



The morphology and relationships of the walking mud spiders of the genus *Cryptothele* (Araneae: Zodariidae)

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ABSTRACT

We revise the relationships of the spider genus *Cryptothele* after reexamination of the morphology of the spinnerets, leg tarsal claws and maxillae with scanning electron microscopy. *Cryptothele* species have a particular conformation of the spinning field of the anterior lateral spigots that is typical of zodariids and close relatives: the field of major ampullate gland spigots, together with their strain sensilla, are invaginated within the field of piriform gland spigots. The implantation of the teeth on the inner side of the leg tarsal claws is also consistent with its placement among zodariids. We added *Cryptothele* to a morphological dataset of zodariid genera, together with the outgroups *Homalonychus* (Homalonychidae) and *Penestomus* (Penestomidae). The phylogenetic analysis concludes that the genus *Cryptothele* is a member of the subfamily Cydrelineae, which by priority is here considered a junior synonym of Cryptothelinae. *Cryptothele* specimens cover most of their body with soil particles which become consolidated as mud, and the debris is probably held in place by curved setae covered by long barbs. The spinnerets, which can be retracted and hidden, as well as the booklungs, are surrounded by a crown of thick setae that are densely covered by short barbs, protecting those areas against soil particles. *Cryptothele* are probably specialized to prey on termites, and their phylogenetic placement indicates that this diet specificity evolved two times independently in zodariids.

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1. Introduction

The tropical spiders of the genus *Cryptothele* were first discovered by L. Koch (1872). Because of their bizarre, cryptic appearance they were placed in a new suborder of their own (Ruditelariae), together with the bird dropping spiders of the genus *Celaenia* Thorell, 1868, now distantly placed in Araneidae. *Cryptothele* specimens have the ability to cover most of their body with soil particles and mud, and hide the retracted spinnerets behind a mud-covered crown of setae. In this way, they attain a strikingly cryptic appearance (Fig. 1), which is the origin of their generic name. So remarkable is their camouflage that they have been called “walking mud spiders” (Koh and Ming, 2013) and even “invisible ground spiders” (Koh, 1989). An early hint of their way of living comes

from a charming report by Abraham (1924: 90), which is worth reproducing here:

“This specimen was kept alive from 25th June 1922 until 14th October 1922 and during that time could only be induced to eat termites. Its method of capturing these was to remain quite still until a termite approached [The spider seemed always to ‘sense’ the proximity of the termite when it was quite a distance away] when it would raise its nearest leg (or legs) up to the air and with them, as it were, guide the insect underneath its (the spider’s) cephalothorax, then it would ‘gather’ the termite into a suitable position for striking by folding its legs under itself and around the insect in such a way that the insect’s head comes just in front of the spider’s fangs. The termite is always bitten on the dorsal surface of the thorax, just behind the head, and as soon as its struggles cease the spider’s legs are brought back to their normal position and the corpse is held by the mandibles and palpi during the process of being eaten.”

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Fig. 1. *Cryptothele* spp., females. (A–D) from Sri Lanka, MJR1393. (A) Dorsal view. (B) Same, prosoma ventral view. (C) Tarsus–metatarsus joint of leg IV, dorsal view, showing clean area near trichobothria and tarsal organ. (D) Same, spinnerets. (E) Male spinnerets, retracted, from Myanmar, MJR1396. (F) *Cryptothele* (CASENT9036335) female from Kuala Belalong, Brunei, Borneo, photo by Griswold. (G) *Cryptothele* sp. female with eggsac (CAS) from Popa Mt, Burma, photo by Dong Lin.

“The normal gait of this specimen reminded one strongly of that of a chameleon each leg being moved with great deliberation and when alarmed the spider would ‘freeze,’ often with one or two legs in the air if it so happened that it had been moving them when the alarm came.”

The observations of Koh (1989: 87) corroborate this: “When a termite approaches, it [the invisible ground spider] raises its front legs in the air, “guides” the termite underneath its cephalothorax, folds its legs around the termite in such a way that the termite’s head is positioned under its fangs, then the spider strikes.” Their cryptic appearance and hidden life style under logs or in the leaf litter has resulted in them being among the rarest species in collections, to the point that only three of the ten species are known from both sexes (Marusik and Omelko, 2012, 2013). All *Cryptothele* species are very similar to each other and are restricted to tropical areas in the Indian Ocean and the western part of the Pacific Ocean.

The affiliation of *Cryptothele* has been contentious, mainly because of the incorrect interpretation of a few diagnostic characters. Simon (1893: 420) found that *Cryptothele* and the zodariid *Cydrela* Thorell, 1873 were almost indistinguishable, including the very peculiar eye arrangement, with the anterior eye row so procurved as to form a trapezium (Fig. 2A). Nevertheless, he maintained *Cryptothele* in its own subfamily Cryptothelinae Simon, 1890 within the zodariids, reporting differences in the tarsal claws, rugous tegument, and sternum. In Koch’s (1872) illustration of the

tarsal claws of *C. verrucosa* L. Koch, 1872, only one of the superior claws has a single tooth, and the rest are smooth; the same observation is reproduced by Simon (1893: 421). The three species of *Cryptothele* available to us all had several teeth on the tarsal claws (see Fig. 8L, M, O). Perhaps the teeth are variable among species, or most likely, the stuck detritus may have impaired Thorell’s and Simon’s observations.

Davies (1985) includes *Cryptothele* in its own family Cryptothelidae, by the supposed presence of a serrula in the maxillae, absent in zodariids. However, Jocqué (1991) noticed that in fact *Cryptothele* did not have a serrula, and suggested that for this reason it might be a basal member of Zodariidae, but refrained from a formal transfer and did not include the genus in his phylogenetic analysis. Later, Wunderlich (2004) sketched a phylogenetic hypothesis with *Cryptothele* and *Homalonychus* Marx, 1891 as sister groups, forming a basal split within Zodariidae. Such a basal placement was argued because of the supposedly ventral implantation of the teeth on the tarsal claws of *Cryptothele*, in agreement with Jocqué (1986), who also reasoned that *Cryptothele* should be excluded from Zodariidae for the same reason. As will be shown below, *Cryptothele* species have tarsal claws that are similar to those of most zodariids, with teeth on their inner sides. Jocqué and Dippenaar-Schoeman (2006) in turn argued that *Cryptothele* is probably a member of Cydreliinae, which should by priority become Cryptothelinae, based on the peculiar eye disposition and the basolateral extension of the endites.

