Phylogeny and host association in *Platygaster* Latreille, 1809

(Hymenoptera, Platygastridae)

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An examination of the known midge host/midge plant host associations for species of *Platygaster* parasitoid wasps seems to indicate a number of natural parasitoid species groups restricted to specific plant families. Midge hosts seem less indicative for platygastrid relationships, but several exceptions from this rule exist. The possible reasons for this are discussed. It is also shown that species of *Platygaster* with known host associations generally prefer midges on plant families which are not the families generally prefered by the midges. Furthermore, a comparison of the known midge host/midge plant host associations for the genera of the "*Platygaster*-cluster" and the "*Synopeas*-cluster" shows great differences in the general preferences of the clusters.

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Introduction

The phylogeny of the very large platygastrid genus *Platygaster*, tiny parasitoids on gall midges (Diptera, Cecidomyiidae), is mostly unresolved. The great problems which meet the investigator are primarily - as in all platygastrids - the few external characters available in a phylogenetic analysis. A further obstacle in the revisionary work is that many species are known only from short dated original descriptions (unknown or unrevised type material). Aspects of the biology (midge host or host plant of midge) are, however, known for about half the described species, so perhaps this could enlighten aspects of the parasitoid taxonomy - as was successfully done e.g. in Braconidae by Griffiths (1964, 1966a, 1966b). A couple of species groups of *Platygaster* were in fact treated by MacGown (1974, 1979), in particular in the later work, on the basis of host plant association. A general overview of the entire genus with regard to host midge and host plant association combined with taxonomic remarks has, however, to my knowledge never been done. Perhaps for good reasons, considering the above mentioned difficulties. At present an arrangement of the species in *Platygaster* – which is a portmanteau genus most unlikely to be monophyletic (MacGown, 1979) – can only be very tentative and preliminary. But some partial conclusions seem to be possible, helping to construct a conceptual "taxonomic sceleton" which surely need a more solid foundation and a lot more bricks of facts to satisfy, but this can only be provided by many further years of alpha taxonomy.

An overview of host association is also relevant for quite another reason: The only modern catalogue (also with notes on biology), i.e. Vlug (1995), took no regard to modern revisions of cecidomyiid taxonomy and nomenclature, at first hand making comparisons very unclear.

Method

A list of species of *Platygaster* was made with their cecidomyiid hosts and the midge host plants (Table 1; author and year of description only mentioned here). Sorted on the basis of midge genus or midge tribe this list only made limited sense with regard to wasp taxonomy (understood as comparative morphology of the *Platygaster*-species as known first-hand by the author or through the literature). Of course, also the phylogeny of Cecidomyiidae is very unresolved, e.g. Oligotrophini and Cecidomyiini being paraphylet-ic groups (Roskam, 1992), making a more reliable parameter desirable. Luckily, sorted by host plant family, a – somewhat fragmentary – pattern seemed to emerge. It invites to make several new suggestions on relationships between species not hitherto considered but quite reasonable with view to some key characters (especially of head and thorax, among the most indicative in platygastrids).

Results

Remarks on Platygaster associated with

- Betulaceae: The two Palaearctic species *betularia* and *betulae* are indeed very similar in biology as well as in morphology (Roskam, 1986), the Nearctic *columbiana*, however, seems to be rather distant, cf. Fouts (1924).
- Chenopodiaceae: P. aphidis and bonessi seem to be species sola, but between the Nearctic P. atriplicis and the Palaearctic P. stefaniolae and stefaniellae there seems to be several key characters in common (structure of head and mesoscutum).
- Compositae: It must be noticed that all species here except four are from the New World. With regard to the descriptions in Kieffer (1926) it seems that the following Neotropical species are rather similar: *P. baccharidis, caulicola, tumoricola, heterothalami* and probably also *luctuosa*, clearly reflecting the greater importance of plant than of midge association for the phylogeny of the wasps (it is perhaps relevant that all their midge hosts form distinct galls, cf. Kieffer (1926)). Also the Nearctic *astericola, huachucae, variabilis,* and *vernoniae* share plant family association as well as several key morphological characters. The same seems to be the case for *actinomeridis* and *artemisiae* (the record of *actinomeridis* from Cesalpiniaceae is doubtful, cf. Fouts (1924)). In contrast, the most surely closely related *rohweri* and *vernoniae* share neither a closely related midge nor plant. But also *solidaginis, striaticeps,* and *utahensis* which seem to have similar structure of head and mesoscutum are all associated with Compositae.
- Coniferae: MacGown (1979: 16) clearly defined the P. contorticornis-group on the peculiar condition of male antennal plate organs (P. contorticornis, confusa, gahani, ponderosae, shastensis, beneficiens, and herricki). To this should most probably be added P. plana Buhl, 1994 and planoides Buhl, 1995 (males and biology unknown). P. rufipes, abicollis, and victoriae form another group on account of antennal plate organ and shape of scutellum according to MacGown (1979). P. zaragozana and juniperi also form a distinct group based on aberrant shape of metasoma, though also diplosidis could belong here. Finally, P. entwistlei and manto share many morphological traits and association with conifers. P. distincta attacks midge species from two genera on the same plant host, Pinus radiata. P. matsutama is a parasitoid on a midge on the needles of Pinus, the very similar P. sugitama on a midge on the needles of Cryptomeria, both in Japan (a parallel biology should be expected from the very similar P. lundensis Buhl, 1997).
- Fabaceae: The similar *P. tuberculi* and *leguminicolae* share midge genus as well as plant family association. (*P. lupinicola* should possibly also be included in this group).
- Fagaceae: There seems to be several key similarities between *P. tumida* and *cynipicola* (in structure of head and thorax). Also, *cynipicola* and *atrae* are very similar, reared from

Table 1. Species of *Platygaster* with known host/plant associations. *Platygaster* names generally according to Vlug (1995). Cecidomyiid names generally according to Gagné (1994) and Skuhravá (1986). Some informations missing or unavailable. Cases of a species just swept on a certain plant not mentioned. Notes: 1) Not host (but probably midge host/prey). 2) New record: *P. sagana* reared from *Rhopalomyia ptarmicae* (Vallot, 1849) on *Achillea ptarmica* L. in Germany (M. Boness leg.).

