THE IMPLEMENTATION OF TAXONOMIC HARMONISATION FOR CANDONINAE (OSTRACODA, CYPRIDOIDEA): A HEURISTIC SOLUTION FOR *FABAEFORMISCANDONA TRICICATRICOSA* (DIEBEL AND PIETRZENIUK)

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Abstract. The concept of Taxonomic Harmonisation (TH) incorporates the search for similarities between taxa mentioned in different data sets and/or taxonomic classification systems, in order to propose a more coherent and homogenous taxonomic system necessary for practical usage in basic and applied scientific activities. For the present project we conceived *Fabaeformiscandona tricicatricosa* as a species defined by a homeostatic cluster of traits with a given temporal persistence, visible in close relationship with other *Fabaeformiscandona* species, like *F. caudata* (Kaufmann), *F. levanderi* (Hirschmann), and *F. siliquosa* (Brady), as well as with *Candona neglecta* Sars which displays analogies in valve shape. We show the advantages to study the above-mentioned taxa by a combination of classic observations in optical microscopy with SEM-techniques and with the treatment of data using geometric morphometrics and multivariate statistics. A protocol for the implementation of the TH of *F. tricicatricosa* is proposed. We offer a differential diagnosis for *F. tricicatricosa* as compared to *F. caudata, F. levanderi, F. siliquosa* and *C. neglecta*. We use for taxonomic diagnostics a combination of aggregate traits like the average of the outline of valves and qualitative traits, like the shape and the position of a ledge on the posterior side of the valves. We propose to add the term "Consensus" to the species defined by the procedure of the taxonomic harmonisation. To differentiate them from other types of species we propose to use the extension *sensu lato* following the Linnean species notation. Comments on the origin and the (palaeo)ecology and (palaeo)biogeography of *F. tricicatricosa* are presented.

Key words: Non-marine ostracods, *Fabaeformiscandona* taxa, taxonomic harmonisation, Consensus species, (palaeo)ecology, (palaeo)biogeography

INTRODUCTION

The concept of Taxonomic Harmonisation (TH) belongs to a more general trend in the modern cultural activities, namely to homogenise terms in order to be accessible to a wider spectrum of specialists, with a priority to those dealing with different computer media (Weinberger, 2011). Harmonisation procedures exist for various domains of economics and politics (Windholz, 2012), as well as in natural sciences. For this latter domain, we will mention as example Cardoso *et al.* (2005) who proposed harmonisation procedures for better usage of biological methods.

Taxonomic Harmonisation incorporates the search for similarities between taxa mentioned in different data sets and/or taxonomic classification systems, in order to propose a more coherent and homogenous taxonomic system necessary for practical usage in basic and applied scientific activities (*cf.* for such an approach related to ostracods the series of Horne *et al.* contributions (2011a, 2011b, 2012).

The practical interests of an efficient identification of *Fabaeformiscandona tricicatricosa* Diebel and Pietrzeniuk, 1969 (below mentioned also with *Ft*) is as following: the species is known as preferring psychrophilic lentic (lacustrine) habitats (both shallow and deep benthic sites) and has a wide geographical range, a Holarctic distribution (Fig. 1). Having these characteristics Fuhrmann (1991) suggested that *F. tricicatricosa* could be an important (palaeo)ecological indicator for cold climate, occurring during the Late Glacial to Recent times. This possibility will be further examined in this publication.

Besides the possibility to use *Ft* as a (palaeo)ecological indicator one should note also the interest for (palaeo)biogeography; it allows to reconstruct the history of the geographic dispersion of this species through time, especially during the last My years. This latter aspect represents a perennial topic of the biogeography of aquatic non-marine organisms in the Northern Hemisphere (*cf.* for a classic monographic treatment of the question, Thienemann, 1950). There

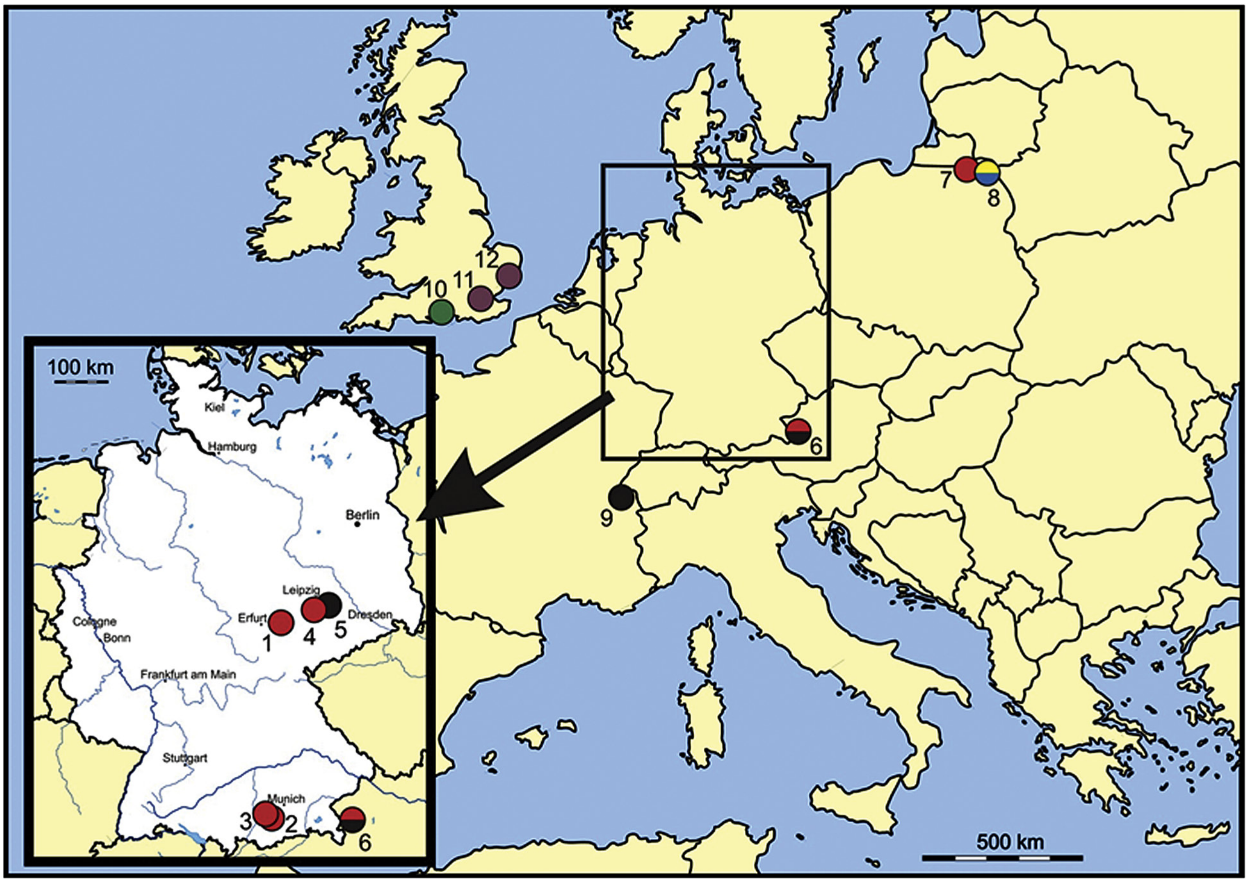


Fig. 1. Representative areas in Western and Central Europe from where specimens of species of the genus *Fabaeformiscandona* and of *Candona neglecta* were studied. **1** – Süssenborn near Weimar, Thuringia, Germany – type locality for *F. tricicatricosa*; **2** – Starnberger See, Seeshaupt (type locality for *F. lozeki*) and Kempfenhausen, 40 km SW of Munich, Bavaria, Germany; **3** – Ammersee, 30 km SW of Munich, Bavaria, Germany; **4** – Zauschwitz, 20 km SW Leipzig, Saxony, Germany; **5** – Neunitz, 20 km SE Leipzig, Saxony, Germany; **6** – Lake Mondsee, Upper Austria (see Fig. 2 for details); **7** – Lake Rospuda Filipowska, 25 km NW of Suwałki, Podlaskie Voivodeship, Poland; **8** – Lake Serwy, 25 km SE Suwałki, Podlaskie Voivodeship, Poland; **9** – Petit-Lac of Lake Geneva, Switzerland; **10** – New Forest National Park, Hampshire, UK; **11** – Central London, UK – "*F. tricicatricosa*" *sensu* Coope *et al.*, 1997; **12** – Little Oakley, Essex, UK – "*F. tricicatricosa*" *sensu* Robinson, 1990. Colours indicate species as follows: red – *Fabaeformiscandona tricicatricosa*, yellow – *Fabaeformiscandona levanderi*, black – *Fabaeformiscandona caudata*, green – *Fabaeformiscandona siliquosa*, blue – *Candona neglecta*, violet – dubious records of *Fabaeformiscandona tricicatricosa*.

are, nowadays, few cases which document, in a satisfactory way, the dynamics of ostracod distribution related to climate changes. We will mention for non-marine ostracods *inter alia* the contribution of Griffiths *et al.* (1998), who discussed the origin and distribution of the predominantly Arctic species *Tonnacypris glacialis* (Sars, 1890) and for the marine ostracods the review of Faranda and Gliozzi (2011), who dealt with the "Northern guests" arriving during the Quaternary in the Mediterranean area.

For a successful TH of this species two questions are of interest:

(**1**) Are all the identifications of *Ft* correct or some of the documented, that is, illustrated and/or discussed morphotypes could belong to different species? From our experience the shape of some morphotypes of *Ft*-valves resembles those of *F. lozeki* (Absolon, 1973), *F. caudata* (Kaufmann, 1900)*, F. levanderi* (Hirschmann, 1912)*, F. siliquosa* (Brady, 1910) or even those of *Candona neglecta* Sars 1887. Therefore, we need to find a set of criteria which will allow to identify *Ft* with more certainty and to test for the accuracy of the above-mentioned identifications.

(**2**) Is really *F. lozeki* (Absolon, 1973) a true junior synonym of *F. tricicatricosa* Diebel and Pietrzeniuk, 1969? The junior synonym of *F. tricicatricosa* Diebel and Pietrzeniuk, 1969 was decided on the unique diagnostic trait which separates both species, namely the number of the mandibular muscle imprints is variable (Fuhrmann, 1991). This argument is here confirmed (*cf.* Fig. 19 F, G) and the synonymy of *F. lozeki* with *F. tricicatricosa* was adopted *inter alia* by von Grafenstein *et al*. (1999b), Fuhrmann (2012), Namiotko *et al.* (2015). However Meisch (2000) and Fuhrmann (2004, 2009) accepted both species. Absolon (1978) and Fuhrmann (2012) noted slight differences in the shape and the size of valves between the Bavarian population at Seeshaupt and Saxony specimens, like those from Zauschwitz. Fuhrmann (2012, p. 72) concluded as following: "Es bedarf weiterer Untersuchungen an umfangenreichen Material, um die taxonomische Stellung der Form *Fabaeformiscandona lozeki* zu klären". This question will be carefully analysed below.

Conceptual issues needed for the taxonomic harmonisation procedure

First of all, we have to propose a definition for species fitting the needs for the implementation of TH. It means we consider from the very beginning (an idea we took from Horne *et al.*, 2011a) that we need an adapted definition usable for fossils which are potentially interesting for palaeoecologic reconstructions and/or stratigraphic identifications. It means that we accept the idea that we have to treat the concept of species within a pluralistic view. In this latter case, the definition we use and the way we delineate taxonomically our material differs from those using recent material with limbs or molecular biological techniques or for those who use cladistics (*cf.* Dupré, 2001 for such an approach).

Experience with morphologic traits of Candoninae species from various populations dispersed on wide geographic areas and with significant temporal persistence shows that they display at a given level of precision a perceptive stability due to a homeostatic cluster of traits (a kind of phylogenetic inertia). Stable morphologic characters allow us to predict with better than chance probability that they constitute diagnostic traits for the investigated species. Grene and Depew (2004, p. 300) consider such species as „classes whose existence is temporally restricted". Griffiths (1999, p. 224) names such species „classes with historical essence". Hence, for the present project we will conceive *Fabaeformiscandona tricicatricosa* as a species defined by its homeostatic cluster of traits (sensu Boyd, 1999) with a given temporal persistence (historical essence), visible in close relationship with other *Fabaeformiscandona* species of the *Fabaeformiscandona acuminata* species-group, like *F. caudata* (Kaufmann, 1900), *F. levanderi (*Hirschmann, 1912), *F. siliquosa* (Brady, 1910) and with *Candona neglecta* Sars 1887. These five species build what we will call here an "aggregative taxonomic system". This concept stems from our need to find a coherent method for the characterisation of the taxonomic status *of F. tricicatricosa* using relational arguments. The five species mentioned above appear to us as entities which stay in close relationship by their morphological similarities of the valves due, either to phylogenetic relationships, or to convergent evolution. Therefore, the system emerges as a whole through the network of resemblances existing for those species. At a lower level of our taxonomic system, *F. tricicatricosa,* with its various populations distributed in space and time (see next sections) represents also a system with a network of inter-populational relationships.

For the present need of TH we should not go too deep in the individuation of morphological traits for taxonomic definition, as D.J. Horne and co-authors already suggested (Horne *et al*., 2011a). We propose to use the principle of near-decomposability of complex systems of Simon (1962), namely that we should keep a general structure which allows one to see the properties of interest in a taxon at a consensual level of generality. In our study, the taxon "Species" should be identified with traits clearly visible for many cases and/or samples from various places. This is an epistemological approach where the species is defined through consensus arguments (see next, for more arguments). To do this we need to better understand the within and between variability of populations. For this latter approach one of the best examples we have is that of Baltanás and Geiger (1998) who compared the range of variability of the various populations of *Limnocythere inopinata*. For inter-populational variability Baltanás and Geiger (1998, p. 135) used mean values of the valve shapes (called, also, consensus shapes). These latter are important characteristics for each population. The conceptual treatment of the valve variability of *Limnocythere inopinata* allowed a better understanding of ecology and biogeography of this generalist species. A similar approach will be followed in the present study too.

The near-decomposability principle of complexity (in our case of a complex assemblage of ostracods) needs explanation. A system becomes complex (as defined by McShea, 1979, p.84) through "an increasing of … the number of different types of parts or interactions it has. The opposite of complexity is simplicity; systems with few types of parts or interactions are simple." Herbert Simon (1962) proposed to simplify complex systems by decomposing them in subsystems of more homogenous and/or simpler structural units, an approach called "pragmatic holism" (Simon, 1996). To achieve this goal it was proposed to use aggregate variables (e.g. average values for data displaying variability) which should characterise the subsystems (Simon, 1997). Further on, it was proposed to make the distinction between the within variability of subsystems and those existing among subsystems, the former having, generally, a higher variability than the latter. Therefore, the relationships among subsystems are weaker, but not negligible, as compared to those existing within a subsystem. Decomposing, in this way, large sets of variable data, we achieve a dramatic reduction of time for the computation of their variability and we get a heuristic result which allows us to find easier answers to the scientific questions addressed.

Coming to our ostracod problem, the identification of *Fabaeformiscandona tricicatricosa* using the near-decomposability principle of Simon, we have, first, to define the group of taxa with their variability which needs to be clearly identified. We have, then, to understand the degree of variability of the morphology of *F. tricicatricosa* as compared to similar morphological taxa. Using, for the study of the ostracod valves, aggregate data (*e.g.* average values of the valve outlines), geometric morphometrics and multivariate statistics the goal of a taxonomic harmonisation can be heuristically attained (see below the proposed protocol).

The heuristic approach of defining species we propose is based on the view that, generally, it is impossible to get a diagnosis which should apply successfully to all putative *Ft* individuals. Hence, for TH approach we have to leave out the extreme phenotypes (the so-called outliers) and to work with average values (*cf.* also the discussion of Baltanás and Geiger, 1998). Danielopol *et al.* (2011a) discussed problems with identification of specific ostracod taxa and, in a special contribution, Danielopol *et al*. (2011b) proposed the usage of morphological profiles derived from the virtual mean shape of the valves. The fact that ostracodologists could identify correctly in many cases *Ft*, as we can see now *a posteriori,* is due to the intuitive psychological effect of what is called "the Ludwig Wittgenstein's family resemblance principle" (Wittgenstein, 1986). It means that species can be correctly identified by a combination of traits without the need to use the complete taxonomic diagnosis. Note that, within this approach useful for TH, we do not discuss phylogenetic or evolutionary aspects of the related species mentioned above, but just morphological similarities within a given hierarchic taxonomic level. Heuristics used for taxonomic purposes do not offer 100% success when we are confronted also with homeomorphic shapes of valves. This approach will be here documented with a comparative study of an assemblage of species considered for this study as a decomposable system.

MATERIAL AND METHODS OF STUDY

A. Sampling sites and ostracod material (Figs. 1, 2; Tables 1 and 2).

For the present project on the TH of *F. tricicatricosa* we investigated 724 valves, adults and juveniles. Most of this material (606 valves) comes from Lake Mondsee. For comparative purposes we studied *F. caudata* (135 valves), *F. levanderi* (15 valves) and *C. neglecta* (396 valves). Tables 1A and 1B offer a detailed statistics of the 1270 items processed, while Table 2 displays information on juvenile valves used for description of morphological changes during the post-embryonic development. The sampled material was photographed and digitised for morphometrics and multivariate statistical analysis (bi- and multi-variate statistics). Besides our material, we used published figures which were scanned and digitised; all this allowed in-deep (detailed) comparisons.

Lake Mondsee is located in the western part of Austria (the Salzkammergut), about 30 km east of Salzburg. The lake has a surface of about 14 km^2 with the mean and maximum depths of 37 and 68 m, respectively. It was during a long period of time an oligo-mesotrophic lake. With the increase of anthropic pressure the water quality of the lake downgraded, the lake became during a part of the year eutrophic. Benthic ostracod fauna, at sites deeper than 20 m became locally extinct. With the construction of a water purification system and a strong control of nutrient input to the lake, the water quality at the end of 1980 improved. Considering the water temperature of Mondsee, one has to mention that the littoral and sublittoral (down to a depth of approx. 15 m) get, during summer and autumn, temperatures which are above 10-15°C while, during winter, they go down to 4-5°C. In the deeper part of the lake (*i.e.* in the profundal zone at a depth of 40-60 m), the water temperature remains below 10°C, generally at about 5°C, during the whole year. Detailed information on the ostracod research and on the ecological situation of the Lake Mondsee can be found in the monographic study "*Cytherissa* the *Drosophila* of Paleolimnology" (Danielopol *et al*. 1990a), specifically, in various chapters of this volume, *inter alia* Danielopol *et al.* (1990b), Danielopol and Casale (1990), Geiger (1990a, 1990b). For further information, see Lauterbach *et al.* (2011) and Namiotko *et al.* (2015).

The benthic ostracods were thoroughly sampled during a period of 20 years within various research programmes carried on at the Laboratory of Benthos of the Institute for Limnology, at the time belonging to the Austrian Academy of Sciences, mainly during the "*Cytherissa* Project" started in 1982 and funded by the Austrian Science Fund during 1983-1988 (Danielopol *et al*., 1990a). Sampling and processing of ostracod material continued during a European project on the ecology and of evolutionary reproductive modes of ostracods (1994-1997), with published data in Martens (1998). Another important moment for the data acquisition related to the present TH project was the "European Science Foundation-Project" during 2004-2008, with results published in Lauterbach *et al.* (2011) and Namiotko *et al.* (2015). Additionally, a one year scholarship offered to L. Picot by the University of Fribourg (2002-2003) helped to increase our information on benthic ostracods, mainly on *F. tricicatricosa* and *F. caudata* (Picot and Danielopol, *in litt.*).

Figure 2 shows the approximate location of the sites from where we sampled *F. tricicatricosa* and *F. caudata* in Lake Mondsee. *Candona neglecta*, widely distributed in this lake, was for the purpose of the TH project investigated only from one sampling site and from one section of the long core MO-5 at site 9 (see Fig. 2). Table 1A offers a detailed presentation of the material sampled at 10 sites located in Lake Mondsee.

Site 1 – in front of the stream Zellerache, the bottom is sandy and covered with organic debris transported into the lake by the stream. There are few ostracods at the site, and just one valve of *F. caudata* was caught in a sample from 8 m deep.

Site 2 – in front of the Institute for Limnology, the sediment is pelitic and at a depth of 4 m macrophytes develop. *F. tricicatricosa* occurs at a depth of 4 m and 15 m, while *F. caudata* only at a 4 m-deep bottom.

Site 3 – on the western side of the lake, in front of the Golf Club. The subsurface relief is steep and the sediment is sandy-pelitic. At 10-m deep bottom, both *F. tricicatricosa* and *F. caudata* occur, while at a depth of 15 m only the former species exists in our samples.

Site 4 – located in front of the gravel-pit lake, south of the site 3. Few valves of *F. tricicatricosa* were found there.

Site 5 – at the southern part of the lake; it is an area with most of the psychrophilic species which survived the period when the northern basin of the lake was eutrophic. The lower water temperature in this part of the lake compared to the other lake basins is due to the strongly forested surrounding and to a shadow brought by the steep mountain cliffs on the southern shore. Some of the samples were labelled with the SM code, others with the P3 code. These labels exist in the collection deposited at the Universal Museum Joanneum in Graz. As one can see from Table 3, this area offers a high number of valves belonging to living specimens of both *F. tricicatricosa* and *F. caudata*.

Site 6 – is located in the Mooswinkel Bay and it was intensively studied for the benthic ostracods, especially *Cytherissa lacustris*, during 1982-1988 (Danielopol *et al.*, 1990b). *Fabaeformiscandona tricicatricosa* was found just at the transition between the sublittoral and the profundal areas, where the sediment is pelitic and the benthic surface is well oxygenated. It is remarkable that specimens' abundance at a depth of 40 m reduces. Continuing downward, on the lake bottom slope, the sediment becomes anoxic and practically *F. tricicatricosa* does not occur at greater depths.

Sites 7 and 8 – are located in the northern half of the lake basin at depths of 41 and 45 m, respectively. Both sites were affected during the second part of the 20th century by the negative effects of the lake eutrophication (Danielopol *et al.*, 1985, 1990b). *Fabaeformiscandona tricicatricosa* occurs only as sub-recent specimens in the cores at depths varying between 20 cm and 30 cm below the surface. Site 8 offered less individuals of *F. tricicatricosa* as compared to the cores taken at site 7 (*cf.* Table 1).

Site 9 – in front of the Federal Institute for Fisheries in Scharfling at 62-m deep bottom. A long core of 15.5-m length (MO-05) was extracted, in 2005, and investigated by a multidisciplinary team. The values of oxygen and carbon isotopes in ostracod valves were systematically investigated using Candoninae valves, mainly *Candona neglecta*, and for the lower part of the core also using *F. tricicatricosa* (Lauterbach *et al.*, 2011; Namiotko *et al.*, 2015). *Fabaeformiscandona tricicatricosa* appeared in high numbers in the section 02E of the MO-05 core, which covers the composite depth 1113.0-1167.5 cm, representing the calibrated age of 12 576-11 187 BP, *i.e.* both the Younger Dryas and Early Holocene stages (Lauterbach *et al.*, 2011). As regards ostracods, the whole section belongs to the Local Ostracod Assemblage Zone 3 (LOAZ 3), as described in Namiotko *et al*. (2015). The section G of the MO-05 core covers the Late-Glacial period, the section F – the Allerød, while the section D represents Holocene (see Lauterbach *et al.*, 2011 for the core MO-05 chronology). The samples of all these 3 sections contain few adults and many juvenile specimens of *F. tricicatricosa*. This contrasts with the high number of both adults and juveniles in the samples of the section 02E of the core MO-05.

Site 10 – is located in the deepest part of the lake, at 65-m deep bottom. This area was strongly affected by the eutrophication of the lake, during the last century, and ostracod fauna is depauperated (Danielopol *et al.*, 1990b). Only one juvenile valve of *F. tricicatricosa* was recovered at the depth of 9 cm of a short core taken from this site.

The part of the ostracod material we used in this project is deposited in the collection of the Universal Museum Joanneum, Laboratory of Palaeontology, in a series of trays with micropalaeontological cells under the label ESF Mondsee. The trays 12, 13 and 14 contain cells with valves which were photographed and are labelled with the photo-number. A list of the specimens accompanies this material. The photographic material is stored on an external computer hardplate and also deposited at the Laboratory of Palaeontology, Universal Museum Joanneum, Graz.

Starnberger See (or Lake Starnberg) (area no 2 in Fig. 1), situated in southern Bavaria, Germany, ca. 25 km SW of Munich at 584 m a.s.l., is one of the largest (surface area of 56.36 km^2) and deepest (maximum and mean depths of 127.8 and 53.2 m, respectively) lakes in Germany (Nixdorf *et al.*, 2004).

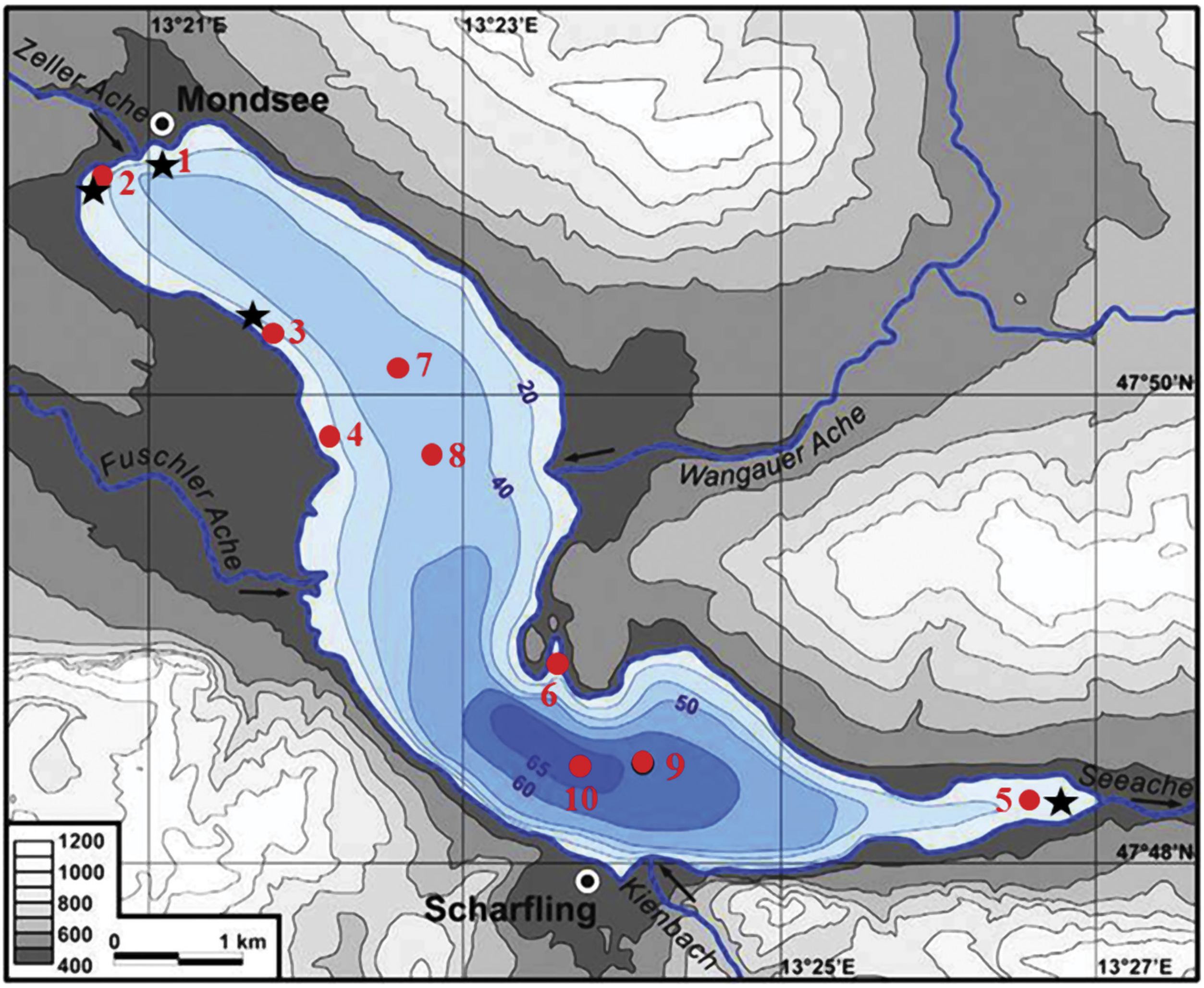


Fig. 2. Bathymetric map of lake Mondsee with the sampling sites were *Fabaeformiscandona tricicatricosa* (red points) and *Fabaeformiscandona caudata* (black stars). Sites 1 – 8 and 10 - Recent and sub-Recent individuals; site 9 – location of the MO-05 coring site with fossil valves of *F. tricicatricosa* from Late Glacial and Holocene layers belonging to sections 1G, 1F, 2E, 1D (*cf*. Lauterbach *et al.*, 2011, p. 255, Fig. 2). Map, modified from Namiotko *et al.*, 2015, p. 24, Fig.1. Additional details for sampling sites, see text.

