

Morphological phylogenetics of the Tenthredinidae (Insecta : Hymenoptera)

Lars Vilhelmsen

Natural History Museum of Denmark, Universitetsparken 15, DK-2100, Denmark.

Email: lbvilhelmsen@snm.ku.dk

Abstract. The Tenthredinoidea is the most diverse superfamily of non-apocritan Hymenoptera. It is also one of the largest herbivorous groups within the order, some species having substantial economic impact. Until very recently, no comprehensive phylogenetic analyses of the superfamily had been undertaken. This paper presents the largest morphological dataset assembled so far for elucidating the phylogeny of the Tenthredinoidea. In total, 129 taxa were scored for 146 characters from the adult head, thorax, wings and ovipositor apparatus. The emphasis of the taxon sample is on Tenthredinidae (104 terminals), which is by far the largest family in the Tenthredinoidea. The results of the cladistic analyses confirm the monophyly of the Tenthredinoidea, the first split being between the Blasticotomidae and the remaining families (Tenthredinoidea s. str., also monophyletic), and the monophyly of all families except Tenthredinidae. The analyses fail to consistently retrieve any of the six currently recognised subfamilies within Tenthredinidae, although core clades of Heterarthrinae, Nematinae, Selandriinae and Tenthredininae are often supported. Diprionidae are placed inside the Nematinae under some weighting conditions. The failure to corroborate the tenthredinid subfamilies might be ascribed to an insufficient character/terminal ratio, but also to problems with the existing classification. Inclusion of characters from the male genitalia and the larval stages as well as molecular data currently being assembled will hopefully lead to a more robust classification of the Tenthredinidae in the future.

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Introduction

The Tenthredinoidea, or true sawflies, are the most diverse lineage of non-apocritan Hymenoptera. The most recent comprehensive compilation reported ~7500 described species in six families and close to 600 genera (Blank *et al.* 2012). Unlike most Hymenoptera, the larvae of Tenthredinoidea are exclusively herbivorous, carnivory having been observed only in a few adults (Jervis and Vilhelmsen 2000). As herbivores, sawfly larvae might have substantial impact on vegetation, in some cases causing serious damage (e.g. Diprionidae). Most sawfly larvae are simple external feeders, resembling typical lepidopteran caterpillars in lifestyle, but within the superfamily more intricate interactions with host plants have repeatedly evolved (e.g. leaf rolling, leaf mining, gall formation; see Gauld and Bolton 1996).

Currently, six subfamilies are recognised in Tenthredinidae (Taeger *et al.* 2010): Allantinae, Blennocampinae, Heterarthrinae, Nematinae, Selandriinae and Tenthredininae. Previously widely recognised subfamilies include Dolerinae and Susaninae, but they are presently included in Selandriinae and Nematinae, respectively. Susaninae, comprising only the small genus *Susana* (10 spp.; Taeger *et al.* 2010), have indeed been repeatedly retrieved as a basal lineage within the Nematinae

in molecular analyses (Nyman *et al.* 2006, 2010; Malm and Nyman 2015; Prous *et al.* 2014).

The tenthredinid subfamilies are mostly defined by combinations of characters from the venation of the forewing (Benson 1952; Goulet 1992). Anyone who has attempted to identify a tenthredinid sawfly has had to deal with an often confusing entry key with characters difficult to visualise, unless properly illustrated, and subfamilies keying out multiple times. Perhaps the most useful key is by Goulet (1992), covering the genera of sawflies in Canada and Alaska, which requires 13 couplets to deal with seven subfamilies of Tenthredinidae (including Susaninae). Only the Tenthredininae key out once, the remaining subfamilies occurring twice except the Nematinae, which make a total of five appearances, including the Susaninae.

Within the last two decades, there has been a surge in papers dealing with the higher-level phylogeny of the Hymenoptera, either focusing on the basal lineages or across the entire order. The culmination has been the recent outputs from the US NSF-funded Hymenoptera Assembling the Tree of Life project (HymAToL) and spinoffs (Vilhelmsen *et al.* 2010; Heraty *et al.* 2011; Sharkey *et al.* 2012; Klopstein *et al.* 2013). These and analyses dealing specifically with the basal symphytan

Table 1. Data matrix
Polymorphisms: 0/1 = A, 1/2 = B

Taxa	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778
<i>Macroxyela ferruginea</i> (XYE)	0010000010	1120000311	1000001001	0101101101	1000000000	0100111010	1010010110
<i>Xyela julii</i> (XYE)	0010000000	1120000200	1000001001	0101101101	1000000000	0100111010	10100?00-0
<i>Onycholyda amplecta</i> (PAM)	0000010100	1020100100	1000100011	1000100101	1000000010	0100111010	1010111100
<i>Cephus pygmaeus</i> (CEP)	0000010100	10001-0200	1000000011	0101000010	10011--010	0101101010	1010010100
<i>Urocerus gigas</i> (SIR)	0010000100	10001-0211	1100000011	010100-0-0	1100010000	0000100110	1000110110
<i>Aproceros leucopoda</i> (ARG)	001000003?	01--000000	0-11200101	1000100100	0111121011	1111?00201	00001100-1
<i>Arge ustulata</i> (ARG)	0001000030	01--000100	0-11200111	1000100110	0111121101	0111000201	00100100-0
<i>Sterictiphora furcata</i> (ARG)	0011000030	01--000100	0-11200111	1000100110	0111121011	1111000201	00001100-1
<i>Blasticotoma filiceti</i> (BLA)	?10000030	2120010200	0-11111111	1101101101	1000111110	0101101111	0000?0110
<i>Blasticotoma f. pacifica</i> (BLA)	000001103?	1120010200	0-11111111	1101101111	1101100000	0101101111	0000111100
<i>Rumaria reducta</i> (BLA)	0000011030	11--010100	0-11111101	1101100101	1101100000	0101101111	00001110-0
<i>Abia fasciata</i> (CIM)	001000002?	0121000200	1111300000	-010111110	1111020100	0111000201	00000100-1
<i>Cimbex femoratus</i> (CIM)	0000000120	0121000100	1111300000	-010111100	0111020110	0111000211	0000011111
<i>Corynis crassicornis</i> (CIM)	1001001120	1021000100	0-11110101	100010-0-0	0101021000	0111000201	0000110111
<i>Pachylosticta albiventris</i> (CIM)	0000000120	1011000111	1111210101	1000101100	1101211000	0111000101	0000110111
<i>Diprion pini</i> (DIP)	0010000001	0010000120	0-11100101	1000111100	0101121000	0001100101	0000010110
<i>Gilpinia polytoma</i> (DIP)	0010000001	0020001200	0-11100101	1000111100	0101121000	0001100101	0000010110
<i>Monocentus juniperi</i> (DIP)	0011000001	0010000200	0-11100101	1000111101	0101121000	0001100201	00000100-0
<i>Neodiprion sertifer</i> (DIP)	0000000001	0010000120	0-11100101	1000111100	0101121000	0001100101	0000010110
<i>Acardulecera dorsalis</i> (PER)	0000000020	2020001100	1111200101	10001000-1	0111121011	1111000201	00101100-1
<i>Conocxa</i> sp. (PER)	0000000020	2020000100	0-11020010	-0001000-1	0111121000	0111000201	00000100-1
<i>Heteroperyyia hubrichi</i> (PER)	0010000001	0010000211	1111100000	-000100100	0111010100	1111000201	00000100-1
<i>Lophyrotoma analis</i> (PER)	0010000001	0010000000	0-11200000	-000100100	0111111100	1110000201	00000100-0
<i>Perga dorsalis</i> (PER)	0010000120	0011000111	1111210010	-100100000	1111021001	1111000201	00101110-1
<i>Phylactophaga froggatti</i> (PER)	0010000020	10?0000111	0-11200110	-1000000-1	0111121010	0111000201	0010?00-1
<i>Acidiphora geceera</i> (All)	0010000010	2010000200	1111110101	1001101101	0101110002	0001101201	0000011100
<i>Allantus cinctus</i> (All)	0011011010	1010000100	0-11110111	1001101111	1101100012	0001100111	0000111100
<i>Allantus</i> sp. (All)	0011011010	1010000100	0-11110111	1001101111	1101100010	0001100111	0000111100
<i>Ametastigia glabrata</i> (All)	0011010010	1010000100	0-11110111	1001101111	1101100010	0101100111	0000111100
<i>Ametastigia pallipes</i> (All)	0011010010	1010000100	0-11110111	1001100111	1101100010	0001100111	0000111100
<i>Apethymus serotinus</i> (All)	0011010010	1010000100	0-11110111	1001100111	1101100010	0101100111	0000111100
<i>Athalia rosae</i> (All)	0011010010	1010000100	0-11110111	1001101111	1101100012	0101100111	0000011100
<i>Dimorphopteryx penguis</i> (All)	0010010010	1010000200	0-11110101	1001101111	1101100012	0101100111	0000011100
<i>Empria</i> sp. (All)	0011000010	2010000100	0-01110101	1001101111	1101100012	0001100101	0000011100
<i>Eopsis beaumonti</i> (All)	0011000010	2010000100	0-01110101	1001101111	1101100012	0101101111	0000010100
<i>Eriocampa ovata</i> (All)	001101101?	2020000100	1111100101	1001101111	0101100010	0001100201	0000101100
<i>Harpiphorus lepidus</i> (All)	011000001?	2010000100	0-111?010?	?001101101	1101100010	000?01101	0000111100
<i>Macrophlytus testaceus</i> (All)	0011011010	1010000100	0-11110111	1001101101	1101100012	0101100111	0000111100
<i>Monostegia abdominalis</i> (All)	0011000001?	1010000100	0-11110111	1001101111	1101100002	0001100111	0000110100
<i>Monstoma pulveratum</i> (All)	001101001?	2020000100	0-11110111	1001101111	1101100012	0000100201	0000010100

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Table 1. (continued)

Taxa	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
	0-11110101	0-11110101	1001101111	10001110-1	0101100000	0002100201	0000101100
<i>Neacitophora bellicornis</i> (All)	0110000010	2010000100	1001101111	10001110-1	0101100000	0002100201	0000101100
<i>Pseudosibla excavata</i> (All)	0010010010	1020000100	1001101111	1012110-1	0101100000	0101100201	0000111100
<i>Taxonus agrorum</i> (All)	0011011010	1020000200	1001101111	11010110-1	1101100010	0101100211	0000111100
<i>Taxonus alboscitellatus</i> (All)	0011011010	1010000100	1001101111	11010110-1	1101100012	0001100211	0000111100
<i>Xenapates braunsi</i> (All)	0011000010	2010-00200	1001101111	10001110-1	1101100012	0001100101	0000111100
<i>Ardis pallipes</i> (Ble)	0111000010	1020000100	1001101111	10101110-1	1101100010	0001?00211	0000011100
<i>Bleniocampa phyllocolpa</i> (Ble)	0110000010?	2020000200	1001101111	10010110-1	1101100010	0001?00211	0000111100
<i>Blenogeries spissipes</i> (Ble)	0010000010	1010000100	1001101111	10001110-1	0101100000	0001100211	00001110-0
<i>Cladardis elongata</i> (Ble)	0110000010	2020000100	1001101111	10031110-1	1101100010	0001100211	0000011100
<i>Claremontia alternipes</i> (Ble)	0110000010	1020000200	1001101111	10031110-1	0101100010	0001100211	0000111100
<i>Distega</i> sp. (Ble)	0010000010	2010000200	1001101101	10101110-0	1101100012	0001?00101	00001100110
<i>Eutomostethus ephippium</i> (Ble)	0110000010?	2020000200	1001101111	10001100-1	0001100000	0001?00201	0000101100
<i>Halidamia affinis</i> (Ble)	0010000010?	1020000100	1001101111	10001110-1	1101100010	0001100211	00001100-0
<i>Monophadnus pallescens</i> (Ble)	0010010010	0000000100	1001101101	10001110-1	0101100010	0001?00211	0000110110
<i>Parachtractus rudis</i> (Ble)	0010010010	0000000100	1001101101	10001110-1	0101100010	0001?00211	0000110110
<i>Parvophora pruni</i> (Ble)	0111000010	0010000200	1001101111	10010110-1	0001100010	0001100201	00000100-0
<i>Perichista albida</i> (Ble)	0111000010	1010000100	1001101101	10001110-1	1101100012	0001?00201	0000111100
<i>Phymatocera aterrima</i> (Ble)	0010100010	0000000100	1001101101	10101110-1	0101100000	0001?00201	0000011100
<i>Rhadnocera nodicornis</i> (Ble)	0010100010	1010000200	1001101101	10010110-1	0101100000	0001100201	00000100-0
<i>Seljukia tenebrosa</i> (Ble)	0010000010	1020000100	1000101111	10001110-1	0101111000	1001100201	0000010110
<i>Stethomostus fuliginosus</i> (Ble)	0010000010	1020000100	1001101111	11110110-1	0101110000	1101100201	00001100-0
<i>Tethida barda</i> (Ble)	0110000010	1020000100	1001101111	10101110-1	0101111000	0001100201	0000010110
<i>Waldheimia carbonarius</i> (Ble)	0110000010	B0100000100	1001101111	10001110-1	0001100012	0001100201	0000101100
<i>Waldheimia devotai</i> (Ble)	0110000010	2010000100	1001101101	10001110-1	1001100012	0001101101	0000101100
<i>Waldheimia ochra</i> (Ble)	0110000010	2010000100	1001101101	10001110-1	1001100012	0001101101	0000101100
<i>Caliroa cerasi</i> (Het)	0110000010	2020000100	1001101111	10001110-1	0001100002	0001100201	0000011100
<i>Endelomyia aethiops</i> (Het)	0110000010	1020000100	1001101111	1001110-1	0101100010	0101?00211	0000011100
<i>Fenusia pumila</i> (Het)	0110000010	1020000200	1000100101	10010110-0	0101110010	0001?01101	00000110-0
<i>Heterarthrus vagans</i> (Het)	0110000010	1020001100	1001100101	00010110-1	1101110010	0001?01001	00001110-0
<i>Metallus pumilus</i> (Het)	0110000010	1010000200	1001101111	10010110-0	1101110010	0101?00001	00001110-0
<i>Nefusa ambigua</i> (Het)	0110000010	2010000200	1001101111	10101110-1	0101110010	0101?01111	00001110-0
<i>Notofenusia surosa</i> (Het)	0100000010	2010000100	1001101111	10001110-0	0101100010	0001101001	00001110-0
<i>Parna tenella</i> (Het)	0100000010	2020000100	1001101101	10110110-1	0101110002	0001?00201	00001110-0
<i>Profenusia pygmaea</i> (Het)	0000000010?	2020000200	1001101111	10031110-1	0101110010	1001100101	00001010-0
<i>Amuronematus amplius</i> (Nem)	0010000010	0000001100	1001101101	10100110-1	1101110000	0001100211	0000010100
<i>Cladius compressicornis</i> (Nem)	0011000010	0000000100	1000101101	10101110-1	1101110010	0001100211	0000110100
<i>Cladius pectinicornis</i> (Nem)	0011000011	00A0000010	1000101101	10101110-1	1101110010	0001100211	0000110100
<i>Cræsus septemtrionalis</i> (Nem)	0011000010	0000001100	1001101111	11101110-1	1101111000	0001100201	0000110100
<i>Craterocerus fraternalis</i> (Nem)	0011000010	0010000100	1001101101	11110110-1	1101100000	1001101211	0000010100
<i>Dineura pullior</i> (Nem)	0010000010	1000000200	1001101101	10110110-1	1101110000	0001100201	0000010110
<i>Dineura viridorsata</i> (Nem)	0010000010	1000000200	1001100101	10110110-1	1101110000	0001100201	0000010110
<i>Fagineura crenativora</i> (Nem)	0011000010	0000000100	1001101101	10100110-1	1101100012	0001100201	0000011100

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Table 1. (continued)

