

Discoveries of Cave Misophrioids (Crustacea: Copepoda) Shed New Light on the Origin of Anchialine Faunas

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Abstract. Phylogenetic relationships between the known genera of the order Misophrioida are examined. Two lineages are identified: one consisting of the family Misophriidae which comprises seven genera, and a new, monotypic family, the Palpophriidae fam. nov.; the other consisting of another new family, the Speleophriidae fam. nov., comprising eight genera. Habitat exploitation by these families is discussed: members of the Misophriidae are primarily hyperbenthic, those of the Palpophriidae and Speleophriidae are primarily cavernicolous in anchialine habitats. The occurrence of misophriids in littoral and submarine caves is interpreted as evidence of a relatively recent landward extension of the habitat range in this family, from a shallow-water hyperbenthic ancestor. The zoogeographic distribution of speleophriids in anchialine caves is interpreted as resulting from a dispersal and colonization episode prior to the closure of the Tethys Sea. The analysis also indicates that deep-water forms may represent a secondary colonization rather than an indication of deep-water ancestry for the entire order. The importance of anchialine habitats as refuges for ancient lineages of copepods is stressed and it is recognised that these fragile habitats should be accorded some measure of protection.

Key words. Phylogeny, Misophriidae, Palpophriidae fam. nov., Speleophriidae fam. nov., zoogeography.

1. INTRODUCTION

The number of genera and species within the order Misophrioida has grown rapidly in the past two decades. In 1980 the order comprised the littoral genus *Misophria* Boeck, 1864 and the bathypelagic genus *Benthomisophria* Sars, 1909 only. The former genus was monotypic, the latter contained just two species (BOXSHALL & ROE 1980). The number of known species doubled in 1983 when BOXSHALL (1983) established three new monotypic genera, *Archimisophria*, *Misophriopsis* and *Misophriella*, collected from the hyperbenthic zone in the deep waters of the North Atlantic. A second species of *Archimisophria* was described from hyperbenthic waters of the South Atlantic at a depth in excess of 1000m off the coast of Brazil (ALVAREZ 1985). The following year the first misophrioid, *Speleophria bivexilla* Boxshall & Iliffe, 1986 was described from an anchialine cave habitat, on Bermuda. By 1989 a further four new genera and six new species had been established all based on material from anchia-

line habitats around the world (BOXSHALL & ILIFFE 1987; HUYS 1988) and the first analysis of the phylogenetic relationships between the genera was undertaken (BOXSHALL 1989).

BOXSHALL (1989) identified two main lineages within the Misophrioida; the *Misophria*-lineage comprising *Misophria*, *Benthomisophria*, *Misophriella* and *Misophriopsis*, and the *Archimisophria*-lineage comprising *Palpophria* Boxshall & Iliffe, 1987, *Dimisophria* Boxshall & Iliffe, 1987, *Speleophria*, *Expansophria* Boxshall & Iliffe, 1987, *Boxshallia* Huys, 1988, and *Archimisophria*. Both of these lineages had a deep-sea hyperbenthic taxon as their most plesiomorphic offshoot, *Misophriopsis* and *Archimisophria* respectively. BOXSHALL (1989) interpreted the results of this analysis of the taxa known at that time as evidence that the misophrioids inhabiting anchialine caves on oceanic islands belong to lineages that originated in the deep-sea. This conflicted with the view of STOCK (1986) that a deep-sea origin of certain anchialine cave taxa on Atlantic islands was unlikely because of an anoxic stage

in the Middle Tertiary that would have wiped out much of the bathyal-abyssal fauna.

The continuing discovery of new misophrioids from anchialine caves (BOXSHALL & ILIFFE 1990; JAUME & BOXSHALL 1996a,b; JAUME et al. 1998), and from hyperbenthic habitats in both shallow waters (BOXSHALL 1990; OHTSUKA et al. 1992), and in deep or high latitude waters (MARTINEZ ARBIZU & SEIFRIED 1996; JAUME & BOXSHALL 1997; HUMES, in press; MARTINEZ ARBIZU & JAUME, pers. comm. 1999) has provided a new and broader perspective on the morphological diversity of this interesting order. The presence of specialised cavernicolous misophrioids in anchialine caves on Mediterranean islands has added to the biogeographical questions surrounding the history of the order. How can we explain the presence of misophrioids on Mediterranean islands when the Mediterranean Sea was dry a mere five and a half million years ago, according to the Messinian Salinity Crisis theory proposed to explain the presence of extensive evaporite deposits around the Mediterranean basin (HSÜ et al. 1973)?

These recent discoveries have provided the new data required for a thorough reexamination of the controversial question of whether the anchialine cave misophrioids descended from ancestors found in deep water or in shallow water hyperbenthic habitats. The objective of this paper is to examine the new evidence relevant to this question by using a phylogenetic analysis of the genera currently comprising the Misophrioida.

Methods

The data matrix has been compiled using published information except for *Palpophria*, the original description of which (BOXSHALL & ILIFFE 1987) is supplemented by and corrected by the examination of new material from the type locality. At present 16 misophrioid genera are regarded as valid, but only 15 are included in the matrix (Appendix 2). *Dimisophria* has been omitted because of the uncertainty concerning the sex and state of maturity of the holotype (BOXSHALL & ILIFFE 1987), the only specimen thus far known. The outgroup is the presumed ancestral calanoid of HUYS & BOXSHALL (1991). A total of 82 characters is included (Appendix 1). These characters are mostly self-explanatory, such as presence or absence of setation elements (Characters 12–19, 36–42, 44–47, 49–51, 53–58, 61–69 and 73–80), but interpretative notes are provided below on certain problematic characters. Male and female antennular segmentation patterns vary and are, therefore, treated separately. A schematic analysis (Fig. 1) is presented to facilitate the identification of homologous segments and setation elements of the antennary exopod. Similarly, a schematic is presented to facilitate the identification of setation elements from the fifth legs of both sexes

(Fig. 2). Anatomical terminology for appendage parts is adopted from HUYS & BOXSHALL (1991).

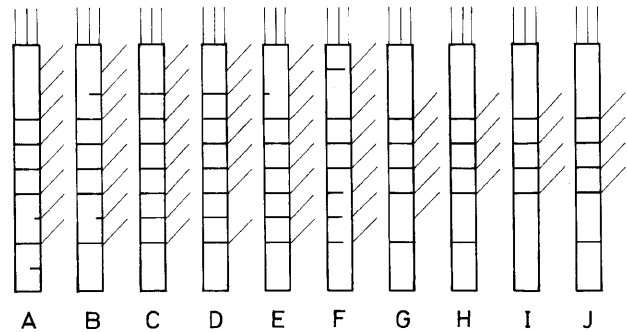


Fig. 1. Schematic representation of the antennary exopod showing presumed segmental homologies between genera of Misophrioida.

A = *Speleophria* (based on *S. gymnesica*); B = *Speleophriopsis* (*S. balearicus*); C = *Expansophria* (*E. galapagensis*); D = *Archimosphria*; E = *Boxshallia*; F = *Huysia*, *Protospeleophria*; G = *Misophria*, *Misophriopsis*, *Stygomisophria*, *Arcticomisophria*, *Fosshageniella*; H = *Misophriella*; I = *Benthomisophria*; J = *Palpophria*.

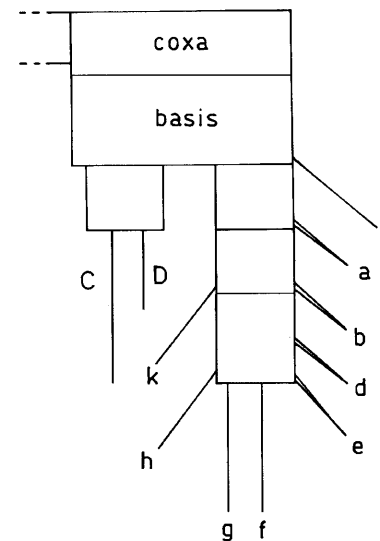


Fig. 2. Schematic representation of the presumed ancestral fifth swimming leg for the Misophrioida, with maximum segmentation and setation. Individual setation elements are identified with letters corresponding to characters 61 to 69 and 73 to 80 in Appendix 1.

Characters

A total of 82 characters was employed in the analysis as listed in Appendix 1. The character matrix is given in Appendix 2.

All characters relating to the segmentation of appendages (characters 1–10, 20–34, 43, 52, 59–60 and 70–72) refer to whether or not particular articulations are expressed in the adult. The term “fused” for compound segments is avoided in the absence of the developmental data which are necessary to distinguish between segments that remain undifferentiated through development and those that secondarily fuse (KARAYTUG & BOXSHALL 1996).

The antennary exopods (characters 43 to 46) of most genera are compared in Figure 1. The key species in interpreting this ramus are *Speleophria gymnesica* Jaume & Boxshall, 1996 and *Huysia bahamensis* Jaume, Boxshall & Iliffe, 1998. In *S. gymnesica* the proximal segment of the exopod carries only a single seta but its double origin is clearly indicated by the retention of an incomplete suture line marking the plane of the articulation between ancestral exopodal segments I and II (JAUME & BOXSHALL 1996a: Fig. 6A). The proximal segment in each of the other genera also carries a single seta: all are similarly interpreted here as double segments. In *H. bahamensis* the compound apical segment is partly subdivided by an incomplete suture line marking the original articulation between ancestral segments IX and X (JAUME et al. 1998: Fig. 2B). Articulations between all other exopodal segments are fully expressed in at least one misophrioid genus (Fig. 1).

