INTRODUCTION

C. Delamare Deboutteville (1957) in a lecture delivered to the French "Société de Biogéographie" noted that one of the aims of the "Actual biogeography" should be the reconstruction of natural histories of various animal lineages. Delamare Deboutteville (op. cit.) emphasised that the best way to achieve such a goal is through treating beside geographical information also data from other search directions like morphology, systematics, ecology and evolution. Our approach here is different, we will use geographical patterns of several species belonging to a non-marine ostracod group, the genus Cryptocandona Kaufmann (Candolinae, Candonidae, Cypridoidae), in order to better discuss the evolutionary problems related to morphological diversity, especially the disparity of the carapace shape, of these taxa.

The genus Cryptocandona Kaufmann, 1900 is an ostracod group, well defined by morphological traits of the limbs; the carapace is narrowly compressed, when seen in dorsal view, and the valves...
are weakly calcified and without ornamentation (Meisch 2000). Within the subfamily Candonaicæ it represents a primitive lineage, considering the fifth limb with three exopodal setae, the seventh limb with a seta on the second endopodal segment and a weekly internal sclerotised hemipenis (Danielopol 1980a, Namiotko & Danielopol 2001).

Since Kaufmann's publication (Kaufmann 1900), at least 15 species, Recent and fossil ones, are considered to belong to this genus (Kempf 1980). Most of them are distributed in Europe, one species (Candona brehmi (Klie)) was discovered in Japan (Klie 1934, Danielopol 1980a). Fossil species were described from the Tertiary and Quaternary deposits in Central Europe (e.g. Absolon 1973, 1978, Krstić 1972, Sokač 1978).

Recent Candona species colonize surface water habitats, those of lakes and springs but also the subsurface environment, riverbed sediments or porous groundwater in alluvial valleys (Meisch 2000). There are a series of exclusively groundwater dwelling species living either in porous groundwater or cave water habitats (see below). A limnetic environment is assumed for one Tertiary fossil species, Candona nociens (Krstić 1972).

The Recent Candona species we shall discuss here, taking in consideration their present-day geographical and ecological distributions (information in Löfler & Danielopol 1978, Danielopol 1980a, Meisch 2000, Namiotko & Danielopol 2001) belong to four distinct groups:

1. Species which live mostly in Western and Central Europe inhabiting mainly epigean (benthic) habitats, seldom subsurface ones, i.e. Candona reducta (Alm).

2. Species which are distributed over the whole Europe inhabiting both surface and subsurface habitats, in this latter case both shallow (hyporheal) and deep porous groundwater habitats, i.e. Candona vavrai Kaufmann.

3. Species which live in porous groundwater habitats either mainly along the valleys of large rivers, like the Rhine, the Rhône, the Danube and their tributaries [i.e. Candona kieferi (Klie)] or mainly along the Carpathians (i.e. Candona matris (Sywula)).

4. Species with restricted geographical distributions and occurring mainly in groundwater habitats, e.g. Candona lerethii (Klie) in Belgium, Candona phreatica (Kiefer and Klie) in Slovenia, Candona dudichi (Klie) in Hungary and Candona brehmi (Klie) in Japan. These latter two species live in cave-water habitats. Note that C. phreatica and C. dudichi were seldom found in surface water habitats connected to groundwater systems (springs) while the other two species were found in deep subsurface waters.

The carapace shape of the Candonaicæ is very diverse. One finds species with carapaces which approximate geometric shapes like the rectangular, trapezoidal or triangular ones (Danielopol 1978, 1980b). It was noted that often interstitial dwelling ostracods, especially those living in marine sands, display carapace shapes which are conspicuously more elongated than those belonging to epigean dwelling species (Elofsen 1941, Hartmann 1973, Danielopol & Hartmann 1986). Non-marine ostracods which live in porous non-consolidated sediments have beside species with elongated carapaces also a rather high number of taxa displaying triangular and/or trapezoidal carapaces (Danielopol 1978, 1980b, Danielopol & Marmonier 1994). Another common feature of interstitial dwelling animals, beside their elongated body shapes, is also their more reduced size, as compared to those of related surface dwelling taxa (Giere 1993, Coineau 2000).

