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### The parasitic wasp genera *Skiapus*, *Hellwigia*, *Nonnus*, *Chriodes*, and *Klutiana* (Hymenoptera, Ichneumonidae): Recognition of the *Nesomesochorinae* stat. rev. and *Nonninae* stat. nov. and transfer of *Skiapus* and *Hellwigia* to the *Ophioninae*

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# The parasitic wasp genera *Skiapus*, *Hellwigia*, *Nonnus*, *Chriodes*, and *Klutiana* (Hymenoptera, Ichneumonidae): Recognition of the Nesomesochorinae stat. rev. and Nonninae stat. nov. and transfer of *Skiapus* and *Hellwigia* to the Ophioninae

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## Abstract

The ichneumonid wasp genera *Skiapus* Morley, *Hellwigia* Gravenhorst, *Nonnus* Cresson, *Chriodes* Förster, and *Klutiana* Betrem are each formally removed from the Campopleginae on the basis of morphological, molecular, and simultaneous analyses using PAUP\* and the optimization alignment program POY. *Skiapus* and *Hellwigia* are shown to form a monophyletic group with the Ophioninae to which they are transferred. *Nonnus* is treated as comprising the Nonninae stat. nov. and *Chriodes* and *Klutiana* (sometimes treated as a junior synonym of *Chriodes*) are treated as comprising the Nesomesochorinae stat. rev. The status of Nesomesochorinae and Nonninae is not fully resolved as they are not consistently recovered as separate groups, forming a single clade in some analyses. We keep them separate because of this uncertainty. Molecular synapomorphies within the D2–3 expansion region of the 28S rDNA gene show the utility of this gene region in determining subfamily-level placement within the higher Ophioniformes.

**Keywords:** *Campopleginae*, *Nonnini*, *parasitoid*, *phylogeny*, *taxonomy*

## Introduction

Much effort has recently been put into obtaining a wide range of ichneumonoids for DNA sequencing projects aimed at answering a range of evolutionary questions (Belshaw et al. 1998, 2001; Broad and Quicke 2000; Belshaw and Quicke 2002; Dowton et al. 2002). As a result, representatives of many genera whose systematic placement has hitherto been

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uncertain have been obtained, and in several cases it is now possible to offer a more definite conclusion about their relationships. Here we use morphological, molecular, and simultaneous analyses to explore the relationships of five genera currently included in the Campopleginae but which do not fit well there and might therefore belong to other groups.

The Campopleginae *sensu lato* is a very large, cosmopolitan ichneumonid subfamily and comprises approximately 70 valid genera and 1836 species (Yu and Horstmann 1997; Wahl 1999). Campoplegines are koinobiont endoparasitoids, nearly all attacking Lepidoptera larvae, though a few taxa use larvae of other groups as hosts, including tenthredinoid symphytans (Hymenoptera), Raphidioptera, Trichoptera and chrysomelid, curculionid and cerambycid beetles (Coleoptera). Although the Campopleginae is an important group of parasitoids from both economic and biological standpoints, there have been very few studies of relationships within the subfamily (Wahl 1991; Dbar 1993; Miah and Bhuyia 2001) and it has been considered to be one of the most taxonomically difficult groups in the Ichneumonidae (Townes 1970; Gauld and Mound 1982; Gauld 1984).

Although the overall limits of the Campopleginae have been relatively stable since Townes' (1970) generic treatment, as with so many ichneumonoid subfamilies, morphological synapomorphies defining it are hardly apparent. Within the Campopleginae there are considerable disagreements about its classification at all levels (Townes 1970; Carlson 1979; Gauld 1984; Wahl 1991). Two aberrant tribes, the Hellwigiini and Nesomesochorini recognized by Townes et al. (1961, 1965) are morphologically distinct from the rest of the Campopleginae and do not appear to fit well there. The hellwigiines have long been considered as a distinct group and Horstmann (1969) went as far as to raise them to subfamily status, the Hellwigiinae, comprising the two genera *Hellwigia* Gravenhorst and *Protohellwigia* Brues. Townes (1970), at almost the same time, continued to treat the Hellwigiini within the Campopleginae (=Porizontinae *sensu* Townes) as a tribe including the genera *Hellwigia* (with which he synonymized *Protohellwigia* Brues) and *Skiapus* Morley.

Wahl (1991) considered the phylogenetic placement of *Rhimphoctona* Förster, a genus with a relatively long ovipositor that attacks wood-boring beetle larvae, with reference to the higher categories within the subfamily. The study included both larval and adult characters and he concluded that the existing tribes were unsound and instead recognized five, less formal, genus groups, although he stated that all were monophyletic. Three of these were monotypic (the *Nemeritis* Holmgren, *Gonotypus* Förster, and *Menaka* Gupta groups), the *Bathyplectes* group included a small number of genera (*Bathyplectes* Förster, *Rhimphoctona*, *Pyracmon* Holmgren, *Nepiesta* Förster, and *Leptoperilissus* Schmiedeknecht), while the *Dusona* Cameron group embraced all the remaining genera (including those previously in the tribes Hellwigiini and Nesomesochorini). *Rhimphoctona* represented a basal group which formed the sister clade to the rest of the subfamily. However, in Miah's (1998) preliminary morphological analyses of campoplegine genera, five genera, included in the *Dusona* group by Wahl (1991, 1999), namely *Skiapus*, *Hellwigia*, *Nonnus*, *Chriodes*, and *Klutiana*, were never recovered with the other members of the subfamily. The first two were associated consistently with the Ophioninae and the latter usually with the Anomaloninae. Molecular analyses have further suggested that neither the Nesomesochorini nor *Hellwigia* are actually campoplegines. In the preliminary molecular and simultaneous molecular and morphological analyses of Quicke et al. (2000), *Nonnus* was found not to cluster with the three other Campopleginae included, though its placement elsewhere was not stable. More recently, the molecular phylogeny presented by Belshaw and Quicke (2002) placed

*Hellwigia* within the Ophioninae and *Nonnus* and *Chriodes* as the sister group of the Anomaloninae, largely in agreement with Miah's morphological trees.

Here we present additional 28S rDNA sequence data, including all the genera of Hellwigiini and Nesomesochorini together with a far denser sampling of campoplegine and related genera. These data are analysed separately and in combination with a morphological data set, based on the individual exemplar genera, using direct optimization to deal with the length variation in the gene fragment used. The results lead us to transfer *Hellwigia* and *Skiapus* to the Ophioninae and to recognize the Nesomesochorinae and Nonninae as subfamilies.

## Materials and methods

### *Selection of taxa*

The Campopleginae belongs to the "Ophioniformes" group of subfamilies as proposed by Wahl (1991). This group currently comprises the Ophioninae, Ctenopelmatinae, Banchinae, Mesochorinae, Metopiinae, Campopleginae, Tatogastrinae, Cremastinae, Tersilochinae, and Anomaloninae, though molecular and morphological data additionally indicate that the Lycorininae, Neorhacodinae, Oxytorinae, Phrudinae, Stilbopinae, and Tryphoninae also belong in the same large clade (Belshaw and Quicke 2002; D. L. J. Quicke et al., in preparation). Within this complex Gauld (1985) and Wahl (1991) suggested Ophioninae and Cremastinae, respectively, as the sister group of Campopleginae. The first hypothesis was supported by the most parsimonious tree (MPT) resulting from analyses of 28S rDNA by Belshaw et al. (1998) without any bootstrap support, and subsequently with high support by Belshaw and Quicke (2002). In the present analyses we therefore selected a number of genera of Ophioninae along with a smaller selection from each of the Anomaloninae, Banchinae, Cremastinae, Ctenopelmatinae, and Tersilochinae, in order to allow us to test the monophyly of Campopleginae *sensu lato*. The Orthopelmatiformes (comprising the genus *Orthopelma* Taschenberg) was selected as the outgroup because in previous molecular and simultaneous analyses it nearly always formed the sister group to the enlarged Ophioniformes group (Quicke et al. 2000).

The genera of Campopleginae included in our analyses covered a wide range of the subfamily based on the cladistic analyses of Miah (1998). Our selection was also influenced by the five genus groups recognized by Wahl (1991), but we were unable to obtain material for sequencing of the *Nemeritis* and *Menaka* groups (both monotypic). The taxa sequenced are listed in Table I together with the EMBL/GenBank accession numbers of the sequences obtained. Morphological characters were scored as far as possible for the same taxa as sequenced, but we also examined a range of other species and scored characters as polymorphic where intrageneric variation was encountered. When larval and internal characters had not been scored for the same species, the data presented are from congeners; no assumptions were made beyond that. We coded taxa for 67 morphological characters (Table II); the matrix is included as the Appendix.

### *Molecular protocols*

DNA was extracted from single mid-legs preserved in absolute ethanol using the ethanol precipitation method with final elution into 30 µl of water. Polymerase chain reactions

Table I. Taxa included in study, their provenance and EMBL/GenBank accessions numbers (arrangement of taxa in accordance with classification resulting from this study).

