The systematics of the south-east Asian genus *Fangensis* Rambla
(Opiliones: Cyphophthalmi: Stylocellidae)

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**Abstract.** The hitherto monotypic opilionid genus *Fangensis* Rambla, 1994 is re-evaluated from new material collected in northern, western and southern Thailand. The original description of *F. leclerci* Rambla (type material not traceable) was based on specimens belonging to at least three distinct species. *Fangensis leclerci* is thus redefined and the binomen restricted to specimens from a cave in northern Thailand only. Three new species are described, *F. spaleus*, sp. nov. and *F. cavernarus*, sp. nov. from two caves in western Thailand and *F. insulanus*, sp. nov. from forests on two islands in southern Thailand. Taxonomic characters are discussed and relationships among *Fangensis* species and between *Fangensis* and other cyphophthalmids are evaluated using morphological data and ~4 Kb of molecular data from three loci, two nuclear ribosomal genes and a mitochondrial coding gene. Overall, data indicate monophyly of Stylocellidae and morphological and ribosomal data suggest monophyly of *Fangensis*, which is in turn divided into two clades, one composed of the three species from northern and western Thailand and the other represented by the species from southern Thailand. Observations on mating in *F. leclerci* are provided.


**Introduction**

*Fangensis leclerci* Rambla, 1994, type species of the hitherto monotypic genus *Fangensis* Rambla, 1994, was described from specimens collected in two caves in northern Thailand (i.e. ‘Tham (= Cave) Klaeb’ = Tham Klaeb Yai (one male, two females, four juveniles) and ‘Tham Mang On’ = Tham Muang On (two juveniles)) and in three caves in western (or western central) Thailand (i.e. ‘Tjam Rawa’ or ‘Tham Kung Rawa’ = Tham Kaeng Lawa (one male), ‘Tham Sai Yok Noi’ = ‘Tham Nam Tok’ = Tham Wang Badan (one juvenile) and ‘Tham Nam’ = Tham Nam Phrathat (one male, one female)) (see Rambla, 1994: 109) (different spellings of Thai names are caused by inconsistent transliteration of the Thai script and by misunderstanding of spoken Thai, which usually does not distinguish between ‘L’ and ‘R’). Owing to lack of eyes (in both sexes) and presence of anal gland pores (in males), this species (and genus) was originally placed in the family Sironidae.

This raised several questions. Is *F. leclerci* really a sironid and thus the only known representative of this family in south-east Asia? Do the populations in northern and western Thailand, which are seemingly restricted to limestone caves and their immediate surroundings and which are separated by more than 500 km, really belong to the same species? Moreover, it is not clear which of the specimens examined by Rambla (1994) is the holotype and, consequently, which of these five caves is the type locality. Rambla (1994: 110) actually did give the description of a male type, but she did not specify which of the three males (from three caves and actually belonging to three distinct species) she examined is the type. Therefore, all specimens mentioned in the original description are to be treated as syntypes. It may also be noted that none of the two caves in northern Thailand that are known to house *Fangensis* is actually located in the district of Fang from which Rambla derived the generic name. Tham Klaeb Yai lies in the Chiang Dao District and Tham Muang On in the Sankamphaeng District (both in Chiang Mai Province).

The doubtful placement in the family Sironidae has been addressed by Giribet (2002; see also Giribet and Boyer 2002), who transferred *Fangensis* to the Stylocellidae. The placement of *Fangensis* within the Stylocellidae is currently followed by the online catalogue of Cyphophthalmi (http://collections.oeb.harvard.edu/Invertebrate/Cyphophthalmi/species.cfm, verified July 2005).

A re-examination of the type material of *F. leclerci* is currently not possible because it has either been misplaced or lost (personal inquiry at the Departament de Biologia...
Animal, Universitat de Barcelona (DBAUB) by G. G. and examination of the entire Rambla collection by A. Pérez-González in August 2004). Safe keeping in DBAUB was assumed by Giribet (2000: 56) but apparently the types have never been deposited in that collection or in a museum. However, our study of new material collected from three of the caves (Tham Klaeb Yai, Tham Nam Phrathat and Tham Kaeng Lawa) from where the males of the type series originate clearly shows that (at least) three species are involved. Therefore, a lectotype designation from the mixed-species syntype series is necessary. As the description of *F. leclerci* appears to be mostly based on the single male from Tham Klaeb Yai in northern Thailand (Rambla, 1994: figs 1, 2, 4, 5, plate III.4 clearly correspond with males examined from this cave, but body measurements do not), Rambla probably considered this specimen as the holotype, though she failed to identify it as such. A further indication for that is found in her type species designation ‘Espèce-type: *Fangensis leclerci* n. sp. (perte de Tham Klaeb, district de Fang au nord de Chiang Mai, Thaïlande)’ (Rambla, 1994: 110). Therefore, we here select the male syntype from Tham Klaeb Yai as the lectotype of *F. leclerci*.

In the following, newly collected specimens from Tham Klaeb Yai, Tham Nam Phrathat and Tham Kaeng Lawa are used to rediagnose the genus *Fangensis*, to redefine its type species, *F. leclerci*, and to describe two additional troglobiomorphic species (habit, see Fig. 1). A third new *Fangensis* species, with more sturdy legs and with eyespots, is described from humid forests in southern Thailand.

**Material and methods**

*Morphological methods*

Males and females of each species were dissected and their genitalia studied as temporary mounts (embedded in glycerine) under a compound microscope. Holotypes were left intact. If only one male paratype was available for dissection, part of the dorsal scutum was removed and the penis extracted from the dorsal side. This left the gonopore complex and the anal region intact for scanning electron microscope (SEM) investigation. To draw and examine details of the gonopore complex of the penis, the dorsal microtrichia were removed by means of micro-scissors whenever possible. If too small for such a manipulation, the penes were made transparent by placing them in warm lactic acid overnight. Ovipositors were made transparent (reversible) in warm glycerine diluted with water; treatment with lactic acid or KOH causes excessive and irreversible swelling.

One male and one female specimen of each species were examined with a FEI Quanta 200 SEM, (Peabody, MA, USA). For each species, the male holotype (non-type for *F. leclerci*) was photographed using a JVC KY-F70B digital camera mounted on a Leica MZ 12.5 stereomicroscope. A series of images (~10) were taken at different focal planes and assembled with the dedicated software package AutoMontage Pro Version 5.00.0271 (Syncroscopy, Frederick, MD, USA).

Measurements were taken using a stereomicroscope and are given in mm. Total body length refers to the distance between midpoint of anterior and midpoint of posterior margin of the dorsal scutum. Lengths of leg and palp articles were mostly measured on their dorsal side, from midpoint of anterior margin to midpoint of posterior margin, except for the leg tarsi. These possess a deep dorso-distal invagination and therefore their maximal lengths are given. Depths were measured on the lateral side, at the widest portion, except for tarsus IV of the male, which was measured behind the adenostyle. Tarsal length does not include the claw. The position of the adenostyle on tarsus IV is given at the more clearly marked distal point, where it abruptly rises from the dorsal surface of the tarsus.

Terminology of penis morphology largely corresponds with that used by Shear (1993) and Schwendinger et al. (2004), but because the ‘setae’ of the penis have no alveolus or articulation and leave stumps when they break off, we here refer to them as microtrichia. Rambla (1994) used the term ‘plaque ovoïde’ (translated as ‘ovoid plate’ by Giribet and Boyer 2002) to describe the modified area on the retro-lateral face of tarsus IV in males of *Fangensis leclerci*. Because this is not really a plate (but a more or less clearly outlined area with a different surface structure) and because it is not ovoid in the new species, we here introduce the alternative term ‘Rambla’s organ’.

