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Contribution to the taxonomy of *Pseudocandona* and four related genera, with the description of *Schellencandona* nov. gen., a list of the Candoninae genera, and a key to the European genera of the subfamily (Crustacea, Ostracoda)

by

Claude MEISCH [1])

Abstract. The chaetotaxy of the cleaning leg of the type species of the podocopid genera *Cryptocandona* Kaufmann, 1900; *Pseudocandona* Kaufmann, 1900; *Fabaeformiscandona* (Krstic, 1972) Danielopol, 1973; and *Candona* Baird, 1845 is illustrated. The setal scheme of the limb is shown to be constant within each of the genera considered, and the taxonomic importance of the scheme is stressed. *Schellencandona* nov. gen. is erected for the species of the *schellenbergi*-group, which were formerly assigned to *Pseudocandona*. Seven species are transferred from *Pseudocandona* into *Fabaeformiscandona*: *Fabaeformiscandona aemonae* (Klie, 1935) nov. comb.; *Fabaeformiscandona bilobata* (Klie, 1938) nov. comb.; *Fabaeformiscandona bilobatoides* (Löffler, 1963) nov. comb.; *Fabaeformiscandona brevicornis* (Klie, 1925) nov. comb.; *Fabaeformiscandona brisiaca* (Klie, 1938) nov. comb.; *Fabaeformiscandona hertzogi* (Klie, 1938) nov. comb.; *Fabaeformiscandona lapponica* (Ekman, 1908) nov. comb.; and *Fabaeformiscandona speleae* (Klie, 1941) nov. comb. Three other new combinations are proposed: *Pseudocandona sarsi* (Hartwig, 1899) nov. comb., *Pseudocandona semicognita* (Schäfer, 1934) nov. comb., and *Pseudocandona triquetroides* (Sywula, 1974) nov. comb. A differential diagnosis of the five genera, and a key to the European genera of the Candoninae are given.

Introduction

The Candoninae is one of the three subfamilies of the Candonidae, the two others being the Cyclocypridinae Kaufmann, 1900 and Paracypridinae Sars, 1923 (see Martens 1992). The species of the first two subfamilies inhabit fresh or brackish waters, while representatives of the last subfamily are found in marine and brackish habitats.

The Candoninae, presently comprising more than 300 living and fossil species, are mainly distributed in the Holarctic. Only the genus *Candonopsis* occurs mainly outside the Holarctic. Species of this subfamily completely lack natatory setae on the

[1]) Musée national d'histoire naturelle, Marché-aux-Poissons, L-2345 Luxembourg (email: claude.meisch@ci.educ.lu).

second antennae (A2) and are thus devoid of any swimming ability. The subfamily includes

(a) benthic species which swim above or dig in the sediment of permanent and/or temporary waters;

(b) stygophilous species, i. e. species occurring in both surface and subterranean waters but with preference for the latter habitat;

(c) stygobitic species, which occur exclusively in hypogean habitats (e. g. all the species of the genera *Mixtacandona* and *Phreatocandona*);

(d) species occurring in humid terrestrial environments (genus *Terrestricandona*).

Genera and type species of the Candoninae are summarized in table 1 (after Martens 1992, modified).

The impetus for the present work came from the faunistic study of the European Candoninae species. When preparing a key to the European candonine genera, it appeared that identification of a number of the genera is at least uneasy and partly relies on (to say the least) a number of subtle characters, such as for instance the number of filaments of the respiratory plate of the maxilliped, the plumose versus smooth structure of the externodistal seta on the penultimate segment of the mandibular palp, and the shape and degree of sclerotization of the 'M'-process in the hemipenis.

Upon examining the appendages of a number of species, the importance of the chaetotaxy of the cleaning limb for the distinction of at least part of the candonine genera became apparent.

At an early stage of the present work I could see that

(a) number and position of the setae of the cleaning limb differed in at least several genera of the subfamily;

(b) the setal scheme of the cleaning leg was constant in at least several genera;

(c) the commonly accepted assignment of a number of species to the genus *Pseudocandona* appeared doubtful.

These observations stimulated me to check the chaetotaxy of the cleaning leg (T3) in a large number of candonine species in order to test the general validity of (b) and (c). The ultimate aim was to discover new features for the identification and characterization of the genera *Candona* s. str., *Cryptocandona*, *Fabaeformiscandona* and *Pseudocandona*.

In recent years, the chaetotaxy of various candonid and cypridid Ostracoda has been used for taxonomic studies (see for instance Danielopol 1978a, and subsequent papers; Martens 1986, and subsequent papers). A general model for the description of the cypridoid chaetotaxy was proposed by Broodbakker & Danielopol (1982). The scheme for the antenna was revised by Martens (1987).

It should be noted that various authors already used the chaetotaxy of the cleaning leg for characterization of a number of candonine genera, mainly *Cryptocandona*, *Mixtacandona* and *Nannocandona* (see Ekman 1914; Alm 1915; Klie 1938d; Petkovski 1969; Danielopol 1978a). So far, however, there has been no comparative study of the T3-chaetotaxy for the genera considered here.

Table 1. - Summary of extant genera and type species of Candoninae.

Genus	Type species
Tribe Candonini	
Baicalocandona Mazepova, 1976	*B. bivia* Mazepova, 1976
Candona s. str. Baird, 1835	*C. candida* (Baird, 1835)
Candonopsis Vavra, 1891	*C. kingsleii* (Brady & Robertson, 1870)
Caribecandona Broodbakker, 1983	*C. trapezoidea* Broodbakker, 1983
Cryptocandona Kaufmann, 1900	*Cr. vavrai* Kaufmann, 1900
Fabaeformiscandona (Krstic, 1972)	*F. fabaeformis* (Fischer, 1851)
Indocandona Gupta, 1984	*I. krishnakanti* Gupta, 1984
Mixtacandona Sywula, 1970	*M. laisi* (Klie, 1938)
Nannocandona Ekman, 1914	*N. faba* Ekman, 1914
Paracandona Hartwig, 1899	*P. euplectella* (Robertson, 1889)
Phreatocandona Danielopol, 1973	*Ph. motasi* Danielopol, 1973
Pseudocandona s. l. Kaufmann, 1900	*Ps. insculpta* (Müller, 1900)
= *Metacandona* Bronstein, 1930	*M. bispinosa* Bronstein, 1930
= *Typhlocypris* (Vejdovsky, 1882) Sostaric, 1888	*T. eremita* (Vejdovsky, 1882)
= *Cavernocandona* Hartmann, 1964	*C. dispar* Hartmann, 1964
= *Alatocandona* Carbonnel, 1969	*A. bronsteini* Carbonnel, 1969
Schellencandona nov. gen.	*S. schellenbergi* (Klie, 1934)
Terrestricandona Danielopol & Betsch, 1980	*T. minuta* Danielopol & Betsch, 1980
= *Terrestricypris* Shornikov, 1980	*T. arborea* Shornikov, 1980
Tribe Namibcypridini	
Danielocandona Broodbakker, 1983	*D. lieshoutae* Broodbakker, 1983
Namibcypris Martens, 1992	*N. costata* Martens, 1992

The present contribution is the first step towards a revision of the Candoninae based on the study of 'soft parts', mainly the chaetotaxy of the cleaning leg, of four genera. In a second phase of the revision, other characters, above all of the antennae and the hemipenis should be considered and characters of the carapace and valves should be included in the study.

Material and methods

As a starting point, illustrations of the cleaning leg of the type species of the genera *Cryptocandona*, *Pseudocandona*, *Fabaeformiscandona*, and *Candona* s. str. are given. The figures are drawn from specimens dissected by the author. As a second step, the setal equipment of the cleaning leg of all known species of *Cryptocandona*, *Pseudocandona*, and *Fabaeformiscandona*, and a large number of species of *Candona* was checked. The verification was either done on dissected specimens from the author's collection of microscopic slides (those species are marked with an asterisk), or on illustrations given in the literature. This allows verification of the hypothesis of the intrageneric constancy of the setal scheme of the cleaning leg within the genera considered. Taxonomic changes inferred from those data are proposed. Finally, a differential diagnosis of the genera considered is given.

Abbreviations: LV, left valve; RV, right valve; A2, antenna; Pr, protopodite; E, endopodite; T1, T2 and T3, first, second and third thoracopods; L, length of carapace; W, width of carapace (dorsal view); specimens of the species marked with an asterisk (*) have been examined by the author.

Structure and chaetotaxy of the candonine cleaning leg

Serial homology of the three thoracopods of the Podocopida

The 5th, 6th and 7th limbs of the podocopid Ostracoda are considered here serially homologous thoracopods (T1, T2 and T3). In the Cytheroidea, the three pairs of thoracopods are subequally developed walking legs. In the remaining podocopid lineages (a) the fifth limb (T1) is more or less strongly transformed into a maxilliped; (b) the sixth limb (T2) is a well developed walking leg; (c) the seventh limb (T3) is transformed into a recurved cleaning leg, except in the Darwinuloidea and Sigillioidea.

