A CLADISTIC ANALYSIS OF HAWAIIAN OPHIONINE WASPS (HYMENOPTERA: ICHNEUMONIDAE)

by

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ABSTRACT

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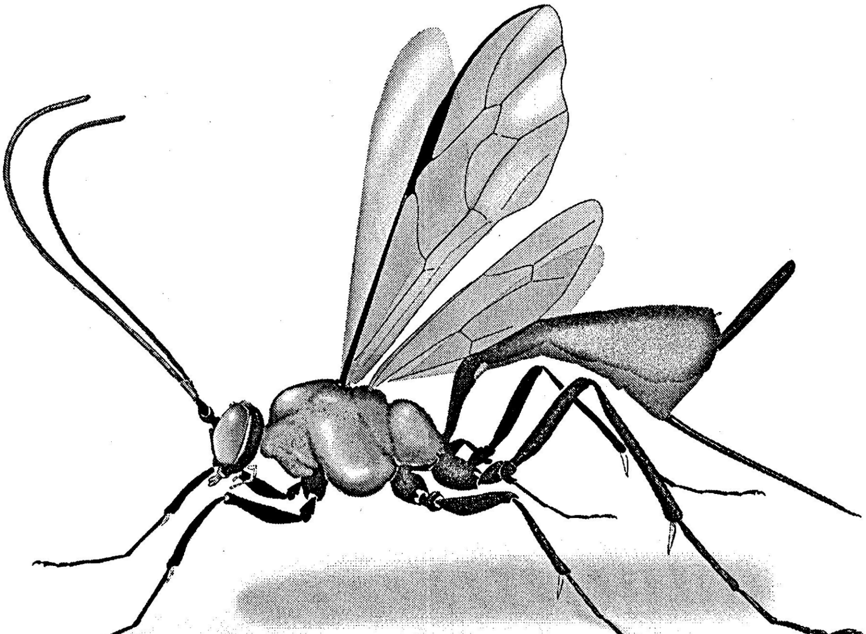
A cladistic analysis was performed on 29 of the 31 known species of Hawaiian ichneumonid wasps of the subfamily Ophioninae, based upon 64 adult morphological characters. Outgroups consisted of 17 species of *Enicospilus*, one species of *Leptophion*, and *Dicamptus* (scored from a genus description). Outside of an undescribed species known only from a single specimen, increased support was found for the existence of one Hawaiian clade of Ophioninae. The group is presently divided into multiple genera, of which most species are placed in the speciose and cosmopolitan genus, *Enicospilus*. Maintenance of the nominal taxa *Pycnophion*, *Banchogastra*, and *Abanchogastra* at generic rank renders *Enicospilus* paraphyletic (as has been noted by other authors) or polyphyletic. Nomenclatural changes are recommended, including those that would serve to ensure, at a minimum, the paraphyly of *Enicospilus*. The consequences of nomenclatural changes necessary to enforce strict monophyly of *Enicospilus* are discussed, as are the distribution and evolution of atypical morphological features unique to the Hawaiian ophionine fauna.

For my grandparents, Jim and Lois



Pycnophion fuscipennis Perkins

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I would like to thank a number of workers at various museums who entrusted me with specimens. In particular, Ian Gauld of the Natural History Museum, London, not only sent me wonderful material, but also encouraged this newcomer to work with a group of wasps which are near to much of his own research. His many publications have set a standard of quality for which I will strive to achieve in my career. I also would like to thank the following persons for specimens and correspondence: Dave Wahl of the American Entomological Institute, Gainesville, FL, U.S.A.; John Huber of the Canadian National Collection, Ottawa, Canada; Robert Zuparko of the California Academy of Sciences, San Francisco, CA, U.S.A; Robert Carlson and David Furth of the U.S. National Museum of Natural History, Washington D.C., U.S.A; and Tino Gonsalves of the Bernice P. Bishop Museum, Honolulu, HI, U.S.A.

I may have never imagined the importance and delight of studying insects if it wasn't for the influence of a number of people at the University of Washington including Ted Pietsch, Brian Urbain, Trevor Anderson, Sharon Collman, and John Edwards.

I also owe much to my family who has remained encouraging and supportive even though I have had to travel far away from them for my studies.

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1. INTRODUCTION

> *"The variability of many of the Hawaiian Ophionini is so excessive, that if similar variation occurs in other tropical countries, the group may well prove one of the most difficult of entomological studies."*
>
> *— R. C. L. Perkins, 1915*

Hawaii has been colonized by ichneumonid wasps perhaps as few as three times. The Ethiopian and Oriental genus *Ecthromorpha* Holmgren and the genus *Spolas* Townes (also known from New Zealand) are the only ichneumonid wasps other than a group of ophionines that are definitively native. The most successful group of native Hawaiian ichneumonid wasps is an array of *Enicospilus* Stephens species, a cosmopolitan and extremely large yet morphologically homogeneous genus of the subfamily Ophioninae. Other ophionine genera are found on these islands but are believed to have arisen from within *Enicospilus* (Cushman 1947; Gauld 1985), yet their generic rank status has remained owing to their highly derived morphology and the impracticability of synonymizing them with *Enicospilus*.

Worldwide *Enicospilus* contains more than 650 species (Gauld 1981). Members are present in most, if not all regions, but diversity is concentrated in tropical areas, with particularly large radiations in New Guinea and Madagascar. Members of *Enicospilus* are typical ophionines in that they are usually large, slender, orange to brown nocturnal parasitoids of larval Lepidoptera; familiar to most entomologists as conspicuous visitors to their light traps. As juvenile koinobiont endoparasitoids, they allow their host to mature until just prior to host pupation. At this time the host is killed, often just after the host constructs its cocoon. The wasp then spins its own cocoon inside that of the host, or exits to do so (Gauld 1985). Species recognition can be relatively easy for such a diverse group owing to the diagnostic arrangements of sclerites that "float" in the discosubmarginal cell of the forewing, and to the extensive treatments of Ophioninae for many regions of the world by Ian Gauld which contain very usable keys and elaborate descriptions and redescriptions of many species (Gauld 1977, 1988; Gauld and Mitchell 1978, 1981; Gauld and Carter 1983).

These insects are strong fliers and disperse widely, as evidenced by their presence on all major tropical island groups in the Pacific. In Hawaii *Enicospilus* has given rise to at least 31 species, including small stout, diurnally active species, species possessing long-straight and long-curved ovipositors, and species with extremely elongate metasomas; all of which are atypical for the genus at large. In fact there is arguably more morphological diversity within the Hawaiian Ophioninae than in the vast diversity of *Enicospilus* outside the islands. And though little is known of their biologies, it is quite likely that these morphological oddities represent adaptive shifts in host usage. This suspicion is based on the striking resemblance of the metasomas of some Hawaiian lineages to other, more distantly related genera of Ophioninae (Fig. 1). One host record supports such a conclusion. *Pycnophion fuscipennis* Perkins has been reported parasitizing larval *Hyposmocoma chilonella* Walsingham (Lepidoptera: Cosmopterygidae) in *Rubus hawaiiensis* (Swezey 1931, 1954). This host is unusual in that it is not exposed. Immatures of this genus conceal themselves within the pith of stems of various plants (Zimmerman 1978; Gauld 1985). Perkins apparently suspected that some members may parasitize Coleoptera given that he stated the cocoons are often found in large numbers when collecting Coleoptera (Perkins 1913).

Intriguingly, there are multiple independent communications of what might be regarded as swarming or lekking behaviors. In an address to the Hawaiian Entomological Society, Perkins (1907), in reference to insects found on the slopes of Mauna Loa, stated the following:

> *"Ophions of various species and genera are extremely numerous, and often scores of individuals may be seen resting under a single large leaf, while frequently a regular swarm flies off, as one disturbs the dead fronds of the large tree-ferns."*

Perkins made similar remarks in 1913.

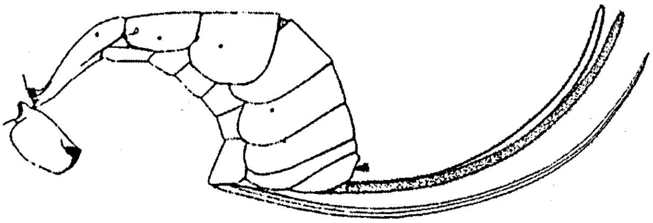
> *"Many are of social habits and crowd together in large numbers at rest. We have seen dozens of examples of a species resting beneath one or two adjoining leaves of a large-leafed tree, so thickly indeed as to hide the surface. At other times they form great flocks in dead hanging fern fronds. These assemblies are sometimes all of the male sex, but sometimes mixed. Sometimes too the species are mixed in these assemblies. So far as we know only* Enicospilus *and* Pleuroneurophion *congregate in this way, the others being more solitary."*

Attention was again called to this phenomenon at another meeting of the Hawaiian Entomological Society (Giffard 1955). The following is in reference to *E. kaalae* Ashmead on the island of Kauai [(*E. henshawi* Ashmead is a junior synonym of *E. lineatus* (Cameron)].

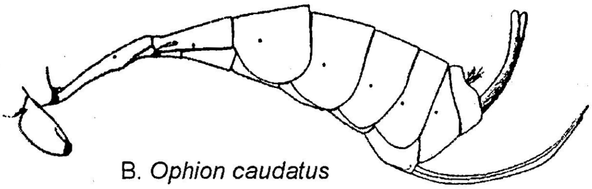
> *"Large numbers of this wasp had assembled in clumps of* Styphelia tameiameiae *and when disturbed they flew out downhill, all in the same direction. Among them there was captured a single specimen of* Enicospilus henshawi *Ashmead."*

1.1 Present Classification

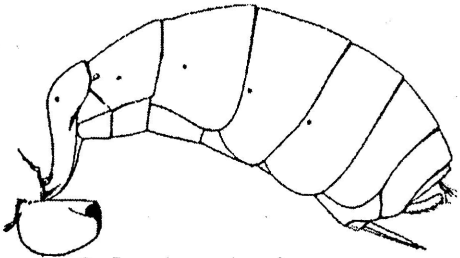
Including undescribed taxa first mentioned in the present work, the Ophioninae of Hawaii consist of 31 species (Table 1). Generic classification has fluctuated but presently these species are arranged in the following four genera: *Enicospilus* (24 species),



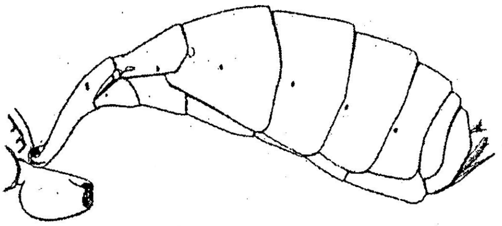
A. *Pycnophion molokaiensis*



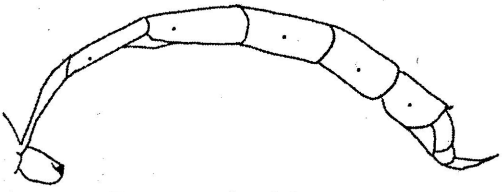
B. *Ophion caudatus*



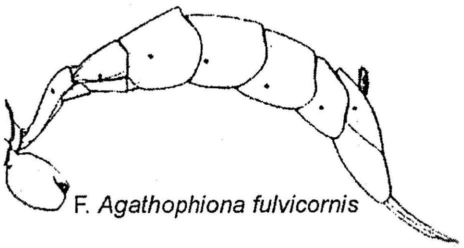
C. *Banchogastra nigra*



D. *Rhynchophion flammipennis*



E. *Enicospilus fullawayi*



F. *Agathophiona fulvicornis*

Fig. 1. A, C, E: metasomas of Hawaiian ophionine wasps. B, D, F: metasomas of non-Hawaiian ophionine wasps (A, B, C, D, F after Cushman1947).

Table 1. Distributions of Hawaiian Opioninae.	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii
Pycnophion fuscipennis Perkins, 1910	X	X			X	
Pycnophion kauaiensis Ashmead, 1901	X					
Pycnophion molokaiensis Ashmead, 1900	X		X		X	
Banchogastra nigra Ashmead, 1900						X
Banchogastra vitreipennis Perkins, 1910	X*	X*			X	X*
Banchogastra species 1					X	
Abanchogastra hawaiiensis (Ashmead, 1901)		X			X	X
Enicospilus (*Enicospilus*) *bellator* Perkins, 1915		x	x			X
Enicospilus (*Enicospilus*) *castaneus* Ashmead, 1901		x	x	X	X	X
Enicospilus (*Enicospilus*) *dispilus* Perkins, 1902	X	X	x	X	X	x
Enicospilus (*Enicospilus*) *funereus* Perkins, 1915					x	
Enicospilus (*Enicospilus*) *kaalae* Ashmead, 1901	X	X	X		X	
Enicospilus (*Enicospilus*) *lineatus* (Cameron, 1883)	X	X	X	x	X	X
Enicospilus (*Enicospilus*) *longicornis* Ashmead, 1901	X	X			X	X
Enicospilus (*Enicospilus*) *melanochromus* Perkins, 1915	X	X			x	
Enicospilus (*Enicospilus*) *molokaiensis Ashmead, 1901*	X	X	X	x	X	X
Enicospilus (*Enicospilus*) *nigrolineatus Ashmead, 1901*	X	X	X	X	X	X
Enicospilus (*Enicospilus*) *pseudonymus* Perkins, 1915					X	
Enicospilus (*Enicospilus*) *tyrannus* Perkins, 1910			x			x
Enicospilus (*Enicospilus*) *variegatus* Ashmead, 1901						X
Enicospilus (*Enicospilus*) *waimeae* Ashmead, 1901	X					x
Enicospilus (*Eremotyloides*) *fullawayi* Cushman, 1944	X	X				
Enicospilus (*Eremotyloides*) *orbitalis* (Ashmead, 1901)	X	X	x		X	X
Enicospilus (*Eremotyloides*) *perkinsi* Cushman, 1944	X					
Enicospilus (*Pleuroneurophion*) *ferrugineus* (Perkins, 1915)					X	
Enicospilus (*Pleuroneurophion*) *hawaiiensis* (Ashmead, 1900)						X
Enicospilus species 1 undescribed			X			
Enicospilus species 2 undescribed						X
Enicospilus species 3 undescribed	X					
Enicospilus species 4 undescribed	X					
Enicospilus species 5 undescribed					X	X
Total 31	17	14	11	5	18	17

lower case "x" denotes distribution records not verified with specimens examined by the author.

