



Archioncaea arabica gen. et sp. nov., a remarkable oncaeid (Copepoda: Poecilostomatoida) from the northern Arabian Sea.

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Abstract: A new genus, *Archioncaea*, is proposed to accommodate a new species of Oncaeidae (Poecilostomatoida) collected from the deep northern Arabian Sea. *A. arabica* gen. et sp. nov. is known from females only and is considered the most primitive oncaeid copepod known to date on account of the combined presence of a trisetose exopod on leg 5 and a long inner coxal seta on leg 1. Other unique plesiomorphic character states are found in the armature of the antennule, maxilla and maxilliped and in the presence of an endopodal surface suture marking the ancestral segmentation of the antenna. *A. arabica* differs from all other oncaeids in the naked endopodal claw of the maxilliped, the presence of distinctly 2-segmented endopods on all swimming legs and the absence of the outer basal seta of leg 5. The discovery of *A. arabica* is of major significance in assessing and polarizing the evolutionary changes of certain characters in the family, such as the ornamentation of mandible blades and the evolution of integumental conical processes on the swimming legs.

Résumé : Un nouveau genre, *Archioncaea*, est créé pour recevoir une nouvelle espèce d'Oncaeidae (Poecilostomatoida) récoltée dans la partie nord profonde de la mer d'Arabie. *A. arabica* gen. et sp. nov. n'est actuellement connue que par les spécimens femelles et l'espèce est considérée comme la plus primitive des copépodes oncaeidés actuellement connus, en raison de la présence à la fois d'un exopodite pourvu de trois soies sur la patte 5 et d'une longue soie interne sur la coxa de la patte 1. D'autres caractères plésiomorphes uniques s'observent dans l'armature de l'antennule, de la maxille et du maxillipède et dans une suture à la surface de l'endopodite, représentant la trace de la segmentation ancestrale de l'antenne. *A. arabica* diffère de tous les autres Oncaeidae par la griffe dégagée sur l'endopodite du maxillipède, la présence d'endopodites à 2 segments sur toutes les pattes nageuses et l'absence de la soie basale externe sur la patte 5. La découverte de *A. arabica* est d'une importance majeure car l'espèce montre l'orientation des changements évolutifs de certains caractères de la famille, tels que l'ornementation des lames mandibulaires et l'évolution des processus tégumentaires coniques sur les pattes nageuses.

Keywords : Copepoda, Poecilostomatoida, *Archioncaea* gen. nov., ancestral, Arabian Sea, plankton.

Introduction

The evolutionary history of the Oncaeidae is largely unknown and the phylogenetic relationships between the

various species are generally poorly resolved. Huys & Böttger-Schnack (1997) recently recognized the diphyletic status of the family, proposed the new family Lubbockiidae to accommodate *Lubbockia* Claus, 1862 and related genera, and retained only *Oncaea* Philippi, 1843, *Conaea* Giesbrecht, 1891 and *Epicalymma* Heron, 1977 in the

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Oncaeidae. Depending on the authority, the speciose genus *Oncaea* has either been amalgamated with *Conaea* and *Epicalymma* forming a single unsurveyable complex (Malt, 1982), or has been regarded as a heterogeneous group that is urgently in need of splitting up in a number of distinct genera (Heron & Bradford-Grieve, 1995), or has been classified as a paraphyletic taxon (Huys & Böttger-Schnack, 1997). A detailed phylogenetic analysis of the three genera is currently in progress and will result in the recognition of more than 20 new genera.

The true diversity of the Oncaeidae is similarly unknown and its relative abundance in copepod assemblages is grossly underestimated in vast areas of the world's oceans. At present, about 86 species have been formally described in the family but in-depth studies carried out on a small geographic scale and using adequate sampling methods indicate that this number represents only the tip of the iceberg. For example, Böttger-Schnack (1996) in her study of Arabian Sea zooplankton recognized 69 putative species of Oncaeidae of which only 19 could be identified as previously described species. Closer examination of her artificially delimited species group 7 (Böttger-Schnack, 1996: p. 1090), resulted in the discovery of a new species displaying a suite of plesiomorphic character states previously unknown in the family. The purpose of this paper is to describe this species in detail on the basis of females and to discuss the phylogenetic implications of this discovery.

