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The evolution of groundwater Cladocera

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Abstract

Cladocera occur in various types of groundwater, but are most common in the underflow of rivers. Numerous surface water species occasionally venture into groundwater; some chydorids are more common in groundwaters than in surface waters; at least three groups within *Alona*, finally, have evolved exclusive groundwater species. The latter show few obvious adaptations to the subterranean habitat, except loss of an eye or total blindness. Some, however, have conserved an array of primitive characters (e.g. on the end-claw of the postabdomen, and the setation of the valve rims) which suggest that the physical protection and relative constancy of the hyporheic has permitted the survival of some ancient taxa.

Introduction

Since 1983, (Dumont, 1983) attention has refocused on the existence of groundwater-dwelling Cladocera, and the field has expanded considerably. Of the numerous older records, which had not received the attention they deserve, quite a few have been reinterpreted as genuine (see Dumont, 1983, 1987; Brancelj & Sket, 1990; Schmidt, 1994, and many older references therein). What has advanced the field most is the finding that the groundwater fauna is composed, besides many surface-water (stygoxenic) species (the list now stands at *c.* 35 spp. – Table 1), of an array of *c.* 10 species entirely limited to a groundwater (stygobitic) mode of life. In addition, *c.* 10 spp. with transitory (stygophilic) ways of life exist (Table 1). Also, the population dynamics and phenology of one river-gravel dweller, *Alona phreatica* Dumont, has now been studied (Sabater, 1987). There is thus little doubt that systematic attention to Cladocera in all sources of groundwater will reveal plenty of undescribed taxa in the future, with possibly quite a few surprises. Available evidence indicates that Cladocera are, on the whole, a much less common structural element of hypogean faunas than, say, the Copepods and the Ostracods. Yet, they may at times be quite abundant, even if often of strictly local occurrence. Thus, of two samples taken a few kilometres apart in the Wadi Surdud, a river in central Yemen, one contained a rich population of *Alona alsafadii*, an undescribed primitive *Alona* species (Dumont & Brancelj, 1994), while the second contained no Cladocera at all. Quite a bit of research will be needed to show whether such localized populations are the rule rather than the exception, and why they are distributed in such a patchy way. Extended surveys using quantitative or, at least, semi-quantitative methods such as that of Beladjal *et al.* (1992), may hopefully be widely applied in the near future.

The aim of the present paper is to explore possible pathways behind the evolution of a groundwater mode of life in the Cladocera.

Taxonomic incidence

Table 1 illustrates convincingly the fact that, while the majority of families of so-called Cladocera are represented in groundwater, it is the chydorids that virtually hold a monopoly on a strict stygobitic mode of life. Within the Chydoridae, there are quite a few genera (*Chydorus*, *Disparalona*, *Rhychotalona*) with species that might be stygophilic, and are therefore only rarely recorded in lakes and rivers (where they are often – and not by chance – found over sandy bottoms, or in sphagnum). There is also a suggestion that some predominantly or exclusively stygobitic species, traditionally placed in *Chydorus* or in *Pleuroxus* (e.g. '*Chydorus*' *piger* and *pigroides*) might in fact better be transferred

Table 1. List of Cladocera (Anomopoda and Ctenopoda) recorded from various types of groundwater (up to October 1993) Categories : X - stygoXenic; ? - stygoPhilic; B - stygoBitic.

