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Asymmetric female genitalia and other remarkable morphology in a new genus of cobweb spiders (Theridiidae, Araneae) from Madagascar

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Symmetry is such a conspicuous feature of life that asymmetries draw our immediate attention. While not uncommon in bilateral organisms in general, asymmetry in spiders is rare. Here I report the first case of antisymmetry in external female genitalia in spiders, in the new genus ***Asygyna*** (Theridiidae: Araneae) from Madagascar. In the nearly 39 000 species of spiders described to date, the external structure of the female genitalia is symmetric. In entelegyne spiders paired external copulatory openings each lead to an internal copulatory duct, whose roughly symmetrical trajectories terminate in paired receptacles, the spermathecae. In *Asygyna*, here exemplified by two new species, ***A. huberi*** and ***A. coddingtoni***, laterality is evident in the internal and external female genitalia. A single copulatory opening leads (either to the left or right depending on the individual) to a single copulatory duct with a distinctly asymmetric trajectory. The duct splits terminally shortly before entering the two spermathecae. The males are symmetric, but possibly only one palp can be used in copulation with each female. If adaptive, the selective forces behind this asymmetry are perplexing, as male access to females seems reduced. However, if males are plentiful, asymmetry may benefit the female by reducing insertion times and thus shortening copulation time, and by tightening her control over which males sire her offspring. *Asygyna* has a range of other bizarre sex-related morphologies, including prosomal pits and a well developed stridulatory mechanism in both sexes, a male proboscis, and simplified palps. A phylogenetic analysis, including 63 taxa and 242 morphological characters, places *Asygyna* in Pholcommatinae, sister to the enigmatic genus *Carniella*.

ADDITIONAL KEYWORDS: antisymmetry – asymmetric epigyna – clypeal proboscis – copulation – mating – Pholcommatinae – prosomal pits – stridulation – theridiid phylogeny.

INTRODUCTION

Symmetry, whether bilateral, radial, or spherical, is one of the more conspicuous characteristics of life. Asymmetries, especially in bilateral organisms, thus stand out and draw our attention. Numerous cases of asymmetries are well documented. Obvious examples include amoeba, mammalian hearts and brains, human handedness, fiddler crab claws, skulls of toothed whales, and pleuronectiform (flat) fish (Ludwig, 1932; see also Huber, 2004). Asymmetric genitalia are known in many insects, including Grylloblattodea (grylloblattids), Dictyoptera (cockroaches and mantids), and Phasmida (walking sticks) (e.g. Thorne & Carpenter, 1992; Grandcolas, 1996), and many Diptera (McAlpine, 1981), as well as in various other organisms, including plathelminths, nematodes, cephalopods, 'cyprinodont' fish, and birds (Ludwig, 1932; Tuxen, 1970).

Strangely, fluctuating asymmetry and teratology apart, the list barely includes spiders, which are highly symmetric (Huber, 2004). A few spiders manipulate a symmetric phenotype; a striking case is the mandatory amputation of one of the two sperm transfer organs in the cobweb spiders *Tidarren* Chamberlin

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& Ivie, 1934 and *Echinotheridion* Levi, 1963 (Branch, 1942; Knoflach & van-Harten, 2000, 2001; Knoflach, 2002). Loss and regeneration of limbs (Uetz *et al*., 1996), and sometimes the wrinkling of otherwise symmetrical epigynal scapes (e.g. in some araneids and pholcids) may lead to apparent asymmetry (Levi, 1973; Huber, 2003). Only recently was the first instance of true asymmetry in spider genitalia explicitly discussed (Huber, 2003, 2004), in the pholcid genus *Metagonia* Simon, 1893 (González-Sponga, 1998). Most species of *Metagonia* have asymmetric internal female genitalia, but symmetric male genitalia. The symmetry of the latter presumably stems from the females being antisymmetric, i.e. both left and right 'handed' individuals occur, thus there may be no selection for asymmetry in the male (Huber, 2004). In *M. mariguitarensis* (González-Sponga, 1998), however, female asymmetry is directional (all are same 'handed'), and the males are directionally asymmetrical as well (Huber, 2004).

A few other cases of asymmetric copulatory duct trajectories are found in spiders, e.g. in some hahniids, including *Neoantistea* Gertsch, 1934 (Opell & Beatty, 1976: figs 12–17, 21–23). In all these cases, the female appears symmetric externally, and has paired genital openings and copulatory ducts that both seem functional. Therefore, to the best of my knowledge, in all of the nearly 39 000 hitherto described species of spiders (Platnick, 2004) whose females are known, their genitalia are, barring imperfections, symmetrical externally. The objective of this paper is to report the first case of asymmetric external spider epigyna, with an unpaired genital opening and a single copulatory duct. I offer some remarks on the evolution of asymmetry. I describe two species in a new genus, *Asygyna*, endemic to Madagascar, and illustrate and discuss the range of remarkable morphological features of these small (~1.3–1.9 mm) spiders. Finally, I test the monophyly and estimate the phylogenetic placement of *Asygyna*, by adding the two species to a published morphological data matrix of Theridiidae (Agnarsson, 2003b, 2004) and running a phylogenetic analysis.

MATERIAL AND METHODS

The specimens were collected as part of the Terrestrial Arthropod Inventory of Madagascar project run by the California Academy of Sciences (CAS) and the Tsimbazaza Botanical and Zoological Park (PBZT). This project is funded by NSF Biotic Surveys and Inventories Program (BSI 0072713), McBean Family Foundation, Lakeside Foundation, and the Schlinger Foundation. I encountered the specimens during a 3-week visit at the CAS (funded by C. Griswold), during which I sorted through the theridiid collection. The specimens were kindly lent to the author by Charles Griswold, curator of Arachnology at the Department of Entomology, CAS.

Specimen preparation

For detailed methodology see Agnarsson (2004). Specimens were examined under a Wild M-5 A dissecting microscope. Male palps were removed with fine tweezers and epigyna were excised and cleaned using sharp needles. First examination took place in 95% ethanol. For expansion, palps were immersed in concentrated KOH (~1 g/mL) for 1 min and then transferred to distilled water where rapid expansion took place in less than 1 min (see Coddington, 1990, modified from Shear, 1967). The trajectory of the male sperm duct and female copulatory duct were examined by immersing the genitalia in methyl salicylate, rendering the cuticle transparent (Holm, 1979).

All drawings of genitalia were made using a compound microscope with a camera lucida with specimens temporarily mounted as described in Coddington (1983). The drawings were then scanned and rendered in Adobe Photoshop. For SEM examination specimens were cleaned ultrasonically for 1 min and then transferred to 100% ethanol overnight. The specimens were then dissected, and most of the specimens were submitted to critical point drying, but male palps were air-dried.

Five SEM preparations were done per species: abdomen of both sexes, prosoma of both sexes with male palp and all legs but the 4th (and one leg 1), removed. Specimens were glued to round-headed rivets using an acetone solution of polyvinyl resin, and then sputter coated with gold-palladium. Digital images were taken of specimens positioned on a sand bed in a small dish with alcohol. Several images were taken at different focal planes and these were assembled using AutoMontage. All digital images (SEM and digital camera) were processed, and all drawings made, in Adobe Photoshop. All plates were composed and labelled in Adobe Illustrator.

Epigyna are here labelled 'right handed' if the genital opening leads to the right side of the animal (i.e. to the left from the viewpoint of the researcher examining a specimen ventrally and cephalic region orientated forward), and 'left handed' if the openings lead to the left.

Classification and cladistic analysis

The specimens were originally identified using an interactive key to world theridiid genera (Agnarsson, 2003a). The specimens matched no existing genus, but keyed out closest to the pholcommatines *Carniella*

Thaler & Steinberger, 1988 (see also Wunderlich, 1995; Knoflach, 1996) and *Proboscidula* Miller, 1970 (see also Levi, 1972; Knoflach, 1995). As the inclusion of these species in either genus would dramatically alter the diagnoses of the genera, and quite possibly render them paraphyletic (*Proboscidula* has never been included in a phylogenetic analysis and only a single *Carniella* species is present in Agnarsson's (2004) study, so a definitive test is, as yet, unattainable), the establishment of a new genus seems a logical solution.

The two new species were scored for the 242 characters of Agnarsson's (2004) study. Character scoring for each species was as follows (the full matrix is available at http://theridiidae.com/cladogramsi.html, and will be submitted to treebase.com):

Asygyna huberi: 0001000100000100122000000000-1101101--0200000000–1-----00-0000100000001010 00100-------000000000100000000100201-0000000000 150011110100110111101 1-101111010100001000 111001?000000121101021100100 1?00010001011-000011011 0?011031???????????00??????

Asygyna coddingtoni: 000100010000001001220000000 000-1101101--0200000000-1-----00-000010000000 101000100-------000000000100000000100201-0000000 000150011110110110111101 1-110111101010000 1000111001?000000121101221100100 1?00010001011 -000011011 0?011031???????????00??????

Cladistic analysis was done with NONA (Goloboff, 1993) through the Winclada shell (Nixon, 2002) using mult*1000 command and the ratchet 'island hopper' with 1000 replications, holding 10 trees and selecting 25 characters for each, and PAUP* (Swofford, 2002) with 1000 random stepwise additions, and subtree-pruning and regrafting branch swapping algorithm (all searches done with both amb – and amb =) searching for minimal length trees under the criterion of parsimony. These search algorithms are heuristic, but guaranteed algorithms (e.g. branch and bound) are not computationally feasible for matrices of this size.

Support for the monophyly of the new genus was estimated using bootstrapping (Felsenstein, 1985) and Bremer support (Bremer, 1988, 1994). Successive weighting (Farris, 1969), was used to choose among the two most parsimonious trees.

Character data was compiled and managed in NEXUS Data Editor 0.5.0. (Page, 2001). I used Winclada 1.00.08 (Nixon, 2002) and MacClade (Maddison & Maddison, 2002) to optimize and trace characters on the preferred tree. Data were transferred from NEXUS Data Editor to Winclada via Mesquite (Maddison & Maddison, 2001), allowing the transfer of character information with the data matrix and thus facilitating data exploration.

Taxonomic note

Simon (1889: 228) described *Thyreobaeus scutiger* Simon, 1889, a new linyphiid genus and species from Madagascar based on a single female. Nothing further has been published on this genus, but based on the original description (in Latin, no figures) *Thyreobaeus* may be a senior synonym of *Asygyna*. It is small (1.6 mm), dark, and with a dorsal scutum (rare in female linyphiids) and a distinctly truncated sternum. However, the type vial (at the Paris Museum) is empty and the type thus presumably lost.

List of abbreviations used in the text

AC	aciniform gland spigot(s)
AG	aggregate gland spigot(s)
ALS	anterior lateral spinneret
C	conductor
CHk	theridiid cymbial hook
CY	cylindrical gland spigot(s)
E	embolus
MA	median apophysis
mAP	minor ampullate gland spigot(s)
MAP	major ampullate gland spigot(s)
PI	piriform gland spigot(s)
PLS	posterior lateral spinneret
PMS	posterior median spinneret
ST	subtegulum
T	tegulum

RESULTS

Altogether, about 50 specimens of *Asygyna* were available to me, all from the Madagascar project of the CAS (see Material and methods). These belong to at least eight species, most have asymmetric external epigyna, and all are internally asymmetric. At present, a revision of the genus is quite premature. Only two of the species are found in several samples, are common enough to justify a detailed (destructive) morphological study, and co-occur in samples sufficiently to match sexes with some confidence. Other species were mixed among samples, and at least three are singletons. Most *Asygyna* specimens are from montane rainforest (1000 m and above), although *A. coddingtoni* seems to prefer lowland dry forest. Specimens were almost exclusively caught by means of beating low vegetation and in pitfall traps, whereas none was caught using the normally most productive techniques, e.g. aerial search at night. Given the rarity of these animals in collections (I am only aware of the CAS specimens) and that they may be easily overlooked in the field (e.g. a Smithsonian expedition to Madagascar in 2001 did not encounter any *Asygyna*), it is quite likely that *Asygyna* contains numerous additional undiscovered species.

