Revisiting *Lepidonella* Yosii (Collembola: Paronellidae): character overview, checklist of world species and reassessment of *Pseudoparonella doveri* Carpenter

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Summary. Characters used in the taxonomy of the genus *Lepidonella* Yosii, 1960 (Collembola: Paronellidae) are listed and discussed. Several new ones are introduced. An overview of pseudopore patterns across Collembola is presented, with several new locations of these structures across Entomobryomorpha. Their interest at different taxonomic level is underlined. The genus *Lepidonella* is redefined. The American species *L. marimuti* Soto Adames & Bellini, 2015 is placed in *incertae sedis* among *Lepidonella*. *Lepidonella* species of the world are listed with synonymies and combinations. The Malaysian troglotic species *Pseudoparonella doveri* Carpenter, 1933 is redescribed in detail, with emphasis on its pattern of antennal chaetae, and transferred to the genus *Lepidonella*. Its close similarity with *L. lecongkieti* Deharveng & Bedos, 1995 from southwestern Vietnam caves is underlined. This disjunct distribution is briefly discussed.

Résumé. Revue du genre *Lepidonella* Yosii (Collembola : Paronellidae) : caractères, liste critique des espèces du monde et ré-assignation de *Pseudoparonella doveri* Carpenter. Les caractères utilisés dans la taxonomie du genre *Lepidonella* Yosii, 1960 (Collembola : Paronellidae) sont répertoriés et discutés. Plusieurs nouveaux caractères sont décrits. Une synthèse des patrons de distribution des pseudopores dans la classe des Collembolés est présentée, avec la mise en évidence de nouvelles localisations de ces structures au sein des Entomobryomorpha. Leur intérêt à différents niveaux taxonomiques est souligné. Le genre *Lepidonella* est redéfini. L'espèce américaine *L. marimuti* Soto Adames & Bellini, 2015 est placée en *incertae sedis* au sein du genre *Lepidonella*. Les espèces de *Lepidonella* du monde sont listées avec synonymies et combinaisons. L'espèce troglotique de Malaisie *Pseudoparonella doveri* Carpenter, 1933 est redécrite en détail, en insistant sur son patron de soies antennaires, et transférée dans le genre *Lepidonella*. Son étroite similarité avec *L. lecongkieti* Deharveng & Bedos, 1995 des grottes du sud-ouest du Vietnam est soulignée. Cette distribution disjointe est brièvement commentée.

Keywords: Taxonomy; checklist; chaetal types; pseudopores; cave fauna

Carpenter (1933) described a remarkable new species of Paronellidae from the Batu Caves in Selangor (Malaysia), *Pseudoparonella doveri*, characterized in its original description by elongate appendages and claws, and lacking eyes (in fact, it has 3 + 3 small eyes, see below). It was at that time the most troglomorphic species of springtails known from Southeast Asia. He assigned it to the genus *Pseudoparonella* Handschin, 1925 on the basis of its short bidentate mucro. Yoshii (1981, 1983) did not accept this assignment, and considered the species as *incertae sedis*. Deharveng (1987, 1988) placed the species in *Troglopedetes* Absolon, 1907 following the redefinition of the genus by Palacios-Vargas et al. (1985). Mitra (1993, 2002) assigned *P. doveri* to the genus *Microparonella* Carpenter, 1916, which he had redefined. *Microparonella* was shown to be a synonym of *Troglopedetes* to which its type species clearly belongs (Deharveng & Bedos 1995), but these authors did not

reassess the taxonomic position of *P. doveri* in this context, which remains therefore uncertain.

With the current acceleration of researches on cave Collembola in Southeast Asia, it is increasingly important for biogeographic knowledge of the region to better place this species taxonomically, which remains the most troglomorphic of Southeast Asia Collembola. We had the opportunity to examine a few specimens of *Pseudoparonella doveri* from the Batu Caves given by Max Moseley and Liz Price, and a paralectotype of the species from the Natural History Museum (NHM) in London. Comparing our specimens to the original description of *Paronella appendiculata* (Schött, 1917), type species of the genus *Pseudoparonella* (Ellis & Bellinger 1973), led us to the conclusion that “*Pseudoparonella doveri*” is not a member of the genus *Pseudoparonella*, in agreement with the authors cited above. The species is neither a *Troglopedetes* as currently understood, as its

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fourth antennal segment is not subdivided. Its inclusion in the genus *Microparonella* has to be abandoned as the genus was found to be based on a species of *Troglopedetes* (Deharveng & Bedos 1995). The short mucro and presence of only two trichobothria on Abd. IV exclude *doveri* from *Cyphoderopsis* Carpenter, 1917 or *Trogolaphysa* Mills, 1938 as well (Thibaud & Najt 1988; Jantarit et al. 2013; Soto-Adames et al. 2014). Conversely, it matches the most recent definition of the genus *Lepidonella* Yosii, 1960 (Deharveng & Bedos 1995; Soto-Adames & Bellini 2015; Bellini & Cipola 2017), except for its reduced eye number, a well-known adaptive character among cave-obligate species.

In this paper, several new or rarely used taxonomical characters are introduced for the taxonomy of *Lepidonella* and Paronellidae. The genus *Lepidonella* is rediagnosed, and a list of its species is given. *Pseudoparonella doveri* is transferred to the genus *Lepidonella*, and redescribed in detail. Its affinities with *L. lecongkietii* Deharveng & Bedos, 1995 from southern Vietnam are emphasized.

Material and methods

The examined specimens include a slide of a paralectotype borrowed from the London NHM and six specimens collected in the Batu Caves by Max Moseley and Liz Price. These last specimens in alcohol were examined and photographed under a Leica (Wetzlar, Germany) MZ16 stereomicroscope, then mounted on slides in Marc Andre II after clearing in lactic acid. Morphological characters were observed and drawn using a Leica DMLB microscope with Differential Interference Contrast (DIC). Photographs were taken with a Jenoptik (Jena, Germany) ProgRes C10+ camera mounted on the microscope. Figures including photos were improved with Photoshop Elements v9 (Adobe Inc., San José, USA).

Abbreviations used in the descriptions

Abd. = abdominal segment; Ant. = antennal segment; mac = macrochaeta; mes = mesochaeta; mic = microchaeta; ms or s-microchaeta = microsensillum auct.; omma = ommatidium, -ia; psp = pseudopore; Scxa = furcal anterior subcoxa; sens or s-chaeta = sensillum or sensory seta auct.; tric = trichobothrium; Th. = thoracic segment; Tita = tibiotarsus.

Nomenclature

We follow Yoshii (1982) for the nomenclature of various morphological structures, Zhang et al. (2016) for clypeal chaetotaxy and Fjellberg (1999) for labial palp. We use the notation of Gisin (1967) for labium basis, with upper case letter for ciliated chaetae, lower case letter for smooth chaetae; we use brackets for mic.

Regarding chaetal categories, the term S-chaeta (Deharveng 1983) is preferred to the term sensillum, considering that a chaeta is best defined as the external part of a sensillum, which is a composite organ. The term chaeta is used instead of seta for coherence with the widely used term “chaetotaxy”, and macrochaeta, microchaeta instead of macroseta, microseta for etymological coherence (chaeta is a Greek root, like macro and micro, while seta is a Latin root). For

dorsal chaetotaxy, we rely (but see below) on the nomenclatures of Szeptycki (1979), Mitra (1993) and Soto-Adames & Bellini (2015). We used most characters listed in Soto-Adames et al. (2014), with some additional ones. The formula of dorsal macrochaetae and trichobothria are given by half-tergite from head to Abd. IV; mac along peri-antennal area, anterior rows of mac on Th. II, lateral mac of Abd. IV and mac of Abd. V–VI are not included in the formula. S-chaetae formulae are given separately for ms and for s, by half-tergite from Th. II to Abd. V.

Most chaetae had fallen during clearing and mounting processes. Sockets of scales can often be distinguished from those of chaetae on slide specimens of Entomobryoidea, but this was not that easy on the few available specimens of *L. doveri*, and we were not able to reconstruct reliably the dorsal chaetotaxic pattern of mesochaetae as thoroughly analyzed by Soto-Adames & Bellini (2015).

