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Systematics and biology of the aberrant intertidal parasitoid wasp *Echthrodesis lamorali* Masner (Hymenoptera : Platygastridae s.l.): a parasitoid of spider eggs

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Abstract. The platygastroid wasp *Echthrodesis lamorali* has been of considerable interest since its description in 1968, primarily because of its highly modified, densely pilose, wingless body, its distribution and unusual biology. The species is endemic to the Cape Peninsula, South Africa, where it is an endoparasitoid of eggs of the marine spiders *Desis formidabilis* (Desidae) and *Amaurobioides africanus* (Anyphaenidae) in the intertidal region. Although a highly aberrant monospecific genus, the phylogenetic relationships of *Echthrodesis* are confused, in part due to convergence in body form across numerous unrelated platygastroid genera. We used sequence data from the nuclear 28S rRNA and 18S rDNA genes, and the mitochondrial cytochrome oxidase 1 (CO1) gene, to determine the phylogenetic affinities of *E. lamorali*. We present a revised taxonomic description for the genus and species, as well as new morphological information on the structure of its mouthparts and ovipositor system. Phylogenetic analyses of molecular data place *E. lamorali* within one of two independent clades of platygastroid wasps that use spider eggs as hosts. *Echthrodesis* is sister to a group of three genera: *Neobaeus* (New Zealand; host unconfirmed); *Mirobaeoides* (Australia; spider eggs); and *Embidobia* (near cosmopolitan; embiid eggs). Details on the biology, behaviour and morphological adaptations of *E. lamorali* are provided.

Additional keywords: morphology, phylogeny, Scelioninae, taxonomy.

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Introduction

The platygastroid wasp *Echthrodesis lamorali* Masner is an endoparasitoid of the egg stage of two intertidal spiders, *Desis formidabilis* (O.P. Cambridge) (Desidae) and *Amaurobioides africanus* Hewitt (Anyphaenidae). It is remarkable in that the species is adapted to a marine environment, becoming completely submersed by sea water and exposed to intensive wave action in the intertidal zone at each high tide (Lamoral 1968; Masner 1968). Presumably due to the exclusive association with this habitat, *E. lamorali* has become highly modified and adapted for life in rocky areas of the intertidal zone. Morphological adaptations include extensive wing reduction in both sexes (Carey *et al*. 2006), a compact body form that probably facilitates movement in very confined spaces and a covering of dense setae (Figs 5, 6), hypothesised to trap air during daily immersion in sea water (Masner 1968). The first two of these morphological traits are likely to be reductional synapomorphies that are exhibited by several genera of Platygastroidea that parasitise spider eggs (e.g. *Baeus* Haliday, *Mirobaeus* Dodd, *Mirobaeoides* Dodd, *Neobaeus* Austin), and are thought to facilitate entry through the silk walls of spider egg sacs (Austin 1988*a*; Austin *et al*. 2005; Stevens and Austin 2007).

On first description, *Echthrodesis* was hypothesised to be closely related to *Embidobia* Ashmead, *Mirobaeus* and

Mirobaeoides (Masner 1968). This relationship was later formalised by Masner and Dessart (1972), who united them within the tribe Embidobiini along with other putatively related genera (*Endecascelio* Masner and Dessart, *Palaeogryon* Masner, *Embioctonus* Masner) (Masner 1976, 1980). *Echthrodesis* differs from these genera in the remarkable pilosity of its body, and from *Embidobia, Palaeogryon* and *Embioctonus* in its host use as these three genera parasitise eggs of Embiidina whereas *Mirobaeus* and *Mirobaeoides* (like *Echthrodesis*) parasitise spider eggs. Galloway and Austin (1984) postulated that the production of silk by such different host groups provided a possible evolutionary link in host exploitation for this tribe.

Following analysis of several morphological characters, including the ovipositor system, and host-use data (Austin 1986,1988*a*; Austin and Field 1997), all platygastroid genera parasitising spider eggs were placed in the single nominal tribe Baeini *s.l.*, whereas previously they had been distributed across three tribes (i.e. Embidobiini, Baeini and Idrini; *sensu* Masner 1976). At the same time, based on the morphology of the mandible and its host associations, *Echthrodesis* was removed from the Embidobiini and placed in the Baeini (Austin and Field 1997). Subsequently, a morphological phylogenetic analysis of the Baeini *s.l.* placed *Echthrodesis* as sister to a terminal clade comprising *Apobaeus* Masner, *Baeus*, *Mirobaeoides* and *Neobaeus* (Iqbal and Austin 2000); however, this study did not include any of the embiid egg parasitoids from the Embidobiini.

Somewhat surprisingly, recent molecular phylogenetic appraisals of platygastroid genera using multiple genes (Carey *et al*. 2006; Murphy *et al*. 2007) have revealed the spider egg parasitoids (i.e. Baeini) to be polyphyletic, with *Baeus*, *Ceratobaeus* Ashmead, *Hickmanella* Austin, *Idris* Foerster and *Odontacolus* Kieffer forming a monophyletic group, and *Mirobaeoides* and *Neobaeus* together forming an independent clade that is sister to *Embidobia*. This relationship supports a possible common origin for parasitising silk-encased host eggs, and two independent origins for parasitising spider eggs within the superfamily, as previously inferred (Masner (1968, 1976; Masner and Dessart 1972). However, an important question in platygastroid systematics remains; what are the evolutionary affinities of *Echthrodesis*? Is it related to the genera in the *Baeus* clade or the *Embidobia–Mirobaeoides–Neobaeus* clade, or does it represent a third independent lineage of platygastroids that exploits spider eggs as hosts?

Here we use sequence data from three genes, the nuclear 28S rRNA and 18S rDNA genes, and the mitochondrial cytochrome oxidase 1 (CO1) gene, to determine the affinities of *E. lamorali* with other lineages of playgastroid wasps. We also present a revised taxonomy for the genus and species, new comparative morphological information on the structure of its mouthparts and ovipositor system, and new field observations of its behaviour and biology in association with one of its host intertidal spiders, *D. formidabilis*, on the Cape Peninsula (South Africa).

Materials and methods

Field collections, observations and imaging

Egg sacs of *Desis formidabilis* were collected from the type locality of *E. lamorali*, 'The Island' at Kommetjie, 26 km south of Cape Town on the Atlantic side of the Cape Peninsula (34°8′24.33″S, 18°19′15.22″E) during July and August 2009 and May and August 2011. Visual searching in perceived optimal areas of the intertidal zone located spider colonies inhabiting limpet shells secured to the undersides of rocks or lodged in rocky crevices. Emergence and subsequent behaviour of *E. lamorali* was observed under a Wild M5A dissecting microscope in the laboratory. Photography of living specimens was undertaken with a Nikon D80 and a Nikkor 105-mm macro lens. Images of live and preserved specimens were acquired using the EntoVision multiple-focus imaging system. This system comprises a Leica M16 microscope with an attached JVC KY-75U 3-CCD digital video camera. Cartograph 5.6.0 was used to merge an image series into a single in-focus image. Lighting was achieved using techniques summarised in Buffington *et al*. (2005), Buffington and Gates (2009) and Kerr *et al*. (2009). Images included in this paper are available on WaspWeb (http://www.waspweb.org), and are archived at Morphbank (http://www.morphbank.net) and in Specimage (http://specimage.osu.edu) (the image database at The Ohio State University).

Specimen preparation

For mouthpart and genitalic dissections, the head and metasoma from both male and female specimens were boiled in 10% lactophenol for 30 min, followed by a distilled-water wash, and then dissected using tweezers (Dumont no. 5) and a no. 2 entomological pin with a sharp tip. The maxillo-labial complex, male aedeagus, female ovipositor and terminal tergites and sternites were extracted. These structures were placed in a micro-concavity slide in 10% NaOH for 30 min, followed by glacial acetic acid for 10 min (maxillo-labial complex, ovipositor and aedeagus) or 30 min (terminal tergites and sternites). Structures were transferred to 70% ethanol (30 min) followed by 96% ethanol (30 min) and clove oil (30 min), then mounted in Canada Balsam. Structures used for SEM examination were dried using hexamethyldisilazane. Microscopic slides were examined using a Euromex GE 3045 microscope and drawings were made using a Reichart drawing tube.

Terms and abbreviations

Morphological terminology generally follows Masner (1980) and Mikó *et al*. (2007), with terms for ovipositor structures following Austin and Field (1997), those for the maxillo-labial complex as labelled in Fig. 1, and those for male genitalia after Johnson (1984). Standard abbreviations are used for the following morphological features: antennomeres (A1, A2, etc); metasomal tergites (T1, T2, etc); metasomal sternites (S1, S2, etc).

Anatomical terms used in the descriptions are linked to concepts in the Hymenoptera Anatomy Ontology (HAO; Yoder *et al*. 2010, Hymenoptera Anatomy Portal (http://portal.hymao.org, accessed on 25 March 2010)) (Table S1, available in the Supplementary Material). Identifiers in the format HAO_XXXXXXX represent concepts in the HAO and are provided to enable readers to confirm their understanding of the concepts being referenced. The identifier can also be used as a URI (universal resource identifier) by appending the identifier to 'http://purl.obolibrary.org/obo/' (e.g. http://purl.obolibrary.

