Danielopolina kornickeri sp. *n.* (Ostracoda, Thaumatocypridoidea) from a western Australian anchialine cave: morphology and evolution

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Danielopolina kornickeri sp. *n.* is described from an anchialine cave in Western Australia. This is the first *Danielopolina* species occurring outside of the Western Hemisphere (Atlantic and Eastern Pacific Oceans and Islands). A cladistic analysis indicates that this species is a primitive taxon of the anchialine cavernicolous clade; the deep-sea dwelling species *Danielopolina carolynae* appears more primitive and does not cluster with the other *Danielopolina* species. The ecological environment of *D. kornickeri* is described. Detailed discussions consider: (1) the shell ornamentation and its relevance to the phylogeny of the Thaumatocyprididae; (2) the antero-dorsal node of the Permian *Thaumatomma* (hypothesized here to be an ocular lens which regressed in the post-Palaeozoic thaumatocypridids); (3) the distal chaetotaxy of the antennae (hypothesized to perform the chemosensorial function known in the aesthetascs of other myodocopids or podocopids); (4) palaeobiogeographical arguments for a shallow marine origin of cavernicolous species *Danielopolina*.

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Introduction

A predictable aquatic community occurs from Australia to the Caribbean (Humphreys 1993a; Yager & Humphreys 1996) in some anchialine habitats (Holsinger 1989, 1992; Yager 1994) that bordered the former Tethys Sea. This community characteristically includes cirolanid isopods, atyid shrimps, ostracods, gammarid amphipods, remipedes and thermosbaenaceans. Such a community has recently been found to occur at the arid tropical coast of Western Australia (Humphreys & Adams 1991; Poore & Humphreys 1992; Bruce & Humphreys 1993; Humphreys 1993a; Yager & Humphreys 1996). In this paper we describe a new species of *Danielopolina* which constitutes the first occurrence of this genus in the Southern Hemisphere and the Indo-west Pacific region.

In spite of more than 20 years of intensive exploration, the diversity and originality of the crustacean faunas inhabiting coastal (anchialine) caves and/or marine crevicular systems continue to surprise us. The first interesting ostracod described from an anchialine cave was *Thaumatocypris orghidani*, an endemic species from Cuba that was considered at the time to be a 'living fossil' (Danielopol 1972). Subsequently, new species and genera were discovered in various anchialine caves, mainly from Atlantic and Eastern Pacific islands and coastal areas (reviewed in Iliffe 1992; Kornicker & Iliffe 1995).

*Thaumatocypris orghidani (*Halocyprida, Thaumatocyprididae) was later referred to the new genus *Danielopolina* (Kornicker & Sohn 1976a). Another nine *Danielopolina* species have been described (Kornicker & Iliffe 1995), most of which are exclusively troglobites, living on oceanic islands or on the continental coasts around the Central Atlantic and in the Pacific (Fig. 1A). *Danielopolina carolynae*, the type species, is the only species of the genus living in the deep sea, at a depth of about 3450 m in the South Atlantic, off Brazil (Kornicker & Sohn 1976a).

The origin of such marine cave fauna has caught the imagination of zoologists for over 100 years. Fuchs (1894)

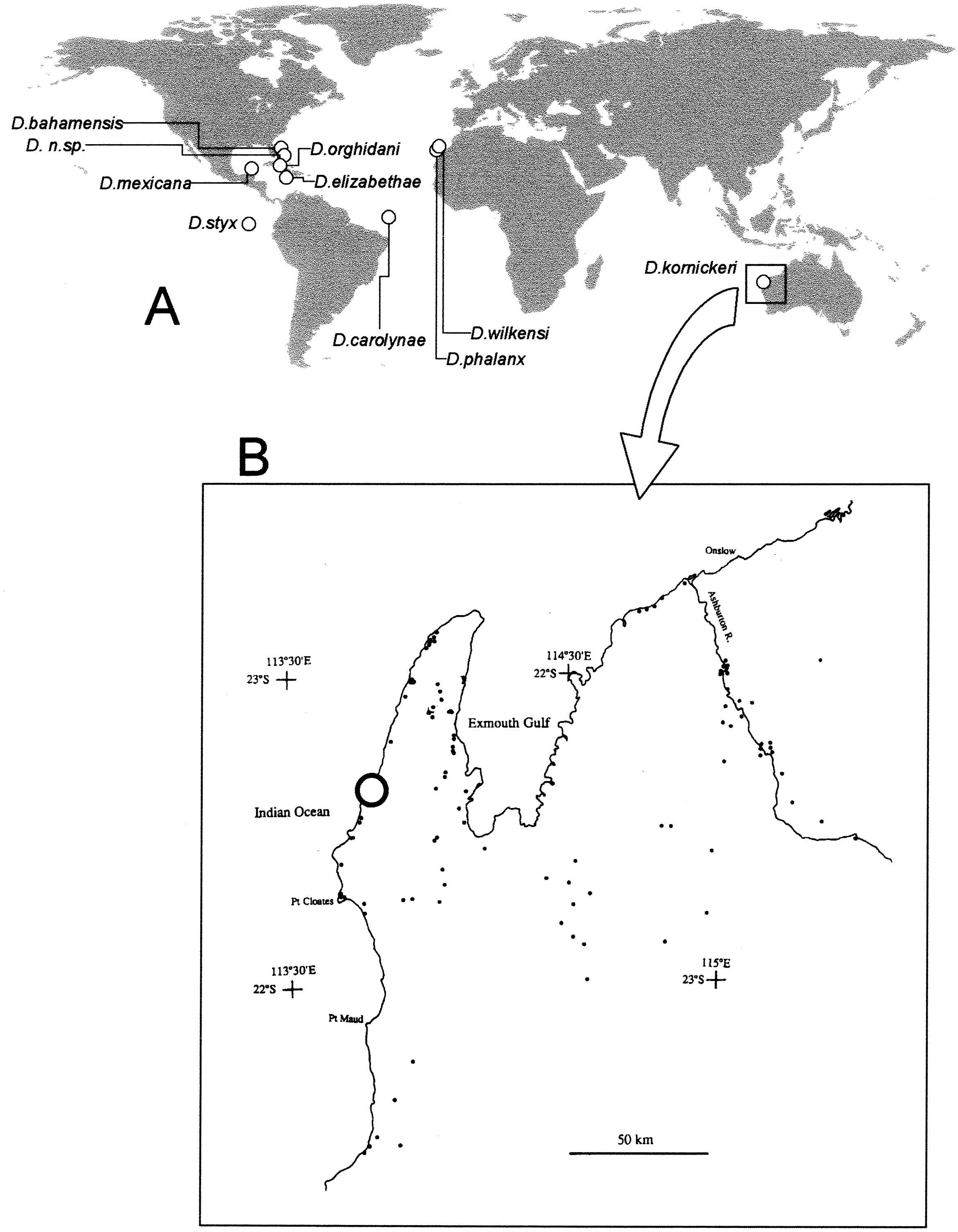

Fig. 1 —A. Geographic distribution of *Danielopolina* species. All are troglobite, anchialine species, except *Danielopolina carolynae*, a deep-sea dwelling species. —B. Map of the type locality of *Danielopolina kornickeri*, nov.sp., in the Cape Range peninsula (Western Australia). The large circle corresponds to the location of the anchialine cave C-28.

suggested that deep-sea dwelling animals, adapted to eternal darkness and a stable environment, could successfully colonize the shallow marine caves. This hypothesis has found new proponents, owing to recent discoveries in anchialine caves. Boxshall (1989) argued that both misophrioid copepods and the ostracods of the genus *Danielopolina* from anchialine caves most probably originated from closely related deep sea forms that colonized deep crevicular systems and subsequently migrated to the shallow marine spelean habitats (see also Jaume & Boxshall 1995, 1996a, 1996b for a different opinion). However, others have argued that shallow benthic thaumatocypridid ostracods could directly and independently colonize either marine shallow caves or the deep sea (Danielopol 1990; Baltanás & Danielopol 1995; Kornicker & Iliffe 1995). The discovery of the thaumatocypridid ostracod *Pokornyopsis feifeli* from the Upper Jurassic (> 150 Ma) in a palaeoenvironment no deeper than 200 m and resembling Recent marine crevicular systems (Aubrecht & Kozur 1995) gives additional support to the shallow water origin of anchialine fauna, an idea strongly defended by Stock (1986; 1994).

