Review and identification keys to the ichneumonid parasitoids (Hymenoptera: Ichneumonidae) of Nearctic *Choristoneura* species (Lepidoptera: Tortricidae)

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Abstract—Wasps of the family Ichneumonidae recorded as parasitoids of *Choristoneura* Lederer (Lepidoptera: Tortricidae) in North America are summarized. A total of 113 species in 45 genera and 11 subfamilies have been reliably reared from 10 species of Nearctic *Choristoneura*. Twenty-one more species are listed as possible parasitoids of Nearctic *Choristoneura*, based on rearings from Palearctic *Choristoneura* species and (or) limited introductions to North America. Well-illustrated identification keys are provided to the subfamilies, all genera, and species of 39 of the genera. The species of *Choristoneura* used as hosts by the 113 ichneumonid species are tabulated, as well as the wasps' geographic ranges. The biological characteristics of the ichneumonid subfamilies parasitizing *Choristoneura* spp. are described and compared. Erroneous *Choristoneura* host records and synonyms for all ichneumonid taxa previously recorded from Nearctic *Choristoneura* spp. are given. *Phaeogenes gaspesianus* Provancher is moved to *Dirophanes* Förster, forming *D. gaspesianus* (Provancher) **comb. nov.** New host records are *Phaeogenes cacoeciae* Viereck and *Scambus hispae* (Harris) on *C. rosaceana* (Harris), *D. gaspesianus* and *Pimpla disparis* Viereck on *C. fumiferana* (Clemens) (*P. disparis* having been introduced to New Brunswick to control the gypsy moth, *Lymantria dispar* (L.)), and *Exochus turgidus* Holmgren on *C. occidentalis* Freeman.

Résumé—On trouvera ici une rétrospective des guêpes de la famille Ichneumonidae signalées comme parasitoïdes de *Choristoneura* Lederer (Lepidoptera: Tortricidae) en Amérique du Nord. En tout, 113 espèces appartenant à 45 genres et 11 sous-familles ont été élevées de façon fiable à partir des 10 espèces nord-américaines de *Choristoneura*. Vingt-et-un espèces additionnelles sont signalées comme parasitoïdes possibles des *Choristoneura* néarctiques, d'après des élevages faits sur des *Choristoneura* paléarctiques et (ou) des introductions de portée limitée en Amérique du Nord. Des clés bien illustrées ont été dressées pour l'identification des sous-familles, de l'ensemble des genres et des espèces de 39 de ces genres. Des tableaux présentent les espèces de *Choristoneura* utilisés comme hôtes par les 113 espèces, ainsi que les répartitions géographiques des guêpes. Une description de la biologie des sous-familles d'ichneumonidés parasitoïdes de *Choristoneura* permet des comparaisons entre les groupes. Une liste est donnée des signalisations d'hôtes et des synonymies erronées pour tous les taxons d'ichneumonidés mentionnés antérieurement comme parasitoïdes de *Choristoneura* néarctiques. *Phaeogenes gaspesianus* Provancher est transféré au genre *Dirophanes* Förster, devenant *D. gaspesianus* (Provancher) **comb. nov.** De nouvelles associations d'hôtes sont signalées: *Phaeogenes cacoeciae* Viereck et *Scambus hispae* (Harris) chez *C. rosaceana* (Harris), *D. gaspesianus* et *Pimpla disparis* Viereck chez *C. fumiferana* (Clemens) (*P. disparis* a été introduit au Nouveau-Brunswick pour contrôler la spongieuse, *Lymantria dispar* (L.)) et *Exochus turgidus* Holmgren chez *C. occidentalis* Freeman.

[Traduit par la Rédaction]

Introduction

Choristoneura Lederer (Lepidoptera: Tortricidae) is a Holarctic and Oriental genus comprised of 38 species (Brown 2005), of which 17 have been recorded from the Nearctic region (Table 1). The genus is of interest because it includes the most damaging forest pest in eastern Canada, the spruce budworm, *C. fumiferana* (Clemens) (Smith *et al.* 2002), as well as other forest pests such as the western spruce budworm, *C. occidentalis* Freeman, and the

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Table 1. *Choristoneura* species in North America and the known number of their ichneumonid parasitoid species.

Choristoneura species	Common name	No. of ichneumonid species reared	Ichneumonid rearing records
C. albaniana (Walker)	None	0	None
C. argentifasciata Heppner	None	0	None
C. biennis Freeman	Two-year-cycle budworm	2	Bradley (1974)
C. carnana (Barnes and Busck)	None	0	None
C. conflictana (Walker)	Large aspen tortrix	27	Torgersen and Beckwith (1974)
C. fractivittana (Clemens)	Brokenbanded leafroller	0	None
C. fumiferana (Clemens)	Spruce budworm	66* (7 introduced)	Blais (1960, 1965); Smith *et al.* (2002)
C. lambertiana (Busck)	None	8	McGregor (1970); Stevens *et al.* (1977)
C. obsoletana (Walker)	None	0	None
C. occidentalis Freeman	Western spruce budworm	32(10?)†	McKnight (1974)
C. orae Freeman, 1967	None	1	Bradley (1974)
C. parallela (Robinson)	Spotted fireworm	1	Franklin (1948)
C. pinus Freeman	Jack pine budworm	22	Walley (1953); Allen *et al.* (1969)
C. retiniana (Walsingham)	None	7‡	Schaupp *et al.* (1991)
C. rosaceana (Harris)	Obliquebanded leafroller	47 (1 introduced)	Li *et al.* (1999)
C. spaldingiana Obratzov	None	0	None
C. zapulata (Robinson)	None	0	None

Note: Scientific names follow Brown (2005) and common names follow the Entomological Society of Canada Insect Common Names Committee (2005) list. Number of ichneumonid species reared refers to the species listed in Table 3 and does not include species listed in Table 4.

*Included in the 66 species reared from *C. fumiferana* are two questionable records (×? in Table 3). These pre-date the revision of *Choristoneura* by Freeman (1967) and no collecting locality was given for either rearing. This means that the host could be *C. fumiferana* or another species such as *C. occidentalis* described by Freeman (1967).

†Ten records of *C. occidentalis* are listed as questionable (×?) in Table 3. Nine are from "*C. fumiferana*" west of the Rocky Mountains from rearings prior to Freeman (1967). These are most likely from *C. occidentalis*, though some of the rearings were possibly from other *Choristoneura* spp., such as *C. biennis*, which also occurs west of the Rockies. The remaining questionable record is from Schaupp *et al.* (1991) (see the following footnote).

‡The seven parasitoids recorded by Schaupp *et al.* (1991) from *C. retiniana* were from mixed collections of *C. retiniana*, *C. occidentalis*, and apparent hybrids of these two species. In Table 3, six of these ichneumonid species are listed as questionably reared (×?) from *C. retiniana* but definitely reared (×) from *C. occidentalis.* This is because other studies have confirmed all the species as parasitoids of *C. occidentalis* except for *Mesochorus flaviceps* Provancher, for which Schaupp *et al.* (1991) is the only record (indicated by "×?" for both *C. occidentalis* and *C. retiniana* in Table 3).

jack pine budworm, *C. pinus* Freeman. It also includes agricultural pests such as the obliquebanded leafroller, *C. rosaceana* (Harris), which feeds on apples (Hagley and Barber 1992) and raspberries (Li *et al.* 1999), and the spotted fireworm, *C. parallela* (Robinson), which is a pest of cranberries (Franklin 1948). Research aimed at reducing the damage caused by these pests has included surveys of the parasitoids of relevant *Choristoneura* species (Table 1). In concert with these surveys, several papers have provided keys to and biological summaries of parasitoids associated with North American *Choristoneura* spp. (chalcidoid wasps, Huber *et al.* 1996; tachinid flies, O'Hara 2005). In terms of active biological control efforts, only four species of *Choristoneura* have received attention: *C. fumiferana* (Clausen 1978; Varty 1984; Smith *et al.* 2002); *C. occidentalis* (Shepherd and Cunningham 1984; Otvos *et al.* 2002); *C. pinus* (Frankenhuyzen 2002); and *C. rosaceana* (Li *et al.* 2002). Active control efforts against *C. occidentalis* and *C. pinus* have been limited to viruses and bacteria, whereas those

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Table 2. Biological characteristics of ichneumonid subfamilies parasitizing *Choristoneura* spp. summarized from Gauld (1991), Gauld *et al.* (1997, 2000, 2002*a*), and Wahl (1993*b*).

Subfamily	Larval location	Development	Mode*	Oviposition location
Anomaloninae	Endoparasitoid	Koinobiont	1°	Larva
Banchinae	Endoparasitoid	Koinobiont	1°	Larva
Campopleginae	Endoparasitoid	Koinobiont	1°	Larva
Cremastinae	Endoparasitoid	Koinobiont	1°	Larva
Cryptinae	Ectoparasitoid	Idiobiont	1° or 2°	Prepupa or pupa
Ichneumoninae	Endoparasitoid	Koinobiont; idiobiont	1°	Larva, prepupa, or pupa
Lycorininae	Ectoparasitoid?	Koinobiont	1°	Larva
Mesochorinae	Endoparasitoid	Koinobiont	2°	Larva
Metopiinae	Endoparasitoid	Koinobiont	1°	Larva
Pimplinae	Ectoparasitoid; endoparasitoid	Idiobiont	1° or 2°	Larva, prepupa, or pupa
Tryphoninae	Ectoparasitoid	Koinobiont	1°	Larva

Note: Biological characteristics pertain only to species known to parasitize *Choristoneura* spp. in North America. For references and more detailed descriptions of biology see the subfamily sections in the text.

*1° denotes a primary parasitoid and 2° denotes a hyperparasitoid.

against *C. fumiferana* and *C. rosaceana* have also included investigation and (or) introduction of parasitoids.

This paper is a review of the family with the most species known to parasitize *Choristoneura* spp. in North America — the Ichneumonidae (Hymenoptera). The purpose of this paper is to (*i*) tabulate and evaluate all records of ichneumonids parasitizing *Choristoneura* spp. in North America; (*ii*) provide illustrated keys to the subfamilies, genera, and most species reared from Nearctic *Choristoneura* spp.; (*iii*) provide general biological information concerning the ichneumonid subfamilies parasitizing *Choristoneura* spp.; and (*iv*) provide up-to-date taxonomy of the ichneumonids associated with Nearctic *Choristoneura* spp.. The use of ichneumonids as biological control agents against *Choristoneura* pests has been hindered by the difficulty of identifying the large number of species involved. It is hoped that this paper will provide biocontrol workers with the tool to allow them to use ichneumonids more effectively to help control *Choristoneura* spp. in North America. In addition, it is expected that there may be benefits to community and population ecologists, who rely on sound taxonomy to ensure correct identification of the species on which they work.

Ichneumonidae

Yu *et al.* (2005) listed 23 331 described extant species and 4929 North American species of Ichneumonidae, making it the most speciose family in the Hymenoptera worldwide (LaSalle and Gauld 1993) and the most speciose insect family in the Nearctic region (Poole and Gentili 1996). In terms of importance to biological control, ichneumonids are possibly the most important group for control of forest pests. They are also one of the main three groups for control of agricultural pests, along with their sister family, the Braconidae, and the superfamily Chalcidoidea (Hymenoptera).

Almost all ichneumonids are parasitoids, meaning that their larvae develop on or in one host and their development invariably leads to the death of the host (Waage and Greathead 1985). The effect of ichneumonids in controlling pests can be substantial. For example, in an outbreak of the pine sawfly *Neodiprion sertifer* (Geoffrey) (Diprionidae) in Hungary in 1936, the level of parasitism of *Exenterus abruptorius* (Thunberg) (Tryphonininae) was 45%–50% in repeated samples taken from over 20 million *N. sertifer* cocoons (Morris 1937).

Currently, there are 40 subfamilies (Gauld *et al.* 2002*a*; Quicke *et al.* 2005) classified in the Ichneumonidae, of which 11 have been reliably recorded from *Choristoneura* species in North America. Members of these subfamilies have different types of host–parasite interaction, including (*i*) larva feeding externally (ectoparasitoid) or internally (endoparasitoid); (*ii*) larval feeding commencing immediately (idiobiosis) or following a delay that allows the host to develop (koinobiosis) (Askew and Shaw 1986); (*iii*) larva feeding on the *Choristoneura*

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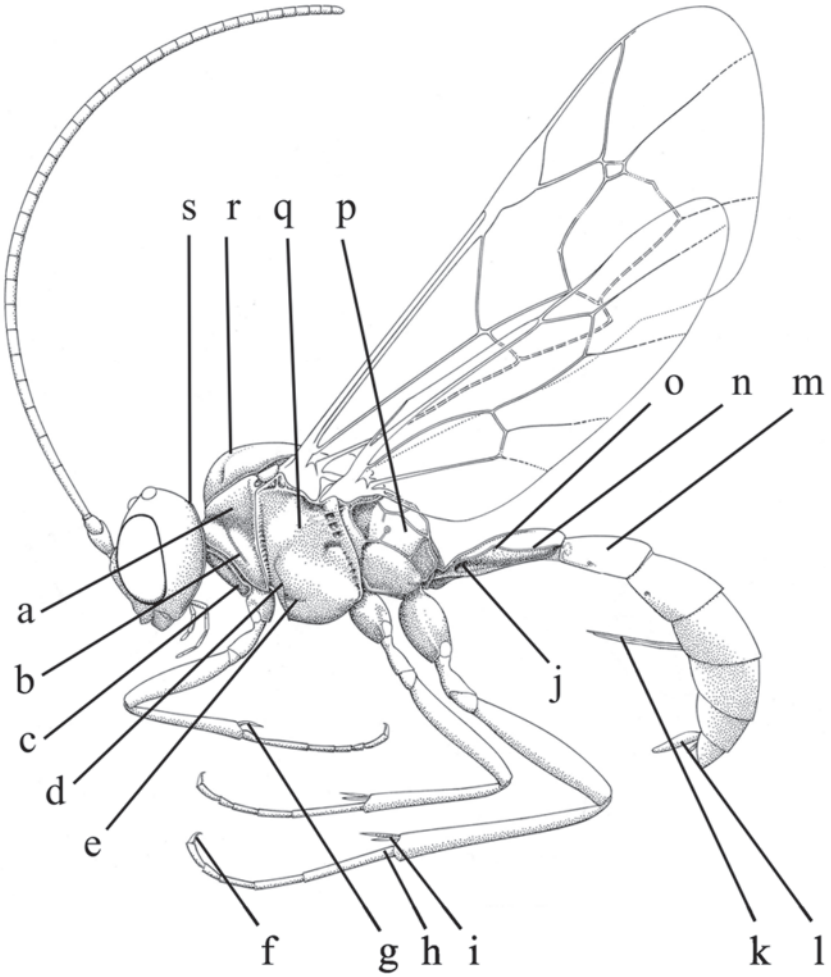
Fig. 1. Ichneumonid wasp, lateral view: a, pronotum; b, epomia; c, propleuron; d, epicnemial carina; e, sternaulus; f, hind tarsal claw; g, fore tibial spur; h, basal segment of the hind tarsus; i, hind tibial spur; j, glymma; k, ovipositor; l, ovipositor sheaths; m, tergite of metasomal segment 2 (T2); n, dorsolateral carina of tergite 1 (T1); o, spiracle of T1; p, propodeum; q, mesopleuron; r, notaulus of the mesoscutum; s, occipital carina.



host (primary parasitism) or on another parasitoid in the *Choristoneura* host (hyperparasitism); (*iv*) development in a *Choristoneura* species that requires another parasitoid species (obligate hyperparasitism) or does not (facultative hyperparasitism); and (*v*) oviposition into different host stages (larva, prepupa, or pupa). This information is summarized in Table 2.

Materials and methods

The ichneumonids included as parasitoids of *Choristoneura* spp. in North America were determined by means of the following criteria: (*i*) examination of reared specimens in the Canadian National Collection of Insects, Ottawa, Ontario, Canada (CNC), American Entomological Institute, Gainesville, Florida, United States of America (AEIC), and Northern Forest Research Centre, Edmonton, Alberta, Canada (NFRC); (*ii*) identification of reared ichneumonids from recent surveys of *C. occidentalis* in British Columbia, *C. fumiferana* in Ontario, and *C. rosaceana* in British Columbia and Quebec; (*iii*) reference to the literature. In the case of literature references, the validity of a record was assessed on the basis of such criteria as a knowledge of host ranges for related taxa, whether or not voucher specimens were deposited and could be examined, and the relative level of authority of determinations of host and parasitoid species.

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Fig. 2. Ichneumonid wasp fore wing (a) and hind wing (b).

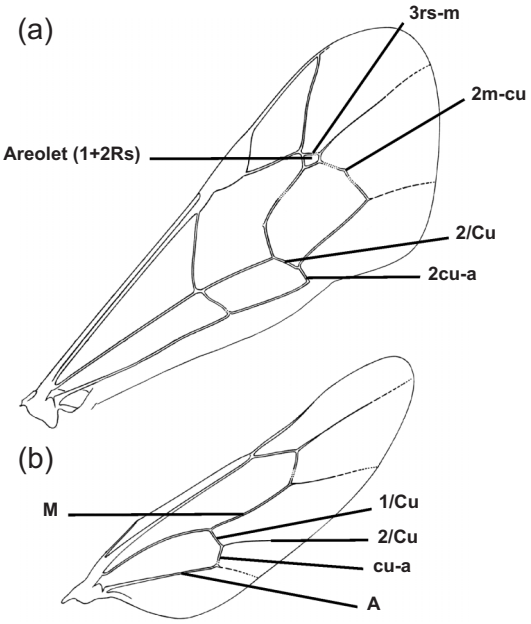
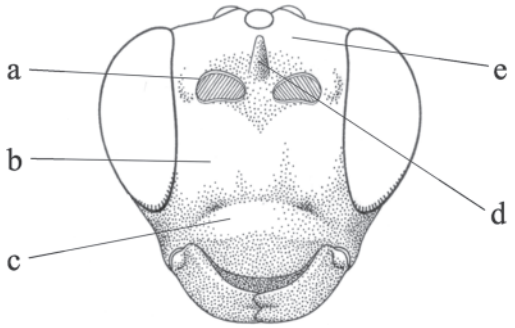


Fig. 3. Ichneumonid wasp head, anterior view: a, antennal socket (torulus); b, supraclypeal area; c, clypeus; d, supra-antennal horn; e, supra-antennal area.



All morphological terms follow Townes (1969) with the following modifications: hypostomal carina for "oral carina", supra-antennal area for "frons", supraclypeal area for "face", gena for "temple", occiput for "postocciput", malar space for "cheek", epicnemial carina for "prepectal carina", laterotergites for "epipleura", gonoforceps for "claspers", and hypopygium for "subgenital plate". The term mesosoma is used for the body region that includes the thorax and the first abdominal segment, the propodeum. The term metasoma is used for the apparent abdomen, with MS1, MS2, *etc.* referring to metasomal segments 1, 2, *etc.*, T1, T2, *etc.* referring to the tergites of metasomal segments 1, 2, *etc.*, and S1 referring to the sternite of metasomal segment 1. Generalized ichneumonid morphology is shown in Figures 1–4. Wing-venation terms (Fig. 2) follow the Comstock–Needham system as updated by Ross (1936) and incorporate the recommendations of Goulet and Huber (1993) except for the naming of the vein that forms the distal edge of fore wing cell 1 + 2Rs (the "areolet" of Townes 1969). This vein is of uncertain origin and is here referred to as vein 3rs-m in conformity with Wahl and Gauld (1998). Abscissae of veins are denoted as follows: 1/Cu means the first abscissa of Cu, 2/Cu the second abscissa, *etc.* The following terms for specialized structures are defined: epomia: a raised ridge (carina) on the pronotum (Figs. 1*b*, 9*c*); glymma: a lateral depression sub-basally on T1 (Figs. 1*j*, 12*f*); notaulus: a longitudinal groove sublaterally on the mesoscutum (Figs. 1*r*, 10*f*); sternaulus: a longitudinal groove subventrally on the mesopleuron (Figs. 1*e*, 9*f*); thyridium: a scarlike transverse depression subanteriorly on T2 (Figs. 8*f*, 12*d*). Line drawings were originally commissioned by Henry Townes in the 1950s and 1960s. I could not add scale bars because they were not present on the original drawings and intraspecific size variation of many species precluded accurate estimation.

Fig. 4. Ichneumonid wasp propodeum (a–d, i–j) and first metasomal segment (e–h), dorsal view: a, medial longitudinal carina; b, spiracle; c, lateral longitudinal carina; d, pleural carina; e, dorsolateral longitudinal carina; f, spiracle; g, dorsal longitudinal carina; h, anterolateral projection; i, posterior transverse carina; j, anterior transverse carina.

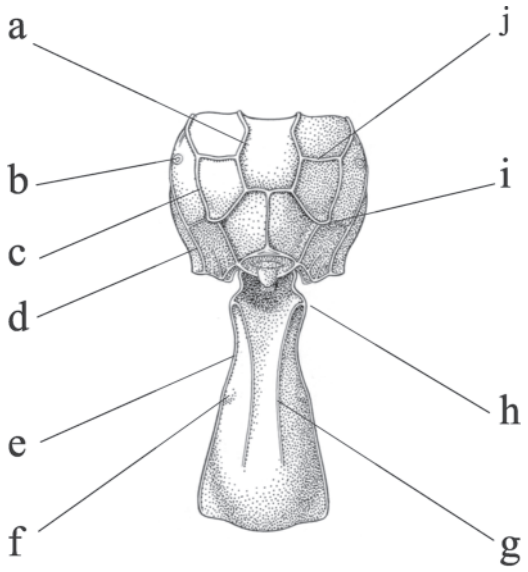


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Table 3. Alphabetical list of ichneumonids reared from or introduced to control *Choristoneura* spp. in North America.

	Choristoneura host[†]											
Ichneumonid species*	bi	co	fu	la	oc	or	pa	pi	re	ro	Region[‡]	Reference(s)
Acropimpla alboricta (Cresson) (Pimplinae)	×	–	×	–	×?	–	–	–	–	×	Widespread	Bradley 1974; Leonard and Simmons 1974; Carolin and Coulter 1959; Carlson 1979
A. pronexus Townes[H]	–	–	×	–	–	–	–	×	–	–	Wyo., N.H., B.C., N.B.	Bradley 1974; Allen *et al.* 1969
Agrypon alpinum (Davis) (Anomaloninae)	–	–	–	–	–	–	–	×	–	–	Widespread	Dixon and Benjamin 1963
A. dioryctriae Dasch	–	–	×	–	×?	–	–	–	–	–	Widespread	Dasch 1984 (reared east + west)
A. prismaticum (Norton)	–	–	×	–	–	–	–	–	–	–	Widespread	Dasch 1984
A. provancheri (Dalle Torre)	–	×	–	–	–	–	–	–	–	–	B.C., N.S., Alaska, Kans.	Torgersen and Beckwith 1974
A. varitarsum (Wesmael)	–	–	–	–	×	–	–	–	–	–	Widespread	Dasch 1984 (reared in west only)
Apechthis annulicornis (Cresson) (Pimplinae)	–	–	×	–	–	–	–	–	–	×	Widespread	Dowden *et al.* 1950; Townes and Townes 1960
A. ontario (Cresson)	–	×	×	–	×	–	–	×	–	×	Widespread	Bradley 1974; Cappuccino *et al.* 1998; Hamel 1977; Walley 1953; Li *et al.* 1999
A. picticornis (Cresson)	–	×	×	–	–	–	–	–	–	×	Widespread	Bradley 1974; Torgersen and Beckwith 1974
Apophua simplicipes (Cresson) (Banchinae)	–	–	–	–	–	–	–	–	–	×	Widespread	Cossentine *et al.* 2004
Campoplex mellipes (Provancher) (Campopleginae)	–	–	×	–	–	–	–	–	–	–	Widespread	Blais 1960
Cephaloglypta murinanae (Bauer) (Banchinae)	–	–	I	–	–	–	–	–	–	–	(Ont., N.B.)	Carlson 1979
Chorinaeus excessorius Davis (Metopiinae)	–	–	×	–	–	–	–	–	–	×	Widespread	Townes and Townes 1959
C. subcarinatus Holmgren	–	–	×	–	–	–	–	–	–	–	Widespread	Townes and Townes 1959
Dirophanes gaspesianus (Provancher) (Ichneumoninae)	–	–	×	–	–	–	–	–	–	–	Widespread	This study (Ont., Que.)
D. maculicornis (Stephens)	–	×	×	×	×	–	–	×	–	–	B.C., N.L., Ore., N.Y., (Ont.)	Torgersen and Beckwith 1974; Blais 1960; Stevens *et al.* 1977; McKnight 1974; Nealis 1991; Carlson 1979
Dusona seamansi (Viereck) (Campopleginae)	–	×	–	–	–	–	–	–	–	–	B.C., Man., Colo.	Walley 1940
Enytus eureka (Ashmead) (Campopleginae)	–	–	–	–	–	–	–	–	–	×	B.C., Alta., Idaho, Calif.	Coop *et al.* 1989

Table 3 (*continued*).

