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Redescription, taxonomy, distribution and ecology of *Cryptocandona dudichi* (Klie, 1930) (Crustacea, Ostracoda)

by

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Abstract: *Cryptocandona dudichi* (Klie, 1930) is redescribed from both the type material and specimens recently collected from springs in the surroundings of the type locality in Hungary. The morphological variability of the species is studied, a differential diagnosis and details of the distribution, ecology and life history are given. The animals from the Baradla cave (type locality) were found to possess two paedomorphic characters: the elongate posterior shape of the adult female carapace and the untransformed seta z2 of the male antenna. The evolutionary significance of these characters is discussed.

1. Introduction

The genus *Cryptocandona* was erected by Kaufmann (1900a, b) for *C. vavrai* described from Switzerland. Both Müller (1912) and Sars (1925) retained the genus as valid, but Klie (in Kiefer & Klie 1927 and Klie 1938), following Alm (1915), lowered the taxon to the rank of a species group, the *cryptocandona*-group, within *Candona* s.l. To date, the validity of the genus *Cryptocandona*, based on characters of both the carapace and appendages, appears firmly established (Danielopol 1980, Baltanás et al. 2000, Meisch 1996, 2000; see the first and the lattermost of these authors for a diagnosis of the genus).

Cryptocandona Kaufm. comprises 13 nominal living species distributed throughout Europe and Japan (Kempf 1980, 1997). The transfer of one species, i.e. *Candona cyproides* (Daday, 1905), described from South America, to the genus *Cryptocandona* by, for instance, Müller (1912) and Kiefer & Klie (1927) is inappropriate (Danielopol 1980, Martens & Behen 1994). The majority of the species of the genus are restricted to springs and waters connected to springs, the hyporheic habitat of streams and alluvial sediments, and caves (Meisch 2000).

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Amongst the genera of the Candoninae, *Cryptocandona* retains a number of primitive characters, mainly the 'fully' developed setal equipment of the cleaning leg (Fig. 3A) (see also Meisch 1996, 2000). The latter character is highly diagnostic and therefore allows easy recognition of the members of the genus.

Recently, the revision of the taxonomy, ecology and distribution of the European species of *Cryptocandona* has been undertaken under the co-ordination by one of us (D.L.D.) (see Baltanás et al. 2000, Marmonier et al. unpublished data, Namiotko & Danielopol in press). The present paper continues this series of contributions.

Cryptocandona dudichi was first described as *Candona dudichi* by Klie (1930) from the Baradla cave in Hungary (see below). Brehm (1953) transferred it to the genus *Cryptocandona*. The species was unrecorded until 2000, when one of us (Z.G.) collected it from both the Baradla cave and springs in the surroundings.

2. Material

The present redescription is based on the type material deposited at the Zoologisches Museum und Zoologisches Institut der Universität Hamburg (= ZMH) as well as on new collections made by one of us (Z.G.) from springs in the surroundings of the Baradla cave, the type locality, and the Baradla cave.

2.1. Type material and type locality

Type-material: (a) one dissected male mounted in glycerine (slide ZMH 340a) prepared by W. Klie and labelled: "*Candona dudichi* n. sp. male, Aggteleker Höhle, 27.XI.29, coll. Dudich"; (b) one dissected female mounted in glycerine (slide ZMH 340b) prepared by W. Klie and labelled: "*Candona dudichi* n. sp. female, Aggteleker Höhle, 27.XI.29, coll. Dudich"; (c) one entire female and two empty female valves as well as two strongly decalcified (?) male valves preserved in an ethanol tube (ZMH 340) labelled: "*Candona dudichi* n. sp., Ungarn, Aggteleker Tropfsteinhöhle, Armensünderhaus, 5350 m, 27. Nov. 1929, coll. Dudich". A holotype was not designated.

Designation of lectotype: the adult dissected syntype female on the sealed slide no ZMH 340b is here designated as lectotype. The remaining specimens of the type material are proposed to be considered paralectotypes.

Type locality: The Baradla cave is situated in the Borsod-Abaúj-Zemplén county, north-eastern Hungary, close to the Slovakian border. Approximate co-ordinates: 20º29' E, 48º29' N (UTM: DU67). Approximate altitude: 450-500 m a.s.l. The cave belongs to an extensive karstic system, with cave openings in Hungary and Slovakia, situated in the Inner West Carpathian Mountains. The type material was sampled from a cave pond at 5350 m from the main entrance, in the part of the cave designated as "Armensünderhaus" at the time of collecting (Klie 1930).

2.2. Other material (leg. Z.G.)

Baradla cave. 11.X.2000: 3 valves.

Nagy-Tohonya spring. Approximate co-ordinates: 20° 31' E, 48° 29' N. Altitude: 260 m.

(a) 11.VI.2000: one adult male (L=0.93 mm) and 4 juveniles (L=0.62-0.64 mm); (b) 11.VIII. 2000: 3 juveniles (L=0.63-0.78 mm); (c) 24.IX.2000: 3 adult males (L=0.91-0.95 mm); 2 adult females (L=0.87-0.89 mm); 1 empty (? male) carapace (L=0.93 mm); 11 juveniles (L=0.30-0.77 mm).

Kecskés spring. Approximate co-ordinates: 20° 38' E, 48° 34' N. Altitude: 320 m. 23.IX. 2000: 4 juvenile LVs (L=0.56-0.86 mm).

Medvekerti spring. Approximate co-ordinates: 20° 37' E, 48° 34' N. Altitude: 340 m. 24.IX.2000. One empty carapace.

This material is deposited in the Hungarian Natural History Museum in Budapest, except the soft parts of two males, one female, five juveniles and one empty carapace from the Nagy-Tohonya spring (24.IX. 2000), which are housed at the University of Gdansk, Poland.

3. Methodology

The 'new' material was collected using a fine-meshed (0.25 mm) hand net. Once concentrated by sieving, ostracods were picked from the sieve residue and transferred into 70% ethanol for permanent storage.

The limb morphology was studied under the light microscope and line drawings were made by the first author with the help of a 'camera lucida' at 500×, 800× or 2000× (oil immersion). Valve outlines of the type specimens were redrawn from photographs printed out from pictures taken with a video camera. Valve dimensions were measured to the nearest 0.01 mm under the microscope at 500×. Valves of the 'new' material were prepared for the SEM and studied by the second author at the SEM laboratory of the Royal Belgian Institute of Natural Sciences in Brussels.

The chaetotaxic notation adopted here follows the model proposed by Broodbakker & Danielopol (1982), as revised for the second antenna by Martens (1987) and the thoracopods by Meisch (1996). Names and abbreviations for the limbs L4-L7 (maxillula and thoracopods T1, T2 and T3) and the caudal rami (furca) follow the scheme proposed by Smith & Martens (2000); terminology for the penis as in Danielopol (1969). The caudal ramus is designated as uropod in Meisch (2000). The taxonomic system follows Martens et al. (1998).

Abbreviations used in text and figures :

A, anterior; a, outer lobe of penis; A1, antennula; A2, antenna; b, inner lobe of penis; CR, caudal ramus; cs, chelate seta; D, distal; d, seta on Pr of L6; d_1, d_2, d_p, setae on Pr of L7; E, endopod; e, setae on EI of L6 and L7; EI – EIV, 1st to 4th podomeres of E; Ex, exterior; Exo, exopod; f, setae on EII of L6 and L7; g, setae on EIII of L6 and L7; G_a, anterior claw of CR; G_M (G_m), major (minor) claw on EIV of A2; G_p, posterior claw of CR; G_{1-3}, anterior and internal claws (or setae) on EIII of A2; H, height; h, medial lobe of penis; h_{1-3}, setae (or claws) on EIV of L6 and L7; In, interior; L, length; *l*, large (relative L of setae or claws); L5, maxilliped (5th limb); L6, walking leg (6th limb); L7, cleaning leg (7th limb); LV, left valve; M, sclerotized internal process of penis; *m*, medium (relative L of setae or claws); Md, mandibula (3rd limb); Mdp, mandibular palp; Mx, maxillula (4th limb); n, number of specimens; P, posterior; pl, plumed seta; Pr, protopod; RV, right valve; S.D., standard deviation; *s*, small (relative L of setae or claws); s_a (s_p), anterior (posterior) seta of CR; S_{1-2}, plumed setae on the 1st podomere of Mdp; t_{1-4}, internal setae on EII of A2 (t_2 and t_3 transformed in males into sensory bristles); W, width; Y, aesthetasc on EI of A2; y_{1-3}, aesthetascs on EII, EIII and EIV of A2, respectively; y_a, aesthetasc on the terminal podomere of A1; z_{1-3}, external setae (or claws) on EIII of A2; α, ß, γ, special setae on the 1st, 2nd and 3rd podomeres of Mdp, respectively. Podomeres used as reference for evaluation of the relative L of setae and claws of the corresponding limb: A1, 4th podomere; A2, EI; Mdp, 3rd podomere; Mx palp, 2nd podomere; L6, EII; L7, EI. All other symbols and their combinations as in Broodbakker & Danielopol (1982).

