A Dufrenoyia (Ammonoidea, Deshayesitidae) fauna from Germany: Evidence for D. furcata Zone deposits at the lower–upper Aptian boundary

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1 **A *Dufrenoyia* (Ammonoidea, Deshayesitidae) fauna from Germany:**

2 **Improving the correlation of the lower/upper Aptian boundary**

3
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5 With 9 figures, and 1 table

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8
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15
16 **ABSTRACT**

17 *Dufrenoyia* is a relevant ammonite genus for discussing the lower/upper Aptian
18 boundary on a supraregional scale. We present the first comprehensive account
19 on the genus from Germany, recording the two index species *Dufrenoyia furcata*
20 and *Dufrenoyia transitoria* from the Ahaus area. This is based on a yet
21 undescribed historical collection by the German nineteenth century palaeontologist
22 Clemens Schlüter. Our stratigraphic conclusions improves the correlation of the
23 poorly-known highest lower Aptian in Germany, particularly with the well-known
24 successions in England and France. An alleged dimorphism in *Dufrenoyia furcata*
25 is discussed.

Keywords. Ammonites; lower Aptian/upper Albian; historical material; northern Germany; Correlations

1. Introduction

Almost 60 years ago Raymond Casey recommended to place the lower/upper Aptian boundary at the last occurrence of *Dufrenoyia*, at the top of the *Tropaeum bowerbanki* Zone, based on the well-exposed Lower Greensand succession in southern England (Casey, 1961). In fact, in the Boreal-Atlantic subrealm *Dufrenoyia furcata* can be used as an alternative to the uppermost lower Aptian zonal index *Tropaeum bowerbanki* (Lehmann, 2015). Although this has been debated over the years (e.g. Kemper, 1971) it is now widely accepted (Reboulet et al., 2011; 2018; 2014). Our current knowledge indicates that the ammonite genus *Dufrenoyia* is a well-established marker for recognizing the lower/upper Aptian boundary in the Boreal as well as in the Tethys (Raisossadat et al., 2008), whereas the distribution of other important markers like *Tropaeum* and *Australiceras* is comparatively restricted (Lehmann et al., 2015).

The Aptian ammonites of the genus *Dufrenoyia* from North Germany described here are a part of a collection assembled in the nineteenth century. At that time, many small clay pits were existing in that area from which a large number of fossils were collected. Nowadays, there is hardly any outcrops left. This is the main reason why only 15 papers illustrating ammonites from *in situ* occurrences from the Aptian in North Germany were published in the past 50 years (Kemper, 1971a, 1973a; Kemper and Zimmerle, 1978; Gaida et al., 1978; Kemper, 1976, , 1982a, , 1995; Weber, 1996; Mutterlose, 1996; Owen in Mutterlose et al., 2003; Hoffmann and Mutterlose, 2011; Vespermann, 2006; Mutterlose and Wiedenroth,

2009; Lehmann et al., 2012; Lehmann et al. , 2016). Among those, ammonite systematic is only addressed in a couple of contributions (Owen *in* Mutterlose et al., 2003; Hoffmann and Mutterlose, 2011) and thus each further account is reasonable.

2. Geological setting

All specimens referred to here have been obtained from the vicinity of the city of Ahaus in northern Germany. During the Early Cretaceous this area was at the western rim of the Lower Saxony Basin (LSB in the following; Fig. 1). The LSB contains a several thousand meters thick sedimentary succession, spanning a time interval from the latest Jurassic to the Late Cretaceous. During Aptian times, the LSB was subdivided by small swells and islands into subbasins, but generally it constituted a large epicontinental sea extending to the Proto-North Sea area, and connected to the (proto-)Atlantic Ocean in the southwest and northwest (Kemper, 1979; Ziegler, 1990). In the distal areas predominately shales were deposited, including the local expression of OAE 1a (e.g. Lehmann et al., 2012), whereas towards the basin margin, silty to sandy dark-grey claystone prevailed (Mutterlose and Böckel, 1998). The material described here comes from a restricted southernmost extension of the LSB called the Alstätte Bay (e.g. Lehmann et al., 2012; von Bargaen and Lehmann, 2014; Schlak et al., 2016; =Alstätte Embayment of Kemper, 1973b and Herngreen et al., 1994). It represents one of several small bays at the southwestern margin of the LSB (Wolburg, 1954; Schott et al., 1969). Sediments of the Alstätte Bay were poorly exposed for many decades and thus very little research was done for many years. This changed fairly recently and a whole series of papers on the temporary EGW section in

Ahaus-Alstätte that was exposed from 2009 to 2019 was published (Hoffmann and Mutterlose, 2011; Lehmann et al., 2012; Bottini and Mutterlose, 2012; Mutterlose and Bottini, 2012; von Bargaen and Lehmann, 2014; von Bargaen et al., 2016; Mutterlose et al., 2014; Schlak et al., 2016; Lübke and Mutterlose, 2016; Lehmann et al., 2016). However, the Ahaus area became a classic area for Aptian palaeontology in Germany already in the 19th century due to a large number of fossiliferous, but now abandon clay pits (e.g. Ewald, 1861; Hilbck, 1867; Ziegler, 1873). It is quite surprising that the material focussed on herein can add quite a few new data to this classical and seemingly well-explored area of palaeontological research in Central Europe.

Figure 1 somewhere near here

3. Material and conventions

3.1 Previously known material

Dufrenoyia is a very rarely reported ammonite from Early Cretaceous deposits of Germany. Already von Strombeck (1858: 444) reported an ammonite, erroneously referred to as *Ammonites Deshayesi*, that is a *Dufrenoyia* since the cross section shows a distinct ventrolateral edge (“Die Kante zwischen Rücken und Seite pflegt dagegen bis ins höchste Alter hervorzustechen”).

