity on thoracic dorsum black. Legs mostly

brownish yellow except fore legs tawny-yellow and hind coxa black. Propodeum black. Gaster with first apparent tergum entirely black; then terga black on dorsum with the sides yellow; last two terga entirely pale brown. Ovipositor sheaths black.

Head about 1.6× as broad as long in dorsal view. Antennal scape as long as pedicel, anellus and first funicular segment combined; pedicel oval, 0.8× shorter than first funicular segment; first funicular segment 2× as long as wide (figure 26). Pronotum and mesoscutum with coarse cross-striae. Scutellum 1.1× as long as broad, the anterior part weakly reticulate-striate, the frenal area reticulated along the frenal line and the remainder nearly smooth with some shallow areolae (figure 139). Forewing stigma roughly oval, about 1.3× as long as wide; upper part of stigmal vein comparatively elongate, 1.1× as long as stigma width; uncus half as long as upper part of stigmal vein (figure 63). Propodeum without median carina. Ovipositor sheaths 1.9× longer than gaster, 0.9× as long as body. Distal part of dorsal valve of ovipositor with blunt teeth (figure 101).

Male

Body length 2.4 mm. Body colour black and yellow. Head black except face, gena and a circumorbital band yellow. Pilosity pale on lower face, black on remainder of head. Antenna mostly brown; scape except distally above and pedicel beneath, yellow. Dorsum of thorax mostly black except two large, hemispherical spots at posterior margin of pronotum, and outer surface of lateral lobe of mesoscutum yellow. Lateral panel of pronotum, tegula, mesepimeron and mesepisternum yellow; metapleuron with yellowish brown patch on ventral margin. Pilosity dark on thoracic dorsum. Legs yellowish brown except hind coxa brown at base. Propodeum black except callus with yellowish brown patch on ventral margin. Gaster dark brown on dorsum of first apparent tergum, and pale amber at side; dorsum of following terga progressively becoming pale amber at posterior margin, each tergum being separated from the preceding by a narrow, brownish yellow band; last two terga entirely tawny-yellow.

Head 1.4× as broad as long in dorsal view. Antennal scape subequal to combined length of pedicel, anellus and first funicular segment; pedicel ovate, subequal to first funicular segment; distal funicular segments quite subquadrate (figure 42). Pronotum and mesoscutum with coarse cross-striae. Scutellum 1.3× as long as broad, the anterior margin wider than the posterior margin of mid-lobe of mesoscutum. Anterior part of scutellum reticulate-striate, the frenal area reticulated below the frenal line and the remainder nearly smooth with some shallow areolae (figure 157). Stigma broadly oval, 1.2× as long as wide, upper part of stigmal vein 0.8× as long as stigma width; uncus half as long as upper part of stigmal vein (figure 81). Propodeum with a fine irregular median carina on anterior part. Aedeagus large, convex, digitus with three teeth (figure 119; Kangas, 1945).

Variation

The above description summarizes that given by Milliron (1949) for the American type material. In the European specimens, body length varied from 2.2 to 3.8 mm in females, from 2.1 to 3.0 mm in males. Female colour was highly variable. The circumorbital band could be reduced to a yellow spot adjacent to the eye on its posterior margin (type material of *M. gronblomi* according to Hussey, 1954b). Milliron (1949) and Bouček (1970b) noticed a frequent absence of the yellow spots on pronotum. Most of the specimens we examined from France and Finland did

not show any yellow colour on thorax except lateral panel of pronotum. Hind coxa could be entirely black. In addition, the gaster colour pattern largely varied in intensity and definition. The carination of propodeum was variable and often consisted of a complete, fine median carina (type material of *M. gronblomi*; Hussey, 1954b). In the European specimens we examined, the relative length of the exserted part of ovipositor varied from 0.9 × to 1.1 × the body length whilst Bouček (1970b) considered that piece as usually longer than body.

Males were also variable in colour. In North America, Milliron (1949) observed specimens much darker than the type material, where most of the yellow markings were absent (especially circumorbital band, spots on pronotum, lateral lobe of mesoscutum and axilla), and mesepimeron, mesepisternum and hind coxa entirely black. However, all the European specimens observed by Bouček (1970b) presented large yellow spots on pronotum, as it also appeared in our specimens from France and Finland. Propodeum carination could consist of a complete, but fine, irregular median carina (type material of *M. gronblomi*; Hussey, 1954b). The carina was double anteriorly in specimens from France.

Sex ratio

Apparently balanced in northern Europe (Annila, 1970).

Hosts

In the native North American areas, develops in seeds of eastern firs, *Abies balsamea* (Peck, 1963; Grissell, 1979; Hedlin *et al*., 1980) and *A. fraseri* (Pursh.) Poir. (Hedlin *et al*., 1980) (Pinaceae). In Europe, it was similarly recorded from seeds of exotic fir species introduced from North America: *A. amabilis* (Annila, 1970), *A. balsamea* (Annila, 1970; Ochsner and Jensen, 1998), *A. concolor* (Annila, 1970; Ochsner and Jensen, 1998) and *A. lasiocarpa* (Annila, 1970) but damage on *A. amabilis* and *A. concolor* was lower in Finland than in the native range (Annila, 1970). It also shifted on to the native *A. sibirica* (Kangas, 1945; Vikberg, 1966; Annila, 1970; Ochsner and Jensen, 1998) and on to several exotic Asian firs of the balsam fir group, which were heavily attacked: *A. nephrolepis* (Annila, 1970), *A. sachalinensis* (Annila, 1970), *A. veitchii* (Annila, 1970; Ochsner and Jensen, 1998; AR). Some other Eurasian fir species were infested but only lightly: *A. alba* (Annila, 1970), *A. bornmülleriana* (Ochsner and Jensen, 1998), *A. holophylla* Maxim. (Annila, 1970), *A. homolepis* (Ochsner and Jensen, 1998), *A. koreana* (Annila, 1970; Ochsner and Jensen, 1998), *A. nordmanniana* (Annila, 1970; Ochsner and Jensen, 1998) and *A. pinsapo* (Ochsner and Jensen, 1998). Annila (1970) assumed that fir species with large cones are less susceptible to colonization by *M. specularis* because of the shortness of its ovipositor.

Distribution

Probably originates from North America (Bouček, 1970b), its present range covering eastern Canada and the eastern USA (Peck, 1963; Grissell, 1979; Hedlin *et al*., 1980). First introduced into northern Europe and extending to western Siberia, it has been recently recorded from western Europe: Denmark (Ochsner, 1998; Ochsner and Jensen, 1998; Jensen and Ochsner, 1999); Finland (Kangas, 1945; Vikberg, 1966; Annila, 1970); France (AR); Russia (Moscow, Siberia; Vikberg, 1966; Bouček, 1970b); Sweden (Hansson, 1991).

Comments

To date, six other species of seed chalcids were observed in seeds of firs in the West Palearctic region: *M. milleri*, *M. pinsapinis*, *M. pinus*, *M. rafni*, *M. schimitscheki* and *M. suspectus*. For separating these species, see the chapter concerning *M. milleri*.

Material examined

Canada: 4♀, 4♂, ex. *A. balsamea*, Tourville-l'Islet, Québec, 9 March 1983 (in laboratory) (GM). **Finland**: 20♀, 20♂, ex. *Abies sibirica* Tuusula, 10 July 1974, E. Annila (AR); 2♀, ex. *A. veitchii*, Bromaru, 1968, E. Annila (MNHN). **France**: 2♀, 2♂, Les Barres (45), ex. *A. veitchii*, Les Barres (45), June 1990, R. Ostermeyer (AR).

Megastigmus spermotrophus Wachtl
(figures 27, 43, 64, 82, 102, 120, 140, 158)

Megastigmus spermotrophus Wachtl, 1893: 26–28. 3♀ and 1♂ syntypes, coll. Mayr (NMW [examined]).

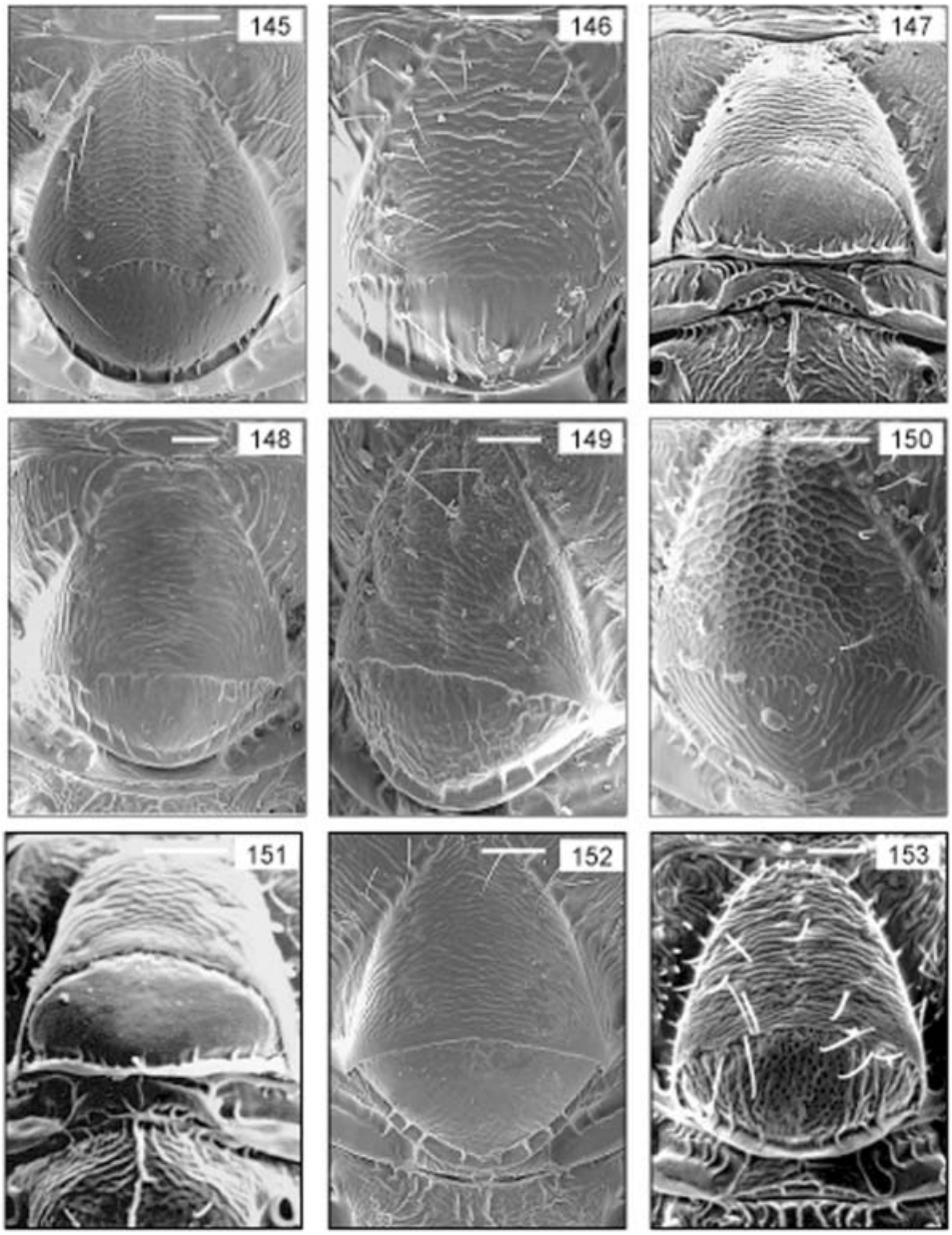
Female

Body length (without ovipositor) 3.3, 3.8 and 4.1 mm. Body colour brownish yellow to orange-yellow. Head brownish yellow, with darker, irregular spots as side of clypeus, on gena and around ocelli. Pilosity pale on lower face, black on remainder of head. Antenna brown except scape yellowish and pedicel and anellus brownish yellow beneath. Thorax mostly brownish yellow, with posterior margin of pronotum lighter, and anterior part of mid-lobe of mesoscutum, outer axilla, and median area of scutellum reddish brown; small black spots present at insertion of wings. Pilosity black on thoracic dorsum. Legs brownish yellow. Propodeum brownish yellow with median area reddish brown. Gaster dark orange-yellow. Ovipositor sheaths black.