4. Classification

Phylum	Arthropoda
Subphylum	Crustacea Pennant, 1777
Class	Ostracoda Latreille, 1806
Order	Podocopida Sars, 1866

Suborder	Podocopina Sars, 1866
Infraorder	Cypridocopina Jones, 1901
Superfamily	Cypridoidea Baird, 1845
Family	Candonidae Kaufmann, 1900
Subfamily	Candoninae Kaufmann, 1900
Tribe	Candonini Kaufmann, 1900
Genus	*Cryptocandona* Kaufmann, 1900

5. Redescriptions

Cryptocandona dudichi (Klie, 1930)

Candona Dudichi Klie, 1930: 165, figs 1-7.
Cryptocandona Duchidi (spelling error) - Brehm, 1953: 10.

5.1. Redescription of the type specimens

Female. LV viewed laterally (Fig. 1A) with an elongated sub-triangular shape. Greatest H slightly less than ½ L and situated just in front of mid-length. Dorsal margin weakly arched, posteriorly sloping more steeply than anteriorly, where a very gentle concavity can be seen. Anterior and posterior valve margins rounded, the posterior one more narrowly than the anterior one. Ventral margin with a slight but distinct convexity in the middle. Calcified part of the inner lamella narrow, on both ends equalling 7.5-8.0% of the valve L. RV (Fig. 1B) : general outline as in the LV, but relatively less high and more elongated; ventral margin concave, without any conspicuous expansion. Carapace viewed dorsally (Fig. 1C) (following Klie 1930) very slender, lanceolate; LV overlaps RV at both extremities; both ends pointed. Greatest W (0.24 mm) situated at mid-length. Surface of valves smooth. Central muscle scar arrangement as characteristic for the tribe Candonini. Fused marginal zones narrow, with straight, short and regularly distributed, dense marginal pore canals.
Measurements
LV (n = 2): L = 0.91-0.92 mm; H = 0.43 mm; H/L = 0.47.
RV (n = 1): L = 0.90 mm; H = 0.40 mm; H/L = 0.44.

A1 (Fig. 1D): I+II: A-2*l*(pl), P-2*l*(pl) / III: A-1*m* / IV: A-1*m*, P-1*m* / V: A-2*l*, P-1*s* / VI: A-2*l*, P-1*m* / VII: A-1*s*-2*l*, P-1*l*-1? / VIII: D-y_a-3*l*.

The distal end of one of the posterior setae of the 7th podomere having not been seen, the relative L of this seta was evaluated as medium (*m*) or large (*l*). The longest anterior setae on the penultimate podomere c. 2.5x as long as the ramus (the last five podomeres combined). Aesthetasc y_a equalling 2.7x the length of the terminal podomere. Sensory part of this aesthetasc c. 1/4 as long as the total length of this organ. L ratios of the last five podomeres (IV-VIII) from proximal to distal as 1.0 : 0.9-1.0 : 0.9-1.0 : 1.3-1.4 : 1.7-1.8. L/W of these podomeres, from proximal onwards: 1.2, 1.3, 1.7, 3.2, 6.4.

A2 (Fig. 1E): Pr: P-1*m* / Exo: D(Ex)-2*s*-1*m* / EI: P-Y, P(D)-1*s*-1*m* / E(II+III): A-2*s*, P-y_1, P(In)-4*s*(t_1-$_4$), D(A)-1*m*(G_2), D(P)-y_2, D(Ex)-3*s*(z_{1-3}), D(In)-2*l*(G_1,G_3) / EIV: D(A)-1*m*(G_M), D(P)-y_3-1*m*, D(Ex)-1*m*(G_m), D(In)-1*s*.

Aesthetasc Y c. 0.5x the length of EI ; sensory part c. 1/2 of the total L of Y. Separation between EII and EIII not expressed; this fused podomere bearing 4 internal 't' setae and 3 external 'z' setae (z_1 claw-like, 0.3x the length of EI). Aesthetascs y_1 and y_2

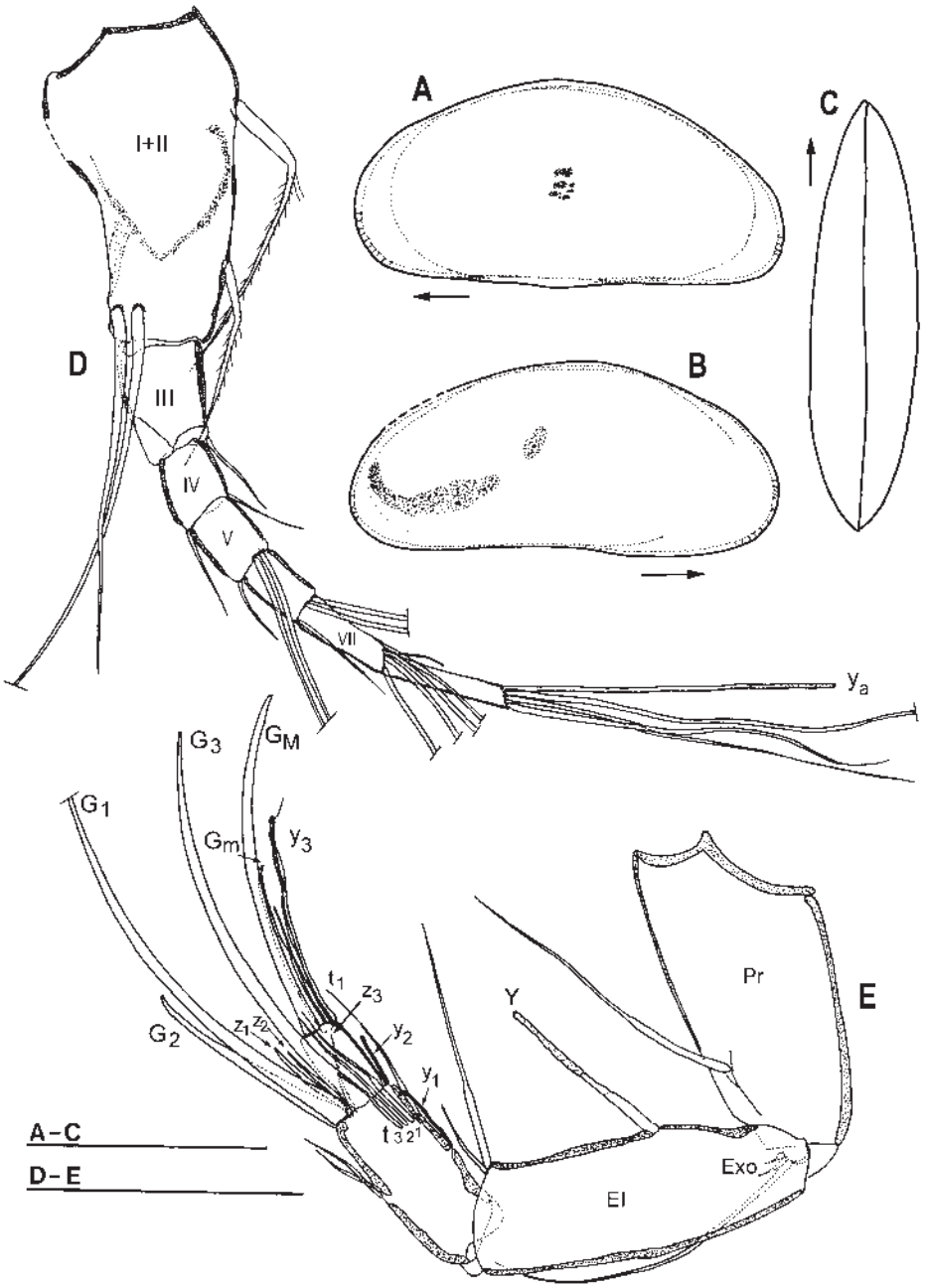


Fig. 1. *Cryptocandona dudichi* (female). A: LV, external view (valve from the tube ZMH 340). B: RV, external view (valve from the tube ZMH 340). C: carapace, dorsal view (redrawn from Klie, 1930). D: A1 (lectotype ZMH 340b). E: left A2, internal view (lectotype ZMH 340b). Scale bars: A-B: 500 µm; C: 528 µm; D-E: 100 µm.

short, sub-equal in L, c. 0.2x as long as EI. Relative lengths of the A2 claws: G_1 = 1.2 (actually slightly more since a very small apical part was broken); G_2 = 0.6; G_3 = 1.2; G_M = 1.0; G_m = 0.5. Terminal podomere additionally to the claws G_M and G_m and the so-called seta 'g' with the postero-distal aesthetasc y_3, the latter basally fused with the neighbouring seta. Aesthetasc y_3 c. 0.6x as long as EI; sensory part of this aesthetasc almost 1/4 of the total L.