If there is a general agreement about the thoracic origin of the 6th and 7th limbs, there has been extensive discussion about the thoracic versus cephalic origin of the 5th limb. The 5th limb was classically considered the 1st thoracopod (see for instance Müller 1894 and subsequent papers; Sars 1925; Klie 1938d; Danielopol 1978a). In contrast, Weygoldt (1960) concluded, mainly from the innervation of the 5th limb in the larval and adult stages of *Cyprideis litoralis*, that the 5th limb has a cephalic origin and hence is a modified 2nd maxilla (Mx2); the leg-like appearance of the 5th limb in the Cytheroidea, Darwinuloidea, and part of the Cypridoidea, etc, should have evolved in response to functional adaptation. The latter view was accepted by Hartmann (1966, 1967, 1968, 1975) in his most influential and comprehensive work on Ostracoda. Almost all modern authors followed Weygoldt's (1960) and Hartmann's (op. cit.) view (see for instance Danielopol 1978b and subsequent papers; Maddocks 1982, 1990; Martens 1986, and subsequent papers; Wouters 1984, and subsequent papers).

However, more recently a different opinion was adopted by Athersuch et al. (1989), who again considered the 5th limb the 1st thoracopod. The same view is adopted here. In the present author's opinion, the thoracic origin of the 5th limb is strongly supported by the obvious homologous structure and chaetotaxy of this limb in all podocopid lineages (for the Macrocyprididae see Maddocks 1990; for the Cypridoidea see the illustrations showing an 'evolutionary series' in Danielopol 1978a: fig. 37).

For comparison with the Candoninae, the thoracopods of *Macrocypris minna,* the type species of the genus *Macrocypris,* are shown (fig. 1). The Macrocyprididae come close to the cypridoid stock (Maddocks 1990), having preserved many primitive characters: for instance, the T1 appears leg-like and incompletely transformed into a maxilliped; the T2 is a well developed walking leg; the T3 (cleaning leg) is distally not transformed into a pincer organ, and the overall setal equipment is well developed (see Maddocks 1990). When the cleaning leg is rotated downwards (fig. 1D), the homology with the walking leg is clear and the homologous segments and setae are readily recognized.

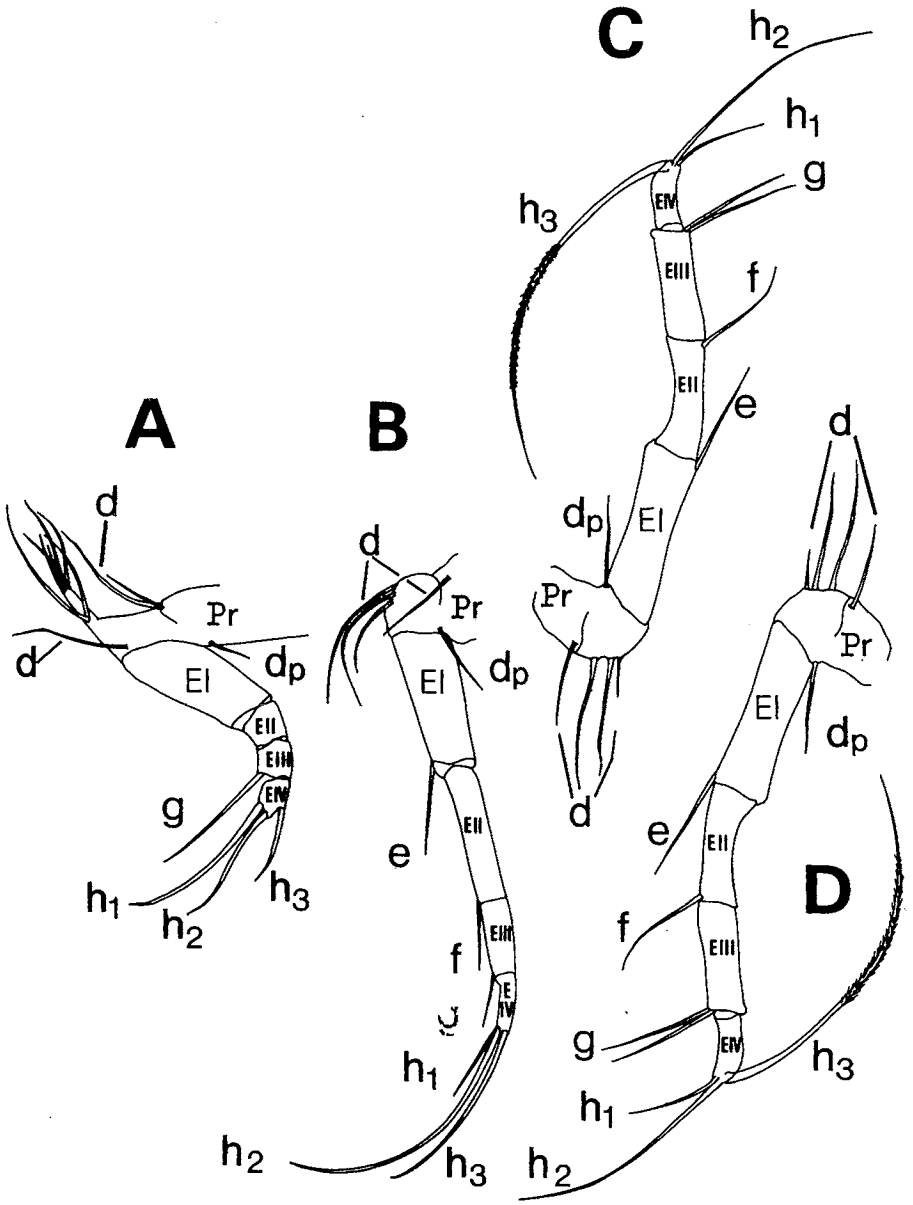


Fig. 1. *Macrocypris minna*. A, B and C, maxilliped, walking and cleaning legs in the 'natural' position; D, cleaning leg rotated downwards to show the homologous setae. See text for explanation. The limbs are not shown at the same scale. Slightly modified from Maddocks (1990).

In the Candoninae, and the Candonidae in general, the T1 has become a 'true' maxilliped (see intermediary stages in Danielopol 1978a: fig. 37), the endopodite of which is modified into a clasping organ in the male; the cleaning leg is similar to that of the Macrocyprididae, although there is a marked trend towards reduction of the setal equipment (see below).

Structure of the candonine cleaning leg

The general structure of the cleaning leg barely varies among the members of the Candoninae (Danielopol 1978a; Broodbakker & Danielopol 1982; also observations of the present author). The T3 comprises four or five segments (podomeres), depending on the fusion or non-fusion of the segments 3 and 4. The basal segment is the protopodite (Pr); the 3 or 4 distal segments are considered the endopodite (E). In a number of candonine species, the endopodite segments II and III have partly fused, a weak separation between the segments being still present. In other species, the fusion of EII and EIII is complete and the leg therefore appears 4-segmented. Segments EII and EIII, whether fused or not, are commonly referred to as the 'penultimate segment' of the cleaning leg. The 5-segmented leg is most certainly the plesiomorphic ('primitive') condition. This is supported by the presence of seta 'f' in some genera (e.g. *Cryptocandona*,). Indeed, a look at the T3 of the type species of all the candonine genera shows that, in the course of evolution, no 'true' setae are added to the complete scheme (see *Cryptocandona*), but that there is, on the opposite, a clear trend towards the loss of one or more setae in many genera (see figs 2 and 3). Thus, the presence of seta 'f' proves that the fusion of two segments has taken place in the species which lack a separation close to the seta 'f'. Most probably, the fusion of the two segments occurred independently, in parallel, within a number of candonine genera.

Chaetotaxy of the candonine cleaning leg

As already stated above, a descriptive model of the chaetotaxy of the Cypridoidea was published by Broodbakker & Danielopol (1982). In that model, the setae of the limbs are identified by the position (proximal/distal; anterior/posterior) and relative length (short/medium/long). For quick identification of the setae a more simple model will be used here. This model is not intended to replace that of Danielopol & Broodbakker (1982). It should be noticed that only the 'true' setae (in the sense of Broodbakker & Danielopol 1982) are considered here; the so-called pseudochaetae are discarded. The setal scheme of the cleaning leg is not sexually dimorphic within the genera considered here.

In the most primitive candonine condition, see for instance *Cryptocandona*, the protopodite bears 3 setae, i. e. 2 'ventral' and 1 'dorsal' setae, here designated as d1, d2 and dp (p for 'posterior'; figs 2 and 3). The letter 'd' is chosen to follow the designation proposed by Martens (1989; 1990; and subsequent papers) for the homologous setae of the protopodite of the walking leg of the Cyprididae. Seta d2 is completely reduced in most of the candonine genera.