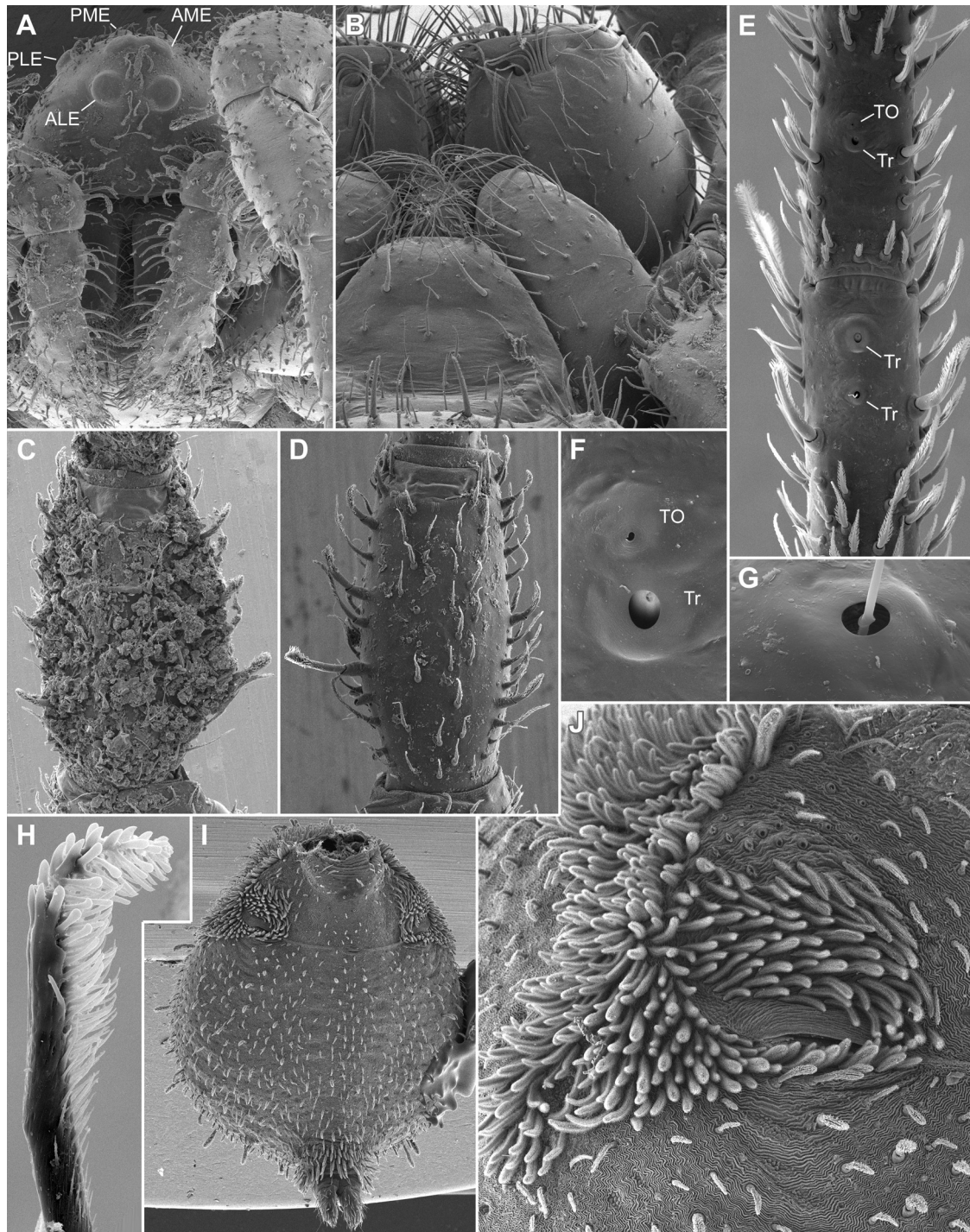


Fig. 2. (A–D, I and J) *Cryptothele alluaudi*, immature. (E–H) *Cryptothele* sp. female from Sri Lanka, MJR1393. (A) Eyes, anterior view. (B) Mouthparts, ventral view. (C) Right tibia I, ventral view, with stuck detritus. (D) Left tibia I, ventral view, sonicated. (E) Tarsal–metatarsal joint of leg I, dorsal view, sonicated. (F) Tarsal organ I and adjacent trichobothrial socket. (G) Trichobothria from metatarsus I. (H) Tibia I, ventral prolateral macroseta. (I) Abdomen, ventral view, sonicated. (J) Same, detail of right booklung showing protective setae (ALE = anterior lateral eye; AME = anterior media eye; PLE = posterior lateral eye; PME = posterior median eye; TO = tarsal organ; Tr = trichobothria).

A recent study using molecular sequences and spinneret anatomy (Miller et al., 2010) revealed that *Homalonychus* and *Zodariidae* are probably closely related, and that the enigmatic *Penestomus* Simon, 1902 formerly placed in *Eresidae*, is indeed a cribellate relative of *zodariids*. The three families *Homalonychidae*, *Penestomidae* and *Zodariidae* show an unusual disposition of the major ampullate gland spigots, which are surrounded by the piri-forms, instead of being placed on a marginal field. The aim of this contribution is to present a detailed study of the relevant morphological characters using scanning electron microscopy, and argue

on the relationships of *Cryptothele* by expanding the quantitative phylogenetic analysis of Jocqué (1991).

2. Material and methods

2.1. Phylogenetic analysis

We used the phylogenetic analysis of the genera of *Zodariidae* of Jocqué (1991) to test the higher affinities of *Cryptothele*, adding the outgroups *Penestomus* and *Homalonychus*, following the results

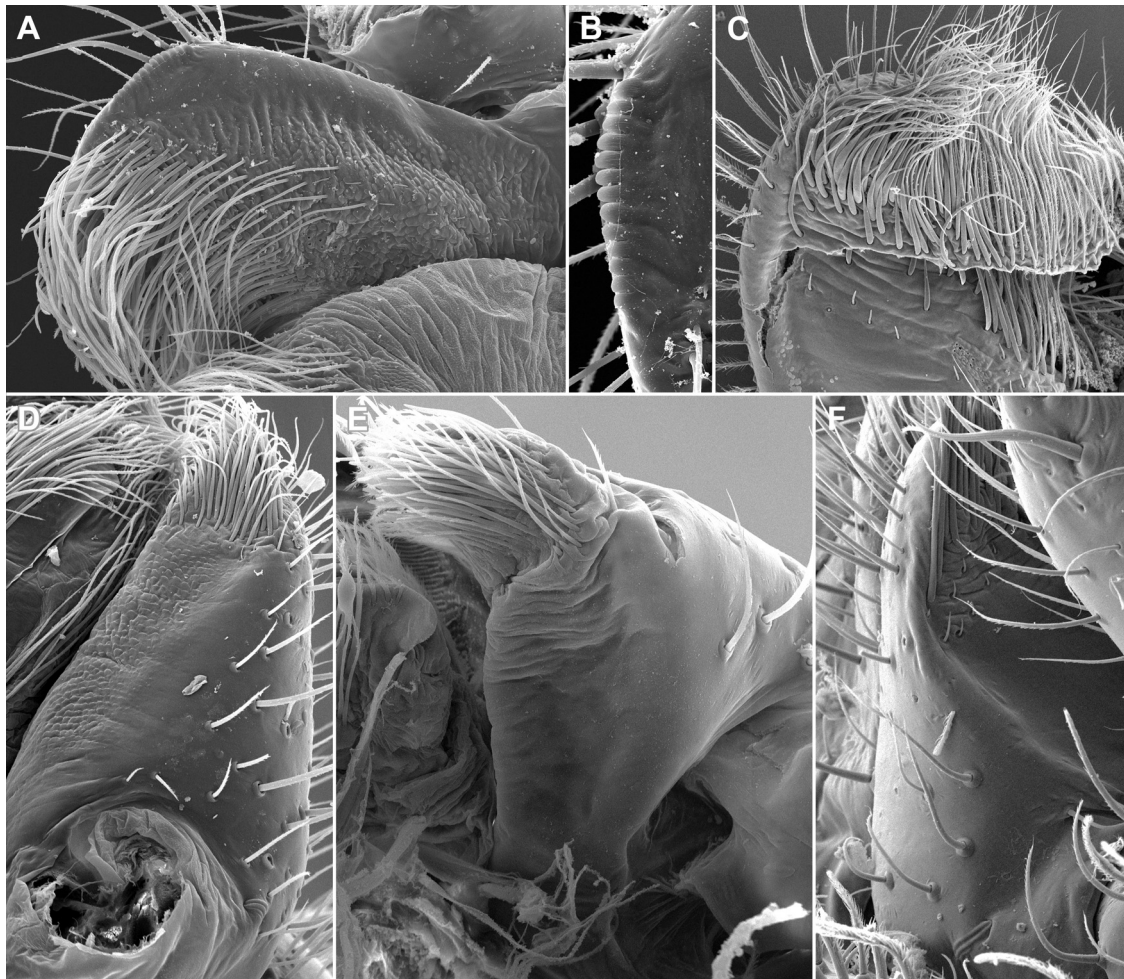


Fig. 3. Maxilla and serrula, dorsal view. (A, B) *Penestomus egazini* (Penestomidae). (C) *Homalonychus theologus* (Homalonychidae). (D) *Platnickia elegans* (Zodariidae). (E) *Zodarion italicum* (Zodariidae). (F) *Cryptothele alluaudi* (Zodariidae).

