

REVISION OF *GRANARIA FRUMENTUM* (DRAPARNAUD 1801) (MOLLUSCA, GASTROPODA, CHONDRINIDAE) SUBSPECIES OCCURRING IN THE EASTERN PART OF THE SPECIES' RANGE

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Abstract *Granaria frumentum* occurring in the eastern part of the species' range (i.e. in Dalmatia, Bosnia-Herzegovina, 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* ssp. 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; Jaekel *et al.*, 1957; Soós, 1943; Fehér & Gubányi, 2001; Damjanov & Likharev, 1975; Irikov & Eröss, 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 accommodated 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-Herzegovina, 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 & Eröss, 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



Figure 1 Schematic distribution map of *Granaria frumentum*, roughly indicating the ranges of subspecies, which are mentioned in the present study. Area, delimited by the frame, is magnified on Fig. 2.

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

Coll. ZE private collection of Zoltán Erőss, 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 Kotschán, 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 AUSTRIA: Niederösterreich, Flatzterwand bei Ternitz, 10.1937, leg. Wochesl (NHMW–K 4.623) – Oberösterreich, Kremsmünster, 01.05.1948, leg. Mahler (NHMW–K 26.753) – CROATIA: Papuk Mts., G, Bojcan, 22.04.2004., leg. LD, JK & DM (HNHM 94634/2) – CZECH REPUBLIC: Karlštejn, 22.07.1995, leg. ZF (HNHM76095/4) – GERMANY: Jena, ex coll. Zoologisches Museum Berlin (HNHM 72695/35) – HUNGARY: Kunpeszér 1 km along the road to Tatárszentgyörgy, UTM: CT61, 26.08.2002, leg. ZF (HNHM 90803/13) – Nagyarsány, S slope of Szársomlyó, 08.08.1976, leg. Gy. Kovács (HNHM60321/51) – Szilvásvár, Istállóskei-bg., UTM: DU52, 12.09.1994, leg. L. Drimmer (HNHM 31470/49) – Pilisborosjenő, brickworks, 08.04.1984, L. Drimmer (HNHM 37670/430) – ROMANIA: “Báziás” [Bazias], 1883. leg. M. Kimakowicz (HNHM 72735/6) – “Hungaria, Nagyenyed” [Aiud], leg. Szilády (HNHM 72697/3) – SERBIA: Petrovaradin, fortress, N 45.2524° E19.873°, 14.11.2001, leg. P.

Sólymos & T. Gaudényi (Coll. PSó) – SLOVAKIA: Malé Karpaty, Smolenice, Jaskiňa Driny, 400 m a.s.l., N48° 30′ 02″ E 17° 24′ 14″, 19.03.2004, leg. ZE & ZF (HNHM 95347/13) – Trenčín, castle hill, 08.08.1990, leg. Gy. Kovács (HNHM 68193/31).

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 $\frac{1}{4}$ whorl behind aperture, then all four main plicae form a knob-like protrusion about $\frac{1}{3}$ 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 [!]

? *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.

Taxon	<i>frumentum</i>	<i>illyrica</i>	<i>hungarica</i>	<i>atracta</i>	<i>subaii</i>
Shell size	small–middle-sized H: 6–8.9 mm W: 2.5–3.1 mm	middle-sized–large H: 8.2–14*** mm W: 2.9–3.7 mm	small–middle-sized H: 5.7–10.3 mm W: 2.5–3.3 mm	middle-sized–large H: 7.4–15.2* (11.4**) mm W: 2.5–3.3* mm	middle-sized H: 6.5–9.7 mm W: 2.3–2.7 mm
Shell shape	ventricose, barrel-shaped	ventricose-fusiform or cylindrical-fusiform	ventricose, barrel-shaped	fusiform–elongated fusiform	fusiform
Cervical swelling	strong	absent–very weak	absent–weak	absent–very weak	weak–moderate
Whorls	moderately convex	flat	moderately convex	moderately convex–flat	convex
Palatal plicae	strong	moderately developed	weak	very weak, infra-palatal usually absent, supra-palatal sometimes absent	moderately developed
Subangular lamella	absent	present, sometimes in two disjoint parts	absent	mostly absent	present, sometimes in two disjoint parts
Striation	moderate–strong	almost smooth–moderate	moderate–strong	weak–moderate	strong

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*)

Material examined BOSNIA-HERCEGOVINA: “Livno” (NHMW 38.528/1) – CROATIA: Omiš, by the bank of Cetina river, 04.08.1972, leg. PS, LP & AS (HNHM 72721/50) – same locality, 13.11.1976, leg. Mikuska & Topál (HNHM 10128/11) – Velebit Mts., 1.5 km N of Obrovac, by the bank of Zrmanja river, 28.06.1997, leg. ZF & LT (HNHM 76134/33) – Istria, S of Kostanjica, 27.07.1987, leg. ÉK & LP (HNHM 70881/142) – Istria, Kotli, gorge of Mirna river (SE of Buzet), N45° 22.10' E14° 0.98', 20.06.2004, leg. ZF & LT (HNHM 94424/11) – Cres, Lubenice, N44° 53' 19" E14° 19' 50", 22.08.2008, leg. ZF & LT (HNHM 97064/50) – Velebit Mts., Starigrad,

Mala Paklenica gorge, 27.06.1997, leg. ZF & LT (HNHM 76102/38).

Description Shell corneous yellowish-brown, usually larger than the nominate form, cylindrical-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, $\frac{1}{3}$ – $\frac{2}{3}$ 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 disjoint 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 $\frac{1}{4}$ whorl behind the aperture, then all four main plicae form a knob-like protrusion about $\frac{1}{3}$ 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 [Valdobbiene, 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 Pontebba to Passo di Pramollo, 800 m a.s.l., 25.07.1999, leg. LP (HNHM 75994/11) – 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* Rossmässler 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 *frm. 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]