Taxon	Provenance	EMBL accession number
<b>Campopleginae</b>		
<i>Bathyplectes</i> sp. ( <i>curculionis</i> species group)	Germany: Bayer Wald	AY593068
<i>Campoplex deficiens</i> Gravenhorst	UK: Hilbre Island	AY593078
<i>Casinaria petiolaris</i> (Gravenhorst)	Hungary	AY593069
<i>Charops</i> sp.	Malaysia (Sabah)	AJ302844
<i>Cryptophion manuei</i> Gauld and Janzen	Costa Rica	AY593070
<i>Cymodusopsis</i> sp.	Belize: Las Cuevas	AY593071
<i>Diadegma mollipla</i> (Holmgren)	South Africa	AJ302851
<i>Dusona</i> sp.	UK: Sheffield	Z97891
<i>Echthronomas facialis</i> (Thomson)	France	AY593072
<i>Eriborus ?terebrans</i> (Gravenhorst)	W. Malaysia: Cameron Highlands	AY593073
<i>Gonotypus melanostoma</i> (Thomson)	UK: Silwood	AY593074
<i>Hyposoter didymator</i> (Thunberg)	Ex laboratory culture	AY593075
<i>Lathrostizus ?lugens</i> (Gravenhorst)	UK: Silwood	Z97892
<i>Leptocampoplex cremastoides</i> (Holmgren)	Germany: Bayer Wald	AY593076
<i>Melalophacharops</i> sp.	W. Malaysia: Cameron Highlands	AY593077
<i>Olesicampe</i> sp.	Germany: Bayer Wald	AY593079
? <i>Phobocampe</i> sp.	Germany: Bayer Wald	AY593080
<i>Rhimphoctona ?grandis</i> (Fonscolombe)	Turkey	AJ302872
<i>Scirtetes robustus</i> (Woldstedt)	UK: Lancashire	AY593081
<i>Tranosema rostrale</i> (Brischke)	Ex laboratory culture	AY593082
<i>Venturia ocybeta</i> (Gauld)	Australia	AY593083
<i>Xanthocampoplex</i> sp.	Australia	AJ302917
<b>Nesomesochorinae</b>		
<i>Chriodes</i> sp.	?Tanzania	AJ302845
<i>Klutiana</i> sp.	Japan	AY593066
<b>Nonninae</b>		
<i>Nonnus</i> sp.	Costa Rica	Z97893
<b>Ophioninae</b>		
<i>Afrophion hymnis</i> (Gauld and Mitchell)	S. Africa: Cape Prov.	AY593084
<i>Alophophion</i> sp.	Falkland Islands	AY593085
<i>Baryatocephalus mocsaryi</i> (Brauns)	Turkey: Sivas	AY593086
<i>Dicamptus seyrigi</i> Delobel	Madagascar	AY593087
<i>Enicospilus ramidulus</i> (Linnaeus)	UK: Silwood	Z97887
<i>Eremotylus marginatus</i> (Jurine)	France: Dordogne	Z97886
<i>Euryophion latipennis</i> (Kirby)	Togo	AJ302854
<i>Hellwigia obscura</i> Gravenhorst	France: Dordogne	AJ302858
<i>Laticoleus infumatus</i> Gauld and Mitchell	Uganda: Kibale	AY593088
<i>Leptophion anici</i> Gauld	Australia	AY593089
<i>Rhynchophion flammipennis</i> (Ashmead)	Costa Rica	AY593090
<i>Skiapus</i> sp.	Tanzania: Amani	AY593067
<i>Thyreodon laticinctus</i> Cresson	Belize: Las Cuevas	AJ302876
<b>Anomaloninae</b>		
<i>Anomalon</i> sp.	Turkey	AJ302838
<i>Barylypa</i> sp.	Papua New Guinea	AY593091
<i>Gravenhorstia (Erigorgus)</i> sp.	Turkey	AY593092
<i>Habronyx</i> sp.	Turkey	AY593093
<i>Trichomma</i> sp.	Malaysia (Sabah)	AJ302878
<b>Cremastinae</b>		
<i>Cremastus spectator</i> Gravenhorst	UK: Gwent	AY593094
<i>Temelucha</i> sp.	Turkey	AY593095

Table I. (Continued.)

Taxon	Provenance	EMBL accession number
<b>Ctenopelmatinae</b>		
<i>Anoncus</i> sp.	UK: Silwood	AY593096
<i>Euryproctus numidicus</i> Schmiedeknecht	Germany: Bayer Wald	AY222798
<i>Glyptorhaestus</i> sp.	Germany: Bayer Wald	AY593097
<i>Perilissus albitarsis</i> Thomson	UK: Silwood	Z97903
<i>Sympherta</i> sp.	Russia: Kaliningrad	AY593098
<b>Tersilochinae</b>		
<i>Allophrys</i> sp.	Belize: Las Cuevas	AY593099
<i>Stethantyx</i> sp.	Belize: Las Cuevas	AJ302874
<i>Tersilochus heterocerus</i> (Thomson)	UK: Harpenden	AY593100
<b>Banchinae</b>		
<i>Banchus volutatorius</i> (Linnaeus)	UK: Hilbre Island	AJ302842
<i>Glypta altamirai</i> Godoy and Gauld	Costa Rica	AY593101
<i>Meniscomorpha zacasta</i> Ugalde and Gauld	Costa Rica	AY593102
<i>Syzeuctus</i> sp.	Belize: Las Cuevas	AY593103
<b>Orthopelmatinae</b>		
<i>Orthopelma</i> sp.	Turkey	AY222799

(PCRs) were carried out in a GeneAmp9600 thermal cycler in 20 µl reactions containing 1.0 µl of DNA extract, 10 pmol of primers (forward: 5' GCG AAC AAG TAC CGT GAG GG 3'; reverse: 5' TAG TTC ACC ATC TTT CGG GTC 3'), 10 nmol of dNTPs (Amersham Pharmacia Biotech: APB), 1.0U of *Taq* polymerase (Bioline), 2 µl of 10 × reaction buffer (2.0 mM MgCl<sub>2</sub>). PCR conditions were 94°C for 30 s, 50°C for 30 s, and 72°C for 60 s (35 cycles with an initial denaturation for 2 min and a final extension for 7 min). PCR products were purified using GFX gel band purification kit (APB) and sequenced directly using *BigDye* terminators.

#### Data analysis

The morphological and molecular data sets were analysed both separately and simultaneously. Morphological data were analysed with maximum parsimony using PAUP\* (Swofford 1998) treating multistate characters as both unordered and with selected characters set as ordered (see below). Initially we searched a large area of tree space by using 10,000 random additions holding only a single tree in memory for branch swapping (TBR) each addition. The shortest trees found were then used as starting trees for further branch-swapping with maxtrees set at 50,000. Successive approximations weighting was carried out on most parsimonious trees using the maximum value of the retention index as the reweighting function (Gauthier et al. 2000).

Analyses involving molecular data were carried out using direct optimization (Wheeler 1996; Gladstein and Wheeler 2001) implemented using the program POY (version 3.0.11a, 20 May 2003) on a supercomputer at the University of Helsinki. The 28S D2–D3 sequences were initially arranged by eye to recognize regions for which homology could be assigned with high confidence. Nineteen putatively homologous regions were then

Table II. Morphological characters and character states used in this study (terminology for body features and wing venation broadly follows Goulet and Huber 1993 and Gauld and Bolton 1996; the naming of propodeal carinae and areas follows Townes 1969).