*Phylogenetic analysis*

In order to test the validity of the genus *Fangensis* and of the family *Stylocellidae*, we undertook phylogenetic analyses of molecular data from specimens of all four species of *Fangensis* and from selected out-groups. The latter include representative stylocellids (*Miopsalis* sp. and *Stylocellus* spp. from various localities in Peninsular Malaysia, Sumatra, Borneo and New Guinea) and species of other families (Table 1). The molecular data utilised include complete 18S rRNA (~1.8 Kb), a 1.3 Kb fragment of 28S rRNA and ~800 bp of the

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Fig. 1. *Fangensis spelaeus*, sp. nov., habitus of male paratype, dorsolateral view. Scale bar: 1.0 mm.
mitochondrial cytochrome c oxidase subunit I (COI) (see Table 1). For detailed protocols on DNA extraction, amplification and sequencing we refer to previous molecular studies on opilionid systematics (see Giribet et al. 2002; Boyer et al. 2005). 18S rRNA was amplified between primer pairs 1F and 9R and sequenced using forward primers 1F, 3F, 18Sa2.0 and reverse primers 4R, 18Sbi, 9R described elsewhere (see Giribet et al. 2002; Boyer et al. 2005). The sequenced fragment, excluding external primers, ranged between 1761 and 1763 bp. The 28S rRNA fragment was amplified with primer pairs 28Sa and 28Sb (a fragment ranging between 1308 to 1324 bp). Internal primers employed for sequencing are the forward primer 28S rd4.8a (5′-GAC TTC CCT CTA CAT CAT-3′) and reverse primer 28S rd5b (5′-CCA CAG CGC ATG ATA AAG ATA-3′) (see Table 1). For COI, we used primers LCO1490 (5′-GGT CAA CAA ATC ATA AAG ATA-3′) and HCOoutout (5′-GTA AAT ATA TGR TGD GCT C-3′) for both amplification and for sequencing.

Phylogenetic analysis under the parsimony optimality criterion was undertaken with the computer programme POY version 3.0 (Wheeler et al. 2002). Nodal support was assessed via 1000 replicates of jackknifing (Farris 1997) and nodal stability was investigated via a sensitivity analysis of 12 parameter sets varying the indel-to-change and transversion-to-transition ratios (Wheeler 1995; Giribet 2003). From activity analysis of 12 parameter sets ranging between 1308 to 1324 bp. Internal primers employed for sequencing are the forward primer 28S rd4.8a (5′-ACC TAT TCT CAA ACT TTA AAT GG-3′) and the reverse primer 28S rd5b (5′-CCA CAG CGC TTC CCT CTA CAT C-3′). This is the first time that this larger fragment has been used for a study on opilionid systematics. For COI, we used primers LCO1490 (5′-GGT CAA CAA ATC ATA AAG ATA-3′) and reverse primer 28S rd5b (5′-CCA CAG CGC TTC CCT CTA CAT C-3′) for both amplification and for sequencing.

Abbreviations of repository institutions

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Table 1. List of specimens used for molecular analysis

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Taxonomy

Genus *Fangensis* Rambla


– Giribet, 2000: 56 (listing under Sironidae); Giribet, 2002: 3 (transfer to Stylocellidae).

Diagnosis

Eyeless stylocellids (*F. insulans*, sp. nov. with eyespots but without cornea), mainly characterised by a bulged or depressed area with a scaly, striate or rugose surface (‘plaque ovoïde’ of Rambla 1994; ‘ovid plate’ of Giribet and Boyer 2002; here termed ‘Rambla’s organ’) on the retro lateral side of tarsus IV (Figs 4C, 9C, 14F, 15B, 19C,G) and by a long pigmented body along the inner surface of each apical lobe of the ovipositor (Figs 6, 11, 16D,E, 21). An unpaired gland pore (Figs 3D, 8D, 13D, 15C, 18D) present at posterior margin of dorsal scutum (area VIII) in males; anal plate of males with (Figs 3D, 18D) or without smooth longitudinal band (corresponding to a similar structure in *Stylocellus sumatranus* Westwood, 1874 and to the anal carina in *S. globosus* Schwendinger & Giribet, 2004); leg claws (especially on posterior legs) in both sexes distally widened and spatulate (in troglobiomorphic species) or cylindrical and hook-shaped (in forest-dwelling species); leg I (in all species) and leg II (in troglobiomorphic species) with a distinct ventral concentration of hairs; tarsus IV of males entire; light spots present dorsally on leg coxae II, close to or
partly covered by anterolateral margin of dorsal scutum (distinct in cave-dwelling species, indistinct in forest-dwelling species); gonopore complex of penis without lobuli laterales.

**Etymology**

The first part of the genus name obviously refers to the northern Thai district of Fang, but the second part is open to speculation. It can be interpreted as an inappropriate Latin adjective ending, or as a Latin noun, ‘ensis’ (= sword). In the former case, the corresponding gender is either masculine or feminine and in the latter case it is masculine. No corresponding explanation is given in the original description and the specific epithet of the type species, the genitive form ‘leclerci’ (= of Leclerc), also does not help to solve this ambiguity. According to article 30.2.4 of the current edition of the International Code of Zoological Nomenclature (ICZN 1999) a genus name formed from neither Latin or Greek, and whose gender was not specified or indicated, is to be treated as masculine.

**Fangensis leclerci** Rambla

(Figs 2–6)


**Type material**

**Northern Thailand:** Chiang Mai Province, Chiang Dao District, close to an underground river inside Tham Klaeb (probably Tham Klaeb Yai), 14.vii.1985, male lectotype (used for SEM study by Rambla; dried, coated and mounted on a SEM stub), here designated from the syntype series (containing three distinct species) in order to clearly define this species. Paralectotypes: 2 females and 2 juveniles from the type locality. Tham Klaeb and Tham Klaeb Yai are different caves, 1.5–2 km apart from each other. Tham Klaeb is short, dry and frequented by tourists, whereas Tham Klaeb Yai is little known, long and has an underground river running through it (see Rigal and Deharveng 1986). The latter was mentioned for ‘Tham Klaeb’ by Rambla (1994: 109). Repository unknown.

**Remarks on the type material**

All other paralectotypes are possibly or clearly not conspecific with the lectotype: two juveniles from outside the same cave (3.viii.1985) may belong to *Stylocellus* sp., specimens of which were collected from leaf litter in the same province (on Doi Suthep; Suzuki 1985) and in a neighbouring province (P. J. Schwendinger, unpublished data). Two juveniles (20.vii.1985) from ‘Tham Mang On’ (= Tham Muang On; over 80 km from the type locality) in Sankamphaeng District may belong to a different *Fangensis* species. One male (16.vi.1986) from ‘Tjam Rawa’ or ‘Tham Kung Lawa’ (= Tham Kaeng Lawa), western Thailand, Kanchanaburi Province, Sai Yok District, belongs to *F. spelaeus*, sp. nov. One juvenile (17.vi.1986) from outside ‘Tham Sai Yok Noi’ (= Tham Wang Badan) possibly belongs to an undescribed *Stylocellus* sp. that was also collected from under bark particles in the same district (P. J. Schwendinger, unpublished data). One male and one female (17.vi.1985) from ‘Tham Nam’ (= Tham Nam Phrathat) in Si Sawat District belong to *F. cavernarus*, sp. nov. All specimens were collected by Phillipe Leclerc (Paris, France). The whereabouts of the type series are unknown.

**Material examined**

**Northern Thailand:** Chiang Mai Province, Chiang Dao District, Tham Klaeb Yai (19°34′33.7″N, 99°03′40.1″E; presumably the type locality), 570 m alt., ~30–150 m inside the limestone cave, dark zone, 10 males (7 in MHNG; 3 in MCZ: 2 in collection (MCZ 62879), 1 used for SEM examination (MCZ 62886)), 10 females (6 in MHNG; 4 in MCZ: 1 in collection (MCZ 62880), 1 used for SEM examination (MCZ 62881), 2 in DNA collection (MCZ DNA100913, DNA100865)), 23–24.xii.2002 (sample TH-02/25). From the same locality, 1 female (MHNG), 23.xii.2004 (sample TH-04/22). All specimens collected by P. J. Schwendinger.
Fig. 3. Scanning electron micrographs of *Fangensis leclerci* Rambla. *A*, body of female, ventral view; *B*, gonostome complex of male; *C*, gonostome complex of female; *D*, anal region of male showing anal gland pore and smooth longitudinal band on anal plate; *E*, anal region of female without modifications.
Diagnosis

Dorsal scutum moderately arched (Fig. 2C), posterior margin (corresponding to tergite VIII) slightly tapering in males and females (Figs 2A,B, 3A). Eyes absent. Ozophores quite long, width across them mostly exceeding width across posterior portion of prosoma region; granules in prosoma region distinctly larger than elsewhere on dorsal scutum (Fig. 2B; see also Rambla 1994; pl. I, figs 1, 2 – SEM micrograph of lectotype). Anal plate of male with a short, wide longitudinal median band of smooth surface in posterior part of plate; tergite IX with smooth median zone (Fig. 3D). Ventral side of tarsus I and II with a concentration of short sensory hairs occupying most of tarsal length (Fig. 4D,E). Tibia IV of male with indistinct subdistal ventral bulge conferring it a pentagonal shape in lateral view (Fig. 4I); tarsus IV of males carrying a small adenostyle at 55% of tarsal length (Fig. 4B,G); Rambla’s organ ovoid in shape, slightly longer than wide, distinctly bulging from retrolateral surface of tarsus IV and set with tiny triangular scales (Fig. 4C,G). Leg claws spatulate (see Rambla 1994: pl. I, fig. 7). Penis with microtrichial formula \( n = 2 \): 3, 7–8, 5/5; ventral side set with tiny denticles distally, ventral microtrichia separated from each other by 4–5 times their diameter, the median one situated proximal to the laterals (Fig. 5A,D); both groups of

