REVISION OF GRANARIA FRUMENTUM (DRAPARNAUD 1801) (MOLLUSCA, GASTROPODA, CHONDRINIDAE) SUBSPECIES OCCurring IN THE EASTERN PART OF THE SPECIES’ RANGE

ZOLTÁN FEHÉR¹, TAMÁS DELI² & PÉTER SÓLYMOS³

¹Hungarian Natural History Museum, H-1088, Baross u. 13, Budapest, Hungary*
²Munkácsy Mihály Museum, H-5600, Gyulai út 1, Békéscsaba, Hungary
³Alberta Biodiversity Monitoring Institute, Department of Biological Sciences, CW 405, Biological Sciences Bldg., University of Alberta, Edmonton, Alberta, T6G 2E9, Canada

Abstract Granaria frumentum occurring in the eastern part of the species’ range (i.e. in Dalmatia, Bosnia-Hercegovina, Montenegro, Serbia, Romania, Bulgaria, Albania and Greece) has been revised. Five morphotypes were recognized in the study area, namely G. f. frumentum (Draparnaud 1801), G. f. hungarica (M. Kimakowicz 1890), G. f. illyrica (Rossmässler 1835), G. f. atracta (Pilsbry 1918) and G. f. subaii spp. n. In our view, morphological differences and the more or less distinct ranges justify treating these morphotypes as distinct taxa, but due to the occurrence of transitional populations, they should only be distinguished at the subspecific level.

Key words Granaria frumentum, taxonomy, the Balkans, Albania

INTRODUCTION

Granaria frumentum (Draparnaud 1801) and its related taxa (= Granaria frumentum s.l. in the sense of Gittenberger (1973)) are distributed in and around the Alps, in the Apennine Peninsula, in the Carpathians, in the Pannonian Basin and in the Balkan Peninsula as far as to the Stara Planina Mountains and Epirus (Alzona, 1971; Bank, 2007; Turner et al., 1998; Klemm, 1973; Lisicky, 1991; Wiktor, 2004; Pintér & Suara, 2004; Reischütz & Sattmann, 1990; Jaeckel et al., 1957; Soós, 1943; Fehér & Gubányi, 2001; Damjanov & Likharev, 1975; Irikov & Erőss, 2008) (Fig. 1).

The majority of the taxa were described superficially, without defined type locality and designated type material. This makes their systematics problematical. Without seeing most of the described taxa Pilsbry (1916–1918) was unable to critically revise this group, therefore he provided only “... a collection of materials rather than an authoritative monograph ...”. In the most recent revision of the family, Gittenberger (1973) also evaded a comprehensive revision by proposing the grouping of G. frumentum s.str., G. illyrica (Rossmässler 1835) and G. apennina (Küster 1850) with the same nominal species, despite declaring that G. frumentum s. str. is not identical either with the southeastern Alpine form G. illyrica or with the Carinthian form G. frumentum s.l. Later, Gittenberger (1984) anticipated a connection between the central European nominate subspecies and other subspecies inhabiting south-east Austria, Italy, Yugoslavia and Romania. In contrast, the Fauna Europaea checklist (Bank, 2007) mentions only two valid taxa, namely G. frumentum and G. illyrica, with the latter treated as an aggregate to include all the related forms from eastern provinces previously described.

Sólymos et al. (2003) have attempted to typify some Central European and Balkan populations by multivariate methods using various continuous and discrete shell characteristics. They found that the typical “illyrica form” (Dalmatian coast) and the typical “frumentum form” (Central Europe) are clearly separated from each other as well as from a third, less coherent group, which consisted of Balkan populations. This seemed to justify the distinction of G. frumentum and G. illyrica as separate taxa, and at the same time support Gittenberger’s (1984) view that G. frumentum s.l. is more heterogeneous morphologically than can be accomodated by two valid taxa.