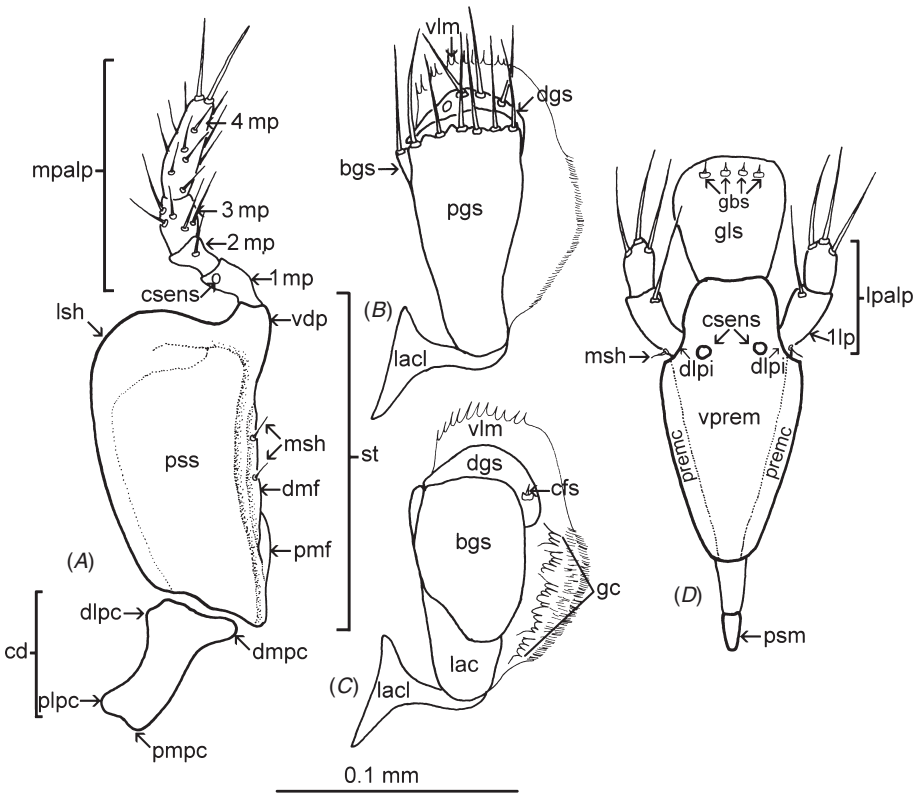

Fig. 1. Morphological terms used for mouthparts in the descriptions of *Echthrodesis*. Abbreviations defined in Table S1. For definitions of terminology see: HAO; Yoder *et al*. 2010, Hymenoptera Anatomy Portal (http://portal.hymao.org).

org/obo/HAO_0000124). URLs in the format http://purl.org/net/hao/HAO_0123456 resolve to the HAO's community-based resource that includes additional images, notes and other metadata.

The external hyperlinks are explicitly cited in the endnotes so that users of the printed version of the paper have access to the same resources, insofar as the external information conforms to standards developed and maintained through the organisation Biodiversity Information Standards (Taxonomic Database Working Group). Taxonomic names, where appropriate, have been registered with Zoobank (http://www.zoobank.org).

The following abbreviations are used for collections: Canadian National Collection of Insects, Ottawa (CNCI); C. A. Triplehorn Insect Collection, Ohio State University, Columbus (OSUC); Iziko South African Museum (SAMC); KwaZulu–Natal Museum, Pietermaritzburg (NMSA); Waite Insect and Nematode Collection, University of Adelaide, Adelaide (WINC).

Project information

This work is a product of the Platygastroidea Planetary Biodiversity Inventory, funded by the USA National Science Foundation (N.F. Johnson and A.D. Austin). One of the primary objectives of this project is to use biodiversity informatics tools to accelerate the taxonomic process and to make real-time collaboration possible within the community of researchers with appropriate expertise. Details on the data associated with specimens can be accessed at the following link: hol.osu.edu, and entering the identifier (e.g. OSUC 497717) in the form [*urn:lsid:biosci.ohio-state.edu:osuc_occurrences:*[specimen ID] where the spaces in the specimen ID are replaced by two underscores (__), i.e. *urn:lsid:biosci.ohio-state.edu:osuc_occurrences:OSUC__*497717.]

Taxon sampling and design of the phylogenetic analyses

To determine the likely relationships of *Echthrodesis*, two analyses were undertaken. In analysis 1, sequence data for the CO1 and 28S rDNA genes were employed for a comprehensive sampling of 22 species (representing seven genera and including *E. lamorali*) of platygastroids known to parasitise spider eggs, plus an additional 10 playgastroid species representing 10 genera associated with a range of insect hosts (Table 1). Of the 22 species that parasitise spider eggs, nine were newly sequenced while the remaining came from either Carey *et al*. (2006) or Murphy *et al*. (2007) (Table 1). Two platygastrids, *Piestopleura* sp. and *Synopeas* sp., were used as outgroups based on the results of Murphy *et al*. (2007).

To further test the relationships of *Echthrodesis*, the Bayesian analysis presented in Murphy *et al*. (2007) was repeated with sequences of *Echthrodesis* added to the dataset (Analysis 2). This analysis employed sequence data for three genes (CO1, 28S rDNA, 18S rDNA; see below for details) and had the advantage of placing *Echthrodesis* among a far greater sampling of taxa across the whole superfamily (86 species

Table 1. Species and sequence data (GenBank numbers) for specimens used for phylogenetic analysis 1

* = sequences taken from Carey *et al*. (2006) or Murphy *et al*. (2007); host data mostly from Austin and Field (1997); vouchers in OSUC = Ohio State University Collection, UA = voucher collection of A. D. Austin, The University of Adelaide

Taxon	Specimen code	Known or likely host group	Locality	COI	28S
Insect-egg parasitoids					
Dyscritobaeus sp. *	UA-M429	unknown	Australia	DQ888385	DQ888441
Embidobia sp.*	UA-M428	Embioptera	Yemen	DQ888386	DQ888442
Gryon sp. *	UA-M430	Heteroptera	Australia	DQ888390	DQ888448
Macroteleia sp.*	UA-M368	Tettigoniidae	Yemen	DQ888393	DQ888454
Oxyscelio sp.*	UA-M422	?Orthoptera	Australia	DQ888399	DQ888465
Phanuromyia sp.*	UA-M372	Fulgoroidea	Costa Rica	DQ888400	DQ888469
Piestopleura sp.*	UA-M318	unknown	Australia	DQ888409	DQ888477
Synopeas sp.*	UA-M334	Cecidomyiidae	Australia	DQ888411	DQ888480
Telenomus crassiclava Nixon*	UA-M304	Lepidoptera	Costa Rica	DQ888419	DQ888491
Trimorus sp.*	UA-M403	Heteroptera	Australia	DQ888424	DQ888498
Spider-egg parasitoids					
Baeus sp. 1	UA-M458	Araneae	Australia	KF679308	KF679321
Baeus sp. 2	UA-M460	Araneae	Australia	KF679319	KF679337
Baeus sp. 3	OSUC248071	Araneae	French Guiana	KF679310	KF679339
Baeus sp. 4	OSUC248075	Araneae	French Guiana	KF679315	KF679333
Echthrodesis lamorali Masner	OSUC173845	Araneae	South Africa	KF679306	KF679329
Echthrodesis lamorali Masner	OSUC173844	Araneae	South Africa	KF679313	KF679331
Echthrodesis lamorali Masner	OSUC173846	Araneae	South Africa	KF679304	KF679335
Hickmanella sp.*	UA-M444	Araneae	Australia	KF679311	KF679332
Idris sp. 1*	UA-M280	Araneae	Australia	DQ888392	DQ888451
Idris sp. 2	UA-M462	Araneae	Australia	KF679314	KF679325
Idris sp. 3*	UA-M144	Araneae	Australia	DQ888391	DQ888450
Idris sp. 4	UA-M443	Araneae	Australia	KF679301	KF679326
Idris sp. 5	UA-M457	Araneae	Australia	KF679299	KF679336
Idris sp. 6	OSUC176058	Araneae	USA	KF679302	KF679327
Idris (*Ceratobaeus*) *masneri* Austin[#]	UA-M449	Araneae	Australia	KF679303	KF679330
Idris (*Ceratobaeus*) sp. 2	UA-M456	Araneae	Australia	KF679317	KF679324
Idris (*Ceratobaeus*) sp. 3	UA-M459	Araneae	Australia	KF679318	KF679328
Idris (*Ceratobaeus*) sp. 4	UA-M442	Araneae	Australia	KF679300	KF679322
Idris (*Ceratobaeus*) sp. 5	OSCUC176054	Araneae	Australia	KF679312	KF679340
Mirobaeoides sp. *	UA-M282	Araneae	Australia	DQ888375	DQ888429
Mirobaeoides sp.*	UA-M464	Araneae	Australia	KF679307	KF679334
Neobaeus novazealandensis Austin*	UA-M438	? Araneae	New Zealand	KF679309	KF679341
Odontacolus sp.	OSUC181562	Araneae	Peru	KF679316	KF679320

representing 59 genera). However, this analysis included only six taxa (including *Echthrodesis*) known to parasitise spider eggs.