Table 1A. Sampling sites in Lake Mondsee and ostracod material used in the present study. For location of the sites see Fig 2. Abbreviations: f – female, m – male, j – juvenile, LV, RV – left and right valves.

Site	Acronym	Depth (m)	f- LV	f- RV	m- LV	m- RV	j- LV	j- RV	Total V	Notes
Fabaeformiscandona tricicatricosa										
2	I (Institute)	4	3	3	3	3	0	0	12	
2	I (Institute)	15	0	0	2	0	0	0	2	
3	GF (Golf Place)	10	22	13	9	2	0	0	46	
3	GF (Golf Place)	15	0	4	6	5	0	0	15	
4	BS (Gravel-pit L)	10	2	2	2	0	0	0	6	SEM
5	SM	6	6	4	1	2	0	0	13	
5	SM	8	0	1	0	3	0	0	4	
5	P3 (0-3 cm)	12	12	7	3	0	0	0	22	
5	SM	15	12	0	8	2	0	0	22	

table 1A (continuation)

Site	Acronym	Depth (m)	f-LV	f-RV	m-LV	m-RV	j-LV	j-RV	Total V	Notes
6	Mo-7	16-18	1	0	3	1	9	9	23	
6	Mo-7	40	0	0	0	0	1	2	3	
7	MO-3 (41)	41	15	23	7	9	0	0	54	
8	MO-3 (45)	45	10	6	2	4	11	7	40	
9	MO-05-2E	62	50	45	15	28	86	90	314	
9	MO-05-1G	62	1	3	0	2	0	2	8	
9	MO-05-1F	62	12	3	3	3	0	0	21	
9	MO-05-1D	62	0	1	0	0	0	0	1	
10	MO-65	65	0	0	0	0	0	1	1	
Fabaeformiscandona caudata										
1	ZW	8		1					1	
2	I	4		2					2	
3	GF	10	1						1	
5	SM	6	8	7	0	0	0	0	15	
5	P-3 (0-3cm)	12	2	3					5	
Candona neglecta										
9	MO-05-2E	62	47	52	28	25	123	115	390	

Table 1B. Sampling sites (except Lake Mondsee) and ostracod material used in the present study. For location of the sites see Fig 1. Abbreviations: f – female, m – male, j – juvenile, LV, RV – left and right valves. Ostracod valves from published data are not listed.

Site	Acronym	Depth (m)	f-RV	f-LV	m-RV	m-LV	j-RV	j-LV	Total V	Notes
Lake Starnberg and surroundings										
Fabaeformiscandona tricicatricosa										
Seeshaupt	SHA	-	5	2	2	0	0	0	9	SEM
Starnberger See	STA	18	4	3	2		2	7	18	
Starnberger See	STA-82/15	50	0	1	0	0	0	0	1	
Kempfenhausen	KM	-	4	4	3	3	0	0	14	SEM
Lake Ammersee										
Fabaeformiscandona tricicatricosa										
Ammersee	AS 85/12	21.5	0	1	0	0	0	0	1	
Zauschwitz										
Fabaeformiscandona tricicatricosa										
Zauschwitz	ZAU	-	14	13	6	6	0	0	39	SEM
Neunitz										
Fabaeformiscandona caudata										
Neunitz	NEU		5	5	0	0	0	0	5	SEM
Lake Rospuda Filipowska										
Fabaeformiscandona tricicatricosa										
Rospuda	ROS12D	12	14	7	7	8	0	0	36	SEM

table 1B (continuation)

Site	Acronym	Depth (m)	f-RV	f-LV	m-RV	m-LV	j-RV	j-LV	Total V	Notes
Fabaeformiscandona caudata										
Rospuda	ROS12D	12	1	0	0	0	0	0	1	
Lake Serwy										
Fabaeformiscandona levanderi										
Serwy	SER17D	17	4	7	2	2	0	0	15	SEM
Candona neglecta										
Serwy	SER17D	17		6						SEM
Lake Geneva										
Fabaeformiscandona caudata										
Petit-Lac	GE	13	17	22	0	0	31	35	105	SEM

Table 2. Ostracod material (left valves) used for reconstruction of developmental trajectories of Candoninae species. Abbreviations: Af and Am – adult female and adult male, A-1 to A-6 – ostracod developmental stages in reversed order from the 8th postembryonic stage (A-1) to the 3rd one (A-6), A-1m – male pre-adult stage.

Species	LV-Origin	Af	Am	A-1	A-2	A-3	A-4	A-5	A-6	A-1m
F. tricicatricosa	MO-05-2E	50	15	16	19	12	20	15	4	1
F. caudata	GE (Petit-Lac)	17	0	10	16	3	2	-	-	-
C. neglecta	MO-05-2E	47	28	31	21	24	20	14	13	2

This is a pre-Alpine, (mono-)dimictic lake with a relatively small drainage basin and a long water renewal time of 21 years (Alefs and Müller, 1999; Nixdorf *et al.*, 2004). Lake Starnberg, likewise several pre-Alpine lakes in Central Europe (compare a section on Lake Mondsee above and on Lake Ammersee below), has experienced in the past decades prominent eutrophication due to a human activity. However, after the introduction of a lake restoration program, in 1970/1980s, continuous monitoring of water quality has shown an improvement in lake trophic conditions (Alefs and Müller, 1999). Lake Starnberg is now mesotrophic with decreased phosphorus loading to less than 10 µg/dm^3 and reasonably well oxygenated hypolimnion with temperatures 3.8-9.0°C at the depth of 15-18 m (von Grafenstein *et al.*, 1999b; Nixdorf *et al.*, 2004). Lake Starnberg has been the subject of various palaeolimnological studies of one of us (U. von Grafenstein), including oxygen isotope records of profundal ostracods since the last glaciation (von Grafenstein *et al.*, 1992, 1999b).

Material for the present study from Lake Starnberg and its surroundings comes from four different collections (see Table 1B).

(**1**) STA – Living specimens of *F. tricicatricosa* were collected by one of us (U. von Grafenstein) in September and November of 1990, from the depth of 18 m located on the western side of a transect perpendicular to the lake isobaths off an island Roseninsel (details in von Grafenstein *et al.*, 1999b).

(**2**) STA-82/15 – The analysed valves of *F. tricicatricosa* were separated by U. von Grafenstein from Late Glacial sediment section of a 140-100 cm depth of a STA 82/15 core taken from the bottom of Lake Starnberg at the depth of 50 m. The section was dated as 15,000-10,000 years BP.

(**3**) KM – Valves originally identified as *F. cf. tricicatricosa* by one of us (R. Fuhrmann) were found in late Holocene sediment sample collected by Gregor in 2002 at Kempfenhausen, on the north-eastern shore of Lake Starnberg. (For the valves studied cf. Table 1B).

(**4**) SHA – This is a topotypical material of *F. lozeki* (*cf.* Table 1B) originating from the Early Holocene lake chalk sample E 1264 from Seeshaupt on the southern shore of Lake Starnberg. The sample comes from the same core (taken near a small pond Gartensee) from which Absolon (1973) described his species *F. lozeki* (sediment samples of Preboreal age taken from a 590 cm-depth below the ground level).

Ammersee (site no 3 in Fig. 1) is a most northern pre-Alpine lake, situated at an altitude of 533 m a.s.l., 20 km SW of Munich, close to Lake Starnberg, and has also been extensively investigated palaeolimnologically by one of us (von Grafenstein *et al.*, 1994, 1996, 1999a, 1999b; Czymzik *et al.*, 2013). Like Lake Starnberg, Ammersee has a glacial-morphologic origin and is reasonably large and deep (surface is 46.6 km^2, maximum depth 81.1 m, mean depth 37.6 m). Although the potential trophic state of this dimictic lake is oligotrophic, due to intensive land use, until the late 1970s, Ammersee underwent a distinct eutrophication, and then, as a result of immense management activities, the trophic conditions of the lake improved, so that, nowadays, Ammersee may be considered mesotrophic. An overview of the geological and morphological characteristics, as well as eutrophication dynamics of the lake, can be found *e.g.* in Alefs and Müller (1999), Nixdorf *et al*. (2004), Vetter and Sousa (2012) and Czymzik *et al*. (2013).

Material of *F. tricicatricosa* from Ammersee (Table 1B), comes from a core AS 85/12 taken from the bottom of Lake Ammersee at the depth of 21.5 m on the west side of the lake in front of Uting. For the present study *Ft* was separated by U. von Grafenstein from Allerød sediment section of a 585-583 cm-depth (dated as 13,000 BP).

Zauschwitz (Site no 4 in Fig. 1) is a village situated 20 km SW of Leipzig in Saxony, Germany. Valves of *F. tricicatricosa* were picked out from a sediment sample of a Middle Weichselian age, collected on 1.08.1973 by R. Fuhrmann from a brickyard (a list of accompanying species and more details in Griffiths, 1995, Griffiths *et al*., 1998 and Fuhrmann, 2012). For the valves here studied *cf.* Table 1B).

Neunitz (Site no 5 in Fig. 1) is a village located 20 km SE of Leipzig in Saxony, Germany. Material of *F. caudata* from this site (*cf.* Table 1B) comes from a sample collected by R. Fuhrmann on 12.04.1982.

Lakes Rospuda Filipowska and Serwy (Sites nos. 7 and 8, respectively - in Fig. 1) are situated at a distance of 25 km from Suwałki in Podlaskie Voivodeship, NE Poland, the coldest climatic region of the country. Both lakes are dimictic and moderate in size and depth, with total surface areas of 3.4-4.6 km^2 and the maximum and mean depth between 38.9 and 41.5 m, and between 14.5-14.6 m, respectively (Jańczak, 1999). The two lakes show, at present, still moderate symptoms of eutrophication, which allow them to be classified as mesotrophic (Serwy) or in transition between meso- and eutrophic (Rospuda Filipowska) (Namiotko, 1996); however, there is an indication that the water quality of Rospuda has declined, in the last few years.

From these two lakes, subrecent valves of four species were used in the present study (Table 1B). A dredge sample taken on 4.09.1988 by T. Namiotko at a depth of 12 m from Lake Rospuda Filipowska yielded *F. tricicatricosa* and *F. caudata*, whereas in a dredge sample taken on 7.09.1988 by T. Namiotko at a depth of 17 m from Lake Serwy *F. levanderi* and *Candona neglecta* were found.

For the documentation of material from Germany and Poland valves were photographed further digitised and, partly, deposited in the collection Ostracoda Danielopol of the Universalmuseum Joanneum.

Lake Geneva (Petit-Lac) (Site no 9 in Fig. 1) is the area where one of us (L. Decrouy) sampled *F. caudata* for his doctoral thesis on the isotope studies using ostracods and their ecological signals. The sampling area is in front of Versoix and *F. caudata* was recovered from benthos samples, at a depth of 13 m. The material consisted of 105 valves (*cf.* Table 1B) which were photographed with both SEM and TLM microscopes and stored as photographic documents. The valves were further used for isotopic analysis. Information on this material was published in Decrouy (2009), Decrouy *et al.* (2012), Decrouy and Vennemann (2014). The photographic material and their digitised version for morphometric analysis are stored as documents in the Data-bank of the TH-project (Danielopol, unpubl.).

B. A PROTOCOL FOR THE IMPLEMENTATION OF TAXONOMIC HARMONISATION

(**1**) Examination of taxa supposed to be morphologically similar and/or phylogenetically related to *Ft*.

(**2**) Search for morphological traits significant for a differential diagnosis.

(**3**) Description of variability of valves within and between sampling sites followed by the construction of a virtual average-profile of the valve shapes and identification of outliers within the data sets.

(**4**) Test of data using geometric morphometric procedures for valve outlines and multivariate statistical methods. Additionally, comparative analysis using other closely related species.

(**5**) Documentation of misidentifications and invalid taxonomic assignments.

(**6**) Presentation of results allowing an improved view on the (palaeo)ecologic and (palaeo)geographic distribution.

C. Analytical methods

The valves were photographed in lateral view using a transmitted light microscope (TLM) Nikon and a Nikon digital camera. Most of the photos were done at the Benthos laboratory of the Institute for Limnology of the Austrian Academy of Sciences, in Mondsee by various members of our working group during a long-term interval (2000 and 2007). A data bank for this material (Ostracoda-photo collection) was created by D. L. D. and his colleagues at the Benthos Laboratory of the Institute for Limnology. Another part of the valves were photographed by T. N. with TLM at the laboratory for Limnozoology of the University of Gdansk. The outlines of the photographed valves were further digitised with the TPSdig software, version 1.37 (Rohlf, 2003) as preparation for morphometric analyses. The photographic documentation with SEM techniques was made mainly at Universalmuseum Joanneum in Graz by M. G. using a JEOL JSM-6610LV. *Fabaeformiscandona caudata* from Lake Geneva (Petit-Lac) was photographed with SEM techniques by L. D. at the Institute of Earth Surface Dynamics of the University of Lausanne.

For the ostracod shell, *i.e.* the carapace with its two valves, the right (RV) and the left (LV) ones, we follow the nomenclature used in Horne *et al.* (2002). For the complex structure of the hemipenis and the female genital lobe we used the preparation technique described in Namiotko *et al.* (2011). For the description of the outlines of valve shapes, we used the bounding box and the control-points algorithm offered by MORPHOMATICA (Fig. 4 A, B, 13, A, B, 23 A, 36 A, 38 E). The advantage of this approach is that we can describe (*i.e.* locate changes) in the shape of the outline of valves in an accurate way (*cf.* Danielopol *et al*., 2011b).

We noticed that the best comparative morphological traits for our *Ft* and its related species are visible on the female RV. This is especially the case of the postero-dorsal ledge, as well as the posterior and the postero-ventral sections of the valve's outline (*cf.* next section). We do not deny the usefulness of examining also the female LV and the male valves which offer useful diagnostic details too but they are less visible as compared to those of the female RV. For instance the male valves of *F. tricicatricosa* differ only slightly from those of *F. levanderi* (compare the former species in Fig. 7 A with the latter in Fig. 19 D).

A combination of transmitted light microscopy (TLM) images combined with SEM-views becomes a necessity for accurate descriptions. Details of the peripheral area of the valves pointing to the details of the radial pores channels complement the general shape of the outline for the same area as photographed with the SEM. For instance, see the complementarity in details of the anterior section of *F. tricicatricosa*, RV (Figs. 5 B and 5 E. or for *F. caudata* Figs. 14, 15 with 16, 17). The combination of the TLM with the SEM allows us to understand that, behind specific surface shapes, there are structures which have definite importance. For *F. tricicatricosa* the lower section of the anterior part of the valve is rounded in the female with equal long radial channels (*cf.* Fig. 5 E), but differs in more substantial ways in the case of the male's valve, where the radial pore channels are within this section longer (*cf.* Fig. 7 E). Same situation for *F. caudata* for instance, the postero-ventral section of the left valve is more developed than its opposite homologue section and more bounded (*cf.* Figs. 16 C and 17 B, D). Note that, within this area, the radial pore channels are longer on the left valve than its homologue section on the right valve.

An important aspect is the observation that morphological differences in the valve shape could be due to the valve curvature. In Fig. 10, A, B, C the difference of the extension of the fused area traversed by radial pore channels are, in our opinion, due to the curvature of the valve, namely the valves in Fig. 10 A and B being more flat displays in the TLM a fused zone in the postero-ventral part larger with longer radial channels than the valve in Fig. 10 C.

Geometric morphometric analysis of the outlines was performed using Linhart's B-spline algorithm (Neubauer and Linhart, 2008) and computed with the computer programme MORPHOMATICA v. 1.6 (Linhart *et al.*, 2006). An important aspect presented here is the usage of virtual consensus profiles for taxonomic descriptions or of standardised shapes. Consensus taxonomic profiles are produced in MORPHOMATICA as a virtual mean shape of valves belonging to the individual outline forming one or several populations of the assumed species on which we produce the TH (*cf.* Figs. 8, 23, 27, 29, 36 – 38 C, D).

For morphometric analyses of our data we used multivariate algorithms, like the non-metric Multi-Dimensional Scaling (N-MDS) and the Canonical Analysis of Principal coordinates (CAP) routines existing in the computer-packages PRIMER version 6 and PERMANOVA+ for PRIMER v.6 (Clarke and Gorley, 2006; Anderson *et al.*, 2008) already discussed in Danielopol *et al*. (2011b, 2014). The N-MDS, allowed us to see in two dimensions the spread of the morphological disparity for various populations (*cf.* Figs. 9, 24, 25). In the present case, especially useful was the CAP analysis which offered us a way to see how well predefined groups can be discriminated or correctly identified.

RESULTS – THE IMPLEMENTATION OF THE HEURISTIC PROCEDURE

A. THE GENERIC AFFILIATION AND THE PRACTICAL DIFFERENTIATION OF THE *FABAEFORMISCANDONA TRICICATRICOSA* FROM SEVERAL MORPHOLOGICALLY RESEMBLING SPECIES

We present below the morphological traits which allow the identification of the taxon *tricicatricosa* Diebel and Pietrzeniuk as belonging to the genus *Fabaeformiscandona* Krstić 1972, specifically to the species-group *acuminata* (for the diagnostic traits of this latter taxonomic group, see Meisch, 2000).

(**1**) The taxon *tricicatricosa* is known by both sexes and in addition to the initially fossil material on which it was described by Diebel and Pietrzeniuk (1969) we find, also, living specimens. The valves are elongated of medium size, the female having about 1.2mm length with a height of about 50-53% of the length (Table 3). Clear sexual dimorphism of the valves (*cf.* Figs. 5 - 7) and of specific limbs (Fig. 22) are visible. The left valve covers the right one and displays better developed cardinal areas, well visible when its outline is superposed on the opposite valve-outline (Fig. 8) and when the data are spread within a 2D multi-dimensional space (Fig. 9). This latter figure displays the N-MDS plot of female RV (n=45) and female LV (n=50) which come from the sample MO-05-2E, Younger Dryas section (*cf.* Lauterbach *et al*., 2011; Namiotko *et al.,* 2015). The diagram suggests significant differences between the RV and the LV-outlines. The Canonical Analysis of Principal Coordinates correctly classified 90.53% of cases.

(**2**) The dorso-posterior margin of the female's valves is straight and placed in oblique position within the section CP d1 – d3 of the valves. The right valve develops a ledge (Figs. 3 B, C, 5 B-D, 7 D, 12 D, E). It is important to note that

Table 3. Information on the size of female RV of *Fabaeformiscandona tricicatricosa*, *F. caudata*, *F. levanderi*, *F. siliquosa* (from Henderson, 1990) and *Candona neglecta*. For geographical location of the sites see Figs. 1 and 2, for site acronyms see Table 1A and 1B.

Site/sample acronym/name	Sample size	Mean length (mm)	Confidence limits (± 95%)	Height (in % of length)	Confidence limits (± 95%)
Fabaeformiscandona tricicatricosa					
Zauschwitz	13	1.15	1.12 - 1.17	52.25	51.81 - 52.65
Lake Rospuda Filipowska ROS12D	13	1.36	1.34 - 1.37	50.90	50.23 - 51.64
Mondsee MO-05-2E	45	1.21	1.20 - 1.22	50.29	50.05 - 50.53
Mondsee MO-3 (41)	23	1.26	1.25 - 1.27	50.50	50.15 - 50.87
Mondsee I, GF and SM (4-15 m)	25	1.24	1.22 - 1.26	50.98	50.64 - 51.32
Seeshaupt	3	1.27	1.25 - 1.29	51.00	49.00 - 52.00
Kempfenhausen	4	1.25	1.20 - 1.30	50.38	49.51 - 51.26
Lake Starnberg	4	1.35	1.33 - 1.38	50.50	50.00 - 51.00
Suessenborn, Germany (Allotype)	1	1.21	-	49.50	-
Fabaeformiscandona caudata					
Lake Geneva GE	12	1.18	1.16 - 1.20	47.27	46.88 - 47.60
Mondsee I (4 m) and SM, P3 (6-12 m)	12	1.145	1.11 - 1.18	48.25	48.08 - 48.42
Neunitz	5	1.22	1.21 - 1.24	46.63	46.20 - 47.00
Fabaeformiscandona levanderi					
Lake Serwy SER17D	8	1.24	1.21 - 1.27	54.36	53.81 - 54.88
Fabaeformiscandona siliquosa					
New Forest, Hampshire, UK	1	~1.4	-	46.80	-
Candona neglecta					
Lake Serwy SER17D	6	1.20	1.17 - 1.23	52.50	51.83 - 54.88

the generotype *Fabaeformiscandona fabaeformis* develops also dorso-posterior ledges (*cf.* Krstić, 1972, Absolon, 1978). Considering the valve-ledge of *F. tricicatricosa*, it appears that this does not exist in the case of *Candona neglecta* Sars (*cf.* Fuhrmann, 2012, Plate 10 and here Fig. 12 A - C).

The female's RV-ledge of *Ft* is represented by a small inflexion of the outer wall delineated at the periphery by the outer margin and at the inner side by a lamellar selvage. Below the ledge one notices small denticulate "buds" (*cf.* Figs. 5 C - D). There are two other living *Fabaeformiscandona* species which display ledges with denticulate "buds" on the posterior margin of the female valve, namely *F. caudata* (Kaufmann) and *F. levanderi* (Hirschmann) (*cf.* Fuhrmann, 2012, Pl. 18-Fig. 2e, Pl. 25-Fig.1e, and here Figs. 14, C – G, 18 D, 19 C). On this latter figure (Fig. 19 C) one sees broken tubular "buds", representing excrescent selvage structures.

(**3**) The anterior vestibulum, narrowly developed (about 1/5th of the valves' length) and with short and densely disposed marginal and sub-marginal channels (*cf.* Fig. 5 E). The selvage on the anterior and the ventral sides poorly developed and sometimes it is difficult to distinguish from the outer margin. A similar situation is visible at *F. caudata* (Fig. 15 B - D) and *F. levanderi* (Fig. 18 B).

(**4**) The valves of the juveniles, especially of the A-2 and A-3 of the *Fabaeformiscandona* we studied, namely *Ft, F. caudata, F. harmsworthi, F. protzi* as well as *Candona (Camptocypria) gratkornensis* display a more oblique dorso-posterior shape (*cf.* Figs. 20 G, 21 B) as compared to the similar stage of *Candona neglecta* which is more rectangular (Fig. 21 A).

(**5**) Considering the limbs of *Ft*, one should note that the female genital process is elongated, digitiform (*cf.* Fig. 22), a characteristic of many species of *Fabaeformiscandona*, differing, in this way, from the similar lobe, of *Candona neglecta* which is flat and widely bent (*cf.* Meisch, 2000, Fig. 26).

(**6**) The hemipenis at *Ft* and *F. levanderi* having a process "a" inserted on the lower half of the lateral side of the peniferum, a characteristic that is visible *inter alia* also in *F. fabaeformis* (Danielopol, 1969) and at *F. tora* (*cf.* Smith and Kamiya, 2007). This process in the case of *Ft* and *F. levanderi* appears bi-lobate (*cf.* Fig. 22). The similar process in the case *C. neglecta* is much larger and starts from the whole lateral margin of the peniferum and appears as rectangular shaped (*cf.* Danielopol, 1969, Meisch, 2000). The proximal half of the M-process of the *Ft*-hemipenis is straight (*cf.* Fig. 22), similar to those of *F. levanderi* and *F. fabaeformis* (*cf.* Danielopol, 1969), differing from those of *C. neglecta* (*cf.* Danielopol, 1969, 1978).

(**7**) There are only four distal setae on the inner side of the 2nd mandibular palp of *Ft*, which characterises the *Fabaeformiscandona acuminata* species-group, including inter alia *F. caudata, F. siliquosa* and *F. levanderi* (Meisch, 2000). It differs from the species group *F. fabaeformis* and the species group *F. balatonica* which display three and five setae, respectively (Meisch, op. cit).

(**8**) The endopodites of the male's 4th limb (clasping appendages), slender and with a low degree of asymmetry, a peculiarity displayed also by *F. levanderi* (*cf.* Meisch, 2000).

(**9**) One fossil species comes closer to the genus *Fabaeformiscandona,* namely *Candona (Camptocypria) gratkornensis* Gross (*cf.* Gross 2008, p. 268, Fig. 5; p. 271, Pl. 2, Fig. 6 and here Fig. 20 E - F) represents an adult female. The dorso-posterior ledge of the right valve of *C. gratkornensis* resembles those of *Ft,* being outside delineated by the outer margin and at the inner side by a well-developed lamellar selvage (Fig. 20 F). The valve described by Gross (2008, *cf.* p. 268, Fig. 5.2 and p. 271, Pl. 2, Fig. 6) belongs to an adult female, while the valve figured in Gross 2008, p. 271, Pl. 2, Fig. 13 is, probably, an A-2 juvenile. The adult and the juvenile RV present the typical oblique dorsal section of *Fabaeformiscandona*. *Candona (Camptocypria) gratkornensis* was found in Mid-Late Miocene deposits of the Styrian Basin, in Austria (Gross 2008), documenting that the present-day *Fabaeformiscandona* species similar to *Ft* belong to an ancient (Tertiary) candonine-group.

B. Proposal for a standardised characterisation of the *F. Tricicatricosa*, with emphasis on the female RV; differential diagnosis for *F. tricicatricosa*, *F. caudata*, *F. levanderi*, *F. siliquosa* and *C. neglecta*

Fuhrmann (2012: p. 72) explicitly wrote that the shape and position of the ledge on the FRV of *Ft* is the key trait which characterises this species: "Bei der gestreckt bohnenförmigen *Fabaeformiscandona tricicatricosa* ist als characteristisches Merkmal ein schmaler Innenrandbereich der posteroventralen inneren Randzone nach innen gebogen, selbst Bruchstücke sind daran erkennbar".

F. tricicatricosa, female RV (Figs. 4 A, 5 A - C, 12 D, E, 20 A - D) is remarkable by ratio H/L of about 50%, but varying between 49-53 % (*cf.* Table 1) with maximum H placed in the central third of the length at about 55% of the valve's length around the CP d5; the dorso-posterior margin around the CP d4, generally, widely arched (*cf.* Fig. 4 A). The maximal curvature located at about 30 % of the maximal height. Most important, the posterior ledge small and rounded placed in the upper half of the outline (see red arrow). The ledge is represented by a very small area of the peripheral margin and a well-developed lamellar selvage; below this curved lamellar structure on the selvage several denticulate "buds" are visible (Figs. 5, C, D). The outline section between CP d1 – d3, straight.

The female left valve presents an elongated posterior ledge (Fig. 6 B). The male's LV, commonly has an angular antero-ventral section and elongated radial channels (Figs. 7 A, B, E, 32 B/15). The male's RV lacks the ledge (Fig. 6 D).

The female genital process, as well as the traits of the hemipenis and of the clasping appendage of the male are similar to those of *F. levanderi* (*cf.* details previous section).