During this study, our primary aim was to identify the Granaria material, which was collected in the recent years in Albania, Bosnia-Hercegovina, Greece, Romania, Serbia and Montenegro, within the framework of the long-term Balkan research project of the Hungarian Natural History Museum and the Munkácsy Mihály Museum (Fehér et al., 2004, Fehér & Erőss, 2009a, b). Due to a lack of sufficient material from the western part of the species’ range, a comprehensive revision of the whole G. frumentum s.l. group is beyond the
scope of this paper, although some consideration of the western taxa is unavoidable because of overlap with forms described or indicated for our study area.

**Material and Methods**

Most of the examined material was collected recently in the study area. Additionally, we investigated other Balkan material (including some from Bulgaria and Croatia) in the collections of the Hungarian Natural History Museum, the Munkácsy Mihály Museum, the Naturhistorisches Museum (Wien) and in the private collections of Péter Subai, András Hunyadi and Zoltán Erőss. The following abbreviations are used for collections:

- **HNHM** Hungarian Natural History Museum, Budapest
- **MMM** Munkácsy Mihály Museum, Békéscsaba
- **NHMW** Naturhistorisches Museum, Wien
- **NHMW–K** NHMW, Klemm Collection
- **NHMW–E** NHMW, Edlauer Collection
- **Coll. AH** private collection of András Hunyadi, Budapest
- **Coll. PS** private collection of Péter Subai, Aachen
- **Coll. PSó** private collection of Péter Sólymos, Edmonton/Budapest

Sampling localities of recently collected material are listed as precisely as possible, with geographic coordinates, if any, given in the format as recorded. Label information of old museum materials are given in quotation marks and, where necessary, explanations are given between parentheses. For reasons of brevity, names of the frequently encountered collectors are abbreviated as follows: ZB = Zoltán Barina, GB = Gusztáv Boldog, LD = László Dányi, TD = Tamás Deli, TDo = Tamás Domokos, ZE = Zoltán Péter Erőss, ZF = Zoltán Fehér, ÉH = Éva Horváth, AH = András Hunyadi, TH = Tamás Huszár, ÉK = Éva Kiss, JK = Jenő Kontschán, JKó = Judit Kóra, KK = Kornél Kovács, DM = Dávid Murányi, CN = Csaba Németh, BP = Barna Páll-Gergely, DP = Dániel Pifkó, LP = László Pintér, PS = Péter Subai, MS = Miklós Szekeres, AS = Anna Szigethy, LT = Lilla Tamás.

**Systematic Account**

On the basis of the shell characters, five more or less distinct morphotypes can be distinguished in the study area. We made an attempt to assign these morphotypes with previously described taxa, based on their type areas (if any) and their original figures and descriptions. We paid
particular regard to the typical *G. frumentum* s. str. and the typical *G. illyrica* forms, which are considered to be the only valid taxa by the latest European checklist (Bank, 2007). One of the five morphotypes was found to be a new taxon, and is formally described below.

**CHONDRINIDAE** Steenberg 1925  
**Genus Granaria** F. Held 1838  
**Type species** *Granaria frumentum* (Draparnaud 1801)  

*Granaria frumentum frumentum* (Draparnaud 1801) (Fig. 3A)  

*Pupa frumentum* Draparnaud 1801: 59  
*Pupa frumentum* Draparnaud, 1805: 65, pl. 3, figs 51–52  
*Pupa frumentum* Rossmässler, 1835: 81–82, fig 34  
*Pupa frumentum* Rossmässler, 1837: 11, pl. 23, fig 310  
*Pupa (Torquilla) frumentum* Westerlund, 1887: 107  
*Abida frumentum* Pilsbry, 1918: 297–298, pl. 42, figs 1–4  
*Abida frumentum* Germain, 1930: 396  
*Abida frumentum* Soós, 1943: 131–133, pl. 5, figs 1–2  