In both new species the female genitalia are distinctly asymmetric (Figs 1B, F, 2F–H, N–P, 6D–F, 7D,

10A–C) with a single copulatory opening that leads to an unpaired copulatory duct. The trajectory of the copulatory duct is complex, especially in *A. coddingtoni* (Figs 1C, D, G, H, 2P), and in both species the duct splits just prior to entering both spermathecae (Fig. 1D, H). The ultimate part of the copulatory pathway is thus symmetrical. As in both species different individual females may be either right or left handed (compare Figs 2N, O, 10A, B), this is an example of antisymmetry (Huber, 2004).

The samples include 15 females of *A. coddingtoni*, and 10 of *A. huberi*. Of the latter, eight are right handed and two left handed, while for *A. coddingtoni* 11 are right handed and four left handed. Unfortunately, these meagre data offer little scope for interpretation, but are possibly suggestive. The chances of ten 'trials' resulting in eight or more of one 'type', assuming random chance, are approximately 0.055 (according to tables of binominal probabilities; chi-square, $P = 0.058$). The chances of 15 'trials' resulting in 11 or more of one 'type' are approximately 0.059 (binominal probabilities; chi-square, $P = 0.071$). Lumping the two species together, the chances of 19 out of 25 specimens being right handed are 0.007 (binominal probabilities; chi-square, $P = 0.009$).

Epigyna apart, females and males, including their sperm transfer organs (palps), appear perfectly symmetrical. But they do show a range of other unusual or unique morphological features. *Asygyna* shares with the pholcommatines *Carniella*, *Craspedisia* Simon, 1894, and *Proboscidula* (together counting only 15 species) the presence of a male proboscis (Figs 2E, K, 4A–C, E, 9B–E, see also Levi, 1963; Knoflach, 1995). While the probosces of *Carniella*, for instance, are similar between species, those of *Asygyna* are diagnostic for each species (compare Figs 4A and 9B). *Asygyna* species have a particularly well developed abdomen–prosoma stridulatory apparatus (Fig. 9A), and females of *A. huberi* are unique among theridiids (see Agnarsson, 2004) in having it no less developed than the male (compare C and D, Fig. 4). *Asygyna* has distinct prosomal warts and pits (Figs 4A–F, 9B–F). Similar modifications are phylogenetically widespread, but relatively uncommon in theridiids (see, e.g. Levi & Levi, 1962; Agnarsson, 2003a, 2004; Knoflach & Pfaller, 2004; Knoflach, 2004), and again the females are unusual in having them no less pronounced than the males (Figs 4D, 9F, also present in females of the cobweb genus *Wirada* Keyserling, 1886). The regular rim of these warts and pits, surrounding the stridulatory area of both sexes is also unusual (Fig. 9A, but a similar pattern is seen in at least some female *Crustulina* Menge, 1868; see Agnarsson, 2004: fig. 42H). Male *Asygyna*, uniquely among theridiids, have a single aggregate gland spigot (AG) fully developed (Figs 6C, 7F), whereas the other one, and the flagelliform (FL) are absent. In most male theridiids (as in other araneoids) the 'araneoid triplet' (the two AGs plus a FL) is absent, but in the few that have the triplet, both the AGs are fully developed (Agnarsson, 2004). Aggregate gland spigots produce sticky material (glue) that is specifically used to wrap-attack prey (e.g. Coddington, 1989); most adult male spiders do not attack prey, and many do not feed at all and are short lived. Unusually, the FL is also nonfunctional (absent) in the female (Figs 6A, B, 8A).

The cladistic analysis resulted in two equally most parsimonious cladograms (L = 748, CI = 36, RI = 73). The new genus *Asygyna* nests within Pholcommatinae, and is sister to *Carniella* in both trees. The two trees differ only in the position of *Robertus*, as sister to *Pholcomma* (tree 1), or as sister to *Carniella* plus *Asygyna* (tree 2). Successive weighting found a single tree identical to tree 2; this is here presented as the preferred hypothesis. Character support for the monophyly of *Asygyna* is robust; the clade is supported by 19 unambiguous synapomorphies, one of which has perfect fit to the cladograms. Several additional putative *Asygyna* synapomorphies (characters not in the matrix of Agnarsson, 2004) were also observed and are described. Bremer (> 10) and bootstrap values (100) also indicate robust support.

DISCUSSION

Asygyna is a morphologically striking spider genus; it includes the first spiders to be described with asymmetric external and internal female genitalia. It is perhaps surprising that their discovery has awaited the 21st century, but it demonstrates how our knowledge of spider diversity is still remarkably incomplete (Coddington & Levi, 1991). The spider fauna of Madagascar is certainly no exception, and the theridiid fauna is mostly unknown. On this large (587 040 km^2) and diverse tropical island, only between 500 and 600 spider species have been recorded to date (Roth *et al*., 2003; Platnick, 2004). In contrast, about the same number of species are known from many small countries in temperate Europe, e.g. Slovenia (about 20 000 km^2), although there also the fauna is relatively poorly known (Kuntner & Šereg, 2002). Only 26 theridiids have been recorded from Madagascar, while 36 are already known from the more than 1000 times smaller, neighbouring Seychelles Islands (Saaristo, 2003; Platnick, 2004). Other recent discoveries in Madagascar include numerous subsocial *Anelosimus* species, described by Agnarsson & Kuntner (2005).

That the 50 available individuals of *Asygyna* belong to at least eight species (of which 3–4 were singletons) suggests that many more await discovery. Additionally, montane forests in many other areas of Madagas-

car remain to be extensively sampled and may hold further species.

The asymmetry of the epigyna is a puzzling evolutionary phenomenon. In most spiders (with the exception of many haplogyne spiders) a male will copulate with a female using both palps, each alternatively entering the corresponding side (ipsilateral insertions are the norm in entelegyne spiders, see Huber, 1998 and references therein). Epigynal asymmetry must result in changes in copulation and sperm induction, with seemingly negative consequences for the male as his access to females (or their eggs) seems reduced. To start with, the male is probably able to transfer less sperm per copulation using only one palp. Also, if each male can only use one of his palp during copulation with a female, and mates again without refilling his 'used' palp, the next female he encounters may be 'wrong handed'. Of course, males may simply recharge their palps upon encountering the next female, but even so, it is hard to imagine female antisymmetry benefiting the male. Possibly the male can enter either side with the same palp, or enter either 'handed' epigyna with both palps. This would likely require two different copulatory positions, and seems rather unlikely as only in a single species of spider, *Tidarren cuneolatum*, alternation between ipsilateral and contralateral palpal insertion has been shown (Knoflach & van-Harten, 2000).

Yet this single case may be particularly relevant as it represents the mirror image of *Asygyna* asymmetry. *Tidarren* males are secondarily antisymmetric due to obligatory amputation of one palp prior to maturation, while the females are symmetric. When a *T. cuneolatum* male encounters a female that has already mated on his ipsilateral side he assumes an unusual copulatory position and achieves contralateral insertion (Knoflach & van-Harten, 2000). However, this ability appears not to be universal amongst the 'single palp males' of *Tidarren* and *Echinotheridion*, and without further data we are left to speculate on the copulation and sperm induction in *Asygyna* species.

Epigynal asymmetry may be easier to explain from the female's perspective. She may, for example, benefit from faster copulation times (more than the relatively short-lived male). Spiders may suffer higher predation risks when copulating and mating only once (one palp) may shorten the period during which they are vulnerable. In another cobweb spider *Achaearanea wau* the female chases away the male after a single (one palp) copulation resulting in rapid mating (Lubin, 1986). However, this argument is weak as many theridiid spiders mate for several hours (Knoflach, 2004), and in *Enoplognatha* spp., the only pholcommatines whose mating biology is well known, copulations last longer, and alternate palpal insertions are more numerous, than in most other theridiids (Knoflach, 2004).

In addition to shorter copulation times, asymmetry may allow the female a tighter control over what male(s) sire her offspring. Epigynal asymmetry can be viewed as a barrier to sperm induction from any particular male. Such barriers are common, as pointed out for example by Eberhard (1996: 336): 'It seems clear that there is something special about sperm transport that often favours the evolution of female traits that make passage difficult'.

Further evidence for female choice comes from the long and tortuous copulatory (insemination) ducts found in both *Asygyna* here described. It is clear that the male embolus cannot reach the spermathecae; rather, the female must transport the sperm. Eberhard (1996) suggests that in spiders tortuous insemination ducts of females probably screen males on the basis of their abilities to introduce sperm deep within the female and to induce her to transport the sperm. The female could benefit from her choosiness through acquisition of 'good attractiveness genes' (Eberhard, 1996) for their male offspring. But long and elaborate ducts may be costly; asymmetry (by halving the material needed for ducts) may also have arisen as a compromise between complexity of ducts and resources available for their 'construction' (see also Ludwig, 1932). Other unusual *Asygyna* morphologies are mostly sex-related and further indicate that sexual selection has played a key role in shaping these spiders.

If asymmetry benefits the female, why then is it so rare? Symmetry could dominate simply because of developmental constraints, the rarity of asymmetric epigyna being explained by the difficulty of breaking away from an age-old developmental pathway. Huber (2004) suggested that the selective factors for asymmetry in genitalia are different in spiders than in insects, as male spiders differ in having paired sperm transfer organs.

Huber (2004) argued that in the case of antisymmetry in female epigyna, there should be no selection for asymmetry in the male palps. Only in the directionally asymmetric pholcid *Metagonia mariguitarensis* are palps also asymmetric (Huber, 2004). As *Asygyna* males are symmetric, it seems likely that the slight observed bias in 'handedness' in the two species is simply an artefact of meagre data. If right handed females were dominant, we would expect differences between the left and right palps of males.

The range of bizarre morphological features of *Asygyna*, including male proboscis, prosomal warts and pits in both sexes, single functional AG in males, and well developed stridulatory mechanism in females of *A. huberi*, raises further considerations. Sexually dimorphic features, such as the proboscis, presumably play a role in mating (or male–male conflict), as do the clypeal modifications in argyrodine theridiids

(e.g. Legendre & Lopez, 1974, 1975; Lopez, Emerit & Juberthie-Jupeau, 1980; Whitehouse, 1987). Stridulatory mechanisms (where present), also play a major role in mating in spiders, but these are almost always sexually dimorphic (Westring, 1843; Barth, 1982 2001; Agnarsson, 2004; Knoflach & Pfaller, 2004; Knoflach, 2004).

It is interesting that the two species differ in this manner; female *A. coddingtoni* have a typically reduced (apparently nonfunctional) stridulatory field compared to the males, while female *A. huberi* almost certainly stridulate. The presence of prosomal pits and aggregate gland spigots in both sexes is also atypical; in most known cases these are also sexually dimorphic. The latter may indicate that males are relatively long lived and perhaps mate often. The different orientation of epigynal openings, posteriorly (*A. huberi*) or anteriorly (*A. coddingtoni*) is yet another atypical feature of these spiders. Most, or all, of these features seem related to mating.