DNA extraction, amplification and sequencing

Specimens were processed in the Austin laboratory at The University of Adelaide (UA specimen codes in Table 1) or in the Johnson laboratory at Ohio State University (OSUC specimen codes in Table 1). For the UA specimens, genomic DNA was extracted from ethanol-preserved tissue using the Puregene® DNA Purification Kit (Gentra Systems Inc.). For the OSUC material, non-destructive DNA extraction was performed using the DNeasy extraction protocol (Qiagen Inc., cat. no. 69506) as modified by C. D. Zhu and J. S. Noyes (unpubl. data): in brief, individual specimens were initially softened in 70% ethanol at room temperature for 2 h; vortexing in step 2 of the published protocol was modified by mixing the reaction gently and incubating at 55°C for 24 h with 40 µL of proteinase K; the mixture was then stored at −20°C for 24 h; the intact specimen was then removed from the tube and prepared for standard mounting; the reaction was incubated for 10 min at 70°C after addition of Buffer AL; then 200 µL of cold ethanol (96–100%) was added to the supernatant; finally, the final suspension of DNA from the column membrane (Step 7) was performed with two washes of Buffer AE previously warmed to 55–70°C.

Partial sequences were obtained from a ~600 base pairs (bp) product obtained by PCR amplification of the mitochondrial protein coding CO1 gene using the primers C1-J-1718 and C1-N-2329 (Simon *et al*. 1994). PCR amplification of an ~800 bp segment of the nuclear 28S rDNA gene, spanning the D2 and D3 segments, was implemented using the primers D2-3665 F and D3-4413 R (Gillespie *et al*., 2005). Amplification of an ~800 bp segment of the nuclear 18S rDNA gene for *E. lamorali* only was implemented using the primers *18S*ai and *18S*bi (Whiting *et al*. 1997).

PCR amplifications were carried out in 25 µL containing PCR buffer, 0.2 mM of each dNTP, 0.4 µM of each primer, 2 mM $MgCl_2$, 0.5 units of AmpliTaq Gold® DNA Polymerase (Applied Biosystems Inc.) and 25–100 ng of genomic DNA. Thermocycling conditions were: an initial denaturation step of 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, an annealing temperature of 50°C for 30s, and an extension temperature of 72°C for 30 s. This was then followed by an additional extension of 72°C for 3 min. PCR products were purified using the Ultraclean™ PCR Clean-up™ Kit (MOBIO Laboratories Inc.). Sequencing reactions were performed using ABI Big Dye Terminator Chemistry and fragments were resolved on an ABI 3700 sequencer.

Sequence alignment and phylogenetic reconstruction

Sequence alignment of the three genes was undertaken following Murphy *et al*. (2007). The CO1 gene was aligned by eye, as few insertion/deletion events were present. The amino acid sequence was translated as a test for the presence of nuclear paralogues, e.g. stop codons. Alignment of both nuclear RNA genes (28S and 18S rRNA) was undertaken using Clustal X (Thompson *et al*. 1997) and employing several gap opening/gap extension schemes (gap to change costs 1 : 1 1 : 2 1 : 5 1:10). Regions of uncertain alignment that varied markedly between different alignment schemes were deleted (Gatesy *et al*. 1993), and a single alignment of each gene was used for subsequent analyses.

Maximum parsimony (MP) analyses were performed in PAUP* 4.0b10 (Swofford 2002) using the heuristic search algorithm with 100 random sequence addition replicates to help eliminate bias from taxon ordering in the datasets. Gaps were treated as missing data and characters were weighted equally. Confidence in the MP trees was assessed from 1000 non-parametric bootstrap pseudo-replications.

Bayesian phylogenetic analyses were performed for each gene alignment separately and for concatenated data using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). The appropriate model of evolution was chosen by the Akaike information criterion using Modeltest (Posada and Crandall 1998) on all data partitions separately (28S rRNA, 18S rRNA and the separate codon positions of CO1). The optimal partitioning strategy was examined using Bayes factor analysis (Brandley *et al*. 2005) comparing the harmonic means of the log-likelihoods of different possible partition combinations, for example: no partitions; three partitions (18S + 28S + CO1); five partitions (18S + 28S + CO1 1st codon pos + CO1 2nd codon pos + CO1 3rd codon pos). The optimal partitioning chosen for 'Analysis 1' was the partitioning of 28S + CO1 1st codon pos + CO1 2nd codon pos (with 3rd codon pos removed), whilst the partitioning for 'Analysis 2' was similar, with the addition of an 18S partition. MrBayes analyses were run across four chains for five million generations sampling every 100 generations, and stationarity was determined from an examination of log-likelihoods and model parameters. Trees recovered before stationarity were discarded and Bayesian posterior probabilities of each bipartition, representing the percentage of times each node was recovered, were calculated from the remaining trees. Multiple runs were performed to assess that parameters were not considerably different at stationarity based on alternate prior probabilities.

Molecular phylogenetic results

Analysis 1

Sequences for CO1 and 28S rDNA were generated for all taxa. The CO1 alignment consisted of 538 bp and contained 233 parsimony-informative sites. *Mirobaeoides* contained an insertion of one codon but all other taxa had uniform sequence lengths. The 28S rRNA alignment consisted of 720 bp and had 288 parsimony-informative sites. A comparison of the topologies and Bayesian support between the gene regions suggested no major phylogenetic incongruence (trees not shown). Given this, the sequence data for the two genes were concatenated for further analysis.

The 1258 bp combined CO1 and 28S rRNA alignment had 521 parsimony-informative sites when the ambiguous regions of 28S rRNA and the third codon position of CO1 were excluded. The Bayesian tree for the concatenated data (Fig. 2) resolves two separate clades associated with parasitising spider eggs; one comprising the genera *Odontacolus, Idris, Hickmanella* and *Baeus* with high Bayesian support (92%), and a second clade comprising *Echthrodesis, Neobaeus* and *Mirobaeoides* with low Bayesian support (61%). *Embidobia* is contained within the latter clade and is sister to *Mirobaeoides* (100%). The MP tree (not shown) was generally less resolved compared with the Bayesian tree but the general pattern was the same with regard to resolving the same two separate spider-egg parasitising clades and the position of *Echthrodesis* and *Embidobia*.

Analysis 2

The Bayesian re-analysis of the Murphy *et al*. (2007) three-gene dataset with the inclusion of *E. lamorali* estimated an almost identical set of relationships as the original study (see Supplementary Fig. 1). As in analysis 1, two independent clades associated with spider eggs were resolved, with *Echthrodesis* being placed in the second clade as sister to *Mirobaeoides* (Bayesian support 96%), and *Embidobia* sister to these two genera (67%). *Neobaeus* was not included in this re-analysis of the 2007 data.

Biology and behaviour

Host spider

Desis formidabilis (Fig. 3*B–D*) inhabits the bolder-strewn intertidal zone (Fig. 3*A*) and lives inside limpet shells, sometimes communally, with up to five (but more commonly one or two) individuals inhabiting a single shell. Eggs are laid within a silken compartmentalised wedge-shaped structure that lines the inside edge of the shell (Fig. 3*A*, *B*). Each compartment comprises a purse-like structure that is sealed from other compartments, but not all of these contain eggs. Each egg sac within a shell consists of five or six compartments, each containing different stages of development from newly oviposited eggs (Fig. 4*B*), through spider embryos to recently emerged spiderlings (1st instar) and older spiders (2nd and, possibly, 3rd instars), which stay inside the sealed compartment. Spider egg batches in individual compartments comprise 8–19 eggs.

