Editorial

In the Spring 2019 issue, I anounced that this year marks the 60th anniversary of scientific publications by the British Arachnological Society. The *Bulletin of the Flatford Mill Spider Group* first appeared in 1959. Ten years later it was superseded by the *Bulletin of the British Arachnological Society*. The name was changed to *Arachnology* in 2013, with the first part of volume 16.

In order to celebrate this anniversary, this Autumn 2019 issue of the journal includes a number of special articles on arachnology in Britain. There are reviews and updated checklists of the British spider, pseudoscorpion, and harvestmen faunas by Alastair Lavery, Gerald Legg, and Mike Davidson, respectively. In addition, there are papers on hybridization between two species of large house spiders in Britain by Geoff Oxford, and on the heritability of lateral banding in *Dolomedes plantarius* by Alice and Stephen Baillie and Helen Smith.

Arachnological research is indeed alive and well in Britain today, increasing our knowledge and understanding of these fascinating animals.

Paul Selden

Changes in the British pseudoscorpion fauna over the last 50 years

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Abstract

Over the past 30 years the British pseudoscorpion fauna and our understanding of it has grown. Three new species have been discovered, two of which, *Larca lata* Hansen, 1884 and *Microbisium brevifemoratum* (Ellingsen, 1903) have viable populations, whilst a third, *Americhernes oblongus* (Say, 1821), is a casual introduction. A further species, *Chthonius* (*Chthonius*) *halberti* (Kew, 1816) was rediscovered in 2016. An atlas was published in 1980 and a revised *Linnean Society Synopsis* in 1998. The rise of computers facilitated the digitization of records from 1992 onwards, and enabled the publication of distribution records online through the author's web site, chelifer.com, and the NBN Atlas. The interest in pseudoscorpions has subsequently blossomed and given rise to a Facebook page and a number of identification courses. All this interest will hopefully further our understanding of the British pseudoscorpion fauna.

Keywords: atlas • Britain • Ireland • neoteny • synopsis

Historical perspective

Britain has a unique reputation for recording, collecting, and understanding its natural world dating back over 300 years. Much of the data accumulated over the years found its way into the Biological Records Centre (BRC) established in 1964 at Monks Wood Experimental Station. (Now based in Wallingford, Oxfordshire and hosted by the Centre for Ecology & Hydrology and also supported by the Joint Nature Conservation Committee). These data were derived from published records, material held in museums, keen individuals, clubs, societies, professional biologists, and national recording schemes whom they continue to support. The BRC's work forms a significant part of the National Biodiversity Network (NBN) established in 1995, Britain's largest partnership for nature, overseen by the NBN Trust. Data are vetted and fed into the online resource the *National Biodiversity Atlas*.

Pseudoscorpions were initially recorded on standard BRC species record cards—2636 records in total (Britain and Ireland). These provided the source data for the publication, in 1980, of the *Provisional Atlas of the Arachnids of the British Isles, Part 1*: *Pseudoscorpions* (Jones 1980). This was a milestone in the understanding of the distribution of our pseudoscorpion fauna and provided the basis for further work. In 1998, the Linnean Society of London together with the Estuarine and Brackish-Water Sciences Association produced the *Synopsis of the British Fauna No. 40: Pseudoscorpions* (Legg & Jones 1998). This publication helped to put the group on the map and encouraged recorders, collectors and researchers to further our knowledge of the group by providing a then up-to-date account and key for false-scorpions.

In 1992, BRC passed the records cards to the author, then at the Booth Museum of Natural History in Brighton, for digitization using the first PC owned by Brighton Council (as it was) running Microsoft Access v. 2.0. the author set up the Pseudoscorpion Recording Scheme, through the British Arachnological Society, to encourage the study of the group. A periodical newsletter, *Galea*, was produced, now incorporated in the BAS Newsletter. Over a period of two years or so the process was completed. These records were (and still are) stored in a Microsoft Access database system and are continually being updated to http:// www.chelifer-.com/?page_id=61, vetted and periodically added to the NBN Atlas. To date (January 2019) there are 8648 on the Atlas with a further 500 to vet and upload. Records and specimens (and images) for identification continue to be sent in and are welcome.
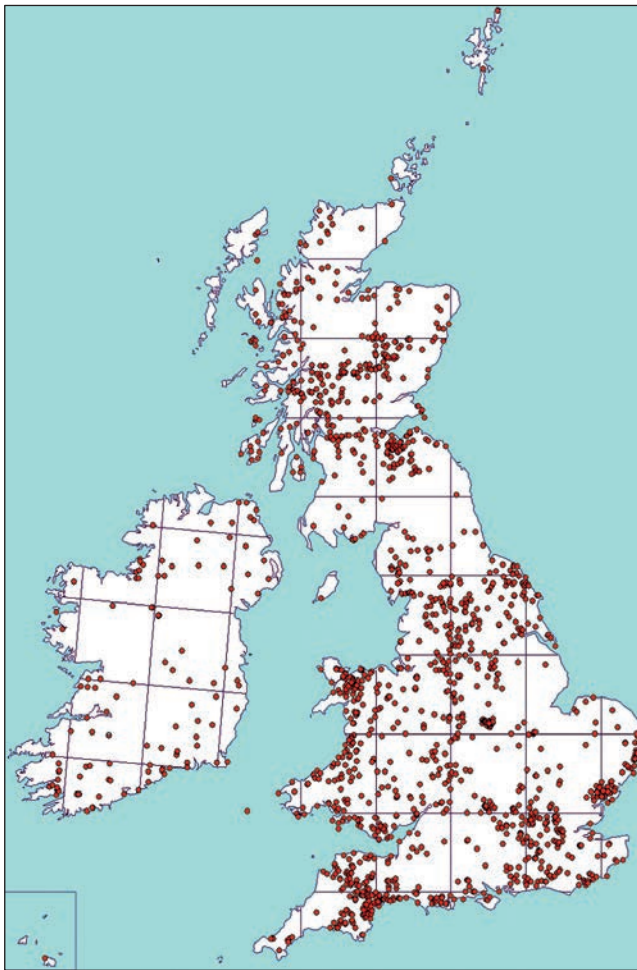
Fig. 1: Distribution map of *Neobisium carcinoides* (2016).

Once digitized, the species records were mapped using the software DMap by Alan Morton. In 2012, the author set up a web site (http://www.chelifer.com) partly devoted to the UK pseudoscorpion fauna. Details of the British pseudoscorpion fauna were and are provided together with descriptions of species, and distribution maps that are periodically up-dated (Fig. 1).

In 2015, Liam Andrews set up the Pseudoscorpion Facebook page. The aim was to provide a forum for identifying and discussing pseudoscorpions and sharing pictures and tips for finding them. As of January 2019, 680 people contribute to this page, providing additional records and helping to further the interests and understanding of pseudoscorpions. His page has proved extremely successful at stimulating the study of pseudoscorpions and contributes are great deal to our knowledge of the species, particularly their distribution. An upsurge in interest in pseudoscorpions, particularly on the Facebook page, followed the publication in 2016 of the Field Studies Council *Illustrated Key to the British False Scorpions* (Legg & Farr-Cox 2016) (Fig. 2). A number of ID courses were subsequently run in various parts of the country. The key is being updated following feedback.

Other records are derived from iRecord a valuable resource for anyone interested in natural history. The goal of iRecord is to make it easier for wildlife sightings to be col-

lated, checked by experts and made available to support research and decision-making at local and national levels. Through this web site, the public can make a real contribution to science and conservation. Verified records are linked to the NBN, thus providing valuable distribution data.

With all these current activities our understanding of the group is ever increasing and will hopefully lead to further discoveries. To date, there are 27 species recorded from the UK & Ireland. Of these 26 are generally recognised as having viable populations and all are included in the Field Studies Council key; *Americhernes oblongus* (Say, 1821) is regarded as an accidental import.

Checklist of British and Irish species of pseudoscorpions
(based on Harvey 2013)

order PSEUDOSCORPIONES Latreille, 1825
suborder EPIOCHEIRATA Harvey, 1992
superfamily Chthonioidea Daday, 1889
  family Chthoniidae Daday, 1889
    tribe Chthoniini Daday, 1889
      ***Ephippiochthonius* Zaragoza, 2017**
        Ephippiochthonius tetrachelatus (Pressler, 1790)
          Dimpled-clawed chthoniid
        Ephippiochthonius kewi Gabbutt, 1966
          Kew's chthoniid[1]
      ***Chthonius* C. L. Koch, 1843**
        Chthonius (*Chthonius*) *halberti* Kew, 1916
          Halbert's chthonid[2]
        Chthonius (*Chthonius*) *ischnocheles* (Hermann, 1804)
          Common chthoniid
        Chthonius (*Chthonius*) *tenuis* L. Koch, 1873
          Dark-clawed chthoniid
        Chthonius (*Chthonius*) *orthodactylus* (Leach, 1817) *s.s.*
          Straight-clawed chthoniid[3]
suborder IOCHEIRATA Harvey, 1992
superfamily Neobisioidea Chamberlin, 1930
  family Neobisiidae Chamberlin, 1930
    subfamily Neobisiinae Chamberlin, 1930
      ***Neobisium* Chamberlin, 1930**
        Neobisium (*Neobisium*) *maritimum* (Leach, 1817)
          Shore neobisiid
        Neobisium (*Neobisium*) *carpenteri* (Kew, 1910)
          Carpenter's neobisiid[4]
        Neobisium (*Neobisium*) *carcinoides* (Herman, 1804)
          Moss neobisiid
      ***Roncus* L. Koch, 1873**
        Roncus (*Roncus*) *lubricus* L. Koch, 1873
          Reddish two-eyed neobisiid
    subfamily Microcreagrinae, Balzan, 1892
      ***Roncocreagris* Mahnert, 1976**
        Roncocreagris cambridgei (L. Koch, 1873)
          Cambridge's two-eyed neobisiid
      ***Microbisium* Chamberlin, 1930**
        Microbisium brevifemoratum (Ellingsen, 1903)
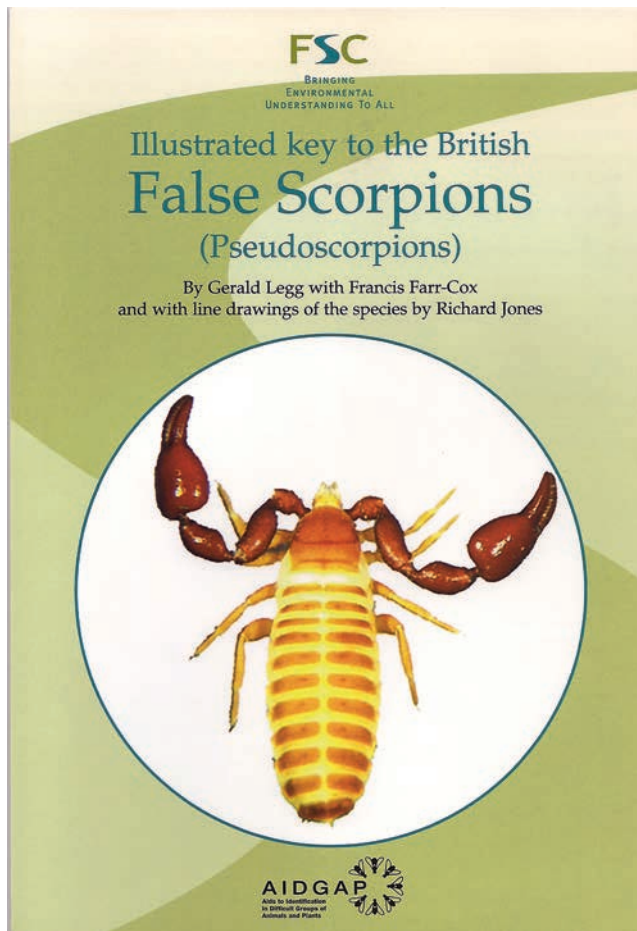   Bog neobisiid[5]
superfamily Cheiridioidea Hansen, 1894

Fig. 2: Front cover of the Field Studies Council *Illustrated Key to the British Pseudoscorpions* (Legg & Farr-Cox 2016).

Fig. 3: *Chthonius halberti* from the upper shore near Kimmeridge, Dorset. © Steve Trewhella, UK Coastal Wildlife.

family Cheiridiidae Hansen, 1894
  subfamily Cheiridiinae Hansen, 1894
    ***Cheiridium* Menge, 1855**
      Cheiridium museorum (Leach, 1817)
        Book chelifer
superfamily Cheliferoidea Risso, 1827
  family Chernetidae Menge, 1855
    subfamily Lamprochernetinae Beier, 1932
    ***Lamprochernes* Tömösvary, 1892**
      Lamprochernes savignyi (Simon, 1881)
        Savigny's shining claw
      Lamprochernes nodosus (Schrank, 1803)
        Knotty shining claw
      Lamprochernes chyzeri (Tömösvary, 1882)
        Chyzer's shining claw
    ***Pselaphochernes* Beier, 1932**
      Pselaphochernes scorpioides (Hermann, 1804)
        Compost chernes
      Pselaphochernes dubius (O. Pickard-Cambridge, 1892)
        Small chernes
    ***Allochernes* Beier, 1932**
      Allochernes powelli (Kew, 1916)
        Powell's chernes
      Allochernes wideri (L. Koch, 1873)
        Wider's tree chernes
    subfamily Chernetinae Beier, 1932
    ***Dinocheirus* Chamberlin, 1929**
      Dinocheirus panzeri (L. Koch, 1873)
        Terrible-clawed chernes
    ***Chernes* Menge, 1855**
      Chernes cimicoides (Fabricius, 1793)
        Common tree chernes
    ***Dendrochernes* Beier, 1932**
      Dendrochernes cyrneus (L. Koch, 1873)
        Large tree chernes
    ***Americhernes* Muchmore, 1976**
      Americhernes oblongus (Say, 1821)
        American chernes[6]
  family Withiidae Chamberlin, 1931
    subfamily Withiinae Chamberlin 1931
    ***Withius* Kew, 1911**
      Withius piger (Simon, 1878)
        Lazy chelifer[7]
  family Cheliferidae Risso, 1827
    subfamily Cheliferinae Risso, 1827
    tribe Cheliferini Risso 1827
    ***Chelifer* Geoffroy, 1762**
      Chelifer cancroides (Linnaeus, 1758)
        House chelifer
    tribe Dactylocheliferini Beier, 1932
    ***Dactylochelifer* Beier, 1932**
      Dactylochelifer latreillii (Leach, 1817)
        Marram grass chelifer
superfamily Garypoidea Simon, 1879
  family Larcidae Harvey 1992
    ***Larca* Chamberlin, 1930**
      Larca lata (Hansen, 1884)
        Oak tree chelifer[8]

Notes on some species and changes to the UK and Irish fauna

[1]*Chthonius tetrachelatus* and *C. kewi* were previously included in the subgenus *Ephippiochthonius* which was raised to full generic status in 2017 by Zaragoza.

[2]*Chthonius halberti* was first recorded in Ireland in 1915 at Malahide, County Dublin (Kew 1916), where it was found beneath stones on the seashore between the levels of orange lichens and *Pelvetia canaliculata* (just above high-water mark). H. W. Kew subsequently collected two speci-

Fig. 4: *Chthonius orthodactylus* from the base of dense grasses, Ditchling Common, Sussex.

mens, which were believed to be the same species, at Axmouth in Devon, under stones on the beach near and below the high-water mark (Muchmore 1968). Attempts in recent years to find the species at Malahide have proven unsuccessful. However, in July 2016, Steve Trewella redis-covered it near Kimmeridge in Devon (Trewella 2016; Fig. 3) where it appears to be abundant and its distribution prob-ably extends along the coast. Beier's (1963) description of *C. halberti* is based upon specimens from the south coast of France and this description does not fit the type specimens of *C. halberti* in the National Museum of Ireland, Dublin (Muchmore 1968). *Chthonius halberti* was considered by some authors to be the type species of the genus *Kewochthonius* and, in 1968, Muchmore redescribed it as *K. halberti* using the Irish and Devon material. Evans & Browning (1954) give the group subgeneric status, using the
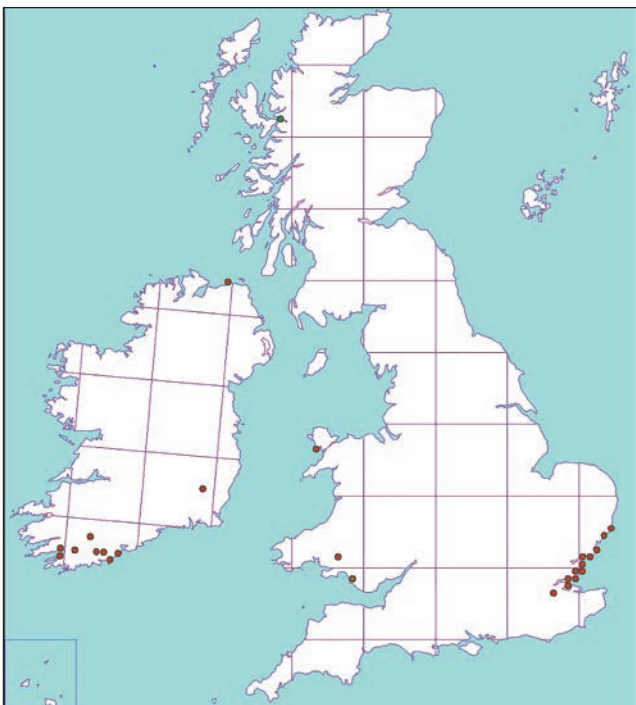

Fig. 6: *Microbisium brevifemoratum* on Sphagnum, Holland.

name *Neochthonius*, but this is incorrect on grounds of page priority. It is now regarded as *Chthonius* (Harvey 2011). Distribution: Europe: Ireland, England, France, Italy, and Portugal (Harvey 2013). A disjunctive range that deserves further study.

[3]*Chthonius orthodactylus*. The status of this species had been put into doubt (Leclerc & Heurtault 1979; see Legg & Jones 1988: 72), but it is distinct enough to be included in the British fauna. It has a wide-ranging, pan-European dis-tribution: Austria, Belgium, Bosnia-Herzegovina, Britain, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Hungary, Ireland, Italy, Netherlands, Romania, Serbia, Slovakia, Slovenia, and Tunisia (Harvey 2013) (Fig. 4).

[4]*Neobisium carpenteri* was originally found in 1909 beneath Arbutus bark and in moss on the coast of Glengar-iff, south-west Ireland. In 1971, further specimens were found in *Sphagnum* moss on the cliff top and, in 1982, in leaf litter. In the 1950s, specimens identified as *N. carpen-teri* were discovered along the Essex coast (Gabbutt 1965). Further ones matching the description have also been found more recently inland in Wales. This rather disjunctive distri-bution deserves further study. The species has been recorded from France, Ireland, and the Netherlands. Beier

Fig. 5: Distribution map of *Neobisium carpenteri* (2016).

Fig. 7: *Larca lata* from a stump of an ancient oak containing the remains of a bird's nest, Windsor, Berkshire.

(1963: 99) noted that it was similar to, and possibly a sub-species of, *Neobisium ischyrum* (Navás, 1918) found in Portugal and Spain which suggested, erroneously (Legg & Jones 1988), a possible link to the Lusitanian fauna—species occurring in southern Ireland that show affinities with those in Iberia and western France (Carpenter 1896). The species has been recorded from Britain, France, Ireland, and the Netherlands (Harvey 2013) (Fig. 5).

[5]*Microbisium brevifemoratum*. This rare species has only been found twice, initially by Steve Judd of Liverpool Museum at Chartley Moss, Staffordshire on 29 July 1994. In 2005, a second one was discovered in *Sphagnum* in Wales. On the continent, it occurs in *Sphagnum* bogs and carr. It resembles a small *Neobisium carcinoides*, but has fewer trichobothria on the palps, the fixed finger with only seven, the movable one with three trichobothria; thus supporting the neotenous condition of the genus *Microbisium*. Hand sorting, Tullgren funnel extraction and suction sampling this habitat in Britain could well uncover further specimens. It occurs throughout Eurasia, and is prevalent in central Europe and Russia through to China (Harvey 2013) (Fig. 6).

[6]*Larca lata* is our rarest species and has only been found at one locality in Windsor Great Park in 1969 (Legg collection). It was collected from nest debris in a decaying ancient oak tree and initially misidentified as *Chelifer cancroides* by Legg (and used to illustrate *C. cancroides* in Legg & Jones 1988). Judson & Legg, 1996 corrected the identification and recorded the species from Britain. This is a typical habitat for this very rare European species which likes shadowy, humid, rot-holes rich in decaying debris or bird and rodent excrement. In Europe it is found in Austria, Britain, Bulgaria, Czech Republic, Denmark, Germany, Latvia, Netherlands, Poland, Romania, Hungary, and Sweden. (Harvey 2013) (Fig. 7).

[7]*Withius piger* is an introduced species (Pickard-Cambridge 1885, 1892) probably with viable populations, unlike the next species. It was first found in 1880. Further specimens have been reported sporadically from various ports, warehouses and farms:

1880, January, Dover, Kent, from an oil mill

1880, near Plymouth, Devon

1886, Hyde, Dorset, from an old building

1886, Avenham Park, Preston, Lancashire; in a rubbish heap

1905–1907, Sheppey, Kent, heap of sugar refuse, rice grain etc

1908, Hendon, Middlesex, in a manure heap

1908, Manchester, Messrs Mosleys rubber warehouse

1916, June, Acton Bridge, near Northwich, Cheshire, in an old bone mill

1917, August, Dunham Park, Cheshire, under oak bark near old mill

1956, December, Aldershot, Hants, grain residues in a disused mill

1974, July, CWS Farm, Withgill near Clitheroe, Lancashire,debris in barley store

1980, September, ship MS Titiv Veles, 7 shed, 9 Dock, Port of Manchester, beneath stack of Turkish Vallonia board from Ismir

It is likely that further examples of this species will be found and should be sought by examining material from warehouses, stores etc.

[8]*Americhernes oblongus* is an introduced alien found in 1991 in Dover. This species had been previously recorded and described as *Chernes insuetus* (Cambridge, 1892), a species that has been synonymized by Judson (1997) with *A. oblongus* and is known from the Americas (Harvey 2013). No viable populations have been recorded since, but it will be worth keeping an eye on ports and the like for any further alien species. During the past 25 years the author has received items from China on two occasions that have contained populations of the cosmopolitan species *Cheiridium museorum*.

Future discoveries

There are currently 861 species (and counting) in 73 genera and 16 families recorded in Europe (Harvey 2011) including 20 or so species from the Asian parts of Russia and Turkey. It would be fair to say that the UK and Ireland may well have hitherto undetected representatives of the European fauna. Possible further discoveries could include. *Lasiochernes pilosus* (Ellingsen, 1910), a species distributed in several European countries (Harvey 2013), including France. It shows a degree of host specificity, since it is almost exclusively found in the subterranean nests of moles containing dead leaves. Such nests have barely received any attention. This species has also been recorded from vole (*Microtus* spp.) and, apparently, pocket gopher nests (*Thomomys* sp.) (Francke & Villegas-Guzman 2006). It would be worthwhile examining other mammal retreats to see if any pseudoscorpions occur, e.g. badger bedding and bat roosts.

There are many cavernicolous species in Europe and they continue to be discovered (Harvey 1991; Ćurčić *et al*. 1997). Entomophilous species may be found particularly associated with wasps and bees, as they are known elsewhere (Judson 1990; Harvey 2015; Ayuka *et al*. 2016).

It would be prudent to examine bird nests, especially those of seabirds and raptors, and caves. For example, *Dinocheirus panzeri* was thought uncommon but, in 1970, an old pigeon loft at the Portaferry marine field station on Strangford Loch yielded hundreds. Work in Slovakia (Christophoryová *et al*. 2010) found eleven pseudoscorpion species associated with 171 nests of 28 different bird species collected in Slovakia, Austria, and the Czech Republic. These included *Cheiridium museorum*, *Dactylochelifer latreillii*, *Chernes hahnii* (C. L. Koch, 1839), *Dendrochernes cyrneus* and *Allochernes wideri*. There was a high proportion of *Pselaphochernes scorpioides* in hoopoe nests with rotting debris, *D. cyrneus* in Eurasian tree sparrow nest boxes, and *A. wideri* in the nests of the tawny owls, the European scops owls, and the European roller. In contrast, *C. hahnii* and *D. latreillii* occurred in the nest

fauna of blackbirds and song thrushes, *C. museorum* in the nests of white wagtails situated on the ground and on buildings, and *C. cancroides* in nests in synanthropic habitats. Christophoryová *et al.* (2010) found that species occurring in nests fall into two groups: those that are accidental (nidixenous species), *viz. Chthonius fuscimanus* Simon, 1900, *C. tetrachelatus*, *Mundochthonius styriacus* Beier, 1971, *Neobisium carcinoides*, *N. crassifemoratum* (Beier, 1928), *N. inaequale* Chamberlin, 1930, *N. sylvaticum* (C. L. Koch, 1835), *Chernes cimicoides*, *C. similis* (Beier, 1932), *C. vicinus* Beier, 1932, *Allochernes powelli*, *Lamprochernes chyzeri*, *L. Nodosus*, and *Larca lata*. The author has also found Chthonius *ischnocheles* in nests. The second group includes those that have a substantial association with nests (nidiphilous species): *C. museorum*, *C. cancroides*, *A. wideri*, D. *cyrneus*, *D. latreilli*, *C. hahnii*, *D. panzeri*, and *P. scorpioides*. The inclusion of *D. latreillii* as a nest associate has not been observed in the British Isles, where the species has a distinctly maritime distribution; perhaps Christophoryová *et al.* (2010) were dealing with a different species.

Species of arthropods new to the region have arrived by a variety of means and been subsequently found in ports, warehouses, stores, timber yards (especially importers), botanical gardens, nurseries, garden centres, etc. Studies of the debris, refugia, and soil fauna of these locations may well yield introduced species of pseudoscorpion. Farm buildings, stables, and chicken houses are also well worth examining as they are under-recorded, and not just for introduced species. Unlike many arthropods, alien pseudoscorpions are unlikely to raise any biosecurity issues.

How to find them

Typically, recorders find pseudoscorpions by hand sampling, sieving, shaking, lifting stones and old tree bark, etc. Such techniques are satisfactory up to a point but, for better, less time-consuming results, other techniques can be deployed. Vacuum sampling of grassland, *Sphagnum*, bogs, heaths, and other appropriate habitats, has proven very effective: a 10-second suck produces finds that would take hours by hand. Girdling trees, especially rotting ones, with corrugated card or bubble-wrap, or the deployment of onion bags filled with hay on tree branches or in rot holes to simulate bird nests provide refugia for some species that can be retrieved at leisure without damage to the tree. Tullgren funnel sampling is extremely effective, and simple solar-powered ones (sunshine permitting) can be used in the field.

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A revised checklist of the spiders of Great Britain and Ireland

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Abstract

A revised checklist of spider species found in Great Britain and Ireland is presented together with their national distributions, national and international conservation statuses and synonymies. The list allows users to access the sources most often used in studying spiders on the archipelago.

Keywords: Araneae • Europe

Introduction

A checklist can have multiple purposes. Its primary purpose is to provide an up-to-date list of the species found in the geographical area and, as in this case, to major divisions within that area. It is also a guide to the names to be used, giving some stability at national level to ever-changing international nomenclature. This list includes United Kingdom and International Union for Conservation of Nature (IUCN) conservation statuses from Harvey *et al.* (2017). Finally, the checklist can provide users with guidance on how to trace current nomenclature to the most frequently used national identification resources, which are often several steps removed from current usage.

This checklist, like its predecessors, covers the archipelago made up of the islands of Great Britain, Ireland, and adjacent smaller islands. This geographical area covers two countries: the Republic of Ireland (RI) and the United Kingdom of Great Britain and Northern Ireland (UK). The four nations of the UK—Wales, Scotland, Northern Ireland, and England—are included, with one of the UK's Crown Dependencies, the Isle of Man. All 212 species recorded from the Isle of Man are found in England, Wales, and all but 2 in Scotland (Spider Recording Scheme 2019). As biogeographically distinct, the other two Crown Dependencies, the Bailiwicks of Jersey and Guernsey (the Channel Islands) are not included. A list of spider species found only on the Channel Islands but not in the rest of Great Britain and Ireland is included in Merrett, Russell-Smith & Harvey (2014).

The island of Ireland, a geographical and biogeographical unit, is differentiated from the political units on the island by using the names Republic of Ireland and Northern Ireland in situations where confusion is possible.

This checklist updates Merrett, Russell-Smith & Harvey (2014). It is the latest in a long series going back to Blackwall (1861), forming an important record of the developing understanding of the spiders of Great Britain and Ireland.

Methods

Selection criteria and lists

The checklist has two main sections; List A contains all species proved or suspected to be established and List B species recorded only in specific circumstances.

The criterion for inclusion in list A is evidence that self-sustaining populations of the species are established within Great Britain and Ireland. This is taken to include records from the same site over a number of years or from a number of sites. Species not recorded after 1919, one hundred years before the publication of this list, are not included, though this has not been applied strictly for Irish species because of substantially lower recording levels.

The list does not differentiate between species naturally occurring and those that have established with human assistance; in practice this can be very difficult to determine.

List A: species established in natural or semi-natural habitats

The main species list, List A1, includes all species found in natural or semi-natural habitats. List A2 contains a small number of species that are established but have not yet been fully described taxonomically. Species with insufficient records to determine their status are given in List A3. This covers species where records are confined to only one site or to very few individuals, with no evidence of reproduction.

The distinction, made in previous checklists, between species confined to artificial habitats such as greenhouses and species largely confined to other buildings has become increasingly difficult to determine and so species formerly listed as greenhouse species are now included in List A1. Species found almost exclusively in anthropic habitats are identified in the list as:

Ag: exclusively or almost exclusively in greenhouse-like structures.

Ah: exclusively or almost exclusively in houses.

Ab: exclusively or almost exclusively in buildings other than homes, such as warehouses and industrial structures.

List B: species recorded from artificial habitats and as imports

List B1 covers species recorded as established populations only in large-scale, artificial climate-controlled areas such as tropical biomes and tropical sections of botanic gardens. The extreme climate modification of these habitats is considered enough to exclude these species from List A.

List B2 contains species regularly imported into Great Britain and Ireland, for example with foodstuffs, but with no evidence that they are established.

Removal of species

While it seems easy to add species to a checklist, it can be more difficult to remove them, especially given the number of lists that can be found in publications and on the internet. These include species which have at some time been recorded in the literature as Great British or Irish but should no longer be considered so. This can be because the species has not been recorded in Great Britain and Ireland for at least 100 years, or as a result of ambiguity about its taxonomic status and distribution, or because it was recorded from Great Britain and Ireland in error. Nearly 50 such species were found in checklists for Great Britain and Ireland, both online and printed, but are not included here. A further publication is planned to explore these records.

Nomenclature

Eighty years ago, Bristowe (1939: 3) wrote "The nomenclature has undergone many changes, and it is feared that we have by no means reached finality yet". Changes in species, genus, and family names are a constant and essential feature of a developing science but have been for years a source of confusion and annoyance at a practical, day-to-day level.

Previous checklists have largely followed international usage but have departed from this, sometimes wisely, on several occasions. This list follows the nomenclature in the current edition of the World Spider Catalog, in this case version 20.0 (World Spider Catalog 2019), last checked on 1st July 2019.

Identification

The use here of currently recognised species names should allow for easy access to world and European literature and to web-based resources. It does, however, present difficulties in using the most commonly consulted identification publications. The inclusion of superseded names from Merrett, Russell-Smith & Harvey (2014) and Roberts (1985, 1987, 1993) should allow users to trace names back through to all these sources. There are currently four main texts used for spider identification in Great Britain and Ireland:

• Bee, Oxford & Smith (2017), covering all families except Linyphiidae, used Merrett, Russell-Smith & Harvey (2014). The second edition (due 2020) will use the names in this list.

• Roberts (1995), again not fully covering Linyphiidae, is close to Roberts (1985, 1987, 1993).

• Roberts (1985, 1987, 1993) remains the major text for species identification in Great Britain and Ireland. All name changes are in the list.

• Locket & Millidge (1951, 1953) and Locket, Millidge & Merrett (1974) are the oldest useful identification guides to spiders in this region. Roberts (1987) listed changes in nomenclature.

Sources and references

Country records are taken from the Spider Recording Scheme (SRS) (2019) for Scotland, England and Wales. The SRS does not cover the island of Ireland; the species listed here for these areas are based on van Helsdingen (1996) and McFerran (1997) with species subsequently included.

The full list of references needed to chart the changing nomenclature and distribution of spiders in Great Britain and Ireland is prohibitively long for a print publication. The references in this paper are only to publications directly used; for nomenclature changes only the paper establishing the current name is listed. To untangle the full references for any species on the list, the online World Spider Catalog in its most recent edition should be used https://wsc.nmbe.ch.

No references are included for Scottish, English, or Welsh country distributions as the records are available on the Spider Recording Scheme (2019). References are given for species recorded here for the first time. Published sources for Irish records later than van Helsdingen (1996) are included.

The Checklist

See Lists A (1–3) and B (1–2) in Tables 1 and 2.

Discussion

A checklist, by its very nature, is always a work in progress and the rapid advance of knowledge at both local and global levels means that lists will be out of date as soon as they are published. However the periodic publication of the list should give some stability to the nomenclature used for spider species within Great Britain and Ireland.

The inclusion for the first time of country listings within this checklist should be viewed as experimental and subject to greater change than the overall list. The lists for England, Wales and Scotland reflect with considerable confidence the known distributions. The list for the island of Ireland is likely to be more provisional. In all cases further records and corrections are very welcome.

Table 3 summarizes the current status of spiders within Great Britain and Ireland.

Acknowledgements

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Table 1: Species found in Great Britain and Ireland.

      List A1: species established in natural or semi-natural habitats.

      List A2: species awaiting taxonomic definition.

      List A3: species with insufficient data to determine status.

      Abbreviations: Countries: E = England: S = Scotland: W = Wales: NI = Northern Ireland: RI = Republic of Ireland. Anthropic Status (AS): Ag = exclusively or almost exclusively in greenhouse-like structures; Ah = exclusively or almost exclusively in houses; Ab = exclusively or almost exclusively in buildings other than homes, such as warehouses and industrial structures. Conservation status: GB = Great Britain designations: NS = Nationally Scarce; NR = Nationally Rare. IU = IUCN international designations: CE = Critically Endangered; E = Endangered; V = Vulnerable; NT = Near Threatened; DD = Data Deficient.

List A1. Species established in natural or semi-natural habitats

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Family ATYPIDAE										
Atypus affinis Eichwald, 1830			E	S	W		RI		NS	
Family SCYTODIDAE										
Scytodes thoracica (Latreille, 1802)			E		W		RI	Ah		
Family PHOLCIDAE										
Pholcus phalangioides (Fuesslin, 1775)			E	S	W	NI	RI	Ah		
Psilochorus simoni (Berland, 1911)			E	S	W	NI	RI	Ah		
Family SEGESTRIIDAE										
Segestria senoculata (Linnaeus, 1758)			E	S	W	NI	RI			
Segestria bavarica C. L. Koch, 1843			E		W				NR	
Segestria florentina (Rossi, 1790)			E	S	W					
Family DYSDERIDAE										
Dysdera erythrina (Walckenaer, 1802)			E	S	W	NI	RI			
Dysdera crocata C. L. Koch, 1838			E	S	W	NI	RI			
Harpactea hombergi (Scopoli, 1763)			E	S	W	NI	RI			
Harpactea rubicunda (C. L. Koch, 1838)		Appendix 2	E						NR	V
Family OONOPIDAE										
Oonops pulcher Templeton, 1835			E	S	W	NI	RI			
Oonops domesticus Dalmas, 1916			E	S	W	NI	RI	Ah		
Family MIMETIDAE										
Ero cambridgei Kulczyński, 1911			E	S	W	NI	RI			
Ero furcata (Villers, 1789)			E	S	W	NI	RI			
Ero aphana (Walckenaer, 1802)			E	S					NS	
Ero tuberculata (De Geer, 1778)			E	S					NS	
Family ERESIDAE										
Eresus sandaliatus (Martini & Goeze, 1778)		*Eresus niger*	E						NR	V
Family ULOBORIDAE										
Uloborus walckenaerius Latreille, 1806			E						NR	NT
Uloborus plumipes Lucas, 1846		not present	E	S	W		RI	Ag		
Hyptiotes paradoxus (C. L. Koch, 1834)			E		W		RI		NS	
Family NESTICIDAE										
Nesticus cellulanus (Clerck, 1757)			E	S	W	NI	RI			
Kryptonesticus eremita (Simon, 1880)	not present	not present			W					
Family THERIDIIDAE										
Episinus angulatus (Blackwall, 1836)			E	S	W	NI	RI			
Episinus truncatus Latreille, 1809			E		W		RI		NS	
Episinus maculipes Cavanna, 1876			E			NI	RI		NS	
Euryopis flavomaculata (C. L. Koch, 1836)			E	S	W	NI	RI		NS	
Lasaeola prona (Menge, 1868)	*Dipoena prona*	*Dipoena prona*	E		W				NR	E
Lasaeola tristis (Hahn, 1833)	*Dipoena tristis*	*Dipoena tristis*	E				RI		NS	
Phycosoma inornatum (O. P.-Cambridge, 1861)	*Dipoena inornata*	*Dipoena inornata*	E	S	W		RI		NS	
Dipoena erythropus (Simon, 1881)			E		W				NR	V
Dipoena melanogaster (C. L. Koch, 1837)			E				RI		NR	E
Dipoena torva (Thorell, 1875)				S					NR	NT
Crustulina guttata (Wider, 1834)			E	S	W		RI			
Crustulina sticta (O. P.-Cambridge, 1861)			E				RI		NS	
Asagena phalerata (Panzer, 1801)	*Steatoda phalerata*	*Steatoda phalerata*	E	S	W	NI	RI			
Steatoda albomaculata (De Geer, 1778)			E		W				NR	
Steadota bipunctata (Linnaeus, 1758)			E	S	W	NI	RI			

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Theridiidae cont.										
Steatoda grossa (C. L. Koch, 1838)			E	S	W	NI	RI	Ab		
Steatoda nobilis (Thorell, 1875)		Appendix 2	E	S	W	NI	RI	Ab		
Steatoda triangulosa (Walckenaer, 1802)		not present	E		W					
Anelosimus vittatus (C. L. Koch, 1836)			E	S	W	NI	RI			
Kochiura aulica (C. L. Koch, 1838)		*Anelosimus aulicus*	E						NS	
Cryptachaea riparia (Blackwall, 1834)	*Achaearanea riparia*	*Achaearanea riparia*	E	S	W		RI		NS	
Cryptachaea blattea (Urquhart, 1886)	not present	not present	E		W					
Cryptachaea veruculata (Urquhart, 1885)		*Achaearanea veruculata*	E							
Parasteatoda lunata (Clerck, 1757)	*Achaearanea lunata*	*Achaearanea lunata*	E		W		RI			
Parasteatoda tepidariorum (C. L. Koch, 1841)	*Achaearanea tepidariorum*	*Achaearanea tepidariorum*	E	S	W	NI	RI	Ag		
Parasteatoda simulans (Thorell, 1875)	*Achaearanea simulans*	*Achaearanea simulans*	E		W					
Phylloneta sisyphia (Clerck, 1757)		*Theridion sisyphium*	E	S	W	NI	RI			
Phylloneta impressa (L. Koch, 1881)		*Theridion impressum*	E	S	W	NI	RI			
Theridion pictum (Walckenaer, 1802)			E	S	W					
Theridion hemerobium Simon, 1914			E		W		RI		NS	
Theridion hannoniae Denis, 1944		not present			W					
Theridion varians Hahn, 1833			E	S	W	NI	RI			
Theridion pinastri L. Koch, 1872			E						NS	
Theridion familiare O. P.-Cambridge, 1871			E	S					NS	
Theridion melanurum Hahn, 1831			E	S	W	NI	RI			
Theridion mystaceum L. Koch, 1870			E	S	W	NI	RI			
Sardinidion blackwalli (O. P.-Cambridge, 1871)	*Theridion blackwalli*	*Theridion blackwalli*	E	S			RI		NS	
Platnickina tincta (Walckenaer, 1802)		*Theridion tinctum*	E	S	W	NI	RI			
Simitidion simile (C. L. Koch, 1836)		*Theridion simile*	E	S	W	NI	RI			
Neottiura bimaculata (Linnaeus, 1767)		*Theridion bimaculatum*	E	S	W	NI	RI			
Paidiscura pallens (Blackwall, 1834)		*Theridion pallens*	E	S	W	NI	RI			
Rugathodes instabilis (O. P.-Cambridge, 1871)		*Theridion instabile*	E		W	NI	RI		NS	
Rugathodes bellicosus (Simon, 1873)		*Theridion bellicosum*	E	S	W		RI		NR	
Rugathodes sexpunctatus (Emerton, 1882)		not present		S						
Coleosoma floridanum (Banks, 1900)	not present	not present	E					Ag		
Enoplognatha ovata (Clerck, 1757)			E	S	W	NI	RI			
Enoplognatha latimana Hippa & Oksala, 1982		Appendix 1	E	S	W		RI			
Enoplognatha thoracica (Hahn, 1833)			E	S	W	NI	RI			
Enoplognatha mordax (Thorell, 1875)		*Enoplognatha crucifera*	E	S	W				NS	
Enoplognatha caricis (Fickert, 1876)	*Enoplognatha tecta*	*Enoplognatha tecta*	E						NR	V
Enoplognatha oelandica (Thorell, 1875)			E						NR	CE
Robertus lividus (Blackwall, 1836)			E	S	W	NI	RI			
Robertus arundineti (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Robertus neglectus (O. P.-Cambridge, 1871)			E	S	W	NI	RI		NS	
Robertus scoticus Jackson, 1914				S					NR	CE
Robertus insignis O. P.-Cambridge, 1907			E						NR	DD
Pholcomma gibbum (Westring, 1851)			E	S	W	NI	RI			
Theonoe minutissima (O. P.-Cambridge, 1879)			E	S	W	NI	RI			
Family THERIDIOSOMATIDAE										
Theridiosoma gemmosum (L. Koch, 1877)			E		W	NI	RI		NS	
Family MYSMENIDAE										
Trogloneta granulum Simon, 1922	not present	not present			W					
Family LINYPHIIDAE										
Ceratinella brevipes (Westring, 1851)			E	S	W	NI	RI			
Ceratinella brevis (Wider, 1834)			E	S	W	NI	RI			
Ceratinella scabrosa (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Walckenaeria acuminata Blackwall, 1833			E	S	W	NI	RI			
Walckenaeria mitrata (Menge, 1868)			E						NR	V
Walckenaeria antica (Wider, 1834)			E	S	W	NI	RI			
Walckenaeria alticeps (Denis, 1952)			E	S	W	NI	RI		NS	
Walckenaeria cucullata (C. L. Koch, 1836)			E	S	W		RI			
Walckenaeria nodosa O. P.-Cambridge, 1873			E	S	W	NI	RI		NS	
Walckenaeria atrotibialis (O. P.-Cambridge, 1878)			E	S	W	NI	RI			
Walckenaeria capito (Westring, 1861)			E	S	W		RI		NS	
Walckenaeria incisa (O. P.-Cambridge, 1871)			E	S	W				NS	
Walckenaeria dysderoides (Wider, 1834)			E	S	W	NI	RI		NS	

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Linyphiidae cont.										
Walckenaeria stylifrons (O. P.-Cambridge, 1875)			E						NR	V
Walckenaeria nudipalpis (Westring, 1851)			E	S	W	NI	RI			
Walckenaeria obtusa Blackwall, 1836			E	S	W				NS	
Walckenaeria monoceros (Wider, 1834)			E	S	W		RI		NS	
Walckenaeria corniculans (O. P.-Cambridge, 1875)			E				RI		NR	CE
Walckenaeria furcillata (Menge, 1869)			E	S	W				NS	
Walckenaeria unicornis O. P.-Cambridge, 1861			E	S	W	NI	RI			
Walckenaeria kochi (O. P.-Cambridge, 1872)			E	S	W	NI	RI		NS	
Walckenaeria clavicornis (Emerton, 1882)			E	S	W	NI	RI		NS	
Walckenaeria cuspidata Blackwall, 1833			E	S	W	NI	RI			
Walckenaeria vigilax (Blackwall, 1853)			E	S	W	NI	RI			
Dicymbium nigrum (Blackwall, 1834)			E	S	W	NI	RI			
Dicymbium nigrum brevisetosum Locket, 1962	*Dicymbium brevisetosum*	*D. nigrum* f. *brevisetosum*	E	S	W	NI	RI			
Dicymbium tibiale (Blackwall, 1836)			E	S	W	NI	RI			
Entelecara acuminata (Wider, 1834)			E	S	W	NI	RI			
Entelecara congenera (O. P.-Cambridge, 1879)			E		W				NS	
Entelecara erythropus (Westring, 1851)			E	S	W	NI	RI			
Entelecara flavipes (Blackwall, 1834)			E	S	W		RI		NS	
Entelecara omissa O. P.-Cambridge, 1902			E				RI		NS	
Entelecara errata O. P.-Cambridge, 1913			E	S	W		RI		NS	
Moebelia penicillata (Westring, 1851)			E	S	W	NI	RI		NS	
Hylyphantes graminicola (Sundevall, 1830)			E	S	W		RI			
Gnathonarium dentatum (Wider, 1834)			E	S	W	NI	RI			
Trematocephalus cristatus (Wider, 1834)			E						NS	
Tmeticus affinis (Blackwall, 1855)			E	S	W		RI		NS	
Gongylidium rufipes (Linnaeus, 1758)			E	S	W	NI	RI			
Dismodicus bifrons (Blackwall, 1841)			E	S	W	NI	RI			
Dismodicus elevatus (C. L. Koch, 1838)			E	S					NR	V
Hypomma bituberculatum (Wider, 1834)			E	S	W	NI	RI			
Hypomma fulvum (Bösenberg, 1902)			E		W	NI	RI		NS	
Hypomma cornutum (Blackwall, 1833)			E	S	W	NI	RI			
Metopobactrus prominulus (O. P.-Cambridge, 1872)			E	S	W	NI	RI			
Hybocoptus corrugis (O. P.-Cambridge, 1875)	*Hybocoptus decollatus*	*Hybocoptus decollatus*	E		W				NS	
Baryphyma pratense (Blackwall, 1861)			E	S	W					
Baryphyma gowerense (Locket, 1965)			E		W	NI	RI		NR	V
Baryphyma trifrons (O. P.-Cambridge, 1863)			E	S	W	NI	RI			
Baryphyma maritimum (Crocker & Parker, 1970)			E						NR	NT
Praestigia duffeyi Millidge, 1954		*Baryphyma duffeyi*	E				RI		NR	E
Gonatium rubens (Blackwall, 1833)			E	S	W	NI	RI			
Gonatium rubellum (Blackwall, 1841)			E	S	W	NI	RI			
Gonatium paradoxum (L. Koch, 1869)			E						NR	E
Maso sundevalli (Westring, 1851)			E	S	W	NI	RI			
Maso gallicus Simon, 1894			E		W				NS	
Minicia marginella (Wider, 1834)		Appendix 2	E				RI		NR	DD
Peponocranium ludicrum (O. P.-Cambridge, 1861)			E	S	W	NI	RI			
Pocadicnemis pumila (Blackwall, 1841)			E	S	W	NI	RI			
Pocadicnemis juncea Locket & Millidge, 1953			E	S	W	NI	RI			
Hypselistes jacksoni (O. P.-Cambridge, 1902)			E	S	W	NI	RI		NS	
Oedothorax gibbosus (Blackwall, 1841)			E	S	W	NI	RI			
Oedothorax fuscus (Blackwall, 1834)			E	S	W	NI	RI			
Oedothorax agrestis (Blackwall, 1853)			E	S	W	NI	RI			
Oedothorax retusus (Westring, 1851)			E	S	W	NI	RI			
Oedothorax apicatus (Blackwall, 1850)			E	S	W		RI			
Trichopternoides thorelli (Westring, 1861)		*Trichopterna thorelli*	E	S	W	NI	RI			
Trichopterna cito (O. P.-Cambridge, 1872)			E						NR	E
Pelecopsis mengei (Simon, 1884)			E	S	W	NI	RI			
Pelecopsis parallela (Wider, 1834)			E	S	W	NI	RI			
Pelecopsis elongata (Wider, 1834)				S					NR	NT
Pelecopsis radicicola (L. Koch, 1872)			E						NR	E
Pelecopsis susannae (Simon, 1914)	not present	not present	E							
Parapelecopsis nemoralis (Blackwall, 1841)	*Pelecopsis nemoralis*	*Pelecopsis nemoralis*	E	S	W	NI	RI			
Parapelecopsis nemoralioides (O. P.-Cambridge, 1884)	*Pelecopsis nemoralioides*	not present	E	S	W		RI		NS	

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Linyphiidae cont.										
Silometopus elegans (O. P.-Cambridge, 1872)			E	S	W	NI	RI			
Silometopus ambiguus (O. P.-Cambridge, 1905)			E	S	W	NI	RI		NS	
Silometopus reussi (Thorell, 1871)			E	S	W	NI	RI			
Silometopus incurvatus (O. P.-Cambridge, 1873)			E	S			RI		NR	V
Mecopisthes peusi Wunderlich, 1972			E	S	W	NI	RI		NS	
Cnephalocotes obscurus (Blackwall, 1834)			E	S	W	NI	RI			
Acartauchenius scurrilis (O. P.-Cambridge, 1872)			E						NR	NT
Trichoncus saxicola (O. P.-Cambridge, 1861)			E	S			RI		NR	V
Trichoncus hackmani Millidge, 1955			E						NR	V
Trichoncus affinis Kulczyński, 1894			E						NR	
Styloctetor romanus (O. P.-Cambridge, 1873)	*Ceratinopsis romana*	*Ceratinopsis romana*	E		W				NR	
Styloctetor compar (Westring, 1861)	*Ceratinopsis stativa*	*Ceratinopsis stativa*	E		W		RI		NS	
Evansia merens O. P.-Cambridge, 1900			E	S	W		RI		NS	
Tiso vagans (Blackwall, 1834)			E	S	W	NI	RI			
Tiso aestivus (L. Koch, 1872)			E	S	W				NS	
Troxochrus scabriculus (Westring, 1851)			E	S	W		RI			
Minyriolus pusillus (Wider, 1834)			E	S	W	NI	RI			
Tapinocyba praecox (O. P.-Cambridge, 1873)			E	S	W	NI	RI			
Tapinocyba pallens (O. P.-Cambridge, 1872)			E	S	W	NI	RI			
Tapinocyba insecta (L. Koch, 1869)			E	S	W	NI	RI		NS	
Tapinocyba mitis (O. P.-Cambridge, 1882)			E						NR	E
Tapinocyboides pygmaeus (Menge, 1869)			E	S					NR	DD
Microctenonyx subitaneus (O. P.-Cambridge, 1875)			E	S	W	NI	RI		NS	
Satilatlas britteni (Jackson, 1913)			E	S	W	NI	RI		NS	
Thyreosthenius parasiticus (Westring, 1851)			E	S	W	NI	RI			
Thyreosthenius biovatus (O. P.-Cambridge, 1875)			E	S	W		RI		NS	
Monocephalus fuscipes (Blackwall, 1836)			E	S	W	NI	RI			
Monocephalus castaneipes (Simon, 1884)			E	S	W	NI	RI		NS	
Lophomma punctatum (Blackwall, 1841)			E	S	W	NI	RI			
Saloca diceros (O. P.-Cambridge, 1871)			E		W		RI		NS	
Gongylidiellum vivum (O. P.-Cambridge, 1875)			E	S	W	NI	RI			
Gongylidiellum latebricola (O. P.-Cambridge, 1871)			E	S	W	NI	RI		NS	
Gongylidiellum murcidum Simon, 1884			E	S	W		RI		NS	V
Micrargus herbigradus (Blackwall, 1854)			E	S	W	NI	RI			
Micrargus apertus (O. P.-Cambridge, 1871)			E	S	W					
Micrargus subaequalis (Westring, 1851)			E	S	W	NI	RI			
Micrargus laudatus (O. P.-Cambridge, 1881)			E		W				NS	
Notioscopus sarcinatus (O. P.-Cambridge, 1872)			E	S	W				NS	
Glyphesis cottonae (La Touche, 1945)			E		W		RI		NR	V
Glyphesis servulus (Simon, 1881)			E		W				NR	NT
Erigonella hiemalis (Blackwall, 1841)			E	S	W	NI	RI			
Erigonella ignobilis (O. P.-Cambridge, 1871)			E	S	W	NI	RI		NS	
Savignia frontata Blackwall, 1833			E	S	W	NI	RI			
Diplocephalus cristatus (Blackwall, 1833)			E	S	W	NI	RI			
Diplocephalus permixtus (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Diplocephalus latifrons (O. P.-Cambridge, 1863)			E	S	W	NI	RI			
Diplocephalus connatus Bertkau, 1889			E						NR	CE
Diplocephalus picinus (Blackwall, 1841)			E	S	W	NI	RI			
Diplocephalus protuberans (O. P.-Cambridge, 1875)			E	S	W				NR	V
Diplocephalus graecus (O. P.-Cambridge, 1872)		not present	E							
Araeoncus humilis (Blackwall, 1841)			E	S	W	NI	RI			
Araeoncus crassiceps (Westring, 1861)			E	S	W	NI	RI		NS	
Panamomops sulcifrons (Wider, 1834)			E		W				NS	
Lessertia dentichelis (Simon, 1884)			E		W	NI	RI		NS	
Scotinotylus evansi (O. P.-Cambridge, 1894)			E	S					NS	
Typhochrestus digitatus (O. P.-Cambridge, 1872)			E	S	W	NI	RI		NS	
Typhochrestus simoni Lessert, 1907			E		W				NR	CE
Diplocentria bidentata (Emerton, 1882)			E	S	W		RI		NS	
Wabasso replicatus (Holm, 1950)		not present		S					NR	V
Erigone dentipalpis (Wider, 1834)			E	S	W	NI	RI			
Erigone atra Blackwall, 1833			E	S	W	NI	RI			
Erigone promiscua (O. P.-Cambridge, 1872)			E	S	W	NI	RI			

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Linyphiidae cont.										
Erigone arctica (White, 1852)			E	S	W	NI	RI			
Erigone longipalpis (Sundevall, 1830)			E	S	W	NI	RI			
Erigone tirolensis L. Koch, 1872				S					NS	
Erigone dentigera O. P.-Cambridge, 1874	*Erigone capra*	*Erigone capra*	E	S	W		RI		NR	
Erigone welchi Jackson, 1911			E	S	W		RI		NR	E
Erigone psychrophila Thorell, 1871			E	S					NR	NT
Erigone aletris Crosby & Bishop, 1928			E	S						
Prinerigone vagans (Audouin, 1826)		*Erigone vagans*	E	S	W					
Mermessus trilobatus (Emerton, 1882)		not present	E							
Mecynargus morulus (O. P.-Cambridge, 1873)		*Rhaebothorax morulus*	E	S	W	NI	RI		NS	
Mecynargus paetulus (O. P.-Cambridge, 1875)		*Rhaebothorax paetulus*		S					NR	V
Semljicola faustus (O. P.-Cambridge, 1900)	*Latithorax faustus*	*Latithorax faustus*	E	S	W	NI	RI		NS	
Semljicola caliginosus (Falconer, 1910)			E	S					NR	E
Donacochara speciosa (Thorell, 1875)			E			NI	RI		NS	
Leptorhoptrum robustum (Westring, 1851)			E	S	W	NI	RI			
Drepanotylus uncatus (O. P.-Cambridge, 1873)			E	S	W	NI	RI			
Leptothrix hardyi (Blackwall, 1850)			E	S	W	NI	RI		NS	
Hilaira excisa (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Hilaira nubigena Hull, 1911			E	S					NR	V
Hilaira pervicax Hull, 1908			E	S	W	NI			NS	
Oreoneta frigida (Thorell, 1872)	*Hilaira frigida*	*Hilaira frigida*	E	S	W	NI	RI			
Halorates reprobus (O. P.-Cambridge, 1879)			E	S	W	NI	RI		NS	
Collinsia inerrans (O. P.-Cambridge, 1885)	*Milleriana inerrans*	*Milleriana inerrans*	E	S	W		RI			
Collinsia distincta (Simon, 1884)	*Halorates distinctus*	*Halorates distinctus*	E	S	W				NS	
Collinsia holmgreni (Thorell, 1871)	*Halorates holmgreni*	*Halorates holmgreni*		S					NS	
Carorita limnaea (Crosby & Bishop, 1927)			E		W	NI	RI		NR	V
Karita paludosa (Duffey, 1971)		*Carorita paludosa*	E			NI	RI		NR	V
Wiehlea calcarifera (Simon, 1884)			E						NR	E
Mioxena blanda (Simon, 1884)			E		W		RI		NR	DD
Caviphantes saxetorum (Hull, 1916)			E	S	W				NR	NT
Asthenargus paganus (Simon, 1884)			E	S	W	NI	RI		NS	
Jacksonella falconeri (Jackson, 1908)			E	S	W	NI	RI		NS	
Pseudomaro aenigmaticus Denis, 1966			E						NR	DD
Ostearius melanopygius (O. P.-Cambridge, 1879)			E	S	W	NI	RI			
Aphileta misera (O. P.-Cambridge, 1882)			E	S	W	NI	RI			
Porrhomma pygmaeum (Blackwall, 1834)			E	S	W	NI	RI			
Porrhomma convexum (Westring, 1851)			E	S	W	NI	RI		NS	
Porrhomma rosenhaueri (L. Koch, 1872)					W		RI		NR	NT
Porrhomma pallidum Jackson, 1913			E	S	W	NI	RI			
Porrhomma campbelli F. O. P.-Cambridge, 1894			E	S	W	NI	RI		NS	
Porrhomma microphthalmum (O. P.-Cambridge, 1871)			E	S	W					
Porrhomma errans (Blackwall, 1841)			E	S	W		RI		NS	
Porrhomma egeria Simon, 1884			E	S	W		RI		NS	
Porrhomma oblitum (O. P.-Cambridge, 1871)			E		W		RI		NS	
Porrhomma cambridgei Merrett, 1994			E						NR	DD
Porrhomma montanum Jackson, 1913			E	S	W	NI	RI		NS	
Agyneta subtilis (O. P.-Cambridge, 1863)			E	S	W	NI	RI			
Agyneta conigera (O. P.-Cambridge, 1863)			E	S	W	NI	RI			
Agyneta decora (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Agyneta cauta (O. P.-Cambridge, 1902)			E	S	W	NI	RI		NS	
Agyneta olivacea (Emerton, 1882)			E	S	W	NI	RI		NS	
Agyneta ramosa Jackson, 1912			E	S	W		RI			
Agyneta innotabilis (O. P.-Cambridge, 1863)	*Meioneta innotabilis*	*Meioneta innotabilis*	E	S	W	NI	RI			
Agyneta rurestris (C. L. Koch, 1836)	*Meioneta rurestris*	*Meioneta rurestris*	E	S	W	NI	RI			
Agyneta mollis (O. P.-Cambridge, 1871)	*Meioneta mollis*	*Meioneta mollis*	E		W	NI	RI		NR	NT
Agyneta saxatilis (Blackwall, 1844)	*Meioneta saxatilis*	*Meioneta saxatilis*	E	S	W	NI	RI			
Agyneta mossica (Schikora, 1993)	*Meioneta mossica*	not present	E	S	W	NI	RI		NS	
Agyneta simplicitarsis (Simon, 1884)	*Meioneta simplicitarsis*	*Meioneta simplicitarsis*	E						NS	
Agyneta affinis (Kulczyński, 1898)	*Meioneta beata*	*Meioneta beata*	E	S	W	NI	RI			
Agyneta fuscipalpa (C. L. Koch, 1836)	*Meioneta fuscipalpa*	not present	E						NR	V
Agyneta gulosa (L. Koch, 1869)	*Meioneta gulosa*	*Meioneta gulosa*	E	S	W	NI	RI		NS	
Agyneta nigripes (Simon, 1884)	*Meioneta nigripes*	*Meioneta nigripes*		S	W				NS	