	Category	Occurrence	Key reference
Daphniidae			
Daphnia longispina O.F.M.	x	Yugoslavia, France	Brancelj & Sket (1990); Schmidt (1994)
D. hyalina Leydig	x	France (Rhone Valley)	Schmidt (1994)
D. cucullata Sars	x	Sweden, France (Rhone Valley)	Schmidt (1994)
D. galeata Sars	x	France (Rhone Valley)	Schmidt (1994)
Ceriodaphnia megops Sars	x	France (Rhone Valley)	Schmidt (1994)
C. reticulata (Jurine)	x	France (Rhone Valley)	Schmidt (1994)
C. dubia Rich.	x	Yugoslavia	Brancelj & Sket (1990)
Scapholeberis mucronata (O.F.M.)	x	France (Rhone Valley)	Schmidt (1994)
S.rammneri Dumont & Pensaert	x	South China cave	personal observation
Simocephalus vetulus (O.F.M.)	x	Yugoslavia; France	Brancelj & Sket (1990); Schmidt (1994)
S. expinosus (Koch)	x	France (Rhone Valley)	Schmidt (1994)
Moinidae			
Moina macrocopa Straus	x	France	Pacaud (1952)
Macrothricidae			
Macrothrix laticornis (Jurine)	P	Yugoslavia	Brancelj & Sket (1990)
M.bialatus Motas & Orgh.	B	Rumania	Motas & Orghidan (1948)
Neothrix sp.	P(?)	Australia	Dumont (1987)
Bosminidae			
Bosmina longirostris (O.F.M)	x	Yugoslavia; France	Brancelj & Sket (1990); Schmidt (1994)
Sididae			
Sida crystallina (O.F.M.)	x	France (Rhone valley)	Schmidt (1994)
Ilyocryptidae			
Ilyocryptus sordidus (Liévin)	x	Rumania, Yugoslavia, France	Dumont (1987); Schmidt (1994)
I. agilis (Kurz)	x	Rumania, Yugoslavia, France	Dumont (1987); Schmidt (1984)
Chydoridae			
Eurycercus lamellatus O.F.M.	x	Yugoslavia; Wales	Brancelj & Sket (1990); personal observation
Acroperus harpae Baird	x	Yugoslavia; France	Brancelj & Sket (1990); Schmidt (1994)
Alona affinis (Leydig)	P	Rumania, Ireland elsewhere in Europe	Motas & Orghidan (1948); Schmidt (1994); Hazelton (1974)

to a separate (sub)genus (Frey, 1993). Yet, at this point in time, the preponderance of *Alona* among the strict stygobitic species is absolutely overwhelming. While at first sight more Macrothricids, and especially Ilyocryptids might have been expected, it should be borne in mind that most – if not all – of these bottom-living species are really mud dwellers, which makes them quite distinct from true groundwater species. The latter are rather to be looked for among species adjusted to scraping the surface of solid substrates, an adaptation quite common among the chydorids (Fryer, 1968).

Morphological distinctiveness

Within *Alona*, we presently know of three species groups that contain an 'evolutionary line' connecting strictly groundwater to surface-water dwelling species: the *Alona protzi*-group (three species), the *Alona*

Table 1. (continued).

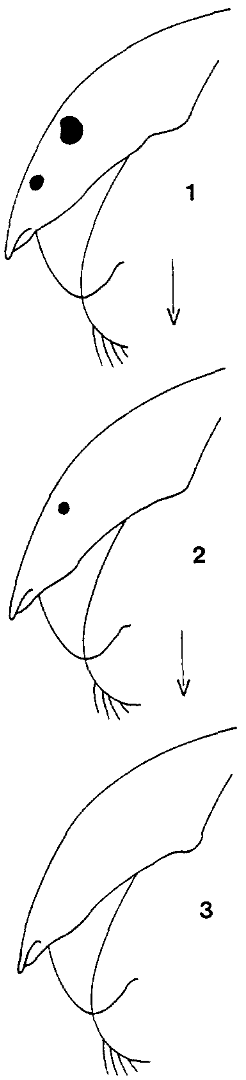
	Category	Occurrence	Key reference
A.quadrangularis (O.F.M.)	P	Widespread in Europe	Beladjal *et al.* (1992)
A.macrops Motas & Orghidan	B	Rumania	Motas & Orgidan (1948)
A.rectangula Sars	x	Sweden & elsewhere in Europe	Husmann & Teschner (1970)
A.guttata group			
A. cf guttata	P	Sweden, Belgium, Australia	Dumont (1992); Beladjal *et al.* (1992)
A.bessei Dumont	B	Central Massif, France	Dumont (1983)
A.intermedia Sars	x	Sweden	Husmann & Teschner (1970)
Alona protzi-group			
(A. protzi Hartwig	P	Rhone gravels, France	Dumont (1987)
(A. smirnovi Petk. & Flössner	B	Springs at Lake Ohrid	Petkovski & Flössner (1972)
(A. phreatica Dumont	B	France, Catalonia	Dumont (1983); Sabater (1987)
Alona diaphana-group			
(A. diaphana Sars	x	Slovenia	Brancelj (1990)
(A. sketi Brancelj	B	Slovenia	Brancelj (1990)
(A. hercegovinae Brancelj	B	Bosnia-Hercegovina	Brancelj (1992)
Alona karua-group			
A. alsafadii Dum. & Branc.	B	Yemen, Wadi Surdud	Dumont & Brancelj (1994)
A. rustica Scott	?	Europe; Brazil	Dumont (1987); Beladjal *et al.* (1992)
Disparalona rostrata (Koch)	x	France, Rhone valley; Slovenia	Brancelj & Sket (1990); Schmidt (1994)
Rhynchotalona falcata Sars	P	Lake Llyndanas (Wales)	leg J. Mertens (1991), unpublished
Chydorus sphaericus (O.F.M.) group	x	Widespread in Europe; Australia	Dumont (1987); Schmidt (1994)
C. ovalis Kurz	x	Slovenia; Croatia	Brancelj & Sket (1990)
C. parvus Daday	P	Sandy shores of Lake Malawi at Senga Bay	personal observation
"Chydorus" piger[1] Sars	P	Slovenia; probably widespread in Europe	Brancelj & Sket (1990)
"Chydorus" pigroides Lillj[1]	B(?)	Uppsala, Sweden	Frey (1976)
Pseudochydorus globus (Baird)	x	France, Rhone valley	Schmidt (1994)
Pleuroxus uncinatus Baird	x	France, Rhone valley	Schmidt (1994)
Pleuroxus aduncus (Jurine)	x	Slovenia	Brancelj & Sket (1990)
P. laevis Sars	x	Slovenia	Brancelj & Sket (1990)
P. denticulatus Birge	x	France, Rhone valley	Schmidt (1994)
Pleuroxus piger[2] (sensu Dumont, 1983)	B	Auvergne, France	Dumont (1983)
Alonopsis elongata Sars	x	Sweden	Husmann & Teschner (1970)
Tretocephala ambigua (Lillj)	x	Croatia	Brancelj & Sket (1990)
Monospilus dispar Sars	x	Rhone valley, France	Schmidt (1994)
Leydigia leydigi (Schoedler)	x	Rumania, Yugoslavia, France	Dumont (1987); Schmidt (1994)
L. acanthocercoides (Fischer)	x	France, Rhone valley	Schmidt (1994)
Camptocercus rectirostris (Schoedler)	x	France, Rhone valley	Schmidt (1994)

