Neglecandona altoides (Petkovski, 1961) nov. comb. and the genus *Neglecandona* Krstić, 2006 (Crustacea, Ostracoda, Candonidae)

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Meisch, C., B. Scharf, R. Fuhrmann & A. Thiéry, 2019. *Neglecandona altoides* (Petkovski, 1961) nov. comb. and the genus *Neglecandona* Krstić, 2006 (Crustacea, Ostracoda, Candonidae). *Bulletin de la Société des naturalistes luxembourgeois* 121: 237–264.

Abstract. The freshwater ostracod *Candona altoides* Petkovski, 1961, a member of the Candoninae Kaufmann, 1900 of Candonidae Kaufmann, 1900 is redescribed from material collected in North Macedonia, Serbia, southern France, Corsica included, and Germany. The species is transferred to the genus *Neglecandona* Krstić, 2006: *Neglecandona altoides* (Petkovski, 1961) nov. comb. The distribution, the ecology, the life history and the fossil record of the species are reviewed. *Neglecandona altoides* nov. comb. is new to France and Italy. The genus *Neglecandona* Krstić, 2006 is reassessed and an amended generic diagnosis based on characters of both the carapace and appendages is provided. 36 extant species are formally transferred to *Neglecandona*. The genus now comprises 39 extant species.

Key words. Ostracoda, Candonidae, Candoninae, *Neglecandona*, *Neglecandona altoides* nov. comb., Branchiopoda, taxonomy, distribution, temporary waters.

1. Introduction

Up to the early 2000s the ostracod genus *Candona* Baird, 1845 was generally considered to comprise two divergent lineages classified as separate species groups: the *candida*-group, with species around *Candona candida* O.F. Müller, 1776, and the *neglecta*-group, with *Candona neglecta* Sars, 1887 as a reference (Klie 1939; Meisch 2000; Petkovski et al. 2002).

Krstić (2006) formally introduced the genus *Neglecandona* for the *neglecta*-group of species, with *Candona lindneri* Petkovski, 1969 as type species and assigned two extant (*N. lindneri* and *N. neglecta*) as well as nine fossil species to the new genus. More recently, one other species, *N. angulata* (G.W. Müller, 1900) Medici et al., 2011 was transferred there (Meisch et al. 2019).

Neglecandona altoides (Petkovski, 1961) nov. comb. was first described from North Macedonia and Bulgaria (Petkovski 1959, 1961, 1964). The original descriptions (Pekovski op. cit) were very brief and comprised illustrations of the left valve, the female posterior end of body, and the penis only. A comprehensive description of the species, including characters of both the carapace and appendages is still missing at present.

The author of the genus *Neglecandona* Krstić, 2006, being a palaeontologist, presented an original diagnosis of the genus based on characters of the carapace only. Therefore, diagnostic features of the soft parts had been missing up to now.

We here present (a) a redescription of *Neglecandona altoides* (Petkovski, 1961) nov. comb. from material collected in North Macedonia, Serbia, France and Germany; (b) an amended diagnosis of the genus *Neglecandona* Krstić, 2006 comprising characters of both the carapace and appendages; (c) the formal transfer of all the species of the former *neglecta*-group of species to the genus *Neglecandona* Krstić, 2006.

Table 1. Distribution of extant populations of *N. altoides* (Petkovski, 1961) nov. comb. Sites with material examined by the present authors are marked with ●, those taken from the literature with o. Site numbers and symbols are the same than those used in Fig. 1.

Abbreviations: A.T., Alain Thiéry; R.F., Roland Fuhrmann; T.P., Trajan Petkovski. *C. bispinosa*, *Cypris bispinosa* Lucas, 1849; *C. candida*, *Candona candida* (O.F. Müller, 1776); *C. lacustris*, *Cypria lacustris* Lilljeborg, 1890; *C. ovum, Cyclocypris ovum* (Jurine, 1820); *C. vidua*, *Cypridopsis vidua* (O.F. Müller, 1776); *E. virens, Eucypris virens* (Jurine, 1820); *H. chevreuxi, Herpetocypris chevreuxi* (Sars, 1896); *H. incongruens*, *Heterocypris incongruens* (Ramdohr, 1808); *H. rotundata*, *Heterocypris rotundata* (Bronstein, 1928); *I. gibba*, *Ilyocypris gibba* (Ramdohr, 1808); *N. lindneri*, *Neglecandona lindneri* (Petkovski, 1969); *P. karamani*, *Paralimnocythere karamani* (Petkovski, 1960); *P. albicans, Pseudocandona albicans* (Brady, 1864); *P. marchica*, *Pseudocandona marchica* (Hartwig, 1899); ad., adult; subad., subadult; juv., juvenile.

Site Fig. 1		Country	Locality	Coordinates	Publication/ date of collection/ collector	Cp or LV lengths (in mm)/Sexes/ ad./subad./juv.	Habitat	Co-occurring ostr. species
1	o	S North Macedonia	Stepanovo/ Gevgelija	41°15'N 25°19'E	Petkovski 1959		Pond	
2	o	N North Macedonia	Aracinovsko blato (near Skopje)	42°00'N 21°25'E	Petkovski 1964		Swampy temporary pools	
3	●	S North Macedonia	Vitačevo highlands, S Kavadarci	41°15'52"N 22°03'16"E	7.4.1975, T.P.	♂ 1.40-1.50 n=5 ♀ 1.37-1.40 n=4	Grassy temp. pools	*H. chevreuxi* *C. ovum*
4	o	Bulgaria	5-6 km from Black Sea	42°19'41"N 27°45'19"E	Petkovski 1964	1 ♀	Swampy roadside pool	
5	●	S Serbia	Near Vlasina reservoir	42°40'42"N 22°20'54"E	2.6.1973, T.P.	♂ 1.43-1.46 n=2 ♀ 1.24-1.31 n=4	Pools in swampy area	*N. lindneri* *C. lacustris* *C. vidua*
6	o	E Montenegro	River Matica	43°N 19°E	Karanovic & Petkovski 1999		Pond	*C. candida* *C. vidua* *P. karamani*
6	o	E Montenegro	Prokletije, spring Medun	42°35'N 19°56'E	Karanovic 2007		Swampy temp. pools in meadowland	
7	●	France, S Corsica	Frasselli pond 1 of Tre Paduli de Frasselli, Natura 2000, FR9400608, 135 m a.s.l.	41°27'12"N 9°10'05"E	19.3.2009, A.T.	1 ♂	Temp. pond	*E. virens* (♀ only)
8	●	France, Var	Bonne Cougne Natura 2000, FR9301621 236 m a.s.l.	43°20'37"N 6°15'36"E	31.10.2001, A.T. 8.12.2008, id. 26.8.2009, id. 20.1.2010, id. 25.4.2010, id. 19.2.2012, id. 28.7.2014, id. 15.1.2014, id. 14.5.2014, id. 13.11.2015, id.	Many spms from 2001-2015, sexes and instars not registered	Temp. pond	*E. virens* *C. bispinosa* *T. lutaria* *I. gibba* *P. albicans*

9	●	France, Var	Évenos, Parc naturel régional de la Sainte-Baume 589 m a.s.l.	43°12'42"N 5°51'10"E	8.6.2012, A.T.	1 ♀ 1.43	Artificial temp. pool	*E. virens H. incongruens*
10	●	France, Var	Figanières, pond 1, 305 m a.s.l.	43°34' 34"N 6°30'52"E	20.1.2010, A.T. 13.11.2011, id.	13 spms: ad. ♂ and ♀ and juv. 22 subad.: 15 ♂ 0.99-1.09 7 ♀ 0.95-0.97	Temp. pond	*E. virens P. marchica*
10	●	France, Var	Figanières, pond 2, 302 m a.s.l.	43°34' 35"N 6°31'3"E	29.1.2012, A.T. 19.2.2012, id. 11.11.2013, id.	3 ad. ♂, 8 ad. ♀, 8 juv. 2 ♂ 8 ad.: 6 ♂ 1.43-1.53 2 ♀ 1.26-1.28	Temp. pond	*E. virens C. ovum P. marchica C. bispinosa*
11	●	France, Var	Lake Redon, Natura 2000, FR9301621, 252 m a.s.l.	43°20'42"N 6°14'10"E	10.1.2012, A.T.	1 ♀ empty cp, 1.33	Temp. pond	*E. virens C. ovum H. rotundata H. salina*
12	o	Italy	Prov. Parma, Langhirano, Costa di Castrignano	44°36'N 10°13'E	Rossetti et al. 2006	♂ 1.56-1.72 n=2 ♀ 1.60-1.63 n=3	Temp. pool	
13	●	Germany, Saxony	Steinbach, NE Borna	51°09'40"N 12°28'58"E (average)	5.9.1981, R.F. 17.1.1983, id. 7.4.1984, id.	♂ 1,28-1.31 n=2 ♀ 1.22 n=1	2 fish ponds	See Material and methods
14	●	Germany, Saxony	Eschefeld near Frohburg	51°02'40"N 12°32'37"E (average)	5.4.1982, R.F. 20.5.1984, id.	♂ 1.34-1.50 n=18 ♀ 1.22-1.31 n=20	5 fish ponds	Idem
15	●	Germany, Thuringia	Windischleuba, NE Altenburg	51°01'20"N 12°28'50"E (average)	9.8.1983, R.F. 15.4.1984, id.	♂ 1.36-1.42 n=3 ♀ 1.21-1.27 n=3	7 fish ponds	Idem

2. Material and methods

2.1. Material studied

The material of *Neglecandona altoides* comb. nov. studied comes from the South of North Macedonia, Serbia, southern France (department of Var in the Provence region, and Corsica), and Germany (Saxony and Thuringia). A detailed list of the sites and the collectors of the samples studied is presented in Table 1.

2.2. Methods

The samples taken by two of us (R.F. and A.T.) and also those collected by T. Petkovski were collected with a hand net. All specimens are preserved in 70% ethanol.

The higher classification follows Horne et al. (2002). The chaetotaxic scheme follows Broodbakker & Danielopol (1982), Martens (1987) for the second antenna, and Meisch (1996, 2000, 2007) for the three pairs of thoracopods (T1-3/L5-L7) and the uropodal ramus (the latter here designated as U-ramus for shortness).

Drawings of the appendages were made by the second author (B.S.) from specimens collected from temporary pools of the Vitačevo highlands, south of Kavadarci in North Macedonia, and pools in a swampy area in the vicinity of Vlasina reservoir in southern Serbia (site numbers 1 and 3 in Fig. 1) (leg. Dr Trajan Petkovski). Both localities were selected for their geographical proximity to the sites where the type material in North Macedonia was collected. Alain Thiéry collected a very large number of samples of various invertebrates in water bodies of the Provence region and Corsica. Identifications of the ostracods were made by the first author.

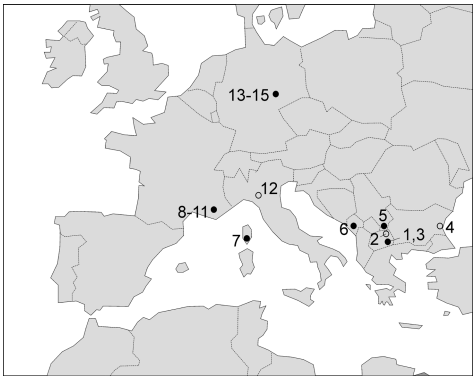


Fig. 1. Distribution of *Neglecandona altoides* (Petkovski, 1961) nov. comb. Same symbols as in Table 1.

The drawings were checked against dissections made from animals coming from the entire material studied (Table 1). SEM images were taken in the SEM-laboraties of the Zoological Institute of the University of Hamburg, Germany (courtesy of Dr Dietmar Keyser), and the Royal Institute of Natural Sciences of Brussels, Belgium (courtesy of Prof. Koen Martens).