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Linyphiidae cont.										
Microneta viaria (Blackwall, 1841)			E	S	W	NI	RI			
Maro minutus O. P.-Cambridge, 1906			E	S	W		RI		NS	
Maro sublestus Falconer, 1915			E	S			RI		NR	E
Maro lepidus Casemir, 1961			E	S	W				NR	E
Syedra gracilis (Menge, 1869)			E	S					NS	
Syedra myrmicarum (Kulczyński, 1882)	not present	not present	E							
Centromerus sylvaticus (Blackwall, 1841)			E	S	W	NI	RI			
Centromerus prudens (O. P.-Cambridge, 1873)			E	S	W	NI	RI			
Centromerus arcanus (O. P.-Cambridge, 1873)			E	S	W	NI	RI			
Centromerus levitarsis (Simon, 1884)			E	S			RI		NR	E
Centromerus dilutus (O. P.-Cambridge, 1875)			E	S	W	NI	RI			
Centromerus capucinus (Simon, 1884)			E						NR	NT
Centromerus incilium (L. Koch, 1881)			E	S					NS	
Centromerus semiater (L. Koch, 1879)			E						NR	E
Centromerus brevipalpus (Menge, 1866)	*Centromerus brevivulvatus*	*Centromerus aequalis*	E	S					NR	E
Centromerus serratus (O. P.-Cambridge, 1875)			E						NR	E
Centromerus albidus Simon, 1929			E				RI		NR	CE
Centromerus cavernarum (L. Koch, 1872)			E						NR	NT
Centromerus persimilis (O. P.-Cambridge, 1912)			E				RI		NR	DD
Centromerus minutissimus Merrett & Powell, 1993			E						NR	DD
Tallusia experta (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Centromerita bicolor (Blackwall, 1833)			E	S	W	NI	RI			
Centromerita concinna (Thorell, 1875)			E	S	W	NI	RI			
Sintula corniger (Blackwall, 1856)			E	S	W	NI	RI		NS	
Oreonetides vaginatus (Thorell, 1872)			E	S	W		RI		NS	
Saaristoa abnormis (Blackwall, 1841)			E	S	W	NI	RI			
Saaristoa firma (O. P.-Cambridge, 1905)			E	S	W	NI	RI		NS	
Macrargus rufus (Wider, 1834)			E	S	W	NI	RI			
Macrargus carpenteri (O. P.-Cambridge, 1894)			E	S					NS	
Bathyphantes approximatus (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Bathyphantes gracilis (Blackwall, 1841)			E	S	W	NI	RI			
Bathyphantes parvulus (Westring, 1851)			E	S	W	NI	RI			
Bathyphantes nigrinus (Westring, 1851)			E	S	W	NI	RI			
Bathyphantes setiger F. O. P.-Cambridge, 1894			E	S	W	NI	RI		NS	
Kaestneria dorsalis (Wider, 1834)			E	S	W	NI	RI			
Kaestneria pullata (O. P.-Cambridge, 1863)			E	S	W	NI	RI			
Diplostyla concolor (Wider, 1834)			E	S	W	NI	RI			
Poeciloneta variegata (Blackwall, 1841)		*Poeciloneta globosa*	E	S	W	NI	RI			
Drapetisca socialis (Sundevall, 1833)			E	S	W	NI	RI			
Tapinopa longidens (Wider, 1834)			E	S	W	NI	RI			
Floronia bucculenta (Clerck, 1757)			E	S	W	NI	RI			
Taranucnus setosus (O. P.-Cambridge, 1863)			E	S	W	NI	RI		NS	
Labulla thoracica (Wider, 1834)			E	S	W	NI	RI			
Stemonyphantes lineatus (Linnaeus, 1758)			E	S	W	NI	RI			
Bolyphantes luteolus (Blackwall, 1833)			E	S	W	NI	RI			
Bolyphantes alticeps (Sundevall, 1833)			E	S	W		RI			
Nothophantes horridus Merrett & Stevens, 1995		not present	E						NR	E
Megalepthyphantes nebulosus (Sundevall, 1830)		*Lepthyphantes nebulosus*	E	S	W	NI	RI			
Lepthyphantes leprosus (Ohlert, 1865)			E	S	W	NI	RI			
Lepthyphantes minutus (Blackwall, 1833)			E	S	W	NI	RI			
Mughiphantes whymperi (F. O. P.-Cambridge, 1894)		*Lepthyphantes whymperi*	E	S	W		RI		NS	
Obscuriphantes obscurus (Blackwall, 1841)		*Lepthyphantes obscurus*	E	S	W	NI	RI			
Tenuiphantes alacris (Blackwall, 1853)		*Lepthyphantes alacris*	E	S	W	NI	RI			
Tenuiphantes tenuis (Blackwall, 1852)		*Lepthyphantes tenuis*	E	S	W	NI	RI			
Tenuiphantes zimmermanni (Bertkau, 1890)		*Lepthyphantes zimmermanni*	E	S	W	NI	RI			
Tenuiphantes cristatus (Menge, 1866)		*Lepthyphantes cristatus*	E	S	W	NI	RI			
Tenuiphantes mengei (Kulczyński, 1887)		*Lepthyphantes mengei*	E	S	W	NI	RI			
Tenuiphantes flavipes (Blackwall, 1854)		*Lepthyphantes flavipes*	E	S	W	NI	RI			
Tenuiphantes tenebricola (Wider, 1834)		*Lepthyphantes tenebricola*	E	S	W	NI	RI			
Palliduphantes ericaeus (Blackwall, 1853)		*Lepthyphantes ericaeus*	E	S	W	NI	RI			
Palliduphantes pallidus (O. P.-Cambridge, 1871)		*Lepthyphantes pallidus*	E	S	W	NI	RI			
Palliduphantes insignis (O. P.-Cambridge, 1913)		*Lepthyphantes insignis*	E	S	W		RI		NS	

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Linyphiidae cont.										
Palliduphantes antroniensis (Schenkel, 1933)		*Lepthyphantes antroniensis*		S					NR	CE
Piniphantes pinicola (Simon, 1884)		*Lepthyphantes pinicola*	E	S	W				NR	
Oryphantes angulatus (O. P.-Cambridge, 1881)		*Lepthyphantes angulatus*	E	S	W	NI	RI		NS	
Improphantes complicatus (Emerton, 1882)		*Lepthyphantes complicatus*		S					NR	NT
Agnyphantes expunctus (O. P.-Cambridge, 1875)		*Lepthyphantes expunctus*	E	S					NS	
Midia midas (Simon, 1884)		*Lepthyphantes midas*	E						NR	E
Helophora insignis (Blackwall, 1841)			E	S	W	NI	RI			
Pityohyphantes phrygianus (C. L. Koch, 1836)			E	S					NS	
Linyphia triangularis (Clerck, 1757)			E	S	W	NI	RI			
Linyphia hortensis Sundevall, 1830			E	S	W	NI	RI			
Neriene montana (Clerck, 1757)			E	S	W	NI	RI			
Neriene clathrata (Sundevall, 1830)			E	S	W	NI	RI			
Neriene peltata (Wider, 1834)			E	S	W	NI	RI			
Neriene furtiva (O. P.-Cambridge, 1871)			E		W				NS	
Neriene radiata (Walckenaer, 1841)			E	S					NR	NT
Microlinyphia pusilla (Sundevall, 1830)			E	S	W	NI	RI			
Microlinyphia impigra (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Allomengea scopigera (Grube, 1859)			E	S	W	NI	RI			
Allomengea vidua (L. Koch, 1879)			E	S	W	NI	RI		NS	
Family TETRAGNATHIDAE										
Tetragnatha extensa (Linnaeus, 1758)			E	S	W	NI	RI			
Tetragnatha pinicola L. Koch, 1870			E	S	W		RI			
Tetragnatha montana Simon, 1874			E	S	W	NI	RI			
Tetragnatha obtusa C. L. Koch, 1837			E	S	W	NI	RI			
Tetragnatha nigrita Lendl, 1886			E		W	NI	RI			
Tetragnatha striata L. Koch, 1862			E	S	W		RI			
Pachygnatha clercki Sundevall, 1823			E	S	W	NI	RI			
Pachygnatha listeri Sundevall, 1830			E	S	W		RI			
Pachygnatha degeeri Sundevall, 1830			E	S	W	NI	RI			
Metellina segmentata (Clerck, 1757)		*Meta segmentata*	E	S	W	NI	RI			
Metellina mengei (Blackwall, 1869)		*Meta mengei*	E	S	W	NI	RI			
Metellina merianae (Scopoli, 1763)		*Meta merianae*	E	S	W	NI	RI			
Meta menardi (Latreille, 1804)			E	S	W	NI	RI			
Meta bourneti Simon, 1922			E		W				NS	
Family ARANEIDAE										
Gibbaranea gibbosa (Walckenaer, 1802)			E	S	W	NI	RI			
Araneus angulatus Clerck, 1757			E						NS	
Araneus diadematus Clerck, 1757			E	S	W	NI	RI			
Araneus quadratus Clerck, 1757			E	S	W	NI	RI			
Araneus marmoreus Clerck, 1757			E	S	W					
Araneus alsine (Walckenaer, 1802)			E	S					NS	
Araneus sturmi (Hahn, 1831)			E	S	W		RI			
Araneus triguttatus (Fabricius, 1775)			E	S	W	NI				
Larinioides cornutus (Clerck, 1757)			E	S	W	NI	RI			
Larinioides sclopetarius (Clerck, 1757)			E	S	W	NI	RI			
Larinioides patagiatus (Clerck, 1757)			E	S	W	NI	RI		NS	
Nuctenea umbratica (Clerck, 1757)			E	S	W	NI	RI			
Agalenatea redii (Scopoli, 1763)			E	S	W	NI	RI			
Neoscona adianta (Walckenaer, 1802)			E		W		RI			
Araniella cucurbitina (Clerck, 1757)			E	S	W	NI	RI			
Araniella opisthographa (Kulczyński, 1905)			E	S	W	NI	RI			
Araniella inconspicua (Simon, 1874)			E						NS	
Araniella alpica (L. Koch, 1869)			E		W				NR	E
Araniella displicata (Hentz, 1847)			E						NR	NT
Zilla diodia (Walckenaer, 1802)			E		W					
Hypsosinga albovittata (Westring, 1851)			E	S	W		RI		NS	
Hypsosinga pygmaea (Sundevall, 1831)			E	S	W	NI	RI			
Hypsosinga sanguinea (C. L. Koch, 1844)			E						NS	
Hypsosinga heri (Hahn, 1831)			E						NR	V
Singa hamata (Clerck, 1757)			E	S	W				NS	
Cercidia prominens (Westring, 1851)			E	S	W				NS	
Zygiella x-notata (Clerck, 1757)			E	S	W	NI	RI			

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Araneidae cont.										
Zygiella atrica (C. L. Koch, 1845)			E	S	W	NI	RI			
Leviellus stroemi (Thorell, 1870)	*Stroemiellus stroemi*	*Zygiella stroemi*	E						NR	NT
Mangora acalypha (Walckenaer, 1802)			E		W		RI			
Cyclosa conica (Pallas, 1772)			E	S	W	NI	RI			
Argiope bruennichi (Scopoli, 1772)			E		W					
Family LYCOSIDAE										
Pardosa agricola (Thorell, 1856)			E	S	W	NI	RI			
Pardosa agrestis (Westring, 1861)			E	S	W	NI	RI		NS	
Pardosa purbeckensis F. O. P.-Cambridge, 1895		*Pardosa agrestis*	E	S	W		RI			
Pardosa monticola (Clerck, 1757)			E	S	W	NI	RI			
Pardosa palustris (Linnaeus, 1758)			E	S	W	NI	RI			
Pardosa pullata (Clerck, 1757)			E	S	W	NI	RI			
Pardosa prativaga (L. Koch, 1870)			E	S	W	NI	RI			
Pardosa amentata (Clerck, 1757)			E	S	W	NI	RI			
Pardosa nigriceps (Thorell, 1856)			E	S	W	NI	RI			
Pardosa lugubris (Walckenaer, 1802)			E	S			RI		NS	
Pardosa saltans Töpfer-Hofmann, 2000		not present	E	S	W		RI			
Pardosa hortensis (Thorell, 1872)			E	S	W					
Pardosa tenuipes C. L. Koch, 1847	*Pardosa proxima*	*Pardosa proxima*	E	S	W				NS	
Pardosa trailli (O. P.-Cambridge, 1873)			E	S	W				NR	V
Pardosa paludicola (Clerck, 1757)			E						NR	E
Hygrolycosa rubrofasciata (Ohlert, 1865)			E						NR	E
Xerolycosa nemoralis (Westring, 1861)			E						NS	
Xerolycosa miniata (C. L. Koch, 1834)			E	S	W				NS	
Alopecosa pulverulenta (Clerck, 1757)			E	S	W	NI	RI			
Alopecosa cuneata (Clerck, 1757)			E		W	NI	RI		NS	
Alopecosa barbipes (Sundevall, 1833)		*Alopecosa accentuata*	E	S	W	NI	RI			
Alopecosa fabrilis (Clerck, 1757)			E						NR	CE
Trochosa ruricola (De Geer, 1778)			E	S	W	NI	RI			
Trochosa robusta (Simon, 1876)			E						NR	V
Trochosa terricola Thorell, 1856			E	S	W	NI	RI			
Trochosa spinipalpis (F. O. P.-Cambridge, 1895)			E	S	W	NI	RI		NS	
Arctosa fulvolineata (Lucas, 1846)			E						NR	NT
Arctosa perita (Latreille, 1799)			E	S	W	NI	RI			
Arctosa leopardus (Sundevall, 1833)			E	S	W	NI	RI			
Arctosa cinerea (Fabricius, 1777)			E	S	W		RI		NS	
Arctosa alpigena (Doleschall, 1852)		*Tricca alpigena*		S					NR	V
Pirata piraticus (Clerck, 1757)			E	S	W	NI	RI			
Pirata tenuitarsis Simon, 1876			E	S	W	NI	RI		NS	
Pirata piscatorius (Clerck, 1757)			E	S	W	NI	RI		NS	
Piratula hygrophila (Thorell, 1872)	*Pirata hygrophilus*	*Pirata hygrophilus*	E	S	W	NI	RI			
Piratula uliginosa (Thorell, 1856)	*Pirata uliginosus*	*Pirata uliginosus*	E	S	W	NI	RI			
Piratula latitans (Blackwall, 1841)	*Pirata latitans*	*Pirata latitans*	E	S	W		RI			
Aulonia albimana (Walckenaer, 1805)			E						NR	CE
Family PISAURIDAE										
Pisaura mirabilis (Clerck, 1757)			E	S	W	NI	RI			
Dolomedes fimbriatus (Clerck, 1757)			E	S	W		RI		NS	
Dolomedes plantarius (Clerck, 1757)			E		W				NR	V
Family OXYOPIDAE										
Oxyopes heterophthalmus (Latreille, 1804)			E						NR	V
Family AGELENIDAE										
Agelena labyrinthica (Clerck, 1757)			E		W		RI			
Textrix denticulata (Olivier, 1789)			E	S	W	NI	RI			
Eratigena agrestis (Walckenaer, 1802)	*Tegenaria agrestis*	*Tegenaria agrestis*	E	S	W		RI			
Eratigena atrica (C. L. Koch, 1843)	*Tegenaria atrica*	*Tegenaria atrica*	E	S	W		RI			
Eratigena duellica (Simon, 1875)	*Tegenaria gigantea*	*Tegenaria duellica*	E	S	W	NI	RI			
Eratigena picta (Simon, 1870)	*Tegenaria picta*	Appendix 1 as *T. picta*	E						NR	V
Eratigena saeva (Blackwall, 1844)	*Tegenaria saeva*	*Tegenaria saeva*	E	S	W	NI	RI			
Tegenaria domestica (Clerck, 1757)			E	S	W	NI	RI			
Tegenaria ferruginea (Panzer, 1804)			E							
Tegenaria parietina (Fourcroy, 1785)			E				RI			
Tegenaria hasperi Chyzer, 1897	not present	not present	E					Ab		

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Agelenidae cont.										
Tegenaria silvestris C. L. Koch, 1872			E	S	W	NI	RI			
Coelotes atropos (Walckenaer, 1830)	from Amaurobiidae	from Agelenidae	E	S	W					
Coelotes terrestris (Wider, 1834)	from Amaurobiidae	from Agelenidae	E	S	W				NS	
Family CYBAEIDAE										
Cryphoeca silvicola (C. L. Koch, 1834)	from Dictynidae	from Agelenidae	E	S	W	NI	RI			
Tuberta maerens (O. P.-Cambridge, 1863)	from Dictynidae	from Agelenidae	E						NR	E
Family HAHNIIDAE										
Antistea elegans (Blackwall, 1841)			E	S	W	NI	RI			
Iberina montana (Blackwall, 1841)	*Hahnia montana*	*Hahnia montana*	E	S	W	NI	RI			
Iberina candida (Simon, 1875)	*Hahnia candida*	*Hahnia candida*	E						NR	V
Iberina microphthalma (Snazell & Duffey, 1980)	*Hahnia microphthalma*	*Hahnia microphthalma*	E						NR	DD
Hahnia nava (Blackwall, 1841)			E	S	W	NI	RI			
Hahnia helveola Simon, 1875			E	S	W	NI	RI			
Hahnia pusilla C. L. Koch, 1841			E	S	W		RI		NS	
Cicurina cicur (Fabricius, 1793)	from Dictynidae	from Agelenidae	E	S	W				NS	
Mastigusa arietina (Thorell, 1871)	from Dictynidae	*Tetrilus arietina*	E						E	RE
Mastigusa macrophthalma (Kulczyński, 1897)	from Dictynidae	*Tetrilus macrophthalma*	E						NR	V
Family DICTYNIDAE										
Dictyna arundinacea (Linnaeus, 1758)			E	S	W	NI	RI			
Dictyna pusilla Thorell, 1856			E	S	W				NS	
Dictyna major Menge, 1869				S					NR	CE
Dictyna uncinata Thorell, 1856			E	S	W	NI	RI			
Brigittea latens (Fabricius, 1775)	*Dictyna latens*	*Dictyna latens*	E	S	W	NI	RI			
Nigma puella (Simon, 1870)			E		W		RI		NS	
Nigma flavescens (Walckenaer, 1830)	not present	*Nigma flavescens*	E							
Nigma walckenaeri (Roewer, 1951)			E							
Lathys humilis (Blackwall, 1855)			E	S	W					
Lathys heterophthalma Kulczyński, 1891	*Lathys nielseni*	Appendix 1	E						NR	V
Lathys stigmatisata (Menge, 1869)			E		W				NR	V
Argenna subnigra (O. P.-Cambridge, 1861)			E		W		RI		NS	
Argenna patula (Simon, 1874)			E	S	W				NS	
Altella lucida (Simon, 1874)			E						NR	CE
Argyroneta aquatica (Clerck, 1757)	from Cybaeidae	from Argyronetidae	E	S	W	NI	RI			
Family AMAUROBIIDAE										
Amaurobius fenestralis (Stroem, 1768)			E	S	W	NI	RI			
Amaurobius similis (Blackwall, 1861)			E	S	W	NI	RI			
Amaurobius ferox (Walckenaer, 1830)			E	S	W	NI	RI			
Family ANYPHAENIDAE										
Anyphaena accentuata (Walckenaer, 1802)			E	S	W	NI	RI			
Anyphaena numida Simon, 1897	not present	not present	E							
Anyphaena sabina L. Koch, 1866	not present	not present	E							
Family LIOCRANIDAE										
Agroeca brunnea (Blackwall, 1833)			E	S	W					
Agroeca proxima (O. P.-Cambridge, 1871)			E	S	W	NI	RI			
Agroeca inopina O. P.-Cambridge, 1886			E		W					
Agroeca lusatica (L. Koch, 1875)			E						NR	E
Agroeca dentigera Kulczyński, 1913		not present			W				NR	DD
Agroeca cuprea Menge, 1873			E	S					NR	NT
Liocranoeca striata (Kulczyński, 1882)	*Agraecina striata*	*Agroeca striata*	E	S	W	NI	RI		NS	
Apostenus fuscus Westring, 1851		Appendix 1	E						NR	V
Scotina celans (Blackwall, 1841)			E	S	W		RI		NS	
Scotina gracilipes (Blackwall, 1859)			E	S	W	NI	RI		NS	
Scotina palliardii (L. Koch, 1881)			E						NR	E
Liocranum rupicola (Walckenaer, 1830)			E		W		RI		NS	
Family PHRUROLITHIDAE	*Corinnidae*	*Clubionidae*								
Phrurolithus festivus (C. L. Koch, 1835)			E	S	W	NI	RI			
Phrurolithus minimus C. L. Koch, 1839			E						NS	
Family CLUBIONIDAE										
Clubiona corticalis (Walckenaer, 1802)			E		W					
Clubiona reclusa O. P.-Cambridge, 1863			E	S	W	NI	RI			

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Clubionidae cont.										
Clubiona subsultans Thorell, 1875				S					NR	NT
Clubiona stagnatilis Kulczyński, 1897			E	S	W	NI	RI			
Clubiona rosserae Locket, 1953			E						NR	V
Clubiona norvegica Strand, 1900			E	S	W				NS	
Clubiona caerulescens L. Koch, 1867			E	S	W				NR	V
Clubiona pallidula (Clerck, 1757)			E	S	W	NI	RI			
Clubiona phragmitis C. L. Koch, 1843			E	S	W	NI	RI			
Clubiona terrestris Westring, 1851			E	S	W	NI	RI			
Clubiona frutetorum L. Koch, 1866		not present					RI			
Clubiona neglecta O. P.-Cambridge, 1862			E	S	W	NI	RI			
Clubiona pseudoneglecta Wunderlich, 1994		not present	E						NR	V
Clubiona frisia Wunderlich & Schütt, 1995		*Clubiona similis*	E						NR	NT
Clubiona lutescens Westring, 1851			E	S	W	NI	RI			
Clubiona comta C. L. Koch, 1839			E	S	W	NI	RI			
Clubiona brevipes Blackwall, 1841			E	S	W	NI	RI			
Clubiona trivialis C. L. Koch, 1843			E	S	W	NI	RI			
Clubiona juvenis Simon, 1878			E				RI		NR	NT
Clubiona diversa O. P.-Cambridge, 1862			E	S	W	NI	RI			
Clubiona subtilis L. Koch, 1867			E	S	W		RI			
Porrhoclubiona genevensis (L. Koch, 1866)	*Clubiona genevensis*	*Clubiona genevensis*	E		W				NR	NT
Porrhoclubiona leucaspis (Simon, 1932)	*Clubiona leucaspis*	not present	E							
Family CHEIRACANTHIIDAE	Clubionidae	Clubionidae								
Cheiracanthium erraticum (Walckenaer, 1802)			E	S	W	NI	RI			
Cheiracanthium pennyi O. P.-Cambridge, 1873			E						NR	E
Cheiracanthium virescens (Sundevall, 1833)			E	S	W	NI	RI		NS	
Family ZODARIIDAE										
Zodarion italicum (Canestrini, 1868)		Appendix 1	E						NS	
Zodarion vicinum Denis, 1935		not present	E						NR	V
Zodarion rubidum Simon, 1914		not present	E						NR	
Zodarion fuscum (Simon, 1870)		not present	E		W				NR	V
Family GNAPHOSIDAE										
Drassodes lapidosus (Walckenaer, 1802)			E	S	W	NI	RI			
Drassodes cupreus (Blackwall, 1834)			E	S	W	NI	RI			
Drassodes pubescens (Thorell, 1856)			E	S	W		RI		NS	
Haplodrassus signifer (C. L. Koch, 1839)			E	S	W	NI	RI			
Haplodrassus dalmatensis (L. Koch, 1866)			E		W				NS	
Haplodrassus umbratilis (L. Koch, 1866)			E						NR	DD
Haplodrassus soerenseni (Strand, 1900)				S					NR	E
Haplodrassus silvestris (Blackwall, 1833)			E	S	W				NS	
Haplodrassus minor (O. P.-Cambridge, 1879)			E		W				NS	
Scotophaeus blackwalli (Thorell, 1871)			E	S	W	NI	RI			
Scotophaeus scutulatus (L. Koch, 1866)		Appendix 2	E					Ah		
Phaeocedus braccatus (L. Koch, 1866)			E						NR	V
Zelotes electus (C. L. Koch, 1839)			E	S	W	NI	RI		NS	
Zelotes latreillei (Simon, 1878)			E	S	W	NI	RI			
Zelotes apricorum (L. Koch, 1876)			E	S	W		RI			
Zelotes subterraneus (C. L. Koch, 1833)		Appendix 1	E	S	W				NS	
Zelotes longipes (L. Koch, 1866)		*Zelotes serotinus*	E						NR	V
Zelotes petrensis (C. L. Koch, 1839)			E						NR	
Trachyzelotes pedestris (C. L. Koch, 1837)		*Zelotes pedestris*	E		W					
Urozelotes rusticus (L. Koch, 1872)		*Zelotes rusticus*	E		W					
Drassyllus lutetianus (L. Koch, 1866)		*Zelotes lutetianus*	E		W		RI		NS	
Drassyllus pusillus (C. L. Koch, 1833)		*Zelotes pusillus*	E	S	W	NI	RI			
Drassyllus praeficus (L. Koch, 1866)		*Zelotes praeficus*	E		W				NS	
Gnaphosa lugubris (C. L. Koch, 1839)			E						NR	V
Gnaphosa occidentalis Simon, 1878			E						NR	NT
Gnaphosa nigerrima L. Koch, 1877		not present	E						NR	V
Gnaphosa leporina (L. Koch, 1866)			E	S	W				NS	
Callilepis nocturna (Linnaeus, 1758)			E		W				NR	IU
Micaria pulicaria (Sundevall, 1831)			E	S	W	NI	RI			
Micaria albovittata (Lucas, 1846)		*Micaria romana*	E						NR	V

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Gnaphosidae cont.										
Micaria alpina L. Koch, 1872				S	W				NR	V
Micaria subopaca Westring, 1861			E	S					NS	
Micaria silesiaca L. Koch, 1875			E						NR	NT
Family MITURGIDAE	Zoridae	Zoridae								
Zora spinimana (Sundevall, 1833)			E	S	W	NI	RI			
Zora armillata Simon, 1878			E						NR	CE
Zora nemoralis (Blackwall, 1861)			E	S	W				NR	V
Zora silvestris Kulczyński, 1897			E						NR	CE
Family ZOROPSIDAE										
Zoropsis spinimana (Dufour, 1820)	not present	not present	E							
Family SPARASSIDAE		Eusparassidae								
Micrommata virescens (Clerck, 1757)			E		W		RI		NS	
Family PHILODROMIDAE		Thomisidae								
Philodromus dispar Walckenaer, 1826			E	S	W		RI			
Philodromus aureolus (Clerck, 1757)			E	S	W	NI	RI			
Philodromus praedatus O. P.-Cambridge, 1871			E	S	W		RI			
Philodromus cespitum (Walckenaer, 1802)			E	S	W	NI	RI			
Philodromus longipalpis Simon, 1870		Appendix 2	E						NS	
Philodromus collinus C. L. Koch, 1835			E							
Philodromus buxi Simon, 1884			E							
Philodromus emarginatus (Schrank, 1803)			E	S		NI			NR	V
Philodromus albidus Kulczyński, 1911			E		W		RI		NS	
Philodromus margaritatus (Clerck, 1757)			E	S					NR	NT
Philodromus rufus Walckenaer, 1826			E							
Rhysodromus fallax (Sundevall, 1833)	*Philodromus fallax*	*Philodromus fallax*	E		W				NR	V
Rhysodromus histrio (Latreille, 1819)	*Philodromus histrio*	*Philodromus histrio*	E	S	W				NS	
Thanatus striatus C. L. Koch, 1845			E		W		RI			
Thanatus formicinus (Clerck, 1757)			E						NR	CE
Thanatus vulgaris Simon, 1870	not present	not present	E	S	W			Ab		
Tibellus maritimus (Menge, 1875)			E	S	W	NI	RI			
Tibellus oblongus (Walckenaer, 1802)			E	S	W	NI	RI			
Family THOMISIDAE										
Thomisus onustus Walckenaer, 1806			E						NS	
Diaea dorsata (Fabricius, 1777)			E		W		RI			
Misumena vatia (Clerck, 1757)			E		W		RI			
Pistius truncatus (Pallas, 1772)			E						NR	CE
Xysticus cristatus (Clerck, 1757)			E	S	W	NI	RI			
Xysticus audax (Schrank, 1803)			E	S	W		RI			
Xysticus kochi Thorell, 1872			E	S	W					
Xysticus erraticus (Blackwall, 1834)			E	S	W	NI	RI			
Xysticus lanio C. L. Koch, 1835			E		W		RI			
Xysticus ulmi (Hahn, 1831)			E	S	W		RI			
Xysticus bifasciatus C. L. Koch, 1837			E	S					NS	
Xysticus luctator L. Koch, 1870			E						NR	E
Xysticus sabulosus (Hahn, 1832)			E	S	W	NI	RI		NS	
Xysticus luctuosus (Blackwall, 1836)			E	S	W		RI		NR	E
Xysticus acerbus Thorell, 1872			E		W				NR	
Bassaniodes robustus (Hahn, 1832)	*Xysticus robustus*	*Xysticus robustus*	E						NR	E
Cozyptila blackwalli (Simon, 1875)	*Ozyptila blackwalli*	*Ozyptila blackwalli*	E						NR	E
Ozyptila scabricula (Westring, 1851)			E		W				NS	
Ozyptila claveata (Walckenaer, 1837)	*Ozyptila nigrita*	*Ozyptila nigrita*	E						NS	
Ozyptila pullata (Thorell, 1875)		not present	E						NR	V
Ozyptila sanctuaria (O. P.-Cambridge, 1871)			E		W		RI			
Ozyptila praticola (C. L. Koch, 1837)			E		W		RI			
Ozyptila trux (Blackwall, 1846)			E	S	W	NI	RI			
Ozyptila simplex (O. P.-Cambridge, 1862)			E		W					
Ozyptila atomaria (Panzer, 1801)			E	S	W	NI	RI			
Ozyptila brevipes (Hahn, 1826)			E		W		RI			
Family SALTICIDAE										
Salticus scenicus (Clerck, 1757)			E	S	W	NI	RI			

Species	2014	Roberts	E	S	W	NI	RI	AS	GB	IU
Salticidae cont.										
Salticus cingulatus (Panzer, 1797)			E	S	W	NI	RI			
Salticus zebraneus (C. L. Koch, 1837)			E						NS	
Heliophanus cupreus (Walckenaer, 1802)			E	S	W	NI	RI			
Heliophanus flavipes (Hahn, 1832)			E	S	W	NI	RI			
Heliophanus auratus C. L. Koch, 1835			E						NR	V
Heliophanus dampfi Schenkel, 1923		Appendix 2	E	S	W				NR	V
Marpissa muscosa (Clerck, 1757)			E	S	W				NS	
Marpissa radiata (Grube, 1859)			E		W				NR	V
Marpissa nivoyi (Lucas, 1846)			E		W		RI		NS	
Sibianor aurocinctus (Ohlert, 1865)		*Bianor aurocinctus*	E	S	W				NS	
Sibianor larae Logunov, 2001	not present	not present	E							
Ballus chalybeius (Walckenaer, 1802)		*Ballus depressus*	E		W				NS	
Neon reticulatus (Blackwall, 1853)			E	S	W	NI	RI			
Neon robustus Lohmander, 1945		not present	E	S	W		RI		NS	
Neon valentulus Falconer, 1912			E						NR	CE
Neon pictus Kulczyński, 1891		not present	E						NR	NT
Euophrys frontalis (Walckenaer, 1802)			E	S	W	NI	RI			
Euophrys herbigrada (Simon, 1871)			E						NR	V
Euophrys petrensis C. L. Koch, 1837	*Talavera petrensis*	*Euophrys petrensis*	E	S		NI	RI		NR	NT
Pseudeuophrys erratica (Walckenaer, 1826)		*Euophrys erratica*	E	S	W	NI	RI		NS	
Pseudeuophrys lanigera (Simon, 1871)		*Euophrys lanigera*	E	S	W		RI			
Pseudeuophrys obsoleta (Simon, 1868)		*Euophrys browningi*	E						NS	
Talavera aequipes (O. P.-Cambridge, 1871)		*Euophrys aequipes*	E	S	W		RI			
Talavera thorelli (Kulczyński, 1891)		App. 2 as *Euophrys thorelli*	E						NR	V
Hypositticus pubescens (Fabricius, 1775)	*Sitticus pubescens*	*Sitticus pubescens*	E	S	W		RI			
Attulus distinguendus (Simon, 1968)	*Sitticus distinguendus*	not present	E						NR	CE
Attulus saltator (O. P.-Cambridge, 1868)	*Sitticus saltator*	*Attulus saltator*	E		W				NS	
Calositticus caricis (Westring, 1861)	*Sitticus caricis*	*Sitticus caricis*	E		W		RI		NR	
Calositticus floricola (C. L. Koch, 1837)	*Sitticus floricola*	*Sitticus floricola*	E	S	W	NI	RI		NR	NT
Calositticus inexpectus (Logunov & Kronestedt, 1997)	*Sitticus inexpectus*	not present	E		W				NS	
Evarcha falcata (Clerck, 1757)			E	S	W		RI			
Evarcha arcuata (Clerck, 1757)			E		W				NS	
Macaroeris nidicolens (Walckenaer, 1802)		not present	E							
Aelurillus v-insignitus (Clerck, 1757)			E	S					NS	
Phlegra fasciata (Hahn, 1826)			E		W				NR	NT
Synageles venator (Lucas, 1836)			E		W				NS	
Myrmarachne formicaria (De Geer, 1778)			E						NS	
Pellenes tripunctatus (Walckenaer, 1802)			E						NR	V
Dendryphantes rudis (Sundevall, 1832)	not present	not present	E							
Hasarius adansoni (Audouin, 1826)	not present	not present	E			NI	RI	Ag		

List A2. Species awaiting taxonomic definition

	2014 Checklist	Family								
Orchestina sp.		Oonopidae	E						NR	CE
Megalepthyphantes cf. *collinus*		Linyphiidae	E							
Lathys sp.	not present	Dictynidae					RI			

List A3. Species with insufficient data to determine status

	2014 Checklist	Family								
Holocnemus pluchei (Scopoli, 1763)	not present	Pholcidae	E					Ab		
Oecobius navus Blackwall, 1859	not present	Oecobiidae	E					Ab		
Islandiana falsifica (Keyserling, 1886)		Linyphiidae			W					
Frontinellina frutetorum (C.L.Koch, 1834)		Linyphiidae	E							
Neriene emphana (Walckenaer, 1841)	not present	Linyphiidae	E							
Tegenaria ramblae Barrientos, 1978		Agelenidae	E							
Trachyzelotes fuscipes (C. L.Koch, 1866)	not present	Gnaphosidae	E							
Synema globosum (Fabricius, 1775)	not present	Thomisidae	E							

B1. Species found only in artificial tropical biomes

	2014 Checklist	**Family**
Spermophora kerinci Huber, 2005	not present	Pholcidae
Nesticella mogera (Yaginuma, 1972)	not present	Nesticidae
Pseudanapis aloha Forster, 1959	not present	Anapidae

B2. Species recorded from imported goods but not established

	2014 Checklist	**Family**
Uroctea durandi (Latreille, 1809)	not present	Oecobiidae
Artema atlanta Walckenaer, 1873	not present	Pholcidae
Steatoda paykulliana (Walckenaer, 1806)		Theridiidae
Cyrtophora citricola (Forsskål, 1775)	not present	Araneidae
Olios sanctivincentii (Simon, 1897)	not present	Sparassidae
Barylestis variatus (Pocock, 1899)	not present	Sparassidae
Heteropoda venatoria (Linnaeus, 1767)	not present	Sparassidae
Philaeus chrysops (Poda, 1761)		Salticidae
Phidippus johnsoni (Peckham & Peckham, 1883)	not present	Salticidae

Table 2: List B: species recorded but not established in natural or semi-natural habitats.

List	**Description**	**E**	**S**	**W**	**NI**	**RI**	**GB & I**
A1	Established species	644	449	492	315	418	665
A2	Established but not fully described	2				1	3
A1 + A2	Established in Great Britain and Ireland	646	449	492	315	419	668
A3	Status not known	7		1			8
A1 + A2 + A3	Recorded in Great Britain and Ireland	653	449	493	315	419	676
B1	Artificial biomes only						3
B2	Imports						9

Table 3: Summary. Abbreviations: E = England; S = Scotland; W = Wales; NI = Northern Ireland; RI = Republic of Ireland; GB = Great Britain; I = island of Ireland.

The British harvestman (Opiliones) fauna: 50 years of biodiversity change, and an annotated checklist

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Abstract

The British harvestman fauna amounted to 22 species in 1969, and increased by almost 30% to 31 species in the following 50 years. The recent additions are discussed, and an updated checklist is provided. Although some of these species had been considered as relicts, there is little evidence to suggest that they are anything other than recent immigrants, with distributions and patterns of spread largely consistent with that view. Possible future immigrants or overlooked species are considered, along with some of the pressures driving change.

Keywords: non-native species • recording scheme

Introduction

As part of a celebration of the first publication of this journal in 1969 (originally the *Bulletin of the British Arachnological Society*) this paper reviews the rapid and surprising changes in the composition of the British harvestman (Opiliones) fauna during the past half century.

The first harvestman-related article in the *Bulletin* was a note by Jochen Martens (1969) confirming the identity of the British species of *Nemastoma* as *N. bimaculatum* rather than the similar *N. lugubre*. Martens (1969: 24) noted that 'In spite of good diagnostic characters (even macroscopical by size) the two species are mixed by all modern authors, following Roewer who has combined the names to "*Nemastoma lugubre-bimaculatum*".' The theme of identity confusion recurs regularly in the following decades and many more changes in the fauna were to come.

Here, I will consider the changes which have taken place over the past 50 years, explore the reasons for them, and speculate on what the next half century might bring for the British harvestman fauna. One enduring feature since 1969 has been Prof. Martens's continuing contribution (e.g. Wijnhoven & Martens 2019).

British Harvestman Recording Scheme

The distribution data used in this review come from the British Arachnological Society (BAS) Harvestman Recording Scheme (HRS), formerly the Opiliones Recording Scheme (ORS). The ORS started in 1973, was originally run by the Biological Records Centre (BRC) (now part of the Natural Environment Research Council), and was later jointly administered by the BAS and BRC. Since 2005, the scheme has been administered solely by the BAS.

The HRS dataset is largely the result of the recording efforts of a large number of amateur naturalists. Data have also come from specific research studies or general biodiversity and ecological research. The data would not exist without volunteer recorders.

The publication of the Linnean Society's first Synopsis *of the British Fauna* was on Harvestmen (Savory 1948) and was a major step in promoting the group as worthy of study. This publication has gone through a further three editions authored by Sankey & Savory (1974), Hillyard & Sankey (1989), and Hillyard (2005); it is now out of print and significantly out of date.

In 1973, John H. P. Sankey was coordinating the BRC Recording Scheme, with records being submitted on a standard record card. BRC published a Provisional Atlas (Sankey 1988). After John's death, Paul D. Hillyard further developed the BRC scheme leading to the publication of a new *Synopsis* (Hillyard 2005), with distribution maps based on data held by the BRC. The scheme then passed to Peter Nicholson at a time when the database had moved from BRC to be administered by the BAS itself. The author is the most recent custodian. Currently, the HRS data sit alongside the BAS spider data on the SRS website and can be accessed via http://srs.britishspiders.org.uk. In addition to distribution maps and records there are various resources including species accounts, photographs, and identification aids.

Distribution maps

Savory (1948), in his *Synopsis* provided lists of counties where each species had been found. Distribution maps for British harvestmen were first produced by Bristowe (1949) who recognised 21 species and mapped his own and other published records at the county level, with significant recorder bias. Sankey & Savory (1974), in their *Synopsis*, followed the same mapping format but with the benefit of a much larger dataset. The *Provisional Atlas* (Sankey 1988), and all subsequent mapping of the scheme, has been at hectad level but still with large areas of the country unrecorded and clear biases towards certain well-worked areas.

The 1988 atlas used 11,244 computerized and validated records. By 1998 there were a further 10,000 records. As of August 2019, there are about 59,600 records.

Checklist of British harvestmen

An updated and annotated checklist of British species, which replaces the last published checklist (Hillyard 2005). Changes from previous versions are highlighted in **bold**.

suborder LANIATORES
  family Phalangodidae
    ***Scotolemon doriae* Pavesi, 1878**
      relict or possible introduction [1] [#]
suborder DYSPNOI
  family Nemastomatidae

Nemastoma bimaculatum (Fabricius, 1775)

Mitostoma chrysomelas (Hermann, 1804)

Nemastomella bacillifera (Simon, 1879)

= *Centetostoma bacilliferum* (Simon, 1879) [2] [#]

     relict or possible introduction

family Trogulidae

Trogulus tricarinatus (Linnaeus, 1767)

Anelasmocephalus cambridgei (Westwood, 1874)

family Sabaconidae

***Sabacon viscayanus ramblaianus* Martens, 1983**

=*Sabacon viscayanum ramblaianum* (Martens, 1983) [3] [#]

     relict or possible introduction

suborder EUPNOI

family Phalangiidae

   subfamily Oligolophinae

Oligolophus tridens (C. L. Koch, 1836)

Oligolophus hanseni (Kraepelin, 1896)

Paroligolophus agrestis (Meade, 1855)

Paroligolophus meadii (O. Pickard-Cambridge, 1890)

Lacinius ephippiatus (C. L. Koch, 1835)

Odiellus spinosus (Bosc, 1792)

     established introduction

Mitopus morio (Fabricius, 1799)

   subfamily Phalangiinae

Phalangium opilio Linnaeus, 1758

   subfamily Opilioninae

Opilio parietinus (De Geer, 1778)

Opilio canestrinii (Thorell, 1876)

     recent introduction

Opilio saxatilis C. L. Koch, 1839

   subfamily Platybuninae

Megabunus diadema (Fabricius, 1779)

***Rilaena triangularis* (Herbst, 1799)**

= *Platybunus triangularis* (Herbst, 1799) [4]

Platybunus pinetorum C. L. Koch, 1839

     recent introduction

Lophopilio palpinalis (Herbst, 1799)

family Sclerosomatidae

   subfamily Scleosomatinae

Homalenotus quadridentatus (Cuvier, 1795)

   subfamily Gyinae

***Dicranopalpus caudatus* Dresco, 1948**

     relict or possible introduction [5] [#]

***Dicranopalpus ramosus* (Simon, 1909)**

     recent introduction [5]

***Dicranopalpus larvatus* (Canestrini,1874)**

     recent introduction [6]

   subfamily Leiobuninae

Leiobunum rotundum (Latreille, 1798)

Leiobunum blackwalli Meade, 1861

***Leiobunum gracile* Thorell, 1876**

= *Leiobunum tisciae* Avram, 1971 [7]

     recent introduction

***Leiobunum* sp. A**

     recent introduction [8]

Nelima gothica Lohmander, 1945

     relict or possible introduction [#]

Notes

It is possible that some or all of these are previously undetected relict species, consistent with former geographical linkage to the Pyrenees/Iberia. Alternatively they may be relatively recent introductions, sometimes indicated by rapid range expansion, e.g. in *Sabacon*, but this might equally be due to climate change allowing them to expand from their refugial areas.

[1] *Scotolemon doriae* has recently been reported from Plymouth. (Bilton 2018).

[2] *Centetostoma bacilliferum* is now in the genus *Nemastomella* (Schönhofer 2013). The genus name *Nemastomella* was introduced by (Mello-Leitão 1936) for an Iberian species, *N. integripes*, then synonymized with *N. dubia* by Staręga (1986). Staręga (1986) attached to the still-valid genus name 11 Iberian species including *bacillifera* (Simon, 1879); Schönhofer (2013) validated this decision.

[3] *Sabacon* - change of gender (Schönhofer 2013).

[4] *Rilaena triangularis* was moved back to the genus *Platybunus* by Hillyard (2005). The justification for this is unclear and it has been restored to *Rilaena* for consistency with other European checklists and until the relationship between these genera is resolved.

[5] The presence in Britain of *Dicranopalpus caudatus* and *D. ramosus* was established by Wijnhoven & Prieto (2015).

[6] *Dicranopalpus larvatus* was discovered in the Scilly Isles, Guernsey, and the Isle of Wight in February 2019.

[7] The *Leiobunum rupestre* species group was reviewed by Martens & Schönhofer (2016). This concluded that *Leiobunum gracile* was the earliest available name for *L. tisciae*.

[8] An unknown species of *Leiobunum* has been spreading across Europe since about the year 2000 (Wijnhoven, Schönhofer & Martens 2007) this has so far remained unnamed and has been known as *Leiobunum* sp. A in the interim.

Kury (2012), in his synopsis of available checklists, cited three versions of the British list, with only two species being added in that period (Table 1). Each of these lists covers the British Isles, i.e. the archipelago of Britain and Ireland. Currently, the BAS collates distribution data for harvestmen within Britain only. It is perhaps unfortunate that this useful biogeographic zone has been split. A checklist for the island of Ireland was published by Cawley (2002) which lists 17 species. Surprisingly, there appear to have been no additions since then (https://maps.biodiversityireland.ie/Dataset/56).

For comparison, Table 2 includes a selection of recent checklists from northern and central Europe. These show a wide range of diversity depending both on size and location of the geographical region, from four species on Iceland to 141 on the Iberian Peninsula.

It can be seen that a northern European archipelago like Britain, which was significantly affected by the last glaciation, has a relatively limited fauna compared to larger countries and regions like France, Italy, and Iberia, which have a larger bioclimatic range and greater biodiversity, due to the

Author	Region	No. species
Sankey & Savory (1974)	British Isles	22
Hillyard & Sankey (1989)	British Isles	23
Hillyard (2005)	British Isles	25

Table 1: British checklists.

large area and number of relict species with restricted ranges.

Accordingly, Italy has about 40% endemic harvestman species (Chemini 1995) and the Iberian Peninsula 70% (Prieto 2008). Kury (2002) listed the U.K. as having three endemic species, but in fact there are none.

Additions to the British fauna

The British harvestman fauna can be divided into three fairly discrete groups:

Natives, which may have survived the last glaciation or gradually moved in, under their own ambulatory power, as the ice retreated.

Historic immigrants, which came along with traded goods and human migrants. Long transit times probably led to poor survival so it is likely there were few introductions during this period. For example, *Opilio parietinus* and *Odiellus spinosus*, although present in the nineteenth century lists, are predominantly synanthropic, i.e. associated with human activities.

Recent immigrants arriving during the major trade boom of the twentieth–twenty-first centuries. This was an age of increasingly rapid transport, giving maximum opportunity for survival in transit. These harvestmen are largely associated with synanthropic habitats. There are nine species which fall within the nominal 50 year timeframe but two earlier arrivals are included for discussion (Table 3). The change in number of species over time is given in Table 4.

Harvestmen do not have the distributional advantages of spiders with their silk-mediated ballooning, or pseudoscor-

Publication	Region	No. species
Bezděčka, Bezděčková & Kvamme (2017)	Iceland	4
Bezděčka, Bezděčková & Kvamme (2017)	Faroe Islands	5
Bezděčka, Bezděčková & Kvamme (2017)	Finland	17
Cawley (2002)	Ireland	17
Bezděčka, Bezděčková & Kvamme (2017)	Sweden	21
Bezděčka, Bezděčková & Kvamme (2017)	Norway	23
Bezděčka, Bezděčková & Kvamme (2017)	Denmark	25
Vanhercke (2004)	Belgium	26
Current paper (2019)	Britain	31
Muster & Meyer (2014)	Luxembourg	31
Wijnhoven (2009)	Netherlands	34
Bliss & Martens (1995)	Germany	45
Delfosse (2004)	France	120
Chemini (1995)	Italy	120
Prieto (2008)	Iberian Peninsula	141

Table 2: Selection of current European checklists.

Species	Date
Nelima gothica	< 1935
Dicranopalpus caudatus	< 1957
Dicranopalpus ramosus	< 1970
Sabacon viscayanus ramblaianus	< 1981
Nemastomella bacillifera	< 1988
Opilio canestrinii	< 1999
Platybunus pinetorum	< 2008
Leiobunum gracile	< 2009
Leiobunum sp. A	< 2009
Scotolemon doriae	< 2017
Dicranopalpus larvatus	< 2018

Table 3: Estimated arrival date in Britain of recent immigrants.

pions, which use phoresy (grabbing on with their chelicerae to other, more mobile animals). There seems to be no evidence that harvestmen use their chelicerae to hitch a lift, but who knows what tiny nymphs get up to?

For almost all British harvestmen, the known distribution is strongly affected by recorder bias. The highest population of active recorders is in southern Britain which increases the likelihood of discoveries being made there first, followed by a probable wave of recognition as recorders realise a new species might be in their patch and positively look for it.

In general, most species enter through the south of Britain where most goods arrive via main transport hubs for onward distribution. However, some species appear to leapfrog to distant parts of the country, probably by rapid (containerized) road and rail transport, e.g. *Opilio canestrinii* in Moray, Scotland.

It is well recognised that what we consider as non-native species are often described as being synanthropic. In their review of non-native species in Canada's boreal zone, Langor *et al*. (2014: 372) found that "A large proportion of such species are associated with disturbed anthropogenic habitats such as urban areas, agricultural landscapes, transportation and communication corridors, and industrial developments". Most of the species discussed below are most readily found in such habitats and several are commonly encountered when resting on walls of buildings.

In his important publication on the faunal connections between Europe and North America, Lindroth (1957) reviewed the fauna of Newfoundland, which he considered to be more affected by introduced European species than any other part of North America. The greatest concentration of those species was to be found in the south east, the main area of trade and population originating in Britain.

Time period	Total no. British species	Change in no. species
1855	13	
-1890	19	+6
-1969	22	+3
-1988	23	+1
1990 to 1999	25	+2
2000 to 20009	26	+1
2010 to 2019	31	+5

Table 4: Change in number of species.
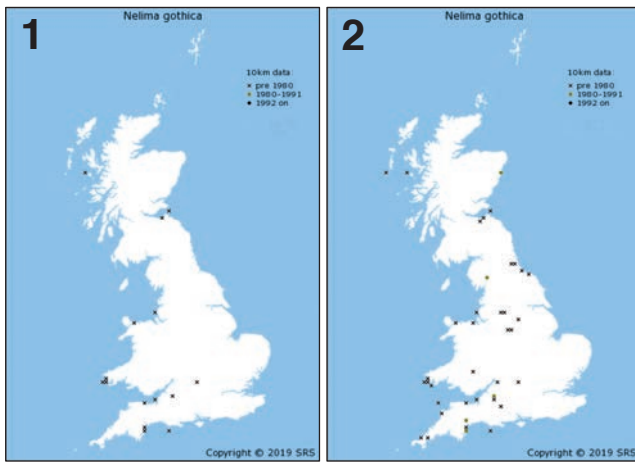
Maps 1–2: Distribution of *Nelima gothica*. **1** up to 1950; **2** up to 2019.

Maps 3–4: Distribution of *Sabacon viscayanus ramblaianus*. **3** up to 1980; **4** up to 2019.

When considering whether a species was an introduction he used several evidence criteria: historical (i.e. when did it first appear in survey data), geographical (whether the distribution was disjunct), ecological (whether largely synanthropic), biological, and taxonomic. For a long time, Newfoundland was run as a summer base for British fishermen, largely from ports in the south-west of England. Sailing ships in ballast crossed the Atlantic, returning at the end of the fishing season with their cargoes, usually destined for southern Europe, from whence they returned again in ballast. Clearly, this gave opportunities for British organisms to be carried to North America (in ballast material) and possibly European species to be picked up, again in ballast, on the return journey to the ports of south-west England. This type of trade link might be replicated with other British ports, e.g. the extensive trade with Baltic ports.

The idea that European species of molluscs living on Newfoundland islands were relict species was dismissed by Lindroth and linked instead to the use of small, off-shore islands as ballast dumping grounds. This may be of relevance in a British harvestman context for species such as *Nelima gothica*, which first turned up in Britain at various island and coastal locations and has since spread inland. Coincidentally, Lindroth (1957) mentioned information regarding ballast heaps at Poole Harbour which may have come from the Iberian Peninsula around 1905. He also suggested that this may be relevant in any discussion of a Lusitanian element in the British fauna.

Lindroth (1957) noted a wide range of ballast types, including soil, sand, gravel, rocks, lime, and builder's rubble, used during the age of sail. Of course, many products are imported, which might contain invertebrates such as harvestmen. The horticultural trade is a prime suspect, particularly where plants are transported with soil.

A biodiversity hotspot has been identified in South Wales (e.g. Gregory *et al*. 2018), which includes several molluscs and millipedes, and is thought to result from accidental importation with iron ore or other materials for use in the local coal and iron and steel industries. The harvestman *Sabacon viscayanum ramblaianum* is common in the same area.
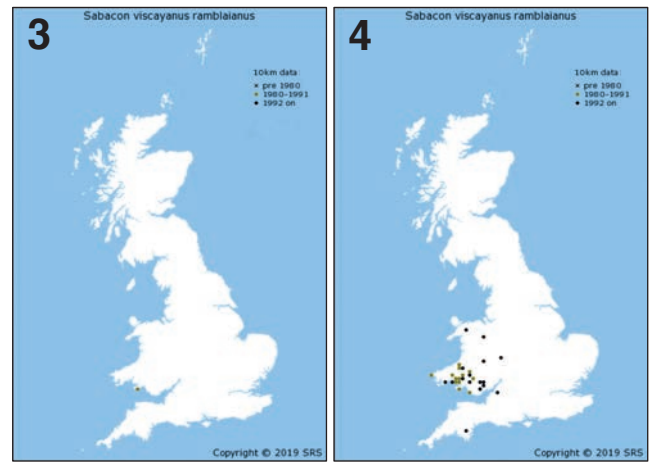
Nelima gothica **Lohmander, 1945** (Maps 1–2)

The first twentieth century addition to the British list was *Nelima gothica*. This species was found in Britain on the Island of Skokholm, off the coast of south Wales (Bristowe 1935). Bristowe reported that it was also found on the Isle of May (east Scotland) only a month later by R. M. Lockley, the owner of Skokholm. Was this species an overlooked native or a recent introduction? It was for some time considered an island/coastal species (much like the spider *Erigone aletris*) but is now more widespread and occurs well inland (Maps 1–2). It originated in northern Spain and the Pyrenees (Martens 1978) and perhaps spread via France and the Baltic, where it was first recognised on the island of Gotland. This looks a little like the sort of shipping-related introduction discussed by Lindroth (1957) in Newfoundland, establishing itself on the coast and then spreading inland. It is worth noting that the first records of *N. gothica* in the Netherlands, in 2012, were in a recent extension to Rotterdam harbour (Noordijk *et al* 2015).

Sabacon viscayanum ramblaianum **Martens, 1983** (Maps 3–4)

The first British record of *Sabacon viscayanum ramblaianum* was from the Gower Peninsula, South Wales (Abbott 1981) and determined by Martens (1983). *Sabacon* has been found in woodland litter and debris but, as Hillyard (2005) noted, some of the locations are associated with abandoned industrial sites, and it has been found in more open brownfield situations below logs, rocks, and in moss, where there is sufficient moisture for this delicate species. This is another Pyrenean harvestman that was initially thought to be a possible relict species in Britain. However, more recently it has been recognised that there is a suite of invertebrate taxa in industrial areas of South Wales and south-west England which may be linked to the import of bulk mineral resources such as iron ore for smelting, rock, aggregate, and general ships' ballast (Gregory *et al*. 2018). *Sabacon* has also started to spread north and east through Wales
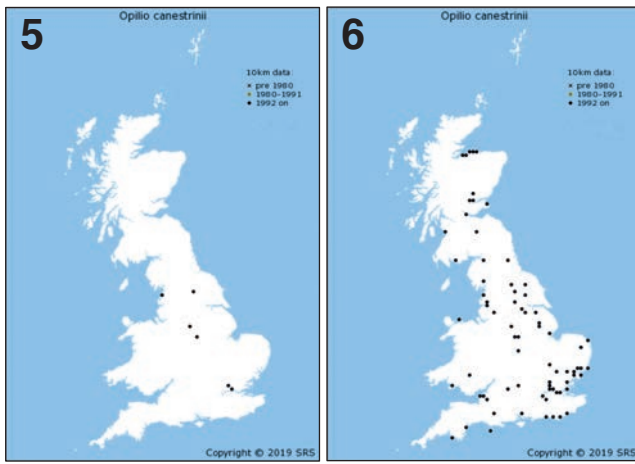
Maps 5–6: Distribution of *Opilio canestrini*. **5** up to 2010; **6** up to 2019.

Maps 7–8: Distribution of *Dicranopalpus ramosus* agg. **7** up to 1990; **8** up to 2019.

and expanded into England by 1999. In 2014, it was discovered in Devon in south-west England, perhaps another area where an industry-linked introduction has taken place (Maps 3–4). Hillyard (1999) discussed its possible relict status based on its habitat preferences in Britain (Abbot 1981), but it is more likely to be an introduction given its association with post-industrial sites.

By the third edition of the *Synopsis* (Hillyard 2005), a further two species of harvestman had been added to the British list:

Nemastomella bacillifera (Simon, 1879)

Nemastomella bacillifera was first found in a small area of Devon (Smithers & Hogg 1991), centred around a disused railway and quarry on the outskirts of Plymouth. More recently, it has been found in a cemetery closer to the centre of the city but otherwise has shown no inclination to expand its range very far. This is another species probably originating in the Pyrenees and is usually found under stones, in grass tussocks, etc. A possible route for introduction was suggested by P. Smithers (in Sankey 1993) via the china clay industry links between Plymouth and Spain.

Opilio canestrinii (Thorell, 1876) (Maps 5–6)

This is generally considered to be an Italian species (e.g. Martens 1978), which has spread rapidly across Europe in recent years. The arrival of *Opilio canestrinii* in Britain had been predicted (Sankey 1986; Hillyard & Sankey 1989) some time before it was discovered in 1999, in the Lea Valley in Essex by Peter Harvey (Hillyard 2000). This species has since spread widely throughout Britain, extending at least as far as the Moray coast in Scotland. Suggestions that this species has had a negative impact on *O. parietinus* and *O. saxatilis* in other parts of its expanded European range does not yet appear to be the case in Britain.
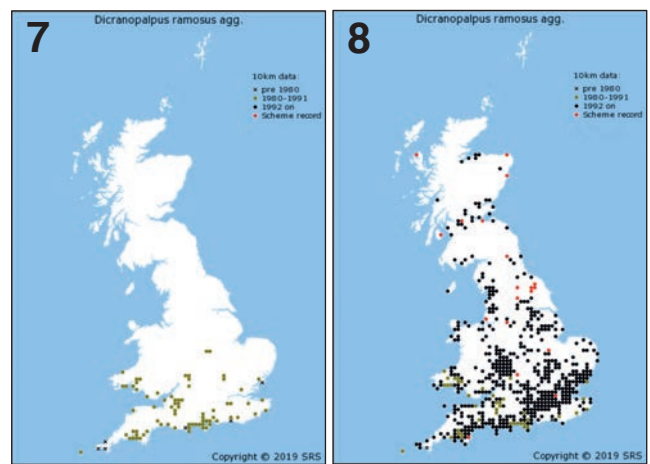
Dicranopalpus caudatus Dresco, 1948 (Maps 7–8)

Sankey & Savory (1974) listed this species as being first found in Britain at Bournemouth on the south coast in 1957, but not identified as *D. caudatus* until further specimens were collected in Hove, Sussex (Sankey & Storey 1969). A male and female, collected in Hove in 1967, had been sent to Jochen Martens (Martens 1978, figs. 712–715) as *D. ramosus*. The material is still available. Its identity oscillated back and forth between *D. caudatus* and *D. ramosus* until Wijnhoven & Prieto (2015) confirmed the presence of two species of *Dicranopalpus* in Britain, with *D. caudatus* the earlier introduction in the south of England. The description in Sankey & Savory (1974) is clearly of *D. caudatus*.