* somewhat questionable because this record is from a male specimen and I am not fully confident that male *B. nigra* can as of yet be adequately distinguished from male *B. vitreipennis*.

Pycnophion Ashmead (three species), *Banchogastra* Ashmead (three species), and *Abanchogastra* Perkins (one species). The latter three are strictly Hawaiian and were said to be "allied to" and "almost certainly derived within" *Enicospilus* by Cushman (1947) and Gauld (1985), respectively. Despite this, both authors preferred classifications that retain their generic status. The subgenus rank has generally not been used in the classification of *Enicospilus* at large, but Cushman (1944, 1947) recognized two species of *Pleuroneurophion* Ashmead and three of *Eremotyloides* Perkins as Hawaiian subgenera of *Enicospilus*. He placed the remaining members of Hawaiian *Enicospilus* in the nominal subgenus, *Enicospilus*.

1.2 Taxonomic History

As is the case for many Hawaiian insects, the first specimens of ophionine ichneumonid wasps were collected in Hawaii in the late 1800's by the minister and naturalist Thomas Blackburn. He lived on the islands from 1877–1883 and in this time sent many insects to specialists in London including four ophionine wasps to Cameron who described them as male-female pairs of two species of the genus *Ophion* Fabricius, namely *O. nigricans and O. lineatus* (Cameron 1883). In 1900, Ashmead listed the new Hawaiian genera *Pycnophion* and *Banchogastra* in a key and in 1901 described these and a number of species. He placed one of these species in the Nearctic and Neotropical genus *Athyreodon* Ashmead (junior synonym of *Thyreodon* Brullé) and assigned to it the specific epithet *hawaiiensis*. This species was again described by Perkins (1902) as the new genus and species *Abanchogastra debilis*. Thus, the senior specific epitaph for this species dates to Ashmead (1901) but the genus *Abanchogastra* dates to Perkins (1902).

Ashmead's misidentifications and treatment of conspecific individuals was considered "extraordinary" by Perkins (1915). To his credit Perkins sorted out his actions and communicated them in 1915. In this work Perkins treated all of the known Hawaiian ophionines, and recognized as new six species and one genus (*Eremotyloides*). He also presented a key, checklist with synonyms, bibliography and described many important characters for distinguishing taxa.

After Perkins' revision, a few references to Hawaiian Ophioninae appeared mainly as published notes taken during meetings of the Hawaiian Entomological Society, but nothing taxonomic appeared until Cushman (1944) treated the Hawaiian *Enicospilus* and *Abanchogastra*. In this work he presented a very usable key, a checklist, described additional taxa, and made comments related to phylogeny. Mysteriously, he makes no mention of the Hawaiian genera *Pycnophion* or *Banchogastra*, despite presumably having access to these within the National Museum where he worked. Cushman relegated *Eremotyloides* and *Pleuroneurophion* to subgenera of *Enicospilus* and synonymized a number of nominal taxa under *E. lineatus*. Since Cushman's treatment, no additional Hawaiian Ophioninae have been described; however the generic classification has oscillated among the opinions of several authors. Townes (1945), synonymized all Hawaiian genera with *Enicospilus* in his catalogue of Nearctic Ichneumonidae. In 1947 Cushman still recognized *Pycnophion* and *Banchogastra* as genera but not *Abanchogastra* in his generic revision of the Ophionini. In this work Cushman presented the first detailed generic descriptions for *Pycnophion* and *Banchogastra*. Townes, Townes, and Gupta (1961) took the same position as Townes 1945 but later Townes (1971) elevated *Banchogastra* and *Pycnophion* to genus status. Gauld's phylogenetic analysis and classification of the genera of Ophioninae (1985) continued to recognize these taxa as well as *Abanchogastra* at the generic rank, an arrangement upheld in the Catalogue of World Ichneumonidae by Yu and Horstmann (1997). The only author to provide justification for these actions was Gauld, who argued that the impractical consequences of synonymizing the Hawaiian genera with *Enicospilus* were sufficient to maintain a paraphyletic *Enicospilus*.

1.3 Phylogenetics

The monophyly of the Hawaiian Ophioninae has not been demonstrated, yet has been suspected on the basis of their similarity (Gauld personal communication). Furthermore, Cushman (1944) described them as "a very distinct group within the genus" and went on to cite "a peculiarly fine, mat sculpture" shared among species. This stands as the only previously cited character evidence that would strengthen suspicions of monophyly by these authors.

The endemic Hawaiian genera (i.e. *Pycnophion*, *Abanchogastra*, and *Banchogastra*) have been supported as a natural group. Gauld (1985) cited a lack of alar sclerites, possession of straight, rather slender Rs+2r, loss of the last third or so of the lateral scutellar carinae, and a centrally interrupted posterior mesosternal carina as evidence. He went on to discuss the possible relationships among these three taxa and found evidence for both *Abanchogastra* + (*Pycnophion* + *Banchogastra*) and *Banchogastra* + (*Pycnophion* + *Abanchogastra*) but not the third possible combination. Gauld also highlighted the similarities of an *Enicospilus* species from the Marquesas islands (*E. moea* Cheesman) to the Hawaiian genera and speculated that this, rather than any species of Hawaiian *Enicospilus*, may be the closest species to the clade of Hawaiian endemic genera.

As for the taxa presently recognized as subgenera of *Enicospilus* (*Eremotyloides* and *Pleuroneurophion*), no one has specifically argued for their monophyly per se, but these hypotheses can be presumed by the very nature of the characters that led to their recognition. *Eremotyloides* was erected to contain species with a greatly elongate metasoma and a short, up-curved ovipositor; *Pleuroneurophion* for species with long, straight ovipositors and 1m-cu with an angulate thickening (ramellus).

Cushman (1944) highlighted a few groups of species and the characters they share. He reported that *E. molokaiensis*, *E. melanochromus*, and *E. kaalae* have a large fenestra occupying nearly half the area and fully three-fourths the width of the apical portion of the discocubital (discosubmarginal) cell, with a small pyriform or oval proximal sclerite lying at the lower proximal angle, closer to the discocubitus (1m-cu), mostly or entirely proximad a line perpendicular to the costa (pterostigma) through the base of the radial (marginal) cell; the discocubitus (1m-cu) (except in *E. kaalae*) more or less thickened in the middle and sometimes angulate or subangulate, but without a ramellus; the second discoidal (second discal) cell with upper and lower margins subparallel for fully half its length; and the aedeagus with the apical, bulblike swelling not rising above the general dorsal margin. Cushman also noted that *E. castaneus*, *E. dispilus*, *E. bellator*, *E. lineatus*, *E. funereus*, and *E. waimae* share the following: fenestra rather small, about as broad as long and underlying much less than half length of basal abscissa of radius (Rs+2r), proximal sclerite quite variable in size and shape, and sometimes absent, but when present always distad a line perpendicular to costal (pterostigma) margin at base of radial (marginal) cell, rarely (*E. bellator*) fenestra reduced to a narrow area without a sclerite; aedeagus with apex very strongly swollen below and above. *Enicospilus castaneus*, *E. dispilus*, *E. bellator* share a transversely flat and very densely and coarsely punctate scutellum with unusually high carinae; unusually long malar space; second discoidal (second discal) cell long and narrow with its upper and lower margins parallel in about its apical third; male with apical tarsal segments strongly depressed and parallel-sided or even a little broader basad middle than at apex.

1.4 Present Study

The following analysis is the first to consider the entirety of the Hawaiian Ophioninae in a phylogenetic context, and the first numerical analysis. It is designed as a test of the monophyly of the group as a whole as well as that of the nominal Hawaiian genera

(*Pycnophion*, *Banchogastra*, and *Abanchogastra*), the subgenera of *Enicospilus* (*Pleuroneurophion*, *Eremotyloides*), and species-group concepts of Cushman (1944). The evolution of morphological oddities (e.g. various ovipositor lengths, stout body form, etc.) and zoogeography within the archipelago is considered and discussed with respect to hypotheses of phylogeny presented herein.

2. MATERIALS AND METHODS

2.1 Taxa Sampled and Material Examined

Characters of 29 of the 31 species of Hawaiian Ophioninae were coded. All known species of *Pycnophion*, *Banchogastra*, and *Abanchogastra* were coded as well as all Hawaiian *Enicospilus* with the exception of *E. funereus* Perkins and *E. tyrannus* Perkins (species sensu Cushman 1944). Additionally five undescribed Hawaiian species of *Enicospilus*, here referred to as *E.* species 1, *E.* species 2, *E.* species 3, *E.* species 4, and *E.* species 5, as well as one undescribed species of *Banchogastra* (*B.* species 1). Seventeen non-Hawaiian *Enicospilus* species were coded as outgroup taxa to test the puted monophyly of the entirety of the Hawaiian Ophioninae (Table 2). Selection of these outgroup taxa was largely limited to those taxa in the Snow Entomological Collection of the University of Kansas as well as an assortment of species from the California Academy of Sciences and the Canadian National Collection. Given the extreme diversity of these wasps in the Indo-Pacific, particularly New Guinea, and given that many other Hawaiian insect taxa appear to have colonized Hawaii from the West, including the two other Hawaiian ichneumonid radiations (the genus *Spolas* is known from Hawaii and New Zealand and *Ecthromorpha* occurs in the Ethiopian, Oriental, and Australian regions), a bias towards species occurring in these regions was employed in the selection of outgroup taxa. *Leptophion*, a genus of the same genus-group as *Enicospilus* (Gauld 1985), was coded to serve as the root, and *Dicamptus*, a genus considered even closer to *Enicospilus* (Gauld 1985) was also coded from a generic description (Gauld 1985).

Material for study was acquired from the following institutions: The Natural History Museum, London, England; American Entomological Institute, Gainesville, Florida, U.S.A.; Canadian National Collection, Ottawa Canada; California Academy of Sciences, San Francisco, California, U.S.A.; U.S. National Museum of Natural History, Washington D.C., U.S.A.; Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.; and the Snow Entomological

Table 2. Outgroup taxa.	Locality	Repository	Specimen Identifier
Enicospilus outgroup species 1	New Guinea	CAS	DJB-03-SN-455
Enicospilus outgroup species 2	West Sumatra	CAS	DJB-03-SN-456
Enicospilus melanocarpus Cameron	Malaysia	CAS	DJB-03-SN-457
Enicospilus outgroup species 4	Papua New Guinea	CAS	DJB-03-SN-473; 474; 475
Enicospilus outgroup species 5	Papua New Guinea	CNC	DJB-03-SN-479
Enicospilus outgroup species 6	Papua New Guinea	CNC	DJB-03-SN-460; 480
Enicospilus outgroup species 7	Borneo	CNC	DJB-03-SN-461
Enicospilus outgroup species 8	Malaysia	CAS	DJB-03-SN-462
Enicospilus pseudantennatus Gauld & Mitchell	Australia	CNC	DJB-03-SN-451
Enicospilus outgroup species 10	Papua New Guinea	CNC	DJB-03-SN-464
Enicospilus outgroup species 11	Papua New Guinea	CAS; CNC	DJB-03-SN-458; 459; 465; 476; 477; 478
Enicospilus outgroup species 12	New Guinea	CNC	DJB-03-SN-466
Enicospilus insularis (Kirby)	Australia; New Zealand	CNC	DJB-03-SN-467; 463
Enicospilus purgatus (Say)	U.S.A. (Kansas)	KU	DJB-03-SN-469; 488; 489; 490
Enicospilus outgroup species 15	Papua New Guinea	CNC	DJB-03-SN-481; 482
Enicospilus flavoscutellatus (Brullé)	Costa Rica	KU	DJB-03-SN-483; 487; 491
Enicospilus moea Cheesman			
Leptophion sp.	Australia	KU	DJB-03-SN-525
Dicamptus spp.*			

* coded from generic description (Gauld, 1985).

Collection, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, U.S.A.

2.2 Terminology

Morphological terminology generally follows that of Gauld and Mitchell (1978, 1981) and Gauld (1988). Terminology for integument sculpture follows Harris (1979). Tergal numbers are in reference to the metasoma.

2.3 Characters and Character States

All characters used in this study are derived from adult morphology. Most are externally visible in dry pinned insects but several are only visible upon dissection of apical metasomal segments. The species descriptions and keys presented by Perkins (1915) and Cushman (1944, 1947) offered many morphological characters that were found to be phylogenetically useful. Additionally, many characters used by Gauld (1985) in his generic analysis of the subfamily were found to vary within the ingroup and were thus used in this analysis. Characters that showed discrete variation were preferred. When characters showing continuous variation were employed, coding was performed by establishing one state encompassing the range of variation found in the outgroups and additional states were established for variation outside of that range. Characters were coded as "-" when they were not applicable to a species (e.g. when absent).

1. Compound eyes:

(0) strongly rounded outwardly.
(1) weakly convex and less rounded outwardly.
(2) much reduced.

2. Occipital carina dorsally:
(0) complete.
(1) absent dorsally.

3. Diagonal groove and pubescence on mandible:
(0) with groove running diagonally on mandible from basal area (near anterior condyle) to between teeth, and accompanied by a line of pubescence originating from groove.

(1) without such groove and pubescence.

4. Basal width of mandibular teeth:
(0) upper tooth clearly widest.
(1) about the same width.
(2) lower tooth clearly widest.

5. Relative lengths of mandibular teeth:
(0) virtually equally in length.
(1) upper clearly longer than lower.
(2) upper tooth reduced.

6. Taper of mandible:
(0) weakly tapered so that apex (distance measured between teeth apices) is more than half as broad as base.
(1) mandible more strongly tapered such that apex is 0.30–0.50 times as wide as base.
(2) the apex less than 0.30 times as wide as base.