of Miller et al. (2010) from molecular markers. There have been several additions to the known diversity of Zodariidae after the generic review of Jocqué (1991), mainly by Jocqué himself and collaborators, in some cases with partial phylogenetic analyses of focal groups, but those have not challenged the main hypotheses of relationships in the family (see Dankittipakul et al., 2012). The main changes involve the relationships within Zodariinae and Lachesaninae (see Jocqué, 1992, 1995; Benjamin and Jocqué, 2000), two groups rather distant from the putative relatives of *Cryptothele*. We used the same characters as in Jocqué (1991) with the original numeration, and added two more: the presence or absence of the serrula (uninformative, as only one of the outgroups has the serrula), and the disposition of the major ampullate gland spigot field on the anterior lateral spinnerets. We also tested the addition of two terminals to the dataset, *Procydrela procursor* Jocqué, 1999 and *Rotundrela rotunda* Jocqué, 1999, which were suggested as close relatives of Cydrelininae (Jocqué, 1999), and corrected two scorings in character 28 (eyes in two rows in *Caesetius* Simon, 1893 and *Psammoduon* Jocqué, 1991, after Jocqué, 1991: 113, 123). The dataset is deposited in TreeBase with accession number 15507.

We analyzed the phylogenetic dataset with TNT version 1.1 (Goloboff et al., 2008). As a search strategy we used 50 addition sequences followed by tree-bisection-reconnection branch-swapping, each followed by 100 iterations of the parsimony ratchet (TNT commands: *ratchet: iter 100; mult = ratchet repl 50 tbr hold 10; bb = fillonly*). This heuristic search produced hits to the

minimum value in about 50% of the replicates. With such a number of hits to the same best trees, it is likely that the optimal trees were found.

In the original analysis Jocqué used higher a priori weights for some complex or unusual characters. Here we explored the effect of (a) these a priori character weights, (b) equal weighting, and (c) implied weighting against homoplasy, with constant of concavity $k = 1$ to 8 (Goloboff, 1993). The results of the 10 weighting regimes are summarized as a sensitivity value on the tree under equal weights; a value of 1 means that only one weighting regime produced the group as monophyletic (e.g., in Fig. 9, Cryptothelinae + Storenomorphinae), and a value of 10 means that the group is insensitive to weighting regimes (e.g., Fig. 9, Cryptothelinae). A few characters originally inactivated because of high homoplasy were left inactive here.

2.2. Observation of specimens

For the examination using a scanning electron microscope (SEM) the samples were critical point dried and coated with gold-palladium. We used a FEI-XL30 or Leo 1450VP standard SEM, or Hitachi-S4700 field emission SEM, all under high vacuum. Detritus in *Cryptothele* specimens was removed by sonication in 80% ethanol for approximately 5 s. Complementary observations of the location of major ampullate gland spigots were obtained for some zodariids using a Leitz stereomicroscope.

2.3. Material

We examined the following specimens for this study. **Amaurobiidae:** *Pimus napa* Leech, 1972, from USA (specimens referred to in Griswold et al., 2005). **Austrochilidae:** *Thaida peculiaris*, Karsch, 1880, from Argentina and Chile (specimens referred to in Griswold et al., 2005). **Homalonychidae:** *Homalonychus theologus* Chamberlin, 1924 from USA (specimens referred to in Ramírez, 2014). **Penestomidae:** *Penestomus egazini* Miller et al., 2010 from South Africa (female CASENT9024964, male CASENT9024985). *Penestomus planus* Simon, 1902 from South Africa (3 females, 1 male subadult, 1 immature MACN-Ar 30767). **Sicariidae:** *Sicarius rupestris* (Holmberg, 1881) (male and female from Argentina, ARAMR881, 882). **Tengellidae:** *Tengella radiata* Kulczyński, 1909, from Costa Rica (specimens referred to in Griswold et al., 2005). **Zodariidae:** *Cryptothele alluaudi* Simon, 1893 from Seychelles (7 immatures MRAC 143.081). *Cryptothele* spp. from Myanmar (1 male

CAS ARAMR147; 1 female CAS ARAMR146), Sri Lanka (1 female in AMNH MJR-732, 733), Borneo (1 female CASENT9036335). *Cybaeodamus taim* Lise, Ott and Rodrigues, 2009 from Argentina (7 males 9 females 5 immatures MACN-Ar MJR-670 to 674). *Cyrioctea aschaensis* Schiapelli and Gerschman, 1942 from Argentina (6 females 2 immatures MACN-Ar MJR-667 to 669). *Platnickia elegans* (Nicolet, 1849) from Chile (female MACN-Ar 31089). *Storenomorpha paguma* Grismado and Ramírez, 2004, from Vietnam (specimens referred to in Grismado and Ramírez, 2004). *Zodarium italicum* (Canestrini, 1868) from Germany (male and female, ZFMK MAI-90 to 98). Disposition of major ampullate gland spigots observed with stereomicroscope in: *Antillorena pollii* Simon, 1887, from Jamaica (male MACN-Ar 31082); *Hermippus septemguttatus* Lawrence, 1942 from South Africa (female MACN-Ar 11406); *Tenedos brescoviti* Jocqué and Baert, 2002, from Argentina (female and immatures MACN-Ar 10510); *Mallinella* sp. from Benin (female, AMNH, ARAMR759); *Habronestes raveni* Baehr, 2003, from Australia (male and female