Taxa	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778
<i>Hemichroa australis</i> (Nem)	0011000010	0-11100101	1001101111	11110110-1	1101110000	0A01100211	0000010100
<i>Hoplocampa</i> sp. (Nem)	0011000010	0-11200101	1001101111	10101110-1	0101100000	0101100201	0000010110
<i>Nematinus steini</i> (Nem)	0011000010	0-11100101	1001101101	10110110-1	0101100000	0001100201	0000010100
<i>Nematus caeruleocarpus</i> (Nem)	0011000010	0-11100101	1001101101	10100110-1	1101110000	0001100211	0000010100
<i>Neopareophora liturata</i> (Nem)	0010000010	0-11100101	1001000101	10100110-?	1101110010	0001100201	00000100-0
<i>Pachynematus clitellatus</i> (Nem)	0010000010	0-11100101	100110A111	10100110-1	1101100000	0001100211	0000010110
<i>Pikonomia alaskense</i> (Nem)	0011000010	0-11100101	100110???	10100110-1	1101110000	0001100211	0000010110
<i>Pontania proxima</i> (Nem)	00100000A0	0-11100101	1001100101	10100110-1	1101110010	0001?00201	0000010100
<i>Pristicampus incisus</i> (Nem)	0010000010	0-11100101	1001100101	10100110-?	1101110000	0001?00211	0000010110
<i>Pristiphora ? angulata</i> (Nem)	0010000010	0-11100101	1001100111	10100110-0	1101100000	0001100211	0000010110
<i>Pseudodineura fuscata</i> (Nem)	001000001?	0-11100101	1001101111	10101110-1	0101100000	0001?00201	00000100-0
<i>Susana annulata</i> (Nem)	0010000010	0-11100101	1001101101	110121?0-1	1101110000	0001100211	0000010110
<i>Adeleta nova</i> (Sel)	001000001?	0-11100001	1001101111	10001110-1	1101100010	0001?00211	00000100-0
<i>Adiaclena nigripictus</i> (Sel)	0110000010	0-11100101	1001101101	10101110-1	0101110010	0001100201	0000011100
<i>Aneugmenus padi</i> (Sel)	011000001?	0-11100101	1001101111	10110110-1	1101110010	0001?00211	0000011100
<i>Canonias rufiventris</i> (Sel)	0110011010	0-11100101	1001100101	10112110-0	1101100012	0001100211	0000010100
<i>Dolerus nitens</i> (Sel)	0011000010	0-11101111	1001101111	11001110-1	1101100010	0000100211	0000010110
<i>Dolerus pratensis</i> (Sel)	0011000010	0-11110111	1001101111	11011110-1	1101100000	0001100211	0000010110
<i>Dulophanes</i> sp. (Sel)	0100001000	0-11100101	1001101111	10100110-0	1001110010	0001?00201	0000011100
<i>Heptamelus dalibomi</i> (Sel)	000000002?	0-11100101	1000101111	11012110-1	1101100010	0101?00211	0000011100
<i>Heptamelus</i> sp. (Sel)	0010000020	0-11100101	1000101111	11012110-1	1101100010	0101?00211	0000011100
<i>Nesoselandria mortio</i> (Sel)	0110000010	0-11100101	1001101101	00111110-0	1101110010	0101100211	0000011100
<i>Plaumammia aemula</i> (Sel)	0010000010	0-11100101	1000101111	10110110-0	1101100010	0101100201	0000011100
<i>Proselandria roseomaculata</i> (Sel)	011000001?	0-11100101	1001101111	10101110-0	1101100012	0001?00201	000001?0110
<i>Pseudohemiphetus runari</i> (Sel)	0011000020	0-11110101	1000101111	11012110-1	1101100010	0101?00211	00000110-0
<i>Rocallia japonica</i> (Sel)	0010000010	0-11100101	1001101111	10011110-1	1101100010	0001?00211	0000011100
<i>Selandria serva</i> (Sel)	0110000010	0-11100101	1001101111	10110110-1	0101110010	0001100201	0000010110
<i>Stromboeceria nigricans</i> (Sel)	0010010010	0-11100101	1001101111	10110110-0	1101100000	0001?00201	0000011100
<i>Stromboecerus delicatulus</i> (Sel)	0010010010	0-111?0101	1001101111	10110110-?	1101100010	0001?00201	0000011110
<i>Strongylogaster multifasciata</i> (Sel)	0011010010	0-11101010	1001100111	11110110-1	1101100010	0001100211	0000010100
<i>Aglaostigma fulvipes</i> (Ten)	0010000101	0-11100101	1001111111	10110110-1	1101100010	01011002A1	0000010100
<i>Corymbas koreana</i> (Ten)	0011011010	0-11101111	1001101111	11012110-1	1101100000	0001100201	0000011100
<i>Filacus alpinus</i> (Ten)	0000010010	0-11101010	1001101111	11012110-1	1101100010	0001100211	0000011100
<i>Lagium atroviolaceum</i> (Ten)	0011011010	0-11100101	1001101111	11012110-1	1101100010	0001100211	0000011100
<i>Leucopelmonus annulicornis</i> (Ten)	0001011010	0-11100101	1001101111	10012110-1	1101100012	0001100111	0000011100
<i>Macrophya duodecimpunctata</i> (Ten)	1011011010	0-11101010	1001101111	11010110-1	1101100010	0101100211	0101101010
<i>Pachyprotasis rapae</i> (Ten)	0011011010	0-11101111	1001101111	11012110-1	1101100010	0001100211	0101101010
<i>Perineura rubi</i> (Ten)	0011011010	0-11100101	1001101101	10010110-1	1101100012	0001100111	0000011100
<i>Rhogogaster punctulata</i> (Ten)	0011011010	0-11101111	1001111011	11012110-1	1101100012	0001100201	0000010100
<i>Rhogogaster viridis</i> (Ten)	0011011010	0-11101111	1001111011	11012110-1	1101100012	0001100201	0000010100
<i>Sciapteryx consobrina</i> (Ten)	0001011010	0-11101111	1001101111	11010110-1	1101100000	0001?00211	0000010100
<i>Siobla sturmi</i> (Ten)	0010011010	1111110111	1001101111	11012110-1	1101100010	0101100211	0000010100

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Table 1. (continued)

Taxa	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Tenthredo kochleri</i> (Ten)	1001011010	1020000300	1001101111	1001101111	1101100010	0001100201	0000110100
<i>Tenthredo scrophulariae</i> (Ten)	1001011010	1020000300	1001101111	1001101111	1101100010	0001100211	0000110100
<i>Tenthredopsis ornata</i> (Ten)	0011011010	1010000100	1001101111	1001101111	1101100000	0001100201	0000110101
<i>Zaschionyx montana</i> (Ten)	0011011010	1010000300	1001101111	1001101111	1101100010	0101100211	0000110100
Taxa	Characters						
	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
	8888888889	9999999990	0000000001	1111111112	2222222223	3333333334	444444
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	123456
<i>Macroxyela ferruginea</i> (XYE)	00121000-1	0102100100	0103100--0	1101110101	-00000100?	--00000??0	?0?-0-
<i>Xyela julii</i> (XYE)	00120000-1	0102100110	0103100--1	0101110110	0010001001	--00000000	10?-00
<i>Onycholyda amplecta</i> (PAM)	10120000-0	0102100110	0103100--1	1101110110	0?????????	??????????	??????
<i>Cephus pygmaeus</i> (CEP)	1000-100-0	0102100101	0123101--1	1001110111	-011202000	0000000002	101-10
<i>Urocerus gigas</i> (SIR)	0111?000-0	0112101100	0113100--0	1011110111	-110002000	4000000002	100-10
<i>Aprocerus leucopoda</i> (ARG)	-100-11001	00-20-2010	1101?-100	0001110?0-1	-000000-10	0110011--0	-10000
<i>Arge ustulata</i> (ARG)	1102011001	00-20-1110	1102?-1110	0001100111	-00002-10	0110021--0	-10000
<i>Sterictiphora fuscata</i> (ARG)	-100-01011	00-20-2000	1102?-1110	0011100111	-010?0?-10	0110001--0	-10000
<i>Blasticotoma filiceti</i> (BLA)	0100-1?1-1	01101111?0	01?3100???	?0011?1110	1?????000	000000000?	?0?-10
<i>Blasticotoma f. pacifica</i> (BLA)	01010101-1	01101101-0	0103100--0	100110?110	1010001000	0000000000	101-10
<i>Runaria reducta</i> (BLA)	0101010101	0A-01101-0	0103100--0	1001100110	1010001002	2000000000	101-10
<i>Abia fasciata</i> (CIM)	-000-10010	00-01101-0	1132?-1110	000111?110	0011221110	0110010112	001101
<i>Cimbex femoratus</i> (CIM)	-001010010	00-01101-1	1133111--0	0001110110	0010--110	0010000112	?0?101
<i>Corynis crassicornis</i> (CIM)	0000-10010	00-01101-1	0122?-1110	0001110110	0010200210	0110000112	001001
<i>Pachylosticta aliventris</i> (CIM)	0000-10001	00-01101-1	0132?-1110	00011A0110	0?????????	??????????	??????
<i>Diprion pini</i> (DIP)	0101001001	00-10-0110	0113101--0	0011100111	-010?2210	0011020010	001001
<i>Gilpinia polytoma</i> (DIP)	0102001000	00-10-0100	0113101--0	0011100111	-010?2210	0011020010	001001
<i>Monoctenus juniperi</i> (DIP)	1102000001	00-10-0110	0112?-1110	1011100111	-010001?10	0011020010	001001
<i>Neodiprion sertifer</i> (DIP)	0101001011	00-10-0110	0113101--0	0011100111	-010000210	0011020010	001001
<i>Acordulecera dorsalis</i> (PER)	-100-10000	00-00-01-0	0110-1110	00110-00-1	-01--1-10	0100001--0	-10000
<i>Conocoxa</i> sp. (PER)	-100-00001	00-10-1110	0110-1110	00110-00-1	-010?0?-10	0001001--0	-10000
<i>Heteroperveia hubrichi</i> (PER)	-100-10000	00-20-0110	0111?-101	00110-?0-1	-011001-10	0001001--0	-10000
<i>Lophyrotoma analis</i> (PER)	0100-10000	00-20-10-0	1100?-1110	10110-00-1	-??????????	??????????	??????
<i>Perga dorsalis</i> (PER)	0100-10000	00-20-1110	0130?-101	00010-00-1	-000000-10	0110001--0	-10000
<i>Phylacteophaga frogatti</i> (PER)	0100-10000	00-20-0110	0120?-1110	00110-?0-1	-010?2-10	00010?01--0	-10010
<i>Acidtophora gecera</i> (All)	1101000000	00-2?11011	0123100--0	10000-0111	-111212210	--10010012	101000
<i>Allantus cinctus</i> (All)	0101010000	00-01101-1	0113100--0	10000-0111	-010000110	0110000012	101011
<i>Allantus viennensis</i> (All)	0101010000	00-01101-1	0123100--0	00000-?101	-010001110	0110000012	101110
<i>Allantus</i> sp. (All)	0101010000	00-01101-1	0113100--0	10000-?111	-??????????	??????????	??????
<i>Ametastigma glabrata</i> (All)	0101010000	00-2110101	0103100--0	10000-0111	-1100001110	0110000012	101210

(continued next page)

Table 1. (continued)

Taxa	Characters									
<i>Ametastigia pallipes</i> (All)	0000000000	0000000001	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
<i>Apethymus serotinus</i> (All)	8888888889	9999999990	0000000001	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
<i>Athalia rosae</i> (All)	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Dimorphopteryx penguis</i> (All)	0101010000	00-01101-1	0103100--1	0103100--1	0103100--1	0103100--1	0103100--1	0103100--1	0103100--1	0103100--1
<i>Empria</i> sp. (All)	0101010000	00-01101-1	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0
<i>Eopsis beaumonti</i> (All)	0100-10000	00-21101A1	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0
<i>Eriocampa ovata</i> (All)	0101010000	00-2110111	0113100--1	0113100--1	0113100--1	0113100--1	0113100--1	0113100--1	0113100--1	0113100--1
<i>Harpiphorus lepidus</i> (All)	1001010000	01101101-0	01B3100--1	01B3100--1	01B3100--1	01B3100--1	01B3100--1	01B3100--1	01B3100--1	01B3100--1
<i>Macrophlytus testaceus</i> (All)	0101000000	00-01101-1	0123100--0	0123100--0	0123100--0	0123100--0	0123100--0	0123100--0	0123100--0	0123100--0
<i>Monostegia abdominalis</i> (All)	0101010000	00-2110111	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0
<i>Monsonia pulveratium</i> (All)	0101010000	00-2110111	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0
<i>Neacidiphora bellicornis</i> (All)	0000-10000	00-2110111	0103100--0	0103100--0	0103100--0	0103100--0	0103100--0	0103100--0	0103100--0	0103100--0
<i>Pseudosiobla excavata</i> (All)	0101011010	00-2110111	0123100--0	0123100--0	0123100--0	0123100--0	0123100--0	0123100--0	0123100--0	0123100--0
<i>Taxonus agrorum</i> (All)	0101010000	00-2110101	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0
<i>Taxonus albocutellatus</i> (All)	0101010000	00-2110101	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0
<i>Xenapates braunsi</i> (All)	1101010000	00-2110101	0103100--0	0103100--0	0103100--0	0103100--0	0103100--0	0103100--0	0103100--0	0103100--0
<i>Ardis pallipes</i> (Ble)	0101010000	00-2110101	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100
<i>Blennocampa phyllocolpa</i> (Ble)	0101010000	00-2110110	0121?-101	0121?-101	0121?-101	0121?-101	0121?-101	0121?-101	0121?-101	0121?-101
<i>Blennogaster spissipes</i> (Ble)	0101010000	00-2110110	0102?-----	0102?-----	0102?-----	0102?-----	0102?-----	0102?-----	0102?-----	0102?-----
<i>Cladardis elongatula</i> (Ble)	0101010000	00-21101A0	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100
<i>Claremontia alternipes</i> (Ble)	0101010000	00-2110110	01B1?-100	01B1?-100	01B1?-100	01B1?-100	01B1?-100	01B1?-100	01B1?-100	01B1?-100
<i>Distega</i> sp. (Ble)	0101010000	00-2110101	0101?-100	0101?-100	0101?-100	0101?-100	0101?-100	0101?-100	0101?-100	0101?-100
<i>Eutomostethus ephippium</i> (Ble)	1101010000	00-2110110	0101?-011	0101?-011	0101?-011	0101?-011	0101?-011	0101?-011	0101?-011	0101?-011
<i>Halidamia affinis</i> (Ble)	0100-10000	00-2110110	0101?-010	0101?-010	0101?-010	0101?-010	0101?-010	0101?-010	0101?-010	0101?-010
<i>Monophadnus pallescens</i> (Ble)	0101010000	00-2110111	0111?-101	0111?-101	0111?-101	0111?-101	0111?-101	0111?-101	0111?-101	0111?-101
<i>Paracharactus rudis</i> (Ble)	0101010000	00-2110110	01A1?-100	01A1?-100	01A1?-100	01A1?-100	01A1?-100	01A1?-100	01A1?-100	01A1?-100
<i>Pareophora pruni</i> (Ble)	0101010000	00-2110110	0101?-000	0101?-000	0101?-000	0101?-000	0101?-000	0101?-000	0101?-000	0101?-000
<i>Periclistia albida</i> (Ble)	0101010000	00-2110110	0111?-000	0111?-000	0111?-000	0111?-000	0111?-000	0111?-000	0111?-000	0111?-000
<i>Phymatocera aterrima</i> (Ble)	0101010000	00-2110110	0111?-010	0111?-010	0111?-010	0111?-010	0111?-010	0111?-010	0111?-010	0111?-010
<i>Rhadnocera nodicornis</i> (Ble)	1101010000	00-2110110	0A01?-010	0A01?-010	0A01?-010	0A01?-010	0A01?-010	0A01?-010	0A01?-010	0A01?-010
<i>Seljukia tenebrosa</i> (Ble)	0101010000	00-2110110	1103111?--0	1103111?--0	1103111?--0	1103111?--0	1103111?--0	1103111?--0	1103111?--0	1103111?--0
<i>Stethomostus fuliginosus</i> (Ble)	0101010000	00-2110111	0111?-101	0111?-101	0111?-101	0111?-101	0111?-101	0111?-101	0111?-101	0111?-101
<i>Tethida barda</i> (Ble)	0101010000	00-2110110	01A1?-100	01A1?-100	01A1?-100	01A1?-100	01A1?-100	01A1?-100	01A1?-100	01A1?-100
<i>Walldheimia carbonarius</i> (Ble)	1101010000	00-21101A1	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100
<i>Walldheimia devototi</i> (Ble)	0101010000	00-21101A1	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100
<i>Walldheimia ochra</i> (Ble)	0101010000	00-2110111	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100	0111?-100
<i>Caliroa cerasti</i> (Het)	0101010011	00-2110110	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0
<i>Endelomyia aethiops</i> (Het)	0101010001	00-2110110	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0	0113100--0
<i>Fenusia pumila</i> (Het)	0100-10001	00-01101-0	0111?-011	0111?-011	0111?-011	0111?-011	0111?-011	0111?-011	0111?-011	0111?-011
<i>Heterarthrus vagans</i> (Het)	1000-10011	00-01101-0	0103100--1	0103100--1	0103100--1	0103100--1	0103100--1	0103100--1	0103100--1	0103100--1
<i>Metallus pumilus</i> (Het)	0101010011	00-01101-0	0101?-101	0101?-101	0101?-101	0101?-101	0101?-101	0101?-101	0101?-101	0101?-101
<i>Nefusa ambigua</i> (Het)	1101010011	00-01101-0	0101?-100	0101?-100	0101?-100	0101?-100	0101?-100	0101?-100	0101?-100	0101?-100

(continued next page)

Table 1. (continued)

Taxa	0000000000	0000000001	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
<i>Aglaostigma fulvipes</i> (Ten)	0101001010	00-21101A1	0113111--0	10011A0111	0110001110	0101000012	101010			
<i>Corymbas koreana</i> (Ten)	0102001010	00-2110111	01230----0	1001111101	-011--110	0110000011	101011			
<i>Filacus albipes</i> (Ten)	0101011010	00-2110101	0113111--0	1001110111	-110000110	0110000012	101001			
<i>Lagium atrovitaceum</i> (Ten)	0101011010	00-2110101	0123111--0	100A101111	-0110001110	0100000012	101010			
<i>Leucopelmonus amulicornis</i> (Ten)	0101001010	00-2110101	0123111--0	10000-0111	-010002110	0110000012	101011			
<i>Macrophya duodecimpunctata</i> (Ten)	0101011010	00-2110101	0122?-----0	1001110111	-111002110	0110000011	101111			
<i>Pachyprotasis rapae</i> (Ten)	0101011010	00-2110101	0112?-----0	1001110111	-010?0?110	0110000011	101110			
<i>Perineura rubi</i> (Ten)	0101011010	00-2110101	0112?-----0	1001101101	-010002110	0100000011	101110			
<i>Rhogogaster punctulata</i> (Ten)	0101011010	00-2110101	01120----0	1001100111	-010002110	0110000011	?01111			
<i>Rhogogaster viridis</i> (Ten)	0101011010	00-2110101	0123111--0	0001110111	-0100001110	0110000011	101111			
<i>Sciapteryx consobrina</i> (Ten)	0101011010	00-2110101	0113111--0	1001110101	-010002110	0100000011	101111			
<i>Siobla sturmi</i> (Ten)	0101001010	00-2110111	0123100--0	1001110111	-011001110	0100000011	?01?0?			
<i>Tenthredo koehlerii</i> (Ten)	0100-11010	00-2110101	0113111--0	1001110111	??00000000	??00000000	??0000			
<i>Tenthredo scrophulariae</i> (Ten)	0101011010	00-2110111	01B3111--0	1001110101	-111002110	0110000012	101111			
<i>Tenthredopsis ornata</i> (Ten)	-102011010	00-2110101	0113111--0	1001110111	-010002110	0107000012	101010			
<i>Zaschionyx montana</i> (Ten)	1001011010	00-2110100	01120----0	1001100111	-010?0?010	0100000012	10?110			

grade of Hymenoptera (e.g. Vilhelmsen 1997, 2001; Schulmeister *et al.* 2002; Schulmeister 2003a; Ronquist *et al.* 2012; Malm and Nyman 2015) have placed the Tenthredinoidea as either the second or third lineage to branch off from the base of the hymenopteran tree. There is thus no doubt that the superfamily branched off before the evolution of the parasitoid–carnivorous lifestyle displayed by the majority of the Hymenoptera. The Tenthredinoidea retains the ancestral herbivorous lifestyle of the order (see Vilhelmsen and Turrisi 2011), unlike other major herbivorous lineages within Hymenoptera (e.g. bees, fig wasps, gall wasps) which evolved from carnivorous or parasitoid ancestors.