7. Torsion of mandibles:
(0) mandible untwisted, i.e. mandible base and teeth in same plane.
(1) upper tooth rotated posteriorly from 5–50°, such that the upper tooth is positioned posterior to lower tooth to some degree in frontal aspect.
(2) mandible twisted more than 50°.

8. Malar space of male:
(0) nearly half (0.35–0.60) as long as basal width of mandible.
(1) distinctly less than half (<0.35) as long as basal width of mandible.
(2) distinctly longer (>0.60) than half basal breadth of mandible.

9. Malar space of female:
(0) nearly half (0.35–0.60) as long as basal width of mandible.
(1) distinctly less than half (<0.35) as long as basal width of mandible.
(2) distinctly longer (>0.60) than half the basal breadth of mandible.

10. Ocelli:

(0) large, the rims of the outer ones almost touching compound eyes or with only small space between margin of compound eye and lateral ocellus.
(1) reduced, space between compound eye and lateral ocellus at about 0.25 diameter of ocellus.
(2) strongly reduced, space between compound eye and lateral ocellus at greater than 0.50 diameter of ocellus.

11. Flagellum segment number in female:
(0) greater than 52 segments.
(1) less than 52 segments.

12. Flagellum segment number in male:
(0) greater than 53 segments.
(1) less than 53 segments.

13. Micro-sculpture of hind coxa:
(0) without indication of minute, imbricate network of semi-homogeneous angulate (approximately hexagonal) cells.
(1) with minute, imbricate network of fine, scratch-like semi-homogeneous angulate (approximately hexagonal) cells. They appear flat, both in highlighted and shaded areas of coxae and do not effect the surface of the integument in terms of light reflection (appearing glossy) or elevation.
(2) with minute, imbricate network of semi-homogeneous angulate (approximately hexagonal) cells that are not flat but weakly to somewhat strongly colliculate (in areas of highlights may appear flat or scale-like, but in shaded parts each cell can be seen to be slightly raised medially).

These micro-sculpture characteristics can usually be seen in many places on the integument but is often most conspicuous on the hind coxae. State two effects the overall appearance of light reflection. Instead of appearing glossy, the integument appears somewhat dull and mat. Each cell reflects light at the center of the raised area and is shadowed in the depressed areas between cells resulting in many pinpoint highlights rather than continuously glossy areas.

14. Secondary sculpture on hind coxae (sculpture overlying that described in character 13):

(0) no sculpture, or extremely weak localized sculpture, on areas other than dorsal area nearest trochanter.
(1) overlying micro-sculpture, consisting of rugulose, rugose, or foveolate areas broadly in areas other than dorsal area nearest trochanter.

15. Epicnemial carina:
(0) complete, extending from ventral midline to middle anterior of mesopleuron.
(1) absent ventrally near midline.

16. Scutellar carinae:
(0) absent.
(1) short, reaching to or not quite to center of scutellum.
(2) nearly complete, reaching 0.8 or more of length of the scutellum.

17. Dorsal surface of scutellum:
(0) convex.
(1) more or less flat.

18. Scutellar sculpture:
(0) granulate and smooth with scattered punctures or pits.
(1) densely pitted and/or rugose.

19. Propodeal sculpture posteriorly:
(0) extremely heavily carinate or areolate.
(1) lightly rugulose or coriaceous.

20. Metapleura:
(0) moderately convex.
(1) strongly convex.

21. Anterior transverse carina of propodeum in female:
(0) present.
(1) absent, only apparent medially, or otherwise vestigial.

22. Anterior transverse carina of the propodeum in male:

(0) present.

(1) absent, only apparent medially, or otherwise vestigial.

23. Longitudinal propodeal impression:

(0) absent, dorsum of propodeum convex or more or less flat.

(1) medial longitudinal shallow depression apparent.

24. Separation between propodeum and metapleuron:

(0) with carina, complete or present in part, either anteriorly or posteriorly.

(1) without carina (furrow may be present).

25. Posterior transverse carina of the mesosternum:

(0) complete.

(1) absent, weak or evanescent medially.

26. Position of 1m-cu in relation to Cu1b in forewing (Gauld's cubital index):

(0) widely separated, by at least 0.29 the length of Cu1b

(1) separated by about 0.50 times the length of Cu1b.

(2) separated by less than 0.29 the distance of 1 Cu1b.

27. 1m-cu in forewing (variable 1):

(0) without medial thickening.

(1) with slight medial thickening.

(2) with ramellus (vein stub or very strong medial thickening).

28. 1m-cu in forewing (variable 2):

(0) not strongly arched medially, obtuse angle formed by imaginary lines connecting proximal most point of 1m-cu, the anterior most point along 1m-cu (near midpoint) and point most distal is greater than 129°.

(1) strongly arched medially, obtuse angle formed by imaginary lines connecting proximal most point of 1m-cu, anterior most point along 1m-cu (near midpoint) and point most distal is less 130°.

29. Base of Rs+2r in forewing:

(0) emerges from pterostigma at an angle about the same as angle of the main shaft of Rs+2r.

(1) emerges from pterostigma at an angle slightly greater than main direction of Rs+2r.

(2) emerges from pterostigma at a much steeper angle then main direction of Rs+2r, such that an imaginary line projected by the base of Rs+2r crosses the abscissa of M between 2m-cu and 3rs-m in its posterior half.

30. Rs+2r in forewing:

(0) nearly straight with slight medial convexity or slightly sinuous.

(1) perfectly straight.

(2) strongly convex or sinuous medially.

31. Taper of Rs+2r in forewing:

(0) thickest medially.

(1) tapered from thick basally to thin distally.

(2) slender throughout.

32. Pterostigma:

(0) broad and triangular.

(1) long, not abruptly narrowed proximally, but narrowed rather abruptly distally.

(2) long, slender and evenly tapered.

33. Pubescence of discosubmarginal cell centrally (excluding fenestra):

(0) rather densely and uniformly hirsute.

(1) clearly less dense, especially centrally.

34. Fenestra in discosubmarginal cell (well defined glabrous area):

(0) present.

(1) absent or vestigial.

35. Fenestra length (not applied to vestigial fenestra):

(0) long, reaching clearly beyond half the length of Rs+2r.

(1) not long, reaching to about the midpoint of Rs+2r (in most species just past end of thickened portion of vein).

(2) reduced, extending to clearly less than half the distance of Rs+2r.

36. Fenestra width:
(0) very wide, extending close to 1m-cu.
(1) not reaching to near 1m-cu.

37. Proximal alar sclerite (variable 1):
(0) present.
(1) absent.

38. Proximal alar sclerite (variable 2):
(0) positioned closer to Rs+2r than 1m-cu.
(1) positioned closer to 1m-cu than Rs+2r.

39. Proximal alar sclerite (variable 3):
(0) positioned distad of an imaginary line drawn perpendicular through pterostigma through base of marginal cell.
(1) positioned basad of an imaginary line drawn perpendicular through pterostigma through base of marginal cell.

40. Central alar sclerite:
(0) present.
(1) absent.

41. Distal alar sclerite:
(0) present.
(1) absent.

42. Length of 3rs-m/length of abscissa of M between 2m-cu and 3rs-m in forewing:
(0) greater than 0.35.
(1) less than 0.35.

43. Position of cu-a in forewing:
(0) distinctly proximal to the base of Rs&M (abscissa of M+Cu between cu-a and Rs&M/cu-a greater than 0.40).
(1) near base of Rs&M or anterior of it.

44. Position of distal abscissa of Cu1 in hindwing:

(0) well posterior of midpoint between M and 1A (at least 2/3 the distance).
(1) near midpoint point between veins M and 1A.

45. Hind apical tarsus in male:
(0) broadening toward apex and not strongly arched.
(1) strongly arched and parallel sided (or even slightly broader basad of middle).

46. Shape of hind pretarsal claw in male:
(0) long axis of claw and axis of apical tooth angled at about 90 degrees to one another or somewhat short and evenly curved (view outside surface).
(1) long and with long axis of claw and axis of apical tooth clearly angled greater than 90 degrees to one another (view outside surface).

47. Spines of fore tibia:
(0) multiple scattered spines clearly apparent on outer surface.
(1) spines absent or clearly reduced (isolated and weak).

48. Thyridia of tergum II:
(0) displaced posteriorly, leaving a scar between itself and the tergal margin.
(1) close to the anterior margin of the tergum.

49. Female tergum III:
(0) 1.2–2 times longer than maximum width.
(1) length less than maximum width.
(2) at least 2.5 times longer than width.

50. Female tergum IV:
(0) 1–1.3 times longer than wide.
(1) wider than long.
(2) greater than 1.3 times longer than wide.

51. Female tergum V:
(0) less than 1.2 times longer than wide.
(1) greater than 1.5 times longer than wide.

52. Female tergum VI:
(0) wider than long.
(1) longer than wide.

53. Female tergum VII (variable 1):
(0) generally square shaped or rectangular, width not more than twice length (measured at postero-ventral angle).
(1) much wider (more than 2x) than long.
(2) much elongate.

54. Female tergum VII (variable 2):
(0) midpoint of dorsum (lengthwise) about the same as midpoint of ventral margin.
(1) ventral anterior margin projected well anterior of dorsal anterior dorsal margin.

55. Female tergum VII (variable 3):
(0) dorsum of tergum continuous throughout length.
(1) dorsum of tergum invaginated anteriorly such that hemitergites are only narrowly attached.

56. Female sternum VII:
(0) rectangular and not projecting beyond apex of metasoma or produced ventrally.
(1) enlarged, at rest extending beyond apex of metasoma and/or produced strongly ventrally.

57. Tergum III in female:
(0) laterally compressed throughout.
(1) anterior portion not laterally compressed, posterior part laterally compressed.
(2) not laterally compressed.

58. Position of spiracles of tergum II:
(0) behind midpoint.
(1) at or before midpoint.

59. Ovipositor length:
(0) short (less than half length of metasoma).

(1) long, lengthened distal of swelling.
(2) long, lengthened basal of swelling.

60. Ovipositor shape:
(0) straight.
(1) up-curved.
(2) down-curved.

61. Aedeagus (variable 1):
(0) short and stout.
(1) slender.
See figures in Cushman (1944).

62. Aedeagus (variable 2):
(0) more or less straight.
(1) clearly curved anteriorly.

63. Parameres:
(0) not symmetrical above and below, dorsal apex pointed, ventral apex rounded, dorsal surface from flat to concave.
(1) symmetrical above and below, rounded evenly apically or somewhat pointed (but not at a dorsal apex).

64. Color:
(0) largely yellow or yellow with dark (more or less black) areas.
(1) generally orange to deep red that often grades into brown or black in some areas.

2.4 Analysis

A parsimony analysis of 64 adult morphological characters was performed on taxa selected as outlined above. The data matrix (Table 3) was created using Winclada (Nixon 1999) and heuristic searches for parsimonious trees as well as Bootstrap and Jackknife tree searches were performed with Nona (Goloboff 1993). The heuristic search parameters consisted of 1000 replications. Search strategy was set to "Multiple TBR + TBR (mult*max*)"

Table 3. Character state matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Pycnophion molokaiensis	0	0	0	0,1	0	1	1	?	0	1	1	?	2	0
Pycnophion kauaiensis	0	0	0	0,1	0,1	2	1	2	2	2	1	?	2	0
Pycnophion fuscipennis	0	0	0	1	0	1	1	?	1	1	1	?	2	0
Banchogastra nigra	2	0	1	1	1	1	1	-	-	2	1	?	2	0
Banchogastra vitreipennis	2	0	1	0,1	1	1	1	-	-	2	1	?	2	0
Banchogastra species 1	2	0	1	1	1	2	1	-	-	2	?	1	2	0
Abanchogastra hawaiiensis	0	1	0	1	0,1	2	2	1	1	0	1	1	2	0
Enicospilus bellator	0	0	0	1	0	1	1	0	0	0	0	0	2	1
Enicospilus castaneus	1	0	0	1	0	1	1	0	0	0	1	0	2	1
Enicospilus dispilus	1	0	0	1	1	1	1	1	0	0	0,1	0	2	1
Enicospilus lineatus	0	0	0,1	1	1	1	1	1	1	0	0,1	0	2	0
Enicospilus species 1	0	0	1	1	1	1	1	?	0	0	0	?	1	0
Enicospilus waimeae	0	0	1	1	1	2	1	?	1	0	0	?	2	0
Enicospilus pseudonymus	0	0	0	2	2	1	1	0	?	0	?	0	2	1
Enicospilus kaalae	0	0	0	1	0	1	1	1	1	0	1	0	2	1
Enicospilus melanochromus	0	0	0	1	0	1	1	1	?	0	?	0	2	0
Enicospilus molokaiensis	0	0	0	1	1	1	1	1	0	0	1	0,1	2	0
Enicospilus longicornis	0	0	1	1	1	1	1	1	1	0	1	0	2	0
Enicospilus nigrolineatus	0	0	0	1	1	1	1	1	0	0	0	0	2	0
Enicospilus variegatus	0	0	0	1	1	1	1	0	0	0	0	0	1	0
Enicospilus species 2	0	0	0	1	1	2	1	?	0	0	0	?	2	0
Enicospilus ferrugineous	0	0	0	1	1	2	1	?	1	0	?	?	2	0
Enicospilus hawaiiensis	0	0	0	1	1	1	1	0	1	0	1	1	2	0
Enicospilus species 3	0	0	0	1	1	1	1	1	1	0	1	1	2	0
Enicospilus species 4	0	0	0	0	1	2	1	1	1	0	1	0	2	0
Enicospilus fullawayi	0	0	0	1	0	1	1	1	1	0	1	1	2	0
Enicospilus orbitalis	0	0	0	1	0	1	1	1	1	0	1	0,1	2	0
Enicospilus perkinsi	0	0	0	1	0	1	1	1	1	0	1	?	2	0
Enicospilus species 5	0	0	0	0	0	1	1	?	0	1,2	1	?	2	0
Enicospilus pseudantennatus	0	0	0	2	?	1	1	?	0	0	0	0	1	0
Enicospilus outgroup species 1	0	0	0	1	1	1	1	?	1	0	0	?	1	0
Enicospilus outgroup species 2	0	0	0	2	1	1	1	?	0	0	0	?	1	0
Enicospilus melanocarpus	0	0	1	2	1	1	1	?	0	0	0	0	1	0
Enicospilus outgroup species 4	0	0	0	1	0	1	1	0	1	0	0	0	1	0
Enicospilus outgroup species 5	0	0	0	1	1	1	1	?	1	0	0	?	1	0
Enicospilus outgroup species 6	0	0	0	1	1	2	1	1	1	0	0	0	1	0
Enicospilus outgroup species 7	0	0	0	1	1	2	1	1	?	0	?	0	1	0
Enicospilus outgroup species 8	0	0	0	0	1	1	1	?	1	0	0	?	0	0
Enicospilus insularis	1	0	1	0	1	1	0	?	1	0	0	0	1	0
Enicospilus outgroup species 10	0	0	0	1	1	1	1	?	0	0	0	?	1	0
Enicospilus outgroup species 11	0	0	0	1	1	1	1	1	1	0	0	0	1	0
Enicospilus outgroup species 12	0	0	0	1	0	1	1	?	1	0	0	?	1	0
Enicospilus purgatus	0	0	0	1	1	1	1	0	0	0	0	0	1	0
Enicospilus flavoscutellatus	0	0	0	1	1	1	1	1	0	0	0	0	1	0
Enicospilus moea	0	0	0	2	1	1	1	?	1	0	0	?	1	0
Enicospilus outgroup species 15	0	0	0	1	1	1	2	1	1	0	0	?	0	0
Leptophion sp.	0	0	0,1	1	0	0	0	?	1	0	0	0	0	0
Dicamptus spp.	?	0	0,1	1	0	0	0	?	?	0	0	0	?	?

