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# ON THE CARAPACE SHAPE OF SOME EUROPEAN FRESHWATER INTERSTITIAL CANDONINAE (OSTRACODA)

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Abstract.—The interstitial Candoninae have a large number of species with trapezoidal triangular and widely arched carapace shapes. Some of the interstitial Candoninae display carapaces with extreme morphological features, e.g. a very elongate shape with a pointed posterior, a triangular shape with a large dorsal protuberance.

It is suggested that such species, as *Mixtacandona elegans* Danielopol & Cvetkov and *Phreatocandona motasi* Danielopol, with elongate carapaces and pointed posterior should have a low fecundity. The Candoninae species with this extreme type of carapace shape are known also from the sublittoral of Lake Baikal (*''Candona'' fossiliformis* Mazepova) and from the eastern Paratethys during the Pliocene (*Pontoniella schemachensis* Mandelstam). It is hypothesized that the elongate carapace shape with a pointed posterior is an adaptation less suited for Candoninae living in unpredictable surface habitats but acceptable for those species inhabiting physically and/or biologically stable habitats which exist over geological epochs.

The Freshwater Interstitial Candoninae of Europe

The subfamily Candoninae (sensu Danielopol, 1976, 1978) contains a high number of true interstitial species living in freshwater habitats in Europe (Danielopol, 1977). This subfamily is also one of the most "species-rich" ostracod groups living in European surface waters (Löffler & Danielopol, 1978). The Candoninae are creeping forms with unpigmented carapace and eye.

I consider "true interstitital" ostracods to be species found in interstitial or in interstitial and cavernous aquatic habitats, which show eye reduction and/or long antennal aesthetascs "Y" (see Danielopol, 1973). In cases where data on these characteristics is not available, species recorded exclusively from the above mentioned habitats are referred to as "true interstitial" forms (Table 1). Several species are not included in this category because reliable data about their typical habitat is lacking (see Danielopol, 1978).

The carapace shapes of the interstitial Candoninae can be roughly classified as follows: a) almost rectangular; b) elongate, slightly triangular; c) widely arched dorsally; d) "highly" triangular; e) trapezoidal; f) elongate with pointed posterior. Table 1 presents data available for the interstitial Table 1.—The freshwater interstitial Candoninae recorded in Europe (i—interstitial habitat; k—karstic habitat; a—almost rectangular; b—elongate, slightly triangular; c—widely arched dorsally; d—"highly" triangular; e—trapezoidal; f—elongate with pointed posterior). Data from Danielopol, 1978; Danielopol & Cvetkov, 1979; Sywula, 1976.

Taxa	Habitat	Shape	Height
Pseudocandona			
eremita (Vejdovsky) s.l.	i + k	d	>1/2
zschokkei (Wolf)	i	e	>1/2
puteana (Klie)	i	d	>1/2
schellenbergi (Klie)	i	e	>1/2
triquetra	i + k	d	>1/2
belgica (Klie)	i	e	>1/2
hertzogi (Klie)	i	e	>1/2
brisiaca (Klie)	i	с	>1/2
insueta (Klie)	i	e	<1/2
bilobata	in part work in the second	с	>1/2
spelaea (Klie)	i + k	а	1/2
dichtliae (Brehm)	i	e	>1/2
szöcsi (Farkas)	i	d	>1/2
bilobatoides (Löffler)	i	с	<1/2
pseudoparallela (Löffler)	i	а	1/2
profundicola (Löffler)	seminoper i	а	1/2
tyrolensis (Löffler)	those is pecies i.m.	а	1/2
altoalpina (Löffler)	i	a	1/2
rouchi Danielopol	i + k	e	>1/2
delamarei Danielopol	i	а	>1/2
Ps. n. sp. aff. eremita	i	d	>1/2
mira Sywula	i	e	<1/2
Cryptocandona			
phraeticola (Klie)	ie (sen i u Dadieloj	b	<1/2
leruthi (Klie)	na univit i digena	b	<1/2
kieferi (Klie)	i	b	<1/2
juvavi (Brehm)	i	b?	<1/2?
matris Sywula	i	b	>1/2
Fabaeformiscandona			
latens (Klie)	i	a	>1/2
wegelini Petkovski	i and i and i	а	<1/2
Candonopsis			
boui Danielopol	i (1996) i	b	<1/2
Phreatocandona			
motasi Danielopol	i	f	<1/2
Mixtacandona			
laisi (Klie)	i	e	<1/2
stammeri (Klie)	i + k	e	<1/2
chappuisi (Klie)	i i	e	<1/2
transleithanica (Löffler)	ugnani v hand	a	<1/2