Material examined ALBANIA: Periferi Berat, Dardhë, beneath N slope of Çuka Partizan, 800 m a.s.l., N40° 44.584' E20° 07.628', 09.04.2006, leg. ZE, ZF, AH, DM (HNHM 97019/17, Coll. AH/17, Coll. ZE/17) – Periferi Skrapar, 4 km E of Terovë, valley of Lumi i Tomoricës, at the Terovë junction [fluvial flotsam], N40° 42.860' E20° 13.349', 25.08.2006, leg. ZF, AH, TH & DM (HNHM 97060/3, Coll. AH/3) – Periferi Dibrë, 3 km E of Fushë-Lurë along the Cidhnë–Fushë-Lurë road, 1220 m a.s.l., N41° 48.819' E20° 14.171', 29.06.2007, leg. LD, ZE, ZF, AH & DM (HNHM 97024/6) – Periferi Dibrë, 3 km W of q. e Murrës, 31 km W of the L. i Drinit te Zi, 975 m a.s.l., N41° 38.792' E20° 11.411', 26.06.2003, leg. ZE, ZF, JK & DM (HNHM 93674/9) – Periferi Dibrë, beneath Cidhnë, gorge of Pr. i Setës, at the hydroelectric station, 510 m a.s.l., N41° 45.036' E20° 15.754', 10.10.2005, leg. TD & ZF (HNHM 97050/1) – Periferi Dibrë, 1 km W of Cidhnë along the footpath to Gurrë-Lurë, gorge of Pr. i Setës, 680 m a.s.l., N41° 45.111' E20° 15.665', 10.10.2005, leg. TD, ZE, ZF & DM (HNHM 97022/3, Coll. ZE/3) – same locality, N41° 45.123' E20° 15.145', 12.04.2006, leg. ZE, ZF, AH & DM (HNHM 97021/4, Coll. AH/4, Coll. ZE/4) – Periferi Dibrë, ca. 2 km W of Cidhnë along the footpath to Gurrë-Lurë, gorge of Pr. i Setës, 730–750 m a.s.l., N41° 45.036' E20° 15.754', 10.10.2005, leg. ZE & DM (HNHM 97057/1, MMM 90716/1, Coll. ZE/1) – Periferi Dibrë, ca. 3 km W of Cidhnë along the footpath to Gurrë-Lurë, gorge of Pr. i Setës, 730 m a.s.l., N41° 45.428' E20° 14.333', 12.04.2006, leg. ZE, ZF, AH & DM (HNHM 97056/1) – Periferi Kukës, 1 km S of Resk along the Kukës–Peshkopi road, 690 m a.s.l., N41° 55.558' E20° 23.224', 26.06.2007, leg. LD, ZE, ZF, AH & DM (HNHM 97025/5) – Periferi Kukës, Kolesjan–Resk, along the Kukës–Peshkopi road, 1 km N of the Ploshtan junction, 670 m a.s.l., N41° 57.597' E20° 23.689', 09.10.2005, leg. TD, ZE, ZF & DM, (HNHM 97048/1) – Periferi Mirditë, Bisak, 2 km on the road towards Klos, by the right bank of Lumi i Fani i Vogël, 430 m a.s.l., N41° 53.37' E20° 07.25', 08.04.2001, leg. ZE, ZF & KK (HNHM 85749/7) – Periferi Shkodër, ca. 1.5 km upstream from dam at Koman,

Liqeni i Komanit, right bank, 180 m a.s.l., N42° 07.302' E19° 49.882', 14.04.2006, leg. ZE, ZF, AH, DM (HNHM 97020/2, Coll. AH/3, Coll. ZE/3) – Periferi Shkodër, ca. 12 km upstream from dam at Koman, Liqeni i Komanit, right bank, 170 m a.s.l., N42° 11.229' E19° 52.173', 15.04.2006, leg. ZE, ZF, AH & DM (HNHM 97059/10, Coll. AH/10, Coll. ZE/10) – Periferi Shkodër, ca. 15 km upstream from dam at Koman, Liqeni i Komanit, right bank, 170 m a.s.l., N42° 12.321' E19° 53.507', 15.04.2006, leg. ZE, ZF, AH & DM (HNHM 97014/2, Coll. AH/2, Coll. ZE/2) – Periferi Shkodër, ca. 15.5 km upstream from dam at Koman, Liqeni i Komanit, right bank, 180 m a.s.l., N42° 12.640' E19° 53.677', 15.04.2006, leg. ZE, ZF, AH & DM (HNHM 97015/2, Coll. AH/1, Coll. ZE/1) – Periferi Shkodër, ca. 17.5 km upstream from dam at Koman, Liqeni i Komanit, right bank, 170 m a.s.l., N42° 13.550' E19° 53.542', 15.04.2006, leg. ZE, ZF, AH & DM (HNHM 97016/1) – Periferi Shkodër, ca. 18 km upstream from dam at Koman, a left side-valley of Liqeni i Komanit, 170 m a.s.l., N42° 13.613' E19° 54.300', 15.04.2006, leg. ZE, ZF, AH & DM, (HNHM 97017/3, Coll. AH/2, Coll. ZE/2) – Periferi Tropojë, 11 km S of Bajram Curri, gorge of Pr. i Shijës, 220 m a.s.l., N42° 17.927' E20° 01.731', 07.10.2005, leg. TD, ZE, ZF & DM (HNHM 97049/1) – Periferi Tropojë, 3 km W of the Lumi i Valbonës mouth on the Fierzë–Tetaj road, 226 m a.s.l., N42° 15.784' E19° 59.400', 07.10.2005, leg. TD, ZE, ZF & DM (HNHM 97058/3, MMM 90714/2, Coll. ZE/2) – Periferi Tropojë, Dragobi (14 km N of Bajram Curri), gorge of Pr. i Thatë, 540 m a.s.l., N42° 26.184' E19° 59.079', 06.10.2005, leg. TD, ZE, ZF & DM (HNHM 97055/3, MMM90712/3, Coll. ZE/3) – Periferi Tropojë, over Gurorë, 3 km N of the Lumi i Valbonës mouth, 289 m a.s.l., N42° 17.206' E20° 01.287', 07.10.2005, leg. TD, ZE, ZF & DM (HNHM 97052/1, MMM 90713 /1) – BULGARIA: Belogradchik–Oresec, 18.07.1984, leg. ÉK & LP (HNHM 37436/112) – Cerepis monastery, 08.08.1978, leg. LP (HNHM 34872/6) – Rabisa, Magura cave, 19.07.1984, leg. ÉK & LP (HNHM 37439/2) – Ritlite, 08.08.1978, leg. LP (HNHM 41400/4) – BOSNIA-HERCEGOVINA: “Bosnien: Foča” (NHMW/1) – “Mrtvanje, Bjelasnica” (NHMW 30.28/20) – “Vucjaluka, Bosn.” (NHMW 32.346 /4) – “Travnik” (NHMW 38.315 /1) – Travnik, above the city, ca. 750 m a.s.l., 18.08.1987, leg. PS (Coll. PS 16934/4) – Konjic, N43° 40.04'