In contrast to the recent advances in resolving especially basal hymenopteran relationships at the superfamily level, there have until very recently not been any comprehensive studies targeting the phylogeny of the Tenthredinoidea. Even the analyses with the largest samples from the superfamily (e.g. Schulmeister 2003a; Ronquist *et al.* 2012) are substantially under-represented with regards to tenthredinoids, especially the largest family, the Tenthredinidae. Nyman *et al.* (1998, 2000, 2006, 2010) performed pioneering molecular analyses on the subfamily Nematinae to unravel their phylogeny and co-evolution with their host plants; Leppänen *et al.* (2012, 2013) similarly explored the leaf-mining Heterarthrinae. Isaka and Sato (2014) did a molecular phylogeny of mostly Palaearctic Selandriinae and estimated the time of origin and initial diversification for the subfamily to the Early Cretaceous.

Recently, Wetz and Vilhelmsen (2014) compiled a dataset of ovipositor system characters also with emphasis on Nematinae. However, they did not have enough characters to obtain satisfactorily resolved and robust results. Better results for Nematinae were obtained by Prous *et al.* (2014), who employed three molecular markers and revised the genus classification for the subfamily. The predominantly Australian–South American family Pergidae was subjected to a combined analysis by Schmidt and Walter (2014), but the rest of the Tenthredinoidea were inadequately sampled for elucidating relationships within the superfamily.

Nevertheless, some relationships at the higher level are repeatedly retrieved. The Tenthredinoidea are always well supported, and the basal split is almost always (but see Sharkey *et al.* 2012) between the Blasticotomidae, a small and rare family of fern-feeders, and the rest, the Tenthredinoidea s. str. (Vilhelmsen 2001). Within the latter, the clade Argidae+Pergidae is usually well supported. The Cimbicidae+Diprionidae+Tenthredinidae frequently form a clade, although Vilhelmsen (2001) placed the Cimbicidae as sister to Argidae+Pergidae. The Cimbicidae+Diprionidae+Tenthredinidae are not consistently resolved, the Cimbicidae+Diprionidae sometimes forming a monophylum (e.g. Schulmeister 2003a; Klopstein *et al.* 2013; Malm and Nyman 2015), sometimes not (Heraty *et al.* 2011; Ronquist *et al.* 2012). Significantly, all analyses except Boevé *et al.* (2013) failed to retrieve the Tenthredinidae as monophyletic, even with a small taxon sample (e.g. Heraty *et al.* 2011); usually, representatives of the genus *Athalia* fall outside the family.

Two studies have recently been published by Boevé *et al.* (2013) and Malm and Nyman (2015), the first to include a

Table 2. Character list*Head*

1. *Eyes ventrally*: (0) at most slightly converging (Fig. 1A–E); (1) distinctly converging ventrally, reaching medially of lateral margins of clypeus (Fig. 1F).
2. *Dorsal tentorial pit*: (0) indistinct, continuous with ventral groove to torulus (Fig. 1A, D, F); (1) distinct circular pit separated from torulus by raised cuticle (Fig. 1B, C, E).
3. *Epistomal sulcus*: (0) absent or weakly developed, without corresponding internal ridge (Fig. 1A, B, D, F); (1) present, distinct, with ridge (Fig. 1C, E).
4. *Anterior margin of clypeus*: (0) more or less straight (Fig. 1A–C, E); (1) deeply incurved (Fig. 1D, F).
5. *Postocular pit*: (0) absent (Fig. 2A, C, D); (1) small pit immediately posterior to eye present ventrally (Fig. 2B).
6. *Occipital carina laterally*: (0) absent (Fig. 2B, C); (1) present (Fig. 2A, D).
7. *Occipital carina dorsally*: (0) absent (Fig. 2B–D); (1) present, at least reaching occipital sulcus (Fig. 2A).
8. *Ventral head sclerotisation*: (0) absent (Vilhelmsen 2011: fig. 5A); (1) present (Vilhelmsen 2011: fig. 5B).

Antenna

9. *Number of antennal segments*: (0) more than nine; (1) nine (Fig. 3A, B, D–F); (2) five to eight (Fig. 3C); (3) four or fewer (ordered).
10. *Lateral projections in males*: (0) absent; (1) present (Fig. 3A).
11. *Pedicellus*: (0) shorter than wide (Fig. 3A, B); (1) 1–1.5× as long as wide (Fig. 3D, F); (2) 1.5× as long as wide or longer (Fig. 3C, E) (ordered).
12. *Third antennomere*: (0) not conspicuously enlarged (Fig. 3A–F); (1) enlarged, comprising at least a third of total length of antenna (Beutel and Vilhelmsen 2007: fig. 2A).
13. *Antennomeres 3 and 4*: (0) 3rd shorter than 4th (Fig. 3A, B); (1) 3rd equal to or, at most, 1.5× longer than 4th (Fig. 3E); (2) 3rd at least 1.5× longer than 4th (Fig. 3C, D, F) (ordered).
14. *Apical antennomeres*: (0) not conspicuously modified (Fig. 3A–F); (1) one or more apical antennomeres forming distinct club.

Mouthparts

15. *Labrum, position*: (0) anterior to tips of mandibles (Vilhelmsen 2011: fig. 1A, B); (1) posterior to tips of mandibles (Vilhelmsen 2011: fig. 1C).
16. *Labrum, tormae*: (0) separate apodemes; (1) fused medially, forming continuous bar.
17. *Mandible, profile*: (0) left mandible gradually tapering to apex in lateral view (Fig. 2A, B, D); (1) subdivided, with broad base and abruptly tapered distal part (Fig. 2C).
18. *Left mandible apical teeth*: (0) one; (1) two (Fig. 1C–E); (2) three (Fig. 1A); (3) four (ordered).
19. *Maxilla, number of palpal segments*: (0) six; (1) five or fewer.
20. *Labium, number of palpal segments*: (0) four; (1) three.

Pronotum

21. *Length*: (0) pronotum short dorsally of transverse pronotal sulcus (Fig. 4A, D, F); (1) long dorsally of transverse pronotal sulcus (Fig. 4B).
22. *Orientation*: (0) pronotum oblique posterior to transverse pronotal sulcus (Vilhelmsen 2000b: fig. 2A, E, F); (1) vertical posterior to transverse pronotal sulcus (Fig. 4B).
23. *Posterodorsal corner*: (0) without notch (Vilhelmsen 2000b: fig. 2A, E, F); (1) with distinct notch above anterior thoracic spiracle (Fig. 4A–F).
24. *Posterolateral margin*: (0) straight (Vilhelmsen 2000b: fig. 2A, E); (1) with incurvation accommodating anterior thoracic spiracle (Fig. 4A–F).
25. *Mesopleural attachment*: (1) pronotum separate from anterior mesopleural margin (Vilhelmsen 2000b: fig. 2A); (1) pronotum articulating with mesopleuron below spiracle (Fig. 4B, D, F); (2) pronotum fused with mesopleuron below spiracle for only short distance (Fig. 4A); (3) pronotum fused with mesopleuron below spiracle for entire distance (ordered).

Propectus

26. *Propleuron, dorsal cervical sclerite*: (0) absent or broadly fused with rest of propleuron (Fig. 5B, C); (1) sclerite present, at most attached to propleuron for short distance posteriorly (Fig. 5A, D).
27. *Propleuron, cervical line*: (0) absent (Fig. 5B–D); (1) present, cervical sclerite partly separated from rest of propleuron (Fig. 5A).
28. *Propleuron, propleural sulcus*: (0) absent (Fig. 5B); (1) sulcus and corresponding internal ridge present (Fig. 5A, C, D).
29. *Propleuron, medioventral margins*: (0) entirely separate medially (Fig. 6A, C); (1) abutting medially for at least a short distance (Fig. 6D).
30. *Propleuron, katepisternum*: (0) absent (Fig. 6A, C); (1) present (Fig. 6B, D).
31. *Propleuron, configuration of katepisternum*: (0) adjacent to lateral procoxal articulation (Vilhelmsen 2000b: fig. 17B, C); (1) separate from lateral procoxal articulation (Fig. 6B, D).
32. *Prosternum, laterosternal sclerites*: (0) absent or fused with prosternum (Fig. 6A, C, D); (1) independent sclerite present (Fig. 6B).
33. *Prosternum, anterolateral corner*: (0) separate from the propleuron (Fig. 6B–D); (1) fused with the posteroventral corners of the propleuron (Fig. 6A).
34. *Fore leg, calcar*: (0) anterior fore tibial spur simple, straight (Basibuyuk and Quicke 1995: fig. 2F–I); (1) anterior fore tibial spur curved, bifid (Basibuyuk and Quicke 1995: fig. 2B, E).
35. *Fore leg, inner apical protibial spur*: (0) absent; (1) present.
36. *Fore leg, tips of apical protibial spurs*: (0) pointed and sclerotised (Basibuyuk and Quicke 1995: fig. 2H, I); (1) blunt and membranous (Basibuyuk and Quicke 1995: fig. 2F, G).

Mesonotum

37. *Length of median mesoscutal sulcus*: (0) short, terminating at least 0.75 own length from scutellar sulcus (Fig. 7A–C); (1) distance between posterior end and scutellar sulcus at most 1/2 length of median sulcus (Fig. 7D).
38. *Notauli*: (0) absent or reduced, terminating well before midline of mesoscutum posteriorly (Fig. 7B); (1) fully developed, almost reaching midline posteriorly (Fig. 7A, C, D).

(continued next page)

Table 2. (continued)

39. *Notauli configuration*: (0) no difference between anterior and posterior part (Fig. 7A, D); (1) anterior part narrow, posterior part wider, with depression (Fig. 7C).
40. *Postscutellum*: (0) absent or reduced (Fig. 7A); (1) present, distinct (Fig. 7C, D).
- Mesopectus*
41. *Postspiracular sclerite*: (0) absent (Vilhelmsen 2000b: fig. 1); (1) present (Fig. 4A–F).
42. *Prepectus*: (0) absent or fused with adjacent sclerite (Fig. 4A); (1) independent sclerite present (Fig. 4E, F).
43. *Anterodorsal part of mesopleuron*: (0) not set off from surrounding part (Fig. 4A–C, F); (1) raised and/or separated by groove, line etc. (Fig. 4D, E)
44. *Posterior thoracic spiracle*: (0) spiracle visible in lateral view (Fig. 4A, F); (1) spiracle concealed in lateral view by mesopleuron (Fig. 4B–E).
45. *Posterodorsal margin of mesopleuron*: (0) straight in lateral view (Fig. 4D, E); (1) with incurvation at posterior thoracic spiracle (Fig. 4A, C, F); (2) with raised flap lateral to spiracle (Fig. 4B) (unordered).
46. *Prospinasternum*: (0) separate from mesopleuron (Vilhelmsen 2000b: fig. 1B, 7A); (1) fused with anterior mesopleural margin (Fig. 4A).
47. *Prospinasternal sulcus*: (0) small or absent (Vilhelmsen 2000b, Fig. 7A); (1) large (Fig. 4A).
48. *Mesopseudosternal sulcus*: (0) absent or weakly developed with no corresponding internal structure (Fig. 4B–F); (1) well developed with corresponding internal ridge (Fig. 4A).
49. *Mesopseudosternal sulcus configuration*: (0) not reaching anterior margin of mesopleuron; (1) extending to anterior margin of mesopleuron (Fig. 4A).
50. *Mesospinasternal apodeme*: (0) absent (Vilhelmsen 2000a: fig. 7D); (1) present, receiving metafurco-mesospinal muscles (Vilhelmsen 2000a: fig. 7C).
51. *Anterior mesofurcal arm*: (0) absent or reduced (Vilhelmsen 2000a: fig. 7D); (1) present, elongate (Vilhelmsen 2000a: fig. 7C).
52. *Lateral mesofurcal arm*: (0) short (Heraty *et al.* 1994: figs 3, 4); (1) elongate, extending towards mesopleuron (Vilhelmsen 2000a: fig. 7C, D).
- Metanotum*
53. *Insertion point of mesoscutello-metanotal muscle*: (0) not on a conspicuous structure (Fig. 8B–D); (1) on ring-like structure medially on anterior metanotal margin (Fig. 8A).
54. *Connection to 2nd phragma*: (0) sclerotised, at most separated by short membranous part (Vilhelmsen 2000a: figs 8A, 11A); (1) separated by extensive membranous area (Vilhelmsen 2000a: figs 9A, 10A).
55. *Lateral metanotal process*: (0) absent or short, blunt; (1) slender, projecting ventrally and/or medially.
56. *Shape of cenchrus*: (0) less than twice as broad as long (Fig. 8B–D); (1) at least twice as broad as long (Fig. 8A); (2) more than three times as broad as long (Vilhelmsen 2000a: fig. 3B) (ordered).
57. *Posterior part of cenchrus*: (0) membranous and inflected, devoid of hooks (Fig. 8B–D); (1) not inflected, hooks extend across entire surface (Fig. 8A).
58. *Apodeme for lateral metanoto-metapleural muscle*: (0) absent or small; (1) present, conspicuous.
59. *Metapostnotum size*: (0) shorter than 1/2 length of T1 (Fig. 8A, C, D); (1) at least as long as 1/2 length of T1 where longest (Fig. 8B).
- Metapectus*
60. *Anepimeron anteriorly*: (0) not expanded, metapleural arm clearly visible (Fig. 9C); (1) expanded anteriorly and dorsally, convex (Fig. 9A); (2) arm elongate and slender, not expanded distally (Fig. 9B, D) (unordered).
61. *Anterior margin of metapleuron*: (0) without apodeme dorsally (Fig. 9B–D); (1) with distinct apodeme ventral to anapleural cleft (Figs 9A, 10A).
62. *Anapleural cleft*: (0) absent (Fig. 9C, D); (1) present (Fig. 9A, B).
63. *Metapleuron configuration with T1*: (0) at most abutting (Fig. 9B–D); (1) fused (Fig. 9A).
64. *Metapleural apodeme*: (0) at most shallow ridge present (Vilhelmsen 2000a: fig. 7B); (1) distinct apodeme present (Vilhelmsen 2000a: fig. 7D).
65. *Metapleuron posteroventral apodeme*: (0) absent (Vilhelmsen 2000a: fig. 7D); (1) present, accommodating posterior pl3-fu3 muscle (Vilhelmsen 2000a: fig. 7C (t24)).
66. *Paracoxal notches*: (0) absent (Fig. 10A–D); (1) present (Vilhelmsen 2000a: fig. 6B).
67. *Paracoxal sulcus and ridge*: (0) curving anteriorly (Fig. 10A, C); (1) curving posteriorly (Fig. 10B, D).
68. *Paracoxal sulcus termination*: (0) at posterior margin of metepisternum (Fig. 10D); (1) in middle of metepisternum (Fig. 10B, C); (2) in metapleural sulcus close to anterior margin of metepisternum (Fig. 10A) (unordered).
69. *Anterior metafurcal arms*: (0) absent or weakly developed (Vilhelmsen 2000a: fig. 7D); (1) well developed (Fig. 10C).
70. *Lateral metafurcal arms*: (0) short (Vilhelmsen 2000a: fig. 7A); (1) well developed, extending laterally (Vilhelmsen 2000a: fig. 7D).
71. *Metathoracic trochantin*: (0) absent; (1) present, receiving muscle (Vilhelmsen 2000a: figs 8B, 11B).
72. *Hind femur length*: (0) shorter than hind tibia (excl. trochantellus); (1) approx. equal to hind tibia.
73. *Preapical hind tibial spurs*: (0) absent; (1) present.
74. *Apical hind tibial spurs*: (0) short, not much longer than apical breadth of tibia; (1) length at least 2× apical breadth of hind tibia.
75. *Hind basitarsus length*: (0) shorter than tarsomeres 2–4; (1) equal to or longer than tarsomeres 2–4.
76. *Hind tarsal pulvilli*: (0) absent from tarsomeres 1 and 2; (1) present on tarsomeres 1–4.
77. *Hind tarsal claw basal lobe*: (0) absent or weakly developed; (1) present, distinct.
78. *Hind tarsal claw*: (0) simple, without additional tooth; (1) bifid.
79. *Hind tarsal claw teeth length*: (0) of subequal length (when bifid); (1) inner tooth much shorter than apical.
- Abdominal T1*
80. *T1 medially*: (0) subdivided by median longitudinal line (Fig. 8A, B, D); (1) fused medially, entire (Fig. 8C).
81. *T1 membranous patch*: (0) small, T1 inner margins subparallel at least anteriorly (Fig. 8A, B); (1) well developed, T1 inner margins diverging for almost entire length (Fig. 8D).

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Table 2. (continued)

82. *T1, metalaterophragmal lobe*: (0) absent or weakly developed (Vilhelmsen 2000a: fig. 4A, C); (1) present, distinct (Fig. 8B, C; Vilhelmsen 2000a: fig. 4B, D).