Three setation characters were included relating to the maxilliped (characters 49–51). The plesiomorphic 6-segmented condition of the maxillipedal endopod is retained in genera such as *Speleophriopsis* and *Boxshallia*, which possess a separate first endopodal segment bearing either 1 or 2 setae (JAUME & BOXSHALL 1996a; HUYS 1988). In many other genera the first endopodal segment is not differentiated, the endopod is 5-segmented and the basis bears only 3 setae, so that there is no evidence of the first endopodal segment, together with its setae, having been incorporated into the basis. In the genera with a 5-segmented endopod and no additional setae on the basis, the character used is the absence of the setae derived from the first endopodal segment, irrespective of whether a segment bearing these setae is defined or not.

Important characters are represented by the setation of the fifth swimming legs in both sexes (characters 61 to 69 and 73 to 80). This leg is typically sexually dimorphic so the sexes are treated separately. The setation elements can be identified by reference to the lettering system given in Figure 2.

Analysis

The analysis was performed using PAUP 3.11, produced by D. Swofford. All characters were treated as IRREVERSIBLE UP following the analysis of HUYS & BOXSHALL (1991) which demonstrated that oligo-

merization was the dominant mode of evolutionary transformation with the copepods. This generates longer, less parsimonious trees. A BRANCH AND BOUND search was employed and bootstrap values were calculated for the 50% majority consensus tree.

2. RESULTS

Four trees of branch length = 183 were generated. Bootstrap values were calculated by heuristic search and the bootstrap 50% majority consensus tree is adopted here (Fig. 3).

There are two main lineages. One lineage comprises *Misophria*, *Benthomisophria*, *Misophriella*, *Misophriopsis*, *Stygomisophria*, *Fosshageniella*, *Arcticomisophria* and *Palpophria*. It is defined by the following shared apomorphies: failure to express articulation XXVI–XXVII in female antennule, loss of aesthetasc

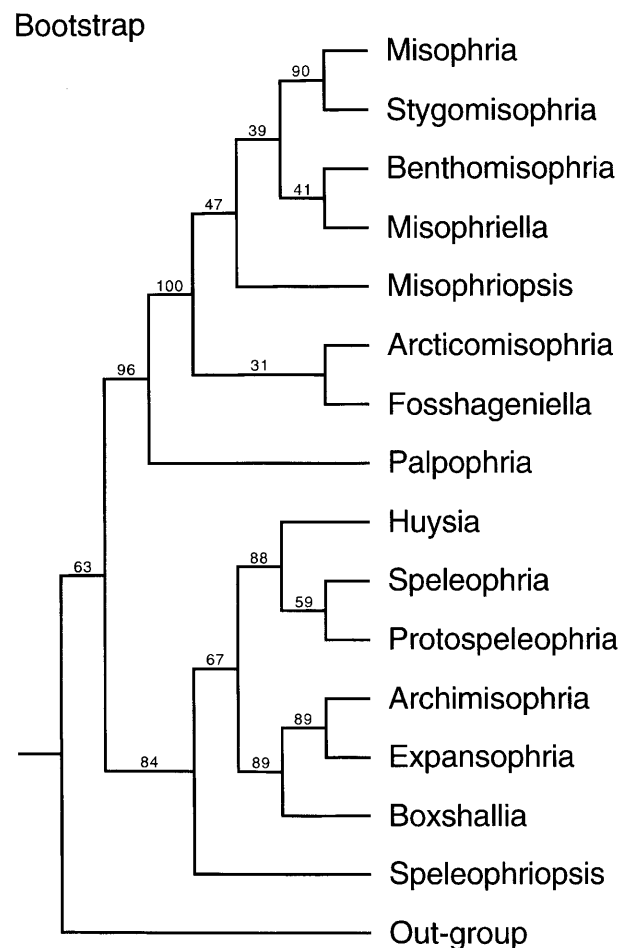


Fig. 3. Bootstrap 50% majority consensus tree, depicting inferred phylogenetic relationships between genera of Misophrioida [Length 183]. Numbers at each node indicate bootstrap support.

on segment III of female antennule, complete failure to express articulation between segments IX and X in antennary exopod, loss of seta from antennary exopodal segments II and IX, loss of maxillary exite seta, loss of seta representing praecoxal endite and seta(e) representing first endopodal segment in maxilliped, loss of outer seta originally carried on endopodal segment 5 of maxilliped, failure of expression of coxa-basis articulation in female fifth leg, loss of outer spine on second exopodal segment and proximal inner seta on third exopodal segment of female fifth leg.

The exclusion of *Palpophria* allows the definition of a core *Misophria*-group on the basis of the following shared apomorphies: failure to express articulations II–III, III–IV, IV–V, V–VI, IX–X, X–XI and XI–XII in female antennule, loss of aesthetascs from segments VII, XI, XX and XXVI in female antennule, failure to express articulations II–III, III–IV, IV–V, V–VI, X–XI, XI–XII, XIX–XX, XXI–XXII, XXII–XXIII, XXIV–XXV, XXV–XXVI and XXVI–XXVII in male antennule, loss of seta from antennary exopodal segment VIII, and loss of outer spine on second exopodal segment of male fifth leg.

The other lineage comprises seven genera *Speleophriopsis*, *Speleophria*, *Huysia*, *Protospeleophria*, *Archimiosophria*, *Boxshallia* and *Expansophria*. It is defined by the following shared apomorphies: loss of aesthetasc from segments XIV, XVIII and XX of female antennule and from segments V, XIV and XVIII of the male antennule, loss of proximal seta from inner margin of second endopodal segment of leg 1, loss of subapical seta from apex of endopod of both female and male fifth legs.

The topology presented in the bootstrap 50% majority consensus tree (Fig. 3) is used here as the basis for a proposed division of the Misophrioida into three families. The Misophriidae, comprises the core *Misophria*-group of seven genera as defined by the synapomorphies above. The Misophriidae is a relatively homogeneous group of mostly hyperbenthic taxa and is solidly supported by the analysis, with a bootstrap value of 100. Relationships within the Misophriidae are not well resolved and have low bootstrap values. The monotypic Palpophriidae fam. nov. is the sister-group of the Misophriidae. The third family, the Speleophriidae fam. nov., consists of the other lineage identified in the analysis and comprises the seven genera listed above. The Speleophriidae is well supported with a bootstrap value of 84. These three families are formally diagnosed below. The position of *Dimiosophria* is equivocal but it is tentatively placed in the Speleophriidae.

Family Misophriidae Brady, 1878

Emended Diagnosis: Body cyclopiform; prosome comprising cephalosome and 4 free pedigerous somites;

first pedigerous somite concealed beneath carapace-like extension of posterior margin of dorsal cephalic shield. Urosome 6-segmented in male, indistinctly 5-segmented in female due to partial fusion of genital and first abdominal somites to form genital double-somite; 4 free abdominal somites in male, 3 in female. Prosome-urosome articulation between fourth and fifth pedigerous somites (podoplean position). Genital apertures paired in both sexes, located ventrally at posterior border of genital somite in male, in anterior third of genital double-somite in female; or with single common pore in female. Seminal receptacles fused. Copulatory pores paired.

Rostrum small, defined at base or fused to dorsal cephalic shield. Caudal rami with 7 setae or with seta I lacking. Nauplius eye absent. Antennules 17 to 19-segmented in female; typical compound segments as follows: II–VI, IX–XII and triple apical segment XXVI–XXVIII: compound segments sometimes incorporating additional segments, such as II–VII, II–VIII or IX–XIII. Aesthetascs typically present only on segments XVI, XVIII, XXI, XXV and XXVIII; lacking on other segments. Antennules 12 to 15-segmented in male, bilaterally symmetrical, geniculate with geniculation located between segments homologous with XX and XXI of the female; typically with compound segments II–VI, XIX–XX, XXI–XXIII, and XXIV–XXVIII; often with compound segments incorporating additional segments such as, IX–XII or IX–XIII. Sheath typically present on segment XV in male, partly enclosing segment XVI. Aesthetascs typically present on segments I, III, V, VII, IX, XI, XIV, XVI, XVIII, XXI, XXIV, and XXVIII.

Antenna biramous with 6-segmented exopod and 3-segmented endopod; coxa unarmed, basis typically with 2 inner setae. First to third endopodal segments with 1, 5 and 7 setae respectively. First exopodal segment derived from fused ancestral segments I and II, second from segments III and IV, third to fifth representing ancestral segments III to VIII, sixth representing fused ancestral segments VIII–X; maximum setal formula 0, 2, 1, 1, 1, 3. Labrum an undivided muscular lobe.

Mandible with large coxal gnathobase and biramous palp; exopod typically 6-segmented but segments usually incompletely expressed; setal formula 0, 2, 1, 1, 2 or 1, 1, 1, 1, 2; endopod 2-segmented, setal formula 1/2, 6/8; basis bearing 1 seta at most on inner margin. Paragnaths separate.

Maxillule with large praecoxal endite bearing about 15 elements; coxa with single endite bearing up to 6 setae, and vestigial epipodite incorporated into segment, represented by up to 8 setae; basis lacking seta on outer margin; 2 widely separated basal endites present, proximal endite well developed, with up to 4 setae; distal en-

dite largely incorporated into segment, represented by up to 4 setae; exopod 1-segmented with maximum of 11 setae, endopod indistinctly 2-segmented, proximal segment representing double segment; setal formula (4, 4), 6: maxillary setation often reduced.

Maxilla 6-segmented; praecoxa and coxa each with 2 endites, endite formula 4/7, 3, 3, 3; allobasis with well developed proximal (basal) endite forming a claw bearing up to 4 setae, distal (endopodal) endite vestigial, represented by 2 or 3 setae; outer coxal seta absent; free endopod 3-segmented, setal formula 2, 2, 4; setation of maxilla often reduced.

Maxilliped 7-segmented, comprising syncoxa with 3 endites, basis and 5-segmented endopod, with ancestral first endopodal segment not expressed; praecoxal and coxal endite formula 0, 1, 3, 2, or further reduced; praecoxal seta lacking; basis typically with 3 setae; endopod setal formula 2, 2, 2, 2, 5.

