Odd partnerships among middle Eocene (Bartonian) *Nummulites*: Examples from the Transylvanian (Romania) and Dorog (Hungary) Basins

Szabolcs-Attila Kövecsi,1, Lóránd Silye,1, György Less,2,3, Sorin Filipescu

1. Introduction

Nummulitids are Cenozoic calcareous benthic foraminifera (Racey, 2001), which lived in marine, warm, normal saline, oligotrophic environments, within the photic zone (Reiss and Hottinger, 1984; Beavington-Penney and Racey, 2004). The individuals have large (i.e. from 1 mm to a few cm), planispirally-coiled, generally lenticular tests, which are subdivided into numerous chambers. Trimorphism, frequently observed in recent larger benthic foraminifera (LBF) populations, has not yet been proven in fossil *Nummulites* species (Mateu-Vicens et al., 2012). Therefore, their life cycle is regarded as dimorphic in this study: the asexually reproduced megalospheric generation, with small tests (A forms), is alternating with the sexually reproduced microspheric generation, with large tests (B forms).

*Nummulites* tests are the dominant components of thick Paleogene sedimentary deposits, usually limestones, and sandy-clayey limestones. They have a widespread occurrence in the northern (Arni, 1965; Aigner, 1982, 1985) and southern (Papazzoni, 2008) Neotethyan margin throughout the Eocene. Some of them are characterized by the dominance of one or two *Nummulites* taxa, and the unusually low ratio (frequently < 100) between A and B forms. These deposits were called “nummulitic banks” and interpreted as autochthonous accumulations (Arni, 1965), although later this interpretation was questioned by Aigner (1982, 1985). This generated a long lasting debate regarding the autochthonous vs. allochthonous nature of the nummulitic banks (see discussions in Papazzoni, 2008; Mateu-Vicens et al., 2012; Seddighi et al., 2015). It was recently shown however, that the presence of a clayey or micritic cement between the *Nummulites* in a nummulitic bank, might be a clear sign of the autochthonous deposition (Papazzoni, 2008). Furthermore, Seddighi et al. (2015) demonstrated that contrary to the previous findings of Jorry et al. (2006), even imbricated *Nummulites* tests present in nummulitic banks should be considered autochthonous, because the nummulitic tests can reach a hydrodynamically stable orientation after a very short transportation time. Therefore one might conclude that at least some nummulitic banks preserved autochthonous LBF assemblages, whilst the hydrodynamic behaviour of the nummulitic tests needs further investigation.

One of the relationships between co-existing LBF species is the “odd partnership”. This term was first introduced by Hottinger (1999) to define a relationship between two sympatric species, which bear...
structurally identical or very similar adult shells, but markedly differ in their protoconch and adult test size. The odd partnership or odd pair was interpreted as a particular adaptation to seasonal changes in the environment, which makes it possible for both partners to benefit optimally from the periodical change of the carrying capacity of a given habitat (Hottinger, 1999).

The LBf assemblages offer the best examples in the fossil record or in recent habitats for the odd pairs. However, the existence of such a relationship between the highly diverse and stratigraphically important nummulitids has only been speculated, but never described (see Hottinger, 1999).

The purpose of this paper is to describe in detail the first record of an ‘odd partnership’ (sensu Hottinger, 1999) in the case of middle Eocene (Bartonian) Nummulites species.

2. Geological and stratigraphical setting

The studied Eocene nummulitic accumulations are exposed in the north-western part of the Transylvanian Basin, Romania and in the Dorog Basin, Hungary (Fig. 1).

2.1. Transylvanian Basin

In the Transylvanian Basin, nummulitic accumulations belong to the lowermost Paleogene tectonostratigraphic megasequence (Krézsek and Bally, 2006). The continental Jibou Formation (Hofmann, 1879) forms the lower part of this megasequence (Fig. 2). This formation is transgressively covered by the upper Lutetian to lower Priabonian Călata Group (Rusu, 1995) of shallow marine to offshore stratigraphic units referred to as Foidaș, Căpușu, and Mortănușa Formations, and the Viiște Limestone (Rusu, 1995; Filipescu, 2001). The Căpușu Formation (Popescu, 1978) is a ~25 m thick sedimentary sequence deposited in a shallow marine (inner shelf with tidal regime) environment. It consists of sandy marls, bioclastic and oolitic limestones and nummulitic sand-clays. In the top of the formation storm-dominated outer shelf shales (Proust and Hosu, 1996) interfinger with, or are covered by a 2 to 10 m thick nummulitic accumulation (Rusu et al., 2004). This succession can be studied in many outcrops scattered on over an area of ~40 km × 5 km in the NW Transylvanian Basin (Răileanu et al., 1968). The most striking feature of the accumulation is the overwhelming dominance of well-preserved Nummulites perforatus shells. However, in low numbers, similarly well preserved Nummulites beaumonti shells are also present, and the nummulitic shells are embedded in a fine-grained matrix (Papazzoni and Sirotti, 1995; Papazzoni, 2008). This sedimentary sequence was interpreted as a nummulitic bank (Papazzoni and Sirotti, 1995; Rusu et al., 2004). Its age is regarded as early Bartonian (Schaub, 1981; Rusu, 1995), based on the nummulitic assemblages referring to the SBZ 17 Zone of Serra-Kiel et al. (1998).

