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Taxonomic Revision, Molecular Phylogeny and Zoogeography of the huntsman spider genus *Eusparassus* (Araneae: Sparassidae)

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I would like to dedicate my dissertation

to my family

for all their motivations, loves and supports,

in particular to my parents,

my wife Maryam and my son Bardia

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Abstract

The spider genus *Eusparassus* Simon, 1903 (Araneae: Sparassidae: Eusparassinae; stone huntsman spider) is revised worldwide to include 30 valid species distributed exclusively in Africa and Eurasia. The type species *E. dufouri* Simon, 1932 is re-described and a neotype is designated from Portugal. An extended diagnosis for the genus is presented. Eight new species are described: *Eusparassus arabicus* Moradmand, 2013 (male, female) from Arabian Peninsula, *E. educatus* Moradmand, 2013 (male, female) from Namibia, *E. reverentia* Moradmand, 2013 (male, female) from Burkina Faso and Nigeria, *E. jaegeri* Moradmand, 2013 (male, female) from South Africa and Botswana, *E. jocquei* Moradmand, 2013 (male, female) from Zimbabwe, *E. borakalalo* Moradmand, 2013 (female) from South Africa, *E. schoemanae* Moradmand, 2013 (male, female) from South Africa and Namibia and *E. mesopotamicus* Moradmand and Jäger, 2012 (male and female) from Iraq, Iran and Turkey. 22 species are re-described six of them are transferred from the genus *Olios* Walckenaer, 1837. Six species-groups are proposed: the *dufouri*-group [8 species: *E. dufouri*, *E. levantinus* Urones, 2006, *E. barbarus* (Lucas, 1846), *E. atlanticus* Simon, 1909, *E. syrticus* Simon, 1909, *E. oraniensis* (Lucas, 1846), *E. letourneuxi* (Simon, 1874), *E. fritschi* (Koch, 1873); Iberian Peninsula to parts of north-western Africa], *walckenaeri*-group [3 species: *E. walckenaeri* (Audouin, 1826), *E. laevatus* (Simon, 1897), *E. arabicus*; eastern Mediterranean to Arabia and parts of north-eastern Africa], *doriae*-group [7 species: *E. doriae* (Simon, 1874), *E. kronebergi* Denis, 1958, *E. maynardi* (Pocock, 1901), *E. potanini* (Simon, 1895), *E. fuscimanus* Denis, 1958, *E. oculatus* (Kroneberg, 1846) and *E. mesopotamicus*; Middle East to Central and South Asia], *vestigator*-group (3 species: *E. vestigator* (Simon, 1897), *E. reverentia*, *E. pearsoni* (Pocock, 1901); central to eastern Africa and an isolated area in NW India], *jaegeri*-group [4 species: *E. jaegeri*, *E. jocquei*, *E. borakalalo*, *E. schoemanae*; southern and south-eastern Africa], *tuckeri*-group [2 species: *E. tuckeri* (Lawrence, 1927), *E. educatus*; south-western Africa). Two species, *E. pontii* Caporiacco, 1935 and *E. xerxes* (Pocock, 1901) cannot be placed in any of the above groups. Two species are transferred from *Eusparassus* to *Olios*: *O. flavovittatus* (Caporiacco, 1935) and *O. quesitio* Moradmand, 2013. 14 species are recognized as misplaced in *Eusparassus*, thus nearly half of the described species prior to this revision were placed mistakenly in this genus. Neotypes are designated for *E. walckenaeri* from Egypt, *E. barbarus*, *E. oraniensis* and *E. letourneuxi* (all three from Algeria) to establish their identity. The male and female of *Cercetius perezi* Simon, 1902, which was known only from the immature holotype, are described for the first time. It is recognized that the monotypic and little used generic name *Cercetius* Simon, 1902 — a species, which had been known only from the immature holotype — as a synonym of the widely used name *Eusparassus*. The case proposal 3596 (conservation of name *Eusparassus*) is under consideration by ICZN.

The first comprehensive molecular phylogeny of the family Sparassidae with focus on the genus *Eusparassus* is investigated using four molecular markers (mitochondrial COI and 16S; nuclear H3 and 28S). The monophyly of *Eusparassus* and the *dufouri, walckenaeri* and *doriae* species-groups are recovered with the latter

two groups more closely related. The monophyly of the *tuckeri*-group is not supported and the position of *E. jaegeri* as the only available member of the *jaegeri*-group is not resolved within the *Eusparassus* clade. DNA samples of the *vestigator*-group were not accessible for this study. The origination of the genus *Eusparassus* around 70 million years ago (MA) is estimated according to molecular clock analyses. Using this recent result in combination with some biogeographic and geological data, the Namib Desert is proposed as the place of ancestral origin for *Eusparassus* and putative Eusparassinae genera.

Further analyses are done on the phylogenetic relationships of Sparassidae and its subfamilies. The Eusparassinae are not confirmed as monophyletic, with the two original genera *Eusparassus* and *Pseudomicrommata* in separate clades and only the latter clusters with most other assumed Eusparassinae, here termed the "African clade". Monophyly of the subfamilies Sparianthinae, Heteropodinae *sensu stricto*, Palystinae and Deleninae is recovered. The Sparianthinae are supported as the most basal clade, diverging considerably early (143 MA) from all other Sparassidae. The Sparassinae and genus *Olios* are found to be polyphyletic. The Sparassidae are confirmed as monophyletic and as most basal group within the RTA-clade. The divergence time of Sparassidae from the RTA-clade is estimated with 186 MA in the Jurassic. No affiliation of Sparassidae to other members of the 'Laterigradae' (Philodromidae, Selenopidae and Thomisidae) is observed, thus the crab-like posture of this group was proposed a result of convergent evolution. Only the families Philodromidae and Selenopidae are found members of a supported clade. Including a considerable amount of RTA-clade representatives, the higher-level clade Dionycha is not but monophyly of the RTA-clade itself is supported.

1. INTRODUCTION

It is estimated that nearly 8.7 million eukaryotic species are living on earth, of those 86% still await to be identified by taxonomists (Mora et al. 2011) and for spiders, the order Araneae, over 2/3 of their diversity is claimed to await discovery (Agnarsson et al. 2013). The accelerating biodiversity loss on earth provides an urgent need to increase the knowledge of the survived species diversity.

1.1. Motivation and preface to this study

It was in 2006 when I visited the Senckenberg Research Institute and Natural History Museum (SMF) during a short time scientific visit targeting taxonomy of the hermit crabs from the Persian Gulf (my MSc thesis at the University of Tehran), via “the Middle Eastern biodiversity network project” funded by the DAAD. Three years later (Sep 2009), I have awarded a PhD scholarship from the Ministry of Science, Research and Technology of Iran to study the taxonomy and phylogeny of spiders in SMF as a student of the Goethe University, Frankfurt am Main. There were three main reasons for this shift (from crabs to spiders). First was my great interest in Arachnida. Secondly I found studying taxonomy of spiders a research gap area not even in Iran but also in the entire Middle Eastern countries where the spider fauna is so diverse and unique but at the same time not well investigated. Third reason points toward SMF itself that houses one of the richest spider collections in the world and employed a renowned spider taxonomist such as Dr Peter Jäger. I have had a great opportunity to learn about taxonomy, nomenclature and systematics as well as phylogeny, biogeography and evolutionary history of spiders in general and Sparassidae in detail.

The huntsman spiders or giant crab spiders of the family Sparassidae Bertkau, 1872 are among the most diverse families of spiders. Despite they comprises the largest spiders in the world, most of the genera are not investigated. For instance, it is surprising that of the 33 genera known from Africa just two have been revised prior to this study. The genus *Eusparassus* Simon, 1903 is one of these unrevised genera. *Eusparassus* was previously included 29 nominal species, a heterogeneous assemblage of taxa. They are distributed from Africa to parts of Eurasia. Moreover, *Eusparassus* is unique among the sparassid genera by having a well preserved fossil

dated back to the Eocene era (Dunlop et al. 2011). All these facts highlight the genus as a fruitful subject for a taxonomic, phylogenetic and biogeographic study.

I have started my research on spiders by revising the cave dwelling genus *Spariolenus* Simon, 1880 in Iran leading to the description of four new species (Moradmand and Jäger 2011). Then I focused on the taxonomic revision of *Eusparassus* which resulted in two revisionary publications (Moradmand and Jäger 2012a; in Eurasia) and (Moradmand 2013; in Africa and Arabia) and one case proposal to the International Commission on Zoological Nomenclature (ICZN) (Moradmand and Jäger 2012b). I presented three lectures and one poster of my results in International (2010, Poland: Siedlce) and European (2012, Slovenia: Ljubljana) congresses and also two talks as scientific visitor in 2011 at the Natural History Museum (NHM London) and in 2012 at the Royal Museum for Central Africa (MRAC Tervuren). These two latter scientific visits were sponsored by SYNTHESYS for studying the type series at noted spider collections. The most time consuming task during the revision was to find and borrow the (sometimes hidden) type material from various collections in Europe and Africa. Additionally to NHM and MRAC, I had an opportunity to visit the rich spider collections of the Muséum National d'Histoire Naturelle (MNHN Paris), Zoological Museum, University of Copenhagen (ZMUC) and Museum für Naturkunde (ZMB Berlin). I have learnt new scientific methods and techniques by participating in the "Phylogenetic systematics and molecular dating course" in ZMUC (2011), the "Geographic Information System" (GIS) workshop and the "Species Distribution Modelling" (SDM) course which two latter were held in GRADE (Goethe Graduate Academy, Frankfurt).

After performing the taxonomic review, I classified *Eusparassus* species into species-groups and tried to raise evolutionary hypotheses about speciation, relationships of species-groups, historical biogeography and the systematic position of the genus *Eusparassus* within the Sparassidae (see chapter 3.2). To verify these hypotheses I focused on molecular phylogeny and molecular clock analyses (see chapter 3.3). Additionally to *Eusparassus*, the range of the sampled taxa expanded gradually while my study was the first comprehensive phylogenetic analysis on Sparassidae as well. Thus, representatives of other Eusparassinae genera in particular and Sparassidae in general were included in my research as well as members of the RTA-clade (see chapter 3.3).

1.2. General introduction to spider classification

Spiders, Order Araneae, are one of the most diverse groups of animals belonging to the class Arachnida. They are chelicerate arthropods and share the trait chelicerae with other well-known orders, i.e. Scorpiones, Opiliones and Acari (Foelix 2010). Currently, taxonomists classified more than 44,000 known spider species into 112 families (Platnick 2013). The Araneae are divided into three suborders: Mesothelae (the oldest group with autplesiomorphic character, e.g. segmented opisthosoma), Mygalomorphae (Tarantulas and their relatives) and Araneomorphae. The Araneomorphae exhibit a vertical form of fangs (labidognath) in comparison to Mygalomorphae which have parallel fangs (orthognath).

The Araneomorphae include the majority (>90%) of spider species (Foelix 2010). Some of them have a special spinning plate close to spinnerets named cribellum. Araneomorphae with and without cribellum are called cribellate and ecribellate, respectively. According to the complexity of the copulatory structures, Eugene Simon in his “Historie Naturelle des Araignées” (1892–1903), separated the ecribellate spiders into haplogynes (simple copulatory organs) and entelegynes (complex copulatory organs). Entelegynes are usually divided into Trionycha (legs with three tarsal claws) and Dionycha (legs with two tarsal claws). Another higher level synapomorphy among a relatively large group of entelegynes is the retrolateral tibial apophysis on the male palpal tibia (RTA). The group with representatives sharing this character is called RTA-clade (Coddington and Levi 1999).

Within RTA-clade, four families: Sparassidae Bertkau, 1872 (giant crab spiders), Selenopidae Simon, 1897 (wall crab spiders), Philodromidae Thorell, 1870 (running crab spiders) and Thomisidae Sundevall, 1833 (“true” crab spiders) are grouped under name ‘Laterigradae’. They share the character of laterigrade legs which characterize by a crab-like posture (Latreille 1802). As noted above, most of the spider classification dates back to 19th century and as mentioned by Foelix (2010) that the “...natural system of classification is still very much a matter of controversy”.

1.3. Family Sparassidae

The family of huntsman spiders or giant crab spiders, Sparassidae, are composed of small to very large hunting spiders occurring worldwide. Living in various habitats from humid rain forest of Amazon to arid sand dunes of Sahara (Jäger and Kunz 2005; Rheims 2010) and from sea level to high altitudes (~4000) (Moradmand and Jäger 2012a), they represents one of the highly diverse and successful groups of spiders. Sparassidae currently comprises 85 genera and 1132 described species (Platnick 2013). According to previous section on spider classification, Sparassidae are araneomorph, ecribellatae and entelegyne spiders. They are considered dionychans and placed in the RTA-clade but their systematic position and relationships to other families is unclear (Agnarsson et al. 2013).

Simon (1897, 1903), Järvi (1912-1914), Petrunkevitch (1928) and Roewer (1954) proposed classifications for Sparassidae. Simon (1897) classified Sparassidae in seven sub groups (Sparassinae, Heteropodinae, Palystinae, Staianinae, Sparianthinae, Clastinae and Chrosiodermatinae). Hogg (1903) placed most of the Australian endemic genera in his new group Deleninae. Simon (1903) proposed a new subfamily Tibellomatinae. Järvi (1912-1914) proposed Eusparassinae, Polybetinae and Micrommatinae using exclusively the female copulatory characters while previously just those of somatic characters for classification including eyes arrangement and shape of body were applied. Petrunkevitch (1928) combined Polybetinae and Deleninae under Eusparassinae. Croeser (1996) revised Palystinae and Jäger (1998) proposed synapomorphies for Heteropodinae and Sparianthinae. But, the status of the majority of Sparassidae subfamilies is still unknown. Moreover, the majority of the Sparassidae genera are not revised and consequently the systematic position of them within the family is quite unknown. The monophyly of the family and currently known subfamilies has never been tested excluding for the endemic Australian subfamily Deleninae (Agnarsson and Rayor 2013).

1.4. Genus *Eusparassus* and Eusparassinae, a historical review

The genus *Eusparassus* was erected by Simon (1903) and the type species is *Eusparassus dufouri* Simon, 1932. The designation of the type species of *Eusparassus* has a long and a relatively complicated history. It was due to the

problematic generic name *Sparassus* Walckenaer, 1805 and specific name *argelasius* by Walckenaer (1805). The original description of the genus *Sparassus* was based on five species currently placed in three genera: three species now in the genus *Micrommata* Latreille, 1804 [sub *S. samaragdulus* (Fabricius, 1793), *S. roseus* (Clerck, 1757) and *S. ornatus* (Walckenaer, 1802)], a juvenile of *Heteropoda venatoria* (Linnaeus, 1758) [sub *S. pallens* (Fabricius, 1794)] and a single male of the genus *Olios* Walckenaer, 1837 (sub '*Sparassus argelasius*') from Bordeaux, France. Walckenaer (1805) presented no description of '*S. argelasius*' which is therefore a nomen nudum. The following year, Walckenaer (1806) provided a description and illustration of this male under the name *Sparassus argelasius*. Although Simon (1903) doubted that *Sparassus* was a junior synonym of *Micrommata*, Jäger (1999) proposed the synonymy of *Sparassus* with *Micrommata*. Latreille (1818) examined two female specimens from Spain and described them under the name '*Micromata argelasia*' (*Micromata* is an incorrect original spelling of *Micrommata* in Latreille (1804)). Unfortunately he misidentified the species (Walckenaer's male was an *Olios* species and Latreille's female was an *Eusparassus* species). Simon (1903) established his new genus *Eusparassus*, and designated Latreille's (1818) misidentified *Micrommata argelasia* female specimens as the type species. The misidentification by Latreille (1818) was pointed out by Simon (1932) who described *E. dufouri* as the type species of the genus *Eusparassus* referring to the misidentified Spanish females of Latreille (1818). Simon (1932) was the first reviser of this case who also presented a description and illustration of Walckenaer's '*Sparassus argelasius*' under the generic name *Olios*. The type species of *Eusparassus* was misidentified under the name '*E. argelasius*', thus *dufouri* was selected as the valid specific name for the type species of the genus *Eusparassus* by Simon (1932).

For the reasons mentioned above, *Eusparassus* and *Olios* were not explicitly diagnosed to date and many misidentifications and misplacement are expected. Even some contributors used the generic name *Sparassus* (e.g. Levy 1989) for *Eusparassus* species following Bonnet (1958). Levy (1989) in a brief review on some *Eusparassus* species (sub *Sparassus*) re-described *E. walckenaeri* (Audouin, 1826) and proposed some diagnostic characters to identify *Eusparassus* species (e.g. female vulva and colouration of ventral opisthosoma). Prior to current study, *Eusparassus* comprised 29 nominal species (Platnick 2013) (see Table 1) and most of them were known by a single sex and by their original description.

Table 1. The nominal species of *Eusparassus* known prior to this revision (modified from Platnick catalogue).

	sex	*Eusparassus* species	Synonyms	records
1	male, female	*barbarus* (Lucas, 1846)		Algeria
2	male	*bicorniger* (Pocock, 1898)		East Africa
3	juvenile	*concolor* Caporiacco, 1939		Ethiopia
4	male	*cornipalpis* Strand, 1906		Ethiopia
5	male, female	*dufouri* Simon, 1932 *		Western Mediterranean
6	male, female	*dufouri atlanticus* Simon, 1909		Morocco
7	male, female	*dufouri maximus* Strand, 1906		Algeria, Tunisia
8	juvenile	*flavovittatus* Caporiacco, 1935		Karakorum
9	male, female	*fulviclypeus* Strand, 1906		Ethiopia
10	male, female	*fuscimanus* Denis, 1958		Afghanistan
11	juvenile	*laterifuscus* Strand, 1908		Madagascar
12	male, female	*letourneuxi* (Simon, 1874)		Algeria, Tunisia
13	male, female	*levantinus* Urones, 2006		Spain
14	male	*lilus* Strand, 1907		Java
15	male, female	*nanjianensis* (Hu and Fu, 1985)		China
16	female	*nigrichelis* Strand, 1906		Ethiopia
17	male, female	*oculatus* (Kroneberg, 1875)		Central Asia
18	male, female	*oraniensis* (Lucas, 1846)	*Ocypete fritschi* Koch, 1837	North Africa
19	female	*palystiformis* Strand, 1907		South Africa
20	female	*pontii* Caporiacco, 1935		Karakorum
21	male	*potanini* (Simon, 1895)		China
22	female	*quinquedentatus* Strand, 1906		West Africa
23	male	*rufobrunneus* Caporiacco, 1941		Ethiopia
24	juvenile	*sexdentatus* Strand, 1906		West Africa
25	female	*shefteli* Chamberlin, 1916		Peru
26	juvenile	*subadultus* Strand, 1906		Ethiopia
27	male, female	*syrticus* Simon, 1909		Algeria, Tunisia
28	female	*ubae* Strand, 1906		East Africa
29	male, female	*walckenaeri* (Audouin, 1826)	*Sparassus doriae* Simon, 1874; *E. kronebergi* Denis, 1958	Eastern Mediterranean to Afghanistan

Moreover, the diagnostic characters within *Eusparassus* species were incomplete. Early diagnoses for *Eusparassus* species were based mostly on

unreliable and variable somatic characters. *Eusparassus* is currently placed in Eusparassinae along with some proposed African genera. But, the systematic position of *Eusparassus* and Eusparassinae genera within Sparassidae is uncertain, since the majority of the Sparassidae genera are not revised to date. Simon (1897) placed *Euparassus* (sub *Sparassus*) in Sparassinae. After creating the genus *Eusparassus*, Simon (1903) placed it along with several other genera in Delenineae. Järvi (1912) proposed the new subfamily Eusparassinae (sub “Eusparasseae”) for *Eusparassus* along with the genera *Pseudomicrommata* Järvi, 1914 and *Rhitymna* Simon, 1897. Jäger and Kunz (2003) proposed the re-establishment of Eusparassinae by noting some synapomorphies and supposed that some endemic African genera to be potentially included in this subfamily. The systematics of these taxa is obscure and no comprehensive taxonomic revision has been carried out so far.

1.5. Aims of my dissertation

The aims of this dissertation are:

First, to revise the genus *Eusparassus* Simon 1903 (Araneae: Sparassidae) in its entire geographical distribution, to define the genus and to clarify the status of its species and to propose species-groups, based on morphological characters of somatic and copulatory organs.

Second, to apply a wide range of molecular markers of the broadest possible sample of *Eusparassus* species and Sparassidae genera (with focus on Eusparassinae) to test the monophyly of the morphologically proposed species-groups, genus *Eusparassus*, subfamily Eusparassinae and family Sparassidae, and also to clarify the position of *Eusparassus* within Sparassidae and subsequently Sparassidae within RTA-clade by reconstructing phylogenetic trees.

Third, to explore the phylogenetic relationships associated with the distributional patterns and geological events to propose evolutionary scenarios for the origin of *Eusparassus* and its zoogeography.

2. MATERIAL AND METHODS

2.1. Morphological studies

Specimens for morphological investigation were mostly obtained from the large spider collections (public and private) in Europe, Africa and North America (see list of “collections and curators” in chapters 3.1 and 3.2).

Examination, measurements and illustration of the specimens were performed using a Leica MZ 165C stereomicroscope equipped with a drawing tube. Measurements included the prosoma, opithosoma and all leg joints as well as eyes and all eye distances. The diagnostic characters were illustrated and/or photographed including somatic characters: chelicerae (ventral view), anterior part of prosoma focusing on eyes (dorsal view) and copulatory characters: male palp (three views: prolateral, ventral, retrolateral), female epigyne (dorsal and ventral views) and vulvas (anterio-dorso-lateral view). Male palps were dissected from patella joint and were observed in 70% ethanol. Using forceps and fine needles, the hairs covering the bulb and the base of RTA were removed for a better view on the structures. Female epigynes after dissection and cleaning from hairs and soft tissue surrounding vulva were submerged in 96% lactic acid for clear observation of the internal duct system. A Canon EOS 50D installed on the Microscope was used to photograph the specimens and their structures. Details of characters used for the descriptions and diagnoses of *Eusparassus* are summarized in Fig. 1.

Subsequent art works on the illustrated and photographed characters were carried out by computer programs Adobe Photoshop CS3, CorelDRAW X5 and Inkspace.

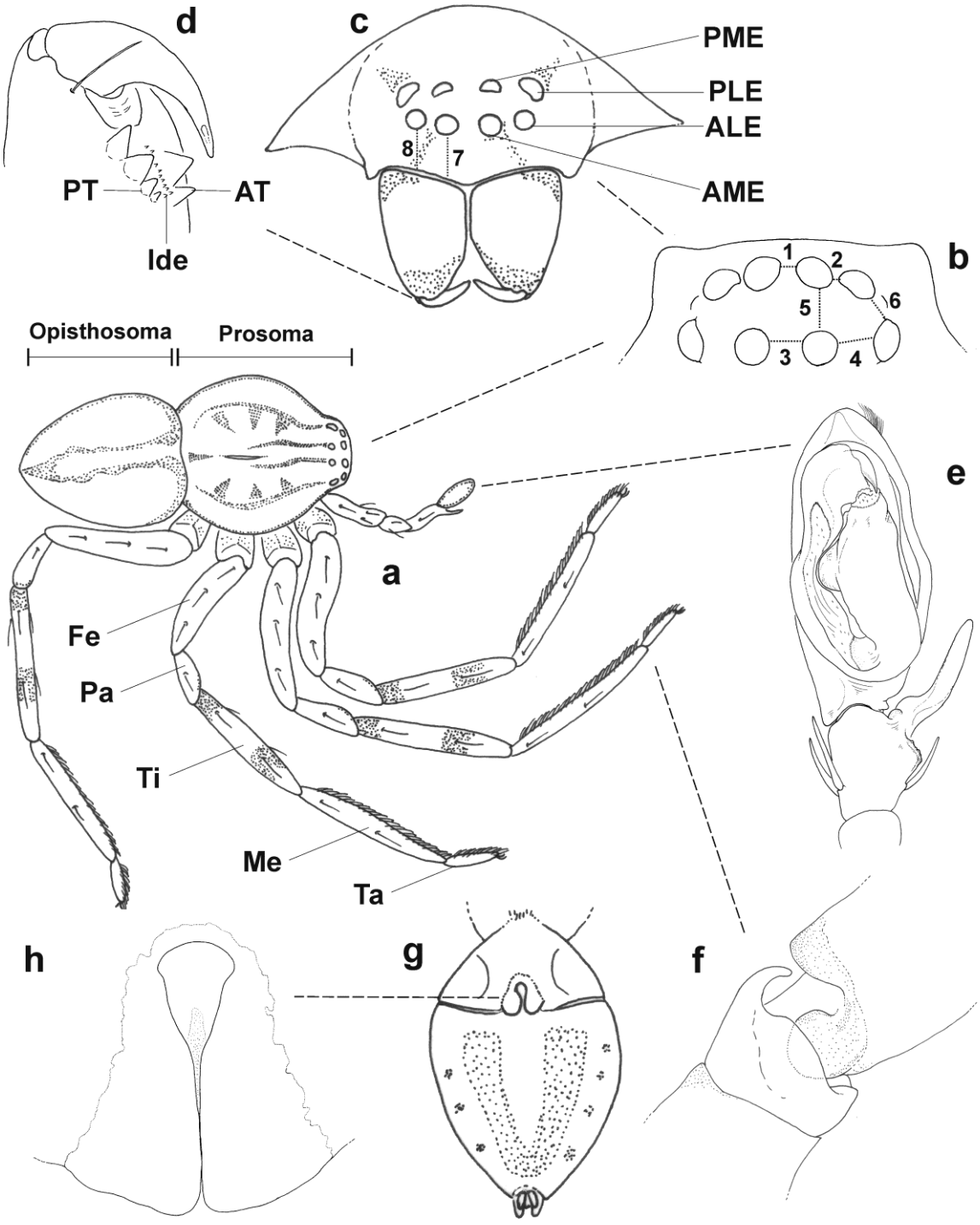

FIGURE 1. Schematic illustration of the structures used for examination, measurements and description of *Eusparassus* sp. (a) specimen, dorsal view, Fe: femur, Pa: patella, Ti: tibia, Me: metatarsus, Ta: tarsus; (b, c) eye arrangement and measurement areas: AME: anterior median eyes, ALE: anterior lateral eyes, PME: posterior median eyes, PLE: posterior lateral eyes; 1 AME-AME, 2 AME-ALE, 3 PME-PME, 4 PME-PLE, 5 AME-PME, 6 ALE-PLE, 7 clypeus height at AME, 8 clypeus height at ALE (b dorsal view, c frontal view); (d) chelicera, AT: anterior teeth, PT: posterior teeth, Ide: intermarginal denticles; (e) male palp, ventral; (f) soft trilobate membrane; (g) opisthosoma of female, ventral; (h) female epigyne, ventral.

2.2. Molecular studies

Tissues of the fresh sparassid specimens used for molecular studies were mostly obtained from the "spider tissue collection for DNA analysis" (SD) deposited in the Arachnology section, Senckenberg Research Institute. Additional specimens were sampled by the author in Ethiopia (2011) and by colleagues from different parts of the distribution range (see Chapter 3.3: Table 1). The majority of outgroup sequences were extracted from GenBank (see Chapter 3.3: Table 2). For details see chapter 3.3: Material and methods.

Gene selection. Four gene markers were analysed to reconstruct the phylogeny including two mitochondrial genes cytochrome *c* oxidase subunit I (COI, 648 bp; barcoding region), 16S rRNA (16S, ~500–510 bp) and two nuclear gene 28S rRNA (28S; ~780 bp) and Histon 3 (H3; 327 bp). These markers represent a comprehensive selection of data from both mitochondrial and nuclear protein-coding and ribosomal genes: COI as the DNA-barcoding region to address species-species relationships (after Barrett and Hebert 2005), 16S to address deeper phylogeny among genera and finally 28S and H3 both nuclear genes with slower gene evolution to address the relationships at the deeper nodes of the phylogenetic trees (after Hausdorf 1999; Dimitrov et al. 2012).

DNA Isolation. Genomic DNA was isolated using CTAB method after Wallace (1987; Bayer and Schönhofer 2013). Portions of muscle tissues of the legs were cut into small pieces and dried at room temperature, and were subsequently additionally air dried using a heater (at 40°C). The dried tissues were homogenised in 753 µl homogenisation solution [750 µl CTAB (Cetyltrimethylammoniumbromid) (2%), 0.1 M Tris-HCl (pH 8), 1.4 M NaCl (Natriumchlorid), 2.5 mM EDTA (Ethylendiamintetraacetic acid), 2% SDS (Sodium dodecylsulfat, Natriumsalt), 1.5 µl ß-Mercaptoethanol (14.3 M); 1.5 µl Proteinase K (15 mg/ml)]. The mixture left at 60°C for 2–3 hrs (or overnight) on a heating block with shaker for a full digestion. By following centrifugation (13000 rpm, 10 min), the precipitate components and upper foams were removed and supernatant liquid recovered. Using a standard phenol-chloroform-isoamylalcohol solution (after Sambrook and Russell 2001), the supernatant was recovered up to three times with 1.5 volumes, followed by centrifugation (12000 rpm, 12 min). During the final chloroform-isoamylalcohol extraction step, the DNA was precipitated using 1/10 volume 3 M Na-acetate, pH 5.2

and 2.5 volumes of ice cold absolute ethanol at –20°C. The solution incubated at minus 20°C over night. Following centrifugation (12000 rpm, 20 min), supernatant discarded and DNA pellet washed with 500 µl Ethanol 70% (-20°C) in ice box followed by final centrifugation (12000 rpm, 5 min, at 4°C). The air dried DNA pellet was dissolved in 20 µl ultrapure, sterile H_2O. Spectrophotometry was applied to determine the concentration of the extracted DNA.

***PCR amplification*.** For the PCR, the partial fragments of mitochondrial genes COI and 16S and the nuclear genes 28S and H3 were amplified using the primer pairs and PCR termocycling details presented in chapter 3.3: Table 3. The amplification was performed in 25 µl final volume containing 13.95 µl of ultra pure water (dd H_2O), 2.5 µl of 10*Polymerase-buffer, 0.4 µl of each primer (100 pmol/µl), 1.5 µl of dNTPs (2.5 mM), 3.5 µl of MgCl2 (25 mM), 2.5 µl of the genomic spider DNA templates (30–35 ng/ µl) and 0.25 µl of *Taq* DNA polymerase. PCR products were purified using the QIAquick PCR purification kit (Qiagen).

Sequencing and editing. The purified fragments were sequenced using BigDye Terminator Cycle Sequencing Kit v. 3.1 using primers as mentioned above. Sequencing was carried out from both forward and reverse for better evaluation and easier editing. Sequences were edited manually by viewing the chromatographs in BioEdit (Hall 1999) and CodonCode Aligner (v. 4.1.1, Codon Code Corporation). All newly sequenced markers (chapter 3.3: Table 1) will be deposited in the Genbank after acceptance of the manuscript (chapter 3.3). Because of the relatively huge number of samples, most of the DNA extractions, PCR and all sequencing were carried out by Scientific Research and Development GmbH (SRD), Bad Homburg, Germany.

Alignment. The sequences were curated and aligned using ClustalW implemented in MEGA (v.5.2.1) (Tamura et al. 2012). 28S and 16S were further aligned with MAFFT v7 (Katoh and Standley 2013). Concatenation of the four different markers were done using Mesquite v2.75 (Maddison and Maddison 2011).

Phylogenetic analyses. To verify the edited sequences MEGA (v.5.2.1) (Tamura et al. 2012) was used by running Neighbor-Joining analysis under the Kimura 2-Parameter model. Models of nucleotide substitution and sequence evolution were evaluated for each gene under different alignment strategies using jModeltest v0.1.1

(Posada 2008). The estimated models were further used to test phylogenetic relationships among taxa under Bayesian inference (BI) (using MrBayes v3.2.1 after Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Parallel to BI analyses, the phylogenetic relationships were tested using Maximum likelihood inference (using raxmlGUI v0.95 after Silvestro and Michalak 2011) The resulted trees were viewed and manipulated in Figtree v. 1.4. (available at http://tree.bio.ed.ac.uk/software/figtree/). The divergence time among taxa were estimated by BEAST v1.7.2 (Drummond et al. 2012) by calibrating BI trees using fossil and biogeographic data.

2.3. Distributional data processing

Eusparassus species locality data were obtained from collection labels and direct sampling in the field using GPS. Internet sources such as Google Earth: http://www.earth.google.com used to verify the accuracy of the localities. The online global gazetteers version 2.2 (http://www.fallingrain.com/world) was used to find correct name of places and also states and provinces of the country of distribution. It also provided geographical coordination for the species locations when the coordinates were not recorded by the samplers. All formats were converted to decimal degree to be mapped in DIVA-GIS version 7.4.0 (available at http://www.diva-gis.org/, Hijmans et al. 2005).

3. RESULTS

The results of this study are presented in three chapters. **Chapter 3.1** is about the taxonomic revision of the genus *Eusparassus* in Eurasia. In **chapter 3.2** I present an overview on the systematics of *Eusparassus* along with the revision of Afro-Arabian species. And finally, in **chapter 3.3** the molecular phylogenetic relationships of *Eusparassus*, Eusparassinae and Sparassidae are investigated.

Anlage 1

Erklärung über Anteile der Autoren/Autorinnen an den einzelnen Kapiteln der Promotionsarbeit

Titel der Publikation/ des Manuskripts: **Taxonomic revision of the huntsman spider genus *Eusparassus* Simon, 1903 (Araneae: Sparassidae) in Eurasia**

Was hat der/die Promovierende bzw. was haben die Co-Autoren/Autorinnen beigetragen[#]	Name des/der jeweiligen Autors/Autoren/Autorin*
(1) Entwicklung und Planung	Majid Moradmand (90%) Peter Jäger (10%)
(2) Durchführung der einzelnen Untersuchungen/ Experimente	Majid Moradmand
(3) Erstellung der Daten-sammlung und Abbildungen	Majid Moradmand
(4) Analyse/Interpretation der Daten	Majid Moradmand
(5) übergeordnete Einleitung/ Ergebnisse/Diskussion	Majid Moradmand (98%) Peter Jäger (2%)

[#]Bei 2, 3 und 4 bitte kurze inhaltliche Angaben der jeweiligen Anteile, bei 1 und 5 reichen prozentuale Angaben

*Mehrfacheintragungen möglich

Als Autoren/Autorinnen werden solche Personen bezeichnet, die an der Arbeit in Bezug auf die genannten Punkte in einer Weise mitgewirkt haben, dass sie für die ausgewiesenen Passagen (mit) verantwortlich sind. Personen, die an der Arbeit mitgewirkt haben, jedoch nicht in diese Kategorie fallen, sollten in der Danksagung Erwähnung finden.

Datum/Ort

05/09/2013 Frankfurt am Main

Unterschrift Promovend/Promovendin

M. Moradmand

Datum
zustimmende Bestätigung der vorgenannten Angaben

Unterschrift Betreuer/Betreuerin

Chapter 3.1. Taxonomic revision of the genus *Eusparassus* Simon, 1903 (Araneae: Sparassidae) in Eurasia

This chapter is based on the following paper in a slightly modified version.

Status: **published (28 September 2012)**

Type of publication: **Research Article**

Journal: **Journal of Natural History**

Citation: **Moradmand, M. and Jäger, P., 2012. Taxonomic revision of the huntsman spider genus *Eusparassus* Simon, 1903 (Araneae: Sparassidae) in Eurasia. *Journal of Natural History*, 46 (39-40), 2439–2496.**

Abstract

The huntsman spider genus *Eusparassus* Simon, 1903 in Eurasia is revised to include 13 valid species. The type species is redescribed, and additional diagnostic characters are presented for the genus. Neotypes are designated for *Eusparassus dufouri* Simon, 1932 from Portugal, and *Eusparassus walckenaeri* (Audouin, 1826) from Egypt to establish their identity. Consequently, *E. kronebergi* **stat. nov.** Denis, 1958 from Afghanistan and *E. doriae* **stat. nov.** (Simon, 1874) from central Iran which were considered junior synonyms of *E. walckenaeri* are re-established as valid species. Lectotypes and paralectotypes are designated for: *E. kronebergi* **stat. nov.**, *E. maynardi* (Pocock, 1901) **comb. nov.** and *E. pearsoni* (Pocock, 1901) **comb. nov.** Two new synonymies are proposed: *E. nanjiangensis* (Hu & Fu, 1985) as junior synonym of *E. potanini* (Simon, 1895) from Xinjiang Uyghur autonomous region in China and *E. doriae* **stat. nov.** as senior synonym of *E. fontanieri* (Simon, 1880). Three new combinations are proposed: *Eusparassus xerxes* (Pocock, 1901) **comb. nov.** from Makran coast in Pakistan and Iran, *E. maynardi* (Pocock, 1901) **comb. nov.** from Baluchistan in Pakistan and *E. pearsoni* (Pocock, 1901) **comb. nov.** from Ghats in India (all transferred from the genus *Olios* Walckenaer, 1837). The latter two species are proposed as valid species and are removed from junior synonymy with *E. xerxes* **comb. nov.** One new species is described: *E. mesopotamicus* **spec. nov.** (male and female) from Iraq and Iran. New geographical records are presented: *E. pontii* Caporiacco, 1935 and *E. kronebergi* **stat. nov.** are recorded for the first time from India. *E. fuscimanus* Denis, 1958, *E. oculatus* (Kroneberg, 1846) and *E. levantinus* Urones, 2006 are redescribed using new material. *E. lilus* Strand, 1907, described from Java, is proposed as *nomen dubium* because the type material could not be found and no longer seems to exist. Misplaced *Olios flavovittatus* **comb. nov.** (Caporiacco, 1935) from Karakoram is transferred from the genus *Eusparassus*. Almost all the species are redescribed for the first time and illustrations from male and female copulatory organs including intraspecific variations are provided using a large number of specimens.

Keywords: Eusparassinae, neotype, lectotype, new species, Eurasia

INTRODUCTION

Eusparassus Simon, 1903 are medium to large sized huntsman spiders which are among the foremost arthropod predators of deserts and semiarid areas (Levy 1989). Silken papery retreats, stuck firmly to underside of large flat stones, are used as a shelter for moulting and hiding during the day (Figure 1A). Females lay their eggs enclosed in a silken sac inside the retreat (Gerhardt 1928; Levy 1989; Gabriel 2011). They are distributed accross part of the Old World from Southern Africa to Mediterranean Europe and through the Middle East into Central and South Asia. The single Neotropical report of the genus, "*Eusparassus shefteli*" Chamberlin, 1916 is not congeneric with *Eusparassus* (based on original illustrations and picture of holotype female epigyne) and actually belongs to the genus *Polybetes* Simon, 1897 (Cristina Anne Rheims, personal communication). Thus, *Eusparassus* spp. are restricted to Africa and Eurasia.

Currently, *Eusparassus* comprises 28 nominal species, of which 10 are described from Eurasia and 18 from Africa (Platnick 2012). The majority of the species are known merely by a single gender and by their original description, thus they have never been recorded since. Some species were placed originally or subsequently in the genus *Olios* and therefore the necessity to investigate their types was unavoidable. The systematics of the taxon is obscure and no comprehensive taxonomic revision has been carried out so far. It was only Levy (1989) who in a small revisionary work, emphasized on the female's copulatory organs and the lateral view of the vulva as a diagnostic character, and redescribed *E. walckenaeri* (sub *Sparassus*). Presently, definitions of characters and species boundaries of *Eusparassus* species are incomplete. As in other groups of spiders, early diagnoses were based mostly on variable somatic and non-copulatory characters, which poorly defined species boundaries. *Eusparassus* show a striking uniformity in somatic and copulatory characters. These similarities in traits as well as some intraspecific variations have challenged a discrimination of species. The challenging taxonomy of *Eusparassus* was admitted by previous workers as well (i.e., Denis 1947; Levy 1989; Jäger and Yin 2001).

FIGURE 1. (A) Papery retreats of *Eusparassus walckenaeri* underside of flat stones in Mügla, Turkey, (B) Habitus of *E. walckenaeri* at the entrance of its retreat, (C) Habitus of *Eusparassus mesopotamicus* **spec. nov.** from Birecik, Turkey. Photos by D. Kunz (A, B) and B. Göcmen (C).

Eusparassus was erected by Simon (1903) to replace nominal species published under the name *Sparassus* by Simon in 1880. The type species is *E. dufouri* Simon, 1932, designated originally sub misidentified "*Eusparassus argelasius*". Simon (1903: 1020) proposed the synonymy of *Sparassus* Walckenaer, 1805 with *Micrommata* Latreille, 1804. The time lapse between proposing the genus and describing the type species was due to the taxonomic puzzle of the generic name *Sparassus*. At that time, it had been subjected to complex disputes. It was in use simultaneously for species of *Olios* Walckenaer, 1805 and *Eusparassus* (Simon 1874 and 1895; Pocock 1901). Some workers (Bonnet 1958; Levy 1989) originally used *Sparassus* for describing and recording species of *Eusparassus* until *Sparassus* was considered by Jäger (1999) as a junior synonym of *Micrommata*. Simon (1897) classified the Sparassidae by means of eyes (pattern and size) in seven sub groups and placed *Sparassus* in Sparassinae (sub "Sparasseae"). After creating the genus *Eusparassus*, Simon (1903) classified his new genus along with several other genera in Delenineae (sub "Deleneae"). Järvi (1912, 1914) proposed a new subfamily Eusparassinae (sub "Eusparasseae") for three genera *Eusparassus*, *Pseudomicrommata* Järvi, 1914 and *Rhitymna* Simon, 1897, according to similarities in female copulatory structures. *Rhitymna* was later revised and proved to belong to a different phylogenetic lineage (Jäger 2003). Järvi's classification appeared in Petrunkevitch (1928) who emphasized some somatic characters and combined Järvi's and Simon's classifications. Recently, Eusparassinae was re-established by Jäger and Kunz (2003) who found some synapomorphies in both somatic and genital characters, transferred an endemic African genus *Arandisa* Lawrence, 1938 and proposed some other endemic South African genera to be potentially included in this subfamily.

The recently investigated *Eusparassus* fossil in Baltic amber, *E. crassipes* (Koch and Berendt, 1854), uncovered the long existence of the genus which can be dated back to at least 44–49 Ma, during Eocene (Dunlop et al. 2011). Modern widespread distribution of the genus across the Old World and its long existence at least from early Tertiary till present (~50 million years) demonstrate its evolutionary success. The extant individuals occur in a diverse range of elevations from the semi-arid areas at sea level to the mountainous highlands, c. 4000 m, the highest altitude recorded to date for members of Sparassidae. In the present paper, we deal with the Eurasian species excluding Arabia. The *Eusparassus* fauna of the Arabian Peninsula is mostly related to Northern African elements which will be considered in a revision of African representatives. In this context, we provide descriptions of 13 *Eusparassus* species and designate neotypes, lectotypes and paralectotypes to fix species identities.

MATERIAL AND METHODS

The specimens were examined, measured and illustrated using a Leica MZ 165C stereomicroscope equipped with a drawing tube. Male palps were observed in 70% ethanol. Hairs covering the bulb as well as the base of RTA were removed with forceps and fine needles. Hairs surrounding distalo-ventral margin of cymbium and around RTA are partially illustrated in male palps. Female epigynes were dissected and soft tissue surrounding vulva was removed using minute entomological pins (model Sphinx V2A 0.1 x 12 mm). Subsequently, epigynes were submerged in 96% lactic acid to observe the internal duct system. For a better understanding of the internal duct system, we provide a drawing from anterio-dorso-lateral view of left vulvas. In this view, there is no need to cut the lateral lobes of epigyne and is suitable for type material which should be treated with care. The dorsal view of vulva is not illustrated (except Figure 3B). The order of species is arranged from West (Portugal) to East (India) in the geographical distribution range. Geographic coordinates extracted subsequently from the web site http://www.fallingrain.com/world/ are given in parentheses.

All measurements are in millimetres. Size classes of spiders are according to Jäger (2001: 14). Measurements of palps are listed as: total length [femur, patella, tibia, cymbium]; legs as: total length [femur, patella, tibia, metatarsus, tarsus]. Abbreviations used throughout the text: AB — anterior bands of epigynal field, ALE — anterior lateral eyes, AME — anterior median eyes, AMLL — anterior margin of LL, dRTA — dorsal RTA, EF — epigynal field, EFB — epigynal field bridge, LL — lateral lobes, MS — median septum, PLE — posterior lateral eyes, PME — posterior median eyes, PMLL — posterior margin of LL, RTA — retrolateral tibial apophysis, vRTA — ventral RTA, SD — Sparassidae DNA numbers in SMF, SS — slit sensillum, T — tegulum, TL — turning loop, I–IV — 1st to 4th leg. Palp and leg spination are presented in the following format: prolateral, dorsal, retrolateral and ventral (the latter only if present). Parentheses and slashes are used to state spination variation within a single specimen and among different specimens, respectively. Since most of the specimens are old and long preserved, we provide a general pattern of colouration in the genus description paragraph. Species specific colouration is given briefly in species description.

Collections and curators

CRB — Collection of Robert Bosmans, Brussells

IOZB — Institute of Zoology, Chinese Academy of Sciences, Beijing (Li Shuqiang)

MCSN — Museo Civico di Storia Naturale "Giacomo Doria", Genoa (Maria Luisa Tavano)

MHNG — the Muséum d'histoire naturelle, Genève (Peter Schwendinger)

MIZ — Zoological Museum, Polish Academy of Science, Warsaw (Dominika Mierzwa)

MVHN — Museu Vallencià d'Historia Natural, Vallencià (Sergio Montagud Alario)

MMB — Moravian Museum, Brno (Petr Bañař)

MNCN — Museo Nacional de Ciencias Naturales, Madrid (Javier Sánchez Almazán)

MNHN — Muséum National d'Histoire Naturelle, Paris (Elise-Anne Leguin, Christine Rollard)

MNM — Museo Civico di Storia Naturale di Milano, Milan (Andrea Sabbadini, Carlo Pesarini)

MZH — Finish Museum of Natural History, University of Helsinki (Ritva Talman)

NHM — Museum of Natural History, London (Janet Beccaloni)

NHMW — Naturhistorisches Museum, Vienna (Christoph Hörweg)

NRM — Swedish Museum of Natural history, Stockholm (Gunvi Lindberg, Kjell Arne Johanson)

SMF — Senckenberg Research Institute, Frankfurt am Main (Julia Altmann, Peter Jäger)

SNSD — Senckenberg Naturhistorische Sammlungen, Dresden (Katrin Schniebs)

SZMN — Siberian Zoological Museum, Novosibirsk (Galina Azarkina)

ZIP — Zoological Institute, Academy of Science, St. Petersburg (Kirill Mikhailov)

ZMB — Museum für Naturkunde, Berlin (Anja Friederichs, Jason Dunlop)

ZMMU — Zoological Museum of Moscow state University, Moscow (Kirill Mikhailov)

ZMUC — Zoological Museum, University of Copenhagen (Nikolaj Scharff)

ZSM — Zoologische Staatssammlung München, Munich (Stefan Friedrich, Roland Melzer)

TAXONOMY

Family Sparassidae Bertkau, 1872

Subfamily Eusparassinae Järvi, 1912

Genus *Eusparassus* Simon, 1903

Micrommata [part] – Latreille, 1818: 517; Dufour, 1820: 299, pl. 2 (misidentification).

Sparassus [part] – Walckenaer, 1830: 108, pl. 7, fig. 1; Walckenaer, 1837: 584, 585; Simon, 1880: 290; Bonnet, 1958: 4098; Levy, 1989: 138, fig. 20. (misidentification).

Eusparassus Simon, 1903: 1020, 1023, 1025– Strand, 1906: 630; Strand, 1907: 437 ; Strand, 1908: 19; Simon, 1909: 31; Järvi, 1912: 57, 175, fig. 49, pl. 4, figs 9, 10; Järvi, 1914: 173–175; Reimoser, 1919: 200; Petrunkevich, 1928: 155; Gravely, 1931: 238; Schenkel, 1936: 9, 283; Roewer, 1928: 118, pl. 2, figs 38–39; Roewer, 1955: 775; Roewer, 1962: 4, figs 82–84; Caporiacco, 1935: 216, pl. 6, f. 4; Caporiacco, 1939: 353; Caporiacco, 1941: 109, f. 40; Denis, 1945: 54; Denis, 1947: 49, pl. 2, f. 12; Denis, 1958: 102, f. 30; Barrientos & Urones, 1985: 356, figs 4, 5; Jäger, 1999: 1, 4, 6; Song et al. 1999: 467, f. 268H, K; Jäger, 2001: 16, 18, figs a–c, ä, ö; Jäger & Yin, 2001: 132; Jäger and Kunz, 2005: 168, 169, figs 205–213; Urones, 2006: 100, figs 1–43; Dunlop et al. 2011; Deltshev, 2011: 28; Gabriel, 2011: 9–12, figs 2, 9.

Notes. Simon (1903) created the generic name *Eusparasus* to substitute it for the name *Sparassus*; because he suspected that *Sparassus* was a junior synonym of *Micrommata* (Simon 1903: 1020). He designated the type species as *Eusparassus argelasius* denoted by a new replacement name (nomen novum) for misidentified *Micrommata argelasia* (published in Latreille 1818). Since this species could be mistaken with *Olios argelasius*, the type species of *Olios* Walckenaer, 1805 (sub *Sparassus argelasius*) Simon (1932) proposed *Eusparassus dufouri* as a new species.

Type species. *Eusparassus dufouri* Simon, 1932 by original designation in Simon (1903) sub *E. argelasius*, female from Spain.

Extended diagnosis. *Eusparassus* spp. can be diagnosed from the other two monotypic genera of Eusparassinae by the number of ventral tibial spines: I–IV 4 (6 in *Arandisa* and *Pseudomicrommata*) and by relative diameters of AME which is subequal to or larger than ALE (smaller than ALE in the other two genera); *Eusparassus* spp. are recognisable by the shape of copulatory structures: parallel embolus and tegulum constructing a U-shaped structure, embolus membrane covering partially embolus tip; dRTA strong and straight, in

contrast to dRTA, vRTA small and weakly developed (Figures 2A, 11G, 19A); Female epigyne characterized by two large triangular lateral lobes, LL parallel and in contact on the median longitudinal suture,diverging strongly at posterior margins and slightly at anterior margins, and circumscribing MS entirely (Figures 3A, 4C) or partially (Figures 5F, 8A, 16A, 21A); in vulva, dorsal view, two parallel copulatory ducts, straight and fully or partially hyaline, folded and membranous (Figure 3B).

Redescription. Medium to large Sparassidae, body length 10 mm (e.g. *E. oculatus*) to 30 mm (e.g. *E. xerxes* **comb. nov.**); prosoma slightly longer than wide; Leg length formula 2 4 1 3 (most of species) or 2 4=1 3; eyes arranged in two rows, anterior row slightly recurved and posterior row relatively straight, eyes about subequal in size, AME slightly larger than or subequal to ALE and PME smaller than PLE; Basal segment of chelicerae at distal retromarginal end with 1 (Figures 2E, 7B) to 3 or 4 thick bristles (Figures 19E, 22D), in most species onlyone bristle; Chelicerae with 2 anterior and 3 to 6 posterior teeth, Cheliceral furrow with (Figure 4B) or without denticles (Figures 2E, 9B, 21D); ventral tibial spines: I–IV 4, spination of other parts variable but in most species: Palp 131, 101, 1111, 1013; Legs: Femur I–III 323, IV 322; Patella I–IV 101; Tibia I–IV 2024/2224; Metatarsus I–III 2024, IV 3034/3036; male palp as in diagnosis with embolus originating at 6:30 – o´clock – position running first distally and bent retrolaterally, tip of embolus pointing in various angles and with diverse shapes, embolus and tegulum form a U-shaped structure in ventral view; small and hyaline conductor situated at distal end of tegulum and covering partially tip of embolus (Figures 11E, 12B) ; Female epigyne consisting of two large triangular lateral lobes, LL parallel and in contact on the median longitudinal suture; MS soft and hyaline (Figure 5F) or hard and sclerotised (Figure 22E), EF fusing anteriorly and constructing EFB (Figures 17F, 20A) or not (Figure 16A); internal duct system with glandular pores situated in a depression (Figures 5G, 6B, D) or on a projection (Figures 2C, 8B, 22F).

Colouration. Pale grey to dark brown spiders, with uniform colouration of body (Figure 1C) or clearly patterend body and banded legs (Figure 1B), ventral opisthosoma with distinct dark marking (Figure 23B–D) or pale (Figure 23A), dorsal opisthosoma with a pattern of small chevrons on posterior half.

Eusparassus dufouri Simon, 1932

Figures 2 (A–E), 3 (A–C), 23C

Micrommata argelasia (Walckenaer, 1805) – Latreille, 1818: 517 (misidentification, description of female, Spain); Dufour, 1820: 299, pl. 2 (misidentification).*Sparassus argelasius* – Walckenaer, 1830: 108, pl. 7, fig. 1 (misidentification, male); Walckenaer, 1837: 584 (misidentification, female); Simon, 1875: 334 (misidentification); Simon, 1880: 290 (misidentification)
Eusparassus argelasius – Simon, 1903: 1020, 1025 (type species designation, new replacement name, description of the genus) – Järvi, 1912: 57, 175, figs 9, 10, 49, pl. 4; Järvi, 1914: 175; Roewer, 1928: 118, pl. 2, figs 38–39 (misidentification).
E. dufouri Simon, 1932: 890 (new replacement name). – Barrientos & Urones, 1985: 356, figs 4, 5; Urones, 2006: 102, figs 1–24.
Sparassus dufouri (Simon) – Levy, 1989: 138, fig. 20.

Type material: (syntype females unavailable, see notes below), **Neotype:** male (SD 815), Portugal: *Distrito de Portalgere*, Montalvão, [39˚36' N, 07˚31' W] 6 May 2011, S. Henriques leg. (SMF)
Other material examined. PORTUGAL: 1♂ (SD 834), 1♀ (SD 822), with same data as for neotype (SMF); 1♂, Pulo do Lobo, May 2011, S. Henriques leg. (SMF, SD 838); 1♀,*Distrito de Beja*: Serpa, Altenju, May 2011, S. Henriques leg. (SMF, SD839); 1♂, 1♀, *Pomarao*, 120 m, (37°34.5′ N 7°32.100′W) 19–22 May 2006, Cardoso et al. leg. (ZMUC); **SPAIN:** 1♂, 1♀, *Huelva Province:* Alajar, Aracena, (37°53′28″N 6°33′40″W) 7 July 1969, A. Senglet leg. (MHNG); 2♂♂, *Jaén Province*: Sierra de Cazorla, Guadalquivir, (37°56′12″N 02°57′30″W), 24 July 1971, A. Senglet leg. (MHNG); 1♂, 1♀, Cordoba, 3 June 1909 (MNCN); 1♀, Rabida, June 1959, V. Buddenbrock leg. (SMF).
Diagnosis. Closely related to *E. levantinus* but differing from it by much more stout embolus tip and more sickle-like dRTA in ventral view (Figure 2A, C); EM sheath-like and covering part of embolus tip in retrolateral view (Figure 2B); vulva differing from that of *E. levantinus* by glandular process located on a continuous part distinguishable from turning loop (Figure 3C).
Redescription. Male (n=8)
Medium-sized *Eusparassus* species; total length: 9.9–13.8, prosoma length 5.5–6.8, prosoma width 5.3–6.6, anterior width of prosoma 2.6–3.5, opisthosoma length 4.5–7.0, opisthosoma width 3.0–4.5. Eyes subequal, eye diameters (neotype): AME 0.40, ALE 0.32, PME 0.31, PLE 0.34; eye interdistances: AME-AME 0.22, AME-ALE 0.10, PME-PME 0.43, PME-PLE

0.42, AME-PME 0.32, ALE-PLE 0.22, clypeus height at AME 0.20, clypeus height at ALE 0.27.

Chelicerae with 2 anterior and 3 posterior teeth, cheliceral furrow without denticles; Basal segment of chelicerae at distal end close to base of fangs with 1 bristle (Figure 2E).

Leg formula: 2 4 1 3. Measurements of palp and legs (neotype): Palp 8.3 [2.7, 1.2, 1.0, 3.4], I 25.9 [7.2, 2.3, 6.8, 7.3, 2.3], II 28.7 [8.3, 2.9, 7.6, 7.5, 2.4], III 24.3 [7.2, 2.6, 6.1, 6.3, 2.1], IV 26.7 [7.9, 2.3, 6.8, 7.4, 2.3].

Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323/424, IV 321/322/422; Patella I–IV 000(1)/101; Tibia I–IV 2024/2224; Metatarsus I–III 1014/2024, IV 3034/3(4)036.

Palp. as in diagnosis with cymbium nearly two times longer than tibia; tegulum shorter than embolus and tip of embolus proximad, embolic projection consists of a large sheath-like part distally and a hyaline part proximally (Figure 2A– C).

Female (n=6)

Total length: 16.2–17.5, prosoma length 8.0–8.5, prosoma width 6.7–7.7, anterior width of prosoma 4.3–4.5, opisthosoma length 8.2–9.0, opisthosoma width 4.5–6.0. Eye diameters: AME 0.45, ALE 0.41, PME 0.34, PLE 0.40; eye interdistances: AME-AME 0.35, AME-ALE 0.16, PME-PME 0.60, PME-PLE 0.58, AME-PME 0.48, ALE-PLE 0.42, clypeus height at AME 0.27, clypeus height at ALE 0.35.

Chelicerae with 2 anterior and 3 or 4 posterior teeth, Cheliceral furrow without denticles. Basal segment of chelicerae at distal end close to base of fangs mostly with 1 bristle or 2 bristles.

Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 8.7 [2.3, 1.5, 1.7, 3.2], I 26.1 [7.5, 3.4, 6.2, 6.8, 2.2], II 28.5 [8.5, 3.5, 7.0, 7.3, 2.2], III 24.2 [7.4, 3.2, 5.7, 5.8, 2.1], IV 26.7 [8.0, 3.1, 6.3, 7.1, 2.2].

Spination. Palp 131, 000 (001), 1111, 1013; Legs: Femur I–III 323/(3)424, IV 322(1)/422; Patella I–IV 000(1)/101; Tibia I–IV 1014/2024; Metatarsus I–III 2024, IV 3034/3036.

Epigyne/vulva. As in diagnosis, epigyne is longer than wide, AMLL are fused together and circumscribe MS entirely, EFB present and combined with AMLL (Figure 3A).

Colouration. Olive-brown with clearly banded legs; ventral opisthosoma with a V-shaped dark marking (Figure 23C).

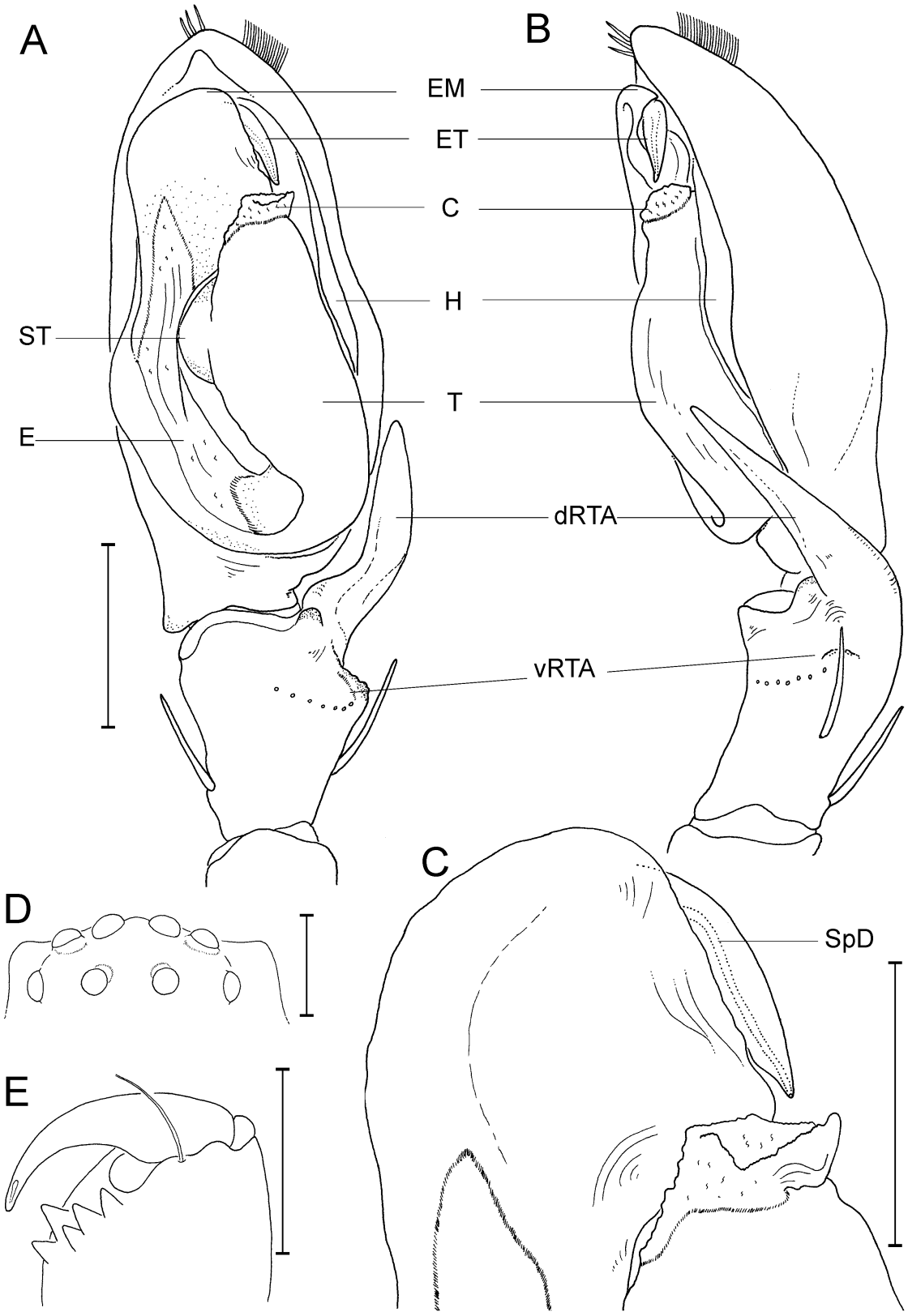

FIGURE 2. *Eusparassus dufouri* Simon, 1932, neotype male from Chanca, Portugal (SMF). (A) left palp, ventral, (B) left palp, retrolateral, (C) tip of embolus and conductor, ventral, (D) eye arrangement, (E) left chelicera, ventral. Abbreviations: C — Conductor, dRTA — dorsal retrolateral tibial apophysis, E—Embolus, EM—Embolus membrane, ET— Embolus tip, H—Haematodocha, SpD— Sperm duct, ST— Subtegulum, T—tegulum, vRTA — ventral retrolateral tibial apophysis. Scale bars: (A, B, D, E) 1 mm, (C) 0.5 mm.

Taxonomic notes. In the description of the genus *Sparassus*, Walckenaer (1805: 40) just listed *Sparassus argelasius* without a description (*nomen nudum*) along with the following nominal species: *S. samaragdulus* (Fabricius, 1793), *S. pallens* (Fabricius, 1794), *S. roseus* (Clerck, 1757) and *S. ornatus* (Walckenaer, 1802) [for more details see Jäger (1999: 3)]. One year later (1806: 146, table 2) he published a description and illustration of a male under the name *Sparassus argelasius*, a misidentification that was later transferred to the genus *Olios*. Walckenaer's original description of *Sparassus* was actually based on species of the previously established genus *Micrommata* Latreille, 1804 and a single male of *Olios argelasius*. Latreille (1818) examining two female specimens from Spain tried to describe the female of Walckenaer's species, "*Sparassus argelasius",* and transferred it to *Micrommata* (sub *Micromata argelasia*), but he failed to identify it correctly. This misidentification was pointed out later by Simon (1903: 1025), who described his new genus *Eusparassus*, cited Latreille's description and indicated the type species as *E. argelasius* Latreille. Nevertheless, Latreille's misidentification was based on Walckenaer (1905) and the species name was preoccupied by *Olios argelasius* (sub *Sparassus*). Simon (1932: 890) realized this confusion when he described and illustrated *O. argelasius* (Walckenaer) and proposed *E. dufouri* as a new replacement name (*nomen novum*) to substitute the previously established name *E. argelasius*. Simon noted that "the species described under name *Sparassus argelasius* Latreille (in Simon 1875: 334) must take the new name (*nom. nov.*) as *Eusparassus dufouri*". Prior to proposing the genus *Eusparassus*, Simon (1875: 334, 1880: 290) used the nominal species "*Sparassus argelasius*" to describe *E. dufouri*. In the literature, *Sparassus* itself was used to record not only different species but also different generic taxa including *Micrommata*, *Olios* and *Eusparassus*.

Neotype designation. According to all the facts noted, Simon (1932) did not designate any name-bearing type specimen subsequently while referring to Latreille (1818). According to Article 72.4.2 of ICZN when a new nominal species-group taxon (*E. dufouri*) is based on a published misidentification by an earlier author (*M. argelasia* Lat.), the type series consists of

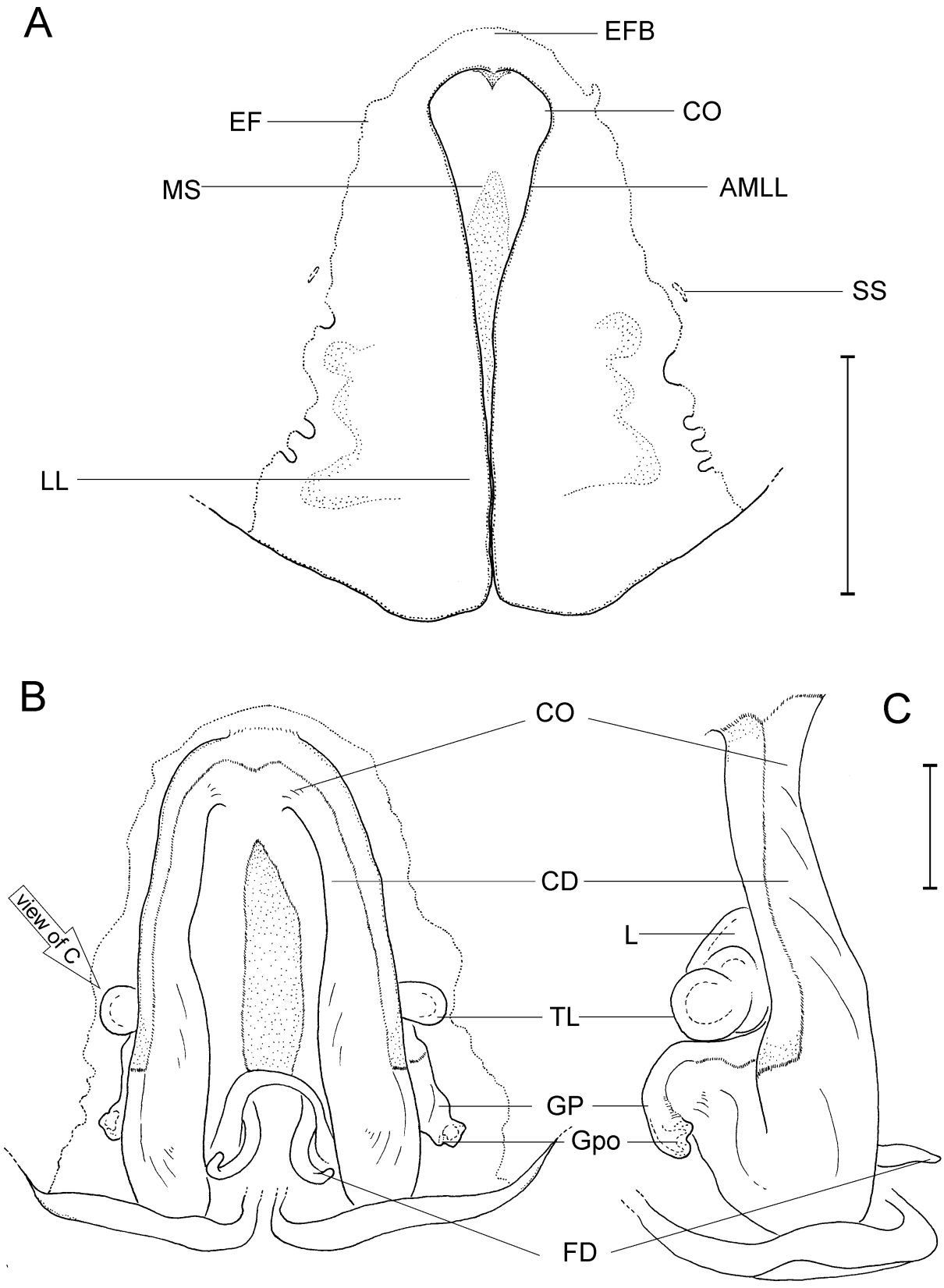

FIGURE 3. *Eusparassus dufouri* Simon, 1932, female from type locality (SMF), (A) epigyne, ventral (B) vulva, dorsal (C) left vulva, anterio-dorso-lateral. Abbreviations: AMLL—anterior margin of LL, CD— Copulatory duct, CO— Copulatory opening, EF— epigynal field, EFB— epigynal field bridge, FD— Fertilization duct, GP— Glandular process, GPo— Glandular pores, L—Lumen, LL— lateral lobes, MS— median septum, PMLL — posterior margin of LL, SS — slit sensillum, TL — Turning Loop, Scale bars: (A, B) 1 mm, (C) 0.5 mm.

the specimens which had been misidentified. No material of Latreille can be traced in MNHN and it is generally understood that none exists. Consequently, it is necessary to designate a neotype for *E. dufouri* at this time to establish its identity, define the nominal taxon objectively and avoid taxonomic confusion with similar and closely related species in the Iberian Peninsula (i.e. *E. levantinus* Urones, 2006), in Northern Africa [i.e. *E. oraniensis* (Lucas, 1846)] and in eastern Mediterranean (i.e. *E. walckenaeri*). There are two forms in the Iberian Peninsula, *E. dufouri* of uncertain identity, and *E. levantinus*, which was described by Urones (2006). The latter species is distributed in Eastern and Southern Spain while it is replaced by *E. dufouri* in western Iberian Peninsula. Accordingly, a neotype is designated for *E. dufouri* from western Iberian Peninsula in the border of Portugal and Spain, in Montalvão. Based on the distribution map presented by Urones (2006) and also distribution records of the present study, type locality is selected to be as far as possible from the distribution range of *E. levantinus*. Specimens were freshly collected and DNA samples are available.

Doubtful record. Simon (1932: 890) stated that the single report of the species from France (Pyrenees-Orientales) was actually collected from a shipment from Spain, Iberia.

Known geographical distribution and habitat. Western Iberian Peninsula in Spain and Portugal, mostly under stones; under old tree bark in the southeast of Portugal (Barrancos Valley), including *Eucalyptus* trees. (S. Henriques, personal observation).

Eusparassus levantinus Urones, 2006

Figures 4 (A–G), 23D

Eusparassus levantinus Urones, 2006: 108–112, figs 25–43 (description and illustration of male and female from Spain, holotype male and paratype female examined).

Type material examined. Holotype: male, **SPAIN: Castellon Province**, Almeria (La Mosquera), 20 May 2004, S. Montagud leg. (MVHN 200504LM1); **Paratype:** 1 female, Enix, Almeria, 18 April 1973, M. Rambla leg. (MNCN 20.02/16315)

Other material examined. SPAIN: 1♂, Andalusia, Almeria, Cabo de Gata, 36° 43′ 18.8″ N, 2° 11′ 34.69″ W, 21 May 2011, S. Henriques leg. (SMF); 1♂, Andalusia, reared by S. Heist, 25 June 2005, B. Hayen ded. (SMF); 1♀, Andalusia, Medina-Sidonia, Algeleurus, 36°28′N 5°55′W, 300 m altitude, T. Zieger leg. (SMF); 1♀, Andalusia, Medina-Sidonia, Algeleurus, 36°28′N 5°55′W, 300 m altitude, T. Zieger leg. (SMF); 1♀, Andalusia, 4 September 2001, St.

Heist leg. (SMF); 1♀, Valencia Province: between Pego and Val de Ebo, 405 m altitude, Macchia with few interspred trees, under stone, 2 June 2010, S. Huber and A. Schönhofer leg. (SMF)

Diagnosis. Similar to *E. dufouri* but distinguished by shape of embolus tip, which is smaller, slimmer and pointed in ventral view, and dRTA which is straighter (Figure 4E–G); in vulva, glandular pores situated on a semicircular process which is fused to entire body of vulva (Figure 4D), in contrast they are present on a separated curved structure in *E. dufouri* females.

Redescription

Male (n=3)

Medium *Eusparassus* species; Total length: 12.4–14.8, prosoma length 5.9–7.8, prosoma width 4.7–6.2, anterior width of prosoma 2.3–3.3, opisthosoma length 6.5–7.0, opisthosoma width 4.0–4.6. Eye diameters: AME 0.43, ALE 0.42, PME 0.36, PLE 0.46; eye interdistances: AME-AME 0.29, AME-ALE 0.10, PME-PME 0.48, PME-PLE 0.58, AME-PME 0.32, ALE-PLE 0.31, clypeus height at AME 0.35, clypeus height at ALE 0.40.

Chelicerae with 2 anterior and 3 posterior teeth, Cheliceral furrow without denticles.

Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 11.1 [3.1, 1.4, 1.3, 5.3], I 29.6 [8.1, 3.4, 7.1, 8.2, 2.8], II 32.8 [9.2, 3.9, 7.8, 9.1, 2.8], III 27.7 [8.2, 3.3, 6.4, 7.1, 2.7], IV 30.9 [8.9, 3.2, 7.3, 8.8, 2.7].

Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323/424, IV 322/422; Patella I–IV 000(1)/101; Tibia I–IV 2224; Metatarsus I–III 1014/2024, IV 3034/3036.

Palp. As in diagnosis, with cymbium longer than tibia, embolic projection developed, embolus tip pointed proximad, dRTA strong and flattened, vRTA pointed in ventral view (Figure 4E–G).

Female (n=4)

Total length: 17.6–19.7, prosoma length 7.1–8.7, prosoma width 5.8–7.0, anterior width of prosoma 3.7–4.3, opisthosoma length 10.5–11.0, opisthosoma width 6.5–7.0. Eye diameters: AME 0.42, ALE 0.41, PME 0.35, PLE 0.41; eye interdistances: AME-AME 0.33, AME-ALE 0.15, PME-PME 0.54, PME-PLE 0.56, AME-PME 0.51, ALE-PLE 0.43, clypeus height at AME 0.21, clypeus height at ALE 0.33.

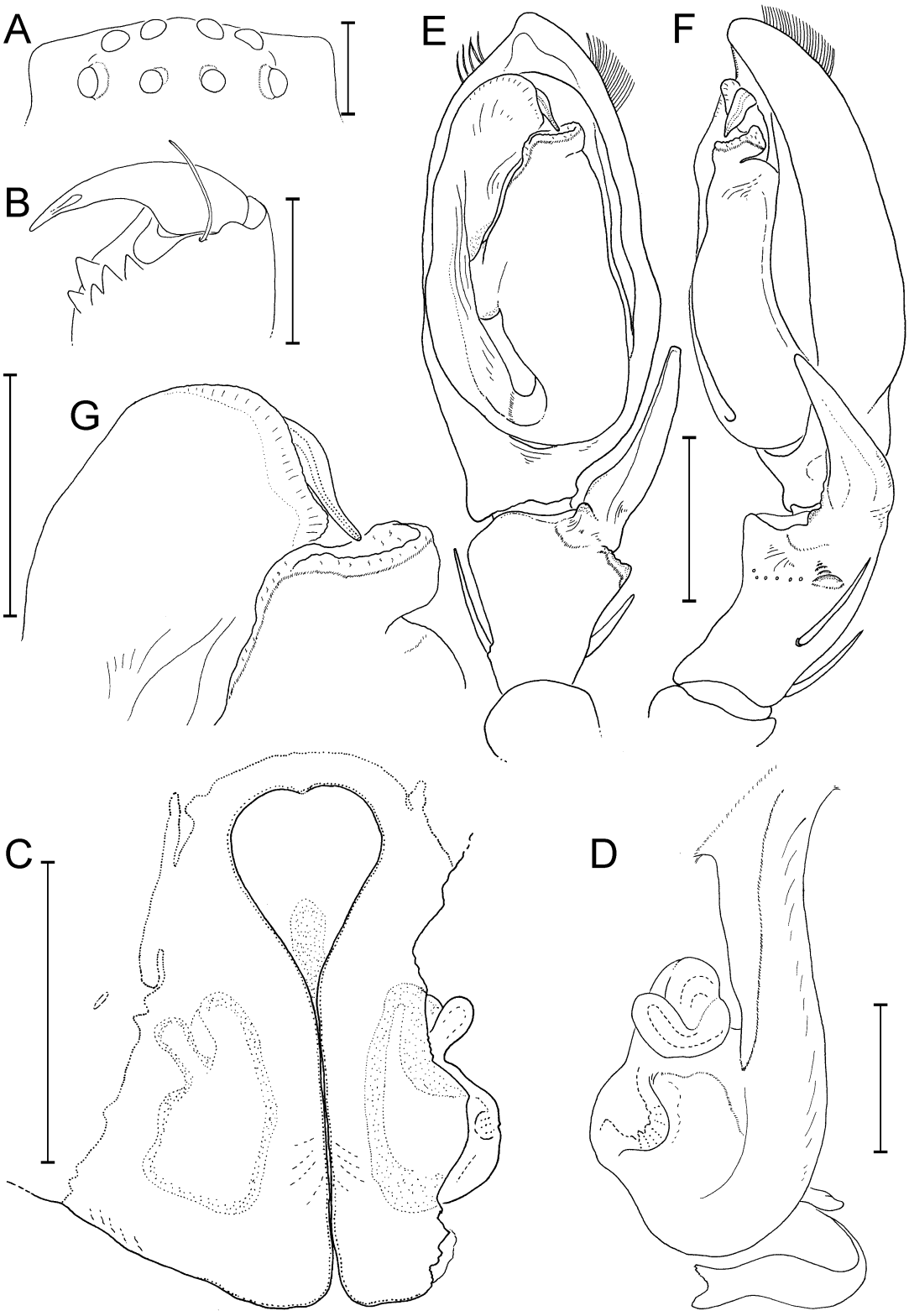

FIGURE 4. *Eusparassus levantinus* Urones, 2006, female paratype (A–D) from Almeria, Spain, (A) eye arrangement, (B) left chelicera, ventral, (C) epigyne, ventral, (D) left vulva, anterio-dorso-lateral; Male (E–G) from Andalusia, Spain, (E) left palp, ventral, (F) left palp, retrolateral, (G) tip of embolus and conductor, ventral. Scale bars: (A–C, E, F) 1 mm, (D, G) 0.5 mm.

Chelicerae with 2 anterior and 3 posterior teeth, cheliceral furrow without denticles; basal segment of chelicerae at distal end with 1 bristle (Figure 4B).

Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 9.8 [3.1, 1.4, 2.1, 3.2], I 29.0 [8.2, 4.0, 7.0, 7.5, 2.3], II 32.2 [9.5, 4.2, 7.8, 8.4, 2.3], III 27.4 [8.3, 3.6, 6.5, 6.7, 2.3], IV 30.0 [9.1, 3.3, 7.3, 8.0, 2.3].

Spination. Palp 131, 000/001, 1111, 1013; Legs: Femur I–III 323/424, IV 322/422; Patella I–IV 000(1)/101; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034/3036.

Epigyne/vulva. As in diagnosis. Epigyne longer than wide; MS encircled entirely by AMLL, the latter fused together (Figure 4C); turning loop with antro-ventrad elongated tip (Figure 4D).

Colouration. Olive brown spider; ventral of opisthosoma with a dark V-shaped marking (like that of *E. dufouri*) but with an additional median band (Figure 23D).

Known geographical distribution and habitat. Eastern and southern Iberian Peninsula in Spain, mostly coastal areas under stones.

Eusparassus walckenaeri (Audouin, 1826)

Figures 1B, 5 (A–G), 6 (A–G), 23A

Philodromus walckenaerii Audouin, 1826: 390, pl. 6, fig. 1 (description of female, type not designated).

Philodromus linnaei Audouin, 1826: 390, pl. 6, fig. 2 (description of male, type not designated) [synonymy by Simon1906].

Drassus civilis Reuss, 1834: 207 (description of juvenile; holotype, immature, Egypt: Sinai: Tor, 1827 Rüpell leg., SMF 4575 examined).

Sparassus walckenaeri – Walckenaer, 1837: 585 (transfer).

Ocypete tersa C. L. Koch, 1837: 83, fig. 305 (description of female; from Greece, type not available) [synonymy by Levy 1989]; C. L. Koch, 1845: 39, figs 980–981.

Sparassus tersa – Simon, 1880: 291 (in part, material from Greece, MNHN, examined).

Eusparassus tersa – Järvi, 1912: 57, fig. 48, pl. 4, figs 4–8 (transfer); Järvi, 1914: 173.

Sparassus cambridgii Simon, 1874: 257 (description of juvenile, from Egypt) [synonymy by Simon 1880].

Sparassus validus Thorell, 1875a: 80 (description of female; holotype, female, Taur. Merid., Ent.etikett nr=232, Nordmann leg. MZH 20.492, examined) [synonymy by Levy 1989] – Thorell, 1875b: 124.

Sparassus cognatus O. Pickard-Cambridge, 1876: 588 (description of female; syntypes, one female and 10 immatures, Egypt, not examined) [synonymy by Levy 1989].
Sparassus fontanieri Simon, 1880: 294 (description of male, holotype, locality not clear, MNHN, examined) [synonymy by Levy 1989].
Sparassus extensipes Karsch, 1880: 383, pl. 12, fig. 12. (description of male, holotype, male, Egypt: Cairo, not examined) [synonymy by Simon1906].
Sparassus linnaei – Kulczyn'ski, 1901: 43 (transfer, one male examined from Cairo in MIZ).
Sparassus walckenaeri – Pavesi, 1880: 364; 4; Levy, 1989: 132–138, figs 3–18
Sparassus walckenaerius – Simon, 1880: 292.
Heteropoda civilis – Strand 1916: 36 (Unjustified combination).
Eusparassus walckenaeri – Strand 1908: 24; Simon, 1906: 1168; Denis, 1947: 50, pl. 2, figs 14–16.); Deltshev, 2011: 28; Gabriel, 2011: 9–12, figs 2, 9.

Type material: (type female from Egypt not designated, unavailable, see notes below) **Neotype:** male, with label "**Egypt: Cairo**" (30° 3' 0N, 31° 15' 0E), 1971 (SNSD).
Other material examined. EGYPT: 1♂, 1♀, with same data as for neotype (SMF); 1♂, Cairo, with label: "*Sparassus linnaei*, Cairo, det. Kulczyński, F.1691" (MIZ 212984). **PALESTINE:** 2♂♂, surrounding of Nablus, 25 June 1999, A. Hussein leg (CRB); 2♂♂, surrounding of Nablus, 6 May 1999, A. Hussein leg (CRB). **ISRAEL:** 1♀, Sede Boqer, Negev desert, between Béer Sheva and Mituzpe Ramon, 6–29 May 2003, M. Rezac leg. (SMF); 2♀♀, 10 juveniles, Jerusalem, F.166 (MIZ 212984). **LEBANON:** 1♀, Amioun, 1944, H.B. Cott leg., (NHM 1950.3.30.124); **JORDAN:** 1♀, Dana Natural Reserve, Wadi Dana, (30° 41' N, 35° 37' E), under stones, 16 April 2004, J. Altman & J. Meier leg. (SMF, SD8); 1♀, Petra, Al-Habis, April 1983, J. Wittenberg & Kinzelbach leg., (SMF); 1♀, Amman, Pine forest, July 2007, J. Wiehele leg. (SMF); 2♀♀, Al-Bala, 10 km SE of Suwaylih, Al-Fuhays, summer 1980, F. Krupp & W. Schneider leg. (SMF); **SYRIA:** 13♂♂, 4♀♀, 5 juveniles, ***Golan***, camp Faüar, June 1981, K. Kollnberger leg. (NHMW); 1♀, Damascus (ZMB); **IRAQ:** 1♀, Al-Anbar Province: Lake Tharthar (33° 58' N, 43° 11' E), 23 March 1986, M. Carl leg. (SMF); 1♀, Baghdad, Kálová leg. PGD 312003 (MMB); **TURKEY:** 1♀, Taurus Mountains, with label: [type, *Sparassus validus* Thorell 1875, Aranea, Taur. Merid., Ent.etikett nr=232] Nordmann leg. (MZH 20.492); 1♀, Muğla Province, Güllück Yeni Oba, 26 August 2010, R. Zeelen & D. Kunz leg. (SMF); 1♂, Muğla Province, Bafa Gölü/Bafa Lake, 7 September 2010, R. Zeelen & D. Kunz leg. (SMF); 1♀, Ankara, Güvecci, 25 October 2006, D. Kunz leg. (SMF); 1♂, Turkish Riviera, 25 km N of Anamur, mountain meadow, July 2007, S. Huber leg. (SMF); 1♀, Izmir, in crevices inside retreat, 24 April 1992, W. Braunstein leg. (SMF);

GREECE: 1♂, Laconia, 4 km NE of Jithion, with rivulet across the shore (Near East Excursion), 5 August 1980, R. Kinzelbach leg (SMF); 1♂, Northern Aegean region, Sámos Island, near Vouliótes [=Vourilótoi], (37° 47' N, 26° 51' 30" E), 400 m Altitude, 25 June 2003, V. Vignoli leg (SMF); 1♀, Sámos Island, 26 June 2003, V. Vignoli leg. (SMF); 1♀, Lesbos Island, between Molivos and Kalloni, 3 July 2003, V. Vignoli leg. (SMF); 1♂, ***Sporades***, Skiathos Island (39° 10' N, 23° 29' E), 31 May 1979, Liebegott leg. (SMF 30846/1); 1♂, Thessaly, Volos, A. Schönhofer leg. (SMF 30846); 1♀, Lemnos Island, August 1976, A. de Caboga leg (MHNG); 3♀♀, Cyclades, Paros Island, Parikia, 25 June 1968, A. Senglet leg. (MHNG); 3♀♀, Cyclades, Naxos Island, Polichni, 6 August 1968, A. Senglet leg. (MHNG); 1♀, Central mainland, Phthiotis (=Phthiotida), Tragana, (38° 38' N, 23° 06' E) 5 June 1980, A. Senglet leg. (MHNG); 1♀, Crete Island, Lassithi, Exo Mouliana, 18 May 1970, A. Senglet leg. (MHNG); 1♂, Crete Island, Aptera, (SMF4618); 1♂, Crete Island, Stanion, 16 May 1979 J. Wunderlich leg. (SMF); 1♂, Arcadia, Paralia Astros, marshy area along mouth river Tanos, 26 May 1998, R. Bosmans leg. (CRB); 1♂, Attica, Thoriki, Velatouri, 16 May 1974, P. Goemare leg. (CRB); 1♂, Euboea (=Evia) Island, Psachna E., 100m, stones around ruin in open maquis shrubland, 10 May 2001, R. Bosmans leg. (CRB); 1♂, Peloponnese, Geráki, (36° 59' 44.11" N, 22° 43' 22.02" E), 25 February 2011, F. Šťáhlavský & M. Peprný leg. (SMF); **CYPRUS:** 1♂, Phapos, May 1994, T. Zugles leg (SMF); 1♀, Protaras, Ayios Elias Village, 17 May 1997, P.J. Haymoz leg (MHNG); **ITALY:** 1♂, 4 juveniles males, Etruria (1896.VIII.181 NHMW).

Diagnosis. The species can be recognised by a combination of somatic and genital characters. Males can be distinguished by hyaline and slender ET pointed retrolaterad in left palp and twisted at its distal end (Figure 5E). In female, AMLL not fused anteriorly (Figures 5F, 6A, C) (i.e., fused in *E. dufouri*); glandular pores located on a circular depression in vulva, behind loop (Figures, 5G, 6B, D) (i.e., *E. mesopotamicus* **spec. nov.** and several other species on a projection part). Mostly a patch of intermarginal denticles (3–20) is present in cheliceral furrow (Figures 5B, 6E–G) (usually absent or if present 1 or two denticles in other Eurasian species).

Redescription.

Male (n=33)

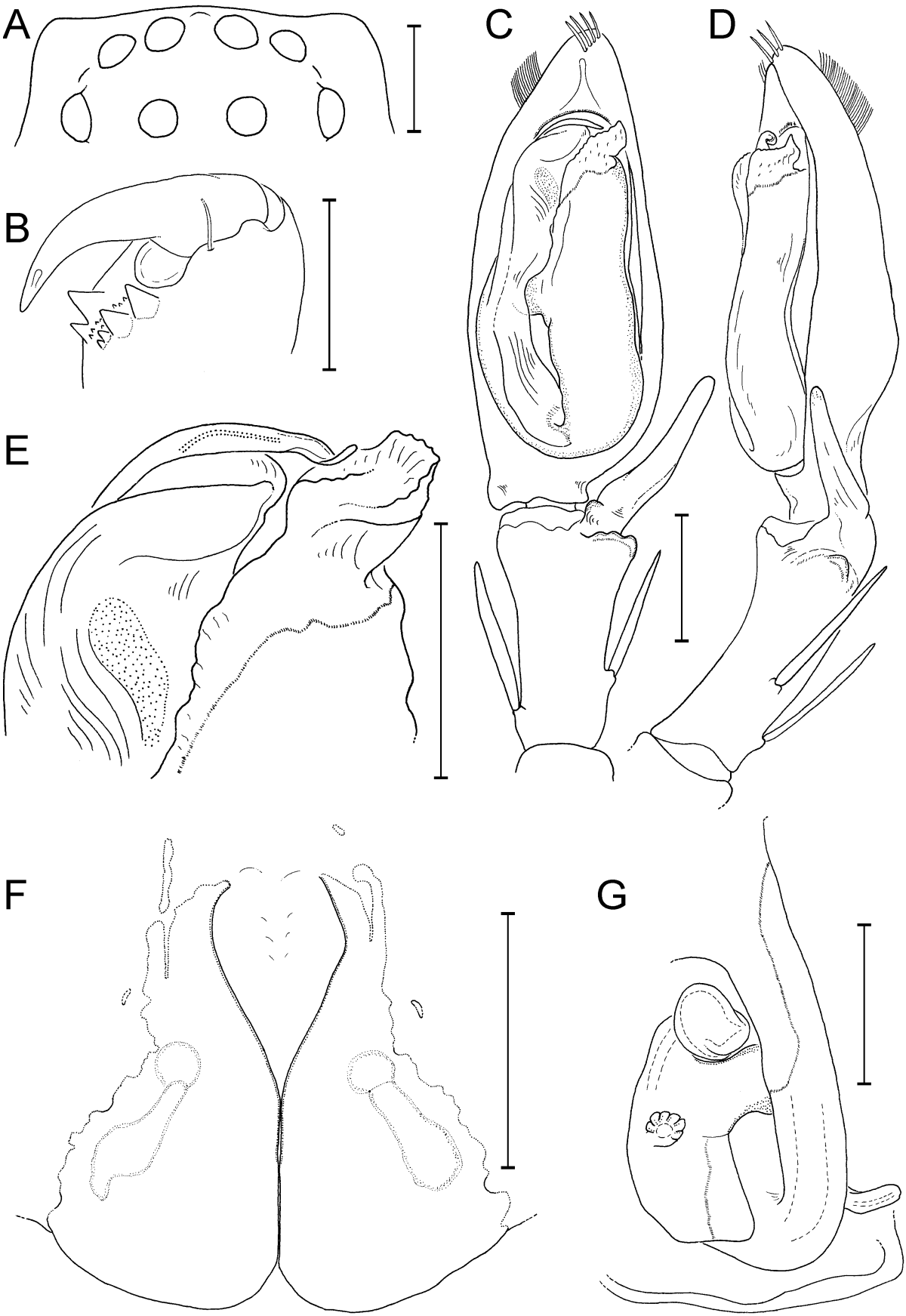

FIGURE 5. *Eusparassus walckenaeri* (Audouin, 1826), neotype male (A–E) from Cairo, Egypt (SMF). (A) eye arrangement, (B) left chelicera, ventral, (C) left palp, ventral, (D) left palp, retrolateral, (E) tip of embolus and conductor, ventral; female (F–G) from type locality (F) epigyne, ventral (G) left vulva, anterio-dorso-lateral. Scale bars: (A–D, F) 1 mm, (E, G) 0.5 mm.

Medium to large Sparassidae (body length 10–20 mm)

Total length: 13.4–20.6, prosoma length 6.1–8.6, prosoma width 5.7–7.8, anterior width of prosoma 2.8–4.0, opisthosoma length 7.3–12.0, opisthosoma width 4.3–6.4. Eye diameters (neotype): AME 0.47, ALE 0.50, PME 0.48, PLE 0.55; eye interdistances: AME-AME 0.25, AME-ALE 0.06, PME-PME 0.38, PME-PLE 0.50, AME-PME 0.50, ALE-PLE 0.31, clypeus height at AME 0.33, clypeus height at ALE 0.47.

Chelicerae with 2 anterior and 4 to 6 posterior teeth, Cheliceral furrow with denticles (Figure 5B); the number of denticles is variable (3–20), 3 to 10 denticles arranged in a single line (Figure 6E–G) or cluster of 10 to 20 denticles (Figure 5B); variation in denticles is not correlated to geographical distributions or to sexes. In one case even without denticles (one female from Damascus, Syria, ZMB). Basal segment of chelicerae at distal end in most cases with a single bristle (Figure 5B) or two bristles (Figure 6G);

Leg formula: 2 4 1 3. Measurements of palp and legs (neotype): Palp 13.2 [3.6, 1.8, 2.1, 5.7], I 44.6 [12.0, 4.7, 12.1, 12.3, 3.5], II 49.8 [13.5, 4.4, 14.1, 14.3, 3.5], III 41.5 [12.0, 4.0, 11.5, 11.0, 3.0], IV 46.0 [12.7, 4.0, 12.4, 13.5, 3.4].

Spination. Palp 131, 000/101, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 000(1)/101; Tibia I–IV 2024/2224; Metatarsus I–III 2024, IV 3036.

Palp. As in diagnosis with cymbium and tibia elongated, Cymbium longer than tibia, ET slender and hyaline, dRTA flattened dorso-ventrally, vRTA prominent and triangular in ventral view (Figure 5C, D).

Female (n=33)

Total length: 16.9–25.3, prosoma length 6.0–10.0, prosoma width 5.2–8.6, anterior width of prosoma 3.6–5.0, opisthosoma length 10.9–15.3, opisthosoma width 6.5–10.5. Eye diameters (female from the neotype locality): AME 0.50, ALE 0.47, PME 0.46, PLE 0.51, eye interdistances: AME-AME 0.24, AME-ALE 0.07, PME-PME 0.43, PME-PLE 0.42, AME-PME 0.38, ALE-PLE 0.22, clypeus height at AME 0.43, clypeus height at ALE 0.52. Eyes subequal.

Chelicerae with 2 anterior and 4 to 5 posterior teeth, Cheliceral furrow with denticles. Dentition variable, as in males. For instance, in three females (MHNG) obtained from Naxos

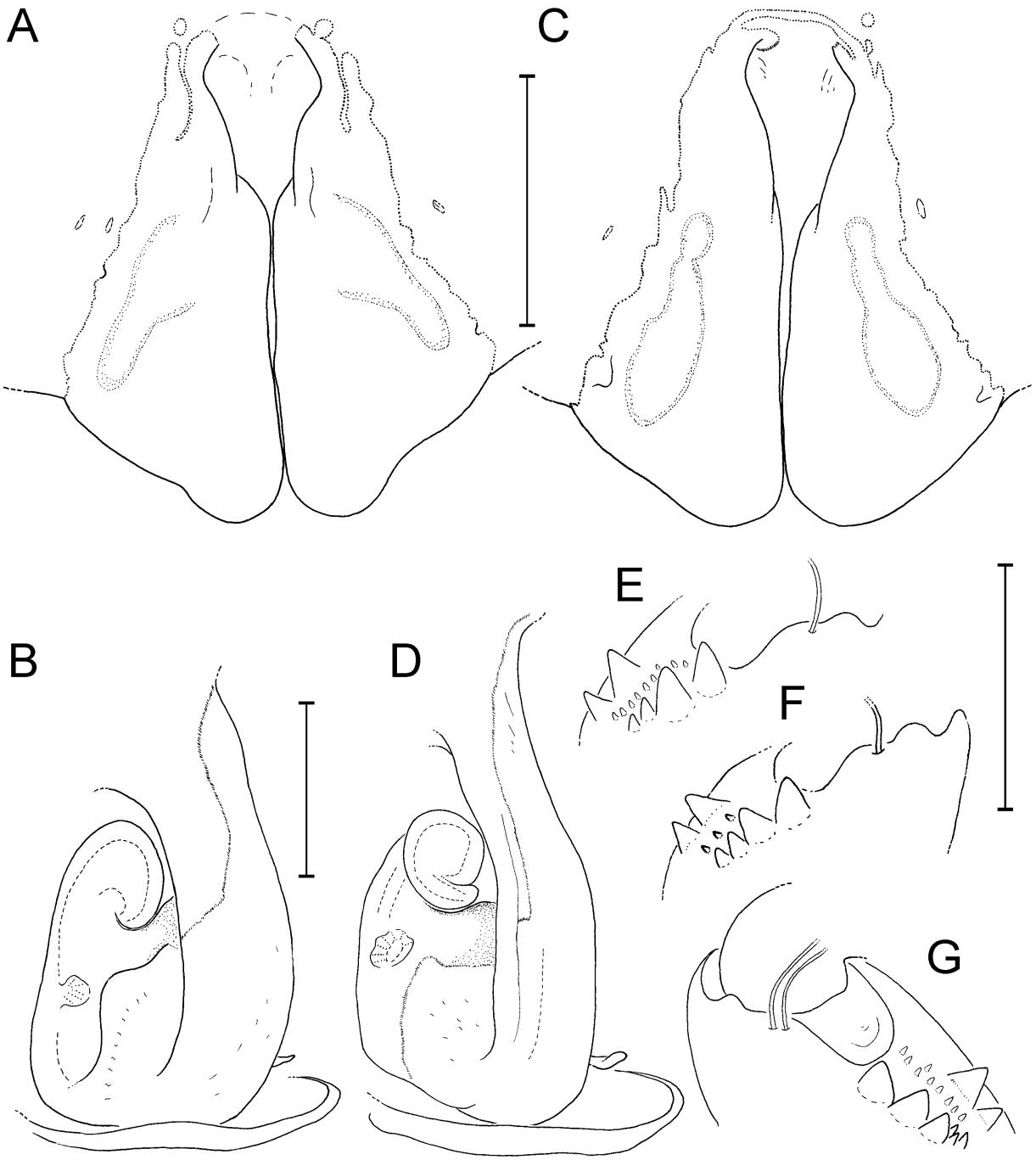

FIGURE 6. *Eusparassus walckenaeri* (Audouin, 1826), female copulatory organ variations, (A–B): Female from Greece, Samos Island, (A) epigyne, ventral (B) left vulva, anterio-dorso-lateral; (C–D): Female from Turkey, Milas: (C) epigyne, ventral (D) left vulva, anterio-dorso-lateral; (E–G) variations in chelicerae: number of bristles and intermarginal denticles, ventral. Scale bars: (A, C, E–G) 1 mm, (B, D) 0.5 mm.

Island (Aegean region, Greece), intermarginal denticle variations are observed. A female from Cyprus has no denticles at the cheliceral furrow but the copulatory organ is assumed to the species. Specimens from Greece (Paros, Lakonia, Skiathos, Samos and Lesbos Islands) in most cases have a line of denticles.

Leg formula: 2 4 1 3. Measurements of palp and legs (female from the neotype locality): Palp 9.8 [3.0, 1.5, 1.8, 3.5], I 31.5 [8.6, 3.7, 8.4, 8.5, 2.3], II 34.4 [10.0, 4.0, 9.1, 8.8, 2.5], III 29.6 [8.8, 3.5, 7.7, 7.4, 2.2], IV 32.6 [9.6, 3.1, 8.5, 9.0, 2.4].

Spination. Palp 131, 000/001, 1111, 1013; Legs: Femur I–III 323, IV 322; Patella I–IV 000(1)/101; Tibia I–IV 2024/2224; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis, with slight variations in epigyne relative length; epigyne may be elongated beyond epigynal furrow (Figure 6A, C); EFB in most specimens absent (Figures 5F, 6A), but if present only as thin bridge (Figure 6C).

Colouration. Dark brown to orange-brown in Turkey and Greece to milky cream in the Negev desert with darker patterns on prosoma; legs with distinct darker bands; dorsal opisthosoma with a series of small chevron-like patterns, ventral opisthosoma without marking (Figure 23A).

Remarks. Type material of *E. walckenaeri* was collected by French naturalist J. C. Savigny (1777–1851), who accompanied Napoleon on his military expedition to Egypt (1798–1801). Savigny was responsible for studying and collecting invertebrates (Fransen et al. 1997). Back in Paris, he produced his famous plates for the "Description de l'Egypte" in which he illustrated the type specimens (plate 6, figures 1, 2) but without any description. Audouin (1826) briefly explained Savigny's illustrations. In his sketchy explanation, Audouin proposed two names for the same species in the same plate. He named the female, figure 1, "*Philodromus walckenaerii*" and the male, figure 2, "*P. linnaei*". The type specimens cannot be traced since he never designated any (Alderweireldt 1996) therefore the plates were treated as the only 'types' for the name (Brignoli 1978). Since no name-bearing type material (other than the plate) is known to be extant, it is necessary to establish a neotype to maintain nomenclatural stability and reduce taxonomic confusion with morphologically similar species [i.e. *E. doriae* (Simon, 1874) **stat. nov.,** *E. kronebergi* Denis, 1958 **stat. nov.**] within the distribution range.

