

Possible Boundaries between *Pseudoalbaillella* and *Follicucullus* (Follicucullidae, Albaillellaria, Radiolaria): An Example of Morphological Information from Fossils and Its Use in Taxonomy

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Recently, a middle Permian radiolarian species was reassigned from *Follicucullus monacanthus* Ishiga et Imoto to *Pseudoalbaillella monacantha* on the basis of the diagnoses of the genera *Pseudoalbaillella* Ormiston et Babcock and *Follicucullus* Holdsworth et Jones. This revision results in redrawing of the boundary between the genera; however, different boundaries could be drawn using different perspectives. As an example of fossil morphological information and its use in taxonomy, this article discusses possible boundaries from the traditional, diagnostic, phylogenetic and evolutionary perspectives. We advocate using the diagnostic boundary (between *Ps. monacantha* and *F. porrectus* Rudenko) to avoid taxonomic confusion and inconvenience.

Key words: Morphology, Taxonomy, Radiolaria, Generic Boundary, Permian

1. Introduction

Organisms have been classified as per their morphological characteristics since the taxonomic scheme in the eighteenth century as represented by Linnæus (1735). Subsequently, the idea of evolution, established by Darwin (1859), has been incorporated in taxonomy. In the mid-twentieth century, phylogenetic taxonomy was proposed by Hennig (1950, 1965). Taxonomists have attempted to classify organisms on the basis of these ideas using new methods and ideas such as phenetics and molecular phylogenetics. Numerous species concepts have been proposed (e.g. Mayden, 1999; Hey, 2001; Benton and Pearson, 2001) and thereby recent taxonomy includes several perspectives in addition to that of morphology. Moreover, the genus concept has been defined using several perspectives (Winston, 1999). Allmon (1992) discussed the genus concept in the fossil record and proposed the following: 1) the 'phylogenetic' or 'cladistic' concept, 2) 'phenetic' or 'gap' concept and 3) 'hybridization' concept. However, extinct fossil groups that have no relationship to living organisms cannot provide some types of direct information (e.g. molecular genetics). Consequently, classification of extinct fossils emphasizes morphology. The issues of how information can be extracted from the morphologies of extinct fossils, and how this information can be used in taxonomy are important and a matter for debate.

Radiolarians, which are marine protozoans, possess a siliceous skeleton and have inhabited the oceans from the

Cambrian¹ Period until the present day (De Wever *et al.*, 2001). This study focuses on the extinct fossil genera of radiolaria, *Follicucullus* Ormiston et Babcock and *Pseudoalbaillella* Holdsworth et Jones. These genera belong to the Family Follicucullidae Ormiston et Babcock of the Order Albaillellaria Deflandre. Our recent work revised the generic classification of one radiolarian species: from *Follicucullus monacanthus* Ishiga et Imoto to *Pseudoalbaillella monacantha* (Ito *et al.*, 2015). This revision was based on the diagnostic characteristics of the genera. Several researchers have considered that *Pseudoalbaillella* evolved into *Follicucullus* during the middle Permian² (e.g. Ishiga *et al.*, 1982; Ishiga, 1986; De Wever *et al.*, 2001). Our revision results in redrawing of the generic boundary; however, different boundaries can be drawn using other perspectives. The shells of *Follicucullus* and *Pseudoalbaillella* are characterized by simple features; therefore, we believe that this boundary problem is a good example of the use of extinct fossil morphology in taxonomy. This article discusses the possible boundaries between *Follicucullus* and *Pseudoalbaillella* from the traditional, phylogenetic and evolutionary perspectives in addition to the perspective using the generic definitions.

2. Possible Boundaries

2.1 Traditional definition

Ormiston and Babcock (1979) established the genus *Follicucullus*. Holdsworth and Jones (1980) established *Pseu-*

¹Cambrian: the oldest period in the Phanerozoic (ca. 540–485 Ma).

²Permian: the newest period in the Paleozoic (ca. 300–250 Ma).