2.2. Dorog Basin

The Eocene in the western part of the Dorog Basin corresponds to two major depositional sequences. The lower sequence (late Lutetian to early Bartonian), consists of the Dorog, Csernye and Csolnok Claymarl Formations and corresponds to the transgressive part of the Eocene lower depositional cycle (Less et al., 2000; Kercsmár, 2010). The lower Bartonian Tokod Formation represents the regressive part of the lower depositional cycle. It is transgressively covered by the upper Bartonian to Priabonian upper depositional sequence (Fig. 3), referred to as the Szőc Limestone and the Padrág Marl Formation (Less et al., 2000; Kercsmár, 2010). The Tokod Formation consists of grayish clayey marls with Nummulites at its base and abundant mollusc shells in its lower part, which are covered by shallow-marine and fluvial sandstones interlayered with coal at the top. Well-developed nummulitic banks are present in the lower part of this lithostratigraphic unit (Budai et al., 2008). These consist almost exclusively of well-preserved N. perforatus shells, although Nummulites...
striatus (Bruguière, 1792) tests with the same preservation are sporadically present in the grey clayey matrix (Kercsmár, 1995). The nummulitic assemblage is indicative of the lower Bartonian SBZ 17 Zone of Serra-Kiel et al. (1998), hence an early Bartonian age can be assigned to the nummulitic bank in the Dorog Basin (Less et al., 2000).

2.3. Main facies of the studied sections

The exposures studied in the Transylvanian Basin are usually a few meters high, and up to ~10–15 m wide and were logged and sampled at relatively high resolution (Fig. 4 and Appendix A). The size of the outcrop M allowed logging at three different parts of the outcrop. The MV
outcrops are located 40 to 160 m apart from each other and expose almost entirely the same rock body and can thus be easily correlated. Although the Vă1 outcrop is located nearby, its correlation to the MV 1–4 outcrops is difficult. However, its stratigraphic position suggests that the Vă1 outcrop exposes the deposits below the MV 1–4 outcrops. Even if there are unexposed strata between them, the Gi1-3 outcrops can be also put in stratigraphic order (Fig. 4).

The Nummulites perforatus bank of the Tokod Formation was sampled in a small outcrop in Bajót, Komárom-Esztergom County, Dorog Basin.

The most widespread sedimentary facies, structures and Nummulites biofabric-types observable at outcrop level are:

1. Shallow erosional scours filled with very weakly cemented nummulitic floatstone/rudstone. The packstone/wackstone matrix composed of fine-grained sediments and chaotically stacked, well-preserved N. perforatus A forms, and N. beaumonti (both A and B forms) fill the space between the chaotically stacked N. perforatus B forms. This facies is present in the lower part of outcrop M (Fig. 4 and Appendix A).

2. Weakly cemented nummulitic rudstone/floatstone with chaotically stacked N. perforatus B forms. The N. perforatus B forms are embedded in a packstone/wackstone matrix, which consists of fine-grained sediments and chaotically stacked, well-preserved N. perforatus A forms, and N. beaumonti or N. striatus (both A and B forms). This is the most common facies type in the studied banks, observable in outcrops MV1-4, Vă1, Gi1-3, and Ba1 (Figs. 4, 5).

3. Nummulitic rudstone/floatstone with in contact or edgewise imbricated N. perforatus B forms. The fine-grained nummulitic packstone/wackstone matrix comprises mainly of chaotically stacked, well-preserved N. perforatus A forms and sandy clays (Appendix A). This lithofacies occurs in the upper part of exposure M, above a major erosional surface (Fig. 4 and Appendix A).

4. Nummulitic floatstone with linear accumulation of N. perforatus B forms. The apparently not sorted nummulitic packstone matrix consist of fine-grained sediments and chaotically stacked, well-preserved Nummulites perforatus A forms, although sometimes N. beaumonti (both A and B forms) are also present (Figs. 4, 5 and Appendix A). This lithofacies occurs in the upper part of a few outcrops i.e. M, MV1, MV2 and is dominant in the Vă2 outcrop.

3. Material and methods

Twenty-six samples were collected from ten different outcrops (Figs. 1, 4, 5 and Appendix A) of the N. perforatus bank in the Transylvanian Basin. They represent rock fragments composed of Nummulites specimens mostly loosely bound together by a clayey or sandy matrix.
One sample, consisting of rock fragments (nummulitic specimens in a clay matrix), was collected in Bajót, Komárom-Esztergom County, Dorog Basin.

The collected samples were dried at room temperature, and then about 2 kg sediment (always rock fragments, and not isolated specimens) from each sample was wet sieved using a 63 μm sieve. The dried >63 μm residue was split and ¼ of each residue was used for further analysis.

The biometrical measurements were performed on Nummulites A and B forms using two different approaches. The Nummulites A forms were measured using the following method: 50 randomly selected specimens of N. perforatus, and all N. beaumonti and N. striatus specimens present in the studied residue (1/4 split) were measured per sample (Tables 1 and 2) in order to record the diameter (D) and thickness (T) of their test. The internal diameter of the protoconch (C) was also measured using the following method: 50 randomly selected specimens of N. perforatus, and all N. beaumonti and N. striatus specimens present in the washing residues of each sample.