First finds attributed to a species that is now included in *Dufrenoyia* were mentioned by Ewald (1861: 338; not 1860 as cited by von Koenen 1902) from the Ahaus area (Barler Berg) as *Ammonites furcatus*. The same specimens were later briefly described by von Koenen (1902: 202-204), referring to them as *Hoplites furcatus* Sowerby. Besides 10 specimens from the Ahaus area von Koenen (1902) mentions two doubtfully conspecific specimens from Weenzen, Duingen area, in

the Hildesheim district. More recently, Kemper (1964: 42) referred to one of these specimens in the University of Münster collection as *Dufrenoyia dufrenoyi* (d'Orbigny, 1840) [sic] – apparently the only specimen that survived until then. Kemper (1971: pl. 26, fig. 2) figured *Dufrenoyia furcata* and since his figure captions refers to being a part of the University of Münster collection it can be assumed that he refers to the same specimen and actually revised his earlier identification. In fact, this historical specimen remained the only material depicted in the literature from Germany and consequently Kemper (1976: pl. 24, fig. 1 and, 1995: pl. 5, fig. 2) refigured this important find.

3.2 New material and conventions

One of us (JL) was visiting the historical collection of Clemens August Schlüter (Fig. 2A) as a part of the University of Bonn collection in 2016, recognizing that the Aptian/Albian part of this collection was scientifically not explored yet. All of the material is housed in the Goldfuß-Museum für Paläontologie, University of Bonn, Germany. Its acronym is IGPB (for “Institut für Geowissenschaften, Paläontologie, Bonn”). Since these specimens are of historical importance additional to their scientific value, no preparation works have been done to reveal the suture lines. However, IGPB KrU16-5 is a slightly worn internal mould that shows the suture. We used the suture terminology of Wedekind (1916), as applied by Kullmann and Wiedmann (1970) and modified by Korn et al. (2003): E - external lobe, A - adventive lobe (that is L of traditional nomenclature), U - umbilical lobe (I - internal lobe is not applicable for the present material). The E/A (that is E/L of traditional nomenclature) is the saddle between E and A and A/U (L/U of traditional nomenclature) and corresponds to the saddle between A and U. The

differentiation into U_2 and U_3 is used here according to the conclusions on suture ontogeny of *Dufrenoyia* by Schindewolf (1967). For most specimens it was not possible to give conch dimensions, D represents the diameter, U the width of the umbilicus (further details and measurements see [Supplementary data](#)).

The nineteenth century palaeontologist Schlüter (Fig. 2A) became famous by publishing 164 papers on Late Cretaceous and Devonian fossils from North Germany in between 1859 and 1902 (Steinmann, 1908; Riegraf and Scheer, 1991b, b). Many of Schlüter's papers are based on fossils collected by himself, he was a successful collector from an early age (Steinmann, 1908). During the first part of his career he almost exclusively published on Late Cretaceous fossils from Germany and in 1878 this changed and he also concentrated on the description of Devonian fossils (Riegraf and Scheer, 1991a). In fact, Early Cretaceous fossils never drawn his attention, except for a paper on glacial erratics (Schlüter, 1874). This is one reason why he never worked on the fossils at hand, but also because he borrowed it to J. Ewald who used it together with a collection of von der Marck from the same locality to give an overview, however, without figuring them (Ewald, 1861). Nevertheless, the Ewald (1861) paper presents identifications that are referred to in the recent literature as doubtful (Klein and Bogdanova, 2013: 125) and thus it is relevant to figure all of the original material that survived here.

Figure 2 somewhere near here

In this respect it is astonishing that Edwin Kemper never used the collection of the University of Bonn. Kemper was a geologist and palaeontologist widely known for his comprehensive work on the Early Cretaceous of the LSB in Germany (e.g.

Kemper, 1982b; Kemper, 1987). His work comprised Aptian ammonites quite intensively, but although he used historical material from various sources, he probably overlooked Schlüter's collection, because the latter was widely-recognized for his collection of Late Cretaceous and Devonian fossils only. This assumption is underlined by a statement in his famous "Bentheimführer" (Kemper, 1976) that there is nice material is kept in the collection of Münster University and the Natural History Museum in Enschede (The Netherlands).

3.3 Locality details

In 1853 quarrying first exposed Aptian sediments in the Ahaus area (Ewald, 1861). This exposure is now long covered again, but together with succeeding clay pit activities it is known today as the classical Barler Berg near Ahaus locality for fossils in Germany (Kemper 1976; Lehmann et al., 2012). Most of the specimens described here are, however, lettered in red "Wüllen" (Fig. 2C). Besides, some of these have an additional label associated in the specimen box that states "Wüllen bei Ahaus, Unterer Gault, C. Schlüter leg." Some labels show that Schlüter identified the *Dufrenoyia* specimens correctly based on the state of the art of his time. Several identifications are given on the labels associated, and in one case (old inventory number 223, IGPB KrU16-5) a label is fixed on the specimen with that information and the identification "*Ammonites furcatus* Sow. = *A. Dufrenoyi* d'Orb." (Fig. 2B). Apparently, Schlüter was aware of his finds, but simply did not do the scientific work by himself (compare 3.2). Some fossils in the collection are labelled with the locality name "Barler Berg", as also indicated by red letters on the specimens (e.g. IGPB KrU15-13, a phylloceratid; IGPB KrU15-10, a pleurotomariid gastropod). In this case the year of collecting is given (1899, respectively 1864). A

