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Shape variation in Australian *Poltys* species (Araneae: Araneidae)

Helen M. Smith
Australian Museum,
6 College St., Sydney,
NSW 2010, Australia

Summary

Preliminary work on the revision of Australian *Poltys* species indicated that there is an unusually large range of intraspecific variation in abdomen shape. These variants are conspecific, as has been confirmed by DNA analysis of different shape morphs within one species and the rearing of two different morphs from the same eggsac of another species. The major predators of *Poltys* are thought to be birds and wasps, which hunt primarily by sight. This wide range of phenotypes could be an effective camouflage strategy. Similar plasticity of form could be obfuscating the taxonomy of related genera and other taxa which use similar methods of concealment.

Introduction

Araneid spider taxonomy has traditionally used abdomen shape and, to a lesser extent, coloration, as key features for species determination and many old types were based on immature animals showing variant morphology. Modern taxonomists have recognised far greater plasticity in certain taxa. For instance, some of the genera treated by Levi, e.g. *Micrathena* and *Wagneriana* (Levi, 1985, 1991) have varying numbers of abdominal tubercles and often exhibit bilateral asymmetry. However, to some extent the presence or absence of a certain number of such features may still be used in the definition of a particular species. With this sort of concept of what constitutes reasonable variation I began work on the araneid genus *Poltys* C. L. Koch, 1843.

Poltys occurs throughout much of the equatorial and southern Old World and Australasia and includes a variety of bizarre body shapes. In Australia the genus is represented by about ten species in three species groups (H. M. Smith, in prep.). All are active at night in finely meshed orb webs and rest camouflaged on various trees and shrubs during the day. The females of two of these groups are primarily mimics of dead twigs (Fig. 1), while those of the third group, found only in the northern half of Australia, tend to be of a rounded form and resemble dead buds, fruit or galls. Males are very small compared with females and their abdomens rarely develop beyond a slightly extended oval.

Work on the revision of the Australian species of *Poltys* was started on the female specimens in the collection of the Australian Museum in Sydney and initially targeted specimens from SE New South Wales. These had previously been identified as a number of different species, reflecting a variety of shapes and colour forms. Figure 2 shows an example of each basic form as outlines of dorsal and lateral views of the abdomen. However, examination revealed that whilst the epigynes were somewhat variable, this variation was not consistent with any particular abdominal form. Furthermore, there seemed to be a continuum of body shape variation and complexity of ornamentation; could these forms represent only one species? A limited DNA study was undertaken to test this hypothesis. In addition, abdominal shape development was studied whilst raising young spiders of a similar species from Lord Howe Island. A species of the rounded form from Japan (identified as *Poltys illepidus* C. L. Koch) has also been studied by Ogasawara (2000).

The DNA work was facilitated by the donation of primers after completion of an unrelated study on lycosid spiders. A future, more complete DNA study on all Australian *Poltys* species will include a sequence which has been more widely used on araneids (e.g. that used by Piel & Nutt, 1997) and a nuclear sequence.

Material and methods

(1) DNA study

Specimens

Nine specimens were collected from the Sydney area and frozen at $-80\,^{\circ}$C. These represented variants on the major shape forms (Fig. 3). Alcohol-preserved specimens collected outside the Sydney area, but identified with that material, as well as several other species, were also sequenced as controls.

DNA extraction

Two or three legs were removed from each specimen and used directly for DNA extraction (fresh frozen specimens), washed in ddH_2O (initial spirit specimens), or rehydrated through a series of solutions (later spirit specimens). DNA was extracted by one of three methods. For the initial batch of nine specimens (frozen fresh material) a Gentra PUREGENE®DNA Isolation

Fig. 1: *Poltys* sp. subadult female in resting position on a dead twig. Specimen photographed at Hornsby, Sydney.

Kit was used, with slight modifications to the manufacturer's method: RNase digestion was omitted and a wide-bore pipette was used to minimise shearing. Extractions from specimens stored in 75% ethanol were performed either by the CTAB method of Saghai-Maroof *et al.* (1984) or using a Qiagen DNeasy™ Tissue Extraction Kit (04/99), following protocol B for insects with the substitution of 200 µl CTAB for PBS in step 2. DNA pellets were rehydrated in 50 µl ddH_2O except those extracted using the Qiagen kit, which were eluted in 100 µl. Two µl samples were run on 1.2% agarose gels containing ethidium bromide (in TBE buffer) and examined for UV induced fluorescence. Depending on the apparent quantity of DNA, samples were used either undiluted or diluted 10 or 20 times.