Table 3. Character state matrix (continued).

	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Pycnophion molokaiensis	1	0	1	0	1	1	0	?	0	0	1	1	0	0
Pycnophion kauaiensis	?	0	0,1	0	1	1	1	1	0	0	1	0	0	0
Pycnophion fuscipennis	1	0	0	0	1	1	1	?	0	0	1	1	0	0
Banchogastra nigra	1	0	1	0	1	0	0	?	0	1	1	1	0	0
Banchogastra vitreipennis	0,1	0	1	0	1	0	0	0	0	0	0	0,1	0	0
Banchogastra species 1	1	0	1	0	1	0	?	0	0	1	0	1	0	0
Abanchogastra hawaiiensis	0	0	0	0	1	0	1	0	0,1	1	1	0,1	0	0
Enicospilus bellator	0	1	0	1	1	0	1	1	0	1	0	0	0	0
Enicospilus castaneus	0	1	0	1	1	0	0	1	0	1	0	0	0	0
Enicospilus dispilus	0	1	0	1	1	0	0	0	0	1	0	0,1	0	0
Enicospilus lineatus	0	0	0	0	1	0	1	0,1	1	0	0	0	0	0
Enicospilus species 1	0	0	0	1	1	0	0	?	0	0	0	0	0	0
Enicospilus waimeae	0	0	0	1	1	0	0	?	0	1	0	0	0	1
Enicospilus pseudonymus	0	0	0,1	1	1	0	?	1	0	1	1	0	0	0
Enicospilus kaalae	0	0	0	1	1	0	0	1	0	0	0	0	0	0
Enicospilus melanochromus	0	0	0	1	1	0	?	1	0	1	1	0	1	0
Enicospilus molokaiensis	0	0	0	1	1	0	0	1	0	0,1	0	0	1	0
Enicospilus longicornis	0	0,2	1	0	1	0	0,1	1	0	1	0	0	0	0
Enicospilus nigrolineatus	0	0	0	1	1	0	0	0	0	1	0	0	0	0
Enicospilus variegatus	0	0,2	0	1	1	0	0,1	1	0	1	0	0	0	0
Enicospilus species 2	0	0	0	1	1	0	0	?	0	0	0	0	0	0
Enicospilus ferrugineous	0	0	0	0	1	0	1	?	0	1	0	0	2	1
Enicospilus hawaiiensis	0	0	0	0	1	0	1	1	0	0	0	0	2	1
Enicospilus species 3	0	0	0	0	1	0	1	1	0	0	0	0	2	1
Enicospilus species 4	1	2	0	0	1	0	1	1	0	1	0	0	0	1
Enicospilus fullawayi	0	0	0	0	1	0	1	1	1	1	0	0	0	0
Enicospilus orbitalis	0	0,1	0	0	1	0	1	1	1	1	0	0	0	1
Enicospilus perkinsi	0,1	0	0	0	1	1	1	1	0,1	0	0,1	0	0	1
Enicospilus species 5	1	2	0	0	1	0	1	?	0	0	1	0	0	1
Enicospilus pseudantennatus	0	0	0	0	1	0	0	?	0	0	0	0	0	0
Enicospilus outgroup species 1	?	1	0	0	0	0	0	?	0	0	0	0	0	0
Enicospilus outgroup species 2	0	1	0	0	0	0	0	?	0	0	0	0	0	0
Enicospilus melanocarpus	0	1	0	0	0	0	0	?	0	0	0	0	0	0
Enicospilus outgroup species 4	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 5	0	0	0	?	0	0	0	?	1	0	0	0	0	0
Enicospilus outgroup species 6	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Enicospilus outgroup species 7	0	1	0	1	0	0	?	0	0	0	0	0	0	0
Enicospilus outgroup species 8	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Enicospilus insularis	0	0	0	1	1	0	0	?	0	0	0,1	0	0	0
Enicospilus outgroup species 10	0	1	0	0	1	0	0	?	0	0	0	0	0	0
Enicospilus outgroup species 11	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 12	0	0	0	0	1	0	0	?	0	0	0	0	0	0
Enicospilus purgatus	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Enicospilus flavoscutellatus	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Enicospilus moea	1	0	0	1	1	1	0	?	0	0	1	0	0	0
Enicospilus outgroup species 15	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Leptophion sp.	0	0	0	0	1	0	0,1	?	0	0	1	1	0	1
Dicamptus spp.	0	0	0	?	0	?	0	0	?	?	0	0,1	0	?

Table 3. Character state matrix (continued).

	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Pycnophion molokaiensis	0	1	2	2	1	1	-	-	1	-	-	1	1	0
Pycnophion kauaiensis	0	1	2	1	1	1	-	-	1	-	-	1	1	0
Pycnophion fuscipennis	0	1	2	2	1	1	-	-	1	-	-	1	1	0
Banchogastra nigra	0	1	2	1	0	1	-	-	1	-	-	1	1	0
Banchogastra vitreipennis	0	1	2	2	0	1	-	-	1	-	-	1	1	0
Banchogastra species 1	0	1	2	1	0	1	-	-	1	-	-	1	1	0
Abanchogastra hawaiiensis	1	1	2	0	0	1	-	-	1	-	-	1	1	0
Enicospilus bellator	0	0	1	1	0	0	1	1	1	-	-	1	1	0
Enicospilus castaneus	0	0	0	1	0	0	1	1	0	0	0	1	1	0
Enicospilus dispilus	0	0	0	1	0	0	1	1	0	0	0	0	1	0
Enicospilus lineatus	0	0	0	1	0	0	1	1	0	0	0	1	1	0
Enicospilus species 1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Enicospilus waimeae	1	0	0	1	0	0	1	1	0	0	0	1	1	0
Enicospilus pseudonymus	0	1	2	1	0	1	-	-	1	-	-	1	1	0
Enicospilus kaalae	0	0	0	1	0	0	1	0	0	1	1	1	1	0
Enicospilus melanochromus	0	0	1	1	0	0	0	0	0	1	1	1	1	0
Enicospilus molokaiensis	0	0	0	1	0	0	0	0	0	1	1	1	1	1
Enicospilus longicornis	1	0	0	1	0	0	1	1	0	0	0	0	1	0
Enicospilus nigrolineatus	0	0	0	1	0	0	0	1	0	0	0	1	0	0
Enicospilus variegatus	0	0	1	1	0	0	1	1	0	0	0	1	1	0
Enicospilus species 2	1	0	0	1	0	0	1	0	0	0	0	1	1	0
Enicospilus ferrugineous	2	1	0	1	0	0	2	1	1	0	0	1	1	0
Enicospilus hawaiiensis	2	0	0	1	0	0	2	1	1	-	-	1	1	0
Enicospilus species 3	2	0	0	1	0	0	1	1	?	?	?	?	0,1	0
Enicospilus species 4	1	0	1	1	0	0	1	1	1	-	-	1	1	0
Enicospilus fullawayi	0	3	0	1	0	0	0	0	0	1	0	1	1	1
Enicospilus orbitalis	1	0	1	1	0	0	2	1	1	-	-	1	1	1
Enicospilus perkinsi	0,1	0	0	1	0	0	2	1	0	0	0	1	1	0
Enicospilus species 5	0	2	0	0	0	0	0	1	0	0	0	1	0	1
Enicospilus pseudantennatus	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 1	2	2	0	2	0	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 2	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Enicospilus melanocarpus	2	0	0	2	0	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 4	2	1	0	2	0	0	0	0	0	0	0	1	0	0
Enicospilus outgroup species 5	1	0	1	2	0	0	1	0	0	0	0	1	1	0
Enicospilus outgroup species 6	2	0	0	2	0	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 7	0	0	1	2	0	0	0	0	0	0	0	?	?	0
Enicospilus outgroup species 8	2	1	0	1	0	0	0	0	0	0	0	0	?	0
Enicospilus insularis	0,1	0	0	1	0	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 10	1	0	0	1	0	0	0	0	0	0	0	0	1	0
Enicospilus outgroup species 11	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 12	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Enicospilus purgatus	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Enicospilus flavoscutellatus	1	0	0	2	0	0	0	0	0	0	0	0	0	0
Enicospilus moea	1	0	2	2	0	0	0	1	1	-	-	1	1	0
Enicospilus outgroup species 15	0	0	0	2	1	0	0	0	0	0	0	0	0	0
Leptophion sp.	1	1	1	1	0	0	1	1	1	-	-	1	1	0
Dicamptus spp.	0	0,2	1	1,2	?	0	?	?	0	?	?	?	?	0,1

Table 3. Character state matrix (continued).

	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Pycnophion molokaiensis	0	1	?	?	0	1	1	1	0	0	1	1	0	0
Pycnophion kauaiensis	0	1	0	0	0	1	1	1	0	0	1	1	0	0
Pycnophion fuscipennis	0	1	?	?	0	0	0	1	0	0	1	1	0	0
Banchogastra nigra	0	1	?	?	0	1	1	1	0	0	?	?	?	0
Banchogastra vitreipennis	0	1	0	0	0	1	1	1	0	0	?	?	?	0
Banchogastra species 1	1	1	0	0	0	1	1	1	0	0	?	?	?	?
Abanchogastra hawaiiensis	0	1	0	0	1	0	0	0	0	0	1	0	0	0
Enicospilus bellator	0	0	1	1	1	0	0	0	0	0	?	0	?	0
Enicospilus castaneus	1	0	1	1	1	0	0	1	0	0	0	0	?	0
Enicospilus dispilus	0,1	0	1	1	1	0	0	1	0	0	0	0	0	0
Enicospilus lineatus	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Enicospilus species 1	1	0	?	?	0	0	0	0	0	0	?	0	0	0
Enicospilus waimeae	1	0	0	0	1	0	0	0	0	0	?	0	0	0
Enicospilus pseudonymus	1	0	0	1	1	0	0	0	0	0	?	?	?	?
Enicospilus kaalae	1	0	0	0	1	0	0	0	0	0	1	0	0	1
Enicospilus melanochromus	1	0	0	0	1	0	0	0	0	0	?	?	?	?
Enicospilus molokaiensis	1	0	0	0	1	0	0	0	0	0	1	0	0	1
Enicospilus longicornis	0,1	0	0	0	1	0	0	0	0	0	0	0	0	1
Enicospilus nigrolineatus	1	0,1	0	0	1	0	0	0	0	0	0	0	0	0
Enicospilus variegatus	1	0	1	1	1	0	0	0	0	0	?	0	?	0
Enicospilus species 2	1	0	?	?	1	0	0	0	0	0	?	0	?	0
Enicospilus ferrugineous	1	0	?	?	1	0	0	1	0	0	?	?	?	0
Enicospilus hawaiiensis	1	0	0	0	1	0	0	1	0	0	1	0	0	0
Enicospilus species 3	0,1	0	0	0	1	0	0	1	0	0	?	0	?	0
Enicospilus species 4	0,1	1	0	0	1	0	0	0	0	0	0	0	0	0
Enicospilus fullawayi	1	0	0	0	1	0	2	2	1	1	?	0	?	1
Enicospilus orbitalis	1	0	0	0	1	0	2	2	1	1	0	0	1	1
Enicospilus perkinsi	1	0	0	0	0	0	0	2	0	0	?	0	1	0
Enicospilus species 5	1	0	?	?	1	0	2	2	1	1	2	0	0	0
Enicospilus pseudantennatus	1	0	?	?	0	0	0	0	0	0	?	?	?	0
Enicospilus outgroup species 1	1	0	?	?	0	0	0	0	0	0	?	?	?	0
Enicospilus outgroup species 2	1	0	?	?	0	0	0	0	0	0	?	?	?	0
Enicospilus melanocarpus	1	1	?	?	0	0	0	0	0	0	?	?	?	0
Enicospilus outgroup species 4	1	0	0	0	0	0	0	0	0	0	?	?	?	0
Enicospilus outgroup species 5	1	0	?	?	0	0	0	0	0	0	?	?	?	1
Enicospilus outgroup species 6	1	0	0	0	0	0	0	0	0	0	?	?	?	0
Enicospilus outgroup species 7	1	0	0	0	0	0	0	0	0	0	?	?	?	?
Enicospilus outgroup species 8	1	0	?	?	0	0	0	0	0	0	?	?	?	0
Enicospilus insularis	1	0	?	?	0	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 10	1	0	?	?	0	0	0	0	0	0	?	?	?	0
Enicospilus outgroup species 11	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Enicospilus outgroup species 12	1	0	?	?	0	0	0	0	0	0	?	?	?	0
Enicospilus purgatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Enicospilus flavoscutellatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Enicospilus moea	1	1	?	?	1	0	0	0	0	0	?	?	?	0
Enicospilus outgroup species 15	1	0	0	0	0	0	0	0	0	0	?	?	?	0
Leptophion sp.	1	0	0	0	0	0	0	2	0	0	?	?	?	?
Dicamptus spp.	0,1	0	0	0	?	0	?	0	?	?	?	?	?	?