Fig. 4. Scanning electron micrographs of *Fangenis leclerci* Rambla. *A*, distal part of left chelicera of male, retrolateral view; *B*, adenostyle; *C*, Rambla’s organ; *D*, tarsus I of male, retrolateral view; *E*, tarsus II of male, retrolateral view; *F*, tarsus III of male, retrolateral view; *G*, tarsus IV of male, retrolateral view; *H*, tarsus IV of female, retrolateral view; *I*, tibia IV of male, retrolateral view.
dorsal microtrichia touching each other in the middle and not covering anterolateral parts of penis (Fig. 5B,E); gonopore complex with very wide lobus medialis and narrow lacinia dorsalis almost reaching distal margin of penis (Fig. 5C,F). Ovipositor ($n = 3$) with a pair of long terminal setae and with sensitive process carrying fairly few branches; ventroproximal plates of apical lobes short, each one with only three setae; pigmented bodies of apical lobes distinct; receptaculata seminis ovoid (Fig. 6).

**Variation**

Range of measurements in males ($n = 7$) and females ($n = 6$; in parentheses): body length 2.91–3.13 (3.07–3.24), width across ozophores 1.52–1.60 (1.55–1.69), greatest width (in opisthosoma region) 1.61–1.71 (1.69–1.83). Variation in shape of penes ($n = 2$), see Fig. 5, in shape of ovipositors ($n = 3$), see Fig. 6.

**Remarks**

Rambla’s (1994: 110) measurements of the unspecified male holotype slightly exceed the size range that we observed for males of this species.

The conspicuous tooth-like anterolateral processes on leg coxae II illustrated for the female of *F. leclerci* by Rambla (1994: fig. 6) are shorter, basally wider and less distinct in specimens examined from Tham Klaeb Yai, but clearly more distinct in specimens from Tham Kaeng Lawa (*F. spelaeus*, sp. nov.) and Tham Nam Phrathat (*F. cavernarus*, sp. nov.).

Rambla’s illustrations (1994: fig. 4b, pl. 3, figs 1, 2) of the tarsus IV of the male seemingly does not refer to *F. leclerci*,

![Fig. 5. *Fangensis leclerci* Rambla, genitalia of two males: *A*–*C*, male 1; *D*–*F*, male 2. *A*, *D*, total penis, ventral view; *B*, *E*, same, dorsal view; *C*, *F*, gonopore complex, dorsal view. LM, lobus medialis; LD, lacinia dorsalis. Scale bars: 0.1 mm.](image)
although she states that only one male and one female from Tham Klaeb were used for SEM examination. The adenostyle in her pictures is quite narrow, and the Rambla’s organ is distinctly striate like in *F. cavernarus*, sp. nov. (Figs 14B, F, 15B), whereas in *F. leclerci* the adenostyle is straight and the Rambla’s organ is scaly (Fig. 4B, C, G).

The illustration of a penis in the original description (Rambla 1994: fig. 5) corresponds with the penes of males from Tham Klaeb Yai examined. The ovipositor illustrated by Rambla (1994: fig. 7) is obviously swollen (presumably by KOH treatment), does not show its internal structure and is difficult to identify. The presence of only three setae on each ventroproximal plate of the apical lobes of the ovipositor indicates that it belongs to *F. leclerci*, but the plates themselves appear too long for that species (cf. Fig. 6). It is possible that Rambla drew the ovipositor of the female from ‘Tham Nam’ (= Tham Nam Phratat), which is now assigned to *F. cavernarus*, sp. nov. The two female paratypes of that species possess quite long proximal ovipositor plates set with three to four setae (Fig. 16D, E).

**Distribution**

Known only from Klaeb Yai Cave, ~30 km north of Chiang Dao. A detailed description of this cave, including topography, was given by Rigal and Deharveng (1986).

It needs to be verified if the population in the ‘Mang On’ (= Muang On) Cave (east of Chiang Mai, ~80 km away from Tham Klaeb Yai; see Deharveng and Brouquisse 1986), known from two juveniles (Rambla 1994: 109), also belongs to this species. P. J. S. found no opilionids in the Muang On Cave, a local tourist attraction, during short visits in December 2002, 2003 and 2004.

**Natural history**

*Fangensis leclerci* was found in the dark part of the cave, most animals on wet loam next to the underground river, one specimen on stal. A pair was caught in copulation, with the male hanging on the underside of the female, his legs tightly embracing her body. Both animals were facing in opposite directions and the male was vividly palpitating the anal region of the female with his pedipalps in an alternating manner. After ~10 min the animals were disturbed, they partly separated, and the female dragged the male behind her for a short distance until he became loose. A second pair was observed in the cave in premating behaviour: the male attempted to mount the female from behind while both were walking. They separated – probably owing to disturbance during observation – and did not assume the mating position.

Direct sperm transfer via copulation may not be employed in all cyphophthalmids. Karaman (2005) illustrated and discussed the use of spermatophores for two species of *Cyphophthalmus* in Serbia. In Malaysia, one of us (P. J. S.) collected three *Stylocellus* females, each with a spermatophore (similar to that described by Karaman) attached to its gonostome.

In captivity, the animals dug short burrows into wet, soft soil, where they took shelter when disturbed.

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**Fig. 6.** *Fangensis leclerci* Rambla, tips of ovipositors of three females, ventral view. A, most setae omitted, insertions of setae on proximoventral plates indicated by circles (apical lobes slightly deformed due to treatment with KOH); B, all setae illustrated (apical lobes slightly deformed due to treatment with lactic acid); C, all setae illustrated (untreated). PB, pigmented body of apical lobe; RS, receptaculum seminis; SP, sensitive process; TS, terminal seta. Scale bars: 0.1 mm.
**Fangensis spelaeus**, sp. nov.
(Figs 1, 7–11; Table 2)


**Material examined**

**Holotype.** Male (MHNG, sample TH-03/01), western (or western central) Thailand, Kanchanaburi Province, Sai Yok District, Tham Kaeng Lawa (14°17′59.1″N, 98°58′59.3″E), 150 m alt. (~50–100 m inside limestone cave; dark zone), 30.iv.2003.

**Paratypes.** Thailand: 7 males (5 in MHNG, TH-02/02, TH-03/01; 1 in MCZ 62882; 1 used for SEM examination (MCZ 62883)) and 9 females (6 in MHNG, TH-02/02 (including 'allotype'), TH-03/01; 3 in MCZ: 1 in collection (MCZ 62888), 1 used for SEM examination (MCZ 628333), another for DNA analysis (MCZ DNA100669)) from the type locality, 7.vii.2002, 30.iv.2003. All specimens collected by P. J. Schwendinger.

**Diagnosis**

Blind, long-legged species (Fig. 1), different from the similar *F. leclerci* in: body larger, more slender; dorsal scutum less arched in central part; ozophores less prominent; width at posterior portion of prosoma region always greater than width across ozophores; posterior scutal margin in males more rounded (more truncate in females) (Figs 7A,B, 8A cf. Figs 2A,B, 3A); granules in prosoma region not distinctly larger than elsewhere on dorsal scutum (Fig. 7B cf. Fig. 2B); anal plate of males without modification (Fig. 8D cf. Fig. 3D); tibia IV of males with pronounced subdistal ventral bulge (Fig. 9I); tarsus IV of males carrying a larger adenostyle at ~51% of tarsal length and a more elongate Rambla’s organ with striate surface (Fig. 9B,C,G cf. Fig. 4B,C,G). Penis with more strongly pointed appearance and more numerous, much deeper dorsal microtrichia; ventral microtrichia situated closer to each other, the median one(s) more distally than the laterals; lacinia dorsalis of gonopore complex wider, lobus medialis much narrower (Fig. 10 cf. Fig. 5). Ovipositor with sensitive process carrying more branches; ventroproximal plate of each apical lobe longer, with more setae (5 v. 3) (Fig. 11 cf. Fig. 6).

