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# Revision of the genus *Pseudobryobia* McGregor, 1950 (Acari, Tetranychidae)

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## Original research

### ABSTRACT

The species of the tetranychid mite genus *Pseudobryobia* are revised mainly based on data published in the literature. Following a survey of the classification history of the genus, emphasizing the changes that occurred in the morphological characters used in its definition, we briefly discuss their relative importance for the genus delimitation. As a result, we provide amended diagnoses for the genera *Pseudobryobia* and *Bryobia* and transfer 7 species from *Pseudobryobia* to *Bryobia*. Species belonging to the genus *Pseudobryobia* bear two setae on coxisternal plate II, one pair of tenent hairs on all the empodia and are distributed in the Nearctic biogeographic zone. Conversely, some species previously assigned to the genus *Pseudobryobia* bear one seta on coxisternal plate II, two rows of tenent hairs on empodia II-IV, and are recorded in the Palearctic and Afrotropical biogeographic zones. These species are transferred to the genus *Bryobia*. The following nomenclature changes resulting from the revision are proposed: *B. (Bryobiopsis) abbatelloi* new combination, *B. (B.) anacantha* reinstated combination, *B. (Allobia) bucharica* reinstated combination, *B. (B.) eurotiae* reinstated combination, *B. (A.) japonica* reinstated combination, *B. (B.) neoephedrae* new combination, *B. (A.) nikitensis* reinstated combination. We recognise six subgenera for *Bryobia*, as previously considered by other authors, and also treat *Nuciforaella* Vacante (1983) as a junior synonym of *Bryobia* (*Allobia*) Livshits and Mitrofanov, 1971. A key to the species of *Pseudobryobia* is also provided.

**Keywords** phytophagous mites; Bryobiinae; morphology; systematics

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## Introduction

Among the Bryobiini, the genus *Pseudobryobia* is the second largest genus in terms of species number, but is far behind the genus *Bryobia*, with 18 and 136 species, respectively (Migeon and Dorkeld, 2006-2017). This genus was established by McGregor (1950) mainly to accommodate some morphological characters of a new species of bryobiine mite collected in Mexico, *Pseudobryobia bakeri*. Since its formation, this genus was alternatively synonymized with the genus *Bryobia*, considered as a subgenus of *Bryobia*, and reinstated as a full genus; its diagnosis was also amended several times (e.g. Wainstein (1960); Tuttle and Baker (1968); Livshits and Mitrofanov (1972); Baker and Tuttle (1972); Meyer (1987)). Wainstein (1960) and Livshits and Mitrofanov (1971), who were actively involved in the taxonomical status of *Pseudobryobia*, both mentioned that the separation between the genera *Pseudobryobia* and *Bryobia* needed further research. Confusion regarding the definition of these genera was

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confirmed recently when *B. longisetis* Reck, 1947 was moved from the genus *Pseudobryobia* to the genus *Bryobia* (Auger and Migeon, 2014) when, according to Vacante (1983) and to Barbar (2018), the assignment of *P. nikitensis* to *Pseudobryobia* may be inappropriate because of an unusual location of the fourth pair of dorsocentral setae. More recently, Zeity and Srinivasa (2019) went further by proposing the reinstatement of the genus *Nuciforaella*, and moving *P. nikitensis* (Livshits & Mitrofanov, 1969) and *P. japonica* (Ehara & Yamada, 1968) from the genus *Pseudobryobia* to *Nuciforaella*. Based on the morphological similarities of current designations, we think that the genus assignation of additional species of *Pseudobryobia* should be re-examined and probably could be assigned to the genus *Bryobia*. However, instead of changing a few species, we believe that a full revision of the genus *Pseudobryobia* is desperately needed to clarify the taxonomy of this group.

To this end, we conduct a thorough historical taxonomic review of the genus *Pseudobryobia*, paying particular attention to the characters used for its delineation. Our findings result in a significant revision of the genus *Pseudobryobia*.