Material and methods

Oncaeids were collected at two localities in the northern Arabian Sea during Cruise 5/3 of R/V Meteor (MINDIK), using a multiple opening-closing net with a mesh size of 0.05 mm. Further locality details are given below under "Material examined". The plankton was initially fixed in 4% formaldehyde-seawater solution buffered with hexamethylene tetramine and later transferred into a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol, and 94.5% filtered seawater (Steedman, 1976).

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England). Drawings have been prepared using a camera lucida on a Zeiss Axioskop or Leitz Dialux microscope equipped with differential interference contrast. Scale bars are given in μm .

Total body length and the ratio of prosome to urosome (excluding caudal rami) were calculated as the sum of the middorsal lengths of individual somites measured in lateral view. In the case of telescoping somites these lengths are measured from the anterior to the posterior margin along the dorsal curvature. This approach differs from that traditionally used in oncaeid taxonomy, where the

telescoping of somites is not considered in length measurements.

The descriptive terminology applied to segmentation and setation of body appendages is adopted from Huys & Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1 - P6, first to sixth thoracopods; exp, exopod; enp, endopod; exp (enp)-1(-2, -3), to denote the proximal (middle, distal) segment of a ramus.

Type material is deposited in the collections of The Natural History Museum, London (NHM) and the Zoologisches Institut und Museum an der Universität Hamburg (ZMH).

Systematics

Order POECILOSTOMATOIDA Thorell, 1859

Family ONCAEIDAE Giesbrecht, 1892

Archioncaea gen. nov.

Diagnosis. - Oncaeidae. Body cyclopiform, prosome broad-oval. P2-bearing somite without dorsoposterior projection in ♀. Cephalosome without lateral lobate extensions. Genital double-somite ♀ barrel-shaped, not swollen dorsally, slightly constricted bi-laterally; with several transverse spinule rows ventrally in posterior half. First and second postgenital somites distinctly shorter than anal one. Anal somite with wide anal opening; operculum bare. Exoskeleton thinly chitinated.

Male unknown; sexual dimorphism presumably present in antennule segmentation and armature, maxilliped, genital segmentation and ornamentation, and P6.

Antennule 6-segmented in ♀ with armature formula 1-[3], 2-[10], 3-[6], 4-[4 + ae], 5-[2 + ae], 6-[6 + (1 + ae)]. Aesthetascs well developed.

Antenna not prehensile. Enp-1 with lobate projection; abexopodal margin with row of large, strong spinules. Enp-2 distinctly shorter than enp-1, with transverse surface suture marking original segmentation; posterior surface with rows of spinules; lateral armature consisting of 3 well developed, bare or minutely pinnate setae and 1 strong, unipinnate claw; distal armature consisting of 4 strong, pinnate setae, 2 long naked setae and well developed posterior seta.

Labrum weakly bilobate. Anterior margin with patch of long spinules medially, flanked by pair of large teeth and several denticles laterally. Posterior margin with median concavity fringed with dentiform processes; lateral portions with strong tooth and small denticles.

Mandible with 2 blades and 2 setae. Blades fused basally along posterior surface. Dorsal blade spinulose along entire dorsal margin, bipinnate in distal half. Dorsal element longest, setiform, multipinnate.