Forewing

83. *Subcosta*: (0) at most short transverse vein present; (1) distinct, separate longitudinal vein extending at least half length of costal cell.
84. *Subcosta anterior branch*: (0) entirely absent (Fig. 11A, B); (1) not tubular and/or interrupted (Fig. 11D); (2) tubular, reaching vein C (Fig. 11G) (ordered).
85. *Subcosta anterior branch position*: (0) proximal to M – Sc+R junction (Fig. 11D, G); (1) distal to M – Sc+R junction.
86. *Costal cell in middle*: (0) higher than width of veins C and R combined (Fig. 11D); (1) shorter than or equal to width of veins C and R combined (Fig. 11A, B).
87. *Vein R configuration*: (0) straight throughout (Figs 11A, G, 12C); (1) with distinct bend at cell 1M (Figs 11B, 12E, F).
88. *Cell 1M*: (0) angular anteriorly (Figs 11C, 12A); (1) rounded anteriorly (Fig. 11A).
89. *Vein M junction to Sc+R*: (0) very close to Rs+M junction (Figs 11F, 12A); (1) some distance from Rs+M junction (Figs 11E, G, H, 12E, F).
90. *Veins m and 1m-cu configuration*: (0) more or less parallel (Fig. 12A, B, E); (1) convergent (Fig. 11B, H).
91. *Rs+M proximal part*: (0) more or less straight (Fig. 12B); (1) strongly recurved (Fig. 12C, D).
92. *1st abscissa of Rs*: (0) absent or very short (Fig. 11B); (1) present (Fig. 11A).
93. *Shape of 1st abscissa of Rs*: (0) anterior end more proximal than posterior; (1) posterior end more proximal than anterior.
94. *Abscissa of Rs*: (0) entirely absent as tubular vein between cells 1R and Rs (Figs 11G, H, 12A); (1) present only partly as tubular vein between cells 1R and Rs (Fig. 11D); (2) fully developed, might have bulla (Fig. 12B, D, E) (ordered).
95. *Cross vein 2r*: (0) absent (Fig. 11B–D, F, G); (1) present (Figs 11A, E, H, 12A, D).
96. *Cross vein 2r position*: (0) proximal or opposite 2r-m; (1) distal to 2r-m (Figs 11A, E, H, 12A, D).
97. *Tip of radial cell*: (0) on anterior wing margin (Figs 11D, F, 12F); (1) retracted from anterior wing margin (Fig. 11C); (2) radial cell open (Fig. 11B) (unordered).
98. *Cross vein 2r-m*: (0) absent (Figs 11C, 12C); (1) present (Figs 11D–G, 12D).
99. *Rs – 2r-m/2r-m – 3r-m distance, measured along vein Rs*: (0) Rs to 2r-m longer than 2r-m to 3r-m (Figs 11G, 12E); (1) 2r-m to 3r-m as least as long as Rs to 2r-m (Fig. 11B, D).
100. *1m-cu/Cu1 angle*: (0) veins meeting in angle less than 110 degrees (Figs 11B, H, 12B); (1) veins meeting in angle more than 120 degrees (Fig. 12A, E, F).
101. *Veins 1m-cu and 2m-cu*: (0) inserts on M in different cells (Fig. 11D, F); (1) both insert on M in cell 1RS (Fig. 11C, E, G).
102. *Cross vein 3r-m*: (0) absent; (1) present.
103. *Cu-a insertion*: (0) 1/2 × cu-a length or more from base of Cu1 (Figs 11A, 12B); (1) 1/4 to 1/2 × cu-a length from base of Cu1 (Fig. 11D); (2) 1/4 or less × cu-a length from base of Cu1 (Fig. 12A); (3) cu-a in apposition to M (Fig. 11E) (ordered).
104. *Posterior anal vein and cross vein 1a*: (0) entirely absent (Fig. 11C); (1) posterior anal vein absent proximally of 1a (Figs 11B, G, H, 12B); (2) present for short distance proximally and distally (Figs 11E, F, 12F); (3) present along entire length of anterior anal vein (Figs 11A, D, 12A, C–E) (ordered).
105. *Cross vein 1a*: (0) absent (Fig. 12D); (1) present (Figs 11A, D, 12A, C, E).
106. *Cross vein 1a position*: (0) in distal half of anal cell, distal to incurvation (Figs 11A, D, 12A, C); (1) in proximal half of anal cell, at incurvation (Fig. 12E).
107. *Cross vein 1a configuration*: (0) oblique (Figs 11A, 12A, C); (1) straight (Figs 11D, 12E).
108. *Vein 3a*: (0) curved (Fig. 12B); (1) straight (Fig. 11G, H).
109. *Vein 3a apex*: (0) not divided at apex (Fig. 11G, H); (1) bifid (Fig. 12B).

Hindwing

110. *Distal hamuli placement*: (0) en echelon (Basibuyuk and Quicke 1997: figs 5C, 6); (1) aligned (Basibuyuk and Quicke 1997: fig. 5B).
111. *Secondary hamuli*: (0) absent (Basibuyuk and Quicke 1997: fig. 2D); (1) present (Basibuyuk and Quicke 1997: fig. 2C).
112. *Subcosta*: (0) absent (Fig. 13A, B); (1) present.
113. *Cell R1*: (0) entirely closed off by veins (Fig. 13A, C, E, F); (1) open distally, vein R1 incomplete (Fig. 13B, D).
114. *Cross vein 3r-m*: (0) absent (Fig. 13C, D); (1) present (Fig. 13A, B, E, F).
115. *Cross vein m-cu*: (0) absent (Fig. 13C, D); (1) present (Fig. 13A, B, E, F).
116. *Veins 3r-m/m-cu configuration*: (0) 3r-m less than own length away from m-cu (Fig. 13A, B); (1) 3r-m at least own length away from m-cu (Fig. 13F).
117. *Marginal vein*: (0) absent (Fig. 13D); (1) present at least in males (Fig. 13E).
118. *Posterior anal vein*: (0) absent or at least partly reduced (Fig. 13B, D); (1) present, complete (Fig. 13A, C, E, F).
119. *Length of anal cell*: (0) as long as cell 1Cu posteriorly (Fig. 13F); (1) shorter than cell 1Cu (Fig. 13A, C, E).

Abdomen

Characters 122–127 have been illustrated and discussed in Weltz and Vilhelmsen (2014).

120. *Pleural region of abdominal terga*: (0) separate from terga s. str. (Vilhelmsen 2001: fig. 5A, B); (1) fused with terga s. str. (Vilhelmsen 2001: fig. 5C).
121. *Abdominal spiracle position*: (0) ventral to membranous subdivision of terga (Vilhelmsen 2001: fig. 5A); (1) dorsal to membranous subdivision of terga (Vilhelmsen 2001: fig. 5B).
122. *T8, anterolateral corners*: (0) without extension; (1) with extension.

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Table 2. (continued)

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123. *T9, anterior flanges*: (0) continuous medially at least through thickened posterior rim; (1) not continuous medially.
124. *Cercus*: (0) length/mid-breadth ratio at most 2; (1) length/mid-breadth ratio between 2 and 5; (2) length/mid-breadth ratio at least 5 (ordered).
125. *Length of cercus/medial length of tergum 10*: (0) at most 0.7; (1) between 0.7 and 1; (2) at least 1 (ordered).
126. *Length of cercus/medial length of tergum 9 + tergum 10*: (0) at most 0.5; (1) between 0.5 and 1; (2) at least 1 (ordered).
127. *Medial length of tergum 10/medial length of tergum 9*: (0) at most 1; (1) between 1 and 2; (2) at least 2 (ordered).
- Ovipositor*
- Characters 128–146 have been illustrated and discussed in Weltz and Vilhelmsen (2014).
128. *Length of 3rd valvula/length of part of 3rd valvula from level of median bridge to posterior end*: (0) at most 1.3; (1) between 1.3 and 1.9; (2) at least 1.9 (ordered).
129. *Banding pattern on 1st and 2nd valvula*: (0) absent; (1) present.
130. *Lamnium of 1st valvula*: (0) comprising at least half of length; (1) comprising slightly less than half of length; (2) comprising short distance distally only (ordered).
131. *Distribution of sawteeth on 1st valvula*: (0) present along at least half of length; (1) present along between half and third of length; (2) present along third of length; (3) present along quarter of length; (4) present for less than quarter of length (ordered).
132. *Serrulae on sawteeth*: (0) absent; (1) present on sawteeth of 1st valvula.
133. *Lateral part of 1st valvula*: (0) without hairs; (1) with hairs.
134. *Ctenidia laterally on 1st valvula*: (0) absent; (1) present on annuli.
135. *Spurettes laterally on 1st valvula*: (0) absent; (1) present on annuli.
136. *Aulax on 1st valvula*: (0) entirely on dorsal margin of 1st valvula; (1) displaced ventrally on medial wall of 1st valvula for less than half of length; (2) displaced ventrally on medial wall of 1st valvula for at least half of length (ordered).
137. *Second valvifer and 3rd valvula*: (0) at least partly separated by membranous area; (1) totally fused.
138. *Second valvifer*: (0) continuous with median bridge at least through weakly sclerotised strip; (1) entirely separated from median bridge by membrane.
139. *Posterodorsal part of 2nd valvifer*: (0) do not project posteriorly of ventral margin of 2nd valvifer; (1) produced posteriorly of ventral margin of 2nd valvifer.
140. *Distal part of dorsal flange*: (0) curving dorsomedially; (1) curving dorsally; (2) more or less straight (unordered).
141. *Anterodorsal parts of 3rd valvulae*: (0) fused/continuous medially; (1) at least slightly separated medially.
142. *Second valvula*: (0) separate from opposite apically; (1) fused with opposite apically.
143. *Lengths of 2nd valvulae*: (0) equal; (1) unequal.
144. *Less sclerotised zones of 2nd valvula*: (0) put together, comprising clearly less than half of length of lamnium; (1) put together, comprising about half of length of lamnium; (2) put together, comprising clearly more than half of length of lamnium (ordered).
145. *Sawteeth on 2nd valvula*: (0) absent; (1) present on dorsal margin.
146. *Annuli of 2nd valvula*: (0) ventral terminations without tufts of hairs; (1) ventral terminations with tufts of hairs.
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substantial number of exemplars sampled broadly across the Tenthredinidae. Boevé *et al.* (2013) assembled a dataset comprising 100+ tenthredinid taxa, but only a dozen outgroup taxa to explore the evolution of larval chemical defenses. Furthermore, many genera are represented by more than one terminal (*Monophadnus* by no less than nine), so in total 64 tenthredinid genera are included (Boevé *et al.* 2013: fig. 3). These were sequenced for two mitochondrial and one nuclear gene. This dataset retrieved the Tenthredinidae as monophyletic, but did not reproduce the existing subfamily classification. Interestingly, Heptamelini (*Heptamelus* + *Pseudoheptamelus*) and *Athalia* spp. were placed as successive outgroups to all remaining Tenthredinidae.

Malm and Nyman (2015) have a more balanced taxon sample, including ~80 exemplars of Tenthredinidae, as well as 40 representatives from the other tenthredinoid families. Despite the lower number of tenthredinid terminals, almost as many genera (61) are included as in Boevé *et al.* (2013). With data from nine protein coding genes Malm and Nyman (2015) were able to produce robust results and properly test the subfamily classification of the Tenthredinidae,

something no previous study has accomplished. The subfamilies Nematinae and Tenthredininae are retrieved as well supported, as well as core clades of Allantinae (except *Athalia* spp., *Eriocampa* and *Eusunoxa*) and Selandriinae (except Heptamelini: *Heptamelus* + *Pseudoheptamelus*). More problematic are the Blennocampinae and Heterarthrinae, the latter being placed as two separate clades within the Blennocampinae. Malm and Nyman (2015) even retrieved all Tenthredinidae except Heptamelini as monophyletic, although not with strong support. *Athalia* spp. were sister to all Tenthredinidae except Heptamelini. Consequently, Malm and Nyman (2015) suggested elevating Heptamelini to family status (Heptamelidae).

The current study presents the largest taxon sample assembled for exploring relationships across the Tenthredinidae and the placement of the other tenthredinoid families relative to Tenthredinidae. A correspondingly high number of morphological characters have been scored for this endeavour. The aim is to test the existing subfamily classification of the Tenthredinidae and provide a baseline for improving it, as well as revealing characters that might be useful for purposes of identification.

Materials and methods*Material examined*

In total, 129 terminals were included in the analyses: five non-tenthredinoid outgroups, three Argidae, three Blasticotomidae, four Cimbicidae, four Diprionidae, six Pergidae and 104

Tenthredinidae. Within the latter, the six subfamilies (according to Taeger *et al.* 2010) were represented as follows: 21 Allantinae, 20 Blennocampinae, 9 Heterarthrinae, 20 Nematinae, 18 Selandriinae and 16 Tenthredininae. The dissected specimens are stored in the Natural History Museum of Denmark, University of Copenhagen.

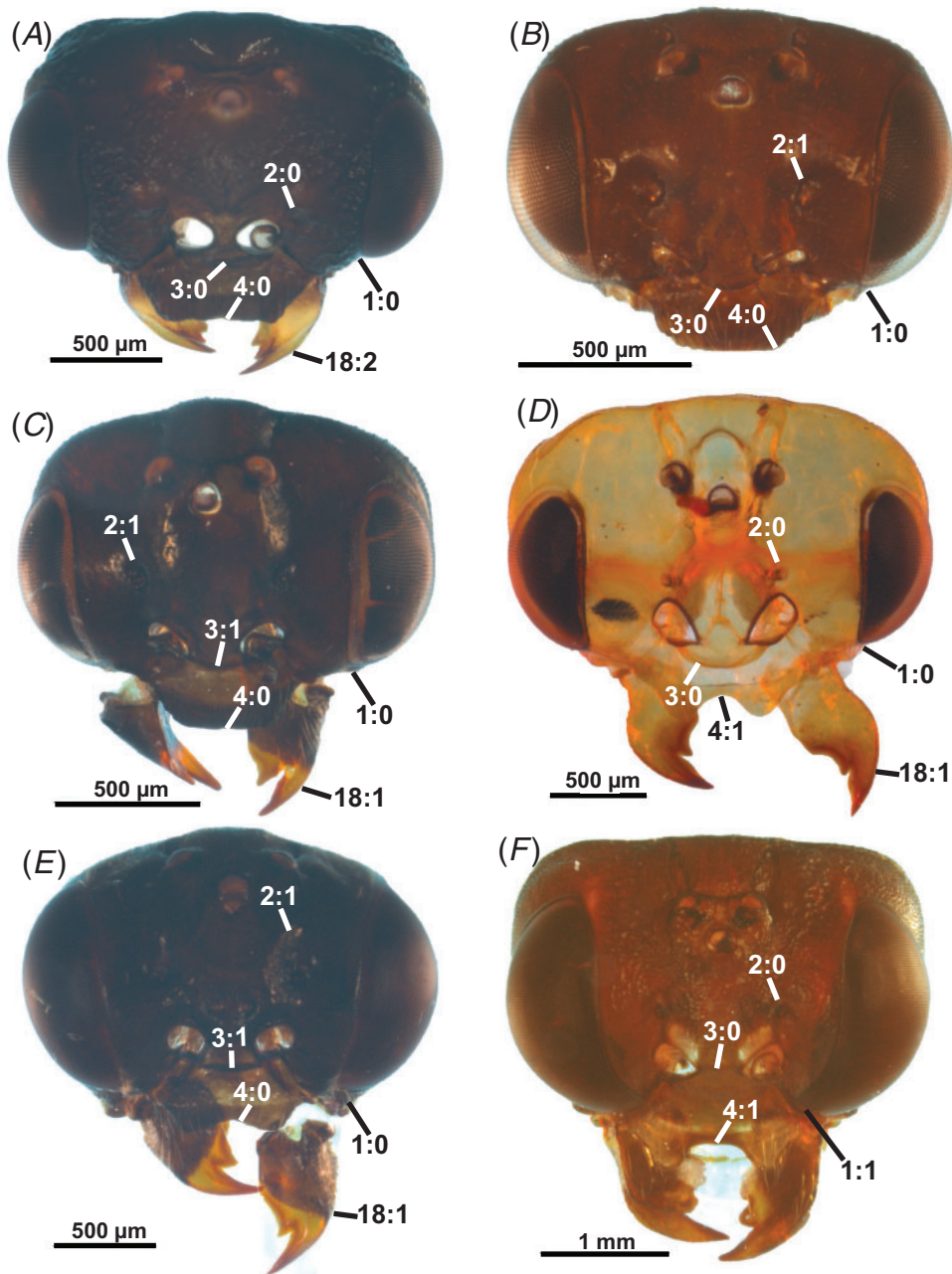


Fig. 1. Anterior view of head of: (A) *Blasticotoma filiceti* Klug, 1834 (Blasticotomidae); (B) *Blennocampa phyllocolpa* Viitasaari and Vikberg, 1985 (Tenthredinidae, Blennocampinae); (C) *Endelomyia aethiops* (Gmelin, 1790) (Tenthredinidae, Heterarthrinae); (D) *Hemichroa australis* (Serville, 1823) (Tenthredinidae, Nematinae); (E) *Aneugmenus padi* (Linné, 1760) (Tenthredinidae, Selandriinae); (F) *Tenthredo scrophulariae* Klug, 1817 (Tenthredinidae, Tenthredininae). Character states indicated by numbers.

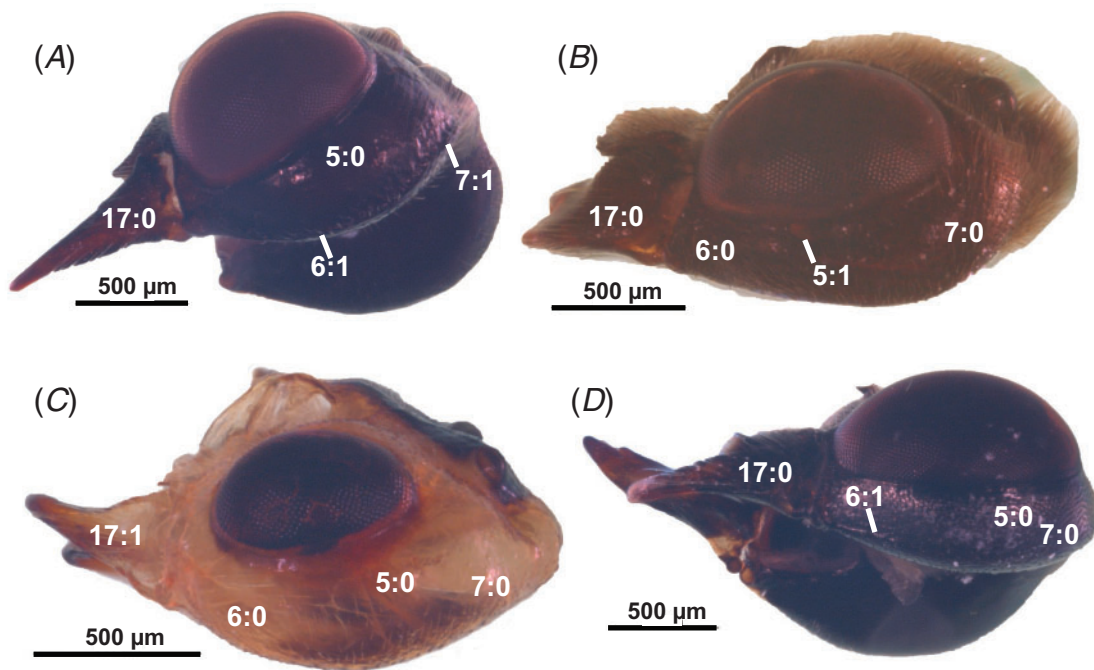


Fig. 2. Lateral view of head of: (A) *Taxonus agrorum* (Fallén, 1808) (Tenthredinidae, Allantinae); (B) *Phymatocera aterrima* (Klug, 1816) (Tenthredinidae, Blennocampinae); (C) *Pachynematus clitellatus* (Serville, 1823) (Tenthredinidae, Nematinae); (D) *Filacus albipes* (Provancher, 1895) (Tenthredinidae, Tenthredininae). Character states indicated by numbers.