Swimming legs 1 to 4 biramous, with 3-segmented rami; members of each leg pair joined by intercoxal sclerite; inner coxal seta and outer seta on basis present, inner spine on basis of first leg. Spine and seta formula for legs 1 to 5 as follows:

	coxa	basis	exopodal segments	endopodal segments
leg 1	0-1	1-1	I-1; I-1; III,I,4	0-1; 0-2; 1,2,3
leg 2	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,2,3
leg 3	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,2,3
leg 4	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,2,2
leg 5 (f)	0-0	1-0	I-0; 1/2,I,1	2
leg 5 (m)	0-0	1-0	I-0; 0-1; 2,I,2	2

Setation often reduced or modified by transformation of setae into spines. Fifth legs primitively biramous; members of leg pair joined by intercoxal sclerite; praecoxa sometimes present, usually absent; coxa and basis separate or fused; basis with outer seta; inner coxal seta absent; exopod 1 to 2-segmented and bearing up to 5 setal elements in female, and 1 to 3-segmented with up to 7 setae in male; endopod 1-segmented and bearing 1 or 2 setae in both sexes. Fifth legs uniramous due to loss of endopod in some genera; exopod often reduced. Sixth legs typically confluent in female, separate in *Misophriella* and in males, represented by opercular plate closing off genital openings. Eggs loosely attached to female urosome, not contained in sacs.

Type-genus: *Misophria* Boeck, 1865

Included genera:

Arcticomisophria Martínez Arbizu & Seifried, 1996

Benthomisophria Sars, 1909

Fosshageniella Jaume & Boxshall, 1997

Misophria Boeck, 1865

Misophriella Boxshall, 1983

Misophriopsis Boxshall, 1983

Stygomisophria Ohtsuka, Huys, Boxshall & Itô, 1992

Remarks

This is a well defined family, with all genera sharing numerous diagnostic apomorphies, particularly related to the segmentation patterns of the antennules.

Family Palpophriidae fam. nov.

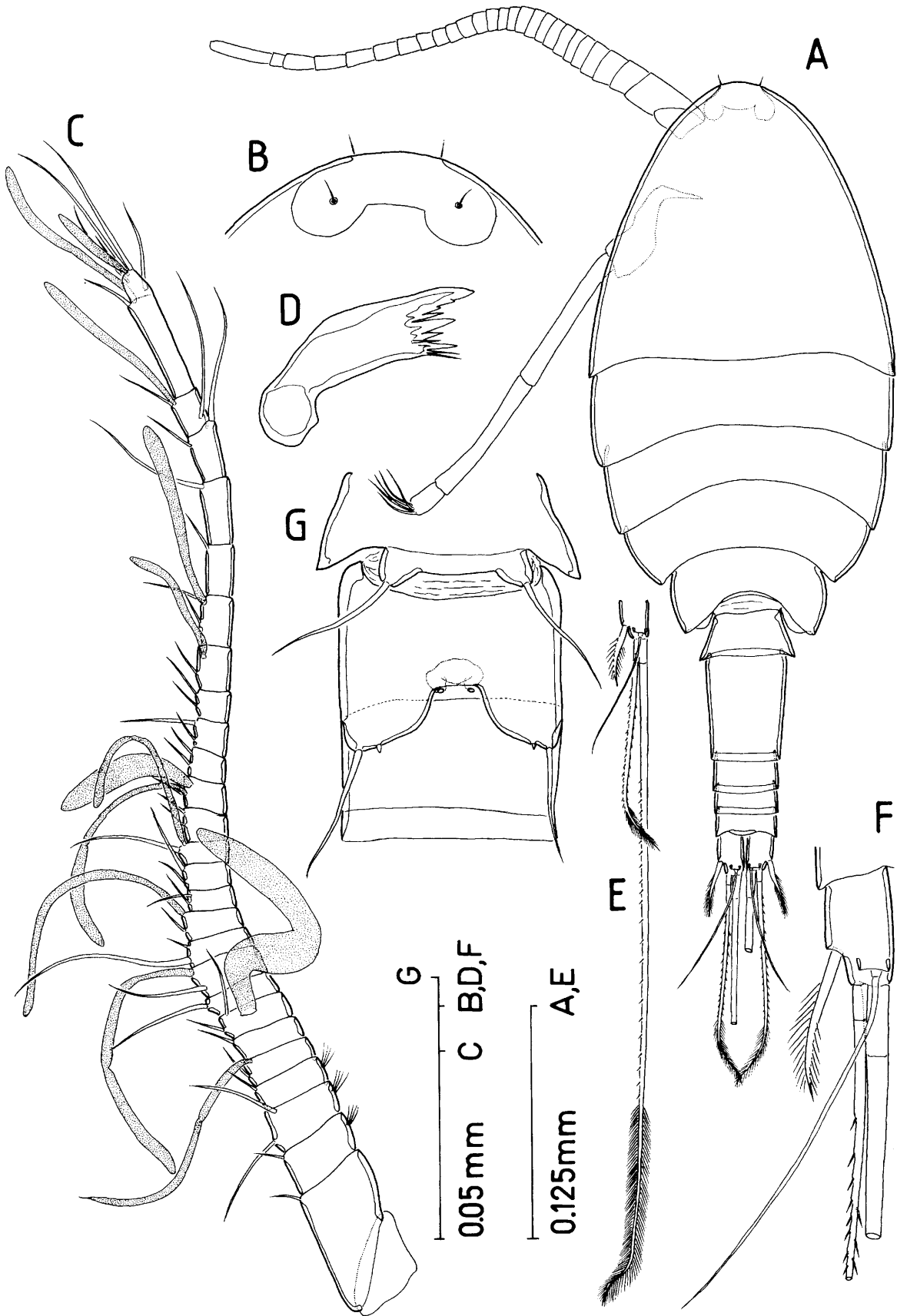
Diagnosis: Body cycloform (Fig. 4A); prosome comprising cephalosome and 4 free pedigerous somites; first pedigerous somite free, not covered by carapace-like extension. Urosome indistinctly 5-segmented in female due to partial fusion of genital and first abdominal somites to form genital double-somite; 3 free abdominal somites in female. Prosome-urosome articulation between fourth and fifth pedigerous somites (podoplean position). Genital apertures paired, located ventrally in anterior third of genital double-somite in female (Fig. 4G). Seminal receptacles fused. Paired copulatory pores located medially, adjacent to genital apertures. Caudal rami with 4 setae (Fig. 4E, F).

Rostrum bilobed (Fig. 4B). Nauplius eye absent. Antennules 26-segmented in female (Fig. 4C); apical segment triple, representing ancestral segments XXVI to XXVIII. Aesthetascs present on segments V, VII, IX, XI, XIV, XVI, XX, XXI, XXV, (XXVI and XXVIII).

Antenna biramous with indistinctly 7-segmented exopod and 2-segmented endopod (Fig. 5A); coxa and basis unarmed; proximal endopodal segment unarmed, distal with 2 medial and 7 apical setae; first exopodal segment derived from fused ancestral segments I and II, second to sixth representing ancestral segments III to VII, seventh representing ancestral segments VIII–X; setal formula 0, 1, 1, 1, 1, 1, 4. Labrum an undivided muscular lobe. Mandible with coxal gnathobase (Fig. 4D) and elongate uniramous palp due to loss of exopod. Paragnaths lobate.

Maxillule (Fig. 5B) with large praecoxal endite bearing 15 elements; coxa with single endite bearing 3 setae; vestigial epipodite incorporated into segment and represented by 2 setae; basis lacking seta representing exite on outer margin; proximal basal endite well developed with 3 setae; distal endite not defined; exopod 1-segmented with 1 seta; endopod distinctly 2-segmented; setal formula 2, 6.

Maxilla indistinctly 5-segmented (Fig. 5C); syncoxa with 3 endites, formula 3, 3, 2; allobasis with well developed proximal (basal) endite forming claw bearing 2 setae (1 stout seta plus a tiny seta derived from incorporated first endopodal segment); free endopod 3-seg-