Results

Morphological characters

Below we list and comment on some important morphological characters for the taxonomy of *Lepidonella*. Several are newly introduced characters, and a few are overlooked features drawn from various papers of Yoshii (mostly, 1981, 1982).

Pseudopores

Figure 2. Pseudopores were first discovered by Gisin (1963) on tergites and coxae I and II of Entomobryidae, then distally on manubrium (Gisin 1964). Later on, they were observed in other locations in Isotomidae (Deharveng 1979), Poduromorpha (Deharveng 1983), Entomobryidae (Lukic et al. 2015) and Tomoceridae (Yu et al. 2014). In fact, they are also present in other locations not mentioned in the literature, as listed below for *Lepidonella doveri*:

- (1) Apically on antennal segments II and III, probably firstly mentioned on Ant. III of *Paronella vivieni* Barra, 1969 by Barra (1969). Christiansen & Reddell (1986) call them lenticular organs. Bellini & Cipola (2017) mention a “discrete shallow subapical organite on Ant. IV” that we have not observed in other Entomobryoidea so far, which is perhaps a pseudopore.
- (2) Externally to antennal basis on head in the peri-antennal area (initially mentioned in Neanuridae, Deharveng 1983).
- (3) Externally on coxae I, II and III [initially mentioned by Hühner (1962) as “chitinringe”, and by Gisin (1963)].
- (4) On manubrium between its basis and the genital plate, probably those observed in *Coecobrya* by Zhang & Dong (2014) and Zhang et al. (2018), as a group of 2–3 in *L. doveri*.

- (5) Dorsodistally on manubrium (initially mentioned in Gisin 1964).
- (6) Basally on dentes (new location, observed in many Entomobryidae).
- (7) Laterally on Abd IV along anterior subcoxa margin, already mentioned in Mateos & Greenslade (2015) in several Lepidocyrtinae.
- (8) Dorsally, 1 + 1 on each tergite from Th. II to Abd. IV (present in all Entomobryoidea, all Tomoceridae, and probably Isotomidae).

The line of pseudopores located behind the posterior line of chaetae on Abd. IV tergite in *Troglopedetes* Absolon, 1907 (Deharveng 1988), *Cyphoderopsis* Carpenter, 1917 (Jantarit et al. 2013), *Trogolaphysa* Mills, 1938 (Soto-Adames & Taylor 2013) and *Cyphoderus* Nicolet, 1842 (Jantarit et al. 2014) has not been observed in *L. doveri* and in *L. lecongkieti* and is not reported in other species of the genus (Zeppelini & Oliveira 2016). The presence of these pseudopores is a strong putative synapomorphy of (Troglopedetinae + Cyphoderidae), that separates them from other Paronellidae and Entomobryidae.

In five other locations where pseudopores may be present in some Entomobryoidea, they were not detected in *Lepidonella*, due to unfavorable preparations or real absence: (i) anterointernally on the peri-antennal area of head (figured in Jantarit et al. 2014, p. 7); (ii) apically on Ant. I (Lukic et al. 2015); (iii) on thoracic sternites (observed in *Lepidocyrtus* sp., unpublished); (iv) between tenaculum and ventral tube (observed in *Lepidocyrtus* sp. and *Cyphoderus* sp., unpublished); and (v) on the central part of Abd. IV tergite in *Lepidocyrtus curvicolis* Bourlet, 1839, as figured by Mateos (2008). A large number of pseudopores are at least present on the manubrium of Tomoceridae (Yu et al. 2014), that have never been observed in *Lepidonella*, nor in other Entomobryomorpha. Evidence is therefore increasing that these tiny pseudopores have diversified distribution patterns that provide (or may provide) powerful characters at all taxonomic levels.

Eyes arrangement. When the complete set of eyes (8 + 8) is present, they may be arranged as two main different patterns in Entomobryoidea: either in two parallel lines with omma G anterior to or at level of F (most atmobiotic Paronellidae s. l.), or in a compact group, with G posterior to F. This last pattern is the only one reported in *Lepidonella* and known in soil Paronellidae (*Paronella* spp., *Trogolaphysa* spp.).

Ventral complex of labrum. Figure 3D. The presence of two slightly asymmetrical multi-toothed combs as described here for *L. doveri* has been already reported in a number of Entomobryoidea, for instance by Rusek (1971) in *Willowsia nigromaculata* (Lubbock, 1873) and in *Cyphoderus asiaticus* Yosii, 1959; by Palacios-Vargas

et al. (1985) in *Trogolaphysa* spp.; by Yoshii (1982) in *Acrocyrtus heterolepis* (Yosii, 1959); Gruia (1984) in *Pseudosinella* (*Plumosinella*) *kenchristianseni* Gruia, 1984; Deharveng & Gouze (1986) in *Pseudosinella cabidochei* Deharveng & Gouze, 1986; and Jantarit et al. (2014) in *Cyphoderus* spp. These combs are also present in the Hypogastruridae *Triacanthella madiba* Janion, D'Haese & Deharveng, 2012 (Janion et al. 2012) and in several Isotomidae (Fjellberg 1979). They are associated in many (all?) species with a pair of thin, sinuous, unequal tubules (that we propose to name tongues), located side by side, which are however not mentioned in most cited cases. They show low inter-specific and inter-generic variations among Entomobryoidea. Conversely, they are more or less reduced in Isotomidae where a distal brush, never found in Entomobryoidea, tends to develop between the combs and the distal edge of the labrum (Fjellberg 1979; Potapov 2001); in the few studied Tomoceridae where this labral part is described, only the distal brush is clearly seen (Lukic et al. 2010).

Labium basis. Figures 3A, 4A, B. The succession of ciliated/smooth chaetae along the proximal edge of labium basis is widely used to separate species of Entomobryoidea following Gisin (1967). In *L. doveri*, on 4 specimens examined, chaeta M2 was asymmetrical in one specimen (ciliated/smooth), and some variability has often been reported in chaetae M of various species in the literature. This character should therefore be used cautiously as a diagnostic character. Chaeta L2 is similar in size to L1 in *L. doveri*, as well as in most species of Entomobryoidea, whereas it is reduced to a minute mic in *Troglopedetes* (Deharveng 1988), *Cyphoderopsis* (Jantarit et al. 2013) and *Campylothorax* (Mari Mutt, 1987). Labium basis chaetotaxy may therefore provide interesting generic or supra-specific characters in Paronellidae s. l., though information is still lacking for a large number of species.

Maxillary outer lobe. Figure 3C. The number of sublobal hairs is known in only 5 species of *Lepidonella*. In the two cave species *L. doveri* and *L. lecongkieti*, there are 4 hairs, of which one is much smaller than the others. In *L. nigrofasciata* (Handschin, 1928) and *L. oudemansi* (Yoshii, 1983), there are 3 subequal hairs, but the fourth minute additional hair observed in the above species may have been overlooked. The American species *L. zeppelinii* Soto-Adames & Bellini, 2015 departs from the previous four Asian species in having only two sublobal hairs (Soto-Adames & Bellini 2015), a number frequent among other Paronellidae s. l. Conversely, the presence of 4 sublobal hairs including one much smaller than others is retrieved in Entomobryidae like *Entomobrya nivalis* (Linnaeus, 1758) after Fjellberg (2007), *Pseudosinella argentea* Folsom, 1902 after Soto-Adames (2010), or in

Verhoeffiella absoloni Kseneman, 1938 after Lukic et al. (2015).

Complete dorsal chaetotaxy. Dorsal chaetotaxy has been analyzed in detail by Soto-Adames & Bellini (2015) for the South American species *L. zeppelinii* but is unknown in other species of the genus. Only macrochaetotaxy and S-chaetotaxy are described here for *L. doveri*, as the state of available slides were too poor to allow a detailed description of their chaetotaxy.

Femoral organ. Femoral organ is a group of modified chaetae, thick, subcylindrical and rather short, located on the femur of leg III. It is the main diagnostic character which separates *Lepidonella* (without femoral organ) from *Bromacanthus* Schött, 1925 (with femoral organ) according to Mitra (2003). In *L. nigrofasciata*, Yoshii (1983) figures a rather dense group of chaetae in the place of the femoral organ, that he did not consider to represent the femoral organ itself, as chaetae were not morphologically modified. Femoral organ is absent in *L. doveri* and in *L. lecongkieti* (unpublished data), supporting their inclusion in *Lepidonella* rather than in *Bromacanthus*.