It is important that we attempt to establish whether this species is still extant in its original range (Carlos Prieto, personal communication), and establish its current range. Because of the previous confusion between *D. caudatus* and *D. ramosus*, these are mapped together as *D. ramosus* agg. Maps 7–8 show changes in the distribution of the species aggregate pre- and post-1990. It seems likely, if the distributions can be untangled, that *D. caudatus* has not extended so far from its original locations, and *D. ramosus* has been the more aggressive colonizer. Recent records for *D. caudatus* have been published by Richards (2019) from the Scilly Isles and Sheffield. Further critical examination of voucher specimens (old and new) is required to clarify the current distribution of these species.

Dicranopalpus ramosus (Simon, 1909) (Maps 7–8)

Wijnhoven & Prieto (2015) gave good descriptions of both species, thus allowing relatively easy separation of adult males based on leg length and penis morphology. Females are quite variable and, although there are apparently good characters given, they may not be totally reliable, especially if based on photographs.

D. ramosus appears to have been a later introduction, probably in the 1970s, and has spread rapidly throughout Britain. The collection of John Sankey (now in the Natural
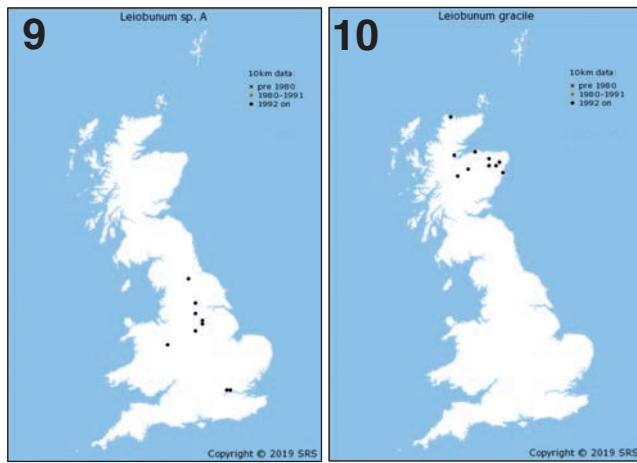
Maps 9–10: Distributions of: **9** *Leiobunum* sp. A. up to 2019; **10** *Leiobunum gracile* up to 2019.

History Museum, London) contains a previously unnamed specimen from Hengistbury Head, Bournemouth (24 September 1980), which has now been identified (M. B. Davidson) as a male *Dicranopalpus ramosus*.

Hillyard (1999) recorded the recent rapid spread of what was probably *D. ramosus*, reaching Lancashire and Yorkshire. It appears to have arrived Edinburgh by 1995, but no other Scottish records appeared until 2008, since when it has become widespread (Davidson 2010), reaching as far north as the Moray Coast and Uig on the Isle of Skye.

It is strange that nowhere in the British literature does anyone apparently comment on the presence of the distinctive Zorro mask in the males of *D. ramosus*, and the discrepancy with published British descriptions, including Hillyard (2005). Brown (1984: 7) noted: "A very distinct form was found at Worcester Terrace, Clifton, which possessed a very striking black dorsal median stripe which extended from the ocularium to the end of the abdomen. An adult female of the same nature was captured at Claverton". This sounds like a female *D. ramosus*, but there is no mention of males with a distinctive mask across the ocularium. Although Richards (2010a), in his excellent photoguide, included photographs of male *D. ramosus* with a mask, no reference was made to this in the text. However, it appears that this is an unreliable character, with evidence of a mask on some *D. caudatus* whilst not all *D. ramosus* have it (Wijnhoven & Prieto 2015), and animals get darker with age. Richards (2019) specifically mentioned a male *D. caudatus* from the Scilly Isles with a mask.

Wijnhoven & Prieto (2015: 33) suggested that "it is still premature to propose *D. caudatus* as a native species for England, as the possibility of an introduction from the Iberian Peninsula cannot be excluded. Then again, an introduction within a short time span of two congeneric species would seem highly unlikely". However this argument may be less valid given the appearance of yet another *Dicranopalpus* (see below) and the recent addition of two species of *Leiobunum*.

Platybunus pinetorum C. L. Koch, 1839

The first report and a description of this species was by Richards (2010b) from the Sheffield area in June 2010. A visit to Edinburgh by the author (Davidson 2012) found what was assumed to be the first Scottish record of *P. pinetorum*, on the crags of Arthur's Seat. However, while examining specimens in the Glasgow Museum's store, more were unearthed which, not surprisingly, had been keyed out as *Rilaena triangularis*. These had been collected in Glasgow by Richard Weddle in 2008 and 2009 (Davidson 2013) and apparently represent the first British specimens: another example of a species hiding in plain sight.

P. pinetorum has now spread itself thinly between Moray in Scotland and Northampton in England. It is probably easily overlooked due to its colouration, and is often found on walls, but also on tree trunks in woodland.

Leiobunum sp. A (Map 9)

Wijnhoven, Schönhofer & Martens (2007) alerted the harvestman community to the rapid spread through Europe of an unidentified *Leiobunum*. Its biology in the Netherlands has been described by Wijnhoven (2011). It was not long before this strikingly very large, long-legged harvestman was being reported in Britain. The first record was in 2009 at Worksop, with other records stretching from Richmond, south through Yorkshire and Derbyshire, to Shrewsbury in the west and more recently the London area.

It is of some interest that the two recent introductions in this genus *L*. sp. A and *L. gracile* (see below) have quite separate distributions in Britain (Davidson 2016). The former appears to be restricted to England and Wales, while the latter is only found in Scotland. It will be well worth scrutinising specimens and photographs of *Leiobunum* in each of these core areas for the other species. While much depends on the lighting, these species can be separated by the colour created by their microsculpture, with *L*. sp. A generally a dark metallic green and *L*. gracile blueish.

At the time of writing, *L*. sp. A remains unnamed but has become part of ongoing research into the complex taxonomy of the *Leiobunum rotundum* species group to which it belongs. Its likely origin is in the western Iberian region, among a group of closely related species (Hay Wijnhoven, personal communication).

Very recently, a DNA barcode was produced for this species by Grant Brown of St Andrews University (Brown 2019). His preliminary phylogenetic analysis of available barcodes for species in this genus suggests a close affinity between *L*. sp. A and *L. rotundum*.

Leiobunum gracile Thorell, 1876 (Map 10)

Leiobunum gracile (formerly *L. tisciae*) was first discovered in a rural graveyard near Huntly, Aberdeenshire (Davidson 2009). An adult female was found in June 2008 behind a gravestone leaning against a wall. Further speci-

mens, including males, were found in Aberdeen (its probable first point of introduction) and were identified by Axel Schönhofer. The taxonomy of the *L. rupestre* group, to which *L. gracile* belongs, was reviewed by Martens & Schönhofer (2016). As discussed above, it is strange that it has not been found, so far, south of Aberdeen. Neither has *L.* sp. A been found in Scotland (this is consistent with *L. gracile* being a forest dweller from central European mountains with a secondary distribution in northern European countries, while *L.* sp. A originates in the Iberian Peninsula). Hillyard & Sankey (1989) also mentioned a record, of what is now *L. gracile*, from Derbyshire in 1975 (Martens 1978), which they discounted due to doubts about its origin and failure to find any more specimens. However, this record is valid (Axel Schönhofer, personal communication). The small series of specimens in the J. Martens collection is also mentioned in Martens & Schönhofer (2016), including the collection number. It is possible that this find represents an older introduction, which then may have died out. The Scottish records probably stem from separate wave of introductions. It is worth looking again in the Derbyshire area for this species, and it is possible that *L. gracile* may have been confused with the even larger *L.* sp. A.

Scotolemon doriae Pavesi, 1878

Not only is this a new species to Britain, but it also adds the family Phalangodidae. It was first discovered at the end of 2017 (Bilton 2018) in a graveyard in Plymouth, Devon. This remains the only location for this remarkable soil-dwelling harvestman, which was found below stones which were partly embedded in the soil. This is a small (body length < 2 mm), orange coloured, mite-like harvestman with a strangely tentative, *Oonops*-like gait. Bilton also reported that *Nemastomella bacillifera* was also found at this site, which suggests that both species, which are only found in the Plymouth area and in synanthropic locations, are almost certainly introduced.

Originally described from Italy, it has also been found in Corsica, southern France and Croatia. Iorio & Delfosse (2016) recently reported *S. doriae* from Paris.

Dicranopalpus larvatus (Canestrini, 1874)

In first draft of this paper, I wrote: "It should be noted that there are other species of *Dicranopalpus* which could turn up in Britain, so specimens should be examined carefully." So it was only with mild surprise to hear of the discovery of *D. larvatus*. However, what was even more surprising was to learn that it had been found in very quick succession, over less than two weeks, in the Scilly Isles, Guernsey (Channel Islands) and the Isle of Wight (Richards 2019). It will be interesting to see if and how long it takes to reach the British mainland. This is a ground-living species which is mature in the winter, consistent with the February date of these finds. *D. larvatus* is quite different from both *D. ramosus* and *D.*

caudatus and should be easily identifiable from photographs.

Coincidentally, Wijnhoven & Martens (2019) had a paper describing this rare species on the cusp of publication, when this species was found, which includes a note on this discovery. Previously, *D. larvatus* had been found in Italy, Sicily and, more recently, Sardinia (a suspected introduction from Sicily or the Italian mainland).

Leiobunum limbatum L. Koch, 1861

It is too early to claim *L. limbatum* as an established British species; however, a photograph which appears to be of this species, taken in August 2019 at Colne in Lancashire, was posted to the inaturalist.org website in October 2019 (Paul Richards, personal communication).

This is an alpine species (Martens 1978), the native range of which includes the French Alps, Austria, southern Germany, northern Italy, and Slovenia. Like several other *Leiobunum* species, it has shown a remarkable ability to spread. According to Rozwałka & Staręga (2012), it has become established across Germany, Poland, the Czech Republic, Slovakia, and southern Sweden. It is normally found in dry forest habitats and rocky places but appears to have adapted to man-made habitats across its expanded range. It seems quite likely that this species is capable of establishing itself in Britain, and this may be confirmed in 2020.

Miscellaneous species

During the period under discussion, a number of possible species have failed to survive, including *Nelima fuscifrons*, found near Edzell in Scotland (Sankey 1953) and later considered to be a variety of *L. rotundum* (Martens 1978), and *Mitopus ericaeus* (Jennings 1982) has been downgraded to a variety (Martens 1988), at least for now.

Patterns of introduction

In the species considered above, two or three distinct patterns of introduction and subsequent spread can be discerned. The long legged, late arrivals *O. canestrinii*, *P. pinetorum*, *L.* sp. A, and *L. gracile* appear to have arrived and very quickly spread to mostly inland locations across Britain. *D. ramosus* probably falls into this group. Long legs and adaption to drier habitats appear to facilitate dispersal, probably using road and rail transport.

The second group includes *D. caudatus*, *Sabacon*, *Nemastomella*, and perhaps *Scotolemon* and *D. larvatus*. These are smaller species that have arrived in coastal regions and have taken some time to establish themselves and, only in the case of the first two, made any headway in spreading. These are perhaps held back by their smaller size and a need for moisture, which may slow their spread. Only

time will tell what the small, short-legged *D. larvatus* will do.

Nelima gothica appears to be quite different, having arrived in coastal regions (probably overlooked for some time), initially spreading round the coast (by several separate introductions?) and then gradually moving inland. It was perhaps initially limited by climate.

Possible future introductions: or are they already here?

A number of species have been considered as possible additions to the British harvestman fauna based on their existing propensity to spread in Europe or because they may have been overlooked.

Although the British population of *Nemastoma* was confirmed as belonging to *N. bimaculatum* (see above), there remains the possibility that this and *N. lugubre* are both present (Hillyard 1998). The group was first disentangled (and the GB situation clarified) by Gruber & Martens (1968) and then Martens (1978). The morphological differences were also given by Meidell & Stol (1990).

Sankey & Savory (1974) suggested that *Platybunus bucephalus*, *Leiobunum rupestre*, and *Laccinius horridus* were potential future immigrants. However, the arrival of *Platybunus bucephalus* and *Leiobunum rupestre* is less likely. *P. bucephalus* is a mountain-dwelling species which avoids mild lowlands. The same holds true for *L. rupestre*, at least in most cases (see Martens 1978; Komposch & Gruber 2004). Prior to Martens & Wijnhoven's (2016) publication, northern lowland populations were affiliated to *L. rupestre*, but that turned out to be false.

More recently, Hay Wijnhoven (personal communication 2018) suggested that "both *Nelima sempronii* and *Nelima doriae* would be good candidates to cross the Channel. *N. doriae* is much more widespread in France than previously thought, and both do well in disturbed, semi-natural habitats. Other candidates might include *Lacinius horridus* and *Nemastoma dentigerum*". Axel Schönhofer (personal communication) suggested the possibility of an additional species of *Trogulus* turning up in the calcareous areas of southern and south-eastern Britain. There are good indications that more than one species in present; see also Martens (1988).

Conservation: pressures & priorities?

As far as we are aware, no native species of British harvestman has become extinct in the last 200 years. In fact, biodiversity has continued to increase (as in many other invertebrate groups) and there is little sign of this trend ending.

Britain's native fauna is undoubtedly impoverished due to past glaciations and early loss of land bridges. So, with a 30% increase in the last 50 years, are non-native species to be welcomed, or should they be seen a threat to the survival of the less aggressive natives?

Undoubtedly, humans have facilitated their arrival throughout history by importing them in cargoes. Opportunities for successful establishment have increased with the advent of rapid transport, by land, air and sea, and the sheer volume of materials transported around the world. Of particular relevance to harvestmen is the movement of horticultural products, especially plants with and without soil.

An unattributed and undated, (probably J. Sankey pre-1988) attempt to assess the conservation status of British harvestmen tended to emphasise seemingly rare species, which we might now accept as non-natives: *D. ramosus / caudatus*, *L. gracile* (first time round), and *Sabacon viscayanum* or, in the case of *M. ericaeus*, a variety of a very variable and common species. With hindsight we might be more inclined to highlight the vulnerabilities of the soil-dwelling species such as *Anelasmocephus cambridgei*, *Trogulus tricarinatus*, and *Homalenotus quadridentatus*. These are all species that might find it difficult to adapt to, or avoid, the current changes in climate and other pressures on the natural environment.

Of course, even species such as *Nemastomella bacillifera*, which we now consider as non-native, may become of high conservation concern in a European context, as environmental change affects their native range. Britain could become a refugium, post-warming rather than peri-glacial!

Conclusions

During the past 50 years, the number of British harvestman species has increased by almost 30%, from 22 to 31: a 35% increase since 1900. It would appear that these discoveries have all been a result of recent introductions through human activities. It is expected that this trend will continue, with several species known to be spreading in Europe or otherwise likely to arrive in the next shipping container from who knows where. A warming climate may well assist this trend.

Of particular interest is the group of species that may have originated on the Iberian Peninsula. Some were previously considered as Lusitanian relicts but it now seems more likely they are recent introductions.

The majority of recent discoveries have been of the larger, long-legged, species which are easily photographed for identification by specialists. However, there is still a need for voucher specimens for morphological examination and now the possibility of DNA barcoding.

Although our fauna has continued to increase in number our knowledge of the biology and ecology of individual species has not followed a similar trend. In the words of T. H. Savory (1979: 9) anyone "who is seeking a subject for research is strongly recommended to consider the Opiliones. The order holds rich possibilities in a field that is almost untilled". However, judging by the amount of harvestman related activity on the internet their appeal has now broadened to a wider cross-section of naturalists and the general public, and in the next 50 years the prospects for opilionology look bright.

Acknowledgements

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Non-additive effects on the morphology of hybrids between two species of large house spiders, *Eratigena saeva* and *E. duellica* (Araneae: Agelenidae)

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Abstract

Hybridization and introgression in the wild between two species in the *Eratigena atrica* group of large house spiders, *E. duellica* and *E. saeva*, are well documented. However, the morphology of known F_1 hybrids and subsequent F_2 and backcross generations has not previously been explored. The phenotypes of these interspecific offspring have implications for the ease of introgression and for the morphological identification of individuals of hybrid origin. Here, the progeny from laboratory crosses are analysed using both simple characters and multivariate statistical techniques. F_1 hybrids in both sexes are, morphologically, significantly biased towards *E. duellica* but backcross progeny tend to resemble their non-F_1 parents more than expected in a model of additive, unlinked quantitative trait loci (QTL). It is possible that loci on the X-chromosomes affect the phenotype or that there are maternal influences. These biases may have consequences for the ease and direction of gene flow between the species. While female F_1 hybrids can be distinguished from pure parents, for later generations, and for all generations of males, confusion with the parental species is highly likely and may have affected previous conclusions.

Introduction

Hybridization is now widely recognized as a major phenomenon in evolution (Stebbins 1959; Harrison 1993; Arnold 1997; Abbott *et al.* 2013) and can result in both increases and decreases in species diversity (Levin, Francisco-Ortega & Jansen 1996; Rhymer & Simberloff 1996; Ellstrand & Schierenbeck 2000; Seehausen 2004, 2006). In the mid-1900s, hybridization, in animals at least, was considered a rare phenomenon (e.g. Mayr 1963) but early landmark studies (reviewed in Harrison 1993) revealed that the formation of hybrid zones and subsequent gene exchange (introgression) between species were much more prevalent than previously thought (Dowling & Secor 1997; Barton 2001; Baack & Rieseberg 2007). The dynamics of hybrid zones in terms of the factors that determine their structure, width, and the geographical concordance of different genetic markers has received much attention (e.g. Barton & Hewitt 1985; Carneiro *et al.* 2013; Shurtliff 2013), but here, the focus of interest is on the ultimate consequences of gene exchange for species diversity.

An increase in species as a result of hybridization can occur in a number of situations, for example when the parent taxa are adapted to specific environments but hybrids can exploit different ones (Anderson 1948; Moore 1977; Gray, Marshall & Raybould 1991; Rieseberg *et al.* 2003; Mallet 2007; Bailey, Eroukhmanhoff & Sætre 2013). Conversely, if one species vastly outnumbers a second, hybridization may lead to the latter being completely swamped genetically, effectively becoming extinct (Levin, Francisco-Ortega & Jansen 1996; Rhymer & Simberloff 1996; Roberts *et al.* 2010; Todesco *et al.* 2016). If the species are numerically more equal, gene flow may be such that the two original entities fuse into one intermediate species (Rhymer & Simberloff 1996; Bettles *et al.* 2005; Taylor *et al.* 2005: Seehausen 2006; Todesco *et al.* 2016; Kearns *et al.* 2018). This process is often called 'speciation in reverse' (see Oxford & Croucher (2014) for a critique of this term). In this paper, I explore the morphological effects of hybridization between the large house spiders *Eratigena saeva* and *E. duellica* (Agelenidae) and consider their implications for the future integrity of the two species.

These two spider species are placed in what was originally called the *Tegenaria atrica* group (Locket 1975; Merrett 1980), comprising *T. saeva* Blackwall, 1844, *T. duellica* (= *gigantea*) Simon, 1875, and *T. atrica* C. L. Koch, 1843 (Agelenidae). More recently, Bolzern, Burchardt & Hanggi (2013) argued that these species, and some others previously placed in the genus *Tegenaria*, should be moved to a new genus, *Eratigena*, a suggestion well supported by both molecular and morphological evidence. They also proposed that, because the three species do not fall out as distinct groups in phylogenies based on mtDNA sequences and, they asserted, their sample of mainly continental European specimens could not be separated reliably on morphological grounds, they should be regarded as just one, albeit variable, species: *E. atrica*. However, Oxford & Bolzern (2018) demonstrated that, in Britain, continental Europe and North America, the three species can indeed be identified morphologically. They hypothesized that the sharing of some mtDNA haplotypes by *E. saeva* and *E. duellica* is likely to be a result of both incomplete lineage sorting and contemporary hybridization and introgression.

Over most of England and Wales, *E. saeva* and *E. duellica* occur allopatrically, with the former in the West Country and Wales and the latter in the east and the Midlands (Merrett 1980; Croucher *et al.* 2007), distributions that seem to have been stable for at least a century (Oxford 2009). Their ranges overlap to some extent in the county of Dorset and northwards along the Welsh border. In northern England and Scotland these species appear to have been largely absent until the 1960s (Oxford 2009). As they colonized, their geographically distinct, east–west distributions blurred and, from Yorkshire and Lancashire northwards, both species can be found throughout (Oxford & Smith 1987; Croucher 1998; Croucher *et al.* 2007; Oxford 2011). The third species, *Eratigena atrica*, has a much more limited distribution in Britain, with self-sustaining populations known only from the area around Newcastle upon Tyne and possibly in the Perth–Dundee region of Scotland (Oxford & Smith 2014).

Cross code	Cross	Mate No.	Egg sacs	Males		Females		Total M	Total F	Total
				No. isol.	No. box	No. isol.	No. box			
Ps(1)	*s* × *s* (1st gen)	2	3	18	0	11	0	18	11	29
		11	3	23	0	9	0	23	9	32
		13	4/2	22	0	9	0	22	9	31
		18	5	24	0	15	0	24	15	39
				87	0	44	0	87	44	131
Pd(2)	*d* × *d* (1st gen)	5	3	15	0	16	0	15	16	31
		10	2	20	0	10	0	20	10	30
		14	3/2	8	0	11	0	8	11	19
		19	4/2	13	0	5	0	13	5	18
				56	0	42	0	56	42	98
Ps(3)	Orig *s*							7	9	16
Pd(4)	Orig *d*							4	8	12
Ps(5)	*s* × *s* (2nd gen)	104	5	9	9	1	9	18	10	28
		110[+]	2*/4*	7	1	4	1	8	5	13
		114[+]	3	3	0	1	0	3	1	4
		115[+]	3/4	6	3	2	5	9	7	16
		123	3/4	8	4	2	8	12	10	22
		130[+]	1/5	10	7	1	2	17	3	20
				43	24	11	25	67	36	103
Pd(6)	*d* × *d* (2nd gen)	103	2/1	1	0	2	0	1	2	3
		109[+]	2*	6	0	4	0	6	4	10
		113[+]	2/1	1	0	3	0	1	3	4
		116[+]	1/2	6	0	2	1	6	3	9
		122	3	8	2	4	2	10	6	16
		128	2/3	8	2	2	2	10	4	14
		129	3/5	7	4	4	2	11	6	17
		132[+]	2	7	0	2	2	7	4	11
				44	8	23	9	52	32	84
F1(7)	*d* × *s* (1st gen)	12	6	30	0	18	0	30	18	48
Bs(8)	*s* × F₁	101	1/2	6	0	2	0	6	2	8
		111	3*	5	0	5	0	5	5	10
		112	1/2*	7	0	4	0	7	4	11
		119	2/3	9	7	1	2	16	3	19
		133	1	5	0	2	0	5	2	7
				32	7	14	2	39	16	55
Bd(9)	*d* × F₁	102	2/3	5	0	4	0	5	4	9
		105	1/2	3	0	5	0	3	5	8
		106	2	3	0	3	0	3	3	6
		120	1/3	9	1	2	0	10	2	12
		121	2	5	0	8	0	5	8	13
		131	4	10	3	0	0	13	0	13
				35	4	22	0	39	22	61
Bs(10)	F₁ × *s*	117	1	1	0	4	1	1	5	6
Bd(11)	F₁ × *d*	124	3/4	6	3	7	0	9	7	16
F2(12)	F₁ × F₁	118[+]	3/2	2	0	4	0	2	4	6
		125[+]	3/6	17	4	2	3	21	5	26
		126[+]	1/2	4	0	1	0	4	1	5
		127[+]	1	2	0	1	0	2	1	3
		137[+]	2/3	8	4	3	2	12	5	17
		138[+]	4	13	2	5	6	15	11	26
		139[+]	3	14	1	4	6	15	10	25
		141[+]	3	16	4	5	4	20	9	29
				76	15	25	21	91	46	137

Table 1: **Cross codes** 1 to 6 comprise intraspecific matings (pure species), with the offspring of the original parents presented first (Ps(1), Pd(2)) because these were used as the DFA training set (see text). Then follow: the original parents (Ps(3), Pd(4)); the intraspecific offspring from the second generation (Ps(5), Pd(6)); the only successful interspecific cross (F1(7)); reciprocal backcrosses with *saeva* (Bs(8), Bs(10)); reciprocal backcrosses with *duellica* (Bd(9), Bd(11)); crosses between two F₁ hybrids (F2(12)). Under **Cross**, the female parent is shown first (*s* = *E. saeva*; *d* = *E. duellica*; F₁ = first-generation hybrid). **Mate No.** indicates the identifiers for individual crosses. Those that derive from sib-sib matings, used as controls for the production of the F₂ generation (see text) are indicated with a +. **Egg sacs** indicate the number from each female parent that provided data in the present analysis; where the contribution to male and female offspring differed in this respect females are shown first. * denotes cases where the products of two egg sacs were pooled. Under **Males** and **Females**, No. isol. denotes the number of individuals separated from the rest of the brood and reared in isolation; **No. box** shows the number that matured in boxes containing several members of the same brood (see text). **Totals** are shown beneath each Cross code in grey highlight.

Where the ranges of *E. saeva* and *E. duellica* meet, in the parapatric zone of southern England and Wales and more extensively in northern England and Scotland, individuals with intermediate palp and epigyne characteristics are found (Merrett 1980; Oxford & Smith 1987; Oxford & Plowman 1991; Croucher *et al*. 2007). Indeed, there is evidence that good *E. saeva* and good *E. duellica* in Yorkshire are morphologically more similar than are the species taken from the allopatric areas further south (Oxford & Smith 1987; Croucher 1998; Croucher *et al*. 2007), suggesting considerable ongoing introgression. There is no evidence for hybridization between *E. atrica* and either of the other two species around Newcastle upon Tyne (Oxford & Smith 2014). Croucher, Oxford & Searle (2004), and Oxford & Bolzern (2018) showed that *E. saeva* and *E. gigantea* are

more closely related to each other than they are to *E. atrica*, which might explain this difference.

Laboratory crosses between and within *E. saeva* and *E. duellica* show that the success of interspecific matings is very low compared to that of intraspecific matings (Kennett & Dalingwater 1986; Croucher 1998; Oxford & Croucher 2014). The barrier to hybridization seems to be purely mechanical, and prevents the correct engagement of the palp and epigyne for long enough to permit sperm transfer (Oxford & Croucher 2014). What has not been investigated to date is the morphology of known F_1 and F_2 offspring and those of F_1s reciprocally backcrossed to both parents, and what this might imply for interspecific interactions.

Although geometric morphometrics methods are increasingly used to analyse differences in shape between populations and taxa (e.g. Zelditch, Swiderski & Sheets 2012), the handling time per specimen is considerably greater than making standard measurements under a microscope. There is, therefore, a trade-off between the ability of this technique to capture the fine details of shape and the number of specimens that can be processed. In addition, many who might want to assess the possible hybrid status of individual spiders may not have access to geometric morphometric tools.

Here, I apply simple morphometric techniques to the off-spring from a subset of the laboratory matings used by Oxford & Croucher (2014). The objectives were: 1) to explore the phenotypic expression of diagnostic characters in progeny from known intra- and interspecific crosses; 2) to provide guidance on the interpretation of individuals with specific characteristics found in the wild; and 3) to consider the implications of the results in terms of continuing gene flow and introgression between the taxa.

Methods

Collection, rearing and crossing of spiders

The original parents of the crosses considered here were collected from the wild in their penultimate or pre-penultimate instars during late summer, 2008, using a fishing technique (Oxford & Croucher 1997). They were reared to maturity in isolation in the laboratory. Oxford & Croucher (2014) provided details of rearing and crossing conditions and other procedures; their collection sites are shown in fig. 1 of that paper. Briefly, all parents originated in allopatric areas of west Wales (*E. saeva*) and central/eastern England

A. Female

Character	Raw data			Standardized data			
	saeva	*duellica*	*d-s*	$\%_1$	Cum $\%_1$	$\%_2$	Cum $\%_2$
RSW/RLW	703.8528	233.959	-469.894	63.6	63.6	68.6	68.6
RWMN	-6170.34	-6374.96	-204.617	7.6	71.2	8.2	76.8
in_out	3.604613	-8.33765	-11.9423	7.3	78.5		
RWMN/RH	4730.811	4870.04	139.229	6.3	84.8	6.8	83.6
RSW	-74.8051	-387.93	-313.125	5.3	90.1	5.7	89.3
PROL	-110.199	-93.7696	16.42945	2.4	92.5	2.6	91.9
SMX	294.1372	139.6228	-154.514	2.4	94.9	2.6	94.5
SWMX	281.34	134.0449	-147.295	1.2	96.2	1.3	95.9
RH	2101.181	2156.768	55.58686	1.2	97.4	1.3	97.2
RWMX	-22.8942	-64.402	-41.5078	0.9	98.3	1.0	98.2
RLW	451.6755	401.4286	-50.2469	0.9	99.2	1.0	99.1
APR	139.5618	113.3788	-26.183	0.7	99.9	0.7	99.8
PROW	168.3124	166.8263	-1.48606	0.1	100.0	0.2	100.0
Constant	-1377.23	-1027.93	349.3056				

B. Male

Character	Raw data			Standardized data	
	saeva	*duellica*	*d-s*	%	Cum %
TCL	1297.35	1065.498	-231.852	29.2	29.2
CW	179.3618	571.3396	391.9778	23.5	52.7
CANG	-257.074	124.9475	382.0212	21.0	73.7
PROL	-50.257	-38.8539	11.40312	11.6	85.3
PROW	-41.7288	-30.5499	11.17893	7.9	93.1
TW	65.09362	40.79195	-24.3017	2.7	95.9
CL	13.00879	46.80062	33.79182	2.3	98.1
TWMX	154.2885	123.4747	-30.8138	1.9	100.0
Constant	-678.736	-517.627	161.1089		

Table 2: **A** female coefficients from discriminant function analysis (DFA) of all characters using raw (mm or ratio) measurements across Ps(1) and Pd(2), the training set. The coefficients are subtracted (*d - s*, *duellica - saeva*) to provide an equation for deriving DF scores for individual spiders. Also shown are the % contribution of each character to the separation of the species from a DFA of measurements standardized to have zero mean and unit standard deviation. These will be independent of absolute character size. $\%_1$ is the percentage contribution of the summed, unsigned coefficients arranged in rank order of importance and Cum $\%_1$ the cumulative percentages. Results from a second analysis omitting the qualitative character in_out (see text) are shown as $\%_2$ and Cum $\%_2$; the rank order is unchanged. **B** male coefficients from discriminant function analyses (DFA) of all characters using raw (mm) measurements across Ps(1) and Pd(2), the training set. See above for an explanation of other columns. Female characters: PROW = maximum prosoma width; PROL = maximum prosoma length; APR = tip of apophysis to the posterior edge of the receptacle (spermathecal) opening; RWMX = maximum width between receptacle openings; RWMN = minimum width between receptacle openings; RLW = receptacle opening long width; RSW = receptacle opening short width; RH = top of receptacle opening to epigastric furrow; in_out = whether the anterior end bends out (+1), in (-1) or neither way (0) for each spermatheca (scores summed); SWMX = maximum spermatheca width; SMX = total length of a spermatheca. Male characters: PROW and PROL, see above; TCL = maximum tegulum + conductor length; TW = tegulum width; TWMX = maximum tegulum width; CW = conductor width; CL = conductor length; CANG = conductor angle.

(*E. duellica*), well away from the zone of species overlap. Some males were involved in more than one cross. The specimens used here comprise Group 3 (original crosses) and Group 4 (second-generation crosses), as defined by Oxford & Croucher (2014). Some individuals were removed at various times from the rest of the brood and reared to maturity in isolation, whereas others were allowed to mature within the brood boxes.

Only one intraspecific cross in Group 3 was successful and therefore one or both parents of all subsequent crosses involving the F_1 offspring derived from this pairing. As F_2 progeny were, necessarily, a result of sib × sib matings, similar crosses were established within species to examine any effects of inbreeding. On maturity, progeny were, like their parents, preserved in 70% ethanol and are retained at the University of York.

Morphometrics

Characters examined were those used by Oxford & Bolzern (2018) with the exception, in females, of the distance from the epigastric furrow to the major constriction in the spermathecal width (CSW). This measure was used by Oxford & Bolzern (2018) to help distinguish *E. atrica* from *E. saeva* and *E. duellica*, and is therefore not relevant here. Characters are listed in the legend to Table 2. Measurements were made using a Reichert binocular microscope fitted with an eyepiece graticule and fixed objective lenses, and are expressed here in millimetres (unless otherwise stated). For males, most measurements were made on the right palp but, if the left was already removed, that was the one used. Croucher (1998) showed that in these species there is no directional asymmetry in palp morphology. For females, the epigyne was excised and external measurements made. Internal characters of cleared epigynes were examined from a dorsal aspect after a brief period of dehydration in absolute ethanol followed by immersion in clove oil.

As stressed by Oxford & Bolzern (2018) the correct and consistent orientation of palps and epigynes is critical if measurements are to be reliable. Merrett (1980) specified the appropriate orientation for males, and Oxford (2008) for females. In the present study, male and female material was assembled separately in large plastic boxes (three for males, two for females) in a random order. During examination, tubes were picked, again at random, from these boxes and the specimens measured blind. The source of the individual was only revealed and noted once all measurements had been recorded. This double-random-selection approach ensured that unconscious bias did not affect the results.

The raw measurements analysed in this paper, after conversion to millimetres, are available to download from Zenodo (https://zenodo.org) doi: 10.5281/zenodo.3517194

Statistical analyses

For each sex, discriminant function analysis (DFA) was use to generate weighted multiple regression equations incorporating all morphological characters derived from the offspring of *saeva* × *saeva* Ps(1) and *duellica* × *duellica* Pd(2) crosses as the training set—individuals regarded as exemplars of their respective species (for cross nomenclature see Table 1). Because there are only two taxa in the training set, for simplicity the coefficients and constants for *saeva* were subtracted from those for *duellica* ($d - s$). To generate a score for each individual, each character (i) measurement (m_i), in millimetres or a ratio, was multiplied by the $d_i - s_i$ coefficient for that character, summed over the total number of characters measured (n) and the $d_c - s_c$ constant added. More formally:

$$\text{DF score} = \sum_{i=1}^{n} m_i(d_i - s_i) + (d_c - s_c)$$

The mean score for the training sets is zero.

Applying this equation to the offspring of other crosses enabled their morphology to be compared, relative to that of the training set. The original parents collected from the wild were the obvious training set to use but were too few in number. Instead, they were classified together with the other crosses. For females, one internal character, whether the anterior end of the spermatheca bends in or out, is qualitative and in some cases was not altogether clear. Parallel DFAs were run with and without this character. Differences between DF scores for the separate matings were tested in a one-way analysis of variance with appropriate post-hoc comparisons.

The value of the coefficient associated with each character in the DFA will in part be a function of physical size. In order to isolate which features most clearly differentiate the training taxa independently of absolute character size, measurements of each character were standardized to have zero mean and unit standard deviation across both training sets using $(x_i - \bar{x})/sd$; where x_i represents each individual measurement and $\bar{x}$ and sd are, respectively, the mean and standard deviation across all individuals in the training set. When subjected to DFA the resulting coefficients directly reflect the character's relative importance in the classification.

For males, Merrett (1980) identified a simple plot of maximum tegulum + conductor length (TCL) *v.* maximum carapace (prosoma) length (PROL) that clearly separated the three species in the *Eratigena atrica* group. Regression lines for the separate species are usually parallel but differ in elevation. Merrett plots were used to compare the offspring of the various crosses. Regression lines were tested for differences in slopes and elevations with an analysis of covariance (ANCOVA) and appropriate post-hoc, pairwise comparisons made using the Holm-Sidak method (Holland & Copenhaver 1987).

Where appropriate, sequential Bonferroni corrections were made (Rice 1989). Statistical analyses used Minitab 17, SigmaPlot 14 and Microsoft Excel 2010 packages.
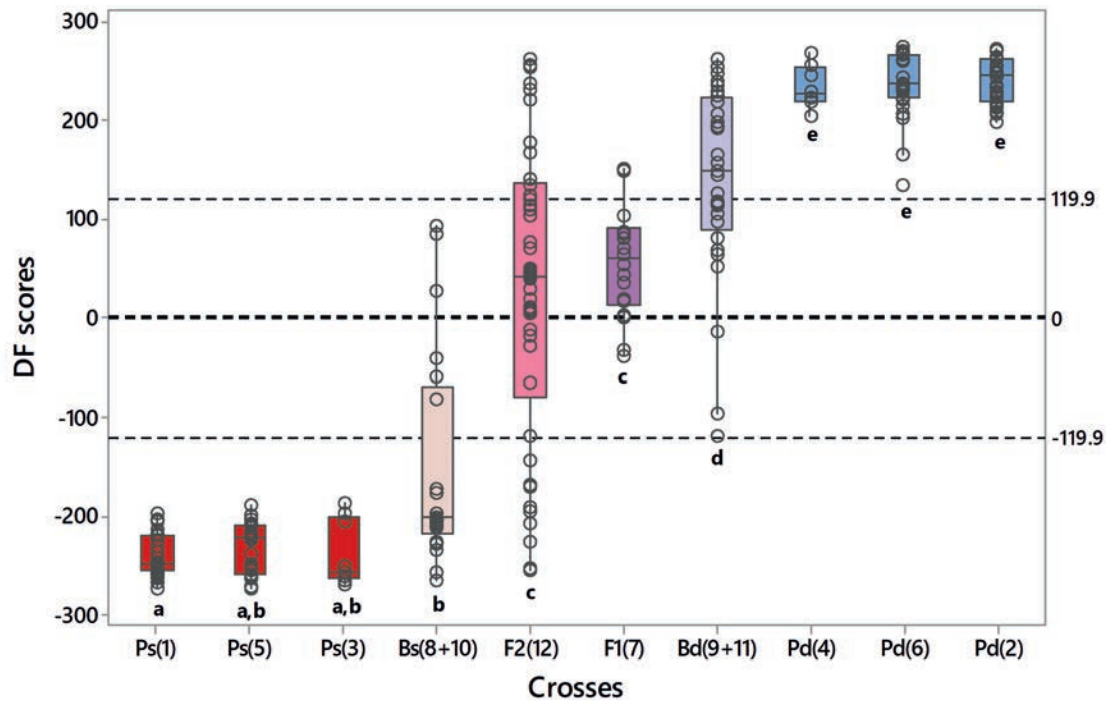
Fig. 1: Box and whisker plot of female DF scores, based on raw measurements or ratios, for individuals from different crosses. Sources are as follows: Red = *E. saeva* Ps(1,3,5); Blue = *E. duellica* Pd(2,4,6); shades of purple/red/blue = F_1 hybrids F1(7), backcross $F_1 \times$ *saeva* Bs(8+10), backcross $F_1 \times$ *duellica* Bd(9+11), F_2 generation F2(12). The heavy dashed line shows the DF score that is mid-way between the parental species. The lighter dashed lines indicate the expected scores for progeny derived from the backcrosses to *E. saeva* (lower) and to *E. duellica* (upper) on the assumption of the additivity of quantitative trait loci (QTLs). Individual data points are shown as open circles, the interquartile ranges as coloured boxes and the medians by a horizontal line with each box. Letters below each box show the outcome of a post-hoc test (see text). Samples sharing a letter are not significantly different. For cross codes see the legend to Table 1.

Results

Measurements were made on a total of 482 males and 285 females. The breakdown of the various crosses is shown in Table 1, with their nomenclature as used in this paper indicated in the first column. A small number of individuals had dried out and these are not included. Although a number of backcrosses of s × F_1 (Bs8) and d × F_1 (Bd9) were made, for logistical reasons only one backcross of F_1 × s Bs(10) and two of F_1 × d Bd(11) were set up, and one of the last cross was unsuccessful. In the majority of analyses, data from the reciprocal crosses were pooled (i.e. Bs(8+10) and Bd(9+11)). The relative success of the various crosses, in terms of number of young emerging from egg sacs and their mean viabilities, has been considered elsewhere (Oxford & Croucher 2014).

The effect of rearing conditions

As mentioned, some individuals were reared in isolation for the later part of their development whereas others reached maturity in the original brood boxes (Table 1). The latter were more likely to have been in competition for food and might have matured at a smaller body size (measured by PROL). One-way ANOVAs (variances not assumed equal) were used to test this hypothesis. Only three crosses, Ps(5), Pd(6) and F2(12), contained sufficient numbers of isolated *v*. box-reared females for comparisons to be made (Table 1). In one case, Ps(5), box-reared individuals were, on average, larger than those reared in isolation whereas in the other two

cross types, box-reared spiders were smaller, in one case, Pd(6), significantly so ($p = 0.016$). For males, comparisons were made within Ps(5), Pd(6), Bs(8+10), Bd(9+11) and F2(12) (Table 1). In no case was the mean PROL significantly different between the rearing conditions. In three cases the means for those reared in isolation was slightly greater than for those reared together, and in two cases the reverse was true. The eight tests across both sexes assess the same null hypothesis; none of them was significant after applying a sequential Bonferroni correction. The evidence suggests that rearing conditions did not markedly affect the overall size of individuals within crosses. Further analyses of the same crosses using one-way ANOVA on the RSW/RLW ratio in females, and ANCOVA on the relationship between TCL and PROL in males, failed to show any sign that box-reared spiders differed from those reared individually in these critical respects (as discussed below). For the rest of the analyses, data were therefore pooled across the two rearing conditions within crosses.

Discriminant function coefficients

The coefficients from DFAs based on raw data (mm or ratios) from the training set of pure *E. saeva* Ps(1) and pure *E. duellica* Pd(2) are shown in Table 2. The table also shows the percentage contribution for each character from DFAs (details not shown) on standardized data (zero mean, unit standard deviation) free from the influence of absolute size. For females, the percentage contribution to the separation is also given for a DFA on transformed data that excludes the

Cross	Adj. mean	Std. error	95% confidence limits lower	upper
Pd(2+4)	1.198	0.00355	1.191	1.205
Pd(6)	1.199	0.00386	1.191	1.206
Bd(9+11)	1.239	0.00397	1.231	1.247
F1(7)	1.279	0.00502	1.269	1.289
F2(12)	1.283	0.00291	1.277	1.289
Bs(8+10)	1.322	0.00434	1.313	1.33
Ps(1+3)	1.343	0.00288	1.337	1.348

Table 3: Adjusted means and their 95% confidence intervals from an ANCOVA of TCL against PROL (covariate) for the male data. Small data sets have been pooled as indicated, and Ps(5) omitted (see text). All adjusted means are significantly different from one another except for Pd(2+4) and Pd(6), and for F1(7) and F2(12).

qualitative character reflecting the direction of the anterior bend of the spermathecae (in_out). The ratio of receptacle short width (RSW) to receptacle long width (RLW) in females contributes nearly 64% towards the separation of the taxa, which rises to almost 70% if the in_out character is ignored. The second most important measurement is the minimum width between the receptacles (RWMN), followed by the in_out character. For males, tegulum + conductor length (TCL), conductor width (CW) and conductor angle (CANG) are of similar magnitude and together contribute almost 75% towards the separation of the taxa. All DFA scores discussed below are based on all characters and raw (mm or ratio) measurements.

Females

Discriminant function scores

Fig. 1 shows a plot of DFA scores for females for the various crosses using the coefficients in Table 2. The training sets, Ps(1) and Pd(2), original parents, Ps(3) and Pd(4), and subsequent intraspecific crosses, Ps(5) and Pd(6), are clearly separated by species. A one-way ANOVA (variances not assumed to be equal) on DF scores from all crosses shown in Fig. 1 was highly significant ($F_{(9, 69.2)}$ = 1730.35; p < 0.001). Results from a post-hoc Games-Howell pairwise comparison test are indicated in Fig. 1. Thus, the intraspecific *saeva* and *duellica* crosses are internally consistent and the F_1 and F_2 generations form a homogeneous group clustered at the centre. In this analysis, the $F_1 \times$ *saeva* backcross offspring Bs(8+10) cluster with Ps(3) and Ps(5) whereas the offspring from the $F_1 \times$ *duellica* crosses, Bd(9+11) form a separate group.

Scores for the F_1 hybrids, F1(7), are intermediate between the two parents but shifted significantly from the expectation of zero towards *duellica*, with a mean of 54.9 (Ryan-Joiner normality test, p > 0.1; one-sample t-test, NH = 0, p = 0.001). Note that the null hypothesis for this comparison is different from the less specific null hypothesis tested above. For the F_2 generation, F2(12), however, although there is also a slight bias towards *duellica*, the mean score (28.1) is not significantly different from zero (Ryan-Joiner normality test, p > 0.075; one-sample t-test, NH = 0, p = 0.225). For the combined backcross $F_1 \times$ *saeva*,
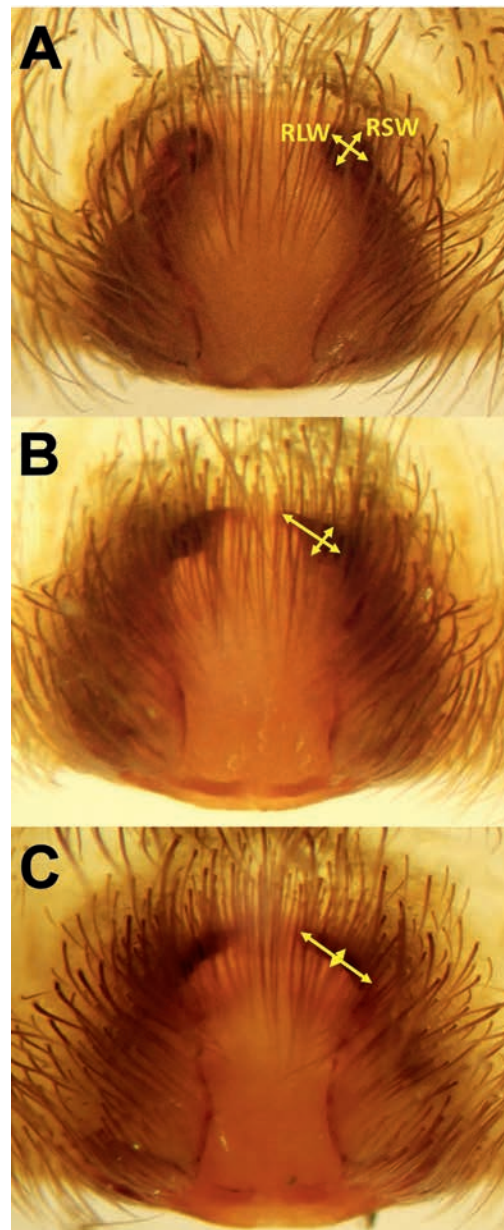
Fig. 2: The female characters receptacle short width (RSW) and receptacle long width (RLW), whose quotient is diagnostic for pure species and indicative for some hybrids. **A** *Eratigena saeva*; **B** F_1 hybrid; **C** *E. duellica*. Note that these measurements do not refer to the same structures across species. RSW is the width of the receptacle (more accurately, the spermathecal) opening in *E. saeva* and hybrids, but is just the width of the heavily chitinized brow ridge in *E. duellica*. Likewise, RLW is the length of the fully chitinized brow ridge in *E. duellica* but the width of the receptacle opening in *E. saeva*.

Bs(8+10), the mean would be expected, *a priori*, to be midway between the predicted F_1 mean (zero) and the mean of the *saeva* training set (-239.786) i.e. -119.893. The distribution of scores for Bs(8+10) was not normally distributed (Ryan-Joiner normality test, p < 0.01). A Wilcoxon Signed Rank test showed that the observed median (-202.0) was not significantly different from the expected value (p = 0.135). Scores for the second backcross, $F_1 \times$ *duellica*, Bd(9+11), are similarly not normally distributed (Ryan-Joiner normality test, p = 0.027) and a Wilcoxon Signed Rank test against a theoretical value of 119.893 was not significant (observed median = 147.8; p = 0.147). In both backcross comparisons,
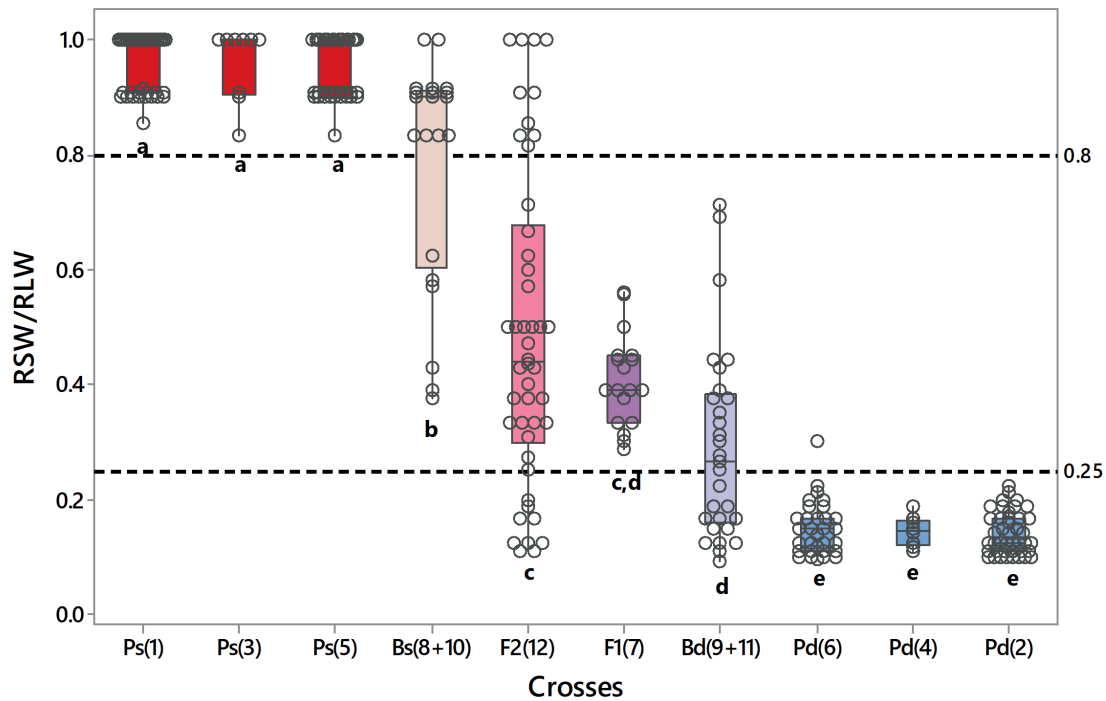
Fig. 3: Box and whisker plot of the ratio RSW/RLW in female offspring. The dashed lines show the empirical limits of variation within *E. saeva* (upper line) and *E. duellica* (lower line). For further explanation, see legends to Fig. 1 and Table 1.

however, the observed medians are shifted towards the non-F_1 parental value.

The reciprocal backcrosses were initially combined because a one-way ANOVA involving all crosses showed that they were not significantly different (not shown) and some sample sizes were small. However, sample sizes permitting, it is possible to test specifically the separate reciprocals against the theoretical expectations. The backcross with an *E. duellica* mother, Bd(9), had a mean offspring DF score of 144.4 (n = 22) and those with an F_1 mother, Bd(11), a mean score of 119.1 (n = 7). Although neither differ significantly from the expectation of 119.893 (Ryan-Joiner normality test, $p = 0.057$; one-sample t-test, NH = 119.9, $p = 0.251$ and Ryan-Joiner normality test, $p = 0.032$; one-sample Wilcox signed rank test, NH = 119.9, $p = 0.554$, respectively), the progeny with the *duellica* mother had, on average, higher DF scores i.e. are more *duellica*-like than progeny from the reciprocal. For the reciprocal backcrosses to *E. saeva*, the equivalent analyses showed that when the mother was *saeva*, the mean offspring DF score was -132.4 (n = 16) and when the mother was an F_1 the mean score was -208.04 (n = 5) (Ryan-Joiner normality test, $p = 0.05$; one-sample t-test, NH = -119.8, $p = 0.68$ and Ryan-Joiner normality test, $p > 0.1$; one-sample t-test, NH = -119.8, $p < 0.001$, respectively). Thus, an F_1 mother produces offspring that are more *saeva*-like than the reciprocal.

One-way ANOVAs (variances not assumed to be equal) of DF scores from inbred *v.* outbred individuals from Ps(5) and Pd(6) showed that they were not significantly different ($F_{(1, 33.5)} = 0.13$; $p = 0.723$ and $F_{(1, 24.2)} = 0.48$; $p = 0.495$, respectively).

RSW/RLW ratios

The major female character separating taxa in the DFA is the ratio of RSW/RLW (Table 2, Fig. 2), plotted in Fig. 3. A one-way ANOVA (variances not assumed to be equal) on this ratio was highly significant ($F_{(9, 71.3)} = 1501.59$; $p < 0.001$) and the results of post-hoc Games-Howell pairwise comparison tests indicated in Fig. 3. Values for F1(7) and Bd(9+11) overlap, as do those for F1(7) and F2(12), but otherwise crosses are significantly different. Fig. 3 suggests that *E. saeva* can be recognized as having ratios > 0.8 whereas *E. duellica* has ratios < 0.25, as indicated by the dashed lines. There was one *E. duellica* in Pd(6) with an unusual cavity below the chitinized ridge (RLW) which accounts for it appearing above the 0.25 line. All F_1 hybrids, F1(7), fall in the range 0.25 to 0.8 while the $F_1 \times$ *saeva*, Bs(8+10) and the $F_1 \times$ *duellica*, Bd(9+11) backcross offspring straddle the 0.8 and 0.25 lines, respectively. The F_2 offspring, F2(12), span the full range of values.

Males

Discriminant function scores

Results of a one-way ANOVA (variances not assumed to be equal) on the DF scores and post-hoc Games-Howell pairwise comparison tests are given in Fig. 4. The intraspecific crosses clearly fall out as separate groups; indeed the only overlap is between Pd(6), where n = 4, and Bd(9+11). The absolute numerical value of the DF scores is smaller than for females partly because fewer characters are included. Scores for the F_1 hybrids, F1(7) are intermediate between the two parents but are significantly shifted from
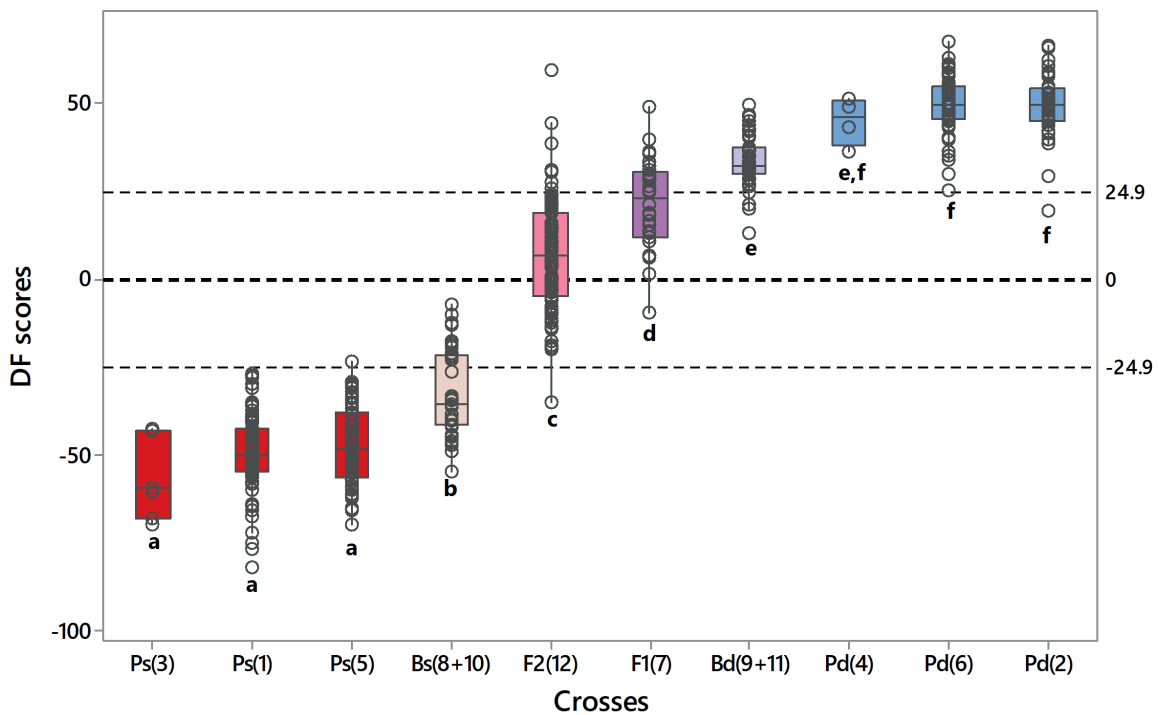
Fig. 4: Box and whisker plot of male DF scores, based on raw measurements, for individuals from different crosses. The heavy dashed line shows the DF score
that is mid-way between the parental species. The lighter dashed lines indicate the expected scores for progeny derived from the backcrosses to *E. saeva*
(lower) and to *E. duellica* (upper) on the assumption of the additivity of quantitative trait loci (QTLs). For further explanation, see legends to Fig. 1
and Table 1.

the expectation of zero towards *duellica*, with a mean of
21.4 (Ryan-Joiner normality test, $p > 0.1$; one-sample t-test,
NH = 0, $p < 0.001$). For the F_2 generation there is a lesser,
but still significant, bias towards *duellica* with a mean score
of 6.6 (Ryan-Joiner normality test, $p > 0.1$; one-sample t-
test, NH = 0, $p < 0.001$). For the backcross $F_1 \times$ *saeva*,
Bs(8+10), the mean would, *a priori*, be expected to be
midway between the predicted F_1 mean (zero) and the mean
of the *saeva* training set (-49.868) i.e. -24.934. The distribu-
tion of scores for Bs(8+10) is significantly different from
this expectation with a mean of -32.8 (Ryan-Joiner normal-
ity test, $p > 0.1$; one-sample t-test, NH = -24.934, $p < 0.001$).
Likewise, for the second backcross $F_1 \times$ *duellica*, Bd(9+11),
scores were significantly different from the expectation,
with a mean of 33.4 (Ryan-Joiner normality test, $p > 0.1$;
one-sample t-test, NH = 24.934, $p < 0.001$). For both back-
crosses, the means of the offspring were biased in the direc-
tion of the non-F_1 parent. One-way ANOVAs (variances not
assumed to be equal) of DF scores from inbred *v.* outbred
individuals within Ps(5) and Pd(6) showed that they were
not significantly different ($F_{(1, 64.4)} = 0.21$; $p = 0.645$ and
$F_{(1, 34.3)} < 0.01$; $p = 0.945$, respectively).

The only backcrosses for which numbers allow a dissec-
tion into reciprocal matings involved a *duellica* parent,
Bd(9) and Bd(11). The mean DF scores are virtually identi-
cal: 33.4 for Bd(9) [n = 39] and 33.2 for Bd(11) [n = 9] and
biased towards *duellica*. Testing against the expectation of
24.9 shows both to be highly significant (Ryan-Joiner nor-
mality test, $p > 0.1$; one-sample t-test, NH = 24.9, $p < 0.001$
and Ryan-Joiner normality test, $p > 0.1$; one-sample t-test,
NH = 24.9, $p = 0.001$, respectively). For Bs(8) the DF score
was -33.1, significantly more *saeva*-like than expected

(Ryan-Joiner normality test, $p = 0.1$; one-sample t-test, NH
= -24.9, $p < 0.001$).

