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# Systematics of the Spider Family Deinopidae with a Revision of the Genus *Menneus*

*Jonathan A. Coddington,  
Matjaž Kuntner, and  
Brent D. Opell*

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## ABSTRACT

Coddington, Jonathan A., Matjaž Kuntner, and Brent D. Opell. Systematics of the spider family Deinopidae with a revision of the genus *Menneus*. Smithsonian Contributions to Zoology, number 636, iv + 61 pages, 32 figures, 1 table, 2012. The enigmatic and rare spiders of the family Deinopidae are known for their extremely large ocelli and their unique habit of casting their small cribellate webs over nocturnal pedestrian or aerial prey. Although the monophyly of the family has not been controversial, deinopid descriptive systematics has been neglected since the original species descriptions. The first goal of this monograph is to test the monophyly of Deinopidae and its genera and thus to establish a phylogenetically informed taxonomy of the species. We provide the first phylogeny of this family on the basis of 53 morphological and 3 behavioral characters scored for 17 deinopid species and 2 outgroups. Extant deinopid spiders belong to two genera: the larger pantropical *Deinopis* MacLeay, 1839, diagnosed by the extreme size of their posterior median eyes, and the smaller *Menneus* Simon, 1876, of the Old World (sub)tropics with normally sized eyes. *Avella* Pickard-Cambridge, 1877, and *Avellopsis* Purcell, 1904, are junior synonyms of *Menneus* as their type species are nested throughout *Menneus* phylogeny. The second goal is to revise the non-*Deinopis* species of Deinopidae. Here, we recognize, diagnose, illustrate, describe, and phylogenetically place the 14 known *Menneus* species. Africa currently has six species: *Menneus camelus* Pocock, 1902, from South Africa; *M. capensis* (Purcell, 1904) new combination from Western Cape, South Africa; *M. darwini* new species from Tanzania; *M. dromedarius* Purcell, 1904 (removed from synonymy of *M. camelus*), from South Africa and Madagascar; *M. samperi* new species from Kenya, Tanzania, and Uganda; and *M. tetragnathoides* Simon, 1876 (*M. affinis* Tullgren, 1910 new synonym), from Angola, Malawi, and Tanzania. Australasia currently has eight species: *M. aussie* new species from eastern Australia and New Caledonia; *M. bituberculatus* new species from Queensland and Indonesian West Papua; *M. superciliosus* (Thorell, 1881) from eastern Australia; *M. nemesio* new species from New South Wales; *M. neocaledonicus* (Simon, 1889) from New Caledonia; *M. quasimodo* new species from Western Australia; *M. trinodosus* Rainbow, 1920 (*Deinopis insularis* Rainbow, 1920, new synonym), from Queensland and New South Wales; and *M. wa*, new species, from Western Australia. We propose *Avella angulata* L. Koch, 1878, *Avella despiciens* O. P.-Cambridge, 1877, and *Avella unifasciata* L. Koch, 1878, as nomina dubia. *Paleomicromenneus lebanensis* Penney, 2003, the earliest known fossil, is similar to *Menneus*. *Menneus* is phylogenetically sister to *Deinopis*, and within *Menneus* we recover a grade of Australasian species that includes the African *M. capensis*, followed by a distal clade of African species with peculiar asymmetric somatic morphology.

Cover images, from left to right: *Menneus camelus* female with web from South Africa (photo by M. Kuntner); *Deinopis spinosa* female from Florida, USA (photo by J. A. Coddington); *Menneus capensis* female with web from South Africa, (photo by M. Kuntner).

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# Systematics of the Spider Family Deinopidae with a Revision of the Genus *Menneus*

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## INTRODUCTION

The “ogre-faced” spiders of the family Deinopidae are known for their unusual morphology, natural history, and rarity. MacLeay personally discovered and described the first deinopid in 1839, writing (p. 10), “I found *Deinopis*, with the last mentioned genus [*Ctenus*] and *Dolomedes*, under stones in the island of Cuba. It must be assigned to the *Wolfspinnen* of Koch, but it is very unlike any of them hitherto known.” MacLeay must have meant the lower faces of large boulders, where it would not be unusual to find *Ctenus*, *Dolomedes*, or, indeed, *Deinopis* spinning a web positioned to envelope prey walking on the stone surface. However, to temperate biologists used to turning over small rocks in search of cursorial spiders, MacLeay’s description probably conveyed entirely the wrong impression (or perhaps MacLeay entirely misremembered the circumstances). Lacking any further biological data, several generations of arachnologists continued to speculate that deinopids were a branch of cursorial hunting spiders (e.g., O. P. Cambridge, 1877; Thorell, 1881, 1886). Doleschall (1859) reported that *Deinopis* were collected from a “large irregular web spun between trees, in the center of which the spider sits with the anterior legs extended along the body axis” (as paraphrased by Simon, 1892:209). Marx (1889: 341) added to the confusion by reporting that the discoverer of *D. spinosa*, W. S. Barnard, remembered it as being “on a large horizontal web, which resembled very much that of *Agalena*, but he could not find a tubular retreat attached to the web, as is the case with *Agalena*.”

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Akerman (1926), studying *Menneus*, was the first to describe the 1–2 cm sized web (Figures 1a,d, 2b–d) and the remarkable attack behavior in which the animal grasps the corners of the web with the anterior tarsi and lunges (actually drops) toward prey to envelop it with the extremely extensible web. Since Akerman, Baum (1937), Roberts (1954), Clyne (1967, 1968), Mascord (1970), Robinson and Robinson (1971), Theuer (1954), Austin and Blest (1979),

Coddington (1986a, 1986b), Coddington and Sobrevila (1987), Larsen (1992), and Getty and Coyle (1996) all observed the same specialized architecture and attack behavior. Theuer (1954: 37) studied *D. spinosa* extensively and saw the same web and behavior in animals that he felt sure were “no more than 3–4 days old.” However, Mascord (1982:5) wrote, “I photographed recently a small net at my home which was only 5mm wide by 3.4mm deep, and, although it was similar in appearance, it does not have the cribellate strands of an adult net,” and Raven (1992) offered further details on newborn *Deinopis* biology. The web intrigued biologists since its discovery, but not until Eberhard (1982) clarified the basic ethological apomorphies defining the orb web did Coddington (1986a) confirm that the deinopid architecture was plausibly homologous (Figure 2d). Since then deinopids have figured prominently in studies of spinnerets (Peters, 1982; Coddington, 1989), the comparative morphology of silks (Eberhard and Pereira, 1993), and exemplars in phylogenetics (reviewed in Coddington et al., 2004; Coddington, 2005).

Deinopid morphology was similarly enigmatic to classical authors. C. L. Koch (1850:41) erected a new family for *Deinopis*, but that, of course, did not solve the problem of their relationships (although he suggested Salticidae). Subsequent authors mostly suggested affinities with other, more or less large-eyed families such as lycosids, pisaurids, oxyopids, or even salticids, or cribellates such as hypochilids, eresids, or agelenids. Simon described *Menneus* in 1876 and immediately realized from the distinctive palpal morphology that *Deinopis* was closely related but made no comment concerning the placement of the pair. O. P. Cambridge (1877:558) said, “Dinopides, including the genus *Avella* described below, contains now three genera and is an exceedingly remarkable group; and I confess that its systematic position is, as yet, a puzzle to me.” Walckenaer, as well as MacLeay, who founded it, placed “*Dinopis* in the family Lycosides, between which and the Salticides I have at present left it, though that place will probably not long retain it. I cannot, however, agree with Dr. L. Koch, who places *Dinopis* in the family Eresides. . . . I would rather suggest that its place is near to the Agelenides, though in the absence of any knowledge of its habits it is impossible to speak with certainty upon this point.” Convinced of the monophyly of the Cribellatae, Simon (1892:205–210) placed deinopids as a subfamily of Uloboridae, but his reasoning was essentially phenetic rather than phylogenetic. Berland (1932:373) followed Simon, and based on Akerman’s observations directly related the deinopid web to the uloborid orb. Petrunkevitch (1923, 1928, 1933) disagreed only as to rank, restoring Dinopinae [sic] to its own family.

Millot (1933) strongly supported Dinopidae because of the many differences in internal anatomy with Uloboridae, and since then the group has usually been regarded as a distinct family (Platnick, 2010).

*Deinopis*, of course, is well known for its huge posterior median eyes (Figure 3a). In photographic terms, the eyes are about 0.77 mm f/0.58 lenses, thus extremely wide angle, and extremely “fast,” or sensitive to light (Blest and Land, 1977). They considered deinopid posterior median ocelli to be the largest of any invertebrate: the largest they measured in *D. subrufus* were 1.40 mm in diameter, and *subrufus* is not a particularly large species. They estimated that *Deinopis* posterior median eyes gathered proportionately about 2000× the amount of light as a diurnal eye, either human or salticid. The physiology of the posterior median eyes is as impressive as their form. Blest and coauthors published a series of papers (Blest and Land, 1977; Blest, 1978; Blest et al., 1978a, 1978b, 1979, 1980; Laughlin et al., 1980; Blest and Price, 1981) that showed that *Deinopis* destroyed most of the photosensitive membrane in these eyes at dawn and resynthesized it at dusk, saying, “*Dinopis* might almost be said to make a new retina every day” (Blest, 1978:479). Clearly, the enlarged eyes in *Deinopis* facilitate visual predation under dark conditions.

Deinopids also deserve to be better known for their extraordinary genitalia. Many authors have remarked on the distinctive male round tegula, round alveoli, and spiraled emboli (Figure 4a–e). Females are comparably equipped (see Figure 9d). As we explain further below, these apomorphies apparently enable extreme rotation of the bulb during copulation. Although not illustrated here, some *Deinopis* females have more than 20 twists or coils in the copulatory ducts, and their males may have correspondingly spiraled emboli (see, e.g., Kuntner et al., 2008: fig. 20). Although no one has studied the detailed sexual biology of any species, the central median apophysis probably anchors the bulb in the epigynum and does not rotate. Neither, obviously, does the cymbium. Instead the tough, highly spiraled median apophysis membrane and basal hematodocha must unwind as many times as the male embolus rotates itself into the female copulatory ducts. Multicellular animals famously have never evolved true axles, wheels, or even repetitive rotation of body parts, but *Deinopis* may hold the world record for trying.

Despite their circumtropical distribution and notoriety, deinopids are unusually rare in collections and apparently in the field, considering that they are large (body length 1–2 cm), free-living animals favoring habitats that naturalists and collectors intensely sample (Figures 1, 2). Judging

from collections borrowed for this study, the current global total for Deinopidae is about 300 adult specimens of only 57 nominal species (Platnick, 2010). The 14 species of the genus *Menneus*, the main subject of this paper, are known from only 135 adult animals from 106 distinct localities worldwide. By the beginning of the twentieth century, only two *Menneus* adults had been collected, and, by 1950, only 15. From 1950 until the present, however, 122 adults have been collected, possibly because naturalists now realize the importance of collecting at night (see Figure 8b). If one supposes that all species with viable populations have ranges large enough so that taxonomists would regard them as occupying at least two “localities,” one may apply “Chao2” estimators (Colwell, 2008) to obtain a rough lower-bound estimate of the actual richness of a clade or lineage. Four of the 14 *Menneus* species are known from single localities, and two are known from only two, yielding an estimate of clade richness of 30 species, or roughly double the currently known total. Of course, such statistical estimators assume random constant sampling effort, which is clearly false (Figure 8b), but the method at least provides an approximation of the magnitude of undiscovered *Menneus* diversity.

As a family, Deinopidae is comparably rare. Average abundance in quantitative samples from either the Old World or New World tropics (Cameroon, Madagascar, Thailand: Coddington, unpublished data; Tanzania: Sorensen et al., 2002; Peru: Silva and Coddington, 1996; Bolivia: Coddington et al., 1991, 1996; Guyana: Coddington et al., 2009; Tobago: Coddington, unpublished data) is 0.9 adults per 1,000 individuals—among the lowest local abundances of any families from these inventories.

Because Deinopidae are cribellate and spin orb webs, the family has featured prominently in the controversy over the monophyly of the orb web (Opell, 1979; Coddington, 1986a, 1986b; Coddington and Levi, 1991; Bond and Opell, 1998; Coddington et al., 2004). Ethological and morphological evidence to date places Deinopidae consistently as the sister group of Uloboridae, forming Deinopoidea, and the latter as sister to the ecribellate, primitively orb-spinning Araneoidea (Coddington, 1986a, 1986b, 1990a, 1990b; Scharff and Coddington, 1997; Griswold et al., 1998, 1999, 2005). Some molecular analyses, however, have not recovered a monophyletic Orbiculariae (e.g., Wu et al. (2002), but see Garb et al. (2006) and Blackledge et al. (2009) who find support for the group).

This paper revises the genus *Menneus* worldwide and establishes the generic classification of Deinopidae. It also provides a morphologically and ethologically based estimate of the species level phylogeny of the former and

cladistically based definitions of relevant higher taxa. We expect to follow this paper with a worldwide revision of *Deinopis*, but, given the length of time this study has been underway, it seems worthwhile to publish these results now in order to facilitate *Menneus* species identification.

Classically, *Menneus* is a genus of southern Africa and Australia. Earlier authors recognized 13 species (Platnick, 2010). Six species were from Africa: *camelus* from KwaZulu-Natal, *dromedarius* and *capensis* (as *Avellopsis*) from the Cape Province, South Africa, *affinis* from East Africa, and *tetragnathoides* from the Congo. Seven species were from Australia, New Guinea, and adjacent islands (mostly treated as *Avella*): *angulatus* and *superciliosus* from Queensland, *despiciens* from Queensland and New South Wales, *unifasciatus* from New South Wales, *neocalledonius* from New Caledonia, *reticulatus* from New Guinea, and *trinodosus* from Lord Howe Island. One fossil species, *M. pietrzeniukae*, is known from Baltic Amber but seems to be a juvenile female (Wunderlich, 2004; Dunlop et al., 2009). Owing mainly to the tendency of nineteenth century authors to describe as new species juveniles of obviously new lineages, such as *Menneus*, many older names are nomina dubia. Deinopid species are surprisingly difficult to diagnose, even with genitalic characters. Species concepts based only on somatic features are best suppressed.

## METHODS AND MATERIALS

A total of 135 adult *Menneus* specimens were examined, representing 113 species records. Localities are listed as written on museum labels (usually direct quotes) without interpretation of abbreviations. In square brackets we provide the collection acronym, the specimen code (if any), count, and sex of specimens, as well as decimal latitude and longitude.

## ABBREVIATIONS

The following museum abbreviations are used subsequently throughout the text, and we thank the curators, collection managers, and associated staff for their help in providing specimens and loans:

### Museums

AMNH	American Museum of Natural History, New York, USA
AMS	Australian Museum, Sydney, Australia
BMNH	The Natural History Museum, London, UK

CAS	California Academy of Sciences, San Francisco, USA	MH	median hematodocha
EMUC	Essig Museum University of California, Berkeley, USA	ML	midline
Filmer	Martin Filmer Private Collection, Johannesburg, South Africa	MS	modified spigot
MCSNG	Museo Civico di Storia Naturale, "Giacomo Doria," Genoa, Italy	NSS	nonsticky spiral
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA	OC	o'clock
MNHN	Muséum National d'Histoire Naturelle, Paris, France	PC	paracribellar spigot
Murphy Coll.	John Murphy Private Collection, Hampton, UK	PLS	posterior lateral spinneret
NMP	Natal Museum, Pietermaritzburg, South Africa	PME	posterior median eye
QM	Queensland Museum, Brisbane, Australia	PMS	posterior median spinneret
RMCA	Musée Royal de l'Afrique Centrale, Tervuren, Belgium	Rl	lower radius
SAM	South African Museum, Cape Town, South Africa	Rm	middle radius
SANC	South African National Collection, Pretoria, South Africa	Ru	upper radius
SMNH	Swedish Museum of Natural History, Stockholm, Sweden	SEM	scanning electron microscope
TM	Transvaal Museum Pretoria, South Africa	ST	subtegulum
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA	T	tegulum
WAM	Western Australian Museum, Perth, Australia		
ZMUC	Zoological Museum, University of Copenhagen, Denmark		

#### Other Abbreviations

AC	aciniform spigot
AL	alveolus
ALE	anterior lateral eye
ALS	anterior lateral spinneret
AME	anterior median eye
BH	basal hematodocha
CB	cymbium
CY	cylindrical spigot
E	embolus
FL	frame line
MAP	major ampullate spigot
mAP	minor ampullate spigot

MH	median hematodocha
ML	midline
MS	modified spigot
NSS	nonsticky spiral
OC	o'clock
PC	paracribellar spigot
PLS	posterior lateral spinneret
PME	posterior median eye
PMS	posterior median spinneret
Rl	lower radius
Rm	middle radius
Ru	upper radius
SEM	scanning electron microscope
ST	subtegulum
T	tegulum

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#### TAXONOMY

All measurements, including those on figures, are reported in millimeters, made using a microscope micrometer eyepiece. Prosoma and opisthosoma length and height

were measured in lateral view, and their widths were measured in dorsal view, all at widest points (prosoma height measured at head region). Eye widths are maximum diameters of the eye lens; eye separations were measured between lenses. See "MORPHOLOGY" for detailed descriptions of family apomorphic and diagnostic features. All other taxonomic methods are standard in spider systematics.

#### ILLUSTRATIONS AND IMAGING

Older illustrations were rendered on Vellum® film or fine-grained coquille board and further rendered with black, soft Prismacolour® pencils. These artworks were scanned and further manipulated with Photoshop CS3. The newer illustrations were made with a Visionary Digital imaging system, equipped with a Canon 40d digital camera body and an Infinity K2 microscope using Olympus metallurgical objectives. Image "stacks" were combined with Helicon Focus 4.0 and further manipulated in Photoshop CS3 extended. Scanning electron microscope images were captured using an Amray 1810 SEM at the Smithsonian's National Museum of Natural History Scanning Electron Microscope Facility.

#### PHYLOGENETIC METHODS

For deinopid exemplars, we used all *Menneus* and three *Deinopis* species, and for outgroups, we used *Uloborus diversus* and *Dictyna arundinacea*. Specimens examined for phylogeny were as follows.

#### Outgroups

*Dictyna arundinacea*: ♀ ♂ - USNM, N Sakhalin Okha District Pil'tun Bay, A. M. Basarukin, 6–7.1991.

*Uloborus diversus*: ♀ - USNM, Fresno Co. Chase Orchard Navel. 9.iv.74.

#### Ingroups

*Deinopis spinosa*: ♀ ♂ - USNM, FL, Alachua Co., Devil's Millhopper St. Pk., mixed hardwoods. J. Coddington, 2.viii.1985.

*D. lamia*: ♀ - Coll. Alayon, El Veral. Guanahacabibes, ix.1981; M-La Chispa, Ballesteros, T. De Collantes. ix.1981, Col J. Santos.

*D. cylindrica*: ♀ - Natal Mus, South Africa, KwaZulu-Natal, Lake Sibayi, Rhodes Univ. Exped., vi.1966; M-PAN, Zambesi (no further data).

*Menneus camelus*: ♀, South Africa, Johannesburg, dried branches in garden, M Filmer, 20.iii.1988;

- ♂ - Natal Museum, South Africa, KwaZulu-Natal, Amanzimtoti, Inanda Nature Res, 3030BB?, P Reavell, 20.iv.1981.
- M. capensis*: ♀ - SAM, South Africa, Cape Prov, Cape Town, Newlands Forest, Paradijs' Stream, N Larsen, 9.v.1991; ♀ ♂ - USNM, South Africa, Western Cape, Cape Town, Table Mtn. NP, Newlands Forest. 33°58.934'S 18°26.686'E. Alt. 159 m, Leg. Kuntner & al., 4.v.2006.
- M. darwini*: ♂ - All material examined (see "TAXONOMY").
- M. dromedarius*: ♂ - NMP (NM 5894): South Africa, KwaZulu-Natal, Ngoyi Forest, Lawrence & al., ii.1953. ♀ - CAS (CASENT9012406): Madagascar, Toliara, Réserve Privé Berenty, Forêt de Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, ER30 beating low vegetation, 35 m, 24°57'25"S 46°16'17"E, B. L. Fisher et al. BLF5318, 3-8.ii.2002.
- M. samperi*: ♀ ♂ - All material examined (see "TAXONOMY").
- M. tetragnathoides*: ♂ - lectotype - MNHN, "Congo" (Angola, Cabinda, Chinchoxo); RMCA, Malawi, Chintheche, R Jocqué, 2.v.1978.
- M. aussie*: ♀ ♂ - QM, Australia, QLD, Rundle Range, 24.iii.1975.
- M. bituberculatus*: ♀ - QM, Australia, QLD, Upper Brookfield, pittraps, rainforest, Raven & Green, 6.x.1981.
- M. nemesio*: ♀ - AM, Australia, NSW, Wamberal, MR Gray, 7.xii.1983; ♂ - CAS, Australia, NSW, 5 mi N Hawkesbury r. br., 150 m, Ross & Cavagnaro, 3.xii.1962.
- M. neocaledonicus*: ♀ ♂ - QM, New Caledonia, Aoupinie, 20 km NE Poya, 650 m, Monteith & Cook, 18.v.1984.
- M. quasimodo*: ♀ holotype (see "TAXONOMY").
- M. superciliosus*: ♀ ♂ - AM, Australia, QLD, Edmonton, NC Coleman, 29.ix.1969.
- M. trinodosus*: ♀ - AM, Australia, QLD, Eurimbula, SE Gladstone, rainforest site 4, 24°11'S, 151°50'E, C Horseman, iii.1975; ♂ - QM, Australia, QLD, Kroombit Tops (Three Moon Ck.), 45 km SSW Calliope rainforest, Davies & Gallon, 9.xii.1983.
- M. wa*: ♀ ♂ - All material examined (see "TAXONOMY").

*Menneus* species, as noted in the Introduction, are rare spiders. Four *Menneus* species are only known from a single sex: *M. tetragnathoides* and *M. darwini* only from males and *M. bituberculatus* and *M. quasimodo* only from

females. Because so few adults were available, we avoided as much as possible destructive sampling of specimens, such as dissections or SEM preparations. The use of light microscopy alone meant that phylogenetically informative features were necessarily macroscopic and scarce. We found only 56 potentially informative characters among the 19 taxa (see Phylogeny). We used Mesquite (Maddison and Maddison, 2009) to maintain the matrix and NONA 2.0 (Goloboff, 1993) in combination with Winclada 1.00.08 (Nixon, 2002) for tree searches using unweighted parsimony.

## MORPHOLOGY

Millot (1933) mentioned several deinopid apomorphies. The cephalothoracic intestinal diverticulae of Uloboridae are solely supra-oesophageal and simple. Four pairs of diverticulae lead to the walking legs and one anterior pair enter the mouth area. Both *Deinopis baubo* and *Menneus camelus* have one system homologous to the uloborid condition and an extra system of sub-oesophageal diverticula, which Millot regarded as unique in spiders. In addition, deinopids have a sixth pair of diverticulae beneath the homologs of the uloborid anterior diverticulae: these serve the bases of the pedipalps and the labrum. *Deinopis*, uniquely, has the right anterior diverticula (dorsal view) enlarged and expanded to form the “frontal diverticule” in a semilunate shape immediately behind the lateral eyes.

Deinopidae have several sorts of body setae: blunt, plumose, and feathery setae (Figure 5a–d). Chelicerae always bear anterior and posterior teeth, but the number varies within and between species (Figure 5c).

The fourth metatarsus, as in all cribellate spiders, bears a calamistrum (Figure 5e). The fourth tarsus has a ventral comb of distinctive setae, and the retrolateral claw is reduced (Figure 5f). Male legs are relatively much longer than female legs (Figure 1a–c), and male legs I and II are additionally modified in various ways (see characters 31–37, below, and Figure 3c–e).

Deinopids present a complete complement of spinnerets and spigots (Figure 7a). The cribellum is entire and broad, with the annulate cribellate spigots apparently clustered more densely on the anterior cribellum surface (Figure 7b,c). The ALS have a fairly extensive piriform field, and the major ampullate field, unusually among spiders, contains multiple functional major ampullate spigots (Figure 7d). The PMS bear a single anterior minor ampullate spigot, multiple apical aciniform spigots, an extensive field of anterior paracribellar spigots (with annulate

shafts), and an extensive posterior field of cylindrical spigots (Figure 7e). The PLS have a distal “modified” spigot (putative homolog of the uloborid pseudoflagelliform and araneoid flagelliform spigot), multiple aciniform spigots, and an extensive basal brush of cylindrical spigots (Figure 7f). Male epiandrous spigots are grouped (Figure 6a), smooth, and set in deep pockets (Figure 6b).

The ventral surface of the deinopid anal tubercle has a modified field of setae, symmetric and oriented toward the midline (Figure 6c).

Deinopid palpal bulbs are built on a simplified plan (Figure 4a,b), which probably reflects exacting functional requirements. The embolus is always a thin, relatively flat, spiral sclerite, and the number of coils correlates, to some extent, with the number of coils of the female copulatory ducts. (For the 12 deinopid taxa of Table 1 known from both sexes, the correlation coefficient,  $r^2$ , is 0.51 and  $p = 0.08$ .) The embolus has a complex cross section (Figure 6f) with an inner ridge and an adjacent groove. The ridges and grooves of a given loop probably engage adjacent loops. This reinforcing mechanism may aid the male to insert the tip of the embolus all the way into the spermathecae of the female during copulation. The tip of the embolus may have subdistal structures whose function is enigmatic (Figure 6f).

The tegulum has only a single apophysis other than the embolus, which is probably the homologue of the uloborid and araneoid median apophysis (Figure 6d–f), not the conductor (contra Kuntner et al., 2008: fig. 20). The deinopid median apophysis is compact, and the apical part is always more or less hook-shaped (Figure 15g), with the concavity facing the median or apical margin of the palp. The basal part often has a lobe (Figures 6e, 10j), more or less visible in ventral view. The apical hook probably engages the epigastric rim adjacent to the median plate, or septum, of the female epigynum (Figure 22e–g) during copulation, thus locking the bulb to the epigynum. The median apophysis is flexibly attached to the tegulum, via a coiled, tough, tendon-like membrane. The tegulum is also highly modified. The ejaculatory duct is a simple spiral. The walls of the tegulum are smooth, and it is shaped like a squat sphere. There are no lateral projections. It is firmly attached to the subtegulum. The subtegulum is small and contains the fundus of the reservoir. It is attached to the cymbium by the extremely coiled, tough, basal hematodocha (Figure 4b).

We hypothesize that these features of the palp cooperate in a special copulatory mechanism. In order to introduce the embolus tip into the female spermathecae, the tegulum apparently rotates a number of times as the basal hematodocha expands, thus screwing the embolus into the

**TABLE 1.** Phylogenetic character matrix. See “Character Descriptions” for explanation of the 56 characters and their states; see “Phylogenetic Methods” for list of exemplar taxa and sources. A dash (-) indicates inapplicable data; a question mark (?) indicates unknown data.

Terminal taxa	Character number					
	10	20	30	40	50	56
<i>Dictyna arundinacea</i>	00-0000000	00-0000--0	002100--00	00000000-0	100---30-	00-000
<i>Uloborus diversus</i>	00-0000000	00-0001000	000-00--00	0000000100	000-0--20-	00-010
<i>D. cylindrica</i>	1101000100	10-0011001	000-011001	11111110-1	0014010111	100???
<i>D. spinosa</i>	1101001111	1101011001	000-011010	0000000101	0010000011	110121
<i>D. lamia</i>	1101001110	10-0011001	000-011010	000000?101	0010000011	110???
<i>Menneus bituberculatus</i>	0100011211	00-1011100	000-01002?	???????????	???????????	???????
<i>M. trinodosus</i>	0100011211	0101011100	100-010210	0000000101	1111011111	10021
<i>M. capensis</i>	0100011211	00-0011000	0011110111	0000000101	1110011112	100121
<i>M. superciliosus</i>	0100011201	00-0011000	0110110121	0000001101	1112100313	00021
<i>M. neocalaledonicus</i>	0100010111	00-0000--0	100-010200	11100110-1	1114100010	000???
<i>M. quasimodo</i>	0110010101	00-0011000	100-01003?	???????????	???????????	???????
<i>M. wa</i>	0110011211	00-0011000	0111110121	111111?101	1113000013	000???
<i>M. aussie</i>	0110011201	00-0011000	1011110151	1111111101	1112100013	000???
<i>M. nemesio</i>	0110011111	00-0011000	1111110131	11111110-1	1112100213	100???
<i>M. camelus</i>	0110111211	0111111110	100-010120	1111111111	1114100012	101121
<i>M. tetragnathoides</i>	???????????	???????????	??????????0	111111?111	1111100113	001???
<i>M. dromedarius</i>	0110111211	0101011110	100-010140	1111111111	1113100113	000???
<i>M. darwini</i>	???????????	???????????	??????????0	1111111111	1112100113	001???
<i>M. samperi</i>	0110111211	0111111110	110-010130	1111111111	1113100113	1001??

copulatory ducts. All spider palps rotate as they expand, but the morphology of the deinopid palp seems specialized to rotate to an exaggerated extent. If the median apophysis is fixed to the epigynum during copulation, it cannot rotate. Likewise, the cymbium cannot rotate. However, via the median apophysis membrane and similarly coiled basal hematodocha, the tegulum can “unwind” through as many revolutions as there are coils, thus imparting a spiral motion to the embolus.

The female genitalia (Figure 23e–g) are entelegyne, unlike some genera of uloborids. Externally, the epigynum is simple, consisting of a median plate bordered laterally by the thickened rims of the epigastric furrow. Between the median plate and the thickened rims lie paired copulatory slits (Figure 27e,f). The thickened margins of the epigastric furrow adjacent to the median plate are excavated to a greater or lesser extent on their dorsal surface, thus forming a small hollow that probably engages the male median apophysis during copulation.

Internally, the copulatory ducts spiral around the fertilization ducts (e.g., Figure 27g). In posterior and

dorsal view, the left copulatory duct, for example, spirals counterclockwise from the epigynum toward the spermatheca. The entrance to the copulatory duct is at the basal, wider portion of the median plate of the epigynum, more or less at the bottom of the copulatory slits. The fertilization ducts are heavily sclerotized and long (probably additional synapomorphies for Deinopidae). These thickened ducts might serve as a stiffening support or anchor for the coil of copulatory ducts. The lumen of the duct is quite straight. Sometimes the wall of the fertilization ducts are reinforced with auger-like spiral thickenings, to which the inner margins of the copulatory duct may be fused. The initial curve of the fertilization duct passes along the margin of the lateral epigynal margins and generally is quite visible in posterior view as a darkly sclerotized area adjacent to the rim of the median epigynal plate (Figure 23g).

Although the distal sclerotized portions of the female genitalia are often massive, actual limits of spermathecae are often difficult to discern. Glandular pore fields in *Deinopis* seem to be limited to the apical portion of the spermathecae.

## PHYLOGENY

Table 1 gives the matrix for 19 terminals and 56 phylogenetic characters and character states, which are described below.

### CHARACTER DESCRIPTIONS

#### *Female Somatic Morphology*

1. *Female PME setal fringe:* (0) absent (Figure 18a); (1) present (Figure 3a). The posterior median eyes of female *Deinopis* have an encircling fringe of short, broad, modified setae.
2. *Female ALE tubercle:* (0) absent (Opell, 1979: fig. 23); (1) present (Figure 3a). The ALE of all known deinopids occur on prominent tubercles such that the eyes point ventrolaterally. The animals hunt ventral side up and this feature evidently enables the lateral eyes to see above and to the sides.
3. *Female ALE tubercle:* (0) small (Figure 3a); (1) large (Figure 25d). In some *Menneus* species the ALE tubercle is notably longer.
4. *Female AME/PME ratio:* (0)  $\geq 0.50$  (Figure 25d); (1)  $\leq 0.30$  (Figure 3a). All *Deinopis* species have greatly enlarged posterior median eyes.
5. *Female clypeal setae:* (0) absent (Figure 25d); (1) present (Figure 18a). Some *Menneus* species have noticeably thicker and larger setae medially on the margin of the female clypeus.
6. *Female cheliceral setal conformation.* (0) multiple, irregular (Figure 10a); (1) distinct medial and frontal macrosetae (Figure 28b). *Menneus* species have two pairs of distinct cheliceral macrosetae.
7. *Female endite trichobothria:* (0) absent; (1) present (Figure 5b). The endite bears, usually, two basal shorter and two distal longer trichobothria that point in notably different directions than the surrounding setal fields.
8. *Female sternum:* (0) broad; (1) setose knob (Figure 5a); (2) pointed (Figure 31k). The sternum posterior apex may be relatively broadly truncated, a blunter knob bearing setae, or sharply pointed.
9. *Female sternum pattern:* (0) uniform or mottled; (1) light median band (Figure 20d). The sternal color pattern may be uniform to mottled or with a median light band.
10. *Female posterior carapace white mark:* (0) absent; (1) present (Figure 32a). The posterior carapace margin may have a white V-shaped guanine mark.