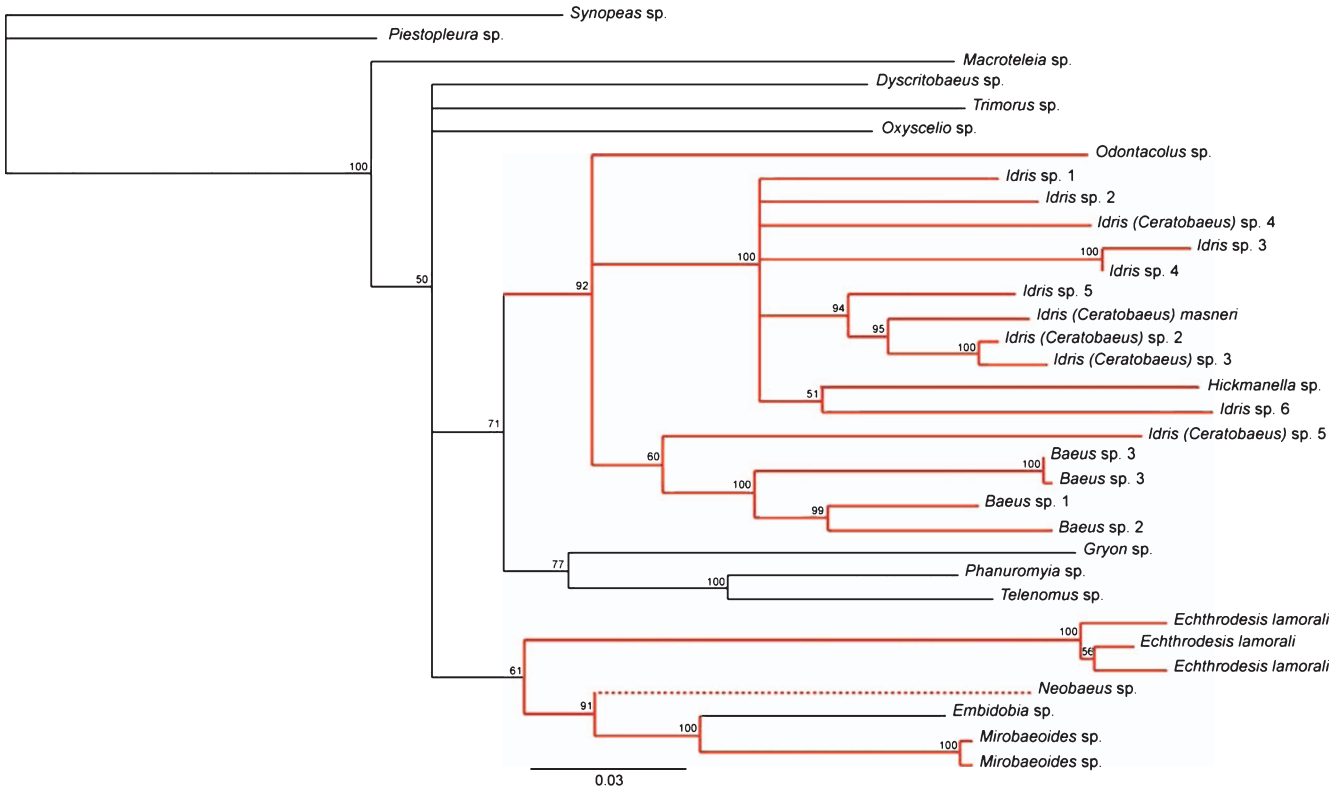

Fig. 2. Phylogeny based on the Bayesian analysis of nuclear 28S rRNA and mitochondrial CO1 gene sequences (with 3rd base removed). Red solid lines = taxa known to parasitise spider eggs; red broken line = taxon suspected of parasitising spider eggs; black lines = taxa that parasitise eggs of insect hosts (see Table 1).

Wasp development and emergence

A single wasp develops and pupates within each host egg, as is the norm for platygastroids (Austin *et al*. 2005), although there are some exceptions such as *Platygaster zosine* Walker, which is polyembryonic (Austin *et al*. 2005), and *Telenomus monilicornis* Ashmead, *T. dendrolimi* Matsumura and *T. fariai* Lima, which are gregarious (5–10 wasps emerging from one host egg) (Johnson 1984). During wasp development, the off-white, circular host eggs change shape and colour such that just before wasp emergence they have become more ovoid, brown in colour and papery. Adult wasps chew their way out of their host egg, with males usually emerging slightly before females.

Mating

Male wasps actively 'wrestle' each other for an opportunity to mate with a female. As many as three males may be involved in a tussle over a female that is chewing her way out of her host egg. The male actively antennates the female on her head and mesosoma and touches her with his mandibles, appearing to almost bite her behind the head. The male straddles the front portion of the female that is protruding from the host egg and may help to chew the exit hole allowing the female to escape. Once she is free, the male mounts her from behind, antennating and appearing to bite her head and pronotum. The latter action may involve mandibular gland secretion. Soon after, the male moves backwards such that his metasoma is overlapping the female's metasoma. He may briefly clean his aedeagus with his back legs before inserting it into the female in a downwards and forward movement of the metasoma. During copulation the male clasps the female's metasoma with his fore and mid legs. The act of copulation lasts for 7–9 s, after which the male immediately dismounts and loses interest in the female. Other males may subsequently attempt to copulate with her, but have not been observed to be successful. Males often mount other males, straddling them from behind and repeatedly antennating as they do with females, occasionally attempting to insert their aedeagus.

Oviposition

Wasps chew a small circular exit hole in the silken egg sac to escape, with often more than one exit hole being produced (Fig. 4*A*), sometimes adjacent to each other. Female wasps proceed to search for other egg sac compartments within the same limpet-shell retreat. They chew a circular entrance hole, just large enough for them to fit through, in the side wall of a compartment containing early-stage host eggs. Once inside the compartment, the female antennates the surface of the eggs (Fig. 4*B*) and, if the eggs are acceptable, proceeds to oviposit into each egg individually (Fig. 4*C*, *D*). Up to three females have been observed ovipositing inside a single egg compartment, with each having chewed its own entrance hole in the side of the silken sac. Host-egg mortality within a parasitised egg batch was 100% ($n = 7$). The sex ratio of hatching wasps is skewed, being highly female-biased with only 15 males reared from 118 parasitised eggs.

Fig. 3. *Desis formidabilis*. (*A*) Habitat, type locality of *E. lamorali*; (*B*) habitus, in limpet shell nest; (*C*) head, anterior view, showing chelicerae; (*D*) two spiders in same nest with pink egg sac on right.

Taxonomy

Echthrodesis Masner

(Figs 1, 5*A–D*, 6*A–D*, 7*C*, 8*A–F*, 9*D–I*)

urn:lsid:zoobank.org:act:4F559F0A-0816-4537-BC0D-995A5ED098EA
urn:lsid:biosci.ohio-state.edu:osuc_concepts:476
Echthrodesis Masner, 1968: 197; Johnson, 1992: 370 (catalogued); Austin & Field, 1997: 39 (description of ovipositor system).
Type species: *Echthrodesis lamorali* Masner, by monotypy and original designation.

Diagnosis

Among genera in the tribes Embidobiini and Baeini, *Echthrodesis* shares with *Endecascelio* a labial palp comprising two sclerites and the presence of a conspicuous principal carina on the stipes that is distolaterally angled. *Echthrodesis* is easily separated from *Endecascelio* and all genera in the Embidobiini and Baeini by the dense pilosity of its body (although *Neobaeus* is moderately hairy on the dorsal surface). It differs from *Neobaeus* and *Baeus* in having narrow laterotergites attached to the sternites (rather than wide and free laterotergites). In addition, *Echthrodesis* differs from *Neobaeus, Mirobaeus* and *Mirobaeoides* by having a rounded (rather than a carinate) vertex and hirsute eyes, and from *Embidobia* by the 4–2 palpal formula, having the metasoma broadly and closely abutted to the mesosoma (i.e. sessile in female, sub-sessile in male), and a basally narrowed and longitudinally costate T1. Like *Baeus*, *Neobaeus* and *Mirobaeoides*, *Echthrodesis* has T2 of the metasoma as the longest tergite, whereas in *Mirobaeus* and virtually all baeine genera T3 is the longest (N.B. in *Baeus* and *Mirobaeoides* T1 is often vertical and hidden by the posterior mesosoma so that the first visible tergite (=T2) appears to be the longest and should not be mistaken for T1).

Description

Head. Occipital carina complete. Frons flat to weakly convex. Ocular ocellar line (the shortest distance between the inner orbit of the eye and the outer margin of the lateral ocellus; OOL) > ocellar diameter. Submedian carina on frons absent. Orbital carina on frons absent. Central keel on frons present, short. Lower portion of central keel simple. Torulus orientated anterolaterally to lateral. Fan-like striae arising from anterior mandibular articulation. Malar sulcus present. Setation of compound eye present, very short. Genae densely setose.

Mouthparts (Fig. 1). Labrum internal, hidden beneath clypeus. Mandibles tridentate. Mandibular dentition transversely orientated. Maxillo-labial complex (MLC):