Neotype designation. The detailed locality in which Savigny collected the types was not recorded. According to the history of the expedition, it is assumed that most likely the collecting took placed around Cairo, since the scientists' team spent most of the time there (Fransen et al. 1997). Thus, Cairo is though to be putatively the type locality of this species. We select it from as nearly as practicable from the original type locality. Two males and one female sampled in Cairo were found in the collection of SNSD, and one male is here designated as neotype. The neotype male and the other male and female from the type locality, Cairo (determined by the neotype) fit well with the illustrations of original plate 6,

including general habitus, eye arrangements, chelicera and also accurate illustrated male palp (plate 6, figure 2d).

Note on doubtful records in Europe. A single male and four juveniles from Etruria, Italy (NHMW) were found to be conspecific with *E. walckenaeri*. Levy (1989) considered this material to be mislabelled, since there are no other records from Italy. In addition to these specimens, we found a vial containing three immatures from Sicily in NHMW which show somatic characters (presence of intermarginal denticles in chelicera, pale ventral opisthosoma and eyes arrangements) that agree well with those of *E. walckenaeri* description. Further records of *E. walckenaeri* in Europe from "Crimea, Ukraine" (sub *Sparassus validus*) [misunderstanding by Simon (1880) and Levy (1989)] is probably incorrect since both the original description and label mention "Taur." which refers to Taurus Mountains in western Turkey, Anatolia.

Known geographical distribution and habitat. The distribution range is restricted to eastern Mediterranean countries from Egypt to Greece and its eastern most distribution to Iraq in the Middle East. They are found in semidry areas under flat stones. In Greece, it is recorded that they are trogloxene, sporadically occurring underground (Deltshev 2011).

Eusparassus mesopotamicus spec. nov.

Figures 7 (A–E), 8 (A–E)

Type material. Holotype: male, **IRAN:** ***Khuzestan Province:*** Shush (32° 11' 39" N, 48° 14' 37" E), with label: Perse, Suse, 1904, de Morgan leg. (MNHN).

Paratypes (1♂, 2♀♀) **IRAN:** ***Khuzestan Province*****:** 1♂ with same data as for holotype (MNHN); 1♀, Ahwaz, semiarid desert, 1961, Schübart leg. (SMF); 1♀, 20 km north of Ahwaz, March 1958, Frank leg. (SMF).

Additional material examined. 1♀, **IRAQ:** Najaf, 19 July 1937, W.P. Kennedy leg. (NHM 1949.1.4.14).

Etymology. The species is named after Mesopotamia (the Land of Rivers), largely corresponding to modern day Iraq, south-eastern Turkey and south-western Iran where the species is distributed. adjective.

Diagnosis. Males can be distinguished from other congeners by the robust embolus tip which is S-shaped and directed proximo-distad in left palp, ventral view (Figure 7E), females are

similar to those of *E. walckenari* but differ in having glandular pores on distal end of glandular projection of vulva (Figure 8B, D, E); they differ from females of *E. doriae* **stat. nov.** in having AMLL of epigyne more extended and MS longer than wide (Figure 8A, C) in the latter species MS is wider than long.

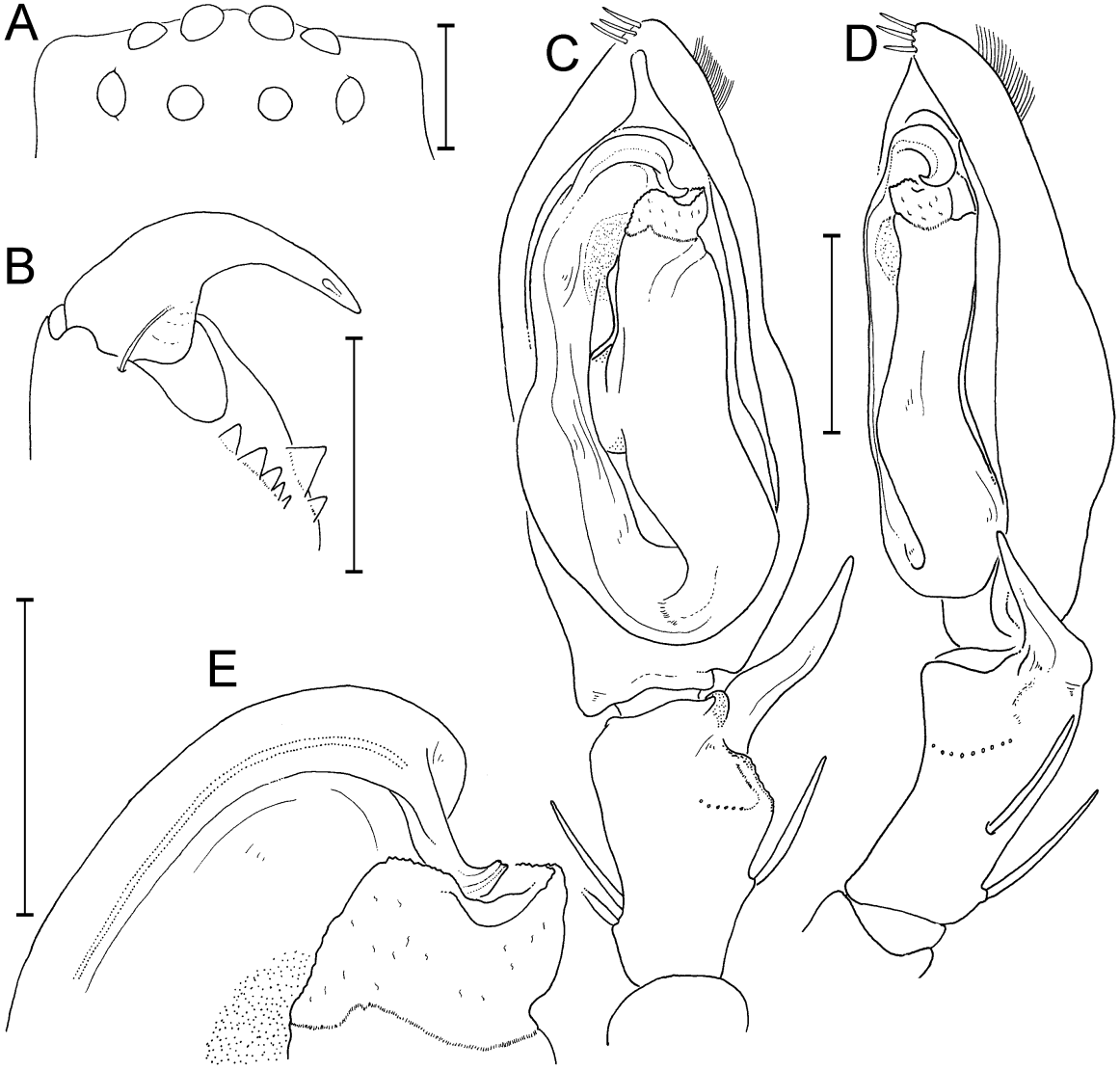

FIGURE 7. *Eusparassus mesopotamicus* **spec. nov.**, holotype male from Shush, Khuzestan Province, Iran. (A) eye arrangement, (B) left chelicera, ventral, (C) left palp, ventral, (D) left palp, retrolateral, (E) tip of embolus and conductor, ventral. Scale bars: (A–D) 1 mm, (E) 0.5 mm.

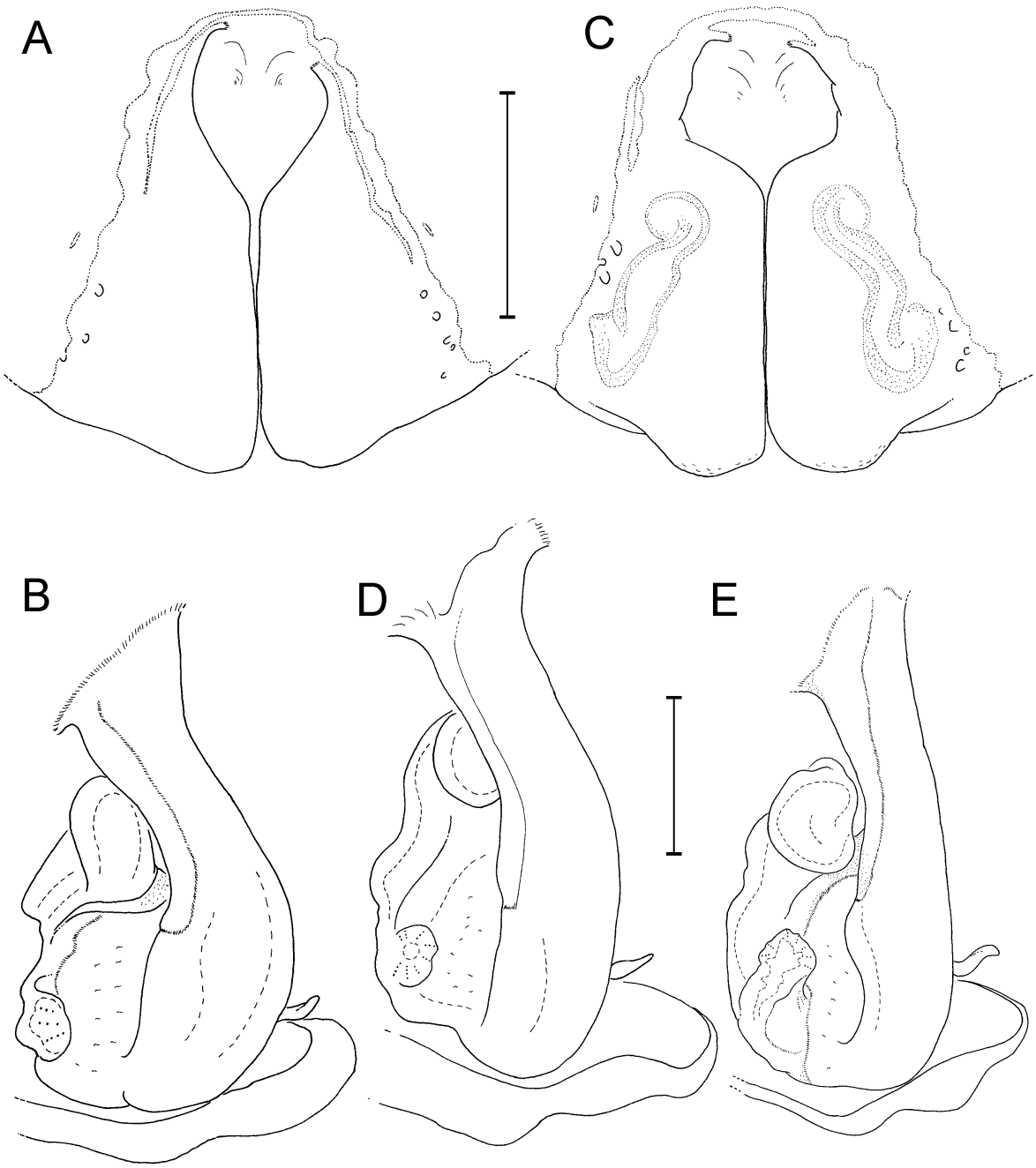

FIGURE 8. *Eusparassus mesopotamicus* **spec. nov.**, (A–B) paratype female, from Ahwaz, Khuzestan Province, Iran: (A) epigyne, ventral (B) left vulva, anterio-dorso-lateral; (C–D) paratype female, same locality, variations (C) epigyne, ventral (D) left vulva, anterio-dorso-lateral; (E) female from Nejef, Iraq: variation left vulva, anterio-dorso-lateral. Scale bars: (A, C) 1 mm, (B, D, E) 0.5 mm.

Description. Male (n=2)

Males medium-sized; holotype, total length: 16.1, prosoma length 7.6, prosoma width 6.7, anterior width of prosoma 3.5, opisthosoma length 8.5, opisthosoma width 5.5. Eye diameters: AME 0.46, ALE 0.40, PME 0.35, PLE 0.40, AME-AME 0.30, AME-ALE 0.08, eye interdistances: PME-PME 0.52, PME-PLE 0.46, AME-PME 0.45, ALE-PLE 0.28, clypeus height at AME 0.35, clypeus height at ALE 0.43.

Chelicerae with 2 anterior and 5 posterior teeth, cheliceral furrow without denticles (Figure 7B). Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 10.2 [2.5, 1.0, 1.2, 5.5], I 29.4 [8.2, 2.7, 8.1, 8.3, 2.1], II 32.2 [8.9, 3.0, 9.2, 8.6, 2.5], III 25.6 [7.3, 2.5, 7.2, 6.8, 1.8], IV 30.5 [8.6, 2.5, 8.1, 9.0, 2.3].

Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 001/101; Tibia I–IV 2124/2224; Metatarsus I–III 2024, IV 3034.

Palp. As in diagnosis with cymbium nearly two times longer than tibia, cymbium stout, dRTA shortened, when compared to cymbium, vRTA broad and not pointed (Figure 7C, D).

Female (n=3)

Total length: 20.5–25.5, prosoma length 8.5–9.5, prosoma width 7.0–7.8, anterior width of prosoma 4.3–4.7, opisthosoma length 12.0–16.0, opisthosoma width 7.2–9.5. Eye diameters: AME 0.55, ALE 0.47, PME 0.42, PLE 0.47. Eye interdistances: AME-AME 0.31, AME-ALE 0.08, PME-PME 0.67, PME-PLE 0.68, AME-PME 0.55, ALE-PLE 0.38, clypeus height at AME 0.35, clypeus height at ALE 0.45.

Chelicerae with 2 anterior and 5 to 6 posterior teeth; cheliceral furrow without denticles. Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 10.7 [3.5, 1.5, 2.0, 3.7], I 35.9 [10.3, 4.2, 9.5, 9.4, 2.5], II 39.3 [11.2, 4.5, 10.2, 9.8, 2.6], III 31.4 [9.3, 4.0, 8.3, 7.5, 2.3], IV 37.4 [11.3, 4.0, 9.7, 10.2, 2.2].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321/322; Patella I–IV 000; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034.

Epigyne/vulva. As in diagnosis with EFB present as narrow band, AMLL developed but not fused together, AMLL encircled partially MS (Figure 8A, C).

Colouration [in ethanol]. Cream to pale orange; ventral opisthosoma pale in colour.

Known geographical distribution. Iran (Khuzestan Province), Iraq (Najaf) and Turkey (Hakkari Province).

Eusparassus doriae (Simon, 1874) **stat. nov.**

Figures 9 (A–E), 10 (A–D)

Sparassus doriae Simon, 1874: 254, pl. 5, fig. 6 (description of male and female; syntypes, one male and female, examined).
Sparassus tersa – Simon, 1880: 291 (Simon listed *Sparassus doriae* as synonym of *S. tersa*, material from Iran).*Eusparassus tersus* – Roewer, 1955: 775 (misidentification; one male, one female and 2 juveniles examined, from Iran, Roewer collection, SMF).

Type material. Syntypes: 1 male, 1 female, **IRAN:** ***Tehran Province:*** Tehran, 1862–63, G. Doria leg. [(label: Jar n. 1663, Simon n. 1.557–Tehran (Doria) sub *Eusparassus tersa*] (MNHN).

Other material examined. 1♂ and 4♀♀, **IRAN:** ***Kerman Province:*** 1♂, 1♀, 2 juveniles, Jiroft, Maskun, [(label: Arachn. Coll. Rwr.-Ltd. No. 11454, *Eusparassus tersus* (C. L. Koch, 1838), Iran, Sabzawaran, Roewer det.1955), "Osterreichische Iran-Expedition 1949/50"], F. Starmühlner, H. Löffler and P. Kaltenbach leg. (SMF RII/11454); **IRAN:** ***Yazd Province*****:** 2♀♀, 10 km north east of Bafq, Bafq, 1258 m, 10 April 2004, V. Vignoli & P. Crucitti leg. (SMF); 1♀, West of Baghdad-Abad, Taft, 1502 m, 9 April 2004, V. Vignoli & P. Crucitti leg. (SMF). 1subadult ♀, 5 km south west of Taft, 1556 m, 13 April 2004, V. Vignoli & P. Crucitti leg. (SMF).

Diagnosis. Males differ from other congeneric males by tip of embolus leaf-like and directed retrolatero-proximad in left palp, ventral view (Figure 9E), dRTA compared to *E. walckenaeri* is slimmer and bent proximally, dRTA and vRTA are more widely spaced (Figure 9C, D). Females can be distinguished by epigynal field as long as wide (longer than wide in *E. mesopotamicus* **spec. nov.**) and AMLL are not extended anteriorly (Figure 10A, C) (extended in *E. walckenaeri*).

Description.

Male (n=2) [syntype first]

Prosoma length 6.7 (6.2), prosoma width 5.6 (4.7), anterior width of prosoma 3.1 (2.8), opisthosoma length 7.0 (6.7), opisthosoma width 4.5 (4.2). Eye diameters: AME 0.40, ALE 0.35, PME 0.33, PLE 0.36, Eye interdistances: AME-AME 0.20, AME-ALE 0.05, PME-PME

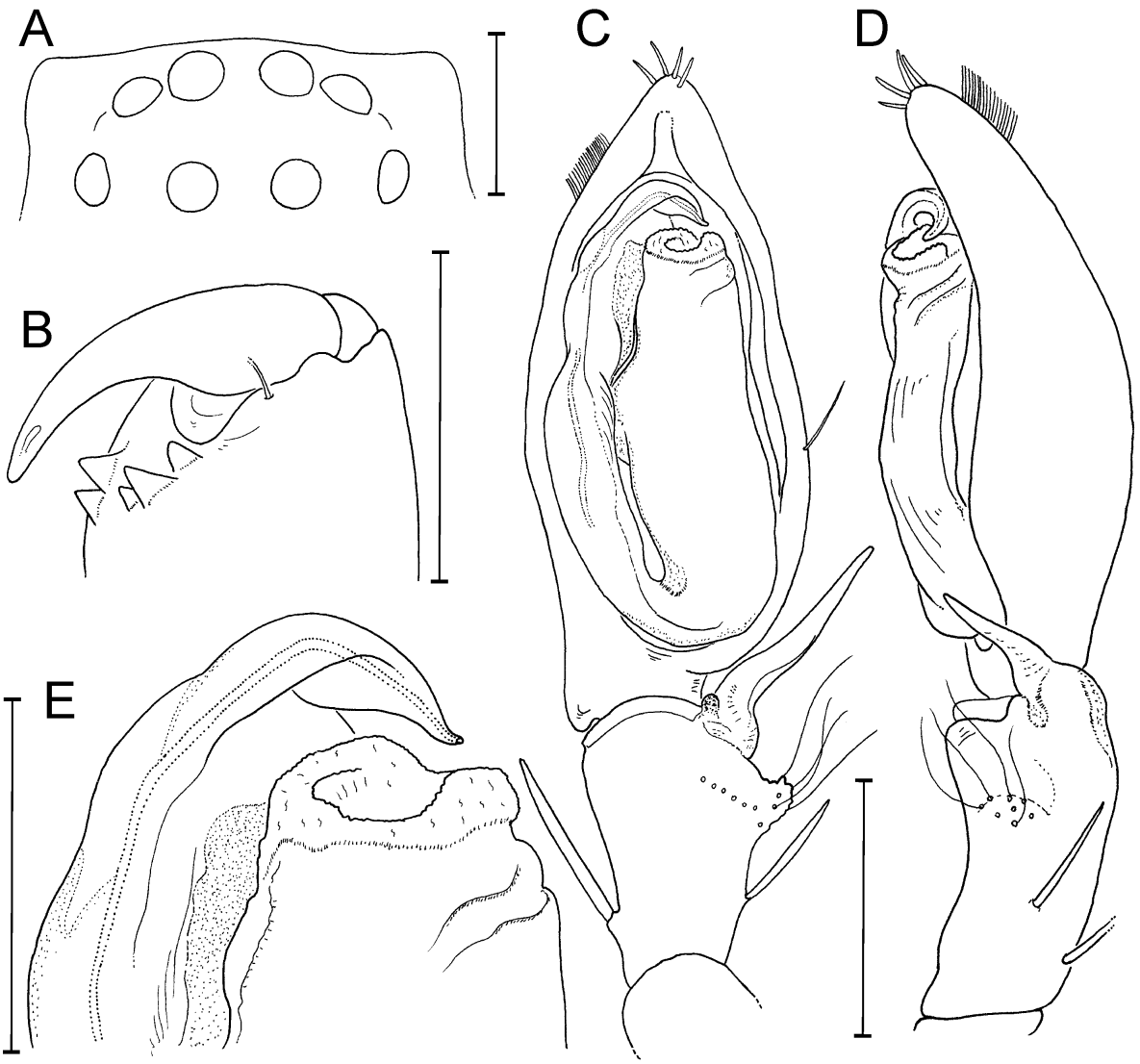

FIGURE 9. *Eusparassus doriae* (Simon, 1874) **stat. nov**., male from Jiroft, Kerman Province, Iran. (A) eye arrangement, (B) left chelicera, ventral, (C) left palp, ventral, (D) left palp, retrolateral, (E) tip of embolus and conductor, ventral. Scale bars: (A–D) 1 mm, (E) 0.5 mm.

0.37, PME-PLE 0.37, AME-PME 0.37, ALE-PLE 0.25, clypeus height at AME 0.18, clypeus height at ALE 0.27.

Chelicerae with 2 anterior and 3 posterior teeth; cheliceral furrow without denticles (Figure 9B). Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 8.5 [2.6, 1.2, 1.4, 2.9], I 30.4 [8.4, 3.1, 8.1, 8.2, 2.6], II 32.6 [9.3, 3.2, 9.0, 8.6, 2.5], III 27.7 [8.3, 2.9, 7.3, 7.1, 2.1], IV 32.2 [9.3, 2.7, 8.5, 9.2, 2.5].

Spination. Palp 131, 101, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 101; Tibia I–IV 2224; Metatarsus I–III 2024, IV 3034.

Palp. as in diagnosis with cymbium longer than tibia, vRTA developed (Figure 9C, D).

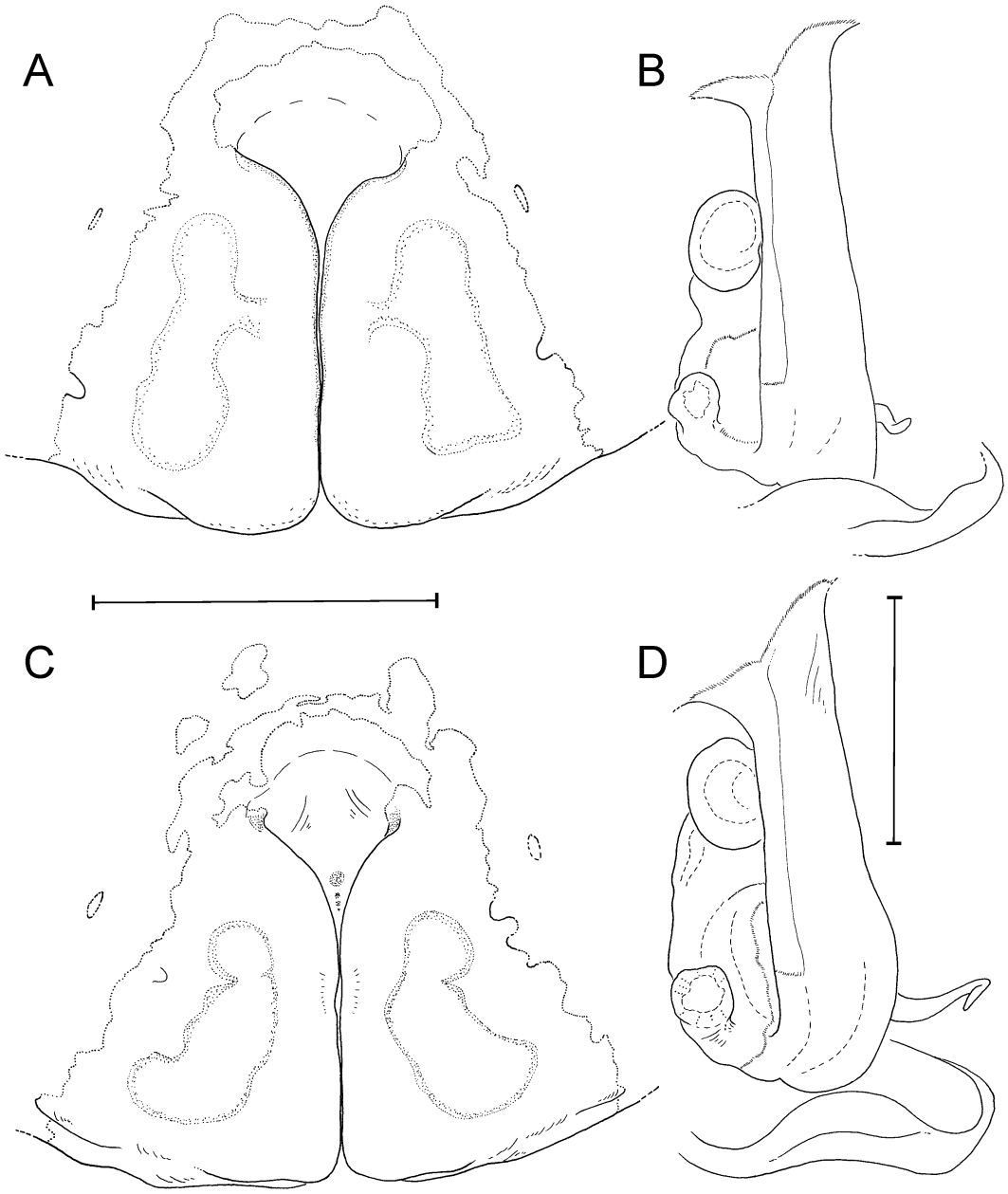

FIGURE 10. *Eusparassus doriae* (Simon, 1874) **stat. nov**., (A–B) syntype female from Tehran, Iran (A) epigyne, (B) left vulva, anterio-dorso-lateral; (C–D) female from Bafq, Yazd Province, Iran (C) epigyne, (D) left vulva, anterio-dorso-lateral. Scale bars: (A, C) 1 mm, (B, D) 0.5 mm.

Female (n=5)

Total length: 11.8–15.2, prosoma length 6.5–8.7, prosoma width 5.3–6.5, anterior width of prosoma 3.3–4.5, opisthosoma length 8.0–11.2, opisthosoma width 3.5–7.5. Eye diameters (syntype): AME 0.44, ALE 0.40, PME 0.36, PLE 0.38; Eye interdistances: AME-AME 0.20, AME-ALE 0.05, PME-PME 0.36, PME-PLE 0.42, AME-PME 0.40, ALE-PLE 0.23, clypeus AME 0.24, clypeus ALE 0.35.

Chelicerae with 2 anterior and 3 or 4 posterior teeth, cheliceral furrow without denticles; Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 7.4 [2.2, 1.1, 1.6, 2.5], I 22.8 [6.5, 2.8,

6.0, 5.8, 1.7], II 25.6 [7.7, 3.2, 6.7, 6.2, 1.8], III 21.6 [6.6, 2.7, 5.6, 5.2, 1.5], IV 25.5 [7.8, 2.7, 6.6, 6.7, 1.7].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 322; Patella I–IV 000; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034.

Epigyne/vulva. Epigyne as in diagnosis, EFB is wide, MS is wider than long (Figure 10A, C); vulva as in diagnosis with glandular pores situated at distal end of glandular process (Figure 10B, D).

Colouration. [in ethanol] cream to pale orange, dorsal opisthosoma with a patch and series of small chevron-like patterns and additional dots, ventral opisthosoma pale.

Remarks. *E. doriae* **stat. nov**. is here re-established. The species was described by Simon (1874) based on material obtained by Italian naturalist Giacomo Doria from Tehran (1862–63). Unfortunately, types in MCSN could not be traced and were most probably destroyed because of floods occurring in 1970 and 1990 (M.L. Tavano, personal communication). However, in the Simon collection (MNHN) we found one male and one female (syntypes) from the same expedition, which were taken to Paris by Simon. After the original description by Simon (1874), he himself in 1880 mistakenly synonymised the species with *Sparassus tersa* (C.L. Koch), currently a junior synonym of *E. walckenaeri*. Following Simon, Roewer (1955) working on material of "Austrian Iran-Expedition (Österreichische Iran-Expedition 1949/50)" from central Iran, Kerman Province misidentified the material as *E. tersus*. Subsequently, Levy (1989) moved this species to *E. walckenaeri*. *Sparassus fontanieri* Simon, 1880 is another nominal species for which the type material was probably collected from Iran. The type material was collected by M. Fontanier but the type locality is not clear, as stated by Simon (1880: 75): "...origin uncertain, probably from Persia (=Iran)...". Despite not locating the type specimen, Levy (1989) synonymised *E. fontanieri* with *E. walckenaeri*. The holotype male was recovered by us from MNHN and proved to be a synonym of *E. walckenaeri* , as Levy (1989) clarified. However, we found out that *E. doriae* **stat. nov.** is the only widespread *Eusparassus* species in central Iran.

Known geographical distribution and habitat. This species is distributed in Central Iran (Tehran, Kerman and Yazd Provinces). It occurs under large flat stones in dry mountainous areas (V. Vignoli personal observation) and near orchards under stones (first author personal observation).

Eusparassus kronebergi Denis, 1958 **stat. nov.**

Figure 11 (A–G)

Eusparassus kronebergi Denis, 1958: 99, figs 26–28 (description of male and female; syntypes: one male, one female, examined, **lectotype and paralectotype here designated**).
Sparassus walckenaeri – Levy 1989: 134 (listed *Sparassus kronebergi* as synonym of *S. walckenaeri*).

Type material: Lectotype: male, **AFGHANISTAN:** ***Seistan***, Faizabad, 14 February 1949, K. Paludan leg. (ZMUC 5671); **Paralectotype**: 1 female, ***Farah Province:*** Farah, (station 87), 18 June 1948, K. Paludan leg. (ZMUC 5675).
Other material examined. 2 ♂♂, **INDIA:** ***Rajasthan***, Suratgarh, D. Hummel leg. (NRM).
Diagnosis. Males of *E. kronebergi* can be distinguished from other congeners by vRTA (compared to that of *E. walckenaeri*) not well developed (Figure 11C, D) and embolus tip directed retrolateralo-distad, in ventral view (Figure 11E); in contrast to *E. walckenaeri*, epigyne with MS as wide as long, and to *E. doriae* **stat. nov.**, EF longer than wide (Figure 11F); vulva with a distinct crest laterally (Figure 11G).
Redescription.
Male (n=3) [lectotype first]
Males medium-sized. Total length: 12.8–18.2, prosoma length 5.6–8.9, prosoma width 4.8–7.6, anterior width of prosoma 2.6–3.7, opisthosoma length 7.2–9.3, opisthosoma width 4.5–5.5. Eye diameters (lectotype): AME 0.37, ALE 0.33, PME 0.32, PLE 0.33, eye interdistances: AME-AME 0.19, AME-ALE 0.07, PME-PME 0.40, PME-PLE 0.48, AME-PME 0.35, ALE-PLE 0.22, clypeus height at AME 0.23, clypeus height at ALE 0.38.
Chelicerae with 2 anterior and 4 posterior teeth; Cheliceral furrow without or with a single denticle, distal end of cheliceral basal segment with a single bristle (Figure 11B); Leg formula: 2 1 4 3. Measurements of palp and legs: Palp 10.5 [3.5, 1.6, 2.0, 3.4], I 26.6 [7.4, 2.9, 6.7, 7.3, 2.3], II 28.0 [7.9, 3.0, 7.5, 7.2, 2.4], III 23.4 [6.8, 2.6, 6.0, 6.1, 1.9], IV 26.2 [7.8, 2.5, 7.0, 7.5, 2.4].
Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 001/101; Tibia I–IV 2024/2224; Metatarsus I–III 2024, IV 3034.
Palp. As in diagnosis, with cymbium longer than tibia.

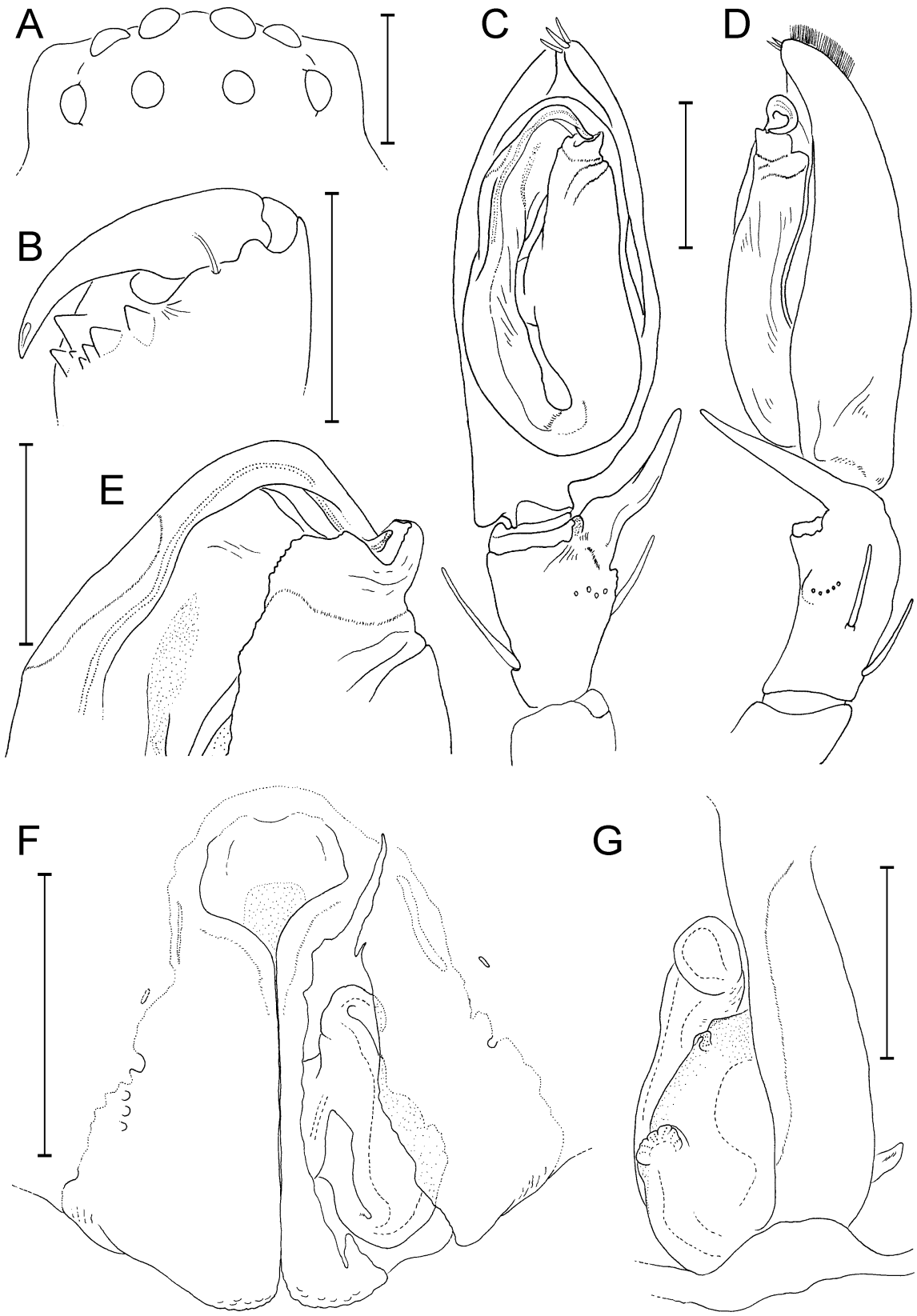

FIGURE 11. *Eusparassus kronebergi* Denis, 1958 **stat. nov**., (A–E) lectotype male from Faizabad, Sistan, Afghanistan. (A) eye arrangement, (B) left chelicera, ventral, (C) left palp, ventral, (D) left palp, retrolateral, (E) tip of embolus and conductor, ventral; (F–G) paralectotype female from Farah, Farah Province, Afghanistan (F) epigyne, (G) left vulva, anterio-dorso-lateral. Scale bars: (A–C, E) 1 mm, (D, F) 0.5 mm.

Female (n=1) paralectotype:

Prosoma length 4.8, prosoma width 3.9, anterior width of prosoma 2.6, opisthosoma length, opisthosoma width. Eye diameters: AME 0.34, ALE 0.30, PME 0.28, PLE 0.32, eye interdistances: AME-AME 0.20, AME-ALE 0.05, PME-PME 0.37, PME-PLE 0.31, AME-PME 0.26, ALE-PLE 0.16, clypeus height at AME 0.18, clypeus height at ALE 0.28.

Chelicerae with 2 anterior and 3 to 4 posterior teeth; cheliceral furrow without denticles. Leg formula: 24=13 (leg IV and I are the same size). Measurements of palp and legs: Palp 6.6 [1.8, 0.9, 1.3, 2.6], I 18.6 [5.2, 2.2, 4.8, 4.7, 1.7], II 20.1 [5.9, 2.5, 5.3, 4.9, 1.8], III 16.5 [4.8, 2.1, 4.2, 3.9, 1.5], IV 18.7 [5.6, 2.1, 4.9, 4.5, 1.6].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321; Patella I–IV 000; Tibia I 1024, II 2024, III (1014)2024, IV 2024; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF longer than wide, EFB present (Figure 11F); vulva has two separate glandular parts located near a ridge laterally (Figure 11G).

Colouration. [in ethanol] pale brown, dorsal opisthosoma with a patch and series of small chevron-like patterns, ventral opisthosoma pale.

Remarks. Morphological evidence allows this species to be withdrawn from the synonymy (Levy 1989) with *E. walckenaeri*. Syntypes were collected in Afghanistan during "the 3rd Danish Expedition to Central Asia". These are one male and one female collected allopatrically. There is the possibility that they are not conspecific. Consequently, to designate a unique bearer of the name of the nominal species (Article 74), we select the male to be the lectotype of *E. kronebergi* **stat. nov.** to fix the status of the species. Two other males sampled from Rajastan were found to be conspecific. This is the first record of the species from India

Known geographical distribution. Western Afghanistan; India: Rajastan (new record).

Eusparassus fuscimanus Denis, 1958

Figures 12 (A–D), 13(A–F), 14 (A–E)

Eusparassus fuscimanus Denis, 1958: 100, fig. 29 (description of female; syntypes, two females, Afghanistan, examined). – Roewer, 1962: 4, figs 82–84 (description of male; Lund collection, not available).
Sparassus fuscimanus – Levy, 1989: 137, fig. 27.

Type material: Syntypes: 1 female, **AFHANISTAN:** ***Nuristan***, Wama (35° 7' 15 N, 70° 44' 30 E), 2250 meters, under stone, 17 April 1948, K. Paludan leg. (ZMUC 5670); 1 female and 1 juvenile, **Afghanistan:** Central Afghanistam: ***Puistagoli***, Koh-i-baba, 1 July 1948, N. Haarløv leg. (ZMUC 5673).
Other material examined. 1♂, 5 ♀♀, **AFGHANISTAN**: ***Nangarhar Province***: Jalal-abad (34° 25' 34 N, 70° 27' 5 E)**:** countryside of Jalal-abad: 1♂, 01 March 1965, D. Povolnỳ leg. (MMB); 10 km east of Jalal-abad: 1♀, 620 m altitude, 22 February 1966, Povolnỳ and Tenora leg. (18 MMB); 12–20 km east of Jalal-abad: 1♀, 600 m altitude, 8 March 1966, Povolnỳ and Tenora leg. (27 MMB); Jalal-abad: 1♀, 580 m altitude, 15 April 1967, D. Povolnỳ leg. (97 MMB); Jalal-abad: 1♀, 580 m altitude, 3 May 1967, D. Povolnỳ leg. (114 MMB); Dareyhe-Nur (34° 44' 11" N, 70° 39' 28" E), 1♀, 2470 m altitude, 19 March 1967, D. Povolnỳ leg. (114 MMB).

Diagnosis. Female epigyne similar to that of *E. doriae* **stat. nov.** in having EF as long as wide but can be differentiated by AMLL extended anteriorly (Figure 13C, E), vulva exhibits a lateral ridge which separates the hyaline part of copulatory duct from the more sclerotised part of internal duct system (Figure 13D, F), this ridge is absent in vulvas of *E. doriae* **stat. nov.** *Eusparassus fuscimanus* can also be distinguished by the eye interdistances (Figure 13A), AME-ALE is spaced ½ of AME-AME (as in *E. pontii*) since in *E. doriae* **stat. nov.** this relative distance is ¼. Male can be distinguished from other *Eusparassus* males by long and enlarged embolus tip pointed proximad not covered by EM (Figure 12D).

Redescription.

Male (n=1)

Total length: 16.1, prosoma length 8.1, prosoma width 6.4, anterior width of prosoma 3.5, opisthosoma length 8.0, opisthosoma width 6.0. Eye diameters: AME 0.43, ALE 0.40, PME

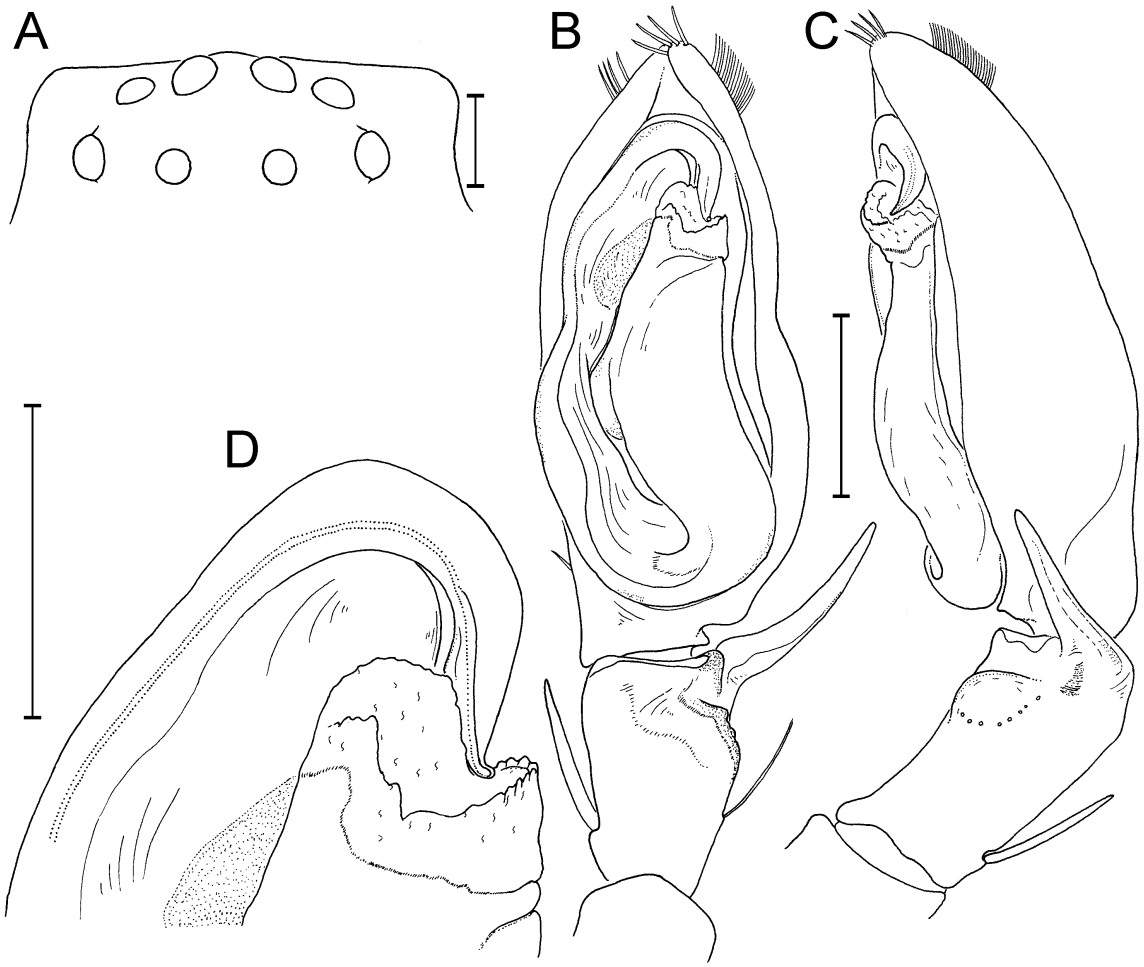

FIGURE 12. *Eusparassus fuscimanus* Denis, 1958, male from Jalalabad, Nangarhar Province, Afghanistan. (A) eye arrangement, (B) left palp, ventral, (C) left palp, retrolateral, (D) tip of embolus and conductor, ventral. Scale bars: (A–C) 1 mm, (D) 0.5 mm.

0.33, PLE 0.38, eye interdistances: AME-AME 0.19, AME-ALE 0.11, PME-PME 0.53, PME-PLE 0.47, AME-PME 0.31, ALE-PLE 0.24, clypeus height at AME 0.27, clypeus height at ALE 0.35.

Chelicerae with 2 anterior and 6 posterior teeth; cheliceral furrow without denticles. Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 9.9 [3.5, 1.4, 1.3, 3.7], I 34.3 [9.3, 3.8, 9.2, 9.5, 2.5], II 37.4 [10.4, 4.1, 10.1, 10.3, 2.5], III 31.4[9.1, 3.5, 8.5, 8.2, 2.1], IV 35.3 [10.0, 3.4, 9.5, 10.0, 2.3].

Spination. Palp 131, 101(0), 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 101; Tibia I–IV 2224; Metatarsus I–III 2024, IV 3034.

Palp. As in diagnosis with cymbium approximately two times longer than tibia, dRTA slender and pointed distally, vRTA broad (Figure 12B, C); stout ET not covered by EM (Figure 12D).

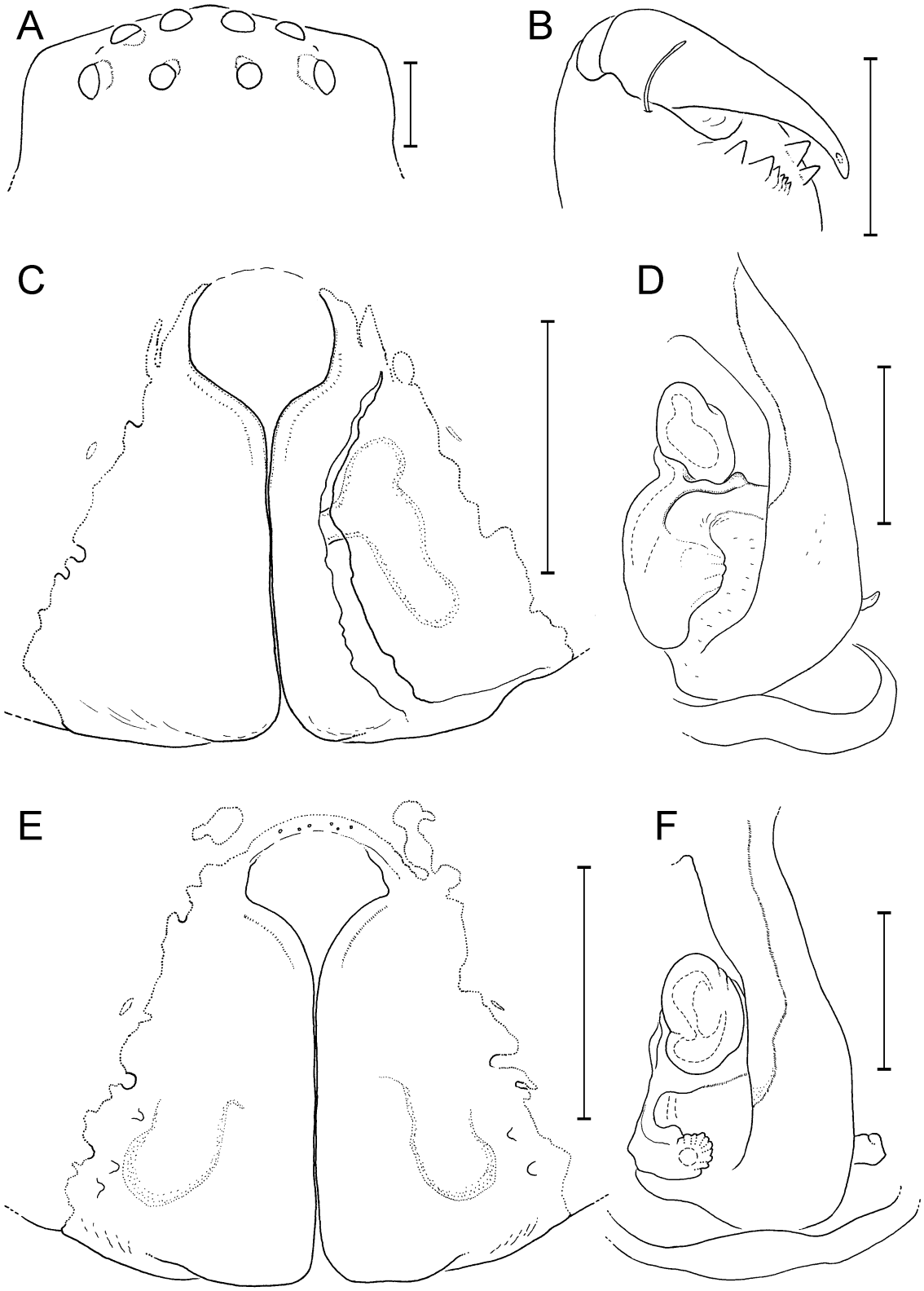

FIGURE 13. *Eusparassus fuscimanus* Denis, 1958, (A–D) syntype female from Nuristan, Wama, Afghanistan (A) eye arrangement, (B) left chelicera, ventral, (C) epigyne, ventral (D) left vulva, anterio-dorso-lateral; (E–F) syntype female from Puistagudi, Kohi-baba, Afghanistan (E) epigane, ventral (F) left vulva, anterio-dorso-lateral. Scale bars: (A–C, E) 1 mm, (D, F) 0.5 mm.

Female (n=7):
Total length: 16.1–18.3, prosoma length 5.9–8.0, prosoma width 5.0–6.3, anterior width of prosoma 3.0–4.0, opisthosoma length 10.2–10.3, opisthosoma width 7.0–7.3. Eye diameters: AME 0.42, ALE 0.36, PME 0.35, PLE 0.34, eye interdistances: AME-AME 0.28, AME-ALE 0.18, PME-PME 0.55, PME-PLE 0.53, AME-PME 0.47, ALE-PLE 0.41, clypeus height at AME 0.24, clypeus height at ALE 0.35.

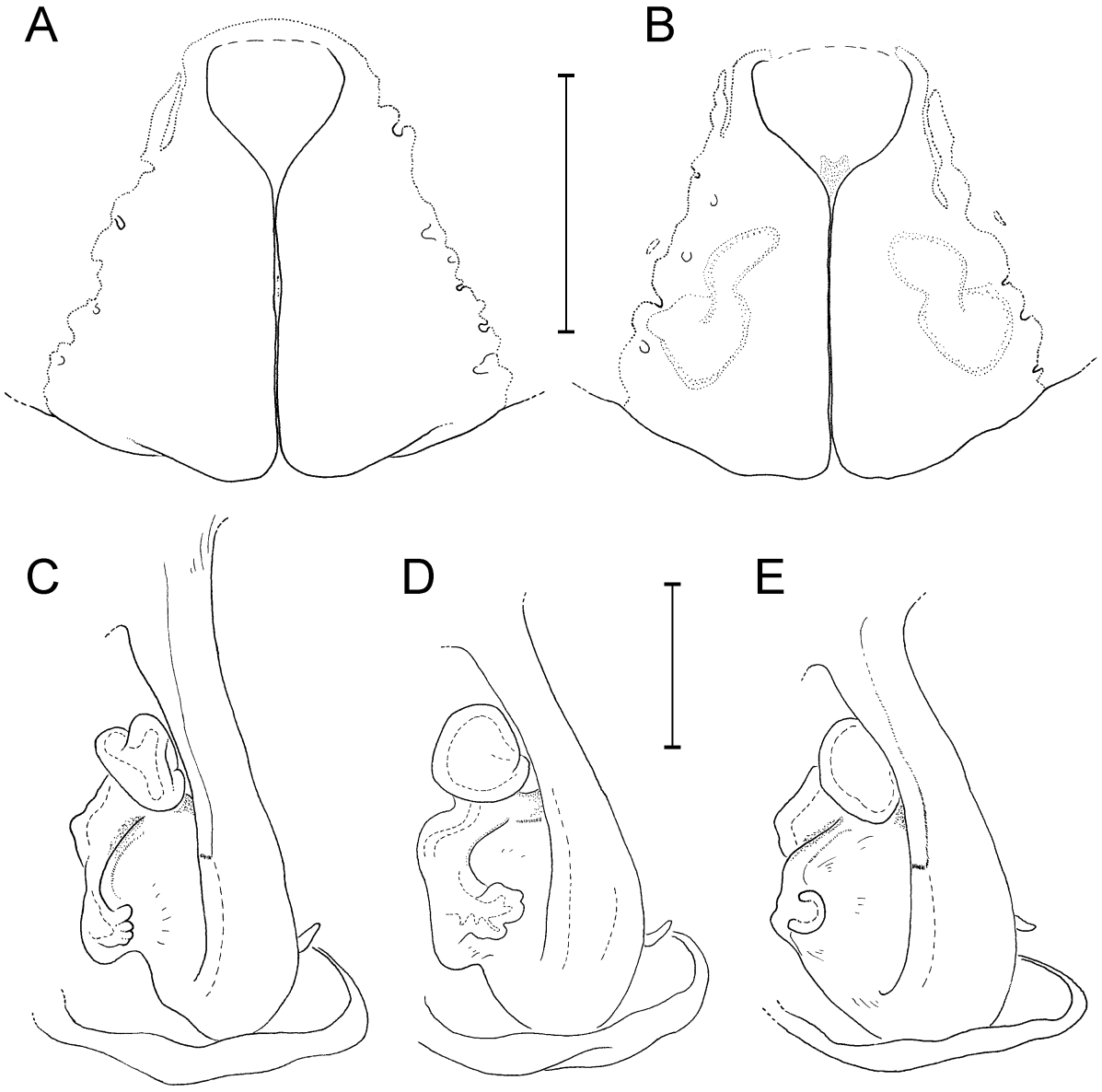

FIGURE 14. *Eusparassus fuscimanus* Denis, 1958, variations in females from Jalalabad, Nangarhar Province, Afghanistan (A) epigyne, ventral (B) left vulva, anterio-dorso-lateral; (C) epigyne, ventral (D) left vulva, anterio-dorso-lateral; (E) left vulva, anterio-dorso-lateral, variation from Dareye-noor, Afghanistan. Scale bars: (A, C) 1 mm, (B, D, E) 0.5 mm.

Chelicerae with 2 anterior and 4 to 8 posterior teeth, posterior teeth start with 3 large distal and 1–5 small proximal teeth, cheliceral furrow without denticles (Figure 13B).

Spination: Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321; Patella I–IV 000; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034. Leg formula: 2 4 1 3. Measurements of palp and legs of the largest female syntype: Palp 8.8 [2.8, 1.4, 1.6, 3.0], I 23.3 [6.7, 3.0, 5.9, 5.6, 2.1], II 27.0 [8.1, 3.4, 6.8, 6.7, 2.0], III 23.1 [7.0, 3.1, 5.8, 5.4, 1.8], IV 25.9 [7.9, 3.0, 6.5, 6.7, 1.8].

Epigyne/vulva. As in diagnosis, EF as wide as long or slightly wider than long (Figure 14A, C); vulva with TL slightly variable in shape (Figure 14B, D, E).

Colouration [in ethanol]. Cream to pale orange, dorsal opisthosoma with a patch and series of small chevron-like patterns and additional dots, ventral opisthosoma pale.

Remarks. The type specimens were collected during "the 3rd Danish Expedition to Central Asia" in Afghanistan conducted by K. Paludan (South and East) and N. Haarløv (North, West and Centre) from May to August 1948. The specimens, two females and one juvenile, were deposited in ZMUC and described later by Denis in 1958. Knut Lindberg (1892–1962) from Lund, Sweden, conducted an expedition to Afghanistan between 1957 and 1960. Later on, Roewer (1962) found one female and one male in the collection of Knut Lindberg (MZLU) and described the male for the first time. Unfortunately, this material could not be traced. Fortunately, an important and rich collection of spiders from Jalal-Abad, Afghanistan exists in MMB which was included in the present study; several females and one male of *E. fuscimanus* are properly described here.

Known geographical distribution and habitat preferences. *Eusparassus fuscimanus* is recorded from a dry wooded valley in Wama, Nuristan (1500 m) to higher elevation in the Baba Mountain range, central Afghanistan (3500 m). Spiders were found under stones.

Eusparassus oculatus (Kroneberg, 1875)

Figures 15 (A–E), 16 (A–E)

Sparassus oculatus Kroneberg, 1875: 29, pl. 5, fig. 45 (description of male and female; syntypes, one male and two females, examined). – Levy, 1989: 137, figs 28–29.

Eusparassus oculatus – Denis, 1958: 102, fig. 30 (transfer, one female from Afghanistan, examined); Reimoser, 1919: 200; Schenkel, 1936: 9, 283; Song et al., 1999: 467, fig. 268; Jäger & Yin, 2001: 132.

Type material: Syntypes: 1 male, 1 juvenile, **UZBEKISTAN:** ***Samarqand province*** (=***Turkestan)***, Samarkand, 1870, Narkevich leg. (ZMMU 4261); **Syntypes:** 2 females, 1 juvenile, **UZBEKISTAN:** ***Samarqand province*** (=***Turkestan)***, Samarkand, 1870, Narkevich leg. (ZMMU 1358).

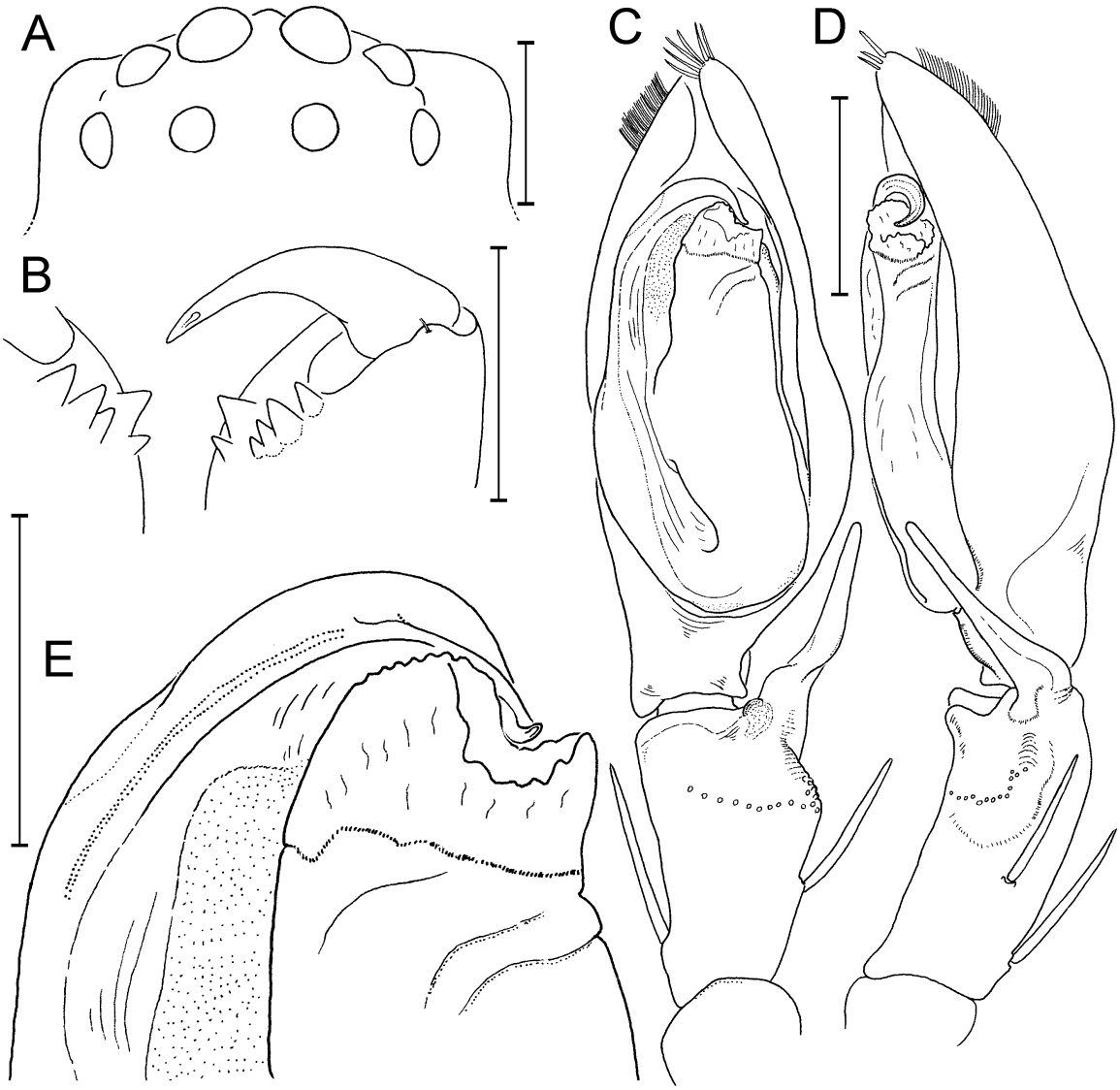

FIGURE 15. *Eusparassus oculatus* (Kroneberg, 1875), male from Zarafshan, Uzbekistan. (A) eye arrangement, (B) left and part of right chelicera, ventral, (C) left palp, ventral, (D) left palp, retrolateral, (E) tip of embolus and conductor, ventral. Scale bars: (A–D) 1 mm, (E) 0.5 mm.

Other material examined. UZBEKISTAN: 2 ♂♂, 1 ♀, ***Navoiy Province,*** Zarafshan, 20 April 1998, A. V. Gromov leg. (SZMN); 2 ♂♂, 1 ♀, 1 juvenile, Babatagh, Mt. Range near Ak-Mechet, summer 1999, O. V. Lyakhov leg. (SZMN); 1 ♂, 2 juveniles, *Navoiy Province*, Zarafshan, 20 July 1998, A. V. Gromov leg. (SZMN); 1 ♀, Turkestan (SMF13366); **TAJIKISTAN:** 2 ♀♀, Aktau Range, near Gasavuti, 16 April 1973, A. P. Kohonean leg. (SZMN); 1 ♂, Gazavuti, Vakhsh riverside, 18 April 1974, A. P. Kononenko leg. (SZMN); 1 ♂, Hyssaz, Mt. Range near Shuzkhak, 23 May 1974, Naszetdinov leg. (SZMN); **TURKEMINISTAN:** 1 ♀, 30 km NE of Gazhgy, Kushka, Badkhyz Reserve, 09 April 1993, D. Logunov leg. (SZMN); 1 ♀, 12 km N of Chemenedit, 18 April 1994, A. A. Zyuzin leg. (SZMN); 1 ♀, Badkhyz Reserve, Kzyl-Dzhar Canyon, A. Gulikov leg. (SZMN); 1 ♂,

Ashgabad, Croweb leg. (ZMB 31200); **AFGHANISTAN:** 1 ♀, Herat (st. 76), 14 June 1948, Central Asiatische Expedition. (ZMUC).

Diagnosis. This is the only *Eusparassus* species in Eurasia with AME strikingly larger than the other eyes (1.5 times larger than ALE) (Figure 15A). *E. oculatus* can also be recognizable by ET short and pointed proximo-ventrad (Figure 15E) (larger and stouter than in *E. kronebergi* **stat. nov.**); vRTA broad and not well developed (Figure 15C, D) (in contrast, that of *E. potanini* enlarged and prominent); in contrast to other species' females, EFB absent and AMLL not developed around MS laterally (Figures 16A, B).

Redescription.

Male (n=8):

Total length: 10.1–15.1, prosoma length 5.1–6.3, prosoma width 4.5–5.6, anterior width of prosoma 2.5–3.1, opisthosoma length 5.0–8.8, opisthosoma width 2.6–4.5. Eye diameters: AME 0.51, ALE 0.33, PME 0.34, PLE 0.33; eye interdistances: AME-AME 0.17, AME-ALE 0.08, PME-PME 0.43, PME-PLE 0.42, AME-PME 0.33, ALE-PLE 0.26, clypeus height at AME 0.27, clypeus height at ALE 0.33.

Chelicerae with 2 anterior and 3 to 5 posterior teeth, cheliceral furrow without denticles (Figure 15B). Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 9.7 [3.2, 1.3, 1.6, 3.6], I 35.0 [9.5, 3.5, 9.2, 9.8, 3.0], II 38.6 [10.4, 3.7, 10.5, 10.8, 3.2], III 31.8 [9.2, 3.1, 8.5, 8.3, 2.7], IV 36.6 [10.5, 3.0, 9.5, 10.6, 3.0].

Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 000/101; Tibia I–IV 2024/2124; Metatarsus I–III 2024, IV 3034.

Palp. As in diagnosis with embolus tip short, vRTA not well developed, dRTA slender and directed ventral-distad (Figure 15C, D).

Female (n=11):

Total length: 15.7–23.5, prosoma length 6.2–7.0, prosoma width 5.0–5.6, anterior width of prosoma 3.0–3.5, opisthosoma length 9.5–16.5, opisthosoma width 6.5–10.3. Eye diameters (largest female, MM96): AME 0.49, ALE 0.35, PME 0.31, PLE 0.34, eye interdistances: AME-AME 0.23, AME-ALE 0.07, PME-PME 0.48, PME-PLE 0.45, AME-PME 0.38, ALE-

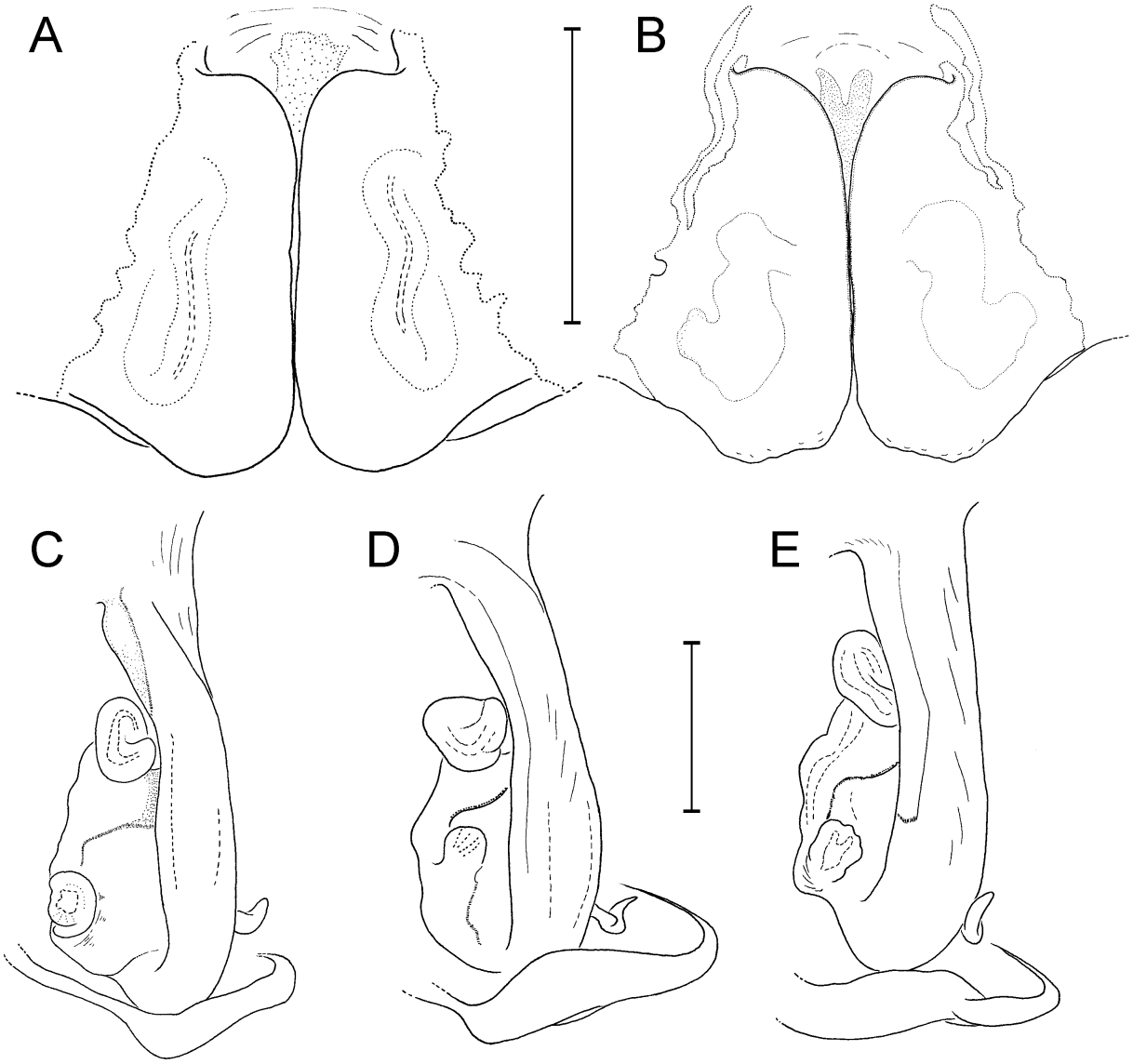

FIGURE 16. *Eusparassus oculatus* (Kroneberg, 1875) (A) epigyne, ventral, of syntype female from Samarkand, Uzbekistan; (B–C) female from Zarafshan, Uzbekistan (B) epigyne, ventral (C) left vulva, anterio-dorso-lateral; (D) variation of vulva, female from Tajikistan, (E) variation of vulva, female from Turkmenistan. Scale bars: (A, B) 1 mm, (C–E) 0.5 mm.

PLE 0.27, clypeus height at AME 0.31, clypeus height at ALE 0.40. Eyes other than AME are in similar size range, AME largest.

Chelicerae with 2 anterior and 3 to 5 posterior teeth. Cheliceral furrow without denticles. Leg formula: 2413. Measurements of palp and legs (largest female, MM96): Palp 8.7 [2.5, 1.3, 1.8, 3.1], I 27.2 [7.6, 3.5, 7.0, 6.9, 2.1], II 29.8 [8.7, 3.5, 8.2, 7.2, 2.2], III 24.3 [7.3, 3.0, 6.3, 5.7, 2.0], IV 28.4 [8.5, 3.0, 7.2, 7.6, 2.1].

Spination. Palp 131, 000/001, 1111, 1013; Legs: Femur I–III 323, IV 322; Patella I–IV 000/101; Tibia I–IV 2024/2124; Metatarsus I–III 2024, IV 3034.

Epigyne/vulva. As in diagnosis with AMLL parallel to epigastric furrow, AMLL not extended anterioraly, EFB absent (Figure 16A, B); in vulva, glandular pores are located at the tip of a projection, TL slightly variable in shape among different specimens (Figure 16 C–E).

Colouration [in ethanol]. pale cream, dorsal opisthosoma with a patch and series of small chevron-like patterns and additional dots, ventral opisthosoma pale.

Remarks. The type material was collected during the "Scientific Expedition to Turkestan" conducted by Alexis Fedtschenko to Central Asia, Samarkand. After its original description by Kroneberg (1875) from Uzbekistan, it was recorded again by Denis (1958) from Afghanistan. Here we present further new records from Tajikistan and Turkmenistan based on material deposited in SZMN.

Known geographical distribution. Central Asia including Afghanistan, Uzbekistan, Tajikistan, Turkmenistan and China: Xinjiang Uyghur.

Eusparassus potanini (Simon, 1895)

Figure 17 (A–G)

Sparassus potanini Simon, 1895: 340–341 (description of male; holotype, male, examined).

Eusparassus potanini Reimoser, 1919: 200.

Heteropoda nanjiangensis Hu & Fu, 1985: 92–93, figs 1–7. [description and illustration of male and female; female holotype, male paratype, label: Tulufan (Putaogou), Xinjiang Uygur Autonomous Region, 5.7. 1982, by J. L. Hu) IOZB, examined] – Hu & Wu, 1989: 310, figs 248, 1–7. **New synonymy**

Sparassus nanjianensis – Levy, 1989: 134 (suspected synonymy).

Eusparassus nanjianensis – Song et al., 1999: 467, fig. 268H, K.

Eusparassus nanjiangensis – Jäger & Yin, 2001: 132.

Type material: Holotype: male, **CHINA:** ***Nan-Shan-Kou***, Tjan-Shan, 10 June 1877, M.G. Potanin leg. (ZIP 164).

Additional material examined. CHINA: ***Xinjiang Uyghur*****:** 1 ♀, Kashi (Kashgar), 5 July 1975 (IOZB); 1 ♀, Kashi (Kashgar), 15 July 1996. (IOZB 107); 1 ♂, 1 ♀ and 2 juveniles, Jarkend, 1909, G. Raquelle leg. (NRM); 1 ♀, Turpan, Jh. Basfus leg. (ZMB); 2♀♀, (Label: Turkestan)**:** Kashgar. (SMF 6085); 1 ♂, 1 immature ♀, Kashgar, E. Turkestan D. Lamsdell leg. (NHM 1889.4.25.2-3).

Diagnosis. Males of *E. potanini* are characterised by a combination of characters including beak-like dRTA, a deep retro-lateral incision at proximal part of cymbium (Figure 17C) and broad retrolatero-distad embolus tip (Figure 17E); in female epigyne, EFB present but distinctly separated from AMLL, approximately as long as MS length (Figure 17F).

Redescription.

Male (n=4) [Holotype first]

Males medium-sized. Total length: 14.2–17.3, prosoma length 7.4–7.8, prosoma width 6.2–6.6, anterior width of prosoma 3.1–3.3, opisthosoma length 6.8–9.5, opisthosoma width 4.4–5.1.

Eye diameters (holotype): AME 0.47, ALE 0.44, PME 0.36, PLE 0.45, AME-AME 0.22, eye interdistances: AME-ALE 0.10, PME-PME 0.42, PME-PLE 0.46, AME-PME 0.31, ALE-PLE 0.21, clypeus height at AME 0.37, clypeus height at ALE 0.42.

Chelicerae with 2 anterior and 4 or 5 posterior teeth. Cheliceral furrow without denticles (Figure 17B). Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 10.3 [3.2, 1.5, 1.7, 3.9], I 35.6 [10.0, 3.4, 9.5, 9.3, 2.4], II 38.9 [10.6, 4.1, 10.7, 10.8, 2.7], III 31.6 [9.6, 3.4, 8.8, 8.5, 2.3], IV 36.6 [10.5, 3.4, 10.0, 10.3, 2.4].

Spination. Palp 131, 001, 1111; Legs: Femur I–III 323, IV 322/321; Patella I–IV 101; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034.

Palp. As in diagnosis with dRTA proximally wide and pointed distally, vRTA is triangular in ventral view (Figure 17C).

Female (n=6):

Total length: 15.7–19.6, prosoma length 7.3–8.1, prosoma width 6.0–7.0, anterior width of prosoma 3.5–4.0, opisthosoma length 8.4–11.5, opisthosoma width 6.0–8.1.

Eye diameters: AME 0.48, ALE 0.40, PME 0.38, PLE 0.43, eye interdistances: AME-AME 0.28, AME-ALE 0.13, PME-PME 0.47, PME-PLE 0.50, AME-PME 0.36, ALE-PLE 0.23, clypeus height at AME 0.38, clypeus height at ALE 0.43.

Chelicerae as in males. Cheliceral furrow without denticles. Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 9.4 [2.8, 1.3, 1.7, 3.6], I 31.6[9.0, 3.8, 8.4, 8.3, 2.1], II 33.7 [9.8, 3.8, 9.2, 8.5, 2.4], III 28.4 [8.6, 3.4, 7.5, 6.7, 2.2], IV 32.2 [9.7, 3.2, 8.6, 8.3, 2.3].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 322; Patella I–IV 000; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034.

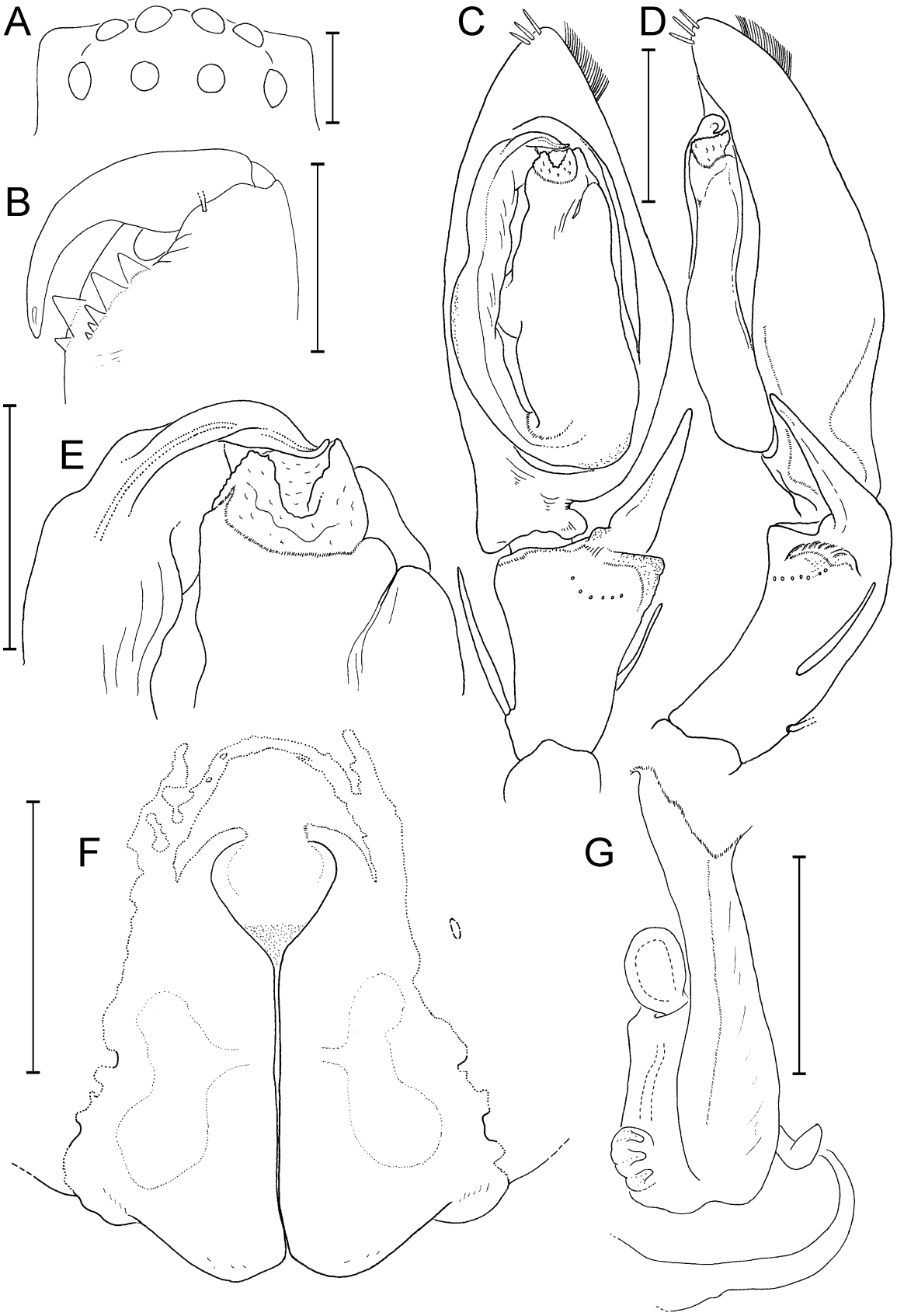

FIGURE 17. *Eusparassus potanini* (Simon, 1895), (A–E) holotype male from Nan-Shan-Kou, Tjian-Shan, China. (A) eye arrangement, (B) left chelicera, ventral, (C) left palp, ventral, (D) left palp, retrolateral, (E) tip of embolus and conductor, ventral; (F–G) female from Jarkend, Oyghur Autonomous region, China (F) epigyne, (G) left vulva, anterio-dorso-lateral. Scale bars: (A–D, F) 1 mm, (E, G) 0.5 mm.

Epigyne/vulva. As in diagnosis with EF longer than wide, AMLL well developed anteriorly but not encircling MS entirely, EFB distinctly separated from AMLL (Figure 17F); glandular pores located on a globular process of vulva (Figure 17G).

Colouration [in ethanol]. cream to dark yellow, ventral opisthosoma pale.

Remarks. The description and illustration of *E. nanjiangensis* (sub *Heteropoda nanjiangensis*) by Hu and Fu (1985), as well as examination of the type series, match the male holotype of *E. potanini*. Additional females (along with sympatric males) examined from around the type locality, revealed conspecifity of them with the holotype female of *E. nanjiangensis*. Herewith, this species is proposed as a junior synonym of *E. potanini*.

Known geographical distribution. Autonomous region in Xinjiang Uyghur, China, the most northeastern distribution range of *Eusparassus* species.

Eusparassus pontii Caporiacco, 1935

Figure 18 (A–E)

Eusparassus pontii Caporiacco, 1935: 216, pl. 6, fig. 4 (description of female; syntypes, two females, examined).

Type material: Syntypes: 1 female, **PAKISTAN: *Karakoram*,** Pajue oasis, 3500 m, 28 July 1929 (MNM); 1 female, Tsock meadow, 3940 m, 11 May 1929 (MNM); 1 juvenile, Tolti oasis, 2400 m, 20 April 1929 (MNM).

Additional material examined. 1 ♀, 2 immatures, **INDIA: *Kashmir:*** 1 ♀, 1 juvenile, Ladakh, Shey, Trockerhay, 3400 m, 2 June 1976, J. Martens leg. (SMF); 1subadult female, Ladakh, J. Martens leg. (SMF).

Diagnosis. Epigyne resembles that of *E. kronebergi* **stat. nov.** in having EFB fused to AMLL bordering MS (Figure 18C) but differ from it by the presence of a strong continuous ridge at lateral side of vulva and one large glandular process (Figure 18D, E), in contrast vulva of *E. kronebergi* **stat. nov.** has two small and separated glandular parts; It can also be distinguished

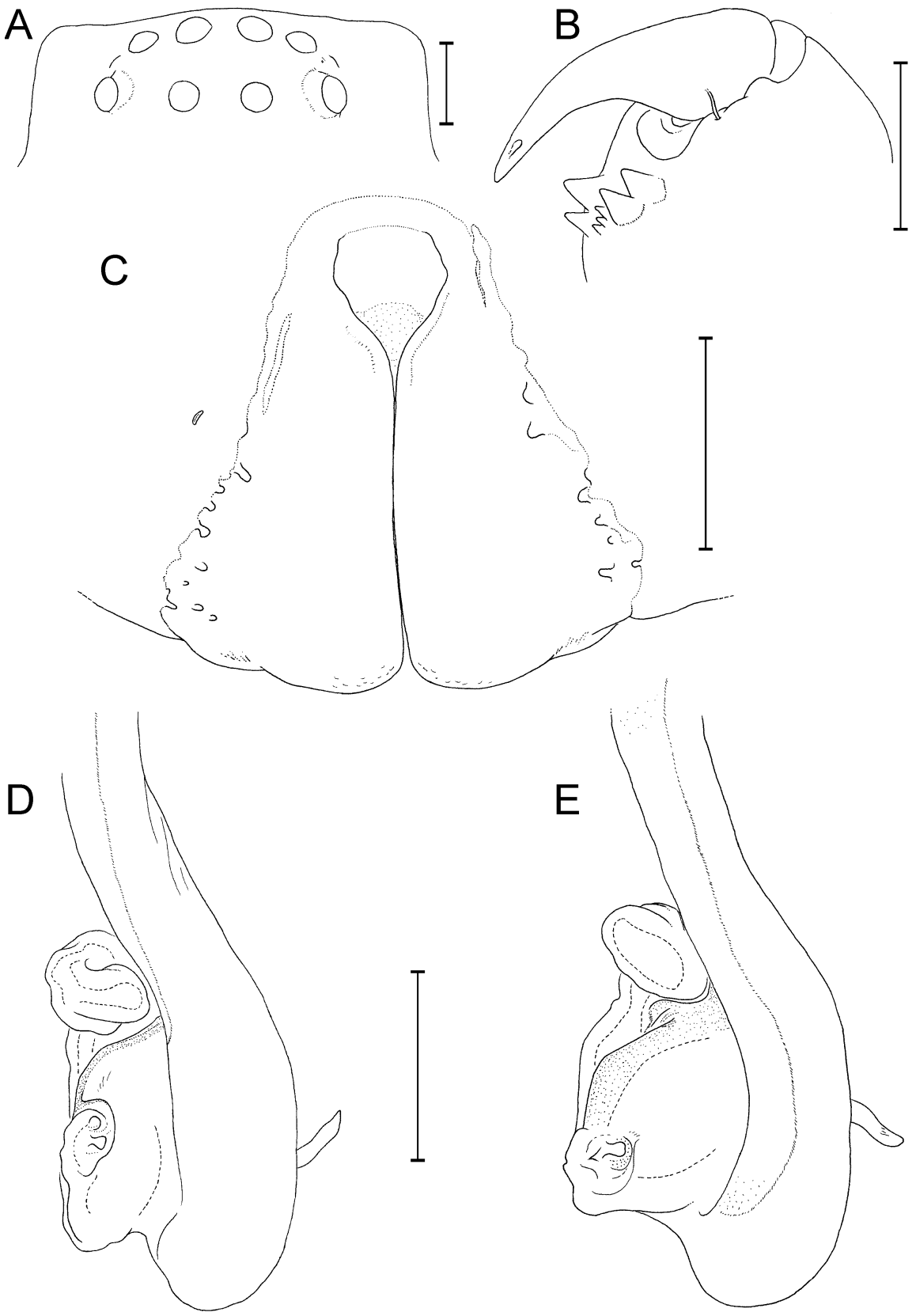

FIGURE 18. *Eusparassus pontii* Caporiacco, 1935, (A–D) syntype female from Karakoram, Pakistan (A) eye arrangement, (B) left chelicera, ventral (C) epigyne, ventral (D) left vulva, anterio-dorso-lateral; (E) variation of left vulva, anterio-dorso-lateral. Scale bars: (A–C) 1 mm, (D, E) 0.5 mm.

by the eye interdistances: AME-ALE spaced ½ of AME-AME (as in *E. fuscimanus*) but differ from this later species in having EF longer than wide (Figure 18C).

Redescription.

Female (n=3):

Total length: 14.9–18.9, prosoma length 6.4–9.1, prosoma width 5.7–7.8, anterior width of prosoma 3.2–4.7, opisthosoma length 8.5–9.8, opisthosoma width 6.5–7.4. eyes are the same size, eye diameters: AME 0.39, ALE 0.41, PME 0.40, PLE 0.40; eye interdistances: AME-AME 0.28, AME-ALE 0.15, PME-PME 0.43, PME-PLE 0.62, AME-PME 0.53, ALE-PLE 0.35, clypeus height at AME 0.32, clypeus height at ALE 0.46.

Chelicerae with 2 anterior and 4 to 6 posterior teeth; cheliceral furrow without denticles (Figure 18B). Leg formula: 21=43. Measurements of palp and legs: Palp 10.6 [3.3, 1.6, 1.9, 3.8], I 34.7 [9.6, 4.3, 8.7, 9.5, 2.6], II 37.7 [10.7, 4.5, 10.1, 9.6, 2.8], III 31.1 [9.5, 3.8, 8.2, 7.3, 2.3], IV 34.6 [10.3, 3.9, 8.8, 9.1, 2.5].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321/322; Patella I–IV 000; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034/3036.

Epigyne/vulva. As in diagnosis with two large black triangular LL, AMLL not fused but bordered by EFB (Figure 18C); Vulva with a bulge at the area of glandular processes and marked by a continuous ridge (Figure 18D, E).

Male. Unknown.

Colouration [in ethanol]. Reddish brown, dark brown chelicera, dorsal opisthosoma with a patch and series of small chevron-like patterns and additional dots, ventral opisthosoma with pale markings.

Remarks. The type specimens were collected during "the Italian Mission to Karakoram (1929-VII)". One of the type localities is Pajue, a campsite in K2 Mountain. The species is recorded from high elevations (~4000 m), the highest altitude recorded for Sparassidae so far. This is the first record of the species after its original description outside the type locality in Indian Himalaya, Ladakh.

Known geographical distribution and habitat. High altitudes in mountainous Himalaya in Pakistan: Karakoram, K2 Mountain and India (new country record): Ladakh.

Eusparassus xerxes (Pocock, 1901) **comb. nov.**

Figures 19 (A–F), 20 (A–D), 23B

Sparassus xerxes Pocock, 1901: 489–490 (description of male and female; syntypes, examined).
Olios xerxes – Gravely 1931: 240–241, figs 5A, 6A (transfer); Sethi & Tikader 1988: 35, figs 157–162.

Type material: Syntypes: 3 ♂♂, 1 ♀, 10 immatures, **IRAN: *Bushehr Province***: 1 male, 1 female, 1 juvenile, Bushehr (sub Bushier), F.W. Townsend leg. (NHM 1882.109); 4 subadult males, 3 juveniles, Port Reshire near Bushier, F.W. Townsend leg. (NHM 0.5.9.36.41); 1 subadult male, 1 subadult female, 1 juvenile, Bushier, F.W. Townsend leg. (NHM 7.88.33); 1 male, **PAKISTAN: *Baluchistan Province***: Ormara, Makran Coast, F.W. Townsend leg. (NHM 1899.10.6.7); 1 male, Ormara, Makran Coast, F.W. Townsend leg. (NHM 0.5.6.20).
Additional material examined. 1 ♂, 5 ♀♀**, PAKISTAN:** 1 ♂, 4 ♀♀, ***Azad Kashmir***: Panjur (Mozaffarabad: Kupwara, 34° 28' 10" N, 73° 39' 0" E), E. Zugmayer leg. (ZSM A20110058); 1♀, ***Azad Kashmir***: Kedsch, E. Zugmayer leg. (ZSM A20110051).
Diagnosis. Large *Eusparassus* species (largest female: body length 30 mm, legspan 14 cm), with diagnostic vase-like black marking on venter of opisthosoma in both genders (Figure 23B) which is absent in most Eurasian species (except *E. dufouri* and *E. levantinus* which is V-shaped). Palp similar to that of *E. fuscimanus* but differing in relative cymbium/tibia length: cymbium more than two times longer than tibia in *E. fuscimanus*, as opposed to *E. xerxes*, less than two times. ET more extended distally in *E. fuscimanus* than *E. xerxes* (Figure 19A–C).
Redescription.
Male (n=4):
Total length: 21.3–24.8, prosoma length 10.8–12.3, prosoma width 9.5–10.0, anterior width of prosoma 5.4–5.8, opisthosoma length 10.5–12.5, opisthosoma width 7.0–7.7. Eye diameters: AME 0.61, ALE 0.60, PME 0.57, PLE 0.60; eye interdistances: AME-AME 0.32, AME-ALE 0.15, PME-PME 0.61, PME-PLE 0.57, AME-PME 0.64, ALE-PLE 0.40, clypeus height at AME 0.41, clypeus height at ALE 0.51.
Chelicerae with 2 anterior and 3 or 4 posterior teeth. Cheliceral furrow without denticles. Four thick inclined bristles at distal end of basal segment (Figure 19E). Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 15.2 [5.3, 2.2, 2.6, 5.1], I 56.7 [16.2, 5.3, 15.7, 15.8,

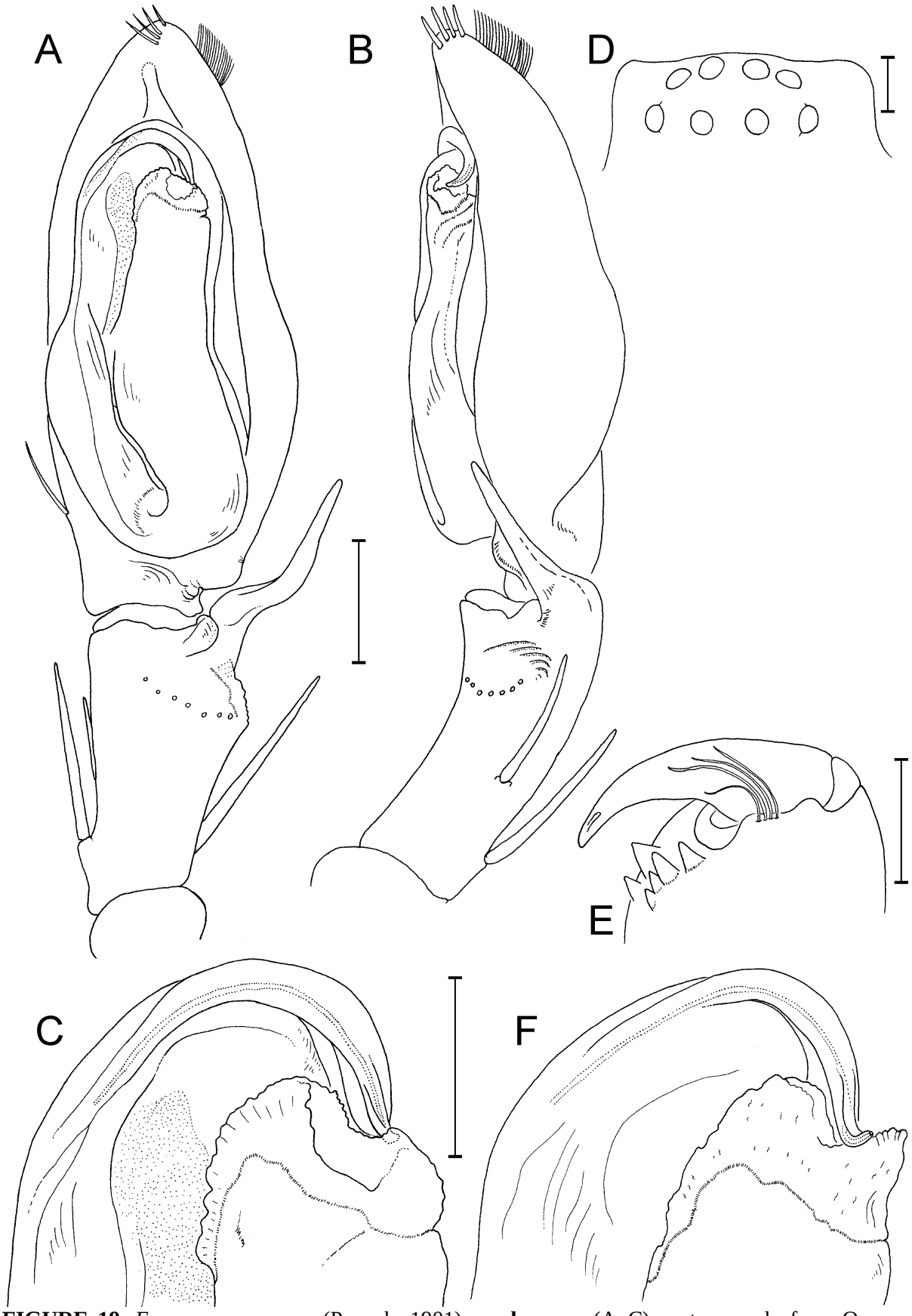

FIGURE 19. *Eusparassus xerxes* (Pocock, 1901) **comb. nov.**, (A–C) syntype male from Ormara, Makran coast, Pakistan: (A) left palp, ventral, (B) left palp, retrolateral, (C) tip of embolus and conductor, ventral; (D–F) syntype male from Bushehr, Persian Gulf coast, Iran: (D) eye arrangement,

(E) left chelicera, ventral, (F) tip of embolus and conductor from left palp, ventral. Scale bars: (A, B, D, E) 1 mm, (C, F) 0.5 mm.

3.7], II 63.1 [17.5, 6.0, 17.3, 18.5, 3.8], III 53.5 [15.7, 5.5, 14.5, 14.4, 3.3], IV 60.3 [17.0, 5.3, 16.3, 18.0, 3.7].

Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 000/101; Tibia I–IV 2024/23(2)24; Metatarsus I–III 2024, IV 3034/3036.

Palp. As in diagnosis with dRTA strongly bent and vRTA is not well developed, palp generally elongated, cymbium longer than tibia (Figure 19A, B); ET pointing proximo-ventrad (Figure 19C, F).

Female (n=6):

Total length: 21.5–29.8, prosoma length 10.5–13.0, prosoma width 8.4–10.7, anterior width of prosoma 6.0–7.3, opisthosoma length 11.0–16.8, opisthosoma width 8.2–10.5. Eye diameters: AME 0.63, ALE 0.62, PME 0.60, PLE 0.64; eye interdistances: AME-AME 0.43, AME-ALE 0.17, PME-PME 0.70, PME-PLE 0.78, AME-PME 0.70, ALE-PLE 0.50, clypeus height at AME 0.55, clypeus height at ALE 0.60.

Chelicerae with 2 anterior and 3 or 4 posterior teeth. Cheliceral furrow without denticles. Leg formula: 2 4 1 3. Measurements of palp and legs: Palp 15.5 [4.8, 2.3, 3.2, 5.2], I 51.9 [14.7, 6.1, 13.3, 14.5, 3.3], II 55.3 [16.1, 6.2, 15.0, 14.7, 3.3], III 47.1 [14.5, 5.5, 12.5, 11.8, 2.8], IV 52.4 [15.7, 5.5, 13.7, 14.3, 3.2].

Spination. Palp 131, 001, 1111, 1013; legs: Femur I–III 323, IV 322; Patella I–IV 000 (001); Tibia I–IV 2024–21(2)24; Metatarsus I–III 2024, IV 3034 (3036).

Epigyne/vulva. EF longer than wide, AMLL well developed but not fused together, EFB present but not combined to AMLL; EF longer than wide (Figure 20A, C); vulva generally short and compact, glandular pores situated on a widened semicircular process (Figures 20B, D).

Colouration [in ethanol]. Prosoma and legs reddish brown with creamy opisthosoma, ventral opisthosoma as diagnosis.

Remarks. Gravely (1931), using an unreliable character at generic level (number of distal bristles at basal segment of chelicerae), transferred *E. xerxes* **comb. nov.** (sub *Sparassus* and along with unjustified former junior synonyms: *E. pearsoni* **comb. nov.** and *E. maynardi* **comb. nov.**) to *Olios*. *Eusparassus pearsoni* **comb. nov.** and *E. xerxes* **comb. nov.** have three and four bristles, respectively, whereas one bristle appears in most *Eusparassus* spp. This is

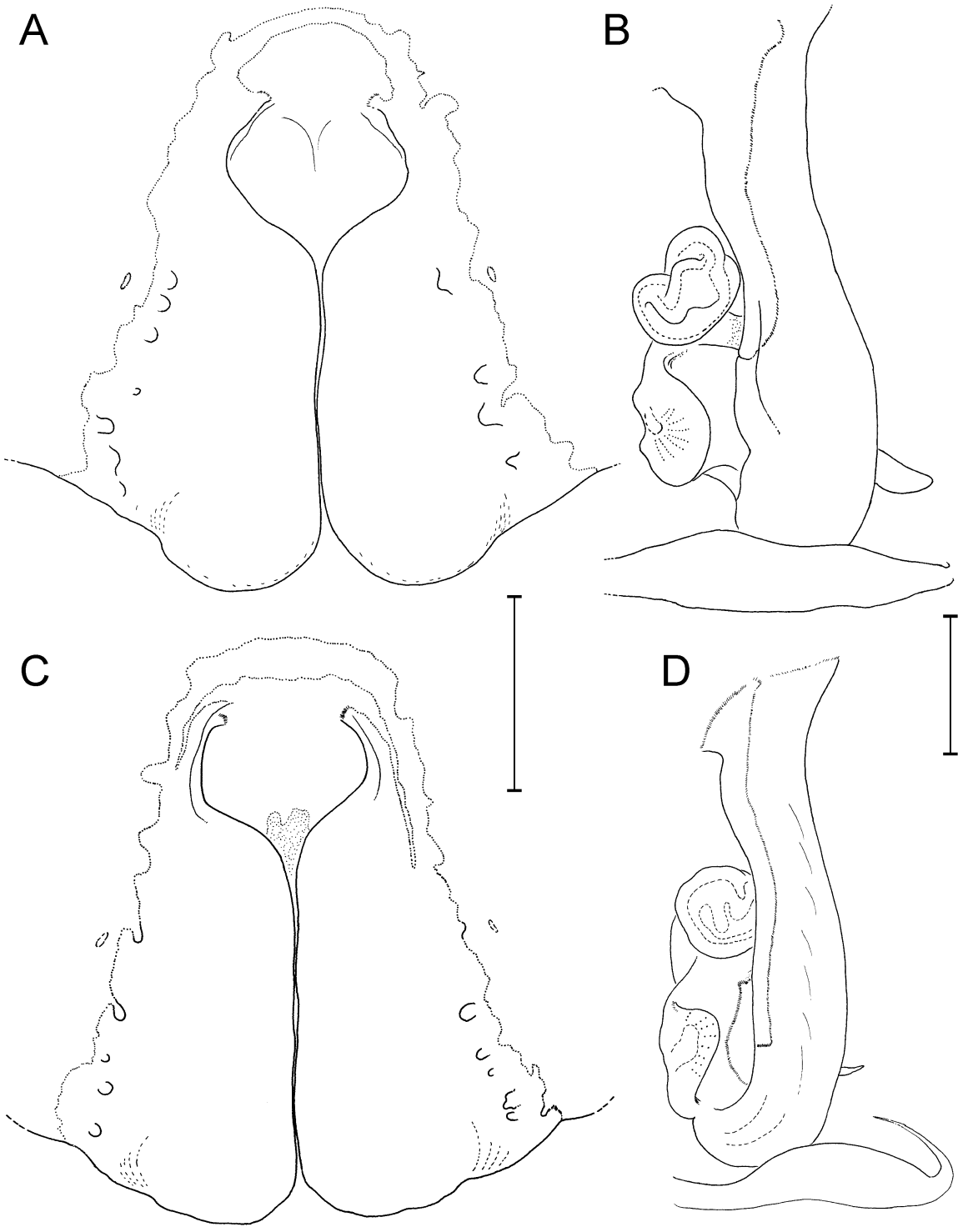

FIGURE 20. *Eusparassus xerxes* (Pocock, 1901) **comb. nov.**, (A–B) syntype female from Bushehr, Persian Gulf coast, Iran: (A) epigyne, ventral (B) left vulva, anterio-dorso-lateral; (C–D) female from Kedsh, Azad Keshmir, Pakistan: (C) epigyne, ventral (D) left vulva, anterio-dorso-lateral. Scale bars: (A, C) 1 mm, (B, D) 0.5 mm.

the largest *Eusparassus* species in Eurasia (legspan 14 mm). After its original description from Makran coast in Iran and Pakistan (Pocock 1901), we describe conspecifics from Central Pakistan in Kashmir. The species exhibit dorsal tibial spines normally absent in other

Eusparassus species. Ventral marking of opisthosoma resembles some *Eusparassus* species in African Sahara and Arabia.