The A/B ratios were determined using 1 mm and 6 mm mesh sieves and only for the N. perforatus, because the other two taxa had a very low abundance. Because the N. perforatus A and B forms have a significant size difference, it is easy to separate them by sieving the entire >63 μm residue: the smaller A forms of N. perforatus remain in the 1–6 mm fraction, whilst the B forms are present in the >6 mm fraction. In order to obtain a good estimate of the number of the A form specimens present in a given sample, first we measured the weight of all the N. perforatus A forms present in the 1–6 mm fraction of the dried residue’s ¼ split. Then we measured the weight of 100 randomly selected N. perforatus A form specimens picked from the split of the same size fraction. The total number of N. perforatus A form specimens present in a sample was estimated using the Eq. (1)

\[ A_f = \frac{A_t}{A_{100}} \times 100 \]  

(1)

where \( A_t \) stands for the total number of Nummulites A forms in one sample, \( A_t \) represents the weight of all Nummulites A forms present in the sample, and \( A_{100} \) marks the weight of 100 specimens of Nummulites A forms randomly selected from the same sample.

All B forms present in the same sample splits were counted, giving the value of \( B_t \). Finally, the A/B ratio for the assemblages present in one sample was calculated with the formula

\[ A_f/B_t = A_{f/100}/B_t \]  

(2)

### Table 1

Biometrical data of the studied Nummulites A form (megalospheric) specimens. N - number of studied specimens, s.e. - standard error. Please note that the N of Nummulites beaumontii or Nummulites striatus represents the number of all specimens found in a sample, whilst in the case of Nummulites perforatus N refers to number of randomly selected specimens from a sample. Samples M3 and M5 were collected at the same stratigraphic level located above the strata with samples M1, M2 and M4.