## Material and methods

Our study is based on a literature review dealing with the genus *Pseudobryobia*. The literature concerning species that were assigned to this genus at least once and works allowing a better delineation of the genus were also accessed. In some cases, particularly when important data from the literature were unclear or missing, we had the opportunity to access some type specimens or specimens belonging to the species required. This occurred several times and concerned *P. abbatiielloi* Smiley & Baker, 1995, *P. canescens* Baker & Tuttle, 1972, *P. curiosa* (Summers, 1953), *P. drummondi* (Ewing, 1926), *P. ephedrae* (Tuttle & Baker, 1968), *P. filifoliae* (Tuttle & Baker, 1968), *P. japonica* (Ehara & Yamada, 1968), *P. knowltoni* Tuttle & Baker, 1976 and *P. namae* (Tuttle & Baker, 1964). Type specimens of *P. japonica* (National Museum of Nature and Science, Tsukuba : NSMT Ac-1303637, paratype) and specimens of *P. abbatiielloi* (3 and 11 slides of mites collected in Yemen and Saudi Arabia, respectively) were examined by Dr Tetsuo Gotoh (Ibaraki University, Japan) and by Dr Fahad Jaber Alatawi (King Saud University, Saudi Arabia), respectively. Other type specimens were examined by the senior author in Dr Baker's collection (USDA, Systematic Entomology Laboratory, National Museum of Natural History, Smithsonian Institution, Maryland Beltsville, Washington DC.)

## Results and discussion

### Historical taxonomic review of *Pseudobryobia*

In 1950, McGregor established the genus *Pseudobryobia* with *P. bakeri* as type species and he also moved *Petrobia drummondi* to this genus. Despite a detailed diagnosis of *Pseudobryobia*, McGregor did not analyse relatedness to other closely related genera. In McGregor's description, the genus is defined as follows: forelegs barely exceeding body, other shorter; peritreme enlarging distally somewhat septate or lobed, not protruding externally; empodia with a pair of tenent hairs; dorsum with striated integument bearing short setae.

Pritchard and Baker (1955) criticized the McGregor's genus description as insufficient for generic distinction, focusing only on the peritreme as its defining character state. They regarded this feature as intraspecifically variable, possibly due to slide mounting variation. For this reason, Pritchard and Baker disagreed with McGregor and argued that *Pseudobryobia* is a synonym of *Bryobia*.

Wainstein (1960) considered that there were too many differences between typical species belonging to the genus *Bryobia* and both *P. bakeri* and *P. drummondi*. Nevertheless, as among the genus *Bryobia* some species are morphologically "intermediate" between the two genera, he demoted the genus *Pseudobryobia* to subgeneric rank among the genus *Bryobia*. Species

belonging to this subgenus had the following characters: peritremal enlargement not obvious, sometimes weakly developed; the empodium of leg I padlike with one pair of tenent hairs, those on legs II-IV with one pair or two rows of tenent hairs and the prodorsum without anterior lobes or with these lobes greatly reduced. Based on these criteria, in addition to *P. bakeri* and *P. drummondi*, Wainstein also placed in this subgenus *Bryobia curiosa* Summers, 1953 and *B. longisetis* Reck, 1947. We note that Wainstein's (1960) "anterior lobes" are equivalent to the prodorsal or propodosomal lobes that bear setae  $v_1$  and  $v_2$  in some bryobiine mites, and are not homologous with the "narrow semihyaline plate [...] devoid of setae" noted by McGregor (1950) for *P. bakeri*.

Tuttle and Baker (1968) continued to treat *Pseudobryobia* as a synonym of *Bryobia*. They proposed an amended diagnosis of the genus *Bryobia* and noted variability of some key characters that were previously used to separate this genus and *Pseudobryobia*: i.e. the shape of peritremal ends varying from simple to anastomosed and the presence or absence of propodosomal projections. In line with this, they described and placed among the genus *Bryobia* two new species of *Bryobia* that bear no propodosomal lobes: *B. ephedrae* and *B. filifoliae*.

Livshits and Mitrofanov (1971) were the first to use a new morphological character, the coxal setal count of leg II, to distinguish between the genera *Pseudobryobia* (two setae on coxa II) and *Bryobia* (one seta on coxa II). This was made possible thanks to a correspondence with E. W. Baker who informed them that all the American species previously placed or described among the genus (or subgenus) *Pseudobryobia* (*P. drummondi*, *P. bakeri*, *P. curiosa*, *P. agropyra* (Morgan, 1960), *P. ephedrae*, *P. namae*, and *P. filifoliae*) have two setae on coxa II. Thus, to accommodate species without or with poorly developed prodorsal lobes but having one seta on coxa II, Livshits and Mitrofanov (1971) erected the new subgenus *Allobia* among the genus *Bryobia* into which they transferred three species: *P. japonica*, *P. longisetis* and *P. nikitensis*. The diagnosis of *Allobia* is quite close to that of *Pseudobryobia* but differs by the number of setae on coxa II and the arrangement of dorsal setae  $f_1$  and  $f_2$ : i.e., coxal formula 2-1-1-1; prodorsal lobes absent or poorly developed; distance between setae  $f_1$  greater than distance between setae  $f_2$  with setae  $f_1$  and  $f_2$  well separated, positioned laterally.