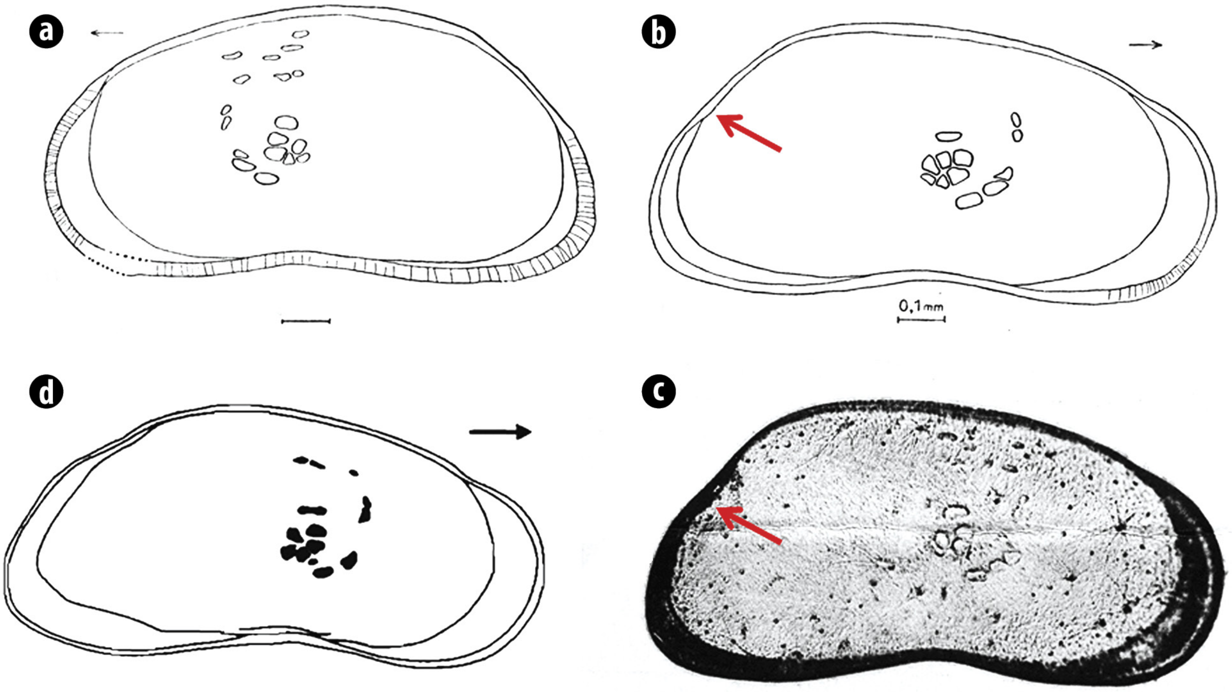


Fig. 3. *Fabaeformiscandona tricicatricosa* **A-C** - Original illustration of the female L and R valves (from Diebel and Pietrzeniuk, 1969; A, B - p. 474, text-figs. 6a, 6b; **C** - Pl. 8, Fig. 6). Red arrow points to the ledge of the RV; **D** - *F. siliquosa* (Brady, 1910), female R valve (from Henderson, 1990, p. 101, Fig. 40).

F. caudata, female RV (Figs. 13 A, 14 A - D, 16 A - D), displays a H/L of about 46 – 48 % (*cf.* Table 1) with maximum height placed in the section between CP d5-d6 (Fig. 13 A); the posterior ledge is long and the dorsal outline between CP d1-d3 is convex (Fig. 13 A). A straight line of the outline visible between CP d1 -m1 section (Fig. 13 A). The transition from the dorsal to the posterior side widely bent between CP d4 - d7. Maximal curvature, at about 25% of the maximal height. The posterior end of the left valve more pointed than the RV and forming a spoon-like shape well visible in TLM (Fig. 17 A, B, D). The genital process, is well developed, triangular-shaped (*cf.* Kaufmann, 1900, Brady 1910, Meisch, 2000). This is also visible at the juvenile stage A-1 (photo made by Decrouy, unpublished).

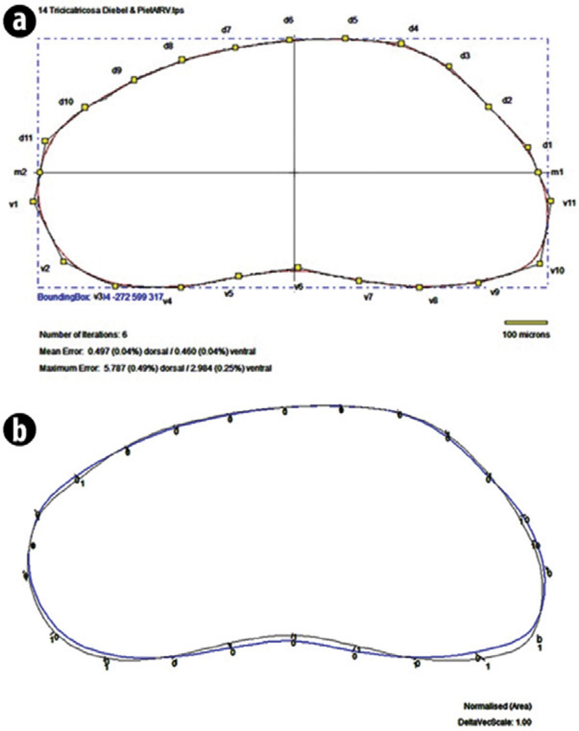


Fig. 4. Protocol for the description of ostracod outlines using the computer programme MORPHOMATICA; **A** - *F. tricicatricosa,* outline of the allotype valve of Diebel and Pietrzeniuk, 1969 (*cf.* here Fig. **3 B**) (reversed view in a bounding box using the non-standardised for surface algorithm); **B** – *F. tricicatricosa* – Superposition of female outlines, RV calculated with the standardised for surface algorithm; blue line (0) allotype from Diebel and Pietrzeniuk, 1969, p. 474, Fig. 6B; black line (1) allotype of *F. lozeki* from Absolon, 1973, p. 77, Fig. 35B. The outlines calculated with 24 control points; the mean and maximum errors approximation given as percentages of the dorsal and ventral halves (*cf.* Brauneis *et al.* 2008).

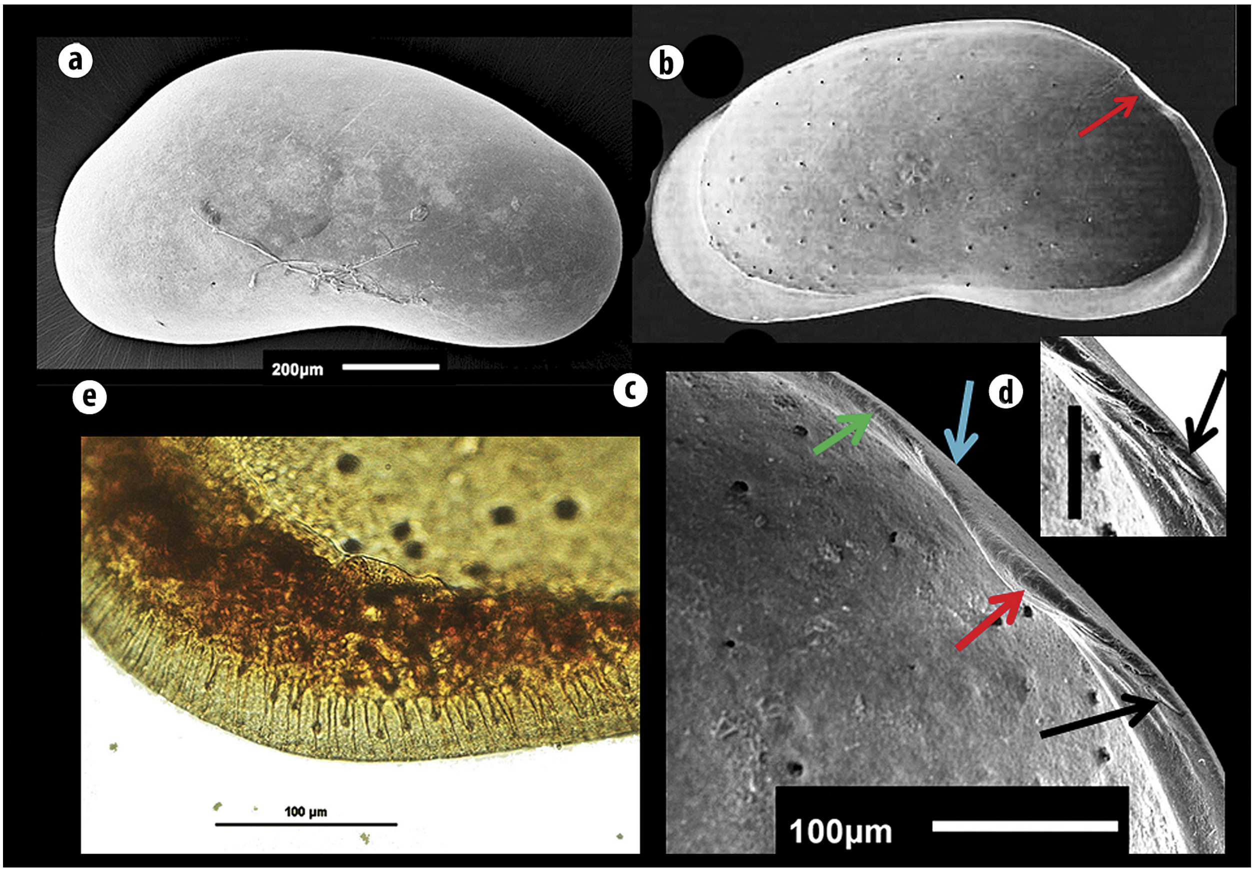


Fig. 5. *Fabaeformiscandona tricicatricosa,* (Zauschwitz), adult female RV: **A, B** –external and internal, lateral view; **C – E** – inner lateral view, details; **C-D** – posterior ledge; **E** – anteroventral section with the fused zone of the peripheral and radial channels of the setae. Note the dense number of distal opening channels interspaced with sub-distal radial channels opening on the lateral external side of the valve. Red arrow points to the ledge, blue arrow shows the outer valve margin, black arrow points to a „bud", green arrow marks the selvage; **A** – SEM microphotographs of a valve deposed at Universal Museum Joanneum, Graz (photo M. Gross); E – TLM-picture (photo T. Namiotko); scale in **D** – 50 mµ.

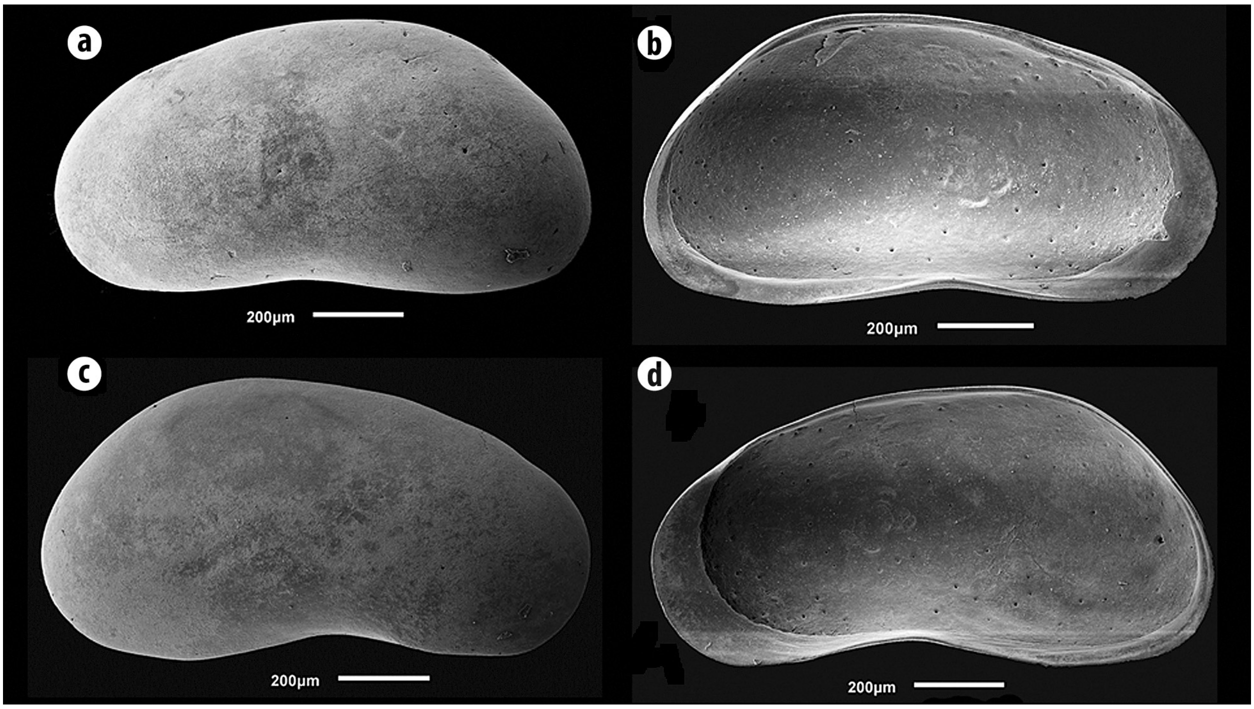


Fig. 6. *Fabaeformiscandona tricicatricosa*, (Zauschwitz), adult valves, SEM view: **A, B** – female LV, **A** – external view, **B** – inner view same valve as in **A**; **C, D** male RV, **C** - external view, **D** – inner view same valve as in **C**; all material deposed at Universal Museum Joanneum, Graz (photo M. Gross).

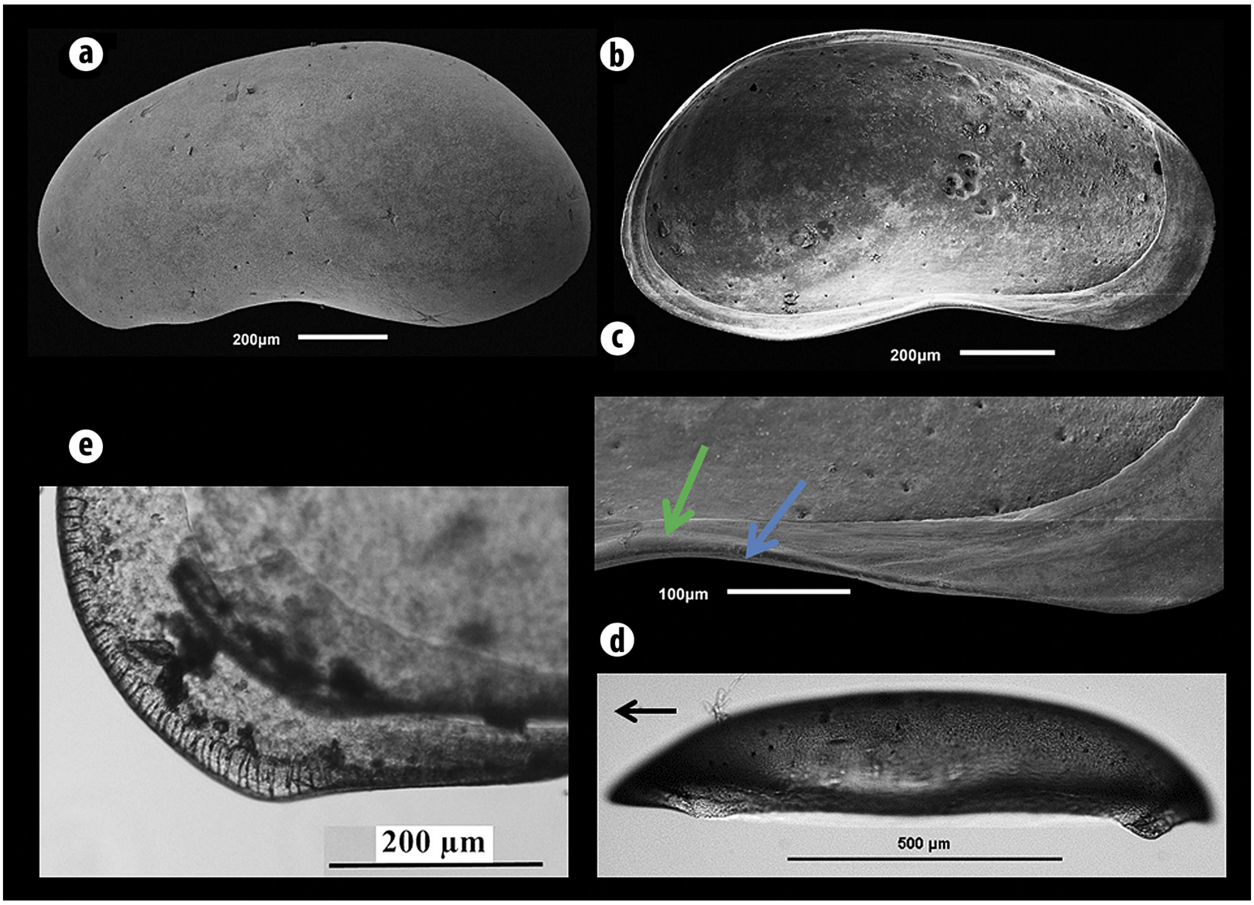


Fig. 7. *Fabaeformiscandona tricicatricosa*, (Zauschwitz), adult valves, SEM view: **A - C** – male LV; **A** – external view; **B, C** – inner view of the same male LV, **B** – general view, **C** – detail of **B** in the central part of the ventral area, (all material deposed at Universal Museum Joanneum, Graz, photo M. Gross); **D** – dorsal view in TLM of a female RV Zauschwitz (photo T. Namiotko), note the well-developed posterior ledge; **E** – detail of male LV valve, Mondsee, site MO-P3, Ostra-Photo No. 7198 antero ventral area in TLM with elongated radial channel on the antero-ventral corner (photos numbers refer to the Ostracod-photo Bank of Data developed by D. L. Danielopol at the Limnological Institute in Mondsee, during the period 2000 and 2007, and deposed at the Universalmuseum Joanneum and/or available from D. L. D.). Blue arrow marks the outer margin, green arrow points to the selvage.

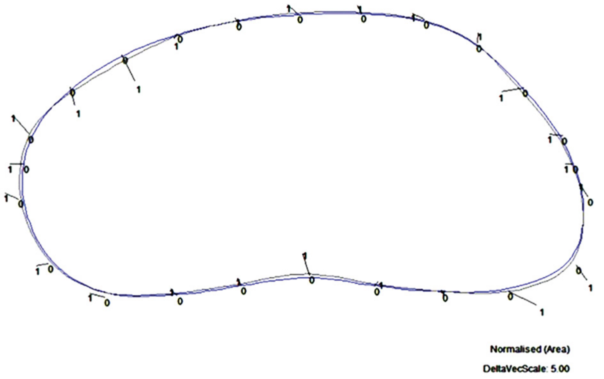


Fig. 8. *Fabaeformiscandona tricicatricosa*, (Mondsee, site 9, sample MO-05-2E), adult female valves, superposition on the mean outline of 50 LV (0) the mean outline of 45 RV (1) using in MORPHOMATICA the standardised for equal surface algorithm.

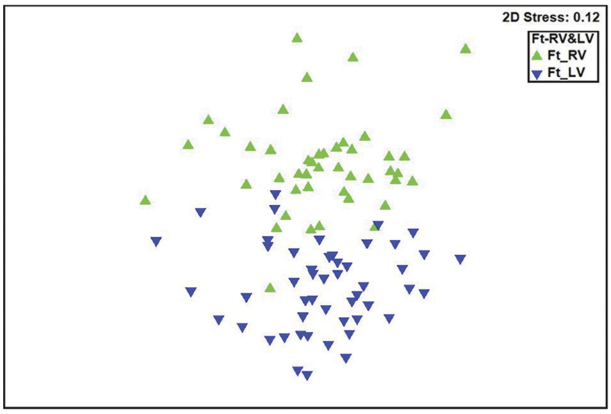


Fig. 9. *Fabaeformiscandona tricicatricosa*, (Mondsee, site 9, sample MO-05-2E), non-metric Multi Dimensional Scaling plot (N-MDS) of adult female valves, RV (n-45, in green) and LV (n-50, in blue).

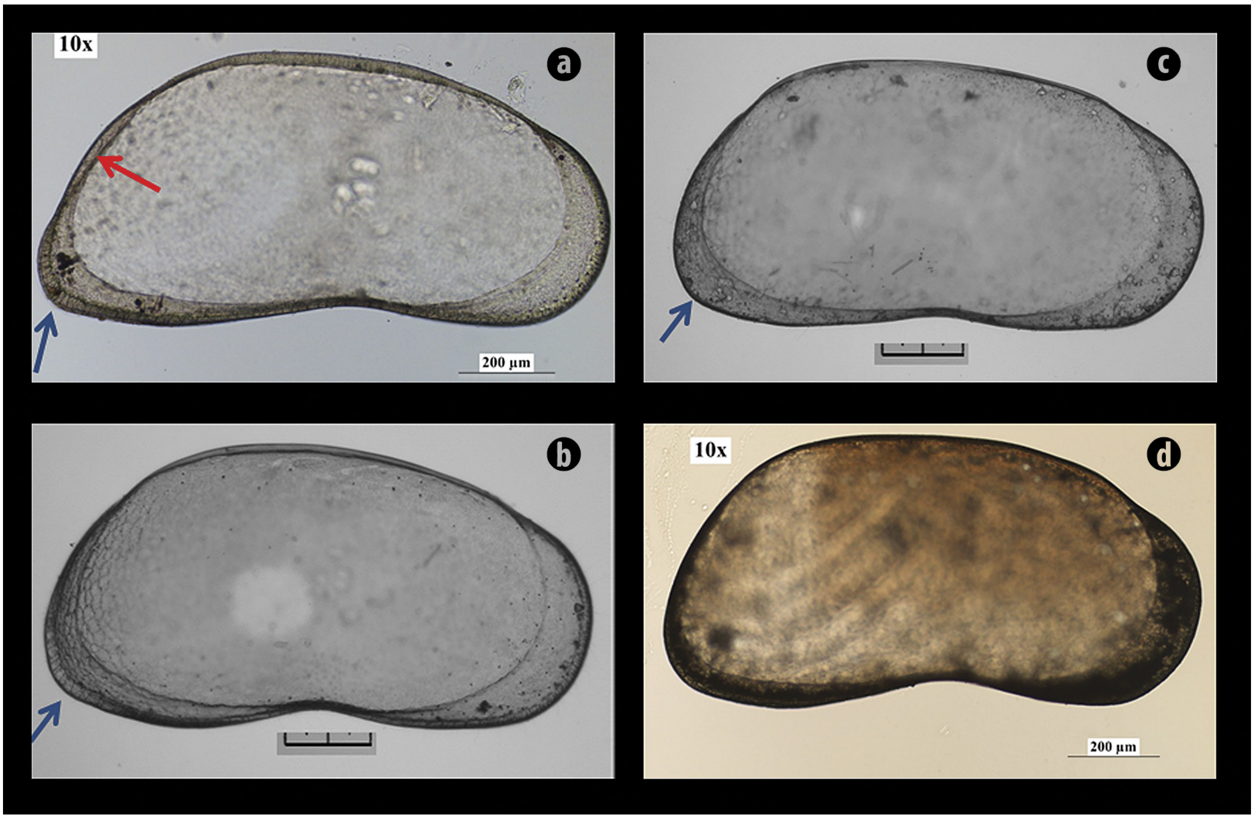


Fig. 10. A - *Fabaeformiscandona caudata*, (Mondsee), female RV in TLM, Mondsee, site 5 (sample 6m), Ostra-photo No. 7166; **B** – **D** – *F. tricicatricosa* in TLM, **B-C**, Mondsee, site 7 (sample 41m); **B** – female RV-Ostra-photo No. 247; **C** – female RV- Ostra-photo No. 252; **D** – male RV – Mondsee, site 9, sample MO-05-2E, Ostra- photo No. 5507; Red arrow points to the postero-dorsal ledge, blue arrow indicates the postero-ventral margin with the radial channels. Scale in **B** and **C,** 180 µm.

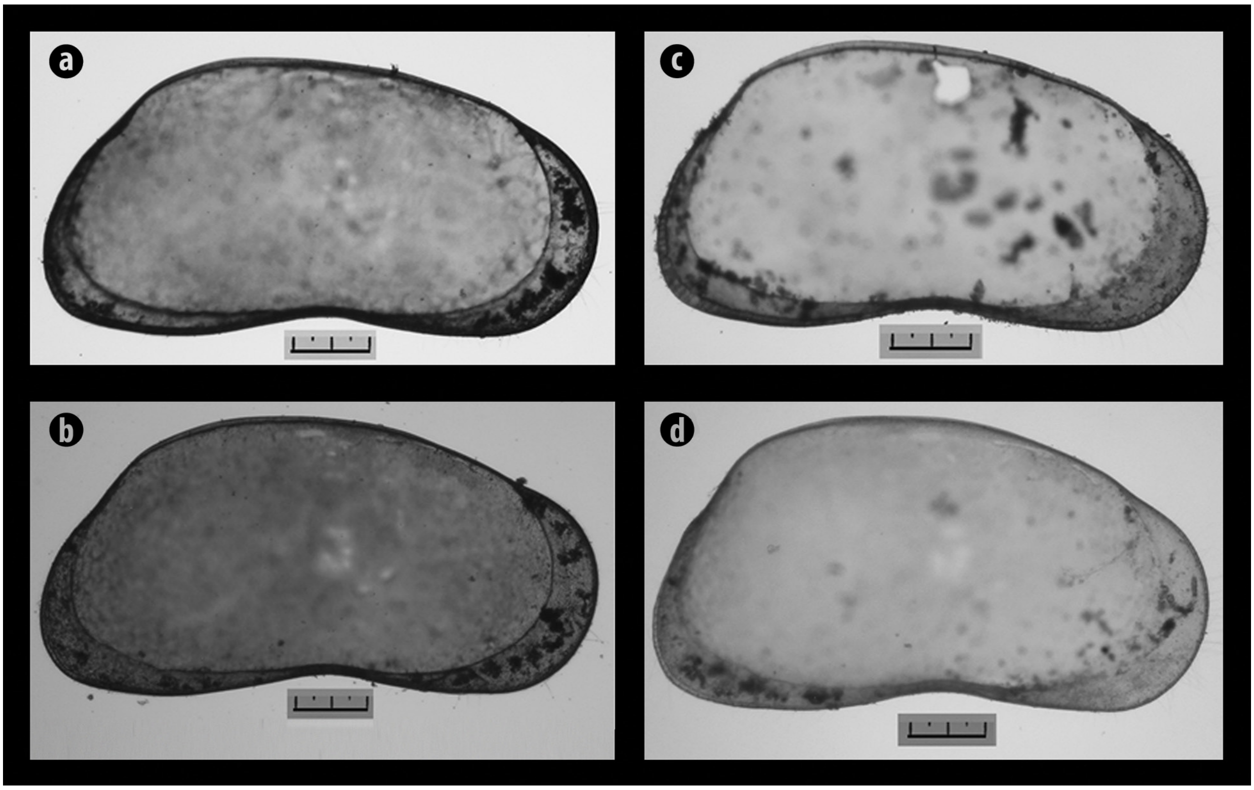
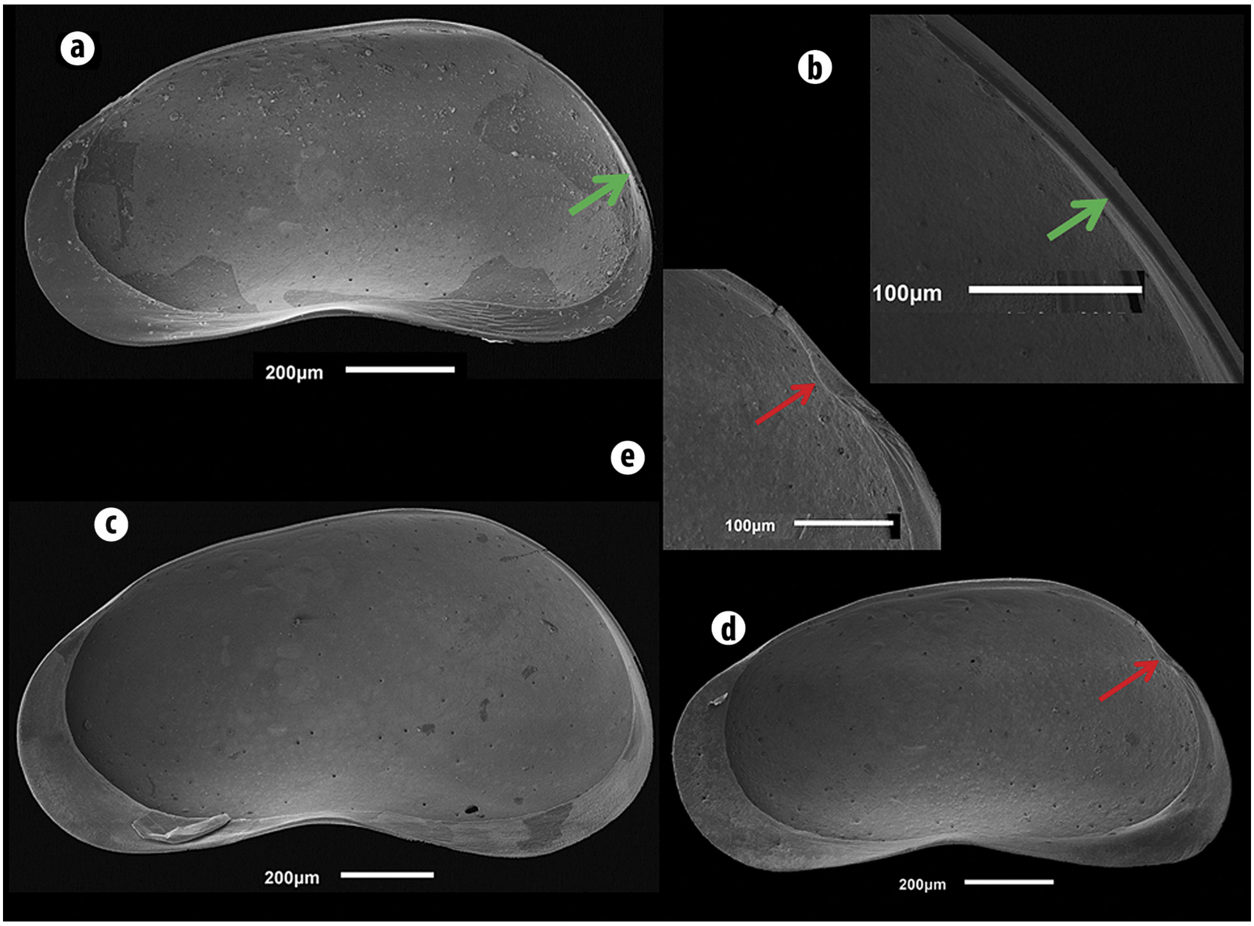
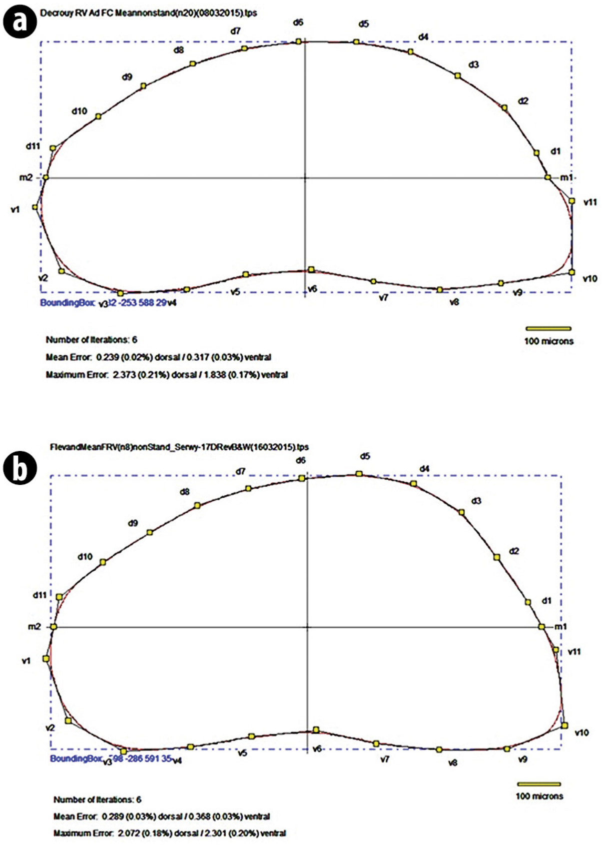


Fig. 11. *Fabaeformiscandona tricicatricosa,* (Mondsee), female RV in TLM, variability of the general form from two littoral-sublittoral samples: **A, B**- Mondsee, site 3 (sample 10 m), Ostra-photos No. 117 and 133; **C, D** – Mondsee, site 2 (sample 4m), Ostra-photos No. 119 and 125. Scale in **A** – **D**, 160 µm.