Species of ostracods co-occurring with *N. altoides* in ponds in Saxony and Thuringia (Germany) are too many to be included in Table 1 and they are therefore presented here below. All species were collected and identified by R.F. When the first two authors disagree with the taxonomic status of a given species, the species is marked with 'syn. of …, fide …, at the first occurrence (not repeated later in the lists).

Steinbach (locality 13 in Table 1). Adults: *Fabaeformiscandona fabaeformis*, *Pseudocandona insculpta*, *Ilyocypris monstrifica*, *Physocypria kraepelini*, *Cypria ophtalmica*, *Cypridopsis vidua*, *Potamocypris arcuata*, *Potamocypris unicaudata*, *Limnocythere inopinata*. Juveniles only: *Neglecandona neglecta*, *Fabaeformiscandona caudata*, *Pseudocandona parallela* (syn. of *Pseudocandona albicans*, fide Meisch et al. 2019), *Candonopsis kingsleii*. Valves only: *Candona candida*, *Dolerocypris fasciata*, *Ilyocypris biplicata* (syn. of *I. gibba*, fide Meisch et al. 2019), *Ilyocypris gibba*, *Cypris pubera*, *Plesiocypridopsis newtoni*.

Eschefeld (locality 14 in Table 1). Adults**:** *Candona candida*, *Neglecandona neglecta*, *Fabaeformiscandona caudata*, *Fabaeformiscandona protzi*, *Pseudocandona insculpta*, *Pseudocandona parallela*, *Cyclocypris humilis* (?syn. of *C. ovum*, fide Meisch et al. 2019), *Cyclocypris ovum*, *Physocypria kraepelini*, *Cypria ophtalmica*, *llyocypris bradyi*, *Bradleystrandesia hirsuta*, *Eucypris virens*, *Cypridopsis vidua*, *Potamocypris unicaudata*, *Limnocythere inopinata*. Juveniles only: *Candonopsis kingsleii*, *Ilyocypris biplicata*, *Cypris pubera*. Valves only: *Fabaeformiscandona fabaeformis*, *Ilyocypris gibba*, *Ilyocypris monstrifica*, *Bradleystrandesia affinis* (syn. of *B. reticulata*, fide Meisch et al. 2019), *Notodromas monacha*, *Plesiocypridopsis newtoni*.

Windischleuba (locality 15 in Table 1). Adults: *Cyclocypris ovum*, *Physocypria kraepelini*, *Tonnacypris lutaria*, *Plesiocypridopsis newtoni*, *Cypridopsis vidua*, *Potamocypris arcuata*, *Potamocypris unicaudata*. Juveniles only: *Fabaeformiscandona caudata*, *Pseudocandona insculpta*, *Pseudocandona parallela*. Valves only: *Candona candida*, *Fabaeformiscandona fabaeformis*, *Ilyocypris biplicata*, *Ilyocypris gibba*, *Ilyocypris monstrifica*, *Cypris pubera*, *Eucypris virens*, *Bradleystrandesia affinis*, *Notodromas monacha*, *Heterocypris incongruens*, *Limnocythere inopinata*.

Abbreviations used in text and figures. RV and LV, right valve and left valve. L, length of carapace and/or valves; W, width of carapace; A1 and A2, first antenna (antennule) and second antenna; Md-palp, mandibular palp, Mx1, maxillula, first maxilla; Mxp, first thoracopod T1, maxilliped; T2, second thoracopod, walking leg; T3, third thoracopod, cleaning leg; Uropodal ramus, U-ramus; SEM, scanning electron microscope. M-piece, inner medial process of the penis; myr, million years. Authors' names are abbreviated with their initials. ICZN, International Code of Zoological Nomenclature.

3. Results

3.1. *Neglecandona altoides* (Petkovski, 1961) nov. comb.

Systematic position of *Neglecandona altoides* (Krstić, 2006) nov. comb.

Class Ostracoda Latreille, 1802 (Ostrachoda; as Ostracoda in Latreille 1808)
Order Podocopida G.O. Sars, 1866
Suborder Cypridocopina Baird, 1845
Superfamily Cypridoidea Baird, 1845
Family Candonidae Kaufmann, 1900
Subfamily Candoninae Kaufmann, 1900
Tribe Candonini Kaufmann, 1900

Genus *Neglecandona* Krstić, 2006

Type species: *Neglecandona lindneri* (Petkovski, 1969) Krstić, 2006.

Type material and type locality. The type material of *N. altoides* (Petkovski, 1961) is deposited in the Natural History Museum in Skopje under an unknown registration number (Karanovic 2012). Petkovski (1959, 1961) reported the finding of his material of *N. altoides* nov. comb. in both southern and northern North Macedonia (Stepanovo in the municipality of Gevgelija and Aracinovsko blato, a swampy area in the environs of Skopje, respectively). No holotype having been designated, Petkovski's (op. cit.) type material consists of syntypes, and the mentioned localities constitute the type locality (Articles 73.2.3. and 76 of ICZN).

Material studied (see Table 1). The material studied by the present authors is deposited in the collections of C.M., B.S., and R.F.

Description of *Neglecandona* (Petkovski, 1961) nov. comb. (Figs 2-12)

Female (Figs 2-10). Carapace elongated in lateral view, greatest H situated approximately at 2/3 of L; dorsal margin conspicuously straight and oblique, steeply sloping towards the anterior end. LV extends beyond RV at both ends. Carapace moderately inflated in dorsal view, greatest W approximately situated at 2/3 L. Postero-ventral inner marginal calcified lamella of RV with c. 5 tiny parallel ridges resembling wrinkles (Figs 2C, 3C, 4C, 5A). These wrinkles absent from the LV.

Valves with a pearly lustre; posterior valve surface sometimes with a reticulated ornamentation (Fig. 6); pore canals in the anterior areas spine-shaped, mimicking tiny external spines at high magnification in the stereomicroscope.

A1 (Fig. 7A) 7-segmented. Apical natatory setae approximately as long as the combined 6 terminal segments. Aesthetasc ya moderately long, slightly shorter than the length of the combined two distal segments. Apical seta of terminal segment weakly reinforced, claw-like. Rome's organ absent, Wouters' organ not seen.

A2 (Fig. 7B, C). Basal segment proximally with one long seta, ventro-distally with one short, feathered, one normal seta and a ventro-distally long seta. Exopodite with one long and two short setae. Aesthetasc Y relatively short. Four t-setae present, the longest slightly extending beyond distal end of terminal segment. Setae z1, z2 and z3 short, z1 slightly reinforced. Terminal claws relatively short, the longest (G1) slightly longer than the two combined terminal segments. G2 slightly reduced in length.

Mandibular palp (Fig. 8A). Setal group of the 2nd segment with four equally long setae, a beta-seta and one short feathered seta present; gamma seta of penultimate segment feathered.

Maxillula (Mx1) (Fig. 8B). Palp two-segmented, distal segment asymmetrical in shape; both teeth bristles of third masticatory process smooth.

Maxilliped (Mxp, T1) (Fig. 8C). Palp one-segmented, distally with setae h1-3. Setae a, b and d present.

Walking leg (T2) (Fig. 9A) without special characters; seta d1 present, d2 missing.

Cleaning leg (T3) (Fig. 9B) 5-segmented, penultimate segment divided; basal segment with setae d1 and dp (d2 missing); setae g and h1-3 present, setae e and f absent.

U-ramus (Fig. 10A). Basal part inflated; seta sp well developed, approximately extending to the distal end of the ramus.

Genital fold (or lobe; Fig. 10A-E) roundly protruding, somewhat variable in shape, sometimes slightly asymmetrically developed on both sides; distally rounded to angularly rounded, with or without a small round, sometimes tit-shaped expansion.

Male (Figs 2-5, 11, 12, 17A-B). Carapace conspicuously sexually dimorphic, significantly larger than in the female and postero-ventrally inflated. Postero-ventral marginal zone of RV without the tiny wrinkles seen in the female.

A2 (Fig. 11A,B). Penultimate segment subdivided, with two male bristles (transformed setae t2 and t3); setae z1 and z2 modified into claws. Prehensile organs slightly asymmetrically built; right organ with a broad distal end; left organ distally thin, finger shaped (Fig. 11C.D). U-ramus basally not inflated (Fig. 9C).

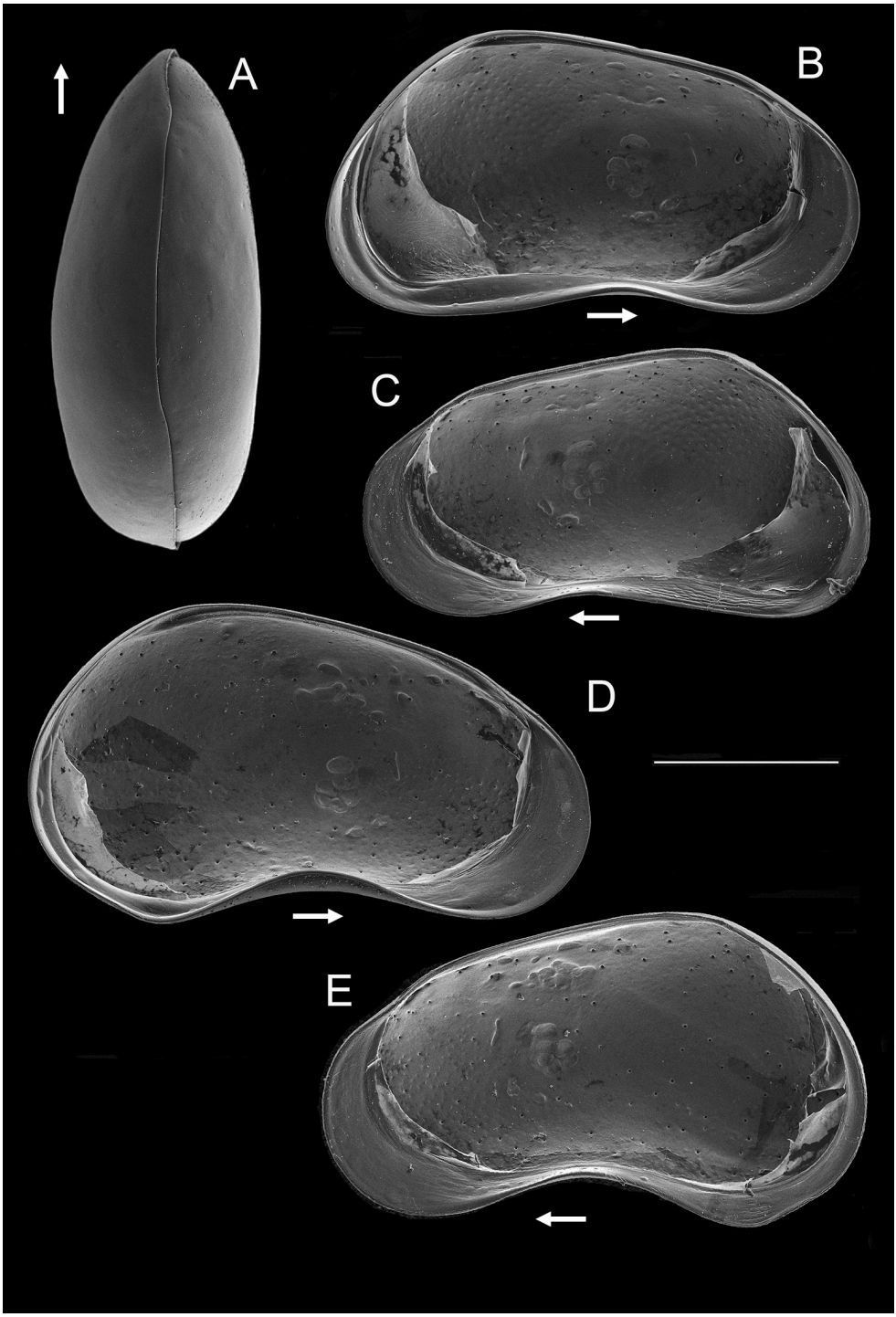


Fig. 2. *Neglecandona altoides* (Petkovski, 1961) nov. comb. A, male carapace in dorsal view. B, C, female LV and RV, internal view. D, E, male LV and RV, internal view. Scale bar: 500 µm. A, Serbia; B-F, southern North Macedonia, highlands of Vitačevo, south of Kavadarci. Arrows point anteriorly in all SEM images.