As a result, Livshits and Mitrofanov (1972) and Baker and Tuttle (1972) independently felt that *Pseudobryobia* should have a full generic status and proposed to reinstate it. Both contributions provided new diagnoses of the genus in which the number of coxal setal count was raised: in specimens belonging to the genus *Pseudobryobia* the coxal formula is 2-2-1-1 versus 2-1-1-1 in the genus *Bryobia*. In addition, Baker and Tuttle (1972) re-emphasized the positions of dorsocentral setae  $f_1$ : in *Pseudobryobia*, the dorsocentral  $f_1$  setae are located in the normal longitudinal dorsal position and are not marginal.

By the same logic, when Mitrofanov (1973) described a new bryobiine mite (*Pseudobryobia eurotiae* (Mitrofanov, 1973)) meeting the criteria of *Pseudobryobia*, excepting the coxal formula, he created the new subgenus *Bryobiopsis* defined as follows: outer lobes minute, in the form as small tubercles and not separated from inner lobes by a deep incision; setae  $c_3$  in line with  $c_1$  and  $c_2$ ; setae  $f_1$  well separated from  $f_2$  and in central position (not lateral), coxal formula 2-1-1-1.

Smith Meyer (1974) decided to follow Baker's opinion and mentioned that *Pseudobryobia* species can be separated from *Bryobia* by their coxal formulae. She therefore defined *Pseudobryobia* as species without propodosomal lobes, a coxal setal formula of 2-2-1-1, and also noted the position of setae  $f_1$ . She defined the latter feature as setae  $f_1$  either closer together than the first pair of setae  $c_1$ , or in line with the latter, unlike the genus *Bryobia* in which setae  $f_1$  are further apart than setae  $c_1$  and located more laterally.

Tuttle *et al.* (1976) provided an updated diagnosis of the genus *Pseudobryobia* that is a composite of that previously proposed by Baker and Tuttle (1972) and by Meyer (1974): in species belonging to this genus, in addition to the absence of prodorsal lobes and to a coxal setal count of 2-2-1-1, setae  $f_1$  are located in normal position (i. e. not laterally, more or less in line with the other dorsocentral setae). In the same year, Tuttle and Baker (1976) described a

new bryobiine mite species, *P. knowltoni* but, surprisingly, they did not provide any information about its coxal setal count.

Vacante (1983) noted a discrepancy in the assignment of *P. nikitensis*, which has no prodorsal lobes but bears only one seta on coxa II and has setae  $f_1$  in a lateral position. He considered that this species should belong to a morphologically “intermediate” genus between the genera *Bryobia* and *Pseudobryobia*. Thus, to accommodate the characters of this species, he created the monospecific genus *Nuciforaella* with the type species *N. nikitensis*. It must be noted that until recently this new genus was not recognized in later acarological works like Smith Meyer (1987) and Bolland *et al.* (1998).

In the subsequent contributions dealing with the genus *Pseudobryobia* by Mitrofanov *et al.* (1987), Meyer (1987) and Baker and Tuttle (1994), these authors continued to emphasize the absence of a prodorsal projection, the coxal formula and the location of setae  $f_1$  in separating this genus from *Bryobia*. Despite the interest in these morphological traits, when Baker and Tuttle (1994) described two new species, *P. antennaria* Baker & Tuttle, 1994 and *P. konoii* Baker & Tuttle, 1994, they did not provide their coxal formulae. In 1987, Mitrofanov *et al.* discovered an additional character for distinguishing the two genera: duplex setae on tarsus III are associated in *Bryobia* versus dissociated in *Pseudobryobia*.