Segment 2 (EI) has one distal seta, designated as 'e'. This seta too is lost in most candonine genera.

In the primitive condition, segments 3 and 4 (EII and EIII) are separated and each of them bears a 'postero'-distal seta, here designated as 'f' and 'g'. Seta 'f' is commonly referred to as the 'medial seta of the penultimate segment'; it is completely reduced in most candonine genera.

The terminal segment (segment 5 or EIV) bears 3 terminal setae, here designated as h1, h2 and h3.

The setae d1-2 of both the walking and cleaning legs are most certainly the remains of a greater number of protopodite setae. In Macrocyprididae (see Maddocks 1990), the protopodite of the walking leg bears 4 or 5 'd'-setae, and the cleaning leg has usually 4 'd'-setae. The protopodite of both legs obviously results from the fusion of at least two segments. No attempt is made here to homologuise the setae d1 and d2 of the T3 of the Candoninae with one or the other of the more numerous 'd'-setae of the T3 of *Macrocypris*. The setae dp is most probably the remain of a reduced exopodite.

The homology of the T3-setae 'e', 'f', 'g' and h1-3 with the antero-distal setae of the segments EII, EIII and the terminal claw and ajacent setae of the walking leg (fig. 1) is self-evident. The terminal T3-seta h2 appears homologous with the terminal claw of the candonine walking leg, while h1 and h3 are the homologs of the two small setae adjacent to the terminal claw of the walking leg.

It should be noticed that only the setal scheme, i. e. the presence or absence of the setae d1-2, 'e', 'f', 'g' and h1-3, is considered important here. The degree of development (length and thickness) of the different setae is taxonomically unimportant at the generic level.

Taxonomic descriptions

Classification (after Maddocks 1982 as modified by Martens 1992)

Subphylum Crustacea Pennant, 1777
Class Ostracoda Latreille, 1806
Subclass Podocopa Müller, 1894
Order Podocopida Sars, 1866
Suborder Podocopina Sars, 1866
Infraorder Cypridocopina Jones, 1901
Superfamily Cypridoidea Baird, 1845
Family Candonidae Kaufmann, 1900
Subfamily Candoninae Kaufmann, 1900

Genus *Cryptocandona* Kaufmann, 1900

Type species and taxonomic history

Cryptocandona vavrai Kaufmann, 1900. Synonym: *Cr. juvavi* Brehm, 1953.

Cryptocandona was erected by Kaufmann (1900) to include one single species, *Cr. vavrai*, described as new from Switzerland.

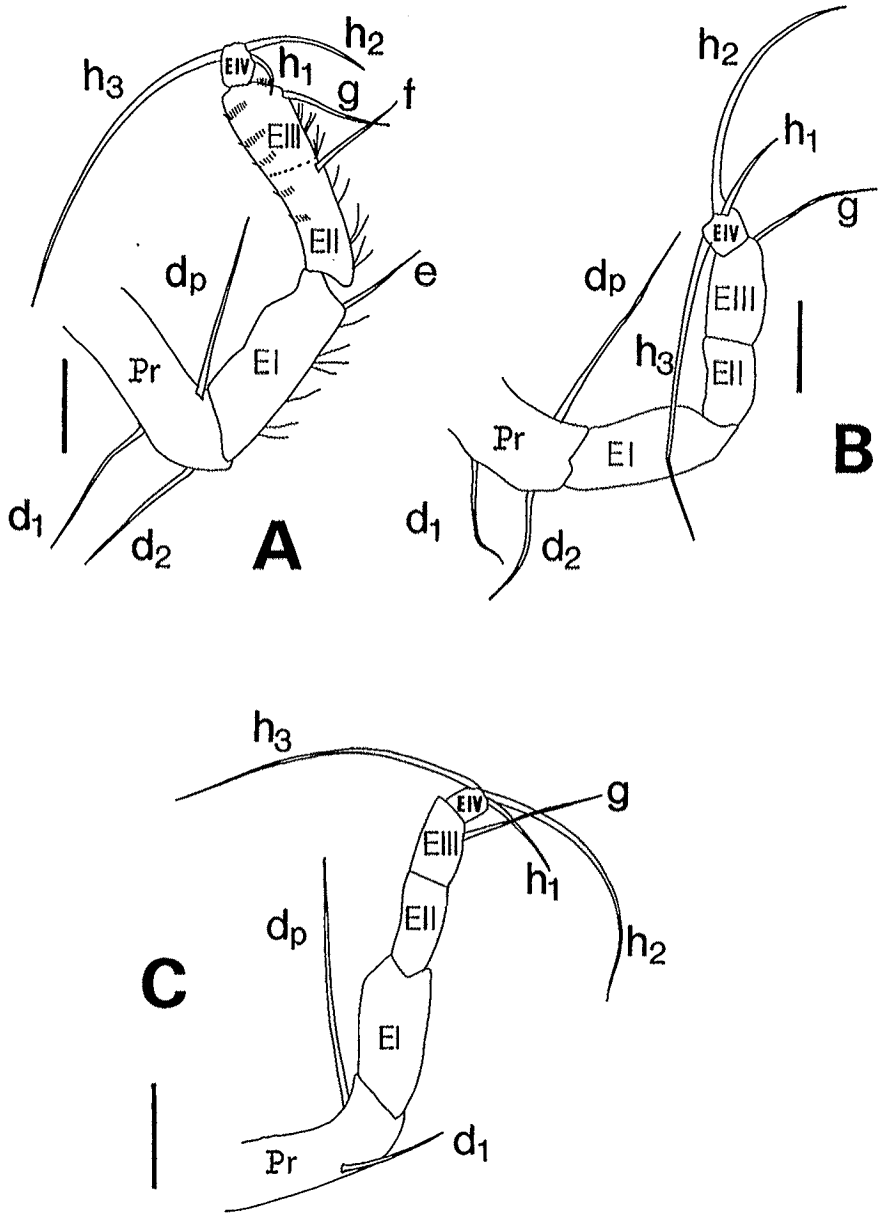


Fig. 2. - Cleaning leg of A, *Cryptocandona vavrai;* B, *Pseudocandona insculpta*; C, *Fabaeformiscandona fabaeformis*. Scale bars, 50 µm. See text for explanation.

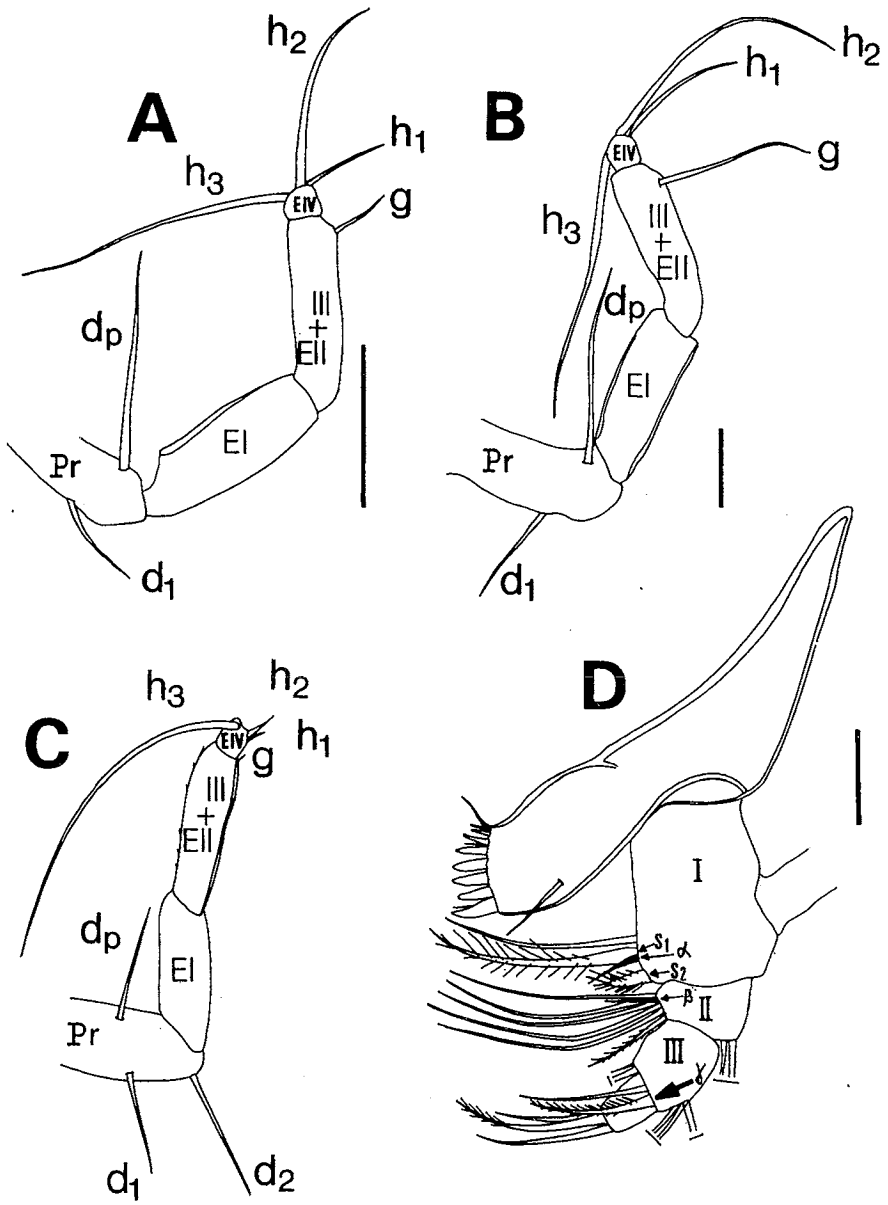


Fig. 3. - Cleaning leg of A, *Schellencandona belgica* nov. comb.; B, *Candona candida;* C, *Mixtacandona laisi*; D, mandible and mandibular palp of *Candona candida.* See text for explanation. Scale bars, 50 µm. (C redrawn from Klie 1938e).