Filamentous organ. The presence of filamentous organs laterally on Abd. III has been observed in several poorly delimited genera of Lepidocyrtinae (Yoshii 1982, p. 34; Yoshii & Suhardjono 1989, 1992; Mateos & Greenslade 2015). Surprisingly, these organs are also present in *L. doveri* and in *L. lecongkieti*, at the same place as in the species of “*Ascocyrtus* (*Cinctocyrtus*)” Yoshii & Suhardjono, 1989 cited in Yoshii & Suhardjono (1992). In *L. lecongkieti*, they are constituted by a tuft of very long chaetae (up to 450 µm) inserted laterally on Abd. III. In *L. doveri*, only the sockets of these chaetae were visible. In both species, the filamentous organ was seen in a few specimens only.

Coxal complex. Figure 8G, H, I. The coxal pattern of mac and psp seems to be rather stable across many Entomobryoidea, and that of *Lepidonella doveri* is quite similar to those described for *Heteromurtrella puertoricensis* Mari-Mutt, 1979 (Mari-Mutt 1979), *Lepidocyrtus flexicollis* Gisin, 1965 (Mateos 2008), and *Verhoeffiella absoloni* Kseneman, 1938 (Lukic et al. 2015) for instance.

Claw complex. Figure 8D, E, F. In most *Lepidonella*, the unguiculus is clearly truncated, with four exceptions: *L. doveri* and *L. lecongkieti*, which are the only cave species in the genus, and *L. subcarpenteri* Denis, 1948 and *L. zeppelinii*. This last species is the only representative of the genus in America and departs by several characters from other *Lepidonella*. A re-examination of *L. subcarpenteri* is needed, in order to re-evaluate the taxonomic value and evolutionary significance of unguiculus morphology.

Ventral tube morphology. Ventral tube is long, slightly longer than head in *L. lecongkieti*, *L. doveri* and

undescribed species of Southeast Asia, and relatively longer in cave than in soil species. Its apical part is a large exsertile vesicle *sensu* Willem (1900) [= terminal tubule in Yoshii (1981)], a structure often well developed in Paronellidae *s. l.* It is mentioned and figured under the name “protrusible sac” by Carpenter (1916) in the description of the genus *Microparonella* and of *Lepidonella flava* (Carpenter, 1916). The protrusible structure is smooth, subdivided in two paired parts and oriented obliquely forward, towards the mouth, in the examined species of *Lepidonella* preserved in ethanol, with anterior diverticule reduced to a short swelling.

Multiplets on dens. Figure 10B, C. The arrangement of chaetae in multiplets is well known on Th. II of many Entomobryoidea [multiplets *sensu* Szeptycki (1979)]. In *L. doveri* and in *L. lecongkieti* scales are arranged in a similar way on dentes (Deharveng & Bedos 1995), as it is also observed on the dens of *Cyphoderopsis* spp. (Jantarit et al. 2013). This pattern, though less obvious, also exists in some Lepidocyrtinae, like *Pseudosinella* (*Plumosinella*) *kenchristianseni* (Gruia 1984).

Lateral organ of Abd. V–VI. The lateral organ of Yoshii (1989) is a conspicuous invaginate paired structure located on each side at the joint between Abd. V and Abd. VI of several Entomobryidae. It is absent in *Lepidonella* and has not been reported so far among Paronellidae *s. l.*, but was observed in *Callyntrura* sp. (unpublished).

Taxonomy

Family Paronellidae Börner, 1906

(*sensu* Absolon & Kseneman, 1942)

Subfamily Bromacanthinae Mitra, 1993

(*sensu* Bromacanthini Mitra, 1993)

Genus *Lepidonella* Yosii, 1960

Type species: *Lepidonella tokiokai* Yosii, 1960 (Bougainville in Solomon Islands)

Diagnosis of the genus (*: character known in the type species)

Similar to Lepidocyrtinae in body shape, at least for smallest species. Medium to large size (1–2.7 mm)*. Head perpendicular to body in specimens stored in alcohol*. Body curvature well marked at level of the middle or posterior part of Th. III, Th. II not protruded*. Dark pigment present as patches on the body (soil species)*, or body unpigmented or very lightly and uniformly pigmented (cave species). Flexed-cross mac absent. Scales present on the body*, present dorsally on Ant. I*, on Ant. I–II or absent, and present on furca at least ventrally. Scales finely and uniformly sculptured, hyaline to slightly beige, rounded to oval. Omma 3 + 3 to 8 + 8*. Extra-ocular structure *sensu* Mitra (1972) absent. Labrum

granulated area with anterior U-shape indentation*. Maxillary outer lobe with 3 or 4 sublobal hairs (2 in *L. zeppelinii*). Antennae shorter (surface species) or longer (cave species) than body; first segment shorter than head. Fourth antennal segment neither subdivided nor annulated, without apical bulb* (except in *L. marimuti*). Metafemoral organ absent*. Trochanteral organ well developed*. Posterior row of mes present on head*. Macrochaetotaxy very reduced on head and body*. Trichobothrial pattern as 1/0,0/0,2,3,2. Trichobothrial complexes well differentiated, with short and strongly enlarged mes. Filamentous organ present in *L. doveri* and *L. lecongkietii*, unknown in other species. Posterior line of pseudopores absent on Abd. IV. Lateral organ absent at the suture of Abd. V–VI. Manubrial spines absent. Two longitudinal rows of numerous spines on dentes (23–110)*. Distal lobe and enlarged distal chaetae on dens absent. Mucro plump, short, with 3–4 teeth*, apically inserted on dens.

Note

The type species of the genus, *Lepidonella tokiokai*, was described from Solomon Islands on a single specimen. It has never been revised since its original description, which is globally accurate. The state of many of the characters subsequently introduced, e.g. pseudopore distribution, is however unknown in this species as well as in most other species of *Lepidonella*. Compared to previous definitions of the genus (Carpenter 1916; Deharveng & Bedos 1995; Mitra 2003; Soto-Adames & Bellini 2015), the main changes in the current diagnosis concerns eye number that may be as few as 3 + 3, pigmentation which may vary from large dark patches to uniformly white, and antenna length which may vary from shorter to longer than body. Several characters newly introduced need to be checked on a larger number of species. Dorsal chaetotaxy of *Lepidonella* is “complete or almost complete” according to Soto-Adames & Bellini (2015, p. 31). However, this observation concerns only two species, of which one is *incertae sedis* (*L. marimuti* from Antillas), and the other one, *L. zeppelinii* from Brazil, is the only other species known from America which departs from its congeners by the reduced chaetotaxy of its maxillary outer lobe. No information on dorsal chaetotaxy is available for *Lepidonella* of Southeast Asia and Australasia.

List of species of *Lepidonella* in the current definition of the genus

Complete references for the current species of *Lepidonella* as well as those which have been previously considered as *Lepidonella* but are now placed in other genera are drawn from the unpublished lists of Bellinger et al. (1996–2017). We selected here the most significant citations, i.e. new combinations, or additional distribution data. All citations

from the works of Deharveng & Bedos (1995), Mitra (2003) and Soto-Adames & Bellini (2015) are included. Later references include citations giving additional locations or new combinations, and those in the recent review of the genus by Soto-Adames & Bellini (2015). Complete reports of species citations anterior to 2007 or 2015, depending on species, may be found on the web (Bellinger et al. 1996–2017).

Lepidonella annulicornis (Oudemans, 1891)

Sira annulicornis Oudemans 1891: 87 (Java)
Seira annulicornis in von Dalla Torre 1895: 12 (“Am. insulae”)
Paronella (Sira) annulicornis in Schäffer 1898: 409 (n. comb.)
Paronella annulicornis in Schött 1901: 329 (n. comb.); Denis 1933: 267 (Sunda islands, India); Absolon & Kseneman 1942: 25 (Sumatra); Denis 1948: 281 (Vietnam)
Callyntrura annulicornis in Yosii 1966a: 50 (n. comb., sp. inquirenda); Yosii 1966b: 377 (Java)
Microparonella annulicornis in Yoshii 1981: 38 (n. comb.); Yoshii & Greenslade, 1993: 76 (Sulawesi)
Lepidonella annulicornis in Mitra 1992: 212 (n. comb.); Deharveng & Bedos 1995: 22 (erroneously given as n. comb.); Mitra 2003: 80 (erroneously given as n. comb.); Soto-Adames & Bellini 2015: 337

The Oudemans paper is dated 1890–1891. We therefore quote it as 1891. The report from India by Denis (1933) is probably a mistranslation of “Ost Indies” (nowadays Indonesia) from the title of the paper of Oudemans (1891). The record of the species from “Am. insulae” (American insulae) by von Dalla Torre (1895) is a geographical misplacement, as the species has never been recorded in America. The record of the species from India by Denis (1933) is also a geographical misplacement: the author probably misunderstood the title of Oudemans (1891) paper as referring to India, having overlooked that the species was described from Java.