<table>
<thead>
<tr>
<th>Outcrop</th>
<th>Sample no.</th>
<th>Taxon</th>
<th>N</th>
<th>Protoconch C (μm)</th>
<th>Diameter D (mm)</th>
<th>Thickness T (mm)</th>
<th>T/D</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean ± s.e.</td>
<td>Mean ± s.e.</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>M5</td>
<td>N. perforatus</td>
<td>50</td>
<td>816</td>
<td>21.7 ± 0.08</td>
<td>2.25 ± 0.05</td>
<td>0.570 ± 0.010</td>
</tr>
<tr>
<td></td>
<td>M4</td>
<td>N. perforatus</td>
<td>50</td>
<td>844</td>
<td>22.7 ± 0.11</td>
<td>2.34 ± 0.05</td>
<td>0.592 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>M3</td>
<td>N. perforatus</td>
<td>50</td>
<td>808</td>
<td>22.7 ± 0.08</td>
<td>2.05 ± 0.05</td>
<td>0.567 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>M2</td>
<td>N. perforatus</td>
<td>50</td>
<td>799</td>
<td>25.2 ± 0.11</td>
<td>2.06 ± 0.06</td>
<td>0.587 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>M1</td>
<td>N. perforatus</td>
<td>50</td>
<td>814</td>
<td>21.8 ± 0.10</td>
<td>2.16 ± 0.05</td>
<td>0.604 ± 0.013</td>
</tr>
<tr>
<td>MV1</td>
<td>MV1B</td>
<td>N. perforatus</td>
<td>50</td>
<td>909</td>
<td>24.4 ± 0.11</td>
<td>2.07 ± 0.07</td>
<td>0.611 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>MV2</td>
<td>N. perforatus</td>
<td>50</td>
<td>880</td>
<td>24.1 ± 0.11</td>
<td>1.14 ± 0.06</td>
<td>0.576 ± 0.022</td>
</tr>
<tr>
<td></td>
<td>MV2A</td>
<td>N. perforatus</td>
<td>50</td>
<td>790</td>
<td>20.8 ± 0.09</td>
<td>2.12 ± 0.06</td>
<td>0.573 ± 0.012</td>
</tr>
<tr>
<td></td>
<td>MV3</td>
<td>N. perforatus</td>
<td>50</td>
<td>830</td>
<td>24.9 ± 0.10</td>
<td>1.97 ± 0.05</td>
<td>0.535 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>MV3D</td>
<td>N. perforatus</td>
<td>50</td>
<td>830</td>
<td>24.9 ± 0.10</td>
<td>1.38 ± 0.06</td>
<td>0.742 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>MV3C</td>
<td>N. perforatus</td>
<td>50</td>
<td>731</td>
<td>23.4 ± 0.10</td>
<td>1.07 ± 0.04</td>
<td>0.623 ± 0.027</td>
</tr>
<tr>
<td></td>
<td>MV3B</td>
<td>N. perforatus</td>
<td>50</td>
<td>823</td>
<td>26.6 ± 0.13</td>
<td>2.07 ± 0.06</td>
<td>0.547 ± 0.015</td>
</tr>
<tr>
<td></td>
<td>MV3A</td>
<td>N. perforatus</td>
<td>50</td>
<td>847</td>
<td>19.3 ± 0.12</td>
<td>2.11 ± 0.06</td>
<td>0.600 ± 0.015</td>
</tr>
<tr>
<td></td>
<td>MV3B</td>
<td>N. perforatus</td>
<td>50</td>
<td>847</td>
<td>19.3 ± 0.12</td>
<td>1.41 ± 0.05</td>
<td>0.754 ± 0.015</td>
</tr>
<tr>
<td></td>
<td>MV4</td>
<td>N. perforatus</td>
<td>50</td>
<td>716</td>
<td>25.1 ± 0.10</td>
<td>1.92 ± 0.06</td>
<td>0.560 ± 0.010</td>
</tr>
<tr>
<td></td>
<td>MV4B</td>
<td>N. perforatus</td>
<td>50</td>
<td>790</td>
<td>26.6 ± 0.10</td>
<td>2.06 ± 0.05</td>
<td>0.587 ± 0.013</td>
</tr>
<tr>
<td></td>
<td>MV4A</td>
<td>N. perforatus</td>
<td>50</td>
<td>813</td>
<td>21.1 ± 0.10</td>
<td>1.89 ± 0.05</td>
<td>0.585 ± 0.012</td>
</tr>
<tr>
<td></td>
<td>V31</td>
<td>N. perforatus</td>
<td>50</td>
<td>780</td>
<td>22.2 ± 0.14</td>
<td>2.02 ± 0.07</td>
<td>0.554 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>V31C</td>
<td>N. perforatus</td>
<td>50</td>
<td>814</td>
<td>24.3 ± 0.13</td>
<td>1.94 ± 0.06</td>
<td>0.539 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>V31B</td>
<td>N. perforatus</td>
<td>50</td>
<td>799</td>
<td>16.6 ± 0.13</td>
<td>1.94 ± 0.06</td>
<td>0.539 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>V31A</td>
<td>N. perforatus</td>
<td>50</td>
<td>927</td>
<td>26.7 ± 0.09</td>
<td>2.12 ± 0.06</td>
<td>0.509 ± 0.009</td>
</tr>
<tr>
<td></td>
<td>V32</td>
<td>N. perforatus</td>
<td>50</td>
<td>764</td>
<td>27.0 ± 0.07</td>
<td>1.77 ± 0.04</td>
<td>0.538 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>V32C</td>
<td>N. perforatus</td>
<td>50</td>
<td>770</td>
<td>24.1 ± 0.09</td>
<td>2.01 ± 0.05</td>
<td>0.552 ± 0.013</td>
</tr>
<tr>
<td></td>
<td>V32A</td>
<td>N. perforatus</td>
<td>50</td>
<td>906</td>
<td>21.2 ± 0.10</td>
<td>2.19 ± 0.05</td>
<td>0.575 ± 0.012</td>
</tr>
<tr>
<td></td>
<td>G1</td>
<td>N. perforatus</td>
<td>50</td>
<td>818</td>
<td>24.4 ± 0.08</td>
<td>2.04 ± 0.06</td>
<td>0.461 ± 0.010</td>
</tr>
<tr>
<td></td>
<td>G1</td>
<td>N. perforatus</td>
<td>50</td>
<td>812</td>
<td>23.6 ± 0.10</td>
<td>1.81 ± 0.06</td>
<td>0.431 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>G2</td>
<td>N. perforatus</td>
<td>50</td>
<td>871</td>
<td>22.6 ± 0.09</td>
<td>1.82 ± 0.06</td>
<td>0.521 ± 0.012</td>
</tr>
<tr>
<td></td>
<td>G2A</td>
<td>N. perforatus</td>
<td>50</td>
<td>785</td>
<td>23.0 ± 0.11</td>
<td>2.09 ± 0.05</td>
<td>0.574 ± 0.018</td>
</tr>
<tr>
<td></td>
<td>G3</td>
<td>N. perforatus</td>
<td>50</td>
<td>920</td>
<td>22.3 ± 0.10</td>
<td>2.56 ± 0.06</td>
<td>0.615 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>Ba1</td>
<td>N. perforatus</td>
<td>21</td>
<td>179</td>
<td>7.4 ± 0.10</td>
<td>1.60 ± 0.06</td>
<td>0.637 ± 0.017</td>
</tr>
</tbody>
</table>
4. Results

4.1. Identified assemblages and their geographic distribution

The *Nummulites*-assemblages recovered from the Eocene deposits of the Transylvanian Basin (Plate 1) are markedly different in their species composition, and geographic distribution. Our investigation suggests, that in the easternmost located area, around Gilău (outcrops Gi1, Gi2, Gi3), the LBF assemblages comprise only *N. perforatus* (Fig. 1, Tables 1 and 2). However, about 25 km west of Gilău, around Huedin, the LBF assemblages consist mostly of *N. perforatus* in association with *N. beaumonti* (outcrops M, MV1, MV2, MV3, V1). In this area only at two locations (outcrops MV4 and V2) were identified assemblages which consist only of *N. perforatus*. The LBF assemblage recovered from the Eocene of the Dorog Basin (outcrop Ba1), Hungary, situated far west from the Transylvanian Basin consists of *N. perforatus* in association with *N. striatus* (Fig. 1; Tables 1, 2; Plate 1).

