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The genus *Folsomides* in the Hòn Chông hills, Vietnam (Collembola: Isotomidae)

Louis Deharveng[1*], Anne Bedos[1] & Marko Lukić[2]

Abstract. The *Folsomides* species of the Hòn Chông hills in the southwestern part of the Mekong plain in Vietnam are listed. Six species have been collected, of which five belong to the *parvulus* group. Three of these species, among the most common Collembola in the tropics, are cosmopolitan or pantropical (*F. parvulus*, *F. pseudoparvulus*, and *F. centralis*). The synonymy of *F. parvulus* (2+2 remote Omma) and *F. pseudoparvulus* (2+2 adjacent Omma) is not supported by their local and global distribution patterns, nor by the morphological stability of their differential character, eyepatches, within Hòn Chông populations. We propose to recognise, within the *F. parvulus* species group, a *F. parvulus* complex for three closely related species: *F. parvulus* with 2+2 remote eyepatches, each with one Omma; *F. pseudoparvulus* with 1+1 patches, each with two adjacent Omma; and *F. americanus* that would uncover species with 1+1 pigmented Omma, awaiting information on its ocular variability. *F. parvulus* and *F. pseudoparvulus* are present in Hon Chong, *F. americanus* is not. *Folsomides* cf. *semiparvulus* is recorded from one sample in littoral habitat. Two new species of the *Folsomides parvulus* group, restricted to a single cave (*F. anops*, new species) or two caves (*F. whitteni*, new species), are described. *F. anops*, new species, is characterised by two regressive characters unique in the genus: absence of eyes and absence of unguiculus. *F. whitteni*, new species, differs from other *Folsomides* by a combination of characters, namely 1+1 Omma, tenaculum with two rami and without chaeta, mucro bidentate, dens with one or two chaetae, manubrial chaetotaxy reduced (10–13 chaetae in total). Extinction risks of these two rare species due to on-going quarrying of the karstic Hòn Chông hills and caves are emphasized.

Key words. cave fauna, troglobite-edaphobite, troglobite-guanobite, threatened habitats, quarrying, threatened species

INTRODUCTION

The Hòn Chông karst is a cluster of tiny hills scattered on the alluvial plain in southwestern Vietnam and Cambodia, west to the Mekong delta, and covered by a remarkable calcicolous vegetation (Le, 1970, 1974; Figs. 1–3). Mostly degraded today in dense and low bushes, it formerly included some fine stands of rather dense forest that have been destroyed by uninterrupted quarrying from the end of the last century. Biological exploration of the soil and cave fauna of these hills was carried out during the last two decades, and revealed a rich and original fauna, characterised by a number of endemic taxa of invertebrates: Gastropoda (Vermeulen et al., 2007, 2009), Arachnida (Makol & Gabrys, 2005; Schwendinger & Martens, 2006; Judson, 2007, 2017; Fernandez et al., 2014, 2015), Pauropoda (Scheller, 2004), Diplopoda (Golovatch et al., 2009, 2014, 2016; Mauriès et al., 2010), Coleoptera (Deuve, 1996; Ferrer, 2004, 2006; Meregalli & Osella, 2007; Jałoszyński, 2017), Hymenoptera (Roncin, 2002), and Hemiptera (Williams, 2004). Collembola exhibit a similar richness in endemics, but most of their species remain undescribed (Deharveng & Bedos, 1995, 1996; Bedos & Deharveng, 2000; Janion et al., 2013). The fauna includes an exceptionally high proportion of narrow-range and relictual species, unmatched so far in any other area of Southeast Asia (Deharveng et al., 2009). These soil and cave communities are critically threatened by limestone quarrying (Fig. 3), and several species limited to one or two tiny hills are on the verge of extinction (Mylroie & Tronvig, 1997; Ives, 2012).

Intensive sampling effort was carried out during the last two decades and yielded detailed information on the invertebrate diversity in soils and caves of the Hòn Chông region. In spite of this, each sampling campaign continues to bring taxa new to science and of high taxonomic interest. The last important sampling campaign was organised in October 2014. The material collected at this occasion contained a diversity of Collembola, including several new species which had never been obtained during previous campaigns. The present paper is devoted to the genus *Folsomides* Stach, 1922 in Hòn Chông. Synonymies within the species complex of *Folsomides parvulus* are questioned, an important issue for two reasons: *F. americanus* and *F. parvulus* (both from the *F. parvulus* group) are probably the most common species or forms of Collembola in tropical regions, and *F. parvulus*

[1]Institut de Systématique, Evolution, Biodiversité (ISYEB), CNRS, Muséum national d'Histoire naturelle, Sorbonne Université, EPHE, Université des Antilles, 45 rue Buffon, 75005 Paris, France; Email: dehar.louis@wanadoo.fr (*corresponding author)

[2]Croatian Biospeleological Society, Demetrova 1, HR - 10 000 Zagreb, Croatia

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is the type species of the genus. The distribution of the six species of the genus present in Hòn Chông is discussed. Two new extremely rare species are described from caves of the Hòn Chông area: *Folsomides anops*, new species, characterised by a strong reduction of eyes, unguiculus and furca, and *Folsomides whitteni*, new species.

MATERIAL AND METHODS

Litter and soil outside caves as well as guano and soil inside caves were intensively sampled in the Hòn Chông hills, using mostly a Berlese-Tullgren device to extract the arthropods. Pitfall traps filled with 95% ethanol were used in one of the surveyed caves. Collected material was stored in 95% ethanol. *Folsomides* specimens used for morphological descriptions were prepared on slides in Marc-André 2 after clearing in lactic acid. They were examined and drawn under an optical microscope LEICA DMLB with DIC (Differential Interference Contrast) on which a camera lucida was mounted. Photographs were taken with a ProgRes camera C10+ mounted on the microscope. Figures including photos were edited with Photoshop Element v9 (Adobe Inc., San José, USA).

The following abbreviations are used in the text and figures: Abd., abdominal segment; Ant., antennal segment; AIIIO, Ant. III organ; mac, mes, mic: macrochaeta, mesochaeta, microchaeta; Md, Mdl, and Ml: dorsal, dorso-lateral, and lateral macrochaetae of tergites after Deharveng (1987), corresponding to SA, M, and L of Fjellberg (1993); Omma, ommatidia; Scxa, anterior furcal subcoxa; Scxp, posterior furcal subcoxa; Th., thoracic segment; Tita, tibiotarsus.

Maxillary structures are named after Fjellberg (1984), and ventro-labral structures after Deharveng et al. (2018). 'Sensory' chaetae (sensilla auct.) on antennae and body are considered as a same category, S-chaetae (Deharveng, 1983). Notation of antennal chaetae follows Deharveng (1983) and Potapov (2001) when applicable. Notation of AIIIO chaetae follows Deharveng (1983: 50), starting from the external S-microchaeta of the organ (S1, S2, S3, S4, and S5) instead of Chen & Christiansen (1993: 13) who numbered these AIIIO S-chaetae in the reverse order for Lepidocyrtinae (5, 4, 3, 2, 1). Notation of tibiotarsal chaetae follows Lawrence (1977), Deharveng (1983), Fjellberg (1993), and Potapov (2001).

Hang and Nui, the Vietnamese words for cave and hill, have been used in the text associated to cave and hill names.

TAXONOMY

Order Entomobryomorpha Börner, 1913

Family Isotomidae Schäffer, 1896

Folsomides Stach, 1922

Type species. *Folsomides parvulus* Stach, 1922.

Remarks. The two new species described in this paper have the characteristic habitus of most species of the genus *Folsomides*, as well as its main chaetotaxic characters. However, *Folsomides anops*, new species, is affected by a strong regression of eyes, unguiculus, and furca, which makes necessary to update the genus description and to redefine the group of *Folsomides parvulus* to which it belongs. The similarity of *Folsomides* with the genus *Isotomodella* Martynova, 1967 was stressed by Potapov & Stebaeva (2002). With the complete loss of eyes of *F. anops*, new species, described here, one of the few morphological differences between the two genera (presence/absence of eyes) vanishes. Eyes are however known to be a labile and adaptive character in a number of lineages of Collembola, and several other characters listed by these authors and assumed to be non-adaptive remain valid to separate the two genera, in particular details of the S-chaetotaxy of tergites, chaetotaxy of ventral tube (3+3 latero-distal chaetae in *Folsomides* vs. usually 4+4 in *Isotomodella*), and morphology of hind body (last two abdominal segment 'broken' vs. 'not broken' in profile).

Redescription of the genus *Folsomides*. A detailed definition of the genus is given by Fjellberg (1993), Potapov (2001), and Palacios-Vargas & Villarreal-Rosas (2013). It is corrected here for Omma and unguiculus due to their absence in *F. anops*, new species. Other characters are unchanged.

Body long and cylindrical, with an abrupt bend in dorsal profile between Abd. IV and V. Small size, usually less than 1 mm. Cuticle smooth, with only primary granules. Body hairs smooth (or faintly serrate towards tip of abdomen), acuminate. Macrochaetae variable, straight, generally poorly developed. Anal spines absent. Head with 0–6 Omma on each side. PAO present, elongate. Two prelabral chaetae. Maxillary palp simple or bifurcate, three sublobal hairs. Maxilla and mandibles unmodified. Post-labial chaetae 3+3. Antennae without apical bulb, with several more or less thickened subcylindrical chaetae. Thorax without ventral chaetae. Tergites of thorax and abdomen with 33/22224 S-chaetae, in midtergal position on Abd. I–III. S-microchaeta formula 10/000 to 11/111, antero-lateral one always present on Th. II. Ventral tube with 3+3 latero-distal and two posterior chaetae. Furca present. Tenaculum with 2–4 teeth on each side, chaeta present or absent. Ventro-apical chaetae absent on manubrium. Dens always shorter than manubrium, not crenulated, with 1–6 dorsal and 0–3 ventral chaetae. Mucro present, at most with two teeth, or absent. Mucronal chaeta absent. Tibiotarsi I and II with a reduced set of chaetae, 19 or 20 in total, with chaetae B4 and B5 on tibiotarsi I–II either absent or present as a single midline chaeta. Clavate tenent hairs absent. Claws simple, without teeth. Unguiculus present or absent.