Lepidonella ceylonica (Yosii, 1966)

Microparonella ceylonica Yosii 1966b: 378 (Sri Lanka)
Lepidonella ceylonica in Mitra 1993 (n. comb.): 86; Deharveng & Bedos 1995: 22 (erroneously given as n. comb.); Mitra 2003: 80 (erroneously given as n. comb.); Soto-Adames & Bellini 2015: 337

Lepidonella doveri (Carpenter, 1933)

Pseudoparonella doveri Carpenter 1933: 220 (Malaysia); Absolon & Kseneman 1942: 23; Moseley 2004: 81
Troglopedetes doveri in Deharveng 1987: 167 as n. comb.; Deharveng 1988: 97; Fanciulli et al. 2003: 203
?Microparonella doveri in Yoshii 1981: 41; Yoshii 1983: 11 (as *incertae sedis*)
Microparonella doveri in Mitra 1993: 54 (n. comb., without justification); Mitra 2002: 70 (n. comb., with justification)

Lepidonella duodecimoculata (Prabhoo, 1971)

Microparonella duodecimoculata Prabhoo 1971: 43 (India)

Lepidonella duodecimoculata in Deharveng & Bedos 1995: 22 (n. comb.); Soto-Adames & Bellini 2015: 337

***Lepidonella flava* (Carpenter, 1916)**

Microparonella flava Carpenter 1916: 44 (Seychelles)
Syn. *Paronella seychellesiensis* Salmon 1964: 545 (replacement name)
Microparonella seychellensis in Yoshii 1981: 38 (misspelling for *seychellesiensis* Salmon 1964)
Lepidonella flava in Deharveng & Bedos 1995: 22 (n. comb.); Soto-Adames & Bellini 2015: 337

Paronella seychellesiensis was proposed as a replacement name for *flava* by Salmon (1964) as a result of the synonymy of *Microparonella* with *Paronella* Schött, 1893, which already included the species *Paronella flava* Carpenter, 1916 described from Myanmar. However, the transfer of *P. seychellesiensis* (= *M. flava*) into the genus *Lepidonella* led to the decision being reversed and *P. seychellesiensis* being synonymized with *Lepidonella flava* (Deharveng & Bedos 1995).

***Lepidonella incerta* (Handschin, 1925)**

Pseudoparonella incerta Handschin 1925: 255 (Sumatra)
Microparonella incerta in Yoshii 1983: 11 (n. comb.)
Lepidonella incerta in Deharveng & Bedos 1995: 22 (n. comb.); Mitra 2003: 80 (erroneously given as n. comb.); Soto-Adames & Bellini 2015: 337

According to Soto-Adames & Bellini (2015, p. 337), “the original species description is very brief, and the color pattern described suggests that *L. incerta* may be a senior synonym of *L. oudemansi*.”

***Lepidonella kei* (Yoshii & Suhardjono, 1992)**

Microparonella kei Yoshii & Suhardjono 1992: 47 (Kei Island, Indonesia)
Lepidonella kei in Deharveng & Bedos 1995: 22 (n. comb.); Soto-Adames & Bellini 2015: 337

***Lepidonella lecongkieti* Deharveng & Bedos, 1995**

Lepidonella lecongkieti Deharveng & Bedos 1995: 23 (Vietnam)
Lepidonella lecongkieti in Soto-Adames & Bellini 2015: 337

***Lepidonella nigrofasciata* (Handschin, 1928)**

Pseudoparonella nigrofasciata Handschin 1928: 262 (Java)
Handschinella nigrofasciata in Yosii 1966a: 50 (n. comb.)
Bromacanthus nigrofasciatus in Yoshii 1981: 41 (incertae sedis)
Microparonella nigrofasciata in Yoshii 1983: 8 (n. comb.)
Lepidonella nigrofasciata in Deharveng & Bedos 1995: 22 (n. comb.); Mitra 2003: 80 (erroneously given as n. comb.); Soto-Adames & Bellini 2015: 337

***Lepidonella oudemansi* (Yoshii, 1983)**

Microparonella oudemansi Yoshii 1983: 7 (Malaysia)
Lepidonella oudemansi in Deharveng & Bedos 1995: 22 (n. comb.); Mitra 2003: 80 (erroneously given as n. comb.); Soto-Adames & Bellini 2015: 337

The color pattern of *L. oudemansi* recalls that of *L. incerta*. Soto-Adames & Bellini (2015: 337) consider on this basis that the two species might be synonyms.

***Lepidonella papuana* (Womersley, 1937)**

Pseudoparonella papuanus Womersley 1937: 208 (Papua New Guinea)
Lepidonella papuanus in Mitra 2003: 82 (holotype examined, n. comb.)

The assignation of this species to *Lepidonella* by Mitra (2003) was overlooked in Deharveng & Bedos (1995) and Soto-Adames & Bellini (2015).

***Lepidonella picta* (Schäffer, 1898)**

Paronella picta Schäffer 1898: 410 (Papua New Guinea: New Britain)
Lepidonella picta in Mitra 1992: 212 (n. comb.); Mitra 2003: 74, 80 (Solomon Islands) (erroneously given as n. comb.)

This species was overlooked in the lists of Deharveng & Bedos (1995) and Soto-Adames & Bellini (2015).

***Lepidonella subcarpenteri* (Denis, 1948)**

Paronella subcarpenteri Denis 1948: 279 (Vietnam, Cambodia)
Microparonella subcarpenteri in Yosii 1966b: 379 (n. comb.)
Lepidonella subcarpenteri in Mitra 1993: 86 (n. comb.); Deharveng & Bedos 1995: 22 (erroneously given as n. comb.); Mitra 2003: 80 (erroneously given as n. comb.); Soto-Adames & Bellini 2015: 337

***Lepidonella tokiokai* Yosii, 1960**

Lepidonella tokiokai Yosii 1960: 33 (Solomon Islands); Soto-Adames & Bellini 2015: 337
Microparonella tokiokai in Yoshii 1981: 37 (n. comb.); Greenslade 1994: 105 (Australia)

The incorporation of the genus *Lepidonella* into *Microparonella* by Yoshii (1981) implied the transfer of its type species, *L. tokiokai*, to *Microparonella*, though the species itself was not cited in the paper.

***Lepidonella zeppelinii* Soto-Adames & Bellini, 2015**

Lepidonella zeppelinii Soto-Adames & Bellini 2015: 332 (Brazil).

The presence of two sublobal hairs on the maxillary palp (Soto-Adames & Bellini 2015, p. 333) separates this American species from the four Asian species in which this character is known.

Incertae sedis

***Lepidonella marimuti* Soto-Adames & Bellini, 2015**

Microparonella incerta Mari-Mutt 1987: 404 (Puerto Rico), *nec* Handschin 1925: 255 (Sumatra).