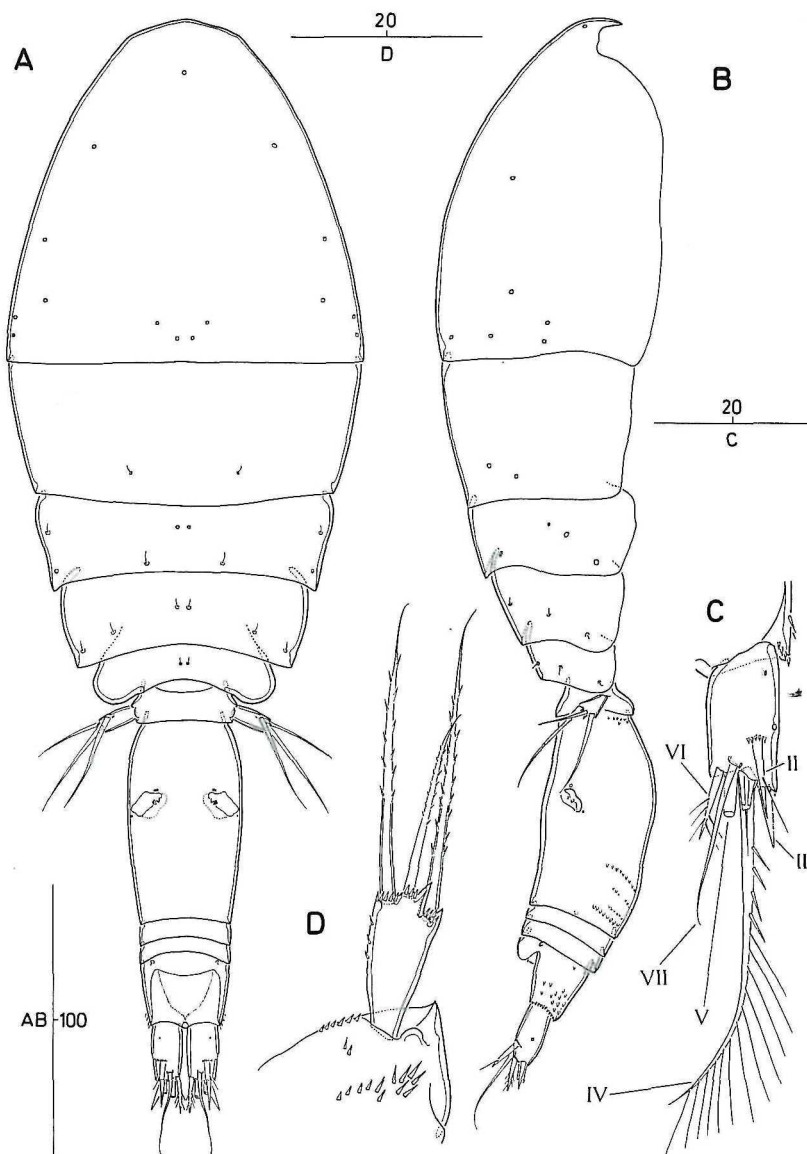


Figure 1. *Archioncaea arabica* gen. et sp. nov. (♀). A, habitus, dorsal; B, same, lateral; C, right caudal ramus, dorsal; D, P5, lateral.

Figure 1. *Archioncaea arabica* gen. et sp. nov. (♀). A, habitus, vue dorsale; B, habitus, vue latérale; C, rame caudale droite, vue dorsale; D, P5, vue latérale.

Maxillule weakly bilobate; elements of praecoxal arthrite closely set together, outermost element spiniform and bearing transverse row of spinules.

Maxilla with allobasis shorter than syncoxa; allobasal claw with transverse surface suture marking original fusion plane.

Maxilliped ♀ slender. Basis without ornamentation on posterior surface; anterior surface with hyaline serrate flap along most part of palmar margin and with long setules distally; both palmar elements setiform and naked; distal

seta slightly shorter than proximal one. Enp-1 completely separate. Enp-2 with slender, naked claw, short outer seta and vestigial inner setule.

P1 with long, plumose inner coxal seta. Basis without inner basal seta. Endopod 2-segmented; enp-2 outer spine stout, with broad serrate hyaline flanges; distal inner seta shortest, closely set to 5th inner seta.

P2-P4 exopods with short outer spines; those of exp-2 and proximal spine of exp-3 very small. Distal spine of exp-3 long, with broad outer serrate flange.

P2-P4 endopods 2-segmented. Enp-2 very long and slender; without conical processes on P2 and P3 but pore present between both apical spines. Enp-2 inner distal spine long; outer distal spine well developed in P2; outer spine absent in P3-P4.

Swimming leg armature formula:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-0	I-0;I-1;III,I,4	0-1;I,6
P2	0-0	1-0	I-0;I-1;II,I,5	0-1;I,II,5
P3	0-0	1-0	I-0;I-1;II,I,5	0-1;0,II,4
P4	0-0	1-0	I-0;I-1;II,I,5	0-1;0,II,3

P5 represented by subrectangular exopod with 1 lateral and 2 apical, pinnate setae; outer basal seta absent. Genital apertures of ♀ large; located near midregion of dorsal surface of genital double-somite; each operculum with minute spinous process and vestigial spine.

Caudal ramus about 1.7 times as long as wide, without conspicuous dorsal expansion surrounding base of seta VII. Seta I absent; seta II spiniform, with lateral setule and dorsally displaced; seta III spiniform; seta IV proximally unipinnate and distally plumose; condition of seta V unknown; seta VII bare, distinctly shorter than IV; seta VI spiniform and pinnate.