Head about 1.5 × as broad as long in dorsal view. Antennal scape 1.1 × as long as pedicel, anellus and first funicular segment combined; first funicular segment elongate (2 × as long as wide), 1.1 × longer than the following segments (figure 27). Pronotum distinctly wider than long. Pronotum and mesoscutum with dense cross-striae. Scutellum 1.2 × as long as broad, the anterior part reticulate-striate, the frenal area nearly smooth with a limited reticulation just below the frenal line and short, weak longitudinal wrinkles (figure 140). Six pairs of bristles on scutellum. Forewing stigma elongate-oval, 1.9 × as long as wide; upper part of stigmal vein comparatively elongate, about 0.9 × as long as stigma width; uncus very short, 0.3 × as long as upper part of stigmal vein (figure 64). Propodeum with a median carina more pronounced anteriorly. Ovipositor sheaths 0.9 × as long as body. Distal part of dorsal valve of ovipositor with blunt teeth, except the terminal one (figure 102).

Male

Body length 3.1 mm. Body colour dark lemon yellow. Head lemon yellow except black spots surrounding ocelli, which are partially coalescent. Pilosity pale on lower face, black on remainder of head. Antenna light brown except scape yellowish and pedicel yellowish beneath. Thorax mostly dark lemon yellow with a few black patterns: a transverse band at anterior margin of pronotum; a bilobed, transverse band at anterior margin of mid-lobe of mesoscutum, a spot on outer axilla, and a band on lateral panel of metanotum. Pilosity on thoracic dorsum black. Legs



FIGS 145–153. Electroscan photographs of scutellum of male *Megastigmus*. (145) *M. aculeatus*; (146) *M. amicorum*; (147) *M. atedius*; (148) *M. bipunctatus*; (149) *M. milleri*; (150) *M. nigrovariegatus*; (151) *M. pictus*; (152) *M. pinsapinis*; (153) *M. pinus*. Same origins as in (32–38, 76). Scale bars = 100 μm.

yellowish. Propodeum entirely black. Gaster with the first two apparent terga black on dorsum; remainder of gaster dirty yellow.

Head about 1.5 × as broad as long in dorsal view. Scape as long as pedicel, anellus and first funicular segment combined; first funicular segment elongate, twice as long as wide, 1.2 × as long as the following segments (figure 43). Pronotum and

mesoscutum with dense cross-striae. Scutellum 1.2× as long as broad, the anterior part reticulate-striate, the frenal area nearly smooth with a limited reticulation just below the frenal line and short, weak longitudinal wrinkles (figure 158). Forewing stigma more oval than that of female, only 1.4× as long as wide, with upper part of stigmal vein less elongate, about 0.6× as long as stigma width; uncus 0.4× as long as upper part of stigmal vein (figure 82). Propodeum with a distinct median carina. Penis medium-sized, conical, sinuated at the apex; digitus with four teeth (figure 120).

Variation

The above description corresponds to the type material. In the other specimens we examined, body length varied from 2.8 to 4.3 mm in females, from 2.7 to 3.8 mm in males. Female colour was a little variable. Most specimens from Europe and New Zealand fitted the type description. However, lighter individuals were observed where body was entirely light orange-yellow (e.g. at Vielsaam, Belgium). Specimens darker than the type were not uncommon. The darkest ones presented reddish brown stripes on sides of pronotum and on anterior margin of lateral lobe of mesoscutum, a black band on anterior margin of propodeum, and the black spots at insertion of wings extended in a black line along sutures of tegula and acropleuron (e.g. in France and Finland). Gaster was deep amber, much darker than thorax in these individuals. The relative length of the exserted part of ovipositor varied from 0.9× to 1.1× the body length.

Male predominant colour varied from lemon-yellow to orange-yellow. In light specimens, the circumocellar spots on head was quite absent, the bilobed band on mid-lobe of mesoscutum reduced to a light brownish, thin stripe extending along the anterior suture, the propodeum was yellow, and the first two apparent terga of gaster showed only narrow brown stripes on dorsum (e.g. specimens from Lavercantière seed orchard, France). In darker specimens, the circumocellar spots were completely coalescent, and a number of black patterns were observed on thorax: a band on anterior margin of pronotum and anterior half of mid-lobe of mesoscutum, a spot on outer axilla and lateral panel of metanotum (e.g. specimens from arboretum of Les Barres, France). The median carina on propodeum could be absent or interrupted.

Sex ratio

Highly variable according to location and year (Milliron, 1949; Hussey, 1955b). Sex ratio was strongly skewed in favour of males in some cases (Roques, 1981).

Hosts

Specific to seeds of *Pseudotsuga* spp. (Pinaceae). In the native North American areas, both varieties of Douglas-fir, *P. menziesii* (var. *glauca* [Beissn.] E. Murray and var. *menziesii* [Mirb.] Franco) are attacked as well as bigcone Douglas-fir, *P. macrocarpa* (Milliron, 1949; Keen, 1958; Peck, 1963; Grissell, 1979; Hedlin *et al*., 1980; Niwa and Overhulsen, 1992). Also recorded from *P. flahaulti* Flous and *P. macrolepis* Flous in Mexico (Cibrian-Tovar *et al*., 1995). However, the specimens developing in *P. macrocarpa* were considered as a distinct subspecies, *Megastigmus spermotrophus nigrodorsatus* Milliron (Milliron, 1949).

In the European areas of introduction, records essentially concerned plantations of *P. menziesii*. In the French arboreta, the typical form of *M. spermotrophus* was

also observed to colonize seeds of several additional exotic species: bigcone Douglas-fir, the Japanese *P. japonica*, and the Mexican *P. guinieri* and *P. rehderi* (Ostermeyer, 1990; AR). Earlier records from seeds of *Abies* spp. (e.g. Hoffmeyer, 1931a; Zacher, 1932; Čermak, 1952; Nikol'skaya, 1952; Lessmann, 1962; Wall, 1984) probably referred to pale specimens of *M. rafni* and those on *Tsuga* (e.g. Hoffmeyer, 1931a) to *M. tsugae* Crosby.

Distribution

Native from western North America, being widespread from British Columbia to California and Mexico (Peck, 1963; Grissell, 1979; Hedlin *et al*., 1980; Cibrian-Tovar *et al*., 1995). Introduced with Douglas-fir seeds to New Zealand (Bain, 1977; Commonwealth Institute of Entomology, 1977; Bouček, 1988) and Europe. Presently widespread all over Europe, even in Mediterranean countries, being recorded from: Austria (Kapuściński, 1966; AR); Belgium (Jamblinne de Meux and Nanson, 1969; Tombuyses, 1993; AR); former Czechoslovakia (Čermak, 1952; Bouček, 1954; Mentberger, 1964; Křístek, 1967, 1968; Křístek *et al*., 1992); Denmark (Hoffmeyer, 1931b; Jespersen and Lomholdt, 1983; Ochsner, 1998; Jensen and Ochsner, 1999); Estonia (Luik and Voolma, 1988); Finland (Annila, 1982; AR); France (Vayssières, 1931; Roques, 1981, 1983; Rappaport and Roques, 1991; Roques and Raimbault, 1998); Germany (Tubeuf, 1930; Gäbler, 1962; Lessmann, 1974a, 1974b; Sellenschlo, 1984a; Schneider, 1985); Great Britain (Laidlaw, 1931; Hussey, 1954a, 1955); Hungary (Györfii, 1956, 1962); Ireland (Commonwealth Institute of Entomology, 1977), Italy (Sorauer, 1953; Roversi *et al*., 1993; Da Ros, 1997; AR); Norway (Wall, 1984); The Netherlands (Oudemans, 1933; AR); Poland (Kozikowski, 1949; Madziara, 1955; Kapuściński, 1966; Schnaider, 1970; Szmidt and Banaszak, 1991); Portugal (AR); Romania (Nanu, 1976, 1980; Nanu *et al*., 1986); Russia (Bekreneva and Tropin, 1975; Nikol'skaya and Zerova, 1978; Stadnickii *et al*., 1978); Spain (AR); Sweden (Trägårdh, 1917); Switzerland (AR); former Yugoslavia (Bouček, 1977).

Comments

No other chalcid species was observed in the seeds of *Pseudotsuga* spp. in the West Palearctic. *M. spermotrophus nigrodorsatus* Milliron, identified in the seeds of *P. macrocarpa* in southern California (Milliron, 1949), was not apparently introduced with the seeds of that species in Europe. According to Milliron (1949), the male differs from that of *M. spermotrophus* by predominantly black patterns on head dorsum (a quadrilateral spot extending from occipital carina to antennal scrobe) and thorax (a large median spot on pronotum; the mid-lobe of mesoscutum mostly black except a narrow yellow stripe along notuli; an oblique spot on lateral lobe of mesoscutum; the frenal line and a complete median longitudinal line on scutellum). No reliable characters were identified for differentiating females, yet.

Confusion may occur between darker specimens of *M. spermotrophus* and lighter specimens of a fir seed chalcid, *M. rafni*. Female can be differentiated by the relative length of the exserted part of ovipositor (1.2 × longer than body in *M. rafni* versus 0.9–1.1 × as long as body in *M. spermotrophus*) and the shape of forewing stigma (uncus comparatively more elongate in *M. rafni*; figures 64, 69). In males of *M. spermotrophus*, stigma is less rounded (1.4 × versus 1.1 × as long as wide in *M. rafni*) and uncus is much less elongate (figures 79, 82). To separate males, Milliron (1949) also used presumed differences in colour patterns (black coloration

never extensive on axilla in darker forms of *M. spermotrophus*) but lighter forms of *M. rafni* may present axilla entirely yellow.