Ichneumonid species*	*Choristoneura* host†										Region‡	Reference(s)
	bi	co	fu	la	oc	or	pa	pi	re	ro		
E. montanus (Ashmead)	–	–	×	–	×	–	–	–	×?	–	Ont., N.B., Ore., Mont.	McGugan and Blais 1959; Niwa *et al.* 1987; Schaupp *et al.* 1991
Erigorgus stenotus Dasch (Anomaloninae)	–	×	–	–	–	–	–	–	–	–	B.C., Maine, Calif., N. Mex.	Dasch 1984
Exeristes comstockii (Cresson) (Pimplinae)	–	–	×?	–	–	–	–	×	–	–	Widespread	Townes and Townes 1960; Walley 1953
Exochus albifrons Cresson (Metopiinae)	–	–	–	–	–	–	–	×	–	×	Widespread	Allen *et al.* 1969; Bradley 1974
E. nigripalpis Thomson	×	–	×	×	×	×	–	×	×?	×	Widespread	Bradley 1974; Blais 1960; Stevens *et al.* 1977; Schaupp *et al.* 1991
E. turgidus Holmgren	–	–	–	–	×	–	–	–	–	–	Widespread	This study
E. washingtonensis (Davis)	–	×	–	–	–	–	–	–	–	–	Alaska, N. Mex., Que., W. Va.	Torgersen and Beckwith 1974
Gelis tenellus (Say) (Cryptinae)[H]	–	–	×	–	–	–	–	×	–	–	Widespread	Wilkes and Anderson 1947; Walley 1953
Glypta alberta Dasch (Banchinae)	–	–	–	–	–	–	–	–	–	×	Y.T., Wyo.	Dasch 1988
G. albonotata Dasch	–	–	×	–	–	–	–	–	–	×	Widespread	Dasch 1988
G. choristoneurae Dasch	–	–	×	–	–	–	–	–	–	–	Alta., Ont.	Dasch 1988
G. conflictanae Dasch	–	×	×	–	–	–	–	–	–	×	Alaska, N.L., Calif., Nebr.	Dasch 1988
G. erratica Cresson	–	×	×	–	–	–	–	×	–	×	Widespread	Dasch 1988
G. fumiferanae (Viereck)	–	×	×	×	×	–	–	×	×?	×	Widespread	Prentice 1955; Dasch 1988; Schaupp *et al.* 1991; Hagley and Barber 1992
G. imitator Dasch	–	–	–	–	–	–	–	×	–	–	Alta., N.L., Wis., Del.	Dasch 1988
G. infrequens Dasch	–	–	–	–	–	–	–	–	–	×	Idaho	Dasch 1988
G. longipalpus Dasch	–	–	×	–	–	–	–	–	–	–	Y.T., Alta., Sask., N.L.	Dasch 1988
G. longiventris Cresson	–	–	–	–	–	–	–	–	–	×	Wis., Conn., Que., N.C.	Dasch 1988
G. partita Dasch	–	–	×	–	–	–	–	–	–	–	Ont., Mich.	Dasch 1988
G. pilula Dasch	–	–	×	–	–	–	–	–	–	–	Que.	Dasch 1988
G. rufiscutellaris Cresson	–	×	–	–	–	–	–	–	–	–	Widespread	Dasch 1988
G. rufofasciata Cresson	–	–	×	–	–	–	–	–	–	×	B.C., N.L., Calif., N.J.	Dasch 1988
G. tortricis Dasch	–	–	–	–	–	–	–	–	–	×	B.C., N.L.	Dasch 1988
G. transversa Dasch	–	–	×	–	–	–	–	–	–	–	Ont., Conn.	Dasch 1988

Table 3 (*continued*).

Ichneumonid species*	*Choristoneura* host†										Region‡	Reference(s)
	bi	co	fu	la	oc	or	pa	pi	re	ro		
G. tricincta Provancher	–	–	×	–	–	–	–	×	–	×	Alaska, N.S., Ore., N.Y.	Dasch 1988
G. variegata Dasch	–	–	–	–	–	–	–	–	–	×	B.C., Calif., Mont.	Cossentine *et al.* (2007)
Hercus fontinalis (Holmgren) (Tryphoninae)	–	×	×	–	–	–	–	–	–	×	Widespread	Gupta 1984; Townes *et al.* 1992
Habronyx aclerivorus (Rohwer) (Anomaloninae)	–	–	×	–	×	–	–	–	–	×	Widespread	Dasch 1984
Hyposoter annulipes (Cresson) (Campopleginae)	–	×	–	–	–	–	–	–	–	–	Widespread	Torgersen and Beckwith 1974
Ichneumon audax Cresson (Ichneumoninae)	–	–	×	–	×	–	–	–	–	–	B.C., Colo., N.Y.	Dowden *et al.* 1950; Wilkes *et al.* 1948; this study
I. gestuosus Cresson	–	–	×	–	–	–	–	–	–	–	B.C., Ont., Maine	Bradley 1978; Carlson 1979
Ischnus inquisitorius (Müller) (Cryptinae)	–	×	–	–	×?	–	–	–	–	×	Widespread	Townes and Townes 1962; Carolin and Coulter 1959; Doğanlar and Beirne 1978
I. minor Townes	–	–	–	–	×?	–	–	–	–	–	Widespread	Townes and Townes 1962
Isoperus coelebs (Walsh) (Pimplinae)	–	–	×	–	–	–	–	–	–	–	Widespread	Dowden *et al.* 1950
I. stercorator (Fabricius)	–	–	–	–	–	–	–	–	–	×	Widespread	Townes and Townes 1960
Itoplectis conquisitor (Say) (Pimplinae)[P or H]	–	×	×	×	×	–	×	×	–	×	Widespread	Bradley 1974; Stevens *et al.* 1977; McKnight 1974; Franklin 1948; Nealis 1991
I. evetriae Viereck	–	–	×	–	–	–	–	–	–	–	Widespread	Townes and Townes 1960
I. maculator (Fabricius)[P or H]	–	–	I	–	–	–	–	–	–	–	(Ont., Ore.)	Carlson 1979
I. quadricingulata (Provancher)[P or H]	–	×	×	×	×	–	–	×	–	×	Widespread	Torgersen and Beckwith 1974; Bradley 1974; McGregor 1970; McKnight 1974; Li *et al.* 1999
I. vesca Townes	–	–	×	–	×	–	–	–	–	–	Alaska, N.L., N. Mex., Maine	Bradley 1974; McKnight 1974
I. viduata (Gravenhorst)	–	–	–	–	×?	–	–	–	–	×	Alta., Sask., N.W.T., Calif., N. Mex., Wyo.	Carolin and Coulter 1959; Townes and Townes 1960
Lissonota acrobasidis (Ashmead) (Banchinae)	–	×	×	–	–	–	–	–	–	×	Widespread	Townes and Townes 1978
Lycorina albomarginata (Cresson) (Lycorininae)	–	–	–	–	–	–	–	–	–	×	Man., N. Mex., Maine, Ga.	Carlson 1979

Table 3 (*continued*).

Ichneumonid species*	*Choristoneura* host†										Region‡	Reference(s)
	bi	co	fu	la	oc	or	pa	pi	re	ro		
Mastrus laplantei Mason (Cryptinae)	–	–	×	–	–	–	–	–	–	–	Alaska, B.C., Man., N.L.	Carlson 1979
Meniscomorpha mirabilis (Cresson) (Banchinae)	–	–	–	–	–	–	–	–	–	×	Widespread	Townes and Townes 1978
Mesochorus argaleus (Dasch) (Mesochorinae)[H]	–	–	–	–	–	–	–	×	–	×	Y.T., Que., Ore., S.C.	Dasch 1971
M. flaviceps Provancher[H]	–	–	×	–	×?	–	–	×	×?	–	Widespread	Dasch 1971; Schaupp *et al.* 1991
M. gemellus Holmgren[H]	–	–	×	–	×	–	–	–	×?	–	B.C., N.L., Calif., N.Y.	Dasch 1971; Niwa *et al.* 1987; Schaupp *et al.* 1991
M. lanceolatus (Dasch)[H]	–	–	×	–	–	–	–	–	–	–	B.C., N.B., Wis., N.Y.	Dasch 1971
M. nuncupator (Panzer)[H]	–	–	–	–	–	–	–	×	–	–	Widespread	Dasch 1971
M. sylvarum Curtis[H]	–	–	×	–	–	–	–	–	–	×	Widespread	Blais 1965; Dasch 1971
M. uniformis Cresson[H]	–	–	×	–	–	–	–	–	–	–	Widespread	Dasch 1971
Oedemopsis scabricula (Gravenhorst) (Tryphoninae)	–	–	–	–	–	–	–	–	–	I	(B.C.)	Loan and Doğanlar 1980
Orgichneumon calcatorius (Thunberg) (Ichneumoninae)	–	–	×	–	–	–	–	–	–	–	B.C., N.S., Wis., Fla.	Bradley 1978
Parania geniculata (Holmgren) (Anomaloninae)	–	–	×	×	–	–	–	–	–	–	Widespread	Dasch 1984; Stevens *et al.* 1977
Patrocloides montanus (Cresson)(Ichneumoninae)	–	–	×	–	–	–	–	–	–	–	Widespread	Bradley 1978
P. perluctuosus (Provancher)	–	–	×	–	–	–	–	–	–	–	B.C., N.L., N.H.	Bradley 1978
Phaeogenes cacoeciae (Viereck) (Ichneumoninae)	–	×	–	–	–	–	–	–	–	–	Alaska, Man., Wyo., N.Y.	Torgersen and Beckwith 1974; this study (*rosaceana* B.C., N.Y.)
Phytodietus burgessi (Cresson) (Tryphoninae)	–	×	–	–	–	–	–	–	–	×	Widespread	Loan 1981; Prentice 1955
P. conflictanae Loan	–	×	–	–	–	–	–	–	–	–	B.C., Sask., Calif., Nebr.	Loan 1981
P. fumiferanae Rohwer	–	–	I	×	×	–	–	–	×?	–	B.C., Mont., Ariz., N. Mex., (Ont., Que., Maine, N.Y.)	Carlson 1979; Schaupp *et al.* 1991; Wilkes 1946: introduced and established in east
P. improbanae Loan	–	–	–	–	×?	–	–	–	–	–	Widespread	Loan 1981

Table 3 (*continued*).

Ichneumonid species*	*Choristoneura* host†										Region‡	Reference(s)
	bi	co	fu	la	oc	or	pa	pi	re	ro		
P. pleuralis Cresson	–	–	–	–	–	–	–	–	–	×	Widespread	Loan 1981
P. polyzonias Forster	–	–	I	–	–	–	–	–	–	–	(Ont.)	Carlson 1979
P. vulgaris Cresson	–	×	×	–	–	–	–	–	–	×	Widespread	Loan 1981; Hagley and Barber 1992
Pimpla aequalis Provancher (Pimplinae)[P or H]	–	–	–	×	–	–	–	–	–	×	Ont., N.S., Colo., Fla.	Stevens *et al.* 1977; Hagley and Barber 1992
P. disparis Viereck	–	–	I	–	–	–	–	–	–	–	(Ont., Va., Nebr.)	Kamijo 1973; Schaefer *et al.* 1989; this study
P. pedalis Cresson	–	×	×	–	×	–	–	×	–	–	B.C., N.L., Calif., Md.	Torgersen and Beckwith 1974; Bradley 1974; McKnight 1974
P. punicipes (Cresson)	–	–	–	–	–	–	–	–	–	×	Pa., Tex.	Biddinger *et al.* 1994
P. sanguinipes Cresson	–	–	–	–	×?	–	–	–	–	–	B.C., Calif., Mont., Tex.	Townes 1944
P. turionellae (Linnaeus)	–	–	I	–	–	–	–	–	–	–	(N.S., Ont., Conn., Idaho, Mass., Minn., N.J., N.Y.)	Graham 1958; Bartlett *et al.* 1978
Pristomerus baumhoferi Cushman (Cremastinae)	–	–	–	–	×	–	–	–	–	–	B.C., Sask., Calif., Alaska	Dasch 1979
Scambus atrocoxalis (Ashmead) (Pimplinae)	–	–	–	–	×?	–	–	–	–	–	Alaska, N.W.T., B.C., N.L.	Townes 1944
S. brevicornis (Gravenhorst)	–	–	–	–	–	–	–	–	–	×	B.C., N.L., Calif., N.J.	Carlson 1979; Li *et al.* 1999
S. buolianae (Hartig)	–	–	I	–	–	–	–	–	–	–	(Ont.)	Carlson 1979
S. canadensis Walley	–	×	×	–	–	–	–	–	–	–	Alaska, Ore., Ont., N.S.	Bradley 1974
S. decorus Walley	–	–	×	–	–	–	–	–	–	×	Alaska, B.C., N.L., Wis., N.H., Maine	Bradley 1974; Doğanlar and Beirne 1978
S. hispae (Harris)[P or H]	–	×	×	–	×	–	–	×	–	×	Widespread	Bradley 1974; McKnight 1974; this study for *C. rosaceana*
S. planatus (Hartig)	–	–	×	–	–	–	–	–	–	–	Alaska, B.C., Ont., N.S.	Bradley 1974
S. transgressus (Holmgren)	–	–	–	–	×	–	–	–	–	–	B.C., Calif., Idaho, Mont.	Carlson 1979
S. vesicarius (Ratzeburg)	–	–	–	–	–	–	–	–	–	×	B.C., Que., Calif., Minn.	Hagley and Barber 1992

Table 3 (*concluded*).

Ichneumonid species*	*Choristoneura* host†										Region‡	Reference(s)
	bi	co	fu	la	oc	or	pa	pi	re	ro		
Sinophorus teratis (Weed) (Campopleginae)	–	–	×?	–	–	–	–	–	–	–	B.C., N.L., Idaho, Nebr., Wis., Maine, N.Y., Ga.	Sanborne 1984
Sphelodon phoxopteridis (Weed) (Banchinae)	–	–	–	–	–	–	–	–	–	×	B.C., Que., Minn., Fla.	Biddinger *et al.* 1994
Syspasis tauma (Heinrich) (Ichneumoninae)	–	–	×	–	–	–	–	–	–	–	Sask., Que., Minn., S.C.	Heinrich 1961*a*
Temelucha evetriae (Cushman) (Cremastinae)	–	–	–	–	×	–	–	–	–	–	Wash., Calif., S.D., Tex.	Shea *et al.* 1984
T. forbesi (Weed)	–	–	×	–	–	–	–	×	–	–	Sask., P.E.I., N.D., Fla.	Dasch 1979
T. platynotae (Cushman)	–	–	–	–	–	–	–	×	–	–	Widespread	Dasch 1979
T. rhyacioniae (Cushman)	–	–	–	–	×	–	–	×	–	–	Alta., Que., Mont., Colo., Maine, W. Va., Ga.	Allen *et al.* 1969; Shea *et al.* 1984
Theronia atalantae (Poda) (Pimplinae)$^{P\ or\ H}$	–	–	×	–	×?	–	–	–	–	–	Widespread	Dowden *et al.* 1950; Carolin and Coulter 1959
Tranosema rostrale (Brischke) (Campopleginae)	–	×	×	–	×	–	–	–	–	×	B.C., Ont., Que., N.B., Colo., Maine, N.Y.	Cusson *et al.* 1998; Blais 1960; McKnight 1974
T. tenuifemur (Walley)	–	–	×	–	–	–	–	–	–	–	B.C., Ont., N.B.	Miller and Renault 1976
Tranosemella praerogator (L.) (Campopleginae)	–	×	–	–	×	–	–	–	×?	×	Alaska., B.C., Calif., Tex.	Torgersen and Beckwith 1974; Schaupp *et al.* 1991; Li *et al.* 1999
Triclistus emarginalus (Say) (Metopiinae)	–	–	–	–	–	–	–	–	–	×	Widespread	Bradley 1974
Trieces crassipes Walley (Metopiinae)	–	×	–	–	–	–	–	–	–	–	B.C., Ont., Que., Sask.	Bradley 1974

Note: Synonyms of species names are listed in Appendix A.

*A superscript "H" denotes an obligate hyperparasitoid and "P or H" a facultative hyperparasitoid.

†Host names are abbreviated as follows: bi, *C. biennis*; co, *C. conflictana*; fu, *C. fumiferana*; la, *C. lambertiana*; oc, *C. occidentalis*; or, *C. orae*; pa, *C. parallela*; pi, *C. pinus*; re, *C. retiniana*; and ro, *C. rosaceana*. "×" denotes a rearing record; "–" denotes a lack of rearing record; "I" denotes an introduced (either deliberately or accidentally) species; and "×?" denotes a reared species, but the host species is in question.

‡A "widespread" species is found throughout North America; otherwise, provinces and states are the most westerly, easterly, *etc.* regions recorded. Regions in parentheses are areas to which a species has been introduced or has subsequently spread.

Table 4. Holarctic ichneumonid species reared from *Choristoneura* spp. in the Palaearctic region, but not yet reared from *Choristoneura* spp. in the Nearctic region.

Ichneumonid species	Palaearctic host	Nearctic range*	Reference(s)
Apechthis compunctor (Linnaeus) (Pimplinae)	*C. hebenstreitella* (Müller)	Mass. (I for *Lymantria dispar* Linnaeus)	Horstmann 1971; Crossman and Webber 1924
Apechthis quadridentata (Thomson)	*C. murinana* (Hübner)	Ont., Que. (I for *C. fumiferana*)	Carlson 1979
Apechthis rufata (Gmelin)	*C. hebenstreitella*; *C. murinana*	Ont. (I, only 18 specimens for *C. fumiferana*)	Carlson 1979
Campoplex rufipes Gravenhorst (Campopleginae)	*C. murinana*	Eastern Canada (I, only 3 specimens for *C. fumiferana*)	Bucher 1953; Bartlett *et al.* 1978
Chorinaeus funebris (Gravenhorst) (Metopiinae)	*C. murinana*	Widespread	Mills and Kenis 1991
Coelichneumon deliratorius (Linnaeus) (Ichneumoninae)	*C. murinana*	B.C., Que., Maine, Ga.	Schimitschek 1964
Diadegma armillatum (Gravenhorst) (Campopleginae)	*C. murinana*	Ore. (I for *Yponomeuta malinella* Zeller)	Franz 1941; Unruh *et al.* 2003
Diadegma chrysostictos (Gmelin)	*C. diversana* (Hübner, 1817); *C. murinana*	Ont., Que., Mich., Conn. (I, only 3 specimens for *C. fumiferana*)	Schimitschek 1964; Bartlett *et al.* 1978
Dolichomitus terebrans (Ratzeburg) (Pimplinae)	*C. murinana*	B.C., Que., Nfld., Calif., N.C.	Zwölfer 1961
Exeristes roborator (Fabricius) (Pimplinae)	*C. murinana*	Ont., Que., Calif., Fla. (I for *Ostrinia nubilalis* Hübner)	Wiackowski 1957; Baird 1925
Gregopimpla inquisitor (Scopoli) (Pimplinae)	C. murinana	Ont. (I, only 38 specimens for *C. fumiferana*)	Schimitschek 1964; Carlson 1979
Herpestomus brunnicornis (Gravenhorst) (Ichneumoninae)	*C. murinana*	B.C., Wash. (I for *Y. malinella*)	Zwölfer 1956; Cossentine and Kuhlmann 2002
Hypsicera femoralis (Geoffrey) (Metopiinae)	*C. murinana*	Alaska, Que., Calif., N.C.	Bucher 1953
Liotryphon strobilellae (Linnaeus) (Pimplinae)	*C. murinana*	B.C., Que., Calif., N.Y.	Čapek *et al.* 1982 (cited from Yu *et al.* 2005)
Lissonota folii Thomson (Banchinae)	*C. murinana*	B.C., Nfld., Calif., Mass.	Mills and Kenis 1991
Pimpla aquilonia Cresson (Pimplinae)	*C. diversana*	B.C., Nfld., Alaska, Tenn.	Momoi 1973
Pimpla rufipes (Miller)	*C. murinana*	Mass. (I for *L. dispar*)	Zwölfer 1961; Coulson *et al.* 1986

Table 4 (*concluded*).

Ichneumonid species	Palaearctic host	Nearctic range*	Reference(s)
Scambus inanis (Schrank) (Pimplinae)	*C. murinana*	B.C., N.W.T., N.S., Neb.	Aubert 1969
Sinophorus turionum (Ratzeburg) (Campopleginae)	*C. murinana*	Ont., Ohio, N.Y. (I for *Rhyacionia buoliana* (Denis and Schiffermüller) and *O. nubilalis*)	Pisica and Petcu 1967 (cited from Yu *et al.* 2005); Coppel and Arthur 1954
Temelucha decorata (Gravenhorst)	*C. murinana*	N.Y.	Cushman 1928
Tranosemella coxalis (Brischke)	*C. murinana*	Alaska, Alta., Que., Nfld.	Schimitschek 1943 (cited from Yu *et al.* 2005)

*"I" denotes species that were introduced to the Nearctic region.

Overview of ichneumonids reared from Nearctic *Choristoneura* spp.

Ten *Choristoneura* species have been identified as hosts for ichneumonids in North America. Table 1 gives the number of ichneumonid species reared from each of the *Choristoneura* species, the common names of the *Choristoneura* species, and references to selected host-parasitoid rearing literature and (or) review articles. The number of ichneumonid species reared from each host species ranges from only 1 for *C. orae* Freeman and *C. parallela* up to 66 species for *C. fumiferana*. Huber *et al.* (1996) listed 31 ichneumonid species from *C. fumiferana*, therefore this study more than doubles this figure, as well as confirming ichneumonid rearing records from *C. biennis* Freeman, *C. orae*, and *C. parallela* (all omitted from Huber *et al.* 1996).

In total, 113 ichneumonid species in 45 genera have been reliably reared from and (or) introduced to control *Choristoneura* species in North America. Table 3 lists the 113 species, known rearings from *Choristoneura* spp., the geographic range for each wasp, and selected references. References listed include one or more host records for each ichneumonid, but not all relevant references are cited in all cases. Yu *et al.* (2005) and Yu and Horstmann (1997) provide an exhaustive list of references. Twenty-one additional species are listed in Table 4. These species may parasitize *Choristoneura* spp. in North America but have not yet been reliably reared. They are included in Table 4 for three reasons: (*i*) they are native to both the Nearctic and Palaearctic regions but have been reared from *Choristoneura* spp. only in the Palaearctic region; (*ii*) they are known to parasitize *Choristoneura* spp. in the Palaearctic region and were introduced to North America to control other pests, but have yet to be reared from *Choristoneura* spp. in North America; (*iii*) they were introduced to North America to control *Choristoneura* spp. but were introduced in such small numbers that there was little or no chance of establishment. Table 5 lists rearing records from the literature that are likely incorrect, based on errors in identifying wasp or host. This table does not include errors that are due to changes in host nomenclature (*e.g.*, western rearings prior to Freeman 1967), which are corrected in Table 3 where verification was possible. Appendix A provides a list of synonyms of ichneumonid taxa reared from Nearctic *Choristoneura* spp., and is included because of the many synonyms that may have been used in

Table 5. Erroneous records of ichneumonid rearing from Nearctic *Choristoneura* species.

Ichneumonid species	Stated host	Reference	Reason to reject
Cylloceria melancholica (Gravenhorst) (Cylloceriinae)	*C. fumiferana*	Dasch 1992	Cylloceriinae reliably reared from Tipulidae (Diptera) only
Dichrogaster crassa (Provancher) (Cryptinae)	*C. pinus*	Dixon and Benjamin 1963 (as *Otacustes*)	Genus parasitizes Chrysopidae (Neuroptera)
Perilissus coloradensis (Ashmead) (Ctenopelmatinae)	*C. occidentalis*	McKnight 1974	Ctenopelmatinae almost always on sawflies (Hymenoptera)
Pyracmon hyalinus (Provancher) (Campopleginae)		Walley 1953 (as *Limneria*)	Genus likely only parasitizes Coleoptera
Syrphoctonus sp. (Diplazontinae)	*C. pinus*	Dixon and Benjamin 1963	Diplazontinae are parasitoids of Diptera
Woldstedtius flavolineatus (Gravenhorst) (Diplazontinae)	*C. fumiferana*	Dasch 1964	Diplazontinae are parasitoids of Diptera

earlier literature. Finally, identification keys for the species of 39 of the 45 genera reared from Nearctic *Choristoneura* spp. are provided below (see the introduction to the keys for details regarding the remaining 6 genera).