The questions addressed in this contribution are:

1. Is the carapace shape of Candona a valid taxonomic character? For most organisms shape is under tight (phylo)genetic control making individuals within a lineage morphologically similar to each other. This is a feature that taxonomists have used since long time ago as the basis of their daily work. When morphologies (indeed a multidimensional trait) are arranged according to their relationships we obtain the so-called empirical morphological space (see McGhee 1999). It is expected for morphologically different species to occupy different positions in the morphospace. Unfortunately, not a single point but a cloud of them correspond to each species in the morphospace because shape is far from being an invariant trait. Genetic diversity, ecophenotypic variability and phenotypic plasticity all contribute to morphological disparity within a clade. Only when clouds of points representing species in the morphospace do not overlap, species can be safely discriminated on the basis of shape alone. Thus, understanding (and explaining) disparity patterns of Candona, as compared to other Candonaicæ would allow to progress toward better systematics of the Candonaicæ. It is well known that this latter scientific aspect is far from achieving the consensus of palaeontologists and neontologists. For instance one should compare the differences existing between the taxonomic system used by Mandelstam & Schneider (1963) and Krstic (1972) for the fossil candonines with those used by Danielopol (1978) or Meisch (2000) for Recent ones.

2. Is morphological diversity of carapace shapes of Candonaicæ species related to any geographical pattern? Because gene flow must be very reduced between populations living in patchy environments (for instance, groundwater habitats) a larger morphological disparity is expected.
Table I. – Material used for the morphological analysis (R-right, L-left, V-valve; see also text).

<table>
<thead>
<tr>
<th>CODE</th>
<th>SPECIES</th>
<th>VALVES</th>
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<th>COUNTRY</th>
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<tr>
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</tr>
<tr>
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<td>HUNGARY</td>
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<td>LV</td>
<td>Hermalle sous Argenteau</td>
<td>BELGIUM</td>
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<td>LV</td>
<td>Tekovice Luzany</td>
<td>SLOVAKIA</td>
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<td>LV</td>
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<td>YUGOSLAVIA</td>
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<td>Clou de la Fou</td>
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<td>LV</td>
<td>Sigistel</td>
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<td>Izverna</td>
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<td>LV</td>
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<td>LV</td>
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<td>RV</td>
<td>Strwiąż stream</td>
<td>POLAND</td>
</tr>
<tr>
<td>32</td>
<td></td>
<td>RV, LV</td>
<td>Bogdan Voda</td>
<td>ROMANIA</td>
</tr>
</tbody>
</table>

(3) Is morphological diversity of carapace shapes of Cryptocandona species related to any ecological pattern? Ecological conditions of groundwater habitats, especially the living space in porous systems, are assumed to be more homogenous and more constraining than those existing in benthic water habitats (Gibert et al. 1994, Coineau 2000). One could expect hence, that the carapace shapes of hypogean species living within non-consolidated porous sediments converge toward some adaptively functional type, e.g. the elongated and miniaturised one.

The present contribution belongs to a larger project dealing with the reconstruction of the evolutionary pathways of the Cryptocandona lineage. The revised morphology and systematics of the species assigned to this Candona河北省 genus will be published separately (e.g. Namietko & Danielopol 2001, Marmonier et al. MS, etc).

MATERIAL AND METHODS

(1) Geographical and ecological information: We present briefly here the general geographical (Fig. 1) and ecological distribution of the species used for our morphometric analysis. For the special material which documents our contribution we add detailed information on the geographical location and the habitat type. The ostracod material discussed here is represented by carapaces and/or valves of adult females (Table I).

Cryptocandona vovrai Kaufmann, 1900 – The species is very common in the whole Europe (Löffler & Danielopol 1978, Meisch 2000). It occurs in both lentic habitats of lakes (littoral and the profundal ones) as well as in lotic habitats, springs, slow flowing streams; it colonises subsurface water both the shallow ones (the hyporheal of running waters) as well as deep groundwater in alluvial valleys. As the species is very eurythermal it occurs commonly in southern and northern Europe.

The original material of Kaufmann (and a figure of the valve here used from Kaufmann’s monograph 1900) stems from a marshy area with helocrene at Gentilino, W Lugano, Switzerland. We integrated in our data set also the outline of a specimen figured by Hartmann-Hiller (1977) originating from the Harz area, Germany. The following material was directly investigated by us: (1) Grumelange in Belgium, near the boarder with Germany, a spring sampled by C Meisch; (2) hyporheal in the Dusznicka Bystrzycka stream, 15 km W Klodzko, Poland; (3) Šuncuiș, a well accessing to porous groundwater, 45 km ESE Oradea, Romania; (4) Sigistel, between Nucet and Ștei, a well accessing to porous
groundwater, Romania; (5) Izverna, hyporheal in front of the Izverna cave, 15 km W Baia de Aramă, Romania; (6) Adamello-Brenta Natural Park, GA-1B spring, 40 km NW Trento, Italy; (7) Alas, hyporheal on the Lachein stream, 10 km SSW Saint-Girons, Ariège, France; (8) Arcine, a well accessing to porous groundwater, 20 km E Lyon, France; (9) Clou de la Fou, near Saint Paul de Fenouillet, marshy system, 30 km WNW Perpignan, France.