The recent discovery of a rich and diversified fauna in anchialine caves in Western Australia, including the genera *Halosbaena* (Thermosbaenacea), *Haptolana* (Cirolanidae), *Liagoceradocus* (Hadziidae) and *Lasionectes* (Remipedia) (Poore & Humphreys 1992; Bruce & Humphreys 1993; Humphreys 1993a, 1993b; Yager & Humphreys 1996), congeneric with marine troglobites of the Atlantic, corroborate the hypothesis that the origin of the anchialine troglobites originated from an ancient epigean fauna that existed in the Tethys Sea at least since the Mesozoic (Iliffe *et al.* 1983, 1984; Wilkens *et al.* 1986; Kornicker & Iliffe 1989a; Humphreys 1993a, 1993b).

Here, we describe a new species of *Danielopolina* and compare its morphology and geographical distribution with those of the other known Thaumatocyprididae so as to elucidate the origin and evolution of the cave dwelling thaumatocypridids.

Material and Methods

Collections were made by divers, using hand-held nets, bottles and traps. All diving was conducted under the standards of the Cave Divers Association of Australia. Details of the water sampling and profiling are given in Yager & Humphreys (1996). In essence, physical and chemical data were obtained from above and below the pycnocline; and the physical characteristics (temperature, conductivity, dissolved oxygen, pH) were profiled through the upper 22 m using a submersible data logger and tethered probes.

For the description and systematic treatment of the Myodocopa Halocyprida we followed Kornicker & Iliffe (1995). Cladistic analysis were run with Paup 3.1 (Swofford 1993) and performed on female character set only. We looked for a more stable, less *assumption-dependent*, phylogenetic hypothesis. Assumptions were therefore kept to a minimum and no polarities were fixed (Wilson 1992). All characters have been treated as unordered 'Fitch' (Fitch 1971), i.e. characters are allowed to reverse direction in search for the shortest tree, except those referring to the carapace (characters 2–4 in Table 1). The evolutionary sequence hypothesized by Kornicker & Iliffe (1995) for ornamentation (character 4) was here assumed. The presence of anterior ridges and a posterior dorsal process was also considered to be primitive states. Multistate taxa were interpreted as having polymorphisms.

Order HALOCYPRIDA Dana, 1853
Suborder HALOCYPRIDINA Dana, 1853
Superfamily THAUMATOCYPRIDOIDEA Müller, 1906
Family THAUMATOCYPRIDIDAE Müller, 1906
Genus *Danielopolina* Kornicker & Sohn, 1976a
Danielopolina kornickeri, sp.*n.* (Figs 2A-D, 3A-F)

Holotype. One dissected adult female (WAM C24366). Carapace preserved in alcohol (WAM C24367), the other was destroyed while dissecting.

Paratypes. One dissected adult male (WAM C24368)(carapace preserved in ethanol, WAM C24369), one dissected adult female (WAM C24370) (carapace preserved in ethanol, WAM C24371), plus 12 undissected individuals (WAM C24372). All with sizes similar to the dissected adults. From the type locality, 26.v.1995, in saline water, A. A. Poole, D. Warren & W. F. Humphreys, lot BES 4295.

Type locality. Cave C-28, Cape Range peninsula, Western Australia (2225S 11346E)(Fig. 1B), 7.viii.1993, in saline water. A.A. Poole, D.Warren, W.F. Humphreys & R.D. Brooks, lot BES 2486 (WAM XX-96).

Etymology. Named for Prof. L.S. Kornicker (Smithsonian Institution, Washington, DC) who contributed substantially to the description of new ostracod Myodocopa taxa from spelean habitats.

Differential Diagnosis. The family Thaumatocyprididae contains the recent living genera *Thaumatocypris* G.W. Müller, 1906; *Thaumatoconcha* Kornicker & Sohn, 1976 *and Danielopolina, and the fossil genera Thaumatomma Kornicker & Sohn, 1976 and Pokornyopsis Kozur, 1974* (Kornicker & Sohn 1976a). The new species is assigned to the genus *Danielopolina*, because of the shape and length of the anterior processes of the valves (conical and of medium length) and the presence on the 6th limb of 2 setae on the 1st exopodial joint, at the dorsal corner (Thaumatocypris has only one seta and a spine, *Thaumatoconcha* displays 3 setae; the anterior conical processes are moreover very long in

Table 1 Character data set used for cladistic analysis of phylogenetic relationships.

	Characters																																			
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Thaumatocypris G. W. Müller, 1906	L	P	P	I	1	1	1	3	1	1	2	?	1	2	1	4	?	9	0	2	1	7	4	2	6	9	0	3	8	2	1	0	3	1	2	7
Thaumatoconcha Kornicker & Sohn	L	P	A	(UO)	1	1	0	(32)	2	1	3	0	1	2	1	4	(32)	(98)	0	(32)	1	(76)	(765)	3	(89)	(78)	0	2	(89)	(32)	1	0	2	3	2	6
Danielopolina kornickeri nov.sp.	M	A	A	R	1	1	0	2	2	1	3	1	2	2	1	3	1	9	1	2	1	7	4	3	5	8	0	3	8	2	1	0	3	2	1	7
D. phalanx Kornicker & Iliffe, 1995	M	A	A	O	0	1	0	1	2	1	3	1	0	2	1	3	1	9	0	2	1	7	3	3	5	9	0	3	8	2	0	0	3	2	3	4
D. elizabethae Kornicker & Iliffe, 1992 (male)	S	A	P	R	0	0	2	3	2	0	3	0	0	2	1	4	?	8	0	2	1	6	3	3	4	8	0	3	7	1	1	0	2	2	1	3
D. styx Kornicker & Iliffe, 1989 (IInstar IV)	S	A	A	E	0	1	0	3	2	1	3	0	0	1	1	4	4	9	0	2	1	6	3	3	5	8	0	3	5	0	0	0	2	2	1	4
D. mexicana Kornicker & Iliffe, 1989	M	A	P	I	0	1	0	1	2	1	3	1	0	2	1	3	1	9	0	2	1	6	3	3	5	8	0	3	7	2	0	0	2	2	2	5
D. bahamensis Kornicker & Iliffe, 1989	S	A	A	R	0	0	0	1	2	1	3	0	0	2	1	3	1	8	0	2	1	6	3	3	3	8	0	3	7	2	0	0	1	2	2	3
D. wilkensi Hartmann, 1985	S	A	P	R	0	1	0	1	2	1	3	0	0	2	1	3	1	8	0	2	1	6	3	3	4	8	0	3	7	2	0	0	2	2	2	6
D. orghidani (Danielopol, 1972)	S	A	P	E	1	1	0	1	2	0	3	0	0	2	0	3	1	8	0	2	1	6	3	3	4	6	1	2	8	1	1	0	2	2	2	3
D. carolynae Kornicker & Sohn, 1976	L	P	P	E	1	1	0	2	2	0	3	1	0	2	1	4	1	9	1	3	1	6	4	2	?	10	1	2	9	3	1	1	2	2	2	6
D. n.sp. Kornicker & Iliffe (in press)	S	A	P	E	0	1	0	1	2	0	3	0	0	2	1	2	1	8	0	2	0	6	3	3	4	6	0	3	6	2	0	0	2	2	2	3

Carapace:
1) Size: Large(L)/Medium(M)/Small(S)
2) Anterior ridges: Present(P)/Absent(A)
3) Posterior Dorsal Process: Present(P)/Absent(A)
4) Ornamentation: Smooth(O)/Spines(I)/Reticulate Papillae(E)/Reticulate Ridges(R)/Punctate(U)

1st Antenna:
5) 2nd Joint-Ventral (bristles)
6) 2nd Joint-Dorsal (bristles)
7) 3rd + 4th Joint-Terminal ventral (bristles)
8) 5th Joint-Ventral (bristles)
9) 7th Joint-Ventral (bristles)
10) 7th Joint-Dorsal (bristles)
11) 8th joint (bristles)

2nd Antenna:
12) Protopodite (bristles)
Endopodite 13) 1st joint-ventral (bristles)
14) 1st joint-dorsal (bristles)
15) 2nd joint-lateral (bristles)
16) 2nd joint-terminal (bristles)
17) 3rd joint
Exopodite 18) Number of joints
19) 1st joint (bristles)

Mandible:
20) Basale, posterior margin (bristles)
Endopodite 21) 1st joint-dorsal (bristles)
22) 3rd joint

Maxilla:
Endopodite 23) 1st joint-anterior (bristles)
24) 1st joint-posterior (bristles)
25) 2nd joint (bristles)

5th Limb:
Exopodite 26) 1st joint (bristles)
27) 2nd joint-ventral/terminal (bristles)
28) 3rd joint (bristles)