**Description**

Total length of male holotype (female ‘allotype’ in parentheses) 3.32 (3.73), width across ozopores 1.46 (1.52), greatest width (at posterior portion of prosoma region) 1.58 (1.70); length: width ratio 2.1 (2.2).

**Dorsal scutum** quite slender, width at posterior portion of prosoma region clearly exceeding width across ozophores and equal or slightly greater than width in opisthosoma region (Fig. 7B). Central part of dorsal scutum fairly flat (Fig. 7C); posterior margin (corresponding to tergite VIII) evenly rounded and with quite small anal gland pore in males (Figs 7A,B, 8D), relatively narrower and slightly truncate in females (Fig. 8A,E).

**Ventral prosomal complex** typical for stylocellids: males with coxae IV meeting in the midline for a distance of about the gonostome length, females with coxae IV completely separated by gonostome; gonostome of both sexes almost circular, in females much larger than in males; lateral walls of gonostome formed by elevated postero-proximal processes of coxae IV; these processes slightly larger and situated more posteriorly in females; posterior margin of gonostome in both sexes formed by a short opisthosomal sternite with straight or rounded anterior margin in males (Fig. 8B) and straight anterior margin in females (Fig. 8C).

**Anal region.** Anal plate and tergite IX in both sexes unmodified, without smooth areas (Fig. 8D,E).

**Chelicerae** (Fig. 9A) relatively stout, furnished with numerous long setae. Proximal article with granular surface, carrying spike-like granules on ventral and proventral side, a transversal dorsal crest, a small, scale-like anteroventral (retroventral) process and a low, widely rounded posteroventral mound. Second article fairly robust, dorsal side almost completely

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**Fig. 7. Fangensis spelaeus**, sp. nov., body of male holotype. A, ventral view; B, dorsal view; C, lateral view.
Fig. 8. Scanning electron micrographs of *Fangensis spelaeus*, sp. nov. *A*, body of female, ventral view; *B*, gonostome complex of male; *C*, gonostome complex of female; *D*, anal region of male showing anal gland pore and unmodified anal plate; *E*, anal region of female without modifications.
ornamented with small granules between base and joint of movable finger. Proximal article of male holotype (female ‘allotype’ in parentheses) 1.01 (1.06) long, 0.37 (0.42) deep; second article 1.15 (1.21) long, 0.25 (0.28) deep, movable finger 0.42 (0.44) long, 0.09 (0.09) deep, 37% (36%) of second article length. Dentition of cutting edges uniform and similar on both cheliceral fingers, composed of ~10 denticles.

**Palp** without processes. Length/depth (length:depth ratio in parentheses) of palpal articles (from trochanter to tarsus) of male holotype [of female ‘allotype’ in square brackets]: 0.37/0.12 (3.1) [0.36/0.15 (2.4)]; 0.67/0.14 (4.8) [0.70/0.15 (4.7)]; 0.36/0.14 (2.6) [0.40/0.15 (2.7)]; 0.53/0.11 (4.8) [0.57/0.11 (5.2)]; 0.48/0.10 (4.8) [0.49/0.11 (4.5)]; total length 2.41 [2.52]. Palpal claw 0.09 (0.10) long.

**Fig. 9.** Scanning electron micrographs of *Fangensis spelaeus*, sp. nov. A, left chelicera of male, retrolateral view; B, adenostyle; C, Rambla’s organ; D, tarsus I of male, retrolateral view; E, tarsus II of male, retrolateral view; F, tarsus III of male, retrolateral view; G, tarsus IV of male, retrolateral view; H, tarsus IV of female, retrolateral view; I, tibia IV of male, retrolateral view.
Legs (Fig. 9D–I) long and slender, surface of all articles setose and granular, claws (especially on posterior legs) distally widened and spatulate. Ventral sides of tarsi I and II with a concentration of short sensory hairs occupying most of tarsal length (Fig. 9D,E). No longitudinal dorsal grooves present on leg tarsi. Tibia IV of male with pronounced sub-distal ventral bulge (Fig. 9I). Tarsus IV of male carrying an adenostyle fringed at the tip (Fig. 9B,G); position of distal base of adenostyle at 51% of tarsal length; Rambla’s organ with striate surface, only slightly bulging from retrolateral face, elongate in direction of leg axis, ~2 times longer than wide (Fig. 9C,G). Tarsus IV of female without modifications (Fig. 9H). For measurements, see Table 2.

Penis (Fig. 10) short, typical of stylocellids. Microtrichial formulas \((n = 3)\): 3, 10, 8+8; 3, 9, 7+8; 4, 10, 8+8; some microtrichia with denticles on their shafts. Ventral side of penis ornamented with tiny denticles in distal part; 3–4 ventral microtrichia set back from distal margin, their bases separated by ~2–3 times their diameters; median microtrichia/microtrichium situated distal to lateral microtrichia (Fig. 10A,D,G). Broadly rounded or slightly invaginated distal margin of penis with 9–10 apical microtrichia. Dorsal

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Fig. 10. Fangensis spelaeus, sp. nov., genitalia of three males: A–C, male 1; D–F, male 2; G, male 3. A, D, G, total penis, ventral view; B, E, same, dorsal view; C, F, gonopore complex, dorsal view. Scale bars: 0.1 mm.
side of penis with two groups of microtrichia touching each other in the middle and completely covering apex of penis; bases of dorsal microtrichia forming a procured row (Fig. 10B,E); these microtrichia exceptionally deep, their ventral, more distally situated margins giving the false impression of a parallel row. Tips of all penis microtrichia bent towards each other (Fig. 10B; pressed apart on the microscopic slide in Fig. 10E), giving the penis a distinctly pointed appearance. Gonopore complex (Fig. 10C,F) with wide, subapically slightly constricted lacinia dorsalis with broadly rounded distal margin; lobus medialis quite narrow, with angular distal margin and prominent lateral parts carrying small lateral processes but no digiti.

Ovipositor (Fig. 11) composed of two apical lobes and 41–44 circular articles ($n=2$), each of the latter furnished with eight equally long setae (proximal article with fewer setae). Each apical lobe carrying several setae, including a long terminal seta, a sensitive process with a dense group of simple or furcate branches with slightly hooked tips, and five setae on each ventroproximal plate. A long, slender pigmented body present in distal half of each lobe; a similar body with a more complicated structure lying in its posterior half; a somewhat ovoid receptaculum seminis near its base.

Table 2. Leg measurements (in mm) of new Fangensis species

<table>
<thead>
<tr>
<th>Leg</th>
<th>Trochanter</th>
<th>Femur</th>
<th>Patella</th>
<th>Tibia</th>
<th>Metatarsus</th>
<th>Tarsus</th>
<th>Total</th>
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<td></td>
<td>length/depth</td>
<td></td>
<td></td>
<td></td>
<td>length/depth</td>
<td></td>
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<tr>
<td>Fangensis spelaeus, sp. nov., male holotype</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>I</td>
<td>0.35/0.21 (1.7)</td>
<td>1.14/0.22 (5.1)</td>
<td>0.52/0.23 (2.2)</td>
<td>0.75/0.21 (3.6)</td>
<td>0.36/0.19 (1.9)</td>
<td>1.03/0.20 (5.2)</td>
<td>4.15</td>
</tr>
<tr>
<td>II</td>
<td>0.35/0.21 (1.7)</td>
<td>1.14/0.22 (5.2)</td>
<td>0.49/0.23 (2.1)</td>
<td>0.68/0.21 (3.2)</td>
<td>0.35/0.19 (1.8)</td>
<td>1.00/0.20 (5.0)</td>
<td>4.01</td>
</tr>
<tr>
<td>III</td>
<td>0.35/0.23 (1.5)</td>
<td>1.06/0.25 (4.2)</td>
<td>0.47/0.27 (1.7)</td>
<td>0.57/0.25 (2.3)</td>
<td>0.35/0.19 (1.8)</td>
<td>0.84/0.22 (3.8)</td>
<td>3.64</td>
</tr>
<tr>
<td>IV</td>
<td>0.42/0.22 (1.9)</td>
<td>1.36/0.30 (4.5)</td>
<td>0.59/0.30 (2.0)</td>
<td>0.74/0.30 (2.5)</td>
<td>0.37/0.20 (1.9)</td>
<td>0.93/0.29 (3.2)</td>
<td>4.41</td>
</tr>
</tbody>
</table>