Md consists of the first basal podomere of Pr (coxa) and a 4-segmented palp (second podomere of Pr and 3 podomeres of E). Coxa heavily chitinized and elongated, the ventral masticatory part (Fig. 2B) with one relatively long lateral seta, distally with 7 stout teeth and groups of various setae between them; ventrally with one hirsute seta.

Mdp (Fig. 2A): I: In-1*s*(α)-1*s*(S_2:pl)-1*m*-1*m*(S_1:pl) / II: Ex-1*m*-1*l*, In-1*s*(ß)-1*m*-3*l* / III: Ex-2*m*-1*l*, In-1*s*-3*m*, D-1*m*(ɣ)-1*m* / IV: D-4*s*-2*m*(G).

Second Md-palp podomere internally with five setae: ß-seta short and slender; a group of 3 equally long and smooth setae; one similar but shorter seta which is set more apically. The ɣ-seta smooth, similar in shape and length to the adjoining distal seta. The two claws of the terminal podomere 1.3x as long as the third palp podomere. Rake-like organ (Fig. 2C) with 11 teeth.

Mx with a branchial plate, three masticatory processes and a 2-segmented palp (Fig. 2D): I: Ex-2*m*-2*l* / II: D-4*s*-2*m*(cs).

L5 (maxilliped) (Fig. 2F). Pr bearing two anterior unequal 'a' setae and two exterior setae 'b' and 'd'. Masticatory process (endite) apically with a group of 14 setae. Exo (respiratory plate) with 3 plumed setae. E with 3 apical sub-equal setae.

L6 (walking leg) (Fig. 2E): Pr: A(D)-1*s*(d) / EI: A(D)-1*s*(e) / EII: A(D)-1*s*(f) / EIII: A(D)-2*s*(g) / EIV: P-1*s*(h_3), D-1*s*(h_1)-1*l*(h_2: G). Terminal claw serrated, 2.6x as long as EII.

L7 (cleaning leg) (Fig. 3A): Pr: Ex-2*m*(d_1,d_2), In-1*l*(d_p) / EI: P-1*s*(e) / EII: P-1*s*(f) / EIII: P-1*s*(g) / EIV: D-1*s*(h_1)-1*m*(h_2)-1*l*(h_3).

Cleaning leg conspicuously slender, 5-segmented; EII/EIII separation very weakly developed. Relative lengths of the 3 apical setae: h_1 = 0.3; h_2 = 0.7; h_3 = 1.9. Other setae as characteristic for the genus.

CR and genital lobe (Fig. 3B). Posterior CR-margin straight, anteriorly slightly rounded in the basal part. Length ratios of the anterior margin, s_a, G_a, G_p, s_p and the distance between s_p and G_p : 100 : 15 : 68 : 55 : 15 : 27. Genital lobe posteriorly with an obtuse conical expansion. Maximum oocyte diameter: c. 0.08-0.10 mm.

Male. Two decalcified valves of the tube ZMH 340 probably belonged to the dissected male of the slide ZMH 340a, but could not be allocated with confidence. The decalcification of these valves made any measurements and drawings impossible. Following Klie (1930), the male carapace, although longer and relatively broader in dorsal view, is similar in outline to that of the female.
Measurements after Klie (1930): carapace L = 0.98 mm; H = 0.48 mm (thus H/L = 0.49); W = 0.25 mm.

A1 (Fig. 3C): I+II: A-2*l*(pl), P-2*l*(pl) / III: A-1*m* / IV: A-1*s*, P-1*m* / V: A-2*l*, P-1*m* / VI: A-2*l*, P-1*m* / VII: A-1*s*-2*l*, P-2*l* / VIII: D-y_a-3*l*.

Setal equipment of A1 similar to that of the female. Aesthetasc y_a 2.5x as long as the terminal podomere; sensory part c. 1/4x the total length of that organ. L ratios of the

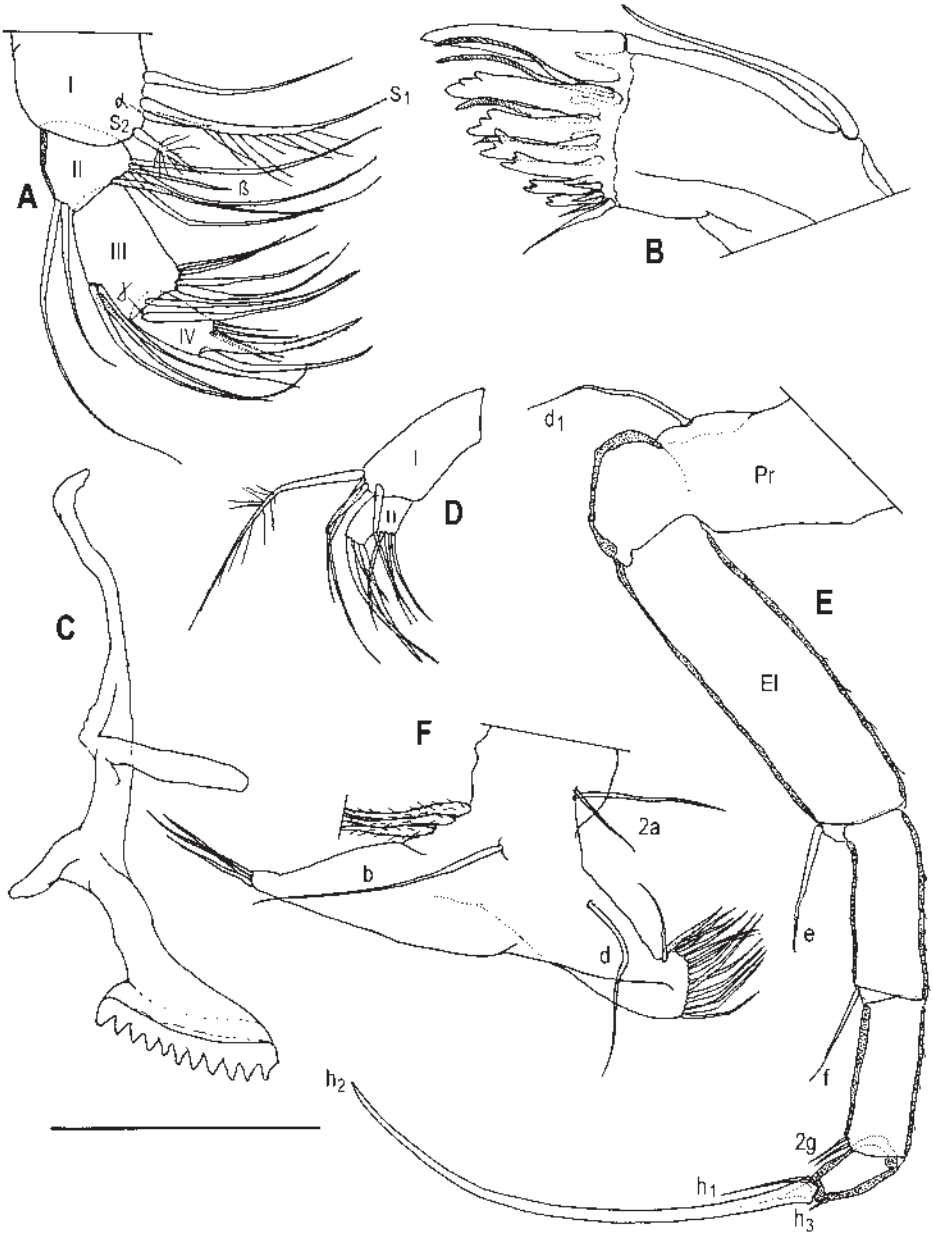


Fig. 2. *Cryptocandona dudichi* (female, lectotype ZMH 340b). A: Mdp. B: Md, distal part of coxal plate. C: rake-like organ. D: Mx palp. E: L6. F: L5. Scale bar: A, D-F: 100 µm; B-C: 40 µm.