4.2. Biometry of the studied *Nummulites* specimens

The average diameter (D) of the *N. perforatus* A form specimens recovered from the Transylvanian Basin varies between 3.28 and 4.19 mm, and the thickness (T) between 1.89 and 2.55 mm (Table 1). The values of *N. perforatus* A forms from the Dorog Basin are of the same order of magnitude, although they are slightly higher: the average D is 4.20 mm, whilst the average T is 2.56 mm. The diameter and thickness of the recovered *N. beaumonti* A forms and *N. striatus* A forms are roughly two times smaller, *N. beaumonti* A form specimens recovered only from the Transylvanian Basin have an average D between 1.63 and 2.34 mm, and a T between 0.68 and 1.43 mm, whereas the average D and T values obtained for *N. striatus* A forms from the Dorog Basin are 2.55 mm and 1.60 mm, respectively (Table 1). The average T/D ratio of the *N. perforatus* A forms is between 0.43 and 0.62, which is close to the average T/D ratio of the *N. beaumonti* (0.41–0.75) and *N. striatus* A forms (0.64).

The protoconch diameter (C) shows also large difference between the *N. perforatus* and *N. beaumonti* or *N. striatus* A forms. The mean C of the *N. perforatus* B forms varies between 109 and 186 μm, whilst the mean C of the *N. beaumonti* A forms is between 109 and 186 μm in the samples from the Transylvanian Basin. The LBF-assemblage from the Dorog Basin shows a similar difference between the mean C (920 μm) of the *N. perforatus* A forms, and the mean C (179 μm) of *N. striatus* A forms (Table 1).

The average thickness (D) of *N. perforatus* B forms is one order of magnitude greater than that of the *N. beaumonti* or *N. striatus* B forms (Table 2). Moreover, there is no discernible size difference between the A and B forms of *N. beaumonti* and *N. striatus*, respectively, whilst the *N. perforatus* B forms are 4–5 times larger in diameter (D) than the A forms. The mean T/D ratio of the recovered *N. perforatus* B forms is between 0.321 and 0.552. These values are considerably smaller than the T/D ratio of the *N. perforatus* A forms. The very rare *N. beaumonti* or *N.
The studied nummulitic assemblages have an A/B ratio between 19 and 135 (see Table 2). In half of the outcrops i.e. MV1, MV2, VA1 and Gi2, the A/B ratio decreases upwards (Fig. 4). The minimum decrease of the A/B ratio was observed in outcrop Gi2, where this ratio decreases upsection from 70 to 39, whilst the maximum decrease upsection (97 to 15) was recorded in exposure MV1. This means a decrease from 1.8 to 6.5 times of the A/B ratio upwards. In other outcrops (MV3, MV4, VA2) the A/B ratios increased upwards between 2 and 2.45 times, resulting in an increase of the A/B ratio from 54 to 106 (MV3) or from 35 to 86 (VA2). However the upward increase or decrease of the A/B ratio in the studied outcrops is not consistently related to any change of the biofabrics or sedimentary structures (Fig. 4) and the T/D of the N. perforatus specimens is quite constant, even if the A/B ratio of the assemblages shows variability (Fig. 6a).

In order to record the variations of the A/B ratio along the same stratigraphic level, the same strata were logged at different places. At the M outcrop the A/B ratio changed laterally along the strata from 39 (M1) through 112 (M2) to 47 (M4). The vertical change of the A/B ratio at this outcrop was either dropping from 112 (M2) to 80 (M3) in the central part of the exposure, or increasing from 47 (M4) to 98 (M5) in a laterally equivalent part of the section.

5. Discussion

5.1. Autochthonous or allochthonous assemblages?

Recent LBF are adapted to various hydrodynamic regimes and species with different shapes can effectively withstand water motion (Briguglio and Hohenegger, 2011). However, modern LBF do not form banks. As a consequence, the usefulness of modern LBF accumulations for the interpretation of fossil nummulite banks is somewhat limited. Instead, one has to rely mostly on the interpretation of sedimentary and taphonomic features and on experimental studies on Nummulites to determine if the studied nummulite banks consist of autochthonous, paraautochthonous or allochthonous assemblages.

The Nummulites A and B form specimens are well preserved, most commonly TS 1 on the taphonomic scale for Nummulites of Beavington-Penney (2004), but TS 0 specimens are also common (see Plate 1). The TS 0 state of preservation suggests in situ deposition, whilst the TS1 indicates that the specimens suffered moderate transportation over very short distance by wave-motion (Beavington-Penney, 2004). This is in good agreement with the most common Nummulites biofabrics observed in the Transylvanian and Dorog Basins. The chaotic stacking found in the nummulitic limestones is either interpreted as the result of wave action (Racey, 2001), or of bioturbation (Beavington-Penney et al., 2005). The presence of the shallow, wave related-scours (e.g. outcrop M) supports the former interpretations, but where the scour belts are absent, the second interpretation cannot be ruled out. The decimetre scale linear accumulations of the Nummulites tests suggest parautochthonous wave or current winnowed accumulations (Aigner, 1985; Racey, 1995; Racey, 2001) or in situ compaction of the shells (Racey, 2001). The rarely observed imbrications (they occur only in the upper part of outcrop M) are features related to unidirectional transport (Beavington-Penney et al., 2005), and they might be related to storm events (Beavington-Penney et al., 2006). However, transport of the Nummulites shells most probably occurred only over very short distances, and they remained in their original bioicoenosis, as suggested by the taphonomic features in combination with the experimental results of Nummulites shell transport (Sedighi et al., 2015) or settling velocity (Briguglio and Hohenegger, 2011).