▲ **Fig. 12.** *Candona neglecta* (Lake Serwy), SEM photos, **A** – **C** adult valves, **A-B**, female, **C** – male, **B** – detail of the posterior section of the valve. Green arrow indicates the selvage without a ledge; **D** – **E**, *Fabaeformiscandona tricicatricosa* (Seeshaupt), female RV, inner view; red arrow points to the posterior ledge. Material deposed at Universal Museum Joanneum, Graz (photo M. Gross).



◀ **Fig. 13. A** - *Fabaeformiscandona caudata,* (Lake Geneva, Petit-Lac), outline of the mean shape of 20 females RV reversed representation, using the bounding box in MORPHOMATICA and the non-standardised for size algorithm; **B** - *F. levanderi,* (Lake Serwy), mean shape-outline of 8 females RV, calculated as for Figure **A**.

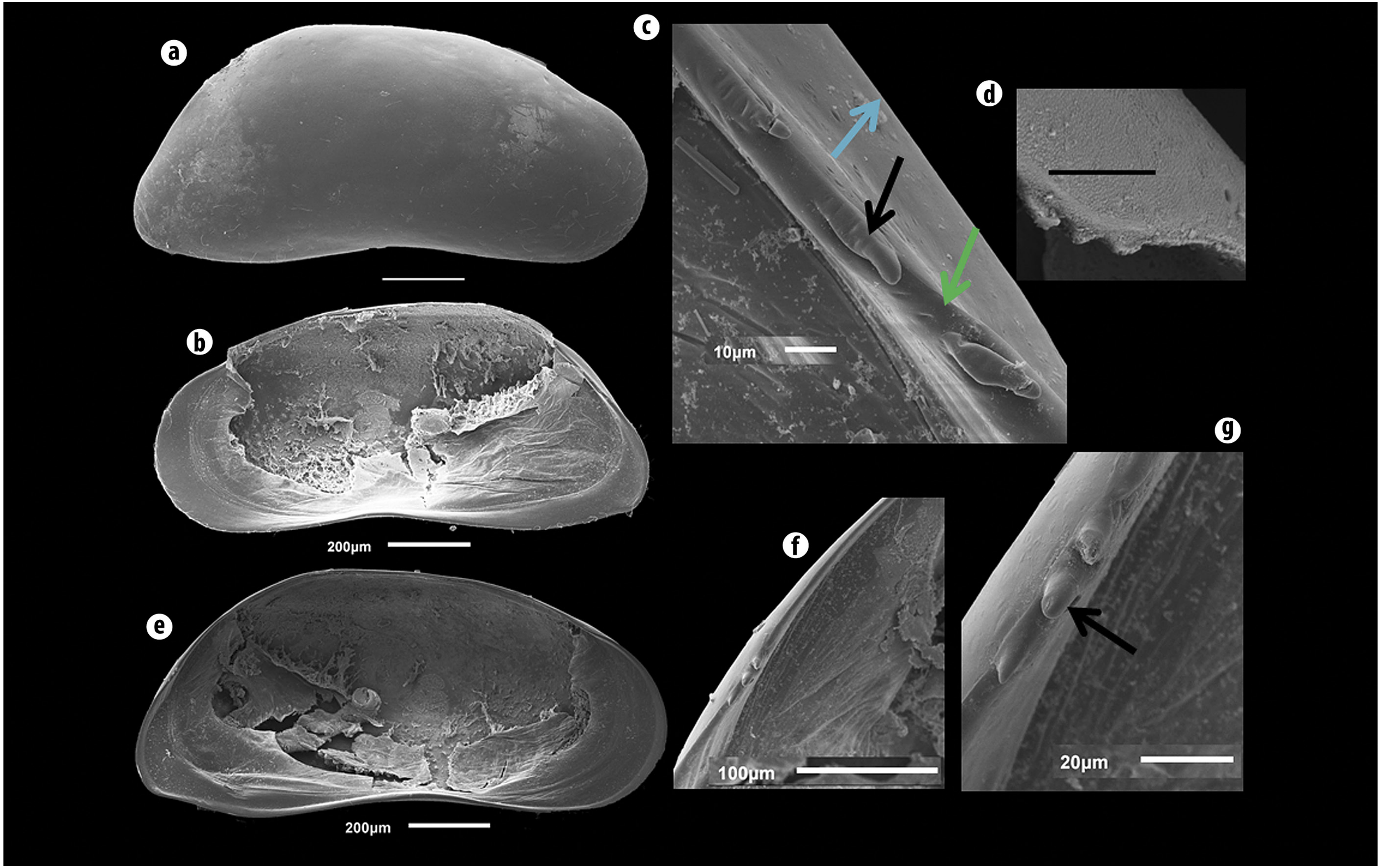


Fig. 14. *Fabaeformiscandona caudata (*Neunitz), SEM photos, adult female; **A – D** – RV; **E – G** – LV; **A, B, E** - Lateral view, external (**A**) and internal (**B, E**) view, general; **C, D, F, G** –details of the posterior ledge inner lateral view; Except **D** (photo Decrouy) all photos M. Gross, Joanneum Graz; blue arrow shows the outer valve margin, black arrow points to a „bud“, green arrow marks the selvage; scale of **D** – 20 µm. Material deposed at the Universalmuseum Joanneum, Graz.

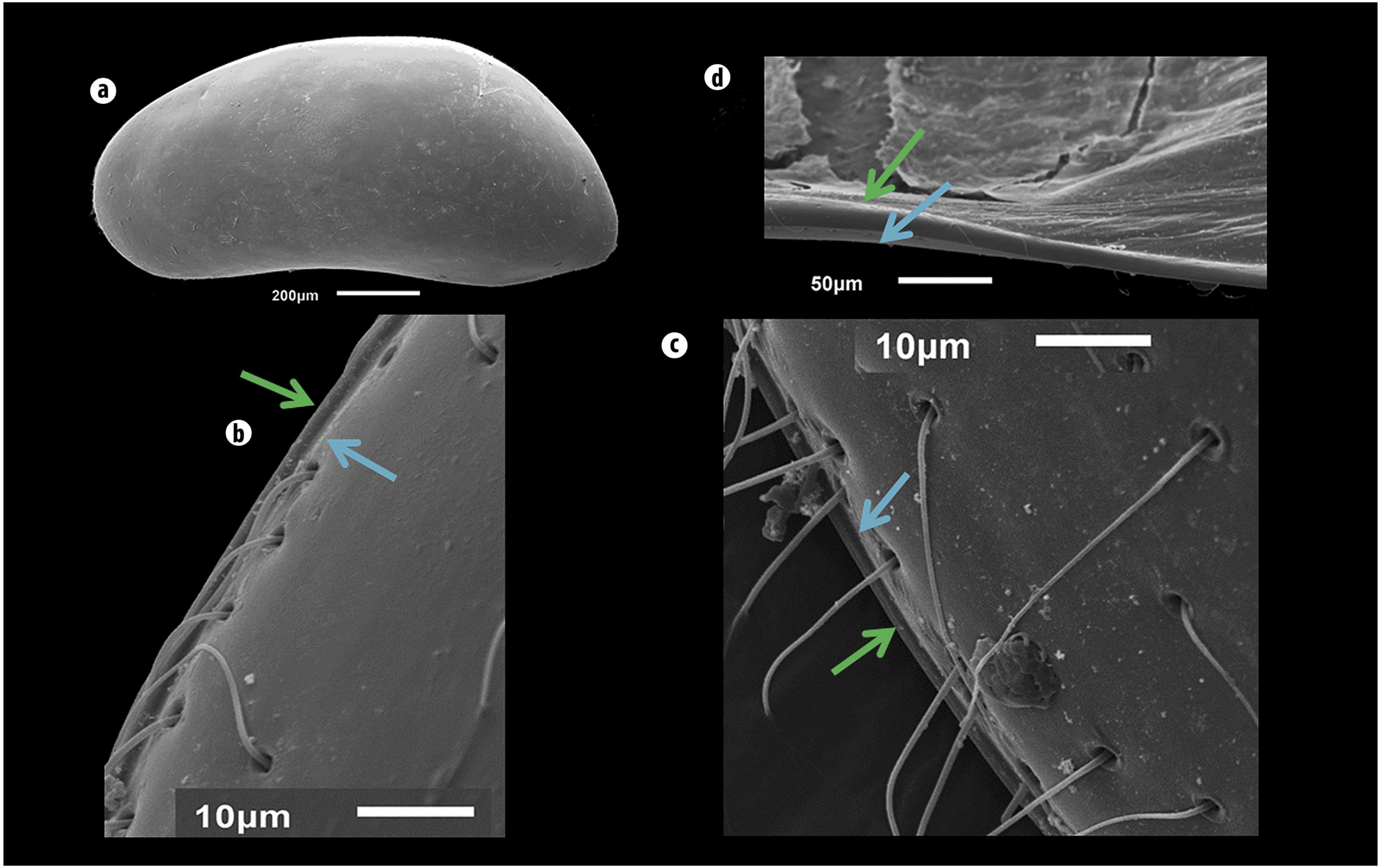


Fig. 15. *Fabaeformiscandona caudata (*Neunitz), Adult female LV, SEM photos; **A** –external view; **B – C** – details of **A**; **B** – anterior marginal side, upper third ; **C** – lower anterior marginal side; **D** – inner ventral side, central section. Blue arrow marks the outer margin, green arrow points to the selvage. Material deposed at the Universalmuseum Joanneum, Graz.

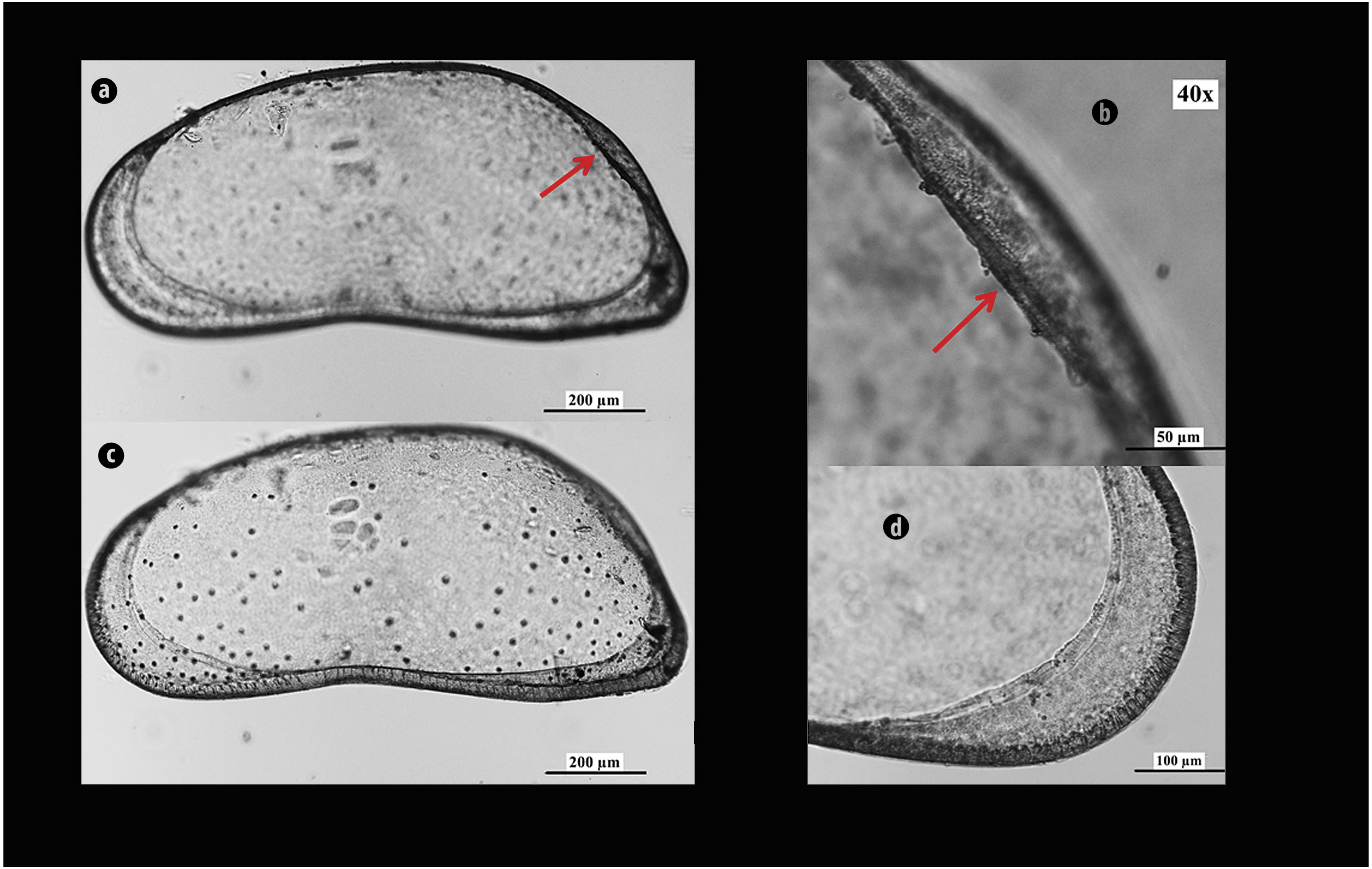


Fig. 16. *Fabaeformiscandona caudata* (Mondsee, site 5, sample 6m), Adult female RV (Ostra-photo No. 7166); **A-C** - inner side; **A** - general view, focusing on the posterior lamellar ledge; **B** - detail of the ledge (*cf.* red arrow); **C** – general view, focusing on the anterior and posterior vestibula as well as on the ventral fused zone with radial channels; **D** – detail of the anterior third of the RV, external view.

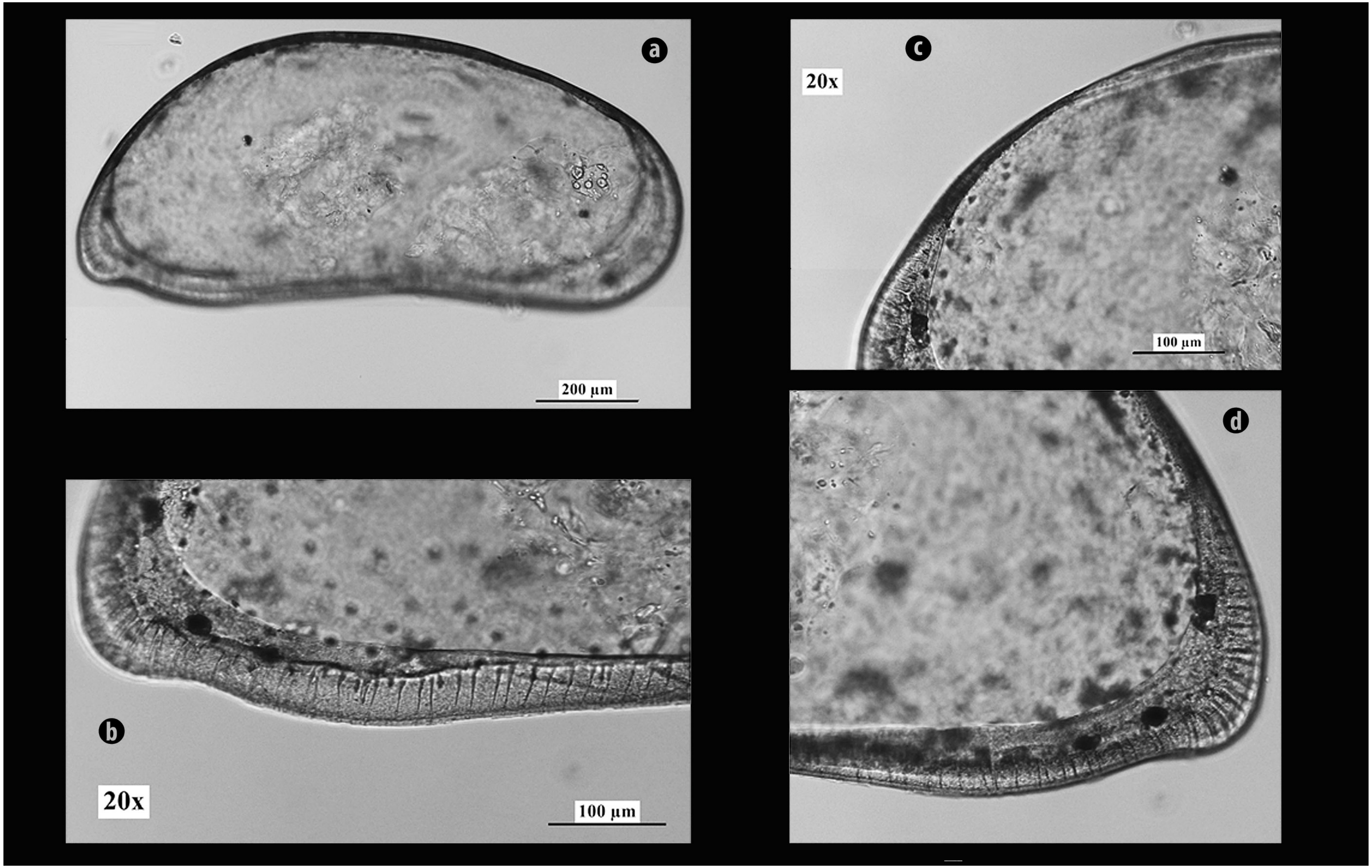


Fig. 17. *Fabaeformiscandona caudata (*Mondsee, site 5, sample 12m), Adult female LV (Ostra-photo No. 7176); **A, B** – inner side; **A**- general view; **B** - detail of the postero-ventral side; **C, D** – outer side; **C** – detail of the antero-dorsal section of the outline; **D** - detail of the postero-ventral side focusing on the postero-ventral fused zone with radial channels.

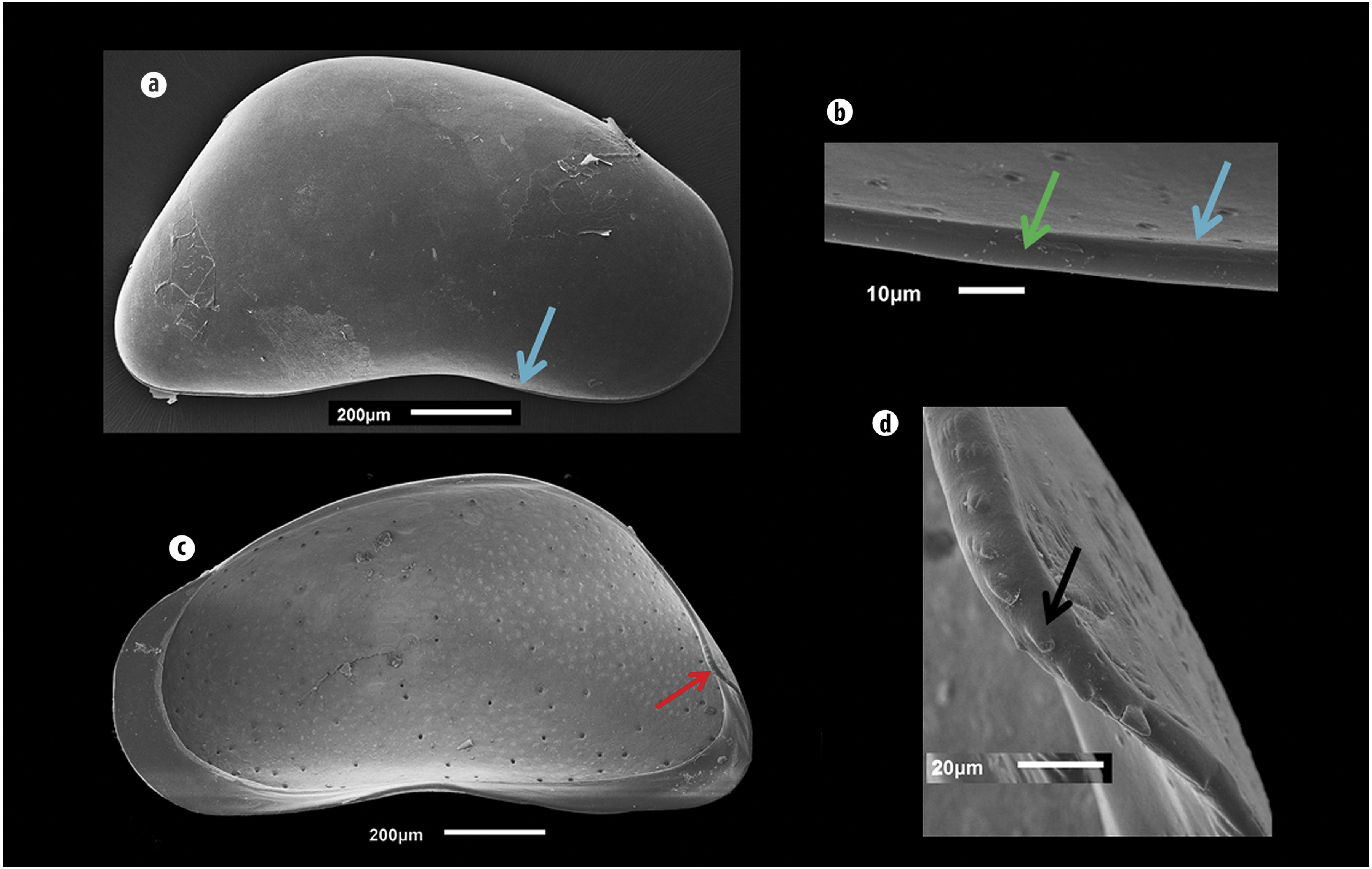


Fig. 18. *Fabaeformiscandona levanderi* (Lake Serwy) adult female RV: **A** – external side (blue arrows indicates place of the detail in **B**); **B** – peripheral antero-ventral section (blue arrow points to the outer margin, green arrow marks the selvage); **C** – same valve, internal side (red arrow indicates the posterior ledge); **D** – detail of the ledge with the „buds“ (black arrow points to one of them). Material deposed at the Universalmuseum Joanneum, Graz.

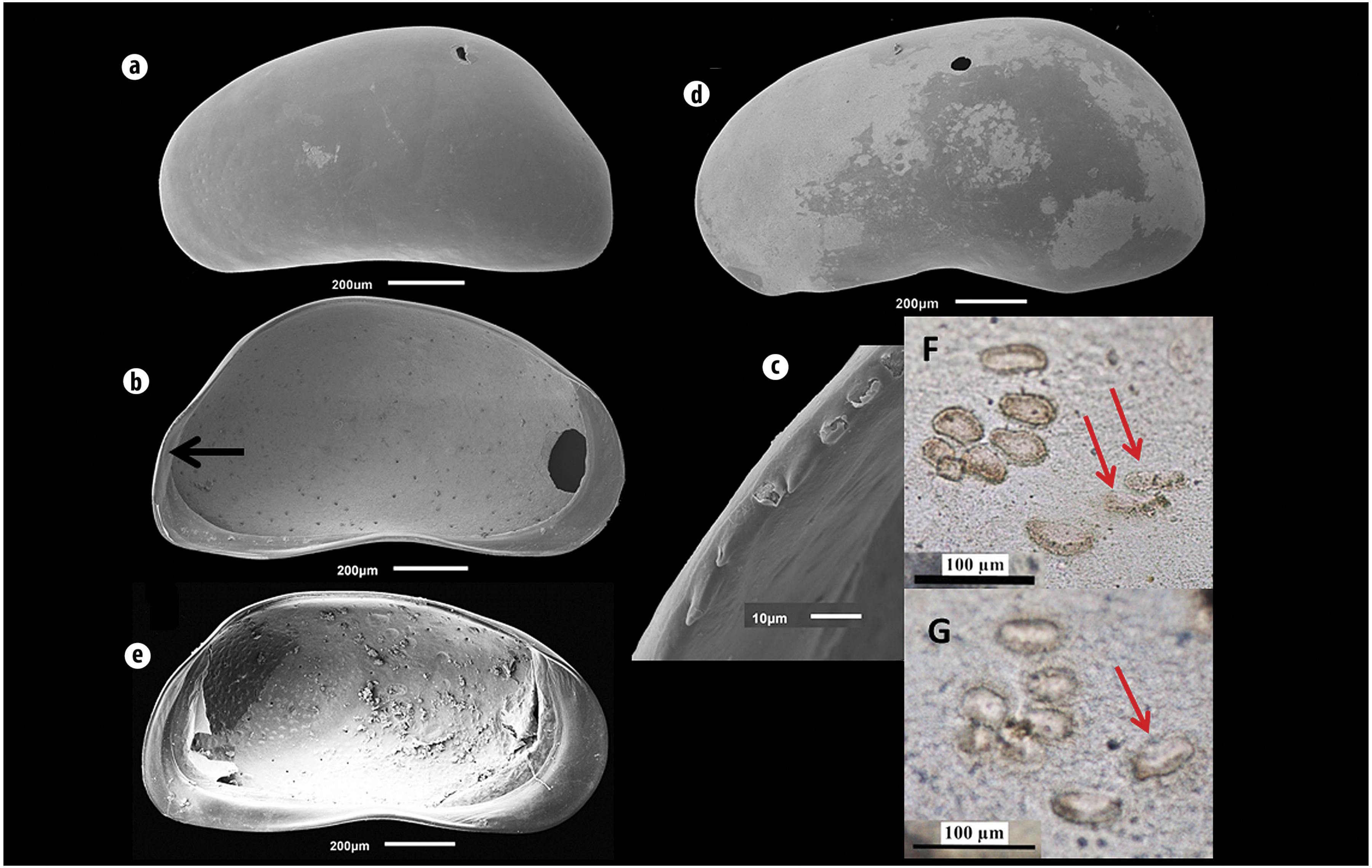


Fig. 19. A – D – *Fabaeformiscandona levanderi* (Lake Serwy) adult LV; **A** – female external view; **B** – female inner view (black arrow points out to the area for the detail showed in **C**); **C -** detail from **B**; **D** – male external view; **E – G** - *F. tricicatricosa* (Mondsee); **E** – specimen from site 4; **F, G** – central adductor and mandibular muscle imprints of two females LV, inner view, site 5, 12 m deep. Red arrows indicate the variable mandibular imprints, namely divided in specimen **F**, simple in specimen **G**.