Character number	Morphological character and states
1	Clypeal bristles: (0) not in a regular transverse row at ventral margin; (1) in the form of a very regular comb of strong bristles.
2	Clypeus: (0) not extended beyond tentorial pits; (1) extended beyond tentorial pits (Sanborne 1986; Wahl 1991).
3	Clypeus and face: (0) separated by a groove or depression; (1) not separated by a groove (Gauld 1985; Wahl 1991).
4	Number of flagellomeres: (0) 40 or fewer; (1) more than 40.
5	Median flagellar segments: (0) longer than wide or quadrate; (1) at least 1.05 times wider than long.
6	Antenna length: (0) less than fore wing; (1) equal to or greater than fore wing.
7	Ocelli: (0) small, separated from eye by more than 0.5 times their diameter; (1) enlarged, nearly touching eyes.
8	Emargination of eyes adjacent to antennal sockets: (0) weak or absent; (1) moderate; (2) strong (Townes 1970; Miah 1998). [ordered]
9	Inner margin of eyes: (0) parallel; (1) weakly converging ventrally; (2) moderately to strongly converging ventrally. (Townes 1970; Kusigemati 1983; Sanborne 1986). [ordered]
10	Anterior tentorial pits: (0) closer to eye than to mandible; (1) closer to mandible than to eye.
11	Colour of setae on face and mesosoma: (0) silvery; (1) pale brown to black.
12	Maxillary palp: (0) five-segmented; (1) with four or fewer segments.
13	Labial palp: (0) four-segmented; (1) with three or fewer segments.
14	Mandible shape: (0) weakly tapered, apex (measured before separation of distal teeth) more than 0.5 times as broad as base; (1) 0.4–0.5 times as broad as base; (2) less than 0.3 times as broad as base. [ordered]
15	Labrum: (0) projecting, strongly sclerotized; (1) not projecting and not usually strongly sclerotized.
16	Epomia: (0) present; (1) absent (Wahl 1991).
17	Propleuron: (0) without lateroventral posteriorly projecting flange; (1) with lateroventral posteriorly projecting flange (Wahl 1991).
18	Notauli: (0) present; (1) absent.
19	Sternaulus: (0) present and sharp at least up to mid-length of mesopleuron; (1) absent.
20	Mesopleural fovea: (0) absent or very weak; (1) present and well-developed.
21	Mesopleuron: (0) without diagonal groove or depression extending from upper anterior corner; (1) with such a groove or depression.
22	Metepisternal pit: (0) absent; (1) present.
23	Posterior transverse carina of mesosternum: (0) incomplete; (1) complete (Wahl 1991).
24	Submetapleural carina: (0) incomplete, not extended to form a flange anteriorly; (1) complete, forming a narrow flange; (2) expanded into a broad flange anteriorly. [ordered]
25	Propodeum surface: (0) not irregularly coarsely rugose-areolate; (1) irregularly coarsely rugose-areolate.
26	Median section of anterior transverse propodeal carina (M in Townes 1969, Figure E): (0) present; (1) absent.
27	Median section of posterior transverse propodeal carina (N in Townes 1969, Figure E): (0) present; (1) absent.
28	Propodeal spiracles: (0) round to short elliptical; (1) elongate, at least three times longer than wide.
29	Fore wing: (0) without an adventitious vein; (1) with well-defined, adventitious vein running parallel to and removed from the hind margin of cell 3-Cu. This has been recognized previously as an autapomorphy of the Ophioninae. A similar vein occurs in a number of scattered cases in other subfamilies (Groteini, <i>Grotea anguina</i> Cresson; Poemeniinae, <i>Ganodes balteatus</i> Townes, <i>Rodrigama gamezi</i> Gauld; Gravenhorstiini, <i>Gravenhorstia</i> Boie spp.), but it is never so long or well defined, usually tends towards the hind margin of the wing and is often obfuscated in a brown cloud. Wahl (1990) considers that an adventitious vein, similar to the ophionine condition, occurs in Tatogastrinae, but our observations of <i>Tatogaster</i> Townes reveals only a poorly defined infuscation in this area, similar to the condition in many ichneumonids.



Table II. (Continued.)

Character number	Morphological character and states
30	Pterostigma of fore wing: (0) wide, less than 2.5 times longer than broad; (1) slender, more than 2.5 times longer than broad.
31	Fore wing vein Rs <sub>2r</sub> meeting pterostigma: (0) at about 30° and rather straight; (1) at 30–45°; (2) at an angle greater than 45°. [ordered]
32	Marginal cell of fore wing: (0) short; (1) long; (2) very long (Gauld 1984, 1985). [ordered]
33	Vein cu-a of fore wing in respect of Cu: (0) weakly to strongly inclivous; (1) vertical or reclivous.
34	Veins around areolet: (0) not thickened; (1) thickened.
35	Fore wing with: (0) two rs-m cross-veins, forming an areolet; (1) one rs-m cross-vein.
36	Cross-vein rs-m of fore wing (when only one present, that is 2rs-m or 3rs-m is lost): (0) proximal to vein 2m-cu; (1) distal or opposite (interstitial) to vein 2m-cu. Wahl (1991) considers that the two different veins which may be involved can effectively be distinguished by whether the remaining one is proximal or distal to vein 2m-cu. However, the condition in <i>Skiapus</i> is very nearly interstitial, and we prefer not to make any assumption of which vein this is.
37	Fore wing veins 2rs-m and 3rs-m: (0) arising independently from Rs; (1) with a common section from Rs, that is, the areolet is petiolate.
38	Vein Rs of hind wing: (0) shorter than; (1) equal to; (2) longer than rs-m.
39	Vein M+Cu of hind wing with apical third of first abscissa: (0) strongly curved; (1) straight or at most weakly curved.
40	Basal 0.6 of M+Cu: (0) spectral or absent; (1) distinct and present.
41	Distal abscissa of Cu of hind wing: (0) distinct and pigmented; (1) spectral or absent.
42	If distal abscissa of hind wing vein Cu present then Cu&cu-a of hind wing: (0) intercepted; (1) not intercepted.
43	Basal hamuli of hind wing: (0) situated well away from wing base, not on tubular vein; (1) very close to wing base, on proximal spur of tubular or strongly sclerotized vein C.
44	Distal hamuli of hind wing: (0) widely separated; (1) closely spaced.
45	Number of distal hamuli: (0) 9 or more; (1) 6–8; (2) fewer than 6. [ordered]
46	Membrane of fore wing: (0) uniformly setose; (1) with glabrous area.
47	Membrane of forewing: (0) without alar sclerite(s); (1) with sclerites.
48	Apex of fore tibia: (0) simple; (1) with a strong tooth-like projection.
49	Fore and mid-tibiae of female: (0) simple, widest at about mid-length; (1) clavate.
50	Pecten of claws: (0) not reaching apex; (1) reaching apex.
51	Pecten of claws if reaching apex: (0) straight; (1) sinuous (Gauld 1985; this also occurs in a small number of other taxa (Ctenopelmatinae, <i>Ctenopelma luciferum</i> (Gravenhorst)—female only; Mesochorinae, <i>Cidaphus rostratus</i> Dasch; Cremastinae, <i>Xiphosomella Szépligeti</i> sp.).
52	Hind tibial fringe of setae: (0) simple; (1) strongly incurved in the middle, longest setae anteriorly, shortest medially.
53	Bridge separating spurs and tarsus of mid- and hind tibia: (0) absent; (1) present.
54	Length of first metasomal segment: (0) less than second segment; (1) 0.95–1.05 times length of second segment; (2) longer.
55	Suture between first metasomal tergite and sternite: (0) incomplete or absent; (1) complete.
56	Spiracles on first metasomal segment: (0) more than 0.7 distance from the base; (1) less than 0.65 distance from base.
57	First metasomal sternite: (0) long, medially reaching more than 0.7 along tergite; (1) shorter, not reaching beyond 0.65.
58	Glymma on first metasomal tergite: (0) absent; (1) present (see Wahl 1991).
59	Second metasomal tergite: (0) with thyridia; (1) without thyridia.
60	Metasomal tergite 2: (0) not striate; (1) longitudinally striate.
61	Third metasomal tergite and laterotergite: (0) completely separated by crease; (1) not or only partially separated.
62	Exposed portion of ovipositor: (0) longer than metasoma; (1) of medium length, shorter than metasoma, but longer than depth of apical part of metasoma; (2) short, at most equal to depth of apical part of metasoma. [ordered]
63	Number of rectal pads: (0) 2; (1) 4–6; (2) 10 or more (see Miah 1998; Quicke et al. 1999).

Table II. (Continued.)

Character number	Morphological character and states
64	Prelabium of final instar larva; (0) with 6 or fewer sensilla; (1) with 8 or more sensilla. A larger number of sensilla is also found in the Banchinae ( <i>Banchus</i> group).
65	Final instar larvae prelabial sclerite: (0) absent or very lightly sclerotized and only represented by lateral arms; (1) present and sclerotized.
66	Final instar larva prelabial sclerite when sclerotized: (0) transverse or curved; (1) triangular; (2) "Y"-shaped (see Short 1978; Wahl 1991).
67	Final instar larval epistoma: (0) complete; (1) largely unsclerotized, especially medially.

identified and split into separate blocks to enable more thorough POY searches to be carried out. The following POY commands were used for all runs:

```
-fitchtrees -norandomizeoutgroup -random 50 -multibuild 10 -treefuse -fuselimit 50 -noleading
-slop 5 -checkslop 2 -buildmaxtrees 2 -maxtrees 2 -impliedalignment -holdmaxtrees 50 -driftspr
-drifttbr -numdriftspr 5 -numdrifttbr 5 -seed -1
```

The data were run with gap:substitution cost ratios of 2:1, 3:1, and 4:1. For simultaneous molecular and morphological analyses, all morphological polymorphisms were treated as unknown, all characters were treated as unordered and all state changes assigned the same cost as a substitution.

## Results

### *Morphological analysis*

The MPTs obtained, either with all characters unordered (Figure 1a) or with selected ones ordered (Figure 1b) were essentially similar, though the strict consensus tree of the latter was somewhat less resolved. Neither recovered the Campopleginae as monophyletic, but instead it was paraphyletic with respect to the Anomaloninae, Banchinae, Ctenopelmatinae, and Ophioninae in all cases and also with respect to the Cremastinae in non-successive approximation trees. The Nesomesochorini (*Chriodes*, *Klutiana*, and *Nonnus*) was recovered as monophyletic in all analyses. *Skiapus* and *Hellwigia* were included in the large polytomy in both the unordered and ordered analyses (Figure 1a, b), but in the successive approximations trees (Figure 1c) were associated with a derived clade comprising the Ophioninae and Anomaloninae.