The in situ position of the studied assemblages is supported by the floatstone facies observed on the outcrop level in some places, which is usually interpreted as a result of autochthonous accumulation, whilst the rudstone/floatstone facies present in other places might be the result of autochthonous/parautochthonous deposition (Racey, 2001). The presence of fine-grained, non-calcareous and not cemented sediment in the matrix of the floatstones and rudstone/floatstones observable in all studied exposures was regarded as a clear sign of the autochthonous deposition on the nummulitic banks in the Transylvanian Basin (Papazzoni, 2008).

Jorry et al. (2006) suggested that Nummulites shells of different size might have similar hydrodynamic behaviour, because they have a rather similar density. Even so, the threshold of shear velocity of a Nummulites test of 2 cm diameter is significantly different to that of a shell with a diameter of about 2 mm (Jorry et al., 2006). This means that size sorting should occur during mass transport. The co-occurrence of large and small tests thus rules out the possibility of any considerable transport within the studied nummulitic banks.

Furthermore, observations on recent LBF having comparable test sizes demonstrated that: (1) regardless of their taxonomic affinities and their shape, the T/D ratio of species living in the same environment is very similar; and (2) the T/D ratio of closely related species having very similar test architecture is almost identical (Renema, 2005). However, there is no significant relationship between the T/D ratio of the almost entirely lenticular B forms and the A/B ratio of the studied assemblages (Fig. 6a). This suggests that the observed changes in the A/B ratio are not the result of sedimentary processes. Additionally, the recovered Nummulites A forms regardless to their taxonomical affinities and occurrences have a very similar diameter, T/D ratios, and an inflated lenticular shape, even if the diameter of their protoconch differs markedly in size (Fig. 6b). These observations further supports our conclusion that any significant transportation or selective winnowing of the studied Nummulites assemblages can be ruled out.

Summarizing, based on the preservation state of the tests, the facies types and the lack of shape variability, we conclude that the studied nummulite banks in the Transylvanian and Dorog Basins preserve (para-)autochthonous (when imbrication is present) or autochthonous (any other case) assemblages deposited on a shore face.

5.2. Odd pairs within the nummulitic assemblages

There is a considerable test size difference between the N. perforatus A and B-generations, however this does not apply for N. beaumonti and...
The specimens of the N. beaumonti and N. striatus had roughly half (A forms) or one order of magnitude smaller (B forms) adult test sizes than the A- and B-generation tests of N. perforatus. The N. perforatus A forms were considerably larger during their embryonic stage than the A forms of N. beaumonti and N. striatus (Tables 1 and 2). Such a considerable size difference between two species, which are taxonomically closely related, and share the same habitat can be interpreted as an ‘odd partnership’ sensu Hottinger (1999), or an ‘odd pair’ sensu Hottinger (2006). This particular phenomenon was compared to the relationship between Don Quijote and Sancho Panza, therefore Hottinger (1999) called the larger, more abundant and diverse partner ‘Don’ after Don Quijote, whilst the smaller, rare, and more uniform partner was named ‘San’ after Sancho Panza.

The observed co-occurrence of two taxa of the same genus with significantly different size (the large-sized N. perforatus together with the small-sized N. beaumonti) in the Bartonian of the Transylvanian Basin, led us to define the N. beaumonti as the ‘San’ partner, and the N. perforatus as the ‘Don’ partner of such an odd pair. Based on the same observation regarding the size, co-occurrence and taxonomical affinity in the Bartonian of the Dorog Basin, we conclude that another odd pair can be defined there: the San partner is represented by N. striatus and the Don partner is N. perforatus as in the case of the odd pair observed in the Transylvanian Basin. Although several odd pairs have been already described among foraminifera (Table 3), only one potential odd pair was pointed out so far by Hottinger (1999) within the highly diverse groups of Nummulites, with Nummulites variolarius as San partner and Nummulites leavigatus as Don partner reported from the lower Lutetian of the Paris Basin. Hottinger based his assumption on data from Blondeau (1972), but this potential odd pair in Nummulites has never been investigated, or described in details.

5.3. Paleoecology of the Nummulites odd pairs

Recent LBF live in symbiosis with photosynthetic algae (Haynes, 1965; Leutenegger, 1977; Hottinger, 1982; Leutenegger, 1984; Hallock, 1985; Lee and Hallock, 1987), and they are adapted to stable, tropical to warm-temperate, shallow marine, oligotrophic environments (Hottinger, 1983; Hallock, 1985). Because they depend on their symbions and the amount of light necessary for those, they tend to develop tests with large surface/volume (Hohenegger, 2009), or small T/D ratio. Nevertheless, there is a limit on shell thinning as they need to balance light optimisation with hydrodynamic stability (Hottinger, 1997; Hohenegger, 2009).

Among recent LBF the occurrence of odd pairs is generally restricted to species living in the subtropical or tropical shallow marine upper photic zone. In these regions seasonality has an important effect on environmental conditions (Hottinger, 1999), including changes of salinity (Levy, 1994), and/or nutrient supply (Lee et al., 1991).