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Таха	Habitat	Shape	Height
löffleri Danielopol	i	e	>1/2
botosaneanui Danielopol	i	e	<1/2
pietrosanii Danielopol & Cvetkov	i	b	<1/2
elegans Danielopol & Cvetkov	i	f	<1/2
Mixtacandona n. sp.	i	d	>1/2
Mixtacandona sp. aff. chappuisi	i	e	= <1/2
pseudocrenulata Schäffer	i + k?	e	<1/2
cottarellii n. sp. (in litt.)	i	e	<1/2
juberthieae Danielopol	i	e	<1/2
Nannocandona			
stygia Sywula	i	e	<1/2

Candoninae. Similar carapace shapes also exist in the surface-dwelling Candoninae (review in Danielopol, 1978).

Hartmann (1973) showed that among the marine creeping interstitial ostracods (mainly Cytheracea) the elongate carapace (height less than 1/2 the length) is most commonly found. From Table 1 one can see that 41% of the freshwater interstitial species have carapaces with maximal height of more than <sup>1</sup>/<sub>2</sub> the carapace length. One should notice too that the carapace shapes of many species are trapezoidal, "highly" triangular and dorsally widely arched. Some of the European interstitial Candoninae have carapaces with extreme morphological features. Mixtacandona elegans Danielopol & Cvetkov (Fig. 1A, B) from southeastern Bulgaria has the most dorsoventrally depressed and elongate carapace of all the Candoninae (Danielopol & Cvetkov, 1979). Two other subterranean Candoninae display similar carapace shapes, i.e. Mixtacandona ljovuschkini (Rudjakov) from a cave in Transcaucasia (Rudjakov, 1963) and Phreatocandona motasi Danielopol (Fig. 1C, D) from the southern Carpathians in Romania (Danielopol, 1980). Mixtacandona n.sp. (Fig. 1F) lives in the same habitat and area as M. elegans. This species has the largest dorsal protuberance occurring in the Candoninae, i.e. 1/4 the total height (Danielopol & Cvetkov, 1979). The only epigean Candoninae I could find with similar extreme morphological characteristics is "Candona" fossiliformis Mazepova (Fig. 1E), a species which lives in the sublittoral of Lake Baikal between 20 and 50 m depth (Mazepova, 1970; Löffler, pers. comm.). This species has an elongate carapace with a pointed posterior. A similar species has been recorded by Mandelstam et al. (1962) and Vekua (1975) from the Pliocene deposits of the eastern Paratethys in the southwest of the Soviet Union (i.e. Pontoniella schemaschensis Mandelstam, Fig. 3B). This species lived in a shallow Caspi-brackish environ-

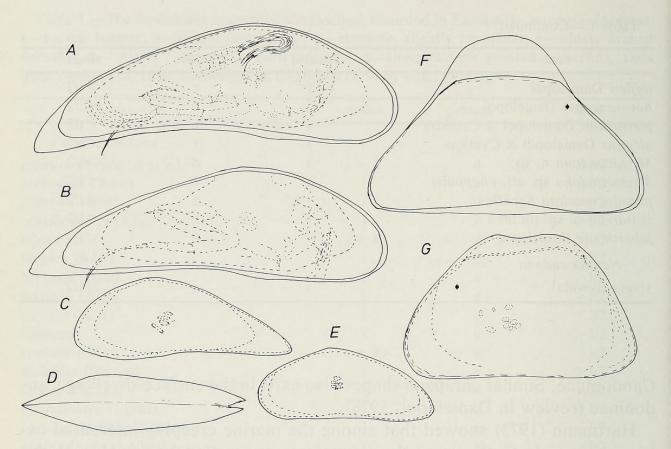


Fig. 1. A, B, Mixtacandona elegans,  $\delta$  and  $\varphi$  carapaces (Zvetdetz); C, D, Phreatocandona motasi,  $\varphi$ , (Jiblea); C, left valve; D, Carapace, dorsal view; E, "Candona" fossiliformis (Lake Baikal); F, Mixtacandona n. sp.,  $\varphi$ , (Zvetdetz); G, Pseudocandona dorsoconcava,  $\varphi$  (Lake Baikal).

ment. The specimen of *Pseudocandona dorsoconcava* (Bronstein) figured here (Fig. 1G) was found in Lake Baikal at 20 m depth. It has a very conspicuous dorsal protuberance (1/7) of the total height located in the anterior half of the carapace). No other surface Candoninae has been recorded with such a high dorsal protuberance.