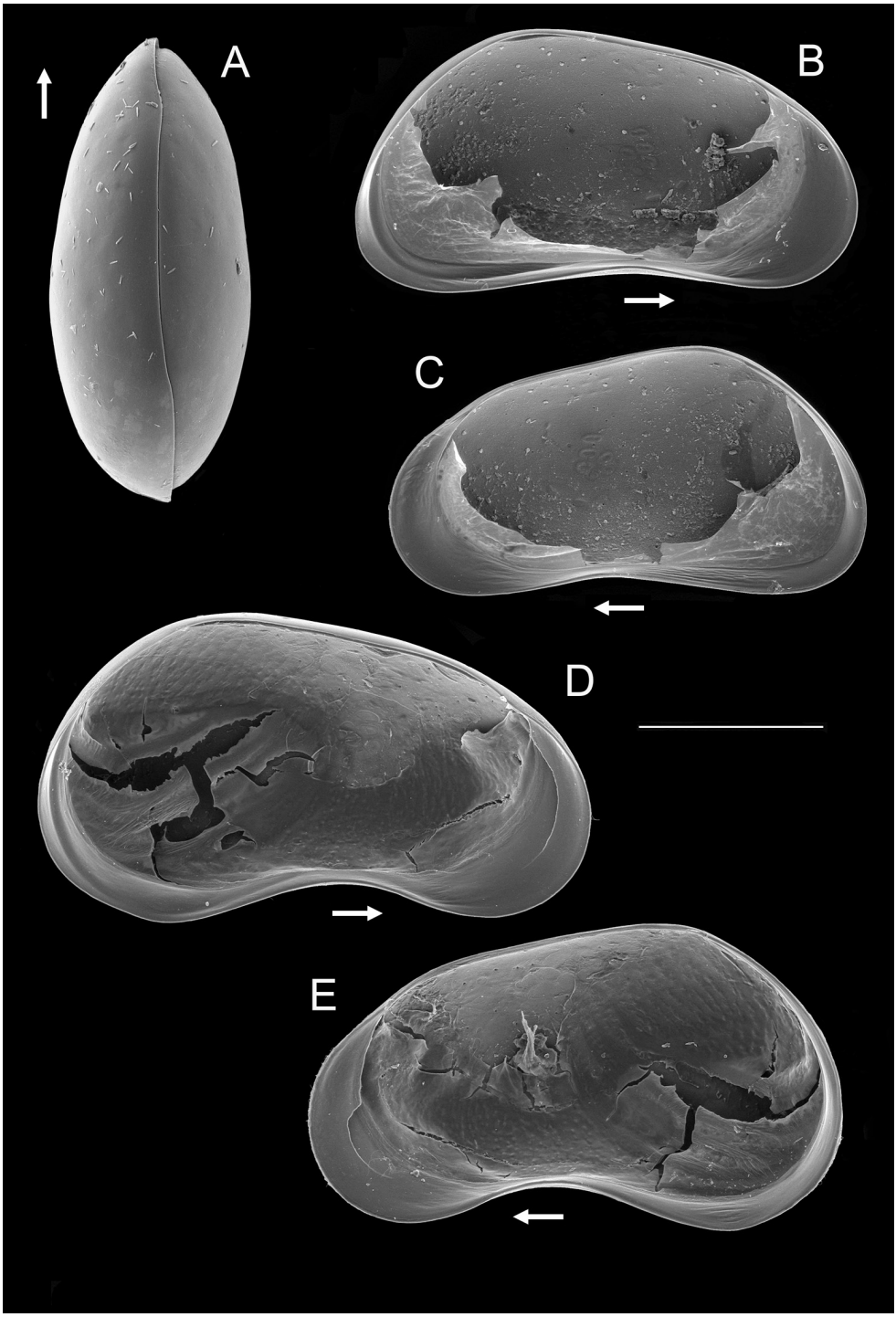


Fig. 3. *Neglecandona altoides* (Petkovski, 1961) nov. comb. A, female carapace in dorsal view. B, C, female LV and RV, internal view. D, E, male LV and RV, internal view. Scale bar: 500 µm. A, B, C, Figanières 1; D, E, Figanières 2. France.

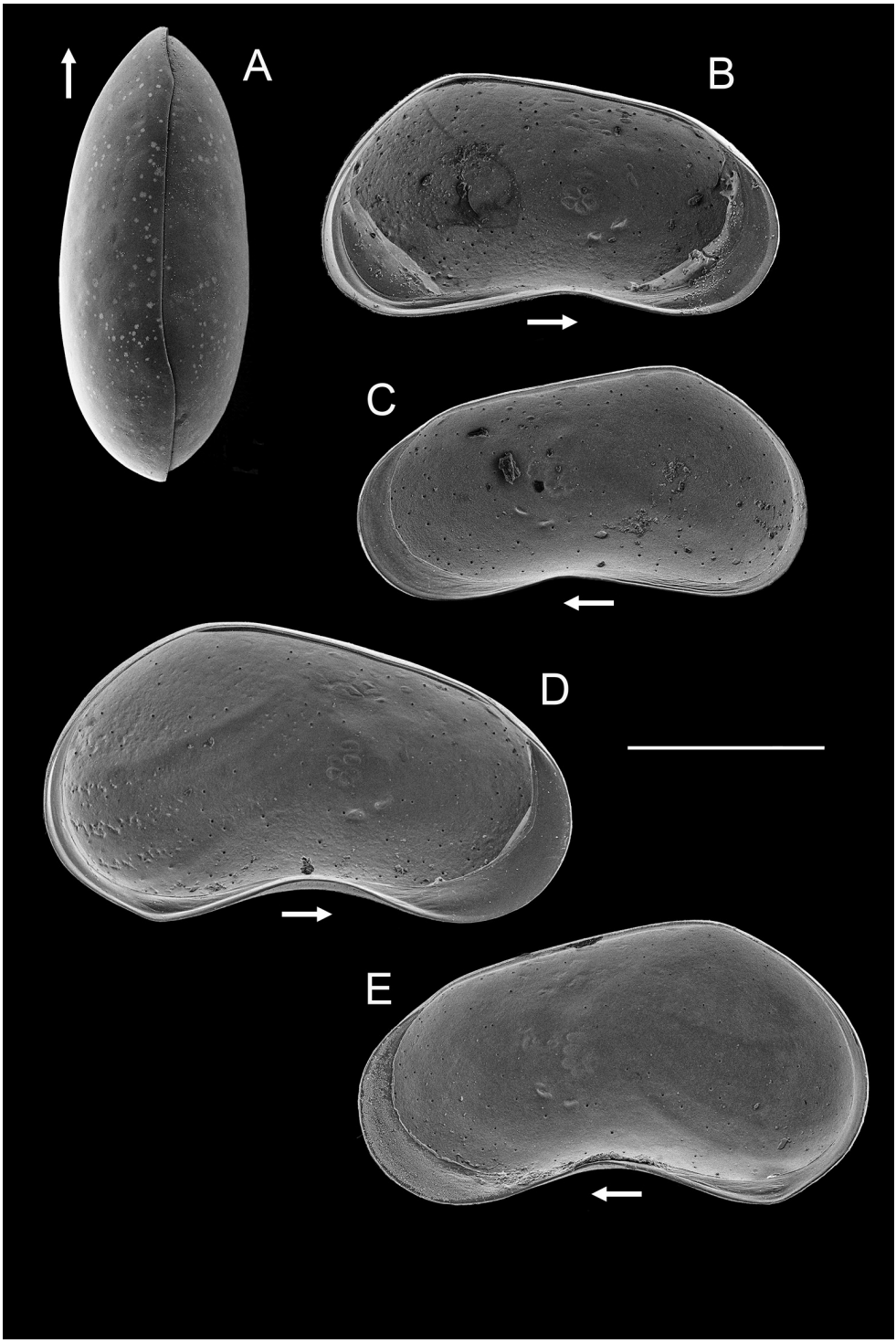


Fig. 4. *Neglecandona altoides* (Petkovski, 1961) nov. comb. A, female carapace in dorsal view. B, C, female LV and RV, internal view. D, E, male LV and RV, internal view. Scale bar: 500 µm. Eschefeld, Saxony, Germany.

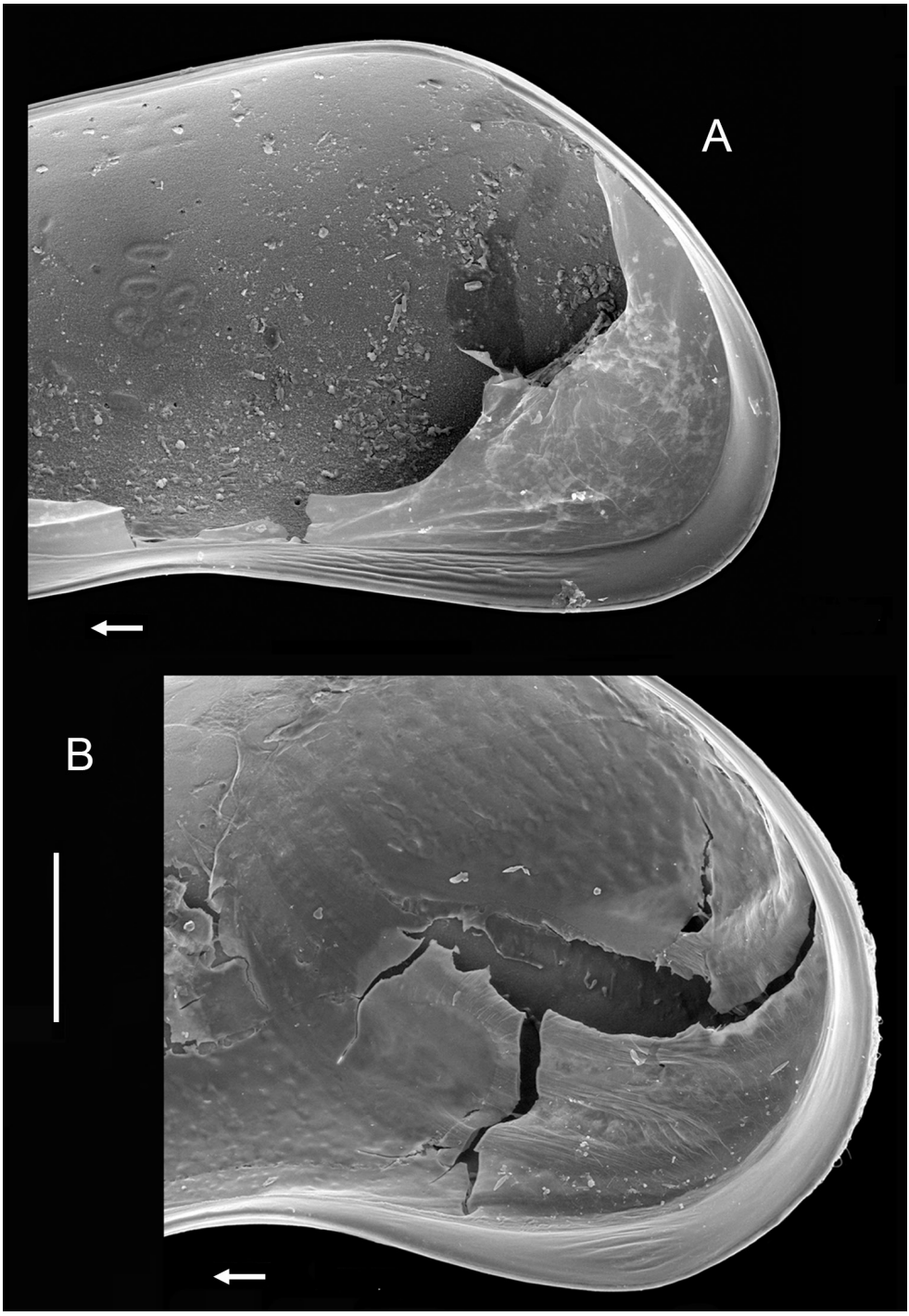


Fig. 5. *Neglecandona altoides* (Pekovski, 1961) nov. comb. A, RV of female, inner postero-ventral marginal area. See rows of 'wrinkles'. B, RV of male; the postero-ventral margin is conspicuously inflated. The 'wrinkles' seen in the female are missing in the male RV, but there are a few tiny shallow grooves at the very posterior end of the ventral margin. Scale bar: 200 µm. A, Bonne Cougne; B, Figanières 2, France.