*Cryptocandona reducta* (Alm, 1914) – A mainly epigean dwelling species colonising various lotic and lentic habitats in the Western, Northern and Central Europe (Löffler & Danielopol 1978, Meisch 2000). It is a psychrophilic species which colonises also deep lakes like Loch Ness in Scotland (Griffiths et al. 1993); it occurs seldom in southern Europe e.g. in Auvergne, France (Scharf & Keyser 1991). *C. reducta* colonises infrequently groundwater habitats, i.e. the hyporheal of streams and porous groundwater in alluvial sediments along valleys. Alm (1914) described this species using material from springs at Renô in the province Finnmark (Norway). We used for the present contribution the outline of *C. reducta* published by Alm (1914). From Absolon’s monograph on candonines (Absolon 1978) we used the outline of *C. reducta* drawn by this author from a female caught in a spring at Hut' near Jablonec nad Nisou, Czech Republic. Additional material used, stems from
material deposited in our collections: (1, 2) two limno-
crene springs (Q-98, D-94) at Hausrück, 15 km NNW
Vöcklabruck, Upper Austria; (3) superficial sediments (a
10 cm deep layer below the bottom) of Broadstone,
Stream, 30 km NNE Brighton, East England, UK (the
streambed at this site is dominated by fine sandy sedi-
ment, J. Araya- Schmid leg. and pers. comm. to DLD);
(4) a well dug in alluvial sediments, 20 m inland from
the River Bôbr at Brázkowa, 15 km W Walbrzych,
Poland (leg. T Sywula and pers. comm. to TN); (5) spring at
Olsing, close to Bastendorf, Luxembourg (leg. C Meisch
and pers. comm. to DLD and TN).
Cypriostoma kieferi (Klie, 1938) – This stegobitic
species was found in Western and Central Europe within
the drainage basins of the Rhine, Rhône and the Danube
(Klie 1938, Marmonier & Creuzet des Chateilliers 1992,
Rogulj et al. 1993, Danielpol & Baltanás 1996, Meisch
2000). In Eastern Europe it occurs, near the Black Sea,
coast, in Romania (see below). It lives mainly in porous
groundwater of shallow and deep alluvial sediments.
It occurs seldom in springs or at the surface of gravelly sedi-
ments when groundwater strongly exfiltrates (Danielpol
et al. 2000).

For this species we used drawings from Absolon
(1978), Marmonier (1988) and Marmonier et al. (MS) as
well as material from DLD collection. Material from fol-
lowing six sites were studied: (1) a groundwater sample at
Blatnica, 15 km S Martin in Slovakia (Absolon 1978); (2)
a limnocrene spring at Lutter, near Benfeld on the
Rhône, 30 km S Strasbourg, France (Marmonier et al.
MS); (3) a limnocrene spring at Lutter, near Benfeld on the
Rhône, 30 km S Strasbourg, France (Marmonier et al.
MS); (4) porous groundwater of alluvial sediments near
Orgeux and Arcolat, in the Saône plain, 30 km N Dijon,
France (Marmonier 1988); (5) porous groundwater of allu-
vial sediments of an abandoned channel of the Ain,
closely located to the Rhône river, at Saint Maurice de
Goordan, 15 km NE Lyon, France (Marmonier et al.
MS); (5) porous groundwater in alluvial sediments of the
Danube floodplain at Vienna, samples from Lobau (the
piemeters A-1, in Danielpol 1953 and A-81, in Pos-
pisil 1994), Austria; (6) porous groundwater from alluvial
sediments deposited in the village Lumina, 15 km NW
Constanta, Romania.
Cypriostoma matris (Sywula, 1976) – A stegobitic
species occurring mainly along the Carpathians in Po-
land and in north-eastern Romania. It was also found in
a number of wells accessing to groundwater in alluvial
sediments of the river Vistula in the Lublin Upland, Po-
land (Skalski 1982). The type material came from a well
dug in alluvial sediments in Cisna (Bieszczady Moun-
tains). The material used here originates from 2 sites in
Poland (1-2) and one in Romania (3): (1) a well dug in
alluvial sediments at Niedzim, 20 km W Bielsko
Biała; (2) a hyporheic site on Strwiąż stream, 30 km
SSE Sanok; (3) a well accessing to the alluvial sedi-
tments at Bogdan Voda (Cudna) in the Iza Valley, 55 km
E Baia Mare.

