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# A new, endemic genus of Anomaloninae (Hymenoptera, Ichneumonidae) from St Helena

Gavin R. Broad[1]

1 *Department of Life Sciences, the Natural History Museum, Cromwell Road, London SW7 5BD*

Corresponding author: *Gavin R. Broad* (g.broad@nhm.ac.uk)

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## Abstract

A new genus, *Helenanomalon* **gen. n.**, of the ichneumonid subfamily Anomaloninae is described for two newly described species, *Helenanomalon ashmolei* **sp. n.** and *H. bonapartei* **sp. n.** *Helenanomalon* species are endemic to the remote South Atlantic island of St Helena, where they are the only known anomalonines. Unusually amongst anomalonines, there seems to be pronounced sexual dimorphism. The possible affinities of *Helenanomalon* are discussed.

## Keywords

Taxonomy, new genus, new species, south Atlantic, UK overseas territory

## Introduction

The remote, southern Atlantic island of St Helena (a UK overseas territory) has, unsurprisingly, a very small fauna of endemic Hymenoptera. Being 1,960 km from the nearest landmass (Africa), only a few Ichneumonoidea have colonised the island under their own steam, although a variety of tramp species have been inadvertently introduced. The invertebrate fauna of two key areas of St Helena was recently catalogued by Ashmole and Ashmole (2004) and Mendel et al. (2008), with the latter report based on extensive material collected in the Central Peaks area of the island in 2005–2006. Amongst the five species of Ichneumonidae collected in that survey were two male

specimens of the subfamily Anomaloninae that could not be identified to genus. There are also two published mentions of an undescribed anomalonine genus from St Helena. A short note by Ian Gauld, in his revision of the genera of Anomaloninae (Gauld, 1976), on an undescribed genus from St Helena, led to the rediscovery of a further male specimen in the Natural History Museum (hereafter BMNH) collection. Anomaloninae specimens collected in the Eastern Arid Area of the island by the Belgian expeditions of 1965–1967 are mentioned in a report on the ichneumonoid fauna of St Helena by Decelle (1976) as having been identified as a new genus by Henry Townes. The two females are deposited in Musée de l'Afrique Centrale (Tervuren) (hereafter RMCA) and were labelled as a 'new genus of Gravenhorstiini' by Henry Townes in 1972. These five specimens seem to be the only specimens of Anomaloninae to have been collected on St Helena.

Assigning the St Helena anomalonines to a genus, or defining a new genus to accommodate them, has proved problematic. Gauld's (1976) analysis of anomalonine relationships informed his redefinitions of the genera but was based on phenetic analysis of morphological characters. I had hoped to reanalyse Gauld's data using cladistic methods, and to include the St Helena specimens, as a test of their generic status. However, Gauld did not include a character matrix in his paper, stating that the data had been deposited in the BMNH library. Unfortunately, there is no trace of any such documents in either the library or the archives of BMNH. Given the information provided by Gauld in his generic revision, it is impossible to reconstruct his character matrix so a new genus is proposed here on the basis of character combinations that seem to preclude its placement in any described genus, and some apomorphic characters that attest to its long evolutionary independence from other lineages. I.D. Gauld and H.K. Townes had, probably independently, concluded that the males seen by Gauld and the females seen by Townes represented an undescribed genus. The males and females of this new genus are dissimilar in numerous ways, necessitating the description of two separate species.

## Materials and methods

Specimens are deposited in the Natural History Museum, London (BMNH) and the Musée de l'Afrique Centrale (Tervuren) (RMCA). Originally, three males were deposited in BMNH and two females in RMCA. Through the kind cooperation of Eliane de Coninck, curator at RMCA, one of each sex were exchanged so that both institutes now hold both sexes and both species.

Morphological terminology follows Gauld (1991). The format of the generic description follows that of Gauld (1976), for ease of comparison with other anomalonine genera, including numerous indices that Gauld (1976) employed. Photographs were taken using a Canon EOS 450D digital camera attached to a Leica MZ12 stereomicroscope. Partially focused photographs were combined using Helicon Focus software.