Fangensis spelaeus, sp. nov., female ‘allotype’

I 0.38/0.23 (1.7) 1.22/0.23 (5.3) 0.57/0.25 (2.2) 0.82/0.21 (3.9) 0.37/0.20 (1.9) 1.09/0.21 (5.2) 4.45
II 0.37/0.25 (1.5) 1.22/0.22 (5.5) 0.53/0.26 (2.0) 0.70/0.23 (3.1) 0.37/0.20 (1.8) 1.06/0.22 (4.8) 4.25
III 0.37/0.26 (1.4) 1.14/0.25 (4.6) 0.51/0.27 (1.9) 0.64/0.25 (2.6) 0.37/0.19 (1.9) 0.93/0.25 (3.7) 3.96
IV 0.47/0.25 (1.9) 1.51/0.26 (5.8) 0.65/0.30 (2.2) 0.84/0.36 (2.4) 0.40/0.21 (1.9) 1.14/0.26 (4.4) 5.01

Fangensis cavernarus, sp. nov., male holotype

I 0.40/0.26 (1.5) 1.42/0.25 (5.7) 0.64/0.25 (2.6) 0.93/0.22 (4.2) 0.40/0.21 (1.9) 1.26/0.23 (5.5) 5.05
II 0.40/0.26 (1.5) 1.40/0.25 (5.7) 0.61/0.27 (2.3) 0.82/0.25 (3.3) 0.40/0.21 (1.9) 1.19/0.25 (4.8) 4.82
III 0.42/0.27 (1.6) 1.24/0.27 (4.6) 0.58/0.30 (1.9) 0.69/0.27 (2.6) 0.37/0.19 (1.9) 0.93/0.25 (3.7) 3.96
IV 0.47/0.28 (1.8) 1.58/0.32 (4.9) 0.73/0.32 (2.3) 0.89/0.35 (2.5) 0.44/0.22 (2.0) 1.12/0.33 (3.4) 5.01

Fangensis cavernarus, sp. nov., female ‘allotype’

I 0.41/0.27 (1.5) 1.43/0.27 (5.3) 0.64/0.27 (2.4) 0.96/0.25 (3.8) 0.41/0.22 (1.9) 1.26/0.25 (5.0) 5.11
II 0.41/0.27 (1.5) 1.40/0.26 (5.5) 0.62/0.27 (2.3) 0.85/0.23 (3.4) 0.41/0.22 (1.9) 1.19/0.26 (4.6) 4.89
III 0.42/0.28 (1.6) 1.30/0.27 (4.8) 0.59/0.30 (2.0) 0.72/0.28 (2.6) 0.40/0.21 (1.9) 1.04/0.30 (3.5) 4.36
IV 0.52/0.30 (1.7) 1.68/0.33 (5.1) 0.74/0.32 (2.3) 0.99/0.31 (3.2) 0.48/0.23 (2.1) 1.25/0.30 (4.2) 5.66

Fangensis insulanus, sp. nov., male holotype

I 0.50/0.39 (1.3) 1.35/0.39 (3.5) 0.72/0.34 (2.1) 0.81/0.33 (2.5) 0.45/0.27 (1.7) 1.13/0.28 (4.0) 4.96
II 0.47/0.34 (1.4) 1.22/0.37 (3.3) 0.66/0.36 (1.8) 0.66/0.34 (1.9) 0.42/0.25 (1.7) 1.03/0.27 (3.8) 4.46
III 0.47/0.37 (1.3) 1.16/0.41 (2.8) 0.63/0.39 (1.6) 0.55/0.39 (1.4) 0.41/0.25 (1.6) 0.91/0.31 (2.9) 4.13
IV 0.61/0.39 (1.6) 1.44/0.49 (2.9) 0.74/0.44 (1.7) 0.78/0.44 (1.8) 0.42/0.28 (1.5) 1.10/0.37 (3.2) 5.09

Fangensis insulanus, sp. nov., female ‘allotype’

I 0.47/0.37 (1.3) 1.25/0.37 (3.4) 0.70/0.33 (2.1) 0.75/0.28 (2.7) 0.42/0.25 (1.7) 1.05/0.27 (3.9) 4.64
II 0.44/0.34 (1.3) 1.13/0.34 (3.3) 0.63/0.34 (1.9) 0.61/0.33 (1.8) 0.39/0.23 (1.7) 0.95/0.25 (3.8) 4.15
III 0.44/0.34 (1.3) 1.06/0.39 (2.7) 0.59/0.34 (1.7) 0.56/0.37 (1.5) 0.38/0.25 (1.5) 0.85/0.30 (2.8) 3.88
IV 0.59/0.36 (1.6) 1.44/0.44 (3.3) 0.70/0.41 (1.7) 0.74/0.39 (1.9) 0.42/0.28 (1.5) 1.03/0.33 (3.1) 4.92
Variation

Range of measurements in males \((n = 7)\) and females \((n = 7);\) in parentheses): body length 3.11–3.33 (3.35–3.74), width across ozophores 1.34–1.42 (1.38–1.54), greatest width (at posterior portion of prosoma region) 1.52–1.64 (1.50–1.69). Two males with a clearly rounded posterior margin of the gonostome. Variation in shape of penes \((n = 3)\), see Fig. 10; variation in shape of ovipositors \((n = 2)\), see Fig. 11. Two males have deformed legs: one with a short tarsus but without a metatarsus on its right leg I, the other with a strongly reduced tarsus budding directly from the patella of its right leg II.

Distribution

Known only from Kaeng Lawa Cave in western (western central) Thailand. This cave (under the name ‘Tham Rawa’) was briefly described and illustrated by Brouquisse (1987). Rambla (1994: 109) also studied a single juvenile, which she attributed to *F. leclerci*, from a ‘milieu endogé’ (probably under stones) near ‘Sai Yok Noi Cave’ (= Wang Badan Cave), which is ~15 km east of Kaeng Lawa Cave and ~20–25 km south of Nam Phrathat Cave (locality of *F. cavernarus*, sp. nov.). The identity of that specimen is unclear and needs to be established from new material.

Natural history

The animals examined were all found in the wide, dark part of the cave, which is temporarily illuminated for tourists. The opilionids, however, appear not to be much disturbed by that. All were found walking in the open, near the base of the cave walls or of large stalagmites, on the wet, loamy cave floor and on stal wettened by water dripping from the cave ceiling. No such opilionids were found in the dry parts of the cave or under debris, garbage or discarded bamboo poles at some distance from the cave walls. As in *F. leclerci*, this species also seems to require high humidity and is probably not able to survive the seasonally dry environment outside caves in that area.

Etymology

Latin: ‘spelaeus’ (-a, -um); adjective of ‘spelaeum’ (= cave), originating from the Greek ‘spelaion’.

*Fangensis cavernarus*, sp. nov.

*(Figs 12–16; Table 2)*


Material examined

**Holotype.** Male (MHNG), western (or western central) Thailand, Kanchanaburi Province, Si Sawat District, Tham Nam Phrathat (14°23′53.6″N, 99°04′52.6″E), 570 m alt. (~300–600 m inside limestone cave; dark zone).

**Paratypes.** Thailand: 1 male (in MCZ 62884, used for SEM examination) and 4 females (3 in MHNG (including ‘allotype’); 1 in MCZ, used for SEM examination (MCZ 62885) and for DNA analysis (MCZ DNA101460)), same data as for holotype. All specimens collected by P. J. Schwendinger, 17.vii.2004, sample TH-04/01.

Diagnosis

Different from *F. spelaeus*, sp. nov. in: body slightly larger, with a pair of dark paramedian stripes in prosoma region of dorsal scutum (Fig. 12B); gonostome of males relatively larger, longer than distance of contact between left and right coxa IV (Fig. 13B cf. Fig. 8B); anal gland pore of males distinctly larger (Figs 13D, 15C cf. Fig. 8D); subdistal bulge on tibia IV of males smaller and situated retroventrally (Fig. 15A cf. Fig. 9f) (ventrally in *F. spelaeus*, sp. nov.); adenostyle thinner (Fig. 14B cf. Fig. 9B), situated slightly more distally (at 56% of tarsal length; in *F. spelaeus*, sp. nov. at 50%); Rambla’s organ more elongate (Figs 14F, 15B)

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![Fig. 12. *Fangensis cavernarus*, sp. nov., body of male holotype. A, ventral view; B, dorsal view; C, lateral view.](image-url)
Fig. 13. Scanning electron micrographs of *Fangensis cavernarum*, sp. nov. A, body of female, ventral view; B, gonostome complex of male; C, gonostome complex of female; D, anal region of male showing large anal gland pore and unmodified anal plate; E, anal region of female without modifications.
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cf. Fig. 9C,G); penis with less pointed appearance, ventral microtrichia more closely spaced, lobus medialis carrying a pair of small lateral digiti (Fig. 16A–C cf. Fig. 10); ovipositor with fewer (6–7 v. 10) setae on both ventroproximal plates of apical lobes, proximal portion of pigmented paramedian bodies inside apical lobes different in shape (Fig. 16D,E cf. Fig. 11).