Primers and PCR

Spider-specific nested primers designed by Colgan *et al.* (2002) to amplify a 260 bpr sequence of Cytochrome Oxidase I were used: (Spider CO I F5′ CCTGGGAGTTTATTAGGGGATGATC and Spider CO I R5′ GGATATACAGTTCAACCAGCTCC). Amplification was carried out using 1 µl of appropriately diluted sample product, 3.5 mM $MgCl_2$, Buffer IV (10 ×, 20 mM $(NH_4)_2SO_4$, 750 mM Tris-HC1 pH 9.0, 0.1% Tween) (Advanced Biotechnologies), 0.05 mM dNTP, 12.5 pmol primers and 0.5 Units of Red Hot™ thermostable DNA polymerase in a total volume of 25 µl with oil overlay. A control using 1 µl ddH_2O instead of DNA was included. The PCR profile was 94 °C for 3 min, 45 °C for 1 min, 72 °C for 1 min–one cycle; 94 °C for 30 sec, 55 °C for 30 sec, 72 °C for 45 sec–35 cycles; and 94 °C for 30 sec, 55 °C for 30 sec, 72 °C for 3 min–one cycle. Two µl of each reaction product was resolved and UV visualised on 2% agarose gels containing ethidium bromide. All PCR products for sequencing were purified using the QIAquick™ PCR Purification Kit, following manufacturer's instructions varying the amount of ddH_2O for elution (step 8) depending on the concentration of DNA.

Cycle sequencing

Samples were sequenced in both directions using the Big Dye DyeDeoxy™ terminating sequencing method using 1 µl purified PCR product, 1 µl BigDye™ Terminator Mix, 0.8 µl primer (5.0 pM/µl) and 7.2 µl Buffer IV (made up as before) with an oil overlay. They were cleaned by ethanol/sodium acetate precipitation and run on an Applied Biosystems 310 Gene Analyser®. Some samples were problematic (eventually primer degeneration was identified as the cause) and were mostly sequenced using a 20 µl reaction (up to 8 µl PCR product, 2–4 µl BigDye™ Terminator Mix, 0.8 µl primer and ddH_2O or Buffer IV up to 20 µl).

Sequence alignment

The 5′ and 3′ strands of the DNA sequences were matched using the Sequence Navigator™ package. Sequences were aligned using default values for parameters in CLUSTAL W (Thompson *et al.*, 1994) and manually surveyed to check and improve if needed. The BLAST search option was used to compare sequences for the Sydney specimens to GENBANK.

(2) Rearing

Two eggsacs were laid in captivity by *Poltys* sp. females collected on Lord Howe Island in December

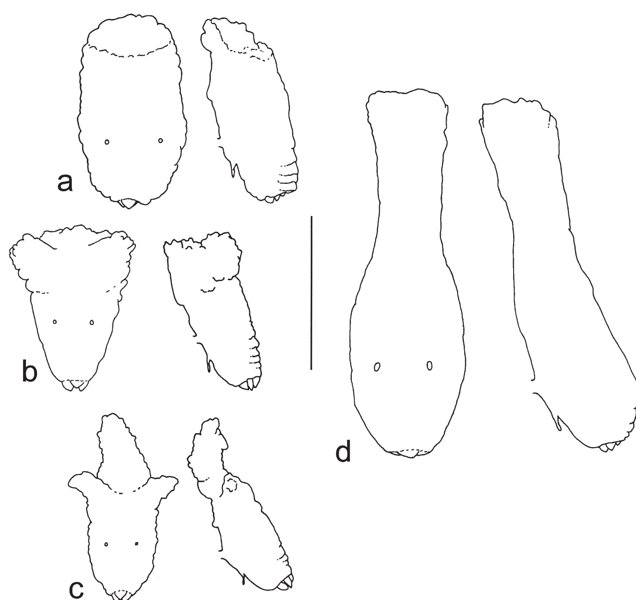

Fig. 2: Outlines of female *Poltys*, main abdomen shapes seen in the Sydney area, dorsal (left) and lateral views. **a** Truncated "tower"; **b** Well-developed humeral tubercles but little central "tower"; **c** Medium to well-developed "tower" with definite humeral bumps; **d** Tall "tower" with minimal or no humeral bumps. Specimens: a = Lane Cove; b = Beecroft; c = Ku-ring-gai Chase NP; d = Lane Cove. Scale line = 5 mm.