couple of labels associated with the *Dufrenoyia* material states that they were collected from “Wüllen” in 1863 (IGPB KrU18-10) respectively 1865 (IGPB KrU-14-25). However, Wüllen is the name of the next larger settlement and is used synonymous with “Barler Berg”, that is a more precise name for indicating where the former pits were located (Fig. 3). We assume both locality names are used synonymous by Schlüter who, however, apparently did not changed the name used for this collecting locality at one point in time. We call the locality Barler Berg here, since “Wüllen” is widely used in the literature to refer to a former limestone quarry (Riegraf, 1997) of Late Cretaceous (Turonian) age (e.g. Wittler, 2003; Wiese, 2009; Karl et al., 2012) and even a formation in the Turonian of Westphalia is named after Wüllen (Niebuhr et al., 2007).

Figure 3 somewhere near here

The Barler Berg locality is also called “an der Frankenmühle” (von Strombeck, 1858; Ewald, 1861), referring to the name of a farmyard about 1 km WSW of the Frankenmühle, as clarified by Kemper (1976: figure caption to pl. 24, fig. 1; Fig. 3). This locality name was alternatively spelled “Frankemölle” (Bentz 1930) or “Frankenmölle”, see Kemper 1976) in historical times. Hosius (1860: 68) reports an alternation of glauconitic marlstones and iron-containing sandstones, sometimes silicified, of varying hardness from the Frankenmühle locality. The matrix of the specimens at hand are in general accordance with this observation. All specimens show a carbonaceous matrix and mostly this contains many coarse quartz grains (Fig. 2B), almost all are reddish and this indicates that they are rich in iron, but there is are also a few specimens

preserved in a light grey claystone. In fact, there are is an examples where a specimen preserved in grey claystone is associated with a specimen in carbonaceous matrix in the same box and the same label in the collection (IGPB KrU14-25 and IGPB KrU14-25b). Although these two preservations indicate an origin from beds of contrary rock types, this is in accordance with the alternation of different lithology at one and the same spot as described by Hosius (1860).

4. Systematic palaeontology

Suborder Ammonitina Hyatt, 1889

Superfamily Deshayesitoidea Stoyanow, 1949

Family Deshayesitidae Stoyanow, 1949

Dufrenoyia Kilian and Reboul, 1915

Preliminary remarks. Among Cretaceous ammonoids, the Deshayesitidae show a particularly large variability. As already outlined by Bersac and Bert (2015) and Lehmann et al. (2016), many of the species and even genera described are in need of a critical evaluation.

Several attempts have been made in the last two decades to evaluate the intraspecific variability of the western European populations of *Dufrenoyia*. Large number of specimens show that there is a considerable variability in the course of time, but also in the individual assemblages (fossil “populations”) that are from a short stratigraphic interval. Such “populations” were investigated from France by Martin (2003) and Dutour (2005). Interestingly these two authors outlined the variability of the French “populations”, but reached different systematic conclusions regarding the number of taxa represented. According to Martin (2003)

all specimens from SE France, including *Dufrenoyia dufrenoyi* (d'Orbigny, 1841), fall within the range of variation of *Dufrenoyia furcata* (J. de C. Sowerby, 1836). To the difference, Dutour (2005) retains three successive palaeospecies (? forming a chronospecies): *Dufrenoyia furcata*, *Dufrenoyia praedufrenoyi* Casey, 1964 and *Dufrenoyia dufrenoyi*. Since, a quantitative study of more than 1200 specimens from Spain was conducted by García and Moreno-Bedmar (2010), who concluded that sexual dimorphism occurs in *D. furcata*. These later authors did not directly address the distinction between *D. furcata* and *D. dufrenoyi*, even so they kept the two species separate.

The Mediterranean faunas on which those population studies were carried out are based on juvenile pyritized internal moulds (diameter < 30 mm) that cannot be compared with our material. With two exceptions, our material represents later growth stages with a diameter ranging from 50 to 75 mm. Preserved suture lines indicate a reconstructed diameter of at least 100 mm for some specimens.

The collection herein studied compares best with the *Dufrenoyia* from the Lower Greensand of England monographed by Casey (1964, 1980). The variability of these forms was recently addressed since by Bersac and Bert, 2012), who concluded that the many taxa described by Casey fall within the range of variation of two palaeospecies: *Dufrenoyia furcata* (J. de C. Sowerby, 1836) and *Dufrenoyia dufrenoyi* (d'Orbigny, 1841).

Bersac and Bert (2012: 219 and 223) were aware of the limited quality of their database that was compiled from literature data and photographic material. They already pointed out that “the specimens studied from the Monograph were initially selected by Casey to illustrate an essentially typological taxonomic division, and

thus they were not sampled in order to conduct a population study” and that “the number of specimens per sample is low to very low”.

Regarding *Dufrenoyia*, the quantitative study performed by those authors is based on 31 specimens originating from three different geographic and geological settings (Hythe Beds, Kent; Carstone, Norfolk and Ferruginous Sands, Isle of Wight). The precise stratigraphic position in the *T. bowerbanki* Zone of at least a third of the material studied is either vague, inferred or unknown (Casey, 1961, 1964). In our opinion, the conclusions reached by Bersac and Bert (2012) can only be regarded as a working hypothesis.