Type and only species. - *Archioncaea arabica* gen. et sp. nov.

Etymology. The generic name is derived from the Greek *archi*, meaning first, and alludes to the primitive position of genus in the Oncaeidae. The trivial name refers to the type locality in the northern Arabian Sea. Gender: feminine.

Archioncaea arabica gen. et sp. nov.

Material examined

Northern Arabian Sea, central part, 18° 00' N 66° 25' E: Stn. 496; *R/V Meteor* leg 5/3b: holotype ♀ dissected on 8 slides (NHM reg. no. 1997.716) and paratype ♀ dissected on 2 slides (NHM reg. no. 1997.717). Collected 12 May 1987 with MSN 0.05mm net (haul 1/2); depth 1050-1250 m; total water depth 3035 m.

Northern Arabian Sea, central part, 18° 00' N 66° 25' E: Stn. 496; *R/V Meteor* leg 5/3b: paratype ♀ (slightly damaged) in alcohol (NHM reg. no. 1997.718) and paratype ♀ (slightly damaged) in alcohol (ZMH reg. no. K-38245). Collected 12 May 1987 with MSN 0.05mm net (haul 2/2); depth 450-600 m.

Northern Arabian Sea, near coast of Oman, 20° 44' N 59° 40'E: Stn. 347; *R/V Meteor* leg 5/3a: paratype ♀ in alcohol

(NHM reg. no. 1997.719). Collected 5 April 1987 with MSN 0.05mm net (haul 5/4); depth 1450-1650 m; total water depth 2510 m.

Northern Arabian Sea, near coast of Oman, 20° 44' N 59° 40'E: Stn. 347; *R/V Meteor* leg 5/3a: paratype ♀ in alcohol (partly deteriorated). Collected 5 April 1987 with MSN 0.05mm net (haul 7/4); depth 350-400 m. Retained in personal collection of R. Böttger-Schnack.

Description

Female (Figs.1-5).

Total body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 465 µm.

Exoskeleton thinly chitinated. Prosome 4.7 times length of urosome, excluding caudal rami, 4 times urosome length including caudal rami. Leg 2-bearing somite without conspicuous dorso-posterior projection in lateral aspect (Fig. 1B). Integumental pores and sensillae on prosome as indicated in Fig. 1A-B.

Proportional lengths (%) of urosomites are 12.1 : 55.8 : 5.4 : 6.1 : 20.6. Proportional lengths (%) of urosomites and caudal rami are 10.3 : 47.7 : 4.7 : 5.2 : 17.6 : 14.5.

Genital double-somite about 1.6 times as long as maximum width (measured in dorsal aspect) and twice as long as postgenital somites combined; largest width measured at posterior margin; slightly constricted at about halfway the double-somite and just posterior to genital apertures (Fig. 2C). Ventral surface with minute spinules around anterior margin; posterior third with several transverse spinular rows, posteriormost raised (Fig. 2B). Paired genital apertures large, located dorsolaterally at about halfway the distance from anterior margin of genital double-somite; closed off by vestigial sixth legs with armature represented by 1 minute spinous process and 1 vestigial spine (Fig. 2D). Two secretory pores on dorsolateral surface associated with genital apertures (Fig. 2D).

First and second postgenital somites very short; first one with 2 short sensilla lateroventrally and 2 pores dorsolaterally.

Anal somite distinctly tapering posteriorly; 1.75 times wider (maximum) than long; slightly longer than caudal rami (Fig. 2C); ventral surface with spinular pattern as in Fig. 2B. Anal opening very wide; anterior margin (operculum) smooth. Short sensillum discernible on either side of anal opening. Posterior margin of somite with fine spinules ventrally and laterally.

Caudal ramus (Fig. 1C) about twice as long as wide. Armature consisting of 6 elements: seta II dorsally displaced, spiniform, with long setule laterally; seta III spiniform, minutely unipinnate; seta IV with ornamentation along outer margin only (spinules proximally and long

setules distally); condition of seta V unknown (broken in all specimens examined); seta VI short, spiniform and pinnate; seta VII naked, shorter than seta IV. Dorsolateral margin with 2 secretory pores.