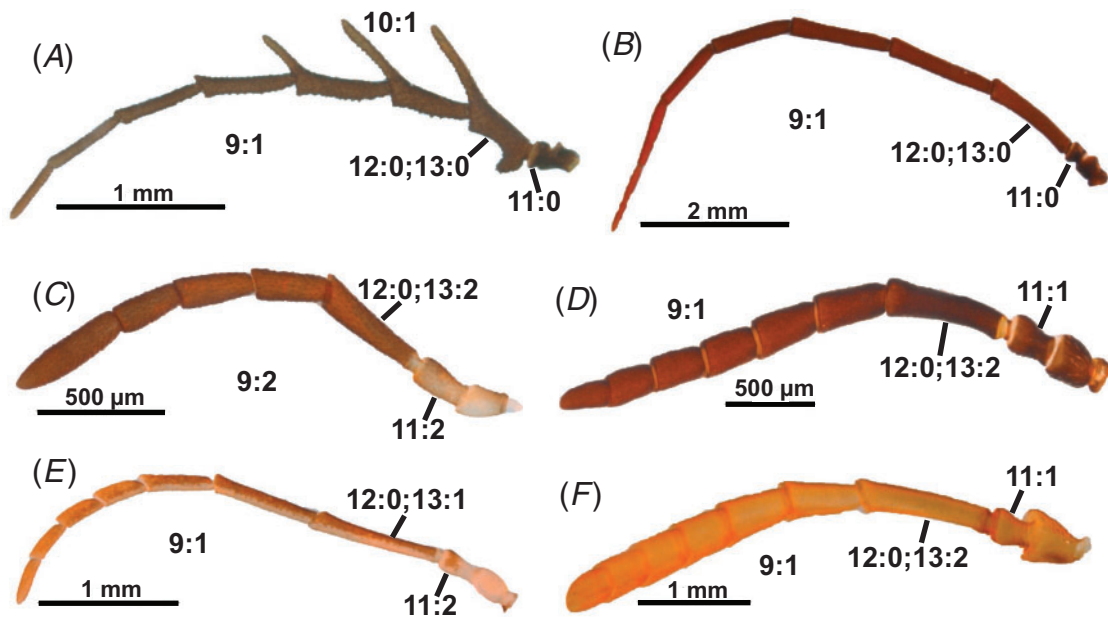


Fig. 3. Antennae of: (A) *Cladius pectinicornis* (Geoffroy, 1785) (Tenthredinidae, Nematinae); (B) *Craesus septentrionalis* (Linné, 1758) (Tenthredinidae, Nematinae); (C) *Heptamelus dahlbomi* (Thomson, 1870) (Tenthredinidae, Selandriinae); (D) *Selandria serva* (Fabricius, 1793) (Tenthredinidae, Selandriinae); (E) *Strombocerus delicatulus* (Fallén, 1808) (Tenthredinidae, Selandriinae); (F) *Tenthredo scrophulariae* Klug, 1817 (Tenthredinidae, Tenthredininae). Character states indicated by numbers.

The Tenthredinidae are most diverse in the northern hemisphere, and the majority of the terminals included come from the Palaearctic. However, efforts have been made to also include some of the rarer taxa from the Afrotropical and Neotropical regions. For further details of the material examined, see Table S1 (available as Supplementary Material on the journal website).

Dissections, imaging and character scoring

Most specimens were preserved in 70% ethanol before dissection. Dissection and scoring of characters were carried out under a Leica MZ16 APO or Leica M205C dissecting microscope (Leica Microsystems, Wetzlar, Germany). Dissected material was stored and examined in glycerin. Selected features (antennae, labrum, labiomaxillary complex, hind tarsi) were mounted on

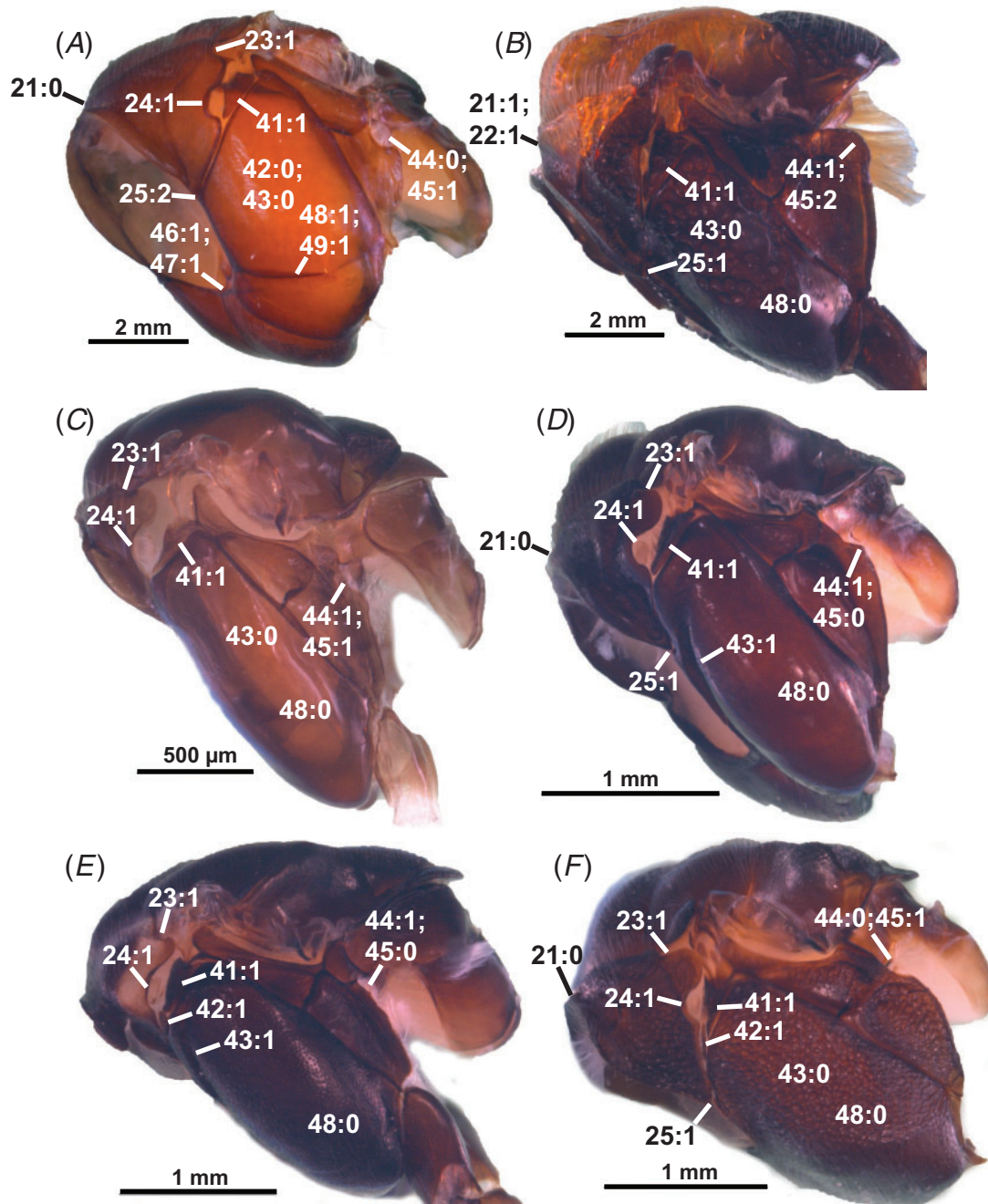


Fig. 4. Lateral view of pronotum and mesothorax of: (A) *Arge ustulata* (Linné, 1758) (Argidae, Arginae); (B) *Eriocampa ovata* (Linné, 1760) (Tenthredinidae, Allantinae); (C) *Rocalia japonica* Naito, 1988 (Tenthredinidae, Selandriinae); (D) *Stethomostus fuliginosus* (Schrank, 1781) (Tenthredinidae, Blennocampinae); (E) *Craterocercus fraternalis* (Norton, 1872) (Tenthredinidae, Nematinae); (F) *Dolerus nitens* Zaddach, 1859 (Tenthredinidae, Selandriinae). Character states indicated by numbers.

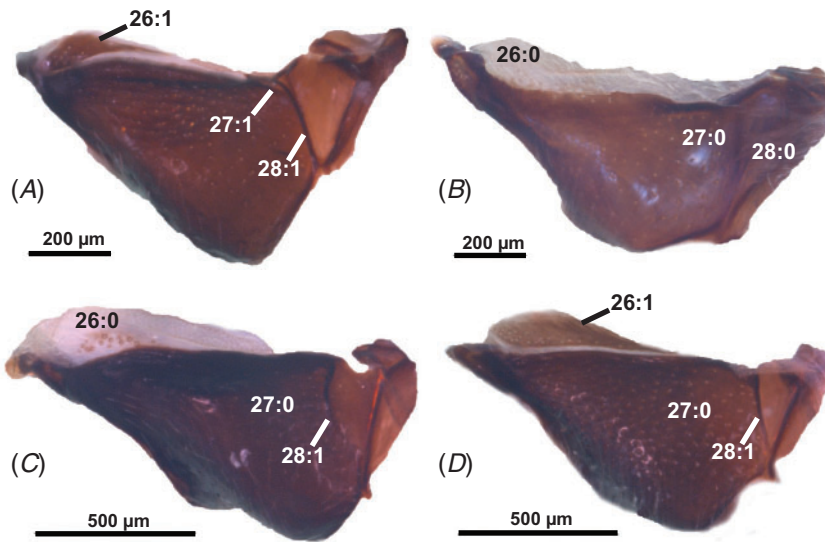


Fig. 5. Lateral view of propectus of (A) *Blasticotoma filiceti* Klug, 1834 (Blasticotomidae); (B) *Lophyrotoma analis* (Costa, 1864) (Pergidae, Pteryperginae); (C) *Nematus caeruloecarpus* Hartig, 1837 (Tenthredinidae, Nematinae); (D) *Dolerus nitens* Zaddach, 1859 (Tenthredinidae, Selandriinae). Character states indicated by numbers.

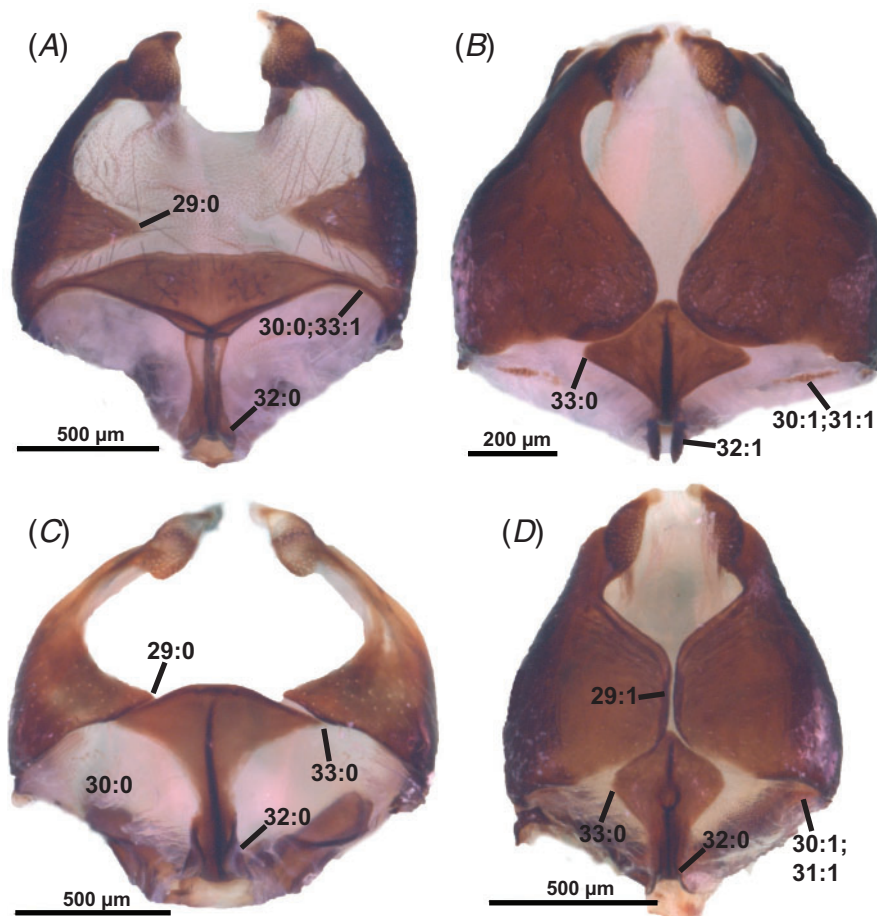


Fig. 6. Ventral view of propectus of: (A) *Abia fasciata* (Linné, 1758) (Cimbicidae, Abiinae); (B) *Blasticotoma filiceti* Klug, 1834 (Blasticotomidae); (C) *Heteroperreyia hubrichi* Malaise, 1955 (Pergidae, Perreyinae); (D) *Allantus cinctus* (Linné, 1758) (Tenthredinidae, Allantinae). Character states indicated by numbers.

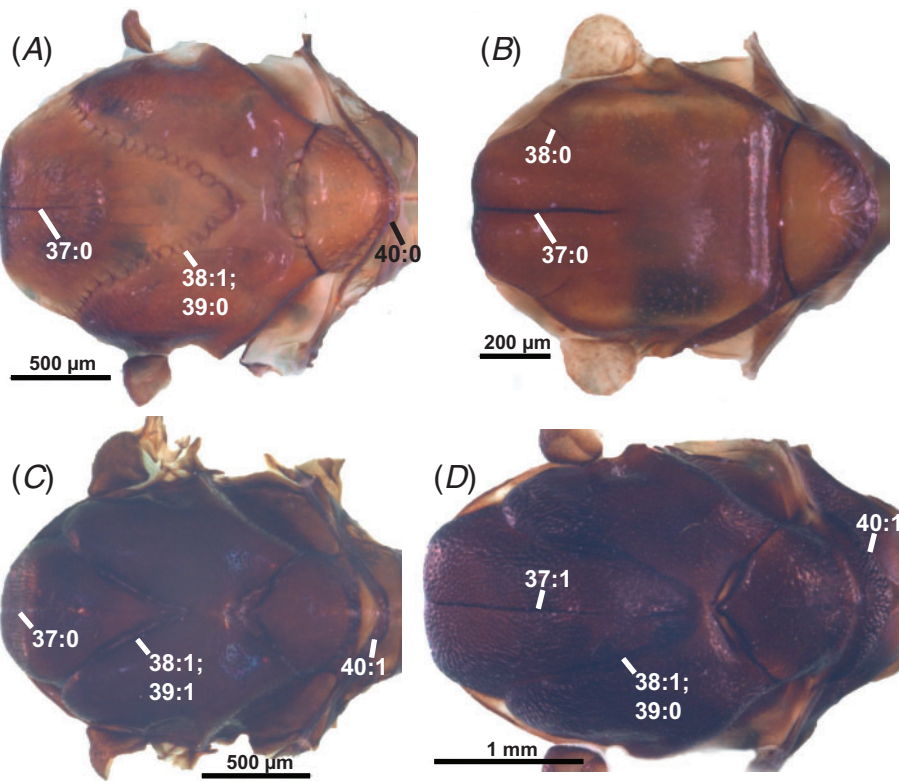


Fig. 7. Dorsal view of mesonotum in: (A) *Aproceros leucopoda* Takeuchi, 1939 (Argidae, Sterictiphorinae); (B) *Arcodulecera dorsalis* Say, 1836 (Pergidae, Acordulecerinae); (C) *Ametastegia glabrata* (Fallén, 1808) (Tenthredinidae, Allantinae); (D) *Nematus caeruloecarpus* Hartig, 1837 (Tenthredinidae, Nematinae). Character states indicated by numbers.

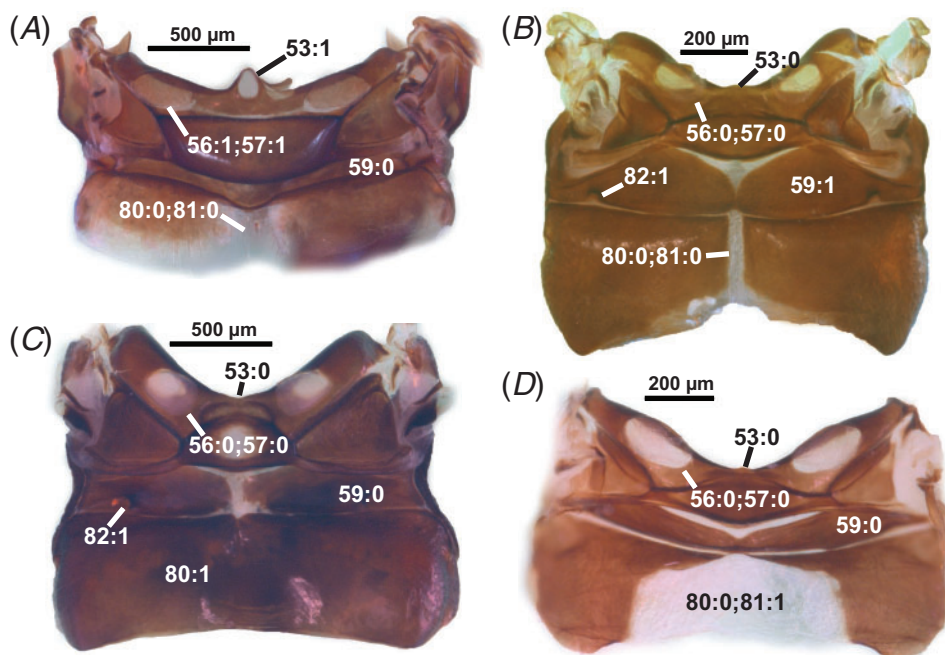


Fig. 8. Dorsal view of metanotum in: (A) *Lophyrotoma analis* (Costa, 1864) (Pergidae, Pteryperginae); (B) *Ametastegia pallipes* (Spinola, 1808) (Tenthredinidae, Allantinae); (C) *Tenthredopsis ornata* (Serville, 1823) (Tenthredinidae, Tenthredininae); (D) *Hoplocampa* sp. (Tenthredinidae, Nematinae). Character states indicated by numbers.

slides in Entellan (Merck KGaA, Darmstadt, Germany) and examined in a Leitz compound microscope. Images of specimens in glycerin were taken with a Leica DFC 450C digital camera mounted on a Leica MZ 16A dissecting microscope (Leica Microsystems). Wings were temporarily mounted on slides in glycerin during imaging. Compound images were compiled from image stacks with Zerene Stacker (Zerene Systems, Richland, WA, USA). Final images were cleaned up in Adobe Photoshop before being assembled into plates with Adobe Illustrator (Adobe Systems, San Jose, CA, USA). Cladograms reproduced were exported as PDFs from Mesquite, and modified in Adobe Photoshop and Illustrator.