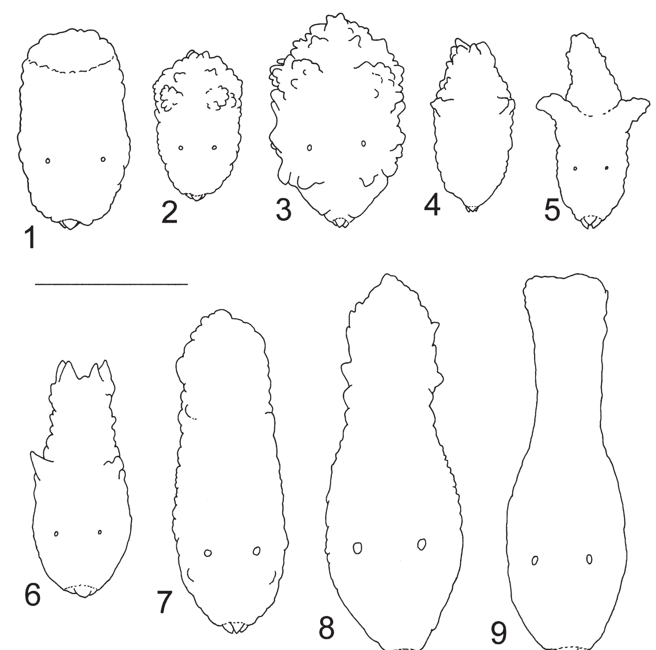

Fig. 3: The nine female Sydney specimens used for DNA work. Specimens 4 and 5 from Ku-ring-gai Chase NP, all others from Lane Cove. All drawn to same scale (line = 5 mm).

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Sp 1   Sydney 1-9        AGTTGTATAA   TGTAATTGTA   ACTGCTCATG   CTTTTGTAAT   AATTTTTTTT   ATAGTAATAC
Sp 1   S coast           ..........   ..........   ..........   ..........   ..........   ..........
Sp 1   Vic coast         ..........   ..N.....N.   ..........   ..........   ..........   ..........
Sp 1   40ml scrub        ..........   ..........   ..........   ..........   ..........   ..........
Sp 2   LHI               ..........   .........G   ..........   ..........   ..........   ..........
Sp 3   Rockhmptn         ....A.....   .........T   ..........   .......T..   ..........   .....T..G.
Sp 4   NT                .A........   ...T.....T   ..........   ..........   G.........   ........G.

Sydney 1-9 (cont.)       CGATCTTAAT   TGGGGGATTT   GGAAATTGAT   TAGTTCCATT   AATGTTAGGG   TCTCCTGACA
S coast (cont.)          ..........   ..........   ..........   ..........   ..........   ..........
Vic coast (cont.)        ..........   ..........   ..........   ..........   ..........   ..........
40ml scrub (cont.)       ..........   ..........   ..........   ..........   ..........   ..........
LHI (cont.)              .A..T.....   ......G...   ..........   ....G..G..   .........A   .GC..C..T.
Rockhmptn (cont.)        .T..T..G..   ......T...   ..........   .......T..   ..........   G.C..C..T.
NT (cont.)               .TG.G..G..   ...A..T..C   ........G.   ....G..G..   ......G...   G.......T.