## Results

### Taxonomy

***Helenanomalon* gen. n.**
http://zoobank.org/BAC8F2BC-DF2C-4B4F-A29A-6063811E4697

**Type species.** *Helenanomalon bonapartei* sp. n.

**Description.** Eye surface with short hairs, shorter than spaces between them; eyes convergent ventrally; occipital carina complete, dorsally closer to rear ocellus than diameter of ocellus, ventrally reaching mandible base separate from hypostomal carina (difficult to see on the female specimens of *H. ashmolei* sp. n., cannot confirm for both species); frons simple, lacking median longitudinal or transverse carinae. Antenna long, potentially sexually dimorphic, simple in ♂ of *H. bonapartei* sp. n., very short and distinctly clubbed in ♀ of *H. ashmolei* sp. n., with subapical flagellomeres shorter and wider than basal flagellomeres (Fig. 6); flagellum lacking white band; scape from 1.4–2.3× pedicel, truncate at shallow angle. Clypeus truncate (Fig. 3), edge thin and slightly outcurved; mandible strongly narrowed, slightly twisted, with upper tooth 2.0–2.6× lower tooth. Maxillary palp with five segments, labial palp with four (in *H. bonapartei* sp. n., cannot confirm for *H. ashmolei* sp. n.), apical palpomere very small. [Cardo not dissected out.]

Pronotum rather short dorsally with narrow, sharply defined transverse furrow, anterior edge of furrow continuing ventrally as carina close to and parallelling anterior edge of pronotum; posterior, dorsal corner of pronotum not covering spiracular sclerite; lower anterior corner lacking tooth, rounded anteriorly. Mesoscutum steeply rounded anteriorly without an apical concavity. Notauli present or absent; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina reaching to about lower ⅓ of mesopleuron, dorsally distant from anterior margin of mesopleuron, medio-ventrally weakly raised; sternaulus absent; only short, median section of posterior transverse carina of mesosternum present.

Fore coxa smooth; fore tibial spur with long comb of macrotrichia on inner surface with membranous flange posterior to comb. Mid tibia with two spurs. Hind trochanter dorsally 2.0–3.0× as long as trochantellus, ventrally 1.0×; hind tarsi of ♂ not swollen; hind tarsal claws abruptly curved, fully pectinate (Fig. 5a), or weakly curved with only basal pecten (Fig. 5b).

Fore wing with *Rs* straight; 2*rs-m* basal to 2*m-cu*; 1*m-cu* and *Cu*1*a* basally separate (Fig. 9a,b). 1st subdiscal cell approximately parallel-sided. Hind wing with 6 (♀) or 9–10 (♂) hamuli on vein *R*1; distal abscissa of *Cu*1 present, but not joining *cu-a*+basal section of *Cu*1 (nervellus) (Fig. 9a), or absent (Fig. 9c).

Petiolar index:
PI (distance from anterior margin of 1st metasomal spiracle to base of 1st tergite / distance from posterior margin of spiracle to apex of 1st tergite) = 2.19–2.68.

Fore wing indices:
CI (length of *Cu*1 between 1*m-cu* and *Cu*1*a* / length of *Cu*1*b* between *Cu*1*a* and 1*A* = 0.82–1.27;
BI (shortest distance between *Cu*1 and 1*A* at distal end of 1st subdiscal cell / shortest distance between *Cu*1 and 1*A* at proximal end of 1st subdiscal cell) = 1.09–1.13;
DBI (length of *Cu*1between *cu-a* and 1*m-cu* / length of 1*m-cu* between *Cu*1 and 2+3*rs-m*) = 0.49–0.51;
ICI (length of 2+3*rs-m* / length of *M* between 2+3*rs-m* and 2*m-cu*) = 0.60–1.23;
MI (length of *Rs* / length of *Rs*+2*r*) = 1.60–1.89.

Hind wing index:
RI (length of *Rs* between *R*1 and 1*r-m* / length of 1*r-m* between *Rs* and *M*) = 1.25–1.38.

Propodeum reticulate, with longitudinal, median depression; spiracle about 1.6× as long as broad; apex of propodeum extending about 0.3–0.4× length of hind coxa. Metasoma elongate.

♀ genitalia. Ovipositor sheath 1.2× length of tergite 3; ovipositor lacking dorsal notch but pre-apically markedly swollen, higher and wider here than basal or apical sections, apical 0.3 of dorsal valves of ovipositor very narrow, slightly decurved (Fig. 7).

♂ genitalia. Metasomal tergites 8+9 (syntergum of Gauld 1976) entire; 8th sternite roundly produced posteriorly; parameres (=gonosquamae) approximately rectangular; gonolacinia smoothly curved, with median tooth; distivolsella not wholly visible in available specimens; aedeagus in profile distally swollen, convex dorsally with apical, dorsal projection, ventrally membranous with whole membranous area covered with minute spinules, not laterally expanded (Fig. 8).

**Etymology.** Named after the type locality, St Helena, and the type genus of the subfamily, *Anomalon*.

**Remarks.** The two available female specimens of *H. ashmolei* sp. n. are, in part, encrusted with glue and dirt so it is not possible to see all of the characters that can be observed in the male specimens of *H. bonapartei* sp. n. Sexual dimorphism seems to be pronounced in this genus, although each species is known from one sex only; see discussion below on the species status of specimens.