The last contribution dealing with *Pseudobryobia* by Smiley and Baker (1995) generated confusion. Indeed, in their diagnoses of the genera *Pseudobryobia* and *Bryobia*, they reversed the coxal formula between the two genera so that the coxal formula 2-2-1-1 was assigned to the genus *Bryobia* and 2-1-1-1 to *Pseudobryobia*. This mistake has not been without consequence because in the wake of the Smiley and Baker’s new descriptions, they also synonymized the subgenus *Bryobiopsis* (see Mitrofanov (1973) above) with the genus *Pseudobryobia*. This makes sense with the flawed new diagnoses proposed as until this contribution the subgenus *Bryobiopsis* only differed from *Pseudobryobia* by the number of setae on the coxa II (1 seta present in species belonging to the subgenus *Bryobiopsis*). This supports the idea that their mistake in the coxal formulae may be not simply a typing error.

In the same contribution, they also described a new species, *P. abbatielloi*, but as they did not provide its setal formula, one has to wonder how many setae are present on its coxa II. Following their reasoning, the synonymy of the sub-genus *Bryobiopsis* with *Pseudobryobia*, we may anticipate that *P. abbatielloi* bears one seta on its coxa II.

Following this contribution several species were moved to the genus *Pseudobryobia*: i) Ehara (1996) transferred *B. japonica* to the genus *Pseudobryobia* because of the absence of prominent prodorsal lobes over the gnathosoma (Gotoh, personal communication); ii) Bolland *et al.* (1998) moved 4 species from the genus *Bryobia* to *Pseudobryobia*: *B. anacantha* (Strunkova & Mitrofanov, 1983), *B. agropyra*, *B. bucharica* (Strunkova & Mitrofanov, 1983) and *B. nikitensis*. As these four species do not bear the same number of setae on coxa II, the new combinations provided by Bolland *et al.* (1998) make sense if we accept that these authors did not take into account the coxal setal formula to distinguish between the genera *Bryobia* and *Pseudobryobia*. Moreover, in some of these species, the dorsocentral setae are arranged in a longitudinal row whereas in others setae  $f_1$  are near the body margin (e.g. *P. agropyra*, *P. drummondi*, *P. neoephedrae* Bolland *et al.*, 1998 and *P. bucharica*, *P. japonica*, *P. nikitensis*, respectively). Therefore, the dorsal setal pattern is overlooked as a possible or important characteristic to delineate taxa, and a characteristic not used by these authors when creating new taxonomic assignments. The only character shared by all the species Bolland *et al.* (1998) merged into taxa into the genus *Pseudobryobia* is the absence of propodosomal lobes over the gnathosoma.

Auger and Migeon (2014) transferred *P. longisetis* (*sensu* Bolland *et al.*, 1998) back to the genus *Bryobia* using key morphological characters defined by Livshits and Mitrofanov (1972), by Baker and Tuttle (1972) and by Meyer (1974) to distinguish between the genera *Bryobia* and *Pseudobryobia*.

The last contribution dealing with *Pseudobryobia* reinstated the genus *Nuciforaella* and transferred *P. nikitensis* and *P. japonica* (*sensu* Bolland *et al.*, 1998) to this genus (Zeity and



Srinivasa, 2019). Their proposal was based on Vacante's opinion which considered that the morphological characteristics of the genus *Nuciforaella* represent an intermediate state between the genera *Bryobia* and *Pseudobryobia* (Vacante, 1983).

## Morphological characters and genus delineation

Table 1 presents the potentially informative morphological character states that may separate *Bryobia* from the species of *Pseudobryobia* as currently defined by Bolland *et al.* (1998). As the setal count on coxa II was agreed by most of the acarologists to reliably distinguish the genera *Pseudobryobia* and *Bryobia* ((Livshits and Mitrofanov, 1971); Livshits and Mitrofanov (1972); Baker and Tuttle (1972); Meyer (1974); Tuttle *et al.* (1976); Mitrofanov *et al.* (1987); Meyer (1987); Baker and Tuttle (1994)), we organize the taxa according to this morphological trait (displayed in the 3rd column in the Table I): species bearing two setae on coxa II are gathered and provided first. Arranged thus, some character states are shown to be highly variable, especially the shape of the distal end of the peritreme and the shape of the dorsohysterosomal setae. However, the location of setae  $f_1$ , the number of tenent hairs on empodium I-IV and the state of the duplex setae on tarsi III and IV do not vary among the species group bearing 2 setae on coxa II. Some of these traits are shared by species with one seta on coxa II, but two morphological criteria are congruent and distinguish two distinct species groups among this genus: a species group with 2 setae on coxa II, having empodia II-IV with a pair of tenent hairs and exclusively Nearctic in geographical distribution; and a group with one seta on coxa II, bearing empodia II-IV with two rows of tenent hairs and having Palearctic and Afrotropical distributions.