**Type locality** France (but see Remarks)

**Material examined**  

*Description* Shell ventricose-cylindric, tapering abruptly (in the upper third); somewhat transparent, corneous yellowish-brown, with opaque whitish, strong, cervical swelling behind aperture; distinctly and regularly striate. Whorls moderately convex. Angular lamella strongly thickened on the right side where it joins the peristome, a short, deeply placed lamella (spiral lamella) beyond its inner end. Collumellar and subcollumellar lamellae subequal, remote from peristome; supracollumellar lamellae small and almost immersed or wanting. Four long, conspicuous plicae present: lower palatal is the longest and strongest, penetrating to mid-dorsal line; upper palatal nearly or quite as long; infrapalatal and basal plicae are shorter within. Suprapalatal, upper palatal and infrapalatal plicae become weaker and shallower ¼ whorl behind aperture, then all four main plicae form a knob-like protrusion about ¼ whorl behind the aperture. Short suprapalatal or sutural plicae may be seen deep within the aperture. All plicae conspicuous externally as light lines. Lip reflected, thickened and whitish, preceded by a shallow crest (Table 1).

*Remarks* Although Draparnaud (1801) did not define a type locality explicitly, as he was dealing with the fauna of France, it is generally assumed that the taxon’s *area typica* is France (e.g. Kokshoorn & Gittenberger, 2008).

*Granaria frumentum illyrica* (Rossmässler 1835)  
(Figs 3K–L)  

*Pupa frumentum var. illyrica* Rossmässler 1835: 82  
*Pupa frumentum var. illyrica* Rossmässler, 1837: 11, pl. 23, fig 312  
*Pupa pachygastra* Rossmässler 1837: 11, pl. 23, fig 314 [1]  
? *Pupa cylindracea* Rossmässler 1837: 12, pl. 23, fig 315  
*Pupa (Torquilla) frumentum var. illyrica* Westerlund, 1887: 107 [in part]  
*Pupa (Torquilla) frumentum var. pachygastra* Westerlund, 1887: 107
Table 1 Main shell morphological characteristics of *Granaria frumentum* subspecies. Literature data refer to the following synonyms: * = *fusiformis* Küster; ** = *minor* Küster; *** = *cylindracea* Rossmässler.

<table>
<thead>
<tr>
<th>Taxon</th>
<th><em>frumentum</em></th>
<th><em>illyrica</em></th>
<th><em>hungarica</em></th>
<th><em>attracta</em></th>
<th><em>subaii</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Shell size</td>
<td>small–middle-sized</td>
<td>middle-sized–large</td>
<td>small–middle-sized</td>
<td>middle-sized large</td>
<td>middle-sized</td>
</tr>
<tr>
<td>H: 6–8.9 mm</td>
<td>H: 8.2–14*** mm</td>
<td>H: 5.7–10.3 mm W: 2.9–3.7 mm</td>
<td>H: 7.4–15.2* (11.4**) mm W: 2.5–3.3* mm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W: 2.5–3.1 mm</td>
<td>W: 2.5–3.3 mm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shell shape</td>
<td>ventricose, barrel-shaped</td>
<td>ventricose-fusiform or cylindric-fusiform</td>
<td>ventricose, barrel-shaped</td>
<td>fusiform–elongated fusiform</td>
<td>fusiform</td>
</tr>
<tr>
<td>Cervical swelling</td>
<td>strong</td>
<td>weak–moderate</td>
<td>convex</td>
<td>convex</td>
<td></td>
</tr>
<tr>
<td>Whorls</td>
<td>moderately convex</td>
<td>moderately convex</td>
<td>moderately convex</td>
<td>moderately convex</td>
<td></td>
</tr>
<tr>
<td>Palatal plicae</td>
<td>strong</td>
<td>moderately developed</td>
<td>weak</td>
<td>very weak, infrapalatal usually absent, suprapalatal sometimes absent</td>
<td></td>
</tr>
<tr>
<td>Subangular lamella</td>
<td>absent</td>
<td>present, sometimes in two disjoined parts</td>
<td>absent</td>
<td>mostly absent</td>
<td>present, sometimes in two disjoined parts</td>
</tr>
<tr>
<td>Striation</td>
<td>moderate–strong</td>
<td>almost smooth–moderate</td>
<td>moderate–strong</td>
<td>weak–moderate</td>
<td>strong</td>
</tr>
</tbody>
</table>