Fig. 6. *Neglecandona altoides* (Petkovski, 1961). Scanning electron micrograph of the reticulated ornamentaton in the posterior valve area. Female, Figanières 2, France. Scale bar: 20 µm.

Zenker's organ (Fig. 12D) with 6 internal rings of spines. Penis as in Fig. 12A-C. M-piece strongly developed, distally moderately curved, apically rounded. (Fig. 12A-C). Penes and Zenker's organs usually visible through the valves.

Size of females 1.1-1.6 mm (usually 1.3-1.4 mm); males 1.3-1.7 mm (usually 1.4-1.6 mm). Males always present.

Intraspecific variation

The animals of both sexes from southern Europe – the Balkans, Italy and southern France – are somewhat larger than those found in central Europe (Germany) (see Table 1). It is presently unknown if this variation in size is due to environmental (climatic) factors or not.

The female genital fold is roundly protruding, often smooth, sometimes with a small tit-shaped process or some wrinkles; the folds are asymmetrically shaped in some specimens (Fig. 10B-E). It should be noticed that the shape of the fold depends, at least in part, on the position of the posterior end of body under the microscope. The M-piece of the penis, which is an important differentiating feature among species in the genus *Neglecandona*, always comprises a rounded, somewhat hook-shaped distal part in *N. altoides* nov. comb. (Fig. 12A-B). Here again the visible shape somewhat depends on the position under the microscope.

No variation was seen in the composition of the setal group on the 2nd Md palp segment: in all the specimens of both sexes dissected by the present authors, it consisted of four equally long setae; this character is a diagnostic feature of the genus *Neglecandona*.

Differential diagnosis

N. altoides nov. comb. is easily recognized from its congeners by the combination of the following three features: (a) its large size, usually 1.3-1.4 mm in the females; usually 1.4-1.6 mm in the males; (b) the long, straight and conspicuously sloping dorsal margin and (c) the shape of the M-piece in the penis (Fig. 12A, B); the M-piece of the penis of *N. altoides* nov. comb. is similar to that of *N. lindneri*, but clearly differs from that of *N. natronophila* (Fig. 12E) and that of *N. neglecta* (Fig. 27H, I in Meisch 2000).

Ad (a): Although there may be an overlapping variation in size with *N. neglecta, N. lindneri* and *N. vernalis* in some individuals of *N. altoides*, the presence, in a given sample, of at least a few individuals of *N. altoides* larger than the largest known specimens of any of the three other species allows the unambiguous identification of *N. altoides*.

Ad (b): For detailed comparisons of the carapaces and valves of *N. altoides* and the three close relatives mentioned above, we refer to the detailed descriptions and differentiating features provided by Fuhrmann (2012b). Noticeably, the carapaces of both sexes of *N. natronophila* nov. comb. appear very similar in shape to those of *N. altoides* nov. comb.

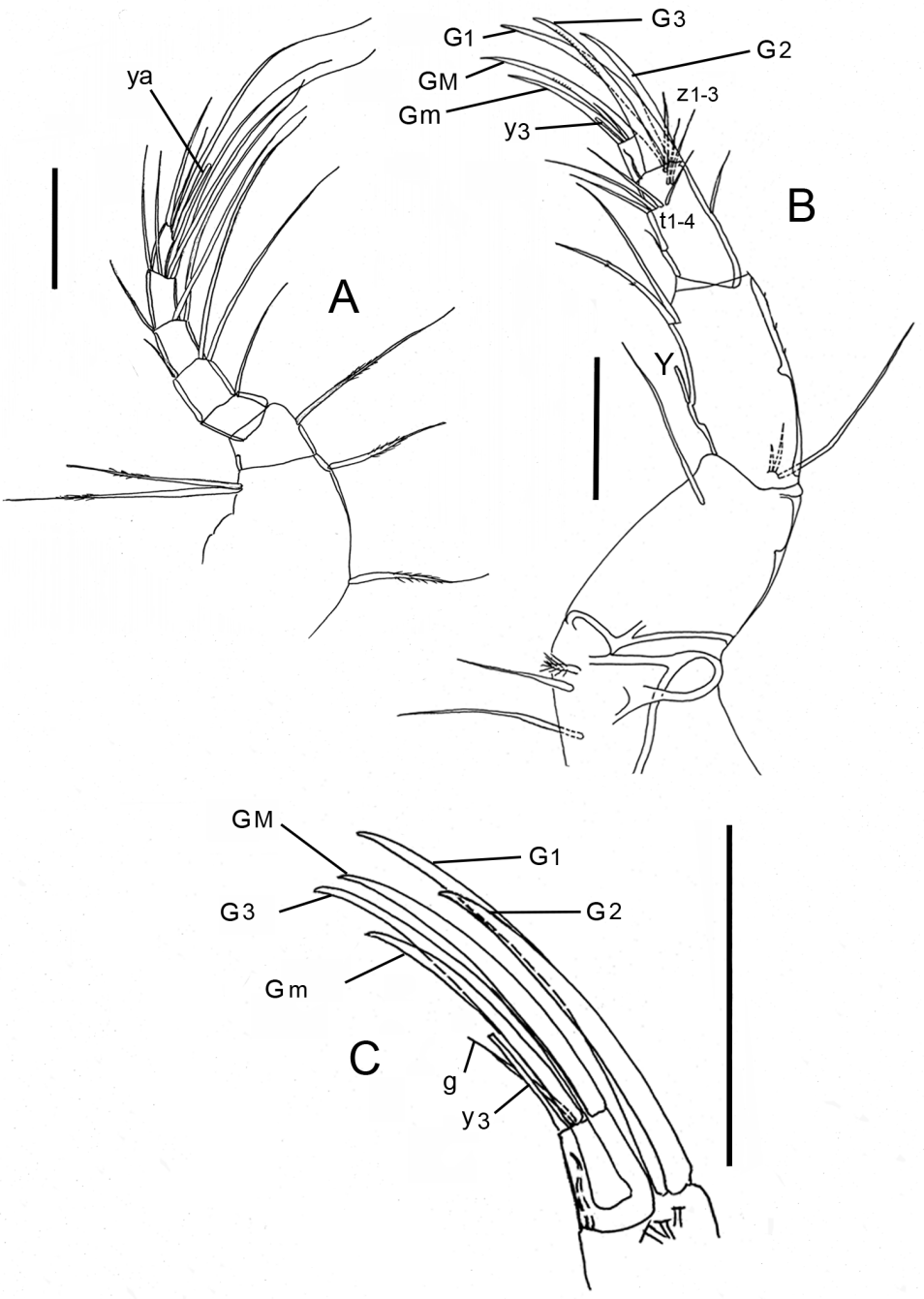


Fig. 7. *Neglecandona altoides* (Petkovski, 1961) nov. comb. Female. A, antennule. B, antenna, A2. C, distal end of antenna. Scale bars: 100 μm.

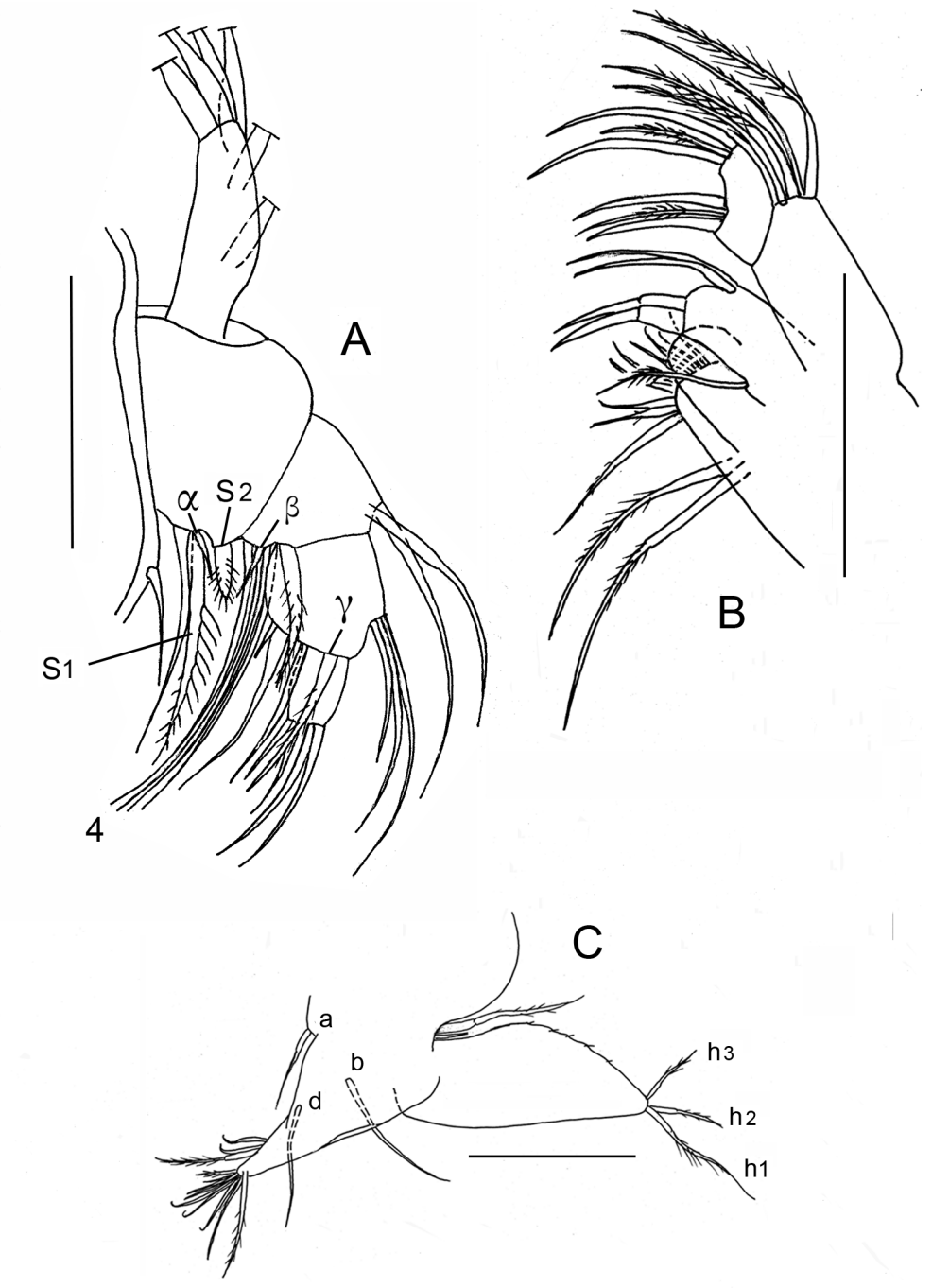


Fig. 8. *Neglecandona altoides* (Petkovski, 1961) nov. comb. Female. A, mandibular palp. B, maxillula. C, maxilliped (modified T1). Scale bars: 100 μm.