E17° 57.54', 23.04.2000, leg. ZE & ZF (HNHM 83356/1) – “Sarajevo”, 1886, leg. Kimakowicz (HNHM 72743/5) – MONTENEGRO: Gušinj S 2 km, Alipašini Izvori, 935 m a.s.l., N42° 33.014' E19° 49.486', 04.10.2005, leg. TD, ZE, ZF & DM (HNHM 97054/1) – Ibar Valley, 1 km SW of Spiljani, 829 m a.s.l., N42° 54.410' E20° 20.062', 12.10.2005, leg. TD, ZE, ZF & DM (HNHM 97035/3, Coll. EZ/2) – between Ribarice and Rožaje (20 km S of the Tutin junction), UTM: DN34, 19.07.1972, leg. LP, PS & AS (HNHM 34880/10, HNHM 34877/14, HNHM 72738/13, Coll. PS 1827/11) – Durmitor, Crno Jezero, UTM: CN47, 15.08.1987, leg. PS (Coll. PS 13454/5) – KOSOVO: Beli Drim spring, UTM: DN43, 19.07.1972, leg. LP, PS & AS (HNHM 34875/6, HNHM 72747/5, Coll. PS 1826/5) – Novoselo (Novosellë), spring of the Beli Drim (Burimi i Drinit te Bardhë), 580 m a.s.l., N42° 44.239' E20° 18.408', 12.10.2005, leg. TD, ZE, ZF & DM (HNHM 97061/1, MMM 90717/1, Coll. ZE/1) – ROMANIA: “Zalasd b. Vajdahunyad” [Zalasd stream near Hunedoara], 1883, leg. M. von Kimakowicz (HNHM 72736/7) – “Govasdia b. Vajdahunyad” [Govăjdia near Hunedoara], 1883, leg. M. von Kimakowicz (HNHM 72746/6) – “Vajdahunyad, Schlossberg” [Hunedoara, castle hill], 1883, leg. M. von Kimakowicz (HNHM 72745/6) – “Piatra Barului, Strell-tal”, 1883, leg. M. von Kimakowicz (HNHM 72727/6) – “Békás-szoros” [Cheile Bicazului], 11.04.1973, leg. Gy. Kovács (HNHM 68180/13) – Capațina Mts., 2 km N of Baile Olanesti, 16.08.1999, leg. ZE, ZF & KK (HNHM 75995/22) – between Pestera and Baița (20 km N of Deva), 14.08.1999, leg. ZE, ZF & KK (HNHM 75996/7) – Domogled Mt. near Baile Herculane, 25.07.1997, leg. ZE & ZF (HNHM 76111/14) – Crivadia, Viadukt Crivadia (15 km NW of Petrosani), 15.08.1999, leg. ZE, ZF & KK (HNHM 75997/11) – 3 km SE of Steierdorf, 24.07.1997, leg. ZE & ZF (HNHM 76101/1) – Turda, Cheile Turzii, 26.07.1977, leg. Gy. Kovács (HNHM 68175/96) – Hunedoara, castle, 14.08.1999, leg. ZE, ZF & KK (HNHM 75998/4) – Munții Piatra Craiului, NW of Podu Dâmboviței, Cheile Dâmboviței toward Sătic, limestone gorge, 740 m a.s.l., N45° 25' 13.7" E25° 11' 34.5", 30.04.2008, leg. TD, ÉH, JL, BP & PS (MMM 90582/12) – Munții Piatra Craiului, N of Dâmbovicioara, limestone gorge 1–2 km upstream of the village, 30.04.2008, leg. TD, ÉH, JL, BP & PS (MMM 90583/7) – Munții Poiana Ruscă,

before Govăjdia (SW of Hunedoara), S-exposed limestone cliffs, 260–300 m a.s.l., N45° 43' 53.4" E22° 50' 33.2", 26.04.2008, leg. TD, ÉH, JL, BP & PS (MMM 90584/155) – Munții Făgăraș, N of Brădet (NE of Curtea de Argeș), Vâlsan gorge, 675 m a.s.l., N45° 20' 04" E24° 44' 21", 01.05.2008, leg. TD, ÉH, JL, BP & PS (MMM 90585/1) – Munții Piatra Craiului, E of Podu Dâmboviței, Cheile Cheii, limestone gorge, 30.04.2008, leg. TD, ÉH, JL, BP & PS (MMM 90586/9) – Munții Vâlcă, N of Pârvulești (N of Târgu Jiu), valley (gorge) of the Șușița Seacă, 390 m a.s.l., N45° 09' 27.5" E23° 11' 46.4", 03.05.2008, leg. TD, ÉH, JL, BP & PS (MMM 90587/14) – Munții Piatra Craiului, N of Podu Dâmboviței (between Podu Dâmboviței and Dâmbovicioara) gorge, 30.04.2008, leg. TD, ÉH, JL, BP & PS (MMM 90588/12) – Munții Vâlcă, 3–4 km N of Cloșani (N of Baia de Aramă), slopes with limestone cliffs on the left side of the Motru, 03.05.2008, leg. TD, ÉH, JL, BP & PS (MMM 90589/1) – Munții Vrancea, near Lepșa (NW of Focșani), conglomerate walls on the right side of Cheile Tișița Mică, 600 m a.s.l., N45° 56' 25.5" E26° 35' 05.7", 27.04.2008, leg. TD, ÉH, JL, BP & PS (MMM 90590/2) – Munții Vrancea, near Lepșa (NW of Focșani), Pasul Soveja, on limestone conglomerate cliffs, 27.04.2008, leg. DT, ÉH, JL, BP & SP (MMM 90591/1) – Jud. Caraș-Severin, Nera Gorge, SE Potoc, at the confluence of Chichiregu and Bleiului streams, 160 m a.s.l., N44° 54' 08.8" E21° 44' 54.5", 20.04.2007, leg. TD, TDo, BP & PS (MMM 90592/151) – Jud. Gorj, 1.4 km N Vâlcele (= NE of Tismana), 310 m a.s.l., N45° 05' 44.9" E22° 58' 31.8", 17.04.2007, leg. TD, TDo, BP & PS (MMM 90593/34) – Jud. Mehedinți, Cheile Romenutei (in Cerna Valley) ca. 40 km E of Băile Herculane, 420 m a.s.l., N45° 04' 28.3" E22° 37' 13.2", 19.04.2007, leg. TD, TDo, BP & PS (MMM 90594/13) – Jud. Mehedinți, W Ponoarele (= SW Baia de Aramă), near Zăton cave, 18.04.2007, leg. TD, TDo, BP & PS (MMM 90595/5) – Jud. Gorj, valley of Motru-Sec river, NW Cloșani, limestone, 350 m a.s.l., N45° 04' 14.2" E22° 46' 34.3", 17.04.2007, leg. TD, OD, BP & PS (MMM 90596/34) – Jud. Gorj, N Cloșani, Motru river, right side, limestone, 340 m a.s.l., 17.04.2007, leg. TD, TDo, BP & PS (MMM 90598/50) – Jud. Gorj, 1.5 km N of Palovragi, 100–300 m N of Palovragi cave, 620 m a.s.l., 16.04.2007, leg. TD, TDo, BP & PS (MMM 90599/8) – Jud. Caraș-Severin, Minis valley, Cascada Bigâr (= 1.6 km SE of Anina),