Keys to the ichneumonids reared from Nearctic *Choristoneura* spp.

The following keys will identify North American ichneumonid species that have reliable host records from *Choristoneura* spp., except for those of the following six genera: *Agrypon* Förster (5 species), *Glypta* Gravenhorst (18 species), *Temelucha* Förster (4 species), *Mesochorus* Gravenhorst (7 species), *Scambus* Hartig (9 species), and *Phytodietus* Gravenhorst (7 species). Townes and Townes (1962) provided reliable keys to the Nearctic species of *Scambus*. Because males and females of *Scambus* need to be keyed out separately and many figures are required for species identification, the information is not repeated here but readers are referred to those keys. For the other five genera, the existing species keys are difficult, if not impossible, to use without an extensive reference collection and (or) type material. Revisions of those keys, and (or) the genera, are required before species in these genera can be reliably identified. References to these genera are provided in the subfamily sections of the key should the reader wish to attempt species identifications; however, this is not recommended because it could easily lead to incorrect identifications and the addition of further erroneous species records to the literature.

Key to ichneumonid subfamilies reared from Nearctic *Choristoneura* spp.

1. Areolet large and diamond-shaped (rhombic) (Fig. 5*a*) **and** supraclypeal area ventral to antennae, with transverse ridge extending between eyes (Fig. 7*a*); fore wing length less than 6 mm. *Female*: ovipositor long and needle-like, thin, and parallel-sided from base to near apex with sharp point, without a strong dorsal subapical notch or ventral apical ridges (sheaths may need to be separated from ovipositor to see notch and ridges). *Male*: genitalia with gonoforceps modified into two long, hairless, rod-like stylets apically (Fig. 17*b*) (not to be confused with female ovipositor sheaths, which bear hairs and cover a medial ovipositor) . . . . . Mesochorinae (*Mesochorus*) (p. 32)

— Areolet various: open (vein 3rs-m absent) (Fig. 5*c*), pentagonal (Fig. 5*b*), triangular (Fig. 5*e*), irregularly quadrangular (Fig. 5*f*) or, rarely, if more or less diamond-shaped, then supraclypeal area without a ridge (as in Fig. 4*b*); fore wing lengths various: longer than 6 mm in some specimens. *Female*: ovipositor sometimes needle-like but stout in some specimens, with ventral ridges apically (Fig. 16*a*) or with a dorsal subapical notch (Fig. 16*b*). *Male*: genitalia with gonoforceps wide and rounded apically and bearing hairs 2

2(1). Metasomal T1 with spiracle posterior to middle (Fig. 12*e*), in dorsal view either petiolate (slender anteriorly and medially but with posterior part strongly widened) (Fig. 13*a*) or cylindrical (slender and parallel-sided anterior of spiracle and only slightly widened posteriorly) (Fig. 13*c*) 3

— Metasomal T1 with spiracle at or anterior to middle of tergite (Fig. 1), in dorsal view gradually widening posteriorly (Fig. 13*b*). 8

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3(2). Clypeus with a dense fringe of parallel setae protruding ventrally from apical edge; areolet open (as in Fig. 5*c*); tarsal claws simple (as in Fig. 15*c*); propodeum with longitudinal and transverse carinae (Fig. 11*e*). *Female*: ovipositor with ventral valve having weakly sclerotized medial region (Fig. 16*d*) and dorsal valve without a subapical notch . . . . . Tryphoninae (*Hercus*, in part) (p. 36)

— Features not exactly as above. Clypeus without setae or, if setae present, not protruding from edge and (or) not dense and parallel; areolet open (as in Fig. 5*c*) or closed (as in Figs. 5*b*, 5*e*, 5*f*); tarsal claws simple (as in Fig. 15*c*), pectinate (as in Fig. 15*d*) or with a large basal tooth (as in Fig. 15*e*); propodeum with or without longitudinal and (or) transverse carinae (as in Figs. 11*c*, 11*d*, 11*f*). *Female*: ovipositor with ventral and dorsal valves equally sclerotized (as in Fig. 16*a*) and dorsal valve sometimes with a subapical notch (Fig. 16*b*) 4

4(3). Areolet pentagonal, the cell either closed (Fig. 5*b*) or open, but if open, then pentagonal shape still apparent (Fig. 5*d*); metasoma dorsoventrally depressed, with T4 and T5 wider than high; propleuron with ventroposterior corner not produced into a lobe (as in Fig. 1*c*); T1 without lateral depression (glymma) (Fig. 12*e*). *Female*: ovipositor with ventral valve having distinct ridges apically (Fig. 16*a*) or ridges absent, dorsal valve without a subapical notch (as in Fig. 16*a*) 5

— Areolet triangular (Fig. 5*e*), quadrangular (Fig. 5*f*), or open (Fig. 5*c*), but never pentagonal; metasoma laterally compressed, with T4 and T5 higher than wide; propleuron with ventroposterior corner produced into an angulate lobe that in most species touches or overlaps pronotum (Fig. 9*a*); T1 with lateral depression (glymma) (Fig. 12*f*) or without (Fig. 12*e*). *Female*: ovipositor with ventral valve smooth apically (Fig. 16*b*) and dorsal valve with a subapical notch, this either obvious (Fig. 16*b*) or less obvious because ovipositor distal to notch quite slender 6

5(4). Mesopleuron with sternaulus extending more than one-half length (Fig. 9*f*); T2 without longitudinal striations anterior to transverse scarlike depression (thyridium) (Fig. 8*e*); areolet closed (Fig. 5*b*) or open (Fig. 5*d*). *Female*: ovipositor extending greatly beyond apex of metasoma. . . . . Cryptinae (3 genera) (p. 25)

— Mesopleuron with sternaulus absent or extending no more than one-half length of mesopleuron (as in Fig. 1*e*); T2 with longitudinal striations anterior to thyridium (Fig. 8*f*) (at least some longitudinal wrinkling laterally); areolet closed (as in Fig. 5*b*). *Female*: ovipositor not or barely extending beyond apex of metasoma . . . . . Ichneumoninae (6 genera) (p. 25)

6(4). Propodeum with network of thin, irregular raised sculpture (reticulations) (Fig. 11*b*); areolet open (as in Fig. 5*c*); clypeus with apical edge pointed medially (Fig. 7*b*) . . . . Anomaloninae (4 genera) (p. 16)

— Propodeum without reticulations, surface smooth with distinct carinae in most specimens (as in Fig. 11*a*); areolet open (as in Fig. 5*c*) or closed (Fig. 5*f*); clypeus with apical edge truncate (as in Fig. 7*d*) or uniformly rounded (as in Fig. 7*c*) 7

7(6). Supraclypeal area with at least some white, yellow, or orange markings and separated from clypeus by a strong groove (as in Fig. 10*c*); middle and hind legs with tibial spurs separated from base of tarsus and from each other by sclerotized regions, tibial apex thus with three separate points of insertion (Fig. 15*b*); areolet open (as in Fig. 5*c*) . . . . . Cremastinae (2 genera) (p. 25)

— Supraclypeal area entirely black, either not or only weakly separated from clypeus by a groove (Fig. 10*b*); middle and hind legs with tarsus and tibial spurs not separated by sclerotized regions, tibial apex thus with one large point of insertion (Fig. 15*a*); areolet open or closed. . . . . Campopleginae (7 genera) (p. 17)

8(2). Supraclypeal area, in anterior view, with a medial triangular process projecting dorsally between antennal sockets (Fig. 7*f*) and not separated from clypeus, both structures, in lateral view, therefore forming a continuous, strongly convex bulge (Fig. 10*d*). *Female*: ovipositor short, not extending beyond apex of metasoma . . . . . Metopiinae (4 genera) (p. 32)

— Supraclypeal area, in anterior view, without a medial triangular process between antennal sockets (as in Fig. 7*c*) and separated from clypeus by a groove at least laterally, both structures, in lateral view, therefore not forming a continuous bulge (Fig. 10*c*). *Female*: ovipositor short or long, extending beyond apex of metasoma in most specimens. 9

9(8). T2–T4, in dorsal view, with three deep grooves delineating a medial triangular area on each tergite (Fig. 14*a*); pronotum with epomia strong and ending dorsally in a swollen area (Fig. 9*e*) (best seen in dorsolateral view); metanotum (region posterior to base of hind wing) with strongly projecting lateral lobe touching projection on dorsolateral corner of propodeum (Fig. 8*d*) . . . . . Lycorininae (*Lycorina albomarginata* Cresson) (p. 31)

— T2–T4, in dorsal view, with or without grooves delineating a medial triangular area on each tergite, most species with tergites smooth (as in Fig. 14*c*) or with only oblique grooves delineating anterolateral corners (as in Figs. 14*b*, 14*d*); pronotum with or without epomia, but if epomia present, then not projecting dorsally as a swollen area (as in Fig. 9*c*); metanotum without projecting lobe touching dorsolateral corner of propodeum 10

10(9). Areolet open (as in Fig. 5*c*) 11

— Areolet closed (as in Figs. 5*e*, 5*f*) 12

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11(10). T2–T4 with deep oblique grooves joined medially (chevron-shaped depression) (Fig. 14*b*); tarsal claws pectinate (as in Fig. 15*d*). *Female*: ovipositor with a dorsal subapical notch, ventral valve uniformly sclerotized, and without an egg attached ventrally . . . . . Banchinae: Glyptini (4 genera) (p. 16)

— T2–T4 without oblique grooves (as in Fig. 14*c*); tarsal claws simple (Fig. 15*c*). *Female*: ovipositor without a dorsal subapical notch, ventral valve with a weakly sclerotized medial region, and in some specimens with an egg attached ventrally (Fig. 16*d*) . . . . Tryphoninae: Oedemopsini (in part) (2 genera) (p. 36)

12(10). Metapleuron with submetapleural carina produced anteriorly as a strong lobe (Fig. 11*a*); propodeum with strong posterior transverse carina only (Fig. 11*d*) (vestiges of medial longitudinal carinae present medially in *Lissonota acrobasidis*). *Female*: ovipositor with a strong dorsal subapical notch (Fig. 16*b*), without a dorsal swelling (nodus), and without strong ventral teeth . . . . . Banchinae: Atrophini (2 genera) (p. 16)

— Metapleuron with submetapleural carina not produced anteriorly into strong lobe; propodeum with carinae various: either complete (Fig. 11*c*), with longitudinal carinae only, or with no carinae (not with only posterior transverse carina). *Female*: ovipositor without a dorsal subapical notch, although a dorsal subapical swelling (nodus) and (or) strong, ventral teeth (Fig. 16*a*) present in some specimens 13

13(12). Propodeum without carinae; tarsal claws strongly pectinate (Fig. 15*d*) . . . . . Tryphoninae: Phytodietini (*Phytodietus*) (p. 36)

— Propodeum with at least pleural carina and most species with anterior section of medial longitudinal carinae as well; tarsal claws simple (Fig. 15*c*) or with a basal tooth (Fig. 15*e*) . . . . . Pimplinae (8 genera) (p. 33)

Subfamily Anomaloninae

Anomalonines are primary koinobiont endoparasitoids of Lepidoptera or, more rarely, Coleoptera. They lay their eggs in the host larva (Table 2) and emerge from the pupa (Gauld *et al.* 1997). Eight species from four genera have been reliably reared from six species of *Choristoneura* in North America (Table 3), but in general they are reared relatively rarely.

Literature: Dasch (1984) revised the North American genera and species. Gauld *et al.* (1997) revised the Costa Rican genera (most of which are also Nearctic) and included a good summary of their biology.

Key to Anomaloninae reared from Nearctic *Choristoneura* spp.

1. Fore wing with base of cell 2M pointed because vein 2cu-a joins Cu basal to union of m-cu and Cu (Fig. 6*a*) . . . . . *Parania geniculata* (Holmgren)

— Fore wing with base of cell 2M truncate because vein 2cu-a joins Cu distal to union of veins m-cu and Cu (Fig. 6*b*) 2

2(1). Mesoscutum with notaulus absent or present only as a weak depression anteriorly; mesopleuron with epicnemial carina short, not extending dorsally more than 0.1 height of pronotum and its dorsal end curving slightly posteriorly away from pronotum. . . . . *Erigorgus stenotus* Dasch

— Mesoscutum with notaulus present (Fig. 10*f*); mesopleuron with epicnemial carina extending dorsally at least 0.2 height of pronotum and dorsal end either straight or curving anteriorly towards pronotum (as in Fig. 6*f*). 3

3(2). Fore wing vein 2/Cu equal or longer than vein 2cu-a (Fig. 6*c*); fore coxa without a transverse ventral carina . . . . . *Habronyx aclerivorus* (Rowher)

— Fore wing vein 2/cu shorter than vein 2cu-a (Fig. 6*d*); fore coxa with a transverse ventral carina or sharply angulate anterior margin . . . . . *Agrypon* (5 species)

Subfamily Banchinae

Banchines are primary koinobiont endoparasitoids of Lepidoptera. They lay their eggs in the host larva (Table 2) and emerge from the prepupa (Gauld *et al.* 2002*a*). This is one of the most prevalent subfamilies parasitizing *Choristoneura* in North America, with 23 species from 6 genera reliably reared from 7 *Choristoneura* species (Table 3). *Glypta* has the greatest number of species (18) recorded from Nearctic *Choristoneura* spp., but the size of the genus (314 described Nearctic species) contributes to difficulty in identifying specimens to species. *Glypta fumiferanae* (Viereck) has been reared from seven species of *Choristoneura* and is a prevalent parasitoid of *C. fumiferana* in eastern North America (Dowden *et al.* 1948) and of

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C. occidentalis west of the Rocky Mountains (Carolin and Coulter 1959). *Glypta variegata* Dasch and *Apophua simplicipes* (Cresson) are important parasitoids of *C. rosaceana* in the southern interior of British Columbia (Cossentine *et al.* 2004; Cossentine *et al.* 2007) and *G. erratica* Cresson is a prevalent parasitoid of *C. conflictana* in Alaska (Torgersen and Beckwith 1974). *Cephalolglypta murinanae* (Bauer) was introduced from Europe to Ontario and New Brunswick on four occasions (1950, 1955, 1956, and 1973) to help control *C. fumiferana*, but despite this, it does not appear to have become established (Carlson 1979).

Literature: Townes and Townes (1978) and Dasch (1988) revised the North American Atrophini and Glyptini, respectively. Gauld *et al.* (2002*a*) revised the Costa Rican genera of the subfamily (many of which are also Nearctic) and included a good summary of their biology and comments on generic limits.

Key to Banchinae reared from Nearctic *Choristoneura* spp.

1. T2 with strong oblique grooves meeting medioanteriorly (Fig. 14*b*) . . . . . 2 (Glyptini)
— T2 without oblique grooves . . . . . 5 (Atrophini)
2(1). T1 with a pair of sharp basolateral teeth (Fig. 13*d*); body predominantly white to light yellow; antenna with a white band medially . . . . . *Sphelodon phoxopteridis* (Weed)
— T1 without basolateral teeth; body predominantly black or orange; antenna uniformly coloured . . . 3
3(2). Head with dorsoposterior region deeply excavated (Fig. 10*a*) . . . *Cephaloglypta murinanae* (Bauer)
— Head with dorsoposterior region not excavated 4
4(3). Fore tibial spur reaching or surpassing middle of first tarsomere; head with supra-antennal area lacking a horn or dorsally concave, cuplike protrusion medially . . . . . *Apophua simplicipes* (Cresson)
— Fore tibial spur not reaching middle of the first tarsomere; head with supra-antennal area with or without a horn or dorsally concave, cup-like protrusion medially. . . . . *Glypta* (18 species)
5(1). Areolet open (as in Fig. 5*c*) . . . . . *Meniscomorpha mirabilis* (Cresson)
— Areolet closed (as in Fig. 5*e*). . . . . *Lissonota acrobasidis* (Ashmead)

Subfamily Campopleginae

Campoplegines are primary koinobiont endoparasitoids, mostly of Lepidoptera. They lay their eggs in the host larva (Table 2) and emerge from the pupa (Wahl 1993*b*). Nine species from seven genera have been reared from five species of *Choristoneura* in North America and some species can be moderately abundant on *Choristoneura* spp. For example, *Tranosema rostrale* (Brischke) has been reared frequently from low-density populations of *C. fumiferana* in Canada and the United States of America (Cusson *et al.* 1998). Species of this subfamily are some of the most difficult to identify to species, partly because the limits of some genera are poorly defined. The key below was constructed only to differentiate campoplegine species previously recorded from *Choristoneura* spp., and it should not be assumed that other species reared from *Choristoneura* spp. in the future will key out to the correct genus when this key is used. For example, almost all *Campoplex* spp. have a closed areolet and therefore would not key out to *C. mellipes* (Provancher), which has an open areolet. The key should therefore be used with caution and species identities confirmed by reference to original descriptions and (or) reference material.

Literature: Townes (1970) revised the world genera. Keys to North American species are not available for most genera that have species reared from *Choristoneura* spp., except for *Dusona* Cameron (Walley (1940) as *Campoplegidea*) and *Sinophorus* Förster (Sanborne 1984). Cusson *et al.* (1998) differentiated *T. rostrale* from *Enytus montanus* (Ashmead). Torgersen and Beckwith (1974) provided a key to the species they reared from *C. conflictana* in Alaska, including *Hyposoter annulipes* (Cresson) and *Tranosemella praerogator* (Linnaeus).

Key to Campopleginae reared from Nearctic *Choristoneura* spp.

1. Propodeal spiracle elongate (Fig. 6*f*); eyes with inner margin strongly indented opposite antennae (as in Fig. 7*c*); areolet large and receiving vein 2m-cu near middle . . . . . *Dusona seamansi* (Viereck)
— Propodeal spiracle round or elliptical; eyes with inner margin not or only slightly indented opposite antennae; areolet open (as in Fig. 5*c*) or small (Fig. 5*f*) and when closed, receiving vein 2m-cu distal to middle . . . 2

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Fig. 5. Fore wing, apical half: a, *Mesochorus* sp.; b, *Ischnus* sp.; c, *Glypta* sp.; d, *Mastrus* sp.; e, *Phytodietus* sp.; f, *Hyposoter* sp.

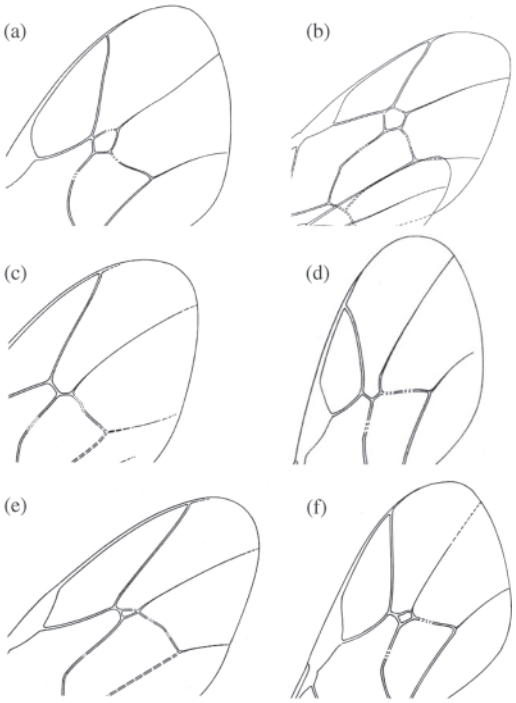
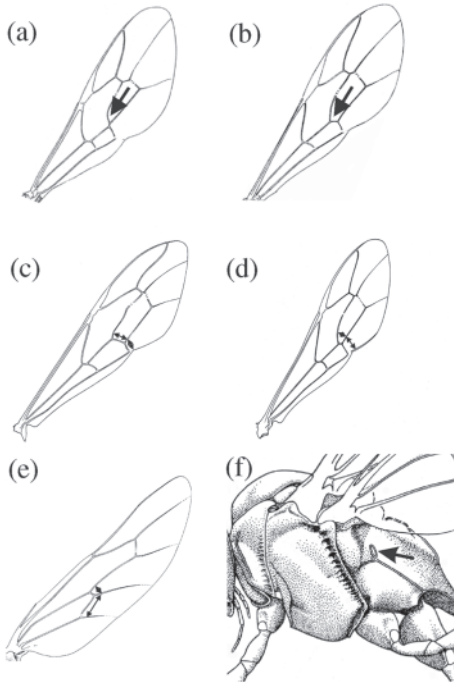


Fig. 6. a–d, fore wing: a, *Parania* sp.; b, *Agrypon* sp.; c, *Habronyx* sp.; d, *Agrypon* sp. (the arrow in a and b indicates the basal region of cell 2m and the arrows in c and d indicate the relative lengths of veins 2/Cu (above) and 2cu-a (below); e, hind wing, *Pimpla* sp. (the arrows indicate the relative lengths of vein 1/Cu (above) and cu-a (below); f, thorax and propodeum, lateral view, *Dusona* sp. (the arrow indicates the propodeal spiracle).



2(1). Areolet open (as in Fig. 5*c*) 3
— Areolet closed (as in Fig. 5*f*) 6
3(2). T1 without glymma (Fig. 12*e*), or glymma only a shallow groove; S1, in lateral view, strongly convex near base, horizontal suture between S1 and T1 near midheight of segment (Fig. 12*e*); hind tibia banded, pale at base, and with sub-basal and apical dark bands . . . . . *Campoplex mellipes* (Provancher)
— T1 with glymma as a deep pit (as in Fig. 12*f*); S1, in lateral view, flat near base, horizontal suture between S1 and T1 ventral to midheight of segment (as in Fig. 12*f*); hind tibia uniformly coloured, or if banded, then its base dark 4
4(3). Hind tibia uniformly coloured or only slightly darker basally and apically, but not forming discrete, conspicuous bands 5
— Hind tibia strongly banded, light medially, and with black to brown bands basally and apically . . . . . *Enytus eureka* (Ashmead)
5(4). *Female*: middle coxa reddish brown. *Male*: fore and middle coxae yellowish brown; scape black to dark brown with at most a slightly paler reddish brown spot ventrally . . . . . *Tranosema rostrale* (Brischke) (in part, specimens with open areolet)
— *Female:* middle coxa black to dark brown. *Male*: fore and middle coxae pale yellow; scape black to brown dorsally but completely pale yellow ventrally . . . . . *Enytus montanus* (Ashmead)
6(2). Propodeum with a median longitudinal trough crossed transversely by many striations; T1 without glymma, or glymma only a shallow groove; S1 in lateral view strongly convex near base, horizontal suture between S1 and T1 near midheight of segment (as in Fig. 12*e*) . . . . *Sinophorus teratis* (Weed)
— Propodeum without a median longitudinal trough, or if slightly concave medially, then without striations; T1 with glymma as a deep pit (as in Fig. 12*f*); S1, in lateral view, flat near base, horizontal suture between S1 and T1 below midheight of segment (as in Fig. 12*f*) 7

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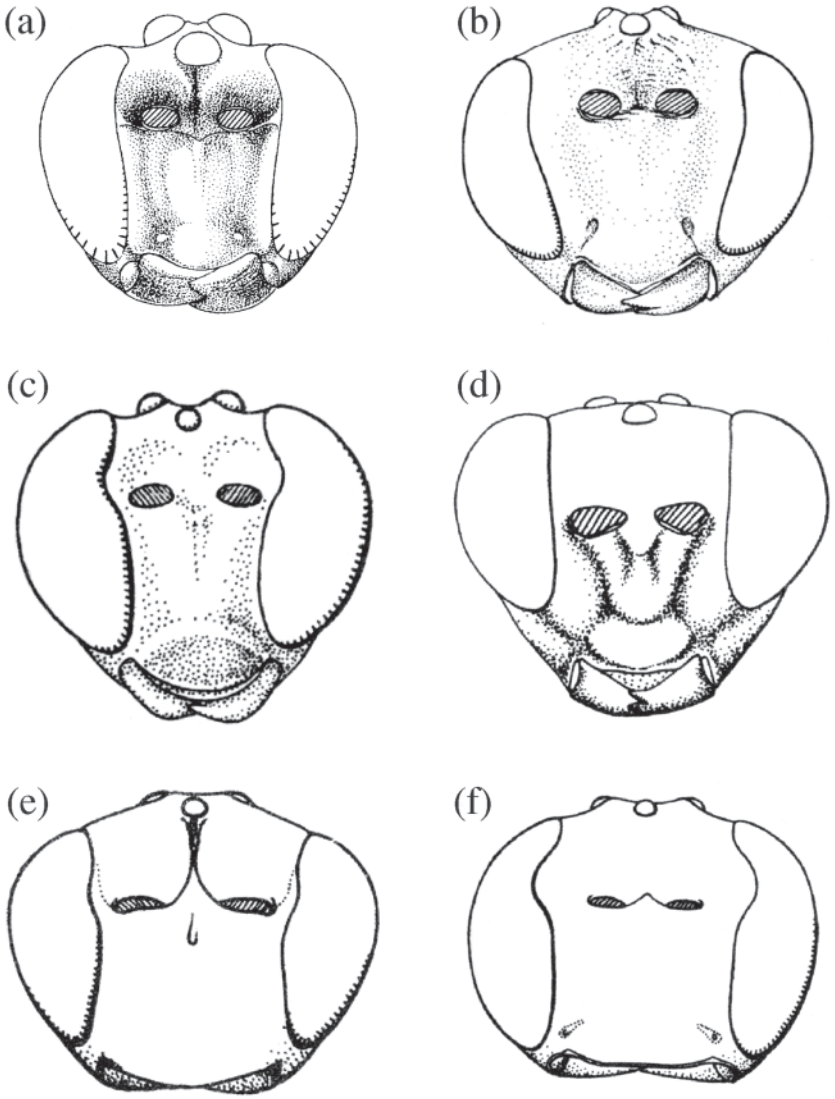
Fig. 7. Head, anterior view: a, *Mesochorus* sp.; b, *Agrypon* sp.; c, *Apechthis* sp.; d, *Ischnus* sp.; e, *Triclistus* sp.; f, *Trieces* sp.