Mazepova (1970) suggested that "Candona" fossiliformis from Lake Baikal has phylogenetic affinities with the fossil species belonging to the Candona of the group lobata from the Paratethys and with the Recent "Candona" ljovuschkini from Transcaucasia. Danielopol & Cvetkov (1979) showed that "Candona" ljovuschkini belongs to the Candona group mixta, now considered a valid genus, Mixtacandona Klie (Danielopol, 1977/1978). This species has the 2nd thoracic leg with 2 short and 1 long distal setae, the clasping palps of the maxilla slightly asymmetric and with digitiform tips, characteristics that can be found in all the Mixtacandona species. Mixtacandona ljovuschkini has close affinities with Mixtacandona elegans. Phreatocandona motasi Danielopol has 3 short setae on the exopodite of the antenna, a long distal seta on the 1st thoracopod; the 2nd thoracopod is similar to those of Pseudocandona, having distally 3 long setae. In these

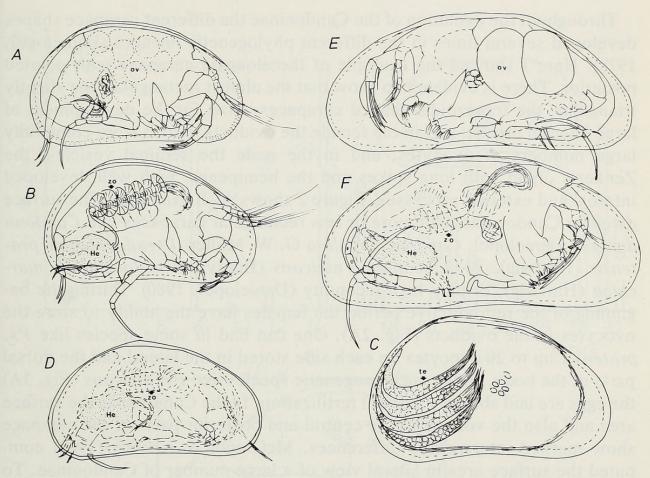


Fig. 2. Epigean (E) and hypogean (Hy) Candoninae: A, B, Pseudocandona pratensis, ♀,
(E), (Dourdou); C, Pseudocandona aff. pratensis, ♂, (E). (Seewinkel, temporary pond nr. 12);
D, Pseudocandona n. sp. aff. eremita, ♂, (Hy), (Jiblea); E, F, Mixtacandona aff. chappuisi,
♀, ♂, (Hy), (Bogdan Voda) (ov—ovocytes, zo—Zenker's organ, He—hemipenis, te—testes).

peculiarities *Phreatocandona* differs from other genera of Candoninae. *"Candona" fossiliformis* has the antennae, the clasping palps of the maxilla and the thoracopods similar to those of *Pseudocandona* species. These data suggest that the elongate carapace shape with an extremely pointed posterior, occurring in species found in both ground water (in Europe) and in Lake Baikal, was produced by parallel evolution in related phylogenetic lineages.

## The Functional Importance of the Carapace Shape in the Candoninae

Why within the Candoninae does this characteristic carapace shape, very elongate and pointed, occur only in species which live in subterranean habitats, in Lake Baikal and in the Paratethys? To answer this question one has to understand, first of all, the functional importance of the carapace. Secondly one has to find what such different environments as the groundwater (in southeastern Europe), the eastern Paratethys Sea (e.g. during the Pliocene) and the sublittoral of Lake Baikal have in common.