Other species

The genus comprises at present 12 nominal living epigean and hypogean species (Danielopol 1980b; Kempf 1980, also working copy of 1995), which are distributed throughout central and northern Europe and Japan (Palaearctic).

Differential diagnosis of *Cryptocandona*

Carapace ca 1 mm long, elongate in lateral view, distinctly laterally compressed in dorsal view. Male A2 5-segmented (penultimate segment subdivided) and with male bristles (transformed t2 and t3 setae). Mandibular palp: setal group of the 2nd segment with 3 setae (this segment with 2+3 setae); externo-distal seta ('gamma'-seta) of the penultimate segment smooth (not plumose). Respiratory plate of the maxilliped with 3 filaments. Cleaning leg: protopodite with 3 setae (d1-2 and dp); distal seta of segment 2 (EI) (seta 'e') present; penultimate segment (EII+III) with a medial and a distal setae (setae 'f' and 'g'); terminal segment with 1 long and 2 short setae (setae h1-3).

Important literature: Ekman (1914), Klie (1938a, d), Danielopol (1978a, 1980b).

T3-chaetotaxy

Within the Candoninae, the setal equipment of the cleaning leg of the species of this genus is most complete. In *Cr. vavrai*, all setae, i. e. d1-2, dp, 'e', 'f', 'g', and h1-3 are present (fig. 2A); the penultimate segment is usually undivided; there is a weak subdivision in some specimens.

The T3-setal equipment of all known species of the genus has been checked; it is identical with that of the type species, except for the missing data mentioned below: *Cr. brehmi* Klie, 1934 (Bronstein, 1947); *Cr. dudichi* (Klie, 1930) Brehm, 1953; *Cr. kieferi* * (Klie, 1938) Danielopol, 1980; *Cr. leruthi* (Klie, 1936) Danielopol, 1980; *Cr. longipes* (Ekman, 1908) G.W. Müller, 1912 (Pr not described nor illustrated); *Cr. matris* (Sywula, 1976) Danielopol, 1980 (T3 not illustrated; setae d1-2 and dp, 'g' and h1-3 mentioned in the text). *Cr. phreaticola* (Kiefer & Klie, 1927) Brehm, 1953; *Cr. pygmaea* (Ekman, 1908) G.W. Müller, 1912 (Pr not described nor illustrated); *Cr. reducta* * (Alm, 1914) Sars, 1925; *Cr. riongessa* Bronstein, 1947 (Pr not described nor illustrated);

Cr. angustissima (Ekman, 1914) Danielopol, 1980. The T3-setal scheme is similar to that of the type species of the genus, except for the protopodite, for which Ekman's (1914) figure shows only two setae (d2 and dp). The absence of the seta d1 is probably due to an error of observation.

In 8 of the 12 known species the setal scheme of the cleaning leg is similar to that of the type species. In 4 species the chaetotaxy is only partially known but does not contradict the scheme found in the type species. From these data it may be inferred that the setal scheme of the cleaning leg is constant within *Cryptocandona* and hence appears to be an important diagnostic feature of the genus.

Genus *Pseudocandona* Kaufmann, 1900

Type species

Candona insculpta Müller, 1900. Unused senior synonym: *Cypris pubescens* Koch, 1837 = *Candona pubescens* (Koch) sensu Hartwig 1899.

Taxonomic history

Pseudocandona was erected by Kaufmann (1900) for one single species, *Ps. pubescens* (Koch, 1837), - now considered an unused senior synonym of *Ps. insculpta* (Müller, 1900) - extracted from *Candona* s. l. In Kaufmann's (1900) view *Pseudocandona* differs from *Candona* solely in the absence of sexually dimorphic characters on the male antenna. The male A2 of *Ps. insculpta* is indeed similar to that of the female: the penultimate segment is undivided, and the t2 and t3-setae are untransformed (the so-called male bristles are missing).

Triebel (1963) transferred the species of the *rostrata* and *compressa* groups from *Candona* into *Pseudocandona*, which he considered a subgenus of *Candona*. Petkovski (1969) accepted Triebel's view but considered *Pseudocandona* a separate genus.

Petkovski's (1969) broad definition of *Pseudocandona* - the genus now includes species with a dimorphic male A2 (penultimate segment subdivided and with male bristles - has been adopted by a majority of modern authors (see for instance Danielopol 1973, 1978a,b, and subsequent papers; Broodbakker 1983a; Broodbakker & Danielopol 1982; Wouters 1989; Meisch et al. 1990; Martens et al. 1992; Krstic 1993; Griffiths & Evans 1995), and is also adopted in the present work.

Reassessment of *Pseudocandona* Kaufmann, 1900 sensu lato

According to Danielopol (1978b: 58), *Pseudocandona* is characterized by the combination of the following features: (a) respiratory plate of the maxilliped with 2 filaments; (b) medial seta of the penultimate segment of the cleaning leg (= seta 'f') absent; (c) 'M'-process of the hemipenis flat and proximally only weakly sclerotized.

Pseudocandona s. l. comprises ca 75 Recent species distributed throughout the Holarctic. The genus has been subdivided into six species groups (see Danielopol & Hartmann 1986): the *rostrata-*, *compressa-*, *zschokkei-*, *eremita-*, *schellenbergi-*, and *caribbeana*-groups. Additionally, there are (a) a number of species without group-assignment (see below), and (b) ca 28 species which are endemic in lake Baikal in Siberia.

Remark. It should be noticed that only the last character (the structure of the 'M'-process) clearly differentiates *Pseudocandona* from the related genera *Candona* s. str. and *Fabaeformiscandona*. Moreover, the taxonomy of the genus *Pseudocandona* remains unclear at present and it is not possible to give a really satisfactory diagnosis of the genus. This because

(1) a number of species are represented by parthenogenetically reproducing females only. The assignment of those species to the genus *Pseudocandona* appears uncertain. This problem may be solved with the help of the chaetotaxy of the cleaning leg (see below);

(2) Triebel (1963) and Broodbakker & Danielopol (1982) showed that the species from lake Baikal in Siberia assigned to *Pseudocandona* are not closely allied to the European species of the genus, but rather belong to a separate phylogenetic lineage (see also Martens et al. 1992a,b). Therefore it is here suggested to remove the Baikal-species from *Pseudocandona*. The Baikal-species probably belong to one or even more as yet undescribed genera, the taxonomy of which, however, will not be discussed here.

(3) The commonly accepted assignment of the species of the *schellenbergi*-group to *Pseudocandona* appears doubtful. This taxonomic problem will be solved with the help of the chaetotaxy of the cleaning leg (see below).

T3-chaetotaxy

Setal scheme of the cleaning leg of the type species, *Ps. insculpta* (Müller, 1900) (fig. 2B): protopodite with 3 setae (d1, d2, and dp); setae 'e' and 'f' lost; 'g' present; h1-2 well developed, h3 distinctly shorter.

Species of the ***zschokkei*-group.** Type: *Ps. zschokkei* (Wolf, 1920) Bronstein, 1939.

Carapace trapezoidal in lateral view; valves with shallow pits which are most dense in the central valve area. Setal group on the second segment of the mandibular palp with 3 setae (this segment with 2+3 setae). This group, which has been established by Danielopol (1978a), includes four stygobitic species (see Danielopol & Hartmann 1986): *Ps. delamarei* Danielopol, 1978; *Ps. dichtliae* (Brehm, 1953) Danielopol, 1986; *Ps. rouchi* Danielopol, 1978; *Ps. zschokkei* (Wolf, 1920) Bronstein, 1939.

