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Nomenclature to describe the transition from multiserial to uniserial chamber arrangement in benthic foraminifera

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ABSTRACT – We define terms used to describe the transition from a trochospiral, multiserial or biserial chamber arrangement to a uniserial chamber arrangement in benthic foraminifera. The morphological transition from a trocho-, multi- or biserial to a uniserial chamber arrangement may be abrupt, or form a morphological progression through transitional stages defined as 'loosely biserial', 'lax-uniserial' and, finally, 'loosely uniserial'. The precise meanings of the intermediate stages ending in uniseriality are defined here by means of examples using foraminiferal models. We introduce the new terms ‘Cryptobiserial’, ‘Cryptotriserial’ and ‘Cryptotrochospiral’ to describe the chamber arrangement in genera with uniserial stages that preserve the sense of coiling of the previous trochospiral, triserial or biserial stages.

KEYWORDS: foraminifera, morphology, ontogeny, chamber arrangement

INTRODUCTION
The transition from a multiserial to a biserial to a uniserial chamber arrangement is seldom abrupt or straightforward among benthic foraminifera, but is often characterized by intermediate stages. Such foraminiferal morphologies are transitional biformed, gradually changing their chamber arrangement during ontogeny from biserial to uniserial (see Hottinger, 2006). In the literature a number of loosely defined terms can be found to describe the transition to uniseriality, such as ‘loosely biserial’, ‘a tendency to become uniserial’ or ‘irregularly uniserial’. However, these terms themselves are not used consistently and are not found defined in Hottinger’s (2006) popular glossary of terms used in foraminiferal research.

As part of an effort to revise and update the descriptions of the agglutinated foraminiferal genera, we believe it is useful to precisely define the terms used to describe the transitional or intermediate stages between a multiserial or biserial chamber arrangement and uniserial growth, as so many of the agglutinated genera exhibit such behaviour. As Hottinger (2006) states in the introduction to his glossary: ‘The alternating arrangement of the shell cavities is a very fundamental and widespread pattern of the foraminiferal architecture’. The biserial chamber growth pattern is known mainly from the class Rotaliata (Mikhalevich, 2000, 2005; Mikhalevich & Debenay, 2001), which possess multilocular tests with low (brevithalamous), often globular, chambers and agglutinated or calcareous walls. This chamber arrangement is distinct in both benthic and planktonic habitats. Surprisingly, the only documented benthic-planktonic (tychoplagic) taxon is also biserial (Darling et al., 2009). Therefore, the purpose of this paper is to properly define these morphological terms to ensure that their use is consistent and well understood by foraminiferal researchers.

TERMS USED TO DENOTE THE TRANSITION FROM A BISERIAL TO A UNISERIAL CHAMBER ARRANGEMENT
Examples of the transitional stages between a biserial and uniserial chamber arrangement were generated using the moving reference model described by Łabaj et al. (2003) and by Tyszka & Topa (2005). This model accurately produces simulated foraminiferal morphologies that can be found in nature. Figure 1 illustrates the transition from biseriality to uniseriality and the intermediate stages are defined below.

Biserial
A trochospiral chamber arrangement with about 180° between consecutive chambers, thus producing two rows of chambers (Hottinger, 2006). In other words, it is an alternating chamber arrangement that creates two series of chambers. This latter definition neglects the term ‘trochospiral arrangement’ because the biserality might be generated without a helicoidal chamber pattern, i.e. directly from a planispiral arrangement (see Tyszka & Topa, 2005). In true biserial forms (Figs 1.1, 1.2) the chambers comprising each row share a common horizontal or oblique suture between them. Furthermore, two series of rows create a common ‘zigzag’ suture, which separates both series from each other.

Loosely biserial
Chambers are arranged in two alternating rows, but the chambers within a row barely make contact with one other (Figs 1.3, 1.6, 1.7). In lateral view, the sutures separating the terminal chambers extend obliquely from one side of the test to the other. They form an extended ‘zigzag’ suture, nearly lacking any horizontal sutures between chambers sharing the same series.
Lax-uniserial
The chamber arrangement is truly intermediate between biserial and uniserial, such that the ultimate chamber is only in contact with the penultimate chamber (Figs 1.3, 1.4, 1.6, 1.7). The chambers are cuneate and alternate in position and the sutures between chambers are oblique. The centre points of the chambers still preserve a biserial arrangement. The term was introduced by Neagu & Neagu (1995) to describe the genera *Hagimashella* and *Bicazammina*. The genus *Eobigenerina* described by Cetean *et al.* (2008) has a lax-uniserial stage between the initial biserial stage and the terminal uniserial stage. Loeblich & Tappan (1987) described this type of coiling as ‘alternating in a loose biserial’ in the case of *Haeuslerella*.

Alternating uniserial
The axis of growth has a zigzag form, but each segment (or rectilinear portion) of the zigzag consists of more than two chambers (Figs 1.8, 1.9). Where the growth axis shifts direction, chambers are cuneate and sutures are oblique. In the rectilinear segments, sutures are orthogonal to the growth axis. This term was introduced by Łabaj *et al.* (2003) to describe this shape based on models of foraminiferal architecture. This alternating uniserial architecture is observed in the species *Ammobaculites pauperculus* Zheng, 2001, which was described as ‘curved and twisted’ in the rectilinear portion (Zheng & Fu, 2001). In this species each segment of the zigzag consists of 3–4 chambers.