Throughout the evolution of the Candoninae the different carapace shapes developed several times in the different phylogenetic lineages (Danielopol, 1978). Here I showed the example of the elongate carapace with pointed posterior. There is evidence to show that the almost rectangular, the slightly triangular, the trapezoidal shaped carapaces allow for the development of large internal organs: e.g. in the female the oviducts, which store commonly large numbers of ovocytes; and in the male the seminal vesicles, the Zenker's organ with long spikes and the hemipenes, with well developed internal and external processes. Figure 2 shows such examples. The surface dwelling Candoninae with more or less rectangular carapaces like Candona dancaui Danielopol, Candona angulata G. W. Müller, Pseudocandona pratensis (Hartwig), Pseudocandona albicans (Brady), Pseudocandona marchica (Hartwig), display high fecundity (Danielopol, 1980). During the beginning of the reproductive period the females have the ability to store the ovocytes in the oviducts (Fig. 2A). One can find in some species like Ps. pratensis up to 20 ovocytes on each side stored in the lateral and the dorsal parts of the body. In the parthenogenetic species like Ps. albicans (Fig. 3A) the eggs are laid abruptly without fertilization. In the Candoninae the surface area and also the volume of the central and posterior parts of the carapace show marked interspecific differences. McGregor & Kesling (1969) computed the surface area in lateral view of a large number of Candoninae. To permit a comparison they expressed the data in terms of converted areas of the carapace using the following formula

$$Ca^{CA} = \frac{CA}{(L^{CA})^2} \times 100$$

where Ca<sup>CA</sup> is the converted area, CA is the area of the carapace in lateral view, L<sup>CA</sup> is the maximal length of the carapace. Table 2 (part A) shows the converted areas of several epigean Candoninae (females) living in shallow water bodies. The second part (B) of the table shows the values for the 4 species with elongate carapace shape and pointed posterior. The latter group has the lowest values. Kesling (1965) and McGregor & Kesling (1969) pointed out that the interspecific differences in the converted areas are due to differences in the shape of the posterior part of the carapace which holds the reproductive organs. Table 3 supports this idea. It shows the converted area of the anterior <sup>1</sup>/<sub>3</sub> and of the posterior <sup>2</sup>/<sub>3</sub> of the carapace (see also Fig. 3B), calculated by the following:

$$Ca^{A} = \frac{A}{(\frac{1}{3} L^{CA})^{2}} \times 100 \text{ and } Ca^{P} = \frac{P}{(\frac{2}{3} L^{CA})^{2}} \times 100$$

Ca<sup>A</sup> and Ca<sup>P</sup> are the converted areas respectively of the anterior <sup>1</sup>/<sub>3</sub> and the posterior <sup>2</sup>/<sub>3</sub> of the carapace, A and P are areas of the respectively anterior

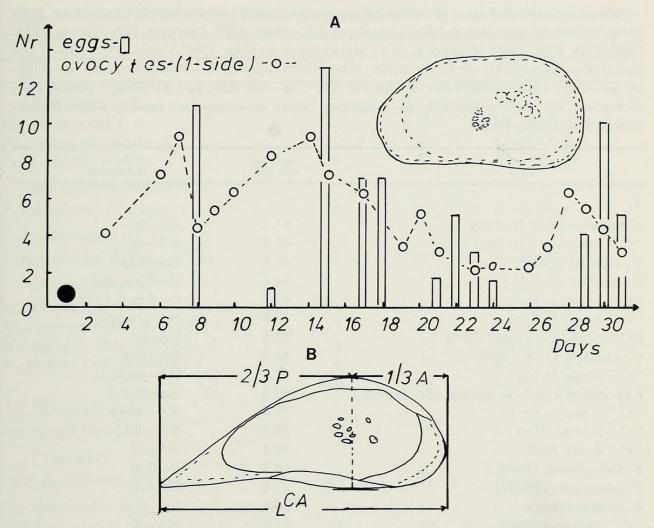


Fig. 3. A, *Pseudocandona albicans*,  $\Im$ , the evolution of the ovocyte number in the oviduct and the egg laying rhythm (•—the last molt); **B**, *Pontoniella schemachensis*, left valve (after Vekua, 1975).

<sup>1</sup>/<sub>3</sub> and the posterior <sup>2</sup>/<sub>3</sub> carapace in lateral view.  $L^{CA}$  is the maximal length of the carapace. Whereas the converted area of the anterior part varies within a narrow range, that of the posterior <sup>2</sup>/<sub>3</sub> varies to a larger extent. All the epigean Candoninae listed here have almost rectangular, elongate, slightly triangular, "highly" triangular and trapezoidal carapaces. Most of these species are widely arched posteriorly. The male copulatory organ as well as the clasping organs are normally held in the inner carapace space, i.e. within the space limited by the inner margin of the carapace (Fig. 2B, D, F).