[1] Generic allocation likely incorrect.
[2] Not the same species as "Chydorus' piger.

karua-group (two species), and the *Alona diaphana*-group (three species).

From a combination of the character states encountered in these eight taxa, we can establish that:

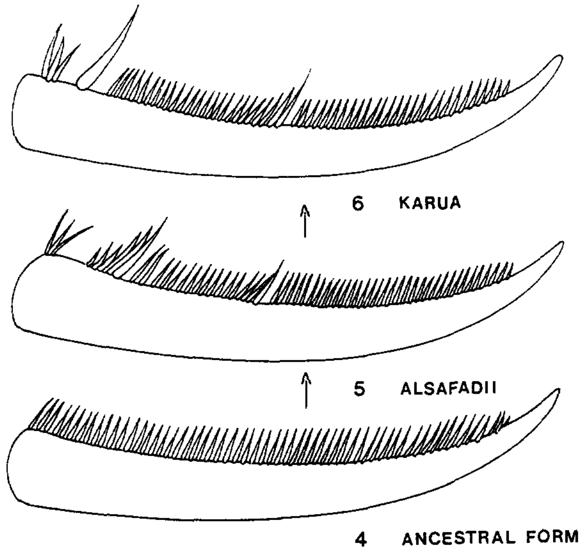
1. *eye and ocellus pigmentation is lost* (Figs 1–3): in *all* species that, at least, at times occur in surface waters, both an eye and an ocellus occur. Two groundwater forms (*A. smirnovi*, *A. alsafadii*)



Figs 1–3. Progressive eye-pigment reduction in *Alona* as an adaptation to subterranean life. 1. surface-living species (e.g. *A. karua*); 2. groundwater species (e.g. *A. smirnovi*, *A. alsafadii*); 3. cave-dwelling species (e.g. *A. sketi*, *A. hercegovinae*).

only show a pigmented ocellus. Two blind cave-dwellers (*A. sketi*, *A. hercegovina*) have neither.

2. *feeding appendages*: in the two hypogean species in which the fine structure of the trunk limbs has been described in sufficient detail (*A. sketi* and *A. alsafadii*) only minute differences in structure with their surface-dwelling relatives were observed. These could not be related to differences in habitat, but rather represented species-specific characters (Brancelj, 1990, 1992; Dumont & Brancelj, 1994).