Loosely uniserial
Chambers are arranged in a single row along a straight or slightly meandering axis (Fig. 1.10), but sutures between chambers are not necessarily orthogonal to the growth axis. In loosely uniserial forms, chambers can be chaotic and irregular, as in the genus *Subreophax*.

Uniserial
Chambers arranged in a single row (Hottinger, 2006). The axis or growth is rectilinear and sutures between chambers are horizontal or orthogonal to the growth axis (Fig. 1.5). If the

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**Fig. 1.** Foraminiferal models illustrating the transition from biseriality to uniseriality (modified from Łabaj *et al.*, 2003). 1–2, biserial; 3, loosely biserial to lax-uniserial; 4, lax-uniserial to uniserial; 5, uniserial; 6, planispiral to loosely biserial to lax-uniserial to uniserial; 7, biserial to loosely biserial to lax-uniserial; 8, alternating uniserial with a twisted aspect; 9, alternating uniserial with a zig-zag pattern; 10, loosely uniserial.
Chambers are externally arranged in a single row and sutures Pseudouniserial. These terms are introduced below.

Nature of the uniserial part, which typically displays rotation of preserve the sense of coiling of the earlier part of the test. In such (or observations of the shape of the chamber interiors viewed in view from an external view; however, dissection of some foraminifera term uniserial describes the nature of the chamber arrangement growth axis is gently curved, the sutures may be oblique. The (1961) with respect to his genus Loeblich & Tappan (1987) used the term ‘pseudobiserial’ to (1961). Drawings of the genus Pseudoreophax Clavulina (Fig. 2).

Pseudouniserial
Chambers are externally arranged in a single row and sutures between chambers are horizontal or subhorizontal. Loeblich & Tappan (1985) used the term to describe their genus Gyroval- vulina, which has chambers arranged terminally in a loose spiral. Chambers gradually become broader and fewer per whorl, until each chamber extends more than half the distance around the test but is not completely uniserial. The spiralling nature of the terminal chamber is illustrated by the alternating position of the apertural tooth, which projects obliquely within the chamber cavity. Pseudouniserial coiling may be characterized further as cryptobiserial, cryptotriserial, etc. depending upon the angle successive chambers make with respect to previous chambers.

Cryptobiserial, cryptotriserial, cryptotrochospiral, etc. (new terms)
Chambers are externally arranged in a single row and sutures between chambers are horizontal, but the internal structure of the test reveals that a sense of coiling still exists, for example the position of the aperture or internal connections alternates between chambers, or twists from one chamber to the next. Chambers within the uniserial part typically rotate with respect to one another. This feature was first pointed out by Geroch (1961) with respect to his genus Pseudoreophax (Fig. 2). Loeblich & Tappan (1987) used the term ‘pseudobiserial’ to describe this mode of coiling, though we prefer the term ‘cryptobiserial’. In their description of the genus Clavulina, which is initially triserial and externally terminally uniserial, Loeblich & Tappan (1987) observed that successive toothplates in the uniserial part of the type species are orientated 120° apart, reflecting the original triseriality of the test. In general, the spiralling nature of cryptobiserial or cryptotriserial forms can be determined only by observing the internal structure of the test or asymmetries of the aperture, including the orientation of the apertural tooth in successive chambers, if present.

DISCUSSION AND CONCLUSIONS
In addition to the simple transition from biserial to uniserial, more complex trimorphic chamber arrangements are found that also include the transition from biserial to uniserial patterns. The most distinctive are triserial–biserial–and–uniserial genera, such as the agglutinated Spiroplectinata or calcareous Uvigerina, or planispiral–biserial–uniserial tests, as in the genus Plecte- eratidus recently described by Kaminski et al. (2009). These ontogenetic transitions, as well as the results of foraminiferal modelling, show that biseriality is morphogenetically related to uniseriality and planispirality (see Tyszka, 2006).

The morphogenetic reason for the transition from a biserial to a uniserial chamber pattern seems to be connected to the transition between apertures, which are responsible for the change in chamber growth (see Mikhailievich & Debenay, 2001). This true transition is usually (but not necessarily) associated with the change from basal apertures in the biserial arrangement, through areal apertures, to terminal apertures in the wholly uniserial chamber arrangement.

As mentioned previously, the biserial chamber arrangement is known mainly from the class Rotaliata (sensu Mikhailievich). Within this class, the calcareous Rotaliida sensu lato (Bowser et al., 2006), with simple biserial and coiled biserial morpho- types, form a monophyletic clade based on molecular phylogenetic evidence, including the closely related Bolivina and Brizalina, as well as cassidulinids (Schweizer et al., 2008). The same clade includes the genus Uvigerina, which shows transitions from a triserial through loosely triserial, then biserial and, finally, to a lax-uniserial chamber arrangement. These results once again show that molecular phylogeny is closely linked with morphological evolutionary trends.

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