Sydney 1-9 (cont.)       TAGCTTTTCC   TCGAATAAAT   AATTTAAGAT   TTTGATTGCT   ACCACCTTCG   TTATTTTTAT
S coast (cont.)          ..........   ..........   ..........   ..........   ..........   ..........
Vic coast (cont.)        .G........   ..........   ..........   ..........   ...-------   ----------
40ml scrub (cont.)       .G........   ..........   ..........   ..........   ..........   ..........
LHI (cont.)              .G........   ..........   ..........   ....G.....   T.....A..A   ..........
Rockhmptn (cont.)        .......C..   ...C......   ..........   ........T.   G..T..A..A   C.......G.
NT (cont.)               .G........   ......G...   ........G.   .......AT.   ...G.....A   ..G.....GC

Sydney 1-9 (cont.)       TAATTGTATC   TTCTATAGTA   GAGATAGGGG   TT
S coast (cont.)          ..........   ..........   ..........   ..
Vic coast (cont.)        ----------   ----------   ----------   --
40ml scrub (cont.)       ----------   ----------   ----------   --
LHI (cont.)              ..G.......   ..........   ..........   ..
Rockhmptn (cont.)        ..G.A.....   ......G..G   ..A.....A.   .A
NT (cont.)               .GN.G.....   ......N..T   ........N.   .A
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Fig. 4: DNA sequences: Sydney 1–9=specimens outlined in Fig. 3; S coast=near Bateman's Bay, New South Wales (species 1); Vic coast=near 90 Mile Beach, Victoria (species 1); 40 ml scrub=40 Mile Scrub, N. Queensland (species 1); LHI=Lord Howe Island (species 2); Rockhmptn=Rockhampton, Queensland (species 3, commonly referred to as *P. illepidus* C. L. Koch); NT=Humpty Doo, Northern Territory (species 4, related to *P. turriger* Simon). A dot (.) indicates base is the same as the reference sequence (Sydney 1–9); A, C, G, T are bases; N is inconclusive data for that point; a dash (-) indicates no data (sequence ended).

2000. Forty spiderlings from each were transferred into individual vials and raised as far as possible under the same conditions. The diet consisted primarily of houseflies hatched from commercially supplied pupae, supplemented by pollen and moths. This was mashed with a few drops of water using a pestle and mortar, and portions of the mix were stuck to the inside of the vial lid. The reared spiders were unable to make orb webs in the confined space, but seemed to accept this mix, despite it not being living prey. Males were mostly killed after maturing, but females were grown on as far as possible and moved into larger vials when necessary. More detailed information on rearing techniques and spider development will be included in a later publication.

All DNA and reared specimen material is housed in the collections of the Australian Museum, Sydney.

Results

(1) DNA study

The nine specimens from the Sydney area had exactly the same sequence over the 260 base pair section of mitochondrial DNA examined (Fig. 4, primer sequences not shown). This was rather a surprising result, since there had proved to be considerable variation in the lycosid study for which the primers were originally designed. To ensure that there was no contamination between samples and to check that this sequence was informative in the current group a number of other specimens were then added to the experiment. Specimens thought to be of the same taxon from outside Sydney from the south coast of New South Wales (shape similar to Fig. 2c), the Victorian coast and from 40 Mile Scrub, North Queensland (both tall, similar to Fig. 2d) also had identical or closely matching sequences, these indicating the variation within the geographical range of the species (all "sp. 1" in Fig. 4). Two of these sequences are incomplete, owing to the primer problem referred to under "methods". The sequencing successfully separated other *Poltys* taxa and the sequences of three examples are given here for comparison. Species 2 was from Lord Howe Island (the taxon used for the rearing experiment); species 3 was a species commonly referred to as *P. illepidus* from Rockhampton, Queensland; species 4 was related to *P. turriger* Simon and was from the Northern Territory.

Although this sequence is rather suboptimal in variability for *Poltys*, the differences were sufficient to show definite differences between taxa and indicate that it is highly probable that the nine Sydney specimens are of the same species. The BLAST search showed the sequence of the nine Sydney specimens to be unique, suggesting this is not a result of contamination with other organisms such as bacteria.

(2) Rearing

There were initial differences between hatchlings from the two eggsacs. Those from eggsac A (laid 18 December 2000, started emerging 9 January 2001) were small and very numerous (300–400); those from eggsac B (laid

c. 18 December 2000, started emerging 11 January 2001) were larger and there were far fewer (*c*. 150). Of the 40 separated from each eggsac, sex ratios were approximately 50/50 (19♂ 17♀ 4? from A; 18♂ 18♀ 4? from B; ?s died while too young to determine the sex). Of the juvenile females, 12 from A and 14 from B progressed through enough moults (and the remains were left in good enough condition) to be certain of their eventual shape.