Based on morphology alone we can do little but speculate, but there is clearly a fascinating field of study awaiting the ethologist in the study of *Asygyna* mating and copulation. What effect does female handedness have, and how do males deal with it? What role does stridulation play, and how do females of *A. coddingtoni* and *A. huberi* differ behaviourally in this respect? Do species with genitalia opening of different orientation differ in their mating position? What is the role of the proboscis, and the prosomal warts and pits? Are males relatively long-lived? Do they mate multiple times? Equally important will be detailed taxonomic study, consequent on the availability of more specimens, followed by the reconstruction of *Asygyna* phylogeny, to offer insight into the evolution of these spiders.

Asygyna is clearly a Pholcommatinae (*sensu* Agnarsson, 2004) and the phylogenetic analysis places it sister to the enigmatic genus *Carniella*. Characters uniting the two genera include presence of a clypeal proboscis, absence of a trichobothrium on metatarsus III, absence of a TTA, leg IV being the longest in the female. Unfortunately, I did not have access to any specimens of *Proboscidula* or *Craspedisia*. It is quite possible that either of these may be more closely related to *Asygyna* than is *Carniella*. The monophyly of *Proboscidula, Craspedisia*, and *Carniella* has not been tested cladistically. The future inclusion of these genera, preferably including examples of at least two species each, is required in order to test their monophyly, and for a more accurate placement and a stronger test of the monophyly of *Asygyna*. It would also answer the interesting question concerning whether the male proboscis is homologous in all genera or has evolved convergently in two or more. Interestingly, these related genera occur in widely disparate areas, mostly on different continents. A phylogenetic framework is also essential to unravel their biogeography.

Asygyna is a remarkable spider genus whose range of bizarre morphological features provides a framework for a variety of future studies, for ethologists, taxonomists, systematists and biogeographers alike. Its discovery demonstrates the importance of pilot studies; all available specimens stem from a discovery project in an understudied, highly diverse area, Madagascar. More targeted fieldwork is now essential to cast light on the many questions posed by *Asygyna*.

TAXONOMY

ASYGNA GEN. NOV.

Type species: ***Asygyna* huberi sp. nov**.

Etymology: the genus name is a merger of the words 'asymmetric' and 'epigyna'; gender is feminine.

Diagnosis: Asygyna resembles the related pholcommatine genera *Proboscidula* (Miller, 1970; Levi, 1972; Knoflach, 1995) from mainland Africa, *Carniella* (Thaler & Steinberger, 1988; Wunderlich, 1995; Knoflach, 1996), which is found from Europe to Africa and Thailand, and *Craspedisia* (Simon, 1894; Levi & Levi, 1962; Levi, 1963) from the Neotropics. All share some of the synapomorphies of Pholcommatinae (see Agnarsson, 2004), such as cymbial hook on ectal margin, cymbial hook tapered, and PLS AG parallel. All four also have a male clypeal proboscis, a single tibial trichobothrium on female palp (also in Theonoe), and a single trichobothrium, or none (*Carniella*, also Theonoe), on male palpal tibia. *Asygyna* differs from *Proboscidula*, *Carniella* and *Craspedisia* by prosomal tubercles in females, from *Carniella* and *Craspedisia* by a regular rim of tubercles around the prosomal stridulatory ridges, and from *Proboscidula* and *Carniella* also by their presence in males. It differs from all three by embolus spiralling counter-clockwise (in left palp), and epigynum asymmetrical. Further characters may include a single male AG fully developed (vs. none in *Carniella*, unknown in *Proboscidula* and *Craspedisia*), and absence of FL in both sexes. *Asygyna* differs from *Proboscidula* and *Craspedisia* by having a simple palp (conductor and theridiid tegular apophysis absent). *Asygyna* differs from *Carniella* and *Craspedisia* by the presence of a scutum, and from *Carniella* by the presence of three colular setae (two in *Carniella*, unknown in *Craspedisia*), rugose prosoma, and a distal cymbial hook.

Description: small pholcommatine theridiids, total length 1.37–1.89 mm, sexes similar in size (Figs 2A–E, I–M). Male with clypeal proboscis (Figs 4A–C, E, 9B–D), carapace as wide or wider than long in both sexes (excluding the male proboscis), dark brown, cov-

ered with warts and pits, formed by elevated and modified setal bases (Figs 2A–E, I–K, 4A–F, 9B–F). Posterior tip of male and sometimes female carapace with well developed stridulatory ridges, not separated medially (Figs 4C–D, 9A, E). Stridulatory ridge field surrounded by a regular row of warts (Fig. 9A). Sternum wider than long, extending between coxae IV, broad posteriorly and terminating abruptly without tapering (Figs 4B, 9C), light brown with a darker rim (Fig. 2C). Eyes variable, AME or PME sometimes larger than laterals, PME sometimes juxtaposed (Figs 2I, J, 4C, D, 9E, F). Chelicerae with 2–4 prolateral teeth, none retrolaterally (Fig. 5A, B), male fangs and cheliceral teeth sometimes enlarged (Fig. 5A). Legs relatively short and stout, leg IV slightly the longest, legs I and II subequal, legs III shortest, brown, femora and sometimes tibia darker (Fig. 2B). Tarsal organ proximal (0.25–0.40) on all leg tarsi, distal on female palpal tarsus. Trichobothrium on metatarsi slightly proximal (0.4–0.45), absent on IV and apparently sometimes on III. Leg tibia with 2–4 dorsal trichobothria (Fig. 10F), female palpal tibia with a single trichobothrium (Figs 5E, 10G). Tarsal claws stout, with few teeth (Fig. 5C), female palpal claw small, with few, or no teeth (Fig. 5D). Tarsal comb distinct (Fig. 9G), comb setae with simple, straight hooks (Fig. 9H), also present on female palp (Fig. 5D). Abdomen as wide or wider than long, round and quite flat, dorsally grey-brown with a white rim, covered with a hard sclerotized scutum (Figs 2A–E, I–M, 5G, 8E, 10E). Ventrally with a large sclerotized, glabrous plate from around the pedicel to the epigastric fold, a white spot posterior to the epigastric plate, remainder of venter and sides light grey, covered with small sclerotized platelets (Fig. 2L, M). A distinct 'disc' around pedicel (Figs 2L, M, 6D, G–H, 7D, 8F, G) anteriorly, with paired rows of 3–5 large stridulatory picks in males (Figs 6G, 8G), and sometimes females (Fig. 6H, absent in 8F). Colulus large and fleshy, bearing three setae (Figs 6D, 7E, 8C). Spinnerets situated terminally, surrounded by a sclerotized ring (Figs 5G, H, 8D, E). Spinnerets with relatively few spigots (see Agnarsson, 2004). Anterior lateral spinnerets with a small piriform field of 5–10 spigots (Figs 6A, 7E, F, 8B). Posterior median spinnerets with two aciniforms (Figs 6A, 7E, F, 8A), posterior lateral spinnerets with only three aciniforms (Figs 6B, C, 8A). Two posterior lateral spinneret aggregates in females, only one of them enlarged and flattened in the typical theridiid fashion (Figs 6A, B, 8A), males apparently with a single functional aggregate spigot (Figs 6C, 7F), the other aggregate and the flagelliform are visible as raised scars. Posterior lateral spinneret flagelliform spigot absent (Figs 6B, C, 8A). Male palpal tibia typical theridiid cup shaped, with a narrow base and broad tip, but tibial rim not with a distinct row of long setae (Figs 1, 7A–C). A single trichobothrium on palpal tibia (Figs 1, 7C). Cymbium with a cymbial hook on margin, distinctly tapered as in most pholcommatines. Median apophysis large with a broad hood distally, involved in the bulb–cymbium lock mechanism. Embolus highly variable, theridiid tegular apophysis absent in examined species. Epigynum usually asymmetrical externally (Figs 2F–H, N–P, 6D–F, 10A–C) with a single copulatory opening leading to the right or left side of the animal depending on the individual (Fig. 2N–P). A single copulatory duct with a complex asymmetric trajectory, splits terminally before entering the two spermathecae (Figs 1B–D, F–H). Epiandrous gland field small, with 1–3 well separated pairs of fusules (Figs 5F, 10D).

Phylogenetics: the monophyly of *Asygyna* is here supported by 19 unambiguous morphological synapomorphies (Fig. 11). The genus belongs to Pholcommatinae and is here sister to *Carniella* (Fig. 11). It is related to other pholcommatines with a proboscis (*Carniella*, *Craspedisia*, *Proboscidula*), but the rarity of these genera has hitherto forbidden their inclusion in the data matrix. The exact placement of *Asygyna* thus awaits further phylogenetic analyses.

Natural history: Asygyna has been collected in northern and eastern Madagascar (between 12 and 21° south, Fig. 12). Most specimens (*A. huberi* and undescribed species) were encountered in rainforest, mostly montane, at elevations between 1000 and 1500 m, but *A. coddingtoni* seems to prefer lowland dry forests. Most specimens were collected by beating low vegetation. No further data exists on their natural history.

ASYGYNA HUBERI SP. NOV. (FIGS 1A–D, 2A–H, 3–6)

Types: female holotype and male paratype from Madagascar, Antananarivo Province, 3 km 41° NE of Andranomay, 11.5 km 147° SSE of Anjozorobe, 18°28.24′S, 47°57.36′E, 1300 m, 5–13.xii.2000, from montane rainforest, col. C. E. Griswold *et al.* (BLF2543), in CAS.

Additional material examined: Data as types BLF2543 (2xx, 2yy), BLF2398 (1yy), BLF2544 (3yy). Antananarivo Province, 7 km SE of Andasibe National Park (Perinét), 18°58′S, 48°27′E, 5.ix.2001, montane forest, beating foliage, D. Ubick. in CAS (1yy). Antananarivo Province, Réserve Spéciale d'Ambohitantely, Forêt d'Ambohitantely, 20.9 km 72° NE of d'Ankazobe, 18°13.31′S, 47°17.13′E, 1410 m, 17–22.iv.2001, montane rainforest, beating low vegetation, C. E. Griswold *et al.* in CAS (1yy). Fianarantsoa Province, 29 km SSW of Ambositra, Ankazomivady, 20°46.6′S, 47°09.9′E, 1700 m, 7.i.1998, montane