*Abida illyrica* Pilsbry, 1918: 303–304, pl. 42, figs 8–9

*Abida frumentum pachygastra* Pilsbry, 1918: 302, pl. 42, figs 7, 10, 11

? *Abida illyrica cylindracea* Pilsbry, 1918: 305, pl. 45, figs 1–2

*Abida frumentum illyrica* Soós, 1943: 132

Type locality “Illyrien” (*illyrica*), “Dalmatien” (*pachygastra and cylindracea*)


Description Shell corneous yellowish-brown, usually larger than the nominate form, cylindric-fusiform (tapering more gradually); surface almost smooth to the naked eye. Whorls almost entirely flat. No or weakly developed cervical swelling behind aperture. Peristome widened but not recurved as per *frumentum* (trumpet-like in side-view). Subangular lamella always present, ½–¾ of the length of angular lamella, outer end either outside or in the same line as the angular. Outer parts of subangular and angular usually fuse or agglutinate, inner parts more or less diverge. Sometimes, subangular consists of two disjoined parts: a short node outside and a somewhat longer part (accessory lamella) behind that. Spiral lamella is usually longer than that of *frumentum*. Four long, conspicuous palatal plicae present. The suprapalatal, upper palatal and infrapalatal become weaker and shallower ¼ whorl behind the aperture, then all four main plicae form a knob-like protrusion about ½ whorl behind the aperture. Small accessory plica(e) may
sometimes be seen over the suprapalatal, and/or between upper palatal and suprapalatal plicae (Table 1).

Remarks Two other forms were described from the vicinity of this taxon’s area typica; Pupa pachygastra and Pupa cylindracea. The original description of Pupa pachygastra is based on only three specimens, which are very different in size, and with the number of palatal folds unequal (five or six), but otherwise, the shape of the depicted specimen resembles G. f. illyrica. Specimens with accessory palatal plicae can sometimes be found in G. f. illyrica populations, therefore we think that Rossmässler’s description is based on three atypical G. f. illyrica specimens. In contrast, the other taxon, Pupa cylindracea Rossmässler 1837, also described from Dalmatia, is more difficult to associate with typical G. f. illyrica. The depicted specimen looks somewhat different from typical G. f. illyrica and, moreover, the description does not deal with the subangular lamella, nor is the type locality defined precisely. Pilsbry (1916–1918) mentions this taxon from Almissa [Omiš], but the material from Omiš we studied did not contain any specimens looking like the one depicted by Rossmässler (1837). It is conceivable that Rossmässler’s description was based on an abnormal G. f. illyrica specimen, therefore the name is retained as a possible synonym. Alternatively, it might better be treated as a nomen dubium.

It is generally believed, that this taxon ranges westwards as far as the southern Alps. Forms occurring in the southern Alps are often treated as G. illyrica (Westerlund 1887; Gittenberger, 1973; Klemm, 1973; Turner et al., 1998; Falkner et al., 2002; Bank, 2007). We have studied only limited material from this area [Valdobbiate, Monte Cesen, 530 m a.s.l., N45° 54’ 42” E11° 59’ 43”, 11.04.2006, leg. LD & JK (HNHM 97028/2) – Torbole, near Lake Garda, 23.08.1956, leg. Hässlein (HNHM 72750/2) – along the road from Pontebb to Passo di Pramol, 800 m a.s.l., 25.07.1999, leg. LP (HNHM 75994/1) – Torri de Benaco, near Lake Garda, 65 m a.s.l., N45° 36’ 48” E10° 41’ 20”, 12.04.2006, leg. LD & JK (HNHM 97063/1)]. Regarding their general appearance (i.e. shape and size of the shell, ribbing and shape of the whorls), the small number of examined southern Alpine material seem similar to the Dalmatian populations with the remarkable difference that subangular and accessory lamellae are missing (Fig. 3M). Due to the lack of material from the southern Alps, we cannot judge how constant these latter characters are and if they have any systematic relevance. Preliminary molecular studies indicate that the southern Alpine and Dalmatian clades are well separated (Kokshoorn & Gittenberger, 2008; Kokshoorn, unpublished observation). In the meantime, therefore, we treat only the Dalmatian populations as G. f. illyrica in the strict sense (Figs 1, 2, 3K–L; Table 1).