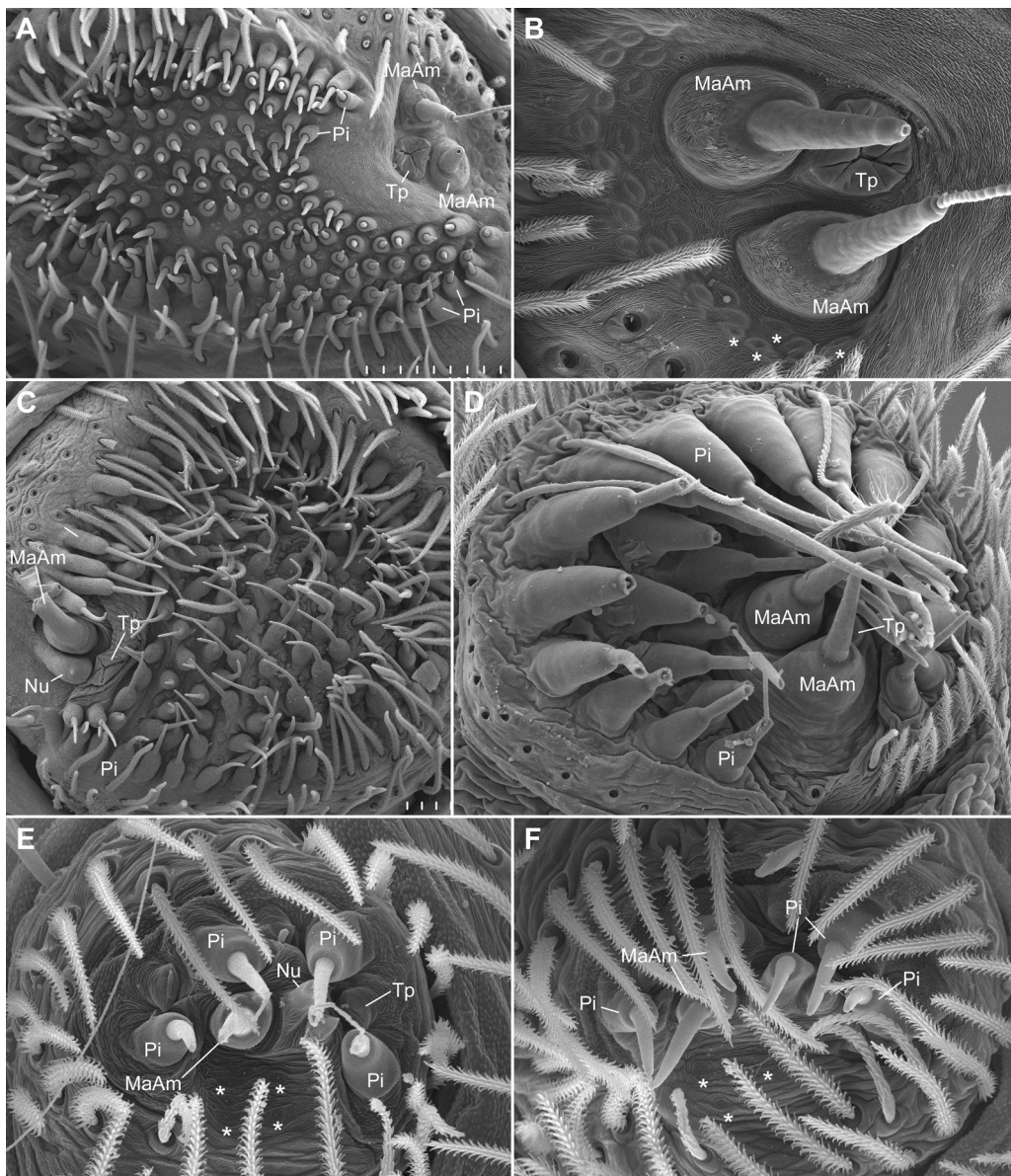


Fig. 4. Spinning field of anterior lateral spinnerets. (A) *Thaida peculiaris* (Austrochilidae) female, right. (B) Same, detail of field of major ampullate spigots (only some of the many sensilla are marked with asterisks). (C) *Tengella radiata* (Tengellidae) male, left. (D) *Homalonychus theologus* (Homalonychidae) female, left. (E) *Penestomus egazini* (Penestomidae) male, left. (F) Same, female left. (Asterisks below strain sensilla of major ampullate field). MaAm = Major ampullate gland spigot, Nu = nubbin, Pi = piriform gland spigot, Tp = tartipore.

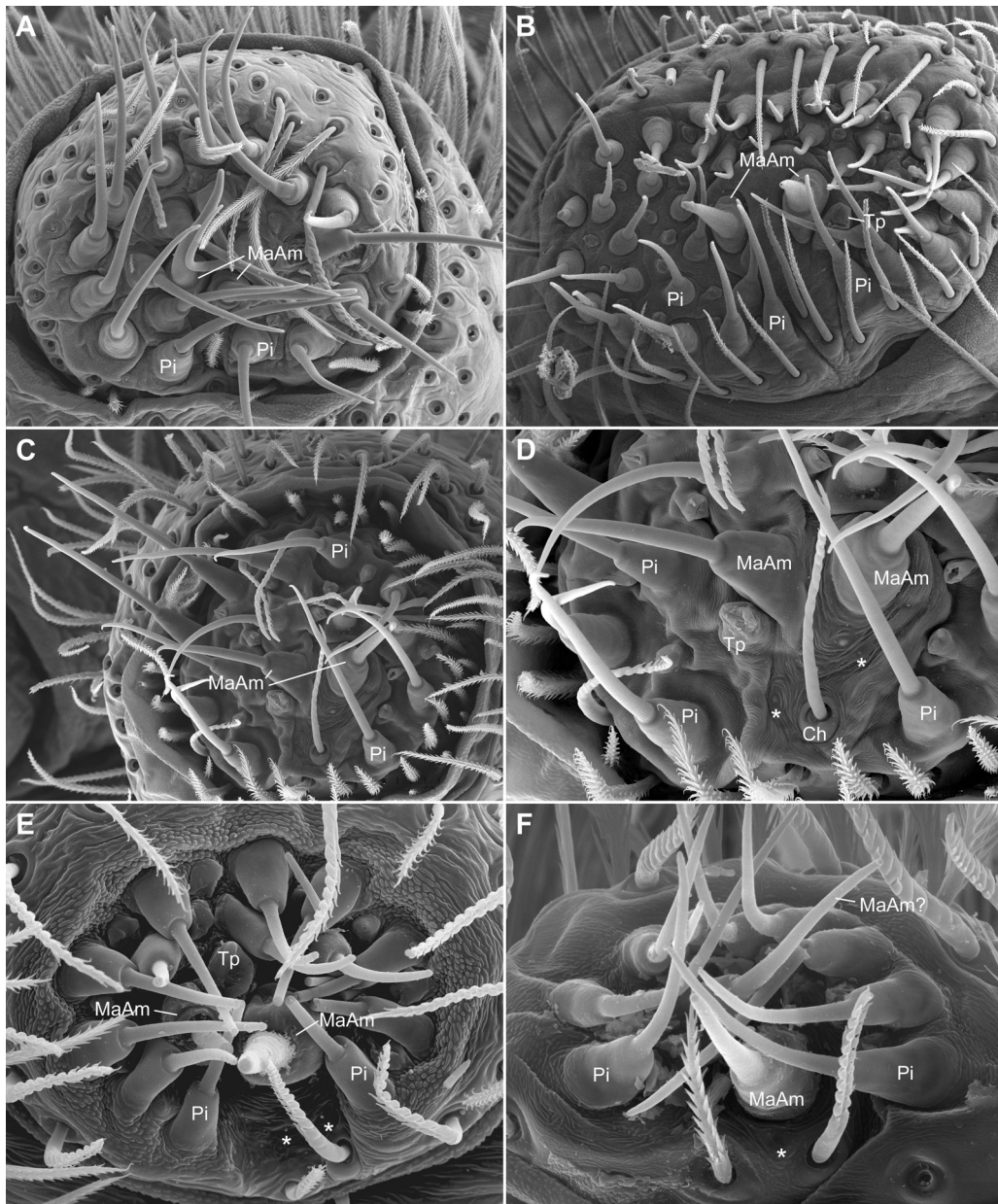


Fig. 5. Spinning field of anterior lateral spinnerets of Zodariidae. (A) *Cybaeodamus taim* female, left. (B) *Storenomorpha paguma* female left ALS. (C) *Cyriotea aschaensis* female right ALS. (D) Same, detail of MaAm field invaginated among piriform spigots, asterisks on MaAm field sensilla. (E) *Platnickia elegans* male, right. (F) *Zodarion italicum* male, right. (Asterisks below strain sensilla of major ampullate field). Ch = chemosensory seta, MaAm = Major ampullate gland spigot, Pi = piriform gland spigot, Tp = tartipore.

QM SP101); *Cicynethus florumfontis* Jocqué, 1991, from South Africa (male MACN-Ar 11344); *Diores* cf. *triarmatus* from South Africa (female MACN-Ar 12899). Repository acronyms are as follows: AMNH, American Museum of Natural History, New York; CAS, California Academy of Sciences, San Francisco; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MRAC, Musée royal de l'Afrique Centrale, Tervuren; QM, Queensland Museum, Brisbane; ZFMK, Zoologisches Forschungsmuseum Alexander Koenig, Bonn.