The *Folsomides parvulus* group
(Table 1)

This group was proposed by Fjellberg (1993) for two species, *F. parvulus* (including several species considered as

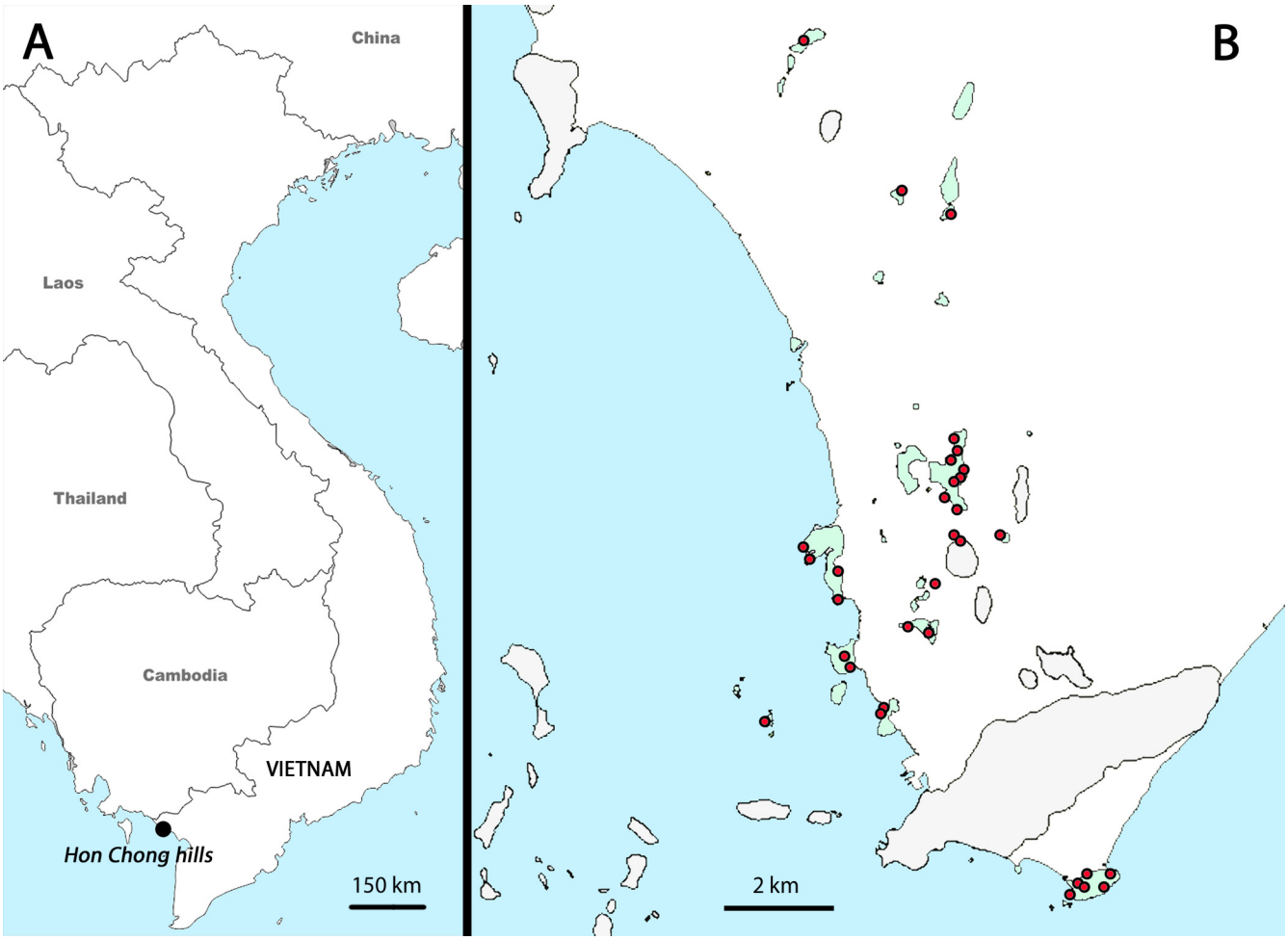

Fig. 1. A, location of Hòn Chông hills in Vietnam; B, records of *Folsomides centralis* in Hòn Chông hills. Pale green, limestone hills; pale grey, non-limestone hills.

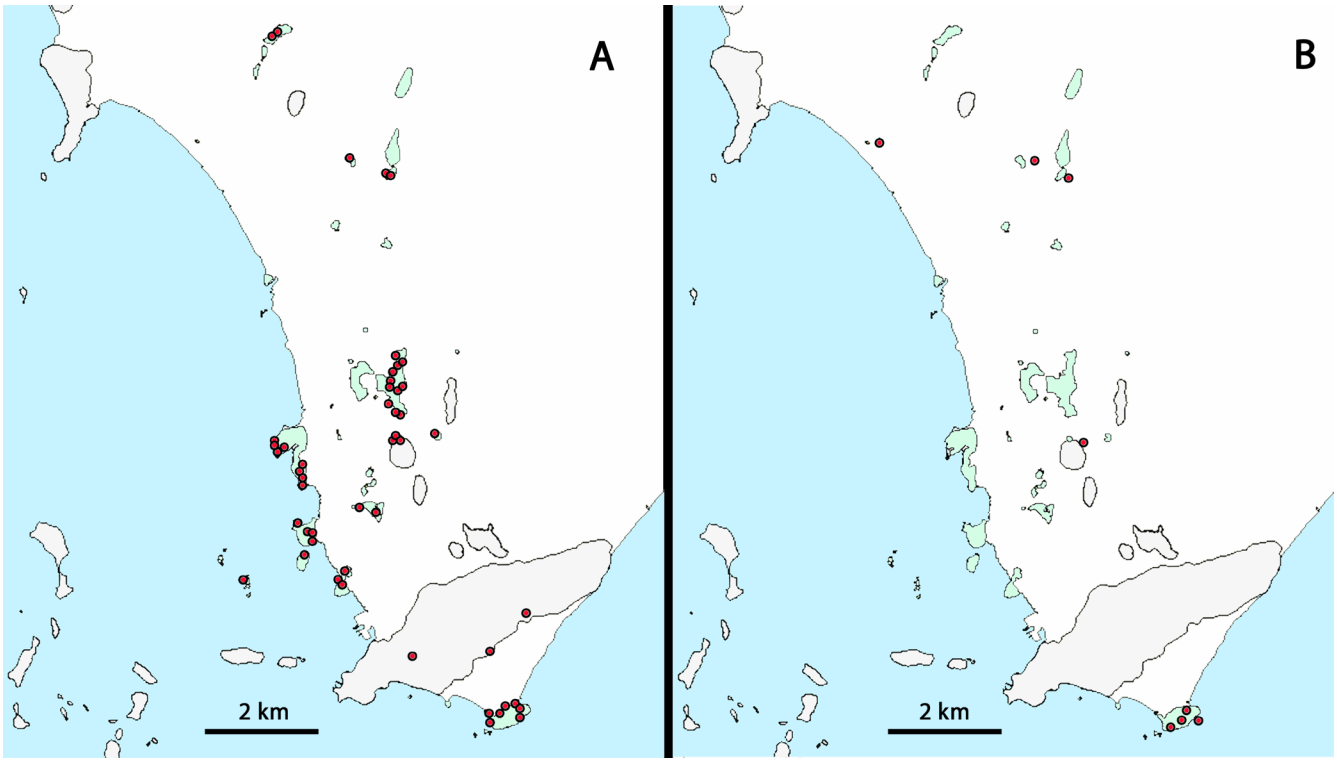

Fig. 2. A, records of *Folsomides parvulus* in Hòn Chông hills; B, records of *Folsomides pseudoparvulus* in Hòn Chông hills. Legend as in Fig. 1.

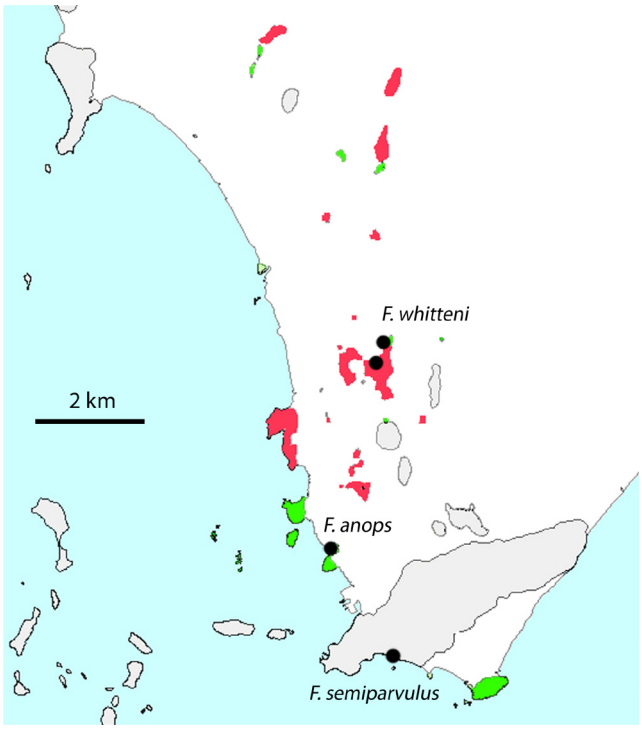

Fig. 3. Records of *Folsomides anops*, *F.* cf. *semiparvulus*, and *F. whitteni* in Hòn Chông hills. Legend as in Fig. 1; red, hills planned to be erased by quarrying.

synonyms) and *F. semiparvulus*. It was characterised at that time by the medial S-chaeta located posteriorly and close to the macrochaeta Md on Abd. IV tergite (between Md and Mdl in other *Folsomides*), body without pigment and 1–2 Omma per side (Potapov, 2001). With the inclusion of the new species of Hòn Chông, this definition has to be modified for eye number, from 1 or 2 to 0–2 Omma per side. This group includes five of the six species of *Folsomides* collected in Hòn Chông: *F. anops*, new species, *F.* cf. *semiparvulus*, *F. parvulus*, *F. pseudoparvulus*, and *F. whitteni*, new species. Other species are listed in Table 1, including several of uncertain taxonomic status.