310 m a.s.l., N45° 00' 12.7" E21° 57' 34.5", 19.04.2007, leg. TD, TDo, BP & PS (MMM 90600/4) – Jud. Gorj, Cheile Pocrui, N of Pocrui (NE Baia de Arama), 06.07.2007, leg. GB, TD & JKó (MMM 90601/31) – Jud. Gorj, 4 km N of Runcu, Cheile Sohodolului, 450 m a.s.l., 06.07.2007, leg. GB, TD & JKó, (MMM 90602/5) – Jud. Mehedinti, Băile Herculane–Domogled, Cheile Jelărăului, 08.07.2007, leg. GB, TD & JKó (MMM 90603/5) – Jud. Mehedinti, Jupânesti (between Baia de Arama and Portile de Fier), Epuran cave, 407 m a.s.l., N44° 50' 04" E22° 34' 10", 07.07.2007, leg. GB, TD & JKó, (MMM 90604/9) – Jud. Mehedinti, Băile Herculane, Pestera Hotilor, 05.07.2007, leg. GB, TD & JKó (MMM 90605/5) – Jud. Mehedinti, 3 km S Baia de Arama, near cave, N44° 59' 42" E22° 47' 13", 07.07.2007, leg. GB, TD & JKó (MMM 90606/8) – Jud. Caras-Severin, E of Coronini (limestone wall, near bank of Danube), 85 m a.s.l., N44° 39' 52" E21° 41' 56", 04.07.2007, leg. GB, TD & JKó (MMM 90607/2) – Jud. Mehedinti, Cheile Romenutei (in Cerna Valley) ca. 40 km E of Băile Herculane, 420 m a.s.l., N45° 04' 28.3" E22° 37' 13.2", 05.07.2007, leg. GB, TD & JKó (MMM 90608/1) – Jud. Caras-Severin, between Moldova Nou and Padina Mate, forest (Fagus, Caprinus, Ruscus) with limestone rocks, 299 m a.s.l., N44° 44' 15" E21° 42' 57", 04.07.2007, leg. GB, TD & JKó (MMM 90609/2) – Jud. Caras-Severin, between Moldovita and Moldova Nou, limestone wall, 444 m a.s.l., N44° 47' 05" E21° 42' 07", 04.07.2007, leg. GB, TD & JKó (MMM 90610/38) – Jud. Mehedinti, Cazanele Mari, near Dubova (bank of Danube), 08.07.2007, leg. GB, TD & JKó (MMM 90611/654) – SERBIA: Glozanica E, roadside bush, N43° 37' 30" E22° 13' 11", 02.04.2006, leg. TD, TDo, K. Nacsá & BP (MMM 90581/4) – Cerovica–Sastavci, gorge, 01.07.1984, leg. ÉK & LP (HNHM 45805/42, HNHM 95343/1) – Đerdap Mts., Golubinje N, quarry, N44° 34' 09" E22° 14' 44", 13.10.2006, leg. LD, JK & DM (HNHM 97030/12) – Manasija monastery, E of Despotovac, 260 m a.s.l., N44° 06' 00" E21° 27' 48", 04.07.2008, leg. TD, BP & PS (MMM 90564/151) – Golubac, fortress, N44° 39' 36" E21° 38' 17", 13.07.2004, leg. ZB & DP (HNHM 97018/7) – same locality, N44° 39' 30" E21° 39' 45", 12.10.2006, leg. LD, JK & DM (HNHM 97013/12) – Gornjak monastery, 22.07.1990, leg. L. Németh (HNHM 89266/6) – Pirot, Gradišnička gorge, 400 m a.s.l., N43° 11' 11" E22° 35' 48", 09.07.2008, leg. TD, BP & PS (MMM 90569/16) –

Grnčar (ca. 25 km S of Bela Palanka), 370 m a.s.l., N43° 01' 14" E22° 21' 51", 09.07.2008, leg. TD, BP & PS (MMM 90570/5) – Niška Banja, Jelašnička gorge, 390 m a.s.l., N43° 16' 53" E22° 03' 44", 06.07.2008, leg. TD, BP & PS (MMM 90565/186) – Kalna N 1.5 km, 350 m a.s.l., N43° 25' 45" E22° 25' 03", 09.07.2008, leg. TD, BP & PS (MMM 90571/6) – E end of the Mali Kazan gorge, 74 m a.s.l., N44° 36' 49" E22° 16' 31", 11.07.2008, leg. TD, BP & PS (MMM 90568/35) – Knjaževac S 5 km along the road to Pirot, 260 m a.s.l., N43° 32' 11" E22° 17' 07", 10.07.2008, leg. TD, BP & PS (MMM 90563/9) – Levovik (near Soko Banja), 01.07.1984, leg. ÉK & LP (HNHM 45806/5) – Ljuberađa NE, along the road to Gorčini, near spring, 460 m a.s.l., N43° 01' 49" E22° 23' 20", 09.07.2008, leg. TD, BP & PS (MMM 90566/21) – Luka, Stol Mt., 600 m a.s.l., 11.07.2008, leg. TD, BP & PS, (MMM 90572/14) – Pirot, fortress, 360 m a.s.l., N43° 09.558' E22° 34.866', 22.03.2002, leg. ZE, ZF & AH (HNHM 89617/2, Coll. AH/2) – same locality, 09.07.2008, leg. TD, BP & PS (MMM 90574/24) – 1 km W of the Grža junction, along the Paracin–Zaječar road, 280 m a.s.l., N43° 51.46' E21° 36.87', 11.04.2004, leg. ZE, ZF & AH (HNHM 94421/27, Coll. AH/24) – Batrage, 4 km along the road to Ribarice, UTM: DN55, 19.07.1972, leg. LP, PS & AS (HNHM 34880/10, HNHM 72739/10, Coll. PS 1823/7) – E of Rožaje, 1030 m a.s.l., 22.07.2008, leg. ZE & AH (Coll. AH/11) – Sičevo, Nišava valley, 10.07.1972, leg. LP, PS & AS (HNHM 72732/184) – Vratarnica S 1 km (near Zaječar), N43° 46' 38" E22° 18' 47", 26.07.1997, leg. ZE, ZF & KK (HNHM 76124/7) – Stubič W, Kanyon Reke Zamne (ca. 2 km E of Plavna), N44° 17' 32" E22° 16° 39", 11.07.2008, leg. TD, BP & PS (MMM 90573/21) – Užice S 2 km along the road towards Nova Varoš, 514 m a.s.l., N43° 51.06' E19° 49.24', 27.06.1996, leg. ZE & ZF (HNHM 76098/4) – same locality, N43° 51.06' E19° 49.24', 06.04.2001, leg. ZE, ZF & KK (HNHM 85746/11) – same locality, 15.10.2008, leg. LD, ZF, JK & DM (HNHM 97029/8) – Zlot, Zlotska pečina, N44° 01' 48" E21° 57' 46", 13.04.2003, leg. ZE & AH (Coll. AH/16) – Zlot NW, Lazareva pečina, 260 m a.s.l., N44° 01' 44" E21° 57' 28", 05.07.2008, leg. TD, BP & PS (MMM 90562/11) – Pazariste W 1 km (near Novi Pazar), at the Sebečevo junction, 588 m a.s.l., N43° 07.910' E20° 24.963', 12.10.2005, leg. TD, ZE, ZF & DM (HNHM 97062/4, MMM 90718/4, Coll. EZ/4) – same locality, 16.07.1985, leg. ÉK & LP (HNHM 30877/22) – Požega N