3. Results

The general morphology of *Cryptothele* is consistent with its placement in Zodariidae. The chelicerae have very short fangs, without teeth (Figs. 1B and 2B), the clypeus is high, with the anterior eye row strongly procurved making the characteristic disposition

2–4–2 reported for some cydreline (Fig. 2A), and the posterior spinnerets are very short and devoid of spigots, except of the presence of the cylindrical gland spigots in adult females (Fig. 6A–B, E–F). In the following paragraphs we discuss in more detail some character systems that are important for the systematics of Zodariidae.

3.1. Serrula

Zodariids are well known for lacking the serrula on the maxillae (Fig. 3D and E), and *Cryptothele* is no exception (Fig. 3F). The serrula was lost many times in other entelegyne spider groups, such as desids, corinnids, zorids, prodidomids, trochanteriids, gallieniellids, and also in a variety haplogynes and mygalomorphs (e.g., see Jocqué and Dippenaar-Schoeman, 2006; Griswold et al., 2005). The structure is also absent in *Homalonychus* (Fig. 3C) but present in *Penestomus* (Fig. 3A and B). The serrula was scored as Character

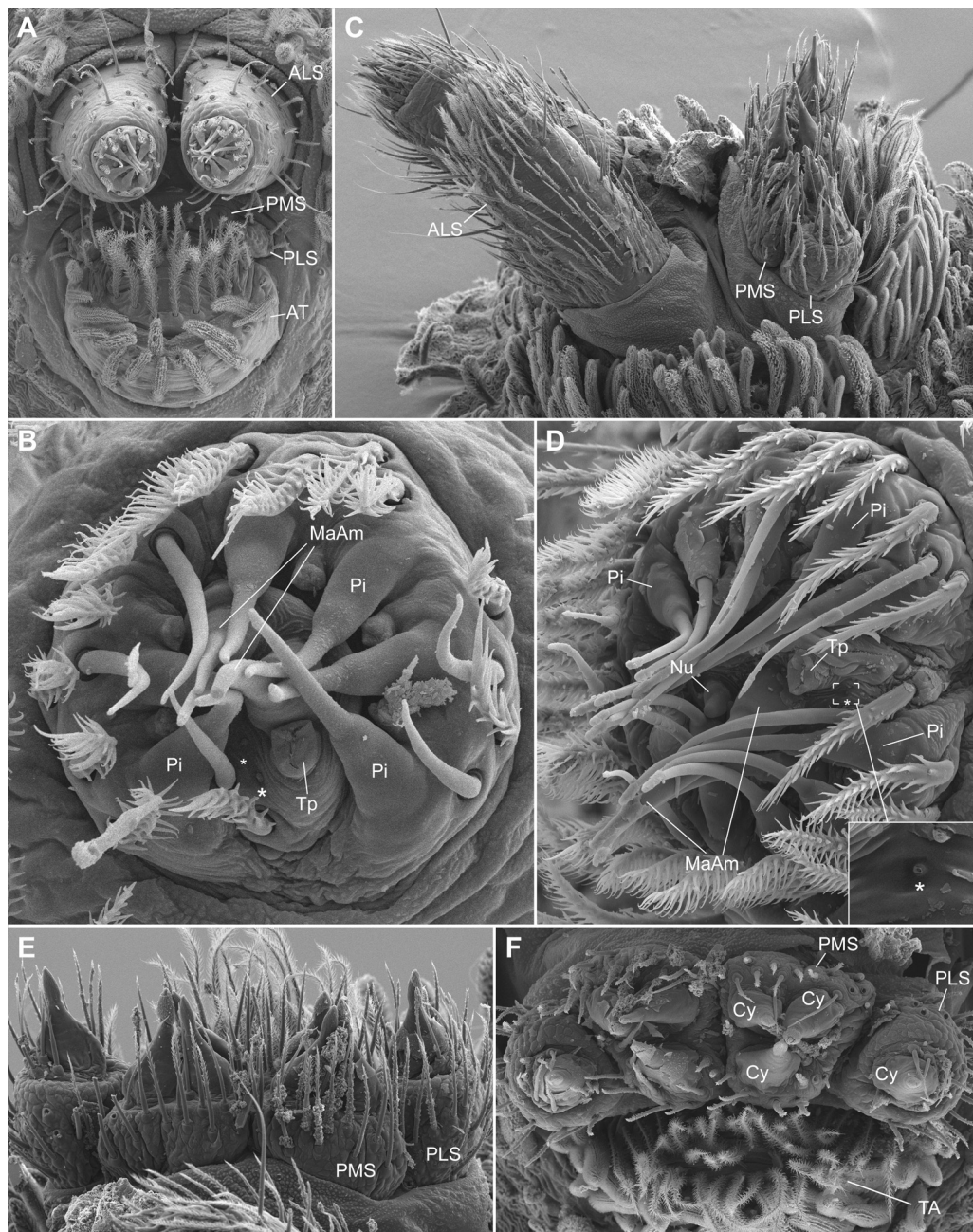


Fig. 6. Spinnerets of *Cryptothele*, ultrasound cleaned. (A) *Cryptothele alluaudi*, immature. (B) Same, left anterior lateral spinneret, inset to strain sensilla of major ampullate field. (C) *Cryptothele* sp. from Sri Lanka (MJR-733) spinnerets, left lateral view. (D) Same, left anterior lateral spinneret, inset to strain sensilla of major ampullate field. (E) Same, posterior spinnerets, posterior view. (F) Same, ventral view. ALS = anterior lateral spinneret, AT = anal tubercle, Cy = cylindrical gland spigot, MaAm = Major ampullate gland spigot, Nu = nubbin, PLS = posterior lateral spinneret, Pi = piriform gland spigot, PMS = posterior median spinneret, Tp = tartipore.

80: (0) present, (1) absent; the character is however uninformative for our taxon sample, as only *Penestomus* has the serrula in this dataset.

3.2. Spinnerets and spigots

Preserved specimens of *Cryptothele* often have the spinnerets retracted behind a crown of protective setae (Fig. 1D and E). The anterior lateral spinnerets are well developed, two-segmented and supplied with spigots (Fig. 6A–D). In contrast, both pairs of posterior spinnerets are very short, a frequent characteristic among zodariids (Fig. 6C, E–F). In males and immatures (Fig. 6A) the posterior spinnerets are only represented by a short nubbin with few setae, devoid of any spigot. Only adult females develop large cylindrical

spigots on the posterior spinnerets, three on the medians and one on the laterals, and a short but definite distal article in the posterior lateral spinnerets, distinguished as a strip of cuticle with setae (Fig. 6E–F).

3.3. The invagination of the major ampullate gland spigot field

Entelegyne spiders have a conserved pattern of two major ampullate gland spigots (MaAmp) on the mesal margin of the anterior lateral spinneret spinning field, and a larger field of piriform gland spigots (Pi) occupying most of the remaining surface of the spinning field (Fig. 4A–C; Griswold et al., 2005: 58; Ramírez, 2014). The MaAmp spigots are placed on a plate, more sclerotized than the surrounding cuticle, provided with characteristic sensilla (Fig. 4A).