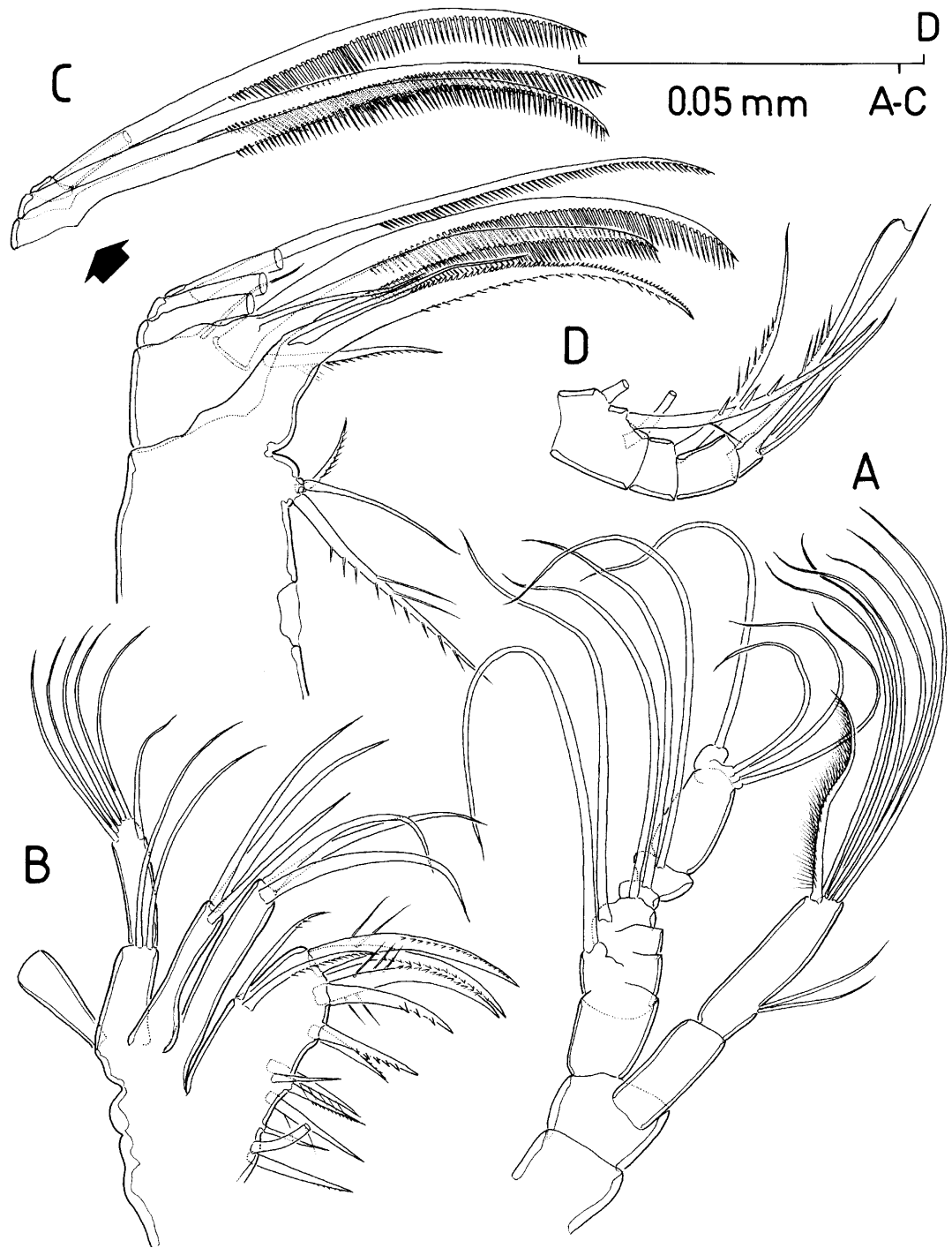


Fig. 5. *Palpophria aestheta* Boxshall & Iliffe, adult female. A, right antenna, medial; B, maxillule (armature of basal epipodite and exopod unresolved); C, maxilla (proximal endite on syncoxa missing); D, detail of maxilliped endopod.

Fig. 4. *Palpophria aestheta* Boxshall & Iliffe, adult female. A, body, dorsal (notice extreme elongation of mandibular palp); B, rostrum, ventral; C, left antennule, ventral; D, cutting edge of mandibular gnathobase; E, detail of relative lengths of caudal ramus setae; F, left caudal ramus, dorsal; G, fifth pedigerous somite with fifth legs and genital double-somite, ventral.

mented, setal formula 1, 1, 3. Maxilliped 6-segmented, comprising syncoxa, basis and 4-segmented endopod; syncoxa with 4 distally located setae; basis with 3 setae; endopodal setal formula 3, 1, 1, 3 (Fig. 5D).

Swimming legs 1 to 4 biramous, typically with 3-segmented rami except endopod 2-segmented in leg 1; members of each leg pair joined by intercoxal sclerite; inner coxal seta and outer seta on basis present, inner seta on basis of first leg only. Spine and seta formula for legs 1 to 4 as follows:

	coxa	basis	exopodal segments	endopodal segments
leg 1	0-1	1-I	I-1; I-1; III,I,4	0-1; 1,2,5
leg 2	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,2,3
leg 3	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,2,3
leg 4	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 0,2,2

Fifth leg reduced to lobe armed with single seta (Fig. 4G). Sixth legs confluent in female, armed with seta plus tiny spine.

Type-genus: *Palpophria* Boxshall & Iliffe, 1987

Included genera:

Palpophria Boxshall & Iliffe, 1987

Remarks

This family is most readily characterised by the unique state of the mandible. The elongate, uniramous mandibular palp (Fig. 4A) is one of the most unusual found in the entire Copepoda. There are numerous other important characters. The first leg has a 2-segmented endopod but it retains all eight of the setae that are primitively present in genera with a 3-segmented endopod, for example *Misophriopsis*. This unique state is reflected in the PAUP analysis which indicates that the 2-segmented endopod appears independently on at least three occasions: in the Palpophriidae and in *Speleophriopsis* and the *Protospeleophria/Speleophria/Huysia*-group within the Speleophriidae.

Examination of a new specimen of *Palpophria aestheta* Boxshall & Iliffe, 1987 (BMNH Reg.No. 1988.205) revealed several inaccuracies in the original description. In particular the antennule bears an aesthetasc on segment V and another on the very apex (derived from segment XXVIII) that were previously overlooked, and because a segmental boundary was overlooked the aesthetascs shown on segments 8, 10, 13, 15, 19, 20 and 25 should have been attributed to segments IX, XI, XIV, XVI, XX, XXI and XXVI, respectively (Fig. 4C). The antennary exopod is indistinctly 7-segmented with a setal formula of 0, 1, 1, 1, 1, 1, 4 (Fig. 6A), rather than 6-segmented. There is an additional seta on the prae-

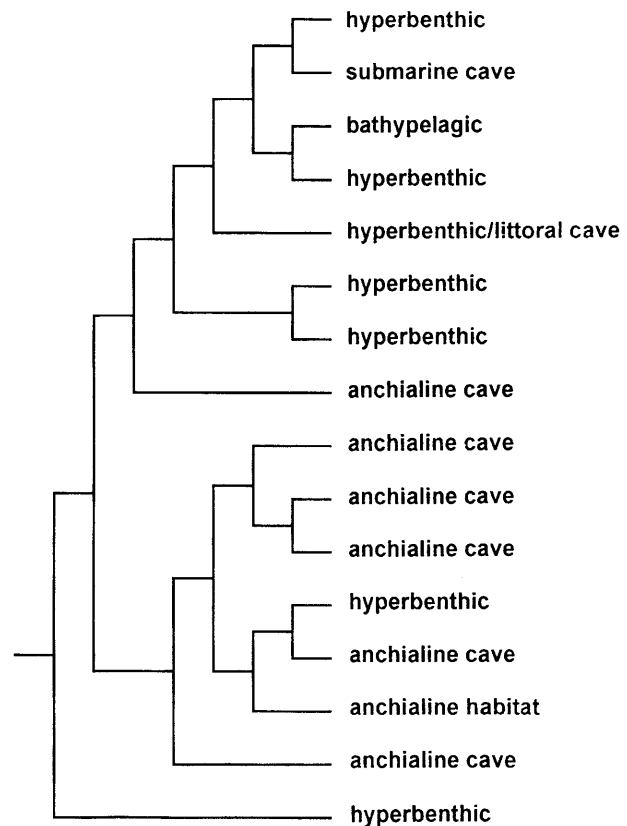


Fig. 6. Habitat cladogram indicating major shifts in habitat utilization in the Misophrioida.

coxal arthrite of the maxillule, 1 less on the coxal endite, and the endopodal formula is 2, 6 rather than 0, 5 (Fig. 5B). The maxilla is indistinctly 5-segmented due to the presence of three rather than two free endopodal segments (Fig. 5C), armed with 1, 1, 2 not 1, 3 as given by BOXSHALL & ILIFFE (1987), and the distal syncoxal endite carries only 2 setae. The apical segment of the maxillipedal endopod carries 3 setae (Fig. 5D), not 2 as originally given. The armature of the sixth legs comprises a seta plus a tiny spine (Fig. 4G).

Family Speleophriidae fam. nov.

Diagnosis: Body cycloform; prosome comprising cephalosome and 4 free pedigerous somites. First pedigerous somite free, carapace-like extension of posterior margin of cephalosome typically absent, present and covering first pedigerous somite only in *Archimiso-phria*. Urosome 6-segmented in male, indistinctly 5-segmented in female due to partial fusion of genital and first abdominal somites to form genital double-somite; 4 free abdominal somites in male, 3 in female. Prosome-urosome articulation between fourth and fifth

pedigerous somites (podoplean position). Genital apertures paired in both sexes, located ventrally at posterior border of genital somite in male, in anterior third of genital double-somite in female; or with single common pore in female. Seminal receptacles fused. Copulatory pores paired.

Rostrum defined at base, variable in size. Caudal rami with 7 setae or with seta I lacking. Nauplius eye absent. Antennules 26 to 27-segmented in female; apical segment double, comprising fused ancestral segments XXVII and XXVIII. Antennules 23 to 27-segmented in male, bilaterally symmetrical, geniculate between segments homologous with XX and XXI of the female; sometimes with segments XIX and XX fused proximal to geniculation and XXI and XXII fused distal to geniculation but apparently without fusion of segments either side of geniculation in *Speleophriopsis* and *Huysia*. Male antennule with sheath on segment XV partly enclosing segment XVI; sheath secondarily absent in genera such as *Archimisophria*.

Antenna biramous with 6 to 8-segmented exopod and 3-segmented endopod; coxa unarmed, basis with 1 or 2 inner setae, first to third endopodal segments with 2, 5 and 7+2 setae respectively: first exopodal segment derived from fused ancestral segments I and II; second to seventh typically representing ancestral segments III to VIII, segment 8 typically representing fused ancestral segments IX–X; segment X partly defined only in *Huysia*; additional fusions present in some genera; maximum setal formula 1, 1, 1, 1, 1, 1, 1, 4: antennal setation often further reduced. Labrum an undivided muscular lobe.

Mandible with large coxal gnathobase and biramous palp; exopod 5-segmented, setal formula 1, 1, 1, 1, 2; endopod 2-segmented, setal formula 4, 8 or reduced; basis bearing 0 to 3 setae on inner margin. Paragnaths separate.