6th Limb:
29) Precoxal + Coxal + Basale (bristles)
30) 1st + 2nd joint-midventral (bristles)
31) 1st + 2nd joint-dorsal (bristles)
32) 1st + 2nd joint-terminal ventral (bristles)
33) 3rd joint
34) Endopodite (bristles)

Furca:
35) Articulated claws
36) Non-articulated claws

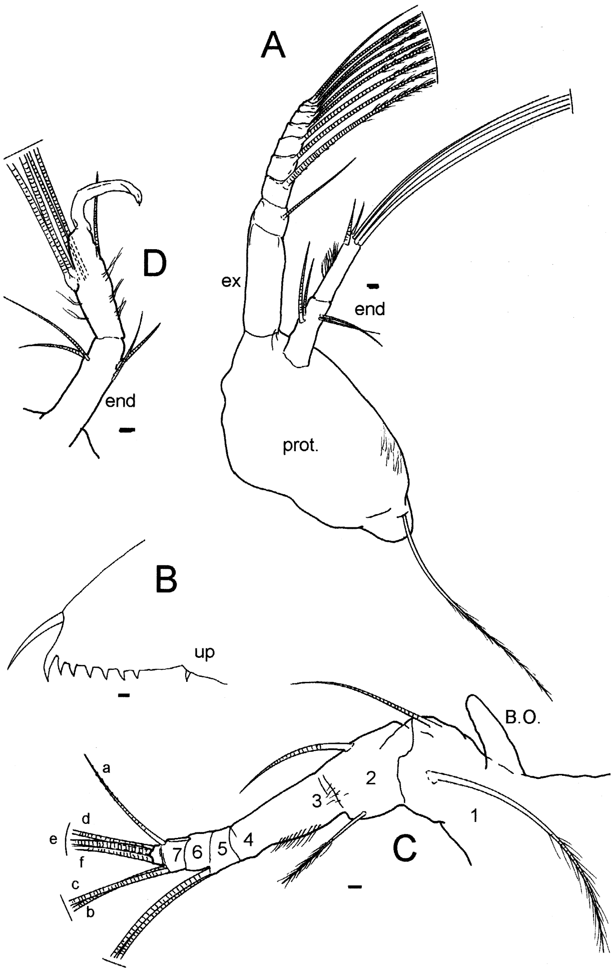

Fig. 2 A–C. *Danielopolina kornickeri*, new species, holotype, adult female. —A. Second antenna (only proximal part of long bristles shown). —B. Lamella of furca. —C Bellonci organ and first antenna (only proximal part of long bristles shown). —D. *Danielopolina kornickeri*, adult male, endopodite of second antenna (only proximal part of long bristles shown). Scale: small black bars = 10 Mm. Symbols: prot = protopodite; end = endopodite; ex = exopodite; up = unpaired process; B.O. = Bellonci organ.

Thaumatocypris while they are very attenuated in *Thaumatoconcha*).

Danielopolina kornickeri sp.*n.* has a unique feature not seen in any other Thaumatocyprididae taxa, i.e. the 2nd antenna has 2 setae on the ventral side of the 1st joint of the endopodite. It also displays characters that occur exclusively in the *Danielopolina* anchialine cavernicolous taxa, i.e. the medium size of the carapace and the lack of anterior ridges. A large number of unarticulated spines on the furca (7) and of setae on the anterior margin of the 1st endopodial joint of the maxilla (4) are traits which one finds in *Thaumatocypris* and to a lesser extent (the latter trait) in *D. carolynae*. Other similarities with this latter species are: 2 ventral setae on the 5th joint of the 1st antenna and 1 seta on the 1st exopodial joint of the 2nd antenna.

Female Description. Carapace poorly calcified and delicate, subrounded in lateral view, with straight dorsal margin near hinge. Margin between anterior and anteroventral triangular processes concave (Fig. 4B). These processes with conical projections of medium length; with extremities open and with a membranous finger-form process emerging from the hollowed projection (the latter breaking easily, and lacking in some specimens). Posterior and ventral margins evenly rounded, without posterodorsal process.

Ornamentation (Fig. 4B). Reticulated, with continuous walls in the periphery, becoming discontinuous and even disappearing close the centre.

Carapace size: length (including anterior triangular process) 0.85 mm, height 0.56 mm.

First antenna (Fig. 2D). First joint with 2 setae (1 long ventral and 1 shorter dorsal). Second joint with 1 dorsal seta at midlength and 1 subterminal ventral bristle. Third and fourth joints fused bearing ventral setulae. Fifth joint with 2 terminal ventral bristles. Sixth joint bare. Seventh joint with 1 short-terminal dorsal seta (a-bristle) bearing short marginal spines and 2 terminal ventral setae (b-and c-bristles) with some minute widely spaced spines. Eighth joint bearing 3 terminal bristles. Setae of the joints 1–5 ringed to the tip. Rings in the distal setae b, c, of the joints 7 and e, f of the distal segment use to be less conspicuous in the proximal areas.

Second antenna (Fig. 2A). Protopodite with one fairly long seta on posterior edge and setulae near the ventroproximal corner. Endopodite 2-jointed (3rd joint fused to the 2nd one): first joint with 4 ringed setae (2 dorsal and 2 ventral); second joint with short ringed dorsal seta inserted on lateral side and 3 long filament-like, terminal setae near ventral margin; small third joint fused to second joint, with short-terminal bristle. Exopodite 9-jointed: first joint divided into long proximal and short distal parts, the distal part bearing a ventral short bristles; setae of joints 28 ringed, with natatory hairs and, at least some, with minute spines widely spaced; ninth joint with two bristles, 1 short and 1 long, both with natatory setulae.

Mandible. Basale (Fig. 3A): tooth of endite with 5 triangular cusps (all bare); posterior edge of endite spinous (hairy), with 2 short ringed distal seta (distal of these tubular); anterior margin of endite with 1 long ringed seta near midlength; 5 ringed setae (4 long, 1 short) near midlength of the lateral side of endite (indeed, one is on the posterior edge), and one short ringed distal bristle: medial side of basale near dorsal margin with 2 ringed setae (ventral of these shorter); dorsal margin of basale with cluster of spines at apex. Endopodite 3-jointed (Fig. 3C): first joint with

