



Fig. 1. Sketches showing evolutionary transition from *Pseudoalbaillella* to *Follicucullus* with boundaries. PT: pseudothorax.

doalbaillella and *Parafollicucullus* Holdsworth et Jones. Ishiga et al. (1982) described *F. monacanthus* and regard *Parafollicucullus* as a synonym³ of *Pseudoalbaillella*. They suggested that this species had originated from *Pseudoalbaillella fusiformis* (Holdsworth et Jones), i.e. they drew the generic boundary between *Ps. fusiformis* and *F. monacanthus*. Kozur and Mostler (1989) established the genus *Ishigaconus* Kozur et Mostler, containing only *I. scholasticus* (Ormiston et Babcock). Kozur (1993) assigned both *Ps. fusiformis* and *F. monacanthus* to the genus *Parafollicucullus*. Wang and Yang (2007, 2011) and Wang et al. (2012) re-assigned *F. monacanthus* to the genus *Pseudoalbaillella* on the basis of the evolutionary sequence from *Ps. fusiformis* to *Ps. monacantha*. The classification of Ishiga et al. (1982) has been followed by most researchers so far. The traditional boundary between *Pseudoalbaillella* and *Follicucullus* had been substantially drawn between *Ps. internata* and *Ps. monacantha*, because *Ps. fusiformis* and *Ps. internata* had been undivided until the establishment of *Ps. internata* by Wang et al. (2012).

2.2 Diagnosis

Ito et al. (2015) placed *Ps. monacantha* in the *Pseudoalbaillella* according to the original diagnostic characteristics of the genus. The terminologies of *Pseudoalbaillella* and *Follicucullus* are shown in Fig. 1. The shell of *Pseudoalbaillella* is composed of three parts, an apical cone, a winged pseudothorax and a pseudoabdomen (Holdsworth and Jones, 1980); that of *Follicucullus* consists of an apical portion and a weakly inflated to subspherical region (Ormiston and Babcock, 1979). Moreover, *Pseudoalbaillella* has

wing(s) whereas *Follicucullus* has no wing in the original diagnoses. *Pseudoalbaillella monacantha* consists of three parts with a wing; *F. porrectus* Rudenko is composed of two parts and lacks wings. Consequently, the diagnostic boundary should be drawn between *Ps. monacantha* and *F. porrectus*. However, the shell of *F. scholasticus* is not composed of two obvious parts. If the diagnosis is strictly applied, this species is not *Follicucullus*.

2.3 Phylogenetics (cladistics)

Phylogenetic taxonomy approves of holophyletic⁴ taxa but denies polyphyletic⁵ taxa in principle (e.g. Hennig, 1965). Evolutionary taxonomy, which embraces partially phylogenetic taxonomy, prefers the use of holophyletic taxa although taxonomists debated (e.g. Grant, 2003; Rieppel, 2005; Brummitt, 2005; Ebach et al., 2006; Hörandl, 2006, 2007; Hörandl and Stuessy, 2010).

Zhang et al. (2014) proposed the *Follicucullus* phylogenetic model, which regards *Ps. monacantha* as *F. monacanthus*. The model proposes that this species evolved into both *F. dilatatus* Rudenko and *F. porrectus*. In other words, *Ps. monacantha* is the ancestor of two distinct *Follicucullus* species plus their descendants. In this case, *Follicucullus* is a biphyletic taxon if *Ps. monacantha* is included in *Pseudoalbaillella* (Fig. 2A); however, if *Ps. monacantha* is included in *Follicucullus*, as described by Zhang et al. (2014), then *Follicucullus* is a holophyletic taxon (Fig. 2B). Thus,

³Synonym: one of two or more different taxonomic names that have been applied to the same taxon.

⁴Holophyletic: a group of organisms descended from a common ancestor, and that contains all descendants from this ancestor (based on Hörandl and Stuessy, 2010).

⁵Polyphyletic: a group of organisms that contains descendants from three or more different common ancestors (with two ancestors, biphyletic is the appropriate term) (after Hörandl and Stuessy, 2010).