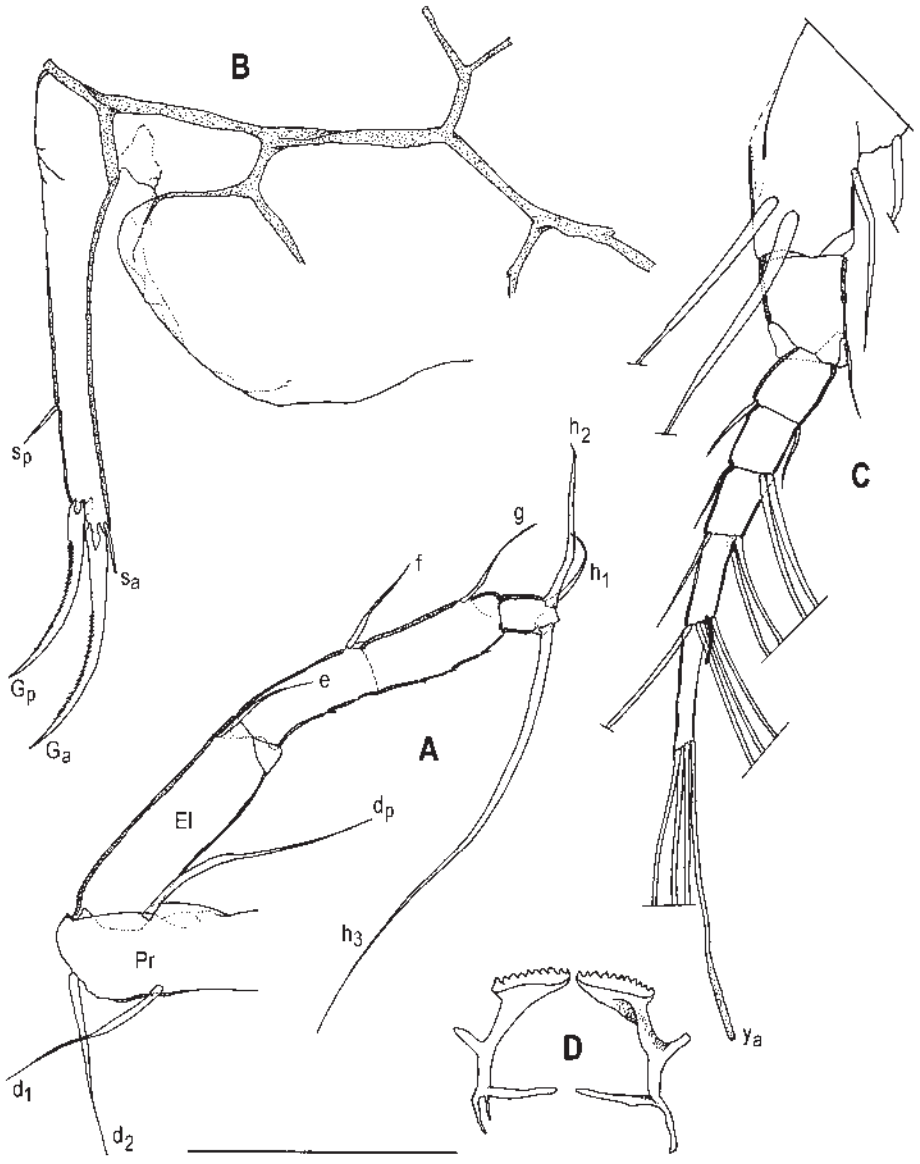


Fig. 3. *Cryptocandona dudichi* (A-B: female, lectotype ZMH 340b; C-D: male, paralectotype ZMH 340a). A: L7. B: CR, its attachment and genital lobe. C: A1. D: rake-like organs. Scale bar: A-B: 125 µm; C-D: 100 µm.

last five podomeres (IV-VIII) from proximal to distal: 1.0 : 0.9 : 1.0 : 1.4 : 1.8. L/W ratio of these podomeres, from proximal onwards: 1.2; 1.3; 1.7; 3.5; 7.0.

A2 (Fig. 4A): Pr: P-1*m* / Exo: D(Ex)-2*s*-1*l* / EI: P-Y, P(D)-1*s*-1*m* / EII: A(D)-2*s*, P-y_1, D(In)-3*s*(t_1,t_3,t_4)-1*m*(t_2) / EIII: D(P)-y_2, D(A)-1*l*(G_2), D(Ex)-2*s*(z_2,z_3)-1*l*(z_1:G), D(In)-1*s*(G_1)-1*s*(G_3) / EIV: D(A)-1*m*(G_M), D(P)-y_3-1*m*, D(Ex)-1*s*(G_m), D(In)-1*s*.

Endopod 4-segmented. Aesthetasc Y relatively slightly shorter than in the female, equalling 0.5x the length of EI; sensory part of this aesthetasc c. 1/2 of the total L. Setae t_2 and t_3 transformed into male bristles, 0.5x and 0.4x as long as EI, respectively; t_1 as long as t_3; t_4 very short. Relative lengths of the claws and setae of EIII and EIV as: G_1 (claw) = 0.4; G_2 (claw) = 1.3; G_3 (seta) = 0.5; z_1 (claw) = 1.1; z_2 (seta) = 0.5; z_3 (seta) = 0.4; G_M (claw) = 1.0; G_m (claw) = 0.4. Aesthetasc y_3 basally fused with the adjoining seta. Aesthetasc y_3 0.5x as long as EI.

Rake-like organ (Fig. 3D) with 10-11 teeth.

Mdp and Mx without sexual dimorphism.

L5 (maxilliped) (figs 4B-C). Pr and Exo as in the female. The two E developed into asymmetrically shaped prehensile palps (clasping organs), each composed of one podomere. Right palp larger, arched and distally helmet-shaped; the left one more regularly curved.

L6 (walking leg) as in the female.

L7 (cleaning leg) without sexual dimorphism. Relative lengths of the 3 apical setae as: h_1 = 0.3; h_2 = 0.7; h_3 = 1.9.

CR. Posterior claw and both setae relatively longer than in the female. Length ratios of the anterior margin, s_a, G_p, s_p and the distance between s_p and G_p as 100 : 17 : 66 : 17 : 34. Both G_a were broken.

Penis (Fig. 4D). Outer lobe ‘a’ well developed, approximately square-shaped; inner lobe ‘b’ distally rounded; medial lobe (h) wide and short. Distal end of the M process elongated.

Zenker’s organ (Fig. 4E) relatively short, with 7 internal spinous whorls.

5.2. Comments on the original description

There are several minor inaccuracies in Klie’s (1930) original description of the species.

a) Size of carapace and shape of valves. The valves of both the female type specimens and the ‘new’ material are distinctly smaller and more elongated than indicated by Klie (op. cit.) : 0.91-0.92 mm versus 0.96 mm. Similarly, the male carapaces from the new material are 0.91-0.93 mm long (the male type specimens are unsuitable for measurements to be taken), while Klie (op. cit.) mentions 0.98 mm. Measurements on the new material were independently taken by two of us (T.N. and C.M.).

b) Female A1. Our measurements indicate that the terminal segment is more elongated (L/W = 6.4 and even more in males) than indicated by Klie (1930; L/W = 5). The precise measurement of the longest A1-setae is, in general, uneasy; our estimation (2.5x the length of the last five combined podomeres) is slightly different from Klie’s statement (2x as long as the combined IV-VIII).

c) Female A2. According to Klie (1930), G_1 is approximately 4.5x as long as EIV; actually, this claw appears to be longer (at least 4.8x as long as EIV).