Material examined

Austria: 1♀, 'seeds from Austria, 1941' (MNHN). **Belgium**: 6♀, 5♂, ex. *Pseudotsuga menziesii*, Fenffe, May 1993, F. Tombuyses (AR). **Finland**: 3♀, 2♂, ex. *P. menziesii*, Kirkkunomi, Båtvik, January 1994 (in laboratory), M. Pulkinnen (AR). **France**: 35♀, 30♂, ex. *P. menziesii*, Lavercantière (46), May 1986 (AR); 11♀, 15♂, ex. *P. menziesii*, Les Barres (45), May 1981 (AR); 4♀, 3♂, ex. *P. macrocarpa*, Les Barres, May 1981 (AR); 1♀, 2♂, ex. *P. guinieri*, Les Barres, May 1990, R. Ostermeyer (AR); 3♀, 2♂, ex. *P. rehderi*, Les Barres, May 1990, R. Ostermeyer (AR); 8♀, 12♂, ex. *P. japonica*, Angers (49), May 1989 (AR). **Germany**: 11♀, 5♂, ex. *P. menziesii*, Bergach, May 1993 (AR). **Italy**: 10♀, 9♂, ex. *P. menziesii*, Amborzasco (Liguria), May 1993, A. Battisti (AR); 6♀, 5♂, ex. *P. menziesii*, Vallombrosa (Toscana), May 1992, A. Battisti (AR); 6♀, 5♂, ex. *P. menziesii*, Acquerino (Toscana), May 1992, A. Battisti (AR); 2♀, 3♂, ex. *P. menziesii*, Etroubles (Aosta), May 1992, M. Kenis (AR); 10♀, 12♂, ex. *P. menziesii*, Sila (Calabria), May 1993, A. Battisti (AR); 1♀, ex. *P. menziesii*, Paluzza (Friul), May 1993, A. Battisti (AR). **The Netherlands**: 2♀, 4♂, ex. *P. menziesii*, Ede, May 1991 (AR); 2♀, 3♂, ex. *P. menziesii*, Vaals (LI), May 1991 (AR). **New Zealand**: 3♀, 2♂, ex. *P. menziesii*, Roturoa, September 1993, N. Kay (AR). **Poland**: 2♀, 2♂, ex. *P. menziesii*, Beskid Żywiecki, Nadleśnictwo Ujsoły, June 1987 (MS). **Portugal**: 15♀, 13♂, ex. *P. menziesii*, Amarante, May 2000, (AR). **Spain**: 22♀, 23♂, S. Breixo, Guitiriz, ex. *P. menziesii*, May 1992, G. Vega (AR). **Switzerland**: 23♀, 15♂, ex. *P. menziesii*, Birmensdorf (ZU), May 1993 (AR). **USA**: 12♀, 10♂, ex. *P. menziesii*, California, 1994, N. Rappaport (AR).

Megastigmus strobilobius Ratzeburg
(figures 28, 44, 65, 83, 103, 121, 141, 159)

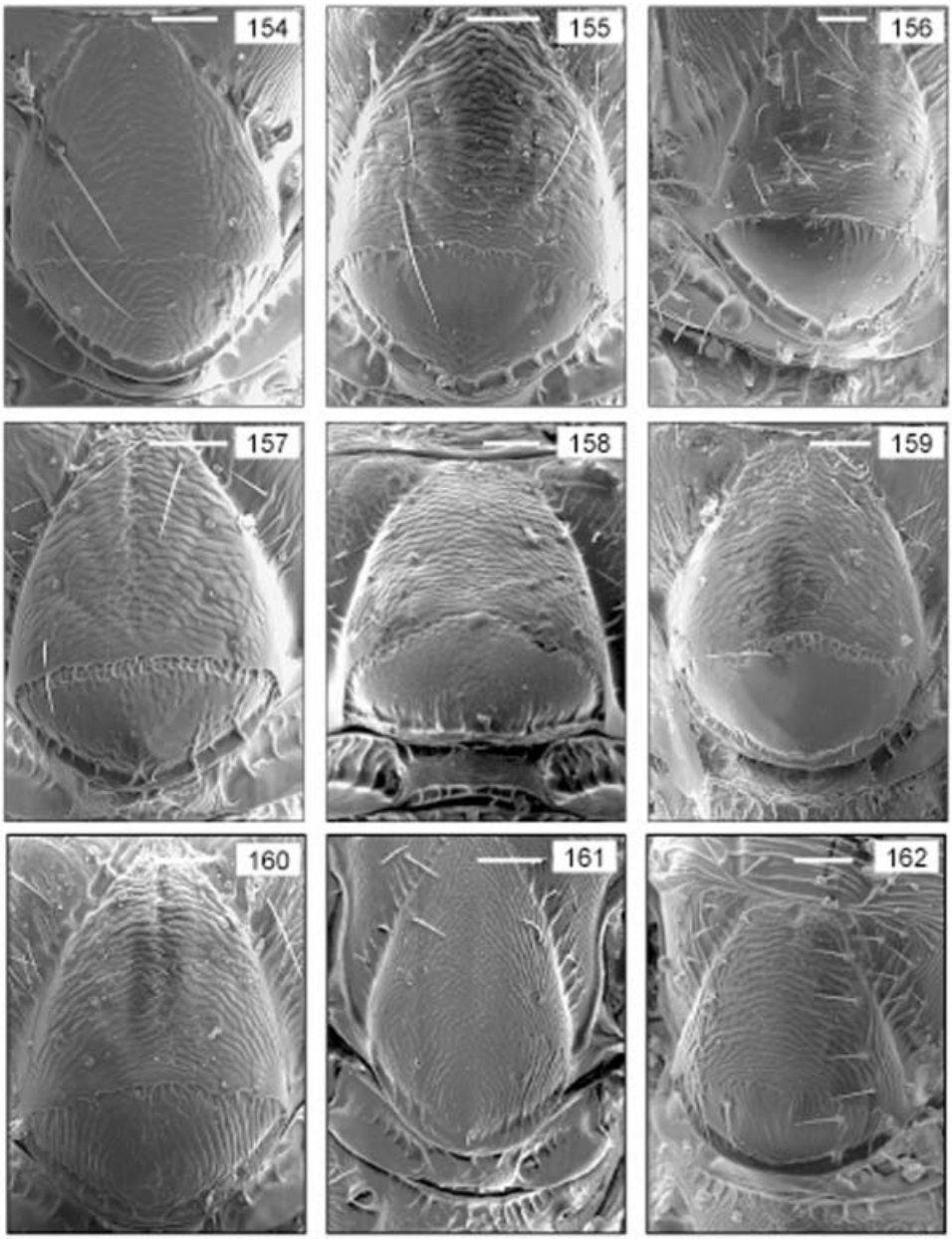
Megastigmus strobilobius Ratzeburg, 1848: 182. ♀, number unknown, Germany (destroyed probably in World War II according to Graham, 1969).

Megastigmus abietis Seitner, 1916: 309–311. 1♀ and 2♂ Syntypes, 'Fichtensamen', Austria (NMW, [examined]). Synonymy by Escherich 1938: 368.

Female

Body length (without ovipositor) 3.7 mm (erroneously estimated at 4.0 mm in the original description; Seitner, 1916). Body colour mostly black. Face yellowish brown connected to a circumorbital yellow band extending to the occipital area, remainder of head black. Pilosity pale on lower face, black on remainder of head. Antenna light brown. Pronotum black with a bright yellow cross-band in front of hind margin, the band being very narrowly interrupted in the middle, remainder of thoracic dorsum black. Lateral panel of pronotum, prepectus and tegula yellow; mesopleuron dark brown, metapleuron black. Pilosity black on thoracic dorsum. Fore coxa brownish yellow at the base, mid- and hind coxa black; remainder of legs yellow. Wings subhyaline, the basal cell of forewing with 12 hairs on the disc. Propodeum entirely black. Dorsum and antero-lateral parts of gaster black, latero-ventral parts yellowish brown. Ovipositor sheaths dark brown.

Head 1.4× as broad as long in dorsal view. Antennal scape elongate, as long as combined length of pedicel, anellus and two first funicular segment; pedicel large, 1.1× longer than first funicular segment; second funicular segment and following



FIGS 154–162. Electroscan photographs of scutellum of male *Megastigmus*. (154) *M. pistaciae*; (155) *M. rafni*; (156) *M. schimitscheki*; (157) *M. specularis*; (158) *M. spermotrophus*; (159) *M. strobilobius*; (160) *M. suspectus*; (161) *M. transvaalensis*; (162) *M. wachtli*. Same origins as in (39–47). Scale bars = 100 μm.

segments sub-quadrate (figure 28). Pronotum and mesoscutum with coarse cross-striae, very arcuate near the posterior margin of the mid-lobe of mesoscutum. Scutellum 1.2 × as long as broad, the anterior part with coarse cross-striation, the frenal area smooth with only a few short carinae expanding from the frenal line

(figure 141). Forewing stigma ovale-elongate, about 1.8 × as long as wide; upper part of stigmal vein elongate, about as long as stigma width; uncus 0.6 × as long as upper part of stigmal vein (figure 65). Propodeum with a median carina. Ovipositor sheaths 0.9 × as long as body, 1.1 × as long as gaster and thorax combined. Distal part of dorsal valve of ovipositor with a large third median tooth (figure 103).

Male

Body length 3.2 and 3.7 mm (estimated at 3.75–4.0 mm in the original description; Seitner, 1916). Body colour black and yellow. Head mostly yellowish brown except occiput and ocellar area black. Pilosity pale on lower face, black on remainder of head. Scape brown, yellowish beneath; remainder of antenna light brown. Thoracic dorsum black except a bright yellow cross-band on posterior part of pronotum, the band being very narrowly interrupted in the middle, and a brownish, indefinite spot on external side of lateral lobe of mesoscutum. Lateral panel of pronotum, prepectus, lower mesepimeron, lower mesepisternum, tegula and acropleuron yellow. Upper mesepimeron and upper mesepisternum light brown, metapleuron black. Pilosity black on thoracic dorsum. Fore coxa almost entirely yellow except a narrow, indefinite brownish yellow band at the base, mid-coxa yellow, hind coxa black, remainder of legs yellow. Wings subhyaline, the basal cell of forewing with 14 hairs on the disc. Propodeum black except callus light brown. Dorsum and antero-lateral parts of gaster black, latero-ventral and apical parts yellowish brown.

Head about 1.3 × as long as broad in dorsal view. Antennal scape elongate, 1.1 × as long as pedicel, anellus and first funicular segment combined; second funicular segment and following ones more elongate than in female, about 1.5 × as long as wide (figure 44). Pronotum and mesoscutum with coarse cross-striae, very arcuate near the posterior margin of the mid-lobe of mesoscutum. Scutellum 1.2 × as long as broad, the anterior part with coarse cross-striation tending to reticulation, the frenal area mostly smooth with short longitudinal carinae forming a limited reticulated area below the frenal line (figure 159). Forewing stigma rounded, about 1.2 × as long as wide; upper part of stigmal vein elongate but comparatively smaller than in female, about half as long as stigma width; uncus 0.9 × as long as upper part of stigmal vein (figure 83). Propodeum with a median carina. Aedeagus medium-sized, rounded; digitus with four teeth (figure 121).