13 km on the road to Valjevo, 27.06.1996, leg. ZE & ZF (HNHM 76109/1) – Kosjerić SE 2 km, on the Valjevo–Požega road, 390 m a.s.l., N43° 58.03' E19° 57.67', 06.04.2001, leg. ZE, ZF & KK (HNHM 85753/6) – Bukovi S 1 km on the Valjevo–Požega road, 27.06.1996, leg. ZE & ZF (HNHM 76122/13) – Bukovi N 1 km on the Valjevo–Požega road, ca. 400 m a.s.l., N44° 09.68' E19° 52.90', 06.04.2001, leg. ZE, ZF & KK, (HNHM 85752/10) – Valjevo S 14 km on the road to Požega, 500 m a.s.l., N44° 10.787' E19° 52.277', 19.10.2002, leg. ZE, ZF, JK & DM (HNHM 91363/53) – Valjevo S 13 km on the road to Požega, 420 m a.s.l., N44° 09.623' E19° 52.985', 03.10.2005, leg. TD, ZE, ZF & DM (HNHM 97053/2, MMM90711/3, Coll. ZE/3) – Nišava gorge, Oštravica E 1 km, 300 m a.s.l., N43° 20.141' E22° 07.983', leg. ZE, ZF & AH (HNHM 89665/15).

Transitional form to *G. f. frumentum*. ALBANIA: Periferi Dibrë, Selishtë, (along the Peshkopi–Burrel road, 18 km W of the bridge of Lumi i Drinit te Zi) 800 m a.s.l., N41° 37.617' E20° 16.277', 26.06.2003, leg. ZE, ZF, JK & DM (HNHM 93675/3) – Periferi Dibrë, bridge of Lumi i Drinit te Zi (between Draj-Reç and Zall-Reç) 306 m a.s.l., N41° 53.282' E20° 18.991', 09.10.2005, leg. TD, ZE, ZF & DM (HNHM 97051/3, MM 90715/3, Coll. ZE/3) – BOSNIA-HERCEGOVINA: “Zwornik” (NHMW E-24.067) – “Vares Bezirk Sarajevo” (NHMW 41279) – “Vlasic Bosnien” (NHMW K-31692) – S slope of Vlasič Mt., 12 km from Travnik, 1450 m a.s.l., 16.04.2000, leg. ZE & ZF (HNHM 89828/10) – ROMANIA: “Déva, Schlossberg” [Deva, castle hill], 1883. leg. M. Kimakowicz (HNHM 72730/6) – SERBIA: Štrbac N 5 km (near Knjaževac), N43° 31' 34" E 22° 17' 20", 26.07.1997, leg. ZE, ZF & KK (HNHM 76121/3) – Zlot, Zlotska pečina, 20.07.1984, leg. ÉK & LP (HNHM 37438/79) – Nišava gorge 3 km E of Sičevo, ca. 300 m a.s.l., N43° 20.141' E22° 07.983, 22.03.2002, leg. ZE, ZF & AH (HNHM 89666/7).

Transitional form to *G. f. atracta*. BOSNIA-HERCEGOVINA: “Plasa b. Jablanica” (NHMW 33566) – “Trebovic Bosnien” (NHMW 30.281/11) – “Berg Stolac” (NHMW K-61.066) – Velež Mts., Humilišani (10 km E of Potoci), 01.04.1999., leg. ZE, ZF & KK (HNHM 75974/15) – Biambare pečina, 42 km NNE of Sarajevo, 16.07.2008, leg. ZE & AH (Coll. AH/27) – MONTENEGRO: Tara valley, 12 km E of Đurđevica Tara, N43° 04.356' E19° 23.002', 18.04.2000, leg. ZE & ZF

(HNHM 83349/2) – Tara valley, Budečevica, 2 km towards Pljevlja, UTM: CN67, 13.08.1987, leg. PS (Coll. PS 13534/7) – NW of Donja Dobrilovina, 15.07.1985, leg. ÉK & LP (HNHM 30879/1) – Gornja Dobrilovina, UTM: CN76, 16.08.1987, leg. PS (Coll. PS 13501/2) – Donja Bukovica, UTM: CN46, 28.06.1996, leg. ZE & ZF (HNHM 76103/2) – between Bioče and Morača Manastir, leg. F. Seidl (NHMW K-63.553/1) – Morača valley, 1.7 km S of Morača Monastir, 296 m a.s.l., N42° 45' 11" E19° 23' 27", 03.04.2006, leg. TD, TDo, K. Nacsa, BP (MMM 90580/2) – Gradac S 1 km, along the Šavnik–Niksič road, 28.06.1996, leg. ZE & ZF (HNHM 83354/6) – Treskavac Mts, Pošćenje (near Šavnik), at the N end of Kanjon Nevidio, bank of Komarnica Reka, 950 m a.s.l., N42° 59.298' E19° 04.070', 10.10.2008, leg. LD, ZF, JK & DM (HNHM 97037/7) – Treskavac Mts, N of Pošćenje (near Šavnik), 1008 m a.s.l., N42° 58.894' E19° 04.100', 10.10.2008, leg. LD, ZF, JK & DM (HNHM 97036/14) – SERBIA: Zlatibor Mts., between Dobrošolica and Draglica, N43.60° E19.72°, 27.06.1996, leg. ZE & ZF (HNHM 76128/12) – Velika Župa (S of Prijepolje), N43° 19' 55" E19° 39' 05", 06.04.2001, leg. ZE, ZF & KK (HNHM 85754/1) – Buče N 4 km on the road to Hercegovačka Goleša, 650 m a.s.l., N43.49° E19.42°, 17.07.2008, leg. ZE & AH (Coll. AH/20).

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.