### *Molecular analysis*

The trees obtained from the three different POY analyses (with different gap:substitution ratios) were very similar and strict consensus trees for each are given in Figure 2a–c. In all cases the Campopleginae excluding *Chriodes*, *Klutiana*, *Nonnus*, *Skiapus*, and *Hellwigia* was monophyletic whereas Ctenopelmatinae was paraphyletic at least with respect to the Campopleginae and in the case of the 2:1 and 4:1 also with respect to the Ophioninae. In all cases, *Skiapus* and *Hellwigia* were recovered monophyletic with, and usually separately inside, the Ophioninae. In all analyses *Chriodes*, *Klutiana*, and *Nonnus* were monophyletic with Anomaloninae and in 3:1 and 4:1 *Nonnus* was recovered inside the Anomaloninae as the sister group of *Trichomma* Wesmael.

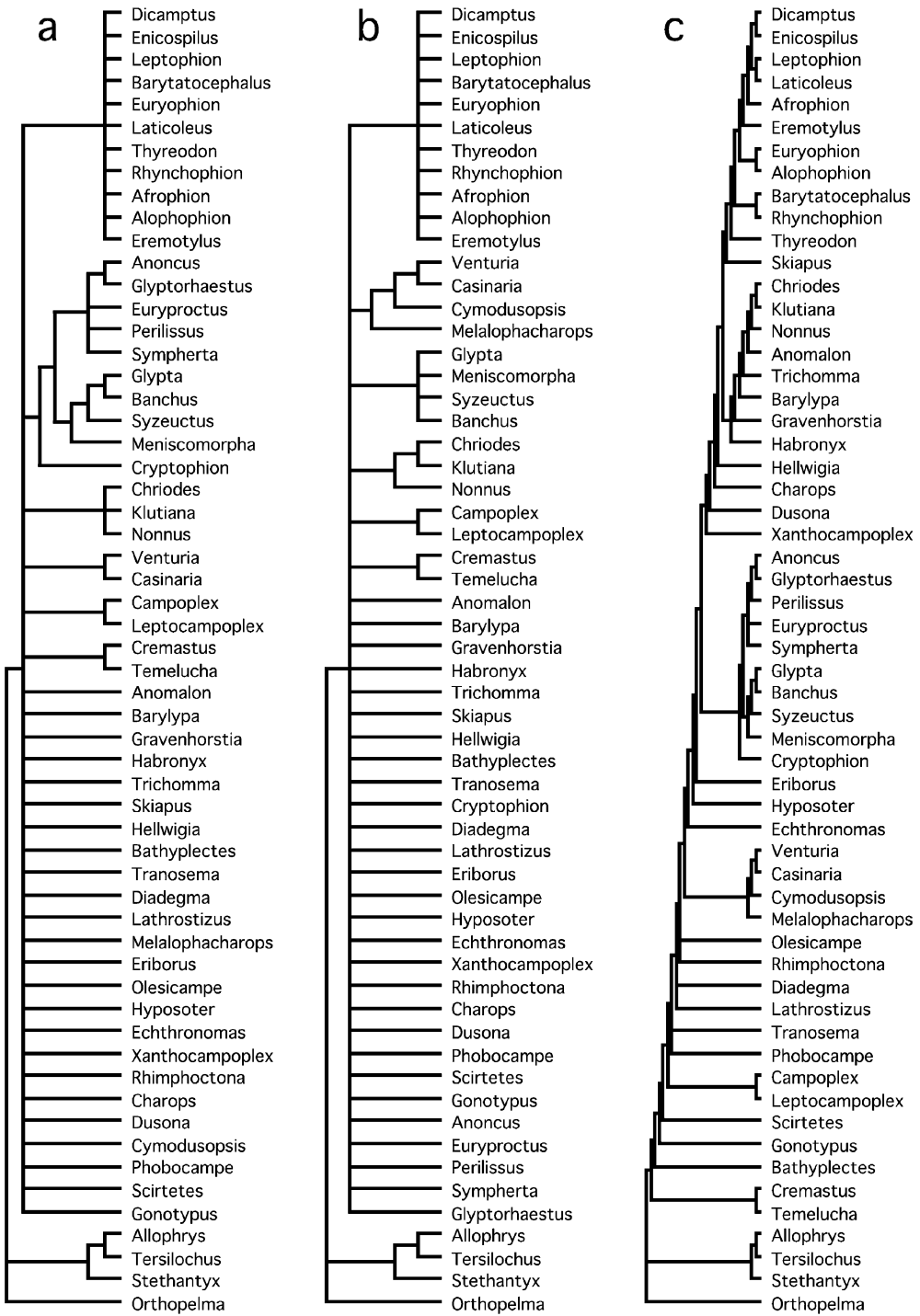


Figure 1. Strict consensus of: (a) MPTs with all characters unordered; (b) MPTs when selected characters treated as ordered; (c) after successive approximations weighting with selected characters treated as ordered.

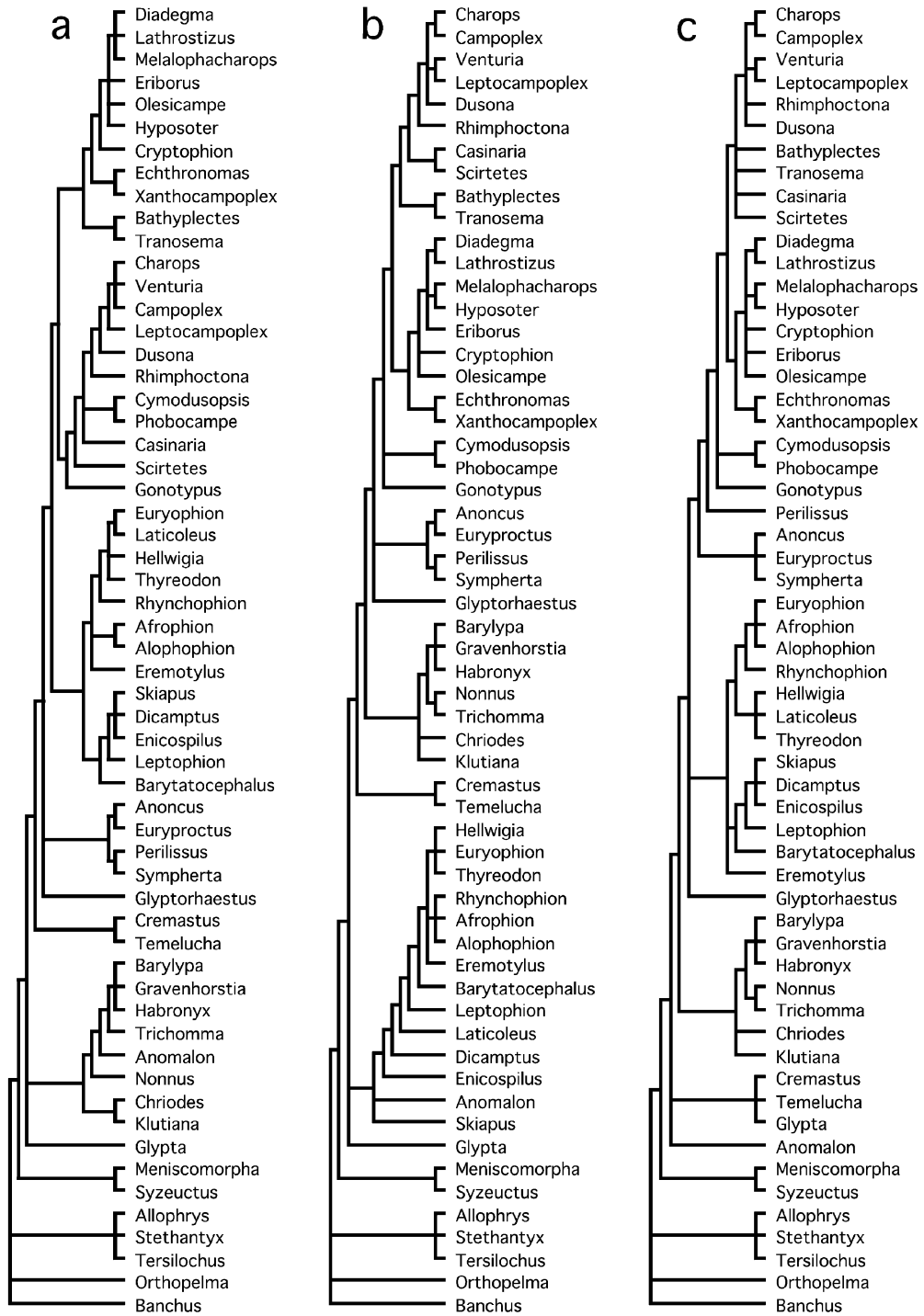


Figure 2. Strict consensus of trees obtained from optimization alignment analysis of molecular data with gap:substitution ratio set at (a) 2:1, (b) 3:1, and (c) 4:1.