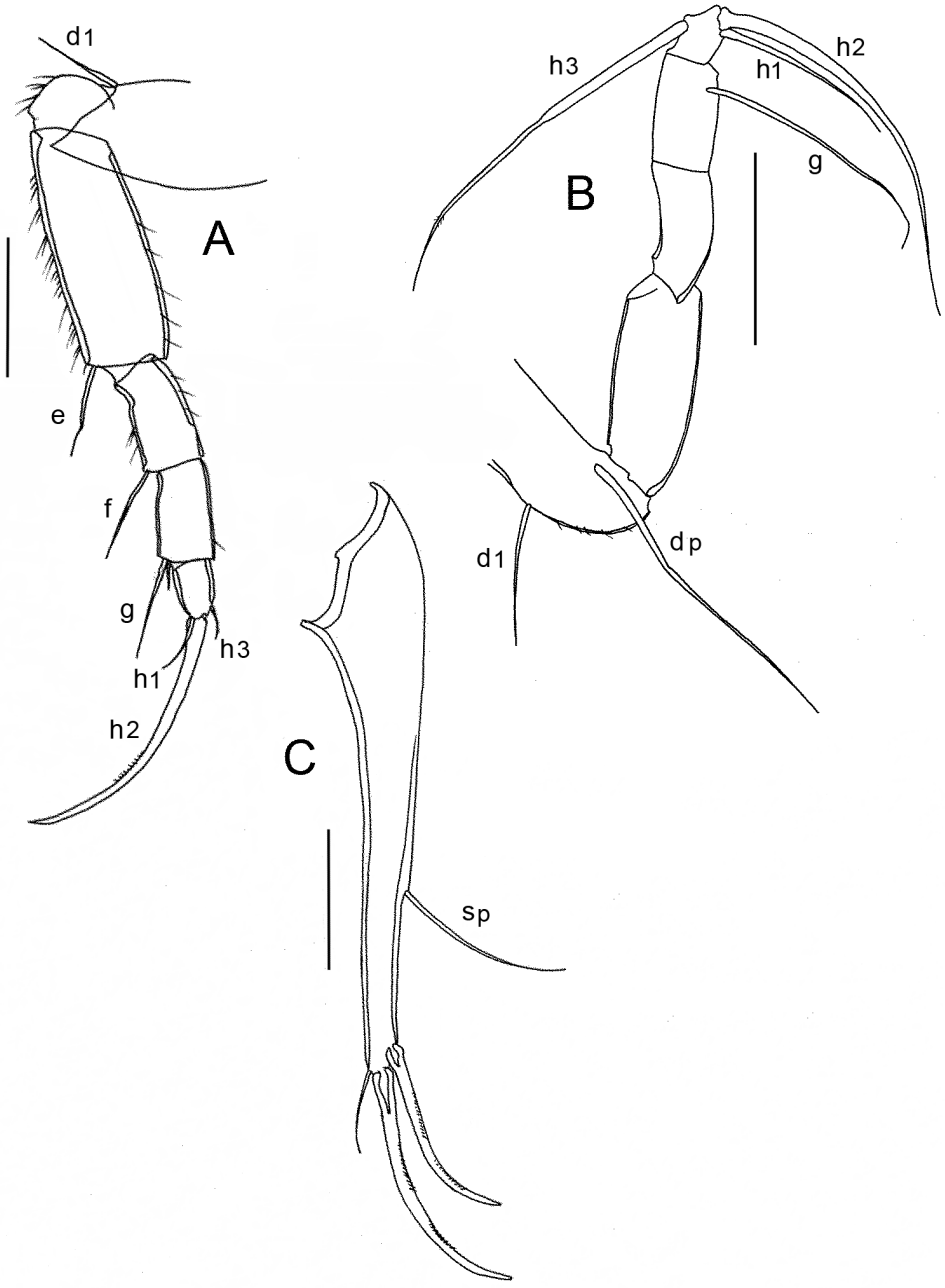


Fig. 9. *Neglecandona altoides* (Petkovski, 1961) nov. comb. Female. A, 2nd thoracopod, walking leg. B, third thoracopod, cleaning leg. Male. C, U-ramus. Scale bars: 100 μm.

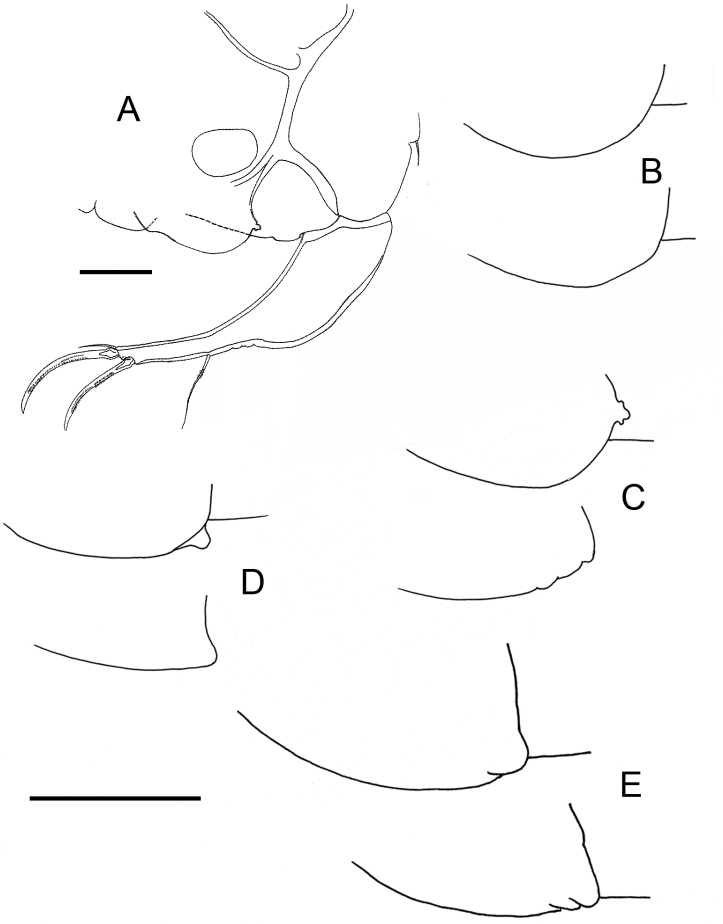


Fig. 10. *Neglecandona altoides* (Petkovski, 1961) nov. comb. Female. A, rear end of body, showing the genital fold, the U-ramus and its attachment. B-E, variation in shape of the genital fold, both folds of a given female are shown. Scale bars: 100 µm.

Ad (c): One of us (B.S.) checked the M-pieces of one male of *N. vernalis* nov. comb. (leg. R.F.) and found them to be similar to those seen in *N. neglecta*. The penal M-piece alone allows unambiguous distinction of *N. altoides* nov. comb. from *N. neglecta*, *N. vernalis* nov. comb. and *N. natronophila* nov. comb.

Taxonomic remarks

(1) Petkovski (1959) briefly described three unnamed varieties of *Candona neglecta* which differ in their valve outlines in lateral view, the shape of the female genital lobe and the shape of the M-piece. Two years later, the same author (Petkovski 1961) elevated one of these varieties (his variety 2) to species rank as *Candona altoides* n. sp., without any description and illustrations, but with referring to the figures 56-58 in his earlier (Petkovski 1959) publication. Following Petkovski (1959, 1961) *C. altoides* is diagnosed as follows: in lateral view, the dorsal margin of the females is conspicuously high at the posterior end, steeply sloping anteriorly (distinctly less so in *C. neglecta*) and the terminal branch of the M-piece appears distally rounded (Fig. 12A-C herein) (distally straight in *C. neglecta*). Petkovski (1966) reviewed the shape of the M-piece of various species of the *neglecta*-group, with *C. altoides*' M-piece belonging to his type IV (Petkovski 1966: Figs 8-9; compare with Fig. 12A-C).

(2) Petkovski (1969: 93) says that he formerly misidentified his samples of *Candona altoides* recorded from Novo Mesto in Slovenia (Petkovski 1959) and others from

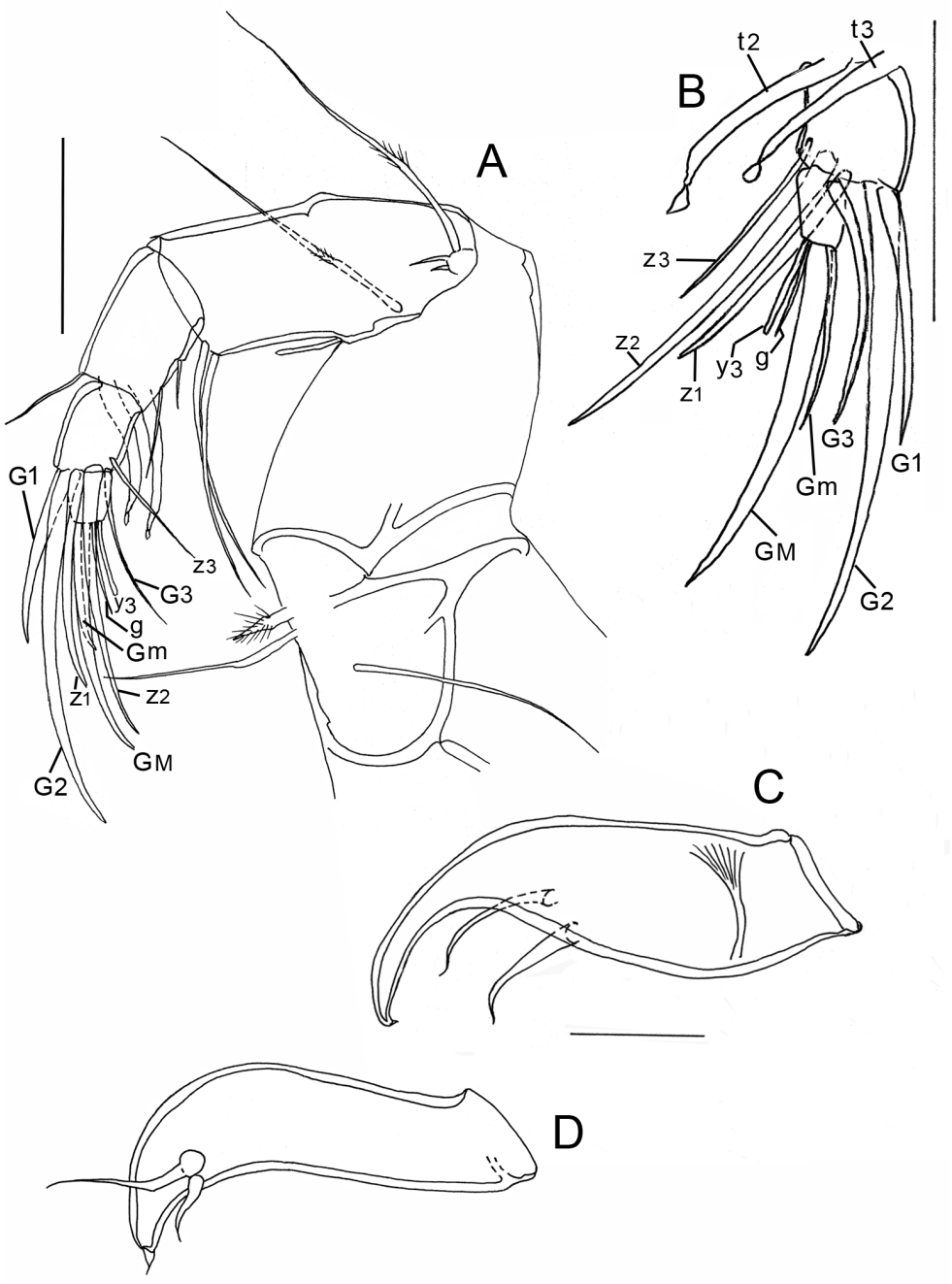


Fig. 11. *Neglecandona altoides* (Petkovski, 1961) nov. comb. Male. A, antenna. B, distal end of antenna. C and D, left and right prehensile organs. Scale bars: 100 µm.