Description

Total length of male holotype (female ‘allotype’ in parentheses) 3.66 (4.04), width across ozopores 1.58 (1.64), greatest width (in opisthosoma region) 1.91 (1.97); length:width ratio 1.9 (2.1).

Dorsal scutum slender, width at posterior portion of prosoma region greater than width across ozopores but smaller than width in opisthosoma region; central part of dorsal scutum fairly flat (Fig. 12C), its posterior margin evenly rounded in males (Fig. 12A,B) and slightly truncate in females (Fig. 13A).

Ventral prosomal complex typical for stylocellids: males with coxae IV meeting in the midline for a distance clearly shorter than gonostome length (Fig. 13B), females with coxae IV completely separated by gonostome (Fig. 13C); gonostome of males distinctly smaller than in females; lateral walls of gonostome formed by elevated postero-proximal processes of coxae IV, these processes about equally long in both sexes; posterior margin of gonostome in both sexes formed by a short trapezoidal opisthosomal sternite with straight or indistinctly rounded anterior margin (Fig. 13B,C).

Anal region. Anal gland pore of males exceptionally large (Figs 13D, 15C). Anal plate and tergite IX of male

Fig. 14. Scanning electron micrographs of Fangenis cavernarus, sp. nov. A, left chelicera of male, retrolateral view; B, adenostyle; C, tarsus I of male, retrolateral view; D, tarsus II of male, retrolateral view; E, tarsus III of male, retrolateral view; F, tarsus IV of male, retrolateral view; G, tarsus IV of female, retrolateral view.
unmodified, without smooth areas (Fig. 13D), as in female (Fig. 13E).

Chelicerae (Fig. 14A) relatively stout, furnished with numerous long setae. Proximal article with granular surface, carrying a providental row of relatively large denticles (spike-like granules), a transversal dorsal crest, a small, scale-like anteroventral (retroventral) process and a low, widely rounded posteroventral mound. Second article fairly robust, almost completely ornamented with small granules between base and joint of movable finger. Proximal article of male holotype (female ‘allotype’ in parentheses) 1.06 (1.21) long, 0.42 (0.43) deep; second article 1.31 (1.38) long, 0.31 (0.31) deep, movable finger 0.51 (0.52) long, 0.11 (0.11) deep, 39% (38%) of second article length. Dentition of cutting edges uniform and similar on both cheliceral fingers, composed of ~10 denticles.

Palp without processes. Length/depth (length:depth ratio in parentheses) of palpal articles (from trochanter to tarsus) of male holotype [of female ‘allotype’ in square brackets]: 0.38/0.15 (2.5) [0.38/0.15 (2.5)]; 0.83/0.16 (5.2) [0.84/0.16 (5.3)]; 0.43/0.15 (2.9) [0.46/0.16 (2.9)]; 0.64/0.12 (5.3) [0.65/0.12 (5.4)]; 0.57/0.12 (4.8) [0.58/0.12 (4.8)]; total length 2.85 [2.91]. Palpal claw 0.11 (0.11) long.

Legs (Figs 14C–G, 15A) long and slender, surface of all articles setose and granular, claws (especially on posterior legs) distally widened and spatulate. Ventral sides of tarsi I and II with a concentration of short sensory hairs occupying most of tarsal length (Fig. 14C,D). No longitudinal dorsal grooves present on leg tarsi. Tibia IV of male with distinct subdistal retroventral bulge (Fig. 15A). Tarsus IV of male carrying a relatively long, thin adenostyle with a fringed tip (Fig. 14B,F); position of distal base of adenostyle at 56% of tarsal length; Rambla’s organ slightly bulging from retrolateral face, elongated in direction of leg axis, ~3 times longer than wide (Figs 14F, 15B). Tarsus IV of female without modifications (Fig. 14G). For measurements, see Table 2.

Penis (Figs 16A–C) short, typical of stylocellids. Microtrichial formula \(n = 1\): 3, 9, 7+7; many microtrichia with a few denticles on their shafts. Ventral side of penis ornamented with tiny denticles in distal part; three ventral microtrichia set back from distal margin, their bases separated by about their diameters, the median microtrichium situated slightly distal to lateral microtrichia (Fig. 16A). Distal margin of penis moderately invaginated, carrying nine apical microtrichia. Dorsal side of penis with deep microtrichia (as in *F. spelaeus*, sp. nov.); no median gap between dorsal microtrichia of left and right side; microtrichial bases not fused, arranged in a curved row (Fig. 16B). Gonopore complex (Fig. 16C) with paddle-shaped, distally widely rounded lacinia dorsalis; lobus medialis quite narrow, its apex distinctly projecting beyond distal margin of lacinia dorsalis, carrying a small lateral digitus and a more proximal process on each side.

Ovipositor (Fig. 16D,E) composed of two apical lobes and 40–43 circular articles (\(n = 2\), each of the latter (except the proximal one) furnished with eight equally long setae. Each apical lobe carrying several setae, including a long terminal seta, a sensitive process with a dense group of simple or bifurcate branches with slightly hooked tips, and 3–4 setae on the ventroproximal plate. A long, slender, pigmented body present in the distal half of each lobe; a similar body with a more complicated structure lying in its proximal half; an ovoid or sac-like receptaculum seminis situated near its base.

Variation

Range of measurements in males (\(n = 2\)) and females (\(n = 4\); in parentheses): body length 3.66–3.74 (3.86–4.04), width across ozopores 1.56–1.58 (1.60–1.65), maximum width (in opisthosoma region) 1.91–1.99 (1.95–1.97).
In the anal gland pore of the holotype two openings of gland ducts are visible; the male paratype shows three such openings. The ovipositor of one of the females dissected has ovoid receptacles and six setae on both ventral plates of the apical lobes (Fig. 16D), the other female dissected has rather elongate receptacles and seven setae on both plates (Fig. 16E).

**Distribution**

*Fangensis cavernarus*, sp. nov. is known only from the type locality, a limestone cave through which flows an underground river. A description and a map of this cave (under the name ‘Tham Nam’) were published by Brouquisse (1987: 34–35).

**Natural history**

*Fangensis cavernarus*, sp. nov. was collected ~300–600 m inside Nam Phrathat Cave. All animals were slowly walking about on slightly sloping, wet loam (quite deep and very sticky in some places) on both sides of an underground river. The animals were very scattered and appeared to be distinctly less abundant than the other cave-dwelling *Fangensis*

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**Fig. 16.** *Fangensis cavernarus*, sp. nov., genitalia. *A*, total penis, ventral view; *B*, same, dorsal view; *C*, gonopore complex of same penis, dorsal view (one apical microtrichium situated more ventrally and not illustrated); *D, E*, tips of ovipositors of two females, ventral view; *D*, all setae illustrated; *E*, most setae omitted, insertions of setae on proximoventral plates indicated by circles. *D*, digitus. Scale bars: 0.1 mm.
species. When approaching the animals in the cave to a distance of 1–1.5 m without stepping on the substrate on which they were sitting, they turned away, increased their pace and fled towards the cave wall. These blind opilionids are obviously very sensitive to vibratory or olfactory stimuli.

Etymology
Latin: ‘cavernanus (-a, -um)’, adjective of ‘caverna’ (= cave).

*Fangensis insulanus*, sp. nov.
(Figs 17–21; Table 2)
*Fangensis* sp. Giribet & Boyer, 2002 (cladistic analysis at generic level).

Material examined
**Holotype.** Male (MHNG, sample TH-04/12), southern Thailand, Phuket Province, Ko (= Island) Siray (7°53′06.8″N, 98°26′13.6″E), 30 m alt., 5.ix.2004.


**Other material examined.** Thailand: 1 large juvenile (MHNG, TH-03/15), 23.v.2003 and 3 large juveniles (MCZ DNA100388), 12.vii.2000 from the type locality. All specimens collected by P. J. Schwendinger.