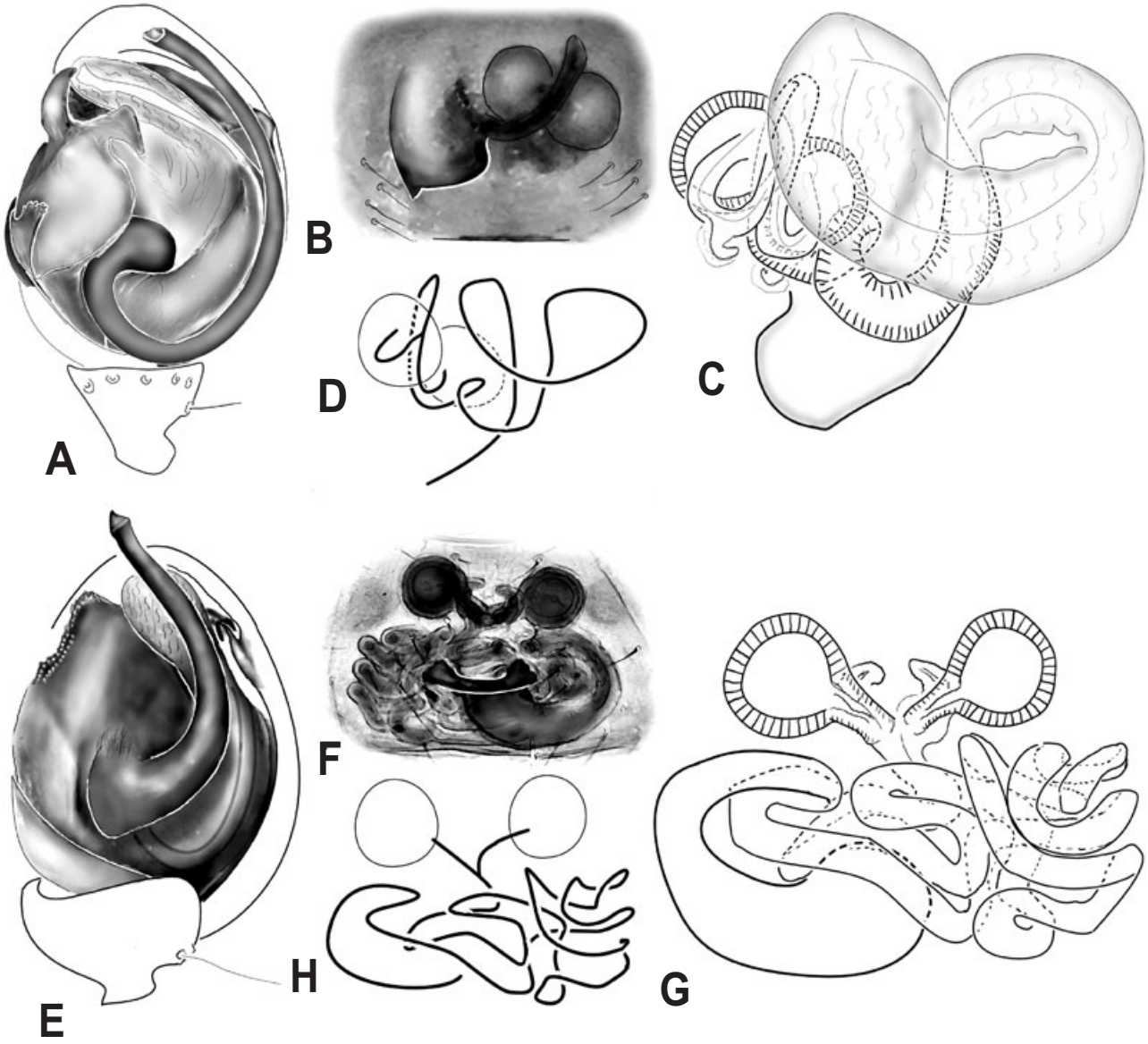

Figure 1. A–C, ***Asygyna huberi* sp. nov.** A, left palp ventral; B, epigynum. C, schematic drawing of the cleared epigynum, dorsal view. D, pathway of the copulatory duct. E–H, ***Asygyna coddingtoni* sp. nov.** E, left palp ventral. F, epigynum. G, schematic drawing of internal epigynum, dorsal view. H, pathway of the copulatory duct.

rainforest, sifted leaf litter, B. L. Fisher, in CAS (1xx). Fianarantsoa Province, Ranomafana National Park, Vohiparara, Piste Touristique, 21°13.6′S, 47°24.0′E, *c*. 1000 m, 23.iv.1998. C. E. Griswold *et al.* in CAS (1yy, identification doubtful, specimen differs slightly in epigynum and eye arrangement).

Etymology: species epithet is a patronym in honor of Bernhard Huber, an avid student of spider genitalia, asymmetry and sexual selection.

Diagnosis: males of *Asygyna huberi* differ from *A. coddingtoni* by a rounded proboscis (Figs 4A–C, E), ventral spines on femora, especially femur III, large cheliceral teeth and fang (Fig. 5A), and by details of the palpal organ, including a simple tegulum lacking an ectal rim, and a longer and thinner embolus (Figs 1A, 3A–F). Females differ by having fully developed stridulatory mechanism, both abdominal SPR (Fig. 6H) and prosomal ridges (Fig. 4D), and by details of the epigynum, copulatory opening scoop-shaped and facing posteriorly, copulatory ducts much shorter (Fig. 1B–D). Both sexes differ from *A. coddingtoni* in having PME equal in size to other eyes (Figs 2A, B, D–E).

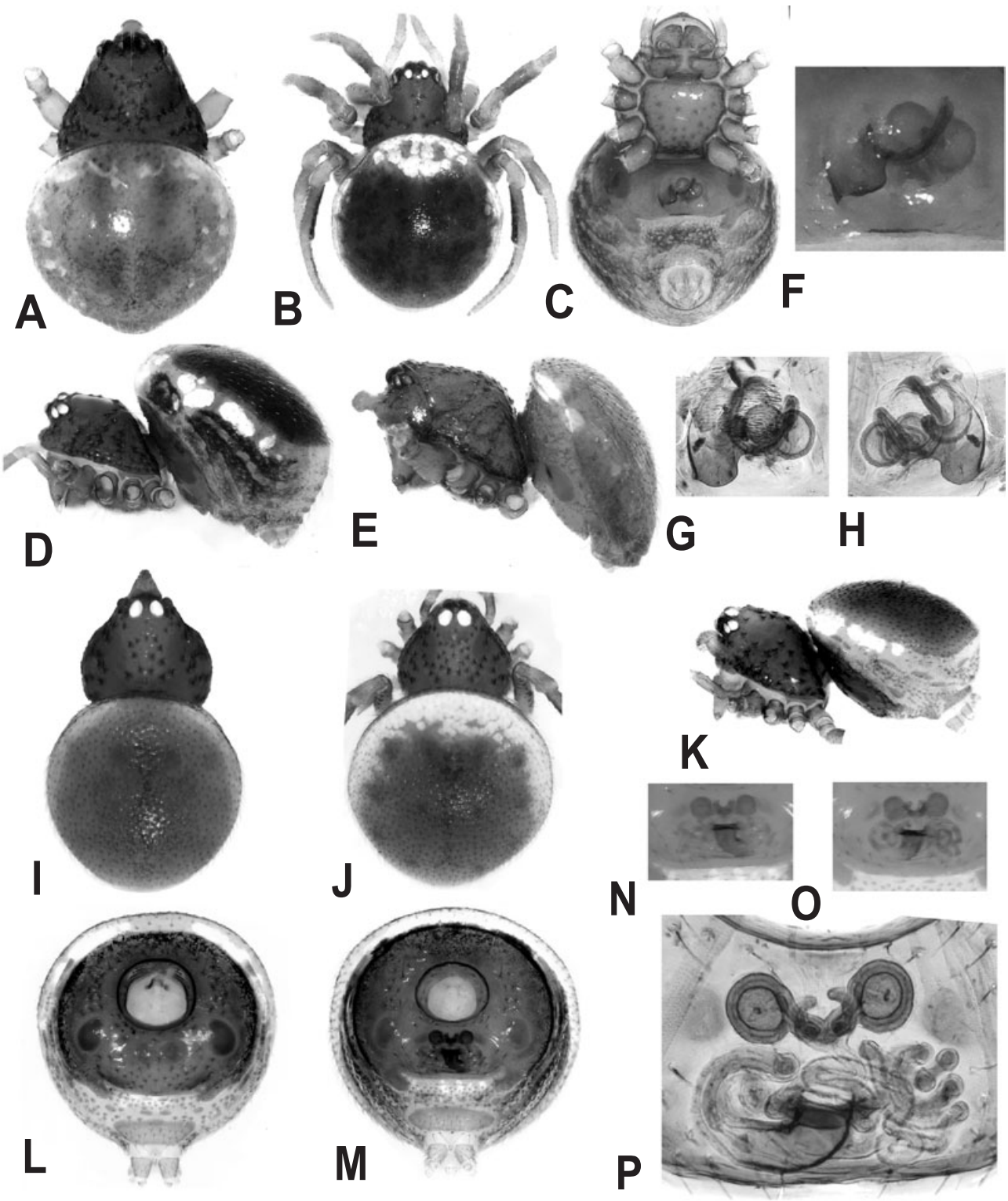

Figure 2. Photographs. A–H, ***Asygyna huberi* sp. nov.** A, male dorsal. B, female dorsal. C, female ventral. D, female profile. E, male profile. F, 'right handed' epigynum. G, cleared 'right handed' epigynum ventral. H, same dorsal. I–P, ***Asygyna coddingtoni* sp. nov.** I, male dorsal. J, female dorsal. K, male profile. L, male abdomen ventral. M, female abdomen ventral. N, 'left handed' epgiynum. O, 'right handed' epigynum. P, details of a cleared 'right handed' epigynum.

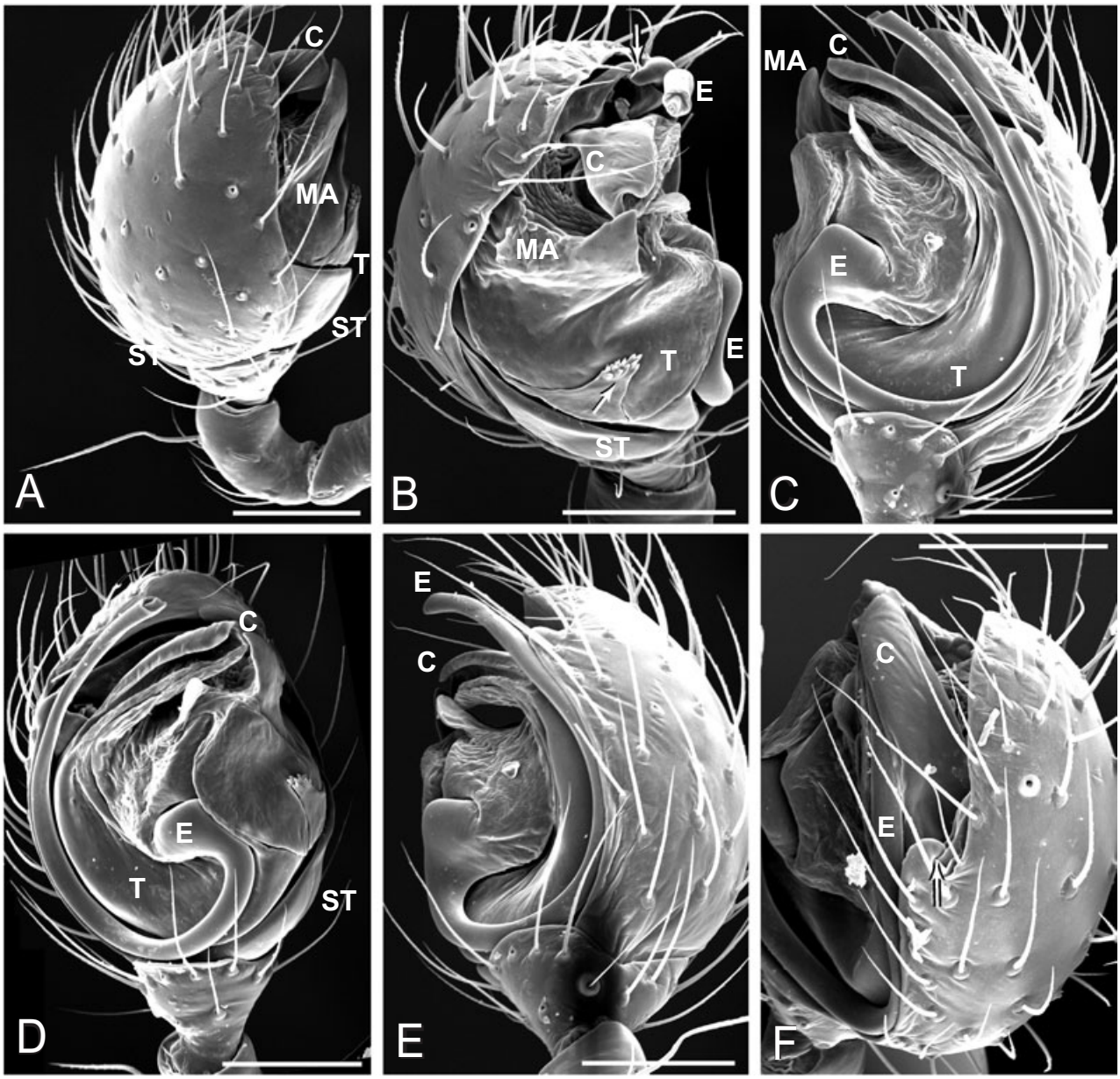

Figure 3. ***Asygyna huberi*** **sp. nov.** male palp. A, mesal. B, submesal. C, ventral. D, right palp ventral, left and right palps appear identical. E, ectal. F, ectocaudal. Scale bars: A–F, 100 μm.