Known geographical distribution. From Southern Iran (Bushehr port in the Persian Gulf) to Makran Coast and Central Pakistan (Baluchistan and Azad Kashmir Provinces).

Eusparassus maynardi (Pocock, 1901) **comb. nov. stat. nov.**

Figure 21 (A–E)

Sparassus maynardi Pocock, 1901: 490 (description of female and male; syntypes, one adult and two subadult females, three subadult males, **lectotype adult female and paralectotypes immatures here designated) [**see note below].

Olios xerxes – Gravely 1931: 240–241 (in part, misidentification and unjustified synonymy); Sethi & Tikader 1988: 35 (in part, misidentification).

Type material: Lectotype: female, **PAKISTAN:** ***Baluchistan Province***, Baluchistan, F.W. Townsend leg. (NHM 1900.3.13.5.6); **Paralectotypes:** 2 subadult males and 1 immature female**:** 1 subadult male, Baluchistan, F.W. Townsend leg. (NHM 1900.3.13.5.6); 1 subadult male, 1 subadult female, ***Sindh Province,*** Jacobabad, H.M. Phipson leg. (NHM 1899.4.10.24.29).

Note. The type material of *E. maynardi* consists of one adult female and several immatures. Consequently, in order to maintain species identity, the adult female is designated here as lectotype.

Additional material examined. PAKISTAN: 2♀♀, ***Sindh Province***: with label "Jacobabad, H.M. Phipson/*Sparassus pallescens* Pocock Type", Jacobabad, H.M. Phipson leg. (NHM 1899.7.10.27. 9); 1♀**,** ***Azad Kashmir***: Kedsch, E. Zugmayer leg. (ZSM A20110052)

Diagnosis. The combination of characters, including absence of EFB, long slender epigyne and not fused AMLL (Figure 21A, E) distinguishes *E. maynardi* **comb. nov.** from remaining congeners. This species lacks any black marking on venter of opisthosoma (unlike *E. xerxes* **comb. nov.**).

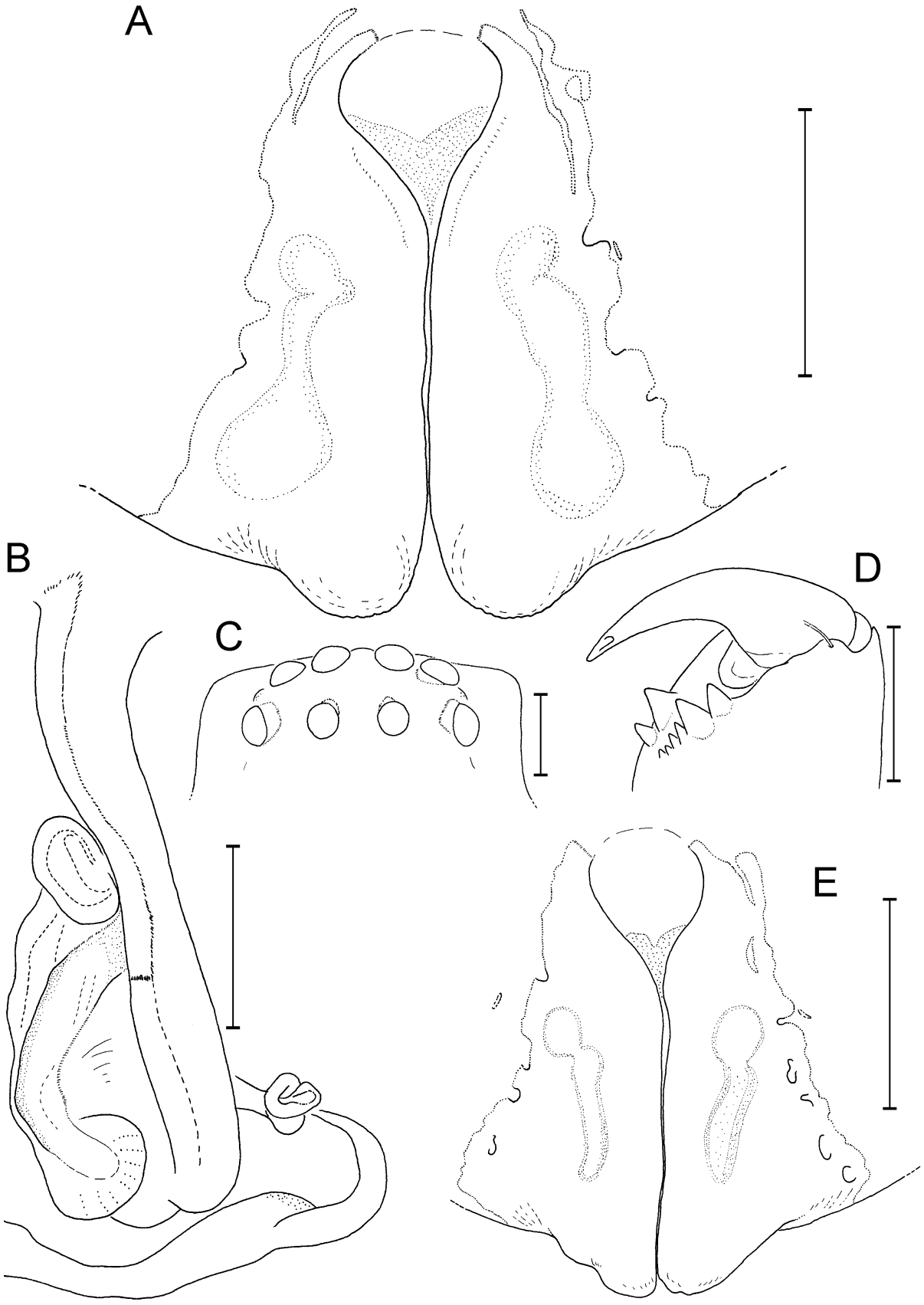

FIGURE 21. *Eusparassus maynardi* (Pocock, 1901) **comb. nov. stat .nov.**, (A–D) lectotype female from Baluchistan, Pakistan: (A) epigyne, ventral (B) left vulva, anterio-dorso-lateral (C) eye arrangement, (D) left chelicera, ventral, (E) variation of epigyne, ventral, female from Jacobabad, Sindh Province, Pakistan. Scale bars: (A, C–E) 1 mm, (B) 0.5 mm.

Redescription.

Female (n=4) [lectotype is the largest female]:

Total length: 15.7–20.4, prosoma length 7.0–9.2, prosoma width 6.0–7.6, anterior width of prosoma 3.4–4.3, opisthosoma length 8.7–11.2, opisthosoma width 5.0–8.1. Eye diameters of (lectotype): AME 0.54, ALE 0.47, PME 0.44, PLE 0.45, eye interdistances: AME-AME 0.27, AME-ALE 0.06, PME-PME 0.46, PME-PLE 0.53, AME-PME 0.35, ALE-PLE 0.26, clypeus height at AME 0.48, clypeus height at ALE 0.58.

Chelicera with 2 anterior and 4 to 6 posterior teeth; cheliceral furrow without denticles; one bristle at distal end of cheliceral basal segment (Figure 21D). Leg formula: 2 4 1 3. Measurements of palp and legs (lectotype): Palp 11.6 [3.5, 1.7, 2.3, 4.1], I 37.3 [10.4, 4.5, 10.1, 10.0, 2.3], II 40.4 [11.6, 4.6, 11.1, 10.5, 2.6], III 34.4 [10.4, 4.2, 9.3, 8.3, 2.2], IV 39.1 [11.1, 4.0, 10.5, 10.8, 2.7].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 322(3); Patella I–IV 000; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034.

Epigyne/vulva. As in diagnosis, with EF longer than wide, MS partially sclerotised (Figure 21A, E); longitudinal ridge at lateral side of vulva, glandular pores located on a semispherical process (Figure 21B).

Male. Unknown.

Colouration [in ethanol]. Yellowish brown with irregular darker pattern on prosoma, , ventral opisthosoma without marking.

Remarks. Additional conspecific females have been found close to the type locality in Baluchistan. In NHM there were two females from Jacobabad, Pakistan labelled by Pocock under name "*Sparassus pallescens*". The name has never been published and looks to be a provisional name by Pocock. We found these females to be conspecific with *E. maynardi* **comb. nov**. It seems that Gravely (1931) considered generic diagnostic characters of the genus *Eusparassus* to synonymise this species (as well as *E. pearsoni* **comb. nov.**) with *E. xerxes* **comb. nov.** He stated that he failed to distinguish *E. maynardi* "vulva" (=epigyne) from those of the latter species.

Known geographical distribution. Pakistan: Baluchistan, Sindh and Azad Kashmir Provinces.

Eusparassus pearsoni (Pocock, 1901) **comb. nov. stat. nov.**

Figure 22 (A–F)

Sparassus pearsoni Pocock, 1901: 492–493 (description of female; syntypes examined, **lectotype and paralectotypes designated**) [see notes below].
Olios xerxes – Gravely 1931: 240–241 (in part, misidentification and unjustified synonymy); Sethi & Tikader 1988: 35 (in part, misidentification).

Type material: Lectotype: female, **INDIA:** ***Poona***, Ghats, Madan leg. (NHM 99.11.2.177.199); **Paralectotypes: INDIA:** 13 ♀♀ and 30 juveniles, same data as for lectotype (NHM 99.11.2.177.199); 3 ♀♀, with label "*Sparassus pearsoni* Poc. East Khandesh, R. Pearson coll. Robt. Wroughton (p.)" (NHM 99.9.21.5.24.525); 33 ♀♀, with label: "Poona Dist., Bombay Nat. Hist. Soc./ Poona Dist" (NHM 1899.9.21.526-546); 85 ♀♀ and several immatures, with label "*Sparassus pearsoni* Poc. Pimparner (W. Khandesh), R. Pearson coll. Robt. Wroughton (p.)" (NHM).
Note. Among this relatively huge number of syntypes, we found several immature specimens of *Olios* sp. and *Eusparassus* sp. Hence, to maintain the status and verify the identity of the species, an adult female from Poona, Ghats in India is designated as lectotype.
Diagnosis. *Eusparassus pearsoni* **comb. nov**. can easily be distinguished from remaining species by its peculiar MS of epigyne heart-shaped and fully hardened and sclerotised (Figure 22A, E).
Redescription. Female (n=135):
Total length: 16–21, prosoma length 7.5–9.4, prosoma width 6.4–8.2, anterior width of prosoma 4.0–5.2, opisthosoma length 8.5–11.6, opisthosoma width 5.2–6.8. Eyes of lectotype, eye diameters: AME 0.62, ALE 0.45, PME 0.38, PLE 0.44; eye interdistances: AME-AME 0.30, AME-ALE 0.15, PME-PME 0.68, PME-PLE 0.75, AME-PME 0.48, ALE-PLE 0.32, clypeus height at AME 0.53, clypeus height at ALE 0.61 (Figure 22C).
Chelicera with 2 anterior and 3 or 4 posterior teeth; cheliceral furrow without denticles; three bristles at distal end of cheliceral basal segment (Figure 22D). Leg formula: 2 4 1 3.

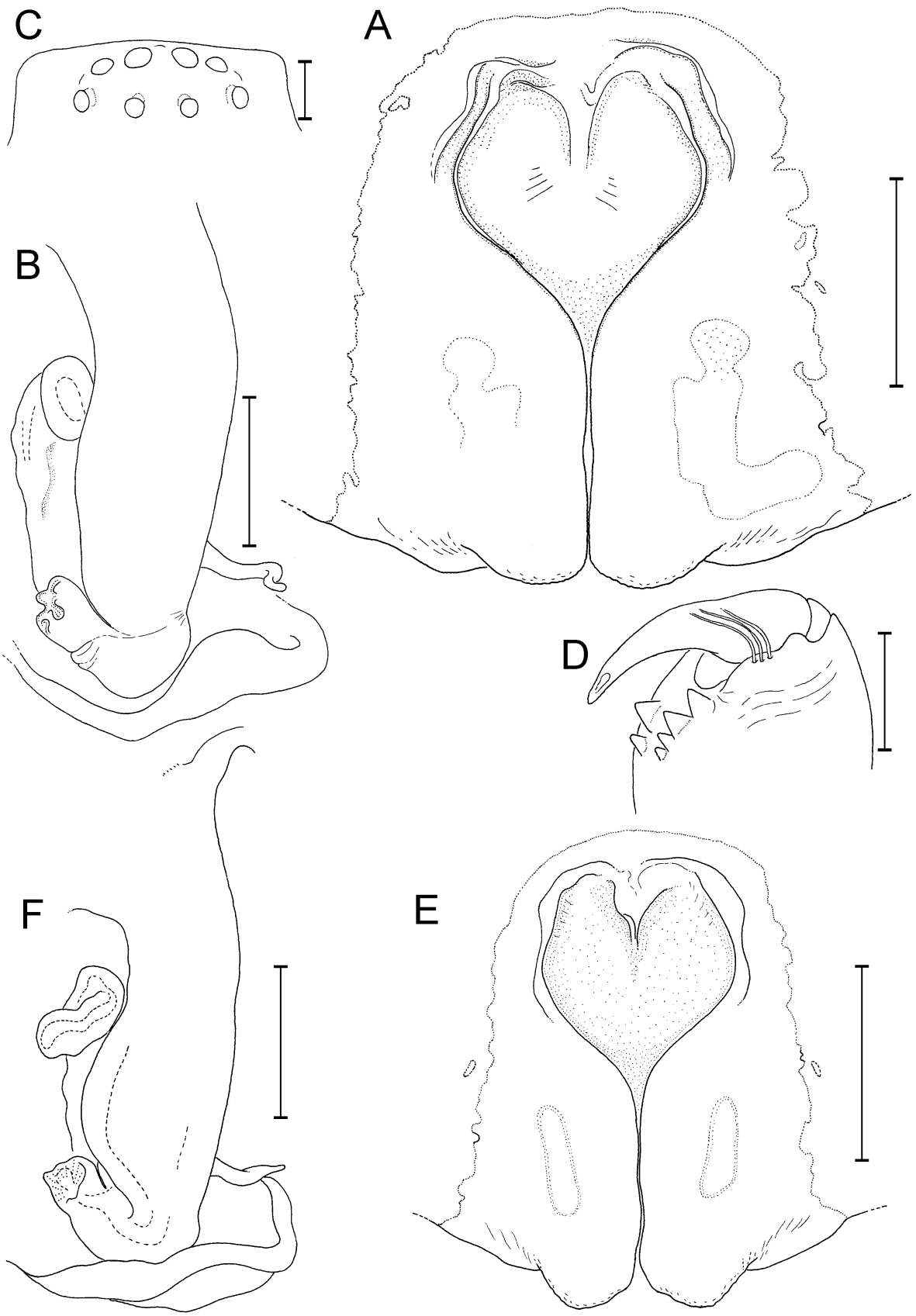

FIGURE 22. *Eusparassus pearsoni* (Pocock, 1901) **comb. nov.stat .nov .**, (A–D) lectotype female from Poona, western Ghats, India: (A) epigyne, ventral (B) left vulva, anterio-dorso-lateral (C) eye arrangement, (D) left chelicera, ventral; (E–F) paralectotype female from Eastern Khandesh, India, (E)

variation of epigyne, ventral (F) variation, left vulva, anterio-dorso-lateral. Scale bars: (A, C–E) 1 mm, (B, F) 0.5 mm.

Measurements of palp and legs (lectotype): Palp 10.4 [3.3, 1.5, 2.0, 3.6], I 30.1 [8.8, 4.3, 7.2, 7.8, 2.0], II 32.5 [9.8, 4.2, 8.0, 8.3, 2.2], III 29.0 [9.1, 4.0, 6.8, 7.1, 2.0], IV 31.5 [9.6, 3.7, 7.7, 8.4, 2.1].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 322; Patella I–IV 000/001; Tibia I–IV 0024/2024; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis with MS enlarged, EF quadrate in shape; EFb combined with AMLL; AMLL are not fused but continued into hardened MS (Figure 22A, E); vulva with glandular pores located at tip of glandular process (Figure 22F).

Male. Unknown.

Colouration [in ethanol]. Reddish brown with dark patches on prosoma, gray opisthosoma, ventral opisthosoma pale.

Remarks. Gravely (1931) erroneously synonymised *E. pearsoni* **comb. nov.** along with *E. maynardi* **comb. nov.** with *E. xerxes*, despite noting the peculiar differences in the epigyne of *E. pearsoni*, which is noticeably distinguishable from *E. xerxes* **comb. nov.** Pocock (1901), in "the Fauna of India series", did not include illustrations to his description of all his new species. Later, Gravely (1931) only provided drawings of *E. xerxes*. Consequently, the drawings of *E. pearsoni* (as well as *E. maynardi*) have never appeared in publications before and are presented here for the first time.

Known geographical distribution. Known only from the type localities including Khandesh, Ghats and Poona (=Pune) in Indian Peninsula.

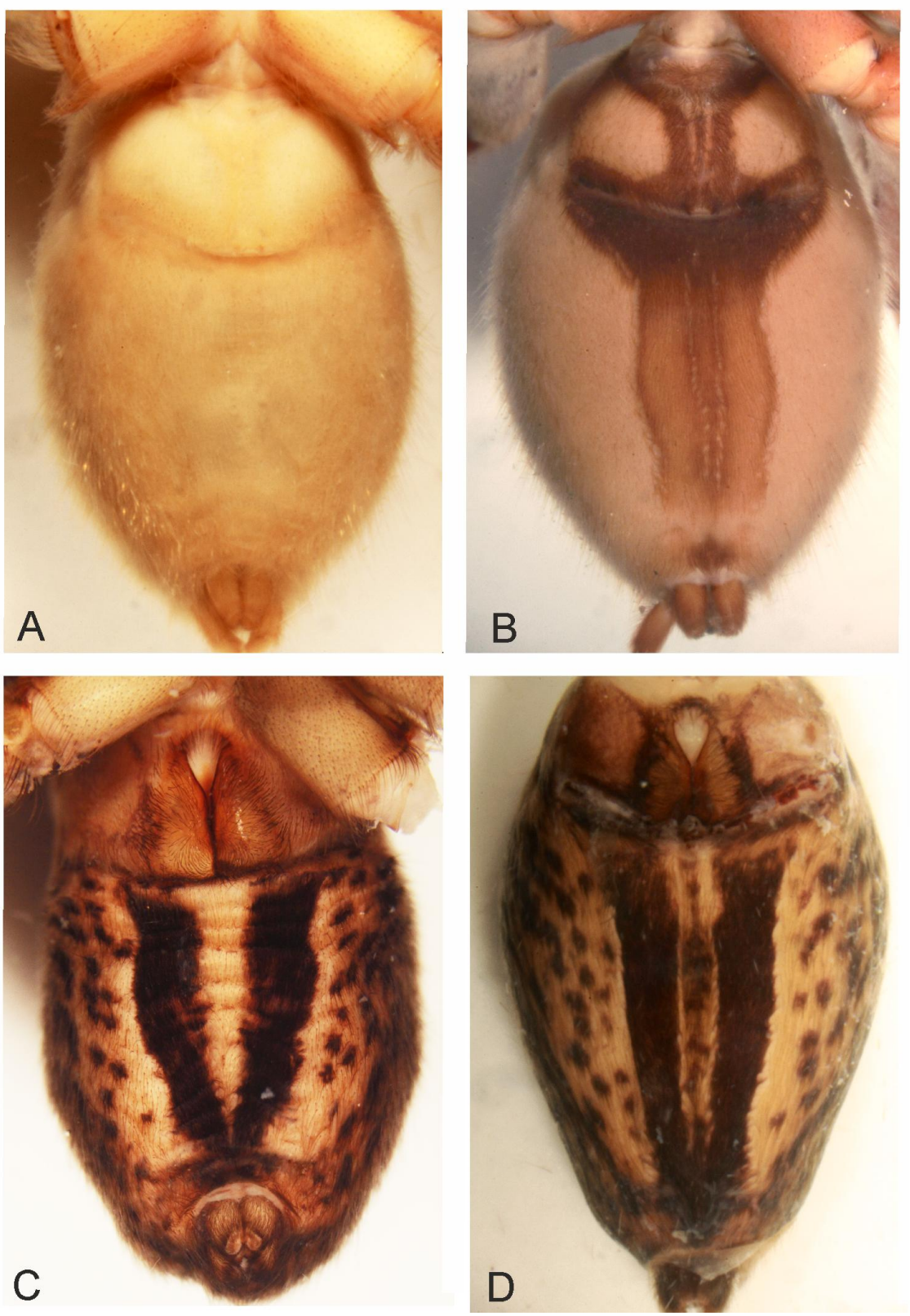

FIGURE 23. ventral opisthosoma colouration, (A) *Eusparassus walckenaeri*, (B) *E. xerxes* **comb. nov.**, (C) *E. dufouri*, (D) *E. levantinus*.

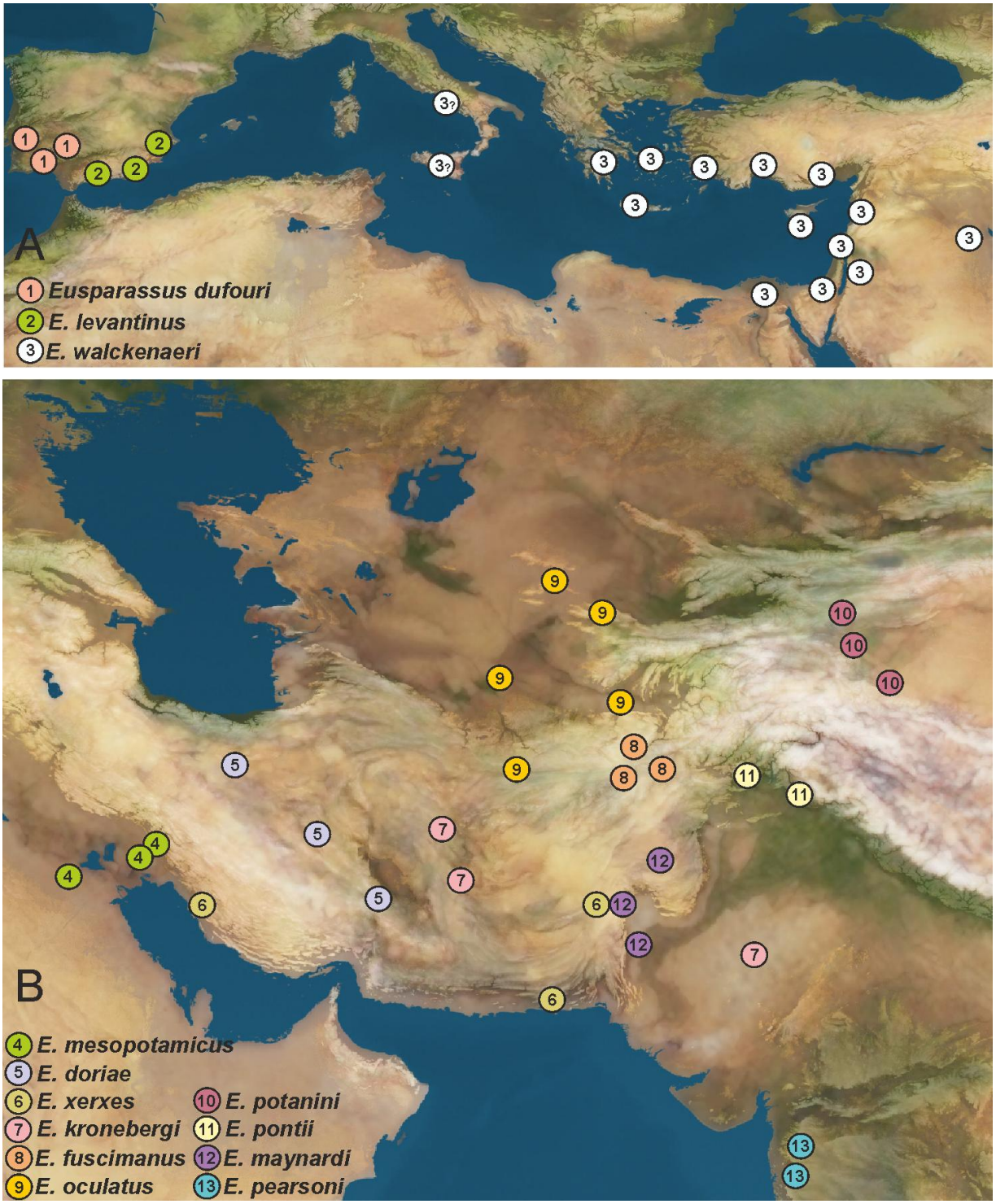

FIGURE 24. Distribution map of Eurasian *Eusparassus* species in (A) Mediterranean region, (B) Middle East, Central and South Asia.

Misplaced Species

Eusparassus lilus Strand, 1907 **nomen dubium**

Eusparassus lilus Strand, 1907: 437 (description of male, from Java in Indonesia, holotype in Zoologische Institute Tübingen, destroyed in 2nd WW).

Remarks. Strand (1907) did not provide any drawing of the species and the description does not include any diagnostic character of *Eusparassus*. According to the known distribution range and preferable habitats of *Eusparassus* species, Java is thought to be out of distributional limits. The species probably belongs to *Olios* and this genus is proved by Jäger (2003) to occur in Java [e.g., *O. nigrifrons* (Simon, 1897)]. The species is considered a *nomen dubium* until the holotype is recovered.

Olios flavovittatus (Caporiacco, 1935) **comb. nov.**

Eusparassus flavovittatus Caporiacco, 1935: 217, pl. 5, fig. 11 (description of juvenile; holotype from Karakoram, juvenile, examined).

Type material: Holotype: juvenile (severely damaged), **PAKISTAN:** ***Karakoram***, Garhi, agris aridis, altitude 1200 m, April 1929 (MNM).

Remarks. This badly damaged juvenile was received from MCSM. Only parts of right chelicerae, the prosoma and opisthosoma are available. Examination of eye pattern and prosoma, which is as long as wide, as well as presence of several bristles (>7) at distal end of chelicera basal segment (instead of one or maximum four bristles in *Eusparassus* spp.) revealed that the species should actually be transferred to *Olios*.

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Chapter 3.2. Systematics and Zoogeography of *Eusparassus* with revision of the African and Arabian species

This chapter is based on the following paper in a slightly modified version.

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Abstract

An overview on the systematics of the stone huntsman spider genus *Eusparassus* Simon, 1903 and an identification key to the known species are presented. Six species-groups are proposed. The *walckenaeri* group (3 species, Eastern Mediterranean to Arabia and parts of North-Eastern Africa), *dufouri* group (8 species, Iberian Peninsula to parts of North-western Africa), *vestigator* group (3 species, Central to Eastern Africa and an isolated area in India), *jaegeri* group (4 species, Southern and South-Eastern Africa), *tuckeri* group (2 species, South-Western Africa) and *doriae* group (7 species, Middle East to Central and South Asia). Two species, *E. pontii* Caporiacco, 1935 and *E. xerxes* (Pocock, 1901) could not be placed in any of the above groups. The species from Africa and Arabia are revised. The following ten species are re-described: *Eusparassus barbarus* (Lucas, 1846), *E. atlanticus* Simon, 1909 **stat. nov.**, *E. syrticus* Simon, 1909, *E. oraniensis* (Lucas, 1846), *E. letourneuxi* (Simon, 1874), *E. fritschi* (Koch, 1873) **stat. rev.**, *E. walckenaeri* (Audouin, 1826), *E. vestigator* (Simon, 1897) **comb. nov.**, *E. laevatus* (Simon, 1897) **comb. nov.** and *E. tuckeri* (Lawrence, 1927) **comb. nov.** The latter three species are transferred from *Olios* Walckenaer, 1837. Seven new species are described: *Eusparassus arabicus* **spec. nov.** (male, female) from Arabian Peninsula, *E. educatus* **spec. nov.** (male, female) from Namibia, *E. reverentia* **spec. nov.** (male, female) from Burkina Faso and Nigeria, *E. jaegeri* **spec. nov.** (male, female) from South Africa and Botswana, *E. jocquei* **spec. nov.** (male, female) from Zimbabwe, *E. borakalalo* **spec. nov.** (female) from South Africa and *E. schoemanae* **spec. nov.** (male, female) from South Africa and Namibia. Three taxa, *E. dufouri maximus* Strand, 1906 **syn. nov.,** *E. rufobrunneus* Caporiacco, 1941 **syn. nov.** and *Olios furcatus* Lawrence, 1927 **syn. nov.** are proposed as junior synonyms of *E. oraniensis*, *E. vestigator* **comb. nov.** and *E. tuckeri* **comb. nov.** respectively. Males of *E. atlanticus* **stat. nov.** and *E. fritschi* **stat. rev.** are described for the first time as in the female of *E. vestigator* **comb. nov.** Neotypes are designated for *E. barbarus*, *E. oraniensis* and *E. letourneuxi* (all from Algeria). The male and female of *Cercetius perezi* Simon, 1902, which was known only from the immature holotype, are described here for the first time. This resulted in recognizing the monotypic and little used generic name *Cercetius* Simon, 1902 as a synonym of the widely used name *Eusparassus*. Nearly all the species are illustrated for the first time. *Eusparassus concolor* Caporiacco, 1939 is transferred to *Olios* Walckenaer, 1837 and the replacement name *Olios quesitio* is proposed because of secondary homonymy. For the majority of the species, new geographical records are presented. The systematics and zoogeography of the currently known species and species groups are discussed. A brief note on the copulation process of *E. walckenaeri* is presented.

Key words: taxonomy, Eusparassinae, *Cercetius*, identification key, copulation process, evolutionary hypothesis.

INTRODUCTION

Members of the spider genus *Eusparassus* Simon, 1903 (Sparassidae: Eusparassinae) are among the most conspicuous arachnid predators in arid and semiarid deserts of Africa and most parts of Eurasia. As these spiders inhabit stony habitats and build their retreats underside of large flat stones and also in the crevices of rocks (Levy 1989, Gabriel 2011), the common name "stone huntsman spiders" is proposed here. They are small to very large huntsman spiders distributed in Africa and Eurasia. The fossil stone huntsman spider, *E. crassipes* (Koch & Berendt, 1854) from Eocene era found in Northern Europe amber fossil, is dated back to approximately 50 Ma (Dunlop *et al.* 2011). Recently, Moradmand and Jäger (2012a) revised the Eurasian representatives (excluding Arabia) and provided an historical review of the systematics of the genus. They provided diagnostic characters of the genus *Eusparassus* and recognized 13 valid species in Europe, the Middle East, and Central and South Asia. Before that, the genus had never been revised with the exception of a brief review by Levy (1989) who re-described *E. walckenaeri* (sub *Sparassus*) and mentioned some diagnostic characters (e.g. female vulva and colouration of the ventral opisthosoma) for species identification, along with a revision of some Middle Eastern Sparassidae.

The systematic position of *Eusparassus* within Sparassidae remains vague, since the majority of Sparassidae genera have not yet been revised. Simon (1897a) placed *Eusparassus* (sub *Sparassus*) in his proposed "Sparasseae" group. Later, Simon (1903) moved the genus to another group named "Deleneae" along with several other genera. Simon's classifications were based on somatic characters, e.g. the arrangement of eyes. Järvi (1912, 1914) was the first who applied characters of the copulatory organs (exclusively female) to classify Sparassidae. He proposed the subfamily Eusparassinae Järvi, 1912 (sub "Eusparaseae") for *Eusparassus* including the genera: *Pseudomicrommata* Järvi, 1914 and *Rhitymna* Simon, 1897. Of these two genera, only the African endemic *Pseudomicrommata*, known as the grass huntsman spider, has some kind of similarities to *Eusparassus*. Jäger (2003) proposed that *Rhitymna* represent a different phylogenetic lineage in Asia. Jäger and Kunz (2003) in a congress abstract proposed some diagnostic characters for Eusparassinae and assumed that a number of African endemic genera could be placed in this subfamily (e.g. *Arandisa* Lawrence, 1938).

Huntsman spiders in Africa and Arabia have received little taxonomic attention (Jäger & Kunz 2005). Despite having great diversity and living in various habitats, the majority of the African huntsman spiders remained unexplored compared to their relatives in other parts of the

world. Dippenaar-Schoeman and Jocqué (1997) gave an historical review of systematic research into the huntsman spiders of Africa (sub Heteropodidae). Jäger and Kunz (2005) provided an overview of the known genera of the huntsman spiders and presented a generic identification key for Africa and nearby regions. They listed 33 nominal genera, and of these, only two have been revised to date: the Afrotropical genus *Palystes* L. Koch, 1875 (by Croeser 1996) and the Afro-Asian genus *Cebrennus* Simon, 1880 (by Jäger 2000). The nominal and monotypic genus *Cercetius* Simon, 1902 from Afro-Arabia is considered to be a senior synonym of *Eusparassus* (Moradmand & Jäger, 2012b). An official proposal (case number 3596) was submitted to the International Commission on Zoological Nomenclature (ICZN) to conserve the name *Eusparassus* by giving it precedence over the forgotten name *Cercetius* (Jäger & Moradmand 2012b). The case is under consideration by ICZN, and until a ruling has been made, prevailing usage of the names is to be maintained (ICZN 1999: Article 82). Palaeogeographically closely related to Africa, the Arabian Peninsula is totally neglected in the case of studying sparassids except for a few sparsely recorded species (e.g. Simon 1902; Levy 1989; Jäger 2000; Jäger 2006).

In this paper, an overview of all the known *Eusparassus* species is provided and the Afro-Arabian representatives are revised investigating all the available types and a large number of specimens from the major European and African spider collections. Although 18 nominal species are known from Afro-Arabia (Platnick 2013), the taxonomic status of the majority of these species is not clear. However, following the present study and that of Moradmand and Jäger (2012a), 30 valid species of *Eusparassus* are identified, of which 25 species are known by both sexes and 5 species by females alone. An identification key to all the known species is presented here.

MATERIAL AND METHODS

Material for this study was mostly obtained from the large spider collections in Europe and Africa (listed below). Additional specimens were sampled by colleagues from different areas within the *Eusparassus* distribution range. The spiders have a cryptic life style in subterranean habitats including crevices in rocks and under large flat stones, where they construct their large papery retreats (Fig. 52c). They are strikingly agile and tricky to be caught. The typical method for sampling Sparassidae (using a headlight to trace reflecting eyes at night) seems to be non effective in these spiders. They are mainly collected inside their retreats by turning over the

inhabited stones by day and removing the spider from their retreats. The use of pitfall traps (R. Bosmans, in Algeria) and Malaise traps (A. van Harten, in Yemen) are two additional methods that seem to be effective for collecting stone huntsman spiders, especially males (see data on labels).

Examination, illustration and measurements of the specimens follows Moradmand and Jäger (2012a), using a Leica MZ 165C stereomicroscope equipped with a drawing tube. Photos of the copulatory structures and habitus were taken using a Canon EOS 50D camera installed on the microscope. The arrangement of the species in the text is according to species groups and follows the geographical distribution range from North (Sahara) to South (Southern Africa).

Measurements are given in millimetres. Size classes of spiders are according to Jäger (2001) as follows: small (3–10 mm), medium (11–20 mm), large (21–30 mm) and very large (>30 mm). Measurements of palps are listed as: total length [femur, patella, tibia, cymbium]; legs as: total length [femur, patella, tibia, metatarsus, tarsus]. Palp and leg spination are presented in the following format: prolateral, dorsal, retrolateral and ventral (the latter only if present). Parentheses and slashes are used to state spination variation within a single specimen and among different specimens, respectively. At the beginning of every description part, the given MM number (serial number used by the author to measure and/or illustrate the material) is noted for the single measurement of a particular specimen (i.e., eye sizes), but for the range measurements (i.e., total length) the sum number of studied specimens are noted.

Abbreviations used throughout the text:

AB — anterior bands of epigynal field,

ALE — anterior lateral eyes,

AME — anterior median eyes,

AMLL — anterior margin of lateral lobes,

CD — copulatory duct,

CO — copulatory opening,

DK—field numbers used by Dirk Kunz,

dRTA — dorsal RTA,

E — embolus,

EF — epigynal field,

EFB — epigynal field bridge,

EM — embolus membrane,

ET — embolus tip,

GP — glandular process,

Gpo — glandular pores,

H — haematodocha,

L — lumen,

LL — lateral lobes,

MM — serial numbers used by the author for measured and/or illustrated material,

MS — median septum,

Msa — membraneous sac,

PLE — posterior lateral eyes,

PME — posterior median eyes,

PMLL — posterior margin of LL,

RTA — retrolateral tibial apophysis,

vRTA — ventral RTA,

ST — subtegulum,

SD — Sparassidae DNA numbers in SMF,

SpD — sperm duct,

SS — slit sensillum,

T — tegulum,

TL — turning loop,

Vsh — vulva shadow,

I–IV — 1st to 4th leg.

Collections and curators

AMNH— American Museum of Natural History, New York (Norman Platnick)

BMSA (NMBA) — National Museum, Bloemfontein (Leon N. Lotz, Trudie Peyper)

CCM — Collection of Christoph Muster, Putbus

CRB — Collection of Robert Bosmans, Gent

HECO — Hope Entomological Collection, Oxford (Zoë Simmons)

ICEAD — Invertebrate Collection of Environment Agency, Abu Dhabi (Anitha K. Saji)

MHNG —Muséum d'histoire naturelle, Genève (Peter Schwendinger)

MIZ — Zoological Museum, Polish Academy of Science, Warsaw (Dominika Mierzwa)

MNHN — Muséum National d'Histoire Naturelle, Paris (Christine Rollard)

MNM — Museo Civico di Storia Naturale di Milano, Milan (Andrea Sabbadini, Carlo Pesarini)

MRAC — Musée Royal de l'Afrique Centrale, Tervuren (Rudy Jocqué)

MZH — Finish Museum of Natural History, University of Helsinki (Ritva Talman)

MZUF —Natural History Museum "La Specola", Florence (Luca Bartolozzi)

NHM —Natural History Museum, London (Janet Beccaloni)

NHMW — Naturhistorisches Museum, Vienna (Christoph Hörweg)

NMB — Naturhistorisches Museum, Basel (Ambros Hänggi)

NMNW — National Museum of Namibia, Windhoek (Tharina Bird)

NMSA — KwaZulu Natal Museum, Pietermaritzburg (Debbie Jennings, Audrey Ndaba)

PPRI — ARC Plant Protection Research Institute, Gauteng, Pretoria (Ansie Dippenaar-Schoeman)

SAMC — Iziko South African Museum, Cape Town (Dawn Larson)

SMF — Senckenberg Research Institute, Frankfurt am Main (Julia Altmann, Peter Jäger)

SNSD — Senckenberg Naturhistorische Sammlungen, Dresden (Katrin Schniebs)

ZMB — Museum für Naturkunde, Berlin (Anja Friederichs, Jason Dunlop)

ZMH — Zoological Museum, University of Hamburg (Hieronymus Dastych)

ZMUC — Zoological Museum, University of Copenhagen (Nikolaj Scharff)

ZSM — Zoologische Staatssammlung, Munich (Stefan Friedrich, Roland Melzer)

Identification key to species of *Eusparassus*

In the following key, a combination of the somatic and copulatory characters are used, nevertheless, species identification should be confirmed by checking the detailed diagnoses and descriptions given in the text for each species. The key should be used with special care when identifying females. Species descriptions of the *doriae* group as well as *E. pearsoni* (Pocock, 1901) (*vestigator* group), *E. pontii* Caporiacco, 1935 and *E. xerxes* (Pocock, 1901) (both incertae sedis), *E. dufouri* Simon, 1932 and *E. levantinus* Urones, 2006 (both *dufouri* group) are given in Moradmand and Jäger (2012a). The character ventral opisthosoma dark marking must be used with special care as preserved specimens could have been faded. Since *Cercetius perezi* is regarded congeneric (retained usage until ICZN decision on case 3596), this species is included in the *Eusparassus* key.

1. Cheliceral furrow with intermarginal denticles (e.g. Fig. 1f)……..2

– Cheliceral furrow without intermarginal denticles (e.g. Fig. 13e).....16

2. Male [unknown in *E. borakalalo* **spec. nov.**]……..3

– Female…….....9

3. Palp with enlarged and bulged ST (e.g. Fig. 35a)…….....4

– Palp with small and hidden ST behind T (e.g. Fig. 1a)……....6

4. dRTA bifurcated at its tip (Figs 35a, b) [Zimbabwe]……...……...***jocquei* spec. nov.**

– dRTA pointed and not bifurcated at its tip……....5

5. ET triangular and flattened proximally and pointed distally (Fig. 31c) [South Africa: Northern Cape Province]……...***schoemanae* spec. nov.**

– ET slender and curved at its distal end (Fig. 29c) [South Africa].....***jaegeri* spec. nov.**

6. dRTA bent toward cymbium and pointed disto-ventrad (Fig. 4a) [Horn of Africa to Arabia]……..... ***laevatus***

– dRTA directed distad……...….7

7. Ventral opisthosoma with large solid black marking (Fig. 57b), ET directed distad (Fig. 42c, f) [Arabia and Horn of Africa]…….***Cercetius perezi***

– Ventral opisthosoma pale, ET directed retrolaterad (e.g. Fig. 1d)……....8

8. Palp and dRTA robust, PE and AE roughly subequal (Figs 1a–e) [Eastern Mediterranean to Egypt and Algeria]…….***walckenaeri***

– Palp and dRTA elongated and slender, PE distinctly larger than AE (Figs 7a–d) [Arabian Peninsula]……...…….***arabicus* spec. nov.**

9. Epigyne with AMLL fused together anteriorly (e.g. Fig. 32a)…….……..10

– Epigyne with AMLL not fused together anteriorly (e.g. Fig. 2a)……...…....14

10. Epigyne with MS clearly visible posteriorly (Fig. 36a) [Zimbabwe]……....***jocquei* spec. nov.**

– Epigyne with MS not visible posteriorly (LL are in contact)...11

11. Vulva composed of several bulbous parts in TL (Figs 43c, d) [Horn of Africa to Arabia]……..***Cercetius perezi***

– Vulva different (with single large TL)……...……....12

12. MS as long as wide, CD and MS partially to fully sclerotized (Figs 30a–d) [South Africa]…….……..***jaegeri* spec. nov.**

– MS longer than wide and membranous, CD hyaline……...……...…….13

13. EF longer than wide (Figs 32a, 33a) [South Africa: Northern Cape Province]..... ***schoemanae* spec. nov.**

– EF wider than long (Figs 34a, f) [South Africa]…….. ***borakalalo* spec. nov.**

14. PE distinctly larger than AE (Fig. 7d), EF bridge present, (Fig. 8a) [Arabian Peninsula]…….... ***arabicus* spec. nov.**

– PE and AE nearly equal, EF bridge mostly absent……..15

15. MS as wide as long, MS length ¼ EF length, vulva with Gpo situated in a depression in connection with collar form a continuous ridge (Figs 5a–c) [Horn of Africa to Arabia]…. ***laevatus***

– MS mostly longer than wide, MS length ½ of EF length, vulva with Gpo situated in a depression separated from collar part (Figs 2a–c) [Eastern Mediterranean to Egypt and Algeria]…….. ***walckenaeri***

16. Male [unknown in *syrticus, pearsoni, maynardi, pontii*]…….....17

– Female.....35

17. Ventral opisthosoma with distinct dark marking……..18

– Ventral opisthosoma lacking distinct dark marking……....28

18. vRTA well developed: as long as one-third of dRTA (e.g. Fig. 25a)……...……...19

– vRTA not well developed: less than one-third of dRTA.....20

19. ET flat and wide with a pointed triangular process, dRTA robust and flattened dorso-ventrally (Figs 27a–c) [Burkina Faso and Nigeria]……...…. ***reverentia* spec. nov.**

– ET and dRTA different (Figs 25a–c) [Eastern Africa: Ethiopia, Kenya and Tanzania]……..... ***vestigator***

20. EM with projecting bulge covering proximal end of ET in ventral view (Figs 20a–c) [Eastern Morocco]……...…. ***fritschi***

– EM without any projecting bulge……...….21

21. ET directed proximad (Fig. 11a)……..22

– ET pointing in different direction……..……..23

22. ET robust and flat, dRTA sickle-like (Figs 11a, b), ventral opisthosoma with V-shaped marking (Fig. 48b) [Western Iberian Peninsula]……... ***dufouri***

– ET slim, dRTA more straight (Fig. 60c), V-shaped marking with additional median band (Fig. 48d) [Eastern Iberian Peninsula]…….…….. ***levantinus***

23. AE larger than or subequal as PE…….24

– PE generally larger than AE, PLE largest.....27

24. ET directed retrolaterad (Figs 12a, c) [Morocco].....***atlanticus***
– ET directed ventrad (Fig. 22c), PLE subequal to PME……..25
25. ET flattened, dRTA bent toward cymbium, directed ventrad (Figs 15a–c) [Northern Algeria]……..……..……..***barbarus***
– ET slim, dRTA directed distad (Figs 22a–c).....26
26. Small to medium *Eusparassus* species (16 to 18 mm) with ventral opisthosoma marking more solid in fresh samples and V-shaped in preserved ones (lines of marking are bold dark) (Fig. 49f) [North-Eastern Algeria].....***letourneuxi***
– Large *Eusparassus* species (21 to 25 mm), a vase-like black marking on ventral opisthosoma (Fig. 56d) [Iran to Pakistan].....***xerxes***
27. ET directed retrolaterad, vRTA pointed and triangular in ventral view (Figs 17a–c, 62a) [Algeria to Morocco].....***oraniensis***
– ET directed distad, vRTA broad and not pointed (Figs 42a–c, 66a, e).....***Cercetius perezi***
28. Embolus long and ET slender (e.g. Figs 37a–c).....29
– ET short and robust.....30
29. Palpal structures strongly elongated, embolus covered by slender embolus membrane (Figs 40a–c) [Southern Namibia].....***educatus* spec. nov.**
– Embolus membrane projected into a folded part close to ET (Figs 37a–c) [Northern Namibia, Angola].....***tuckeri***
30. AME strikingly larger (~1.5 times) than other eyes (Fig. 58e) [Central Asia].....***oculatus***
– AME subequal to or <1.5 times larger than others.....31
31. ET proximad, long and robust (Fig. 67c) [Afghanistan].....***fuscimanus***
– ET shorter and directed in different orientations.....32
32. vRTA rounded and not well developed (e.g. Fig. 68a).....33
– vRTA pointed and clearly triangular (e.g. Fig. 68e, see chapter 3.1:Moradmand & Jäger, 2012a: fig 17C).....34
33. ET slim (Fig. 67e) [Afghanistan to Rajasthan in India].....***kronebergi***
– ET robust (Fig. 68a) [Iran, Iraq and Turkey].....***mesopotamicus***
34. dRTA straight and beak-like, distal end of ET pointing distad (Fig. 68e) [China: Xinjiang Uyghur].....***potanini***
– dRTA with a slight bend in proximal half, ET leaf-like, distal end of ET pointing proximad (Fig. 67a) [Central Iran].....***doriae***

35. Ventral opisthosoma with distinct dark marking.....36
– Ventral opisthosoma lacking distinct dark marking.....48
36. MS widened (approximately as wide as EF), fully sclerotized and prominent (e.g. Figs 63b, d, f), chelicerae usually with more than two thick bristles (max. five bristles) at ventral base of fangs.....37
– MS small, hyaline to partially sclerotized, chelicerae mostly with one thick bristle (max. two bristles).....39
37. MS heart-shaped (Fig. 63f), femur spination 323 [India: Western Ghats].....***pearsoni***
– MS quadrangular (Fig. 63b), femur spination 424.....38
38. GP separated from CD by most of its entire length (Figs 26b, c) [East Africa: Tanzania to Ethiopia].....***vestigator***
– GP attached to CD by most of its entire length (Figs 28b, c) [Burkina Faso, Nigeria].....***reverentia* spec. nov.**
39. PE generally larger than AE, PLE largest.....40
–AE larger than or subequal to PE.....42
40. Vulva with several bulbous parts in the turning loop (Figs 43b–d) [Arabia to Horn of Africa].....***Cercetius perezi***
– Vulva different.....41
41. TL extending CD laterally (at least slightly) in dorsal view, GP small (Figs 18b, 19b) [Algeria to Morocco].....***oraniensis***
– TL invisible and covered by CD in dorsal view, GP enlarged (Figs 24b, c) [Tunisia].....***syrticus***
42. AMLL not encircling MS entirely, ventral opisthosoma with a vase-like black marking [Iran to Pakistan].....***xerxes***
– AMLL encircling MS entirely, ventral opisthosoma with a V-shaped or solid black marking.....43
43. EF quadrangular (e.g. Fig. 23a).....44
– EF rather triangular (e.g. Fig. 13a).....45
44. MS semicircular (Figs 23a, f, 61f) [North-Eastern Algeria].....***letourneuxi***
– MS triangular (Figs 16a) [North-Western Algeria].....***barbarus***
45. PLE very small (PLE ~1.4 times smaller than AME) (Fig. 21d); MS and EF mostly as long as wide (Fig. 21a) [Morocco].....***fritschi***
– Eyes different; EF distinctly longer than wide.....46

46. Lacking a sclerotized longitudinal strip on dorsal MS (Fig. 13b), ventral opisthosoma with a solid dark marking (Fig. 49b) [Morocco].....***atlanticus***

– A sclerotized longitudinal strip on MS present in dorsal view (e.g. Fig. 16b), ventral opisthosoma with a V-shaped dark marking.....47

47. GP located on a continuous part distinguishable from turning loop; ventral opisthosoma with a clear V-shaped marking (Fig. 48b) [Western Iberia].....***dufouri***

– GP situated on a semicircular process which is fused to entire body of vulva; V-shaped marking with an additional median band (Figs 48d, f) [Eastern Iberia].....***levantinus***

48. AMLL fused together and encircling MS entirely (e.g. Fig. 65b).....49

– AMLL not fused together and not encircling MS entirely (e.g. Fig. 67d).....50

49. Vulva ducts and TL coiled and twisted (Fig. 41c) [Namibia].....***educatus* spec. nov.**

– Vulva ducts and TL simple, straight and spherical, respectively (Fig. 38c) [Namibia].....***tuckeri***

50. EF bridge absent (e.g. Fig. 68d)……..51

– EF bridge present (e.g. Fig. 68f).....52

51. EF distinctly longer than wide, AMLL strongly developed (Fig. 66f), eyes subequal [Pakistan: Baluchistan].....***maynardi***

– EF nearly as long as wide, AMLL not developed (Fig. 68d), AME strikingly largest (Fig. 58e) [Central Asia].....***oculatus***

52. EF bridge distinctly separated from AMLL and not bordering MS (Fig. 68b) (see also Moradmand and Jäger 2012a: fig. 10A).....53

– EF bridge fused to AMLL and bordering MS.....55

53. EF as long as wide, AMLL not extended anteriorly (Fig. 67b) [Central Iran].....***doriae***

– EF longer than wide, AMLL extended anteriorly (e.g. Fig. 68b).....54

54. EF bridge distinctly separated from AMLL, approximately as long as MS length (Fig. 68f) [China: Xinjiang Uyghur].....***potanini***

– EF bridge separated from AMLL, but less than MS half length (Fig. 68b) [Iran, Iraq and Turkey].....***mesopotamicus***

55. EF as wide as long or slightly wider than long (Fig. 67d) [Afghanistan].....***fuscimanus***

– EF clearly longer than wide.....56

56. MS as wide as long (Fig. 66g) [Pakistan: Karakoram; India: Ladakh].....***pontii***

– MS distinctly wider than long (Fig. 67f) [Afghanistan to Rajasthan in India].....***kronebergi***

Taxonomy & Systematics

Family Sparassidae Bertkau, 1872

Subfamily Eusparassinae Järvi, 1912

Genus *Eusparassus* Simon, 1903

Type species: *Eusparassus dufouri* Simon, 1932, subsequent designation by Simon (1932). The type species was misidentified by Simon (1903) under the name "*E. argelasius*" sensu Latreille, 1818. The females misidentified by Latreille (1818) under the name "*Micrommata argelasia*" were type specimens which are not available. Thus, the neotype was designated from Montalvão (Portugal), re-described and illustrated by Moradmand and Jäger (2012a) [for more details on the nomenclature, see Moradmand and Jäger (2012b)].

Micrommata Latreille, 1804 [part]. Latreille 1818: 517; Dufour 1820: 299, pl. 2 (misidentification).

Sparassus Walckenaer, 1805 [part]. Walckenaer 1830: 108, pl. 7, fig. 1; Walckenaer 1837: 584, 585; Simon 1874: 252; Simon 1880: 290; Simon 1897b: 388; Bonnet 1958: 4098; Levy 1989: 138, fig. 20 (misidentification).

Olios Walckenaer, 1837 [part]. Pocock 1901: 489–493; Lawrence 1927:42, pls 2, 3, figs 29, 67.

Cercetius Simon, 1902: 253 (description of juvenile, holotype examined from Dibba, Persian Gulf). Simon 1903: 1020, 1023, 1026; Jäger & Kunz 2005: 170, figs 201–204 (illustration of juvenile holotype) [see the nomenclatural note in the description of *Cercetius perezi* Simon, 1902, below].

Eusparassus Simon, 1903: 1020, 1023, 1025. Simon 1909: 31; Järvi 1912: 57, 175, fig. 49, pl. 4, figs 9, 10; 1914: 173–175; Reimoser 1919: 200; Petrunkevich 1928: 155; Gravely 1931: 238; Schenkel 1936: 9, 283; Roewer 1928: 118, pl. 2, figs 38–39; 1955a: 775; 1962: 4, figs 82–84; Caporiacco 1935: 216, pl. 6, fig. 4; 1939: 353; 1941: 109, fig. 40; Denis 1937: 1050; 1938: 388; 1945: 54; 1947: 49, pl. 2, fig. 12; 1958: 102, f. 30; Barrientos & Urones 1985: 356, figs 4, 5; Jäger 1999: 1, 4, 6; 2001: 16, 18, figs 13 a–c, ä, ö; Song *et al.* 1999: 467, f. 268H, K; Jäger & Yin 2001: 132; Jäger & Kunz 2005: 168, 169, figs 205–213; Urones 2006: 100, figs 1–43; Dunlop *et al.* 2011: 519, figs 1–3; Deltshev 2011: 28; Gabriel 2011: 9–12, figs 2, 9; Moradmand & Jäger 2012a: figs 1–23.

Eusparassus (Doubtful usage). Strand 1906a: 630; 1907a: 437; 1907b: 671; 1908b: 19.

Diagnosis. *Eusparassus* is easily diagnosable from other members of subfamily Eusparassinae by the presence of two pairs of ventral tibial spines on legs I–IV (three pairs in *Pseudomicrommata*, *Arandisa*, *Leucorchestris* Lawrence, 1962 and *Carparachne* Lawrence, 1962); from *Olios* (subfamily Sparassinae) by a combination of characters including the presence of intermarginal denticles in some *Eusparassus* spp. (absent in *Olios* spp.), presence of a single bristle on the anterior margin of cheliceral basal segment below fangs but that number can reach a maximum of five (mostly >10 in *Olios* spp.). However, the best characters to distinguish between these two morphologically closely similar genera are those of the copulatory structures. In *Eusparassus* spp. the male palp is characterized by embolus and tegulum nearly of the same length arranged as a U-shaped structure, presence of embolus membrane (EM) [EM can be considered a well developed pars pendula, personal communication with C.A. Rheims], lack of any tegulum apophysis (Fig. 1); female epigyne shows two large lateral lobes (LL), and simple straight copulatory ducts leading to a more complex turning loop (TL) (Fig. 2).

Description. See chapter 3.1: Moradmand and Jäger (2012a).

Natural history and habitat preferences. The knowledge on the biology of stone huntsman spiders is quite scanty. They produce large silken papery retreats attached to the underside of stones or in crevices of rocks. They hide during the day in these retreats and also use them to moult in. The excuvia are mostly found within the abandoned retreats (personal observation). Females construct a sealed egg-sac inside the larger retreat and guard it until the spiderlings hatch. In *E. walckenaeri* (Audouin, 1826), it took nearly one month from pre-larval stage to hatching stage (Gabriel 2011). Like most Sparassidae, the stone huntsman spiders are nocturnal predators. They are known from semi-arid pine forest in the Atlas Mountains and the borders of the Sahara in Northern Africa to the Wahiba sand dunes and Wadis in Arabia, from the Mediterranean area to Central Asian deserts and the slopes of the Himalayas, and throughout the Eastern and Southern African Savannah to the arid borders of the Namib and Kalahari deserts. They can occur in very high elevations above sea level (e.g., *E. pontii* up to 3000–4000 m in Himalayas, Moradmand & Jäger 2012a). Earlier biological notes are restricted to some observations on the species *E. walckenaeri* by Gerhardt (1928, 1933) who documented his observations on the mating behaviour of this species (sub *Sparassus* sp. from Greece). Gabriel (2011) published his observations of the developments of spiderlings and some parasites and predators from Turkey.

Copulation. The first photographical documentation of the copulation process of palp and epigyne in the genus *Eusparassus* is recorded and presented here. Combining knowledge of the morphology of the copulatory structures in *Eusparassus* spp. and the detailed documentation on how they function in action provide some valuable data on the functional morphology of the pedipalp and epigyne. Juvenile specimens of *E. walckenaeri* were collected by Dr Peter Jäger in the Negev desert (during the 26th European congress of Arachnology) in September 2011. Specimens were reared in captivity until they reached maturity in August 2012. On the 7th of August, the female was housed in a glass terrarium (30cm diameter x 20cm high) and one day later, the male was introduced into the terrarium. A few minutes later, the male started searching and tracing the female. Suddenly he attacked her and tried to grab her by the legs and chelicerae but the female autotomized one leg and escaped. He fed on the leg of the female and subsequently killed a cricket roaming in the terrarium but did not consume it. The male approached the female again. This time the female did not struggle and the male seized her, face to face, using both his legs and chelicerae. He gently bit the female's pedicel area between prosoma and opisthosoma and held her with his legs (Fig. 44a). They remained in this position for a few seconds until the female was totally subdued and did not move till the end of mating. The male attempted to reach the female's epigyne, first from her right side using his left palp but without inserting his embolus (Figs 44b–d). Then he shifted to the left side of the female. The process of coupling palp and epigyne was initiated by anchoring the RTA (dRTA) into the posterior margin of epigyne between the lateral lobes (Figs 45a, d), the male stretched his right palp next, which suddenly expanded and the embolus was inserted into the copulatory opening (Fig. 45b). This observation (inserting dRTA into posterior margin between lateral lobes of epigyne) gives some evidence about a similar structure in the vulva which was recently recognized in the species of the genus *Sinopoda* Jäger, 1999. This structure was named membranous sac (Msa) and is supposed to hold the dRTA during copulation (Jäger 2012). The Msa can be mistaken for intermediate tissue and muscles around vulva, and is usually removed during vulva preparation since its presence restricts the view on scleriotized vulva structures.. The Msa in *Eusparassus* species is located medially between the fertilization ducts (Figs 11d, e). Another modification in the female copulatory organ might be the following: *Eusparassus* species with a more robust dRTA have special modifications dorsally of the median septum, from a simple hyaline structure (Fig. 2b) to a sclerotized longitudinal band (Fig. 16b) and even a complex folded structure (Fig. 36b).

Species groups

Species groups are recognized by a combination of somatic characters and those of copulatory structures of male and female. Six species groups are proposed: ***walckenaeri* group** (3 species), ***dufouri* group** (8 species)**,** ***vestigator* group** (3 species); ***jaegeri* group** (4 species); ***tuckeri* group** (2 species) and ***doriae* group** [7 species, description of members presented in Moradmand & Jäger (2012a)]. *Eusparassus xerxes* (Pocock, 1901), *E. pontii* Caporiacco, 1935 and *Cercetius perezi* Simon, 1902, could not be placed in any proposed species groups and are listed at the end of the description. In the following section species are listed according to species-groups. For every group the diagnosis, species composition and distribution range are presented. In this paper the representatives from Africa and Arabia are re/described. For description of the species from Europe, the Middle East, Central and South Asia, see Moradmand and Jäger (2012a).

walckenaeri species group

Diagnosis. Chelicerae with intermarginal denticles (Figs 1f, 5e, 7e, 10c); ventral opisthosoma lacking any dark marking (Fig. 46d); male palp with ST small in size (compare to *jaegeri* group) and situated behind EM (Figs 1b, 4a, 7a, 9a); AMLL of epigyne not fused (Figs 2a, 5a, 8a, 10a); there is no GP, and Gpo situated in a depression on vulva (Figs 2c, 3b, 5c, 8c, 9f, 10e).

Species composition. Three species: *Eusparassus walckenaeri* (Audouin, 1826), *E. laevatus* (Simon, 1897) **comb. nov.** and *E. arabicus* **spec. nov.**

Distribution. Eastern Mediterranean to North-Eastern Africa and Arabian Peninsula (Fig. 70a).

Eusparassus walckenaeri (Audouin, 1826)

Figs 1–3, 46a–e, 59a, b

Philodromus walckenaerii Audouin, 1826: 390, pl. 6, fig. 1 (description of female, Egypt; no type series designated).

Philodromus linnaei Audouin, 1826: 390, pl. 6, fig. 2 (description of male, Egypt, no type series designated) [synonymy by Simon 1906].

Drassus civilis Reuss, 1834: 207 (description of juvenile; holotype, immature, examined) [synonymy by Levy 1989].
Sparassus walckenaeri (Audouin). Walckenaer 1837: 585 (transfer); Pavesi 1880: 364; 4; Levy 1989: 132–138, figs 3–18.
Ocypete tersa C. L. Koch, 1837: 83, fig. 305 (description of female; from Greece, type not available) [synonymy by Levy 1989]. C. L. Koch 1845: 39, figs 980–981.
Sparassus cambridgii Simon, 1874: 257 (description of juvenile, from Egypt) [synonymy by Simon 1880].
Sparassus validus Thorell, 1875a: 80 (description of female; holotype female, MZH, examined) [synonymy by Levy 1989]. Thorell 1875b: 124.
Sparassus cognatus O. Pickard-Cambridge, 1876: 588 (description of female; syntypes, one female and 10 immatures, Egypt, not examined) [synonymy by Levy 1989].
Sparassus extensipes Karsch, 1880: 383, pl. 12, fig. 12. (description of male, holotype, male, Egypt: Cairo, not examined) [synonymy by Simon 1906].
Sparassus walckenaerius (Audouin). Simon 1880: 292.
Sparassus tersa (C. L. Koch). Simon 1880: 291 (in part, material from Greece, MNHN, examined).
Sparassus linnaei (Audouin) Kulczyn'ski. 1901: 43 (transfer) (one male examined from Cairo in MIZ).
Eusparassus walckenaeri (Audouin). Simon, 1906: 1168; Strand 1908b: 24; Denis 1947: 50, pl. 2, figs 14–16.); Deltshev 2011: 28; Gabriel 2011: 9–12, figs 2, 9; Moradmand and Jäger 2012a: 2453, figs 1B, 5–6, 23A (designation of neotype, neotype male from EGYPT examined).
Eusparassus tersa (C. L. Koch). Järvi 1912: 57, fig. 48, pl. 4, figs 4–8 (transfer); Järvi 1914: 173.
Heteropoda civilis (Reuss). Strand 1916: 36 (unjustified combination).

Type material. Neotype of *E. walckenaeri* (subsequent designation by Moradmand and Jäger 2012a): male, **EGYPT:** ***Muhafazat al Qahirah***: Cairo [N 30° 3', E 31° 15'], 1971 (SNSD 52); **Holotype** of *Drassus civilis* (designated by Reuss 1834): immatere, **EGYPT:** ***Sinai***: Tor, 1827 Rüppell leg. (SMF 4575); **Holotype** of *Sparassus validus* (designated by Thorell, 1875a): female, **TURKAY:** Taurus Mountains, (label: Taur. Merid., Ent.etikett nr=232), Nordmann leg. (MZH 20.492).

Other material examined. (16♂♂, 18♀♀): EGYPT: 1♂, 1♀ (MM 121), with same data as for neotype (SNSD); ***Muhafazat al Qahirah***: 1♂, Helwan, March 1901, in house (NHM); 1♂, Fayid, gravel area, 15 April 1947, J.H. Graham leg. (NHM 1948.10.11.7); 1♂, Cairo, with label: "*Sparassus linnaei,* Cairo, det. Kulczyński, F.1691" (MIZ 212984); ***Muhafazat al Qina***: 1♂ (MM3), 2♀♀ (MM17, MM206), Luxor (Al Uqsur), Thebes (SMF 5557); ***Muhafazat al Jizah*:**

1♂ (MM7), Al Jizah (=Gizeh) (SMF 5576); ***Muhafazat al Suways***: 1♀, Djebel Genaifa, W of Suez Canal, 9 June 1947, G. Konieczny leg. (SMF); 3♂♂, 7♀♀, 1 juv., "*Prof. J. Omer-Cooper SIWA Expedition 1935*", *Libyan Desert*, Siwa Oasis, 20–30 May (2♀♀, 1 juv.: NHM 1936.2.12.94–96, 2♂♂: NHM 1936.2.12.97–98), 29 April (1♂: NHM 1936.7.10.6), 22 July (1♀: NHM 1936.2.12.176), August (1♀: NHM 1936.2.12.157), 22 August (1♀: NHM 1936.2.12.177), 30 August (1♀: NHM 1936.2.12.560); 1♂, 2♀♀, 18 October 1985, Sörensen & Kollend leg. (ZMUC); **LIBYA**: ***Baladiyat al Kufrah***: 1♂, Jebel Uweinat, Karkur Talh [N 21° 54', E 024° 58'], "Mission Scientifique Belge", 25 October 1968 (MRAC 135886); 1♀, *Baladiyat Shahhat*, Susa (=Soussa) (MNHN 227.61); **SUDAN:** ***Wilayat al Khartoum***:1♂, Khartoum, July 1909, S.S. Floman leg. (NHM 09.10.13.1048); 1♀, 1 juv., Khartoum, October 1979, El Hamin El Rayal leg. (MRAC 152086–87); ***Wilayat al Bahar al Ahmar***: 1♀, Gabet al Maadin, 20 km S of Mohammed Qul., 21 September 1960, Prof. J. C. Thompson leg. (NHM); **ALGERIA**: ***Wilaya d' El Oued***: 1♂, 1♀, El Oued, C.I.E. coll: 13593-1559, 1953, L. Past al Ag leg. (NHM); ***Wilaya d' Illizi***: 1♂, Fort Polignac, C.I.E. coll: 13593-3585, September 1953, L. Pastal Ag leg. (NHM); ***Wilaya d' Tamanghasset***: 1♀, 1 juv., Tamarnaset, C.I.E. coll: 13593, 1953, L. Past al Ag leg. (NHM); **TUNISIA**: ***Gouvernorat de Gafsa***: 1♂, Gafsa, 1904, Weiss leg. (MNHN); ***Gouvernorat de Kebili***: 1♂. Kebili, Zaafrane 15 km w Douz, N 33° 26' 44.2", E 8° 54' 7.6", 21 May 2007, C. Muster leg. (CCM).

Diagnosis. Embolus tip (ET) retrolaterad and subsequently twisted distad (Fig. 1d); dRTA extending latero-distally (Fig. 1b); MS (compared to that of *E. laevatus* **comb. nov.**) enlarged and longer than wide (Figs 2a; 3a, c). [see also diagnosis for *walckenaeri* species group above].

Description. Male (ranges: n=17, single measurement: MM7):

Measurements. Medium sized; total length 13.6–16.7, prosoma length 7.1–8.4, prosoma width 6.0–7.2, anterior width of prosoma 2.8–3.8, opisthosoma length 6.5–8.3, opisthosoma width 5.0–5.8. Eye diameters: AME 0.50, ALE 0.48, PME 0.47, PLE 0.51; eye interdistances: AME-AME 0.20, AME-ALE 0.06, PME-PME 0.44, PME-PLE 0.52, AME-PME 0.42, ALE-PLE 0.30, clypeus height at AME 0.63, clypeus height at ALE 0.69.

Chelicerae. Chelicerae with 2 anterior and 3 to 5 posterior teeth (first three larger with additional smaller ones); cheliceral furrow with 8 to 20 intermarginal denticles; mostly with one bristle at distal end of cheliceral basal segment (Fig. 1f).

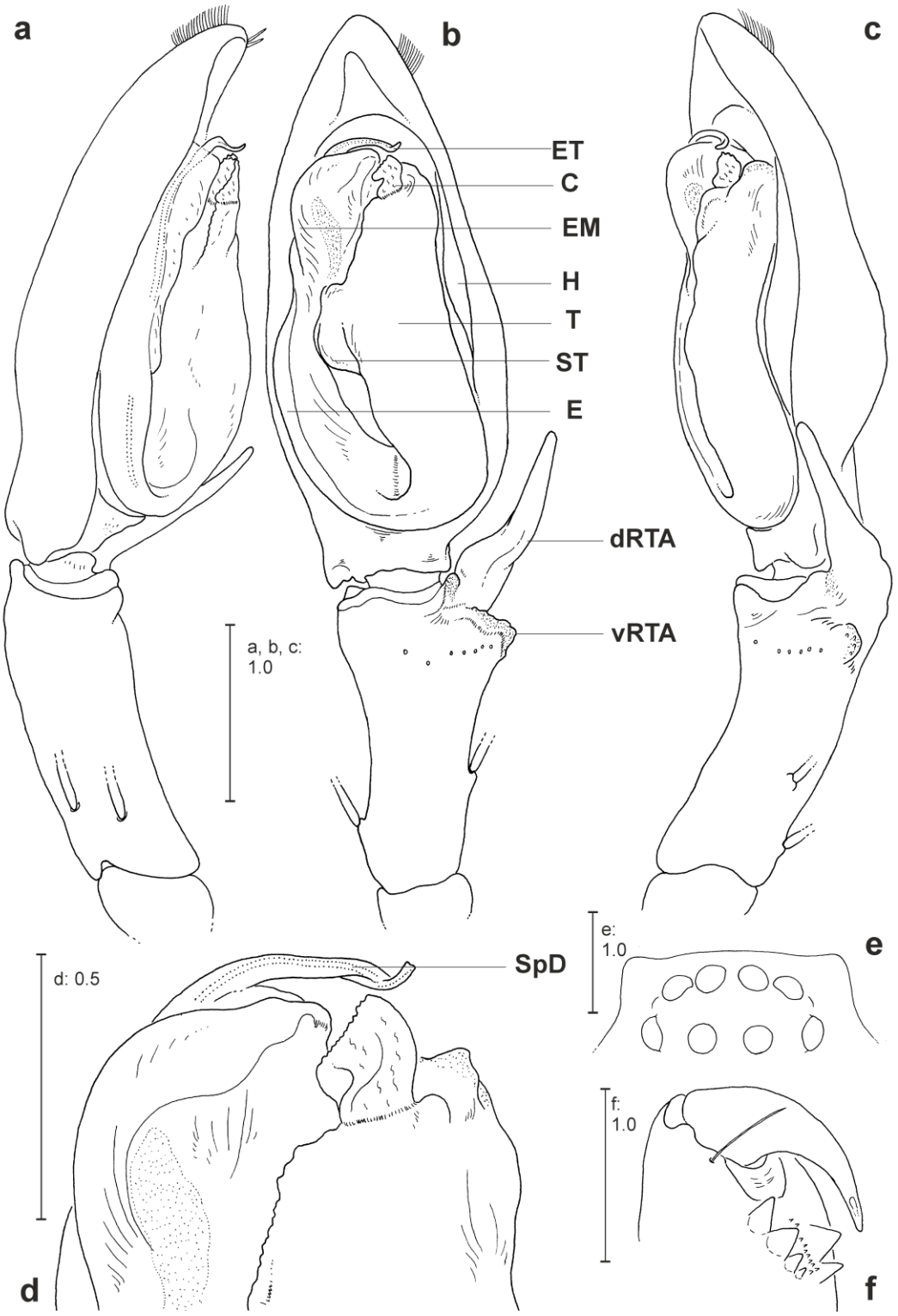

FIGURE 1. *Eusparassus walckenaeri* (Audouin, 1826), male from EGYPT: Thebes (SMF). (a–c) left palp (a prolateral, b ventral, c retrolateral); (d) tip of embolus and conductor, ventral; (e) eye arrangement, dorsal; (f) right chelicera, ventral. Abbreviations: C — Conductor, dRTA — dorsal retrolateral tibial apophysis, E — Embolus, EM — Embolus membrane, ET — Embolus tip, H — Haematodocha, SpD — Sperm duct, ST — Subtegulum, T — tegulum, vRTA — ventral retrolateral tibial apophysis.

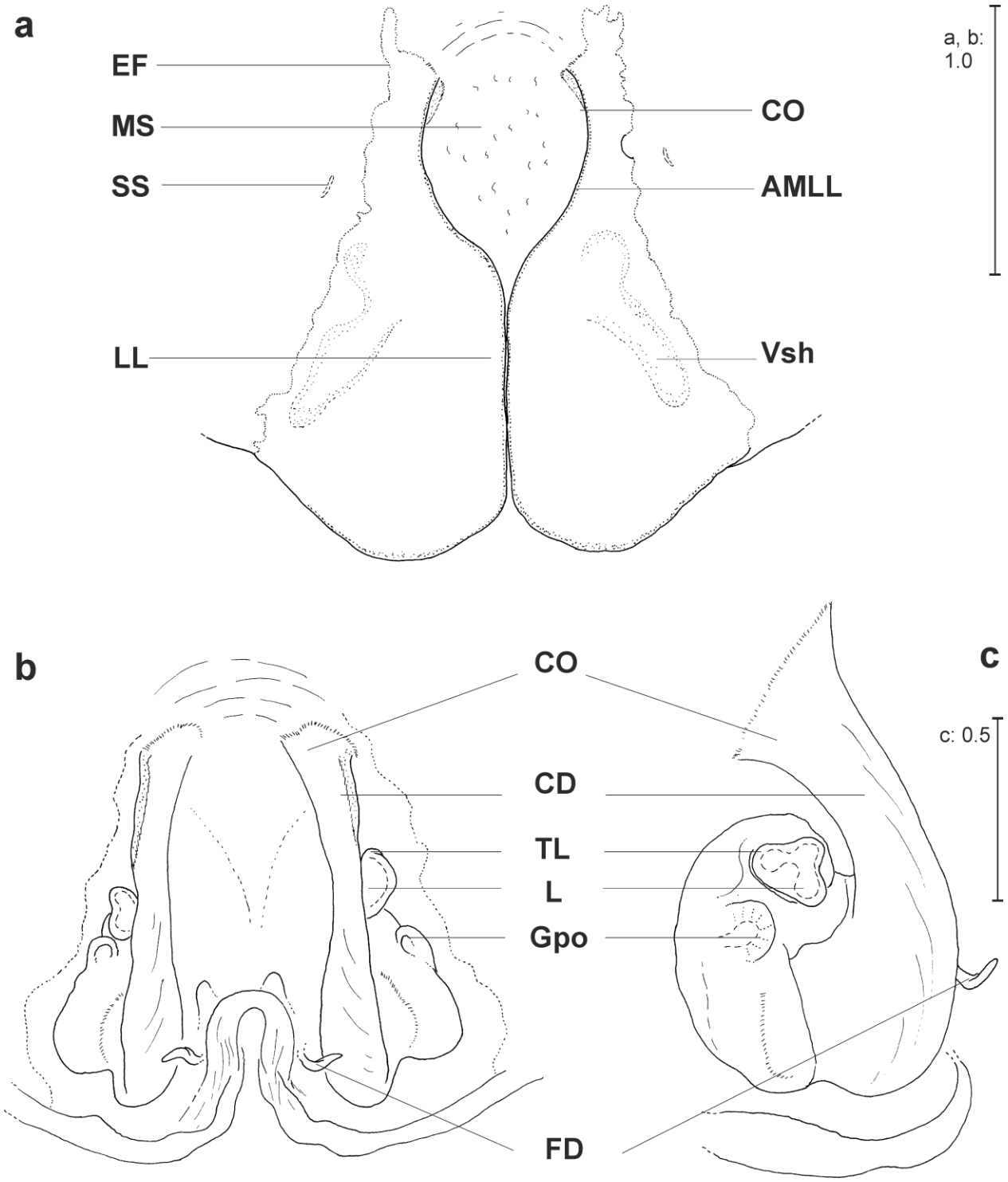

FIGURE 2. *Eusparassus walckenaeri* (Audouin, 1826), female from EGYPT: Thebes (SMF). (a) epigyne, ventral; (b) vulva, dorsal (c) left vulva, anterio-dorso-lateral. Abbreviations: AMLL — anterior margin of lateral lobes, CD — copulatory duct, CO — copulatory opening, EF — epigynal field, FD — fertilization duct, Gpo — glandular pores, L — Lumen, LL — lateral lobes, MS — median septum, SS — slit sensillum, TL — turning loop, Vsh — vulva shadow.

Legs. Leg formula: II IV I III. Measurements of palp and legs (MM7): Palp 11.8 [3.8, 1.7, 2.2, 4.1], I 44.7 [12.0, 4.6, 12.2, 12.3, 3.6], II 48.1 [13.1, 4.8, 13.4, 13.2, 3.6], III 40.8 [11.7, 4.2, 11.2, 10.6, 3.1], IV 45.5 [12.5, 4.0, 12.0, 13.7, 3.3].

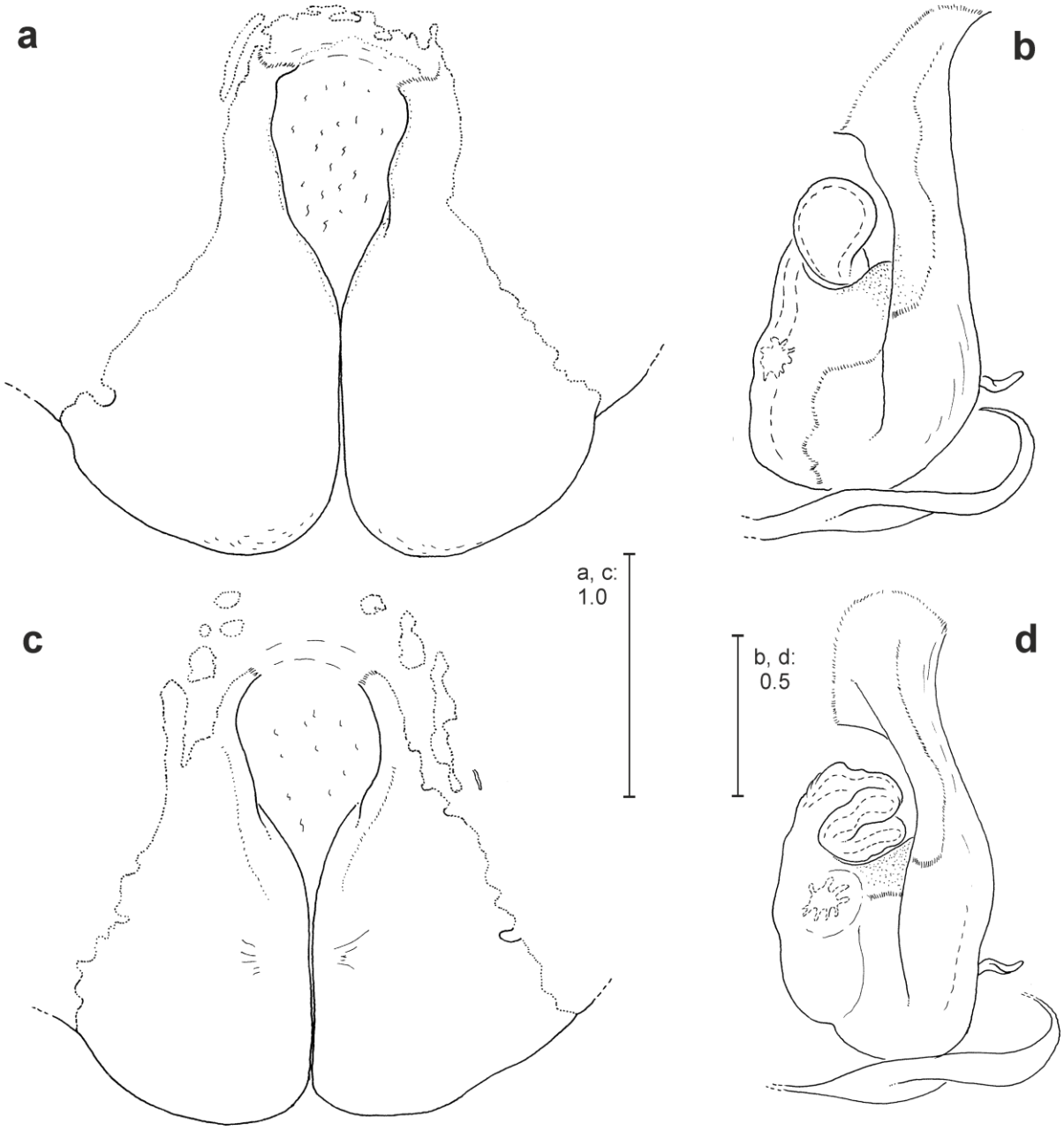

FIGURE 3. *Eusparassus walckenaeri* (Audouin, 1826), variation: (a, b) female from LIBYA (MRAC); (c, d) female from ALGERIA (NHM). (a, c) epigyne, ventral; (b, d) left vulva, anterio-dorso-lateral.

Spination. Palp 131, 001/101, 1111; Legs: Femur I–III 323, IV 321/322; Patella I–IV 001/101; Tibia I–IV 2124/2224; Metatarsus I–III 2024, IV 3036.

Palp. As in diagnosis with cymbium less than two times longer than tibia (Fig. 1c); ET hyline and not covered by EM ventrally (Fig. 1d); vRTA pointed and triangular in ventral view (Fig. 1b).

Female (ranges: n=18, single measurement: MM17):

Measurements. Medium to large sized; total length 17.8–26.6, prosoma length 7.5–10.1, prosoma width 6.4–8.7, anterior width of prosoma 3.7–5.0, opisthosoma length 10.3–16.5, opisthosoma width 7.2–11.0. Eye diameters: AME 0.47, ALE 0.42, PME 0.44, PLE 0.51; eye interdistances: AME-AME 0.19, AME-ALE 0.08, PME-PME 0.41, PME-PLE 0.57, AME-PME 0.50, ALE-PLE 0.39, clypeus AME 0.71, clypeus ALE 0.65.

Chelicerae. Chelicerae as in males.

Legs. Leg formula: II IV I III. Measurements of palp and legs. Palp 12.0 [3.6, 1.8, 2.5, 4.1], I 36.6 [10.0, 4.5, 9.2, 9.7, 3.2], II 40.6 [11.3, 4.9, 10.5, 10.7, 3.2], III 34.3 [10.1, 4.1, 8.8, 8.5, 2.8], IV 38.7 [11.0, 4.1, 9.7, 10.7, 3.2].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321/322; Patella I–IV 000/001; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034/3036.

Epigyne/vulva. As in diagnosis with EF slightly longer than wide (Fig. 2a) or as wide as long (Figs 3a, c); MS lacking a sclerotized strip dorsally (Fig. 2b); TL of vulva simply spherical (Fig. 3b) or folded (Fig. 3d).

Colouration (Live). Varies from dark brown with darker W-shaped distinct pattern on prosoma, a series of chevrons on dorsal opisthosoma and surrounding additional dark patches; legs clearly banded (Figs 46 a, c–e) to a milky cream body decorated with fewer dark patches on prosoma and opisthosoma, femora not banded with dark rings (Fig. 46b); ventral opisthosoma lacking dark marking (Fig. 46d).

Remarks. Species boundaries in *walckenaeri* species group remain obscure, despite distinguishing three valid species. Since *E. walckenaeri* shows a great similarity in copulatory structures in a vast area, it requires an additional and robust molecular investigation to uncover potential hidden diversity. For example, specimens from the Seychelles (MRAC 144729) examined by Benoit (1978) were studied and confirmed to be an *Eusparassus* sp. of the *walckenaeri* species group. Levy (1989) and Saaristo (2010) mentioned this record referring to Benoit (1978) but it seems that they did not study the specimens, as no illustration of the specimens appeared in their publications. These specimens closely resemble undescribed species from Eastern Africa and Arabia and were probably introduced to the islands by ships. Benoit

(1978) stated that *E. walckenaeri* was introduced to the Seychelles Islands from the Mediterranean region. These specimens resemble *E. walckenaeri* but the diagnostic characters are neither sufficient to describe a new species nor to list them under *E. walckenaeri*. These speciemens are larger and more robust than *E. walckenaeri* and the epigyne has dorsally an additional sclerotized median band on the MS (Figs 9d, e; 10a–b), Gpo is located in a small circular depression on vulva but with considerable distance from TL (Figs 9f, 10e), compared to that of *E. walckenaeri*. The specimens from Somalia and Sudan have a similar dark pattern as *E. walckenaeri* group but with white background (Fig. 46f) (instead of dark brown or creamy as in other *walckenaeri* group members). DNA barcoding from freshly collected samples hopefully will assist in any final decision.

Known geographical distribution and habitat. From Greece in the North to Chad in the South and from Algeria in the West to Iraq in the East (Fig. 70a), collected near vicinities of villages, orchards, stony deserts, living under stones.

Eusparassus laevatus (Simon, 1897) comb. nov.

Figs 4–6, 47a–c, 59c, d

Sparassus laevatus Simon, 1897c: 388 (description of female, listing field numbers of one male and one female). [Syntypes, NHM, examined]

Olios laevatus (Simon) Roewer 1955b: 695 (unjustified transfer).

Type material. Syntypes (designated by Simon 1897c): 1♀, 1♂, **ETHIOPIA**: 1♀, West of Shebelle River, (label: *Sparassus laevatus* Simon, Type, W of Shebeli River, 15.12.94), (NHM 97.11.10.55); 1♂ Shebelle River, (label: *Sparassus laevatus* Sim, Shebeli, 1.9.94) (NHM).

Other material examined. (17♂♂, 15♀♀): **ETHIOPIA**: ***Afar Region***: 1♂, Awash National Park, RAS Hotel, 08° 59'N, 040° 10' E, in gravely area, 5 October 1988, A. Russell-Smith leg. (MRAC 236211); 1♂, Awash National Park, RAS Hotel, 08° 59'N, 040° 10' E, in Caravan, 18 February 1986, A. Russell-Smith leg. (MRAC 236152); **DJIBOUTI**: ***Tadjourah Region***: 3♂♂, 4♀♀, Tadjoura, Randa, 1958 [label: Coloniales Cote francaise de Somalies, Tadjoura, Roünda,

1958] (MNHN); **SOMALIA**: ***Nugal***: 1♂, Run, Valle del Nogal, July 1969 (MRAC 173159); ***Gobolka Woqooyi Galbeed***: 1♀, Somaliland, NE Hargeshia, 1111 m, 8 July 2011, F. Kovařík

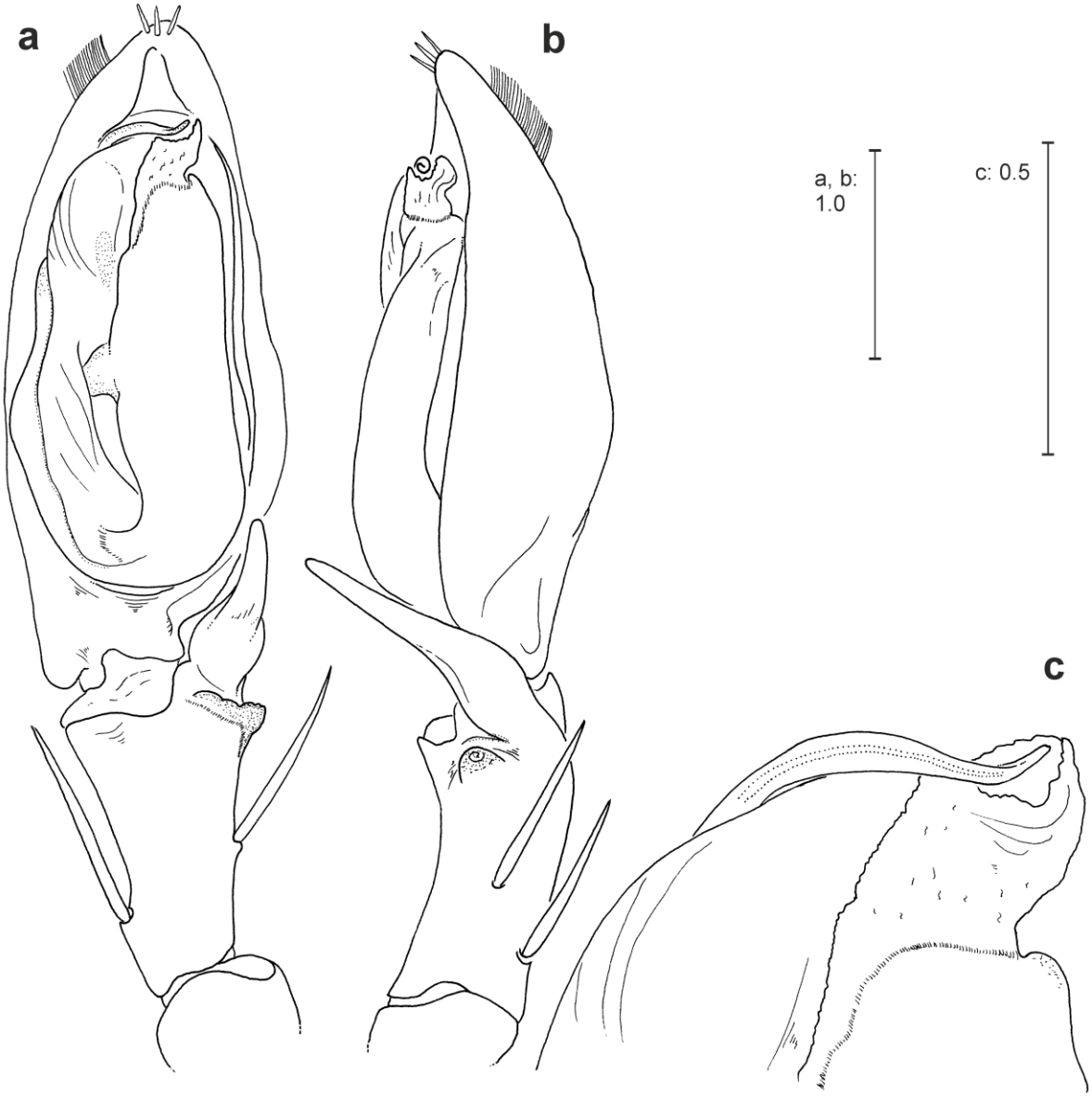

FIGURE 4. *Eusparassus laevatus* (Simon, 1897) **comb. nov.**, syntype male from Ethiopia: Shebelle River (NHM). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral.

leg. (SMF, SD841, MM163); **YEMEN**: ***Muhafazat al Mahwit***: 1♂, 1♀, Ar Rujum, 16 October 2000–15 January 2001, in Malaise trap, A.van Harten & A. M. Hayer (15.26 N, 43.40E, 1900 m) leg. No. 1500 (SMF); 2♂♂, Ar Rujum, 9 April–5 June 2001, in Malaise trap, A. van Harten leg. No. 1500 (SMF); 1♂, 2♀♀, Al Lahima, 1 January–8 April 2001, in Malaise trap, A. van Harten leg. No. 1368 (SMF); 1♂, 1♀, 12 km NW of Mankha, 5 May–6 July 2001, in Malaise trap, A. van Harten leg. No. 1795 (SMF); ***Muhafazat Hadramawt***: 1♀, Hadhramaut, D. Anderion (NHM

94.11.1); 1♀, Haraz Mountain, Southern slope of Al Lan, 2600 m, 23 June 2010, V. Hula & J. Niedobová (SMF, SD 813, MM164); **SAUDI ARABIA**: 1♂, Arabian, A. B. Derewal leg. (NHM 99.12.2.16); ***Al Bahah***: 1♂, Bani Sar, 29 February–7 March 1984, W. Büttiker leg. (NMB); 2♂♂, 1♀, An-Namas, 17 April 1980, 2380 m, W. Büttiker leg.(NMB); 1♂, 1♀, An-Namas, 19 September 1980, 2380 m, W. Büttiker leg. (NMB); 1♀, Wadi Damad, 800 m, 24 September 1981, W. Büttiker leg. (NMB); **OMAN**: 1♂, Mudhaybi, 530 m, N 22˚ 12', E 58˚ 06', camp 12, 12 March 1986, W. Büttiker leg. (NMB); ***Muhafazat Zufar***: 1♀, ca. 40 km NE Dhofar, Tawi Atayr, Wadi Hinna, Salah Collection permit granted to Prof. Weygoldt No.07/2000, 23 September 2000, S. Huber leg. (SMF, MM32); **UNITED ARAB EMIRATES**: ***Ra's al Khaymah***: 1♀, Wadi Shawkah, 5–12 May 2007, in water trap, A. van Harten leg. (SMF, MM49)

Diagnosis. Closely similar to *E. walckenaeri* but males differ in shape and direction of dRTA which extends disto-ventrally (Fig. 4a); female differ in having MS reduced in size (Figs 5a; 6a, d); Gpo situated in an indentation in connection with TL collar forming a continuous ridge (Figs 5b–c, 6b–c) [see also diagnosis for *walckenaeri* species group above].

Description. Male (ranges: n=18, single measurement: syntype):

Measurements. Medium sized; total length: 12.3–15.7, prosoma length 5.8–7.5, prosoma width 4.5–6.7, anterior width of prosoma 2.1–3.6, opisthosoma length 6.5–8.2, opisthosoma width 3.5–5.2. Eye diameters: AME 0.50, ALE 0.40, PME 0.37, PLE 0.43, Eye interdistances: AME-AME 0.20, AME-ALE 0.01, PME-PME 0.36, PME-PLE 0.38, AME-PME 0.39, ALE-PLE 0.23, clypeus height at AME 0.25, clypeus height at ALE 0.41.

Chelicerae. Chelicerae with 2 anterior and 4 or 5 posterior teeth; cheliceral furrow with intermarginal denticles.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 9.4 [3.1, 1.1, 1.7, 3.5], I 35.0 [9.2, 3.6, 9.6, 9.7, 2.9], II 37.1 [10.2, 3.7, 10.0, 10.3, 2.9], III 30.9 [9.0, 3.1, 8.0, 8.2, 2.6], IV 35.2 [10.0, 3.0, 9.1, 10.2, 2.9].

Spination. Palp 131, 001/101, 1111; Legs: Femur I–III 323, IV 321/322; Patella I–IV 001/101; Tibia I–IV 2124/2224; Metatarsus I–III 2024, IV 3036.

Palp. As in diagnosis with cymbium longer than tibia but not more than twice tibia length (Fig. 4b); vRTA pointed and triangular (Fig. 4a); ET retrolaterad first and slightly distad (Fig. 4c).

Female (ranges: n=17, single measurement: syntype):

Measurements. Medium sized; total length: 16.3–18.1, prosoma length 7.0–8.6, prosoma width 6.2–7.5, anterior width of prosoma 3.5–4.3, opisthosoma length 9.3–9.5, opisthosoma width 6.3–6.5. Eye diameters: AME 0.51, ALE 0.37, PME 0.36, PLE 0.41; Eye interdistances: AME-AME

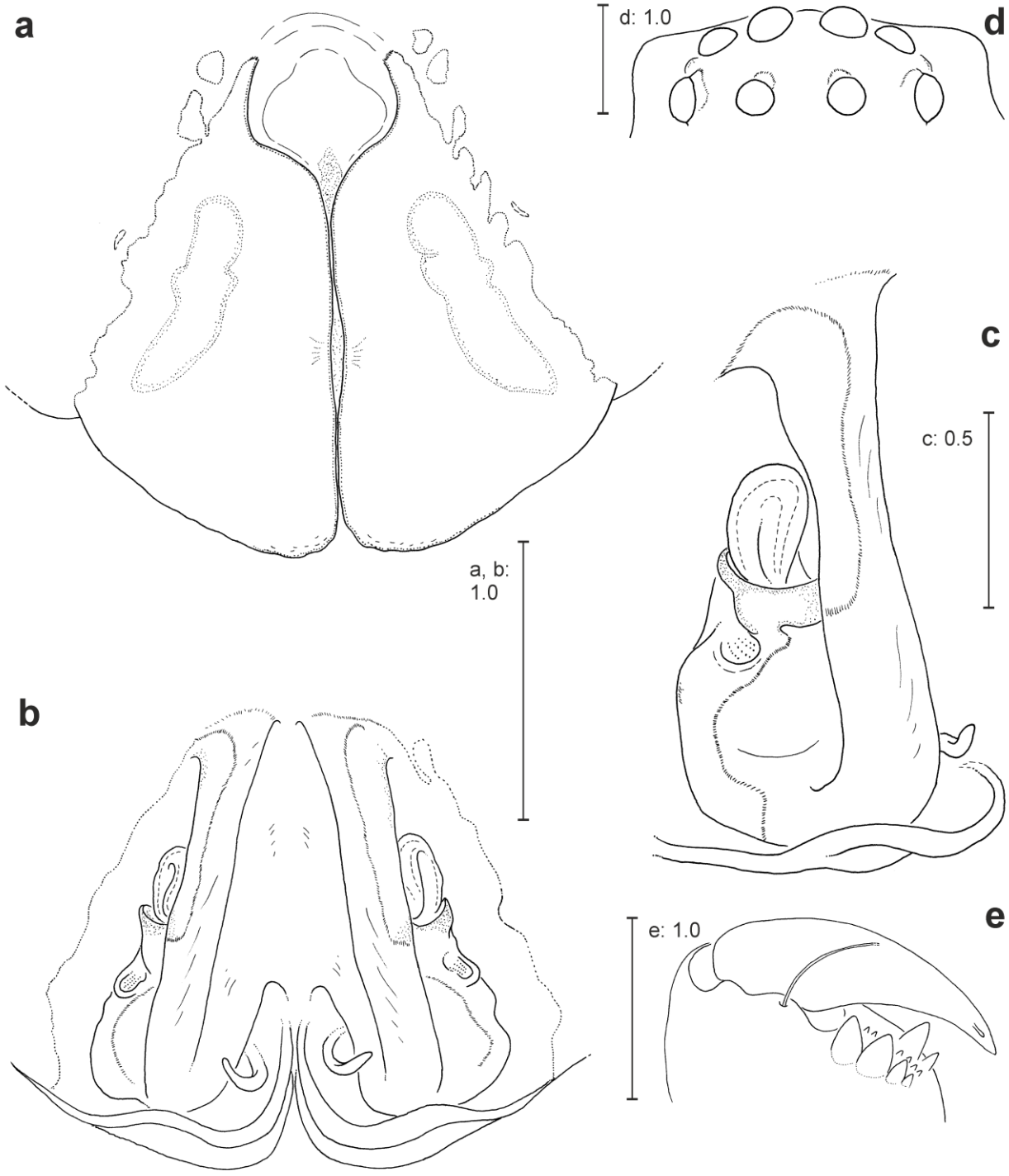

FIGURE 5. *Eusparassus laevatus* (Simon, 1897) **comb. nov.**, syntype female from Ethiopia: W of Shebelle River (NHM). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) eye arrangement, dorsal; (e) right chelicera, ventral.