Downloaded by [University of Bath] at 15:57 13 February 2014

*Simultaneous analysis of molecular and morphological data*

The trees obtained from the three simultaneous analyses (with different gap:substitution ratios) were very similar and are presented in Figure 3a–c. In all cases the Campopleginae excluding *Chriodes*, *Klutiana*, *Nonnus*, *Skiapus* and *Hellwigia* was recovered as monophyletic and formed a sister group to a monophyletic Ctenopelmatinae, and in turn these were the sister group to the Cremastinae. In all trees *Skiapus* formed a sister group to the Ophioninae plus *Hellwigia*, the latter being recovered in a derived position with *Euryophion* Cameron and *Thyreodon* Brullé. In the 2:1 tree (Figure 3a) *Chriodes*, *Klutiana*, and *Nonnus* form a monophyletic group which is the sister group of the Anomaloninae plus Ophioninae (including *Skiapus* and *Hellwigia*). With a 3:1 gap:substitution ratio *Nonnus* remained in that position while *Chriodes* and *Klutiana* appeared as the sister group of the Cremastinae, Ctenopelmatinae and the restricted Campopleginae (Figure 3b). With the highest gap:substitution ratio, *Chriodes*, *Klutiana*, and *Nonnus* were again recovered as monophyletic, but here forming a sister group to a clade comprising Ophioninae (including *Skiapus* and *Hellwigia*), Anomaloninae, the restricted Campopleginae, Ctenopelmatinae, and Cremastinae.

**Discussion and conclusions**

That the Campopleginae *sensu lato* were not recovered as monophyletic in the analysis of morphological data set, despite inclusion of several characters normally considered as synapomorphies for the subfamily (for example, the silvery setae of the face, lack of a distinct groove between the clypeus and face and, where known, the Y-shaped prelabial sclerite of the final instar larva) is not too surprising since the Ichneumonidae are well known to show high levels of morphological homoplasy. This may explain why many studies treat groups at subfamily level rather than including representative genera or large numbers of characters.

The 28S rDNA sequence data, on the other hand, reveal several substitutions that appear to be synapomorphies for the Campopleginae with the exceptions of *Skiapus*, *Hellwigia*, *Nonnus*, *Chriodes*, and *Klutiana*. Some of these are highlighted in Figure 4. The sequences obtained for *Skiapus* and *Hellwigia* both possess the two obvious molecular synapomorphies characteristic of all members of the Ophioninae sequenced to date [for example, inserts in fragments 3 and 4 in Figure 4 (boxed)] and lack the synapomorphies of the Campopleginae [for example, substitutions in fragments 1 and 2 in Figure 4 (black circles)]. Thus it is not surprising that *Skiapus* and *Hellwigia* are recovered in a monophyletic clade with the Ophioninae in the POY trees. However, these two genera are not recovered together either in purely molecular or simultaneous analyses, and the DNA sequence fragments shown in Figure 4 suggest why. Within the Ophioninae a number of *Enicospilus* species possess a four-base insertion in the D2 28S rDNA (Figure 4 fragment 3) that is present (albeit without base homology) in *Skiapus*. Given the lack of base homology and the fact that this is just a two-base pair insertion within an already variable piece of DNA, it would be unwise to attribute too much to this. All Ophioninae (*sensu* Gauld, 1985) may possess a high number of rectal pads, whereas campoplegines either possess the putatively plesiomorphic number (six) or fewer (four or five) (Pampel 1914; Quicke et al. 1999). The number of ophionine genera examined (just three) is, however, inadequate to draw conclusions about whether the whole subfamily is characterized by the large number of rectal pads (a character state, incidentally, also shared by the Anomaloninae, Rhyssinae, and some Acaenitinae in the Ichneumonidae, and by the genus

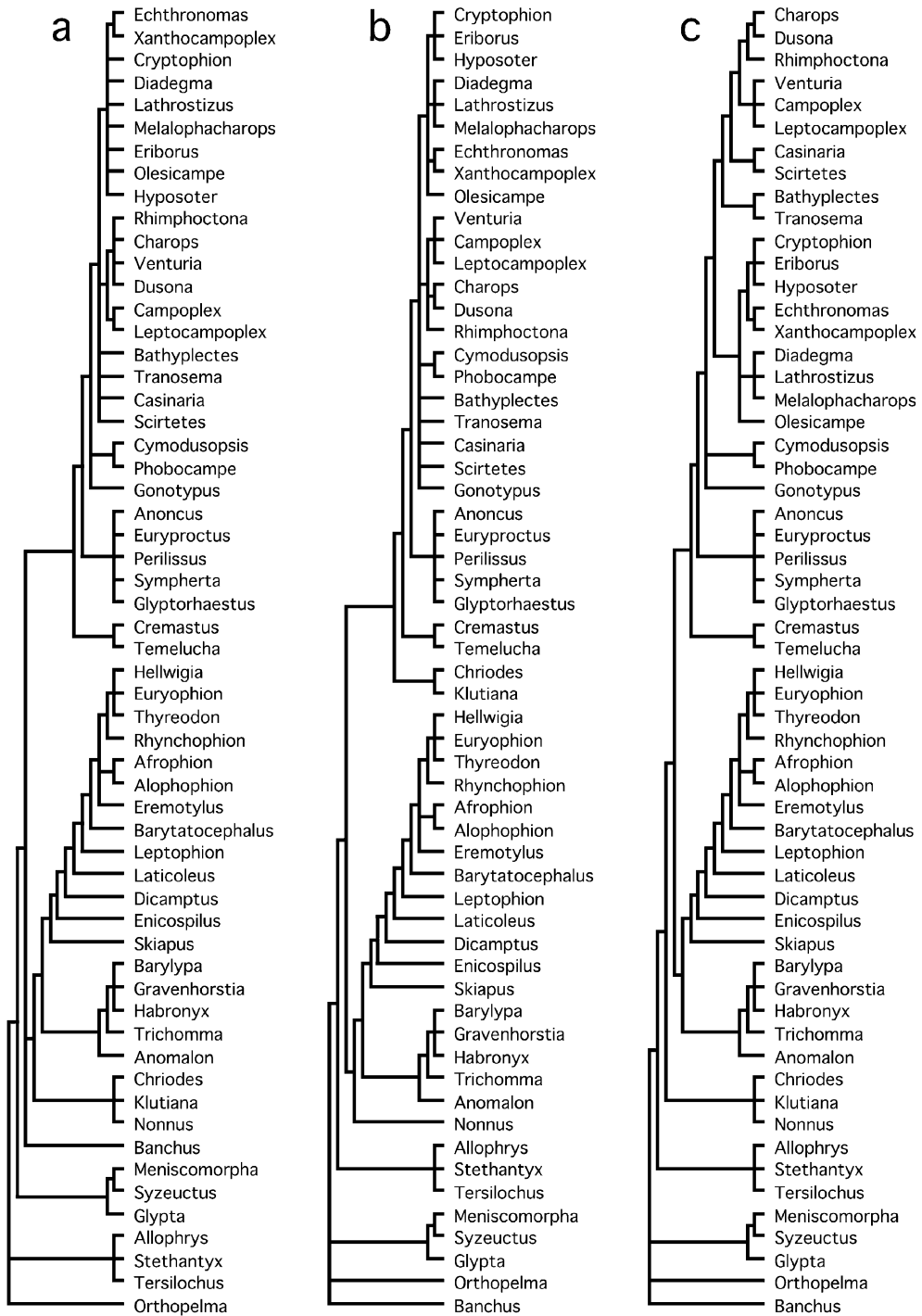


Figure 3. Strict consensus of trees obtained from simultaneous optimization alignment analyses of morphological and molecular data with gap:substitution ratio set at (a) 2:1, (b) 3:1, and (c) 4:1.