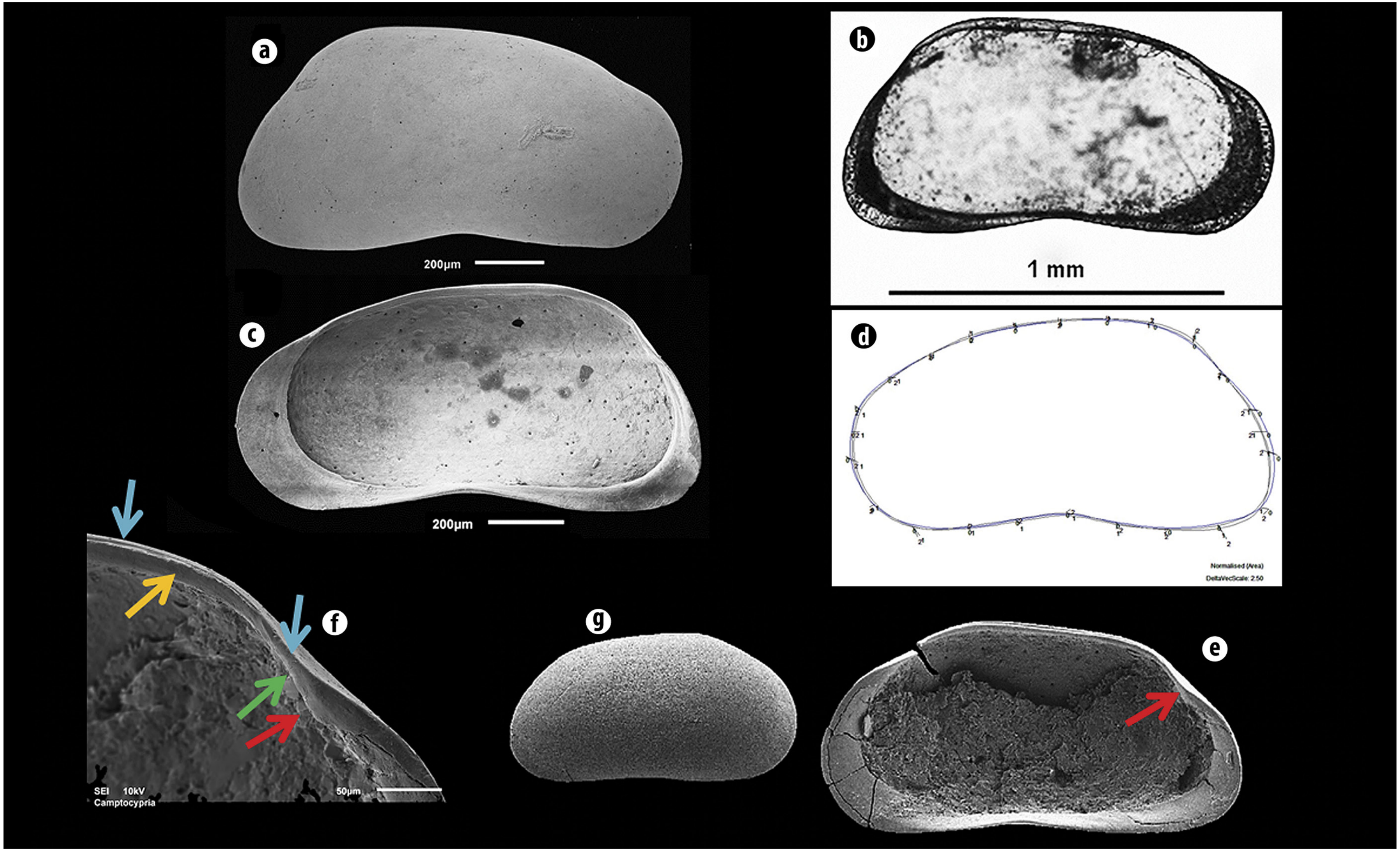


Fig. 20. A – D - *Fabaeformiscandona tricicatricosa* (Kempfenhausen-Starnberger See), female RV: **A, C** – outer and inner SEM-view; **B** - TLM-view of **A** (valve No. 6, photo T. Namiotko); **D** - Superposition on the allotype outline of *F. tricicatricosa* of Diebel and Pietrzeniuk (0) of Mean outline of 3 RV, Starnbergersee Rec. 18 m deep (1) and of the mean outline of 4 RV from Kempfenhausen (2), standardised for equal surface area; **E-G** – *Camptocypria* (alias *Fabaeformiscandona) gratkornensis,* RV: **E** – adult female (Holotype), inner view(from Gross, 2008, p. 271, Pl., Fig. 6); **F** – dorso-posterior detail of the holotype; **G** – A-2? RV juvenile stage (from Gross, 2008, p. 271, Pl. 2, Fig. 13); red arrow points to the posterior ledge, blue arrow marks the outer margin, green arrow points to the selvage, yellow arrow shows the hinge lamella. Material deposed at the Universalmuseum Joanneum, Graz.

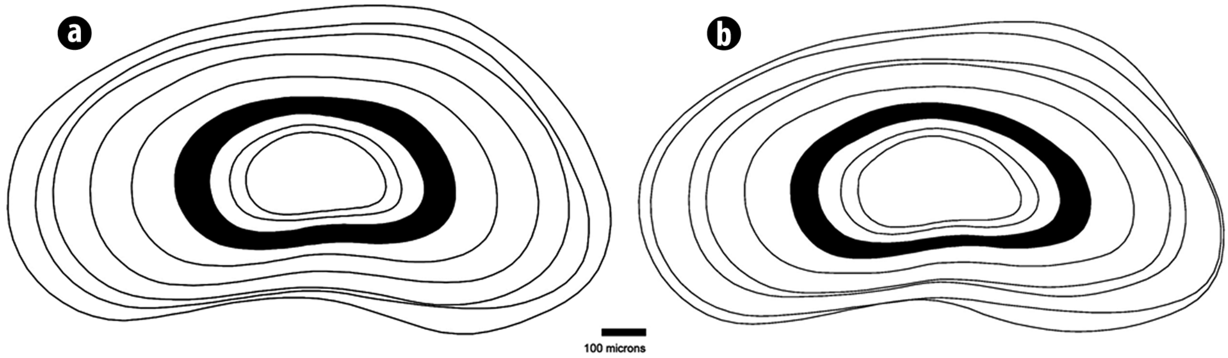


Fig. 21. Developmental trajectories of shells belonging to *Candona neglecta* (**A**) and *Fabaeformiscandona tricicatricosa* (**B**) from the Mondsee site 9, sample MO-05-2E. The superposition of the outlines in non-standardised for shape algorithm, follows concentrically, from the periphery toward the centre: A-m, A-1 m, A-f, A-1 f, A-2, A-3, A-4 and A-5. The general shape of A-3 stage is figured in black.

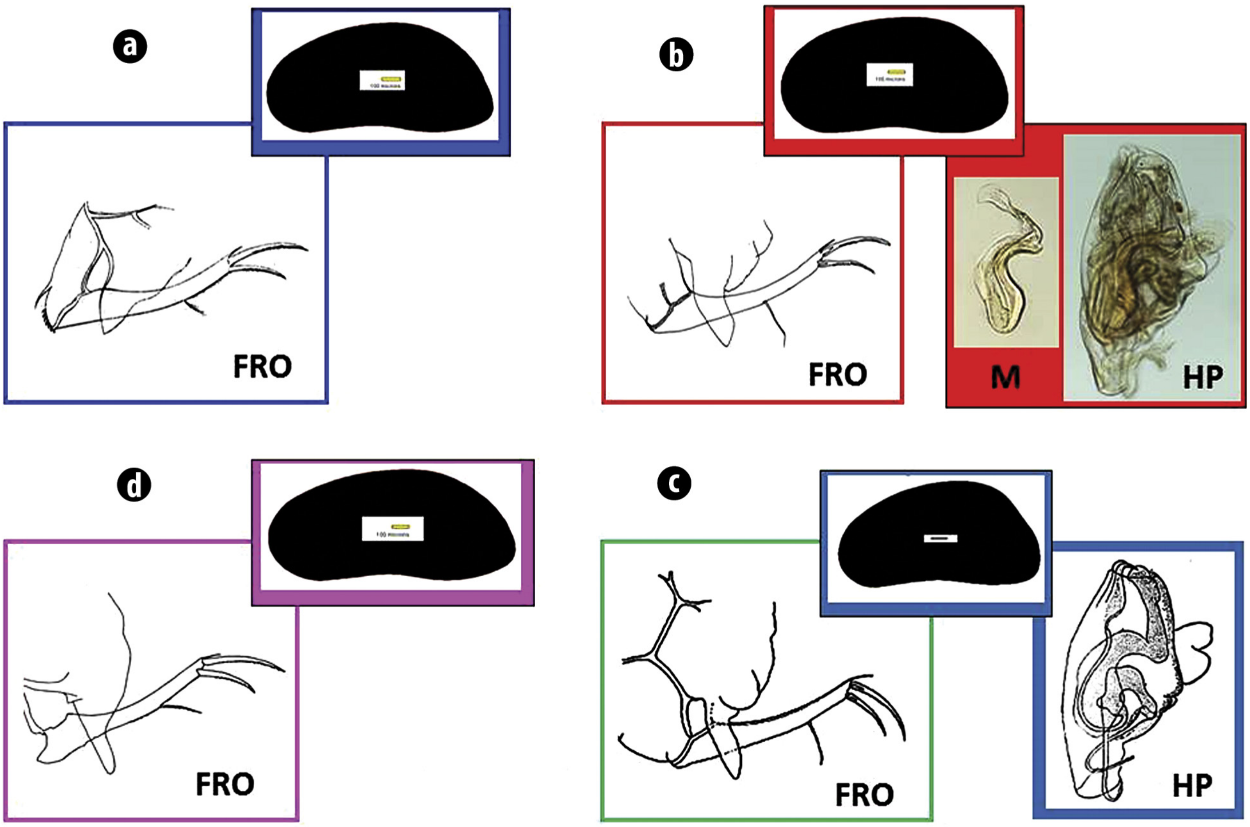


Fig. 22. Comparative morphology of limbs of three related *Fabaeformiscandona* species; in black, their specific valve shapes: **A** – *F. caudata* (from Kaufmann, 1900, Pl. 26, Fig. 23); **B** - *F. tricicatricosa* (Rospuda lake, hemipenis photo Namiotko); **C** – *F. levanderi* (from Petkovski, 1977, p.55, Figs. 9 and 13); **D** – *F. siliquosa* (from Henderson, 1990, p. 101, Fig. G). FRO – female's reproductive organ; HP – hemipenis with the penis process M (photo Namiotko).

F. levanderi, female RV (Figs. 13 B, 18 A - D), displays a H/L of about 56% (*cf.* Table 1) with maximum height placed in the posterior third of the dorsal section around the CP d5; the posterior ledge is placed in the lower half of the outline; the section m1-d3 straight.

The shape of the male's valve resembling those of *F. tricicatricosa* (Fig. 19 D). The posterior section of the outline of the LV more bent than those of *F. tricicatricosa* (*cf.* Fig. 7 A). At the antero-ventral part of the LV and RV a slight tuberosity develops (*cf.* Fuhrmann, 2012, Plate 25, Figs. 2 A, D, E).

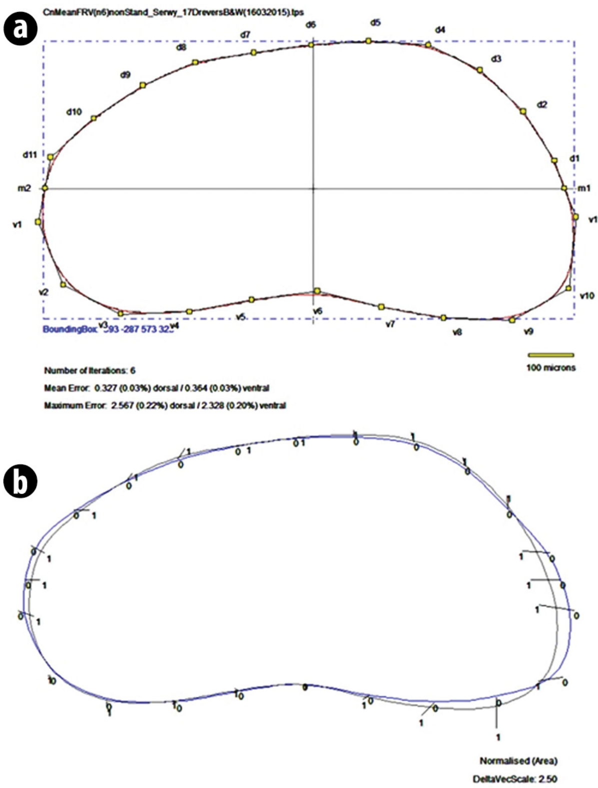


Fig. 23. *Candona neglecta* and *Fabaeformiscandona tricicatricosa* outlines: **A** –mean outline of 6 female RV (reversed view in a bounding box). **B** – superposition in their standardised shape for equal surface, computed by MORPHOMATICA, allotype of *F. tricicatricosa* (0) and the mean outline of 6 RV of *C. neglecta* (1).

F. siliquosa is characterised by elongated valves with a rounded posterior outline (*cf.* Brady 1910 and here Fig. 3 D). It resembles, in some way, *Ft* (*cf.* Fig. 37 B) by the roundness of the posterior section. The maximal height is 46.8 % of the length (*cf.* Table 3).

C. neglecta, female RV (Figs. 12 A – B) has no posterior ledge, the posterior section between CP d1-d3 slightly convex, the H/L of about 52-55 % (*cf.* Table 3) laying in the posterior third of the dorsal section.

The male displays a widely bent postero-ventral section and a ventral concave one in the middle of the valve (Fig. 12 C). The limbs differ from the *Ft* as follows: the male's endopodite of the 4th limb with a strong asymmetry between the left and the right one, the hemipenis with a process M presenting a large bent basis, the lateral process of the peniferum rectangular shaped (*cf.* Danielopol, 1969). The female genital process flat and widely bent.

C. THE PROBLEM OF THE OUTLIERS; HOW TO RECOGNISE THEM?

The outline shape of some isolated valves within a population of *F. tricicatricosa* displays notable deviations from the usual pattern. For instance, in the case of littoral specimens from Mondsee, there is a whole series of shapes, from elongated to notably high ones (Fig. 11 A – D), this latter (Fig. 11 D) resembling *F. levanderi* (Fig. 18 A). For the purpose of TH they can be removed from the analysis. The existence of outliers can also be detected when size is considered, namely within a sample of 12 female RV from the Mondsee littoral site 3, one valve is much larger than the whole group (*cf.* Fig. 29 A). Note that we found a similar case in the sample MO-05-2E containing many female-RV of *C. neglecta*. There are also elongated valves of *F. tricicatricosa* which resemble those of *F. caudata* (*cf.* Figs. 10 A, B, 31 A – D). These outliers do not play for the present project a role as we use, mainly, mean shape outlines or consensus profiles.

We did not consider an outlier a whole sample of valves which deviates conspicuously from the standard pattern of the valves taken as references, especially, when such valves display other typical traits characteristic for a given species. Such a case is the sample of Kempfenhausen which displays the typical morphological traits of *Ft*, like the straight section CP d1 – d3 of the dorso-ventral margin and the small posterior ledge (Fig. 20 A - C), but where the mean (consensus) shape of the RV differs slightly from the outline of the allotype of *Ft* (*cf.* Fig. 20 D). These differences are within the range of variability of the specimens from different sites of this species. The dissimilarity degree expressed as Euclidean distance between the former couple of consensus outlines is 26.85 and that between the Absolon's (1973) right valve outline from Seeshaupt and Kempfenhousen mean shape, is 29.05.

D. THE NEAR-DECOMPOSABILITY ALGORITHM AS PROCEDURE FOR TAXONOMIC HARMONISATION OF *F. TRICICATRICOSA*

For the present study we consider *F. tricicatricosa, F. caudata, F. levanderi, F. siliquosa* and *Candona neglecta* to build a system-unit whereas each species represents a subsystem (*cf.* arguments in the previous section). We will investigate the disparity of the RV-shape for the *Ft*-female at three spatial scales, namely at local sites, like the Lake Mondsee, at a continental level, namely at the European scale. Finally, the distribution of the species at its intercontinental scale is examined.

a. The local (site) scale

We take as example the variation of valves from *Ft* populations occurring in Lake Mondsee at different places and different time periods. Figure 24 displays the range of dispersion of the valve shape for several samples from the deep zone of the lake, at the sites 7 and 9 (*cf.* Fig. 2). The sample MO-41m (site 7) is represented by sub-Recent valves of *Ft* prior to the local extinction of this species during the eutrophication of the lake in the second part of the last century where the sediment became organogenically enriched (*cf.* Danielopol and Casale, 1990). The sample from the site 9 was extracted from a long-core (MO-05) that we analysed for palaeo-climate multi-proxy reconstruction (Lauterbach *et al.*, 2011; Namiotko *et al.*, 2015). Section 2E of the MO-05 core represents a cold phase during the Younger Dryas beginning of the Holocene period, during which the lake was oligotrophic and the sediment accumulation was represented mainly by fine grained minerals from the surrounding area (Lauterbach *et al.*, 2011; Namiotko *et al.*, 2015). A few specimens of *Ft* were studied from the late-Glacial section 1G of the MO-05 core and from the Holocene section 1D corresponding to the early Holocene. The disparity distribution in a bi-dimensional morphospace using the N-MDS analysis (Fig. 24) shows relatively good separation of the shape of the YD-valves from those of the sub-recent one of the MO-41m. The three valves of *Ft* from the Late-Glacial section cluster with the YD-valves and the Holocene valve of section D is located within the cloud of the MO-41m sample.

Figure 25 shows the comparative dispersion of disparity of the valves between the two profundal sites discussed above and a littoral-sublittoral sample coming from the fringe of the lake, at the sites 2, 3 and 5 from depths which do not exceed 15m deep. Results obtained after performing a CAP to the same data are displayed in Fig. 26. This latter procedure allows to determine how well classified are the three samples. The MO-052E and the MO-41m samples were correctly identified with a probability exceeding 75 % while the littoral-sublittoral sample attains a rate of 72% of correct identification. If we eliminate this latter sample and we recalculate the CAP-distribution just for the two profundal samples we get a degree of correct identification, above 95%. This is due to the fact that the pattern of both the form (*i.e.* the shape calculated dependent on the real size) as well as of the shape (*i.e.* the real size is eliminated and the calculation is done on a standardised surface unit) the two samples differ conspicuously (Fig. 27 A, B). This latter representation displays the superposition of the mean outlines of the samples from the deep part of Lake Mondsee. One can see that the consensus outline of the sample MO-41m is larger than those of the MO-05-2E, especially, on the upper part of the anterior and posterior sections of the outline, as well as on the ventral part. One will notice also differences in the length of the valves and their H/L ratio (*cf.* Table 3).This aspect of disparity is a clear demonstration of the presence of an environmental impact on the shape and form of the valve. For the comparative case of the profundal habitats of Mondsee we know that the degree of seasonal thermal fluctuations are attenuated (see discussion in Namiotko *et al.*, 2015), probably ± 2-3 C° degree around the annual mean of temperature evaluated to 4-6 C°. We hypothesize that the phenotypic differences between the YD-consensus outline (MO-05-2E sample) and those of the subrecent one (MO-41m) are due to the trophic state of the lake, namely the last hundred years, the trophic state of the lake switched from an oligotrophic state to a meso-eutrophic one, as discussed in Namiotko *et al.* (2015). A similar ecophenotypic situation is visible also in the case of *Candona neglecta* from the same periods and sites (Danielopol and Namiotko, *in litt.*).

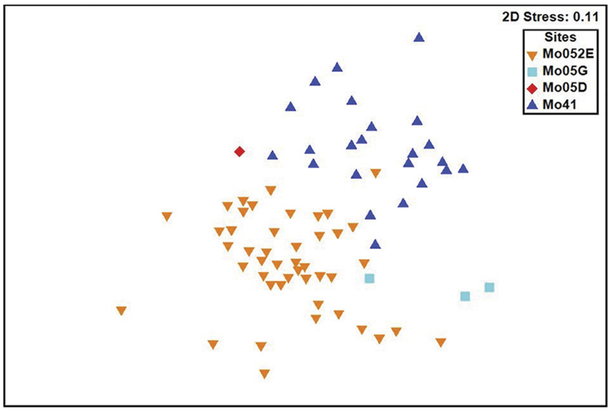


Fig. 24. *Fabaeformiscandona tricicatricosa* – non-Metric multi-Dimensional Scaling (N-MDS) plot of female RV-shapes from Mondsee site 7, samples MO-41m (n-23), and site 9, MO-05, sections-2E (n-43), G (n-3) and D (n-1).

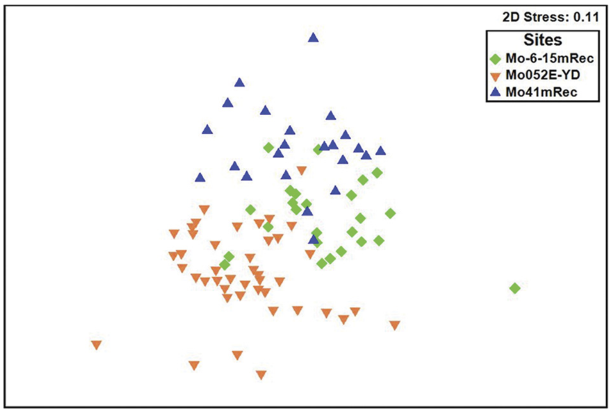
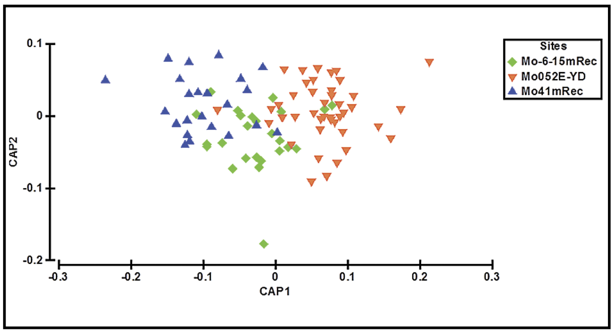


Fig. 25. *Fabaeformiscandona tricicatricosa* – non-Metric multi-Dimensional Scaling (N-MDS) plot of female RV-shapes from Mondsee site 7, samples MO-41m (n-23), site 9, sample MO-05-2E (n-44) and site 5, sample MO-6-15m (n-25).



▲ **Fig. 26.** *Fabaeformiscandona tricicatricosa* – Canonical Analysis of Principal coordinates (CAP) plot of female RV-shapes from Mondsee site 7, samples MO-41 (n-23), site 9, sample MO-05-2E (n-44), site 5, sample MO-6-15m (n-25).

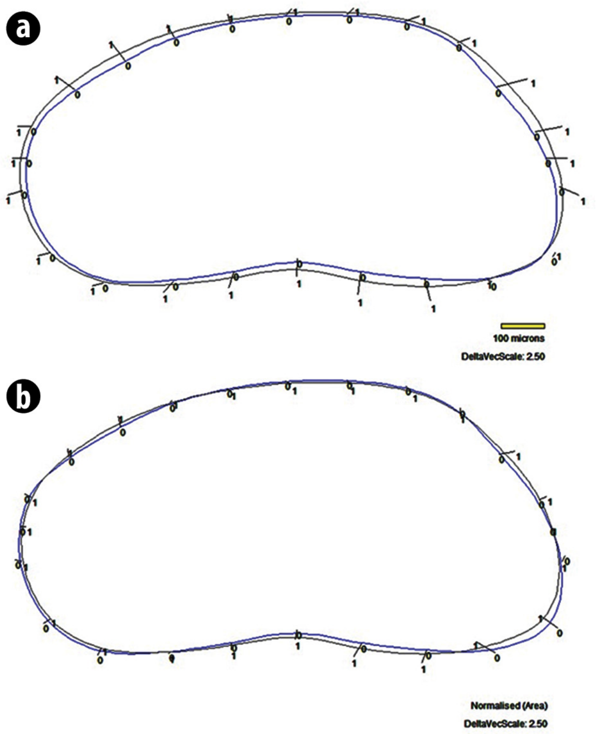


Fig. 27. *Fabaeformiscandona tricicatricosa* – superposition of mean female RV-shapes from Mondsee site 9, 44 valves from MO-05-2E outline blue (0) and 23 valves sub-Recent at site 7 MO-41m (1). **A** – outlines represented in non-standardised for equal surface algorithm; **B** - same items in standardised for surface algorithm; all data computed with MORPHOMATICA. ▶

b. The regional (continental) scale

We started our characterisation of *Ft* comparing the female RV which stems from Central Germany (Süssenborn, near Weimar) as figured by Diebel and Pietrzeniuk (1969) with the female from Seeshaupt in Bavaria (located at the southeast part of Starnbergersee) figured by Absolon (1973) and considered a new species, *F. lozeki* (*cf.* Fig. 4, B). Later on *F. lozeki* was considered a synonym of *F. tricicatricosa* (*e.g.* Fuhrmann, 1991). As one can see from the superposition of the valves of the two morphotypes standardised for equal surface, the Süssenborn exemplar displays a wider posterior curvature with the maximal bending placed within the outline section of the CP v10 - v11 (Fig. 4 A, B). The morphotype of Absolon displays the posterior maximal bending, in a slightly lower position, within the section CP v9 – v10 (*cf.* Fig. 4 B). These data confirm the observation of Fuhrmann (2012, p. 72) who mentioned that the valve morphology of the Absolon's *F. lozeki* is slightly different from those of Diebel and Pietrzeniuk (1969). Documentation of the valves of *F. tricicatricosa* from Zauschwitz in Saxony by Fuhrmann (2012) points out to morphological differences of this population as compared to the Bavarian *F. lozeki*. However, it was not clear enough if such a difference is so important to keep the validity of both species. This problem will be discussed afterwards, with arguments derived from our investigation using geometric morphometrics and multivariate statistics.

Figure 28 displays the results of a comparative analysis of the diversity of the female RV of *Ft* from the southern part of Central Europe and a more northern site in Central Europe, in Saxony using Canonical Analysis of Principal coordinates (CAP). For the southern area, we used a sample from Mondsee, MO-052E (n – 45), one from Seeshaupt, namely 2 valves from the *locus typicus* of *F. lozeki* sampled by A. Absolon, (*cf.* his publication, 1973) and 3 valves from Starnbergersee sampled by one of us (*cf.* von Grafenstein *et al.*, 1999b). We compared the disparity of the outlines with those of 13 valves from Zauschwitz in Saxony, sampled by R. F. (*cf.* Fuhrmann, 2012). We note a clear separation of the Zauschwitz sample from those located in the southern part of Central Europe. The CAP analysis shows a 100% discrimination of the former sample from the other ones. This is apparently a confirmation of Fuhrmann's suspicions of existing two closely related *Fabaeformiscandona* species, as discussed previously. Moreover, we compared the disparity of the Zauschwitz sample (Zausch) with a sample from Lake Rospuda in Poland (ROS, n - 13).