11. *Female dorsal femur I:* (0) normal; (1) bulging (Figure 3b). The basal, dorsal femur is sometimes expanded into a bulge or knob.
12. *Female femur III ventral hair brush:* (0) absent; (1) present. The retrolateral surface of femora III and IV sometimes have a distinct brush of long setae.
13. *Female femur III hair brush length:* (0) short; (1) long. The third femoral hair brush may be short or long.
14. *Female femur IV hair brush:* (0) absent; (1) present.
15. *Female coxae III–IV pleural bar:* (0) absent; (1) present. Some deinopids have sclerotized bars between the third and fourth coxae, which join carapace to sternum.
16. *Female tarsus IV retrolateral claw teeth:* (0) normal; (1) reduced (Figure 5f, arrow). The fourth tarsal retrolateral claw may be smaller and may bear fewer, smaller teeth than the prolateral claw.
17. *Female abdominal form:* (0) smooth (Figure 28c); (1) tuberculate (Figure 10d). Deinopid females generally have paired dorsal abdominal tubercles.
18. *Female abdominal tubercle position:* (0) median-anterior (Figure 25b,c); (1) posterior (Figure 31c,d). Abdominal tubercles may be either median or posterior.
19. *Female abdominal tubercle symmetry:* (0) symmetric (Figure 20c); (1) asymmetric (Figures 1d, 18c). Almost all deinopids have abdominal tubercles, but in some *Menneus* species the tubercles are greatly enlarged and single, either left or right, and both states may occur in the same species.
20. *Female abdomen proportion:* (0) width/length  $> 0.4$ ; (1) width/length  $< 0.4$  (Figure 11d). The *Deinopis* abdomen is relatively longer and thinner than other taxa in this study.
21. *Female ventral abdominal dark band:* (0) mottled/solid (Figure 30d); (1) paired (Figure 27d). The abdomen bears a median ventral dark area, which in some species is mottled or nearly solid and in others it is paired.
22. *Female abdominal ventral guanine pattern:* (0) mottled (Figure 11c); (1) paired conspicuous guanine spots (Figure 20d). Some species have paired, relatively anterior, ventral abdominal guanine spots or patches.
23. *Female dorsal posterior abdominal pattern:* (0) mottled (Figure 11d); (1) paired longitudinal narrow bands (Figure 27c); (2) median dark band.
24. *Female dorsal posterior abdominal pattern shape:* (0) straight to undulating (Figure 30c); (1)

- marked, regular undulations, chevron-like (Figure 27c).
25. *Female abdominal mid-dorsal color pattern:* (0) longitudinal mottled or light band (Figure 28c); (1) transverse light bar (Figure 27c).
- #### Female Genital Morphology
26. *Female epigynal median area:* (0) chamber or thin septum (Opell, 1979: fig. 43); (1) broad, plate-like septum. The median epigynal area of deinopids always bears a well-developed median septum that appears as a broad plate (Figure 10e).
27. *Female epigynal median plate:* (0) flat (Figure 18f); (1) involute (Figure 10e). In ventral view the anterior lateral margins of the median septum of *Deinopis* is excavated so that the septum appears to have a pronounced neck.
28. *Female epigynal septum lateral margins:* (0) subrectangular (Figure 9b); (1) triangular (Figure 25f); (2) subparallel (Figure 31e). The overall outline of the epigynal median septum may be wider than long (subrectangular), triangular, or longer than wide (subparallel).
29. *Female number of copulatory duct turns:* (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6. The number of copulatory duct turns in deinopids can be quantified in various ways, depending on where the duct turns are considered to start and end. The least ambiguous seems to be to count them from figures representing a particular orientation. Consequently, we quantify duct turns in dorsal view, as the number of apparent turns on the lateral margin of the copulatory/fertilization duct complex (e.g., Figure 28g, 1 turn; Figure 27g, 4 turns). The number of turns in *M. quasimodo* is ambiguous; we code it as state three.
- #### Male Somatic Morphology
30. *Male carapace shape:* (0) pear-shaped, sides of thoracic region parallel (Figure 22h); (1) diamond-shaped, sides of thoracic region narrowing posteriorly (Figure 25h). As in females, male carapace shape varies informatively, either the plesiomorphic pear shape or a more angular diamond shape.
31. *Male tibia II distal end:* (0) normal; (1) with apophysis (Figure 3d). Tibia II of some males bears a prolateral strong apophysis at the metatarsal joint. This and the next two characters pertain to distal tibial modifications and are distributed identically for this taxon sample, but we code all three conditions because the morphology of each is distinct.
32. *Male tibia-metatarsus condyle:* (0) normal; (1) stout (Figure 3d). The ectal condyle of the male tibia-metatarsal joint is sometimes stronger and stouter than normal.
33. *Male tibia II tip:* (0) normal; (1) swollen (Figure 3d). In addition to the previous modifications, the male tibia II distal tip may be significantly broader or swollen.
34. *Male distal Mt II setae:* (0) normal; (1) curved and/or stout (Figure 3e). The distal end of metatarsus II bears several setae, of which the dorsal and/or prolateral may be distinctly longer, curved, or stouter in some species.
35. *Male Mt-Ta II joint:* (0) normal; (1) ball and socket (Figure 3e). The metatarsus-tarsal joint in some species is modified, with the metatarsus bearing a distal, dorsal protruding knob that fits into a corresponding socket on the tarsus.
36. *Male Ta II dorsal setae:* (0) normal; (1) spatulate (Figure 3e). The dorsal surface of male tarsus II may bear a longitudinal field of short, spatulate setae.
37. *Male Ta I form:* (0) entire; (1) divided (Figure 3c). Like the tibia, the male tarsus I may be divided.
38. *Male abdominal form:* (0) strictly cylindrical (Figure 10i); (1) more oval and tuberculate (Figure 20i). As in the females, some species have prominent dorsal abdominal tubercles. Tubercles in males can vary greatly in size.
39. *Male abdominal tubercle symmetry:* (0) paired (Figure 20i); (1) unpaired (Figure 24d). As in females, male abdominal tubercles may be paired or single and either left or right.
- #### Male Genital Morphology
40. *Male cymbial form:* (0) oval, elongate (Opell, 1979: fig. 47); (1) round, hemispherical (Figure 4e). In ventral view, deinopid cymbia are remarkably circular in outline, and in lateral view nearly hemispherical.
41. *Male apical cymbial margin:* (0) smoothly rounded (Figure 4b); (1) pointed (Figure 4e). In some males the distal margin of the cymbial alveolus is rounded, and in others it is pointed.
42. *Male apical cymbial setae:* (0) absent (Figure 4a,b); (1) present (Figure 4e). Some males have

- noticeable tufts of curved, often white setae on the apical margin of the alveolus.
43. *Male tegulum form*: (0) elongate, oval (Opell, 1979: fig. 46); (1) round, radially symmetric (Figure 14b). In ventral view, all deinopid tegula are remarkably circular in outline.
  44. *Median hematodocha position*: (0) 12–(4–6); (1) 2–(4–5); (2) 4–(7–8); (3) 6(8)–9(11); (4) (10–11)–(1–2). The span of the median hematodocha insertion on the tegulum in ventral view varies both in position and extent and is often diagnostic for species. It can be quantified as occupying various sectors of an imaginary “clock” (Figure 14b “10–2,” e “11–4,” h “6–9”). In an attempt to constrain the proliferation of singleton character states, we occasionally subsume variation between species, thus (10–11)–(1–2) means a span of 10–11 OC to 1–2 OC.
  45. *Median apophysis base*: (0) smoothly rounded (Figure 14e); (1) with knob (Figure 15b,e,h). In ventral view, the base of the median apophysis may be rounded or produced into a blunt or somewhat acutely pointed knob.
  46. *Median apophysis distal lobe*: (0) relatively broad, subrectangular (Figure 22l); (1) relatively narrow, elongate (Figure 10j). In ventral view, the distal tip of the median apophysis may be fairly narrow, such that the basal portion of the median apophysis is easily visible or broad such that no part of the basal portion shows.
  47. *Median apophysis distal lobe curvature*: (0) abruptly angled (Figures 4e, 15g); (1) gently curved (Figure 17f). In retrolateral or prolateral view, the median apophysis may either bend sharply, at almost a right angle, or its curve may be gradual and gentle.
  48. *Embolic coil width: tegulum width*: (0) << 1; (1) < 1; (2) subequal; (3) > 1. In ventral view, the diameter of the outermost embolic coil may be much less (Figure 16h), slightly less (Figure 14h), subequal (Figure 16e), or greater than (Figure 17b) the diameter of the tegulum.
  49. *Embolic form*: (0) curved (Opell, 1979: fig. 47); (1) spiraled (Figure 4c). Outgroups such as Uloboridae may have distinctly curved emboli, but all deinopid emboli are strongly and often extremely spiraled.
  50. *Embolic coil number*: (0) 2; (1) 2.5; (2) 3; (3) 3.5 or more. The same issue that arises when quantifying female copulatory duct turns or twists (character 29) also pertains to quantification of male embolic turns. In *Menneus* the tip of the embolus of a normal palp terminates close to the cymbium apex. Coils are counted to the nearest half rotation, from illustrations of ventral views, beginning from the tip of the embolus until it disappears beneath the median apophysis (e.g., Figure 14b [3.5 turns], e [2.5 turns]).
  51. *Embolus tip form*: (0) simple, attenuate (Figure 24e,f); (1) distally widened (Figure 10j,k). In ventral view, the embolus tip may be simply attenuate or needle-like, or it can be expanded or widened subapically.
  52. *Embolus tip symmetry*: (0) entire (Figure 20k, l); (1) excavated (Figure 11m). The embolus tip may be symmetric (whether widened or not) or asymmetric, with one side of the embolus prolonged into a narrow, delicate tip.
  53. *Embolus tip*: (0) bent smoothly away from embolus coil (Figure 14f); (1) relatively straight (Figure 14i). In retrolateral view, the tip of the embolus may lie in the plane of the embolic coils or may abruptly bend away from the tegulum toward the median apophysis.

#### Behavior

54. *Female eggsac form*: (0) oval to flattened (Opell, 1979: fig. 254); (1) spherical (Figure 2e). All known deinopid eggsacs are markedly spherical, whereas most spider eggsacs, and in this case those of the outgroups, are more or less flattened and oval. Deinopid egg sac walls are also relatively dense and hard.
55. *Web architecture*: (0) sheet; (1) orb with many radii (Opell, 1979: pl. 8); (2) orb with few radii (Figure 2d). All known deinopid webs are bilaterally symmetric, modified orbs (Coddington, 1986a) with three radii on each side. Although the web architecture of *Menneus* is known only for a few species, all show the expected deinopid architecture.
56. *Sticky silk area size*: (0) much larger than spider (Opell, 1979: pl. 8); (1) subequal to spider size (Figure 2c). Most web-spinning spiders spin webs much larger than their body size. Deinopids make webs whose sticky silk area is roughly 1–2 cm at rest and thus comparable to the body size and leg span of the spider.

## RESULTS

The matrix of Table 1 yields a single tree of length 131 under unweighted parsimony, with consistency index 0.54 and retention index 0.69 (Figure 8a). Although Figure 8a is the single most parsimonious explanation for the data of Table 1 and a testable hypothesis, the matrix is so sparse that applying measures of nodal support would be pointless (most nodes within *Menneus* would show low levels of support, at best). All 131 steps are mapped on Figure 8a. Ambiguous mappings were usually resolved with fast optimization, thus allocating homoplasy to secondary loss, but for several features, slow optimization seemed more appropriate. Deinopidae, *Deinopis*, and *Menneus* are monophyletic, and their synapomorphies are discussed in “TAXONOMY.” Of note, secondary sexual characters affecting male first and second legs evolve in a block at the node subtending *Menneus wa*. Large posterior median eyes are a *Deinopis* synapomorphy. Deinopid web architecture (Figures 1a,d, 2b–d) is a family synapomorphy. Given that *Deinopis* is circumtropical and *Menneus* is limited (mostly) to the Old World tropics, the family must predate the breakup of Gondwana. The biogeography as mapped on the cladogram (Figure 8a) suggests that the origin of *Menneus* may be Australasian. The cladistic position and African distribution of *M. capensis* among Australasian species is therefore anomalous. The earliest known fossil, *Paleomicromenneus lebanensis* (Penney, 2003), is Cretaceous (*M. pietzenikae* and other juveniles are known from Baltic amber; Wunderlich 2004), but by that time, Africa and Australasia had already rifted apart. Given the uncertainty as to the true ages of lineages, and, most importantly, the paucity of known specimens and severe undersampling bias, the biogeographic pattern cannot be ascribed at this point either to vicariance or dispersal. A distal clade of species is unique to Africa (Figure 8a) and defined by an unusual synapomorphy: the ability to develop asymmetric (i.e., left or right) abdominal tubercles. This feature, in addition to the family-level apomorphies of femoral setal fringes, mottled coloration, and daytime resting postures, no doubt form a complex of adaptations promoting crypsis.

## TAXONOMY

### DEINOPIDAE C. L. KOCH, 1850

**DIAGNOSIS.** Entelegyne cribellate spiders; females with median epigynal plate and copulatory ducts

coiling around long, heavily sclerotized fertilization ducts (Figure 23g), males with unique, flat, round tegulum held in a round, hemispherical cymbium, embolus long, coiled around a single tegular apophysis, hypothesized to be the median apophysis homologue (Figure 4a–e). Both sexes with anterior lateral eyes on distinct, ventrally oriented tubercles (Figure 10a,b,f,g). Tapetum absent from all secondary eyes. Fourth tarsal retrolateral claw teeth reduced (Figure 5f). Web architecture and attack behavior unique, a highly reduced and stylized orb web, about the same size as the body length of the spider, held in the anterior legs, and actively used to envelop aerial or pedestrian prey (Figures 1a,d, 2b–d). Egg sac probably unique: a hard, brown sphere attached to leaves or buried in leaf litter (Figure 2e).

**COMPOSITION.** Three lineages, *Menneus*, *Deinopis*, and *Paleomicromenneus*, treated as genera. *Paleomicromenneus lebanensis* Penney 2003 is known only from Cretaceous Lebanese amber (Penney, 2003). The male specimen is small (2.86 mm body length) but otherwise fits comfortably into the family, resembling *M. capensis* in genitalic form.

**SPECIES DIAGNOSTIC CHARACTERS.** While external epigynum shape varies to some extent, the internal morphology (especially size, proportion, and number of coils of copulatory duct) is diagnostic. In males, the relative origin of the median hematodocha, the orientation of the median apophysis, and the position of the embolus tip, and its morphology, are diagnostic (Figures 14–17). In local faunas, abdominal form and coloration can be valuable identification clues (e.g., Figure 1b).

**DISTRIBUTION.** Tropics and subtropics worldwide, extending to temperate SW Australia, from sea level to as much as 2300 m.

### *Deinopis* MacLeay, 1839

*Deinopis* MacLeay, 1839:9.—Platnick, 2010. Type species *D. lamia* MacLeay, 1939, by monotypy.

*Dinopis*: Bonnet, 1956.—Lehtinen, 1967:230, 306.

**NOTES.** Original genus spelling is used (MacLeay, 1839; Platnick, 2010), not the unjustified emendation *Dinopis* (as in Bonnet, 1956). The name is feminine (Bonnet, 1956).

**DIAGNOSIS.** Synapomorphies in this analysis that define *Deinopis* are: the PME are less than a diameter apart and extremely enlarged (at least 3× the AME diameter) with a fringe of setae (characters 1 and 4, Figure 3a). Female first femora are distally enlarged (character

11, Figure 3b). *Deinopis* abdomens, although not unique among spiders in their proportions, are usually much longer than wide (character 20, Figure 9a).

**DESCRIPTION.** Large spiders, female total length from 15 to 28 mm, males from 12 to 23 mm. Body and legs usually gray to brown. Cephalothorax elongate, with a narrow cephalic region (Figure 9a,e), and a long, narrow sternum, prolonged posteriorly (Figure 5a). Eyes as diagnosed, with ALE on tubercles (Figures 10a,b,f,g; 11a,b,i,j). Chelicerae with conspicuous pro- and retrolateral teeth, sometimes also with small denticles close to posterior rim (Figure 5c). Very long legs with leg formula 1, 2, 4, 3. Abdomen cylindrical, usually many times longer than wide, with or without prominent paired tubercles (Figures 9a,e, 10c,d,h,i, 11c,d,k,l). Female epigyna inconspicuous, median septum triangular to rectangular, with small round spermathecae and long copulatory ducts coiled around straight sclerotized fertilization ducts (Figures 9b-d, 11e-h). Male palpal tegulum partly covered with conspicuous embolus coiled around median apophysis. Embolus makes 1.5 to many turns; embolic tip tapered, flattened, or sinuate (Figures 9f, 10j, 11m).

**SPECIES.** The genus currently contains 46 species (Platnick, 2010). However, our generic revision in preparation will recognize approximately 30 valid species.

**DISTRIBUTION.** Tropics, subtropics worldwide.

### **Paleomicromenneus Penney, 2003**

*Palaeomicromenneus* Penney 2003: 571. Type species *Palaeomicromenneus lebanensis* Penney 2003, by monotypy.

**NOTES.** Penney (2003) described this species based on a single male from Lebanese amber. On the basis of the size (2.9 mm) of the type species, the genus is probably valid. Features used to diagnose modern species (embolus position, median apophysis form, median hematodocha extent) were not visible in the fossil specimen.

### **Menneus Simon, 1876**

*Menneus* Simon, 1876:218.—Lehtinen, 1967:217, 306.—Platnick, 2010.

Type species *Menneus tetragnathoides* Simon, 1876, by monotypy.

*Avella* Pickard-Cambridge, 1877:574 [see Cambridge, O. P., in References].—Lehtinen, 1967:217, 306.—Platnick, 2010. Type species *Avella despiciens* Pickard-Cambridge, 1877, from Rockhampton, Queensland, Australia, by monotypy. NEW SYNONYMY.

*Avellopsis* Purcell, 1904: 128.—Lehtinen, 1967:217, 306.—Platnick, 2010.

Type species *Avellopsis capensis* Purcell, 1904, from Kalk Bay Mountain, South Africa, by monotypy. NEW SYNONYMY.

**NOTE.** The name is masculine (Bonnet, 1957).

**DIAGNOSIS.** *Menneus* are easily recognized as deinopid spiders in which the PME are always at least a diameter apart and of relatively normal size ( $AME/PME \geq 0.40$ , Figure 18a,b,g,h). Synapomorphies for the genus at this point are subtle. *Menneus* have distinct frontal and medial cheliceral setae (character 6, Figures 20b, 25d), the carapace usually has a distinct posterior guanine patch (character 10, Figure 32a), and the cymbium bears a distal group of long, curving setae (character 42, Figure 4e).

**DESCRIPTION.** Medium sized spiders, female total length from 7.2 to 19.5 mm, males from 5.0 to 13.6 mm. Body and legs usually gray to brown, with patches of white and black. Cephalothorax elongate, pear or diamond shaped (Figures 18b,h, 20a,g). Eyes as diagnosed, with ALE on pronounced elongate tubercle, AME usually on smaller tubercle (Figure 19a,b). Sternum longer than wide, relatively acute posteriorly (Figure 20d). Long legs with leg formula 1, 2, 4, 3 (Figures 1a-d, 2a-c,e). Abdomen cylindrical, longer than wide, usually with a single (all African species except *capensis*) (Figure 18c,d,i,j) or paired dorsal tubercles (*capensis* and all Australasian species except *neocaledonicus*) (Figure 20c,i). Female epigyna relatively small, triangular, with inconspicuous posterior copulatory openings (Figure 18e,f), spermathecae round, unlobed, long thick copulatory ducts coiled around long straight fertilization ducts (Figures 22g, 23g). Male palpal cymbium round, apically pointed, ventral palp view exposes median hematodocha at edge of flat tegulum; tegulum partly covered with conspicuous embolus coiled around median apophysis. Embolus makes 2–4 turns; embolic tip tapered, flattened, or sinuate (Figures 14–17).

**SPECIES.** We currently recognize 14 *Menneus* species, six from Africa, and eight from Australasia. Several old Australasian names were based on juvenile specimens, and because species are often sympatric and can only be identified confidently from adults, we regard these names as nomina dubia (see below).

**DISTRIBUTION.** Central and southern Africa, Madagascar, Australia, New Guinea and New Caledonia (Figures 12, 13).

## KEY TO MENNEUS SPECIES

1. Africa or Madagascar ..... 2  
Australasia ..... 11
2. Males ..... 3  
Females ..... 8
3. Embolic coils in ventral view less than tegular width [Figure 14c,f] ..... 4  
Embolic coils subequal to or greater than tegular width [Figures 14i, 15i] ..... 5
4. Embolic coils much less than tegular width, median apophysis distal lobe broad and flat [Figure 14a–c] ..... *M. camelus*  
Embolic coils slightly less than tegular width, median apophysis distal lobe narrow, extended [Figure 14d–f] ..... *M. capensis*
5. Embolus tip bent away from tegulum in prolateral view [Figure 15c,f], median apophysis distal–basal lobe axis points to 2 OC [Figure 15b,e] ..... 6  
Embolus tip relatively straight and parallel to tegulum in prolateral view [Figures 14i, 15i], median apophysis distal–basal lobe axis points to 1 OC [Figures 14h, 15h] ..... 7
6. Median hematodocha in ventral view begins at roughly 6 OC, median apophysis in pro- or retrolateral view relatively flat [Figure 15a–c] ..... *M. dromedarius*  
Median hematodocha in ventral view begins at roughly 8 OC, median apophysis in pro- or retrolateral view relatively rounded [Figure 15d–f] ..... *M. samperi*
7. Median apophysis in pro- or retrolateral view rounded [Figure 14g–i], embolus tip at 10:30 OC ..... *M. darwini*  
Median apophysis in pro or retrolateral view flat and angled [Figure 15g–i], embolus tip at 11:30 OC ..... *M. tetragnathoides*
8. Copulatory duct turns three or fewer ..... 9  
Copulatory duct turns four or more ..... 10
9. Copulatory ducts with one full turn (or two if counting lateral margins in dorsal view) [Figure 20f] ..... *M. capensis*  
Copulatory ducts with two full turns (or three if counting lateral margins in dorsal view) [Figure 18k] ..... *M. camelus*
10. Copulatory ducts with three full turns (or four if counting lateral margins in dorsal view) [Figure 23g] ..... *M. samperi*  
Copulatory ducts with four full turns (or five if counting lateral margins in dorsal view) [Figure 22g] ..... *M. dromedarius*
11. Males ..... 12  
Females ..... 17
12. Embolic coils less than tegular width [Figures 16i, 17f,i] ..... 13  
Embolic coils subequal to or greater than tegular width [e.g., Figures 16e, 17a,b] ..... 15
13. Embolic coils only about half the tegular width [Figure 16i] ..... *M. neocaledonicus*  
Embolic coils more than half the tegular width [Figure 17f,i] ..... 14
14. Median apophysis distal lobe narrow, only slightly curved [Figure 17d–f] ..... *M. trinodosus*  
Median apophysis distal lobe broad, abruptly curved [Figure 17g–i] ..... *M. wa*
15. Embolus tip abruptly curved away from tegulum [Figure 17a,c] ..... *M. superciliosus*  
Embolus tip gradually curved away from tegulum [Figure 16c,f] ..... 16
16. Median apophysis in ventral view subrectangular [Figure 16b] ..... *M. aussie*  
Median apophysis in ventral view curved, lunate [Figure 16e] ..... *M. nemesis*
17. Abdominal tubercles absent [Figure 28c] ..... *M. neocaledonicus*  
Abdominal tubercles present ..... 18
18. Abdominal tubercles posterior [Figures 26c, 31c] ..... 19  
Abdominal tubercles anterior or median [Figures 25b, 30c] ..... 20
19. Abdominal tubercles single, not bifid [Figure 31c] ..... *M. trinodosus*  
Abdominal tubercles bifid [Figure 26c] ..... *M. bituberculatus*
20. Abdomen extends caudally beyond the spinnerets [Figure 27c,d] ..... *M. nemesis*  
No caudal abdominal extension ..... 21
21. Copulatory ducts with only two full spirals (or three counting lateral margins in dorsal view) [Figures 30g, 32g] ..... 22  
Copulatory ducts with three or more full spirals ..... 23
22. Abdomen relatively narrow, lateral margins mottled [Figure 30c,d] ..... *M. superciliosus*  
Abdomen wide, with conspicuous lateral brown spots [Figure 32c,d] ..... *M. wa*
23. Copulatory ducts with three or four full spirals (or four or five counting lateral margins in dorsal view) [Figure 29g is ambiguous] ..... *M. quasimodo*  
Copulatory ducts with five full spirals (or six counting lateral margins in dorsal view) [Figure 25g] ..... *M. aussie*

## AFRICAN SPECIES

***Menneus camelus* Pocock, 1902**

FIGURES 2A–C, 2E, 4E, 12, 14A–C 18, 19

*Menneus camelus* Pocock, 1902:325 (♀).—Lehtinen, 1967:247, fig. 40 (see *M. dromedarius* for incorrect synonymy).—Penney, 2003:572, figs. 1–3 (♂).—Platnick, 2010.

**TYPES.** Holotype female from Durban, Natal, South Africa, in BMNH, examined.

**DIAGNOSIS.** Female *camelus* differ from all *Menneus* except *M. dromedarius* and *M. samperi* by the usual presence of an unpaired abdominal tubercle (Figure 18c,d,i,j, but see variation). They differ from *M. dromedarius* and *M. samperi* by the epigynum with only two full (or three, counted as visible lateral margins in dorsal view) wide copulatory duct coils (Figure 18k). The median hematodocha in ventral view (left palp) spans 11–2 OC, the embolus tip lies at about 11 OC, and the median apophysis–basal lobe axis lies at about 2 OC (Figure 14b). The embolus makes 3.25 coils and is relatively straight and parallel to the tegulum in prolateral view (Figure 14c), and, unlike all other African *Menneus*, the embolic coils are narrower than the tegular width in ventral view (Figure 14a–c).

**DESCRIPTION.** Female from Umkomaas River, KwaZulu-Natal. Total length 14 mm. Carapace 5.3 mm long; 2.3 mm wide. Abdomen 8.8 mm long; 5.0 mm wide. Cephalic width 0.4× carapace width. PME diameter 1 mm; PME separation 1.9 diameters. AME/PME 0.7; AME separation 2.5 AME diameters; closer to PME than to clypeal margin. ALE/PME 0.8; ALE tubercle large, eye's lower edge 2/3 or more diameters from clypeus margin (Figure 18a,g); ALE 1.5 diameters below clypeal margin. PLE/PME 0.8; PLE separation 7.2 PLE diameters; PLE 1.3 diameters behind PME. Clypeus 3.1 AME diameters. Chelicerae with 5 to 7 promarginal teeth; 4 retromarginal teeth; frontal macrosetae in transverse line; laterals stout. Sternum 0.5× as wide as long; maximum width at coxa I. First femur length 11.7 mm; with 5 prolateral macrosetae; patella + tibia I, 14.2 mm; metatarsus I, 12.5 mm; tarsus I, 3 mm. Lengths of patella + tibia II, 11.4 mm; III, 5.2 mm; IV, 6.5 mm. Calamistrum 0.4 metatarsus IV length.

Male from Amanzimtoti, KwaZulu-Natal. Total length 8.5 mm. Carapace 3.8 mm long, 2.2 mm wide. Abdomen 5.0 mm long, 2.0 mm wide. Cephalic width 0.6× carapace width. PME diameter 0.25 mm; PME separation 2 diameters. AME/PME 0.7; AME separation 2.4 AME diameters; equally spaced between PME and clypeal

margin. ALE/PME 0.6; ALE tubercle large; ALE 2 diameters below clypeal margin. PLE/PME 0.7; PLE separation 6 PLE diameters; PLE 1.7 diameters behind PME. Clypeus 1.2 AME diameters. Chelicerae with 4 promarginal teeth; 4 retromarginal teeth; additional 2 or 4 small denticles close to retromargin. Sternum 0.5× as wide as long. First femur length 10.5 mm; with 3 prolateral macrosetae; patella + tibia I 13.6 mm; metatarsus I 15.0 mm; tarsus I 4.3 mm. Lengths of patella + tibia II, 9.9 mm; III, 4.6 mm; IV, 6.0 mm. Tarsus I divided, with proximal portion distinctly swollen. Terminal portion of metatarsus II with curve bordered posteriorly by stout seta. Dorsal surface of tarsus II with stout setae extending down most of its length. Palpal femur length 2.6× cymbium length.

**VARIATION.** In both sexes the usually unpaired abdominal tubercle varies in size and shape. A female collected at Gwala-Gwala had a paired tubercle (Figure 2a) unlike her conspecific from the same locality. Embolus relative length varies. Female body length ranges from 7.7 to 19.5 mm ( $n = 31$ ), and males from 7.2 to 9.5 ( $n = 9$ ).

**NATURAL HISTORY.** *Menneus camelus* employs the usual deinopid hunting strategy including a backward strike (M. Kuntner, pers. obs.; Figures 1d, 2a–c).

**DISTRIBUTION.** South Africa (Figure 12).

**SPECIMENS EXAMINED.** **SOUTH AFRICA:** Gauteng Prov., Johannesburg, dried branches in garden, M Filmer, 20.iii.1988, [Filmer Coll: 1 ♀; -26.2: 28.03]. Gauteng Prov., Northcliff, Johannesburg, in bushes in garden, L Prendini, 4.iv.1988, [Murphy Coll.: 1 ♂; -26.14: 27.97]. Gauteng Prov., outside Pretoria, in low bush near buildings, M Filmer, [Filmer Coll.: 1 ♂; -25.74: 28.19]. Gauteng Prov., Pretoria, HK Monro, iii.1952, [NMP: NM 5886, 1 ♀; -25.74: 28.19]. Gauteng Prov., Pretoria, A Viljoen, 8.iv.1981, [SANC: AcAT/82/342/ 1 ♀; -25.74: 28.19]. Gauteng Prov., Pretoria, in house, C Cilliers, iv.1986, [SANC: AcAT/86/40/, 1 ♀; -25.74: 28.19]. Gauteng Prov., Pretoria, in garden, C. Kok, 4.vi.1979, [SANC: AcAT/79/295/, 1 ♀; -25.74: 28.19]. Gauteng Prov., Pretoria, V/d. Mark, 10.x.1973, [SANC: AcAT/76/1714, 1 ♀; -25.74: 28.19]. Gauteng Prov., Pretoria North, M Greyling, [TM: 1 ♀; -25.74: 28.19]. Gauteng Prov., Pretoria, Agric. Building, in toilet, A vd-Berg, [SANC: AcAT/83/322/, 1 ♂; -25.74: 28.19]. Gauteng Prov., Weavind Park, Pretoria, on wall, S vdBerg, 30.iii.1985, [SANC: AcAT/85/133/, 1 ♀; -25.74: 28.19]. KwaZulu-Natal, Amanzimtoti, Inanda Nature Res., 3030BB?, P Reavell, 20.iv.1981, [NMP: NM 14065, 1 ♂; -30.09: 30.85]. KwaZulu-Natal, Charters Creek, St. Lucia, forest, 28°12'S 32°26'E, Doyen & Griswold, 19–21.xi.1985, [NMP: 1 ♀, 2 juveniles; -28.2: 32.43].