Phylogenetic analyses

The character matrix (see Table 1) was assembled in Mesquite 2.75 (Maddison and Maddison 2011). The dataset was

analysed with TNT 1.1. (Goloboff *et al.* 2008). The following characters were treated as ordered: 9, 11, 13, 18, 25, 56, 84, 94, 103, 104, 124–128, 130, 131, 136, 144. Space for 1 000 000 trees was reserved in memory. Traditional searches were run for equal and implied weights analyses with 10 000 replications, saving 100 trees per replication. The root was *Macroxyela*. K values for implied weights analyses were set to 1–15, 20, 25 and 30 in turn. Character evolution was explored in Mesquite.

Character list

The character list is presented in Table 2. Many of the characters examined here are extracted and modified from previous studies conducted in a phylogenetic context: head and mouthparts (Vilhelmsen 1996, 1999, 2011), thorax (Vilhelmsen 2000a, 2000b) and ovipositor system

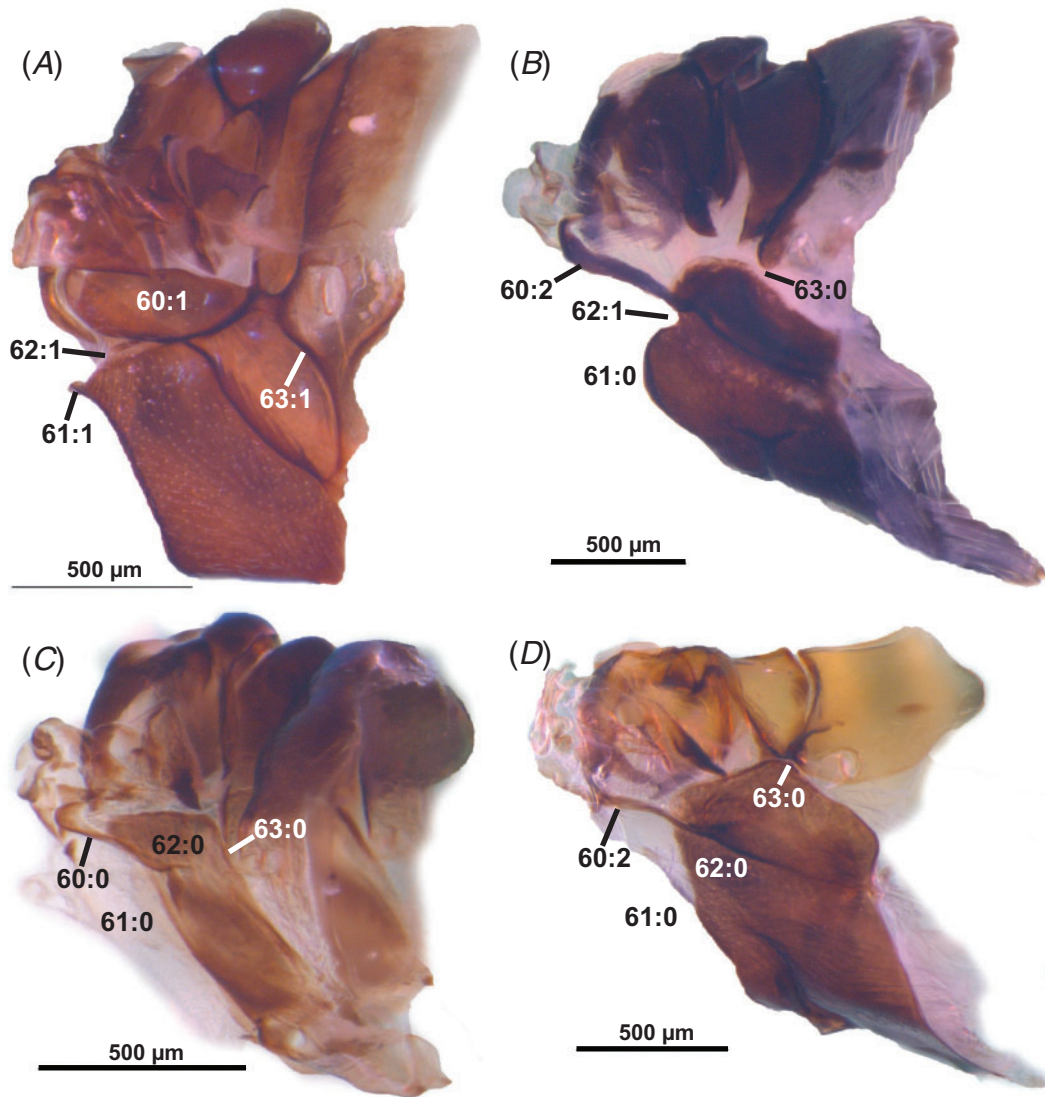


Fig. 9. Lateral view of metathorax in: (A) *Lophyrotoma analis* (Costa, 1864) (Pergidae, Pteryperginae); (B) *Eopsis beaumonti* Benson, 1959 (Tenthredinidae, Allantinae); (C) *Heterarthrus vagans* (Fallén, 1808) (Tenthredinidae, Heterarthrinae); (D) *Leucopelmonus annulicornis* (Harrington, 1893) (Tenthredinidae, Tenthredininae). Character states indicated by numbers.

(Vilhelmsen 2000c; Weltz and Vilhelmsen 2014). Other sources of characters are some of the existing comprehensive keys for ‘Symphyta’: Benson (1952, 1958), Goulet (1992) and Zhelokhovtsev *et al.* (1994). The male genitalia of the basal Hymenoptera were examined by Schulmeister (2001, 2003b), but this character system falls outside the scope of the present contribution, as do characters from larval anatomy (Yuasa 1922; Maxwell 1955). Previous compilations of morphological characters relevant for tenthredinoid relationships are found in Vilhelmsen (2001) and Schulmeister (2003c).

Results and discussion

The equal weights (EW; Fig. 14) analysis produced 3628 trees of length 1448 steps. The shortest trees were retrieved only in very few replications. Resolution was generally poor, the base of the Tenthredinoidea s. str. forming a large polytomy. The only major clades supported were the Nematinae and a clade comprising Diprionidae + (Cimbicidae + (Argidae + Pergidae)).

The implied weights analyses (IW) usually produced only one tree (Figs 15, 16); however, the topology of the tree differed substantially according to the *k* value implemented, and the most fit tree was only retrieved in very few replications. The deeper relationships especially were highly

unstable, but subfamilies and even in some cases genera (e.g. *Allantus*, *Cladius*, *Dolerus*) within Tenthredinidae were not supported in most analyses. In the following, only the relationships that could be observed across a substantial range of analytical settings are discussed.

Blasticotomidae and Tenthredinoidea s. str. were always monophyletic and sister groups. The families Argidae, Cimbicidae, Diprionidae and Pergidae were always monophyletic, Cimbicidae + (Argidae + Pergidae) always coming out as a clade (CAP in Figs 14–16). Diprionidae was the sister to this clade in the EW and IW analyses with *k* > 12 (Fig. 16). However, when *k* was 1–12, Diprionidae was placed inside the Nematinae (Fig. 15), as sister to *Cladius pectinicornis*. ‘Tenthredinidae’ was never monophyletic, Argidae, Cimbicidae, Diprionidae and Pergidae always being nested inside.

The shifting position of the Diprionidae was intriguing. The position within Nematinae, even within the genus *Cladius*, is supported by several putative synapomorphies: presence of lateral projections on the male antennae (char. 10:1; only shared with *Cladius pectinicornis* and two pergids), anterior fore tibial spur simple (char. 34:0), and well developed ctenidia laterally and ventrally displaced aulax medially on first valvula (chars 134:1 and 136:2; see also Weltz and Vilhelmsen 2014). However, the alternative position as sister to Cimbicidae + (Argidae + Pergidae) would be supported by the

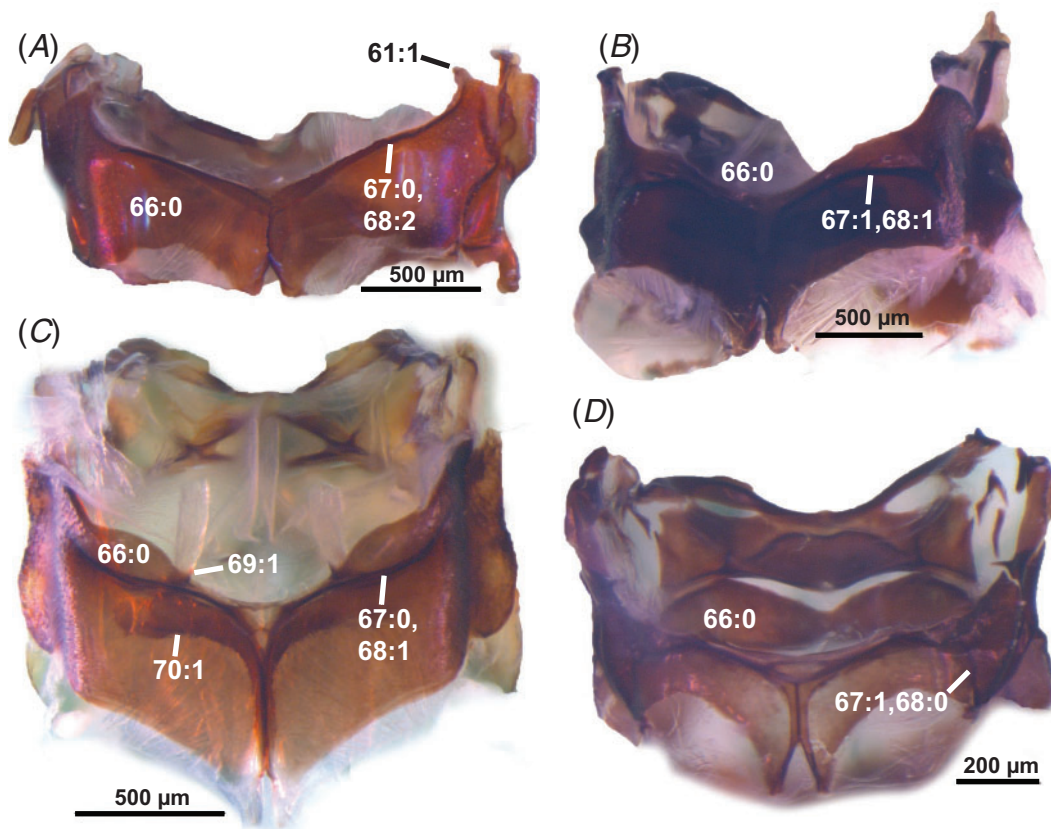


Fig. 10. Ventral view of metathorax in: (A) *Lophyrotoma analis* (Costa, 1864) (Pergidae, Pteryperginae); (B) *Eopsis beaumonti* Benson, 1959 (Tenthredinidae, Allantinae); (C) *Leucopelmonus annulicornis* (Harrington, 1893) (Tenthredinidae, Tenthredininae); (D) *Notofenusia surosa* (Konow, 1905) (Tenthredinidae, Heterarthrinae). Character states indicated by numbers.

cenchus configuration (chars 56:2, 57:1) and ovipositor characters (chars 133:1, 140:0). Furthermore, no analyses including molecular data have placed Diprionidae inside Nematinae (Schulmeister 2003a; Nyman *et al.* 2006; Ronquist *et al.* 2012; Boevé *et al.* 2013; Malm and Nyman 2015).

The Cimbicidae are always placed as the sister to Argidae + Pergidae, supported by the fusion between the first abdominal tergum and the metapleuron (char. 63:1), the absence of the posteroventral apodeme for the posterior pleuro-furcal muscle (char. 65:0; probably correlated with 63:1), the first abdominal tergum not being subdivided medially (80:1; reversed in some argids and pergids), and the absence of the anterior branch of the subcosta and the costal cell being short (chars 84:0 and 86:1; likely also correlated). Most other analyses place Cimbicidae in a clade with Diprionidae and Tenthredinidae, often as sister to Diprionidae (Schulmeister 2003a; Nyman *et al.* 2006; Malm and Nyman 2015). Apparently there is support for this relationship from the molecular but also some morphological data, e.g. male genitalia (Schulmeister 2003b).

Allantinae were never monophyletic, the majority of the taxa usually coming out at the base of Tenthredinoidea s. str. in

one or two larger clades (often including non-allantines), but always with some taxa scattered across the phylogeny. *Harpiphorus* was sister to all other Tenthredinoidea s. str. in all IW analyses (Figs 15, 16). *Athalia* is a rogue taxon, usually falling outside major clades. At $k > 7$ and EW, *Athalia* is sister to *Eriocampa*. Recent comprehensive molecular analyses have placed *Athalia* as sister to all other Tenthredinidae (Boevé *et al.* 2013) or all except Heptamelini (Malm and Nyman 2015).

Blennocampinae was never monophyletic, but usually scattered across the phylogeny as small clades or grades. Indeed, in the most comprehensive identification manuals (Benson 1952; Goulet 1992) this subfamily is among the last to key out and is mainly characterised by not having the characters used to delimit the other subfamilies. In Boevé *et al.* (2013) blennocampines are mixed with allantine and heterarthrine taxa; in Malm and Nyman (2015) the subfamily is paraphyletic with respect to Heterarthrinae and the allantine *Eusunoxa*. Blennocampinae seems to be something of a taxonomic waste basket.

The Heterarthrinae were never retrieved as monophyletic. A core clade comprising *Fenusia*, *Heterarthrus*, *Metallus*,

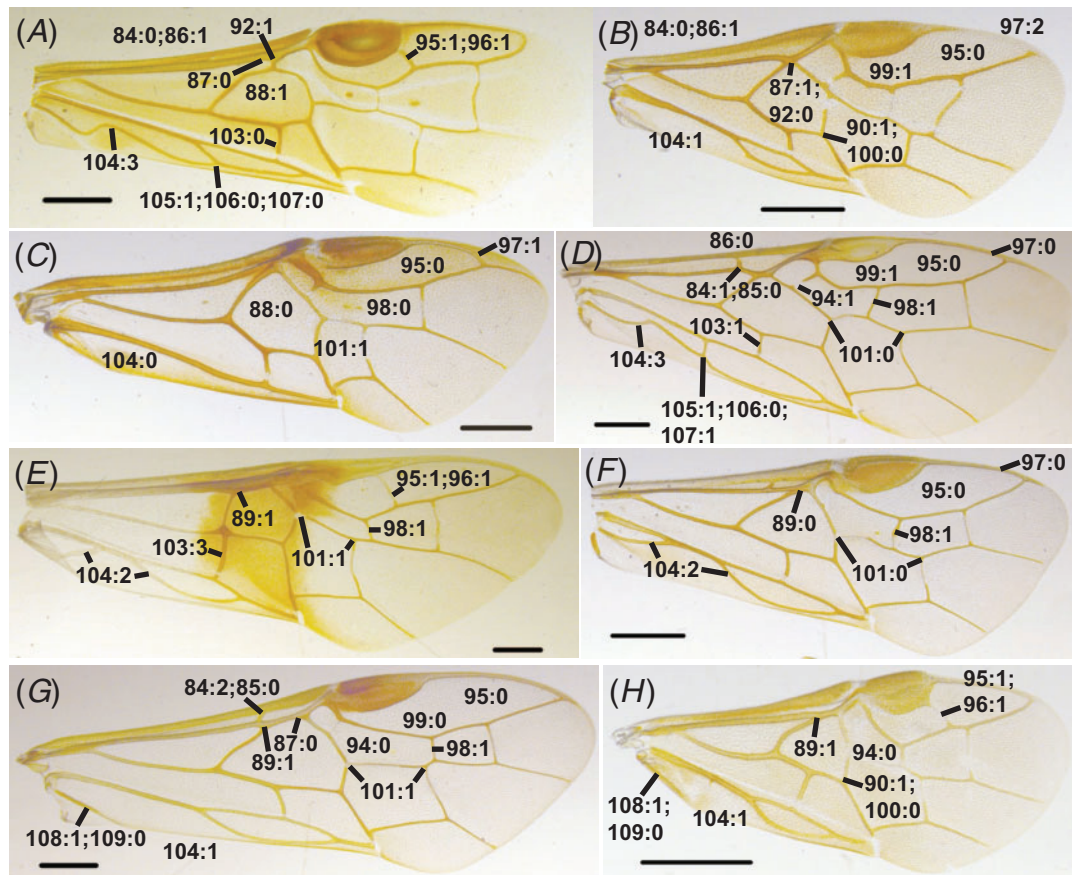


Fig. 11. Forewing of: (A) *Blasticotoma filiceti* Klug, 1834 (Blasticotomidae); (B) *Aproceros leucopoda* Takeuchi, 1939 (Argidae, Sterictiphorinae); (C) *Lophyrotoma analis* (Costa, 1864) (Pergidae, Pteryperginae); (D) *Neodiprion sertifer* (Geoffroy, 1785) (Diprionidae, Diprioninae); (E) *Abia fasciata* (Linné, 1758) (Cimbicidae, Abiinae); (F) *Cladius pectinicornis* (Geoffroy, 1785) (Tenthredinidae, Nematinae); (G) *Nematus caeruleocarpus* Hartig, 1837 (Tenthredinidae, Nematinae); (H) *Profenusia pygmaea* (Klug, 1816) (Tenthredinidae, Heterarthrinae). All scales 1 mm.