7(6). Hind tibia banded (white to yellow medially and black to brown apically and basally to sub-basally) . . . 8
— Hind tibia not banded (brown or orange, except blending to slightly darker orangish brown apically) . . . . . *Tranosema* Förster 9
8(7). Hind tibia with base dark to light brown (darker than white to yellow medial band). *Female*: ovipositor length about twice apical depth of metasoma . . . . . *Tranosemella praerogator* (Linnaeus)
— Hind tibia with base white to yellow, same shade as medial white to yellow band (sub-basal dark band present, but clearly not extending to base). *Female*: ovipositor about as long as or slightly longer than apical depth of metasoma . . . . . *Hyposoter annulipes* (Cresson)
9(7). Middle coxae dark brown. *Male*: hind tibia completely dark brown . . . *Transosema tenuifemur* (Walley)
— Middle coxae light to medium orangish brown. *Male*: hind tibia predominantly orange . . . . . *Tranosema rostrale* (Brischke) (in part, specimens with closed areolet)

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Fig. 8. a–c, head, anterior view: a, *Scambus* sp.; b, *Oedemopsis* sp.; c, *Hyposoter* sp. (the arrows in b compare height to width of clypeus); d, thorax, lateral view, *Lycorina* sp. (the inset shows the hook of the metanotum overlapping the propodeum); e, f, T2, dorsal view: e, *Ischnus* sp. (the arrow points to the area near the base of T2 that lacks longitudinal striations); f, *Patrocloides montanus* (the arrows point to strong longitudinal striations anterior to the thyridium).

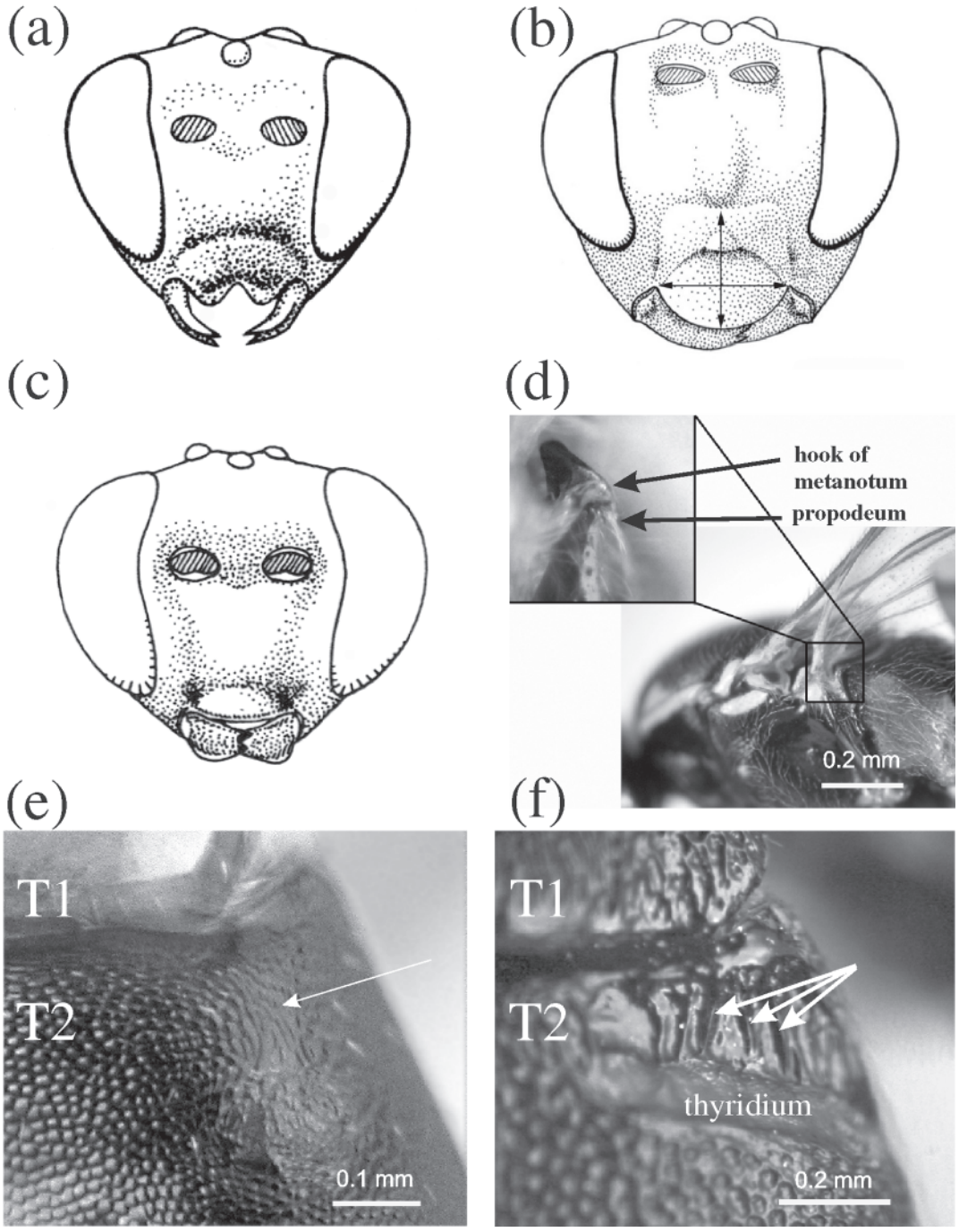

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Fig. 9. Head and (or) thorax, lateral view: a, *Sinophorus* sp.; b, *Chorinaeus* sp.; c, *Pristomerus* sp.; d, *Gelis* sp.; e, *Lycorina* sp.; f, *Mastrus* sp. (the arrow indicates the lobe of the propleuron in a, the dorsolateral groove of the pronotum in b, the epomia of the pronotum in c and e, and the sternaulus in f; contrast the length of the sternaulus with "e" in Figure 1).

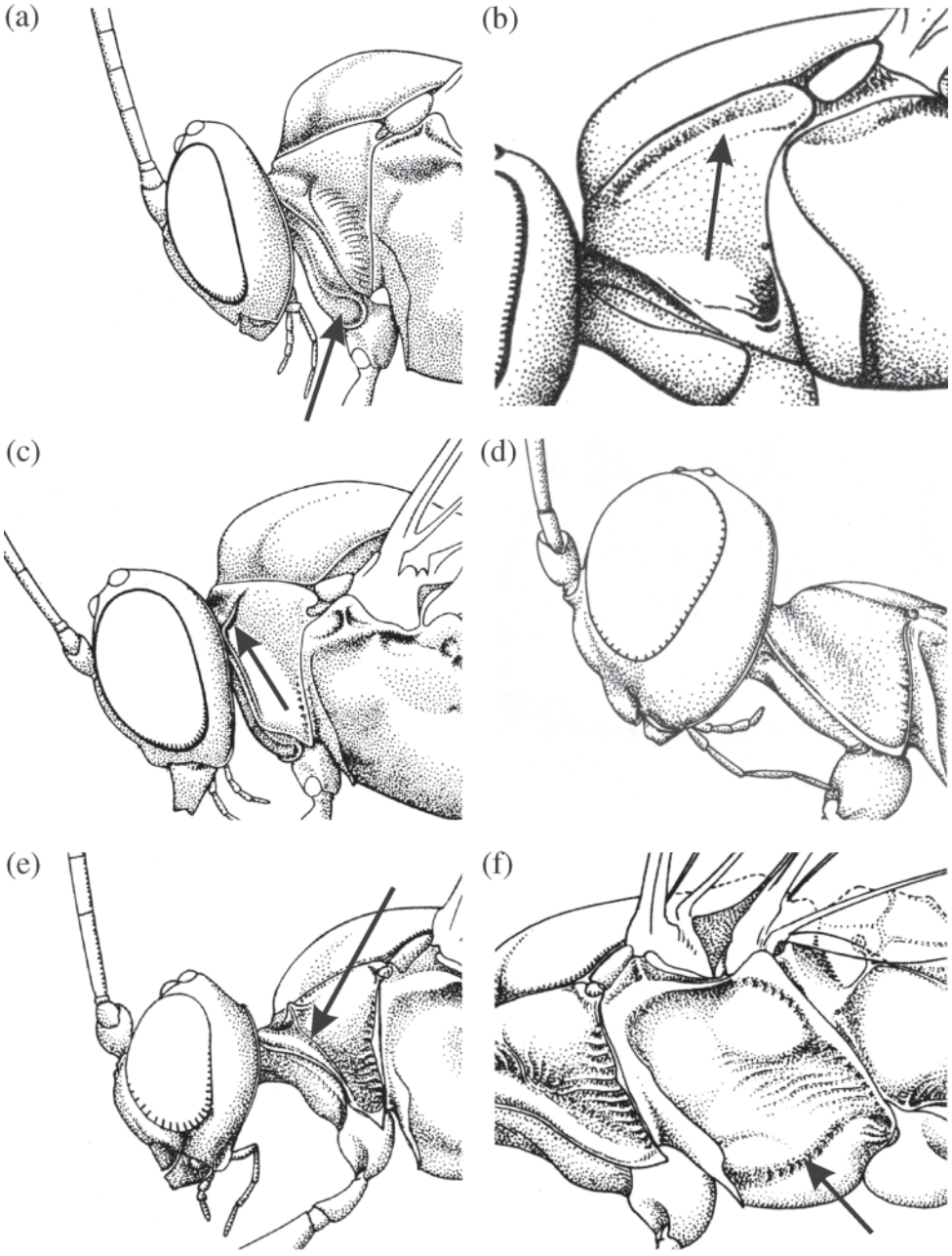

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Fig. 10. a, head, dorsal view, *Cephaloglypta murinanae*; b–e, head, lateral view: b, *Dusona seamansi*; c, *Glypta conflictanae*; d, *Exochus albifrons*; e, *Hyposoter* sp. (the arrow points to the clypeal groove in c and the absence of a groove in b and d); f, habitus, *Habronyx aclerivorus* (the enlarged area shows the notaulus).

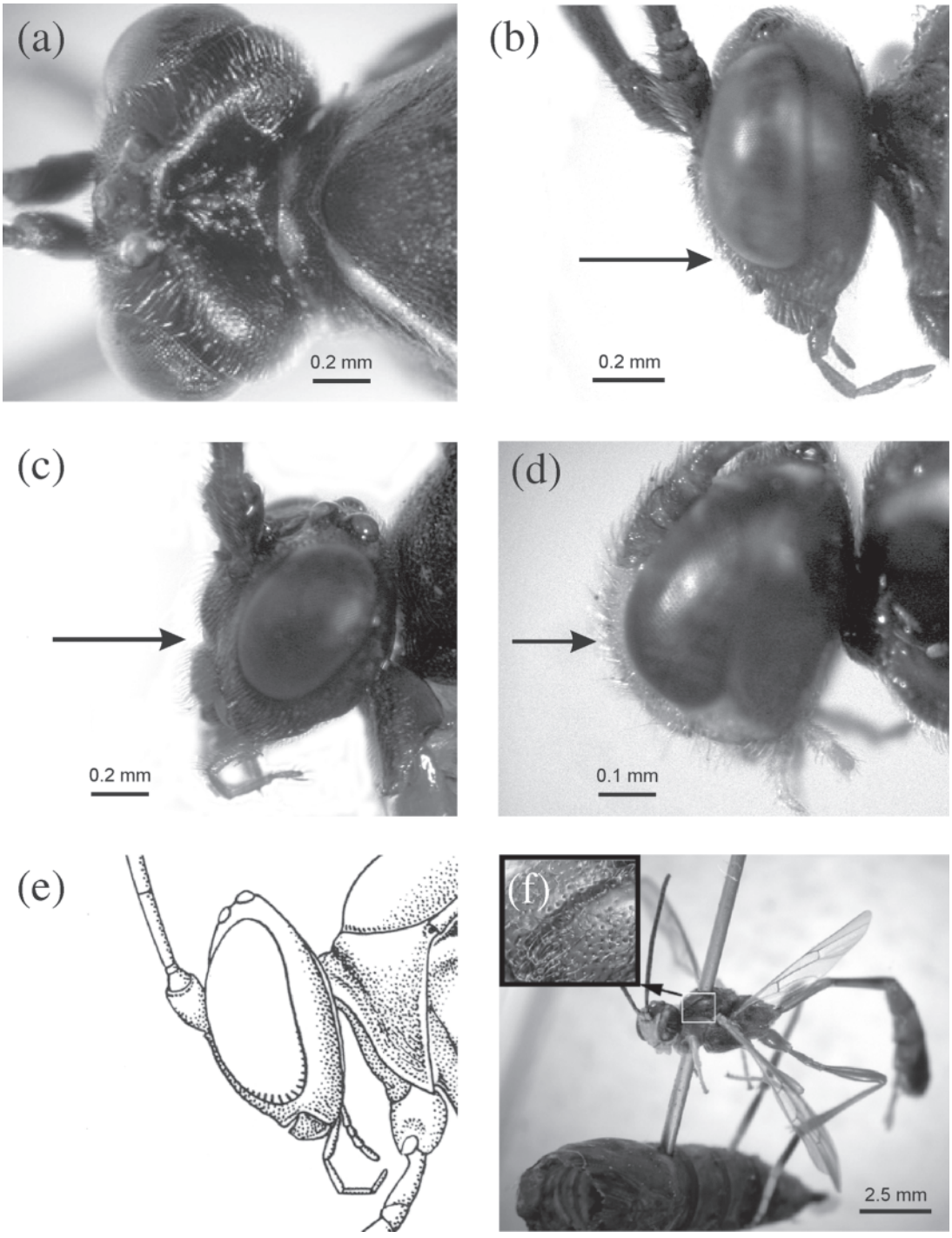

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Fig. 11. a, b, propodeum, lateral view: a, *Apophua* sp.; b, *Habronyx* sp. (the arrow in a indicates the submetapleural carina produced ventrally as a lobe); c–f, propodeum, dorsal view: c, *Mastrus* sp.; d, *Meniscomorpha* sp.; e, *Hercus* sp.; f, *Oedemopsis* sp.

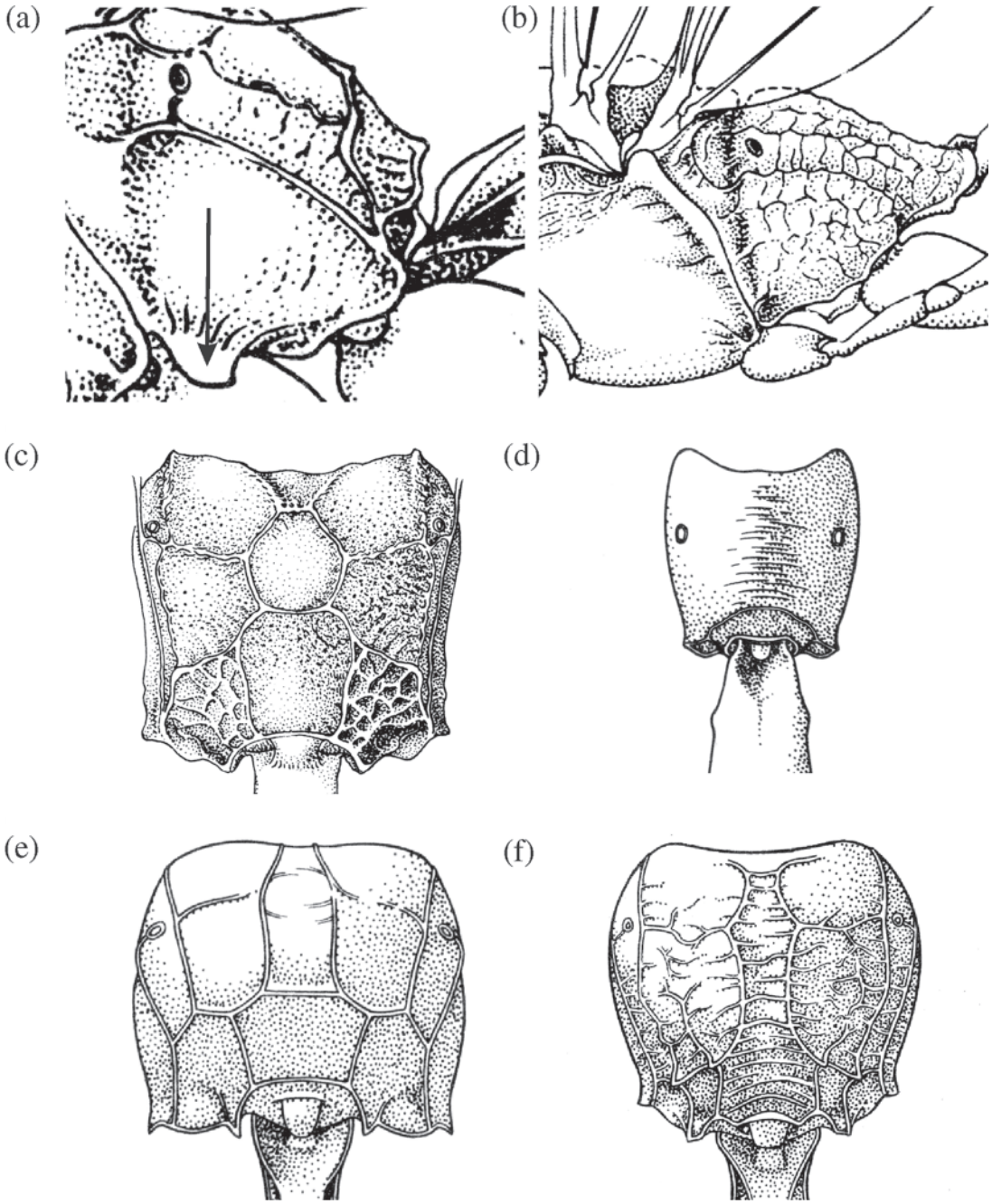

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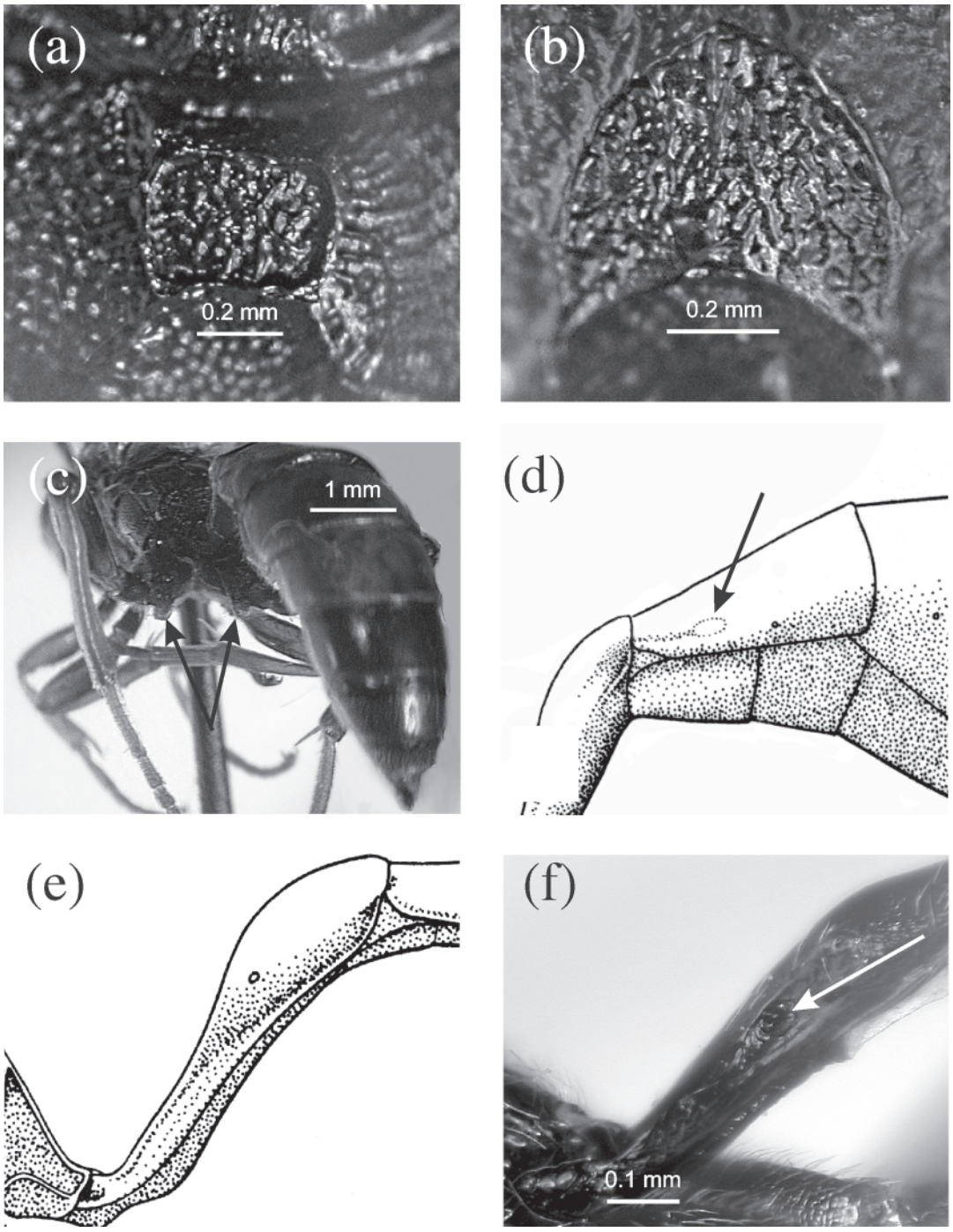
Fig. 12. a, b, propodeum, dorsal view of areolar region: a, *Patrocloides montanus*; b, *Orgichneumon calcatorius*; c, thorax and abdomen, posterolateral view, *Phaeogenes cacoeciae* (the arrows indicate keels on the hind coxae); d–f, anterior part of the metasoma, lateral view: d, *Dusona* sp.; e, *Campoplex* sp.; f, *Tranosemella praerogator* (the arrow in d indicates the thyridium of T2 and the arrow in f indicates the glymma of T1).



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Subfamily Cremastinae

Cremastines are primary koinobiont endoparasitoids of Lepidoptera or Coleoptera. They lay their eggs in the host larva (Table 2) and emerge from the penultimate or final larval instar (Gauld *et al.* 2000). Five species from two genera have been reared from three species of *Choristoneura* in North America (Table 3), although only relatively rarely. *Temelucha* is a large genus (137 described Nearctic species), which contributes to difficulties in identifying specimens to species.