### *Helenanomalon bonapartei* sp. n.

http://zoobank.org/302F71B2-114A-41D1-896D-66C0E57B84A5
Figs 1, 3a, 4a, 5a, 8, 9a

**Description.** Male. Fore wing length 6.7–7.9 mm in ♂. Antenna with 33 (1 specimen)–36 (2 specimens) flagellomeres; all flagellomeres longer than wide and about equal width; antennal flagellum 1.2× length of fore wing (Fig. 1); scape 2.3× pedicel; distance between eyes ventrally c.0.8× distance dorsally (Fig. 3a); mandible more weakly

**Figure 1.** Holotype ♂ of *Helenanomalon bonapartei* sp. n.; scale bar = 10 mm.

twisted than in *H. ashmolei* sp. n., upper tooth 2.0× lower tooth. Head and mesosoma covered in closely spaced, silvery setae, but sparser than in *H. ashmolei* sp. n. (Fig. 4a); metasoma, beyond first tergite, covered in slightly sparser setae; notauli strongly im-

pressed and narrow medially but faint on anterior slope and posteriorly disappearing in rugosity (Fig. 4a). Head rugose, matt, pronotum rugose-punctate laterally, dorsally punctate, mesoscutum punctate, rugose posteriorly, mesopleuron punctate, transversely striate dorsally, mesosoma with shiny interspaces between obvious punctures. Hind trochanter dorsally 3.0× as long as trochantellus, ventrally 1.0×; hind tarsal claws abruptly curved, fully pectinate (Fig. 5a). First sternite without convexity sub-basally. Fore wing (Fig. 9a) with *cu-a* slightly distal to *Rs&M*; hind wing with 9–10 hamuli on vein *R*1; distal abscissa of *Cu*1 with distal section reaching wing membrane, proximally distant from *cu-a*+basal section of *Cu*1 (nervellus). Petiolar index 2.68; fore wing indices: CI 0.82; BI 1.09; DBI 0.49; ICI 1.23; MI 1.60; hind wing index: RI 1.25.

Colour. Red, paler than in *H. ashmolei* sp. n.; face, inner orbits, underside of scape bright yellow; frons and antennal flagellum black; mesosoma red with black on middle of median lobes of mesoscutum, mesoscutum posteriorly, mesopleuron dorsally, ventrally, mesosternum, propodeum dorsally, metasternum, upper division of metapleuron, postscutellum. Scutellum (mesoscutellum) black anteriorly, medially, ivory or yellow posteriorly and laterally. Following parts ivory: palps, pronotum dorso-posteriorly, ventro-posteriorly, propleural lobe, subalar prominence, fore and mid coxae and trochanters, fore trochantellus, mid trochantellus ventrally, hind trochanter and trochantellus ventrally. Hind coxa apically, dorsally, trochanter and trochantellus, femur basally, tibia and tarsus dark brown/black. First and second metasomal tergites black, remainder of metasoma and legs red.

Female: unknown.

**Material examined.** Holotype ♂ 'St Helena: High Peak Malaise trap: xii.2005–1.2006 S15°58.7' W5°44.0' c.752m UTM:02/068 18 82/1903', 'St Helena Peaks Project N.P. Ashmole, M. Ashmole, H. Mendel & E. Thorpe BMNH(E) 2006-9', specimen number BMNH(E) #1022370 (BMNH).

Paratypes: 1 ♂ 'St Helena: Peak Dale gumwoods: 24.i.2006: off foliage (2096)', 'St Helena Peaks Project N.P. Ashmole, M. Ashmole, H. Mendel & E. Thorpe BMNH(E) 2006-9' (RMCA); 1♂ 'St Helena Knollcombes 16.x.1957 C.R. Wallace', specimen number BMNH(E) #1022371 (BMNH).

**Etymology.** Named after the most famous inhabitant of St Helena, Napoleon Bonaparte, who was exiled there from 1815 until his death in 1821.