Variation

The above description corresponds to the type material of *M. abietis*. In the other examined specimens, body length varied from 2.3 to 3.7 mm in females, from 2.2 to 3.7 mm in males. Female colour was a little variable. The yellow band on pronotum could be continuous, without interruption in the middle (Bouček, 1970b; a few specimens we examined from France). The band could also vary in size (large to tiny) and colour (bright to dirty yellow). In a few male specimens of Poland, the lateral parts of thorax and legs were entirely yellow except hind coxa. In both sexes, the number of hairs on the disc of forewing basal cell varied from 10 to 18 (Bouček, 1970b). In both sexes, the median carina on propodeum was often interrupted in the middle.

Sex ratio

Balanced. Seitner (1916) noticed 43.3% of males (161♂:211♀) in Austria whilst this proportion varied from 38 to 66% in the populations observed by Skrzypczyńska and Roques (1987) in France.

Hosts

Develops primarily in seeds of spruces (*Picea* spp., Pinaceae) native to northern Eurasia, Norway spruce, *P. abies* (among others, Seitner, 1916; Kapuściński, 1966; Cankov, 1974; Del Favero and Masutti, 1974; Nanu, 1976, 1980; Stadnickii *et al*., 1978; Roques, 1983; Skrzypczyńska and Roques, 1987) and Siberian spruce, *P. obovata* (Stadnickii *et al*., 1978). The chalcid extensively colonized plantations outside the natural range of these species (Roques, 1983). In addition, it shifted to closely related Asian spruce species planted in French arboreta: the Caucasian *P. orientalis* (Roques, 1983), *P. asperata* and *P. montigena* from western China, and *P. glehnii* from the islands of northeastern Asia (Da Ros *et al*., 1993), the latter species being also attacked by *M. ezomatsuanus* in its native range (Kamijo, 1962). *M. strobilobius* was also observed in seeds of the North American *Picea pungens* planted in Denmark (USNM). Earlier records on *Abies* spp. (e.g. Sorauer, 1953; Lessmann, 1962; Edomskii, 1965; Gusev, 1984; Wall, 1984; Křístek *et al*., 1992), *Pseudotsuga* and *Tsuga* (Křístek *et al*., 1992) are likely to represent misidentifications.

Distribution

Western Europe to Lake Baïkal, at least: Austria (Seitner, 1916); Belgium (AR); Bulgaria (Cankov, 1974); former Czechoslovakia (Čermak, 1952; Bouček, 1970b; Křístek *et al*., 1992); Denmark (Hoffmeyer, 1929, 1931b; Jespersen and Lomholdt, 1983; Ochsner, 1998; Jensen and Ochsner, 1999; USNM); Estonia (Luik and Voolma, 1988); Finland (Kangas, 1940; Annila, 1966, 1984); France (Roques, 1983; Trosset and Roques, 1986; Skrzypczyńska and Roques, 1987; Ostermeyer, 1990; Da Ros *et al*., 1993; AR); Germany (Holste, 1922); Great Britain (Hussey, 1954a; Bouček, 1970b); Hungary (Wall, 1984); Italy (Del Favero and Masutti, 1974); Lithuania (Milishaukas, 1976; Saksons, 1976; Dumchius, 1984; AR); Norway (Wiersma, 1978); Poland (Szmidt, 1953; Madziara-Borusiewicz, 1961, 1965; Kapuściński, 1966; Skrzypczyńska, 1982, 1986, 1989a; Skrzypczyńska and Roques, 1987; but rare in the 1990s, Witteczek, 1998); Romania (Tudor *et al*., 1973; Istrate and Ceianu, 1975; Nanu, 1980; Nanu *et al*., 1986); Russia: from Arkhangelsk and European part to Altaï Mts, Irkutsk and Tiumen (Nikol'skaya, 1952; Jakovlev, 1961; Edomskii, 1965; Stadnickii, 1971; Golutvina *et al*., 1972; Voroncov, 1975; Nikol'skaya and Zerova, 1978; Stadnickii *et al*., 1978 as *M. abietis*; Edomskii, 1980; Zerova and Seryogina, 1994); Sweden (Wiersma, 1978); Slovakia (Kelbel, 1997); Ukraine (Padii, 1974; Stadnickii *et al*., 1978); Yugoslavia: Bosnia (Fitze, 1959).

Comments

In the West Palearctic, seeds of some spruce species (e.g. *P. orientalis*) were also infested by an exotic chalcid introduced from North America, *M. atedius*. Diagnostic characters to separate the two species are given in the chapter concerning *M. atedius*. Another species, *M. ezomatsuanus* Hussey and Kamijo, was recognized in the Far East and its western limit is not precisely known. We examined specimens from northeastern China (1♀ from *Picea koraiensis* Nakai, Moershan, Heilongjiang, 4 June 1993, AR) and Japan (1♂ from *P. jezoensis*, Teshio, Hokkaido, 17 May 1956, K. Kamijo leg.; 1♀ from *P. ghlenii*, Teshio, Hokkaido, 27 May 1956, K. Kamijo leg.). Females of *M. ezomatsuanus* are distinguished by a smooth frenal area and a comparatively shorter exserted part of ovipositor, which is as long as thorax and gaster combined and only 0.8 × as long as body whereas these values reach 1.1 and 0.9 in *M. strobilobius*, respectively. Males have a more elongate antennal scape, as

long as the combined length of the first two funicular segments, according to Kamijo's observations (1962). Another species from southwestern China, *M. likiangensis* Roques et Sun, is easily differentiated by the presence of extended yellow patterns on thorax (posterior and lateral margins of pronotum, latero-posterior margin of mid-lobe and outer surface of lateral lobes of mesoscutum, antero-lateral parts of scutellum, and inner angle of axilla, and dorsellum; Roques *et al*., 1996).

Material examined

Austria: 1♀, 2♂ syntypes *M. abietis*, ex. *Picea abies*, Seitner (NMW). **Belgium**: 6♀, 3♂, ex. *P. abies*, Gilbuschheck, May 1993, Belgium Forestry Office (AR); 1♀, 1♂, ex. *P. abies*, Cote des Forges, May 1993, Belgium Forestry Office (AR). **Denmark**: 1♀, ex. *P. pungens*, 13 May 1974 (USNM). **France**: 7♀, 4♂, ex. *P. abies*, Névache (05), elev. 1550 m, July 1981, (AR); 4♀, 4♂, ex. *P. abies*, Amance (54), July 1980 (AR); 6♀, 5♂, ex. *P. abies*, Meygal Forest (43), July 1980, (AR); 2♀, 2♂, ex. *P. abies*, Les Barres (45), July 1991, R. Ostermeyer (AR); 1♀, 1♂, ex. *P. abies*, Malbuisson Forest (25), May 1993, French National Forestry Office (AR); 2♀, 3♂, ex. *P. asperata*, Les Barres June 1990, R. Ostermeyer (AR); 2♀, 3♂, ex. *P. glehnii*, Les Barres, June 1991, R. Ostermeyer (AR); 6♀, 5♂, ex. *P. montigena*, Les Barres, June 1991, R. Ostermeyer (AR); 5♀, 4♂, ex. *P. obovata*, Les Barres, June 1990, R. Ostermeyer (AR). **Lithuania**: 2♀, 2♂, ex. *P. abies*, Kaunas, 27 May 1982; 6♀, 6♂, ex. *P. abies*, Kaunas, May 1993, O. Dumchius (AR). **Poland**: 1♂ ex. *P. abies*, Powroźnik Forest, 7 March 1980 (laboratory conditions) (MS); 15♀, 5♂, ex. *P. abies*, Beskid Sądecki Mts, June 1987 (MS); 1♂, ex. *P. abies*, Wisła, Beskid Śląski Mts, April 1997 (cone coll. October 1995), M. Kozioł (MS).

Megastigmus suspectus Borries

(figures 5, 8, 29, 45, 66, 84, 104, 122, 142, 160)

Megastigmus suspectus Borries, 1895: 29. ♀ Syntypes (number unkown), Bornholm, Denmark (?ZMUC, according to Hussey, 1954b; not found in ZMUC [not examined]).

Megastigmus piceae Seitner, 1916: 315–317. 3♀ syntypes, Idria, 'Tannensamen' (NMW [examined]). Synonymy by Escherich, 1938: 369.

Megastigmus bornmülleriana Hussey, 1957: 253. Holotype ♀, Yenice, Turkey (BMNH [examined]). Synonymy by Bouček, 1970b: 269.

Female

Body length (without ovipositor) 5.2 mm. Body mostly black with a few yellowish patterns. Head with face yellow except a brown, triangular patch on clypeus and a small brown spot on supraclypeal area; remainder of head with a large black patch extending from antennal scrobe to frons, ocellar area, occiput, temple and reaching outer part of gena; eye surrounded by yellow on ventral margin. Pilosity mostly black on head, including lower face. Antenna brown with scape yellow beneath. Thorax mostly black, except lateral panel of pronotum yellow. Pilosity black on thoracic dorsum. Legs brownish yellow, with fore- and mid-coxa black at the base but yellow apically and hind coxa entirely black; remainder of legs brownish yellow except hind femur brown dorsally. Propodeum black. Gaster dark brown to black on dorsum, brownish yellow latero-ventrally. Ovipositor sheaths black.

Head 1.5× as broad as long in dorsal view. Antennal scape as long as pedicel, anellus and first funicular segment combined (figure 29). Pronotum and mesoscutum with coarse cross-striae, the striae being V-shaped near the posterior margin of the

mid-lobe of mesoscutum. Scutellum 1.3 × as long as broad, the anterior part reticulate-striate, the frenal area longitudinally wrinkled (figure 142) or reticulate (Hussey, 1957). Forewing stigma very elongate, 2.6 × as long as wide; upper part of stigmal vein comparatively very elongate, 1.6 × as long as stigma width; uncus 0.5 × as long as upper part of stigmal vein (figures 8, 66). Propodeum with a double median carina (Hussey, 1954). Ovipositor sheaths 1.1 × longer than body. Distal part of the dorsal valve of ovipositor with a large second tooth (figure 104).

Male

Body length 3.8 mm. Body colour black and yellow. Head mostly yellow except a rounded, brown marking at the centre of each cheek, and a black patch extending on frons, ocellar area, occiput and temple and reaching gena. Pilosity mostly dark on lower face, but including some pale hairs, remainder of head with black pilosity. Antenna brown with scape and pedicel yellowish beneath. Thoracic dorsum entirely black. Lateral panel of pronotum, prepectus, mesopleuron yellow except a light brown patch on upper mesepisternum and lower mesepimeron. Fore coxa yellow, mid-coxa light brown, hind coxa black except apical extremity yellow; remainder of legs yellow. Propodeum black. Gaster with dorsum dark brown except on last tergum; lateral and ventral parts orange-yellow except first sternum and base of second sternum dark brown.