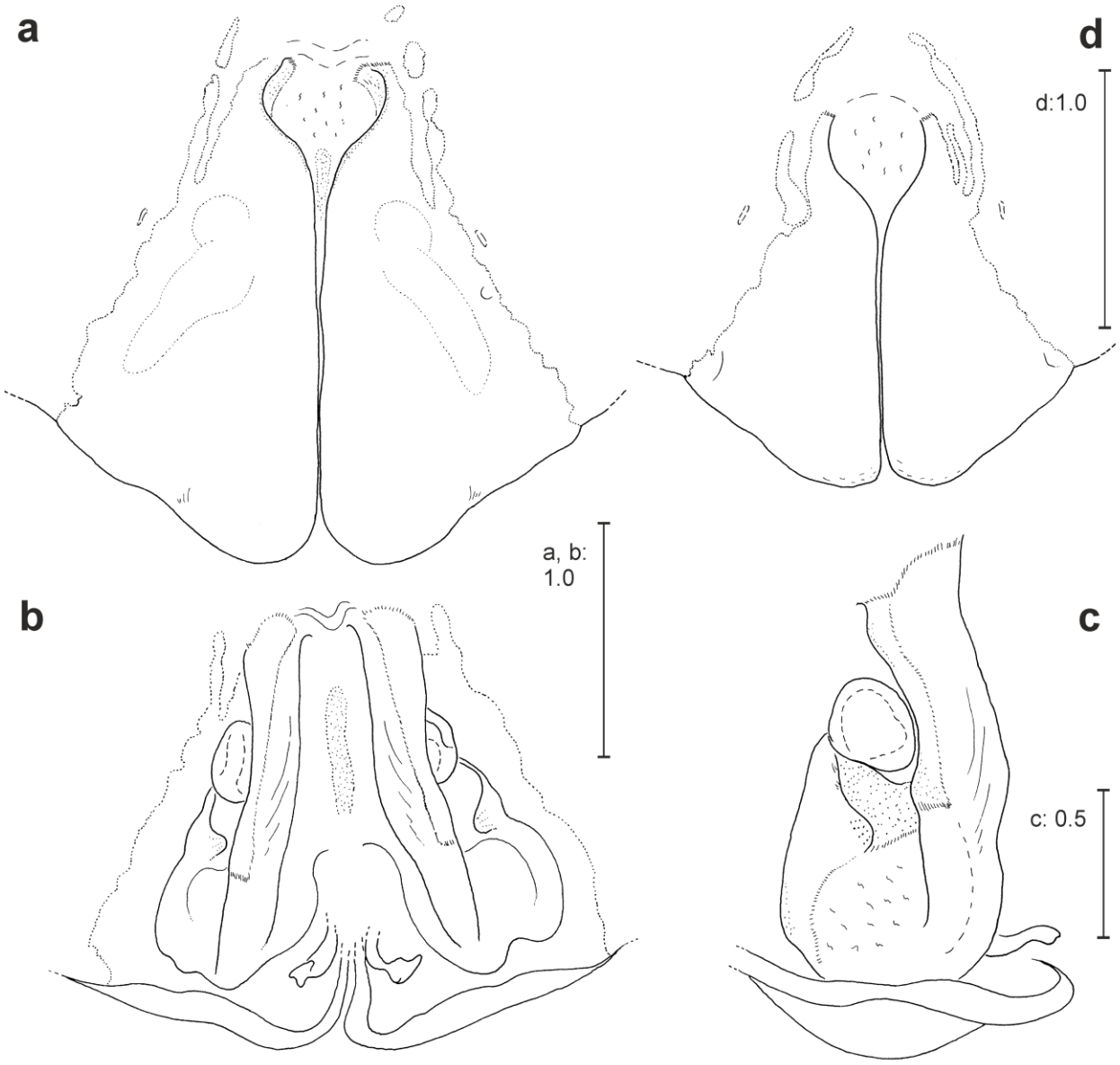

FIGURE 6. *Eusparassus laevatus* (Simon, 1897) **comb. nov.**, variation in females from Arabian Peninsula: (a–c):female from Yemen (SMF); (d) female from United Arab Emirates (SMF). (a, d) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral.

0.23, AME-ALE 0.05, PME-PME 0.50, PME-PLE 0.45, AME-PME 0.37, ALE-PLE 0.23, clypeus AME 0.43, clypeus ALE 0.56.

Chelicerae. Chelicerae with 2 anterior and 3 to 5 posterior teeth, cheliceral furrow with 8 to 20 intermarginal denticles; one bristle at distal end of cheliceral basal segment (Fig. 5e).

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 10.0 [2.8, 1.5, 2.0, 3.7], I 29.7 [7.8, 3.7, 7.7, 8.0, 2.5], II 32.5 [9.2, 3.7, 8.5, 8.6, 2.5], III 26.8 [8.2, 3.2, 6.7, 6.6, 2.1], IV 30.7 [9.1, 3.1, 7.8, 8.3, 2.4].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321/322; Patella I–IV 000/001; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034/3036.

Epigyne/vulva. As in diagnosis with EF slightly wider than long (Fig. 5a) or as long as wide (Figs 6a, d); longitudinal sclerotized strip on MS present (Fig. 6b) or absent (Fig. 5b); CD short, vulva robust and compact (Figs 5c, 6c) compared to other *walckenaeri* group members.

Colouration (Live). Yellowish brown with distinct dark pattern on prosoma, dorsal opisthosoma with a long cardiac mark, legs clearly banded (Fig. 47b) to paler bands (Fig. 47c); specimen in ethanol reddish brown with pale body (Fig. 47a).

Remarks. Simon (1897c) described only the female of *E. laevatus* **comb. nov.** but he listed two different field numbers corresponding to specimens collected from the type locality, Shebelle River (Simon 1897c: 389). My investigation in the collection of NHM revealed that the second number (1.9.94) refers to a male sympatrically collected from the type locality and definitely examined by Simon (1897c). According to Article 72.4.1 of the Code (ICZN 1999), the male belongs to the type series, and is, as the female, a syntype. The type specimens were collected by the American investigator, A.D. Smith during "The first expedition from Somaliland to Lake Lamu" in 1893–94. The female is redescribed but the male, even though it is a syntype, is described for the first time.

Known geographical distribution and habitat. East Africa from southern Ethiopia to the horn of Africa in Somalia and Djibouti (new country record), and the Arabian Peninsula in Yemen (new country record), Saudi Arabia (new country record) and Oman (new country record) (Fig. 70a).

Eusparassus arabicus spec. nov.

Figs 7–8, 47d–e, 59e–f

Type material. Holotype: male, **SAUDI ARABIA: *Mintaqat ar Riyad*:** Wadi Mizbil [N 24˚ 30', E 46˚ 25'], 13 April 1977, W. Büttiker leg. (NMB-ARAN 20666).

Paratypes (4♂♂, 1♀)**: SAUDI ARABIA:** 1♂, same data as for holotype (SMF); ***Mintaqat al Hail*:** 1♀, Wadi Naqben [in Jebel Aja Mountain], N 27˚ 41', E 41˚ 38', 1050 m, 27 May 1981, W. Büttiker leg. (NMB-ARAN 20667); ***Mintaqat Makkah*:** 1♂**,** Abha, Asir Mountains**,** 2200 m, April 1977, Dr. C. Lowe leg. (NHM); 1♂, Abulat Island, Red Sea, "Mission de la Calypso Mer Rouge 1952", Cherbounier leg. (MNHN); **UNITED ARAB EMIRATES**: ***Dubayy***: 1♂, Barasti, Jumeriah, 1964, Peck leg. (AMNH).

Etymology. The specific name is taken from the type locality. Adjective.

Diagnosis. This is the only *walckenaeri* group member with PLE distinctly larger than AME (~1.2 times) (Figs 7d, 47d–e); male palp closely similar to that of *E. walckenaeri* (especially ET) but can be easily recognized by the more slender and longer dRTA and less developed vRTA (Fig.7a–b) [see also diagnosis for *walckenaeri* species group above].

Description. Male (ranges: n=5, single measurement: holotype):

Males medium-sized; total length 13.2, prosoma length 6.7, prosoma width 5.8, anterior width of prosoma 2.8, opisthosoma length 6.5, opisthosoma width 4.6. Eye diameters: AME 0.44, ALE 0.50, PME 0.46, PLE 0.53, eye interdistances: AME-AME 0.14, AME-ALE 0.02, PME-PME 0.30, PME-PLE 0.33, AME-PME 0.38, ALE-PLE 0.25, clypeus height at AME 0.35, clypeus height at ALE 0.40.

Chelicerae. Chelicerae with 2 anterior and 3 to 4 posterior teeth, cheliceral furrow with intermarginal denticles (Fig. 7e).

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 10.6 [3.6, 1.6, 2.2, 3.2], I 40.4 [10.7, 4.2, 11.2, 11.5, 2.8], II 44.9 [12.1, 4.2, 12.8, 12.7, 3.1], III 38.6 [11.1, 3.7, 10.9, 10.3, 2.6], IV 41.4 [12.0, 4.0, 11.4, 11.3, 2.7].

Spination. Palp 131, 001, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 001/101; Tibia I–IV 2124/2224; Metatarsus I–III 2024, IV 3036.

Palp. As in diagnosis with generally elongated and slender palp, cymbium slightly longer than tibia, dRTA elongated, vRTA not pointed (Figs 7a–b); ET retrolaterad and twisted at its distal end, ET covered partially by conductor (Fig. 7c).

Female (n=1, paratype):

Large sized; total length: 21.3, prosoma length 8.5, prosoma width 7.6, anterior width of prosoma 4.3, opisthosoma length 12.8, opisthosoma width 8.5. Eye diameters: AME 0.51, ALE 0.56, PME 0.54, PLE 0.63. Eye interdistances: AME-AME 0.15, AME-ALE 0.01, PME-PME 0.41, PME-

PLE 0.46, AME-PME 0.53, ALE-PLE 0.41, clypeus height at AME 0.42, clypeus height at ALE 0.55.

Chelicerae. Chelicerae with 2 anterior and 3 posterior teeth; cheliceral furrow with 10 intermarginal denticles.

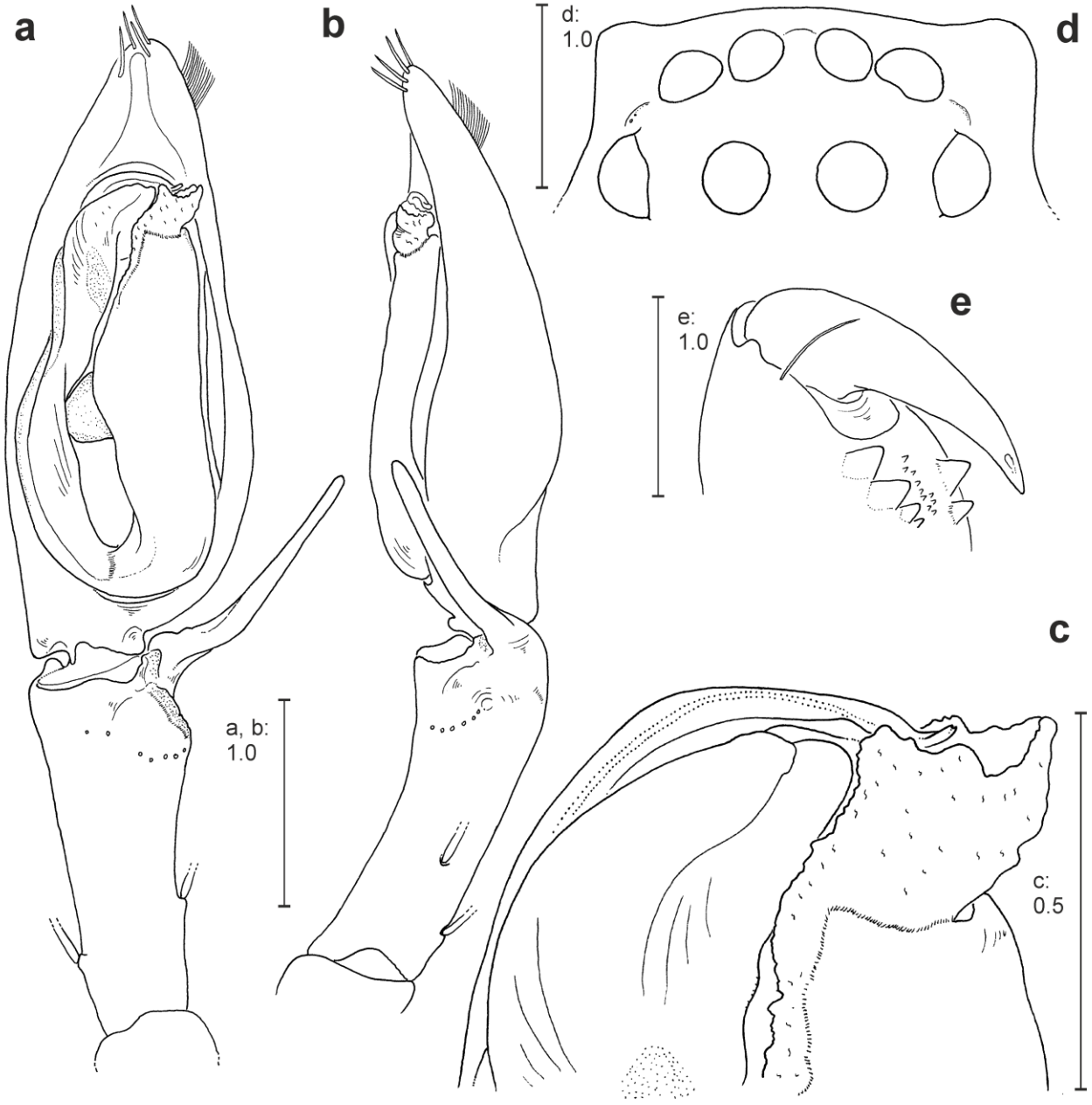

FIGURE 7. *Eusparassus arabicus* **spec. nov.**, holotype male from Saudi Arabia: Wadi Mizbil (NMB). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) right chelicera, ventral.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 11.6 [3.5, 1.7, 2.3, 4.1], I 36.4 [10.2, 4.3, 9.4, 9.8, 2.7], II 40.4 [11.3, 4.6, 11.5, 1.3, 2.7], III 34.8 [10.5, 4.0, 9.3, 8.6, 2.4], IV 38.3 [11.0, 4.0, 10.2, 10.5, 2.6].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 322; Patella I–II 000, III–IV 001; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3036.

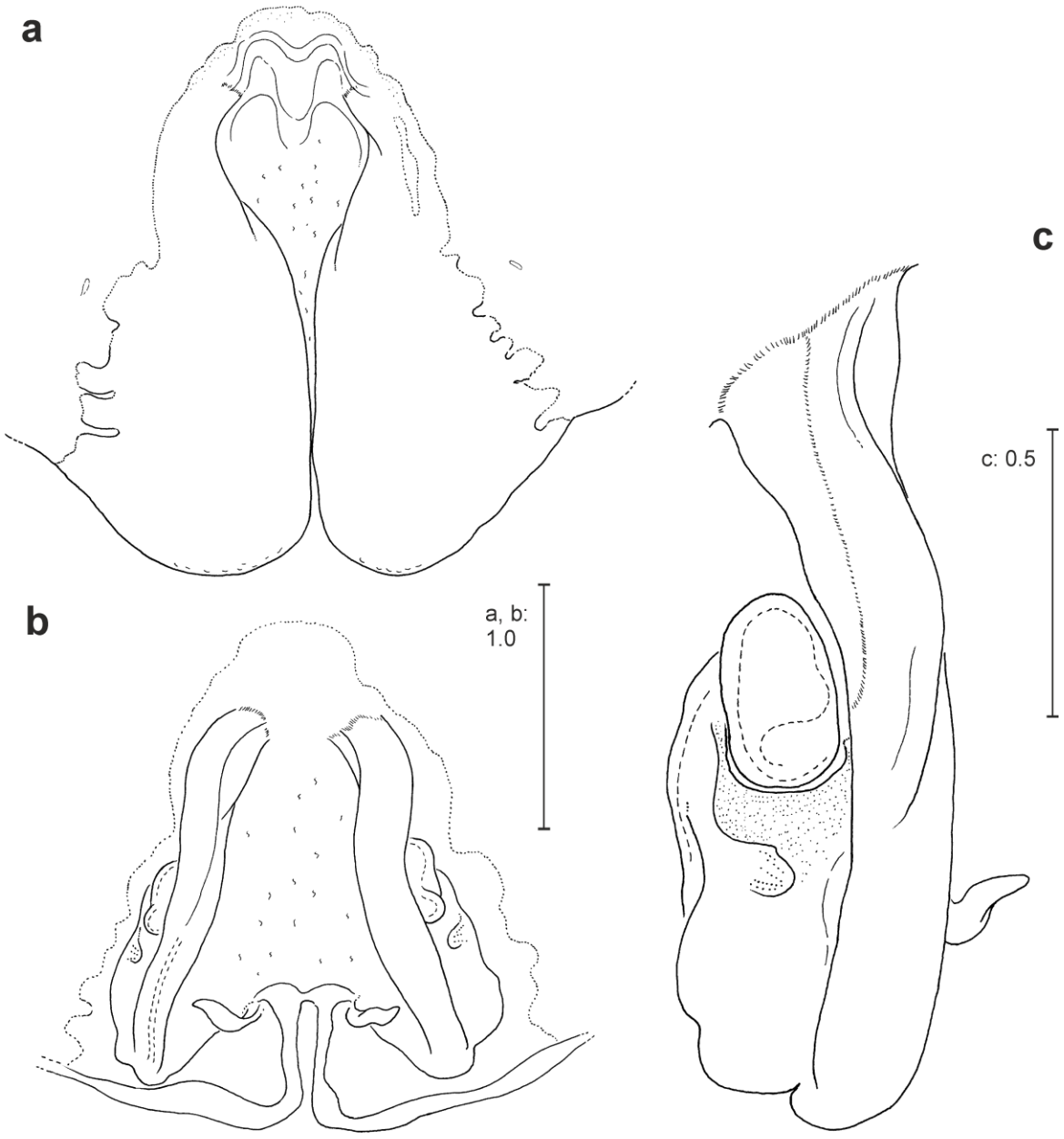

FIGURE 8. *Eusparassus arabicus* **spec. nov.**, paratype female from Saudi Arabia: Hail: Wadi Naqben (NMB). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral.

Epigyne/vulva. EF slightly longer than wide, EF fused anterioly with a bridge but AMLL not encircling MS entirely (Fig. 8a); CD membranous (Fig. 8b), TL spherical and robust (Fig. 8c).

Colouration [in ethanol]. Reddish to yellowish brown with darker W-shaped patches on prosoma, remains of cardiac mark on dorsal opisthosoma and legs with pale bands (Figs 47d, e).

Known geographical distribution and habitat. Endemic to Northern Arabian Peninsula collected from wadis and oases (Fig. 70a).

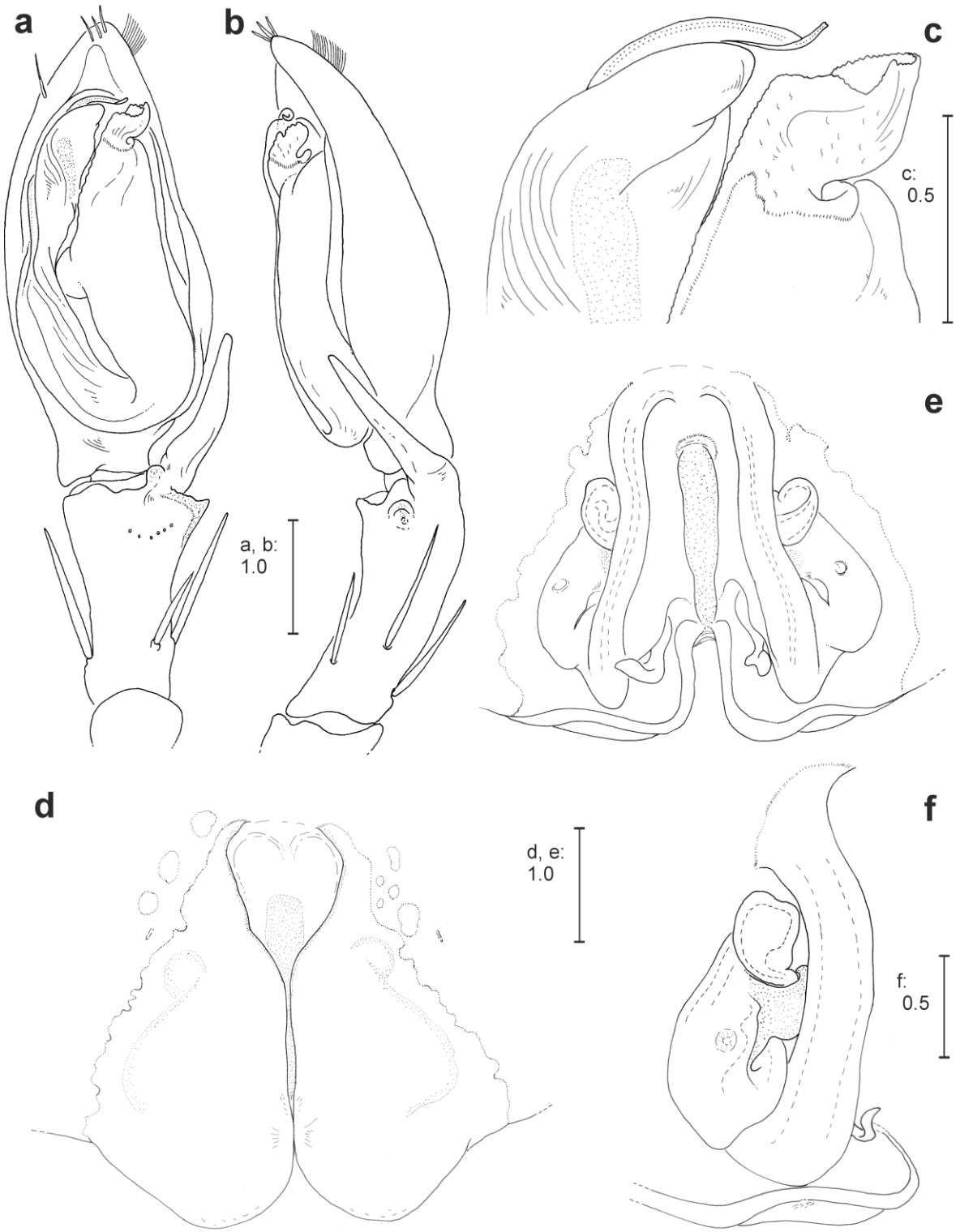

FIGURE 9. *Eusparassus* sp. (*walckenaeri* group) male and female from Djibouti (MNHN). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) epigyne, ventral; (e) vulva, dorsal; (f) left vulva, anterio-dorso-lateral.

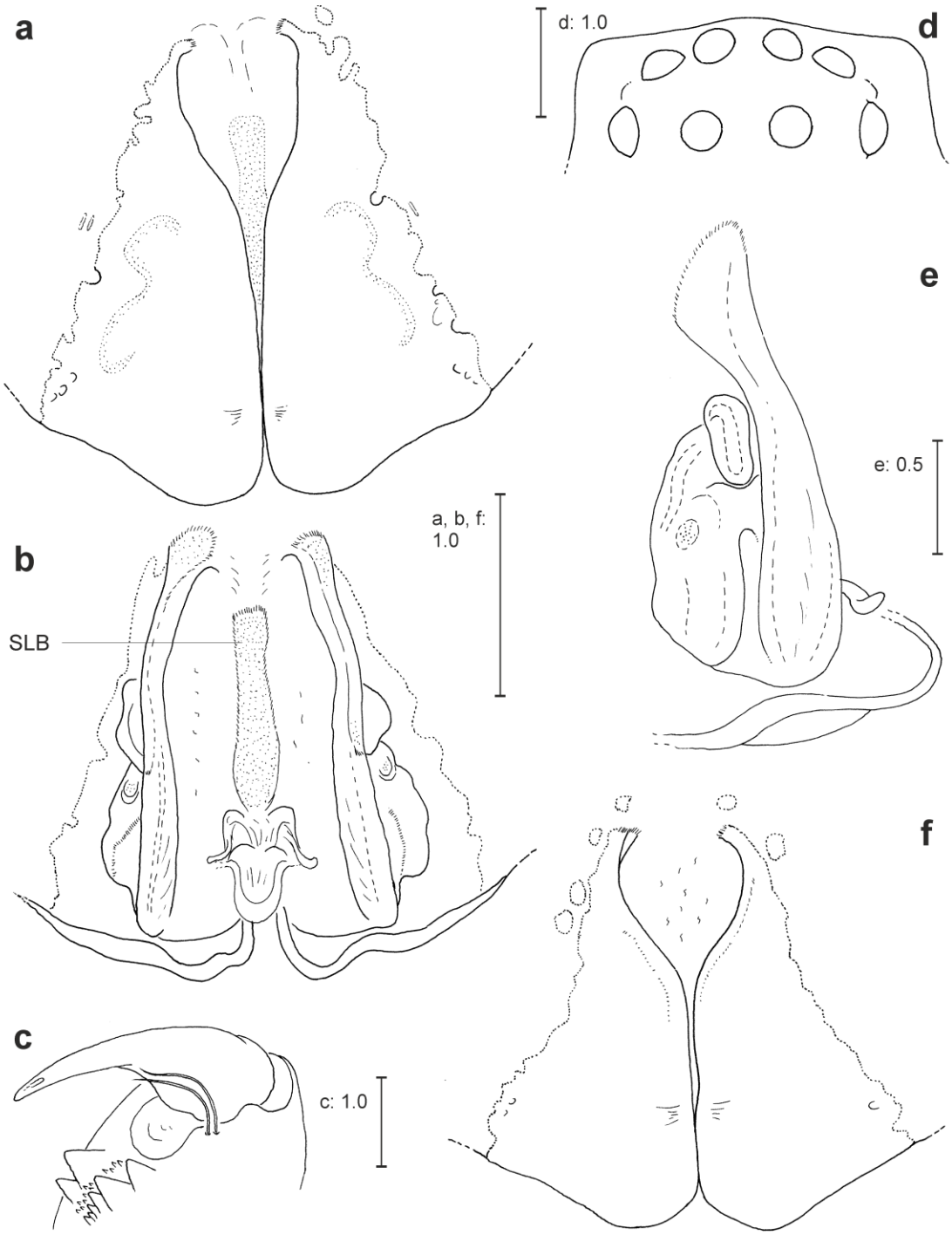

FIGURE 10. *Eusparassus* sp. (*walckenaeri* group): (a–d) female from Seychelles (MRAC); (e–f) female from Saudi Arabia (SMF, MM33). (a, f) epigyne, ventral; (b) vulva, dorsal; (c) left chelicera, ventral; (d) eye arrangement, dorsal (e) left vulva, anterio-dorso-lateral. SLB — sclerotized longitudinal band.

dufouri species group

Diagnosis. Opisthosoma ventrally with a distinct dark marking (Figs 48b, d; 49b, f); chelicerae without intermarginal denticles (Figs 13e, 15d, 23e); male palp with ST reduced in size and mostly not visible (Figs 12a, 15a, 17a, 20a, 22a); female epigyne with fused AMLL encircling MS entirely (Figs 11c, 13a, 16a, 18a, 21a, 23a, f)

Species composition. Eight species: *Eusparassus dufouri* Simon, 1932; *E. barbarus* (Lucas, 1846); *E. oraniensis* (Lucas, 1846); *E. fritschi* (Koch, 1873) **stat. rev.**; *E. letourneuxi* (Simon, 1874); *E. atlanticus* Simon, 1909 **stat. nov.**; *E. syrticus* Simon, 1909 and *E. levantinus* Urones, 2006.

Distribution. From Iberian Peninsula (Portugal and Spain) to North-western Africa (Morocco, Algeria, Tunisia and Libya) (Fig. 70b).

Remarks. Identification of females in the *dufouri* group is difficult; therefore a combination of characters must be used to identify the species, including eye pattern and structures of vulvas. Males are easily distinguishable by the shape of RTA and ET. *Eusparassus fritschi* **stat. rev.** is removed from synonymy with *E. oraniensis*. *Eusparassus atlanticus* **stat. nov.** which was subspecies of *E. dufouri* is elevated to species level, for comparison the nominate species (*E. dufouri*) is illustrated (Figs 11a–e) [for more details see Moradmand and Jäger 2012a: figs 2–3, 23C].

Eusparassus atlanticus Simon, 1909 stat. nov.

Figs 12–14, 49a–b, 60e–f

Eusparassus argelasius atlanticus Simon, 1909: 30 (description of female) [syntypes, MNHN, examined], [in Platnick (2013) as *E. dufouri atlanticus*]. **Elevated to species level.**

Sparassus syrticus (Simon). Levy 1989: 137, figs. 22–23 (misidentification, illustration of ♀). [1♀, MNHN, examined].

Type material. Syntypes (designated by Simon 1909)**:** 7♀♀ and 1 immature ♀, **MOROCCO: *Region de Doukkala-Abda*:** Djebel Demnata (=Demnate), Jar N. 1669, Simon N. 5732 (MNHN).

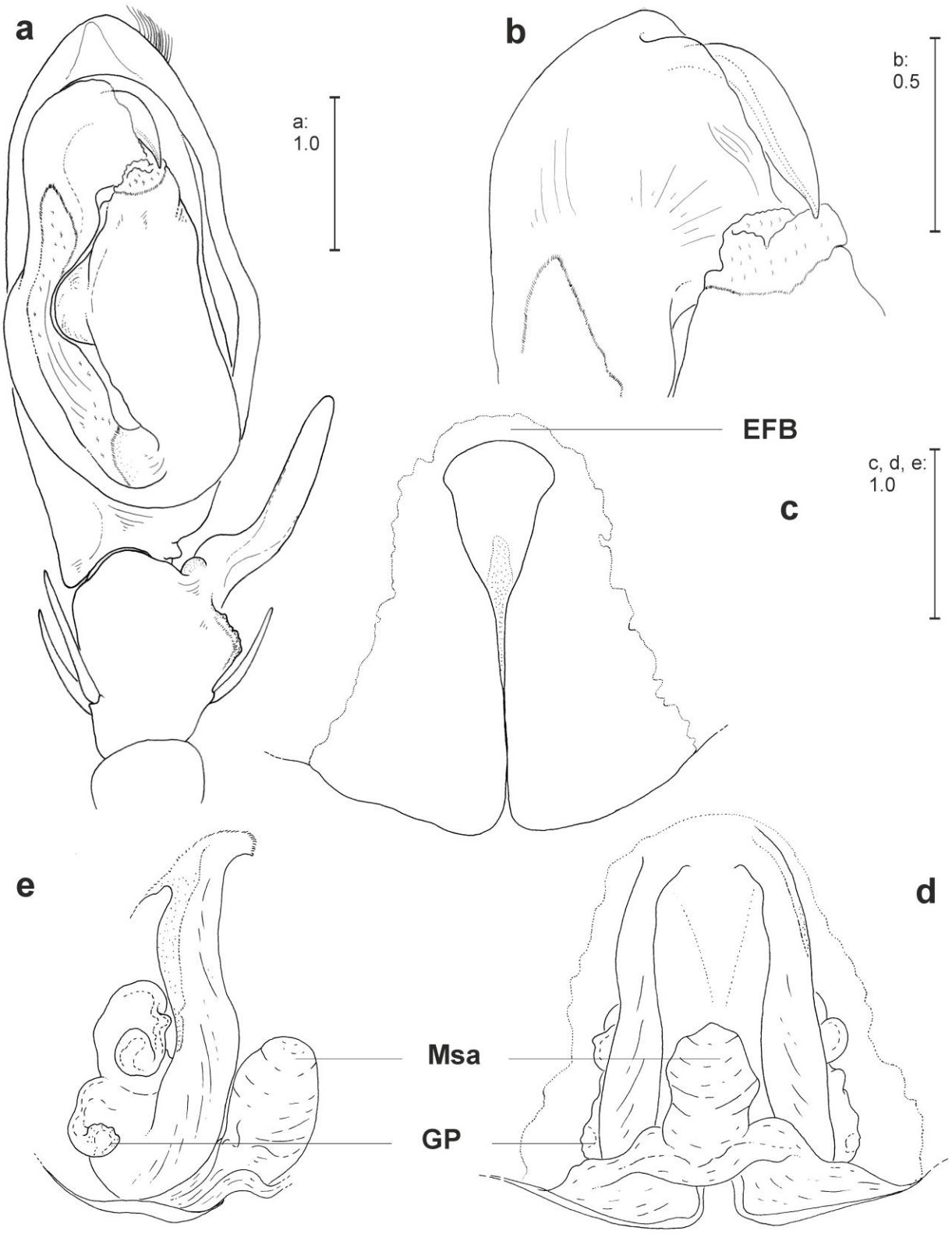

FIGURE 11. *Eusparassus dufouri* Simon, 1932, male and female from Portugal (SMF). (a) left palp, ventral; (b) embolus tip and conductor, ventral; (c) epigyne, ventral; (d) vulva, dorsal; (e) left vulva, anterio-dorso-lateral. Abbreviations: EFB — epigynal field bridge, GP — glandular process, Msa — membranous sac, expanded.

Other material examined. MOROCCO: *Region de Marrakech-Tensift-Al Haouz*: 1♂, 1♀, Marrakesh, Sidi Mimoun, G. Buchat leg. 1903 (MNHN); ***Region de Souss-Massa-Draa*:** 1♀ (MM21), ca. 20 km S of Tizi-n-Test, under stone in retreat, 23 July 2000, S. Huber leg. (SMF).

Diagnosis. Male differentiated by simple pointed and retrolaterad ET (Fig. 12c) and slightly curved dRTA (Fig. 12a); compared to other congeners in *dufouri* group, LL and MS more elongated (Figs 13a, 14a, b) [see also diagnosis for *dufouri* species group above].

Description. Male (n=1, MM 191):

Measurements. Medium sized; total length 13.3, prosoma length 6.5, prosoma width 5.8, anterior width of prosoma 2.7, opisthosoma length 6.8, opisthosoma width 4.7. Eye diameters: AME 0.37, ALE 0.28, PME 0.26, PLE 0.31; eye interdistances: AME-AME 0.25, AME-ALE 0.15, PME-PME 0.40, PME-PLE 0.47, AME-PME 0.35, ALE-PLE 0.30, clypeus height at AME 0.20, clypeus height at ALE 0.28.

Chelicerae. Chelicerae with 2 anterior and 4 posterior teeth; cheliceral furrow lacking intermarginal denticles.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 8.7 [2.8, 1.2, 1.4, 3.3], I 30.0 [8.2. 3.1, 7.3, 8.6, 2.8], II 32.9 [9.2, 3.1, 8.3, 9.5, 2.8], III 27.1 [7.9, 2.7, 6.5, 7.4, 2.6], IV 30.7 [8.8, 2.6, 7.5, 9.1, 2.7].

Spination. Palp 131, 101, 1111; Legs: Femur I 324, II 424, III 324, IV 322; Patella I–IV 101; Tibia I–IV 2224; Metatarsus I 1014, II–III 2024, IV 3036.

Palp. As in diagnosis with cymbium twice as long as tibia; vRTA not well developed (Figs 12 a, b); EM not covering ET in ventral view (Fig. 12c).

Female (ranges: n=9, single measurement: syntype):

Measurements. Medium sized; total length 16.6–18.8, prosoma length 7.2–8.6, prosoma width 6.5–7.8, anterior width of prosoma 4.1–4.5, opisthosoma length 9.4–10.2, opisthosoma width 5.7–6.2. Eye diameters: AME 0.53, ALE 0.42, PME 0.40, PLE 0.44; eye interdistances: AME-AME 0.30, AME-ALE 0.15, PME-PME 0.51, PME-PLE 0.65, AME-PME 0.42, ALE-PLE 0.35, clypeus height at AME 0.47, clypeus height at ALE 0.62. Eyes subequal; AME slightly larger than others (Fig. 13d).

Chelicerae. Chelicerae with 2 anterior and 3 to 5 posterior teeth, intermarginal denticles absent (Fig. 13e).

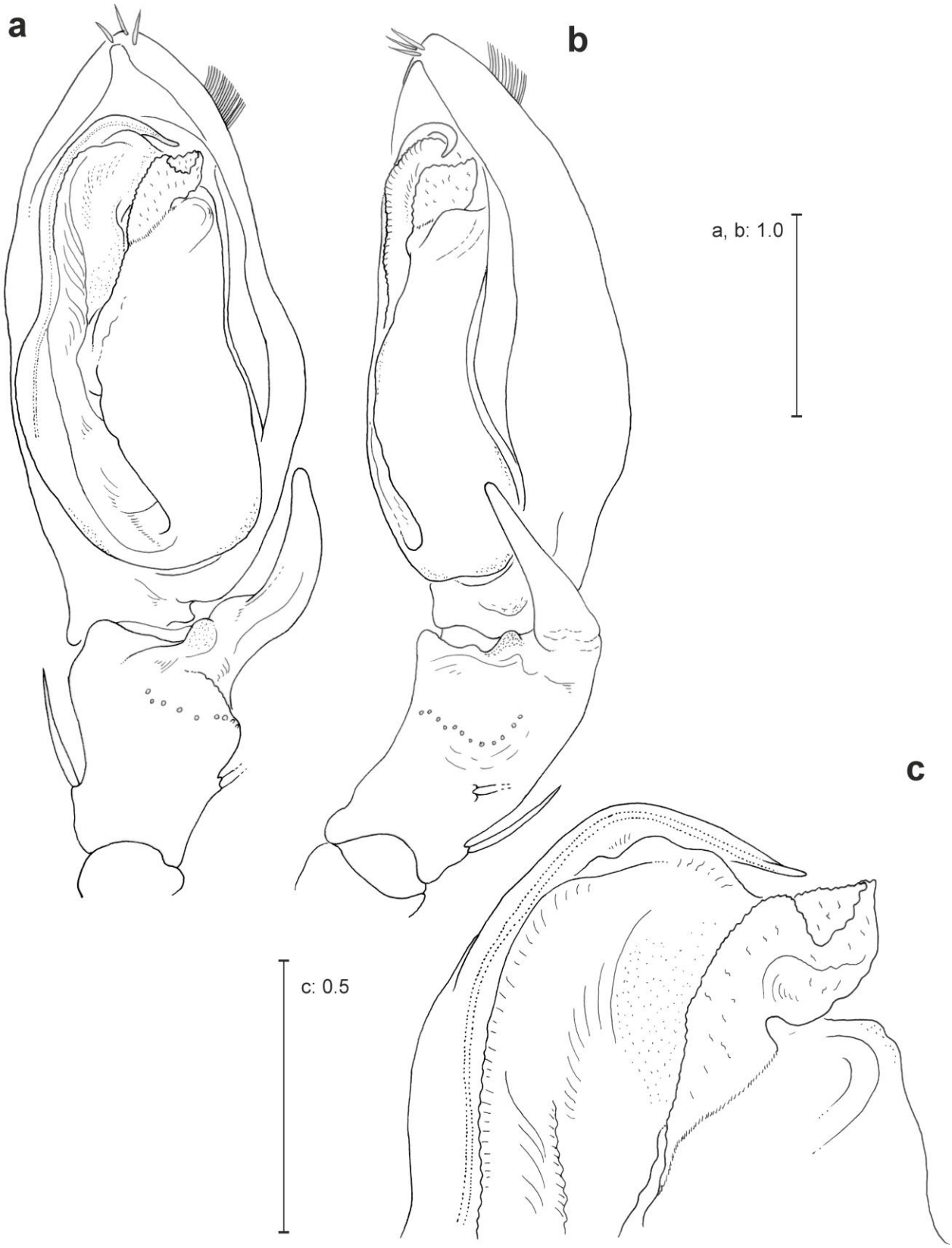

FIGURE 12. *Eusparassus atlanticus* Simon, 1909 **stat. nov.**, male from Morocco: Sidi Mimoun (MNHN). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral.

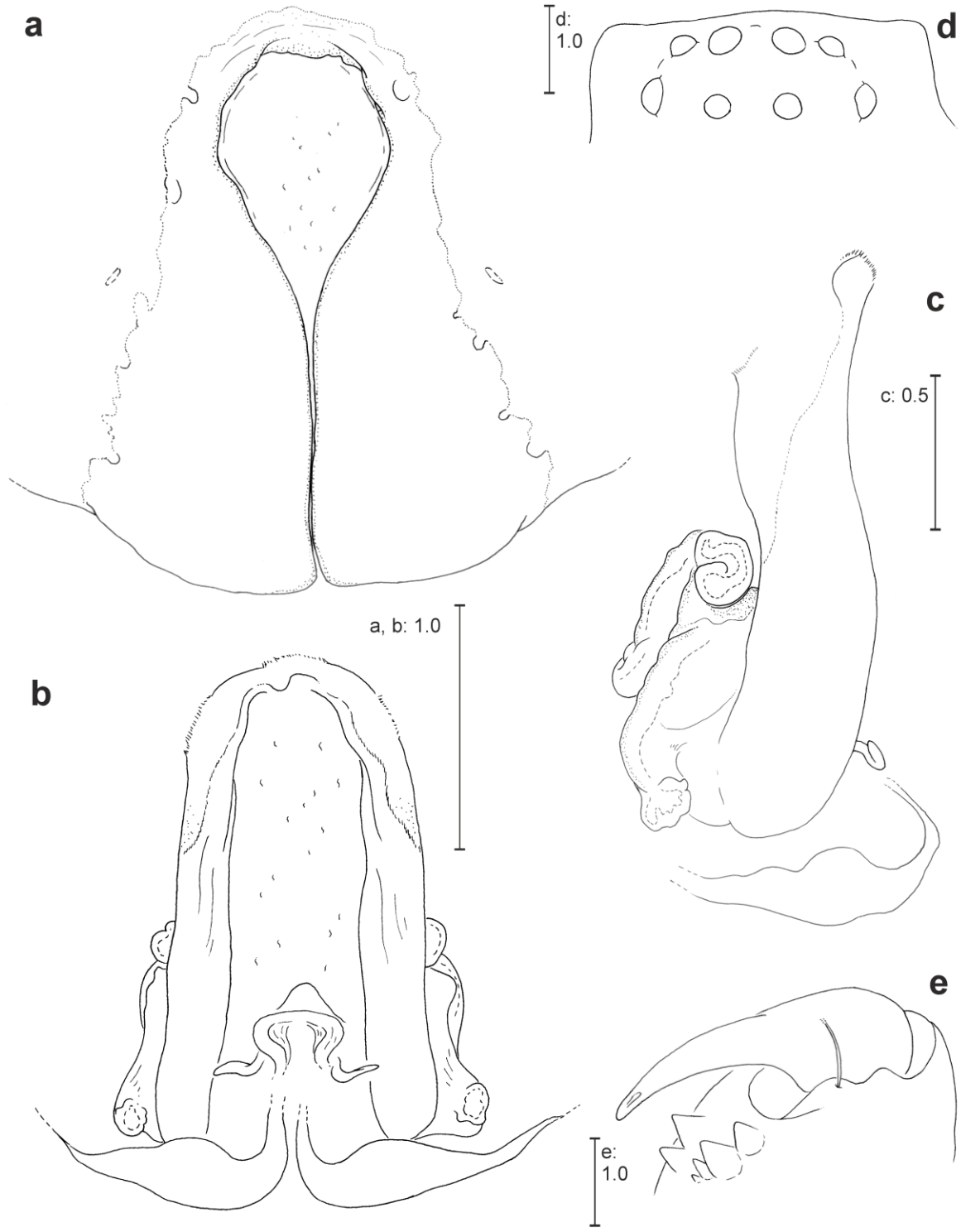

FIGURE 13. *Eusparassus atlanticus* Simon, 1909 **stat. nov.**, syntype female from Morocco: Djebel Damnata (MNHN). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) eye arrangement, dorsal; (e) left chelicera, ventral.

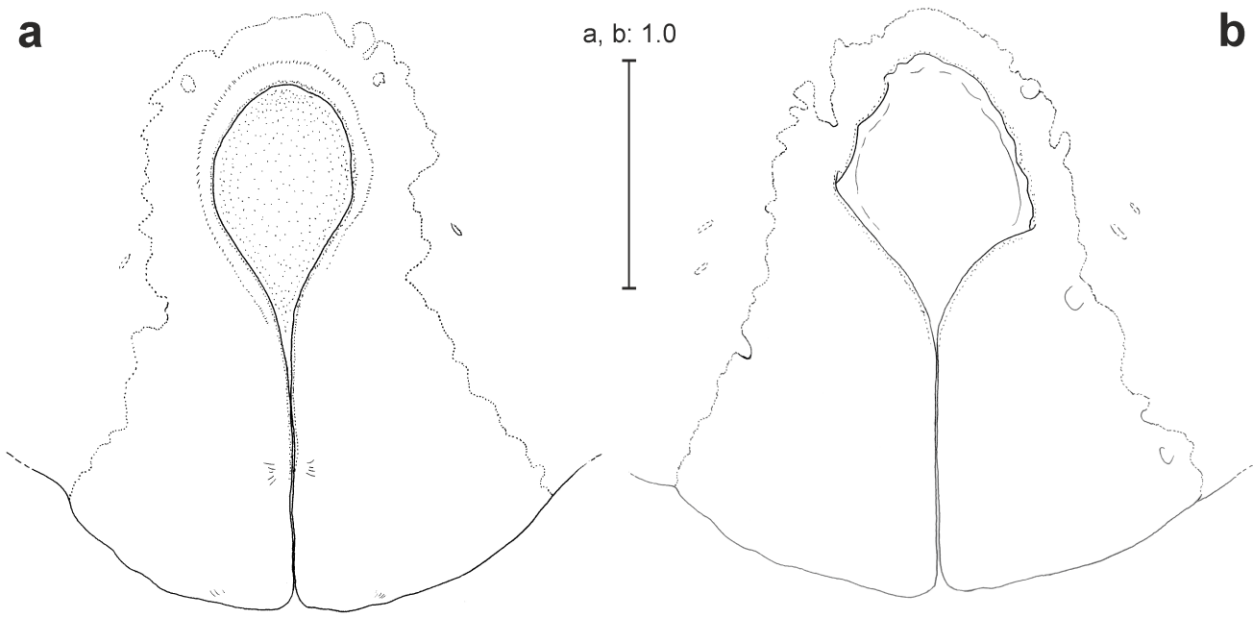

FIGURE 14. *Eusparassus atlanticus* Simon, 1909 **stat. nov.**, variation in syntype females from Morocco: Djebel Damnata (MNHN). (a, b) epigyne, ventral.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 10.5 [3.1, 1.6, 2.0, 3.8], I 30.6 [8.6, 3.9, 7.3, 8.4, 2.4], II 33.1 [9.7, 4.1, 8.2, 8.6, 2.5], III 29.2 [8.8, 3.7, 7.0, 7.3, 2.4], IV 32.4 [9.7, 3.6, 7.8, 8.8, 2.5].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 424, IV 321/423; Patella I–IV 000/101; Tibia I–IV 0004/2024; Metatarsus I 0004/1014, II 1014/2024, III 2024, IV 3034/3036.

Epigyne/vulva. As in diagnosis with EF generally elongated; MS longer than wide, hyaline (Figs 13a, 14b) to fully sclerotized (Fig. 14a); vulva with glandular process (Fig. 13c).

Colouration [in ethanol]. Reddish brown, prosoma with transverse dark lines leading to fovea, dorsal opisthosoma with series of large chevrons at proximal end turning smaller gradually at distal end, legs clearly banded (Figs 49a–b); ventral opisthosoma with a uniform compact dark marking below epigastric furrow (Fig. 49b).

Remarks. *E. atlanticus* **stat. nov.** is elevated from subspecies to species level here. In the original description, Simon (1909) emphasized on the dark marking of the ventral opisthosoma and placed this species under *E. dufouri* (sub *E. argelasius atlanticus*). After *E. dufouri* was defined by Moradmand and Jäger (2012a), the description of the male and female of *E. atlanticus* **stat. nov.** revealed that this species must be considered as its own valid species and not a subspecies. The male is described here for the first time.

Known geographical distribution and habitat. Western Morocco in Atlas Mountains, under stones, and gravel in dry river beds.

Eusparassus barbarus (Lucas, 1846)

Figs 15–16, 51a–b, 61a–b

Olios barbarus Lucas, 1846: 202, pl. 11, fig. 10 (description of male and female, from Algeria: Algiers, Constantine, Lacalle, type material not located in MNHN, presumably lost). Neotype designated here (for justification see remarks).

Sparassus barbarus (Lucas). Simon 1874: 262 (transfer).

Eusparassus barbarus (Lucas). Reimoser 1919: 177 (listing and transfer).

Type material: Neotype: male, **ALGERIA**: ***Wilaya de Ain Defla***: Teniet el Haad [N 35° 52' 16'', E 2° 1' 41'']*,* 1800 m, Cedar Forest, 19 February 1988, R. Jocqué & R. Bosmans leg. (MRAC 168777).

Other material examined. ALGERIA: 1♀, with same data as for neotype (MRAC); ***Wilaya de Batna*****:** 1♂, Jebel Metlili, N 35° 15', E 5° 38', Pine forest, 1000m altitude, 13 April 1987, R. Jocqué leg. (MRAC 167560); ***Wilaya de Biskra*****:** 1♀, Biskra, King leg. (ZSM A20110054); ***Wilaya de Tizi Ouzou*****:** 1♂, Djurdjura Mountain, Tala Guilet, 1600m, April 1983, H. Franz leg. (SMF); ***Wilaya de Adrar*****:** 1♀, Great Atlas Mountains, Tadlest [N 29° 18', E 0° 16'], 2250 m, 20 June 1930 (SMF 4604); 2♂♂, 6♀♀, 42 juveniles, 1866–67, W.T. Taczanovski leg. [label: *Olios barbarus* Luc., Algeria 1866-67, leg & det. WT. Taczanovski] (MIZ F15); **TUNISIA:** 1♂, 1959, Kahmann leg. (SMF).

Diagnosis. Male differs from other congeners by ET flattened dorso-ventrally and ET pointing first proximad and then ventrad (Fig. 15c); It resembles that of *E. letourneuxi* but differs in dRTA bending toward cymbium (Figs 15a, b); epigyne similar to that of *E. letourneuxi* but differs from it by the triangular-shape of the MS (Fig. 16a) (semicircular in *E. letourneuxi*) [see also diagnosis for *dufouri* species group above].

Description. Male (ranges: n=6, single measurement: neotype):

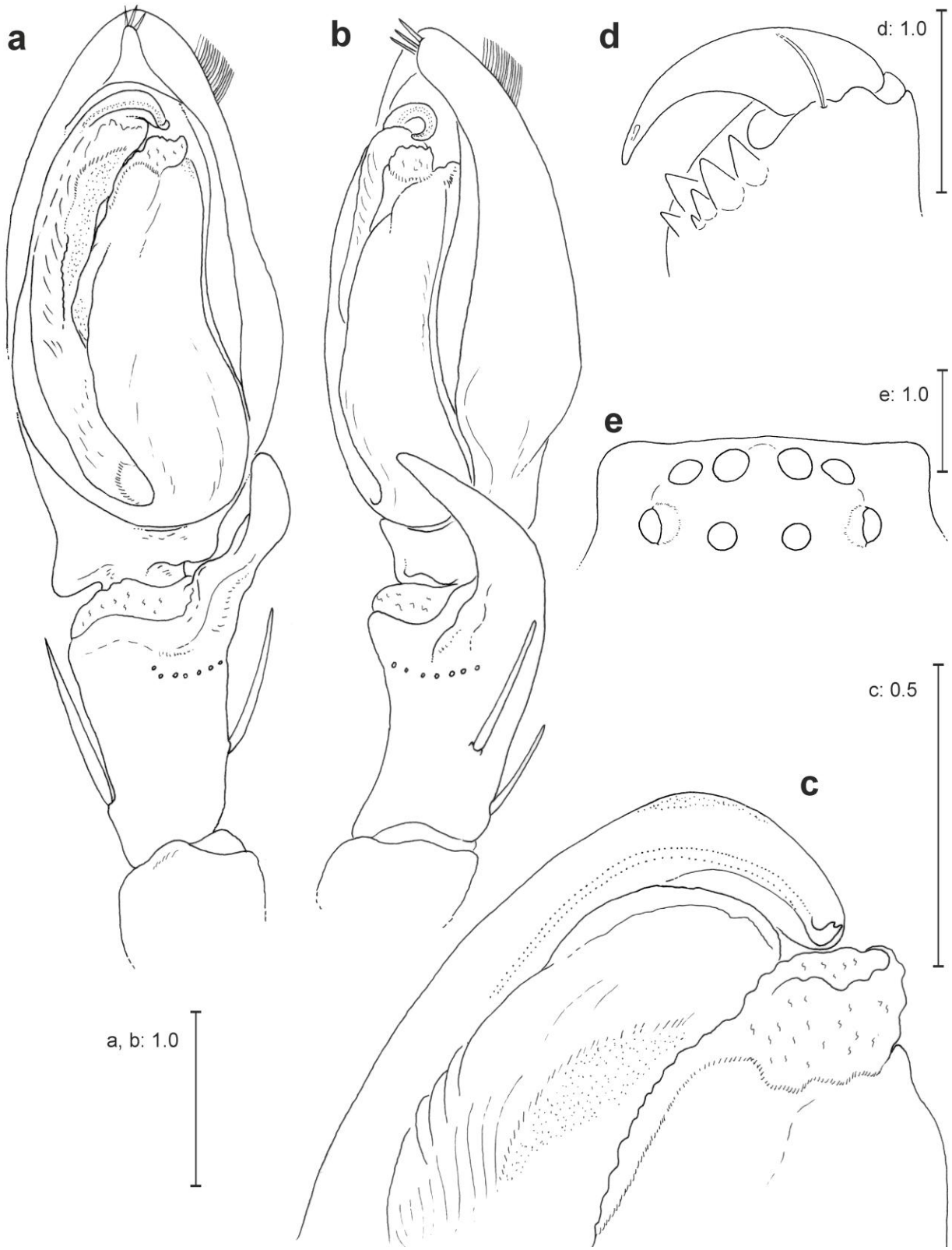

FIGURE 15. *Eusparassus barbarus* (Lucas, 1846), neotype male from Algeria: Teniet el Haad (MRAC). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) left chelicera, ventral; (e) eye arrangement, dorsal.

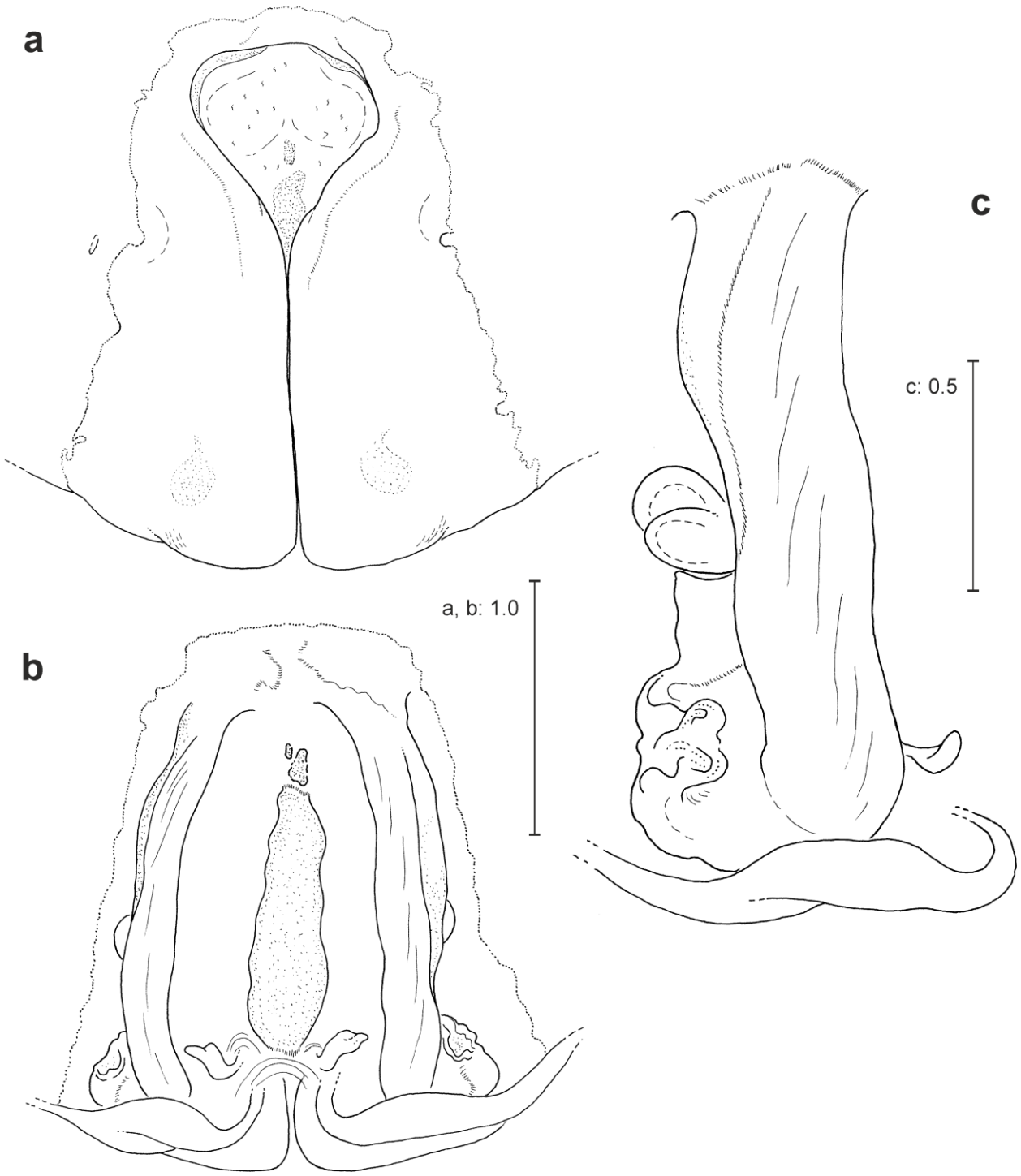

FIGURE 16. *Eusparassus barbarus* (Lucas, 1846), female from the type locality, Algeria (MIZ). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral.

Measurements. Medium sized; total length: 16.5–17.6, prosoma length 7.0–7.6, prosoma width 6.4–6.8, anterior width of prosoma 3.3–3.4, opisthosoma length 9.5–10, opisthosoma width 5.6–6.0; Eye diameters: AME 0.43, ALE 0.38, PME 0.32, PLE 0.41; eye interdistances: AME-AME

0.27, AME-ALE 0.17, PME-PME 0.43, PME-PLE 0.51, AME-PME 0.37, ALE-PLE 0.30, clypeus height at AME 0.35, clypeus height at ALE 0.40. AME largest (Fig. 15e).

Chelicerae. Chelicerae with 2 anterior and 4 posterior teeth; cheliceral furrow without intermarginal denticles (Fig. 15d).

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 9.4 [3.0, 1.4, 1.5, 3.5], I 30.5 [8.5, 3.6, 7.5, 8.4, 2.5], II 33.2 [9.4, 3.4, 8.5, 9.1, 2.8], III 28.3 [8.5, 3.1, 7.0, 7.2, 2.5], IV 31.2 [9.1, 3.2, 7.5, 8.8, 2.6].

Spination. Palp 131, 101, 1111; Legs: Femur I 324(5)/424, II–III 324(3)/424, IV 423/(3)424; Patella I–IV 101; Tibia I–IV 21(0)24/2224; Metatarsus I–III 1014/2024, IV 3034/3036.

Palp. As in diagnosis, with cymbium approximately twice as long as tibia; dRTA widened dorso-ventrally, vRTA small in size and shifted toward cymbium in ventral view (Figs15 a–c).

Female (ranges: n=9, single measurement: MM 205):

Measurements. Medium to large sized; total length: 17.5–22.5, prosoma length 7.0–10.2, prosoma width 6.1–8.6, anterior width of prosoma 3.8–5.1, opisthosoma length 10.5–12.5, opisthosoma width 7.5–8.0. Eye diameters: AME 0.54, ALE 0.41, PME 0.42, PLE 0.46; eye interdistances: AME-AME 0.36, AME-ALE 0.14, PME-PME 0.65, PME-PLE 0.75, AME-PME 0.45, ALE-PLE 0.28, clypeus height at AME 0.50, clypeus height at ALE 0.60.

Chelicerae. Chelicerae as in males.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 10.7 [3.2, 1.7, 2.0, 3.8], I 31.7 [9.1, 4.3, 7.5, 8.5, 2.8], II 35.0 [10.2, 4.5, 8.5, 9.0, 2.8], III 30.7 [9.4, 4.2, 7.2, 7.3, 2.6], IV 33.7 [10.2, 3.8, 8.1, 8.8, 2.8].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–II 324/424, III 424, IV 322/423; Patella I–IV 000/101; Tibia I–IV 0004/2024; Metatarsus I–III 0004/ 2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF longer than wide (Fig. 16a); MS hyaline with a longitudinal sclerotized strip dorsally (Fig. 16b); GP present (Fig. 16c).

Colouration [in ethanol]. Reddish cream, prosoma with a dark Y-shaped patch and additional transverse lines, opisthosoma with a brown band along the entire length and additional small patches (Figs 51a–b); opisthosoma ventrally with V-shaped marking with bold inner lines (Fig. 51b).

Remarks. Lucas (1846) described two species (sub *Olios*) currently assigned to the genus *Eusparassus*: *E. barbarus* and *E. oraniensis*. The type material is not available at MNHN and

presumed to be lost, as confirmed by other researchers (i.e. Azarkina & Logunov 2006) and verified by author's direct investigation in MNHN. Fortunately, Lucas (1846) illustrated the habitus and eye arrangement, and provided a description of the colouration of the ventral opisthosoma. The illustration of prosoma in *O. barbarus* is unique. This colouration is recognized in this study among some *Eusparassus* specimens found nearby the type locality. Since *E. barbarus* can easily be mistaken with the similar parapatric species *E. letourneuxi*, one male is designated here as neotype to avoid taxonomic problems and misidentification in the future. The eye arrangement and colouration of the neotype correspond to the original drawings and description.

Known geographical distribution and habitat. From Northern Algeria to Tunisia, up to 1800 meters altitude in mountainous pine and cedar forests, found under stones.

Eusparassus oraniensis (Lucas, 1846)

Figs 17–19, 50, 62a, b

Olios oraniensis Lucas, 1846: 201, Pl. 11, fig. 9 (description of female, from Algeria: Oran: Djebel Santon, Santa Cruz [N 35°42′25.3″, W 0°39′55.34″], type material not located in MNHN, presumably lost). Neotype designated here (for justification see remarks).

Sparassus currax Blackwall, 1858: 429 (description of male, holotype from Algeria, not located in HECO, presumably lost).

Sparassus oraniensis (Lucas). Simon 1874: 255 (description of male, material not located in MNHN, presumably lost); Simon 1880: 291; Levy 1989: 137, fig. 21.

Eusparassus argelasius maximus Strand, 1906a: 630 (description of male and female) [syntypes from Algeria (South-west): Naâma Province*:* Tiout oase, lost in Stuttgart collection]. **New synonymy.**

Eusparassus oraniensis (Lucas). Strand 1908b: 23.

Eusparassus argelasius oraniensis (Lucas). Simon 1909: 31.

Eusparassus dufouri oraniensis (Lucas). Denis 1947:49, pl. 2, fig.12 (illustration of female from Egypt: Siwa, material not located in NHM, probably misidentified).

Type material: Neotype: female, **ALGERIA:** ***Wilaya de Oran***, 1906, Scherer leg. (ZSM A20110055).

Other material examined. ALGERIA: 1♀, with same data as for neotype (ZSM A20110056); ***Wilaya de Bechar***: 1♀, Beni Ounif, March 1955, Fittkau leg. (ZSM A20110053); ***Wilaya de Biskra***: 1♀, 1 juv., Biskra, September 1912 B.H. Boxtux leg. (NHM 1948.11.29.4-5); 2♀♀, Biskra, 1903 (NHM 10.10.29.26.27); **MOROCCO:** ***Region de Guelmim-Es Semara***: 1♂, N 28 56′11.54″, W 8 57′10.08″, point 37, September 2011, S. Henriques leg. (SMF, SD843); ***Region de Souss-Massa-Draa*****:** 1♂, 1♀, Anti-Atlas, between Tizuit and Tafraut, 2 km E of Kerdouss, 1100m, under stone, 22 July 2000, S. Huber leg. (SMF); 1♀, Anti-Atlas, ca. 15km S of Igherm, under stone, 28 August 2001, S. Huber leg. (SMF); 1♂, Zagora, December 2008, G. Ackermann leg. (SMF, SD444); 1♂, E of Bou Rbia, N 30°07′60.2″, W 6°23′0.27″, 16 September 1999, H. Nickel leg. (SMF); ***Region de Meknes-Tafilalet*****:** 1♂, Erg Chebbi, N 31°16′12.69″, W 3°59′28.50″, 760m, under stone, 13 July 2009, J. Achenberg leg. (SMF, SD615, MM9); 1♂, Meski, around water source, 29 July 1971, R. Jocqué leg. (MRAC 154281).

Diagnosis. PLE largest (unique character within the group, Fig. 18d), ET retrolaterad first, slightly proximad, finally distad (Fig. 17c); vulva robust and widened as in *E. syrticus* but differring from it in having smaller and spherical GP (Figs 18b, c) [see also diagnosis for *dufouri* species group above].

Description. Male (ranges: n=5, single measurement: MM 9):

Measurements. Medium to large sized *Eusparassus* species [largest male (MM9) with 13.3 cm legspan]. Total length 14.2–24.8, prosoma length 7.8–11.5, prosoma width 6.8–11.3, anterior width of prosoma 3.5–5.6, opisthosoma length 6.4–13.3, opisthosoma width 4.0–9.1. Eye diameters: AME 0.62, ALE 0.64, PME 0.61, PLE 0.75; eye interdistances: AME-AME 0.28, AME-ALE 0.09, PME-PME 0.64, PME-PLE 0.70, AME-PME 0.80, ALE-PLE 0.57, clypeus height at AME 0.53, clypeus height at ALE 0.66. PLE larger than others.

Chelicerae. Chelicerae with 2 anterior and 3 to 5 posterior teeth; cheliceral furrow lacking intermarginal denticles.

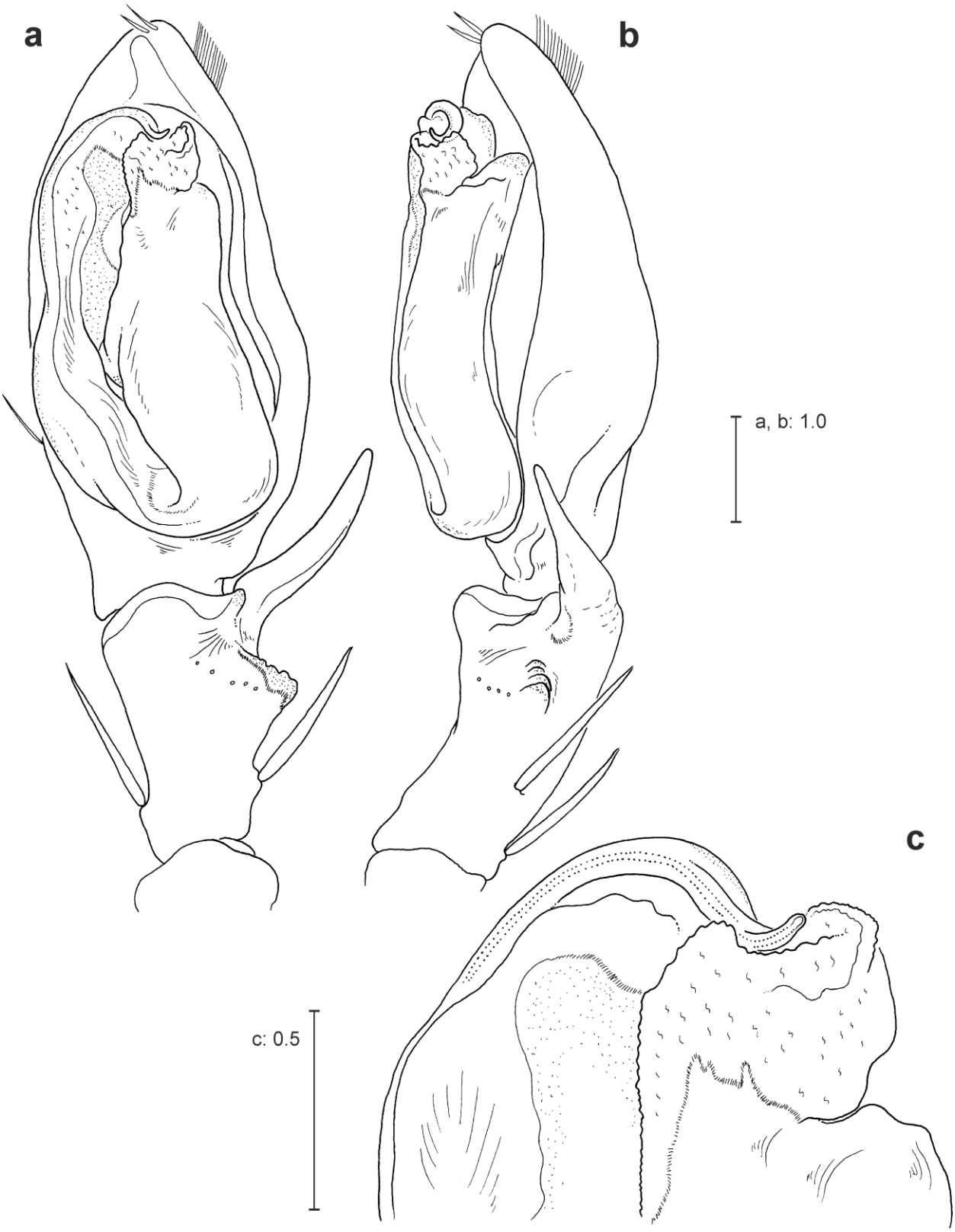

FIGURE 17. *Eusparassus oraniensis* (Lucas, 1846), male from Morocco: Erg Chebbi (SMF). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral.

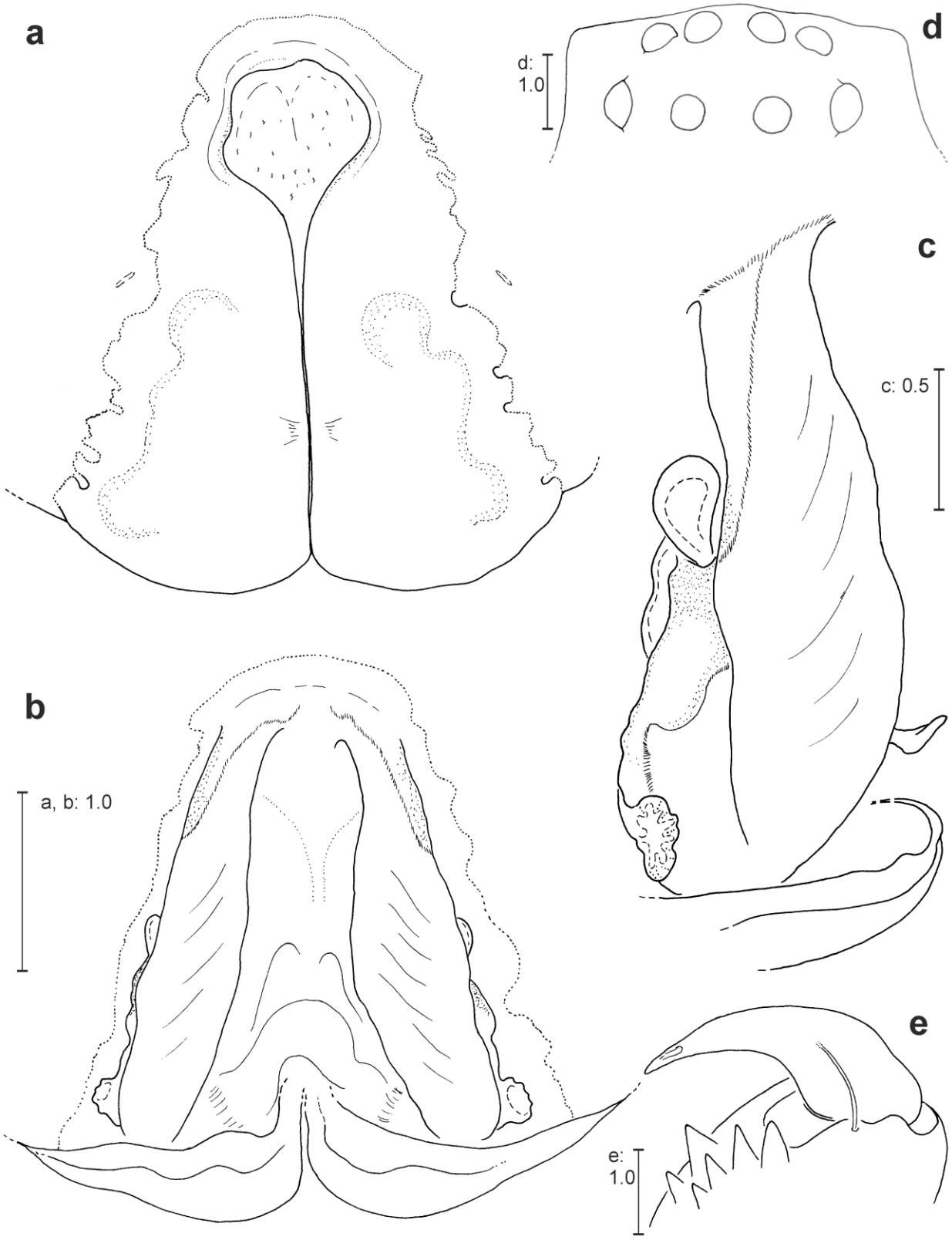

FIGURE 18. *Eusparassus oraniensis* (Lucas, 1846), neotype female from Algeria: Oran (ZSM). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) eye arrangement, dorsal; (e) left chelicera, ventral.

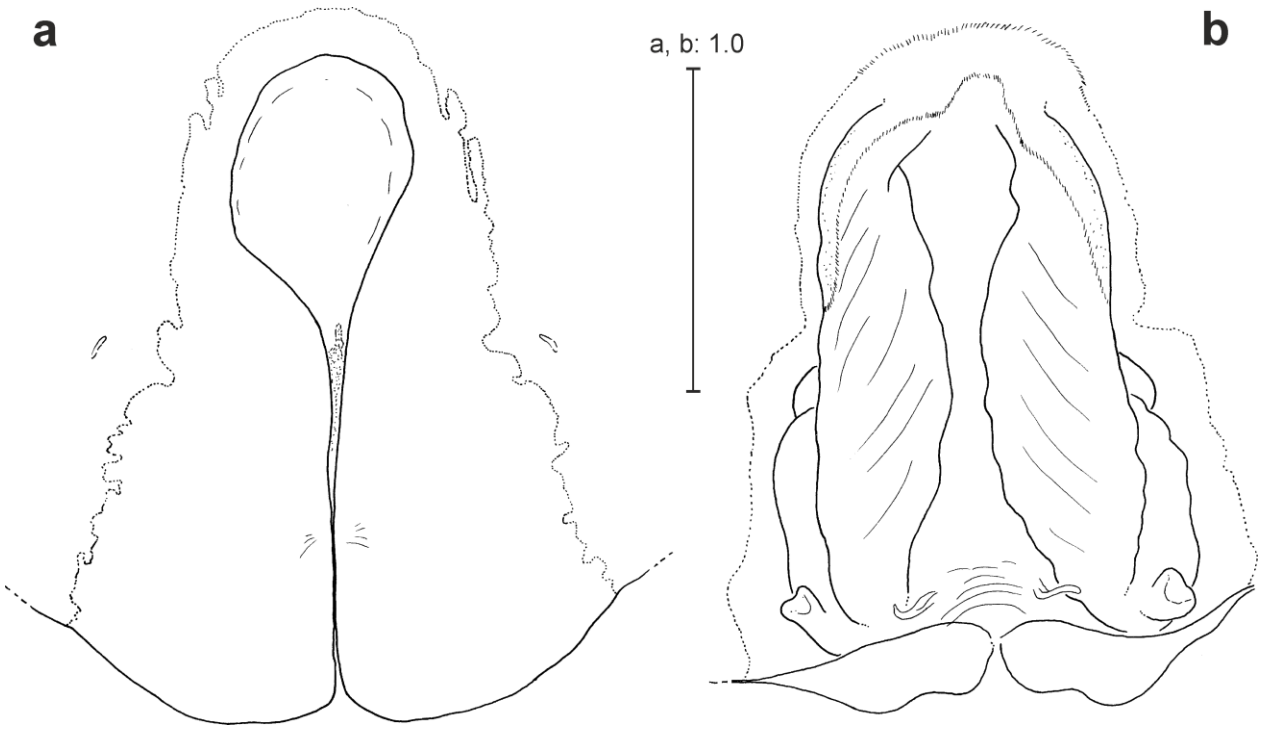

FIGURE 19. *Eusparassus oraniensis* (Lucas, 1846), variation in female from Morocco (SMF). (a) epigyne, ventral; (b) vulva, dorsal.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 15.5 [5.2, 2.6, 2.3, 5.4], I 55.5 [15.5, 5.6, 15.0, 15.7, 3.7], II 57.9 [16.1, 5.8, 15.5, 16.7, 3.8], III 51.1 [15.5, 5.4, 13.3, 13.8, 3.1], IV 56.7 [16.7, 5.1, 14.5, 16.6, 3.8].

Spination. Palp 131, 001, 1111; Legs: Femur I–III 424, IV 333/433; Patella I–IV 101; Tibia I–IV 2(1)224; Metatarsus I–III 1014/ 2024, IV 3034/3036.

Palp. As in diagnosis with robust cymbium longer than tibia; vRTA pointed and triangular in ventral view (Figs 17a, b); ET hardened and sclerotized (Fig.17c).

Female (ranges: n=8, single measurement: neotype):

Measurements. Medium to large sized *Eusparassus* species. Total length (neotype) 29.5, prosoma length 6.7–11.5, prosoma width 5.8–9.7, anterior width of prosoma 3.5–5.4, opisthosoma length 8.5–18.0, opisthosoma width 5.5–15.0. Eye diameters: AME 0.64, ALE 0.63, PME 0.61, PLE 0.68; eye interdistances: AME-AME 0.33, AME-ALE 0.08, PME-PME 0.67, PME-PLE 0.60, AME-PME 0.85, ALE-PLE 0.53, clypeus height at AME 0.43, clypeus height at ALE 0.52. PLE largest (Fig. 18d).

Chelicerae. Chelicerae dentition as in males (Fig. 18e).

Legs. Leg formula: II IV I=III. Measurements of palp and legs: Palp 15.8 [4.2, 2.2, 2.4, 5.0], I 42.7 [12.4, 5.2, 10.7, 11.3, 3.1], II 48.6 [13.8, 5.7, 12.7, 13.2, 3.2], III 42.9 [12.9, 5.1, 10.6, 11.3, 3.0], IV 47.8 [14.0, 5.0, 12.1, 13.5, 3.2].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 424, IV 422/423; Patella I–IV 000/101; Tibia I–IV 2024/2224; Metatarsus I–III 2124/2224, IV 3036.

Epigyne/vulva. As in diagnosis with EF longer than wide (Figs 18a, 19a); MS as long as wide (Fig. 18a) or longer than wide (Fig. 19a); FD partially (Fig. 19b) to fully sclerotized (SMF, MM 192 from Algeria: Beni Ounif).

Colouration. Creamy gray or yellowish brown, prosoma with distinct radial small dark bands especially along posterior eyes, opisthosoma with a longitudinal band in which outer lines are dark. Femora of legs without any band, but two clear dark patches on tibia ventrally (Figs 50a–b); ventral opisthosoma with a uniform dark marking with a notch at its anterior side (Fig. 50c).

Remarks. Lucas (1846) provided an illustration and a detailed description of colouration of this species, and noted that the ventral opisthosoma is decorated with two dark brown longitudinal bands, which meet in their posterior part, resembling the letter V. This character can be seen in specimens preserved for a long time in several species of the *dufouri* group. Even a compact marking in a freshly collected specimen can turn into V-shaped marking after preservation. In the illustration of *O. oraniensis* (Lucas 1846: pl. 11, fig. 9) no pattern is present on dorsal opisthosoma and no dark bands on the legs are illustrated, the body is uniformly coloured. This can be generally observed in specimens preserved for a long period. Lucas (1846) named the species after the type locality, the Oran region in the north-western part of Algeria. One *Eusparassus* specimen collected from Oran (deposited in ZSM) is designated here as neotype to avoid confusion with similar parapatric species of the group.

Known geographical distribution and habitat. Western Algeria and South-Eastern Morocco, under stones near to water sources.

Eusparassus fritschi (Koch, 1873) stat. rev.

Figs 20–21, 49c–d, 61c–d

Ocypete fritschi C. Koch, 1873: 114 (description of female, syntypes, SMF, examined)
Sparassus oraniensis (Lucas). Simon 1880: 291 (unjustified synonymy). **Removed from junior synonymy.**

Type material. Syntypes (designated by Koch 1873)**: 2♀♀, MOROCCO: *Region de Marrakech-Tensift-Al Haouz*:** Mtouga [label: 2 Types, *Ocypete fritschi* C. Koch, Marroko: Mtüga] 1872, Fritsch & Rein leg. (SMF 4569).

Other material examined. MOROCCO: *Region de Souss-Massa-Draa*: 4♂♂, 2♀♀, Agadir, April 1939, L. Bulaud (MNHN); 2♀♀, 1juv, Tafraoute, camp place, 21 August 1999, H. Nickel (SMF); 1♂ (MM 198), 1♀, June 1986, Wirtz leg. (SMF); ***Region de Marrakech-Tensift-Al Haouz*:** 1♂ (MM 194), Tizi-n-Test, Taroudannt, Buland leg. (MNHN); 1♂, Atlas, river gravel at Ouirgane, May 1976, 1200 m, P. Hillyard leg. (NHM); 5♀♀, 1sub♀, S.E. of Marrakesh, Lala Aziza (MNHN 6550); ***Region de Taza-Al Hoceima-Taounate*:** 2♀♀, Taza Province, Taza (N 34° 12' 36, W 4° 0' 36), 19 May 1936 (SMF 4656); ***Region de Meknes-Tafilalet*:** 1♀, Azrou, 28 May 1930 (SMF 4603).

Diagnosis. Compared to other group members, it is the only species with posterior eyes (especially PME) distinctly reduced in size (~1.4 times smaller than AME) (Fig. 21d); male distinguished easily from other congeners by EM with a projected bulge (Fig. 20c); epigyne with MS and EF as long as wide (Fig. 21a) [see also diagnosis for *dufouri* species group above].

Description. Male (ranges: n=7, single measurement: MM 198):

Measurements. Males of medium size. Total length 14.6–16.7; prosoma length 7.1–8.2, prosoma width 6.0–7.1, anterior width of prosoma 3.2–3.5, opisthosoma length 7.5–8.5, opisthosoma width 5.0–5.3. Eye diameters: AME 0.46, ALE 0.38, PME 0.37, PLE 0.40; eye interdistances: AME-AME 0.21, AME-ALE 0.07, PME-PME 0.42, PME-PLE 0.47, AME-PME 0.35, ALE-PLE 0.25, clypeus height at AME 0.32, clypeus height at ALE 0.37.

Chelicerae. Chelicerae with 2 anterior and 4 or 5 posterior teeth; cheliceral furrow lacking intermarginal denticles.

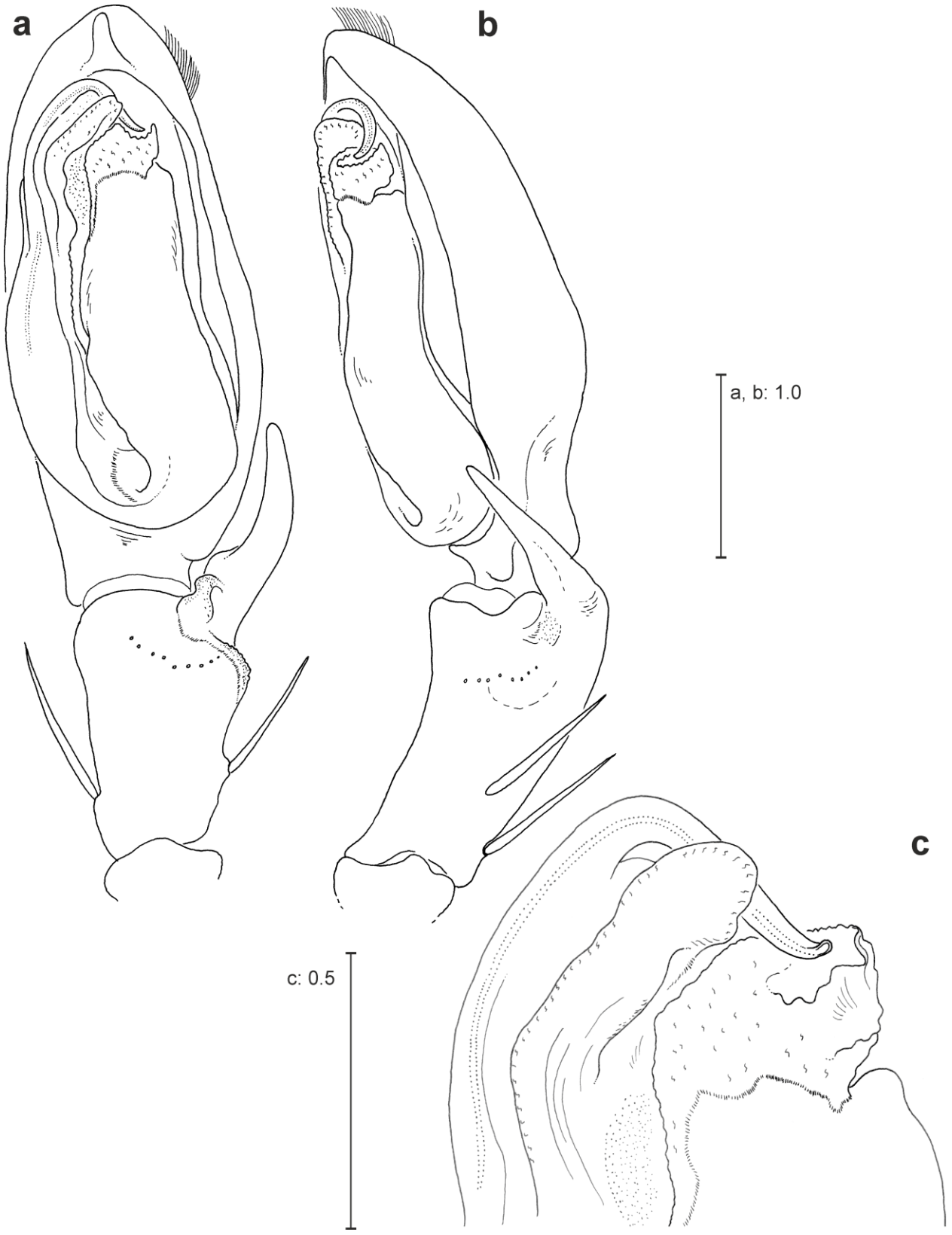

FIGURE 20. *Eusparassus fritschi* (Koch, 1873) **stat. rev.**, male from Morocco (SMF). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral.

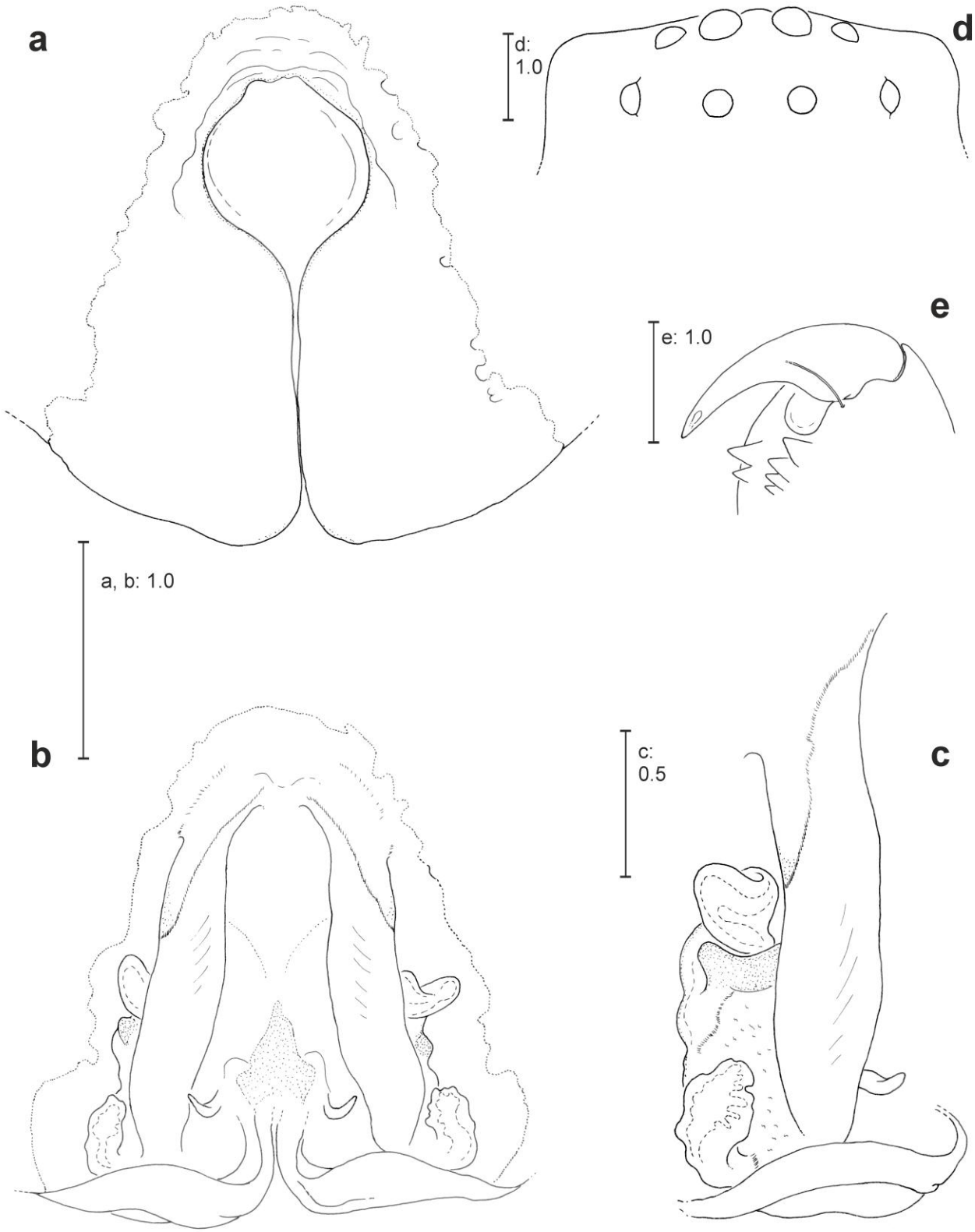

FIGURE 21. *Eusparassus fritschi* (Koch, 1873) **stat. rev.**, syntype female from Morocco: Mtuga (SMF). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) eye arrangement, dorsal; (e) left chelicera, ventral.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 9.9 [3.1, 1.5, 1.7, 3.6], I 35.5 [9.9, 3.7, 9.0, 9.8, 3.1], II 38.9 [11.1, 3.8, 10.2, 10.6, 3.2], III 33.1 [9.8, 3.4, 8.5, 8.6, 2.8], IV 37.8 [10.9, 3.3, 9.4, 11.1, 3.1].

Spination. Palp 131, 001, 1111; Legs: Femur I 324/424, II 323/424, III 424, IV 322/422; Patella I–IV 101; Tibia I–IV 2224; Metatarsus I 1014, II–III 2024, IV 3036.

Palp. As in diagnosis with ST not visible; vRTA rounded and weakly developed; cymbium longer than tibia (Figs 20a, b); ET pointing first proximad and distally ventrad; hyaline EM bulging and covering part of ET (Fig. 20c).

Female (ranges: n=10, single measurement: syntype):

Measurements. Females of large size. Total length 20.8–25.0, prosoma length 8.8–10.0, prosoma width 7.5–9.4, anterior width of prosoma 4.6–6.0, opisthosoma length 12.0–15.0, opisthosoma width 7.0–10.0. Eye diameters: AME 0.50, ALE 0.43, PME 0.38, PLE 0.36; eye interdistances: AME-AME 0.33, AME-ALE 0.16, PME-PME 0.60, PME-PLE 0.75, AME-PME 0.56, ALE-PLE 0.46, clypeus AME 0.45, clypeus ALE 0.53. AE distinctly larger than PE, with AME distinctly larger than others (Fig. 21d).

Chelicerae. Chelicerae with 2 anterior and 4 or 5 posterior teeth, cheliceral furrow lacking intermarginal denticles; one bristle at distal end of cheliceral basal segment (Fig. 21e).

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 11.5 [3.4, 1.8, 2.2, 4.1], I 34.1 [9.4, 4.5, 8.1, 9.3, 2.8], II 36.7 [10.7, 4.5, 9.0, 9.7, 2.8], III 31.6 [9.7, 4.0, 7.6, 7.8, 2.5], IV 36.1 [10.3, 4.3, 8.8, 10.0, 2.7].

Spination. Palp 131, 101, 1111, 1013; Legs: Femur I 223/224/424, II–III 424, IV 322/422; Patella I–IV 000; Tibia I–II 0004/2024, III–IV 2024; Metatarsus I–III 1014/2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF as long as wide (Fig. 21a) or slightly longer than wide, longitudinal band on MS (dorsal view) weakly developed (Fig. 21b), GP well developed (Fig. 21c).

Colouration [in ethanol]. Reddish brown with series of chevron like patterns on dorsal opisthosoma, legs banded (Figs 49c–d), ventral opisthosoma with V-shaped dark marking (Fig. 49d).

Remarks. Koch (1873) described two females from the Mtuga Plateau, Morocco. He noted the general similarities in traits between this species and *E. walckenaeri* (sub *Ocypete tersa*). Simon (1880) listed this species as synonym of *E. oraniensis* but with a question mark (sub *Sparassus oraniensis*). Probably he did not see the syntypes, but referred to the colouration of the ventral

opisthosoma for his judgment. The dark marking is a diagnostic character in all members of the *dufouri* group. In *E. fritschi* **stat. rev.** clear differences exist between the characters of the copulatory organs (especially the newly discovered male) compared to other species. Thus, species rank is re-established and the male is described here for the first time.

Known geographical distribution and habitat. The Atlas Mountains in Morocco, river gravel under stones.

Eusparassus letourneuxi (Simon, 1874)

Figs 22–23, 49e–f, 61e–f

Sparassus letourneuxi Simon, 1874: 252–253, pl. 5, fig. 8 (description of male, syntypes from Algeria: Constantine Prov., and around Algiers, not located in MNHN, presumably lost). Levy 1989: 137, figs. 24–26 (illustration of female). **Neotype designated here**.

Eusparassus letourneuxi (Simon). Strand 1908b: 19 (transfer); Denis 1938: 388; Denis 1947: 50, Pl. 2, fig. 13 (description of female).

Eusparassus dufouri kabylianus Denis, 1937: 1050 (description of male and female) [synonymy by Denis 1938].

Type material: Neotype: female, **ALGERIA:** ***Wilaya de Tizi Ouzou:*** Kabylie region: Yakouren [N 36° 44', E 4° 27'], [label: *Eus. letourneuxi* E.S., Kabilia, Yakouren, C.M. 1905] (MNHN 22629).

Other material examined. ALGERIA: 2♀♀, with same data as for neotype (MNHN). ***Wilaya de Blida:*** 1♂, 1♀, Atlas Blidéen, Djebel Ferroukha, Gellaï, 1350 m, pitfalls in planted *Cedrus* forest, 20 June 1987–9 May 1988, R. Bosmans leg. (CRB). ***Wilaya de Tizi Ouzou:*** 2♀♀, Tala Guilef, 1550–2000 m, litter in old, open *Cedrus* forest, 29 April 1984, R. Bosmans leg. (CRB); 1♀, Massif du Djurdjura, Col de Tizi N'Kouillal, 1700 m, among stones in montane grassland, 22 October 1982, R. Bosmans leg. (CRB); 1♂, Massif du Djurdjura, Tala Guilef, 1420 m, pitfall in grassland in *Cedrus* forest, 20 June 1993, R. Bosmans leg. (CRB); ***Wilaya de Bejaia*:** 1♀, Oued Daas, 15 m, beach near river mouth, 22 May 1988, R. Bosmans leg. (CRB). ***Wilaya de***

***M'sila*:** 1♀, Djebel Maadid, 1500 m, *Quercus ilex* forest, 9 March 1990, R. Bosmans leg. (CRB); ***Wilaya de Boumerdes*:** 1♂, entre Toulmout et Keddara, 500 m, 27 April 1989, R. Bosmans leg. (CRB). ***Wilaya de Tissemsslit*:** 2♂♂, Theniet El Had, around Djebel Meddad, 1780 m, 19 February 1988, R. Bosmans leg. (CRB); 1♂, Theniet-el-Had, Djebel Meddad, 1450 m, stones mixed *Cerdrus atlanticus* and *Querqus faginea* forest, 18 May 1988, R. Bosmans leg. (CRB). ***Wilaya de Bouira*:** 1♂, Massif du Djurdjura, Tikjda, 1450 m, among stones around Hotel, 17 September 1987, R. Bosmans leg. (CRB).

Diagnosis. Resembles *E. barbarus* in having a short ET but differs by having a slimmer ET (Fig. 22c) and dRTA directed distad (Figs 22a, b); female epigyne with unique MS semicircular (Figs 23a, f) [see also diagnosis for *dufouri* species group above].

Description. Male (ranges: n=7, single measurement: MM 195):

Measurements. Medium sized. Total length 15.6–17.8, , prosoma length 7.1–8.3, prosoma width 6.3–6.7, anterior width of prosoma 3.3–3.8, opisthosoma length 8.5–9.5, opisthosoma width 5.0–5.5. Eye diameters: AME 0.45, ALE 0.35, PME 0.32, PLE 0.38; eye interdistances: AME-AME 0.26, AME-ALE 0.12, PME-PME 0.38, PME-PLE 0.55, AME-PME 0.34, ALE-PLE 0.28, clypeus height at AME 0.25, clypeus height at ALE 0.38.

Chelicerae. Chelicerae as in females.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 8.9 [2.5, 1.3, 1.5, 3.6], I 31.9 [8.6, 3.3, 8.0, 9.0, 3.1], II 34.2 [9.4, 3.2, 8.9, 9.7, 3.0], III 29.2 [8.5, 3.2, 7.1, 7.6, 2.8], IV 32.5 [9.1, 3.1, 8.0, 9.3, 3.0].

Spination. Palp 131, 101, 1111; Legs: Femur I 323(4)/324, II–III 324/424, IV 322/422/423; Patella I–IV 001/101; Tibia I–IV 2224; Metatarsus I–III 1014/2024, IV 3036.

Palp. As in diagnosis with cymbium nearly twice as long as tibia, dRTA sickle-shaped and vRTA not developed (Figs 22a, b); ET shortened distally but robust proximally (Fig. 22c).

Female (n=9):

Measurements. Neotype: Total length: 18.8, prosoma length 7.4, prosoma width 6.3, anterior width of prosoma 3.8, opisthosoma length 11.2, opisthosoma width 7.0. Eye diameters: AME 0.50, ALE 0.34, PME 0.35, PLE 0.41; Eye interdistances: AME-AME 0.28, AME-ALE 0.13, PME-PME 0.43, PME-PLE 0.51, AME-PME 0.31, ALE-PLE 0.28, clypeus AME 0.37, clypeus ALE 0.41. AME largest and ALE smallest (Fig. 23d).

Chelicerae. Chelicerae with 2 anterior and 3 or 5 posterior teeth, cheliceral furrow lacking intermarginal denticles; one bristle at distal end of cheliceral basal segment (Fig. 23e).

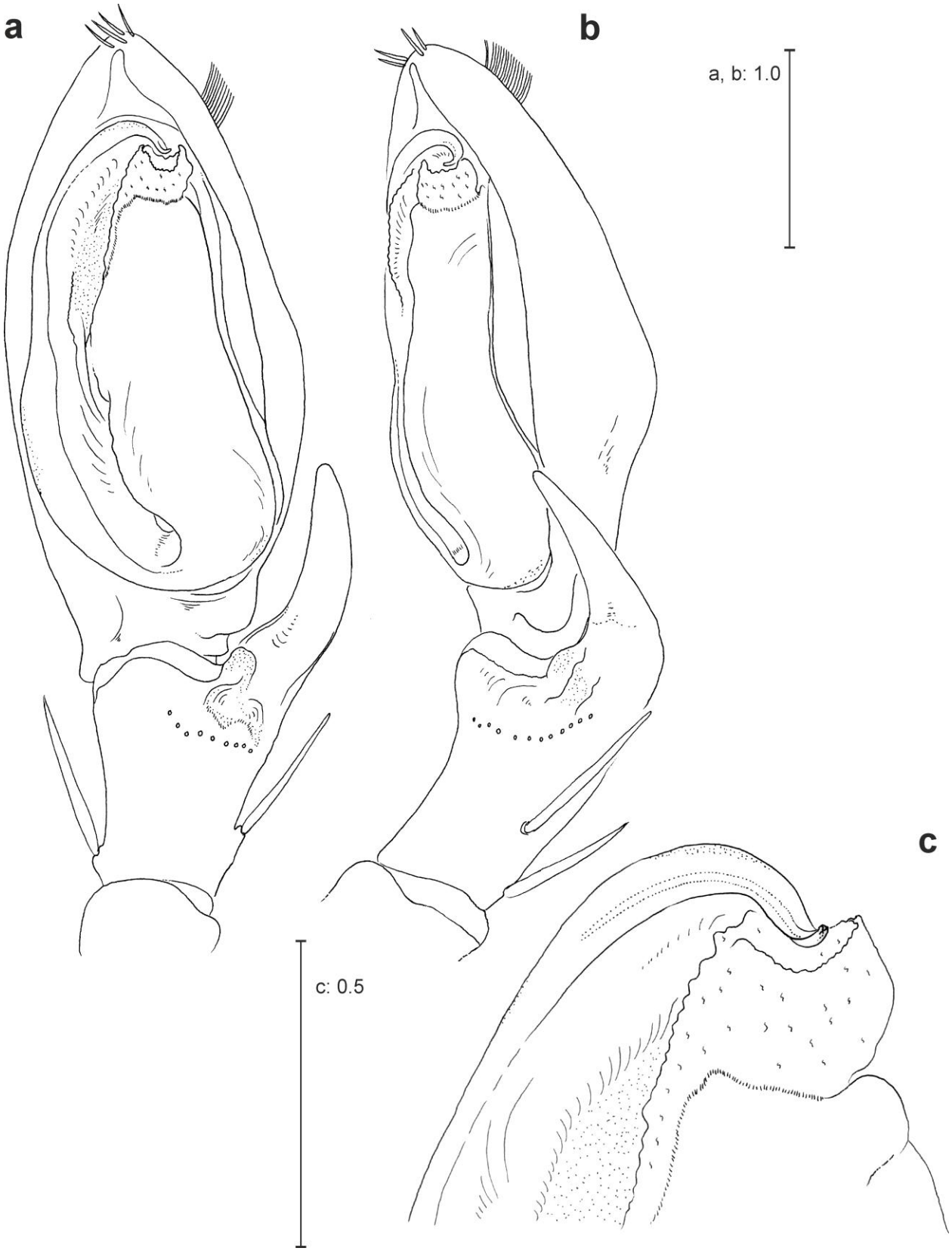

FIGURE 22. *Eusparassus letourneuxi* (Simon, 1874), male from Algeria: Djebel Ferroukha (CRB). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral.