Dufrenoyia furcata (J. de C. Sowerby, 1836)

Figs. 4.A-J, 5, 6

1836 *Ammonites furcatus* J. de C. Sowerby in Fitton, p. 339, pl. 14, fig. 17

1925 *Dufrenoyia furcata*; Burckhardt, p. 17; pl. 10, figs. 12, 13 (refigured holotype of J. de C. Sowerby 1836)

1930 *Dufrenoyia furcata*; Spath, p. 435

1964 *Dufrenoyia furcata* (J. de C. Sowerby); Casey, p. 378, pl. LXII, fig. 2a-c (= holotype of J. de C. Sowerby, 1836), fig. 3a-b, pl. LXIII, fig. 1, pl. LXV, fig. 1a-b, text-fig. 134d (= reproduction of J. de C. Sowerby, 1836, pl. 14, fig. 17), text-fig. 135, 136a-c.

1964 *Dufrenoyia formosa* Casey, p. 395, pl. LXIII, fig. 3, pl. LXV, fig. 3, pl. LXVI, fig. 4, 5a-b, text-fig. 140h.

1964 *Dufrenoyia mackesoni* Casey, pl. LXII, fig. 4a-b ; pl. LXIII, fig. 5a-b ; pl. LXV, fig. 4a-b ; text-fig. 140d.

275 1968 *Dufrenoyia furcata* (J. de C. Sow.); Kemper, pl. 24, fig. 1 (= Kemper 1971a
276 and 1976, both pl. 24, fig. 1).

277 1971b *Dufrenoyia furcata* (J. de C. Sow.); Kemper, pl. 26, fig. 2 (= Kemper,
278 1968, 1971a, as well as Kemper 1976: each pl. 24, fig. 1).

279 1995 *Dufrenoyia furcata* (J. de C. Sow.); Kemper, pl. 5, fig. 2 (= Kemper, 1968,
280 pl. 24, fig. 1).

281 2015 *Dufrenoyia furcata*; Lehmann, Fig. 15.2 (holotype refigured)

282

283 Remarks. Full revision of *D. furcata* is beyond the scope of the present
284 contribution. A full list of citations is given by Klein and Bogdanova (2013), who did
285 not revise the species. Additionally, specimens attributed to this species were
286 illustrated by Delanoy et al. (2013), Pictet et al. (2016) and Bersac and Bert
287 (2019).

288

289 *Material.* 15 specimens, IGPB KrU14-13, IGPB KrU14-14, IGPB KrU14-25a, IGPB
290 KrU17-5a, IGPB KrU17-5b, IGPB KrU17-5c, IGPB KrU17-8a, IGPB KrU17-8d,
291 IGPB KrU17-11, IGPB KrU17-12, IGPB KrU17-13, IGPB KrU18-10, KrU18-8b,
292 IGPB KrU18-11, IGPB KrU18-22; probably conspecific is KrU14-25b, short and
293 distorted fragments referred to as *Dufrenoyia* sp. because of their poor
294 preservation.

295

296 **Figures 4, 5 and 6 somewhere near here**

297 *Description.* Specimens IGPB KrU17-5a and IGPB KrU17-5b are juveniles that
298 compare with the early whorls of IGPB KrU.17-8b. At a diameter of 25 to 30 mm,
299 the coiling is moderately involute (U/D around 0.29, see [Supplementary data](#)) with

300 a C whorl section. Both specimens are densely ribbed with usually one secondary
301 rib in between two primary ribs (10 primary and 11 secondary ribs per half whorl in
302 IGPB KrU17-5a: Fig. 4.E). Height of the onset of secondary ribs varies strongly,
303 either on the lower third of the flank high or at about mid-flank. All ribs weaken on
304 the ventral area. They bear small clavate tubercles on the ventral shoulder. A
305 smooth siphonal band can be observed. This feature is less expressed on IGPB
306 KrU17-5a (Fig. 4.E) than in IGPB KrU17-5b (Fig. 4.F).

307 IGPB KrU17-5c (Fig. 4.D) is a poorly preserved fragment of a juvenile marked by
308 coarser ornamentation and well expressed ventrolateral clavi and smooth siphonal
309 band.

310 Most specimens at hand are mid-size with a maximum reconstructed diameter
311 ranging from 50 to 100 mm. The coiling is moderately involute (U/D around 0.26,
312 see [Supplementary data](#)) with a subrectangular whorl section. The flanks are
313 ornamented by very strong, radiate and flexuous ribs, with primary ribs very
314 prominent and high on the lower and mid flank of most specimens even.

315 This is less marked on IGPB KrU14-14 (Fig. 4.I) that is distorted, but nevertheless
316 differs from all other specimens by a shallower umbilical wall and a more evolute
317 coiling; additionally, the flexuous ribbing is generally prorsiradiate and not radiate.

318 IGPB KrU17-11 (Fig. 5) is distorted and thus the ribbing is less distinct on the right
319 side of the shell, but the left side better retains the original inflation of the shell and
320 here the strength of ribbing is as prominent as usually at this growth stage.

321 However, ribbing in IGPB KrU17-11 is less flexuous and denser compared to other
322 specimens of the same size.

323 The last rib preserved in IGPB KrU17-13 (Fig. 6; estimated diameter of 70 mm,
324 maximum whorl height of 30 mm) is standing closer compared to previous ribs and

the last three ribs are clearly thinner than previous ones; additionally a broadening of the body chamber is noted at the aperture. Furthermore, the umbilical wall is shallower for the last quarter of the whorl compared to the other specimens and the coiling appears more evolute.

There are in between 9-10 primary and secondary ribs per half whorl (Table 1). Secondary ribs are regularly alternating with primary ribs to the exception of IGPB KrU17-8d (Fig. 4.B) where a pair of secondary ribs can be observed between to primary ribs. All specimens show ventrolateral clavi united by transversal ribs across the siphonal area (i.e. without smooth siphonal band), giving the venter a tabulate appearance in cross section with clear ventrolateral edges and a flat venter in between.