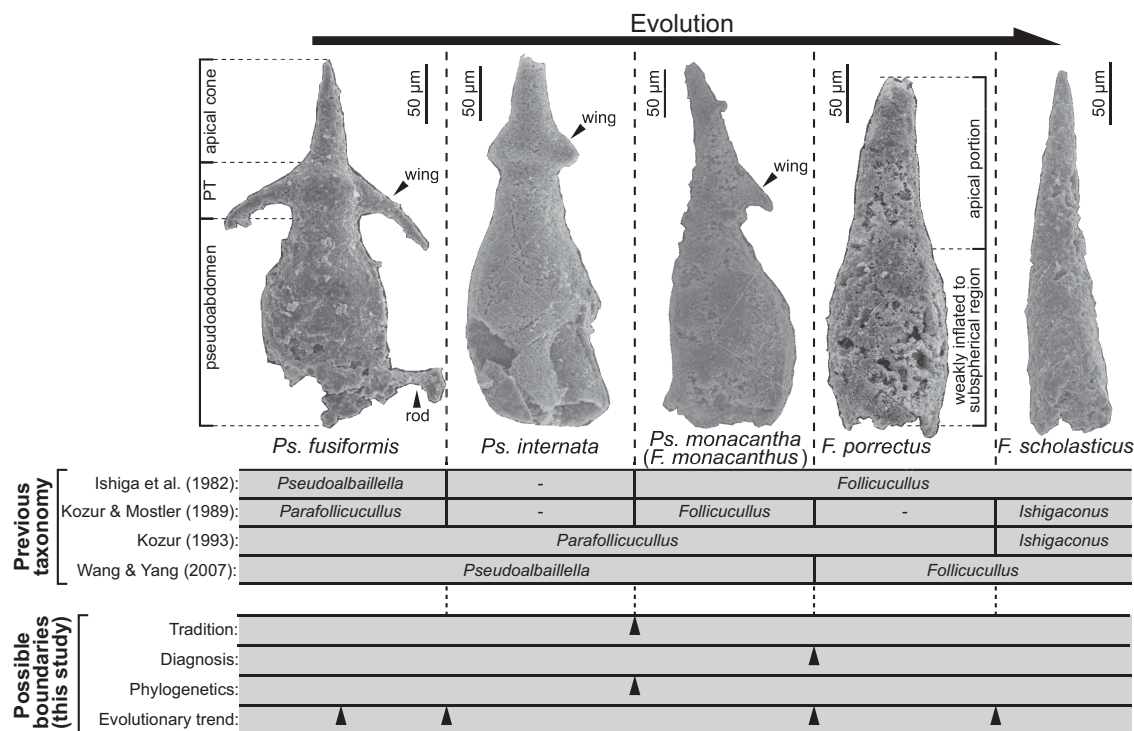


Fig. 1. Sketches showing evolutionary transition from *Pseudoalbaillella* to *Follicucullus* with boundaries. PT: pseudothorax.

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,

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).

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

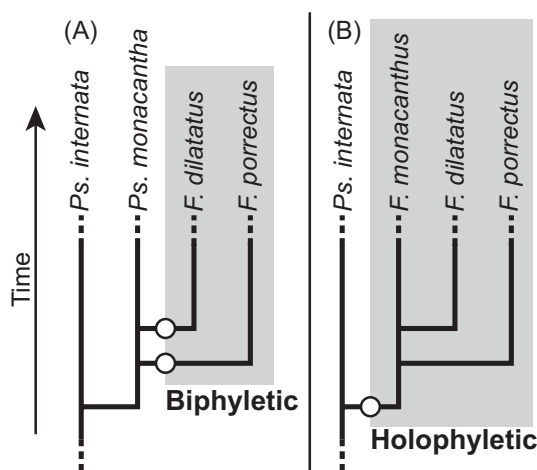


Fig. 2. Simplified evolutionary trees from *Pseudoalbaillella* to *Follicucullus*. Branches are based on the phylogenetic model proposed by Zhang *et al.* (2014). Gray parts indicate *Follicucullus*; open circles are ancestor of *Follicucullus*. (A) Case of *Ps. monacantha*. (B) Case of *F. monacanthus*.

the boundary between *Pseudoalbaillella* and *Follicucullus* should be drawn as shown in Fig. 2B from the perspective of phylogenetic and possibly evolutionary taxonomy.

2.4 Evolutionary trend

The evolutionary trend from *Pseudoalbaillella* to *Follicucullus* is characterized by simplification: the shells of these species had reduced wing(s) and gradually became slimmer (Fig. 1). Observations on the endoskeletons of living radiolaria (e.g. De Wever *et al.*, 2001) indicate that the skeletons of *Pseudoalbaillella* and *Follicucullus* were contained within protoplasmic bodies (i.e. ectoplasm). Thus, the simplification of the shell may reflect simplification of the organisms' bodies. Size reduction of fossil organisms caused by palaeoenvironmental stress is well known (e.g. Guex, 2006; Twitchett, 2007). In the case of the Albaillellaria, Guex *et al.* (2014) highlighted retrograde evolution of *Albaillella* around the end-Permian mass extinction.