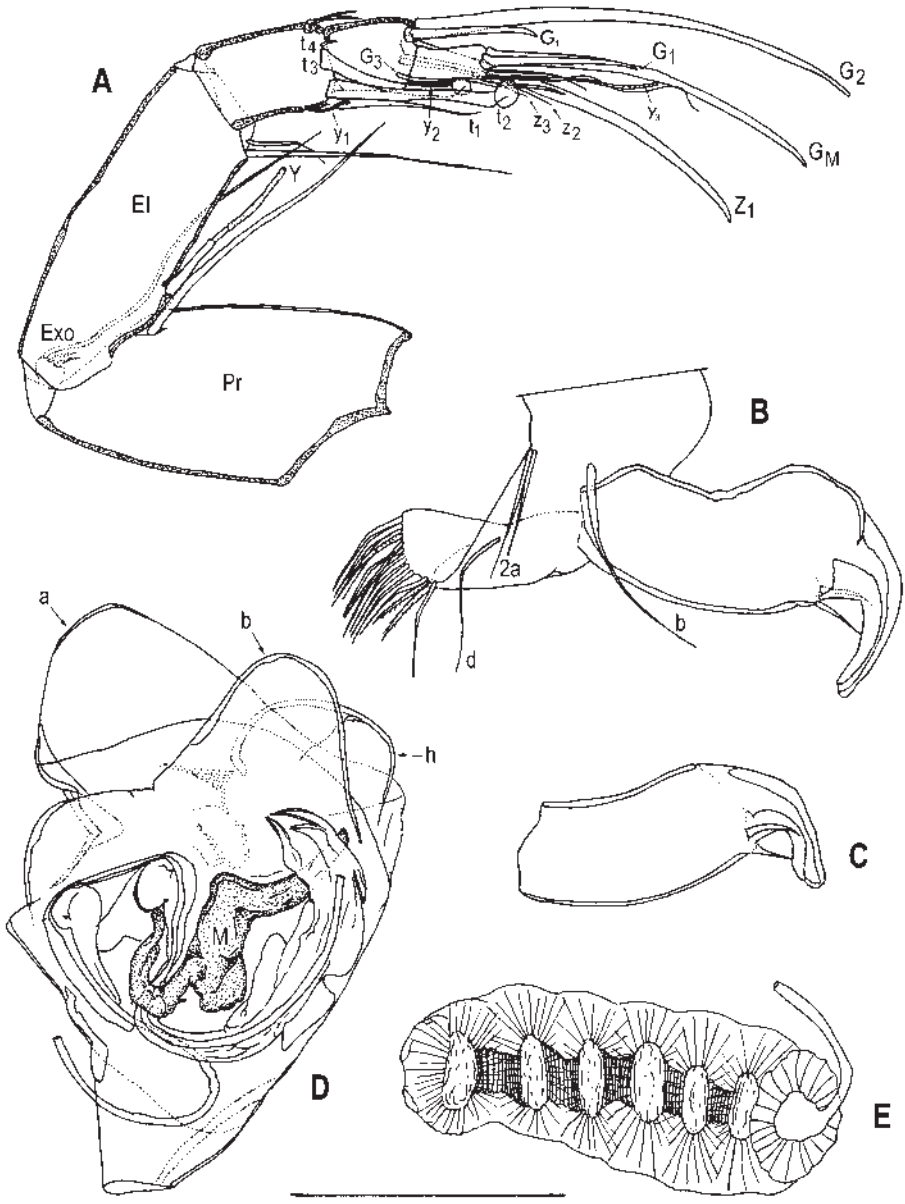


Fig. 4. *Cryptocandona dudichi* (male, paralectotype ZMH 340a). A: left A2, internal view. B: right L5 with prehensile palp. C: left prehensile palp. D: right hemipenis, internal view. E: Zenker's organ. Scale bar: A-C: 100 µm; D: 125 µm; E: 164 µm.

d) Female L7 (cleaning leg). Klie (op. cit.) writes: h_1 1.5x as long as EIV; h_2 2x as long as h_1, and h_3 almost 4x as long as h_2. Our observations were as follows: h_1 1.4x as long as EIV; h_2 2.2x as long as h_1 and h_3 almost 3x as long as h_2 (in the male even less). The main inconsistency concerns the longest seta h_3. Klie's (op. cit.) observation is most certainly erroneous since we did not notice the lack of the c. 50 μm long distal part of this seta in the lectotype.

e) Female CR. Contrary to Klie's (op. cit.) indication (s_p shorter than half the distance between G_p and s_p), s_p is actually slightly longer than half the G_p-s_p distance.

f) Male A2. Klie (op. cit.) notes that both male bristles extend beyond the distal end of EIV. Actually, only t_2 extends slightly beyond the end of the terminal segment; t_3 either reached the distal end of that segment or is slightly shorter.

g) Male left prehensile palp. The trunk is actually more rounded than in Klie's (op. cit.) description and figure.

h) Penis. The outer lobe 'a' overlaps the inner lobe 'b' (not the opposite as mentioned by Klie, op. cit.). It should be noticed that the relative length of the lobes depends somewhat on the position of the penis under the microscope and this may explain Klie's (op. cit.) erroneous observation.

5.3. Comparison of the type specimens with the new material and additional description

5.3.1. Carapace

The carapaces of the two type females from the Baradla cave (L=0.91-0.92 mm) are larger than those of the two available females collected on 24.IX.2000 in the spring Nagy Tohonya (L=0.87-0.89 mm). However, since sample sizes are low, this could be a fortuitous bias.

Valve shapes reveal other differences (compare Fis 1A,B and 5-6). The valves of the cave females are more elongated (H/L for LV=0.47 versus 0.48-0.50); both the posterior and anterior valve margins appear more acuminate that those of the spring females. In general, the cave females display a carapace shape similar to that of the last stage juveniles from the spring. Male valves from the type series were not suitable for size and shape comparisons.

It has to be stressed here that, at least in the sample taken on 24.IX.2000 in the spring Nagy Tohonya, the carapace length was sexually dimorphic (figs 5 and 6). Mean L of male LV (± S.D.)=0.925 ± 0.019 mm (n = 4); female LVs: 0.880 ± 0.014 mm (n = 2). These differences are marginally statistically significant (Student t-test: t = 2.882; d. f. = 4; p = 0.045). In contrast, the carapace shape does not display any significant differences between the sexes. As an addition to the description of the species, the carapace size of the last five juvenile stages and the adults from the Nagy-Tohonya population is shown in Fig. 7.

5.3.2. Appendages

Careful comparison of the type specimens with those recently collected from springs did not reveal any taxonomically significant dissimilarities. Most probably, the differences listed in Table 1 express the intraspecific variability of the species.