Table 1 somewhere near here

Discussion. The Barler Berg material illustrates well the ontogenetic stage 2 (ventrolateral clavi bordering the smooth siphonal band) and 3 (ventrolateral clavi united by transversal ribs) of the genus *Dufrenoyia* as defined by Casey (1964). Specimens IGPB KrU17-5a (Fig. 4.E) and IGPB KrU17-5b (Fig. 4.F) clearly shows that the beginning of ontogenetic stage 3 is at about 25 to 30 mm. This is typical of the *Dufrenoyia* from the lower part of the *Tropaeum bowerbanki* Zone (*D. transitoria* Subzone) of the Lower Greensand.

Among those, *Dufrenoyia formosa* and *Dufrenoyia mackesoni* corresponds best to most of the specimens at hand. Even so their morphology is more slender than that of the holotype of *Dufrenoyia furcata* (refigured here, Fig. 7) with a slightly more involute coiling, a slightly narrower whorl section and a somewhat finer

350 ribbing, we consider them as conspecific. This is in agreement with Bersac and
351 Bert (2012) treatment of those taxa.

352

353 **Figure 7 somewhere near here**

354

355 Among the juvenile specimens from Barler Berg IGPB KrU17-5b (maximum
356 diameter 25mm, maximum diameter around 12 mm; Fig. 4.F) corresponds well to
357 alleged macroconchs of same size figured by García and Moreno-Bedmar (2010)
358 in its comparatively to microconchs fine and less dense ribbing of primary and
359 secondary ribs, and a siphonal zone that gets smooth by a discontinuous ribbing
360 across the venter. In contrast IGPB KrU17-5a (Fig. 4.E, reconstructed maximum
361 diameter 30mm, maximum whorl height 14mm) shows continuous ribs across the
362 venter, and pretty distinct ventrolateral bullae, as well as a dense ribbing and thus
363 could be regarded as a microconch. We cannot see a fairly evolute coiling in our
364 juvenile microconch though, however, it needs to be emphasized that the
365 conclusions by García and Moreno-Bedmar (2010) are based on a sample size
366 that is statistically significant. The advantage of our material compared to that of
367 Martin (2003) and García and Moreno-Bedmar (2010) is that it represents adult or
368 at least subadult specimens that are supposed to show indications for dimorphism
369 more clear than juveniles, particularly modifications of the mature body chamber
370 (Klug et al., 2015). Another advantage is that some also allow – at least to some
371 extend - an assessment of the juvenile stage morphology. The features of IGPB
372 KrU17-13 (Fig. 6) described above (broadening of section and modified ribbing at
373 the aperture, umbilical wall shallower, coiling more evolute) probably indicate that
374 it reached maturity at its estimated maximum diameter of 70 mm (maximum whorl

height 30 mm). Contrary specimen IGPB KrU17-22 does not show signs of maturity although it is larger. This fragment (maximum whorl height of 35 mm) is still septate at its initial part preserved, and the estimated diameter is larger than 120 mm.

The irregularity of ribbing in this group of ammonites is remarkable. It is well-known from systematic descriptions that primary and secondary ribbing is not perfectly alternating in *Dufrenoyia*. Additionally, in several cases an individual primary rib on one side of the shell corresponds to a secondary rib on the other in our material (IGPB KrU14-14: Fig. 4.I; IGPB KrU17-12: Fig. 4.J, IGPB KrU14-25a: Fig. 4.G) and occasionally pathologies occur (IGPB KrU14-13: Fig. 4.C; IGPB KrU17-12: Fig. 4.J) or other irregularities in ornament occur (IGPB KrU17-8d: Fig. 4.B). A pretty extensive occurrence of pathologies could be related to a partially demersal life style (e.g. Keupp and Ilg, 1992, 1994), but the general abundance of irregularities is difficult to explain.

To summarize the *Dufrenoyia* material at hand is varying much. A sexual dimorphism is not apparent in our material and the morphological disparity might be also explained by a wide range of phenotypic plasticity.

Distribution. In the eponymous zone widely distributed in Europe (England, Germany, France, Spain), Turkmenistan, northern Caucasus in Russia, Mangyshlak peninsula in Kazakhstan (Casey, 1964; Kemper, 1976; Ropolo et al., 2006; García and Moreno-Bedmar, 2010). Not all of the non-European occurrences are certain, as well as the records from Egypt (Aly, 2006) and Japan (Obata et al., 1982).

400 *Dufrenoyia transitoria* Casey, 1961

401 Figs. 8, 9

402

403 1961 *Dufrenoyia transitoria* sp. nov., Casey, p. 594; pl. 83, figs. 3a-b.

404 1964 *Dufrenoyia transitoria* Casey, Casey, p. 388, pl. LXV, fig. 6, pl. LXVI, fig. 2a-b

405 (= CASEY, 1961, pl. 83, fig. 3a-b), fig. 3a-b, text-fig. 140b, 141, 142.

406

407 A specimen from Spain that is doubtfully representing the species from our point of
408 view was figured by Moreno-Bedmar et al. (2012: appendix fig. 6i)

409

410 *Material.* 2 specimens, IGPB KrU16-5 (former inventory number 223) and IGPB
411 KrU18-23.

412

413 *Description.* The best preserved specimen (IGPB KrU16-5) is a half whorl,
414 representing a part of a phragmocone and a partial body chamber with a
415 maximum whorl height of 47 mm and a reconstructed maximum diameter of
416 around 95 mm (Fig. 8).

