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Original article

Two ammonite species under the same name: Revision of *Deshayesites deshayesi* (d'Orbigny, 1841) based on topotype material (Lower Aptian, Lower Cretaceous, Northeast of France)

Deux espèces d'ammonites sous un même nom : révision de Deshayesites deshayesi *(d'Orbigny, 1841) sur la base de matériel topotypique (Aptien inférieur, Crétacé inférieur, Nord-Est de la France)*

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ABSTRACT

After a review of the current state of knowledge about the classical Lower Aptian (Lower Cretaceous) ammonite index-species *Deshayesites deshayesi* (d'Orbigny, 1841) and the problems concerning the acceptation of this species, a topotype sample of 159 *Deshayesites* from the *Argiles à Plicatules* Formation (Paris Basin, northeastern France), including the lectotype of the latter species, is studied statistically. According to the Deshayesitidae evolutionary pattern highlighted by Bersac and Bert (2012), the present study shows that the whole studied population from the *Argiles à Plicatules* Formation belongs actually to a single species with a large intraspecific variability under the Dipolar Variation. Nothing supports the hypothesis of polyzonality of the level that provides the *Deshayesites* within the *Argiles à Plicatules*. The characteristics of the *Deshayesites* studied relate the latter to *Deshayesites annelidus* Casey, 1963 rather than to what is usually considered to be *D. deshayesi*. Consequently, *D. deshayesi* is revised, *D. annelidus* is treated as a junior synonym of *D. deshayesi*, and the species previously usually considered as *D. deshayesi* has to be renamed in *D. multicostatus* Swinnerton, 1935. Accordingly, it is proposed to move the limit of the *D. deshayesi* Zone downward.

Mots clés :
Deshayesites deshayesi
Ammonoidea
Biostratigraphie
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RÉSUMÉ

Après un état des lieux des connaissances concernant *Deshayesites deshayesi* (d'Orbigny, 1841), espèce index ammonitique classique de l'Aptien Inférieur (Crétacé Inférieur) et des problèmes concernant son acceptation, nous avons effectué une étude statistique d'un échantillon topotypique de 159 *Deshayesites* des *Argiles à Plicatules* (bassin de Paris, Nord-Est de la France) comprenant le lectotype de l'espèce. Sur la base des modalités évolutives des Deshayesitidae proposées par Bersac et Bert (2012), le présent travail montre que la population de *Deshayesites* des *Argiles à Plicatules* appartient à une seule et même espèce présentant une importante variabilité intraspécifique selon la Loi de Variation Dipolaire et que le niveau livrant les *Deshayesites* des *Argiles à Plicatules* n'est pas polyzonal. Il s'avère que les caractéristiques de cette population de *Deshayesites* sont celles de l'espèce *Deshayesites annelidus* Casey, 1963 et non

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celles de ce qui est jusqu'à présent considéré comme étant *D. deshayesi*. *D. deshayesi* est donc révisée en conséquence, *D. annelidus* est considérée comme un synonyme mineur de *D. deshayesi*, et il est proposé de renommer *Deshayesites multicostatus* Swinnerton, 1935 l'espèce jusqu'à présent considérée comme étant *D. deshayesi*. Il est donc proposé de déplacer vers le bas la limite de la Zone à *D. deshayesi*.