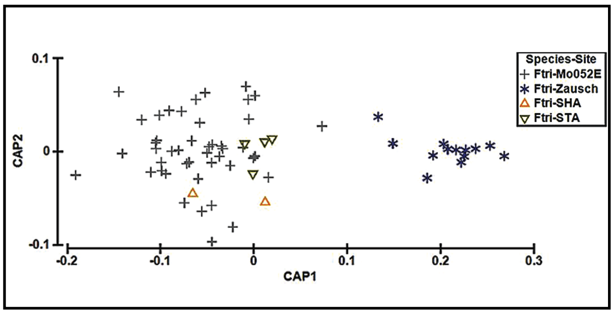


Fig. 28. *Fabaeformiscandona tricicatricosa* – Canonical Analysis of Principal coordinates (CAP) of female RV-shapes from Mondsee samples MO-05-2E (n-44), Zauschwitz-ZAUSCH (n-13), Starnberger lake-STA (n-3), Seeshaupt-SHA (n-2).

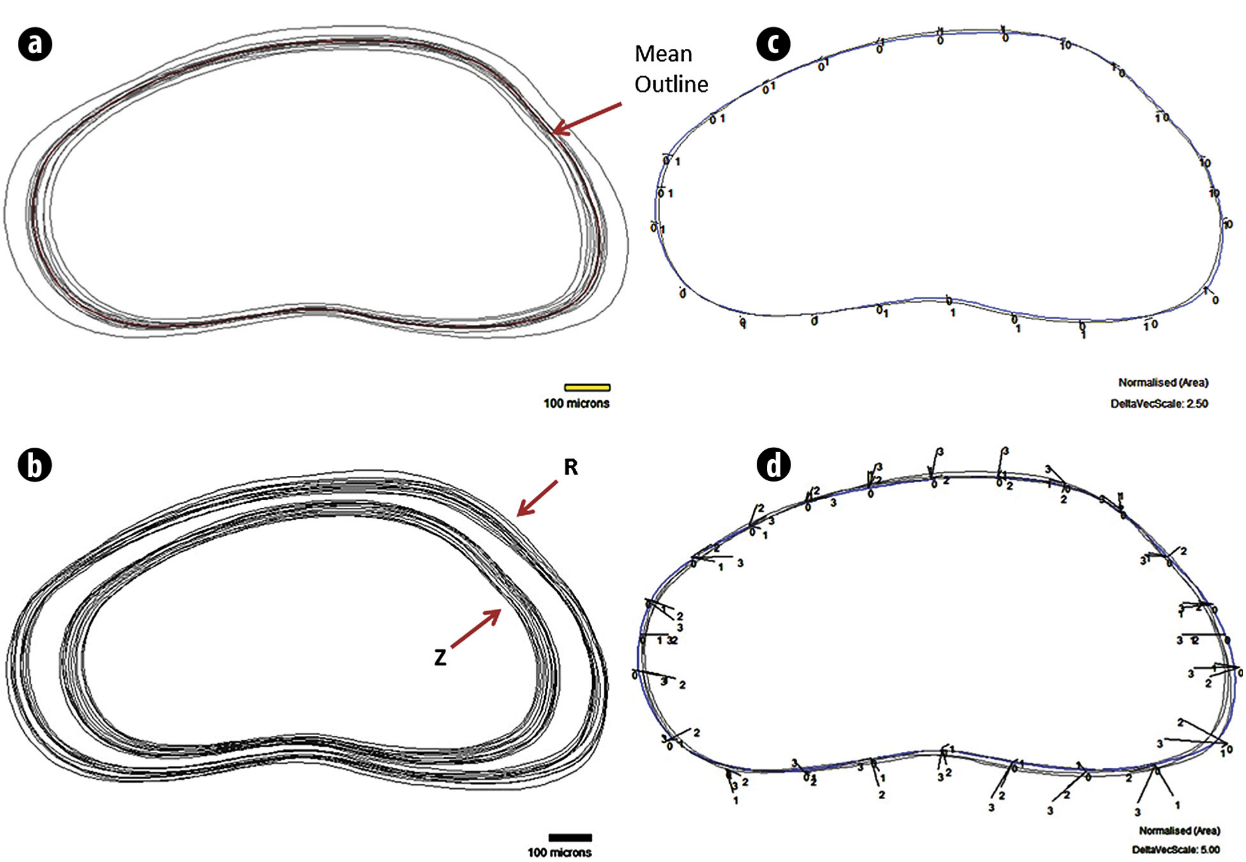


Fig. 29. *Fabaeformiscandona tricicatricosa* – female RV; **A** – Mondsee, site 5, sample 6-superposition in non-standardised for equal surface algorithm (n-12), mean outline in red colour; **B** - Superposition of Rospuda outlines (R) in non-standardised for equal surface algorithm (n-13) on Zauschwitz-outlines (Z) in non-standardised for equal surface algorithm (n-13); **C** - same as **B** but expressed as mean outlines in the standardised for equal surface algorithm of MORPHOMATICA, Rospuda (0) and Zauschwitz (1); **D** - superposition in standardised for equal surface algorithm of *F. tricicatricosa*, allotype, RV (0) and mean outlines for the samples MO-05-2E (1), MO-41m (2) and Zauschwitz (3).

Figure 29 B displays in superposition of the form of outlines the 2 samples. One notices the difference of size, the former sample displaying a more reduced size (*cf.* also comparative values in Table 3). However, if we superpose the consensus outlines of the 2 samples using the standardised for surface algorithm in MORPHOMATICA (*cf.* Fig. 29 C) we note the close similarity between their shapes.

We continued our comparative study of *Ft* superposing consensus valves of two samples from Mondsee, MO-052-2E and MO-41m compared to the Zauschwitz consensus outline and using as reference the allotype of Diebel and Pietrzeniuk (Fig. 29 D) calculated from the data presented above and using the algorithm of standardised surfaces in MORPHOMATICA. We note that the mean outline of Zauschwitz resembles more, especially in the postero-ventral side, to those of the consensus outline of the sample MO-41m and differs from those of MO-05-2E which resemble more the allotype of *tricicatricosa*. We interpret this as an argument for existing ecophenotypic differences of shape visible even at a regional scale and, therefore, we can avoid the rehabilitation of the idea of two species, *F. tricicatricosa* and *F. lozeki*.

Another aspect which has to be discussed here is the location of fossil *Ft* southern from the Alps area, namely in Croatia and in Serbia. Sokač (1978) mentioned *F. lozeki* from Middle and Upper Pleistocene deposits at Posavina, Prevlaka and *F. tricicatricosa*, in deposits dated as Middle Pleistocene, in Slavonja, at Gradište. Here we figured the female RV of Sokač (1978, Pl. 14, Fig. 9). This morphotype is remarkable by its posterior section (between the CP v11 and d3) practically, straight, with a postero-ventral widely bound section between the CP d3 – d5, approximating an angle of 165°. The maximal postero-ventral curvature lies by about 18.5% of the maximal height, this latter representing 51% of the maximal length of the valve (*cf.* Fig. 33 C).

The valve figured by Krstić (2006, Pl. 20, Fig. 10, here Fig. 33 D) stems from a sample of the upper part of the Upper Paludinian or Malezi zone (considered the limit of the Pliocene for the Paludinian lake) from the Bačka Trough in Serbia. It represents the only record from the Tertiary, albeit at the limits with the Quaternary. Even so, most of the European *Ft* stem from Middle and Upper Quaternary layers and continue with Holocene and Recent records (see next section for more details). As compared to the Croatian material and further with those of the Prealpine zone in Upper Austria and Bavaria, the Serbian *Ft* has a slightly higher H/L ratio (52.5%) and a maximal curvature in the postero-ventral section at about 28.5 % of the H; in this way, this morphotype resemble the mean-shape of the Zauschwitz population from Central-East Germany (*cf.* Table 1). This is surprising because one would expect more similarity with the valves from southern part of Central Europe (we will discuss again this aspect in the next section).

We integrate now the data for the outline disparity of *Ft*, comparing it to those of various populations of the other species belonging to our taxonomic assemblage formed by *F. caudata, F. levanderi* and *Candona neglecta*. Figure 30 shows in a CAP-display a clear separation between the populations belonging to *F. caudata* (namely those of Lake Geneva Petit-Lac), Mondsee, Lake Rospuda in Poland and Neunitz in Germany, from the complex of population of *Ft* and from *F. levanderi*. Notably, only one valve of *Ft* clustered with *F. caudata* and, at a closer examination (*cf.* Fig. 31 A-D), it can be said that this valve represents an outlier of the MO-05-2E sample and not a misidentification of *Ft*. Especially, when we superpose on the extremely elongated *F. tricicatricosa* valve (Fig. 31 A) those of a *C. caudata* from Fig. 31 B we note that the dorso-posterior segment of the outline between CP d1 – d3 is straight, while that superposed of *F. caudata* is convexly bended within this CP d1 – d3 section of the outline.

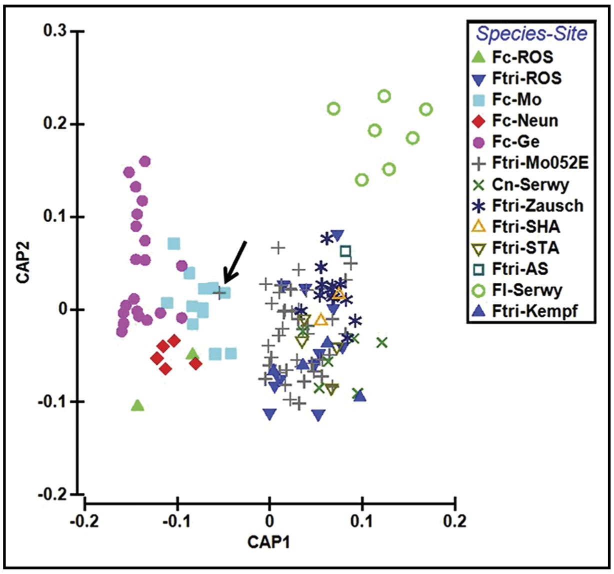


Fig. 30. Canonical Analysis of Principal coordinates (CAP) plot of female RV for different populations belonging to *F. tricicatricosa* (Ftri), *F. caudata* (Fc), *F. levanderi* (Fl), *C. neglecta* (Cn), from various sites: lake Rospuda (ROS), Mondsee (Mo), (site 9 sample MO-05-2E), Neunitz (Neun), Lake Geneva, Petit-Lac (Ge), Lake Serwy, Zauschwitz (Zausch), Seeshaupt (SHA), Starnbergersee (STA), Ammerssee (AS), Kempfenhausen am Starnbergersee (Kempf). Arrow indicates a specimen of *F. tricicatricosa* belonging to the sample MO-05-2E (valve No. 5671 in Ostra-Photo coll.) placed in the cloud of *F. caudata* belonging to the sample 6m from site 5 (valve No. 329 in Ostra-Photo coll.).

If we repeat a CAP analysis using only the *Fabaeformiscandona* data aggregated in the three main taxa, *Ft, F. caudata* and *F. levanderi* we obtain a very high rate of discrimination (*i.e.* between 97.5 % and 100 %). This is another indication for distinguishing, at least in Europe, of only one species, *Ft*, as target for this project of taxonomic harmonisation. An interesting aspect is represented by the similarity in shape of the 6 valves of *C. neglecta* from Lake Serwy which cluster with the complex of *Ft*-valves (*cf.* Fig. 30). The minimal differences which exist between the posterior within the section CP d1 – d3 and the ventro-posterior one do not allow discriminating those species with the B-splines algorithm implemented in MORPHOMATICA. This problem will be discussed in more detail below (in the next section).

We did not add here two records of *Ft*. Robinson (1990) mentions this taxon in the UK at Little Oakley, Essex in a Middle Pleistocene section. Coope *et al.* (1997) recorded *F. lozeki* in samples excavated in London on the upper terrace of the Thames closely located to Natural History Museum Gardens (The Ismaili Centre). It is assumed that the climate was of arctic tundra type. We will demonstrate below that these two identifications are wrong; the valves belong to the genus *Candona*, the *neglectoid*-complex of taxa.

c. The global (intercontinental) scale

We continue now with the last step of our comparative study for delineation of a standard profile of *F. tricicatricosa* within our TH project, namely with the examination of the valve disparity at the intercontinental scale considered also as a global approach. There are two records from Quaternary sites of Siberia. The first one is the record of Wetterich *et al.* (2009) and the description of *Ft* originates from samples coming from the Dimitry Laptev strait in the NE Siberia at 73°N latitude. The samples come from Quaternary exposure-sections dated as Eemian and Late Glacial/Holocene. The sediments were deposited in shallow lakes with a summer temperature approximated to 10-19°C. This water temperature is close to what is known for pre-alpine lakes, like Mondsee (*cf. inter alia*, Geiger, 1990a. 1990b; Dokulil, 2014). Figure 32 here presents the valves for female and male illustrated by Wetterich *et al.* (2009, p. 88, Fig. 13/13-16). As compared to Fuhrmann's material illustrated and discussed above, the Wetterich *et al.* female-RV has a lower posterior curvature at about 25.5% of the maximal valve height (the mean value of the female RV of the outlines from Zauschwitz displays the maximal curvature at 31.3% of the maximal H.

A second record is that of Schornikov (2008), coming from Krasnyj Yar on the Ob' river, a site at the 56°N. We figure here Schornikov's material for *F. tricicatricosa* (*cf.* Fig. 33 A/14 the female RV and the male LV, respectively, Fig 33. A/15). The RV of *Ft* presented by Schornikov ressembles much with the mean outline of the Zauschwitz valves, both have the same H/L ratio of 51.25 % (as calculated from our data using MORPHOMATICA, with the bounding box subroutine) and the posterior maximum curvature lay above 25% while, for the

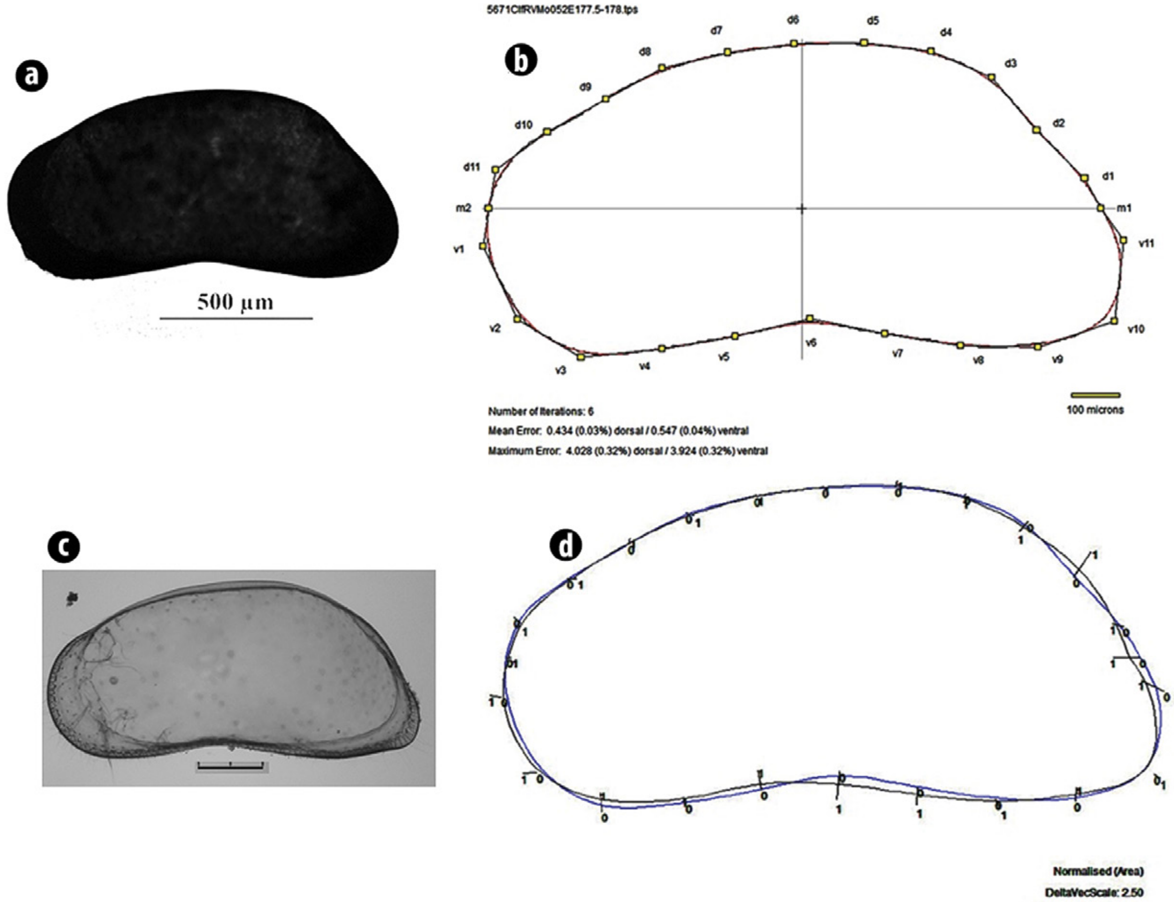


Fig. 31. *F. tricicatricosa* example of outlier resembling *F. caudata*. **A, B** - *F. tricicatricosa* female RV from sample MO-05-2E (valve No. 5671 in Ostra-Photo coll.); **C** – female RV *F. caudata* (valve No. 329 in Ostra-Photo coll. from site 5, sample 6m, scale 200µm). **D** – superposition in standardised for equal surface of *F. tricicatricosa*, valve No. 5671 (0, blue outline) and *F. caudata,* valve No. 329 (1).

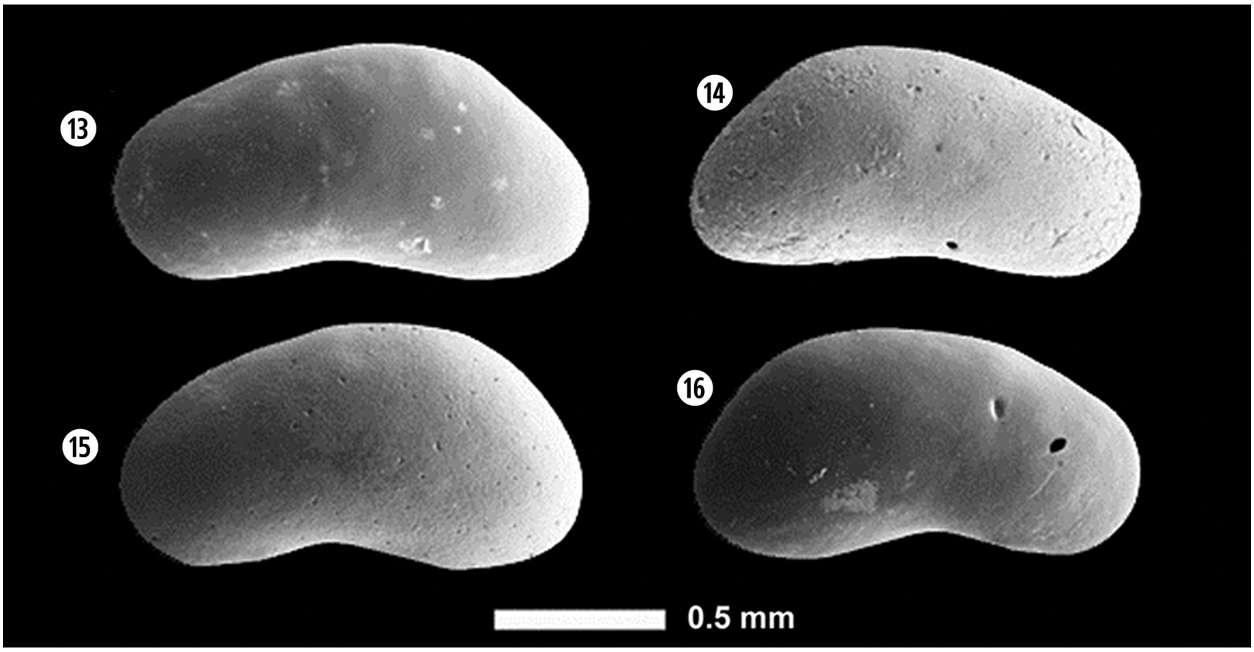


Fig. 32. *Fabaeformiscandona tricicatricosa* –specimens from Siberia, Dmitri Laptev Strait. SEM images from Wetterich et al., 2009, Fig-plate **13** (images: **13** - female LV, **14**-female RV**, 15**-male LV, **16**-male RV).

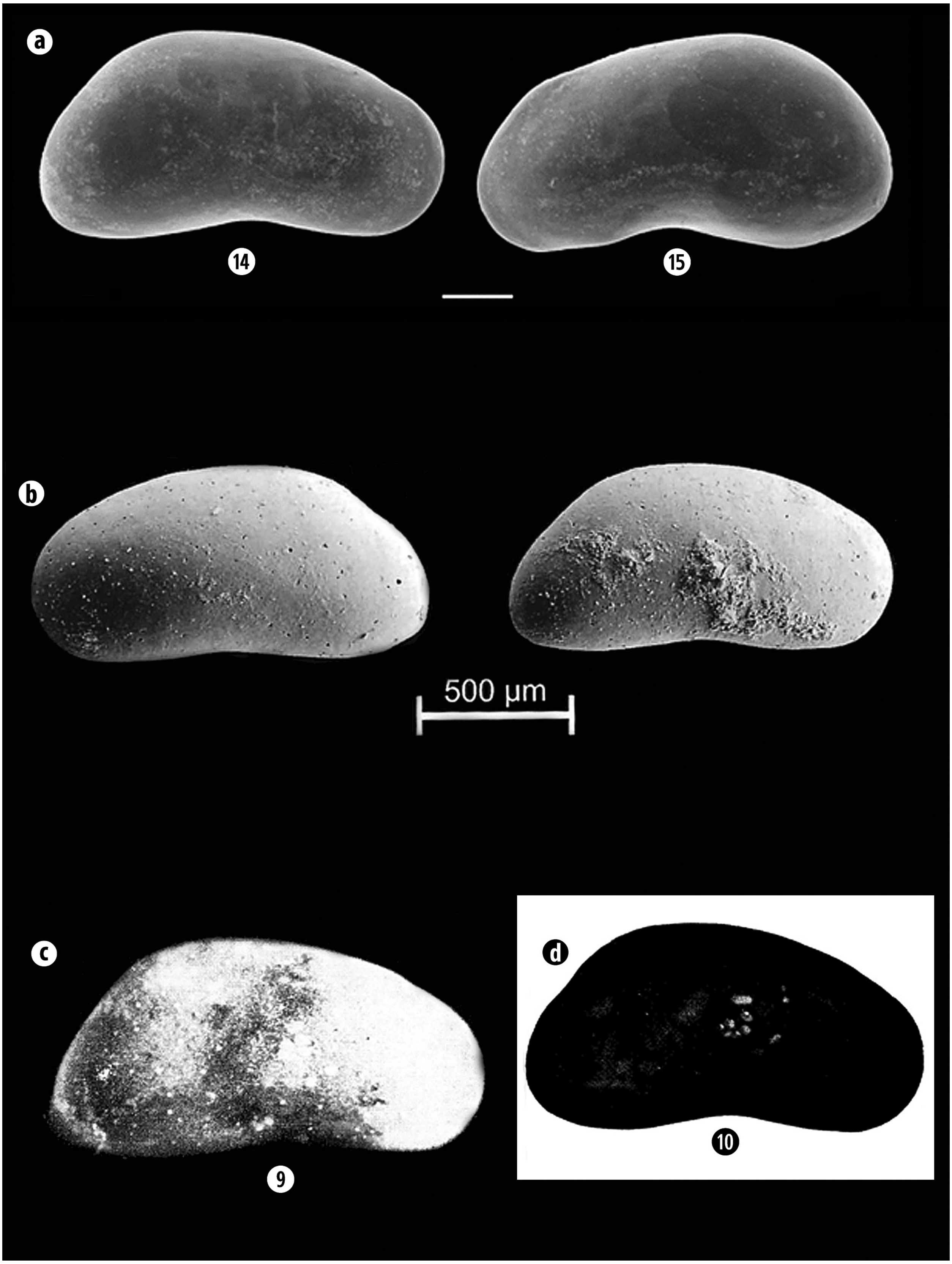


Fig. 33. *F. tricicatricosa* from various sites: **A** – female RV and male LV from Krasnyj Yar on Obi River (from Schornikov, 2008, Pl. **1**, Figs.**14** and **15**), bar scale-size 0.2 mm; **B** – female LV and RV from Herschel's Island lake, Canadian Arctic (from Lenz *et al.,* 2012, Pl. **1**, Figs. **a2** and **a3**); **C** – female RV from Croatia, Slavonija (from Sokač, 1978, Pl. **14**, Fig. **9**). **D** – female RV from Serbia, Vojvodina, Malezi zone of Paludina lake (from Krstić, 2006, Pl. **20**, Fig. **10**).

Siberian valve, it is by 28 % of the maximal height which is an indication for a widely large bending posterior section of the outline.

Finally, a third Quaternary site for arctic conditions where Ft was discovered was presented by Lenz *et al.* (2012). The site is located at the Herschel Island, at 69°N in the Canadian Arctic. Here we reproduce in Fig. 33 B the female's valves of *Ft* published by Lenz *et al.* (2012, p. 33, Fig 2a and 3a). The RV, as compared to the European and Siberian similar valves, is more elongate and more pointed posteriorly; the H/L is only 49.37% and the maximal curvature lays at 24% of the height.

With the global repertoire of *Fabaeformiscandona tricicatricosa* and its position within the complex of related or similar morphological taxa we proceed now to a canonical analysis of principal coordinates on the outline of the female RV. We are confronted with two types of data, those for which we analysed samples with at least 3 individuals and those extracted from the published information where only one item was available. We homogenise the two types of data producing for the samples with at least 3 valves, a mean (or consensus) outline using the routine subprogramme of MORPHOMATICA. With this new data-set we produce a standard consensus profile using the CAP-routine in PRIMER-PERMANOVA (*cf.* Figs. 34, 35). The canonical analysis of the CAP searches the best probabilistic solution for discriminating *a priori* defined groups, also providing us an estimate of the error rate of such solution with the percentage of correctly classified items. Therefore, we present the data of figure 34 grouped within the focal species of interest for our project, using a heuristic *a priori* decision (*cf.* Fig. 35). The result of this multivariate analysis shows that *Fabaeformiscandona tricicatricosa* is in 81.92% cases correctly classified, this means that, from 11 items of *Ft*, 9 were recognised as belonging to this species, while one was classified with *C. neglecta* (the morphotype of the Kempfenhausen consensus outline) and one with *F. siliquosa* (namely the outline of the Diebel and Pietrzeniuk, allotype). All the 3 records of *F. caudata* are 100% correctly classified. The outline of the two *C. neglecta* and those of *F. tricatricosa* (*sensu* Robinson, 1990) that we identified *a priori* as *Candona* of the *neglectoida* group occupy in the morphospace a peripheric position as compared to the cluster of *F. tricicatricosa*. We operate again a qualitative filtering of the data plotted in Fig. 35. We recognise that the morphotype of Kempfenhausen and those of Diebel and Pietrzeniuk's allotype have a posterior ledge typical to the standard description of *Ft* (as presented above). We produce now for the 11 morphotypes allocated to this species a consensus profile of the outline (Fig. 36 A). We propose this latter representation to be accepted as the common denominator for *F. tricicatricosa (sensu lato)*, the result of our taxonomic harmonisation procedure. The question necessary now to answer is, to what kind of practical application this virtual taxonomic harmonised profile can be used within different kinds of ostracodological research.

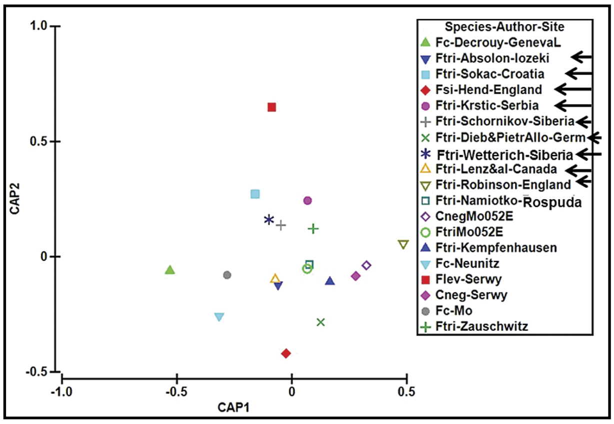


Fig. 34. Canonical Analysis of Principal coordinates (CAP) plot of female RV-shapes; only mean shapes are represented when the sample has more than one valve; **Fc** – *F. caudata*; **Ftri** – *F. tricicatricosa*; **Fsi** – *F. siliquosa*; **Flev** – *F. levanderi*; **Cneg** – *Candona neglecta*; Mo – Mondsee. Arrows indicate the data with one individual extracted from published data.