Lepidonella marimuti Soto-Adames & Bellini 2015: 337 (US Virgin Islands, Dominican Republic) (Replacement name)

?*Microparonella incerta* in Deharveng & Bedos 1995: 22 (*incertae sedis*)

Yoshii (1983, p. 11) placed *Pseudoparonella incerta* Handschin in the genus *Microparonella*. Hence, the species described as *Microparonella incerta* by Mari-Mutt (1987) was a homonym and should have been renamed. Deharveng & Bedos (1995), having shown that *Microparonella* was a synonym of *Lepidonella*, placed *incerta* Handschin in this last genus, but they mentioned that there was a doubt (underlined below) about the assignation of *incerta* Mari-Mutt to *Lepidonella*: “*Microparonella incerta* Mari Mutt, 1987 (Puerto Rico), s’il s’agit bien d’un *Lepidonella*, devient un homonyme junior de *L. incerta* (Handschin, 1925)”. Actually, as stressed by Soto-Adames & Bellini (2015), *L. marimuti* is very isolated within *Lepidonella*, by its apical bulb on Ant. IV and its tridentate mucro, but also by the presence of several ciliated labral chaetae, and hardly modified accessory chaetae of its trichobothrial complexes. Apical bulb on Ant. IV has a high taxonomic value given its distribution among suprageneric taxa in most Entomobryoidea (except in *Lepidocyrtus* s. l. and *Pseudosinella*, notoriously known to be phylogenetically heterogeneous). On these grounds, *L. marimuti* is considered here as *incertae sedis*. Description or redescription of more Southeast Asia species of the genus would be necessary to validate these conclusions.

Species transferred to *Trogolaphysa*

Because of the presence of three trichobothria on Abd. IV, two species placed in *Lepidonella* by Deharveng & Bedos (1995) were transferred to the genus *Trogolaphysa* by Soto-Adames & Bellini (2015).

***Trogolaphysa monomaculata* (Barra, 1969)**

Paronella (*Microparonella*) *monomaculata* Barra 1969: 212 (Gabon)
Lepidonella monomaculata in Deharveng & Bedos 1995: 22 (n. comb.)

Trogolaphysa monomaculata in Soto-Adames & Bellini 2015: 337 (n. comb.)

***Trogolaphysa vivieni* (Barra, 1969)**

Paronella (*Microparonella*) *vivieni* Barra 1969: 207 (Gabon)

Lepidonella vivieni in Deharveng & Bedos 1995: 22 (n. comb.)
Trogolaphysa vivieni in Soto-Adames & Bellini 2015: 337 (n. comb.)

Redescription of *Lepidonella doveri* (Carpenter, 1933)

Type locality. Malaysia: Selangor: Gombak: Batu Caves: Dark Cave (X = 101.684132°; Y = 3.237908°; alt = 85 m).

Type material. The species was described based on several specimens according to Carpenter (1933): “Selangor: Batu Cave; several, July 1926; in side passage, Dark Cave, swimming in large numbers on stream, coll. C. Dover, 10 September 1926”. Mitra (2002) mentions having seen one lectotype and one paralectotype in his review of the genus *Microparonella*. We examined a single type specimen (to be considered as a paralectotype) from the Natural History Museum of London, labeled “Batu Caves, Selangor, Malaysia, July 1926, BM1934-80”.

Material examined (all from type locality). One type specimen on slide from the NHM (London).

One specimen on slides (dissected), 14.VI.2003, Max Moseley leg. (MAL-CMM309).

One specimen on slide, 2.VII.2003, by hand, Max Moseley leg. (MAL-CMM310).

Two specimens on slides (dissected) including one male, 4.VII.2003, cave, by hand, Max Moseley leg. (MAL-CMM318).

Two females on slides (dissected), chamber D, 21.VIII.2003, by hand, Liz Price leg. (MAL-Liz01).

Description.

Habitus. Figure 1A, C. Length: 2.3–2.7 mm. Color: pale yellow according to original description; specimens in ethanol whitish with very small, almost inconspicuous microdots of bluish grey pigment especially behind eye spots; 2 or 3 small black separated eye patches on each side with 3 ommata (Figure 1D). Extraocular structure *sensu* Mitra (1972) absent. Slender, with elongate legs, furca and antennae. In lateral view, head down perpendicularly to the body. Body strongly bent at the level of Th. II but not humped, straight backwards or slightly arched at the level of Th. III–Abd. II (Figure 1A, C). Th. II more than 1.5 as long as Th. III; Abd. IV about 4 times longer than Abd. III (Figure 1A).

Pseudopores. Figure 2. Pseudopores present as round flat disks, larger than mac sockets on various parts of the body: antennae, head, tergites, coxae, manubrium and dens. On antennae, psp located ventroapically between the tip of antennal segments and the chaetae of the apical row, or just below apical row of chaetae (absent or not detected on Ant. I, 1 on Ant. II and 2 on Ant. III). On head, 1 or 2 psp located externally on peri-antennal area, difficult to observe. On tergites, 1 + 1 psp close to the axis from Th. II to Abd. IV, and a file of 4 conspicuous psp on Abd. IV along the suture

Figure 1. *Lepidonella*, photos (A, B, C, stereomicroscope; D, microscope). A, habitus of *L. doveri* (asymmetrical antennae); B, habitus of *L. leongkietii*; C, anterior part of *L. doveri*; D, anterior part of head and ocular patches of *L. doveri*, with recognized sockets marked in black. Scales: 1 mm (A, B); 0.5 mm (C); 0.1 mm (D).

with the anterior furcal subcoxa. Coxae I, II and III with 2–(3), 3–(4) and 1–2 psp respectively, located close to longitudinal rows of chaetae described below. On manubrium, 3 dorsobasal psp close to genital plate and 2 + 2 apical ones. Dens dorsally with a line of 4 psp on the proximal third.

Chaetae. More detail later in the description of antennae, tergites, legs and furca. Ordinary chaetae differentiated into ciliated to serrated mac and mes, some enlarged and modified (in trichobothrial complexes), smooth mes (distally on Tita), smooth pointed mic (on Ant. I, on pretarsus and on anal valves), and weakly ciliated mic (on Tita and femora). Mac ill-differentiated from large mes on Abd. IV. S-chaetae of various morphologies. Dense cover of overlapping scales on head and body. Scales present on Ant. I–II, on manubrium and dentes, absent on legs and ventral tube. Scales roundish or oval, never pointed, of variable size, hyaline, adorned with many minute spicules in irregular lines. Two types of S-chaetae on tergites, like in other Entomobryoidea (more details in Zhang & Deharveng 2015): ms (S-chaetae type 1 in Jantarit et al. 2013; or microsensillum in Soto-Adames et al.

2014) short, opaque, pointed and S (S-chaetae type 2 in Jantarit et al. 2013; lateral sensillum in Soto-Adames et al. 2014) slightly longer, thinner, rod-like, hyaline. Dorsal macrochaetae: 0/0,0/0,0,(3),2

Trichobothrial pattern: 1/0,0/0,2,3,2 by half tergite.

Mouthparts. Figures 3, 4. Clypeal area (Figure 3F) with 12 chaetae (and an extra-chaeta asymmetrically in the examined specimen), not matching exactly any of the patterns described in Zhang et al. (2016), but close to that of *L. nigrofasciata* as illustrated by Yoshii (1983: 9). Distal border of the apical non-granulated area of the labrum with a relatively narrow median intrusion into the granulated area dorsally (Figure 4C); apical edge not adorned with spines. Ventrodistal complex of labrum well differentiated, asymmetrical, with 2 distal combs of 11–12 and 8–9 teeth and an axial pair of sinuous tubules (Figure 3D). Labral formula 4/5,5,4; prelabral chaetae bent and ciliated, labial chaetae smooth and acuminate; labral chaetae of the distal row slightly shorter than those of the median and proximal row (30

Figure 2. *Lepidonella doveri*, photos (microscope). Pseudopores on different body parts. **A**, Ant. II, ventroapically; **B**, Th. III; **C**, Abd. III; **D**, two pseudopores of the lateral group on Abd. IV; **E**, Coxa 1; **F**, Coxa 2; **G**, **H**, between manubrial basis and genital plate. Scales: 25 μ m (E, F, G); 10 μ m (A, B, C, D, H).

vs 39 and 46 μ m), their socket almost fused to the integument.

Maxillary outer lobe with 1 papillate chaeta, 1 basal chaeta and 4 sublobal hairs of which the upper one is 4 times shorter than the others (Figure 3C).

Labium (Figures 3A, 4A, B). Chaetae of labial basis as M1M2(R)EL1L2 or M1m2(R)EL1L2. Chaetae M1 and E subequal, ciliated; m2 or M2 as long as M1, smooth or ciliated (asymmetrically in one specimen); R reduced to a short and thick ciliated spine; L1 and L2 ciliated, other chaetae of the submentum smooth and acuminate, of similar size. Labial palp similar to that described by Fjellberg (1999) for *Troglopedetes* sp., with strong papillate chaetae. Number of guards for each major papillate chaetae as: h (2), A (0), B (5), C (0), D (4) and E (4). Lateral process subcylindrical, not reaching the apex of papilla E. Five smooth proximal chaetae.