### *Helenanomalon ashmolei* sp. n.

http://zoobank.org/EECE67E9-2D77-4903-9559-9CD0EB8FF929

Figs 2, 3b, 4b, 5b, 6, 7, 9b,c

**Description.** Female. Fore wing length 3.6–3.7 mm. Antenna with 16–17 flagellomeres, apical two flagellomeres of partly fused but still with obvious division between them, apical flagellomere 3.7× penultimate flagellomere, penultimate 6 flagellomeres of antenna as wide as or wider than long, apical flagellomere at widest 1.8× as wide


**Figure 2.** Holotype ♀ of *Helenanomalon ashmolei* sp. n.

as first flagellomere; antennal flagellum 0.6× fore wing (Fig. 2); scape 1.4× pedicel; distance between eyes ventrally c.0.7× distance dorsally (Fig. 3b); mandible more strongly twisted than in *H. bonapartei* sp. n., upper tooth 2.6× lower tooth. Head and

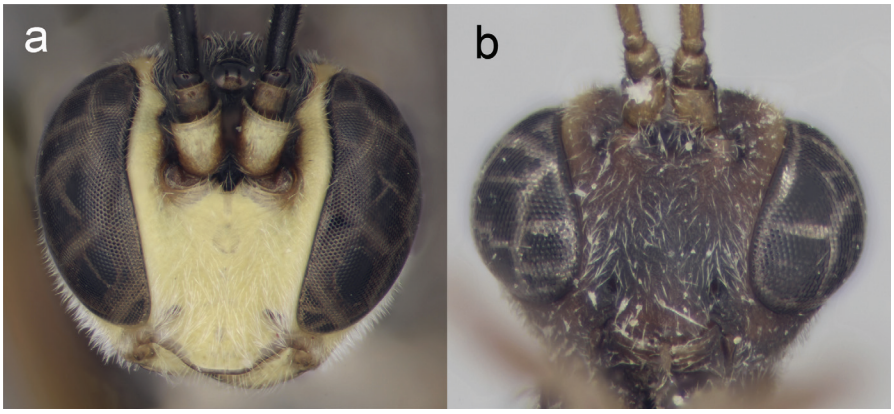


**Figure 3.** Face of **a** holotype ♂ of *H. bonapartei* sp. n. and **b** holotype ♀ of *H. ashmolei* sp. n.

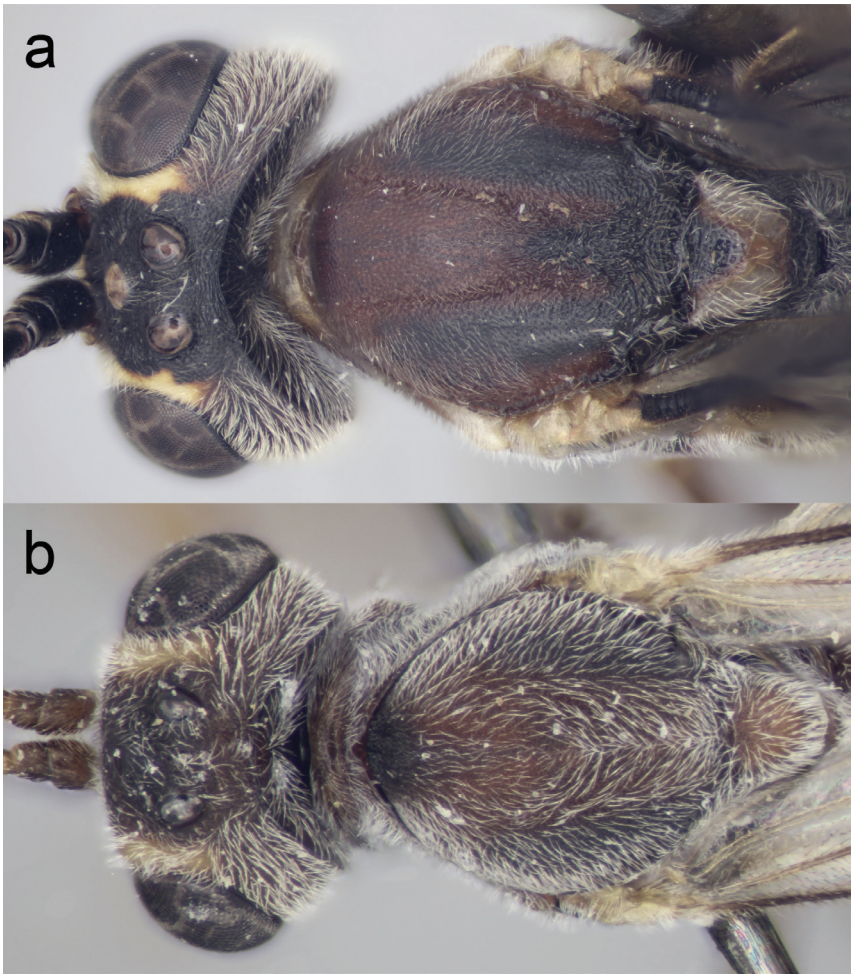


**Figure 4.** Mesoscutum of **a** holotype ♂ of *H. bonapartei* sp. n. and **b** holotype ♀ of *H. ashmolei* sp. n.

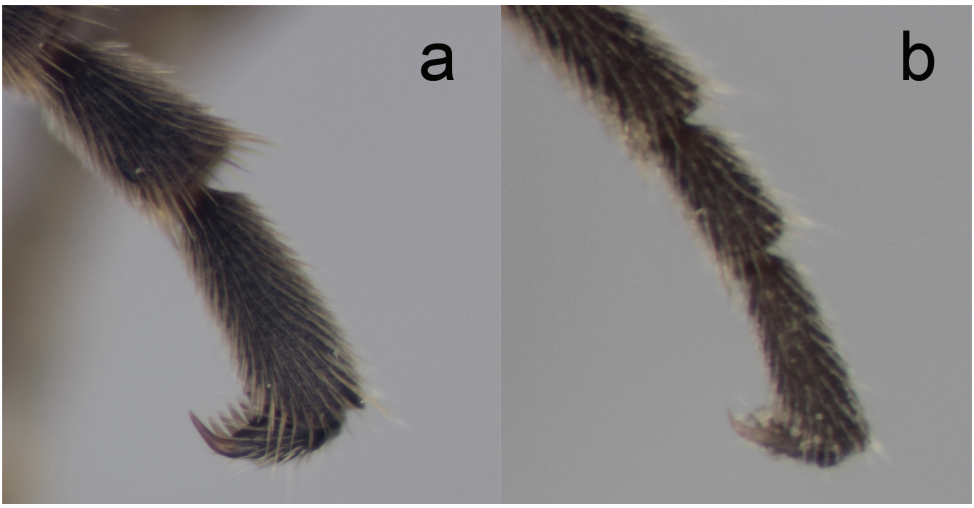


**Figure 5.** Hind tarsal claw of **a** holotype ♂ of *H. bonapartei* sp. n. and **b** holotype ♀ of *H. ashmolei* sp. n.

**Figure 6.** Antenna of holotype ♀ of *H. ashmolei* sp. n.

mesosoma covered in closely spaced, silvery setae, denser than in *H. bonapartei* sp. n. (Fig. 4b); metasoma, beyond first tergite, covered in slightly sparser setae; notauli absent (Fig. 4b), no rugose area on mesoscutum. Head and mesosoma predominantly of granulate appearance, rugose, matt, impunctate. Hind trochanter dorsally 2.0× as long as trochantellus, ventrally 1.0×; hind tarsal claws weakly curved with only basal pecten (Fig. 5b). First metasomal sternite with marked convexity sub-basally. Fore wing (Fig. 9b) with *cu-a* slightly proximal to *Rs&M*; hind wing (Fig. 9c) with 6 hamuli on vein *R*1; distal abscissa of *Cu*1 absent but with slight angulation on nervellus (*cu-a*+ *Cu*1). Petiolar index 2.19; fore wing indices: CI 1.27; BI 1.13; DBI 0.51; ICI 0.60; MI 1.89; hind wing index: RI 1.38.