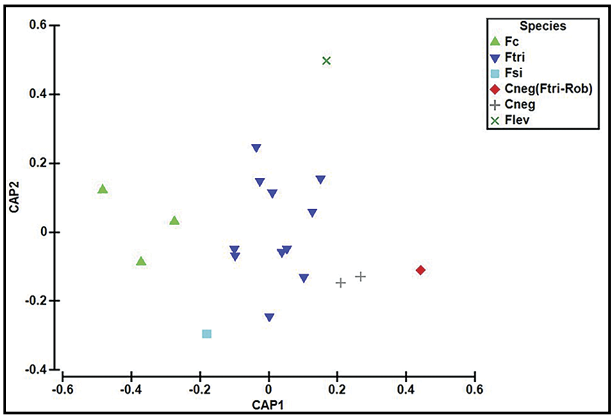


Fig. 35. Same CAP plot of female RV-shapes as in Fig. **34** but reducing the data only to species: *F. caudata* (**Fc**), *F. tricicatricosa* (**Ftri**), *F. siliquosa* (**Fsi**), F. *levanderi* (**Flev**), *C. neglecta* (**Cneg**); Rob - Robinson.

DISCUSSION – PRACTICAL APPLICATIONS

A. The interest of the virtual profile of the valve outline of *F. Tricicatricosa* for ostracodological research

The virtual profile of the female RV of *Ft* presented within a standardised bounding box (Fig. 36 A) is an innovation for the practice of common identification and rapid characterisation of ostracod valves. We recognise immediately the diagnostic traits already presented using the allotype of Diebel and Pietrzeniuk (1969), namely the H/L ratio about 50% which gives the idea of an elongated valve shape, the posterior section of the outline within the section CP d1 - d3, in oblique position and appearing as a straight line, finally the maximal curvature which is in the lower third of the posterior outline.

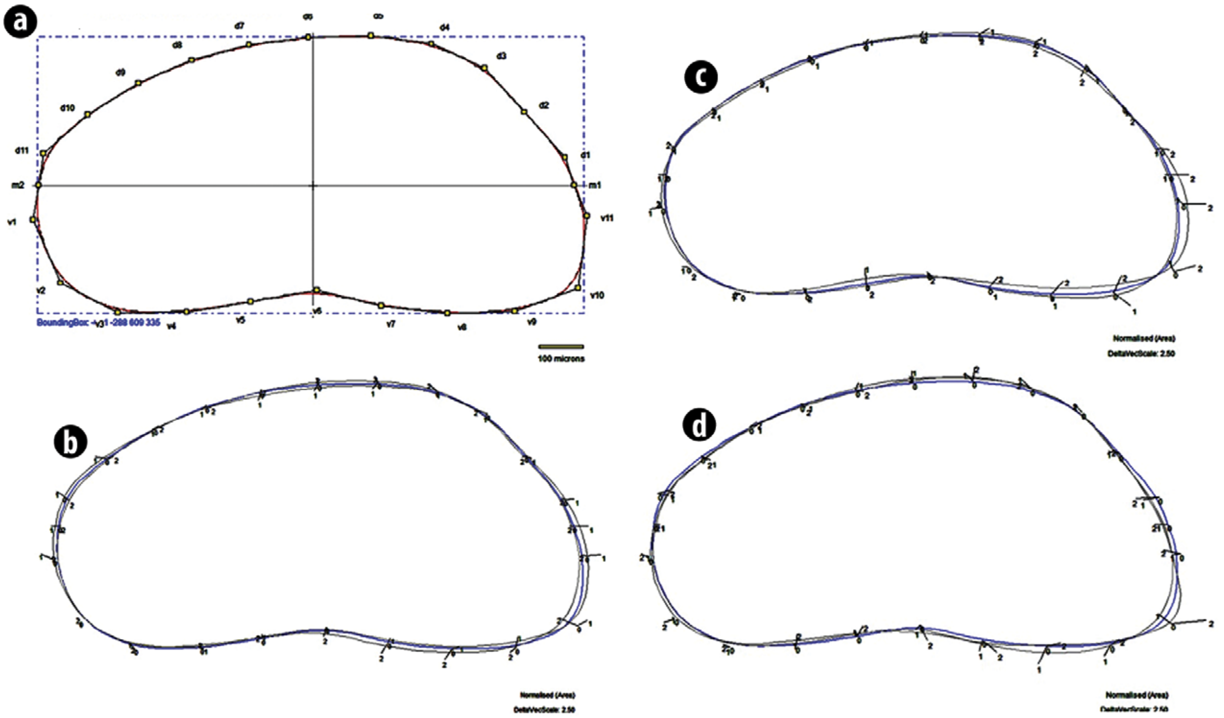


Fig. 36. *F. tricicatricosa* outlines : **A** – Virtual mean profile of 11 valve types from Fig. 35 (reversed view in a bounding box); **B – D** superpositions on the Virtual mean profile (0, blue outline) of female RV of specimens figured by various authors: **B** – superposition of the allotype of *F. tricicatricosa* of Diebel and Pietrzeniuk, p. 474,text-fig.**6b** (1) and the consensus outline of *F. tricicatricosa* of the Zauschwitz-sample (2); **C** – superposition of the female RV of Schornikov 2008, Pl. **1**, Fig. **15** (1) and of Lenz *et al.* 2012, Pl. **1**, Fig. **a3** (2); **D** – superposition of the female RV of Krstić, 2006, Pl. **20**, Fig. **10** (1) and Sokač Pl **14**, Fig. **9** (2).

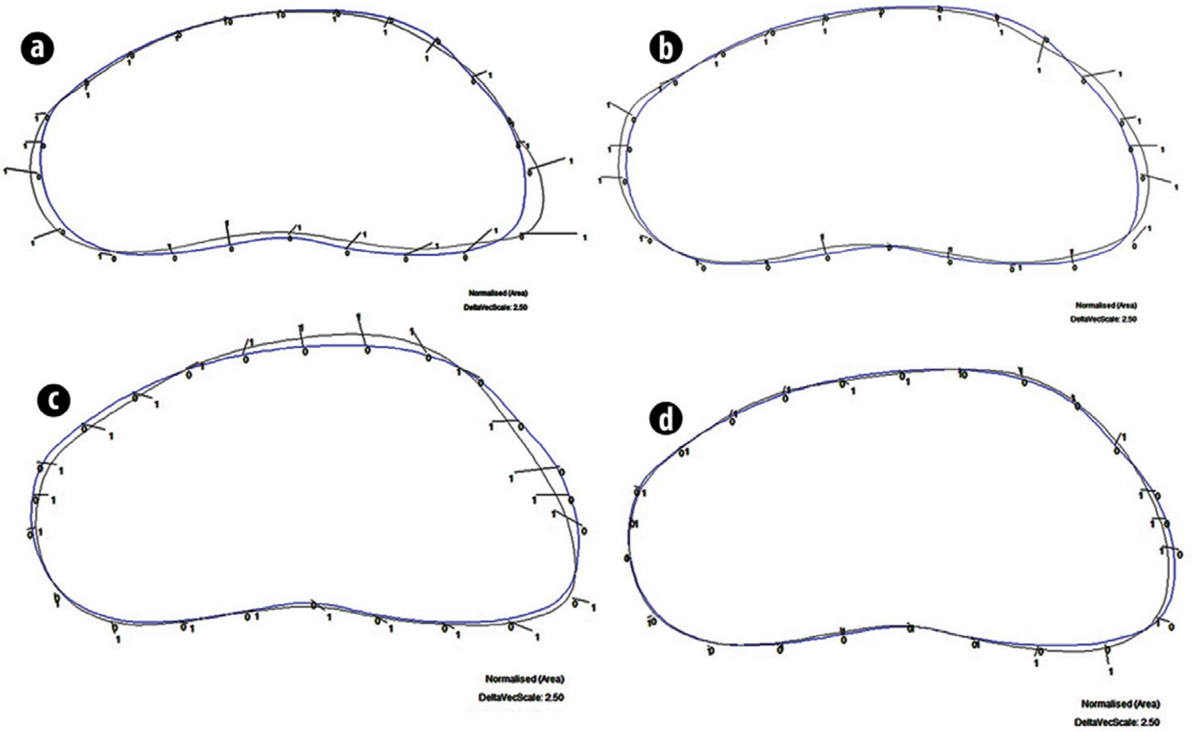


Fig. 37. A - Superimposition of outlines of the female RV on the Virtual Profile of *F. tricicatricosa,* derived from the set of 11 outlines in standardised for equal surface algorithm (0), *F. caudata,* consensus outline of the Lake Geneva-PetitLac sample (1); **B** – Virtual Profile outline of *F. tricicatricosa* as in **A** (0), *F. siliquosa,* from Fig. **40C**, p. 101, in Henderson, 1990 (1); **C** - Virtual Profile outline of *F. tricicatricosa* as in **A** (0), *F. levanderi* consensus outline of the Lake Serwy (1); **D** - Virtual Profile outline of *F. tricicatricosa* as in **A** (0), *C. neglecta* consensus outline of the Lake Serwy (1).

Figure 36 B shows that when we superpose on the virtual taxonomic harmonised outline of *F. tricicatricosa* in standardised for equal surface (using the subroutine of MORPHOMATICA) of the allotype RV of Diebel and Pietrzeniuk (1969) we note strong similarities of the 2 shapes. A slight divergence occurs between the virtual outline as reference and the mean outline of the Zauschwitz population namely the postero-ventral section is more inward placed pointing out to the larger curvature of this latter morphotype but this remains in the range of the shape differences observed for various populations of *Ft*. Figure 36 C is a confirmation for the similarity between Schornikov's valve of Krasnyj Yar and the European morphotypes while the more elongated and postero-ventrally pointed outline of Lenz *et al.* (2012) is also here in a comparative way well visible.

Finally one can see in Fig. 36 D that the two southern fossil morphotypes of Sokač (1978) and Krstić (2006) display stronger posterior differences as compared to the virtual-standard outline of *F. tricicatricosa*.

It is important now to draw a distinction between the virtual-standard outline of *Ft* and related taxa of our conceptual system. Figure 37 A point out to the distinction between the reference outline and the consensus outline of *F. caudata*, the population from lake Geneva (this one is the original place from where Kaufmann (1900) described this species). We note on the superposition representation of the two outlines that the latter species is more elongated and pointed in the ventral third of the posterior section; it is more arched, surpassing the straight section of *Ft,* slightly in the area of d1-d2 and strongly in the CP d3-d5 section.

Figure 37 B confirms the main diagnostic trait offered by Brady (1910) for *F. siliquosa*, namely a widely round posterior margin as compared to the virtual *Ft*. As with *F. caudata* the valve is more elongated surpassing on both sides, anterior and the posterior ones the reference outline of *Ft*. Continuing with Fig. 37 C we note the strong distinction between the virtual *F. tricicatricosa* and the mean outline of *F. levanderi* from Lake Serwy. Finally, Fig. 38 D documents the near shape superposition between the reference *Ft* and the consensus outline of *C. neglecta* from Lake Serwy.

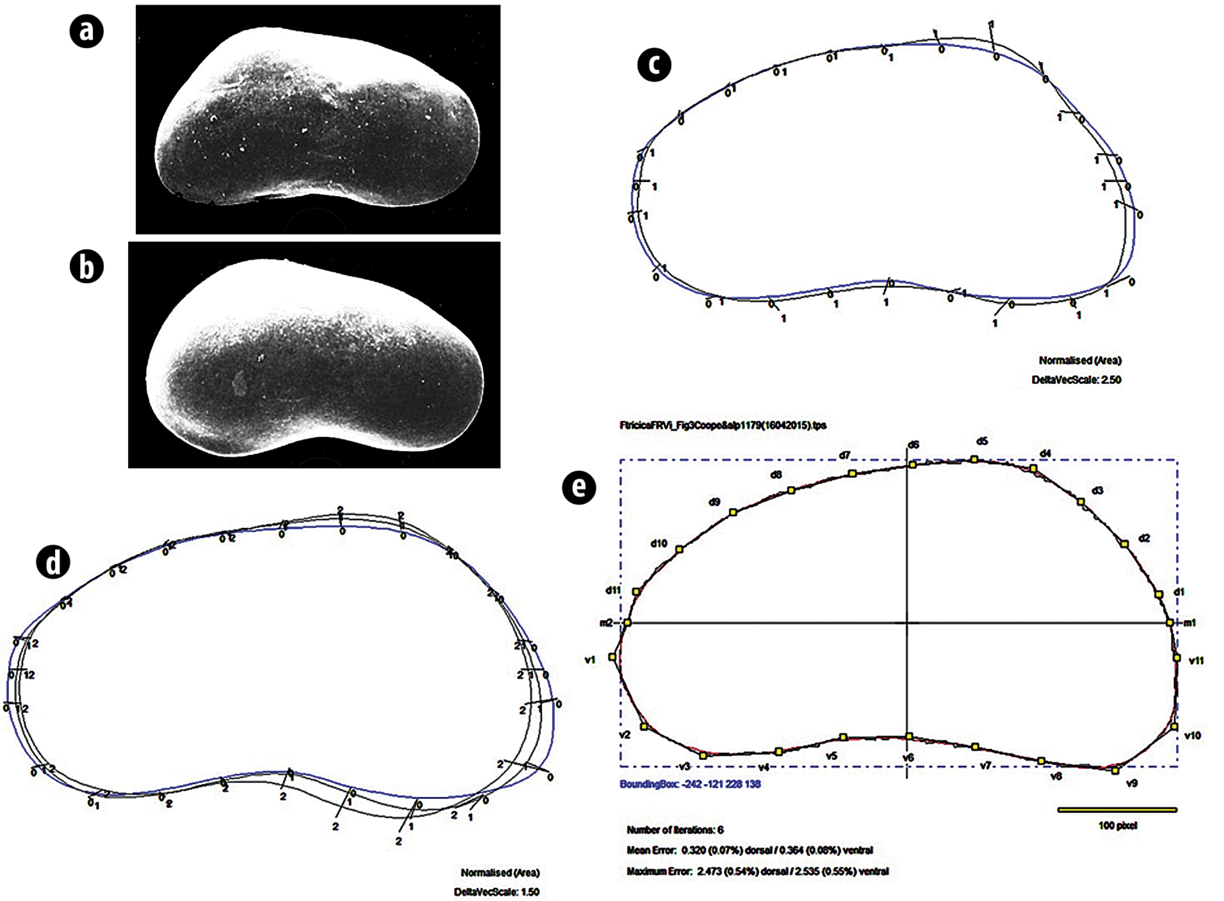


Fig. 38. *F. tricicatricosa*, **A** – female RV; **B** – male RV (from Robinson, 1990, Pl. 1, Figs. **11a**, **11b**); **C** - Superimposition on the female RV of the Virtual Profile of *F. tricicatricosa,* derived from the set of 11 outlines in standardised for equal surface algorithm (0) of the female RV of Robinson's figure **11b** (here **A**) (1); **D** – superposition on the consensus outline of 28 male RV of *F. tricicatricosa* from the sample MO-05-2E (0), the consensus outline of *C. neglecta* of 25 male RV from the sample MO-05-2E (1) and the Robinson's male outline from Fig. **11a**, here **B** (2); **E** - *F. tricicatricosa* female RV from Coope *et al.* 1997, Fig. **9-3**, in reversed view and within bounding box.

In conclusion, the virtual-standard profil of *Fabaeformiscandona tricicatricosa* is an excellent tool for reference of species when no type material is available. It offers comparative information which helps further to improve the taxonomy of given species. Below we present this aspect.

B. TAXONOMIC PROBLEMS

The taxonomic harmonisation procedure of *Fabaeformiscandona tricicatricosa* allows us now to address solutions to two practical taxonomic questions related to this species.

a. Fabaeformiscandona tricicatricosa as Consensus Species

For the present study of *F. tricicatricosa* we used as identification criteria a combination of aggregate traits (e.g. average or consensus outline-shape) combined with qualitative traits (e.g. the shape and position of the ledge). We propose to name such a defined taxon Consensus Species. To distinguish a Consensus Species by name from the classic Linnean species we propose to extend the nomenclature by adding *sensu lato* in breackage after the species name.

The Consensus Species concept as proposed here for *Ft* differs slightly from the Ecological Species concept of van Valen (1976, p. 233). This latter author coined the term Ecological Species for "a lineage which occupies an adaptive zone minimally different from that of any other lineage, and which evolves separately from all lineages outside its range".

Ft as Consensus Species, differs epistemologically from the Ecological Species concept of van Valen (op. cit.) because the ecological valence of our species here analysed is much wider than those of the related species *F. caudata*. The former species lives in different adaptive zones, like the littoral and in the profundal zones of lakes with prevailing cold water characteristics. It differs from *F. caudata* which occurs only in the littoral-sublittoral habitats of lakes. Therefore, there is a partial overlapping of ecological properties with *F. caudata* and only a part of the ecological range is specific to *Ft*. Therefore, in our opinion, it does not exactly cover the requirements of the Ecological species concept of van Valen (1976). Consensus Species differs from the Phylogenetic Species concept of Rosen (1979). This author sees geographically constrained groups of individuals characterised by unique apomorphous traits, as the unit of evolutionary significance. Other specialists like Racovitza (1912) and/or Nelson and Platnick (1981) define evolutionary species as simply the smallest sample of self-perpetuating organisms that have a unique origin and unique sets of characters which are kept during long periods of time. Such species, following their supporters, are historical entities (see, for more discussion, Wilkins, 2011).

It is important to note that the systemic approach we use here is not completely new. We find already in the publications of Nicolae Botnariuc (*e.g.* Botnariuc, 2003) the idea that species belong to, both a taxonomic hierarchy, and to a general systemic hierarchy, as an organizational unit of living mater. Danielopol and Cristescu (2015) and Danielopol and Tabacaru (2015) offered a review of these ideas and stressed out that species in the Botnariuc's conception is a system unit, something that resembles the views presented here. Therefore defining species based on systems theory merits in the future more scrutiny.

We have also to mention the evolutionary genetic concept used by ostracodologists like Koen Martens, Isa Schön and their colleagues. Working with biological molecular techniques which are able to reconstruct the evolutionary pathways of present living ostracods belonging to various *Bennelongia* ostracod-populations the above mentioned colleagues proposed to consider the divergent *Bennelongia* groups as evolutionary genetic species (*cf.* Martens *et al*., 2013).

Finally, it appears that the Consensus Species concept, as here documented for *F. tricicatricosa,* will find many applications especially in the case of ostracods species where molecular biology techniques are not available or as in the case of fossil species where a robust taxonomy is needed. The Candoninae data (*Camptocypria* sp., *Caspiocypris* ex gr. *alta*) presented by Stoica *et al*. (2016) come to our mind as potential examples for future research using procedures of taxonomic harmonisation, as here demonstrated.

b. Taxonomic confusions - Proposals for remediation

b.1. Confusion of F. tricicatricosa with F. caudata

Danielopol and colleagues who studied the living and subfossil ostracod fauna of Mondsee mentioned *F. caudata* as an inhabitant of the lake at deep sites (*cf.* Danielopol *et al*., 1988, 1993; Danielopol and Casale, 1990). It is now well demonstrated that this species lives in littoral-sublittoral habitats, generally to depth less than 30 m deep (*cf.* Decrouy *et al.*, 2012 for Lake Geneva (Petit-Lac) in Switzerland, Fuhrmann, 2012 for various lakes in Germany, Namiotko *et al.*, 2015 for Lake Mondsee, in Austria).

The confusion of Danielopol and co-authors (op. cit.) is due to the fact that in lake Mondsee both species, *F. caudata* and *Ft* co-occur. This latter species presents morphotypes which resemble the shape of the former species, namely there are female-valves with more elongated and pointed postero-ventral shapes. However when we compared the mean-shape of the female RV of *Ft* with those of *F. caudata* we noted clear differences as mentioned above.

b.2. Confusion of F. tricicatricosa with species of the complex Candona group neglectoida

We showed above that the outlines of the left and the right valves of *Ft* only slightly diverge from *C. neglecta* from Lake Serwy. Therefore to separate the quasi-homeomorphic valves of *Ft* and *C. neglecta* it appears necessary to apply the criterion of the presence or absence of the posterior ledge existing at *Ft* as earlier discussed.

Robinson (1990) who studied Middle Pleistocene (Cromerian age) at Little Oakley, Essex identified the candonines here figured as Fig. 38 A (female RV) and Fig. 38 B (male RV) as *F. lozeki*. Using the superposition technique of MORPHOMATICA and the virtual outline of *Ft (sensu lato*) (see Fig. 38 C) we recognise that the Robinson's *F. lozeki* belongs to a *Candona* sp. *ex gr. neglecta*. The female RV of Robinson displays a H/L ratio of 54.4% and the angle between the posterior segments d3-d4 and d4-d5 represents about 125°. *F. tricicatricosa* is more elongated displaying a H/L ratio of about 50% to 52% and the homologue dorso-posterior angle is about 160°. Considering the male RV (Fig. 38 B) we used the consensus outline of *F. tricicatricosa* from the sample MO-052E derived from 28 valves and the mean outline of 25 male-outlines of *C. neglecta* from the same site and sediment section as *Ft*. The displays of Fig. 38 C and Fig. 38 D confirm clearly our original hypothesis that the Robinson's candonids belong to *Candona* and more specially to the *neglectoida* species complex.

Coope *et al.* (1997) identified *Ft* in Pleistocene samples from the channel of river Thames at London. When the Coope's valve is displayed within a bounding box (Fig 38 E) we note that the H/L is 55%, a value commonly found for species of *Candona* belonging to the *neglectoida*-complex. The posterior margin within the section d1-d3 is externally bended the maximal curvature is at about 30% of the maximal height. We conclude that the material identified as *Ft* in Coope *et al.* (op. cit.) belongs to a taxon closely related to *C. neglecta*.

b.3. Unnecessary assignment of Fabaeformiscandona tricicatricosa to other generic taxa

The taxonomic name *Ložecandona* was first mentioned in Krstić (2003), as *nomen nudum* for a subgenus of *Candona*. In Krstić (2006, p. 169) *Ložecandona* is considered as genus and got a short diagnosis. Following its author *Ložecandona* should include *F. levanderi, F. lozeki* and *F. tricicatricosa*. The main diagnostic character mentioned by Krstić (2006) is inconclusive, namely she considers as the distinctive generic trait the presence of a posterior ledge (either on the left valve or on both valves), an argument already used by Krstić (1972) for *Fabaeformiscandona* Krstić. The two genera of Krstić *(i.e. Fabaeformiscandona* and *Ložecandona)* are placed in a tribus Varicandonini Krstić and Guan, 2000, beside the genus *Varicandona* Sywula, 1970. This latter genus has as generotype the species *F. protzi* (Hartwig). Sywula (1974) in his monograph of the Polish ostracods and for species like *F. protzi, F. levanderi* etc. discarded the genus *Varicandona* and adopted a taxonomic solution similar to those of Klie (1938), namely the genus *Candona* contains various subgenera. For the species-groups *fabaeformis* and *acuminata*, Sywula used as a subgenus the taxonomic name *Eucandona* proposed by Daday (1900). However this latter taxon even in its revised version of Karanovic (2006) remains invalid. J. Daday in his monograph *Ostracoda Hungariae* (1900, pp. 242-248) refers for the new genus *Eucandona* as first species, what now is called *Pseudocandona rostrata* (Brady and Norman, 1889). Because no type species for *Eucandona* was proposed, the ICZN Code (version 2000) sees in the article 67.2.2, the fixation of type species prior 1930 the first species mentioned in the new genus. But as this latter species is misidentified we have to consider *Eucandona* as an invalid genus and for stability of the taxonomic system of Candoninae it is better to continue to use the long year established name *Fabaeformiscandona* which appears in standard taxonomic synthesis like the Meisch's "Freshwater Ostracoda of Western and Central Europe" (Meisch, 2000) and those of Martens and Savatenalinton (2011).

C. ON THE ORIGIN AND THE GEOGRAPHIC DISTRIBUTION OF *FABAEFORMISCANDONA TRICICATRICOSA* (SENSU LATO)

It was repeatedly documented that *Ft* prefers psychrophilic habitats (Absolon, 1973, p. 88; Fuhrmann and Pietrzeniuk, 1990a, p. 177; Meisch, 2000, p. 118; Fuhrmann, 2012, p.72, Namiotko *et al.*, 2015). Figures 39 and 40, as well as Appendix 1, offer an overall view on the geographic records we could find in the literature concerning *Fabaeformiscandona tricicatricosa*. This information, synthesized for the first time here, will allow to construct an alternative hypothetical scenarios for the origin and dispersion of this species.

The data of Schornikov (2008) and Wetterich *et al.* (2009) from northern Siberia as well as the more recent data of Lenz *et al.* (2012) from a western Canadian Arctic lake confirm this ecological situation. However this species was found also in the Eemian interglacial at Gröbern in Central Germany (Saxony) during warmer climatic conditions (*cf.* Fuhrmann and Pietrzeniuk, 1990a). These authors explain this exception to the above mentioned pattern through the preferential distribution of the species in the hypolimnion of a palaeo-lake where water-temperature was "cooler" than those of the epilimnion.

In Central Europe *Ft* colonises deep lakes on both sides of the Alps, on the northern part one should mention Starnbergersee, Ammersee, Mondsee and on the southern side Überlingersee, a subsidiary of lake Constance (for a more detailed bibliography, *cf.* Absolon, 1978, Fuhrmann and Pietrzeniuk, 1990b, Meisch, 2000, Fuhrmann, 2012).

More interesting is the presence of *Ft* during Middle Pleistocene in Croatia, at two localities in the Slavonia, south-east from Zagreb (Sokač, 1978). The presence here of psychrophilic species is interpreted by Sokač, (1978, p. 39) as following: "the appearance of the "cold forms" mentioned here points to the conclusion that the climate was colder than at present". This hypothesis is confirmed by the results of Banak *et al*. (2015) who used isotopic analysis on the calcite of terrestrial gastropods of Eastern Croatia in an area located close to those investigated by Sokač (1978). Nowadays, because *Ft* does not exist anymore in this area, one could hypothesize that this species spread from the northern areas of Europe during a cool climate periods and retired or got locally extinct once the climate during the Holocene improved. Beside Faranda and Gliozzi (2011), Martínez-García *et al.* (2015) offered such examples of marine ostracods which expanded southward their distribution, during the Late Pleistocene along the coast of Western Europe.

The most remarkable occurrence of *Ft* is that mentioned by Krstić (2003) and Krstić (2006) in Serbia (Vojvodina). The species occurs as fossil in the Upper Paludinian beds, in the Southern Bačka trough, dated as Upper Pliocene-Lower Pleistocene (the *Ilyocypris malezi* zone). These deposits correspond apparently to a warm/temperate stage (Nenadić and Gaudenyi, 2013). This site represents the most southern occurrence of *Ft* and needs an explanation. Interesting enough, Danielopol *et al*. (1990) mentioned that the present-day psychrophilic species *Cytherissa lacustris* Sars occurred in the Lower Pleistocene in the Megalopolis Basin (Northern Greece), while now it exists in central and northern Holarctic zones. Coming back to *Ft* we showed here that it presents morphologic similarities with the late Middle Miocene species *Fabaeformiscandona gratkornensis*, therefore, the presence of Ft at the end of the Pliocene in the Paludina Lake in Serbia could indicate the existence of wider thermic ecological preferences and, possibly, a wider geographic distribution prior to the specialisation to the psychrophilic environment of the Quaternary in the Central and Northern part of the Palaearctic.

Griffiths *et al.* (1998) for their present-day Arctic species *Tonnacypris glacialis* proposed the following scenario: this Eucypridini belongs to a lineage which was during the optimal warm/temperate climate widely extent in Europe. It adapted during the Middle Pleistocene to cold water habitats existing in the northern part of the Holarctic. This species had "the ability to track advancing and retreating ice-masses throughout Pleistocene glacial and interglacial cycles…" (*cf.* Griffiths *et al.*, op. cit., page 523). This scenario fits well *Ft*, too which exists, now, in areas, formerly, covered by glaciation. It presupposes, as in the case of *T. glacialis*, a rapid spread during the Middle-Upper Pleistocene in Central and Northern Europe, as well as in Siberia and the Arctic Canada (Figs. 39, 40).

In the scenario proposed for the origin and dispersion of *T. glacialis*, Griffiths *et al*. (1998) mentioned the possibility of local morphological differentiation as a microevolutionary process leading to Arctic endemic fauna. Even if the arguments were not strong enough for the *Tonnacypris* species, this aspect deserves to be discussed for *Ft*. As mentioned above, Fuhrmann (2012) foresaw the existence of closely related taxa to *Ft*, namely *F. lozeki* spread in the southern part of Germany (Bavarian deep lakes) as a different taxon from *Ft* represented in the northern part of this country, namely in Saxonia.