Literature: Dasch (1979) revised the North American species. Gauld *et al.* (2000) revised the Costa Rican species and included a summary of their biology.

Key to Cremastinae reared from Nearctic *Choristoneura* spp.

1. T1 with lateral margins widely separated ventrally (Fig. 13*e*); T2 with a thyridium (as in Fig. 12*d*). *Male*: hind femur with a ventral tooth subapically. *Female*: hind femur with a minute tooth or bump . . . . . *Pristomerus baumhoferi* Cushman
— T1 with lateral margins curving to meet each other ventrally or fused with sternum ventrally (Fig. 13*f*); T2 without a thyridium. *Both sexes*: hind femur without a tooth . . . . . *Temelucha* (4 species)

Subfamily Cryptinae

The Cryptinae is the largest ichneumonid subfamily, with over 4600 described species in 395 genera (Yu *et al.* 2005), but no species are highly prevalent on Nearctic *Choristoneura* spp. Only four species in three genera have been recorded from five host species (Table 3). The subfamily is biologically diverse. Most species are idiobiont ectoparasitoids (Table 2) of insects in several orders (Townes and Townes 1962), but some are endoparasitic and (or) koinobiont and a few prey as larvae on spider egg sacs. In addition, some are facultative hyperparasitoids, including *Gelis tenellus* Say, which is known only from parthenogenetic females (Allen 1962).

Literature: Townes and Townes (1962) revised the North American species of Cryptini, including *Ischnus* Gravenhorst. Townes (1983) revised the North American genera of Phygadeuontini, including *Mastrus* Förster and *Gelis* Thunberg, but did not provide species keys for these two genera, nor are any useable keys available from previous authors.

Key to Cryptinae reared from Nearctic *Choristoneura* spp.

1. Areolet closed (Fig. 5*b*); propodeum without longitudinal carinae (except pleural carina). *Male*: supraclypeal area with white to yellow markings along inner orbit of eyes . . . . . *Ischnus* 3
— Areolet open (Fig. 5*d*); propodeum with longitudinal carinae, at least the medial longitudinal carinae posteriorly. *Male*: supraclypeal area not marked with white to yellow 2
2(1). *Only females known*: fore wing clear with two darker brown regions, one near where vein M + Cu divides into M and Cu and the other posterior and distal to stigma (this usually forming a band across entire wing); pronotum with epomia absent (Fig. 9*d*) . . . . . *Gelis tenellus* Say
— *Both sexes*: fore wing uniformly clear; pronotum with epomia present (as in Fig. 9*c*) . . . . . *Mastrus leplantei* Mason
3(1). Scutellum with lateral carinae extending about 0.4 times its length (Fig. 16*e*) . . . . . *Ischnus inquisitorius* (Müller)
— Scutellum without lateral carinae except at its extreme base (Fig. 16*f*) . . . . *Ischnus minor* (Townes)

Subfamily Ichneumoninae

Ichneumonines are endoparasitoids of Lepidoptera (Wahl 1993*b*). They oviposit in either the larva, prepupa, or pupa (Table 2) but always emerge from the pupa (Heinrich 1961*a*). Some females (*e.g.*, *Ichneumon* spp.) hibernate as adults (Heinrich 1961*a*), which is unusual because most ichneumonids spend the winter as a larva or pupa. Nine species from six genera have been reared from five species of Nearctic *Choristoneura* (Table 3). Most species are rarely reared from *Choristoneura* spp., but *Dirophanes maculicornis* (Stephens) is the most important pupal parasitoid of *Choristoneura* spp. in some areas. For example, Jaynes and Drooz (1952) reported rates of parasitism up to 15% on *C. fumiferana* in Maine, and Torgersen and Beckwith (1974) found that it was the dominant pupal parasitoid on

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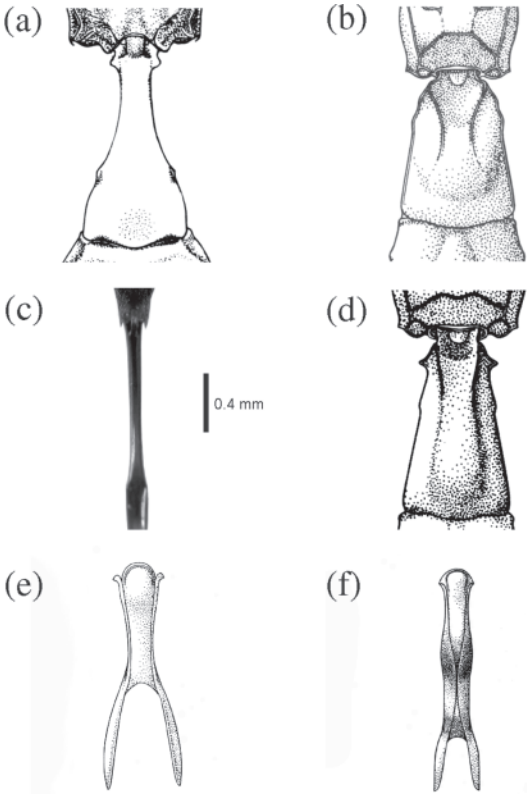
Fig. 13. a–d, MS1, dorsal view: a, *Ischnus* sp.; b, *Glypta* sp.; c, *Agrypon alpinum*; d, *Sphelodon phoxopteridis*; e, f, MS1, ventral view: e, *Pristomerus* sp.; f, *Temelucha* sp.



C. conflictana in Alaska (in both studies this species is listed as *D. hariolus* (Cresson)).

Literature: Heinrich (1961*a*, 1961*b*, 1961*c*, 1961*d*, 1962*a*, 1962*b*, 1962*c*) revised all the tribes, except the Alomyiini, "with particular reference to the northeastern region of North America". The keys for some genera include all the North American species, but for others, western and (or) southern species are not included and (or) will not key. No recent keys are available for the genera of Nearctic alomyiines, although Allen (1968) provided a key to the species of Nearctic *Phaeogenes* Wesmael and commented on the differences between *Dirophanes* Förster and *Phaeogenes*.

Comments

Dirophanes maculicornis was introduced into Ontario in the 1950s to help control *C. fumiferana* (Carlson 1979). Carlson (1979) decided that *D. maculicornis* was conspecific with the North American species *D. hariolus,* but Diller (1981) stated that the two species are distinct. Neither author provided justification for their decisions. Later, Schönitzer *et al.* (2006) revised *Dirophanes* and concluded that *D. hariolus* and *D. maculicornis* are distinct. Their study suffered from insufficient material of *D. hariolus*, whereas the present study suffers from insufficient material of *D. maculicornis*. Neither their use of colour nor differences in the hind coxal tooth or sculpture of T2 and T3 consistently distinguish the two species. Mandibular tooth length may offer a diagnostic character but this needs to be quantified across both species including a wider geographic sample of *D. hariolus*. *Dirophanes hariolus* is a widespread, variably coloured species (head and thorax range from orange to black). *Dirophanes maculicornis* generally has a black head and thorax. It was previously thought that white marks on the scutellum were specific to *D. maculicornis*; however, a series of CNC reared male *D. hariolus* from Kamloops, British Columbia show a transition in the scutellum from partly white to completely black. Morley (1903) also states that rarely, the scutellum of female *D. maculicornis* in Europe can be completely black. With respect to punctation, the same holds true: *D. hariolus* is variable (*e.g.*, the distance between punctures of the male gena ranges from punctures almost touching to greater than the puncture diameter) and *D. maculicornis* falls within this range (distance ranges from touching each other to separated by nearly the puncture diameter). Examination of specimens at AEIC confirms these findings (D. Wahl, personal communication). The best character that unites *D. hariolus* and *D. maculicornis* is the elongate tooth on the female hind coxa. The shape of this tooth varies throughout the range of *D. hariolus* from sharply carinate to apically rounded (D. Wahl, personal communication), but it is always much longer than that of any other species of *Dirophanes* except *D. maculicornis* and there are no quantifiable differences in this tooth between these two "species". The question of whether or not these two species are synonymous remains unclear and perhaps could be answered through molecular sequence analysis. Because of this uncertainty and to be consistent with the recent North American literature, I use the name *D. maculicornis*, following Carlson (1979) who believed the two species are synonymous. In addition, *Phaeogenes gaspesianus* Provancher, 1882 is moved to *Dirophanes* forming *Dirophanes gaspesianus* (Provancher) **comb. nov.** The transfer is made because this species has a straight hypostomal carina near the mandible and a strong notaulus anteriorly, and the form of the keel on the hind coxa of the female is like that of other species of *Dirophanes*. The

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Fig. 14. a–f, T2, dorsal view: a, *Lycorina* sp.; b, *Glypta erratica*; c, *Scambus* sp.; d, *Acropimpla alboricta*; e, *Chorinaeus* sp.; f, *Trieces* sp. (the arrow in d indicates the shallow oblique groove on T2 and the arrow in e and f indicates the lateral longitudinal carina on T2).

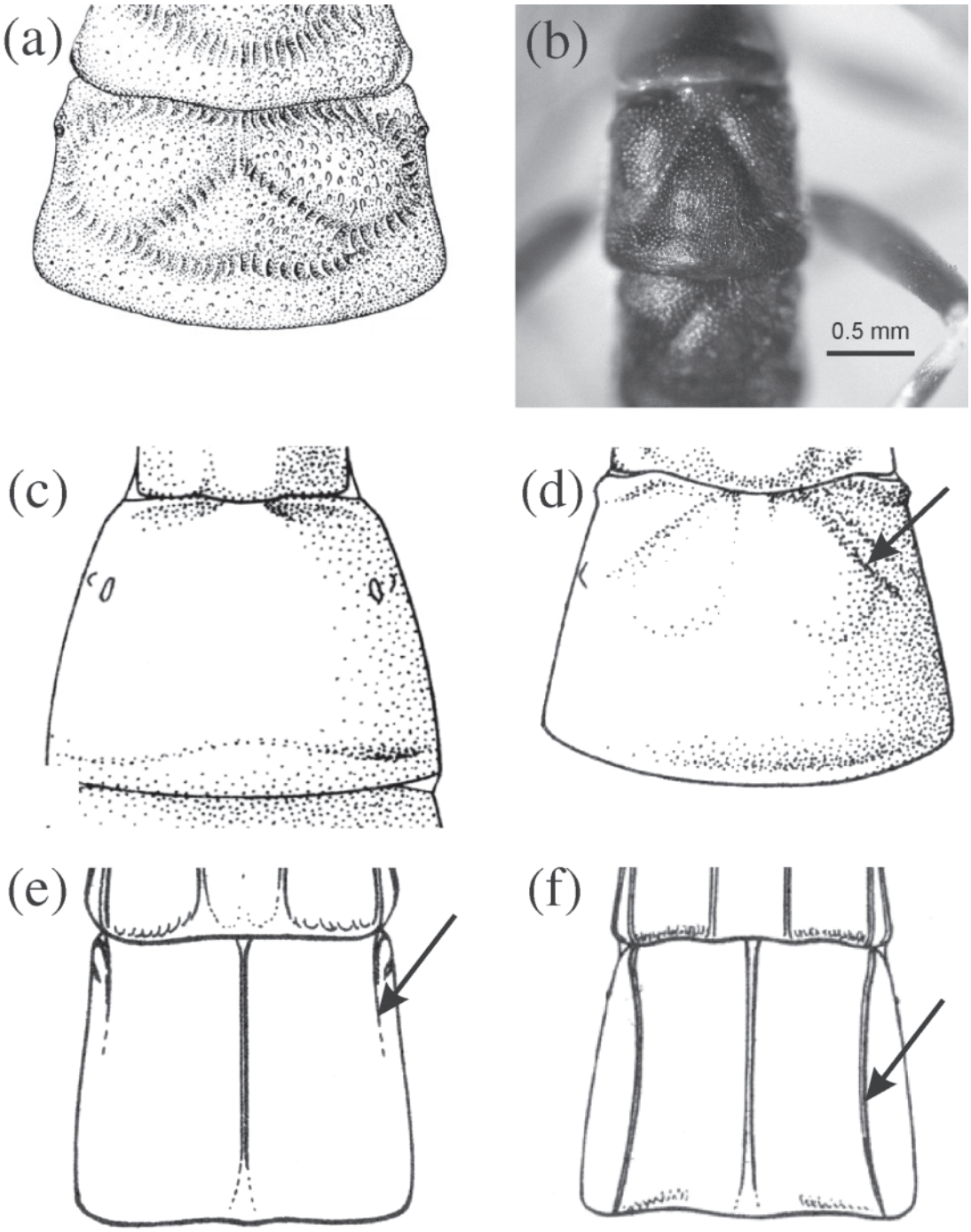

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Fig. 15. a, b, hind tibia, apical view with spurs and tarsus removed: a, *Glypta fumiferanae*, b, *Pristomerus* sp.; c–f, tarsal claws: c, *Pimpla pedalis*; d, *Phytodietus fumiferanae*; e, *Apechthis annulicornis*; f, *Theronia atalantae*.

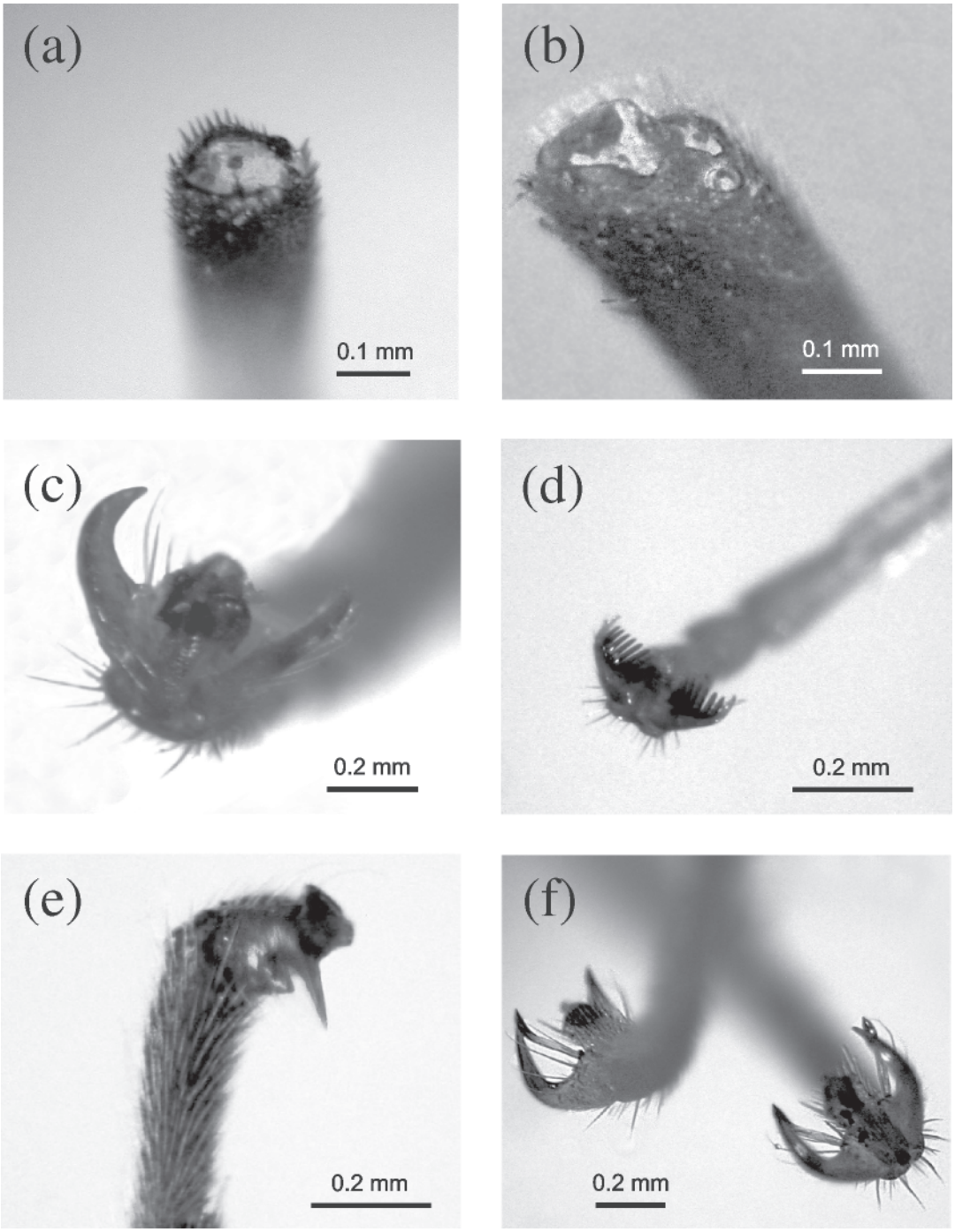

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Fig. 16. a–d, ovipositor: a, *Pimpla aquilonia*; b, *Sinophorus teratis*; c, *Apechthis annulicornis*; d, *Hercus* sp. (the arrow in b indicates the dorsal subapical notch); e, f, scutellum, dorsal view: e, *Ischnus migrator*; f, *Ischnus minor* (the arrow in e and f indicates the length of the lateral carina of the scutellum); g, h, metasoma, ventrolateral view: g, *Exochus nigripalpis*; h, *Exochus washingtonensis* (the arrow in g and h indicates the laterotergite of MS3).

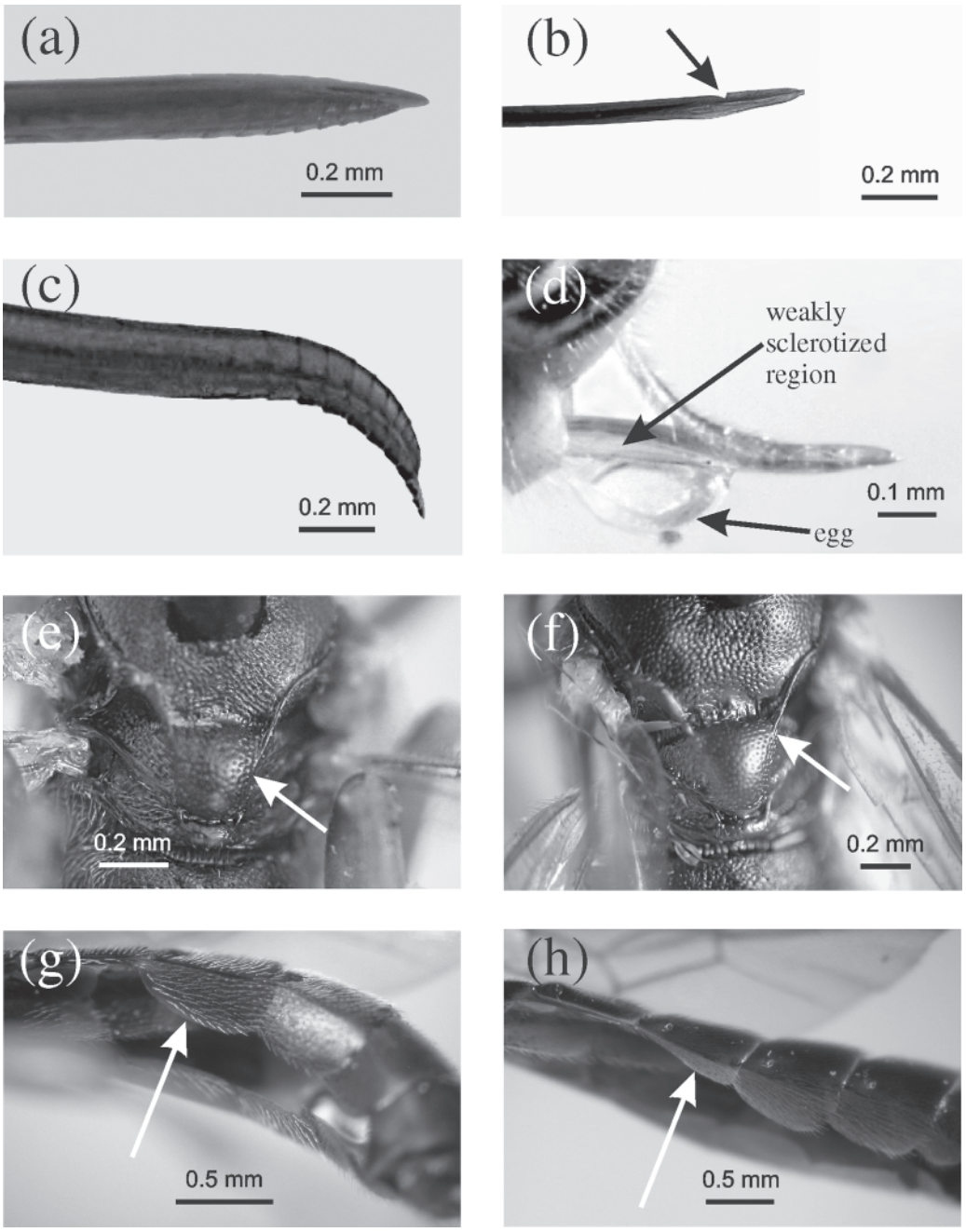

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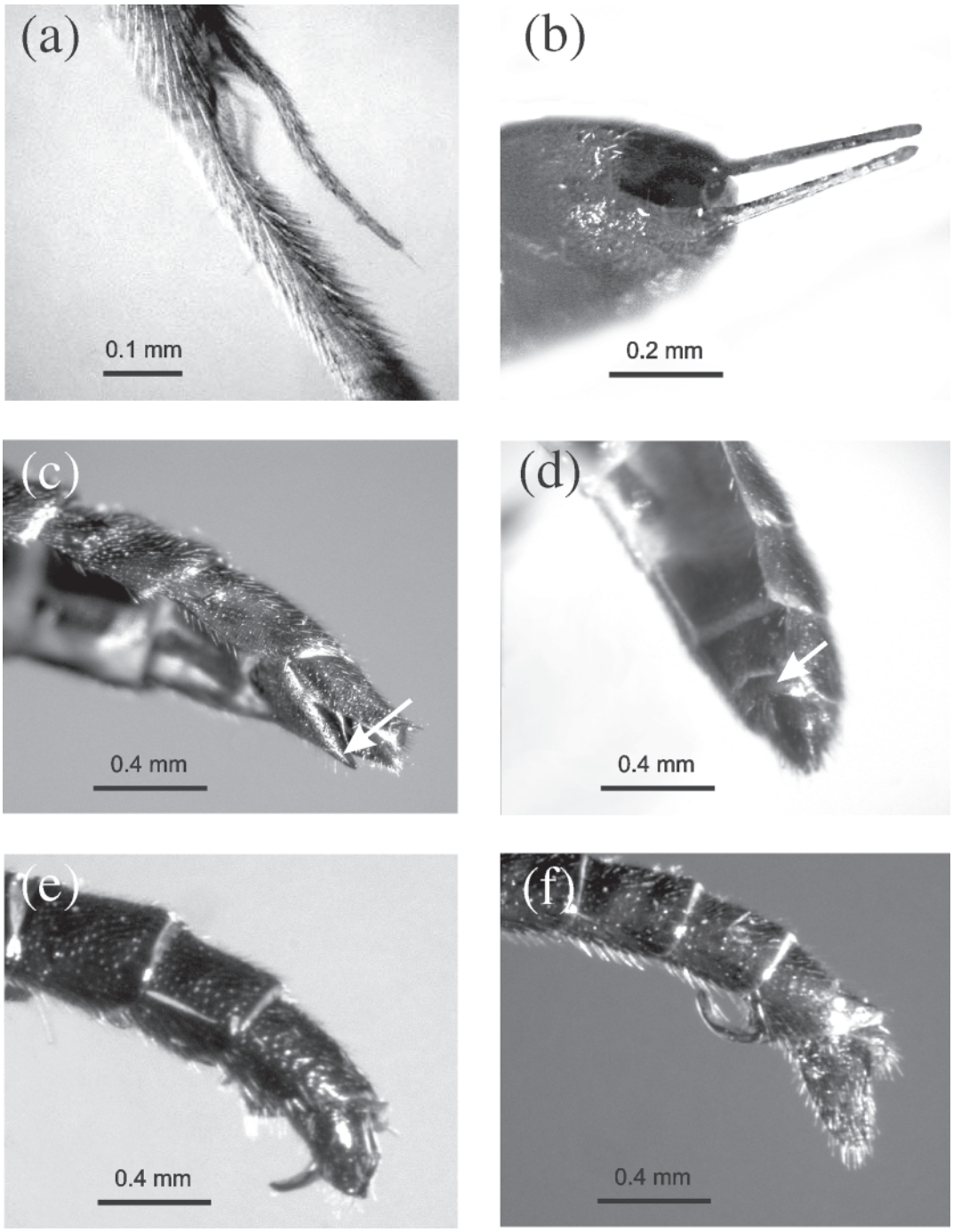
Fig. 17. a, basal tarsomere of foreleg and tibial spur, *Phytodietus* sp., lateral view; b–f, posterior metasomal segments of male, showing the hypopygium and gonoforceps: b, ventral view, *Mesochorus* sp.; c, d, ventrolateral view: c, *Pimpla* sp.; d, *Scambus hispae*; e, f, lateral view: e, *Acropimpla pronexus,* f, *Acropimpla alboricta* (the arrows in c and d indicate the hypopygium).