KwaZulu-Natal, Dukuduku, forest in deep shade, on herbs, 28°23'S 32°90E, P Reavell, 18.i.1980, [NMP: NM 12952, 1 ♀; 28.38: 30.59]. KwaZulu-Natal, Greater St. Lucia Wetlands Park, Gwala Gwala forest, 28°23.042'S 32°24.436E, Leg. Kuntner & al., 28.iv.2006, [USNM: 1 ♀; -28.384: 32.4073]. KwaZulu-Natal, Greater St. Lucia Wetlands Park, Gwala Gwala forest, 28°23.042'S 32°24.436'E, Leg. Kuntner & al., 28.iv.2006, [USNM: 1 ♀; -28.384: 32.4073]. KwaZulu-Natal, Greytown, [RMCA: 146.144, 1 ♀, 4 juveniles; -29.06: 30.59]. KwaZulu-Natal, Kosi Bay, Toppin, ii.1906, [NMP: NM 2048, 1 ♂, 4 juveniles; -26.89: 32.88]. KwaZulu-Natal, Mtunzini, Twin Streams Farm, coastal dune forest, 28°57'S 31°46'E, Griswold & al, 19.i.1984, [NMP: 2 ♀; -28.95: 31.77]. KwaZulu-Natal, Natal [no further data], Coll CM, [MNHN: 1 ♂, 1 ♀, 5 juveniles; -28.52: 30.9]. KwaZulu-Natal, Natal, Zululand [no further data], [MNHN: AR 166, 1 ♀, 8 juveniles; -28.52: 30.9]. KwaZulu-Natal, Ngotshe, Togkekry, 27°46'S 31°36'E, TW Schofield, 12.iv.1968, [NMP: NM 12406, 2 ♀; -27.77: 31.6]. KwaZulu-Natal, Pietermaritzburg, RF Lawrence, v.1957, [NMP: NM 6836, 1 ♀; -29.61: 30.37]. KwaZulu-Natal, Pietermaritzburg, RF Lawrence, iv.1957, [NMP: NM 5302, 1 ♀; -29.61: 30.37]. KwaZulu-Natal, Pietermaritzburg, Holliday, x.1944, [NMP: NM 4269, 1 ♂; -29.61: 30.37]. KwaZulu-Natal, Pietermaritzburg, RF Lawrence, vii.1944, [NMP: NM 4261, 1 ♂; -29.61: 30.37]. KwaZulu-Natal, Pietermaritzburg, E Pratt Yule, iv.1941, [NMP: NM 3350, 1 ♀; -29.61: 30.37]. KwaZulu-Natal, Pietermaritzburg, Townbush forest, R Oberprieler, 27.ii.1984, [SANC: AcAT/84/442/, 1 ♀; -29.61: 30.37]. KwaZulu-Natal, St. Lucia Game Reserve, Fanie's Island, 25m, M Ramirez, 31.iii–4.iv.2001, [AMNH: 1 ♂; -28.11: 32.43]. KwaZulu-Natal, Stella Bush, HW Bell Marley, ii.1916, [SAM: B 2173, 1 ♀; -33.93: 18.85]. KwaZulu-Natal, Tembe Elephant Park, 115m, M Ramirez, 9–12. iv.2001, [AMNH: 1 ♀; -27.04: 32.42]. KwaZulu-Natal, Umkomaas River, [BMNH: 1 ♀, 4 juveniles; -30.2: 30.79]. KwaZulu-Natal, Winkel Spruit, 30°06'S 30°51'E, C Ackerman, xii.1916, [NMP: NM 1913, 1 ♀; -30.1: 30.85]. Limpopo Prov., Meetse-a-Bophelo mission, on roof of bus, M Zwiegelaar, 11.iv.1977, [SANC: AcAT/77/891/, 1 ♀; -24.25: 30.45]. Mpumalanga, Badplaas Embuleni Nature Reserve, grassveld savanna, in wooded area, 1100m, 25°57'12"S 30°33'15"E, D & S Ubick, 28.iii.2001, [CAS: 1 ♀; -25.953333: 30.554167]. [no data; TM: 8962, 1 ♀]. W Transvaal, Rustenberg, AL Capener, ii.1965, [NMP: NM 9431, 1 ♀; -33.5: 24.5]. Weenen, TD Walsh, 25.vii.1934, [NMP: 1511 Weenen Walsh, 1 ♀; -28.85: 30.08].

### ***Menneus capensis* (Purcell, 1904), new combination**

FIGURES 1A–C, 12, 14D–F, 20

*Avellopsis capensis* Purcell 1904:128 (♂♀).—Lehtinen, 1967:217, figs. 33, 37 (transfer from Uloboridae).—Platnick, 2010.

**TYPES.** Lectotype female in SAM hereby designated, examined. Vial with lectotype contains three labels: one in ink stating “Dinopidae TYPE *Avellopsis capensis* Purcell ACC. NO. 12330 SAM/ARAN 3176. Side of Kalk Bay Mountain. N.F. Purcell. 3/1902”; one photocopied stating “MUS CAPE TOWN lectotype/PTL*Avellopsis capensis* Purcell, 1904.”; and one in pencil stating “12330 Side of Kalk Bay Mountain 3/02 by W.F.P. of *Avellopsis capensis* Purc.” Paralectotype female from Camps Bay is immature.

**DIAGNOSIS.** Female *Menneus capensis* differ from all other African species by the diamond-shaped abdomen with paired abdominal tubercle (Figure 20c,d). Copulatory ducts with one and a half spirals (or two counting lateral margins in dorsal view) (Figure 20f). The median hematodocha in ventral view (left palp) spans 12–4 OC, the embolus tip lies at about 11 OC, and the median apophysis–basal lobe axis lies at about 8:30 OC (Figure 14e), is narrow, and is gently curved in prolateral view (Figure 14e,f). The embolus makes 2.5 coils, and is bent away from the tegulum in prolateral view (Figure 14f).

**DESCRIPTION.** Female from Newlands Forest, Cape Town, South Africa. Total length 10 mm. Carapace 3.4 mm long; 2.5 mm wide. Abdomen 6.6 mm long; 4.8 mm wide. Cephalic width 0.7× carapace width. PME diameter 0.3 mm; PME separation 1.2 diameters. AME/PME 0.5; AME separation 1.9 AME diameters; closer to PME than to clypeal margin. ALE/PME 0.5; ALE tubercle large; ALE 1 diameter below clypeal margin. PLE/PME 0.8; PLE separation 5.2 PLE diameters; PLE 1.4 diameters behind PME. Clypeus 2 AME diameters. Chelicerae with 4 promarginal teeth; 4 retromarginal teeth; additional 4 small denticles close to retromargin. Sternum 0.8× as wide as long; maximum width at coxa I. First femur length 6.6 mm; with 5 prolateral macrosetae; patella + tibia I, 7.2 mm; metatarsus I, 6.4 mm; tarsus I, 1.4 mm. Lengths of patella + tibia II, 6.5 mm; III, 4.1 mm; IV, 4.2 mm. Calamistrum 0.3 metatarsus IV length.

Male from Cape Province, Goudini. Total length 6.5 mm. Carapace 3.2 mm long; 2 mm wide. Abdomen 3 mm long; 1.4 mm wide. Cephalic width 0.5× carapace width. PME diameter 0.2 mm; PME separation 1.2 diameters. AME/PME 0.5; AME separation 1.8 AME diameters;

closer to clypeal margin than to PME. ALE/PME 0.6; ALE tubercle large; eye's ventral edge 2/3 or more diameters from clypeus margin; ALE 0.6 diameters below clypeal margin. PLE/PME 0.5; PLE separation 4 PLE diameters; PLE 2.2 diameters behind PME. Clypeus 0.8 AME diameters. Chelicerae with 2 promarginal teeth; 3 retromarginal teeth; median frontal macrosetae distal to laterals; laterals attenuate. Sternum 0.9× as wide as long. First femur length 9.4 mm; with 4 prolateral macrosetae; patella + tibia I 10.5 mm; metatarsus I 12.1 mm; tarsus I 1.9 mm. Lengths of patella + tibia II, 8.6 mm; III, 4.8 mm; IV, 5.2 mm. Tarsus I undivided. Terminal portion of tibia II unmodified. Terminal portion of metatarsus II without distal curve in dorsal view. Dorsal surface of tarsus II without stout setae. Palpal femur length 2.1× cymbium length.

**VARIATION.** Female body length ranges from 8.5 to 11.4 mm ( $n = 7$ ), and males from 5.0 to 7.0 ( $n = 3$ ).

**NATURAL HISTORY.** The species inhabits forests around Table Mountain, Cape Town (N. Larsen, pers. comm.). We have recently collected fresh material from Newlands Forest, Cape Town. The web and predatory habits are typical of deinopids (Figure 1a–c). The spiders were found to build their webs close to the ground, typically under boulders adjacent to water.

**DISTRIBUTION.** Western Cape, South Africa (Figure 12).

**SPECIMENS EXAMINED.** **SOUTH AFRICA:** Cape Prov., Camps Bay, WF Purcell, [SAM: 748 SAM/ARAN 3177, 1 juvenile; -33.95: 18.37]. Cape Prov., Cape Town, Newlands Forest, Paradijs Stream, N Larsen, 9.v.1991, [SAM: C 2453, 2 ♀; -33.98: 18.44]. Cape Prov., Cape Town, Newlands Forest, Paradijs Stream, N Larsen, v.1991, [SAM: C 1864, 1 juvenile; -33.98: 18.44]. Cape Prov., Cape Town, Newlands Forest, Paradijs Stream (NL153), N Larsen, 9.v.1991, [SAM: C 1858, 1 ♀; -33.98: 18.44]. Cape Prov., Cape Town, Newlands Forest, Paradijs Stream (NL154), N Larsen, 9.v.1991, [SAM: C 1859, 1 ♂; -33.98: 18.44]. Cape Prov., Kalk Bay Mountains, WF Purcell, iii.1902, [SAM: Acc. No. 12330 SAM/ARAN 3043, 14 juveniles; -33.93: 18.46]. Cape Prov., side of Kalk Bay Mountain, WF Purcell, iii.1902, [SAM: Acc. no. 12330 SAM/ARAN 3176, 1 ♂; -33.93: 18.46]. Western Cape, Cape Town, Table Mtn. NP, Newlands Forest, 159 m, 33°58.934'S 18°26.686'E, M Kuntner & al, 4.v.2006, [USNM: 1 ♀; -33.9822: 18.4448]. Western Cape, Cape Town, Table Mtn. NP, Newlands Forest, 159 m, 33°58.934'S 18°26.686'E, M Kuntner & al, 4.v.2006, [USNM: 1 ♂; -33.9822: 18.4448]. Western Cape, Cape Town, Table Mtn. NP, Newlands Forest, 159

m, 33°58.934'S 18°26.686'E, M Kuntner & al, 4.v.2006, [USNM: 1 ♀; -33.9822: 18.4448]. Western Cape, Cape Town, Newland Forest Preserve, SE Table Mtn., indigenous forest, 33°58'S 18°28'E, N Larsen, K Muller, S Prinsloo, D & S Ubick, 4.iv.2001, [CAS: 1 ♂, 1 ♀; -35.08: 18.47]. Western Cape, Table Mountain, Capetown, Fernwood Gully, indigenous forest, 150 m, 33°58'S 18°27'E, CE Griswold, 18.xii.1996, [CAS: 1 ♀; -33.97: 18.53].

### ***Menneus darwini*, new species**

FIGURES 12, 14G–I, 21

**TYPES.** Holotype male: **TANZANIA:** Iringa, Mufindi Dist., Uzungwa Scarp For. Res., canopy fog, 1515 m, 08°30'S 35°52'E, McKamey & al, 4.iii.1996, [ZMUC: 1 ♂; -8.5: 35.87].

**ETYMOLOGY.** Named for Charles Darwin in honor of the 150th anniversary of the publication of *On the Origin of Species* and the 200th anniversary of his birth. Gender is masculine.

**DIAGNOSIS.** Male *Menneus darwini* is most similar to *M. dromedarius*, *M. tetragnathoides*, *M. camelus*, and *M. samperi* among African species. The median hematodocha in ventral view (left palp) spans 4:30–8 OC, unlike any other African species, the embolus tip lies at about 10:30 OC, and the median apophysis–basal lobe axis lies at about 1 OC (Figure 14h). The embolus makes 3.5 coils, and the tip is straight rather than bent away from the tegulum in prolateral view (Figure 14i).

**DESCRIPTION.** Female unknown.

Male (holotype). Total length 8.7 mm. Carapace 3.5 mm long. Carapace 2.4 mm wide. Abdomen 5.0 mm long. Abdomen 2.5 mm wide. Cephalic width 0.4× carapace width. PME diameter 0.3 mm; PME separation 1.7 diameters. AME/PME 0.7; AME separation 1.8 AME diameters; equidistant between PME and clypeal margin. ALE/PME 0.7; ALE tubercle large; eye's ventral edge 2/3 or more diameters from clypeus margin; ALE 1 diameter below clypeal margin. PLE/PME 0.8; PLE separation 5.2 PLE diameters; PLE 1.3 diameters behind PME. Clypeus 0.8 AME diameters. Chelicerae with 3 promarginal teeth; 7 retromarginal teeth; median frontal macrosetae absent (or inconspicuous); laterals attenuate. Sternum 0.5× as wide as long. First femur length 10.7 mm; with 4 prolateral macrosetae; patella + tibia 12.4 mm; metatarsus I 12.7 mm; tarsus I 3.5 mm. Lengths of patella + tibia II, 9.1 mm; III, 3.7 mm; IV, 4.9 mm. Tarsus I divided. Terminal portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II with curve

bordered posteriorly by stout seta. Dorsal surface of tarsus II with stout setae extending down most of its length. Palpal femur length  $2.3 \times$  cymbium length.

**VARIATION.** Known only from holotype male.

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** Only known from the type locality, Tanzania.

### ***Menneus dromedarius* Purcell, 1904**

FIGURES 12, 15A–C, 22

*Menneus dromedarius* Purcell, 1904:127 (♀).—Lehtinen, 1967:247, fig. 40.

Here removed from synonymy of *M. camelus* (contra Lehtinen, 1967).

**TYPES.** Holotype female from Pirie Bush, King Williamstown, Natal, South Africa, in SAM, spec. no. 11536, examined. Type label reads: "... F. A. Pym, March, 1902."

**NOTE.** Four females recently collected in Madagascar fit well into the known variation of South African *M. dromedarius*.

**DIAGNOSIS.** Female *M. dromedarius* differ from other known African females by having copulatory ducts with four full spirals (or five counting lateral margins in dorsal view; Figure 22g). The median hematodocha in ventral view (left palp) spans 6–10 OC, unlike any other African species, the embolus tip lies at about 11:30 OC, and the median apophysis–basal lobe axis lies at about 2 OC (Figure 15b). The embolus makes 3.5 coils and is bent away from the tegulum in prolateral view (Figure 15c).

**DESCRIPTION.** Female from Kleinmond, Cape Province, South Africa. Total length 8.8 mm. Carapace 3.2 mm long; 1.9 mm wide. Abdomen 5.4 mm long; 3.0 mm wide. Cephalic width  $0.8 \times$  carapace width. PME diameter 0.23 mm; PME separation 2.6 diameters. AME/PME 0.6; AME separation 2.1 AME diameters; closer to PME than to clypeal margin. ALE/PME 0.7; ALE tubercle large; ALE 2 diameters below clypeal margin. PLE/PME 0.8; PLE separation 7.4 PLE diameters; PLE 2 diameters behind PME. Clypeus 3 AME diameters. Chelicerae with 4 promarginal teeth; 4 or 5 retromarginal teeth. Sternum  $0.5 \times$  as wide as long; maximum width at coxa I. First femur length 6.5 mm; with 3 prolateral macrosetae; patella + tibia I, 7.5 mm; metatarsus I, 6.2 mm; tarsus I, 1.6 mm. Lengths of patella + tibia II, 5.4 mm; III, 2.6 mm; IV, 3.5 mm. Calamistrum 0.5 metatarsus IV length.

Male from Grahamstown. Total length 10 mm. Carapace 4.7 mm long. Carapace 3 mm wide. Abdomen 5.1 mm long. Abdomen 2.2 mm wide. Cephalic width  $0.6 \times$

carapace width. PME diameter 0.3 mm; PME separation 1.8 diameters. AME/PME 0.6; AME separation 1.7 AME diameters; closer to PME than to clypeal margin. ALE/PME 0.5; ALE tubercle large; eye's ventral edge 2/3 or more diameters from clypeus margin; ALE 1.9 diameters below clypeal margin. PLE/PME 0.7; PLE separation 7.3 PLE diameters; PLE 1.8 diameters behind PME. Clypeus 0.9 AME diameters. Chelicerae with 3 promarginal teeth; 1 retromarginal teeth; median frontal macrosetae distal to laterals; laterals attenuate. Sternum 0.5× as wide as long. First femur length 11.9 mm; with 4 prolateral macrosetae; patella + tibia I 15.7 mm; metatarsus I 16 mm; tarsus I 5.2 mm. Lengths of patella + tibia II, 11.4 mm; III, 5.5 mm; IV, 6.9 mm. Tarsus I divided, with proximal portion distinctly swollen. Terminal portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II with curve bordered posteriorly by stout seta. Dorsal surface of tarsus II with stout setae extending down most of its length. Palpal femur length  $2.8 \times$  cymbium length.

**VARIATION.** In both sexes the unpaired abdominal tubercle varies in size and shape. Female body length ranges from 10.0 to 17.5 mm ( $n = 5$ ), and males from 10.0 to 13.3 ( $n = 5$ ).

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** South Africa, Madagascar (Figure 12). Copenhagen (ZMUC) has a specimen of *M. dromedarius* with a label saying only "Cameroon" and no other data. At this time we regard this as a locality error.

**SPECIMENS EXAMINED.** **MADAGASCAR:** Toliara, Réserve Privé Berenty, Forêt de Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, gallery forest, general collecting night, 35 m, 24°57'25"S 46°16'17"E, BL Fisher et al. BLF5319, 3–8.ii.2002, [CAS: CASENT9012443, 1 ♀; -24.956944: 46.271389]. Toliara, Réserve Privé Berenty, Forêt de Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, ER30 beating low vegetation, 35 m, 24°57'25"S 46°16'17"E, BL Fisher et al. BLF5318, 3–8.ii.2002, [CAS: CASENT9012406, 1 ♀; -24.956944: 46.271389]. Toliara, Réserve Privé Spéciale de Cap Sainte Marie 12.3 km 262°W Marovato, spiny forest/thicket EH21 beating low vegetation, 200 m, 25°34'54"S 45°10'6"E, BL Fisher et al. BLF5502, [CAS: CASENT9012629, 1 ♀, 1 juvenile; -25.581667: 45.168333]. Toliara, Réserve Privé Spéciale de Cap Sainte Marie, 12.3 km 262°W Marovato, spiny forest/thicket EH21 beating low vegetation, 200 m, 25°34'54"S 45°10'6"E, BL Fisher et al. BLF5505, [CAS: CASENT9012682, 1 ♀; -25.581667: 45.168333]. **SOUTH AFRICA:** Cape Prov., Diepwalle Forest Sta., 22 km NE Knysna, indigenous forest, 1800 ft, 33°57'S 23°10'E, Griswold & Griswold, 10.i.1985, [NMP: 1 ♂; -33.95: 23.17].

Cape Prov., Kleinmond, on ground in fynbos vegetation, S Neser, 16.xii.1985, [SANC: AcAT/86/13/1, 1 ♀; -34.34: 19.02]. Eastern Cape, Grahamstown, behind bookcase, 33°18'S 26°32'E, PMC Croeser, 26.i.1979, [NMP: 1 ♂; -33.3: 26.53]. KwaZulu-Natal, Ngoyi Forest, Lawrence & al., ii.1953, [NMP: NM 5894, 1 ♂, 1 juvenile; -28.83: 31.66]. Transvaal, Barberton, 25°47'S 31°03'E, RF Lawrence, iii.1960, [NMP: NM 7966, 1 ♂; -25.78: 31.05]. Fairy Glen Farm, Bathurst, forest floor, RF Lawrence, 25.i.1980, [SANC: AcAT/82/127/1, 1 ♂; -33.5: 26.82].

### ***Menneus samperi*, new species**

FIGURES 12, 15D–F, 23

**TYPE.** Holotype male in NMP from Kenya, Kaibos; see locality data below.

**ETYMOLOGY.** Named for Cristián Samper K., Director of the National Museum of Natural History, Smithsonian Institution, in recognition of his leadership and contributions to biodiversity science. Gender is masculine.

**DIAGNOSIS.** Female *Menneus samperi* differ from other known African females by having copulatory ducts with three full spirals (or four counting lateral margins in dorsal view) (Figure 23g). The median hematodocha in ventral view (left palp) spans 8–11 OC, the embolus tip lies at about 12 OC, and the median apophysis–basal lobe axis lies at about 2 OC (Figure 15e). The embolus makes 3.5 coils and is bent away from the tegulum in prolateral view (Figure 15f). Both males and females have noticeably long third femoral setal fringes.

**DESCRIPTION.** Female from Tanzania. Total length 10.5 mm. Carapace 4.4 mm long; 2.9 mm wide. Abdomen 6.1 mm long; 4.3 mm wide. Cephalic width 0.7× carapace width. PME diameter 0.23 mm; PME separation 3.3 diameters. AME/PME 0.8; AME separation 2.2 AME diameters; equidistant between PME and clypeal margin. ALE/PME 0.7; ALE tubercle large; ALE 2.7 diameters below clypeal margin. PLE/PME 1.0; PLE separation 7.8 PLE diameters; PLE 1.7 diameters behind PME. Clypeus 1 AME diameters. Chelicerae with 4 promarginal teeth; 7 retromarginal teeth. Sternum 0.5× as wide as long; maximum width at coxa I. First femur length 10.6 mm; with 3 prolateral macrosetae; patella + tibia I, 12.1 mm; metatarsus I, 11.3 mm; tarsus I missing. Lengths of patella + tibia II, 10.0 mm; III, 4.6 mm; IV, 5.4 mm. Calamistrum 0.3 metatarsus IV length.

Male (holotype). Total length 7.6 mm. Carapace 3.3 mm long. Carapace 2.2 mm wide. Abdomen 4.1 mm long. Abdomen 2.2 mm wide. Cephalic width 0.6×

carapace width. PME diameter 0.19 mm; PME separation 2.6 diameters. AME/PME 0.97; AME separation 1.9 AME diameters; closer to clypeal margin than PME. ALE/PME 0.8; ALE tubercle large; eye's ventral edge 2/3 or more diameters from clypeus margin; ALE 1.8 diameter below clypeal margin. PLE/PME 1.1; PLE separation 5.8 PLE diameters; PLE 1.0 diameters behind PME. Clypeus 0.8 AME diameters. Chelicerae with 4 promarginal teeth; 1 retromarginal tooth; median frontal macrosetae absent (or inconspicuous); laterals attenuate. Sternum 0.6× as wide as long. First femur length 8.5 mm; prolateral macrosetae absent; patella + tibia 11.0 mm; metatarsus I 11.4 mm; tarsus I 3.2 mm. Lengths of patella + tibia II, 8.2 mm; III, 3.4 mm; IV, 4.3 mm. Tarsus I divided. Terminal portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II with curve bordered posteriorly by stout seta. Dorsal surface of tarsus II with stout setae extending down half of its length. Palpal femur length 2.0× cymbium length.

**VARIATION.** Only one male known. Female body length ranges from 13.0 to 15.0 mm ( $n = 2$ ). The Uganda female had 4–5 first femoral macrosetae.

**NATURAL HISTORY.** The Uganda female was collected with a typical deinopid spherical eggsac, 9 mm in diameter.

**DISTRIBUTION.** Eastern Africa (Kenya, Tanzania, Uganda; Figure 12).

**SPECIMENS EXAMINED.** **KENYA:** Kaibos, indigenous forest, 01°12'N 35°08'E, B Lamoral, 23.v.1980, [NMP: 1 ♂; 1.2: 35.13]. **TANZANIA:** Bukoba Dist., Minzero Forest Reserve, 01°05'S 31°30'E, M Andersen, x.1998, [ZMUC: 1 ♀; -1.08: 31.5]. **UGANDA:** Kabale Dist., Ruhizha Bwindi Impenetrable NP, "Nature Trail," forest, 2300 m, 01°03'S 29°47'E, CE Griswold, 13–16. ix.1996, [CAS: 1 ♀; -1.05: 29.78].

### ***Menneus tetragnathoides* Simon, 1876**

FIGURES 12, 15G–I, 24

*Menneus tetragnathoides* Simon 1876:219 (♂).—Simon, 1892:210, figs. 155, 156.—Platnick, 2010.

*Menneus affinis* Tullgren, 1910:91, pl. 1, fig. 2 (♂).—Platnick, 2010. NEW SYNONYMY.

**NOTES.** Platnick (2010) notes that Berland (1914:53) considered *M. affinis* as a junior synonym of *M. tetragnathoides*, which was not accepted subsequently. Our examination of the holotype confirms such synonymy.

**TYPES.** *Menneus tetragnathoides* syntype series of one male and two immatures in MNHN, examined, lectotype male designated here. Vial with lectotype contains two labels, one stating "AR 163" and the other "Museum Paris AE 163 *Menneus tetragnathoides* Sim. Congo TYPE." According to Simon (1876) the type material was collected by Louis Petit ca. 1876 at "Chinchonxo in Congo" (today in Angola, Cabinda, Chinchoxo, -5.166667: 12.116667). The remaining specimens have been designated as paralectotypes.

Holotype male *M. affinis* in SMNH, examined, label reads "Kilimandjaro, Kibonoto, Colleg. Y. Sjot."

**DIAGNOSIS.** The median hematodocha in ventral view (left palp) spans 3–6 OC, the embolus tip lies at about 11:30 OC, and the median apophysis–basal lobe axis lies at about 1 OC (Figure 15h). The embolus makes 3.5 coils and is relatively straight and parallel to the tegulum in prolateral view (Figure 15i).

**DESCRIPTION.** Female unknown.

Male from Malawi, Chintheche. Total length 9.8 mm. Carapace 4.2 mm long; 2.3 mm wide. Abdomen 5.4 mm long; 2.6 mm wide. Cephalic width 0.3× carapace width. PME diameter 0.3 mm; PME separation 1.8 diameters. AME/PME 0.7; AME separation 1.4 AME diameters; closer to clypeal margin than to PME. ALE/PME 0.6; ALE tubercle large; eye's ventral edge 2/3 or more diameters from clypeus margin; ALE 1.4 diameters below clypeal margin. PLE/PME 0.8; PLE separation 7.2 PLE diameters; PLE 1.3 diameters behind PME. Clypeus 0.7 AME diameters. Chelicerae with 4 promarginal teeth; 1 retromarginal teeth; frontal macrosetae absent. Sternum 0.5× as wide as long. First femur length 10.5 mm; with 3 prolateral macrosetae; patella + tibia I 15.3 mm. Lengths of patella + tibia II, 12.3 mm; III, 4.6 mm; IV, 5 mm. Terminal portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II with distal curve in dorsal view, bordered by prolateral stout seta. Dorsal surface of tarsus II with stout setae extending down most of its length. Palpal femur length 3× cymbium length.

**VARIATION.** Male body length ranges from 9.5 to 11.0 mm ( $n = 2$ ).

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** West and East Africa (Cabinda, Malawi, Kilimanjaro) (Figure 12).

**SPECIMENS EXAMINED.** ANGOLA: Cabinda, "Chinchonxo," 05°10'S 12°07'E, Louis Petit, ca. 1876, [MNHN: AE 163, 1 ♂, 2 juveniles; -5.17: 12.12]. MALAWI: Chintheche, R Jocque, 2.v.1978, [RMCA: no. 153.633, 1 ♂; -11.83: 34.16]. TANZANIA: Kilimanjaro,

Kibonoto [Kibongoto], Y. Sjot, xii.1905 [SMNH: 1 ♂; -3.18: 37.09].

#### AUSTRALASIAN SPECIES

##### ***Menneus aussie*, new species**

FIGURES 13, 16A–C, 25

**ETYMOLOGY.** "Aussie" is a fifth declension feminine Latin noun, meaning "from Australia."

**TYPES.** Holotype male designated here, in QM, from Rundle Range; see below.

**DIAGNOSIS.** Female *M. aussie* have paired median dorsal abdominal tubercles, like *M. superciliosus*, *M. nemesio*, *M. quasimodo*, and *M. wa*, but, uniquely, have copulatory ducts with five full spirals (or six counting lateral margins in dorsal view; Figure 25g). The median hematodocha in ventral view (left palp) spans 6–9 OC, the embolus tip lies at about 11:30 OC, and the median apophysis–basal lobe axis lies at about 2 OC (Figure 16b). The embolus makes 3.25 coils and is bent away from the tegulum in prolateral view (Figure 16c).

**DESCRIPTION.** Female from Australia, NSW, "Avalon Bch." Total length 10.6 mm. Carapace 4 mm long; 3 mm wide. Abdomen 6.8 mm long; 4.2 mm wide. Cephalic width 0.5× carapace width. PME diameter 0.3 mm; PME separation 1.5 diameters. AME/PME 0.7; AME separation 1.4 AME diameters; equidistant between PME and clypeal margin. ALE/PME 0.6; ALE tubercle large, eye's lower edge 2/3 or more diameters from clypeus margin; ALE 0.7 diameters below clypeal margin. PLE/PME 0.9; PLE separation 4.7 PLE diameters; PLE 1.6 diameters behind PME. Clypeus 1 AME diameters; lacking large marginal macrosetae. Chelicerae with 4 promarginal teeth; 5 retromarginal teeth; median frontal macrosetae proximal to laterals. Sternum 0.7× as wide as long; width at coxae I and II about equal. First femur length 8.9 mm; with 6 to 7 prolateral macrosetae; patella + tibia I, 9.7 mm; metatarsus I, 10 mm; tarsus I, 1.8 mm. Lengths of patella + tibia II, 9.1 mm; III, 5.1 mm; IV, 5.2 mm. Calamistrum 0.4 metatarsus IV length.

Male (holotype) from Australia, ME. Queensland, Rundle Range. Total length 10.5 mm. Carapace 4 mm long. Carapace 2.9 mm wide. Abdomen 6.5 mm long. Abdomen 3 mm wide. Cephalic width 0.4× carapace width. PME diameter 0.3 mm; PME separation 1.1 diameters. AME/PME 0.6; AME separation 1.5 AME diameters; closer to clypeal margin than to PME. ALE/PME 0.7; ALE tubercle large; eye's ventral edge 2/3 or more diameters

from clypeus margin; ALE 1.3 diameters below clypeal margin. PLE/PME 0.9; PLE separation 3.4 PLE diameters; PLE 1.8 diameters behind PME. Clypeus 1 AME diameters. Chelicerae with 2 promarginal teeth; 1 retromarginal teeth; median frontal macrosetae proximal to laterals; laterals attenuate. Sternum 0.7× as wide as long. First femur length 13.4 mm; with 6 prolateral macrosetae; patella + tibia I 14.9 mm; metatarsus I 16.2 mm; tarsus I 4.3 mm. Lengths of patella + tibia II, 12.2 mm; III, 7 mm; IV, 7.2 mm. Tarsus I divided and of uniform width. Terminal portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II with curve bordered posteriorly by stout seta. Dorsal surface of tarsus II with stout setae extending down most of its length. Palpal femur length 2.9× cymbium length.

**VARIATION.** The female from New Caledonia lacks the typical abdominal tubercles, which are consistently present in Australian specimens. Female body length ranges from 9.0 to 12.0 mm ( $n = 6$ ), and males from 9.3 to 9.8 ( $n = 2$ ).

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** Australia (Queensland, New South Wales), New Caledonia (Figure 13).

**SPECIMENS EXAMINED.** AUSTRALIA: NSW, Avalon Bch., B Collins, 11.xi.1972, [AMS: KS 16841, 1 ♀; -33.64: 151.33]. NSW, Manly, NO Fletcher, 6.v.1945, [AMS: KS 16840, 1 ♀; -33.8: 151.29]. QLD, Dandabah, Bunya NP, VED, 6.iii.1976, [QM: 2 ♀; -27.36: 152.93]. QLD, Lamington NP, O'Reillys, night collecting, RR&VED, 16.xi.1977, [QM: 1 juvenile; -28.22: 153.13]. QLD, Rundle Range, 24.iii.1975, [QM: 4 ♂, 3 ♀; -23.65: 150.97]. QLD, Rundle Range, R Kohout, 24.iii.1975, [QM: 2 ♂, 2 ♀; -23.65: 150.97]. NEW CALEDONIA: Col d'Amieu Forest Stn., 400 m, Monteith & Cook, 8.v.1984, [QM: 1 ♀; -21.58: 165.76].

### ***Menneus bituberculatus*, new species**

FIGURES 13, 26

**TYPES.** Holotype female designated here, in QM, from Upper Brookfield; see below.

**ETYMOLOGY.** Named for the bifid posterior abdominal tubercles, an adjective.

**DIAGNOSIS.** Uniquely in *Menneus*, symmetric abdominal tubercles in *M. bituberculatus* are doubly paired (Figure 26c). Female *M. bituberculatus* have copulatory ducts with two full (or three if counting lateral margins) spirals (Figure 26g).