Merrett plots

As mentioned above, Merrett (1980) introduced plots of
prosoma length (PROL) against combined tegulum + con-
ductor length (TCL) as a means of differentiating taxa
within the *Eratigena atrica* group. Homogeneity of slopes
of these plots was tested with an ANCOVA, with PROL as
covariate. For this analysis, data from the reciprocal back-
crosses were pooled and the small samples of Ps(3) and
Pd(4) combined with Ps(1) and Pd(2), respectively. The ini-
tial ANCOVA showed that there was a significant interac-
tion term ($F_{(7, 466)} = 2.30$; $p = 0.026$) indicating that the slopes
of the TCL on PROL plots for the different crosses were het-
erogeneous. Inspection of the data suggested that Pd(5) had
a steeper slope that the other crosses. A re-examination of
the individuals from Pd(5) exerting maximum leverage on
the slope of the regression line showed that they had been
measured correctly. With Pd(5) data removed, the slopes
were no longer heterogeneous ($F_{(6, 401)} = 0.903$; $p = 0.486$)
(Fig. 5). In a post-hoc test (Holm-Sidak method), all pair-
wise comparisons of adjusted means (elevations: Table 3)
were significant different except for Pd(6) *v.* Pd(2+4), all
intraspecific *E. duellica* crosses, and F1(7) *v.* F2(12). Resid-
uals from the common regression line are plotted in Fig. 6,
where data within pure species are combined as Ps(1+3) and
Pd(2+4+6). Thus, the elevation of the Merrett plots accu-
rately identifies intraspecific and backcross offspring as sep-
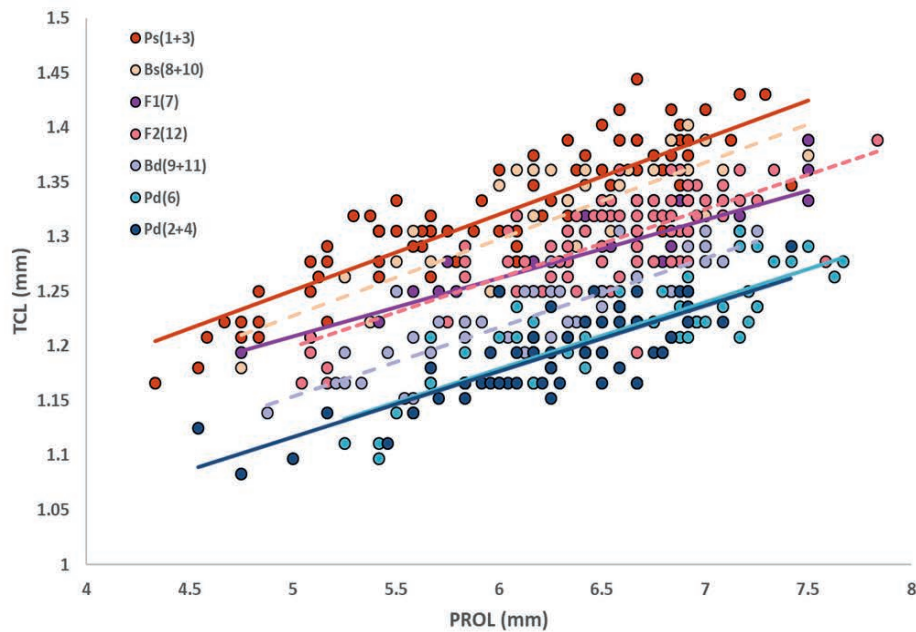
Fig. 5: Merrett plots of TCL v. PROL for all crosses except for Ps(5) (see text). For cross codes see the legend to Table 1.

arate, statistically significant, groups but not the F_1 and F_2 generations.

Comparisons of the backcross progeny residuals were made against expectations assuming additivity, as before. For Bs(8+10) the progeny were significantly more *saeva*-like than expected (Ryan-Joiner normality test, $p > 0.1$; one-sample t-test, NH = 0.0346, $p = 0.004$), whereas for Bd(9+11) the difference was not significant (Ryan-Joiner normality test, $p > 0.1$; one-sample t-test, NH = -0.0378, p

= 0.19) although there was a slight bias towards *saeva* (Fig. 6). Similar analyses for F1(7) and F2(12) progeny showed that F1(7) was not significantly different from expectation (Ryan-Joiner normality test, $p > 0.1$; one-sample t-test, NH = -0.0015, $p = 0.056$), but F2(12) was (Ryan-Joiner normality test, $p > 0.1$; one-sample t-test, NH = -0.0015, $p < 0.001$). Both are biased towards *saeva*.

Merrett plots, however, are of no use when individuals are to be classified. Here, the conductor angle (CANG) can
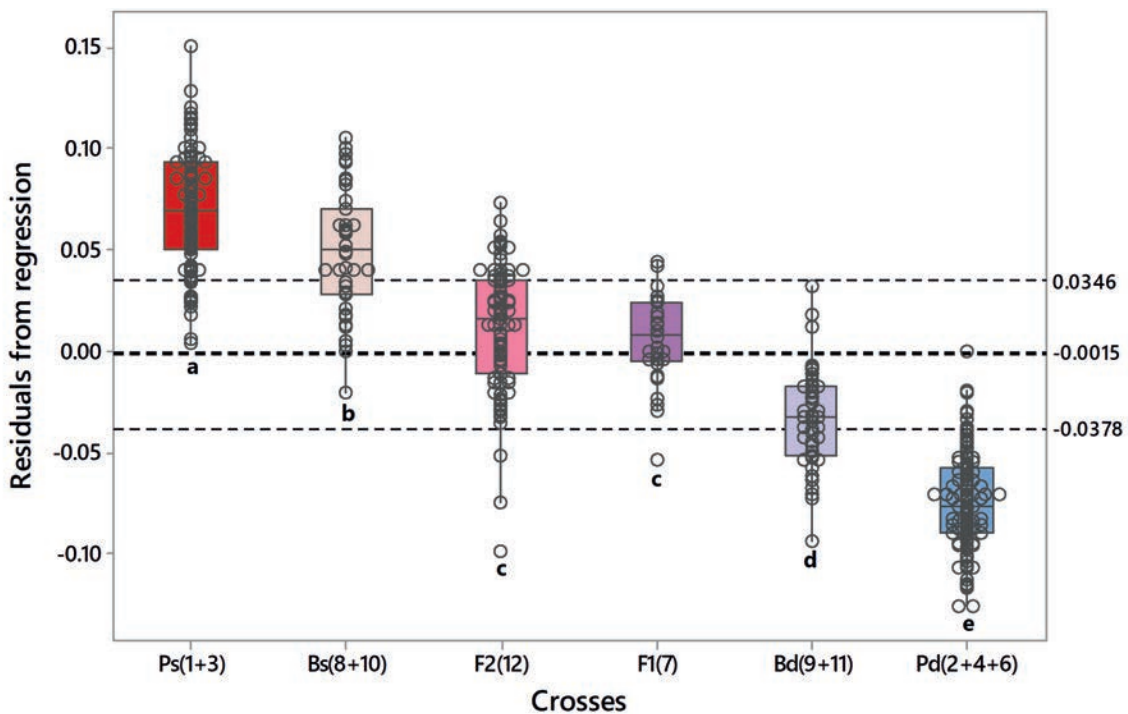
Fig. 6: Box and whisker plot of residuals from the common regression line fitted to male TCL v. PROL data. The heavy dashed line shows the mid-point residual value between the means for pooled pure *E. saeva* and *E. duellica* crosses (but not Ps(5) – see text). The mid-point is not zero because all data contributed towards the common regression line and not just the pure crosses. The lighter dashed lines indicate the expected scores for progeny derived from the backcrosses to *E. saeva* (upper) and to *E. duellica* (lower) on the assumption of the additivity of quantitative trait loci (QTLs). For further explanation, see legends to Fig. 1 and Table 1.
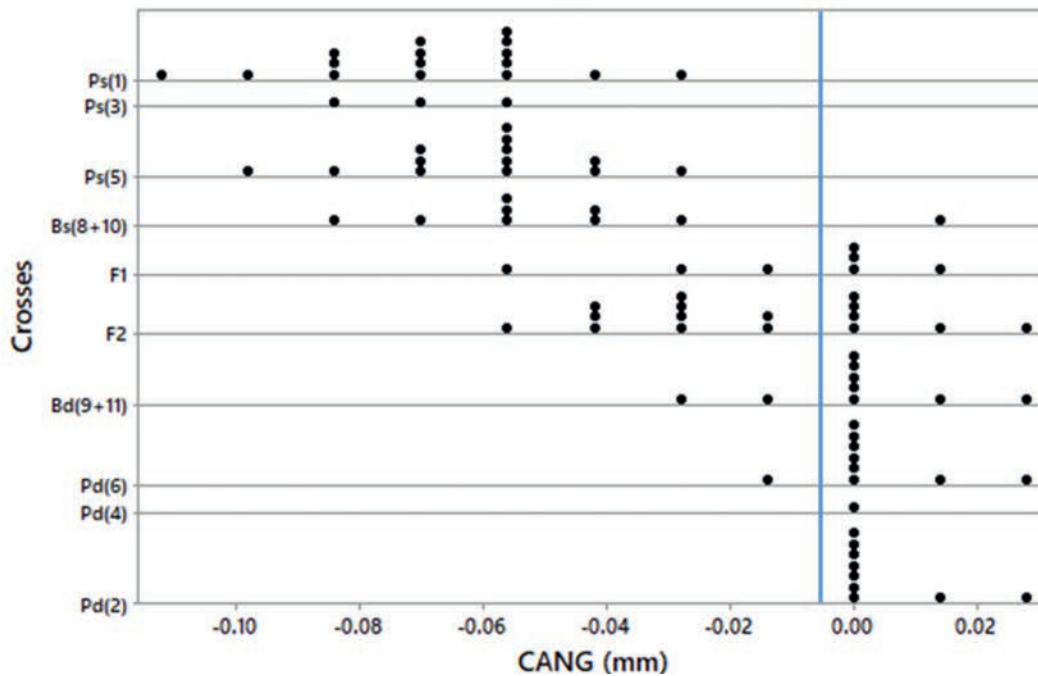
Fig. 7: Dotplot of male character CANG. For the pure species, negative values indicate *E. saeva* and values of zero or above, *E. duellica* (with one exception), as indicated by the blue line. Each symbol represents up to seven observations. For cross codes see the legend to Table 1.

help, with intraspecific *E. saeva* offspring, Ps(1), Ps(3) and Ps(5), having negative values, and *E. duellica*, Pd(2), Pd(4) and Pd(6), slightly positive values or, more often, zero (Fig. 7). Just one individual from Pd(6) fell the wrong side of this threshold. The other crosses broadly concurred with the results of the DFA presented above. F_1 hybrids more resembled *E. duellica* in this respect, but F_2 offspring were more evenly balanced. Backcross generations tended to be more similar to their pure-species parents but with a small number of outliers.

Discussion

Intra- and inter-specific laboratory crosses between *Eratigena saeva* and *E. duellica* were initially set up to investigate their propensity to hybridize (Croucher 1998; Oxford & Croucher 2014). The earlier matings established by Croucher (1998) stopped at the F_1 generation, but a later series of crosses (see Oxford & Croucher 2014) continued to the F_2 generation and included reciprocal backcrosses to both parents; analyses of these data allow important insights into the potential for, and effects of, gene flow between the two species and its future evolutionary implications.

The spiders available for these analyses were reared under two differing sets of conditions, and so it was essential to establish whether this affected their morphologies. Two comparisons suggest not. When the morphology of spiders used as the original parents, Ps(3) and Pd(4), which had developed almost entirely under natural conditions, are compared with intraspecific progeny reared for one, Ps(1) and Pd(2), or two, Ps(5) and Pd(6), generations under standard laboratory conditions, the data are homogeneous (Figs. 1, 3–7). Second, individuals raised for the later part of their

development in isolation are not significantly different in overall size to those reared in the original brood boxes under more crowded conditions. Although the boxes received more food than did isolated individuals, the number in a box was not easy to discern, especially in the early developmental stages, and so the *pro rata* feeding rates were only very approximately the same. Size matters because the DFA analyses used mostly raw measurements, and the larger an individual on average, the greater will be its DF score. These results support the arguments made by Oxford & Croucher (2014) that laboratory conditions are not too dissimilar from those encountered by the species in the wild, and that differences between different crosses are not a consequence of environmental influences.

Hybridization rates between *E. saeva* and *E. duellica* in the laboratory are extremely low (<3% compared with 87% for intraspecific crosses) (Oxford & Croucher 2014; Oxford 2016), and all the F_2 and backcross generations considered here derived from the offspring of a single, successful interspecific mating. Oxford & Croucher (2014) showed that in terms of numbers of viable young produced, sib matings are as successful as matings between unrelated individuals. The present data give no indications that DF scores of progeny of inbred and outbred crosses differ significantly for either sex.

In a previous study (Oxford & Bolzern 2018), the focus was on whether species in the *Eratigena atrica* group clustered in morphological space and, if they did, how many clusters there were. It was appropriate there to make no prior assumptions about the group affinity of individuals and so a principal component analysis was employed. Here, the starting point involved specimens collected from allopatric populations of two of the *Eratigena atrica* group species and the enquiry concerns the morphological rela-

Cross code	Cross	Parents		Progeny				
		Female	Male	Female	Male	X-ratio in females	X-ratio in males	Autosome ratio
F1(7)	$d \times s$	$X_1X_1X_2X_2$	$\mathbf{X_1X_2}$	$X_1\mathbf{X_1}X_2\mathbf{X_2}$	X_1X_2	1 : 1	1 : 0	1 : 1
F2(12)	$F_1 \times F_1$	$X_1\mathbf{X_1}X_2\mathbf{X_2}$	X_1X_2	$X_1X_1X_2X_2$	X_1X_2	3 : 1	1 : 1	1 : 1
				$X_1\mathbf{X_1}X_2\mathbf{X_2}$	$X_1\mathbf{X_2}$			
				$X_1X_1X_2\mathbf{X_2}$	$\mathbf{X_1}X_2$			
				$X_1\mathbf{X_1}X_2X_2$	$\mathbf{X_1X_2}$			
Bs(8)	$s \times F_1$	$\mathbf{X_1X_1X_2X_2}$	X_1X_2	$\mathbf{X_1}X_1\mathbf{X_2}X_2$	$\mathbf{X_1X_2}$	1 : 1	0 : 1	1 : 3
Bs(10)	$F_1 \times s$	$X_1\mathbf{X_1}X_2\mathbf{X_2}$	$\mathbf{X_1X_2}$	$X_1\mathbf{X_1}X_2\mathbf{X_2}$	X_1X_2	1 : 3	1 : 1	1 : 3
				$\mathbf{X_1X_1}X_2\mathbf{X_2}$	$X_1\mathbf{X_2}$			
				$X_1\mathbf{X_1X_2X_2}$	$\mathbf{X_1}X_2$			
				$\mathbf{X_1X_1X_2X_2}$	$\mathbf{X_1X_2}$			
Bd(9)	$d \times F_1$	$X_1X_1X_2X_2$	X_1X_2	$X_1X_1X_2X_2$	X_1X_2	1 : 0	1 : 0	3 : 1
Bd(11)	$F_1 \times d$	$X_1\mathbf{X_1}X_2\mathbf{X_2}$	X_1X_2	$X_1X_1X_2X_2$	X_1X_2	3 : 1	1 : 1	3 : 1
				$X_1X_1X_2\mathbf{X_2}$	$X_1\mathbf{X_2}$			
				$X_1\mathbf{X_1}X_2X_2$	$\mathbf{X_1}X_2$			
				$X_1\mathbf{X_1}X_2\mathbf{X_2}$	$\mathbf{X_1X_2}$			

Table 4: Chromosome segregation in the various crosses. **Bold Xs** derive from *E. saeva* parents; roman Xs from *E. duellica* parents. The ratio columns show the average relative proportion of *duellica*-derived X-chromosomes (roman) and *saeva*-derived X-chromosomes (**bold**) in female and male progeny, and the average proportions of unlinked autosomes inherited from each original parent in both sexes.

tionships between these *a priori* species and their known F_1, F_2 and backcross generations. Discriminant function analysis (DFA) was therefore used to derive the weighting of characters which maximally separate the two pure species in the training set.

A striking observation from the crosses described here is the general bias of F_1 progeny towards the morphology of *E. duellica*, as shown in female DF scores, when the RSW/RLW ratio alone is considered, male DF scores and possibly CANG, but not in the elevation of the Merrett plot where there is a non-significant bias towards *saeva*. This suggests that the effects of the quantitative trait loci (QTLs) underlying at least some of the diagnostic characters are not simply additive. In addition, the backcross generations resemble their non-F_1 parent in DF scores more than expected on the assumption of additivity, in males significantly so. It appears that something other than simple dominance of some *duellica* QTLs is influencing the DF scores (of which, in females, RSW/RLW is a major contributor). The observed biases could potentially be explained by either a maternal effect, in which offspring resemble the maternal species more than expected from an additive model, or the influence of QTLs on the sex chromosomes. A third possibility is that epistatic interactions between genetic elements from the two species resulted in the failure of some classes of offspring, thus biasing the results. Although this hypothesis cannot be ruled out, Oxford & Croucher (2014) showed that the number of live spiderlings produced by the various crosses were not significantly different.

Most spiders exhibit a multiple X-chromosome system of sex determination. In *E. atrica s.l.*, males are reported as X_1X_2 (often written $X_1X_2$0, with the 0 indicating the lack of a Y-chromosome) and females $X_1X_1X_2X_2$ (Revell 1947; Král 1995), in common with approximately 70% of spiders (Král *et al.* 2006; Araújo *et al.* 2012). The specimens Král (1995) used, if from the Czeck Republic, were almost cer-

tainly *E. atrica s.s.*, as this species is widespread in eastern Europe while *E. duellica* and *E. saeva* are absent (Nentwig *et al.* 2019). At the time of Revell's (1947) study, the species currently known as *E. duellica* and *E. saeva* were combined as *Tegenaria atrica* while the present-day *E. atrica s.s.* was known as *Tegenaria larva* (Oxford 2018). Revell is highly likely to have collected local specimens for his study which, given the location of the John Innes Horticultural Institution (Merton Park, Surrey) where he worked, were almost certainly *E. duellica* (see map in Croucher *et al.* 2007). Finally, Jiří Král and I. M. Ávila Herrera (personal communcation) have recently confirmed that *E. saeva*, too, has an identical sex-chromosome system.

The expected segregation of sex chromosomes and autosomes from the two species in the various crosses is shown in Table 4. In order to explain the biases seen, it is necessary to postulate a (partial) dominance effect of *duellica* over *saeva* QTLs on the X-chromosomes. It is assumed that QTLs on the autosomes are additive and unlinked. Table 5 evaluates the expectations from both the X-chromosome and maternal effect hypotheses against the results of this study and assumes that any maternal effect lasts for just one generation.

While acknowledging the uncertainty in predicting some outcomes, Table 5 suggests that, on the basis of current data, results tend to match the X-chromosome model predictions rather better than those of a maternal effect. The necessary assumption of a partial dominant influence of *duellica* QTLs on the X-chromosomes complicates this model. It should be stressed that here only DF scores have been considered and that, on Merrett plots, the residuals of hybrid progeny show a consistent and, in some cases significant, opposite bias in the direction of *saeva*, adding another layer of complexity.

A better evaluation of these possible models would come from an examination of backcross and F_1 progeny from the mating, *E. saeva* female × *E. duellica* male if, indeed, pair-

Cross code	Cross	X-chromosome expected		Maternal effect expected		observed	
		Female	Male	Female	Male	Female	Male
F1(7)	*d* × *s*	*d*	*d*	*d*	*d*	***d***	***d***
F2(12)	F₁ × F₁	*d*	*d*	=	=	*d*	***d***
Bs(8)	*s* × F₁	*s*?	*s*	*s*	*s*	*s*	***s***
Bs(10)	F₁ × *s*	*s*	*s*?	=	=	***s***	n/a
Bd(9)	*d* × F₁	*d*	*d*	*d*	*d*	*d*	***d***
Bd(11)	F₁ × *d*	*d*	*d*	=	=	=	***d***

Table 5: Expectations from models of X-chromosome and maternal influences on DF scores. *d* = deviation towards *duellica*; *s* = deviation towards *saeva*; *s*? = uncertain expectation depending on the relative contributions of X-chromosome and autosomal QTLs; = = no deviation in either direction (assuming a maternal effect lasts for just one generation); n/a, insufficient data to perform a test. Under observed, letters in **bold** are formally significant (see text). The chromosome model assumes that autosomal QTLs are codominant and unlinked, and that *duellica* QTLs on the X-chromosome are partially dominant over *saeva* QTLs.

ings of this type are possible. Both successful interspecific crosses reported by Oxford & Croucher (2014) were *E. duellica* female × *E. saeva* male out of a total of 30 pairings this way round, and 36 reciprocals. In a preliminary report, Kennett & Dalingwater (1986) mentioned 23 interspecific crosses between individuals from allopatric populations, none of which was successful. However, both (reciprocal) interspecific crosses using individuals from sympatric populations produced live young. As Oxford & Croucher (2014) noted, the parents of these crosses may well have had hybrid origins; as shown here, backcross and F₂ generation progeny can closely resemble pure *E. saeva* and *E. duellica*. These productive interspecific crosses may therefore tell us little about the possibility of successful, allopatric *E. saeva* female × *E. duellica* male matings. Indeed, Croucher's (1998; Croucher *et al*. 2007; Oxford & Croucher 2014) generation of interspecific offspring from parents from the parapatric zones in southern England might also have used introgressed individuals.

The morphological biases demonstrated here have implications for species interactions. Oxford & Croucher (2014) showed that mechanical incompatibility represents the major obstacle preventing hybridization between *E. saeva* and *E. duellica*. Earlier work by Croucher (1998), based on a very small sample, suggested that F₁ hybrids might have been less viable under laboratory conditions; this was not found in the later study. A possible consequence of F₁ hybrid progeny morphologically more resembling *E. duellica* (in the present example) might be a greater likelihood of them successfully backcrossing to the *E. duellica* parent, thus biasing the direction of gene flow between the species. If so, gene flow from *E. saeva* to *E. duellica* should, initially at least, be greater than *vice versa*. However, if the reciprocal cross of *E. saeva* female with *E. duellica* male is possible and equally likely in the wild, these biases with respect to differential introgression might even themselves out on a broad geographical scale. If this is the case, and given the apparent rarity of the initial hybridization event, biased gene flow might vary locally, depending on which interspecific reciprocal happened, by chance, to have been successful.

Non-symmetrical gene flow between the two *Eratigena* species has been recognised in several field surveys. Using allozyme markers, Croucher (1998) showed that, in parapatric zones on the south coast of England, *E. duellica* appeared to contain a higher proportion of *E. saeva* genes than the parapatric *E. saeva* sample contained *E. duellica* genes. However, as shown here, because F₁ hybrids can resemble *E. duellica* it is possible that some of Croucher's south coast specimens identified as *E. duellica* were, in fact, mistaken F₁ hybrids, as he acknowledged (Croucher 1998). Oxford & Smith (1987) showed that, on a Merrett plot, the regression lines for *E. duellica* from Yorkshire were shifted towards *E. saeva* compared with the line for Merrett's (1980) own data, mostly obtained from southern England. In contrast, all the lines for *E. saeva* coincided, suggesting no shift towards *E. duellica*. Using data collected a decade later, however, Croucher (1998) and Croucher *et al*. (2007) demonstrated in samples from the York region that *E. duellica* now displayed uniformity on Merrett plots and that *E. saeva* had shifted towards *E. duellica*. Multivariate analyses showed the same trends. The reasons for this apparent reversal are unknown but may reflect the continuing, dynamic nature of hybridization in the north of England (Oxford 2009, 2011, 2016).

Asymmetrical introgression is common in a variety of organisms (e.g. Miralles *et al*. 2016; Ley & Hardy 2017), including other spiders (Lattimore *et al*. 2011), and results from a number of mechanisms. In the grasshoppers *Chorthippus biguttulus* and *C. brunneus*, for example, female preference for male song in interspecific F₁ and F₂ progeny involves a dominance effect (as suggested here), which leads to asymmetric gene flow between the species (Gottsberger & Mayer 2019). In contrast, there are strong maternal influences on behaviour in female hybrids of another species pair, *Chorthippus biguttulus* and *C. mollis* (von Helversen & von Helversen 1975). In the present case, asymmetric introgression appears to be simply a result of non-symmetrical (i.e. non-additive) genitalia morphology in hybrids, which directly affects mating success; there is no evidence for post-zygotic barriers to gene exchange (Oxford & Croucher 2014, but see Croucher 1998, as mentioned above).

It has been argued that, where an individual of one *Eratigena* species is introduced to an area dominated by the other and interspecific offspring are produced, the genes of the former will be swamped and its phenotype effectively hybridized away (Croucher *et al*. 2007; Oxford 2011), as has been demonstrated in other species (e.g. Roberts *et al*. 2010; Todesco *et al*. 2016). This may explain, in part, the remarkably clear distribution patterns, for synanthropic species, of *E. saeva* and *E. duellica* in southern England and Wales (Croucher *et al*. 2007). If the introduced individual is a female, the only genetic signature remaining will be the mitochondrial haplotype (Croucher, Oxford & Searle 2004; Oxford & Bolzern 2018). The results above shown just how rapidly, from a morphological perspective, such an assimilation can take place.

If, as demonstrated here, F_1 progeny of the two *Eratigena* species can sometimes be mistaken for *E. duellica* (and possibly *E. saeva* if reciprocal hybridization is possible) morphological identification is compromised if specimens are taken from a geographical area containing both species. This possible misidentification is enhanced in F_2 and backcross generations where offspring can appear identical to either of the pure species. Nuclear molecular markers differentiating the species can be used to trace ancestry for several hybrid generations (e.g. Nussberger *et al.* 2013; Von Holdt *et al.* 2013; Scott, Glenn & Rissler 2019) but eventually they too cease to be useful.

There is a dearth of morphological studies on hybridization between spider species with which to compare the present results. As far as I am aware, the only analysis of this kind involves *Lycosa ammophilia* and *L. ericeticola* (Lycosidae) (Reiskind & Cushing 1996). These authors described a 300 m wide hybrid zone where the two species meet in northern Florida, USA. Within this zone, males were sampled along a transect across the hybrid zone, classified as parental or hybrid and examined with respect to five morphological measurements using PCA and ratio plots. Hybrids were intermediate between the two parents and significantly different from both. On this basis, the authors suggested that the hybrids were F_1s and that there was very little, if any, introgression. However, the change in the mean ratio with position along the transect (their fig. 12) hints of asymmetrical introgression, with gene flow between the hybrids and *L. ericeticola* but not between the hybrids and *L. ammophila*. Pairing experiments in the laboratory provided no evidence for differences within and between species with respect to courtship and copulatory behaviour.

In conclusion, the present study has shown that the inheritance of diagnostic characters in *E. saeva* and *E. duellica* is not consistent with a simple model of additive, unlinked QTLs. This bias might be caused by a maternal (or even a grandmaternal) effect or, perhaps more likely, by additional, partially dominant QTLs on the X-chromosomes. Whatever the underlying cause, in the present case at least, the effect produces average DF scores in F_1 and F_2 progeny biased towards *E. duellica*, and in backcross progeny towards that of the non-F_1 parent. The implications of the bias in the F_1 offspring is that gene flow into *E. duellica* might initially be easier than in the reverse direction, but we have no information on the morphology of the F_1 generation produced by the reciprocal mating. What the data demonstrate is that recognising F_1 hybrid individuals from simple morphological measurements is reliable for females but not for males. In backcross progeny, some can be identified as being of hybrid origin but others will be confused with the pure species. The approximately intermediate morphology of F_1 hybrids and the full fertility of subsequent back- and intercross generations explain the apparent incipient collapse of reproductive integrity and morphological convergence observed in areas where species widely overlap, such as in the north of England (Croucher *et al.* 2007; Oxford 2011, 2016).

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The heritability of lateral banding in *Dolomedes plantarius*

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Abstract

Pale lateral bands that contrast with somatic colouration are common to many semi-aquatic spider species and may contribute to camouflage. *Dolomedes plantarius* is dimorphic for the presence or absence of a broad, pale, lateral band on the abdomen and cephalothorax. Here, we investigate the heritability of this banding pattern by assessing the proportion of banded progeny in broods of spiderlings for which the phenotype of one or both parents was known. Our results indicate a single-gene system of inheritance with the banded allele dominant to the unbanded. This finding offers a simple way to investigate various aspects of the biology of this rare spider, which is classified as vulnerable to extinction. We consider the implications for further understanding the mating system of *D. plantarius* and for studying the function and maintenance of banding in wild populations.

Keywords: camouflage • colour polymorphism • inheritance • Mendelian ratios • Pisauridae

Introduction

Most invertebrates are, of necessity, masters of subterfuge, whether for escape from predators or access to prey. Although some achieve this through the pattern, colour, and behavioural mechanisms constituting different forms of mimicry (Jamie 2017), most use camouflage to make them difficult to distinguish from their background. The latter are generally divided into those that match their background using cryptic patterns and colours that sample it randomly, and others that have disruptive coloration, with highly contrasting patterns breaking up their outline (Endler 1981, Cuthill *et al.* 2005). Although crypsis and disruption are usually presented as alternative mechanisms of camouflage, both may potentially be deployed in the same species (Schaeffer & Stobbe 2006). Spiders present many examples of both strategies, although crypsis is the more common, with species such as the sand-matching *Rhysodromus fallax*

(Sundevall, 1833) and leaf-matching *Nigma walckenaeri* (Roewer, 1951) presenting classic examples. Some species have evolved the ability to match a variety of backgrounds by reversible colour changes such as those in *Misumena vatia* (Clerck, 1757) (Gabritschevsky 1927; Théry & Casas 2009) but, in most species, colour and pattern are directly genetically determined (Oxford & Gillespie 1998).

The family Pisauridae appears to present examples of both camouflage strategies. Within the genus *Dolomedes* Latreille, 1804, for example, some species are highly cryptic, matching the tree bark or mud surfaces typical of their habitat, while the many semi-aquatic species tend to have a more uniform, dark, ground colour often with highly contrasting light lateral bands (Fig. 1A) on the cephalothorax and abdomen (Carico 1973; Dondale & Redner 1990). These bands also feature in the closely allied semi-aquatic genera *Nilus* O. Pickard-Cambridge, 1876 and *Perenethis* L. Koch, 1878. The lycosid genus *Pirata* Sundevall, 1833, exhibits similar variation, with pale lateral bands a common feature of the semi-aquatic species, such as *Pirata piscatorius* (Clerck, 1757).

Many pisaurid species are polymorphic with respect to their colour and pattern, including lateral banding. These polymorphisms have led to considerable taxonomic confusion, for example with *Pisaura lama* Bösenberg & Strand, 1906, *Dolomedes sulfureus* L. Koch, 1878 (Yaginuma 1986), and *D. horishanus* Kishida, 1936 (Tanikawa 2003), formerly being split on the basis of their contrasting morphs. Several *Dolomedes* species are polymorphic for the presence of lateral banding, with certain individuals lacking it altogether. In those investigated to date, these polymorphisms are genetically determined and so offer a potential route for investigating the function of the bands and their maintenance in the population. *Dolomedes raptor* Bösenberg & Strand, 1906, is sexually dimorphic, with broad white lateral stripes present only in the males (Lin *et al.* 2015). *Dolomedes sulfureus* and *D. horishanus* both exhibit pattern polymorphisms which are genetically determined but not sex limited, and include morphs with and without lateral bands (Yaginuma 1986 and Tanikawa 2003, respectively). In *D. sulfureus*, the polymorphism has been bred out through successive generations and comprises three distinct forms, one of which is unbanded (Nakahira 1979). A more complex, sex-limited colour and pattern variation, including lateral banding, occurs in *Megadolomedes australianus* L. Koch, 1865 (Davies & Raven 1980).

Although lateral bands may provide disruptive camouflage, there has been little work on their function. *Dolomedes* species are ambush hunters. The semi-aquatic species typically use emergent perches where they can sit with their front tarsi in contact with the meniscus to detect approaching prey and predators via their sophisticated mechanosensory system (Bleckmann & Barth 1984). In this situation, the lateral band looks very similar to the curved reflection of sunlight on the meniscus around emerging plant stems, as well as to dead leaves of aquatic plants (Fig. 2). In the nocturnally active *D. raptor*, there is evidence that the contrasting bands attract flying insects (Lin *et al.* 2015),
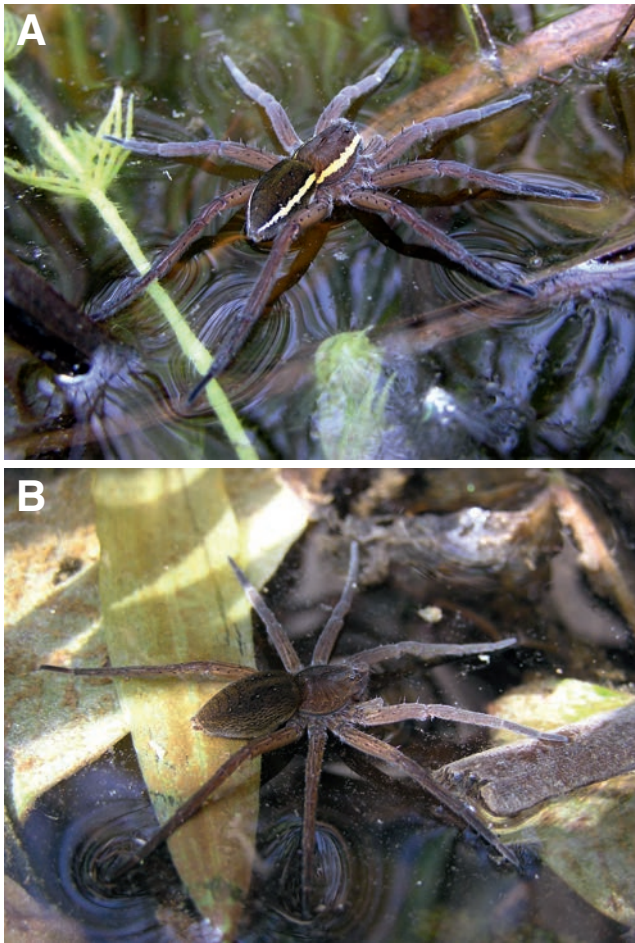
Fig. 1: *Dolomedes plantarius*. **A** with lateral band; **B** without lateral band.

Fig. 2: Cryptic nature of banded *Dolomedes plantarius* with sunlight on the meniscus.

but the position of the lateral bands makes it unlikely that this is an important function in *Dolomedes* species that prey predominantly on aquatic invertebrates. Although *Dolomedes* species have very poor eyesight, and can hunt effectively when blinded (Williams 1979), Lin *et al.* (2015) further showed that the male's white bands have a role in courtship recognition in this sexually dimorphic species.

In the semi-aquatic *Dolomedes plantarius* Clerck, 1757, one of only two *Dolomedes* species in western Europe, both sexes are dimorphic for the presence of conspicuous pale lateral bands. An unbanded morph (Fig. 1B) is widely reported, e.g. from the Netherlands (Helsdingen 1993), Germany (Harms *et al.* 2009; Unruh 2008), France (Bonnet 1930; Lecigne 2006), Sweden (Sollfors 2019), Spain (Bellvert *et al.* 2013), Italy (M. Paschetta, personal communication), and in the three remnant British populations. At one of these (Redgrave and Lopham Fen, East Anglia) it occurs at frequencies of up to 28% (HS, unpublished data) and has been recorded for over 60 years. Indeed, the species was first definitively described from Britain at this site in 1956 as a fortuitous result of the polymorphism. Dr Eric Duffey encountered an unbanded female, alerting him to the possibility that this was *D. plantarius* rather than the much commoner *D. fimbriatus* (Duffey 1958), in which entirely unbanded morphs have not been described.

Although clearly dimorphic for the presence of lateral bands, many other aspects of colour and pattern in *D. plan-*

tarius are highly variable. This includes the width and colour of the lateral band (from white through creamy-yellow, infrequently to a pale brown that contrasts poorly with the body colour) and the extent to which it is solid or broken. It also includes the ground colour of the body (from black to pale brown), and presence of white dorsal spots on the abdomen. The lateral bands can differ in colour between moults (e.g. Fig. 3) and between the carapace and abdomen, and are often more muted in adult females. Much of this variation in colour and pattern is likely to be determined by multiple genes (Oxford & Gillespie 1998). However, the long-term persistence of the banding dimorphism at fairly constant frequencies in wild populations, suggests that it may be under simple genetic control maintained by balancing selection.

Here, we use the ratios of banded to unbanded progeny in broods of both captive- and wild-mated *D. plantarius* to determine whether their frequencies conform to expectations of a genetically determined trait. We discuss the potential of our results for furthering understanding of both the maintenance of the dimorphism in *D. plantarius* populations, and the function of the lateral band. The implications of our results for sexual strategy in *D. plantarius*, and the relevance of this to the conservation of this species, which is currently classed as Vulnerable to extinction both in Britain and internationally (World Conservation Monitoring Centre 1996; Harvey *et al.* 2017), are considered.

Methods

Provenance of the spiders

All of the spiders assessed originated from one or other of the two populations known from England: at Redgrave and Lopham Fen in East Anglia (52°22′N 1°00′E), and on the Pevensey Levels in East Sussex (50°51′N 0°20′E).

In Britain, *Dolomedes plantarius* is fully protected under Schedule 5 of the Wildlife and the Countryside Act 1981 (as amended). Our assessments were made under licenses

Fig. 3: *Dolomedes plantarius* showing a change from white to cream banding upon moulting.

Year	Brood	Parental phenotypes ♀×♂	Progeny phenotypes		Proportion banded
			B	**U**	
2009	1	U×B	37	38	0.493
2009	2	U×B	46	33	0.582
2009	3	B×B	46	16	0.742
2009	4	B×B	80	0	1.000
2009	5	U×U	0	79	0.000
2009	6	B×B	36	0	1.000
2009	7	U×B	47	32	0.595
2010	8	B×B	83	0	1.000
2010	9	B×B	91	0	1.000
2010	10	U×B	5	6	0.455
2010	11	B×B	96	0	1.000
2010	12	B×B	95	0	1.000
2010	13	U×B	63	0	1.000
2010	14	B×B	55	27	0.671
2010	15	U×B	47	48	0.495
2010	16	U×B	28	28	0.500
2010	17	U×U	0	94	0.000
2010	18	U×B	44	43	0.506
2010	19	B×B	77	0	1.000
2010	20	B×U	33	41	0.466
2010	21	B×B	90	2[1]	0.978
2010	22	B×B	73	0	1.000
2012	23	B×B	153	51	0.750

Table 1: Results of crosses for broods in which the phenotype of both parents was known (U = unbanded, B = banded). [1] These individuals are thought to have been misclassified. For further details see text.

issued by Natural England, mostly using animals that were being used to evaluate and deliver a conservation translocation programme to reduce the extinction risk (Smith 2018). This inevitably limited the pairings that were possible, and particularly restricted the availability of unbanded individuals, which occur at relatively low frequency.

The broods assessed

Data on 47 broods were collected over five years, between 2009 and 2013. In 2009, most of the data came from animals used to assess captive rearing methodologies at the John Innes Centre, Norwich. These were third-generation descendants of a single banded female collected from the Pevensey Levels in 2005. No unbanded males were available, so a single individual was collected from Redgrave and Lopham Fen to increase the number of possible band-morph combinations. Seven crosses were made under standardized conditions in a laboratory arena (Table 1). Each female was presented sequentially with different males, which were removed if there was a clear behavioural rejection, until a successful copulation was observed. No further mating opportunities were presented to ensure single paternity and to reduce the chance of losing males to the rare but present risk of post-copulatory cannibalism.

In subsequent years (2010 and 2012) a further 16 broods from laboratory-mated parents were evaluated for banding ratios. These resulted from reciprocal crosses, made in preparation for a translocation programme, between spiders caught as sub-adults from the two English populations. As in 2009, the numbers of crosses and the band morph combinations were determined by the availability of mature spiders and their willingness to mate (Table 1).

A second set of 24 broods, in which only the maternal parent was known, was also evaluated for banding ratios. Twenty-one of these came from females caught at Redgrave and Lopham Fen when either gravid or already carrying an egg sac, and so both the paternal morph and the number of matings was unknown (Table 2). The spiderlings from these broods were captive reared for approximately three months before being used to stock new populations established in East Anglia as part of the translocation programme (Smith 2018). The remaining three broods (Table 2: brood numbers 24–26) in which only the maternal parent was definitely known, came from spiders caught for the reciprocal crosses made in 2010 (above). These were caught as newly emerged adults, rather than subadults, and so we could not be certain that they were previously unmated.

All of the brood parents were photographed to provide a detailed record of their banding morphology.

Assessing banding ratios in spiderling broods

The numbers of banded and unbanded spiderlings were assessed in randomly selected sub-samples of each brood. A maximum of 80 spiderlings per brood was assessed in 2009. In subsequent years, subsamples of 100 were assessed from larger broods (mean brood size >500) while all spiderlings were assessed from smaller broods (Tables 1 & 2). Spiderlings were reared in captivity until the banding morph was distinguishable. When they first emerge from the egg sac, spiderlings are guarded by their mother in a nursery web for approximately five days before dispersing. At this stage they all look very similar, with a dorsal band, and often an impression of lateral bands created by the translucency of the integument and by a scattering of white hairs (Fig. 4A). Dispersal stage spiderlings were reared individually in ventilated 15 mm test tubes lined with damp cotton wool, and fed with small Diptera every two to three days; this rearing

Fig. 4: *Dolomedes plantarius* spiderlings. **A** ~10 days old; **B** ~20 days old, banded morph; **C** ~20 days old unbanded morph. Scale bars = 1 mm.

method prevented cannibalism and usually delivered survival rates between 80 and 95% over the first three months of life. It was first possible to assess whether or not they had lateral bands by the third post-emergence instar, when they were around three weeks old (Fig. 4B–C).

In 2009, the first year in which we made assessments, all observations were made by two independent observers (AB and HS) and re-checked after at least one further moult. Growth rates varied considerably between spiderlings within each brood and microscopical examination was used to assess banding in the smallest individuals. Assessments were consistent between observers. Whether or not the spiders were banded was entirely consistent between instars, although band colour was less so; band morph also remained constant in a sample of spiders from each of the 2010 broods that was reared through to maturity and checked after each moult. In 2010, 2011, and 2013, all assessments were made by the same observer (HS). In 2012, the broods were shared between different institutions for captive rearing. The original observer (HS) assessed a small sub-sample of each brood but remaining subsamples were assessed by other, inevitably less experienced, observers. A very small number of assessment errors arose from the difficulty of evaluating the smallest individuals.

Analyses

Ninety-five percent binomial confidence limits for the proportion banded were calculated for each brood. Based on our initial finding in 2009 that the banding ratios in the broods appeared to conform with simple Mendelian ratios consistent with the parental phenotypes, and with banded dominant to unbanded, we tested against the expectation that our population contained genotypes BB (homozygous banded), BU (heterozygous banded) and UU (homozygous unbanded). Thus we expect broods to be binomial samples from populations determined by parental genotypes as follows:

Both parents banded	BB × BB	100% banded
	BB × BU	100% banded
	BU × BU	75% banded
One parent banded	BB × UU	100% banded
	BU × UU	50% banded
Both parents unbanded	UU × UU	0% banded

Broods were classified as having an expectation of 0%, 50%, 75% or 100% banded based on the nearest of these values to the observed banding proportion consistent with parent phenotypes. We fitted binomial Generalized Linear Models (Nelder & Wedderburn 1972) to test for differences in banding frequencies between groups and to obtain mean banding frequencies with confidence intervals for each group. We present means and confidence intervals back transformed to the linear scale. Analyses are presented separately for broods where both parent phenotypes were known and for broods where only the maternal phenotype was known.

For broods that had values around 50% or 75% we also tested against the relevant expectation using χ^2 tests (Zar 1999). We first tested for differences between broods within one category using a heterogeneity χ^2 test. Assuming the result was non-significant we then combined the data across broods and tested against the expected proportion banded. In cases where we expect 100% or 0% banding there should be no variation in the results so statistical testing is unnecessary. All analyses were carried out in R version 3.6.0 (R Development Core Team 2018).

Year	Brood	Maternal phenotype	Progeny phenotypes		Proportion banded
			B	U	
2010	24	B	48	41	0.539
2010	25	B	85	0	1.000
2010	26	B	67	0	1.000
2011	27	B	69	0	1.000
2011	28	B	86	0	1.000
2011	29	B	78	0	1.000
2011	30	B	206	84	0.710
2011	31	B	180	80	0.692
2011	32	B	100	0	1.000
2011	33	B	100	0	1.000
2011	34	B	108	37	0.745
2011	35	B	44	55	0.444
2011	36	U	0	100	0.000
2012	37	B	94	44	0.681
2012	38	U	168	1[1]	0.994
2012	39	B	137	0	1.000
2012	40	B	142	2[1]	0.986
2012	41	B	164	61	0.729
2012	42	B	122	0	1.000
2013	43	B	86	99	0.465
2013	44	B	68	32	0.680
2013	45	B	88	12	0.880
2013	46	B	75	26	0.743
2013	47	U	57	68	0.456

Table 2: Results of crosses for broods in which only the maternal phenotype was known. [1] These individuals are thought to have been misclassified. For further details see text.

Fig. 5: Proportion of banded spiderlings for each brood in which both parental phenotypes were known; broods ordered according to proportion banded. Error bars show 95% binomial confidence limits and colours indicate parent phenotypes (B = banded: U = unbanded).

Results

In 2009, the results of the nine crosses made in a laboratory arena between and within the two banding morphs of *D. plantarius* very clearly conformed to Mendelian ratios, with the proportion of banded individuals at either zero or 1.0, or close to 0.5 or 0.75 (Table 1). The pairing with two unbanded parents (brood 5) produced only unbanded progeny, pairs with two banded parents produced either all banded or *c*. 75% banded progeny: results consistent with a simple single-gene system of inheritance in which the banded allele is dominant. We therefore tested these broods, and those from subsequent years, for departure from the expectations of this system.

In subsequent years, among broods where both parental phenotypes were known, around 0.2% of spiderlings appear to have been misclassified (5 of 2216 spiderlings recorded). Eleven broods had banding ratios of exactly 1.0 or zero, while a single brood (Table 1: brood 21) was recorded as having 90 banded and two unbanded individuals. Among broods where only the maternal phenotype was known, 10 had banding proportions of either 1.0 or zero, while two broods had ratios of one unbanded to 168 banded and two unbanded to 142 banded respectively (Table 2: broods 38 and 40). Given the difficulties of classifying some small spiderlings we consider that the five records of unbanded spiderlings within these broods are the result of misclassification. This gives a proportion misclassified as 0.0021 (2/959) for broods with both parents known, and 0.0024 (3/1257) for broods with one parent known. In reporting and interpreting the subsequent analyses we assume a very small error rate in the classification of spider-

lings and do not reject our hypothesis of simple Mendelian inheritance based on these five records.

All of the 23 broods for which both parental phenotypes were known had banding ratios consistent with a simple Mendelian model of inheritance. Ten had banding ratios at or close to 1.0, three had banding ratios close to 0.75, eight had banding ratios close to 0.5 and two broods had a banding ratio of 0.0 (Fig. 5). A generalized linear model gave estimated proportions banded, and confidence intervals, that were consistent with this classification (Table 3), while χ^2 tests indicated no significant deviations from our expected ratios of 0.75 (test for heterogeneity between broods $\chi^2 = 1.920$, df = 2, p = 0.383; test against proportion banded = 0.75 $\chi^2 = 0.751$, df = 1, p = 0.386) and 0.5 (test for heterogeneity between broods $\chi^2 = 5.401$, df = 7, p = 0.611; test against proportion banded = 0.50 $\chi^2 = 0.583$, df = 1, p = 0.445). Of the ten broods with banding proportions at or close to 1.0, nine had two banded parents and one had one banded and one unbanded parent. The parents of all three broods close to 0.75 were both banded while those of the eight broods close to 0.5 had one banded and one unbanded parent. Both parents of the two broods with a banding ratio of 0.0 were unbanded (Table 1).

One of the broods with a banding ratio of 0.0 (Table 1: brood 17) was initially assessed as having unbanded maternal and banded paternal phenotypes. However, close examination of the father's pattern showed only a very narrow white line fringing the lower margin of the carapace (Fig. 6A). All other males assessed as banded had a broader white line slightly higher on the flank of the cephalothorax (Fig. 6B). It therefore appears to be the inheritance only of the latter band that is controlled by the simple Mendelian system identified here.

Most of the 24 broods from wild-caught females which mated prior to capture, for which only the maternal phenotype was known, showed a similar pattern to those for which both parental phenotypes were known (Table 2; Fig. 7), although there are indications of some multiple paternity. Eleven broods had banded to unbanded morph ratios at or close to 1.0 (see above on misclassifications), seven broods

Parental type	No. broods	Proportion banded	95% confidence interval
Both phenotypes known			
0.00	2	0.000	not estimable[1]
0.50	8	0.516	0.475–0.558
0.75	3	0.730	0.681–0.774
1.00	10	0.990	0.999–0.999[2]
One phenotype known			
0.00	1	0.000	not estimable[1]
0.50	4	0.472	0.428–0.516
0.75	4	0.727	0.694–0.757
1.00	11	0.997	0.992–0.999[2]
Multiple paternity 1[3]	3	0.687	0.645–0.726
Multiple paternity 2[3]	1	0.880	0.800–0.930

Table 3: Comparison against Mendelian expectations of the mean proportions of banded individuals in broods in which both parental phenotypes were known and those in which only one phenotype was known. [1] Confidence intervals cannot be estimated where all individuals in a category have the same phenotype. [2] The model is bounded 0–1, so one or two offspring with a recorded phenotype that is inconsistent with our predictions give rise to a confidence interval that does not quite overlap the expected value. [3] For explanation of multiple paternity categories see text.

Fig. 6: Male *Dolomedes plantarius*. **A** with carapace margin band only; **B** with lateral band on the carapace and its lower margin.

had banding ratios close to 0.75 (but see further details below), four broods had ratios close to 0.5 and one brood had a ratio of 0.0. One of the 2013 broods (Table 2: brood 45), with a banded maternal phenotype, had a ratio of banded to unbanded spiderlings of 0.880 (95% confidence interval 0.800–0.936) which differs significantly from the Mendelian expectations and is not consistent with a single pairing, suggesting that this individual was multiply mated.

Again, a generalized linear model provides estimates consistent with Mendelian outcomes (Table 3). Of the 11 broods with banding proportions at or close to 1.0, ten were produced by banded females and one by an unbanded female. Seven broods with banding ratios close to 0.75 (Table 2: broods 30, 31, 34, 37, 41, 44, 46) were all pro-duced by banded females. Although there was no significant difference in proportion banded across these seven broods ($\chi^2 = 3.156$, df = 6, p = 0.789), the overall banding ratio of 0.71 differed significantly from 0.75 ($\chi^2 = 10.275$, df = 1, p = 0.001). The three of these broods with the lowest proportions banded (0.680, 0.681, and 0.692) may have involved multiple paternity. The remaining four broods showed no significant difference in the proportion banded ($\chi^2 = 0.764$, df = 3, p = 0.858) and their combined banding ratio did not differ from a predicted value of 0.75 ($\chi^2 = 2.2081$, df = 1, p = 0.137).

The four broods with banding ratios close to 0.5 (Table 2: broods 24, 35, 43, 47) did not differ significantly in the proportion banded ($\chi^2 = 2.087$, df = 3, p = 0.555) and their overall banding ratio did not differ from 0.5 ($\chi^2 = 1.574$, df = 1, p = 0.210). Finally, one brood from an unbanded female had all unbanded offspring.

Overall, these results from broods in which mating took place in the wild, and only the maternal phenotype is known, are consistent with our analysis for broods in which both parental phenotypes were known. However, it seems likely that at least four of these 25 broods involved multiple paternity.

Discussion

Our results from 47 broods of spiderlings show that the lateral banding dimorphism in both male and female *Dolomedes plantarius* is controlled by a simple Mendelian system of inheritance in which the banded allele is dominant. This system controls the presence or absence of pale bands on the side of the carapace and abdomen. It does not appear to control the presence of a very narrow white band at the lower edge of the carapace in many males. Further work is needed to determine the frequency of this band and its pattern of inheritance.

The lateral bands were usually first identifiable in the third post-emergence instar. They appeared consistently
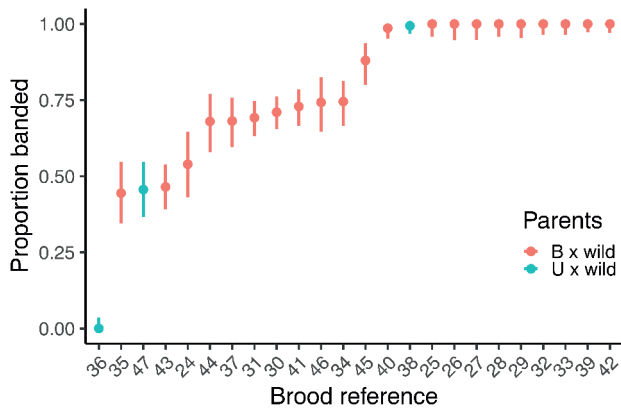
Fig. 7: Proportion of banded spiderlings for each brood in which only the maternal phenotype was known, with broods ordered according to proportion banded. Error bars show 95% binomial confidence limits and colours indicate maternal phenotypes (B = banded, U = unbanded).

thereafter, although they varied in their colour, intensity/solidity, and width between moults, and between individuals. Our results are not consistent with those of Helsdingen (1995), who reported loss of banding in some captive-reared *D. plantarius* at ecdysis, with some, but not other, individuals regaining it after a few days. Duffey (1995) did not observe any unbanded morphs among small juveniles he saw at Redgrave and Lopham Fen, and speculated that banding is lost in some individuals as they mature. However, later, more intensive field studies at the same site found unbanded morphs at similar frequencies in small juveniles and in adults (HS, unpublished data).

The simple Mendelian inheritance of the lateral band in *D. plantarius* offers potential for better understanding of the mating system of this species. Although each of our broods in which the female mated only once, and the paternal phenotype was known, conformed to the Mendelian model, we found that four of the broods from wild-caught adult females that were potentially multiply mated differed significantly in their banding proportion from our Mendelian expectation. Vugdelic (2006) found evidence of multiple paternity in a single female *D. plantarius* caught with an egg sac from one of the sites from which we obtained our stock (the Pevensey Levels). The female subsequently produced two more fertile sacs; sperm storage to fertilize later broods is the norm in this species in Britain, where male numbers decline rapidly by early August but fertile egg sacs can be produced as late as October. Using some progeny from each sac, analysis of six microsatellite loci in 30 individuals inferred a minimum of two fathers, with one male genotype having more offspring than the other in the first two but not the third brood. Vugdelić analysed only one other brood, which resulted from a mating of laboratory-reared virgin parents. In this case, genotype frequencies were consistent with single paternity.

A combination of further laboratory and field work is needed to establish the frequency of polyandry, and the resulting extent of multiple paternity. The possibility of polyandry in a species of such high conservation concern is of more than academic interest because of its potential for

increasing effective population size and maintaining genetic diversity through inbreeding avoidance (Sugg & Chesser 1994; Maklakov & Lubin 2006; Cornell & Tregenza 2007). In common with many spider species, *D. plantarius* males are promiscuous, showing courtship behaviour towards multiple females at once and to unreceptive females, including subadults, those already carrying egg sacs, and even to recently dead individuals (HS, unpublished data). It is much more difficult to assess the extent to which females mate multiple times; they are usually hidden under emergent vegetation and courtship can be protracted over several hours. Multiple matings do not guarantee multiple paternity because of the possibilities of post-copulatory sperm competition and cryptic female choice (Toft & Drengsgaard 1999; Eberhard 2004). Although our laboratory-mated females did not have an opportunity to mate more than once, they exhibited choice, often rejecting several potential partners before mating successfully. In only one case was the potential for further mating clearly diminished by the male embolus breaking in the epigyne.

Our new findings concerning the inheritance of the banding dimorphism in *D. plantarius* offer possibilities for advancing our understanding of its maintenance in the population and the adaptive significance of lateral bands in this and other semi-aquatic pisaurids. With frequencies of the recessive, unbanded morph below 30% in all three British populations, and consistently so over a 28 year period at Redgrave & Lopham Fen (HS, unpublished data), the dimorphism appears to be atypical of others described in spiders, where the recessive morph is usually the more frequent in natural populations (Oxford & Gillespie 1998). Both courtship and hunting in *D. plantarius* are diurnal activities; although, apart from egg sac and nursery construction, the extent of nocturnal activity is unclear. This species hunts on, above, and below water, and is itself a potential target for both vertebrate predators and invertebrate parasitoids. These traits suggest many possible elements of spatial and temporal environmental heterogeneity that might differentially favour either the banded morph through disruptive camouflage or the unbanded morph through crypsis. Factors other than camouflage may also be at play. Tso *et al.* (2002) found that a persistent, genetically determined melanic morph in *Nephila maculata* had significantly reduced body surface UV reflectance and foraging success, although there was no direct evidence of causation. They suggested that melanic individuals may have advantages in thermal properties or in reduced visibility to predators and parasitoid hymenopterans, including those with UV perception. The unbanded morphs may also benefit from their low frequency in the population because of frequency dependent foraging by predators (Bond 2007), or dietary wariness (Franks & Oxford 2009).

Finally, our understanding of the inheritance of lateral bands in *D. plantarius* offers the possibility of using significant changes in banding ratios in the wild to identify critical population changes in this threatened species. These could include founder effects during colonization of new habitat,

and genetic drift and bottlenecks in small, isolated and declining populations.

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Selenops ef sp. nov. (Araneae: Selenopidae) from Cambodia: first record from an Asian cave

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Abstract

Selenops ef sp. nov. (male) is described from Cambodia, Battambang Province. It represents the first record from a cave in Asia. A distribution map of *Selenops* species in Asia is given and the cave-dwelling habit of the new species is discussed.

Keywords: copulatory organ • habitat • new species • systematics • taxonomy

Introduction

The genus *Selenops* Latreille, 1819 consists currently of 129 described species, seven of which occur in Asia (World Spider Catalog 2018). Two of them have been described quite recently: *S. muehlmannorum* Jäger & Praxaysombath, 2011 from southern Laos, and *S. ab* Logunov & Jäger, 2015 from north-central Vietnam (Jäger & Praxaysombath 2011; Logunov & Jäger 2015). Both have similar copulatory organs and fall into one species group. In the present paper another species from this group is described as new to science. It was recorded from a cave in north-western Cambodia.

There are only a few cases known where spiders of the family Selenopidae have been found in caves, e.g. in the Americas: *S. debilis* group from the USA (Crews 2011), *S. juxtlahuaca* Valdez, 2007 from Mexico (Valdez 2011), *S. submaculosus* Bryant, 1940 from the Bahamas (Crews 2011), *S. curazao* Alayón-García, 2001 from the Netherlands Antilles (Crews 2011), *S. mexicanus* Keyserling, 1880 from Costa Rica (Crews 2011), *S. bifurcatus* Banks, 1909 from El Salvador (Crews 2011), and in Australia: *Karaops* sp. (Crews unpublished data). In all cases, spiders of the respective species have been recorded also outside the cave and are considered opportunistic invaders (Crews personal communication). The new species described in this paper represents the first case of a *Selenops* found in a cave in Asia.

Material and methods

Material is preserved in 70% denatured ethanol. Examination and drawings were carried out with a Leica MZ16 stereomicroscope with camera lucida attachment. All measurements are in millimetres. Leg spination pattern lists prolateral, dorsal, retrolateral and ventral spines separately. Palp and leg lengths are listed as: total (femur, patella, tibia,

metatarsus, tarsus). Arising points of tegular appendages in males are described as clock positions of the left palp.

Abbreviations used in the text: ALE = anterior lateral eye, AME = anterior median eye, d = dorsal, p = prolateral, PLE = posterior lateral eye, PME = posterior median eye, RTA = retrolateral tibial apophysis, v = ventral, I–IV = leg numbers. Museum collections: SMF = Senckenberg Museum, Frankfurt am Main, Germany (P. Jäger).

Selenopidae Simon, 1897

***Selenops* Latreille, 1819**

***Selenops ef* sp. nov.** (Figs. 1–5)

Type material: holotype ♂, CAMBODIA: Battambang Province, Phnum Proek district, Chakrey commune, Domnak Ampil village, Phnom Khbai Hong Tak, La Ang Som Nak Poa, 13°321′43.0″N 102°21′56.1″E, 224 m, in cave, H. Steiner leg., by hand, 24 January 2018 (SMF).

Etymology: the species name is an arbitrary combination of letters and, like in *Selenops ab*, the shortest possible name (two letters) indicating the small size of this new species; term in apposition.