Platygaster species	host taxon (genus, tribe)	gall type	host plant taxon (genus, family)
abicollis MacGown & Osgood, 1971		leaf (needle) gall	Abies, Coniferae
acciculosis Drake, 1969	Diarthonomyia, Oligotrophini	stem/leaf gall	Chrysanthemum, Compositae
acciculosis Drake, 1969	Zeuxidiplosis, Cecidomyiini	leaf gall	Hypericum, Hypericaceae
actinomeridis (Ashmead, 1893)	Lasioptera, Lasiopterini		Gleditsia, Cesalpiniaceae
actinomeridis (Ashmead, 1893)			Actinomeris, Compositae
actinomeridis (Ashmead, 1893)	Contaviaia Canidamuijai		Verbesina, Compositae
americana Ashmead, 1887 antennariae (Ashmead, 1893)	Contarinia, Cecidomyiini Rhopalomyia, Oligotrophini	leaf (needle) gall bud gall	Verbesina, Compositae Baccharis, Compositae
aphidis Ashmead, 1893	Aphis, Homoptera1)	predatory midge	Chenopodium, Chenopodiaceae
apicalis Thomson, 1859	Lasioptera, Lasiopterini	stem gall	Rubus, Rosaceae
artemisiae (Ashmead, 1893)	Lasiopiera, Lasiopierini	gall	Artemisia, Compositae
ashmeadiana Huggert, 1973	Dasineura, Oligotrophini	cone	Picea, Coniferae
ashmeadiana Huggert, 1973	Chilophaga, Alycaulini	stem (culm) gall	Aristida, Graminaceae
astericola (Ashmead, 1893)		gall	Aster, Compositae
asynaptae (Ashmead, 1893)	Asynapta, Asynaptini	gall	Salix, Salicaceae
athamas Walker, 1835	Bayeria, Oligotrophini	bud gall	Euphorbia, Euphorbiaceae
athamas Walker, 1835	Wachtliella, Oligotrophini	leaf gall	Rosa, Rosaceae
athamas Walker, 1835	Dasineura, Oligotrophini	terminal bud (unswollen)	Salix, Salicaceae
atrae Fouts, 1924	Procecidochares, Tephritidae1)	stem gall	Daucus, Umbelliferae
atriplicis (Ashmead, 1893)		gall	Atriplex, Chenopodiaceae
attenuata Walker, 1835	Haplodiplosis, Cecidomyiini	stem depressions	Graminaceae
attenuata Walker, 1835	Dasineura, Oligotrophini	flower without swelling	Alopecurus, Graminaceae
australis (Dodd, 1916)		bud	Careya, Barringtoniaceae
baccharidis Kieffer, 1910	Cecidomyia, Cecidomyiini	stem swelling	Baccharis, Compositae
beneficiens MacGown, 1979	Dasineura, Oligotrophini	cone	Picea, Coniferae
betulae (Kieffer, 1916)	Semudobia, Oligotrophini	fruit swelling	Betula, Betulaceae
betularia Kieffer, 1916	Semudobia, Oligotrophini	fruit swelling	Betula, Betulaceae
bonessi Buhl, 2000	Stefaniella, Lasiopterini	stem gall	Atriplex, Chenopodiaceae
brevistriata Kieffer, 1916	Iteomyia, Oligotrophini	leaf gall	Salix, Salicaceae
burkei (Rohwer, 1917)	Retinodiplosis, Cecidomyiini	under bark	Pinus, Coniferae
californica (Ashmead, 1893)	Rhopalomyia, Oligotrophini	gall	Baccharis, Compositae
canestrinii (Rondani, 1866)	Dasineura, Oligotrophini	leaf sheat	"cereals", Graminaceae
carinifrons (Brues, 1910)	On any in Angle and I'' at		Ficus, Moraceae
caryae Ashmead, 1893	Caryomyia, Asphondyliini	gall	Carya, Juglandaceae
caulicola Kieffer, 1910	Meunieriella, Camptoneuromyiini	stem swelling	Baccharis, Compositae
cecconii Kieffer, 1913 cecconii Kieffer, 1913	Dasineura, Oligotrophini Psectrosema, Oligotrophini	stem without gall stem gall	<i>Salix,</i> Salicaceae <i>Tamarix,</i> Tamaricaceae
cecidomyiae Ratzeburg, 1852	Dasineura, Oligotrophini	stem swelling	Salix, Salicaceae
coloradensis (Ashmead, 1893)	Rhopalomyia, Oligotrophini	bud gall	Salvia, Labiatae
columbiana Fouts, 1924	Dasineura, Oligotrophini	bud gall	Alnus, Betulaceae
compressicornis (Thomson, 1859)	Thecodiplosis. Cecidomyiini	leaf (needle) without gall	
contorticornis Ratzeburg, 1844	Kaltenbachiola, Oligotrophini	cone	Picea, Coniferae
corni Kieffer, 1916	Craneiobia, Oligotrophini	leaf gall	Cornus, Cornaceae
coronatus (Brues, 1910)	Asphondylia, Asphondyliini	loar gan	Mikania, Compositae
cottei Kieffer, 1913	Lasioptera, Lasiopterini	stem gall	Daucus, Umbelliferae
cruciferarum Kieffer, 1916	Dasineura, Oligotrophini	flower gall	Raphanus, Cruciferae
cynipicola (Ashmead, 1893)	Neuroterus, Cynipidae1)	3	Quercus, Fagaceae
demades Walker, 1835	Wachtliella, Oligotrophini	bud gall	Erica, Ericaceae
demades Walker, 1835	Dasineura, Oligotrophini	leaf margin rolls	Malus, Rosaceae
diplosidis (Ashmead, 1893)	Retinodiplosis, Cecidomyiini	leaf (needle) without gall?	Pinus, Coniferae
diplosidis (Ashmead, 1893)			Picea, Coniferae
diplosisae Risbec, 1956	Orseolia, Cecidomyiini	stem gall	Oryza, Graminaceae
distincta Fouts, 1926	Thecodiplosis, Cecidomyiini	leaf (needle) gall	Pinus, Coniferae
distincta Fouts, 1926	Cecidomyia, Cecidomyiini	pitch mass	Pinus, Coniferae
dryomiae Dieuzeide, 1927	Dryomyia, Oligotrophini	leaf gall	Quercus, Fagaceae
entwistlei Buhl, 1997	Oligotrophus, Oligotrophini	bud gall	Juniperus, Coniferae
equestris Spittler, 1969	Haplodiplosis, Cecidomyiini	stem depressions	Agropyron, Graminaceae
equestris Spittler, 1969	Haplodiplosis, Cecidomyiini	stem depressions	Triticum, Graminaceae
erdosi (Szelényi, 1958)			Phragmites, Graminaceae
ericeti Rondani, 1877	Dasineura, Oligotrophini	gall	Erica, Ericaceae
eriphyle Walker, 1835	Rhopalomyia, Oligotrophini	bud gall	Artemisia, Compositae
eryngii Kieffer, 1916	Lasioptera, Lasiopterini	stem swelling	Eryngium, Umbelliferae
etsuhoae Buhl, 1998	Etsuhoa, Cecidomyiini	terminal bud gall	Juniperus, Coniferae
eurotiae (Ashmead, 1893)	Firmer Teather divide at)	gall	Eurotia, Chenopodiaceae
euurae (Ashmead, 1893) exigue Fouts, 1926	Euura, Tenthredinidae1) Dasineura, Oligotrophini	gall (on inquiline)	<i>Salix,</i> Salicaceae <i>Salix,</i> Salicaceae
		udii (on monitine)	Jan Oducaciaci