**DESCRIPTION.** Female (holotype). Total length 11.5 mm. Carapace 3.8 mm long; 2.6 mm wide. Abdomen 7.5 mm long; 3.3 mm wide. Cephalic width 1.5× carapace width. PME diameter 0.2 mm; PME separation 3.7 diameters. AME/PME 0.8; AME separation 1.8 AME diameters; equidistant between PME and clypeal margin. ALE/PME 0.7; ALE tubercle small, eye's lower edge contiguous with clypeus margin; ALE 0.8 diameters below clypeal margin. PLE/PME 1; PLE separation 6.1 PLE diameters; PLE 0.6 diameters behind PME. Clypeus 0.2 AME diameters. Chelicerae with 4 promarginal teeth; 4 retromarginal teeth; frontal macrosetae in transverse line; laterals attenuate. Sternum 0.6× as wide as long; maximum width at coxa II. First femur length 7.8 mm; with 6 prolateral macrosetae; patella + tibia I, 9.1 mm; metatarsus I, 8.9 mm; tarsus I, 1.8 mm. Lengths of patella + tibia II, 7.8 mm; III, 3.3 mm; IV, 3.7 mm. Calamistrum 0.4 metatarsus IV length.

Male. Unknown.

**VARIATION.** Unknown.

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** Australia (Queensland), probably New Guinea, based on immature male record (Figure 13).

**SPECIMENS EXAMINED.** AUSTRALIA: QLD, Upper Brookfield, pit traps, rainforest, Raven & Green, 6.x.1981, [QM: 1 ♀, 1 juvenile; -27.49: 152.86]. INDONESIA: West Papua, Hollandia [Jayapura], rain forest, 250ft, H Hoogstraal, xii.1944, [AMNH: 1 juvenile; -2.53: 140.71], identification uncertain.

### ***Menneus superciliosus* (Thorell, 1881)**

FIGURES 13, 17A–C, 30

*Avella superciliosa* Thorell, 1881:200 (♀).—Lehtinen, 1967: 217 (transfer from *Menneus*).—Platnick, 2010.

*Menneus superciliosus* Rainbow, 1911:124.

**TYPES.** Adult female from Somerset, Cape York, in MCSNG, examined. Vial with holotype contains three labels, one in pencil stating "Avella superciliosa Thor. Typus Ragni Austr. Males. p. 200. sp. 122 Somerset (Cape York) 1875. rac. D'Alb.," one in ink "Avella superciliosa Typus! Thorell (Ann. Mus. XVII, p. 200) Somerset (Capo York) 1875 – L. M. D'Albertis," and one in ink stating, stating "Museo Civico di Storia Naturale di Genova Avella superciliosa Typus! Thorell Somerset (Capo York) leg. L. M. D'Albertis, 1875."

**DIAGNOSIS.** Among Australian *Menneus* with paired median dorsal abdominal tubercles female *M. superciliosus* closely resemble *M. wa* in having copulatory ducts with two full spirals (or three counting lateral margins in dorsal view) (Figure 30g). Female *M. superciliosus* and *M. wa*, apart from their apparently disjunct distributions, are difficult to distinguish. *Menneus superciliosus* seem to have narrower, more elongate abdomens and lack the brown lateral abdominal spot (Figure 30c,d). The median hematodocha in ventral view (left palp) spans 4–6 OC, the embolus tip lies at about 1 OC, and the median apophysis–basal lobe axis lies at about 2:30 OC (Figure 17b). The embolus makes 3.5 coils and is bent away from the tegulum in prolateral view (Figure 17c).

**DESCRIPTION.** Female (paratype) from Mount Cook. Total length 10.7 mm. Carapace 4.2 mm long; 2.7 mm wide. Abdomen 5.1 mm long; 4.3 mm wide. Cephalic width 0.7× carapace width. PME diameter 0.3 mm; PME separation 1.7 diameters. AME/PME 0.8; AME separation 1.5 AME diameters; closer to PME than to clypeal margin. ALE/PME 0.9; ALE tubercle large, eye's lower edge 2/3 or more diameters from clypeus margin; ALE 1.6 diameters below clypeal margin. PLE/PME 0.8; PLE separation 3.8 PLE diameters; PLE 1.8 diameters behind PME. Clypeus 1.8 AME diameters. Chelicerae with 5 promarginal teeth; 5 retromarginal teeth; median frontal macrosetae proximal to laterals; laterals stout. Sternum 0.7× as wide as long; maximum width at coxa I. First femur length 9.4 mm; with 4 prolateral macrosetae; patella + tibia I, 12.6 mm; metatarsus I, 10.8 mm; tarsus I, 1.9 mm. Lengths of patella + tibia II, 9.8 mm; III, 5.3 mm; IV, 5.5 mm. Calamistrum 0.3 metatarsus IV length.

Male (holotype) from Mt. Cook. Total length 8 mm. Carapace 3.4 mm long. Carapace 2.4 mm wide. Abdomen 4.5 mm long. Abdomen 1.7 mm wide. Cephalic width 0.5× carapace width. PME diameter 1.1 mm; PME separation 1.4 diameters. AME/PME 0.8; AME separation 1.3 AME diameters; equidistant between PME and clypeal margin. ALE/PME 0.6; ALE tubercle large; eye's ventral edge 2/3 or more diameters from clypeus margin; ALE 0.6 diameters below clypeal margin. PLE/PME 0.8; PLE separation 7 PLE diameters; PLE 1.6 diameters behind PME. Clypeus 1 AME diameters. Chelicerae with 6 promarginal teeth; 6 retromarginal teeth; median frontal macrosetae distal to laterals; laterals attenuate. Sternum 0.5× as wide as long. First femur length 9.8 mm; with 7 prolateral macrosetae; patella + tibia I 11.1 mm; metatarsus I 13 mm; tarsus I 2.5 mm. Lengths of patella + tibia II, 9.2 mm; III, 4.9 mm; IV, 5 mm. Tarsus I divided and of uniform width. Terminal

portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II without distal curve. Dorsal surface of tarsus II without stout setae. Palpal femur length 2.6× cymbium length.

**VARIATION.** Female body length ranges from 7.2 to 13.5mm ( $n = 21$ ), and males from 7.0 to 9.5 ( $n = 9$ ).

**NATURAL HISTORY.** Label data suggest the standard deinopid web.

**DISTRIBUTION.** Australia (Queensland, New South Wales; Figure 13).

**SPECIMENS EXAMINED. AUSTRALIA:**  
NSW, Royal Nat Park, R Mascord, 9.xii.1967, [AMS: KS 16861, 1♂; -34.12: 151.06]. NSW, Royal Nat Park, R Mascord, 9.xii.1967, [AMS: KS 16836 2♀; -34.12: 151.06]. NSW, Royal Nat Park, A Speechley, 14.iii.1969, [AMS: KS 16847, 1♂; -34.12: 151.06]. NSW, Tarre, MR Gray FN1839, [AMS: KS 9371, 1♂; -31.91: 152.46]. QLD, 2.5 km SW Mt Hartley, 35 km S Cooktown, Monteith & al., 23.iv.1982, [QM: 2♀; -15.79: 145.21]. QLD, Beating 12 m Scrub Site 20 NE Q, 15°50'S 145°19'E, RM VED, 22.xi.1975, [QM: 1♂; -15.83: 145.32]. QLD, Bellenden Ker Range, Cableway base Stn, 100 m, Earthwatch, 17.x.1981, [QM: 1♂, 1♀, 3 juveniles; -17.27: 145.92]. QLD, Cairns, RG Wind, viii.-ix.1838, [MCZ: 1♀; -16.92: 145.79]. QLD, Cape Tribulation NE QLD, Monteith, Yates & Thompson, 22ix-7x.1982, [QM: 1♀; -16.09: 145.45]. QLD, Davies Creek, NC Coleman, 11.i.1972, [QM: 1♀; -17: 145.57]. QLD, Edmonton, RE Mascord, 27.vii.1971, [AMS: KS 16834, 1♀; -17.02: 145.74]. QLD, Edmonton, NC Coleman, 29.ix.1969, [AMS: KS 16868, 2♂, 1♀; -17.02: 145.74]. QLD, Home Rule NEQ, night collecting, in web holding net, TT&VED, 31.x.1974, [QM: 1♀; -15.73: 145.29]. QLD, Homevale Riverine Rainforest, 1.iv.1975, [QM: 1♀; -21.72: 148.7]. QLD, Kellep Hut, Windsor Tb, ANZSES Exp, xii.1980, [QM: 1♂; -27.43: 153.04]. QLD, Kenilworth State Forest, R Raven, 14.ii.1972, [QM: 1♀; -26.59: 152.72]. QLD, Koonawarra Cmpgrd. Kianagarow Track Bunya Mts. NP, El Schlinger, 29.i.1978, [EMUC: 1♀; -26.79: 153.08]. QLD, Michaelsens Farm Mt Cotton, vine thicket, V Gallon, 20.xi.1983, [QM: 1♀; -27.62: 153.24]. QLD, Mt Cook, site 34, RR&VED, 12.xi.1975, [QM: 1♂, 1♀; -15.49: 145.26]. QLD, Mt Finlay, site 29, RM JC VED, 2.xii.1973, [QM: 1 juvenile; -15.82: 145.35]. QLD, OF Kroombit Tops SEQ, R Raven, 25.ii.1982, [QM: 2♀; -24.42: 150.97]. QLD, Palm Cove, NC Coleman, 10.xi.1971, [QM: 1♀; -16.75: 145.63]. QLD, The Hummock Mt Hedley, on shrub on path, VE Davies, [QM: 1♀;

-15.75: 145.3]. QLD, Somerset, LM D'Albertis, 1875, [MCSNG: 1♀; -10.76: 142.56].

### *Menneus nemesio*, new species

FIGURES 13, 16D–F, 27

Lehtinen, 1967:217, fig. 41

**TYPES.** Male holotype (CAS) and two female paratypes (AMS); see below.

**ETYMOLOGY.** Noun in apposition, named for Alexander Nemesio Coddington.

**DIAGNOSIS.** *Menneus nemesio* is unique in having a prolonged abdominal caudal extension beyond the spinnerets (Figure 27c–d,j–k). Females have copulatory ducts with four full spirals (Figure 27g). The median hematodocha in ventral view (left palp) spans 5–7 OC, the embolus tip lies at about 11 OC, and the median apophysis–basal lobe axis lies at about 1 OC (Figure 16e). The embolus makes 3.5 coils and is bent away from the tegulum in prolateral view (Figure 16f).

**DESCRIPTION.** Female from Wamberal. Total length 10.9 mm. Carapace 3.2 mm long; 2.2 mm wide. Abdomen 7.4 mm long; 2.8 mm wide. Cephalic width 0.6× carapace width. PME diameter 0.2 mm; PME separation 1.3 diameters. AME/PME 0.7; AME separation 1.6 AME diameters; equidistant between PME and clypeal margin. ALE/PME 0.9; ALE tubercle large, eye's lower edge 2/3 or more diameters from clypeus margin; ALE 0.3 diameters below clypeal margin. PLE/PME 0.9; PLE separation 4.1 PLE diameters; PLE 1.9 diameters behind PME. Clypeus 1.5 AME diameters. Chelicerae with 4 promarginal teeth; 4 retromarginal teeth; median frontal macrosetae proximal to laterals; laterals stout. Sternum 0.7× as wide as long; width at coxae I and II about equal. First femur length 7.6 mm; with 4 to 6 prolateral macrosetae; patella + tibia I, 8.6 mm; metatarsus I, 8.6 mm; tarsus I, 2 mm. Lengths of patella + tibia II, 8 mm; III, 5.7 mm; IV, 5 mm. Calamistrum 0.3 metatarsus IV length.

Male (holotype). Total length 8.2 mm. Carapace 2.8 mm long. Carapace 2 mm wide. Abdomen 5.5 mm long. Abdomen 1.2 mm wide. Cephalic width 0.5× carapace width. PME diameter 0.1 mm; PME separation 1.8 diameters. AME/PME 0.8; AME separation 0.6 AME diameters; closer to clypeal margin than to PME. ALE/PME 1; ALE tubercle large; eye's ventral edge 2/3 or more diameters from clypeus margin; ALE 1 diameters below clypeal margin. PLE/PME 0.8; PLE separation 3.8 PLE diameters;

PLE 2.4 diameters behind PME. Clypeus 1.1 AME diameters. Chelicerae with 3 promarginal teeth; 1 retromarginal teeth; median frontal macrosetae present, but laterals absent. Sternum 0.6× as wide as long. First femur length 8.8 mm; with 3 prolateral macrosetae; patella + tibia I 10.3 mm; metatarsus I 12.4 mm; tarsus I 2.9 mm. Lengths of patella + tibia II, 8.4 mm; III, 4.9 mm; IV, 5.2 mm. Tarsus I divided and of uniform width. Terminal portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II with curve bordered posteriorly by stout seta. Dorsal surface of tarsus II with proximal stout setae. Palpal femur length 2.3× cymbium length.

**VARIATION.** Both females vary in the degree of pigmentation; only one male is known. Female body length ranges from 10.5 to 11.5 mm ( $n = 2$ ).

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** New South Wales (Figure 13).

**NOTES.** Lehtinen (1967:217, fig. 41) illustrated the epigynum of a female specimen in the British Museum (BMNH: 19.9.18.5733), which currently bears a label “*Avella despiciens*.” However, the holotype of *M. despiciens*, at Oxford, is juvenile and therefore a nomen dubium (see below). The BMNH female, illustrated by Lehtinen, is *M. nemesio*.

**SPECIMENS EXAMINED.** AUSTRALIA: NSW, 5 mi N Hawkesbury R. br., 150 m, Ross & Cavagnaro, 3.xii.1962, [CAS: 1♂; -33.53: 151.19]. NSW, Epping, Sydney, N Allan, 30.viii.1969, [AMS: KS 16866, 1♀; -33.77: 151.08]. NSW, Sydney, no collector or date, BMNH: 19.9.18.5733, 1♀; -33.86: 151.2]. NSW, Wamberal, MR Gray, 7.xii.1983, [AMS: KS 13622, 1♀; -33.42: 151.45].

### *Menneus neocaledonicus* (Simon, 1889)

FIGURES 13, 16G–I, 28

*Avella neo-caledonica* Simon, 1889:242 (juvenile).

*Menneus neocaledonicus*: Simon, 1892:210.—Berland, 1924:174, figs.11–15 (♂).

*Avella neocaledonica*: Platnick, 2010.

**TYPES.** Presumed syntypes (2 juveniles) from Noumea in MNHN, examined.

**DIAGNOSIS.** Unlike other *Menneus* species, female *M. neocaledonicus* abdomen is more or less fusiform, lacks any prominent tubercles (Figure 28c,d), the copulatory ducts make a single full spiral (Figure 28g), and the male lacks short stout setae on metatarsus II. The

median hematodocha in ventral view (left palp) spans 9–12:30 OC, the embolus tip lies at about 11 OC, and the median apophysis–basal lobe axis lies at about 3 OC (Figure 16h). The embolus makes 2 coils and is bent away from the tegulum in prolateral view (Figure 16i). The embolus takes only half the size of the tegulum in ventral view.

**DESCRIPTION.** Female from Aoupini. Total length 16 mm. Carapace 5.1 mm long; 2.9 mm wide. Abdomen 5.5 mm long; 2.9 mm wide. Cephalic width 1.6× carapace width. PME diameter 0.2 mm; PME separation 2.4 diameters. AME/PME 0.9; AME separation 1.6 AME diameters; closer to PME than to clypeal margin. ALE/PME 0.8; ALE tubercle small, eye's lower edge contiguous with clypeus margin; ALE 0.6 diameters below clypeal margin. PLE/PME 0.8; PLE separation 6.3 PLE diameters; PLE 2.2 diameters behind PME. Clypeus 0.8 AME diameters. Chelicerae with 4 promarginal teeth; 6 retromarginal teeth; frontal macrosetae in transverse line; laterals attenuate. Sternum 0.5× as wide as long; maximum width at coxa II. First femur length 14.4 mm; with 4 prolateral macrosetae; patella + tibia I, 16 mm; metatarsus I, 15.7 mm; tarsus I, 3.2 mm. Lengths of patella + tibia II, 12.4 mm; III, 8.4 mm; IV, 9.2 mm. Calamistrum 0.3 metatarsus IV length.

Male from Aoupini. Total length 14 mm. Carapace 4.5 mm long. Carapace 2.2 mm wide. Abdomen 9.1 mm long. Abdomen 1.7 mm wide. Cephalic width 1.2× carapace width. PME diameter 0.2 mm; PME separation 2.2 diameters. AME/PME 1; AME separation 1.3 AME diameters; equidistant between PME and clypeal margin. ALE/PME 0.8; ALE tubercle small; eye's ventral edge contiguous with clypeus margin; ALE 0.8 diameters below clypeal margin. PLE/PME 0.9; PLE separation 5.2 PLE diameters; PLE 1.8 diameters behind PME. Clypeus 0.1 AME diameters. Chelicerae with 4 promarginal teeth; 5 to 6 retromarginal teeth; frontal macrosetae in transverse line; laterals attenuate. Sternum 0.5× as wide as long. First femur length 16.4 mm; with 4 prolateral macrosetae; patella + tibia I 17.7 mm; metatarsus I 10.9 mm; tarsus I 4.5 mm. Lengths of patella + tibia II, 12.9 mm; III, 8.4 mm; IV, 9.4 mm. Tarsus I divided and of uniform width. Terminal portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II with curve bordered posteriorly by stout seta. Dorsal surface of tarsus II without stout setae. Palpal femur length 3× cymbium length.

**VARIATION.** Female body length ranges from 15.5 to 17.0 mm ( $n = 2$ ); only one male is known.

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** New Caledonia (Figure 13).

**SPECIMENS EXAMINED.** NEW CALEDONIA:

Aoupinié, 20 km NE Poya, 650 m, Monteith & Cook, 18.v.1984, [QM: 1♂, 1♀; -21.15: 165.31]. Mandjelia, above Pouebo, 6–750, Monteith & Cook, 11.v.1984, [QM: 1♀; -20.4: 164.57]. Noumea, Savae, [MNHN: AR 165, 2 juveniles; -22.23: 166.47].

### ***Menneus quasimodo*, new species**

FIGURES 13, 29

**TYPES.** Holotype female, designated here, in poor condition in WAM from Norseman; details below.

**ETYMOLOGY.** Named after Victor Hugo's famous literary character, Quasimodo, the hunchback of Notre Dame. The holotype spider resembles Quasimodo in having a "wart" and a "hump" (Figure 29c). Gender is masculine.

**DIAGNOSIS.** The single female has multiple median and frontal macrosetae. The epigynum of the only female is slightly damaged, so that the number of copulatory duct spirals is ambiguous—either three or four full spirals (or four or five counting lateral margins in dorsal view; Figure 29g). The paired, relatively anterior, abdominal tubercles are markedly large and truncate, and the female lacks the abdominal extension beyond the spinnerets that characterizes *M. nemesio*.

**DESCRIPTION.** Female (holotype). Total length 8.8 mm. Carapace 3.3 mm long; 2.2 mm wide. Abdomen 5.3 mm long; 4.6 mm wide. Cephalic width 0.42× carapace width. PME diameter 0.21 mm; PME separation 0.27 diameters. AME/PME 0.67; AME separation 1.64 AME diameters; closer to clypeal margin than PME. ALE/PME 0.67; ALE tubercle large, eye's lower edge 1/3 diameter from clypeus margin; ALE only slightly below clypeal margin. PLE/PME 0.62; PLE separation 5.69 PLE diameters; PLE 2.46 diameters behind PME. Clypeus 1.8 AME diameters. Chelicerae with 2 promarginal teeth; 3 retromarginal teeth; multiple macrosetae on median and frontal surfaces. Sternum 0.8× as wide as long; widest at coxae I. First femur length 7.1 mm; with 4 prolateral macrosetae; patella + tibia I, 7.5 mm; metatarsus I, 7.4 mm; tarsus I, 1.4 mm. Lengths of patella + tibia II, 7.4 mm; III, 4.4 mm; Leg IV missing.

**VARIATION.** Unknown.

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** Western Australia (Figure 13).

SPECIMENS EXAMINED. AUSTRALIA: WA, Norseman, 32°12'S 121°46'E, "senex," 1926, [WAM: 26/465, 1♀; -32.2: 121.77].

### ***Menneus trinodosus* Rainbow, 1920**

FIGURES 13, 17D-F, 31

*Menneus trinodosus* Rainbow, 1920:230, pl. 28, figs. 3, 4 (♀).

*Deinopis insularis* Rainbow, 1920:229, pl. 28, figs. 1, 2 (♂). NEW SYNONYMY.

*Avella trinodosa*: Lehtinen, 1967:217 (transfer from *Menneus*).—Platnick, 2010.

*Avella insularis*: Lehtinen, 1967:217, fig. 38 (transfer from *Deinopis*).—Coddington, 1990a:11, fig. 44 (♂).—Platnick, 2010.

**TYPES.** Holotype female of *M. trinodosus* in South Australian Museum, Adelaide, examined (Australia, NSW, Lord Howe Island: see Entomology Insecta Register I11509, no latitude given, no longitude given, A. M. Lea, 12/1915–1/1916, SAM: N1981233 and ARA 5325). Holotype male of *D. insularis* in South Australian Museum, examined (Australia, NSW, Lord Howe Island: see Entomology Insecta Register I11508, A. M. Lea, 12/1915–1/1916, SAM: N1981232 and ARA 5325).

**DIAGNOSIS.** Uniquely in *Menneus*, female *M. trinodosus* have posterior paired abdominal tubercles, the anterior portion of the epigynum is blunt; in ventral view the spermathecae are large, and the copulatory ducts make one full spiral (or two if counting lateral margins; Figure 31c,d,g). The median hematodocha in ventral view (left palp) spans 1–6 OC, the embolus tip lies at about 11 OC, and the median apophysis–basal lobe axis lies at about 2:30 OC (Figure 17e). The embolus makes 2.5 coils and is bent away from the tegulum in prolateral view (Figure 17f).

**DESCRIPTION.** Female from Gladstone. Total length 11.7 mm. Carapace 4.1 mm long; 2.7 mm wide. Abdomen 7 mm long; 3.1 mm wide. Cephalic width 1.5× carapace width. PME diameter 0.2 mm; PME separation 3 diameters. AME/PME 0.9; AME separation 1.9 AME diameters; equidistant between PME and clypeal margin. ALE/PME 0.7; ALE tubercle small, eye's lower edge contiguous with clypeus margin; ALE 0.6 diameters below clypeal margin. PLE/PME 1; PLE separation 6.5 PLE diameters; PLE 1.7 diameters behind PME. Clypeus 0.5 AME diameters. Chelicerae with 4 promarginal teeth; 5 to 6 retromarginal teeth; frontal macrosetae in transverse line; laterals attenuate. Sternum 0.6× as wide as long; maximum width at coxa II. First femur length 8.1 mm;

with 8 to 9 prolateral macrosetae; patella + tibia I, 8.1 mm; metatarsus I, 8.7 mm; tarsus I, 2.1 mm. Lengths of patella + tibia II, 8.1 mm; III, 3.6 mm; IV, 4.2 mm. Calamistrum 0.3 metatarsus IV length.

Male from Burdaberg. Total length 9.1 mm. Carapace 3.3 mm long. Carapace 2 mm wide. Abdomen 5.6 mm long. Abdomen 1.8 mm wide. Cephalic width 0.6× carapace width. PME diameter 0.2 mm; PME separation 2.5 diameters. AME/PME 1.1; AME separation 1.2 AME diameters; closer to PME than to clypeal margin. ALE/PME 0.7; ALE tubercle small; eye's ventral edge contiguous with clypeus margin; ALE 0.6 diameters below clypeal margin. PLE/PME 1; PLE separation 4.9 PLE diameters; PLE 1.5 diameters behind PME. Clypeus 0.1 AME diameters. Chelicerae with 4 promarginal teeth; 3 to 4 retromarginal teeth; frontal macrosetae in transverse line; laterals attenuate. Sternum 0.6× as wide as long. First femur length 9.6 mm; with 6 to 7 prolateral macrosetae; patella + tibia I 8.6 mm; metatarsus I 8.7 mm; tarsus I 2.1 mm. Lengths of patella + tibia II, 11.4 mm; III, 3.2 mm; IV, 3.7 mm. Tarsus I undivided. Terminal portion of tibia II with stout condyles. Terminal portion of metatarsus II without distal curve. Dorsal surface of tarsus II without stout setae. Palpal femur length 2.2× cymbium length.

**VARIATION.** While in most females the abdominal tubercles are posterior as illustrated, in some this is less pronounced. Female body length ranges from 9.1 to 18.0 mm ( $n = 9$ ), and males from 7.0 to 9.1 ( $n = 10$ ).

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** Australia (Queensland, New South Wales, including Lord Howe Island) (Figure 13).

**SPECIMENS EXAMINED.** AUSTRALIA: NSW, L. H. I. 25 [Lord Howe I.], in grass-litter, [AMS: KS 16843, 2♀; -31.55: 159.08]. NSW, L. H. I. 39 [Lord Howe I.], [AMS: KS 16846, 1♀; -31.55: 159.08]. NSW, Lord Howe Island, Intermediate Hill, Big Creek, malaise-trough, tall forest #5, 50 ft, S & J Peck, 18.v.1980, [AMNH: 1♂; -31.55: 159.08]. NSW, Minnamurra Falls Res., C Horseman, 20.iv.1982, [AMS: KS 9204, 1♀, 1 juvenile; -34.62: 150.85]. QLD, Bulburin (Forestry nursery), NW Bundaberg, rainforest site 3A, 580 m, 24°31'S 151°29'E, Gray & Horseman, iii.1975, [AMS: KS 0092, 4♂; -24.52: 151.48]. QLD, Bulburin SF, 24°31'S 151°29'E, [QM: 2♂, 2♀; -24.52: 151.48]. QLD, Bulburin SF, 24°31'S 151°29'E, [QM: 1♂; -24.52: 151.48]. QLD, Eurimbula, SE Gladstone, rainforest site 4, 0 m, 24°11'S 151°50'E, C Horseman, iii.1975, [AMS: KS 0256, 1♀; -24.18: 151.83]. QLD, Finch Hatton, RK&VED, 7.iv.1975, [QM: 1♂, 1♀, 2 juveniles; -21.14: 148.63]. QLD, Kroombit Tops (Three Moon Ck.), 45 km SSW Calliope, rainforest, Davies &

Gallon, 9.xii.1983, [QM: 1♂, 1 juvenile; -24.49: 151.2]. QLD, Kuranda (12 mi N of), Coleman & Mascord, 30.i.1972, [AMS: KS 16867 1♀; -16.82: 145.63]. QLD, Malaan S.F., RR&VED, 20.iv.1978, [QM: 1♂, 1 juvenile; -17.58: 145.58]. QLD, Mt. Goonaneman, nr Childers, 670 m, Davies & Raven, 3.xi.1980, [QM: 1♀; -25.12: 152.18]. QLD, Spear Ck nr Mt Mallay, CNVF Site 34, RR&VED, 5.xi.1975, [QM: CNVF Site 34?, 1♂, 1♀, 7 juveniles; -16.68: 145.33].

### ***Menneus wa, new species***

FIGURES 13, 17G–I, 32

**TYPES.** Holotype male from Denmark and three paratype females from Quaalup Homestead and Quaranup Road, all in WAM; details below.

**ETYMOLOGY.** Named for Western Australia, construed as a noun in apposition.

**DIAGNOSIS.** Among Australian *Menneus* with paired median dorsal abdominal tubercles female *M. wa* closely resemble *M. superciliatus* in having copulatory ducts with two full spirals (or three counting lateral margins in dorsal view; Figure 32g). *Menneus wa* seem to have broader, shorter, abdomens with a lateral brown abdominal spot (Figure 32c,d). The median hematodocha in ventral view (left palp) spans 6–9 OC, the embolus tip lies at about 11 OC, and the median apophysis–basal lobe axis lies at about 1:30 OC (Figure 17h). The embolus makes 3.5 coils and is bent away from the tegulum in prolateral view (Figure 17i).

**DESCRIPTION.** Female from Quaranup Rd. Total length 10.8 mm. Carapace 3.3 mm long; 2.2 mm wide. Abdomen 7.6 mm long; 5.6 mm wide. Cephalic width 0.3× carapace width. PME diameter 0.23 mm; PME separation 0.28 diameters. AME/PME 0.7; AME separation 1.6 AME diameters; closer to PME than clypeal margin. ALE/PME 0.7; ALE tubercle large, eye's lower edge 1/3 diameter from clypeus margin; ALE only slightly below clypeal margin. PLE/PME 1.0; PLE separation 3.7 PLE diameters; PLE 1.6 diameters behind PME. Clypeus 1.8 AME diameters. Chelicerae with 4 promarginal teeth; 4 retromarginal teeth; median frontal macrosetae proximal to laterals; laterals stout. Sternum 0.6x as wide as long; widest at coxae II. First femur length 7.1 mm; with 5 prolateral macrosetae; patella + tibia I, 7.8 mm; metatarsus I, 7.6 mm; tarsus I, 1.5 mm. Lengths of patella + tibia II, 7.2 mm; III, 4.4 mm; IV, 4.6 mm. Calamistrum 0.35 metatarsus IV length.

Male (holotype). Total length 8.5 mm. Carapace 2.8 mm long. Carapace 2 mm wide. Abdomen 5.8 mm long.

Abdomen 1.9 mm wide. Cephalic width 0.4× carapace width. PME diameter 0.23 mm; PME separation 1.1 diameters. AME/PME 0.57; AME separation 1.6 AME diameters; closer to clypeal margin than to PME. ALE/PME 0.83; ALE tubercle large; eye's ventral edge 1.2 or more diameters from clypeus margin; ALE 0.1 diameters below clypeal margin. PLE/PME 1.0; PLE separation 3.7 PLE diameters; PLE 1.15 diameters behind PME. Clypeus 1.54 AME diameters. Chelicerae with 4 promarginal teeth; 5 retromarginal teeth; median frontal and lateral macrosetae missing (or absent?). Sternum 0.6x as wide as long. First femur length 9.8 mm; with at least 3 prolateral macrosetae; patella + tibia I 11.3 mm; metatarsus I 12.7 mm; tarsus I missing. Lengths of patella + tibia II, 8.8 mm; III, 5.4 mm; IV, 5.7 mm. Terminal portion of tibia II with stout condyles and prolateral apophysis. Terminal portion of metatarsus II with curve bordered posteriorly by stout seta. Dorsal surface of tarsus II with proximal stout setae. Palpal femur length 2.3× cymbium length.

**VARIATION.** Three females range in length from 11.0 to 12.5 mm. Two of three females had conspicuous brown spots on the lateral abdominal surface. Only one male is known.

**NATURAL HISTORY.** Unknown.

**DISTRIBUTION.** Western Australia (Fig. 13)

**SPECIMENS EXAMINED.** AUSTRALIA: WA, Denmark, inside house, 34°58'S 117°21'E, R. P. McLellan, 2iii1994, [WAM: 97/2350, 1♂; -34.97: 117.35]. WA, Quaalup Homestead, night collecting, 34°17'S 119°26'E, MS Harvey & JM Waldock, 25.v.1994, [WAM: 97/2351, 1♀; -35.08: 117.92]. WA, Torndirrup Nat. Pk., Quaranup Rd., 35°05'S 117°55'E, MS Harvey & JM Waldock, 25.iv.1990, [WAM: 97/2352, 1♀; -34.28: 119.43]. WA, Torndirrup Nat. Pk., Quaranup Rd., 35°05'S 117°55'E, MS Harvey & JM Waldock, 25.iv.1990, [WAM: 97/2353, 1♀; -33.97: 18.45].

### ***Menneus pietrzeniukae* Wunderlich, 2004**

?*Menneus pietrzeniukae* Wunderlich 2004:892 (juv.), figs. 1–6.

**TYPES.** Juvenile female from Tertiary Baltic amber forest, Paleontological Museum of the Humboldt University Berlin, MB.A114, collected by Simon. Not examined.

**NOTES.** Judging from Wunderlich (2004, fig. 6), the specimen is juvenile, which otherwise would make the name a nomen dubium. However, given that it is a Baltic Amber fossil and that other fully diagnosable specimens may be discovered in the future, we leave it to future authors to decide formally the status of this name.

## NOMINA DUBIA

***Avella angulata* L. Koch, 1878**

*Avella angulata* L. Koch, 1878:1037, pl. 91, fig. 1 (♀).—Platnick, 2010.

*Menneus angulatus*: Rainbow, 1911:123.—Davies, 1988:282, fig. 7 (♂).

**TYPES.** Female holotype in Hamburg, examined.

**NOTES.** The specimen consists only of the cephalothorax and legs. The abdomen is missing. It is unclear if the animal was adult. Without the epigynum, or even knowledge of the form of abdominal tubercles, no known *Menneus* species can be unambiguously linked to this name.