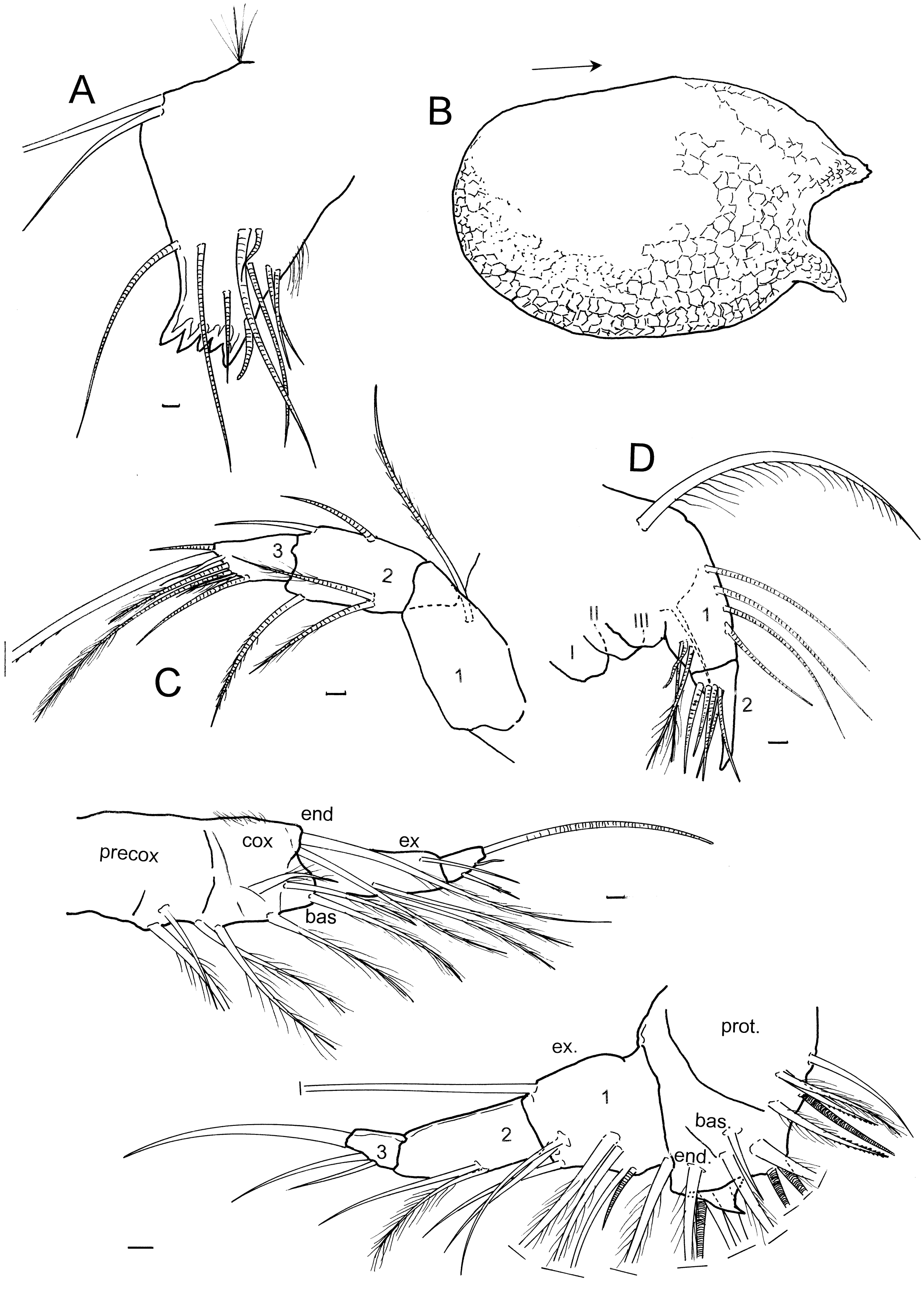

Fig. 3 A–F. *Danielopolina kornickeri*, new species, holotype, adult female. —A. Basale of mandible. —B. Complete specimen from right side. —C. Endopodite of mandible. —D. Maxilla (endite I, II and III with bristles not shown). —E. Sixth limb (epipodial bristles not shown). —F. Fifth limb (epipodite not shown). Scale: small black bars 10 Mm. Symbols: prot = protopodite; end = endopodite; ex = exopodite; precox = precoxale; cox = coxale; bas = basale.

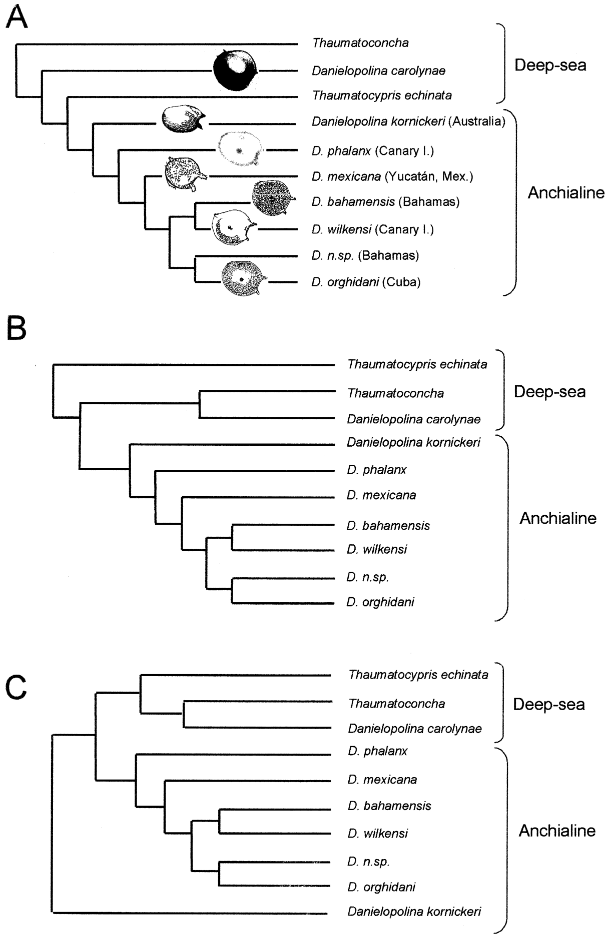

Fig. 4 A–C. Cladogram of the hypothesized relationships among the Thaumatocyprididae. Unrooted tree resulting from an unweighted, unordered character analysis of the data in Table 1 has a length of 87 steps, CI = 0.770, HI = 0.345, RI = 0.647, and RC = 0.495. —A. Tree rooted using *Thaumatoconcha* as outgroup. —B. Tree rooted using *Thaumatocypris* as outgroup. —C. Tree rooted using *Danielopolina kornickeri* sp.*n.* (if it would be a different genus) as outgroup.

dorsal seta at midlength; second joint with 1 ringed terminal ventral bristle, 2 ringed medial setae on ventral margin, 2 dorsal setae (1 ringed medial, 1 spine-like terminal); third joint with 1 long claw-like seta and 6 ringed setae (1 terminal dorsal, 1 subterminal ventral and 4 terminal).

Maxilla (Fig. 3D). Coxale with long stout plumose dorsal bristle. Basale with 2 long setae (1 proximal ventral near base of endite III; 1 medial at joint midwidth). Endopodite: 2-segmented, first joint with 4 long ringed bristles along anterior margin, and 3 distal setae near posterior margin; second joint with 1 anterior stout, straight, nonarticulated, terminal bare claw and 5 setae with bases medial or lateral.

Fifth limb (Fig. 3F). Epipodite with 3 groups of plumose bristles, 2 groups with 5 setae and 1 group with 4 bristles. Protopodite with 5 setae (1 tubular). Basale with 6 setae (1 short ringed claw-like, 2 long plumose, 3 slender ventral tubular). Endopodite with 6 setae (1 small medial tooth-like, 2 long sclerotized ventral claw-like, 2 long plumose ringed ventral, 1 ventral tubular). Exopodite 3-jointed: first joint with 8 bristles: 7 ventral (or slightly lateral) and 1 very long dorso-apical; second joint with two ventral setae at midlength (one plumose, one bare); third joint with 3 setae (1 longest claw-like, 1 medium claw-like and 1 short).

Sixth limb (Fig. 3E). Epipodite with 3 groups of plumose setae (the dorsal and the ventral groups with 5 bristles, the group in the middles with 4 bristles). Precoxale with 2 plumose bristles. Coxale with 2 plumose bristles. Basale with 4 setae (1 bare, 3 plumose). Small endopodite with 2 long plumose bristles. Exopodite: first and second joints fused with 2 long ventral setae (1 bare, 1 plumose) and 1 bare dorsal subterminal bristle; third joint with 3 bare setae (1 long claw-like, 2 short).

Seventh limb. Elongate with two terminal bristles.

Furca (Fig. 2C). Each lamella with 1 anterior, articulated claw and 7 nonarticulated spines. Stout unpaired process (up) on posterior of body just proximal to lamellae.

Bellonci organ (Fig. 2D). Elongate, well developed.

Genitalia. Not observed.

Carapace pigmentation and ocular structures absent.

Male Description. Size, shape and ornamentation similar to those of adult female. Chaetotaxy like in the female except for following characters:

First antenna. third and fourth joints fused, fourth joint with 2 long ventral filament-like setae (no such setae in the female). Similar pattern (female without terminal setae and male with 2 bristles) occur in *D. phalanx*, *D. wilkensi*, *D. bahamensis*, and *Danielopolina* sp.*n.* (Kornicker & Iliffe, in press). *D. elizabethae*, a species for which only the male has been described (Kornicker & Iliffe 1992) also has 2 terminal setae on the 4th joint in the first antenna. 5th joint with 3 filament-like setae (2 in the female), the ventral of these is broader and with 3 widely separated hook-like spines. That seta does not bear hook-like spines either in *D. phalanx* ['...short triangular spines followed by longer slender hair-like spines' (Kornicker & Iliffe 1995)] or in *D. bahamensis* ['...abundant, short, distal hairs' (Kornicker & Iliffe 1989b). A quite similar seta has been described for *D. wilkensi* but on the first joint of the 1st antenna.

Second antenna. 1st joint of the endopodite with two 2 ringed dorsal and 2 ringed ventral bristles, like in the female; 2nd joint with 4 terminal setae (3 in the female) and a short ringed dorsal bristle; 3rd joint small with a hook-like terminal process (Fig. 3B).

Copulatory organ. A recurved process tapering to narrow tip. No posterior styliform process (like the one described for *D. elizabethae*) was found.

Habitat. *Danielopolina kornickeri* sp. *n*. was collected from Bundera Sinkhole (karst index C-28) on the Cape Range peninsula, Western Australia (Fig. 1B). This anchialine cave is located 1.7 km inland from the Indian Ocean. The cave has a single entrance from a flooded sinkhole and is inclined at 30 to the horizontal. The cave was penetrated by cave divers to a depth of 32 m.