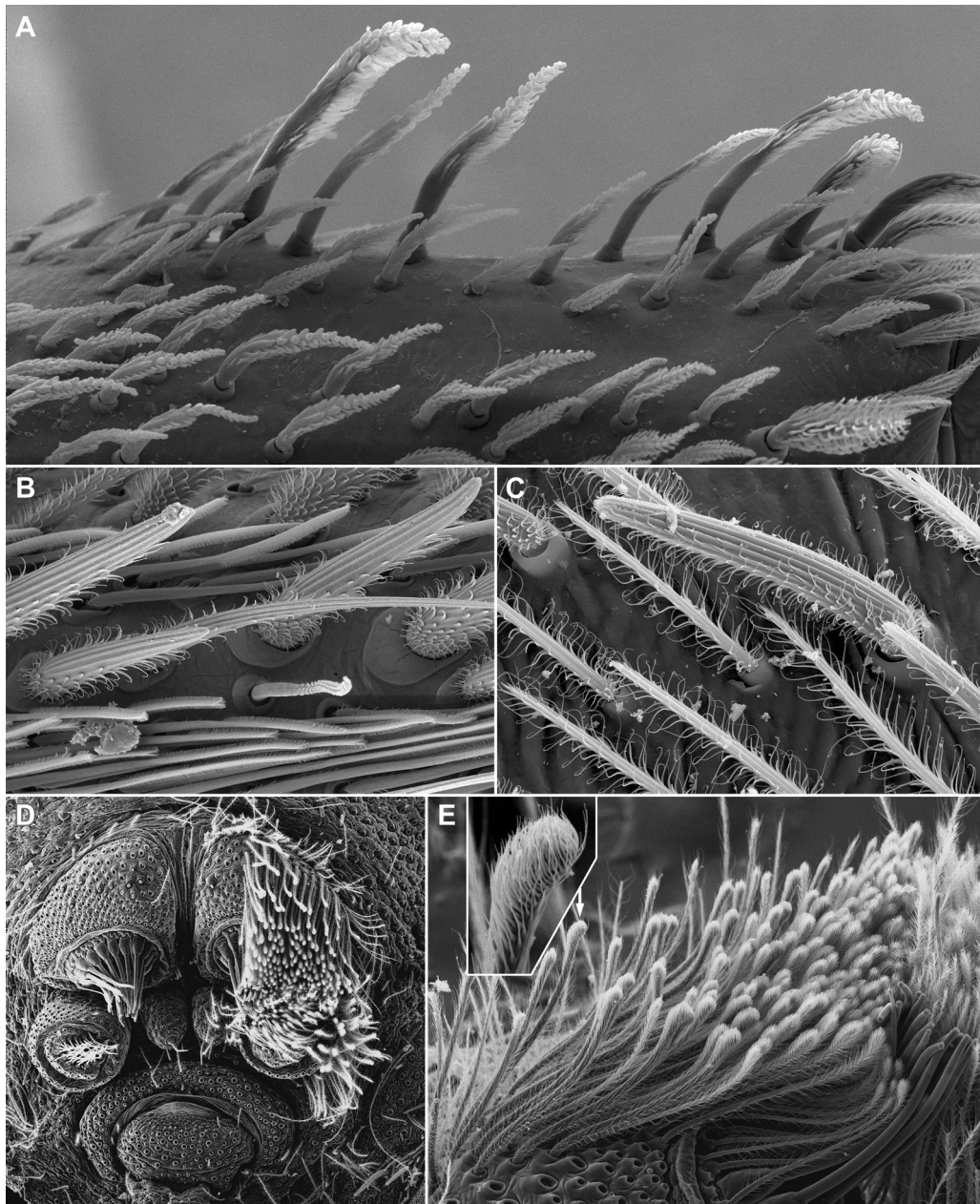


Fig. 7. Morphology of setae, ultrasound cleaned. (A) *Cryptothele* sp. (Zodariidae) female MJR1393, tibia I prolateral side, dorsal view. (B) *Homalonychus theologus* (Homalonychidae), tarsus I, ventral. (C) *Sicarius rupestris* (Sicariidae), opisthosoma. (D) Spinnerets of female *Sicarius rupestris* (Sicariidae), ventral view; most setae were shaved on one side, to expose spigots. (E) Same, lateral view of anterior lateral spinneret, showing dense cluster of protective setae (inset to tip of one seta).

These sensilla are strain detectors similar to the slit sensilla, with a dendrite ending in a pore, and are used to survey the tension of the dragline (Gorb and Barth, 1996). We use here the MaAmp field sensilla to assist the identification of MaAmp spigots.

In *Homalonychus* the MaAmp field is partially invaginated, with one MaAmp in a central position, the other close to the mesal margin (Fig. 4D). A similar configuration occurs in *Penestomus* (Fig. 4E–F).

In zodariids the MaAmp field is well invaginated, with the MaAmp spigots centrally on the Pi field. Both fields are demarcated by furrows or wrinkles, with a narrow stretch of the MaAmp field still connected to the mesal margin (Fig. 5, 6B). The identity of the MaAmp spigots is confirmed by the strain sensilla (asterisks in Figs. 5 and 6). As often occurs in adult entelegynes, the female of *Cryptothele* has one MaAmp and the second is represented by a nubbin (see Townley and Tillinghast, 2003). Both are centrally

placed, and the strain sensilla confirm the identification (Fig. 6D). The examination of an immature specimen revealed the complete spigot complement, with two MaAmp spigots in a longitudinal to oblique line (Fig. 6B).

An extensive survey of the spinneret morphology of entelegyne spiders (Griswold et al., 2005; Ramírez, 2014) revealed only three cases of similarly arranged MaAmp spigots. One is the zoropsid *Uliodon* L. Koch, 1873 with a similar disposition as in zodariids, another is the corinnid *Oedignatha* Thorell, 1881, with a disposition as that of *Homalonychus* and *Penestomus* (Ramírez, 2014), and a third is the titanoeid *Pandava laminata* (Thorell, 1878) (Almeida-Silva et al., 2010: Fig. 29), also like zodariids. Zoropsids, titanoeids and corinnids are clearly not potential close relatives of zodariids (see Raven and Stumkat, 2005; Griswold et al., 2005; Miller et al., 2010; Bosselaers and Jocqué, 2002), hence these are considered homoplastic occurrences of the same configuration.