As regards the taxa considered to be synonyms of G. illyrica by the Fauna Europaea checklist (Bank, 2007), such as Pupa adjuncta Rossmässler 1837, Abida frumentum brelihi Bole 1969, Pupa frumentum var. castanea Gredler 1879, “Pupa crassilabris De Betta 1852, Pupa frumentum var. curta Küster 1843, Pupa frumentum var. elongata Rossmässler 1837, Pupa frumentum var. gigantea Schröder 1911 and Pupa frumentum var. minor Rossmaßler 1837, which were described from the southern-southeastern Alpine region (indicated by “?” in Fig. 1), their systematic positions are hard to judge, but even if they are synonyms, they belong more probably to the southern Alpine form than to G. f. illyrica in the strict sense.

Though G. apennina is also considered a G. illyrica synonym by Bank (2007), we are inclined to follow Pilsbry (1916–1918) and Gittenberger (1973) in considering G. f. apennina (Küster 1850) as a distinct taxon. Though only a few lots were studied from Central Italy [Gola di Celano, bei Avezzano, Abruzzi, 17.08.1968, leg. W. Fauer, Coll. PS 11522/2 and Assisi, Rocca Maggiore, 29.05.1979, leg. LP, HNHM 37442/1], they fit Pilsbry’s (1916–1918: 305–306, pl. 42, figs 12–16) description well, differing characteristically from G. f. illyrica by their very tumid shape, long subangular and conspicuous cervical swellings (Fig. 3N).

Granaria frumentum hungarica (M. Kimakowicz 1890) (Figs 3B–J)

Torquilla frumentum frn. curta var. Illyrica Kimakowicz, 1883: 44
Pupa (Torquilla) frumentum var. Illyrica Westerlund, 1887: 107 [in part]
Torquilla frumentum var. Hungarica Kimakowicz 1890: 236–238
Abida frumentum hungarica Pilsbry, 1918: 301–302, pl. 42, fig 5
Abida frumentum hungarica Soós, 1943: 132

Type locality “Ungarn . . . in Siebenbürgen . . . Südabdachung der transsilvanischen Alpen” [=in the northwestern part of present Romania]


Description Shell ventricose-cylindric, tapering abruptly (in the upper third); in form and size agreeing with type form; somewhat transparent corneous yellowish-brown; distinctly and regularly striate; striation more obsolete than that of the nominal subspecies. Weak or no cervical swelling behind the aperture. Whorls convex. Only the lower palatal plica well developed, other three palatal plicae are much weaker than those of the nominal form. Subangular lamella always missing, angular lamella simply built or at most somewhat thickened in front (Table 1).

Remarks Before 1890, Kimakowicz treated this taxon as Torquilla frumentum illyrica (Kimakowicz, 1883). Although there are some original Kimakowicz lots in the HNHM, which are labelled so and are supposed to be in Kimakowicz’s hand before the description of the Torquilla frumentum hungarica, there is nothing on the label to prove this, so by caution, these lots are not considered as syntypes.
There are some populations where the cervical swelling of some or all of the specimens are more developed than that of the typical *G. f. hungarica*, forming a kind of transition to typical *G. f. frumentum*. The distribution of this feature does not show any distinct pattern, on the contrary, transitional forms occur within the whole range of the *G. f. hungarica* subspecies, sometimes very close to typical populations (e.g. in the Travnik area, in the Nišava gorge, near Zlot, in the Dibrë area, etc.). This indicates that the development of the cervical swelling in this species might be a repeatedly occurring evolutionary event.

There are some populations in Bosnia and Montenegro where the shell shape is less ventricose and the palatal plicae are weaker than those of the Transylvanian – i.e. typical – populations. As these populations occur in the area where the range of *G. f. hungarica* overlaps with that of *G. f. atracta*, it is supposed to be a hybrid form of the two subspecies (Fig. 2).