Danielopolina kornickeri sp. nov. was collected only beneath a density interface in the vicinity of which a layer of strong H_2S concentrations is encountered and below which the water is hypoxic (c. 1.0 mg/l O_2).

Physical and chemical conditions are described in detail in Yager & Humphreys (1996) and only a synopsis is given here.

A well marked temperature inversion at ≈8 m depth raised the water temperature from ≈23–26 °C. Conductivity increased across the temperature inversion from ≈30–38 mS cm^{-1} at 25 °C while there was a correspondingly decrease in pH from ≈8.1–7.6. Dissolved oxygen decreased with depth to c. 1 mg/l at a depth of 22 m. Additional detailed work on the site (September 1997) has revealed that there is a series of hydrogen sulphide layers with increasing depth associated with hypoxic conditions and very low redox values. The fine distribution of *D. kornickeri* with respect to these rapidly changing physicochemical conditions remains to be established.

There is some indication that, despite the remote location, the cave waters are enriched with nutrients (Yager & Humphreys 1996), with values that fall within the range reported for grossly polluted anchialine caves on Bermuda (Iliffe *et al*. 1984a).

The site lies outside conservation reserves and no other site is known in Australia giving access to deep anchialine habitat.

Associated Fauna. Locality C-28 has been sparsely sampled and more species are expected. Several taxa in addition to *Danielopolina kornickeri* sp. *n*. occur below the pycnocline in the cave, *viz*. *Lasionectes exleyi* Yager & Humphreys (Crustacea: Remipedia), *Liagoceradocus branchialis* Bradbury & Williams (Crustacea: Hadziidae), *Stygiocaris stylifera* Holthuis (Decapoda: Natantia: Atyidae) and *Milyeringa veritas* Whitely (Perciformes: Eleotridae). As most taxa were taken in a diver-hauled plankton net, the exact location of the remaining biota is largely unknown, but the following probably occur only above the pycnocline: the algae *Rhizoclonium?tortuosum* (Dillw.) Kuetz. (Chlorophyta: Cladophoraceae) and *Lamprothamnium papulosum* (Wallr.) J.Gr. (Charophyta: Characeae), and the invertebrates Spionidae (Annelida: Polychaeta), *Halicyclops* sp. nov. (Copepoda: Cyclopidae), other ostracods, *Iravadia* sp. (Mollusca: Iravadiidae), gerrids (Hemiptera) and *Kiefferulus intertinctus* (Chironomidae, Diptera). The stygofauna of the Cape Range peninsula generally includes, in addition to *Stygocaris stylifera and Milyeringa veritas*, the sympatric occurrence of a number of other taxa with Tethyan disjunct distributions including the genera *Haptolana* (Isopoda: Cirolanidae), *Halosbaena* (Thermosbaenacea), *Ophisternon* (Pisces: Synbranchiformes) and gammarid amphipods (Humphreys 1993a, b; Barnard & Williams 1995).

Phylogenetic relationships

Baltanás & Danielopol (1995) discussed the relationships in the Thaumatocyprididae using a cladistic approach, and concluded that a deep-sea origin for the group is not supported by existing evidence. Instead, a shallow-water Tethyan origin seemed to be a more plausible hypothesis. Since then, a new *Danielopolina* species has been described from Bahamas (Kornicker & Iliffe, in press) offering us the chance to enlarge the original data matrix in both number of species and of characters included. Given that setation differs between males and females and during ontogeny, at least for some characters (Kornicker & Iliffe 1995), *D. styx* and *D. elizabethae* were removed from the analysis because adult females were not described in these species (Kornicker & Iliffe 1989b, 1992).

Kornicker & Sohn (1976b) proposed a phylogenetic scheme for the Thaumatocyprididae in which *Thaumatocypris* and *Thaumatoconcha* were considered the sister group of *Danielopolina*, all three genera sharing a common ancestor back in the Palaeozoic. *Thaumatocypris* is a monospecific genus (type species: T. *echinata*) known from bathypelagic environments in the Indian Ocean (Kornicker & Sohn 1976a). *Thaumatoconcha*, on the contrary, is quite a diverse lineage with 13 species described mainly from deep-sea environments in the Southern Hemisphere (see Kornicker & Iliffe 1995 for a list). Thus, we have used *Thaumatocypris* and *Thaumatoconcha* as outgroups for the cladistic analysis. One most parsimonious unrooted tree was obtained.

Kornicker & Sohn (1976b; Fig. 2) suggested that the thaumatocypridids evolved from the familiy Entomoconchidae and that *Thaumatoconcha* and *Thaumatocypris* are a monophyletic group. However, it was not possible to root the tree according to that hypothesis so the exact form of evolutionary descent comes under discussion. Two trees were generated, each rooted differently with taxa hypothesized to be the outgroups for *Danielopolina*: *Thaumatoconcha* (Fig. 5A), and *Thaumatocypris* (Fig. 4B).

The first tree (Fig. 4A) suggests a close relationship between *Thaumatocypris* and the anchialine *Danielopolina*