Diagnosis: small spider with body length of male: 5.2. Palpal structures very similar to those of *S. ab* in having a similarly shaped RTA with two branches, a median apophysis with two branches and a relatively short embolus (Figs. 1–2), but can be distinguished by: ventral RTA smaller than dorsal RTA (with same size in *S. ab*); median apophysis with distal branch long and slender, retrolateral branch conical (distal branch short and stout, retrolateral branch only slightly pointed apically in *S. ab*); embolus base rounded and embolus tip in 11 o'clock position (embolus base slender and tip in 12 o'clock position in *S. ab*).

Description of holotype male: carapace length 2.2, width 2.5, anterior width of carapace 1.7, opisthosoma length 3.0, width 2.2. Eyes: AME 0.17, ALE 0.09, PME 0.18, PLE 0.23, AME–AME 0.11, AME–PME 0.02, ALE–PLE 0.15. Cheliceral furrow with 3 promarginal, 2 retromarginal teeth. Spination: palp femur d012, tibia p2, v1; legs: femur I p110, d111, II–IV d111; patella I–IV 000; tibia I–II v2222, IV v100; metatarsus I–II v222. Leg formula (23)41. Measurements of palp and legs: Palp 2.7 (0.9, 0.4, 0.5, -, 0.9), I 9.2 (2.8, 0.9, 2.5, 2.1, 0.9), II 11.3 (3.5, 1.0, 3.1, 2.6, 1.1), III 11.3 (3.8, 1.0, 3.0, 2.5, 1.0), IV 9.9 (3.4, 0.9, 2.5, 2.2, 0.9).

Palp as in diagnosis (Figs. 1–2). RTA arising sub-proximally from tibia with slender ventral RTA and broad dorsal RTA, the latter distally pointed. Embolus arising from tegulum in 7.30 o'clock position, short and only slightly bent. Conductor arising from tegulum in 1 o'clock position, prominent with retrolaterad pointed tip. Median apophysis arising from tegulum in 2 o'clock position with distal branch curved, ventrad, retrolateral branch large, ventrad. Narrow spermophor visible in ventral view in proximal tegulum and at base of embolus and in retrolateral view.

Colouration: carapace and legs pale yellowish brown. Carapace dorsally with faint pattern of two broad longitudi-
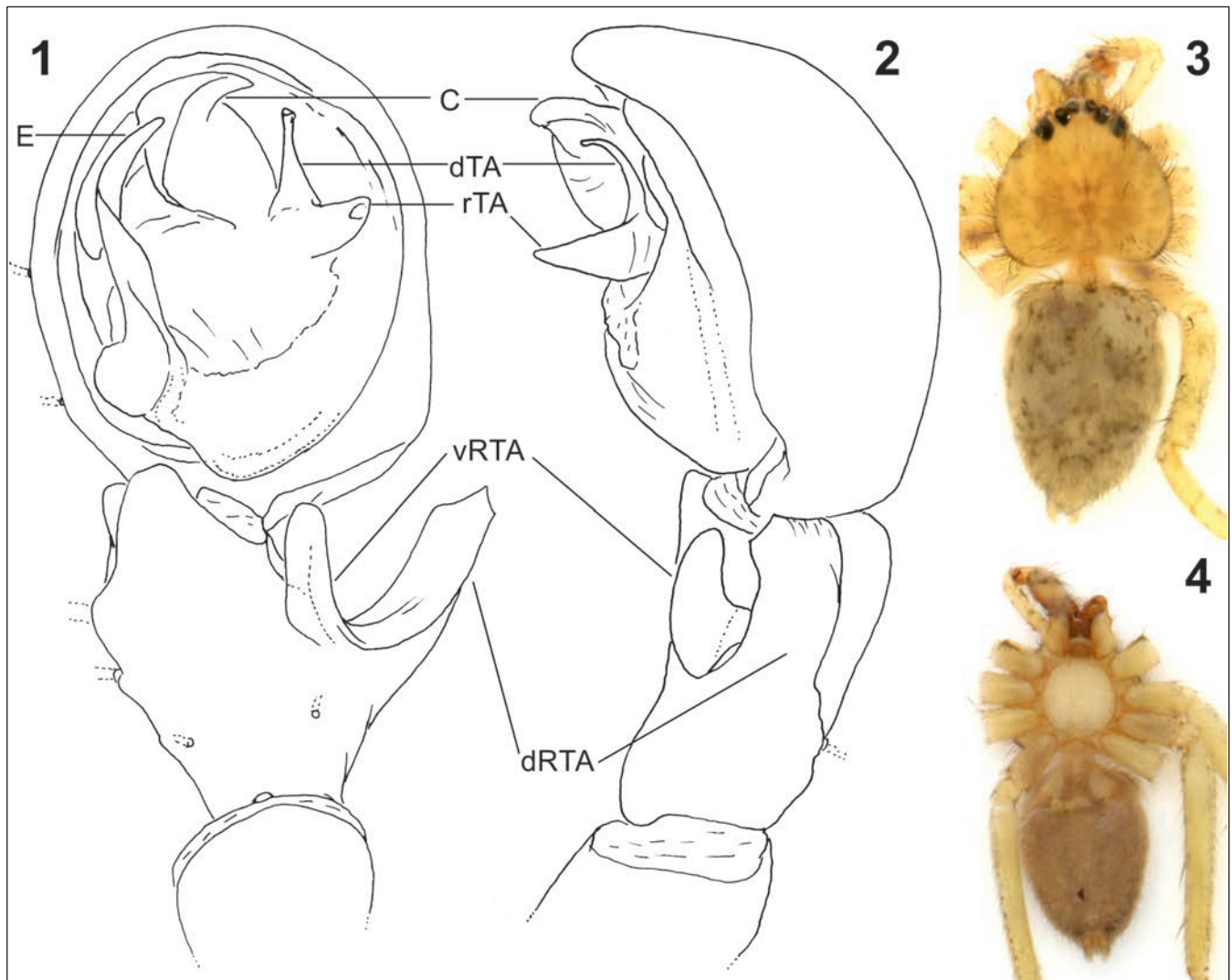
Figs. 1–4: *Selenops ef* sp. nov. from north-west Cambodia, holotype male. **1** left palp, ventral aspect; **2** left palp, retrolateral aspect; **3** habitus, dorsal aspect; **4** habitus, ventral aspect. C = conductor, E = embolus, dMA = distal branch of median apophysis, dRTA = dorsal RTA, rMA = retrolateral branch of median apophysis, vRTA = ventral RTA.

nal bands and additional marginal bands, fovea with dark patch. Chelicera with dark pattern frontally, legs spotted. Sternum, gnathocoxa and labium pale yellowish without pattern. Opisthosoma generally greyish, dorsally irregularly spotted, ventrally without distinct pattern (Figs. 3–4).

Female unknown.

Distribution: known only from the type locality (Fig. 5).

Ecology: the spider has been recorded from a chamber of a cave *c*. 15 m away from an upper cave entrance. The cave is 532 m long. The following organisms have been recorded together with the new species: Chiroptera, Reptilia (*Cyrtodactylus* sp.), *Thereuopoda longicornis*, *Phrynichus orientalis*, Pholcidae, Ctenidae, Diplopoda, Isopoda, Blattodea, Tenebrionidae (2 spp.), other Coleoptera; close to guano: Coleoptera, Formicidae, Reduviidae, Raphidophoridae, Hemiptera (Steiner, personal communication). Additional records should show whether the species is a troglobiont or an opportunistic invader as the species mentioned in the introduction.

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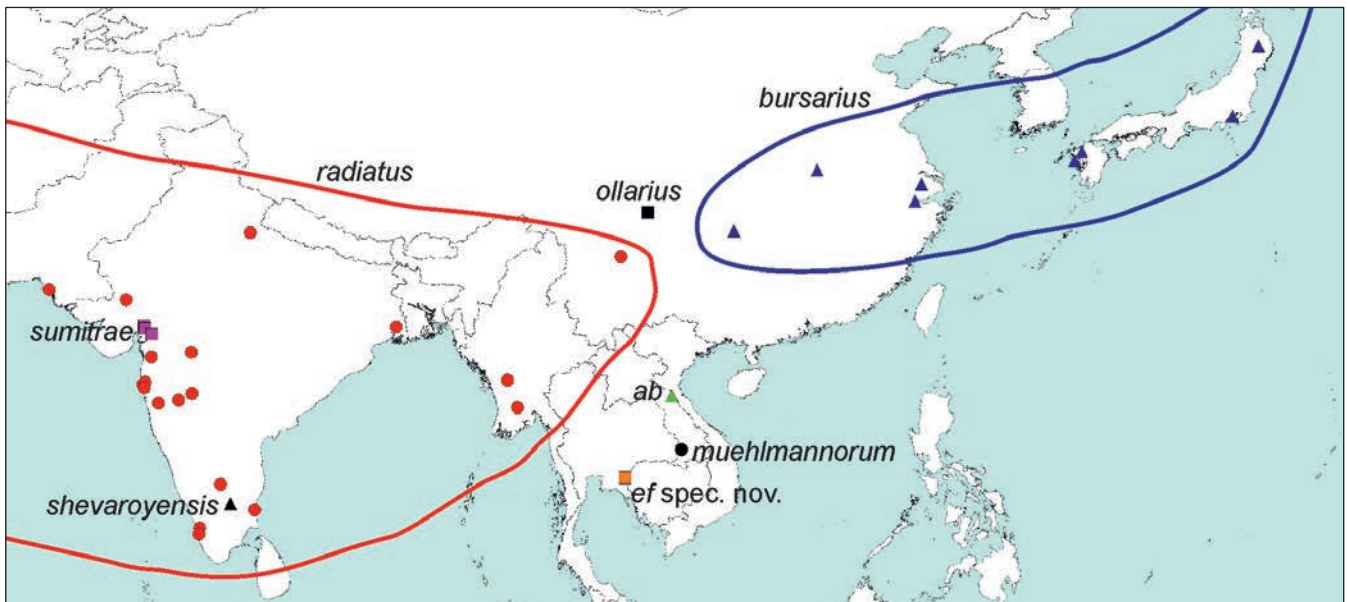
Fig. 5: Distribution records of *Selenops* species in south, east, and south-east Asia (Korean and few other records could not be included because of missing coordinates; distribution ranges of *S. radiatus* (red dots) and *S. bursarius* (blue triangles) considered rough estimates according to present knowledge; range of *S. radiatus* continues to southern Europe and tropical Africa).

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Note on the replacement name for the preoccupied genus *Linga* Lavery & Snazell, 2013 and the synonymy of the type species *Linga orqueta* Lavery & Snazell, 2013 (Araneae: Linyphiidae)

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Abstract

A new genus name is proposed to replace the preoccupied genus *Linga* Lavery & Snazell, 2013: *Notolinga* **n. gen.** The type species *Linga orqueta* Lavery & Snazell, 2013 is presented as a junior synoym of *Neriene fuegiana* Simon, 1902; therefore, *Notolinga fuegiana* **n. comb.** is established.

Introduction

Simon (1902) established a new species, *Neriene fuegiana* Simon, 1902, with a short description of the adult female and no figures, from material collected in Argentinean Tierra del Fuego in 1892/93. No type was designated. Material was deposited in Muséum national d'Histoire Naturelle in Paris and the Zoological Museum in Hamburg. Petrunkevitch (1911) transferred the species to *Oedothorax* without justification and without stating explicitly that he had examined any specimens. In 2007, Miller redescribed and illustrated a Paris specimen MNHN 14110 as '*Oedothorax*' *fuegianus* (Simon, 1902), stating that the specimen was the holotype and concluding that it was misplaced in the genus *Oedothorax*.

Dupérré & Harms (2018) redescribed and illustrated the species as *Neriene fuegiana*, using material from the Zoological Museum in Hamburg. They considered Miller's attribution of holotype to be invalid and designated the female specimen (ZMH-A0000758) as lectotype and MNHN 14110 as a paralectotype.

Lavery & Snazell (2013) described a new species, *Linga orqueta* from the Falkland Islands, with male and female type material deposited in the Natural History Museum London: holotype BMNH(E) 2013-82 1038669, allotype BMNH(E) 2013-82 1038670. Recently, new specimens of *Linga orqueta* were found in Argentinean Tierra del Fuego (Ramírez *et al*. 2018). After comparing the illustrations and photographs presented by Dupérré & Harms (2018), Lavery came to the conclusion that *Linga orqueta* is a junior synoym of *Neriene fuegiana* Simon, 1902.

Peter Coxhead (personal communication) pointed out that *Linga* was preoccupied by a bivalve mollusc (de Gregorio 1884) in contravention of International Commission on Zoological Nomenclature rules, necessitating a new genus

be established for the spider. Therefore, the new genus name, *Notolinga* n. gen. is proposed and the new synonym of *Linga orqueta* Lavery & Snazell, 2013 = *Neriene fuegiana* Simon, 1902 is recognized.

Notolinga n. gen.

Notolinga is created to replace the pre-occupied genus *Linga* (de Gregorio, 1884).

Diagnosis and description: Notolinga has the same diagnosis, description, and phylogenetic relationships as the former genus *Linga* in Lavery & Snazell (2013).

Etymology: The genus name is composed of the prefix Noto, from the Greek *notos* meaning south, added to Linga for Elizabeth Ling Lavery (Lavery & Snazell, 2013). The gender is feminine.

Included species: Only *Notolinga orqueta* comb. nov.

Distribution: Argentina (Tierra del Fuego), Falkland Islands (Islas Malvinas).

Notolinga fuegiana n. comb.

Neriene fuegiana Simon, 1902: 17 (description of ♀, type material not originally defined).

Oedothorax fuegianus Petrunkevitch (1911): 262.

'*Oedothorax*' *fuegianus* Miller (2007): 244, fig. 186C. MNHN 14110 (invalid holotype designation)

Linga orqueta Lavery & Snazell, 2013: 50, figs. 37–43. ♂ BMNH(E) 2013-82 1038669, ♀ BMNH(E) 2013-82 1038670. **NEW SYNONYMY**

Neriene fuegiana Dupérré & Harms (2018): 4, fig. 4A–C (♀). (Lectotype designation ZMH-A0000758).

Notolinga fuegiana **NEW COMBINATION**

Type material by designation (Dupérré & Harms 2018): Female lectotype (Hamburg, ZMH-A0000758); Paralectotype (Paris, MNHN 14110).

Distribution: Argentina (Tierra del Fuego), Falkland Islands (Islas Malvinas).

Discussion

Notolinga fuegiana (Simon, 1902) n. comb. is fully illustrated in Lavery & Snazell, 2013, figs. 37–43 and the female in Dupérré & Harms (2018) fig. 4. The dimensions of the Paris specimen, MNHN 14110 in Miller (2007), the Hamburg specimen ZMH-A0000758 in Dupérré & Harms (2018) and all female specimens known from the Falkland Islands are given in Table 1. Measurements outwith the range in Lavery & Snazell 2013 are highlighted. The only significant outlier is the surprisingly large overall length given in Simon (1902), which may be a transcription error. Table 2 compares descriptions of the species from the literature.

Measurement	L&S max	L&S min	Miller	D&H	Simon
Cephalothorax length	0.68	0.57	0.67	0.59	
Cephalothorax width	0.48	0.45	0.48	0.48	
Abdomen length	0.89	0.61	0.73		
Overall length	1.46	1.11	1.40	1.74	2.70
Leg 1 tibia length	0.39	0.33	0.35		
Tibia ratio (length/width)	0.23	0.19	0.23		
Trichobothrium on mt 1	0.46	0.37	0.41	0.45	
Sternum length	0.40	0.33	0.39		
Sternum width	0.38	0.32	0.35		
Clypeus width	0.08	0.05	0.09		
Tibia length	0.39	0.33	0.35		
Metatarsus length	0.29	0.22	0.28		
Tarsus length	0.29	0.26	0.27		

Table 1: Dimensions in mm. L&S = Lavery & Snazell (2013); D&S = Dupérré & Harms (2018).

	Simon in D&H	Miller	L&S
Cephalothorax	pale yellow	pale yellow	orange, faint striae
Eyes	on black rings		on black patches
Abdomen dorsal	white, medial stripe with 4–5 faint brown transverse lines	light grey, faint medial stripe, lateral patches	white, medial stripe and 4 posterior transverse bands
Abdomen ventral	reddish-brown	darker than dorsum	orange suffused black

Table 2: Descriptions. L&S = Lavery & Snazell, 2013; D&S = Dupérré & Harms (2018).

Conclusions

Comparison of the general appearance and female genitalia show clearly that the Paris and Hamburg specimens belong to the Neotropical genus *Notolinga* n. gen. rather than the Holarctic genera they were allocated to in the earlier literature. The details of the genitalia, dimensions (Table 1), and descriptions (Table 2) show that *Linga orqueta* Lavery & Snazell, 2013 and *Neriene fuegiana* Simon, 1902 are the same species. This combination removes the only species of *Oedothorax* listed for South America in the World Spider Catalog (2019).

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Another one bites the gift: sexual behaviour in a *Trechaleoides* species

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Abstract

In some spiders, nuptial gifts consist of prey or inedible items wrapped in silk by males and offered to females during courtship. Such gifts occur in the Neotropical family Trechaleidae, of which most species are semi-aquatic, associated with watercourses in riparian habitats. Here, we describe the sexual behaviour of the South American species *Trechaleoides keyserlingi* and report the presence of nuptial gift-giving behaviour for the first time in the genus.

Keywords: nuptial gifts • spiders • Trechaleidae

Introduction

Nuptial gifts are non-gametic materials transferred between the sexes (usually from males to females) during courtship and/or mating; they may increase, decrease, or be neutral to fitness success of both sexes (Vahed 1998; Lewis & South 2012). Nuptial gifts have been classified into two types: endogenous when secreted by the males, or exogenous when produced using materials from the surroundings (Lewis & South 2012). In spiders, some oral nuptial gifts (i.e. gifts that are consumed by the female) can be both endogenous and exogenous, as they consist of collected materials like fresh prey (nutritive gifts), prey leftovers or plant parts (worthless gifts) which are wrapped in silk by the males (Bristowe 1958; Costa-Schmidt, Caricao & Araújo 2008; Albo *et al*. 2011; Albo *et al*. 2014). After silk wrapping, the males court and offer the gift package to females (Bristowe 1958; Costa-Schmidt, Caricao & Araújo 2008). Nutritive oral gifts are consumed by the females during copulation. Thereby, they increase the reproductive success of the males that transfer more sperm and thus acquire more descendants (Stålhandske 2001; Albo & Costa 2010; Albo *et al*. 2011), and also of the females that obtain more food and thus produce more eggs (Toft & Albo 2015; Pandulli-Alonso, Quaglia & Albo 2017).

In contrast to insects, in which nuptial gifts are widespread and have evolved independently in several orders (Lewis *et al*. 2014), this trait is very infrequent in spiders. From 120 families and 48,306 species known (World Spider Catalog 2019), only 10 species have been reported with nuptial gifts in the form of prey wrapped in silk. They belong to two families: five species from the Palaearctic Pisauridae (Bristowe & Locket 1926; Nitzsche 1988; Itakura 1993, 1998; Silva & Carico 2012) and five species from the Neotropical Trechaleidae (Silva 2005; Costa-Schmidt, Caricao & Araújo 2008; Albo 2009; Silva & Lise

2009; Silva & Lapinski 2012). With the exception of the pisaurid *Pisaura mirabilis* (Clerck, 1757) and the trechaleid *Paratrechalea ornata* (Mello-Leitão, 1943), that have been extensively studied in latter years (Albo *et al*. 2014; Costa-Schmidt 2015), most information comes from casual observations of males carrying nuptial gifts in the field.

The family Trechaleidae includes semi-aquatic species associated with watercourses, and is characterized by having flexible tarsi as a morphological adaptation to living in these habitats (Carico 2005). Similar to Lycosidae, which is its sister group (Albo *et al*. 2017), females carry their disc-shaped egg sac attached to their spinnerets (Carico 2005). The family contains 16 genera distributed from Argentina to the United States, except for one in Japan (World Spider Catalog 2019). The genus *Trechaleoides* Carico, 2005 is distributed in southern South America, from Brazil to Uruguay (Carico 2005). This genus includes only two species: *T. biocellata* (Mello-Leitão, 1926) and *T. keyserlingi* (F. O. Pickard-Cambridge, 1903) (Carico 2005), the latter being catalogued with priority for conservation in Uruguay (Ghione *et al*. 2017). Very little is known about the biology of *T. keyserlingi* (Carico 2005); here we aim to contribute with basic information on its sexual behaviour.

Material and methods

A total of 20 large juvenile, subadult, and adult individuals were collected for behavioural experiments during the period from 2013 to 2015 in the localities of Paso Guerrero (32°18′56.90″S 57°54′5.30″W) and Rincón de Pérez (32°10′6.68″S 57°26′30.97″W), Paysandú, Uruguay. All collected specimens were transferred to the laboratory and kept separately in individual plastic containers (8 cm diameter × 7 cm high) with pebbles as substratum and water provided by wet cotton wool. Juvenile and subadult individuals were raised in a warm room at 25.1°C (± 0.1 SD) to accelerate their development. They were fed two houseflies (*Musca domestica*) three times a week. Moults were registered once a week until sexual maturity. Once the spiders reached adulthood, they were moved to an experimental room with temperature averaging 19.8°C (± 0.3 SD) and 73.8% (± 0.8 SD) humidity, maintaining the same feeding regime. For trials we used glass terraria (20 × 29 × 15 cm) with pebbles as substrate and water supplied in a Petri dish. Since *T. keyserlingi* is a crepuscular and nocturnal spider (Carico 2005), observations were carried out after 6 pm. Approximately three hours before trials, all individuals were fed a housefly; this procedure allowed us to avoid possible effects of starvation, mainly in males that may eat the prey instead of producing a nuptial gift. The maximum time of the experiments was three hours.

Observations were made approximately at 20 days of adult age, since studies of *P. ornata* showed them to be most sexually active and receptive after that time (Klein, Trillo & Albo 2012). Two days before the trials, each female was placed in an experimental terrarium allowing her to deposit
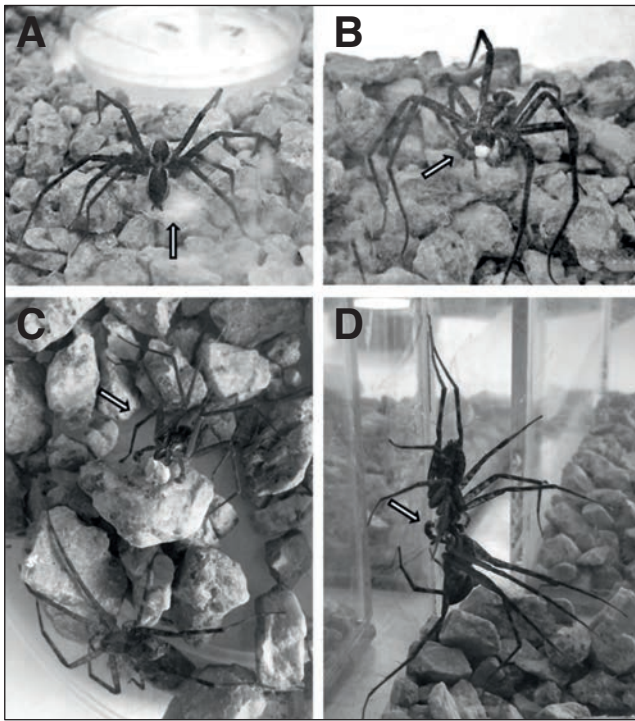
Fig. 1: *Trechaleoides keyserlingi* (Trechaleidae) during nuptial gift construction and courtship. **A** "basal plate spinning": the male deposits silk threads directly from the spinnerets forming a silk sheet; **B** "final manipulation": the male wraps the gift using leg III which draws silk from the substrate. **C** male and female during pre-copulatory courtship; "hyperflexion": male (above) exposes the nuptial gift to the female (below); **D** "female acceptance": female (above) grasp with her chelicerae the nuptial gift offered by the male (below). The arrow indicates all behavioural units.

silk threads. In other gift-giving species, the silk contains pheromones that stimulate male courtship (Lang 1996; Albo, Costa-Schmidt & Costa 2009). At the start of the trials, we offered, carefully with forceps, a housefly to each male. When the fly had been captured and was held in the chelicerae, the male was transferred to the experimental terrarium with the female. The terrarium was divided into two parts by a white paper barrier, and the male was placed in the part not containing the female. Subsequently, the barrier was removed and contact between the sexes was allowed. We described behavioural units of nuptial gift construction and courtship in *T. keyserlingi* following the terminology (with few modifications) used for the related gift-giving species *P. ornata* by Costa-Schmidt, Carico & Araújo (2008) and Albo, Costa-Schmidt & Costa (2009). We analysed the number of silk-wrapping bouts, duration of silk wrapping (calculated as the sum of the durations in all individual silk-wrapping bouts) and total duration of nuptial gift construction (time from the beginning of first bout to the last one, including time spent by males handling and carrying the gift without wrapping). We also registered and analysed courtship behaviour and mating occurrence. Data analysis was performed using the PAST statistical package (Hammer, Harper & Ryan 2003).

Results

All males courted and offered the prey gift to females (N = 20), but only 7 (35%) of the gifts were wrapped in silk, as the other 13 (65%) were offered unwrapped. During silk wrapping, the following male behavioural units were observed: 1) "basal plate spinning": deposition of silk threads by spinning over the pebbles forming a silken sheet (Fig. 1A); 2) "prey placement": placing the prey in the centre of the basal plate; 3) "silk covering": covering the prey by silk deposition as in 1) but with larger diameter; 4) "drumming": tapping with the pedipalps over the silk construction and around the prey; 5) "gift grabbing": holding the package with the chelicerae while extending the pair of legs I, II and IV; 6) "final manipulation": wrapping the gift from the substrate using the third pair of legs while holding it with the pedipalps and chelicerae (Fig. 1B). Males performed this complete sequence of silk wrapping (from 1 to 6) on average 2 times (± 0.8 SD) consequently adding more silk to the package. The total nuptial gift construction took 17.7 (± 8.3 SD) minutes while total silk wrapping duration took 12.4 (± 7.1 SD) minutes.

Male courtship started with the stage of mate searching, where males walked performing "stroboscopic movements" while carrying the housefly (unwrapped or wrapped in silk) in his chelicerae. This behavioural unit consists of the male alternating forelegs vibrations in the air and against the substrate towards the female, sometimes following the female's silk threads with his pedipalps. Once both sexes were close to each other the pre-copulatory courtship and physical contact occurred, during which the male performed "lateral tapping" with his forelegs above female's body (dorsal part). This was followed by both sexes adopting the "hyperflexion posture": legs positioned backwards and the male exposing the nuptial gift (Fig. 1C). The female accepts to mate by grasping the nuptial gift offered by the male ("female acceptance"; Fig. 1D). The frequency of mating was 75% since five females never accepted the male. Female acceptance and mating occurred in 57% of the cases where males offered wrapped gift and in 85% where they offered unwrapped gifts.

Discussion

This is the first record of nuptial gift-giving behaviour for the genus *Trechaleoides*, adding a new species possessing this sexual trait in spiders. This reproductive strategy has been described in several species from the family Trechaleidae, such as in the genera *Paratrechalea* (Costa-Schmidt, Caricao & Araújo 2008) and *Trechalea* (Silva 2005; Silva & Lise 2009). The natural history and sexual behaviour of the sister species *T. biocellata* is unknown (Carico 2005) but, interestingly, Albo (2009) exposed couples with successful copulations but with no observations of nuptial gift-giving behaviour, suggesting the absence of the trait in this species.

This is the second detailed description of courtship in a Neotropical spider with nuptial gifts in the form of prey. Courtship in *T. keyserlingi* resembles the one observed in *P.*

ornata, though several particularities exist between the two species. For example, *T. keyserlingi* showed a very low frequency of nuptial gift construction, as only one third of the males wrapped the prey in silk compared with 50–60% in *P. ornata* (Albo, Costa-Schmidt & Costa 2009; Albo & Costa 2010). In contrast, both species performed a similar number of silk wrapping bouts during gift construction: in *T. keyserlingi* we found a maximum of three, while in *P. ornata* between two and four have been observed (Albo, Costa-Schmidt & Costa 2009). Finally, total gift construction duration seems also to be similar, averaging almost 20 min in *T. keyserlingi* (this study) and 13.9 min (± 4.3 SD) in *P. ornata* (Albo, Costa-Schmidt & Costa 2009).

This study will encourage further research on the sexual behaviour in both *Trechaleoides* species, which may produce evidence of how frequent is the nuptial gift-giving behaviour in the genus, and suggest hypotheses on the evolution of this sexual trait.

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A new species of *Siler* (Araneae: Salticidae) from Japan

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Abstract

An unidentified *Siler* species has been recorded from the central Ryukyus in Japan, but the taxonomic status of the species has not been clarified sufficiently until now. To make clear the taxonomic identity of the species, in addition to a morphological comparison with other Japanese congeners, we performed molecular analysis based on partial sequences of mitochondrial cytochrome oxidase subunit I (mt-COI). As the results, we concluded the unidentified species from the central Ryukyus is new to science. Therefore, we describe this species as *Siler rubrum* sp. nov. in the present paper. *Siler rubrum* sp. nov. is very similar to *S. collingwoodi* (O. Pickard-Cambridge, 1871). However, males of *S. rubrum* sp. nov. can be distinguished from the latter by the length of the tibial apophysis and the shape of the tegulum on the pedipalp. Females of *S. rubrum* sp. nov., in contrast, lack distinct diagnostic characters compared with males, but can be distinguished from *S. collingwoodi* by slight differences in the shape of the copulatory duct.

Keywords: Chrysillini • jumping spider • Nansei Islands • Ryukyu Islands • taxonomy

Introduction

The genus *Siler* Simon, 1889 (Araneae: Salticidae) comprises brightly coloured species, and some of them are known as myrmecophagic spiders (Jackson *et al.* 1998; Touyama, Ihara & Ito 2008). In current taxonomy, the genus *Siler* consists of nine species, all of which are distributed from southern to eastern Asia (World Spider Catalog 2019).

Including one unidentified species, three *Siler* species have been recorded from Japan until now. *Siler cupreus* (Simon, 1889) is a common species in Japan, widely known from the main islands to the Ryukyu islands. *Siler collingwoodi* (O. Pickard-Cambridge, 1871) has been found in the southern Ryukyu Islands (also known as the Yaeyama Islands) (Baba 2010). In addition to these known species, an undescribed species has been recorded from Amami-Oshima, Okinoerabu-jima, and Okinawa-jima islands, which belong to the central Ryukyus (Chikuni 1989; Baba

& Suguro 2019; Tanikawa personal observation). Although this species can be distinguished from the other Japanese *Siler* by colour patterns in males, the taxonomic conclusion has been postponed because of the similarity in the copulatory organs with *S. collingwoodi*.

To make clear the taxonomic status of the unidentified *Siler* species from the central Ryukyus, we made a morphological comparison between the unidentified species and *S. collingwoodi* in detail, and also performed a DNA analysis based on mitochondrial COI, including all Japanese congeners. As a result of morphological comparison and molecular analysis, the species distributed in the central Ryukyus is distinguishable from *S. collingwoodi* and is not identifiable as any of the known species of the genus, so we describe a new species *S. rubrum* sp. nov. in this paper. The results of the molecular analysis are discussed after the description.

Materials and methods

Sampling and morphological examination

All materials were collected from several sites in the Ryukyus and main islands of Japan by various methods, including beating, sweeping and visual searching, and preserved in 75% (v/v) ethanol. Morphological characteristics were observed under a Nikon SMZ1000 and Wild M3Z stereomicroscopes. To examine the copulatory organs of the male, the left pedipalp was cut. The epigynum of the female was dissected and treated in proteinase K from a Qiagen DNeasy Tissue Kit (Qiagen, Inc., Valencia, CA, USA) to remove the muscle. All measurements were made with an ocular micrometer on the stereomicroscope. Photographs were taken with Olympus E-M1 Mark II and TG5 digital cameras. Abbreviations: ALE = anterior lateral eye, AME = anterior median eye, PLE = posterior lateral eye, PME = posterior median eye, distances between eyes are expressed as e.g. ALE–AME. All measurements are in mm.

Molecular analysis

We performed DNA sequence analysis of mitochondrial DNA cytochrome oxidase subunit I (mt-COI) on part of specimens of *S. rubrum* sp. nov., *S. collingwoodi* and *S. cupreus* obtained from Japan (for collection locations see Table 1). The salticid *Phintella abnormis* (Bösenberg & Strand, 1906), was used as the outgroup. Genomic DNA was extracted from ethanol-preserved spiders by using a Qiagen DNeasy Tissue Kit (Qiagen). DNA was amplified in a TaKaRa TP650 thermal cycler (Takara Bio, Inc., Otsu, Shiga, Japan). PCR reactions (50 μL) included 5 μL of genomic DNA, 4 μL of dNTP mix, 1 μL of each primer, 0.38 μL of TaKaRa ExTaq DNA polymerase (Takara Bio), 5 μL of buffer, and 33.62 μL of sterile distilled H_2O. The mt-COI partial sequence was amplified with the primers LCOI-1498 and HCOI-2198 (Folmer *et al*. 1994). The reactants were initially denatured for 2 min at 94°C; this was followed by
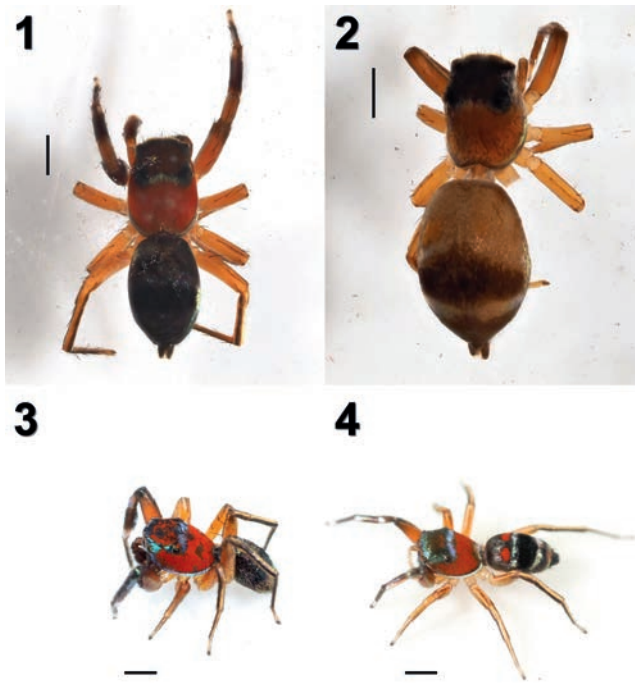
Figs. 1–4: *Siler rubrum* sp. nov. **1** male, dorsal view (in alcohol) (NSMT-Ar16974); **2** female, dorsal view (in alcohol) (NSMT-Ar16975); **3** male, dorso-lateral view; **4** female, dorso-lateral view. Scale bars = 1 mm.

Figs. 5–8: Copulatory organs of *Siler rubrum* sp. nov. **5** male pedipalp, ventral view; **6** same, retrolateral view; **7** epigynum, ventral view; **8** vulva, dorsal view. Scale bars = 0.1 mm.

40 cycles of 15 s at 94°C, 20 s at 47°C and 30 s at 72°C, with no final extension. The PCR products were then sequenced by the Takara Bio Dragon Genomic Center (Takara Bio, Yokkaichi, Japan) using an Applied Biosystems 3730xl DNA Analyzer (Life Technologies Japan, Ltd., Tokyo, Japan) and a BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems). Sequences were aligned by using ClustalW implemented in BioEdit software (Hall *et al*. 2011) and then trimmed to retain only the shortest sequence common to all samples. We constructed the neighbour-joining tree in MEGA 7 software (Kumar *et al*. 2016).

To clarify whether *S. rubrum* sp. nov. can be distinguished from other congeners by differences in DNA sequences (i.e. barcoding gap), we performed the Automatic Barcode Gap Discovery (ABGD) method (available at https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html):

this method detect significant differences in intraspecific and interspecific pairwise distances without *a priori* species hypothesis (Puillandre *et al*. 2012). The ABGD analysis was performed with default parameters (Pmin = 0.001, Pmax = 0.100, Steps = 10, X = 1.5, Nb bins = 20). We utilized uncorrected p distances because they are thought to be more conservative for genetic distance analyses of closely related species (Srivathsan & Meier 2012).

All mt-COI sequences obtained have been deposited in the DDBJ database. The type specimens designated here have been deposited in the collection of the Department of Zoology, National Museum of Nature and Science, Tokyo.

Species	Sample code	Sex	Locality	Collector	Accession No.
Siler rubrum sp. nov.	SL_03	♀	Yamato-Village, Amami-Oshima Island, Kagoshima Pref.	K. Yamamuro	LC485233
Siler rubrum sp. nov.	SL_05	♀	Yamato-Village, Amami-Oshima Island, Kagoshima Pref.	K. Yamamuro	LC485231
Siler rubrum sp. nov.	SL_40	♂	Nago-City, Okinawa-jima Island, Okinawa Pref.	A. Tanikawa	LC485232
Siler rubrum sp. nov.	SL_46	♂	Nago-City, Okinawa-jima Island, Okinawa Pref.	A. Tanikawa	LC485234
Siler rubrum sp. nov.	SL_56	♀	Shoryudo-Cave, Okinoerabu-jima Island, Kagoshima Pref.	T. Yamasaki	LC485237
Siler rubrum sp. nov.	SL_57	♀	Shoryudo-Cave, Okinoerabu-jima Island, Kagoshima Pref.	T. Yamasaki	LC485238
Siler rubrum sp. nov.	SL_59	♂	Shoryudo-Cave, Okinoerabu-jima Island, Kagoshima Pref.	T. Yamasaki	LC485239
Siler collingwoodi	SL_60	♂	Otomi, Iriomote-jima lsland, Okinawa Pref.	H. Yoshitake	LC485240
Siler collingwoodi	SL_61	juv.	Otomi, Iriomote-jima lsland, Okinawa Pref.	H. Yoshitake	LC485241
Siler collingwoodi	SL_62	♀	Otomi, Iriomote-jima lsland, Okinawa Pref.	H. Yoshitake	LC485242
Siler collingwoodi	SL_63	♀	Otomi, Iriomote-jima lsland, Okinawa Pref.	H. Yoshitake	LC485243
Siler collingwoodi	SL_64	juv.	Komi, lriomote-jima Island, Okinawa Pref.	H. Yoshitake	LC485244
Siler collingwoodi	SL_65	juv.	Uehara, lriomote-jima Island, Okinawa Pref.	T. Ebihara	LC485245
Siler collingwoodi	SL_90	♀	Nozoko, Ishigaki-jima Island, Okinawa Pref.	Y. Suzuki	LC485246
Siler cupreus	SL_47	♀	Saruga-jo Valley, Tarumizu-shi, Kagoshima	T. Yamasaki	LC485235
Siler cupreus	SL_53	♀	Okawa-fall, Yakushima Island, Kagoshima	T. Yamasaki	LC485236
Phintella abnormis	Ar_314	♂	Kannondai, Tsukuba, Ibaraki	Y. G. Baba	LC485230

Table 1: Specimens used for molecular analysis.
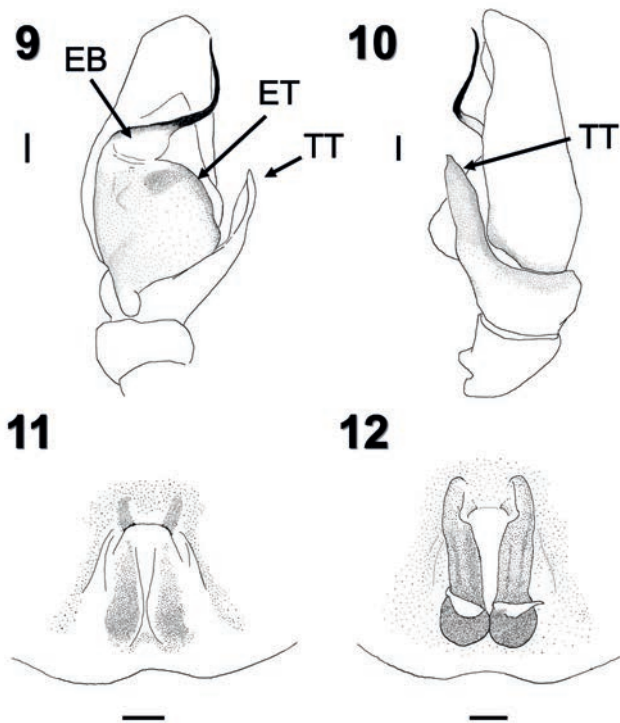
Figs. 9–12: *Siler rubrum* sp. nov. **9** male pedipalp, ventral view; **10** same, retrolateral view; **11** epigynum, ventral view; **12** vulva, dorsal view. Arrows indicate the tip of the tibial apophysis (TT), upper edge of the tegulum (ET) and embolic base (EB). Scale bars = 0.1 mm.

Figs. 13–16: Copulatory organs of *Siler collingwoodi* (O. Pickard-Cambridge, 1871). **13** male pedipalp, ventral view; **14** same, retrolateral view. **15** epigynum, ventral view; **16** vulva, dorsal view. Arrows indicate the tip of the tibial apophysis (TT), upper edge of the tegulum (ET) and embolic base (EB). Scale bars = 0.1 mm.

Salticidae Blackwall, 1841

***Siler* Simon, 1889**

***Siler rubrum* sp. nov.** (Figs. 1–12)

Silerella sp.: Chikuni (1989): 283, fig. 38.

Type series: Holotype ♂, JAPAN: Chinase, Amami-Oshima Is., Kagoshima Pref., 10 April 2015, Y. G. Baba leg. (NSMT-Ar16974). Paratypes: 3♀ 1♂, 30 May 2009, Yamato-Village, Amami-Oshima Is., Kagoshima Pref., K. Yamamuro leg. (NSMT-Ar16975; sample code for molecular analysis, SL03, 05); 1♂, 18 September 2003, Tatsugo-cho, Amami-Oshima Is., Kagoshima Pref., Y. G. Baba leg. (NSMT-Ar16976); 1♀, 17 September 2011, Yuwan, Amami-Oshima Is., Kagoshima Pref., T. Suguro leg. (NSMT-Ar16977); 1♂, 10 April 2015, Chinase, Amami-Oshima Is. Kagoshima Pref., Y. G. Baba leg. (NSMT-Ar16978)

Other material examined: JAPAN: Okinoerabu-jima Is., Kagoshima Pref., 1♀, 11 July 2013, Shoryudo, T. Yamasaki leg.; 1♀, 12 July 2013, same; 1♀1♂, 13 July 2013, same; Okinawa-jima Is., Okinawa Pref.; 1♀, 15 August 2009, Nago city, A. Tanikawa leg.; 1♂, 11 September-2010, same; 1♀, 12 September 2010, same; 1♂, 22 September 2010, same; 1♀, 12 October 2010, same; 1♂15 January 2011, same; 1♀, 12 September 2011, same; 1♂ 1 May 2017, same; 2♀, 7 July 2017, same.

Species examined for comparison: *Siler collingwoodi* (O. Pickard-Cambridge, 1871): Iriomote-jima Is., Okinawa

Pref., 1♂,12 August 1985, Ohara, A. Tanikawa leg.; 1♀, 15 March 2013, Otomi, H. Yoshitake leg.

Etymology: The specific name is derived from the bright red of the male cephalothorax.

Diagnosis: This new species is easily distinguished from congeners other than *S. collingwoodi* by general appearance and the shape of the copulatory organs: *S. rubrum* sp. nov. resembles *S. collingwoodi* in general appearance, but males can be distinguished by the following characteristics: 1) Differences in the colour patterns of the cephalothorax and abdomen: *S. rubrum* has a bright red throughout the cephalothorax (Figs. 1, 3), whereas in *S. collingwoodi* a wide area of the cephalothorax is covered with blue hairs. Also, whereas the abdomen of *S. rubrum* is dark with no stripes, *S. collingwoodi* has red and silver patterns and black streaks on the abdomen (Figs. 1, 3). 2) Differences in the copulatory organ. The embolic base is very swollen in *S. rubrum* (Fig. 9 EB), but less so in *S. collingwoodi* (Fig. 13 EB). In addition, the retrolateral tibial apophysis of *S. rubrum* is longer than that of *S. collingwoodi*. The tip of the retrolateral tibial apophysis extends beyond or is in the same position as the anterior edge of the tegulum (Fig. 9 TT), but that of *S. collingwoodi* does not (Fig. 13 TT). Females of both species are almost the same in general appearance, but the female of *S. rubrum* can be distinguished from that of *S. collingwoodi* by the copulatory duct: in *S. rubrum*, the duct extends to spermatheca without curving (Fig. 12), but it curves in *S. collingwoodi* (Fig. 16).
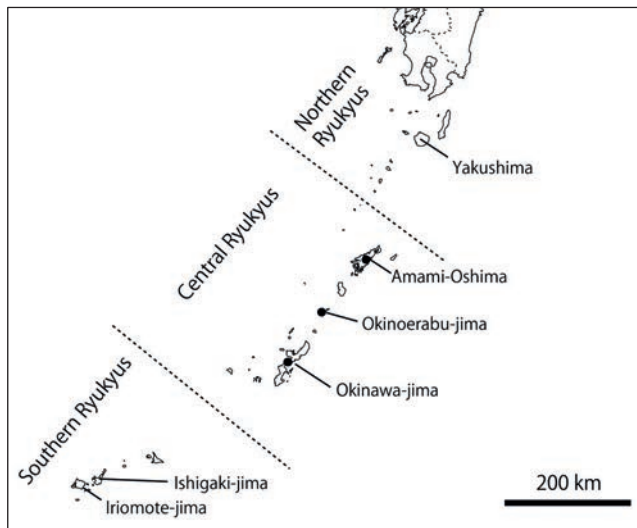
Fig. 17: Map of Ryukyu Islands, Japan, showing the distribution of *Siler rubrum* sp. nov.

Fig. 18: Phylogenetic tree of Japanese *Siler* species, based on partial mt-COI sequences obtained by the neighbour-joining method for the species examined. Scores at each node are bootstrap values (1000 replicates, fewer than 90 omitted). Scale bar shows substitutions per site.

Description: On the basis of the holotype ♂ and paratype ♀, measurements in parentheses indicate the range among other specimens we examined. Body length: ♂ 5.88 (3.63–5.88), ♀ 5.63 (4.38–6.25). Carapace length: ♂ 2.63 (1.63–2.63), ♀ 2.13 (1.75–2.50). Carapace width: ♂ 2.13 (1.38–2.13), ♀ 1.88 (1.38–1.88). Eye fields: ALE–ALE: ♂ 1.52 (1.12–1.52), ♀ 1.45 (1.12–1.52); PLE–PLE: 1.70 (1.24–1.70), ♀ 1.67 (1.24–1.73); ALE–PLE: ♂ 1.12 (0.88–1.21), ♀ 1.12 (1.00–1.24); ALE–PME: ♂ 0.61 (0.45–0.61), ♀ 0.63 (0.39–0.67); ALE–PLE/carapace length: ♂ 0.43 (0.43–0.55), ♀ 0.53 (0.42–0.71); ALE–ALE/PLE–PLE: ♂ 0.89 (0.87–0.96), ♀ 0.87 (0.82–0.90); AME diameter: ♂ 0.45 (0.36–0.52), ♀ 0.45 (0.33–0.48); ALE/AME: ♂ 0.53 (0.50–0.62), ♀ 0.53 (0.47–0.60); ALE/PLE: ♂ 1.14 (0.88–1.33), ♀ 1.00 (0.78–1.29); PME/PLE: ♂ 0.29 (0.25–0.33), ♀ 0.25 (0.22–0.29).

Leg lengths are shown in Table 2.

Male pedipalp. Embolus long, bent sideways and then bending again and running anteriorly, slightly undulating (Figs. 5, 6, 9–10). Tegulum extended posteriorly, with small ventral protuberance in its anterior half (Figs. 5, 19). Tibial apophysis bending slightly.

Female copulatory organ. Epigynum with longitudinal slit medially (Figs. 7, 11). Copulatory opening located at anterior margin of epigynum longitudinal slit. Copulatory duct extending posteriorly without curving, and connected spherical spermatheca (Figs. 8, 12).

Colouration and markings: Male. Carapace fundamentally red emarginated with silver hairs in the living condition. Eye field covered with bluish hairs. Leg I tibia, patella

and femur dark brown, tarsus light brown; legs II–IV light brown. Abdomen shiny and dark (Fig.3). In the ethanol-soaked condition, whole body colour dark and brownish compared to the living condition (Fig. 1).

Female. Carapace basically red, covered with bluish hairs in the living condition; emarginated with white hairs. Leg I tibia, patella and femur dark brown; tarsus light brown; legs II–IV light brown. Dorsum of abdomen covered with silver hairs, except for characteristic red marking and black stripes (Fig. 4). In the ethanol-soaked specimen, whole body colour dark and brownish compared to the living condition (Fig. 2).

Variation. Colouration and markings vary widely with the degree of hair loss.

Distribution: Japan, Central Ryukyus (Amami-Oshima, Okinoerabu-jima and Okinawa-jima Islands) (Fig. 17).

Discussion

Classification of species based on morphological differences was also supported by the results of DNA sequence analysis, as described below. We obtained partial sequences (525 bp) of mt-COI DNA from the specimens. The rooted neighbour-joining phylogenetic tree (Fig. 18) placed each of *S. rubrum* sp. nov., *S. collingwoodi* and *S. cupreus* in different clades. The ABGD method also showed that these *Siler* specimens can be distinguished into three species by barcoding gaps. The p-distances (number of base differences per site) were as follows: within *S. rubrum* sp. nov., 0.006–0.012; between *S. rubrum* sp. nov. and *S. collingwoodi*, 0.051–0.062; and between *S. rubrum* sp. nov. and *S. cupreus*, 0.042–0.053. This result suggests that the specimens in the central Ryukyus (i.e. those collected from the Okinoerabu-jima, Amami Oshima and Okinawa-jima islands; Table 1) was mutually similar among the islands, and that it could be distinguished in terms of DNA sequences from *S. collingwoodi* distributed in the southern Ryukyus, as well as from *S. cupreus* distributed in the main islands and the northern Ryukyus.

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	2.00/1.50	0.94/0.81	1.44/1.06	1.06/0.81	0.63/0.50	**6.06/4.69**
II	1.56/1.25	0.69/0.69	1.00/0.88	0.88/0.69	0.63/0.44	**4.75/3.94**
III	1.56/1.38	0.69/0.69	1.00/0.88	1.25/0.63	0.56/0.44	**5.06/4.44**
IV	1.94/1.75	0.81/0.69	1.56/1.38	1.75/1.38	0.69/0.69	**6.75/5.88**

Table 2: Measurements of leg segments of *Siler rubrum* sp. nov. (♂/♀, mm)

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Corrigendum: Partial antimicrobial and biochemical profiles of *Agelenopsis naevia* Walckenaer, 1842 (Araneae: Agelenidae) venom

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In a paper published in *Arachnology* last year (Ahmed, Shehu & Ndams 2018), the spider used in the experiments was identified as *Agelenopsis naevia* Walckenaer, 1842 (Agelenidae). It has since been pointed out that this species is not known to occur outside North America (World Spider Catalog 2019). Consequently, specimens were obtained and identified by Tony Russell-Smith as *Hippasa* Simon, 1885 sp. (Lycosidae), a genus known from West Africa but not previously recorded from Nigeria (World Spider Catalog 2019). Only juveniles were collected, so a specific identification was not possible.

Acknowledgments

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Redescription of a poorly known insular spider *Labahitha gibsonhilli* (Araneae: Filistatidae)

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Abstract

An illustrated redescription of *Labahitha gibsonhilli* (Savory, 1943) known only from two syntype females from Christmas Island, is given. The species is re-diagnosed and the lectotype and paralectotype are designated. *Labahitha gibsonhilli* differs from *L. oonopiformis* (Bristowe, 1938), the only other known congener, in having a reversed-cordate sternum, as well as in the shape of the receptacles.

Keywords: Araneae • Australia • Christmas Island • Indian Ocean • lectotype • Prithinae

Introduction

The genus name *Labahitha* Zonstein, Marusik & Magalhaes, 2017 was recently proposed to replace the preoccupied *Mystes* Bristowe, 1938. This genus is currently known from two species: the generotype *Labahitha oonopiformis* (Bristowe, 1938) and *L. gibsonhilli* (Savory, 1943)—the latter was recently transferred from *Filistata* Latreille, 1810 (Zonstein & Marusik 2019). The type species of the genus was redescribed in detail by Zonstein, Marusik & Magalhaes (2017), but *L. gibsonhilli* remains known only from the original description, lacking any illustrations (World Spider Catalog 2019).

We recently obtained spider material from the Oxford University Museum of Natural History, containing one vial labelled *Filistata gibsonhilli*. A study of the two females and the label revealed that the specimens represent syntypes, although the label bears no indication of the status of the vial content. The aim of the present paper is to present a redescription of *L. gibsonhilli* and its comparison with the type species *L. oonopiformis*.

Material and methods

Specimens were photographed with a Canon EOS 7D camera attached to an Olympus SZX16 stereomicroscope at the Zoological Museum, University of Turku, Finland. Digital images were montaged using CombineZP image stacking software. The endogyne was cleared in a KOH/water solution until the soft tissues were dissolved. Photographs were taken in dishes with a polyurethane layer on the bottom, using tiny pins to hold the specimens in the required position. All measurements are given in millimeters.

Abbreviations used in the text: ALE = anterior lateral eyes, AME = anterior median eyes, Fe = femur, Mt = metatarsus, OUMNH = Oxford University Museum of Natural History, Pa = patella, PLE = posterior lateral eyes, PME = posterior median eyes, Ta = tarsus, Ti = tibia.

Labahitha Zonstein, Marusik & Magalhaes, 2017

Labahitha Zonstein, Marusik & Magalhaes 2017: 305 (introduced as a replacement name for *Mystes* Bristowe, 1938, preoccupied by *Mystes* Champion, 1895); Zonstein & Marusik (2019: 85).

Remarks: The genus currently comprises only two species: the type species *L. oonopiformis* (Bristowe, 1938) from the Malay Peninsula, and *L. gibsonhilli* (Savory, 1943) from Christmas Island, considered below. However, there are also several undescribed species putatively belonging to *Labahitha*. If so, this genus may have a relatively wide distribution in archipelago areas of the Indian and Pacific Oceans (see Zonstein *et al*. 2017).

In our previous paper (Zonstein, Marusik & Magalhaes 2017), we noted that the endogyne bears inner and outer receptacles, although there is only one pair of receptacles, each possessing a wide stalk and well separated from the globular head of the receptacle. Both species have pore gland areas in the same location (antero-mesally, Figs. 4, 7).

Labahitha gibsonhilli (Savory, 1943) (Figs. 1–5)

Filistata gibsonhilli Savory, 1943: 355 (♀); Roewer (1955): 1281.
Labahitha gibsonhilli: Zonstein & Marusik (2019): 86 (transfer from *Filistata*).

Types: AUSTRALIA: lectotype ♀ (designated here) and paralectotype ♀, Christmas Island, north shore, 1939, A. C. Gibson-Hill (OUMNH-2010-093; examined). Type specimens were desiccated, making it impossible to clean the endogyne properly and provide better figures of carapace.

Diagnosis: Females of *L. gibsonhilli* differ from those of *L. oonopiformis* by the shape of both the sternum and the endogyne. The sternum in *L. oonopiformis* extends between coxae IV (Fig. 6) while in *L. gibsonhilli* it does not do so (Fig. 2). In *Labahitha gibsonhilli* the head of the receptacle (Rh) is wider than its thumb-like stalk (Sr) whereas in *L. oonopiformis* the receptacle is twice as small as the stalk. The head of the receptacle in *L. gibsonhilli* is hemispherical
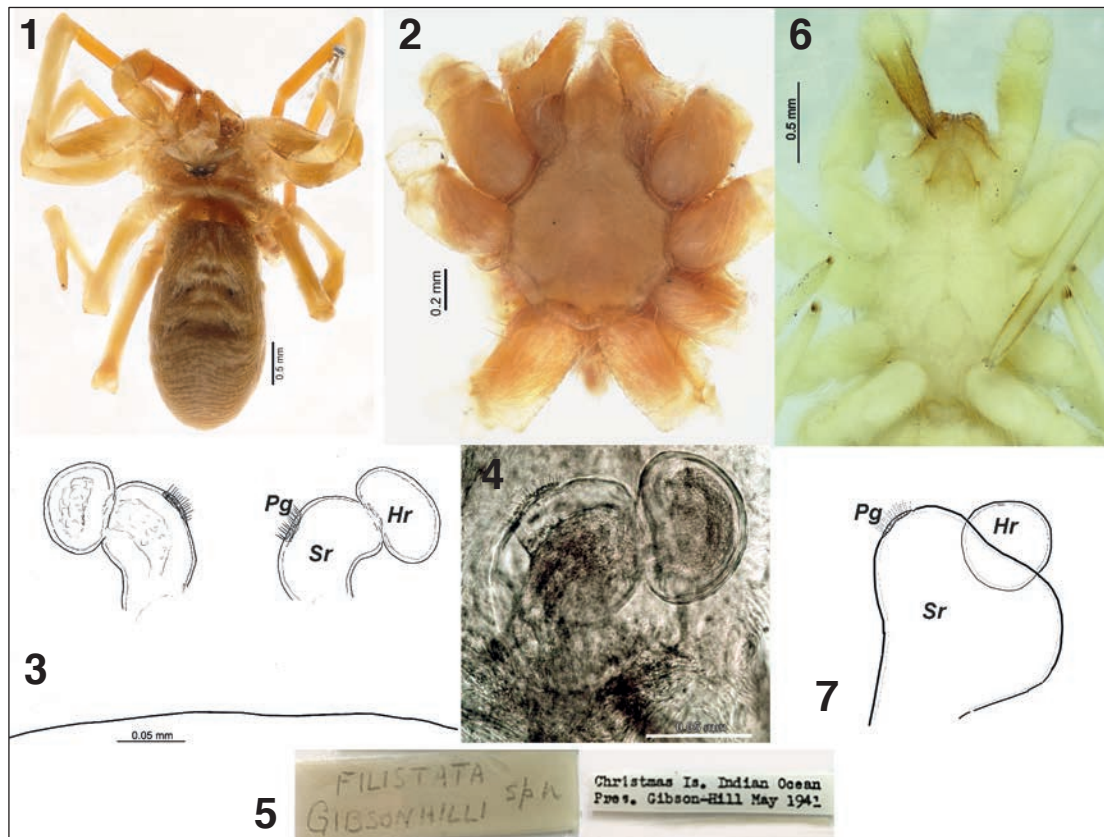
Figs. 1–7: *Labahitha gibsonhilli* (1–5) and *L. oonopiformis* (6–7). **1** habitus of lectotype female, dorsal; **2, 6** prosoma, ventral; **3** endogyne of paralectotype, dorsal; **4, 7** right receptacle, dorsal; **5** original labels. Abbreviations: Hr = head of receptacle, Pg = pore glands area, Sr = stalk of receptacle.

but spherical in *L. oonopiformis*. The two species also differ by the shape of the receptacle stalk and stalk interdistances (cf. Figs. 3–4 and 7).

Redescription of female lectotype: Habitus as in Fig. 1. Measurements: total length 4.0; carapace ~1.6 (deformed and bent, true length unknown), 1.50 wide; clypeus 0.50 long, chelicera 0.10 long; abdomen 2.50 long, 1.35 wide. Eye sizes and interdistances: AME 0.093, ALE 0.13, PME 0.086, PLE 0.071; AME–AME 0.028, ALE–ALE 0.16. Carapace, sternum, chelicera, palp and legs medium yellowish brown, with slightly paler clypeus, femora, patellae and tibiae I–II and entire legs III–IV. Eye tubercle brown, eyes with dark-brown and partially fused bordering. Abdomen dorsally and ventrally uniformly greyish brown. Sternum reversed-cordate (Fig. 2) not extended between coxae IV. Palpal femur wider than femur I. Palp and leg measurements:

	Fe	Pa	Ti	Mt	Ta	Total
Palp	1.00	0.50	0.60	-	0.75	2.85
I	2.00	0.60	1.65	1.40	0.85	6.50
II	1.50	0.55	1.25	1.25	0.75	5.30
III	1.25	0.50	1.00	1.05	0.60	4.40
IV	1.80			missing		

Endogyne as in Figs. 3–4, with a pair of receptacles. Receptacles composed of broad thumb-like stalk (Sr) and hemispherical head (Hr), stalk and head well separated by constriction. Stalks separated by about one diameter, bent laterally, with distinct pore gland area (Pg) antero-mesally. Receptacle heads interspaced by almost 3 diameters.