Maxillule with large praecoxal endite bearing about 15 elements; coxa with single endite bearing up to 6 setae, and vestigial epipodite incorporated into segment, represented by up to 8 setae; basis with 1 seta on outer margin in *Speleophriopsis* and *Speleophria* representing exite, seta usually lacking; 2 widely separated basal endites present, proximal endite well developed, with up to 4 setae; distal endite largely incorporated into segment, represented by up to 4 setae; exopod 1-segmented with maximum of 11 setae, endopod with 2 free segments, proximal segment representing double segment; setal formula (3, 3), 6: maxillary setation often reduced.

Maxilla 6-segmented; praecoxa and coxa each with 2 endites, endite formula 4/7, 3, 3, 3; allobasis with well developed proximal (basal) endite forming a claw bearing up to 4 setae, distal (endopodal) endite vestigial, represented by 2 or 3 setae; outer coxal seta absent; free

endopod 3-segmented, setal formula 2, 2, 4; setation of maxilla often reduced.

Maxilliped 9-segmented, comprising praecoxa with 1 endite, coxa with 3 endites, basis and 6-segmented endopod, with proximal endopodal segment free or incompletely fused to basis; praecoxal and coxal endite formula 1, 2, 4, 3, or reduced; praecoxal seta often lacking; basis with 2 or 3 setae; endopodal setal formula 2, 3, 3, 2, 2+1, 5; ancestral first endopodal segment not differentiated in *Archimisophria*, (free endopod 5-segmented); maxillipedal setation often reduced.

Swimming legs 1 to 4 biramous, typically with 3-segmented rami except endopod of leg 1 often 2-segmented due to failure of second and third segments to separate; members of each leg pair joined by intercoxal sclerite; inner coxal seta and outer seta on basis present, inner seta on basis of first leg only. Maximum spine and seta formula for legs 1 to 5 as follows:

	coxa	basis	exopodal segments	endopodal segments
leg 1	0-1	1-I	I-1; I-1; III,I,4	0-1; 0-2; 1,2,3
leg 2	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,2,3
leg 3	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,2,3
leg 4	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,2,2
leg 5 (f)	0-0	1-0	I-0; (I-1; II,I+1,0)	1
leg 5 (m)	0-0	1-0	I-0; (I-1; II,I+1,1)	1

Setation often reduced or modified by transformation of setae into spines.

Fifth legs primitively biramous; members of leg pair joined by intercoxal sclerite; praecoxa usually absent; coxa and basis separate or fused; basis with outer seta; inner coxal seta absent; exopod typically 2-segmented and bearing up to 7 setal elements in female; 2 or 3-segmented and with up to 8 setae in male; endopod 1-segmented and bearing 1 seta in both sexes, or reduced to single seta as in *Boxshallia*. Fifth legs usually uniramous due to loss of endopod; entire fifth leg absent in *Expansophria apoda* Boxshall & Iliffe, 1987. Sixth legs confluent in female, separate in male, represented by opercular plate closing off genital openings.

Type-genus: *Speleophria* Boxshall & Iliffe 1986

Included genera:

Archimisophria Boxshall, 1983

Boxshallia Huys, 1988

Expansophria Boxshall & Iliffe, 1987

Huysia Jaume, Boxshall & Iliffe, 1998

Protospeleophria Jaume, Boxshall & Iliffe, 1998

Speleophria Boxshall & Iliffe 1986

Speleophriopsis Jaume & Boxshall, 1996

(*Dimisophria* Boxshall & Iliffe, 1987)

Remarks

This new family corresponds to the *Archimisophria*-group identified by BOXSHALL (1989) enlarged by the addition of genera described since 1989, but with *Palpophria* excluded. The above diagnosis does not take into account the characters of *Dimisophria*, which is only tentatively included in this family. Its position must be reassessed after the discovery of new material.

The new family is diagnosed by shared apomorphies relating to loss of aesthetascs from the antennules of both sexes, loss of at least the proximal seta from the inner margin of the second endopodal segment of leg 1, and by loss of the subapical seta from the endopod of the fifth legs. All of these synapomorphies are losses of setation elements. There are several diagnostic plesiomorphies including the retention of a seta on each of the second and eighth ancestral segments of the antennary exopod. Many other plesiomorphic states are exhibited by members of this new family, although not by all. Such plesiomorphies include the retention of the praecoxal seta, the inner seta on the first endopodal and outer seta on the fifth endopodal segment of the maxilliped, the retention of the outer spine on the second exopodal segment of the female fifth leg, and the retention of the seta representing the exite on the maxillulary basis.

Archimisophria fits least well into this family. It shares important apomorphies with members of the family Misophriidae, including the failure of expression of the ancestral first endopodal segment on the maxilliped and the loss of the outer seta from the penultimate segment of this endopod. The topology of Figure 3 indicates these are convergent states. It is also the only speleophriid with a fully developed carapace-like extension of the cephalic shield enclosing the first pedigerous somite. Even though the relationships between *Archimisophria*, *Expansophria* and *Boxshallia* are well supported (bootstrap values = 89), it is possible that, as our knowledge of misophrioid taxa increases, the position of *Archimisophria* might change from that suggested in the working hypothesis presented in Figure 3,

3. HABITAT UTILIZATION

Substituting habitat types for names of genera in Figure 3 provides a simple indication of the main trends in habitat use in the Misophrioida (Fig. 6). The family Misophriidae emend. is a hyperbenthic group, with most of its 12 species occurring in the hyperbenthos over a wide range of depths. The genus *Misophriopsis*, for example, contains species known from deep oceanic (3000 m) and from shallow (8–9 m) coastal waters (BOXSHALL 1983, 1990). A new species of *Misophriop-*

sis has now been discovered from Cova de na Mitjana on Mallorca and is currently being described (JAUME, pers. comm. 1999). The discovery of the new species suggests a direct route by which coastal cave habitats can be colonized from the shallow hyperbenthic. Cova de na Mitjana is not a true anchialine cave. The cave lake is extremely closely linked with the nearby coastal water as indicated by the detectable wave action within the cave. The wave action ensures mixing in the cave lake so the water column is not stratified (with an overlying freshwater lens and deeper poorly oxygenated layers), as in typical anchialine caves. In these respects Cova de na Mitjana fits the definition of a littoral cave - a coastal marine cave opening below sea level, containing air plus sea water but lacking terrestrial influence. This classification is supported by the presence in the cave lake of a typical benthic marine fauna including ophiuroids, the eyed shrimp *Palaemon serratus* (Pennant), and a conger eel *Conger conger* (Linnaeus, 1758). The presence of *Misophriopsis* in such a cave is unremarkable since it can be viewed as a mere landward extension from its normal hyperbenthic habitat.

A similar route might be hypothesised to explain the presence of *Stygomisophria kororiensis* (BOXSHALL & ILIFFE 1987), the sister taxon of the shallow water hyperbenthic genus *Misophria* (Fig. 3), in South Point Cave, on the island of Koror, Palau. South Point is a submarine cave (a void completely filled with seawater) in close contact with the coastal waters, as evidenced by the detectable tidal current, the full or near full salinity and the range of associated fauna which includes sponges, hydroids, polychaetes, crustaceans and fishes (BOXSHALL & ILIFFE 1989). The occurrences of *S. kororiensis* and the new *Misophriopsis* species in coastal marine caves of the littoral and submarine types are the result of independent colonization events (Fig. 6). These two types of marine caves can be viewed as ecotones, transitional zones between the open sea and true anchialine systems, which have a marked terrestrial influence particularly in the form of fresh water input. Misophriids have colonized these ecotones but have not successfully penetrated anchialine systems.

The presence of members of the Misophriidae in such coastal marine caves is an indication of one possible origin of anchialine copepod faunas - by direct range extension from the shallow water hyperbenthos. A similar but vertical, rather than landward, range extension has occurred within the family in the case of *Benthomisophria*. The two species of this genus are distributed in oceanic waters from depths of 2000 to 4000 m but the greatest concentrations were found in the hyperbenthic zone just above the sea bed (BOXSHALL & ROE 1980). These species are still associated with the hyperbenthos but exploit a greater part of the bathypelagic water column above it.

The single species of the Palpophriidae occurs in Jameos del Agua, the classic anchialine system on Lanzarote (BOXSHALL & ILIFFE 1987). Its startling suite of autapomorphies suggests that it represents an ancient and distinct lineage. The sister group of the Misophriidae-Palpophriidae clade is the Speleophriidae (Fig. 3), which comprises primarily specialised anchialine taxa. These relationships could be interpreted as evidence that the presence of *Palpophria* in the anchialine Jameos del Agua represents the retention of an ancestral habitat association and that the divergence of the Misophriidae was linked to its colonization and to exploitation of the hyperbenthic. However, we prefer the less parsimonious alternative, that the presence of the Palpophriidae in anchialine habitats results from an independent colonization, distinct from that of the Speleophriidae.

The members of the family Speleophriidae are almost exclusively known from anchialine habitats. The only exception is *Archimiosophria*, the two species of which inhabit the hyperbenthic community in the deep Atlantic Ocean (BOXSHALL 1983; ALVAREZ 1985). The nearest relatives of *Archimiosophria* therefore occur in anchialine habitats, as also indicated by the earlier analysis (BOXSHALL 1989), however, the topology of the new cladogram (Fig. 3) suggests that the deep-water genus *Archimiosophria* descended from ancestors inhabiting anchialine systems in shallow water, rather than vice versa. This would appear to support the contention (STOCK 1986) that a deep-water origin for such anchialine cave taxa is unlikely.

HUYS & BOXSHALL (1991) in their review of copepod evolutionary history commented that each of the ten recognised orders of copepods had its origins in the marine benthic/hyperbenthic zone. At some point the ancestral stock of the Speleophriidae, or of the entire Misophrioida, must have colonized the anchialine regime and undergone evolutionary diversification while remaining primarily associated with this extremely specialized habitat type. This ancestral colonization is the key event in the history of the Speleophriidae and we view it as both more ancient and qualitatively different from the repeated colonization of littoral and submarine caves exhibited by the Misophriidae, because it requires a greater degree of adaptation to the more extreme hydrographic conditions and the oligotrophic nature of anchialine systems.