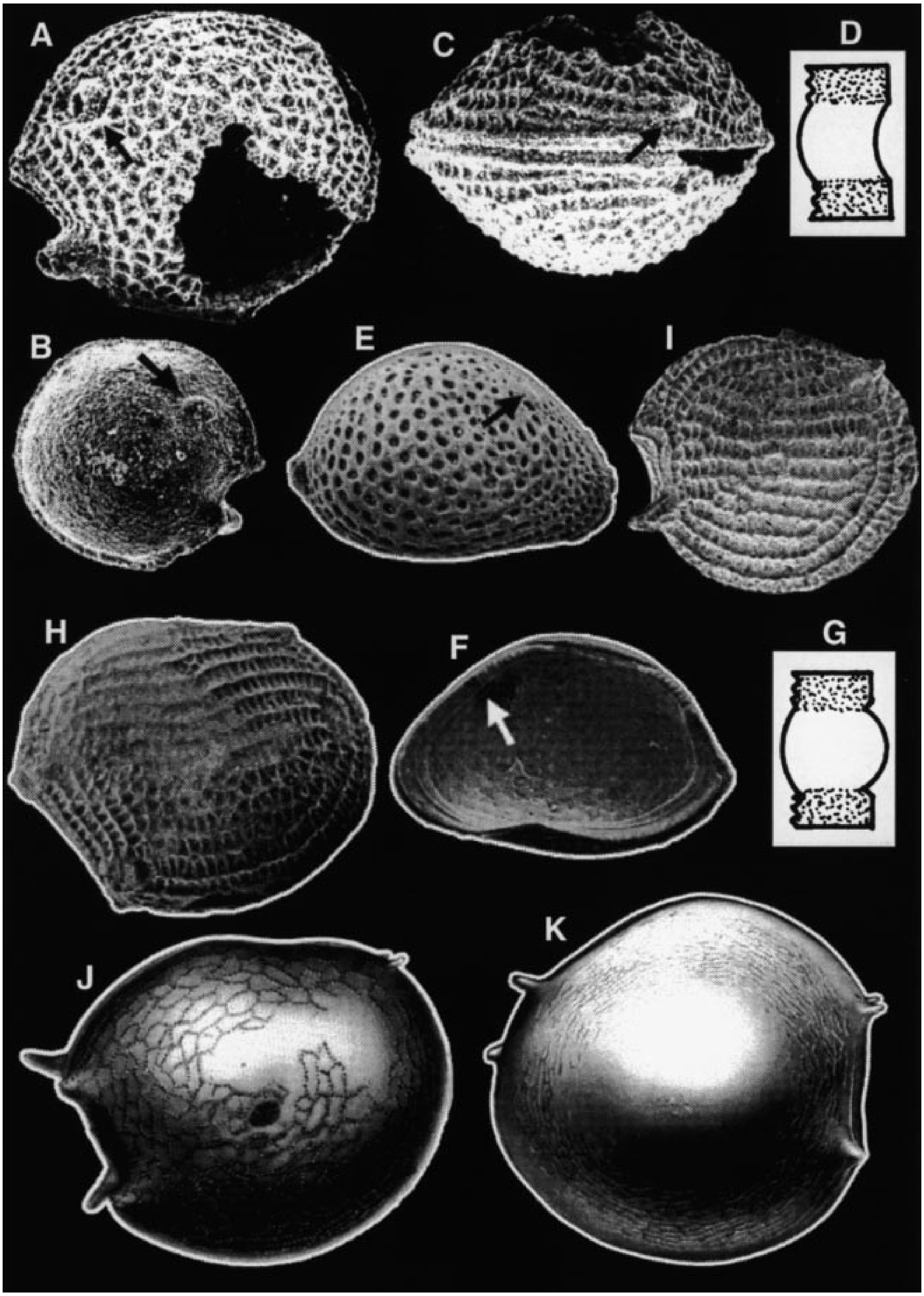

Fig. 5 A–C, *Thaumatomma piscifrons.* —A. Left valve, external side. —B. Left valve, internal side. —C. Carapace, ventral side. —D. Diagrammatic representation of the carapace convexo-concave lens-like structures. —E, F. *Foveoleberis foveolata.* —E. right valve, external side. —F. Right valve, internal side. —G. Diagrammatic representation of the carapace convexo-convex lens-like structures. —H, *Pokornyopsis bettenstaedti*, left valve, external side. —I. *Pokornyopsis feifeli*, left valve, external side. —J. *Danielopolina orghidani*, left valve, external side. —K. *Danielopolina carolynae*, right valve, external side; (A-C, H-K, from Kornicker & Sohn 1976a; E, F,from Malz 1980, D, G, after Bonaduce & Danielopol 1988; arrows point to the anterodorsal node and/or to the carapace lens-like structure).

species. This is an unlikely supposition, since sexual characters are considered to be good indicators of phylogenetic relationships and males of *Thaumatocypris echinata* lack the antennal prehensile structures which are characteristic in *Thaumatoconcha* and *Danielopolina* species (Rudjakov 1993); remember that cladistic analysis has been performed on female character set only. Differences in antennal prehensile structures could be due to the incomplete heterochronic development of the male in T. *echinata* as compared to the full developmental morphology in the case of the *Danielopolina* and *Thaumatoconcha* males. Such cases were documented for the hypogean candonids, e.g. *Pseudocandona delamarei* Dan. by Danielopol (1978; p. 142).

The second tree (Fig. 4B) results in a phylogenetic hypothesis closer to that of Kornicker & Sohn (1976b). All anchialine *Danielopolina* species form a monophyletic group and share a common ancestor with *Thaumatocypris* and *Thaumatoconcha*. However, *D. carolynae* is not included among its congeners but closer to the deep-sea genus *Thaumatoconcha*. In both cases two main conclusions can be drawn: (1) All anchialine species seem to be monophyletic. *Danielopolina kornickeri* sp.*n*., shares a common ancestor with all other anchialine species suggesting that both the Australian and the Atlantic (– western Pacific) branches diverged a long time ago. This agrees with the hypothesis of a Tethyan origin for the group (Baltanás & Danielopol 1995). and also with other evidence on Recent and fossil ostracods. First, species of the closely allied genus *Pokornyopsis* were recovered from various parts of the Western Tethys during the Late Triassic and the Jurassic (Aubrecht & Kozur 1995; Lethiers *et al*. 1998; J.P. Colin, pers. comm. to DLD). Second, strong evidence suggest that a colonization-speciation route starting in the southern end of the Tethys and running towards the West existed for various podocopid ostracod lineages (Whatley 1986; Titterton & Whatley 1988). This seems to be also the case for the thaumatocyprids of the lineage *Pokornyopsis* — *Danielopolina* here discussed; (2) *Danielopolina carolynae* is closer to *Thaumatoconcha* than to the anchialine *Danielopolina* species. This does not necessarily mean that *D. carolynae* is actually a *Thaumatoconcha* species, but poses some questions about whether is it or not a true *Danielopolina.*

Because *Danielopolina kornickeri* sp.*n*. has two ventral setae on the 1st joint of the 2nd antenna (see above for a comparison with other *Danielopolina* species), one could argue that this species is indeed the representative of a new genus. If this is to be accepted (we leave this decision for a future taxonomical revision of the Thaumatocyprididae) then its lineage could be used as a third option to root the tree, as it could have been the earliest derived taxon in the group. This phylogenetic hypothesis (Fig. 4C) suggests a branching event leading to deep-sea (and bathypelagic) species on the one hand, and to anchialine species on the other. This result also supports the hypothesis that *Danielopolina* is indeed a paraphyletic group and of Tethyan origin as well as a colonization route from the East (Australian realm) to the West for the whole group.

Discussion

Shell Ornamentation — relevance to the phylogeny of the Thaumatocyprididae

Kornicker & Sohn (1976b) considered the Recent *Danielopolina* species, living in marine caves and in the deep sea, to be closely related to, possibly descended from, Jurassic thaumatocypridids that looked like *Pokornyopsis feifeli* Triebel. Aubrecht & Kozur (1995) suggested that, as the carapaces of *Danielopolina* spp. are morphologically similar to those of the fossil *Pokornyopsis* species [*P. feifeli* (Triebel 1941) and *P. bettenstaedti* (Bartenstein 1949)], *Danielopolina* should be considered a junior synonym of *Pokornyopsis.*

Consideration of the ornamentation of the valves of Thaumatocyprididae together with ecological and/or palaeoecological information offers new support to the phylogenetic model of Kornicker & Sohn (1976a) and shows the existing differences between the shallow benthic thaumatocypridids and those inhabiting marine caves and/or deep-sea.

Kornicker & Iliffe (1995) recognized six types of ornamentation on the outer surface of the valves of the Thaumatocyprididae: (1) reticulate with walls of continuous ridges; (2) reticulate with walls of discontinuous ridges; (3) reticulate with papillate walls; (4) nonreticulate spinous; (5) nonreticulate smooth; (6) non-reticulate punctate and suggested that these represented an 'evolutionary' sequence. They noted that representatives of the Permian *Thaumatomma* and the Jurassic *Pokornyopsis* display the most primitive ornamentation pattern (i.e. type 1) while the Recent dwelling thaumatocypridids belonging to the genera *Thaumatocypris*, *Danielopolina*, and *Thaumatoconcha* display one of the other five ornamentation types.

We do not consider *Danielopolina* to be synonymous with *Pokornyopsis* for the following reasons. The two Jurassic *Pokornyopsis* species (*P. feifeli* and *P. bettenstaedti*) have strongly calcified valves with 1–3 peripheral concentric ribs which delineate within the central area, more or less horizontal ridges (Fig. 5I-J), traits that were used in the diagnosis of the genus *Pokornyopsis* (Kozur 1974). Large fossae, more or less rectangular, are formed by the intersection of the continuous ridges with vertical and less well developed muri. These characteristics, together with other established thaumatocypridid carapace traits, such as compressed ventro-posterior margin, straight anterior margin delineated by two anterior tubercle-like processes, slightly bent dorsal margin delineated by an anterior and a postero-dorsal tubercle-like processes (Müller 1906; Kozur 1974; Kornicker & Sohn 1976a) form the necessary diagnostic characters of the genus *Pokornyopsis*. No other thaumatocypridid genus display this combination of traits.

Thaumatomma piscifrons, *Pokornyopsis feifeli* and *P. bettenstaedti* lived in marine waters of less than 200 m deep (Kornicker & Sohn 1976a; Aubrecht & Kozur 1995). Compared to the deep-sea dwelling representatives of the genera *Thaumatoconcha* and *Danielopolina*, these species have well-calcified valves with strongly developed external ornamentation (Fig. 5A,C,H-K). *Danielopolina* and *Thaumatoconcha* species which live in the deep sea and the spelean systems display poorly calcified valves with less developed ornamentation which may reflect low metabolic activity. This latter is common for various deep-sea and/or spelean dwelling species (e.g. review in Childress 1995; Vandel 1965). *Danielopolina* species have reticulate valves with poorly developed and discontinuous ridges [*D. bahamensis* (Kornicker & Iliffe 1989), *D. elizabethae* (Kornicker & Iliffe 1992)], or with minute papilllate muri [the deep-sea dwelling *D. carolynae* and the troglobite species *D. orghidani* (Danielopol 1972, 1976; Kornicker & Sohn 1976a; Kornicker & Iliffe 1995)]. Most of the reticular cells have longitudinally elongated polygonal shapes (Fig. 5 J). Other troglobite *Danielopolina* species have smooth shells or the papillae are transformed into small spines (*D. mexicana*; Kornicker & Iliffe 1989b).