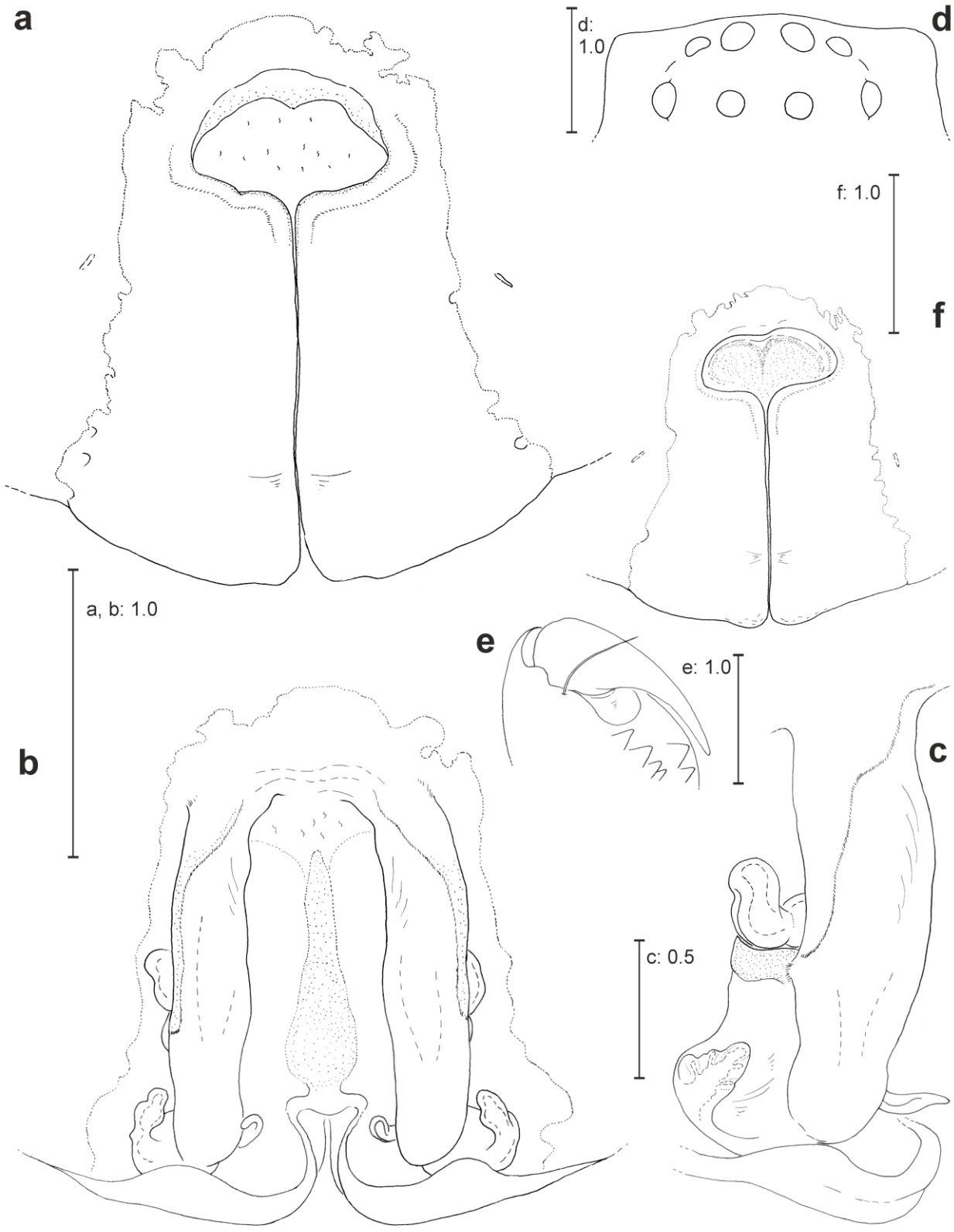

FIGURE 23. *Eusparassus letourneuxi* (Simon, 1874), neotype female from Algeria: Yakouren (MNHN). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) eye arrangement, dorsal; (e) right chelicera, ventral; (f) variation in epigyne, ventral.

Legs. Leg formula: IV II I III. Measurements of palp and legs: Palp 8.3 [2.4, 1.4, 1.6, 2.9], I 25.3 [7.1, 3.5, 6.0, 6.6, 2.1], II 25.0 [7.2, 3.2, 6.1, 6.3, 2.2], III 23.6 [7.3, 3.1, 5.5, 5.6, 2.1], IV 26.3 [7.8, 3.0, 6.2, 7.1, 2.2].

Spination. Palp 131, 101, 1111, 1013; Legs: Femur I 224/324, II–III 123/424, IV 421/422; Patella I–IV 000/101; Tibia I–II 0004/2024, III–IV 2024; Metatarsus I–III 1014/1024/2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF approximately quadrangulate in shape (Figs 23a, f); MS partially (Fig. 23a) to fully sclerotized (Fig. 23f); MS dorsally with a sclerotized strip (Fig. 23b); vulva equipped with a glandular process (GP) (Fig. 23c).

Colouration [in ethanol]. Yellowish brown or reddish brown, dorsal opisthosoma dark brown with small series of yellow chevrons, legs (tibia and femur) clearly banded (Fig. 49e); ventral opisthosoma with V-shaped dark marking in which the mark is not filled with dark colour but is only outlined as "V" with especially the inner lines bold (Fig. 49f).

Remarks. The type specimens were collected from Northern Algeria in Constantine Province and around the capital city Algiers (Simon 1874: 253). Unfortunately, the type series could not be located in MNHN neither could the other male specimens identified by Simon. Exceptionally, in this species, females are easily recognized by the shape of the MS of epigyne. Several different tubes containing *E. letourneuxi* females and juveniles were found in MNHN. Among them a female collected near to the original type locality from Kabylie: Yakouren was selected and designated as neotype to clarify the species identity and reduce taxonomic problems in distinguishing this species from closely similar species in nearby regions of Western Algeria (*E. oraniensis*), Eastern Algeria (*E. barbarus*) and Southern Tunisia (*E. syrticus*). The designated neotype was identified by Simon as *E. letourneuxi* as clearly indicated by his abbreviation "E.S" on the label, confirming that the specimen is correctly identified to *E. letourneuxi*. Several sympatric male and female from different localities were used to describe the male.

Known geographical distribution and habitat. North-Eastern Algeria in the Atlas Mountains, inhabiting stony areas of mountainous grassland, Cedar and Oak forests.

Eusparassus syrticus Simon, 1909

Figs 24, 51c–d, 62c

Eusparassus argelasius syrticus Simon, 1909: 30–31 (description of female). [2 female and 1 immature syntypes from Tunisia, MNHN, examined] 1 female lectotype designated here, (for justification see remarks).

Eusparassus dufouri syrticus (Simon). Denis 1945: 54.

Type material. Lectotype: female**, TUNISIA: *Governorat de Tataouine*:** Tataouine [N 32° 25' 32", E 10° 10' 29"] (label: *Eus. argel. syrticus* E.S. Tunesia S of Triholitaine, Tatahouine), Jar number: 1668, Simon number: 22701 (MNHN).

Diagnosis. Copulatory duct very robust and wide like that of *E. oraniensis* but differing from it by TL not visible in dorsal view (Fig. 24b) and having larger and semispherical GP overlapping with distal end of CD (Fig. 24c) [see also diagnosis for *dufouri* species group above].

Description. Female (lectotype):

Measurements. Large sized *Eusparassus* species; total length 22.8, prosoma length 9.5, prosoma width 8.6, anterior width of prosoma 4.8, opisthosoma length 13.3, opisthosoma width 9.0. Eye diameters: AME 0.55, ALE 0.60, PME 0.55, PLE 0.62; eye interdistances: AME-AME 0.23, AME-ALE 0.05, PME-PME 0.50, PME-PLE 0.51, AME-PME 0.62, ALE-PLE 0.39, clypeus height at AME 0.52, clypeus height at ALE 0.58. PLE largest; LE larger than ME (Fig. 24d).

Chelicerae. Chelicerae with 2 anterior and 3 posterior teeth, intermarginal denticles absent (Fig. 24e).

Legs. Leg formula: IV II I III. Measurements of palp and legs: Palp 11.2 [3.5, 1.7, 2.2, 3.8], I 34.4 [10.0, 4.3, 8.6, 9.1, 2.4], II 36.2 [10.7, 4.4, 9.4, 9.2, 2.5], III 34.1 [10.7, 4.0, 8.4, 8.5, 2.5], IV 37.5 [11.7, 3.8, 9.2, 10.2, 2.6].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 424, IV 423; Patella I–IV 101; Tibia I–IV 2024; Metatarsus I 1014, II–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF longer than wide, MS as long as wide (Fig. 24a); CD widened and covered by TL, only parts of GP extending beyond CD in dorsal view of vulva (Fig. 24b); GP enlarged (Fig. 24c).

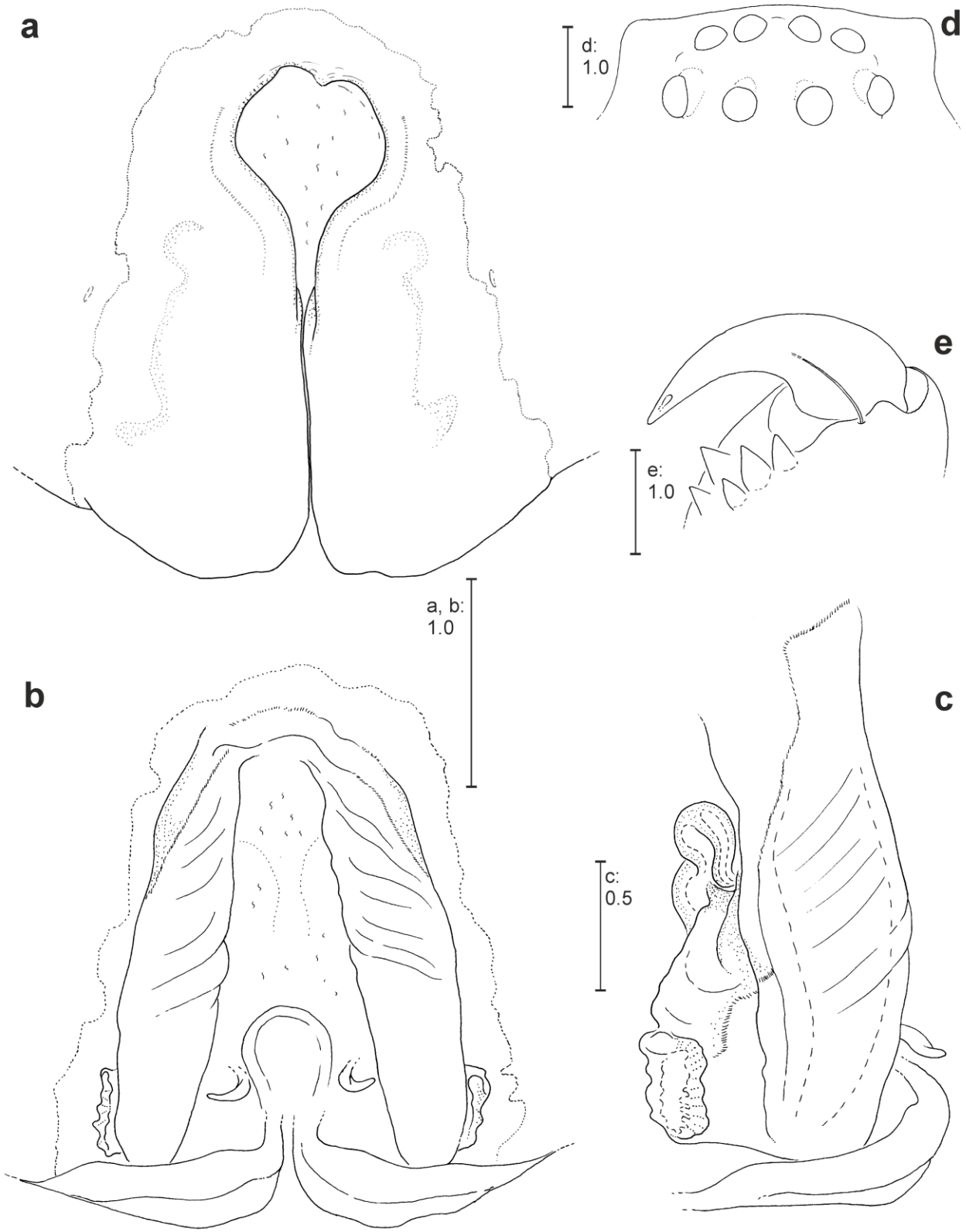

FIGURE 24. *Eusparassus syrticus* Simon, 1909, lectotype female from Tunisia: Tataouine (MNHN). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) eye arrangement, dorsal; (e) left chelicera, ventral.

Colouration [in ethanol]. Reddish brown with banded legs: femur with a distal dark band, tibia with two strong bands (Fig. 51c); ventral opisthosoma with a robust V-shaped dark marking (Fig. 51d).

Male: unknown.

Remarks. The type series consists of two females and one immature female. The one medium sized female belongs to the known species *E. barbarus*. The larger female and immature female both belong to the same species. Thus, in order to conserve the specific name *syrticus*, this latter female is selected and designated here as lectotype. Levy (1989: 137, figs 22–23) studied one female (sub *Sparassus syrticus*) from Morocco but it was a misidentification and the species is actually belonged to *E. atlanticus* **stat. nov.**

Known geographical distribution. Southern Tunisia (type locality).

vestigator species group

Diagnosis. Chelicerae without intermarginal denticles, one to four retromarginal bristles at distal end of cheliceral basal segment (Figs 25e, 28d); ventral opisthosoma with a distinct dark marking (Figs 52b, f, 53c); male with unique prominent and elongated vRTA (at least one third of dRTA length) (Figs 25a, 27a); epigyne with AMLL fused together and entirely encircling MS, epigyne with MS noticeably enlarged and fully sclerotized (Figs 26a, d; 28a).

Species composition. Three species: *E. vestigator* (Simon, 1897) **comb. nov.**; *E. reverentia* **spec. nov.**; *E. pearsoni* (Pocock, 1901) (for latter species description, see Moradmand & Jäger 2012a).

Distribution. Central to Eastern Africa and an isolated area in South Asia (India) (Fig. 71a).

Eusparassus vestigator (Simon, 1897) comb. nov.

Figs 25–26, 52a–b, 63a–b

Sparassus vestigator Simon, 1897c: 388 (description of male and immature female syntypes). [syntypes, male and subadult female, NHM, examined]

Eusparassus rufobrunneus Caporiacco, 1941: 109, fig. 40 (description and illustration of male, two male syntypes), [syntypes, two males, MZUF, examined]. **New synonymy.**

Olios vestigator (Simon). Roewer 1955b: 695 (unjustified transfer).

Type material. Syntypes of *Sparassus vestigator* (designated by Simon 1897c)**:** 1♂, 1 subadult ♀, **ETHIOPIA:** ***between Oromia and Somali Regions***: male, West of Shebelle River, (label: *Sparassus vestigator* Simon, W of Shebeli River, 15.12.94) (NHM 97.11.10.56), subadult female, Shebelle River (label: *Sparassus vestigator* Simon, Type, 5.6.95) (NHM); **Syntypes** of *Eusparassus rufobrunneus* (designated by Caporiacco 1941): 2♂♂, **ETHIOPIA:** ***Southern Nations Region:*** 1♂, El Dire, "Missione Biologica Sagan=Omo, 1939, Prof. Edoardo Zavattari", 18 May 1939 (MZUF), 1♂, Elolo, "Missione Biologica Sagan=Omo, 1939, Prof. Edoardo Zavattari", 16 July 1939 (MZUF).

Other material examined. 6♂♂, 5♀♀, **ETHIOPIA**: 1♂, Valley of the Omo River, field number 6, 14 May 1969, D. Houin leg. (MNHN); 1♀, Valley of the Omo River, field number 27, 7 August 1972, O.F. Rodhain leg. (MNHN); **SOMALIA**: 1♀, Somaliland, Bohalgarshan, 28 October 1895 (NHM 97.11.10.54); **KENYA**: ***Rift Valley Province***: 4♂♂, 1♀ (MM 170), Northern Turkana, Kenya colony, "Lake Rudolf Rift Valley Expedition 1934", February–June 1934, V.E. Fuchs leg. (NHM); 1♀, Lake Baringo area, dry bed of Kapinga River, 16 May 1975, A. J. Penniman leg. (AMNH); ***Central Province:*** 1♀, Mangu, Lome, Prof. Kobert leg. (ZMB); 1♀, Mangu, 3 March 1935, Dr. B. Beuzon leg. (ZMUC); **TANZANIA**: ***Zanzibar Region***: 1♂, Zanzibar, Hildebrandt leg. (ZMB).

Diagnosis. Male palpal morphology similar to that of *E. reverentia* **spec. nov.** but differing in having more slender ET lacking pointed triangular process and more slender dRTA (Figs 25a–c); female differentiated by elongated GP parallel to copulatory duct (CD) (Figs 26b, c) [see also diagnosis for *vestigator* species group above].

Description. Male (ranges: n=9, single measurement: syntype):

Measurements. Medium to large sized; total length 18.2–20.2, prosoma length 8.2–10.0, prosoma width 6.8–8.3, anterior width of prosoma 3.7–4.6, opisthosoma length 10–10.2, opisthosoma width 5.5–7.3. Eye diameters: AME 0.46, ALE 0.35, PME 0.34, PLE 0.35; eye interdistances: AME-AME 0.22, AME-ALE 0.10, PME-PME 0.43, PME-PLE 0.42, AME-PME 0.31, ALE-PLE 0.20, clypeus height at AME 0.25, clypeus height at ALE 0.35. AME largest, other eyes subequal (Fig. 25d).

Chelicerae. Chelicerae with 2 anterior and 4 or 5 posterior teeth; cheliceral furrow without intermarginal denticles (Fig. 25e).

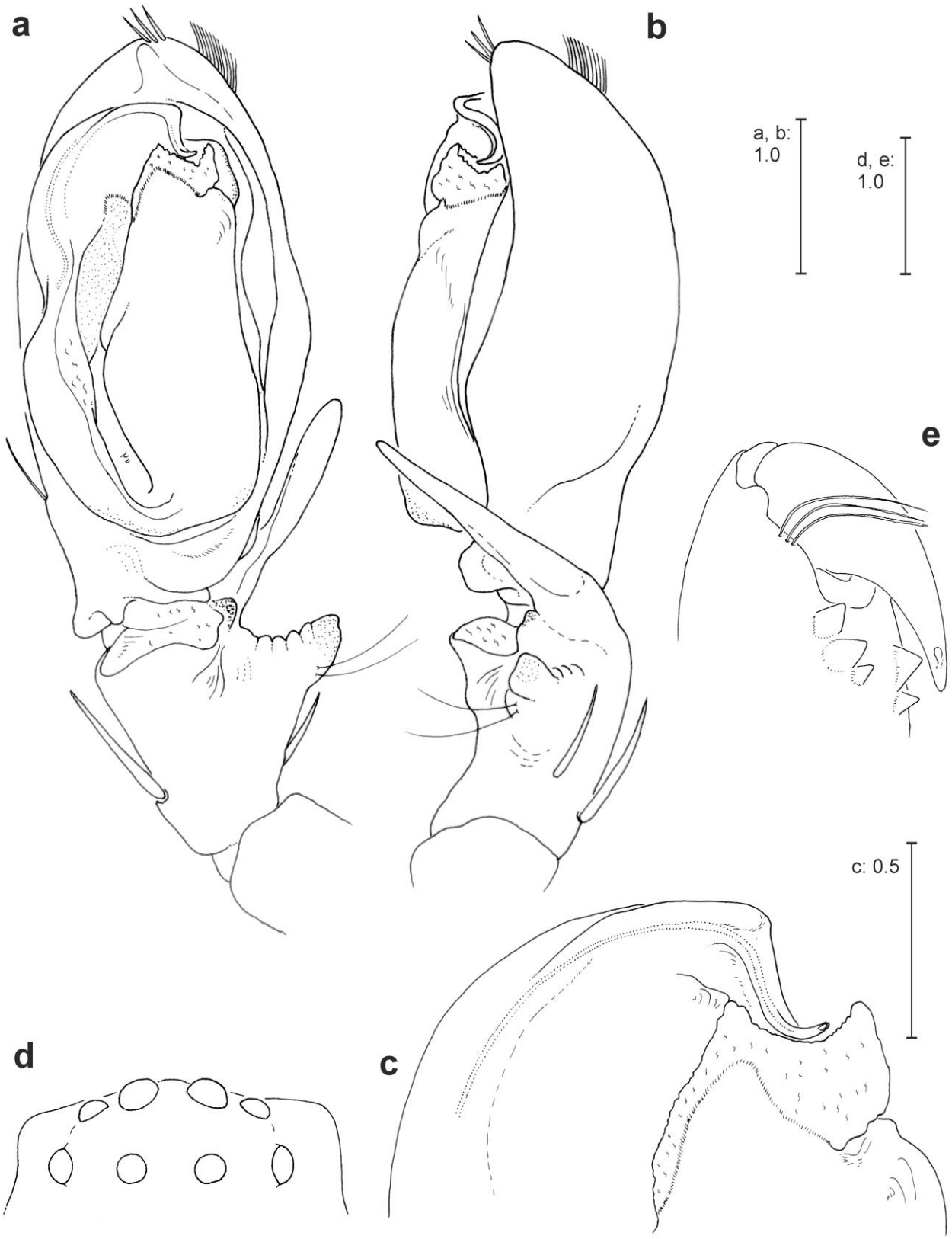

FIGURE 25. *Eusparassus vestigator* (Simon, 1897) **comb. nov.**, syntype male from Ethiopia: west of Shebelle River (NHM). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) left chelicera, ventral.

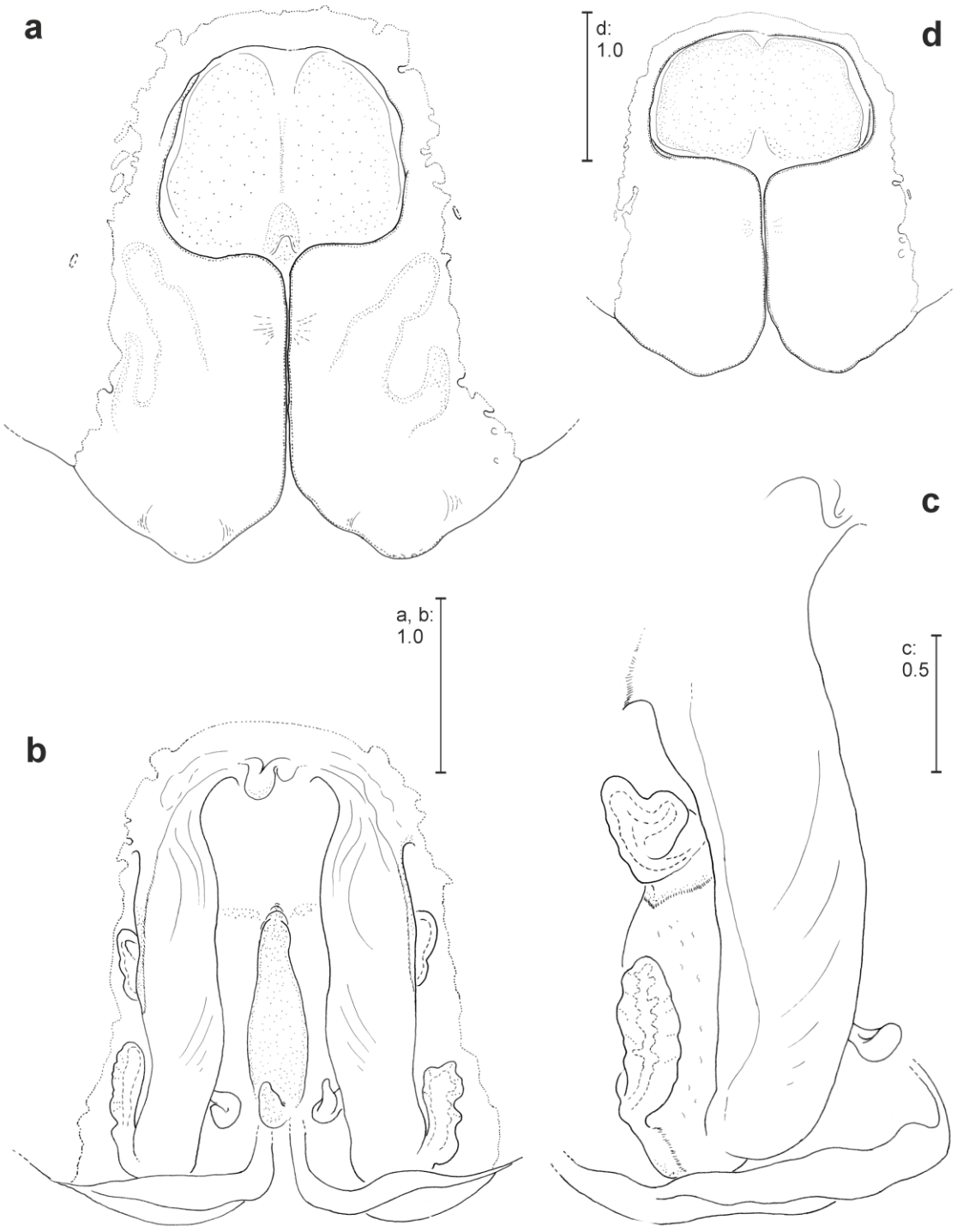

FIGURE 26. *Eusparassus vestigator* (Simon, 1897) **comb. nov.**, female from Kenya: Northern Turkana (NHM). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) variation in epigyne, ventral.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 8.5 [2.8, 1.3, 1.4, 3.0], I 30.1 [8.4, 3.2, 7.5, 8.5, 2.5], II 33.4 [9.5, 3.5, 8.4, 9.3, 2.7], III 27.3 [8.1, 3.0, 7.0, 7.2, 2.0], IV 31.6 [9.1, 2.7, 7.8, 9.7, 2.3].

Spination. Palp 131, 101, 1111; Legs: Femur I–III 424, IV 323/422/423; Patella I–IV 101; Tibia I–IV 2224; Metatarsus I–III 2024, IV 3036.

Palp. As in diagnosis with cymbium more than twice as long as tibia (Fig. 25b); E and T expanded and covering ST (Fig. 25a); ET directed proximad and retrolaterad at its distal end (Fig. 25c).

Female (ranges: n=5, single measurement: MM 170):

Measurements. Medium to large sized; total length 18.5–21.7, prosoma length 8.5–9.7, prosoma width 7.7–8.5, anterior width of prosoma 4.8–5.2, opisthosoma length 10.0–12.0, opisthosoma width 6.5–7.5. Eye diameters: AME 0.61, ALE 0.46, PME 0.45, PLE 0.45; eye interdistances: AME-AME 0.38, AME-ALE 0.20, PME-PME 0.63, PME-PLE 0.77, AME-PME 0.47, ALE-PLE 0.32, clypeus AME 0.45, clypeus ALE 0.62, eye arrangement as in males.

Chelicerae. Chelicerae with 2 anterior and 3 to 5 posterior teeth, cheliceral furrow without intermarginal denticles; one to four retromarginal bristles at distal end of cheliceral basal segment.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 7.4 [2.2, 1.1, 1.6, 2.5], I 22.8 [6.5, 2.8, 6.0, 5.8, 1.7], II 25.6 [7.7, 3.2, 6.7, 6.2, 1.8], III 21.6 [6.6, 2.7, 5.6, 5.2, 1.5], IV 25.5 [7.8, 2.7, 6.6, 6.7, 1.7].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 424, IV 422/423; Patella I–IV 000/101; Tibia I–IV 2024/2224; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF longer than wide; sclerotized MS as long as wide (Fig. 26a) or slightly wider than long (Fig. 26d); large, robust CD and GP, GP long; a median longitudinal sclerotized band on MS dorsally (Figs 26b, c).

Colouration [in ethanol]. Reddish brown to yellowish cream with dark bands on legs, dorsal opisthosoma with a longitudinal dark band composed of fused chevron patterns, ventral opisthosoma with V-shaped dark marking with inner lines bold (Figs 52a–b); live colouration is brownish gray with black patches on body and bands on legs (Fig. 52d).

Remarks. Like other *Eusparassus* species described before 1903, this species was originally placed in *Sparassus* by Simon (1897c) (along with *E. laevatus* **comb. nov.**). Roewer (1955b) made an unjustified combination and transferred the species to *Olios*. *Eusparassus rufobrunneus*

Caporiacco, 1941 **syn. nov.** is proposed here as a junior synonym. The two syntype males from southern Ethiopia exhibit congruent diagnostic characters similar to the syntype male of *E. vestigator*. The syntype female is an immature specimen, thus the female is here described for the first time. Unlike most of *Eusparassus* spp., *E. vestigator* and the other two known species in the *vestigator* group bear more than two thick retromarginal bristles at the distal base of chelicerae.

Known geographical distribution and habitat. East Africa in southern Ethiopia (type locality), Somalia (new country record), Kenya (new country record) and Tanzania (new country record) (Fig. 71a). Found under stones near dry river beds.

Eusparassus reverentia spec. nov.

Figs 27–28, 53, 63c–d

Type material. Holotype: male, **BURKINA FASO: *Houet Province*:** Bobo Dioulasso [N 11˚11', W 4˚17'], 1965, B. Steinstra leg. (MRAC 128181).
Paratype: NIGERIA: *Plateau State:* 1♀, Jos [N 9˚56', E 8˚53'], female with hatched spiderlings (second instar) in papery egg sac, 7–26 April 1963, E. Bouquiaux leg. (MRAC 123751).

Diagnosis. Closely similar to *E. vestigator* **comb. nov.**, but male differing by flatter and wider ET equipped with pointed triangular process (Fig. 27c), and more robust dRTA flattened dorso-ventrally (Figs 27a, b). Female differing in the shape of GP attached to main vulva by most of its length (in *E. vestigator* **comb. nov.** separated) (Figs 28b, c) [see also diagnosis for *vestigator* species group above].
Etymology. The specific name is a Latin translation derived from the German phrase "Ehrfurcht vor dem Leben" (English: "the reverence for life"), in honour of the idea of Dr Albert Schweitzer (1875–1965) who was awarded the Nobel Peace Prize (1952) because of it. The idea could be defined in the following statement by J. Brabazon: "...we are brothers and sisters to all living things, and owe to all of them the same care and respect that we wish for ourselves." Term in apposition.
Description. Male (n=1, holotype):

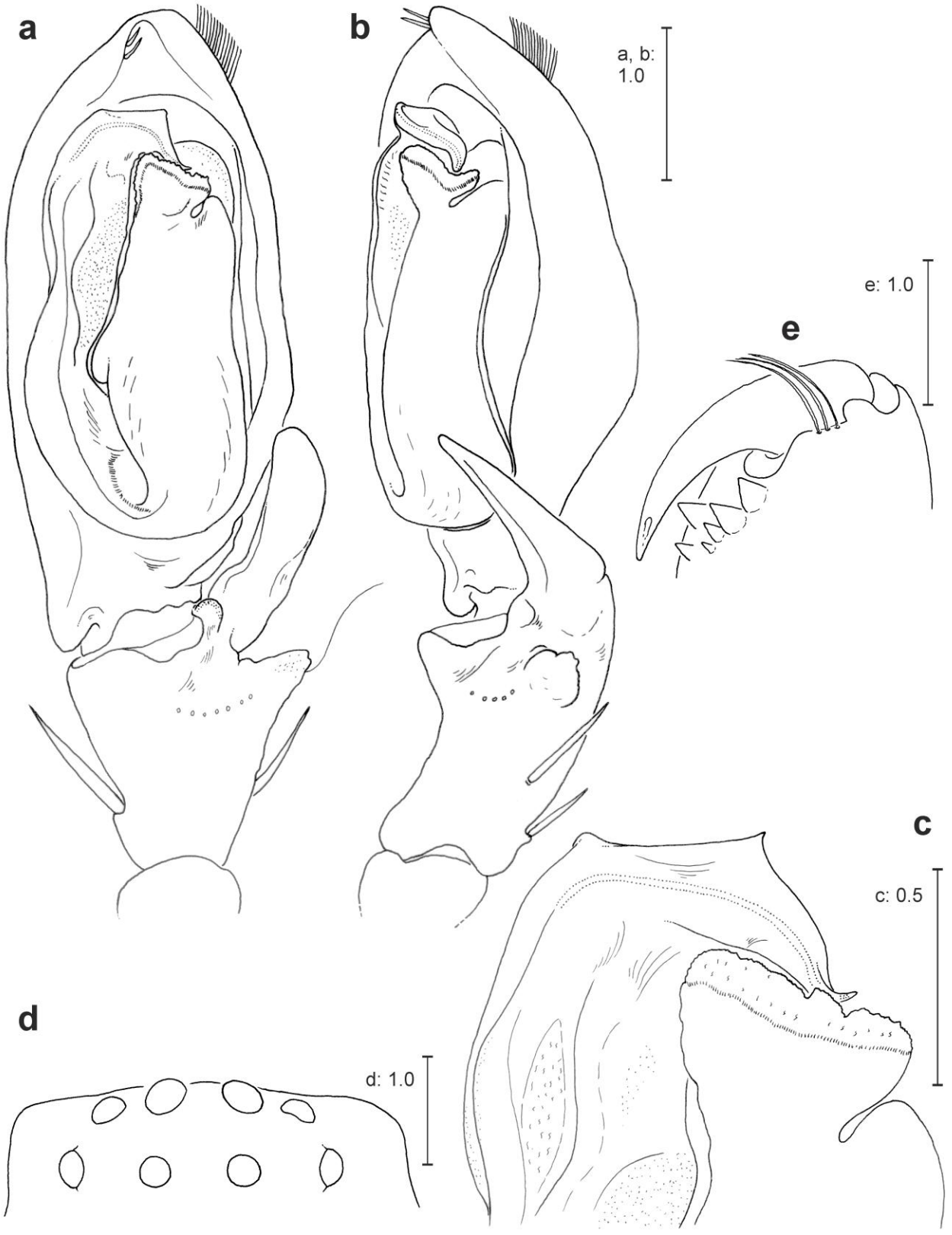

FIGURE 27. *Eusparassus reverentia* **spec. nov.**, holotype male from Burkina Faso: Bobo Dioulasso (MRAC). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) left chelicera, ventral.

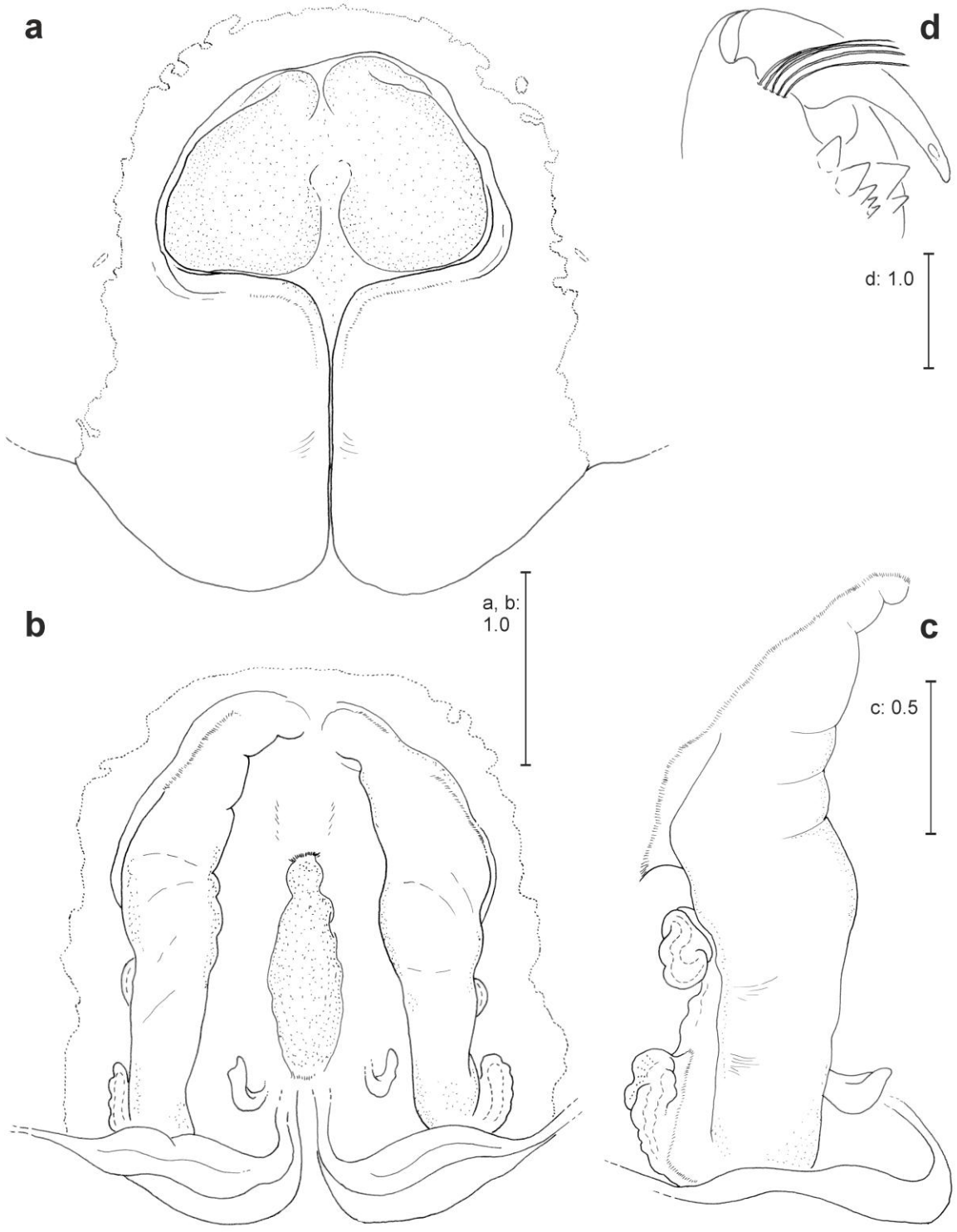

FIGURE 28. *Eusparassus reverentia* **spec. nov.**, paratype female from Nigeria: Jos (MRAC). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) right chelicera, ventral.

Measurements. Male medium sized; total length 15.1, prosoma length 8.6, prosoma width 7.3, anterior width of prosoma 4.2, opisthosoma length 6.5, opisthosoma width 3.5. Eye diameters:

AME 0.53, ALE 0.45, PME 0.40, PLE 0.46; eye interdistances: AME-AME 0.32, AME-ALE 0.16, PME-PME 0.55, PME-PLE 0.65, AME-PME 0.40, ALE-PLE 0.32, clypeus height at AME 0.40, clypeus height at ALE 0.45. AME largest, lateral eyes subequal (Fig. 27d).

Chelicerae. Chelicerae with 2 anterior and 4 posterior teeth, cheliceral furrow lacking intermarginal denticles (Fig. 27e).

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 11.1 [3.7, 1.6, 1.7, 4.1], I 37.3 [9.8, 4.2, 9.5, 10.7, 3.1], II 40.6 [11.5, 4.2, 10.2, 11.5, 3.2], III 34.6 [10.2, 3.6, 8.6, 9.5, 2.7], IV 38.9 [11.0, 3.7, 9.6, 11.5, 3.1].

Spination. Palp 131, 101, 1111; Legs: Femur I–III 424, IV 322; Patella I–IV 101; Tibia I–IV 2224; Metatarsus I–III 2024, IV 3036.

Palp. As in diagnosis with cymbium more than twice as longer as tibia (Fig. 27b); ET with a pointed triangular process (Fig. 27c).

Female (n=1, paratype):

Measurements. Female large sized; total length 22.8, prosoma length 9.8, prosoma width 8.6, anterior width of prosoma 5.5, opisthosoma length 13.0, opisthosoma width 8.2. Eye diameters: AME 0.58, ALE 0.45, PME 0.38, PLE 0.47; eye interdistances: AME-AME 0.50, AME-ALE 0.22, PME-PME 0.82, PME-PLE 0.70, AME-PME 0.69, ALE-PLE 0.48, clypeus height at AME 0.52, clypeus height at ALE 0.65.

Chelicerae. Chelicerae with 2 anterior and 5 posterior teeth.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 10.4 [3.1, 1.7, 2.0, 3.6], I 31.9 [9.1, 4.1, 8.2, 8.6, 2.7], II 34.0 [10.1, 4.4, 8.2, 8.6, 2.7], III 28.9 [8.6, 4.0, 6.8, 7.2, 2.3], IV 32.8 [9.6, 3.8, 8.0, 8.7, 2.7].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 424, IV 322; Patella I–IV 001; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF slightly longer than wide but MS is distinctly wider than long (Fig. 28a); CD partially to fully sclerotized , GP not well developed but parallel to CD (Figs 28b, c)

Colouration [in ethanol]. Reddish brown with darker bands on tibiae and femora of the legs, ventral opisthosoma with a V-shaped dark marking (Figs 53 a–c).

Remarks. The holotype male and paratype female both share the same somatic characters including eyes arrangement, leg formula, spination pattern, cheliceral dentition and presence of

the ventral opisthosoma dark marking and three to five thick bristles at the retromarginal side of chelicerae basal segment.

Known geographical distribution and habitat. From Burkina Faso to Nigeria (Jos Plateau) in Central Africa (Fig. 71a).

jaegeri species group

Diagnosis. Intermarginal denticles of chelicerae present (Figs 29e, 31e, 35e); in female epigyne, AMLL fused together and encircling MS entirely (Figs 30a, 32a, 34a, 36a); male palp exhibiting an obviously enlarged sub-tegulum (Figs 29a, 31a, 35a).

Species composition. Four species: *E. jaegeri* **spec. nov.**, *E. jocquei* **spec. nov.**, *E. schoemanae* **spec. nov.** and *E. borakalalo* **spec. nov.**

Distribution. From Southern Africa to Zimbabwe (Fig. 71b).

Eusparassus jaegeri spec. nov.

Figs 29–30, 54a, 64a, d

Type material. Holotype: male, **SOUTH AFRICA:** ***Gauteng Province:*** 20 km NE of Pretoria, S 25˚36.321', E 28˚19.450', under stone in retreat, collected at night, 8 September 2004, D. Kunz leg. (SMF, SD295, MM52).

Paratypes (7♂♂, 5♀♀)**: SOUTH AFRICA:** ***Gauteng Province*****:** 1♀, Pretoria, Baviaanspoort, under stones, 22 October 1988, M. Filmer leg. (PPRI 90/387); 1♀, Western Transvaal, 4 April 1987, H. Uys leg. (PPRI 88/354); ***Limpopo Province:*** 1♀, Roodeplaat, S 25˚36.052', E 28˚19.731', 1226 m, under stone in retreat, 13 July 2004, D. Kunz leg. (SMF, SD34, MM51); 1♀, Klein Kariba, S 24º50'59", E 28º20'20", 26 November 1996, A.V.D Berg leg. (PPRI 97/163). ***North West Province*****:** 1♂, Borakalalo Nature Reserve, label: **"**Buphuthatswana", S 25˚, E 27˚, October 1986, M. Filmer leg. (PPRI 87/720); 1♂, same data as previous (PPRI 87/75); 1♂, same data as previous, April 1986 (PPRI 87/131); 1♂, same data as previous, 20 November 1986 (PPRI 87/120); 1♂, Magaliesberg, May 1990, L. Prendini leg. (PPRI 91/1435); 1♂, Farms Elandsfontein/Buffelshoek, 37 km W of Thabazimbi, under stone in cocoon, area covered with dry leaves, 3 November 1979, M. Stiller leg. (PPRI 80/174), 1♂, Buffelspoort dam, Rustenburg

District, under dry bark of protea stump, 14 October 1979, M. Stiller leg. (PPRI 80/185); **BOTSWANA:** 1♀, Rooikop, 15 January 1994, A. Harington leg. (PPRI 2001/96).

Other material examined. SOUTH AFRICA: ***Limpopo Province*****:** 2♀♀, 6 juveniles, Makapan, S 23º 10' 60", E 28º 36' 0", (MNHN 16.851); 1♀, ***Northen Cape Province:*** Kimberley (MNHN 13.037).

Etymology. The species is named in honour of Dr Peter Jäger (SMF) in recognition of his scientific support of this project and also his invaluable help, motivation and encouragement; noun in genitive.

Diagnosis. Males differing from congeners by slender and curving ET pointing smoothly distad at its distal end (Fig. 29c) and dRTA with a ventral bulge (Figs 29a, b); epigyne with two large triangular processes at posterior margine of lateral lobes (LL) (Fig. 30a) [see also diagnosis for *jaegeri* species group above].

Description. Male (ranges: n=8, single measurement: holotype):

Measurements. Males medium sized; total length 13.5, prosoma length 5.7–6.3, prosoma width 4.7–5.8, anterior width of prosoma 2.5–3.1, opisthosoma length 7.8–8.0, opisthosoma width 4.0–4.7. Eye diameters: AME 0.40, ALE 0.30, PME 0.25, PLE 0.27; eye interdistances: AME-AME 0.20, AME-ALE 0.06, PME-PME 0.38, PME-PLE 0.44, AME-PME 0.28, ALE-PLE 0.24, clypeus height at AME 0.23, clypeus height at ALE 0.31. AME largest (>1.5 times larger than PME) (Fig. 29d).

Chelicerae. Chelicerae with 2 anterior and 4 or 5 posterior teeth (3 or 4 larger teeth followed by smaller ones), cheliceral furrow with median line of 3 to 5 intermarginal denticles (Fig. 29e).

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 6.9 [2.2, 1.1, 1.1, 2.5], I 24.2 [6.5, 2.1, 6.0, 6.5, 2.1], II 28.2 [7.8, 2.7, 7.3, 8.2, 2.2], III 22.5 [6.5, 2.3, 5.5, 6.2, 2.0], IV 25.0 [7.0, 2.3, 6.2, 7.4, 2.1].

Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323(423), IV 322; Patella I–IV 101; Tibia I–IV 2224; Metatarsus I–III 2024, IV 3036.

Palp. As in diagnosis with cymbium more than twice as long as tibia (Fig. 29b), dRTA beak-like and vRTA wide and triangular in ventral view (Fig. 29a); ET retrolaterad with distal tip bent at right angle (Fig. 29c).

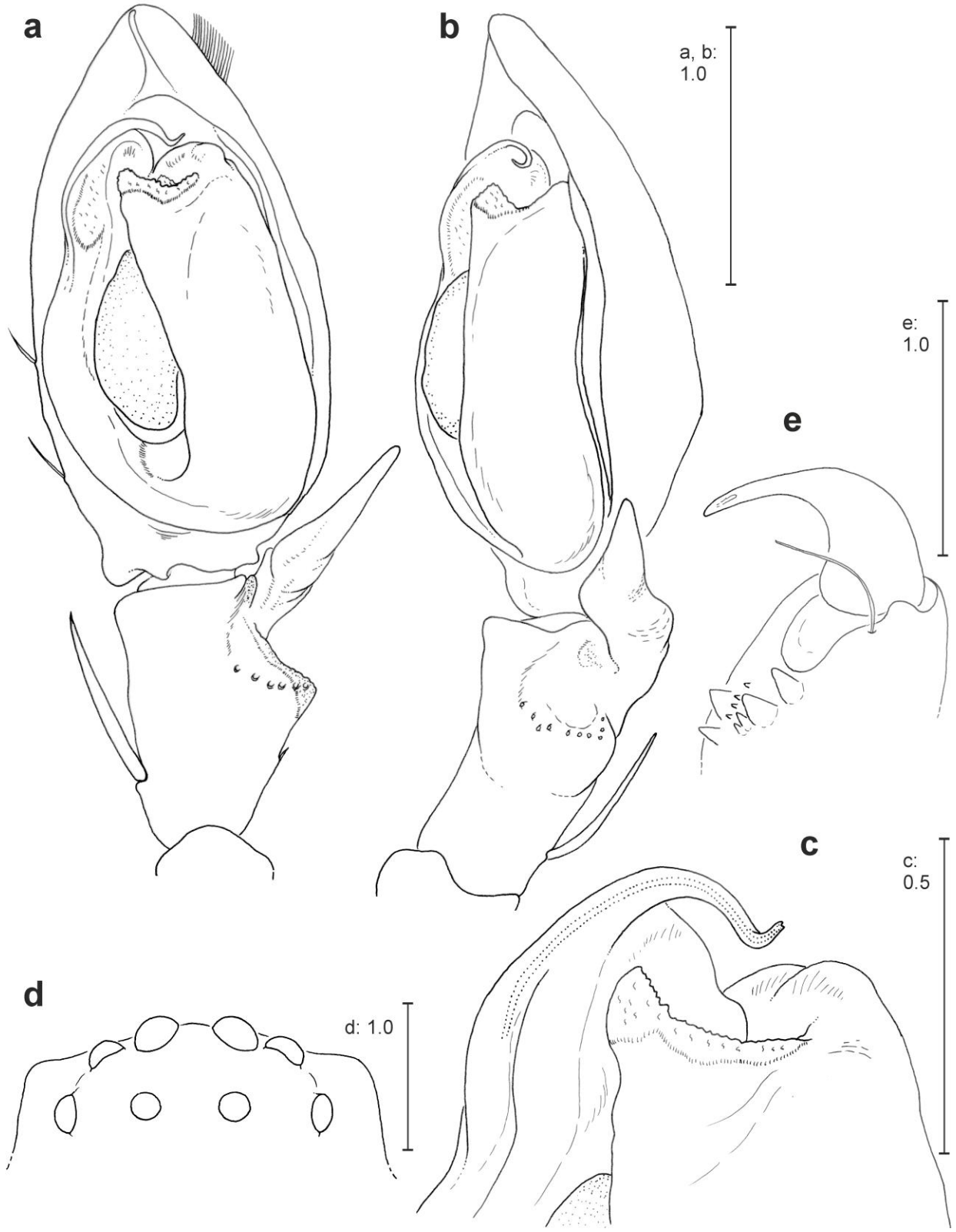

FIGURE 29. *Eusparassus jaegeri* **spec. nov.**, holotype male from South Africa: NE of Pretoria (SMF). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) left chelicera, ventral.

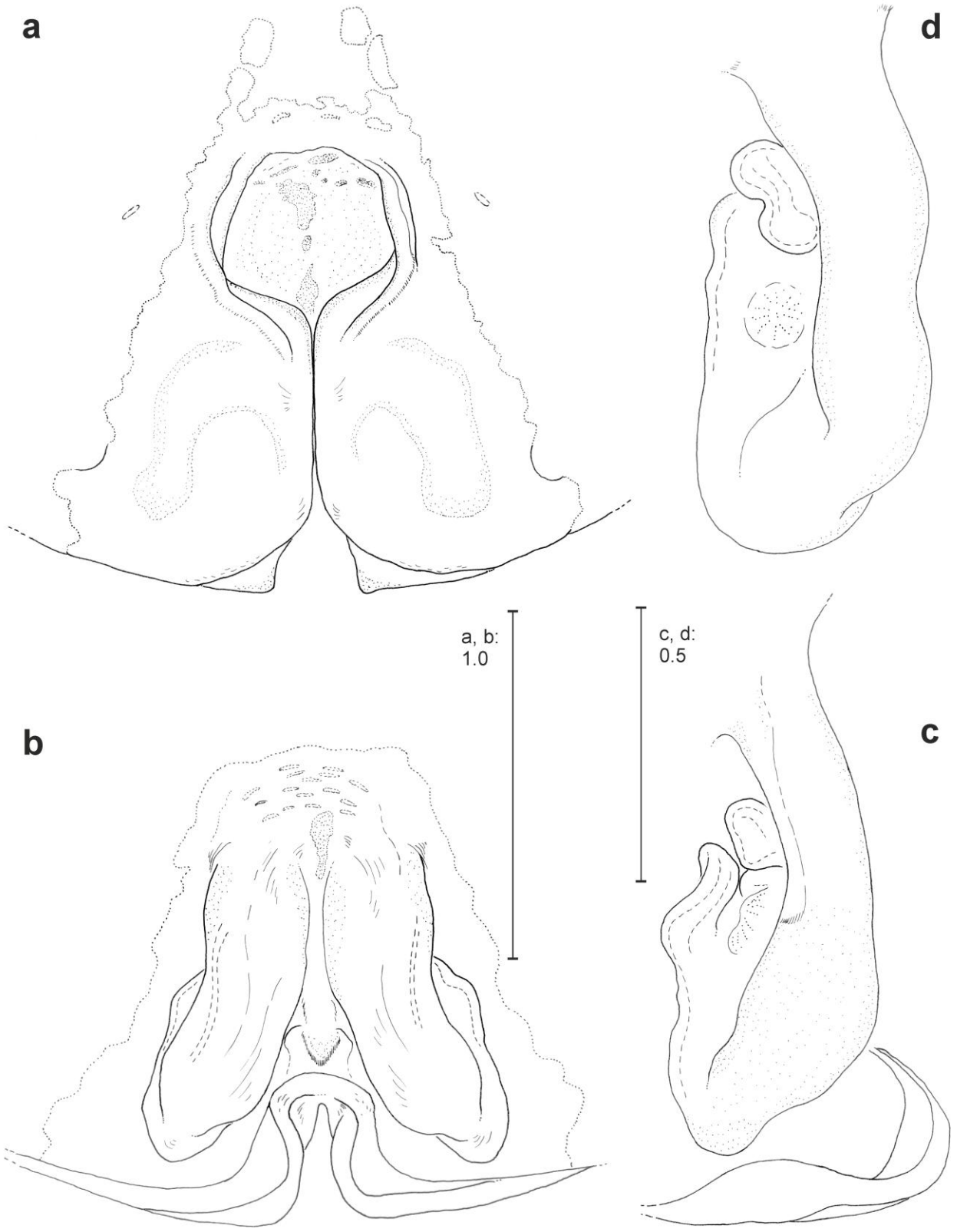

FIGURE 30. *Eusparassus jaegeri* **spec. nov.**: (a–c) paratype female from South Africa: NE of Pretoria (SMF); (d) female from South Africa Klein Kariba (PPRI). (a) epigyne, ventral; (b) vulva, dorsal; (c–d) left vulva, anterio-dorso-lateral.

Female (ranges: n=8, single measurement: paratype MM51):

Measurements. Medium sized; total length: 13.4–19.2, prosoma length 5.3–7.2, prosoma width 4.8–6.3, anterior width of prosoma 3.0–3.8, opisthosoma length 8.1–12.0, opisthosoma width 5.2–7.6. Eye diameters: AME 0.45, ALE 0.34, PME 0.31, PLE 0.35; eye interdistances: AME-AME 0.31, AME-ALE 0.10, PME-PME 0.51, PME-PLE 0.52, AME-PME 0.32, ALE-PLE 0.25, clypeus height at AME 0.34, clypeus height at ALE 0.40.

Chelicerae. Chelicerae dentition as in males. AME largest.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 7.4 [2.3, 1.2, 1.5, 2.4], I 24.7 [6.6, 3.3, 5.9, 6.8, 2.1], II 27.3 [7.5, 3.5, 6.6, 7.5, 2.2], III 22.9 [6.7, 2.8, 5.4, 6.0, 2.0], IV 25.1 [7.0, 2.8, 6.0, 7.2, 2.1].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321/322; Patella I–IV000/101; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis with MS enlarged, roundish and bulged outward ventrally (Fig. 30a), CD massive and dark in colour and fully to partially sclerotized (Fig. 30b), GP reduced in size and situated close to TL (Figs 30c, d).

Colouration. Body uniformly coloured with pale brownish gray hairs and a longitudinal darker strip on dorsal opisthosoma (Fig. 54a)

Known geographical distribution and habitat. South Africa: central region and Botswana collected from retreats under stones covered by bushes. One specimen sampled with an *Euprosthenops* sp. (Pisauridae).

Eusparassus schoemanae spec. nov.

Figs 31–33, 54b–c, 64b, e

Type material. Holotype: male, **SOUTH AFRICA:** ***Northern Cape Province*****:** Namaqualand, Lieliefontein, S 30.39˚, E 18.28˚, 1048 m, Malaise trap, 28 October 2001, (PH II6), C. Mayer leg. (ZMB 48505).

Paratypes (2♂♂, 2♀♀)**: SOUTH AFRICA:** ***Northern Cape Province*****:** 1♂, with same data as for holotype (SMF); 2♀♀, Kamiesberg Mountain, 22–24 km E of Kamieskroon, S 30˚ 18', E 18˚ 05', 4–5 November 1985, C. Griswold, J. Doyen & T.M. Griswold leg. (NMSA 20184); 1♀,

Farm Loeriesfontein, Aberdeen, Great Karroo, under stone, 1972–73, M. Stiller leg. (PPRI 80/194); **NAMIBIA:** ***Karas Region***: 1♂, Near Kodaspiek, 3 September 1992, S. Neser leg. (PPRI 92/543).

Other material examined. SOUTH AFRICA: ***Northern Cape Province:*** 4♀♀, Calvinia, 10 km N of Loeriesfontein, [S 30.58˚, E 19.26˚, 3152 m], 22 October 1990, L.N. Lotz leg. (BMSA 5490).

Etymology. The specific name is a patronyme in honour of Dr Ansie Dippenaar-Schoeman who promotes the arachnological science in Africa; noun in genitive case.

Diagnosis. Small-sized *Eusparassus* species. Male with diagnostic triangular ET and lobe of EM projecting behind base of conductor on tegulum (Figs 31a, c). Epigyne and MS elongated (Figs 32a, 33a); vulva with hump-like glandular process (Figs 32c, 33b) [see also diagnosis for *jaegeri* species group above].

Description. Male (ranges: n=3, single measurement: holotype):

Measurements. Small-sized species. Total length 10.4, prosoma length 4.6, prosoma width 3.8, anterior width of prosoma 2.1, opisthosoma length 5.8, opisthosoma width 3.5. Eye diameters: AME 0.38, ALE 0.25, PME 0.24, PLE 0.27; eye interdistances: AME-AME 0.17, AME-ALE 0.06, PME-PME 0.38, PME-PLE 0.25, AME-PME 0.20, ALE-PLE 0.12, clypeus height at AME 0.17, clypeus height at ALE 0.25. AME largest, other eyes subequal (Fig. 31d).

Chelicerae. Chelicerae with 2 anterior and 4 to 6 posterior teeth (3 or 4 larger teeth followed by smaller ones), cheliceral furrow with 2 to 5 intermarginal denticles close to anterior teeth (Fig. 31e).

Legs. Leg formula: II IV=I III. Measurements of palp and legs: Palp 6.0 [2.0, 0.8, 1.1, 2.1], I 22.4 [5.9, 2.3, 5.8, 6.4, 2.0], II 24.8 [6.7, 2.5, 6.5, 7.0, 2.1], III 20.3 [5.8, 2.1, 5.2, 5.5, 1.7], IV 22.5 [6.4, 2.2, 5.7, 6.2, 2.0].

Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323(422), IV 322(332); Patella I–IV 000/001; Tibia I–IV 2024/2124; Metatarsus I–III 2024, IV 3034/3036.

Palp. As in diagnosis with cymbium approximately twice as long as tibia (Fig. 31b); T and ST bulged and expanded, dRTA pointing distad and vRTA hump-like (Fig. 31a).

Female (ranges: n=7, single measurement: paratype MM 182):

Measurements. Small sized; total length: 8.5–10.2, prosoma length 4.5–5.5, prosoma width 4.0–4.7, anterior width of prosoma 2.3–2.7, opisthosoma length 7.0–9.3, opisthosoma width 4.2–5.8.

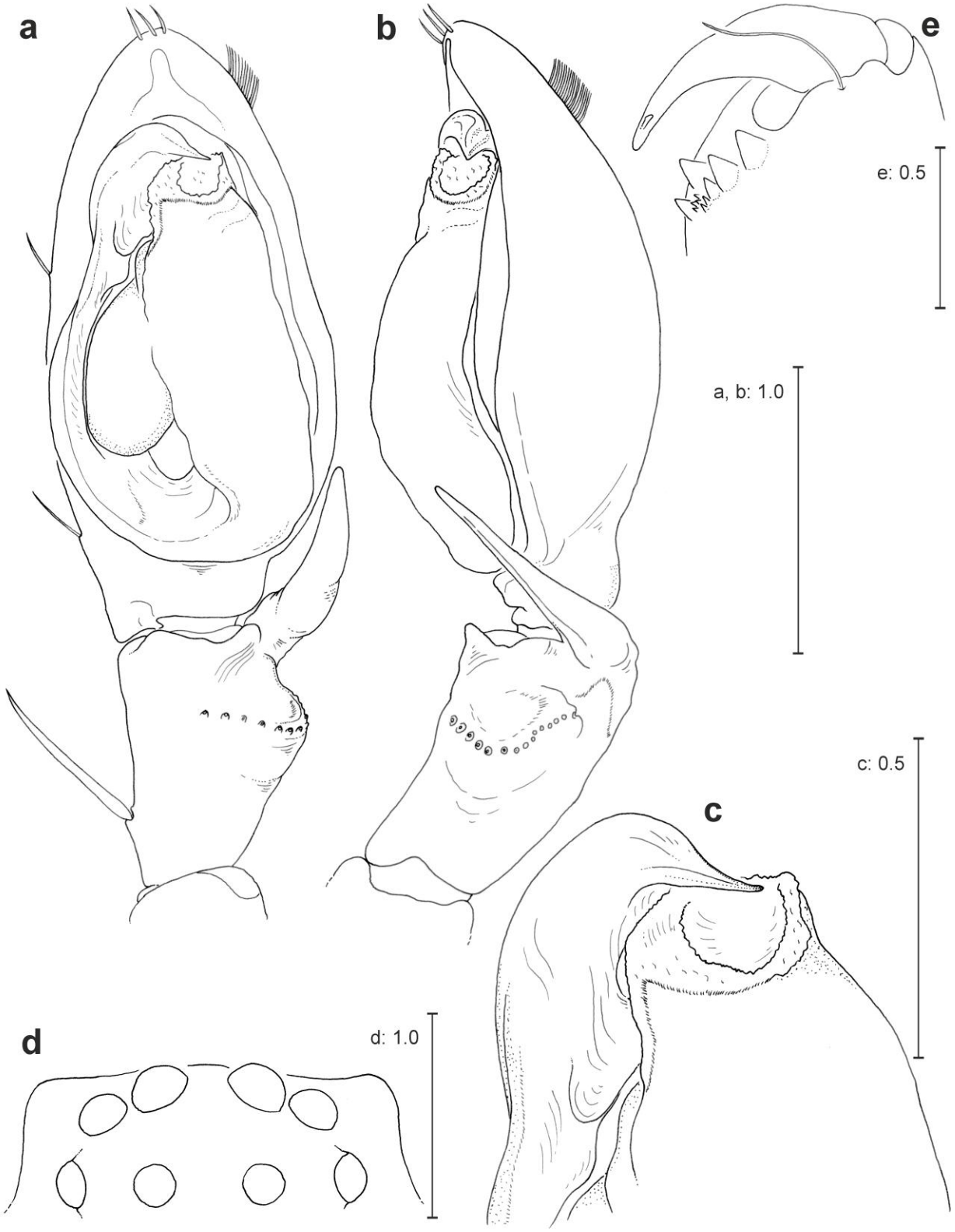

FIGURE 31. *Eusparassus schoemanae* **spec. nov.**, holotype male from South Africa: Namaqualand (ZMB). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) left chelicera, ventral.

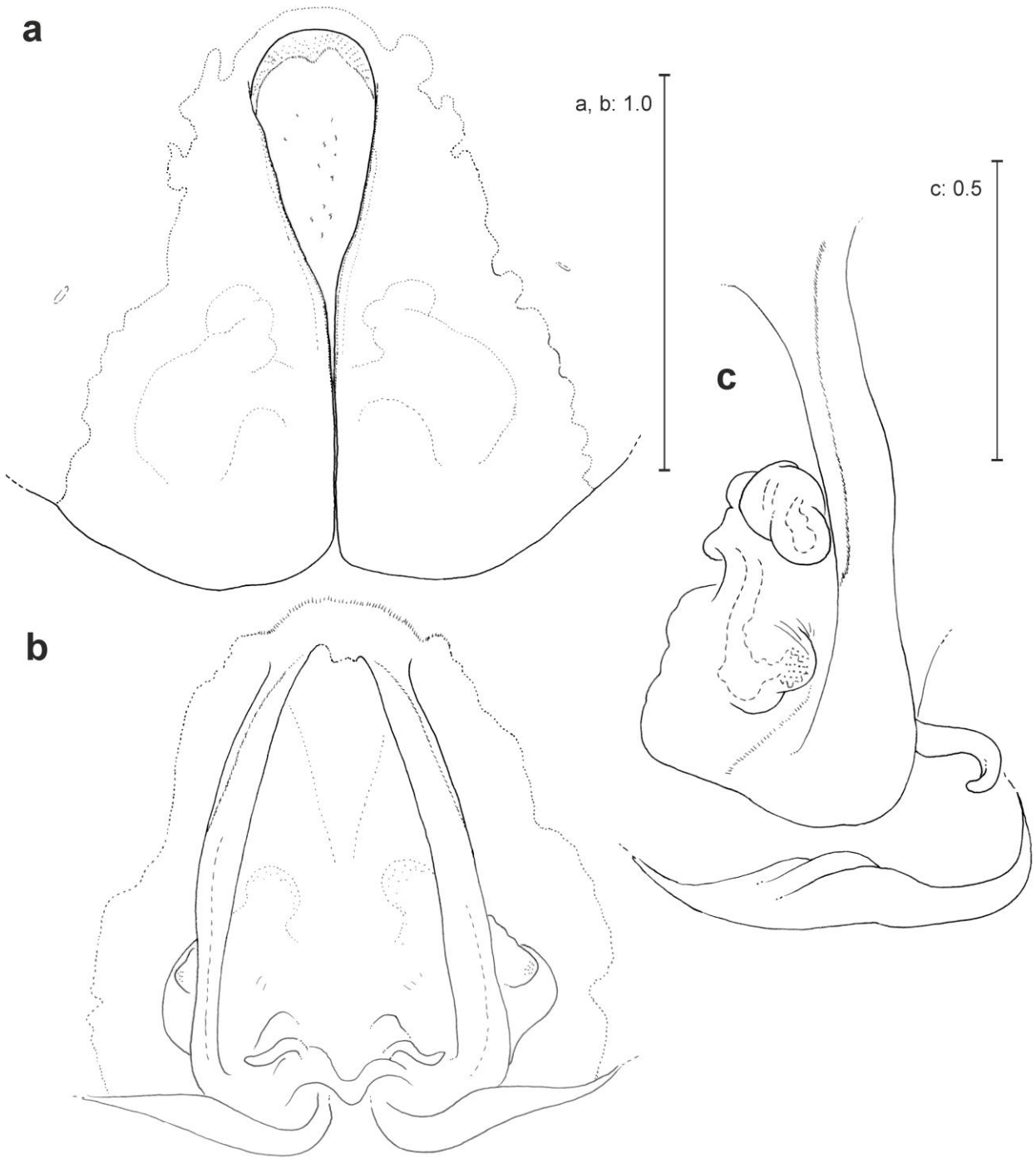

FIGURE 32. *Eusparassus schoemanae* **spec. nov.**, paratype female from South Africa: E of Kamieskroon (NMSA). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral.

Eye diameters: AME 0.37, ALE 0.30, PME 0.26, PLE 0.28; eye interdistances: AME-AME 0.26, AME-ALE 0.07, PME-PME 0.43, PME-PLE 0.45, AME-PME 0.28, ALE-PLE 0.23, clypeus height at AME 0.20, clypeus height at ALE 0.28.

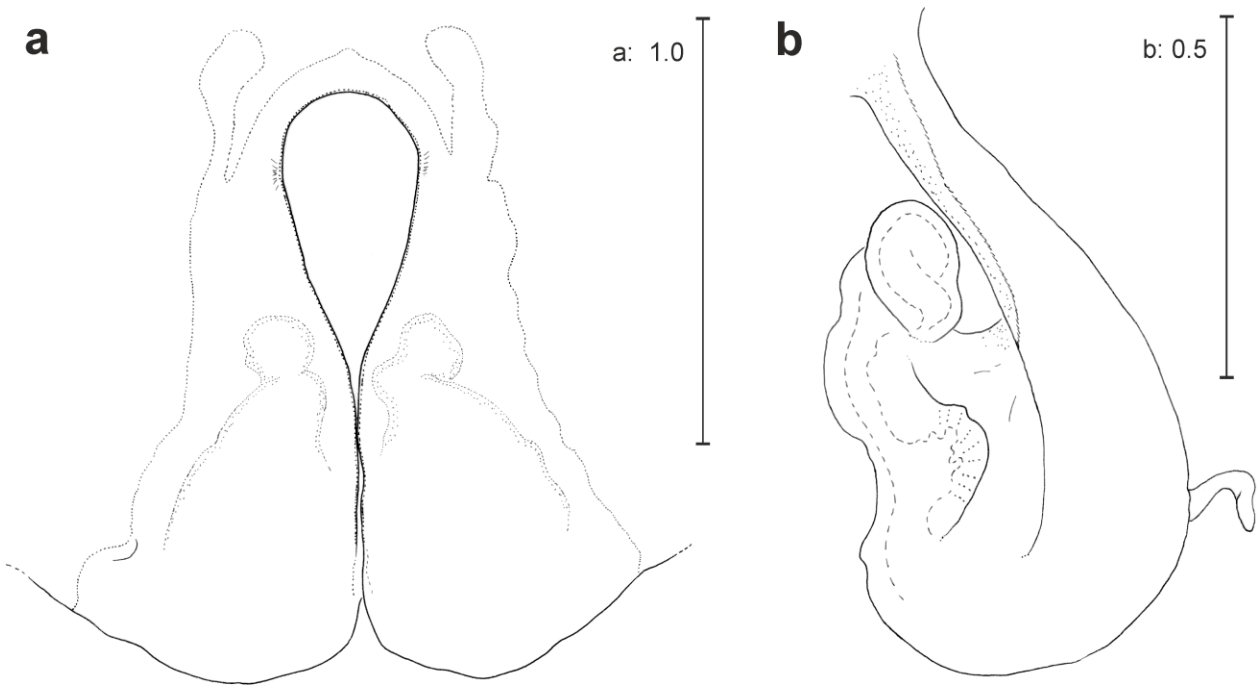

FIGURE 33. *Eusparassus schoemanae* **spec. nov.**, paratype female from South Africa: Aberdeen (NMSA). (a) epigyne, ventral; (b) left vulva, anterio-dorso-lateral.

Chelicerae. Chelicerae dentition as in males, sometimes with fewer intermarginal denticles.

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 6.6 [1.8, 1.0, 1.4, 2.4], I 19.4 [5.3, 2.5, 4.8, 5.4, 1.6], II 21.2 [6.1, 2.1, 5.3, 6.1, 1.6], III 17.3 [5.1, 2.0, 4.2, 4.5, 1.5], IV 19.4 [5.6, 2.1, 4.6, 5.5, 1.6].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321/322; Patella I–IV000/001; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis, epigyne with hyaline MS generally elongated (Figs 32a, 33a), anterior bands of epigynal field present (Fig. 33a), CD narrow and TL hidden behind MS dorsally (Fig. 32b).

Colouration [in ethanol]. Prosoma and legs uniformly yellowish brown, opisthosoma brownish gray dorsally with a line of small dark chevrons (Figs 54b–c).

Known geographical distribution and habitat. South Africa (Northern Cape) and Namibia (Fig. 71b); under stones at higher elevations in mountains.

Eusparassus borakalalo spec. nov.

Figs 34, 55c, 64g

Type material. Holotype: female, **SOUTH AFRICA: *Limpopo Province*:** Borakalalo Nature Reserve, Rust de Winter, S 25.15˚, E 28.29˚, in grass, April 1986, M. Filmer leg. (PPRI 87/137, MM65).

Paratype (1♀)**: SOUTH AFRICA: *Gauteng Province*:** 1♀, Johannesburg, October 1995, A. Harrington leg. (PPRI 2001/94, MM68).

Etymology. The species is named after the type locality; noun in apposition.

Diagnosis. This species is the only known member of the *jaegeri*-group whose EF is distinctly wider than long (Figs 34a, f) [see also diagnosis for *jaegeri* species group above].

Description Female (n=2) [holotype first with measurements of paratype in parenthesis]:

Measurements. Medium sized; total length 12.1, prosoma length 6.4 (5.7), prosoma width 5.7 (4.9), anterior width of prosoma 3.4 (3.1), opisthosoma length 9.3 (7.0), opisthosoma width 5.1 (4.5). Eye diameters: AME 0.41, ALE 0.30, PME 0.28, PLE 0.33; eye interdistances: AME-AME 0.27, AME-ALE 0.11, PME-PME 0.48, PME-PLE 0.50, AME-PME 0.25, ALE-PLE 0.23, clypeus height at AME 0.30, clypeus height at ALE 0.35. AME largest (~1.4 times larger), others subequal (Fig. 34e).

Chelicerae. Chelicerae with 2 anterior and 4 or 5 posterior teeth (2 or 3 larger teeth followed by smaller ones), cheliceral furrow with a median line of 8 to 10 intermarginal denticles (Fig. 34d).

Legs. Leg formula: II IV I III. Measurements of palp and legs: Palp 7.0 [2.1, 1.2, 1.5, 2.2], I 22.3 [5.9, 3.0, 5.3, 6.1, 2.0], II 24.9 [7.0, 3.0, 6.2, 6.7, 2.0], III 20.5 [5.7, 2.5, 4.8, 5.1, 1.8], IV 23.1 [6.1, 2.5, 6.1, 6.4, 2.0].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321(322); Patella I–IV 000; Tibia I–IV 0004/2024; Metatarsus I–III 2024, IV 3036/3034.

Epigyne/vulva. As in diagnosis with AMLL straight (Fig. 34a) or with bulge (Fig. 34f), posterior margin of LL expanded laterally (Fig. 34a); CD slender and in connection with membranous MS, TL visible in dorsal view (Fig. 34b); glandular pores restricted to small circular depression on vulva (Fig. 34c).

Colouration [in ethanol]. Yellowish brown, opisthosoma darker dorsally with a line of small dark chevrons (Fig. 55c).

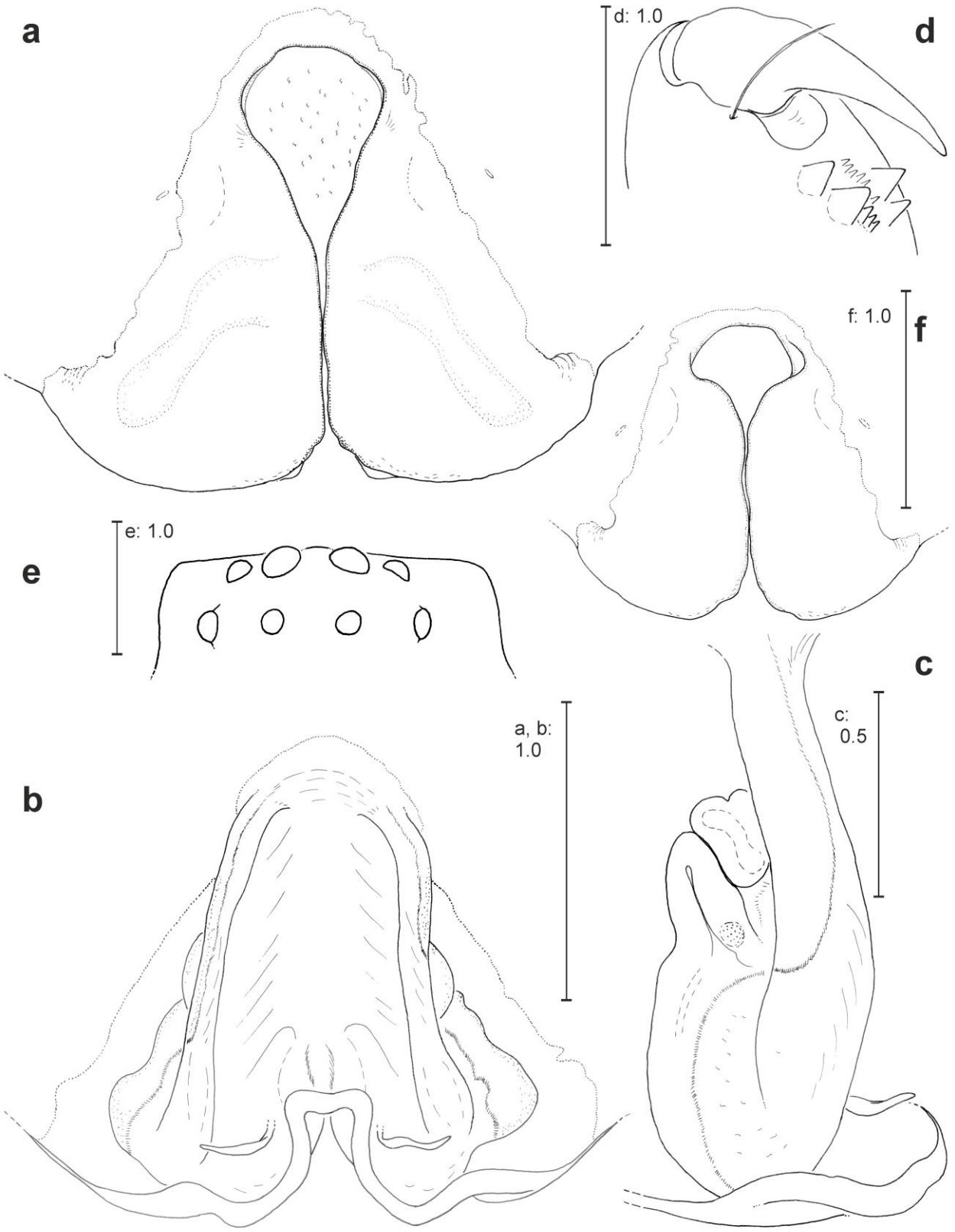

FIGURE 34. *Eusparassus borakalalo* **spec. nov.**, (a–e) holotype and (f) paratype female from South Africa: Borakalalo Natural Reserve. (a, f) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) right chelicera, ventral; (e) eye arrangement, dorsal.

Male. Unknown.

Known geographical distribution and habitat. South Africa (central), sympatric in some area with *E. jaegeri* **spec. nov.**, collected in grass.

Eusparassus jocquei spec. nov.

Figs 35–36, 55a–b, 64c, f

Type material. Holotype: male, **ZIMBABWE: *Matabeleland North Province*:** Bulawayo (S 20°8'60, E 28°34'60, 1351 m) [label: Rhodesia: Bulawayo], November 1964– January 1965, S. Bucklin leg., MM201 (MRAC 128093).

Paratypes: 5♂♂, 1♀ (MM202), 2 juveniles, with same data as for holotype (4♂♂, 1♀ MRAC; 1♂ SMF).

Other material examined. 1♀, "Ostafrika" [=East Africa] (potentially Tanzania, Mozambique, Rwanda or Burundi; see remarks below), December 1904, W. Triesler leg. (ZMB).

Etymology. The species is named in honour of Dr Rudy Jocqué (MRAC). The visit of the author to MRAC coincided with his retirement. The author would like to dedicate the name of this conspicuous species to him in recognition of his long time of productive arachnological research especially on African spiders; noun in genitive case.

Diagnosis. This is the only *Eusparassus* species whose male's dRTA is bifurcated at its distal end (Figs 35a, b) and female epigyne with MS clearly visible posteriorly (Fig. 36a) [see also diagnosis for *jaegeri* species group above].

Description. Male (ranges: n=6, single measurement: holotype):

Measurements. Males medium-sized. Total length 12.0–13.8, prosoma length 5.7–6.3, prosoma width 4.6–5.4, anterior width of prosoma 2.7–3.0, opisthosoma length 6.3–7.5, opisthosoma width 4.0. Eye diameters: AME 0.47, ALE 0.33, PME 0.31, PLE 0.34; eye interdistances: AME-AME 0.18, AME-ALE 0.08, PME-PME 0.42, PME-PLE 0.45, AME-PME 0.33, ALE-PLE 0.22, clypeus height at AME 0.23, clypeus height at ALE 0.37. AME largest, other eyes subequal (Fig. 35d).

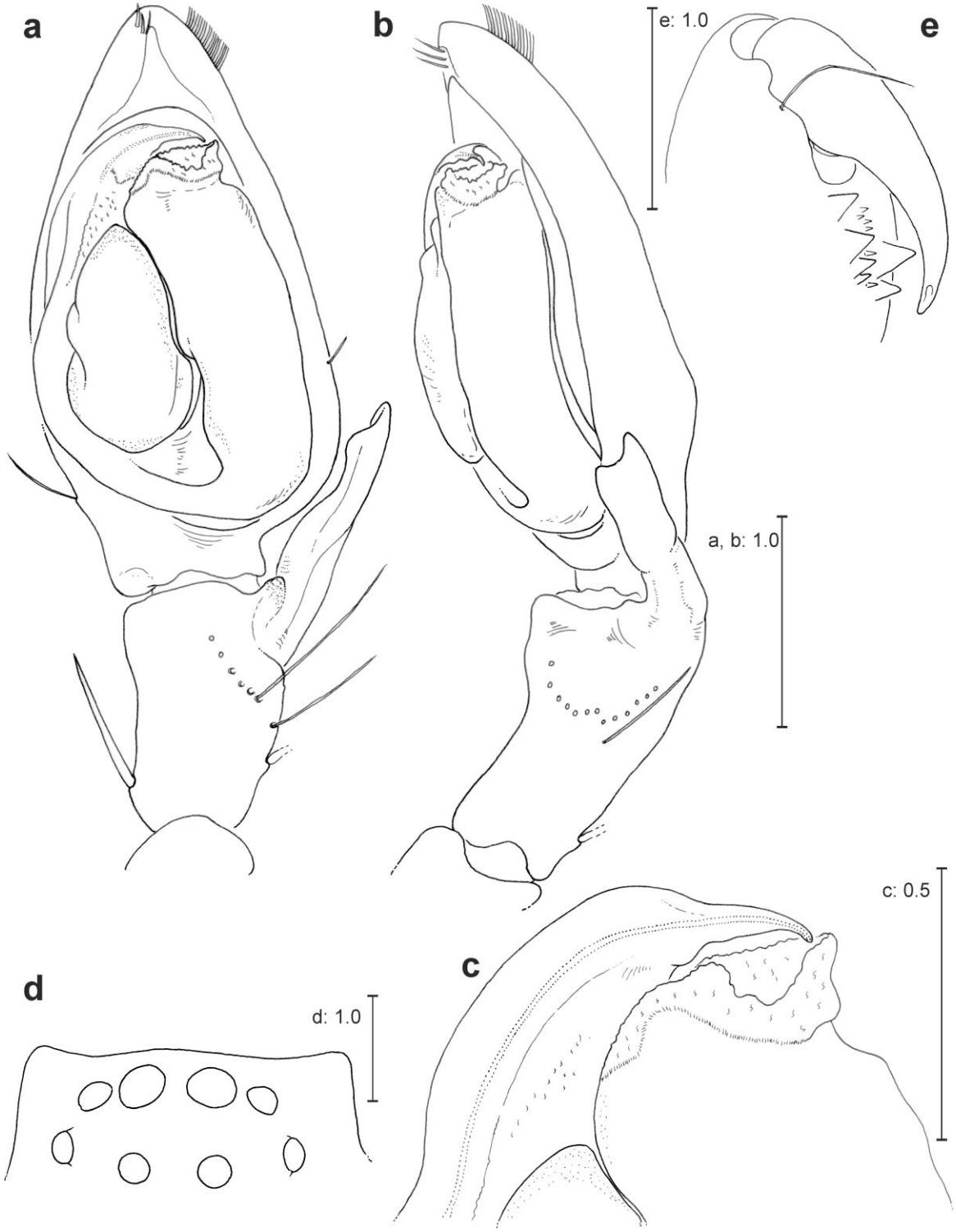

FIGURE 35. *Eusparassus jocquei* **spec. nov.**, holotype male from Zimbabwe: Bulawayo (MRAC) (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) right chelicera, ventral.

FIGURE 36. *Eusparassus jocquei* **spec. nov.**, paratype female from Zimbabwe: Bulawayo (MRAC). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral.

Chelicerae. Chelicerae with 2 anterior and 3 or 4 posterior teeth, cheliceral furrow with a line of 7 to 10 intermarginal denticles (Fig. 35e).

Legs. Leg formula: II I IV III. Measurements of palp and legs: Palp 8.3 [2.8, 1.2, 1.3, 3.0], I 29.8 [7.9, 3.1, 7.5, 8.7, 2.6], II 32.0 [8.7, 3.3, 8.3, 9.1, 2.6], III 26.8 [7.7, 2.8, 6.7, 7.4, 2.2], IV 29.1 [8.1, 2.7, 7.2, 8.7, 2.4].

Spination. Palp 131, 001, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 001/101; Tibia I–IV 2124/2224; Metatarsus I–III 2024, IV 3036.

Palp. As in diagnosis with weakly developed vRTA, ST huge and cymbium approximately twice as long as tibia (Figs 35a, b); ET wide and only distally narrowed, ET directed retrolaterad first and ending proximad at its distal end (Fig. 35c).

Female (n=2, single measurement: paratype):

Measurements. Medium sized. Total length 17.1; prosoma length 6.7, prosoma width 5.6, anterior width of prosoma 3.6, opisthosoma length 10.4, opisthosoma width 7.5. Eye diameters: AME 0.45, ALE 0.33, PME 0.31, PLE 0.33; eye interdistances: AME-AME 0.25, AME-ALE 0.13, PME-PME 0.45, PME-PLE 0.51, AME-PME 0.33, ALE-PLE 0.23, clypeus height at AME 0.35, clypeus height at ALE 0.45.

Chelicerae. Chelicerae dentition like as male.

Legs. Leg formula II I IV III. Measurements of palp and legs: Palp 7.5 [2.3, 1.1, 1.4, 2.7], I 23.7 [6.3, 2.9, 5.7, 6.7, 2.1], II 25.6 [7.0, 3.0, 6.2, 7.2, 2.2], III 20.0 [6.1, 2.2, 4.8, 5.3, 1.6], IV 22.3 [6.5, 2.5, 5.4, 6.3, 2.1].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321; Patella I–IV 000/001; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF nearly as wide as long; MS thoroughly visible between lateral lobes (Fig. 36a); MS folded and in connection with extra membranous parts forming an inverse pocket visible in dorsal view between CDs (Fig. 36b); glandular pores restricted to a small depression near TL (Fig. 36c).

Colouration [in ethanol]. Yellowish cream prosoma with dark brown dorsal opisthosoma decorated with a chevron pattern, ventral opisthosoma pale in colour (Figs 55a–b).

Remarks. The copulatory structures of *E. jocquei* **spec. nov.** are strikingly different from other members of *jaegeri* group including the bifurcated dRTA and the distinctly visible MS between LL. However, it contains all the diagnostic characters of *jaegeri* species group. A female was found in ZMB, with label information “Ostafrika” [=German for “East Africa”]. German East Africa used to be a German colony at the date of collecting (1904) which included what are now modern Tanzania, Rwanda, Mozambique and Burundi. Since the majority of the former German

colony currently comprises the modern countries Tanzania and Mozambique, the specimen was probably collected from one of these countries.

Known geographical distribution and habitat. Known from the type locality and probably Tanzania or Mozambique in Southeast Africa.

tuckeri species group

Diagnosis. Lacking intermarginal denticles in chelicerae (Figs 37e, 40e); female epigyne with AMLL fused together and encircling MS entirely (Figs 38a, 41a); male palps with an enlarged sub-tegulum (not as large as those of *jaegeri*-group) and very long embolus tip, embolus much longer relative to tegulum compared to other species groups; EM developed and forming a process covering ET partially (Figs 37a–c) to completely (Figs 40a–c).

Species composition. Two species: *E. tuckeri* **comb. nov.**, *E. educatus* **spec. nov.**

Distribution. South-west Africa: Namibia and Angola (Fig. 71b).

Eusparassus tuckeri (Lawrence, 1927) comb. nov.

Figs 37–39, 56b, 65a–b

Olios tuckeri Lawrence, 1927: 42, pl. 3, fig. 67 (description and illustration of male) [holotype ♂, examined]. **New combination**.

Olios furcatus Lawrence, 1927: 41, pl. 2, fig. 29 [syntype ♀ examined and designated as lectotype] [paralectotype ♂, undescribed genus] **New synonymy** (for justification see remarks).

Type material. Holotype of *Olios tuckeri* (designated by Lawrence 1927): male, **NAMIBIA: *Kunene Region***: Kunene River [label: Type, 1♂, Sparassidae, *Eusparassus tuckeri* lawr., South West Africa, Kunene R., c1712BC, R.F. Lawrence 1922, Shelf no. SAM/Aran 2639] (SAMC B7124); **Lectotype** of *Olios furcatus* (designated here): female, **NAMIBIA: *Kunene Region***: Kunene River [label: South West Africa, Kunene R. c 1712BC, March 1923, R.F. Lawrence, Acc.no. B6625, Shelf no. SAM/Aran 2427] (SAMC B6625).

Other material examined. NAMIBIA: ***Kunene Region*:** 1♂, Epupa Falls, DK 334, 22 February 2005, D. Kunz leg. (SMF); 1♂, 1♀, 1sub♀, 1 juvenile, Etosha National Park, Sprokieswoud, 19˚ 05' S, 15˚ 37' E, 10 October 1986, under stones, E. Griffin leg. (NMNW 40564); 1♀, Etosha Pan, 18˚ 50' S, 16˚ 20' E, 4 March 1969, B. Lamoral & R. Day leg. (NMSA 12519); 2♂♂, Etosha National Park: Halali, 19˚ 01' S, 16˚ 29' E, 16 December 1993, B.M. Ullig leg. (ZMB); 2♀♀, SW of Windhoek, December 1929, R. Tucker leg.(SAMC 5162). ***Oshikoto Region*:** 2♀♀, Tsumeb, 1920, E. Koodig leg. (SAMC 4810). ***Otjozondjupa Region*:** 2♀♀, Road B8, S 19˚16.962', E 18˚26.935', 1233 m, 19 October 2009, M. Forman leg. (SD 802 & 803, SMF); 2♀♀, Grootfontein, 1919, R. M. Lightfoot leg. (SAMC 4625); **ANGOLA:** ***Namibe Province*:** 1♂, Parque Nacional de Iona (Iona National Park), 31 km S of Tombor, S 16˚20'36.1", E 12˚26'21.1", 241m, 11 January 2006, under stones, dense silk retreats, T. & C. Bird leg. (NMNW 45826); 1♀, 30–45 km NE of Namibe, 14˚ 55' 25.6" S, 12˚ 22' 11.7" E, 316 m, 12 January 2006, TB 06/36, T. & C. Bird leg. (NMNW 45828); 1♀, Parque Nacional de Iona, 52 km NW of Espinheira, S 17˚04'26.9", E 12˚03'40.9", 564 m, 10 January 2006, dense silk retreats under stones, T. & C. Bird leg. (NMNW 45829); 1♀, Iona district, "Espaniera" (Espinheira), mountainous desert on grassy plain in between, 14 July 1996, R. Harris leg. (PPRI 96/595).

Diagnosis. Males easily distinguishable by long and slender ET directed proximad and by folded process of EM extending beyond ET retrolaterally (Figs 37a–c); females vulva with simple and straight CD and TL (Figs 38b–c, 39c) [compared to *E. educatus* **spec. nov.** with complicated vulvas] [see also diagnosis for *tuckeri* species group above].

Description. Male (ranges: n=6, single measurement: holotype):

Measurements (holotype first). Total length 8.7–10.1, prosoma length 4.2–5.1, prosoma width 3.5–4.7, anterior width of prosoma 1.8–2.6, opisthosoma length 4.5–5.0, opisthosoma width 3.0–4.1. Eye diameters: AME 0.32, ALE 0.25, PME 0.23, PLE 0.27. Eye interdistances: AME-AME 0.20, AME-ALE 0.06, PME-PME 0.36, PME-PLE 0.30, AME-PME 0.24, ALE-PLE 0.20, clypeus height at AME 0.09, clypeus height at ALE 0.17. AME largest, ALE and PME subequal and smaller than PLE (Fig. 37d).

Chelicerae. Chelicerae with 2 anterior and 3 or 4 posterior teeth; cheliceral furrow without intermarginal denticles (Fig. 37e).

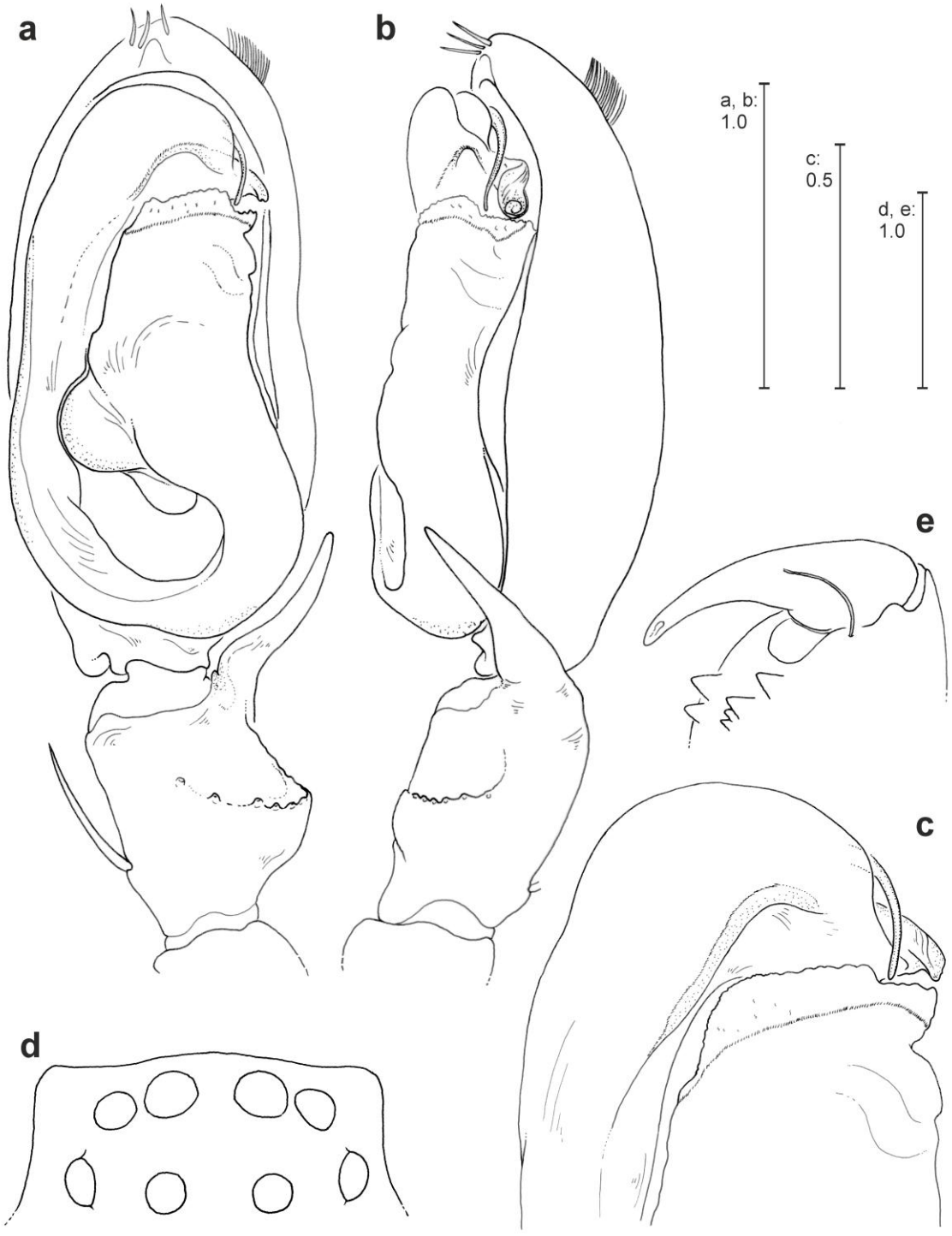

FIGURE 37. *Eusparassus tuckeri* (Lawrence, 1927) **comb. nov.**, holotype male from Namibia: Kunene Riverside (SAMC). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) right chelicera, ventral.

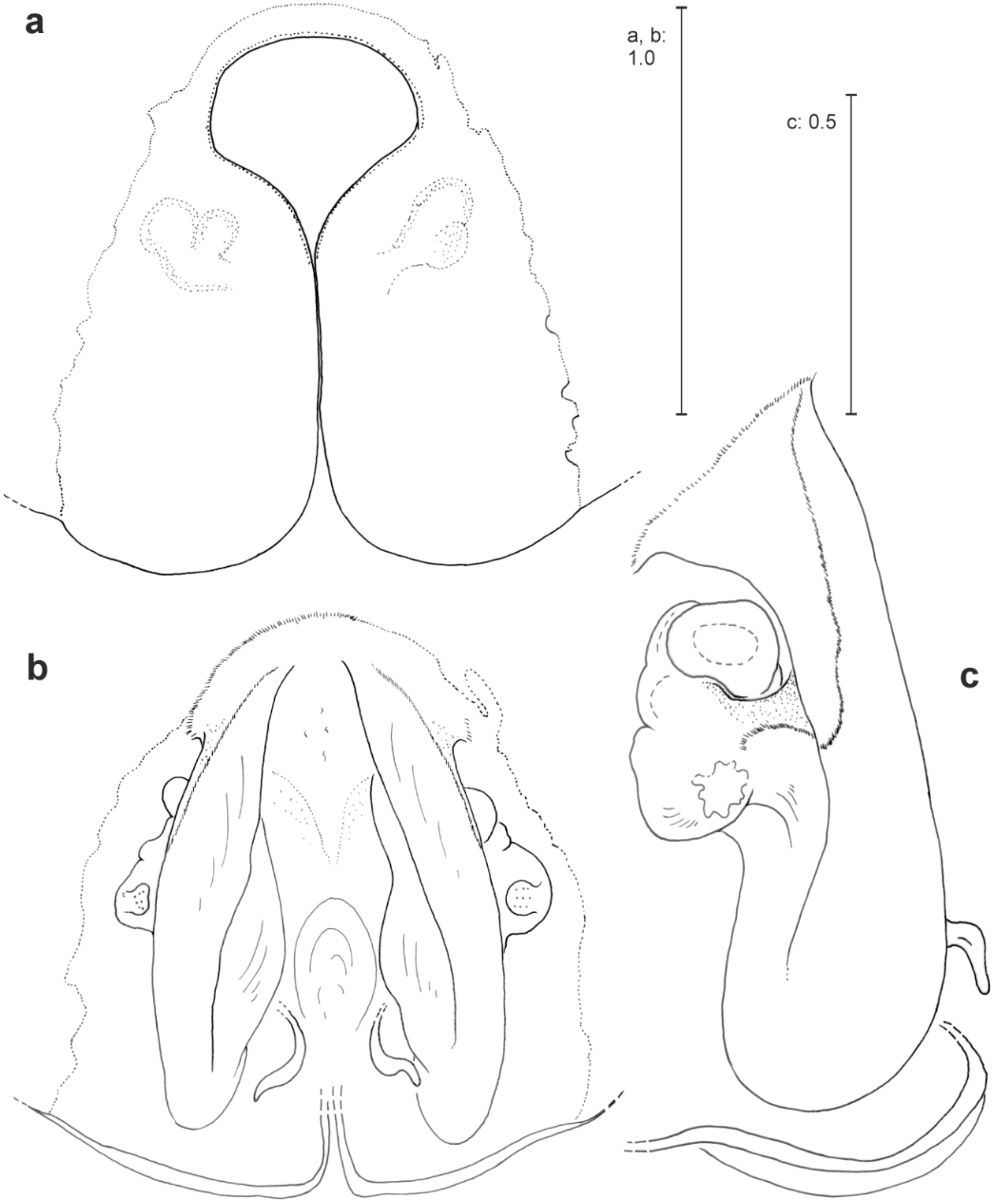

FIGURE 38. *Eusparassus tuckeri* (Lawrence, 1927) **comb. nov.**, female from Namibia: Kunene Riverside [lectotype female of "*Olios furcatus*" (SAMC)]. (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral.