The T3-setal scheme of *Ps. zschokkei* is identical with that of the type species of the genus; that of the three other species remains unknown.

Species of the ***eremita*-group.** Type: *Ps. eremita* (Vejdovsky, 1882). Carapace triangular in lateral view; LV overlapping the RV with a dorsal hump; valves with shallow pits above all in the area of the central muscle scars. Setal group on the second segment of the mandibular palp with 3 setae (this segment with 2+3 setae). This group was introduced by Danielopol (1978a). For a detailed diagnosis see Danielopol (1982a).

The *eremita*-group includes 8 stygobitic species (Danielopol & Hartmann 1986): *Ps. cavicola* (Klie, 1935) Danielopol, 1982; *Ps. dispar* (Hartmann, 1964) Danielopol, 1971; *Ps. eremita* (Vejdovsky, 1882) Danielopol, 1971; *Ps. pretneri* Danielopol, 1978; *Ps. puteana* (Klie, 1931) Danielopol, 1971; *Ps. serbani* Danielopol, 1982; *Ps. trigonella* (Klie, 1931) Danielopol, 1971 (Pr unknown); *Ps. szoecsi* (Farkas, 1958) Petkovski, 1969 (= *Ps. pannonicola* (Löffler, 1960) Danielopol, 1982).

The T3-setal scheme of 7 of those species is identical with that of the type species of *Pseudocandona;* that of *Ps. dispar* remains unknown.

Species of the ***rostrata*-group.** Type: *Ps. rostrata* (Brady & Norman, 1889) Carbonnel, 1969. Carapace not trapezoidal or triangular in lateral view. Setal group on the second segment of the mandibular palp with 3 setae (this segment with 2+3 setae). This group was introduced by Hartwig (1901).

The setal scheme of the cleaning leg of the following species is identical with that of the type species of the genus: *Ps. rostrata* (Brady & Norman, 1889) Carbonnel, 1969; *Ps. hartwigi* * (Müller, 1900) Wouters 1989; *Ps. lobipes* (Hartwig, 1900) Wouters, 1989; *Ps. marchica* (Hartwig, 1899) Carbonnel, 1969; *Ps. sarsi* * (Hartwig, 1899) nov. comb.; *Ps. slavei* Petkovski, 1969; *Ps. stagnalis* (Sars, 1890) Meisch & Broodbakker, 1993; *Ps. antilliana* Broodbakker, 1983; *Ps. geratsi* Broodbakker, 1983.

The T3-protopodite chaetotaxy of *Ps. tyrolensis* (Löffler, 1963) Danielopol, 1980 remains unknown. The species was described from one single female specimen and is only known from the original description. The small carapace size and the morphology of the furca show that this specimen probably belongs to the juvenile stage of a species of *Pseudocandona*.

Species of the ***compressa*-group.** Type: *Ps. compressa* (Koch, 1838) Danielopol, 1973. Carapace not trapezoidal or triangular in lateral view. Setal group on the second segment of the mandibular palp with 5 setae (this segment with 5+2 setae). *Ps. insculpta*, the type species of the genus, belongs to this group, which was introduced by Hartwig (1901).

The setal scheme of the cleaning leg of the following species is identical with that of the type species of the genus: *Ps. albicans* * (Brady, 1864) Danielopol, 1973; *Ps. compressa* * (Koch, 1838) Danielopol, 1973 (=*Ps. crispata* (Klie, 1926)); *Ps. insculpta* (Müller, 1900); *Ps. pratensis* * (Hartwig, 1901) Danielopol, 1980; *Ps. sucki* * (Hartwig, 1901) Danielopol, 1980; *Ps. morimotoi* (McKenzie, 1972) Danielopol, 1986 (Pr unknown); *Ps. semicognita* (Schäfer, 1934) nov. comb.

Remarks. (1) *Ps. pseudoparallela* (Löffler, 1961) Danielopol, 1980 is so far only known from the original description and record from the interstitial groundwater of the upper Danube catchment area in southwestern Germany. According to Löffler (1961; text only) the protopodite of the cleaning leg bears two setae. The characters of the carapace and appendages point to the synonymy with *Ps. albicans* (see also Nüchterlein 1969). The description of the T3-protopodite is probably erroneous.

(2) *Ps. profundicola* (Löffler, 1960) Danielopol, 1980 is so far only known from the type locality in Burgenland, Austria. The setal equipment of the protopodite of the cleaning leg was not described nor illustrated. The setal scheme of the endopodite is identical with that of the type species of the genus. The species is most probably identical with *Ps. albicans*.

(3) *Ps. altoalpina* (Löffler, 1963) Danielopol, 1980 is only known from one single specimen collected in Tyrol, Austria. The original description lacks indications on the setal equipment of the protopodite of the cleaning leg. *Ps. altoalpina* too is most probably synonymous with *Ps. albicans* (see also Nüchterlein 1969).

Species of the ***caribbeana*-group.** Type: *Ps. caribbeana* Broodbakker, 1983.

Carapace trapezoidal with rounded anterior and posterior margins. Second segment of the mandibular palp with 2 + 3 setae. Seta h1 of T3 2-2.5 x the length of the terminal segment. This group was erected by Broodbakker (1983; see also Danielopol & Hartmann 1986) for two species described from the Caribbean area, *Ps. caribbeana* and *Ps. cubensis*, and two others, *Ps. marengoensis* and *Ps. jeanneli*,

from the USA. All four species are stygobites. For a detailed diagnosis of this species-group see Broodbakker (1983).

The setal scheme of the cleaning leg of *Ps. caribbeana* is identical with that of the type species of *Pseudocandona* (see Broddbakker 1983).

Remarks. (1) *Ps. cubensis* Broodbakker, 1983. The T3-setal scheme is identical with that of the type species of the genus, except for the protopodite; according to the original description (text and figure), the latter has only two setae (d2 absent). Since the species is closely related to *Ps. caribbeana*, which has a T3-protopodite with 3 setae, this is most remarkable. Future investigations should clarify the taxonomic status of this species.

(2) *Ps. marengoensis* (Klie, 1931) Danielopol, 1973. The original description by Klie (1931) lacks any description of the setal equipment of the T3-protopodite. But the species comes very close to *Ps. jeanneli* (Klie, 1931) Danielopol, 1986, described in the same publication, for which Klie (1931) illustrates a T3-protopodite with 3 setae. Therefore the presence of 3 setae on the T3-protopodite of *Ps. marengoensis* is highly probable.

Species of the ***schellenbergi*-group**. Synonym: *simililampadis*-group (see Hartmann & Danielopol 1986). Type: *Candona schellenbergi* Klie, 1934.

This group was introduced by Danielopol (1978b) to include the following stygobitic species: *Pseudocandona schellenbergi* (Klie, 1934) Danielopol, 1978; *Ps. belgica* * (Klie, 1937) Danielopol, 1978; *Ps. insueta* (Klie, 1938) Danielopol, 1978; and *Ps. simililampadis* Danielopol, 1978.

The T3-setal scheme of those four species is identical with that of *Ps. insculpta*, type species of *Pseudocandona*, except for the missing d2-seta of the protopodite (fig. 3A). See the discussion below.

Species with no group-assignment. The following species of *Pseudocandona* are classified without group-assignment (see Danielopol & Hartmann 1986): *Ps. aemonae* Klie, 1935 (Danielopol, 1986); *Ps. bilobata* (Klie, 1938) Danielopol, 1980; *Ps. bilobatoides* (Löffler, 1963) Danielopol, 1980; *Ps. brevicornis* (Klie, 1925) Wendling & Scharf, 1992 = *Candona (Typhlocypris) limnocrenica* Sywula, 1971; *Ps. brisiaca* (Klie, 1938) Danielopol, 1980; *Ps. hertzogi* (Klie, 1938) Danielopol, 1980; *Ps. speleae* (Klie, 1941) Danielopol, 1973.

The setal scheme of the cleaning leg of those species is identical with that of the type species of *Pseudocandona*, except for the protopodite, which has only two setae (seta d2 absent). The scheme is actually similar to that of *Fabaeformiscandona* and the transfer of those species into that genus is proposed below (see *Fabaeformiscandona*).

Remark. *Ps. breuili* (Paris, 1920) Danielopol, 1986 should be added to the list of species without group assignment. Paris' (1920) illustration of this rather enigmatic species shows a protopodite without any setae. This, however, is very implausible and most probably erroneous. Living specimens of *Ps. breuili* have been reported from a cave in Spain (Paris 1920) and a spring in eastern Germany (Pietrzeniuk 1985; leg. R. Fuhrmann). The species, which is here provisionally kept within *Pseudocandona*, needs to be redescribed.