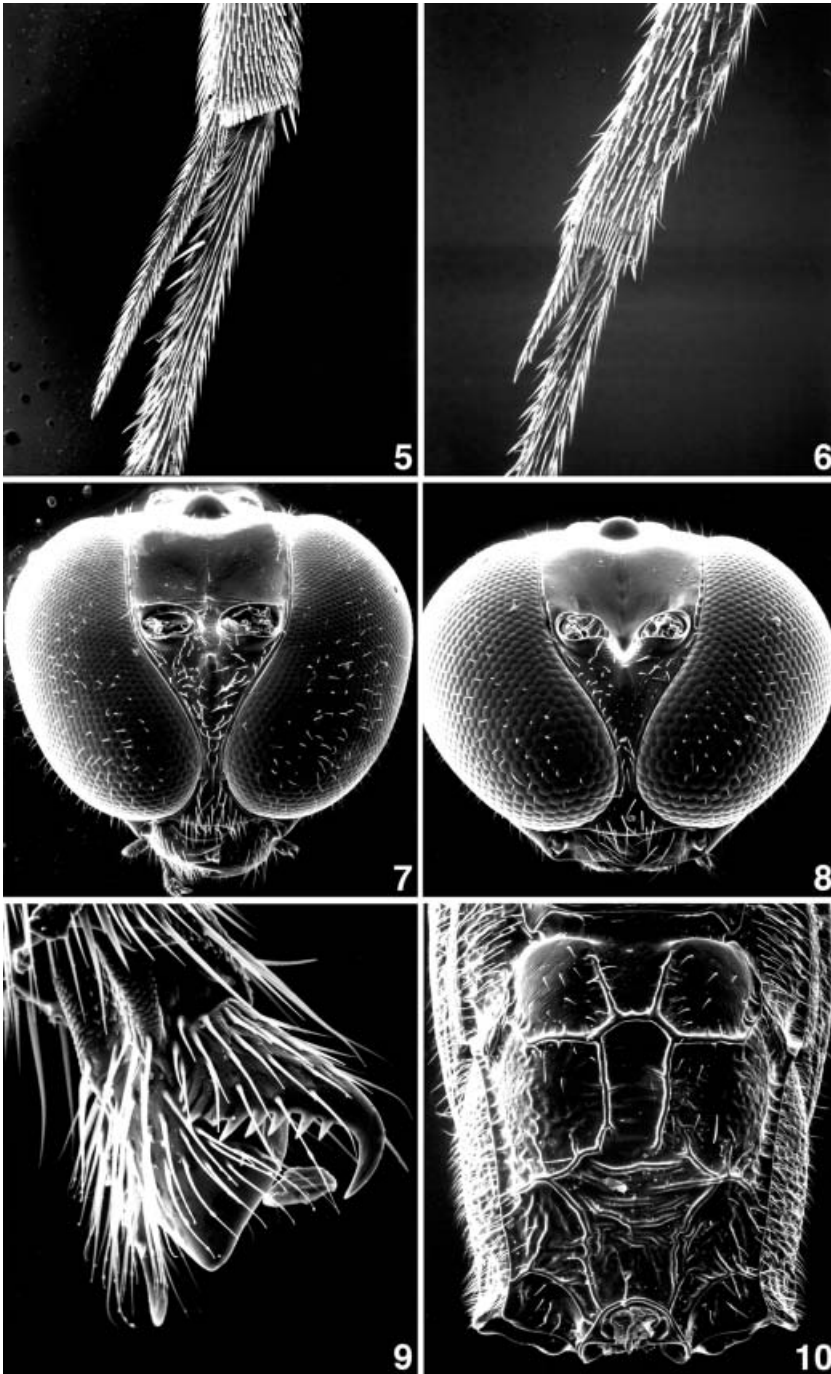
Taxon	Fragment 1	Fragment 2	Fragment 3	Fragment 4
<b>Anomaloniinae</b>				
<i>Anomalon</i> sp.	CCGAAAGATCGAAT	CCTGGCGATTGCGCG	CGCGTTCTCT ---- CGCCTCGCGGGC	GCGCGG ---- CAGACCCC
<i>Barylypa</i> sp.	CCAAAAGATNGNAT	CNCGGCRNCNCGGGTN	CGCGCGTAA ---- CGCTTCGCGGGC	GCGCGG ---- CAGACCCC
<i>Gravenhorstia</i> sp.	NNNAAAGATCGAAT	CTCGGTCAGTGCGCG	CGCGCGTAA ---- CGCTTCGCGGGC	GCGTGG ---- CAGACCCC
<i>Habronyx</i> sp.	CCAAAAGATCGAAT	CTCGGACAGTGCGCG	CACCGGTAA ---- CGCTTCGCGGGC	CGGTGG ---- CAGACCCC
<i>Trichomma</i> sp.	CCAAAAGATCGAAT	TCCCGCGAGCGGGC	CGCGGGCAA ---- CCGCTTCGCGGGC	TCGTGG ---- CAGACCCC
<b>Reclassified taxa</b>				
<i>Chriodes</i> sp.	CCAAAAGATCGAAT	CCC GGCGCGTGTGCG	CGCGTGCAA ---- CGCTTCGCGGGC	GCGTGG ---- CAGACCCC
<i>Klutiana</i> sp.	CCAAAAGATCGAAT	CCC GGCGCGTGTGCG	CACGTGCAA ---- CGCTTCAGCGGC	GCGTGG ---- CAGACCCC
<i>Nonnus</i> sp.	CCAAAAGATCGAAT	CTCGGGCGCCGAGCG	CGCGCGTCA ---- CGCTTCGCGGGC	GCGCGG ---- CAGACCCC
<i>Skiapus</i> sp.	CCGAAAGATCGAAT	TCCGGCGCTTCCGCG	CACCGGTAC <b>GGCA</b> CCCTTCGCGGGC	ATGTGG <b>CTGA</b> CAGATCCC
<i>Helwigia obscura</i>	CCAAAAGATCGAAT	CCTGGCAGATCGCGG	TA-GTGTAC <b>G--G</b> CGCTTACGGGC	ATGTGG <b>CTGA</b> CAGACCCC
<b>Ophioninae</b>				
<i>Aphrophion hynnii</i>	CCAAAAGATCGAAT	CCAGACACCCGTGCG	CAITGTAC <b>G--A</b> CGCTTACGGGC	ATGTGG <b>CTGA</b> CAGACCCC
<i>Allophopion</i> sp.	CCAAAAGATCGAAT	CCAGGCACGTGTGCG	CAITGTAC <b>G--A</b> CGCTTACCGGC	ATGTGG <b>CTGA</b> CAGACCCC
<i>Barytaocephalus mocsaryi</i>	CCAAAAGATCGAAT	CCTGGCACGCGTGGC	CAITGTAC <b>G--A</b> CGCTTACGGGC	ATGTGG <b>CTGA</b> CAGACCCC
<i>Dicamptus seyrii</i>	CCAAAAGATCGAAT	CCAGGCGCTTGTGCG	CAITGTAC <b>G--A</b> CGNTTCGCGGGC	ATGTGG <b>CTGA</b> CAGACCCC
<i>Enicospilus ramidulus</i>	CCGAAAGATCGAAT	CCAGGCGCGTGTGCG	CATCGGTAC <b>GCGA</b> CGCTTCGCGGGC	ACGTGG <b>CTGA</b> CAGACCCC
<i>Eremotilus marginatus</i>	CCAAAAGATCGAAT	CCTGGCACGTGTGCG	CATGTGTAC <b>G--A</b> CGCTTACCGGC	ATGTGG <b>CTGA</b> CAGACCCC
<i>Euryophion latipennis</i>	CCAAAAGATCGAAT	CCTGGCGCGTGGCG	CATGTGTAC <b>G--A</b> CGCTTACGGGC	ATGTGG <b>CTGA</b> CAGACCCC
<i>Thyreodon laticinctus</i>	CCAAAAGATCGAAT	CCTGGCACGTGGCG	CATGTGTAC <b>G--A</b> CGCTTACGGGC	ATGTGG <b>CTGA</b> CAGACCCC
<b>Campopleginae</b>				
<i>Bathyplectes</i> sp.	CCAAAAGTTCGAAT	CCTGGCAATTGTGCG	CATATGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Casiniaria petiolaris</i>	CCAAAAGTTCGAAT	CCTGCAATTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Charops</i> sp.	CCAAAAGTTCGAAT	CCTGGCAATTGTGCG	CATACGTCA ---- CGCTTACGGGC	GTGTGG ---- CAGACCCC
<i>Cryptophion manueli</i>	CCAAAAGTTCGAAT	CCGGCGA-TGCGCG	CATGTGTTA ---- CGCTTACCGGC	ATGTGG ---- CAGACCCC
<i>Cynodisopsis</i> sp.	CCAAAAGTTCGAAT	CCTGGCAATTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Diadegma mollipila</i>	CCAAAAGTTCGAAT	CCGGCGA-TGTCGC	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Disona</i> sp.	CCAAAAGTTCGAAT	CCTGGCAATTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Eriborus terebrans</i>	CCAAAAGTTCGAAT	CCGGCGA-TGCGCG	CAITGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Hyposoter didymator</i>	CCAAAAGTTCGAAT	CCGGCGA-TGTCGC	CAITGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Lathrostizus lugens</i>	CCAAAAGTTCGAAT	CCGGCGA-TGTCGC	CAITGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>?Phobocampe</i> sp.	CCAAAAGTTCGAAT	CCTGGCAATTGTGCG	CAITGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Rhimphoctona grandis</i>	CCAAAAGTTCGAAT	CCTGGCAATTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Tranosema rostrale</i>	CCAAAAGTTCGAAT	CCTGGCAATTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Venturia ocybeta</i>	CCAAAAGTTCGAAT	CCTGGCAATTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Xanthocampoplex</i> sp.	CCAAAAGTTCGAAT	CCTGGCGA-TGTCGC	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<b>Cremastinae</b>				
<i>Cremastus spectator</i>	CCAAAAGATCGAAT	CCTGGCGCTCGTGGC	CGITTTGTTA ---- CGCTTACGGGC	ACGCGG ---- CAGACCCC
<i>Temelucha</i> sp.	CCAAAAGATCGAAT	CCTGGCGCTAGCGGC	CGITTTGTTA ---- CGCTTACGGGC	ATGCGG ---- CAGACCCC
<b>Ctenopelmatinae</b>				
<i>Anoncus</i> sp.	CCAAAAGATCGAAT	CCAGGCACGTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Euryproctus numidicus</i>	CCAAAAGATCGAAT	CTTGGCACGTGTGCG	CATGTGTTA ---- GCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Glyptorhaestus</i> sp.	CCAAAAGATCGAAT	CCGGCGCTTGTGCG	CATGTGTTA ---- NGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Perillissus albitarsis</i>	CCAAAAGATCGAAT	CCTGGCACGTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGTGG ---- CAGACCCC
<i>Sympherta</i> sp.	CCAAAAGATCGAAT	TCTGGCACGTGTGCG	CATGTGTTA ---- CGCTTACGGGC	ATGCGG ---- CAGACCCC

Figure 4. Partial alignments (arrangements) of four parts of the 28S D2 rDNA gene for representatives of the Campopleginae, Cremastinae, Ctenopelmatinae, and Ophioninae (aligned by eye) showing molecular synapomorphies for Campopleginae (1 and 2) and Ophioninae (3 and 4). Fragment 1 corresponds to bases 11–24, fragment 2 to bases 47–62, fragment 3 to bases 203–225 (in box) and fragment 4 to bases 236 (in box) to 244 in the alignment shown in Belshaw et al. (1998, Figure 1).