417 The ribbing is prominent on the flanks, but not very strong, and generally irregular.

418 The strength of the primary ribs is variable. Some are well individualised while

419 others tend to fade on the lower third of the flank. Some secondary ribs are

420 intercalated and arise on the lower third of the flank or at mid-flank; others are

421 branching from the primary ribs at an umbilical bullae; and thus have almost the

422 same appearance as the primary ribs. There are 30 primary and secondary ribs

423 per half a whorl. The ribs are very strong across the venter, more prominent

424 compared to the flanks. In cross section the venter is tabulate, with a rounded

ventrolateral edge and a very slightly arched venter between the edges. The flanks are broadest on the lower third of the flank. The umbilical seam is well-rounded.

A second fragment with a whorl height of about 90 mm is slightly worn, with dense, weak but fairly broad and slightly flexuous ribs that are most prominent near the umbilicus and at the ventrolateral edge. Occasionally secondary ribs are intercalated that arise on the upper flank; the ribs are crossing the venter less prominently.

Figure 8 and 9 somewhere near here

Although the surface of IGPB KrU16-5 is slightly worn the characteristics of the suture line is fairly well-visible on the penultimate suture of the right side of the shell (Fig. 9). The E lobe is slender and high, the A lobe is the most prominent element of the suture line, trifold and barely symmetrical. Lobe U_2 is trifold and asymmetrical. The U_3 is very small, located just above the umbilical edge, in comparison with the U_2 , and little frayed. The E/A saddle is broader than the A lobe and shows a deep and moderately broad incision in the middle. The A/ U_2 saddle is prominent, symmetrical, with a deep and moderately broad incision in the middle.

Discussion. An early tendency to weak ornament (called “rapid degeneration of sculpture” by Casey, 1964) is characteristic for this species and the cross-section matches well the cross section given by Casey (1964: Fig. 140b). The suture line was described by Casey (1964: 388) as „with subquadrate ventral lobe and symmetrically trifold first lateral lobe“. His ventral lobe corresponds to the external

lobe and the first lateral lobe is the A lobe (see conventions in chapter 3.2). A subquadrate external lobe is also reported for the earliest ontogeny by Schindewolf (1967), in a juvenile suture referred to as representing *Dufrenoyia dufrenoyi*, but the E is well-visible in IGPB KrU16-5 and is in fact higher and slender. IGPB KrU16-5 agrees in having a trifid A, however, it is not symmetrical. Lobes and saddles are less regularly frilled with stouter folioles and lobules (*sensu* Yacobucci and Manship, 2011) compared to the suture lines figured by Casey (1964: pl. 66, fig. 3a, b; text-fig. 141), and thus the general appearance of the suture line is less symmetrical in IGPB KrU16-5. The surface of IGPB KrU16-5 is slightly worn and it is most likely that these differences are due to a less favourable preservation of this feature compared to the Lower Greensand specimens.

Bersac and Bert (2016) regards *Dufrenoyia transitoria* as one of the slender morphologies of *D. furcata*. In our opinion, *D. transitoria* has a highly distinctive dense and irregular ribbing style that do not compare with any other *Dufrenoyia* from the Lower Greensand. As such, we believe that the species should be kept separate until more material comes available to discuss Bersac and Bert's view.

Distribution. Outside England and Germany, the species was identified the Paris basin (Amédéo and Matron, 2004). Occurrences from Romania (Avram, 1976) and southeast France (Ropolo et al., 2006) are poorly documented (ventral view not illustrated) and cannot be ascertained. Moreno-Bedmar et al. (2010) illustrated a single specimen from Spain that superficially match *D. transitoria*. The ribbing style and ventral area are closer to those of *D. dufrenoyi* from the same locality than to typical *D. transitoria*.

5. Biostratigraphy and correlations

Kemper (1971) introduced a new biostratigraphical scheme for the Aptian of NW-Germany that was derived from the stratigraphical scheme for the Lower Greensand in southern England established by Casey (1961 and succeeding publications). Kemper (1971, 1995) used both, *Dufrenoyia furcata* and *Tropaeum bowerbanki*, as a zonal index to characterize the highest lower Aptian (Fig. 10).

The occurrence of both species was later used to correlate the lower/upper Aptian boundary between both areas (Casey et al., 1998), although the British scheme is formally slightly different. Casey (1961) defined a *Tropaeum bowerbanki* Zone, subdivided into a *Dufrenoyia transitoria* Subzone at the base and a *Chelonicerias* (*Chelonicerias*) *meyendorfi* Subzone at the top. This interval characterises the uppermost lower Aptian and the genus *Dufrenoyia* ranges from its base to close to its upper limit (Casey et al 1998: Fig. 6).

Casey et al. (1998) retained this zonation, and unequivocally stated that they regard the *Tropaeum bowerbanki* Zone as a synonym for the *Dufrenoyia furcata* Zone (p. 530). A correlation with the West Mediterranean province is thus clear, in fact a *Dufrenoyia furcata* Zone is widely used in this part of the Tethys (Reboulet et al., 2009; 2011; 2018; 2014), but obscured by different zonal names. This is the reason why we prefer to use a *Dufrenoyia furcata* Zone. It makes sense to homogenize the biostratigraphical zonation since *D. furcata* can be recognized in a much wider area than *Tropaeum bowerbanki*.