Mandible head strong, asymmetrical (left one with 4 teeth, right one with 5 teeth); molar plate with one strong pointed basal tooth, and 4–(5) very strong inner distal teeth, identical in both mandibles.

Maxilla head (Figures 3B, 4D, E, F) with a 3-toothed claw and several stout ciliated lamellae; lamella 2 large and broad, lamella 3 well developed; several other lamellae present, but homologies are uncertain; a thin elongate structure, arising from the basis of the maxilla head, reaches claw basis; close to it is a spiny structure 10 μ m long (Figures 3B, 4E, F).

Hypopharynx with many long, thin or thick pointed teeth.

Antennae. Figures 1A, 5. Antennae longer than the body, about 3.7 times as long as cephalic diagonal. Lengths of antennal segments I to IV in μ m: 284/568/625/852 (N = 1), similar to the values of the original drawing of Carpenter (1933) (273/466/602/943). Antennal segments entire, not sub-segmented or annulated; in at least one specimen, antennae asymmetrical, one normal with 4 segments, the other one shortened with 3 segments (Figure 1A). A large cuticular notch devoid of chaetae ventrodistally on Ant. I and II,

Figure 3. *Lepidonella doveri*. Mouthparts and ventral side of head. **A**, labium basis; **B**, maxilla, with its two special structures; **C**, maxillary outer lobe; **D**, ventrodistal part of labrum; **E**, ventral chaetotaxy of head; **F**, clypeus. Legend: filled circles, chaeta sockets; U symbols, scale sockets. Scales: 50 μm (E); 20 μm (A, F); 10 μm (B, C, D).

without (Ant. I) or with 1 pseudopore (Ant. II), not differentiated on Ant. III. Ant. III with at least one ventrodistal psp. Ant. IV. not subdivided, without apical bulb; dorsoexternal subapical organite relatively large ($3.5 \times 1 \mu\text{m}$ to $4 \times 1.3 \mu\text{m}$) swollen, oval, slightly enlarged medially, inserted dorsally at 35–45 μm from the apex (Figure 5G).

Antennal scales subequal, small ($7\text{--}9 \times 4\text{--}5 \mu\text{m}$), oval, present dorsally on Ant. I (Figure 5B) and Ant. II, absent on Ant. III–IV.

Other antennal chaetae of various types (Figure 5A), arranged in a complex pattern rather similar to those described in *Cyphoderopsis* (Jantarit et al. 2013) and in *Cyphoderus* (Jantarit et al. 2014).

- Ciliated mac, very long (108–120 μm), flexuous, thinner than ciliated mes, tapering, relatively hyaline. A few basally on Ant. II, absent on Ant. I, III and IV.

- Ciliated mes, short to long (15 to 75 μm), curved, thick basally, tapering, relatively hyaline. Numerous on all antennal segments, mostly ventrally on Ant. I, small and subequal on Ant. IV (Figure 5F, G).
- Mic (10–20 μm), straight, smooth, $\pm$ spiny. Located ventrobasally (3) and dorsobasally (3) on Ant. I (Figure 5B); dorsobasally (3) on Ant. II; not seen on Ant. III; absent on Ant. IV.
- Finely serrated mes (23–26 μm), curved, distinctly thinner than rugose mes, subcylindrical, relatively hyaline. Present on Ant. IV except in its distal part, absent on Ant. I, II and III
- Rugose mes, rather short (10–18 μm), straight or weakly curved, thick, subcylindrical, blunt apically, hyaline. Present on Ant. II, on Ant. III and on Ant. IV except in its distal part (Figure 5G); absent on Ant. I.

Figure 4. *Lepidonella doveri*, photos (microscope). Mouthparts. **A, B**, labium triangle, with m2 smooth (A) or M2 ciliated (B); **C**, distal part of labrum with its non-granulated intrusion; **D, E, F**, maxilla head at three focus. Legend: x, y, special structures of the maxilla head; 2, 3, lamellae 2 and 3 of the maxilla head. Scales: 20 μm (B); 10 μm (A, C, D, E, F).

- Long sens (35–40 μm), flexuous, smooth, thin, subcylindrical, hyaline. Located ventrally on Ant. I (Figure 5C); absent on Ant. II, III and IV.
- Erected sens (24–25 μm on Ant. III; 20–23 μm on Ant. IV), straight, almost perpendicular to the integument contrary to other chaetae, often curved at tip, smooth, thin, acuminate, more refractive than other chaetae. Present internodistally on 2/3 on Ant. III (Figure 5D) and all along Ant. IV, especially numerous in its distal part (Figure 5G); absent on Ant. I and Ant. II.
- Swollen sens, rather short (7.5–11.5 μm), straight, smooth, ribbed, rounded apically, hyaline. Absent on Ant. I and not seen on Ant. II; two located externodistally, close together, in AIIIO of Ant. III (Figure 5F); absent on Ant. IV.
- Short sens (6–14 μm), curved or straight, smooth, slender, thickened basally or subcylindrical, hyaline. Located ventrally on Ant. I and Ant. II (Figure 5C); present in distal 2/3 on Ant. III (Figure 5D, E) and on Ant. IV except in its distal part (Figure 5G).

- microsens (3–4 μm), smooth, thick, subcylindrical, hyaline. Located in AIIIO, internally to swollen s-chaetae (Figure 5F), absent elsewhere.

Head. Figures 1D, 3E, F. On head, mac limited to antennal lines (8–9 mac on each side); dorsal mes short (12–13 μm), subequal, indistinctly serrated, pointed, symmetrically arranged (Figure 1D). Pattern of mes incompletely visible on a single specimen; on anterior part of the head, mes arranged similarly to those of *L. zeppelinii*, but with additional mes near the antennal line, and fewer along the suture line; those of the posterior row slightly stronger. All postlabial chaetae distinctly to strongly ciliated, pointed rather than acuminate distally, scattered among a cover of large oval scales (45×40 to 60×50 μm) (Figure 3E). Dorsal scales smaller than ventral ones (20×14 to 28×22 μm). Cephalic trichobothria short, close to and posteroexternal to ocular area.

Tergites. Figures 6, 7. Tergite chaetae of six types as usual in the group: ordinary chaetae of various size, ciliated or

Figure 5. *Lepidonella doveri*. Antennae. **A**, types of chaetae (M, mac; m, mes; μ , mic; f, fine, serrated; r, rugose; S, long sens; e, erected; w, swollen; s, short sens; ms, micro-sens; see text for description); **B**, dorsobasal mic, one scale and scale sockets of right Ant. I; **C**, ventroexternal chaetotaxy of the proximal half of right Ant. I; **D**, **E**, externodistal part of left Ant. III, ventrally (**D**) and dorsally (**E**); **F**, Ant. III; **G**, distal part of Ant. IV with subapical organite. Legend: r, rugose type chaetae (**D**); U shapes, scale sockets (**B**); empty circles, chaeta sockets; struck circle, pseudopore (**D**); 1 to 6, S-chaeta numbering of Ant. III. Scales: 30 μ m (**C**); 25 μ m (**D**, **E**, **G**); 20 μ m (**A**, **B**, **F**).

serrated, modified mes of trichobothrial complexes, short S-chaetae (S and ms), S-like chaetae, trichobothria and scales. Dense clothing of round to oval scales (15–40 μ m long), mixed with sparse, short, slightly serrated, subequal mes (9–15 μ m), symmetrically arranged. State of material examined did not allow to reconstruct accurately the detailed pattern of dorsal mes on tergites.

Trichobothrial complexes of Abd. II, III and IV well differentiated (**Figure 6C, D, E**), comprising of short, thick, often triangular modified mes, strongly ciliated unilaterally. Trichobothrial complex of Abd. II with 3 modified mes anterior to internal tric and, 2 modified mes anterior to external tric (possibly more). Trichobothrial complex of Abd. III with 3 modified mes anterior to internal tric and 7 close to lateral tric.

