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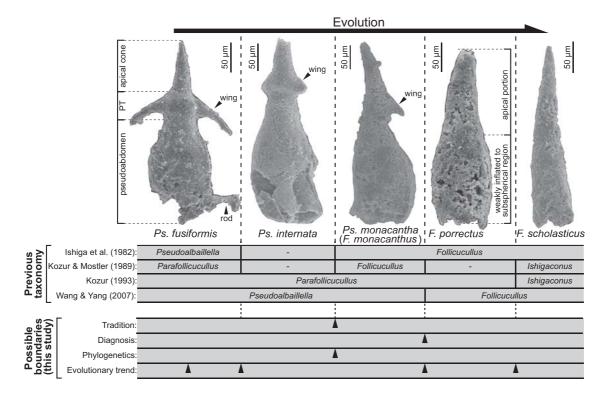


Fig. 1. Sketches showing evolutionary transition from Pseudoalbaillella to Follicucullus with boundaries. PT: pseudothorax.

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) reassigned 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 Pseudoal-baillella 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 descendents from three or more different common ancestors (with two ancestors, biphyletic is the appropriate term) (after Hörandl and Stuessy, 2010).