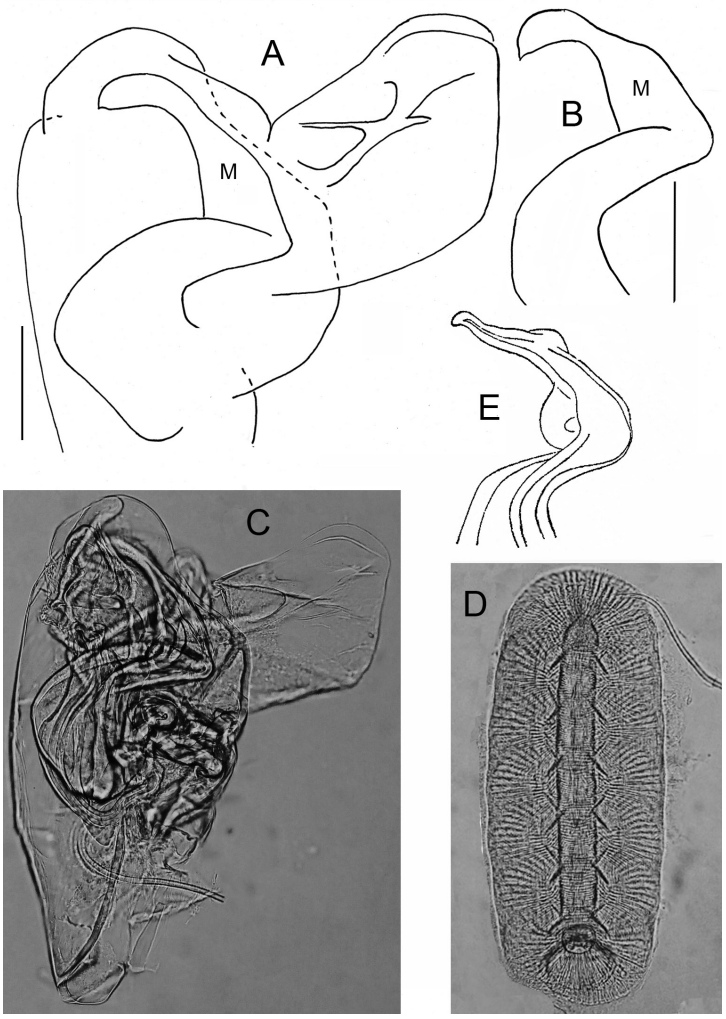


Fig. 12. *Neglecandona altoides* (Petkovski, 1961) nov. comb. (A-D) and *Neglecandona natronophila* (Petkovski, 1969) nov. comb. (E) A, penis of a specimen from the south of the town of Kavadarci, Macedonia. B, M-piece of a specimen from Germany, Saxony. C, penis in transmitted light. D, Zenker's organ. E, M-piece (from Petkovski 1969, Fig. 44). Scale bars: 100 µm, except for E.

Romania. Following Petkovski (1966) the Slovenian and Romanian specimens actually belong to *Candona lindneri* Petkovski, 1969. We agree with the latter identifications on the basis of the illustrations of the M-piece provided by the author (Petkovski 1969).

(3) Rossetti et al. (2006) reported the finding of an unnamed *neglecta*-like species (*Candona* sp. A) collected from a temporary pool at Costa di Castrignano in the province of Parma, Italy. The taxonomic characters mentioned by the authors, mainly so the size of the carapace – 1.60-1.63 mm for three females; 1.56 and 1.72 mm for two males – and the *N. lindneri*-like shape of the penal M-piece, clearly show that these specimens belong to *N. altoides*. This is the first record of the species from Italy.

Distribution (Table 1 and Fig. 1)

N. altoides nov. comb. is presently known from the Balkans (Serbia, Montenegro, North Macedonia), Bulgaria, southern France, Corsica included, Italy, and Germany. These records make us believe that the species has a wide circum-mediterranean distribution. Also, we suspect the species to have been overlooked or misidentified in samples collected from other countries around the Mediterranean (such was the case in Italy, as mentioned above). The northernmost records, those from Saxony and

Thuringia appear somewhat enigmatic at first sight. The German sites, indeed, are geographically disconnected from the main distribution area in the south. Most likely, specimens of *N. altoides* nov. comb. were carried to the north by migrating birds. Ducks would then have been the perfect candidates for spreading the animals from pond to pond in the region. Ostracods are indeed well known to survive the transport on the feet and plumage of water birds and to survive the passage as well through the gut of birds (e.g., Frisch et al. 2007, Brochet et al. 2010).

Ecology

Petkovski's (1959, 1961) *altoides*-animals were collected from a temporary pool at Stepanovo in the municipality of Gevgelija, in the very southeast of North Macedonia, as well as from several temporary pools near Skopje, the capital of North Macedonia. Petkovski (1964) reported the finding of one single female of *C. altoides* from the environs of the estuary of the Ropotamo river, c. 5-6 km away from the Black Sea in SW Bulgaria.

In general, all known records of *N. altoides* nov. comb. come from temporary water bodies, with the exception of fish ponds in eastern Germany (Table 1). The survival and reproduction of *N. altoides* in these ponds might be seen in relation with the annual management of these water bodies. Indeed, the ponds are generally emptied of their water in autumn, with some temporary shallow pools remaining at the bottom, this until the ponds will be refilled in spring.

The *altoides*-ponds in southwestern France, Corsica included, are all temporary water bodies under mediterranean climate. All of them, with the exception of Figanières 1 and 2, are located in nature protection areas (Table 1). For images of the ponds at Bonne Cougne, Figanières 1 et Redon, see Fig. 13-16; for further pictures, aerial ones taken from drones included, see Thiéry 2017).

Water depth at Redon, is mostly less than 60-100 cm. Of the French ponds studied, only the pond at Bonne Cougne reaches a depth of 3 meters in winter. The annual variation of a number of environmental factors in the French ponds is presented in Table 2.

The pond situated near Évenos is an artificial pond on granitic subtrate in a former rock quarry, with a maximum depth of 60-70 cm. In the South of Corsica, the temporary pond in Tre Paduli de Frasselli similarly overlies a granitic substrate; it has a maximum depth of 20-25 cm (Paradis et al. 2009).

Bonne Cougne: a second annual flooding with underground waters from the underlying karst is reponsible for the increase in electrical conductivity from 210 µS/cm to 600-650 µS/cm. In Lake Redon, salty groundwater often mixes with water from rainfall, in which case conductivity reaches 900 µS/cm, or even 1 mS/cm in spring.

Aquatic vegetation: In lake Redon, the presence of *Artemisia molinieri* (endemic) and *Damasonium polyspermum, Lythrum tribracteatum* was noted. At Frasselli, *Isoetes velata*, *Ranunculus ophioglossifolius*, and *Pulicaria vulgaris*, three protected species were found. At Bonne Cougne, eleven species of Charophyceae were observed, which makes this pond to be one of the most charophyte rich in southern France (Souliè-Marsche & Thiéry, unpubl.). Large populations of *Glyceria fluitans* and *Ranunculus peltatus* subsp. *baudotii* have developed at Bonne Cougne (A.T., unpubl.).

Large branchiopods (Crustacea, Branchiopoda) were collected from Bonne Cougne, Redon and Figanières 1 and 2: the anostracan *Linderiella massaliensis* Thiéry & Champeau, 1988 (endemic in southwestern France), together with *Chirocephalus diaphanus* Prévost, 1803 from Bonne Cougne; *C. diaphanus* and the notostracan *Lepidurus apus* (L, 1758) from lake Redon (Thiéry & Champeau 1988; Meglécz & Thiéry 2005). In the temporary pond at Évenos, large branchiopods are represented by *Chirocephalus diaphanus* only (Thiéry 2017).

Life history

Petkovski (1964) noted that juveniles of *N. altoides* from temporary pools in the environs of Skopje appear from late October to November, depending on the refilling of the pools after the summer drought. In southern France and Corsica, adult males and females were exclusively collected from November to March. Col-



Fig. 13. Temporary pond at Bonne Cougne, France, flooded on 25 April 2010. Photo: A. Thiéry.



Fig. 14. Bonne Cougne, dry pond on 28 August 2017. Photo: A. Thiéry.

lections made during the other months of the year yielded juveniles only. In the German fish ponds, adults were present in the samples taken in January and April; from May to September, only juveniles were found. *N. altoides* thus appears to reach sexual maturity in the winter months, with egg laying occurring in spring.

Fossil record

N. altoides nov. comb. has a relatively rich fossil record, which ranges from the Miocene and Pliocene to the Pleistocene and Holocene. The known records are presented in Table 3.

The fossil records in central Germany predominantly come from sediments deposited during glacial periods, mainly in (a) temporary small water bodies with a muddy bottom, (b) small lacustrine basins (locality Neumark-Nord; Fuhrmann & Pietrzeniuk 1990b, 2010, Fuhrmann 2006b, 2008, 2017); and (c) tundra over loess (locality Großstorkwitz; Fuhrmann 2019b). Fossils of *N. altoides* dating from the Holocene were mainly found in sediments deposited in riverine palaeomeanders.

3.2. Genus *Neglecandona* Krstić, 2006

Amended diagnosis

A genus with the characters of the tribe Candonini Kaufmann, 1900 of the subfamily Candoninae Kaufmann, 1900.

Carapace mostly 1.0-1.7 mm in size, more rarely 0.8-1.0 mm long. LV always larger than RV, overlapping the latter both anteriorly and posteriorly in both sexes. Carapace moderately wide in dorsal view, with W/L c. 0.40. Carapace elongated in lateral view, dorsal margin almost straight to straight, except in a number of species endemic to lake Ohrid.



Fig. 15. Temporary pond Figanières 1, France, 17 March 2013. Photo: Gabriel Nève.



Fig. 16. Temporary Lake Redon, France, 5 December 2002. Photo: A. Thiéry.

Carapace of males slightly larger than that of females, postero-ventrally inflated. Anterior valve area in species with elongated valves with spine-shaped, anteriorly directed normal pore canals. Posterior valve area often with a delicate reticulate pattern consisting of tiny grooves, perpendicularly oriented to the lines of the reticulation (Fig. 6).

Valves with a pearly lustre, whitish grey to (slightly) transparent in species living at greater depths in lakes.

Md palp, 2nd segment: setal group with 4 setae (with one possible exception: 5 setae in *N. paionica* (Petkovski, 1959)); gamma-seta on penultimate segment feathered.