Cypriostoma leruthi (Klie, 1936) – A stegobitic
species from Belgium, living in the groundwater of the
alluvial sediments of the Meuse (Maas) river, at Her-
malle sous Argenteau, 15 km N Liège. Additional infor-
mation in Namiotko & Danielpol (2001). The material
here used belongs to the type series of the species, depo-
sited at the Zoological Museum of the University of
Hamburg (ZMH 341).

Cypriostoma phreaticola (Kiefer & Klie, 1927) –
An apparently stegobitic species from Slovakia, found in
porous groundwater habitats, a well at Tekákovské Luzany
(40 km SE Nitra), in riverbed sediments at Zliechov and
in two springs located about 150 km N from the type loc-
ality. Additional information in Namiotko & Danielpo-
l (2001). The material here used belongs to the type
series of the species, deposited at the Zoological Mu-
seum of the University of Hamburg (ZMH 344).

Cypriostoma dudichi (Klie, 1930) – A troglobitic
species from Hungary, found on the bottom of a
 drip-pool in the Barlang cave, at Aggtelek, 45 km NE
from Miskolc (Klie 1930). The material here used rep-
sents valves from the type series of the species, deposi-
ted at the Zoological Museum of the University of
Hamburg (ZMH 340). C. dudichi were found recently in
a karstic spring closely located to the above mentioned
cave (Z. Gido leg. pers comm C Meisch to us).

Cypriostoma brehmi (Klie, 1934) – A troglobitic
species from Japan, found on the Island Honshu, 120 km
NW Tokyo in the cave Hinuwagara (on the bottom of a
drip-pool). The figure used here is redrawn from Klie
(1934). As comparative material we used published in-
formation on the carapace or valves for the following
species:

Cypriostoma noccens (Kršči, 1972) – A fossil Ter-
iary species known only from limnic sediments strati-
ographically identified as the Lower part of the Lower
Pannonian, at Belgrade, Yugoslavia. The outline of the
valve used here comes from the original description of
Kršči (1972).

Candonopsis boui Danielpol, 1981 – A stegobitic
species living in Southern France. It is known from the
riverbed sediments (hyporheal) of the Tarn river at Avalas (the
valve figured here) and alluvial sediments near Albi
at Go (Danielpol 1981, Danielpol & Hartmann 1986).

Candonopsis valida (O.F. Müller, 1776) and Candona
neglecta Sars, 1887 – Both species are very common in
Europe, living in both surface (lotic and lentic habitats)
as well as in groundwater (Löffler & Danielpol 1978,
Roca & Baltanás 1993, Meisch 2000). They are known as
fossils especially in Quaternary deposits of Europe (e.g.
Absolon 1978). The outlines of the female valves of
these species used in our morphometric study were
They belong to both Recent and fossil (Middle and
Upper Pleistocene) material from various localities in
Czech and Slovak Republics and one in Alberta, Canada.

2) Acquisition of data and morphometric analysis:
Ostracod shape analysis can be addressed in different
ways. Landmark methods, including Procrustes appro-
aches, have been extensively used with well ornamented
species (Kaesler & Foster 1987, Reymert et al. 1988,
Abe et al. 1988, Reymert & Bookstein 1993, Reymert
1995). However, difficulties for defining landmarks in
smooth or poorly ornamented ostracods have favoured
methods based on outlines (Kaesler & Waters 1972,
Kaesler & Madocks 1984, Schweitzer et al. 1986,
Burke et al. 1987, Schweitzer & Lohmann 1990, Bal-
tanás & Geiger 1998). Among outline methods, Elliptic
Fourier analysis is known to produce reasonable results
with biological shapes (Rohlf & Archie 1984, Lastrel
1997, McLellan & Endler 1998) and has been used here.

Outline data (400-600 points per contour) were ac-
quired from drawings using tpsDig software (Rohlf 1998).
Sources of drawings are detailed in section (1). The ori-
gen of coordinates describing each outline was placed at
the centroid (centre of gravity) of each valve. In order to make left and right valves comparable left ones were flipped horizontally. Only female outlines were included in the raw data set. Sexual dimorphism is known to be large in some Cryptocandona species thus contributing to overall morphological variability. The aim of the study, however, is to explore patterns in morphological variability at the specific and the between-population levels, not within populations or between sexes.