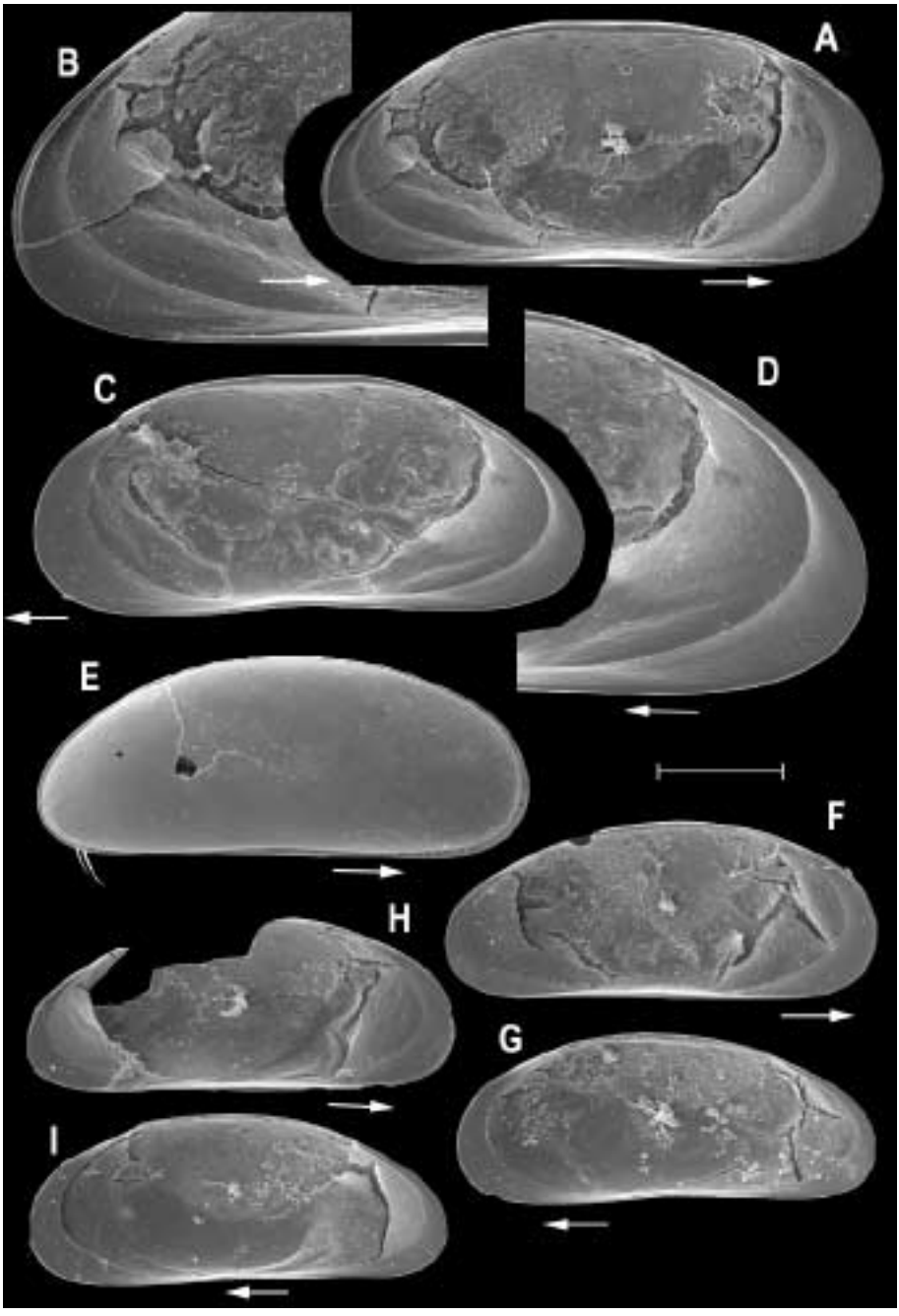


Fig. 5. *Cryptocandona dudichi*. Adult female (A-D) and juveniles (E-I). A: LV; B: posterior detail of LV; C: RV; D: posterior detail of RV; E: juvenile carapace; F and G: juvenile LV and RV; H and I: juvenile LV and RV. All single valves in internal view. Scale bar 0.20 mm for A, C and E-I.

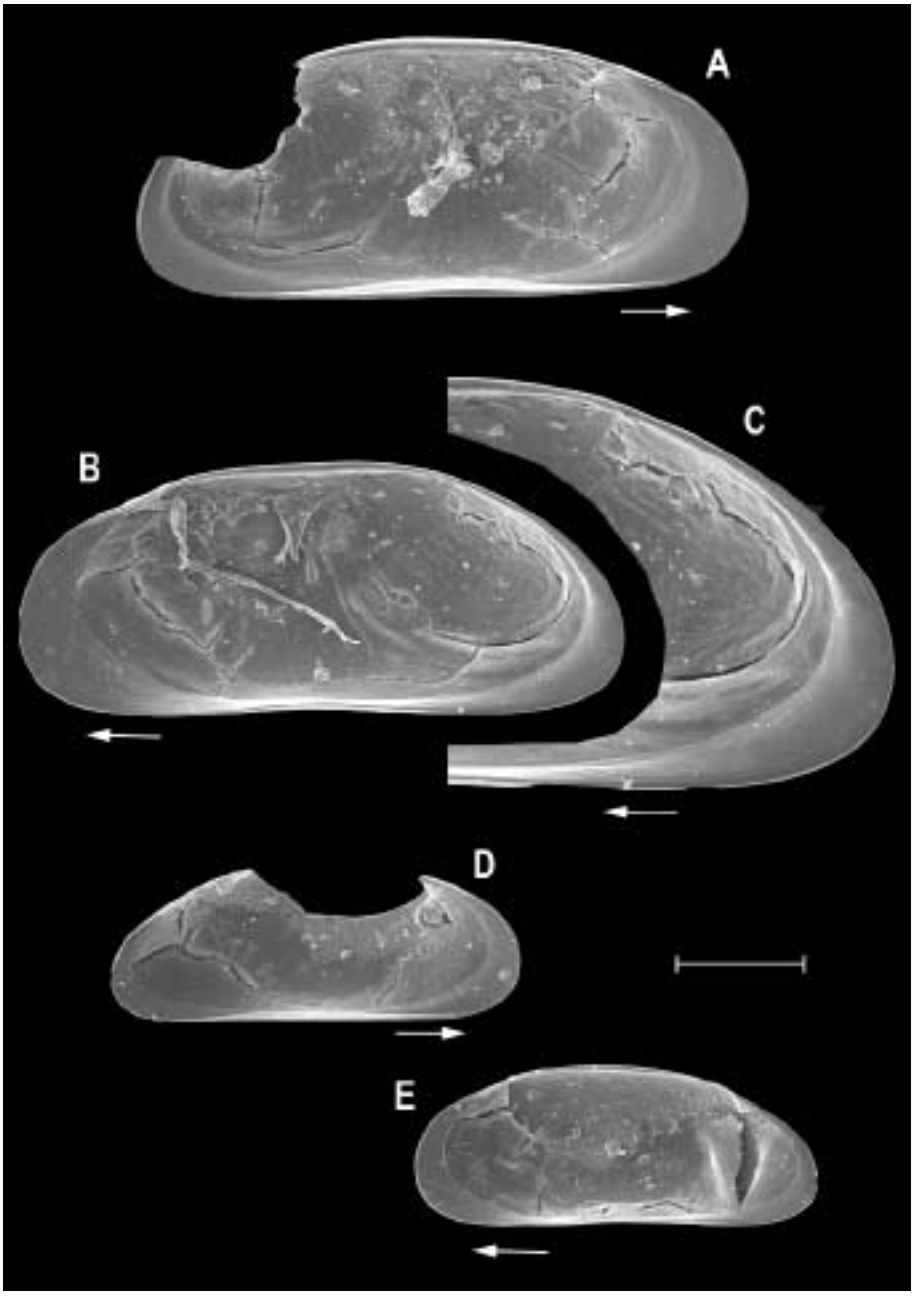


Fig. 6. *Cryptocandona dudichi*. Adult male (A-C) and juvenile (D-E). All valves in internal view. A: LV; B: RV; C: posterior detail RV; D and E: juvenile LV and RV. Scale bar 0.20 mm for A-B and D-E.

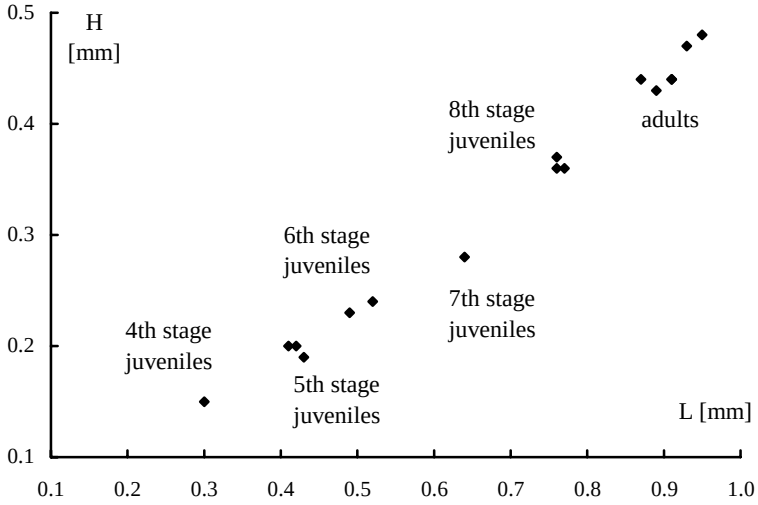


Fig. 7. *Cryptocandona dudichi*. Scatter plot of length versus height of juvenile and adult carapaces. Nagy-Tohonya spring, 24.IX.2000.

However, we would like to stress that in the females from the springs, the claws and/or aesthetascs of the antennae (G1, Y, and y_3, in particular), the mandibular and maxillular palps, and the walking legs were relatively longer than in the cave animals.

In contrast, the A1-podomeres V and VII of the cave animals were longer than those of the spring animals. The same is true for the two setae of the caudal ramus.

A very similar pattern of variability was noticed in the males (Table 1). The spring animals possessed longer setae on A2 (in particular the male bristles, setae t_1 and the sensory part of the aesthetasc y_3). The male paralectotype had relatively longer A1-podomeres; the same was true for the seta h_3 on L7, the posterior claw and the posterior seta on CR.

The question arises whether the differences in the above mentioned lengths are adaptations to the respective habitat (cave or spring). We therefore measured the absolute length (in µm) of the endopodial A2 and L6 (walking leg) podomeres combined with their longest claws (G_2 of the male A2, G_1 of the female A2 and h_2 of L6). Finally, the length ratio of the endopod combined with its longest claw and the carapace was calculated. The results are shown in Table 2.

It can be seen that the total absolute L of the female A2 and L6 are greater in the cave animals (types) than in those from the springs (Table 2, column A). However, when these limb lengths are expressed in combination with the carapace length, the opposite relation is found (Table 2, column B). Differences, in both cases, rank within the range of 2-3% and are considered insignificant. Similar values were calculated for the male antennae (3% difference between cave and spring animals).

The cave and spring males differed also in the degree of development of z_2 of A2. In the males collected from the cave, z_2 is a seta; it is stronger developed, claw-like in the males coming from the spring. The female z_2 is always a seta.