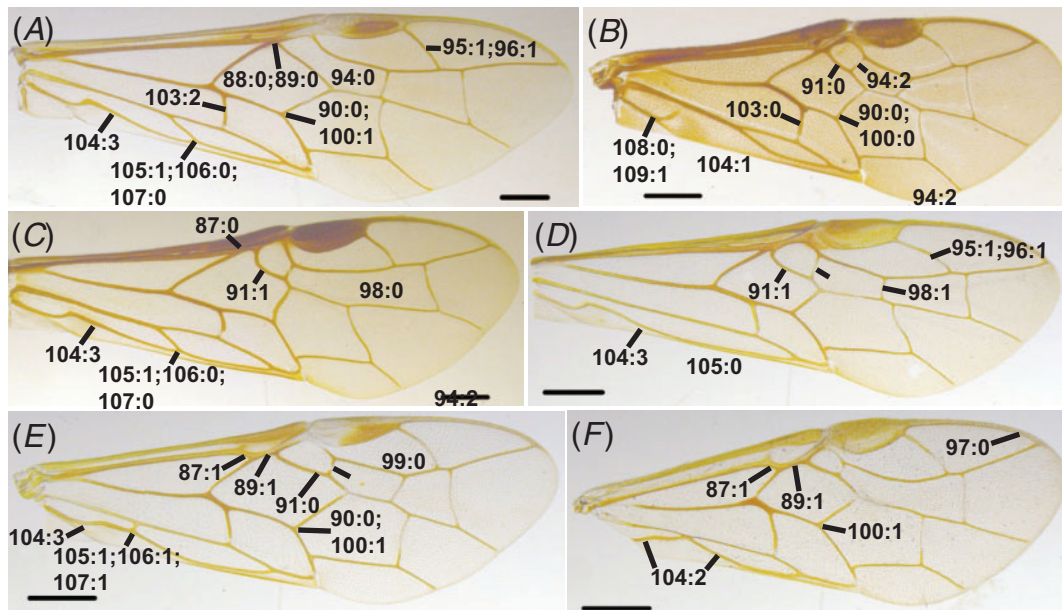


Fig. 12. Forewing of: (A) *Macremphytus testaceus* (Norton, 1861) (Tenthredinidae, Allantinae); (B) *Eutomostethus ephippium* (Panzer, 1798) (Tenthredinidae, Blennocampinae); (C) *Dolerus pratensis* (Linné, 1758) (Tenthredinidae, Selandriinae); (D) *Strongylogaster multifasciata* (Geoffroy, 1785) (Tenthredinidae, Selandriinae); (E) *Leucopelmonus annulicornis* (Harrington, 1893) (Tenthredinidae, Tenthredininae); (F) *Perineura rubi* (Panzer, 1803) (Tenthredinidae, Tenthredininae). All scales 1 mm.

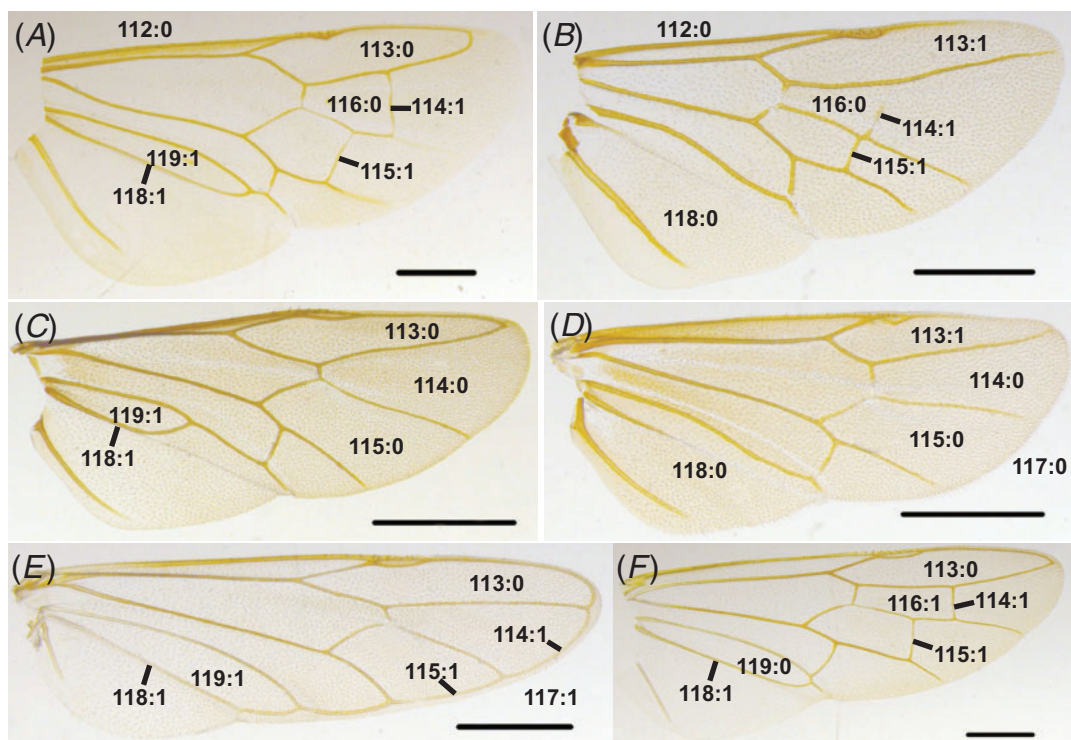


Fig. 13. Hindwing of: (A) *Blasticotoma filiceti* Klug, 1834 (Blasticotomidae); (B) *Aproceros leucopoda* Takeuchi, 1939 (Argidae, Sterictiphorinae); (C) *Eutomostethus ephippium* (Panzer, 1798) (Tenthredinidae, Blennocampinae); (D) *Heterarthrus vagans* (Fallén, 1808) (Tenthredinidae, Heterarthrinae); (E) *Taxonus agrorum* (Fallén, 1808) (Tenthredinidae, Allantinae); (F) *Strongylogaster multifasciata* (Geoffroy, 1785) (Tenthredinidae, Selandriinae). All scales 1 mm.

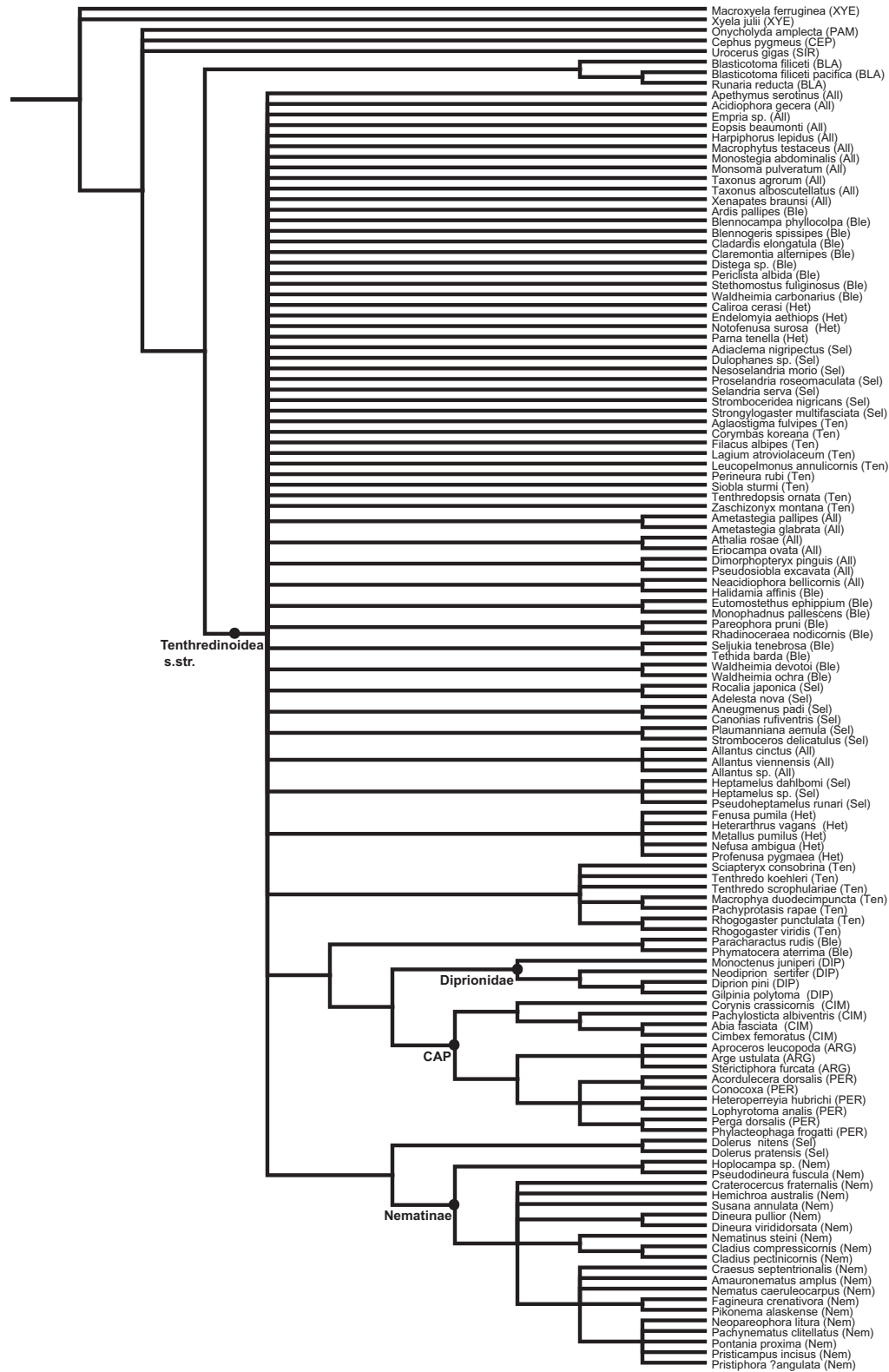


Fig. 14. Strict consensus of 3628 trees of length 1448 steps, obtained by equal weights analysis. Abbreviations: All, Allantinae; ARG, Argidae; BLA, Blasticotomidae; Ble, Blennocampinae; CAP, Cimbicidae-Argidae-Pergidae clade; CEP, Cephidae; CIM, Cimbicidae; DIP, Diprionidae; Het, Heterarthrinae; Nem, Nematinae; PAM, Pamphiliidae; PER, Pergidae; Sel, Selandrinae; SIR, Siricidae; Ten, Tenthredininae; XYE, Xyelidae.

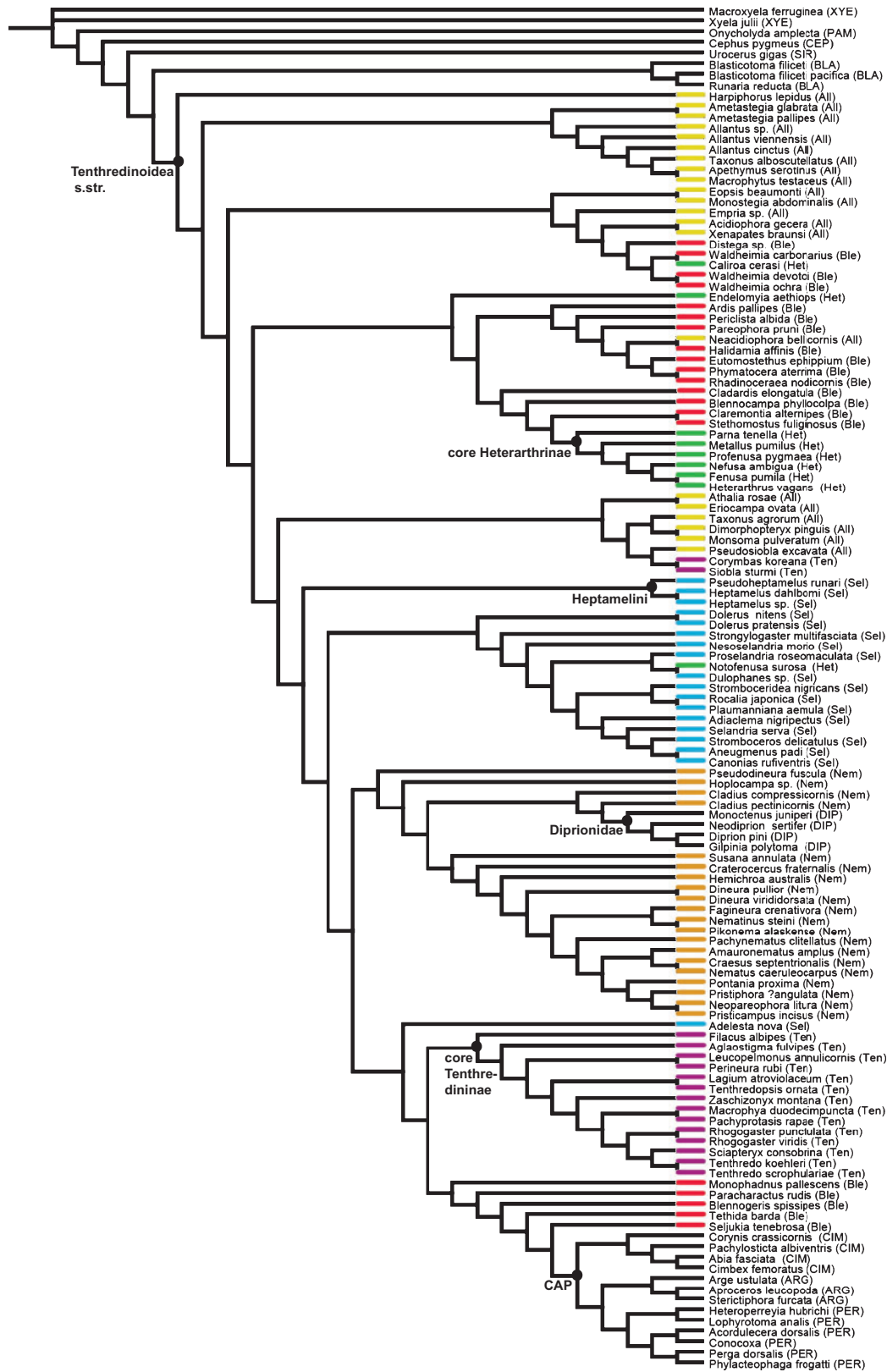


Fig. 15. Most fit tree of fit 57.52315, obtained by implied weights analysis with concavity constant $k = 10$. Abbreviations as in Fig. 14. Subfamilies in Tenthredinidae colour-coded: Allantinae, yellow; Blennocampinae, red; Heterarthrinae, green; Nematinae, orange; Selandrinae, blue; Tenthredininae, violet.

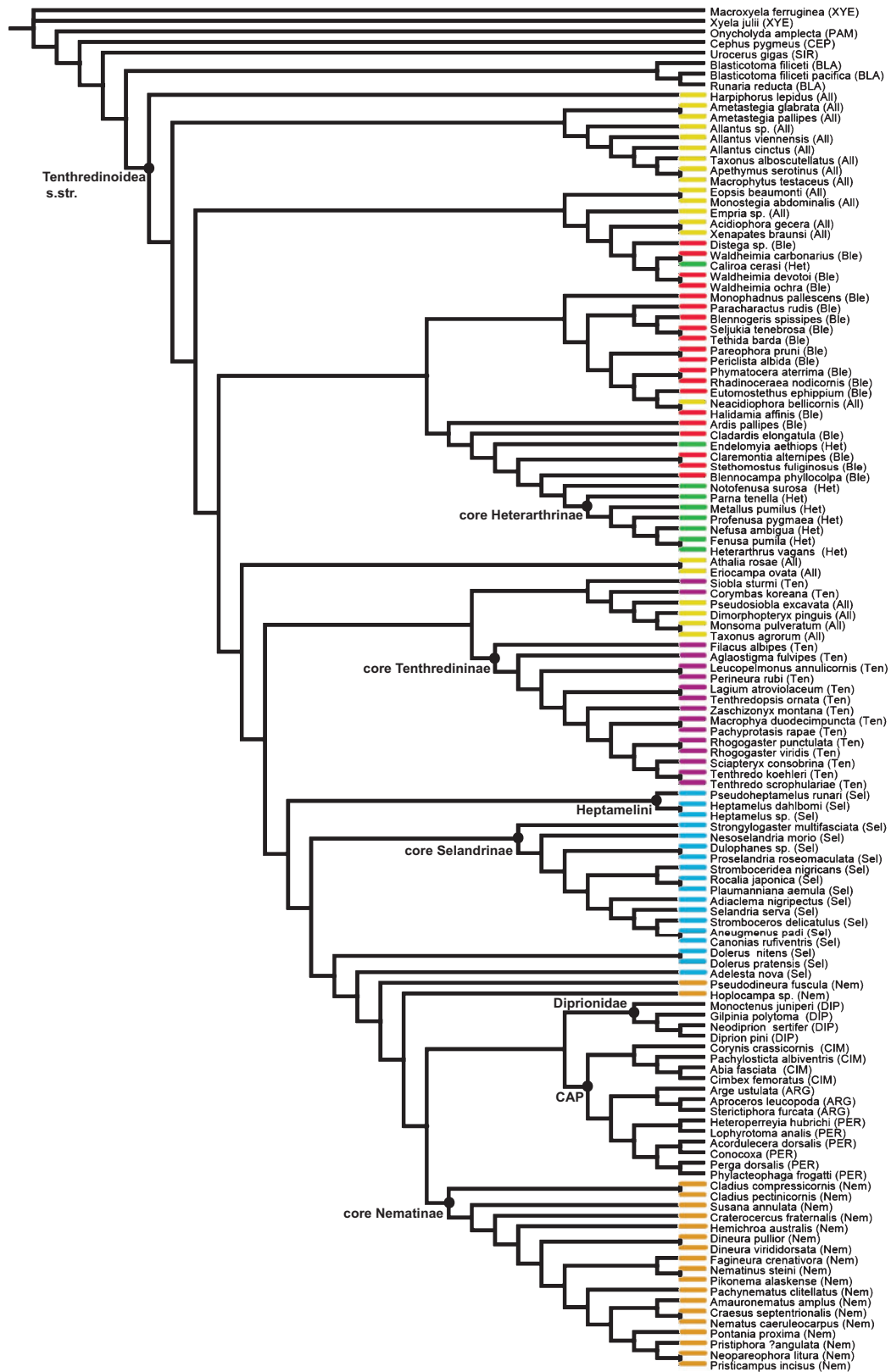


Fig. 16. Most fit tree of fit 38.94650, obtained by implied weights analysis with concavity constant $k = 20$. Abbreviations as in Fig. 14. Subfamilies in Tenthredinidae colour-coded: Allantinae, yellow; Blennocampinae, red; Heterarthrinae, green; Nematinae, orange; Selandrinae, blue; Tenthredininae, violet.