A comparative study has been made in the following 21 Candoninae species of the area of the inner carapace space (ICA), excluding the calcareous lamellar area, and of the lateral surface area of the hemipenis (HeA) (Fig. 4A): 1. *Mixtacandona elegans* (Hy), 2. *M. laisi vindobonensis* (Hy), 3. *M. pietrosani* (Hy), 4. *Mixtacandona* sp. aff. *chappuisi* (Hy), 5. *M. löffleri* (Hy), 6. *M. cottarellii* n. sp. (Hy), 7. *M. tabacarui* (Hy), 8. *Can-* Table 2.—Converted areas of equivalent carapaces (lateral view) in female Candoninae. Data compilation from Danielopol, 1978; Danielopol & Cvetkov, 1979; Delorme, 1970; Furtos, 1933; Hoff, 1944; Klie, 1938; Mazepova, 1970; McGregor & Kesling, 1969; Vekua, 1975. (**Ba**—Lake Baikal; **Eu**—Europe; **H**—Holarctic realm; **NA**—North America; **P**—Palearctic realm; **d**—ditches; **gw**—interstitial groundwater; **ll**—littoral lakes; **m**—marshes; **pp**—permanent ponds; **rp**—rock pools; **sc**—shallow channel; **tp**—temporary ponds; **tr**—temporary running water; **s**—sub-littoral; **sl**—shallow lakes).

Таха	Converted area (%)	Distribution	
<b>A</b> .	1.7 always Sg	charamples. The side	
Candona mülleri Hartwig	63.2	Eu—tp	
"C." renoensis Gut. & Bens.	48.8	NA—tp	
C. weltneri Hartw.	46.6	Eu—ll,tp	
C. candida (O.F.M.)	44.4	H—ll,pp,tp,d	
"C." neglecta Sars	43.7	P—d,m,ll,pp,tp,tr	
"C." truncata Furt.	43.6	NA—m,pp,tp	
Pseudocandona sucki (Hartw.)	42.4	Eu—tp	
C. angulata G. W. Müll.	42.5	Eu—ll,tp	
"C." distincta Furt.	41.6	NA—m,sc,sl	
Fabaeformiscandona hyalina (Br. & Rob.)	40.8	Eu—m,ll,sl	
"C." scopulosa Furt.	39.4	NA—m,rp	
"C." eriensis Furt.	39.3	NA—ll,rp	
"C." acuta Hoff.	39.3	NA—tr	
F. fabaeformis (Fisch.)	38.3	P—ll,tp	
F. acuminata (Fisch.)	37.6	H—ll,tp	
F. fragilis (Hartw.)	36.0	Eu—ll,tp	
"C." ohioensis Furt.	33.8	NA—ll	
B.			
Phreatocandona motasi Dan.	27.0	Eu—gw	
"C." fossiliformis Mazep.	25.5	Ba—s	
Mixtacandona elegans Dan. & Cvetk.	22.9	Eu—gw	
Pontoniella schemachensis Mand.	20.1	Paratethys	

donopsis kingsleii (E), 9. C. boui (Hy), 10. Pseudocandona compressa (E), 11. Ps. simililampadis (Hy), 12. Pseudocandona n. sp. aff. eremita (Hy), 13. Ps. pratensis (E), 14. Ps. rouchi (Hy), 15. Ps. delamarei (Hy), 16. Ps. brevipes (E), 17. Fabaeformiscandona fabaeformis (E), 18. Candona weltneri (E), 19. C. dancaui (E), 20. C. fasciolata (E), 21. C. neglecta (E).