Danielopolina kornickeri sp.*n.* has an interrupted ridge running more or less parallel, but peripheral to the outer margin of the valve along the ventro-posterior side; together they form regular rectangular cells (Fig. 4B) such as are found in the fossil *Pokornyopsis* species. In our opinion, this morphological similarity supports the phylogenetical hypothesis of Kornicker & Sohn (1976b; fig. 3) in which the *Danielopolina* group is derived from *Pokornyopsis*. *Thaumatomma piscifrons*, considered by Kornicker & Sohn (1976b) a collateral group of the lineage *Pokornyopsis-Danielopolina*, presents deep fossae with irregularly shaped cells and with only a slight tendency to form concentric ridges (Fig. 5A,C). These morphological features seems to represent a more primitive state compared to the concentric peripheral ridges and to the well defined fossae of *Pokornyopsis* and add additional support to the phylogenetical model of Kornicker & Sohn (op. cit.) in which the thaumatocypridids are derived from a common ancestor closer to the Devonian *Checontonomus* (Entomoconchidae). Thaumatocypridids first separated as the Permian *Thaumatomma*, followed, during the Mesozoic, by the *Pokornyopsis-Danielopolina* group.

The similarity between the carapace ornamentation of *D. orghidani* and *D. carolynae* (thin reticulation with papillate structures) are most probably homoplasic resulting from convergence due to the similar environmental conditions found in the deep sea and the shallow marine caves.

The 'Anterodorsal Node' of Thaumatomma — Its Hypothetical Function

Kornicker & Sohn (1976a) noted that the Permian ostracod *Thaumatomma piscifrons* has a peculiar antero-dorsal structure on the carapace, which superficially resembles the 'eye spot' of some podocopid ostracods such as Xestoleberididae. They called this structure the 'antero-dorsal node', but could not explain its possible function. Reconsideration of the 'antero-dorsal node' described by Kornicker & Sohn (1976a) and the 'eye spot' structures of the Xestoleberididae, presented by Bonaduce & Danielopol (1988), suggests a possible function that we expand upon below.

Taumatomma piscifrons has, on the outer hand, a smooth, convex tubercle, delineated by a basal annular depression (Fig. 5A-C), while on the interior side of the valve the antero-dorsal node is concave. Bonaduce & Danielopol (1988) showed that those Xestoleberididae species which are specialized to live in strongly illuminated habitats display on the valves, lens-like structures which help the transmission of light to lateral ocelli. They found four types of carapace lenses, namely, plano-concave, convexo-convex (Fig. 5G), convexo-concave (Fig. 5D) and plano-convex. As the shape of the 'antero-dorsal node' corresponds to the convexo-concave lens, as expressed in the Holocene xestoleberidid *Ornatoleberis morkhoveni* (Bonaduce & Danielopol 1988), we therefore hypothesize that the peculiar node of *Thaumatomma* is a 'carapace lens' playing a similar function with the 'ocular nodes' of the above mentioned xestoleberidids. The light, which could be concentrated by the carapace lens of *T. piscifrons* should be further transmitted to a dermal photosensitive zone. Apparently such a dermal area exists in *Bathyconchoecia septemspinosa* (L. S. Kornicker, pers. comm. to D.L.D.) which displays a large pigmented spot on the antero-dorsal node (Kornicker & Angel 1975). It is necessary to point out that *Thaumatomma piscifrons* was found in sediments which were deposited during the tropical Late Permian conditions (Kornicker & Sohn 1976a) in a persistent (in a geological time sense) '...favourable environment, in shallow sunny waters at a considerable distance from contaminating sediment or turbulent waves' (Grant *et al.* 1991; p.489).

No lens-like structures are found in the *Danielopolina* species which live in darkness, or in the oldest known *Pokornyopsis* species, *P. bettenstaedti*, which presumably lived in a poorly illuminated environment. Did the ancestor of the *Pokornyopsis-Danielopolina* lineage have a lens-like structure, similar to those of *Thaumatomma*, which

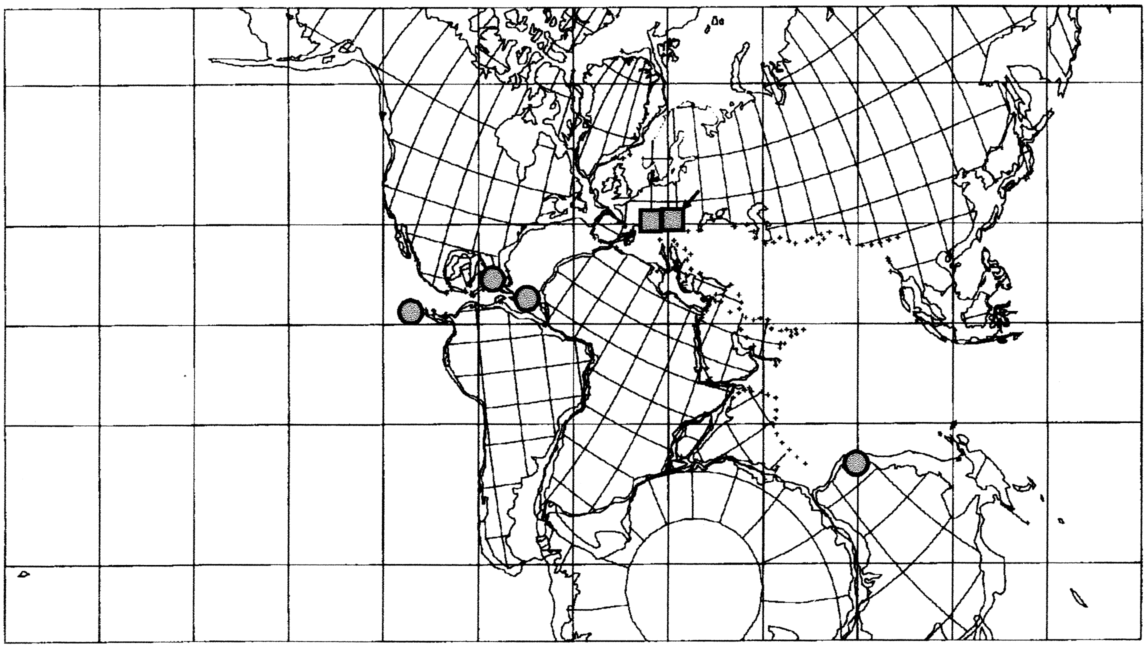

Fig. 6 Locations for recent *Danielopolina* species (circles) and the fossil *Pokornyopsis feifeli* (squares) placed on a palaeogegraphic map showing the position of landmasses in the Jurassic with the Tethys ocean situated between the separating tectonic plates (map from Smith & Briden 1977).

was subsequently lost during life in a poorly illuminated environment? A similar hypothesis was proposed, with a spelean origin, for extant surface-dwelling halocyprid ostracods that lack ocular structures (Angel & Iliffe 1987). However, we consider that the regression of optic structures of surface dwelling thaumatocypridids could have occurred in poorly illuminated benthic habitats. Such an environmental situation is known from shallow-water and higly productive aquatic systems (Sweerts & Rudd 1986). Hallam (1975) and Tyszka (1994), mentioned for various Jurassic epicontinental shallow facies in Europe the presence of fine grained sediments forming a benthic 'soupy ground'. During the Late Triassic and the Jurassic abundant populations of *Pokornyopsis* (various species) inhabited the Western Tethys (Aubrecht & Kozur 1995; Lethiers *et al.* 1998; J.P. Colin, pers. comm. to DLD). Some of the thaumatocypridid species like *Pokornyopsis bettenstaedti* experienced such conditions (Bartenstein 1949). Similar reduction of ocular lenses in trilobites which lived in benthic muddy habitats of the shelf in the Tethys during the Devonian were described by Feist (1995). The regression of ocular structures for benthic animals which adopt a fossorial life was recently analysed for marine gammaridean Amphipoda by Thurston & Bett (1993). These authors showed that even at shallow depths (i.e. less than 200 m) eyeless amphipods occur and the colonization of the deep sea by representatives of some groups was repeated many times. This information is in line with our hypothesis that photoreceptor structures can regress even in shallow benthic and poorly illuminated habitats and that there are crustacean groups which are more prone to penetrate and/or to adapt to aphotic environments than others. Preadapted blind epigean thaumatocypridids could, in principle, have actively colonize the shallow marine caves along the Tethys, since the Mesozoic (Aubrecht & Kozur 1995; Danielopol *et al.* 1996).