Twenty harmonics were computed as descriptor for each outline rendering a total of 77 coefficients per specimen. These coefficients were mathematically normalised to be invariant to rotation and starting position of the outline trace (Persson et al. 1985).

It is very important to stress that shape alone, not size, is the trait under enquiry. Size is a feature that changes among species and individuals too. And although allometric scaling suggests that some interplay must exist between size and shape in non-marine ostracods, such relationship has not been described yet. In order to remove size effect, Fourier coefficients have been normalised for size too (Persson et al. 1985).

3) Representation of the multidimensional morphospace: Fourier coefficients are but numerical descriptions of valve shape, so they can be used to define positions within a multidimensional space which describe morphological relationships among items in it. We call this an empirical morphospace (McGhee 1999). It is important to underline that a morphospace like that is context dependent, i.e., morphospace features and the positions of ostracods in it change according the amount and kind of objects under study. Building an empirical morphospace directly from our series of Fourier coefficients implies to end up with a high order morphospace (77-dimensions) which is difficult to visualise and of limited use. Ordination techniques, like principal component analysis (PCA), allow us to reduce dimensionality in the original morphospace so that most of the variance in the original data set is summarised in few dimensions. Therefore, a PCA has been performed on the covariance matrix of centered data (a total of 65 valves belonging to 12 species in 3 genera). Having the original data projected onto the new morphospace defined by PCA it is easy to explore relationships among shapes using euclidean distances because principal components are, by definition, uncorrelated (orthogonal). Multidimensional Scaling (MDS) arrange "objects" (valve outlines) in a two-dimensional space so as to reproduce the observed euclidean distances and, hence, relationships among them.

RESULTS

Shape comparisons

Fig. 2 shows items under study arranged on a two-dimensional morphospace. It has been produced by applying multidimensional scaling (MDS) on the matrix of euclidean distances measured on the space produced by PCA. Only 15 principal components were extracted given that they explain more than 99% of total variation in the raw data set. Dimensions 1 and 2 in the plot have been scaled different, otherwise all the points would lined up along the horizontal axis given that variability in the vertical dimension is very low. Now, it is important to stress several points concerning how the methods here employed work. First, all the analyses are directed towards the identification of major quantitative changes. It means that subtle qualitative changes will be undervalued. Second, Fourier harmonics run from the general to the particular. In other words, lower-rank harmonics (order 1, 2,...) account for the general shape of the object considered (e.g. elongated, rounded, etc.) whereas higher-rank harmonics account for the small details in valve outline. Because lower-rank Fourier harmonics are associated with higher numbers and a large variability, their contribution to the final arrangement of items in the empirical morphospace is larger than the contribution of higher-rank harmonics. This is not an undesirable property of the method as far as it is reasonable to value changes in general shape more than changes in small fine details. But once similarities or differences in general shape has been established, a morphologist or a taxonomist will likely be highly interested in such fine details. That is why dimension-2 in the plot (Fig. 2) has been enhanced, because it directly refers to changes in shape which are of minor quantitative importance but which are qualitatively relevant. Differences existing between left and right outlines, those valves belonging to the same population (=locality) normally cluster close in the morphospace.

All Cryptocandona species cluster together in the MDS plot (Fig. 2). Still, C. nocens and C. dudichi seem to fall apart. It is adequate here to remember that distances (gaps) in the vertical dimension have been enhanced and do not reflect large quantitative changes but subtle ones. In those species for which several populations have been included degree of overlap is high. There is a gradient in shape (dimension 1) running from C. redacta to C. vavrai, with C. kieferti and C. matris in a central position. This gradient relates to changes in eccentricity of valve outline. Elongated valves (low height/length ratio) are placed on the right side of the plot, whereas more robust compact shapes (like those of C. candida) are in the left side (Fig. 3A). Dimension 2 in MDS plot relates to changes from quadrangular (lower part) to triangular (upper part) shape in valve outline (Fig. 3B). It is in this dimension that Cryptocandona dudichi and C. nocens differ from their relatives. Cryptocandona dudichi has asymmetric valves, the left one higher and with a ventral protruded margin in its central part, the right valve more straight and the ventral margin slightly concave. The dorsal margin of both valves is widely arched. The maximal height, less than 50% of the length, is located in the anterior half of the valve. The posterior third of the valves is visibly more straight and acuminate than the anterior one.
Fig. 2. - MDS plot summarising similarities in outline shapes among different populations in several Cryptocandona and Candona species. Numbers are for locality codes (see Table 1).