Synonymies in the *Folsomides parvulus* species complex

At a global scale, the *F. parvulus* group includes five species, including the two new species described in this paper, and a cluster of closely related forms that is named here the *F. parvulus* complex (Table 1). This complex is characterised by the presence of 1+1 or 2+2 eyes, a dens with three chaetae, a bidentate mucro, and 6–7+6–7 posterior chaetae on the manubrium. Seven described species can be assigned to this complex (Table 1). Many have been synonymised (Bellinger et al., 2015). *Folsomides parvus* is considered a synonym of *Proisotoma (Folsomides) parvula* by Gisin (1944a: 27) and *F. stachi* a synonym of *Proisotoma (Folsomides) americana* by Gisin (1944b: 52). *F. exiguus* is considered a synonym of *Folsomides americanus* by Denis (1948: 212–215). *F. anophthalamis* is considered a synonym of *F. americanus* by Ellis (1974: 120). *F. americanus* and *F. exiguus* are considered synonyms of *F. parvulus* by Christiansen & Bellinger (1980). *F. pseudoparvulus* is considered a synonym of *F. parvulus* by Poinsot-Balaguer & Barra (1982). In his revision of the genus *Folsomides*, Fjellberg (1993), following Cassagnau & Delamare-Deboutteville (1955), placed all the species cited above as probable synonyms of *F. parvulus*. This broad conception was accepted by Potapov (2001).

These different 'species' or forms can be allocated to three well-defined categories (Mendonça, 1984): forms with 1+1 Omma, forms with 2+2 adjacent Omma (1+1 eyepatches), forms with 2+2 separated Omma (2+2 eyepatches), corresponding respectively in our acceptation to *F. americanus*, *F. pseudoparvulus*, and *F. parvulus*. Other species of the *F. parvulus* complex can be assigned to one of these categories, providing we do not consider the relative size of anterior and posterior Omma as a valuable character. The synonymisation of these three species is based on an assumed intra-population instability in Omma number, position, and size (Cassagnau & Delamare-Deboutteville, 1955; Fjellberg, 1993). Evidence of this variability is in fact limited to a single detailed analysis of Brazilian populations of *Folsomides* published by Mendonça (1984), where she assigned all these forms to *F. americanus*. There is, however, another way to interpret her results. If we consider that specimens with 1+1 Omma, 2+2 adjacent Omma, and 2+2 well-separated Omma correspond to the three 'species' mentioned above, of the 18 studied Brazilian populations with more than two specimens, 11 would be monospecific, six with co-occurrence of *americanus* and *pseudoparvulus*, a single one with co-occurrence of *parvulus* and *pseudoparvulus*, excluding a few aberrant asymmetrical specimens. If only the forms with 1+1 and 2+2 ocular patches are recognised as species (*americanus* + *pseudoparvulus* and *parvulus*), co-occurrence would concern a single of the 18 populations. This pattern clearly suggests a specific difference between the specimens with 1+1 (*americanus* + *pseudoparvulus*) and those with 2+2 ocular patches (*parvulus*), and to a lesser degree between *americanus* and *pseudoparvulus*. It supports the hypothesis of co-occurrence of different species rather than the hypothesis of a single variable species, which would imply similar levels of variability between populations in the absence of recognised environmental impact.

In addition, the patterns of adjacent versus remote Omma in closely related forms of *Folsomides* with 2+2 eyes raise questions about eyes homologies. Poinsot-Balaguer & Barra (1982) consider that the posterior Omma are 'F+G' when remote from the anterior Omma but are probably 'B' when adjacent to the anterior Omma. In other terms, the posterior Omma in the two patterns would not be homologous. If they were homologous and the expression of some variability, it would be a case of strong non-sexual dimorphism unique among Collembola, unknown so far in species with 2+2 adjacent Omma (like *Heteromurus nitidus* (Templeton, 1835)), or 2+2 remote Omma (like several species of *Folsomia* Willem, 1902 or *Paranura* Axelson, 1902). However, the presence in the *F. parvulus* complex of rare asymmetrical specimens (one eye with two Omma on one

Table 1. Comparison of *Folsomides* species of the *parvulus* group for discriminant characters (eyes and furca). Species have been assigned to the *parvulus* group after the literature, though the diagnostic chaetotaxic character of the group is unknown in several of them. Abbreviations: orig, original description.

Species name	Type country	Accepted synonym	eyepatches / Omma by side	mucro	dens chaetae	manubrium chaetae	Notes
A - *F. parvulus* complex							
americanus Denis, 1931	Costa Rica		1/1 or 1/2 adjacent?	bidentate	3	7+7 *	* after Ellis, 1974 (6+6 in Denis, 1931)
anophthalamis Hepburn & Woodrig, 1964	USA	*americanus* in Ellis (1974) ?	0*/1	bidentate	3	7+7 **	* Omma without pigment after Ellis, 1974 (no eyes in orig); ** after Ellis, 1974 (>=4+4 in orig)
exiguus Folsom, 1932	Hawaii	*parvulus* in Christiansen & Bellinger (1980)	2/2 remote	bidentate	3	6+6 *	* after original fig., 4+4 after original text
parvulus Stach, 1922	Slovakia		2/2 remote	bidentate	3 *	7+7 **	* after Ellis, 1976 (2 in orig); **6+6 in holotype
parvus Folsom, 1937	USA	*parvulus* in Gisin (1944a)	2/2 remote	bidentate	3	?	
pseudoparvulus Martynova, 1978	Zaire		1/2 adjacent	bidentate	3	6–7+6–7	
stachi Folsom, 1937	USA	*americanus* in Gisin (1944b) ?	1/1	bidentate	3	7+7	
B - Other species							
anops, new species	Vietnam		0/0	absent	1 or 2	5+5	
monosetis Massoud & Rapoport, 1968	Argentina		2/ ?1	bidentate	1–(2)	6+6	
semiparvulus Fjellberg, 1993	Canarias		2/2 remote	bidentate	2	7+7	
whitteni, new species	Vietnam		1/1	bidentate	(1)–2	10–13	
yucatanicus Kováč & Palacios-Vargas, 1996	Mexico		2/2 remote	absent	2	6+6	

side of head, two remote Omma on the other side, Mendonça [1984]) does not allow to rule out the possibility of a genetic switch between these two morphologies, as intermediate patterns have never been recorded.

Several authors accepted the above synonymies on the basis of assumed morphological variability, while mentioning geographical patterns in the distribution of 1+1 and 2+2 eyes forms. At a broad scale, Christiansen & Bellinger (1980: 616) stated that the 1+1 eyes form is more frequent in the south of the Nearctic region, and the 2+2 eyes form more frequent in the north. Potapov (2001: 256) recognises for the Palearctic region that the '*americanus*' form (1+1 ocular spots) is more frequent in the southwest of the region, the '*exiguus*' form (2+2 remote Omma) more frequent in the southeast. At a finer scale, Fjellberg (1993: 460) accepted the synonymy *americanus-parvulus*, based on Canarias material, where the 1+1 and 2+2 eyepatch forms were often mixed in populations. In the absence of quantified variability analyses in the cited papers, we however ignore if the relative abundance of each form at population level would have been compatible with a classical variability pattern, i.e., limited differences between populations in the ratio between the two forms. In Canarias, Fjellberg (1993) also mentioned some monomorphic populations, a puzzling fact that he considered as a possible result of parthenogenesis. To our knowledge however, such differences between populations are not reported in other parthenogenetic Collembola species. Poinsot (1972: 674) also accepted this synonymy, but questioned its relevance, stressing that populations are monomorphic in Provence (France). Later on, Poinsot-Balaguer & Barra (1982) recognised *americanus* and *parvulus* as independent species on a worldwide basis, but without analyses at population level.

Other authors recognised geographical segregation patterns like the previous ones but considered them as evidence of separate specific status for *F. americanus* and *F. parvulus*. Ellis (1974: 114–115) rejects their synonymy on the grounds that the 1+1 and the 2+2 eyepatch forms are not mixed in populations from Rhodes island in Greece. In 1976, the same author challenged the lumping by Cassagnau & Delamare-Deboutteville (1955) of all *Folsomides* with 1+1 and 2+2 eyes, considering that their study was more "wide sweeping than detailed" at population level, a remark which applies to all papers cited above, except that of Mendonça (1984).