Note: In the description, the collection date is indicated as 1939. However, the collection label in the vial with the types gives the date as May 1941 (Fig. 5). Savory (1943) noted that he received spider material from Christmas Island in February and December of 1940. Thus, the label date could correspond to the date when the material arrived at the Oxford Museum.

Acknowledgements

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Leaf webs of *Emblyna* sp. and *Mallos hesperius* (Araneae: Dictynidae)

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Abstract

The prey capture webs of *Emblyna* sp. and *Mallos hesperius* (Chamberlin, 1916) span gentle curves in the surfaces of single, rigid leaves. They share several traits with orb webs: geometrically regular and approximately planar arrangements of strong, non-sticky lines; geometrically regular arrays of sticky lines laid on these non-sticky lines; and frequent renewal (webs are routinely damaged by rain, and are often largely renewed daily). They generally differ from orbs in that neither the sticky nor the non-sticky lines are organized radially. Comparisons with the webs of 22 other dictynid species in seven other genera reveal little phylogenetic pattern. Comparisons with the orb-like para-orbs of six, distantly related species reveal variable combinations of orb-like traits in different groups, suggesting widespread convergence. New details of possible taxonomic interest concerning how silk is combed from the cribellum are described.

Keywords: flexible design • non-orb webs • leaf form effects on web design

Introduction

Web-building spiders are an ancient evolutionary success story. Prey capture webs probably arose at least 300–310 Ma, araneomorphs 230 Ma, and orb webs 165 Ma ago (Selden, Shih & Ren 2011, 2013; Coddington *et al.* 2019). The long evolutionary histories of both orbs and non-orbs, combined with the large number of spider taxa that build prey capture webs, probably largely accounts for both the high modern diversity of web forms and the repeated convergences on particular web designs (Eberhard in press). One set of especially dramatic convergences involves para-orb webs that resemble modern orb webs in several respects. Para-orbs occur in speices in diverse families, including *Nurscia* (= *Titanoeca*) *albomaculata* (Lucas, 1846) (Titanoecidae) (Szlep 1966), *Matachia livor* (Urquhart, 1893) (Desidae) (Opell 1999, Griswold *et al.* 2005), *Fecenia* spp. (Psechridae) (Robinson & Lubin 1979; Zschokke & Vollrath 1995; Murphy & Murphy 2000; Bayer 2011; Agnarsson *et al.* 2012; Blackledge *et al.* 2012), *Synotaxus* spp. (Theridiidae) (Eberhard 1977, 1995, Eberhard, Agnarsson & Levi 2008), *Oecobius concinnus* Simon, 1893 (Oecobiidae) (Solano-Brenes, Miranda & Barrantes 2018) and cf. *Anarrhotus* (Salticidae) (Hill *et al.* 2019). This report describes para-orbs in yet another family: Dictynidae.

Dictynidae is a large, probably polyphyletic, family (Griswold *et al.* 2005; Agnarsson *et al.* 2012), currently with 469 species in 52 genera distributed worldwide (World Spider Catalog 2019). The genera in this study, *Emblyna* (formerly part of *Dictyna*) and *Mallos*, are in the subfamily Dictyninae (Griswold *et al.* 2005). Although there are various published photos and drawings of the webs of dictynid species in the field (Emerton 1902; Nielsen 1932; Comstock 1967; Bristowe 1958; Shinkai 1979; Shinkai & Takano 1984; Bond & Opell 1997; Blackledge & Wenzel 2001; Smith, Emlen & Pearson 2016) (Table 1), there are apparently no detailed descriptions of dictynid web designs. This neglect is probably due in part to the difficulty of seeing patterns in the complex, tangled webs in the field. Dictynid webs often persist for many days, thus accumulating damage, repairs, and additions (Bond & Opell 1997) that can obscure patterns that may have occurred in the original webs (Eberhard 1987; Benjamin & Zschokke 2003). Additions can be substantial: on average *Dictyna volucripes* Keyserling, 1881 in captivity increased the area of their webs by approximately 50% over a span of 9 days (Blackledge & Wenzel 2001). Variations in available attachment sites are probably also responsible for variations in web designs. Bond & Opell (1997: 393) noted that the web forms of different species of *Mallos* spp. in the field correlated with the form of the substrate, and varied so substantially that it was "nearly impossible to associate a particular web type with any one species".

Several design features that are often associated with dictynid webs are illustrated in Fig. 1A of *Mallos pallidus* (Banks, 1904). They include relatively long aerial lines that span spaces between supports, more or less radial non-sticky lines that converge centrally in a dense array near a relatively protected retreat that is located on or very near the substrate (often near a fork in a twig); and a tendency to build webs on dead, finely branched tips of twigs and plant stems. A few other dictynids apparently live on the surfaces of leaves, including *Dictyna foliacea* (Hentz, 1850) (Comstock 1967), *D. felis* Bösenberg & Strand, 1906 (Shinkai 1979), *M. blandus* Chamberlin & Gertsch, 1958 (Bond & Opell 1997) and *Paradictyna* sp. (Forster 1970), but no webs of these species have ever been carefully described.

This note presents observations on several aspects of the designs of freshly built webs and the building behaviour web of two more dictynid species, *Emblyna* sp. and *Mallos hesperius* that build webs on leaves; it compares their webs with those of other dictynids, and also with other para-orb webs. In addition, one aspect of web construction behaviour that has been previously used to determine affinities among families is analysed in *M. hesperius* and compared with that of other cribellate groups.

Material and methods

Spiders were observed in the field and captivity near San Antonio de Escazu, Costa Rica (9°53′51.41″N 84°08′15.99″W, 1325–1350 m) during the early wet season
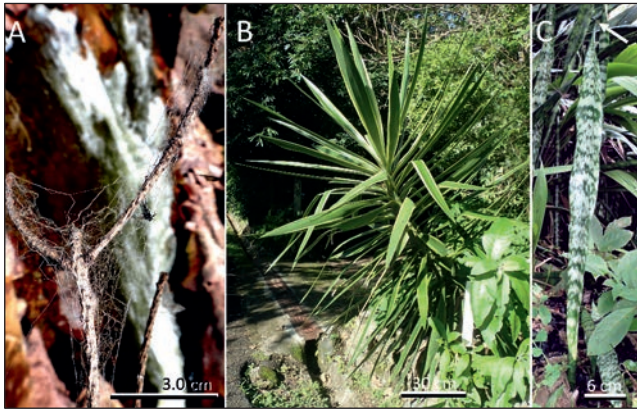
Fig. 1: **A** the web of *Mallos pallidus* in the field near Golden, Colorado, illustrates some typical traits of aerial dictynid webs. It has a tangle of lines built near the tip of a dead branch, with a central retreat where the spider rested on or near the surface of the branch. Several more or less planar arrays of apparently non-sticky lines span spaces between twigs; sticky silk lines are more intensely white in the photo; **B** two *M. hesperius* webs were found near the tips of leaves of this *Yucca guatemalensis* plant; **C** a leaf of *Sanseviera* sp. with an arrow marking the tip.

Fig. 3: The web of a mature female *Emblyna* sp. built in captivity on the distal portion of a *Sanseviera* sp. leaf. **A** overview; **B** close-up showing the many fine lines of the runway (dotted arrows) extending from the lower margin of the floor of the retreat; **C** close-up of the bottom end of the runway (dotted arrow), with spanning lines and where several non-sticky lines, some of which bore zig-zag sticky lines, converged on the same general area (the hub).

in May of 2019 (when it rained more or less daily) and in June and July, when rains were less consistent. Mature females built webs in captivity when they were placed on approximately vertical pieces of the stiff leaves of *Philodendron* sp., *Sanseviera* sp. and *Yucca guatemalensis*; the leaf bases were inserted into small jars that were placed in a closed container with water in the bottom, thus discouraging the spiders from attaching lines to other objects or decamping. Spiders were fed workers of a small dolichoderine ant (*Tapinoma* sp.?) and small nematocerous flies.

I examined webs from the field and captivity under a dissecting microscope, both before and after coating them with talcum powder. Some webs and their leaves were subsequently jarred gently to knock most of the powder from the non-sticky lines but leaving the sticky lines coated. Photos and video recordings at 30 fps were made using an Olympus TG-4 Tough camera. Webs to be photographed were lit from the side to increase contrast.

Fig. 2: A four-day web of a mature female *Emblyna* sp. on the distal portion of a *Sanseviera* sp. leaf. **A** overview of the sticky lines; **B** close-up of the lower portion of the retreat and the upper portion of the prey capture sheet (the dotted arrow marks the runway; the spider rested above the upper limit of this photo); **C** close-up of the middle portion where barely visible fine runway lines (some marked with dotted arrows) and an oblique long spanning line (solid arrow) are visible. This web was first powdered, and then the leaf was jarred repeatedly to remove nearly all the powder from non-sticky lines.

Because webs in the field occurred on elongate, linear leaves that often grew with their tips above their bases (Fig. 1B–C), the words "below" and "down" in the descriptions that follow refer to portions of the web that were closer to the leaf's base, rather than to orientations with respect to gravity. I use the word "line" without implying how many finer fibres (products of single spigots) were included; some lines (but perhaps not others) consisted of many fibres. Species were distinguished in the field by the yellow margins of the cephalothorax and the larger size of *M. hesperius*.

The descriptions below include numerous photos. Because this note is a first, exploratory attempt to describe dictynid web designs in detail, and because it is not yet clear which web traits will prove most informative in comparing different groups, inclusion of abundant photographs seems appropriate. The analyses are relatively qualitative rather than quantitative because, as will be seen below, some aspects of web design appeared to be largely determined by the forms of the leaves on which webs were built. The spiders are very small, and may well occur on other types of leaves with other shapes where I did not learn to search for them. In sum, this paper documents web designs that the spiders are capable of building (as is, of course, typical of studies of spider webs), but it may not document the entire range of web designs that these species build.

The distal portion of the embolus of a mature male of *Emblyna* sp. raised in captivity was thickened, thus making it an *Emblyna* rather than a *Dictyna*; but it did not match any described *Emblyna* species, and may thus be undescribed (D. Ubick personal communication). Specimens of *M. hesperius* matched the description of this species by Bond & Opell (1997). Voucher specimens have been deposited in the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica.
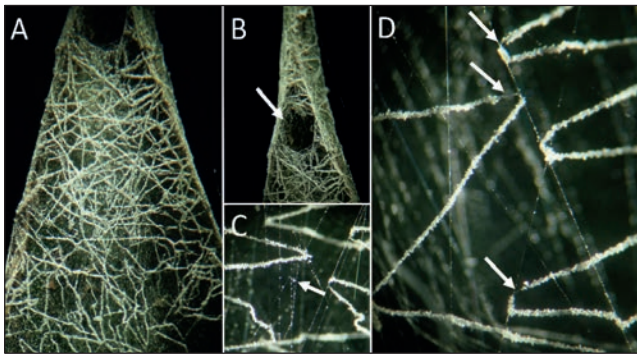
Fig. 4: Details of sticky lines in the web of a mature female *Emblyna* sp. on the distal portion of a *Sanseviera* sp. leaf. **A** the upper end of the planar prey capture sheet just over the retreat has a dense array of sticky lines; **B** the exit hole at the upper end of the retreat, where the floor extends to form the upper wall; **C** fine, non-sticky lines (arrow) were present in the capture sheet; **D** small interruptions in the mat of cribellum silk where it was attached to non-sticky lines (arrows) indicate the direction in which the spider was moving when it laid sticky lines (it was moving upward at all three sites indicated by arrows). This web was first powdered, and then the leaf was jarred repeatedly to remove nearly all the powder from the non-sticky lines.

Results

Emblyna *sp.*

Webs were found in the field on the surfaces of long, stiff leaves of several species (especially *Sanseviera* sp., Asparagaceae) that were somewhat curved transversely (Figs. 1C, 2–6), and also on the surfaces of smaller, stiff, weakly curled leaves of *Citrus* sp. (Rubiaceae). Often the spider rested in a retreat near the distal tip of a long leaf, where the leaf curled more tightly to form a partial tube. The spider closed this tube with a small, dense sheet (Fig. 4A–B), and rested in a small retreat formed by tightly meshed non-sticky lines that formed a floor near the leaf surface and a roof. Some retreats had a small hole at the upper end whose
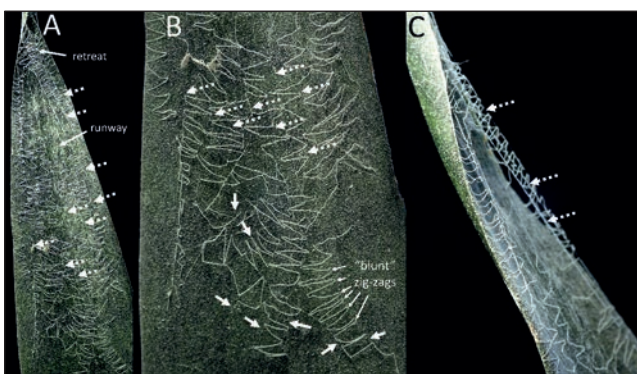
Fig. 5: An *Emblyna* sp. web on a *Sanseviera* sp. leaf that had only a weak transverse curl, but that was somewhat twisted and bent longitudinally, illustrating one likely effect of leaf form on web design. **A** overview showing spanning lines (dotted arrows) and the runway. Most of the spanning lines were nearly parallel with the long axis of the leaf (dotted arrows) except for those at the lower end of the runway; **B** close-up of lower end of runway with spanning lines from above (dotted arrows) ended where other strong non-sticky lines (solid arrows) converged on a central hub area (some of these bore zig-zag sticky lines); **C** the spanning lines and the zig-zag sticky lines attached to them were elevated above the leaf surface in the upper part of the web along both sides of the leaf. This web was first powdered, and then the leaf was jarred repeatedly to remove nearly all the powder from the non-sticky lines.
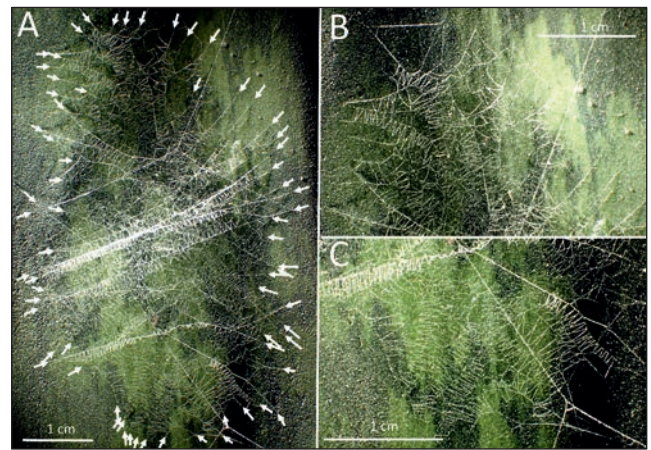
Fig. 6: The more radially symmetrical web of an immature female *Emblyna* sp. found in the field near the centre of a *Sanseviera* sp. leaf (rather than the more customary location near the tip) after 2–3 days without rain. **A** overview, with arrows marking the orientations of the strong non-sticky lines that reached the edge of the web; **B** close-up of the more or less planar upper edge of the web near the leaf surface; **C** close-up of the more or less planar lower edge of the web near the leaf surface.

upper margin was continuous with the floor (Fig. 4B). This hole was on the side opposite the prey capture web, suggesting that it functions as an emergency escape for the spider.

The *E.* sp. webs built in captivity on *S.* sp. leaves had several other consistent traits. Long, approximately parallel non-sticky spanning lines often formed part of a more or less planar prey capture sheet slightly elevated from the leaf's surface, and were composed of multiple strands that splayed apart where they were attached at multiple sites to the leaf (Fig. 7C). This sheet included cribellum lines that were frequently laid in zig-zag patterns between pairs of spanning lines. In some places the cribellum line was attached only once to the non-sticky line, forming a sharp zig-zag (Figs. 3C, 4C–D); more often it was attached more than once, making a blunt zig-zag (Figs. 4D 5B). Additional thin, non-sticky lines were sometimes also present in the prey capture sheet, forming swaths of more or less parallel lines (Fig. 4C). In the upper portion of some webs, especially when the tip of leaf was not strongly curled, the roof of the retreat and the capture sheet were one and the same, and there were cribellum lines in this sheet (Fig. 4A).

Spanning lines were often oriented more or less longitudinally along the length of the leaf (Figs. 2A, 3A) below the site of the retreat, especially on leaves that were partially twisted or bent (Fig. 5A). All such elongate *E.* sp. webs had a tightly meshed runway of fine, more or less parallel, non-sticky lines that was apparently continuous with the retreat floor, extending toward the base of the leaf (Fig. 3B, 5A–C). The runway was up to 5 cm long in webs of mature females. At the lower end of the runway, several long, non-sticky spanning lines diverged, forming a somewhat radial array (Figs. 3C, 5B); adjacent radial spanning lines often had zig-zag cribellum lines attached to them (Figs. 3C, 5A–B).

One exceptional web built near the middle of a straight *Sanseviera* sp. leaf with only a moderately weak transverse fold had a more nearly round outline (Fig. 6A). The spider rested near the centre of this web, in a retreat formed by a

Species	Radial array?	Retreat?	Sharp zig-zag sticky	Blunt zig-zag sticky	Planar?	Aerial?	Tips of branches[1]	Runway?	Reference
Arangina (= *Dictyna*) *cornigera* (Dalmas, 1917)	Yes[2]	Yes	Yes[2]	?[2]	Yes[3]	No[4]	No[4]	?	Marples 1959
Arangina spp.	Yes	Yes	Yes	?	?	No	No	?	Forster 1970
Archaeodictyna consecuta	Yes (some-what)	Yes	?	Yes[5]	Yes[6]	Yes	Yes	?	Nielsen 1932
Argyroneta aquatica (Clerck, 1757)	No	No	No[7]	No[7]	Yes[7]	No[7]	No[7]	No	Bristowe 1958
Ciniflo spp.	?	Tubular, hidden	?	?	On flat surfaces	No (on walls, trunks)	No	?	Bristowe 1958
Dictyna felis	No	?	?	?	Yes?[8]	No[6]	No (on leaf surfaces)	?	Shinkai 1979
Dictyna foliacea	No	No[9]	?	?	On flat surface	No?[6]	No (on leaf surfaces)	?	Comstock 1967
Dictyna latens	No	?	No[10]	No[10]	No	Yes	Yes	?	Nielsen 1932
Dictyna major Menge, 1869, *D. coloradensis*[11] Chamberlin, 1919	?	?	?	?	?	Yes	Yes	?	Smith, Emlen & Pearson 2016
Dictyna foliacia (= *sublata*) (Hentz, 1850)	Yes some-what	Yes (circular opening)	Yes	Yes	Approx.[12]	Yes/No[12]	Yes	?	Comstock 1967
Dictyna uncinata Thorell, 1856	No	?	?	?	Yes (flat surfaces)[13]	No	No	?	Nielsen 1932
Dictyna volucripes	Yes, some-what	Yes (tubular)	Yes[14]	Yes[14]	Weakly?	Yes/No[15]	Yes[15]	?	Emerton 1902; Comstock 1967; Blackledge & Wenzel 2001
Emblyna annulipes (Blackwall, 1846)	slightly	Yes	Yes	Yes	Yes[16]	Yes	Yes	No	Bradley 2013
Emblyna sp.	No[17]	Yes	Yes	Yes	Some	No	No	Yes	This study
Mallos blandus, M. pallidus	?	?	?	?	?	?	No[18]	?	Bond & Opell 1997, Fig. 1
Mallos gregalis (colonial)	No?[19]	Tunnels and chambers	?	?	No	Yes	Yes?	Papery areas beneath surface	Tietjen 1986
Mallos hesperius	No	Yes	Yes	Yes	Some	No	No	Yes	This study
Mallos niveus O, Pickard-Cambridge, 1902, *M. dugesi* (Becker, 1886)[20]	Yes	Yes	Yes	?	Yes	Yes	Yes[21]	No?[22]	Bond & Opell 1997
Mallos spp[23]	Yes	Some	Yes?	Yes	?	?	?	?	Bond & Opell 1997
Mexitlia trivittata	Yes	Yes	No[24]	No[24]	Yes[25]	Yes	Yes[26]	?	Bond & Opell 1997, Opell 1999
Paradictyna spp.	?	No[27]	No (irregular sheet web)	?	Yes?[8]	No[6]	No (on leaf surface)	?	Forster 1970

Table. 1: A tentative summary of web traits in the family Dictynidae. Almost all characterizations are based on only a single data point (often a photograph). The only explicit data on intra-specific variation (Emerton (1902) on *D. volucripes*, Nielsen (1932) on *D. arundinacea*, the present study) suggest high intra-specific variation.

Notes: [1] I know of no statistical demonstration of a preference for the tips rather than more basal portions of plant stems, despite repeated published statements to this effect. [2] web has a ladder design; it was not clear whether the zig-zags were sharp or blunt. [3] "construction of the ladders transverse to a line from the retreat to the margin of the web", but "the upper and lower sheets appear to diverge more often and the retreat is not so obviously a centre of construction". [4] among gravel and rocks in flood bed of river, with retreat under large pebble; aerial nature of web uncertain. [5] clear in figs. 44 of Vol. I, and 116 and 117 of Vol. II of Nielsen (1932). [6] on curved leaf surface. [7] domed sheet built underwater, with no cribellum lines; the sheet functions to hold an air bubble, not as a snare. [8] the strong "horizontal" lines span the parallel edges of a longitudinally curved leaf, so at least these lines were probably approximately planar. [9] spider on surface of web in photo. [10] small loops along vertical foundation lines (apparently similar to *Mexitlia trivittata*). [11] based on one photo with about 50 webs visible; both species were present, but were not distinguished in this study. [12] the web at the tip of small branches in fig. 266 is *D. sublata*; webs were close to flat substrates like windows (Comstock 1967). [13] near grooves in board fences. [14] It was not possible to distinguish sharp from blunt in the web photographs. [15] Emerton (1902) mentioned both walls and the tips of plants. [16] multiple planes around central retreat. [17] except vaguely radial spanning lines at bottom of runway. [18] This categorization is uncertain: webs of both species were described as "built on the tops of *Quercus* leaves" (Bond & Opell 1997: 394); the web in Fig. 1A was not, however, associated with a leaf surface. [19] apparent spanning lines on the outer surface of the communal web were used as walkways by spiders. [20] web forms varied substantially intra-specifically; I have followed the verbal description of "a typical *Mallos* web" and photos of *M. niveus* and *M. dugesi* webs from Bond & Opell (1997); these authors also reported *M. bryanti* webs at the tops of grasses. [21] or near the tips of blades of grass. [22] not distinguishable in photos. [23] The text of Bond & Opell (1997: 393) described a "typical *Mallos*" web without specifying the species. These "typical" traits are listed in this row; the traits visible in web photos of particular species from this same study (which do not all match this "typical" description) are given in other rows in this table. [24] cribellar threads were "deposited in a looped fashion [on long support lines] reminiscent of *Miagrammopes*" (apparently similar to *D. latens*) (Bond & Opell 1997: 394). [25] planar nature not mentioned in verbal description, but seems apparent in web photo. [26] based on one photograph; another, apparently communal web (borders between webs were not mentioned) was "inside [the] corrugated walls of the culvert were covered with webs of hundreds of *M. trivittata* …" (Bond & Opell 1997: 394). [27] rests "on the surface of the leaf not on the web itself".
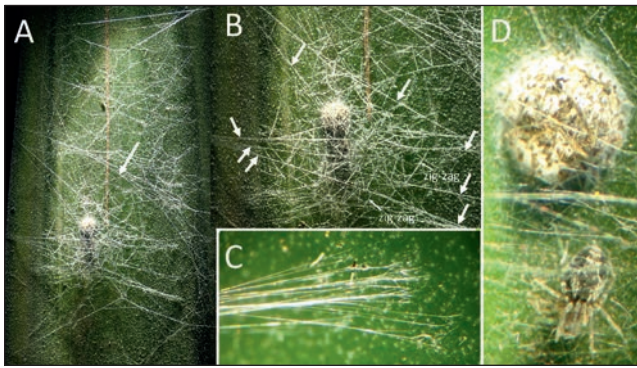
Fig. 7: Details of webs and an egg sac of *Emblyna* sp. in captivity. **A** overview of the egg sac and web built below the lower edge of a previous web; **B** close-up of the egg sac web with spanning lines (arrows) and zig-zag sticky lines attached to them; **C** detail of how the fine lines in a spanning line splayed apart where they were attached to the leaf surface; **D** close-up of the spider and her sac, with small pieces of dark detritus incorporated in the smooth surface of the sac.

Fig. 9: Close-up views of a two day-old web of a mature female *Mallos hesperius* built on a vertical leaf in captivity. **A** view from above, showing the curved sheet of non-sticky lines near the leaf surface (floor), the denser sheet spanning the fold in the leaf (roof), and the spider resting on the floor; **B** non-sticky (solid arrow) and cribellum silk (dotted arrow) lines connecting the floor with the roof; **C** lateral view of the spider resting on the floor and the central dense portion of the roof; **D** close-up of prey capture sheet of another web in which most powder had been removed from non-sticky lines, showing zig-zag sticky lines and bundles of fine non-sticky lines; **E** close-up of lines in this same web seen under a dissecting microscope that included non-sticky and cribellum lines; **F** a closer view of one cribellum line, showing the scalloped edges of the mass of cribellum fibers and the shining curly reserve warp line in the center of the mass. The web was unpowdered except in B.

densely meshed roof and floor of non-sticky lines near the surface of the leaf; there was no clear escape hole to the outside. Several more or less horizontal spanning lines ran across the fold of the leaf, and bore zig-zag cribellum silk lines. Above (Fig. 6B) and below (Fig. 6C) this central area there were approximately planar and somewhat radial arrays of non-sticky lines nearer to the leaf's surface, and these bore dense arrays of zig-zag sticky lines. The relationship of these upper and lower sheets with the roof and floor was not clear. This web may have been the result of several days of building activity, as there had been no rain during the previous 2–3 days.

In some cases it was possible to determine the direction the spider had been moving while laying a cribellum line by noting sites where the mat of cribellum fibrils became narrower just following an attachment to a spanning line (Fig.

4D) (similar narrowing occurs when an uloborid leaves a radius just after having made an attachment) (Eberhard 2019, in press). In 18 such zig-zag lines the spider was moving toward the retreat in 78%, and away from the retreat in 22% of the cases ($\chi^2 = 5.6$, df = 1, p < 0.05). It was not possible to make confident deductions for most attachments, however.

One spider built an egg sac in captivity, below the lower edge of a prey capture web that she had constructed the day before (Fig. 7A). She built new lines over the sac that included both spanning lines and zig-zag cribellum lines (Fig. 7B). There were multiple bits of dark detritus on the smooth external surface of the sac (Fig. 7D).

Mallos hesperius

Spiders were found on the surfaces of horizontal or upwardly directed leaves of plants with large, stiff, and at least slightly concave leaves, including *Agave attenuata* and *Yucca guatemalensis* (both Agavaceae) (Fig. 1B), and *Crinum* sp. (Amaryllidaceae). In captivity, spiders built webs on similar leaves and, in one case, across the shallow fold at the central vein of a *Philodendron* sp. (Araceae) leaf that was oriented approximately vertically (Figs. 8–11).

Although webs varied substantially (especially comparing those built in the field with those built from scratch in captivity) (e.g. Fig. 11), they had several consistent traits. The spider rested in the small space between a sparse curved sheet very close to the leaf surface (floor in Fig. 9A–C) and a denser roof (Figs. 9C, 10A,C). There were numerous long, strong, non-sticky spanning lines that were often approximately parallel to each other (Figs. 8, 11B,D). These were attached to the leaf on either side of the central vein, and

Fig. 8: A view perpendicular to the plane of a powdered two day-old web built by a mature female *Mallos hesperius* on a vertical fragment of a leaf in captivity. The right side of the web was slightly farther from the leaf surface because the leaf curled more sharply. The sticky cribellum lines are thicker than non-sticky lines due to greater accumulations of talcum powder. Most sticky lines were in the planar capture sheet, but a few zig-zag sticky lines near the bottom margin of the web were closer to the leaf.

Fig. 10: Close-up views of webs of the mature female *M. hesperius* in Fig. 8. **A** the abrupt transition between the roof on the left, with its dense mesh of lines with no geometrically consistent orientations, and the rest of the capture sheet; **B** close-up showing how long spanning lines consisted of multiple thinner lines that splayed apart where they were attached separately to the leaf surface; **C** the zig-zag lines of cribellum silk on the prey capture sheet, with the spider and her egg sac below; **D** a mass of bluish silk covered the lumpy surface of the white egg sac seen under a dissecting microscope.

Fig. 12: Views of a mature female *Mallos hesperius* combing cribellum silk onto the surface of an egg sac. **A** dorso-posterior view; **B** somewhat more latero-posterior view, showing how the tip of the tarsus of her combing leg IV rested on the other, supporting leg IV, and how her spinnerets were spread (traced from a video recording).

supported a large and approximately planar capture sheet farther from the leaf surface (Figs. 8, 9A, 10A). At least some spanning lines were composed of multiple fine lines (Fig. 9D) that splayed apart where they were attached to the leaf (Figs. 7C, 8, 10B). A few short lines, including both cribellum and non-sticky lines, connected the floor to the prey capture sheet and the roof (Fig. 9B). The long spanning lines were stiff when I broke them, and I sensed a distinct snap each time I broke one by pulling on it. In contrast with the drag lines of araneid spiders, broken spanning lines did

Fig. 11: Overviews of a field web of an *M. hesperius* that was found on a leaf of *Yucca guatemalensis* the day after a rain (A, B), and the smaller, (somewhat less heavily powdered) web built by the same spider on a clean leaf of the same species after a single day in captivity (C, D). **A** overview of field web; **B** close-up of upper portion of field web (which had a roof and a floor that are not clear in the photo), showing many long supporting lines (dotted arrows), and sparse zig-zags of sticky lines (solid arrows). Most spanning lines were either approximately perpendicular to the longitudinal axis of the leaf or at an angle of about 45° to it; **C** overview of the web built after one day in captivity, showing long, approximately parallel spanning lines (dotted arrows); **D** close-up showing several spanning lines and swaths of fine, short, approximately parallel non-sticky lines (solid arrows) in the prey capture sheet; there were few sticky lines.

not collapse or curl up on themselves or ripple in weak air currents. Spanning lines were not nearly strong enough to bend the stiff leaves on which webs were built.

In webs built on more deeply curved leaves (e.g. Fig. 11), the roof was below, and largely separate from, the prey capture sheet. On a flatter leaf it formed the part of the central area of the prey capture sheet, and was directly dorsal to the spider where the sheet of non-sticky lines was especially densely meshed (Fig. 8). In one case, the roof was slightly larger in diameter than the spider, and extended about a body length below her, slightly elevated from the leaf surface (Fig. 8). There were some cribellum lines on the surface of this central dense sheet (Fig. 8). The rest of the prey capture sheet extended beyond the edges of this central sheet in different directions; the overall shape varied in different webs. The sheet included strong, non-sticky spanning lines, cribellum lines that formed zig-zag patterns (Figs. 8, 9D) (at least in some places), and swaths of additional thin, non-sticky lines (Fig. 9D, 10A, 11D) whose density varied.

Cribellum lines in a fresh web proved on close examination to have a mat of cribellum fibrils whose margins were scalloped, and a central, shiny, curly, reserve warp line (Eberhard & Pereira 1993) (Fig. 9E, F). In 7 cases in which it was possible to determine the direction the spider had been moving when producing a zig-zag sticky line, she was moving toward the retreat in 71%, and away from it in 29% of the cases.

One spider in captivity laid a white, flattened, paper-like egg sac that was attached broadly to the leaf surface and whose outer surface had bumps corresponding to the outlines of the eggs within (Fig. 10C, D). Seen from the side, the surface of the sac was covered with a thick, bluish mass of silk (Fig. 10D) that resembled cribellum silk but no curly reserve warp lines were seen.

Video recordings of one spider combing silk from her cribellum onto the capture sheet and onto the surface of an egg sac showed that the tarsus of the leg IV that combed silk from the cribellum was bent so that its tibia was near the cribellum and the tip of its tarsus rested on the tarsus of the

Taxon	Point where supporting leg is contacted by combing leg	Point on combing leg that contacts supporting leg	Legs cross?	Reference
Mallos hesperius (Dictynidae)[a]	Basal tarsus	Tip of tarsus	No	Present study
Uloborus diversus (Uloboridae)	Metatarsus	Tip of tarsus	No	Eberhard 1988
Zosis geniculata (Uloboridae)	Metatarsus	Tip of tarsus	No	Eberhard 1988
Tengella radiata (Kulczynski, 1909) (Zoropsidae)	Distal metatarsus	Tarsus(?)	Yes	Eberhard 1988
Stegodyphus sarasinorum (Eresidae)	Basal metatarsus	Tarsus	No	Eberhard 1988
Psechrus ca. *torvus* Bayer, 2012 (Psechridae)	Metatarsus	Metatarsus or tarsus	Yes	Eberhard 1988
Psechrus sp. (Psechridae)	Distal metatarsus	Tarsus	Yes (?)	Griswold *et al.* 2005
Oecobius concinnus (Oecobiidae)	Distal metatarsus	Tip of tarsus	No	Solano-Brenes 2018, pers. comm.
Austrochilus forsteri Grismado, Lopardo & Platnick, 2003 (Austrochilidae)	Base of tarsus	Tip of tarsus	No	Griswold *et al.* 2005
Badumna sp. (Desidae)	Distal metatarsus	Tip of tarsus	No	Griswold *et al.* 2005

Table 2: Points of contact between combing and supporting legs IV when silk is combed from the cribellum.

Note: [a] In the drawing of Bristowe (1958), the dictynid *Ciniflo similis* differed from *M. hesperius* in having the combing tarsus resting on the metatarsus rather than on the tarsus of the supporting leg, and the posterior lateral spinnerets were directed posteriorly rather than spread. It is uncertain, however whether the drawing was made from a photograph and can be trusted for these minor details.

other, supporting leg IV (Fig. 12). Both legs IV moved rapidly backward and forward in synchrony. At some moments the legs appeared to make on the order of 10–15 brushing movements per second, but the movements were too rapid to determine the frequency confidently. Both the anterior lateral and the posterior lateral spinnerets were spread wide during combing behaviour (Fig. 12); I was not able to distinguish periodic medial closing movements of the posterior lateral spinnerets in the videos, as occurred in the uloborids *Uloborus walckenaerius* (Peters 1984) and in similar video recordings of *Zosis geniculata* (Eberhard in press).

Spiders attacked prey by running to them from the retreat and biting them. The prey ceased struggling within a minute or two, and the spider then dragged it backward to the retreat. Spiders did not wrap prey during or following attacks; they sometimes walked under silk lines, sometimes on top of them.

Discussion

Comparisons with other dictynids

Several of the web structures described here have not, to my knowledge, been noted previously in dictynid webs: a tightly meshed retreat of non-sticky lines with a floor, a roof, and an escape hole; more or less parallel spanning lines that form part of a more or less planar prey capture sheet; a runway of fine, non-sticky lines from the retreat to distant portions of the prey capture sheet; additional swaths of fine, non-sticky lines in the prey capture sheet that in some cases are more or less parallel with each other; and the cable-like nature of spanning lines that are composed of multiple fine lines that splay apart where they are attached individually to the substrate. The zig-zag patterns of cribellum silk lines (ladders) that often ran between pairs of long straight non-sticky lines are, in contrast, typical of the webs

of other dictynids (Table 1). Although direct observations of behaviour are still lacking, the ladder pattern suggests that a pair of non-sticky lines is laid first, followed by sustained cribellum silk production, with the spider often though not always moving inward from the periphery of the web, and that the cribellum line is attached at relatively regularly spaced to these two non-sticky lines. A second similarity with other dictynids was the gradual addition of lines to their webs over multiple nights, as in *Dictyna volucripes* (Blackledge & Wenzel 2001) and *M. gregalis* (Simon, 1909) (Tietjen 1986). These similarities and differences occur in comparisons in intra-generic comparisons of species in both *Emblyna* and *Mallos* (Table 1). Except for *Argyroneta*, currently available data suggest that the details of web designs are relatively uniform and evolutionarily flexible in dictynids.

Probably some of the most distinctive characteristics of *E.* sp. and *M. hesperius* webs are consequences of their being built against the surfaces of large, stiff, slightly curved leaves of a taxonomically diverse set of plant species. The nearly planar shapes of these leaves imposed an approximately planar form on the spiders' webs. The leaves also apparently affected the overall form of the web, as illustrated comparing the elongate forms of *E.* sp. webs that had a retreat very near the tip of a *S.* sp. leaf (Figs. 2–3, 5) with the rounded outline of a web of the same species built in the central portion of a *S.* leaf (Fig. 6). More systematic observations will be needed, however, to document the effect of leaf shape on web shape. Substrate form has also been thought to have strong effects on web form in other dictynids (Bond & Opell 1997). It is conceivable that the runways of *E.* sp. were not original design features but, instead, accumulations of drag lines laid as the spider moved on its finished web; this doubt emphasizes the need for direct observations of building behaviour.

This flexibility in design may account for the apparent lack of match between the pattern of differences among dic-

Taxon	Planar web	Radial non-sticky lines	Regular array sticky lines	Spiral array of sticky lines	Sticky zig-zag	Silk Hub	Retreat in substrate	Aerial hub	Frame lines
Typical orb weavers (Uloboridae and Araneoidea)	Yes	Yes[1]	Yes	Yes	Yes[2]	Yes	No	Yes	Yes
Oecobius conccinus (Oecobiidae)	Yes	Yes[3]	Yes[4]	Yes[4]	No	Yes	No[5]	No	No
Nurscia albomaculata[6] (Titanoecidae)	Yes	Yes (strongly branched)	Moderate	No	Yes	Yes/?	Yes	No/?	No
Fecenia spp. (Psechridae)	Yes	Yes (strongly branched)	Yes	Yes	Yes	Yes	Yes[7]	Yes	Yes
Matachia livor[8] (Desidae)	Yes	Yes (branched)	Yes	No	Yes	Yes	Yes	No	No
Synotaxus spp. (Synotaxidae)	Yes	No	Yes	No	Yes	No	No	No	Yes
cf. *Anarrhotus* sp. (Salticidae)	Yes	Yes	No sticky lines	-	-	Yes	No	Yes	No
Mallos hesperius (Dictynidae)	Yes (varied)	No	Moderate	No	Yes (at least some)	No[9]	No	No	No
Emblyna sp. (Dictynidae)	Yes (varied)	Mostly no[10]	Moderate	No	Yes (at least some)	Yes[11]	No	No	No

Table 3: Orb-like traits in the webs of the following para-orb taxa (names followed by references in parentheses): *Oecobius cocinneus* (Solano-Brenes, Miranda & Barrantes 2018); *Nurcia* (= *Titanoeca*) *albomaculata* (Szlep 1966); *Fecenia* spp. (Robinson & Lubin 1979; Zschokke & Vollrath 1995; Murphy & Murphy 2000; Bayer 2011; Agnarsson *et al.* 2012; Blackledge *et al.* 2012); *Matachia livor* (Opell 1999; Griswold *et al.* 2005); *Synotaxus* spp. (Eberhard 1977, 1995); cf. *Anarrhotus* (Hill *et al.* 2019); *Mallos hesperius* and *Emblyna* sp. (present study).

Notes: [1] branched in some groups but not others. [2] often at least some zig-zags (turn backs in the spiral) when the orb is asymmetrical. [3] radial lines have branches that are relatively small with respect to total length. [4] sticky lines clearly relatively circular; spiral organization less certain. [5] retreat in silken tent on exposed surface. [6] *N. albofasciata* (Strand, 1907) (= *T. nipponica*) (Shinkai & Takano 1984) and another titanoecid *Goeldia* sp. (Griswold *et al.* 2005) also have moderately regularly arranged sticky lines; a web of *G.* sp. had zig-zag patterns of sticky lines, and an approximately radial pattern of non-sticky lines around a sheltered retreat. [7] retreat in curled leaf suspended in web. [8] the web of *Matachia* sp. figured in (Griswold *et al.* 2005) is similar in all respects mentioned here. [9] floor of web on which spider rests is not part of the planar prey capture web. [10] except in somewhat radial lines at the bottom of the runway in elongate webs, and in more nearly circular webs near the middle of a leaf. [11] radial organization weak

tynid webs in Table 1 and the taxonomic affinities of the species. For instance, in both *Mallos* and *Dictyna*, some species built aerial webs while other congeners built leaf webs; the two species with loops of sticky silk on long non-sticky lines were in different genera: *Mexitlia trivittata* (Banks, 1901) and *Archaeodictyna consecuta* (O. Pickard-Cambridge, 1872) (= *Dictyna latens*). As suggested by the lack of strong phylogenetic patterns, it is possible that some of the differences between the species of this study and other dictynids may due only to the lack of detailed studies rather than to true differences.

In particular, I speculate that other dictynid species that apparently build leaf webs, such as *Dictyna foliacea*, *D. felis*, and *M. blandus* (Table 1), may also share web traits with the species of this study, including similarly approximately planar webs and spanning lines with zig-zag cribellum lines attached to them. Photographs of the webs of *Dictyna foliacea* (Comstock 1967) and *D. felis* (Shinkai & Takano 1984) showed that the spider apparently rested on the surface of a large leaf rather than in a protected retreat near a stem or a fork in a stem, and that the prey capture lines were very near the surface of the leaf. The lack of previous descriptions of dictynid leaf webs may be due (at least in part) to the difficulty of seeing the details of these small spiders' webs without first coating their webs with powder.

The frequently planar or nearly planar nature of the array of spanning lines in the capture sheets of *M. hesperius* and *E.* sp. webs probably resulted from the fact that the gently curled edges of a leaf defined an approximate plane. When a leaf had more substantial relief (e.g. a bend, or a deeper valley between the curled edges), the web was less planar and more three-dimensional (Figs. 5, 11).

A important possible limitation of the data on web forms in this study is that webs may also occur on other plant species where I did not search. The spiders are small and inconspicuous, and neither species was associated with any particular species of plant. Because leaf forms very likely influenced web designs, the bias in my searches could have biased the web designs that I found. For instance, the lack of runways in the webs of *M. hesperius* may have resulted from my having only found webs of this species on leaves that were not as narrow as those where I found *E.* sp. More precise measurements of leaf forms and a larger sample of webs will be needed to test for possible additional designs not described here, and to quantify substrate effects on web designs.

Dictynid webs are often thought to be long lived (e.g. Korenko (2017) on *Dictyna pusilla* Thorell, 1856). Surely this is true in many species, especially those that live in relatively dry habitats where webs are not damaged by rain; here they often accumulate large amounts of dust and detritus (e.g. Fig. 1A; Bond & Opell 1997). In contrast, the webs of the two species of this study were often largely destroyed (especially the cribellum lines) by rain. Most sticky lines in the webs of both species in the field were probably renewed every few days, at least during the rainy season. This observation, combined with observations of substantial additions to webs by *D. volucripes* over the space of several days webs in captivity (Blackledge & Wenzel 2001) imply a greater level of dynamism than has usually been associated with many non-orb webs (Eberhard in press).

Leg positions during combing

The ways that one leg IV supports the other leg while it is combing out cribellum silk from the cribellum vary in different families according to their phylogenetic affinities (Eberhard 1988; Griswold *et al*. 2005) (Table 2). The positions and movements of legs IV of *M. hesperius*, as expected from recent phylogenies (Garrison *et al*. 2016; Dimitrov *et al*. 2017), were similar to those of other derived cribellate species. Observations to date have concentrated only on specifying which leg supports the combing leg and whether this supporting leg moves during combing. Table 2 suggests, however, that additional details such as which portions of legs IV contact each other during combing may constitute as yet unexploited sources of phylogenetic information. Further observations are needed.

Egg sacs

The filistatid *Kukulcania hibernalis* (Hentz, 1842) (Barrantes & Ramírez 2013) and the uloborids *Uloborus diversus* Marx, 1898 and *Zosis geniculata* (Olivier, 1789) (Eberhard unpublished) resemble *M. hesperius* in placing cribellum silk on the outer surfaces of their egg sacs. Presumably these sticky lines function to defend against egg predators or parasites. The apparent absence of reserve warp lines in the egg sac cribellum silk of *M. hesperius* may be unusual; this detail has not been checked in the egg sacs of other species. I know of no other species in which mats of cribellum silk are known to lack reserve warp lines (Griswold *et al*. 2005; Opell 2012).

The egg sac web built by *E*. sp. included two recognizable patterns of lines present in prey capture webs: spanning lines and zig-zag cribellum lines. These similarities emphasize the functional flexibility of these types of lines.

Other para-orbs

Comparisons with the orb-like para-orb webs of other, distantly related spider taxa (Table 3) show how several of the orb-like traits in *M. hesperius* and *E*. sp. webs have evolved convergently, but in different combinations, in other taxa. With the possible exception of zig-zag sticky lines, which are known from other dictynids (Table 1), as well as several other cribellate groups such as the austrochilid *Thaida peculiaris* Gertsch & Zapfe, 1955 (Griswold *et al*. 2005), the gradungulid *Progradungula otwayensis* Milledge, 1997 (Michalik *et al*. 2019), the eresid *Stegodyphus sarasinorum* Karsch, 1892 (Eberhard 1988), and the phyxelidid *Xevioso orthomeles* Griswold, 1990 (Griswold *et al*. 2005), outgroup comparisons suggest that the para-orb design features listed in Table 3 evolved independently of each other. This combination of diversity and repeated convergence is common in spider webs in general (Eberhard in press), and presumably stems from the long evolutionary history of spider prey capture webs that contain sticky lines. The orb web design trait that is least often

found in para-orbs is frame lines; they are shared with only *Fecenia* spp. para-orbs (Table 3). The secondarily derived omission of frame lines observed in orbs built in small spaces (Eberhard in press) suggests that frame lines in para-orbs may be associated with relatively aerial webs.

Acknowledgements

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The sexual behaviour of the Neotropical wolf spider *Lycosa inornata* (Araneae: Lycosidae), with comments on maternal behaviour

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Abstract

Lycosa inornata Blackwall, 1862 is a small wolf spider that inhabits open environments from Uruguay and, like other wolf spiders, little is known of their sexual behaviour, which we describe here. Male courtship behaviour includes leg rubbing, leg vibration and pedipalp drumming, as well as leg waving. Females respond to male courtship by running towards them and shoving them with her legs and body. Receptive females lower their body on the substrate and slightly raise and twist the abdomen, facilitating the mounting and subsequent pedipalp insertions. Copulation lasts less than an hour, has two behavioural copulatory patterns and one haematodochal expansion per pedipalp insertion, in turn intercalated by pedipalp chewing. Pattern I consists of several insertions with the same pedipalp before a side change. Pattern II consists of a single pedipalp insertion before a side change. Females construct a single egg sac within 40–45 days after copulation and an average of 65 spiderlings emerge after 35 days. As occurs in other species of lycosid, *L. inornata* presents a low rate of sexual cannibalism. This study adds to the few descriptions of sexual and reproductive behaviours in wolf spiders and we hope it will increase knowledge of this diverse family of spiders.

Keywords: copulation • courtship • offspring • Uruguay

Introduction

With approximately 224 species known to date, the genus *Lycosa* Latreille, 1804 is one of the most diverse within the Lycosidae family (World Spider Catalog 2019). However, little is known about the sexual behaviour and copulatory patterns of most of the species (Stratton *et al*. 1996; Dolejš, Kubcova & Buchar 2010). Recently, Castro-O'Neil (2010) recognized seven valid species of this genus in Uruguay: *L. auroguttata* (Keyserling, 1891), *L. carbonelli* Costa & Capocasale, 1984, *L. erythrognatha* Lucas, 1836, *L. inornata* Blackwall, 1862, *L. passerina* Mello-Leitão, 1941; *L. poliostoma* (C. L. Koch, 1847), and *L. thorelli* (Keyserling, 1877). However, we only know the courtship and copulatory patterns of two of them: *L. carbonelli* and *L. thorelli* (Costa & Capocasale 1984).

Lycosa inornata is a small lycosid which occurs in Brazil and Uruguay (Castro-O'Neil 2010; Aisenberg, Toscano-Gadea & Ghione 2011; World Spider Catalog 2019). The species is characterized by moderate sexual dimorphism, with an average body length of 13 mm in males and 15 mm in females. Both sexes have a dark brown colour on the body, becoming darker in the males towards the anterior of the cephalothorax. In the males the chelicerae, and the ven-tral part of the coxae, and trochanters of the first and second pair of legs are dark, this colouration is absent in females. The abdomen of all individuals has an arrow-shaped design pointing towards the anterior (Aisenberg, Toscano-Gadea & Ghione 2011).

The biology of the species is nearly unknown but, like other species of Lycosidae, *L. inornata* is closely linked to open pasture environments (Jocqué & Alderweireldt 2005; Aisenberg, Toscano-Gadea & Ghione 2011). This species is active during the night, and it is possible to observe the females at the edge of pastures capturing prey during the warm months (November–March). The males are very agile and walk easily on the grass. It is common to find them in sympatry with *L. thorelli*, *L. carbonelli*, and other Uruguayan wolf spiders, such as *Schizocosa malitiosa*, *L. poliostoma*, and *L. erythrognatha* (Toscano-Gadea personal observation).

The objective of our study is to describe, for the first time, the courtship and copulation of *L. inornata*. With this information we contribute to the knowledge of the reproductive behaviour of this family and help to clarify the relationship between the different species of wolf spiders.

Material and methods

We collected 50 juveniles of *L. inornata* during November and December 2016, in Villa Serrana, Department of Lavalleja, Uruguay (34°19′26.68″S 55°19′07.43″W). All spiders were collected at night using headlamps. In the laboratory, the spiders were housed individually in Petri dishes (diameter 9.5 cm, height 1.5 cm) with a thin layer of sand as substrate and a piece of cotton soaked in water. We fed all individuals twice a week with a mixed diet of mealworm larvae (*Tenebrio molitor* Linnaeus, 1758, Coleoptera: Tenebrionidae) and cockroaches (*Blaptica dubia* Serville, 1839, Blattodea: Blattellidae). The individuals were monitored daily to determine the exact date they reached adulthood. We used only virgin males and females and, with the exception of cases in which females cannibalized males prior to copulation, we did not reuse individuals. Room temperature and humidity during breeding and trials was (mean ± SD) 25.0 ± 1.3 °C, range 23–26.5 °C, and 56.9 ± 6.9 %, range 50–71 %, respectively, and the photoperiod was 12:12 h light:dark.

For the trials, we used square glass containers (15 × 15 × 5 cm, L × W × H), with sand and soil as the substrate and a container with water. Females were placed in the arenas 48–72 h before each trial for the deposition of draglines, which have chemical signals for sexual encounters (Costa 1979; Costa & Capocasale 1984; Foelix 2011). Females and males were selected randomly. Males were carefully placed in the arena on the opposite side from the females. All the trials were performed between 1000–1600 h, in the absence of sunlight and under a 40-watt red light located 50 cm from the containers. We video-recorded all trials with a Sony DCR-SR45 video camera with night-shot mode. The trials ended after the males dismounted or after 30 min if they did

Behaviour	Description	Sex
Stillness	Stay without movement.	♀/♂
Locomotion	Slow walking movements, alternating with motionless.	♀/♂
Contact	During courtship, the male touches any part of the female body and orientates towards her.	♂
Leg vibration	Horizontal agitation (at an angle of approximately 10°), parallel to the substrate but not touching it. This agitation is very fast and involves one or both legs I and II, or an alternate combination of each of them.	♂
Palpal drumming	Fast and alternating movements of the pedipalps against the substrate with variable frequency. This behaviour starts when the pedipalps contact the silk left by the female on the substrate.	♂
Leg vibration + palpal drumming	The male performs leg vibration and palpal drumming simultaneously. This unit can alternate with moments of stillness.	♂
Leg waving	Rapid rise and fall of both legs I, extended at an angle of 45°–60° with respect to the substrate.	♂
Rubbing	Ipsilateral alternate scraping of one leg against another, usually legs I against legs II, or legs II against legs III.	♂
Run	Male quick getaway after female push (see below). A few moments later, he resumes the courtship.	♂
Push	When the female detects the courting male nearby, she quickly runs and shoves him with her legs and body.	♀
Turn	Female orientation towards the approaching male courting.	♀
Leg blocking	The female raises legs I and blocks the male's attempt to mount her.	♀
Body lowering	Female lowers her body and touches the substrate, allowing the male to mount.	♀
Abdominal elevation	With the cephalothorax resting on the substrate, the female lifts and rotates her abdomen, allowing the male to climb on her body.	♀
Attack and cannibalism	The female pounces on the courting male, killing and consuming him.	♀
Mounting	Male climbs on the female's back, placing himself in the opposite direction of the female, as occurs in the typical copulatory position of wolf spiders.	♂
Palpal insertion	Introduction of the embolus in one of the female genital openings. During each insertion, the haematodocha of the pedipalp expands (ejaculation) and the spines of the hind legs become erect.	♂
Palpal chewing	Pedipalp moistening movements performed by the male in between palpal insertions.	♂
Side change	The male switches the pedipalp to insert in the other female genital opening. When inserting the left pedipalp , the male leans to his right side, surrounding the female abdomen with the left front leg and separating the fourth female leg with his other front leg. When the right pedipalp is inserted, the reverse arrangement occurs.	♂
Abdominal vibration	Fast shaking of the abdomen during copulation that occurs axial (from one side to another) and sagittal (up and down), alternately.	♂
Palpal rubbing	The male performs a series of rapid movements with the free pedipalp (the one that is not inserted in the epigyne), touching the area near the epigyne, female's legs II–III, and cephalothorax.	♂
Pseudo-locomotor movements	Legs movements when the male is still mounted on the female but close to dismounting. Movements are as if walking but staying on the female.	♂
Dismounting	The male descends from the female's back, followed by a quick escape.	♂
Catalepsy	Permanency without any movement after male dismounting.	♀

Table 1: Description of the behaviours performed by *Lycosa inornata* during courtship and copulation.

not copulate. We used JWatcher software (Blumstein, Evans & Daniel 2000) to analyse the occurrences and durations of the behavioural units. All statistical analyses were performed with the PAST program (Hammer, Harper & Ryan 2003). The Shapiro-Wilk and Levene tests were used for analysing normality and homogeneity of variance, respectively. To compare the behavioural characteristics between both copulatory patterns (duration, number of insertions and side changes) we used the parametric Student's t-test (non-paired samples) and non-parametric Mann-Whitney U-test (non-paired samples).

Male ages during the trials averaged 12.8 ± 4.7 days after the last moult, whereas the corresponding female ages were 11.9 ± 8.0 days. We recorded courtship latency (period between male placement in the arena and the occurrence of first courtship unit), courtship duration (from first courtship behaviour to mounting), copulation duration (from mounting to dismounting), number of pedipalp insertions and number of side changes. We removed the male immediately if the female attacked him. Voucher specimens were deposited at the Arachnological Collection of Facultad de Ciencias, Montevideo, Uruguay.

Results

We performed 32 trials during January 2016: 14 ended in copulation, 16 ended after 30 min without mounting, and the remaining two ended in sexual cannibalism during courtship. We analysed the sexual behaviour of the 14 successful couples and registered 24 behavioural units. A catalogue of the behaviours is shown in Table 1, and a flow chart of the courtship is shown in Fig. 1.

Courtship behaviour

Courtship lasted 10.6 ± 12.7 min (range 0.3–39.3). In all cases the males began the courtship once they touched the silk deposited on the substrate by the females. Courtship involved the movement of several legs and the pedipalps at the same time. Generally, males started courtship vibrating their legs (leg vibration) (Fig. 2) and scraping them together (rubbing). These behaviours are followed by pedipalp drumming (palpal drumming) (Fig. 3). Leg vibration and palpal drumming occured at the same time as the courtship advanced (leg vibration + palpal drumming), and usually
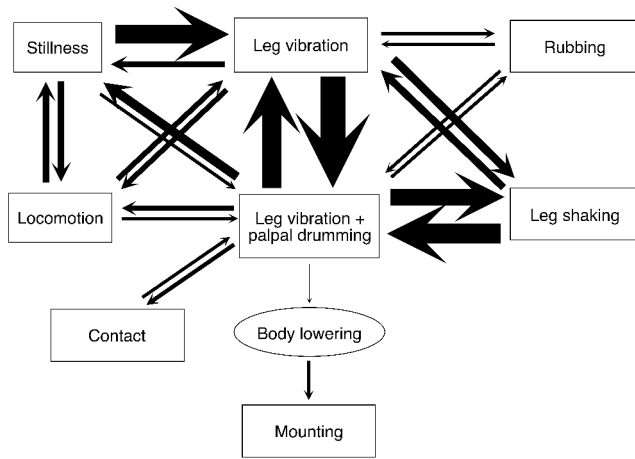
Fig. 1: Flow chart of courtship and copulation behaviours in *Lycosa inornata*. Male behavioural units within boxes and female behavioural units within ovals. Behavioural units that occurred less than ten times were not included in the diagram. 1 mm arrow thickness corresponds to 14 unit occurrences during courtship and copulation.

Fig. 2: Schematic representation of leg vibration behavioural unit performed by the male during courtship. Arrows show the movement of legs I.
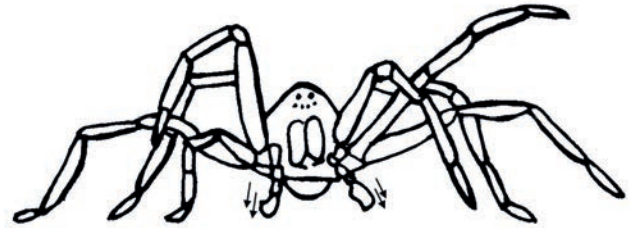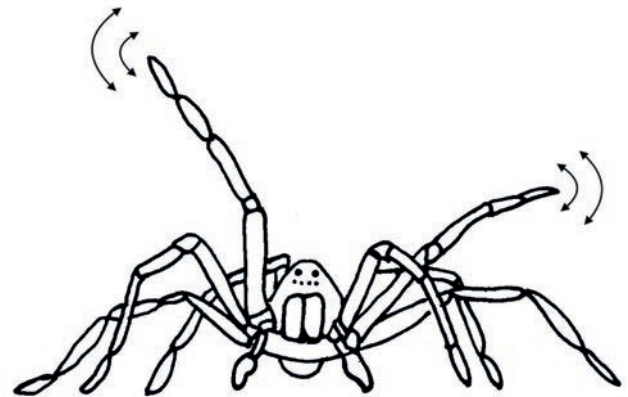

Fig. 3: Schematic representation of palpal drumming behavioural unit performed by the male during courtship. Arrows show the pedipalp movements.

Fig. 4: Schematic representation of leg waving behavioural unit performed by the male during courtship. Arrows show the movement of the legs.

alternated with their legs waving (Fig. 4). During courtship, some females remained motionless (stillness) or walked slowly (locomotion). The male only orientated his courtship towards the female when he was close to her (approximately 2–3 cm) and if she performed any movement. If the female remained still, the male usually continued courting and passed by her without detecting her presence.

In half the cases (n = 7) the females quickly pushed the male with her body during courtship (push), after which the male moved back and resumed courtship (run). In 12 cases (85.7 %), immediately before the male mounted the female, she pressed her cephalothorax onto the substrate (body lowering) and, in ten of these 12 cases, the female slightly elevated her abdomen and rotated it (abdominal elevation). Once she adopted this position, the male immediately climbed on the female's back (mounting). In two cases, the female adopted a different position, raising legs I and II and opening her chelicerae. The male responded to this behaviour by retreating but maintaining the courtship (waving legs I and II and performing pedipal drumming) and touching the female's legs with his legs I and II, before finally mounting her. We never observed females performing leg movements to guide the males prior to the mount, like those observed in *S. malitiosa* (Costa 1979) or *L. poliostoma* (González & Toscano-Gadea personal observation).