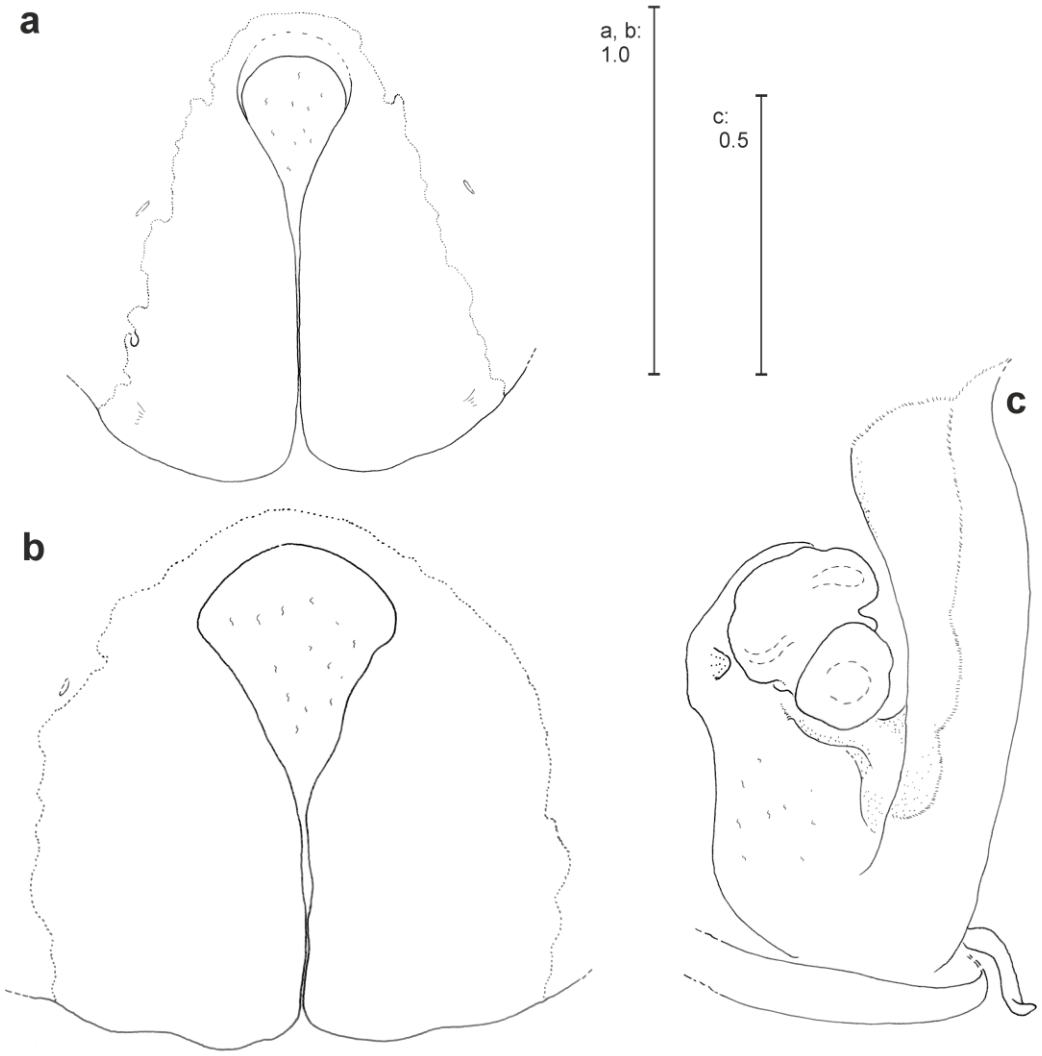

FIGURE 39. *Eusparassus tuckeri* (Lawrence, 1927) **comb. nov.**, females from Angola (NMNW). (a, b) epigyne, ventral; (c) left vulva, anterio-dorso-lateral.

Legs. Leg formula: II IV=I III. Measurements of palp and legs: Palp 5.5 [1.7, 0.8, 0.9, 2.1], I 19.4 [5.5, 1.9, 5.1, 5.3, 1.6], II 23.2 [6.3, 2.2, 6.1, 6.7, 1.9], III 17.1 [5.0, 1.7, 4.1, 4.5, 1.8], IV 19.4 [5.5, 1.7, 4.9, 5.7, 1.6].

Spination. Palp 131, 001; Legs: Femur I–III 323, IV 322; Patella I–IV 101; Tibia I–IV 2124/2224; Metatarsus I–III 2024, IV 3034.

Palp. As in diagnosis with cymbium ~2.5 times longer than tibia; dRTA shortened and vRTA hump-like (Figs 37a, b).

Female (ranges: n=14, single measurement: lectotype):

Measurements (lectotype first). Total length: 12.2–14.3 prosoma length 4.6–6.1, prosoma width 3.9–5.0, anterior width of prosoma 3.0–3.3, opisthosoma length 7.6–8.2, opisthosoma width 4.0–5.2. Eye diameters: AME 0.36, ALE 0.26, PME 0.25, PLE 0.31; eye interdistances: AME-AME 0.24, AME-ALE 0.05, PME-PME 0.42, PME-PLE 0.43, AME-PME 0.21, ALE-PLE 0.17, clypeus AME 0.15, clypeus ALE 0.20.

Chelicerae. Chelicerae with 2 anterior and 3 posterior teeth, cheliceral furrow with intermarginal denticles; one bristle at distal end of cheliceral basal segment.

Legs. Leg formula: II IV=I III. Measurements of palp and legs: Palp 5.4 [1.4, 0.7, 1.0, 2.3], I 16.5 [4.7, 2.1, 4.1, 4.2, 1.4], II 19.1 [5.4, 2.3, 4.8, 5.1, 1.5], III 14.0 [4.2, 1.7, 3.3, 3.4, 1.4], IV 16.9 [4.7, 2.2, 4.0, 4.6, 1.4].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321/322; Patella I–IV 000/001; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3034.

Epigyne/vulva. As in diagnosis with EF slightly longer than wide (Fig. 38a), but in some specimens clearly longer than wide (Figs 39a, b); AMLL arch-shaped and LL enlarged laterally (Figs 38a, 39a, b); vulva with part of glandular pores shifted close to TL (Figs 38b, c; 39c).

Colouration [in ethanol]. Yellowish brown with uniform body colour in prosoma and legs; dorsal opisthosoma with a darker band and surrounding dark patches (Fig. 56b).

Remarks. The type specimens were collected during the museum (SAMC) expedition to Kunene River in 1923. Lawrence (1927) described male and female of a single species under two different specific names. He classified them in the genus *Olios*. At that time, usage of the generic names *Eusparassus* and *Olios* was a subject of disputes, as the genera were not explicitly diagnosed. Simon (1932) was the first reviewer who distinguished between the genera *Olios* and *Eusparassus* (for more details see Moradmand and Jäger 2012b). However, this problem existed until recently as these two genera are very similar in terms of somatic characters and many transfers have been proposed (Moradmand & Jäger 2012a). Lawrence (1927) found two different male morphs and one female morph from the same locality, Kunene River. He described a male under the name *tuckeri* using a single male specimen. For some unexplained reason he described the female of *tuckeri* under the name *furcatus* along with a different male. This strange male (Lawrence 1927: fig. 68) belongs to a different, undescribed genus of Eusparassinae. According to the original description by Lawrence (1927), specific name *furcatus* is clearly assigned to the female. There are two main reasons for this judgment: first, Lawrence (1927) didnot list the accession number of the male (SAMC B6751) in the description, second he gave differential

diagnosis just for the female. Thus, *O. furcatus* sensu Lawrence, 1927 is explicitly the female. Accordingly, the female and male of *O. furcatus* are designated as lectotype and paralectotype, respectively. The female (lectotype of *Olios furcatus*) was misidentified by Lawrence and is clearly the conspecific female of *E. tuckeri* **comb. nov.** Finding of several sympatric males and females confirms this decision. Consequently, *O. furcatus* is proposed to be the junior synonym of *E. tuckeri* **comb. nov.** The paralectotype male of *Olios furcatus* resembles the genus *Eusparassus* in many somatic and genital characters but belongs to an undescribed genus. The vial of these specimens contained several male and also a female with a pre-epigyne, this female was probably overlooked by Lawrence.

Known geographical distribution and habitat. Northern Namibia and southern Angola (new country record) (Fig. 71b).

Eusparassus educatus spec. nov.

Figs 40–41, 56a, 65c–d

Type material. Holotype: male, **NAMIBIA: *Kunene Region*:** NE of Juriesdraai, Palmwag Lodge, under roof, S 19˚53.246', E 13˚56.203', 3 March 2005, DK 378, D. Kunz leg. (SMF).

Paratypes (4♂♂, 5♀♀)**: NAMIBIA: *Kunene Region*:** 1♂, campsite Warmquelle, under roof, S 19˚8.299', E 13˚48.830', 2 March 2005, DK376, D. Kunz leg. (SMF); 1♂, campsite Warmquelle, under roof, S 19˚ 8.299', E 13˚ 48.830', 3 March 2005, (DK 377, SD 341), D. Kunz leg. (SMF); 1♂, 2♀♀, Epupa Falls, S 17˚0.122', E 13˚14.714', 23 March 2005, D. Kunz leg. (SMF, 1♂, DK 337, SD 530, 1♀, DK336, SD332). ***Karasburg District:*** 1♂, Farm Augurabis 109, Gaapriver, S 27˚27'04.0", E 17˚42'18.9", 556 m, 25 August 2005, TB 05/174, EduVentures 7th Expedition in Fish River Canyon (NMNW 47510). ***Erongo Region*:** 1♀, Brandberg, Hungarob River side, S 21˚13.25', E 14˚31.03', 700 m, Pitfall row 2, 27 April 2000, K. Meakin leg. (NMNW 45421); 1♀, Brandberg, Numas Plateau (NMNW 35237); 1♀, N of Keetmanshoop, W. 1910–11, Kramer leg., Dr Werner ded. 28 August 1912 (ZMH).

Etymology. The specific name "educatus" is a Latin term (adjective) meaning "to train" or "to bring up a child". It referrs to "the EduVentures Programme", an educational program by NMNW aiming to explore and collect the biodiversity data within the remote areas of Namibia

and educating children who have in most cases disadvantaged lives. One paratype male was collected during "the EduVentures 7th Expedition" by these children. This new species is the first species described from their material and named to promote this educational project and support these children.

Diagnosis. This unique species can be easily diagnosed by strongly elongated palpal structures, especially the slender embolus, which is covered by the similar long EM (Figs 40a–c, 41d); female vulva is uniquely coiled and twisted and has an extra small glandular process (Figs 41b, c) [see also diagnosis for *tuckeri* species group above].

Description. Male (ranges: n=5, single measurement: holotype):

Measurements (holotype first). Males medium-sized. Total length 11.1–16.3, prosoma length 6.0–8.2, prosoma width 5.4–6.8, anterior width of prosoma 2.9–3.5, opisthosoma length 5.1–8.1, opisthosoma width 2.3–5.5. Eye diameters: AME 0.52, ALE 0.48, PME 0.42, PLE 0.51; eye interdistances: AME-AME 0.20, AME-ALE 0.03, PME-PME 0.43, PME-PLE 0.53, AME-PME 0.41, ALE-PLE 0.28, clypeus height at AME 0.37, clypeus height at ALE 0.48. AME and PLE approximately equal (Fig. 40d).

Chelicerae. Chelicerae with 2 anterior and 3 to 5 posterior teeth, cheliceral furrow without intermarginal denticles (Fig. 40e).

Legs. Leg formula: II I IV III. Measurements of palp and legs: Palp 11.3 [3.6, 1.3, 2.1, 4.3], I 36.0[10.0, 4.4, 9.7, 9.8, 2.1], II 41.5 [11.6, 4.7, 11.7, 10.8, 2.7], III 32.4 [9.8, 4.0, 8.6, 7.9, 2.1], IV 34.2 [10.0, 3.7, 9.1, 9.3, 2.1].

Spination. Palp 131, 000/001, 1111; Legs: Femur I–III 323, IV 322; Patella I–IV 001/101; Tibia I–IV 2124/2224; Metatarsus I–III 2024, IV 3034/3036.

Palp. As in diagnosis with cymbium approximately 2.5 times longer than tibia; dRTA very slim, vRTA rounded and not well developed; embolus very narrow, covered by hyaline and folded embolus membrane (EM) (Figs 40a–c), E and EM loosely connected (Fig. 41d).

Female (ranges: n=5, single measurement: paratype MM 52):

Measurements. Medium-sized; total length 16.7–19.0, prosoma length 8.1–8.5, prosoma width 6.8–7.4, anterior width of prosoma 3.8–4.3, opisthosoma length 8.6–10.5, opisthosoma width 5.0–7.5. Eye diameters: AME 0.48, ALE 0.50, PME 0.44, PLE 0.56; eye interdistances: AME-AME 0.24, AME-ALE 0.02, PME-PME 0.50, PME-PLE 0.45, AME-PME 0.46, ALE-PLE 0.28, clypeus height at AME 0.38, clypeus height at ALE 0.50.

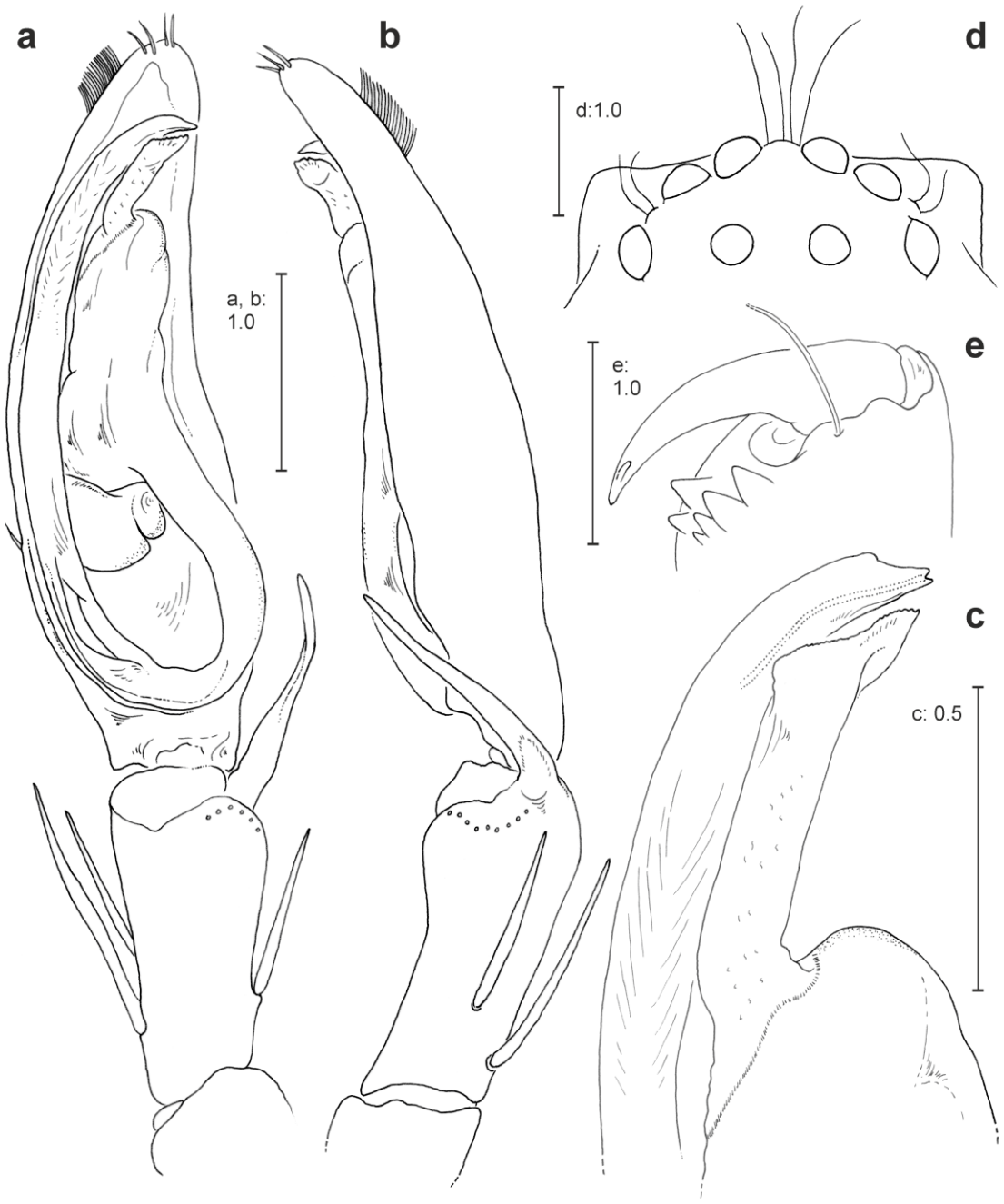

FIGURE 40. *Eusparassus educatus* **spec. nov.**, holotype male from Namibia: NE of Juriesdraai (SMF). (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) right chelicera, ventral.

Chelicerae. Chelicerae with 2 anterior and 3 to 5 posterior teeth, cheliceral furrow without intermarginal denticles.

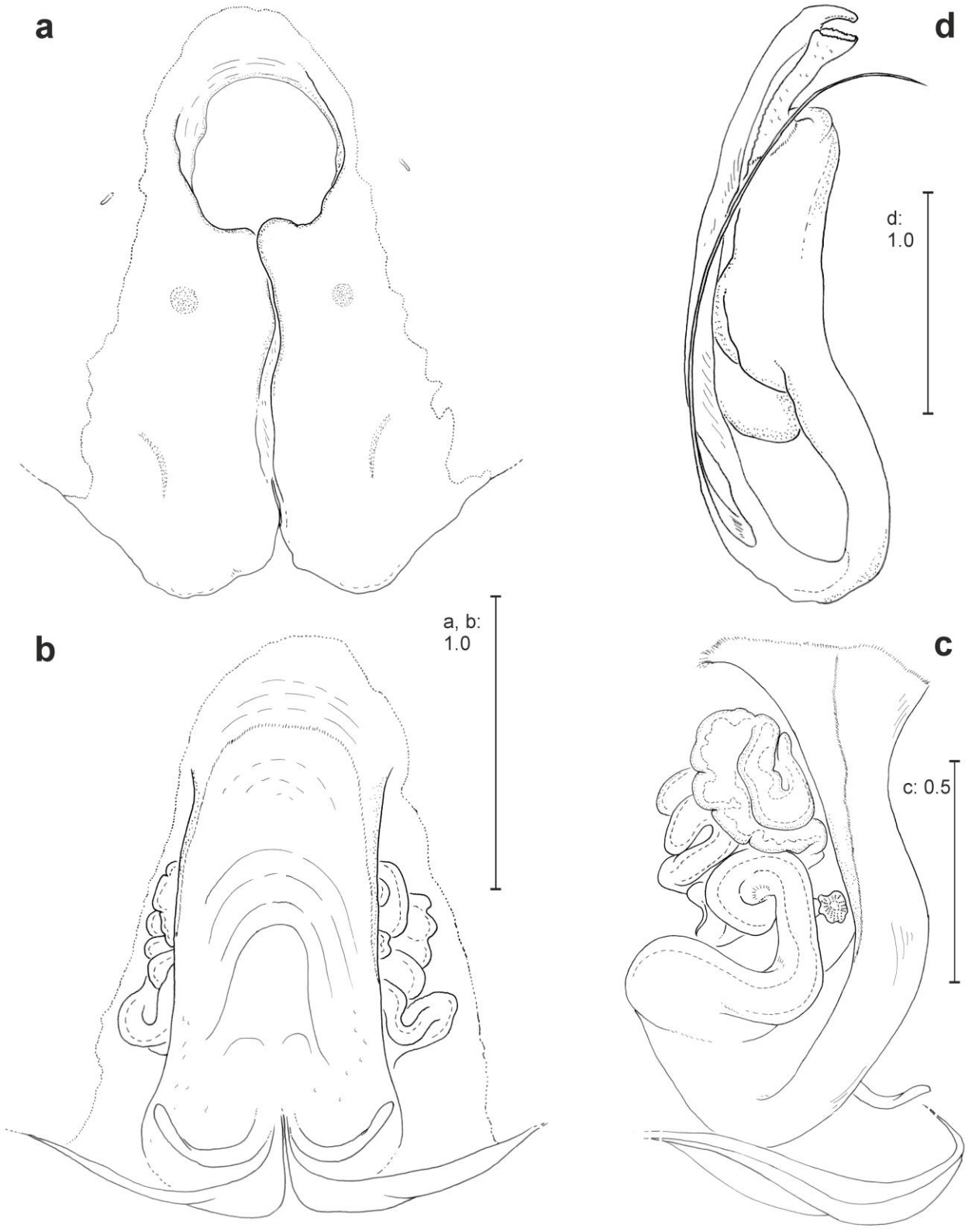

FIGURE 41. *Eusparassus educatus* **spec. nov.**, (a–c) paratypes from Namibia: Epupa Falls (SMF). (a) epigyne, ventral; (b) vulva, dorsal; (c) left vulva, anterio-dorso-lateral; (d) male's bulbus with separated embolus from embolic membrane, ventral.

Legs. Leg formula: II I IV III. Measurements of palp and legs: Palp 8.3 [2.5, 1.2, 1.3, 3.3], I 26.5 [7.3, 3.3, 7.1, 7.2, 1.6], II 28.5 [8.3, 3.4, 7.8, 7.3, 1.7], III 23.5 [7.1, 3.0, 6.1, 5.8, 1.5], IV 24.8 [7.3, 2.7, 6.5, 6.7, 1.6].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 322; Patella I–II 000, III–IV 001; Tibia I–IV 2024; Metatarsus I–III 2024, IV 3036.

Epigyne/vulva. As in diagnosis with EF longer than wide (Fig. 41a), MS hyaline and connected to CD in dorsal view (Fig. 41b); vulva coiled in series of complex loops (Fig. 41c)

Colouration. Yellowish cream with dark black marks on prosoma and dorsal opisthosoma, legs distinctly with strong black bands (Fig. 56a).

Known geographical distribution and habitat. Relatively widely distributed throughout Namibia, collected from desert areas, some specimens under roofs of buildings.

doriae species group

Diagnosis. Chelicerae without intermarginal denticles; ventral opisthosoma pale in colour (Fig. 58b); ST small in size and located behind EM (e.g. Fig. 67a); AMLL of epigyne not fused anteriorly (e.g. Fig. 67b); GP present.

Species composition. Seven species: *Eusparassus doriae* (Simon, 1874); *E. oculatus* (Kroneberg, 1875); *E. potanini* (Simon, 1895); *E. maynardi* (Pocock, 1901); *E. kronebergi* Denis, 1958; *E. fuscimanus* Denis, 1958 and *E. mesopotamicus* Moradmand and Jäger, 2012 (for full descriptions, see chapter 3.1: Moradmand & Jäger 2012a).

D**istribution.** From the Middle East to Central and parts of South Asia (Fig. 72a).

Species with unclear group affiliation

The following three species, *Eusparassus xerxes* (Pocock, 1901), *E. pontii* Caporiacco, 1935 and *Cercetius perezi* Simon, 1902 cannot be placed in the species groups recognized above. They show a transition in character states. *Eusparassus pontii* is closely allied to the members of the *doriae* group but differ from them by having a distinct dark marking on the ventral opisthosoma (Fig. 56f). *Eusparassus pontii* is also similar to *E. xerxes* (presence of ventral opisthosoma marking) but differs by having a single bristle instead of four at the basal segment of the

chelicerae. This species is probably derived from the members of the *doriae* group in the Himalayas. For full description of *E. pontii*, see Moradmand & Jäger 2012a. The distribution of these three species is shown in Fig. 72b.

Eusparassus xerxes (Pocock, 1901)

Figs 56c–d, 66c–d

Sparassus xerxes Pocock, 1901: 489–490 (description of male and female; syntypes, NHM, examined).
Olios xerxes (Pocock). Gravely 1931: 240–241, figs 5A, 6A (transfer); Sethi and Tikader 1988: 35, figs 157–162.
Eusparassus xerxes (Pocock). Moradmand and Jäger 2012a: 2481, figs 19, 20, 23B (transfer; redescription and illustration of male and female syntypes).

Type material: Syntypes (designated by Pocock 1901)**:** 3 ♂♂, 1 ♀, 1 immatures, **IRAN: *Bushehr Province***: 1 ♂, 1 ♀, 1 juvenile, Bushehr (sub Bushier), F.W. Townsend leg. (NHM 1882.109); 1 ♂, **PAKISTAN: *Baluchistan Province***: Ormara, Makran Coast, F.W. Townsend leg. (NHM 1899.10.6.7); 1 ♂, Ormara, Makran Coast, F.W. Townsend leg. (NHM 0.5.6.20).
Material examined. UNITED ARAB EMIRATES: *Ajman*: 1♂, S of Al Manamah, Wadi Siji, 1995, Ziegler leg. (SMF).

Remarks. This is the first record of *E. xerxes* from the Arabian Peninsula. According to the distribution range of *E. xerxes*, it occurs along the Northern strip of the Persian Gulf in Iran to the Makran Coast and central parts of Pakistan (Fig. 72b). However, it was not surprising to encounter this species on the Southern shores of the Persian Gulf. This single male specimen has all the diagnostic character of this species. In addition to the characters of copulatory structure, it has the diagnostic vase-like dark marking on the opisthosoma ventrally (Fig. 56d). For detailed species description, see Moradmand and Jäger (2012a: 43).
Systematic position. *Eusparassus xerxes* is similar to the *dufouri* and *vestigator* groups due to the presence of the dark marking on the ventral opisthosoma, but the females differ in having not fused AMLL of epigyne. It is similar to *doriae* group in the latter character. *Eusparassus xerxes* has four thick bristles, a character shared with the *vestigator* group, but it differs in lacking the autapomorphic character of the *vestigator* group, the strongly developed vRTA. Consequently, *E.*

xerxes could not be placed in any of the *vestigator*, *doriae* or *dufouri* groups. Its geographical distribution also supports this intermediate status.

Known geographical distribution. From the Middle East [Iran and UAE (new country record)] to Pakistan (Fig. 72b).

Cercetius Simon, 1902

The monotypic genus *Cercetius* was erected by Simon (1902) based on a juvenile specimen. The genus and its type species, *C. perezi* Simon, 1902 have never been explicitly diagnosed prior to this study. Examination of the type material revealed that *Cercetius* falls into the synonymy of *Eusparassus* as defined by Moradmand and Jäger (2012a). To maintain stability of nomenclature case proposal 3596 was submitted to ICZN to give the widely used name *Eusparassus* Simon, 1903 priority over *Cercetius* (for details see Moradmand & Jäger 2012b). In accordance with Article 82.1 of the Code, the prevailing usage of names is maintained until the ruling of the Commission is published. Therefore, both generic names *Eusparassus* and *Cercetius* are used in this paper, and formal synonymization is postponed until final ICZN decision.

Cercetius perezi Simon, 1902

Figs 42–43, 57, 66a–b, e

Cercetius perezi Simon, 1902: 253 (description of juvenile, holotype examined); Simon 1903: 1020, 1023, 1026 (juveniles, new geographic records from Somalia); Jäger and Kunz 2005: 170, figs. 201–204 (illustration of holotype).

Type material. Holotype (designated by Simon 1902)**:** juvenile, **UNITED ARAB EMIRATES:** Dibba, Persian Gulf shore, [label: Golfe persique: Dibba, St. XLV, Mission Bonnier–Perez, Cotes-Arabie, March–April 1901, MM. J. Bonnier & Ch. Perez leg. (MNHN 1658-21936)].

Other material examined (9♂♂, 6♀♀). **UNITED ARAB EMIRATES:** ***Abu Dhabi***: 1♂, Dibba, Sweihan, N 24˚28', E 55˚22', 160 m altitude, collected by NARC (National Avian Research Centre), 14 September 1993 (ICEAD, MM1); 1♂, 2 immatures, Persian Gulf shore,

Suwayhan (=Sweihan), April 1970, C. Williams leg. (MNHN, MM158). **OMAN:** 2♂♂, 1♀ (MM 30), Mudhaybi, N 22˚12', E 58˚06', 530 m altitude, camp.p., Oman Eastern Sand Project, 12 March 1986, W. Büttiker leg. (NMB); 1♀, Al-Araqi, September 2000, S. Huber leg. (SMF); 1♂, 2 immatures, Wadi Matam, Wahiba, N 21˚53', E 58˚17', 170 m altitude, 31 January 1986, Oman Eastern Sand Project (NMB); ***Ad Dakhiliyah*:** 1♀, outside of Fallah cave, September 2000, S. Huber leg. (SMF); ***Mintaqat Masqat***: 1♀, near Rusayl, N 25˚33', E 58˚15', March 1984, W. Cookson leg. (NMB); ***Mintaqat al Sharghiah*:** 1♂, Msirah, February 1979, K. M. Guichard leg.(NHM); 1♂, Central Oman, N 22˚25', E 56˚45' [south of Jebel Karwr Mountain, Al-Dakhiliah], sand desert, A. J. Wart leg. (NHM 26.7.63); ***Mintaqat Zufar***: 2 immatures, near Thamarit, Dhofar, N 17˚42', E 54˚02', 450 m, under tyre on soft sand, 24 March 1980, J. N. Barnes leg. (NHM). **YEMEN:** ***Muhafazat Shabwah*:** 1♂, 1♀, 1 immature, Sayhut, between Al-Mukalla and border of Oman, 5–8 March 1995, B. Schätti leg. (MHNG); ***Tihama Region*:** 1♀, Tihama, Northern Yemen, 1985, F. Schüffe leg. (SMF). **SOMALIA:** ***Somaliland:*** 1♂, near Berbera, N 10˚14'25", E 45˚04'55.4", 407 m, 9 July 2011, T. Mazuch & F. Kovarik leg. (SMF, SD 840). **DJIBOUTI:** ***Region d' Obock***: 1♀, Obock, 22 February 1893, M. Maindron leg. (MNHN).

Diagnosis. Large-sized and robust hairy species (total length: male 24 mm, female 28 mm, leg span up to 13.5 cm) with diagnostic uniform large black marking covering ventral opisthosoma posteriorly and partially around epigastric furrow (Fig. 57b) in both sexes; males with short and slender embolus tip pointing distad in ventral view, embolus membrane composed of folded hyaline layers (Figs 42a–c); vulva composed of several bulbous parts at turning loop, glandular pores present on a small process (Figs 43b–d).

Description. Male (ranges: n=9, single measurement: MM 1):

Measurements. Medium to large sized; total length 16.8–23.8, prosoma length 8.5–12.3, prosoma width 7.4–10.4, anterior width of prosoma 4.2–6.2, opisthosoma length 8.3–11.5, opisthosoma width 5.5–8.5. Eye diameters: AME 0.70, ALE 0.75, PME 0.57, PLE 0.80; eye inter-distances: AME-AME 0.23, AME-ALE 0.04, PME-PME 0.54, PME-PLE 0.55, AME-PME 0.60, ALE-PLE 0.38, clypeus height at AME 0.45, clypeus height at ALE 0.58. PLE largest, posterior eye row recurved (Fig. 42d).

Chelicerae. Chelicerae with 2 anterior and 3 to 5 posterior teeth, cheliceral furrow usually with 1 or 2 intermarginal denticles close to anterior teeth; basal segment of chelicerae at distal end retro-marginally with 1 bristle (Fig. 42e).

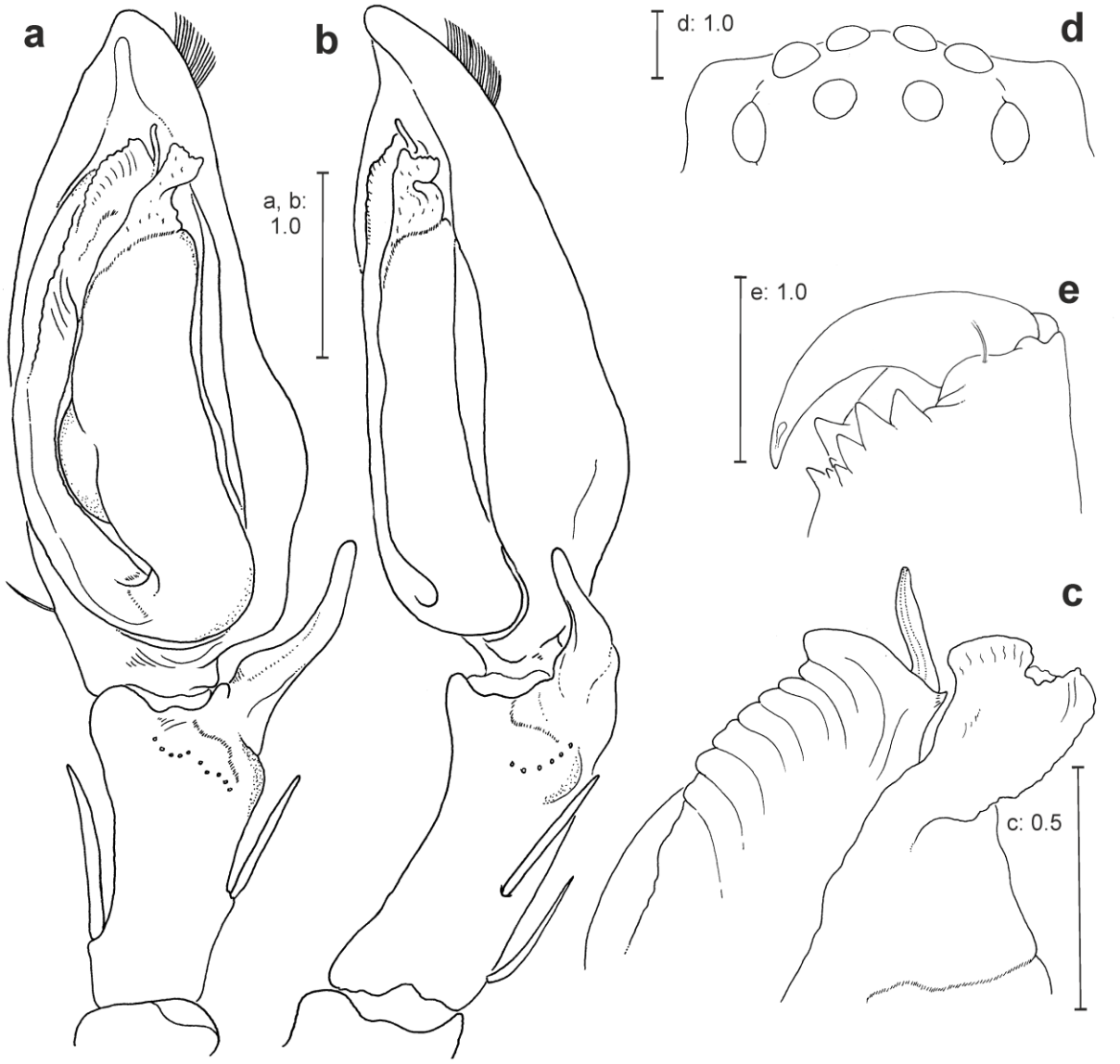

FIGURE 42. *Cercetius perezi* Simon, 1902, males from Suwayhan (=Sweihan), Dibba, Persian Gulf shore, United Arab Emirates. (a) left palp, ventral; (b) left palp, retrolateral; (c) embolus tip and conductor, ventral; (d) eye arrangement, dorsal; (e) right chelicera, ventral.

Legs. Leg formula: II I IV III. Measurements of palp and legs (largest male): Palp 16.3 [5.5, 2.3, 2.8, 5.7], I 54.2 [14.6, 6.8, 14.5, 14.3, 4.0], II 57.2 [16.5, 7.5, 16.1, 15.5, 3.6], III 52.7 [15.7, 6.1, 14.3, 13.1, 3.5], IV 53.2 [15.9, 6.0, 14.5, 13.3, 3.5].

Spination. Palp 131, 001, 1111; Legs: Femur I–III 323, IV 321; Patella I–IV 000(1)/101; Tibia I–IV 2224; Metatarsus I–III 2(1)024, IV 3034/30(1)36.

Palp. As in diagnosis with cymbium longer than tibia; tegulum shorter than embolus; dRTA long and slender with slight median bent, vRTA weakly developed (Figs 42a, b); tip of embolus

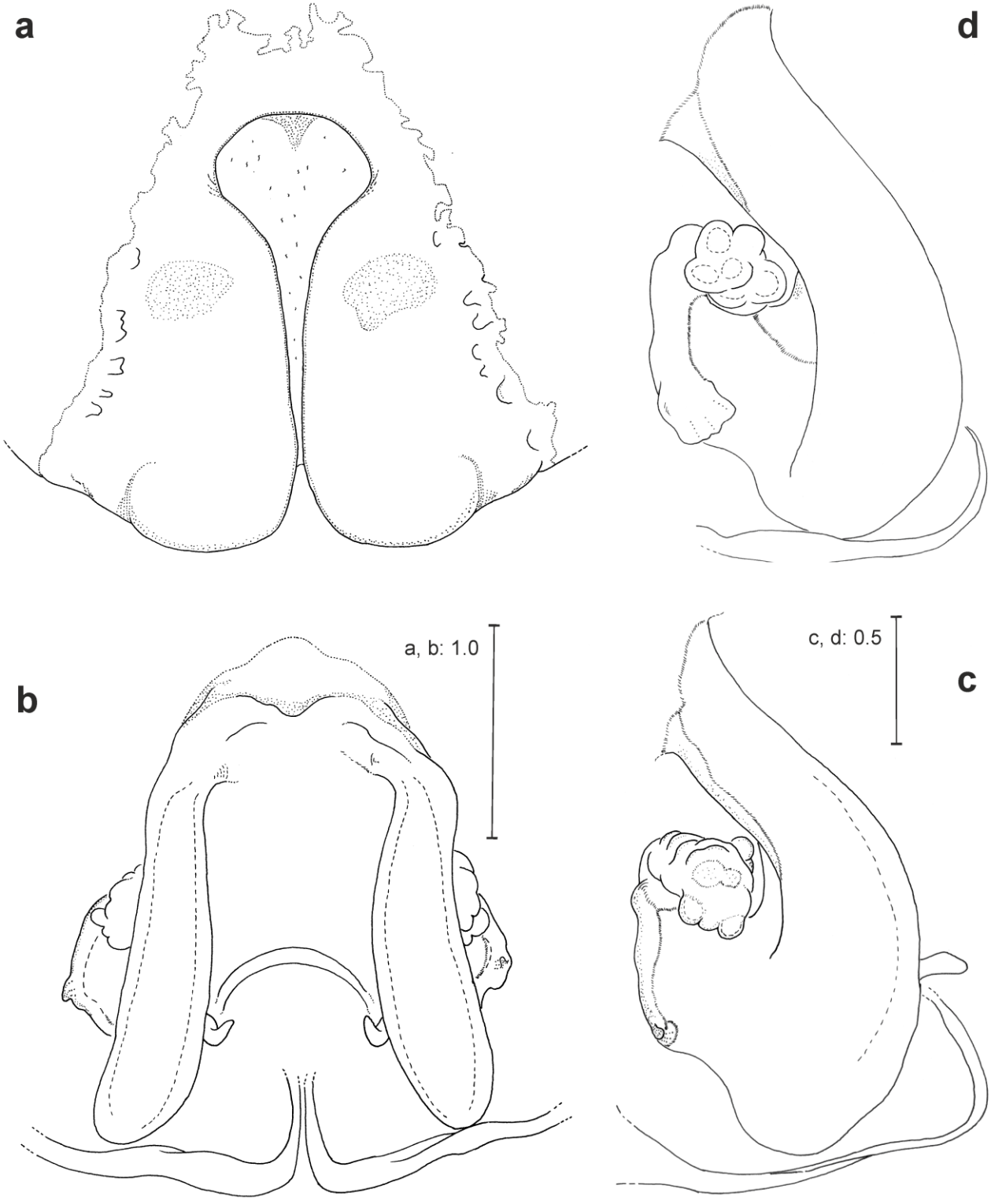

FIGURE 43. *Cercetius perezi* Simon, 1902: (a–c) female from Oman: Mudhaybi; (d) female from Oman: Fallah. (a) epigyne, ventral; (b) vulva, dorsal; (c–d) left vulva, anterio-dorso-lateral.

hyaline and worm-like, embolic membrane consisting of folded layers distally; conductor elongated (Fig. 42c).

Female (ranges: n=7, single measurement: MM 30):

Measurements. Medium to large sized; total length 21.5–28.0, prosoma length 9.5–12.5, prosoma width 8.6–11.1, anterior width of prosoma 5.7–7.5, opisthosoma length 12.0–15.5, opisthosoma width 7.8–11.0. Eye diameters: AME 0.81, ALE 0.84, PME 0.70, PLE 0.88; eye interdistances: AME-AME 0.33, AME-ALE 0.20, PME-PME 0.85, PME-PLE 0.95, AME-PME 0.90, ALE-PLE 0.75, clypeus height at AME 0.65, clypeus height at ALE 0.70.

Chelicerae. Chelicerae with 2 anterior and 3 or 4 posterior teeth, Cheliceral furrow with 1 or 2 intermarginal denticles close to anterior teeth or without denticles. Basal segment of chelicerae at distal end retro-marginally with a single bristle.

Legs. Leg formula: II I IV III. Measurements of palp and legs: Palp 16.3 [5.0, 2.5, 3.1, 5.7], I 46.4 [13.5, 6.5, 11.4, 11.8, 3.2], II 51.9 [14.9, 6.6, 14.0, 13.2, 3.2], III 44.4 [13.7, 6.0, 11.1, 10.8, 2.8], IV 45.6 [14.3, 5.8, 10.9, 11.4, 3.2].

Spination. Palp 131, 001, 1111, 1013; Legs: Femur I–III 323, IV 321; Patella I–IV 101; Tibia I–IV 22(1)24; Metatarsus I–III 2(1)024, IV 3034/3036.

Epigyne/vulva. As in diagnosis with epigyne composed of two large triangular lateral lobes, epigynal field slightly longer than wide, anterior margin of lateral lobes fused together and encircling MS entirely, epigynal field bridge (EFB) present and not separated from anterior margin of lateral lobes (Figs 43a, b).

Colouration. A freshly collected single male was obtained from Somalia whose prosoma and dorsal opisthosoma is creamy-white with shiny white hairs dorsally on legs (Fig. 57a); preserved specimens are reddish-brown spiders with darker scopula hairs on metatarsus and tarsus; prosoma margins, anterior part of prosoma around eyes, chelicerae and dorsal side of femora covered with dense white hairs (Figs 57a, c), in contrast, sternum, coxae of legs and basal segment of chelicerae covered with dense black hairs, ventral opisthosoma with large black marking posterior to and around epigastric furrow (Fig. 57b).

Systematic position. The somatic features and the copulatory organs of *Cercetius perezi* correspond well with the *Eusparassus* delimitation as given in Chapter 3.1 [Moradmand and Jäger (2012a)] and in this paper. The presence of intermarginal denticles of chelicerae, eyes arrangement, leg formula, spination pattern and the presence of dark marking at ventral opisthosoma are all somatic characters which are present in the immature holotype and the newly

discovered adult specimens from the type locality. However, *C. perezi* cannot be affiliated with any of the known species groups. This species embodies some synapomorphies of the *dufouri* group (e.g. dark marking of ventral opisthosoma, epigyne with AMLL encircling MS entirely) and also some of the *jaegeri* and *walckenaeri* groups (presence of intermarginal denticles in some specimens). *Cercetius perezi* is likely to belong to an intermediate lineage among the noted *Eusparassus* species groups. The geographical distribution between the three groups mentioned above supports this hypothesis.

Currently known distribution and habitats. Eastern and southern Arabian Peninsula in the United Arab Emirates (type locality), Oman (new country record) and Yemen (new country record), horn of Africa in Somalia and Djibouti (new country record) (Fig. 72b). Specimens were collected in wadis, sandy substrates, gravel plains and from under stones in deserts.

Misplaced species

"Eusparassus" bicorniger (Pocock, 1898)

Sparassus bicorniger Pocock, 1898: 519, pl. 41, fig. 9 (description and illustration of male), [holotype male, label: type, Ndi, Weiss Rd. Camp, by Steuart Betton/ Nd (Weiss Rd Camp), Aug 4–25, 1897, NHM 94.11.20.61, examined].

Eusparassus biocorniger (Pocock) Strand 1908b: 22 (unjustified combination).

Remarks. The species cannot be categorized in any known Sparassidae genus, and it certainly does not belong to the genus *Eusparassus.* More likely it is a member of an undescribed genus which would be grouped within the subfamily Sparassinae, when more material (especially the conspecific female) from the type locality is recovered. The holotype was most likely collected between Mombasa and Lake Victoria in Kenya, formerly known as "British East Africa".

"Eusparassus" laterifuscus Strand, 1908

Eusparassus laterifuscus Strand, 1908a: 5 (description of juvenile) [subadult male holotype, Madagascar, 18 Decemper 1885, A. Stumpff leg., SMF 4571, examined].

Remarks. The subadult male holotype was collected from Madagascar. The combination of somatic characters clearly distinguishes it from *Eusparassus*: three anterior teeth in chelicerae (two in *Eusparassus*), a patch of several intermarginal denticles close to anterior teeth (scattered or in a line in *Eusparassus*, if present) and the number of ventral tibial spines: I–II 8, III–IV 6 (I–IV 4 in *Eusparassus*); the species is tentatively classified in *"Rhitymna" saccata* group and is actually an undescribed genus endemic to Madagascar (Peter Jäger, unpublished data). There is no other record of the genus *Eusparassus* from Madagascar.

"Eusparassus" ubae Strand, 1906 nomen dubium

Eusparassus ubae Strand, 1906a: 684 (description of female) [type from Uba in East Africa, lost, see Renner 1988: 322]; Strand 1908c: 41, pl. 2, fig. 8 (redescription and illustration of epigyne).

Remarks. The sketchy illustration of the epigyne by Strand (1908c) reveals that this species does not belong to the genus *Eusparassus*, as it lacks the diagnostic triangular lateral lobes and the median septum is visible throughout median line posteriorly. However, it cannot be affiliated with any sparassid genus.

"Eusparassus" palystiformis Strand, 1907 nomen dubium

Eusparassus palystiformis Strand, 1907a: 541 (description of female) [type from Capeland in South Africa, Museum Lübeck, lost]; Strand 1907b: 671.

Remarks. According to the original description, this species could not be placed in the genus *Eusparassus*, as its legs have three pairs of ventral tibial spines (two pairs in *Eusparassus*).

Strand (1907a) expressed doubts on placing his new species in *Eusparassus* by using a question mark.

Remarks on Ethiopian types of Strand. The type specimens of the following four species were unfortunately destroyed during World War II (Renner 1988). The excursion of the author to Ethiopia (June 2011) as well as investigations in major spider collections in Europe resulted in the recognition of two known valid species of *Eusparassus* distributed in the country, namely *E. laevatus* **comb. nov.** (East and North-East), and *E. vestigator* **comb. nov.** (South). These two species were described before those of Strand. Therefore, Strand's species are most likely junior synonyms of *E. laevatus* **comb. nov.** and/or *E. vestigator* **comb. nov.**.

"Eusparassus" cornipalpis Strand, 1906 nomen dubium

Eusparassus cornipalpis Strand, 1906a: 631 (description of male), [type from Mane River in Ethiopia, lost, see Renner 1988: 322].

"Eusparassus" nigrichelis Strand, 1906 nomen dubium

Eusparassus nigrichelis Strand, 1906a: 631 (description of female), [type from Mane River in Ethiopia, lost, see Renner 1988: 322].

"Eusparassus" fulviclypeus Strand, 1906 nomen dubium

Eusparassus fulviclypeus Strand, 1906a: 630 (description of male and female), [types from Mane River and Ginir-Daua in Ethiopia, lost, see Renner 1988: 322].
Olios fulviclypeus (Strand). Caporiacco 1940: 843 (transfer).

"Eusparassus" subadultus Strand, 1906 nomen dubium

Eusparassus subadultus Strand, 1906a: 631 (description of subadult female), [type from Maki-Abassa Lake in Ethiopia, lost, see Renner 1988: 322].

Remarks on West-African types of Strand. The descriptions of the following two species by Strand (1906b) are based on a highly variable character, namely the number of cheliceral retro-marginal teeth. *Eusparassus* spp. show intra and interspecific variation in this character [three to six teeth (three larger and one to three smaller ones)]. Unfortunately, both type specimens were destroyed in Stuttgart (Renner 1988).

***"Eusparassus" quinquedentatus* Strand, 1906 nomen dubium**

Eusparassus 5-dentatus Strand, 1906b: 71–73 (description of female from Ghana [sub Gold Coast], lost, original incorrect spelling).

Eusparassus quinquedentatus (Strand) Roewer 1954: 675 (justified emendation).

"Eusparassus" sexdentatus Strand, 1906 **nomen dubium**

Eusparassus 6-dentatus Strand, 1906b: 73 (description of juvenile, from Togo: Lome, lost, original incorrect spelling).

Eusparassus sexdentatus (Strand) Roewer 1954: 675 (justified emendation).

Olios quesitio comb. nov. et replacement name

Replacement name for *Eusparassus concolor* Caporiacco, 1939: 353 (description of subadult male) [subadult male holotype, Ethiopia: Moyale, 13 May 1973, Prof. Zavattari leg., MZUF 212, examined] (preoccupied by *Olios concolor* Keyserling, 1884: 682, pl. 21, fig. 29).

Etymology. The largest Sparassidae genus in terms of species number, *Olios*, needs a comprehensive revision to uncover its hidden diversity and several misplacements. "Quesitio" is the Latin translation for the term "investigation", referring to the need for taxonomic revision of *Olios* spp. Noun in apposition.

Remarks. The subadult male holotype was collected by Prof Edoardo Zavattari from Borana region in Southern Ethiopia. The combination of somatic characters revealed that the specimen

belongs to the genus *Olios* based on eye arrangement, equal length and width of prosoma, absence of intermarginal denticles, presence of two to five thick bristles at retromarginal side of chelicerae basal segment and spotted legs. The new combination is a secondary homonym of *Olios concolor* Keyserling, 1884 (currently considered a junior synonym of *O. giganteus* Keyserling, 1884), therefore a replacement name is proposed here.

Systematics and zoogeography

With completion of this revision, 30 species of the stone huntsman spiders, genus *Eusparassus* are known (including *C. perezi*), of which 27 species are classified into six species groups and the rest three species are listed as incertae sedis. All species groups show a continuous range of distribution, fully to partially separated from nearby groups. The intermarginal denticles of chelicerae are present in just two species groups namely *walckenaeri* and *jaegeri* (present also in some specimens of *C. perezi*, but in different pattern). Thus, it could be assumed that these two groups are phylogenitically closely related. Consequently, the recently discovered *Eusparassus* fossil (amber), *E. crassipes*, is probably allied to one of these groups, since its chelicerae have distinct intermarginal denticles (Dunlop *et al.* 2011: figs 2e–f). The *jaegeri* group is endemic to Southern Africa (Fig.71b) which is far from the locality of *E. crassipes* in Northern Europe. Thus, *E. crassipes* is probably closely related to the *walckenaeri* group whose distribution range extends into the Eastern Mediterranean region (Fig.70a). The remaining four species groups lack any intermarginal denticles on their chelicerae. Nevertheless, the presence of intermarginal denticles could be also the result of homoplasy and gain and loss of the character might have been taken place several times during the evolution of the members. The *dufouri* and *vestigator* groups are related in terms of the presence of the dark marking ventrally on the opisthosoma and the spination of the legs femora (I–IV 424, exception *E. pearsoni* 323). The disjunctive distribution of the isolated member of *vestigator* group, *E. pearsoni* in India, far from its closest relatives in Eastern Africa (Fig. 71a) can be explained by the following hypothesis: the occurrence of this species in Indian plate is a secondary distribution of its ancestral stock from Eastern Africa. The Indian subcontinent was not totally isolated from Africa after its separation from Gondwanaland. India was reattached to northeast Africa via Greater Somalia around 65–60 MYA (million years ago), on its northward drift toward Eurasia (Briggs 2003). The hypothesized

ancestor of *E. pearsoni* may have dispersed from Eastern Africa to Western India at that time. A similar scenariao was proposed for the distribution of the genus *Mallinella* Strand, 1906 (Zodariidae) by Dankittipakul *et al.* (2012). The *doriae* group - distributed in the Middle East to parts of Central and South Asia - might have evolved from the *walckenaeri* group by losing their intermarginal denticles. The *tuckeri* group represents an endemic lineage in Southwest Africa (Fig.71b). Since most parts of the distribution range of *Eusparassus* species are not explored yet, more species are to be expected, especially in the transition zones between different species groups.

The stone huntsman spiders inhabit semidry and dry deserts. Tectonic drifts have caused major changes in the position of the continents and consequently those of deserts. Many of the current deserts are geologically young, but in contrast, the world's oldest desert is believed to be the Namib Desert, originating from some 55 MYA (Ward 2009). Since the close relatives of *Eusparassus* and Eusparassinae (e.g. *Pseudomicrommata*, *Arandisa*, *Leucorchestris* and *Carparachne*) are living in the Namib Desert and nearby regions, this area is a potential centre of origin of *Eusparassus* spp. This hypothesis of a southern African origin of *Eusparassus* is supported by the absence of representatives in the Americas, Madagascar and Australia (previous records from these regions proved to be misidentifications). Thus, *Eusparassus* does not have a Gondwanan distribution and probably evolved after the breakup of the supercontinent Gondwanaland, which was completed in Early Cretaceous at around 110–100 MYA (Briggs 1995). Diversification of the genus and area expansion probably occurred during the Tertiary.

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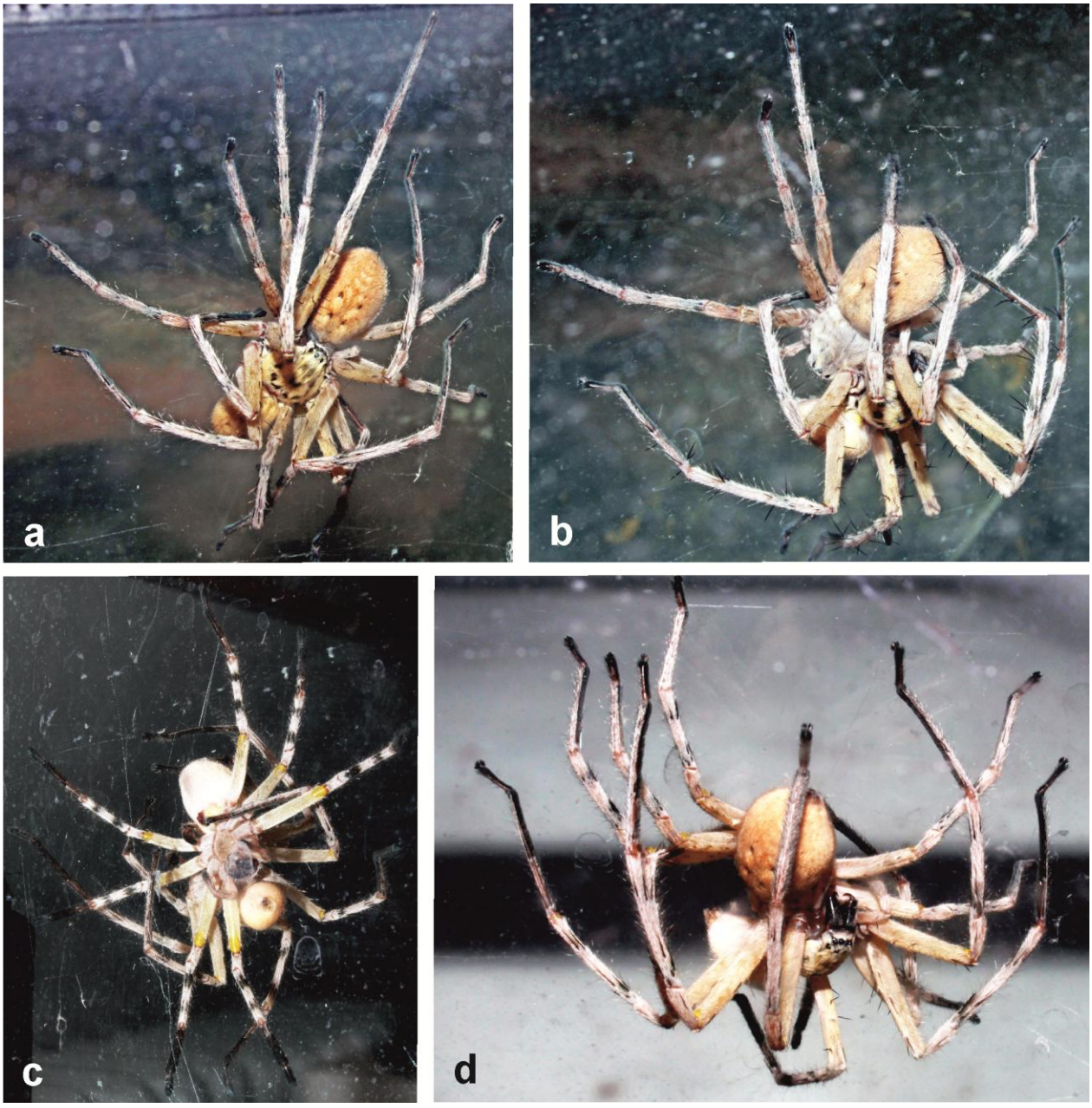

FIGURE 44. *Eusparassus walckenaeri* (Audouin, 1826), pre-copulating movements. (a, c) male hold the female by chelicerae and legs; (b, d) male try to reach female's epigyne from right side of female using his left palp, fixing and evaluating the position.

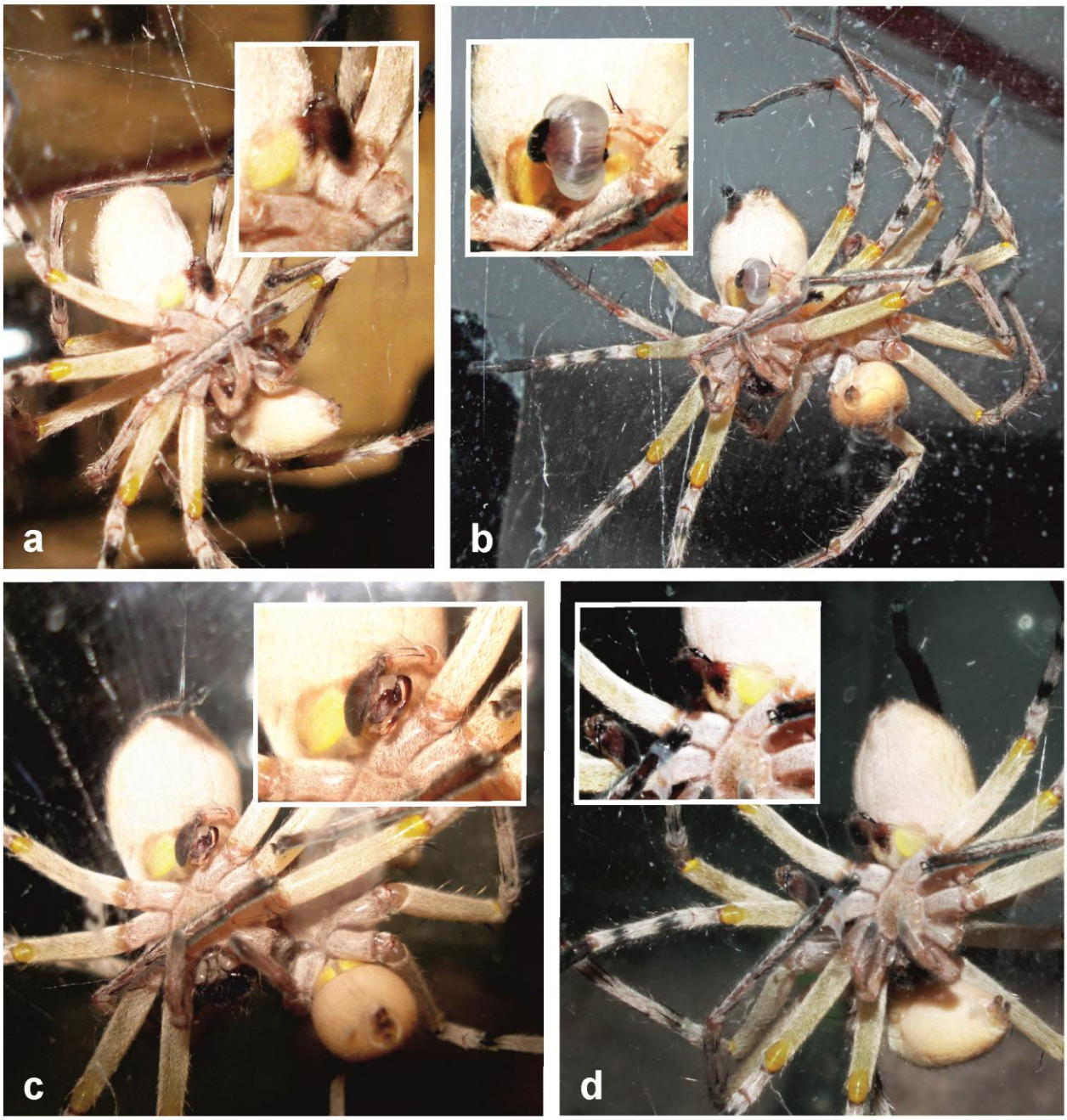

FIGURE 45. *Eusparassus walckenaeri* (Audouin, 1826), copulation. (a–c) male' right palp coupling female's epigyne (a) dRTA inserted into the posterior slit between lateral lobes of epigyne; (b) palp expanded and embolus inserted into copulatory openings (CO); (c) palp expansion is over and embolus is thrown out from CO, palp remain in this position for few seconds; (d) the same process initiated by the left palp, this time from the right side of female.

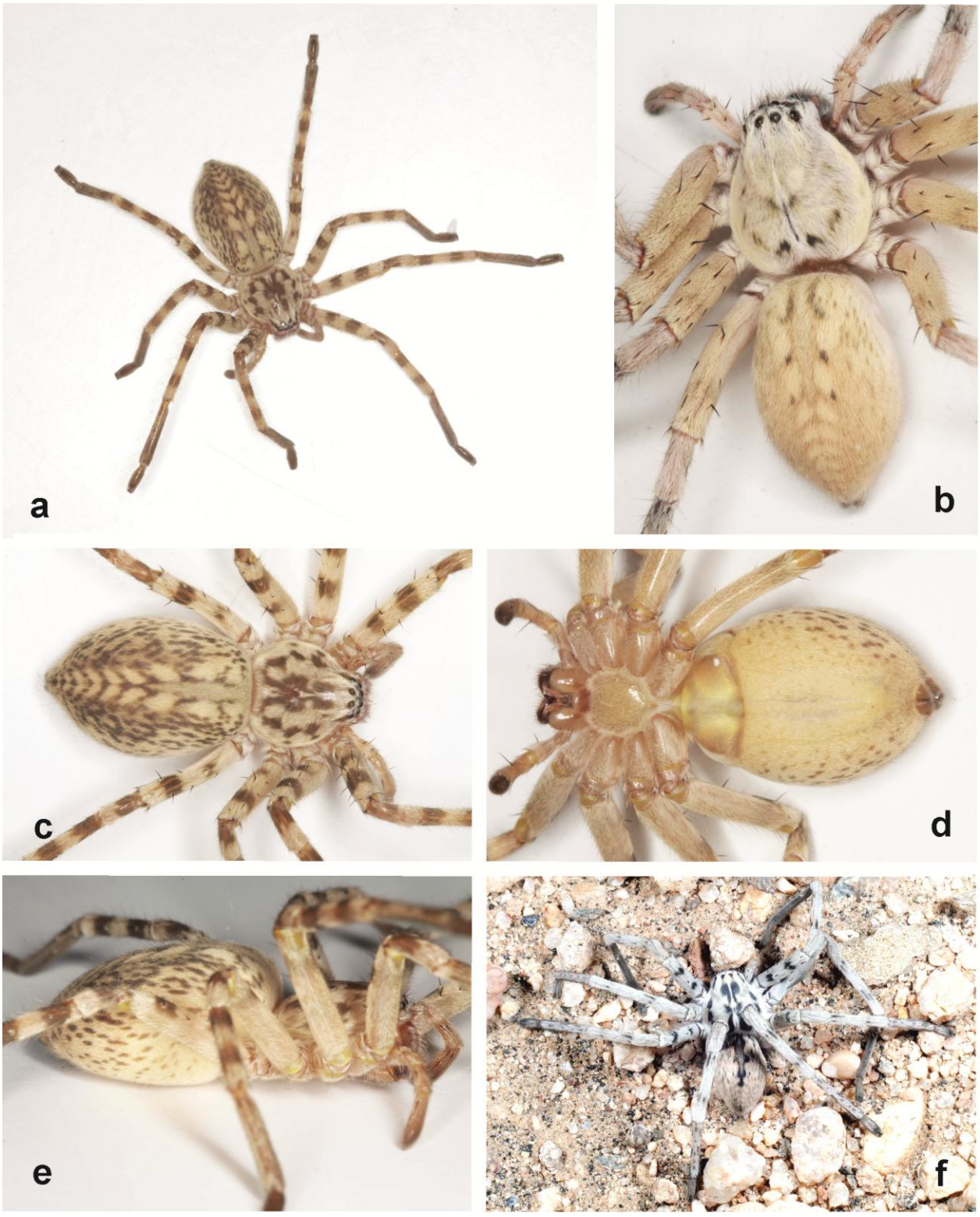

FIGURE 46. Habitus of alive specimens of the *walckenaeri* group. (a–e) *Eusparassus walckenaeri* (Audouin, 1826) (a, c–e from Mügla, Turkey, b from Negev Desert, Israel); (f) *Eusparassus* sp. from Somalia, S of Berbera. Photos by P. Jäger (a–e) and F. Kovařík (f).

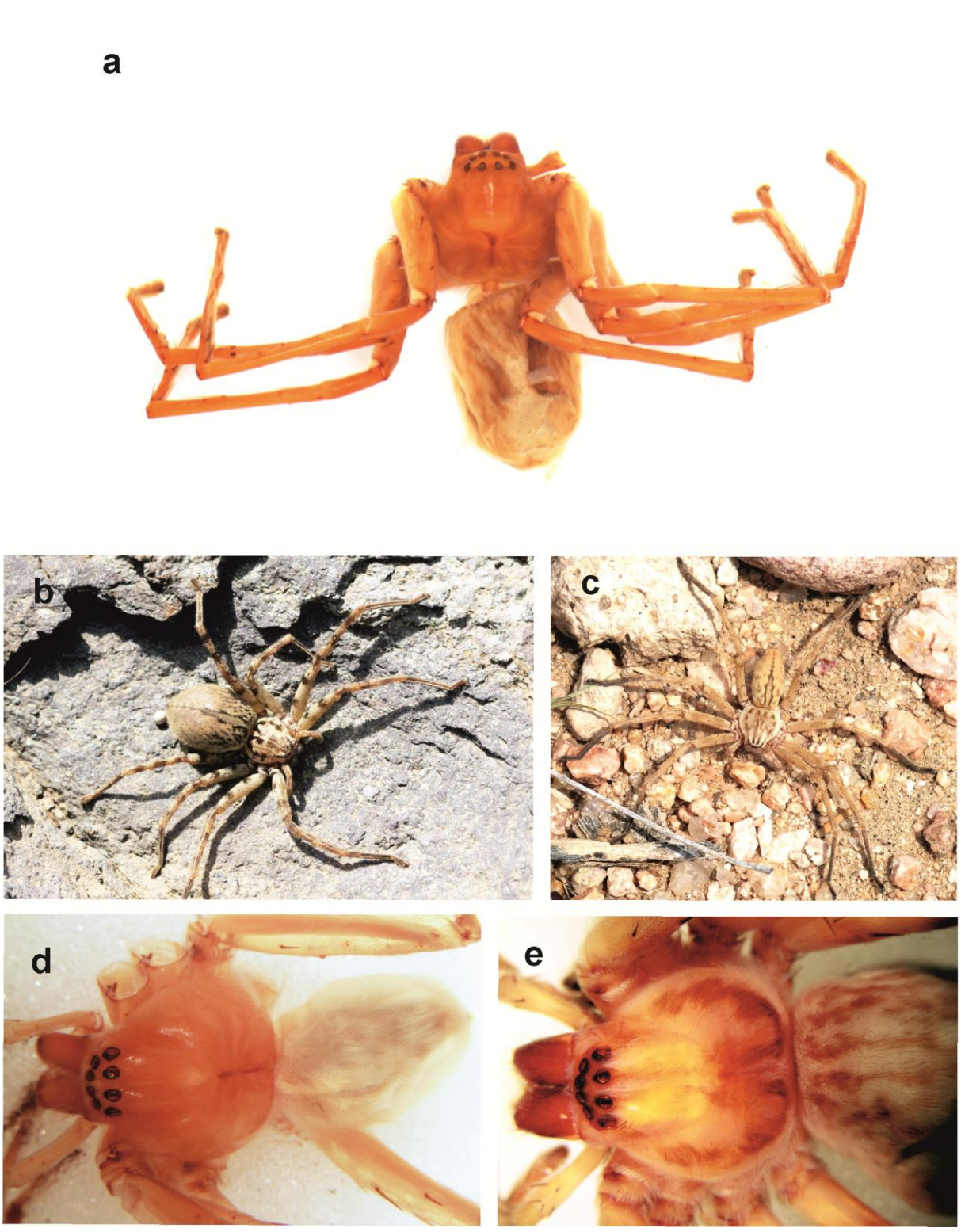

FIGURE 47. Habitus of species of the *walckenaeri* group. (a–c) *Eusparassus laevatus* (Simon, 1897) **comb. nov.** (a syntype female, b–c alive female specimen: b from Yemen, c from Somalia); (d–e) *Eusparassus arabicus* **spec. nov.** (d holotype male, e paratype female). Photos by V. Hula (b) and F. Kovařík (c).

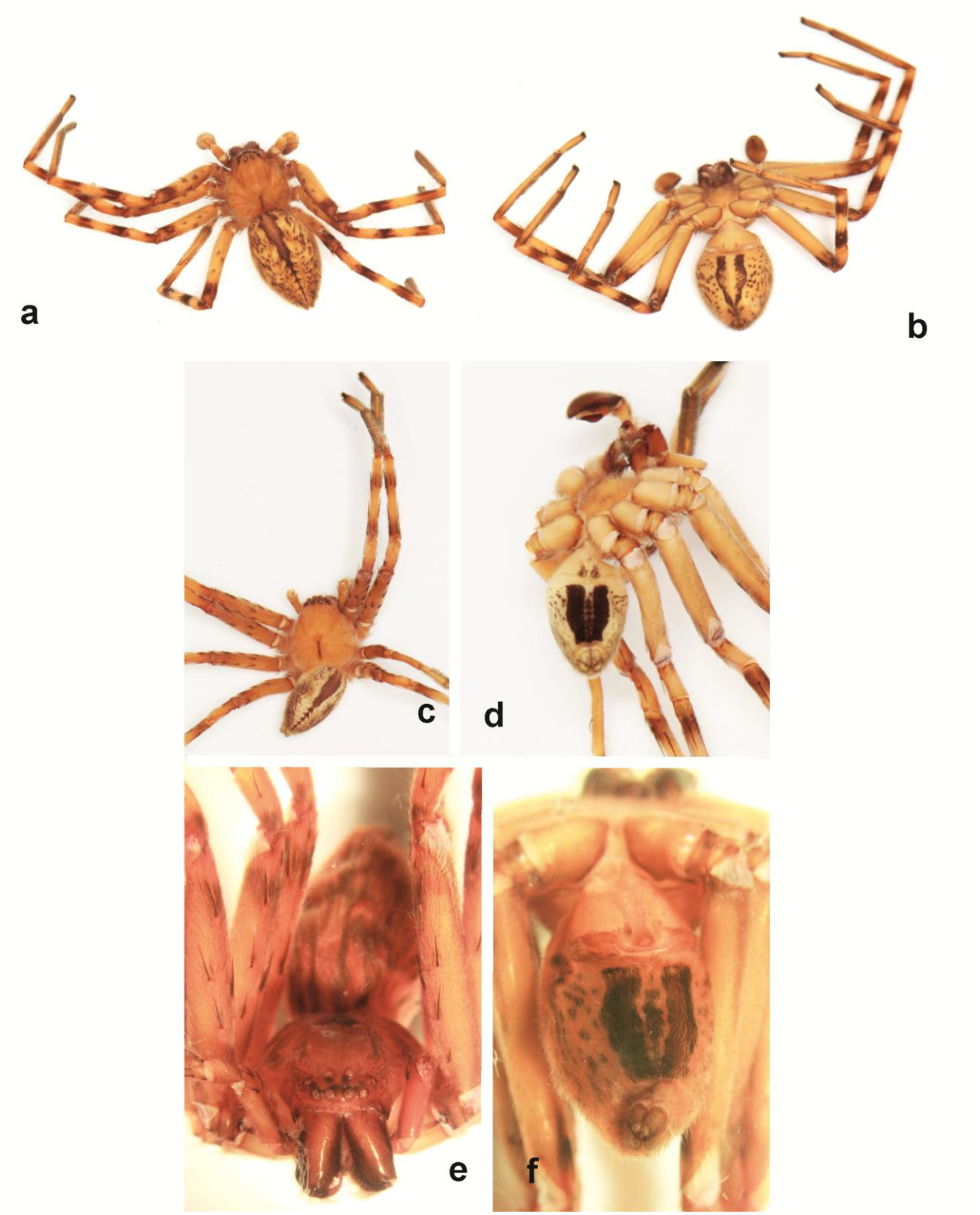

FIGURE 48. Habitus of species of the *dufouri* group. (a–b) *Eusparassus dufouri* Simon, 1932; (c–f) *Eusparassus levantinus* Urones, 2006. (a, c) dorsal, (b, d, f) ventral, (e) frontal.

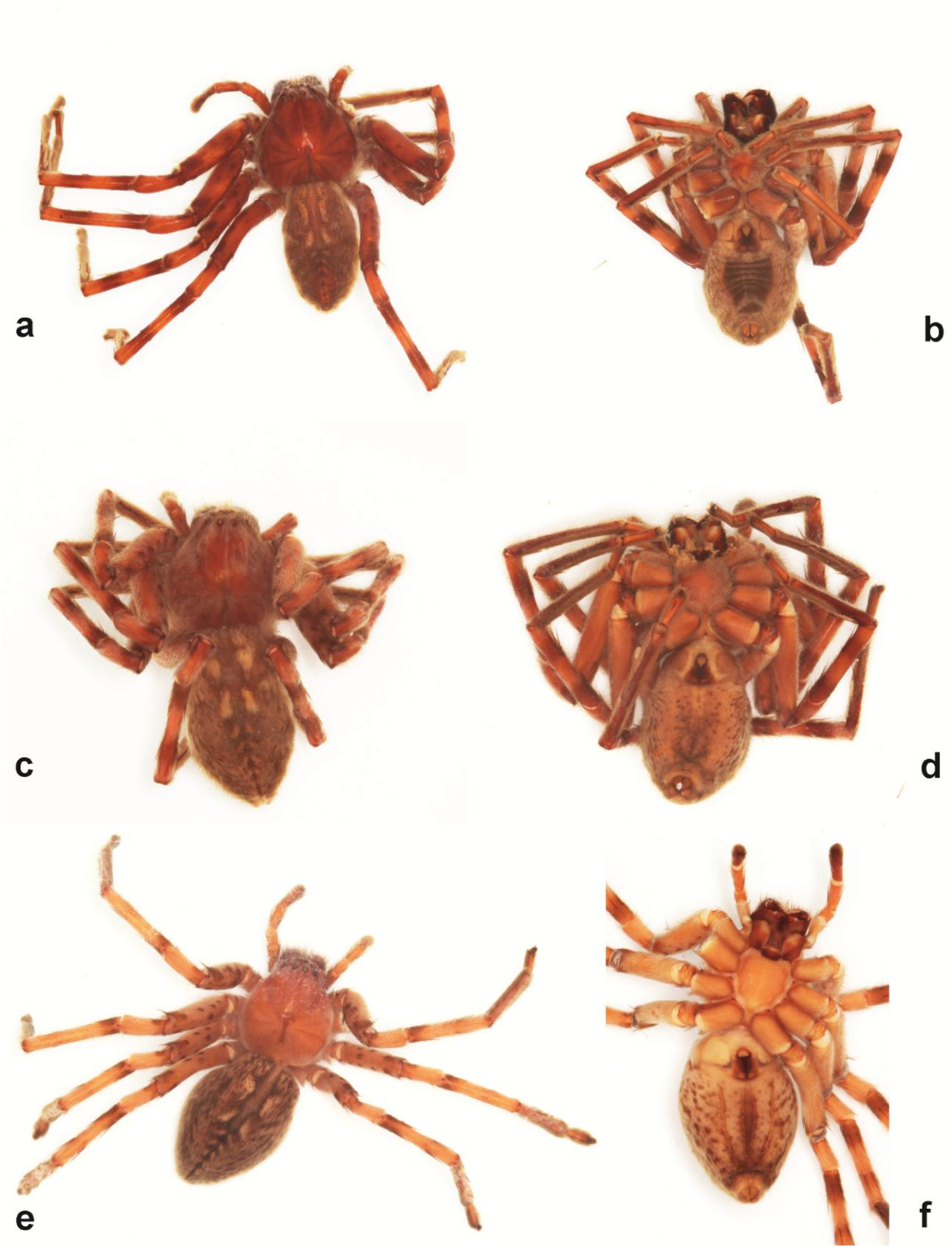

FIGURE 49. Habitus of species of the *dufouri* group. (a–b) *Eusparassus atlanticus* Simon, 1909 **stat. nov.**, syntype female; (c–d) *Eusparassus fritschi* (Koch, 1873) **stat. rev.**, syntype female; (e–f) *Eusparassus letourneuxi* (Simon, 1874), female. (a, c, e) dorsal, (b, d, f) ventral.

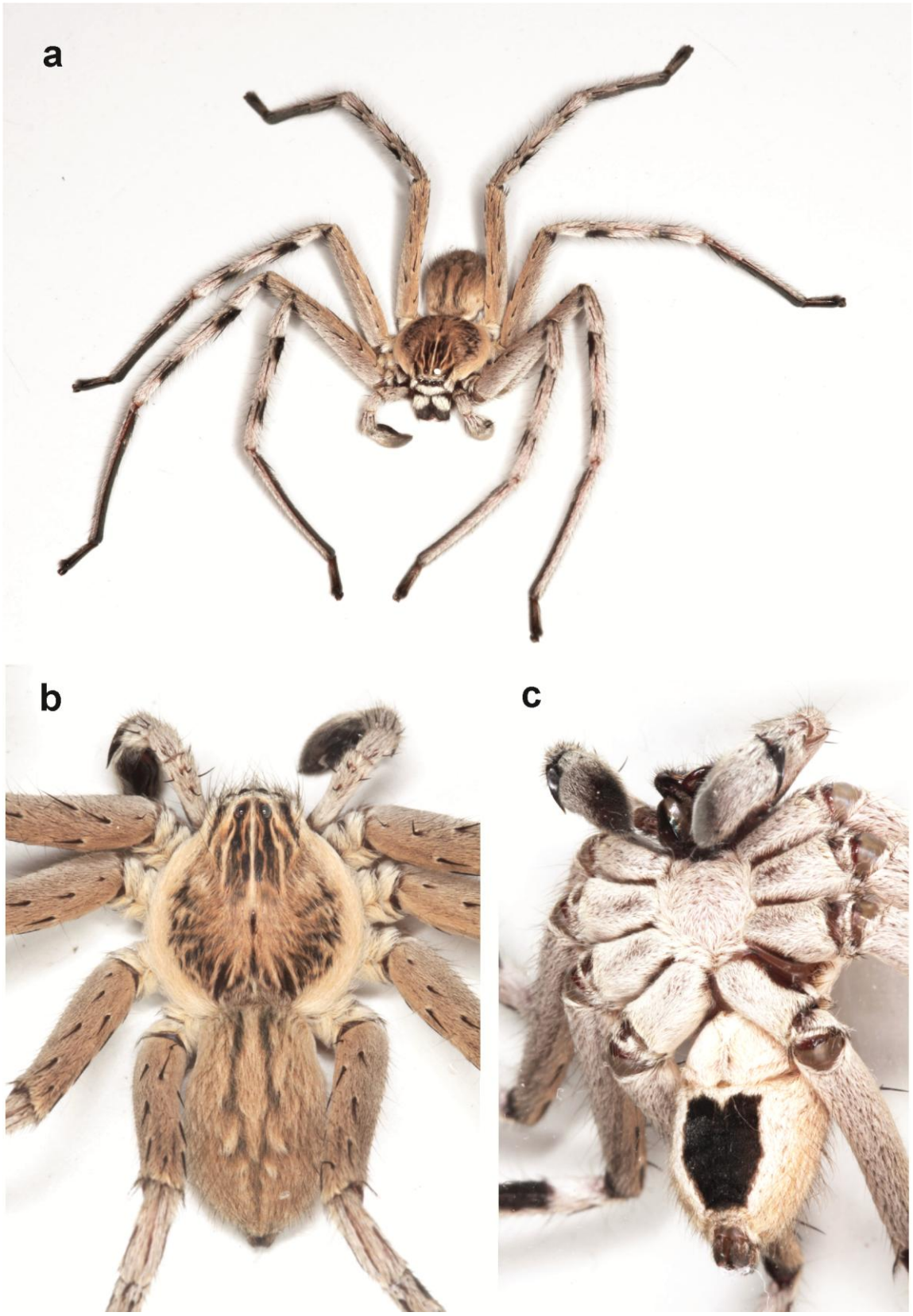

FIGURE 50. Habitus of *Eusparassus oraniensis* (Lucas, 1846), *dufouri* group, alive male specimen from Morocco. (a) entire animal, (b) close up, dorsal, (c) ventral.

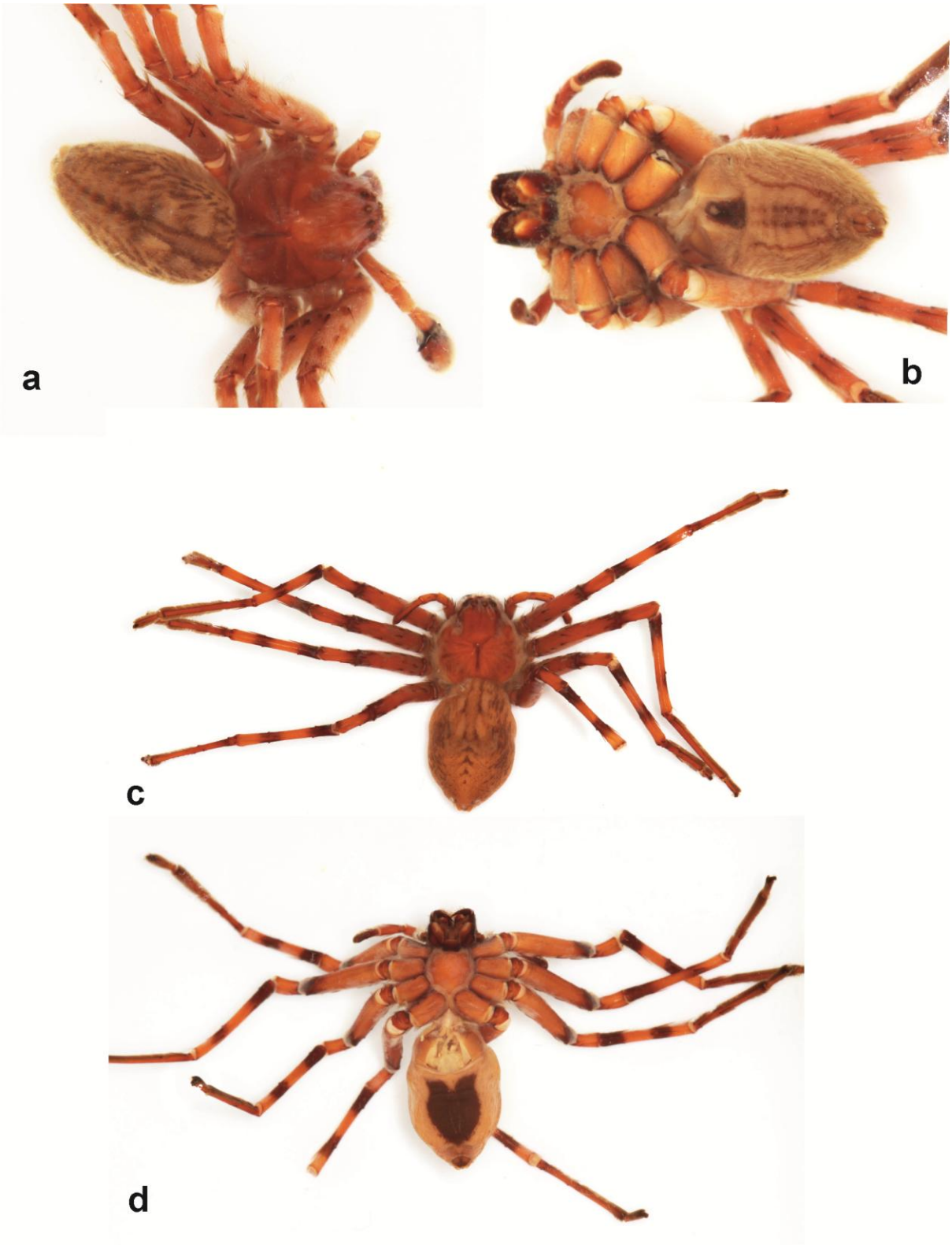

FIGURE 51. Habitus of species of the *dufouri* group. (a–b) *Eusparassus barbarus* (Lucas, 1846) female from Algeria; (c–d) *Eusparassus syrticus* Simon, 1909, lectotype female from Tunisia. (a, c) dorsal, (b, d) ventral.

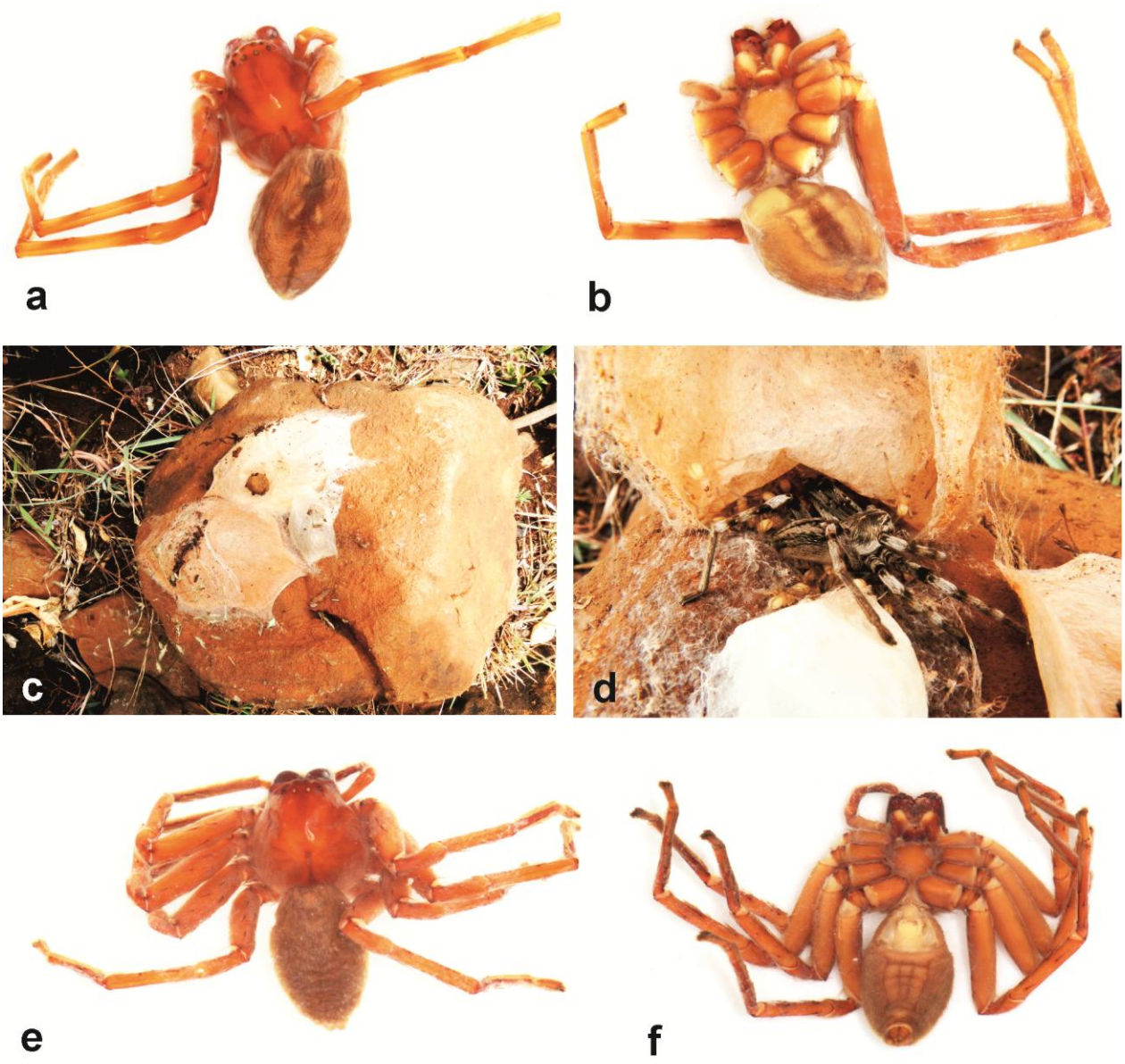

FIGURE 52. Habitus and habitat of species of the *vestigator* group. (a–d) *Eusparassus vestigator* (Simon, 1897) **comb. nov.**, (a–b syntype subadult female, c retreat under stone, d opened retreat with female and spiderlings inside); (e–f) *Eusparassus pearsoni* (Pocock, 1901) lectotype female. (a, e) dorsal, (b, f) ventral. Photos (c, d) by V. Trailin taken in Sof Omar, Ethiopia.

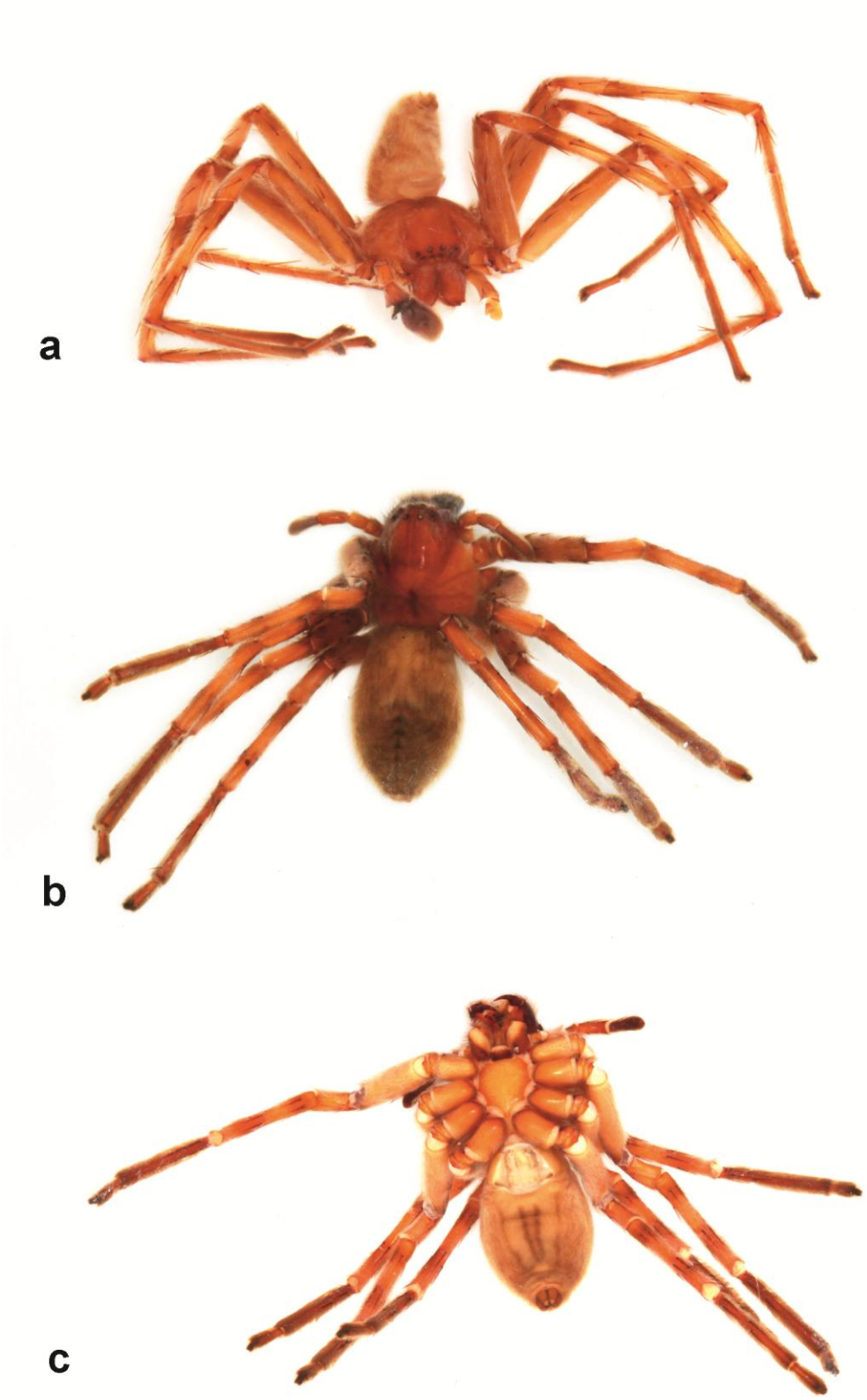

FIGURE 53. Habitus of *Eusparassus reverentia* **spec. nov.**, *vestigator* group. (a) holotype male from Burkina Faso, frontal; (b–c) paratype female from Nigeria (b dorsal, c ventral).

FIGURE 54. Habitus of species of the *jaegeri* group. (a) *Eusparassus jaegeri* **spec. nov.,** alive male, holotype; (b–c) *Eusparassus schoemanae* **spec. nov.** (b holotype male, c paratype female), all from South Africa. Photo (**a**) by D. Kunz.

FIGURE 55. Habitus of species of the *jaegeri* group. (a–b) *Eusparassus jocquei* **spec. nov.,** paratype male from Zimbabwe; (c) *Eusparassus borakalalo* **spec. nov.**, holotype female from South Africa.

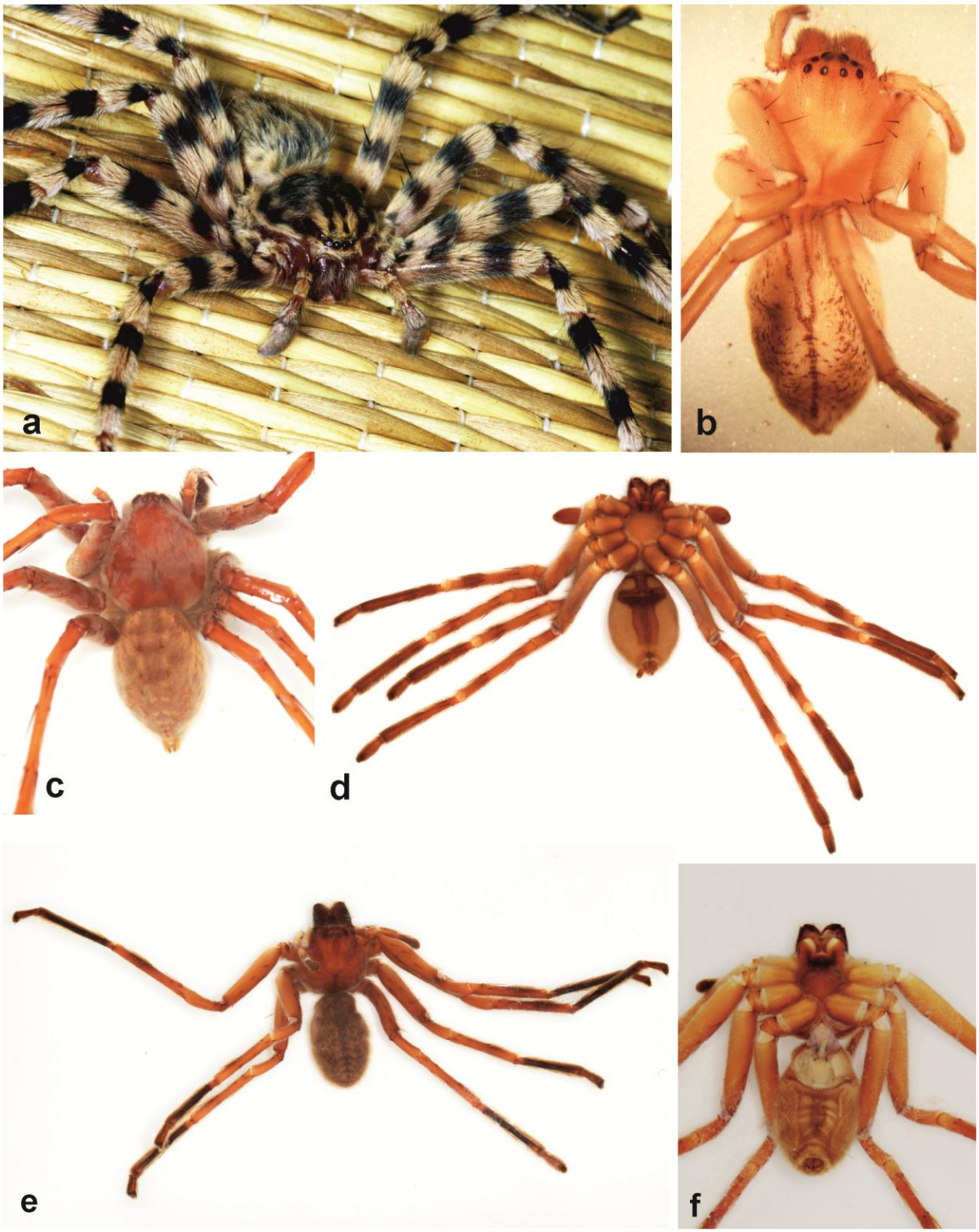

FIGURE 56. Habitus and ventral views of *Eusparassus* spp. (a) *Eusparassus educatus* **spec. nov.** paratype male from Namibia; (b) *Eusparassus tuckeri* (Lawrence, 1927) **comb. nov.**, female from Namibia; (c–d) *Eusparassus xerxes* (Pocock, 1901) (c syntype male from Pakistan, d syntype subadult male from Iran); (e–f) *Eusparassus pontii* Caporiacco, 1935, female from Ladakh, Himalayas, India.

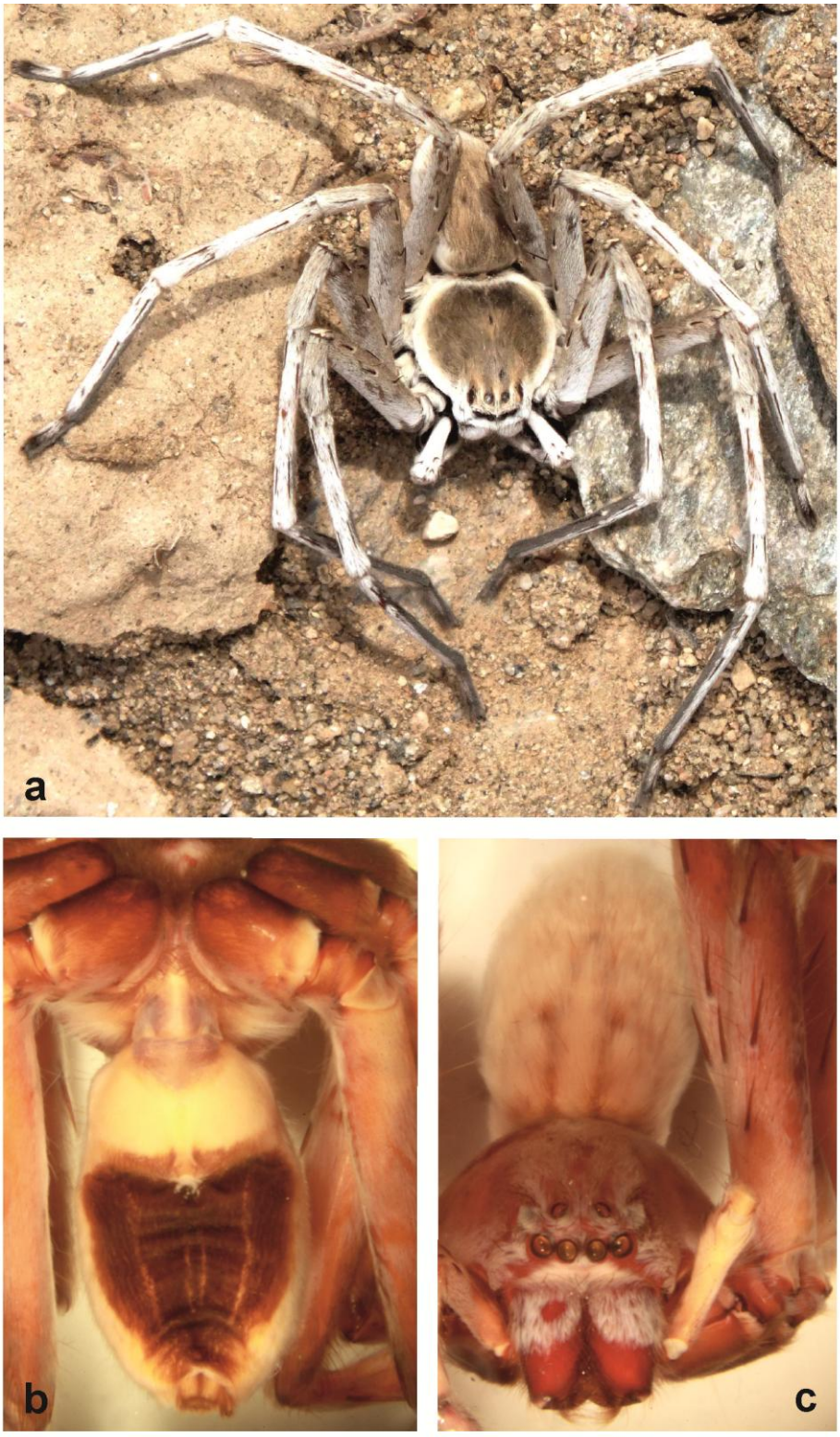

FIGURE 57. *Cercetius perezi* Simon, 1902, habitus and colouration. (a) alive male from Somaliland, near Berbera, Somalia; (b–c) preserved male from Wadi Matam, Wahiba, Oman (b ventral opisthosoma colour pattern, c frontal view). Photo (a) by F. Kovařík.