From our own observations based on thousands of specimens from tropical Asia and Africa, it appears that well-marked distribution patterns exist, though in some areas 1+1 and 2+2 eyes forms may co-exist. For instance, *Folsomides* of the *parvulus* complex we have examined from Ivory Coast have generally the eye pattern of *F. pseudoparvulus* described from Zaire (currently Democratic Republic of Congo): 2+2 adjacent Omma in 1+1 elongated eye spots. Conversely, in Southeast Asia, the *F. parvulus* morphology (2+2 remote Omma) is largely dominant and stable across populations. Syntopy of *F. parvulus* and *F. pseudoparvulus* may occur locally, but the two species are usually in unequal proportions, as illustrated on Table 2 for populations of the Hòn Chông area. Such segregation patterns suggest that *F. parvulus* and *F. pseudoparvulus* might be independent species.

The status of *F. americanus* is less clear. Original figure of Denis (1931) shows a single rounded patch representing the eye and the author states explicitly that "On ne trouve jamais qu'une seule corneule saillante, tout contre le postantennal" [in all cases, there is a single protruding corneule, located against the postantennal], i.e., unlike that of *F. pseudoparvulus* which is elongate (Martynova, 1978). However, he adds "... en dessous un amas de pigment, pouvant manquer, et dans lequel on distingue généralement un mais parfois aussi 2 ou même trois corps ressemblant a des cristallins" [...underneath a heap of pigment, which may be missing, and in which there is generally one but sometimes also 2 or even three bodies resembling crystalline lenses]. This description is confusing, and it lets open the possibility that the number of Omma may vary in *F. americanus*. Subsequently, Collembologists identified all forms with one eyepatch by side, including *F. pseudoparvulus*, as *Folsomides americanus* (or *F. parvulus* when *F. americanus* was considered a synonym of *F. parvulus*), without mentioning the number of Omma (Cassagnau & Delamare-Deboutteville, 1955; Ellis, 1974; Poinsot-Balaguer & Barra, 1982). Mendonça (1984) recognised however two forms among the 1+1 eyepatch species, one with 1+1 Omma and one with 2+2 adjacent Omma, as well as a small proportion of asymmetrical specimens. Twelve specimens from Apaican (Costa Rica), identified by Denis (1931) as *F. americanus*, are grouped on a same slide with "syntypes" as labelled in the collections of the Muséum National d'Histoire naturelle (Paris, France), though the type localities in the original description do not include this locality. All had 1+1 small and round eyepatches, and apparently constituted of 1+1 Omma.

In this context, we propose to recognise provisionally three "species" in the *F. parvulus* complex: *F. parvulus* with 2+2 remote eyepatches, each with one Omma; *F. pseudoparvulus* with 1+1 slightly elongated patches, each with two adjacent Omma; and *F. americanus* with 1+1 Omma, each in a small circular patch. The difference between *F. americanus* and *F. pseudoparvulus* is however often problematic. Examination of fresh topotypic specimens of *F. americanus*, as well as analyses of eye pattern variability at population level coupled with molecular approaches in various regions of the world will be necessary to test this species hypothesis. In any case, the taxonomic structure of the *F. parvulus* complex is likely to be more complicated than it appears from this preliminary approach.

The *Folsomides* species of the Hòn Chông karst

Six species of *Folsomides* are present in the Hòn Chông karst. One (*F. centralis*) belongs to the *centralis* group, five belong to the *parvulus* group as defined above, of which two are new to science and described hereafter. Both are also the only subterranean species of the genus *Folsomides*.

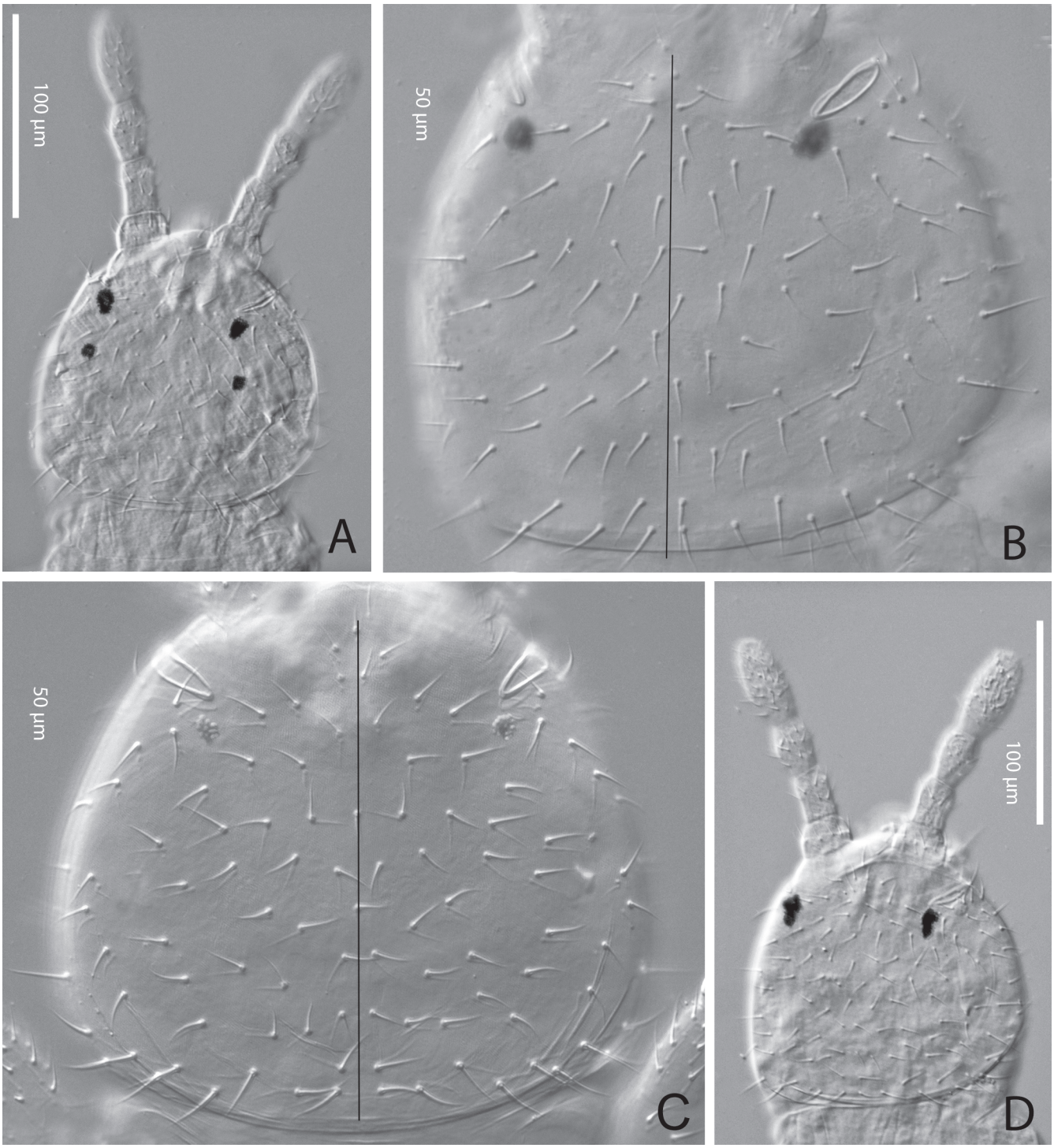

Fig. 4. Dorsal side of head with eyespots. A, *Folsomides parvulus* from Hòn Chông (2+2 remote Omma); B, *F.* cf. *americanus* from France (1+1 Omma); C, *F. whitteni*, new species, (1+1 Omma); D, *F. pseudoparvulus* from Hòn Chông (2+2 adjacent Omma).

***Folsomides centralis* (Denis, 1931)** (Fig. 1B). This species was recorded from Hòn Chông hills by Deharveng et al. (2009). Described from Costa Rica, it is characterised by the medial S-chaeta of Abd. IV located between macrochaetae Md and Mdl, body pigment present, six eyes on each side of the head, and nine chaetae on dens. Not recorded so far from Africa (except in Canary Islands), it is very common in tropical America and tropical Asia, where it often lives in syntopy with *F. parvulus* or *F. pseudoparvulus* in various kinds of soils. In Hòn Chông, *F. centralis* is almost as abundant as *F. parvulus* in all kinds of soils. It is sometimes present in guano and in various cave debris. The species is parthenogenetic.

***Folsomides parvulus* Stach, 1922** (Fig. 2A). This species was recorded from Hòn Chông hills by Deharveng et al. (2009). Described from Slovakia (Stach, 1947, formerly Hungary in original description), it is characterised among the *F. parvulus* group by its two widely separated eyes on each side of the head (Fig. 4A). Common in dry habitats in temperate regions, it is widespread and very abundant in all kinds of soil habitats in tropical countries. With *Isotomiella*

symetrimucronata Najt & Thibaud, 1987, *F. parvulus* is the dominant species of Collembola in the soil and litter of the Hòn Chông karst, occasionally encountered in cave guano. It is especially abundant in disturbed habitats, where it can reach very high density. The species is parthenogenetic, and cosmopolitan in its current taxonomic acceptation.

***Folsomides pseudoparvulus* Martynova, 1978** (Fig. 2B). This species was recorded from Hòn Chông hills by Deharveng et al. (2009) under the name *F. americanus*. Described from Zaire in Africa, it is characterised among the *F. parvulus* group by its two adjacent eyes on each side of the head (Fig. 4D) (one eye only on *F. americanus*, like on Fig. 4B, though this character would have to be confirmed on topotypical specimens). The species is widespread and often very abundant in soils of tropical America and Africa, and to a lesser extent of Southeast Asia. In Hòn Chông, *F. pseudoparvulus* is rarer than *F. parvulus* (Table 2). The species is parthenogenetic and pantropical in the acceptation proposed here (see above).