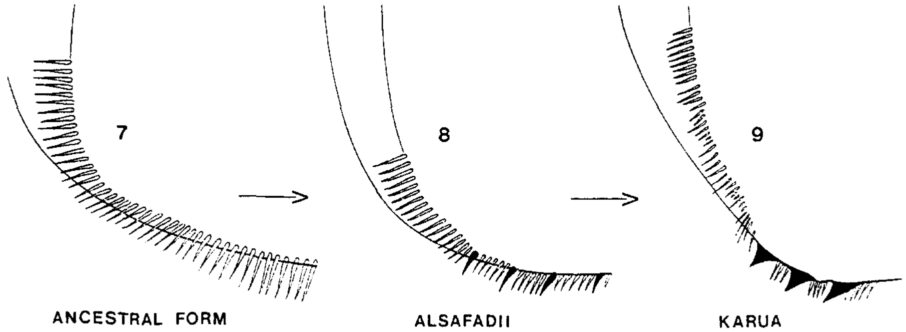
Figs 4–6. The evolution of the external pecten of the end-claw in the *A. karua*-group. The ancestral form is hypothetical.

3. *Postabdomen*: all species-groups with hypogean representatives have, in addition to the usual dorsal spines, fans of lateral fascicles of stiff setae on the postabdomen. The significance of these to a groundwater mode of life is, at present, unclear. The endclaw of the postabdomen is adorned with a number of pectens, and a basal spine in all cases. Most of these are trendless, but an interesting exception is offered by *A. karua* (and *A. hispanica*) and *A. alsafadii*, where the basal spine is seen (Figs 4–6) to be composed of a number of fused (fusion incomplete in *alsafadii*) denticles derived from the basal outer pecten.
4. *valve rim adornments*: like in the preceding case, the *A. karua* group is the only one to contain a trend: the ventro-posterior rim in *A. karua* is differentiated into a zone with setae, a series of strong, sclerotized teeth, and a row of setules of haphazard length moving up the distal valve margin. In *A. alsafadii*, it is clear (Figs 7–9) that these structures are all modified setae.

Discussion

Adaptation versus conservation

Loss of optical perception (eyes, ocelli) is widespread in a lightless environment. However, it remains unclear



Figs 7–9. The evolution of the setation along the posterior section of the carapace valves. The ancestral form is hypothetical.

whether this is irreversible (genetic) or reversible (phenetic). Cases of – possibly reversible – loss of eyes and of body pigmentation have indeed been documented from other groups, e.g. fishes. (Thinès & Proudlove, 1986).

At present, we have no means of determining whether in Cladocera, the loss of eye and/or ocellus pigmentation is a fixed trait. The fact that eye loss does occur, however, confirms that Cladocera in a cave environment respond to environmental selective pressures exactly as any other animal would. Other structural adaptations, such as in the trunk limbs, are doubtful, and of the same order as 'any' interspecific differences, as stated earlier.

In addition, the adornment of the postabdominal claw in *A. alsafadii*, as well as the setation along its valve rim, cannot be interpreted as an adaptation to subterranean life. Yet, both sets of characters clearly suggest a conserved character state, which throws a new light on the origin of the basal spine of the postabdomen, as well as the valve setation and denticulation. The most primitive character state appears to have been a postabdominal claw with a uniform external longitudinal pecten, which, by a process of spinule fusion, gradually transformed into a basal spine, some isolated basal spinules, and two separate external pectens (Figs 4–6). Likewise, the valve setation may originally have consisted of a row of uniform setae, which later specialized into ventral setae of different length, fused among each other and with the carapace to become carapace teeth, or spinules and setules of variable length running up along the inner distal margin of the valves (Figs 7–9).

Surprisingly, therefore, some of the truly groundwater *Alona* appear to be conserved primitive species, rather than highly specialized ones. Because many more such species, as yet undiscovered, may exist, it is anticipated that continued surveys of different types of groundwater may significantly advance our insight into the origin and evolution of these Anomopoda.

The survival of such ancient taxa in the Cladocera is probably for the same reason as in other crustacean groups (e.g. the Syncarida) (Schminke, 1986): the physical protection and relative constancy of the hyporheic environment acted as a refuge in which otherwise vulnerable ancient species found enough shelter to survive.

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