Fig. 3. - Main trends in shape change along dimensions displayed in MDS plot.
Cryptocandona nocens, as figured by Krstić (1972) and here Figs. 3 and 4, has an outline resembling those of C. reducta, i.e. the dorsal margin, clearly arched, the posterior third is higher than the anterior one and widely rounded. The maximal height located in the central area, represents less than half of the maximal length (48%). The ventral margin is straight.

For most of the Cryptocandona species the empirical morphological space overlap. This unexpected effect can be better understood from a detailed assessment of each species.

Cryptocandona vavrai has rectangular carapace shapes with the posterior third generally slightly larger than the anterior one, e.g. the individual figured by Kaufmann (1900) from Switzerland, those of north Italy or those of Belgium. Maximal height lays in the posterior third and represents between 47% and 51% of the maximal length. This valve shape comes closer to those of C. kieferi. The dorsal margin can be angular in some populations like those of Sigişel and Şuncuşi with the angle formed at the maximal height of the valve or can be more rounded, like those of Arcine or those of Clou de la Fou. The valve shape of this latter population resemble those of C. reducta. Individuals of Izverna and Alas displays an attenuated arched dorsal margin. The ventral margin is practically straight in all the populations. Shapes on ends of the shape range are a very large one belonging to the Grumelange (Belgium) population and the most straight one belonging to the Izverna population.

Cryptocandona reducta displays elongated valves with the dorsal margin arched, maximal height in the central part representing 45% - 48% of the maximal length. The anterior and posterior sectors of the dorsal margin are more or less straight; the anterior and posterior with more or less symmetrical rounded margins. The ventral margin is straight. The specimen figured by Alm (op.cit.) and those from Poland have more rounded dorsal margins resembling to C. brehmi. The general carapace of the Austrian populations are more triangular appearing more closer to C. kieferi. Outermost shapes are from Hut (Slovakia), which is the largest, and from Broadstone stream (East England) with the most elongated shape. Some of the C. reducta valves resemble those of C. matis due to their triangular appearance.

Cryptocandona kieferi has rectangular carapaces with the maximal height in the posterior third, 46%-50% of the maximal length; the dorsal margin widely convex, approaching a straight line in the inter-cardinal zone. The anterior and posterior margins broadly rounded while the ventral margin is straight. Individuals from Rhine and the Danube (Lobau, at Vienna) displays a more rounded and higher posterior third of the valves, while individu-
Fig. 4. – Disparity and shape trends in valve outlines displayed as their projections onto first principal component (84 % variance explained arranged). Disparity (inset upper left, grey bars) is measured as the amount of morphospace occupied (range of values in the axis). Sample size is also shown (black bars).
slightly arched, the posterior margin in the upper part straight, the passage to the ventral margin rounded. The ventral margin is straight or slightly concave.

*Candona neglecta* displays bean-shaped valves, more or less rectangular with anterior and posterior margins widely rounded, the latter one larger than the former one. The maximal height located in the posterior third and represents between 51-55% of the maximal length. The dorsal inter-cardinal margin straight and obliquely laying. The ventral margin is slightly concave.

**Biogeographic patterns**

No geographic pattern appears to exist, e.g. no latitudinal or longitudinal gradient can be identified in the analyses with regard to shape variability among populations in the several *Cryptocandona* species here considered.

**Morphological disparity**

Morphological disparity can be approached as the amount of morphospace occupied by a taxon. In this case we took advantage of the fact that most variability in the data (84%) is explained by first principal component extracted by PCA. So, projections of the valves onto that axis allow us to get an estimate of variability within each group (Fig. 4). Unfortunately this measurement is biased by sample size (Foote 1993). Larger samples result in larger shape ranges and, hence, more variability. Despite that drawback of the method and although no statistical significance can be attached to observed disparity, still some interesting details emerge. *Cryptocandona kieferi*, the groundwater dwelling species, shows the largest disparity among *Cryptocandona* species. This is a remarkable observation because *C. kieferi* is less well represented (8 items in 6 localities) than *C. vavrai* (20 items in 11 localities) or *C. reducia* (10 items in 6 localities) (Figs. 1, 4). Although out of the scope of this paper, it is worth noting the variability in *Candona candida* is the largest of all. Indeed this is a not too surprising result considering that the series of outlines used for representing this species comes from a wide temporal (middle Pleistocene to Recent) and spatial (Bohemia to Canada) range (Absolon 1978).