The shapes noted in the Lord Howe Island population were similar to those of the Sydney animals shown in Fig. 2, except that none representing the truncated form (2a) were found and the two large humeral tubercles in form 2b were often extremely well developed. However, almost all of the 20 female Lord Howe specimens were taken within three weeks of each other and not all forms may have been represented in the sample.

Figure 5 indicates the shapes of the females which produced each eggsac and the shapes of their offspring. Both of the females were basically of the form illustrated in Fig. 2d, but a proportion of the offspring of each were closest to the shape of Fig. 2b (middle rows, Fig. 5). Those shown in the bottom rows in Fig. 5 were similar in shape to their mothers. None of the other forms were seen, although the sample size was too small to attach any confidence to this observation. It should be noted that several of the illustrated specimens were considerably shrivelled — the greatest effect being on the height of the central "tower". This especially affected the two females which laid eggsacs, probably because these were initially frozen for future DNA work before the abdomens were transferred to alcohol. These were considerably taller in my initial sketches so a small approximate sketch has been put in alongside the outline, which was drawn direct from the specimen in its present state. The number of moults which each specimen had undergone is also given, as this indicates that certain specimens were still growing towards their final shape. The moult which occurs as the animals leave the eggsac has not been included.

Female specimens that were nearing maturity were mostly rather small compared with wild-caught specimens. Growth-retardation in captive-reared spiders has been recorded in a number of taxa, e.g. by Miyashita (1986, 1988) and may be a result of a simplified diet or restricted movement. However, beyond moult 5 or 6 specimens appeared to have all the complexity of features of normal adults and there is no reason to suspect that small size affected their form. No females matured, although sub-adults with probably only one moult to go were obtained. In this study, and in other *Poltys* specimens that I have reared through different stages of their life history, there has been no evidence to suggest that growth forms, once achieved, ever change to a less complex or different form, although protrusions may shrink somewhat in starved specimens.

These results support those of Ogasawara (2000) who apparently reported abdominal shapes with or without