Cleaning leg: basal segment with 2 setae (d1 and dp); penultimate segment always subdivided.

Female genital lobe roundly protruding, sometimes posteriorly with a small expansion, the latter sometimes tit-shaped. U-ramus strongly developed, basal part inflated in the female. Penis: Distal lateral lobe subquadrate; M-piece strongly developed, with a transverse portion at about mid-length.

Sexual dimorphism: Carapace of males slightly but significantly larger than that of the female, posterior end of carapace postero-ventrally inflated. A2: penultimate segment subdivided, with two male bristles (transformed setae t2 and t3); setae z and claws G1-3 modified. Male prehensile organs (transformed T1-palps) asymmetrically built, right organ distally broadly rounded, left organ distally finger shaped. U-ramus: basal part not inflated. Males always present.

Type species: *Neglecandona lindneri* (Petkovski, 1969) Krstić, 2006 (by original designation). Type locality: North Macedonia.

Table 2. Environmental factors in the French ponds at Bonne Cougne, Redon, Figanières 1 and Frasselli.

Locality	Date	pH	Electrical conductivity C_{25} [µS/cm]	Turbidity [NTU]	Dry residue [g/L]	Organic matter [%]
Bonne Cougne	18/11/2008	7.9	354	-	0.213	30.00
	13/04/2009	7.8	413	1.17-2.71	0.213	25.0
	27/08/2009	7.6	298	3.07-9.03	0.133	30.56
	30/09/2009	7.8	298	13.84-21.9	0.093	8.33
	06/12/2009	7.6	271	1.92-5.05	0.173	15.0
	28/02/2010	7.8	298	6.78-13.30	0.200	33.33
	18/04/2010	7.7	261	0.21-0.52	0.120	19.44
	06/06/2010	7.8	281	1.14-2.15	0.147	55.55
	18/07/2010	7.5	269	1.19-4.46	0.120	22.22
	13/11/2011	7.5	212	81.1-86.6	0.200	0
	01/01/2012	7.6	289	5.18-48.2	0.200	20.0
	29/01/2012	7.7	313	0.74-7.51	0.147	27.78
	22/06/2014	8.3	442	0.74-3.10	0.267	25.0
	18/07/2015	7.7	286	2.82-5.86	0.173	61.66
	26/10/2015	8.1	529	34.0-39.0	0.387	24.07
	13/11/2015	8.0	635	163-287	0.680	11.84
Redon	26/12/2002	8.0	364	-	-	-
	16/01/2003	7.8	398	-	-	-
Figanières	17/03/2017	7.4	334	-	-	-
Frasselli	27/02/2009	7.4	353	-	-	-

Differential diagnosis

The species of *Neglecandona* Krstić, 2006 are readily recognized from those of the genus *Candona* Baird, 1845 s. str. by the combination of the following features: carapace elongate in lateral view, with a long and (almost) straight dorsal margin (carapace less elongated, straight dorsal margin shorter and/or slightly rounded in *Candona*). Mandibular palp: setal group of 2nd segment with 4 setae (5 in *Candona*). Cleaning leg (T3): penultimate segment subdivided (always undivided in *Candona*). Males always present (missing or rare in some species of *Candona*, e.g. *Candona candida* (O.F. Müller, 1776) Baird, 1845). It should be noticed, however, that the elongate carapace-character does not apply to part of the species endemic to Lake Ohrid (see Taxonomic remark no 6 below).

Taxonomic remarks

(1) Before 2006 there had been at least three attempts to establish the *neglecta*-group of species either as a subgenus of *Candona* Baird, 1845 or as a separate genus: *Candona* (*Neglectocandona*) Krstić, 1993; *Candona* (*Neglecandona*) Krstić, 1995; and *Neglecandona* Krstić & Guan, 2001. These attempts are to be considered taxonomically invalid because no type species was designated neither for the two subgenera nor the genus (Article 13.3. of the ICZN). The oblivion was corrected when Krstić (2006) reintroduced the genus *Neglecandona* and designated *Candona lindneri* as type species of the genus.

(2) Krstić (2006) did not provide a diagnosis of the new genus, as she obviously referred to the description published in her previous work (Krstić 1995). The diagnosis is here amended, mainly so to include the morphology of the appendages.

(3) Somewhat surprisingly Krstić (2006) designated *Candona lindneri* Petkovski, 1969 as type species of *Neglecandona*, while *Candona neglecta* Sars, 1887 would have been a more obvious choice. Krstić (2006: 145) writes that she was motivated by the fact that *N. lindneri* was 'best studied both ecologi-

Table 3. Fossil records of *N. altoides* (Petkovski, 1961) nov. comb. Abbreviation: *C. neglecta*, *Candona neglecta*.

Country	Locality	Coordinates	Authors	Stratigraphical range
Germany	Süßenborn near Weimar, Thuringia	50°59'10"N 11°24'05"E	Diebel & Pietrzeniuk 1969, pl. 7: 6-8 (as *C. neglecta*, fide Fuhrmann 2012b)	Middle Pleistocene (Cromer-complex)
	Neumark-Nord (Geiseltal), Saxony-Anhalt	51°19'01"N 11°54'05"E	Fuhrmann & Pietrzeniuk 1990b, 2010 Fuhrmann 2006b, 2008, 2017	Middle Pleistocene (Warthian cold stage) Upper Pleistocene (Weichselian cold stage)
	Burgtonna, Thuringia	51°04'24"N 10°43'54"E	Diebel & Pietrzeniuk 1978, pl. 49: 3-5; 7-8 (as *C.* cf. *neglecta*, fide Fuhrmann 2012b)	Upper Pleistocene (Weichselian cold stage)
	Schadeleben near Ascherleben, Saxony-Anhalt	51°49'56"N 11°21'11"E	Fuhrmann 2012a	Upper Pleistocene (Weichselian cold stage)
	Gröbern, Saxony-Anhalt	51°41'40"N 12°26'58"E	Fuhrmann & Pietrzeniuk 1990a	Upper Pleistocene (Weichselian cold stage)
	Lützkendorf (Geiseltal), Saxony-Anhalt	51°18'06"N 11°50'42"E	Fuhrmann, unpublished	Upper Pleistocene (Weichselian cold stage)
	Großstorkwitz near Pegau, Saxony	51°10'58"N 12°14'49"E	Fuhrmann 2019b	Upper Pleistocene (Weichselian cold stage)
	Grechwitz near Grimma, Saxony	51°13'30"N 12°46'03"E	Fuhrmann 2019b	Upper Pleistocene (Weichselian cold stage)
	Schkeuditz near Leipzig, Saxony	51°23'30"N 12°12'54"E	Fuhrmann 2019a	Holocene
	Pegau, Saxony	51°10'23"N 12°15'13"E	Fuhrmann, unpublished	Holocene
	Salziger See near Seeburg, Saxony-Anhalt	51°28'36"N 11°41'11"E	Wennrich 2006, pl. 1: H-I (as *C. neglecta*, fide Fuhrmann 2012b)	Holocene
Kosovo	Metohija	42°19'41"N 27°45'19"E	Krstić 1975, as *C.* (*Candona*) aff. *altoides*	Upper Pliocene
Turkey (review in Beker et al. 2008)	Various regions in Turkey	-	Freels 1980, as *C.* (*Candona*) cf. *altoides*	Upper Miocene – Pliocene – Lower Pleistocene
	Adana, S Turkey	37°0'N 36°19'E	Nazik et al. 1992, as *C.* (*Candona*) *altoides*	Pliocene
	Sivrihisar, Central Anatolia	39°27'N 31°32'E	Tunoğlu et al. 1995, as *C.* (*Candona*) *altoides*	Pliocene
	Istanbul	41°00'N 28°57'E	Şafak et al. 1999, as *C.* (*Candona*) *altoides*	Pliocene

cally and morphologically' and 'is available to all researchers' from samples deposited in the Institute of Zoology in Hamburg. However, it is presently known that *N. neglecta* is widespread in central Europe and that its populations outnumber those of *N. lindneri* there (e.g., Meisch 2000, Fuhrmann 2012b; also recent findings by the present authors), and that therefore Krstic's (2006) remarks rather apply to *N. neglecta* and not *N. lindneri*. This, however, does not affect the status of *N. lindneri* as type species of the genus.

(4) The posterior area of the valves of some individuals of various species of *Neglecandona* display a delicate reticulated ornamentation (Krstić 2006; Fuhrmann 2012b: plate 6, Fig. 1f;

Fig. 6 herein). Though it can be recognized in the stereomicroscope, the structure of the reticulation is best seen in the SEM. This reticule is not restricted to the genus *Neglecandona,* its presence has indeed been reported from various other candonine species, e.g. *Fabaeformiscandona myllaina* Smith & Kamiya, 2007 and *Fabaeformiscandona alchichica* (Cohuo et al. 2017) (see original species descriptions).

(5) Up-to-now only three extant species had been formally allocated to *Neglecandona* Krstić, 2006 (Table 4). We here transfer 36 other species, which formerly had all been attributed to the *neglecta*-group of *Candona* s.l. We refrain from transferring any fossil species to *Neglecandona* as this would go beyond the scope of the present work.

(6) Species endemic to Lake Ohrid. Of the 39 species presently assigned to *Neglecandona*, 22 are considered endemic to Lake Ohrid (Table 4), with two additional species – *N. dedelica* (Petkovski, 1969) nov. comb. and *N. paloskii* (Petkovski et al., 2002) nov. comb. – being so far only known from sites located on the banks of that lake. Lake Ohrid, which is estimated to have originated

Table 4. Extant species allocated to *Neglecandona* Krstić, 2006. All the species in the list were originally attributed to the genus *Candona* s.l. Baird, 1835. The species are listed alphabetically, except for *N. lindneri, N. neglecta,* and *N. angulata*, which previously were already in *Neglecandona*. Abbreviations: N Macedonia, North Macedonia.

	Species of *Neglecandoa* Krstić, 2006	Distribution	Remarks
1	*N. lindneri* (Petkovski, 1969) Krstić, 2006	Palaearctic	Type species of *Neglecandona* Krstić, 2006
2	*N. neglecta* (Sars, 1887) Krstić, 2006 Syn.: *N. scharfi* (Hahn, 1990) nov. comb. (fide Meisch 2000)	Palaearctic	
3	*N. angulata* (G.W. Müller, 1900) Medici et al., 2011	Holarctic	
4	*N. acricauda* (Mikulić, 1961) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (sublitoral and profundal zones)
5	*N. altoides* (Petkovski, 1961) nov. comb.	Serbia, Montenegro, North Macedonia, Bulgaria, southern France, Corsica included, Italy, Germany	Temporary ponds, fish ponds in Germany
6	*N. bimucronata* (Klie, 1937) nov. comb.	Montenegro, Bosnia, N Macedonia, Slovenia	
7	*N. dalmatina* (Petkovski et al., 2002) nov. comb.	Croatia	
8	*N. dedelica* (Petkovski, 1969) nov. comb.	N Macedonia	Spring swamp on the SE bank of Lake Ohrid
9	*N. depressa* (Klie, 1939) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (sublitoral and profundal zones)
10	*N. expansa* (Mikulić, 1961) nov comb.	N Macedonia/Albania	Endemic to Lake Ohrid (litoral and profundal zones)
11	*N. fasciolata* (Petkovski, 1961) comb. nov.	N Macedonia	
12	*N. formosa* (Mikulić, 1961) nov. comb	N Macedonia/Albania	Endemic to Lake Ohrid (sublitoral zone)
13	*N. goricensis* (Mikulić, 1961) nov. comb	N Macedonia/Albania	Endemic to Lake Ohrid (sublitoral zone)
14	*N. hadzistei* (Petkovski et al., 2002) nov. comb. *Candona hadzistei* nom. nov. pro *C. parvula* Mikulić, 1961 nec Sars, 1926	N Macedonia/Albania	Endemic to Lake Ohrid (litoral and profundal zones)