**Figure 2** *Granaria frumentum* material from the southeastern part of the species’ geographical range. Black square: *G. f. frumentum*; white square: *G. f. hungarica*, typical form; grey square: *G. f. hungarica*, transitional form to *G. f. frumentum*; grey diamond: *G. f. hungarica*, transitional form to *G. f. atracta*; black–white diamond: *G. f. atracta*, typical form; black dot: *G. f. subaii*, typical form; wite dot: *G. f. subaii*, populations with partly or fully reduced subangular lamella; black triangle: *G. f. illyrica*, typical form; white triangle: *G. f. cf. illyrica*, southern Alpine form; black reversed triangle: *G. f. apennina*. Dotted line indicates the “Kronstadt–Klausenburg line”, which separates the ranges of *G. f. hungarica* and *G. f. frumentum* in the opinion of Kimakowicz (1890).

**Granaria frumentum atracta** (Pilsbry 1918)
(Figs 3O–P)

*Pupa fusiformis* Küster 1845: 83–84, pl. 12, figs 4–5 – non Deshayes 1835 non C.B. Adams 1854

*Pupa fusiformis var minor* Küster 1845: 84, pl. 12, figs 6–7 – non Rossmässler 1837

? *Pupa fusiformis var.* Pfeiffer, 1868: 313 [described in the footnote]

? *Pupa eximia* Westerlund 1875: 33

*Pupa (Torquilla) fusiformis* Westerlund, 1890: 46

? *Pupa (Torquilla) eximia* Westerlund, 1890: 46

*Abida atracta* Pilsbry 1918: 327–328, T. 45 figs 18–19 [nom. nov. for *fusiformis* Küster]

*Abida puella* Pilsbry 1918: 328, T. 45 fig 17 [nom. nov. for *minor* Küster]


Type locality “Budua in Dalmatien am Boden nahe am Meere” (but see Remarks).

Description Shell medium-sized to large; rufous-to yellowish-brown; shape elongate fusiform; surface very finely striatulate. Whorls moderately convex to almost flat; last whorl subcristate-compressed below. No or weakly developed cervical swelling behind the aperture. Peristome whitish or flesh coloured. Subangular lamella usually missing. Palatal plicae moderately to strongly reduced: infrapalatal rudimentary; palatalis inferior conspicuous, emerges to the peristome; palatalis superior weak, sometimes emerges to the peristome; suprapalatal very weak, usually does not emerge to the peristome (Table 1).

Remarks As Pupa fusiformis is a preoccupied name, Pilsbry (1916–1918) introduced a new name, Abida atracta. The situation is more complicated due to a variety of Pupa fusiformis which was described by Pfeiffer (1868). Though Pfeiffer did not nominate this variety, Westerlund (1875), without seeing any material and based only on Pfeiffer’s description, named it Pupa exima, an elevation to species level. The lack of an illustration, the unknown type locality and the superficial description do not allow us to decide unambiguously the systematic position of Pupa exima. The shell width, given as 4.5 mm, leaves us unconvinced that Pupa exima can be equated with G. f. atracta, and we therefore suggest it be treated as a nomen dubium.

Although the type locality of Pupa fusiformis is given as Budua [Budva], we did not see any Granaria material from Budva or from the Montenegrin sea-coast. As the molluscan fauna of this region is otherwise well represented in the collections examined, we can reasonably conclude that this species is absent from the area. Küster’s description may well be based on flotsam-collected material.

Granaria frumentum subaii ssp. n.
(Figs 3Q–S, 4A–D)

Granaria frumentum illyrica Reischütz & Sattmann 1990: 257.

Holotype 1 sh, type locality, 18.08.2007, leg. ZF & LT, HNHM 96905.

Paratypes 29 sh, 5 sp, type locality, 18.08.2007, leg. ZF & LT, HNHM 96906/34; 56 sh, type locality, 25.05.2006, leg. ZB, TD & DP, MMM 90574/53 and MMM 90577/3.

Type locality Albania, Periferi Përmet, Benjë, gorge of Lumi i Lengaricës, 335 m a.s.l., N40° 14.68' E20° 26.26'.