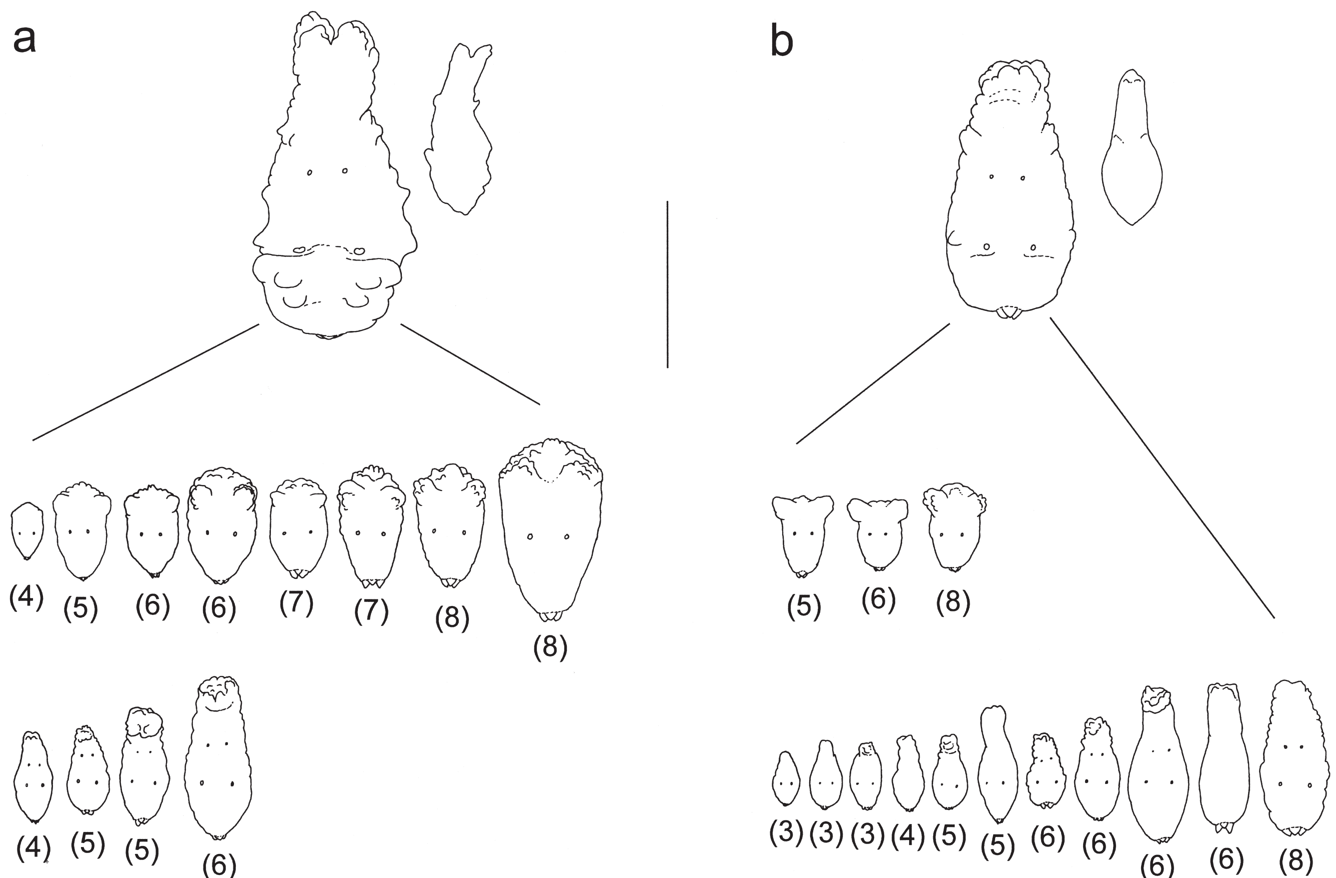

Fig. 5: Lord Howe Island *Poltys*. **a** Top, female A, preserved outline (left) and small sketch of shape in life; below, shapes of juvenile females raised from female A's eggsac, separated into rows based on shape (number of moults before death in brackets); **b** Ditto for female B. Scale line = 5 mm.

humeral bumps and with or without a central "tower" (the paper is in Japanese, but the figures appear self-explanatory). However the variations in the "round-abdomened" species of *Poltys*, both in Japan and in Australia, are rather less extreme than those seen in the twig-mimicking forms examined here. Ogasawara's figures of the epigynes would suggest that the Japanese species known as *P. illepidus* is not the same as the Australian species for which the DNA sequence is given in this paper.

Discussion

These results demonstrate that, for *Poltys* at least, variation in abdominal shape within a species may be extreme. Because of parallel shape variations between species and generally poor illustrations of epigynal features in type descriptions it is unlikely that any species can be positively identified without a direct comparison with type material. Several Australasian types are still to be located, and the identity of the type species for the genus, *Poltys illepidus* C. L. Koch, 1843, is in doubt (especially so as it was described from a "female" specimen with no abdomen and hence no epigyne). There are also implications for the taxonomy of some other araneid species which depend upon camouflage for protection. There may be other taxa exhibiting similarly variable morphology in which the significance of the variation could be misinterpreted. In particular, some of the other genera included in the Poltyeae Simon, 1895 (*Cyphalonotus*, *Kaira*, *Homalopoltys* and *Pycnacantha*) might be expected to show similar tendencies if they are indeed closely related. The New World genus *Kaira* O. P.-Cambridge, 1889, is the only one of these genera which has been revised (Levi, 1993). Levi's illustrations show that females of *Kaira* are at least superficially very similar to those of *Poltys* and there is a similar variety of abdominal shapes in the genus. Given that specimens are fairly rare in collections and that according to Levi the epigyne is difficult to study it is possible that some of the less well-known species could be variant morphological forms.