***Avella despiciens* O. P.-Cambridge, 1877**

*Avella despiciens* O. P.-Cambridge, 1877:574, pl. 57, fig. 10 (♀) [see Cambridge, O. P., in References].—Lehtinen, 1967:217, fig. 41 (misidentification).—Platnick, 2010.

*Menneus despiciens*: Rainbow, 1911:124.

**TYPES.** Juvenile female (?) holotype in Oxford, examined (Australia, QLD, Rockhampton, E. W. Janson, 1877, OUMNH; Bottle no. 169, 1 juvenile). See Note under *M. nemesio*.

***Avella unifasciata* L. Koch, 1878**

*Avella unifasciata* L. Koch, 1878:1035, pl. 90, fig. 6 (♂).—Platnick, 2010.

*Menneus unifasciatus*: Rainbow, 1911:124.

**TYPES.** The holotype male cannot be located and is presumed lost.

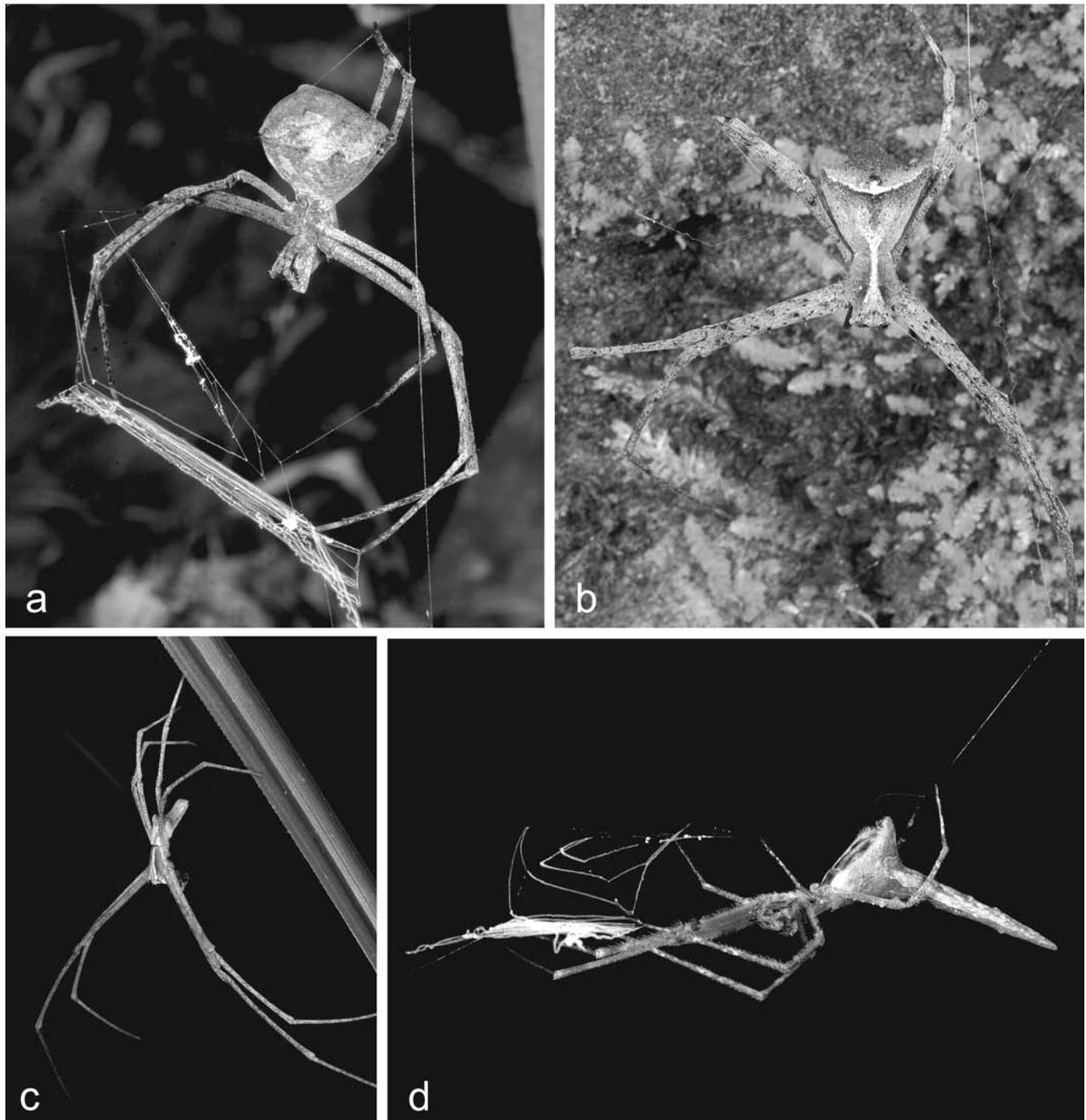
**FIGURES**

FIGURE 1. *Menneus* natural history: a–c are *Menneus capensis*, Cape Town; (a) female holding web; (b) subadult female dorsal; (c) male; (d) *Menneus camelus*, female from Sodwana Bay, KwaZulu-Natal, holding web (note unpaired abdominal tubercle).

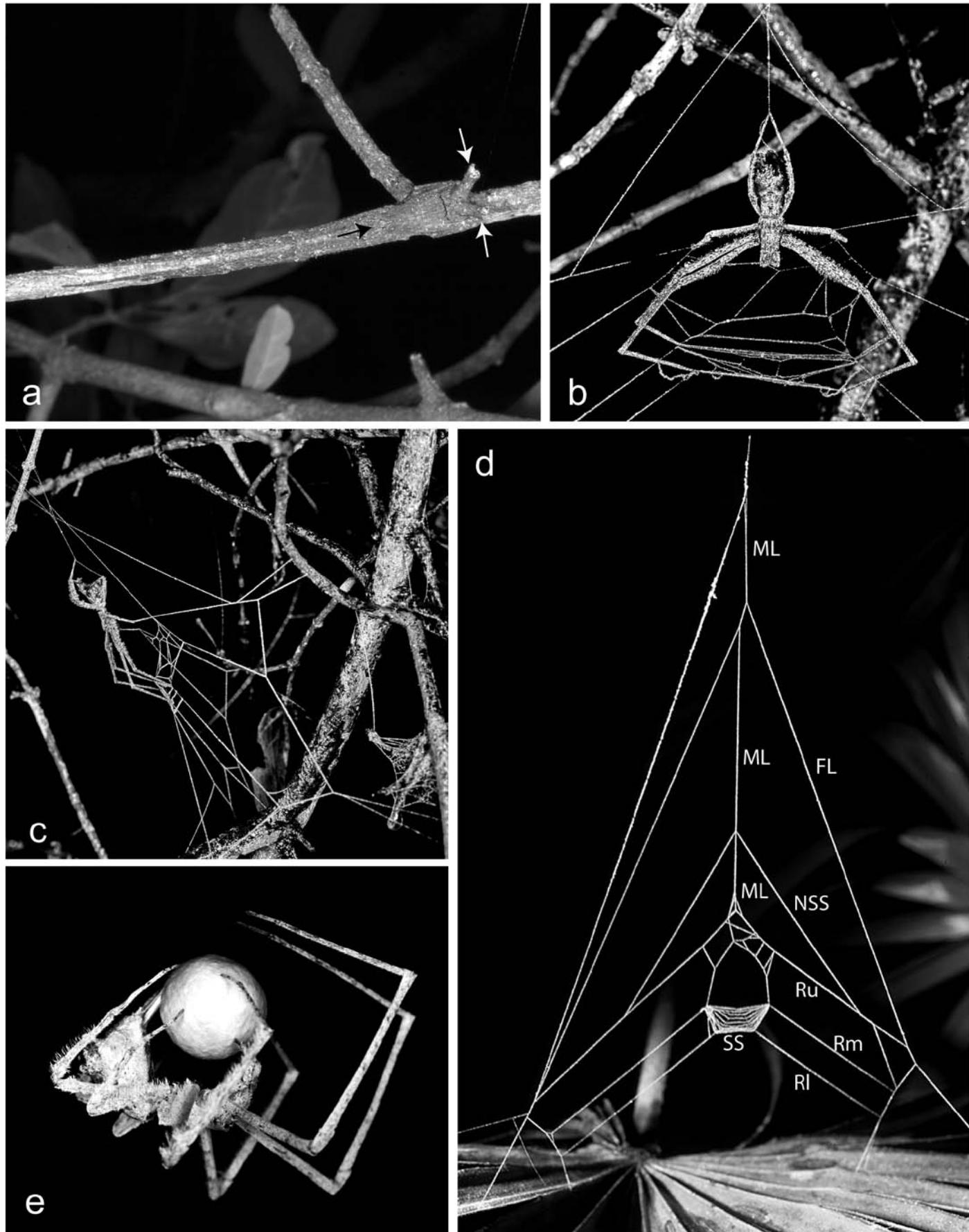


FIGURE 2. (facing page) Deinopid natural history: (a) *Menneus camelus* female from Gwala-Gwala, KwaZulu-Natal, in cryptic posture on twig, head marked with black arrow, note unusual morphology with paired abdominal tubercles (white arrows); (b, c) presumed female *Menneus camelus* in its web, voucher from Fanies Island, KwaZulu-Natal, not available for examination; (d) web of *Deinopis spinosa*, redrawn from Coddington and Sobrevila (1987); (e) presumed female *Menneus camelus* spinning her eggsac, voucher from Sodwana Bay, KwaZulu-Natal, not available for examination.

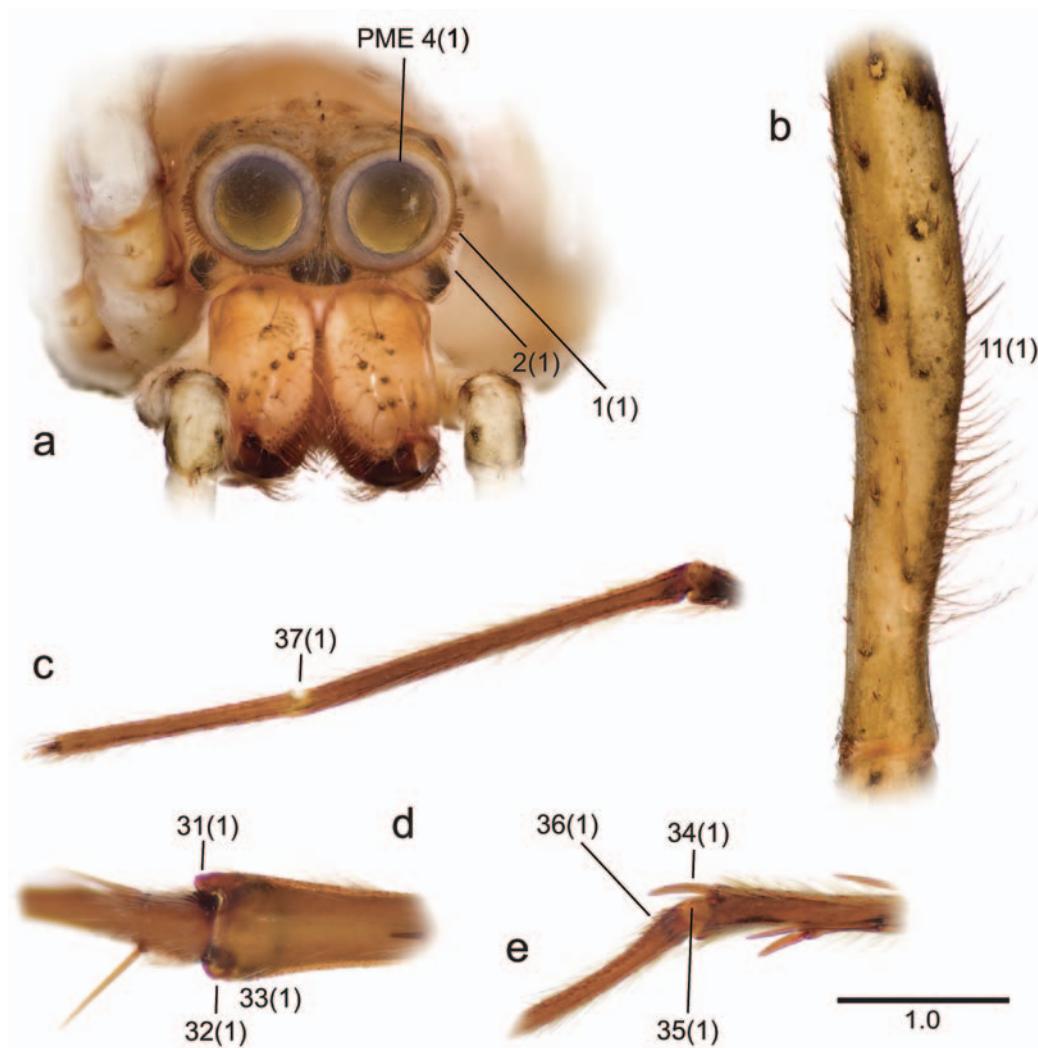


FIGURE 3. Deinopid somatic morphology: a, b are *Deinopis spinosa*, female from Florida, (a) frontal view of prosoma and (b) dorsal view of first left femur; c, e are *Menneus aussie*, male from Queensland: (c) first left tarsus, (d) distal second left tibia, and (e) second left metatarsus-tarsus joint. Numbers = characters (states); see text.

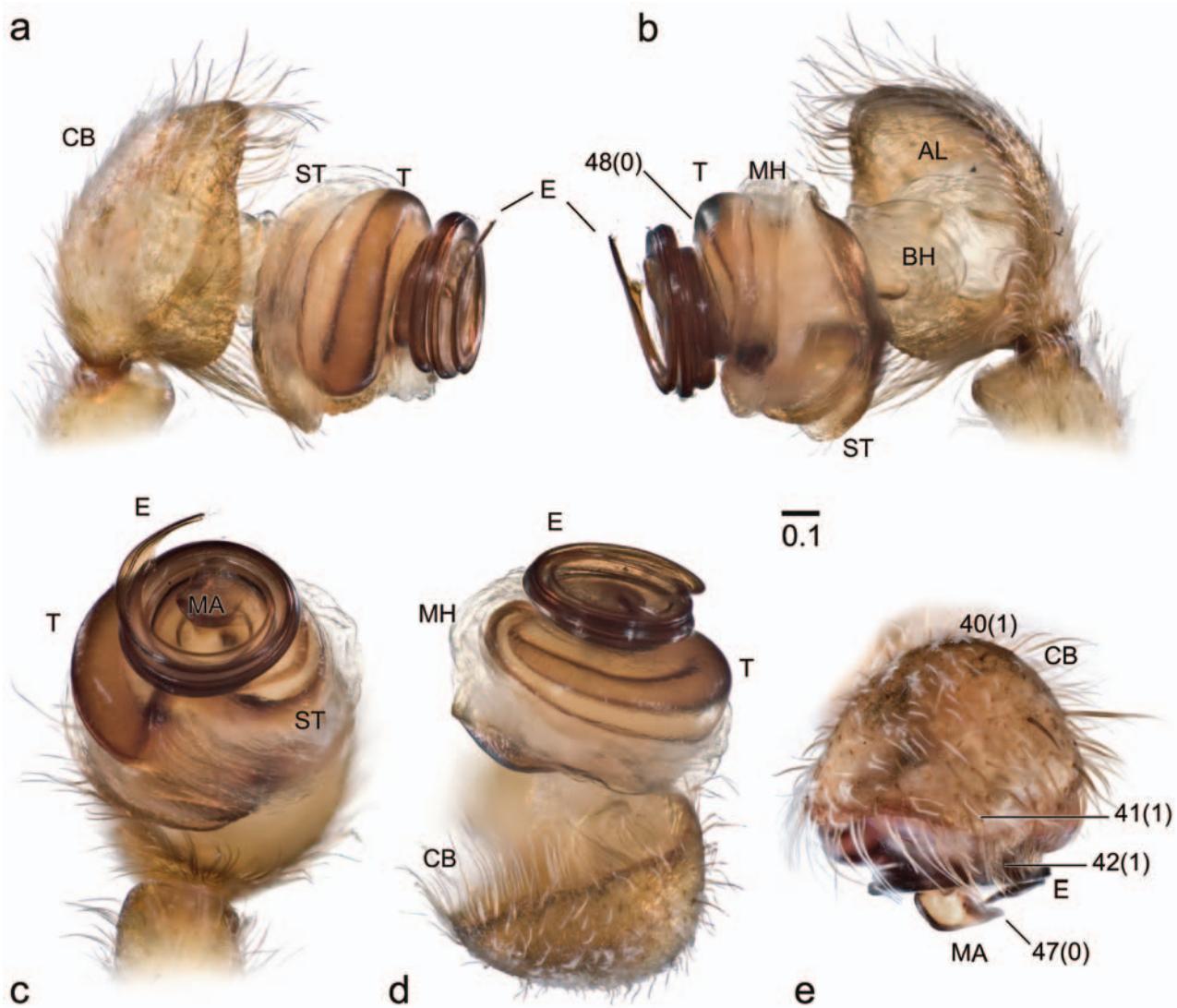
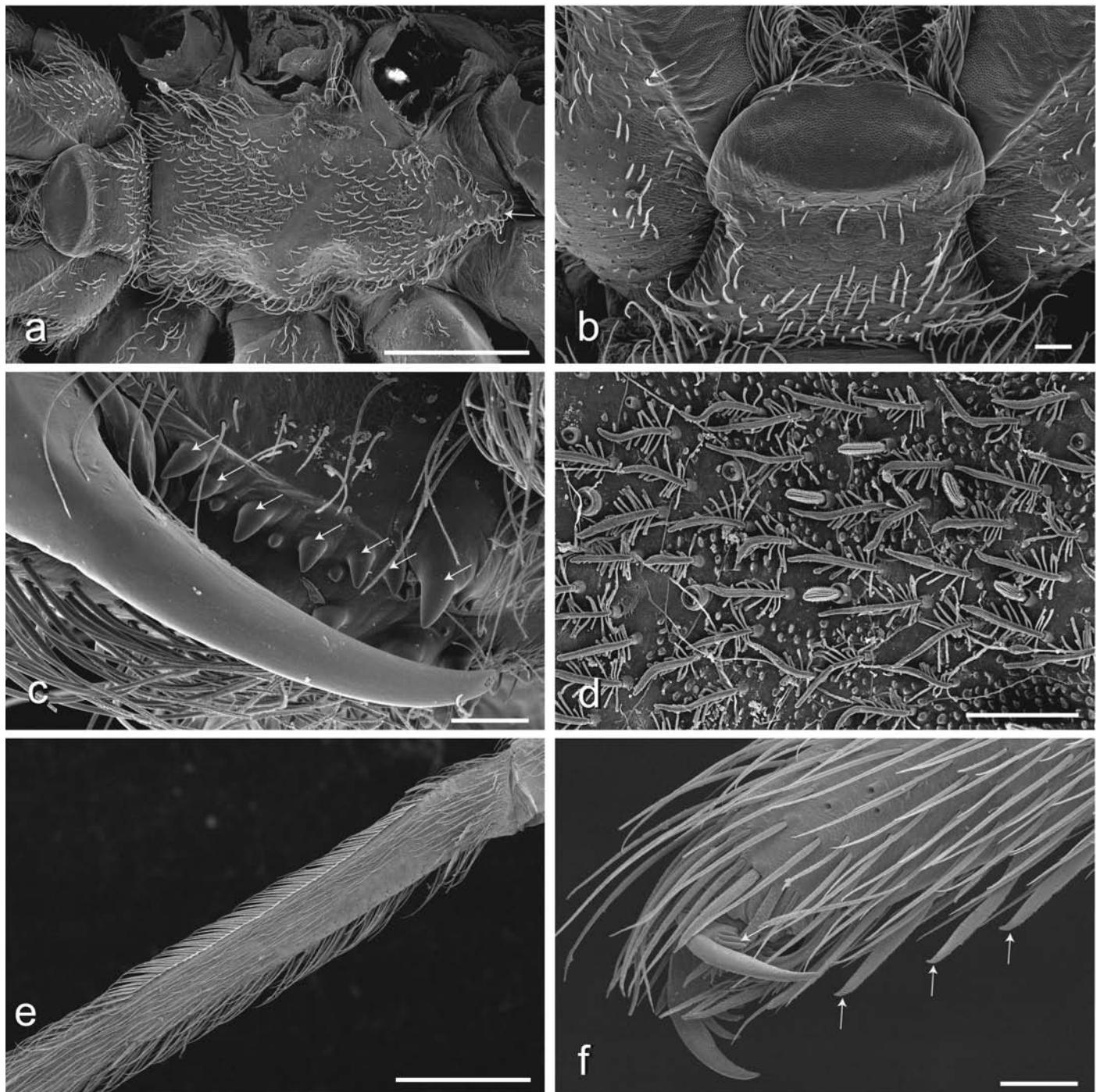
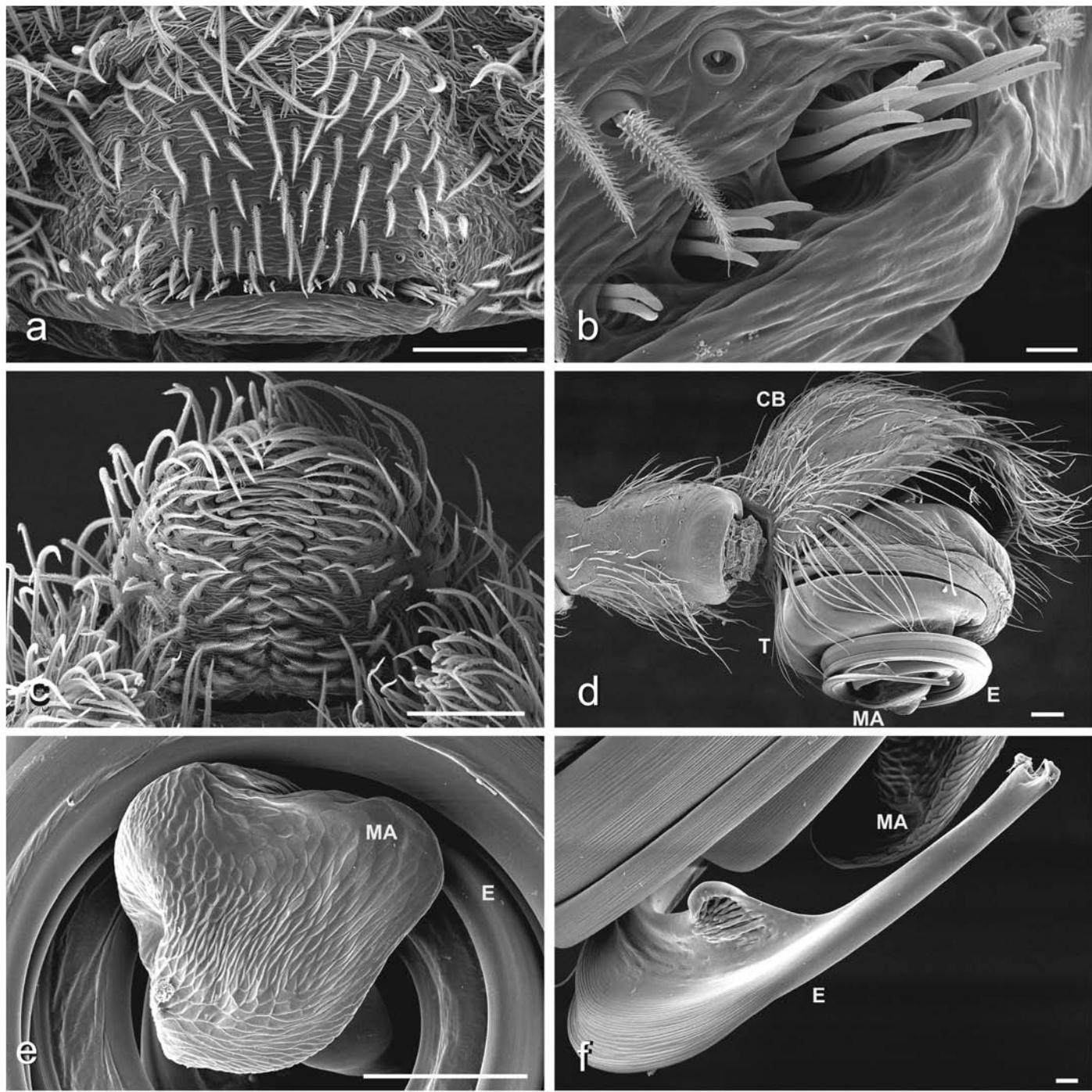


FIGURE 4. Deinopid male palpal morphology: a-d are *Deinopis spinosa*, expanded left palp in (a) prolateral, (b) retrolateral, (c) ventral, and (d) apical view; (e) *Menneus camelus* from South Africa, apical view.



**FIGURE 5.** Deinopid female morphology (*D. spinosa*): (a) sternum, ventral view, showing setose knob (arrow); (b) labium, endites, trichobothria (arrows); (c) detail of chelicera, ventral view, showing teeth (arrows) and denticles; (d) detail of carapace showing feathery, blunt, and plumose setae; (e) metatarsus IV showing calamistrum; (f) tarsus IV claws showing reduced retrolateral teeth (arrow) and ventral tarsal deinopoid setal comb (arrows). All scales = 0.1 mm, except a = 1 mm.



**FIGURE 6.** Deinopid male morphology (*D. spinosa*): (a) epiandrous spigots, ventral view; (b) detail of epiandrous spigots, ventral view; (c) anal tubercle, ventral view; (d) left palp, prolateral view; (e) median apophysis, ventral view; (f) detail of embolus tip. All scales = 0.1 mm, except b and f = 0.01 mm.

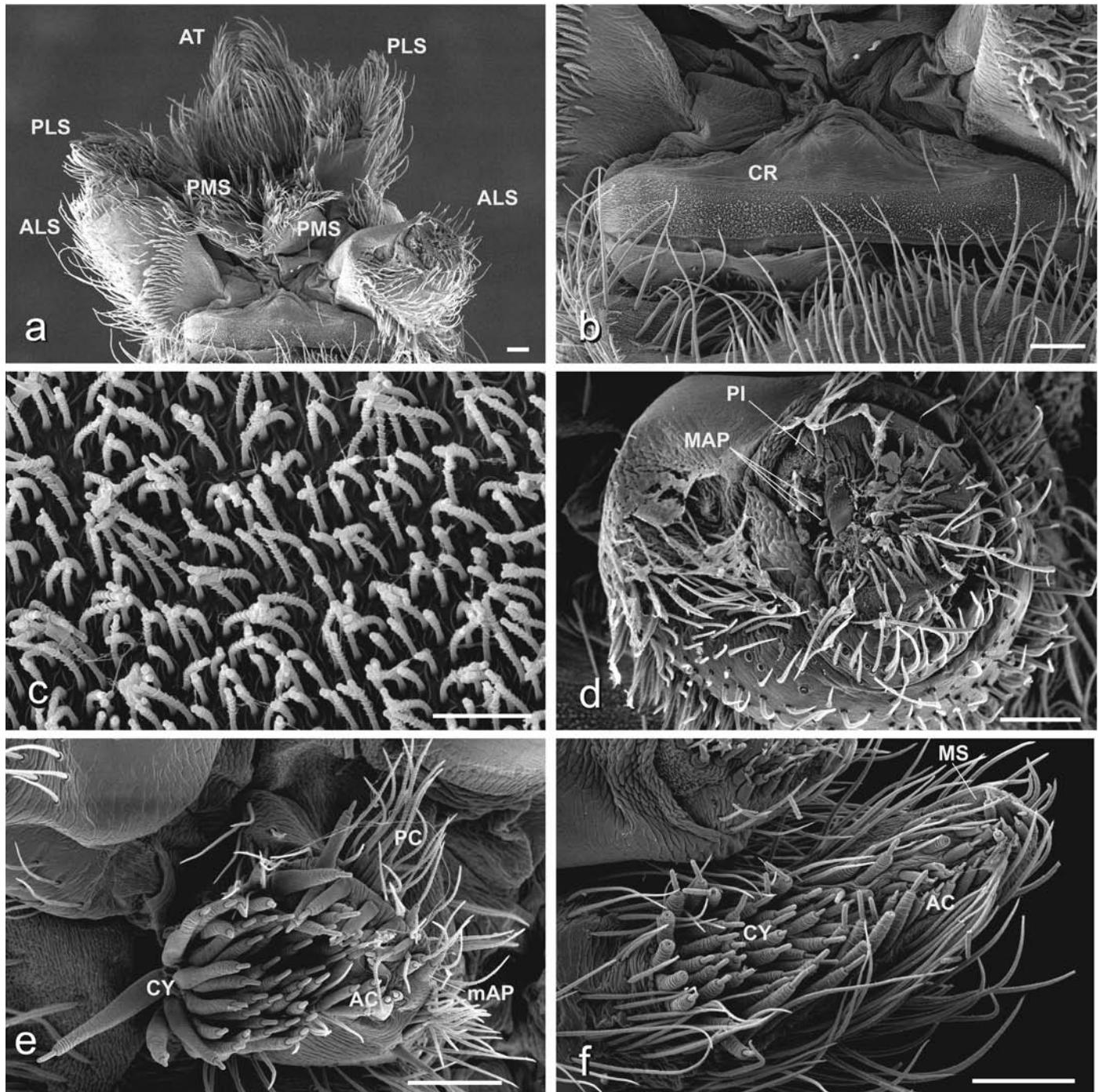


FIGURE 7. *Deinopis spinosa* female spinneret morphology, all ventral views: (a) spinneret overview; (b) cribellum; (c) cribellar spigot detail; (d) ALS with MAP and PI spigots; (e) PMS with mAP, AC, PC, and CY spigots; (f) PLS with CY, AC, and MS spigots. All scales = 0.1 mm, except c = 0.01 mm.

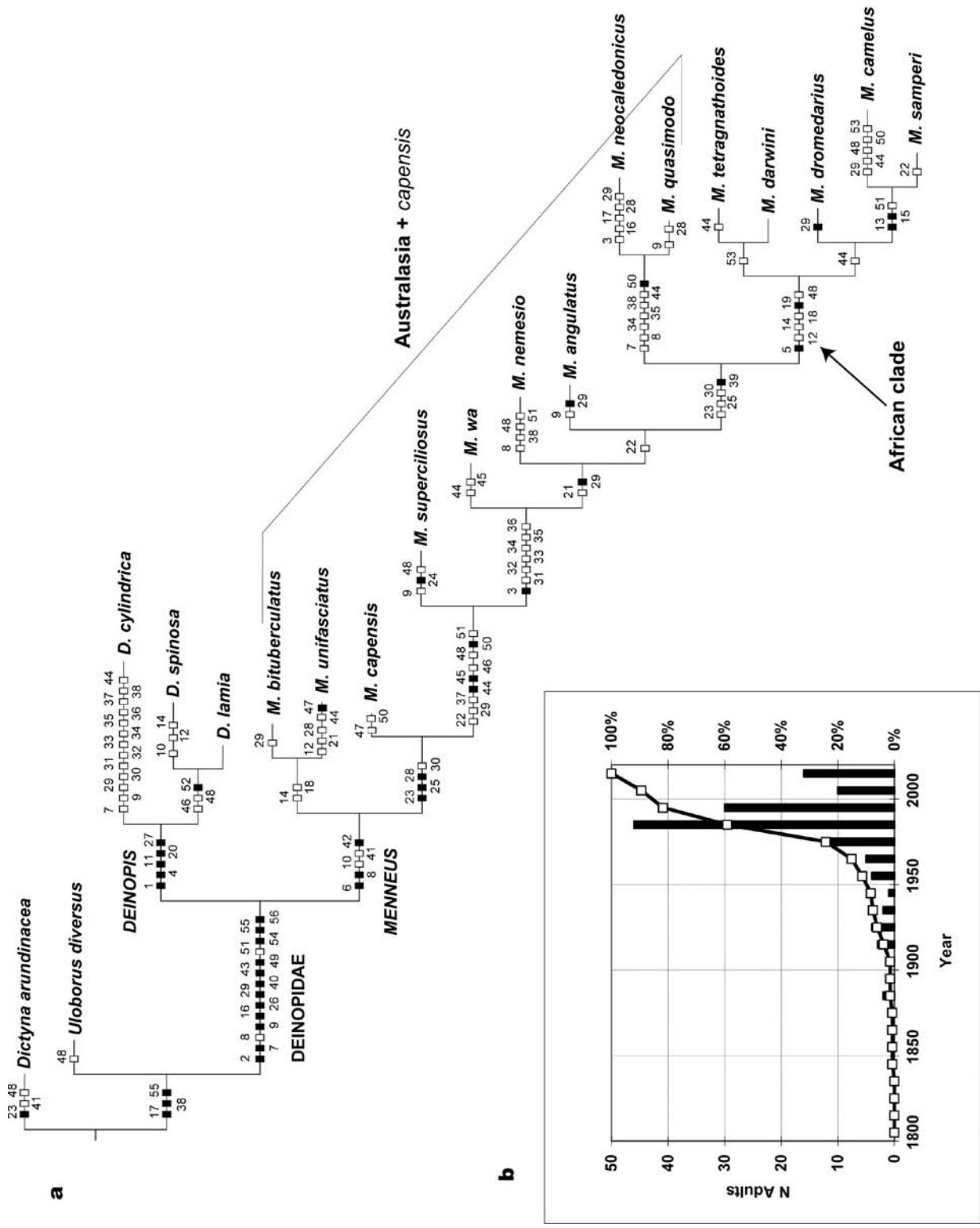


FIGURE 8. (a) Cladogram for outgroups, *Deinopis* exemplars, and all *Menneus* species. Length 131, ci 0.54, ri 0.69. All 131 steps are mapped on the tree, open ticks are characters with homoplasy, solid without. Ambiguous optimizations (5, 7–9, 12, 14, 18–19, 28–29, 34–35, 38–39, 41, 44–45, 47–48, 50, 55), were resolved to maximize homology of states and minimize parallel origin. (b) Growth of deinopid museum collections from 1800 to the present, by decade.