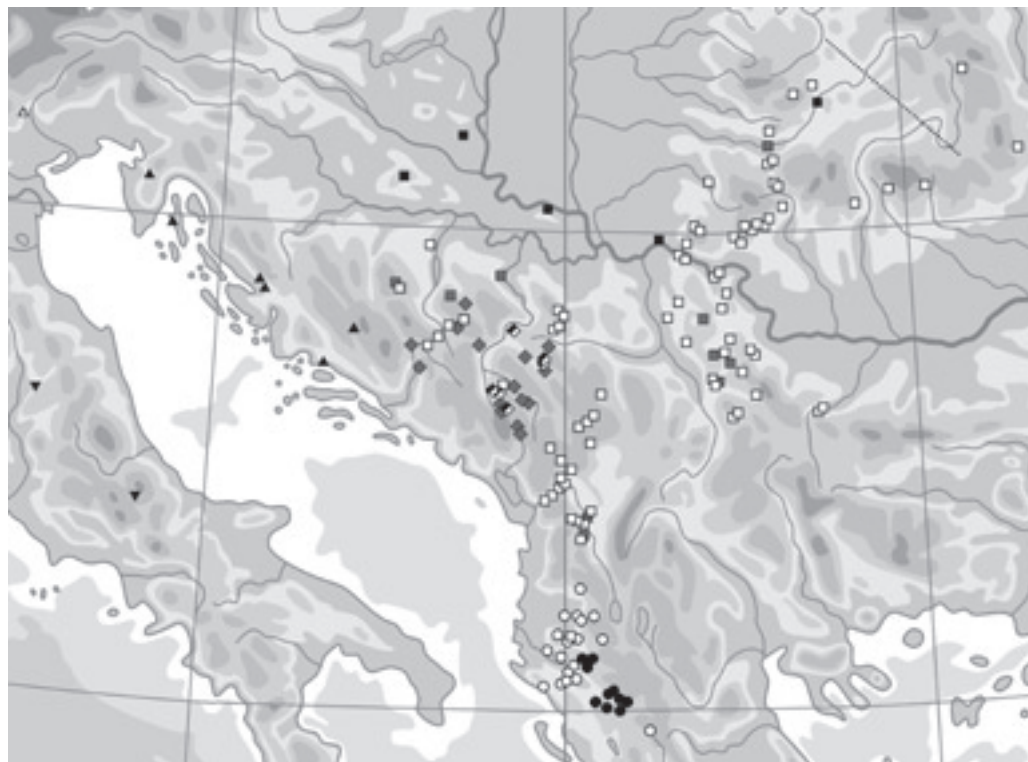


Figure 2 *Granaria frumentum* material from the southeastern part of the species' geographical range. Black square: *G. f. frumentum*; white square: *G. f. hungarica*, typical form; grey square: *G. f. hungarica*, transitional form to *G. f. frumentum*; grey diamond: *G. f. hungarica*, transitional form to *G. f. atracta*; black-white diamond: *G. f. atracta*, typical form; black dot: *G. f. subaii*, typical form; white dot: *G. f. subaii*, populations with partly of 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).

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).

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: 73

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]

? *Abida eximia* Pilsbry 1918: 328–329.

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

Material examined BOSNIA-HERCEGOVINA: Drina valley, Međeđa, viadukt Brodar, opposite to the Lim confluence, N43.74° E19.21°, 17.07.2008, leg. ZE & AH (Coll. AH/29) – MONTENEGRO: Treskavac Mts, Šavnik, Glava Šavnika, 862 m a.s.l., N42° 57.732' E19° 05.585', 09.10.2008, leg. LD, ZF, JK & DM (HNHM 97038/19) – Sinjajevina Mts, Boan W 3 km, bank of Bukavica Reka, along the Šavnik–Kolašin road, 1007 m a.s.l., N42° 57.042' E19° 10.410', 10.10.2008, leg. LD, ZF, JK & DM (HNHM 97039/5) – “Durmitor Westhang” (NHMW E-20.787/1) – “Durmitor” (NHMW E-21.626/7) – SERBIA: 2 km SW of Bistrica (along the Nova Varoš–Prijepolje road, 1 km S of the Priboj junction), 430 m a.s.l., N43° 28.64' E19° 38.70', 06.04.2001, leg. ZE, ZF & KK (HNHM 85748/8) – Zlatar Mts., 7 km N of Prijepolje, N43° 28' 02" E19° 39' 04", 27.06.1996, leg. ZE & ZF (HNHM 76137/1).

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 eximia*, 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 eximia*. The shell width, given as 4.5 mm, leaves us unconvinced that *Pupa eximia* 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 subaia 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 90576/53 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. ZE (Coll. ZE/36) – Periferi Skrapar, 4 km SE of Çorovodë towards Zogas, by the right side of the canyon of Lumi i Osumit, 400 m a.s.l., N40° 29.68' E20° 16.23', 12.04.2001, leg. ZE, ZF & KK (HNHM 85745/4) – Periferi Skrapar, Mali i Ostrovicës, S of Faqekuq, gorge of Pr. i Krishovës, 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°