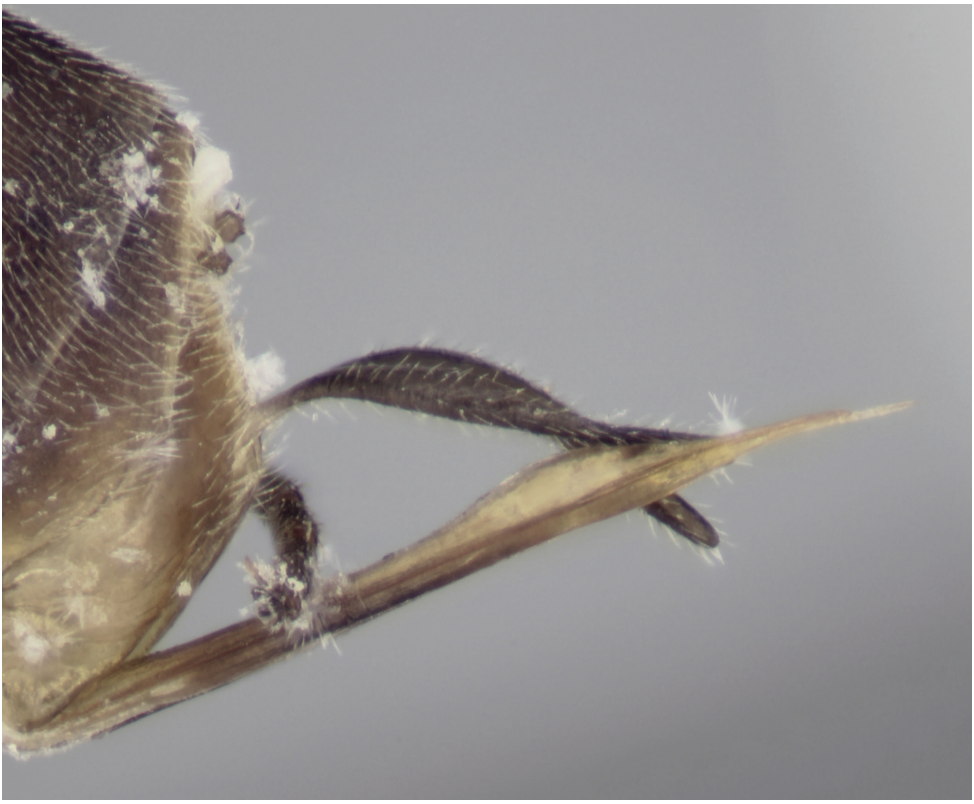

**Figure 7.** Ovipositor of holotype ♀ (RMCA) of *H. ashmolei* sp. n.

Colour. Basically dark red; fore and mid legs and hind femur paler red; extreme base of hind femur, apex of hind trochanter, yellow; antenna basally paler red; inner orbits from antennal sockets to hind ocelli dull yellow; metasoma extensively orange-red in holotype ♀, darker red in paratype ♀.

Male: unknown.

**Material examined.** Holotype ♀ 'Sainte-Hélène: Est Prosperous Bay Plain 800-900 ft. 5.II.1967', 'Coll. Mus. Tervuren Seconde Mission Zoologique à Sainte-Hélène J. Decelle, N. et J. Leleup' (RMCA).

Paratype ♀ same data except 1000-1100 ft, 29.IV.1967, specimen number BMNH(E) #1022369 (BMNH).

**Etymology.** Named after Philip and Myrtle Ashmole, who have done so much to encourage the study and conservation of the unique fauna of St Helena.

## Discussion

Only six species of Ichneumonidae have been recorded from St Helena, namely *Diadegma mollipla* (Holmgren), *Diplazon laetatorius* (Fabricius), the endemic subspe-

**Figure 8.** Genitalia of paratype ♂ (RMCA) of *H. bonapartei* sp. n.

cies *Echthromorpha agrestoria atrata* Holmgren, the endemic species *Netelia insulicola* (Morley), and now *Helenanomalon ashmolei* sp. n. and *H. bonapartei* sp. n. (note that Yu et al. (2012) mistakenly list *Diadegma semiclausum* (Hellén) from St Helena, citing Wagener et al. (2006), who actually only record *D. mollipla* from the island). It seems surprising that there is an endemic genus on this island, given that two of the other ichneumonids (*Diadegma mollipla* and *Diplazon laetatorius*) are widespread, probably introduced, associates of agriculture and the other two are closely related to extralimital species (*Netelia insulicola* to African species and *E. agrestoria atrata* is currently classified as a subspecies of the wide-ranging, polytypic *E. agrestoria* (Swederus)). However,