Discussion

The *zschokkei-*, *eremita-*, *rostrata-*, *compressa-*, and probably also the *caribbeana*-groups must be considered to form the 'taxonomic core' of the genus *Pseudocandona*. The T3-setal scheme confirms this view: it appears identical in all the species of these groups for which it has been described. From the data above I would like to infer the constancy of the T3-setal scheme within the genus *Pseudocandona*.

If this view is accepted, then the observation of a different chaetal scheme in certain taxa should at least cast a strong doubt on the belonging of those species to the genus *Pseudocandona*. This is the case for (1) the species of the *schellenbergi*-group, and (2) a number of species classified without group-assignment. It is here suggested to remove those species from *Pseudocandona* s. l. For a majority of those species the taxonomic transfer is supported by a number of other features (see below).

Pseudocandona sensu stricto

Type species

Candona insculpta G.W. Müller, 1900. Unused senior synonym: *Cypris pubescens* Koch, 1837 = *Candona pubescens* (Koch) sensu Hartwig 1899.

Other species

Pseudocandona s. str. comprises the species of *Pseudocandona* s. l. as defined above minus (a) the ca 28 Baikal species; (b) the 5 species of the *schellenbergi*-group; and (c) 7 species classified without group-assignment. *Pseudocandona* s. str. comprises ca 35 species distributed throughout the Holarctic.

Differential diagnosis

Carapace of medium length, ca 0.8-1.2 mm, variously shaped, usually relatively short and stout, more rarely elongate or triangular in lateral view. Surface of adult valves smooth or pitted, usually (?always) with long, stiff, conspicuous perpendicularly attached setae. LV overlaps RV ventrally. Male A2: penultimate segment subdivided or not; when subdivided then with male bristles (transformed t2 and t3-setae). Mandibular palp: setal group of the second segment with 3 or 5 setae; externo-distal seta of the penultimate segment smooth (not plumose). Maxilliped (T1): respiratory plate with two filaments. Cleaning leg (T3): basal segment (protopodite) with 3 setae (d1-2 and dp); distal seta on the penultimate segment present (seta 'g'); terminal segment with one short seta (h1), and two long setae (h2-3). Zenker's organ with 5+2 rings of spines. Hemipenis: 'M'-process flat and proximally only weakly sclerotized.

Remark. It should be noticed that the T3-setal scheme allows easy distinction of *Pseudocandona* on the one side and *Candona* s. str., *Fabaeformiscandona* and *Schellencandona* nov. gen. on the other side.

Important literature: Kaufmann (1900), Petkovski (1969), Danielopol (1978a, b, 1982), Broodbakker (1983), Danielopol & Hartmann (1986), Martens et al. (1992a, b), Krstic (1993).

Genus *Schellencandona* nov. gen.

Type species

Candona schellenbergi Klie, 1934 is designated the type species of the genus.

Material investigated

Ca 10 adult males, females and juveniles of *Schellencandona belgica* (Klie, 1937) nov. comb. from Saarland, Germany. Leg. James Enright, University of Saarbrücken.

Differential diagnosis

Carapace very small, 0.4-0.6 mm long. Surface of valves smooth or with shallow pits. Eye pigment absent. Male antenna dimorphic: penultimate segment subdivided and with male bristles (t2 and t3-bristles transformed). Mandibular palp: setal group of the second segment with 3 setae (this segment with 2+3 setae); externo-distal seta (gamma-seta) of the penultimate segment smooth (plumose in *Candona* s. str.). Respiratory plate of the maxilliped with 2 setae. Setal equipment of the cleaning leg: basal segment (protopodite) with 2 setae (d1 and dp); penultimate segment (EII+III) with a distal seta (seta 'g'); terminal segment with 2 long (h2-3) and one short (h1) setae. Male A2: penultimate segment subdivided and with male bristles. Zenker's organ with 4+2 rings of spines. Hemipenis: 'M'-process very flat. Ecology: stygobitic species. Distribution: Europe.

Other species

Schellencandona comprises the 4 species of the *schellenbergi*-group established by Danielopol (1978b; see also Danielopol & Hartmann 1986) and formerly assigned to *Pseudocandona*. The new combinations are: *Schellencandona belgica* (Klie, 1937) nov. comb.; *Schellencandona insueta* (Klie, 1938) nov. comb.; *Schellencandona schellenbergi* (Klie, 1934) nov. comb.; *Schellencandona simililampadis* (Danielopol, 1978) nov. comb. *Schellencandona triquetra* (Klie, 1936) nov. comb. is tentatively added to this list (see below).

Important literature: Danielopol (1978b), Danielopol & Hartmann (1986).

Discussion

The establishment of the new genus was foreshadowed by the introduction of the *schellenbergi*-species group within *Pseudocandona* by Danielopol (1978b; see also Hartmann & Danielopol 1986). The author (Danielopol 1978b) stressed that the members of the *schellenbergi*-group differ in two important taxonomic characters from the remaining species of *Pseudocandona*: (a) the Zenker's organ has 4+2 rings of spines (5+2 rings in the remaining species of *Pseudocandona*; *Candona* s. str. and *Fabaeformiscandona* also have 7 rings); (b) the 'M'process of the hemipenis is very flat. The study of the T3-setal scheme (see above) confirms that the species of this group belong to a separate phylogenetic lineage, which is best separated at the generic level.

Schellencandona nov. gen. comes close to *Fabaeformiscandona* and *Candona* s. str., from which it differs mainly in the characters mentioned under (a) and (b) above.

Schellencandona nov. gen. is readily distinguished from *Pseudocandona* by the setal equipment of the basal segment (protopodite) of the cleaning leg: this segment has 2 setae in *Schellencandona* nov. gen.; in *Pseudocandona* s. str. there are 3 such setae (d1, d2 and dp). It should be noticed that the T3-setal scheme is identical in *Candona, Fabaeformiscandona* and *Schellencandona* nov. gen.

All known species of the genus are stygobites. The small size and the absence of the eye pigment are most certainly adaptations to the hypogean way of life. The reduction of the number of spinous rings in the Zenker's organ is probably linked with the reduction in size.

Remarks. (1) *Candona triquetra* Klie, 1936 was assigned to the *rostrata*-group of *Candona* s. l. by Klie (1936) and later transferred into *Pseudocandona*: *Ps. triquetra* (Klie, 1936) Danielopol, 1980. A detailed redescription of the species was given by Marmonier (1988; unpubl. thesis). The T3-protopodite bears 2 setae only (d2 is absent), and the Zenker's organ has only 4+2 spines. The species clearly does not belong to *Pseudocandona* s. str. It is here tentatively transferred into *Schellencandona* nov. gen.

(2) *Candona (Typhlocypris) triquetroides* Sywula, 1974, which is so far only known from southern Poland, comes close to *Candona triquetra* Klie, 1936. As *Typhlocypris* (type species *T. eremita*) is a senior but unused synonym of *Pseudocandona*, the species is here formally transferred into the genus *Pseudocandona*: *Pseudocandona triquetroides* nov. comb. According to the original description, the T3-protopodite, like that of its close relative S. *triquetra*, bears 2 setae (seta d2 is absent). If this shows true, then the species has to be removed from *Pseudocandona* s. str. Further investigation should clarify the generic position of the species.

(3) *Candona (Typhlocypris) mira* Sywula, 1976 = *Pseudocandona mira* (Sywula, 1976) Danielopol, 1980. This species too is so far only known from Poland. According to the original description, the T3-protoprodite is 'perhaps bearing only two setae'. The hemipenis has two well developed distal lobes, the outer one of which draws obliquely away. Sywula (1976) points out that the species stands close to *Candona insueta* Klie (= *Schellencandona insueta* nov. comb.). The present author would like to draw the attention to the close resemblance of the carapace shape of *Ps. mira* with that of *Schellencandona belgica*. The ecology is similar: all three mentioned species are known from wells and/or the interstititial habitat. From these data I would like to conclude that *Ps. mira* probably belongs to *Schellencandona* nov. comb. However, the transfer is not formally proposed here. The description of the Zenker's organ, which remains unknown, should clarify the generic assignment of the species.

Genus *Fabaeformiscandona* (Krstic, 1972) Danielopol, 1973

Type species

Cypris fabaeformis Fischer, 1851.

Other species

The genus comprises ca 12 Recent species (Kempf 1980; also working copy of 1995). Nine newly combined species are added to the list (see below). Distribution: Holarctic.

History

Müller (1900) created the *fabaeformis*- and *acuminata*-groups within *Candona* s. l. Krstic (1972) introduced the subgenus *Fabaeformiscandona* within *Candona* for the members of both species groups. Danielopol (1973; see also 1978a) elevated the subgenus to genus rank.