Description: male (paratype): Total length 1.50. Cephalothorax 0.85 long (0.72 without proboscis), 0.74 wide, 0.66 high, brown, covered with small tubercles (Figs 2A, E, 4A–C, E–F). Sternum wider 1.07 than long 0.71, broad posteriorly, extending between coxae IV (Fig. 4B), coloration and texture as cephalothorax. Abdomen 0.85 long, 1.12 wide, 0.69 high, flat and round with dorsal scutum (Figs 2A, E, 5G, H). Pattern as in Figure 2A. AME largest, others subequal in size about 0.04 in diameter. Clypeus with prominent proboscis, with round smooth tip (Figs 2E, 4A–C, E), clypeus height about 2 × AME diameter. Chelicerae with two prolateral teeth, none retrolaterally (Fig. 5A). Teeth much larger than in female as are cheliceral fangs (compare A and B, Fig. 5). Leg I femur 0.75, patella 0.29, tibia 0.55, metatarsus 0.46, tarsus 0.33. Legs short and leg segments stubby, femur I about five times longer than wide, metatarsus I about seven times longer than wide. Leg formula 1243. Ventral side of femora with a row of small spines, produced by elevated setal bases, most prominent on leg III. Leg colour as carapace, brown, femora and tibia

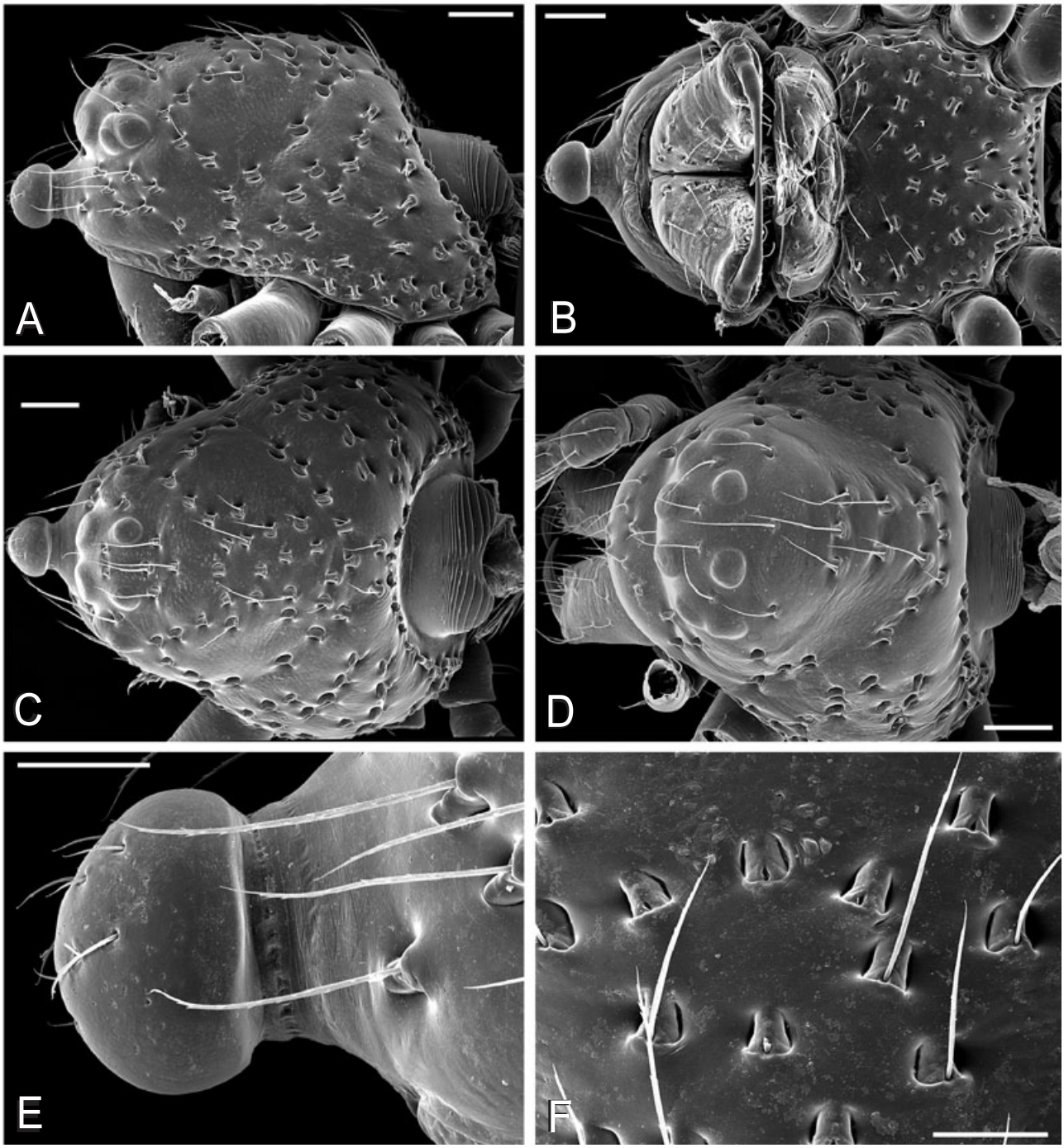

Figure 4. ***Asygyna huberi*** **sp. nov.** A–C, E–F male prosoma. A, profile. B, ventral. C, dorsal. D, female prosoma dorsal. E, details of proboscis. F, details of prosomal pits. Scale bars: A–D, 100 μm, E–F, 50 μm.

darkest. Tibia with dark ventral streak, faint ventral streak also on metatarsi. Tarsal organs slightly proximal (0.40–0.45) on all tarsi. Trichobothria on metatarsi I–II proximal (about 0.40–0.45), absent on metatarsi III–IV. Palpal organ as in Figures 1A and 3A–F, with distinctly tapered cymbial hook, embolus comparatively long and slender, spiraling counter clockwise in the left palp. Conductor long and slender, with a deep furrow for embolus. Single pair of epiandrous gland spigots present (Fig. 5F).

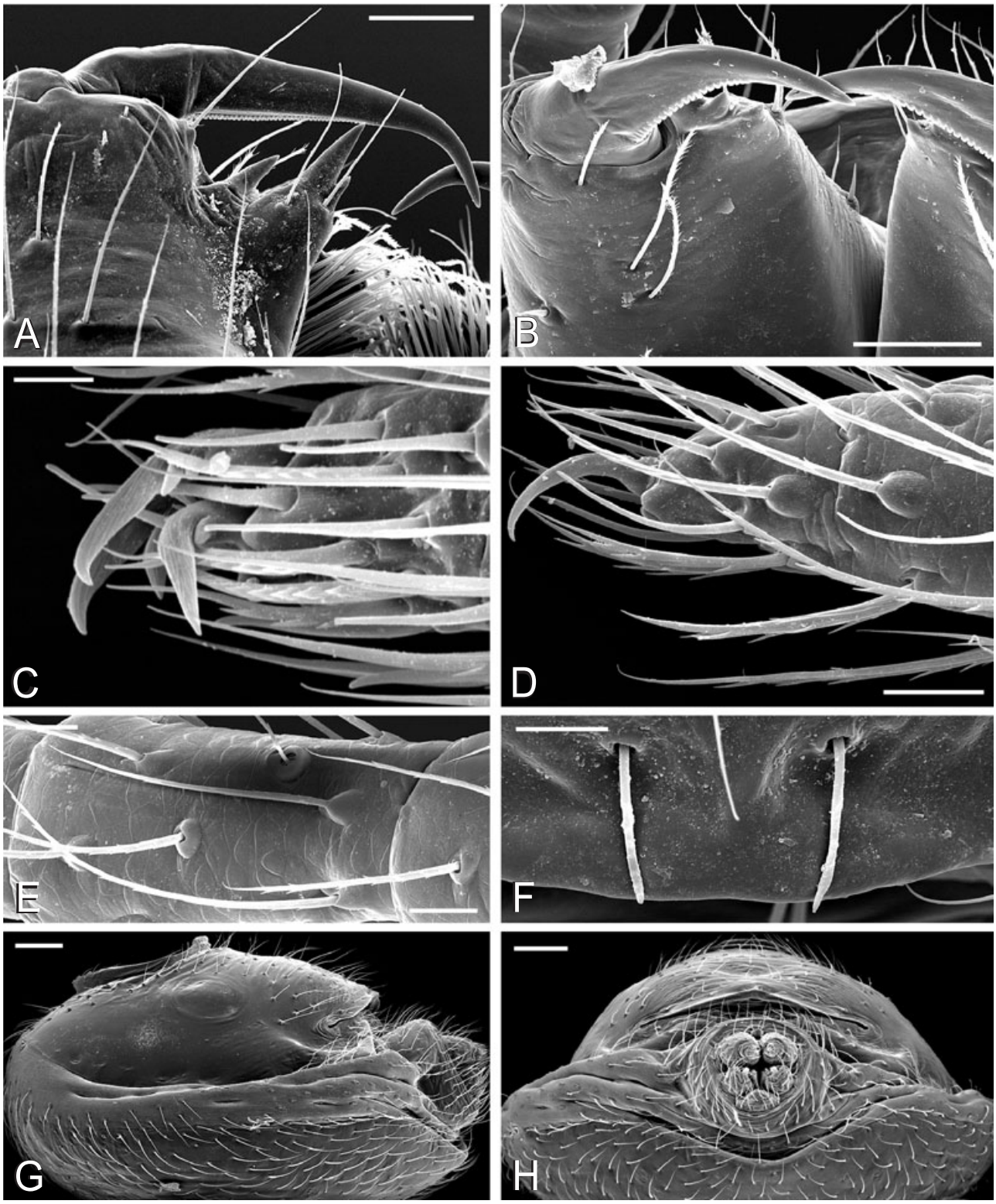

Figure 5. ***Asygyna huberi*** **sp. nov.** A, male cheliceral promargin. B, female cheliceral retromargin, the teeth seen are promarginal. C, female tarsus I claws. D, female palpal claw. E, female palpal tibia dorsal. F, epiandrous gland fusules. G, male abdomen side. H, same, back. Scale bars: G–H, 10 μm; A–B, 50 μm; D–E, 20 μm. C, F, 10 μm.