***Folsomides* cf. *semiparvulus* Fjellberg, 1993** (Fig. 3). This species was recorded from Hòn Chông beach by Thibaud (2002). Described from Canary Islands, it is characterised among the *F. parvulus* group by its 2+2 remote Omma, its dens with two chaetae, its tenaculum with only 2+2 teeth, and the absence of the inner unpaired chaeta of tibiotarsi I–II (Fjellberg, 1993: 460). This species was so far only known from Canary Islands and Mexico (Kováč & Palacios-Vargas, 1996).

Folsomides whitteni, new species

(Figs. 3, 4C, 5A, B, 6, 7A, 8A, B, 9A, 10B; Tables 1, 3)

Type material. Holotype female. Vietnam: Kien Giang Province: Kien Luong, Hòn Chông karst: Nui Bai Voi: Grotte-hôpital, guano, Berlese extraction, coll. Louis Deharveng & Le Cong Man, 29 January 2003 (sample VIET-947). Ten paratypes in alcohol and one on slide, same data as above (sample VIET-947). Three female paratypes on slides, same data as above except soil, Berlese extraction, coll. Quan Mai, 3 March 2004 (sample Vn04Hol-063); about 20 paratypes in alcohol and 4 females on slide, Vietnam: Kien Giang Province: Kien Luong, Hòn Chông karst: Nui Bai Voi: Hang Tai, roots and soil, Berlese extraction, coll. Louis Deharveng & Anne Bedos, 1 December 2006 (samples Vn06-139, Vn06-140).

Type deposition. Holotype, 4 paratypes on slide and 15 paratypes in alcohol in the Muséum National d'Histoire naturelle (Paris, France), 4 paratypes on slide and 15 paratypes in alcohol in the Ho Chi Minh City National University (Vietnam).

Description. Sizes: holotype 0.80 mm, paratypes 0.54 to 0.77 mm. Body colour: white, 1+1 minute pigmented eyes (Fig. 4C). Habitus long and slender (Fig. 5A, B). Pseudopores not seen. Chaetae thin, smooth, and acuminate, differentiated in mes and mac. Dorsal mes subequal, 8.2–10.0 µm long, slightly longer on Abd. V–VI. Mac usually erect, straight, their length given in Table 3.

Antennae (Fig. 6) slightly longer than head. Ant. IV with ordinary chaetae (not counted), about 10 dorsal cylindrical S-chaetae (6–8 µm) and short dorso-external S-chaeta (sm of Potapov [2001]) bent over subapical organite "or", which is very small (Fig. 6B). Ant. III with 21–23 ordinary chaetae. AIIIO classical for family, located dorso-apically with a pair of very short and swollen S-chaetae S3 and S4 (2.3 µm) flanked by two longer, subcylindrical, thickened guard S-chaetae S2 and S5 (6 µm), and with S-microchaeta S1 (2 µm) ventro-externally. Guard S-chaetae S2 and S5 shorter than surrounding ordinary chaetae, thinner and shorter than or subequal to S-chaetae of Ant. IV (6–8 µm). Ant. II with a subcylindrical ventro-external S-chaeta distally, 13 or 14 ordinary mes and 5 basal mic (2 dorsal and a group of 3 ventro-external, larger). Ant. I with 12 ordinary chaetae (a

Table 2. Number of *Folsomides parvulus* (2+2 Omma well separated) and *F. pseudoparvulus* (2+2 adjacent Omma) in some populations of Hòn Chông and Nha Trang. Abbreviations: ratio, ratio of number of *F. pseudoparvulus* to number of *F. parvulus*; asym, number of asymmetrical specimens.

code	habitat	region	*parvulus*	*pseudoparvulus*	ratio	asym
Vn13-242	litter	Nha Trang	12	7	0.58	0
Vn14-058	cave	Nui Hòn Chông	13	2	0.15	0
Vn14-065	litter	Nui Hòn Chông	14	0	0.00	0
Vn14-067	litter	Nui Hòn Chông	19	22	1.16	0
Vn14-068	soil	Nui Hòn Chông	20	1	0.05	0
Vn14-069	litter	Nui Hòn Chông	18	0	0.00	1
Vn14-103	litter	Nui Bai Voi	20	0	0.00	0
Vn14-152	litter	Nui Nai	10	11	1.10	0
VIET-847	soil	Nui Chua Hang	11	14	1.27	0
VIET-846	litter	Nui Chua Hang	5	20	4.00	0
Vn0308-091	litter	Nui Hòn Chông	20	0	0.00	0

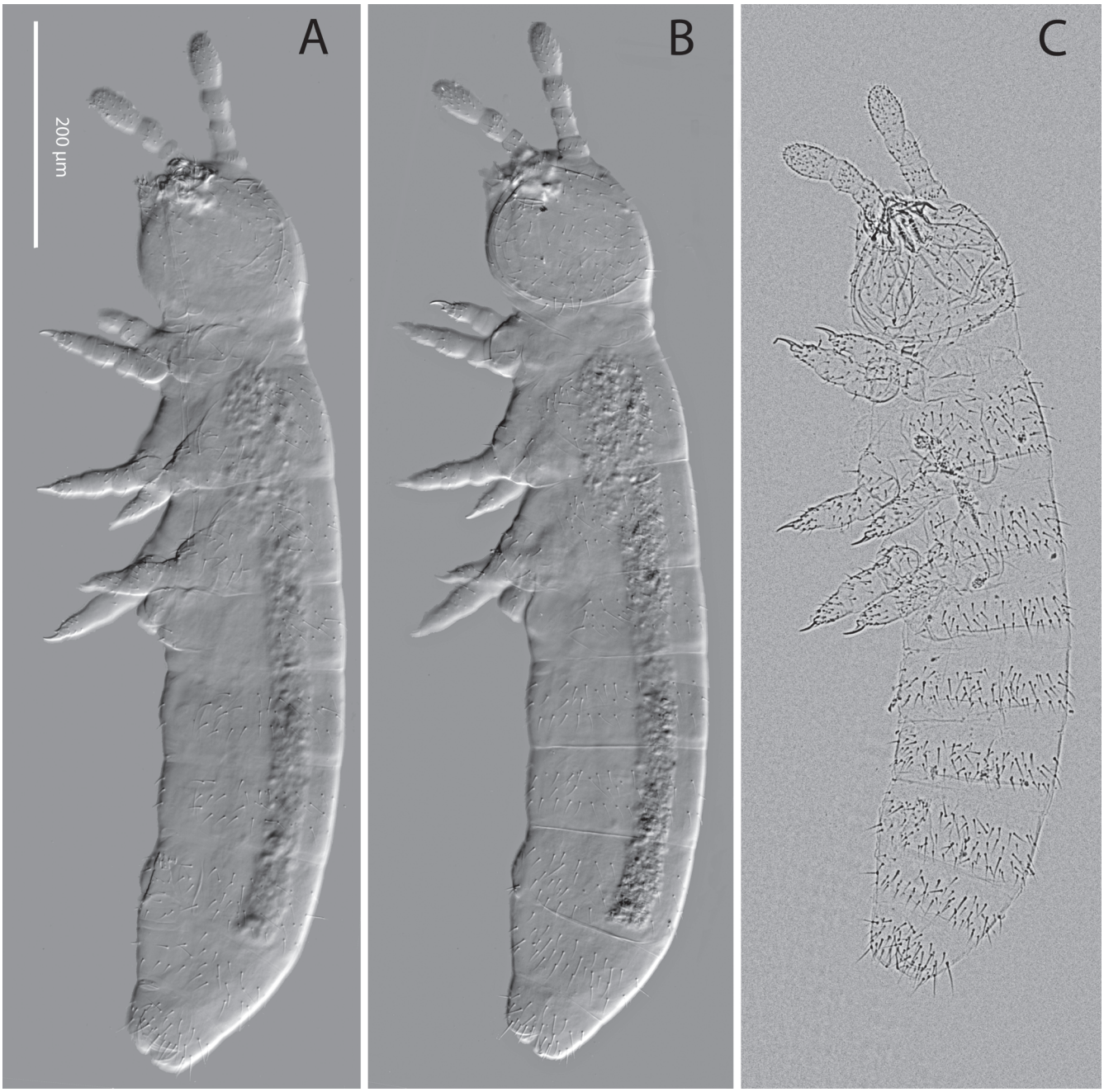

Fig. 5. Habitus. A, B, *Folsomides whitteni*, new species, in ventro-lateral (A) and dorso-lateral (B) views, the same specimen; C, *F. anops*, new species. Same scale for A, B and C.

Table 3. Length in µm of the macrochaetae and p-row ordinary chaetae on the tergites of *Folsomides whitteni*, new species, measured on an adult specimen. Ml, macrochaetae lateral; Mdl, dorso-lateral; Md, dorsal; pr, length of p-row chaetae.

	Ml	**Mdl**	**Md**	**pr**
Th. II	23			10–11.5
Th. III	22			11–12
Abd. I	19			11–12
Abd. II	20			12–14
Abd. III	24			13–15
Abd. IV	22	24	24	14–14.5
Abd. V	23	26	25	15

row of 11 mes and a dorso-basal relatively large mic), 2 subcylindrical thickened S-chaetae of same length ventro-externally, external one thicker, and one minute S-microchaeta close and internal to them.

Ocular plate. Eyes as 1+1 darkly pigmented eyepatches, each eyepatch with one small Omma (diameter 5.1 µm) (Fig. 4C). PAO long (22 µm), narrow, four times as long as eye diameter (Fig. 7A).