Differential diagnosis of *Fabaeformiscandona*

Carapace usually elongate, more rarely triangular in lateral view, usually laterally distinctly compressed. LV usually with a postero-dorsal lobe-like expansion which overlaps the RV. Male A2 dimorphic: penultimate segment subdivided and with male bristles. Setal group of the 2nd segment of the mandibular palp with 3 (*fabaeformis*-group) or 4 (*acuminata*-group) setae; externo-distal seta (gamma-seta) of the penultimate segment smooth (not plumose). Respiratory plate of the maxilliped with 2 filaments. Cleaning leg (T3): protopodite with 2 setae (d1 and dp); setae 'e' and 'f' of EI and EII missing; seta 'g' of EIII present; terminal segment with 2 long (h2 and h3) and one short (h1) setae. Female genital lobe usually with a more or less well developed process which is directed posteriorly. Hemipenis: 'M'-process heavily sclerotized, of simple structure, the proximal part slightly broader than the distal one.

Remarks. (1) Two species groups are recognized: the *fabaeformis*- and the *acuminata*- groups, which at the present state of knowledge are solely distinguished by the number of setae in the setal group on the second segment of the mandibular palp. The setal group has 3 setae in the species of the *fabaeformis*-group, 4 in the *acuminata*-group.

(2) The presence of 2 versus 3 setae on the T3-protopodite allows easy distinction between the species of the genera *Fabaeformiscandona* and *Pseudocandona*. The scheme is similar in *Candona* s. str., *Fabaeformiscandona* and *Schellencandona* nov. gen.

Important literature: Müller (1900), Hartwig (1901), Klie (1938d), Krstic (1972), Danielopol (1973, 1978 a, b).

T3-chaetotaxy

Chaetotaxy of the cleaning leg of *F. fabaeformis* * (type species) (fig. 2C): protopodite with 2 setae (d1 and d2). EII without a seta (seta 'e' lost). EIII: medial seta ('f') missing; 'g' present. Setae h2 and h3 long, h1 short.

Species of the ***fabaeformis*-group.** The setal scheme of the following species is identical with that of the type species of the genus: *F. alexandri* (Sywula, 1981) nov. comb. (protopodite unknown); *F. fabella* (Nüchterlein, 1969) = *F. slesiniaca* (Sywula, 1975) nov. comb.; *F. angusta* (Ostermeyer, 1937) nov. comb.; *F. brisiaca* (Klie, 1938) nov. comb.

Remarks. (1) The T3-chaetotaxy of *F. holzkampfi* (Hartwig, 1900) Wouters, 1989; *F. fragilis* (Hartwig, 1898) Danielopol, 1980; and *F. krstici* (Petkovski, 1969) nov. comb. remains unknown. However, as these three species come very close to *F. fabaeformis*, their T3-setal scheme is most probably identical with that of the type species.

(2) The T3-chaetotaxy of *F. balatonica* too remains undescribed. Although commonly assigned to the *fabaeformis*-group (see Müller 1900; Klie 1938d), the species stands aside within that group, and even within *Fabaeformiscandona*: the setal group of the 2nd segment of the mandibular palp has 5 setae (3 setae in the *fabaeformis*-group; 4 setae in the *acuminata*-group); moreover, the carapace of *F. balatonica* is broadly rounded in dorsal view (laterally compressed in *Fabaeformiscandona*). Both characters fit the diagnosis of the *candida*-group of *Candona* s. str. Therefore, it is here proposed to re-assign *balatonica* to the latter genus: *Candona* s. str. *balatonica* Daday, 1894. However, Dr Dan Danielopol (unpubl.; pers. comm.) informed the present author that in his opinion, mainly because of the structure of the valves and the hemipenis, the species belongs to *Fabaeformiscandona* (Dr Danielopol makes the same remark for *C. levanderi*). There are only scattered records of *C. balatonica* in the literature, and at least part of them appear dubious. The species clearly needs to be redescribed. The synonymy with one of the other species of *Candona* may not be excluded.

(3) *F. lapponica* (Ekman, 1908) nov. comb. The T3-protopodite, as illustrated by Ekman (1914), has 2 setae. Sars' (1925) redescription of the species is accompanied by a figure showing a protopodite with three setae. The latter author's description applies most probably to a species belonging to the genus *Pseudocandona*. The transfer of the species into *Fabaeformiscandona* is confirmed by the structure of the female genital lobe, which has a well developed process that points posteriorly (see Ekman 1914); this process is commonly found in *Fabaeformiscandona;* it is non existant in *Pseudocandona*.

Species of the ***acuminata*-group**. The setal scheme of the following species is identical with that of the type species of the genus: *F. acuminata* (Fischer, 1854) Danielopol, 1980; *F. caudata* (Kaufmann, 1900) Danielopol, 1988; *F. hyalina* (Brady & Robertson, 1870) Danielopol, 1980; *F. latens* * (Klie, 1940) Danielopol, 1980; *F. pennaki* Marmonier & Ward, 1990; *F. protzi* * (Hartwig, 1898) Danielopol, 1988; *F. wegelini* (Petkovski, 1962) Danielopol, 1980.

Discussion

From the data above, it may be inferred that the T3-setal scheme is remarkably constant in *Fabaeformiscandona*. This scheme thus appears to be an important diagnostic feature of the genus.

Seven species formerly ranked without species-group assignment in *Pseudocandona* (see above) are here transferred into *Fabaeformiscandona*: the T3-protopodite of those species has indeed 2 setae only (d2 missing).

The transfer of *Ps. bilobata, Ps. bilobatoides* and *Ps. brevicornis* into *Fabaeformiscandona* is supported by the peculiar strucure of the LV, which bears two dorsal lobe-like expansions that overlap the RV. The generic transfer of *Ps. brisiaca* is confirmed by the structure of the hemipenis, the outer distal lobe of which is laterally attached and draws obliquely away; this character is not found in *Pseudocandona,* but is common in *Fabaeformiscandona*. The transfer of *Ps. brisiaca* is confirmed by the number of setae within the group situated on the 2nd segment of the mandibular palp: the group has 4 setae in *brisiaca* (see Klie 1941); in *Pseudocandona* this group has either 3 or 5 setae.

The new combinations are as follows: *Fabaeformiscandona aemonae* (Klie, 1935) nov. comb.; *Fabaeformiscandona bilobata* (Klie, 1938) nov. comb.; *Fabaeformiscandona bilobatoides* (Löffler, 1963) nov. comb.; *Fabaeformiscandona brevicornis* (Klie, 1925) nov. comb.; *Fabaeformiscandona brisiaca* (Klie, 1938) nov. comb.; *Fabaeformiscandona hertzogi* (Klie, 1938) nov. comb.; and *Fabaeformiscandona speleae* (Klie, 1941) nov. comb.

Remark. *Candona angusta* Ostermeyer, 1937 is assigned to the *rostrata*-group of *Candona* s. l. (see Klie 1938d), which at present ranks within *Pseudocandona* s. str. The species, however, has so far not been formally transferred into that genus. As the T3-protopodite has only two setae (d2 is lost), the species obviously does not belong to *Pseudocandona* s. str. The T3-setal scheme is identical with that of *Fabaeformiscandona* and the (provisional) transfer into that genus is proposed here: *Fabaeformiscandona angusta* (Ostermeyer, 1937) nov. comb. The species needs a redescription and a taxonomic re-examination.

Genus *Candona* s. str. Baird, 1845

Type species

Cypris candida O. F. Müller, 1776 (by Opinion 533 of the International Commission of Zoological Nomenclature).

Other species

More than 1200 nominal Recent and fossil species have been assigned to *Candona* s. l. (Kempf 1980; also working copy of 1995). After extraction of the species ranked within *Cryptocandona, Pseudocandona, Fabaeformiscandona*, etc, the genus *Candona* s. str. comprises at present ca 45 Recent species.

Differential diagnosis of *Candona* s. str.

Carapace relatively broad in dorsal view, with W greater than 1/3 L. Male A2 dimorphic: penultimate segment subdivided and with male bristles. Mandibular palp: setal group of the 2nd segment with 4 (*neglecta*-group) or 5 (*candida*-group) setae; externo-distal seta (gamma-seta) of the penultimate segment plumose (fig. 3D). Respiratory plate of the maxilliped (T1) with 2 filaments. Cleaning leg: protopodite with 2 setae (d1 and dp); setae 'e' and 'f' of EI and EII lost; distal seta ('g') of EIII present; terminal segment with 2 long (h2 and h3) and one shorter (h1) setae. Hemipenis broad and heavily sclerotized; 'D'-process weakly developed, not extending beyond the distal edge of the medial part of the peniferum; 'M'-process well developed and strongly sclerotized, the proximal part broader than the distal one; peniferum usually with a broad distal lobe which is bent towards the dorsal side.

Remarks. (1) Two species-groups are recognized within *Candona* s. str.: the *candida*-group (type: *Candona candida* (O. F. Müller, 1776)) and the *neglecta*-group (type: *Candona neglecta* Sars, 1887). The two groups mainly differ in the number of setae in the setal group situated on the 2nd segment of the mandibular palp: the group has 5 setae in the species of the *candida*-group, 4 setae in the species of the *neglecta*-group.