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present study is the first to record *D. gaspesianus* as a parasitoid of *Choristoneura* (from *C. fumiferana* in Ontario) and the first record of *Phaeogenes cacoeciae* Viereck reared from *C. rosaceana* (in British Columbia and New York State). It is possible that *D. gaspesianus* is a junior synonym of the Palaearctic *Dirophanes callopus* (Wesmael) (D. Wahl, personal communication); however, further study is required prior to formal recognition of this synonymy.

Key to Ichneumoninae reared from Nearctic *Choristoneura* spp.

1. Propodeum with spiracle round to ovoid (as in Figs. 11*b*, 11*d*); clypeus convexly rounded in lateral view. *Female*: hind coxa with a keel or tooth (Fig. 12*c*) 2
— Propodeum with spiracle elongate (as in Fig. 6*f*); clypeus flat in lateral view, middle and lateral edges forming a uniform plane. *Female*: hind coxa without a keel or tooth 4
2(1). Mesoscutum with notaulus absent or barely visible as an indistinct impression anteriorly. *Male*: supraclypeal area completely brown to black . . . . . *Phaeogenes cacoeciae* Viereck
— Mesoscutum with notaulus as a deep groove on anterior quarter. *Male*: supraclypeal area yellow to white in most specimens (a few specimens from British Columbia completely brown) . . . . . *Dirophanes* 3
3(2). Hind tibia orange to brown, without strongly contrasting brown and yellow bands. *Female*: length of tooth on hind coxa greater than width of hind basal tarsomere . . . . . *Dirophanes maculicornis* (Stephens)
— Hind tibia banded, dark brown basally and apically and light yellow to brownish yellow medially. *Female*: length of tooth on hind coxa less than the width of hind basal tarsomere. . . . . *Dirophanes gaspesianus* (Provancher)
4(1). Propodeum with areolar region half-moon-shaped, medial longitudinal carinae curving strongly and continuously into medial portion of anterior transverse carina, two points of union not clearly distinguishable (*i.e.*, basal corners not angulate) (Fig. 12*b*). *Female*: metasoma without a white to yellow apical spot. *Male*: supraclypeal area light-coloured laterally with a vertical dark region medially . . . 5
— Propodeum with areolar region roughly quadrangular, medial longitudinal carinae joining anterior transverse carina at distinct angles (*i.e.*, basal corners angulate) (Fig. 12*a*). *Female*: metasoma with or without a white to yellow apical spot. *Male*: supraclypeal area as above in some specimens but varying from completely light-coloured to completely dark 6
5(4). *Female*: scutellum with black to brown medial longitudinal stripe and white to yellow laterally. *Male*: T1 completely dark posterior to spiracle . . . . . *Syspasis tauma* (Heinrich)
— *Female*: scutellum entirely white to yellow. *Male*: T1 white posterior to spiracle . . . . . *Orgichneumon calcatorius* (Thunberg)
6(4). Body predominantly black to brown **without** metallic blue tint; medium-sized species with body length 8–10 mm. *Female*: metasoma with a white to yellow apical spot; hypopygium short, exposing most of ovipositor (similar to Fig. 17*d*). *Male*: supraclypeal area completely yellow to white . . . . . *Ichneumon* Linnaeus 7
— Body predominantly black to brown **with** slight to strong metallic blue tint; large-bodied species with body length 12–20 mm. *Female*: metasoma without a white to yellow apical spot; hypopygium elongate, exposing only apical portion of ovipositor (similar to Fig. 17*c*). *Male*: supraclypeal area entirely dark with metallic blue tint or at least with dark medial vertical stripe . . . . *Patrocloides* Heinrich 8
7(6). T2 with transverse scarlike regions near base (thyridia) (see Fig. 8*f*) separated by distance slightly greater than width of one thyridium . . . . . *Ichneumon gestuosus* Cresson
— T2 with thyridia separated by distance about one-third width of one thyridium . . . . . *Ichneumon audax* Cresson
8(6). Middle and hind tibia completely dark, fore tibia dark with the inner edge partly yellow but not forming a complete band medially; head, mesosoma, and metasoma with distinct metallic blue tint . . . . . *Patrocloides montanus* (Cresson)
— All tibiae with dark basal and apical bands, medially with a region of white to pale yellow forming a complete band; head and mesosoma black without metallic tinge and metasoma black or with slight metallic blue tint . . . . . *Patrocloides perluctuosus* (Provancher)

Subfamily Lycorininae

The biology of the Lycorininae (*Lycorina* Holmgren) is not well known, but species appear to be koinobionts that lay their egg in the anus of lepidopteran larvae (Shaw 2004) and complete their development as ectoparasitoids (Coronado-Rivera *et al.* 2004). The eggs have a stalk with an anchor similar to that of some Tryphoninae (Coronado-Rivera *et al.* 2004), which suggests that intial development is as an ectoparasitoid, although this has not been confirmed by direct observation. Carlson (1979)

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reported that *L. albomarginata* was reared from *C. rosaceaca*, which is the only record of the subfamily on *Choristoneura* spp.

Literature: Cushman (1920) provided a key to the five Nearctic species under the names *Toxophoroides* Cresson and *Chlorolycorina* Cushman, but both of these are junior synonyms of *Lycorina*.

Subfamily Mesochorinae

Almost all mesochorines for which the biology is known are obligate koinobiont endoparasitic hyperparasitoids of ichneumonoids or, rarely, tachinids (Wahl 1993*b*). The primary host is usually a lepidopteran or sawfly larva. The female probes the primary host's haemocoel with its slender ovipositor and if a parasite larva is encountered, then an egg is laid inside it (Gauld 1984). Emergence is from the prepupa (Allen *et al.* 1969). Seven species of *Mesochorus* have been infrequently reared from five species of *Choristoneura* (Table 3).

Literature: Dasch (1971) revised the North American species of the subfamily. Wahl (1993*a*) subsequently synonymized *Stictopisthus* Thomson under *Mesochorus* so that the *Choristoneura* parasitoids reported in the literature as *S. argaleus* Dasch, *S. flaviceps* (Provancher), and *S. lanceolatus* Dasch are now included in *Mesochorus*. Schwenke (1999) revised the European species and recognized *Stictopisthus* as a discrete genus, but his only justification was that recognition of the genus aided species identification and he provided no characters or analysis to support his action. I follow the classification of Wahl (1993*a*) because he used cladistic methods and clearly showed that species classified in *Stictopisthus* represent a derived group within *Mesochorus*.

Subfamily Metopiinae

Metopiines are endoparasitoids of Lepidoptera (Wahl 1993*b*). They lay their eggs in the host larva (Table 2) and emerge from the pupa (Gauld *et al.* 2002*a*). Those species that lay eggs in leafrollers (*e.g.*, on *C. rosaceana*) most likely enter the leaf roll to oviposit because they have short ovipositors and short, strong legs that help the female pull herself into recesses. This contrasts with most other subfamilies that parasitize leafrollers, which oviposit through the leaf roll and have correspondingly long ovipositors for this purpose (Gauld *et al.* 2002*a*). Eight species in four genera have been reared from nine species of Nearctic *Choristoneura* (Table 3). None of the species are abundant parasitoids of *Choristoneura* spp. in North America, although low numbers have been recovered in many rearing surveys (*e.g.*, Dowden *et al.* 1948; Allen *et al.* 1969; Torgersen and Beckwith 1974). *Exochus nigripalpis* Thomson is remarkable in that it has been reared from eight species of *Choristoneura*, which is more species than any other Nearctic ichneumonid.

Literature: Townes and Townes (1959) revised the Nearctic species. Gauld *et al.* (2002*a*) revised the Costa Rican species and included additional biological information for the genera and redescriptions of some Nearctic species.

Key to Metopiinae reared from Nearctic *Choristoneura* spp.

1. MS3–MS5 with laterotergites (Figs. 16*g*, 16*h*); tarsal claws of fore and middle legs simple (as in Fig. 15*c*) 2
— MS3–MS5 superficially without laterotergites, present only as very narrow, inconspicuous vestiges; tarsal claws of fore and middle legs pectinate at least basally (as in Fig. 15*d*) 6
2(1). Middle tibia with outer spur much shorter than inner spur; areolet open . . . *Exochus* Gravenhorst 3
— Middle tibia with spurs approximately equal in length; areolet closed in most specimens . . . . . *Triclistus emarginalus* (Say)
3(2). Hind coxa and femur dark brown to black; head with medial triangular process between antennal sockets extending dorsally to supra-antennal region as a high, wide lamella with a longitudinal groove (similar to Fig. 7*e*) . . . . . *Exochus turgidus* Holmgren
— Hind coxa and femur orange; head with medial triangular process between antennal sockets not extending dorsally as a high lamella (similar to Fig. 7*f*) 4
4(3). MS3 with laterotergite wedge-shaped (Fig. 16*h*). . . . . *Exochus washingtonensis* (Davis)
— MS3 with laterotergite semicircular to subrectangular (Fig. 16*g*) 5
5(4). Head with supraclypeal area varying from completely black–brown to mostly brown with a narrow lighter area ventral to antennae and between eyes and mandibles; pronotum entirely black except some specimens with a small tinge of yellow in dorsoposterior corner. . . . *Exochus nigripalpis* Thomson
— Head with supraclypeal area completely light-coloured except for small dark vertical stripe medially in some specimens; pronotum with posterior half of dorsal edge of pronotum yellowish white. . . . . *Exochus albifrons* Cresson

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6(1). T2 with lateral longitudinal carinae extending no more than two-thirds length of tergite (Fig. 14*e*); pronotum with broad, shallow groove that parallels upper edge and is most evident posteriorly (Fig. 9*b*) . . . . . *Chorinaeus* Holmgren 7

— T2 with lateral longitudinal carinae extending entire length of tergite (Fig. 14*f*); pronotum without groove paralleling upper edge (as in Fig. 9*d*) . . . . . *Trieces crassipes* Walley

7(6). Hind coxa predominantly brown to black; T1 with dorsal and ventral lateral longitudinal carinae meeting at posterior end of segment at an angle of about 25° . . . . *Chorinaeus subcarinatus* Holmgren

— Hind coxa predominantly orange; T1 with dorsal and ventral lateral longitudinal carinae meeting at posterior end of segment at an angle of about 45° . . . . . *Chorinaeus excessorius* Davis

Subfamily Pimplinae

The Pimplinae is the most biologically diverse subfamily of ichneumonids. Most Ephialtini, including those that parasitize *Choristoneura* spp., are idiobiont ectoparasitoids that oviposit in the immature stages of holometabolous insects (Gauld 1991). However, some other Pimplinae develop as koinobiont ectoparasitoids on immature or adult spiders (Wahl and Gauld 1998), and the larvae of several genera consume multiple eggs in spider egg sacs to complete development and thus are considered predators rather than parasitoids. Some members of the Pimplini are also parasitoids of *Choristoneura* spp. Of these, members of the *Pimpla* group of genera (*Apechthis* Förster, *Itoplectis* Förster, *Pimpla* Fabricius) are idiobiont endoparasitoids of the pupae of Lepidoptera (Gauld 1991). Some species are known to be both primary parasitoids and facultative hyperparasitoids, for example *Itoplectis conquisitor* (Say) (Townes and Townes 1960). The only other member of the Pimplini reared from *Choristoneura* spp. is *Theronia atalantae* (Poda) from the *Theronia* group of genera, which is a pupal idiobiont endoparasitoid (Carolin and Coulter 1959). It appears that *T. atalantae* can be either a primary or a facultative hyperparasitoid and adult females may overwinter, like some ichneumonines (Townes and Townes 1960). In total, 30 species of Pimplinae in 8 genera have been reared from 8 species of Nearctic *Choristoneura*. Some of these species are important controlling agents of *Choristoneura* spp. For example, *Apechthis ontario* (Cresson) and the ichneumonine *D. maculicornis* were the two most abundant parasitoids of *C. fumiferana* in outbreaks in the northeastern United States in the mid-1940s (Jaynes and Drooz 1952). *Apechthis ontario* was also one of the five most abundant parasitoids of *C. occidentalis* in British Columbia in the 1940s (Wilkes *et al.* 1948). *Itoplectis conquisitor* was the second most abundant parasitoid of *C. pinus* after the ichneumonine *D. maculicornis* in eastern Canada in the early 1950s (Walley 1953). The Pimplinae has received the most attention with respect to introductions for biological control (see comments below), perhaps because it is the best known ichneumonid subfamily at the species level and species are relatively large and readily identifiable.

Literature: Townes and Townes (1960) revised the North American species. The parasitoid rearing records they listed for *C. fumiferana* must be cross-referenced to locality to help determine host species because their study preceded the revision of *Choristoneura* by Freeman (1967) (*e.g.*, specimens from British Columbia likely are from *C. occidentalis*, not *C. fumiferana* as Townes cited). Gauld (1991) provided good summaries of the biology of the different groups of pimplines and Gauld *et al.* (2002*b*) provided the most recent classification for the subfamily.

Comments

The nomenclature of the Pimplinae was not stable prior to the early 1990s because of H.K. Townes's failure to recognize Opinion 159 of the International Code of Zoological Nomenclature (1945), which dealt with the application of the ichneumonid names *Ichneumon*, *Pimpla*, and *Ephialtes*. Because of Townes's extensive publications and influence on ichneumonid taxonomy, many works published prior to this time followed his nomenclature. The current work does not recognize Townes's nomenclature, but since many older works cited in this study follow the Townesian system, a comparison of the two sets of names is provided in Table 6. In summary, all references to *Ephialtes* spp. reared from Nearctic *Choristoneura* spp. refer to species correctly assigned to *Apechthis* and all *Coccygomimus* spp. refer to species correctly assigned to *Pimpla* (see Appendix A for a list of all species names). *Pimpla disparis* Viereck is an eastern Palaearctic and Oriental species that was introduced and became established in the eastern United States of America to help control the gypsy moth, *Lymantria dispar*

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Table 6. Comparison of nomenclature for selected pimpline taxa based on acceptance of Opinion 159 of the International Commission on Zoological Nomenclature (1945) versus H.K. Townes's incorrect nomenclature based on the rejection of Opinion 159.

Correct nomenclature	Townes's incorrect nomenclature
Subfamily Pimplinae	Subfamily Ephialtinae
Tribe Ephialtini	Tribe Pimplini
Genus *Ephialtes* Schrank	Genus *Pimpla* Fabricius
Tribe Pimplini	Tribe Ephialtini
Genus *Apechthis* Förster	Genus *Ephialtes* Schrank
Genus *Pimpla* Fabricius	Genus *Coccygomimus* Saussure

Note: No species of *Ephialtes* (Ephialtini) have been reared from Nearctic *Choristoneura* spp., therefore any references to *Ephialtes* spp. in the literature on Nearctic *Choristoneura* spp. refer to species correctly assigned to *Apechthis* (Pimplini).

(Linnaeus) (Schaefer *et al.* 1989). The present study is the first to record it from *Choristoneura* (from *C. fumiferana*) and from Canada (Ontario). In Japan, it has been reared from *Choristoneura diversana* (Hübner) (Kamijo 1973). *Pimpla turionellae* (Linnaeus) was introduced to North America several times in the 1950s in an attempt to control various pests, including *C. fumiferana* in eastern Canada (Bartlett *et al.* 1978), the winter moth, *Operophtera brumata* (Linnaeus), in Nova Scotia (Graham 1958), and the pine shoot moth *Rhyacionia buoliana* (Denis and Schiffermüller) in Ontario (Coppel and Arthur 1954). It is not certain whether it established (Townes and Townes 1960). It has been reared from *C. murinana* in Europe (Mills and Kenis 1991) and from *C. diversana* in Japan (Kamijo 1973). *Itoplectis maculator* (Fabricius) is a Palaearctic species that was introduced to Ontario between 1948 and 1956 in an attempt to control *C. fumiferana*, but apparently did not establish. It was also introduced into Oregon between 1949 and 1954 to help control the omnivorous leaftier, *Cnephasia longana* (Haworth) (Tortricidae) (Dickason and Poonyathawon 1972). It was recovered in 1950 and 1955, but does not appear to have established in Oregon (Carlson 1979). In Europe, *I. maculator* has been reared from *Choristoneura murinana* (Mills and Kenis 1991). The species is facultatively hyperparasitic (Carlson 1979) on several ichneumonids, but it is unclear whether this was known by those attempting to introduce it.

Key to Pimplinae reared from Nearctic *Choristoneura* spp.

1. Propodeum with complete lateral and medial longitudinal carinae and with posterior transverse carina; fore tarsal claws greatly enlarged, simple, with a long, flattened bristle arising near base that extends to tip of claw (Fig. 15*f*); body predominantly orange . . . . . *Theronia atalantae* (Poda)
— Propodeum with only medial longitudinal carinae or no carinae (lateral longitudinal and transverse carinae absent); fore tarsal claws not greatly enlarged and without a long, flattened bristle; body predominantly black to brown. *Female*: fore tarsal claw either with a subapical tooth (Fig. 15*e*) or simple (Fig. 15*c*). *Male*: fore tarsal claw simple 2
2(1). Hind tibia, if banded, with extreme base light (dark band sub-basally). *Female*: ovipositor of various lengths, **but** if projecting beyond apex of metasoma by less than length of metasoma **then** dorsal valve with a distinct subapical angular swelling (nodus). *Male*: hypopygium transverse, apical edge truncate or concave medially (Fig. 17*d*) . . . . . Ephialtini 3
— Hind tibia, if banded, with extreme base dark. *Female*: ovipositor projecting beyond apex of metasoma by less than length of metasoma **and** dorsal valve **without** a distinct subapical nodus (Fig. 16*a*). *Male*: hypopygium triangular, apical edge elongate medially (Fig. 17*c*) . . . . Pimplini (except *Theronia*) 8
3(2). T2 without oblique grooves delineating anterolateral corners, (Fig. 14*c*). *Male*: fore femur sometimes with one or two concave regions ventrally . . . . . *Scambus* (9 species)
— T2 with oblique grooves delineating anterolateral corners (Fig. 14*d*), grooves strong or weak, but definitely present. *Male*: fore femur without concave regions ventrally 4

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4(3). Hind tibia dark except for light area at extreme base. *Female*: ovipositor projecting beyond apex of metasoma by greater than length of fore wing (ovipositor sheath 1.1–1.5 times length of fore wing) . . . . . *Exeristes comstockii* (Cresson)

— Hind tibia banded (light basally and medially and dark sub-basally and apically). *Female*: ovipositor projecting beyond apex of metasoma by less than length of fore wing (ovipositor sheath 0.4–0.7 length of fore wing) 5

5(4). Hind wing with vein 2/Cu distinctly closer to M than to A (vein 1/Cu less than half as long as cu-a) (as in Fig. 6*e*). *Male*: supraclypeal area and clypeus white. *Female*: ventral valve of ovipositor with ridge of basal tooth about 30° from horizontal . . . . . *Iseropus* Förster 6

— Hind wing with vein 2/Cu approximately equidistant between M and A (vein 1/Cu about as long as cu-a) (as in Fig. 2). *Male*: supraclypeal area dark, clypeus white. *Female*: ventral valve of ovipositor with ridge of basal tooth about 15° from horizontal . . . . . *Acropimpla* Townes 7

6(5). Hind tarsus with dark band on apex of second segment occupying 0.2–0.3 length in male and 0.2–0.4 length in female. *Female*: labial palpus white. *Male*: genitalia with gonoforceps strongly narrowed apically into a long point . . . . . *Iseropus coelebs* (Walsh)

— Hind tarsus with dark band on apex of second segment occupying 0.4–0.6 length in male and 0.4–0.8 length in female. *Female*: labial palpus brown. *Male*: genitalia with gonoforceps gradually narrowed into a short, rounded point . . . . . *Iseropus stercorator* (Fabricius)

7(5). Hind femur with about apical 0.3 dark and this blending weakly into orange colour basally; fore wing of most specimens with vein 2m-cu joining areolet distinctly basal to distal corner (as in Fig. 5*f*). *Female*: ovipositor with an evenly curved dorsal subapical swelling (nodus). *Male*: genitalia with gonoforceps short (Fig. 17*e*) . . . . . *Acropimpla pronexus* Townes

— Hind femur with about apical 0.2 dark and this sharply delineated from orange colour basally; fore wing of most specimens with vein 2m-cu joining areolet at or very near distal corner (as in Fig. 5*e*). *Female*: ovipositor with an angular dorsal subapical nodus. *Male*: genitalia with gonoforceps long (Fig. 17*f*) . . . . . *Acropimpla alboricta* (Cresson)

8(2). Eye with inner margin gradually emarginate (not strongly notched) slightly dorsal to antennal socket (as in Fig. 8*a*). *Male*: supraclypeal area black. *Female*: fore tarsal claw simple, without a large basal tooth (Fig. 15*c*) . . . . . *Pimpla* 10

— Eye with inner margin strongly notched slightly dorsal to antennal socket (Fig. 7*c*). *Male*: supraclypeal area of male black, white, or yellow. *Female*: fore tarsal claw with a large basal tooth (7 of 9 species) (Fig. 15*e*) or tooth minute to absent (as in Fig. 15*c*) 9

9(8). *Female*: ovipositor strongly curved ventrally at apex (Fig. 16*c*). *Male*: clypeus and supraclypeal area white to yellow or, in some species, supraclypeal area pale laterally with brown medially . . . . *Apechthis* 18

— *Female*: ovipositor straight (as in Fig. 16*a*). *Male*: clypeus and supraclypeal area completely black to brown . . . . . *Itoplectis* 20

10(8). Hind tibia completely dark brown to black 11

— Hind tibia with a medial light-coloured band or completely orange 12

11(10). Middle and hind coxae black . . . . . *Pimpla disparis* Viereck

— Middle and hind coxae orange . . . . . *Pimpla pedalis* Cresson

12(10). Middle and hind coxae black . . . . . *Pimpla turionellae* (Linnaeus)

— Middle and hind coxae orange 13

13(12). Male. 14

— Female. 16

14(13). Hind tibia completely orange except slightly darkened apically in some specimens . . . . . *Pimpla sanguinipes* Cresson

— Hind tibia with a distinct pale yellow to white submedial band, dark orange–brown to black only basally and apically 15

15(14). Hind femur with apical 0.1–0.2 dark; MS2 with laterotergite (see Figs. 16*g*, 16*h*) about 2.9 times as long as apical width. . . . . *Pimpla aequalis* Provancher

— Hind femur completely orange; MS2 with laterotergite about 2.2 times as long as apical width . . . . . *Pimpla punicipes* Cresson

16(13). Hind tibia dark brown to black basally and apically, submedially with a distinct pale yellow to whitish band . . . . . *Pimpla aequalis* Provancher

— Hind tibia completely orange except slightly darkened apically in some specimens 17

17(16). MS2 with laterotergite (see Figs. 16*g*, 16*h*) narrow, about 4.2 times as long as apical width . . . . . *Pimpla sanguinipes* Cresson

— MS2 with laterotergite wide, about twice as long as apical width . . . . . *Pimpla punicipes* Cresson