4. BIOGEOGRAPHY

The hypothesis that the Speleophriidae has been associated with anchialine habitats since its origin does not immediately help to explain the biogeography of this family. Indeed, the biogeography of this remarkable

group remains difficult to understand. The more speciose speleophriid genera are characterised by their extreme disjunct distributions. The species of *Speleophriopsis* occur on both sides of the Atlantic (Lanzarote and Bermuda), in the Mediterranean (Balearic Islands), the western Pacific (Palau) and Mexico (the Yucatán). Species of *Expansophria* occur in the Atlantic (Lanzarote), western and eastern Pacific (Palau and the Galapagos Islands) and the Mediterranean (Sardinia). Species of *Speleophria* are found in Bermuda and the Mediterranean (Balearic Islands). All other speleophriid genera are currently monotypic. Speleophriids have only ever been found in anchialine habitats and traits of their biology suggest that their dispersal abilities to cross open waters are limited (JAUME & BOXSHALL 1996b). JAUME & BOXSHALL (1996b) inferred that these modern distribution patterns are most likely the result of vicariance events, in particular of the major tectonic events of the opening of the Atlantic (*ca.* 120 Myr BP) and the closure of the Tethys Sea (*ca.* 20 Myr BP). This is essentially the same explanation as outlined by STOCK (1993) for the disjunct distributions of a wide range of stygobiont malacostracans with similarly limited dispersal abilities.

One implication of this "Tethyan track" explanation is that these elements of the anchialine fauna have remained continuously associated with anchialine habitats through these tectonic events and over extended periods of geological time. The main expansion and dispersal of genera such as *Expansophria* and *Speleophriopsis* must have taken place prior to the tectonic events. Modern distributions presumably result from the subsequent fragmentation of ranges and allopatric speciation from ancestral generic stocks that were widely distributed in suitable habitats around the late Mesozoic palaeocoastline of the Tethys Sea. The lack of divergence at the generic level of such widely separated species is remarkable, although as STERRER (1973) indicated, the separation of populations by tectonic movements would not necessarily disrupt or change subterranean habitats, and thus there might be less selective pressure for change.

The key factor now becomes one of persistence since this explanation of spatial discontinuity demands a high degree of temporal continuity. Is it feasible that these speleophriids and their ancestors survived over millions of years in anchialine habitats that were locally subject to profound change in the form of volcanic activity (e.g. Lanzarote, Canary Islands), or the total desiccation of the surrounding sea (e.g. Mallorca, Balearic Islands)? In the absence of data suggesting that speleophriids can survive in open marine waters or in fresh waters, we suggest that it is feasible.

One difficulty with postulating continuity on geological time scales is the apparent transience of particular an-

chialine systems. Some anchialine sites are only recently formed. Using Lanzarote as an example, the first submarine lava flows in the region occupied today by the island commenced about 40 Myr BP and the first subaerial flows about 15.5 Myr BP (ARAÑA & CARRACEDO 1979; COELLO et al. 1992). The Jameos del Agua system is inhabited by five endemic species of speleophriid (BOXSHALL & ILIFFE 1987; JAUME & BOXSHALL 1996a) but was formed by flooding of a lava tube created during an eruption of Volcán de la Corona only 7,000 yr BP (BRAVO 1964). This same lava tube is inhabited by *Speleonectes ondinae* (VALDECASAS 1984), the sister species of which occurs on the Bahamas, on the other side of the Atlantic. Finally, on an even shorter time scale, the small lava pool on Lanzarote inhabited by the speleophriid *Boxshallia* was formed by a lava flow only 200 to 300 yr BP.

The short term colonizations are relatively easy to understand. Evidence from the fauna found in wells and caves around the periphery of Lanzarote indicated that the island's margins are permeated by partly interconnected crevicular habitats on various scales, inhabited by an anchialine stygofauna (WILKENS et al. 1986; BOXSHALL 1989; WILKENS et al. 1993). Newly available habitats could be colonized from elsewhere in this crevicular network. Anchialine regions such as the Canary Islands should be regarded as dynamic complexes of interconnected habitats, the topology of which can change through time. Persistence over timescales of up to 40 Myr is more difficult to explain, although Lanzarote and Fuerteventura may have been continuously or periodically connected by land bridges or shallow water straits with Africa between the late Cretaceous and the Mio-Pliocene (ROTHE & SCHMINKE 1969).

The presence of thalassostygobiontic anchialine faunal elements in the Mediterranean is a special problem because of the so-called Messinian Salinity Crisis, according to which the Mediterranean Sea was dry only 5.5 Myr BP (HSÜ et al. 1973). This is well after the closure of the Tethys Sea (ca. 20 Myr BP) and implies that any anchialine habitats within the Basin would have dried out, causing the extinction of the specialised anchialine fauna. This would contradict the conclusion that the main dispersal of speleophriids into anchialine caves occurred prior to the closure of the Tethys Sea. However, an alternative geochemical interpretation was presented by SONNENFELD (1985) and SONNENFELD & FINETTI (1985) who postulated that the deposition of salts on the floor of the Mediterranean was possible without resorting to a model of total desiccation. It is possible that anchialine habitats with near marine salinities were continuously available within the Mediterranean Basin from Tethyan to recent times, and that these would have served as refuges during the Quaternary glaciations (JAUME & BOXSHALL 1996b).

5. CONSERVATION ISSUES

Despite their specializations misophrioids represent an ancient lineage which separated early from the main copepodan line. They are the podoplean copepod equivalent of "living fossils". Members of the new family Speleophriidae are especially vulnerable to anthropogenic change because all known species occur in only a single cave or cave system. If the cave system undergoes rapid change or becomes polluted these animals simply have nowhere else to go. Some anchialine sites are protected. Jameos del Agua on Lanzarote, for example, is protected as a nature reserve, although it is open to the public for underground music concerts in the natural auditorium. However, the impact of anthropogenic change should be investigated thoroughly if we are to enhance their prospects for survival. Quarrying for limestone has destroyed at least one anchialine cave on Formentera in the Balearics. Even opening caves to the public may create additional problems with artificial lighting stimulating algal growth, disrupting the ecosystem on which these invertebrates depend.

This analysis demonstrates that the basic division of the order Misophrioida into two lineages (BOXSHALL 1989) is relatively robust although a different set of relationships is suggested for *Palpophria* in the current analysis. The differences between the phylogenetic analysis performed by BOXSHALL (1989) and this one are remarkable. Some of these differences are undoubtedly due to the much larger character set and to the new interpretations of characters, in particular to the treatment of compound segments as indicative of the failure of expression of individual segmental articulations. However, the differences also demonstrate that newly discovered anchialine copepod taxa are continuing to generate insight into the complex evolutionary history of this group of crustaceans. In this context, it is highly significant that eight out of the 44 (18%) new families of Copepoda established since 1980 have also been based on newly discovered taxa from anchialine caves. The presence of such a high proportion of novel taxa should heighten awareness of the importance of anchialine habitats as refuges for ancient and phylogenetically-distinct lineages of copepods, and the special conservation needs of these fragile habitats.

6. DISCUSSION

A diverse suite of marine taxa including remipedes, speleophriid misophrioid copepods, epacteriscid calanoid copepods, thermosbaenaceans, pardaliscid amphipods and thaumatocyprid ostracods exhibits similarly extreme, disjunct distribution patterns – with foci at locations including the Canaries, Bermuda, the Gala-

pagos, the Bahamas, Belize, the Balearics, the Yucatán, the Turks & Caicos and northwestern Australia. The presence of some members of this faunal suite has been used as an indication that other members should also be present. WAGNER (1994: 322), for example, in discussing the distribution of the Thermosbaenacea, predicted that remipedes and the ostracod *Danielopolina* Kornicker & Sohn, 1976 would be found in northwestern Australia after the discovery there of *Halosbaena* Stock, 1976 by POORE & HUMPHREYS (1992). The search for unitary explanations of such distribution patterns is, therefore, not surprising.

A deep-sea origin for anchialine cave faunas has been postulated for certain taxa within the Crustacea (FUCHS 1912; HART et al. 1985; KORNICKER & ILIFFE 1985; BOXSHALL 1989). The presence of *Munidopsis polymorpha* Koelbel, 1892, a representative of the mainly deep-sea family Galatheidae, in Jameos del Agua on Lanzarote and in an anchialine cave on El Hierro (P. OROMI, pers. comm.) has been interpreted as evidence of a deep-sea colonization route. A deep-sea link could also be suggested for the Mictacea, which comprises one species in an anchialine cave of Bermuda, and deep-sea species from the western Atlantic and Australia. Deep-sea origins have been postulated to explain the occurrence of the pardaliscid amphipod *Spelaeonicippe* in anchialine caves on both sides of the Atlantic (but see STOCK & VERMEULEN 1982). The deep-sea species *Danielopolina carolynae* was interpreted as plesiomorphic relative to the anchialine species (BOXSHALL 1989) but the recent discovery of a more plesiomorphic form from an anchialine habitat in northwestern Australia allowed BALTANAS & DANIELOPOL (1995) and DANIELOPOL et al. (in press) to challenge this interpretation. Even from the Misophrioida there is now little support for a deep-sea origin. So, although the hypothetical deep-sea origin might be appropriate for the galatheid *Munidopsis polymorpha*, it appears to have very limited application to other anchialine taxa.