**DISCUSSION AND CONCLUSIONS**

(1) Shape description using Elliptic Fourier Analysis combined with Multivariate data analysis conform a powerful tool for comparative studies of the ostracod carapaces. It allows to perceive details unnoticed by current optical inspection with standard perceptual mechanisms. This latter process used by ostracodologists (e.g. Absolon 1978, Krsić 1972, Meisch 2000) established clear patterns or “Gestalts” for the recognition of the general shape of the various *Cryptocandona* species. Our morphometric study shows that the outlines of the various *Cryptocandona* species change smoothly from one specific form to the others. Hence the approach we used here helps to better visualise evolutionary aspects of the carapace morphology of *Cryptocandona* and to better understand the limits of the usage of carapace outlines for the systematics of this group.

(2) The carapace shapes of *Cryptocandona* representatives cluster around the flat rectangular (or elongated) and/or slightly arched morphotypes with no gaps between the various species within the whole morphospace. No high rectangular shapes, like in the case of species belonging to the genus *Candona* (e.g. *C. candida*), no high triangular or trapezoidal shapes, like those of *Mixtocandona* Klie species (Danielopol 1978, Danielopol & Cvetkov 1979) evolved. This fact suggests that the evolvability of the carapace shape (i.e. its evolutionary capacity to transform the morphological form) is developmentally constrained (sensu Wagner 1994 p. 291, i.e. “lack of heritable variation”) and proceeds through small steps as “variations on a theme”. This observation is in line with those of Kemp (1999) who noted that highly integrated morphological structures within a phylogenetic lineage, similar to the ostracod carapace shapes of *Cryptocandona*, are able to change only at a lower extent. The same idea can be expressed in terms of “developmental canalisation” which refers to the production of consisent phenotypes under different environmental and genetic conditions (Møller & Swaddle 1997). It seems that shape in *Cryptocandona* species is a highly canalised trait.

(3) The disparity among patterns of the various *Cryptocandona* species, as represented by their morphospace, is apparently related to their ecological flexibility. The actual geographic distribution of these species is a reflection of their capacity to spread through either surface or subterranean environments and to use the various ecological situations. This is the case with *C. vavrai*, an epigean species which repeatedly colonised groundwater habitats (Namiotko, Marmonier, Horne and Danielopol, in prep). This species has a high disparity and wider geographical distribution. The opposite is the case of *C. reducia*, which seldom colonises deep groundwater habitats, i.e. has more restrictive ecological requirements, displays a lower morphological diversity and the geographical distribution is not so large as compared to the former species. A similar image is displayed by the pair of stygobite species *C. kieferi* and *C. matria*.
However in this latter case the reduced disparity of *C. matris* could be due to the low number of sites and populations represented here. From this information one could infer that the higher degree of disparity of outline shapes for species like *C. vavrai* or *C. kieferi* evolved as adaptive solutions to the local habitats where the different populations settled. Two epigean ostracods, *Eucypris virens* (Jurine 1820) and *Limnocthyere inopinata* (Baird 1843) with both wide ecological and geographical distribution in Europe display similar wide morphological diversities of the valves (Baltanás & Geiger 1998, Yin et al. 1999, Baltanás et al. MS). The limits of our adaptive explanation will be here further discussed (see next paragraph).

(4) The convergent evolutionary state of the morphological form of animals in relation to their specific life habits and ecological space occupied was called by Remane (1943) “Lebensformtypus”. Following Kühnelt (1969) typical animal life-forms for a specific environment (e.g. the porous sandy sediments) are the result of adaptive trends. The disparity of the *Cryptocandona*, as expressed by the various points within the empirical morphospace, does not show a directional trend from the most epigean dwelling species *C. reducta*, to the stygophile *C. vavrai*, leading finally to the exclusively interstitial dwelling species *C. kieferi* or *C. matris*. However, we noticed that within *C. vavrai* and *C. reducta*, the most elongated carapace shapes belong to interstitial dwelling populations. Within the exclusively interstitial species *C. kieferi* and *C. matris* one finds carapaces with both elongated and dorsally arched valves. One could interpret the convergent evolution of these “lebensformtypen” as a non-experimental evidence of natural selection, shaping an adaptive solution for life within the porous space. This observation should stimulate groundwater ecologists to reinvestigate and better describe the local environment where these *Cryptocandona* populations with elongated valves live. Also laboratory experiments could be helpful to better understand the relationships between carapace shape and size of these ostracods and their movement through clastic sediments, within well controlled effective porosities.

Comparing the carapace shape of the cave dwelling species *C. brehmi* with those of epigean *C. reducta* populations and/or the interstitial dwelling *C. matris* we do not see distinct differences which could be interpreted as adaptive solutions to cave life.