It is generally assumed that the species involved in odd partnerships have either different tolerance towards environmental conditions, as suggested by the odd pair Adrosina lucasi and Archaias angulatus from Florida (Levy, 1994), have different feeding modes (Lee et al., 1991), or reproduce in different periods (Zohary et al., 1980; Hottinger, 1999). Hence, the coexistence of two different, closely related species within an odd partnership might reflect either different growth rates, different reproduction periods, and/or life strategies (Hottinger, 1999).
The growth rate of the Nummulites can be very fast when multispiral growth is involved. For instance, Nummulites millecaput, which has the largest known test among Nummulites, could form a test with 10 cm diameter in not >5–6 years (Ferránduez-Cañadell, 2012). However, if multispiral growth is present, it is characteristic only for the microspheric B forms, with the exception of two taxa: N. perforatus and Nummulites cf. dufrenoyi. N. perforatus B forms always show this way of growing, whereas it is rare in A forms (Schaub, 1981; Ferránduez-Cañadell, 2012).

Consequently, the microspheric Don partners (i.e. N. perforatus B form) of the studied odd pairs, most probably lived at least 2 years, based on their average diameter, and assuming a similar growth rate as that of N. millecaput. We consider this a conservative estimate, because the growth rate of LBF shows oscillations (Briguglio and Hohenegger, 2014) due to tidal currents (Eder et al., 2016), and environmental stress (Ferránduez-Cañadell et al., 2014). The N. perforatus B forms would eventually be able to reach their adult test size in the same amount of time as the twice smaller N. beaumonti and N. striatus A forms, if they had higher growth rate and/or a multispiral way of growing. The life span of the San partners - N. beaumonti and N. striatus B forms, which lack the multispiral growth, can be estimated to be about 1 year based on the longevity of the recent nummulitid Operculina ammonoides (Pechex, 1995) and of Amphistegina lobifera (Triantaphyllou et al., 2012). It follows that despite of having multispiral growth, the Don partner reached its adult test size slower than its San partners, but both Don and San partners had a life span long enough to experience seasonal variations of environmental parameters.

The association of a single San partner (Heterostegina operculinoides) with two different Don partners has been already documented by Hottinger (1999). However, the association of the same Don partner, with two different San partners, as in the case of the odd pairs described in the present paper, has never been reported before. Among the species taking part in these nummulitic odd pairs, the Don partner (i.e. N. perforatus) has the most frequent occurrence in the Bartonian (Schaub, 1981). Its association with two different San partners is not the result of its stratigraphic distribution, because both N. beaumonti and N. striatus occurred throughout the Bartonian (Schaub, 1981). The association of N. perforatus with two different smaller nummulitic species might be related to the more restricted paleogeographic distribution of N. beaumonti and N. striatus and/or to the different paleogeographic connections of the two basins. The former assumption is supported by the fact that the N. beaumonti and N. striatus distributions in the northern margin of the Neotethys cover the same area as that of the N. perforatus, but the former species are known from significantly fewer localities (see in Schaub, 1981). Nevertheless, paleogeographic reconstructions suggest a more restricted open sea connections for the Transylvanian Basin than for the Dorog Basin (Kocsis et al., 2014).

The distribution of the nummulitic odd pairs in the Transylvanian Basin reveals another feature. The San partners occur rarely in facies interpreted as a result of high-energy (wave or current dominated) action, whilst the Don partner’s A and B forms are always present in these facies. This suggests, that N. perforatus was more adapted to variable environmental conditions than its San partners N. beaumonti and N. striatus.

The LBF and most of the known odd pairs are regarded as K-strategist species (Hottinger, 1997). Although the same can be thought for the Don and the San partners in the nummulitic odd pairs, we hypothesise, slightly different life strategies, because of the differences observable in their abundance (Tables 1 and 2), life span, mode of growing, and growth rate, occurrence, and paleogeographic distribution. Along the r/K selection continuum, the larger, longer living, and more widely distributed Don partner (N. perforatus) could have been more K-strategist, than the smaller, shorter living, less widely distributed San partners (N. beaumonti and N. striatus). This hypothesis is in agreement with the data on recent odd pairs, which suggest that the smaller, short living San partner is more tolerant towards periodical environmental stress than the larger Don partner (Hottinger, 1999). However, the San partner of the recent odd pairs may occur alone in shallower environment or marginal basin (Hottinger, 1999), and usually have wider geographical distribution (Bassi et al., 2007) than its Don partner. This is not the case in the N. perforatus - N. beaumonti, and N. perforatus – N. striatus odd pairs, which contrary to the common characteristics (see Bassi et al., 2007), show a rare feature: the Don partner has a larger geographic distribution than its San partners, and seems to appear in a wider environmental range. Having a larger and more inflated lenticular shell, the N. perforatus was more adapted to higher energy (e.g. wave dominated) environments due to its size and shape, and made possible for the smaller, but otherwise stress tolerant San partner to colonize an environment where it could not survive alone.

Furthermore, similar to other odd pairs living in shallow water oligotrophic environments characterized by seasonal change (Reiss and Hottinger, 1984; Hottinger, 1987; Hottinger, 1999), the distinct partners of the nummulitic odd pairs could have used different periods for the reproduction. The more K-strategist Don partner might have used the seasons characterized by maximum carrying capacity, whilst the opposite could have been true for the slightly less K-strategist San partners. The dimorphism and the strong difference between the abundance of the A and B forms, might be the result of the same kind of life strategy, but within a single species as suggested by Hottinger (1999).