Material examined ALBANIA: Periferi Berat, Qafa e Gllavës, along the Berat–Këlcyrë road, 900 m a.s.l., N40° 30.17' E19° 59.07', 13.04.2001, leg. ZE, ZF & KK (HNHM 85747/4) – Periferi Ersekë, Maja e Melesinit over Leskovik, 930 m a.s.l., N40° 09.06' E20° 35.69', 03.07.2003, leg. ZE, ZF, JK & DM (HNHM 93676/3) – Periferi Gjirokastër, 3 km NE of Suhë, along the road from Libohovë to Sheper, 425 m a.s.l., N40° 05' 18'' E20° 16' 18'', 12.10.2004, leg. ZF, JK & DM (HNHM 95086/12) – same locality, 14.08.1993, leg. ZF (Coll. ZE/36) – Periferi Skrapar, 4 km SE of Çorovodë towards Zogas, by the right side of the canyon of Lumi i Osumit, upper end, 1070 m a.s.l., N40.56065° E20.39377°, 07.07.2005, leg. ZB, DP & DS (HNHM 95314/1) – Periferi Skrapar, Mali i Tomorrit, 4.8 km NE of Çorovodë towards Radesh, over the gorge of Pr. i Çorovodës, 475 m a.s.l., N40° 31' 25'' E20° 15' 11'', 10.10.2004, leg. ZF, JK & DM (HNHM 95366/12) – Periferi Skrapar, Qafa e Dëvris, NE of Radesh along the road to Zaloshnje, W side of the gorge, 1180 m a.s.l., N40° 33.37' E20°
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Bencë, along the road from Tepelenë to Progonat, 220 m a.s.l., N40° 15' 48'' E20° 00' 25'', 11.10.2004, leg. ZF, JK & DM (HNHM 95108/6) – Periferi Tepelenë, along the road between Tepelenë and Kelcyrë, UTM: DK27, 17.08.1993, leg. ZE (HNHM 83348/1) – Periferi Tepelene, between Bencë and Tepelene, on the left side of L. i Bencës, ca. 2.5 km E of Maja e Tresenikut, 235 m a.s.l., N40.266580° E20.005960°, 02.05.2005, leg. ZB, GK & DP (HNHM 94942/3) – Periferi Vlorë, Dhërmi, along the Vlorë–Sarandë main road, N40° 09' 09'' E19° 38' 08'', 06.07.1996, leg. ZE & ZF (HNHM 76113/19) – Periferi Vlorë, Dhërmi, rocky grassland S of the village, N40° 08' 36” E19° 39’ 44”, 11.05.2006, leg. LD, JK & DM (HNHM 97027/8) – GREECE: Ioannina county, Votonois, stream 1 km E of the village, 662 m a.s.l., N39° 45’ 58” E21° 05’ 50”, 13.05.2006, leg. LD, JK & DM (HNHM 97026/4).

Measurements  Holotype, H: 8.1, W: 2.5 mm.  Paratypes, H: 6.5 to 9.7 mm, W: 2.3 to 2.7 mm.

Diagnosis  Compared to the closest occurring related taxa, this subspecies differs from the nominate form by its more fusiform shell, lesser cervical swelling and the presence of an accessory lamella behind the subangular lamella. From G. f. hungarica (M. Kimakowicz) it differs in its more fusiform shell and the presence of an accessory lamella behind the subangular lamella. From G. f. atracta (Pilsbry) by the better developed palatal plicae and the presence of an accessory lamella behind the subangular lamella. And from G. f. illyrica (Rossmässler) by its smaller and better striated shell and more convex whors.