It is not easy to identify an obvious boundary within the evolutionary simplification from *Pseudoalbaillella* to *Follicucullus* (Fig. 3). The apparent wing reduction began between *Ps. fusiformis* and *Ps. internata*. Meanwhile, wings connecting to rods were illustrated in some specimens of *Ps. fusiformis* in previous studies (e.g. pl. 3, figures 1–6 of Nishimura and Ishiga, 1987; pl. 2, figure 5 of Wang *et al.*, 1994), implying that the boundary should be drawn within *Ps. fusiformis*. Wing reduction was completed between *Ps. monacantha* and *F. porrectus*. The boundary of being slimmer is not determinable because the trend to slimmer was continuous in these species.

3. Concluding Remarks

Taxonomy has advanced towards being a natural rather than an artificial classification. Morphological diagnosis and classification may be artificial. Probably, phylogenetic and evolutionary classifications are nearer to a natural classification. However, the fossil record is not complete (e.g. Forey *et al.*, 2004), so the adoption of phylogenetic and evolutionary classification before their establishment might

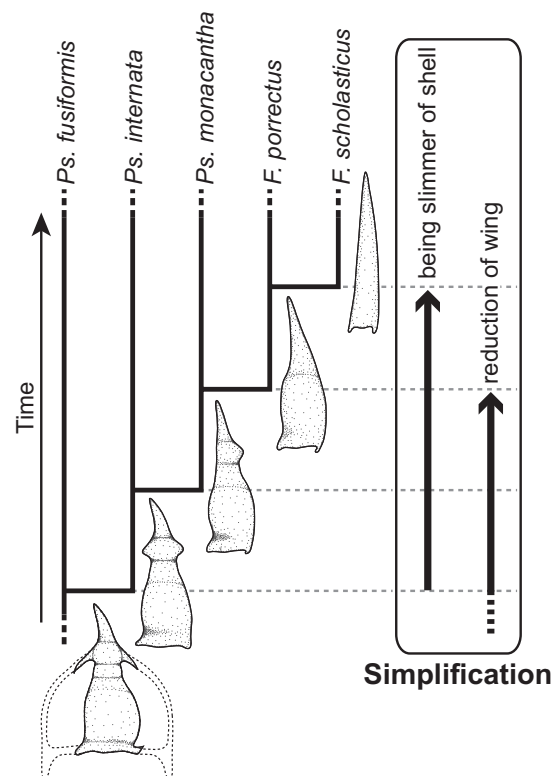


Fig. 3. Simplified evolutionary tree with evolutionary trend of *Pseudoalbaillella* and *Follicucullus*.

cause taxonomic confusion. In addition, some fossils are utilized as a tool for in biostratigraphy and/or identification of facies. A conspicuous character, i.e. artificial classification criterion, is useful as a tool. Hendricks *et al.* (2014, p. 511) stated that 'Genera are arbitrarily circumscribed, non-equivalent, often paraphyletic, and sometimes polyphyletic collections of species. They are useful tools for communication but have no theoretical or biological reality of their own and, whether monophyletic or not, cannot themselves operate in the evolutionary process'.

Diagnostic classification can avoid confusion and inconvenience. We therefore consider that this method should be fundamental to taxonomy on extinct fossils. Meanwhile, where phylogenetic and evolutionary models are well established, an attempt should be made to reassess taxonomy as a contribution to achieving a natural classification. This article described possible boundaries between *Pseudoalbaillella* and *Follicucullus* from the traditional, diagnostic, phylogenetic and evolutionary perspectives. Our proposal can be summarized as follows. The diagnostic boundary is reasonable at present. Phylogenetic classification cannot be ignored; however, the proposed phylogenetic model by Zhang *et al.* (2014) is thus far only a model. Further biometrical and quantitative analyses are necessary for evaluation of the model. If more detailed work confirms the model's validity, the phylogenetic classification is reasonable and the generic diagnoses should be emended. For palaeoecological research that uses evolutionary simplification, use of other classification schemes (i.e. non-official taxonomic terminology) is at present a more realistic and pragmatic option.

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