The correlation between the converted areas of the inner carapace space (Ca<sup>ICA</sup>) and the lateral area of the hemipenis (Ca<sup>HeA</sup>) have been computed (Fig. 4A). There is a significant correlation (P < 0.05) but the coefficient of determination ( $r^2$ ) is only 0.253. This means that only 25% of the variation in one of the 2 variables is explained by the other variable, therefore there is not a close relationship. It is suspected that the large hemipenis processes improve the success of the copulation due to a better sensorial contact with

Таха	Ca <sup>A</sup>	Ca <sup>p</sup>	Distribution
Pseudocandona	West Instead		
Ps. albicans (Br.), 9	77	89	H—(E),ll,m,rp,tp,tr
Ps. compressa (Koch), ♀	77	93	H—(E),ll,tp
Ps. n. sp. aff. eremita, ♂	76	88	Eu—(Hy),gw
Fabaeformiscandona			
F. fabaeformis (Fischer), ♀	78	118	P—(E),ll,tp
Candonopsis			
C. kingsleii Br. & Rob., 9	78	106	H—(E),ll,sc,sl
Mixtacandona			
M. aff. chappuisi, 3	76	87	Eu—(Hy),gw
M. pietrosanii Dan. & Cvetk., 9	73	91	Eu—(Hy),gw
M. tabacarui Dan. & Cvetk., 3	76	86	Eu—(Hy),gw
M. elegans Dan. & Cvetk., 9	78	32	Eu—(Hy),gw
3	76	32	Eu—(Hy),gw
Phreatocandona			
Ph. motasi Dan., 9	84	38	Eu—(Hy),gw
''Candona''			
"C." fossiliformis Mazep., ♀	83	38	B—s
Pontoniella			
P. schemachensis Mand.	76	32	Paratethys

Table 3.—Converted areas of the anterior  $(Ca^A)$  and posterior carapace  $(Ca^P)$  sides in several epigean (E) and hypogean (Hy) Candoninae species (see also explanation in Table 2).

the genital lobes of the female (Danielopol, 1980). I also noticed marked differences in the development of Zenker's organ of several Candoninae belonging to the genera *Mixtacandona*, *Candona*, *Pseudocandona*, *Fabae-formiscandona* and *Candonopsis*, which have high carapace shapes (height more than ½ the length). These species also have large Zenker organs. However, I did not find any significant correlation between the width of Zenker's organ and the maximum height of the inner carapace space (Fig. 4B).

## Relationship between the Carapace Shape and the Environment

Most of the epigean Candoninae listed in Tables 2 and 3 are species with almost rectangular, elongate, slightly triangular carapace shapes. These species are widespread in the Holarctic realm. They live commonly in shallow water bodies which are strongly dependent on the climatic changes of the atmosphere (Klie, 1938; Löffler & Danielopol, 1978; Bronstein, 1947; Delorme, 1970; Furtos, 1933; Hoff, 1942). Such habitats are physically unstable and

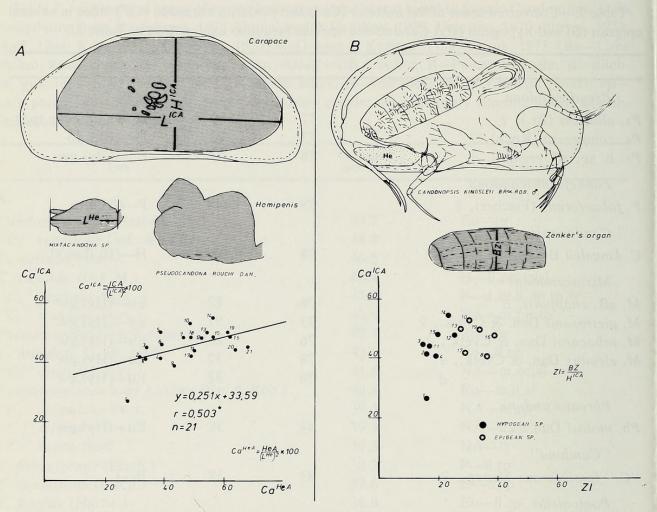


Fig. 4. A, Regression of area of inner carapace space upon lateral area of the hemipenis, with their statistical correlation (see also text); **B**, Relationship between the width of Zenker's organ and the maximum height of the inner space. (The numbers refer to the 21 species mentioned in the text.)

unpredictable. Some of them are short-lived habitats such as temporary ponds, ditches, rock pools, and temporary streams. A great success in reproduction and a high fecundity are at a premium for animals living in unstable water bodies (Southwood, 1976). Comparing the shape of the anterior and posterior part of the carapace of *Mixtacandona elegans*, *Phreatocandona motasi*, "Candona" fossiliformis and Pontoniella schemachensis (Table 3, Fig. 1A, B, C, E), one will notice that the anterior <sup>1</sup>/<sub>3</sub> is highly similar to the other Candoninae quoted above whereas the posterior part is very narrow. These morphological features suggest that the fecundity of these species is low. Further field and laboratory evidence should confirm this prediction.