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18(9). T1 in lateral view convexly rounded dorsally near middle. *Female*: hind tarsal claws without a tooth (as in Fig. 15*c*) . . . . . *Apechthis ontario* (Cresson)
— T1 strongly and angularly raised like a pyramid near middle in lateral view. *Female*: hind tarsal claws with a large tooth (Fig. 15*e*) or tooth absent 19
19(18). *Female*: sclerite covering base of fore wing (tegula) with at least some brown–black at least basally. Hind tibia with a yellowish white band that covers about one-third of tibial length. *Male*: hind tarsus with basal segment predominantly brown, some lighter colour may be present basally and anteriorly but more than half of segment dark . . . . . *Apechthis picticornis* (Cresson)
— *Female*: tegula completely white–yellow. Hind tibia with a yellowish white band that covers about half tibial length. *Male*: hind tarsus with basal segment predominantly white, no more than 0.4 of segment dark . . . . . *Apechthis annulicornis* (Cresson)
20(9). Hind tibia completely orange . . . . . *Itoplectis viduata* (Gravenhorst)
— Hind tibia banded (brown to black basally and apically, lighter coloured submedially) 21
21(20). Female 22
— Male 26
22(21). Mesopleuron with punctures large and dense medially, nearly touching each other in densest areas; metasoma black with some brown or orange laterally, especially on posterior tergites; fore tarsal claw with a broad tooth (as in Fig. 15*e*) . . . . . *Itoplectis maculator* (Fabricius)
— Mesopleuron with punctures fine and less dense medially, separated from each other by their own diameter or greater in densest areas; metasoma almost completely black with brown or orange only on posterior edges of tergites; fore tarsal claw with or without a tooth 23
23(22). Metasomal tergites with a distinct white band on each posterior margin; T3 about 1.6 times as wide as long . . . . . *Itoplectis conquisitor* (Say)
— Metasomal tergites without a white band on each posterior margin (if bands present, they are tan, not white); T3 about 2.1 times as wide as long 24
24(23). Fore tarsal claw with a broad tooth . . . . . *Itoplectis quadricingulata* (Provancher)
— Fore tarsal claw with a minute tooth or tooth absent 25
25(24). Ovipositor sheath about 3.6 times as long as T1; fore wing 4.0–8.5 mm long . . . . . *Itoplectis evetriae* Viereck
— Ovipositor sheath about 2.4 times as long as T1; fore wing 2.5–5.3 mm long . . . . . *Itoplectis vesca* Townes
26(21). Metasomal tergites with a distinct white band on each posterior margin; T4 and T5 polished and with punctures spaced more widely than diameter of puncture . . . . . *Itoplectis conquisitor* (Say)
— Metasomal tergites without a white band on each posterior margin (if bands present, they are tan, not white). T4 and T5 matte with crowded punctures spaced less than diameter of puncture 27
27(26). Scape and pedicel black dorsally and completely yellow ventrally . . . *Itoplectis maculator* (Fabricius)
— Scape and pedicel predominantly black–brown with a small spot of lighter colour near apex of ventral side of scape in some specimens, but dorsal and ventral sides not strongly contrasting 28
28(27). Fore coxa predominantly white to yellow (may be black to brown basally) . . . . . *Itoplectis quadricingulata* (Provancher)
— Fore coxa predominantly black, brown, or orange, not white to yellow except apically in some specimens 29
29(28). Labial palp predominantly brown (partly white in some specimens, but not completely bright white); fore wing 4.0–8.5 mm long . . . . . *Itoplectis evetriae* Viereck
— Labial palp completely bright white; fore wing 2.5–5.3 mm long . . . . . *Itoplectis vesca* Townes

Subfamily Tryphoninae

Tryphonines are koinobiont ectoparasitoids that lay stalked eggs on larval lepidopterans and sawflies (Kasparyan 1973). After hatching, the first-instar larvae remain inside the shell, attached by caudal appendages, and do not complete development until after host pupation (Gerig 1960). The stalk of the egg is embedded deep in the host, which allows host eclosion without sloughing of the egg and associated larva. Nine tryphonine species from three genera have been reared from six species of *Choristoneura*. *Phytodietus fumiferanae* Rowher is an abundant parasitoid of *C. occidentalis* in western North America (Carolin and Coulter 1959) and was successfully introduced into eastern North America to help control *C. fumiferana* (Wilkes 1946). *Phytodietus vulgaris* Cresson is a common parasitoid of *C. conflictana* in Alaska (Torgersen and Beckwith 1974). *Oedemopsis scabricula* (Gravenhorst) is a beneficial invasive accidentally introduced from the Palaearctic region and first found in southwestern British Columbia in the late 1970s (Loan and Doğanlar 1980).

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Literature: Townes *et al.* (1992) revised the North American species of Oedemopsini including those in the genera *Hercus* and *Oedemopsis*. Loan (1981) revised the North American species of the genus *Phytodietus*. Gauld *et al.* (1997) revised the tryphonines of Costa Rica and gave good biological summaries of *Phytodietus* and *Oedemopsis*. Kasparyan (1973) provided an excellent general summary of tryphonine biology and literature.

Key to Tryphoninae reared from Nearctic *Choristoneura* spp.

1. Areolet closed (Fig. 5*e*); propodeum without carinae; fore tibial spur distally curved outwards or straight (Fig. 17*a*), its antennal brush ending considerably before apex of spur . . . . . *Phytodietus* (Phytodietini) (7 species)

— Areolet open (as in Fig. 5*c*); propodeum with strong longitudinal and transverse carinae (Figs. 11*e*, 11*f*); fore tibial spur curved evenly inwards, its antennal brush extending nearly to apex of spur . . . . . (Oedemopsini) 2

2(1). Clypeus about as wide as high, in males evenly convex and in females strongly elevated medially into a beak or nose and appearing to be divided transversely by a downturned parabolic suture (Fig. 8*b*); T2 not shiny, with longitudinal striations between deep, close punctures; propodeum with many fine, thin transverse raised striations between carinae (Fig. 11*f*). . . . . *Oedemopsis scabricula* (Gravenhorst)

— Clypeus about 1.8 times as wide as high and not strongly elevated in either sex (as in Fig. 3*c*); T2 shiny, especially posteriorly, with weak longitudinal striations and very small, sparse punctures; propodeum smooth between carinae except for a few fine, raised striations between medial longitudinal carinae (Fig. 11*e*) . . . . . *Hercus fontinalis* (Holmgren)

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Appendix A

Ichneumonid genera and species associated with *Choristoneura* spp. in North America (from Table 3). Names shown in boldface type are valid. Names shown in regular font are junior synonyms and the corresponding senior synonym is indicated in boldface type at the end of the line.

aclerivorus (Rohwer, 1915) (*Camposcopus*), ***Habronyx***
acrobasidis (Ashmead, 1896) (*Ensimus*), ***Lissonota***
Acropimpla Townes, 1960
acuminator (Müller, 1776) (*Ichneumon*), ***Theronia atalantae***
Adelopimpla Schulz, 1906, ***Lissonota***
Aenoplex Förster, 1869, ***Mastrus***
aequalis Provancher, 1880, ***Pimpla***
aestivale (Viereck, 1921) (*Labrorychus*), ***Agrypon prismaticum***
Aglaocryptus Cameron, 1903, ***Ischnus***
Agrypon Förster, 1860
Agrypum Schulz, 1906, ***Agrypon***
alberta Dasch, 1988, ***Glypta***
albifrons Cresson, 1868, ***Exochus***
albiscutata (Gmelin, 1790) (*Ichneumon*), ***Theronia atalantae***
albomarginata (Cresson, 1870) (Glypta), ***Lycorina***
albomarginata soror (Cushman, 1920) (*Chlorolycorina*), ***Lycorina albomarginata***
albonotata Dasch, 1988, ***Glypta***
alboricta (Cresson, 1870) (*Pimpla*), ***Acropimpla***
aldrichii (Davis, 1898) (*Glypta*), ***Apophua simplicipes***
Alegina Förster, 1869, ***Gelis***
alpinum (Davis, 1898) (*Anomalon*), ***Agrypon***
altalpium (Heinrich, 1952) (*Ephialtes*), ***Scambus brevicornis***
ameformis (Keler, 1937) (*Pimpla*), ***Scambus brevicornis***
Ameloctonus Förster, 1869, ***Hyposoter***
americana Krieger, 1906, ***Theronia atalantae fulvescens***
Amersibia Förster, 1869, ***Lissonota***
Amesolytus Förster, 1869, ***Exochus***
Amyx Schiødte, 1839, ***Lycorina***
Anarthronota Schmiedeknecht, 1900, ***Lissonota***
Androna Cameron, 1911, ***Temelucha***
Anisitsia Viereck, 1912, ***Dusona***
annulata (Ulbricht, 1911) (*Pimpla*), ***Itoplectis viduata***
annulatus (Provancher, 1886) (*Mesoleius*), ***Phytodietus vulgaris***
annulicornis (Cresson, 1870) (*Pimpla*), ***Apechthis***
annulicornis componotus (Davis, 1898) (*Pimpla*), ***Apechthis***
annulipes (Cresson, 1864) (*Mesoleptus*), ***Hyposoter***
anomalus (Morley, 1906) (*Phthorimus*), ***Scambus brevicornis***
Apechthis Förster, 1869
Apechtis Thomson, 1889, ***Apechthis***
Apophua Morley, 1913
Arctodeuon Hellén, 1967, ***Gelis***
arenicola Thomson, 1887, ***Tranosema rostrale***
argaleus (Dasch, 1971) (*Stictopisthus*), ***Mesochorus***
arlequinatus (Geoffrey, 1785) (*Ichneumon*), ***Itoplectis maculator***
Aschistus Förster, 1869, ***Gelis***
ashmeadii (Provancher, 1888) (*Meniscus*), ***Pimpla aequalis***
assertorius (Fabricius, 1793) (*Ichneumon*), ***Ischnus inquisitorius***
Asynida Gistel, 1848, ***Lissonota***
atalantae (Poda, 1761) (*Ichneumon*), ***Theronia***
atalantae fulvescens (Cresson, 1865) (*Pimpla*), ***Theronia***
atalantae gestator (Thunberg, 1824) (*Ichneumon*), ***Theronia***
atalantae himalayensis Gupta, 1983, ***Theronia***
Ateleophadnus Cameron, 1905, ***Scambus***
atriceps (Cresson, 1879) (*Cryptus*), ***Ischnus inquisitorius atricollaris***
atriventris Cresson, 1872, ***Mesochorus sylvarum***
atrocoxalis (Ashmead, 1902) (*Epiurus*), ***Scambus***
atrocoxalis (Cresson, 1870) (*Pimpla*), ***Itoplectis viduata***
audax Cresson, 1877, ***Ichneumon***
augustus (Viereck, 1906) (*Amorphota*), ***Sinophorus teratis***
Austrolissonota Blanchard, 1941, ***Meniscomorpha***
balearicus (Kriechbaumer, 1894) (*Pimpla*), ***Scambus brevicornis***
banksianae Allen, 1967, ***Dirophanes maculicornis***
Barydotira Förster, 1869, ***Gelis***
basizona (Viereck, 1924) (*Campoplex*), ***Tranosemella praerogator***
Bathycetes Förster, 1869, ***Lissonota***
baumhoferi Cushman, 1930, ***Pristomerus***
bicoloripes (Ashmead, 1902) (*Epiurus*), ***Scambus brevicornis***
bicoloripes (Viereck, 1926) (*Amorphota*), ***Dusona seamansi***
bisignatus (Holmgren, 1890) (*Phaeogenes*), ***Dirophanes maculicornis***
Blaptocampus Thomson, 1892, ***Camposcopus*** (subgenus of ***Habronyx***)
Bothynophrys Förster, 1869, ***Lissonota***
Brachypterus Gravenhorst, 1829, ***Ichneumon***
brevicollis Thomson, 1886, ***Mesochorus gemellus***
brevicornis (Gravenhorst, 1829) (*Pimpla*)
brevicornis goniozator Aubert, 1982, ***Scambus brevicornis***
brevicornis rivalis (Habermehl, 1923) (*Epiurus*), ***Scambus brevicornis***
brevis Cushman, 1915, ***Glypta rufiscutellaris***
bruneifrons (Viereck, 1909) (*Pimpla*), ***Iseropus stercorator orgyiae***
brunneus Brischke, 1880, ***Mesochorus nuncupator***
buolianae (Hartig, 1838) (*Pimpla*), ***Scambus***
burgessi (Cresson, 1868) (*Tryphon*), ***Phytodietus***
burkei (Viereck, 1910) (*Ichneumon*), ***Orgichneumon calcatorius***
cacoeciae (Viereck, 1924) (*Campoplex*), ***Tranosema rostrale***
cacoeciae (Viereck, 1924) (*Ephialtes*), ***Itoplectis quadricingulata***
cacoeciae Viereck, 1924, ***Phaeogenes***
calcatorius (Thunberg, 1824) (*Ichneumon*), ***Orgichneumon***
calcatorius albidior Heinrich, 1977, ***Orgichneumon***
Campocineta Schmiedeknecht, 1900, ***Lissonota***
Campoletidea Viereck, 1912, ***Sinophorus***
Campoplegidea Viereck, 1912, ***Dusona***
Campoplex Gravenhorst, 1829
Camposcopus Förster, 1869 (subgenus of ***Habronyx***)
Campothreptus Förster, 1869, ***Oedemopsis***
canadense (Provancher, 1874) (*Anomalon*), ***Agrypon prismaticum***

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canadensis Walley, 1960, ***Scambus***
Catalytus Förster, 1851, ***Gelis***
Cephaloglypta Obrtel, 1956
Chlorolycorina Cushman, 1920, ***Lycorina***
Chorinaeus Holmgren, 1858
choristoneurae Dasch, 1988, ***Glypta***
cingulatolr (Thunberg, 1824) (Ichneumon), ***Pimpla turionellae***
cingulatus (Ratzeburg, 1852) (*Pimpla*), ***Scambus planatus***
clavipes (Davis, 1898) (*Anomalon*), ***Parania geniculata***
Cnemopimpla Cameron, 1903, ***Iseropus***
Coccygomimus Saussure, 1892, ***Pimpla***
coelebs (Walsh, 1873) (*Pimpla*), ***Iseropus***
Coelopimpla Brèthes, 1916, ***Pimpla***
coleophorae (Ashmead, 1890) (*Hemiteles*), ***Gelis tenellus***
Colobacis Cameron, 1901, ***Ichneumon***
colonator (Thunberg, 1824) (*Ichneumon*), ***Theronia atalantae***
comstockii (Cresson, 1880) (*Ephialtes*), ***Exeristes***
concolor (Ratzeburg, 1848) (*Pimpla*), ***Scambus brevicornis***
conflictanae Dasch, 1988, ***Glypta***
conflictanae Loan, 1981, ***Phytodietus***
confusus (Viereck, 1925) (*Campoplex*), ***Hyposoter annulipes***
Conobasta Förster, 1869, ***Glypta***
conodor (Viereck, 1925) (*Campoplex*), ***Enytus montanus***
conquisitor (Say, 1835) (*Cryptus*), ***Itoplectis***
conquisitrix (Schulz, 1906) (*Pimpla*), ***Itoplectis conquisitor***
Coreojoppa Uchida, 1926, ***Ichneumon***
crassipes (Rossi, 1790) (*Ichneumon*), ***Theronia atalantae***
crassipes Walley, 1969, ***Trieces***
Cremastidea Viereck, 1912, ***Temelucha***
cryptocampi (Boie, 1857) (*Pimpla*), ***Scambus vesicarius***
Cryptochorus Aubert, 1965, ***Mesochorus***
Ctenopimpla Cameron, 1899, ***Lissonota***
Daictes Förster, 1869, ***Mastrus***
decoratus Viereck, 1925, ***Campoplex mellipes***
decorus Walley, 1960, ***Scambus***
Delopia Cameron, 1903, ***Dusona***
dentatus (Pic, 1923) (*Phaeogenes*), ***Dirophanes maculicornis***
depressus (Provancher, 1874) (*Hemiteles*), ***Gelis tenellus***
Diblastomorpha Förster, 1869, ***Glypta***
Dihyboplax Enderlein, 1919, ***Pimpla***
dinianae (Fahringer, 1948) (*Phaeogenes*), ***Dirophanes maculicornis***
Dioborus Rao, 1953, ***Agrypon***
Dioctes Förster, 1869, ***Enytus***
Dioratica Förster, 1869, ***Campoplex***
dioryctriae Dasch, 1984, ***Agrypon***
Dirophanes Förster, 1869
disparis Viereck, 1911, ***Pimpla***
diversicolor Viereck, 1912, ***Mesochorus gemellus***
dorsata (Zetterstedt, 1838) (*Bassus*), ***Oedemopsis scabricula***
Dusona Cameron, 1901
Ebiicha Seyrig, 1935, ***Hyposoter***
Echthrodoca Schmiedeknecht, 1900, ***Lissonota***
edmontonensis (Viereck,1925) (*Campoplegidea*), ***Dusona seamansi***
Edrisa Cameron, 1907, ***Mesochorus***
emarginalus (Say, 1829) (*Ophion*), ***Triclistus***
Ensimus Förster, 1869, ***Lissonota***
Enytus Cameron, 1905
epagoges (Cushman, 1917) (*Cremastus*), ***Temelucha platynotae***
Ephialtes Schrank, 1802, ***Apechthis***
Epiurus Förster, 1869, ***Scambus***
Eremochila Förster, 1869, ***Exeristes***
Erigorgus Förster, 1869
erratica Cresson, 1870, ***Glypta***
Erythrocryptus Cameron, 1905, ***Ischnus***
erythropus Viereck, 1909, ***Pimpla sanguinipes***
Erythroscambus Walley, 1960, ***Scambus***
Erythrotheronia Cameron, 1905, ***Theronia***
esucha (Cushman, 1924) (*Ephialtes*), ***Itoplectis quadricingulata***
Eudeleboea Blanchard, 1935, ***Meniscomorpha***
Euichneumon Berthoumieu, 1904, ***Ichneumon***
Eulimneria Schmiedeknecht, 1907, ***Sinophorus***
euphrantae (Schmiedeknecht, 1914) (*Pimpla*), ***Scambus brevicornis***
eureka (Ashmead, 1890) (*Limneria*), ***Enytus***
euurae (Ashmead, 1890) (*Pimpla*), ***Scambus vesicarius***
evetriae (Cushman, 1917) (*Cremastus*), ***Temelucha***
evetriae Viereck, 1913, ***Itoplectis***
evetrivora (Rohwer, 1914) (*Podogaster*), ***Parania geniculata***
examinator (Fabricius, 1804) (*Cryptus*), ***Pimpla turionellae*** *examinatrix* Schulz, 1906, ***Pimpla turionellae***
excavata Obrtel, 1956, ***Cephaloglypta murinanae***
excessorius Davis, 1897, ***Chorinaeus***
Exeristes Förster, 1869
Exeristesoides Uchida, 1928, ***Itoplectis***
exilis Provancher, 1875, ***Ischnus inquisitorius atricollaris***
Exochus Gravenhorst, 1829
facialis Rohwer, 1920, ***Phytodietus burgessi***
femoralis Benoit, 1953, ***Theronia atalantae***
feralis Cresson, 1874, ***Pimpla punicipes***
Fianonia Seyrig, 1952, ***Gelis***
filiforme (Provancher, 1886) (*Anomalon*), ***Agrypon prismaticum***
flavicans (Fabricius, 1793) (*Ichneumon*), ***Theronia atalantae***
flaviceps Provancher, 1879 (*Mesochorus*), ***Mesochorus***
flavicrus Townes and Townes, 1959, ***Chorinaeus subcarinatus***
flavopictus (Rudow, 1883) (*Cryptus*), ***Ischnus inquisitorius***
flavotrochanteratus (Pfeffer, 1913) (*Pimpla*), ***Scambus buolianae***
fontinalis (Holmgren, 1857) (*Eclytus*), ***Hercus***
fontinalis flavens Townes and Gupta, 1992, ***Hercus***
fontinalis pleuralis (Provancher, 1875) (*Orthocentrus*), ***Hercus***
forbesi (Weed, 1887) (*Cremastus*), ***Temelucha***
Foveoglypta Hellén, 1915, ***Glypta***
freyi Hellén, 1949, ***Pimpla turionellae***
frontalis (Zetterstedt, 1838) (*Bassus*), ***Hercus fontinalis***
fulvipes (Cresson, 1864) (*Exochus*), ***Triclistus emarginalus***
fumiferanae (Viereck, 1912) (*Conoblasta*), ***Glypta***
fumiferanae Rohwer, 1922, ***Phytodietus***
fumosus (Ulbricht, 1910) (*Pimpla*), ***Scambus brevicornis***
fuscatus (Walsh, 1869) (*Hemiteles*), ***Gelis tenellus***
fuscicornis (Schrank, 1785) (*Ichneumon*), ***Pimpla turionellae***
gallicola (Giraud, 1872) (*Pimpla*), ***Scambus planatus***
gallicola (Morley, 1908) (*Pimpla*), ***Scambus vesicarius***
gaspesianus (Provancher, 1882) (*Phaeogenes*), ***Dirophanes***
Gelis Thunberg, 1827
gemellus Holmgren, 1860, ***Mesochorus***
geminus (Gravenhorst, 1829) (*Cryptus*), ***Ischnus inquisitorius***
geniculata (Holmgren, 1857) (*Anomalon*), ***Parania***
gestuosus Cresson, 1877, ***Ichneumon***
Gibbonota Heinrich, 1937, ***Lissonota***
gigas (Fahringer, 1943) (*Phaeogenes*), ***Dirophanes maculicornis***
glycinivorellae (Kuwayama, 1928) (*Epiurus*), ***Scambus planatus***
glycinivorellae (Uchida, 1928) (*Epiurus*), ***Scambus planatus***
Glypta Gravenhorst, 1829
Gonioglyphus Seyrig, 1932, ***Lycorina***
gossypii (Ashmead, 1890) (*Pimpla*), ***Scambus hispae***
graminellae (Schrank, 1802) (*Ichneumon*), ***Iseropus stercorator***
Habrocryptus Thomson, 1873, ***Ischnus***
Habronyx (Camposcopus) Förster, 1869
Habronyx (Habronyx) Förster, 1869
Habropimpla Cameron, 1900, ***Pimpla***
hariolus (Cresson, 1867) (*Ichneumon*), ***Dirophanes maculicornis***
hawaiiensis Cameron, 1886, ***Pimpla punicipes***
Hemiepialtes Ashmead, 1906, ***Glypta***
Hemimachus Ratzeburg, 1852, ***Gelis***
Hercus Townes, 1969
hispae (Harris, 1835) (*Ichneumon*), ***Scambus***