The convergence of morphological and geographical criteria demonstrates the importance of the coxal setal formula in the taxonomy of spider mites, and specifically genus delimitation. According to Lindquist (1985), the primitive coxal formula on adult spider mites is 2-2-1-1 but there is a common derivative loss of setae on coxisternal plate II which has only one seta in various genera of Bryobiinae. Among this subfamily, as early as the 1960's, Bagdasarian (1957) and Reck (1959) were the first to reference the coxisternal setal count for genus delimitation and mentioned that 2 setae on coxa I and 1 on coxae II-IV are present in the genus *Bryobia*. Later, several authors included the coxal formula in the diagnoses of the genera *Bryobia* or *Pseudobryobia* (e.g. Baker and Tuttle (1972); Meyer (1974); Vacante (1983); Meyer (1987); Baker and Tuttle (1994)) but also in other genera, suggesting that this character may be fixed among some of them. Unfortunately, this subject is still poorly studied and therefore poorly documented. Although information is lacking on the coxal formula of each known species (data are not always provided in the original descriptions and redescriptions), if we exclude the *Pseudobryobia* species, the number of setae on coxa II generally does not vary between species belonging to the same genus within the Bryobiinae. However, there are some rare exceptions: i) in the genus *Neopetrobia* the usual coxal setal formula is 2-2-1-1 whereas it is 2-1-1-1 in *N. (N.) tarkaensis*; ii) in the genus *Paraplombia* the basic coxal formula is 2-2-1-1 but, in the monotypic subgenus *Brachynychus* it is 4-3-2-2; iii) Smith Meyer (1987) reports that it could vary between 2-3-1-1 and 2-2-1-1 in some species belonging to the subgenera *Anaplombia*. However, these cases are exceptions and therefore not fully comparable with what is observed in the genus *Pseudobryobia*.

To our knowledge, coxal setal variations, comparable in number to that observed in *Pseudobryobia*, also occur in the tetranychine genus *Eutetranychus*. Species of *Eutetranychus* can be separated in two groups using their setal count on coxa II: one group with 1 setae (16 species) and the other with 2 (11 species) (Kamran *et al.*, 2018). Nevertheless, in the genus *Eutetranychus*, geographical distribution of the species does not appear related to their coxal setal formula. For example, among the two newly described species collected in Saudi Arabia, one bears one seta and the other two setae on coxa II (Kamran *et al.*, 2018). Finally, no clear morphological differences between the species of the two subgroups have yet been reported.

However, in our new concept of *Pseudobryobia* the differences in coxal setal formula are related to another discriminant morphological trait: the morphology of the empodia of

**Table 1** Variations in some morphological key characters (used in the literature) of mites belonging to the genus *Pseudobryobia* (*sensu* Bolland *et al.*, 1998) with data on their geographic distribution and their possible genus assignment (as the absence of prodorsal projection over the gnathosoma is shared by all the species, this character is not included in the table).