Table 3. Character state matrix (continued).

	57	58	59	60	61	62	63	64
Pycnophion molokaiensis	1	1	?	1	?	?	?	2
Pycnophion kauaiensis	1	1	?	1	?	?	1	2
Pycnophion fuscipennis	0	0	1	0	?	?	?	1,2
Banchogastra nigra	1	1	0	0	1	?	?	2
Banchogastra vitreipennis	1	1	0	0	1	0,1	1	2
Banchogastra species 1	?	1	?	?	0	0	1	2
Abanchogastra hawaiiensis	0	0	0	0	1	0	1,0	1
Enicospilus bellator	0	0	0	0	0	0	0	1
Enicospilus castaneus	0	0	0	0	0	0	0	1
Enicospilus dispilus	0	0	0	0	0	0	0	1
Enicospilus lineatus	0	0	0	0	0	0	0	1
Enicospilus species 1	0	0	0	0	?	?	?	0
Enicospilus waimeae	0	0	0	0	?	?	?	1
Enicospilus pseudonymus	?	0	?	?	1	?	1	1
Enicospilus kaalae	0	0	0	0	1	1	0	1
Enicospilus melanochromus	?	0	?	?	1	1	0	1
Enicospilus molokaiensis	0	0	0	0	1	0	0	1
Enicospilus longicornis	0	0	0	2	1	1	0	1
Enicospilus nigrolineatus	0	0	0	0	0	0	0	0
Enicospilus variegatus	0	0	0	0	0	0	0	0
Enicospilus species 2	0	0	0	0	?	?	?	0
Enicospilus ferrugineous	0	0	2	0	?	?	?	1
Enicospilus hawaiiensis	0	0	2	0	1	1	0	1
Enicospilus species 3	0	0	2	0	?	?	0	1
Enicospilus species 4	0	0	0	?	1	1	0	1
Enicospilus fullawayi	0	0	0	1	?	?	0	1
Enicospilus orbitalis	0	0	0	1	1	?	0	1
Enicospilus perkinsi	0	0	0	1	1	1	0	1
Enicospilus species 5	0	0	0	0	?	?	?	0
Enicospilus pseudantennatus	0	0	0	0	?	?	?	1
Enicospilus outgroup species 1	0	0	0	0	?	?	?	1
Enicospilus outgroup species 2	0	0	0	0	?	?	?	1
Enicospilus melanocarpus	0	0	0	0	?	?	?	1
Enicospilus outgroup species 4	0	0	0	0	1	0	1	1
Enicospilus outgroup species 5	0	0	0	0	?	?	?	0
Enicospilus outgroup species 6	0	0	0	0	?	?	1	0
Enicospilus outgroup species 7	?	0	?	?	?	?	1	1
Enicospilus outgroup species 8	0	0	0	0	?	?	?	1
Enicospilus insularis	0	0	0	0	?	?	?	1
Enicospilus outgroup species 10	0	0	0	0	?	?	?	1
Enicospilus outgroup species 11	0	0	0	0	1	0	1	0
Enicospilus outgroup species 12	0	0	0	0	?	?	?	2
Enicospilus purgatus	0	0	0	0	?	?	0	0
Enicospilus flavoscutellatus	0	0	0	0	?	?	0	0
Enicospilus moea	0	0	0	0	?	?	?	2
Enicospilus outgroup species 15	0	0	0	0	?	?	1	0
Leptophion sp.	0	0	0	0	?	?	?	0
Dicamptus spp.	0	?	?	0	?	?	?	?

and “Unconstrained search.” Jackknife and Bootstrap tree searches were employed with 1000 replications, 1000 search reps (mult*N), and the “Don’t do max* (TBR)” option was selected. Characters were polarized within the context of the analysis rather than by *a priori* reference to outgroups.

3. RESULTS

The heuristic search found 696 equally parsimonious trees of length 270 steps. Figures 2–4 show the strict consensus of these trees under various optimizations. Bootstrap and jackknife support for many nodes in the consensus tree are not supported by values greater than 50% (Figs 5,6).

4. DISCUSSION AND CONCLUSIONS

4.1 Clades Recovered

With the exception of a single undescribed specimen (*E.* species 1), this dataset provides additional evidence for a single monophyletic clade of Hawaiian Ophioninae, supported at a minimum, by characters 13:2 and 47:1. Character 22:1 may also support this clade, though its absence from the tree shown in figure 2 (slow optimization) indicates that it is equally parsimonious to accept that this character supports a more inclusive node. Mat sculpture (specific characteristics of which are provided under the description of character 13:2) and reduced or absent fore tibial spines (47:1) can be considered unique (but not unreversed) among the taxa selected for this analysis.

Excluding the main cluster of outgroups, and inside of a single basal branch (*E.* species 2), a polytomy of four principal clades and five unplaced species is supported by at least the following characters: 11:1, 24:1, 29:0, 36:1, 64:1. Each of these four principal clades was recovered with substantial support in the Jackknife and Bootstrap trees (i.e. at least 50%), but not with the full complement of species recovered by the consensus tree in all cases.

One principal clade represents the subgenus *Pleuroneurophion*, but in this analysis, an undescribed species (*E.* species 3) is included as a basal member. This group is supported by a number of characters, the most convincing of which are 27:2 (the presence of a stub-like vein, or ramellus, on 1m-cu in the forewing) and 59:2 (a long ovipositor).

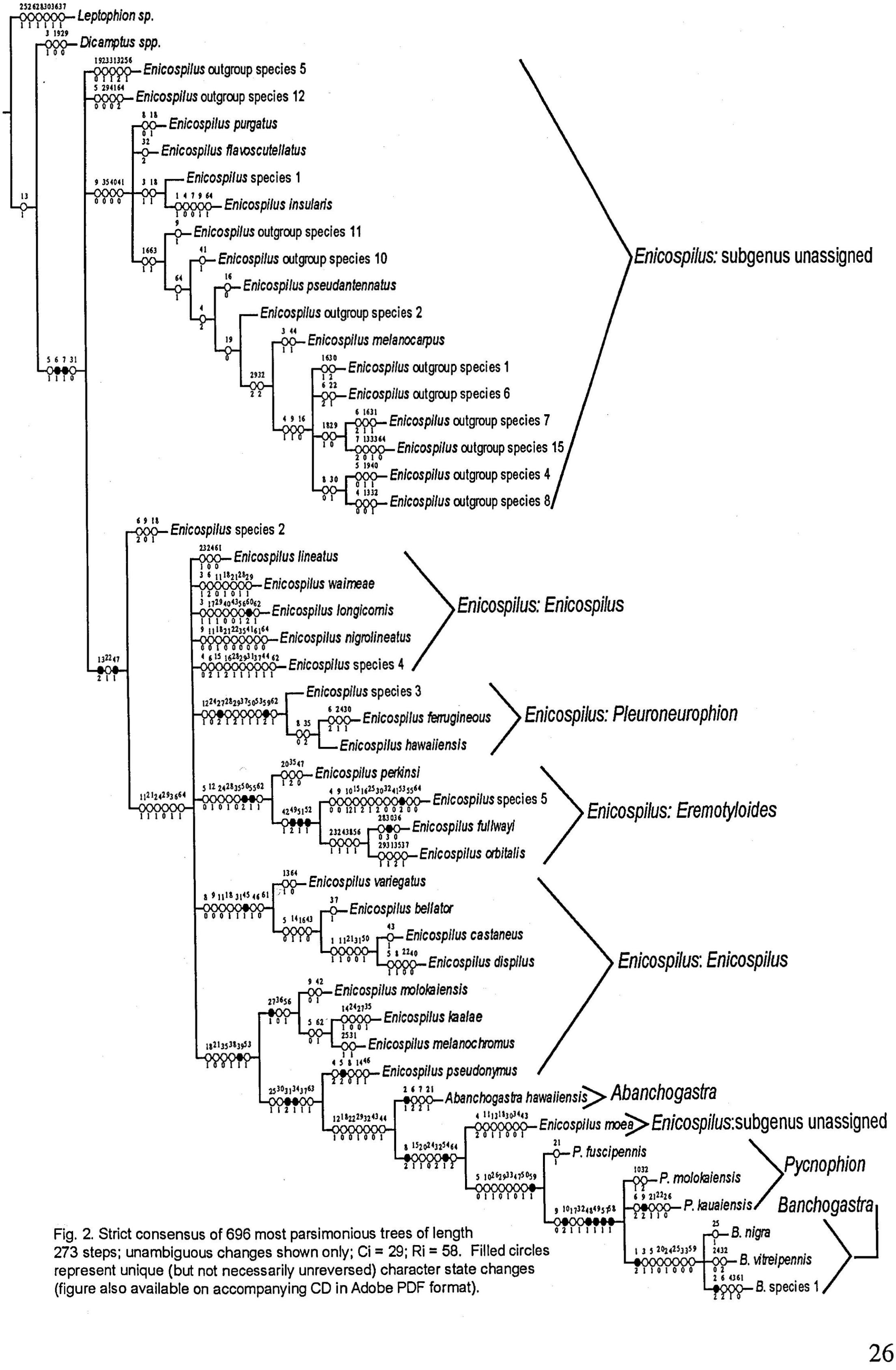


Fig. 2. Strict consensus of 696 most parsimonious trees of length 273 steps; unambiguous changes shown only; Ci = 29; Ri = 58. Filled circles represent unique (but not necessarily unreversed) character state changes (figure also available on accompanying CD in Adobe PDF format).

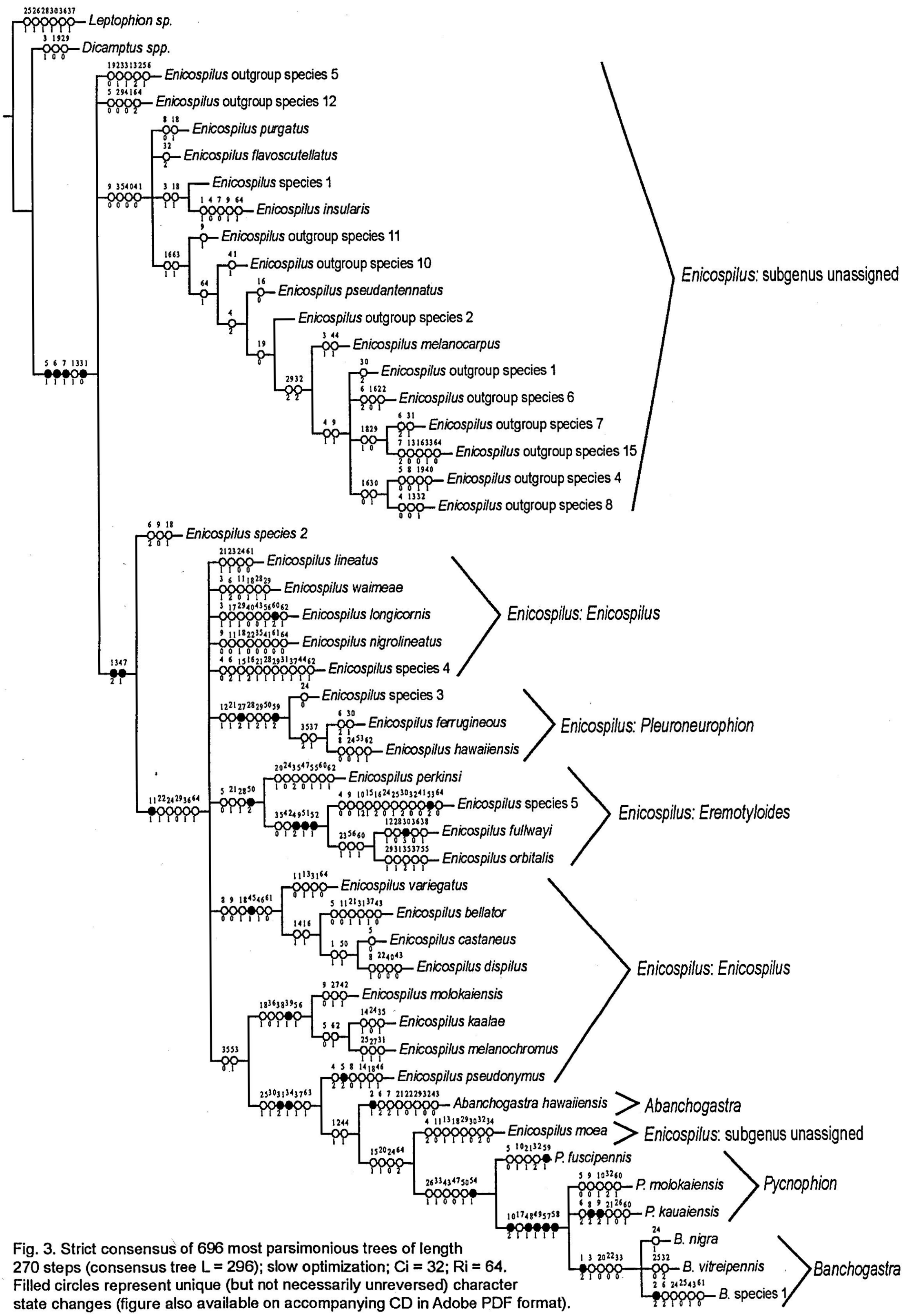


Fig. 3. Strict consensus of 696 most parsimonious trees of length 270 steps (consensus tree L = 296); slow optimization; Ci = 32; Ri = 64. Filled circles represent unique (but not necessarily unreversed) character state changes (figure also available on accompanying CD in Adobe PDF format).