Figure 10 somewhere near here

6. Morphochange and its palaeoenvironmental background

Representatives of the ammonite family Deshayesitidae are widely known as abundant in shallow habitat, less dominant in hemipelagic settings (e.g. the Vocontian basin and Carpathian belt), since we know that *Deshayesites* itself is missing in pelagic deep-water (Mikhailova and Baraboshkin, 2009). Despite the fact that it is a challenging field, some studies try to link the distribution of morphotypes to facies respectively environmental change (Martin, 2003; Lehmann et al., 2016). In the case of *Deshayesites* it has been demonstrated that variability among alleged chronospecies of this family is steered by palaeoenvironmental change and thus might eventually lead to divergent selection (Lehmann et al., 2016).

In southern France, Martin (2003) reports a change to coarser ornamentation through time in *Dufrenoyia*. The average number of ribs per whorl changes from 37 to 28 in the three succeeding “populations” (for each “population” material from different localities is involved) individualised by this author. This trend is interpreted as an adaptive reaction to prograding shallow water facies. This appears to be opposite to the changes interpreted for *Deshayesites* (Lehmann et al., 2016), but agrees with the idea of a principal tendency of strongly tuberculated ammonites, with depressed cross-sections, prefer nearshore deposits (Wilmsen and Mosavinia, 2011). The *Dufrenoyia* material at hand shows primarily a coarse ornament and the high number of quartz grains shows that they were embedded in a turbulent water setting. However, a straightforward transfer of the morphochange pattern observed for *Dufrenoyia* by Martin (2003) to the Barler Berg fauna is impossible. Our coarsely ribbed specimens could be interpreted with corresponding to Martin’s (2003) upper population sample, but the density of ribbing is different and our sample is not statistically relevant. As long as we need

525 to deal with historical collections of *Dufrenoyia* from North Germany this issue
526 cannot be solved any further.

527

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Figure captions, Table caption, Plate caption

Fig. 1. Simplified palaeogeography of the Aptian in northern Europe (small map) and detailed palaeogeography of the southwestern boundary of the Lower Saxony Basin (LSB). APB=Anglo-Paris Basin. 1 and 2: Former Aptian sections. 1: Barler Berg and Frankenmühle, 2: Alstätte EGW section. Assembled after various sources, mainly Schott et al.(1969), Ziegler(1990) and Mutterlose and Böckel (1998).

Fig. 2. A Portrait of Clemens Schlüter (1835-1906) who collected the fossils described here (courtesy of the late J. Wiedmann). **B** Presumably Schlüter's original handwriting on a label sticking on specimen IGPB KrU16-5: "Wüllen bei Ahaus, Unterer Gault, *Amm. furcatus* Sow.: *A. Dufrénoyi* d'Orb., Cl. Schlüter leg.", referring to the Barler Berg locality. **C** Red label (IGPB KrU17-8d) indicating the locality name "Wüllen" on almost all of the specimens in the collection, showing many quartz grains in a carbonaceous matrix.

870

871 **Fig. 3.** Locality map of modern landmarks and assumed sampling localities of the
 872 material described in here. Aptian fossils from this area are either labelled
 873 “Wüllen”, Frankenmühle” (and variations in spelling) or “Barler Berg”, but this all
 874 refers to the couple of potential localities marked in the geological map in the right
 875 lower corner. Geological map after Bentz (1930). The latter author divided the
 876 Cretaceous deposits in several mapping units that are not any longer in use, the
 877 modern age assignment is given in brackets: 1 Kuhfeldschichten, = Kuhfeld Beds
 878 (Valanginian), 2 Gildehauser Sandstein, = Gildehaus sandstone (Hauterivian), 3
 879 “*Hoplites weissii*” beds (lower Aptian), 4 Rothenberg Sandstein, = Rothenberg

880 sandstone (upper Aptian), 5 "*Hoplites tardefurcatus*" beds (Lower Albian), 6
881 "Minimuston", = Minimus claystone (middle Albian), 7 "*Hoplites splendens*" beds
882 (upper Albian, pars), 8 "Flammenmergel" (upper Albian, pars), 9
883 "Cenomanmergel", = Cenomanian marlstone (Lower Cenomanian).
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Fig. 4. *Dufrenoyia furcata* from the Aptian of Barler Berg near Ahaus, Germany. A1–A2, IGPB KrU17-8a. B1–B3, IGPB KrU17-8d. C1–C2, IGPB KrU14-13, note the pathology near the aperture in C1. D1–D3, IGPB KrU17-5c. E1–E3, IGPB KrU17-5a. F1–F3, IGPB KrU17-5b. G1–G3, IGPB KrU14-25a. H1–H2, GPB KrU18-11. I1-2, IGPB KrU14-14. J1–J2, IGPB KrU17-12.

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896 **Fig. 5.** *Dufrenoyia furcata* from the Aptian of Barler Berg near Ahaus, Germany.

897 Note the distortion of the specimen. IGPB KrU17-11.

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Fig. 6. *Dufrenoyia furcata* from the Aptian of Barler Berg near Ahaus, Germany.

Note the denser ribbing close to the aperture and the finer ultimate and penultimate rib compared to all specimens depicted in Fig. 4 this specimen is furthermore distinct by a shallow umbilical wall on the last quarter of the fragment.

IGPB KrU17-13.

Fig. 7. Holotype of *Dufrenoyia furcata* (J. de C. Sowerby, 1836) from the Lower Greensand Group of Hythe, Kent, England. Coll. Fitton, 1911. Original in the British Geological Survey, Geol. Soc. Coll. 2290. Photo of plaster cast made by J. O. Barlow, mould no. 1013 in the Natural History Museum London (photo JL).