Head rounded, 1.2 × as broad as long in dorsal view. Antennal scape smaller (0.9 ×) than pedicel, anellus and first funicular segment combined; first funicular segment 2 × as long as broad, the following segments tending to subquadrate (figure 45). Pronotum and mesoscutum with coarse cross-striae, the striae being V-shaped near the posterior margin of the mid-lobe of mesoscutum. Scutellum 1.3 × as long as broad, the anterior part reticulate-striate, the frenal area with longitudinal carinae (figure 160). Forewing stigma elongate-oval, 1.8 × as long as wide; upper part of stigmal vein comparatively elongate, 1.1 × as long as stigma width; uncus 0.4 × as long as upper part of stigmal vein (figure 84). Propodeum with a sinuous median carina. Aedeagus rounded, smaller than digitus; digitus with four teeth (figure 122).

Variation

The above description is based on the type material of *M. piceae* for female and, from male, on a specimen emerged from *Abies alba* at Piwniczna, Poland (1977, M. Skrzypczyńska leg.), deposited at MNHN. In the other examined specimens, body length varied from 3.5 to 5.7 mm in females, from 3.5 to 4.2 mm in males. The dark markings on lower face of female may be reduced to a small spot on supraclypeal area (type material of *M. bornmülleriana*) or to a brownish spot at the centre of each cheek (some specimens from Poland). Conversely, black could invade most of the face, yellow being limited to a small spot below each torulus, and a lateral band from side of clypeus to gena, then extending along inner egde of eye to parascrobal area (specimens from eastern and southeastern France). The yellow colour on lateral panel of pronotum also disappeared in the type material of *M. bornmülleriana*. Colour variations affected coxae. The fore coxa was entirely yellow and the mid-coxa entirely black in some paratypes of *M. piceae*. Variation in the sculpture of scutellum were also observed. The frenal area could be reticulate (*M. bornmülleriana*; Hussey, 1957). The median carina on propodeum was simple and sinuous in some specimens from Poland but absent in most specimens from the arboretum of Les

Barres, France. The relative length of the exserted part of ovipositor sheaths varied from 1.1 to 1.2 × the body length.

Some males from Poland showed colour patterns lighter or darker than that of the type. Lighter forms presented a face entirely yellow, and lateral parts of thorax quite entirely yellow with only a small, indefinite light brown spot on lower mesepimeron. However, hind coxa always remained mostly black. In darker forms, the thorax was quite entirely jet black with only the lateral panel of pronotum yellow, and the basal part of fore coxa, mid-coxa and hind coxa were black as well as the dorsal part of hind femur, the remainder of legs being yellow.

Sex ratio

Reproduces usually by thelytokous parthenogenesis, only a few males having been recorded (e.g. 3♂:192♀, Skrzypczyńska, 1978; 0♂:441♀, Lessmann, 1974b; 0♀:125♀, Ostermeyer, 1990).

Hosts

Develops primarily in seeds of firs (*Abies* spp., Pinaceae) native to central Europe, North Africa and Asia Minor. Damage was recorded in the natural range of *A. alba* (among others, Kapuściński, 1966; Lessmann, 1974b; Nanu, 1976, 1980; Skrzypczyńska, 1978, 1989b, 1998; Křístek *et al*., 1992; Skrzypczyńska *et al*., 1998), *A. bornmülleriana* (Schimitschek, 1944; Hussey, 1957; Çanakçioglü, 1959, 1969, 1993; Bouček, 1970b), *A. cephalonica* (Kailidis and Georgevits, 1970, 1972), *A. equi-trojani* (USNM), *A. nordmanniana* (Nikol'skaya, 1952; Bouček, 1970b; Stadnickii *et al*., 1978) and *A. numidica* (JPF). The chalcid has extensively colonized plantations of the same species well outside their natural range (e.g. *A. alba*, *A. bornmülleriana*, *A. equi-trojani*, *A. nordmanniana* and *A. pinsapo* in Denmark, Ochsner and Jensen, 1998; *A. cephalonica* in Italy, USNM). Most of the Mediterranean fir species planted in arboreta in France were also attacked (*A. borisii-regis*, *A. cilicica*, *A. nebrodensis*, *A. numidica* and *A. pinsapo*; Roques, 1983; Ostermeyer, 1990; AR). Damage observed in the range of the northern *Abies sibirica* and in that of the far-eastern *A. nephrolepis* (Stadnickii *et al*., 1978) may be caused by *Megastigmus specularis* and *M. borriesi*, respectively. However, *M. suspectus* was observed to shift on *A. sibirica* in French arboreta (AR) as well as on the eastern Asian species, *A. homolepis*, in Denmark (Ochsner and Jensen, 1998). Attacks were recorded on some North American firs introduced in Europe, such as *A. grandis* (McNeill, 1946, Wall, 1984; Křístek *et al*., 1992) and *A. concolor* (Jespersen and Lomholdt, 1983), but Ochsner and Jensen (1998) did not find any damage of *M. suspectus* on North American firs during a large survey in Denmark. Damage to seeds of *Cedrus brevifolia* were also observed, but very scarcely, in French arboreta (Ostermeyer, 1990; AR) as well as damage to *C. atlantica* in southern France (Fabre, unpublished observations). Records on *Picea* species (e.g. Lessmann, 1962) are probably misidentifications to be attributed either to *M. strobilobius* or to *M. atedius*.

Distribution

Widespread over Europe to the Caucasus, at least. Presently recorded from: Austria (Schimitschek, 1935); former Czechoslovakia (Čermak, 1952; Křístek *et al*., 1985, 1992); Denmark (Hoffmeyer, 1931b; Jespersen and Lomholdt, 1983; Ochsner, 1998; Ochsner and Jensen, 1998; Jensen and Ochsner, 1999); France (Roques, 1983; Pintureau *et al*., 1991; AR); Germany (Lessmann, 1974b); Great Britain (Laidlaw, 1931; McNeill, 1946; Hussey, 1954b; Bouček, 1970b); Greece (Kailidis and

Georgevits, 1970, 1972); Hungary (Györfii, 1956); Italy (AR; USNM); Ireland (Bouček, 1970b); Poland (Kozikowski and Kuntze, 1936; Tyszkiewicz, 1949; Kapuściński, 1966; Skrzypczyńska, 1978, 1981b, 1984b, 1985, 1989b, 1996, 1998; Bąk, 1994, 1995, 1999; Skrzypczyńska *et al*., 1998; AR); Romania (Nanu, 1976, 1980; Olenici and Olenici, 2000); Russia: European part to the Caucasus (Milliron, 1949; Nikol'skaya, 1952; Nikol'skaya and Zerova, 1978; Stadnickii *et al*., 1978, as *M. strobilobius*; Zerova and Seryogina, 1994); Sweden (Hansson, 1991); Slovakia (Kelbel, 1995); Turkey (Schimitschek, 1944; Hussey, 1957; Çanakçioglü, 1959, 1968, 1969, 1993; USNM); Ukraine: Crimea (Padii, 1974; Nikol'skaya and Zerova, 1978); Yugoslavia: Slovenia (Seitner, 1916). Also present in North Africa: Algeria (JPF).

Comments

To date, six other species of seed chalcids were observed in fir seeds of the West Palearctic region: *M. milleri*, *M. pinsapinis*, *M. pinus*, *M. rafni*, *M. schimitscheki* and *M. specularis*. For separating these species, see the chapter concerning *M. milleri*.

A species closely resembling those originating from the Far East, *M. borriesi* Crosby was found in seeds of *A. veitchii* in a Danish arboretum (Ochsner, 1998; Jensen and Ochsner, 1999) but its establishment in Europe needs to be confirmed. We examined specimens of *M. borriesi* from Japan (1♀ from *A. sachalinensis*, Bibai, Hokkaido, 12 June 1992, K. Kamijo leg.) and Korea (1♀ from *A. veitchii*, April 1969, D. C. Poe, USNM). The body was entirely black except gaster dark brown. They differed from the female of *M. suspectus* by a much longer scape, about as long as the combined length of the first two and a half of the third funicular segment, a pedicel as long as the first funicular segment, the pilosity mostly pale on lower face, a smooth shining frenal area, and an elongate-oval stigma as Kamijo (1962) already pointed out.

Material examined

Algeria: 1♀, *Abies numidica*, Djebel Ouahch, June 1998 (JPF). **Denmark**: 1♀ (slide), ex. *A. nordmanianna,* Langesø, Fyn, 10 April 1929, Hoffmeyer coll. (ZMUC); 1♀ (slide with wing, head, thorax), ex. *A. nordmanianna,* Langesø, Fyn, 10 April 1929, Hoffmeyer coll. (ZMUC); 4♀ (slide with wings), ex. *A. nordmanianna*, Langesø, Fyn, 1930, Hoffmeyer coll. (ZMUC). **France**: 15♀, ex. *A. alba*, Les Barres (45), May 1981 (AR); 4♀, ex. *A. bornmülleriana*, Les Barres, May 1981 (AR); 6♀, ex. *A. cephalonica*, Les Barres, May 1981 (AR); 5♀, ex. *A. cilicica*, Les Barres, May 1981 (AR); 12♀, ex. *A. nordmanianna*, Les Barres, May 1981 (AR); 2♀, *A. nebrodensis*, Les Barres, May 1993 (AR); 4♀, ex. *A. numidica*, Les Barres, May 1997 (AR); 7♀, ex. *A. pinsapo*, Les Barres, May 1990, R. Ostermeyer (AR); 3♀, ex. *A. sibirica*, Les Barres, May 1990, R. Ostermeyer (AR); 4♀, ex. *A. alba*, La Joux (39), June 1993, French National Forestry office (AR); 10♀, ex. *A. alba*, Gerardmer (88), June 1993, French National Forestry office (AR); 1♀, Rouillon (76), 12 May 1935, Granger (MNHN); 2♀, ex. *Cedrus brevifolia*, les Barres, May 2000, M. Auger-Rozenberg (AR). **Italy**: 2♀, ex. *A. alba*, Vallombrosa (FI), May 2000, M. Auger-Rozenberg (AR); 1♀, ex. *A. cephalonica*, PQ US quarantine service (USNM). **Poland**: 2♂, ex. *A. alba*, Piwniczna, 26 March 1977 (in laboratory); 1♂, ex. *A. alba*, Piwniczna, Łomnica Forest, 29 March 1977 (laboratory conditions) (MS); 1♂, ex. *A. alba*, Piwniczna, 22 February 1980 (laboratory conditions) (MS); 7♀, ex. *A. alba*, Roztoczański Natl. Park, March 1986 (laboratory conditions) (MS); 1♂, ex. *A. alba*, Lesko, Monasterzec Forest, April 1987 (laboratory conditions) (MS). **Slovenia**:

3♀ syntypes *M. piceae*, Idria (NMW). **Turkey**: 1♀, holotype *M. bornmulleriana*, ex. *A. bornmülleriana*, Yenice, 10 March 1956 (ZMUC); 1♀, K. Baş (MNHN); 1♀, ex. *A. equi-trojani*, PQ US quarantine service (USNM).