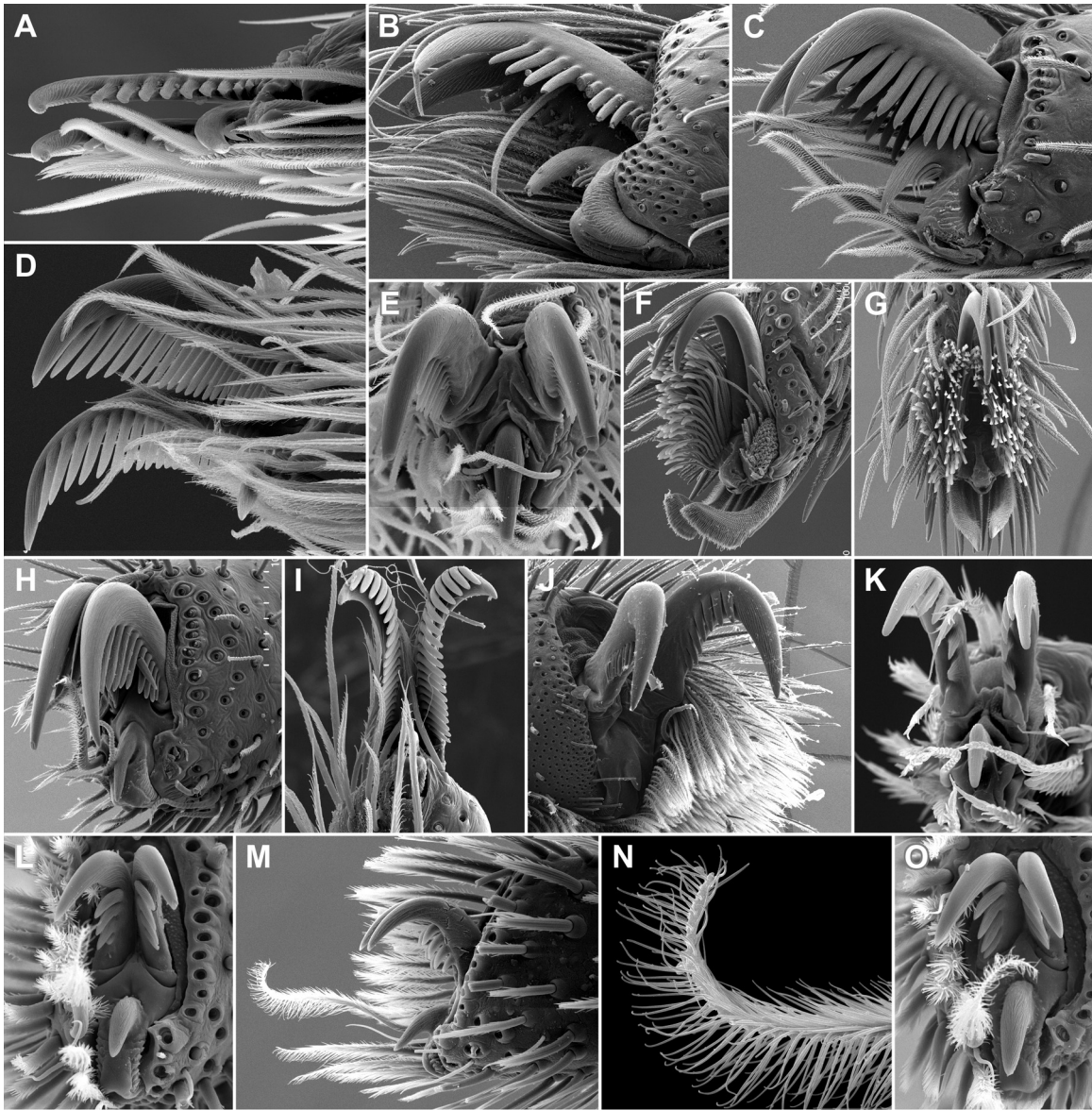


Figure 8. Left tarsal claws. (A) *Thaida peculiaris* (Austrochilidae), leg I (image by Junxia Zhang). (B) *Tengella radiata* (Tengellidae), leg I. (C) *Pimus napa* (Amaurobiidae), leg I. (D) *Penestomus egazini* (Penestomidae), leg I. (E) Same, leg IV. (F) *Homalonychus theologus* (Homalonychidae), leg I. (G) Same, leg IV. (H) *Cyrioctea aschaensis* (Zodariidae), leg I. (I) *Platnickia elegans* (Zodariidae), leg I. (J) *Storenomorpha paguma* (Zodariidae), leg I. (K) *Zodarion italicum* (Zodariidae), leg I. (L, M) *Cryptothele* sp. (Zodariidae, MJR1393), leg I. (N) Same, detail of distal seta. (O) Same, leg IV.

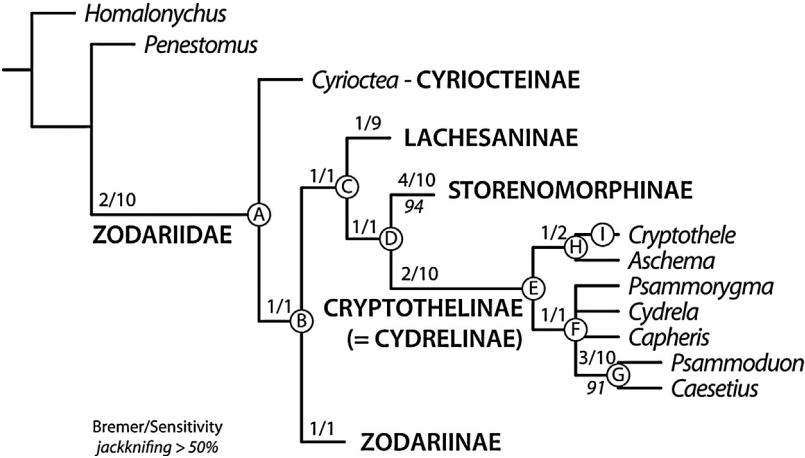


Fig. 9. Summarized strict consensus tree under equal weights (311 steps, more than 2000 trees; dataset modified from [Jocqué, 1991](#), adding outgroups and *Cryptothele*). Support measures and sensitivity upon weighting regimes are indicated on branches (key on bottom left; see [Table 1](#) for synapomorphies).

The placement of the major ampullate gland spigots relative to the piriform gland spigots is scored as Character 81, MaAmp field invagination; (0) MaAmp field on the mesal margin of the anterior lateral spinneret spinning field; (1) MaAmp field partially invaginated within Pi field, MaAmp spigots in a transversal line, with one of the MaAmp spigots still close to the mesal margin; (2) MaAmp field well invaginated within Pi field, MaAmp spigots in a longitudinal line. States were considered ordered, because State 1 is intermediate between 0 and 2. In addition to the outgroups and *Cryptothele*, we were able to examine with SEM the spinnerets of several zodariids: *Cyrioctea* (Cyrioctinae), *Storenomorpha* (Storenomorphinae), *Cybaeodamus*, *Platnickia*, and *Zodariion* (Zodariinae). We were also able to confirm the invagination of the MaAmp field using regular stereomicroscope in other zodariid genera: *Antillorena* (Lachesaninae), *Hermippus*, *Tenedos*, *Mallinella*, *Habronestes* and *Diores* (Zodariinae), and *Cicynethus* (Storenomorphinae). *Cydrela pristina* Dankittipakul and Jocqué (Cydreliinae) has at least one MaAmp among the Pi field (Dankittipakul and Jocqué, 2006; Fig. 4). *Zodariion*, *Mallinella* and *Cryptothele* were scored as State 1, *Cydrela* and *Tenedos* are ambiguous between State 1 or 2, the rest of the zodariids as State 2. At least another zodariine not included in this dataset has the configuration represented by State 2 (*Epicratinus amazonicus* Jocqué and Baert, 2005; Fig. 6).

3.4. Disposition of tarsal claw teeth

In most spiders the superior tarsal claws have a line of teeth on their medial ventral line (Fig. 8A–C). In all zodariids (Fig. 8I–O) except *Cyrioctea* (Fig. 8H) the line of teeth is placed on the internal side of the claws, and that was one of the main lines of evidence for the basal placement of *Cyrioctea* in Zodariidae (Platnick, 1986; Jocqué, 1991). A similar disposition of teeth occurs as well within other entelegyne groups, such as nicodamids, cycloctenids, thomisids, corinnids, liocranids, and several gnaphosoids (Ramírez, 2014). The outgroups considered in this analysis are heterogeneous: while *Homalonychus* lacks teeth (Fig. 8F–G), *Penestomus* has a zodariid-like conformation on the anterior legs, and ventral teeth on the posterior ones (Fig. 8D–E). This of course undermines the support for the placement of *Cyrioctea* as sister to all remaining zodariids. Our examination of *Cryptothele* species, on the other hand, revealed a typical disposition as in derived zodariids (Fig. 8L–M), although the claws are shorter, stouter, and not diverging as in most zodariids, which together with the detritus that usually covers the area make the observation of this character more difficult.