Species names	Authors	Number of setae on coxa II	Setae $f_1$ position	Peritremal enlargement	Dorso-hysterosomal setae shape	Empodium I tentent hairs	Empodium II-IV tentent hairs	Duplex setae on tarsus III	Duplex setae on tarsus IV	Geographic distribution	Genus assignment according to Livshits & Mitrofanov (1971) and Mitrofanov (1973)
<i>P. agropyra</i>	(Morgan, 1960)	2	normal	simple	elongate	1 pair	1 pair	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. antennaria</i>	Baker & Tuttle, 1994	2	normal	developed	spatulate	1 pair	1 pair	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. bakeri</i>	McGregor, 1950	2	normal	simple	subspatulate	1 pair	1 pair	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. canescens</i>	Baker & Tuttle, 1972	2 <sup>a</sup>	normal	developed	subspatulate	1 pair <sup>a</sup>	1 pair <sup>a</sup>	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. curiosa</i>	(Summers, 1953)	2 <sup>a</sup>	normal	simple	spatulate	1 pair <sup>a</sup>	1 pair <sup>a</sup>	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. drummondi</i>	(Ewing, 1926)	2 <sup>a</sup>	normal	developed	elongate	1 pair <sup>a</sup>	1 pair <sup>a</sup>	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. ephedrae</i>	(Tuttle & Baker, 1968)	2 <sup>a</sup>	normal	developed	spatulate	1 pair <sup>a</sup>	1 pair <sup>a</sup>	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. filifoliae</i>	(Tuttle & Baker, 1968)	2 <sup>a</sup>	normal	developed	elongate	1 pair <sup>a</sup>	1 pair <sup>a</sup>	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. knowltoni</i>	Tuttle & Baker, 1976	2 <sup>a</sup>	normal	developed	spatulate	1 pair <sup>a</sup>	1 pair <sup>a</sup>	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. konoi</i>	Baker & Tuttle, 1994	2	normal	poorly developed	elongate	1 pair <sup>b</sup>	1 pair <sup>b</sup>	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. namae</i>	(Tuttle & Baker, 1964)	2 <sup>a</sup>	normal	developed	elongate	1 pair <sup>a</sup>	1 pair <sup>a</sup>	dissociated	dissociated	Nearctic	<i>Pseudobryobia</i>
<i>P. anacantha</i>	(Strunkova & Mitrofanov, 1983)	1	normal	simple	elongate	1 pair	2 rows	associated	dissociated	Paleartic	<i>Bryobia (Bryobiopsis)*</i>
<i>P. bucharica</i>	(Strunkova & Mitrofanov, 1983)	1	marginal	simple	subspatulate	1 pair	2 rows	associated	dissociated	Paleartic	<i>Bryobia (Allobia)<sup>u</sup></i>
<i>P. euraiiae</i>	(Mitrofanov, 1973)	1	normal	simple	elongate	1 pair	2 rows	associated	dissociated	Paleartic	<i>Bryobia (Bryobiopsis)</i>
<i>P. japonica</i>	(Ehara & Yamada, 1968)	1 <sup>c</sup>	marginal	developed	spatulate	2 rows	2 rows	associated	associated	Paleartic	<i>Bryobia (Allobia)</i>
<i>P. neophedrae</i>	Bolland <i>et al.</i> , 1998	1	normal	developed	subspatulate	2 rows	2 rows	associated	associated	Paleartic	<i>Bryobia (Bryobiopsis)</i>
<i>P. nikitensis</i>	(Livshits & Mitrofanov, 1969)	1	marginal	developed	subspatulate	2 rows	2 rows	associated	associated	Paleartic	<i>Bryobia (Allobia)</i>
<i>P. abbatelloi</i>	Smiley & Baker, 1995	1 <sup>d</sup>	normal	simple	elongate	2 rows <sup>d</sup>	2 rows <sup>d</sup>	dissociated	dissociated	Afrotropical	<i>Bryobia (Bryobiopsis)</i>

<sup>a</sup> Data obtained from the examination of type specimens by senior author

<sup>b</sup> After drawings in Tuttle and Baker (1994)

<sup>c</sup> Data obtained from holotype observation by Dr T. Gotoh

<sup>d</sup> Data provided by Dr F. J. Alatawi following the observation of specimens collected in Yemen and Saudi Arabia

\* Subgenus *Bryobiopsis* Mitrofanov (1973)

Coxal formula 2-1-1-1; prodorsal lobes absent or poorly developed; outer lobes not always present, minute or like small tubercles, without deep incision between them and the inner ones; setae  $c_1$ ,  $c_2$  and  $c_3$  in line; setae  $f_1$  in normal position, not contiguous to  $f_2$ .

<sup>u</sup> Subgenus *Allobia* Livshits & Mitrofanov (1971)

Coxal formula 2-1-1-1; prodorsal lobes absent or poorly developed; if present, outer and inner lobes not separated by deep incision; distance between  $f_1$  setae members larger than distance between  $f_2$  members; setae  $f_1$  and  $f_2$  well separated, lateral.

legs II-IV. And, these characters are related to their geographical distribution, which suggests allopatric differentiation on a broad biogeographic scale (e.g. Turelli *et al.* (2001), Barraclough and Vogler (2000)) and reflects two distinct lineages. We therefore propose a revision of the genus *Pseudobryobia* based on the coxal formula, the single pair of tenent hairs on empodia II-IV, and the geographical distribution of *Bryobia* and *Pseudobryobia*.