The reasons why this level of phenotypic plasticity should have arisen in this small group of spiders will be considered more fully in future work. An initial hypothesis is that a combination of predators and the available vegetation will be of greatest importance. Observations so far around Sydney have suggested that certain bird species find *Poltys* extremely palatable, but that they have difficulty locating specimens. In Queensland, *Poltys* specimens of three species have been collected from mudwasp nests (*Sceliphron* sp.: Sphecidae). Other wasp species, notably in the family Pompilidae, also prey exclusively on orb-weaving spiders. Bond & Kamil (1998) used blue jays to demonstrate that apostatic selection (where predators concentrate on abundant prey types whilst ignoring less common ones) can maintain prey polymorphisms in cryptic species. In the case where every potential prey item of a certain species is different in appearance from its neighbours it could be postulated that much of the predation pressure is transferred to more homogeneous species. A study of wasp predation on ant-mimicking salticid spiders by Edmunds (1993) indicated that, like birds, these wasps hunt mainly by sight and appear to use a "searching image", so a similar principle may be applicable.

If these two animal groups are the major daylight predators of *Poltys*, rampant variation in shape and colour could be predator driven but mediated by the need to match the plant background. Main (1999) has discussed similar issues with respect to colour-pattern variations in a western Australian *Carepalxis* L. Koch species which mimics gumnuts in one colour morph. Interestingly, the majority of Western Australian Museum records which Main refers to are from wasp nests. Perhaps these examples, and the *Poltys* recorded from wasp nests, were either less well camouflaged individuals, or there were simply too many of a similar morph in the same locality, allowing the wasps to learn to pick them out as a target. The colour patterns in *Poltys* have not been addressed here. However, in addition to the very variable background coloration there are often patches of colour which greatly enhance the resemblance to, for instance, a broken twig end or lichen patches, and the variations in patterns and colour as well as the morphological variation would further decrease the chances of a predator learning to associate any particular shape with a potential prey item. Colour variation and crypsis are extensively discussed by Oxford & Gillespie (1998) and a number of concepts they present may be applicable to *Poltys*, including the possibility of colour change to match a background.

The remarkable phenotypic plasticity shown by these *Poltys* species almost begs further investigation with respect to genetic and other controlling mechanisms. Among the most basic questions arising from the initial rearing experiments are whether the limited variation seen in the raised spiderlings compared with that in the population and apparent differences in proportions of different-shaped spiderlings which emerged from each eggsac are merely artefacts of having too few samples. Some spiderlings from further eggsacs are currently being raised so that this question can be addressed.

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I am extremely grateful to Sarah Brown, Don Colgan, Denis O'Meally and the other Australian Museum Evolutionary Biology Unit staff who patiently guided me through my first, rather fraught, attempts at DNA sequencing. Thanks also to the NSW National Parks & Wildlife Service and the Lord Howe Island Board for permission to collect specimens; Greta Gray for "spiderling sitting" while I was away; The Australian Museum and Sydney University for funding; Graham Milledge and Gerry Cassis for their support; many other Australian Museum staff who have made helpful suggestions; last, but by no means least, my PhD supervisors Mike Gray and Harley Rose (Sydney University) for all their support and helpful comments.

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Zelotes pyrenaeus, replacement name for *Zelotes mediocris* Simon, 1914 (Araneae: Gnaphosidae)

Francesca Di Franco
Dipartimento di Biologia Animale,
Via Androne 81,
95125 Catania, Italy

and

Theo Blick
Heidloh 8,
95503 Hummeltal, Germany

Di Franco (2002) changed the status of *Zelotes reconditus mediocris* Simon, 1914 from subspecific to specific level. Unfortunately it was overlooked that Kulczyński (1901: 9, pl. 1, fig. 6) had already described *Prosthesima mediocris* from Ethiopia (now Eritrea); only the female of this species is known. *Prosthesima* L. Koch, 1872 and *Zelotes* Gistel, 1848 (which has priority) were both proposed as replacement names for *Melanophora* C. L. Koch, 1833, which was preoccupied in Diptera. Therefore *Zelotes mediocris* (Kulczyński, 1901) is the older and valid name, and we propose herewith the replacement name *Zelotes pyrenaeus* for *Zelotes mediocris* Simon, 1914.

Derivatio nominis: Both hitherto known records of the species are from the Pyrénées near Lourdes (Département Hautes-Pyrénées, France).

Geographical data for the two localities for mapping purposes (with help of <http://www.mapblast.com>):

Bagnères-de-Bigorre: 43.0649°N, 0.1491°E

Ourdon (=Orédon): 43.0360°N, 0.0142°W

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