Mouthparts. Clypeus with 1+3 chaetae. Labral formula ?2/5,5,4. Distal row of labral chaetae papillated; labral edge with 4 roundish swellings; ventro-distally, combs vestigial, untoothed, 2 thin twisted tongues of organ present, both hardly curved. Maxillary outer lobe with bifurcate palp and 3 sublobal hairs. Labium with 4 baso-medial and 5 baso-lateral chaetae. Labial palp not observed in detail. Maxilla stocky, with short but strongly ciliated lamellae, not observed in detail. Mandible short, stocky, with 4 teeth each.

Dorsal chaetotaxy (Fig. 4C, 5B). Dorsal chaetotaxy of head constituted of subequal mes, symmetrically arranged, with 2 or 3 axial chaetae (Fig. 4C). Axial chaetotaxy of Th. II-Abd. V as (5)6,4/3,3,3,4,3 pairs of mesochaetae. One unpaired axial chaeta present in p-row of Abd. V. (absent in one specimen); 3 unpaired chaetae on Abd. VI. Macrochaetotaxy: 1,1/1,1,1,3,3 by half-tergite from Th. II to Abd. V (mac absent on head). S-microchaeta formula 1,0/0,0,1. S-chaeta formula 3,3/2,2,2,2,4. S-microchaetae freely exposed on tergites. All S-chaetae of Abd. I–V in mid-tergal position, anterior to p-row. Internal S-chaetae of Abd. IV close to and behind mac Md (Fig. 8A). S-chaetae of tergites from Th. II to Abd. IV similar in length (6–7 µm) and morphology, subcylindrical, rather thin, about half length of surrounding ordinary chaetae. Those of Abd. V longer (9–11 µm), external pairs distinctly thicker than internal ones (Fig. 8B).

Ventral chaetotaxy (Fig. 5A). Head with 3+3 chaetae along linea ventralis. Chaetae absent on thoracic sternites.

Legs. Chaetotaxy of legs I to III as follows (indicative values): subcoxae I with 1,1,2 chaetae; subcoxae II with 1,5,6 chaetae; coxae with ?,7–8,7 chaetae; trochanter with 7,7,7 chaetae; femora with 13 or 14,12–14,12 chaetae; tibiotarsi with 19,19, 21 chaetae, B4/5 absent on Tita I–II, *x* absent on Tita III. All chaetae thin, smooth and acuminate, none differentiated in tenent hair on Tita. Claw rather thin (12.5–13 µm) without inner tooth; unguiculus reduced (3.5–4.5 µm) (Fig. 9A).

Ventral tube with 3+3 latero-distal and 2 posterior chaetae.

Furca (Fig. 10B). Tenaculum with 2+2 teeth, chaeta on corpus absent. Furcal subcoxae with 3–4 (Scxa) and 2 (Scxp) chaetae. Manubrium with 10–13 posterior chaetae in total (3–4 distal, 2–4 intermediate, 4–6 basal) usually with asymmetries, anterior chaetae absent. Dens very short, slightly longer than claw, with 2 (sometimes 1) posterior

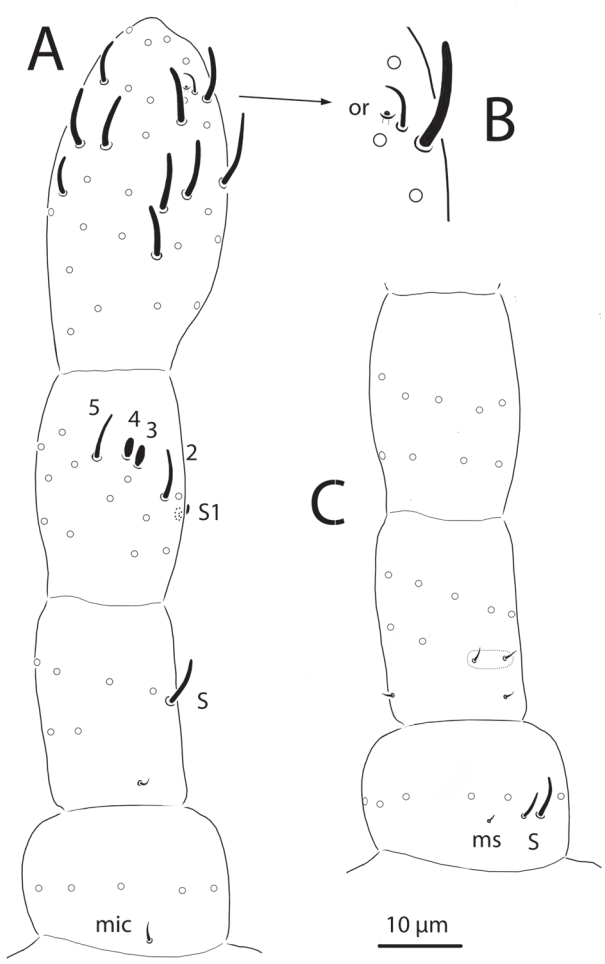

Fig. 6. *Folsomides whitteni*, new species, right antenna. A, Ant. I–IV in dorsal view; B, Organite or on Ant. IV; C, Ant. I–III in ventral view. Two upper ventro-external mic on Ant. II encircled by a dotted line.

chaetae, anterior chaetae absent. Mucro short, bidentate or triangular, fused to dens.

Genital plate. Female genital plate with 1+1 anterior and no posterior mic. Males unknown.

Etymology. The species is named in honour of the late Tony Whitten, in recognition of his tireless dedication to the conservation of the endangered cave faunas of Asia, especially in the Hòn Chông karst.

Discussion. The new species *Folsomides whitteni* belongs to the *parvulus* group, characterised by the internal S-chaetae of Abd. IV close to and behind the mac Md (Fjellberg, 1993). It differs from the other species of this group by the characters listed in Table 1, in particular a reduced furcal chaetotaxy (Fig. 10A, B). It is close to *F. anops*, new species, of the same region, described in this paper, by its strongly reduced eyes and furca, but at a less advanced regressive stage. The female genital plate has 2 mic on its anterior valve and none on its posterior valve, a character shared with *F. monosetis* and *F. pseudoparvulus*, whereas most *Folsomides* and Isotomidae species have 2 mic on each valve in adult. Inter-

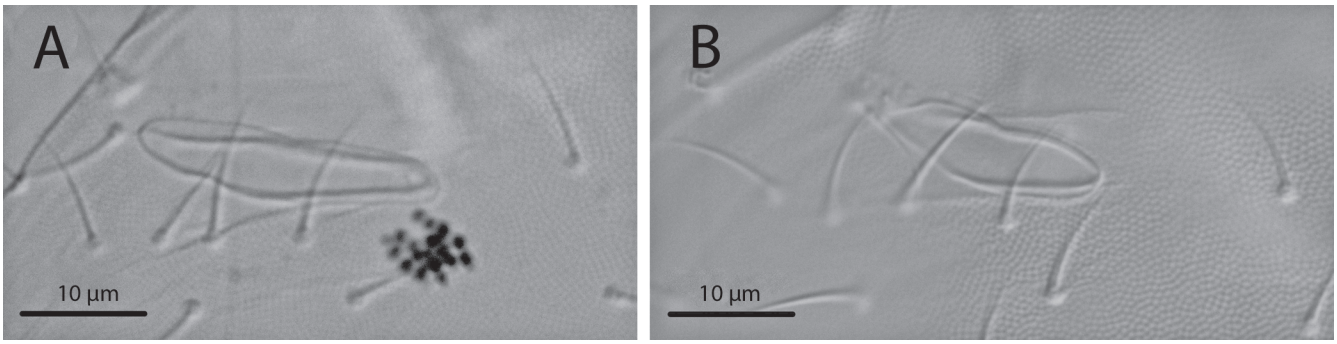

Fig. 7. Post-antennal organ. A, *Folsomides whitteni*, new species; B, *F. anops*, new species.