This revision particularly recalls the works by Livshits and Mitrofanov (1971; 1972) and Mitrofanov (1973). In addition to their definition of the genus *Pseudobryobia* we think that their proposal of six subgenera of *Bryobia* (*Bryobia*, *Lyobia*, *Periplanobia*, *Allobia*, *Bryobiopsis* and *Eharobia*) is robust and, in the present paper, this is particularly the case with the subgenera *Allobia* and *Bryobiopsis*. We share the opinion of Zeity and Srinivasa (2019) that the species *P. nikitensis* and *P. japonica* belong the same taxonomical unit. However, *B. tadjikistanica* Livshits & Mitrofanov, 1969 and, according to our data, *P. bucharica*, should probably also be added to this taxon. In addition, as the morphological characteristics of species placed in the genus *Nuciforaella* correspond to those of the subgenus *B. (Allobia)*, we do not share the view of Vacante (1983) and Zeity and Srinivasa (2019) and we consider the genus *Nuciforaella* as a part of *B. (Allobia)*.

## Genus revision

### *Pseudobryobia* McGregor

*Pseudobryobia* McGregor, 1950:355; *Bryobia (Pseudobryobia)* Wainstein, 1960:113; *Pseudobryobia* Livshits & Mitrofanov, 1972:8; Baker & Tuttle, 1972:2; Meyer, 1974:13; Tuttle *et al.*, 1976:5; Mitrofanov *et al.* 1987:142; Baker & Tuttle, 1994:28; Smiley & Baker, 1995:141. Type-species: *Pseudobryobia bakeri* McGregor

**Genus diagnosis** — Ambulacrum with true claws uncinata, empodia with 1 pair of tenent hairs; 2 pairs of duplex setae on tarsus I, 1 pair on tarsus II, duplex setae on tarsi III and IV dissociated, coxisternal formula 2-2-1-1. Body broadly rounded without anterior cleft, prodorsum without anterior lobes, with 4 pairs of setae, setae  $v_1$  and  $v_2$  sometimes inserted in small to tiny bulges, opisthosoma with 12 pairs of setae, the central fourth pair ( $f_1$ ) in normal position, not marginal; one pair of aggenital ( $ag_1$ ) setae and 3 pairs of pseudanal setae ( $ps_{1-3}$ ), 2 pairs of ventro-caudals ( $h_{2-3}$ ) present ventrally, 1 pair of hypostomal subcapitular seta ( $m$ ).

### *Bryobia* Koch

*Bryobia* Koch, 1836:8-9; Pritchard & Baker, 1955:14; Bagdasarian, 1957:51; Reck, 1959:84; Wainstein, 1960:94; Manson, 1967:78-80; Tuttle & Baker, 1968:4; Livshits & Mitrofanov, 1971:49; Mitrofanov, 1973:12; Meyer, 1974:13; Tuttle *et al.*, 1976:4; Gonzales, 1977:634; Meyer, 1987:8; Mitrofanov *et al.*, 1987:142-143; Baker & Tuttle, 1994:17; Smiley & Baker, 1995:135. Type-species: *Bryobia praetiosa* Koch

**Genus diagnosis** — Ambulacrum with true claws uncinata, empodium with tenent hairs, 1 pair or more on empodium I, more than 1 pair on empodia II-IV; 2 pairs of duplex setae on tarsus I, 1 pair on tarsus II, duplex setae on tarsi III-IV associated or dissociated, coxisternal formula 2-1-1-1. Body broadly rounded without anterior cleft, prodorsum with anterior lobes more or less developed, sometimes absent, with 4 pairs of setae, opisthosoma with 12 pairs of setae, location of central fourth pair ( $f_1$ ) varying from normal to marginal; one pair of aggenital setae ( $ag_1$ ) and 3 pairs of pseudanal setae ( $ps_{1-3}$ ) present, 2 pairs of ventro-caudals ( $h_{2-3}$ ) present ventrally, 1 pair of hypostomal subcapitular seta ( $m$ ).