The strongest alternative to a deep-sea origin is that suggested by the clear Tethyan distributions exhibited by anchialine taxa that never penetrate into the fresher parts of the cave systems. These taxa include the speleophriid misophrioids, the thermosbaenacean *Halosbaena* Stock, 1976 (known from the Caribbean, the Canary Islands and northwestern Australia (WAGNER 1994)), and the remipede genera *Lasionectes* Yager & Schram, 1986 (the Turks & Caicos Islands and northwestern Australia), and *Speleonectes* Yager, 1981 (both sides of the Atlantic). Similarly, species of the ostracod *Danielopolina* are known from the Galápagos Islands, the Caribbean, the Canary Islands, (the South Atlantic – in deep water) and northwestern Australia (BALTANAS & DANIELOPOL 1995). These distribution patterns support the concept of a Tethyan fauna, interpreted as re-

licts of the once widespread, warm-water fauna of the Tethys Sea. (YEATES et al. (1987) and POORE & HUMPHREYS (1992) presented geological and faunistic evidence, respectively, that northwestern Australia should be considered as a remnant of the eastern Tethys belt.) This fauna is regarded as having penetrated anchialine habitats from shallow-water benthic/hyperbenthic origins and may have shown the pre-adaptations referred to by DANIELOPOL, BALTANAS & BONADUCE (1996) as 'the darkness syndrome'.

The Tethyan hypothesis has gained recognition as having the best explanatory power in the study of anchialine faunal distribution patterns. The invasion route into anchialine systems taken in Tethyan times by the ancestors of the Speleophriidae is likely to have been via littoral and submarine caves, directly by range extension from the shallow-water hyperbenthos. The presence of misophriids in modern littoral caves indicates that they can still exploit the same invasion route. The timing of colonization events is thus an important factor since it is probable that some elements of the modern anchialine fauna may have originated in relatively recent, post-Tethyan invasions. The modern anchialine fauna may be a composite of taxa with varying origins and built up over several episodes of colonization, but it appears to exhibit a dominant Tethyan facies.

We interpret copepod families such as the Stephidae and Pseudocyclopiidae, and genera such as *Paramisophria* T. Scott, 1897 within the Arietellidae, as post-Tethyan colonizers. Such taxa are predominantly found in shallow hyperbenthic habitats but occur in marine littoral caves and even in fully anchialine caves. The presence of morphologically indistinguishable populations of a single species, e.g. *Stygocyclopia balearica* Jaume & Boxshall, 1995, in the Balearics and in the Canary Islands (JAUME et al., in press) suggests either that such species can occur outside of the anchialine environment and thus maintain gene flow, or that they are only recent (post-Tethyan) colonists and have yet to diverge morphologically.

As discussed above for the speleophriids, the remaining problem for the Tethyan hypothesis is explaining persistence over long time scales. One factor contributing to the long term persistence of Tethyan relicts in anchialine caves is that sufficiently high water temperatures may have been maintained in some caves to ensure survival during Pleistocene glaciations. JAUME & MARTINEZ (unpublished data) found that in Cova des Burri on Cabrera (the Balearic Islands) the cave lake is permanently stratified with an upper 1.5 m layer of brackish waters (around 15‰) overlying practically marine waters (29–33‰) from 1.5 m to the bottom. Water temperature below the pycnocline is around 17 °C all year round – some 4 °C warmer than the surrounding winter open sea temperature. The superficial

waters are inhabited by taxa which, on Mallorca, penetrate far inland, such as the amphipods *Bogidiella balearica* Dancau, 1973 and *Salentinella angelieri* Ruffo & Delamare, 1952, whereas the waters below the pycnocline are inhabited by strictly marine water stygobionts such as the monotypic *Burrinymysis palmeri* Jaume & García, 1993, the cirrolanid *Metacirrolana ponsi* Jaume & García, 1992 and the fully-tethyan amphipod *Psammogammarus burri* Jaume & García, 1992. According to the geological record, the lowest water temperature postulated for the coldest Pleistocene glaciation is about 7.5 °C (THIEDE 1978; MATEU 1982), i.e. about 5.5 °C lower than the present winter temperature. If the deep water in caves were a constant 4°C warmer than the minimum winter open sea temperature even during the glaciated periods, this indicates that the temperature deep in Mallorcan anchialine caves may have been about 11.5 °C during the coldest glaciation 18000 yr BP. This may have been sufficient to allow the cave to serve as a thermal refuge.

This scenario is similar to that proposed by ILIFFE, HART & MANNING (1983), and MANNING, HART & ILIFFE (1986) to explain the persistence of Bermudian cave fauna during the Pleistocene glaciations, although they also implicated geothermal heating. Even though inshore surface water temperatures around Bermuda may fluctuate between 15 °C in winter to more than 30 °C in summer, at depths below 3 m within the caves, water temperature remains at a relatively constant 20.5 °C all year (ILIFFE et al. 1983). This suggested the possibility of geothermal heating to ILIFFE et al. (1983). If the deeper waters of the caves remained at relatively higher temperatures during the Pleistocene glacial periods, the caves could have served as warm thermal refuges through periods of reduced sea temperature.

Given the varying geological origins of anchialine systems and their distribution across volcanic and karstic regions of different geological age, it is not surprising that no single hypothesis can be advanced to explain how all these anchialine faunas could have persisted over extremely long periods of time. Special case scenarios may be required to account for problematic distributions, such as the presence of Tethyan relicts in caves within the Mediterranean Basin. It may be necessary to generate more, each appropriate for a particular region and its special geological setting and history. Such scenarios may be viewed as competitive and can be tested repeatedly as new sites and faunas are discovered.

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Appendix 1. Characters used in analysis.

Female antennule

- | | |
|-----------------------------------------------|-----------------------------------------------------|
| 1. Articulation between segments I–II: | expressed in adult = 0 / not expressed in adult = 1 |
| 2. Articulation between segments II–III: | expressed in adult = 0 / not expressed in adult = 1 |
| 3. Articulation between segments III–IV: | expressed in adult = 0 / not expressed in adult = 1 |
| 4. Articulation between segments IV–V: | expressed in adult = 0 / not expressed in adult = 1 |
| 5. Articulation between segments V–VI: | expressed in adult = 0 / not expressed in adult = 1 |
| 6. Articulation between segments VI–VII: | expressed in adult = 0 / not expressed in adult = 1 |
| 7. Articulation between segments IX–X: | expressed in adult = 0 / not expressed in adult = 1 |
| 8. Articulation between segments X–XI: | expressed in adult = 0 / not expressed in adult = 1 |
| 9. Articulation between segments XI–XII: | expressed in adult = 0 / not expressed in adult = 1 |
| 10. Articulation between segments XXVI–XXVII: | expressed in adult = 0 / not expressed in adult = 1 |
| 11. Proximal segment (I): | non-inflated dorsally = 0 / inflated = 1 |
| 12. Aesthetasc on antennular segment III: | present = 0 / absent = 1 |
| 13. Aesthetasc on antennular segment VII: | present = 0 / absent = 1 |
| 14. Aesthetasc on antennular segment XI: | present = 0 / absent = 1 |
| 15. Aesthetasc on antennular segment XIV: | present = 0 / absent = 1 |
| 16. Aesthetasc on antennular segment XVIII: | present = 0 / absent = 1 |
| 17. Aesthetasc on antennular segment XX: | present = 0 / absent = 1 |
| 18. Aesthetasc on antennular segment XXI: | present = 0 / absent = 1 |
| 19. Aesthetasc on antennular segment XXVI: | present = 0 / absent = 1 |

Male antennule

- | | |
|-----------------------------------------------|-----------------------------------------------------|
| 20. Articulation between segments II–III: | expressed in adult = 0 / not expressed in adult = 1 |
| 21. Articulation between segments III–IV: | expressed in adult = 0 / not expressed in adult = 1 |
| 22. Articulation between segments IV–V: | expressed in adult = 0 / not expressed in adult = 1 |
| 23. Articulation between segments V–VI: | expressed in adult = 0 / not expressed in adult = 1 |
| 24. Articulation between segments IX–X: | expressed in adult = 0 / not expressed in adult = 1 |
| 25. Articulation between segments X–XI: | expressed in adult = 0 / not expressed in adult = 1 |
| 26. Articulation between segments XI–XII: | expressed in adult = 0 / not expressed in adult = 1 |
| 27. Articulation between segments XII–XIII: | expressed in adult = 0 / not expressed in adult = 1 |
| 28. Articulation between segments XV–XVI: | expressed in adult = 0 / not expressed in adult = 1 |
| 29. Articulation between segments XIX–XX: | expressed in adult = 0 / not expressed in adult = 1 |
| 30. Articulation between segments XXI–XXII: | expressed in adult = 0 / not expressed in adult = 1 |
| 31. Articulation between segments XXII–XXIII: | expressed in adult = 0 / not expressed in adult = 1 |
| 32. Articulation between segments XXIV–XXV: | expressed in adult = 0 / not expressed in adult = 1 |
| 33. Articulation between segments XXV–XXVI: | expressed in adult = 0 / not expressed in adult = 1 |
| 34. Articulation between segments XXVI–XXVII: | expressed in adult = 0 / not expressed in adult = 1 |
| 35. Sheath on segment XV: | present = 0 / absent = 1 |
| 36. Aesthetasc on antennular segment V: | present = 0 / absent = 1 |
| 37. Aesthetasc on antennular segment IX: | present = 0 / absent = 1 |
| 38. Aesthetasc on antennular segment XIV: | present = 0 / absent = 1 |
| 39. Aesthetasc on antennular segment XVIII: | present = 0 / absent = 1 |
| 40. Aesthetasc on antennular segment XXI: | present = 0 / absent = 1 |
| 41. Aesthetasc on antennular segment XXV: | present = 0 / absent = 1 |
| 42. Aesthetasc on antennular segment XXVI: | present = 0 / absent = 1 |