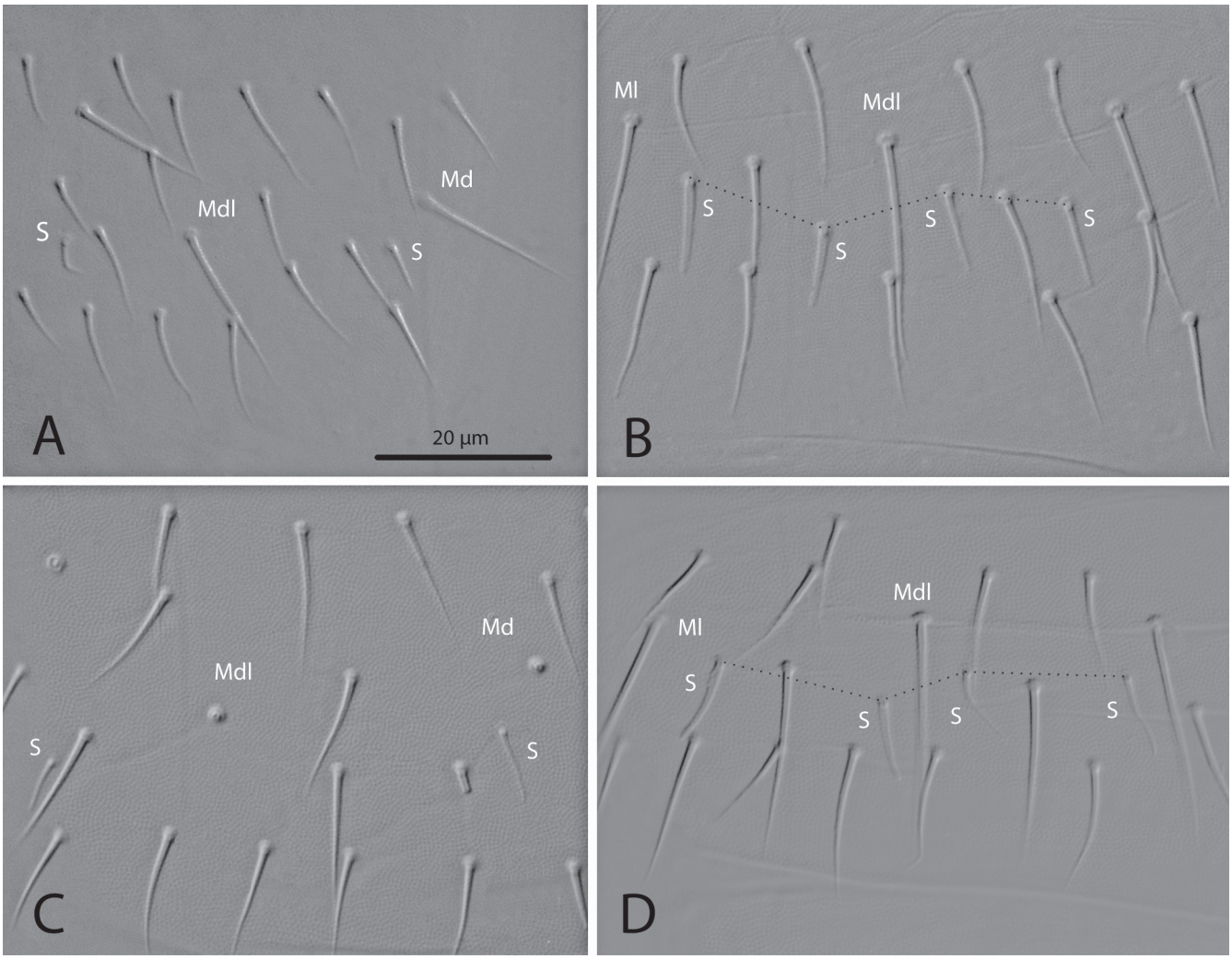

Fig. 8. Dorsal chaetotaxy of Abd. IV and V (left side). A, B, *Folsomides whitteni*, new species, S-chaetae on Abd. IV (A) and on Abd. V (B); C, D, *F. anops*, new species, S-chaetae on Abd. IV (C) and on Abd. V (D). Same scale for A, B, C and D.

Table 4. Length in µm of the macrochaetae and p-row ordinary chaetae on the tergites of *Folsomides anops*, new species, measured on the holotype, an adult or subadult female. Ml, macrochaetae lateral; Mdl, dorso-lateral; Md, dorsal; pr: length of p-row chaetae.

	Ml	**Mdl**	**Md**	**pr**
Th. II	20		(12)	11
Th. III	20		(12)	11
Abd. I	20		(12)	11
Abd. II	20		(12)	11
Abd. III	20		(12)	11
Abd. IV	22	20	22	12
Abd. V	22	25	25	12

specific and intra-specific variations in the number of genital chaetae in the genus *Folsomides* have been already noticed and analysed by Cassagnau & Delamare-Deboutteville (1955). The discriminant value of this character needs however to be confirmed by a larger dataset.

The basal microchaetotaxy of the antennal segments I to III (mbs of Potapov [2001]) exhibit features unusual in Isotomidae, i.e., the absence of dorsal basal mic on Ant. III (Fig. 6A), and the presence of 3 ventral basal mic including two derived from mes close to the classical basal mic of Ant. II (instead of one) (Fig. 6C). These characters have been found in other *Folsomides*, i.e., *F. anops*, new species, *F. parvulus*, *F. pseudoparvulus*, and *F. centralis*, and may have taxonomic value at a supra-specific level.

Ecology and distribution. *Folsomides whitteni*, new species, is restricted to two caves located in the northern part of Nui Bai Voi (Fig. 3), i.e., the Grotte-Hôpital and Hang Tai, which are 500 m apart and belong to unrelated cave systems. The Grotte-Hôpital is the longest cave explored so far in the Hòn Chông karst, with about 1,000 m surveyed (Deharveng et al., 1995; Laumanns, 2011, under the name Hang Moi Chau). It has been heavily disturbed by increasing uncontrolled tourism during the last 20 years. Out of 34 samples taken in terrestrial habitats of the cave, *F. whitteni* was only found in a fruit bat guano pile, at the foot of a high chimney with a small window to outside, in a dark-twilight environment. *F. centralis* is the only other species of the genus occurring in that cave. It was collected twice, once from hanging roots, and once from gravel close to the guano pile where the new species lives. In Hang Tai, a small cave about 10 m long with habitats favourable to cave life, *F. whitteni* was collected at ground level from a dense root-mat in the dark zone. No other *Folsomides* species was collected in the cave. Hang Tai has been completely destroyed by the extension of the Holcim limestone quarry several years ago. *F. whitteni* is therefore, now, restricted to a single guano pile in a single cave heavily threatened by uncontrolled touristic visits. Other caves of the hill did not yield the new species. Fifty-one soil samples were made in Nui Bai Voi outside caves. They contained two species of *Folsomides*: *F. centralis* (14 samples) and *F. parvulus* (28 samples), with the two species mixed in nine samples. In this context, *F. whitteni* may be considered as a rare troglobite-guanobite (Decu, 1986; Deharveng & Bedos, 2018).

Folsomides anops, new species

(Figs. 3, 5C, 7B, 8C, D, 9B, 10C; Tables 1, 4)

Type material. Holotype female (adult or subadult, see discussion). Vietnam: Kien Giang Province: Kien Luong, Hòn Chông karst: Nui Ba Tai: cave west of the hill, from roots and soil, Berlese extraction, coll. Louis Deharveng & Marko Lukić, 3 October 2014 (sample Vn14-017).

Paratype juvenile. Vietnam: Kien Giang Province: Kien Luong, Hòn Chông karst: Nui Ba Tai: cave west of the hill, pitfall trap filled with 95% ethanol, coll. Louis Deharveng & Anne Bedos, 3–16 October 2014 (sample Vn14-177).

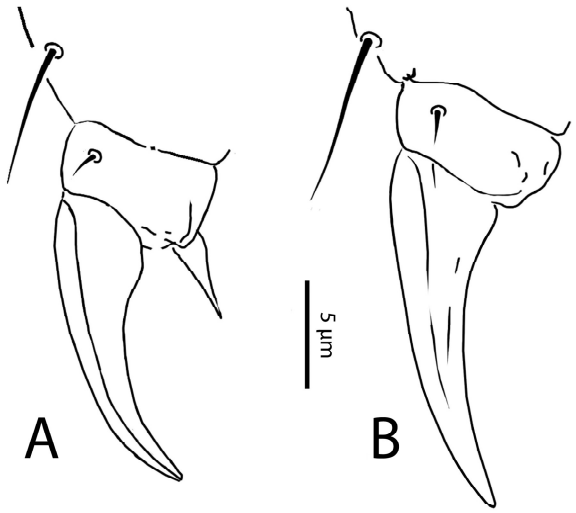

Fig. 9. Claw complex. A, *Folsomides whitteni*, new species; B, *F. anops*, new species.

Type deposition. Holotype in the Muséum National d'Histoire naturelle (Paris, France), paratype in the Ho Chi Minh City National University (Vietnam).

Description. Sizes: holotype 0.75 mm (female, adult or subadult, see discussion), paratype 0.60 mm (juvenile). Body colour: white. Eyes absent. Habitus long and slender (Fig. 5C). Pseudopores as minute circular disks, detected on Th. II-Abd. IV tergites (11/1111 by half tergite), and near the antennal basis (one between PAO and antennal basis). Chaetae thin, smooth, acuminate, differentiated in mes and mac. Dorsal mes subequal, 11–12 µm long from head to Abd. IV, slightly longer on Abd. V–VI. Mac usually erect, straight, their length given in Table 4.

Antennae. Antennae slightly longer than head. Ant. IV with ordinary chaetae (not counted), about 10 large thickened dorsal S-chaetae and a dorso-external S-microchaeta bent over a very short subapical organite "or". Ant. III with about 23 ordinary chaetae. AIIIO located latero-apically and classical for family, dorso-externally with a pair of very short and swollen S-chaetae S3 and S4 (2 µm) flanked by 2 longer, subcylindrical, thickened guard S-chaetae (5.3 µm) and with a ventro-external S-microchaeta S1 (2 µm). Guard S-chaetae S2 and S5 distinctly shorter than surrounding ordinary chaetae (9.7–9.8 µm), thinner and shorter than S-chaetae of Ant. IV (9 µm). Ant. II with a subcylindrical ventro-external S-chaeta and about 13 ordinary chaetae and 5 short basal mic (2 dorsal and group of 3 ventro-external, larger). Ant. I with 12 ordinary chaetae (a row of 11 mes and a dorso-basal relatively large mic), a pair of subequal subcylindrical thickened S-chaetae placed ventro-externally and 1 S-microchaeta close and internal to them.

Ocular plate. Eyes absent; PAO relatively short, narrow, about 0.6 times as long as width of Ant. I (Fig. 7B).