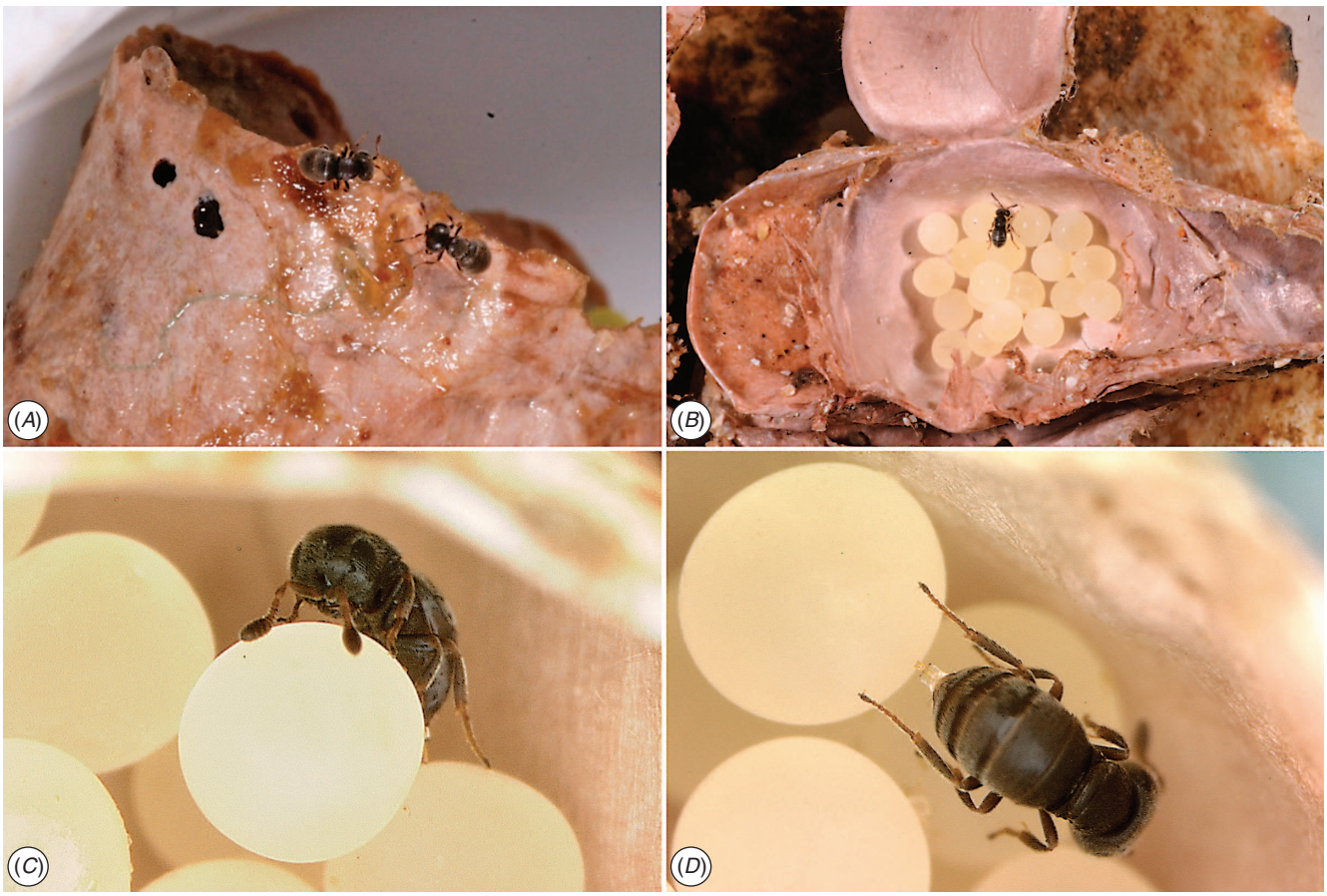

Fig. 4. *Echthrodesis lamorali*. (*A*) Adult wasps exiting natal egg sac showing two chewed exit holes; (*B*) female ovipositing into spider egg within egg sac; (*C*) female holding onto one egg while ovipositing into another; (*D*) close up of ovipositing female showing ovipositor inserted into egg.

maxillae (mx) comprising a well developed cardo (cd), more weakly sclerotised than stipes (st). Shape of cardo: distance between proximal lateral projection (plpc) and distal mesal projection (dmpc) almost equal to distance between proximal mesal projection (pmpc) and distal lateral projection (dlpc). Posterior stipital sclerite (pss) massive, well developed, with median or subapical area broader than basal area. Posterior stipital sclerite devoid of sensilla, except for one or two mechano-sensory hairs (msh), situated near point of insertion of lacinial lever (lacl). Proximomedial stipital flange (pmf) present. Distomedial stipital flange (dmf) present. Principal carina of stipes distolaterally angled (lsh). Ventral dististipital process (vdp) conspicuous. Segmentation of maxillary palps (mpalp) heteronomous. All four sclerites of the maxillary palp with mesal and lateral sides approximately symmetrical, 4th sclerite the longest, ~2.8–3 × as long as wide. Maxillary palpal sclerite sensilla: 1st sclerite (1mp) hairless, with apical large campaniform sensillum (csens); 2nd sclerite (2mp) almost glabrous with 1 or 2 trichoid sensilla in apical half; 3rd sclerite (3mp) covered with relatively short trichoid sensilla, distributed in 1 or 2 transverse rows; 4th sclerite (4mp) covered with numerous trichoid sensilla; apex with two strong trichoid sensilla. Lacinia (lac) concealed. Velum (vlm) with fringed distal edge. Lateral side of galeo-lacinial complex with same degree of sclerotisation as rest of galeo-lacinial complex. Basal galeal sclerite (bgs) postioned sub-apically on galeo-lacinial complex, surrounding lateral side of proximolateral galeal sclerite (pgs). Basal galeal sclerite (bgs) with straight internal edge. Dorsal lobe of basal galeal sclerite with one or two hairs. Proximolateral galeal sclerite (pgs) glabrous. Distal end of proximolateral galeal sclerite (pgs) with two or more setae in one row. Proximolateral (pgs) and distolateral galeal sclerites (dgs) separated by a membranous structure. Distolateral galeal sclerite with setae in a single row. Distolateral galeal sclerite well developed, broader than high. Galeal comb (gc) present. Galeal coeloconicum sensillum (cfs) present on distolateral galeal sclerite (dgs). Postmentum (psm) of normal size. Lateral faces of prementum not continuous posteriorly. Premental carina (premc) visible as a narrow stripe on lateral sides of ventral premental area (vprem). Ventral, premental area (vprem) diamond-shaped. Two symmetrical campaniform premental sensilla (csens) under distolateral premental incisions (dlpi). Trichoid sensilla on ventral premental area absent. Distolateral premental incisions conspicuous. Labial palp (lpalp) present. Segmentation of labial palps heteronomous. Labial palp comprising two sclerites, first sclerite obviously longer than second. Mechano-sensory hairs (msh) on proximal part of 1st sclerite of labial palp (1lp) present. Glossa dorsally with basiconic sensilla (gbs). Ventral side of glossa (gls) glabrous. Glossal styloconic sensilla absent. Four glossal basiconic sensilla (gbs).

Fig. 5. Female of *Echthrodesis lamorali*. (*A*) Habitus, dorsal view; (*B*) habitus, lateral view; (*C*) head, anterior view; (*D*) head and mesosoma lateral view. Scale bars in millimetres.

Antenna. 11 female antennomeres. Radicle positioned parallel to A1. A1 more-or-less cylindrical. A3 of female distinctly shorter than A2. Apical antennomeres of female widened to form antennal clava. Claval formula: 1-2-2-1. 12 male antennomeres. Fifth male antennomere bearing tyloids.

Mesosoma. Transverse pronotal carina absent. Posterolateral edge of pronotum in dorsal view bifid, fitting around tegula. Vertical epomial carina absent. Netrion absent. Flexion of anterior margin of mesoscutum absent, mesoscutum abutting pronotum anteriorly. Skaphion absent. Notauli absent. Mesoscutellum semielliptical, strongly transverse. Apical spines of mesoscutellum absent. Metascutellum absent. Propodeal metasomal depression extending anteriorly to abut metanotum. Lateral propodeal projection absent. Mesopleural pit absent. Posterodorsal margin of mesopleuron rounded. Mesosomal foamy plates absent. Single mid and hind tibial spur. Pretarsal claws with laminate ridges basally. Tegula present. Female apterous; male micropterous with no tubular veins.

Metasoma. Female with 7 terga and 6 sterna. Male with 8 terga and 7 sterna. Metasoma sessile, closely abutting mesosoma. Laterotergites present and narrow. Laterosternites present. T2 slightly longest, T1 and T3 subequal in length. Dorsal setal fields absent. Basal crenulae absent. Apical margin of apical tergum of male evenly arcuate. Anterior margin of S1 straight to weakly concave. Felt fields absent. Apical sternite of male strongly broadened, width 4 × length. Transverse apodeme present in middle of apical sternite of male. Medial longitudinal apodeme of apical sternite of male absent. Apical sternite of female 2.6 × wider than long. Medial longitudinal apodeme of apical female sternite absent. Cerci flat, with 4–5 pairs of bristles, 2 pairs elongate, 2.6 × longer than T6.

Male genitalia. Basal ring aedeagus 0.33 × total aedeagal length, 0.5 × length of aedeagovolsellar shaft. Aedeagal apodemes merged in basal half, distinct apically. Digitus volsellaris apically with four concavities in a single row, three with short digital teeth.

Female ovipositor system. *Ceratobaeus*-type. Ovipositor elongate, 0.65–0.70 × length of metasoma. Proximal arms slender, short, 0.05 × ovipositor length. Gonoplacs elongate, 0.7 × ovipositor length. Second gonocoxa 0.5 × gonoplac

Fig. 6. Male of *Echthrodesis lamorali*. (*A*) Habitus, dorsal view; (*B*) habitus, lateral view; (*C*) head, anterior view; (*D*) head and mesosoma lateral view. Scale bars in millimetres.

length. Proximal part of ventral membranous plate present. Tubular A9 nearly 3 × combined length of T6–T8. Lateral apodemes on T7+T8 short, less than 3 × length of T6.

Morphological comparison of specific characters

There are several characters that are likely to be informative for inferring phylogenetic relationships among tribes and genera of platygastroid wasps (Austin and Field 1997), but these still need assessment within the framework of a comprehensive phylogenetic analysis. The following character systems are likely to be informative.

Female ovipositor system

The most striking difference between *Echthrodesis* and other genera comprising the Embidobiini and Baeini is the absence of a medial apodeme on the apical sternite (Fig. 8*A*) and, to a lesser degree, the shortened lateral apodemes (Fig. 8*D*). The absence of a sternal medial apodeme is known for only nine genera of platygastroids. Other characters, such as the length of the proximal arms, gonoplacs and tubular A9 (Fig. 8*D*, *F*) all need to be assessed across a wider array of taxa as they are likely to show some intergeneric variation, as is known to occur among *Idris* spp. (A. D. Austin, unpubl. data).