Figure 6. *Lepidonella doveri*. Chaetotaxy of tergites and of ventral tube. **A**, dorsal chaetotaxy. **B**, enlargement of the anterolateral S-chaetae of Th. II; **C**, **D**, **E**, enlargement of trichobothrial complex of Abd. II, Abd. III, Abd. IV. **F**, ventral tube, anterior side. Legend: inverted U, scale sockets (C, D, E); small black dots, mes sockets (A, D); larger black dots with numbering, mac sockets (A, D); empty circles, chaetae sockets of ventral tube (F); large blue dots with p, pseudopores (A); struck circles, pseudopores (C, D); black field triangle, modified mes of trichobothrial complex (C, D, E); large circles with central dot and T, trichobothria sockets (C, D, E); blue cross, trichobothria position (A); ms, pointed s-microchaeta; s, hyaline S-chaeta). Scales: 100 μ m (A); 50 μ m (E); 25 μ m (D); 20 μ m (B, C, D).

Trichobothrial complex of Abd. IV with 4 modified chaetae associated to each of the two trichobothria.

S-chaetotaxy (Figure 6A–D) formulae from Th. II to Abd. V: ms as 1,0/1,0,1,0,0; S as 1,?1/0,1,1,n,?. On Abd. IV, a short posterolateral sens and numerous longer S-like or Schaetae. On Abd. V, S-chaetae not distinctly seen. On Abd. II–III and posteriorly on Abd. IV, S and ms are associated to mes in a tandem configuration (Figures 6A, C, D, 7B).

Tergite chaetotaxy with few mac differentiated (Figure 6A). Th. II collar as a row of small mac directed forward, associated with irregularly arranged mes behind them (Figure 7A), and 2–3 irregular rows of shorter mac and mes anterolaterally. Anterolateral sensorial complex of Th. II present, comprising an opaque pointed ms posterior to and side by side with a slightly longer, thinner, hyaline sens. No posterolateral sens detected. No mac detected. Most mes fallen, their

sockets small and difficult to differentiate from scale sockets in our specimens.

Th. III devoid of mac, with more than 14 + 14 mes (2 + 2 posterointernal between the axis and the pseudopores, 8 + 8 posterior, 4 + 4 anterior and several lateral); S and ms not seen.

Abd. I devoid of mac, with at least 6 + 6 mes (of which 1 + 1 between the axis and the pseudopores), and 1 + 1 lateral ms.

Abd. II devoid of mac, with 2 + 2 trichobothria, about 8 + 8 non-modified mes, 5 + 5 modified mes and 1 + 1 S near internal trichobothria (Figure 6C).

Abd. III with 3 + 3 trichobothria, 3 + 3 lateral mac (am6, pm6 and p6), close and external to lateral trichobothria; more than 8 + 8 non-modified mes, 10 + 10 modified mes; 1 + 1 external ms and 1 + 1 internal S, both in tandem with mes (Figures 6D, 7B). Presence of a filamentous organ on each side of Abd. III, constituted of about

Figure 7. *Lepidonella doveri*, photos (microscope). Tergites. **A**, Th. II, anterior line of mac with associated mes; **B**, Abd. III, internal trichobothrial complex including a tandem (mes+ s). Legend: m, 3 sockets of modified mes; p, pseudopore; s, S-chaeta; T, trichobothria. Scales: 15 μ m (A, B).

30 thin and presumably very long mac, but all fallen on our slides.

Abd. IV with 2 + 2 posterointernal mac (B5 and B6), several (6–10) + (6–10) lateral mac ill-differentiated from large mes, more than 20 + 20 thin, slightly serrated S-like mes (18–25 μ m long, some of them possibly smooth S), and 9 + 9 long (about 70 μ m), thin, serrated mes in the posterior row; at least 1 + 1 s-chaetae posterolaterally. No pseudopore behind the posterior line of chaetae, 4 pseudopores along the suture Abd. IV – Scxa (Figure 6A). Chaetotaxy of Abd. V–VI not examined.

Legs. Figure 8. Legs long; Tita of leg III as long as head diagonal, Tita of legs I and II slightly shorter. Legs devoid of scales, covered with ordinary ciliated chaetae of various length, ranging from mic to mac. Coxa of leg I with 2 proximal psp and 6 chaetae posteriorly; coxa of leg II with 11–14 chaetae in anterior row, 9–11 chaetae in posterior row and 3–4 proximal psp in between; coxa of leg III with 4–5 + 8–12 chaetae in anterior row, and 2 proximal psp posteriorly (Figure 8G–I). Trochanteral organ of leg III with 17–21 smooth, straight, unequal spiny chaetae. Femur with a long ventrobasal mac (140–165 μ m), rather thin, 50–60% as long as femur dorsal length; 4–5 shorter mac (60–100 μ m); 5–6 ciliated mic in the proximal half (10–15 μ m long); and a dense cover of mes, 30–100 μ m long (Figure 8A). Tita with strong, slightly sinuous, finely ciliated ventral mes, including 1–2 basal ones longer and thicker than others (70–80 μ m versus 40–60 μ m); dorsally, dense cover of thinner ciliate-serrated mes, and a dorsal row of about 5–11 ciliated mic (10–15 μ m long) (Figure 8A, B, C). The distal whorl of Tita with 9–10 subequal ciliated mes, irregularly arranged, and a thin, acuminate, smooth dorsoapical tenent hair, slightly shorter (85%) than inner edge of claw (35 μ m) and than surrounding ciliated mes (Figure 8E, F); ventrodiscal smooth chaeta of Tita III thick, erected, pointed, rather short (27 μ m, N = 1).

Pretarsal mic minute (2.5–3 μ m). Unguis slender and long (50–60 μ m long, 10.5–12 μ m wide at basis), with (N = 3) or without (N = 2) an unpaired inner tooth at about 72% of inner edge; the claw of the examined paratype had even 2 strong inner teeth, probably a teratological case; a pair of very small, subequal, basal teeth present at 1/8 of inner side of claw (Figure 8E, F); a pair of minute teeth dorsobasally in two specimens, but may be merely the ledge between the smooth and the primary granule areas at the basis of the claw (Figure 8D). Unguiculus about 3/5 as long as inner edge of claw, slightly swollen basointernally, blunt apically, devoid of inner tooth, not truncated, with a minute, often inconspicuous outer tooth at 1/3 of its length (Figure 8E, F).

Ventral tube. Figure 6F. VT four times longer than wide. Lateral flaps with 12–13 + 12–13 chaetae: 6–7 + 6–7 smooth chaetae distally (17–34 μ m), including an external one distinctly longer (48 μ m), and 6 + 6 more hyaline, subequal, ciliated mes proximally (about 20 μ m). Anteriorly, 14 + 14 large chaetae, all ciliated-serrated, including 2 + 2 very large mac side by side distally (Figure 6F). Posteriorly, about 35 mes, all serrated, arranged roughly symmetrically, and 1 + 1 smooth, straight, distal mac close together. The two exsertile vesicles are broad, smooth and short, turned forwards, and devoid of anterior diverticule.

Furca complex. Figures 9, 10. Tenaculum with 4 large teeth of decreasing size from the basal to the distal one of each ramus, on a prominent, irregular body, with a posterobasal strong serrated chaeta bent distally. Mucrodens 1.15–1.30 times longer than manubrium (Figure 10A). Furcal chaetae of 3 types: scales, ciliated chaetae and spines. Inside the manubrium, two thin, straight longitudinal structures running on 3/4 of manubrium length from its apex.

Figure 8. *Lepidonella doveri*. Legs. **A**, femur and proximal part of Tita (leg I); **B**, tibiotarsus (leg II); **C**, two mac and a mes on ventral side of Tita I; **D**, claw II in dorsal view; **E**, Claw I; **F**, claw III (other specimen); **G**, coxa I; **H**, coxa II; **I**, coxa III; **J**, orientation of G, H, I. Legend: empty circles, chaeta sockets; struck circles, pseudopores (G, H, I). Scales: 50 μ m (A, B, G, H, I); 15 μ m (C, D, E, F).

Manubrium ventrally with a dense cover of rounded scales (25–35 $\times$ 20–23 μ m), more elongated and relatively narrow distally (up to 70 $\times$ 25–30 μ m), and 2 + 2 thick ciliated centroapical mes (Figure 9A); scale ornamentation constituted of short spicules arranged in more or less regular lines. Manubrium dorsally covered by subequal ciliated and rather thin chaetae, with approximate symmetrical arrangement and with a streak bearing less or no chaetae medially; a dorsolateral line of 12–13 strong, straight, finely ciliated mac (90–110 μ m) (Figure 9B);

distal area with 4 + 4 ciliated mes and 2 + 2 psp. Presence of 2–3 psp between manubrium basis and genital plate (Figure 2G, H).