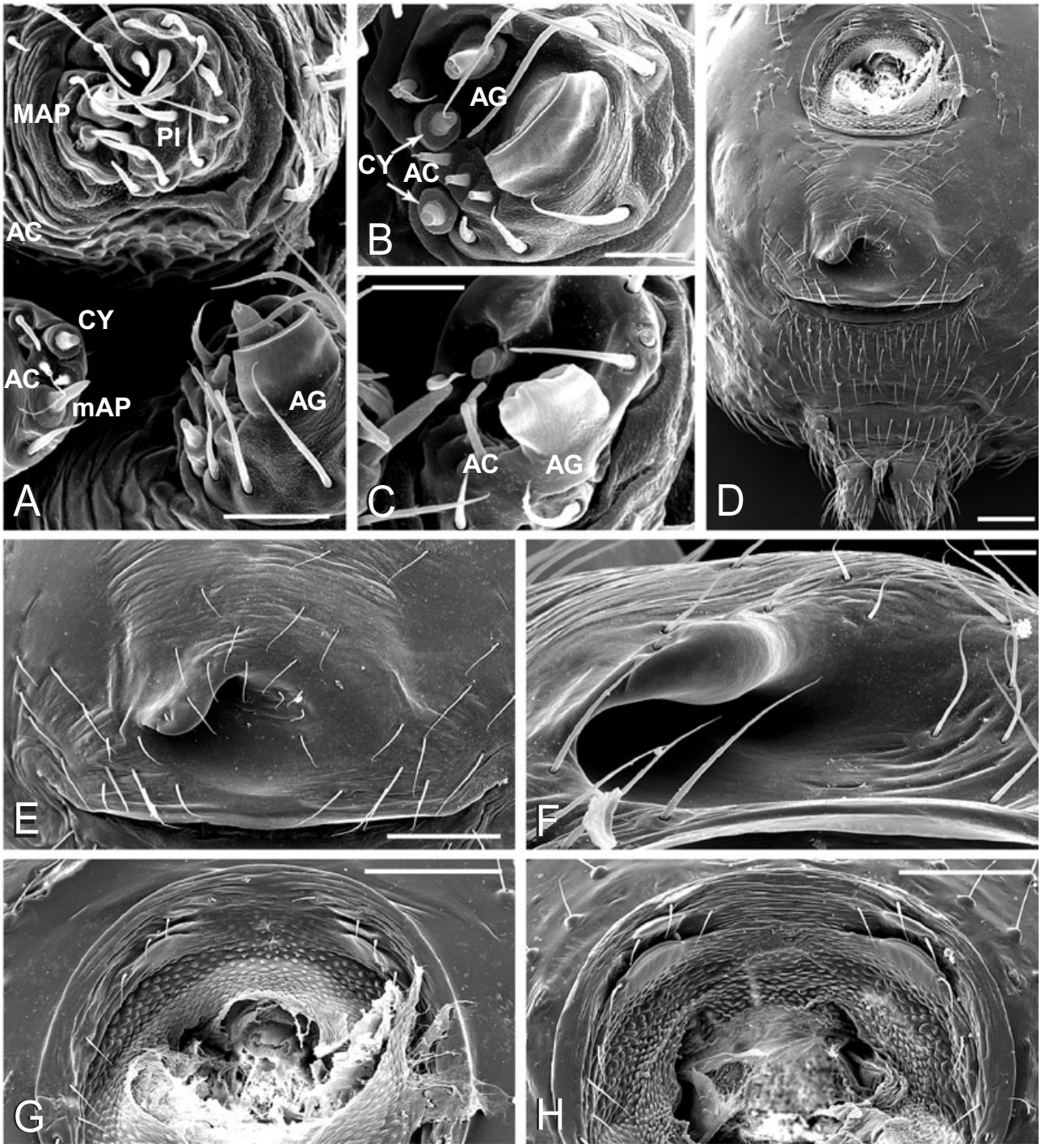

Figure 6. ***Asygyna huberi*** **sp. nov.** A, female left spinning field. B, female PLS, as in other Pholcommatines only one AG is flattened, the other is round. In ***Asygyna*** the FL is furthermore absent. C, male PLS, with one functional and one nonfunctional AG. D, female abdomen ventral. E, epigynum ventral. F, same, caudal. G, female pedicel disc and SPR. H, male pedicel disc and SPR. Scale bars: D, E, G–H 100 μm; A, F, 20 μm; B–C, 10 μm.

Female (holotype): total length 1.89. Cephalothorax 0.59 long, 0.73 wide, 0.64 high, brown. Sternum 0.89 long, 0.94 wide, extending between coxae IV, brown. Abdomen 1.50 long, 1.49 wide, 1.32 high. Pattern as in Figure 2B–D. Eyes subequal in size, about 0.05 in diameter. Clypeus height about 2.5 × AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 0.46,

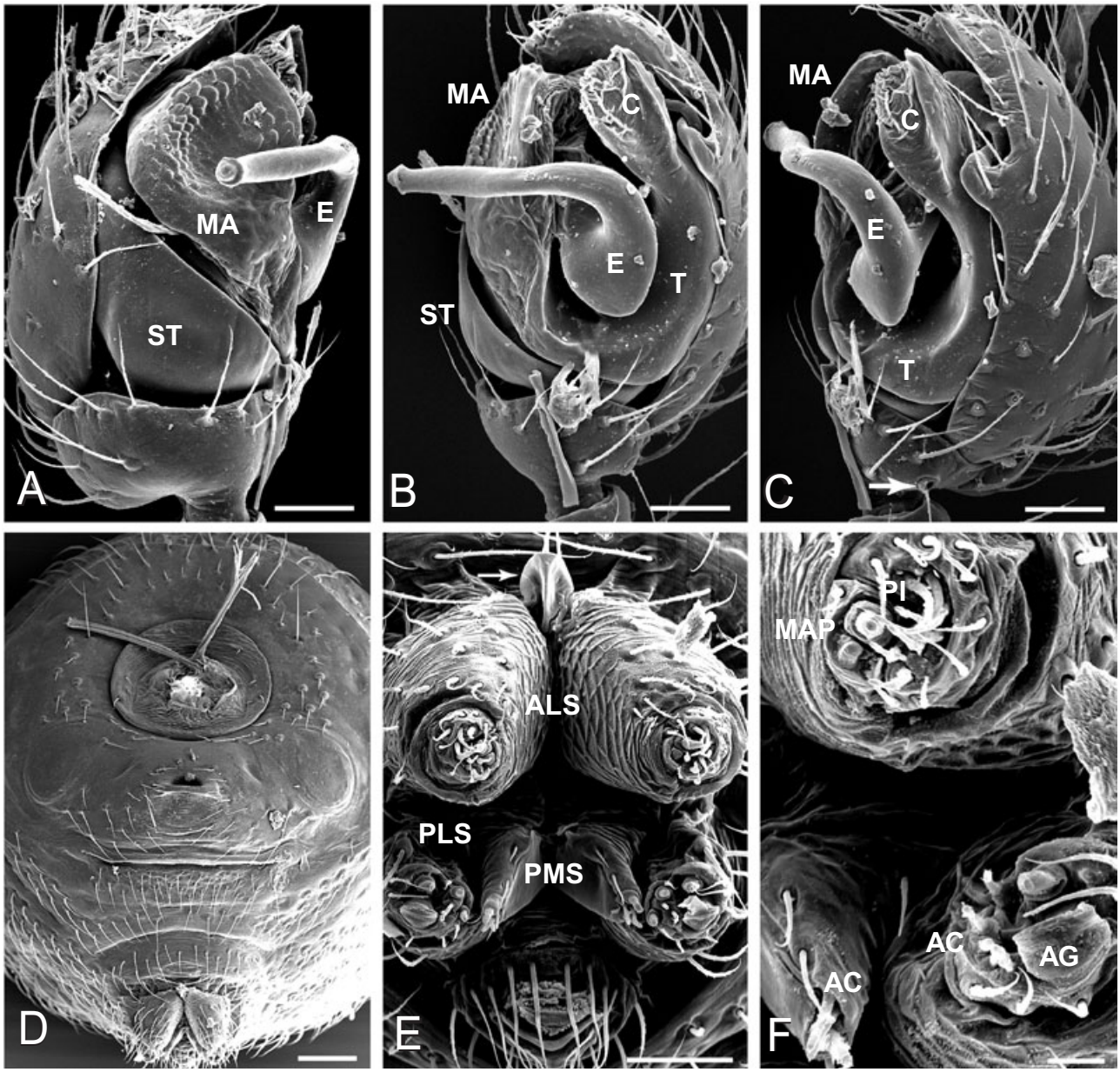

Figure 7. ***Asygyna coddingtoni*** **sp. nov.** A–C, male palp. A, mesal. B, ventral. C, ectal, the tibia has a single trichobothrium (arrow). D, female abdomen ventral. E, female spinnerets, note the large and fleshy colulus (arrow). F, male left spinning field, at least one AG is functional, while the FL appears vestigial. Scale bars: D, 100 μm; A–C, E 50 μm; F, 10 μm.

patella 0.20, tibia 0.33, metatarsus 0.26, tarsus 0.26. Legs short and stubby, femur about 3 times longer than wide, metatarsus I about 4 times longer than wide. Leg formula 4123 with legs 1 and 2 subequal. Leg colour as in male. Tarsal organs proximal (0.25–0.35) on all tarsi, least so on IV. Trichobothria on metatarsi I–II proximal (about 0.30–0.40), absent on metatarsi III–IV. One dorsal trichobothrium on female palpal tibia, 2–3 on leg I tibia, 4 on leg IV. Epigynum with a broad asymmetric copulatory opening, facing posteriorly, and a broad asymmetric funnel, leading either left or right from the opening, long and complex copulatory duct splits terminally before entering the two spermathecae (Figs 1B–D, 2F–H).

ASYGYNA CODDINGTONI SP. NOV. (FIGS 1E–H, 2I–P, 7–10)

Types: Male holotype, and a male and six female paratypes from Parc National d'Ankarafantsika, Forêt

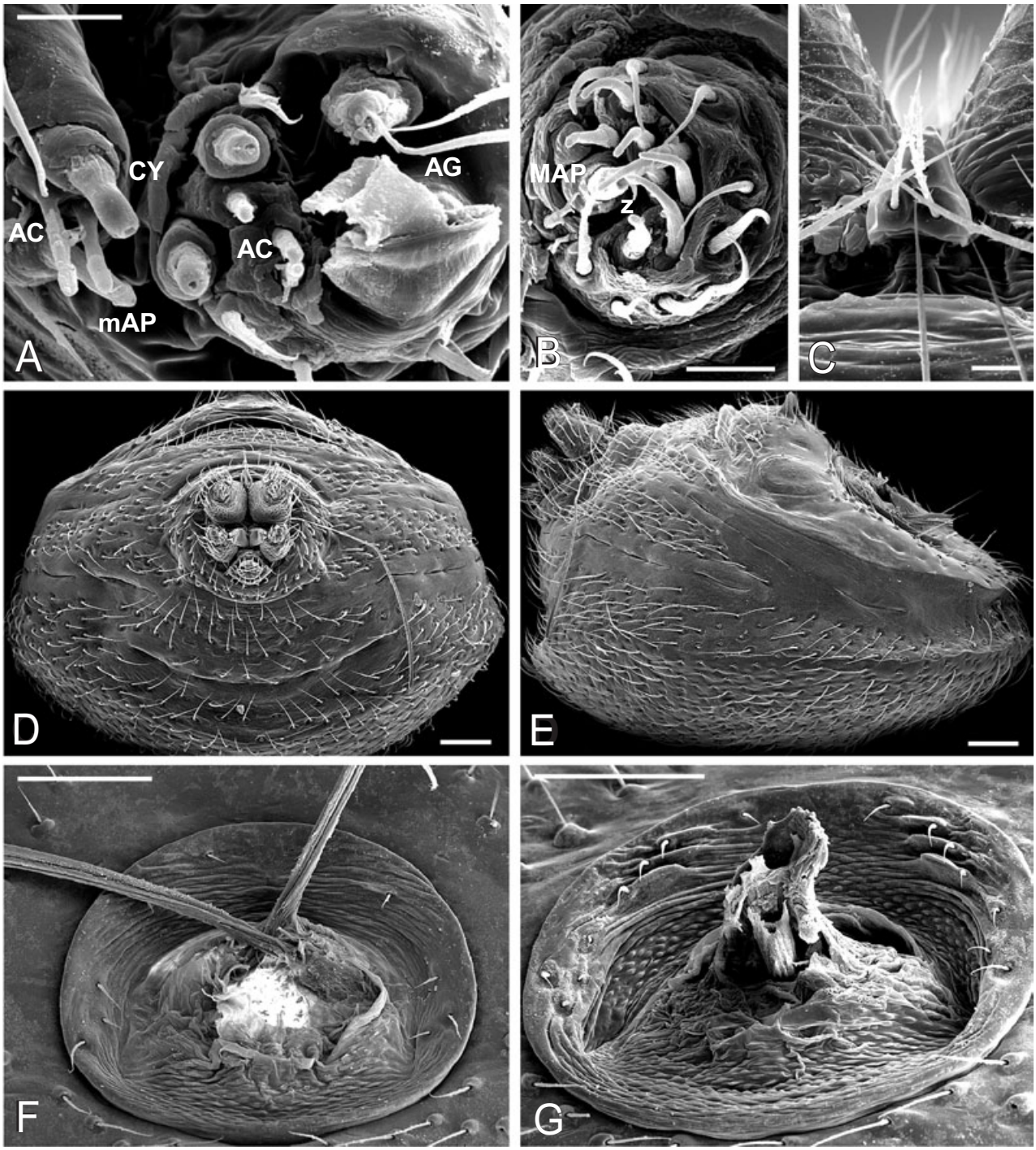

Figure 8. ***Asygyna coddingtoni*** **sp. nov.** A–C, female spinnerets. A, PLS and PMS, apparently the FL is absent. B, ALS. C, colulus, the presence of 3 setae is unusual in Pholcommatinae and a synapomorphy of ***Asygyna***. D, female abdomen posterior. E, same, side. F, female pedicel disc. G, male pedicel disc, note well developed stridulatory picks. Scale bars: D–G, 100 μm; A–C, 10 μm.