1. Introduction and exposition of the problem

The Deshayesitidae are one of the most remarkable ammonite families of the Lower Aptian (Lower Cretaceous) because of their abundance, their morphological diversity and disparity, and their wide geographic extension. Theses aspects make this family a key group for the ammonite biostratigraphy: it has provided – and still provides – most of the index-species of the Lower Aptian ammonite biostratigraphic scales of the Tethyan and Boreal realms since more than one century (Baraboshkin, 2004; Bersac and Bert, 2012; Casey et al., 1998; Hoedemaeker et al., 2003; Reboulet et al., 2006, 2009, 2014 and Fig. 1). Many other species of this family are frequently used for datation, when index-species are lacking. However, this group has suffered from poor biostratigraphic reliability for a long time, due to authors' significant divergences in species interpretation (see Bersac and Bert, 2012 for a discussion). This problem is mainly the result of a typological taxonomic approach of this group: taxa identification (species and genera) and taxonomic productions are based mostly on arbitrary characters without taking into account neither of the evolutionary patterns nor of the intraspecific variability (Bersac and Bert, 2012). The lame result of this kind of approach with such a highly morphologically diversified group is oversplitting (in the sense of De Baets et al., 2012). In the case of the Deshayesitidae, more than one hundred species were described [Klein and Bogdanova (2013) listed 168 potential species, subspecies and varieties spanned into no less than 9 genera]. This pulverization started about two centuries ago (Phillips, 1829) and reached its acme during the 1960–1980s with the significant contribution of Raymond Casey and the soviet authors (Casey, 1963; Glazunova, 1968, 1973). Despite significant improvements in the ammonite taxonomic approach derived from the concept of biological species, for more than 50 years (Callomon, 1963; Dzik, 1985; Kennedy and Cobban, 1976; Tintant, 1963; Westermann, 1966), this pulverization is still active nowadays for the Deshayesitidae (Bogdanova and Mikhailova, 2004; Lukeneder et al., 2013). Nevertheless, some authors have recently studied the Deshayesitidae with a more modern approach (Bersac and Bert, 2012; Dutour, 2005; Garcia and Moreno-Bedmar, 2010; Lehmann et al., 2015; Martin, 2003). These works helped to highlight the evolutionary modalities and the mechanisms of the intraspecific variability in this group (although sometimes variously interpreted by the authors). Bersac and Bert (2012) studied the Deshayesitidae from southern England with such an approach through the data provided mainly by the Raymond Casey's works (Casey, 1961, 1963; Casey et al., 1998). They proposed an evolutionary pattern and a significant taxonomic simplification for this group: they recognized only one chronospecies (*sensu* Simpson, 1961) divided into 8 species and 2 subspecies; they finally redefined these taxa based on the evolutionary characters highlighted. On the other hand, Bersac and Bert (2012) noticed significant differences between *Deshayesites deshayesi* (d'Orbigny, 1841) as usually understood and its own lectotype. Problematically, this latter specimen shows "primitive" evolutionary characters, the most predominantly observed in *D. annelidus* Casey, 1963, which is the mother species of the English population assigned to *D. deshayesi* (here named "English *D. deshayesi*") according to Bersac and Bert (2012). The reinterpretation of *D. deshayesi* by Bersac and Bert (2012) was based on literature data provided by English material, whereas the lectotype of this species comes form a different (but close) paleogeographic area: the eastern Paris Basin (Northeast of France, Fig. 2). The question is to know:

- whether this lectotype is an extreme variant with "primitive" morphology contemporaneous with the "English *D. deshayesi*";
- whether it is contemporaneous with *D. annelidus*.

Bersac et al. (2012) proposed an explanation: they performed a population study based on topotype material, which allowed them to conclude in favour of the second option, and to revise the taxonomy and biostratigraphy accordingly. However, Bersac et al. (2012) studied a small sample (38 specimens, which is however a significant effective statistically), and they exposed their methodology and results very briefly in a short meeting report. A new study is now required to detail the methodology and to test the Bersac et al. (2012)'s hypothesis with a significantly larger topotype sample: this is the aim of the present paper.

Note: to avoid any confusion between the different stratigraphic charts in use (those of Bersac and Bert, 2012; Bersac et al., 2012; Casey et al., 1998; and the standard chart of Reboulet et al., 2014 – see Fig. 1), where the same name of a subzone can sometimes designate two distinct ranges, we adopt here a provisory numbering of the successive subzones without naming them until exposing our final results and their stratigraphic implications. This numbering is explained in Fig. 1.

2. General considerations about the Deshayesitidae of the Anglo-Paris Basin

The Aptian Deshayesitidae are derived from the Barremian Heteroceratidae (an heteromorphic ammonite family) by the recoiling of the shell and the loss of their helical juvenile part (Bogdanova and Mikhailova, 1999, 2004; Delanoy, 1997). The ontogenetic sequence of the southern English Deshayesitidae shows five successive stages (Bersac and Bert, 2012):

- the Globular stage A;
- the stage B of Kossmatella type in the innermost whorls (Plate 3, Fig. 8a–c, 11);
- the stage C with thin and dense main ribs, and with numerous intermediate ribs;
- the stage D with strong ribs with a more spaced and robust ornamentation, and less intermediate ribs;
- the adult stage E (Fig. 3).

The intraspecific variability of the shell shape and ribbing is large and similar between the successive populations regardless to their age (Fig. 3). The main pattern of variability occurs under the Westermann's First Law of Covariation (formerly the Buckman's First Law of Covariation, see Baudouin et al., 2011), which is a special case of the most general Dipolar Variation Law (see Bert, 2013, 2014a, 2014b). It is intricated with the action of heterochronic processes, which modulate the duration of the ontogenetic stages C and D, slender and robust respectively. All the morphologies coexist within an instantaneous population, between extremely