Dens slightly and progressively tapering, ventrally entirely and densely covered by oval, more or less fusi-form scales (Figure 10B), dorsolaterally with 2 rows of spines throughout and some ciliated chaetae dorsally between these rows (Figure 9D). Scales and spines not uniform in size on the whole ventral side of the furca. Dental scales small to medium-size (8 $\times$ 4.5 to 14 $\times$ 8 μ m),

Figure 9. *Lepidonella doveri*. Furca. **A**, ventrodistal chaetae of manubrium; **B**, diagrammatic section of manubrium; **C**, rows of spines on dentes; **D**, diagrammatic section of dens; **E**, Mucro. Legend: U shapes, scale sockets (A); black filled circles, spine sockets of different size (C); struck circles, pseudopores (C); empty circles, chaeta sockets (E). Scales: 100 μm (C); 50 μm (B); 25 μm (D); 10 μm (A, E).

oval-fusiform, rounded apically, densely and regularly covered by minute spinules arranged in lines. Lateral scales and distal scales longer than ventral ones (up to $30 \times 10 \mu\text{m}$).

Scales grouped in multiplets made of 3–6 chaetae on the distal 2/3 of the dens (Figure 10B, C), more irregularly arranged on the 1/3 proximal (Figure 10D). In the multiplets, scales increase in size from the distal to the proximal ones.

Dental spines thick, pointed, small to medium, the shortest ones often swollen proximally, in two longitudinal rows. Dorsointernal row with 84–105 spines, dorsoexternal row with 50–65 spines (Figure 9C). Spines serrated to almost smooth (Figure 10C), with small (from 10–15 μm)

and long (35–40 μm in external row, about 20 μm in internal row) spines interspersed along each row; in the proximal part of the external row, spines are replaced by thick, strong, straight, spiny chaetae (65–80 μm) (Figure 9C).

Thinner, more flexible chaetae present dorsally between the two rows of spines, very variable in size (mes to mac, 20 to 95 μm). In the 1/3 dorsoproximal side of dens, a file of 4–(5) pseudopores (Figure 9C).

Mucro separated from dens, short (subequal or shorter than distal mac and about 20 times shorter than dens, Figure 9C), sclerotized, triangular, with 4 teeth, an apical one rather strong, two anterodistal and a minute proximal tooth (Figure 9E).

Figure 10. *Lepidonella doveri*. Furca, photos (A, stereomicroscope; B, C, D, microscope). **A**, furca in lateral view; **B**, scales arranged in multipler on ventrodistal side of dens; **C**, dental spines and scale multipler on distal part of dens; **D**, ventroproximal scales on dens, not arranged in multipler. Scales: 25 μ m (A, D); 10 μ m (B, C).

Genital plate. Female genital plate with 2 + 2 smooth mic. Male genital plate with 3 + 3 genital mic and 28–30 smooth, short, acuminate circumgenital mes, without modified chaetae.

Discussion

Lepidonella species exhibit two different habitus. Epigeal species are usually characterized by the presence of pigment patches on the body (unclear for *L. flava*), including often darkly pigmented subcoxae. Cave species are characterized by larger size, longer appendages, and absence of pigmented patches except in eyes (body, head and appendages either unpigmented or with a very light uniform coloration). Whether these two morphologies reflect classical adaptations to surface versus cave habitats or correspond to different lineages is unclear, because morphological information is lacking for most soil species. As presently circumscribed, the genus *Lepidonella* is widely distributed in Southeast Asia *sensu lato*, with numerous

undescribed forms from New Guinea to southern China (unpublished data). Only two species are present in America, of *L. marimuti* which is strongly divergent from other species of the genus.

Authors have repeatedly underlined the striking similarity of soil Paronellidae *s. l.* with soil Lepidocyrtinae, expressed in the curvature of their body, their relatively small size and short appendages, the morphology of their scales and their oligochaetosis (Mari-Mutt 1987; Yoshii 1988). Mitra's redefinition of the genus *Lepidonella* in 2003 states that some of its species can be "Lepidocyrtiform" *sensu* Denis (1941). Soto-Adames & Bellini (2015) more recently confirmed the great chaetotaxic similarity with Lepidocyrtinae of the two American species they assign to *Lepidonella*, as well as the basal position of *Lepidonella* among Paronellidae *s. l.* A puzzling observation, even if not conclusive given the low phylogenetic signal brought by COI, is that barcode distance trees often place side by side *Lepidonella* and Lepidocyrtinae species (unpublished). In spite of these

similarities, microdens morphology always allows unambiguous assignment of any species to its family, Paronellidae s. l. or Entomobryidae. It cannot be ruled out therefore that the resemblance between *Lepidonella* and Lepidocyrtinae are the result of selective pressure of their edaphic habitat on one hand (small size, short appendages), and the share of plesiomorphic characters (eye arrangement, trichobothrial pattern) on the other hand. Molecular approaches will be necessary to test these competing hypotheses.

Carpenter (1933) mentions in the original description of *Pseudoparonella doveri* that eyes are “wanting”. In the type specimen we examined, two pigment patches are visible on ocular area, a small posterior one and a larger anterior one, and two or three in all the specimens subsequently collected that we examined (Figure 1A, C, D).

Lepidonella doveri shares with *L. lecongkietii* from Vietnam a typical troglomorphic facies classically linked to subterranean life (Figure 1B): reduced eyes, depigmentation (no color pattern, only very diffuse pigment dots), elongate antennae, legs and claws. The two species are easily recognized from all other *Lepidonella* by this set of characters alone. Among other, non-adaptive characters, several are potentially discriminant but remain undocumented in most species of the genus, in particular its type species, *L. tokiokai*. It is the case of macrochaetotaxy or sublobal hairs of the maxillary outer lobe, where a tiny fourth chaeta present in *L. lecongkietii* (overlooked in Deharveng & Bedos (1995)) and *L. doveri* has not been reported in the three other species of the genus where maxillary outer lobe has been described.

Several character states considered as adaptive to cave life differ between the two species. Two are more “advanced” in *L. doveri*: eye number (3 + 3 versus 6(8) + 6(8)), and tibiotarsal tenent hairs (acuminate versus clavate). Other troglomorphic characters (depigmentation, elongate appendages and claws) are almost identical. Inner teeth on claw tend to disappear in cave adapted Entomobryoidea (Christiansen 1961; Deharveng 1987). This character is present in *L. lecongkietii* and present or absent in *L. doveri*.

The striking similarity between *L. doveri* from Batu Caves (Malay Peninsula) and *L. lecongkietii* from southern Vietnam caves raises a biogeographical problem. They are only 850 km apart in a straight line but separated by the large gulf of Thailand. Intermediate regions along the coast of this sea have many caves where *Lepidonella* have not been recorded so far. Western Cambodia and Southeastern regions of Thailand are poorly known in this respect, but several caves of northern peninsular Thailand and Eastern Thailand were significantly sampled (Deharveng & Bedos 1988; Leclerc et al. 1988; Jantarit et al. 2016) and did not host cave *Lepidonella*. An independent adaptation of surface species of *Lepidonella* to cave life in the two regions cannot be ruled out. However, it is not suggested by the high

similarity between *L. doveri* and *L. lecongkietii* compared to their important differences with surface species of Southeast Asia, though most of these differences concern troglomorphic adaptations. This disjunct distribution could also result from a vicariance event following the last separation of the Sunda Shelf in South-East Asia during the mid-Holocene (c.11,000 years ago), after a long period of direct land connection (Voris 2000; Woodruff 2003; Sathiamurthy & Voris 2006). However, the large Chao Phraya river and its continuation southwards during this period already represented a major barrier between Malay Peninsula and Southwestern Vietnam (Voris 2000; Sathiamurthy & Voris 2006). Further investigations on the limits of cave *Lepidonella* west of Southwestern Vietnam and north of the Malay Peninsula, as well as phylogeographic reconstructions will be necessary to understand the pattern.

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