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Holcogelis Aubert, 1957, ***Gelis***
holmgreni (Schmiedeknecht, 1888) (*Pimpla*), ***Iseropus stercorator***
Hybophanes Förster, 1869, ***Oedemopsis***
Hyposoter Förster, 1869
Ichneumon Linnaeus, 1758
idahoensis Davis, 1898, ***Glypta rufiscutellaris***
Idiosomidea Viereck, 1925***, Dusona***
Ilapinastes Förster, 1869, ***Gelis***
imitator Dasch, 1988, ***Glypta***
improbanae Loan, 1981, ***Phytodietus***
Inareolata Ellinger and Sachtleben, 1928, ***Enytus***
incisa (Gmelin, 1790) (*Ichneumon*), ***Theronia atalantae***
indagatrix (Cresson, 1870) (*Pimpla*), ***Scambus hispae***
infestus (Förster, 1888) (*Epiurus*), ***Scambus brevicornis***
infidelis (Cresson, 1867) (*Ichneumon*), ***Orgichneumon calcatorius***
infrequens Dasch, 1988, ***Glypta***
innominatus (Viereck, 1912) (*Epiurus*), ***Scambus transgressus***
inquisitor (Say, 1829) (*Ichneumon*), ***Iseropus coelebs***
inquisitoriella (Dalla Torre, 1901) (*Pimpla*), ***Iseropus coelebs***
inquisitorius (Müller, 1776) (*Ichneumon*), ***Ischnus***
inquisitorius assimilis (Uchida, 1930) (*Habrocryptus*), ***Ischnus***
inquisitorius atricollaris (Walsh, 1873) (*Cryptus*), ***Ischnus***
inquisitorius meridionator Aubert, 1962, ***Ischnus***
interjectus Gahan, 1914, ***Hyposoter annulipes***
interrupta (Holmgren, 1858) (*Limneria*), ***Tranosemella praerogator***
inversa Cresson, 1870, ***Glypta erratica***
investigatrix (Walsh, 1873) (*Pimpla*), ***Acropimpla alboricta***
Ischnoscopus Förster, 1869, ***Hyposoter***
Ischnus Gravenhorst, 1829
Iseropus Förster, 1869
Isomeris Townes, 1970, ***Lissonota***
Itoplectis Förster, 1869
Jamaicapimpla Mason, 1975, ***Pimpla***
japonica Ashmead, 1906, ***Theronia atalantae gestator***
Kartika Gupta & Gupta, 1976, ***Dusona***
kolthoffi (Aurivillius, 1890) (*Pimpla*), ***Itoplectis quadricingulata***
Labrorychus Förster, 1869
lacticrus (Thomson, 1887) (*Angitia*), ***Tranosemella praerogator***
laevis Viereck, 1925, ***Campoplex mellipes***
Lampronota Curtis, 1832, ***Lissonota***
lanceolatus (Dasch, 1971) (*Stictopisthus*), ***Mesochorus***
laplantei Mason, 1968, ***Mastrus***
laricis Momoi, 1963, ***Cephaloglypta murinanae***
lata (Cushman, 1920) (*Ephialtes*), ***Itoplectis quadricingulata***
lateratorius (Thunberg,1824) (*Ichneumon*), ***Itoplectis maculator***
laticeps (Roman, 1938) (*Angitia*), ***Enytus montanus***
leavitti (Cushman, 1920) (*Ephialtes*), ***Itoplectis quadricingulata***
Leptogelis Ceballos, 1925, ***Gelis***
leucogonos (Gmelin, 1790) (*Ichneumon*), ***Pimpla turionellae***
leucostictos (Gmelin, 1790) (*Ichneumon*), ***Ischnus inquisitorius***
leucozonatus (Ashmead, 1890) (*Glypta*), ***Sphelodon phoxopteridis***
limbata Thomson, 1883, ***Oedemopsis scabricula***
Liotheronia Enderlein, 1919, ***Pimpla***
Lissonota (*Lissonota*) Gravenhorst, 1829
Lissonotoides Benoit, 1955, ***Lissonota***
Lissoscambus Walley, 1960, ***Scambus***
Lissotheronia Cameron, 1905, ***Pimpla***
longicalcar Thomson, 1887, ***Chorinaeus subcarinatus***
longipalpus Dasch, 1988, ***Glypta***
longiventris (Ratzeburg, 1848) (*Pimpla*), ***Scambus planatus***
longiventris Cresson, 1870, ***Glypta***
Lophantium Clément, 1925, ***Lissonota***
Lycorina Holmgren, 1859
maculator (Fabricius, 1775) (*Ichneumon*), ***Itoplectis***
maculator cruentata (Rudow, 1883) (*Pimpla*), ***Itoplectis***
maculatrix (Schulz, 1906) (*Pimpla*), ***Itoplectis maculator***
maculicornis (Stephens, 1835) (*Ichneumon*), ***Dirophanes***
maculipes Cameron, 1903, ***Enytus eureka***
mandibulator (Thunberg, 1824) (*Ichneumon*), ***Tranosemella praerogator***
Mastrus Förster, 1869
Matsumuraius Ashmead, 1906, ***Ichneumon***
melanomerus Viereck, 1925, ***Campoplex mellipes***
melanops (Schrank, 1781) (*Ichneumon*), ***Theronia atalantae***
melitaeae (Ashmead, 1890) (*Hemiteles*), ***Gelis tenellus***
mellipennis Viereck, 1903, ***Theronia atalantae fulvescens***
mellipes (Provancher, 1883) (*Limneria*), ***Campoplex***
Meniscomorpha Schmiedeknecht, 1907
Meniscus Schiødte, 1839, ***Lissonota***
meridionalis (Kriechbaumer, 1887) (*Pimpla*), ***Itoplectis viduata***
meridionator (Aubert, 1961) (*Hybophanes*), ***Oedemopsis scabricula***
Mesochorus Gravenhorst, 1829
mexicanus (Ashmead, 1894) (*Astiphromma*), ***Mesochorus uniformis***
Micromeson Strickland, 1912, ***Gelis***
Mima Davis, 1897, ***Exochus***
minor Townes, 1962, ***Ischnus***
minutus (Weed, 1887) (*Pimpla*), ***Scambus hispae***
mirabilis (Cresson, 1870) (*Meniscus*), ***Meniscomorpha***
mirabilis pleuralis (Ashmead, 1890) (*Clistopyga*), ***Meniscomorpha***
mirabilis pyrodes (Townes, 1978) (*Eudeleboea*), ***Meniscomorpha***
mitralis (Viereck, 1925) (*Campoplex*), ***Hyposoter annulipes***
montana (Cushman, 1920) (*Ephialtes*), ***Itoplectis quadricingulata***
montanus (Ashmead, 1890) (*Ischnoceros*), ***Enytus***
montanus (Cresson, 1864) (*Ichneumon*), ***Patrocloides***
montanus (Cresson, 1865) (*Mesoleptus*), ***Sinophorus teratis***
morleyi (Schmiedeknecht, 1934) (*Pimpla*), ***Scambus vesicarius***
murinanae (Fahringer, 1936) (*Microcryptus*), ***Dirophanes maculicornis***
murinanae (Bauer, 1941) (*Glypta*), ***Cephaloglypta***
murinanae (Bauer, 1942) (*Glypta*), ***Cephaloglypta murinanae***
mussii (Hartig, 1838) (*Pimpla*), ***Iseropus stercorator***
Myrmicromorpha Viereck, 1913, ***Gelis***
nativorus (Walsh, 1869) (*Hemiteles*), ***Gelis tenellus***
Neoarthula Rao, 1953, ***Hyposoter***
Neocremastus Meyer, 1930, ***Temelucha***
Neodelopia Benoit, 1957, ***Dusona***
Neogabunia Brèthes, 1927, ***Pimpla***
neomexicanus (Viereck, 1903) (*Spilocryptus*), ***Ischnus inquisitorius atricollaris***
Neopristomerus Viereck, 1912, ***Pristomerus***
Neozachresta Havrylenko and Winterhalter, 1949, ***Hyposoter***
Nesanomalon Morley, 1913, ***Pristomerus***
Nesopimpla Ashmead, 1906, ***Itoplectis***
nigricoxis (Habermehl, 1918) (*Epiurus*), ***Scambus planatus***
nigripalpis Thomson, 1887, ***Exochus***
nigripalpis subobscurus Townes and Townes, 1959, ***Exochus***
nigripalpis tectulum Townes and Townes, 1959, ***Exochus***
nigripes (Bridgman, 1887) (*Anomalon*), ***Agrypon varitarsum***
nigriscaposus (Thomson, 1877) (*Pimpla*), ***Scambus brevicornis***
nigritarsis (Schmiedeknecht, 1928) (*Ichneumon*), ***Orgichneumon calcatorius***
nigritegulis Constantineanu and Pisica, 1960, ***Pimpla turionellae***
nigroculus (Schrank, 1781) (*Ichneumon*), ***Theronia atalantae***
nigroornatus (Cameron, 1908) (*Otacustes*), ***Gelis tenellus***
nigroscutellatus (Habermehl, 1929) (*Phaeogenes*), ***Dirophanes maculicornis***
nucum (Ratzeburg, 1844) (*Pimpla*), ***Scambus planatus***
nuncupator (Panzer, 1800) (*Ichneumon*), ***Mesochorus***
obesa Cushman, 1917, ***Itoplectis quadricingulata***
occidentalis Heinrich, 1962, ***Patrocloides montanus***
Odontagrypon Cameron, 1906, ***Agrypon***
Oedematopsis Morley, 1908, ***Oedemopsis***
Oedemopsis Tschek, 1869
Omorga Thomson, 1887, ***Campoplex***
Omorgus Förster, 1869, ***Campoplex***
Oncocotta Dasch, 1974, ***Mesochorus***

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ontario (Cresson, 1870) (*Pimpla*), ***Apechthis***
opacellata Desvignes, 1868, ***Pimpla turionellae***
Opisorhyssa Kriechbaumer, 1890, ***Lissonota***
Opodactyla Seyrig, 1932, ***Pimpla***
Orgichneumon Heinrich, 1961
orgyiae (Ashmead, 1896) (*Otacustes*), ***Gelis tenellus***
Orientotheronia Morley, 1913, ***Theronia***
ornatula Walley, 1929, ***Apechthis picticornis***
ostentator (Davis, 1894) (*Meniscus*), ***Meniscomorpha mirabilis pleuralis***
otiosus (Say, 1829) (Ichneumon), ***Orgichneumon calcatorius***
ovalis (Thomson, 1877) (*Pimpla*), ***Itoplectis viduata***
Oxypimpla Noskiewicz & Chudoba, 1951, ***Pimpla***
pacifica (Cushman, 1920) (*Ephialtes*), ***Itoplectis quadricingulata***
pacifica Cushman, 1920, ***Apechthis annulicornis componotus***
padellae Torka, 1918, ***Pimpla turionellae***
paediscae (Ashmead, 1896) (*Agrypon*), ***Parania geniculata***
Paracremastus Szépligeti, 1899, ***Temelucha***
Paragrypon Uchida, 1941, ***Agrypon***
Parania Morley, 1913
Paranomalon Viereck, 1912, ***Erigorgus***
Parapechthis Blanchard, 1936, ***Apechthis***
partita Dasch, 1988, ***Glypta***
parvus Rohwer, 1920, ***Phytodietus pleuralis***
patens (Townes, 1945) (*Horogenes*), ***Enytus montanus***
Patrocloides Heinrich, 1961
pectoralis Townes, 1962, ***Ischnus inquisitorius atricollaris***
pedalis Cresson, 1865, ***Pimpla***
periliti (Ashmead, 1896) (*Otacustes*), ***Gelis tenellus***
perluctuosus (Provancher, 1877) (*Amblyteles*), ***Patrocloides***
Pezolochus Förster, 1850, ***Gelis***
Pezomachus Gravenhorst, 1829, ***Gelis***
Phaeogenes Wesmael, 1845
Philonygmus Förster, 1869, ***Gelis***
phoxopteridis (Weed, 1888) (*Glypta*), ***Sphelodon***
Phytodiaetoides Morley, 1913, ***Pimpla***
Phytodiaetus Agassiz, 1846, ***Phytodietus***
Phytodiaetus Morley, 1908, ***Phytodietus***
Phytodietus (***Phytodietus***) Gravenhorst, 1829
piceae (Cushman, 1935) (*Phaedroctonus*), ***Campoplex mellipes***
picticornis (Cresson, 1870) (*Pimpla*), ***Apechthis***
pictipes (Walsh, 1873) (*Pimpla*), ***Itoplectis conquisitor***
pieridicola (Packard, 1881) (*Campoplex*), ***Mesochorus nuncupator***
Piestetron Dasch, 1974, ***Mesochorus***
pilula Dasch, 1988, ***Glypta***
Pimpla Fabricius, 1804
Pimplidea Viereck, 1914, ***Pimpla***
pimploides Bradley, 1918, ***Dirophanes gaspesianus***
Pimplopterus Ashmead, 1900, ***Lissonota***
plaesseus (Geoffroy, 1785) (*Ichneumon*), ***Itoplectis maculator***
planatus (Hartig, 1838) (*Pimpla*), ***Scambus***
platynotae (Cushman, 1917) (*Cremastus*), ***Temelucha***
plesia Rohwer, 1913, ***Itoplectis evetriae***
Plesiomma Förster, 1869, ***Gelis***
plesius (Viereck, 1912) (*Phygadeuon*), ***Dirophanes maculicornis***
pleturus Davis, 1897, ***Chorinaeus subcarinatus***
pleuralis Cresson, 1865, ***Phytodietus***
pleurivincta (Say, 1835) (*Cryptus*), ***Itoplectis conquisitor***
Poecilopimpla Cameron, 1903, ***Theronia***
politus Provancher, 1883, ***Mesochorus sylvarum***
Polyrhabdus Walsh, 1873, ***Chorinaeus***
polyzonias (Forster, 1771) (*Ichneumon*), ***Phytodietus***
polyzonias fennicus Hellén, 1939, ***Phytodietus***
polyzonias ibericus Habermehl, 1917, ***Phytodietus***
porrectorius (Fabricius, 1787) (*Ichneumon*), ***Ischnus inquisitorius***
praerogator (Linnaeus, 1758) (*Ichneumon*), ***Tranosemella***
pratensis (Pfankuch, 1921) (*Pimpla*), ***Scambus brevicornis***
prismaticum (Norton, 1863) (*Anomalon*), ***Agrypon***
Pristocelus Szépligeti, 1905, ***Pristomerus***
Pristomeridia Ashmead, 1900, ***Pristomerus***
Pristomerus Curtis, 1836
pronexus Townes, 1960, ***Acropimpla***
provancheri (Dalla Torre, 1901) (*Anomalon*), ***Agrypon***
provancheri Dalla Torre, 1901, ***Mesochorus sylvarum***
Pseudacoenites Kriechbaumer, 1892, ***Theronia***
Pseuderipternoides Viereck, 1917, ***Campoplex***
Pseudocasinaria Viereck, 1912, ***Dusona***
Pseudopoemenia Kiss, 1924, ***Scambus***
Pterocormus Förster, 1850, ***Ichneumon***
pterophorae (Ashmead, 1890) (*Limneria*), ***Tranosemella praerogator***
pubescens Hellén, 1915, ***Pimpla turionellae***
pulcherrima (Ashmead, 1898) (*Asphragis*), ***Meniscomorpha mirabilis***
pulchra (Zetterstedt, 1838) (*Bassus*), ***Oedemopsis scabricula***
punctiventris (Thomson, 1877) (*Pimpla*), ***Scambus brevicornis***
puniceus (Schmiedeknecht, 1914) (*Pimpla*), ***Scambus brevicornis***
punicipes Cresson, 1874, ***Pimpla***
quadricinctus (Ashmead, 1894) (*Meniscus*), ***Phytodietus vulgaris***
quadricingulata (Provancher, 1880) (*Pimpla*), ***Itoplectis***
quadripunctata (Schrank, 1781) (*Ichneumon*), ***Theronia atalantae***
Rhadiurginus Hellén, 1967, ***Gelis***
Rhadiurgus Förster, 1869, ***Gelis***
Rhaibaspis Dasch, 1974, ***Mesochorus***
rhenanus (Ulbricht, 1910) (*Pimpla*), ***Scambus vesicarius***
rhyacioniae (Cushman, 1930) (*Cremastus*), ***Temelucha***
Rhynchothyreus Ashmead, 1900, ***Oedemopsis***
Rhythmonotus Förster, 1869, ***Hyposoter***
ribesii (Hensch, 1929) (*Pimpla*), ***Scambus brevicornis***
rogenhoferi Tschek, 1869, ***Oedemopsis scabricula***
rosaceanae (Viereck, 1925) (*Campoplex*), ***Enytus eureka***
rosaceanae (Viereck, 1926) (*Glypta*), ***Apophua simplicipes***
rostrale (Brischke, 1880) (*Limneria*), ***Tranosema***
rostrale albula Momoi, 1968, ***Tranosema rostrale***
rostrale scaponigrum (Ozols, 1959) (*Sinophorus*), ***Tranosema rostrale***
rufescens (Gmelin, 1790) (*Ichneumon*), ***Pimpla turionellae***
ruficoxis (Constantineanu, 1959) (*Phaeogenes*), ***Dirophanes maculicornis***
ruficoxis (Ulbricht, 1909) (*Pimpla*), ***Scambus vesicarius***
rufidorsalis (Uchida, 1932) (*Hybophanes*), ***Oedemopsis scabricula***
rufipes (Provancher, 1874) (*Limneria*), ***Campoplex mellipes***
rufiscutellaris Cresson, 1870, ***Glypta***
rufitegulis Constantineanu and Pisica, 1960, ***Pimpla turionellae***
rufoannulus Hellén, 1915, ***Pimpla turionellae***
rufoannulus Schmiedeknecht, 1934, ***Pimpla turionellae***
rufofasciata Cresson, 1870, ***Glypta***
rufulus (Provancher, 1876) (*Paniscus*), ***Mesochorus uniformis***
rufus (Cameron, 1905) (*Erythrocryptus*), ***Ischnus inquisitorius atricollaris***
rufuscula Davis, 1898, ***Pimpla aequalis***
salicicola (Hensch, 1929) (*Pimpla*), ***Scambus vesicarius***
sanguinipes Cresson, 1872, ***Pimpla***
sanguinolentus (Gmelin, 1790) (*Ichneumon*), ***Ischnus inquisitorius***
sannio Gravenhorst, 1829, ***Ischnus inquisitorius***
scabricula (Gravenhorst, 1829) (*Tryphon*), ***Oedemopsis***
Scambus Hartig, 1838
scanicus (Villers, 1789) (*Ichneumon*), ***Itoplectis maculator***
schmiedeknechti (Ashmead, 1902) (*Himertosoma*), ***Hercus fontinalis***
scutellaris (Wesmael, 1845) (*Phaeogenes*), ***Dirophanes maculicornis***
scutellata (Geoffroy, 1785) (*Ichneumon*), ***Theronia atalantae***
seamansi (Viereck, 1925) (*Campoplegidea*), ***Dusona***
sedulus (Gravenhorst, 1829) (*Cryptus*), ***Ischnus inquisitorius***
segmentator Gravenhorst, 1829, ***Phytodietus polyzonias***
Selenaspis Roman, 1910, ***Acropimpla***
septentrionalis Cushman, 1940, ***Iseropus stercorator orgyiae***
silvanus (Holmgren, 1880) (*Ichneumon*), ***Orgichneumon calcatorius***
simplicipes (Cresson, 1870) (*Glypta*), ***Apophua***

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Sinophorus Förster, 1869
speculator (Scopoli, 1763) (*Ichneumon*), ***Theronia atalantae***
Sphelodon Townes, 1966
spinicoxus (Viereck, 1905) (*Phygadeuon*), ***Dirophanes maculicornis***
stenotus Dasch, 1984, ***Erigorgus***
stercorator (Fabricius, 1793) (*Ichneumon*), ***Iseropus***
stercorator orgyiae (Ashmead, 1896) (*Itoplectis*), ***Iseropus***
stercorator rubrofascialis (Meyer, 1921) (*Pimpla*), ***Iseropus***
Stictopisthus Thomson, 1886, ***Mesochorus***
Stilbonota Stephens, 1835, ***Lissonota***
Stilbopoides Rohwer, 1913, ***Lissonota***
strammentarius (Kriechbaumer, 1890) (*Pimpla*), ***Scambus planatus***
subcarinatus Holmgren, 1858, ***Chorinaeus***
sulcata (Razoumowsky, 1789) (*Ichneumon*), ***Theronia atalantae***
superba (Christ, 1791) (*Ichneumon*), ***Theronia atalantae***
suralis Townes and Townes, 1959, ***Chorinaeus subcarinatus***
sylvarum (Haliday, 1838) (*Cryptus*), ***Mesochorus sylvarum***
sylvarum Curtis, 1833, ***Mesochorus***
Sympratis Förster, 1869, ***Erigorgus***
Syspasis Townes, 1965
tachypus Holmgren, 1860, ***Mesochorus gemellus***
taeniogaster (Viereck, 1912) (*Calliphrurus*), ***Hercus fontinalis pleuralis***
Taiwatheronia Sonan, 1936, ***Apechthis***
talaris Townes and Townes, 1959, ***Chorinaeus subcarinatus***
Tarytia Cameron, 1907, ***Temelucha***
tauma (Heinrich, 1951) (*Coelichneumon*), ***Syspasis***
tecumseh Viereck, 1917, ***Scambus hispae***
Temelucha Förster, 1869
temnopleuris (Cushman, 1920) (*Ephialtes*), ***Itoplectis conquisitor***
tenellus (Say, 1835) (*Cryptus*), ***Gelis***
tenuifemur (Walley, 1963) (*Synetaeris*), ***Tranosema***
teratis (Weed, 1887) (*Limneria*), ***Sinophorus***
Terpiphora Förster, 1869, ***Gelis***
terrestris (Pfankuch, 1921) (*Pimpla*), ***Scambus brevicornis***
Theronia Holmgren, 1859
thuringiacum (Schmiedeknecht, 1907) (*Sinophorus*), ***Tranosema rostrale***
Thymarimorpha Viereck, 1913, ***Dusona***
tibialis (Ulbricht, 1910) (*Pimpla*), ***Scambus brevicornis***
torrenti Ceballos, 1960, ***Exochus turgidus***
tortricidis (Cushman, 1917) (*Cremastus*), ***Temelucha forbesi***
tortricis Dasch, 1988, ***Glypta***
Toxophoroides Cresson, 1873, ***Lycorina***
Tranosema Förster, 1869
Tranosemella Horstmann, 1978
transgressus (Holmgren, 1868) (*Pimpla*), ***Scambus***
transversa Dasch, 1988, ***Glypta***
Trevoria Ashmead, 1900, ***Lissonota***
triangularis (Verhoeff, 1890) (*Pimpla*), ***Scambus buolianae***
Trichionotus Cameron, 1905, ***Agrypon***
Trichonotus Cameron, 1905, ***Agrypon***
tricincta Provancher, 1890, ***Glypta***
Triclistus Förster, 1869
Trieces Townes, 1946
triplicatorius (Thunberg, 1824) (*Ichneumon*), ***Ischnus inquisitorius***
Troctocerus Woldstedt, 1877, ***Scambus***
Tromera Förster, 1869, ***Scambus***
truncatellus (Viereck, 1925) (*Campoplex*), ***Hyposoter annulipes***
turionator (Thunberg, 1824) (*Ichneumon*), ***Pimpla turionellae***
turionellae (Linnaeus, 1758), ***Pimpla***
turionellae basiflava Constantineanu and Ciochia, 1967, ***Pimpla***
turionellae moraguesi Schmiedeknecht, 1888, ***Pimpla***
turionellae nana (Constantineanu, Ciochia, Constantineanu, Mustata, and Ularu, 1967)
(*Coccygomimus*), ***Pimpla***
turionellae tricolor (Constantineanu, Ciochia, Constantineanu, Mustata & Ularu, 1967)
(*Coccygomimus*), ***Pimpla***
turgidus Holmgren, 1858, ***Exochus***
Tyanites Cameron, 1903, ***Ichneumon***
unicolor (Provancher, 1886) (*Anomalon*), ***Agrypon provancheri***
uniformis Cresson, 1872, ***Mesochorus***
Urithreptus Förster, 1869, ***Gelis***
utilis (Norton, 1869) (*Hemiteles*), ***Gelis tenellus***
Vabsaris Cameron, 1903, ***Ichneumon***
varia (Fabricius, 1793) (*Ichneumon*), ***Theronia atalantae***
varia (Olivier, 1792) (*Ichneumon*), ***Theronia atalantae***
variatoria (Fabricius, 1804) (*Cryptus*), ***Theronia atalantae***
variegata Constantineanu, 1954, ***Pimpla turionellae***
variegata Dasch, 1988, ***Glypta***
variegatus (Ashmead, 1890) (*Hemiteles*), ***Gelis tenellus***
variegatus (Schrank, 1785) (*Ichneumon*), ***Pimpla turionellae***
variitarsum Dalla Torre, 1901, ***Agrypon varitarsum***
varitarsum (Wesmael, 1849) (*Anomalon*), ***Agrypon***
varius (Provancher, 1874) (*Cryptus*), ***Ischnus inquisitorius atricollaris***
venablesi (Viereck, 1924) (*Gambrus*), ***Ischnus inquisitorius atricollaris***
ventricosus (Tschek, 1871) (*Pimpla*), ***Scambus planatus***
vesca Townes, 1960, ***Itoplectis***
vesicarius (Ratzeburg, 1844) (*Pimpla*), ***Scambus***
viduata (Gravenhorst, 1829) (*Pimpla*), ***Itoplectis***
Viereckiana Strand, 1914, ***Dusona***
vincta (Schrank, 1781) (*Ichneumon*), ***Theronia atalantae***
vincta (Vollenhoven, 1873) (*Pimpla*), ***Itoplectis maculator***
vittator (Zetterstedt, 1838) (*Tryphon*), ***Mesochorus nuncupator***
vulgaris Cresson, 1870, ***Phytodietus***
vulpes (Christ, 1791) (*Ichneumon*), ***Theronia atalantae***
walshii (Dalla Torre, 1901) (*Pimpla*), ***Itoplectis conquisitor***
washingtonensis (Davis, 1897) (*Mima*), ***Exochus***
Xanthexochus Morley, 1913, ***Exochus***
yakutatensis (Ashmead, 1902) (*Eclytus*), ***Hercus fontinalis***
Zachrestinus Enderlein, 1921, ***Dusona***
Zamesochorus Viereck, 1912, ***Mesochorus***
Zarhynchus Ashmead, 1900, ***Oedemopsis***
Zatranosema Viereck, 1912, ***Campoplex***
zonator (Fabricius, 1793) (*Ichneumon*), ***Ischnus inquisitorius***

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