feltii Fouts, 1920 floricola (Kieffer, 1916) foersteri (Gahan, 1919) foersteri (Gahan, 1919) foutsi Huggert, 1973 fungicola Kieffer, 1916 gahani Fouts, 1924 galenus Walker, 1835 generalii Rondani, 1877 generalii Rondani, 1877 globicola Kieffer & Jörgensen, 1910 graminis (Kieffer, 1916) gyrone Szelényi, 1958 herrickii Packard, 1841 herrickii Packard, 1841 heterothalami Kieffer & Jörgensen, 1910 hiemalis Forbes, 1888 hiemalis Forbes, 1888 hiemalis Forbes, 1888 huachucae (Ashmead, 1893) hyalinipennis (Ashmead, 1887) hybrida Buhl, 1994 hygrophila Kieffer, 1916 iolas Walker, 1835 iteocrypta Kieffer, 1916 iteophilus (Kieffer, 1916) juniperella MacGown, 1979 juniperi MacGown, 1979 juniperina MacGown, 1979 . komugi Ishii, 1953 lampronota Fouts, 1924 . lasiopterae Kieffer & Jörgensen, 1910 leguminicolae Fouts, 1920 leptocera Thomson, 1859 leucanthemi (Kieffer, 1916) libocedri MacGown, 1974 libocedri MacGown, 1974 linearis Fouts, 1924 lineata Kieffer, 1906 longestriata Kieffer, 1916 longestriata Kieffer, 1916 longicaudata (Kieffer, 1906) longula (Kieffer, 1926) lucida Fouts, 1924 luctuosa Kieffer & Herbst, 1911 lupinicola (Ashmead, 1893) lyciicola Kieffer, 1910 lyciicola Kieffer, 1910 mainensis MacGown & Osgood, 1971 mainensis MacGown & Osgood, 1971 malpighii Kieffer, 1916 manto Walker, 1835 marchali Kieffer, 1906 marchali Kieffer, 1906 marchali Kieffer, 1906 matsutama Yoshida & Hirashima, 1979 mayetiolae Kieffer, 1916 mediocris (Brues, 1910) mediocris (Brues, 1910) minutula Dalla Torre, 1898 nigra Nees, 1834 nigra Nees, 1834 nigricoxa Fouts, 1925 nigripes Ratzeburg, 1852 nitida Thomson, 1859 nodicola (Kieffer, 1916) obscura Nees, 1834 obscuripennis Ashmead, 1893 oebalus Walker, 1835 oleae Szelényi, 1940 ornatus Kieffer, 1906 ornatus Kieffer, 1906 oryzae Cameron, 1891

Walshomyia, Oligotrophini Dasineura, Oligotrophini Orseolia, Cecidomyiini

Lestodiplosis, Cecidomyiini *Peromyia,* Peromyiini

Dasineura, Oligotrophini Mayetiola, Oligotrophini Misospatha, Oligotrophini Lasioptera, Lasiopterini Giraudiella, Oligotrophini Mayetiola, Oligotrophini Mayetiola, Oligotrophini

Meunieriella, Camptoneuromyiini Mayetiola, Oligotrophini

Caryomyia, Asphondyllini Cecidomyia, Cecidomyiini Lasioptera, Lasiopterini Dasineura, Oligotrophini Dasineura, Oligotrophini Contarinia, Cecidomyiini

Sitodiplosis, Cecidomyiini Rhopalomyia, Oligotrophini

Meunieriella, Camptoneuromyiini Dasineura, Oligotrophini

Ozirhincus, Lasiopterini Rhopalomyia, Oligotrophini

Lasioptera, Lasiopterini Contarinia, Cecidomyiini Dasineura, Oligotrophini Dasineura, Oligotrophini Mayetiola, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini

Jorgensenia, Centrodiplosini Lyciomyia, Oligotrophini

Paradiplosis, Cecidomyiini

Dasineura, Oligotrophini Craneiobia, Oligotrophini Paradiplosis, Cecidomyiini Dasineura, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini

Thecodiplosis, Cecidomyiini Mayetiola, Oligotrophini Bruggmannia, Asphondyliini

Mayetiola, Oligotrophini Wachtliella, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini Lasioptera, Lasiopterini Mayetiola, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini Dasineura, Oligotrophini flower swelling stem gall gall leaf (needle) without gall cone gall stem without gall stem without gall stem swelling stem gall stem without gall stem (ulm) gall

bud swelling

gall stem without gall

leaf gall resin mass stem swelling siliqua swelling stem swelling bud swelling leaf (needle) gall

flower swelling flower gall

stem gall flower without swelling

swollen achenes

leaf/stem without gall? flower swelling stem swelling leaf gall stem without gall leaf gall cone leaf gall gall stem gall stem gall

leaf (needle) gall leaf gall leaf (needle) without gall leaf gall leaf margin rolls leaf gall

leaf (needle) stem swelling leaf gall

stem without gall leaf margin rolls leaf gall gall siliqua swelling stem swelling stem swelling stem swelling stem gall leaf gall leaf gall stem gall Cedrus, Coniferae Raphanus, Cruciferae Oryza, Graminaceae Ischaemum, Graminaceae Pinus, Coniferae (Fungus) Abies, Coniferae Halimione, Chenopodiaceae Graminaceae Triticum, Graminaceae Baccharis, Compositae Calamagrostis, Graminaceae Phragmites, Graminaceae Triticum, Graminaceae Poa, Graminaceae Heterothalamus, Compositae

Triticum, Graminaceae Bromus, Graminaceae Secale, Graminaceae Heianthus, Compositae Hicoria, Juglandaceae Pinus, Coniferae Phragmites, Graminaceae Brassica, Cruciferae Salix, Salicaceae Juniperus, Coniferae Juniperus, Coniferae Juniperus, Coniferae Graminaceae Baccharis, Compositae

Heterothalamus, Compositae Trifolium, Fabaceae (grass), Graminaceae Chrysanthemum, Compositae Libocedrus, Cupressaceae Viscum (on Libocedrus), Loranthaceae Muhlenbergia, Graminaceae Pyrus, Rosaceae Salix, Salicaceae Salix, Salicaceae Triticum, Graminaceae Cornus, Cornaceae Picea, Coniferae Baccharis, Compositae Lupinus, Fabaceae Lycium, Solanaceae Lycium, Solanaceae

Abies, Coniferae

Abies, Coniferae Cornus, Cornaceae Abies, Coniferae Filipendula, Rosaceae Pyrus, Rosaceae Spiraea, Rosaceae

Pinus, Coniferae Dactylis, Graminaceae Myrsine, Myrsinaceae Psychotria, Rubiaceae Triticum, Graminaceae *Polygonum,* Polygonaceae *Filipendula,* Rosaceae Lupina, Fabaceae Abies, Coniferae Brassica, Cruciferae Salix, Salicaceae Rubus, Rosaceae Salix, Salicaceae Brassica, Cruciferae Olea, Oleaceae Pyrus, Rosaceae Spiraea, Rosaceae Oryza, Graminaceae

pauliani Risbec, 1953 pauliani Risbec, 1953 persicariae Kieffer, 1906 philinna Walker, 1835 philippiae Risbec, 1953 phragmitis (Schrank, 1781) piniphila MacGown, 1979 pinyonicola MacGown, 1979 pleuron Walker, 1835 ponderosae MacGown, 1979 producta MacGown, 1979 prolata MacGown, 1971 pseudotsugae MacGown, 1979 ramachandrai (Rao, 1950) relativa Fouts, 1924 resinosae MacGown, 1979 rhabdophagae MacGown, 1979 riparia Yamagishi, 1980 rohweri Fouts, 1924 rubi (Ashmead, 1893) sagana Walker, 1835 salicicola (Ashmead, 1893) saliciperdae Kieffer, 1913 salvadorae Rao, 1950 sambuci (Kieffer, 1916) scrophulariae (Kieffer, 1916) semiglabra (Girault, 1920) shastensis Fouts, 1924 similis MacGown, 1974 sociabilis Kieffer, 1910 solidaginis (Ashmead, 1887) solidaginis (Ashmead, 1887) solidaginis (Ashmead, 1887) splendidula Ruthe, 1859 stachydis (Kieffer, 1916) stefaniellae Buhl, 2000 stefaniolae Buhl, 1998 stimulator Yamagishi, 1980 striaticeps (Ashmead, 1893) striaticeps (Ashmead, 1893) subterraneus (Kieffer, 1916) subterraneus (Kieffer, 1916) suecicus (Kieffer, 1926) sugitama Yoshida & Hirashima, 1979 szelenyii Huggert, 1975 taras Walker, 1835 taylori MacGown, 1974 tibialis Kieffer, 1905 transsylvanicus (Szelényi, 1958) tuberculi (Kieffer, 1916) tuberosula Kieffer, 1926 tuberosula Kieffer, 1926 tubulosa Brues, 1922 tubulosa Brues, 1922 tumida (Ashmead, 1893) tumoricola Kieffer, 1910 ulmicola Kieffer, 1916 umbraculi (Kieffer, 1916) urnicola Yamagishi, 1980 utahensis (Ashmead, 1893) vaenia Walker, 1835 variabilis Fouts, 1924 verdii Vlug, 1995 vernalis (Myers, 1917) vernoniae (Ashmead, 1893) verrucosa Kieffer, 1916 viburni Kieffer, 1916 victoriae MacGown, 1979 virginiensis (Ashmead, 1893) virgo Day, 1971 viticola (Ashmead, 1893) zangherii Szelényi, 1955 zaragozana Buhl, 1998 zosine Walker, 1835 zosine Walker, 1835