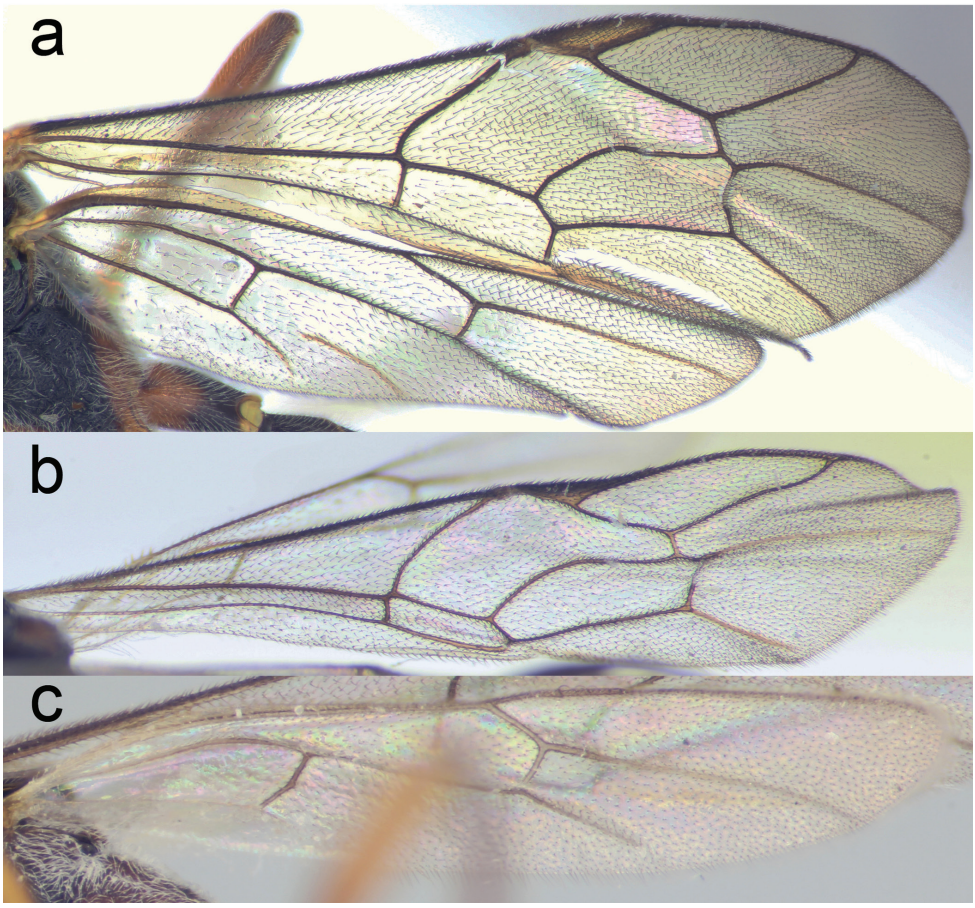


**Figure 9.** Wings of *Helenanomalon* species **a** fore and hind wings of paratype ♂ (BMNH) of *H. bonapartei* sp. n. **b** fore wing of holotype ♀ of *H. ashmolei* sp. n. **c** hind wing of *H. ashmolei* sp. n.

the Central Peaks and Prosperous Bay areas of St Helena are home to other endemic genera of insects and these are clearly areas of special habitat that have allowed the evolution of distinct lineages in great isolation. It should also be noted that the anomalonine fauna of Africa is poorly known, with few species described; the St Helenan insect fauna shows most affinity with the African fauna (Mendel et al. 2008) and the closest relatives of *Helenanomalon* may well be found there.

With one species known only from females and the other only from males, there must remain some doubt as to whether these are really separate species. Given the small anomalonine fauna likely to be present on St Helena, one hypothesis is that these specimens represent the two sexes of the same species, displaying a more extreme sexual dimorphism than is otherwise known within Anomaloninae. In this scenario, females show striking adaptations for locating and accessing hosts, whilst males have rather more generalised morphology. Development in different sizes of hosts will, of course, produce different sizes of adult ichneumonids, even in koinobiont endopara-

sitoids such as anomalonines, and the two females collected so far, much smaller than the males, may simply have developed in rather smaller hosts than the males that have been collected; anomalonines are rarely host-specific, usually accepting hosts across rather taxonomically wide host ranges within particular parasitoid searching niches (e.g., Shaw et al. 2009). However, I favour the alternative hypothesis, that these are separate species. In favour of this are the differences in wing venation; the well-developed notauli in the male but not the female; the larger size of the males, when often it is the females that are larger in ichneumonids; and the fact that the two sexes were collected in different areas of the island, in different habitats (the females in the more arid Prosperous Bay, the males in the wetter Central Peaks area). The sexes do share numerous characters and I am convinced that they are congeneric. The fauna of St Helena has now been better surveyed than that of many remote islands, nevertheless, further collecting should produce more specimens of this genus on St Helena and confirm or refute the taxonomy proposed here. Fresh material would obviously be very useful for DNA sequencing.

An investigation of the evolutionary relationships of *Helenanomalon* would be rewarding in potentially shedding light on the origins of this geographically isolated genus. The classification of Anomaloninae as a whole would certainly repay a detailed phylogenetic study. In Gauld's (1976) key to genera of Anomaloninae, males of *Helenanomalon bonapartei* will fail to travel properly from couplet nine, because the clypeus is truncate apically and the mesoscutum evenly rounded but the notauli are present and strong. Females, and males if the distal abscissa of hind wing vein *Cu*1 is regarded as missing (at couplet five), will reach couplet 40, where they will key to *Habronyx* (*Camposcopus*), but by ignoring the fact that the clypeus does not have a median tooth. Several characters preclude the classification of these specimens in *Habronyx*, such as the apically truncate clypeus, vestigial transverse carina of the mesosternum and the undivided male metasomal tergites 8+9. The aedeagus most closely resembles that of *Habronyx* (*Habronyx*) *australasiae* (Morley), as illustrated by Gauld (1976). The main difficulty faced in trying to place this taxon in Gauld's scheme of relationships is that Gauld's (1976) proposed set of relationships is based on percentage similarity (this work preceded the widespread acceptance of cladistic methods in phylogeny reconstruction) and not on character distributions. In the absence of clades defined by apomorphies we can only suggest that *Helenanomalon* seems to be related to *Trichomma* or *Habronyx*. The former hypothesis is based on overall similarity, including, in some species of *Trichomma*, the lack of a clypeal tooth and the distal abscissa of hind wing vein *Cu*1. *Helenanomalon* differs most obviously in the short setae on the eye and shorter ovipositor than in *Trichomma*. The strong notauli (in the male only though) and various trends, including the short epicnemial caria and short, sparse setae on the surface of the eye, are present in a few species of *Habronyx s.l.*