de Tsimaloto, 18.3 km 46° NE de Tsaramandroso, 16°13.41′S, 46°8.37′E, 135 m, 2–8.iv.2001, col. Fischer, Griswold *et al*. In tropical dry forest, beating low vegetation.

Additional material examined: Antsiranana province, Forêt d'Anabohazo, 21.6 km 247° WSW Maromandia, 14°18.32′S, 47°54.52′E, 120 m, 11–16.iii.2001, tropical dry forest, beating low vegetation, C. E. Griswold *et al.*

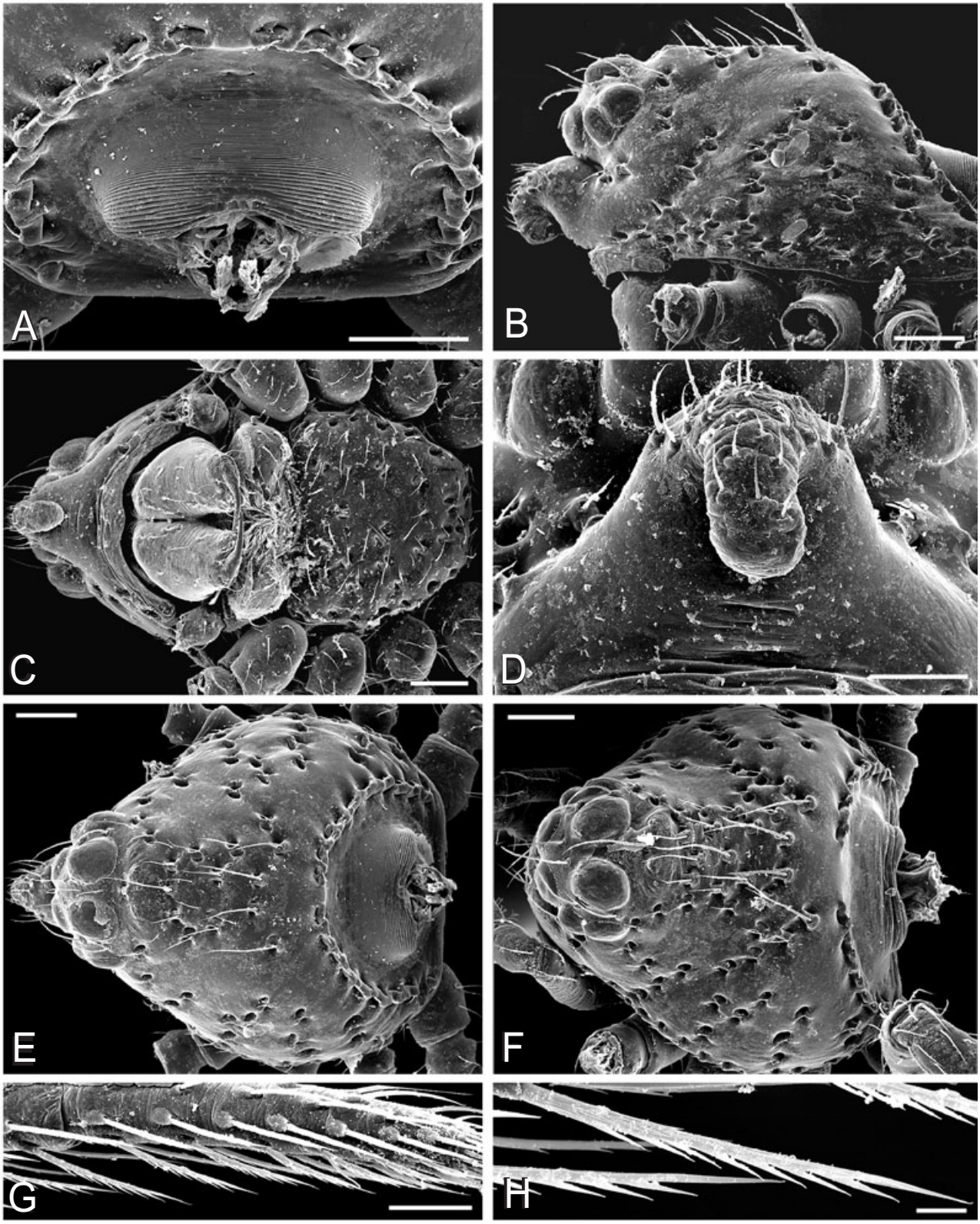

Figure 9. ***Asygyna coddingtoni*** **sp. nov.** A–E, male prosoma. A, details of stridulatory ridges. B, profile. C, ventral. D, details of proboscis. E, dorsal. F, female prosoma dorsal. G, female fourth tarsal comb. H, details of a tarsal comb setae. Scale bars: A–C, E–F, 100 μm; D, G, 50 μm; H, 10 μm.

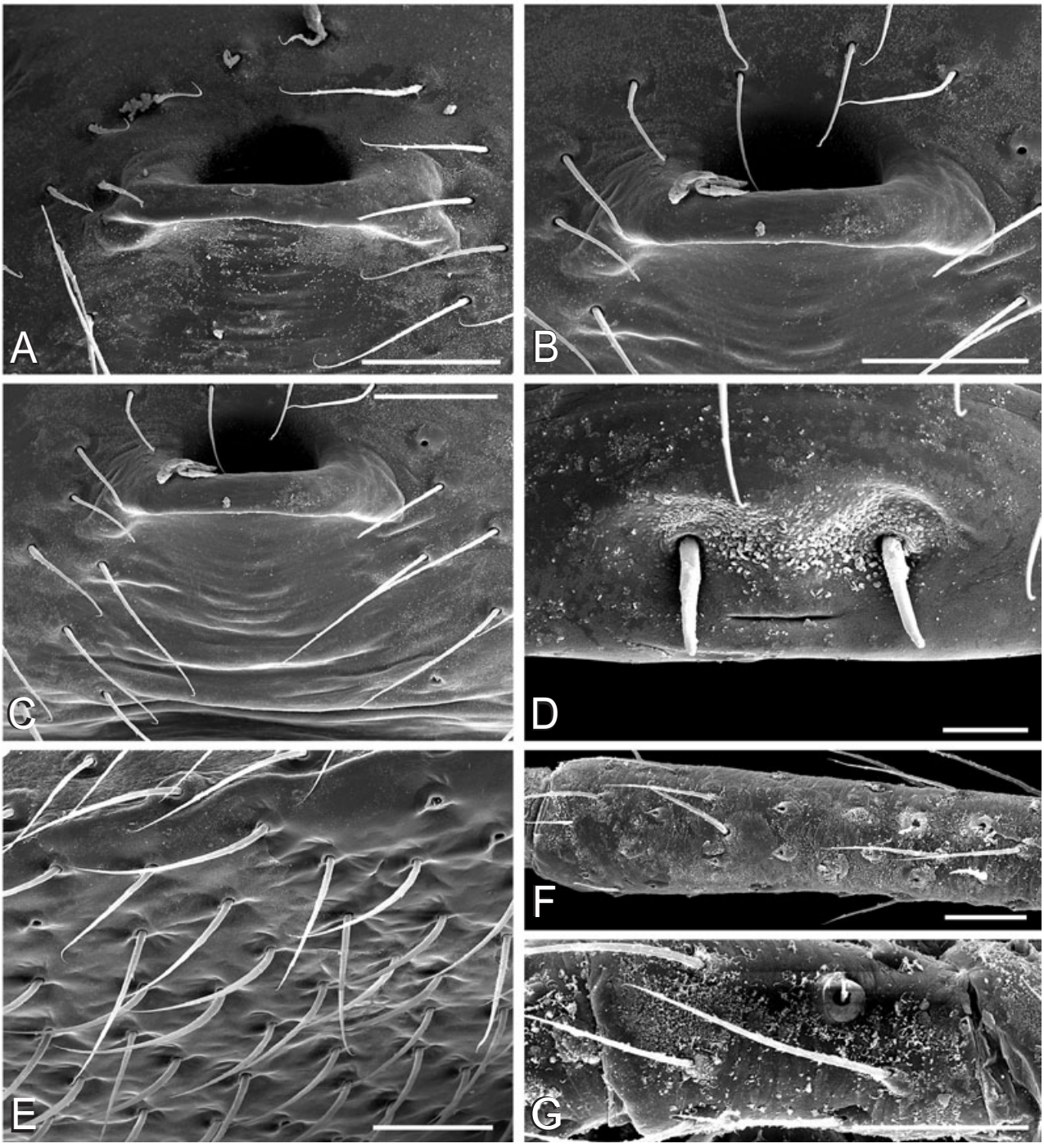

Figure 10. ***Asygyna coddingtoni*** **sp. nov.** A–C, female epigyna. A, 'left' handed. B, 'right' handed. C, same, note the asymmetry in the cuticle under the epigynal opening. D, epiandrous gland fusules. E, surface of scutum, margin with 'normal' abdomen in upper left corner. F, female tibia IV. G, female palpal tibia, with a single trichobotrhium. Scale bars: A–C, E–G, 50 μm; D, 10 μm.

in CAS (1xx, 7yy). Same locality data, J. J. Rafanomezantsoa *et al.* in CAS (1xx). Antsiranana province, Réserve Spéciale de l'Ankarana, 22.9 km 224° SW of Anivorano Nord, 12°54.32′S, 49°6.35′E, 80 m, 10–16.ii.2001, tropical dry forest, beating low vegetation, C. E. Griswold *et al.* BLF2859 (1xx). Mahajanga Province, Réserve d'Ankoririka, 10.6 km 13° NE of Tsaramandroso, 16°16.2′S, 46°2.55′E, 210 m, 9–14.iv.2001,