Wachtliella, Oligotrophini Dasineura, Oligotrophini

Lasioptera, Lasiopterini

Pinyonia, Cecidomyiini Mayetiola, Oligotrophini Contarinia, Cecidomyiini Contarinia, Cecidomyiini

Dasineura, Oligotrophini *Dasineura,* Oligotrophini

Lasioptera, Lasiopterini Rhopalomyia, Oligotrophini2)

Dasineura, Oligotrophini Resseliella, Cecidomyiini Arnoldiola, Oligotrophini Contarinia, Cecidomyiini Rhopalomyia, Oligotrophini

Xenodiplosis, Cecidomyiini Asteromyia, Alycaulini Cecidomyia, Cecidomyiini

Mayetiola, Oligotrophini Ametrodiplosis, Cecidomyiini Stefaniella, Lasiopterini Stefaniola, Lasiopterini Dasineura, Oligotrophini Aspidiotus

Dasineura, Oligotrophini Lasioptera, Lasiopterini Lasioptera, Lasiopterini

Contarinia, Cecidomyiini Giraudiella, Oligotrophini Haplodiplosis, Cecidomyiini Lasioptera, Lasiopterini Lasioptera, Lasiopterini Dasineura, Oligotrophini Dasineura, Oligotrophini Contarinia, Cecidomyiini Sitodiplosis, Cecidomyiini Ledomyia, Ledomyiini Janetiella, Oligotrophini Cincticornia, Asphondyliini Meunieriella, Camptoneuromyiini Janetiella, Oligotrophini Parallelodiplosis, Cecidomyiini Dasineura, Oligotrophini

Procystiphora, Oligotrophini Rhopalomyia, Oligotrophini Thecodiplosis, Cecidomyiini Mayetiola, Oligotrophini

Anabremia, Cecidomyiini Contarinia, Cecidomyiini

Thecodiplosis, Cecidomyiini Giraudiella, Oligotrophini Lasioptera, Lasiopterini Apiomyia, Oligotrophini Etsuhoa, Cecidomyiini Mayetiola, Oligotrophini Mayetiola, Oligotrophini

gall gall leaf margin rolls stem without gall flower gall swollen shoots

leaf (needle) gall stem without gall leaf (needle) gall leaf (needle) gall under bark cone gall gall

bud gall

bud gall cone stem swelling flower swelling leaf gall stem without gall stem gall flower swelling flower swelling gall cone stem gall bud gall leaf gall gall stem gall stem (culm) gall flower swelling stem gall gall bud gall aall

bud gall stem swelling stem swelling

leaf stem gall stem depressions stem gall gall gall stem swelling flower without swelling flower swelling under bark under bark leaf gall stem swelling leaf gall leaf gall (of cynipid) stem gall gall stem fruit swelling leaf (needle fascicle) gall stem without gall gall leaf gall flower swelling hyperparasite? stem gall stem gall stem gall stem gall terminal bud gall stem swelling stem without gall

Vernonia, Compositae Macaranga, Euphorbiaceae Polygonum, Polygonaceae Salix, Salicaceae Philippia, Ericaceae Phragmites, Graminaceae Pinus, Coniferae Pinus, Coniferae Triticum, Graminaceae Pinus, Coniferae Pinus. Coniferae Pinus, Coniferae Pseudotsuga, Coniferae Andropogon, Graminaceae Aster, Compositae Pinus, Coniferae Picea, Coniferae Salix, Salicaceae Pinus, Coniferae Rubus, Rosaceae Achillea, Compositae Salix, Salicaceae Salix, Salicaceae Salvadora, Fabaceae Sambucus, Caprifoliaceae Scrophularia, Scrophulariaceae Vernonia, Compositae Abies, Coniferae Chrysothamnus, Compositae Geoffraea, Fabaceae Solidago, Compositae Solidago, Compositae Aster, Compositae Poa. Graminaceae Stachys, Labiatae Atriplex, Chenopodiaceae Salsola, Chenopodiaceae Salix, Salicaceae Artemisia, Compositae Bigelovia, Compositae Galeobdolon, Labiatae Rubus, Rosaceae Foeniculum, Umbelliferae

Cryptomeria, Taxodiaceae Phragmites, Graminaceae Triticum, Graminaceae Rubus, Rosaceae Polygonum, Polygonaceae Sisymbrium, Cruciferae Sarothamnus, Fabaceae Triticum, Graminaceae Triticum, Graminaceae Quercus, Fagaceae Fraxinus, Oleaceae Quercus, Fagaceae Baccharis, Compositae Ulmus, Ulmaceae Quercus, Fagaceae Salix, Salicaceae Artemisia, Compositae Juncus, Juncaceae Solidago, Compositae Pinus, Coniferae Triticum, Graminaceae Vernonia, Compositae Lathyrus, Fabaceae Viburnum, Caprifoliaceae Pinus, Coniferae Taxodium, Cupressaceae Phragmites, Graminaceae Vitis, Vitaceae Pyrus, Rosaceae Juniperus, Coniferae Avena, Graminaceae Triticum, Graminaceae

different plant families but both from non-cecidomyiid galls (inquiline hosts?). *P. tubulosa* is an extralimital species (subgenus *Cylindrogaster* Huggert, 1980), cf. also Austin & Field (1997).