Table 1. *Cryptocandona dudichi*. Limb characters of the type specimens (Baradla cave) and animals collected from the karst spring Nagy-Tohonya. See text for explanation.

	Character	Cave specimens (types)	Spring specimens
	Females		
A1	ant. and post. setae on podomeres IV and P seta on podomere VI	short	medium
	L ratios of podomeres IV-VIII	1.0 : 0.9-1.0 : 0.9-1.0 : 1.3-1.4 : 1.7-1.8	1.0 : 0.8 : 1.0 : 1.2 : 1.7
	L/W ratios of pod. IV-VIII	1.2; 1.3; 1.7; 3.2; 6.4	1.1; 1.1; 1.6; 2.8; 5.9
A2	relative L of		
	- aesthetasc Y (sensory part)	0.5 (c. 50%)	0.6 (60%)
	- aesthetasc y2	0.2	0.3
	- aesthetasc y3 (sensory part)	0.6 (c. 25%)	0.7 (40%)
	- claw G1	c. 1.2	1.4
	- claw G2	0.6	0.7
	- claw G3	1.2	1.2-1.3
	- claw GM	1.0 (medium)	1.1 (large)
	- free standing seta on EIV	< 0.5 (short)	0.7 (medium)
Mdp	seta S1	medium	large
	relative L of 2 distal claws	1.3	1.5
Mx palp	relative L of outer distal claw	2.4	2.7
	relative L of inner distal claw	2.1	2.4
L6	relative L of h2	2.6	2.7
L7	seta dp	large	medium
CR	relative L of ant. margin : sa : Ga : Gp : sp and dist. sp-Gp	100 : 15 : 68: 55 : 15 : 27	100 : 12 : 67 : 60 : 12 : 27
	Males		
A1	post. seta on podomere V	medium	short
	relative L of y_a	2.5	2.4
	relative L of pod. IV-VIII	1.0 : 0.9 : 1.0 : 1.4 : 1.8	1.0 : 0.8 : 0.8 : 1.2 : 1.6
	L/W ratios of pod. IV-VIII	1.2; 1.3; 1.7; 3.5; 7.0	1.3; 1.2; 1.6; 2.8; 6.7
A2	relative L of		
	- seta t1	0.4 (short)	0.5-0.6 (sh.-medium)
	- male bristle t2	0.5	0.6
	- male bristle t3	0.4	0.5
	- claw G1	0.4	0.3-0.4
	- claw G2	1.3	1.2-1.3
	- seta G3	0.5	0.4-0.5
	- z2	0.5 (seta)	0.4-0.6 (claw-like)
	- seta z3	0.4	0.2-0.4
	- claw Gm	0.4	0.4-0.5
	- aesthetasc y3 (sensory part)	0.5 (50%)	0.4-0.6 (60%)
L7	relative L of seta h3	1.9	1.8
CR	relative L of ant. margin : sa : Ga : Gp : sp : dist. sp-Gp	100 : 17 : ? (broken) : 66 : 17 : 34	100 : 17 : 63 : 51 : c. 10 : 32

Reproductive organs: the penis, the male clasping organs, as well as the shape of female genital lobes of the type animals were in perfect agreement with those collected from the springs. The length of the Zenker's organ of the spring males represented 25% of the carapace length; 27% in the male paralectotype.

Table 2. *Cryptocandona dudichi*. Morphometric data on the absolute lengths of endopodial podomeres and the largest claws of the antennae and walking legs (in µm) in females and males collected from different habitats as well as relative length of these limbs as compared with carapace length. A : absolute L (in µm) of a given limb (antenna or walking leg) combined with its largest claw; B : length ratio (in %) between the absolute L of a given limb and the carapace.

Female antennae							
	L of EI	L of EII+III		L of EIV	L of G1	A (µm)	B (%)
Cave specimens (types)	125	67		33	158	383	42
Spring specimens	114	76		33	157	380	44
Female walking legs							
	L of EI	L of EII	L of EIII	L of EIV	L of h2	A (µm)	B (%)
Cave specimens (types)	133	68	61	33	178	473	51
Spring specimens	125	65	56	33	171	450	52
Male antennae							
	L of EI	L of EII	L of EIII	L of EIV	L of G2	A (µm)	B (%)
Cave specimens (types)	127	46	33	25	162	393	40
Spring specimens	128	51	36	27	162	403	43

6. Differential diagnosis

Only the species of *Cryptocandona* occurring in western and central Europe are considered here, i.e. *C. vavrai* Kaufmann, 1900; *C. reducta* (Alm, 1914)*, C. kieferi* (Klie, 1938); *C. leruthi* (Klie, 1936); *C. phreaticola* (Kiefer & Klie, 1927) and *C. matris* (Sywula, 1976).

C. dudichi differs in the following features from those species.

When seen laterally, the carapace of *C. dudichi* is readily recognized by the approximate mid-length position of the greatest H and above all the postero-dorsal margin which slopes very characteristally towards the posterior end, the latter appearing more narrowly rounded than the anterior one. In *C. reducta*, the greatest H is situated about at mid-length, but both ends are similarly rounded, the carapace appearing therefore almost symmetrically shaped (fig. 82A,B in Meisch 2000). In the remaining species considered here, the greatest H is distinctly situated behind mid-length.

Antennula (A1): (a) Posterior seta on the VIth podomere present; this character is shared with the remaining species, except *C. vavrai,* which lacks this seta; (b) relative L of the terminal (VIIIth) podomere (IVth used as reference) greater than 1.5 in *C. dudichi* and the remaining species, except *C. reducta*, where this value is inferior to 1.5; (c) length ratio of podomeres VII+VIII to the length of podomeres IV+V+VI > 1 in *C. dudichi*, which shares this character with the other species, except *C. reducta*, where this value is inferior to 1.

Cleaning leg (L7): seta h1 relatively long, not recurved downwards, similar to that of the remaining species, except *C. vavrai* (h1 recurved downwards, hook-like in the latter species).

Female genital lobe posterioly with a conical expansion; a similar expansion is present in *C. phreaticola* and *C. matris,* but missing in *C. vavrai, C. kieferi, C. reducta* and *C. leruthi*.

Penis: the outer distal lobe ‘a’ is the longest; this is also seen in *C. matris* (but the lobe ‘a’ of that species bears a characteristic latero-distal inner spine (Sywula 1976: fig. 3e) and *C. phreaticola*.

7. Distribution, ecology, life history and reproduction

Cryptocandona dudichi is presently exclusively known from the Baradla cave and three springs of the karst area in the environs of Aggtelek, close to the Slovakian border, in north-eastern Hungary. From this it might be concluded that the species is endemic to the (West) Carpathians. However, considering that, up to now, the identification of the species was uneasy, it may be that future investigations will expand the known distribution.

Klie (1930) notes that *C. dudichi* was collected four times from two sites in the Baradla cave: (a) a puddle filled in March with thaw water from the karst surface and located at 5350 m from the main entrance to the cave (1 female collected on 29.IX.1929; 2 females and 1 male on 27.XI.1929), and (b) a rock-pool situated at 5750 m from the main entrance (one RV and one LV on 29.VII.1929 and 20.XII.1929, respectively).

Unidentified valves and juveniles of the genus *Candona* s.l. excepted, the only other ostracod in the Baradla-collection examined by Klie (op. cit.) was the epigean *Pseudocandona pratensis* (Hartwig, 1901); the latter did not co-occur with *C. dudichi*.

In 2000, one of us (Z.G.) has carried out extensive investigations into the springs of the Aggtelek karst and the Baradla cave. In November 2000, the sampling in the Baradla cave yielded one single juvenile and a number of empty valves.

From June to August 2000, live animals were found in one spring (Nagy-Tohonya) and empty valves in two others (Medvekerti and Kecskés springs). The three sites are rheocrenic carstic springs.

The Nagy-Tohonya spring, near the village of Jósvafő (about 2.0 km NE of Aggtelek), originates close to the entrance of the Kossuth-cave, being fed by the stream that flows from the cave; the connection with the cave water is subterranean, except at the time of heavily rising water. The animals were collected from the small, slowly flowing branches of the spring, where the substrate was sandy and rich in organic material. No animals were found in the main branch of the spring, the water of which flows very swiftly over gravelly ground. The water of the Nagy-Tohonya spring has a temperature around 13°C, being several degrees higher than that of the other springs in the area; the spring is indeed connected to deep, warm subterranean waters. The Nagy-Tohonya spring flows into the Jósva stream, a tributary of the Bódva stream; the latter flows into the river Sajó, which is a tributary of the river Tisza.