Mixtacandona elegans Dan. & Cvetk. was found in a well from Zvezdets in southeastern Bulgaria near the border with Turkey (Danielopol & Cvetkov, 1979). Phreatocandona motasi was found in a well from Jiblea, near Calimanesti, in the Olt Valley in the southern Carpathians, in Romania

(Danielopol, 1979a). Whereas the short-term temperature fluctuations of the atmosphere in Europe cause thermic fluctuations in the shallow surface water bodies, they have only slight impact on the groundwater. For instance, Kriz (1973) showed that in southern Slovakia the maximum amplitude of the temperature in a well supplied by a shallow aquifer between 1933 and 1970 was only 0.2°C. Moreover, whereas high temperature or severe droughts can easily lead to the desiccation of restricted shallow water bodies above ground, they will affect a groundwater aquifer to a lesser extent, only by modifying its boundaries. These arguments suggested to me that the groundwater habitats of Mixtacandona elegans and Phreatocandona motasi are physically more stable compared to the epigean shallow water bodies. If one considers the geographical position of the localities where M. elegans and Ph. motasi occur one will notice that they are situated on or near old land masses which have existed at least since the beginning of the Neogene (for Bulgaria data see Cvetkov, 1975 and Lüttig & Stephens, 1976; for Romania see maps in Decou & Negrea, 1969). This suggests that the aquifers in the southern Carpathians and in southeastern Bulgaria could have a very long span (millions of years). Lake Baikal is one of the oldest lakes; it has existed at least since the beginning of the Neogene, and according to Kozhov (1963) may have existed since the Oligocene. "The emergence of Baikal as a deep lake with borders approximately of their present shape is dated by Dumitrashko to the end of the Pliocene . . . . " (Kozhov, 1963:270). The sublittoral of Lake Baikal is also a stable environment highly similar to the groundwater habitats. Kozhov (1963:194) mentioned: "The water of the bottom layer in the sublittoral is subjected to much weaker seasonal temperature flucuatuions than the littoral. At a depth of 50 m the annual amplitude of temperature fluctuations does not exceed 5-6°C. The influence of turbulence is practically imperceptible. Light intensity is insufficient for the development of macrophytes . . . .'' In the sample received from Prof. Löffler, collected at 20 m depth in the Baikal, I found besides "Candona" fossiliformis 8 other endemic species of Candoninae, 4 endemic Cytherissa species and a remarkable Cytherid. I could not find any cosmopolitan Siberian ostracod species. This is in keeping with the data reported by Bronstein (1939, 1947) and suggests that in the sublittoral of Lake Baikal the ostracod association is a highly biologically accommodated community where each species has a narrow niche.

During the Pliocene in the central and eastern Paratethys a diverse endemic Candoninae fauna developed (Hanganu & Papaianopol, 1976; Krstic, 1972; Marinescu & Olteanu, 1973/1974; Sokac, 1972; Vekua, 1975, etc.) which recall those of Lake Baikal. From the data presented by the above mentioned authors it seems that there are few cosmopolitan Candoninae dwellers in the Paratethys. This suggests that the Pliocene ostracods from the Paratethys were also species with good competitive possibilities. The endemic Caspi-brackish fauna prospered for several millions of years. Vekua (1975) showed that *Pontoniella schemachensis*, a species with elongate carapace and pointed posterior, lived during the Pontian, Klimmerian and Kuyalnikian in the eastern Paratethys. That means that the species was present there for more than 2.5 million years (using the paleomagnetic time scale proposed by Kochegura & Zubakov, 1978).

## Conclusion

From these data I hypothesize that within the group of Candoninae the elongate carapace shape with a pointed posterior is less suited for widespread species living in unstable surface habitats, but acceptable for species living in physically and/or biologically stable habitats which exist over geological epochs.

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## Addendum

After sending the manuscript to the publisher, Dr. L. Ram (Zoological Survey of India, Patna) sent me the description of a new Candoninae with elongate carapace and pointed posterior. The Indian species lives in groundwater from Bihar.

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