- Graminaceae: The following grouping could tentatively be suggested: 1) *P. virgo, taras,* and *pleuron*; 2) *P. attenuata* and *phragmitis*; 3) *P. gyrone, hiemalis, leptocera, mayetiolae, splendidula,* and *szelenyii. P. attenuata* attacks midges belonging to different tribes on grasses. On the other hand, it is hard to find any parallel associations for the similar species *hiemalis, burkei,* and *eurotiae.*
- Juncaceae: *P. vaenia* is a very aberrant species, and also the only species of the genus known from this plant family (and from the host midge genus).
- Labiatae: *P. subterraneus* and *stachydis* share many key characters as well as association with plant family (midge association less indicative). *P. coloradensis*, on the other hand, is a rare example that midge association is more indicative for close relative (*P. californica*) than plant family association.
- Rosaceae: Though split between two midge tribes the following species seem rather close: *P. apicalis, demades, marchali, ornatus, rubi,* and *subterraneus* (which fits equally well with *stachydis*).
- Salicaceae: Among the wasps associated with this family some three species-groups can possibly be discerned: 1) *P. asynaptae* and *salicicola* (and perhaps *euurae*); 2) *P. iteophilus* and *athamas* (and perhaps *brevistriata*); 3) *P. longestriata, riparia, urnicola,* and *iteocrypta* (from the description in Kieffer (1926) *brevistriata* could also fit in this group). *P. athamas*, on the other hand, is a rare documented case (by Vlug (1985)) of a species which is associated with three plant families (but only one midge tribe).
- Solanaceae: *P. lyciicola* seems to be another example of the importance of plant association overruling midge association.
- Umbelliferae: The similar *P. cottei* and *eryngii* share midge genus as well as plant family association.

That the species of "genus" *Prosactogaster* Kieffer, 1914 (characterised only by long metasoma with anteriorly prolonged 2nd sternite accommodating the extra long ovipositor) are hardly closely related to each other is perhaps supported by their widely different midge and plant associations. The biology of six species is mentioned in Vlug (1995), who treated *Prosactogaster* as a separate genus. The present author regards them as an arbitrary selection of species from a number of *Platygaster* species groups, having convergently developed long ovipositor as a response to interspecific competition for midge hosts living well-protected or relatively deep below the plant surface.

Discussion

Though most of the gall midges in the holarctic region attack Compositae (followed by Salicaceae and Graminaceae according to Richards & Davies (1988)), most *Platygaster* with known biology are associated with Coniferae, closely followed by Graminaceae – only as number three, rather far behind, Compositae (mostly Neotropical). Thus, the pattern mentioned by Memmott & Godfray (1993) that greater parasitoid loads are to be found on hosts on trees and shrubs in comparison with hosts on low-growing plants (explained by an assumed greater difficulty of locating hosts on early successional plants dispersed throughout a habitat) does hardly seem to apply for *Platygaster*, however, with view to their hosts' preference for Compositae the wasp preference for conifers is more significant than its purely numerical value compared to wasps on low-growing plants suggests at first glance.

Spatial distribution, plant architecture and -ultrastructure, typical forms of galls associated with each plant family, microclimate (in e.g. lower vegetation or tree tops), plant/

host chemistry, and history of the geographical distribution of the plants are among the many factors which could concentrate a platygastrid group on certain plant groups, the behavioral and ecological aspects being at least as important in evolution as wasp morphology. Altieri et al. (1993) mention a number of studies showing that several chemical, genetic and architectural attributes of plants can influence parasitoid action on insect hosts (cf. also Quicke (1997: 307)). E.g., it is hardly without evolutionary significance that alkaloids and other allelochemicals involved in plant resistance can be toxic to parasitoids within hosts – perhaps part of an explanation of also the plant associations of *Platygaster* species groups (but as in everything concerning parasitoid seek out particular habitats and are guided by volatiles emanating from plants. "There is thus no doubt that the plant has a huge influence on the evolution and behavioral ecology of host-parasitoid interactions." (Godfray 1994: 353). An understanding of these tri-trophic interactions is not just of theoretical interest. As noted by Sands (2000) it may also be very important when selecting parasitoids for biological control programs.

Probably the development of the species-groups forming the "*Platygaster*-cluster" has been very complex, with several invasions of midges on a plant family by different species-groups taking place, may be following the midge host in co-evolution, leaving their close relatives in the old host plant association, making it today nearly always very difficult to say what is the advanced condition due to the limited information in platygastrid morphology. However, Quicke (1997: 344) remarks that co-cladogenesis appears to be of minor importance in parasitic Hymenoptera, and this also seems to be confirmed by the data in table 1. But it also indicate that many exceptions from simple generalisations could exist. However, even if a species is sometimes reared from another plant family than expected, this says nothing about that it may very possible perform less well than usual on certain hosts due to their host plant (Sands, 2000).

MacGown (1979: 17) for the species-groups considered by him supposed two separate invasions from conifers to non-conifers – or two separate invasions of the conifers by the respective groups. The relatively large diversity of *Platygaster* on Graminacae and Coniferae are no doubt to some degree a reflection on the level of investigation but probably also indicates the relative abundance of this taxonomic assemblage of platygastrids in boreal and subtropical biotopes where life-conditions (e.g. host abundance and distinct seasons) make life in some ways easier for small parasitoids than in the tropics, cf. Godfray (1994: 357).

If the evolution of *Platygaster* species takes place through transference between similar types of galls induced by different midge species, then midge phylogeny is not a reliable guide to wasp taxonomy as a correlation between the taxonomic position of gall midges and the form of their galls is doubtful (Roskam, 1992). E.g., the similar species P. subterraneus and stachydis attack three species of midges which all create swollen deformations on Fabaceae (necessitating the elongated gaster – with long ovipositor – of the parasitoids). Further, P. attenuata and phragmitis attack distinctly related midges living under identical circumstances, i.e. under gall-like depressions or constrictions in cereal crops and *Phragmites*, respectively (Rübsaamen & Hedicke, 1925-39). (The long metasoma of the parasitoids seems to be necessary here because the midge larva live in the stem beneath the sheath, cf. Barnes (1956)). Without pressing the evidence too far, there are also indications of a similar biology for the hosts of P. gyrone, hiemalis, leptocera, mayetiolae, and szelenyii, the midges living at the surface of the plant at least when hatching (Barnes, 1956; Rübsaamen & Hedicke, 1925-39), making a long parasitoid metasoma (and ovipositor) not necessary. P. apicalis, demades, marchali, ornatus, rubi, and subterraneus all seem to parasitise midges in swollen plant deformations, P. demades also in rolled leaf edges (descriptions of host galls in Rübsaamen & Hedicke (1925-39)). It must be

logical, however, that certain midges can be attacked only by parasitoids with a long enough ovipositor – but these parasitoids also have the chance to switch to host nearer the plant surface. The opposite option naturally does not exsist for *Platygaster* species with short metasoma (the length of the female metasoma rather accurately reflects the length of the ovipositor). The possibility of a single *Platygaster* species having different metasomal length according to the relevant host on a specific locality is indicated by Huggert (1974), illustrating the range of morphological variation in *P. depressiventris* Thomson, 1859. (Such intraspecifc variation seems to be widespread in *Platygaster*, possibly facilitating sympatric speciation when a population has adapted to a specific host? Cf. Godfray (1994: 355)) A similar phenomenon was proposed by Gibbons (1979) concerning an ichneumonid genus where ovipositor length provided a means of dividing a single host resource, caused by a sympatric speciation mechanism (competitive speciation).