Both the Medve-kerti and Kecskés springs are located close to the village of Szögliget, at 4.9 km and 6.0 km NNE of Aggtelek. Both flow into the Ménes stream, which is a tributary of the Jósva stream. Medve-kerti is a relatively large, fast flowing, stream-like spring. The substrate at the sampling site consisted of gravel and coarse sand. The Kecskés spring, which originates upside in the hill, is smaller; its substrate consisted mainly of fine grained sand overlaid with small patches of organic sediments.

The data above indicate that *C. dudichi* is a stygobitic species which inhabits caves, the benthic zone of springs, and, possibly, the hyporheic habitat. The findings in 1930

and 2000 (only valves) at Baradla show that the species is a permanent inhabitant of that cave. The occurrence of sexually mature adults from September to late November at Baradla (1930, types) indicates that the species maintains a perennial population in the cave, being therefore a permanent form under cavernicolous conditions. Nothing else is known of the life history.

Reproductive modes of freshwater ostracods appear most diverse and are currently the subject of extensive investigations (for reviews, see the volume edited by Martens 1998). As the samples from both the Baradla cave and the surrounding springs comprise both sexes in about equal numbers, it may be concluded that *C. dudichi* belongs to the species with full bisexual reproduction, a group which includes also *C. matris* and, most probably, *C. kieferi*, *C. leruthi* and *C. phreaticola*. The two remaining western and central European species, *C. vavrai* and *C. reducta*, reproduce mainly parthenogenetically, although populations with so-called 'rare males' were recorded for both. For example, males of *C. reducta*, which species is widely distributed throughout Europe, are to date known from three sites only; recently, no male was found among c. 110 females collected from springs and the interstitial habitats in Luxembourg (leg. R. Gerecke and I. Schrankel, det. C.M., unpublished data). Males appear to be similarly rare in *C. vavrai*, for which too they are so far known from three sites only; the above mentioned recent survey in Luxembourg produced c. 750 females of that species, amongst which one single male was detected. (For a review of the occurrence of males in *C. reducta and C. vavrai* see Meisch 2000).

8. Paedomorphosis in the cave specimens of *C. dudichi*

Paedomorphosis is a general term designating the retention of youthful ancestral features by adult descendants (Gould 1977: 179). The cavernicolous animals of *C. dudichi* exhibit two paedomorphic characters: (a) the carapace shape of the adult female and (b) the z2 seta of the adult male A2 (see above). In itself, this finding is not surprising as paedomorphic characters are known to occur in stygobitic ostracod species (e.g. Danielopol 1978, Danielopol & Cvetkov 1979, Danielopol et al. 1990, Horne et al. 1998, Marmonier et al. unpubl. data) as well as in various other stygobitic animals belonging to groups as diverse as the Crustacea Syncarida (Schminke 1981, Coineau 2000), fishes and amphibians (Sket & Arntzen 1994, Weber 2000, Langecker 2000).

Concerning ostracods, Danielopol et al. (1990) have shown that the carapace shape of the adult females of *Cytherissa lacustris* (Sars, 1863) and *C. tuberculata* Bronshtein, 1930 present a neotenic shape when compared with various other species of *Cytherissa* and/or with members of the related genus *Cyprideis,* e.g., *Cyprideis torosa* (Jones, 1850). The adult male of *Mixtacandona juberthieae* Danielopol, 1978, a stygobitic ostracod, has untransformed, female-like t2 and t3-setae on the antenna, while in the other Candoninae (e.g. the species of the genus *Candona*) these setae are modified into so-called male bristles; similarly, the male A2 endopodial segments 2 and 3 are only partially separated (in general totally so in the other male candonines) (Danielopol 1978). The testes of *Mixtacandona pietrosanii* Danielopol & Cvetkov, 1979 consist of only three seminiferous tubules, while there are generally four such tubules in epigean candonines (Danielopol & Cvetkov 1979). Furthermore, 'immaturity' of a few characters of the carapace (ornamentation, hinge and marginal zones) was found in a number of marine cytheroid genera (Kamyia 1992, Tsukagoshi 1994).

In general, paedomorphosis may result from two distinct processes: (a) progenesis, which is produced by accelerated maturation, and (b) neoteny, which is due to retardation of somatic development (Gould 1977). We believe that the paedomorphic characters of the cave animals of *C. dudichi* (see above) result from neotenic processes, i.e. slowing or arrested growth during post-embryonic development, mainly from the last juvenile stage to the adult one. Neoteny generally affects either the size and shape of the entire body or selected morphological features (Gould 1977, Raff 1996). The comparison of both juveniles and adults of *C. dudichi* from the Baradla cave with spring animals revealed that the neoteny detected affects the carapace shape and the z2-seta.

The particular interest of *C. dudichi* comes from the existence, within one species, of both animals with 'normal' development living in springs and neotenic individuals found in the Baradla cave. In fact, this is the first record of an ostracod having both paedomorphic populations and others with 'normal' development. From the observation that (a) the epigean population has normally developed adults and (b) the carapace shape of the 8th juvenile stage of the spring animals is seen in the adults of the cave animals, we infer that the cave neoteny is the derived state and, consequently, that the spring animals display the primitive condition. From this it follows that the individuals living in the karstic springs do not originate, were not washed out from the cave (this is often seen in springs fed by waters flowing from karstic systems) but belong to populations from which the cave habitats were colonized.

The question arises whether the neotenic characters of *C. dudichi* are adaptations to the cave conditions. The posteriorly elongated carapace could be adapted to the life in interstitial habitats (Coineau 2000), but this must not be considered here; alternatively, this shape could be an adaptation to the oligotrophic conditions of the cave. Future investigations should address this problem through the comparative study of the life histories of the cave and spring animals.

The taxonomic status of the two forms raises another important question. Dealing with a similar problem in the amphibian *Proteus anguinus* from springs and caves in Slovenia, Sket & Arntzen (1994) described the spring animals as belonging to a new subspecies, *P. anguinus parkelj* (the cave animals are assigned to *P. anguinus anguinus*). However, as we did not notice any differences in the morphology of the sexual appendages, which have been shown to play an important function in sexual isolation and speciation (Horne et al. 1998), we consider the spring and cave animals of *C. dudichi* two morphs belonging to one single species. A similar position was recently adopted by Culver & Wilkens (2000) and Weber (2000) for the fish *Astyanax mexicanus*; in that species, the cave animals, which are blind and lack any body pigment, can breed and produce fertile hybrids when brought into contact with individuals from surface waters.

The next question is about the mechanism(s) that induce(s) neoteny in *C. dudichi*. As in troglomorphic cave vertebrates (the fish *Astyanax mexicanus* and representatives of the amphibian genera *Proteus*, *Typhlomolge*, etc), the two paedomorphic characters of the cave animals of *C. dudichi* might result from some genetic or physiological (endocrinal) malfunction occurring during the last stages of the post-embryonic development (discussion in Weber 2000, Langecker 2000). In that case, the evolutionary process is not driven by the selective pressure of cave conditions but is due to 'neutral evolution', which may start either outside or inside the cave. However, Culver & Wilkens (2000) and also Sbordoni et al. (2000) have shown that originally

'neutral' characters may later become adaptive features selected for under given environmental conditions, particularly in caves, where these features may provide an energetic solution to the oligotrophic conditions found there. The neotenic male z2-seta of *C. dudichi* has probably no adaptive value because the energetic expense connected with the reinforcement of that seta into a claw would be minimal; therefore, a neutral evolutionary mechanism is the most parsimonious explanation.

The elongate neotenic carapace shape of the cave animals: this character might be adaptive, as recently speculated by Baltanás et al. (2000). Alternatively, if this shape evolved through neutral processes, then this would be a preadaptive feature which, in the course of evolution and under conditions that specify *K* selection, might be directionally modified into either the triangular or acuminate shape that is seen in a number of other hypogean ostracods. A similar mechanism was described by Culver & Wilkens (2000) for the cave populations of the amphipod *Gammarus minus*. From this it follows that the phylogenetic age of the cavernicolous population (i.e. the time elapsed since the separation from the epigean relatives) is of great importance for the appearance of cave adapted features. Considering various cavernicolous populations with close epigean relatives, both Langecker (2000) and Sbordoni et al. (2000) stress that the slight morphological differences between the epigean and hypogean morphs are due to the evolutionary short time spent by animals within the cave environment. We rather believe that this consideration also applies to the Baradla population of *C. dudichi* and that therefore this ostracod could become a paradigmatic animal for the study of the evolutionary biology of ostracods and evolutionary topics in general.

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