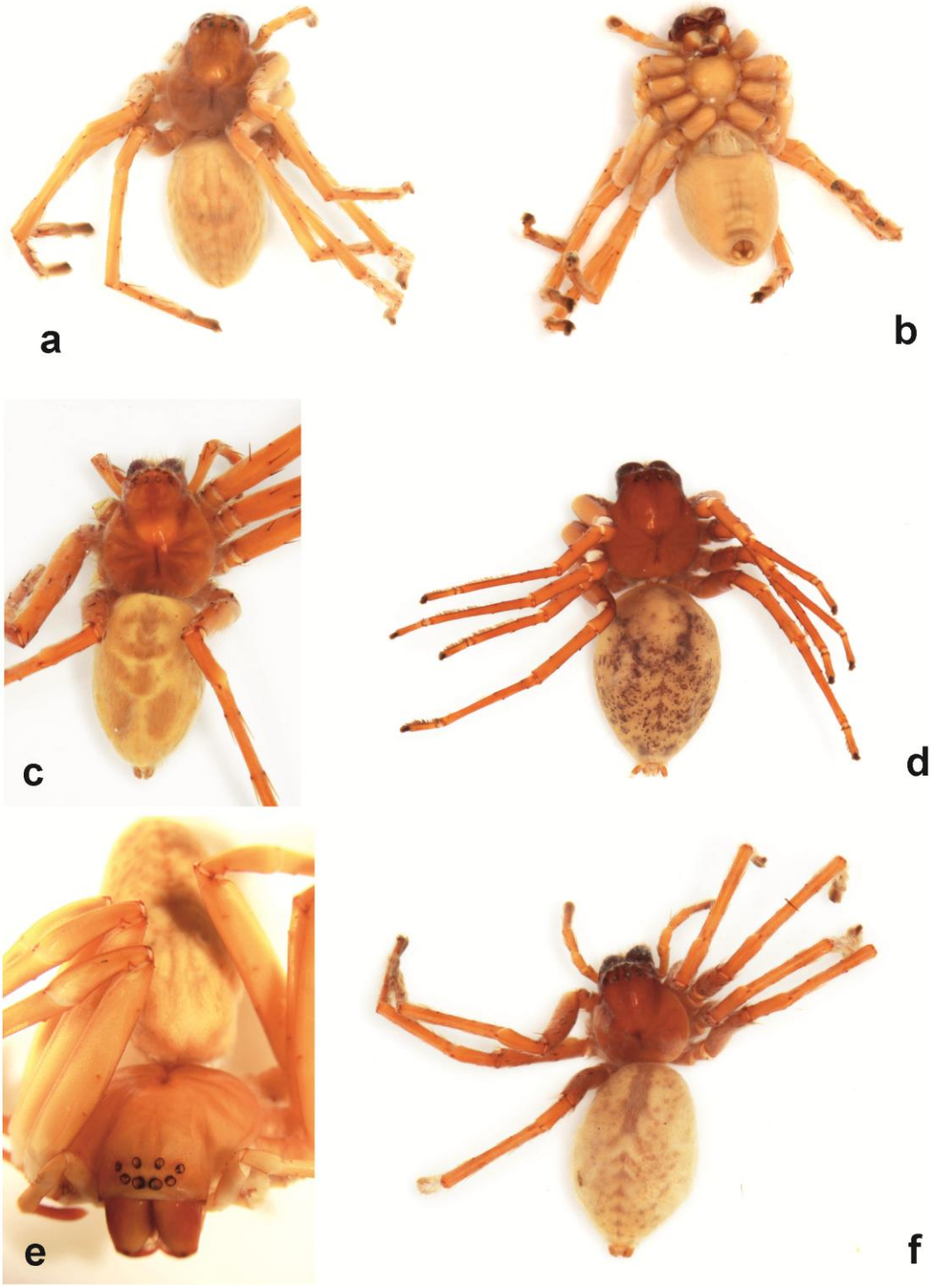

FIGURE 58. Habitus of species of the *doriae* group. (a–b) *Eusparassus doriae* (Simon, 1874) syntype female from Iran; (c) *Eusparassus maynardi* (Pocock, 1901) lectotype female from Pakistan; (d) *Eusparassus fuscimanus* Denis, 1958 female from Afghanistan; (e–f) *Eusparassus oculatus* (Kroneberg, 1875) female from Uzbekistan.

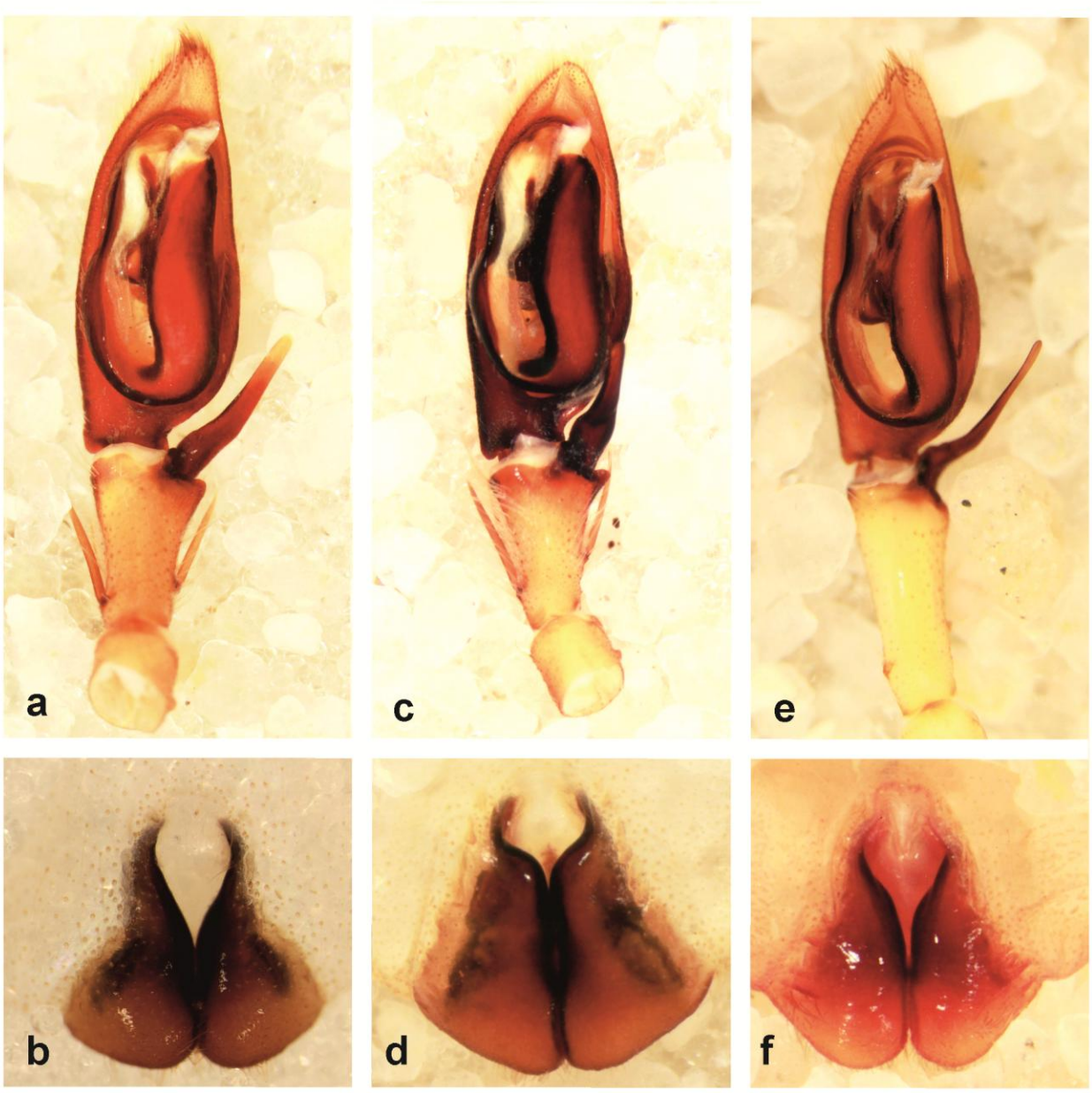

FIGURE 59. *Eusparassus walckenaeri* group. (a–b) *Eusparassus walckenaeri* (Audouin, 1826); (c–d) *Eusparassus laevatus* (Simon, 1897) **comb. nov.**; (e–f) *Eusparassus arabicus* **spec. nov.** (a, c, e) left male palps, ventral; (b, d, f) epigynes, dorsal.

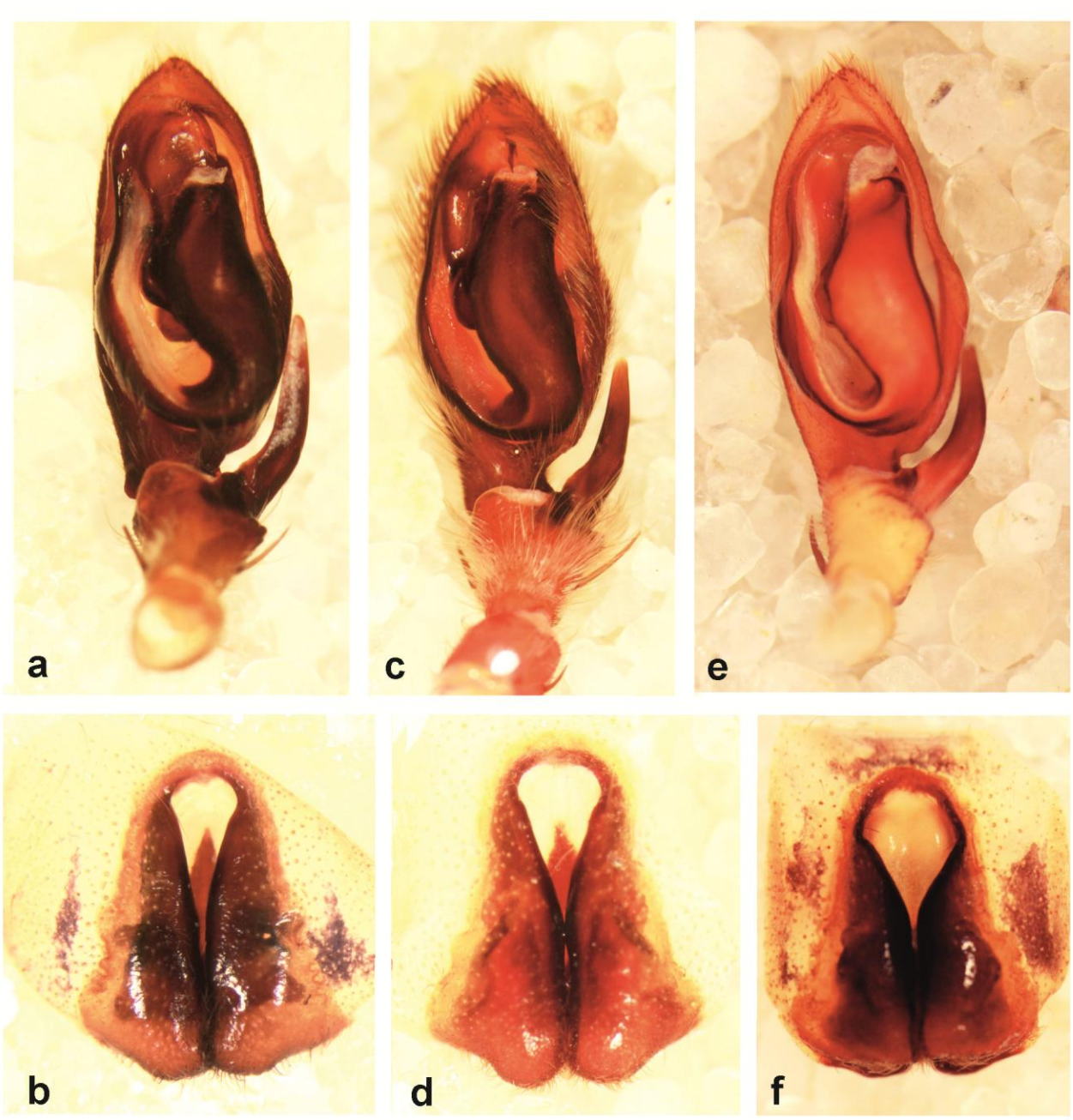

FIGURE 60. *Eusparassus dufouri* group. (a–b) *Eusparassus dufouri* Simon, 1932; (c–d) *Eusparassus levantinus* Urones, 2006; (e–f) *Eusparassus atlanticus* Simon, 1909 **stat. nov.** (a, c, e) left male palps, ventral; (b, d, f) epigynes, dorsal.

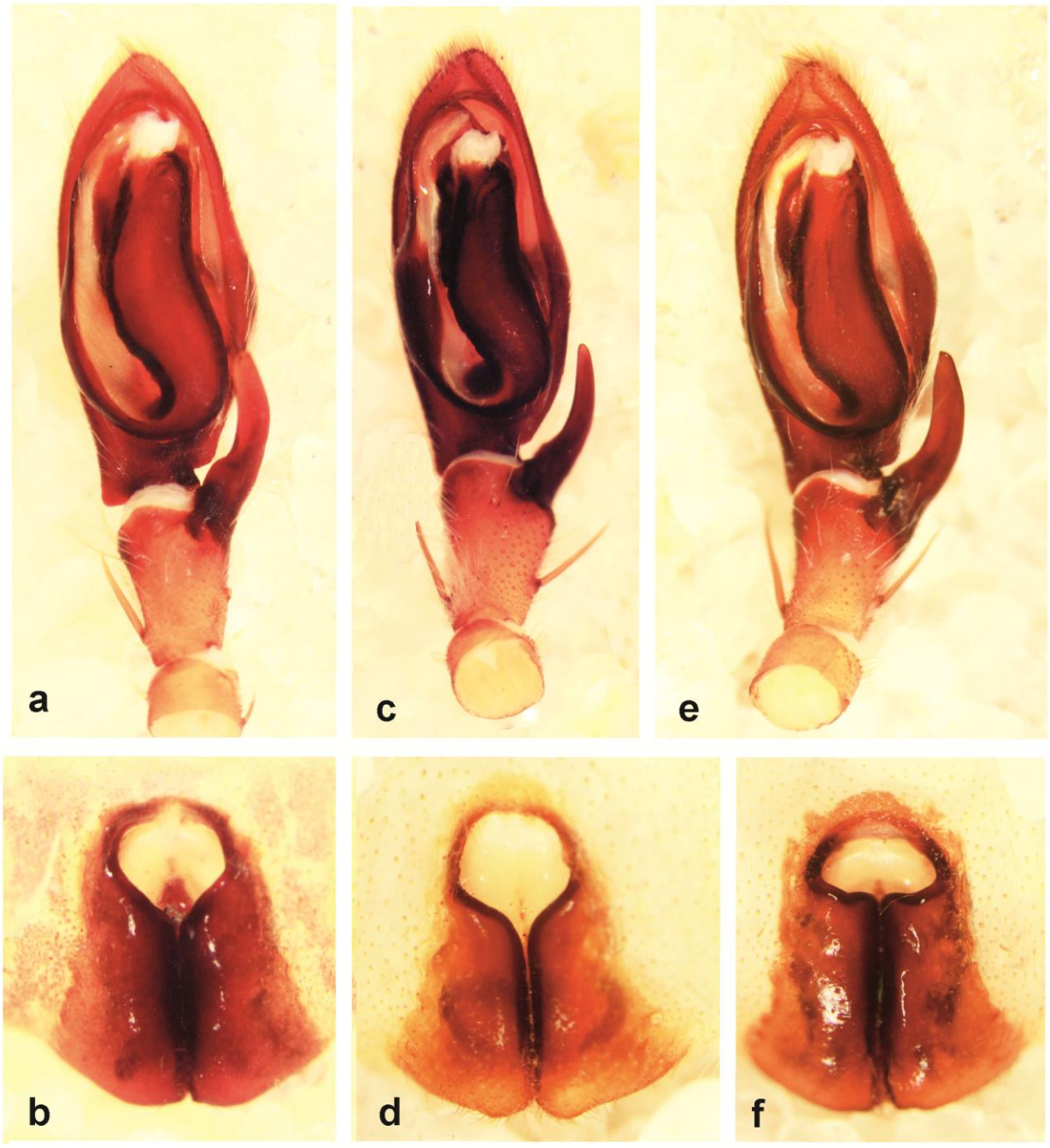

FIGURE 61. *Eusparassus dufouri* group. (a–b) *Eusparassus barbarus* (Lucas, 1846); (c–d) *Eusparassus fritschi* (Koch, 1873) **stat. rev.**; (e–f) *Eusparassus letourneuxi* (Simon, 1874). (a, c, e) left male palps, ventral; (b, d, f) epigynes, dorsal.

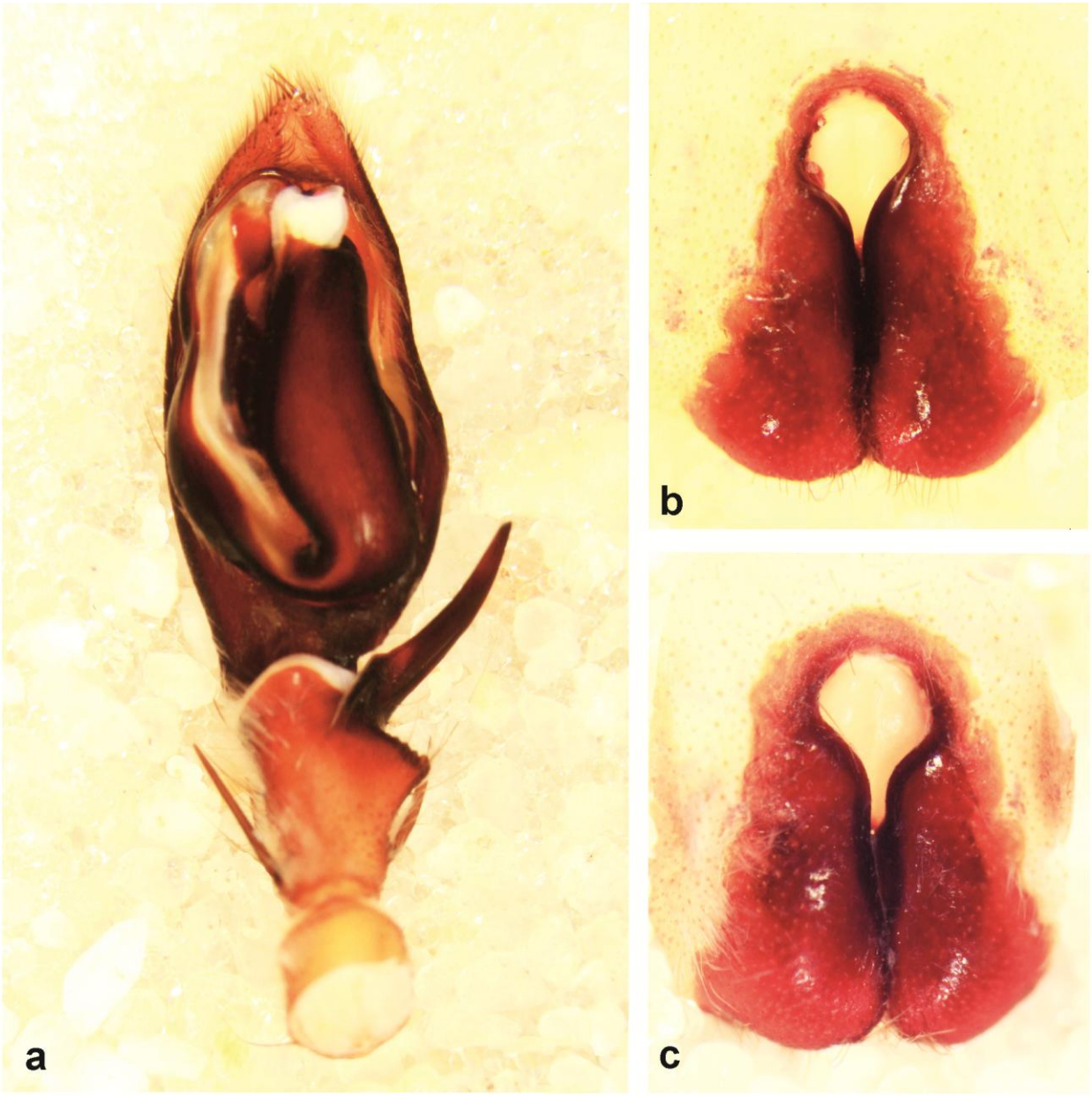

FIGURE 62. *Eusparassus dufouri* group. (a–b) *Eusparassus oraniensis* (Lucas, 1846); (c) *Eusparassus syrticus* Simon, 1909. (a) left male palp, ventral; (b, c) epigynes, dorsal.

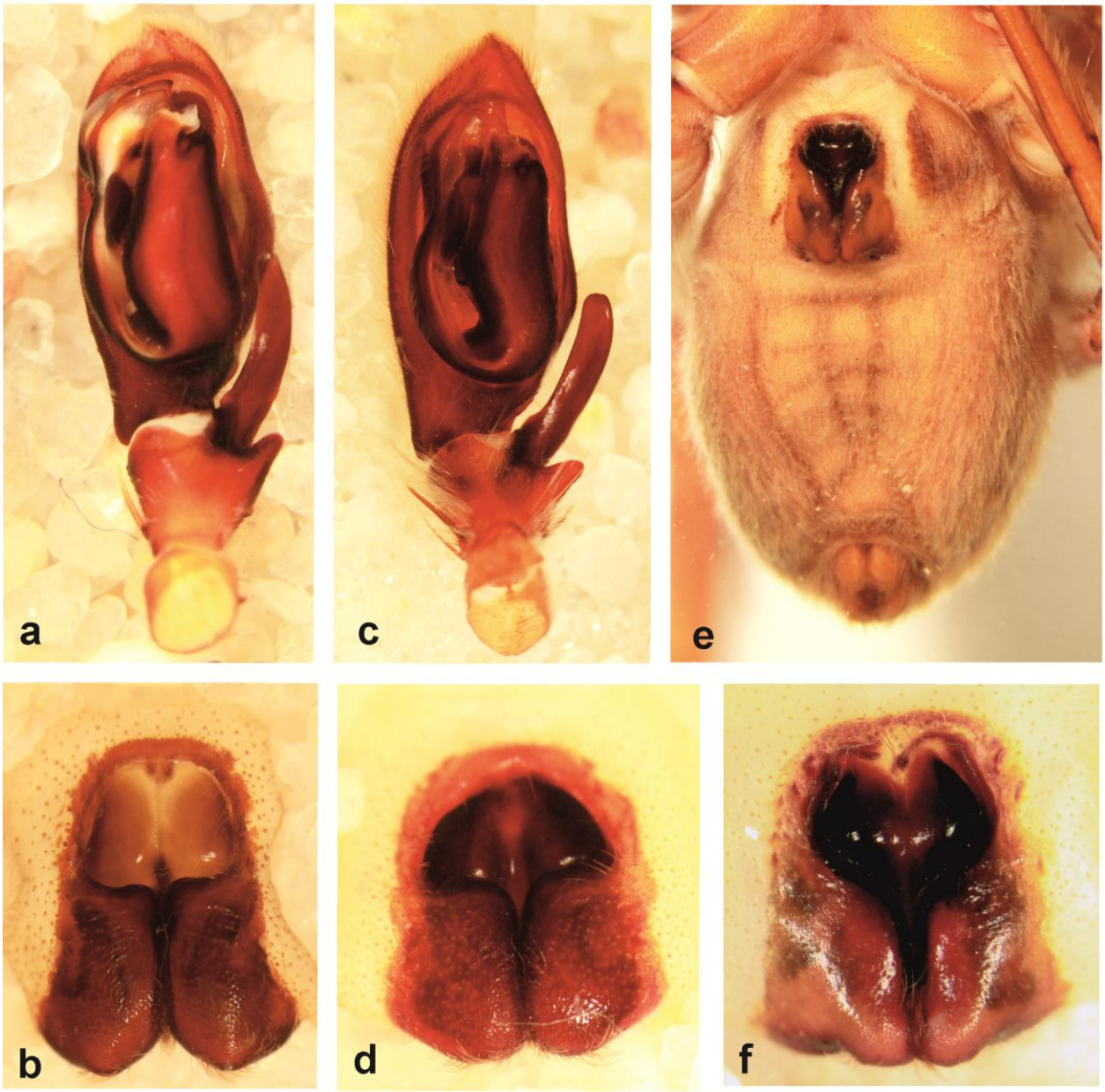

FIGURE 63. *Eusparassus vestigator* group. (a–b) *Eusparassus vestigator* (Simon, 1897) **comb. nov.**; (c–d) *Eusparassus reverentia* **spec. nov.**; (e–f) *Eusparassus pearsoni* (Pocock, 1901). (a, c) left male palps, ventral; (b, d, f) epigynes, dorsal; (e) ventral opisthosoma.

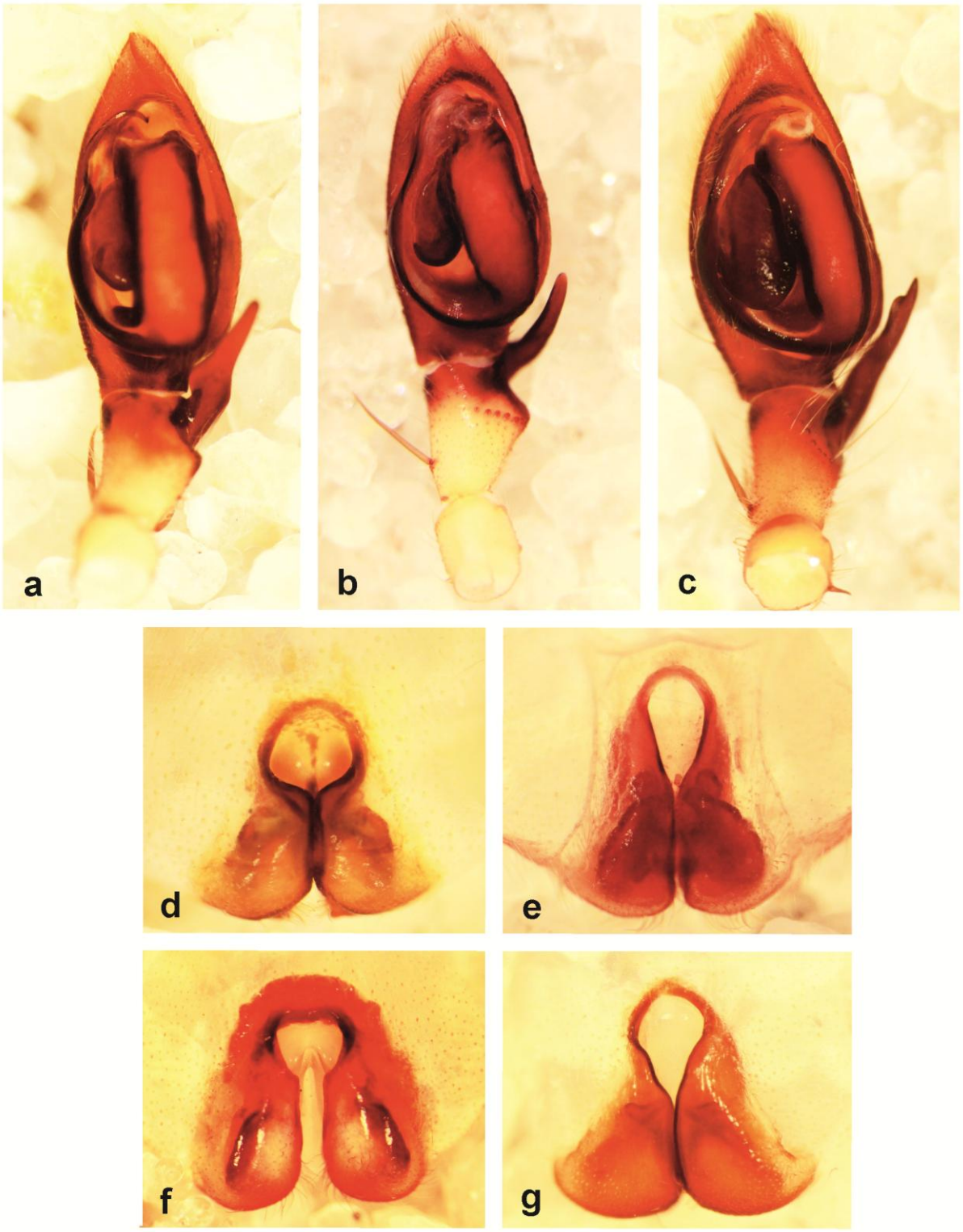

FIGURE 64. *Eusparassus jaegeri* group. (a, d) *Eusparassus jaegeri* **spec. nov.**; (b, e) *Eusparassus schoemanae* **spec. nov.**; (c, f) *Eusparassus jocquei* **spec. nov.**; (g) *Eusparassus borakalalo* **spec. nov.** (a–c) left male palps, ventral; (d–g) epigynes, dorsal.

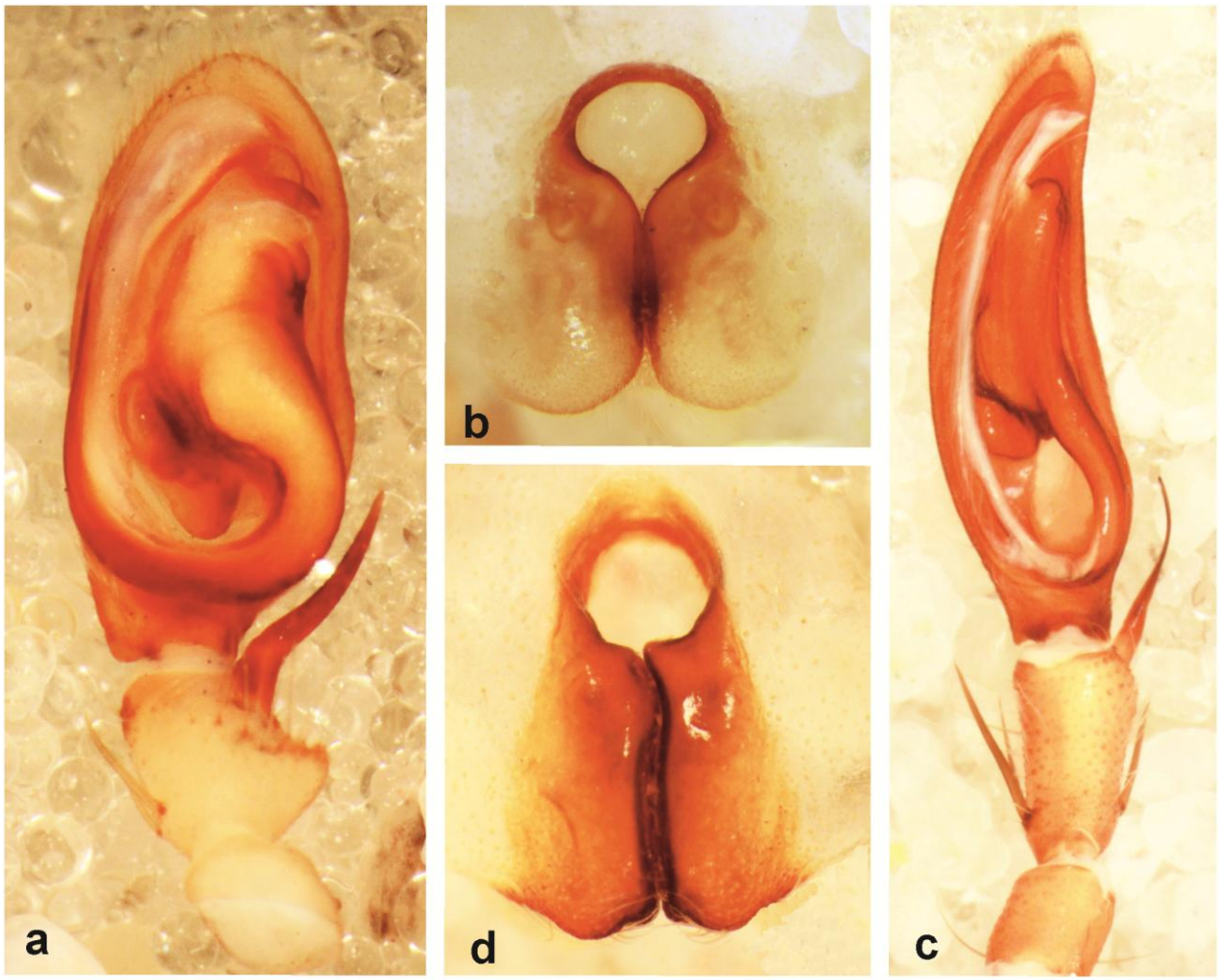

FIGURE 65. *Eusparassus tuckeri* group. (a–b) *Eusparassus tuckeri* (Lawrence, 1927) **comb. nov.**; (c–d) *Eusparassus educatus* **spec. nov.** (a, c) left male palps, ventral; (b, d) epigynes, dorsal.

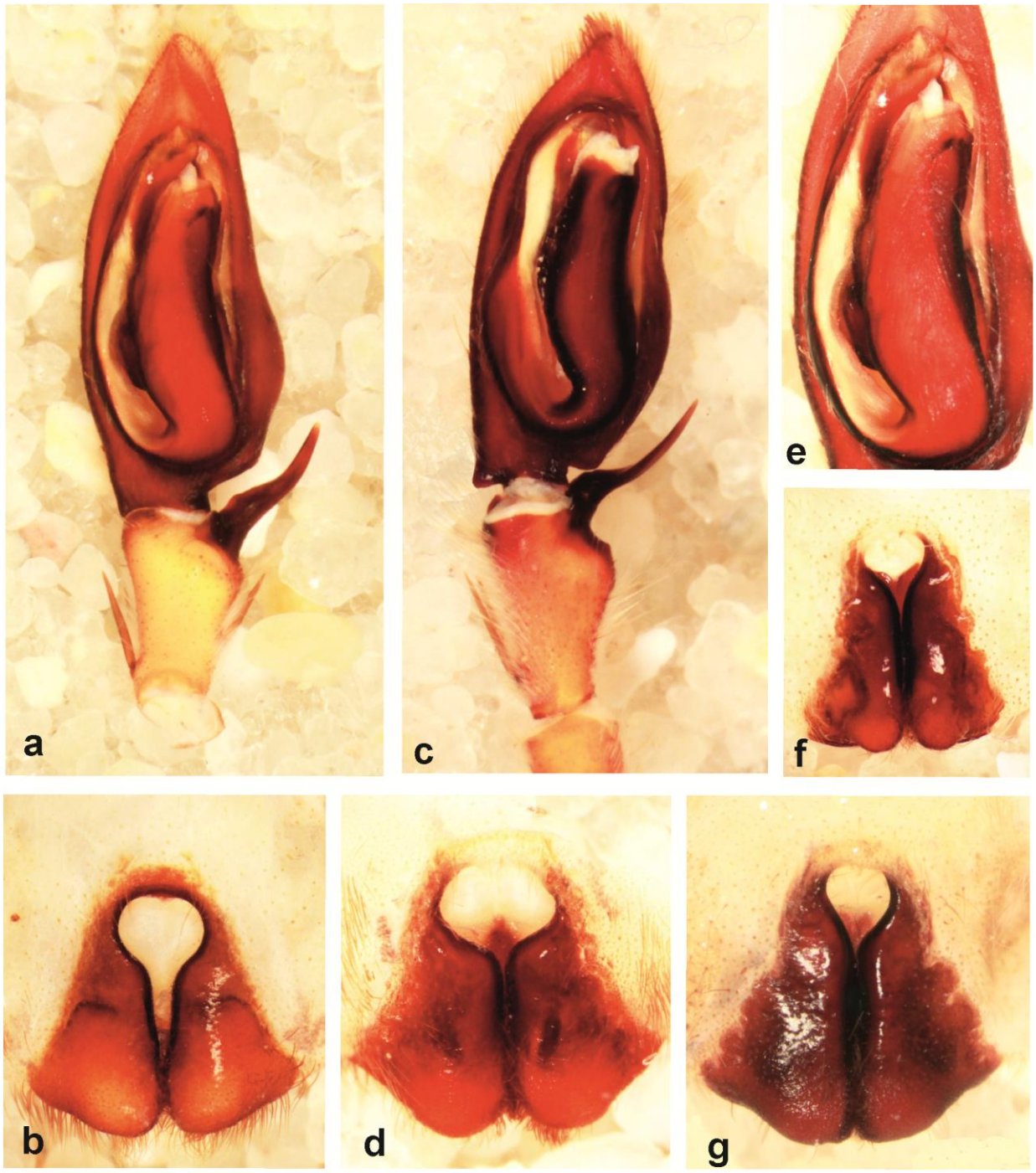

FIGURE 66. (a–b, e) *Cercetius perezi* Simon, 1902; (c–d) *Eusparassus xerxes* (Pocock, 1901); (f) *Eusparassus maynardi* (Pocock, 1901); (g) *Eusparassus pontii* Caporiacco, 1935. (a, c) left male palps, (e) bulbus, ventral (b, d, f, g) epigynes, dorsal.

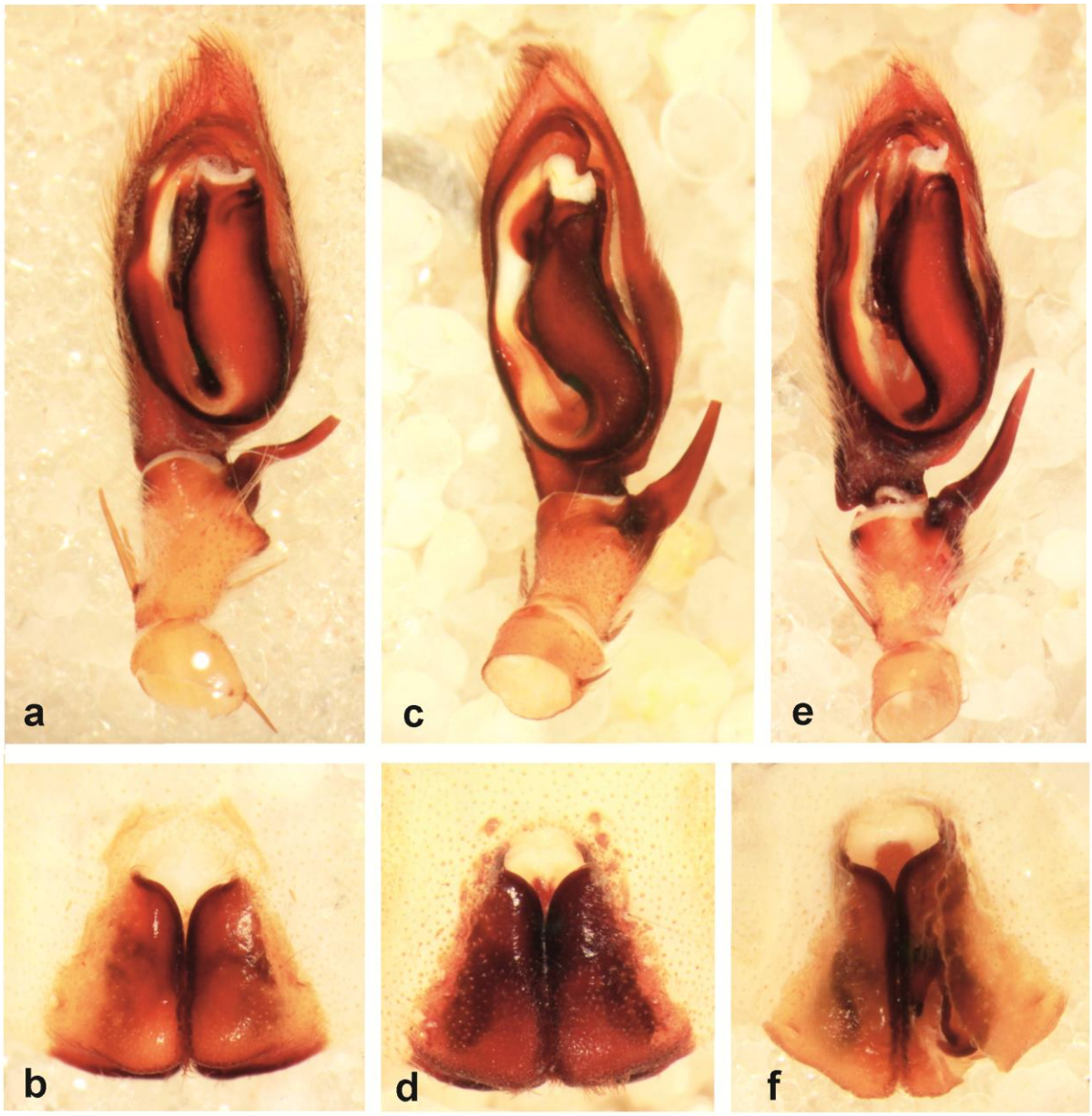

FIGURE 67. *Eusparassus doriae* group. (a–b) *Eusparassus doriae* (Simon, 1874); (c–d) *Eusparassus fuscimanus* Denis, 1958; (e–f) *Eusparassus kronebergi* Denis, 1958. (a, c, e) left male palps, ventral; (b, d, f) epigynes, dorsal.

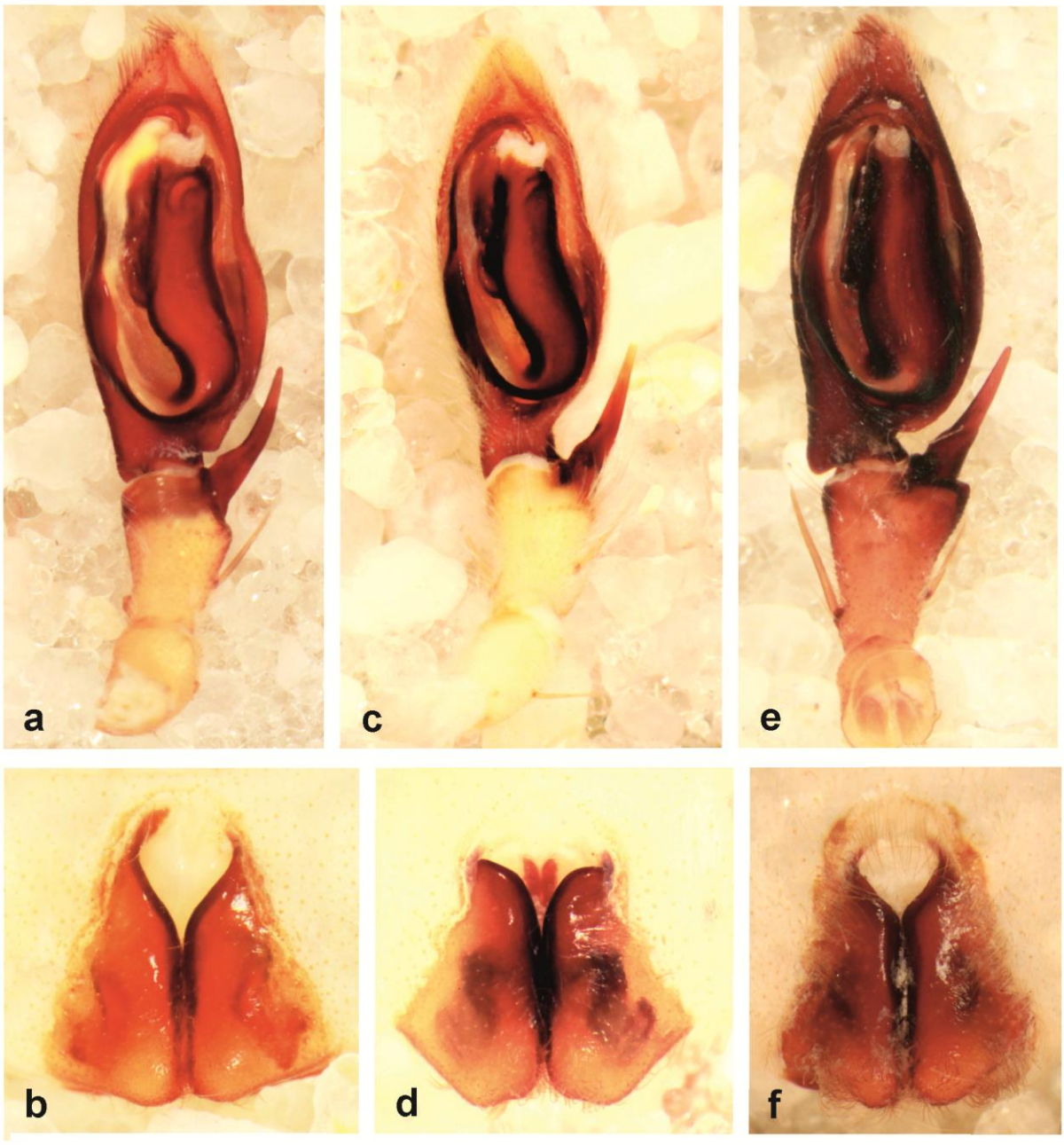

FIGURE 68. *Eusparassus doriae* group. (a–b) *Eusparassus mesopotamicus* Moradmand and Jäger, 2012; (c–d) *Eusparassus oculatus* (Kroneberg, 1875); (e–f) *Eusparassus potanini* (Simon, 1895). (a, c, e) left male palps, ventral; (b, d, f) epigynes, dorsal.

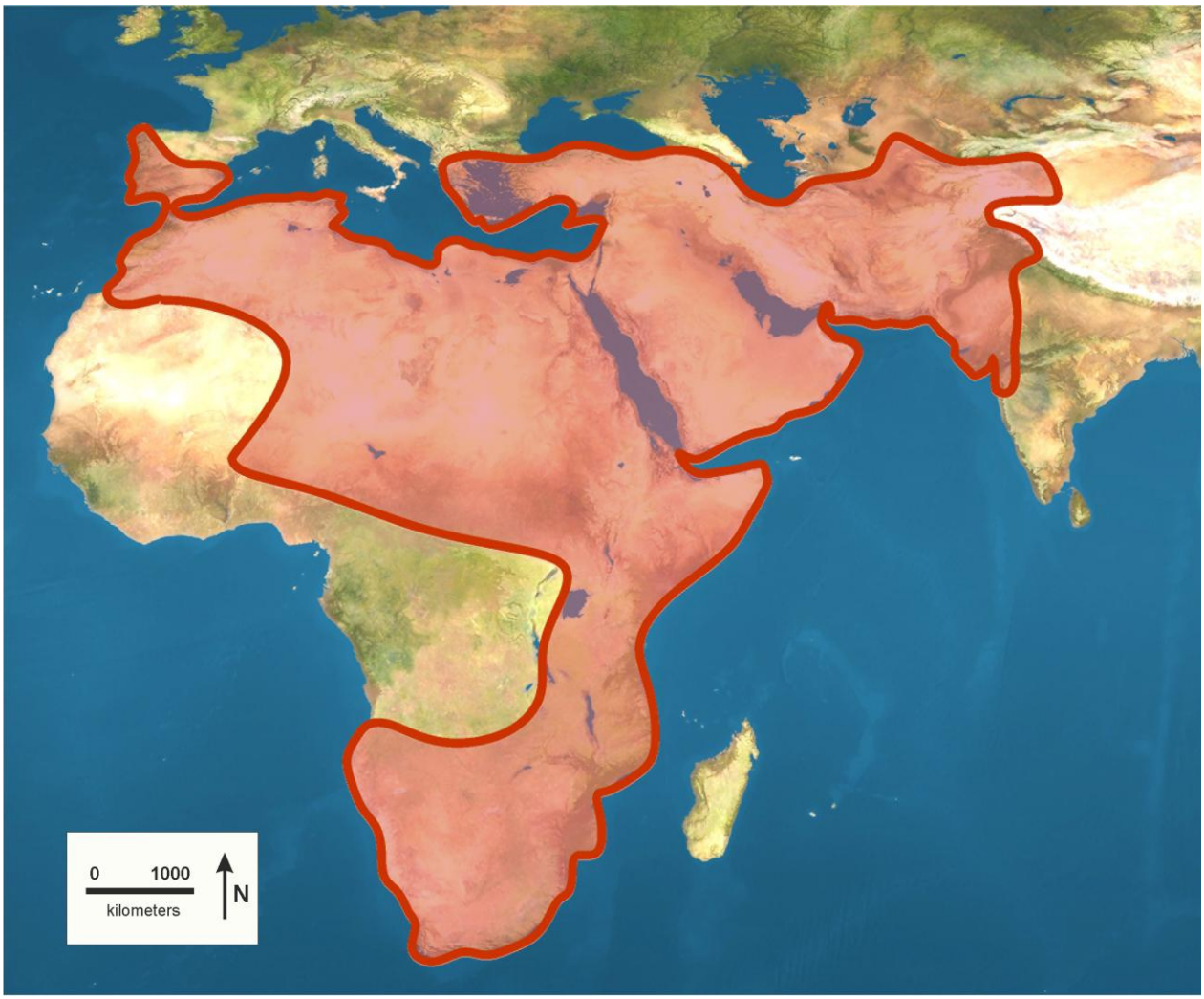

FIGURE 69. Distribution range of *Eusparassus* species.

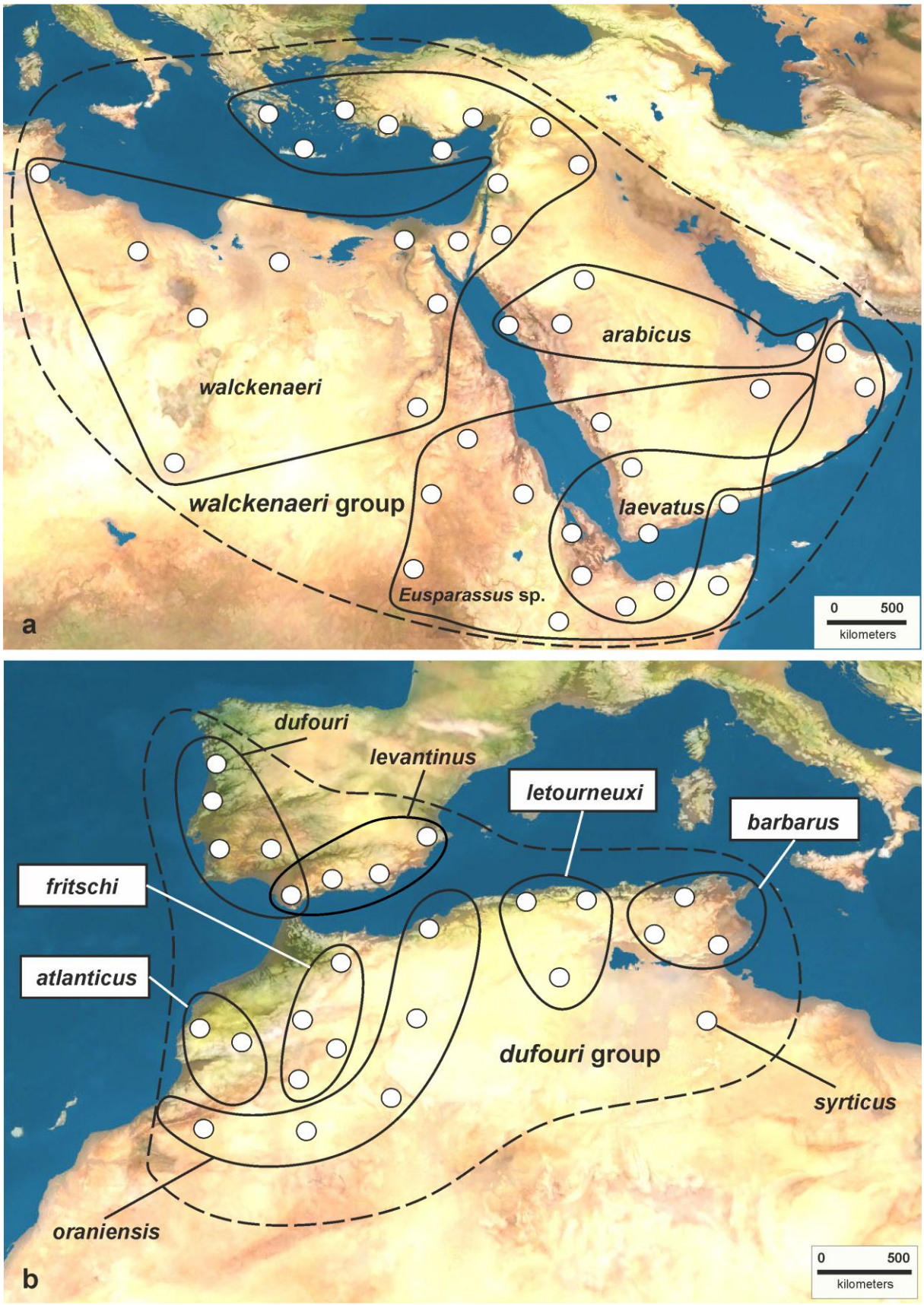

FIGURE 70. Distribution range of (a) *Eusparassus walckenaeri* group; (b) *Eusparassus dufouri* group.

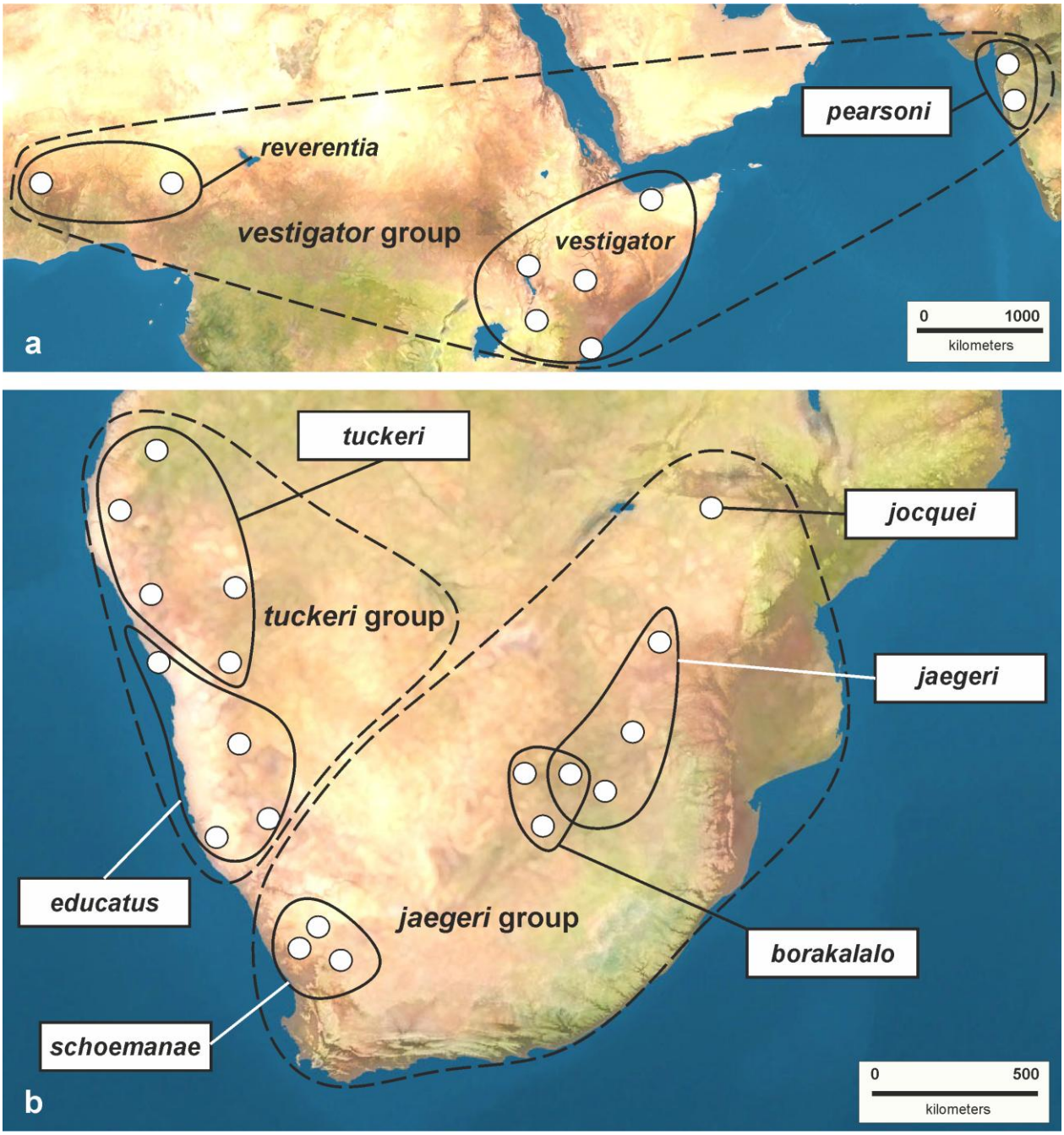

FIGURE 71. Distribution range of (a) *Eusparassus vestigator* group; (b) *Eusparassus tuckeri* and *jaegeri* groups.

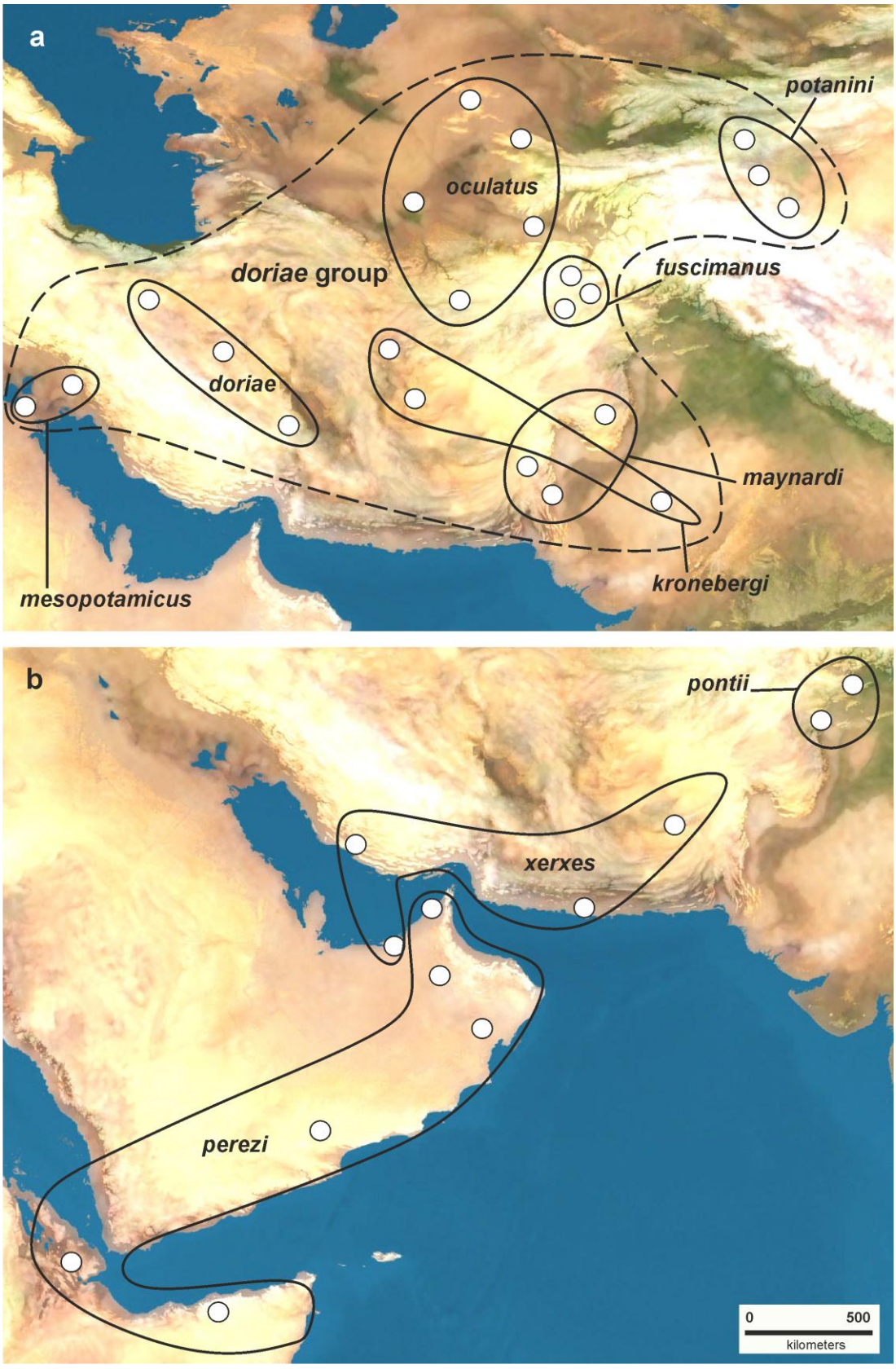

FIGURE 72. Distribution range of (a) *Eusparassus doriae* group; (b) *Eusparassus* incertae sedis and *Cercetius perezi*. (a, b) with the same scale.

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Anlage 1

Erklärung über Anteile der Autoren/Autorinnen an den einzelnen Kapiteln der Promotionsarbeit

Titel der Publikation/ des Manuskripts: **Molecular phylogeny of the huntsman spider family Sparassidae with focus on the genus *Eusparassus* and notes on the RTA-clade and 'Laterigradae'**

	Was hat der/die Promovierende bzw. was haben die Co-Autoren/Autorinnen beigetragen[#]	Name des/der jeweiligen Autors/Autoren/Autorin*
(1) Entwicklung und Planung		Majid Moradmand (85%) Peter Jäger (15%)
(2) Durchführung der einzelnen Untersuchungen/ Experimente	BEAST-Analyse (AS, MM), Phylogenetische Rekonstruktion mit Maximum Likelihood und Bayesian Inference (MM, AS)	Majid Moradmand Axel Schönhofer
(3) Erstellung der Daten-sammlung und Abbildungen	Sammeln von Spinnen für Analysen (PJ, MM), DNA-Extraktion und Sequenzierung (MM), Erstellung der phylogenetischen Matrizen (MM, AS)	Majid Moradmand Axel Schönhofer Peter Jäger
(4) Analyse/Interpretation der Daten	Interpretation der Phylogenetischen Rekonstruktionen (MM, AS), Vergleich verschiedener Methoden und Datensätze (MM)	Majid Moradmand, Axel Schönhofer
(5) übergeordnete Einleitung/ Ergebnisse/Diskussion		Majid Moradmand (85%) Axel Schönhofer (10%) Peter Jäger (5%)

[#]Bei 2, 3 und 4 bitte kurze inhaltliche Angaben der jeweiligen Anteile, bei 1 und 5 reichen prozentuale Angaben

*Mehrfacheintragungen möglich

Als Autoren/Autorinnen werden solche Personen bezeichnet, die an der Arbeit in Bezug auf die genannten Punkte in einer Weise mitgewirkt haben, dass sie für die ausgewiesenen Passagen (mit) verantwortlich sind. Personen, die an der Arbeit mitgewirkt haben, jedoch nicht in diese Kategorie fallen, sollten in der Danksagung Erwähnung finden.

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Chapter 3.3. Molecular phylogeny of Sparassidae with focus on *Eusparassus* and Eusparassinae

This chapter is based on the following manuscript in a slightly modified version.

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Abstract

The molecular phylogeny of the huntsman spider family Sparassidae is comprehensively investigated for the first time using four molecular markers (mitochondrial COI and 16S; nuclear H3 and 28S). Sparassidae was recovered as monophyletic and as most basal group within the RTA-clade. No affiliation to other members of the 'Laterigradae' (Philodromidae, Selenopidae and Thomisidae) was observed, the crab-like posture of this group is assumed a result of convergent evolution. Only the families Philodromidae and Selenopidae were found members of a supported clade together with Salticidae and Corinnidae, while Thomisidae was nested within the higher Lycosoidea. Including a considerable amount of RTA-representatives, the higher-level clade Dionycha was not supported monophyletic. Within Sparassidae monophyly of the subfamilies Heteropodinae *sensu stricto*, Palystinae and Deleninae was recovered. Sparianthinae was supported as the most basal clade, diverging considerably early from all other Sparassidae. Sparassinae and the genus *Olios* were found to be polyphyletic. Eusparassinae was not recovered monophyletic, with the two original genera *Eusparassus* and *Pseudomicrommata* in separate clades and only the latter clustered with most other assumed Eusparassinae, here termed the "African clade". Further focus was on the monophyletic genus *Eusparassus* and its proposed species groups, of which the *dufouri*-, *walckenaeri*- and *doriae*-group were recovered monophyletic with the latter two groups more closely related. The divergence time of Sparassidae and the genus *Eusparassus* were estimated with 186 and 70 million years ago respectively according to molecular clock analyses. An African origin of *Eusparassus* in Namib Desert was proposed.

Keywords: Sparassidae classification; Eusparassinae; Sparassinae, Heteropodinae, Palystinae, Sparianthinae, Dionycha; molecular dating

1. INTRODUCTION

1.1. Family level relationships of the "Laterigradae"

Spiders are the second most diverse order in the Arachnida and important and abundant predators in most terrestrial habitats (Foelix, 2010). Hence it is rather surprising that to date only a small fraction of their diversity has been included in studies on phylogenetic systematics (Agnarsson et al., 2013b; Arnedo et al., 2009; Hedin and Bond, 2006; Miller et al., 2010). Yet, phylogenetic information is lacking for entire families or includes only few representatives of families of up to thousand species. Within such a framework many phylogenetic hypotheses remain to be tested.

Among the currently known families of entelegyne spiders, the families Sparassidae Bertkau, 1872 (giant crab spiders or huntsman spiders), Selenopidae Simon, 1897 (wall crab spiders or flatties), Philodromidae Thorell, 1870 (running crab spiders) and Thomisidae Sundevall, 1833 ("true" crab spiders) share the character of laterigrade legs, that is characterised by a crab-like posture (Latreille, 1802). The characteristic leg position and crab-like locomotion enables laterigrades to manoeuvre more quickly and take refuge in even narrow crevices. Upon this easy to see character Latreille (1802) proposed the name 'Laterigradae' (sub "Latérigrades") for this group of taxa and Simon (1864) used an alternative term "Thomisiformes" for grouping the very same families. Coddington and Levi (1991) followed Latreille and Simon in assuming close phylogenetic relationship, although they noted that homoplasy could be possible. Prior to them, Homann (1971) studied the morphology of the eyes, and found Sparassidae and Philodromidae to have a similar eye structure that is different from Selenopidae. According to these eye structures, Homann (1975) proposed Sparassidae as sister to Philodromidae, and also related Thomisidae with the Lycosoidea. Bayer and Schönhofer (2013) recovered Thomisidae in an uncertain position as either sister group or part of Lycosoidea. Up to date there have been no molecular phylogenetic studies focusing on the inter-familial relationships of these laterigrades, but a few studies explored intra-familial relationships within Selenopidae (Crews and Gillespie, 2010; Crews et al., 2010), Thomisidae (Benjamin et al., 2008) and Sparassidae (Agnarsson and Rayor, 2013). The Philodromidae have not been subject of any molecular phylogenetic studies; except for being treated as outgroup.

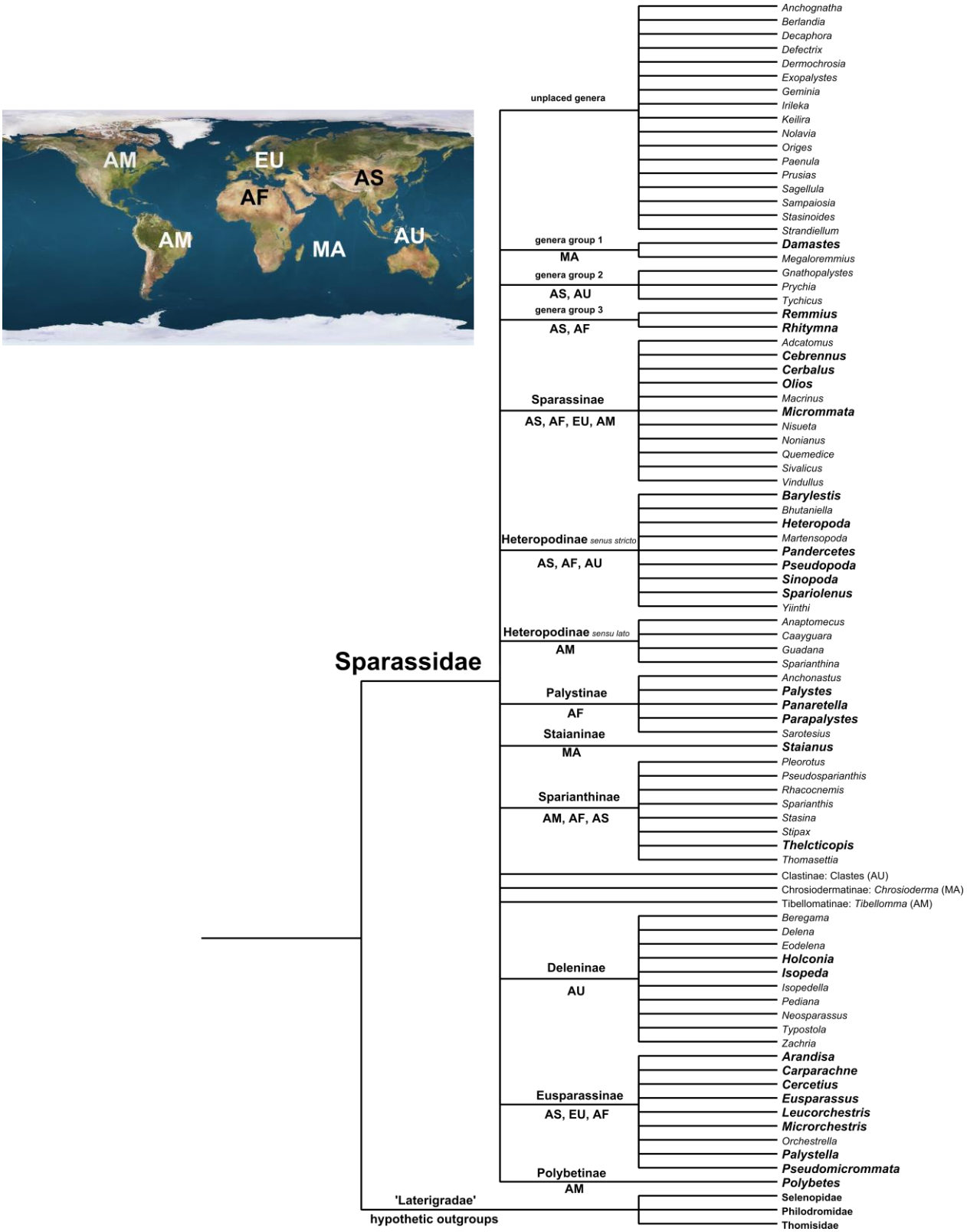

FIGURE 1. The present concept of Sparassidae relationships (modified after Jäger, 1998), with genera included in this study given in bold and larger. The geographic distribution of the groups is indicated at the branches or stated with the genera: AF (Africa), AM (America), AS (Asia), AU (Australia), EU (Europe) and MA (Madagascar).

1.2. Family Sparassidae and its phylogenetic placement

The cosmopolitan family of huntsman spiders, Sparassidae, is composed of small to very large hunting or ambushing spiders (Jäger, 2001). They inhabit a wide variety of mainly tropical to subtropical habitats, ranging from true deserts and semi-deserts over a wide variety of woodland and forest formations up to mountainous highlands (Hirst, 1992; Jäger and Kunz, 2005; Lawrence, 1962; Moradmand, 2013; Rheims, 2010a, b). Frequently recorded from caves (Jäger, 2012; Moradmand and Jäger, 2011), members from South East Asian caves represent the largest known living spiders in terms of leg-span (Jäger, 2005). Sparassidae currently comprises 85 genera and 1132 described species (Platnick, 2013) and the family thus represents one of the most diverse and successful groups of araneomorph spiders. The proposed synapomorphy of Sparassidae is the presence of soft trilobate membranes at the tip of the metatarsi of the walking legs (Petrunkevitch, 1928), which enable better mobility of the tarsi (Clarke, 1984). As another characteristic in Sparassidae Simon (1892: 26, fig. 40) found the tips of the claw tuft setae indented. Homann (1971) suggested the presence of a split rhabdome may be an additional synapomorphy, but studied the pigmentation and structure of the secondary eyes of only a few Sparassidae genera. Within the Entelegynae assemblage of Araneomorphae, Sparassidae are members of the RTA-clade, which are distinguished by the presence of a retrolateral tibial apophysis (RTA) on the pedipalps of males (Coddington and Levi, 1991). Within the RTA-clade Coddington and Levi (1991) and Coddington (2005) treated Sparassidae as a member of Dionycha. The Dionycha clade is solely characterised by its members having two-clawed tarsi and the group is currently composed of several heterogeneous spider families, with its monophyly still largely untested (Agnarsson et al., 2013b; Coddington, 2005).

1.3. Sparassidae subfamilies

Simon (1897, 1903) and Järvi (1912, 1914) were the main contributors towards a classification of Sparassidae into subfamilies. Simon (1897) treated Sparassidae as a subfamily of Clubionidae, and further classified “Sparassinae” into seven sub-groups (Sparasseae, Heteropodeae, Palysteae, Staianeae, Spariantheae, Clastieae and Chrosiodermateae) using somatic characters, mainly those concerning eye morphology (arrangement and size). Hogg (1903) proposed an additional subfamily Deleninae for some Australian endemics. Simon (1903) placed the genera previously classified as Sparassinae into Deleninae and proposed a new subfamily Tibellomatinae for a

monotypic genus based on a juvenile. Järvi (1912, 1914) was the first author who validated Sparassidae as a family. His classification exclusively emphasised characters of the female copulatory organs to propose two new subfamilies (Eusparassinae, Polybetinae) and used Micrommatinae for Sparassinae. These traditional classifications are still considered valid with modifications by Petrunkevitch (1928) and Roewer (1954). In his classification of Sparassidae subfamilies Petrunkevitch (1928) gave priority to somatic characters proposed by Simon. He partially rejected Järvi's classification and included Polybetinae and Deleninae in Eusparassinae. Croeser (1996) revised the Palystinae, but only proposed the transfer of a few genera between subfamilies. Jäger (1998) revised the character states of the subfamilies and recognized synapomorphies for Heteropodinae and Sparianthinae. He stated the status of the remaining subfamilies was far from resolved. Rheims (2007) provided a first morphological cladistics analysis, but due to subsequenly altered coding of several characters she asked to refrain from comparison (C. A. Rheims personal communication). Agnarsson and Rayor (2013) investigated the inter-generic phylogenetic relationships of the Australian Deleninae and proposed them monophyletic, although based on sparse outgroup sampling. Currently, the status of the remaining proposed subfamilies is weakly supported. The current classification concept of Sparassidae modified after Jäger (1998) is presented in Figure 1.

1.4. *Eusparassus* and Eusparassinae

The genus *Eusparassus* Simon, 1903 is the sixth largest genus of the family Sparassidae (Platnick, 2013) and include species which are among the most significant arthropod predators in dry and semidry areas of Africa and Eurasia (Levy, 1989; Moradmand and Jäger, 2012a; Moradmand, 2013). It is also a useful group for investigating phylogenetic relationships and historical biogeography within Sparassidae, as it was recently revised on a global scale (Moradmand and Jäger, 2012a; Moradmand, 2013) and contains the only well assignable fossil of the family. The minimum age of *Eusparassus* is currently dated back to the Eocene, about 44-49 MA, based on the conspicuous and well preserved *E. crassipes* (Koch and Berendt, 1854) found in northern European Baltic amber (Dunlop et al., 2011). Extant *Eusparassus* include 30 species, of which 27 are assigned to six species-groups namely the *dufouri*-, *walckenaeri*-, *doriae*-, *tuckeri*-, *jaegeri*- and *vestigator*-groups (Moradmand, 2013). Aside from the description of several new species, most transfers were from the genus *Olios* Wackenaer, 1837 to *Eusparassus* or vice versa (Jäger et al., 2002; Moradmand and Jäger, 2012a; Moradmand, 2013). Simon (1897)

first placed species of *Eusparassus* (at that time still in *Sparassus*) in Sparassinae. After describing *Eusparassus*, Simon (1903) transferred the genus with other Sparassinae into the Deleninae. Järvi (1912) proposed the new subfamily Eusparassinae for *Eusparassus*, *Pseudomicrommata* Järvi, 1914 and *Rhitymna* Simon, 1897, although *Rhitymna*, was later proposed to be misplaced (Jäger, 2003). Eusparassinae was reaffirmed by Jäger and Kunz (2003), who outlined some synapomorphies for the subfamily and suggested that further African genera should be included (see Figure 1). The monotypic genus *Cercetius* Simon, 1902 is likely to be a synonym of *Eusparassus* (Moradmand and Jäger, 2012b) and a formal case proposal was made to ICZN (International Commission on Zoological Nomenclature) to give *Eusparassus* precedence. Until a final decision usage of both names is retained (ICZN, 1999: Article 82). *Cercetius perezi* could not be affiliated to any species-group proposed by Moradmand (2013).

1.5. Aims of this study

Similarity of morphological traits among different lineages of organisms is not necessarily explained by sharing a common ancestor, but may as well be the result of convergent evolution (Revell et al., 2007). Various evolutionary processes, such as occupying similar habitats (Johnson et al., 2009), are known to cause phenotypic similarity (Bertossa, 2011). Phylogenetic methods have been applied to test characters assumed as diagnostic for the members of the order Araneae (e.g. Miller et al., 2010). However, the present classification still relies on many morphological traits that have yet to be investigated to discriminate between homology and convergence.

Despite being the tenth largest of 112 spider families, Sparassidae was never subject to any comprehensive phylogenetic systematic study. Neither monophyly of Sparassidae and the majority of respected subfamilies has been tested (except for Deleninae; Agnarsson and Raynor, 2013), nor was the position of Sparassidae resolved other than being a member of the family-rich RTA-clade. Most of the many sparassid genera require revision and evaluation of their systematic position within the family and subfamilies. The latter is also true for the recently revised genus *Eusparassus* (Moradmand, 2013) and its subfamily Eusparassinae. Yet, the revision of *Eusparassus* with its six proposed species-groups based on morphological characters provides a good example to evaluate the diagnostic characters used for classification within these taxonomic ranks.

In summary we aim to provide a rigorous insight into the phylogeny of Sparassidae (with a main focus on *Eusparassus* and the Eusparassinae) and its relationships to other spider families, especially those within the RTA-clade. Furthermore, the classification within Sparassidae is revisited, concerning all but the species level, and addressing the following main questions:

1. What is the systematic position of Sparassidae within the RTA-clade? Is the group 'Laterigradae' a valid taxonomic entity or is the laterigrade leg position the result of convergent evolution? Is the Dionycha, based on the single character of two-clawed tarsi, a monophyletic group?

2. Are the family Sparassidae and its currently accepted subfamilies monophyletic?

3. Are the genus *Eusparassus* and its proposed species-groups delineated by Moradmand (2013) monophyletic?

4. When did Sparassidae diverge from RTA-clade relatives? And when did the genus *Eusparassus* originate?

2. MATERIAL AND METHODS

2.1 Taxon sampling

Tissue samples for this study were mainly obtained from the Arachnology section, Senckenberg Research Institute, Frankfurt am Main (SMF) and partially from other spider collections. One leg of each freshly collected spider was preserved in pure 96% EtOH and subsequently stored at minus 28 °C. The specimens were preserved in 70% EtOH and given individual 'SD' numbers (voucher number) which were used as preliminary identification numbers. A list of all voucher specimens with respective SD numbers, their collection localities, deposition institute and the genetic markers investigated with Genbank accession numbers is given in Table 1.

To determine the placement of Sparassidae within the RTA-clade and to test the monophyly of the 'Laterigradae', representatives of 24 of 41 extant spider families now accepted in the RTA-clade were included. This sample of taxa was appropriate to test other relationships proposed for Sparassidae, e.g. if being a member of Dionycha or to revisit its original placement in the Clubionidae. Finally, a number of Orbiculariae, Eresoidea and Palpimanoidea were included to root this RTA-clade ingroup as suggested by previous studies (Agnarsson et al.,

2013a; Griswold et al., 2005; Miller et al., 2010; Spagna and Gillespie, 2008). Sequences for most RTA-clade (non-sparassid) and outgroup taxa were acquired from Genbank (see Table 2).

Monophyly of Sparassidae and the relationships of its major subfamilies were tested by including a comprehensive coverage of taxa from across the overall geographic distribution range of the family, and by including representatives of all larger subfamilies. Geographic sampling covered Africa, Madagascar, Eurasia, Australasia, North America and Central and South America. The representatives of the following historically proposed subfamilies were included in the analyses: Eusparassinae, Sparassinae, Heteropodinae, Palystinae, Polybetinae, Staianinae, Sparianthinae and Deleninae, as well as some presently unplaced genera (see Figure 1). Fresh tissues for the following subfamilies remained unavailable: Clastinae (New Guinea), Chrosiodermatinae (Madagascar) and Tibellomatinae (Venezuela); all are considered monotypic, with Tibellomatinae based on a single juvenile.

To test relationships within *Eusparassus* and the validity of the six *Eusparassus* species-groups proposed by Moradmand (2013) at least two representatives of the *dufouri-*, *walckenaeri-*, *doriae-* and *tuckeri*-group were included. Of the *jaegeri*-group only a single member was available, and no individual of the *vestigator*-group (two species in Central and East Africa and one in India) could be obtained. Additionally, *Cercetius perezi* was included in the analyses to test its relationships with *Eusparassus* group taxa.

2.2 DNA amplification, sequencing and pre-analysis data handling

Extraction of genomic DNA used the CTAB method after Wallace (1987; for details see Bayer and Schönhofer, 2013). The nuclear 28S rRNA gene (28S), Histone H3 (H3) and the mitochondrial cytochrome c oxidase subunit I (COI) and 16S rRNA gene (16S) were amplified using primers and PCR conditions specified in Table 3. These genes have previously shown to be useful for inferring phylogenetic relationships in other groups of spiders (Arnedo et al., 2004; Spagna and Gillespie, 2008; Arnedo et al., 2009; Crews et al., 2010; Miller et al., 2010, Dimitrov et al., 2012; Bayer and Schönhofer, 2013; Dimitrov et al., 2013; Wood et al., 2013). Fragments were purified using the QIAquick PCR purification kit (Qiagen) and sequencing was performed with the BigDye Terminator Cycle Sequencing Kit v3.1, sequencing fragments from both directions, using primers as mentioned. The majority of previously listed procedures were realised by the Scientific Research and Development GmbH, Bad Homburg, Germany (SRD).

Sequence contigs were assembled and edited using DNA Baser v3.5.1 (Heracle BioSoft, http://www.DnaBaser.com) and Sequencher v4.1.4 (Gene Codes Corporation, Ann Arbor, MI). Sequences were initially aligned using MEGA v4.1b (Tamura et al., 2007) checking for correct amino acid translation in COI and H3. To incorporate structural information, 28S and 16S were further aligned with MAFFT v7 (Katoh and Standley, 2013) using the Q-INS-i strategy as recommended by Katoh and Toh (2008). In rare cases, sequences of 28S were manually re-adjusted or sequences removed from the alignment. In some specimens, paralogous copies of H3 and 28S were observed, and excluded from the analyses. Models of sequence evolution were evaluated for each gene using jModeltest v0.1.1 (Posada, 2008) under three substitution schemes (JC, HKY and GTR) on a fixed BIONJ tree, allowing for unequal base frequencies and among-site rate variation and based on the Akaike information criterion. COI and H3 were further partitioned into single codon positions using Mesquite v2.75 (Maddison and Maddison, 2011) and models evaluated for each partition as defined above.

2.3. Alignment strategies and phylogenetic analyses

Aligning deeply divergent taxa introduced many gaps and regions of alignment uncertainty to the 28S and 16S partitions. We thus assumed the composition of taxa would influence our analyses, and investigated changes caused by alternate taxa combinations, thereby also testing the robustness of our data. We investigated taxon combinations as follows:

1) the full data set including all ingroup and outgroup taxa (All-taxa set);

2) all outgroups, but Sparassidae reduced to a set of eight most divergent taxa (see Fig. 2) as predetermined by other analyses (All-outgroups-8-Sparassidae set);

3) Sparassidae reduced to eight taxa as previously defined, all members of the RTA-clade, but other outgroups reduced to *Araneus diadematus* Clerck, 1757 to root this ensemble (RTA-out-8-Sparassidae set);

4) including only Sparassidae and accepting *Thelcticopis* Karsch, 1884 as outgroup, as predetermined by other analyses (Full-ingroup set);

5) as previously defined but reducing terminal taxa in groups with many representatives, e.g. including only two *Eusparassus* species (Full-ingroup-2-*Eusparassus* set).

These taxon combinations allowed evaluation of all initial hypotheses using more than one alignment version. For example the position of Sparassidae within the RTA-clade was estimated in data sets 1, 2 and 3, and the ingroup phylogeny of Sparassidae and the position of Eusparassinae in data sets 1, 4 and 5. For all combinations gene-partitions of 28S and 16S were re-aligned using the described strategies, while this proved unnecessary for the coding genes. For these rRNA genes we also investigated additional alignment versions of the specified five data sets by removing areas of alignment uncertainty using Gblocks (Castresana, 2000; available at http://www.phylogeny.fr/) with least stringent settings. Models were re-evaluated for all partitions of different taxon-combinations or alignment versions (Table 4), and applied to the subsequent analyses. Concatenation and alignment conversion was handled with Mesquite v2.75, while alignment manipulation and curation used MEGA v4.1b (Tamura et al., 2007). For a comparison of the length of all partitions in all data sets see Table 4.

Maximum likelihood analyses (ML) were performed using raxmlGUI v0.95 (Silvestro and Michalak, 2011). Node support was assessed from 1000 non-parametric bootstrap (bt) pseudoreplications (Felsenstein, 1985) as implemented in raxmlGUI (according to Stamatakis et al., 2008). Bayesian inference (BI) topologies were assessed using MrBayes v3.2.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Analyses were run for 5,000,000 to 20,000,000 generations, where the standard deviation of split frequencies had dropped below 0.01, and convergence diagnostics were satisfied for all sampled parameters with few exceptions (ESS >200, PSRF = 1.00; Ronquist et al., 2011). The first 25% of trees were discarded as burn-in, with remaining trees used to reconstruct a 50% majority rule consensus tree. Split frequencies were interpreted as posterior probabilities (pp) of clades. We considered branches receiving 1.00 pp and >87 bt as highly supported (Zander, 2004) and branches receiving >0.94 pp and >69 bt as sufficiently supported.

2.4. Divergence time estimation

Approximate taxon divergence times were estimated from the concatenated data using BEAST v1.7.2 (Drummond et al., 2012), applied to two selected data sets: All-outgroups-8-Sparassidae set and Full-ingroup set with MAFFT alignments. Due to computational limitations, the data were partitioned by genes only, with models set to HKY and invariable sites and gamma as suggested by jModeltest. Nodes were not constrained to be monophyletic and no tree model

operators were removed, allowing BEAST to re-estimate the topology. Analyses were run until ESS values exceeded 200 for all priors, which was after 50,000,000 generations, and checked for convergence using Tracer v1.5. We also investigated changes in the speed of substitutions per lineage using an uncalibrated random local clock model as implemented in BEAST (Drummond and Suchard, 2010). For final analyses in BEAST a Yule model of speciation and a relaxed log-normal clock were set. Clock rates were unlinked and estimated for individual partitions.

For the BEAST analysis only well supported nodes of the All-outgroups-8-Sparassidae set were calibrated using fossil data (see Fig 4). Calibrations (parameters given in parentheses) were set as suggested by Wood et al. (2013) treating them as lognormal distributions with a hard lower bound, based on the minimum age of the fossil, and a soft 95% upper bound to allow significantly older ages:

1) Oecobiidae-Hersiliidae: Penney et al. (2012) state comparable divergence times between Eresidae, Oecobiidae and Hersiliidae, with the common ancestor of Oecobiidae and Hersiliidae known from Lebanese amber (125-135 MA; Penney and Selden, 2011) (parameters: mean 2.3, stdev 1, offset 123 = 5%: 124.9 MA, median: 133 MA, 95%: 174 MA; calibration according to Wood et al., 2013),

2) Salticidae-Philodromidae: with the origin of Salticidae still debated, we used the compelling salticid fossil record as not predating Eocene Baltic amber (Penney and Selden, 2011; parameters: mean 2.3, stdev 1, offset 43 = 5%: 44.9 MA, median: 53 MA, 95%: 94.7 MA),

3) Dictynidae-other families: According to the presence of Dictynidae in Burmese amber (100 MA; Penney and Selden 2011), the divergence with other families is set to slightly predate this deposit (parameters: mean 2.89, stdev 1, offset 96.5 = 5%: 100 MA, median: 114.5 MA, 95%: 189.7 MA; Penney and Selden, 2011; Wood et al., 2013),

4) Lycosidae-Pisauridae: As for the previous family, Pisauridae fossils are present in Burmese amber (100 MA; Penney and Selden 2011). We did not follow Wood et al., (2013), assuming much younger divergence between Lycosidae and Gnaphosidae, as this family relation was not found supported and Gnaphosidae fossils already date back to Baltic amber (Penney and Selden 2011; parameters: mean 2.89, stdev 1, offset 96.5 = 5%: 100 MA, median: 114.5 MA, 95%:189.7 MA).

To constrain the root of the "Full-ingroup set" we applied the divergence age of *Thelcticopis* from all other Sparassidae as based on the analysis of the "All-outgroups-8-

Sparassidae set" (normal distribution; parameters: initial value/mean 163.0, stdev 20 = 2.5%: 130 MA, median: 163 MA, 97.5%: 202 MA). For this set we further calibrated the earliest divergence within *Eusparassus* (mean 1.7, stdev 1.51, offset 43.5 = 5%: 43.96 MA, median: 48.97 MA, 95%: 109.1 MA) using the minimum age based on the amber fossil *E. crassipes* (Dunlop et al., 2011) and the maximum age based on the biogeographic evidence (assuming *Eusparassus* originated after the breakup of Gondwana; Briggs, 1995; Sanmartín and Ronquist, 2004).

3. RESULTS AND DISCUSSION

3.1. Comparison of different alignment strategies and phylogenetic analyses

Different taxon combinations, alignment strategies and reconstruction methods were used to evaluate how they influenced comparable phylogenetic results. In total 20 combinations were investigated. For comparison corresponding data were mapped upon our preferred topologies of the All-outgroups-8-Sparassidae set (Fig. 2) and the Full-ingroup set (Fig. 3), both resulting from ML reconstructions and applying MAFFT alignment.

Including taxa within and outside the RTA-clade significantly increased the number of gapped sites within the 28S and 16S partitions of our alignments, while Gblocks gradually excluded more of these heterogeneous positions. This caused the initial MAFFT alignments to increase in length, but Gblocks to remove larger portions, such that final alignments incorporating more heterogeneous taxa were significantly shorter than before (Table 4). Against expectations, removing outgroup taxa to reduce the amount of alignment uncertainty in the RTA-clade for a clearer phylogenetic signal failed to achieve such results (RTA-out-8-Sparassidae set). While support in the basal nodes of the RTA-clade was generally weak, analyses using multiple outgroups recovered comparable topologies and yielded higher bootstrap values and posterior probabilities (Fig. 2). Only in a few cases and in shallow divergent clades (e.g. within *Eusparassus walckenaeri* (Audouin, 1826) and *E. dufouri* Simon, 1932), support values were found to significantly increase when reducing outgroup taxa (Fig. 3).

Other manipulations more fundamentally influenced the analyses. Removing large portions of 28S and 16S apparently caused significant loss of information on ingroup relationships, as seen in the frequent lower support of Gblocked analyses, especially for the gap-rich All-taxa set (Fig. 3).

This cause is also likely for lower support seen in some outgroup taxa relationships (Fig. 2), but to a much lower extent than seen in the ingroup. In terms of methods we frequently found MrBayes to better support clades than RAxML. MrBayes also showed high support in some reconstructions that did not after processing with Gblocks. No case of high MrBayes support recovered a different phylogenetic constellation than RAxML, as for which both methods remained comparable in supporting the same topology. However, interpretation of results in the absence of, at least sufficient, RAxML support was cautious.

Some results also indicate the need to add more data, e.g. as seen in the values displayed throughout the Clubionoidea+Gnaphosoidea-clade (Fig. 2). Here, variations of the number of outgroup taxa or exclusion of one Clubionidae taxon, as well as cleaning alignments via Gblocks, significantly changed the support for this clade.

In summary no general preference towards a certain combination of taxa, alignment criterion or phylogenetic method is obvious. Our strategy thus proved to be reasonable in recovering differences between single reconstructions, in testing the robustness of our data and in allowing a comparison of phylogenetic results and interpretation of alternatives.

To state a mere observation, ML and BI results showed different performance in terms of supporting comparable phylogenetic splits. While ML was perceived to gradually increase support with increasing strength of the phylogenetic signal, rarely attaining maximum support, BI often quickly and fully supported respective splits. This “all or nothing” behaviour caused BI to support a considerable proportion of splits that received much lower support, often below significance, for ML. However, no case of high MrBayes support recovered a different phylogenetic constellation than RAxML, as for which both methods remained comparable in supporting the same topology.

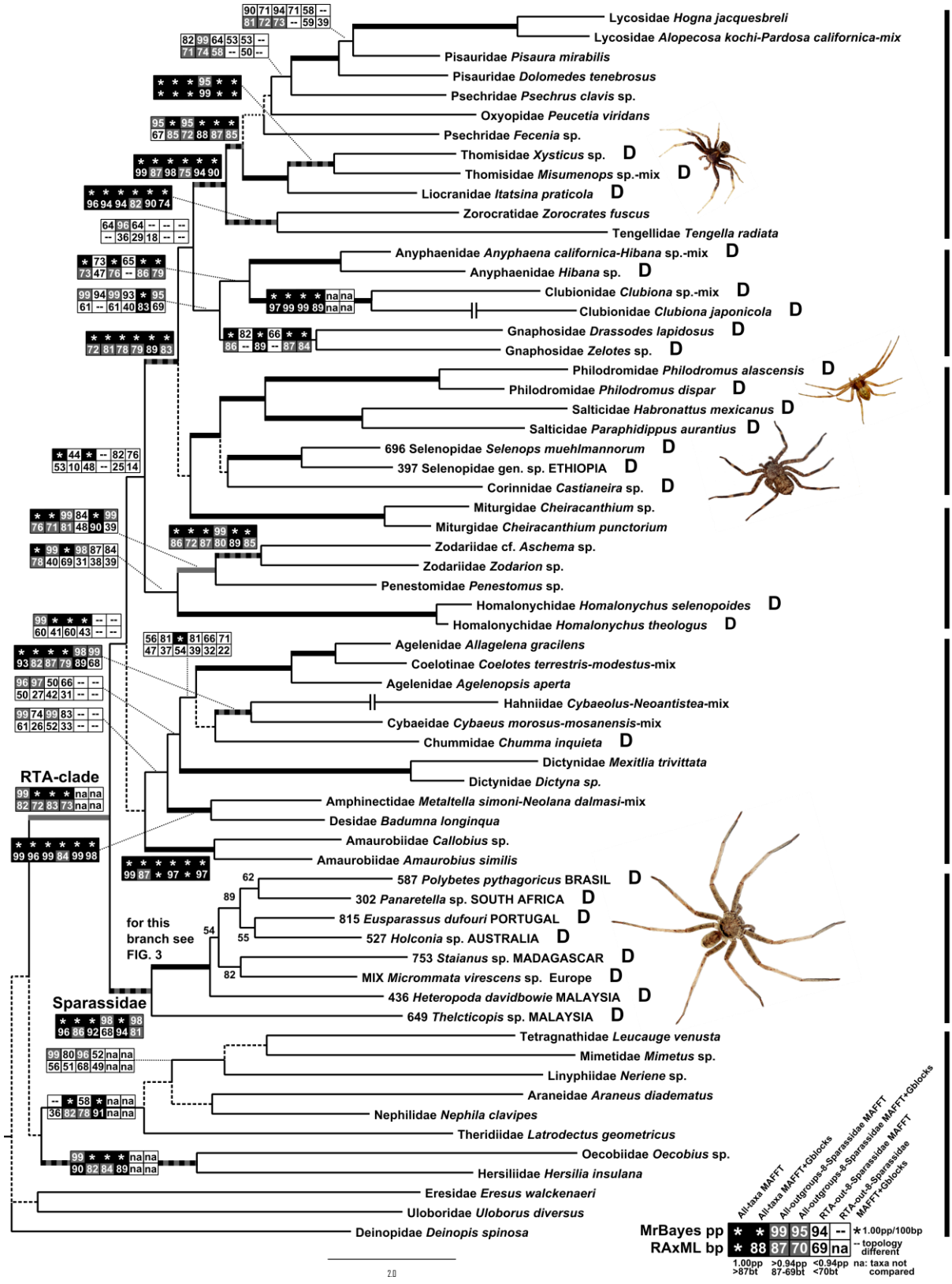

FIGURE 2. Maximum Likelihood tree with all outgroup taxa and a reduced Sparassidae set using MAFFT alignment (All-outgroups-8-Sparassidae set). Results of other analyses are mapped upon this tree, summarizing the overall support for each branch. Bold, black or thin, dashed branches without additional

Fig. 2.continued: table indicate respective support in all compared analyses, with bold, black indicating high support (>87bt, 1.00pp), and thin, dashed no considerable support (<69bt, <0.94pp). For other branches support is given in detail by the associated tables, branch appearance (bold, or shaded) summarises support by at least 2/3 of the analyses and grey indicates sufficiently support (>69bt, >0.94pp). Spider pictures indicate the position of laterigrade groups within the tree and letter "D" indicate the position of Dionycha members; abbreviations Phil. (Philodromidae), Sele. (Selenopidae), Salt. (Salticidae), Cor. (Corinnidae). Terminal branches of *Clubiona japonicola* and the Hahniidae sequence mix were artificially shortened to 1/3 of their actual length.

3.2. RTA-clade, 'Laterigradae' and the position of Sparassidae

The RTA-clade was recovered as a monophyletic group containing Sparassidae in all of our analyses. The monophyly of the RTA-clade was also supported by the analyses of Spagna and Gillespie (2008) and Miller et al. (2010), although these authors did not include Sparassidae. In analyses with all outgroups (Fig. 2), MrBayes consistently supported Sparassidae as sister to all other RTA-clade members, which was only topologically recovered by RAxML. While not fully supported, this still hints towards a basal position of Sparassidae in the RTA-clade. A similar topology of Sparassidae within RTA-clade was recovered by Agnarsson et al. (2013b) with weak support, probably due to the considerable amount of missing data as mentioned by these authors.

Sparassidae and the rest of the 'Laterigradae' are presently considered as "unplaced families" within the higher level clade Dionycha (Coddington, 2005). Yet, in previous molecular studies, Dionycha was not the focus of investigation (Miller et al., 2010; Agnarsson et al., 2013a). Primarily interested in the position of Sparassidae we included 11 family members of Dionycha in our analyses, to eventually comment on the validity of this group, as well. Thus representatives of all currently "unplaced families" within Dionycha were included (according to Coddington, 2005; Dunlop and Penney, 2011: Anyphaenidae, Clubionidae, Corinnidae, Gnaphosidae, Liocranidae, Chummidae, Homalonychidae, Salticidae and the 'Laterigradae' families) (Fig. 2), with the exception of Zoridae. We did not recover Dionycha as a monophyletic entity. The Dionycha members Thomisidae and Liocranidae were firmly nested within a clade otherwise containing only families of the "Higher Lycosoidea". Other Dionycha families were distributed throughout the tree, but without sufficient support from all analyses to reject Dionycha altogether. Two clades exclusively included Dionycha families, one strongly supported (Corinnidae-Salticidae-Philodromidae-Selenopidae), and another one weakly supported (Anyphaenidae-Clubionidae-Gnaphosidae).