## Remarks

Two genera, *Toronobia* Meyer, 1987 and *Strunkobia* Livshits and Mitrofanov, 1972, are morphologically closely related to the genera *Pseudobryobia* and *Bryobia*. In both of them, setae  $f_1$  are in normal position and all the empodia bear one pair of tenent hairs that brings them closer to the genus *Pseudobryobia*. Moreover, in the genus *Strunkobia*, the prodorsal



lobes are absent and duplex setae on tarsi III and IV are dissociated as in *Pseudobryobia*. Nevertheless, in *Strunkobia*, the coxal formula is different (3/4-3/2-1-1), 2 pairs of pregenital setae (*ag*) and 2 pairs of hypostomal setae (*m*) are present. The genus *Toronobia* also differs from *Pseudobryobia* by its coxal formula (2-1-2/3-2) but also by associated duplex on tarsi III and IV and by a reduced (but obvious) conical unique inner prodorsal lobe over gnathosoma that bear  $v_1$  setae, which brings him closer to *Bryobia*.

### Species transferred to the genus *Bryobia*

According to the morphological data displayed in the Table I, 3 species, namely *P. bucharica*, *P. japonica* and *P. nikitensis* do not fit with one of the 3 main criteria of the old diagnosis of the genus *Pseudobryobia*: in these species, members of the fourth pair of dorsocentral setae ( $f_1$ ) are not in their normal position but are displaced marginally. According to the interpretations of Livshits and Mitrofanov (1972) and Mitrofanov (1973), these species would be placed in the sub-genus *Allobia* among the genus *Bryobia* (Table I). Moreover, these species and four others bear 1 seta on coxisternal plate II, two rows of tenent hairs on the empodia II-IV and are only recorded from Palearctic or Afrotropical biogeographic zones. Thus, according to the data provided and the amended genus diagnosis that we propose, the species transferred to the genus *Bryobia* (new and reinstated combinations) are the followings: *B. (Bryobiopsis) abatielloi* n. comb., *B. (Allobia) bucharica* **reinst. comb.**, *B. (A.) japonica* **reinst. comb.**, *B. (A.) nikitensis* **reinst. comb.**, *B. (B.) anacantha* **reinst. comb.**, *B. (B.) eurotiae* **reinst. comb.**, *B. (B.) neoephedrae* **n. comb.**

To date, following this genus revision, 11 species still remain assigned to *Pseudobryobia*, these are: *P. agropyra*, *P. antennaria*, *P. bakeri*, *P. canescens*, *P. curiosa*, *P. drummondi*, *P. ephedrae*, *P. filifoliae*, *P. knowltoni*, *P. kono*i and *P. namae*.

### Key to the species of *Pseudobryobia*

1. Dorsohysterosomal setae set on strong tubercles ..... 2  
— Dorsohysterosomal setae not set on strong tubercles ..... 3
2. Dorsohysterosomal setae long, strong, setae  $d_1$  and  $e_1$  well surpassing setal insertions of the consecutive rows ..... *P. namae* (Tuttle & Baker, 1964)  
— Dorsohysterosomal setae clavate, setae  $d_1$  and  $e_1$  not reaching setal insertions of the consecutive rows ..... *P. canescens* Baker & Tuttle, 1972
3. Stylophore rounded anteriorly ..... 4  
— Stylophore cleft or indented anteriorly ..... 7
4. Peritremal distal end not developed, bulbous ..... *P. bakeri* McGregor, 1950  
— Peritremal end distal end developed ..... 5
5. Distal end of peritreme thumb-finger-like ..... *P. kono*i Baker & Tuttle, 1994  
— Distal end of peritreme anastomosed ..... 6
6. Dorsal setae thickly linear ..... *P. drummondi* (Ewing, 1926)  
— Dorsal setae rodlike, expanded distally ..... *P. filifoliae* (Tuttle & Baker, 1968)
7. Stylophore indented anteriorly ..... 8  
— Stylophore deeply cleft anteriorly ..... 9
8. Prodorsal setae  $v_1$  slightly shorter than setae  $v_2$  ..... *P. antennaria* Baker & Tuttle, 1994  
— Prodorsal setae  $v_1$  about half the length of setae  $v_2$  ..... *P. knowltoni* Tuttle & Baker, 1976

9. Dorsohysterosomal setae elongate, lanceolate, short ..... *P. agropyra* (Morgan, 1960)  
 — Dorsohysterosomal setae spatulate ..... 10
10. Peritremal enlargement simple, bulbous; “U-like” pore present between setae  $f_1$  .....  
 ..... *P. curiosa* (Summers, 1953)  
 — Peritremal enlargement developed, anastomosed; propodosoma cleft between setae  $v_1$ ; leg I  
 at least 1 and 1.5 as long as body ..... *P. ephedrae* (Tuttle & Baker, 1968)

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