Nefusa, *Parna* and *Profenusa* was supported under IW with $k=8-15$, 20 or 25 (Fig. 15). *Notofenusia* was included in this group with $k=11-15$, 20 or 25 (Fig. 16). The core Heterarthrinae corresponds to the ‘true leafminers’ or Heterarthrinae s. str., which was also recovered by Leppänen *et al.* (2012) and Malm and Nyman (2015). In both these analyses, as in the present, the closest relatives of this clade are blennocampine taxa. The Heterarthrinae s. str. are supported by having the tarsal claws simple (char. 78:0; also in *Caliroa*), and having forewing veins m and 1m-cu converging (char. 90:1; also in *Caliroa* and *Endelomyia*). The remaining Heterarthrinae s. lat. included (*Caliroa*, *Endelomyia*) behave as rogue taxa. None of the two molecular analyses placed them with Heterarthrinae s.str. Indeed, their larvae are not leafminers, but external feeders that skeletonise the leaves of their host plants, leaving only the veins (Leppänen *et al.* 2012).

A clade comprising Nematinae with the Diprionidae nested inside was retrieved under IW with k values 4–12; when $k=1-3$, 20, 25; *Hoplocampa* was removed from the other Nematinae. The Nematinae were monophyletic under IW with $k=12-15$, 30 and under EW, in the latter case having *Dolerus* as their sister group (Fig. 14). The core Nematinae (all except *Hoplocampa* and *Pseudodineura*) are supported by the following characters: forewing Rs to 2r-m distance longer than 2r-m to 3r-m distance (char. 99:0), the presence of extensions on the anterolateral corners of the female eighth abdominal tergum and the elongate cerci (char. 124:1, changing to 124:2 within Nematinae). Interestingly, some of the published analyses with the largest sample of Nematinae (Nyman *et al.* 2006, 2010) have *Hoplocampa* as the sister to all other Nematinae in at least some analyses. Furthermore, there is good correspondence between the molecular and morphological topologies for the subfamily, the ‘lower’ genera included in both samples (*Cladius*, *Craterocercus*, *Dineura*, *Hemichroa* and *Susana*) branching off basally (Figs 15, 16).

The Selandriinae were never monophyletic. *Adelesta* was a rogue taxon always placed outside Selandriinae, often as sister to the majority of Tenthredininae (Fig. 15). Under IW with $k=5-6$ and 13–15, almost all Selandriinae came out together, with Heptamelini (*Heptamelus* + *Pseudoheptamelus*) as sister to the rest. Under IW with $k=1-4$ and 7–12, the Heptamelini fell outside Selandriinae, as did *Dolerus* at $k=20$, 25, 30. The core Selandriinae (excluding *Adelesta*, *Dolerus* and Heptamelini) were supported by having the anterodorsal part of the mesopleuron raised (char. 43:1) and having the forewing cross vein 1a absent (char. 105:0). The inclusion of *Dolerus* as sister to this clade (Fig. 15) was supported by the proximal part of the forewing vein Rs+M being strongly recurved, the main character used to define the Selandriinae (e.g. Benson 1952). Heptamelini was always retrieved, even in the EW analyses (Fig. 14), supported by the presence of 5–8 antennomeres (char. 9:2) and with the anterior fore tibial spur simple (char. 34:0).

Dolerus was retrieved as sister to the core Selandriinae by Malm and Nyman (2015), whereas Boevé *et al.* (2013) and Isaka and Sato (2014) put the genus inside the core Selandriinae; *Dolerus* has previously been placed in its own subfamily, the Dolerinae. Both Boevé *et al.* (2013) and Malm and Nyman (2015) placed Heptamelini outside Selandriinae,

as the sister to all Tenthredinidae except *Athalia*, or sister to the remaining Tenthredinidae + (Cimbicidae + Diprionidae), respectively. Isaka and Sato (2014) did not include any members of this tribe. Malm and Nyman (2015) suggested the Heptamelini should be raised to family status. The morphological evidence supports that at least it should be excluded from Selandriinae.

The Tenthredininae were only monophyletic under IW with $k=14$, 15, with *Corymbas* and *Siobla* basal. *Siobla* was a rogue taxon and fell well outside the subfamily when $k=1-13$, 20, 25 or 30, *Corymbas* was also outside when $k=7-13$, these two taxa being sisters (Fig. 15). *Siobla* was placed as sister to all other Tenthredininae by Malm and Nyman (2015), but outside the subfamily by Boevé *et al.* (2013). However, the remaining Tenthredininae were retrieved in all IW analyses of the morphological data. These core Tenthredininae were supported by having the posterior thoracic spiracle concealed by the posterodorsal part of the mesopleuron (char. 44:1), with forewing vein R bent at cell 1M (87:1; both these characters are also present in *Corymbas* and *Siobla*), and forewing Rs to 2r-m distance longer than 2r-m to 3r-m (char. 99:0).

Conclusions

The results of the analyses of the present dataset were satisfactory in the sense that they corroborate previously well established clades (i.e. Tenthredinoidea, Tenthredinoidea s. str., Argidae + Pergidae, all families except Tenthredinidae, which has rarely been retrieved as monophyletic in recent analyses, e.g. Boevé *et al.* 2013). However, they failed to deliver well supported relationships at the subfamily level within Tenthredinidae, despite the dataset being designed to test the existing classification of the ‘family’. This is in contrast to Malm and Nyman (2015), who produced a more robust phylogeny and recovered several of the tenthredinid subfamilies.

The failure to obtain a robust phylogenetic hypothesis with the morphological dataset assembled here might be partly because not enough characters were included relative to the comparatively high number of terminals scored. The ratio of characters (146) to terminals (129) was only slightly above 1, which is apparently insufficient to obtain well resolved and supported relationships. However, the inability to recover the existing subfamily classification was probably also caused by inherent problems with the delimitation of at least some of the subfamilies, as indicated by the results of Malm and Nyman (2015).

To make further progress with the phylogenetics and classification of the Tenthredinidae, it is necessary to explore additional data sources, e.g. morphology of the male genitalia and larvae, as well as molecular markers in addition to those already employed by Malm and Nyman (2015), and analyse all the data together. It is very likely that apart from redefining boundaries of the existing subfamilies, new taxa at this and even the family level will have to be recognised eventually. Indeed, Malm and Nyman (2015) suggested raising the Heptamelini to family rank, given they were consistently placed as sister to all other Tenthredinidae + (Cimbicidae + Diprionidae). Likewise, Boevé *et al.* (2013) found support for elevating *Athalia* to at least subfamily rank. Future combined analyses will hopefully

provide a solid foundation for tenthredinid classification, as well as allow the exploration of the evolutionary history of the family.

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References

- Basibuyuk, H. H., and Quicke, D. L. J. (1995). Morphology of the antenna cleaner in the Hymenoptera with particular reference to the non-aculeate families (Insecta). *Zoologica Scripta* **24**, 157–177. doi:10.1111/j.1463-6409.1995.tb00397.x
- Basibuyuk, H. H., and Quicke, D. L. J. (1997). Hamuli in the Hymenoptera (Insecta) and their phylogenetic implications. *Journal of Natural History* **31**, 1563–1585. doi:10.1080/00222939700770831
- Benson, R. B. (1952). Hymenoptera: 2. Symphyta. Section (b). *Handbooks for the Identification of British Insects* **VI(2b)**, 51–138.
- Benson, R. B. (1958). Hymenoptera: 2. Symphyta. Section (c). *Handbooks for the Identification of British Insects* **VI(2c)**, 139–252 + vi pp.
- Beutel, R. G., and Vilhelmsen, L. (2007). Head anatomy of Xyelidae (Hexapoda: Hymenoptera) and phylogenetic implications. *Organisms, Diversity & Evolution* **7**, 207–230. doi:10.1016/j.ode.2006.06.003
- Blank, S. M., Groll, E. K., Liston, A. D., Prous, M., and Taeger, A. (2012). ‘ECatSym – Electronic World Catalog of Symphyta (Insecta, Hymenoptera).’ Program version 4.0 beta, data version 39 (18.12.2012). Digital Entomological Information, Müncheberg.
- Boevé, J.-L., Blank, S. M., Meijer, G., and Nyman, T. (2013). Invertebrate and avian predators as drivers of chemical defensive strategies in tenthredinid sawflies. *BMC Evolutionary Biology* **13**(198), 1–14.
- Gauld, I. D., and Bolton, B. (1996). ‘The Hymenoptera.’ Second impression. (Oxford University Press: Oxford, UK.)
- Goloboff, P. A., Farris, J. S., and Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786. doi:10.1111/j.1096-0031.2008.00217.x
- Goulet, H. (1992). The genera and subgenera of the sawflies of Canada and Alaska: Hymenoptera. Symphyta. The insects and arachnids of Canada. Part 20. *Agriculture Canada Publication* 1876.
- Heraty, J. M., Wooley, J. B., and Darling, D. C. (1994). Phylogenetic implications of the mesofurca and mesopostnotum in the Hymenoptera. *Journal of Hymenoptera Research* **3**, 241–277.
- Heraty, J., Ronquist, F., Carpenter, J. M., Hawks, D., Schulmeister, S., Dowling, A. P. G., Murray, D., Munro, J., Wheeler, W. C., Schiff, N., and Sharkey, M. J. (2011). Evolution of the hymenopteran megaradiation. *Molecular Phylogenetics and Evolution* **60**, 73–88. doi:10.1016/j.ympev.2011.04.003
- Isaka, Y., and Sato, T. (2014). Molecular phylogenetic and divergence time estimation analyses of the sawfly subfamily Selandriinae (Hymenoptera: Tenthredinidae). *Entomological Science* **17**, 435–439. doi:10.1111/ens.12080
- Jervis, M., and Vilhelmsen, L. (2000). Mouthpart evolution in adults of the basal, ‘symphytan’, hymenopteran lineages. *Biological Journal of the Linnean Society. Linnean Society of London* **70**, 121–146.
- Klopfstein, S., Vilhelmsen, L., Heraty, J. M., Sharkey, M. J., and Ronquist, F. (2013). The hymenopteran tree of life: evidence from protein-coding genes and objectively aligned ribosomal data. *PLoS ONE* **8**, e69344. doi:10.1371/journal.pone.0069344
- Leppänen, S. A., Altenhofer, E., Liston, A. D., and Nyman, T. (2012). Phylogenetics and evolution of host-plant use in leaf-mining sawflies (Hymenoptera: Tenthredinidae: Heterathrinae). *Molecular Phylogenetics and Evolution* **64**, 331–341. doi:10.1016/j.ympev.2012.04.005
- Leppänen, S. A., Altenhofer, E., Liston, A. D., and Nyman, T. (2013). Ecological versus phylogenetic determinants of trophic associations in a plant-leafminer-parasitoid food web. *Evolution* **67**(1493), 1502.
- Maddison, W., and Maddison, D. (2011). Mesquite 2.75. Available: <http://mesquiteproject.org/mesquite/mesquite.html> [accessed September 2011]
- Malm, T., and Nyman, T. (2015). Phylogeny of the symphytan grade of Hymenoptera: new pieces into the old jigsaw(fly) puzzle. *Cladistics* **31**(1), 117. doi:10.1111/cla.12069
- Maxwell, D. E. (1955). The comparative internal larval anatomy of sawflies (Hymenoptera: Symphyta). *Canadian Entomologist* **87**, 1–132.
- Nyman, T., Roininen, H., and Vuorinen, J. A. (1998). Evolution of different gall types in willow-feeding sawflies (Hymenoptera: Tenthredinidae). *Evolution* **52**, 465–474. doi:10.2307/2411082
- Nyman, T., Widmer, A., and Roininen, H. (2000). Evolution of gall morphology and host-plant associations in willow-feeding sawflies (Hymenoptera: Tenthredinidae). *Evolution* **54**, 526–533. doi:10.1111/j.0014-3820.2000.tb00055.x
- Nyman, T., Zinovjev, A. G., Vikberg, V., and Farrell, B. D. (2006). Molecular phylogeny of the sawfly subfamily Nematinae (Hymenoptera: Tenthredinidae). *Systematic Entomology* **31**, 569–583. doi:10.1111/j.1365-3113.2006.00336.x
- Nyman, T., Vikberg, V., Smith, D. R., and Boeve, J.-L. (2010). How common is ecological speciation in plant-feeding insects? A “higher” Nematinae perspective. *BMC Evolutionary Biology* **10**, 266. doi:10.1186/1471-2148-10-266
- Prous, M., Blank, S. M., Goulet, H., Heibo, E., Liston, A., Malm, T., Nyman, T., Schmidt, S., Smith, D. R., Vårdal, H., Viitassaari, M., Vikberg, V., and Taeger, A. (2014). The genera of Nematinae (Hymenoptera, Tenthredinidae). *Journal of Hymenoptera Research* **40**, 1–69. doi:10.3897/JHR.40.7442
- Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D. L., and Rasnitsyn, A. P. (2012). A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology* **61**, 973–999. doi:10.1093/sysbio/sys058
- Schmidt, S., and Walter, G. H. (2014). Young clades in an old family: major evolutionary transitions and diversification of the eucalypt-feeding pergid sawflies in Australia (Insecta, Hymenoptera, Pergidae). *Molecular Phylogenetics and Evolution* **74**, 111–121. doi:10.1016/j.ympev.2014.02.002
- Schulmeister, S. (2001). Functional morphology of the male genitalia and copulation in lower Hymenoptera, with special emphasis on the Tenthredinoidea s. str. (Insecta, Hymenoptera, ‘Symphyta’). *Acta Zoologica* **82**, 331–349. doi:10.1046/j.1463-6395.2001.00094.x
- Schulmeister, S. (2003a). Simultaneous analysis of basal Hymenoptera (Insecta): introducing robust-choice sensitivity analysis. *Biological Journal of the Linnean Society. Linnean Society of London* **79**, 245–275. doi:10.1046/j.1095-8312.2003.00233.x
- Schulmeister, S. (2003b). Genitalia and terminal abdominal segments of male basal Hymenoptera (Insecta): morphology and evolution. *Organisms, Diversity & Evolution* **3**, 253–279. doi:10.1078/1439-6092-00078
- Schulmeister, S. (2003c). Review of morphological evidence on the phylogeny of basal Hymenoptera (Insecta), with a discussion of the ordering of characters. *Biological Journal of the Linnean Society. Linnean Society of London* **79**, 209–243. doi:10.1046/j.1095-8312.2003.00232.x
- Schulmeister, S., Wheeler, W. C., and Carpenter, J. M. (2002). Simultaneous analysis of the basal lineages of Hymenoptera (Insecta) using sensitivity analysis. *Cladistics* **18**, 455–484. doi:10.1111/j.1096-0031.2002.tb00287.x
- Sharkey, M. J., Carpenter, J. M., Vilhelmsen, L., Heraty, J., Liljebblad, J., Dowling, A. P. G., Schulmeister, S., Murray, D., Deans, A. R., Ronquist,

- F., Krogmann, L., and Wheeler, W. C. (2012). Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* **28**, 80–112. doi:10.1111/j.1096-0031.2011.00366.x
- Taeger, A., Blank, S. M., and Liston, A. D. (2010). World catalog of Symphyta (Hymenoptera). *Zootaxa* **2580**, 1–1064.
- Vilhelmsen, L. (1996). The preoral cavity of lower Hymenoptera (Insecta): comparative morphology and phylogenetic significance. *Zoologica Scripta* **25**, 143–170. doi:10.1111/j.1463-6409.1996.tb00156.x
- Vilhelmsen, L. (1997). The phylogeny of lower Hymenoptera (Insecta), with a summary of the early evolutionary history of the order. *Journal of Zoological Systematics and Evolutionary Research* **35**, 49–70. doi:10.1111/j.1439-0469.1997.tb00404.x
- Vilhelmsen, L. (1999). The occipital region in the basal Hymenoptera (Insecta): a reappraisal. *Zoologica Scripta* **28**, 75–85. doi:10.1046/j.1463-6409.1999.00008.x
- Vilhelmsen, L. (2000a). Before the wasp-waist: comparative anatomy and phylogenetic implications of the skeletomusculature of the thoraco–abdominal boundary region in basal Hymenoptera (Insecta). *Zoomorphology* **119**, 185–221. doi:10.1007/PL00008493
- Vilhelmsen, L. (2000b). Cervical and prothoracic skeletomusculature in the basal Hymenoptera (Insecta): comparative anatomy and phylogenetic implications. *Zoologischer Anzeiger* **239**, 105–138.
- Vilhelmsen, L. (2000c). The ovipositor apparatus of basal Hymenoptera (Insecta): phylogenetic implications and functional morphology. *Zoologica Scripta* **29**, 319–345. doi:10.1046/j.1463-6409.2000.00046.x
- Vilhelmsen, L. (2001). Phylogeny and classification of the extant basal lineages of the Hymenoptera (Insecta). *Zoological Journal of the Linnean Society* **131**, 393–442. doi:10.1111/j.1096-3642.2001.tb01320.x
- Vilhelmsen, L. (2011). Head capsule characters in the Hymenoptera and their phylogenetic implications. *ZooKeys* **130**, 343–361. doi:10.3897/zookeys.130.1438
- Vilhelmsen, L., and Turrisi, G. F. (2011). Per arborem ad astra: morphological adaptations to exploiting the woody habitat in the early evolution of Hymenoptera. *Arthropod Structure & Development* **40**, 2–20. doi:10.1016/j.asd.2010.10.001
- Vilhelmsen, L., Miko, I., and Krogmann, L. (2010). Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). *Zoological Journal of the Linnean Society* **159**, 22–194. doi:10.1111/j.1096-3642.2009.00576.x
- Weltz, C.-E., and Vilhelmsen, L. (2014). The saws of sawflies: exploring the morphology of the ovipositor in Tenthredinoidea (Insecta: Hymenoptera), with emphasis on Nematinae. *Journal of Natural History* **48**, 133–183. doi:10.1080/00222933.2013.791941
- Yuasa, H. (1922). A classification of the larvae of the Tenthredinoidea. *Illinois Biological Monographs* **7**, 1–172.
- Zhelokhovtsev, A. N., Tobias, V. I., and Kozlov, M. A. (1994). Volume III: Hymenoptera. Part 6: Symphyta. In 'Keys to the Insects of the European Part of the USSR'. (Ed. G. S. Medvedev.) i–xviii + 432 pp. (Brill: Leiden, The Netherlands.)