6. Conclusions

Three taxonomically closely related species have been observed in the autochthonous Bartonian Nummulites assemblages: N. perforatus and N. beaumonti were recovered from the Transylvanian Basin and N. perforatus and N. striatus from the Dorog Basin. The observed association between two closely related species, having very similar test morphology and structure but significantly different size was interpreted as an example of odd partnership sensu Hottinger (1999). The odd pairs formed by Nummulites beaumonti as San and N. perforatus as Don partner (Bartonian, Transylvanian Basin), and that of N. striatus as San and N. perforatus as Don partner (Bartonian, Dorog Basin) likely lived in an oligotrophic, shallow marine environment within the upper photic zone. The association of the same Don partner with two distinct San partners in two different sedimentary basins is interpreted as the result of the wider paleogeographic distribution, and more abundant occurrence of the Don partner (N. perforatus), as compared to N. beaumonti and N. striatus, the San partners. Our data suggest, that contrary to the odd partners known so far, in the otherwise K-strategist nummulitic odd pairs, the faster growing N. perforatus Don partner was more K-strategist, whilst the smaller San partners N. beaumonti and N. striatus were less K-strategists, and slightly more opportunistic.

Acknowledgments

This work was supported by the Collegium Talentum (SzAK and GL), ROMGAZ (SzAK and SF), the Alexander von Humboldt Foundation (LS), and the National Scientific Fond of Hungary (grant OTKA K 100538). We are grateful to Lukas Jonkers for the corrections made on the manuscript. The comments by Antonino Briguglio and an anonymous reviewer, and the suggestions made by the editor, Frans Jorissen, greatly improved the quality of our work.
Appendix A. View of the studied outcrops with the location of samples, and outcrop view of some lithofacies showing different *Nummulites* biofabric types.
A - outcrop M.
B. Shallow erosional scours filled with nummulitic floatstone/rudstone. The fine grained nummulitoclastic (chaotic stacked, well preserved *Nummulites perforatus* A forms, and *N. beaumonti* A and B forms) packstone/wackstone matrix fills the space between the chaotic stacked *Nummulites perforatus* B forms. Location: outcrop M.

C. Nummulitic rudstone/floatstone. The fine grained nummulitoclastic packstone/wackstone matrix (chaotic stacked, well preserved *Nummulites perforatus* A forms, and *N. beaumonti* A and B forms) fills the gaps between the imbricated (contact and edgewise) or linear accumulated *Nummulites perforatus* B forms. Location: outcrop M.

D. - outcrop MV1; E. - outcrop MV2; F. - outcrop MV3; G. - outcrop MV4; H - outcrop Gu1; I - outcrop Gi2; J - outcrop Gi3; K - outcrop Ba1.

**Appendix B. Taxonomic notes**

Oder Foraminiferida Eichwald, 1830

Family Nummulitidae Blainville, 1827

Genus *Nummulites* Lamarck, 1801

*Nummulites perforatus* (de Montfort, 1808)

pl. 1, figs. c, e, g–i, n–p

1808 *Eugeon perforatus* de Montfort – de Montfort, p. 167.

1853 *Nummulites perforata* d’Orbigny – d’Archiac & Haime, p. 115–120, pl. VI, figs. 1–4.

1972 *Nummulites perforatus* (Monfort) – Bloudeau, p. 161, pl. XXXIV, figs. 7–11.

1981 *Nummulites perforatus* (de Montfort) – Schaub, p. 88–90, figs. 76, 77, pl. 17, figs. 1–10, pl. 18, figs. 1–31, pl. 19, figs. 1–8.

1995 *Nummulites perforatus* (de Montfort) – Papazzoni & Sirotti, p. 73, Pl I, figs. 7–8.

*Nummulites baumonti* d’Archiac and Haime, 1853.

pl. 1, figs. a–b, j, l

1853 *Nummulites Baumonti* d’Archiac & Haime, p. 133–134, pl. VIII, figs. 1–3.

1883 *Nummulites sub-Beaumonti* de la Harpe – de la Harpe, p. 182–183, pl. XXXI, figs. 48–56.


1995 *Nummulites Beaumonti* d’Archiac & Haime – Papazzoni & Sirotti, p. 73, pl I, figs. 9–10.

*Nummulites striatus* (Bruguière, 1792).

pl. I, figs. d, f, k, m

1792 *Camerina striata* Bruguière – Bruguière, p. 399.

1853 *Nummulites contorta* Desh. – d’Archiac & Haime, p. 136–137, pl. 8, figs. 8 a, b.

1929 *Nummulina striata* Bruguière – Rozkosniik, p. 194–195, pl. 6, figs. 6–7 and 20.


**Appendix C. Supplementary data**

Supplementary data associated with this article can be found in the online version, at doi: http://dx.doi.org/10.1016/j.marmicro.2016.07.008. These data include the Google map of the most important areas described in this article.

**References**


de Montfort, D., 1808. Conchyliologie systématique, et classi


de Montfort, D., 1808. Conchyliologie systématique, et classi


de Montfort, D., 1808. Conchyliologie systématique, et classi


de Montfort, D., 1808. Conchyliologie systématique, et classi