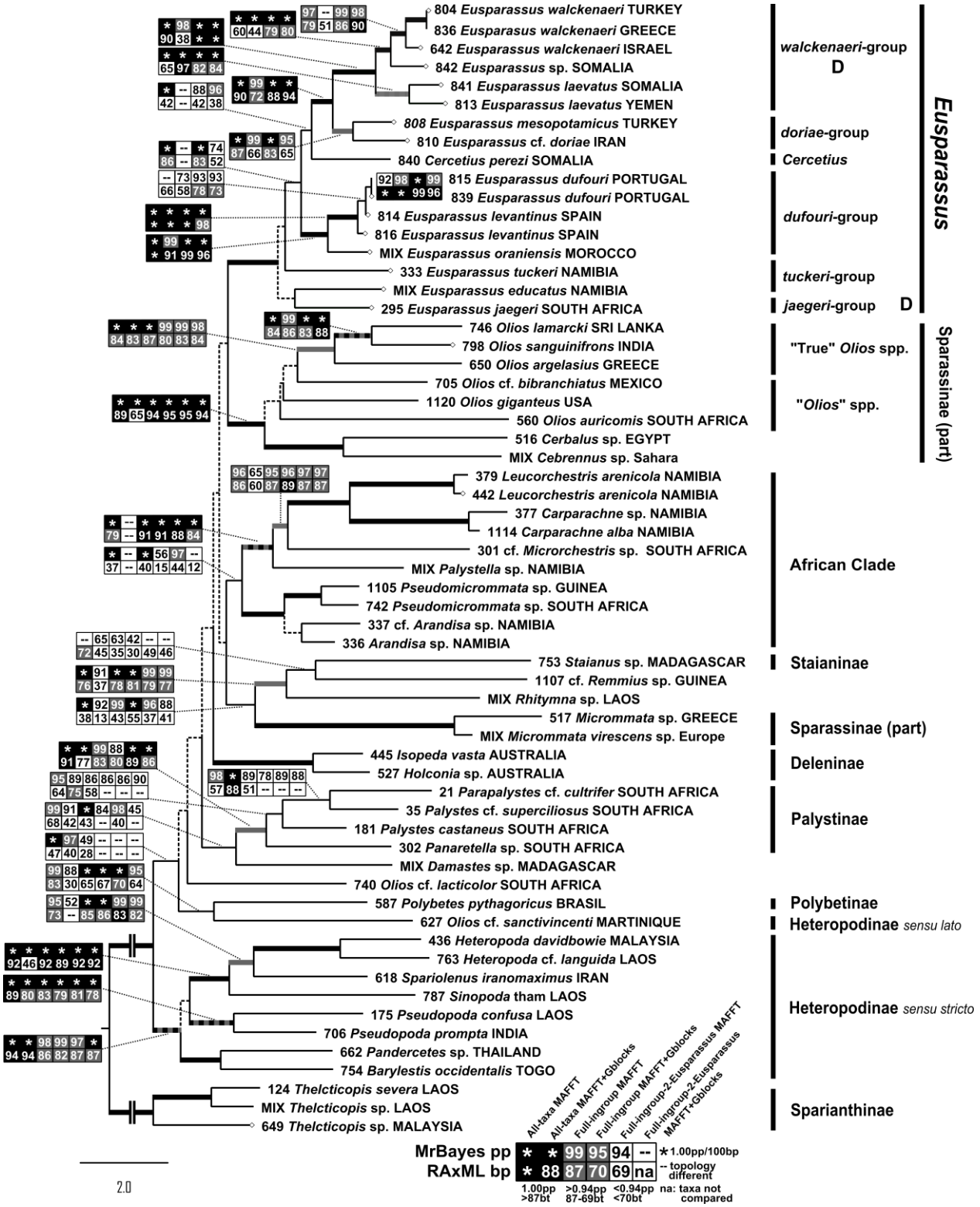

FIGURE 3. Maximum Likelihood tree with all ingroup taxa, using *Thelcticopis* as outgroup (Full-ingroup set). Results of other analyses are mapped upon this tree, summarizing the overall support for each branch (compare legend Fig. 2). Branches separating *Thelcticopis* and all other Sparassidae were artificially shortened to 1/10 of their actual length to fit the layout. The Full-ingroup-2-*Eusparassus* set analysis

Fig. 3.continued: excluded several terminal taxa, especially *Eusparassus* species that are indicated by a diamond. Associated tables feature only results of other analyses (first four columns on the left). Within *Eusparassus* clade, groups with intermarginal denticles in the chelicerae indicated by letter "D".

In contrast the families Chummidae and Homalonychidae were nested within groups containing only non-dionychans (Zodarioidea, Agelenoidea and Amaurobioidea) and Sparassidae is recovered in a basal position without clear affiliation to other RTA-clade families. Other studies treated only a few members of Dionycha (Anyphaenidae,Salticidae, Gnaphosidae; Miller et al., 2010; Agnarsson et al., 2013a), and recovered them as sister to Lycosoidea. Dionycha and Lycosoidea are the two most diverse groups of RTA-clade spiders (Platnick, 2013). Despite having a considerable amount of missing data, Agnarsson et al. (2013b) suggested Dionycha may be a polyphyletic group, a result also indicated by our analyses.

More clearly, the results reject the monophyly of 'Laterigradae' in the sense of Latreille (1802), comprising Sparassidae, Thomisidae, Philodromidae and Selenopidae. Coddington and Levi (1991) assumed that these four families may eventually be clustered near each other, while also acknowledging that the characteristic leg posture might be homoplastic. This habitus is for example also present in the haplogyne spider *Sicarius* Walckenaer, 1847, unrelated to the 'Laterigradae' . Our analyses rather suggest convergent evolution of this habitus, as the groups with crab-like posture appear randomly distributed within the RTA-clade (Fig. 2). Only Philodromidae and Selenopidae were found more closely related, but are separated and sister to the morphologically contrasting families Salticidae and Corinnidae, respectively, with the sister relationships of Philodromidae and Salticidae well supported in all analyses. These four families were also recovered as close relatives in Agnarsson et al. (2013b) but with a different topological arrangement and weak support. Our analyses also nested the family Thomisidae deep within the Lycosoidea with high support and without any relationship towards other 'Laterigradae'. The potential phylogenetic relationship of Thomisidae with the Lycosoidea was also proposed by Homann (1975) and Bayer and Schönhofer (2013). Here all our analyses strongly support Thomisidae as the sister group of Liocranidae and both firmly nested within Lycosoidea. Agnarsson et al. (2013b) gained the same result, yet without recovering Liocranidae as sister to Thomisidae. Coddington and Levi (1991) mentioned Liocranidae to be a polyphyletic family and as we used a taxon (*Itatsina praticola*) different from Agnarsson et al. (2013b; *Agroeca* sp.) these

results require further investigation. Finally, the recovered basal placement of the fourth 'Laterigradae' family Sparassidae does not entirely rule out the possibility of the crab-like posture being a plesiomorphic trait that was lost in most of the divergent RTA families. We believe this a rather unlikely scenario, as the radical morphological changes in the sister families of Selenopidae (Corinnidae) and Philodromidae (Salticidae), the fact that not all Sparassidae exhibit laterigrade legs (e.g., *Micrommata* spp.) and known homoplasy in Haplogynae (*Sicarius*) suggest that leg posture may not necessarily be a good phylogenetic character. The long (laterigrade) legs associated with the presence of scopula and claw tufts may facilitate handling and overpowering dangerous and large preys (Wolff et al., 2013).

Sparassidae was recovered as an independent lineage within the RTA-clade in this study. Its proposed relationship as sister group of Philodromidae (Homann, 1975) can be clearly rejected. Other phylogenetic proposals for Sparassidae are also controversial, regarding the basal and isolated placement of the family. Simon (1897, 1903) treated Sparassidae as a subfamily of Clubionidae. Lehtinen (1967) tentatively placed Sparassidae and Clubionidae in the superfamily Sparassoidea, considering them closely related. Our analyses revealed Clubionidae to be more close to Anyphaenidae and Gnaphosidae, as partly suggested by Coddington and Levi (1991), and Amaurobiidae not contained in the large clade uniting these families.

3.3. Monophyly and Systematics of Sparassidae

The monophyly of Sparassidae was recovered in all datasets, but with different supports (Fig. 2), affirming the proposed synapomorphic characters of the family. The type species of the type genus for Sparassidae, *Micrommata virescens* (Clerck, 1757), is also well nested within the inclusive family clade. *Micrommata* Latreille, 1804 was doubted to belong in the same family as *Heteropoda* Latreille, 1804 by Lehtinen (in Croeser, 1996), but both are clearly recovered in Sparassidae while being in different subfamilies. Our data set also recovered and thus supported the monophyly of most Sparassidae subfamilies and their diagnostic characters as suggested by many previous authors (Simon, 1897, 1903; Hogg, 1903; Järvi, 1912, 1914; Croeser, 1996; Jäger, 1998). Further results for the Sparassidae subfamilies are discussed below, following an order moving from deeper to shallower nodes of the tree shown in Fig. 3.

3.3.1. Sparianthinae

The subfamily is represented here by the genus *Thelcticopis* only, yet a genus featuring all typical synapomorphic characters of Sparianthinae (type genus *Sparianthis* Simon, 1880). The Sparianthinae currently consists of eight genera from tropical South America, Africa and Australasia (Jäger, 2001; Jäger and Kunz, 2005), and members are clearly separable from the rest of Sparassidae by a number of autapomorphic characters. They have much smaller teeth at the posterior chelicera margin than on the anterior margin (both of equal size in other Sparassidae) and the lateral projections of the trilobate membranes always extend beyond the median hook (Jäger, 1998). Our result thus recovered Sparianthinae as sister to the remaining Sparassidae (here termed Non-Sparianthinae) and suggest a very early divergence during the evolution of the family (Figs 2-3).

3.3.2. Heteropodinae

Heteropodinae comprises mostly Australasian genera but also one African genus (Jäger, 2001, 2002; Jäger and Kunz, 2005). With six genera included, our sampling is representative and recovered a well supported monophyletic Heteropodinae *sensu stricto*. All analyses also strongly supported the Heteropodinae in a basal position within the Non-Sparianthinae clade. Synapomorphies for this subfamily are the trilobate membrane with well developed lateral projections and median hook, and chelicerae with three anterior and four to six posterior teeth, intermarginally covered with denticles (mostly a patch of denticles is present close to the three anterior teeth; Jäger, 1998). Within the Heteropodinae the genera *Heteropoda*, *Spariolenus* Simon, 1880 and *Sinopoda* Jäger, 1999 were grouped together with the highest support. *Heteropoda* and *Sinopoda* were already considered closely related given both somatic and copulatory structures (Jäger, 1999b). On the other hand, *Spariolenus* was proposed to be closer to *Barylestis* Simon, 1910 (Jäger, 2006; Moradmand and Jäger, 2011), but was here recovered sister to *Heteropoda*, while *Barylestis* was sister of *Pandercetes* L. Koch, 1875. The placement of the genus *Pseudopoda* [including the type species *P. prompta* (Pickard-Cambridge, 1885)] within the Heteropodinae clade was not fully resolved.

We also included a member of the New World Heteropodinae from the Caribbean Islands (*Olios* cf. *sanctivincenti* (Simon, 1897)) which, according to a personal communication of C. A. Rheims, belongs to an unknown genus misplaced in *Olios*) that did not cluster with the Old World

representatives, despite featuring cheliceral dentition and eye arrangement of this group. While the exact position of this taxon could not be resolved, it was grouped with another Neotropical genus *Polybetes* Simon, 1897, indicating some more geographic influence on the phylogenetic structure within Sparassidae. Closer affiliation with Polybetinae than Heteropodinae also suggests *Olios* cf. *sanctivincenti* to be potentially excluded from the latter and it is here tentatively classified as Heteropodinae *sensu lato* in comparison to the Old World Heteropodinae as *sensu stricto*.

3.3.3. Palystinae

The genera *Palystes* L. Koch, 1875, *Parapalystes* Croeser, 1996 and *Panaretella* Lawrence, 1937 represented a well supported monophyletic group in most analyses (Fig. 3). The grouping is congruent with the subfamily Palystinae and its diagnostic characters studied and proposed by Croeser (1996) and Jäger and Kunz (2010), including eye arrangement and chelicerae with three anterior and three posterior teeth lacking intermarginal denticles. The Palystinae are endemic to tropical Africa (Croeser 1996). According to weak diagnostic characters (Jäger and Kunz, 2010) *Parapalystes* could be considered a synonym of *Palystes*. Our molecular data suggests this possibility, while otherwise the well-defined genus *Palystes* would appear paraphyletic. For further studies on Palystinae the genera *Anchonastus* Simon, 1898 and *Sarotesius* Pocock, 1898 also need to be included.

The Madagascan-Seychellois endemic *Damastes* Simon, 1880 was weakly recovered as a sister taxon to the Palystinae clade. The genus was classified as Deleninae by Simon (1903) but later transferred by Järvi (1912) to a sub-group of Heteropodinae named Toraniformes (Toraniae). Jäger (2002) stated that the systematic placement of the genus within the family is still unclear. Our phylogeny recovered *Damastes* neither close to Deleninae nor Heteropodinae, but the genus also cannot be interpreted as a member of Palystinae or another clade.

3.3.4. Staianinae

This currently monotypic subfamily, based on the genus *Staianus* Simon, 1889, clustered with the genera *Rhitymna* Simon, 1897 and cf. *Remmius* (Fig. 3). The relationship of the three genera is otherwise unresolved, while *Remmius* and *Rhitymna* are considered more closely related based on morphology. *Staianus* is distinctly different from another Madagascan genus *Damastes* (Jäger

and Kunz, 2005), and our molecular data suggests an independent origin of the two endemic genera, as well.

3.3.5. Deleninae

The Australian endemic group Deleninae is here represented by the genera *Holconia* Thorell, 1887 and *Isopeda* L. Koch, 1875, that grouped together with highest support in our analyses. The subfamily was established by Hogg (1903) to include several endemic Australian genera previously classified as Sparassinae by Simon (1897). Hogg (1903) distinguished Deleninae from Sparassinae by the characters of body shape and male palps which is backed here by molecular data. The monophyly of Deleninae was also recovered by Agnarsson and Rayor (2013) based on rich sampling within the subfamily but including few outgroup (e.g. Sparassinae).

3.3.6. Sparassinae

Sparassinae was not recovered as monophyletic in our data set (Fig. 3). The type genus *Micrommata* (as senior synonym of *Sparassus* Walckenaer, 1805) (Jäger, 1999a) does not cluster with its assumed closest relatives *Olios*, *Cebrennus* Simon, 1880 and *Cerbalus* Simon, 1897. The cheliceral features thought to characterise this group may be symplesiomorphic characters (lacking intermarginal denticles and the presence of two anterior and three to six posterior teeth; Jäger, 1998). Because of their general similarity in somatic characters the genera *Eusparassus, Micrommata* and *Olios* were previously summarised under the generic name *Sparassus*. Later, Jäger (1999) gave *Micrommata* priority over *Sparassus*, with the group again split into the three previously synonymous genera. Still, *Olios* remains a special case, being currently the largest Sparassidae genus (Platnick, 2013) and being used as a collective group for many undescribed taxa (Jäger and Kunz, 2005). Rheims (2010b) noted that the genus is most likely polyphyletic, which is supported in our analyses. While most other Sparassidae species of the same genus cluster together with high support, *Olios* cf. *lacticolor* Lawrence, 1952 and *Olios* cf. *sanctivincenti* are placed far from the rest of the included *Olios* species. "True" *Olios* species, can be considered the type species *Olios argelasius* (Walckenaer, 1805), the morphologically similar *O. lamarcki* (Latreille, 1806) and *O. sanguinifrons* (Simon, 1906), are grouped together with strong support. Three other *Olios* species were recovered close to this core group, yet without their interrelationships further resolved. Rheims (2010b) supposed that of these the Nearctic *Olios* species (*giganteus* and *bibranchiatus*) may warrant an independent genus. Morphological

characters (Jäger and Kunz, 2005) are in accordance with our molecular evidence to suggest that the southern African *Olios* species (*auricomis* and *lacticolor*) are different from each other and that *O. lacticolor* should be excluded from the genus. The two Afro-Asian desert dwelling genera *Cebrennus* and *Cerbalus* were grouped together with high support and were sister to the ensemble of the "True" and associated *Olios* species.

3.4. Eusparassinae

The Eusparassinae were not supported as monophyletic in our analyses, but given the unresolved Non-Sparianthinae clade backbone this possibility cannot be entirely rejected. The inferred phylogeny placed the assumed Eusparassinae genera (see Fig. 1) into two separate clades (Fig. 3); one contained the type genus *Eusparassus* and all of its representatives, and the second clade contained the remaining genera (here outlined as African clade) which grouped together with at least sufficient support from half the BI analyses. *Eusparassus* was thus recovered as isolated from *Pseudomicrommata* (both included in the initial composition of the subfamily; Järvi, 1912) and the latter grouped with high support with *Arandisa* Lawrence, 1938, also endemic to Africa and weakly affiliated with others in the African clade (Fig. 3). As noted before, Järvi's (1912, 1914) classification used exclusively the female copulatory characters to group genera and ignored most of the somatic ones. Nevertheless, *Eusparassus* and *Pseudomicrommata* resemble each other in some structures, but also show significant differences in copulatory and somatic characters. For instance, *Pseudomicrommata* (and *Arandisa*) have distinct pockets on the lateral lobes of their epigynes (Jäger and Kunz, 2005) which are lacking in *Eusparassus*. Moreover, the size and arrangement of the eyes and the spination pattern of the legs are very different in the two groups. *Eusparassus* species have the anterior median eyes (AME) always larger or equal to the anterior lateral eyes (ALE) but in the remaining genera AME are smaller than ALE. In *Eusparassus*, legs always have two pairs of tibial spines ventrally while other genera (*Pseudomicrommata* and *Arandisa*) have three. Some *Eusparassus* species have intermarginal denticles in their chelicerae which are always missing in species of other genera. It should be noted that similar structured copulatory organs may have developed independently several times in Sparassidae, as has been shown in other groups of spiders (Forster , 1980). In general, the structure of copulatory organs (particularly in males) is known to evolve and change more rapidly compared to somatic characters (Eberhard, 2010). Thus, the general similarity in copulatory organs is also more likely to reflect a convergent evolution of these organs. The genus

Pseudomicrommata is likely to be subsumed into a group of its own, along with the other African endemic genera *Arandisa*, *Leucorchestris*, Lawrence, 1962, *Carparachne* Lawrence, 1962, *Microrchestris* Lawrence, 1962 and *Palystella* Lawrence, 1928. The phylogenetic relationships between the African clade and *Eusparassus* needs to be further resolved, including with more material and molecular markers.

According to morphological characters, the Asian genus *Rhitymna* was already proposed not belong to Eusparassinae (Jäger, 2003). In agreement, our current phylogeny did not support a close relationship of *Rhitymna* to *Eusparassus* or *Pseudomicrommata*, but placed it within a group encompassing Staianinae, the unplaced cf. *Remmius* and the type of the probably polyphyletic Sparassinae (*Micrommata*) as sister to these three genera.

3.5. *Eusparassus*

The genus *Eusparassus* received strong support, combining all species assigned to this genus including the type species *E. dufouri* Simon, 1932 (using tissue of the neotype). The monophyly of each of the *dufouri*-, *doriae*- and *walckenaeri*-group was recovered, generally with high support (Fig. 3). The phylogenetic results correspond with the majority of the morphological characters (a combination of somatic and genital characters) used to group *Eusparassus* species (Moradmand, 2013). The deep divergence within some species (e.g. *E. levantinus* Urones, 2006 in Iberia or *E. walckenaeri* in Eastern Mediterranean) may indicate the presence of cryptic species. As noted in section 3.3.6 many *Olios* species probably require reassignment, as was done for the species *E. laevatus* (Simon, 1897) and *E. tuckeri* (Lawrence, 1927) now placed in *Eusparassus* (Moradmand, 2013). Our molecular phylogeny supports these nomenclatural acts. In contrast, *O. sanguinifrons*, originally described in *Eusparassus* (Simon, 1906), is here confirmed to be an *Olios* species close to the type species *O. argelasius*, as transferred by Jäger et al. (2002). Another recent taxonomic proposal supported by this study is the synonymy of *Cercetius* with *Eusparassus* (Moradmand and Jäger, 2012b). *Cercetius* is nested within the *Eusparassus* clade, which is also congruent with the morphological information provided by Moradmand (2013). *Cercetius* had not been assigned to any of the proposed *Eusparassus* species-groups and was considered as a lineage intermediate to the *dufouri*- *jaegeri*-, and *walckenaeri*-group. (Moradmand, 2013), a placement not contradicted by the partly unresolved placement of the genus in our analyses. It is for now best retained as a single terminal taxon on the phylogenetic tree, however, the results point to a closer relationship with the *walckenaeri*-, *doriae*- and

dufouri-group than with the *jaegeri*- and *tuckeri*-group members. The *dufouri*-group and *Cercetius perezi* was recovered as sister groups to the *walckenaeri+doriae* clade. One of the main somatic characters proposed to group *Eusparassus* species is the presence of the intermarginal denticles on the chelicerae, present only in the *walckenaeri- and jaegeri*-group (and in some specimens of *Cercetius perezi*). The homology of this character was not recovered in our analyses, as these groups did not form a clade. It is likely that gain of intermarginal denticles has taken place independently in both the *walckenaeri*- and *jaegeri*-group, or was lost in others. The phylogenetic reconstructions strongly supported the *walckenaeri*-group as sister to the *doriae*-group. Moradmand (2013) suggested the *doriae*-group to be a lineage derived from the *walckenaeri*-group in Asia indicated by the loss of the intermarginal denticles of the chelicerae and by other subsequent modifications. Our data suggest that these groups are closely related phylogenetically. The placement of the single representative of the *jaegeri*-group in the tree, *E. jaegeri* Moradmand, 2013, was not further resolved. The *jaegeri*-group is composed of four species endemic to southern Africa (Moradmand, 2013) and its unresolved position might result from the lack of other group members in the tree. The monophyly of the *tuckeri*-group, comprising *E. tuckeri* and *E. educatus* Moradmand, 2013, both endemic to SW Africa, was not recovered, but cannot be rejected either for the insufficient support at the connecting nodes. *Eusparassus educatus* (and to some extent *E. tuckeri*) has an extraordinarily long embolus, unique among *Eusparassus* species (Moradmand, 2013). Finally, the inclusion of more species and additional data is necessary to further resolve the evolutionary history of *Eusparassus*.

3.6. Divergence time and historical biogeography

The divergence between Sparianthinae and other Sparassidae was estimated at 163 MA (95% HPD (highest posterior density) of 127–203 MA) by calibrating the "All-outgroups-8-Sparassidae dataset" using four fossils (Fig. 4). The substitution rate (uncalibrated random local clock) increased slightly from about 0.8 in the outgroup taxa, Sparassidae and the basal Amaurobioidea-Agelenoidea-div.-clade, to 1.0 for the rest of RTA-clade members, but accelerated to 1.4 in the Salticidae-Philodromidae-Corinnidae clade (Appendix 1, Fig. 21). Despite being calibrated, the node age for the divergence of Salticidae-Philodromidae is pulled back considerably, possibly indicating an older age for this node (Hill and Richman, 2009), an issue contradicted and extensively discussed by Penney and Selden (2011).

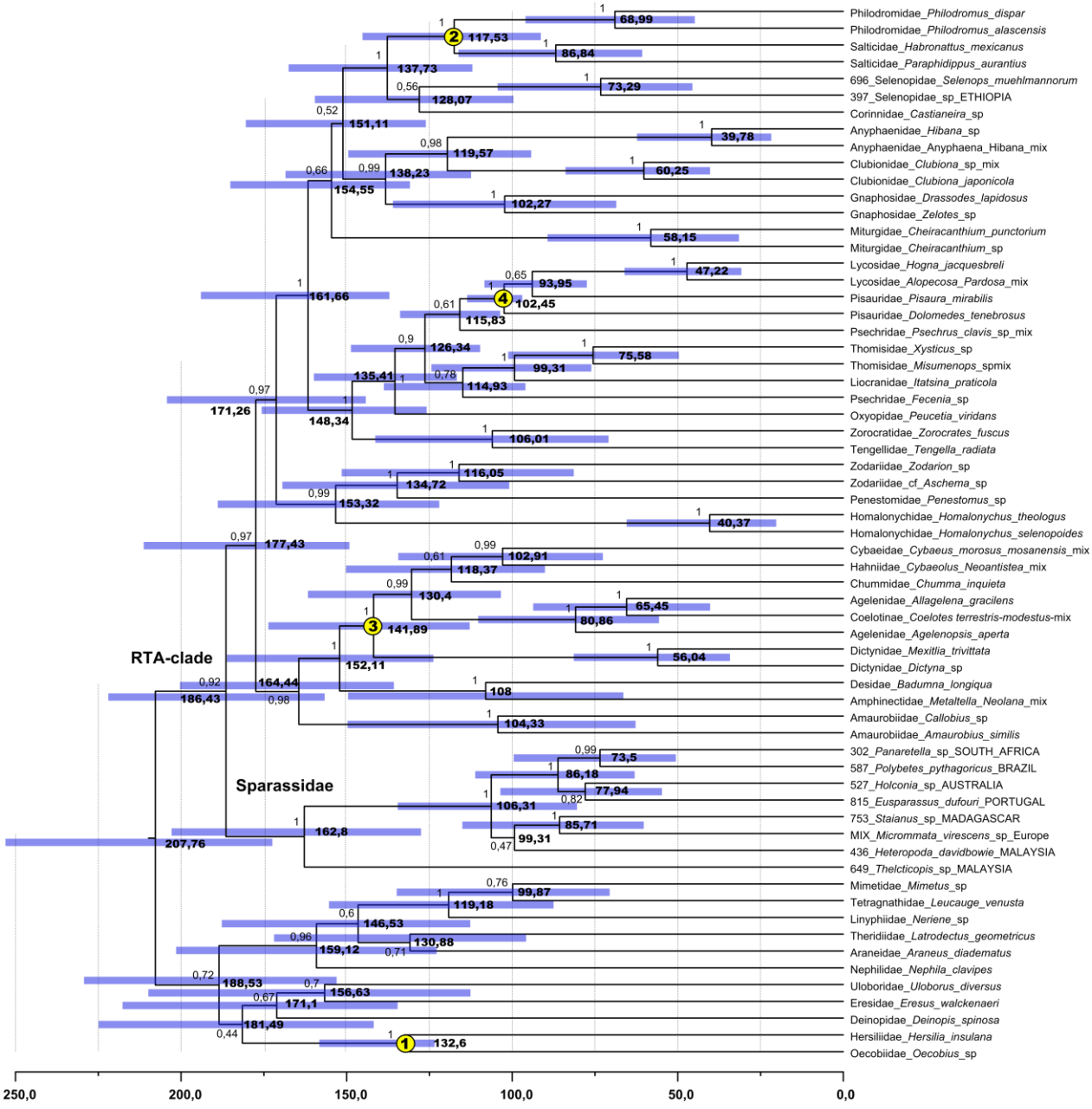

FIGURE 4. Maximum clade credibility tree based on BEAST analysis of the All-outgroups-8-Sparassidae dataset calibrated by four fossil records. Highest posterior density values represent the statistical range of divergence time estimates. Numbers in circles specify calibrated nodes as referred in the Methods.

In comparison to the split from the Sparianthinae, diversification within the Non-Sparianthinae was probably relatively fast, also seen in the unresolved backbone of this group. Both calibrations using outgroup (Fig. 4) and ingroup fossils (Fig. 5), generally agree with the diversification of the Non-Sparianthinae into most clades and subfamilies starting around 105 to 75 Ma., roughly corresponding with the breakup of Gondwana (Briggs, 1995; Sanmartín and Ronquist, 2004).

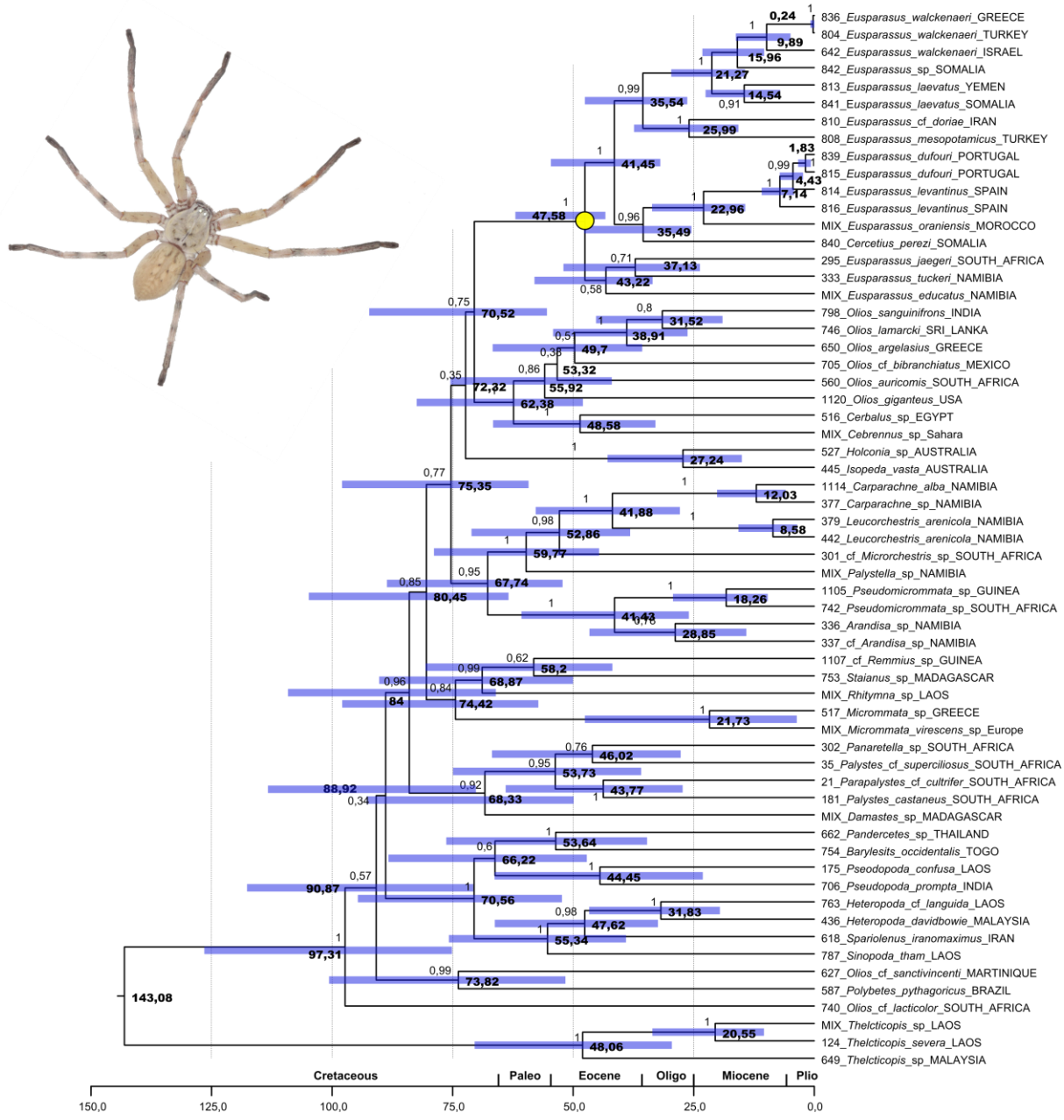

FIGURE 5. Maximum clade credibility tree based on BEAST analysis of the Full-ingroup set of Sparassidae rooted by the divergent time of Sparassidae node from previous analysis (Fig. 4) and calibrated (circle) using an *Eusparassus* fossil and historical biogeography data.

It is important to mention that calibrating the initial diversification within *Eusparassus* (47.5 MA (95% HPD of 43–62 MA; Fig. 5)) pulled the root node of the Full-ingroup set towards a younger date (-20 Ma) in comparison to the calculations based on outgroup fossils (Fig. 4). This might indicate the fossil *E. crassipes* to correspond to a younger node within the genus. Its

intermarginal denticle pattern is present in several groups, none of which *E. crassipes* can be assigned to with certainty. The inferred divergence time within the genus thus may be slightly older as subsequently reported. However, *Eusparassus* likely diverged from other Sparassidae about 70 MA ago and no further diversification into subgroups is obvious for 20 million years.

Based on the distribution of *Eusparassus* groups an African origin is likely. Moradmand (2013) specified a Southern African origin, which is supported by the presence of the oldest lineage of *Eusparassus* and many old lineages within the Non-Sparianthinae (Namibia, South Africa; Fig. 5). This area shows exceptional diversity in desert dwelling organisms with high levels of very old endemism (Barnard et al., 1998; Ward, 2009). The Namib Desert in particular has been highlighted as the oldest desert on earth, with desertification probably already initiating with the Gondwanaland fracturing ca. 130–145 MA (Ward et al., 1983) and permanent aridity from at least 55 MA onwards. This stable environment probably served as a source area for many dry-adapted organisms, as is assumed for *Eusparassus*. The high diversity of the southern African desert-dwelling Sparassidae, with the African clade members mainly distributed within and at the border of the Namib and Kalahari Deserts, and the presence of the more basal *Eusparassus* species (*tuckeri*-group) further supports this assertion. The majority of *Eusparassus* species-groups (five of six) and species (23) occur mainly in Africa and neighbouring regions, e.g., Iberia, with only the members of the *doriae* group (seven species) restricted to Asia.

Other deserts appeared much later, in Asia and North Africa, following a global desertification during the Tertiary, initiating around 23 Ma (Potter and Szatmari, 2009). Considering the much older age of the oldest *Eusparassus* fossil a potential Eurasian origination of *Eusparassus* is unlikely.

The extant species groups of *Eusparassus* generally have different areas of distribution that only exceptionally show considerable overlap. The *dufouri*-group is composed of eight species distributed from the Iberian Peninsula to NW Africa. We found the two Iberian species (*E. dufouri* and *E. levantinus*) closer related to each other compared to the Moroccan *E. oraniensis* (Lucas, 1846). The divergence between *dufouri*- and *walckenari*+*doriae*- clade was estimated 41 MA (95% HPD of 32-55 MA) (Fig. 5).

The *doriae*-group comprises seven species distributed in the Middle East to Central Asia and parts of South Asia and is here represented by two species. The *walckenaeri*-group, occurs in

Eastern Mediterranean to North-Eastern Africa and Arabian Peninsula, and is represented here by two of the three known species from various localities. The phylogeny recovered *doriae*- and *walckenaeri*-group as sister clades with highest support. Their divergence is estimated around 36 MA (95% HPD of 26-48) (Fig. 5), roughly in accordance with the closing of the Turgai Strait (30 MA) that acted as a barrier for most terrestrial biota between the eastern and western Palearctic (Sanmartín et al., 2001). We hypothesize this event to have played a role in diversification of the *doriae*- and *walckenaeri*-group, which could not be tested in the absence of most Asian representatives of the *doriae*-group.

4. CONCLUSIONS

This study is the first to comprehensively tackle the phylogenetic relationships within the large spider family Sparassidae, including its major subfamilies and to investigate further placement and groupings within the RTA-clade. It also provides systematic insight into one of the largest Sparassidae genus *Eusparassus*. For the sheer number of species and genera, our results are a starting point for future research on this conspicuous group of spiders. 1) 'Laterigradae' (Sparassidae, Thomisidae, Philodromidae and Selenopidae) is not recognised as a monophyletic group. Sparassidae is recovered as sister to the rest of the RTA-clade members. Our data also suggests Dionycha to be a polyphyletic ensemble.

2) The family Sparassidae and the subfamilies Sparianthinae, Heteropodinae *sensu stricto*, Palystinae and Deleninae are supported as monophyletic and Sparianthinae are recovered as sister to all other Sparassidae. Sparassinae appeared to be a polyphyletic group. The currently available morphological characters for the classification of Sparassidae generally seem to apply.

3) Eusparassinae is not resolved as a monophyletic group. The branch of the "African clade" consisting of *Carparachne, cf. Microrchestris, Leucorchestris* and *Palystella* comprise morphologically similar genera endemic to southern Africa. At this point, our result suffices to erect a new subfamily for this group or exclude them from Eusparassinae. *Eusparassus* might not be closely related to the African clade genera and if this is further supported, Eusparassinae has to be considered monotypic.

4) *Eusparassus* is recovered as monophyletic with *Cercetius perezi* nested within the group. The monophyly of the *dufouri*-, *doriae*- and *walckenaeri*- group are well supported, while a *tuckeri*-group is not recovered. The *doriae*- and *walckenaeri*-group were found as sister groups and both likely sister to the *dufouri*-group.

5) Sparassidae separated from the other RTA-clade families around 186 MA, and early diverged into Sparianthinae and Non-Sparianthinae (163 MA; Fig. 4). Further divergence happened much later (106–97 MA; Figs 4-5), but surprisingly rapidly in the Non-Sparianthinae.

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Table 1. List of voucher specimens exclusively treated for this study, with respective voucher numbers (SD: Spider DNA collection number in SMF), collection localities and GenBank accession numbers. All species belongs to family Sparassidae except noted. Sparassidae species mentioned first and in alphabetical order.

species	author	SD	Locality	GenBank Accession N.			
				COI	28S	16S	H3
***Arandisa* sp.**	Lawrence, 1938	336	Namibia: Kunene Region, Hobatere Concession	#	#	#	#
Barylestis occidentalis	(Simon, 1887)	754	Togo	#	#	#	#
Carparachne alba	Lawrence, 1962	1114	Namibia: Swakopmund district, Gobabed, Kuiseb River	#	#	#	#
***Carparachne* sp.**	Lawrence, 1962	377	Namibia: Erongo, S of Gobabed	#	#	#	#
Cebrennus rungsi	Jäger, 2000	645	Morocco: Anti-Atlas Range, Ighil,SE of Agadir	#	#	#	#
***Cebrennus* sp.**	Simon, 1880	556	Algeria	#	#	#	#
***Cerbalus* sp.**	Simon, 1897	516	Egypt	#	#	#	#
Cercetius perezi	Simon, 1902	840	Somalia, near Berbera	#	#	#	#
***cf. Arandisa* sp.**	Lawrence, 1938	337	Namibia: Kunene Region, Epupa	#	#	#	#
***cf. Microrchestris* sp.**	Lawrence, 1962	301	South Africa: North Cape Province, Kalahari	#	#	#	#
***cf. Remmius* sp.**	Simon, 1897	1107	Guinea: Mt Nimba	#	#	#	#
***Damastes* sp.**	Simon, 1880	533	Madagascar	#	#	#	#
Eusparassus cf. doriae	(Simon, 1874)	810	Iran: Khorasan Razavi Prov., Gonabad, S of Kakhk	#	#	#	#
Eusparassus dufouri	Simon, 1932	839	Portugal: Beja, Serpa	#	#	#	#
Eusparassus dufouri	Simon, 1932	815	Portugal:Chanca	#	#	#	#
Eusparassus educatus	Moradmand, 2013	530	Namibia: Kunene Region, Epupa Falls	#	#	#	#
Eusparassus educatus	Moradmand, 2013	341	Namibia: Kunene Region	#	#	#	#
Eusparassus jaegeri	Moradmand, 2013	295	South Africa: Gauteng Prov., NE of Pretoria	#	#	#	#
Eusparassus laevatus	(Simon, 1897)	841	Somalia: Hargeshia	#	#	#	#
Eusparassus laevatus	(Simon, 1897)	813	Yemen: Haraz Mts.,southern slope of Mt Al lan	#	#	#	#

Table 1. continued

Eusparassus levantinus	Urones, 2006	814	Spain: Andulacia Province, Ronda	#	#	#	#
Eusparassus levantinus	Urones, 2006	816	Spain: Almeria, Cobodegota	#	#	#	#
Eusparassus mesopotamicus	Moradmand & Jäger 2012	808	Turkey: Hakkari province, Gukurca	#	#	#	#
Eusparassus oraniensis	(Lucas, 1846)	843	Morocco: Gulemim-Es Semara Region	#	#	#	#
Eusparassus oraniensis	(Lucas, 1846)	615	Marocco: Erg Chebbi, Sahara	#	#	#	#
***Eusparassus* sp.**	Simon, 1903	842	Somalia	#	#	#	#
Eusparassus tuckeri	(Lawrence, 1927)	333	Namibia: Kunene Region, Epupa Falls	#	#	#	#
Eusparassus walckenaeri	(Audouin, 1826)	804	Turkey: Mugla Prov., Milas, GüllückYeni Oba	#	#	#	#
Eusparassus walckenaeri	(Audouin, 1826)	642	Israel: Negev, Sede Boqer, W of Midreshet Ben Gurion	#	#	#	#
Eusparasus walckenaeri	(Audouin, 1826)	836	Greece: Peloponnese, Geraki	#	#	#	#
Heteropoda* cf. *languida	Simon, 1877	763	Laos: Champasak Prov., Pakse, That Fane	#	#	#	#
Heteropoda davidbowie	Jäger, 2008	436	Malaysia: Cameron Highlands	#	#	#	#
***Holconia* sp.**	Thorell, 1877	527	Australia, East coast	#	#	#	#
Isopeda vasta	(L. Koch, 1867)	445	Australia	#	#	#	#
Leucorchestris arenicola	Lawrence, 1962	442	Namibia: Gobabeb Field Station	#	#	#	#
Leucorchestris arenicola	Lawrence, 1962	379	Namibia: Karas Region, NE of Luderiz	#	#	#	#
***Micrommata* sp.**	Latreille, 1804	517	Greece: Korfu	#	#	#	#
***Micrommata* sp.**	Latreille, 1804	413	Bulgaria: Rila Mts., Rila Monastery	#	#	#	#
Micrommata virescens	(Clerck, 1757)	16	Germany: Hessen, Lochmühle, Lochborn	#	#	#	#
Olios argelasius	(Walckenaer, 1805)	650	Greece: Perikleia	#	#	#	#
Olios auricomis	(Simon, 1880)	560	South Africa	#	#	#	#
Olios cf. bibranchiatus	Fox, 1937	705	Mexico: Morelos, Oaxtepec	#	#	#	#
Olios cf. lacticolor	Lawrence, 1952	740	South Africa: KwaZulu-Natal, Oribi Gorge Nature Reserve	#	#	#	#
Olios cf. sanctivincenti	Simon, 1897	627	Caribbean: N of Martinique, Le Morne Rouge Island	#	#	#	#

Table 1. continued

Olios giganteus	Keyserling, 1884	1120	USA: Arizona, Cochise Co., S of Kartchner Caverns	#	#	#	#
Olios lamarcki	(Latreille, 1806)	746	Sri Lanka: Southern Province, Ambalangoda	#	#	#	#
Olios sanguinifrons	(Simon, 1906)	798	India: Uttarakhand, Dehra Dun, WII Campus	#	#	#	#
Palystella* cf. *namaquensis	(Lawrence, 1938	363	Namibia: Hardap Region, NE of Sesriem	#	#	#	#
***Palystella* sp.**	Lawrence, 1928	177	Namibia	#	#	#	#
Palystes castaneus	(Latreille, 1819)	181	South Africa	#	#	#	#
Palystes* cf. *superciliosus	L. Koch, 1875	35	South Africa: KwaZulu-Natal, Prestbury	#	#	#	#
***Panaretella* sp.**	Lawrence, 1937	302	South Africa: KwaZulu-Natal, NE of Ndumu	#	#	#	#
***Pandercetes* sp.**	L. Koch, 1875	662	Thailand: Trat Prov., Ko Chang, Khlong Plu school	#	#	#	#
Parapalystes cf. cultrifer	(Pocock, 1900)	21	South Africa: Middelburg, Cape Prov., Great Karroo	#	#	#	#
Polybetes pythagoricus	(Holmberg, 1875)	587	Brasil, Import to Germany	#	#	#	#
***Pseudomicrommata* sp.**	Järvi, 1914	742	South Africa: Free State Prov., Brandfort district	#	#	#	#
***Pseudomicrommata* sp.**	Järvi, 1914	1105	Guinea: Mt Nimba, Ga forest	#	#	#	#
Pseudopoda confusa	Jäger, Pathoumthong & Vedel, 2006	175	Laos: Luang Nam Tha Prov., Luang Nam Tha, Ban Tavan Mai	#	#	#	#
Pseudopoda prompta	(O. P.-Cambridge, 1885)	706	India: Uttarakhand, Joshimath	#	#	#	#
***Rhitymna* sp.**	Simon, 1897	691	Laos: That Fane	#	#	#	#
***Rhitymna* sp.**	Simon, 1897	681	Laos: Luang Phabang Prov., Phou Khoun, Tham Seua	#	#	#	#
Sinopoda tham	Jäger, 2012	787	Laos: Oudomxay Province, Namor District, Tham Na Thong Cave	#	#	#	#
Spariolenus iranomaximus	Moradmand & Jäger, 2011	618	Iran: Ilam Prov., Dehloran, Khofash cave	#	#	#	#
***Staianus* sp.**	Simon, 1889	753	Madagascar: Feow'Nyala, Andasibg-Mantadia N.P.	#	#	#	#
Thelcticopis severa	(L. Koch, 1875)	124	Laos, Luang Nam Tha Province, Muang Sing, Nam Det	#	#	#	#
Thelcticopis severa	(L. Koch, 1875)	405	Laos, Thakek area, Ban Tham	#	#	#	#

Table 1. continued

***Thelcticopis* sp.**	Karsch, 1884	713	Laos: Champasak Province, Pakse, That Fane	#	#	#	#
***Thelcticopis* sp.**	Karsch, 1884	649	Malaysia: Tioman Island	#	#	#	#
Selenopidae: ***Selenops muhlmunnarom***	Jäger & Praxaysombath, 2011	696	Laos: Champasak Province, Pakse, Phou Salao, Felsen	#	#	#	#
Selenopidae gen. sp. ETHIOPIA	#	397	Ethiopia: Oromia, Nec Sar plain	#	#	#	#
Philodromidae: ***Philodromus* dispar**	Walckenaer, 1826	193	Germany: Rheinland-Pfalz, Mainz	#	#	#	#

Table 2. List of specimen's included in the phylogenetic analyses and respective accession numbers extracted from GenBank (http://www.ncbi.nlm.nih.gov/nuccore). The higher level classification follows Dunlop and Penny (2011).

Higher level classification	Taxon	Author	GenBank Accession Numbers			
			CO1	**28S**	**16S**	**H3**
Eresoidea, Eresidae	*Eresus walckenaeri*	Brullé, 1832	FJ948999	FJ948959	AY739892	FJ949037
Eresoidea, Hersiliidae	*Hersilia insulana*	Strand, 1907	FJ949006.1	FJ948966.1	#	FJ949044
Eresoidea, Oecobiidae	*Oecobius* sp.	Lucas, 1846	FJ607579	FJ607540	FJ607466	FJ607617
Orbiculariae, Araneoidea, Araneidae	*Araneus diadematus*	Clerck, 1757	FJ607553	FJ607518	FJ607445	FJ607592
Orbiculariae, Araneoidea, Linyphiidae	*Neriene* sp.	Blackwall, 1833	FJ607576	FJ607539	FJ607465	FJ607614
Orbiculariae, Araneoidea, Nephilidae	*Nephila clavipes*	(Linnaeus, 1767)	FJ525328	FJ525379	FJ525361	FJ525344
Orbiculariae, Araneoidea, Tetragnathidae	*Leucauge venusta*	(Walckenaer, 1841)	FJ607568	FJ607533	FJ607457	FJ607606
Orbiculariae, Araneoidea, Theridiidae	*Latrodectus geometricus*	C. L. Koch, 1841	FJ607567	FJ607532	FJ607456	FJ607605
Orbiculariae, Deinopoidea, Deinopidae	*Deinopis spinosa*	Marx, 1889	FJ525318	FJ525370	FJ525351	FJ525337
Orbiculariae, Deinopoidea, Uloboridae	*Uloborus diversus*	Marx, 1889	FJ525329	FJ525380	FJ525362	FJ525345
Palpimanoidea, Mimetidae	*Mimetus* sp.	Hentz, 1832	FJ607574	FJ607538	FJ607463	FJ607612
RTA Clade, Amaurobioids incertae cedis, Agelenidae	*Agelenopsis aperta*	(Gertsch, 1934)	FJ607552	FJ607517	FJ607444	FJ607591
RTA Clade, Amaurobioids incertae cedis, Agelenidae	*Allagelena gracilens*	(C. L. Koch, 1841)	DQ628606.1	DQ628661.1	#	DQ628652
RTA Clade, Amaurobioids incertae cedis, Agelenidae	*Coelotes terrestris*	(Wider, 1834)	DQ628626.1	DQ628688.1	#	DQ628651.1
Agelenidae	*Coelotes modestus*	Simon, 1880	#	#	AY633875	#

Table 2. continued

RTA Clade, Amaurobioids incertae cedis, Amphinectidae	*Metaltella simoni*	(Keyserling, 1878)	DQ628617	DQ628677	#	#
RTA Clade, Amaurobioids incertae cedis, Amphinectidae	*Neolana dalmasi*	(Marples, 1959)	#	#	#	DQ628655
RTA Clade, Amaurobioids incertae cedis, Amaurobiidae	*Callobius* sp.	Chamberlin, 1947	FJ607559	FJ607524	FJ607450	FJ607598
RTA Clade, Amaurobioids incertae cedis, Amaurobiidae	*Amaurobius similis*	(Blackwall, 1861)	DQ628608	DQ628663	#	#
RTA Clade, Amaurobioids incertae cedis, Amaurobiidae	*Pimus* sp.	Chamberlin, 1947	#	#	#	DQ628646
RTA Clade, Amaurobioids incertae cedis, Miturgidae	*Cheiracanthium* sp.	C. L. Koch, 1839	AY297421	AY297294	AY296712	EF419115.1
RTA Clade, Amaurobioids incertae cedis, Miturgidae	*Cheiracanthium punctorium*	(Villers, 1789)	JN018131	JN018345	#	#
RTA Clade, Amaurobioids incertae cedis, Penestomatidae	*Penestomus* sp.	Simon, 1902	FJ949013.1	FJ948973.1	#	FJ949050.1
RTA Clade, Amaurobioids incertae cedis, Tengellidae	*Tengella radiata*	(Kulczyn'ski, 1909)	DQ628622	DQ628684	#	DQ628649.1
RTA Clade, Amaurobioids incertae cedis, Zodariide	*Zodarion* sp.	Walckenaer, 1826	FJ949024	FJ948984	#	FJ949061.1
RTA Clade, Amaurobioids incertae cedis, Zodariide	cf. *Aschema* sp.	Jocqué, 1991	FJ949009.1	FJ948969.1	#	FJ949046
RTA Clade, Amaurobioids incertae cedis, Zorocratidae	*Zorocrates fuscus*	Simon, 1888	FJ607588	FJ607549	FJ607475	FJ607626
RTA Clade, Amaurobioids, Lycosoidea, Lycosidae	*Alopecosa kochi*	(Keyserling, 1877)	DQ628607	DQ628662	#	DQ628635
RTA Clade, Amaurobioids, Lycosoidea, Lycosidae	*Pardosa californica*	Keyserling, 1887	#	#	JQ280353.1	#
RTA Clade, Amaurobioids, Lycosoidea, Lycosidae	*Hogna jacquesbreli*	Baert & Maelfait, 2008	GU395027	GU395068	#	#
RTA Clade, Amaurobioids, Lycosoidea, Oxyopidae	*Peucetia viridans*	(Hentz, 1832)	FJ607580	FJ607541	FJ607467	FJ607618
Lycosoidea, Pisauridae	*Dolomedes tenebrosus*	Hentz, 1844	FJ607562	FJ607527	FJ607453	FJ607601

Table 2. continued

RTA Clade, Amaurobioids, Lycosoidea, Pisauridae	*Pisaura mirabilis*	(Clerck, 1757)	JX137215	JX137267	#	#
RTA Clade, Amaurobioids, Lycosoidea, Psechridae	*Psechrus clavis*	Bayer, 2012	JX137143	JX137235	AF145263	KC011020
RTA Clade, Amaurobioids, Lycosoidea, Psechridae	*Fecenia ochracea*	(Doleschall, 1859)	JX137157	JX137244	#	KC011018
RTA Clade, Dionycha incertae ceids, Anyphaenidae	*Anyphaena californica*	(Banks, 1904)	DQ628605	DQ628660	AY296713	DQ628633
RTA Clade, Dionycha incertae ceids, Anyphaenidae	*Hibana* sp.	Brescovit, 1991	AY297422	AY297295	AY296713	#
RTA Clade, Dionycha incertae ceids, Chummidae	*Chumma inquieta*	Jocqué, 2001	FJ948991.1	FJ948951.1	#	FJ949030
RTA Clade, Dionycha incertae ceids, Clubionidae	*Clubiona pallidula*	(Clerck, 1757)	HQ924480	#	#	#
RTA Clade, Dionycha incertae ceids, Clubionidae	*Clubiona pseudogermanica*	Schenkel, 1936	#	AY633858	AY633880	#
RTA Clade, Dionycha incertae ceids, Clubionidae	*Clubiona japonicola*	Bösenberg & Strand, 1906	JN817221.1	JN817010.1	JN816587	#
RTA Clade, Dionycha incertae ceids, Corinnidae	*Castianeira sp.*	Keyserling, 1879	AY297419	AY297292	AY296710	#
RTA Clade, Dionycha incertae ceids, Homalonychidae	*Homalonychus selenopoides*	Marx, 1891	AY959938	AY959908	AY955690	FJ949062
RTA Clade, Dionycha incertae ceids, Homalonychidae	*Homalonychus theologus*	Chamberlin, 1924	AY959925	AY959920	#	#
RTA Clade, Dionycha incertae ceids, Philodromidae	*Philodromus* dispar	Walckenaer, 1826	#	#	EU168145	EU157108
RTA Clade, Dionycha incertae ceids, Philodromidae	*Philodromus alascensis*	Keyserling, 1884	GU684172	JQ312075.1	#	#
RTA Clade, Dionycha incertae ceids, Salticidae	*Paraphidippus aurantius*	(Lucas, 1833)	FJ607581	FJ607542	FJ607468	FJ607619
RTA Clade, Dionycha incertae ceids, Salticidae	*Habronattus mexicanus*	(Peckham & Peckham, 1896)	AY297381	AY297251	#	#
Thomisidae	*Misumenops dalmasi*	Berland, 1927	FJ590798	#	DQ174354	EF419123.1

Table 2. continued

RTA Clade, Dionycha incertae ceids, Thomisidae	*Misumenops nepenthicola*	(Pocock, 1898)	#	EF419029.1	#	#
RTA Clade, Dionycha incertae ceids, Thomisidae	*Xysticus* sp.	C. L. Koch, 1835	AY297423	AY297296	AY296714	EU157132
RTA Clade, Dionycha incertae ceids, Liocranidae	*Itatsina praticola*	(Bösenberg & Strand, 1906)	JN817217	JN817006	JN816583	#
RTA Clade, Dionycha incertae ceids, Sparassidae	*Damastes* sp.	Simon, 1880	GQ855822	#	HM575716	HM576227
RTA Clade, Dionycha incertae ceids, Sparassidae	*Eusparassus walckenaeri* (SD 804)	(Audouin, 1826)	#	JX137225	#	#
RTA Clade, Dionycha incertae ceids, Sparassidae	*Leucorchestris arenicola* (SD 442)	Lawrence, 1962	#	JX137222	#	#
RTA Clade, Dionycha incertae ceids, Sparassidae	*Polybetes pythagoricus*	(Holmberg, 1875)	#	#	HM575720	HM576322
RTA Clade, Dionycha incertae ceids, Sparassidae	*Spariolenus iranomaximus* (SD 618)	Moradmand & Jäger, 2011	#	JX137224	#	#
RTA Clade, Dionycha, Gnaphosoidea, Gnaphosidae	*Drassodes lapidosus*	(Walckenaer, 1802)	AY560798	AY560767	AY560683	#
RTA Clade, Dionycha, Gnaphosoidea, Gnaphosidae	*Zelotes* sp.	Gistel, 1848	DQ628624	DQ628686	#	#
RTA Clade, Dictynoidea, Desidae	*Badumna longinqua*	(L. Koch, 1867)	FJ607558	FJ607523	FJ607449	FJ607597
RTA Clade, Dictynoidea, Dictynidae	*Dictyna* sp.	Sundevall, 1833	FJ607561	FJ607526	FJ607452	FJ607600
RTA Clade, Dictynoidea, Dictynidae	*Mexitlia trivittata*	(Banks, 1901)	FJ607573	FJ607537	FJ607462	FJ607611
RTA Clade, Dictynoidea, Hahniidae	*Cybaeolus* sp.	Simon, 1884	FJ948992.1	FJ948952.1	JN816572.1	FJ949031.1
RTA Clade, Dictynoidea, Cybaeidae	*Cybaeus morosus*	Simon, 1886	FJ263792.1	DQ628671	#	DQ628641
RTA Clade, Dictynoidea, Cybaeidae	*Cybaeus mosanensis*	Paik & Namkung, 1967	#	#	JN816569	#

Table 3. Molecular markers and primers used for amplification. The amplification was performed in 25 µl final volume containing 13.95 µl of ultra-pure water (dd H2O), 2.5 µl of 10*Polymerase-buffer, 0.4 µl of each primer (100 pmol/µl), 1.5 µl of dNTPs (2.5 mM), 3.5 µl of MgCl2 (25 mM), 2.5 µl of the genomic spider DNA templates (30–35 ng/ µl) and 0.25 µl of *Taq* DNA polymerase. PCR settings list initial denaturation (id; indicating temperature in °C followed by time in seconds) followed by *n cycles (denaturation: d, anneiling: a, elongation: e) in [], and a terminal elongation (te). References: 1. Bayer and Schönhofer (2013); 2. Bayer (2008; both based on Barrett & Hebert, 2005); 3. based on Simon et al. (1994) modified for this study; 4. based on Crews and Hedin (2006) modified for this study; 5. Hedin and Maddison (2001); 6. Colgan et al. (1998).

Marker	Primer-Name	Primer-Sequence	Ref.	PCR settings
COI	'Heteropoda-fw.'	5'-TCTACTAATCATAAAGATATTGG-3'	1	id95 (300s), [d94 (60s), a56 (60s), e72 (60s)*34], te72 (600s)
	'Heteropoda-rv.'	5'-TCCGGCAGGGTCAAAAAATGA-3'	2	
16S	'LR-N-13398_modified'	5'-CGACTGTTTATCAAAAACAT-3	3	id95 (300s), [d94 (60s), a48 (60s), e72 (60s)*34], te72 (600s)
	'N1-J-12859_modified'	5'-AAGATAGAAACCGACCTGGC-3'	4	
28S	'28SO'	5'-GAAACTGCTCAAAGGTAAACGG- 3'	5	id95 (300s), [d94 (60s), a54 (60s), e72 (60s)*34], te72 (600s)
	'28SC'	5'-GGTTCGATTAGTCTTTCGCC-3'	5	
H3	'H3aF'	5'-ATGGCTCGTACCAAGCAGACVGC-3'	6	id95 (300s), [d94 (60s), a54 (60s), e72 (60s)*34], te72 (600s)
	'H3aR'	5'-ATATCCTTRGGCATRATRGTGAC-3'	6	

Table 4. Models of evolution for each partition and different sets of taxon combinations as calculated by jModeltest. Alignment length did not vary for COI (603bp) and H3 (327bp).

Taxon sets \ partitions	alignment in bp		models of partitions							
	28S	**16S**	**28S**	**16S**	**COI-p1**	**COI-p2**	**COI-p3**	**H3-p1**	**H3-p2**	**H3-p3**
All-taxa set, MAFFT	982	546	GTR+I+G	GTR+G	HKY+I+G	GTR+I+G	HKY+G	SYM+I+G	JC	HKY+I+G
All-taxa set, MAFFT+Gblocks	597	394	GTR+I+G	GTR+I+G	HKY+I+G	GTR+I+G	HKY+G	SYM+I+G	JC	HKY+I+G
All-outgroups-8-Sparassidae set, MAFFT	984	531	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	HKY+G	GTR+G	JC	GTR+G
All-outgroups-8-Sparassidae set, MAFFT+Gblocks	558	384	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	HKY+G	GTR+G	JC	GTR+G
RTA-out-8-Sparassidae set, MAFFT	885	505	GTR+I+G	GTR+G	GTR+G	GTR+I+G	HKY+I+G	SYM+G	JC	GTR+G
RTA-out-8-Sparassidae set, MAFFT+Gblocks	644	405	GTR+I+G	GTR+G	GTR+G	GTR+I+G	HKY+I+G	SYM+G	JC	GTR+G
Full-ingroup set, MAFFT	792	500	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	HKY+I+G	GTR+I	JC	HKY+G
Full-ingroup set, MAFFT+Gblocks	756	446	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	HKY+I+G	GTR+I	JC	HKY+G
Full-ingroup-2-Eusparassus set, MAFFT	790	495	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	HKY+G	GTR+I	JC	GTR+G
Full-ingroup-2-Eusparassus set, MAFFT+Gblocks	756	451	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	HKY+G	GTR+I	JC	GTR+G

4. DISCUSSION

In this chapter I am summarising and linking the three chapters of the results containing two publications (chapter 3.1: Moradmand and Jäger 2012a; chapter 3.2: Moradmand 2013) and one manuscript “under review” (chapter 3.3). I am focusing here on the main results and highlighting the achievements of my study.

4.1. Taxonomic revision and systematics of *Eusparassus* based on morphology

It is essential to any kind of biological research (i.e. performing a study in phylogeny and zoogeography of a group of organisms) to have clearly defined units (species taxon). Prior to this study, the genus *Eusparassus* was not revised and composed of a heterogeneous assembly of several misplaced taxa, some descriptions solely based on a single sex or juveniles and several with nomenclatural ambiguities. Moreover many species were new to science (~27%) and had to be described. *Eusparassus* demonstrates a roughly uniform morphology which hinders the recognition of its diversity (Levy 1989). I have carried out three main steps to revise the genus:

The first step was to define the genus and find out its diagnostic characters to clearly define and distinguish it from the closely similar genera (e.g. *Olios* of the Sparassinae) and putative Eusparassinae members (e.g. *Peseudomicrommata*, *Arandisa*, *Carparachne*, *Leucorchestris* and *Palystella*). For this purpose a neotype for *E. dufouri* Simon, 1932 was designated and re-described as the type species of the genus in order to fix *Eusparassus* identity and avoid further problem in identification of the genus.

Without any doubt, the largest Sparassidae genus in species number (Platnick 2013), *Olios* is the most similar taxon to *Eusparassus* according to somatic characters (Moradmand 2013). This similarity has caused many misidentifications and misplacements between these two genera in the past (Jäger et al. 2002; Moradmand and Jäger 2012a). Along with revising *Eusparassus*, it was necessary for my study to check several types of *Olios* as well. This resulted in transferring six species from *Olios* to *Eusparassus* and conversely two species from *Eusparassus* to *Olios*. According to my results *Eusparassus* could be characterized by a combination

of somatic characters but mainly based on the copulatory organs. The somatic characters include the presence of intermarginal denticles in some *Eusparassus* spp. (absent in *Olios* spp.), presence mostly of a single bristle on the posterior margin of the cheliceral basal segment close to the base of the fangs but that number can reach a maximum of five (mostly >10 in *Olios* spp.). *Eusparassus* is distinguished from the other Eusparassinae genera by the number of ventral tibial spines: I–IV 2 pairs (3 pairs in e.g. *Arandisa* and *Pseudomicrommata*) and by relative diameters of AME which is subequal to or larger than ALE (smaller than ALE in the other genera).

However, like in other groups of spiders the best characters to diagnose *Eusparassus* species were found to be those of the copulatory organs: male palp, female epigyne and vulva (see chapters 3.1, 3.2). Levy (1989) emphasized on the females' copulatory organs and the lateral view of the vulva as a diagnostic character. In substitution, I provided a drawing from anterio-dorso-lateral view of the left half of the vulvas for a better understanding of the internal duct system. Through examination of females, it should be noted here that epigynes must be dissected to examine the vulva, since at least one un-described genus in Africa shows somehow a very similar shape of epigyne (*Olios croseiceps* Pocock, 1898 currently misplaced in *Olios*) which may lead to misidentifications in the future.

Another finding of this study was the synonymy of the monotypic genus *Cercetius* Simon, 1902 with *Eusparassus*. It was concluded after discovery of adult specimens of *Cercetius perezi* from its type locality. Prior to this study, *Cercetius perezi* was known solely from a single immature holotype but male and female were described for the first time (Moradmand 2013). I applied both morphological (see chapter 3.2) and molecular data (see chapter 3.3) to confirm this synonymy. But since the forgotten generic name *Cercetius* was erected one year before *Eusparassus*, thus the case was referred to the International Commission on Zoological Nomenclature for an action under the plenary power (Moradmand and Jäger 2012b) but before any formal decision usage of the both names must be retained (ICZN 1999).

Second step was to distinguish among different *Eusparassus* species. This step was the most time consuming task since I had to get access to several scientific collections and examine all the previously described types for a detailed examination (illustration, measurement and description). Prior to this study, 29 nominal species

were known. I found out that more than 50% of them were misplaced or mistakenly synonymized.

The following 21 species were re-described examining the particular type specimens: *Eusparassus dufouri, E. levantinus, E. atlanticus*, *E. barbarus, E. syrticus*, *E. oraniensis, E. letourneuxi*, *E. fritschi, E. walckenaeri*, *E. laevatus*, *E. vestigator*, *E. tuckeri*, *E. doriae, E. kronebergi*, *E. maynardi*, *E. pearsoni, E. potanini, E. pontii, E. oculatus, E. fuscimanus* and *E. xerxes.* Eight species were described as new to science: *Eusparassus arabicus* (male, female) from the Arabian Peninsula, *E. educatus* (male, female) from Namibia, *E. reverentia* (male, female) from Burkina Faso and Nigeria, *E. jaegeri* (male, female) from South Africa and Botswana, *E. jocquei* (male, female) from Zimbabwe, *E. borakalalo* (female) from South Africa, *E. mesopotamicus* (male, female) from Iran, Iraq and Turkey and *E. schoemanae* (male, female) from South Africa and Namibia.

Males were described for the first time for *E. atlanticus* and *E. fritschi* as in the females of *E. vestigator*. The following species are known only by females: *E. syrticus, E. borakalalo, E. pontii, E. maynardi* and *E. pearsoni.* Neotypes were designated for *Eusparassus dufouri* from Portugal (Chanca), *E. walckenaeri* from Egypt (Cairo), *E. barbarus*, *E. oraniensis* and *E. letourneuxi* (latter three from Algeria) in order to establish their identity and to avoid misidentification with sympatric congeners since their type specimens were either not designated at all or get lost. For the same reason, one specimen from each syntype series of the following species was selected and designated as lectotype: *E. kronebergi* from Afghanistan, *E. maynardi* from Pakistan, *E. pearsoni* from India and *E. syrticus* from Tunisia. Four nominal species *E. oraniensis, E. vestigator*, *E. tuckeri* and *E. potanini* were found to be senior synonyms of *E. dufouri maximus*, *E. rufobrunneus*, *O. furcatus* and *E. nanjiangensis*, respectively.

In contrast, five species were removed from being junior synonyms and re-established as valid species: *E. kronebergi* from Afghanistan and *E. doriae* from central Iran (both previously considered junior synonyms of *E. walckenaeri*), *E. maynardi* from Baluchistan in Pakistan and *E. pearsoni* from Ghats in India (both previously considered junior synonyms of *E. xerxes*) and *E. fritschi* (previously considered a junior synonym of *E. oraniensis*). Six species were transferred from the genus *Olios* to *Eusparassus* including *Eusparassus xerxes*, *E. maynardi, E. pearsoni*, *E. vestigator*, *E. laevatus* and *E. tuckeri.*

I found 14 species misplaced in *Eusparassus* recognizing that nearly half of the described species prior to this revision were misidentified as *Eusparassus*. Two were transferred from *Eusparassus* to *Olios*: *O. flavovittatus* from Pakistan and *O. quesitio* (replacement name for *O. concolor* Caporiacco, 1939) from Ethiopia. Three species ["*Eusparassus*" *shefteli* Chamberlin, 1916 described from Peru, "*Eusparassus*" *bicorniger* (Pocock, 1898) from East Africa and "*Eusparassus*" *laterifuscus* Strand, 1908 from Madagascar] were proven to be misplaced in *Eusparassus* but cannot currently to be assigned to any known Sparassidae genera. The type specimens for the following nine *Eusparassus* species were destroyed but according to their original descriptions they are clearly misplaced in *Eusparassus* and thus recognized as *nomina dubia*: *"Eusparassus" sexdentatus* Strand, 1906; *"Eusparassus" quinquedentatus* Strand, 1906; *"Eusparassus" subadultus* Strand, 1906; *"Eusparassus" fulviclypeus* Strand, 1906; *"Eusparassus" nigrichelis* Strand, 1906; *"Eusparassus" cornipalpis* Strand, 1906; *"Eusparassus" palystiformis* Strand, 1907; *"Eusparassus" ubae* Strand, 1906 and "*Eusparassus*" *lilus* Strand, 1907. Finally, 30 valid *Eusparassus* species (including *C. perezi*) were (re)described, of which 24 are known by both sexes and six only by females.

Third step was to classify species to species-groups. After defining the genus and (re)describing the species, I looked for shared traits among *Eusparassus* species to propose species-groups. A combination of diagnostic characters of both somatic and copulatory structures was applied which led to proposing the following six species-groups (arranged according to species counts):

1) *dufouri* species-group (8 species): *Eusparassus dufouri, E. barbarus, E. oraniensis, E. fritschi*, *E. letourneuxi, E. atlanticus*, *E. syrticus* and *E. levantinus*. The group is distributed in NW Africa to Iberian Peninsula;

2) *doriae* species-group (7 species): *Eusparassus doriae*, *E. oculatus, E. potanini, E. maynardi*, *E. kronebergi*, *E. fuscimanus* and *E. mesopotamicus.* The group is distributed from the Middle East to Central and parts of South Asia;

3) *jaegeri* species-group (4 species): *Eusparassus jaegeri*, *E. jocquei*, *E. schoemanae* and *E. borakalalo*. The group is distributed in southern and SE Africa;

4) *walckenaeri* species-group (3 species): *Eusparassus walckenaeri*, *E. laevatus* and *E. arabicus.* The group is distributed from the eastern Mediterranean to Arabia and parts of NE Africa;

5) *vestigator* species-group (3 species): *Eusparassus vestigator*; *E. reverentia*; *E. pearsoni*. The group is distributed in Central to East Africa and an isolated area in India,

6) *tuckeri* species-group (2 species): *Eusparassus tuckeri*, *E. educatus*. The group is distributed in SW Africa.

Three species could not be affiliated to any species-group proposed above including: *Eusparassus xerxes*, *E. pontii* and *Cercetius perezi*. The two main somatic characters used to classify species to species-groups were the intermarginal denticles in chelicerae and the ventral opisthosoma marking. Just two species-groups (*walckenaeri* and *jaegeri*) have intermarginal denticles in their chelicerae. A distinct dark marking on the ventral opisthosoma is present solely in the *dufouri*- and *vestigator*-group members. However these two characters are present in the specimens of *Cercetius perezi*, too. This species has clearly large solid dark markings like those of the *dufouri*-group members and at the same time some specimens bear intermarginal denticles in their chelicerae. However, *C. perezi* adults show a form of copulatory structures different from these groups.

4.2. Molecular phylogenetics

The phylogenetic relationships of Sparassidae with focus on *Eusparassus* and Eusparassinae were investigated for the first time using four molecular markers (mitochondrial COI and 16S; nuclear H3 and 28S). All of the markers used in this study were verified to be informative in reconstructing phylogenetic relationships of Sparassidae (subfamily Deleninae; Agnarsson and Rayor 2013) and other groups of spiders (i.e. Arnedo et al. 2004; Bayer and Schoenhofer 2013; Crews et al. 2010; Miller et al. 2010; Dimitrov et al. 2012; Dimitrov et al. 2013). For details on this subject see chapter 3.3.

4.2.1. *Eusparassus* and its species-groups

The results of molecular phylogeny were in accordance with the diagnoses of the genus and the proposed morphological affinities to classify *Eusparassus* into species-groups. The genus *Eusparassus* was recovered monophyletic with the type specimen *E. dufouri* nested within (using the DNA of the neotype). The monophyly of

the *dufouri*-, *doriae*- and *walckenaeri*-group were well supported, while that of the *tuckeri*-group was not recovered. In the analyses only one single representative of the *jaegeri*-group was included and of all the proposed species-groups only individuals of the *vestigator*-group were missing which was because of unavailable suitable tissues for DNA isolation of these taxa.

The *doriae*- and *walckenaeri*-group were found as sister clades and both likely sister to the *dufouri*-group. It supported the hypothesis based on the analysis of the copulatory organs that *doriae*- and *walckenaeri*-group members are closely related, despite there are major morphological differences such as presence of intermarginal denticles in the *walckenaeri*-group which is absent in the *doriae*-group. On the other side, the single member of the *jaegeri*-group found to have no close relationships to the *walckenaeri*-group members, although both have intermarginal denticles in chelicerae. It is likely that gain of this character in the *jaegeri*- and *walckenaeri*-group happened independently. The exact position of the *tuckeri*- and *jaegeri*-group within the genus was not resolved. Despite not supported with high values, the monophyly of the *tuckeri*-group cannot be rejected by current analyses.

Cercetius perezi nested well within the *Eusparassus* clade indicating that the morphologic findings (the proposed synonymy) are supported by molecular phylogeny and verifying that representatives of both nominal genera are actually congeners.

4.2.2. Subfamily Eusparassinae

To test the phylogenetic relationships and monophyly of Eusparassinae, all of the originally proposed genera (*Eusparassus, Pseudomicrommata* and *Rhitymna*; by Järvi 1912) and the putative Eusparassinae genera (*Arandisa*, *Carparachne*, *Leucorchestris*, *Microrchestris* and *Palystella*; by Jäger and Kunz 2003) were included. In this sense, Eusparassinae was not recovered as a monophyletic group. It split into two major clades. One clade contained the type species *Eusparassus* with all its representatives (including *Cercetius perezi*) and the second containing the rest of Eusparassinae genera. This branch is named the “African clade” consisting of two subclades: (1) *Pseudomicrommata+Arandisa* and (2) *Carparachne*, cf. *Microrchestris*, *Leucorchestris* and *Palystella.* The “African clade” comprises morphologically similar genera endemic to Africa and mainly southern Africa.

Pseudomicrommata and *Arandisa* were recovered as the closest relatives which is supported by their unique morphological characters such as the presence of epigynal pockets. In the second clade, the Namibian sand dwelling genera *Carparachne* and *Leucorchestris* were recovered as sister taxa and both sister to *Palystella*. *Eusparassus* is different from the “African clade” genera by: anterior median eyes (AME) always larger or equal to anterior lateral eyes (ALE) (the “African clade” members with AME smaller than ALE) and legs ventrally with two pairs of tibial spines (three pairs in the “African clade”). Indeed, some *Eusparassus* species have intermarginal denticles in their chelicerae which are absent in the genera of the African clade. Although *Eusparassus* resemble the “African clade” member particularly by the shape of copulatory structures but it is commonly accepted that genital structures evolve and change more rapidly compared to somatic ones (Eberhard 2010). Consequently, *Eusparassus* might not have any close relationships to African clade genera and the similarity in the noted traits might be the result of convergent evolution. If this hypothesis is further supported, Eusparassinae has to be considered monotypic. At this point, the results are not sufficient to propose a new subfamily for the “African clade” genera or exclude them from Eusparassinae but revisions and more robust phylogenetic results are required before proposing a new taxonomic rank. The exact position of *Eusparassus* within Sparassidae was not resolved. However, the relationship of *Eusparassus* with the rest of Eusparassinae genera might be recovered by adding more data supporting the backbone of the current phylogeny.

The Asian genus *Rhitymna* which was proposed originally to be classified in Eusparassinae (Järvi 1912) was placed separately in a clade containing genera *Staianus*, cf. *Remmius*, and *Micrommata* indicating no relationships to Eusparassinae. This affirmed the note by Jäger (2003) that the genus belongs to a lineage different from Eusparassinae.

4.2.3. Sparassidae and the rest of subfamilies

This study was the first comprehensive phylogenetic research on the family Sparassidae treating the majority of morphological variations and classical subfamilies. The inferred phylogeny supported Sparassidae as a monophyletic group with all available subfamilies nested within as well as the type genus for the family, *Micrommata*. Sparassidae split into two clades, a basal clade containing individuals

of the subfamily Sparianthinae (represented by the genus *Thelcticopis* which features all of the typical characteristics of Sparianthinae) and a larger clade composed of the rest of Sparassidae (termed non-Sparianthinae). This latter result is concordant with morphological evidences since Sparianthinae have a kind of autapomorphic characters when compared to the rest of Sparassidae. It also indicated that Sparianthinae is likely a very early diverging group and is sister to all other Sparassidae.

Within non-Sparianthinae clade the monophyly of the subfamilies Heteropodinae *sensu stricto* (Asia, Africa), Palystinae (Africa) and Deleninae (Australia) were supported. Heteropodinae with representatives of six genera were recovered in a basal position within the non-Sparianthinae clade. However the backbone of the non-Sparianthinae clade was not resolved. The monophyly of Heteropodinae *sensu stricto* is also supported by synapomorphies for this subfamily including the trilobate membrane with well-developed lateral projections and median hook, chelicerae with three anterior and four to six posterior teeth intermarginally covered with denticles (Jäger 1998). Through the investigated taxa, just members of Heteropodinae and two species-groups of *Eusparassus* have intermarginal denticles in their chelicerae. Whether denticles are a plesiomorphic character state in Sparassidae or not could not be tested with the results since the backbone of the tree was not resolved. But it should be noted that the form of cheliceral denticles is different in Heteropodinae *sensu stricto* from those of *Eusparassus*. Mostly a patch of denticles is present close to the three anterior teeth in Heteropodinae (Jäger 2002; Moradmand and Jäger 2011) while in *Eusparassus*, there is a line or scattered denticles throughout cheliceral furrow (Moradmand and Jäger 2012a; Moradmand 2013).

Sparassinae and the genus *Olios* (as the most similar genus to *Eusparassus* in somatic character) appeared to be polyphyletic but further studies require additional taxon sampling. Previously, the polyphyly of *Olios* was suggested by Rheims (2010) and noted by Jäger and Kunz (2005) according to morphological evidences. The genus *Olios* which is distinguished from *Eusparassus* by its morphology (Moradmand and Jäger 2012a, Moradmand 2013) confirmed to be a separate clade by molecular data as well.

The characters of the copulatory organs, trilobite membrane, eye arrangement and cheliceral dentition are currently the available morphological characters for the classification of Sparassidae. The inferred phylogeny revealed that these characters have phylogenetic values at least in the subfamilies Sparianthinae, Heteropodinae *sensu stricto*, Palystinae and Deleninae. However these characters should be applied in combination since possibility of convergence is important to consider.

Very recently Agnarsson and Rayor (2013) tested the phylogenetic relationships of Australian Deleninae. They focused exclusively on Deleninae and the evolution of sociality in its members. Despite they recovered Deleninae monophyletic, but they did not include Sparianthinae, Staianinae and even putative close relatives to Deleninae such as Sparassinae in their analyses.

4.2.4. 'Laterigradae', Dionycha and RTA-clade

Further studies focused on the phylogenetic position of Sparassidae within the order Araneae and test its relationships to assumed closely related families. Sparassidae share the character of crab-like posture (laterigrade position of legs) with the entelegyne families Selenopidae (wall crab spiders), Philodromidae (running crab spiders) and Thomisidae ("true" crab spiders). These families together with Sparassidae were grouped under the name 'Laterigradae' by Latreille (1802) and to date they are all unplaced families within the Dionycha of the RTA-clade. It was assumed that these four crab-like families may eventually be clustered near each other (Coddington and Levi 1991). All representatives of the 'Laterigradae' families and a majority of the RTA-clade families with focus on Dionycha spiders were included in the phylogenetic analyses.

The 'Laterigradae' was not recovered as a monophyletic group thus the similar crab-like leg posture in all four families (Sparassidae, Thomisidae, Philodromidae and Selenopidae) is better explained by evolutionary convergence. As noted above, Sparassidae was placed in an outgroup position towards the rest of the RTA-clade members. Thomisidae was firmly nested within Lycosoidea. However, Philodromidae and Selenopidae were found to be more closely related in a clade together with two family members of contrasting body organisation Salticidae and Corinnidae. 'Laterigradae' families showed no further relationship towards each other which suggest that the term should be abandoned.

The monophyly of Dionycha was not supported in the current phylogeny and this result is in accordance with Agnarsson et al. (2013). The Dionycha was solely erected on the simple character of the two-clawed legs and composed of several heterogeneous spider families (Coddington 2005). The RTA-clade recovered fully monophyletic with Sparassidae nested within the clade using spiders of the non-RTA-clade (Orbiculariae, Eresoidea and Palpimanoidea) as outgroups. This result was also retained by the analyses of Spagna and Gillespie (2008) and Miller et al. (2010), while these authors did not include Sparassidae in their studies.

4.3. Origination and zoogeography of *Eusparassus*

Here I combined the results from molecular dating and phylogeny as well as current knowledge on *Eusparassus* distribution range to discuss about the zoogeography of the genus members.

Extant *Eusparassus* species are distributed across the Old World from southern Africa to Mediterranean region, and from Arabia and Middle East toward Central and South Asia. The previous records of the genus from Madagascar ("*Eusparassus*" *laterifuscus*), Americas ("*Eusparassus*" *shefteli*) and SE Asia ("*Eusparassus*" *lilus*) were proven to be misidentifications (Moradmand and Jäger 2012a; Moradmand 2013). The genus represents one of the evolutionary successful groups of spiders since it exists at least from early Tertiary till present (~50 million years), according to the *Eusparassus* amber fossil record in northern Europe (Dunlop et al. 2011). To trace and discuss the findings of this study on the origin of *Eusparassus*, I should give some notes on the origination of Sparassidae and its comprising subfamilies (see chapter 3.3).

The origin of Sparassidae was dated back to early Jurassic (186 MA) by the molecular dating analyses, when they diverged from the rest of RTA-clade families. Subsequently around 163 MA, the hypothesised Sparassidae ancestor diverged into two clades: the Sparianthinae as basal group and the non-Sparianthinae clade. The further divergence happened rapidly within the non-Sparianthinae much later (106–97 MA) into current diverse groups of Sparassidae [e.g. African clade (Africa), Heteropodinae (Africa, Australasia), Palystinae (Africa), Polybetinae (Americas) and Deleninae (Australia)]. Since the backbone of the phylogenetic relationships among the non-Sparianthinae clade was not resolved, the relationships between

Eusparassus and the African clade genera (as proposed Eusparassinae) cannot be explicitly diagnosed.

However, a hypothesis of *Eusparassus* origination can be proposed based on the molecular dating, historical biogeography and geological events: *Eusparassus* lineage probably originated around 70 MA in SW Africa in the border of the Namib Desert. This hypothesis is supported with the following evidences. Extant and fossil *Eusparassus* species occurred exclusively in Africa and Eurasia meaning that the genus does not have a Gondwanan distribution range and likely originated after the breakup of the supercontinent Gondwanaland. Africa after splitting from other Gondwanaland plates around 110–95 MA remained isolated, stabilized and unchanged until collided and connected with Eurasia in the Paleocene around 60 MA (Sanmartín and Ronquist 2004). But this connection was not still complete to allow dispersal from Africa+Europe to Asia because of a great sea barrier named Turgai Strait which divided the Palearctic into an eastern and western half until 30 MA when the Strait dried up and permitted extensive biotic exchanges (Sanmartín et al. 2001).

Since *Eusparassus* species are representatives of arid to semiarid regions, its origination and dispersal must be connected to desertification and distribution of deserts. The most suitable place for their ancestors could be the transition zone of a desert with stable environment at the estimated divergent time (70 MA). The Namib Desert with the age of 130–55 MA (Ward et al. 1983; Ward 2009) is the best candidate for the ancestral origin of *Eusparassus*. The hypothesis of southern African origin of *Eusparassus* is further supported by the current distribution range of the members of the African clade and also two basal *Eusparassus* species-groups (*tuckeri*- and *jaegeri*-group) within and in the borders of the Namib Desert. The Namib Desert has provided stable environments for its unique diversity of desert dwelling organisms with high levels of endemism (Barnard et al. 1998; Ward 2009). Other deserts of the Old World are much younger, in contrast to the Namib Desert, the Sahara as the largest desert of the world formed not older than 7 MA (Schuster et al. 2006). The Asian deserts appeared or expanded mostly during the global desertification initiating around 23 Ma, in Miocene (Potter and Szatmari 2009).

The proposed six species-groups of *Eusparassus* are distributed in separate geographic regions but partially overlap with neighbouring group distribution range. The inferred phylogeny recovered a clade of *Eusparassus* species with promising

support (outlined here as non-southern African clade) and the southern African group members in a basal position (see chapter 3.3: figs 3, 5). The southern African group including *E. tuckeri* and *E. educatus* (the *tuckeri*-group) and *E. jaegeri* (*jaegeri*-group) recovered in a basal position within the *Eusparassus* clade but their relationships were not resolved. The *tuckeri*-group members are restricted to SW Africa at the borders of the Namib and Kalahari Deserts (Namibia, western South Africa and southern Angola). The *jaegeri*-group are neighbouring them in SE Africa (eastern Namibia, South Africa, Botswana and Zimbabwe). The members of the *tuckeri*- and *jaegeri*-group might be the oldest lineages of *Eusparassus*.

The non-southern African clade subsequently split into two major clades, one containing the *dufouri*-group + *Cercetius perezi* and another one containing *walckenaeri*-group + *doriae*-group members. The first clade separated from the second clade around 41 MA with a common ancestor probably lived in NE Africa and Arabia. The *dufouri*-group members are currently distributed in NW Africa (six species in Tunisia, Algeria and Morocco) and Iberian Peninsula (two species in Spain and Portugal). Most likely the Iberian species originated from NW Africa. However, this could not be tested with the available data since only one representative of NW African (*E. oraninensis*) was included in the analyses. But the results showed that the Iberian species have a more recent common ancestor compared to the Moroccan species around 23 MA. *Cercetius perezi* nested within the non-southern African clade but its exact position was not resolved. Nevertheless, morphological evidences suggest that *C. perezi* could be related to *dufouri*- and *walckenaeri*-group members. The distribution of *C. perezi* among these groups from the Horn of Africa to Arabian Peninsula supports this notion.

Later on, around 35 MA, the *walckenaeri*-group split from the *doriae*-group with their common ancestor probably lived somewhere in the Middle East and/or NE Africa. These two groups recovered to be closely related phylogenetically. The members of the *doriae*-group (seven species) are distributed in the Middle East toward Central Asia and parts of South Asia. The *walckenaeri*-group occurs in eastern Mediterranean and in NE Africa and Arabia. It is likely that the *doriae* lineage diverged from the common ancestor with the *walckenaeri*-group by losing their intermarginal denticles of the chelicerae and subsequent modifications in the copulatory structures. The closing age of the Turgai Strait is in concordant with the

divergent time of the *doriae*- and *walckenaeri*-group. This event might play a role in the divergence of these two groups. Later on in Miocene, a land bridge of arid savannah between Arabia and southern Iran (Shmida, 1985) around where the Persian Gulf is currently present might have affected further exchanges.

The phylogenetic position and relationships of the *vestigator*-group members could not be tested in this study due to missing fresh samples for DNA isolation. The *vestigator*-group composes of three species, two occur in Central and East Africa and one endemic to western India. The presence of this isolated lineage (*E. pearsoni*) in India far from Africa can be explained by secondary distribution of the hypothesised ancestor from eastern Africa to India after the reattachment of the two plates via great Somalia around 65–60 MA.

Finally for the same reason as for the previous, the phylogenetic relationships of *E. xerxes* (from Arabia to Pakistan) and *E. pontii* (Himalayas) to rest of congeners could not be tested. Both species could not be placed in the proposed species groups. They demonstrate a transition in characters between the *dufouri*-, *doriae*- and *walckenaeri*-group. *E. pontii* might have diverged from the *doriae*-group in highlands of the Himalayas and adapted to very high elevations (~4000 m). These entire hypotheses must be tested by a robust phylogeny and molecular dating approach after a rich sampling of the noted taxa.

5. Zusammenfassung

Die Spinnengattung *Eusparassus* Simon, 1903 (Araneae: Sparassidae: Eusparassinae; Stein-Riesenkrabbenspinnen) wird weltweit revidiert, sie umfasst 30 valide Arten ausschließlich aus Afrika und Eurasien. Die Typus-Art *E. dufouri* Simon, 1932 wird wiederbeschrieben und ein Neotypus aus Portugal designiert. Eine erweiterte Diagnose für die Gattung wird vorgeschlagen. Acht neue Arten werden erstmals beschrieben: *Eusparassus arabicus* Moradmand, 2013 (Männchen, Weibchen) von der Arabischen Halbinsel, *E. educatus* Moradmand, 2013 (Männchen, Weibchen) aus Namibia, *E. reverentia* Moradmand, 2013 (Männchen, Weibchen) aus Burkina Faso und Nigeria, *E. jaegeri* Moradmand, 2013 (Männchen, Weibchen) aus Südafrika und Botswana, *E. jocquei* Moradmand, 2013 (Männchen, Weibchen) aus Simbabwe, *E. borakalalo* Moradmand, 2013 (Weibchen) aus

Südafrika, *E. schoemanae* Moradmand, 2013 (Männchen, Weibchen) aus Südafrika und Namibia sowie *E. mesopotamicus* Moradmand & Jäger, 2012 (Männchen und Weibchen) aus dem Irak, Iran und der Türkei. 22 Arten werden wiederbeschrieben, wovon sechs aus der Gattung *Olios* Walckenaer, 1837 nach *Eusparassus* transferiert werden. Sechs Artengruppen werden aufgestellt: die *dufouri*-Gruppe [8 Arten: *E. dufouri*, *E. levantinus* Urones, 2006, *E. barbarus* (Lucas, 1846)*, E. atlanticus* Simon, 1909, *E. syrticus* Simon, 1909, *E. oraniensis* (Lucas, 1846)*, E. letourneuxi* (Simon, 1874), *E. fritschi* (Koch, 1873); Iberische Halbinsel bis Nordwestafrika (teilweise)], *walckenaeri*-Gruppe [3 Arten: *E. walckenaeri* (Audouin, 1826), *E. laevatus* (Simon, 1897), *E. arabicus*; östlicher Mittelmeerraum bis Arabien und Nordostafrika (teilweise)], *doriae*-Gruppe [7 Arten: *E. doriae* (Simon, 1874), *E. kronebergi* Denis, 1958, *E. maynardi* (Pocock, 1901), *E. potanini* (Simon, 1895), *E. fuscimanus* Denis, 1958, *E. oculatus* (Kroneberg, 1846) und *E. mesopotamicus*; Mittlerer Osten bis Zentral- und Südasien], *vestigator*-Gruppe (3 Arten: *E. vestigator* (Simon, 1897), *E. reverentia*, *E. pearsoni* (Pocock, 1901); Zentral- bis Ostafrika und eine isolierte Region in NW Indien], *jaegeri*-Gruppe [4 Arten: *E. jaegeri*, *E. jocquei*, *E. borakalalo*, *E. schoemanae*; Süd- und Südostafrika], *tuckeri*-Gruppe [2 Arten: *E. tuckeri* (Lawrence, 1927), *E. educatus*; Südwestafrika). Zwei Arten, *E. pontii* Caporiacco, 1935 und *E. xerxes* (Pocock, 1901) können keiner der obengenannten Gruppen zugeordnet werden. Zwei Arten werden von *Eusparassus* nach *Olios* transferiert: *O. flavovittatus* (Caporiacco, 1935) und *O. quesitio* Moradmand, 2013. 14 Arten wurden von früheren Autoren fälschlicherweise in die Gattung *Eusparassus* gestellt, damit wurden vor dieser Revision fast die Hälfte der beschriebenen Arten irrtümlicherweise in die falsche Gattung gestellt. Neotypen werden designiert für *E. walckenaeri* aus Ägypten, *E. barbarus*, *E. oraniensis* und *E. letourneuxi* (alle drei letztgenannten aus Algerien), um die Identität dieser Arten eindeutig festzulegen. Männchen und Weibchen von *Cercetius perezi* Simon, 1902 —eine Art, die nur vom juvenilen Holotypus bekannt war— werden erstmals beschrieben. Hierbei wurde festgestellt, dass der kaum benutzte, monotypische Gattungsname *Cercetius* Simon, 1902 ein älteres Synonym des weitverbreiteten und sehr häufig benutzten Gattungsnamens *Eusparassus* ist. Ein Antrag (Nummer 3596), den Namen *Eusparassus* zu schützen, ist bei der Internationalen Kommission für Zoologische Nomenklatur (ICZN) anhängig.

Die Phylogenie der Sparassidae mit dem Schwerpunkt *Eusparassus* wird zum ersten Mal anhand von vier molekularen Markern (mitochondriale Gene COI und 16S; nukleare Gene H3 und 28S) untersucht. Die Monophylie von *Eusparassus* und der *dufouri-, walckenaeri-* und *doriae-* Arten-Gruppen wird nachgewiesen, wobei die beiden letztgenannten Gruppen enger miteinander verwandt sind. Die *tuckeri*-Gruppe ist kein Monophylum, die Position von *E. jaegeri* (als der einzig verfügbaren Art aus der *jaegeri*-Gruppe) innerhalb des *Eusparassus*-Stammbaumes kann nicht aufgelöst werden. DNA-Proben aus der *vestigator*-Gruppe standen für diese Studie nicht zur Verfügung. Anhand der „Molekularen Uhr"-Analyse wird der Ursprung der Gattung *Eusparassus* vor ca. 70 Millionen Jahren vermutet. Anhand der vorliegenden Ergebnisse in Kombination mit biogeographischen und geologischen Daten sind *Eusparassus* und andere mutmaßliche Gattungen der Eusparassinae wahrscheinlich in der Namib-Wüste entstanden.

Weitere Analysen zu den phylogenetischen Beziehungen der Sparassidae und deren Unterfamilien weisen die Eusparassinae als polyphyletisch aus, mit den beiden Gattungen *Eusparassus* und *Pseudomicrommata* in getrennten Linien. Nur die letztere Gattung gruppiert mit den meisten anderen vermuteten Eusparassinae, hier "Afrikanische Gruppe" genannt. Die Unterfamilien Sparianthinae, Heteropodinae *sensu stricto*, Palystinae und Deleninae sind monophyletisch. Die Sparianthinae sind ein basaler Abzweig, welcher sich relativ früh (vor ca. 143 Millionen Jahren) von allen anderen Sparassidae abgetrennt hat. Die Sparassinae und die Gattung *Olios* sind polyphyletisch. Die Sparassidae ist eine monophyletisch Gruppe und innerhalb des sogenannten „RTA-clades" eine basale Abzweigung. Die Abspaltung der Sparassidae vom „RTA-clade" wird vor ca. 186 Millionen Jahre angenommen, also innerhalb des Jura. Es werden keine näheren Beziehungen zu anderen Mitgliedern der ‚Laterigradae' (Philodromidae, Selenopidae und Thomisidae) beobachtet, die krabbenartige Stellung der Beine dieser Gruppe wird als ein Ergebnis konvergenter Evolution angesehen. Nur die Familien Philodromidae und Selenopidae werden als Mitglieder ein- und derselben, unterstützten Untergruppe erkannt. Unter Einbeziehung eines beträchtlichen Anteils von Vertretern des „RTA-clades" werden die übergeordneten „Dionycha" nicht als monophyletisch, der „RTA-clade" selbst aber als monophyletisch unterstützt.

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CURRICULUM VITAE

PERSONAL DATA

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RESEARCH INTERESTS

- Taxonomy, Systematics and Phylogeny of Spiders
- Species Distribution Modelling
- Evolutionary biology and historical biogeography
- Taxonomy and ecology of Hermit Crabs

EDUCATION

Sep 2009 – present: PhD candidate of Biology, Johann Wolfgang Goethe University and Senckenberg Research Institute, Frankfurt am Main, Germany
Oct 2004 – Jun 2007: MSc in Biology-Animal Biosystematics, School of biology, University College of Science, University of Tehran, Iran
Oct 2000 – Oct 2004: BSc in Biology-Zoology, Department of Biology, Faculty of Science University of Isfahan, Iran
Oct 1996 – Oct 2000: High school degree in Experimental Sciences, Shahid-Nilforoosh-Zadeh High School, Isfahan, Iran

HONORS

2011-2012: awarded two research grants from the SYNTHESYS Project (http://www.synthesys.info/), which is financed by the European Community Research Infrastructure Action under the FP7 "Capacities" Program to visit NHM (London) and MRAC (Tervuren) collections.
2010: awarded the best student poster presentation in “die Arachnologische Gesellschaft e.V.” Berlin.
2007- First and excellent degree among MSc students of the Department of Zoology, University of Tehran, Average 18.84 out of 20.
2004 – Exempt from military service by the government of Iran because of being selected as an excellent student.
2004- Ranked **2nd** in Zoological sciences (systematic-physiology-developmental biology) among up to 7000 participants in the National Exam for Entering Nationwide MSc Program in Biological Science.
2004- Ranked **5th** in Medical Entomology and Vectors Control, among up to 500 participants in the National Exam for Entering Nationwide MSc program of Health and medical sciences.

RESEARCH EXPERIENCES AND PROJECTS

09.2009 – present PhD dissertation titled: "Taxonomic revision, phylogeny and zoogeography of the genus *Eusparassus* (Araneae: Sparassidae);

10 - 30.07.2008 conducting a research on spiders taxonomy through the project "Establishment of a Middle Eastern Biodiversity Research, Training and Conservation Network" funded by DAAD in the Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany;

2005 – 2007 MSc Thesis: Taxonomy and Zoogeography of Littoral Hermit crabs (Crustacea: Anomura: Paguridea) of the Persian Gulf and the Gulf of Oman, *Laboratory of Zoology, School of biology, University College of science, University of Tehran*;

01.08 - 30.09.2006 conducting a research on hermit crabs taxonomy through the project "Establishment of a Middle Eastern Biodiversity Research, Training and Conservation Network" funded by DAAD in the Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany;

2005 – 2006 Project on the Biodiversity of the Iranian Coast of the Gulf of Oman, *Laboratory of Zoology, School of biology, University College of science, University of Tehran*;

2002 – 2003 Project on the main benthic Invertebrate Fauna of the Zayande-rood River, Isfahan Province, Iran, *Laboratory of Zoology, Department* of *Biology, Faculty of Science, Isfahan University*

CONGRESSES

September 2012, the 26th European congress of Arachnology, Ljubljana, Slovenia: lecture presentation titled "the stone huntsman spiders - *Eusparassus* Simon, 1903: systematics and zoogeography";

September 2010, "die Arachnologische Gesellschaft e.V." Berlin: Poster titled "Taxonomische Revision der Gattung *Eusparassus* Simon, 1903 (Araneae: Sparassidae): Suche nach diagnostische Merkmalen";

July 2010, the 18th International congress of Arachnology, Poland: lecture titled "On three new species of the genus *Spariolenus* Simon, 1880 (Sparassidae: Heteropodinae) from Iran with comments on taxonomy and zoogeography"; poster titled "Taxonomic revision of the genus *Eusparassus* Simon, 1903 (Araneae: Sparassidae), Part 1: finding diagnostic characters";

March 2006, "the First International Conference on the State of the Gulf Ecosystem: Future and Threats", *UAE University, Al-Ain, United Arab Emirates,* poster presentation titled: "Hermit Crabs (Crustacea: Anomura: Paguridea) of the Persian Gulf: 1- Hormozgan Province"

WORKSHOPS & COURSES

11-15 March 2013, "Isolation, PCR and sequencing of Old DNA", Max Plank Institute for Evolutionary biology, Plön, Germany

27 Feb - 2 Mar 2012, "Species Distribution Modelling (SDM) course", GRADE (Goethe Graduate Academy)

7-11 February 2011, "Geographic Information System (GIS) course I, II", GRADE (Goethe Graduate Academy)

17-28 January 2011, "The Phylogenetic Systematics and Molecular Dating course", Zoological Museum, University of Copenhagen, Denmark

4 December 2009, "Scientific paper writing: develop your own paper!", GRADE (Goethe Graduate Academy)

20 November 2009, "Scientific paper writing: Coping with readers expectations and your own frustration", GRADE (Goethe Graduate Academy)

9 November 2009, "Communication skills" at conferences, GRADE (Goethe Graduate Academy)
December 2006, the first workshop on "the biodiversity conservation imperative: biological, ethical and economic approaches in the Middle East and Europe", University of Tehran and Research Institute Senckenberg

PUBLICATIONS

1) **Moradmand**, **M.,** Schönhofer, A. L., Jäger, P., 2013. Molecular phylogeny of the huntsman spider family Sparassidae with focus on the genus *Eusparassus* and notes on the RTA-clade and 'Laterigradae'. *Molecular Phylogenetics and Evolution*, under review.
2) **Moradmand**, **M**. (2013) The stone huntsman spiders – *Eusparassus* (Araneae: Sparassidae): systematics and zoogeography with revision of the African and Arabian species. *Zootaxa*, 3675 (1), 1–108.
3) **Moradmand**, **M**. and P. Jäger (2012a) Taxonomic revision of the huntsman spider genus *Eusparassus* Simon, 1903 (Araneae: Sparassidae) in Eurasia. *Journal of Natural History***,** 46(39-40), 2439–2496.
4) **Moradmand, M.** and Jäger, P. (2012b) *Eusparassus* Simon, 1903 (Araneae: Sparassidae): proposed conservation of the generic name. *Bulletin of Zoological Nomenclature*, 69(4), 249–253.
5) Naderloo, R., **Moradmand**, **M**., Sari, A. & M. Türkay (2012) An annotated checklist of hermit crabs (Crustacea, Decapoda, Anomura) of the Persian Gulf and Gulf of Oman with five new records and an identification key to the North Indian Ocean genera. *Zoosystematics & Evolution*, 88(1), 63–70.
6) **Moradmand**, **M**. and Jäger, P. (2011) A review on the huntsman spider genus *Spariolenus* Simon, 1880 (Araneae: Sparassidae: Heteropodinae) in Iran with description of four new species. *Zootaxa*, 2910, 46–62.
7) **Moradmand, M.** and Sari, A. (2007a) New record of the hermit crab *Pagurus kulkarnii* Sankolli, 1961 (Anomura, Paguridae) from the Gulf of Oman, Iran. *Zoology in the Middle East*, 42, 112–114.

8) **Moradmand, M.** and Sari, A. (2007b) Littoral Hermit crabs of the Gulf of Oman: A biogeographical approach. *Iranian Journal of Animal Biosystematic*, 3, 25–36.

SCIENTIFIC COMMUNITIES

GRADE (Goethe Graduate Academy)
International society of Arachnology
European society of Arachnology
African society of Arachnology
Iranian society of Arachnology

LANGUAGE SKILLS

Persian (Farsi): mother tongue
English: excellent, TOEFL 2009, paper based
German: intermediate, A2
Arabic: basic

09.Sep.2013 Frankfurt am Main Majid Moradmand