Bellati *et al.* (2014) showed that lakes in the alpine zone and peri-Alps areas were colonised during the Pleistocene by Cladocera from different sources, one boreal and another one from refugial populations that survived in southern parts of Europe. Once they adapted to cold waters they expanded northwards rapidly their territories. The scenario of Bellati *et al*. (2014) could apply to *Ft* too, meaning that we had for the present geographic distribution of two different sources, one coming from the southern Europe towards Central and northern Europe, during an initial phase of colonisation and a second one, during the 2nd part of the Pleistocene from the northern part of the Palaearctic towards Central Europe in one direction and towards the northern part of the Nearctic as second route of migration. It is, especially, this latter dispersal history of interest for palaeoecologists because it allows to reconstruct the thermic evolution of various continental areas during the Pleistocene and the Holocene.

CONCLUSION

(**1**) In order to realise the successful taxonomic harmonisation (TH) process of *Fabaeformiscandona tricicatricosa* for populations represented by both fossil and living individuals, we agreed with the idea of a species concept reflecting a collective ecological identity and recognisable through aggregate traits, like an average shape profile of the valves, as well as through qualitative specific traits. We call it Consensus Species and we suggest continuing to use the traditional Linnean system, but with the extension *sensu lato* added to the species' name. With this concept we want to convey a message that we will express with a quotation from Claridge (2010, p. 105): "We need broadly applicable species concepts and the existing Linnean system of nomenclature, certainly for species names."

(**2**) The best diagnosable morphological traits applied for the TH of *Ft* are those visible on the female RV. This means that we used traits existing on the majority of specimens and/or are, practically, expressed by mean values. Hence, we favoured a Gaussian procedure where outliers were discarded.

(**3**) For the success of the TH of *Ft* it was important to get a morphological profile of the valves using quantitative relational procedures at intra- and interspecific levels. The outline obtained resembles those of the allotype, as originally described by Diebel and Pietrzeniuk, 1969, (Fig. 36 A and B). Therefore, a "consensus virtual profile" can be helpful when no information on the material type exists.

(**4**) For the identification of *Ft*, the Wittgenstein principle of "family resemblance", where only a part of the traits belonging to the species-diagnosis are used, represents a realistic solution.

(**5**) TH implies, also, the critical adoption of the taxonomic system with a wide scientific acceptance by the scientific community. In the case of *Ft*, this is the system of Meisch (2000) combined with those of Martens and Savatenalinton (2011), and in our case already used by Fuhrmann (2012).

(**6**) As a corollary of the TH a reassignment of various taxa misidentified as *Ft* were corrected.

(**7**) Taxonomic Harmonisation, is, in our opinion, an „onerous concept". We paraphrase here the dictum of G.W. Williams (1966, p. 4) on adaptation as an onerous concept, which should be used only where it is really necessary. We consider TH an "onerous concept" because it requires time and energy for competent ostracodologists to produce efficient protocols for the practical identification of species which have potential applications in (palaeo)environmental and/or (pal-

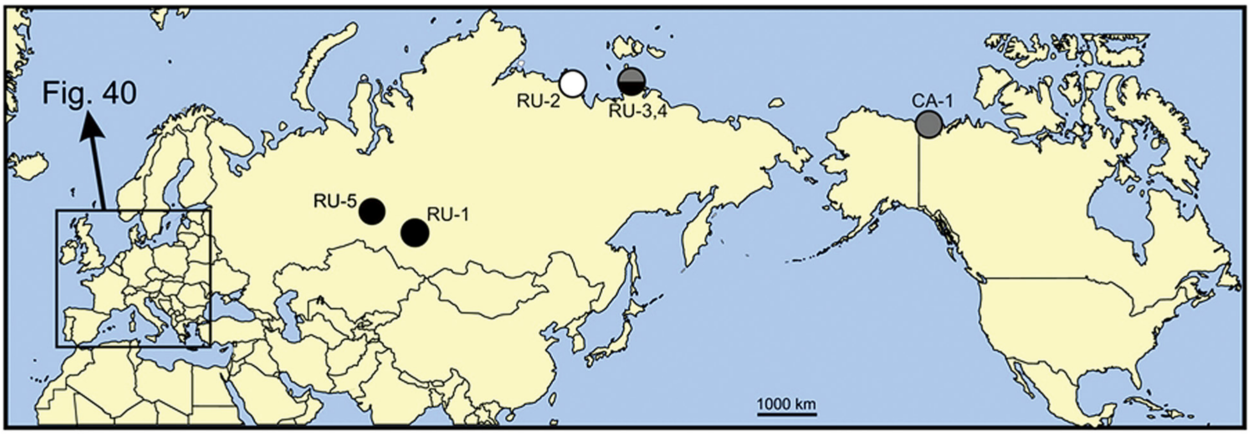


Fig. 39. Modern and fossil extra-European occurrence of *F. tricicatricosa*. White circles = modern and subfossil (historical AD) records, grey circles = Holocene to Late Glacial Maximum records (ca. < 13 000 BP), black circles = Pleistocene records (13 000 – 2 588 000 BP). For details of site designation numbers see Appendix. Figure based on maps downloaded from d-maps.com (*http://www.d-maps.com/carte.php?num_car=18420&lang=en* and *http://www.d-maps.com/carte.php?num_car=125466&lang=en*).

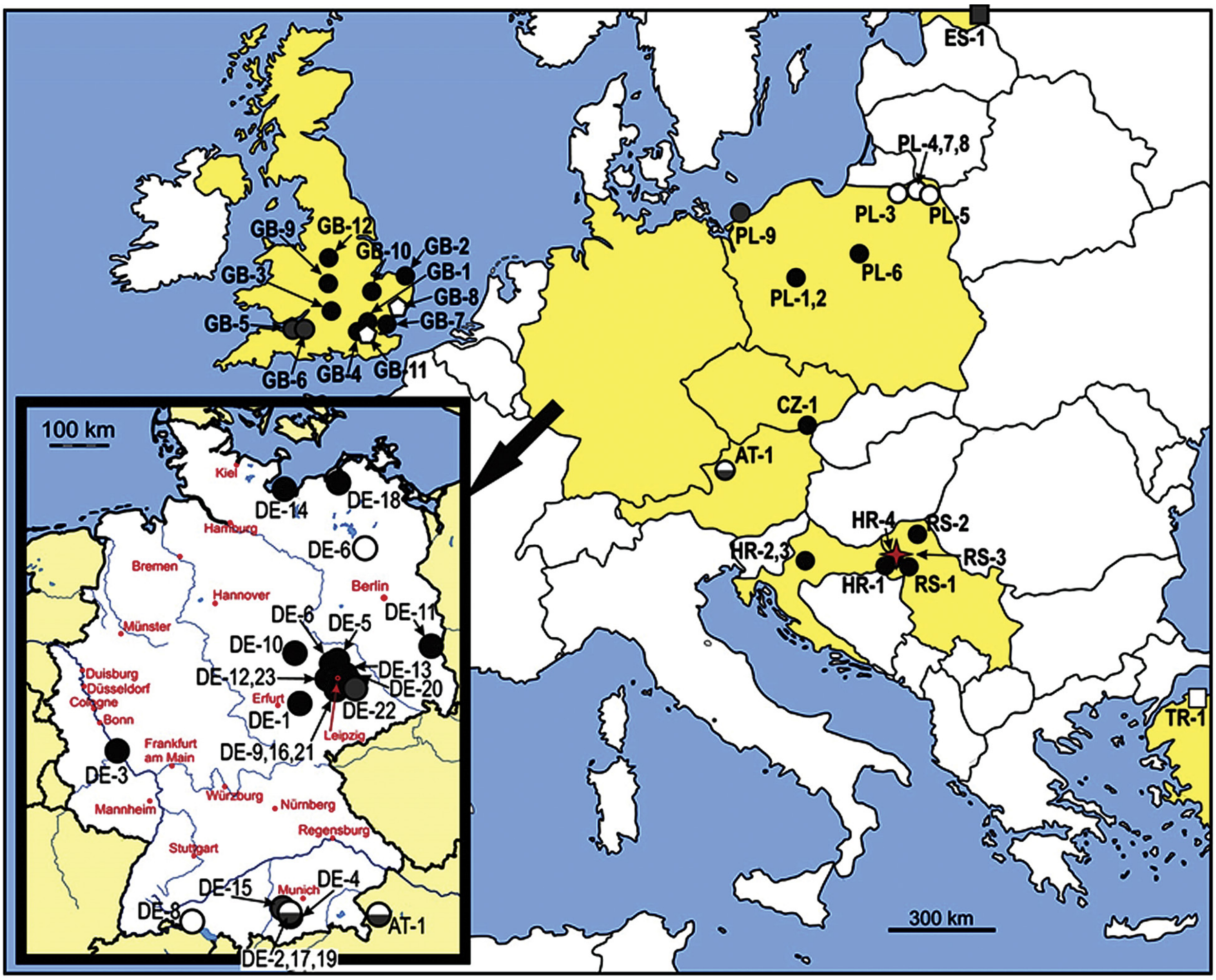


Fig. 40. Modern and fossil occurrence of *F. tricicatricosa* in Europe. White circles = modern and subfossil (historical AD) records, grey circles = Holocene to Late Glacial Maximum records (ca. < 13000 BP), black circles = Pleistocene records (13 000 – 2 588 000 BP), red star = Pliocene record; white pentagons = dubious records (see text for details); white squares = possible records. For details of site designation numbers see Appendix. Figure based on maps downloaded from d-maps.com (*http://www.d-maps.com/carte.php?num_car=2254&lang=en* and *http://www.d-maps.com/carte.php?num_car=14456&lang=en*).

aeo)biogeographic research. This activity, if well done, will be rewarding as we perceive from various ecologic and/or socio-economic projects where "Harmonisation" procedures were successfully implemented offering huge advantages for consensual communication.

(**8**) Finally, the experience we gathered with the TH of *Ft* convinced us that the success of other similar projects depends on the capacity of students to work within a pluridisciplinary context and to permanently discuss their results. Nowadays, this approach can be effectively implemented using modern media-technologies. In this way, our study will be profitable to a wide group of ostracodolgists.

ACKNOWLEDGEMENTS

We dedicate this contribution to our colleague and friend Dr. Radu Olteanu who left us at the end of this year. R. Olteanu contributed substantially to the advancement of our knowledge of the ostracods from the Eastern and Central Paratethys domains. L.P. acknowledges a post-doctoral scholarship from the University of Fribourg to work in the Benthos-laboratory of D.L.D at the Limnology Institute, in Mondsee. The project received support from the Austrian Science Fund (projects P17738-B03 and PI35-B06 to D.L.D.) and is a spinoff of a pluridisciplinary study, within the framework of the European Science Foundation, EUROCORE, Programme EUROCLIMATE (contract No. ERAS-CT-2003-980409 of the European Commission, ESF-project DecLakes) and of the FWF-Project 21748-N21 (*Cyprideis*-Project, attributed to M. G.). We thank the following for technical help: J. Knoblechner, A. Danielopol, A. Stracke, G. Roidmayr, L. Eisl, K. Maier, R. Niederreiter, B. Lahnsteiner (Mondsee), L. Namiotko (Gdansk). Prof. W.E. Piller (Graz) gave logistical support during the last years. We thank, also, for discussion: W.E. Piller, A. Baltanás (Madrid), D.J. Horne (London), A. Lord (Frankfurt-Main), A. Brauer and S. Lauterbach (Potsdam), R. Schmidt (Mondsee), A. Jagsch (Scharfling) and R. Smith (Oroshimo). Finally, we are much indebted to the editors of Geo-Eco-Marina, D. Jipa, N. Panin and C. Vasiliu (all, Bucharest), as well as to the three reviewers of the MS.

APPENDIX 1

Modern and fossil occurrences of *Fabaeformiscandona tricicatricosa* (Diebel and Pietrzeniuk)

The compilation consists of two listings, separately for extra-European and for European records, which are built-up on a country-by-country basis in national alphabetical order. Within the accounts for each country, records are listed in the order of a year of publication. The stratigraphical age of samples, unless otherwise stated, follows division of Quaternary by the International Commission on Stratigraphy in the *Global chronostratigraphical correlation table for the last 2.7 million years* (http://www.stratigraphy.org/upload/QuaternaryChart.pdf): Holocene 0-0.0117 Ma, Late Pleistocene 0.0117-0.126 Ma, Middle Pleistocene 0.126-0.781 Ma and Early Pleistocene 0.781-2.588 Ma. Site code numbers refer to locations shown in Figs. 39 and 40. Abbreviations: CA – carapace, D – dorsal view, DRA – line drawings, F – female, I – inner view, LV – left valve, M – male, O – outer view, RV – right valve, RLM – reflected light microscopy picture, SEM – scanning electron microscopy picture; TLM – transmitted light microscopy picture (*e.g.*, SEM FLVO = scanning electron micrograph of a female left valve in outer view).

NON-EUROPEAN RECORDS

Canada

CA-1: Herschel Island, Yukon – Holocene (Lenz *et al.*, 2012: Fig. 1a2 – SEM FLVO, Fig. 1a3 – SEM FRVO)

Russia

RU-1: Krasnyy Yar, 80 km SW of Tomsk, Tomsk Oblast – Late Pleistocene (Schornikov, 2008: Fig. 14 – SEM FRVO, Fig. 15 SEM MLVO)

RU-2: Samoylov Island, Lena River Delta, Sakha (Yakutia) Republic – modern (Wetterich *et al.*, 2008: as *Fabaeformiscandona* cf. *tricicatricosa*, no pictorial documentation)

RU-3: Bol'shoy Lyakhovsky Island and Oygos Yar on the shore of the Dmitry Laptev Strait, Sakha (Yakutia) Republic – Late Glacial/Holocene and Late Pleistocene (Wetterich et *al.*, 2009: Fig. 13 – SEM FLVO, Fig. 14 – SEM FRVO, Fig. 15 – SEM MLVO, Fig. 16 – SEM MRVO)

RU-4: Oygos Yar on the shore of the Dmitry Laptev Strait, Sakha (Yakutia) Republic – Late Pleistocene (Kienast *et al.*, 2011: Fig. 11 – SEM FLVO, Fig. 12 – SEM FRVO, Fig. 13 – SEM MLVO, Fig. 14 – SEM MRVO)

RU-5: Irtysh River (no more details) – Late Pleistocene (V.A. Konovalova personal comm. to DLD on 5.11.2015 and forthcoming: SEM FLVI).

EUROPEAN RECORDS

Austria

AT-1: Lake Mondsee, Upper Austria – modern, subfossil (historical AD) and Late Glacial to Holocene (Danielopol *et al.*, 1985, 1988 1993 and Yin and Geiger, 1995: as bisexual populations of *Fabaeformiscandona caudata*, no pictorial documentation; Baltanás *et al.*, 2003: as *Fabaeformiscandona lozeki*, no pictorial documentation; Stracke *et al.*, 2008: as *Fabaeformiscandona lozeki*, Fig. – TLM of FLVO, FRVO, MLVO and MRVO; Namiotko *et al.*, 2009 and Namiotko *et al.*, 2015: no pictorial documentation; new data)

Croatia

HR-1: Strizivojna (Borehole V-4), Osijek-Baranja County, Slavonia – Pleistocene (stage not specified) (Sokač, 1978: as *Candona tricicatricosa*, Plate XIII Fig. 5 – RLM FRVO, Fig. 7 – RLM FRVI)

HR-2: Prevlaka (Borehole OS-6), Zagreb County – Middle Pleistocene (Sokač, 1978: as *Candona lozeki*, no pictorial documentation)

HR-3: Prevlaka (Borehole OS-5), Zagreb County – Late Pleistocene (Sokač, 1978: as *Candona lozeki*, Plate XIV Fig. 5 – RLM FLVO, Fig. 7 – RLM FRVI, Fig. 9 – RLM FRVO)

HR-4: Erdut (Borehole DB-2), Osijek-Baranja County, Slavonia – Early Pleistocene (Sokač *et al.*, 1982: as *Candona lozeki*, no pictorial documentation)

Czech Republic

CZ-1: Bulhary, 10 km NW of Breclav, South Moravian Region – Middle Pleistocene (Absolon, 1973: as *Candona lozeki* n. sp., no pictorial documentation)

Estonia

ES-1: Lake Peipus – Holocene (Niinemets, 1999: Plate II Fig. 3 – SEM FLVO and Fig. 4 – SEM FLVI – listed as *Fabaeformiscandona levanderi*, possible record of *F. tricicatricosa*)

Germany

DE-1: Süssenborn, 5 km E of Weimar, Thuringia – Middle Pleistocene (Diebel and Pietrzeniuk, 1969: as *Candona tricicatricosa* sp. n., Text Fig. 6a – DRA FLVO, Text Fig. 6b – DRA FRVO, Text Fig. 6c – DRA FCAD, Plate VIII Fig. 4 – TLM FRVO, Plate VIII Fig. 5 – TLM FLVO, Plate VIII Fig. 6 – TLM FRVO; Absolon, 1978: as *Candona tricicatricosa*, Fig. 45 – DRA of FLVI, FLVD and FRVD)

DE-2: Seeshaupt on the southern shore of lake Starnberger See, 40 km SW of Munich, Bavaria – Late Holocene (Absolon, 1973: as *Candona lozeki* n. sp., Fig. 34a – DRA MLVI, Fig. 34b – DRA MRVI, Fig. 34c – DRA MLVD, Fig. 34e – DRA MCAD, Fig. 35a – DRA FLVI, Fig. 35b – DRA FRVI, Fig. 35c – DRA FLVD, Fig. 35d – DRA FCAD; Absolon, 1978: as *Candona lozeki*, Fig. 46 – DRA of FLVO, FRVO detail, FLVD, FRVD, MLVI and MLVD)

DE-3: Kärlich near Koblenz, Rhineland-Palatinate – Middle Pleistocene (Kempf, 1975: as *Candona tricicatricosa*, no pictorial documentation)

DE-4: Eurach near Penzberg, 50 km S of Munich, Bavaria – Late Pleistocene (Ohmert, 1979: as *Candona lozeki*, Fig. 16 – DRA broken FLVI, Fig. 17 – DRA broken FRVI, Fig. 18 – DRA MRVI)

DE-5: Gröbern, 12 km NE of Bitterfeld, Saxony-Anhalt – Late Pleistocene (Fuhrmann and Pietrzeniuk, 1990a: as *Candona tricicatricosa*, Plate 5 Fig. 1 – TLM FLVO, Fig. 2 – TLM FRVO, Fig. 3 – TLM MLVO, Fig. 4 TLM - MRVO)

DE-6: Grabschütz, 6 km SW of Delitzsch, Saxony – Middle Pleistocene (Fuhrmann and Pietrzeniuk, 1990b: as *Candona tricicatricosa*, Plate 3 Fig. 1 – TLM FLVO)

DE-7: Lake Stechlin, 15 km NE of Rheinsberg, Brandenburg – modern (Fuhrmann and Pietrzeniuk, 1990b: as *Candona tricicatricosa*, no pictorial documentation; new data)

DE-8: Überlingensee of Lake Constance, Baden-Württemberg – modern (Fuhrmann and Pietrzeniuk, 1990b: as *Candona tricicatricosa*, no pictorial documentation)

DE-9: Zauschwitz, 2 km N of Pegau, Saxony – Late Pleistocene (Fuhrmann and Pietrzeniuk, 1990b: as *Candona tricicatricosa*, no pictorial documentation; Griffiths *et al*., 1998: no pictorial documentation; Fuhrmann, 2012: Plate 30 SEM of 1× FLVO, 2× FLVI, 1× FRVO, 2× FRVI, 2× MLVI)

DE-10: Schadeleben and Königsaue, 11 km NW of Aschersleben, Saxony-Anhalt – Late Pleistocene (Fuhrmann and Pietrzeniuk, 1990b: as *Candona tricicatricosa*, no pictorial documentation; Griffiths *et al*., 1998: no pictorial documentation)

DE-11: Cottbus-Nord, 11 km NE of Cottbus, Brandenburg – Middle/Late Pleistocene (Fuhrmann and Pietrzeniuk, 1990b: as *Candona tricicatricosa*, no pictorial documentation; Fuhrmann, 2012: no pictorial documentation)

DE-12: Neumark-Nord, 8 km SW of Merseburg, Saxony-Anhalt – Middle to Late Pleistocene (Fuhrmann and Pietrzeniuk, 1990b and 1990c: as *Candona tricicatricosa*, no pictorial documentation; Fuhrmann, 2004; Fuhrmann, 2006; Fuhrmann and Pietrzeniuk, 2010; Fuhrmann, 2012: no pictorial documentation)

DE-13: Wildschütz, 13 km E of Eilenburg, Saxony – middle Holocene (Fuhrmann, 1991: as *Candona tricicatricosa*, no pictorial documentation)

DE-14: Klein Klütz Höved, Bay of Mecklenburg, Mecklenburg-Vorpommern – upper Middle Pleistocene (Strahl *et al*., 1994: as *Candona tricicatricosa*, no pictorial documentation)

DE-15: Lake Ammersee, 30 km SW of Munich, Bavaria – Holocene (von Grafenstein *et al*., 1994 and 1996 as *Candona tricicatricosa*, no pictorial documentation; von Grafenstein *et al* 1999a: no pictorial documentation)

DE-16: Grossstorkwitz, 2 km N of Pegau, Saxony – Late Pleistocene (Griffiths, 1995; Griffiths *et al*., 1998 and Fuhrmann, 2012: no pictorial documentation)

DE-17: Lake Starnberg, 40 km SW of Munich, Bavaria – modern and Holocene (von Grafenstein *et al*., 1999b: no pictorial documentation; new data)

DE-18: Tessin near Rostock, Mecklenburg-Vorpommern – Late Glacial (Krienke *et al*., 1999: as *Candona tricicatricosa*?, no pictorial documentation)

DE-19: Roseninsel in Lake Starnberg, Bavaria – Holocene (Fuhrmann, 2009: as *Fabaeformiscandona lozeki*, no pictorial documentation)

DE-20: Mahlis, 10 km SW of Oschatz, Saxony – Middle Pleistocene (Fuhrmann, 2012: no pictorial documentation)

DE-21: Schleenhein, 10 km W of Borna, Saxony – Middle Pleistocene (Fuhrmann, 2012: no pictorial documentation)

DE-22: Döbeln-Gärtitz, Saxony – Middle Pleistocene (Fuhrmann, 2012: no pictorial documentation)

DE-23: Neumark-Süd, 10 km SW Merseburg, Saxony-Anhalt – Middle Pleistocene, Late Pleistocene and Holocene (Fuhrmann, 2012: no pictorial documentation)

Poland

PL-1: Poznań-Główna, Greater Poland Voivodeship – Late Pleistocene (Sywula and Pietrzeniuk, 1989: as *Candona lozeki*, Plate LVIII Fig. 5 – TLM MLVO, Fig. 6 TLM MRVO)

PL-2: Poznań-Szeląg, Greater Poland Voivodeship – Late Pleistocene (Sywula and Pietrzeniuk, 1989: Plate LVIII Fig. 3 – TLM FLVO, Fig. 4 TLM FRVO)

PL-3: Lake Rospuda Filipowska, 25 km NW of Suwałki, Podlaskie Voivodeship – modern and subfossil (historical AD) (Namiotko, 1995 and Namiotko and Sywula, 1997: as *Candona (Eucandona) lozeki*, no pictorial documentation; new data)

PL-4: Lake Szelment Wielki, 15 km N of Suwałki, Podlaskie Voivodeship – modern and subfossil (historical AD) (Namiotko and Sywula, 1997: as *Candona (Eucandona) lozeki*, no pictorial documentation; Namiotko *et al*., 2012: no pictorial documentation; new data)

PL-5: Lake Wigry, 15 km SE of Suwałki, Podlaskie Voivodeship – subfossil (historical AD) (Namiotko and Namiotko, 2004: as *Eucandona lozeki*, no pictorial documentation; Namiotko *et al*., 2004: as *Fabaeformiscandona lozeki*, no pictorial documentation)

PL-6: Leszczyno, 15 km NE of Płock, Mazovian Voivodeship – Late Pleistocene (Krupiński *et. al*., 2006: as *Candona lozeki*, no pictorial documentation)

PL-7: Lake Szurpiły, 15 km N of Suwałki, Podlaskie Voivodeship – subfossil (historical AD) (Namiotko *et al*., 2012: no pictorial documentation)

PL-8: Lake Kameduł, 20 km N of Suwałki, Podlaskie Voivodeship, Poland – subfossil (historical AD) (Namiotko *et al*., 2012: no pictorial documentation)

PL-9: Pomeranian Bay, Baltic Sea, Poland – Late Glacial to Holocene (Krzymińska and Namiotko, 2013: Plate IX Fig. 5 – TLM FLVO, Fig. 6 – SEM FRVO, Fig. 7 – TLM MLVO, Fig. 8 – TLM MRVO)

Serbia

RS-1: Bačka NE, Vojvodina – Middle Pleistocene (Krstić, 1988: as *Candona ložeki*, no pictorial documentation)

RS-2: Gornji Breg (K-5-S) near Senta, Vojvodina – Middle Pleistocene (Krstić, 1995: as *Lozekandona tricicatricosa*, no pictorial documentation)

RS-3: Bogojevo, 30 km S of Sombor, Vojvodina – Upper Pliocene (Krstić, 2003: as *Candona (Ložecandona) tricicatricosa*, no pictorial documentation, Krstić, 2006: as *Ložecandona ložeki*, Plate XX Fig. 10 – TLM FRVO)

Turkey

TR-1: Lake Uluabat, Bursa Province – modern (Altinsaçli and Griffiths, 2001: as bisexual populations of *Fabaeformiscandona caudata*, no pictorial documentation, possible record of *F. tricicatricosa*)

United Kingdom

GB-1: Westmill Pit, Vale of St. Albans, Hertfordshire, UK – Middle Pleistocene (Robinson, 1978a: as *Candona tricicatricosa* after Robinson, 1990; Griffiths, 1995: as *Fabaeformiscandona* cf. *tricicatricosa*, no pictorial documentation)

GB-2: West Runton, Norfolk – (Late)Middle Pleistocene (Robinson, 1978b: as *Candona tricicatricosa* after Robinson, 1990)

GB-3: Sugworth, Oxfordshire – Middle Pleistocene (Robinson, 1980: as *Candona tricicatricosa*, no pictorial documentation)

GB-4: Kempton Park, Sunbury, Surrey-on-Thames, UK – Late Pleistocene (Gibbard *et al*., 1981: as *Candona lozeki* after Griffith, 1995)

GB-5: Lower Weare, Somerset – Holocene (Willing, 1985: as *Candona lozeki* after Griffiths, 1995)

GB-6: Clapton, Somerset – Holocene (Willing, 1985: as *Candona lozeki* after Griffiths, 1995)

GB-7: Barling, Essex – Middle Pleistocene (Robinson, 1990: as *Candona tricicatricosa*, no pictorial documentation; Griffiths, 1995) – possibly dubious record: *F. tricicatricosa* not included in the updated ostracod list from the site by Bridgland *et al*. (2001)

GB-8: Little Oakley, Essex – Middle Pleistocene (Robinson, 1990: as Candona tricicatricosa, Plate 1 Fig. 11a – SEM MRVO, Fig. 11b – SEM FRVO; Bridgland *et al*. 1990: as *Candona tricicatricosa*, no pictorial documentation) – dubious record (see text for details)

GB-9: Waverley Wood Pit, Warwickshire – Middle Pleistocene (Robinson, 1990: as *Candona tricicatricosa*, no pictorial documentation; Shotton *et al*., 1993 after Griffiths, 1995)

GB-10: Woodston near Peterborough, Cambridgeshire – Middle Pleistocene (Horton *et al*., 1992: as *Candona* cf. *lozeki*, no pictorial documentation)

GB-11: Ismaili Centre, Central London – Late Pleistocene (Griffiths, 1995; Coope *et al*. 1997: as *Candona lozeki* synonymous with *Fabaeformiscandona tricicatricosa*, Fig. 9.3 SEM RVI) – dubious record (see text for details)

GB-12: Frog Hall Pit near Stretton-on-Dunsmore, Warwickshire – Middle Pleistocene (Griffiths, 1995; Keen *et al*., 1997: as *Fabaeformiscandona lozeki* synonymous with *Fabaeformiscandona tricicatricosa*, no pictorial documentation)

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