3.5. Soil-sticking

The ability of sticking detritus is known for species of many spider genera, such as *Homalonychus* (Homalonychidae), *Sicarius* Walckenaer, 1847 (Sicariidae), *Bradystichus* Simon, 1884 (Pisauridae), *Paratropis* Simon, 1889 (Paratropididae), *Microstigmata* Strand, 1932 (Microstigmatidae), and several Stephanopinae (Thomisidae) (Roth, 1984; Duncan et al., 2007; MJR personal observations on Stephanopinae). Duncan et al. (2007) demonstrated that *Homalonychus* and *Sicarius* convergently evolved similar physical mechanisms for the retention of soil detritus. Both are desert dwellers that have modified setae with long, flexible barbs that adapt to the surface of small sand particles (Fig. 7B and C), thus producing van der Waals forces that stick the particles to the setae. *Cryptothele* specimens have the body covered by soil particles, and usually heavily covered with mud, sometimes with cracks from posterior desiccation (Fig. 1). A few definite parts of the body are clean from debris, such as the chelicerae, mouthparts, copulatory bulb, part of the epigyne and epiandrium, booklung covers and

Table 1

Unambiguous synapomorphies of *Cryptothele* and relatives. Nodes labeled as in Fig. 1.

Node	Synapomorphies
A	Posterior eye row (7): strongly recurved → straight or slightly procurved Tegular apophysis large, free of tegulum (68): present → absent
B	Cheliceral teeth (9): with teeth on both margins → without teeth
C	Endites basolateral extension (13): absent → present
D	Fangs length (15): normal → short (thin part < thick part) Hinged hairs (18): numerous → few, only dorsal
E	Eyes disposition (14): eyes in 2 rows or 2,4,2 → 2,2,4 Posterior spinnerets length (20): long, at least half the AS → short
H	Embolus originating at posterior end of tegulum (64): absent → present
F	Sternum shape (10): sternum oval → triangular
G	Eyes disposition (14): 2,2,4 → eyes in 2 rows or 2,4,2 Tarsal claws (26): 3 claws → 2 claws Chelicerae with mesal field of spinules (45): absent → present
I	Fovea (35): absent → present Spination (37): more developed on III and IV → absent Leg formula (39): 4123 or 4132 → 1243 Female palp triangular, dorsoventrally flat (43): absent → present Two large tegular apophyses (69): absent → present Embolus base separated from tegulum (70): absent → present Fertilization ducts tightly coiled (71): absent → present

spiracles, the spinnerets, the trichobothrial bases and tarsal organ (Fig. 1B–D). The coverage of detritus is generally coincident with the distribution of curved setae (compare Figs. 1C and 2E), whose distal half is covered by long, thick barbs (Figs. 2H and 7A). These might play some role in the retention of particles, although in the specimens heavily covered by mud the barbed ends stick out of the mud surface (Fig. 2C). Placing the spider in an ultrasound cleaner removes much of the detritus (compare Figs. 2C and D), but some still remained stuck directly on the cuticle (Fig. 2D and G), which suggest that the soil particles might be mechanically retained in place by the barbed setae and further consolidated on the cuticle by the addition of water, differing from the small-particles adhesion mechanism of *Homalonychus* and *Sicarius* (Fig. 7B and C), which live in dry environments. While some clean surfaces such as the sensilla on legs are well exposed, the spinnerets and booklungs are surrounded by thick setae with blunt tips, densely covered by short barbs (Fig. 2J), seemingly providing further protection against soil particles, including the crown of setae that covers the spinnerets while retracted (Figs. 1D and 6C). It is noteworthy that species of *Sicarius* have similar setae on the anterior article of their anterior lateral spinnerets (Fig. 7A and B), which suggest that those setae, by a hierarchically sculptured surface design may produce a “Lotus-effect” to protect the spinnerets from dust adhesion (Solga et al., 2007; Koch et al., 2009).

3.6. Relationships

Adding *Cryptothele* and outgroups to the dataset modified from that of Jocqué (1991) results in *Cryptothele* nesting inside Cydreliinae, in any of the 10 weighting regimes here tested, in coincidence with the proposal by Jocqué and Dippenaar-Schoeman (2006), which by priority should be named Cryptothelinae (Fig. 9). The synapomorphies of the subfamily are the same as obtained by Jocqué (1991) (Table 1): the eyes in three rows (Fig. 2A), with a reversion in *Psammoduon* + *Caesetius*, and the extremely short posterior spinnerets (Fig. 6A and C). The detailed placement within the subfamily varies however across weighting regimes. Under equal weights, *Cryptothele* is joined with *Aschema* by the posterior origin of the embolus in the copulatory bulb. In this dataset, if *Cryptothele* is forced as the sister group of *Cydrela* (following the similarity described by Simon, 1893) the grouping would not be supported by any synapomorphy.

We still recovered *Cyrioctea* as sister to all remaining zodariids, even when the outgroups are not decisive on the plesiomorphic disposition of the tarsal claw teeth. Such placement is still supported by the presence of cheliceral teeth in *Cyrioctea* and the outgroups (Character 9), which are usually absent in zodariids. The complete invagination of the major ampullate field (Character 81, State 2) is a potential synapomorphy of zodariids, but ambiguously optimized because of the intermediate condition in *Penestomus* (scored with State 1 or 2). The character has two reversals to State 1, in *Cryptothele* and *Zodarion*.

Adding *Procydrela procursor* and *Rotundrela rotunda* has a more profound impact on the results, which is not surprising, as [Jocqué \(1999\)](#) already discussed the puzzling combination of characters presented by both genera. With these additions, all weighting regimes except equal weights still place *Cryptothele* among cydrelineae. *Procydrela* and *Rotundrela* branch off as successive sister groups of Storenomorphinae, although that is not so stable upon weighting regimes. The backbone of the tree is however considerably altered after these additions (not shown).

4. Taxonomy and discussion

Cryptothelinae L. Koch, 1872

Cryptothelidae L. Koch, 1872: 238 (Cryptotheliden). [Thorell, 1886](#): 326 (Cryptotheloidae). [Davies, 1985](#): 58.

Cryptothelinae: [Simon, 1890](#): 81; 1893: 411, 420. [Petrunkevitch, 1923](#): 179; 1928: 38, 97. [Wunderlich, 2004](#): 1585.

Cydrelineae [Simon, 1893](#): 411, 416. [Petrunkevitch, 1923](#): 179; 1928: 38, 39. [Jocqué, 1991](#): 111. [Wunderlich, 2004](#): 1585. **New synonymy.**

Our study confirms the previous suggestions by [Simon \(1893\)](#) and [Jocqué and Dippenaar-Schoeman \(2006\)](#) of a close relationship of *Cryptothele* with the cydrelineae, thus we formally synonymize Cydrelineae under the older name Cryptothelinae. As noted by [Platnick \(2014\)](#), the name Cryptothelidae is actually older than Zodariidae, which was erected by [Thorell \(1881\)](#), but the precedence of Zodariidae is protected by usage ([ICZN, 1999](#): article 35.5). The precise placement among the cryptotheline genera is however not robustly solved with the current dataset. After examining a larger sample of zodariids, we also show that the invagination of the median ampullate field occurs throughout the main groups of zodariids, although with some reversions from complete to partial invagination (States 2 and 1 of character 81, respectively).

The descriptions by [Abraham \(1924\)](#) and [Koh \(1989\)](#) of *Cryptothele* preying on termites seems stereotyped enough to suggest that species of the genus may be termite specialists, a prey preference that is uncommon in spiders (see [Pekar et al., 2012](#)). Many zodariids seem to be ant specialists, but some species of *Diores* are known to feed on termites, using a mysterious method of prey immobilization by mere contact ([Jocqué and Dippenaar-Schoeman, 1992](#)). An examination of the phylogenetic distribution of prey preferences in zodariids (see [Pekar et al., 2012](#): Fig. 6) leaves little doubt that the specialization on termites appeared independently in *Diores* and *Cryptothele*.

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