*Euurobracon* Ashmead, in the Braconidae). Thus, while our data show convincingly that *Helwigia* and *Skiapus* belong in the same monophyletic group as the Ophioninae, we remain cautious about whether one or both are derived within the Ophioninae or form a sister group to that subfamily.

Whereas the Anomaloniinae are well characterized as a monophyletic group based on morphology (Gauld 1976, 1997), the 28S D2–3 rDNA gene fragment shows no unique synapomorphies (see Figure 4), and no obvious individual substitutions indicate a clear relationship with *Nonnus*, *Chriodes*, and *Klutiana*, though these genera were recovered either monophyletically or as a grade as the sister group of the Anomaloniinae in the purely morphological analyses. However, in the simultaneous analyses (Figure 3) they showed a trend with increasing gap:change values from being a monophyletic sister group of the Anomaloniinae+Ophioninae (Figure 3a), through a polyphyletic state (Figure 3b) to again forming a monophyletic group, but this time as a sister group of the clade comprising all the included taxa except for Banchinae and Tersilochinae (Figure 3c).

*Nonnus*, *Chriodes*, and *Klutiana* share a putatively synapomorphic, medially strongly incurved comb on the inner margin of the hind tibia (Table II: character 52; Figure 6, cf. Figure 5) and, within the Ophioniformes, the clavate fore and mid tibiae of the females (Table II: character 49). Nevertheless, despite the inclusion of these characters, they were



Figures 5–10. Scanning electron micrographs showing features of Campopleginae *sensu stricto* and Nesomesochorinae stat. rev. (5) *Echthronomas* sp. (Campopleginae) hind tibia and basitarsus inner aspect showing unmodified tibial comb. (6–7, 9–10) *Chriodes* sp.: (6) hind tibia and basitarsus inner aspect showing modified tibial comb with medially reduced setae; (7) face; (9) claw showing pecten; (10) propodeum showing areolation. (8) *Klutiana* sp., face.



only recovered as forming a monophyletic group in two of the three simultaneous analyses, thus there is only a weak signal in the combined data set that would support recognition of a single subfamily including *Nonnus*, *Chriodes*, and *Klutiana*. We therefore are here proposing that these be placed in two subfamily-level taxa, the Nonninae for *Nonnus* and the Nesomesochorinae for *Chriodes* and *Klutiana*. The Nesomesochorinae was originally proposed by Ashmead (1905) with type genus *Nesomesochorus* Ashmead (a junior objective synonym of *Chriodes*), and the Nonnini was proposed by Townes et al. (1961).

The Nesomesochorinae and Nonninae can be keyed out together, as the Nonnini, in Townes (1970, p 144) and are recognized by the reduced number of labial palp segments, in addition to the modified hind tibial comb (Table II: character 52). *Chriodes* and *Klutiana* have eyes that converge ventrally so that they are almost touching (Figures 7, 8), the claw is strongly pectinate but not to the apex (Figure 9), and the propodeum has an almost complete set of carinae (Figure 10). *Nonnus* has no especially distinctive morphological features, but they are large wasps with a long ovipositor and white-banded antennae (see Townes 1970, Figure 140). Despite the lack of “ophionoid facies”, the Palearctic genus *Hellwigia* is superficially very like other ophionines, except that it lacks the spurious vein in the fore wing. Its fore wing veins are characteristically sinuous and vein 2m-cu is more or less interstitial (see Townes 1970, Figure 142). *Skiapus* is a highly characteristic genus of medium-sized ichneumonids from Africa. The mandibles are highly aberrant (Figure 11) which are twisted and out-curved, the occipital carina is deeply indented medio-dorsally (Figure 12), the propodeum is very steep posteriorly with two complete transverse carinae located close to its anterior margin (Figure 13), the hind legs are especially long with very large coxae and all legs are strongly spinose (Figure 14). The hind coxa has a tooth ventrally (Figure 15) and the claws are strongly pectinate, though not to the apex and not sinuous as in other ophionines (Figure 16).

Finally, this study emphasizes the value of considering both molecular and morphological data in phylogeny reconstruction since both can provide convincing synapomorphies for groups. In the present example, only molecular data provide convincing evidence for monophyly of the Campopleginae (excluding *Hellwigia*, *Skiapus*, *Nonnus*, *Chriodes*, and *Klutiana*), while most support for the Anomaloninae comes from the morphological data with no molecular synapomorphies in the D2–3 28S rDNA region.

The nomenclatural changes being effected can be summarized thus:

#### CAMPOPLEGINAE

Campoplegoidae Förster, 1869. Type genus *Campoplex* Gravenhorst [misidentified].

Porizonoidae Förster, 1869. Type genus *Porizon* Fallén [?misidentified].

Limneriinae Szépligeti, 1911. Type genus *Limnerium* Ashmead (a junior synonym of *Olesicampe* Foerster).

Charopsinae Viereck, 1918. Type genus *Charops* Holmgren.

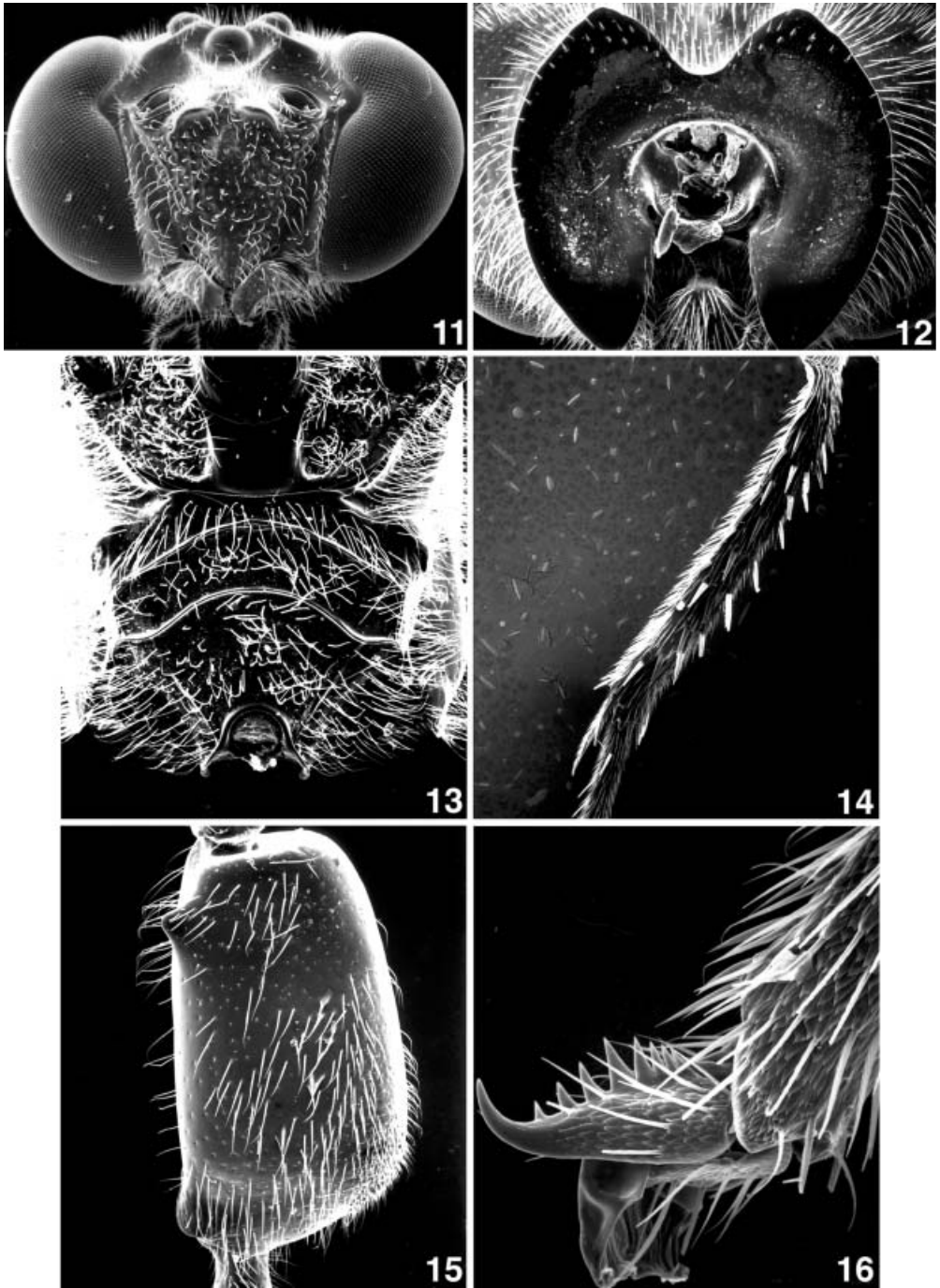
Cryptophioninae Viereck, 1918. Type genus *Cryptophion* Viereck.