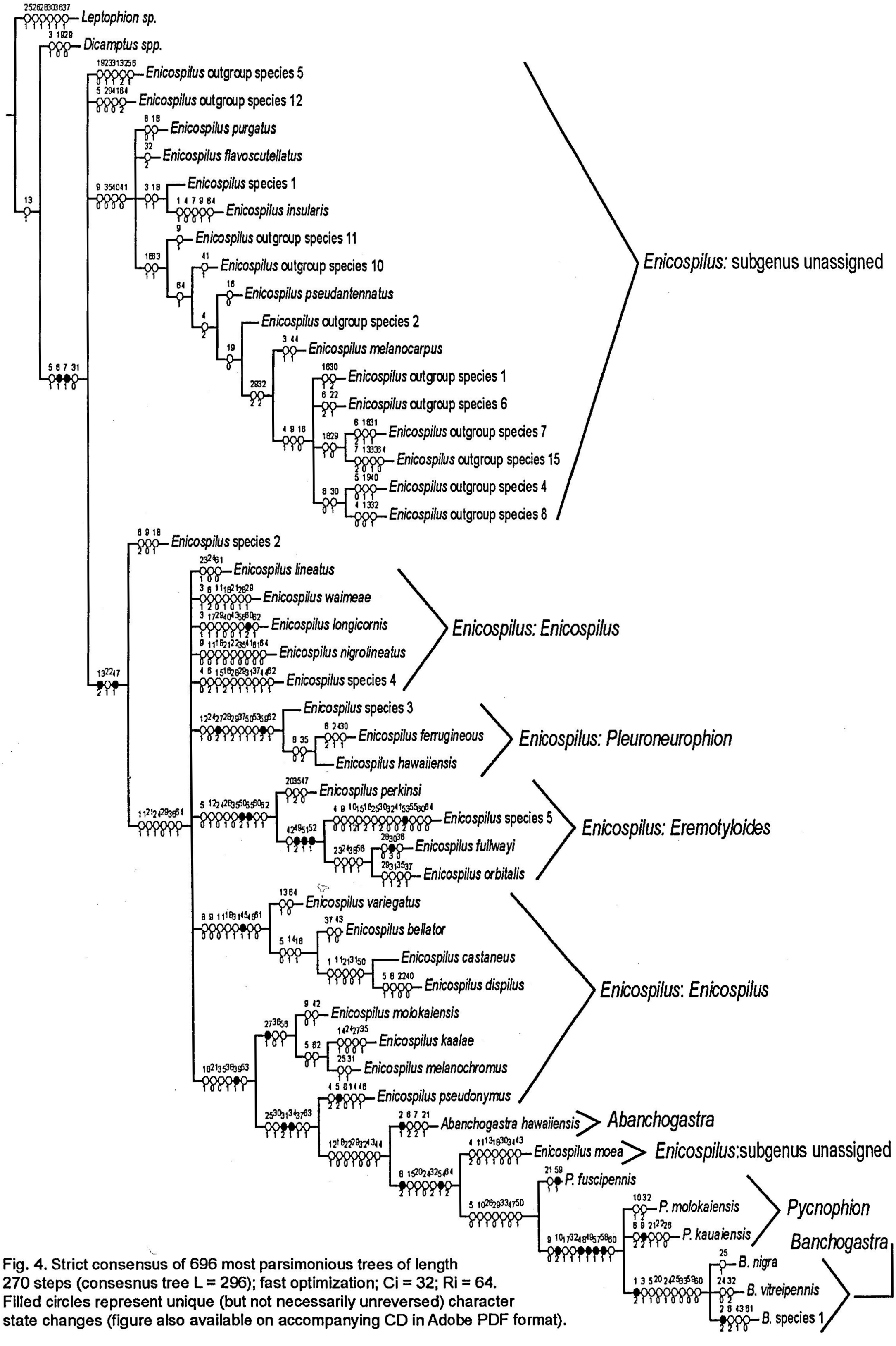


Fig. 4. Strict consensus of 696 most parsimonious trees of length 270 steps (consesnus tree L = 296); fast optimization; Ci = 32; Ri = 64. Filled circles represent unique (but not necessarily unreversed) character state changes (figure also available on accompanying CD in Adobe PDF format).

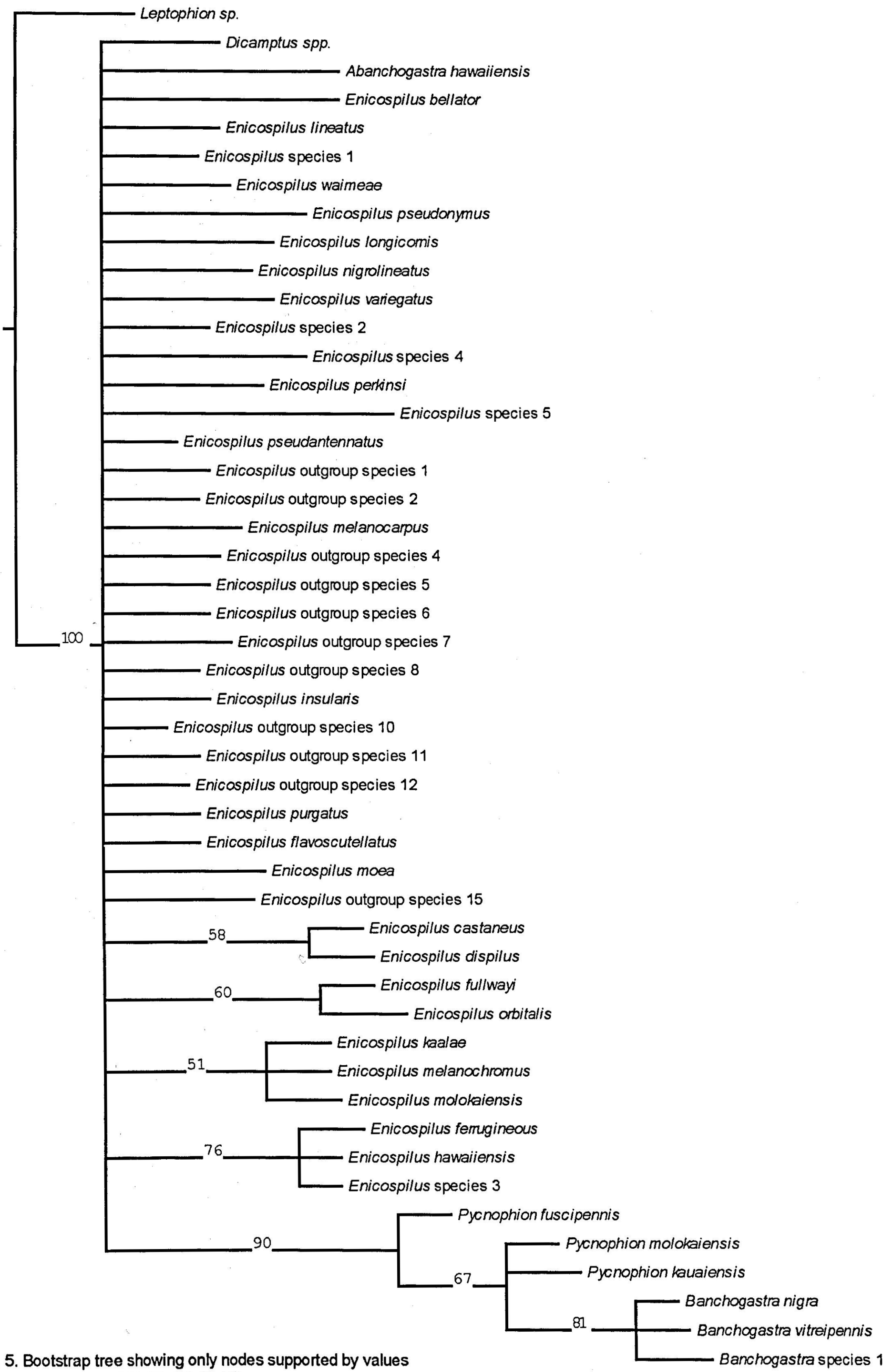


Fig. 5. Bootstrap tree showing only nodes supported by values of 50 or greater. L=459; Ci=19; Ri=29.

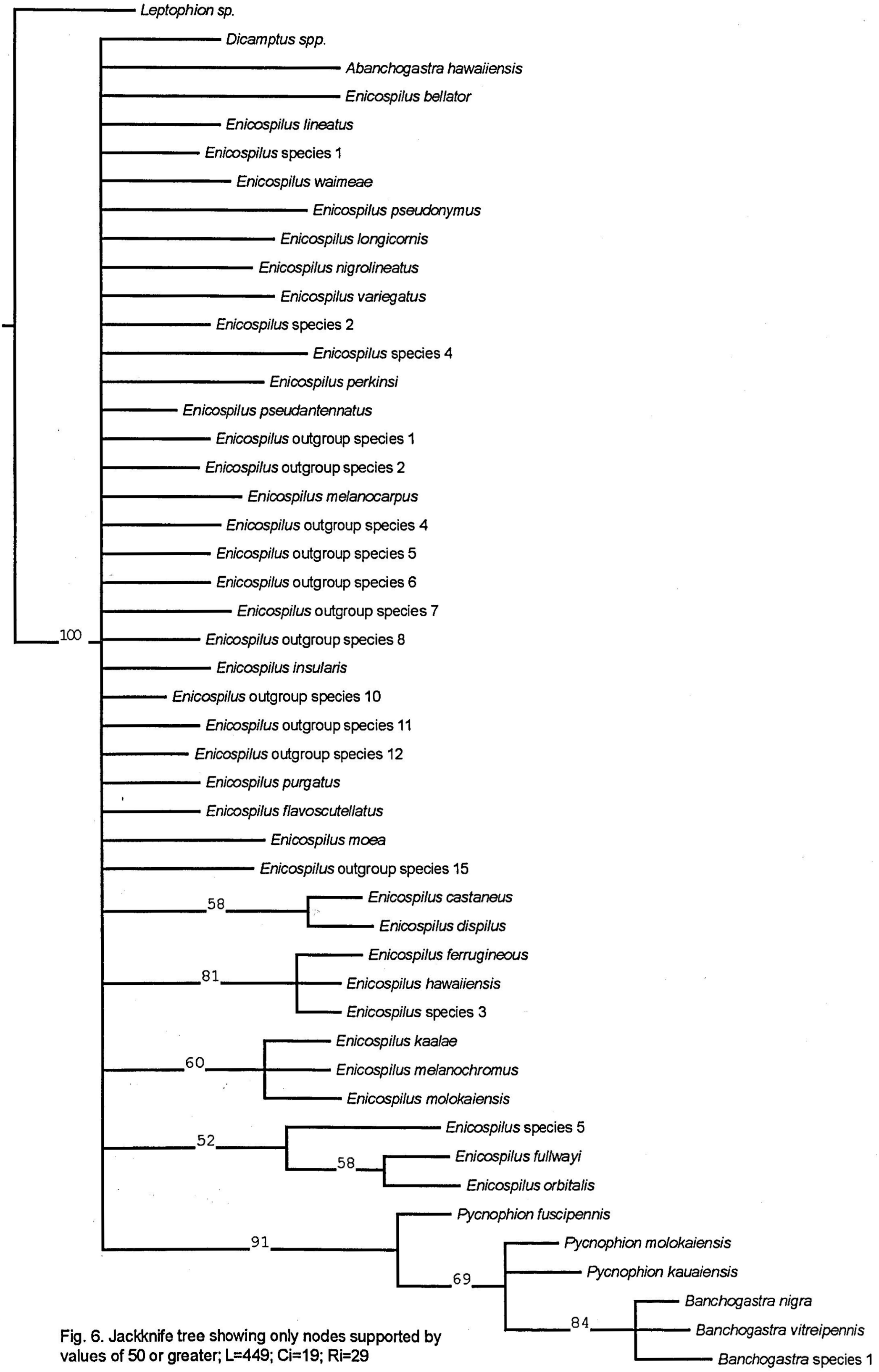


Fig. 6. Jackknife tree showing only nodes supported by values of 50 or greater; L=449; Ci=19; Ri=29

A second principal clade corresponds to the subgenus *Eremotyloides*, with the addition of the highly apomorphic *E.* species 5. Characters supporting this group include elongation of tergum IV (50:2), an invaginated dorsum of tergum VII (55:1), and an up-curved ovipositor (60:1). Whether *E.* species 5 truly belongs to this clade is somewhat suspect given that this hypothesis is contingent upon reversal of a number of characters, including most of those just mentioned, as well as a reversal to account for the presence of multiple, prominent alar sclerites.

A third principal clade is comprised of *E. variegatus*, *E. bellator*, *E. castaneus* and *E. dispilus*. This group was recognized by Cushman (1944), but *E. variegatus* is here added as a basal member. The most compelling characters supporting this clade are 45:1 (apical tarsus in male widened proximally) and 46:1 (apical tooth of pretarsal claw bent outwards).

The last principal clade in the main polytomy contains two subgroups. *Enicospilus molokaiensis, E. kaalae,* and *E. melanochromus* were noted by Cushman (1944) as sharing a large, deep fenestra (36:0), a proximal sclerite that lies posterior and basal in the forewing (38:1, 39:1), and an enlarged female sternum VII (56:1). Sister to this group is a mixed group of *Enicospilus* and the three endemic Hawaiian genera. Gauld (1985) noted that an evanescent posterior transverse carina of the mestosternum could be a character on which to unite the Hawaiian genera, but also noted its occurrence in *E. moea*. In this analysis, an evanescent posterior transverse carina of the mestosternum (25:1) does in fact group these taxa, but with the addition of the Hawaiian species, *E. pseudonymus*. Reinforcing this group are very similar forewing venation (30:1, 31:2), absent or vestigial fenestra (34:1), and evenly rounded parameres (60:1). Remaining members of this clade (i.e. species other than *E. pseudonymus*) are supported most strongly by the posterior position of Cu1 in the hindwing (44:1).