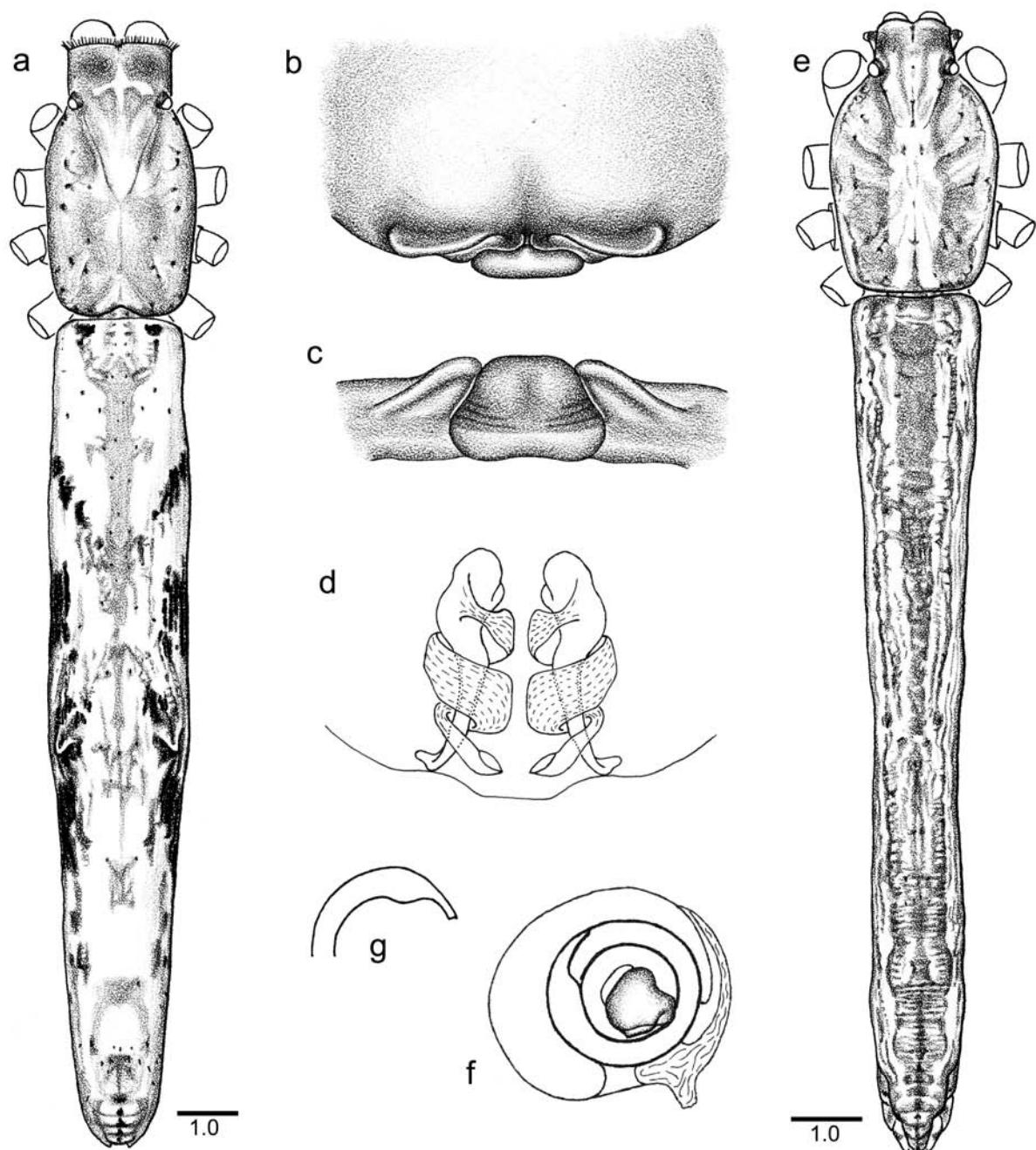
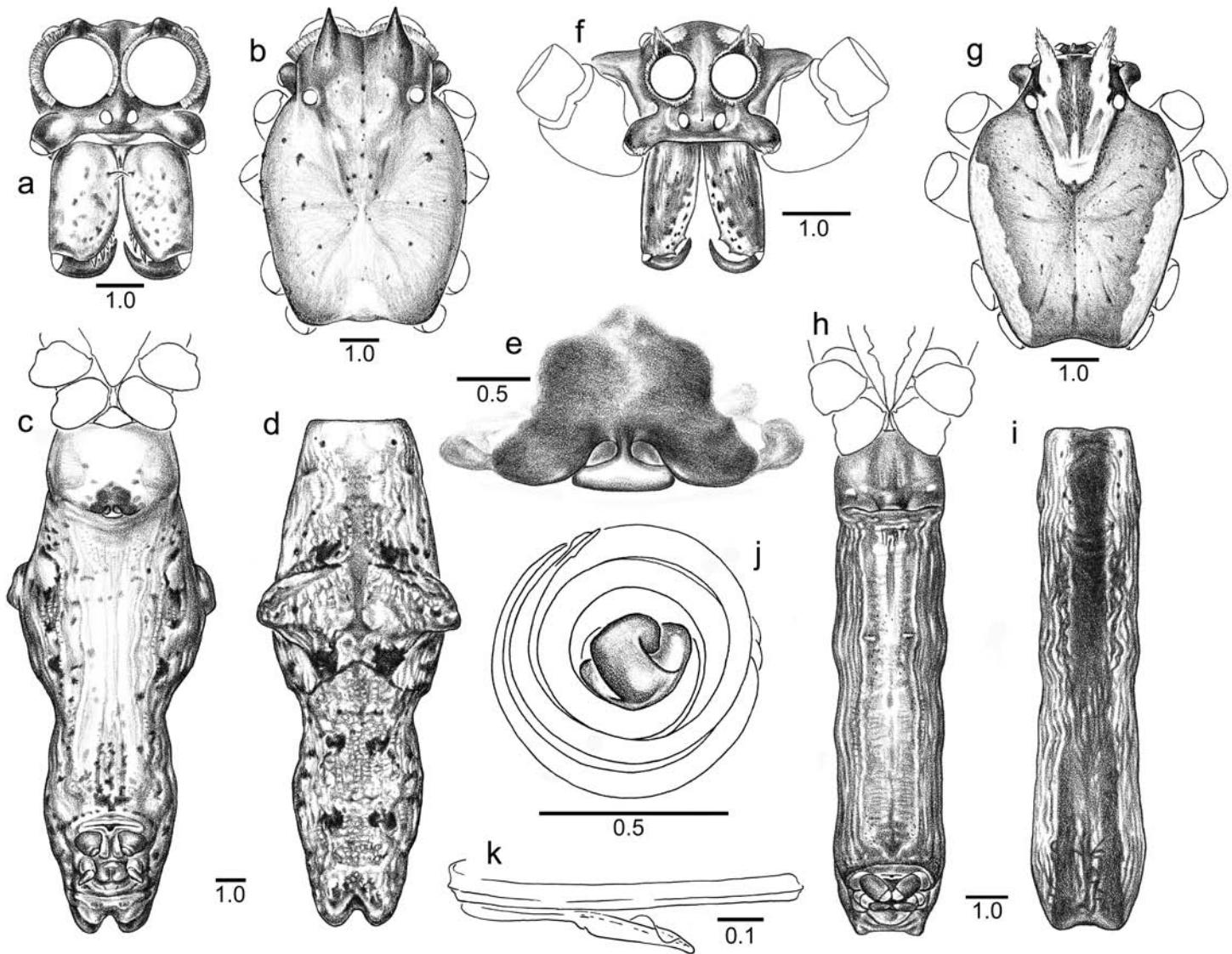


FIGURE 9. *Deinopis lamia*, from Pico Turquino, Cuba: a-d are female; (a) habitus, dorsal; (b) epigynum, ventral; (c) epigynum, caudal; (d) epigynum, dorsal; e-g are male; (e) habitus, dorsal; (f) left palpal bulb, ventral; (g) embolus tip.



**FIGURE 10.** *Deinopis cylindrica*: a–e are female from Lake Sibayi, KwaZulu-Natal; (a) prosoma, frontal; (b) prosoma, dorsal; (c) abdomen, ventral; (d) abdomen, dorsal; (e) epigynum, ventral; f–j are male from Empangeni, KwaZulu-Natal; (f) prosoma, frontal; (g) prosoma, dorsal; (h) abdomen, ventral; (i) abdomen, dorsal; (j) left palpal bulb, ventral; (k) embolus tip.

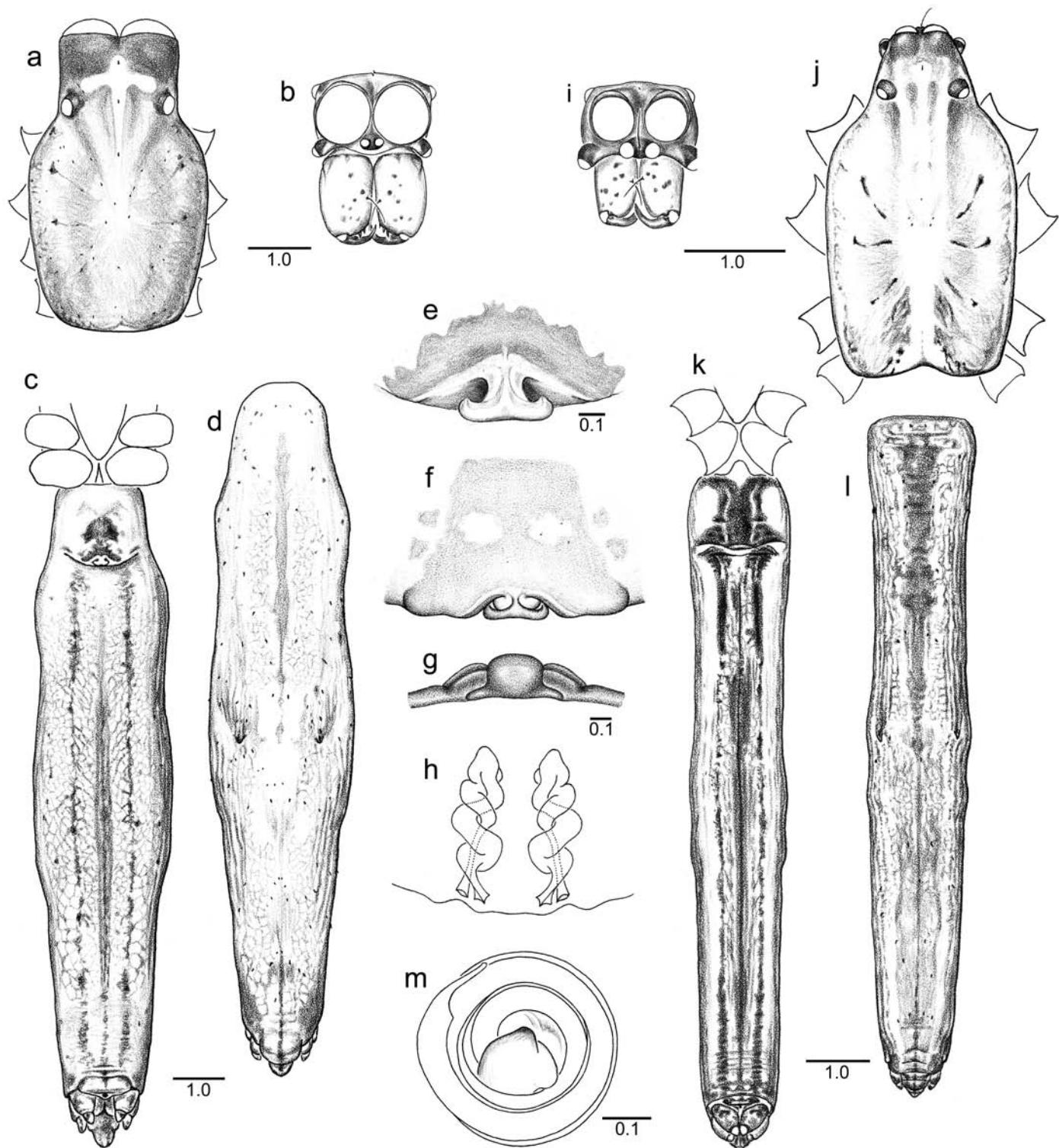
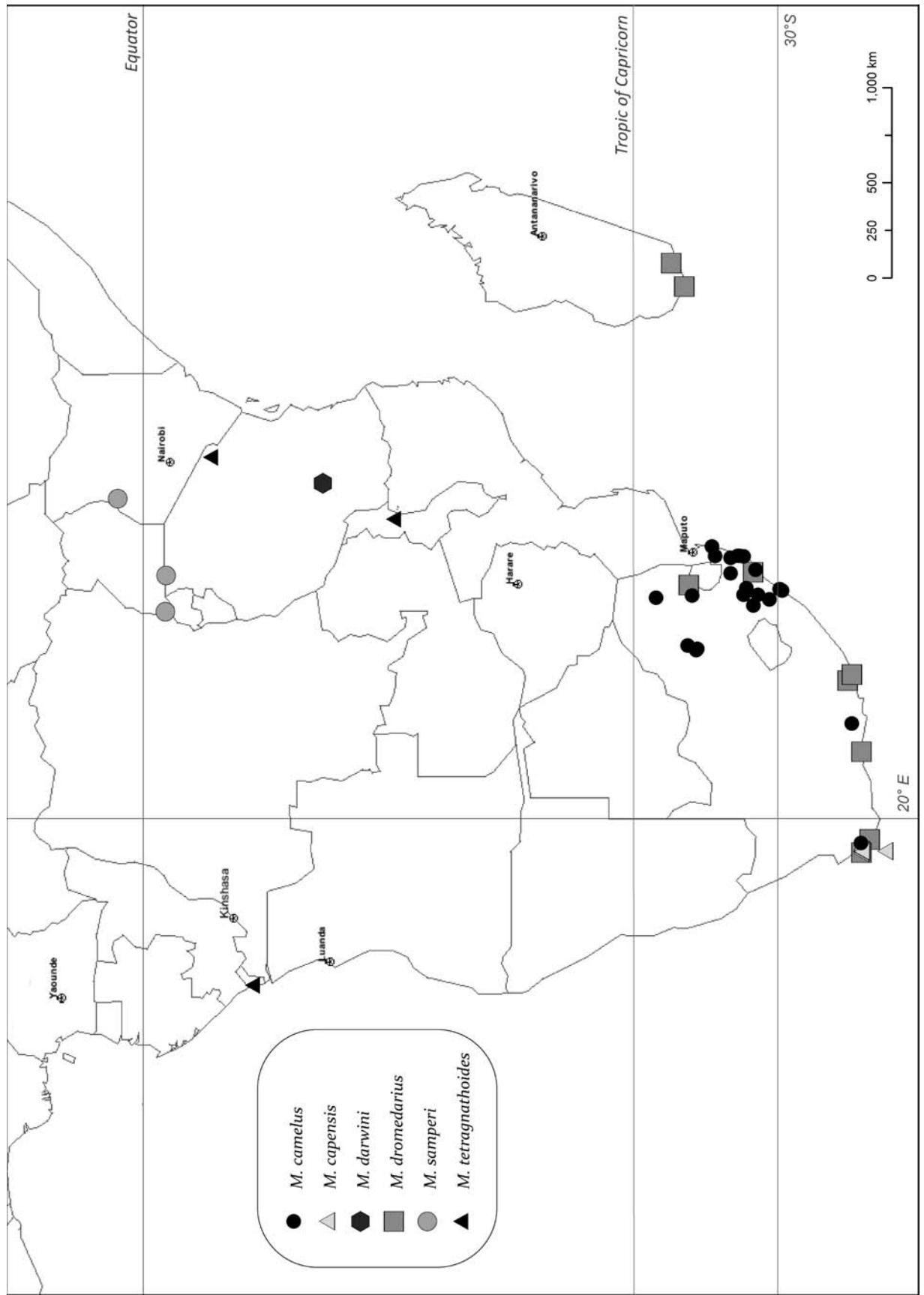
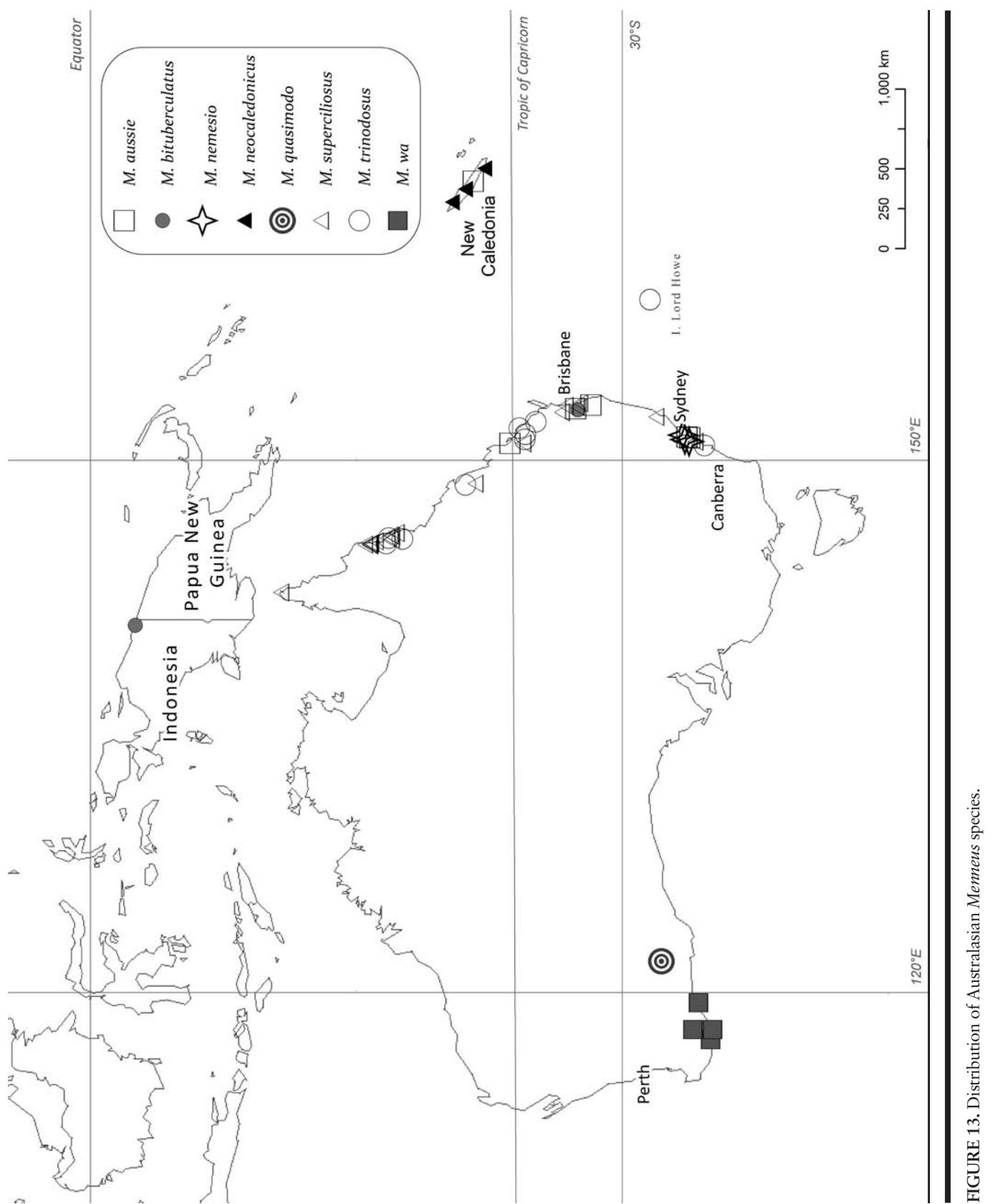
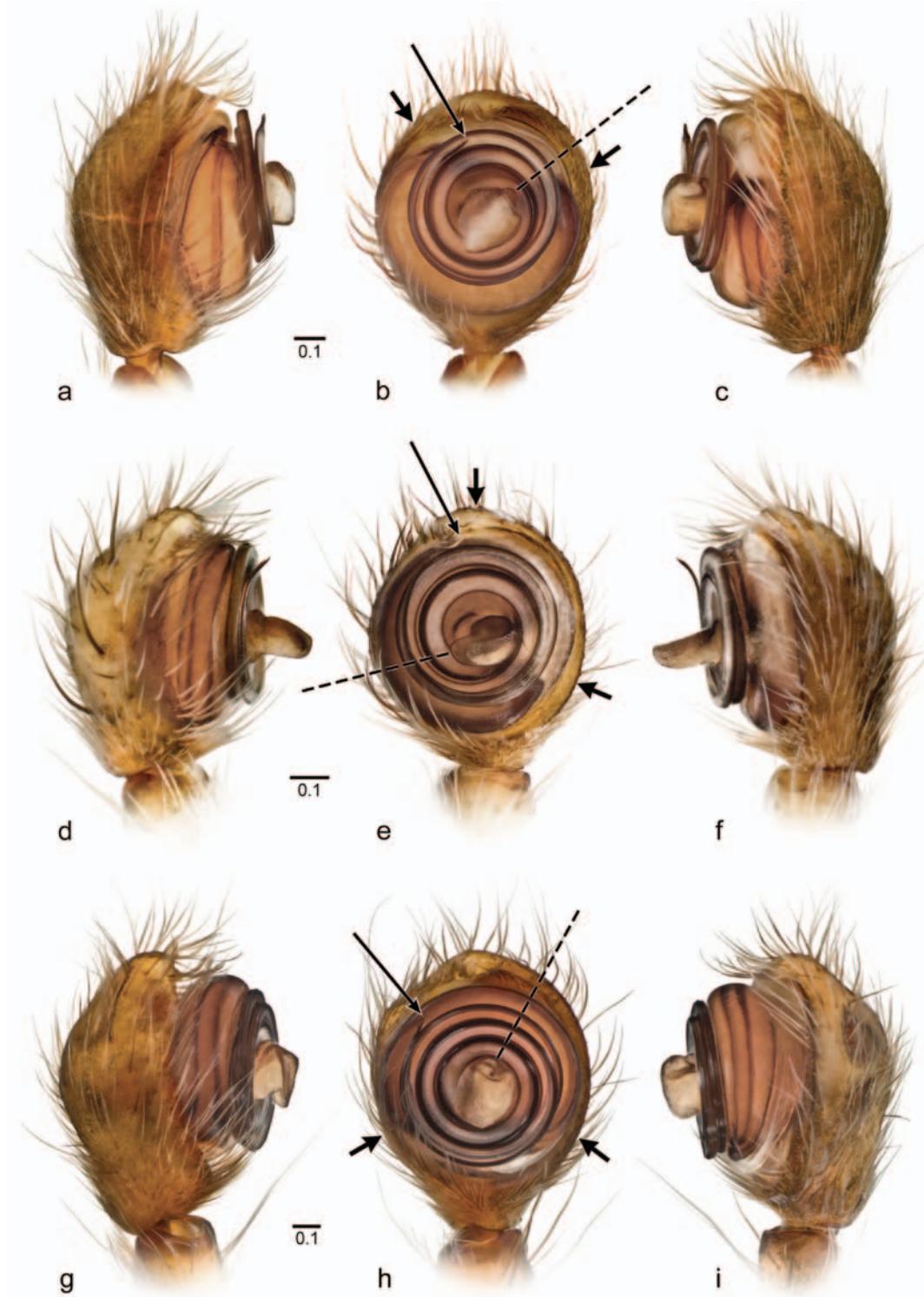


FIGURE 11. *Deinopis spinosa*: a–e are female from Florida; (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, ventral; (d) abdomen, dorsal; (e) epigynum, ventral; f–h are epigynum of female from Jamaica; (f) ventral; (g) caudal; (h) dorsal; i–m are male from Florida; (i) prosoma, frontal; (j) prosoma, dorsal; (k) abdomen, ventral; (l) abdomen, dorsal; (m) left palpal bulb, ventral.

FIGURE 12. Distribution of African *Menenus* species.

FIGURE 13. Distribution of Australasian *Menicus* species.



**FIGURE 14.** *Menneus* male left palps in (left) prolateral, (middle) ventral, and (right) retrolateral view: (a–c) *M. camelus*, (d–f) *M. capensis*, and (g–i) *M. darwini*. Diagnostic features of species in b, e, h: short bold arrows indicate extent of median hematodocha; long slender arrow indicates embolus tip; dashed line indicates the axis of the median apophysis and basal lobe.

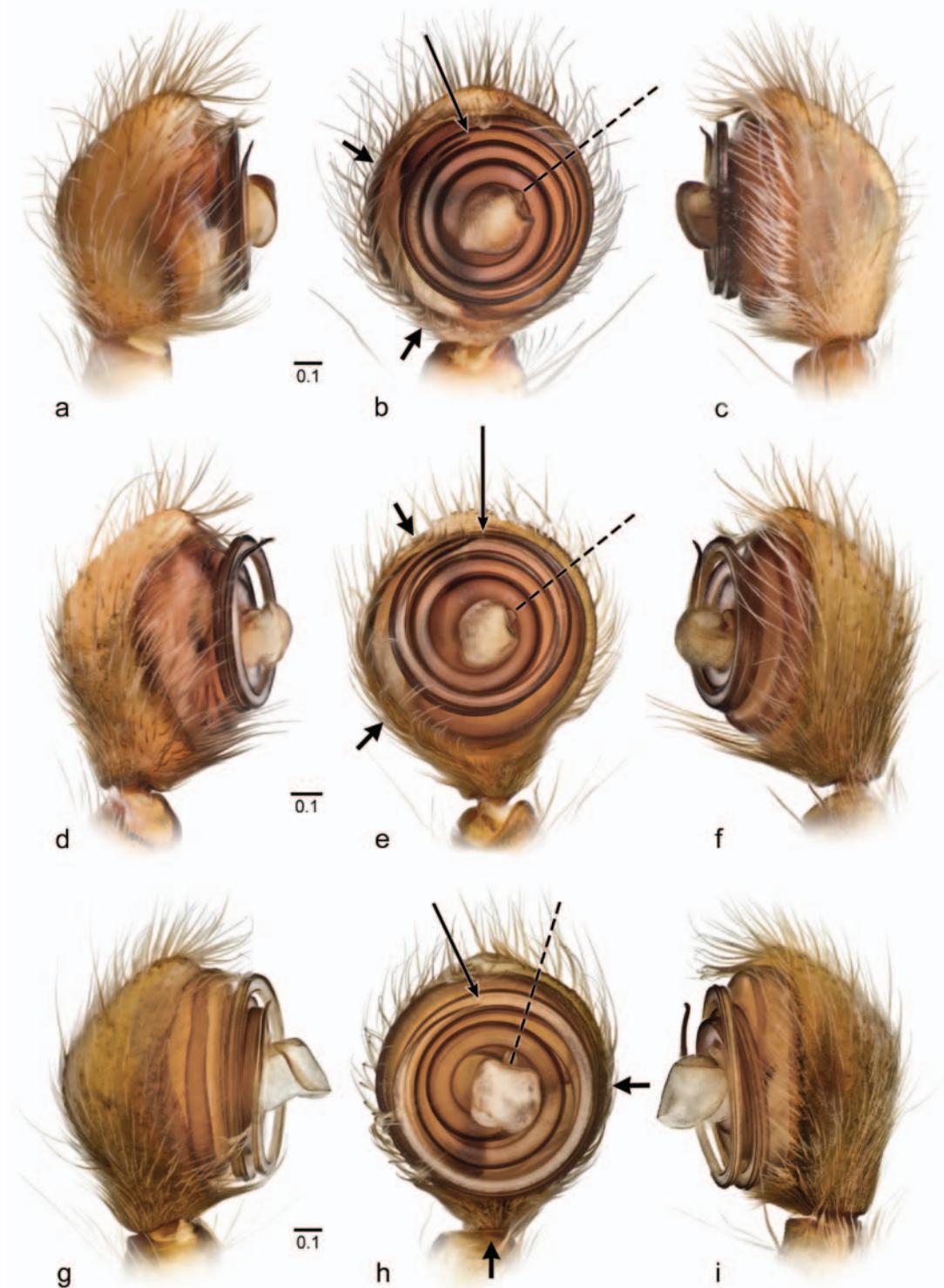
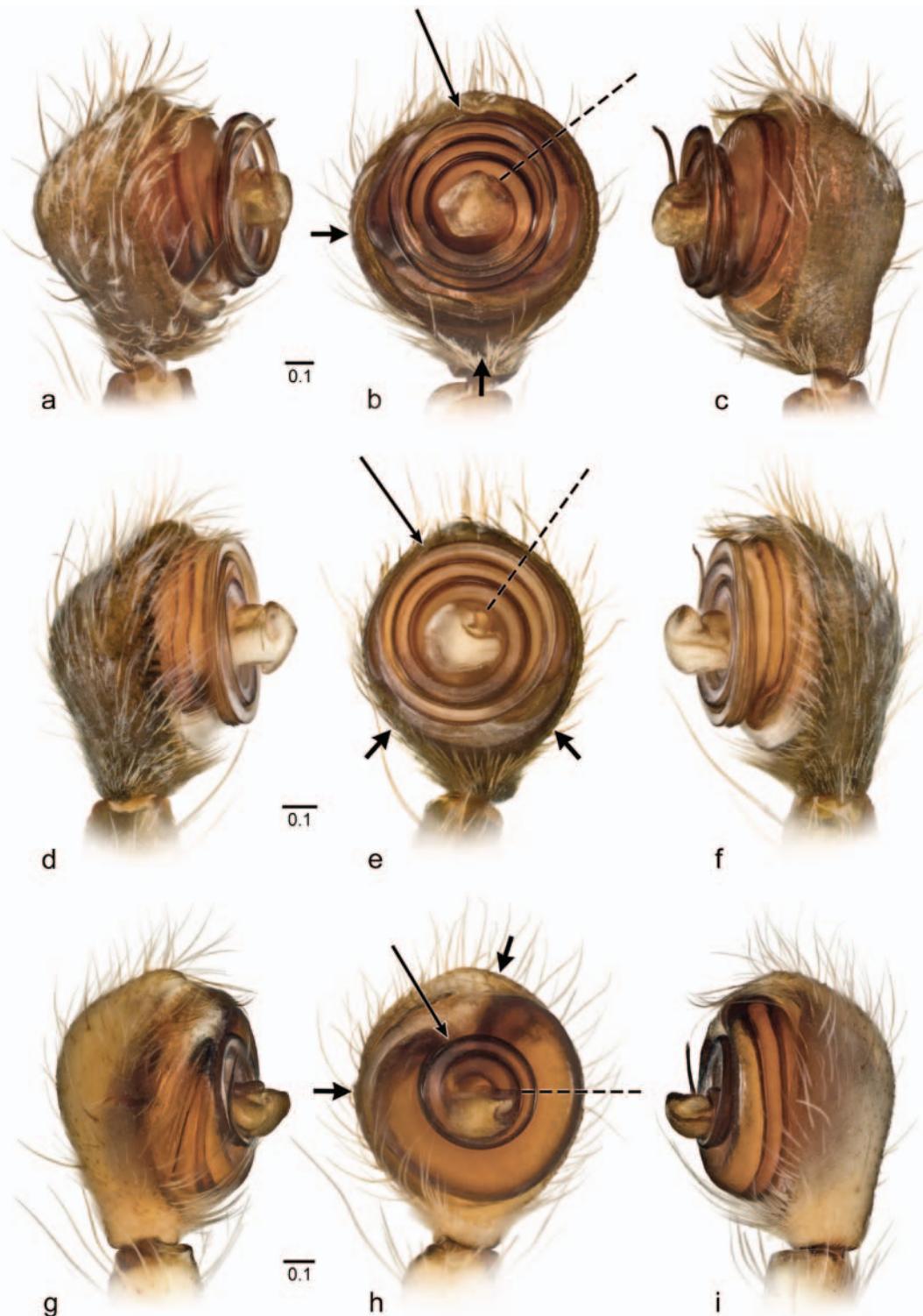
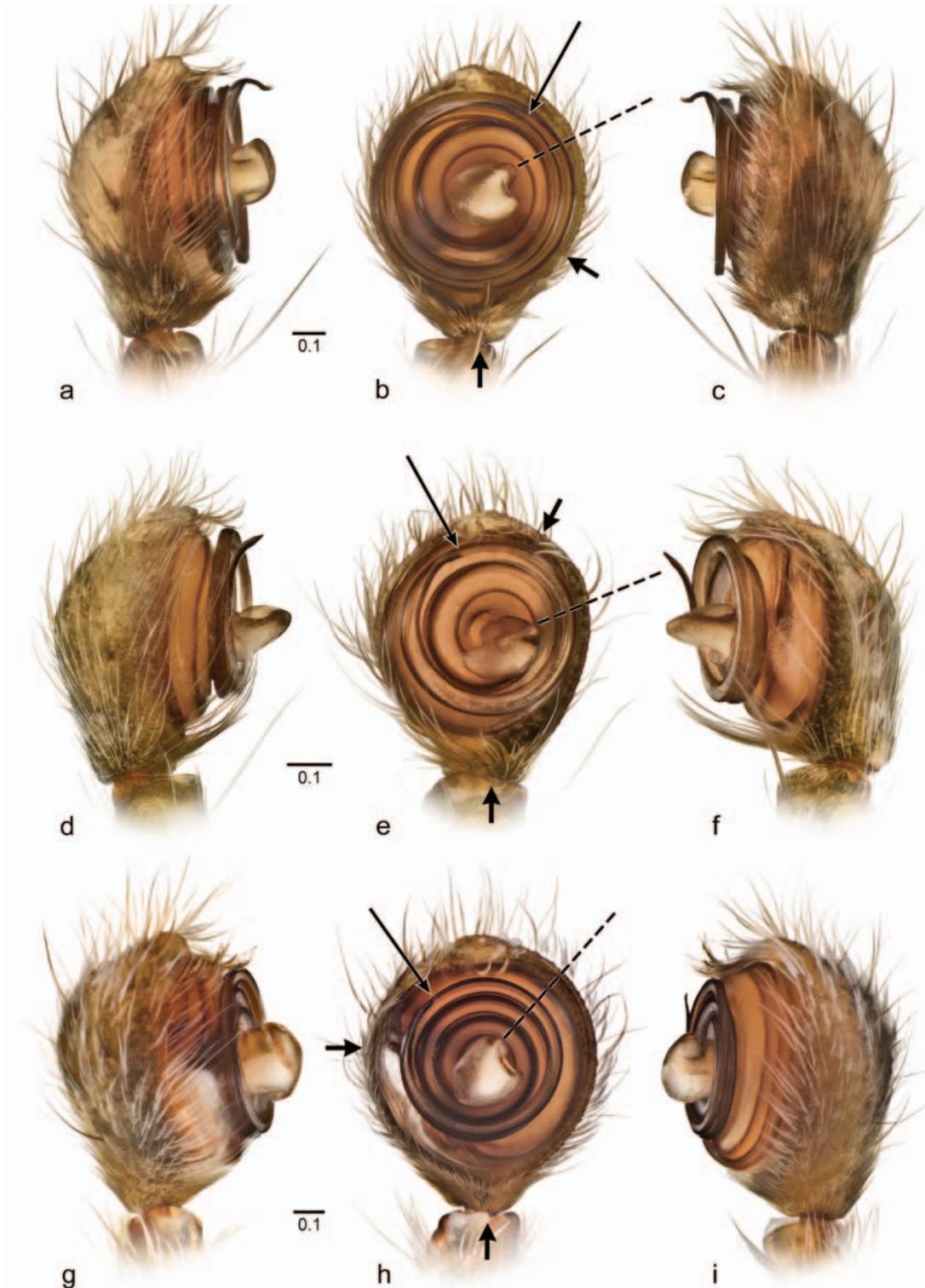


FIGURE 15. *Menneus* male left palps in (left) prolateral, (middle) ventral, and (right) retrolateral view: (a-c) *M. dromedarius*, (d-f) *M. samperi*, and (g-i) *M. tetragnathoides*. Diagnostic features of species in b, e, h: short bold arrows indicate extent of median hematodocha; long slender arrow indicates embolus tip; dashed line indicates the axis of the median apophysis and basal lobe.