Macrini Townes, 1971. Type genus *Macrus* Gravenhorst.

Included genera: the genera listed under Campopleginae by Yu and Horstmann 1997 and Wahl 1999 excluding *Chriodes*, *Klutiana*, *Nonnus*, *Skiapus*, and *Hellwigia*.

#### NESOMESOCHORINAE stat. rev.

Nesomesochorini Ashmead, 1905. Type genus *Nesomesochorus* Ashmead (a junior objective synonym of *Chriodes* Foerster).



Figures 11–16. Scanning electron micrographs showing features of *Skiapus* sp. (Ophioninae). (11) Front of head showing emarginate eyes and twisted mandibles. (12) Back of head showing medially strongly excavated occiput and deflected occipital carina. (13) Metanotum and propodeum showing two complete transverse carinae located close to anterior margin. (14) Tibia of mid-leg, oblique angle, showing strong spines. (15) Hind coxa showing tooth near base. (16) Claw showing pectination.

Mavandini Seyrig, 1935 [incorrectly formed stem]. Type genus *Mavandia* Seyrig (a junior synonym of *Chriodes*).

Included genera: *Chriodes* Förster, *Klutiana* Betrem.

#### NONNINAE stat. nov.

Nonnini Townes, 1961 (in Townes et al. 1961). Type genus *Nonnus* Cresson.

Included genus: *Nonnus* Cresson.

#### OPHIONINAE

Ophionini Shuckard, 1840 (in Swainson and Shuckard 1840). Type genus *Ophion* Fabricius.

Hellwigioidea Foerster, 1869 **stat. rev.** Type genus *Hellwigia* Gravenhorst.

Enicospilini Townes, 1971. Type genus *Enicospilus* Stephens.

Included genera: *Hellwigia* Gravenhorst, *Skiapus* Morley and the genera listed under Ophioninae by Gauld 1985, Yu and Horstmann 1997, and Wahl 1999.

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**Appendix: Morphological data set**

Polymorphisms are abbreviated as follows: a=(0,1); b=(1,2); c=(0,1,2).

<i>Afrophion hynnis</i>	000101121010001111101111011111121011?2110011110001100200000012?????
<i>Allophrys</i>	1000000001011011111010?1010000200110?????1?0120000000200000011?????
<i>Alophophion</i>	000101110010001101101112000010121011?2110011110001100200000012?????
<i>Anomalon</i>	01100000010001010011010021?1101120010?1111?0100000000000001001100?0
<i>Anoncus</i>	0000010010000001111101010010000111010?2010001100100000211110002?????
<i>Banchus volutatorius</i>	00000100110001110111112010?0102100?0211000110000100021111000111101
<i>Barylypa</i>	011000001010111001101101111101221011?111000100000000000001012200?0
<i>Barytatocephalus mocsaryi</i>	000?01010010001101101101011111020011?2110011100001100200000012?????
<i>Bathyplectes</i>	0110000011000010111011010010000000a?000100??200100?00210000?02?0121
<i>Campoplex deficiens</i>	011???00010001111111102001000110010?1010101200000?00110100001?????
<i>Casinara petiolaris</i>	0111010ba0000a10111101?20aa001aca00?11a10101200000?0011000001b10121
<i>Charops</i>	011010021000001011101101011101021010?11100012??000?00210000002?0121
<i>Chriodes</i>	01010101200a1010?00001020000112000?00010011100010?10011000111?????
<i>Cremastus spectator</i>	000001000100011001101102001000010010?0000001100000001210011111?0111
<i>Cryptophion manueli</i>	0101010101000110100001010?100112100?12110101100000?00210110012?????
<i>Cymodusopsis</i>	0110010110000110111110200100100100?11110001200000?0020000001?0121
<i>Diadegma mollipla</i>	011001000100001011?111?100000010100?11110101200000?0021011000b?0121
<i>Dicamptus seyrigi</i>	001101121010021101101101001111120011?2110011110001100200000012?????
<i>Dusona</i>	01111102001000101111010100110102100?02110001000000?0020001001210121
<i>Echthronomas facialis</i>	0111010101?00?011111101001001000?10110101200000?00210110002?0121
<i>Enicospilus ramidulus</i>	000101120010021111101101001111020011?211001111100110020000001221111
<i>Eremotylus marginatus</i>	00010112001000111110110200111221011?2110011010001100200000012?????
<i>Eriborus terebrans</i>	0110010a010001111111102000001021010?2110101200000?00210110002?0121
<i>Gravenhorstia (Erigorus)</i>	010001001010111001101102111101221011?2110001000000000a00001012?00?0
<i>Euryophion latipennis</i>	00010010001000111110110201011220011?21100?1010001100200000012?1111
<i>Euryproctus numidicus</i>	0000110001000010011010?101000111?00?121100011001000000211111002100?1
<i>Glypta altamirai</i>	000000001100011001111112010001020010?211000110000000021111000010101
<i>Glyptorhaestus</i>	00001000010000111110111100000021000?12010001100101000211111002?00?1
<i>Gonotypus melanostoma</i>	011???0001000011111111101000020000?01010001200000?00210?10001?????
<i>Habronyx</i>	010?010120101110011011?2111001221011?2110001000000000000001012100?0
<i>Hellwigia obscura</i>	00100102001a020111101102011101021010?21100?000000?00200001012?????
<i>Hyposoter didymator</i>	0110000101000110111110100100102100?10110101200000?00210110012?0121
<i>Klutiana</i>	00000101201a101010000102000001220010?0010001200010?10011000001?????
<i>Lathrostizus lugens</i>	01100100010000111111110100100011100?11110101200000?00210110001?0121
<i>Laticoleus infumatus</i>	000101121010001111101111001111220011?2110011210001100200000012?????
<i>Leptocampoplex cremastoides</i>	011???000100001?11111101001000210010?101?01200000?00110110001?????
<i>Leptophion</i>	000101111100011110110100111120011?2110011210001100200000012?????
<i>Melalophacharops</i>	011001010100001011011?2001001111010?1111?01200000?0021011000???????
<i>Meniscomorpha zacasta</i>	000001000100011001111112010001121010?2110001100000000211110000?????
<i>Nonnus bianmulatus</i>	00110100101110110010010200010102000?021100010000110100110000001????
<i>Olesicampe</i>	0010000001000011111110100100111100?10010101200000?00210110000?0121
<i>Orthopelma</i>	0100000011000200110100?2000000201010?0011?01200000000211011001000?0
<i>Perilissus albitarsis</i>	00000100a11000101110100100000011100?1211000110010000021111100220111

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<i>Phobocampe</i>	01100000110000111111110100100021000?1b010101200000?00200100002?0121
<i>Rhimphoctona grandis</i>	01110100010000111111110100100112100?01110001100100?00211110011?0121
<i>Rhynchophion flammipennis</i>	000110010010001111101102011111020011?2110011000001100200000012?????
<i>Scirtetes robustus</i>	011001001100001110111101011000110010?1010101200000?00210010001?????
<i>Skiapus</i>	01010102111a111011101101000102020011?21100101001010002000010a21?????
<i>Stethantyx</i>	100000000011011010010?1010000200010?0001?0120000000201110011?00?1
<i>Sympherta</i>	00000100010000101110101101000121100?12110001100100000211111002?00?1
<i>Syzeuctus</i>	00000100010001100111111201010102100?121100011000000002?1110000?0101
<i>Temelucha</i>	000001000110001011101102001000211010?00000011000000012100111110111
<i>Tersilochus heterocerus</i>	1000000001011011011010?1010000200110?0001?01200000000200000011000?1
<i>Thyreodon laticinctus</i>	01010001001001100110111201111121011?211001100000110020000001221111
<i>Tranosema rostrale</i>	01100100000001101111110100100021000?10010a01200000?00211110001?0121
<i>Trichomma</i>	011001012010101001101102111001220011?0110001000000000000001011?00?0
<i>Venturia ocybeta</i>	01100100000000101011010100100111100?0010101200000?0021000001110121
<i>Xanthocampoplex</i>	0110010aaa100010111111010110010b100?12110101100000?0020001000b?a121