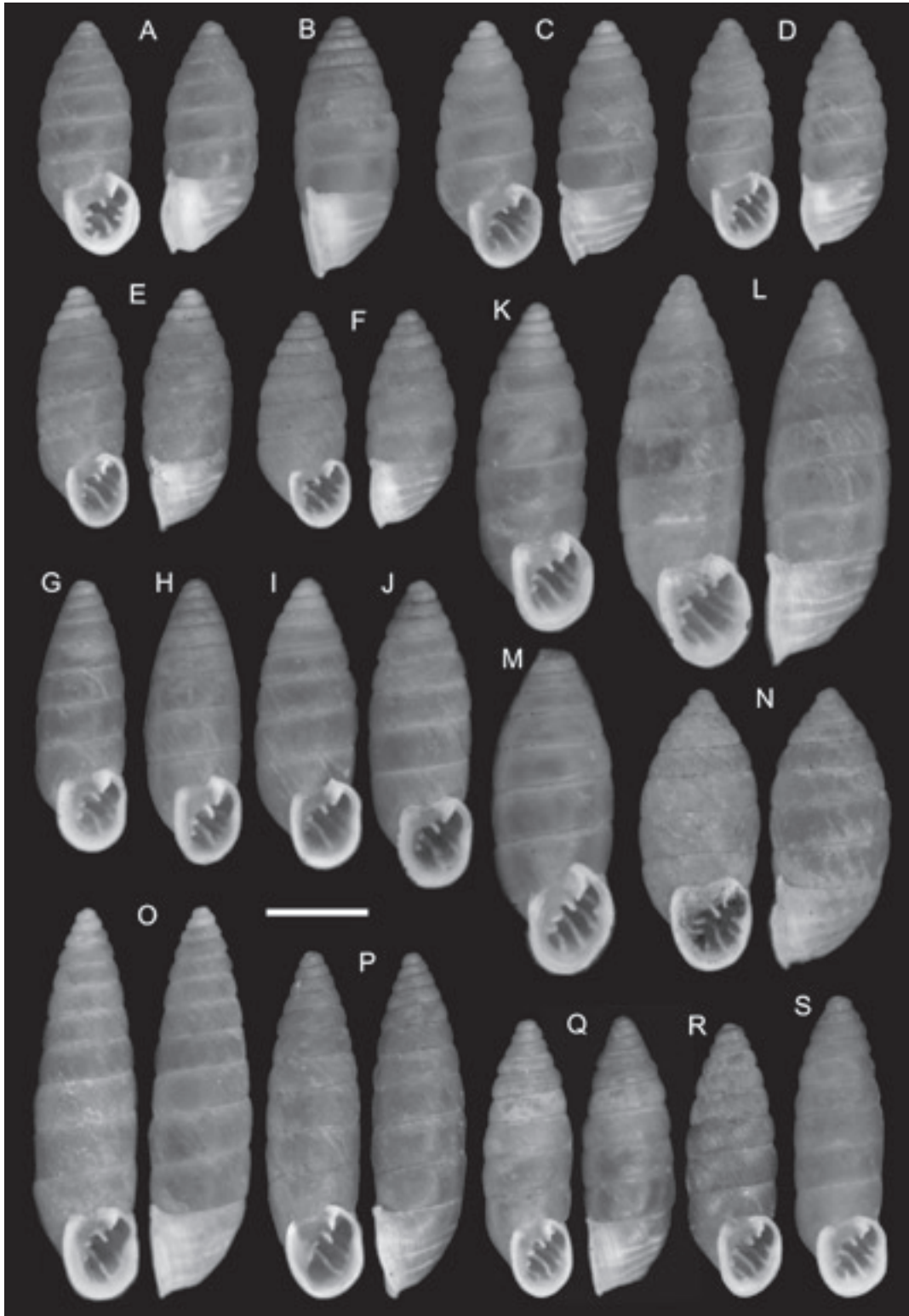


Figure 3 *Granaria frumentum* subspecies. A. *G. f. frumentum*, Pilisborosjenő, HNHM 37670, B. *G. f. hungarica*, transitional form to typical *G. f. frumentum*, Zlot, HNHM 37438, C–J. *G. f. hungarica*, typical form, C. Vajdahunyad, HNHM 72745, D. Zalasd, HNHM 72736, E. Spiljani, HNHM 97035, F. Terovë, HNHM 97033, G–J. *G. f. hungarica*, transitional form to *G. f. atracta*. G. Bučje, Coll. AH, H. Dobrošelića, HNHM 76128, I. Đurđevica Tara, HNHM 83349, J. Donja Dobrilovina, HNHM 30879, K–L. *G. f. illyrica*, K. Lubenice, HNHM 97064, L. Omiš, HNHM 72721, M. *G. f. cf. illyrica*, Torri de Benaco, HNHM 97063, N. *G. f. apennina*, Gola di Celano, Coll. PS 11522, O–P. *G. f. atracta*, O. Bistrica, HNHM 85748, P. Međeđa, Coll. AH, Q–S. *G. f. subatii*, Q. Holotype, Benjë, HNHM 96905, R. Konitsa, Coll. PS 14744, S. Qafa e Gllavës, HNHM 85747. Scale = 3 mm.

16.54', 08.08.2004. leg. ZB, ZF, CN & DP (HNHM 94515/7) – Periferi Skrapar, ca. 15 km NE of Çorovodë, at the Gradec junction, 1000 m a.s.l., N40° 32.61' E20° 16.31', 22.08.2006, leg. ZF, AH, TH & DM (HNHM 96907/30, Coll. AH/30) – Periferi Skrapar, 4.5 km NE of Turbehovë, gorge of Pr.i Krishovës, 1040 m, N40° 33.54' E20° 23.45', 23.08.2006, leg. ZF, AH, TH & DM (HNHM 96908/2) – Periferi Skrapar, 1.5 km N of Qafa e Dëvris, along the road to Zaloshnje, 1110 m a.s.l., N40° 34.29' E20° 17.28', 23.08.2006, leg. ZF, AH, TH & DM (HNHM 96909/3) – Periferi Përmet, Petran, at the confluence of Lumi i Vjosës and Lumi i Lengaricës, 300 m a.s.l., N40° 12.48' E20° 24.86', 13.04.2001, leg. ZE, ZF & KK (HNHM 85756/1) – same locality, 20.05.2006, leg. ZB, TD & DP (MMM 90578/1) – Periferi Përmet, 7 km W of Këlcyrë, by the bank of Lumi i Vjosës, 200 m a.s.l., N40° 17.12' E20° 08.73', 13.04.2001, leg. ZE, ZF & KK (HNHM 85750/10) – same locality, 06.07.1996, leg. ZE & ZF (HNHM 76096/22) – GREECE: Epirus, Kokolajos, N border to Albania, 1988. leg. H. Sattmann (NHMW 102776/9) – 2 km N of Konitsa, leg. P. Reischütz (NHMW 85694/4) – Epirus, N of Konitsa, Topolca stream valley, 600 m a.s.l., UTM: DK73, 26.09.1989. leg. PS & W. Fauer (Coll. PS 14744/94) – Epirus, gorge at the Pogonisko junction of the Konitsa–Molivdokepastos road, 500 m a.s.l., UTM: DK63, 26.09.1989. leg. PS & W. Fauer (Coll. PS 13953/20) – same locality, 16.05.1997. leg. PS & MS (Coll. PS 17083/10) – same locality, 16.07.1990, leg. PS (Coll. PS 15234/33) – Epirus, N side of Vikos gorge near Klidonia, at the old Turkish bridge of the Voidomatis River, 30.07.1975. leg. PS (Coll. PS 10135/4) – Greece, Epirus, 5 km N of Amarandos along the Amarandos–Loutra road, 1400 m a.s.l., UTM: DK74, 12.04.1988, leg. PS (Coll. PS 14915/6) – Epirus, 0.5 km E of Loutra, near Amarandos, 1250 m a.s.l., UTM: DK74, 11.05.1995, leg. PS (Coll. PS 16130/12) – same locality, 16.05.1997. leg. PS & MS (Coll. PS 17052/6) – Epirus, at the bridge of Sarandaporos River between Exohi and Amarandos, 400 m a.s.l., UTM: DK74, 16.07.1990, leg. PS (Coll. PS 15416/10) – Epirus, N side of Sarandaporos gorge, between Exohi and Agia Varvara, 550 m a.s.l., UTM: DK74, 11.05.1990, leg. PS (Coll. PS 16566/7) – same locality, 16.05.1997, leg. PS & MS (Coll. PS 17217/9) – Epirus, Kakolajos, Mt. Dousko, 1100–1200 m a.s.l., UTM: DK53, 12.05.1995, leg. PS (Coll. PS 16011/4).