Gauld (1985) indicated that *E. moea* may be sister to the Hawaiian endemic genera. This may be so, but this analysis found slightly more support for a position as sister to *Pycnophion* + *Banchogastra*. A strongly convex metapleuron (20:1) and a long slender pterostigma (32:2) are among several characters to support this. A clade composed of *Pycnophion* and *Banchogastra* is supported by characters including reduced ocelli (10:1) and a reversal, spines present on fore-tibia (47:0). *Pycnophion* is apparently paraphyletic. A number of characters that group *P. molokaiensis*, *P. kauaiensis* and *Banchogastra* spp. are lacking in *P. fuscipennis*. Among these are the following: thyridia of tergum II displaced to near the anterior margin of the tergum (48:1), further reduction of ocelli (10:2), metasoma not laterally compressed, at least in part (57:1), and spiracles of tergum II at the anterior margin of tergum (58:1). The monophyly of *Banchogastra* is strongly supported by a number of characters, the most convincing of which is the strong reduction of the compound eyes (1:1).

The specific placement of many characters on the consensus tree varies according to the optimization criteria selected (Figs. 2, 3, and 4). For most of these characters, there is no clear justification allowing preference of one criterion over the other. However, for characters that are overwhelmingly rare in *Enicospilus*, slow optimization, which promotes convergences over reversals, is an unfavorable interpretation. For example, character 60:1, an up-curved ovipositor, is interpreted by slow optimization (Fig. 3) as arising independently in the closely related *P. molokaiensis* and *P. kauaiensis*. Given the aberrant nature of the apomorphic ovipositor found in these species, it is appropriate to prefer the equally parsimonious interpretation given by fast optimization, i.e. a single origin of an up-curved ovipositor in the ancestor of *P. molokaiensis* and *P. kauaiensis*, at the cost of accepting a reversal to a straight ovipositor in *Banchogastra*.

4.2 Classification: Cladistics vs. Convenience

The highly derived nature of many Hawaiian taxa, and exactly what rank to assign them, exposes familiar controversy concerning the philosophical basis of classification. Groups such as *Pycnophion* and *Eremotyloides* are undoubtedly very distinctive, and it can be, as Gauld (1985) points out, useful to segregate them from *Enicospilus* for effective communication. Yet the biological reality is that they are in fact derived from *Enicospilus*. Failure to employ a classification consistent with this reality impedes effective communication in certain ways as well. For example, in a popular and widely distributed synopsis of Hawaiian entomology, Howarth and Mull (1992) enumerated Hawaiian genera which contain over 25 species as a proxy for highlighting the large number of explosive radiations among insects in the islands. Because *Enicospilus* contains fewer than 25 Hawaiian species, it was not included in this list. However, had they included species in the endemic genera that have arisen from within *Enicospilus* (which they would have done had they been classified as *Enicospilus*) and just one of the undescribed species, they would have recognized another large species radiation (according to their standard of 25 species). Assigning the apomorphic taxa to genera other than *Enicospilus* impeded communication of this species radiation to a broad audience.

To maintain some nominal genera (i.e. *Pycnophion*) but not others (i.e. *Eremotyloides*) can only be continued in a subjective notion of the degree of difference necessary to do so. Upon naming such groups, Ashmead (1900) and Perkins (1915) obviously believed that they were substantially different from *Enicospilus* to classify them separately. Later workers agreed with some of these genera but not with others, with little consensus among authors. It may seem tolerable to many to allow higher ranks for taxa at the tips of a tree so long as polyphyletic groups do not result. For example, there may be a clade, *Abanchogastra* + (*Pycnophion* + *Banchogastra*), that at worst, only causes the paraphyly of *Enicospilus*. However, it is also quite likely, and in fact supported by the position of *E. moea* in the consensus tree of this analysis, that *Enicospilus* is polyphyletic. Furthermore a problem is encountered in the naming of *E.* species 5. This species is arguably as apomorphic as *Pycnophion* or *Banchogastra*, yet is apparently nested deeper within *Enicospilus*. If one follows the logic which maintains *Abanchogastra*, *Pycnophion* and *Banchogastra*, then establishing a genus for *E.* species 5 might be warranted. However, this action would surely cause polyphyly in *Enicospilus* if this is not already the case. A solution to this situation may be to recognize the classification of Townes (1945), in which all nominal genera are synonymized under *Enicospilus*. This would be the most objective action, but perhaps not the most pragmatic. As stated elsewhere (Gauld 1985), certain inconveniences to communication would become poignant. One would need to refer to the exceptions in apomorphic taxa when speaking of generalities within *Enicospilus*. Furthermore, at least in the short term, classification would be destabilized. *Abanchogastra hawaiiensis* (Ashmead 1901) would become a homonym of *Enicospilus hawaiiensis* (Ashmead 1900). Because the latter has priority, the former would take the next available specific epithet, *debilis* Perkins 1910. A much less desirable result would occur in another case. To synonymize *Pycnophion* with *Enicospilus* would make *P. molokaiensis* Ashmead 1900 a homonym of *E. molokaiensis* Ashmead 1901. Unfortunately, the specific epithet in *Pycnophion molokaiensis* Ashmead 1900 would have priority over that of the widespread and common *Enicospilus molokaiensis* Ashmead 1901. *E. molokaiensis* Ashmead would suddenly refer to an entity other than what is presently referred to by numerous identified specimens. To avoid this confusion, the best action may be to synonymize only *Abanchogastra* under *Enicospilus* (a classification put forth by Cushman 1947 and Townes 1971). This would involve the least nomenclatural change and ensure that *Enicospilus*, though clearly paraphyletic, is not polyphyletic.

Another issue to consider is the use of subgeneric names. Even though Cushman (1944) synonymized *Eremotyloides* and *Pleuroneurophion* under *Enicospilus*, he continued to use these names at the subgenus rank. In addition, he referred to the remaining Hawaiian *Enicospilus* as belonging to the nominal subgenus. Other than this, *Enicospilus* species have generally not been assigned to subgenus. The consensus tree from this analysis indicates that there is likely no cladistic justification for the way in which subgenera of *Enicospilus* are presently employed. The species-group has been extensively used within *Enicospilus* by Gauld and it is seemingly appropriate here as well. A cladistic analysis of species-groups in *Enicospilus* as a whole is needed to find meaningful use for the subgenus rank. Upon completion of such work, *Eremotyloides* and *Pleuroneurophion* may be found appropriate. But until then, it is recommended that these clades be referred to by species-group names, rather than subgenera.

A thorough taxonomic revision that incorporates at least some of the recommendations stated above is needed for the Hawaiian Ophioninae. The most controversial aspect of this revision will be whether to enforce a cladistic classification by synonymizing each of the endemic Hawaiian genera under *Enicospilus* (possibly referring to these clades as species-groups), or to synonymize only *Abanchogastra*, and thus allow a paraphyletic *Enicospilus* to persist by appealing to utility and stability. It is widely accepted that logical consistency between classification and phylogeny is highly desirable in a classification (Wiley 1981). It is also widely accepted that a classification should be stable and maximally useful for communication. In the case of the Hawaiian Ophioninae, there is conflict between these criteria. A worker may try to follow a classification which compromises various criteria, but one may nonetheless be required to prioritize one criterion over others. If legitimate cases exist in which considerations of phylogeny do not take priority over other criteria desired of a classification (a position cladists will be skeptical of), then continued maintenance of endemic Hawaiian ophionine genera, and thus a paraphyletic *Enicospilus*, is arguably justified.

4.3 Distribution and Zoogeography

Multiple wide-ranging *Enicospilus* species were selected as outgroups, both to test the monophyly of the Hawaiian Ophioninae, and as an attempt to find an affinity of the Hawaiian fauna to species from some other part of the world. But from where exactly these insects colonized Hawaii remains unknown. Given that most outgroup taxa are equally removed from the Hawaiian clade (outside of *E.* species 1) in the consensus tree, no light is shed on this matter. Furthermore, given the vagility of *Enicospilus*, many closely related species are widespread. Should the Hawaiian fauna eventually be found allied to such a species-group, Hawaii could still conceivably be colonized from multiple directions.

The exact significance of *E.* species 1, the species that is apparently removed from all other Hawaiian Ophioninae, is unclear. If it is allied to the main Hawaiian clade, it could potentially reveal the origin of the Hawaiian Ophioninae. However this species, known from a single female from Molokai's Kamako'u Preserve, is distinct from all other known Hawaiian *Enicospilus* in its polished sculpture and alar sclerites. Using an existing key to Indo-Papuan ophionine wasps (Gauld and Mitchell 1981), it keys easily to the widespread *E. laqueatus* (Enderlein) of Asia and southern Africa (possibly introduced in the latter, Gauld 1982) and matches fairly well with its description therein, in particular sharing in exact detail the arrangement of alar sclerites. Yet it falls outside the diagnosis of *E. laqueatus* in at least the following respects: longer mandible (though not as long as is in the *E. capensis* species-group); absent notauli; scutellar sculpture and profile; length to width ratios for lower face, labrum, scutellum, hind coxa, hind trochantellus and hind fourth tarsus; pretarsal claws not as pictured for *E. laqueatus*; flagellomeres short and broad; and length of malar space. *Enicospilus laqueatus* is a member of the widespread *E. antefurcalis* species-group. But in *E.* species 1, the flagellar segments are as in the *E. capensis* species-group, the sister group to the *E. antefurcalis* species-group (Gauld 1988). The scutellum, upper mandibular tooth, and pubescence of the 1st subdiscal cell, are seemingly intermediate between *E. capensis* (*E. capensis* species-group) and *E. laqueatus* (*E. antefurcalis* species-group). Thus, *Enicospilus* species 1 may belong to the *E. capensis* species-group, the *E. antefurcalis* species-group (perhaps as an aberrant specimen of *E. laqueatus*), or may be ancestral to both, as evidenced by the intermediate characters.

The mode of origin in Hawaii of *E.* species 1 may be as debatable as its alliance to species-group. Assuming that this is not simply a mislabeled specimen, *E.* species 1 may represent an introduced species (if so it would be the first such record of its kind for *Enicospilus* in Hawaii). Alternatively, if *E.* species 1 is in fact native, it is either the sole representative of a separate introduction into Hawaii, or it is allied to the remainder of the Hawaiian ophionines as a stem taxon. And though *E.* species 1 shares none of the key characters uniting the Hawaiian taxa, it does posses a characteristic diagonally grooved hirsute mandible, a feature that within *Enicospilus* is found in the *E. antefurcalis* group, and its sister group, the *E. capensis* species-group (Gauld 1988). Intriguingly, several Hawaiian species (for example *E. longicornis*, *E. waimae*, and others in extremely reduced forms) posses this trait as well. And though it was not supported in the analysis at large, this feature is suggestive of the notion that *E.* species 1 is allied to the remainder of the Hawaiian Ophioninae. Resolution of the problems created by this specimen is highly desirable. Discovery of additional specimens of *E.* species 1 (or a closely related form in Hawaii) and/or additional character evidence may be necessary to do so.

The position of *E. moea*, a species known only from the Marquesas islands, nested deep within the phylogeny, suggests a dispersal event from Hawaii. Alternatively, the close relation of this species to various Hawaiian Ophioninae could suggest a separate clade resulting from a second colonization event. This hypothesis, however, is less favored than the former, given its position in the phylogeny. It would only become tenable should this section of ophionines (i.e. *E. moea* + (*Pycnophion* + *Banchogastra*)) be shown by another dataset to occupy a more basal position within *Enicospilus*.

Maui, which is neither the largest nor the oldest island, apparently possesses the largest number of species (Table 1). Within the islands, most species are widespread, and those that are not are known from only a few specimens. This is in contrast to many, if not most Hawaiian insect groups that are characterized by high degrees of single island endemism. For example, of the 128 platynine Carabid beetles known from Hawaii, 124 are believed to be restricted to single islands (Liebherr 1997), and each of the 13 species of *Orsonwelles* spiders is a single island endemic (Hormiga et al 2003). Although cladistic biogeographic analysis is perhaps more applicable to groups characterized by high endemism (Nelson and Platnick 1981; Liebherr 1997), some conclusions can be drawn from the area cladogram shown in Figure 7. Allopatric speciation events following dispersal events are often implied by area cladograms of island taxa. However, both inter and intra-island speciation processes are implied by the distribution of various clades of Hawaiian Ophioninae. As shown in Figure 7, speciation on the island of Kauai, followed by dispersal of these species to other islands, without subsequent speciation, is implied by the distribution of *Pycnophion*. In contrast, *Banchogastra* may have evolved out of *Pycnophion*, following one of these dispersal events. Parsimonious explanations for the distribution of *Pleuroneurophion* and *Eremotyloides* also necessitate speciation prior to, as well as after, dispersal events.