(2) The number of setae on the T3-protopodite allows easy distinction of *Candona* s. str. (Pr with 2 setae) and *Pseudocandona* (Pr. with 3 setae). The T3-setal scheme is identical in *Candona* s. str., *Fabaeformiscandona* and *Schellencandona* nov. gen.
(3) Important literature: Danielopol (1978a).

T3-chaetotaxy

Chaetotaxy of the cleaning leg of *Candona candida* (fig. 3B): protopodite with 2 setae (d2 lost). EI without a seta (seta 'e' missing). EII+III: seta 'f' absent, seta 'g' well developed. EIV with two long (h2-3) and one shorter (h1) setae.

Species of the ***candida*-group.** The T3-setal scheme of the following species is identical with that of the type species of the genus: *C. candida* * (Müller, 1776); *C. balatonica* Daday, 1894; *C. dancaui* Danielopol, 1978; *C. improvisa* * Ostermeyer, 1937.

The T3-setal equipment of the following species, which come close to *C. candida*, has not been described, but the respective original descriptions imply that it is identical with that of *C. candida*: *C. devexa* Kaufmann, 1900; *C. sanociensis* Sywula, 1971; *C. studeri* Kaufmann, 1900; *C. weltneri* Hartwig, 1899.

Species of the ***neglecta*-group**. The T3-setal scheme of the following species is identical with that of the the type species of the genus: *C. neglecta* * Sars, 1887; *C. alta* Klie, 1939; *C. cristatella* Klie, 1939; *C. depressa* Klie, 1939; *C. levanderi* Hirschmann, 1912; *Candona marginata* Klie, 1942; *C. marginatoides* Petkovski, 1960; *C. media* Klie, 1939; *C. meerfeldiana* Scharf, 1983; *C. paionica* Petkovski, 1958; C. *trapeziformis* Klie, 1939; *Candona vidua* Klie, 1942.

Remarks. (1) The T3-setal equipment of the following species, which come close to *C. neglecta*, has so far not been described; the original descriptions, however, imply that it is identical with that of *C. neglecta*: *C. altoides* Petkovski, 1961; *C. bimucronata* Klie, 1937; *C. dedelica* Petkovski, 1969; *C. fasciolata* Petkovski, 1961; *C. hartmanni* Petkovski, 1969; C. *lindneri* Petkovski, 1969; *C. lucida* Petkovski, 1969; *C.lychnitis* Petkovski, 1969; *C. natronophila* Petkovski, 1969;

(2) *C. angulata* G.W. Müller, 1900. Müller's (1900; pl. 1: 9) illustration shows a T3-protopodite with 3 setae (d1-2 and d3). To the present author's best knowledge the T3-protopodite of this species has not been illustrated by any subsequent author. The presence of the d2-seta is highly improbable.

(3) *C. scharfi* Hahn, 1990. According to the original description (text and fig. 4; Hahn 1990), the T3-protopodite bears 3 setae; the author's fig. 4 shows two dp-setae, one of which is attached laterally. This observation is highly implausible and hence liable to error.

(4) The T3-setal scheme of the following species remains unknown: C. *muelleri* Hartwig, 1899; *C. holmesi* Petkovski, 1960; *Candona montenigrina* Petkovski, 1961; *Candona strumicae* Petkovski, 1959.

From the data above it is here inferred that the T3-setal scheme is constant within the genus *Candona* s. str. The exceptions mentioned and illustrated in the literature are most probably due to errors of observation.

It should be noticed that the T3-setal scheme of *Candona* s. str., *Fabaeformiscandona* and *Schellencandona* is identical. The presence of 3 versus setae on the T3-protopodite allows easy distinction of those genera from *Pseudocandona* s. str.

Conclusion

From the data presented above it is here inferred that the setal scheme of the cleaning leg is constant within the five candonine genera considered. This scheme thus appears to be an important diagnostic feature at the generic level. It allows easy distinction of the genera *Cryptocandona* and *Pseudocandona* s. str. It is, however, identical in *Candona* s. str., *Fabaeformiscandona* and *Schellencandona* nov. gen.

A brief look at the remaining genera of the subfamily shows that the T3-setal scheme appears to be most probably constant within those genera too, with one noticeable exception, i. e. the genus *Candonopsis*. The latter observation shows that the species of this genus probably do not form a monophyletic lineage; this, however, should be confirmed by a detailed study of all the species assigned to that genus, a study which should also take in account other taxonomic characters.

The study of the T3-chaetotaxy of the candonine genera considered in this work, and also a brief look at the remaining genera of the subfamily, reveal that during evolution (a) no 'true' setae are added to the most complete candonine scheme (see for instance *Cryptocandona*), (b) there is a clear evolutionary trend towards loss of part of the setae (compare figs 1-3), and (c) the homologous setae may be clearly identified by their relative position on the T3 (and also the T1 and T2). For similar remarks on the setae of the podocopid antenna see Maddocks (1976). In *Terrestricandona* all setae, except one of the three terminal setae, are lost.

From a functional point of view, the distal end of the cleaning leg is probably the most important part of the limb. In Cyprididae the two terminal segments of the T3 are modified into a complex pincer organ (see for instance Broodbakker & Danielopol 1982), with a strong reduction in length and specialisation of the three terminal setae h1-3. In the Candoninae the two distal segments are not transformed, the three terminal setae h1-3 being usually well developed. However, in many (?all) species of the *rostrata*-group of *Pseudocandona*, and also in *Cryptocandona vavrai*, the h1-seta is very short, hook-shaped and recurved basally. This could be the first step towards the evolution of a more specialised organ with a function similar to that of the cypridid pincer-organ.

Key to the European genera of the Candoninae

1 (2) Surface of valves covered in a conspicuous reticulate pattern of ridges. Carapace very broad in dorsal view, with both ends markedly rounded genus
genus ***Paracandona***

2 (1) Surface of valves smooth, more rarely pitted; when present, pits are not surrounded with a conspicuous reticulate pattern of ridges **3**

3 (4) Furca: posterior seta absent genus ***Candonopsis***

4 (3) Furca: posterior seta present **5**

5 (6) Walking leg: distal seta of the penultimate segment exceptionally long, ca 2 X the length of the corresponding segment. A2-exopodite with 3 minute setae of subequal length. Hypogean species genus ***Phreatocandona***

6 (5) Walking leg: distal seta of the penultimate segment of 'normal' length, about as long as the corresponding segment, or shorter. A2-exopodite with one very long and 2 minute setae. Epigean and hypogean species **7**

7 (8) Furcal rami short and stout. Carapace 0.4-0.6 mm long. Two hypogean species genus ***Nannocandona***

8 (7) Furcal rami 'normally' shaped, slender. Carapace longer than 0.60 mm in most species. Epigean and hypogean species **9**

9 (10) Cleaning leg: terminal segment with one very long (h3) and two (h1 and h2) conspicuously short setae; distal seta ('g') of the penultimate segment very short (fig. 3C). Hypogean species genus ***Mixtacandona***

10 (9) Cleaning leg: terminal segment with two long (h2 and h3) and one distinctly shorter (h1) setae; seta 'g' of the penultimate segment well developed (figs 2A-C; 3A,B) **11**

11 (14) Cleaning leg: basal segment with three setae (d1, d2 and dp; fig. 2A,B) **12**

12 (13) Cleaning leg, penultimate segment (subdivided or not): medial seta ('f') present (fig. 2A) genus ***Cryptocandona***

13 (12) Cleaning leg, penultimate segment (subdivided or not): medial seta ('f') absent (fig. 2B) genus ***Pseudocandona*** s. str.

14 (11) Cleaning leg: basal segment with 2 setae (d1 and dp; fig. 2C; 3A,B) **15**

15 (16) Carapace broadly rounded in dorsal view, with W/L > 0.40. Penultimate segment of the mandibular palp: externo-distal seta (gamma-seta) plumose (fig. 3D; see arrow) genus ***Candona*** s. str.

16 (15) Carapace laterally compressed in dorsal view, with W/L < 0.40. Penultimate segment of the mandibular palp: externo-distal seta smooth, not plumose **17**

17 (18) Carapace usually longer than 0.60 mm. Setal group of the second segment of the mandibular palp with 3 (group *fabaeformis*) or 4 (group *acuminata*) setae(this segment thus with 2+3 or 2+4 setae). Males (absent in a number of species): Zenker's organ with 5+2 rings of spines. Epigean and hypogean species genus ***Fabaeformiscandona***

18 (17) Carapace 0.40-0.60 mm long. Setal group of the second segment of the mandibular palp with 3 setae (this segment thus with 2+3 setae). Males (always present): Zenker's organ with 4+2 rings of spines. Males always present. Hypogean species genus ***Schellencandona*** nov. gen.

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