Chaetotaxy of the Antennae —The Paradox of a Lack of Sensorial Compensation for the Absence of Ocular Structures

Animals adapted to allobiospheric habitats (i.e. those that are deprived of light and photosynthesizing organisms) develop a complex of traits termed the *darkness syndrome* (Danielopol *et al.* 1996). Beside the regression of ocular structure many allobiospheric animals, living either in subsurface habitats exhibit hyperdevelopment of other sensorial traits, e.g. the blind cave dwelling fish *Astyanax fasciatus* (Cuvier) has a greater number and more strongly developed gustative papillae than do the oculate conspecific fishes living in surface waters (Wilkens 1992). Danielopol (1973) showed that the antennal aesthetascs, i.e. chemo-sensorial setae (for a review of the aesthetasc concept in Crustacea, see Hallberg *et al.* 1992), of several hypogean dwelling candonids (Podocopida) are much longer than those of their epigean relatives.

Planktonic halocyprids (Conchoecinae) have well-developed aesthetascs on the distal segments of the first antenna. For example, female *Conchoecia spinirostris* has four short 'sensory tubes' and one long seta, inserted on the last two antennular segments, while the male has two very long aesthetascs and three setae (Heimann 1979). These aesthetascs or 'sensory tubes' are regionally differentiated into four sections and have a chemo-sensorial function (*ibid.*). By contrast, troglobite species belonging to the genera, *Danielopolina* (Thaumatocyprididae), *Spelaeoecia* and *Deeveya* (Halocyprididae, Deveyinae) have poorly developed aesthetascs (Kornicker & Iliffe 1992), none displaying aesthetascs comparable to those seen in the surface dwelling Conchoecinae. The *Danielopolina* species have three filament-like setae, while *Spelaeoecia* and *Deeveya* have four such setae.

Interestingly enough the marine benthic Sarsiellidae ostracods (Myodocopina), a group within which no species adopted an exclusively troglobiotic life-style, the ocular structures are not regressed and the antennae do not display aesthetascs (see, for an example, Baltanás 1992).

The success of a number of Deeveynae and Thaumatocyprididae ostracods in colonizing subsurface habitats, in contrast to the paucity of other myodocopid taxa, such as the halocyprid Conchoeciidae, that have better developed chemosensory setae, may be due to the different specialization of the aesthetascs in the benthic and pelagic ostracods. The hyperdeveloped antennal aesthetascs in the conchoeciids may be specialized to detect long-range chemical stimuli such as sexual pheromones, useful for life in pelagic waters, while the benthic Halocyprididae and Thaumatocyprididae have aesthetascs which detect short-range stimuli useful to locate food and/or predators in close proximity. Such morphological and functional specialization of the aesthetascs is found in the Mysidacea (Johansson *et al.* 1996) and it may be that ostracods do not require long-range physical and chemical senses within the confines of the cave environment.

Palaeobiogeographical Arguments for a Shallow Marine Origin of Danielopolina Cavernicolous Species

Most of the troglobitic *Danielopolina* species are located within the Central Atlantic area and the unique deep-sea *Danielopolina* species was found at a site closely located to the Brazilian Coast (Fig. 1A). Therefore the hypothesis that the origin of the cavernicolous *Danielopolina* species should be sought in a deep-sea dwelling species (Boxshall 1989) had intuitive appeal. Phylogenetic, ecological/palaeoecological and bio/palaeobiogeographical arguments, as discussed here, point out to a shallow marine origin for the thaumatocypridid cavernicolous species.

We contend that the present day *Danielopolina* troglobites originated from shallow benthic thaumatocypridids that lived on the shelf of the Tethys Sea. We presume that at least some of the surface marine benthic *Danielopolina* ostracods could tolerate lower oxygen conditions as it is known for the *Pokornyopsis* species and therefore could easily colonize the anchialine environment where poorly oxygenated water prevail at the bottom of the cavities (see below). For instance, one should note that present-day *Danielopolina* species are known from both well oxygenated and poorly oxygenated subterranean habitats, e.g. *D. orghidani* in the Grieta Punta Guana, in Cuba, as collected from a well oxygenated habitat (5.7 $mgO_2{\cdot}l^1$, Juberthie *et al.* 1977) while we showed here that *D. kornickeri n.* sp. in the Western Australian cave lives under dysaerobic conditions (dissolved oxygen less than 1 $mgO_2{\cdot}l^{-1}$) and below two H_2S layers (WFH, unpublished). Poorly oxygenated waters are quite common conditions for anchialine fauna (Yager 1994; Yager & Humphreys 1996). A similar situation was postulated for the representatives of the genus *Pokornyopsis*, from Jurassic benthic shallow facies in Germany. While *P. bettenstaedti* lived under poor oxygen conditions during the Early Jurassic (Bartenstein 1949), *P. feifeli* was recorded in the Late Jurassic from a well-oxygenated carbonate facies (Triebel 1941).

Anchialine caves along the margin of the Tethys Sea were colonized by thaumatocypridids at least since the Late Jurassic, as documented by Aubrecht & Kozur (1995) for *Pokornyopsis feifeli*. The deepening of the equatorial area where *Danielopolina carolynae* was found in the South Atlantic near the Brazilian Coast formed later, during the Early Cretaceous (Bonatti *et al.* 1996). The colonization of the region of Western Australia containing the anchialine caves could also have ocurred in the Jurassic as this land area became available for colonization with the break-up of Gondwana (Humphreys *et al.*, in press a), although the adjacent land area had emerged already by the end of the Palaeozoic (Humphreys 1993a, 1993b; Yager & Humphreys 1996). The distribution of the Recent *Danielopolina* species and the distribution of *Pokornyopsis feifeli* are shown in Fig. 6 on a palaeogeographical map of the Late Jurassic. During the Mesozoic most of the places where we now find troglobite *Danielopolina* species could be reached by benthic thaumatocypridids living on the shallow shelf of the Tethys Sea. Interestingly enough, Whatley & Ballent (1995: 963) point out that in the South Atlantic only in the Late Cretaceous did elements of what was to become the Cainozoic bathyal/abyssal fauna colonized the deep water environment. One could argument (as one referee of this paper did) that *Danielopolina carolynae* has its origin in a deep sea ostracod fauna already existing in the lower-latitude of the North Atlantic during Late Jurassic and from where it migrated into the equatorial part of the South Atlantic deep sea. In our opinion if this latter possibility could be the right solution for the deep-sea origin of *D. carolynae*, it does not solve the phylogenetic relationships between this latter and the Atlantic and Western Australian cavernicolous *Danielopolina* species. We document here that they are not phylogenetically closely related. Hence, we consider that the palaeobiogeographical data on the distribution of *Danielopolina* and *Pokornyopsis* provide additional support for the shallow origin of marine cave fauna, an hypothesis that has been rigorously defended by Stock since 1986 and subsequently supported by others (Danielopol 1990; Baltanás & Danielopol 1995; Kornicker & Iliffe 1995; Jaume & Boxshall 1996b).

The present-day distribution of cavernicolous *Danielopolina* species on various islands which were formed during the Tertiary., e.g. the Canary Islands, the Bahamas, Galapagos, etc. could be due to passive transport as hypothesized by Danielopol (1990). This latter author suggested that thaumatocypridids may currently inhabit clastic sediments along continental coasts and as such could be transported passively to marine caves on oceanic islands (e.g. Canary Islands and/or Galapagos). However, as anchialine habitats in fairly close geographical areas such as Cuba, Jamaica, the Bahamas, and the Yucatan Peninsula, have a different thaumatocypridid species in each locality (Kornicker & Iliffe 1995), it suggests that the present-day distribution is not the result of transport by currents from one island to another but results from vicariance events, a hypothesis also consistent with the observed distribution in the anchialine genus *Bahadzia* (Amphipoda, Hadziidae) (Holsinger 1992). The hypothesis that subterranean lineages may move through the subterranean matrix over long periods of geological time has been proposed to explain the presence of ancient lineages within geologically younger rocks, both in the near coastal areas (Humphreys *et al.* in press b) as well as on the shield regions themselves (Poore & Humphreys 1998).

Danielopolina wilkensi and *D. phalanx*, which inhabit an anchialine lava tube in Lanzarote (Canary Islands), are the only known sympatric *Danielopolina* species. They are of especial biogeographical/phylogenetic interest as, according to results shown above (Baltanás & Danielopol 1995; and Fig. 4), they do not belong to the same clade, therefore suggesting successive colonization, an idea repeatedly expressed by Stock from his analyses of the biogeography of anchialine amphipods (e.g. Stock 1993). However, caution is needed in interpreting fine grained patterns in relationships amongst anchialine lineages because the faunas have been poorly sampled and many new species surely await discovery. And we already know that further findings can dramatically change our perceptions of relationships (see, for instance, Baltanás & Danielopol 1995; Jaume & Boxshall 1996b).

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