Mouthparts

The maxillo-labial complex (MLC) of *Echthrodesis* is strikingly different to that of other members of the Baeini and Embidobiini (Fig. 7*A–F*), in part because of the palpal formula (4 : 2 in *Echthrodesis*; 3 : 2 in *Endecascelio*; 2 : 1 in *Embidobia*, *Mirobaeoides*, *Mirobaeus*, *Idris, Embioctonus* and *Palaeogryon*; 1 : 1 in *Baeus*). Although labial palps have one sclerite in *Embidobia*, *Mirobaeoides*, *Mirobaeus*, *Idris* and *Baeus*, these genera can be divided into two groups on the basis of the shape/development of the labial palps: *Baeus* and *Idris* have the labial palps reduced/atrophied and without a mechano-sensory hair on their proximal part, while *Embidobia*, *Mirobaeoides* and *Mirobaeus* have long labial palps and a mechano-sensory hair present on the proximal part. A mechano-sensory hair on the proximal part of the first sclerite of the labial palp also occurs in *Echthrodesis* and suggests the possibility of movement of the

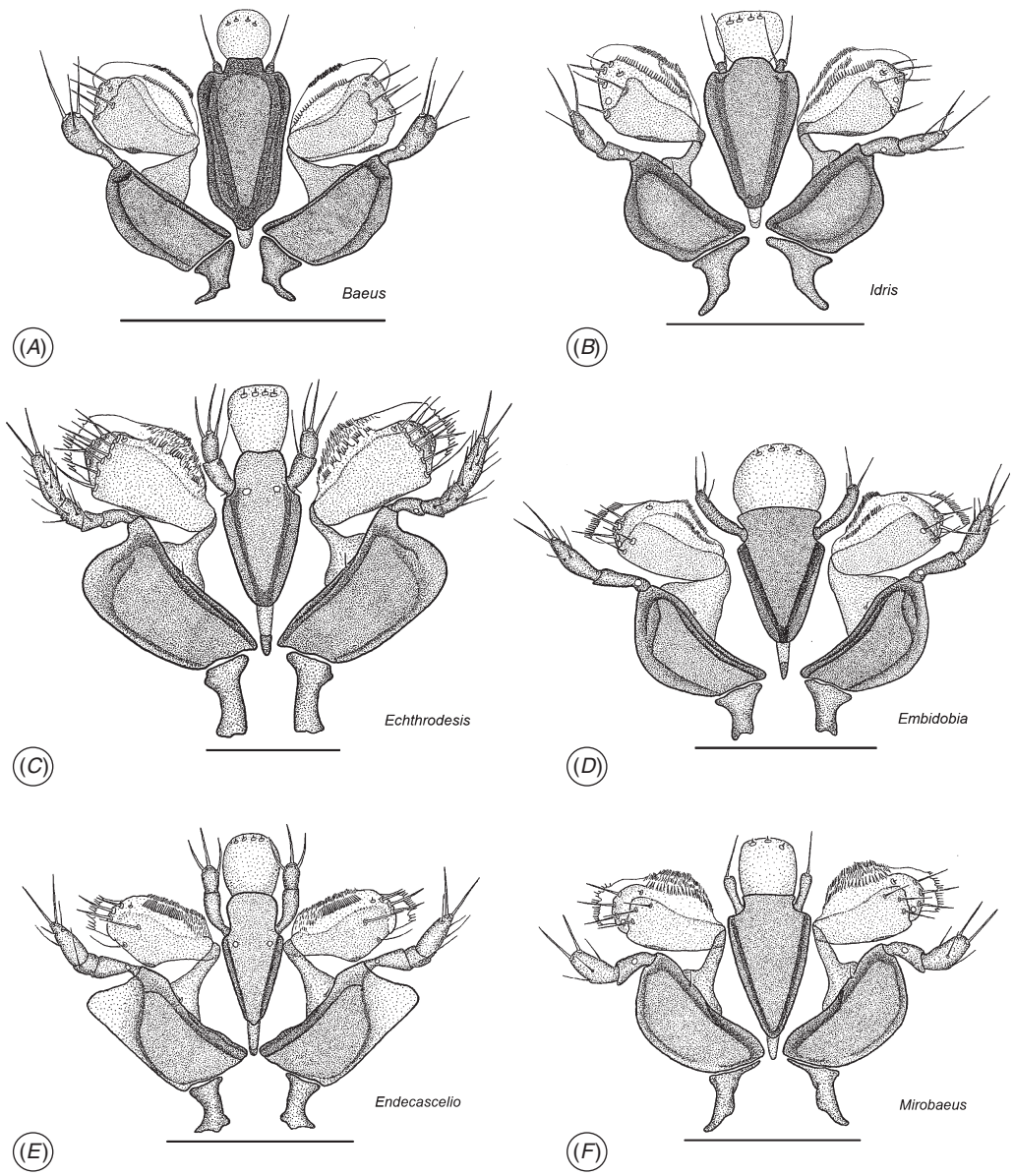

Fig. 7. Maxillo-labial complex. (*A*) *Baeus* sp.; (*B*) *Idris* sp.; (*C*) *Echthrodesis lamorali*; (*D*) *Embidobia* sp.; (*E*) *Endescascelio* sp.; (*F*) *Mirobaeus* sp. Scale bars = 0.1 mm.

labial palps. Its absence may be correlated with a reduction of the length of labial palps and very probably a reduction in movement of this sensory structure. The distal edge of the velum also differs among these genera; it is fringed in *Echthrodesis*, *Embidobia*, *Mirobaeoides* and *Mirobaeus*, but a fringe is lacking in *Idris* and *Baeus*. The postmentum is visible in *Echthrodesis*, *Embidobia* and *Idris*, but is not visible and is probably absent in *Mirobaeus*, *Mirobaeoides* and *Baeus*. Characteristic for all these genera is the absence of trichoid premental sensilla. In *Echthrodesis* and *Idris*, the prementum has two symmetrically campaniform sensilla under the distolateral premental incision, while in *Embidobia*, *Mirobaeus*, *Mirobaeoides* and *Baeus* these sensilla are absent. The glossa has three basiconic sensilla in *Mirobaeus* and *Mirobaeoides*, and four in *Echthrodesis*, *Embidobia*, *Idris* and *Baeus*.

Other potentially useful characters

Most notable are the form of the tarsi and tarsal claws (Fig. 9 comparing *Baeus* and *Echthrodesis*) and the male genitalia (Fig. 8*E*). However, the morphology of these characters has been documented for very few genera, and it will be important to first assess interspecific differences, as is known for the male genitalia of *Telenomus* (Johnson 1984), before their importance at generic level can be assessed.