Mating

The copulatory position of *L. inornata* was the same as that observed in other species of Lycosidae, with the male on top of the female, both oriented in opposite directions (type 3, following Foelix 2011). Copulation lasted 52.0 ± 10.3 min (range 37.4–70.5); it had two consecutive behavioural patterns (patterns I and II), and typically one haematodochal expansion per pedipalp insertion. During mating, the male surrounded the abdomen of the female with his first pair of legs during a side change. The side change consists of an exchange in the use of pedipalps,

going from inserting in one of the female genital opening to the other. The second and third pairs of legs surround the middle part of the female's body while the fourth legs remained extended backwards. At the beginning of copulation, the male changed sides several times before performing the first pedipal insertion with haematodochal expansion, an indirect measure of sperm transfer (Rovner 1971; Toscano-Gadea & Costa 2016). During copulation the female remained immobile.

Pattern I consisted of an insertion in a genital orifice of the female with one haematodochal expansion (rarely two), removal of the pedipalp, pedipalp moistening movements (palpal chewing) and a new insertion of that pedipalp in the same female genital opening. After making a series of insertions with the same pedipalp, the male changed sides and started inserting the other pedipalp, repeating the series in the other female genital opening. The number of insertions per series declined gradually until pattern II began. Pattern II consisted of a series of single insertions with one pedipalp (and a single haematodochal expansion), side change and, again, a single insertion of the other pedipalp in the other female genital opening. Before the side change, males performed a series of rapid movements with the pedipalp that was not being used (the one that was not inserted in the

epigynum) rubbing the female's epigynum, as well as legs II and III and the end of the cephalothorax. Pattern II was maintained until the end of copulation. Sperm transfer was inferred by the expansion of the haematodocha and by the erection of spines of the male hind legs, both due to the increase of haemolymph pressure. Throughout mating, the male performed a series of rapid abdominal vibrations. The male also used the pedipalp not used in sperm transfer to quickly touch the side of the abdomen and the coxae and trochanters of legs III and IV of the female. As copulation proceeded, it was possible to observe silk coming out of the male spinnerets, which could touch the eyes and chelicerae of the female.

The duration of both patterns was similar: pattern I lasted 25.24 ± 6.1 min (range: 15.7–38.7), while pattern II lasted 26.4 ± 9.4 min (range: 13–40.1) (U = 93.5, P = 0.85). Males performed 199.7 ± 31.5 insertions (range: 146–245) during pattern I and 48.9 ± 22.4 insertions during pattern II, (range: 22–103), being significantly more in pattern II than in pattern I (U = 0.0, P < 0.001). The number of side changes during pattern I was 34.9 ± 9.9 (range: 54–24) and during pattern II was 41.6 ± 14.8 (range: 75–21), not showing significant differences between them (t = 1.42, P = 0.17). Ten males started insertions with the left pedipalp and four males started with the right pedipalp.

Before dismounting, males performed a series of pseudo-locomotor movements, as if walking but still mounted and surrounding the female with his legs III (Costa 1979), which ended when the male dismounted (4.0 ± 3.8 min; range: 2–15). After dismounting, six females (43 %) remained completely still (catalepsy) for 2.0 ± 0.9 min (range: 0.9–3.1).

Sexual cannibalism

We observed two cases of pre-copulatory sexual cannibalism; in both cases, the males were performing courtship behaviour prior to the female attack (attack and cannibalism). The attacks were similar to the push that the females perform prior to accepting copulation. No evident differences were observed in the courtship performed by the males that were attacked versus those that were not. One of the females had moulted to adulthood 12 days before, and copulated three days after having cannibalized the male. The other female had nine days of adulthood and copulated seven days after having cannibalized the male.

Maternal behaviour

All females constructed a single white and more-or-less spherical egg sac after copulation and all except one developed until spiderlings emerged from the egg sac. The average number of spiderlings was 65.8 ± 25.3 (range: 23–110). The period elapsed between copulation and construction of the egg sac was 43.5 ± 10.1 days (range: 29–62), while the period between construction of the egg sac and emergence of the spiderlings was 37.1 ± 8.4 days (range: 26–53). Once the spiderlings abandoned the egg sac, they climbed onto the female's abdomen. Females stayed with them until they dispersed (8.8 ± 2.7 days; range: 6–15). Under laboratory conditions, all the females died a few days after the spiderlings descended from their abdomen.

Discussion

Lycosa inornata shares many similarities in courtship behaviour with the other two reported sympatric *Lycosa* spiders: *L. thorelli* and *L. carbonelli*. However, it differs from them in the repertoire, sequence, and apparently also in the frequencies of behaviours. Additionally, the copulation behaviour differs from the other *Lycosa* species mentioned, but resembles that of the sympatric *Schizocosa malitiosa*.

The courtship performed by the males of *L. inornata* is similar to that described by Costa & Capocasale (1984) for *L. carbonelli*. Both species vibrate legs I and II, alternately or simultaneously, shake their forelegs, and rub legs. However, in *L. inornata*, males commonly start courting with leg vibrations, whereas *L. carbonelli* starts with pedipalp drumming (Costa & Capocasale 1984). Additionally, *L. inornata* males seem to perform more frequent and vigorous legs vibrations and leg waving (Toscano-Gadea & González unpubl.). Most of these behaviours have also been observed in *L. thorelli* but, in this last species, the male shows explosive displays with long periods of stillness, and a radical behavioural distinction between his courtship before and after contacting the female. Abdominal vibration during courtship, reported for *L. thorelli* and *L. carbonelli* (Costa & Capocasale 1984), is absent in *L. inornata*. As occurs in other Lycosidae, males of *L. inornata* initiate courtship behaviours only after finding female silken threads. This type of chemical communication is well known in other wolf spiders (Tietjen & Rovner 1982; Costa & Capocasale 1984; Roberts & Uetz 2005; Gaskett 2007; Baruffaldi *et al*. 2010; Uhl & Elias 2011).

The similarities between courtship behaviours of *L. inornata* and *L. carbonelli* could be an adaptation to the characteristics of the microhabitat they occupy. Both species are frequently found at the base of grasses, in direct contact with the substrate. Conspicuous courtships involving visual communication, such as the leg raising of *S. malitiosa* (leg waving according to Costa 1975), *L. poliostoma*, or *L. erythrognatha* (González & Toscano-Gadea personal observation), would not be effective in the microhabitat occupied by *L. inornata*. Nevertheless, behaviours like pedipalp drumming, leg vibration and rubbing could be much more effective under the environmental conditions of dense vegetation (Fernández-Montraveta & Simó 2002; Uetz, Clark & Roberts 2016). In fact, during our experiments we observed that the male could only orient the courtship towards the female after she pushed the male, or when she performed some movement at a short distance (less than 3 cm). These female pushes, in addition to orienting the male during courtship, could be a form of female choice based on male vigour, as occurs in *S. malitiosa* (Aisenberg & Costa 2005). The low level of conspicuous courtship shown by *L. inor-*

nata, as well as similarities in several other behaviours, seems to have much in common with lycosids of similar (small–medium) size, such as *L. carbonelli* and *L. thorelli*, which inhabit similar micro-environments (Costa & Capocasale 1984; Aisenberg, Toscano-Gadea & Ghione 2011). Performing less conspicuous courtships, smaller spider species could avoid predation from larger ones as suggested by Hallander (1970), Pruden & Uetz (2004), and Foelix (2011).

Unexpectedly, the copulation behaviours of *L. inornata* differed not only from the other sympatric *Lycosa* spiders but also from the behaviours reported for the *Lycosa* group in Stratton *et al.* (1996). However, it presents similarities with *S. malitiosa*. While in *Lycosa* species each insertion includes several haematodochal expansions, in *L. inornata* males perform one haematodochal expansion per insertion, as occurs in *S. malitiosa* (Costa 1979). Additionally, *L. inornata* also shares with *S. malitiosa* the occurrence of two copulatory patterns: pattern I, characterized by a series of several insertions per side, and pattern II, characterized by a series of one insertion per side but, unlike *S. malitiosa* (Costa 1979), the duration of both patterns is similar in *L. inornata*.

Both *S. malitiosa* (Costa 1979) and *L. inornata* present a greater delay between insertions during pattern II compared with pattern I. During this delay, the males of *L. inornata* perform palpal rubbing. This behaviour could function as genital stimulation and copulatory courtship, and influence cryptic female choice, as Stratton *et al.* (1996) and Aisenberg & Costa (2005) suggested for other wolf spiders. More studies are needed to assess whether this scenario is occurring in *L. inornata*.

Males of *L. inornata* also perform chewing movements of their pedipalps between insertions, as occurs in *S. malitiosa* (Costa 1979); *Hogna* sp. (Costa & González 2015), and *L. carbonelli* (Costa & Capocasale 1984). *Lycosa inornata* shows a copulation duration similar to that of *L. carbonelli* (Costa & Capocasale 1984), and an intermediate duration within the Lycosidae, based on the data gathered by Stratton *et al.* (1996). We propose that the duration of copulation in *L. inornata* may relate to minimizing the risk of predation, considering the presence of larger and potentially predatory species such as *S. malitiosa*, *L. poliostoma*, and *L. erythrognatha*, which have a duration of copulation over 90 min (Costa 1979; González & Toscano-Gadea personal observation).

Finally, the percentage of females that stay still after copulation in *L. inornata* is higher than in *L. carbonelli* (5.6 %) but lower than in *L. thorelli* (63 %) (Costa & Capocasale 1984) or *S. malitiosa* (90 %) (Costa 1979). The reason for the occurrence of this behaviour is still unknown, but the duration of copulations could influence catalepsy occurrence, since this behaviour is absent in species with short copulations (of a few minutes or less), as occurs in *Pavocosa gallopavo* (Toscano-Gadea & Costa 2016).

As in *S. malitiosa* (Aisenberg *et al.* 2008), the silk coming out of the male spinnerets of *L. inornata* during copulation, would not be related to the catalepsy observed in the

female, since some females remained motionless after copulation and others did not. While this relation was suggested by Becker, Riechert & Singer (2005) in *Agelenopsis aperta* (Gertsch, 1934), more studies are needed to understand the function of these silk remains. It also could be a consequence of the haemolymph pressure during sperm transfer, as occurs in other species of the family (Toscano-Gadea personal observation). We observed that the behaviours performed by the male during mounting and sperm transfer, such as abdominal vibrations, silk threads, and touching the female with the pedipalps, are common to other species of Lycosidae.

As occurs in other small size Uruguayan wolf spiders, sexual cannibalism in *L. inornata* seems to be uncommon (Costa & Capocasale 1984; González *et al.* 2013; Costa & González 2015). This could be explained by the small size of the sexual dimorphism of these species, unlike in other spiders where sexual size dimorphism is evident and sexual cannibalism is frequent (Wilder & Ripstra 2008)

Unlike other species of Lycosidae (Costa 1991; Dolejš, Kubcova & Buchar 2011), females of *L. inornata* did not build shelters during pregnancy or after egg sac construction. *L. inornata* females with egg sacs, and even those carrying offspring on their abdomen, are able to capture small prey, unlike *Tricca lutetiana* (Dolejš, Kubcova & Buchar 2010). However, death of females shortly after the birth of spiderlings is surprising. More studies are needed to determine if it also occurs in natural conditions or is the result of breeding the specimens in the laboratory.

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A new species of *Paraplectana* Brito Capello, 1867 (Araneae: Araneidae) from north-east India

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Abstract

A new araneid species *Paraplectana mamoniae* **sp. nov.**, with a characteristic glossy pink abdomen in females, is described and illustrated based on morphology of individuals collected from Assam, together with notes on its natural history.

Keywords: diagnosis • Jharbari• Kokrajhar• morphology• taxonomy

Introduction

The genus *Paraplectana*, type species *Paraplectana thorntoni* (Blackwall, 1865), was erected by Brito Capello in 1867 with *P. cabindae* as its type, previously described as *Eurysoma thorntoni* by Blackwall in 1865, which later *E. thorntoni* was given new combination as *P. thorntoni* (Blackwall, 1865) by O. Pickard-Cambridge (1879). It is generally recognizable by its abdomen with glossy, elliptical and blackish markings on the dorsum of females. The Afrotropical and Oriental spider genus *Paraplectana* Brito Capello, 1867 consists of 13 nominal species, of which only two species, *P. gravelyi* (Tikader, 1961) and *P. rajashree* Ahmed *et al.* 2015, are known from India (World Spider Catalog 2019). Recent phylogenetic work on Araneidae by Scharff *et al.* (2019) placed *Paraplectana* in the informal group of cyrtarachnines within the ARA clade. The rarity of male individuals in this genus is well known, as noted by Tanikawa (2011). All described individuals of this genus are females, except for *P. sakaguchii* Uyemura, 1938 and *P. tsushimensis* Yamaguchi, 1960, known by both sexes (World Spider Catalog 2019). The spiders of this genus are known to mimic ladybird beetles. These beetles possess noxious chemicals which wreck havoc on taste buds, leading birds to recognize these unsavoury lunch targets from afar and this is a perfect example of Batesian mimicry, in which a species imitates the warning signals to get the protection with its perceived foul taste (Bay 2017). In this paper, we describe a new species *Paraplectana mamoniae* sp. nov. from India.

Materials and methods

Field photographs were taken with Sony DSC-HX90V. Specimens were hand collected, preserved in 80% ethanol and deposited in North Eastern Regional Centre, Zoological Survey of India (NERC- ZSI), Shillong. The microphotographs were taken using a Leica DFC500 HD camera on a Leica M205A stereo microscope using Leica Application Suite (LAS) version 3.8. Soft epignyal tissues were treated in 10% KOH. All measurements are in mm. Leg measurements are given as: total length (femur, patella, tibia, metatarsus, tarsus).

Abbreviations: ALE = anterior lateral eye, AME = anterior median eye, ARA = Araneidae, CD = copulatory duct, CHD = Central Head of Department, DFO = Divisional Forest Officer, FD = fertilization duct, P = promarginal, PCCF = Principal Chief Conservator of Forest, PLE = posterior lateral eye, PME = posterior median eye, R = retromarginal, S = spermathecae, ZSI = Zoological Survey of India.

Paraplectana Brito Capello, 1867

Type species: *Paraplectana thorntoni* (Blackwall, 1865).
Diagnosis: For detailed diagnosis of males see Tanikawa & Harigae (2010) and Tanikawa (2011), and for females see Ahmed *et al.* (2015).

Paraplectana mamoniae sp. nov. (Figs. 1–16)

Types: Holotype ♀ (IV/ARA/ERS–22), India, Assam, Kokrajhar, Jharbari Forest Range (26°36′22.8″N 90°14′45.3″E), 70 m, 2 October 2018, leg. P. Basumatary. Paratype ♀ (IV/ARA/ERS–31) Jharbari Forest Range (26°36′22.8″N 90°14′45.3″E), 70 m, 2 October 2018, leg. P. Basumatary.

Etymology: The specific name is dedicated in memory of Lt. Mamoni Rava (1990–2019). She was an inspiring woman researcher from the Department of Biotechnology, Bodoland University, and a core research worker for Research and Development in Technology Incubation Centre of the department. The name is used as a noun in apposition.

Diagnosis: The female of *Paraplectana mamoniae* sp. nov. is distinguishable from its known congeners by having a characteristic pinkish white abdomen with 18 blackish spots (Figs. 1–5). In contrast, the abdomen is yellowish with 14 blackish spots and venter reddish in *P. coccinella* (Thorell, 1890), abdomen glossy red with 12 black spots in *P. duodecimmaculata* Simon, 1897, abdomen reddish brown with 17 yellowish markings in *P. sakaguchi*, abdomen reddish brown with 12 blackish spots in *P. tushimensis*, abdomen greyish yellow with 14 blackish white patches in *P. gravelyi*, abdomen orange red with 14 blackish spots, venter having blackish patch posteriorly in *P. rajashree*. *P. mamoniae* has a distinct genital morphology: spermathecae large, suboval, narrowly spaced (0.1 mm) (Figs. 15–16); atrium scletorized; short copulatory ducts, uncurved and widely spaced (Figs. 13–14). In contrast, the atrium is slightly scletorized, spermathecae small and ovoid in *P. sakaguchi* (Lee, Yoo & Kim 2015, fig. 1A–B), spermathecae spherical and large, copulatory ducts thin, narrow and long, arising medially from the posterior end of spermathecae and directed distad in *P. gravelyi* (Tikader 1982, figs. 274–276), spermathecae small and widely
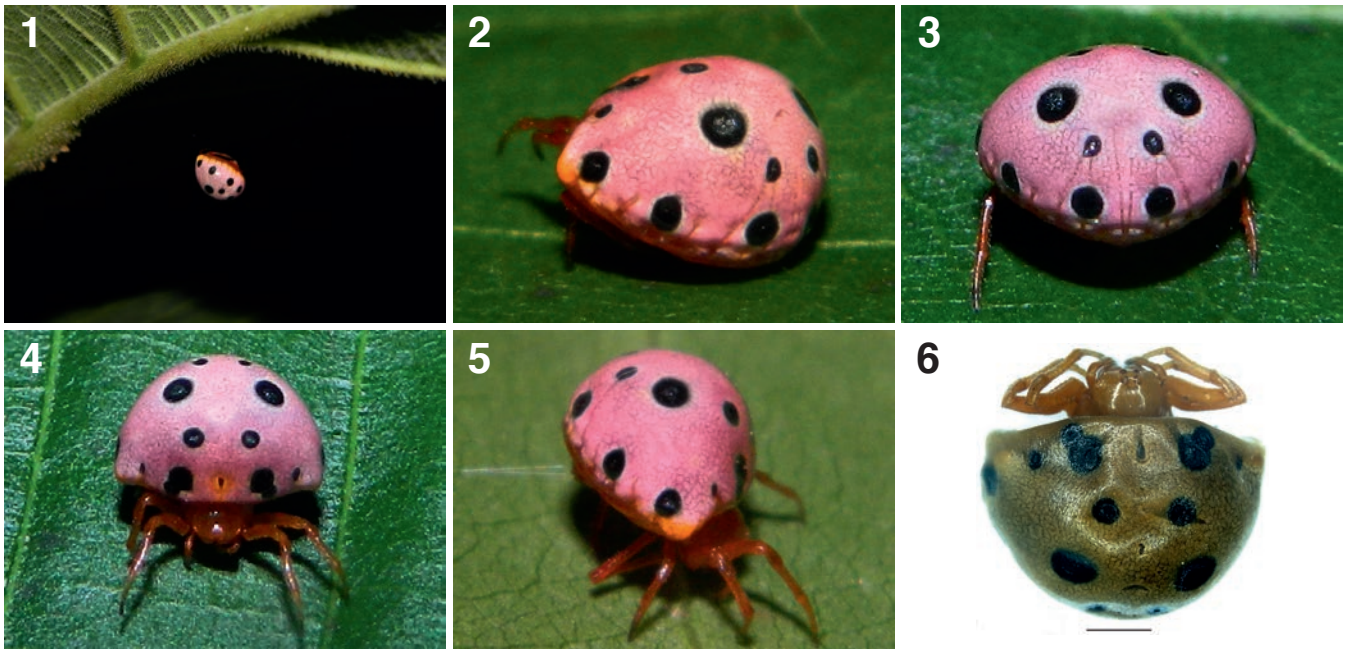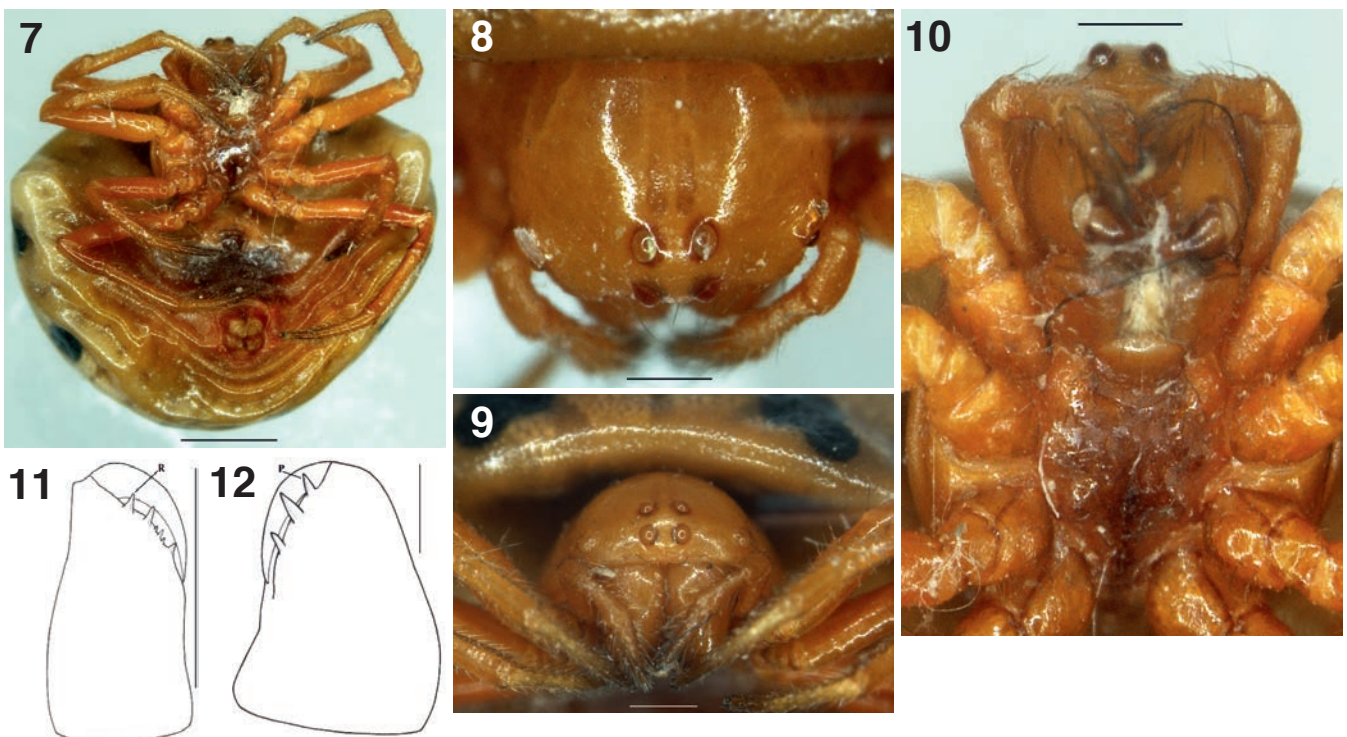
Figs. 1–6: *Paraplectana mamoniae* sp. nov. **1** live habitus, lateral view (on dragline); **2** live habitus, lateral view; **3** same, posterior view; **4** same, frontal view; **5** same, lateral view; **6** preserved habitus, dorsal view. Scale bar = 1 mm.

spaced (0.2 mm), copulatory ducts long, narrowing anteriorly and less spaced posteriorly in *P. rajashree* (Ahmed *et al.* 2015, figs. 1, 6–7).

Description of female holotype (IV/ARA/ERS–22): Total length 5.49; carapace 2.35 long, 3.77 wide; abdomen 3.14 long, 4.31 wide. Carapace reddish orange, raised ocular area (Figs. 6, 8–9). AMEs and PMEs surrounded by narrow blackish ring (Figs. 8–9); eye measurements: AME 0.27, ALE 0.13, PME 0.24, PLE 0.1; interdistances between eyes:

AME–AME 0.26, AME–ALE 0.97, AME–PME 0.18, ALE–ALE 3.05, PME–ALE 1.04, PME–PME 0.26, PME–PLE 1.17, PLE–PLE 3.32. Chelicera, labium and maxilla reddish orange (Figs. 9–10). Chelicera with 3 promarginal and 6 retromarginal teeth (Figs. 11–12). Sternum dark reddish orange and sub-triangular (Fig. 10). Legs reddish orange, covered with numerous pale brownish setae, tarsus leg I–IV blackish brown (Fig. 7). Leg measurements: I 3.15 (1.14 + 0.44 + 0.71 + 0.56 + 0.3), II 3.14 (1.19 + 0.5 + 0.68

Figs. 7–12: *Paraplectana mamoniae* sp. nov. **7** habitus, ventral view; **8** cephalothorax, dorsal view; **9** same, anterior view; **10** same, ventral view; **11** diagrammatic representation of chelicera, ventral view; **12** same, ventral view. Scale bars = 0.2 mm (12); 0.5 mm (11); 1 mm (7–10).
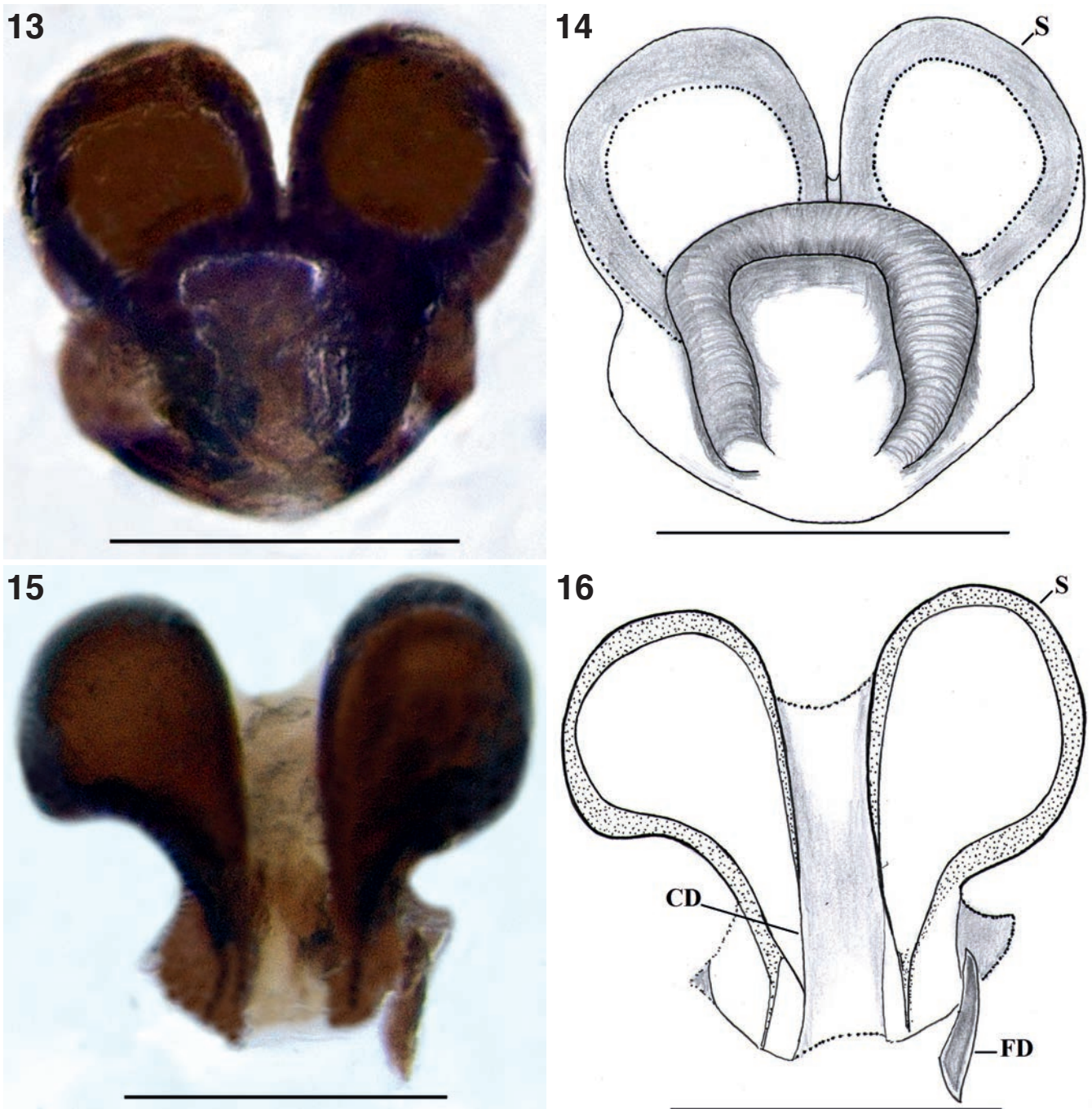
Figs. 13–16: *Paraplectana mamoniae* sp. nov. **13** vulva, dorsal view; **14** diagrammatic representation of vulva, dorsal view; **15** vulva, ventral view; **16** diagrammatic representation of vulva, ventral view. Scale bars = 0.2 mm.

+ 0.54 + 0.23), III 2.03 (0.87+0.3+0.4+0.24+0.22), IV 3.22 (1.37+0.36+0.63+0.53+0.33). Abdomen elliptical, wider than long and blunt anteriorly (Figs. 2–6); dorsum pinkish white with 18 blackish spots (8 medially, 2 anteriorly and 8 laterally) (Figs. 2–5); venter brownish orange with short yellowish longitudinal patch along epigastric furrow and pale blackish patch beneath epigastric furrow (Fig. 7). Body colorations faded from glossy pinkish white to dull brown in preserved individuals (Fig. 6). Epigyne scletorized, slightly elongated posteriorly; spermathecae large, suboval; copulatory ducts short, continuous with spermathecae, arising laterally and directed distad, widely spaced posteriorly; fertilization duct short and narrow, connected with copulatory duct distally (Figs. 13–16).

Male unknown.

Natural history: The new species was found on the abaxial surface of a fig, *Ficus hispida*, constructing a single dragline at a height of 2 m above the ground (Fig. 1). Adult females were observed to be active at night.

Distribution: Assam, India (Fig. 17).

Acknowledgements
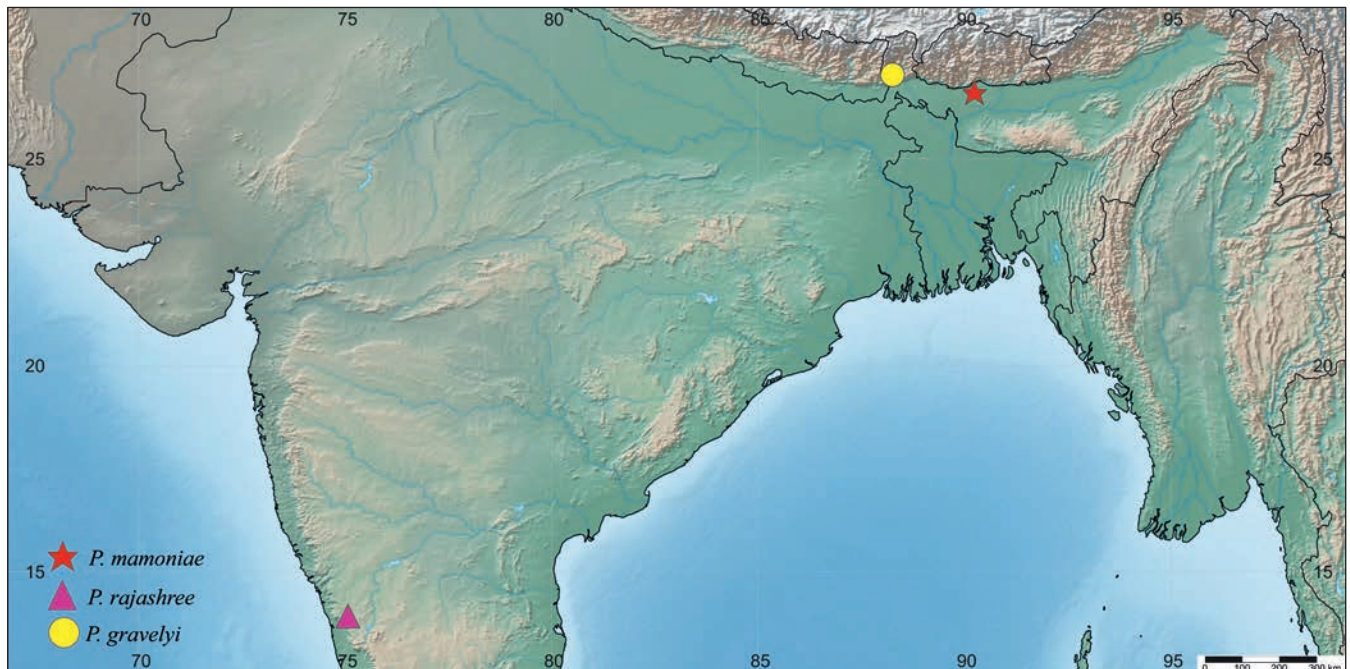
Fig. 17: Type localities of *Paraplectana* species described from India. The type locality of *P. mamoniae* sp. nov. is marked as a red star.

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The first records of *Holothele longipes* (L. Koch, 1875) from Guyana and Panama (Araneae: Theraphosidae)

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Abstract

Specimens of the widely distributed ischnocoline species *Holothele longipes* (L. Koch, 1875) are formally reported from Guyana and Panama for the first time, based on examination of material from the collections of Natural History Museum, London, Oxford University Museum of Natural History and Museo de Invertebrados G. B. Fairchild, Universidad de Panama.

Keywords: biogeography • distribution • Ischnocolinae • morphology • tarantula

Introduction

Karsch (1879) created the genus *Holothele* Karsch, 1879 for *Holothele recta* Karsch, 1879, a species he described from Venezuela. Raven (1985) synonymized five genera (*Euthycaelus* Simon, 1889, *Dryptopelmides* Strand, 1907, *Hemiercus* Simon, 1903, *Schismatothele* Karsch, 1879, and *Scopelobates* Simon, 1903) with *Holothele* but, with the exception of *Dryptopelmides*, all of these genera have since been revalidated by later workers (Rudloff 1997; Guaddanucci & Weinmann 2014; Guadanuuci, Perafán and Valencia-Cuéllar 2017). Raven (1985) suspected that the genus *Stichoplastus* Simon, 1888 also to be synonymous with *Holothele* but did not formally propose this. Rudloff (1997) subsequently considered *Stichoplastus* a junior synonym of *Holothele* in his work.

Recently, Guadanuuci, Perafán & Valencia–Cuéllar (2017) redescribed *Holothele recta* in detail and proposed it to be a junior synonym of *H. longipes* (L. Koch, 1875). They also considered *Dryptopelmides ludwigi* Strand, 1907, *D. rondoni* Lucas & Bücherl, 1972, and *Stichoplastus sanguiniceps* F. O. Pickard-Cambridge, 1898 to be junior synonyms of *H. longipes*. These transferrals resulted in an updated distribution for *H. longipes* spanning six countries: Bolivia, Brazil, French Guiana, Suriname, Trinidad and Tobago, and Venezuela (World Spider Catalog 2019).

In this work, we report the first specimens of *H. longipes* from the countries of Guyana and Panama. These new records, based on examination of material from three natural history museums, extends the distribution of this species both eastwards and northwards.

Materials and methods

Specimens were examined under a Leica MZ12.5 stereomicroscope, photographs of palpal bulbs and tibial apophyses were made using a Canon EOS 6D Mark II attached to a Leica MZ12.5 with images stacked using Helicon Focus software. Abbreviations: BMNH = Natural History Museum, London, OUMNH = Oxford University Museum of Natural History, MIUP = Museo de Invertebrados G. B. Fairchild, Universidad de Panama, ZMH = Zoologisches Museum, Universität Hamburg. The map was made using SimpleMappr (Shorthouse 2010). Authors' emphases in [ ].

Holothele longipes (L. Koch, 1875)

Chaetopelma longipes L. Koch, in Ausserer, 1875: 174, pl. 6, f. 20–21.
Holothele recta Karsch, 1879: 544.
Stichoplastus ravidus Simon, 1889: 208.
Stichoplastus sanguiniceps F. O. Pickard–Cambridge, 1899: 895.
Dryptopelmides ludwigi Strand, 1907: 19.
Stichoplastus ravidus: Schenkel (1953): 2, f. 2a–b.
Dryptopelmides rondoni Lucas & Bücherl, 1972: 234, f. 1–4.
Dryptopelma rondoni: Raven (1985): 152.
Dryptopelma rondoni: Schmidt (1993): 65, f. 96–97.
Dryptopelmides rondoni: Schaefer (1996): 24, f. 10–11.
Holothele longipes: Rudloff (1997): 9.
Holothele recta: Rudloff (1997): 10, f. 1–2.
Holothele rondoni: Rudloff (1997): 10, f. 19.
Holothele sanguiniceps: Rudloff (1997): 11, f. 3–4.
Holothele sanguiniceps: Schmidt (2003a): 17, f. 1–3.
Holothele rondoni: Schmidt (2003b): 109, f. 40–41.
*Holothele sanguiniceps*: Schmidt (2003b): 109, f. 42.
Holothele longipes: Guadanucci, Perafán & Valencia-Cuéllar (2017): 265, f. 1A–G, 2A–F, 3A–D, 4A–F.

Type material: Holotype ♂ *Chaetopelma longipes* BMNH 19.9.18.5728, TRINIDAD: Porto Cabello, Koch coll., examined; holotype ♀, syntype ♀ *Stichoplastus sanguiniceps* BMNH 1895.5.3.1, coll. J. H. Hart and D. W. Ince, examined.

Diagnosis: *H. longipes* can be differentiated from congeners by genital organ morphology. Males can be distinguished by palpal bulb morphology with a thin, elongate embolus with slight curvature at apex (Figs. 1–4). Further distinguished by tibial apophyses morphology, with a taper to the apex of the retrolateral branch (Figs. 5–7). Females can be distinguished by spermathecal morphology, with elongate receptacles, noticeably narrow at the base, but with a varying number of lobes at the apex of the receptacles (see Guadanucci, Perafán & Valencia-Cuéllar 2017).

Distribution: Bolivia, Brazil, French Guiana, Guyana, Panama, Suriname, Trinidad and Tobago, and Venezuela

Other material examined: BRITISH GUIANA: 1♂, 1 imm. BMNH 1939.3.24.48–50, coll. C. A. Hudson, *Holothele longipes* det. D. Sherwood 09/17; VENEZUELA: 1♂, 1♀ BMNH 1903.7.1.128–129, *Holothele longipes* det. D. Sherwood and R. Gabriel 13/04/18; 1♂ BMNH 1905.3.31.61–70, Culata, 3000 m, *Holothele longipes* det.
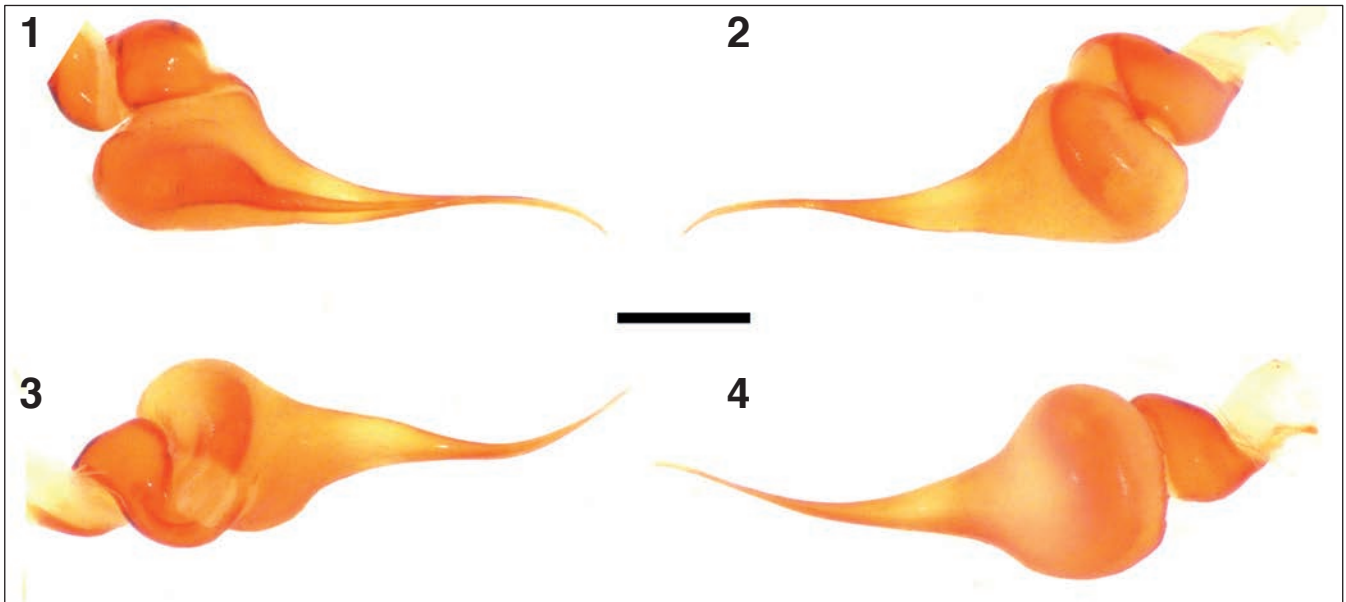
Figs. 1–4: *Holothele longipes* non-type male, BMNH, palpal bulb (left hand side). **1** prolateral view; **2** retrolateral; **3** dorsal; **4** ventral. Scale bar = 1 mm.

D. Sherwood & R. Gabriel 13 April 2018; 2♀ BMNH 1890.10.6, Demerara, coll. W. L. Silater, *Holothele longipes* det. D. Sherwood 09/17; 1♂ BMNH 1905.3.31.24–26, Merida, purch. of Rosenburg, *Holothele longipes* det. D. Sherwood and R. Gabriel 13/04/18; 2♂, 2♀, 1 imm. BMNH 1912.11.11.24–37, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 2018; 1♀ BMNH, Merida, purch. of Rosenburg, *Holothele* sp. found in tube in mixed jar, R. Gabriel 06 March 2009, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 2019; Cojedes Hato Pinero Ilanos plains 8°56′N 68°5′W *c*.150 m, swept August 1990, coll. G. McGavin; 1♂ OUMNH 2006–073; TRINIDAD: 1 ♂ BMNH, Tamana, 21 May 1968, coll. Darlington, *Stichoplastus sanguiniceps* det. DJC 1970, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 2018; 3 imm. BMNH, 16 November 1968, Tamana Caves, coll. Darlington, 16 July 1968, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 2018; 1♂ BMNH 1971/274, Tamana Caves, coll. Darlington, 16 July 1968, *Stichoplastus sanguiniceps* det. DJC 1970, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 2018; 1 imm. ♀ BMNH 1971/296, 19 September 1969, deep part Tamana, 19 January 1968, coll. Darlington, *Stichoplastus sanguiniceps* det. DJC 1970, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 18; 1♀, 1 imm. ♀ BMNH 1971/23/301,

deep part Tamana Cave, 13 December 1968, *Stichoplastus sanguiniceps* det. DJC 1970, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 18; 1♂ BMNH, 1971/298, male is undescribed, coll. Darlington, det. D. J. Clark, *Stichoplastus sanguiniceps* det. DJC 1970, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 2018; 1 imm. ♀, 1 imm. BMNH 1971/297, Tamana Caves, coll. Darlington, 16 October 1968, *Stichoplastus sanguiniceps* det. DJC 1970, *Holothele longipes* det. D. Sherwood & R. Gabriel 13 April 2018; 1 imm. ♂, 1 imm. ♀ BMNH, Mt. Aripo, rotten log, 20 March 1937, 48 AR, Tube 554, some collectors notes, coll. I. T. Sanderson, *Holothele longipes* det. D. Sherwood 09/17; PANAMA: 1♂, 1♀, 1 imm. MIUP, P. N. Darien, Est. Rancho Pirre, 3–17 October 2002, coll. R. Cambra, A. Santos, R. Miranda, P. Gonzales, *Holothele longipes* det. D. Sherwood & R. Gabriel 16 November 2018; BRITISH GUIANA: 1♂, 1♀ OUMNH, 1959, coll. Lampel; BOLIVIA: 1♀ OUMNH, Dep. Cochabamba, Cordillera Mosetenes, Isiboro–Sécure N. P., humid montane forest, 16°13′S 66°24′W, 3 September 2003, ex. colln A. C. Hamel, *Holothele* spp. det. R. Gabriel 30 April 2012, *Holothele longipes* det. D. Sherwood 10 May 2019; SURINAME: 1♀ ZMH A0000884, Paramaribo, coll. J. Michaelis, L. vemd, 31.T.1899, Fam. Aviculariidae, *Holothele longipes* det. D. Sherwood 9 August 2018.
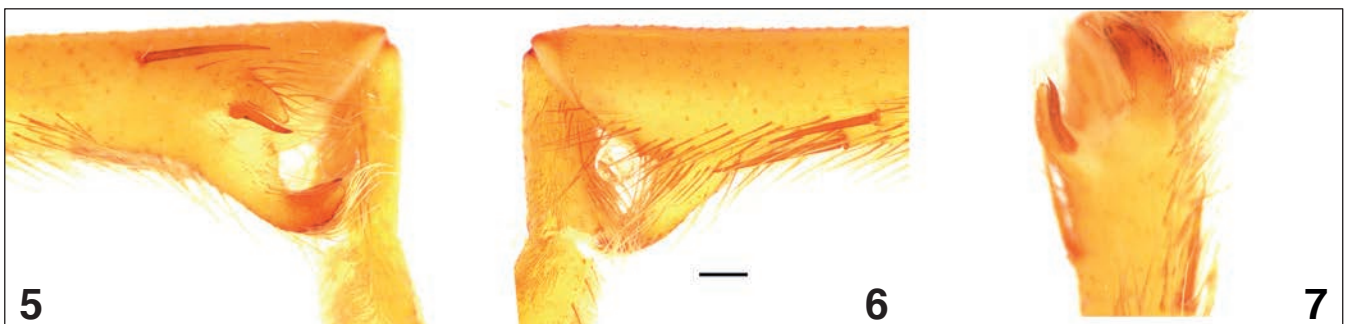
Figs. 5–7: *Holothele longipes* non-type male, BMNH, tibial apophysis (left hand side). **5** prolateral view; **6** retrolateral; **7** ventral. Scale bar = 1 mm.
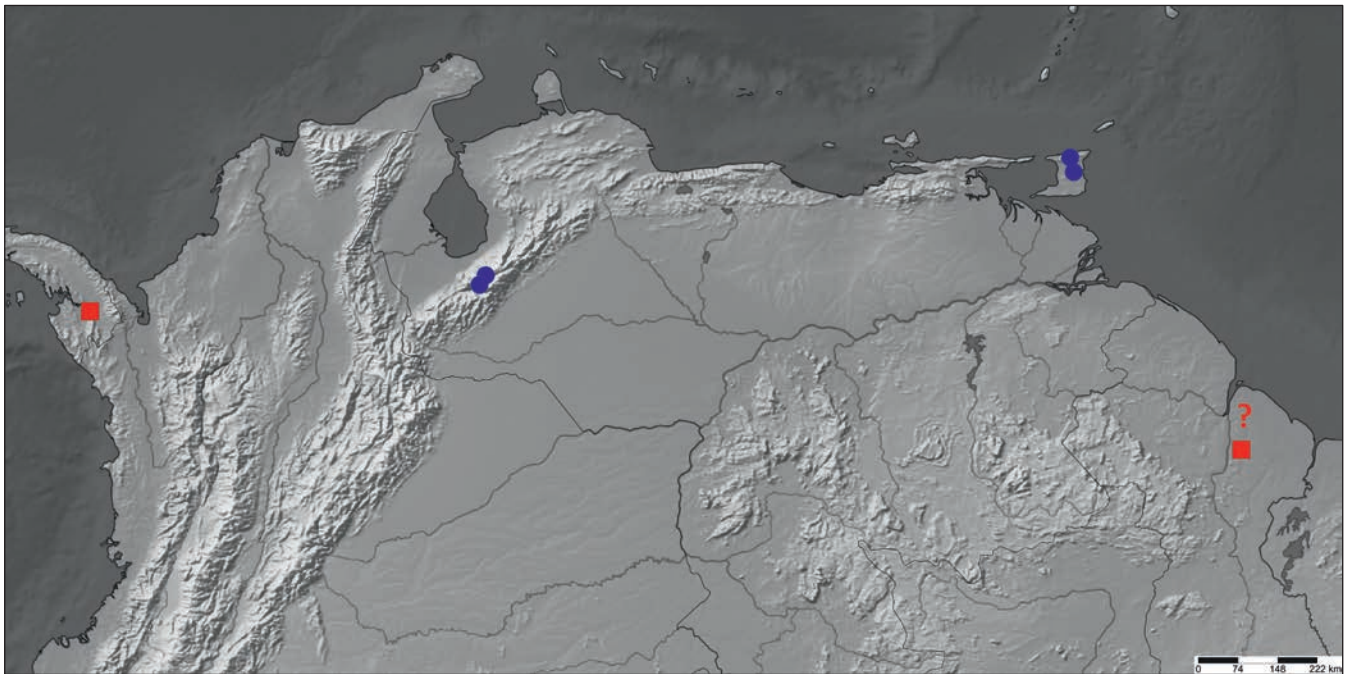
Fig. 8: Map showing the distribution of *Holothele longipes* specimens examined for this work, ■ = new distribution records from this work, ● = specimens from areas already previously reported for this species, **?** = general country indicator, not precise location (based on two specimens (BMNH 1939.3.24.48–50) with simply "British Guiana" for locality data).

Remarks: Whilst working through undetermined Mygalomorphae at the BMNH, two ischnocoline specimens, a mature male and a juvenile, were found in a jar containing other theraphosid species collected from British Guiana in 1939 by C. A. Hudson. Upon closer examination of the male, an abdominal pattern was absent and the palpal bulb and tibial apophyses morphology allied strongly against that of *H. longipes*. We also discovered two mature female specimens collected by W. L. Silater with the locality of Demerara which also corresponds to an area of modern day Guyana. Following the examination of these four specimens, we then examined the type material of *H. longipes* and *S. sanguiniceps* housed at the BMNH to confirm the identifications.

Later, whilst working through jars of undetermined material at OUMNH we found a further male and female of a *Holothele* species collected from British Guiana in 1959 by Lampel also conspecific in morphology with *H. longipes*. These additional specimens in OUMNH confirmed, once again, the distribution of *H. longipes* within the boundaries of modern-day Guyana, and brought the number of specimens of *H. longipes* we were able to examine from the country to six.

We discovered a further three specimens of *H. longipes*, one male, one female, and one immature whilst examining material from MIUP which was collected from the Darien Gap in Panama. Again, morphology demonstrated these three specimens to be *H. longipes* and confirmed the presence of this species within Panama for the first time.

Discussion

The neotropical ecoregion that covers Guyana, Suriname and French Guiana is fairly continuous, consisting of subtropical broadleaf forests (Olson *et al*. 2001). Given the general biogeography of the area and the wide distribution already noted for *H. longipes* in previous works, we do not find it surprising to have found preserved museum specimens of this species collected from within the borders of Guyana. Similarly, given the wide distribution of this species across many habitat types in Colombia (Guadanucci, Perafán & Valencia-Cuéllar 2017) and nearby records from the region of Caribe, we were also not surprised to find specimens from the Darien Gap. Indeed, it is possible this species may occur more northerly in Panama and southerly in Colombia respectively, although this hypothesis will need to be tested through future field work.

In this study, we examined *H. longipes* material from four countries (Fig. 8). The overall present distribution of *H. longipes* covers a significant area of Central and South America across many biogeographical areas. This could raise the possibility of cryptic diversity, especially given that many morphologically conserved species have been found to contain several distinct lineages when subjected to molecular analysis (e.g. Hamilton, Hendrixson & Bond 2016; Ortiz & Francke 2017). However, at present, since molecular characterization has not yet been conducted with *H. longipes*, select morphological characters remain the only robust and viable means of defining the boundaries of this taxon.

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Redescription of *Myrmarachne augusta* (Peckham & Peckham, 1892) (Araneae: Salticidae)

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Abstract

Myrmarachne augusta (Peckham & Peckham, 1892), an ant-mimicking jumping spider (Araneae: Salticidae) is redescribed. This species has only been known from two records and three specimens from Madagascar so far. Its new locality is presented along with a detailed description and discussion on intraspecific variation of colour and morphology in relation to previously recorded specimens.

Keywords: Afrotropical Region • endemic • Madagascar • Myrmarachnini

Introduction

Many spider species are known solely from just a few specimens, which also concerns the majority of Malagasy species from Myrmarachnina (*sensu* Maddison & Szűts 2019). Thus, all information on their biology or distribution significantly contributes to our knowledge. In this article, we present a new record and a redescription of *Myrmarachne augusta* (Peckham & Peckham, 1892) (Araneae: Salticidae), a spider endemic to Madagascar. *Myrmarachne* MacLeay, 1839 is one of the most species-rich genera of jumping spiders, containing presently 188 nominal species (World Spider Catalog 2019). Members of *Myrmarachne*, and some closely related genera, mimic ants; therefore, they share a very similar body type. Identification of species is additionally impeded by a very similar pattern in the male palp structure, intraspecific variability of cheliceral dentition, and changeable morphological features, such as the size of the chelicerae or total dimensions. For females, the task of distinguishing species is no easier, because of the uniformity of their epigyne structure and its high complexity. The most valuable source of information on the genus is the revision by Wanless (1978), it is the only publication in which *M. augusta* was thoroughly depicted, and the last one in which new faunistic data were presented. Moreover, Wanless (1978) attributed to *Myrmarachne cowani* (Peckham & Peckham, 1892) a spider that had been supposed to be merely a different form of *M. augusta*, distinguished by the very large chelicerae, long body, and different cheliceral dentition. We decided to redescribe a male of *M. augusta* based on freshly supplied material, with well visible colours

and hairs. The female of *M. augusta* remains unknown. All measurements are in mm.

Myrmarachne augusta (Peckham & Peckham, 1892)
(Figs. 1–3)

Salticus augustus Peckham & Peckham, 1892: 24, pl. 1, f. 5 (Dm).
Myrmarachne angustiformis Simon (1901): 503 (unnecessary replacement name).
Myrmarachne augusta Wanless (1978): 109, f. 70A-H (m).

Material: MADAGASCAR: Anjozorobe-Angavo Protected Area, 18.4070°S 47.9445°E, *c.* 1300 m, from plants in rainforest, 1♂, 19 April 2017, leg. BINCO. Deposited in the Royal Museum for Central Africa in Tervuren (RMCA ARA 246167).

Measurements: Cephalothorax length 3.7, width 2.0, height 1.6. Eye field length 1.4, anterior width 1.7, posterior width 1.9. Cheliceral length 2.3. Abdomen length 3.6, width 1.9.

Redescription: General appearance as in Fig. 1. Carapace black, delicately pitted, clothed with long thin white hairs. Cephalic part slightly higher than thoracic, not considerably broader. Clypeus very low, with white hairs. Chelicera elongated, broad, horizontal and flattened dorsally, with clear microsculpture in the form of numerous parallel shallow furrows, black, only their tips reddish brown (Fig. 2A). Four teeth on promargin and single tooth on retromargin, paired distal spurs on prolateral margin, fang long without apophysis (Figs. 2A, 3C–D). Endites dark brown with lighter margins, labium and sternum dark brown, labium without a keel. Abdomen slightly constricted, black, covered with white hairs, scutum on the two-thirds of dorsal side, venter black. Spinnerets yellowish grey. Basal segments of legs black, except white yellowish coxae I and trochanters IV and ventral surface of trochanter I and II. Legs I: femora brownish-black, patellae and tibiae yellow with black streaks along sides, metatarsi and tarsi black. Legs II similarly coloured, but metatarsi and tarsi orange yellowish. Legs III and IV black (apart from trochanter IV), their tarsi orange reddish. Legs I with four pairs of ventral spines on tibia and two pairs on metetarsus, legs II with three and two spines respectively, legs III with a single spine on dorsal part of metatarsus. Pedipalps black with reddish brown distal part of cymbium, covered with dense, thick hairs (Fig. 2 B–D). Palpal structure as in Fig. 3A–B, tibial apophysis without flange, which is reduced to a small outgrowth, embolus with pars pendula, encircling the bulb, cymbium without depression complementary to the tibial apophysis, with two apical stout bristles.

Diagnosis: The males of this species can be readily distinguished from congeners by the form of the chelicera, namely by the presence of paired distal spurs on its prolateral margin. This feature is well visible from the dorsal side (Figs. 2A, 3D). The palpal organs are of minor value in recognizing the species because the structure of *Myrmarachne* male genitalia is very uniform; however, the reduced flange
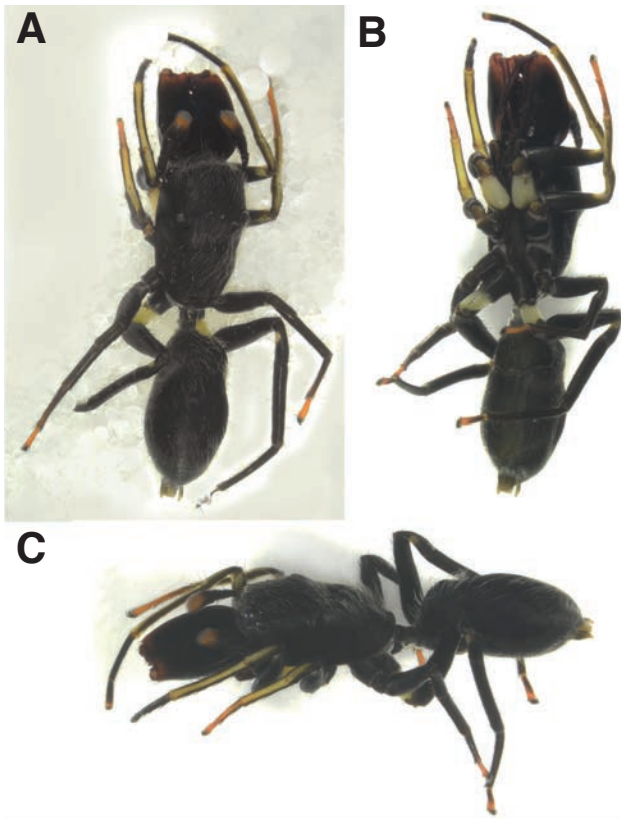
Fig. 1: *Myrmarachne augusta*, male habitus. **A** dorsal view; **B** ventral view; **C** lateral view.

on the palpal tibia, in the shape of a small process, is distinctive.

Variability and distribution

The colouration of the presented specimen does not exactly fit that of the previously reported three specimens (Peckham & Peckham 1892; Wanless 1978). The most striking differences concern whitish coxae I and trochanters IV or yellow tibiae I with longitudinal stripes that are characteristic for our specimen. Only the latter feature is given in the description by Wanless (1978). Our specimen differs also in not having the conspicuous white bands in the constrictions of cephalothorax and abdomen (Peckham & Peckham 1892). Size seems to be variable within the species (Wanless 1978). One of the specimens described by Wanless (1978) had a slightly differently shaped chelicera that was broader and with a different shape of the prolateral spur. The one described here has a different chelicera and shares its shape with the lectotype designated by Wanless. It is premature to draw any taxonomic conclusions based on the known variability of the colouration and morphology. Relationships of *M. augusta* remain unknown. However, considering the high level of endemism, it may be related to one of the Malagasy lineages within the genus, although it may show some superficial resemblance to other species outside Madagascar. Wanless (1978) included it as *species sola*. Edwards & Benjamin (2009) did not consider this species in their study of *Myrmarachne* phylogeny.

The Peckhams (1892) do not give a precise locality for their specimens. The *M. augusta* reported by Wanless (1978) (the one with slightly different cheliceral structure) originated from Antongil Bay in north-east Madagascar. Our record comes from an area situated more centrally on the island, 70 km north-east from the capital Antananarivo (Fig. 4).

The vast majority, i.e. 13 of 14 Malagasy species from the subtribe Myrmarachnina, are endemic to the island (Wanless 1978; World Spider Catalog 2019), only *Hermosa volatilis* Peckham & Peckham, 1892 is thought to live also in some parts of South-East Asia (World Spider Catalog 2019). This example shows how urgent is the thorough reanalysis of this huge species group rather than providing any biogeographical evidence.