15	*N. hartmanni* (Petkovski, 1969) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (litoral zone)
16	*N. holmesi* (Petkovski, 1960) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid
17	*N. jordeae* (Petkovski et al. 2002) nov. comb. *Candona jordeae* nom. nov. pro *C. lucida* Petkovski, 1969 nec Schneider, 1959 *Neglecandona lucida* (Petk., 1969) nov. comb.	N Macedonia	Endemic to Lake Ohrid
18	*N. litoralis* (Mikulić, 1961) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (litoral zone)
19	*N. lychnitis* (Petkovski, 1969) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (shallow litoral zone)
20	*N. macedonica* (Mikulić, 1961) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (sublitoral zone)
21	*N. margaritana* (Mikulić, 1961) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (sublitoral zone)
22	*N. marginata* (Klie, 1942) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (indication on depths missing)
23	*N. marginatoides* (Petkovski, 1960) nov. comb.	N Macedonia/ Albania/Greece	Lake Prespa, Lake Ohrid
24	*N. media* (Klie, 1940) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (profundal zone)
25	*N. meerfeldiana* (Scharf, 1983) nov. comb.	Germany, Spain	
26	*N. meridionalis* (Petkovski, 1958) nov. comb. Syn.: *Candona angulata* f. m*eridionalis* (Petkovski, 1958) nov. comb. (fide Mazzini et al. 2015)	N Macedonia/Greece Eastern Europe	Lake Dojran
27	*N. montenigrina* (Petkovski, 1960) nov. comb.	Montenegro/Albania	Endemic to Lake Skadar
28	*N. natronophila* (Petkovski, 1969) nov. comb.	Serbia, N Macedonia	
29	*N. ohrida* (Holmes, 1937) nov. comb. Syn.: *Neglecandona cristatella* (Klie, 1939) nov. comb. Syn.: *Neglecandona sublitoralis* (Mikulić, 1961) nov. comb. (Fide Petkovski et al. 2002)	N Macedonia/Albania	Endemic to Lake Ohrid (litoral to profundal zone), also adjacent waters
30	*N. ovalis* (Mikulić, 1961) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid (sublitoral zone)
31	*N. paionica* (Petkovski, 1958) nov. comb.	N Macedonia/Greece, Italy? (Pieri et al. 2015)	Lake Dojran
32	*N. paloskii* (Petkovski et al., 2002) nov. comb.	N Macedonia.	Known from type loc. only; a stream on the NE bank of Lake Ohrid
33	*N. peterseni* (Caraion, 1979) nov. comb.	Romania, N Macedonia (as *C.* cf. *peterseni*)	
34	*N. strumicae* (Petkovski, 1959) nov. comb.	N Macedonia	
35	*N. trajani* (Krstić, 1972) nov. comb. *Candona trajani* nom. nov. pro *C. alta* (Klie, 1939) nec Zalanyi, 1929	North Macedonia	Endemic to Lake Ohrid (profundal zone)
36	*N. trapeziformis* (Klie, 1939) nov. comb.	North Macedonia	Endemic to Lake Ohrid (profundal zone)
37	*N. triangulata* (Klie, 1939) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid
38	*N. vernalis* (Fuhrmann, 2008) nov. comb.	Germany (Saxony)	
39	*N. vidua* (Klie, 1942) nov. comb.	N Macedonia/Albania	Endemic to Lake Ohrid

in the Miocene, some 3-5 mio years ago, is known to harbour more than 200 endemic species described, mainly invertebrates and algae, but also fish (e.g., Wagner et al. 2009). As far as ostracods are concerned, ancient Lake Ohrid obviously has been the centre of origin of an endemic species flock belonging to the genus *Neglecandona*. Similar flocks of ostracods are known from other ancient lakes, e.g., lake Baikal in Siberia (c. 28 myr of age), with c. 50 ostracod species and subspecies of the genus *Cytherissa* Sars, 1925, and the African lake Tanganyika (c. 12 myr) with more than 16 endemic ostracod species in at least five genera (Schön & Martens 2012).

In terms of carapace shape, 17 species of *Neglecandona* endemic to Lake Ohrid and adjacent waters present elongated carapaces and exhibit appendages, the penis included, which make them group rather well around *N. lindneri* and *N. neglecta*.

The carapaces of three other Ohrid species, *N. litoralis* (Mikulić, 1961) nov. comb., *N. triangulata* (Mikulić, 1961) nov. comb. and *N. goricensis* (Mikulić, 1961) nov. comb. appear roundly triangular in shape. The appendages of the first two species, the penis included, comply otherwise with the diagnosis of the genus. This is not the case of *N. goricensis* nov. comb., in which the male prehensile organs are rather symmetrically shaped (distinctly asymmetrically in all other species of *Neglecandona*) and the M-piece of the penis lacks the conspicuous transverse portion at mid-length (Mikulić 1961, Fig. 6: 7). These features might cast some doubt on the belonging of this species to the genus *Neglecandona*.

The carapaces of the remaining four species, *N. acricauda* Mikulić, 1961, *N. expansa* Mikulić, 1961, *N. margaritana* Mikulić, 1961 and *N. ohrida* Holmes, 1937 have stocky carapaces in lateral view, differing markedly from the elongated shape seen in, among others, *N. lindneri* and *N. neglecta*. Their appendages, however, the penis included, comply with the diagnosis of the genus.

(7) The taxonomic position of the following three species needs to be discussed.

(a) *N. paionica* (Petkovski, 1958) nov. comb. The 2nd segment of the Md-palp has a setal group with 5 setae, which character rather would exclude the species from *Neglecandona*. However, as all other characters comply with those of the *neglecta*-group, Petkovski et al. (2002) retain the species within that group, and it is therefore provisionally assigned here to the genus *Neglecandona*.

(b) *Candona muelleri* Hartwig, 1999 was generally considered to belong to the *neglecta*-group of species (e.g., Meisch 2000). However, as convincingly pointed out by Karanovic (2006), *Candona muelleri* does not belong there: above all, the female genital lobe (triangularly protruding posteriorly) and the structure of the penis (distal lobe a and M-piece) (see Meisch 2000: 86) do not comply with the diagnosis of *Neglecandona*.

(c) The carapaces and valves of *Candona xizangensis* Huang, 1982 which were repeatedly recorded from lake sediments – those of the surface included – of the southern Tibetan Plateau (e.g., Wrozyna et al. 2009, Frenzel et al. 2010, Peng et al. 2013) are similar to those of *N. neglecta* and therefore the species may well belong to *Neglecandona*. However, as the appendages of this species have so far not been described, we refrain from formally assigning it to the genus *Neglecandona*.

(8) The existence of spine-shape pore canals in the anterior valve area might be seen in relation with the facts that (a) the inner pore openings are c. 3x larger in diameter than the corresponding pore openings on the external valve surface (Fig. 17) and (b) the anterior elongation of the valves during the moults of (late) juveniles.

4. Conclusion

Neglecandona altoides (Petkovski, 1961) nov. comb. has a wide distribution in the Balkans (North Macedonia, Serbia and Montenegro), Bulgaria, southern France, Corsica included, Italy, and eastern Germany. The presently known records point towards a wide distribution in the circum-mediterranean regions in general. It is at present unclear if the rather numerous northernmost extant populations reported from Saxony and Thuringia, Germany, point towards a wider distribution in central and perhaps also western and northern Europe. The German populations may have

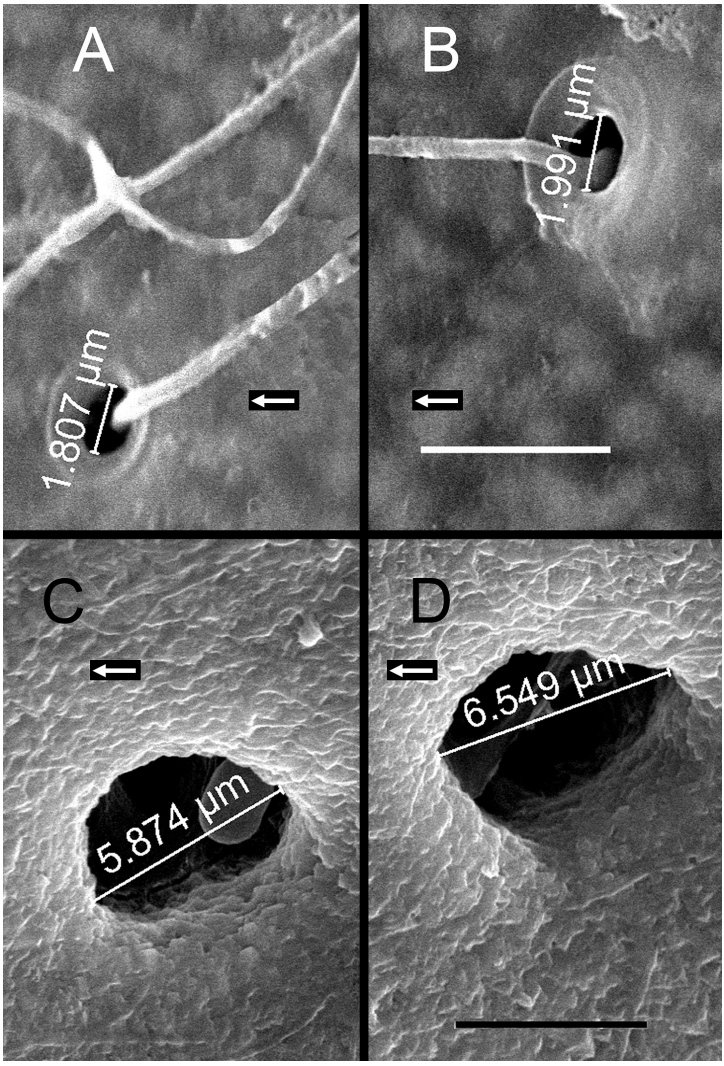


Fig. 17. *Neglecandona altoides* (Petkovski, 1961) nov. comb. Normal pore canals in the anterior area of valves. A and B, two external pore openings carrying each a rim and a seta (LV of an adult male, Figanières 1, France). C and D, internal pore openings (RV of an adult female, Bonne Cougne, France). Internal openings in the anterior valve area are c. 3x larger in diameter than those situated on the external valve surface. Lengths in µm were generated by the SEM. Scale bars: 5 µm. Arrows point anteriorly.

been founded by individuals introduced from the south by migrating birds. Locally living water birds, such as ducks, could have spread the *altoides* ostracods from pond to pond.

The genus *Neglecandona* Krstić, 2006 presently contains 39 extant species. Lake Ohrid, which stretches over the border of North Macedonia and Albania, is a so-called ancient lake, with 3-5 million years in age; it harbours a flock of 24 species of *Neglecandona*, i.e. 61.5 % of the species presently attributed to the genus.

As presently known, the entire genus *Neglecandona* appears to be restricted to the Palaearctic region.

Acknowledgments

We are grateful to Dr Trajan Petkovski, Skopje, for forwarding specimens of *Neglecandona altoides* from North Macedonia and Serbia to two of us (B.S. and R.F.). Julien Cillis is thanked for the technical assistance with the scanning electron microscope (SEM) at the Royal Belgian Institute of Natural Sciences in Brussels (courtesy of Prof. Koen Martens). Renate Walter realised part of the SEM-images at the SEM-laboratory of the Zoological Institute of the University of Hamburg (courtesy of Dr Dietmar Keyser). We thank Dr Karel Wouters for reading the manuscript and suggesting improvements.

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