Of the parasitoids of Salicaceae *P. iteophilus* and *athamas* both seem to live on midges in the terminal buds on *Salix*, *P. longestriata* and *iteocrypta* parasitise in stem galls, *longestriata* also in galls on leaves – perhaps a transition to *brevistriata* which only is known to parasitise galls on leaves. *P. philinna* occurs in 3 midge species, all in *Salix* stems without galls. (Information on host relations as almost always from Vlug (1995), on host biology from Kieffer (1926) and Barnes (1951)).

A reason why *Platygaster* species are less associated with taxonomic entitites of midges than with entities of plants or possibly gall types could be the capability of many midge species to form very different kinds of galls on different parts of the plant, as well as the host range of some midge species which cover up to five plant families (Barnes, 1953). Rather than following its host midges to different plant families (and to different parts of the plant?) a parasitoid would more naturally select other midge species on the same plant, due to the earlier mentioned important role plants play in the host selection process by providing cues to the location of a potential host community, cf. also Vinson (1984) who notes that parasitoids have evolved to respond to cues not only produced by the host, but also cues provided by the food and shelter of the host and associated organisms. A possible cue is a specific type of gall; *Platygaster* species have to my knowledge not at present been reared from different gall types induced by the same midge species, but this could be due solely to lack of investigation.

It is hard to compare on a statistical basis the host plant association of the genera most closely related to *Platygaster*, (the "*Platygaster*-cluster" sensu Austin & Field (1997)), e.g. *Trichacis* Foerster, 1856 and *Isocybus* Foerster, 1856, as these genera are much less rich in known species and furthermore with poorly known biology. Of the seven species of *Trichacis* with known biology, 3 are associated with Graminaceae, and 1 with a plant of each of the following families: Cornaceae, Solanaceae, Malvaceae, and Fagaceae. Of the two species of *Isocybus* with known biology, 1 is associated with a midge on *Brassica* (Cruceferae), 1 with *Carex* (Graminaceae) (Vlug, 1995).

Quite a different picture appears when looking at the slightly more distant "Synopeascluster" sensu Austin & Field (1997), dominated by the very large genus Synopeas Foerster, 1856. The about forty species with host associations noted mostly by Vlug (1995) attack midges on the following plant families: 10 species on Salicaceae, 4 species on Fabaceae, 3 species on Fagaceae, 3 on Anacardiaceae, 3 on Coniferae, 2 on Chenopodiaceae, 2 on Cruciferae, and 1 Synopeas species on each of the following: Aquifoliaceae, Ribesiaceae, Umbelliferae, Myrtaceae, Compositae, Bignoniaceae, Urticaceae, Malvaceae, and Rosaceae. In other words, a remarkable diversity of associations with a very different priority than in *Platygaster*, with Salicaceae being far on the top on the hit list for Synopeas, only number four for *Platygaster*. Furthermore, the most popular plants for *Platygaster* are almost (Coniferae and Compositae) or entirely (Graminaceae) absent as plant association for *Synopeas*. The midges hosts for *Synopeas* are almost equally distributed in Cecidomyiini and Oligotrophini with very few known hosts belonging to other tribes; in *Platygaster* more than twice as many species have hosts in Oligotrophini as in Cecidomyiini.

In conclusion, in morphology as well as in biology there seems to be a deep split between "Synopeas" and "Platygaster", diversifying a long time ago on their hosts in quite different ways. Inside Platygaster s.l. a large number of groups distinct on account of morphology as well as biology are evidently present, but with regard to their interrelatedness and historical development it is at the present level of study only possible to quote Nicolaus Steno's famous dictum: "Pulchra sunt, quae videntur, pulchriora quae sciutur, longe pulcherrima quae ignorantur". ("Beautiful is what we see; more beautiful is what we understand, but by far the most beautiful is what our mind can not contain"). The present synopsis is mostly conjectural and points only to a few tendencies to which future research is recommended to pay attention. But at least it seems to confirm the rule mentioned by Vinson (1984) that there is less tendency for parasitoids to select phylogenetically related hosts than unrelated hosts found on the same plant. It is mentioned by the same source that the widespread evidence of the importance of plants in parasitoid's host location perhaps point to the evolution of the parasitoid habitat in Hymenoptera which may have stemmed from a previous plant-parasite relationship.

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Dansk sammendrag

En undersøgelse af snyltehvepseslægten *Platygaster* for så vidt angår dens mange arters relationer til deres galmyg-værter og disses værtsplanter synes at vise eksistensen af et antal naturlige hvepse-artsgrupper, som er begrænset til galmygværter på bestemte plantefamilier. Galmyggenes slægtskabsforhold synes at have mindre betydning for hvepsenes biologi, men en del undtagelser fra denne regel forekommer. De mulige årsager til disse forhold diskuteres i artiklen, som bringer en opdateret komplet oversigt over kendte *Platygaster*-værts-/værtsplanteforhold. Det vises desuden, at de *Platygaster*-arter, hvis værter kendes, generelt foretrækker myg på plantefamilier i et forhold, der ikke er repræsentativt for den generelle fordeling af galmygarter på plantefamilier. Endelig viser en sammenligning mellem værtsvalget for *Platygaster*-slægtsgruppen og for *Synopeas*-slægts-gruppen store forskelle hvad angår både fordelingen på galmygværter og på plantefamilier.