Megastigmus transvaalensis (Hussey)
(figures 30, 46, 67, 85, 105, 123, 143, 161)

Eumegastigmus transvaalensis Hussey, 1956: 161–162. Holotype ♀, Pretoria, Transvaal, South Africa (BMNH [examined]); 5♀ and 8♂ paratypes, same data as holotype (BMNH, Hussey collection [2♂ examined]). New combination by Bouček, 1978: 129.

Female

Body length (without ovipositor) 3.2 mm (according to Hussey, 1956, the abdomen being nowadays absent on the holotype). Body light to dark orange. Head dirty orange with a tiny black spot at clypeus angles and the area around ocelli darker orange-brown. Pilosity pale on lower face, black on remainder of head. Antenna yellowish brown. Thorax predominantly orange-yellow with the pronotum lighter, and with a narrow, darker orange-brown longitudinal band extending centrally on pronotum, mid-lobe of mesoscutum and scutellum. External sutures of lateral lobes of mesoscutum, axilla and metanotum black. Pilosity black on thoracic dorsum, with only three pairs of hairs on scutellum. Legs dirty yellow. Middle part of propodeum with a black, triangular patch, callus orange-yellow. Gaster mostly light orange-brown; first apparent tergum dark brown, following terga (4–7) with a transverse, narrow rectangular dark brown band becoming soon light brown laterally; apical segments paler yellow-brown. Ovipositor sheaths black.

Head about 1.4× as broad as long in dorsal view. Vertex weakly convex with transverse rugae circularly oblique around ocelli; genal area with fine oblique rugae; occipital area relatively weak. Posterior ocellar line 1.7× as long as ocellocular and lateralocellar lines, and 1.4× as long as occelloccipital line; malar space half as wide as compound eye. Antennal scape elongate, 1.2× as long as combined length of pedicel, anellus and first funicular segment; pedicel nearly (0.9×) as long as first funicular segment; funicular segments 2–5 elongate, about twice as long as wide, the two last ones (6 and 7) tending to subquadrate (figure 30). Pronotum and mesoscutum with strong transverse rugae, coarser than on vertex. Scutellum 1.5× as long as wide, with coarse transverse striations. Frenal line weakly marked, the frenal area with strong longitudinal carinae especially on the lateral parts (figure 143). Forewing stigma oval-elongate, 1.4× as long as broad; uncus elongate, 1.2× as long as upper part of stigmal vein (figure 67); basal cell of forewing with 10 hairs. Propodeum with strong oblique carinae. Ovipositor sheaths about 1.4× as long as gaster, but only 0.6× as long as combined length of gaster and thorax, and 0.5× as long as body. Distal part of dorsal valve of ovipositor with a large third median tooth (figure 105).

Male

Body length 2.7 and 2.8 mm. Body mostly pale orange-yellow except gaster. Head light orange with the area around ocelli darker orange-brown. Pilosity pale on lower face, black on remainder of head. Antenna yellowish brown. Thorax predominantly orange-yellow with the pronotum lighter, and with a narrow, darker orange-brown longitudinal band extending centrally on pronotum, mid-lobe of mesoscutum and scutellum. External sutures of lateral lobes of mesoscutum, axilla

and metanotum black. Pilosity black on thoracic dorsum, with only three pairs of hairs on scutellum. Legs dirty yellow. Propodeum with a black triangular patch in the middle and callus orange-yellow. Dorsum of gaster entirely dark brown, a few patches extending laterally on terga V–VI, remainder of gaster orange-brown.

Head about 1.4 × as broad as long in dorsal view. Antennal scape elongate, 1.1 × as long as combined length of pedicel, anellus and first funicular segment; pedicel nearly (0.9 ×) as long as first funicular segment; following funicular segments elongate, twice as long as wide (figure 46). Pronotum and mesoscutum with strong transverse rugae. Scutellum 1.1 × as long as broad, frenal line weakly marked, the frenal area with strong longitudinal carinae especially on the lateral parts (figure 143). Forewing stigma enlarged, little infuscated, about 1.2 × as long as wide; uncus slightly smaller (0.9 ×) than upper part of stigmal vein (figure 85); basal cell of forewing with 10 bristles. Propodeum with oblique carinae. Aedeagus small, rounded, digitus with three teeth (figure 123).

Variation

The above description is based on the type material from South Africa. In specimens from the West Palearctic, body length varied from 3.0 to 3.5 mm in females, from 2.3 to 3.2 mm in males. Few variations in colour were observed. The central, orange-brown thoracic band completely disappeared in some specimens from Morocco. The black patch on the middle of propodeum could also turn to brown. Gaster dorsum was predominantly black in most specimens from Morocco and Portugal.

Sex ratio

Usually balanced in Morocco (e.g. 46♀:42♂ at Marrakech, AR).

Hosts

The species is probably an endemic, South African species which has host-shifted from native seeds of *Rhus* spp. (Anacardiaceae) into the seeds of *Schinus* spp., which are Anacardiaceae introduced from South America towards most warm areas of the world (Habeck *et al*., 1989; Grissell and Hobbs, 2000). It has been reported from *S. molle* (Hussey, 1956; Bouček, 1978; Grissell, 1979; Habeck *et al*., 1989; AR) and *S. terebinthifolius* (Habeck *et al*., 1989; Perioto, 1997 as *Megastigmus* sp.; AR) but is still capable of attacking *Rhus laevigata* under experimental conditions (Grissell and Hobbs, 2000).

Distribution

Probably present in the major part of the introduction range of *Schinus* spp., everywhere these trees can flower. Reported from South Africa (Hussey, 1956), La Réunion (AR), the USA (California, Florida, Hawaii; Habeck *et al*., 1989), Mexico (USNM), the species has recently been observed for the first time in the native South American range of *Schinus* (Argentina, Brazil; Perioto, 1997 as *Megastigmus* sp.; Grissell and Hobbs, 2000). In the West Palearctic, observed in France (AR), Morocco (AR), Portugal (AR) and Spain (Canary Islands; Grissell, 1979; USNM).

Comments

The pistachio seed chalcid, *M. pistaciae*, was also reported from seeds of *Schinus molle* by Rice and Michalides, 1988, but these authors did not supply the original reference of the record. *M. pistaciae* is morphologically identical to *M. transvaalensis*

except for its larger size (Grissell and Hobbs, 2000). A few specimens closely resembling *M. transvaalensis* were recently obtained in Morocco by one of us (AR) from seeds of another species of Anacardiaceae, *Rhus albida* Schousb. (=*tripartita* D.C.). They may correspond to a closely related South African species, *M. rhusi* (Hussey), which was observed there on *Rhus lancea* L. (Hussey, 1956). Molecular studies are currently under way to determine the degree of genetic relatedness between *M. transvaalensis*, *M. rhusi* and *M. pistaciae* (Grissell and Hobbs, 2000).

Material examined

France: 1♀, ex. *S. molle*, Bormes (83), August 2000, G. Rouault (AR); 1♂, ex. *S. terebinthifolius*, Toulon; September 2000 (AR). **Mexico**: 1♀, ex. *S. molle*, PQ US quarantine service (USNM). **Morocco**: 46♀, 42♂, ex. *S. molle*, Marrakech, February 2000, (AR); 22♀, 18♂, ex. *S. molle*, Chichaoua, October 2000, G. Rouault (AR); 2♀, 1♂, ex. *S. molle*, Agadir, October 2000, G. Rouault (AR). **Portugal**: 1♀, 1♂, ex. *S. molle*, Hortas do Tabual, nr. Sagres, 12 August 2000 (AR); 3♀, 2♂, ex. *S. molle*, Monsanto (Lisboa), September 2000 (AR). **La Réunion Island**: 2♀, ex. *S. terebinthifolius*, St Pierre de la Réunion, 20 December 2000, L. Combes (AR). **Spain**: 1♀, ex. *S. molle*, Tenerife, Canary Islands, May 1962 (USNM). **South Africa**: 1♀, 3♂, ex. *S. molle*, Pretoria, 9 May 1919, J. Jooke (BMNH); 1♀, ex. *S. molle*, 25 October 1919, Riestenburg (Transvaal), J. Jooke (BMNH).

Megastigmus wachtli Seitner
(figures 10, 31, 47, 68, 86, 106, 144, 162)
Megastigmus wachtli Seitner, 1916: 320–321. 2♀ and 2♂ syntypes, Sinj, Dalmatia, Croatia (NMW [examined]).

Female

Body length (without ovipositor) 3.9 and 4.1 mm. Body entirely dirty yellow. Head light yellow. Pilosity pale on face, black on head dorsum. Antenna dark brown, scape and pedicel yellow. Thorax predominantly dirty yellow to straw yellow, with pronotum lighter than other parts, and anterior margin and sides of mesonotum darker, orange to light brownish. Pilosity black on thoracic dorsum. Legs dirty yellow. Wings subhyaline; forewing stigma light brown, without any infuscation. Propodeum brownish yellow. Gaster dirty yellow but base of first apparent tergum brown to black. Ovipositor sheaths black.

Head about 1.2× as broad as long in dorsal view, with large scrobes. Antennal scape very elongate, as long as combined length of pedicel, anellus, first and half of second funicular segments; funicular segments elongate, about twice as long as wide, except the first segment (figure 31). Pronotum and mesoscutum with strong, transverse striae. Scutellum 1.2× as long as broad, the anterior part with coarse transverse striation, the frenal area mostly smooth with a few short longitudinal carinae extending from the frenal line and weak longitudinal wrinkles on the lateral parts (figure 144). Forewing stigma oval-elongate, about 1.6× as long as broad; upper part of stigmal vein comparatively very short, 0.2× as long as stigma length; uncus as long as upper part of stigmal vein (figure 68). Propodeum without median carina. Ovipositor sheaths about 1.3× longer than body. Distal part of dorsal valve of ovipositor with a large third median tooth (figure 106).

Male

Body length 3.5 and 3.8 mm. Body colour mostly dirty yellow. Head light yellow. Face brownish to brownish black, dorsum of head yellowish. Pilosity pale on face, black on remainder of head. Antenna dark brown, except scape and pedicel yellow. Thorax predominantly straw yellow, with pronotum lighter than other parts, and anterior margin and sides of mesonotum darker, orange to light brownish. Pilosity on thoracic dorsum black. Wings very setose; forewing stigma dark brown, surrounded by a distinct infuscation. Propodeum yellowish. Gaster mostly dark brown with more or less large lateral yellow patches; distal segment mostly yellowish.

Head about 1.2 × as broad as long in dorsal view. Antennal scape elongate, 1.1 × as long as combined length of pedicel, anellus, first and half of second funicular segments; funicular segments elongate, twice as long as wide (figure 47). Pronotum and mesoscutum with coarse transverse striae. Scutellum 1.1 × as long as broad, the anterior part densely cross-striated, the frenal area mostly smooth with a few longitudinal wrinkles (figure 162). Forewing stigma enlarged, about 1.4 × as long as wide; upper part of stigmal vein very short, about 0.1 × as long as stigma length; uncus slightly longer than upper part of stigmal vein (figure 86). Propodeum without median carina. Aedeagus small, narrow, sinuated at the apex; digitus with six teeth (figure 10).