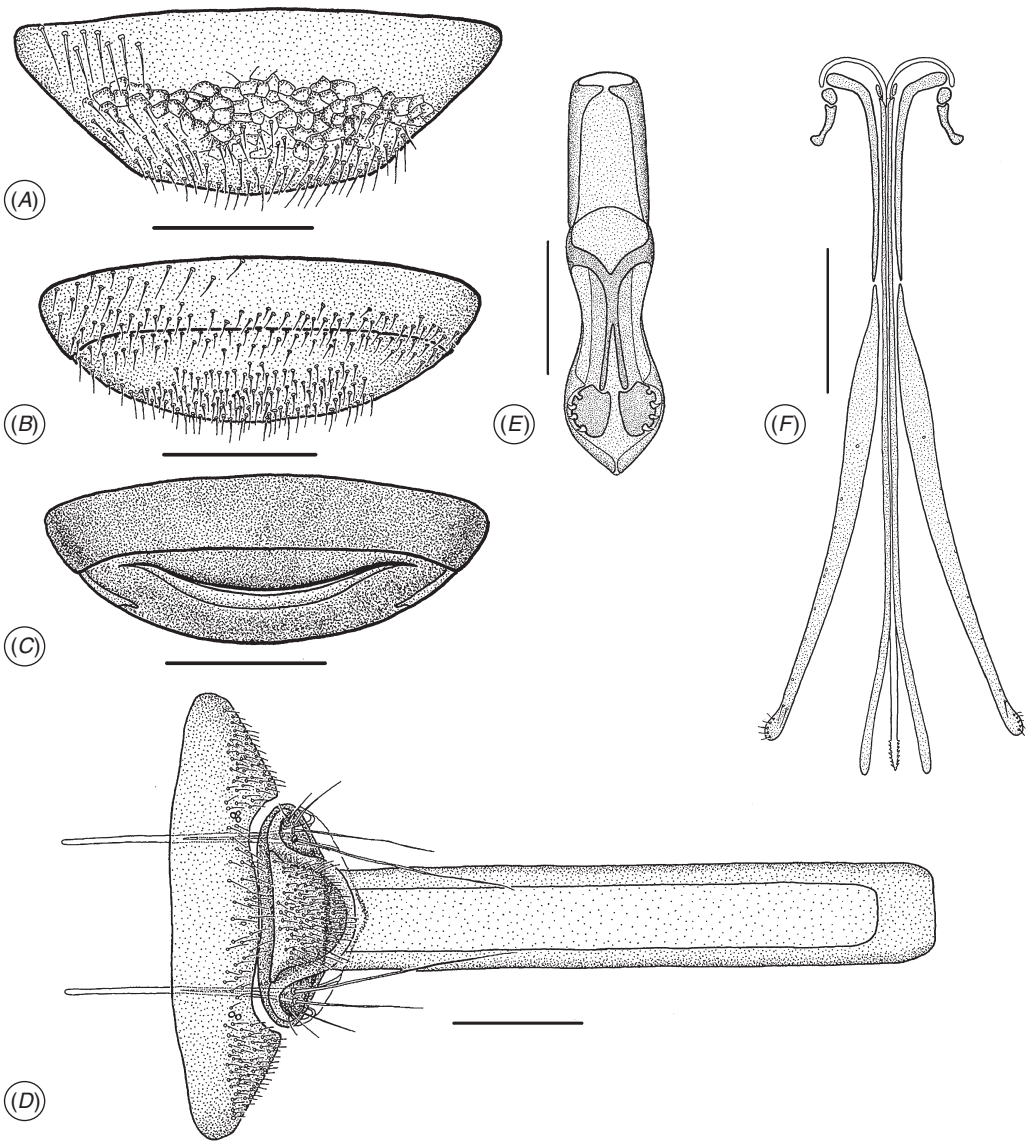

Fig. 8. *Echthrodesis lamorali.* Terminal sternites (*A–C*) and genitalia (*D–F*). (*A*) Last sternite in female without medial apodeme, external view; (*B*) last two sternites in male, external view; (*C*) last two sternites in male, internal view showing developed apodeme correlating with protractor muscles of aedeagus; (*D*) aedeagus; (*E*) ovipositor; (*F*) female T6–T9 showing short lateral apodemes and the exerted part of tubular A9. Scale bars = 0.1 mm.

Echthrodesis lamorali Masner

(Figs 5, 6, 7*A*, 8, 9*D–I*)

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urn:lsid:biosci.ohio-state.edu:osuc_concepts:4283
Echthrodesis lamorali Masner, 1968: 198; Johnson, 1992: 370 (catalogued).

Material examined

Holotype. ♀, **SOUTH AFRICA: [Western Cape]:** Cape Peninsula, Kommetjie, 'The Island', April 1966, B. Lamoral (Type no. 1168, NMSA).
Paratypes. 10♀, 1♂ same data (CNCI, NMSA).
Other material examined. **SOUTH AFRICA: Western Cape:** Kommetjie, upper intertidal zone, 34°07.998′S, 18°19.002′E, 13.v.1972, B. Lamoral, from eggs of *Amaurobioides africanus* Hewitt, 1♀ (OSUC 56500) (OSUC); Kommetjie, The Island, 34°8′24.33″S, 18°19′15.22″E, 5.vii–9.viii.2009, S. van Noort, reared from *Desis formidabilis* (Desidae) eggs, intertidal zone, 73♀, 11♂ (SAM-HYM-P030893, OSUC 173844–173846, OSUC 497717–497726) (OSUC, SAMC, WINC); 22.v.2011, 36♀, 4♂ (SAM-HYM-P044018, OSUC 497727–497736) (SAMC); 34°8.434′S, 18°19.208′E, 9.viii.2011, 9♀ (SAM-HYM-P046358) (SAMC).

Description (modified from Masner 1968)

Body length. 1.1–1.5 mm.
Colour. Generally dark brown to black. Antennae, mandibles and femora dark brown. Tarsi and tibiae

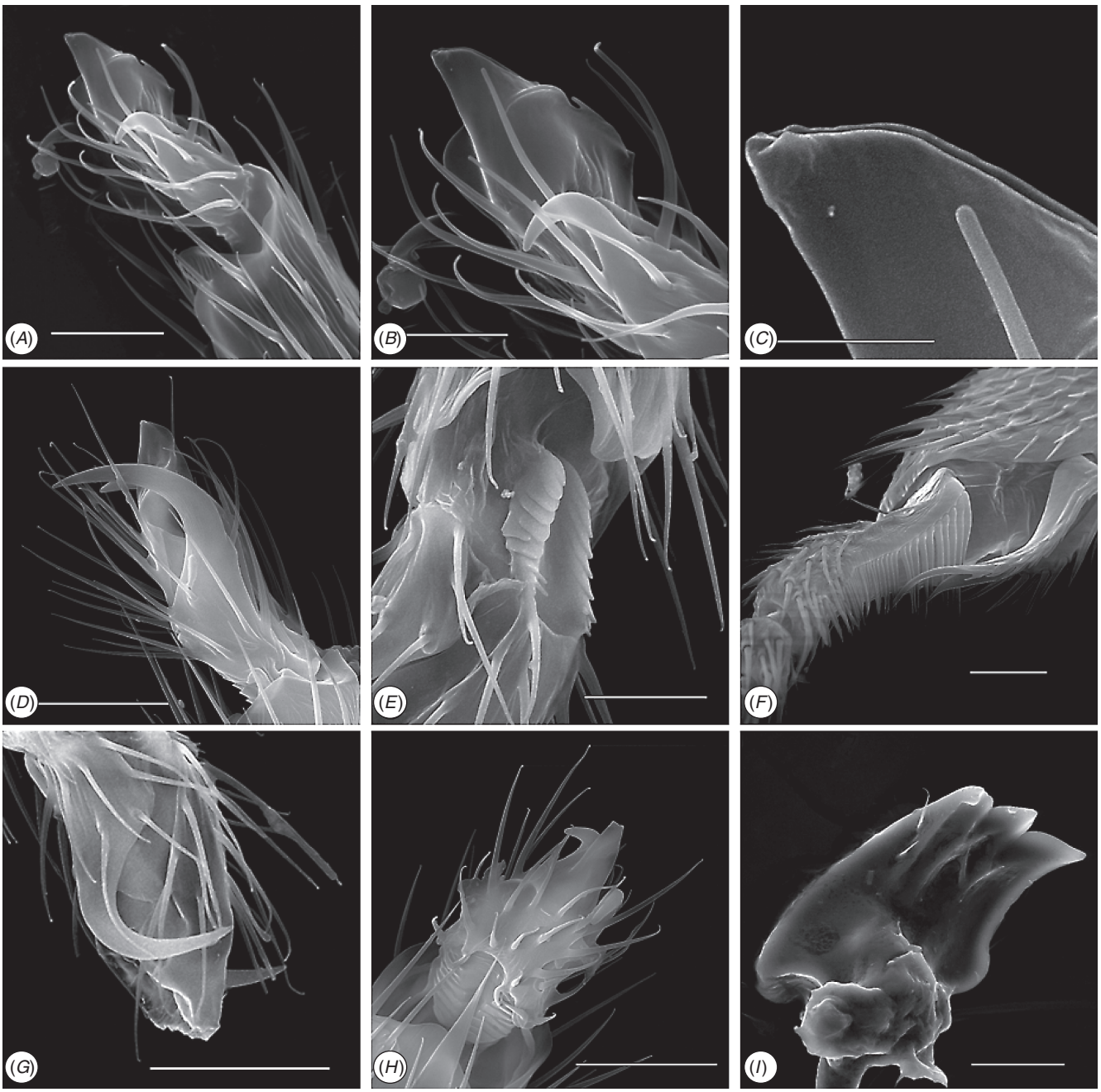

Fig. 9. *Baeus* (*A–C*)*, Echthrodesis lamorali* (*D–I*). (*A*) Fore tarsus, distal segment, claws and pulvillus, scale bar = 10 μm; (*B*) fore tarsus, claws and pulvillus, scale bar = 5 μm; (*C*) pulvillus, scale bar = 2 μm; (*D*) fore tarsus, distal segment, claws and pulvillus, scale bar = 20 μm; (*E*) fore tarsus, detail of claw base, scale bar = 10 μm; (*F*) distal end of fore tibia with modified spurs and proximal fore tarsal segment with comb of setae, scale bar = 20 μm; (*G*) mid leg tarsal claws and pulvillus, scale bar = 20 μm; (*H*) hind leg tarsal claws and pulvillus, scale bar = 20 μm; (*I*) mandible, scale bar = 50 μm.

yellow–brown. Ventral metasoma chestnut brown. Silver pilosity covering body.

Head. Head wider than long (28 : 19). Head 1.22 × wider than mesosoma. Sculpturing scaly–reticulate except for smooth patch around short keel above antennal insertions.

Mesosoma. With same scaly–reticulate sculpturing as head. Shorter than long (16 : 22). Mesoscutellum narrow, length to width (3 : 20). Mesopleuron and metapleuron surface bare and shining.

Metasoma. Moderately broad, 1.67 × longer than wide. Dorsal sculpturing same as on the head and mesosoma, but reticulation more prominent on first three tergites. T1 length to width (11 : 28). T2 length to width (15 : 30). T3 length to width (10 : 28). T4-T6 progressively shorter than T3.

Distribution

Only known from the type locality at Kommetjie, Cape Peninsula, South Africa.

Hosts

Reared from eggs of the intertidal spiders *Desis formidabilis* (Desidae) and *Amaurobioides africanus* (Anyphaenidae). These two spider species commonly commandeer old limpet shells and secure these to rocks or other shells trapped in the boulder-strewn intertidal zone. They exhibit ecological zonation, with *D. formidabilis* inhabiting the lower intertidal zone while *A. africanus* inhabits the upper intertidal zone (Lamoral 1968; Fig. 3*A*).