In several features, such as lack of a clypeal tooth and the form of the epicnemial carina, *Helenanomalon* resembles *Habronyx* (*Austranomalon*) but differs in the truncate, simple clypeus (when truncate in *Austranomalon* then a clypeal tooth is present); the aedeagus has a well-developed, apical, crest-like area; and possible sexual dimor-

phism in tarsal claws, which is the opposite to the condition found in *Austranomalon*, i.e. the male claws in *Helenanomalon* are strongly curved and pectinate, those of the known females weakly curved and scarcely pectinate. Females of *Helenanomalon* have strikingly short antennae, very unusual for an anomalonine, although this autapomorphy does not help place the genus. There are only small differences between some of the genera of Anomaloninae whilst a few genera as currently defined seem to encompass more variation between species classified in the same genus than is found between other genera. *Habronyx* is a good example of the latter, polythetic genus.

The most distinctive feature of *Helenanomalon*, that should render females instantly recognisable, is the short, clavate antennal flagellum of the female (but it is not known if this is true for the unknown female of *H. bonapartei* sp. n.). Males are less easily recognised but have a unique combination of characters, including the apically truncate clypeus, lacking a tooth; the strongly curved, completely pectinate tarsal claws; short, sparse setae on the eye surface; and the incomplete posterior transverse carina of the mesosternum. Females lack notauli and have only basally pectinate claws. Another potential characteristic of the genus is pronounced sexual dimorphism.

## Acknowledgements

Thank you to Howard Mendel and Philip and Myrtle Ashmole for collecting a wealth of insect specimens from St Helena, which prompted me to describe this genus. I am grateful to Eliane de Coninck and Stéphane Hanot for the loan of specimens from Tervuren and for agreeing to the exchange of a female and male between institutes. Harry Taylor at BMNH took the lovely photograph of the holotype male of *H. bonapartei*. I am grateful to Heinz Schnee and Seraina Klopfstein for their helpful reviews of the manuscript, particularly their opinions on the number of species represented by these few specimens.

## References

Ashmole P, Ashmole M (2004) Guide to Invertebrates of Prosperous Bay Plain, St Helena and Illustrated account of species found on the Eastern Arid Area (EAA), including Prosperous Bay Plain, Holdfast Tom and Horse Point Plain. Peebles, Scotland. [cited 2008. http://kidstonmill.org.uk/docs/files%201-5%20together.pdf]

Decelle J (1976) La faune terrestre de l'ile de Sainte-Helene. Troisième Partie 2. Insectes (suite et fin) 15. Hymenoptera 2. Superfam. Ichneumonoidea. Annales du Musée Royale de l'Afrique Centrale, Séries In8º, Sciences zoologiques 215: 162–166.

Gauld ID (1976) The classification of the Anomaloninae (Hymenoptera: Ichneumonidae). Bulletin of the British Museum (Natural History), Entomology 33: 1–135.

Gauld ID (1991) The Ichneumonidae of Costa Rica, 1. Memoirs of the American Entomological Institute 47: 1–589.

Mendel H, Ashmole P, Ashmole M (2008) Invertebrates of the Central Peaks and Peak Dale, St Helena. Report commissioned by the St Helena National Trust, financed by the Overseas Territories Environment Programme (OTEP), 144 pp. http://www.nationaltrust.org.sh/wp-content/uploads/2013/06/Peaks-Invertebrate-Survey-report-2008.pdf

Shaw MR, Stefanescu C, van Nouhuys S (2009) Parasitoids of European butterflies. In: Settele J, Shreeve T, Konvicka M, Van Dyck H (Eds) Ecology of Butterflies in Europe. Cambridge University Press, Cambridge, 130–156.

Wagener B, Reineke A, Löhr B, Zebitz CPW (2006) Phylogenetic study of *Diadegma* species (Hymenoptera: Ichneumonidae) inferred from analysis of mitochondrial and nuclear DNA sequences. Biological Control 37: 131–140. doi: 10.1016/j.biocontrol.2006.01.004, http://www.sciencedirect.com/science/article/pii/S1049964406000326

Yu DS, Achterberg C van, Horstmann K (2012) Taxapad 2012, Ichneumonoidea 2011. Database on flash-drive. www.taxapad.com, Ottawa, Ontario, Canada.