Transitional forms. ALBANIA: “Perat” [= Berat] (NHMW E-16550) – “Albanien, Berat” (NHMW–K 6071/6) – Periferi Berat, Berat, SW side of the castle hill, 100 m a.s.l., N40° 42.34' E19° 56.79', 12.04.2001, leg. ZE, ZF & KK (HNHM 85751/29) – “Tomorgebirge” leg. Winkler (NHMW–K 20338/1) – “Tomorplateau 1300 m” (NHMW K 7060/1) – “Bargullas zur Cafe Glumakes, 1300 m” [Mali i Tomorrit, between Bargullas and Qafa e Kulmakut] ex. coll. Fuchs (NHMW E-16631/9) – Periferi Berat, Mali i Tomorrit, 4 km over Tomorrit i Vogël, towards the ridge, 1400 m a.s.l., N40.687790° E20.128740°, 11.08.2004, leg. ZB, ZF, CN & DP (HNHM 94513/5) – Periferi Berat, Mali i Tomorrit, Kalaja e Tomorrit, 1100 m a.s.l., N40° 41.919' E20° 05.798', 26.05.2004, leg. K. Harnos & DM (HNHM 94377/10) – Periferi Elbasan, 1 km SE of Shkamë (near Mollas), W side of the Maja e Sulovës, 475 m a.s.l., N40° 55.679' E20° 01.833', 29.06.2003, leg. ZE, ZF, JK & DM (HNHM 93673/12) – Periferi Gramsh, Tërvol, gorge of Pr. i Holtit, 250 m a.s.l., N40° 55.562' E20° 13.390', 26.08.2006, leg. ZF, AH, TH & DM (HNHM 97034/1) – Periferi Gramsh, Vinë, 700 m a.s.l., N40° 52.982' E20° 14.660', 04.07.2003, leg. ZE, ZF, JK & DM (HNHM 93672/13) – Periferi Korçë, Maliq W 25 km along the road to Gramsh, at the Gjinikos junction, gorge of Lumi i Devollit, 750 m a.s.l., N40° 41.521' E20° 30.009', 04.07.2003, leg. ZE, ZF, JK & DM (HNHM 93677/7) – Periferi Librazhd, Mirakë, by the right bank of Lumi i Shkumbinit, 210 m a.s.l., N41° 09.940' E20° 14.264', 24.10.2002, leg. ZE, ZF, JK & DM (HNHM 91364/8) – Periferi Mallakastër, S of Greshicë, in the gorge of Pr. i Pavlit, 140–200 m a.s.l., N40° 31.87' E19° 47.55', 14.04.2001, leg. ZE, ZF & KK (HNHM 85755/7) – Periferi Pogradec, Shpellë (4 km SW of Bishnicë), Shkemb i Qytetit, 1140 m a.s.l., N40° 55.258' E20° 26.946', 01.07.2003, leg. ZE, ZF, JK & DM (HNHM 93556/1) – Periferi Tepelenë, 1 km E of the Vjosë bridge near Dragot, along the Tepelenë–Këlcyre road, 180 m a.s.l., N40° 17.930' E20° 05.316', 18.08.2007, leg. ZF & LT (HNHM 97031/100) – Periferi Tepelenë, 1 km SW of Bencë, along the road from Tepelenë to Progonat, 270 m a.s.l., N40° 14' 57" E19° 59' 38", 11.10.2004, leg. ZF, JK & DM (HNHM 95123/1) – Periferi Tepelenë, 13 km W of Këlcyre along the road to Tepelenë, 164 m a.s.l., N40.29530° E20.10669', 20.05.2006, leg. ZB, TD & DP (MMM 90579/16) – Periferi Tepelenë, 2.5 km NE of

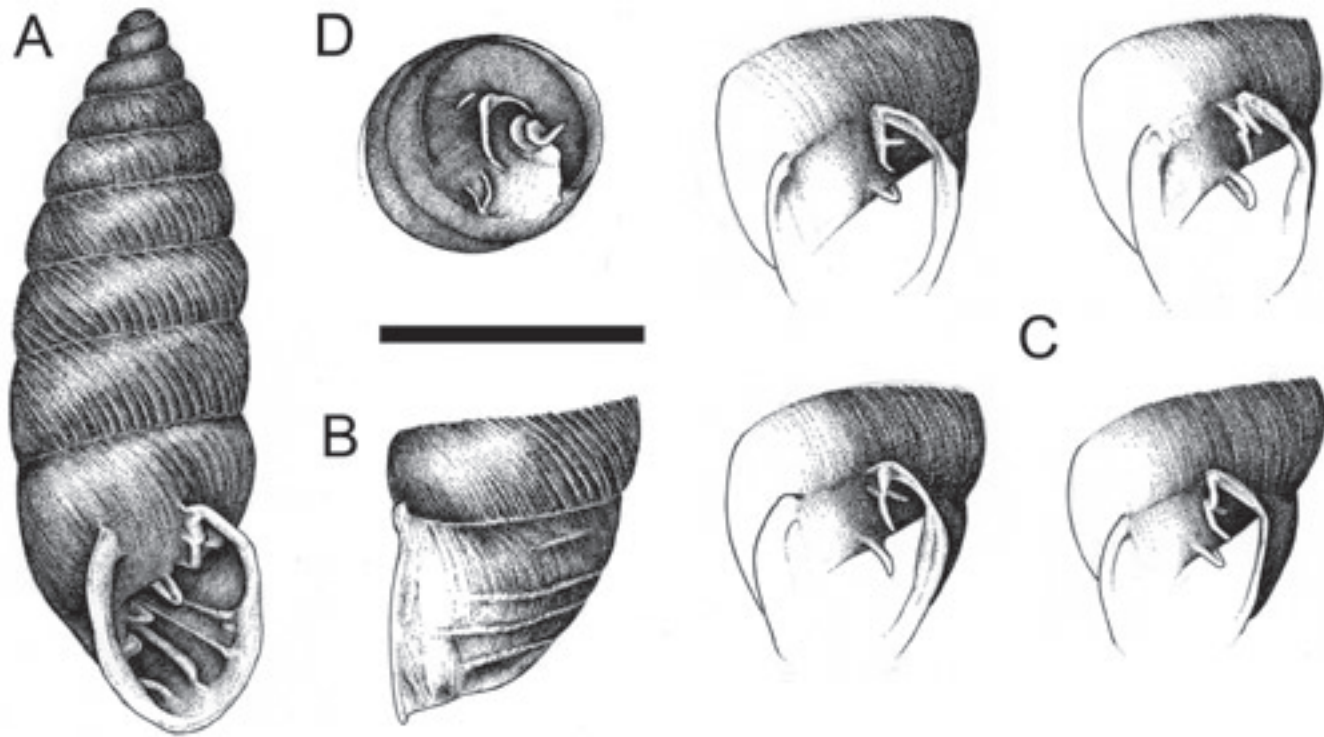


Figure 4 *Granaria frumentum subaii*. A–B. Holotype, Benjë, HNHM 96905, A. frontal view, B. side view of the neck, C. Paratypes, Benjë, MMM 90576, oblique frontal view of four different apertures, to indicate the variation of the structure of the subangular lamella, D. Tepelenë–Këlcyrë, MMM 90579, bottom view of the parietal wall after the ultimate whorl has been partially removed. Scale = 3 mm.

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 Këlcyrë, 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, Votonosi, 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. attracta* (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 whorls.

Description Shell fusiform, tapering gradually; corneous yellowish-brown or reddish-brown; regularly and obliquely striate; comprising 8½ – 9½ convex whorls. 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 ⅓ 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" [Braşov-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. f. frumentum* in the southeastern part of its range, a further two points are worth mentioning. Although this species is believed to live in Macedonia (Jaekel *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 Montenegrin coastal zone. As the Montenegrin 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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