Variation

The above description is based on the type material from Croatia. In the other examined specimens, body length varied from 3.0 to 4.5 mm in females, from 3.0 to 4.3 mm in males. Few variations in female colour were noticed. An additional basal brownish stripe was sometimes observed on pronotum, and dark brownish, narrow lateral stripes were noticed on gaster of females from Tunisia. Males appeared more variable. Specimens lighter than the type were observed in most of the examined populations, these chalcids being quite entirely light yellow except a few brown spots on dorsum of gaster. Darker forms were observed in most populations from Greece and North Africa, especially in Tunisia. These specimens differed from the type colour by the following patterns: thoracic dorsum mostly dark brown with a greyish pronotum and a noticeable black anterior margin of mid-lobe of mesoscutum; mesopleuron, metapleuron and propodeum black except callus dark brown; gaster black except the apical part brown; mid- and hind coxa entirely black; fore coxa, mid-and hind femur black on dorsal part.

Sex ratio

Ratio of males to females varies from 0.5 to 1.7 according to location (Bouaziz and Chakali, 1998; Roques *et al*., 1998a).

Hosts

Develops exclusively in seeds of cypress (*Cupressus* spp., Cupressaceae). Most records concerned damage to the Mediterranean evergreen cypress, *C. sempervirens* (Seitner, 1916; Escherich, 1938; Çanakçioglü, 1959, 1968, 1969; Bouček, 1977; Roques, 1983; Roques and Raimbault, 1986; Bouaziz, 1993). The Moroccan cypress, *C. atlantica*, was also attacked in its natural area (AR). In Europe and North Africa, the chalcid shifted on to some exotic cypress species introduced from California (*C. abramsiana*, *C. arizonica*, *C. bakeri*, *C. goveniana* [Roques *et al*., 1999a; AR] and *C. macrocarpa* [Roques and Raimbault, 1986; Bouaziz, 1993; Bouaziz and Chakali,

1998]) and central America (*C. lusitanica*; AR), but damage was usually limited on these species. Although extensively surveyed in the French seed orchards, some other exotic cypress species did not show any chalcid infestation (*C. cashmeriana* Royle, *C. chenghiana* S. Y. Yu, *C. duclouxiana* Hickel, *C. forbesii* (Jeps.) R. M. Beauchamp, *C. funebris* Hendl., *C. goveniana*, *C. guadalupensis* S. Wats., *C. lusitanica benthami* [Endl.] Carr., *C. macnabiana* Murr., *C. pygmaea* (Lemm.) Sargent, *C. macnabiana* Murr., *C. sargentii* Jepson, *C. torulosa* D. Don.; Roques *et al*., 1999a).

Distribution

Recent genetic studies showed that the species probably originated from the native range of the Mediterranean cypresses, i.e. the southeastern Mediterranean basin (Carcreff, 1996; Roques *et al*., 1999a). At the present time, it is distributed all over the Mediterranean basin, everywhere that cypress has been naturalized. Recorded from most countries of southern Europe: Albania (Roques *et al*., 1999b; AR); France (Roques and Raimbault, 1986; AR); Greece mainland and islands including Crete, Rhodes, Kos and Samos (Roques and Raimbault, 1986; Roques *et al*., 1998, 1999b); Italy (Masi, 1944; Covassi and Binazzi, 1979; Roques and Raimbault, 1986; Guido *et al*., 1995, 1998); Malta (Roques *et al*., 1999b); Portugal (AR); Turkey (Schimitschek, 1944; Çanakçioglü, 1959, 1969, 1993; Roques *et al*., 1999b); former Yugoslavia (Croatia, Montenegro, Slovenia: Seitner, 1916; Escherich, 1938; Bouček, 1977; AR). Observed in North Africa: Algeria (Bouaziz, 1993; Bouaziz and Chakali, 1998); Morocco (El Alaoui El Fels, 1998; AR); Tunisia (Ben Jamaa and Roques, 1998; AR). It is probably present in the other countries extending along the Mediterranean and the Black Sea. Also introduced with cypress seeds into European countries of higher latitudes but climate usually prevented naturalization (Roques and Raimbault, 1986). However, adults were recently found near Paris, in northern France (AR).

Comments

Two other species, *M. amicorum* and *M. atlanticus*, attack cypress seeds within the area. Diagnostic characters allowing species to be separated are given in the chapter concerning *M. atlanticus* for females and in the chapter concerning *M. amicorum* for males.

Material examined

Albania: 3♀, 5♂, ex. *Cupressus sempervirens*, Himaze, August 1987, F. Llubani (AR); 2♀, 2♂, ex. *C. sempervirens,* Tirana, September 1996, G. Demolin (AR); 2♀, 4♂, ex. *C. sempervirens,* Vajkani, September 1996, G. Demolin (AR). **Algeria**: 1♀, 1♂, ex. *C. macrocarpa*, Meurdja Arboretum, 12 May 1993 (in laboratory), K. Bouaziz (AR); 2♀, 4♂, ex. *C. sempervirens*, Meurdja Arboretum, April 1993 (in laboratory), K. Bouaziz (AR). **Croatia**: 2♀, 2♂ syntypes, Sinj, Dalmatia, 11–15 August 1915, Seitner (NMW); 2♀, 9♂, ex. *C. sempervirens*, Dubrovnik, August 1987 (AR). **France**: 2♀, 3♂, ex. *C. abramsiana*, Le Rouet (83), August 1996 (AR); 3♀, 2♂, ex. *C. arizonica*, Thedirac (46), August 1982 (AR); 5♀, 4♂, ex. *C.arizonica*, Les Caunes (83), August 1996 (AR); 1♀, 1♂, ex. *C. bakeri*, Le Caneiret (83), August 1995 (AR); 2♀, 2♂, ex. *C. dupreziana*, Ceyreste (13), August 1996 (AR); 8♀, 3♂, ex. *C. goveniana*, Le Rouet (83), August 1995 (AR); 15♀, 12♂, ex. *C. sempervirens*, Avignon (84), August 1983 (AR); 8♀, 6♂, ex. *C. sempervirens*, Chateau-Arnoux (04), August 1983 (AR); 7♀, 5♂, ex. *C. sempervirens*, Porto (Corsica), August 1983

(AR); 8♀, 8♂, ex. *C. sempervirens*, Fontvieille (13), July 1984 (AR); 8♀, 10♂, ex. *C. sempervirens*, Sospel (06), August 1992 (AR); 7♀, 3♂, ex. *C. sempervirens*, St-Denis (93), September 2000 (AR). **Greece**: 11♀, 15♂, ex. *C. sempervirens*, Pylos (Peloponnesis), August 1991 (AR); 6♀, 7♂, ex. *C. sempervirens*, Eleftheropolis, August 1993, S. Markalas (AR); 3♀, 12♂, ex. *C. sempervirens*, Kavalla, August 1990, S. Markalas (AR); 14♀, 10♂, ex. *C. sempervirens*, Heraklion (Crete), August 1983 (AR); 12♀, 10♂, ex. *C. sempervirens*, Aghios Demetrios (Kos), July 1995; 18♀, 14♂, ex. *C. sempervirens*, Salakos (Rhodos), August 1996 (AR); 22♀, 18♂, ex. *C. sempervirens*, Metamorphosis (Samos), August 1996 (AR). **Italy**: 5♀, 5♂, ex. *C. sempervirens*, Peruggia, July 1985 (AR); 2♀, 4♂, ex. *C. sempervirens*, Bari, August 1987 (AR); 14♀, 12♂, ex. *C. sempervirens*, Fiesole, July 1992 (AR); 9♀, 8♂, ex. *C. sempervirens*, Pisa, July 1992 (AR); 2♀, 1♂, Cogoleto, Liguria, 12 August 1972, Z. Bouček (MNHN). **Malta**: 2♀, 4♂, ex. *C. sempervirens*, Msida, September 1996, J. Buhagiar (AR). **Morocco**: 4♀, 3♂, Marrakech, ex. *C. sempervirens*, September 1997, El Alaoui (AR); 3♀, 2♂, Marrakech, ex. *C. atlantica*, September 1997, El Alaoui (AR). **Portugal**: 1♀, 1♂, ex. *C. lusitanica*, Caldas de Monchique (Algarve) August 1993 (AR); 8♀, 5♂, ex. *C. sempervirens*, Monsanto (Lisboa), August 1993 (AR); 3♀, 2♂, ex. *C. sempervirens*, Montemor o Novo (Evora), August 1993 (AR). **Tunisia**: 5♀, 7♂, ex. *C. sempervirens*, Tabarka, August 1986 (AR); 4♀, 2♂, ex. *C. sempervirens*, Beni Ayeche, August 1995, M. Ben Jamaa (AR); 8♀, 6♂, ex. *C. sempervirens*, Makthar, August 1996, M. Ben Jamaa (AR). **Turkey**: 2♀, 4♂, ex. *C. sempervirens*, Kuşadasi, August 1995 (AR).

Seed chalcids at risk of introduction in the West Palearctic region

A total of 52 additional *Megastigmus* species were reported to develop within tree seeds in zoogeographic regions other than the West Palearctic. Moreover, it is likely that some more species are to be discovered, especially in Asia, Africa and Central America where the seed pest surveys were limited. All these species are of concern to importers of seed stocks in Europe, North Africa and Asia Minor, and caution must be taken with the corresponding seed sources. Most of these species are related to conifers. Pinaceae seeds host 15 additional chalcid species in Asia and North America (table 4). The major part (five species) were observed on firs, *Abies* spp. (three species in Asia and two in North and Central America). Others were reported from *Tsuga* spp. (two species in North America and one in Japan), *Picea* spp. (two species in Asia), *Larix* spp. (one species in North America and one in Japan) and *Pseudotsuga* spp. (two species in Asia). *Pinus* seeds are attacked by at least one more species in North and Central America.

Similarly, 15 additional *Megastigmus* species were recorded from seeds of Cupressaceae in Asia and North America (table 5). Most of them were observed on *Juniperus* spp. (eight species in Central Asia and China, and one in eastern Africa) and *Cupressus* spp. (three species in Asia). Three more species, but yet known only by larvae, may exist in Japan on *Juniperus chinensis* L. (Saito and Yamamoto, 1985) and in China on *J. formosana* Hayata and *J. squamata* Buch. (Roques *et al*., 1995; Roques and Pan, unpublished observations). The seeds of *Chamaecyparis* host two more species (one in Japan, one in North America) whilst another one was recorded on *Thujopsis dolabrata* in Japan.

Relatively few seed chalcids were reported from the other conifer families. One more species was noticed on Taxodiaceae (on *Cryptomeria* spp. in China and Japan). Araucariaceae may also host *Megastigmus* spp. because a specimen emerged from

Table 4. Exotic *Megastigmus* species at risk of introduction in the West Palearctic with imported conifer seeds of the Pinaceae family.