The carapace of *C. dudichi* from a drip pool in the Barlang cave, displays a more acuminate posterior shape (as compared to the anterior part) than those of the other *Cryptocandona* investigated. This could be interpreted as an economy of material and space, an adaptive solution to the oligotrophic cave environment. However to corroborate or refute this hypothesis one needs additional ecological studies. One should note that the adult female of *C. dudichi* displays a carapace shape which resembles those of the 7th juvenile stage of *C. leruith* (for this latter see Namiotko & Daniellopol 2001). This observation suggests that *C. dudichi* with its posterior straight form of the valves is a paedomorphic species.

The fact that *Cryptocandona* populations with both slightly dorsally arched valves and those with a flat dorsal shape, live successfully within the interstitial space of various clastic sediments, suggests that external factors acting through directional selection are not strong enough to shape a distinctly elongated carapace form within this ostracod group. The dorsally arched morphotype exist in various epigean *Cryptocandona* populations too, hence one has to consider this type of carapace form an exaptation (sensu Gould & Vrba 1982). Rouch & Daniellop (1987) noted that the colonisation of subterranean habitats are favoured by epigean preadapted species.

The dorsally arched valves of *Cryptocandona* represent an excellent constructional solution for the strength of their thin calcified walls. Benson (1975) showed that such carapace types are build following the principle of a “catenary arch” in which the thrust in the calcified wall is well equilibrated, i.e. without making necessary additional mass to the extremity of the arch in order to avoid deformations. This latter situation can be seen in various Candoninae (Daniellop 1978, 1980b, 1990). Interesting enough, the principle of the “catenary arch”, realised under natural conditions, was used by the Spanish architect Antonio Gaudi for the design of architectural objects, like those of the cathedral “Sagrada Familia” in Barcelona (Kemp 2000).

(5) The characterisation of the morphological form of the Candoninae valves represents an important aspect of the systematics of this group, especially when dealing with fossil species. Tertiary ostracod fauna, especially in or around the Parasethys in Central and Eastern Europe, is replete with Candoninae displaying a high morphological diversity (e.g. Krstić 1972, Sokač 1972, Olteanu 1995). The taxonomic characterisation of the fossil Candoninae using outline details proceeded in most of the cases by subjective and more or less impressionistic decisions. Hence the systematics of this group, as developed by many ostracodologists, reflects a high degree of arbitrariness. The analysis of valve outlines following the protocols used here allows higher degree of discrimination of morphological forms of Candoninae valves as compared to traditional methods mentioned above. In this way a more objective systematics of the Candoninae can be achieved!
Sbordoni (1993) suggested that the properties of a species can be better defined as a statistical cloud of traits, clustered within a multidimensional space. We suggest here that any taxonomic unit should be defined within a multidimensional morphospace as individualised groups separated from other similar groups by gaps. In our case (the examples used were chosen for comparative purposes only), the data of Recent Cryptocandona and Candonia valve outlines, one could easily define a Cryptocandona pattern within which one could accommodate fossil species, like C. nocens, too. However, the insertion within the empirical morphospace of Cryptocandona the carapace shape of Candonopsis boui, a candonid species belonging to a different phylogenetical lineage (Danielopol 1980a, 1981), forbids us to use solely the valve outline pattern of Cryptocandona as a generic characterisation. This means that fossil candonids with carapace outlines resembling living Cryptocandona species (e.g. C. nocens) can not be allocated, as did Krstic (1972), to this group using only the shape criterion of the valves.

(6) The morphometric method using the Elliptic Fourier algorithm applied on valve outlines gave us a general view on the extension of the variety of carapace shapes within the Cryptocandona group. We avoided to use these information for more specific phylogenetic inferences because of Zelditch et al. (1995) argumentation pointing out that most of the outline-based techniques (one exception being the thin-plate spline decomposed by its partial warps) are inappropriate for phylogenetical reconstructions. However, we intend for future studies on the Candoninaceae to combine outline methods with conventional Procrustes ones. These latter, using landmarks, were successfully used by Benson (1976, 1982, 1983) for evolutionary studies on Recent and fossil marine ostracods. We hope by combining these methods to unveil the biological homologies (sensu Wagner 1989) locked in the structure and the shape of the Candoninaceae carapaces and hence to reconstruct the evolutionary pathways of this group with more accuracy.

In conclusion, the usage of powerful morphometric and multivariate analysis applied to the carapace shapes of various Cryptocandona populations, combined with geographical and ecological information help us to better understand “what exactly, are these forms doing” as Bookstein (1992/1993, p 35) would say. It opens also new avenues for the improvement of the Candoninaceae systematics.

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