References

- Altieri, M.A., J.R. Cure & M.A. Garcia, 1993. The role and enhancement of parasitic Hymenoptera biodiversity in agroecosystems (pp. 257-275). In: J. LaSalle & I.D. Gauld (eds.): *Hymenoptera and biodiversity*. CAB International, Wallingford. 348 pp.
- Austin, A.D. & S.A. Field, 1997. The ovipositor system of scelionid and platygastrid wasps (Hymenoptera: Platygastroidea): comparative morphology and phylogenetic implications. – *Invertebrate taxonomy* 11: 1-87.
- Barnes, H.F., 1951. Gall midges of economic importance. Vol. V: Gall midges of trees. Crosby Lockwood & Son, Ltd., London. 270 pp.
- Barnes, H.F., 1953. The biological approach to the species problem in gall midges (Dipt., Cecidomyidae). – Annales entomologici fennici 19: 2-24.

- Barnes, H.F., 1956. Gall midges of economic importance. Vol. VII: Gall midges of cereal crops. Crosby Lockwood & Son, Ltd., London. 261 pp.
- Fouts, R.M., 1924. Revision of the North American wasps of the subfamily Platygasterinae. Proceedings of the United States National Museum 63(15a): 1-145.
- Gagné, R.J., 1994. *The gall midges of the neotropical region*. Cornell University Press, Ithaca and London. 352 pp.
- Gibbons, J.R.H., 1979. A model for sympatric speciation in *Megarhyssa* (Hymenoptera: Ichneumonidae): competitive speciation. – *American Naturalist* 114: 719-741.
- Godfray, H.C.J., 1994. Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press, Princeton. 473 pp.
- Griffiths, G.C.D., 1964. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). I. General questions of taxonomy, biology and evolution. - *Beiträge zur Entomologie* 14: 823-914.
- Griffiths, G.C.D., 1966. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). II. The parasites of *Agromyza* Fallén. *Beiträge zur Entomologie* 16: 551-605.
- Griffiths, G.C.D., 1966. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). III. The parasites of *Paraphytomyza* Enderlein, *Phytagromyza* Hendel and *Phytomyza* Fallén. – *Beiträge zur Entomologie* 16: 775-951.
- Huggert, L., 1974. Taxonomical studies on the species belonging to *Urocyclops* Maneval (Hym. Proctotrupoidea, Platygastrinae). *Entomologisk Tidskrift* 95: 58-63.
- Kieffer, J.J. 1926. Scelionidae. In: Das Tierreich 48. Walter de Gruyter & Co., Berlin. 885 pp.
- MacGown, M.W., 1974. New nearctic *Platygaster* (Hymenoptera: Proctotrupoidea, Platygastridae): The *coloradensis* group. *Canadian Entomologist* 106: 213-219.
- MacGown, M.W., 1979. The Platygastridae (Hymenoptera: Proctotrupoidea) parasitic on midges (Cecidomyiidae) found on conifers in Canada and the United States. *Information Bulletin* 9, Mississippi Agricultural & Forestry Experiment Station. 144 pp.
- Memmott, J. & H.C.J. Godfray, 1993. Parasitoid webs (pp. 217-234). In: J. LaSalle & I.D. Gauld (eds.): Hymenoptera and biodiversity. CAB International, Wallingford. 348 pp.
- Quicke, D.L.J., 1997. Parasitic wasps. Chapman & Hall, London. 470 pp.
- Richards, O.W. & R.G. Davies, 1988. *Imms' general textbook of entomology*. Tenth Edition (1977, 2nd reprint 1988). Volume 2 (pp. 421-1354). Chapman and Hall, London.
- Roskam, J.C., 1986. Biosystematics of insects living in female birch catkins. IV. Egg-larval parasitoids of the genera *Platygaster* Latreille and *Metaclisis* Förster (Hymenoptera, Platygastridae). – *Tijdschrift voor Entomologie* 129: 125-140.
- Roskam, J.C., 1992. Evolution of the gall-inducing guild (pp. 34-49). In: J.D. Shorthouse & O. Rohfritsch (eds.): *Biology of insect-induced galls*. Oxford University Press, Oxford. 285 pp.
- Rübsaamen, E.H. & H. Hedicke, 1925-1939. *Die Zoocecidien, durch Tiere erzeugte Pflanzengallen Deut*schlands und ihre Bewohner. II. Band. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. 350 pp., with 42 coloured plates.
- Sands, D.P.A., 2000. Taxonomic relationships of parasitoids: poor indicators for their suitability or effectiveness as biological control agents (pp. 410-416). In: A.D. Austin & M. Dowton (eds.): *Hymenoptera: evolution, biodiversity and biological control.* CSIRO Publishing, Collingwood. 468 pp.
- Skuhravá, M., 1986. Family Cecidomyiidae (pp. 72-297). In: A. Soós (ed.): Catalogue of Palaearctic Diptera. 4. Sciaridae-Anisopodidae. Akademiae Kiado, Budapest. 441 pp.
- Vinson, S.B., 1984. Parasitoid-host relationship (pp. 205-233). In: W.J. Bell & R.T. Cardé (eds.): *Chemical ecology of insects.* Chapman and Hall, London. 524 pp.
- Vlug, H.J., 1985. The types of Platygastridae (Hymenoptera, Scelionoidea) described by Haliday and Walker and preserved in the National Museum of Ireland and in the British Museum (Natural History). 2. Keys to species, redescriptions, synonymy. – *Tijdschrift voor Entomologie* 127: 179-224.
- Vlug, H.J., 1995. Catalogue of the Platygastridae (Platygastroidea) of the world. *Hymenopterorum Catalogus*. Pars 19: 1-168.