Fig. 8. *Dufrenoyia transitoria* from the Aptian of Barler Berg near Ahaus, Germany. IGPB KrU16-5.

Fig. 9. Suture of *Dufrenoyia transitoria* from the Aptian of Barler Berg near Ahaus, Germany. IGPB KrU16-5. Left: Continuous line indicates the umbilical seam, dashed line indicates the position of the umbilical edge.

Fig. 10. Position of the *Dufrenoyia furcata* Zone in NW-Germany within a biostratigraphical scheme for the Boreal Aptian and correlation with southern England (Casey 1961, Casey et al. 1998). Note that Kemper (1995) is not formally calling his scheme a zonation, but a succession of index species and that the scheme shown is only applied to the southern part of the Lower Saxony Basin in NW-Germany.

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Specimen number	Primary ribs/ a whorl	Secondary ribs/half a whorl
IGPB KrU25a+b	9	~10
IGPB KrU17-8d	10	10
IGPB KrU17-8a-c	10	~9
IGPB KrU18-11	~9	~9

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950 **Table 1.** Rib density in *Dufrenoyia furcata* from the Barler Berg locality.

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953 Supplementary data

Supplementary data

Table of material used, Lehmann & Bulot, A *Dufrenoyia* (Ammonoidea, Deshayesitidae) fauna from Germany: Improving the correlation of the lower/upper Aptian boundary

Inv.-nb.	Identification	Former identification (given on associated/attached labels)	Description	Individual label associated	Locality given on the (oldest) label/written on specimen	Year obtained by Schlüter (if given)	Figure in present paper	Diameter (D) in mm	Umbilical width (U) in mm	U/D (ratio)	Whorl breadth (wh)	Whorl height (wh)
KrU14-13	<i>Dufrenoyia furcata</i>	none	A quarter of a body chamber fragment with very last part of the phragmocone, pathology close to the aperture	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)		Fig. 4.C1-C2					
KrU14-14	<i>Dufrenoyia furcata</i>	none	Body chamber fragment, about half a whorl; microconch because of more evolute coiling and shallow umbilical wall	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)		Fig. 4.J1-I2					
KrU14-25a	<i>Dufrenoyia furcata</i>	Ammonites furcatus Sow.	Fairly complete specimen and separately a fragment of a couple of ribs	Yes	"Wüllen" (label)	1865 (label)	Fig. 4.G1-G3	~55	14.9	~0.27	19.0	25.6
KrU14-25b	<i>Dufrenoyia</i> sp.	none	Two short fragments (both belong together, need to be glued together; distorted, in claystone preservation (very poor))	No								
KrU16-5	<i>Dufrenoyia transitoria</i>	Ammonites furcatus Sow., A. dufrenoyi d'Orb	Body chamber fragment (slightly more than a quarter whorl) and a small portion of the phragmocone	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen), additional paper label glued on specimen		Fig. 8, Fig. 9 (suture), Fig. 28 (label)					
KrU17-5a	<i>Dufrenoyia furcata</i>	none	Microconch when interpreted as done by Garcia & Moreno-Bedmar 2010: Fig. 1.E	No			Fig. 4.E1-E3	28.8	7.0	0.24		13.6
KrU17-5b	<i>Dufrenoyia furcata</i>	<i>Dufrenoyia furcata</i>	Macroconch when interpreted as done by Garcia & Moreno-Bedmar 2010: Fig. 1.F1 & 1.F2	No, but number "226" on the specimen	Wüllen (on specimen)		Fig. 4.F1-F3	24.4	~7.0	~0.29	7.7	10.8
KrU17-5c	<i>Dufrenoyia furcata</i>	none	Short fragment, microconch when interpreted as done by Garcia & Moreno-Bedmar 2010: Fig. 1.B1 & 1.B2	No	Wüllen (on specimen)		Fig. 4.D1-D3					
KrU17-8a	<i>Dufrenoyia furcata</i>	none	Fairly complete specimen	Yes	Wüllen, b. Ahaus (label)		Fig. 4.A1-A2, Fig. 10					
KrU17-8b	<i>Dufrenoyia furcata</i>	none	Short fragment, a couple of ribs only, belongs to KrU17-8b and needs to be glued together	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)							
KrU17-8c	<i>Dufrenoyia furcata</i>	none	Short fragment, a couple of ribs only, belongs to KrU17-8b and needs to be glued together	Yes	Wüllen, b. Ahaus (label)							
KrU17-8d	<i>Dufrenoyia furcata</i>	none	Fairly complete specimen	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)		Fig. 4.B1-B3, Fig. 2C (label)	48.4	12.6	0.26	13.6	23.5
KrU17-11	<i>Dufrenoyia furcata</i>	none	Distorted body chamber and negative mould of inner whorls	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)		Fug. 5					
KrU17-12	<i>Dufrenoyia furcata</i>	none	Quarter of a body chamber with transition of the phragmocone, small fragment of the penultimate whorl associated	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)		Fig. 4.J1-J2					
KrU17-13	<i>Dufrenoyia furcata</i>	none	Fragment of body chamber, microconch?: more evolute coiling and shallow umbilical wall	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)		Fig. 6					
KrU18-10	<i>Dufrenoyia furcata</i>	Ammonites furcatus Sow. = A. dufrenoyi d'Orb	Body chamber fragment and a small portion of the penultimate whorl	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)	1863 (label)						
KrU18-11	<i>Dufrenoyia furcata</i>	none	Fairly complete specimen, but heavily crushed	Yes	Wüllen, b. Ahaus (label), Wüllen (on specimen)		Fig. 4.H1-H2					

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