**FIGURE 16.** *Menneus* male left palps in (left) prolateral, (middle) ventral, and (right) retrolateral view: (a–c) *M. aussie*, (d–f) *M. nemesio*, and (g–i) *M. neocaledonicus*. Diagnostic features of species in b, e, h: short bold arrows indicate extent of median hematodocha; long slender arrow indicates embolus tip; dashed line indicates the axis of the median apophysis and basal lobe.



**FIGURE 17.** *Menneus* male left palps in (left) prolateral, (middle) ventral, and (right) retrolateral view: (a–c) *M. superciliosus*, (d–f) *M. trinodosus*, and (g–i) *M. wa*. Diagnostic features of species in b, e, h: short bold arrows indicate extent of median hematodocha; long slender arrow indicates embolus tip; dashed line indicates the axis of the median apophysis and basal lobe.

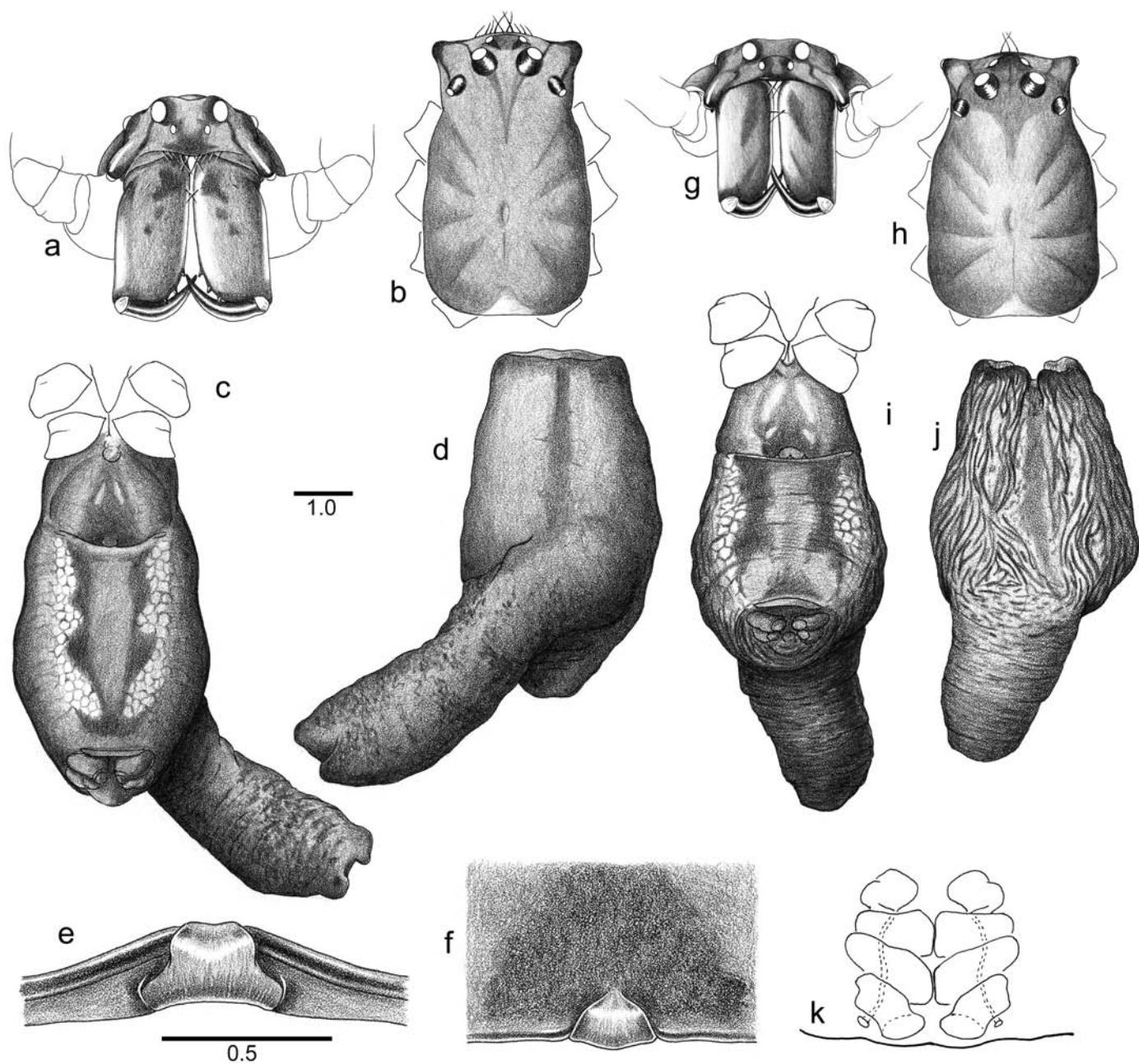


FIGURE 18. *Menneus camelus*: a-f are female from Dukuduku, KwaZulu-Natal; (a) prosoma, frontal; (b) prosoma, dorsal; (c) abdomen, ventral; (d) abdomen, dorsal; (e) epigynum, caudal; (f) epigynum, ventral; g-k are female from Pietermaritzburg, KwaZulu-Natal; (g) prosoma, frontal; (h) prosoma, dorsal; (i) abdomen, ventral; (j) abdomen, dorsal; (k) epigynum, dorsal.

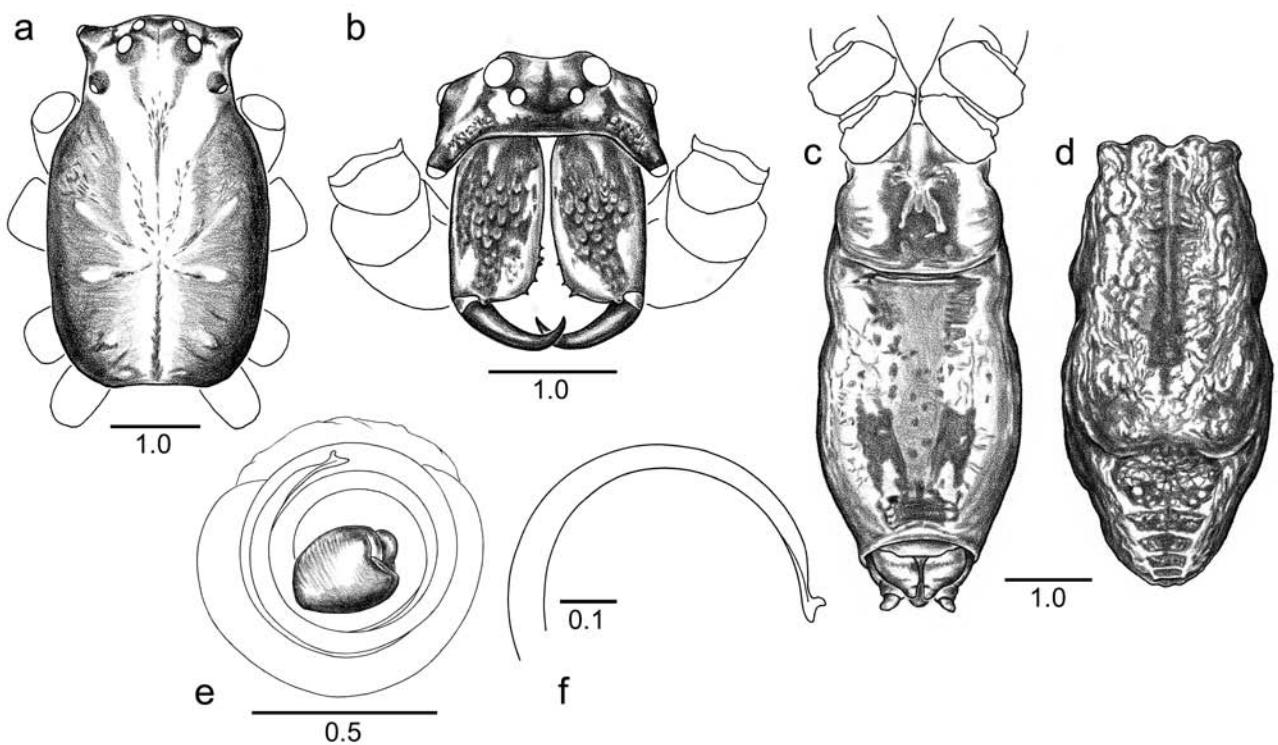
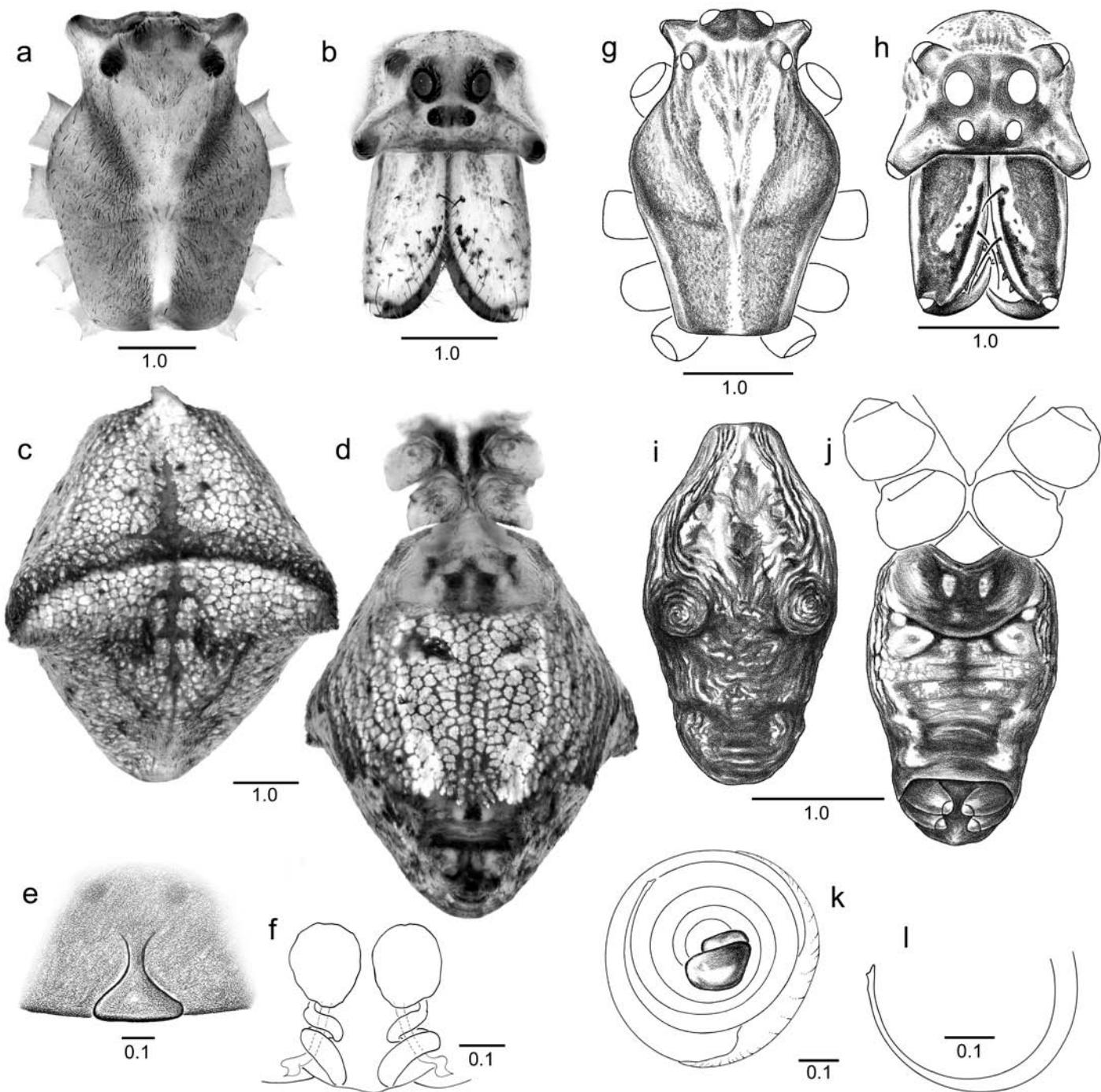


FIGURE 19. *Menneus camelus*, male from Amanzimtoti, KwaZulu-Natal: (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, ventral; (d) abdomen, dorsal; (e) left palpal bulb, ventral; (f) embolus tip.



**FIGURE 20.** *Menneus capensis*: a-f are female from Newlands Forest, Cape Town; (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; (e) epigynum, ventral; (f) epigynum, dorsal; g-l are male from Goudini, Cape Province; (g) prosoma, dorsal; (h) prosoma, frontal; (i) abdomen, dorsal; (j) abdomen, ventral; (k) left palpal bulb, ventral; (l) embolus tip.

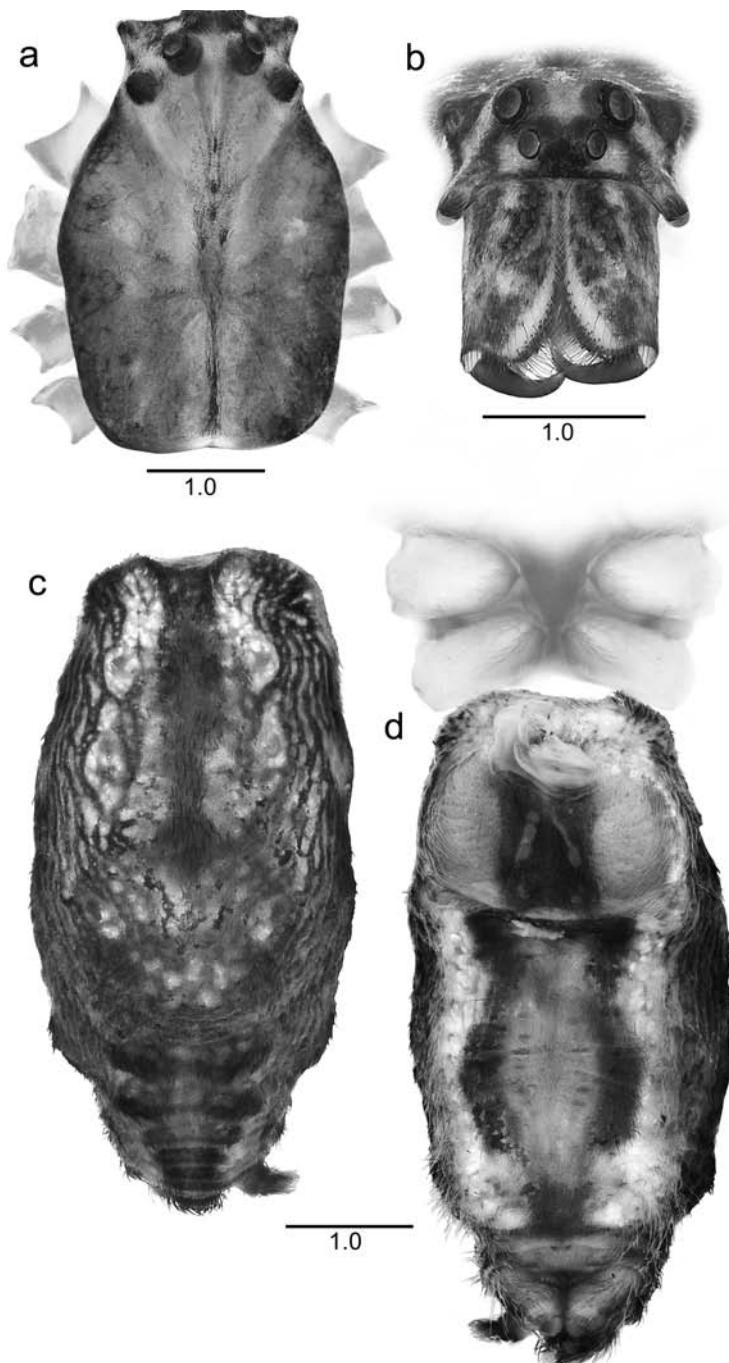
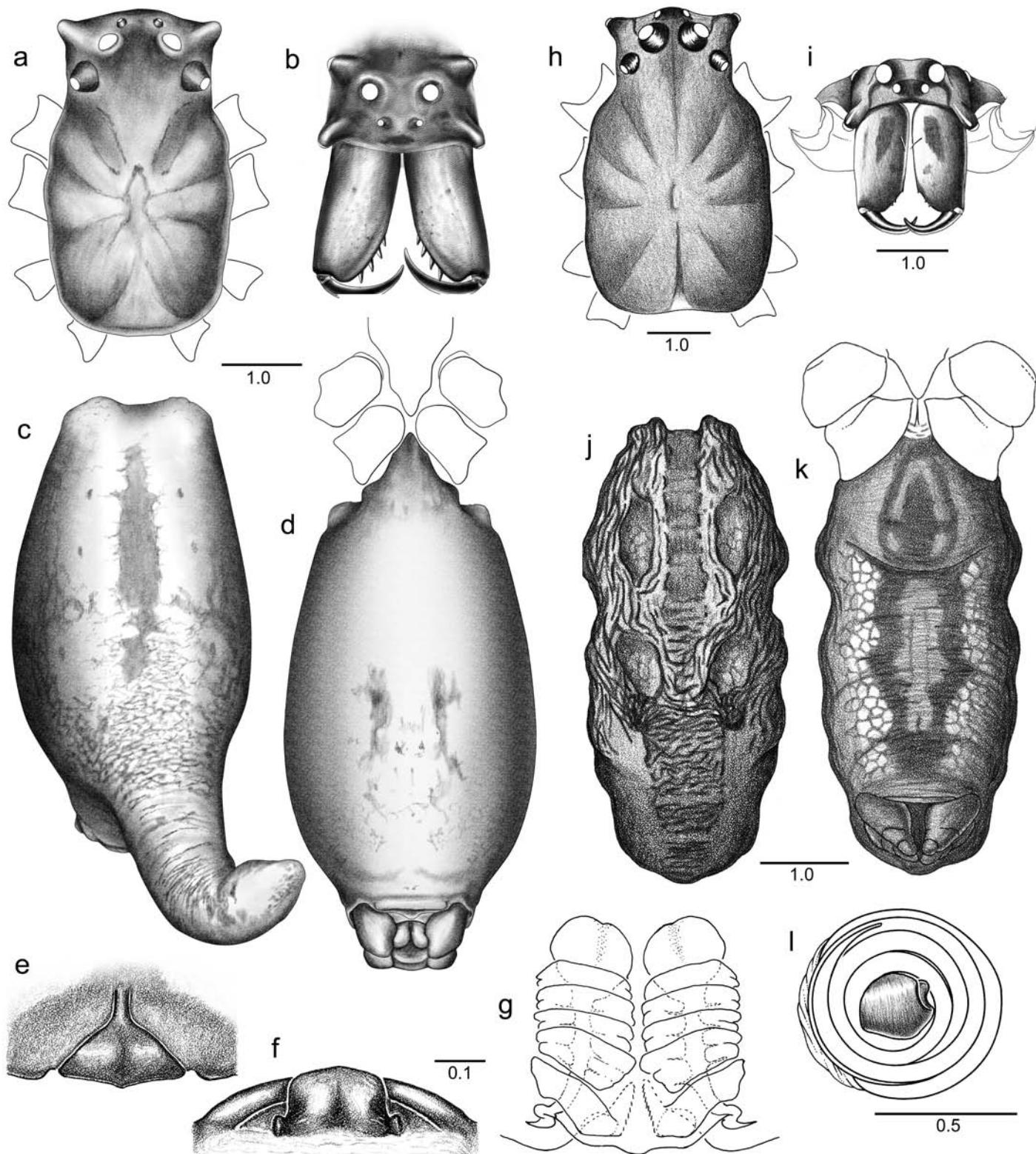


FIGURE 21. *Menneus darwini*, holotype male from Tanzania: (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral.



**FIGURE 22.** *Menneus dromedarius*: a–d are female from Table Mountain, South Africa; (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; e–g are epigynum of female from Kleinmond, South Africa; (e) ventral; (f) caudal; (g) dorsal; h–l are male from Grahamstown, South Africa; (h) prosoma, dorsal; (i) prosoma, frontal; (j) abdomen, dorsal; (k) abdomen, ventral; (l) left palpal bulb, ventral.

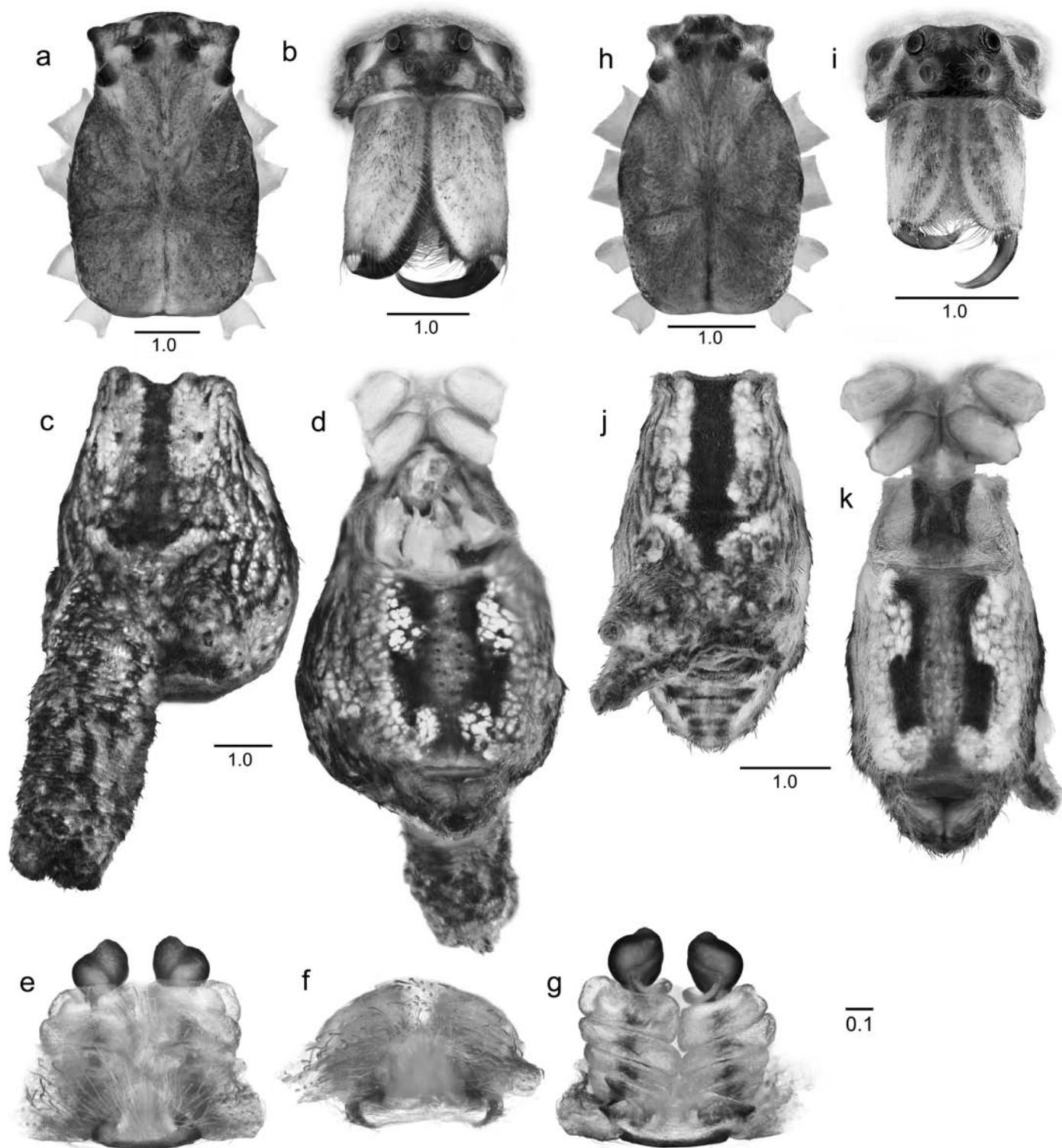


FIGURE 23. *Menneus samperi*: a–d are female from Tanzania; (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; e–g are epigynum of female from Uganda; (e) ventral; (f) caudal; (g) dorsal; h–k are male from Kenya; (h) prosoma, dorsal; (i) prosoma, frontal; (j) abdomen, dorsal; (k) abdomen, ventral.

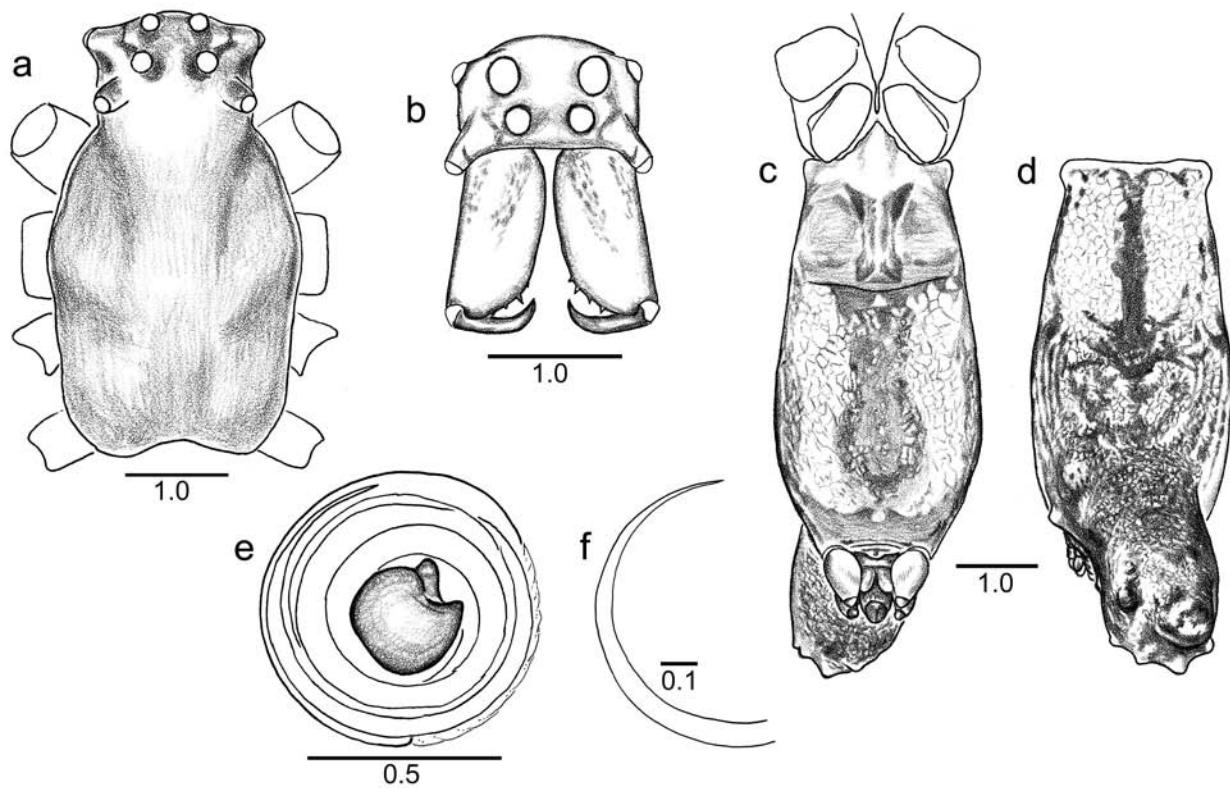


FIGURE 24. *Menneus tetragnathoides*, male from Chintheche, Malawi: (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, ventral; (d) abdomen, dorsal; (e) left palpal bulb, ventral; (f) embolus tip.