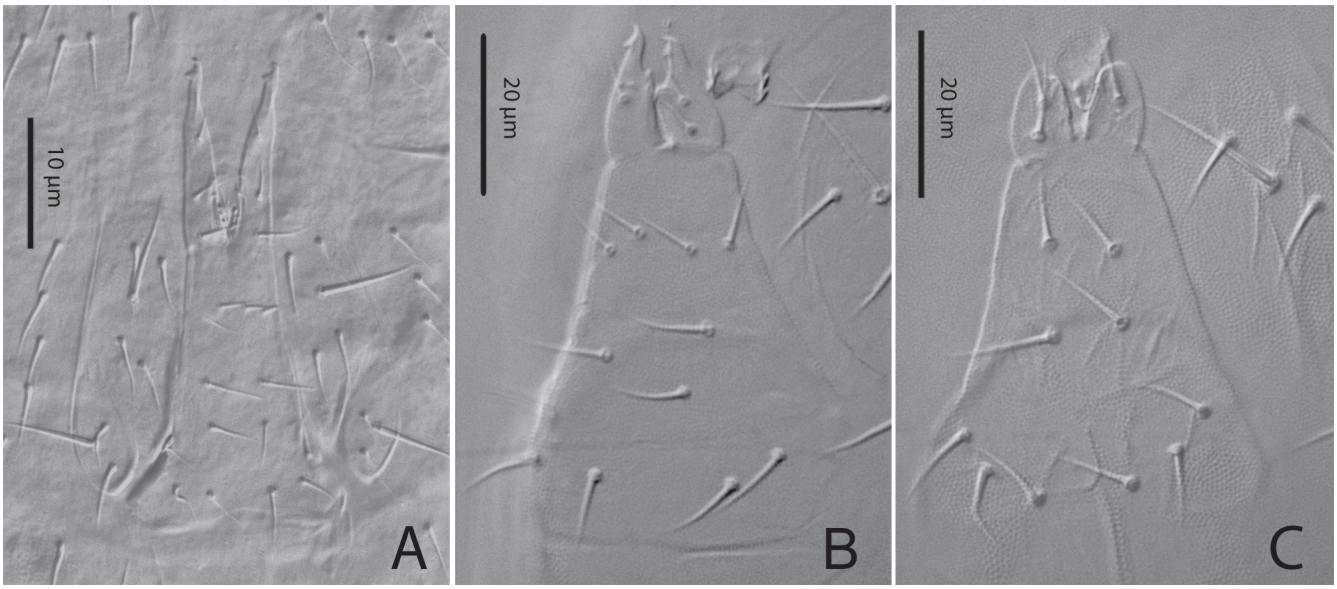

Fig. 10. Furca. A, B, *Folsomides parvulus* from Hòn Chông; B, *F. whitteni*, new species; C. *F. anops*, new species.

Mouthparts. Labrum, labium, maxillary outer lobe and mouthparts not observed in detail. Labium with 4 baso-medial chaetae and 5 baso-lateral chaetae. Lateral process of labial palp thick. Maxilla stocky, with shortly but strongly ciliated lamellae. Both mandibles with 4 teeth.

Dorsal chaetotaxy (Fig. 5C). Axial chaetotaxy of Th. II-Abd. V as 6,4/3,3,3,4,3 pairs of mesochaetae. One unpaired axial chaeta in p-row of Abd. V. Macrochaetotaxy: 1,1/1,1,1,3,3 by half tergite from Th. II to Abd. V (mac absent on head). Dorsal chaetae of medium size (Table 4). S-microchaeta formula 1,0/0,0,0. S-chaeta formula 3,3/2,2,2,2,4. S-microchaetae freely exposed on tergites. All S-chaetae of Abd. I–V in mid-tergal position, anterior to p-row. Internal S-chaetae of Abd. IV close to and behind mac Md (Fig. 8C). S-chaetae of tergites from Th. II to Abd. IV similar in length (5–6.5 µm) and morphology, subcylindrical, rather thin, about half length of surrounding ordinary chaetae. Those of Abd. V longer (9.3–11 µm), external pairs distinctly thicker than internal ones (Fig. 8D).

Ventral chaetotaxy. Head with 3+3 chaetae along linea ventralis. Chaetae absent on thoracic sternites.

Legs. Chaetotaxy of legs I to III as follows (indicative values): subcoxae I with 1,1,1 chaetae; subcoxae II with 1,5,5 chaetae; coxae with 5,7,7 chaetae; trochanter with 5,6–7,5 chaetae; femora with 13,13,13 chaetae; tibiotarsi with 20, 20, ?21 chaetae, B4/5 present on Tita I–II, *x* not detected on Tita III. All chaetae thin, smooth, and acuminate, none differentiated in tenent hair on Tita. Claw thin, without inner tooth; unguiculus totally absent (Fig. 9B).

Ventral tube with 3+3 latero-distal and 2 posterior chaetae.

Furca (Fig. 10C). Tenaculum with 2+2 teeth, chaeta on corpus absent. Furcal subcoxae with 4 (Scxa) and 2 or 3 (Scxp) chaetae. Manubrium with 5+5 posterior chaetae, anterior chaetae absent. Dens very short with 1 or 2 posterior chaetae, anterior chaetae absent. Mucro absent.

Genital plate. Female or subadult female genital plate without anterior and posterior mic. Males unknown.

Etymology. The species is named for its lack of eyes, a character unique among *Folsomides*. From the Greek roots an- (absence of) and -ops (eye).

Discussion. *Folsomides anops*, new species, belongs to the *parvulus* group as defined by Fjellberg (1993), characterised by the internal S-chaetae of Abd. IV close to and behind the mac Md. The new species is described from two specimens, a juvenile and a female adult or subadult. The regression of genital mic seems to be an evolutionary trend in *Folsomides* species of the *parvulus* group compared to other *Folsomides*. The usual pattern in Isotomidae is a pair of mic on the anterior valve and a pair of mic on the posterior valve. In *Folsomides* specimens assumed to be adults however, the absence of the two posterior mic, and even of the two anterior ones on genital plates is mentioned in several forms or species (Cassagnau & Delamare-Deboutteville, 1955). So, it cannot be ruled out that the holotype of *F. anops* is actually an adult with undifferentiated genital mic. In any case, the main diagnostic characters of the species are not age-dependent, and unique in the genus: absence of eyes, absence of unguiculus, and possibly 5+5 chaetae only on the manubrium. The reduced manubrial chaetotaxy is probably not linked to the age of the specimens (one is subadult or adult, see above), as *F. parvulus* and *F. pseudoparvulus* from Hòn Chông have the same manubrial chaetotaxy in adult and in subadult lacking differentiated genital plate. The tibiotarsal chaetotaxy is similar to that of most species of the genus for Tita I and II (20 chaetae with B4/5 present), but the chaeta *x* present in other *Folsomides* has not been detected in *F. anops*.

A blind *Folsomides* is mentioned from Brazil in a table of Mendonça (1984), but it has not been described, and its status is not discussed by the author.

Ecology and distribution. *Folsomides anops* is restricted to a single littoral cave of Nui Ba Tai (Fig. 3), where it was found in or on soil of the dark zone. *F. parvulus* and *F. centralis* are also present in this cave, but not in the same habitat, having been collected from debris and litter in the twilight zone. This is the only one out of the six caves sampled in Nui Ba Tai which yielded *Folsomides* specimens. In contrast, 13 surface samples of Nui Bai Tai contained other species of *Folsomides*, either *F. parvulus* (10 samples), or mixed populations of *F. centralis* and. *F. parvulus* (3 samples). The regressive evolution of several presumably adaptive characters of *F. anops* is probably in relation to a deep soil lifestyle ("euedaphomorphic" morphology after Deharveng & Bedos, 2018). The new species was however absent in the eight deep soil samples taken outside cave in Nui Ba Tai, as well as hundreds of soil samples made in the different hills of the same karst. On this ground, the new species could be qualified as troglobite-edaphobite, being only known from a soil habitat inside a cave.

Conservation issues. The *Folsomides* of the Hòn Chông karst and surrounding areas include both the most common and the rarest species of Collembola of the region. The most common in Hòn Chông, *F. centralis, F. parvulus*, and to a lesser degree *F. pseudoparvulus*, are also among the dominant Collembola in the tropics. The rarest species in the area are only known from a single location (Fig. 3), i.e., one beach (*F.* cf. *semiparvulus* in Binh An), one cave (*F. anops* in Nui Ba Tai) and two caves (one destroyed) of a single hill (*F. whitteni* in Nui Bai Voi).

Folsomides semiparvulus has been described from Canary Islands and was later recorded from Mexico (Kováč & Palacios-Vargas, 1996), Turkey (Skarzynski & Pomorski, 1999), and Brazil (Abrantes & Mendonça, 2007). Its presence in interstitial littoral habitats in Hòn Chông area (Thibaud, 2002), very poorly surveyed and moderately disturbed by human activities, does not allow to consider it as a threatened species. On the contrary, *F. whitteni* and *F. anops* are in a critical situation.

Of the two caves where *F. whitteni* is known to occur, one is highly impacted by unmanaged touristic activities ("Grotte-Hôpital" named after its use during the Vietnam war, or improperly Hang Mo So), the other one (Hang Tai) has been destroyed by quarrying. The whole hill, except the small part of its northern tip where the Grotte-Hôpital is developed, is under intense quarrying, and its caves, where the species was not found so far but which represent potential habitats for it, will all be destroyed within a few years. The species is therefore seriously endangered, though it has not been red-listed so far.

The second rare species, *F. anops*, affected by strong regressive evolution in several morphological characters, is known from a single cave of Nui Ba Tai where it is very rare. A project including a road construction and a chemical plant, recently proposed, was frozen in 2014. If implemented, it would lead to the destruction of a large part of this already tiny hill (0.2 km^2). The species has been red-listed as vulnerable (Deharveng & Bedos, 2016), but given the current quarrying activities and projects in the Hòn Chông area, it could rapidly turn to critically endangered based on IUCN criteria.

These two species add up to an already large number of micro-endemic arthropod and snail species that are critically threatened by limestone exploitation and collateral damages in this tiny karst of Hòn Chông, currently the richest area for deep soil fauna in Southeast Asia (Deharveng et al., 2009).

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