Antenna

- | | |
|------------------------------------------------------------|------------------------------------------------------------|
| 43. Articulation between antennary exopodal segments IX–X: | partly expressed in adult = 0 / not expressed in adult = 1 |
| 44. Seta from antennary exopodal segment II: | expressed in adult = 0 / not expressed in adult = 1 |
| 45. Seta from antennary exopodal segment VIII: | expressed in adult = 0 / not expressed in adult = 1 |
| 46. Seta from antennary exopodal segment IX: | expressed in adult = 0 / not expressed in adult = 1 |

Maxillule

- | | |
|-------------------------------------------------|--------------------------|
| 47. Seta representing exite on maxillary basis: | present = 0 / absent = 1 |
|-------------------------------------------------|--------------------------|

Maxilla

- | | |
|------------------------------|----------------------------------------------------------------------------------------------------------|
| 48. First endopodal segment: | hoop-like, at least partly separate from basis = 0
enlarged, forming notched triangular allobasis = 1 |
|------------------------------|----------------------------------------------------------------------------------------------------------|

Appendix 1. (Continued).**Maxilliped**

49. Seta representing praecoxal endite: present = 0 / absent = 1
 50. Seta(e) derived from first endopodal segment: present = 0 / absent = 1
 51. Outer seta derived from ancestral fifth endopodal segment: present = 0 / absent = 1

Swimming legs

52. Articulation between endopodal segments 2 and 3 of leg 1: expressed in adult = 0 / not expressed in adult = 1
 53. Inner seta on first exopodal segment of leg 1: present = 0 / absent = 1
 54. Proximal seta on inner margin of second endopodal segment of leg 1: present = 0 / absent = 1
 55. Proximal seta on inner margin of third exopodal segment of leg 1: present = 0 / absent = 1
 56. Proximal seta on inner margin of third exopodal segment of leg 2: present = 0 / absent = 1
 57. Proximal seta on inner margin of third exopodal segment of leg 3: present = 0 / absent = 1
 58. Proximal seta on inner margin of third exopodal segment of leg 4: present = 0 / absent = 1

Female fifth swimming leg

59. Articulation between endopod and basis: expressed in adult = 0 / not expressed in adult = 1
 60. Articulation between exopodal segments 2 and 3: expressed in adult = 0 / not expressed in adult = 1
 61. Spine a (outer spine on first exopodal segment): present = 0 / absent = 1
 62. Spine b (outer spine on second exopodal segment): present = 0 / absent = 1
 63. Spine d (proximal outer spine on third exopodal segment): present = 0 / absent = 1
 64. Spine e (distal outer spine on third exopodal segment): present = 0 / absent = 1
 65. Setal element g (inner distal element on third exopodal segment): articulated basally = 0 / fused to segment = 1
 66. Seta h (proximal inner seta on third exopodal segment): present = 0 / absent = 1
 67. Seta k (inner seta on second exopodal segment): present = 0 / absent = 1
 68. Setal element C (subapical seta on apex of endopod): present = 0 / absent = 1
 69. Setal element D (apical seta on apex of endopod): present = 0 / absent = 1

Male fifth swimming leg

70. Articulation between coxa and basis: expressed in adult = 0 / not expressed in adult = 1
 71. Articulation between endopod and basis: expressed in adult = 0 / not expressed in adult = 1
 72. Articulation between exopodal segments 2 and 3: expressed in adult = 0 / not expressed in adult = 1
 73. Spine a (outer spine on first exopodal segment): present = 0 / absent = 1
 74. Spine b (outer spine on second exopodal segment): present = 0 / absent = 1
 75. Spine d (proximal outer spine on third exopodal segment): present = 0 / absent = 1
 76. Spine e (distal outer spine on third exopodal segment): present = 0 / absent = 1
 77. Seta h (proximal inner seta on third exopodal segment): present = 0 / absent = 1
 78. Seta k (inner spine on second exopodal segment): present = 0 / absent = 1
 79. Setal element C (subapical seta on apex of endopod): present = 0 / absent = 1
 80. Setal element D (apical seta on apex of endopod): present = 0 / absent = 1

Body

81. Carapace-like extension from rear margin of cephalosome: absent = 0 / completely enclosing first pedigerous somite = 1
 82. Body tagmosis: gymnoplean = 0 / podoplean = 1

Appendix 2. Character Matrix for PAUP analysis.

Genus Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	OG
1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
2	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
3	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
4	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
5	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
6	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
7	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0
8	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0
9	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0
10	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	0
11	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0
12	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	0
13	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0
14	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0
15	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
16	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0
17	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
18	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
19	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	0
20	1	1	1	?	1	1	?	1	?	?	0	0	0	0	?	0
21	1	1	1	?	1	1	?	0	?	?	0	0	0	0	?	0
22	1	1	1	?	1	1	?	0	?	?	0	0	0	0	?	0
23	1	1	1	?	1	1	?	0	?	?	0	0	0	0	?	0
24	1	1	0	?	1	1	?	0	?	?	0	0	0	0	?	0
25	1	1	1	?	1	1	?	0	?	?	0	0	0	0	?	0
26	1	1	1	?	1	1	?	0	?	?	0	0	0	0	?	0
27	1	1	1	?	0	0	?	0	?	?	0	0	0	0	?	0
28	0	1	1	?	0	0	?	0	?	?	0	0	0	0	?	0
29	1	1	1	?	1	1	?	0	?	?	0	1	1	1	?	0
30	1	1	1	?	1	1	?	0	?	?	0	1	1	1	?	0
31	1	1	1	?	1	1	?	0	?	?	0	0	1	0	?	0
32	1	1	1	?	1	1	?	0	?	?	0	0	0	0	?	0
33	1	1	1	?	1	1	?	0	?	?	0	0	1	0	?	0
34	1	1	1	?	1	1	?	0	?	?	0	0	0	1	?	0
35	0	1	1	?	0	0	?	0	?	?	0	1	0	0	?	0
36	0	0	0	?	?	0	?	1	?	?	1	1	1	1	?	0
37	1	0	0	?	?	0	?	1	?	?	1	1	1	1	?	0
38	0	0	0	?	?	0	?	1	?	?	1	1	1	1	?	0
39	0	0	0	?	?	0	?	1	?	?	1	1	1	1	?	0
40	0	0	0	?	?	0	?	0	?	?	0	1	1	1	?	0
41	0	0	0	?	?	0	?	0	?	?	0	1	1	1	?	0
42	1	1	1	?	?	1	?	1	?	?	0	1	1	1	?	0
43	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0
44	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0
45	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0
46	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0
47	1	1	1	1	1	1	1	1	0	?	0	1	1	1	1	0
48	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
49	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0
50	1	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0

Appendix 2. (Continued).

Genus Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	OG
51	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0
52	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0
53	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
54	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0
55	1	0	0	1	1	0	0	1	1	1	0	1	1	1	0	0
56	1	0	0	1	0	0	?	1	1	1	0	1	1	1	0	0
57	1	0	0	?	?	1	?	1	1	1	0	1	1	1	0	0
58	1	0	0	1	0	0	?	1	1	1	0	1	1	1	0	0
59	1	0	1	1	0	0	1	0	1	1	1	1	1	1	1	0
60	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
61	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0
62	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
63	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0
64	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
65	0	0	0	0	0	0	0	1	1	1	0	0	0	0	?	0
66	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0
67	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
68	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	0
69	0	0	1	0	0	0	1	0	1	1	1	1	0	1	1	0
70	1	1	1	?	0	0	?	0	?	?	0	1	1	0	?	0
71	1	0	1	?	0	0	?	0	?	?	0	1	1	0	?	0
72	1	0	1	?	0	0	?	0	?	?	1	1	1	1	?	0
73	0	1	1	?	0	0	?	0	?	?	0	0	0	1	?	0
74	1	1	1	?	1	1	?	1	?	?	0	1	1	1	?	0
75	1	1	1	?	0	0	?	0	?	?	0	1	1	1	?	0
76	0	0	0	?	0	0	?	0	?	?	0	1	0	1	?	0
77	1	0	1	?	0	0	?	1	?	?	0	0	0	0	?	0
78	1	0	1	?	0	0	?	1	?	?	0	0	1	0	?	0
79	0	1	0	?	0	0	?	1	?	?	1	1	1	1	?	0
80	0	0	1	?	0	0	?	0	?	?	1	1	0	1	?	0
81	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0
82	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0

Key to Taxa:

1 = *Misophria*, 2 = *Misophriopsis*, 3 = *Benthomisophria*, 4 = *Stygomisophria*, 5 = *Arcticomisophria*, 6 = *Fosshageniella*, 7 = *Misophriella*, 8 = *Huysia*, 9 = *Speleophria*, 10 = *Protospeleophria*, 11 = *Speleophriopsis*, 12 = *Archimisophria*, 13 = *Boxshallia*, 14 = *Expansophria*, 15 = *Palpophria*, OG = outgroup.

Note added in proof

While this paper was in press new species of *Misophriella* and *Misophriopsis* have been described from Antarctic waters (MARTÍNEZ ARBIZU & JAUME 1999) and a new species of *Speleophria* found by JAUME, BOXSHALL & HUMPHREYS (unpublished data). The former discovery results in some changes to the data matrix in the case of *Misophriella* which was inadequately described by BOXSHALL (1983). The new species of *Speleophria* is the only one in which the male is known. The addition of male *Speleophria* data to the character matrix given in Appendix 2 does not alter the topology of the tree presented

in Figure 3, although the four trees generated by the revised PAUP analysis were slightly longer (branch length = 188).

JAUME, D., BOXSHALL, G.A. & HUMPHREYS, W.F. (submitted) New stygobiont copepods (Calanoida; Misophrioida) from Bundera sinkhole, an anchialine cenote on North-Western Australia.

MARTÍNEZ ARBIZU, P & JAUME, D. (1999): New hyperbenthic species of *Misophriopsis* and *Misophriella*, first record of misophrioid copepods (Crustacea) from Antarctic waters. *Helgol. Mar. Res.* **53**: 102–117.