4.4 Morphological Evolution

There are several morphological features of various groups in the Hawaiian Ophioninae that are atypical for *Enicospilus* at large. It appears that a long ovipositor has evolved twice from Hawaiian *Enicospilus* species with short ovipositors, the nearly ubiquitous condition for *Enicospilus*. Each species of *Pleuroneurophion* is equipped with a long-straight ovipositor (Fig. 8C). One *Pycnophion* species, *P. fuscipennis* has an ovipositor nearly identical in size and shape to *Pleuroneurophion* species (Fig. 8D), but is likely more closely related to *Enicospilus* with short ovipositors. Close examination further supports separate evolution of these very similar ovipositors. Both *Pleuroneurophion* species and *P. fuscipennis* are marked with a slight swelling in the ovipositor, which in this case, can serve as a marker to identify the location of elongation. In *P. fuscipennis* this swelling is located

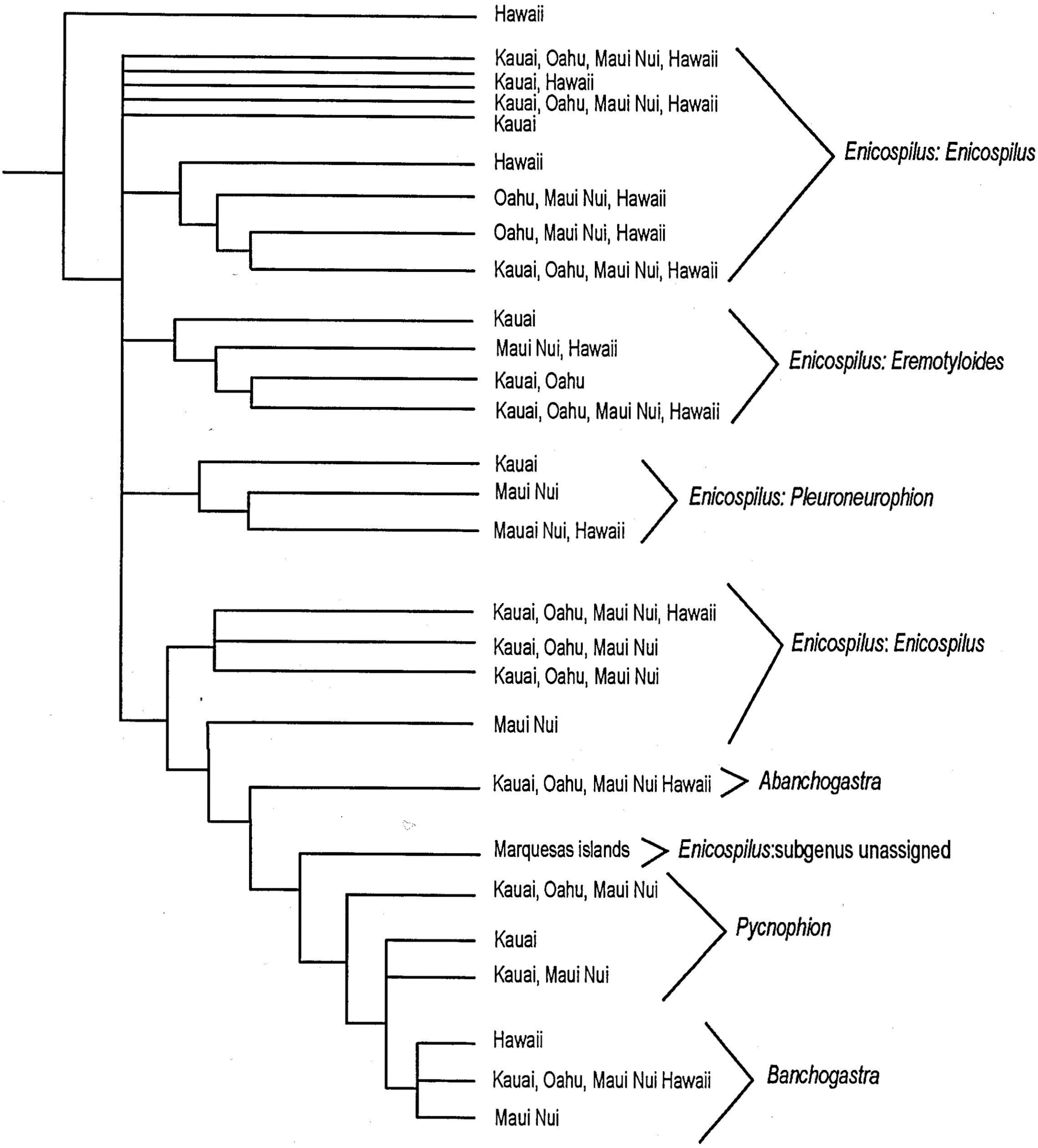


Fig. 7. Area cladogram of the primary clade of Hawaiian Ophioninae

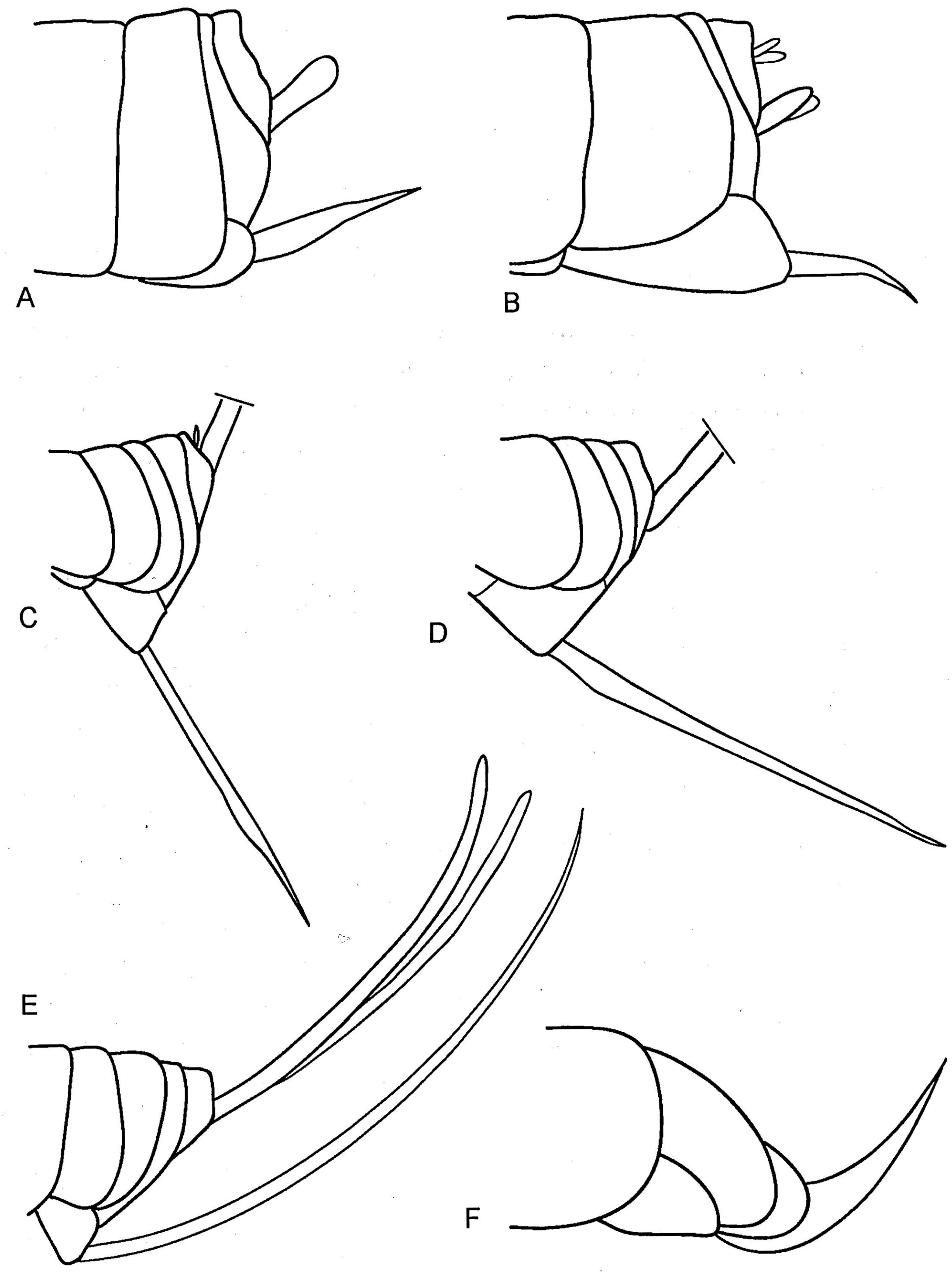


Fig. 8. Ovipositors of Hawaiian Ophioninae. A: *Enicospilus variegatus;* B: *E. longicornis;* C: *E.* (*Pleuroneurophion*) *hawaiiensis;* D: *Pycnophion fuscipennis;* E: *P. molokaiensis;* F: *E.* (*Eremotyloides*) *fullawayi*

basally in the ovipositor (Fig. 8D), and thus, elongation likely occurred distal to the swelling. In contrast, the condition found in species of *Pleuroneurophion*, in which this swelling is distal in the ovipositor (Fig. 8C), implies basal elongation. The evolution of the ovipositor in *Pycnophion* likely occurred in a fashion other than what is suggested by the distribution of character 59 on the tree. The analysis interpreted the ovipositor of *P. fuscipennis* to be an apomorphy for that species and supplies no information about the ovipositors of *P. molokaiensis and P. kauaiensis*. This is because in the latter two species, character 59 was coded as questionable (a swelling could not be identified, a feature needed in order to discriminate between character states one and two). But given that *P. fuscipennis* has a long-straight ovipositor (Fig. 8D), and the remaining species of *Pycnophion* have long, up-curved ovipositors (Fig. 8E), it is plausible that a long-straight ovipositor was derived in an ancestor to all *Pycnophion* species and became further modified as a long, up-curved ovipositor in the ancestor of *P. molokaiensis* and *P. kauaiensis*. Accepting this hypothesis requires one to accept a drastic reversal from a long, up-curved ovipositor to the short ovipositor of *Banchogastra* (Fig. 1C), with no known intermediates. Should a dataset that argues for a monophyletic *Pycnophion* be generated by future work, acceptance of this reversal would not be required. A third species of *Banchogastra* is known only from a single male (*B.* species 1) and seems to resemble *Pycnophion* more than do the described species of *Banchogastra*. If the female is eventually found to have an intermediate ovipositor (up-curved and/or long to any degree), then the reversal from a long, up-curved ovipositor to a short-straight ovipositor will become much more plausible.

Further variation in ovipositor form is found in other groups. Species of *Eremotyloides* have the typical short ovipositor, but in these species, other than *E.* species 5, it is clearly up-curved (Fig. 8F). *Enicospilus* species 4 has an ovipositor that is arguably up-curved, but only slightly so. This is suggestive of an intermediate between the two forms (in the analysis, rather than coding it as "straight" or "up-curved", it was coded as question mark) but a consensus of character data did not support a conclusion. A short, down-curved ovipositor is an apomorphy for *E. longicornis* (Fig. 8B).

Outside of Hawaiian species, ovipositor length is highly conservative among species of *Enicospilus*. Only one species, *E. terebrus* Gauld and Mitchell, from New Guinea and New Britain, has an elongate ovipositor similar to that of *Pleuroneurophion* and *P. fuscipennis*. As pointed out by Gauld and Mitchell (1981), convergence may be assumed in this case based upon a number of other incongruent characters. No species of *Enicospilus* has an ovipositor elongate or curved to the degree found in *P. kauaiensis* or *P. molokaiensis*.

The variety of ovipositors suggests multiple adaptive shifts, in particular shifts that facilitate the attack of concealed larval hosts. As stated above, this is known to be the case for *P. fuscipennis,* but hosts for the remaining *Pycnophion* species are not known. A notable similarity of ovipositors exists between these two species, and that of an oriental species, *Ophion caudatus* (Cushman) (Fig. 1B). This convergence could signal similar hosts, but unfortunately, the host of *O. caudatus* is also not known. Considerable ovipositor diversity can be found among ichneumonids that inhabit nearly every terrestrial ecosystem, typically distributed across a variety of ichneumonid subfamilies. Given the relative paucity of these wasps in Hawaii, it is reasonable to suggest that such ovipositor diversity (and by implication, host diversity) in closely related taxa has arisen in response to the absence of other species with specialized ovipositors in these islands.

Additional metasomal changes occurred in *Pycnophion* and *Banchogastra*. In these taxa, various degrees of compactness and lateral compression of the metasoma are observed. The Ophioninae, and in particular *Enicospilus*, generally have elongate, laterally compressed metasomas. The metasoma is arguably less elongate in *P. fuscipennis*, the most basal of the *Pycnophion* + *Banchogastra* clade, but it clearly has a plesiomorphic, laterally compressed metasoma. The remaining two species of *Pycnophion* have a transversely broadened metasoma anteriorly (through the anterior portion of tergite III), but they are laterally compressed posteriorly. In *Banchogastra* the metasoma is broadened transversely throughout, and notably more compact. In this regard it is similar to the ophionine genus *Rhyncophion* (Fig. 1D). However in the latter, the metasoma remains compressed laterally. Various markers are useful for observing this transformation. *Enicospilus* has distinct, oval, depressed, bare spots (thyridia) in the anterior half of tergum II laterally, that are marked by bare lines or scars between them and the anterior margin. Synapomorphic for the clade *Pycnophion* (other than the basal *P. fuscipennis*) + *Banchogastra*, are thyridia that are positioned at the anterior margin of tergite II (indicative of metasomal shortening).

In contrast to a progressive compaction of the metasoma, is the form found in the species of *Eremotyloides* (Fig. 1E). In this group, a progressive elongation of segments is observed, culminating in *E.* species 5. As in the other forms of the metasoma, this also has at least one analog in an unrelated species outside of Hawaii. The Mexican monobasic genus, *Agathophiona* Westwood similarly has an elongate metasoma (Fig. 1F), and again, the host is unknown.

Progressive loss of alar sclerites to various degrees appears to have been repeated in separate clades. Very few Hawaiian Ophioninae posses a complete set of alar sclerites, such as is common among *Enicospilus*. The basal species of *Pleuroneurophion*, *E.* sp. 3, has a single distinct alar sclerite, yet its intermediate position prevents definitive identification as the central or proximal sclerite. Regardless, it is absent in the remaining two species of this group. In a separate group, a slight vestigial indication of a sclerite is present in the wing of *E. pseudonymus*, and it is completely absent in the remainder of the clade. Accompanying the loss of alar sclerites is reduction of the fenestra, becoming completely hirsute in *Banchogastra*. Progressive loss of alar sclerites has been noted to occur in other insular communities of *Enicospilus*, such as those in Madagascar (Gauld and Mitchell 1978) and the Galapagos islands (Gauld and Carter 1983). It is not clear why this progression has occurred repeatedly among insular communities.

4.5 Future Work

Much remains to be discovered in order to attain a full understanding of the diversity, phylogeny, and biology of the Hawaiian Ophioninae. Cladistic analysis would benefit from the acquisition of two Hawaiian *Enicospilus* species not coded in this analysis, discovery of additional phylogenetically useful characters, the unknown sex for a number of taxa, and new species. A thorough treatment of taxonomy is needed for workers who may wish to collect and identify Hawaiian ichneumonids. Serendipity may be required to find hosts and make meaningful observations, but given the large number of biologists working in the islands, it is plausible to suggest that promoting this poorly-known group may yet result in discoveries that could significantly advance our understanding of the phylogeny, host-ecology, and morphological evolution of these wasps.

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