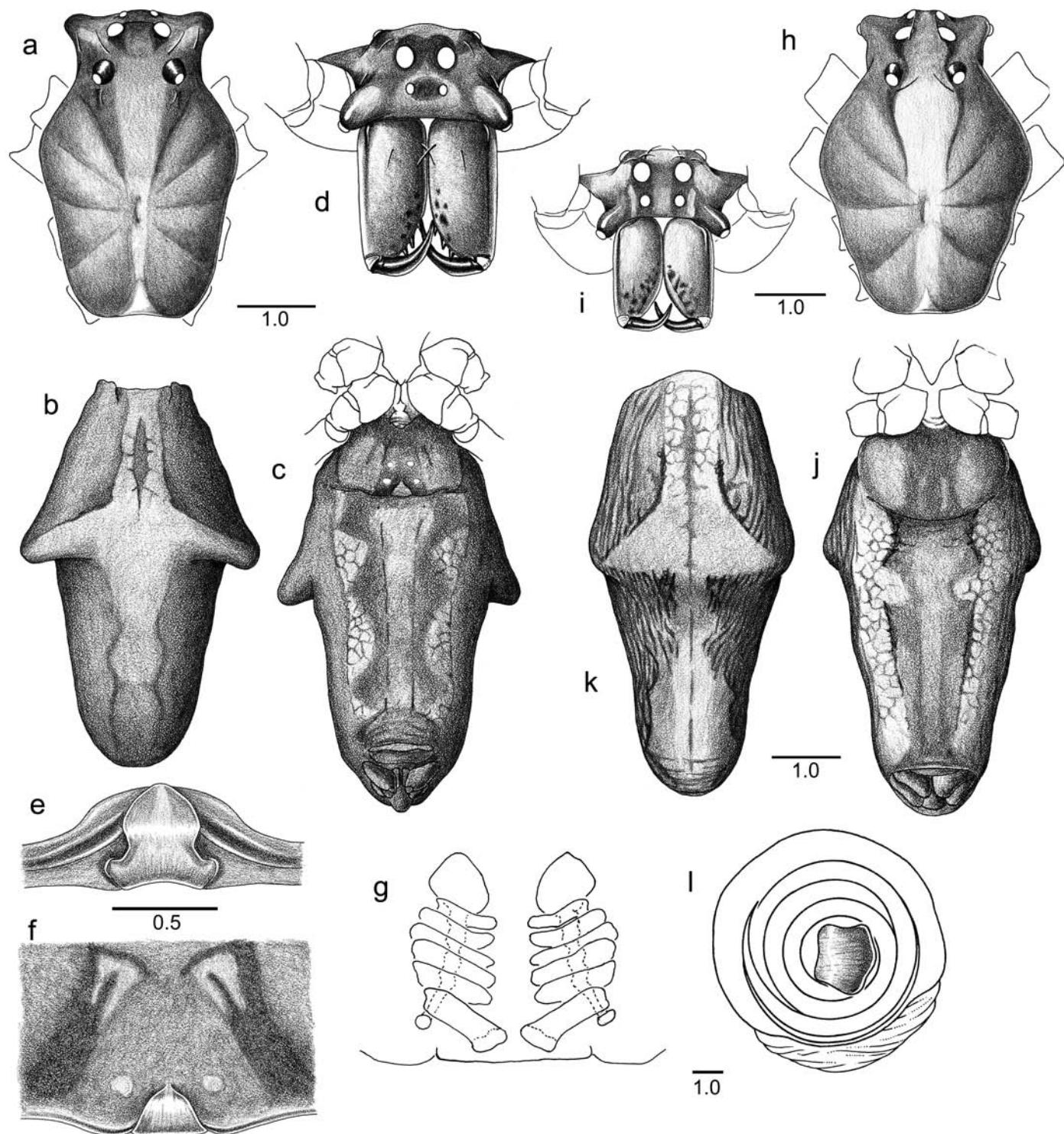


FIGURE 25. *Menneus aussie*: a–g are female from Manly, NSW; (a) prosoma, dorsal; (b) abdomen, dorsal; (c) abdomen, ventral; (d) prosoma, frontal; (e) epigynum, caudal; (f) epigynum, ventral; (g) epigynum, dorsal; h–l are male from Rundle Range, Queensland; (h) prosoma, dorsal; (i) prosoma, frontal; (j) abdomen, ventral; (k) abdomen, dorsal; (l) left palpal bulb, ventral.

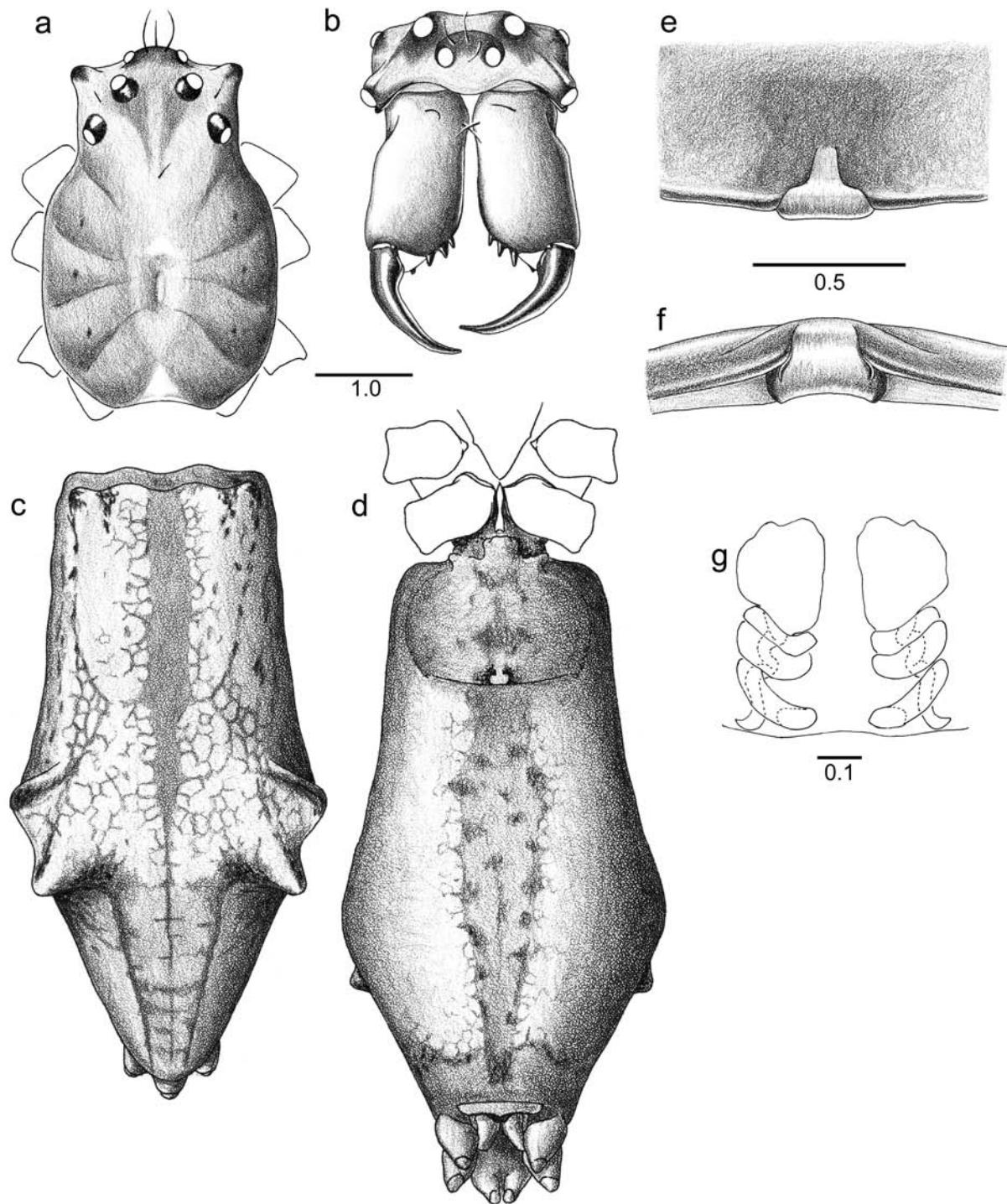


FIGURE 26. *Menneus bituberculatus*, female from Upper Brookfield, Queensland: (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; e–g are epigynum; (e) ventral; (f) caudal; (g) dorsal.

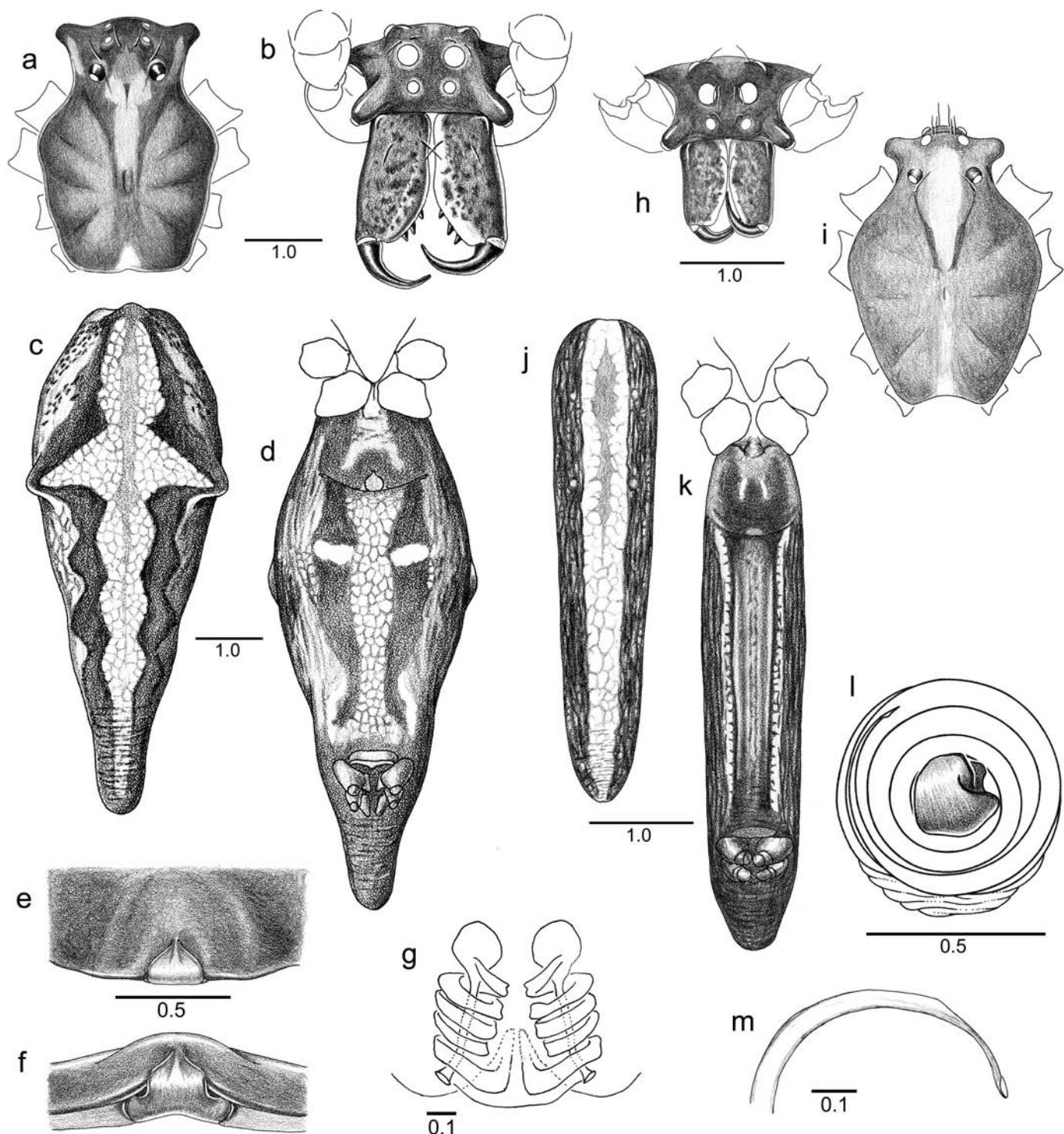
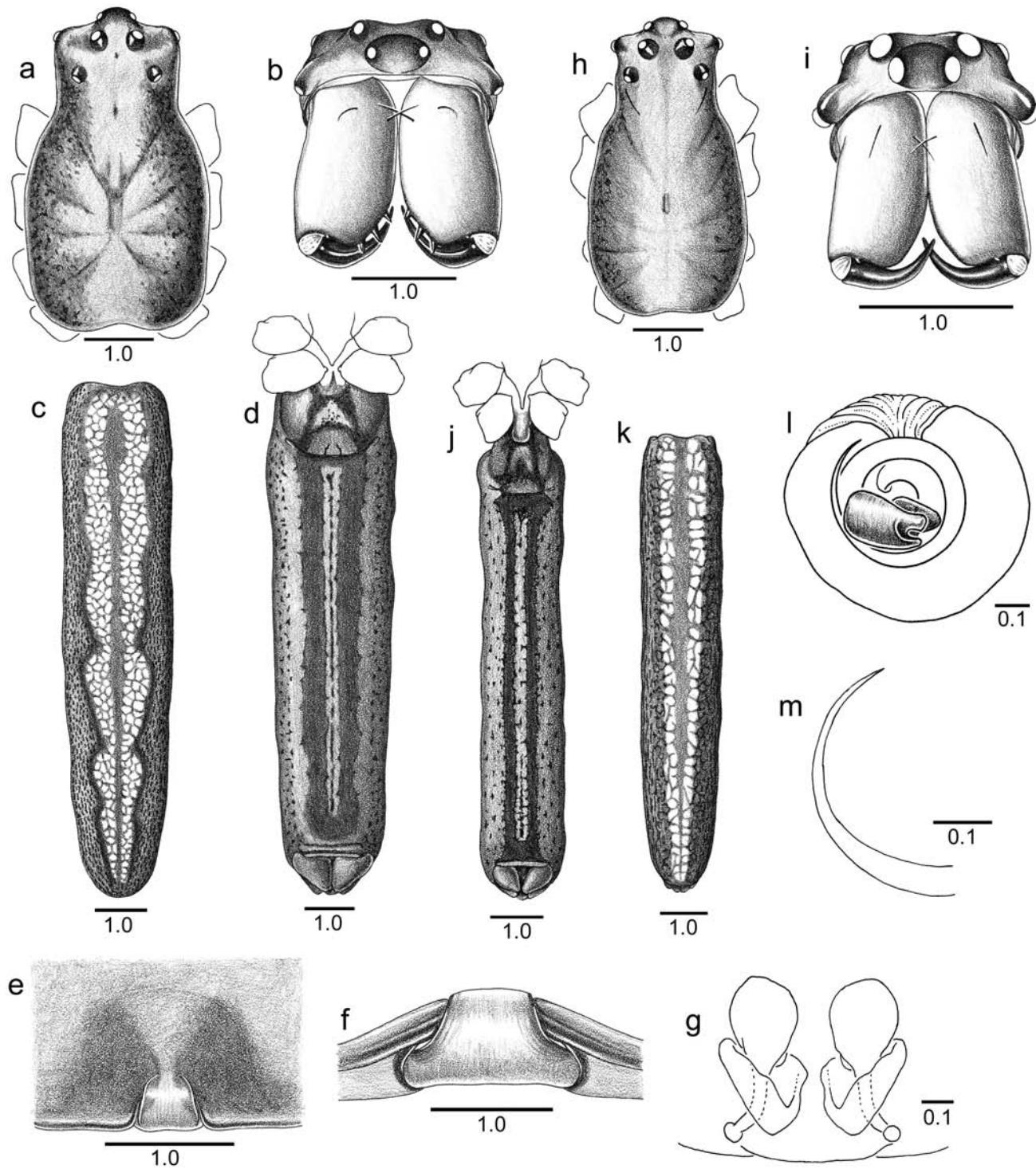


FIGURE 27. *Menneus nemesio*: a–g are female from Wamberal, New South Wales (NSW); (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; e–g are epigynum; (e) ventral; (f) caudal; (g) dorsal; h–m are male from Hawksburg, NSW; (h) prosoma, frontal; (i) prosoma, dorsal; (j) abdomen, dorsal; (k) abdomen, ventral; (l) left palpal bulb, ventral; (m) embolus tip.



**FIGURE 28.** *Menneus neocaledonicus* from Aoupinie, New Caledonia: a–g are female; (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; (e–g) are epigynum; (e) ventral; (f) caudal; (g) dorsal; h–m are male; (h) prosoma, dorsal; (i) prosoma, frontal; (j) abdomen, ventral; (k) abdomen, dorsal; (l) left palpal bulb, ventral; (m) embolus tip.

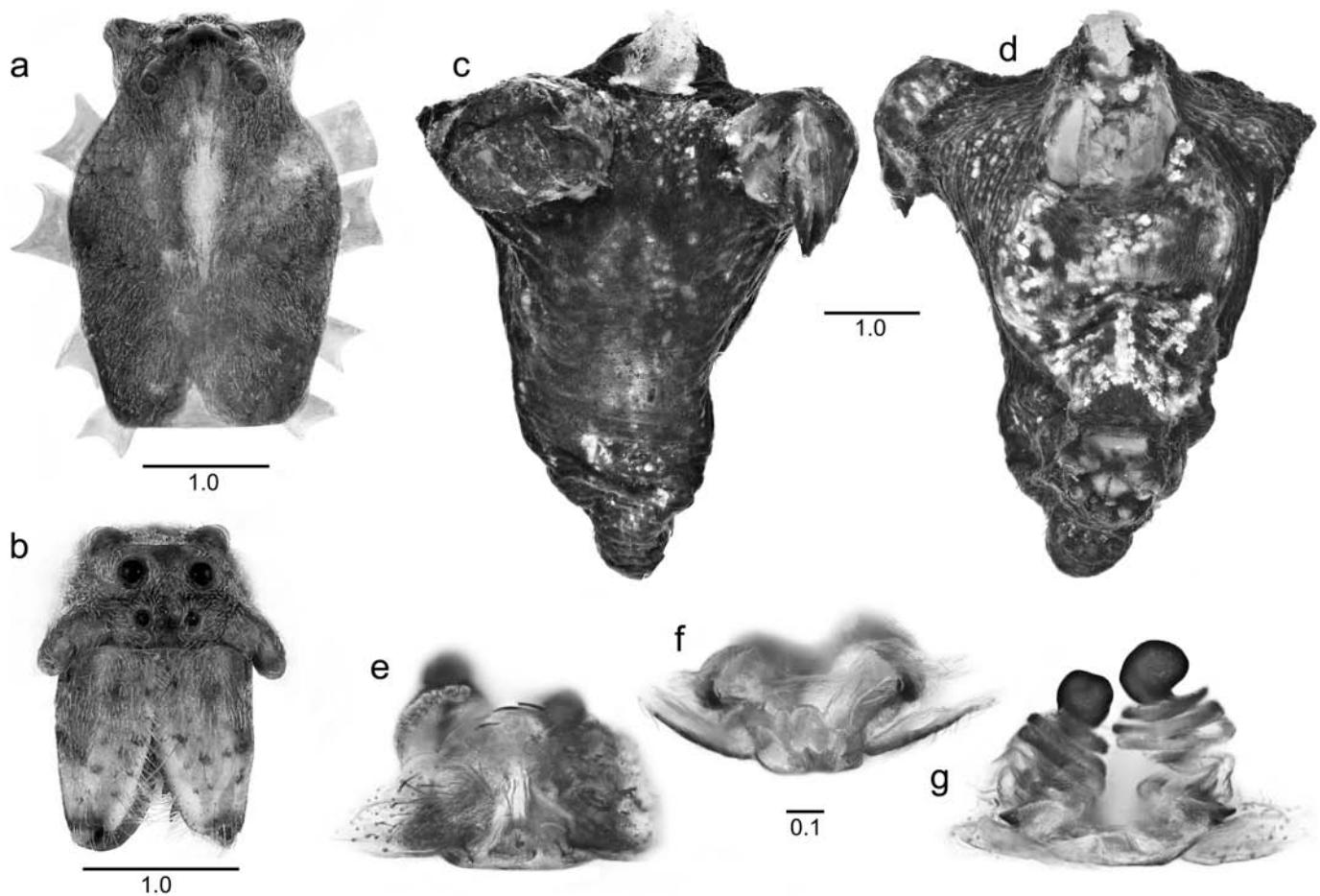


FIGURE 29. *Menneus quasimodo*, female from Western Australia: (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; e–g are epigynum; (e) ventral; (f) caudal; (g) dorsal.

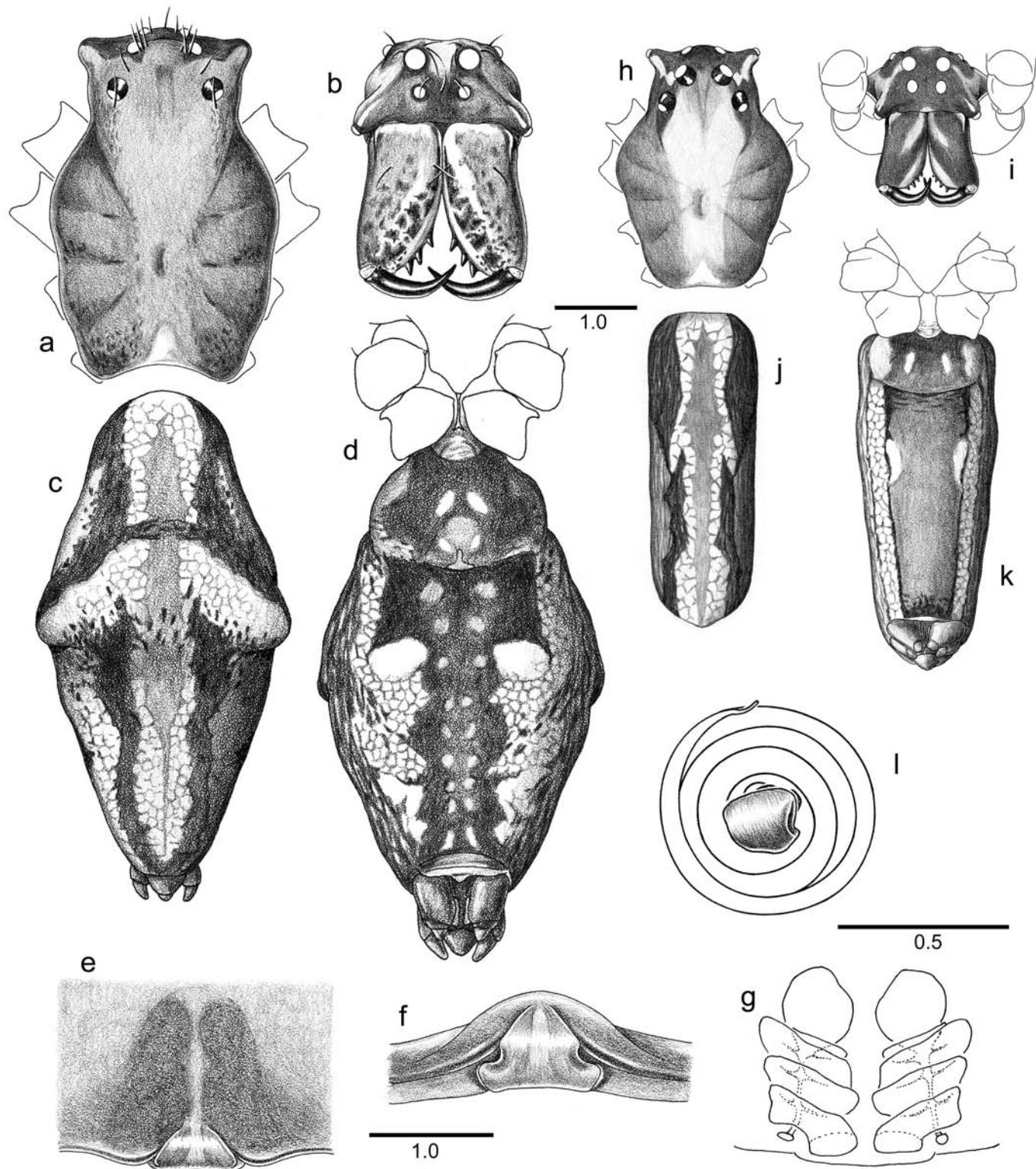


FIGURE 30. *Menneus superciliatus* from Edmonton, Queensland: a-g are female; (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; (e) epigynum, caudal; (f) epigynum, ventral; (g) epigynum, dorsal; h-l are male; (h) prosoma, dorsal; (i) prosoma, frontal; (j) abdomen, dorsal; (k) abdomen, ventral; (l) left palpal bulb, ventral.

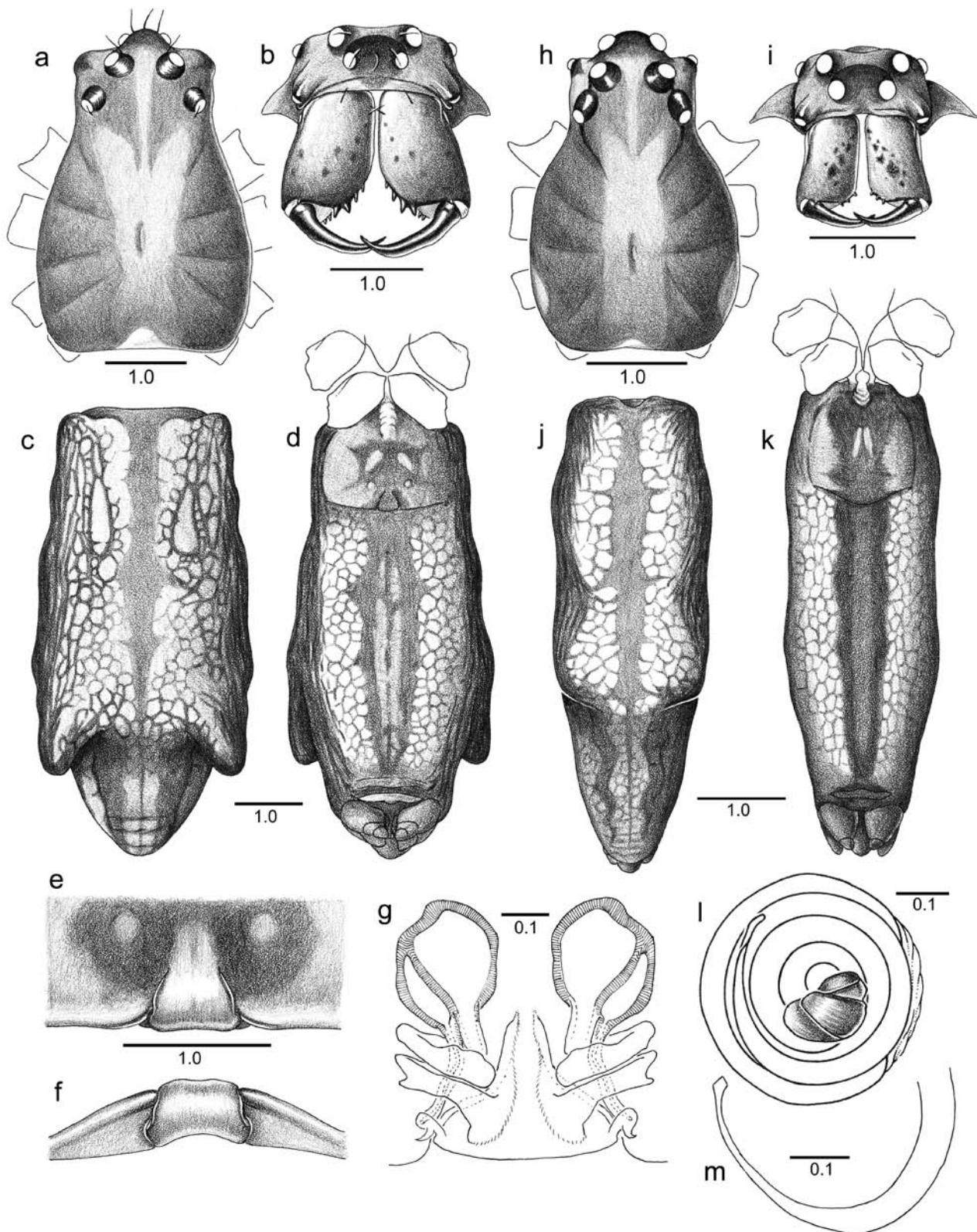


FIGURE 31. *Menneus trimodosus*, a–g are female from Eurimbula, Queensland; (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; e–g are epigynum; (e), ventral; (f) caudal; (g) dorsal; h–m are male from Bundaberg, Queensland; (h) prosoma, dorsal; (i) prosoma, frontal; (j) abdomen, dorsal; (k) abdomen, ventral; (l) left palpal bulb, ventral; (m) embolus tip.

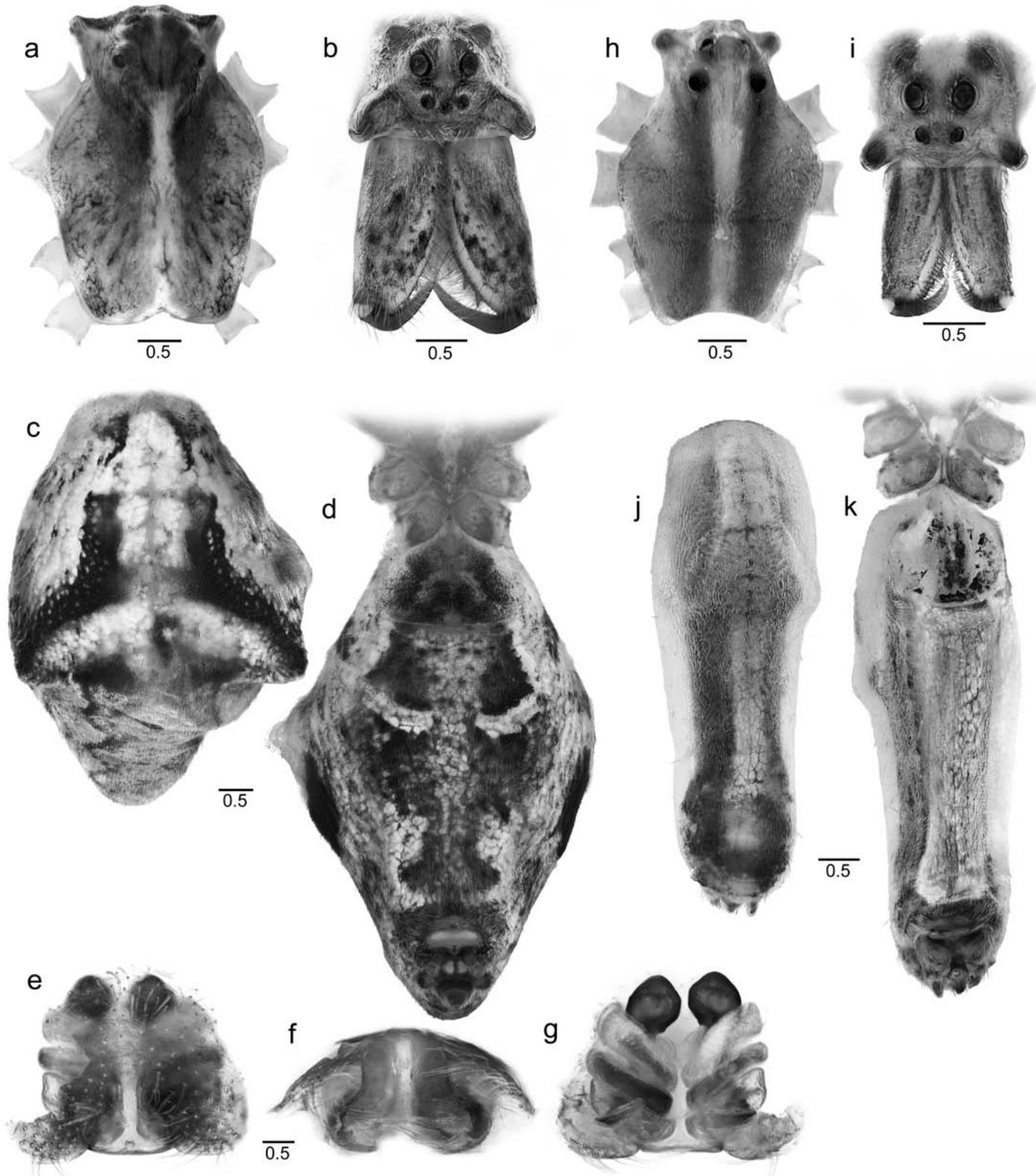


FIGURE 32. *Menneus wa*, from Western Australia: a–g are female; (a) prosoma, dorsal; (b) prosoma, frontal; (c) abdomen, dorsal; (d) abdomen, ventral; e–g are epigynum; (e) ventral; (f) caudal; (g) dorsal; h–k are male; (h) prosoma, dorsal; (i) prosoma, frontal; (j) abdomen, dorsal; (k) abdomen, ventral.

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