Diagnosis
Different from *F. spelaeus*, sp. nov. in: body larger; central part of dorsal scutum flat (Fig. 17C cf. Fig. 7C); eye remnants present as small light spots in all adults (Fig. 17C) but not in juveniles; gonostome of males much wider (Fig. 18B cf. Fig. 8B); anal plate and tergite IX of males with smooth longitudinal median band (Fig. 18D cf. Fig. 8D); legs relatively shorter and stouter, with normal (not spatulate) hook-shaped claws on all tarsi and with longitudinal dorsal grooves on tarsi I and II; ventral concentration of sensory hairs absent on tarsus II (Fig. 19E cf. Fig. 9E); tibia IV of males without ventral bulge (Fig. 19J); tarsus IV of males with a more erect adenostyle at 46% of tarsal length, and a much larger, depressed Rambla’s organ with rugose surface (Fig. 19B,C,G cf. Fig. 9B,C,G); penis without denticles on ventral side, distally wider, with 4–5 ventral microtrichia, only eight dorsal microtrichia, and left and right group of dorsal microtrichia separated by a distinct gap; gonopore complex clearly more remote from distal penis margin, distal margin of lobus medialis slightly invaginated (Fig. 20 cf. Fig. 10); ovipositor with fewer articles, ventroproximal plates of apical lobes much longer and carrying 8–10 setae each; pigmented body along inner surface different in shape; receptacula seminis much longer, sausage-shaped and curled (Fig. 21 cf. Fig. 11).

Description
Total length of male holotype (female ‘allotype’ in parentheses) 4.24 (4.14), width across ozopores 1.87 (1.80), greatest width (at posterior portion of prosoma region) 1.97 (1.92); length: width ratio 2.2 (2.2).

**Dorsal scutum** fairly slender, moderately arched in central part (Fig. 17C), its posterior margin broadly rounded (Figs 17A,B, 18A), with posterior portion of prosoma region strongly bulged laterally, width there exceeding width across ozopores and width in opisthosoma region (Fig. 17B); a small light eyespot (without cornea) present anterior to ozopores (Fig. 17C).

**Ventral prosomal complex** typical for stylocellids: males with coxae IV meeting in the midline for a distance slightly less than the gonostome length; females with coxae IV completely separated by gonostome; gonostome of males very widely sub-quadrangular, with lateral processes situated anteriorly (Fig. 18B); gonostome of females almost circular, with lateral
Fig. 18. Scanning electron micrographs of Fangensis insulanus, sp. nov. A, body of female, ventral view; B, gonostome complex of male; C, gonostome complex of female; D, anal region of male showing anal gland pore and smooth longitudinal band on anal plate; E, anal region of female without modifications.
processes situated more posteriorly (Fig. 18C); posterior margin of gonostome in both sexes formed by a short opisthosomal sternite with straight anterior margin (Fig. 18B,C).

**Anal region.** Anal pore small. Anal plate of males with smooth median band (continuously widening anteriorly) running longitudinally over its surface (in some specimens difficult to see under the light microscope) (Fig. 18D); anal plate of females unmodified (Fig. 18E); smooth median patch on tergite IX of both sexes (Fig. 18D,E).

**Chelicerae** (Fig. 19A) relatively stout, furnished with numerous long setae. Proximal article with granular surface, carrying spike-like granules on ventral and proventral side,
a transversal dorsal crest, a small, knob-shaped anteroventral (retroventral) process — both connected by an indistinct ridge on retrolateral side — and a low, widely rounded posteroventral mound. Second article fairly robust, dorsal side almost completely ornamented with small granules between base and joint of movable finger. Proximal article of male holotype (female ‘allotype’ in parentheses) 1.53 (1.47) long, 0.53 (0.53) deep; second article 1.69 (1.57) long, 0.34 (0.34) deep, movable finger 0.59 (0.56) long, 0.11 (0.11) deep, 35% (36%) of second article length. Dentition of cutting edges confined to distal half, uniform and similar on both cheliceral fingers, composed of ~10 denticles.

**Palp** without processes. Length/depth (length:depth ratio in parentheses) of palpal articles (from trochanter to tarsus) of male holotype [of female ‘allotype’ in square brackets]: 0.47/0.19 (2.5) [0.45/0.20 (2.3)]; 0.88/0.20 (4.4) [0.85/0.20 (4.3)]; 0.59/0.17 (3.5) [0.60/0.16 (3.8)]; 0.64/0.13 (4.9) [0.63/0.13 (4.8)]; 0.49/0.13 (3.8) [0.47/0.13 (6.6)]; total length 3.07 [3.0]. Palpal claw 0.08 (0.08) long.

**Legs** (Fig. 19D–I) stronger than in preceding species, surface of all articles setose and granular, claws normal, not spatulate. Only ventral side of tarsus I (not of tarsus II) with a concentration of short sensory hairs occupying most of tarsal length (Fig. 19D cf. Fig. 19E). Longitudinal dorsal grooves present on leg tarsi I and II (Fig. 19D,E). Tibia IV of male without ventral bulge (Fig. 19I). Tarsus IV of male carrying a short erect adenostyle fringed at the tip; position of distal base of adenostyle at 46% of tarsal length.

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**Fig. 20.** *Fangensis insulanus*, sp. nov., genitalia of two male paratypes from the type locality: A–C, male 1; D–F, male 2. A, D, total penis, ventral view; B, E, same, dorsal view; C, F, gonopore complex, dorsal view. Scale bars: 0.1 mm.
Ramble’s organ developed as a large, shallow depression with rugose surface, occupying most of retro-lateral distal part of tarsus IV (Fig. 19C,G). Tarsus IV of females without modifications (Fig. 19H). Measurements, see Table 2.

Penis (Fig. 20) short, distally quite wide, typical of stylocellids. Microtrichial formula \( (n = 2): 4-5, 8, 8+8-9 \). Ventral side smooth, without denticles on surface; 4–5 ventral microtrichia set back from distal margin, their bases separated by \( \sim 1-2 \) times their diameters; median ventral microtrichia situated more distally than laterals. Distinctly invaginated distal margin of penis with eight apical microtrichia (Fig. 20A,D). Dorsal side of penis with two groups of 8–9 normally deep microtrichia densely set with tiny denticles distally; left and right group of these microtrichia separated by a distinct gap, their bases not fused, arranged in a widely V-shaped row (Fig. 20B,E). Area distal to gonopore complex ornamented with tiny denticles. Gonopore complex distinctly remote from distal penis margin; lacinia dorsalis wide, tongue-shaped, reaching little beyond slightly invaginated distal margin of lobus medialis; the latter relatively short and narrow, carrying bent, finger-like protuberances but no distolateral digit (Fig. 20C,F).

Ovipositor (Fig. 21) composed of two apical lobes and 35 circular articles \( (n = 2) \), each of the latter (except for the most proximal one) carrying eight equally long setae. Apical lobes carrying several setae including a long terminal or slightly subterminal seta situated on or below a more or less distinct terminal ridge, a sensitive process with a dense group of slightly bent, simple or furcate branches, and 8–11 setae on the ventroproximal plate of each apical lobe. Pigmented body along prolateral surface of apical lobes quite wide. Receptacula seminis long, tubular and S-shaped.

Variation
Range of measurements in males \( (n = 8) \) and females \( (n = 6; \) in parentheses): body length 4.03–4.45 \((4.20–4.35)\), width across ozopores 1.75–1.93 \((1.80–1.93)\), greatest width (at posterior portion of prosoma region) 1.88–2.07 \((1.93–2.03)\). Variation in penis morphology \( (n = 2) \), see Fig. 20; variation in ovipositor morphology \( (n = 2) \), see Fig. 21. Two specimens have deformed legs: one male lacks tibia and metatarsus on left leg III, one female lacks its metatarsus and has tibia and tarsus shortened on left leg II.

Distribution
Known from two islands (both very close to each other) off the western coast of southern Thailand.

Natural history
Fangensis insulanus, sp. nov. was sifted and hand collected from the floor of a semi-evergreen rain forest (on Phuket Island) and of an old secondary forest adjacent to remnants of primary forest, situated close to the coast (on Siray Island). Most animals were found under pieces of bark at the base of an old tree with moderately developed buttresses. All were collected under very humid conditions in the rainy season. Sifting during dry periods revealed no such opilionids. They appear to be intolerant of dry conditions, as is also the case in congeneric cave-dwelling species.