Description  Shell fusiform, tapering gradually; corneous yellowish-brown or reddish-brown; regularly and obliquely striate; comprising 8½ – 9½ convex whors. Behind the lip the whitish cervical tract is moderately swollen to barely perceptible. The four principal palatal plicae moderately developed, entering into or past the dorsal mid-line, with a prominence about ½ whorl behind the aperture; upper palatal and infrapalatal plicae somewhat diminished, suprapalatal strongly diminished before the prominence. Occasionally a short fifth palatal plica (sutural) occurs deep inside. Plicae show through
the wall as white lines. Angular and subangular lamellae either separate or fused. A long accessory lamella present behind the subangular, at an acute angle to the angular. Small spiral lamella present deep inside, but scarcely visible without breaking the shell. Parietal lamella starts deeper than angular lamella, but is clearly visible in frontal view. Columellar and subcolumellar lamellae are clearly visible, the former being somewhat larger. Aperture U-shaped with palatal and columellar walls parallel. Peristome white, somewhat reflected and expanded except for the section over the suprapalatal. In frontal view a sinulus can be seen between suprapalatal and angular lamellae. Peristome ends joined by a thin parietal callus.

Derivation of name This taxon is named in honour of our colleague and friend, Péter Subai.

Remarks There are several populations which do not show all of the features which characterize typical populations as defined above. In many which have a typical shell shape the ribbing may be atypical with the subangular lamella missing. In others, shell ribbing can be much weaker than typical shells. However, even in these atypical populations, a few specimens may be found showing more typical features, indicating a basic relationship with typical G. f. subaii populations.

Discussion
In the past century and a half, several taxa of the Granaria frumentum s.l. group have been described. Due to the lack of availability of type materials and the superficial descriptions available in many cases, a complete revision of the species group promises to be very complicated. In common with Gittenberger (1973), we are unwilling to undertake a full review, mostly due to the unavailability of material from the Alpine region. However, the material we were able to access presented a good opportunity to act as a basis for comparison with the morphological variability of the species within the southeastern part of its geographical range. In this way we were able to develop an overall opinion on the taxonomy of the group, as well as to map the subspecific distribution pattern.

We have found five distinct morphotypes in the study area, having more or less distinct ranges with relatively narrow overlapping zones. Accordingly, it seems justified to distinguish more than a single taxon within Granaria frumentum s.l. However, the existence of transitional forms (either when a population consists of specimens which form a transitional series from one morphotype to another or when the whole population bears features transitional between two morphotypes) limits these additional taxa to the rank of subspecies only.

The most widespread subspecies, G. f. hungarica occurs not only in Transylvania but its range seems to involve the eastern part of the Dinaric Mountains, reaching to central Bosnia westwards and to central Albania southwards. It also seems to replace the nominate subspecies south of the Sava River, and in the Carpathians to reach far eastwards beyond the “Kronstadt–Klausenburg line” [Brasov–Cluj] (Fig. 2), which has been defined as the northeastern limit of this taxon by Kimakowicz (1890).

G. f. atracta seems to be restricted to a relatively narrow range in northwestern Montenegro, southwestern Serbia and eastern Bosnia, having numerous transitional populations where its range overlaps with that of G. f. hungarica. Typical G. f. illyrica has been found only in the Adriatic coastal zone between Istria and Central Dalmatia, whereas typical G. f. frumentum has not been found in the Balkans, only in the adjacent part of the Pannonian Basin. In our view, populations occurring in the southeasternmost extension of the species’ range in south Albania and Epirus, belong to a new subspecies, which is here described as G. f. subaii n. ssp.

Regarding the finer-scale distribution of G. frumentum in the southeastern part of its range, a further two points are worth mentioning. Although this species is believed to live in Macedonia (Jaeckel et al., 1957; Stankovic et al., 2006; Bank, 2007), there are hardly any specific Macedonian records in the literature nor did we see any Macedonian material during this study. Therefore we treat its occurrence in Macedonia as doubtful for the time being. Another noteworthy point is that we have not seen any Granaria frumentum material from the Montenegran coastal zone. As the Montenegran coastal area is very well represented otherwise in examined collections, the absence of Granaria most probably reflects a real distribution gap.
Chondrinids are characterized by a relatively fast evolution rate. As most of the known genera in subfamily Chondrininae evolved during the Pleistocene (Gittenberger, 1984), we can reasonably suppose that subspecific differentiation of *G. frumentum* is dated from the Upper Pleistocene and might be caused by range fragmentation during glacial periods. The existing subspecies could be preserved within their own ranges due to subsequent limited dispersal, which is characteristic of the whole genus (Gittenberger, 1984).

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