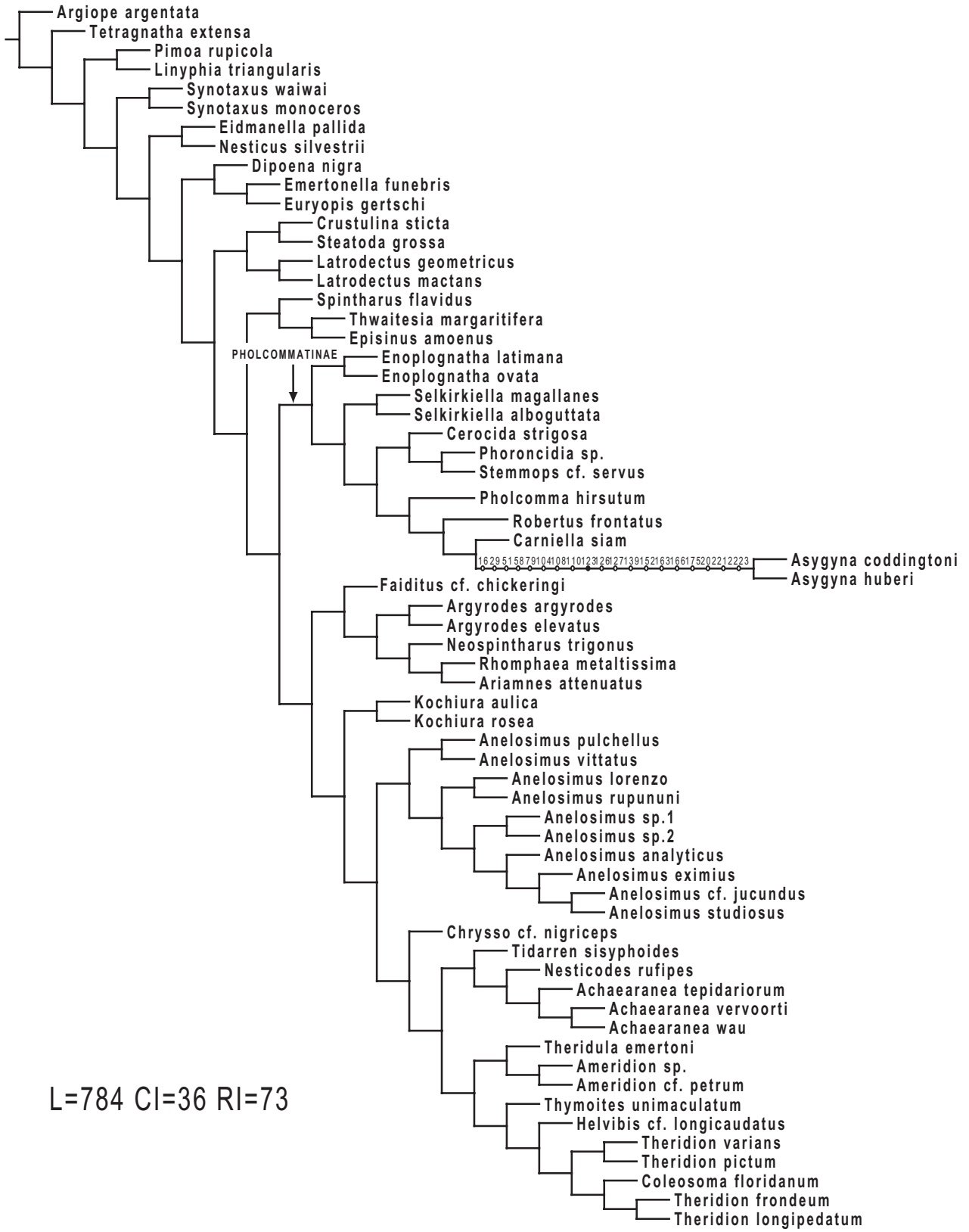

Figure 11. The single most parsimonious tree. Numbers indicate character changes (synapomorphies) on the branch leading to ***Asygyna***. See Agnarsson (2004) for further detail on this phylogeny.

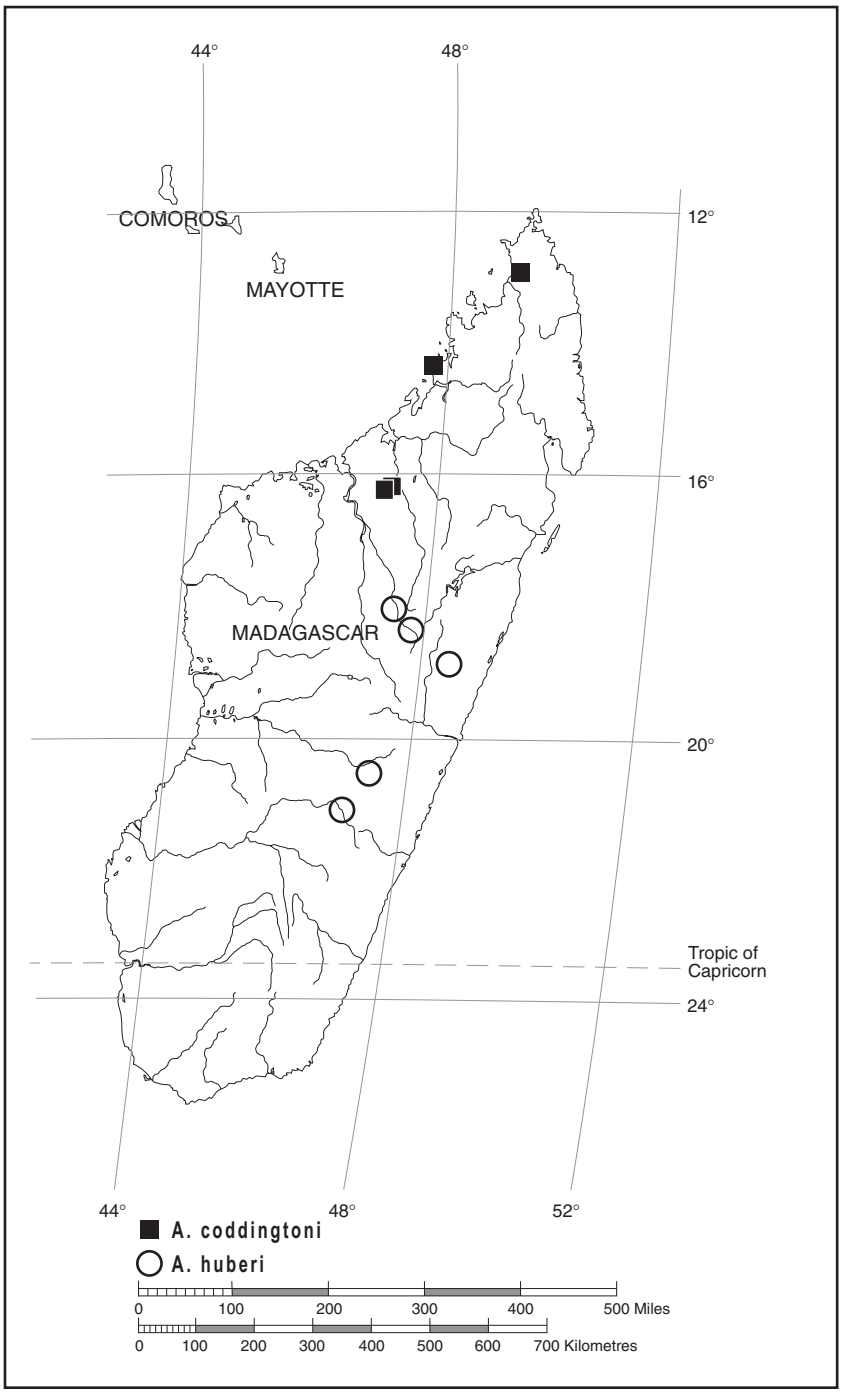

Figure 12. The distribution of records for ***A. huberi* sp. nov.** (open circles) and ***A. coddingtoni* sp. nov.** (filled squares).

tropical dry forest, beating low vegetation, C. E. Griswold *et al.* BLF3666 (2yy).

Etymology: species epithet is a patronym after Jonathan A. Coddington, an inspiring mentor and friend.

Diagnosis: males of *Asygyna coddingtoni* differ from *A. huberi* by a folded tapering proboscis (Figs 2K, 9B–E), lack of ventral spines on femora, small cheliceral teeth, and by details of the palpal organ (Figs 1E, 7A–C), including a conspicuous ectal tegular rim, and a shorter and stouter embolus. Females differ by lacking a stridulatory mechanism, and by details of the epigynum (Figs 1F, G, 10A–C), copulatory opening funnel shaped and facing anteriorly, copulatory ducts much longer and looping many times more. Both sexes differ

from *A. huberi* in having AME larger than other eyes (Figs 2I, J, 9E, F).

Description: male (holotype): Total length 1.56. Cephalothorax 0.72 long (0.65 without proboscis), 0.68 wide, 0.58 high, brown, covered with small tubercles (Figs 2I–K, 9B, E). Sternum slightly wider than long, 0.40 long, 0.41 wide, broad posteriorly, extending between coxae IV, coloration and texture as cephalothorax. Abdomen 0.91 long, 1.02 wide, 0.76 high, round and quite flat, dorsally grey-brown with a white rim, covered with hard sclerotized scutum, ventrally with large sclerotized, glabrous plate around the pedicel, reaching posteriorly to the epigastric fold, a white spot posterior to the epigastric plate, remainder of venter and sides light grey, covered with small sclerotized platelets. PME: largest 0.09 in diameter, very close together, bright pearl-white, lateral eyes smallest. Clypeus with prominent proboscis, with pointy tip bent downwards (Fig. 9B, D), clypeus height about 2.7 × AME diameter. Chelicerae with two prolateral teeth, none retrolaterally. Leg I femur 0.42, patella 0.16, tibia 0.26, metatarsus 0.23, tarsus 0.20. Legs short and leg segments stubby, femur and metatarsus I about 4 times longer than wide. Leg formula 4123, with legs I and II subequal. Leg dark to light brown, legs I–II darker than III–IV, all tibia dark. Tarsal organs not visible in light microscopy. Trichobothria on metatarsi I–II proximal (about 0.40–0.45), absent on metatarsi III–IV. Palp with a narrow tipped, bent cymbial hook, embolus comparatively short and stout, spiralling counter clockwise in the left palp (Figs 1E, 7A–C). Conductor short and broad with a shallow furrow for embolus (Figs 1E, 7B, C). A single pair of epiandrous gland spigots present (Fig. 10D).

Female (paratype): coloration and texture as in male (Figs 2J, M, 9F). Total length 1.37. Cephalothorax 0.58 long, 0.59 wide, 0.45 high. Sternum 0.36 long, 0.38 wide, broad posteriorly, extending between coxae IV. Abdomen 0.98 long, 1.09 wide, 0.74 high. PME: largest 0.09 in diameter, very close together, bright pearl-white (Fig. 2J), lateral eyes smallest. Clypeus without a proboscis (Fig. 9F), clypeus height about 1.7 × AME diameter. Chelicerae with 2–3 prolateral teeth, none retrolaterally. Leg I femur 0.39, patella 0.13, tibia 0.20, metatarsus 0.16, tarsus 0.16. Legs short and stubby, femur about 4 times longer than wide, metatarsus I about 3 times longer than wide. Leg formula 4123. with legs I and II subequal and III only very slightly shorter. Leg colour as in male. Tarsal organs not visible in light microscopy. Trichobothria on metatarsi I–II proximal (about 0.35–0.40), absent on metatarsi III–IV. One dorsal trichobothrium on female palpal tibia, two on leg I tibia, 4 on leg IV. Epigynum with a broad copulatory opening, facing anteriorly, and a broad asymmetrical duct, leading either left, or right, from the opening, two spermathecae, long and complex copulatory ducts (Figs 1, 2N–P, 10A–C).

Natural history: most specimens were collected by beating low vegetation, and some in pitfall traps.

ACKNOWLEDGEMENTS

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