In captivity, juvenile specimens dug burrows (a few centimetres long) into the soil. When disturbed, they first reacted by rubbing secretion from the ozopore over the posterior portion of the dorsal scutum with their third pair of legs and then ran for shelter in their burrows.

Etymology

Results of phylogenetic analysis based on molecular data
An analysis of all three individual loci and two locus combinations (ribosomal: \( 18S \) rRNA + \( 28S \) rRNA; molecular: \( 18S \) rRNA + \( 28S \) rRNA + \( COI \)) under 12 parameter sets resulted in a preferred parameter set using the incongruence length difference (ILD) values at gap cost of 2 with base transformations costing 1 (Table 3). Individual gene trees obtained under such a parameter set are presented in Fig. 22; trees obtained for different combinations of loci are presented in Fig. 23. With the exception of the \( COI \) data alone, all other analyses show monophyly of Stylocellidae (Figs 22, 23) as well as Pettalidae, but not of Sironidae. With respect to Stylocellidae, the \( 18S \) rRNA analysis finds a jackknife

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Fig. 21. Fangensis insulanus, sp. nov., tips of ovipositors of two female paratypes, ventral view. A, all setae illustrated (specimen from Ko Phuket); B, most setae omitted, insertions of setae on proximoventral plates indicated by circles (specimen from the type locality). Scale bars: 0.1 mm.
support value of 99%, but jackknife support is below 50% for the 28S rRNA dataset (Fig. 22). Both the combined analyses of the ribosomal genes (Fig. 23B) and of all three genes (Fig. 23A) find a jackknife support value for Stylocellidae of 89%.

Monophyly of *Fangensis* is supported by individual analyses of 18S rRNA and 28S rRNA (Fig. 22A,B), but is contradicted by the COI dataset (Fig. 22C). The combined analysis of both ribosomal genes (Fig. 23B) is ambiguous with respect to the monophyly of *Fangensis* and monophyly is rejected when the COI data are added (see discussion below) (Fig. 23A). In all cases, *Fangensis* forms two distinct clades, one composed of the three troglobiomorphic species from northern and western Thailand (*F. leclerci*, *F. cavernarus*, sp. nov., and *F. spelaeus*, sp. nov.) and the other represented by two individuals of *F. insulanus*, sp. nov. from the south of the country. Only the COI dataset alone suggests a different relationship, with the northern/western clade appearing paraphyletic (Fig. 22C). Within the northern/western *Fangensis* clade, all analyses except for COI show a sister-group relationship of *F. cavernarus*, sp. nov. and *F. spelaeus*, sp. nov. Irrespective of what data were used, a jackknife support value above 50% was never found for the genus *Fangensis* as a whole.

**Discussion**

**Taxonomy and relationships**

With the discovery of additional species, the genus *Fangensis* now appears to be sufficiently distinct from *Stylocellus*. This was not the case until quite recently (see Schwendinger et al. 2004: 1432). Monophyly is supported by morphological data and also by a large amount of nuclear ribosomal gene data (Fig. 22A,B). The only dataset that contradicts monophyly of *Fangensis* is that of COI (Fig. 22C), which also contributes to ~77% of the total number of steps in the combined analysis of all data. Hence, it is not surprising that such a tree does not show monophyly of *Fangensis*. Although *Fangensis* does not show high jackknife support in the ribosomal tree analyses, its monophyly is fairly stable to parameter set variation, appearing in 7 out of 12 parameter sets for the combined analysis of the ribosomal genes. The failure of our COI analysis to recover *Fangensis* or Stylocellidae as monophyletic groups is not a total surprise. The best-supported cyphophthalmid node in our analyses, the family Pettalidae (see also Giribet and Boyer 2002), is also not monophyletic in the COI analysis (Fig. 22C), even though its molecular support for the other markers is completely unambiguous (100% jackknife support; present under all parameter sets analysed). In fact, Boyer et al. (2005) recently discussed the odd evolution of COI in Cyphophthalmi, where several instances of insertion/deletion events of amino acids have occurred. When compared to many other arthropods, COI seems to have evolved extremely fast in Cyphophthalmi (S. Boyer and G. Giribet, unpublished data), and therefore we prefer to rely on the ribosomal gene data to justify monophyly of *Fangensis*.

Morphological data support the results above. Probable synapomorphies of *Fangensis* are the Rambla’s organ (a bulged or depressed modified area on the retrolateral side of tarsus IV in males; Figs 4C,G, 9C,G, 14F, 15B, 19C,G) and the pigmented bodies along the prolateral side of each apical lobe of the ovipositor (Figs 6, 11, 16D,E, 21). No other stylocellid species examined so far show this combination of characters. In *Stylocellus silhavyi* Rambla, 1991, from Borneo, males do possess a very similar modified area (with a scaly surface as in *F. leclerci*) on the retrolateral side of their tarsus IV, but it is level with the surface of the tarsus (see Rambla 1991: plate I, figs 1, 2) and not elevated or impressed as the Rambla’s organ of *Fangensis* spp. Furthermore, this species possesses well developed eyes. As the internal struc-

Table 3. Tree length and calculated ILD (incongruence length difference) values for the three individual loci (18S: 18S rRNA; 28S: 28S rRNA; COI: cytochrome c oxidase subunit I) and for the combined analyses of the ribosomal (rib) and all (mol) genes at different parameter set values ranging from 111 (equal weights) to 481 (for gaps:transversions:transitions)

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ture of the ovipositor of *S. silhavyi* is unknown and the presence of eyes may be considered plesiomorphic in the Cyphophthalmi (recently we have observed eyes in several species of the family Pettalidae, including all species within the genera *Pettalus* and *Chileogovea*; eyes are also present in the Indian specimens of yet uncertain affinity reported by Bastawade 1992), this species should be re-evaluated for proper generic placement.

The general absence of eyes (eyespots without cornea present in *F. insulanus, sp. nov.*) in *Fangensis* appears to be a
troglobiomorphic adaptation (reduction), but parallel eye reductions within the Stylocellidae have appeared in the cave-dwelling *Stylocellus globosus* (see Schwendinger et al. 2004: 1432) and in the genus *Miopsalis*. Although some of our trees may suggest that lack of eyes in stylocellids may be the plesiomorphic condition (Fig. 22A), other trees find it homoplastic. Until the exact phylogenetic position of *S. globosus* is evaluated, little can be said about the evolution of eyes in Stylocellidae.

Relationships within the genus *Fangensis* are currently interpreted as (*F. insulanus*, sp. nov. (*F. leclerci* (*F. spelaeus*, sp. nov. + *F. cavernarus*, sp. nov.))). The geographically close *F. spelaeus*, sp. nov. and *F. cavernarus*, sp. nov. appear also phylogenetically most closely linked by three morphological synapomorphies: a striate surface of Rambla’s organ, a distinct ventrodorsal bulge on tibia IV of males and remarkably short hairs on tarsus II, and a Rambla’s organ that is bulging from the surface of tarsus IV. *Fangensis insulanus*, sp. nov. is sister to these three species and shares with them the characteristics of the genus: presence of Rambla’s organ on tarsus IV of males (depressed in *F. insulanus*, sp. nov.) and presence of pigmented bodies in the apical lobes of the ovipositor. The same relationships were revealed by our analysis of ribosomal data (Fig. 22A,B).

In this study, we preferred not to include a morphological matrix owing to the lack of a detailed study of many of the undescribed species included in the molecular analysis. For many of these species, key genital characters remain unknown. We expect to present a comprehensive morphological matrix of stylocellids in the near future, once we thoroughly examined all type specimens and the ~40 undescribed species that we currently have in our collections. At that stage we should be able to test many other hypotheses of stylocellid morphological evolution in addition to *Fangensis* monophyly.

**Biogeography**

*Fangensis* is at present only known from northern and western Thailand. Despite extensive collecting by various biospeleologists, no such opilionids were discovered in caves of peninsular Malaysia and of north-eastern and southern Thailand. It is, however, quite likely that *Fangensis* also occurs in Myanmar, in the vicinity of Thailand’s western border.

As for most other cyphophthalmids, *Fangensis* species appear to have fairly restricted distributional ranges. The widest distribution was found in *F. insulanus*, sp. nov., which was collected from two localities ~18 km apart from each other. As this species requires very humid and shaded conditions, it is probably not able to survive outside natural forests. The other three species are adapted to cave life, show...
troglobiomorphic eye loss and limb extension, and are known only from their type localities. They are probably endemic to individual caves or cave systems.

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