Fig. 2: *Myrmarachne augusta*, male. **A** chelicerae, dorsal view; **B** palpal organ, ventral view; **C** palpal organ, retrolateral view; **D** palpal organ, dorsal view.
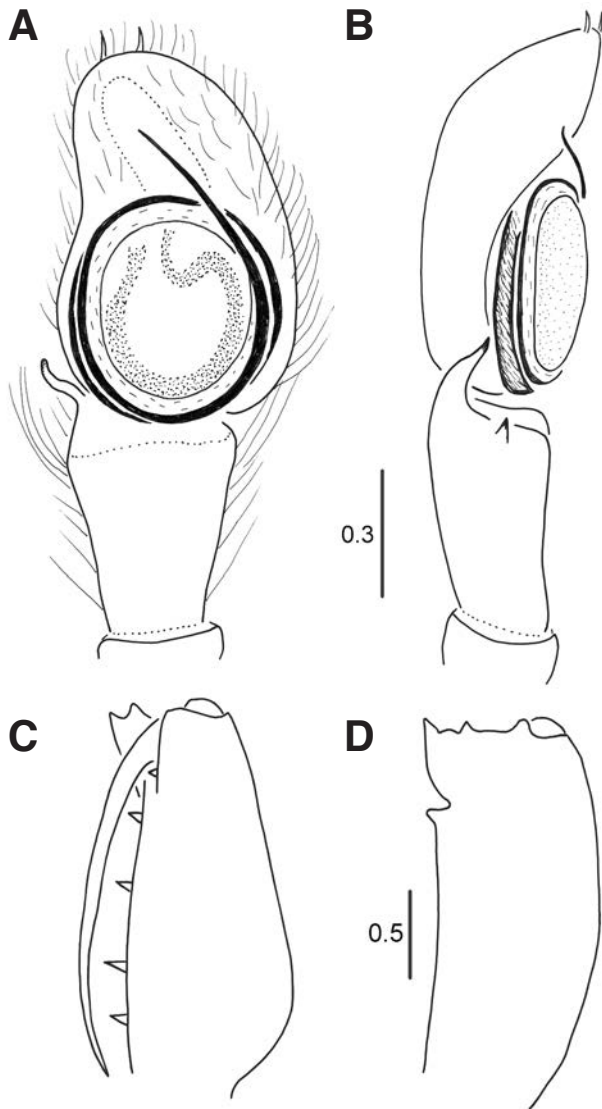
Fig. 3: *Myrmarachne augusta*, male. **A** palpal organ, ventral view;
B palpal organ, retrolateral view; **C** chelicera, ventral view;
D chelicera, dorsal view.

Fig. 4: Collecting sites of *Myrmarachne augusta*; square = previous
record, circle = present record.

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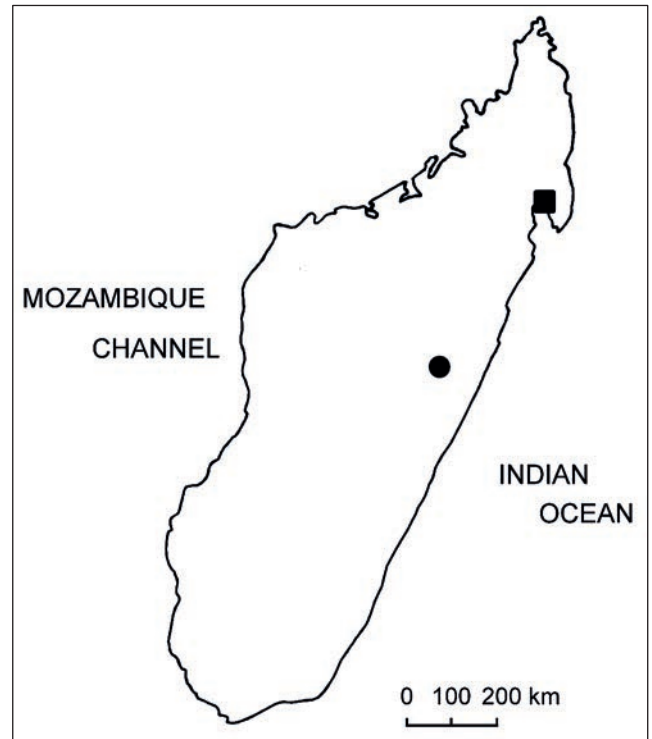of the Myrmarachninae, with rediscovery and redescription of the
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Are trichobothria used in terrestrial prey capture by the yellow scorpion *Tityus serrulatus* Lutz & Mello, 1922 (Buthidae)?

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Abstract

Many arachnids rely on substrate-borne vibrations and air displacement to detect prey. Air-flow stimuli may be detected by long setae called trichobothria, which occur on scorpion pedipalps, but seldom have their functions been addressed in these animals. We tested the hypothesis that trichobothria on scorpion pedipalps are important for capturing terrestrial prey in the scorpion *Tityus serrulatus*. We predicted that scorpions with trichobothria experimentally removed would be less successful in capturing terrestrial prey than the control groups. We also predicted that scorpions without trichobothria would have a higher number of capture attempts, that the latency to detect prey and to the first capture attempts would be higher, and the number of times that scorpions oriented their body towards the prey would be lower. We used an experimental subject and a cricket in an arena with a paper sheet as substrate. We did not find differences in the measured variables between the groups. Other sensory organs, such as basitarsal compound slit sensilla and tarsal hairs would enable scorpions to detect prey by substrate-borne vibrations, compensating for the lack of trichobothria. Our results suggest that the trichobothria of *T. serrulatus* may not be essential to capture terrestrial prey.

Keywords: capture success • filiform hair • foraging • sensory ecology • vibration

Introduction

Arachnids rely on a broad range of sensory organs to acquire environmental information, and mechanoreception is quite extraordinary because of the sensitivity of the organs involved and the wide range of uses. Mechanical stimuli are used in reproduction (Stratton 1997), to avoid predators (Sitvarin *et al*. 2016) and to locate prey (Brownell & Farley 1979a). To detect mechanical stimuli, arachnids rely on organs like tactile setae, slit sense organs and trichobothria (Foelix 1985). Tactile setae are common in arachnids and are sensible to touch (Barth 2002; Foelix 2011). The slit sense organs occur isolated or in groups (Foelix 2011), being responsible for detecting substrate-borne vibrations and for proprioception (Brownell & Farley 1979b; Foelix 2011).

The majority of arachnids possess trichobothria, with the exception of the orders Solifugae, Ricinulei, and Opiliones (Reißland & Görner 1985). In spiders, these setae occur on the legs (Barth 2002), but in scorpions they can only be found on the pedipalps (Hjelle 1990). Trichobothrial setae are usually long and slender, and are inserted in a cavity called a bothrium (Meßlinger 1987); they are extremely sensible to air displacement (Reißland & Görner 1985). Using trichobothria, the spider *Cupiennius salei* (Keyserling, 1877) detects frequencies produced by flies, but the response is affected if these setae are removed (Barth 2002). In scorpions, there are physiological studies on the functioning of trichobothria (Hoffmann 1967; Ignatiev *et al*. 1976). In contrast to the well-studied spiders, behavioural studies on the use of trichobothria and natural prey in scorpions are scarce (Linsenmair 1968; Ashford *et al*. 2018).

As in spiders, it has been shown that scorpion trichobothria allow scorpions to detect and to direct the body toward an airflow stimulus (Linsenmair 1968). Ashford *et al* (2018) found a retreat behaviour in the scorpion *Paruroctonus utahensis* (Williams, 1968) when they simulated an airflow of a moth towards the scorpion. They also found that the specific trichobothrium analysed moves when stimulated by this moth airflow.

The yellow scorpion *Tityus serrulatus* is known for being parthenogenetic (Matthiesen 1962), its broad distribution in Brazil (Brazil & Porto 2010), and its medical importance (Lourenço & Eickstedt 2009). Despite being a common species, there are few behavioural studies, on temperature preference (Hoshino, Moura & De Paula 2005), the use of pectines to detect mechanical stimulus (Mineo, Franco-Assis & Del Claro 2006), description of reproduction by parthenogenesis (Matthiesen 1962), and two behavioural repertoires (Mineo & Del Claro 2003; Colombo & Alencar 2014). As previously mentioned, studies on the use of trichobothria to capture natural prey are scarce in scorpions. Because of comparisons with spiders, these setae are commonly assumed to be used for capturing prey, but there are few quantitative data testing this idea. Therefore, we tested the hypothesis that trichobothria are important in prey capture in *T. serrulatus*.

Methods

Collection and maintenance of animals in the laboratory

We collected the scorpions in November 2015 and June 2016, at the Cemitério de Ribeirão Preto (21°09′29.0″S 47°47′53.2″E), Ribeirão Preto city, São Paulo State, Brazil. We maintained scorpions collected in both years in similar conditions in the laboratory: circular arenas (20 cm diameter × 8 cm high), under ambient temperature (22–24 °C), with paper towel as substrate, water in a cotton ball *ad libitum*, and with constant red lamp illumination. We fed the scorpions with crickets (*Gryllus* sp.) to standardize hunger, and we fed the crickets on dog food (Pedigree®) *ad libitum*. We only used scorpions that had fed previously. Based on data from preliminary trials, all the scorpions were starved for 40 days before the experiment.
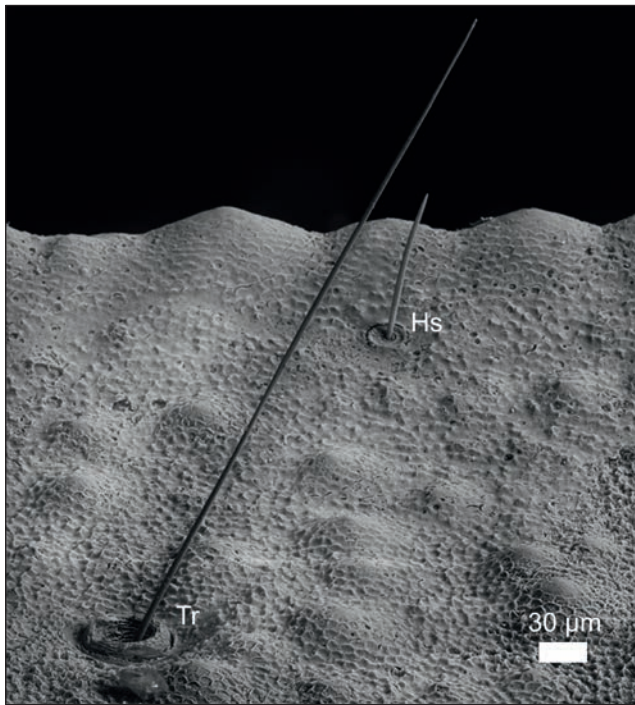
Fig. 1: Trichobothrium (left) and hair sensillum used as control setae (right) on left pedipalp patella of the yellow scorpion *Tityus serrulatus*.

Category	Description
Detection	The scorpion moves one pedipalp away from the other in the horizontal plane, or moves the body forward or backwards, or attempts to capture prey, or stops moving, or orients the body and/or pedipalps toward prey (see next definition). If the prey touches the scorpion, we consider it to have been detected. Some of these behaviours can occur simultaneously.
Body orientation toward prey	The scorpion points one or both pedipalps and rotates the body towards the prey (see Bub & Bowerman 1979; Rein 2003; Stewart 2006; Jiao 2009).
Prey grasp attempt	An attempt to seize and hold the prey with one or both pedipalps, sometimes moving the body towards the prey (see Bub & Bowerman 1979; Rein 2003; Stewart 2006; Jiao 2009)
Grasp success	Hold the prey for at least two seconds with one or both pedipalps (see Bub & Bowerman 1979; Rein 2003; Stewart 2006)

Table 1: Operational definitions of the behavioural categories used in our study in predatory interactions between the scorpion *Tityus serrulatus* and a cricket.

Scorpion anesthesia and immobilization

To remove trichobothria, we needed to have scorpions motionless. Therefore, we first anesthetized each scorpion in a freezer at -22 °C for ~4–5 minutes. Then, to immobilize the scorpion, we placed three paper strips attached on the substrate across the mesosoma and metasoma of the animal, like seat belts. To protect ourselves from the scorpion's sting, we covered the telson with a piece of foam.

Treatments

We had four treatments for our experiment: trichobothria removed (TR, n = 14), control setae removed (CSR, n = 9), control of experimental procedures (CEP, n = 13) and control without handling (CWH, n = 8). We manipulated the scorpions under a stereomicroscope (Leica M125), using forceps to hold the pedipalps while using a razor blade to cut the seta in each treatment. Only setae on the pedipalps were removed. In the TR group, we removed 62 trichobothria (following the pattern of trichobothria distribution in Lourenço 2002), leaving only 10 (five on each internal region of the pedipalp femur), which are on the inferior region, prolaterally on the femur and very difficult to remove. Attempting to remove them was inefficient and stressful to the animals because it required twisting the pedipalp. Removing the trichobothria (or the control setae) of a single individual required ~50 min. Removing 86% (of 72) of the trichobothria should have an effect if they are important for capturing terrestrial prey. In the CSR group, we did everything as described above but only ablated one hair sensillum (see Gaffin, Wennstrom & Brownell 1992; Fig. 1) per adjacent trichobothrium ablated, i.e. we removed the same

number of hair sensilla in CSR as trichobothria in TR. In CEP, we also did everything as above but removed no setae. Instead, we only rubbed the region close to trichobothria with the blade. In CWH we did not manipulate the animals. We waited 15 days before running trials with a manipulated scorpion to minimize putative effects of stress due to our experimental procedure.

Experiment

We used an acrylic circular arena (27 cm diameter) with black paperboard on the walls. The substrate was a paper sheet extended and suspended in a tray with a short marking (2.4 cm) that was later used as a scale in video analyses. We used crickets as a model arthropod prey and not artificial stimuli because we were interested in the use of a specific sensilla in the efficiency or detecting and capturing natural prey. We introduced a scorpion and a cricket (~1 cm) without the third pair of legs (to increase the chances of scorpion capture) in individual vials as far as possible away from each other. After three minutes of acclimation, we released the animals simultaneously and recorded for 11 minutes. During this period, scorpions would often attempt to capture crickets more than once. Only one cricket was offered to each scorpion, which were tested only once. We predicted that scorpions with the most trichobothria removed would: 1 capture less prey, 2 have a lower rate of successful prey capture attempts, 3 have a higher latency to detect prey, 4 have a higher latency to the first prey capture attempt, and 5 have a shorter number of body orientation toward prey than the control groups (see Table 1 for operational definitions). In each test, we introduced the scorpion in the arena rotated ~45° compared with the previous tested animal to minimize possible biases related to external visual stimuli. We alternated the four treatments. We ran the tests from 08:30 pm to 01:45 am. We mounted the camera (Sony HDXR550 mode Night-Shot) perpendicular to the arena. Latency to detect prey and latency to the first prey capture attempt were given the maximum time of 660 seconds for experimental subjects that did move. Differences in the

Variables measured	Treatments and statistics				H and p (Kruskal-Wallis)
	TR	CSR	CEP	CWH	
No. of prey capture attempts per trial	med = 1.2 min = 0 max = 4 (n = 10)	med = 2.8 min = 0 max = 12 (n = 7)	med = 0.8 min = 0 max = 2 (n = 12)	med = 1 min = 0 max = 4 (n = 8)	H = 1.6 p = 0.7
Latency to detect prey (s)	med = 80.1 min = 22 max = 322 (n = 14)	med = 130.4 min = 22 max = 342 (n = 9)	med = 173.2 min = 24 max = 660 (n = 13)	med = 310.6 min = 14 max = 660 (n = 8)	H = 4.90 p = 0.2
Latency to first prey capture (s)	med = 440 min = 76 max = 660 (n = 10)	med = 339.6 min = 54 max = 660 (n = 7)	med = 391 min = 57 max = 660 (n = 12)	med = 497.5 min = 104 max = 660 (n = 8)	H = 2.55 p = 0.5
No. of body orientations	med = 1 min = 0 max = 3 (n = 10)	med = 2.3 min = 0 max = 6 (n = 7)	med = 1.3 min = 0 max = 3 (n = 12)	med = 0.9 min = 0 max = 2 (n = 8)	H = 3.05 p = 0.4

Table 2: Results of the variables measured to test the use of trichobothria in prey detection and capture in the yellow scorpion *Tityus serrulatus*. TR = trichobothria removed, CSR = control setae removed, CEP = control of experimental procedures, CWH = control without handling, med = median, min = minimum, max = maximum.

sample sizes are because some of the videos were not entirely recorded, in which cases we only analysed the available variables.

Analyses

We applied a Shapiro-Wilk test for normality in all experiments, a G-test with Williams correction for the prediction capture success, and a Kruskal-Wallis test for predictions of prey capture attempt, latency to detect prey, latency to the first prey capture attempt, and orientation toward prey. We ran all the tests with BioEstat 5.0 software.

Results

The number of prey capture attempts per trial, latency to detect prey, latency to first prey capture, and number of body orientations did not differ between treatments (Table 1). Crickets would generally walk around the arena, sometimes making pauses. They would usually move in the opposite direction if they touched the scorpion. We did not find significant differences in capture success (G = 0.073, DF = 3, P = 0.995; n (TR) = 10, n (CSR) = 7; n (CEP) = 12, n (CWH) = 8) or any of the other variables measured (Table 2).

Discussion

We did not find differences in the capture success between the treatments. Our results suggest that trichobothria in *T. serrulatus* may not be essential for detecting and capturing at least terrestrial prey and that other sensilla may be involved in prey capture.

A possibility is that scorpions with most trichobothria ablated detected the crickets using substrate-borne vibrations, which can be detected by basitarsal compound slit sensilla, tarsal hairs, and pectines (Brownell & Farley

1979b; Mineo & Del Claro 2006). Thus, those organs would be potential structures used by *T. serrulatus* to compensate for the lack of trichobothria, just as spiders that are still able to find prey without trichobothria (Reißland & Görner 1985).

Scorpions capture a broad range of terrestrial but also of flying prey (review in McCormick & Polis 1990). Flies produce an air flow detected by trichobothria that triggers capture at least in spiders (Klopsch, Kuhlmann & Barth 2013). Air currents simulating moths can also be detected by scorpions (Ashford *et al*. 2018). The spider *Cupiennius salei* jumps toward the air stimulus applied on a leg with intact trichobothria (Barth 2002), but does not jump if the leg lacks trichobothria. Therefore, maybe trichobothria in scorpions are more important in detecting and capturing aerial prey.

Another explanation for why we did not find differences in capture success is that the scorpions would be using the remaining few trichobothria. This would mean that a removal of 86% of the trichobothria would not affect prey capture success, which would suggest another role for these setae besides detecting terrestrial prey. For example, in other arachnids, trichobothria are known to be used in intraspecific communication (Santer & Hebets 2008, 2011), for predator detection (Suter 2003; Ashford *et al*. 2018), and have been suggested to be used during courtship to detect movement of the opposite sex (Brownell 2001).

In summary, our data suggest we should be careful with the assumption that trichobothria are always used for detecting prey. It is possible that at least for some prey in some substrates, these setae may not be required for scorpions to detect and capture prey.

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Two new species of the subfamily Coelotinae (Araneae: Agelenidae) from Central Honshu, Japan

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Abstract

Two new species of the genera *Coelotes* and *Tegecoelotes*, from Central Honshu, Japan, are described under the name of *Coelotes isensis* **n. sp.** and *Tegecoelotes kumadai* **n. sp.** respectively. The former is included in the species group that has four retromarginal teeth on the chelicera, but there is no Japanese species that has a similar form of genital organs when compared to the new species. The latter can be distinguished from all congeneric species by its unique tegulum protruding downward in the male palp. In addition, male of *T. kumadai* is characterized by the leg formula of I–IV–II–III.

Introduction

The subfamily Coelotinae, mainly distributed throughout Asia, is rich in diversity, but many species described up to now are from China (Li *et al*. 2019a,b,c; Zhao *et al*. 2019). In Japan, there are many islands and a complex coastline; in these environments, 11 genera and 119 species of coelotine spiders have been discovered, and 110 of these are endemics (World Spider Catalog 2019). However, poorly surveyed areas still remain, and undescribed species are occasionally discovered in those localities (Okumura 2013, 2017). It has become clear that small specimens collected from Mie Prefecture have unique genital organs in both sexes, which are morphologically different from those of all other coelotine species in Japan. The conductor of the male palp is characterized by beimg short, thick and bifurcate, and the epigyne by its longitudinal and blackish markings stemming from the internal genitalia. In addition, an undescribed species of the genus *Tegecoelotes* has been collected from the Niigata and Nagano Prefectures. *Tegecoelotes* is highly diverse in Japan, where 13 of the 15 species in this genus are known to date. The tegulum of the male palp of newly collected specimens is markedly pointed in lateral view, and no other *Tegecoelotes* species have this unique characteristic (Okumura *et al*. 2009; Okumura, Nishikawa & Ono 2011). In this paper, I describe the two new species mentioned above, in the subfamily Coelotinae, from Central Honshu, Japan, as members of the genera *Coelotes* Blackwall, 1841 and *Tegecoelotes* Ovtchinikov, 1999, and show the characteristic differences between related species.

Methods

Examination and illustration were performed using an Olympus SZX-7 stereomicroscope. In order to examine the genital organs, the left male palp was removed, and the epigyne was dissected and treated in 10% KOH solution to remove muscle as necessary. Photographs were taken using an Olympus E-620 digital camera attached to the microscope. Measurements of respective body parts were performed using a micrometer mounted on an ocular lens. All measurements are given in mm. Leg measurements are given as total length (femur, patella & tibia, metatarsus, tarsus). Descriptive terminology follows Wang (2002) and Ono (2009). Abbreviations: ALE = anterior lateral eye, AME = anterior median eye, CD = copulatory duct, CO = conductor, EM = embolus, ET = epigynal tooth, FD = fertilization duct, LTA = lateral tibial apophysis, MA = median apophysis, MOA = median ocular area, PA = patellar apophysis, PLE = posterior lateral eye, PME = posterior median eye, RTA = retrolateral tibial apophysis, SH = spermathecal head, SP = spermatheca. The voucher specimens are deposited in the collection of the Department of Zoology, National Museum of Nature and Science, Tsukuba (NSMT), Japan.

Family Agelenidae C. L. Koch, 1837

Coelotes isensis n. sp. (Figs. 1, 2)

Japanese name: Ise-yachigumo

Type material: Holotype ♂, Toyokawa Town, Ise City, Mie Pref., 5 October 2003, K. Kumada leg. (NSMT-Ar 16985). Allotype ♀, same data as holotype (NSMT-Ar 16986). Paratypes: 1♂, Ujitachi Town, Ise City, Mie Pref., 8 November 2003, K. Kumada leg. (NSMT-Ar 16987); 1♀ Ujitachi Town, Ise City, Mie Pref., 29 December 2003 K. Kumada leg. (NSMT-Ar 16988).

Other material examined: All specimens were collected from Mie Prefecture, Japan. Eikai, Taiki Town, Watarai County, 4♀♀, 21 October 2000, K. Nojima leg.; Ujitachi Town, Ise City, 4♀♀, 26 November 2003, 2♀♀, 29 December 2003, K. Kumada leg; Maeyama Town, Ise City, 2♀♀, 27 November 2003, K. Kumada leg; Murayama, Minamiise Town, Watarai County, 1♀, 30 December 2018, K. Okumura leg.

Distribution: Mie Prefecture (Fig. 3).

Etymology: The trivial name is derived from the type locality.

Diagnosis: *C. isensis* n. sp. is classified into the group of species that have four retromarginal teeth on the chelicera. However, this species can be distinguished from the other Japanese species by its short, thick and bifurcate conductor in the male palp, and the blackish markings extending longitudinally in the female epigyne.

Description of male holotype: Total length 6.4, carapace 3.4 long, 2.1 wide; abdomen 3.0 long, 1.8 wide; sternum 1.6 long, 1.4 wide. Eye sizes; AME 0.10, ALE 0.16, PME 0.11,

Fig. 1: *Coelotes isensis* n. sp., male, dorsal view.

PLE 0.18. Distances between eyes; AME-AME 0.06, AME-ALE 0.03, PME-PME 0.09, PME-PLE 0.13, AME-PME 0.09, ALE- PLE 0.03. MOA: anterior width 0.26, posterior width 0.31, length 0.30. Leg measurements: I: 8.0 (2.1, 2.7, 2.0, 1.2); II: 7.0 (1.9, 2.4, 1.7, 1.0); III: 6.5 (1.6, 2.2, 1.8, 0.9); IV: 9.0 (2.2, 2.9, 2.7, 1.2).

Palp (Fig. 2A–B): patellar apophysis short, LTA absent, cymbial furrow indistinct, tegulum protruding to the anterior portion of the cymbium, conductor short, thick and bifurcate almost at right angles to each other, embolus flagelliform and short.

Coloration: carapace brown, with blackish brown radial flecks, dorsum of abdomen grayish brown with chevrons,

sternum brown, chelicerae blackish brown, maxillae and labium brown, legs yellowish brown with indistinct ring flecks.

Chericeral promargin with three teeth, and retromargin with four.

Description of female allotype: Total length 6.0, carapace 3.1 long, 2.0 wide; abdomen 2.9 long, 1.8 wide; sternum 1.5 long, 1.2 wide. Eye sizes; AME 0.08, ALE 0.14, PME 0.14, PLE 0.13. Distances between eyes; AME-AME 0.06, AME-ALE 0.06, PME-PME 0.10, PME-PLE 0.14, AME-PME 0.15, ALE-PLE 0.06. MOA: anterior width 0.22, posterior width 0.38, length 0.37. Leg measurements: I: 7.1 (2.0, 2.5, 1.5, 1.1); II: 6.3 (1.8, 2.1, 1.5, 0.9); III: 6.2 (1.7, 2.0, 1.7, 0.8); IV: 8.2 (2.2, 2.7, 2.2, 1.1).

Epigyne and internal genitalia (Figs. 2C–D): epigynal teeth absent, the blackish markings derived from the internal genitalia looks like a shape of *hachi* in kanji, spermathecae thick and close to each other, small spermathecal heads situated in the anterolateral portion of the spermathecae.

Coloration almost same as that of male holotype.

Chericeral promargin with three teeth, and retromargin with four.

Tegecoelotes kumadai n. sp. (Figs. 4–6A,D)

Japanese name: Togari-yamayachigumo

Type material: Holotype ♂, Mt Shindou-san, 169 m, Omi, Itoigawa City, Niigata Pref., 3 October 2018, K. Kumada leg. (NSMT-Ar 16989). Allotype ♀, same data as holotype. (NSMT-Ar 16990). Paratypes: 2♂♂, 3♀♀, same data as holotype. (NSMT-Ar 16991).

Other material examined: All specimens were collected by K. Kumada. Niigata Pref.: Sekigawa, 624 m, Myoukou City, 1♂, 2♀♀, 2 October 2018; Yokozumi, 166 m, Uragawara Ward, Jouetsu City, 12♂♂, 3 October 2018; Hou-
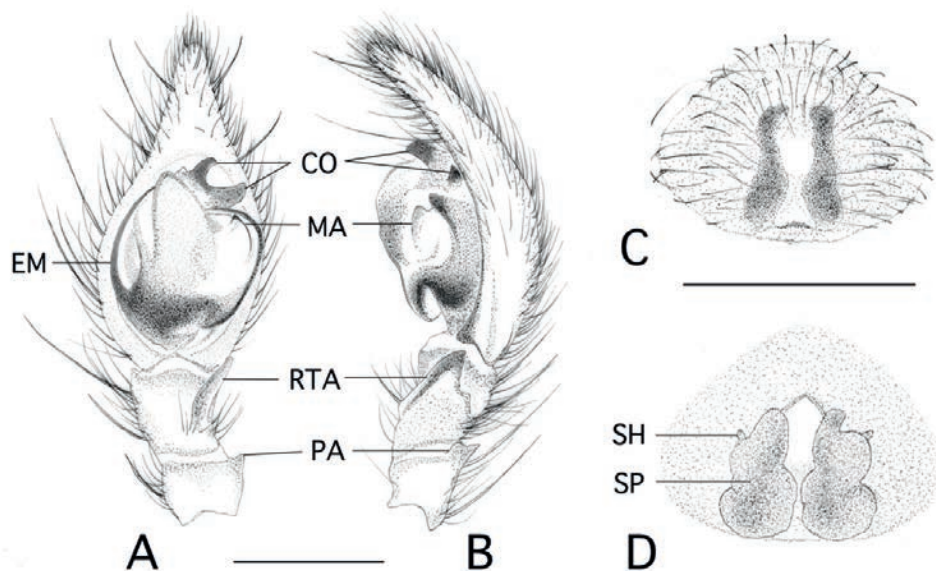

Fig. 2: Genital organs of *Coelotes isensis* n. sp. holotype (A, B), allotype (C) and one of the paratypes (D). **A** male palp, ventral view; **B** same, retrolateral view; **C** epigyne, ventral view; **D** internal female genitalia. Scale bars = 0.5 mm.
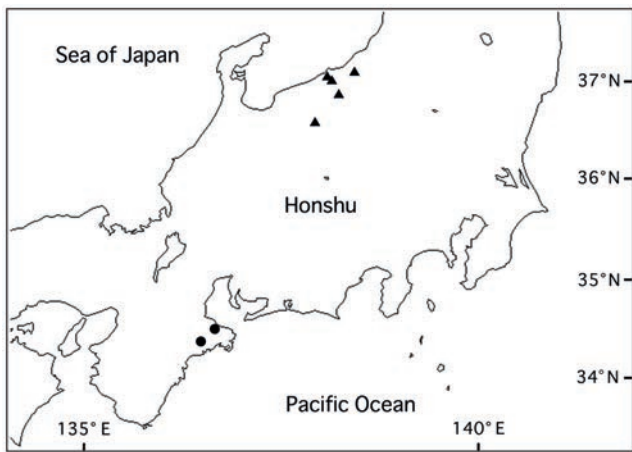
Fig. 3: Distribution of two coelotine species from Central Honshu, Japan. ● = *Coelotes isensis* n. sp.; ▲ = *Tegecoelotes kumadai* n. sp.

jouji, 210 m, Uragawara Ward, Jouetsu City, 1♀, 3 October 2018; Nishihiyama, 490 m, Itoigawa City, 3♂♂, 1♀, 3 October 2018. Nagano Pref.: Iyari, 830 m, Ōmachi City, 6♂♂, 10♀♀, 14 September 2017.

Distribution: Niigata Prefecture, Nagano Prefecture (Fig. 3).

Etymology: The trivial name is dedicated to Mr Ken-ichi Kumada who discovered this new species.

Diagnosis: *Tegecoelotes kumadai* n. sp. resembles *T. michikoae* (Nishikawa, 1977) and *T. secundus* (Paik, 1971) in the general appearance of the genital organs, but can be distinguished from the last species by the structure of the tegulum in the male palp, and the positional relationship of the epigynal teeth and the surface of the anterolateral portion of the epigyne in the female (Fig. 6). The tegulum extremely protrudes in *T. kumadai*, while it is flat in the other species. The epigynal teeth of *T. kumadai* are closer to each other than those of *T. michikoae*. The smooth portions

Fig. 4: *Tegecoelotes kumadai* n. sp., male, dorsal view.

with no setae exist in the anterolateral sides of epigyne in *T. kumadai*, but are indistinct in *T. secundus*.

Description of male holotype: Total length 9.1, carapace 4.2 long, 3.3 wide; abdomen 4.9 long, 2.7 wide; sternum 2.4 long, 2.1 wide. Eye sizes; AME 0.15, ALE 0.24, PME 0.20, PLE 0.18. Distances between eyes; AME-AME 0.10, AME-ALE 0.06, PME-PME 0.18, PME-PLE 0.20, AME-PME 0.18, ALE-PLE 0.05. MOA: anterior width 0.40, posterior width 0.58, length 0.53. Leg measurements: I: 18.6 (4.7,
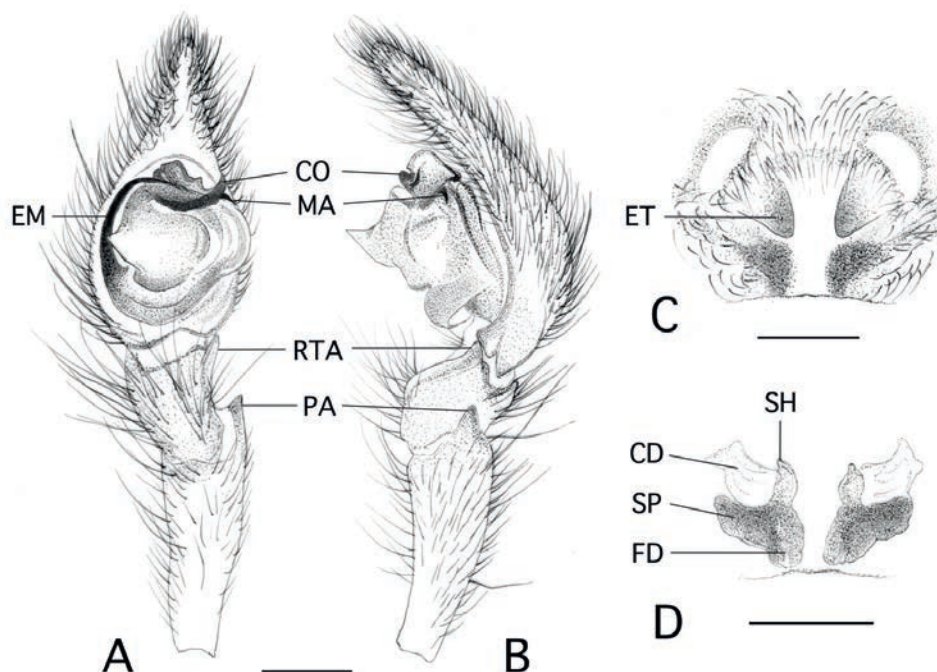

Fig. 5: Genital organs of *Tegecoelotes kumadai* n. sp. holotype (A, B), allotype (C) and one of the paratypes (D). **A** male palp, ventral view; **B** same, retrolateral view; **C** epigyne, ventral view; **D** internal female genitalia. Scale bars = 0.5 mm.
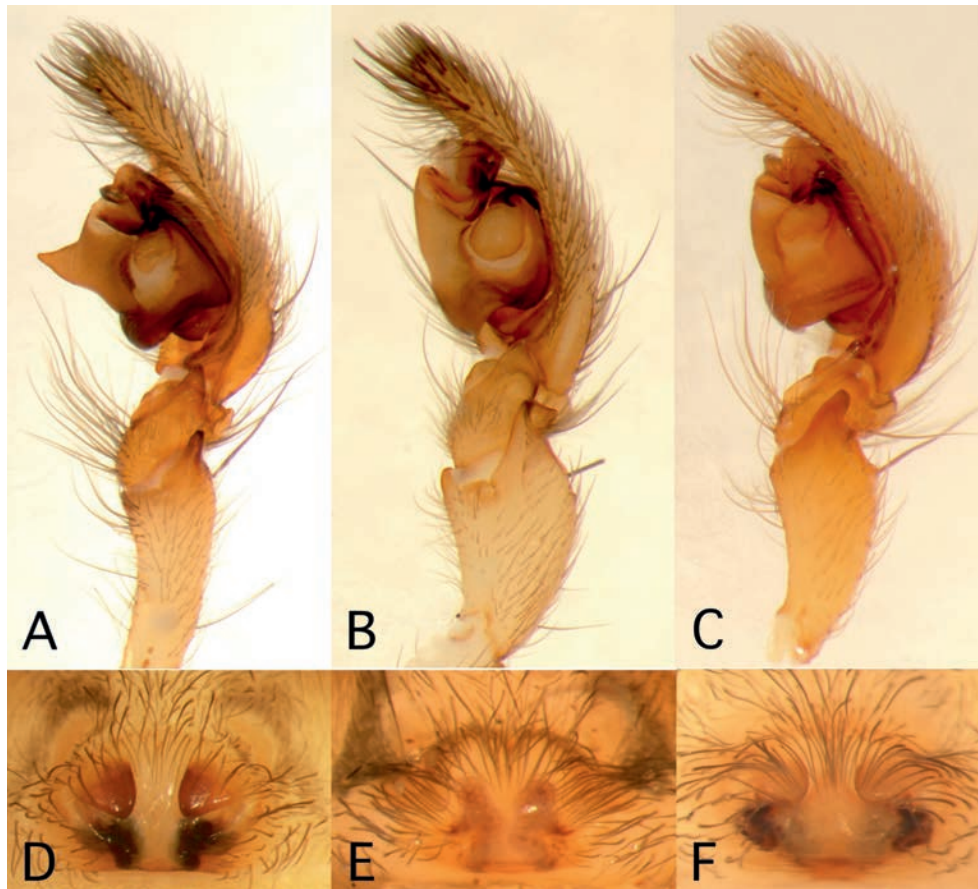
Fig. 6: Comparison of genital organs of three species of *Tegecoelotes*. **A, D** *T. kumadai* n. sp.; **B, E** T. michikoae (Nishikawa 1977); **C, F** *T. secundus* (Paik, 1971).

6.8, 4.5, 2.6); II: 16.4 (4.4, 5.4, 4.2, 2.4); III: 14.5 (4.0, 4.4, 4.1, 2.0); IV: 17.9 (4.6, 5.7, 5.3, 2.3).

Palp (Figs. 5A–B, 6A): patellar apophysis short, LTA extremely small, cymbial furrow short and indistinctive, tegulum protrude to the ventral side and are pointed, conductor curved to the anterior portion of the cymbium, median apophysis small and needle-shaped, embolus flagelliform.

Coloration: carapace brown, with indistinct radial flecks, dorsum of abdomen grayish brown with indistinct chevrons, sternum and labium yellowish brown, chelicerae and maxillae brown, legs yellowish brown without ring flecks.

Chericeral promargin and retromargin with three teeth.

Description of female allotype: Total length 11.1, carapace 5.4 long, 3.5 wide; abdomen 5.7 long, 3.3 wide; sternum 2.5 long, 2.1 wide. Eye sizes; AME 0.18, ALE 0.25, PME 0.18, PLE 0.16. Distances between eyes; AME-AME 0.13, AME-ALE 0.08, PME-PME 0.20, PME-PLE 0.28, AME-PME 0.13, ALE- PLE 0.05. MOA: anterior width 0.49, posterior width 0.56, length 0.59. Leg measurements: I: 15.0 (4.0, 5.2, 3.7, 2.1); II: 13.7 (3.8, 4.5, 3.5, 1.9); III: 12.4 (3.4, 4.1, 3.3, 1.6); IV: 16.1 (4.3, 5.1, 4.7, 2.0).

Epigyne and internal genitalia (Figs. 5C–D, 6D): epigynal teeth broad, and somewhat distant from each other, the blackish markings derived from the internal genitalia situated posterior portion of epigynal teeth, spermathecae Y-shaped and close to each other, copulatory ducts situated in the anterior portion of the spermathecae.

Coloration almost same as that of male holotype.

Chericeral promargin and retromargin with three teeth.

Remarks: The leg formula of coelotine spiders is normally IV–I–II–III, but it has been known to date that in the male of a few species it is I–IV–II–III in Japan (Nishikawa 1983; Okumura, Nishikawa & Ono 2011). In this study, it became clear that the leg formula in the male of *T. kumadai* is also I–IV–II–III.

Acknowledgements

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Density-dependent aggression, courtship, and sex ratio in a fishing spider

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Abstract

Sexual cannibalism is common in spiders and can be advantageous for female fitness by increasing egg production. However, it is possible that, under low mate density, females will be at risk of consuming all of the males they encounter prior to copulation. Cannibalistic females may be able to mitigate the risk of virgin death if they reduce cannibalism rates in response to low mate availability. Here, we attempted to manipulate perceived mate density and observe whether it affected female aggression towards males in the fen raft spider (*Dolomedes fimbriatus*). We predicted that female attack rate would increase in response to an increasing number of male encounters. We also recorded male courtship effort. Despite previous literature finding that *D. fimbriatus* females were highly aggressive towards conspecific males, we found that females only attacked courting males in 14% of encounters. None of these attacks resulted in cannibalism. Moreover, attacks were not associated with how many males the female had previously been exposed to. Male courtship effort decreased in response to repeated exposure to females. Some of the virgin females laid and guarded unfertilized egg cases; this made them unattractive to males, potentially reducing their reproductive lifespan prematurely.

Keywords: mate encounter • sexual cannibalism

Introduction

Behavioural plasticity, the ability of organisms to modify their behaviour to suit the environment, can be vital for sustaining individual fitness in a changing habitat (Chevin, Lande & Mace 2010). The effects of plasticity on individual fitness have also been shown to scale up to the population-level and play a crucial role in predicting population viability (Hoare *et al.* 2007; Chevin, Lande & Mace 2010). This is particularly true for populations in habitats that are rapidly declining in quality due to human impacts. As such, it is now more important than ever to understand how animals change their behaviour in response to different environmental scenarios (Sih, Ferrari & Harris 2011). Behaviours are likely to vary in how influential they for determining the fate of an individual or a population in a changing environment (Schlaepfer, Runge & Sherman 2002). One behaviour that may be particularly important in a changing habitat is mating behaviour, because it is fundamental for facilitating reproduction and the persistence of a population. Many factors may reduce mating success in changing habitats. For example, low population density is a known result of habitat disturbance (Andren 1994) and can negatively affect both individual fitness and per capita growth rate via reduced mate encounter rates (Gascoigne *et al.* 2009). If an organism can alter its reproductive behaviour when potential mates are rare, it may mitigate the reduction in mate encounter rates. In several species there is evidence to suggest that individuals can modify behaviours to maintain mate encounters in sparse populations; for example, by relaxing mate rejection rate or increasing mate searching rate (Lehmann 2007; Holwell *et al.* 2016). How-

ever, it is also possible that some species will be unable to mitigate reductions in mate density by modifying their behaviour, particularly if similar changes in density have not occurred in the recent evolutionary history of the species (Rhainds 2010; Sih, Ferrari & Harris 2011).

One behaviour that might reduce mating rates in a changing habitat is sexual cannibalism (Fisher *et al*. 2018). Sexual cannibalism typically involves a female devouring a male immediately before, during, or immediately after copulation. It has been formally observed in a variety of predatory invertebrates, but has been most commonly reported in spiders (Birkhead, Lee & Young 1988; Elgar & Nash 1988; Arnqvist 1992; Kralj-Fišer *et al*. 2016). In all instances of sexual cannibalism, a reproductive male is removed from the population, potentially increasing male scarcity. Moreover, in the case of pre-copulatory cannibalism, as well as killing a male, females may directly increase their risk of virgin death. Theoretical studies have shown that sexual cannibalism, in particular pre-copulatory cannibalism, can have a negative impact on individual fitness and population viability under certain ecological conditions, in particular low mate density (Wilder, Rypstra & Elgar 2009; Fisher *et al*. 2018; Fisher *et al*. unpublished data). This negative impact of sexual cannibalism could be mitigated if females reduce cannibalism rates in sparse populations. There is evidence of this kind of behavioural plasticity in some cannibalistic species where females reared in low density environments are less likely to cannibalize potential mates (Johnson 2004; Rabaneda-Bueno *et al*. 2008). However, in the absence of behavioural plasticity, females may continue to cannibalize males at a high rate, meaning that the probability a female will consume all of the males she encounters will increase as mate encounter rate decreases. Thus, virgin death rates may increase as a result of low mate density (Wilder, Rypstra & Elgar 2009; Fisher *et al*. unpublished data).

Female fishing spiders (family Pisauridae) are known to be particularly aggressive towards potential mates and, in some species, are known to attempt to cannibalize nearly all approaching males (Arnqvist 1992; Johnson & Sih 2005; Schwartz, Wagner & Hebets 2013, 2016). Furthermore, a lack of variation in cannibalism rates in response to different environmental contexts has also been demonstrated in some fishing spiders (Arnqvist 1992; Johnson 2001); thus, it is possible that cannibalism is not plastic in response to environmental cues for mate density.

Here, we investigate cannibalism in the fen raft spider, *Dolomedes fimbriatus*. *D. fimbriatus* is found throughout Western Europe and is one of only two fishing spiders found in the United Kingdom (Duffey 1995), the other being the congeneric and critically endangered *Dolomedes plantarius* (Smith 2000; Leroy *et al*. 2013). Penultimate instar and adult female *D. fimbriatus* are specialist hunters that rely on areas of freshwater to catch their prey. Due to their specific habitat criteria, populations of *D. fimbriatus* may be particularly vulnerable to decline if habitats are damaged. Indeed, specific habitat requirements may have exacerbated the negative effects of habitat change that led to the recent decline

(Smith 2000) and predicted continued decline of *D. plantarius* (Leroy *et al*. 2013). Discovering whether sexual cannibalism is plastic in response to mate density would help us to understand if cannibalism can accelerate population decline in damaged habitats, and may have implications for the conservation of *Dolomedes* spp. in the UK.

In this study, we manipulated mate encounter rate in adult female *D. fimbriatus* to test whether female aggression is affected by mate availability. We predicted that, to reduce the risk of virgin death, females would be less aggressive towards males when male density was perceived to be lower. We also predicted that older virgin females would be less likely to attack approaching males, again, to reduce their risk of virgin death. Male courtship effort is often thought to signal male quality in cannibalistic spiders (Shamble *et al*. 2009). It has previously been shown that high courtship effort reduces cannibalism risk in spiders (Hebets & Uetz 2000; Prenter, MacNeil & Elwood 2006). As such, we predicted that male courtship latency (a common proxy for courtship effort (Eastwood 1977; Wilgers & Hebets 2012)) would be positively associated with cannibalism. Finally, we predicted that male courtship effort would be energetically constrained and thus decrease in response to repeated exposure to females.

Methods

Recording, collection, and rearing

We collected the spiders at Thursley Common Nature Reserve, which is situated in the south-west of England and is comprised mainly of heathland bog. There is a wooden boardwalk that intersects the reserve that provided a consistent sampling transect and allowed for safe access to the bog pools. We visited the reserve a total of 10 times over two years (2016 and 2017) between the months of April and June. On each visit we walked the entire length of the boardwalk and looked for *D. fimbriatus* in the adjacent pools. Upon locating a spider, the sex of the individual was recorded before an attempt at capture was made. Typically, it is only possible to confidently differentiate between males and females by casual observation after they have reached their penultimate instar. At this stage, males have a considerably smaller thorax and abdomen relative to their leg length, and the legs of the male are thinner than those of the female. A mixture of juvenile and adult males were collected; however, only juvenile females were taken to ensure that all females used in laboratory experiments were virgins. Individuals were then returned to the lab, kept at 22 °C and housed in ventilated 75 × 210 × 130 mm (H × W × D) plastic containers containing water to a depth of ~1 cm and a small piece of slate which formed a dry island that acted as a refuge. Enclosures were cleaned regularly and individuals were fed juvenile crickets (*Gryllus* sp.) *ad libitum*.
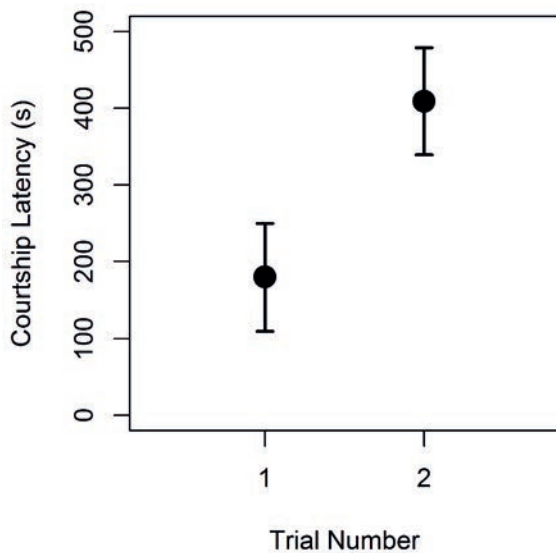
Fig. 1: Mean time taken for a male *Dolomedes fimbriatus* to begin courtship in their first and second exposure to virgin females. Error bars indicate 95% confidence intervals.

Behavioural trials

Behavioural trials took place in large 170 × 530 × 340 mm (H × W × D) enclosures containing water to a depth of ~2 cm. All females used in the trials had been adults for at least 23 days and the mean female age (time since final moult) was 40 days. A small rock was placed at either end of the enclosure to form two islands. Because adult female *D. fimbriatus* have a tendency to become stressed upon being moved between enclosures (A. Fisher personal observation), females were introduced to the trial enclosure the day before the trial took place and were left there overnight. This was intended to reduce the chance of any observed aggression towards the male being the result of stress due to human interference. Leaving females in the enclosure overnight also gave them the opportunity to explore the enclosure and lay down silken draglines. Silken draglines are known to induce courtship behaviour in males of several spider species including *D. fimbriatus* (Tietjehn 1977; Arnqvist 1992). To begin the trial, males were introduced to the rock island at the opposite end of the enclosure to the female. We then recorded the length of time it took before the male began courting the female, and whether or not the female attacked the male. Male courtship and approach behaviour consisted of intermittent bouts of the male using his forelegs to tap the female dragline and the surface of the water, whilst traversing the dragline towards the female. Trials were terminated if the male took longer than 15 minutes to begin courting, stopped courting for over 15 minutes, or made contact with the female. If contact was made, trials were terminated so that males and females would remain as virgins for the subsequent trials. To manipulate mate encounter rate, we introduced a new male to the female on each of the following two consecutive days. Hence females were exposed to three different males, over three days, but all females remained virgin throughout the experiment. Increased exposure to conspecifics in the lab has been

shown to induce density-dependent behavioural responses in other species of predatory invertebrate (Rabaneda-Bueno *et al*. 2008; Brown, Muntz & Ladowski 2012). 17 males were used in trials with 11 females, and no females were paired with the same male twice. After the behavioural trials had been completed, the spiders continued to be cared for in the lab. During this time, five of the virgin females laid and guarded unfertilized egg cases. Further behavioural trials (using the same method) were performed on these females to test whether females continued to attract males after laying an unfertilized egg case.

Statistical analyses

Female aggression was analysed using a Generalized Linear Mixed-effects Model (GLMM) with a binomial error structure. Attack (binary) was the response variable, the fixed effects were: female age (time since final moult), the number of males the female had previously been exposed to, and male courtship latency. Because our experimental design involved repeated measures of the same females, female ID was included in the model as a random effect to avoid pseudoreplication. Male courtship latency in response to repeated exposure to females was analysed using a GLMM with a Gaussian error structure where the response variable was latency to begin courting (seconds) and the fixed effect was trial number. Because repeated measures of the same males were used, male ID was included in the model as a random effect. To test whether an increase in age was associated with a change in courtship latency, we conducted a Spearman's rank correlation test between age increase over trials and courtship latency. Finally, to test how the abundance of males and females changed across the season, a Generalized Linear Model (GLM) with a Poisson error structure was used. The fixed effects were an interaction term between sex and time (number of days from the first day of sampling) and an interaction term between sex and time^2. Time was included as a quadratic term to test for the presence of a non-linear relationship between the abundance of males and females and time. Due to the fact that only five females laid unfertilized egg cases, no formal analysis was carried out on the effect that laying an unfertilized egg case had on male courtship behaviour.

Results

Out of a total of 29 trials, females were only observed attacking males in four of the trials. In all cases, the female attacked the male prior to copulation. Males always managed to escape the female, thus none of these attacks resulted in cannibalism. The likelihood that a female would attack a male was not significantly associated with female age (df = 26, z = 0.194, p = 0.846), the number of males the female had been previously exposed to (df = 26, z = -0.333, p = 0.739), or male courtship latency (df = 26, z = -0.990, p = 0.322). However, courtship latency was significantly greater for males who had previously been exposed to a
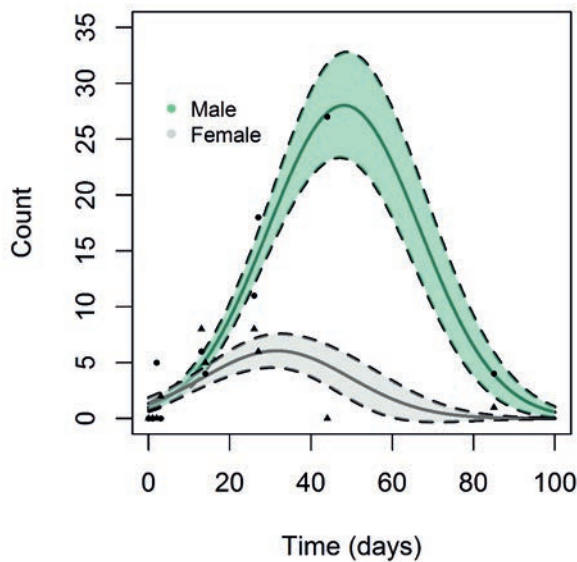
Fig. 2: Male (circular points) and female (triangular points) *Dolomedes fimbriatus* abundance in response to time after 23 April. Data was collected from April–June in 2016 and 2017. Shaded areas indicate 95% confidence intervals

female (Fig. 1: $df = 30$, $z = 2.534$, $p = 0.0223$). There was no significant correlation between the amount of time between the male's first and second encounter with a female and courtship latency (Spearman's rank correlation $\rho = -0.378$, $S = 771.82$, $p = 0.165$), implying that an increase in age was not responsible for the increase in courtship latency. Spiders continued to be cared for in the lab after the behavioural trials were completed. During this time, five virgin females laid and guarded unfertilized egg cases. Upon being exposed to these females, males gave no indication of attempting to court. This suggests that, despite still being virgin, females that lay unfertilized egg cases cease to be attractive to males.

Over the 10 field surveys, 75 males and 30 females were recorded. Although males were more abundant than females, this difference was marginally non-significant ($df = 19$, $z = 1.851$, $p = 0.0642$). Both male and female abundance between the months of April and June had a significant negative relationship with time[2] (Fig. 2: males: $df = 19$, $z = -6.809$, $p < 0.0001$; females: $df = 19$, $z = -2.272$, $p = 0.0231$). There was a marginally non-significant interaction between abundance and sex over the course of the season ($df = 19$, $z = 1.861$, $p = 0.0628$).

Discussion

In this study, *D. fimbriatus* were far less aggressive towards males than has been shown in previous studies on *D. fimbriatus* and other species of the genus *Dolomedes*. Attack rates were very low and we found no effect of female age, perceived mate density or male courtship effort on the likelihood that a female would attack an approaching male. However, we have shown that courtship latency in males increased significantly upon being exposed to a second female, implying that there has not been strong selection for males that have consistent courtship behaviour. We have also shown that females that lay an unfertilized egg case become unattractive to reproductive males, despite the fact that they are still virgins, potentially lowering reproductive rates. Finally, we provide evidence that the sex ratio is male biased, which is common in other spider species (Fromhage, Jacobs & Schneider 2007; Fromhage, McNamara & Houston 2008) and will likely have important implications for mate availability and competition.

In the past, adult female spiders of the genus *Dolomedes* have been shown to be highly aggressive towards reproductive males. In 1992, Arnqvist reported that female *D. fimbriatus* attacked courting males in 87% of encounters. Similarly, female *D. tenobrosus* have been shown to attack males prior to copulation in up to 68% of encounters (Schwartz, Wagner & Hebets 2014). In this study, we found that females only attacked males in 14% of encounters. One reason for these comparatively low attack rates could be female satiation, removing the requirement for females to consume males in order to obtain nutrients (Barry, Holwell & Herberstein 2008). However, this goes against evidence in *D. triton* which suggests that female attack rate is not dependent on female body condition (Johnson & Sih 2005). It could also be that the adaptive benefits of sexual cannibalism vary across different populations of *D. fimbriatus*, thus selecting for variation in aggression across populations. For example, in habitats where individuals are sparse and mate encounter rates are low, females may be selected to maximize their chance of being fertilized by lowering their precopulatory attack rates. Behavioural divergence between populations may be particularly common in *D. fimbriatus*, because their specific habitat requirements and lack of long-range dispersal ability may make populations very isolated (Suter 1999; Vugdelić 2006; Duffey 2012; Leroy *et al*. 2013). As such, genetic mixing with neighbouring populations is highly unlikely to occur, allowing behaviours to evolve to suit particular challenges imposed by specific habitats.

It is fairly common for female spiders and insects to cease to attract males once they have mated, particularly if approaching a female is potentially costly for males due to cannibalism risk (Lelito & Brown 2006; Gaskett 2007). Attractiveness to males is often thought to be associated with pheromone production, so a reduction in the attractiveness of mated females is likely to be due to reduced pheromone production (Roberts & Uetz 2005). Here we report an unusual circumstance in which virgin females cease being attractive to males following the oviposition of an unfertilized egg case. To our knowledge, this has not been shown previously in *Dolomedes* spp. and may not have been found in other spiders. Becoming unattractive to males before being mated is likely to increase a female's probability of dying a virgin, particularly in sparse populations where mate encounter rate is low. As such, one would expect strong selection against this. It may be that encounters with males in the wild are common, and thus the risk of a female remaining unmated is low, meaning that there is little to no advantage of remaining attractive to males for a

long period of time. Male-biased operational sex ratios (OSR) are commonly reported in orb-weaving spiders (Fromhage, Jacobs & Schneider 2007; Fromhage, McNamara & Houston 2008) and have also been seen in *Dolomedes triton* (Zimmermann & Spence 1992). Conditions such as a male-biased OSR, which has been suggested by this study (Fig. 2), may lead to an excess of males being available to females. This would increase the probability that females will mate early in their adult life, and remove the need for females to remain attractive to males for an extended period of time. In addition, there is evidence to suggest that pheromones produced to attract males can bear a significant energetic cost in some species of spider (Baruffaldi & Andrade 2015). Therefore, it may be advantageous for females to stop producing pheromones if they are likely to have mated, as this will allow them to allocate more energetic resources into egg production.

Monogyny is fairly common in spiders, and evidence of male adaptation to monogyny in spiders is perhaps most obvious in instances where males sacrifice themselves after their first copulation to boost the fecundity of the female and delay her re-mating (Andrade 2003; Schwartz, Wagner & Hebets 2013). The occurrence of male-enforced monogyny is often hypothesized to have evolved in response to a low probability that males will get a second opportunity to mate, either because males are likely to be cannibalized by the first female they encounter or because there is a high mortality risk associated with searching for females (Buskirk, Frohlich & Ross 1984; Kasumovic *et al.* 2006). Similarly, there is evidence that high levels of male-male competition may also be enough to facilitate the persistence of monogyny in natural populations (Fromhage, McNamara & Houston 2008). It would therefore be most adaptive for males to invest maximally in their first mating. In some spiders, increasing courtship effort is known to decrease the likelihood of cannibalism prior to copulation. In this study we show a reduction in male courtship effort in response to exposure to a second female. As such, males have not been strongly selected to display consistent courtship behaviour, which could be indicative of a system where males are unlikely to re-mate. However, because female attacks on males were uncommon, our evidence suggests that cannibalism is unlikely to be responsible for a lack of courtship consistency. Theoretical and empirical studies on spider mating systems indicate that male-biased sex ratios may be associated with the evolution of monogyny (Fromhage, Elgar & Schneider 2005; Fromhage, McNamara & Houston 2008; Schneider & Fromhage 2010). Therefore, we suggest that the high male-biased sex ratio demonstrated in this study may create conditions in which male competition is so high that the probability of a male getting access to a second virgin female is very small. Thus, we provide evidence for the hypothesis that male-biased sex ratios may be in part responsible for the evolution of males that are adapted for maximising their reproductive output during a single encounter with a female. It is also worth noting that males are often the dispersing sex in adult spiders (Andrade 2003; Kasumovic *et al.* 2006). Therefore, male *Dolomedes fim-*

briatus may be likely to be travelling between patches of water in search of females. Because we only surveyed spiders found on or immediately near patches of water, our counts may in fact underestimate the abundance of males relative to females.

In this study, we have shown that female aggression towards potential mates can be rare in *Dolomedes* fishing spiders. This goes against the evidence provided by previous studies which show very high attack rates. We therefore think that aggression in *D. fimbriatus* may be population-specific, and that differences across populations could have evolved to mitigate environmental challenges such as reduced mate availability. We also show that virgin female *D. fimbriatus* become unattractive after ovipositing an unfertilized egg case. Although this may not reduce female fitness if females are likely to mate early in their adult lives, in sparse populations where males are rare, it could be that females increase their risk of dying as virgins by laying unfertilized egg cases. Our field data suggest that the OSR may be heavily male biased. This may create high levels of competition among males for access to females, thus reducing the likelihood that males will be able to mate twice. This may explain why we found a significant reduction in male courtship effort in response to males being exposed to a second female. The mating dynamics of *Dolomedes fimbriatus* are still poorly understood but could play a vital role in determining species vulnerability to extinction. We suggest that a cross-population study observing how aggression towards males and female mating rate interacts with natural mate density would be valuable for designing conservation strategies for *Dolomedes*.

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