Discussion

Evolutionary relationships

The previously published molecular studies on platygastroid relationships (Carey *et al*. 2006; Murphy *et al*. 2007) and the new analyses presented here indicate that there are at least two independent clades of platygastroid wasps that exploit spider eggs as hosts. The first clade is by far the most species rich as *Idris s.l.* comprises many hundreds of undescribed species, while the genera in the second clade comprises no more than 50 or so species (A. D. Austin, unpubl. data). *Echthrodesis* belongs to the smaller of the two clades that parasitise spider eggs, suggesting a common origin of association with silk-encased host eggs for *Mirobaeoides, Neobaeus* and *Echthrodesis*. The position of *Embidobia* nested with this clade suggests a potential host-switching event from spider to embiid eggs, lending some credence to the hypothesis that searching for silk as a host substrate may have facilitated this switch (Galloway and Austin 1984). However, the sister genus to *Echthrodesis* will remain elusive until material becomes available for sequencing of several rare genera that putatively belong to this clade, i.e. *Endecascelio*, *Palaeogryon* and *Embioctonus*. Similarly, sequence data are also required for the micropterous genus *Mirobaeus*, which has variously been placed in the Embidoniini (Masner and Dessart 1972; Masner 1976) or the Baeini *s.l.* (Austin 1988*a*; Austin and Field 1997).

A comprehensive phylogenetic analysis of morphological data for platygastroid genera is yet to be undertaken, so independent support for the placement of *Echthrodesis* in a clade with *Neobaeus*, *Mirabaoides* and *Embidobia* is not available. However, such a treatment employing morphology is fraught with the complexity of assessing the degree and extent of homoplasy, given that many genera in the Baeini and Embidobiini display loss or reduction of characters (Austin *et al*. 2005). Underlying historical exposure to similar ecological and environmental parameters has also driven widespread convergent evolution in body form across a diverse range of platygastroid genera, and these will cloud any assessment of phylogenetic relationships based on morphology. Reduction or loss of wings and evolution of a fusiform body shape have clearly arisen independently several times in different lineages of platygastroid wasps (Austin *et al*. 2005). This is well illustrated by the polyphyly of the genera that parasitise spider eggs, with two clades having independently evolved similar morphologies that appear to facilitate their parasitism of silk-encased eggs (Murphy *et al*. 2007). A fusiform body, where the metasoma is broadly abutted to the mesosoma, is commonly associated with cryptic habitats such as leaf litter dwelling and is evident in other unrelated lineages, e.g. *Parabaeus* Kieffer (Sceliotrachelinae), *Platyscelidris* Szabó and *Encyrtoscelio* Dodd (Scelioninae) (Austin *et al*. 2005).

Mouthparts and ovipositor system

Associated with the mouthparts, the maxillary and labial palpal formula also displays likely convergent reduction in segmentation, confounding character polarity assessment. The tribe Embidobiini is characterised by a large range in the palpal formula, with *Echthrodesis* having a palpal formula of 4 : 2, whereas most members of the Baeini and Embidobiini possess a palpal formula of 2 : 1, except *Endecascelio* where it is 3 : 2 and *Baeus* where it is reduced to 1 : 1.

The absence of a median apodeme in the last metasomal sternite (Fig. 8*A*) is characteristic of a generic group with a *Scelio*-type ovipositor, the only known exception being *Aradophagus* (Austin and Field 1997). Among the genera with a *Ceratobaeus*-type ovipositor, only eight genera other than *Echthrodesis* are characterised by a lack of the median apodeme in the last metasomal sternite: *Nixonia* Masner, *Sparasion* Latreille, *Sceliomorpha* Ashmead, *Habroteleia* Kieffer, *Fusicornia* Risbec, *Mantibaria* Kirby, *Neuroscelio* Dodd and *Teleas* Latreille (Austin and Field 1997), all of which are only distantly related to *Echthrodesis*. The median apodeme is one of three points for the attachment of the muscles responsible for the extension and retraction of the ovipositor from the metasoma (Austin and Field 1997). The absence of this apodeme means that ovipositor movement must be achieved in these genera only by the muscles attached to the paired lateral apodemes. The complex configuration of the 2nd gonapophyses assembly present in *Echthrodesis* is characteristic of genera possessing the *Scelio*-type ovipositor system, with the exception of *Doddiella* Kieffer (Austin and Field 1997). The majority of genera possessing the *Ceratobaeus*-type ovipositor system have the second gonapophyses assembly simple, with the exception of *Nixonia*, *Sparasion*, *Sceliomorpha*, *Fusicornia*, *Echthrodesis*, *Anteris* Foerster, *Opisthacantha* Ashmead and *Parascelio* Dodd. In the first five of these genera, the presence of a complex 2nd gonapophyses assembly is associated with absence of the medial apodeme, although the significance of this is unclear.

Morphological adaptations

A diverse range of morphological and physiological adaptations have evolved in adult insects to successfully colonise aquatic environments. These include, for example, reduction or loss of wings (Nondula *et al*. 2004) and the development of breathing siphons and various kinds of physical gills (Hinton 1976); the latter being present in *D. fomidibalis* (Lamoral 1968). However, very few parasitic Hymenoptera are fully aquatic and able to immerse completely to reach submerged hosts. Some notable exceptions are the platygastroid genera *Tiphodytes* Bradley (Spence 1986) and *Thoron* Haliday (Masner 1972; Johnson and Masner 2004) that parasitise the eggs of Gerridae and

Nepidae respectively, the mymarid *Caraphractus cinctus* Walker that parasitises the eggs of Dytiscidae (Jackson 1966), and the ichneumonid *Agriotypus gracilis* Waterson that is ectoparasitic on caddisfly larvae (Aoyagi and Ishii 1991).

In the case of *Echthrodesis*, a likely morphological adaptation includes a covering of dense setae over the body, hypothesised to form a thin plastron of air on submergence (Masner 1968). However, *E. lamorali* might rarely or never be physically immersed in water due to the air trapped within the egg sac and spider retreat inside limpet shells, which might provide sufficient air during submersion at high tide. Spider egg sacs and silk retreats play a critical role in preventing desiccation of eggs and juvenile spiders (Austin 1985, 1988*b*; Hieber 1992) and, hence, are likely to be sufficiently hydrophobic to keep water out. With the asynchronous development of egg clutches within a single egg sac, *Echthrodesis* can complete its life cycle protected inside a single spider retreat and only needs to expose itself to the external environment when it needs to locate new hosts. The host spider population is localised at Kommetjie, Cape Peninsula, and occurs in reasonably high densities such that dispersal to reach new host egg sacs might require movement over only tens of centimetres. Dispersal is likely to occur under favourable conditions at low tide, with the wasps being capable of jumping a short distance (a centimetre or so) when disturbed.

Wing reduction and a fusiform body is likely to facilitate entry to silken egg sacs, as proposed for *Baeus* and *Mirobaeoides* (Austin 1986; Stevens and Austin 2007), as well as being an adaptation in some genera to burrowing through litter or soil (Austin *et al*. 2005). The platygastroid genera that parasitise spider eggs exhibit different oviposition strategies, with some ovipositing from the outside of the egg sac (e.g. *Idris*, *Ceratobaeus*), whereas others burrow through the egg sac walls to reach the eggs within (e.g. *Baeus*, *Echthrodesis*, *Mirobaeoides*). Some of the latter possess highly modified tarsal claws that facilitate access through the sticky silk (Austin 1985). Males of *Echthrodesis* have the specialised body form of females with extremely reduced wings (although they are larger than in the female), a sub-fusiform body and sub-sessile metasoma. The extreme microptery of males and females of *E. lamorali* is, in addition to facilitating host egg sac silk circumvention in females, probably selectively driven by the need to stay in the localised area where the spider population is concentrated. Wings would be a distinct disadvantage, increasing the chance of being blown out to sea on the wind-swept Cape Peninsula. Such lack of sexual dimorphism, where males have the same modified body form as females, is associated with the genetic expression of effective winglessness in platygastroid wasps restricted to precarious habitats such as small oceanic islands, e.g. the baeine *Mirabaeoides pecki* (Austin), an endemic to Lord Howe Island (Austin 1988*a*, 1995).

Biology

The general biology and behaviour of *Echthrodesis* is similar to that documented for other platygastroids that parasitise spider eggs (Vachon 1955; Valerio 1971; Bradoo 1972; Austin 1984*c*; Cobb and Cobb 2004). However, some aspects of the biology of *Echthrodesis* appear to be unique. Since the parasitism rate observed was 100% in each egg batch, it seems likely that once a fecund female has gained access to a sealed egg compartment, she has sufficient eggs to lay in all the host eggs present. Complete mortality of spider eggs has previously not been documented for platygastroids (e.g. Austin 1984*c*, 1988*b*) and might be a function of *Echthrodesis* having several clutches with a small number of eggs. The highly biased female sex ratio suggests local mate competition and high inbreeding, which is not uncommon among platygastroid wasps (Austin *et al*. 2005). Thus, the multiple females attacking eggs in a chamber might all be sisters. Further investigations are required to establish the degree and nature of competition for oviposition resources and whether a female wasp can discern if an egg has been previously parasitised or not, as only a single parasitoid develops in each spider egg. Within an egg sac there are several empty compartments that are sealed and these might act to mislead this parasitoid.

Acknowledgements

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