Species	Range	Host species	References
Species attacking *Abies* spp.			
M. borriesi Crosby	Russia; Korea; Japan	*A. mariesii*; *A. sachalinensis*; *A. sikokiana* Nakai; *A. veitchii*	Escherich, 1938; Shtakel'berg, 1955; Kamijo, 1962; Kobayashi, 1981; Gusev, 1984
M. firmae Kamijo	Japan	*A. firma* Sieb. and Zucc.	Kamijo, 1962
Megastigmus sp.	China	*A. delavayi* Franchet	Roques *et al.*, 1995
M. lasiocarpae Crosby	North America; China	*A. amabilis*; *A. lasiocarpa* var. *lasiocarpa*; *A. sibirica*	Milliron, 1949; Keen, 1958; Hedlin, 1974; Hedlin *et al.*, 1980; Xu and He, 1995
Megastigmus sp.	Mexico	*A. religiosa* (H.B.K.) Schl. and Cham.	Cibrian-Tovar *et al.*, 1986
Species attacking *Larix* spp.			
M. laricis Marcovitch	North America	*L. laricina* (Du Roi) K. Koch	Grissell, 1979; Hedlin *et al.*, 1980; Turgeon, 1994
M. inamurae Yano	Japan	*L. leptolepis*	Kamijo, 1962
Species attacking *Picea* spp.			
M. ezomatsuanus Hussey and Kamijo	Japan; China	*P. obovata*; *P. glehnii*; *P. jezoensis*; *P. koraiensis* Nakai	Hussey and Kamijo, 1958; Kobayashi, 1981; Roques *et al.*, 1995; Xu and He, 1995
M. likiangensis Roques and Sun	China	*P. likiangensis* Pritzel	Roques *et al.*, 1995
Species attacking *Pinus* spp.			
M. albifrons Walker (= *M. grandiosus* Yoshimoto)	North America; Mexico; Honduras; Guatemala	*P. arizonica* Engelm.; *P. ayacahuite* Ehren.; *P. engelmannii* Carr.; *P. hartwegii* Lindl; *P. michoacana* Mart. *P. montezumae* Lamb.; *P. ponderosa* Dougl.; *P. pseudostrobus* Lindl.; *P. rudis* Endl.	Milliron, 1949; Hedlin *et al.*, 1980; Turgeon, 1994; Cibrian-Tovar *et al.*, 1986, 1995; USNM
Species attacking *Pseudotsuga* spp.			
M. pseudotsugaphilus Xu and He	China	*P. gaussenii* Flous	Zhou, 1978; Xu and He, 1995
Megastigmus sp.	China	*P. sinensis* Dode	Roques *et al.*, 1995
Species attacking *Tsuga* spp.			
M. hoffmeyeri Walley	North America	*T. canadensis* (L.) Carr.	Milliron, 1949; Grissell, 1979
M. tsugae Crosby	North America	*T. heterophylla* Raf. (Sarg.); *T. mertensiana* (Bong.) Carr.	Milliron, 1949; Keen, 1958; Hedlin *et al.*, 1980
M. tsugaphilus Kamijo	Japan	*T. sieboldii* Carr.	Kamijo, 1958, 1962

Table 5. Exotic *Megastigmus* species at risk of introduction in the West Palearctic with imported conifer seeds of the Cupressaceae and Taxodiaceae family.

Species	Range	Host species	References
Species attacking *Cupressus* spp.			
M. cupressi Mathur	India	*C. torulosa*	Mathur, 1955; Subba Rao and Hayat, 1986; Narendran, 1994
M. duclouxiana Roques and Pan (= *M. duclouxianae* Xu and He)	China	*C. duclouxiana*; *C. torulosa*	Roques *et al.*, 1995; Xu and He, 1995
M. carinus Xu and He	China	*C. duclouxiana*	Xu and He, 1995
Species attacking *Juniperus* spp.			
M. certus Nikol'skaya	Kirgistan	*J. sabina*; *J. semiglobosa* Regel	Nikol'skaya, 1966; Stadnickii *et al.*, 1978; Zerova and Seryogina, 1994
M. fidus Nikol'skaya	Kirgistan	*J. sabina*; *J. sibirica* Burgsd.	Nikol'skaya, 1966; Stadnickii *et al.*, 1978; Zerova and Seryogina, 1994
M. gravis Nikol'skaya	Georgia	*J. excelsa*; *J. foetidissima* Willd.	Nikol'skaya, 1966; Zerova and Seryogina, 1994
M. juniperi Nikol'skaya	Central Asia; Turkey	*J. seravchanica* Komarov; *J. excelsa*	Nikol'skaya, 1966; Stadnickii *et al.*, 1978; Zerova and Seryogina, 1994; Özkazanç, 1982
M. pingii Roques and Sun	China	*J. pingii* Cheng.	Roques *et al.*, 1995
M. rigidae Xu et He	China	*J. rigida*	Xu *et al.*, 1998
M. sabinae Xu and He	China	*J. convallium* Rehder and Wilson; *J. komarovii* Florin; *J. przewalskii* Komarov; *J. saltuaria* Rheder and Wilson; *J. tibetica* Komarov	Wu *et al.*, 1992, 1993; Xu and He, 1989, 1995, 1998
M. somaliensis Hussey	Eastern Africa	*J. procera* Hochst. ex. Endl.	Hussey, 1955a
M. validus Nikol'skaya	Kirgistan	*J. turkestanica* Komarov	Nikol'skaya, 1966; Stadnickii *et al.*, 1978; Zerova and Seryogina, 1994
Species attacking *Chamaecyparis* spp.			
M. chamaecyparidis Kamijo	Japan	*C. obtusa* (Sieb. and Zucc.) Endl.	Kamijo, 1958, 1962
M. thyoides Kamijo	Canada	*C. thyoides* (L.) B.S.P.	Turgeon *et al.*, 1997
Species attacking *Thujopsis spp.*			
M. thuyopsis Yano	Japan	*T. dolabrata* Sieb and Zucc.	Escherich, 1938; Kamijo, 1962
Species attacking Taxodiaceae			
M. cryptomeriae Yano	China, Japan	*C. fortunei* Hooib.; *C. japonica* D. Don.	He, 1984; Zhang, 1987; Xu *et al.*, 1989; Roques *et al.*, 1995; Xu and He, 1995; Kamijo, 1962; Kobayashi, 1981

Table 6. Exotic *Megastigmus* species at risk of introduction in the West Palearctic with imported seeds of Angiosperms.

Species	Range	Host species	References
Species attacking Rosaceae			
M. cotoneastri Nikol'skaya	Russia; Japan	*Cotoneaster insignis* Pojenk; *C. nummularia* Fisch. and Rey; *C. racemiflorus* (Desf.) Booth ex. Bosse; *C. tauricus* Pojark	Zerova and Seryogina, 1994; Nikol'skaya, 1952
M. fangii Pan and Roques	China	*Rosa helenae* Rehder and Wilson	Pan and Roques, in preparation
M. mali Nikol'skaya	East Asia; Japan	*Pyrus* (= *Malus*) *pallasiana* Juzepczuk; *P. baccata* Borckh.; *Pyrus* sp.	Nikol'skaya, 1956; Kamijo, 1962; Zerova and Seryogina, 1994
M. pourthiaeae Kamijo	Japan	*Pourthiaea villosa* Decne.	Kamijo, 1962
M. amelanchieris Cushman	USA	*Sorbus aucuparia*; *Amelanchier laevis* Wieg. × *humilis* Wieg.; *A. sanguinea* (Pursh.) D.C.; *Pistacia* and *Eucalyptus* (Sorauer, 1953) probably erroneous	Milliron, 1949; Grissell, 1979
M. formosus Milliron	Canada	?*Crataegus* and *Rosa*; swept from *C. coccinea* L. = *C. macrantha* Lodd	Milliron, 1949; Grissell, 1979; USNM
M. gahani Milliron	USA	*Spiraea opulifolia* L. (= *Physocarpus opulifolius* Maxim. ex Koehne) var. *intermedius* (Rydb.) Robinson	Milliron, 1949; Sorauer, 1953
M. physocarpi Crosby	North America	*Spiraea opulifolia*	Milliron, 1949; Grissell, 1979
M. americanus Milliron	North America	*Sorbus* sp. (*aucuparia*)	Milliron, 1949; Gahan, 1951
Species attacking Anacardiaceae			
M. rhusi (Hussey)	South Africa	*Rhus lancea* L	Hussey, 1956; Bouček, 1978
M. thomseni (Hussey)	South Africa	?*Heeria insignis* (Del) O. Ktze	Hussey, 1956; Bouček, 1978
Species attacking Fabaceae (Leguminosae)			
M. albizziae Mukerji	India	*Albizzia* sp., probably *odoratissima* Benth.; *A. Lebeck* Benth. in Hook. (= *A. lebbeck*)	Mukerji, 1950; Subba Rao and Hayat, 1986; Narendran, 1994
M. leeuweni Ferrière	Java	*Dalbergia* (= *Milletia*) *sericea* Springl.	Ferrière, 1929; Milliron, 1949
Species attacking Aquifoliaceae			
M. floridanus Milliron	USA	*Ilex opaca* Aiton; *Ilex* × *attenuata* Ashe (= *I. cassine* L. × *I. opaca*)	Grissell, 1989
Species attacking Hamamelidaceae			
M. distylii Kamijo	Japan	*Distylium racemosum* Sieb. and Zucc.	Kamijo, 1979

seeds of *Agathis* sp. collected at Coimbatore, India (20 January 1916) was observed at USNM. It was identified as *M. indi* Girault but Milliron (1949) qualified this name as *nomen nudum*. Thus, its taxonomic status still remains uncertain. Two additional species, *M. pseudomali* Xu and He and *M. celius* Xu and He, were reported from 'conifer seeds' in China but without any indication of host (Xu and He, 1995).

A total of 15 additional species were recorded from Angiosperm seeds (table 6). Most of them were observed in seeds of Rosaceae (four in the Caucasus and Asia and five in North America) and Anacardiaceae (two in Africa). Two species were described from Asian Fabaceae (Leguminosae) but this family probably hosts more *Megastigmus* species because we observed at USNM several unidentified specimens having emerged from seeds of *Acacia leucophloea* Willd. (from Burma), *Parkia speciosum* Hassk. (from Java) and *Sesbania grandiflora* Poir. (from 'Siam'). Other host families include Aquifoliaceae (one species in North America) and Hamamelidaceae (one species in Japan).

In addition, three species, *M. koebelei* Ashmead from Japan (Ashmead, 1904; Milliron, 1949; Kamijo, 1962). *M. caperatus* Milliron from Canada (?*Picea*, Milliron, 1949) and *M. variegatus* Strand. from Mexico (Milliron, 1949) still have unknown hosts. According to Grissell (1999), *M. sinensis* Sheng reported from bamboo shoots (Graminae) in China (Sheng, 1989) and *M. hypogea* (Hussey) reported from 'oil seed' (?*Helianthus*, Asteraceae; Hussey, 1956), are probably parasitoids. Two other species, *M. mendocinus* Kieffer and Jorgensen (Milliron, 1949) and *M. flavipes* Ashmead (Milliron, 1949; Grissell, 1979) were recently transferred to the genus *Torymoides* (Torymidae) and *Gastrancistrus* (Pteromalidae), respectively (Grissell and Heydon, 1999).

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