Antennule 6-segmented (Fig. 2A), relative lengths (%) of segments measured along posterior non-setiferous margin 10.6 : 14.2 : 35.5 : 14.9 : 12.7 : 12.1. Segment 1 with spinule row along anterior margin. Most setae on segments 1-3 minutely pinnate. Armature formula: 1-[3], 2-[10], 3-[6], 4-

[4 + ae], 5-[2 + ae], 6-[6 + (1 + ae)]. Aesthetascs long, well developed; apical one fused to seta.

Antenna 3-segmented, not distinctly reflexed (Fig. 3A). Coxobasis with pattern of short spinules on both anterior and posterior surfaces; with naked seta at inner distal corner. Endopod segments unequal in length. Proximal endopod segment with inflated outer margin bearing two spinule rows; posterior surface with row of strong recurved spinules. Distal endopod segment short; transverse suture on

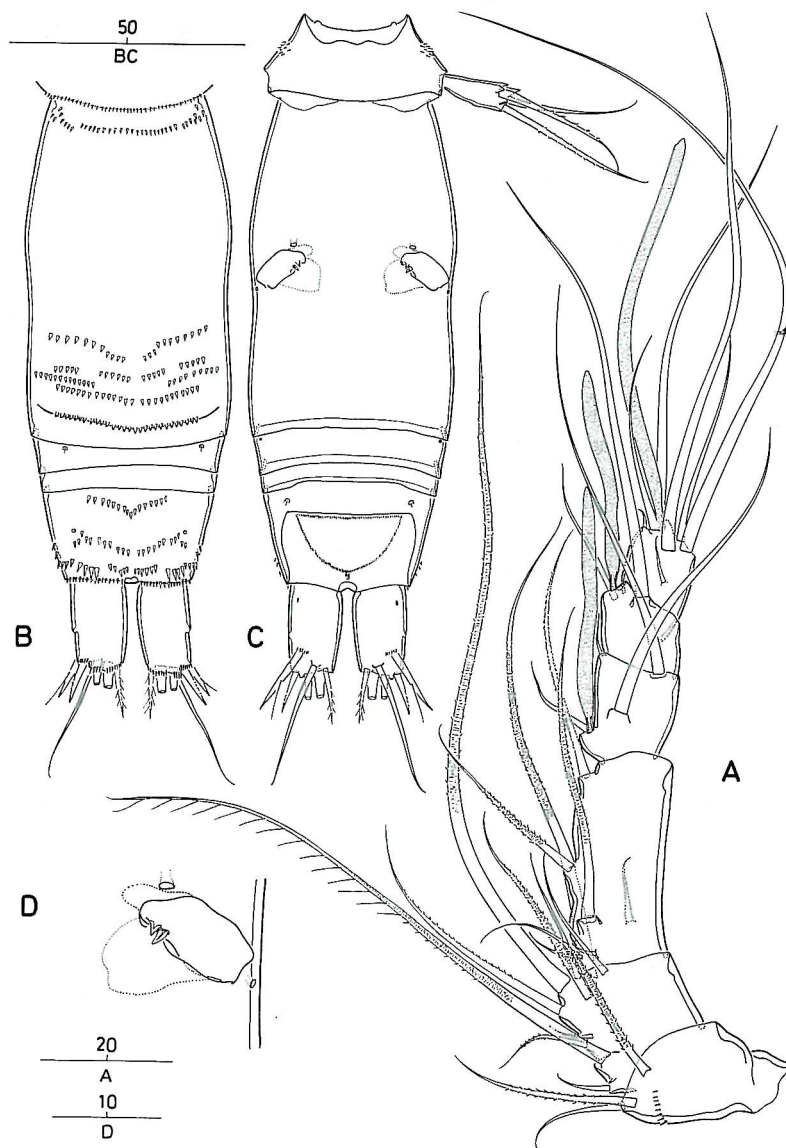


Figure 2. *Archioncaea arabica* gen. et sp. nov. (♀). A, antennule, ventral; B, urosome (excluding P5-bearing somite), ventral; C, urosome, dorsal; D, left genital aperture, dorsal.

Figure 2. *Archioncaea arabica* gen. et sp. nov. (♀). A, antennule, vue ventrale ; B, urosome (sauf somite portant P5), vue ventrale ; C, urosome, vue dorsale ; D, orifice genital droit, vue dorsale.

anterior surface (Fig. 3B) marking original segmentation; posterior surface with 2 rows of fine spinules; lateral armature consisting of 3 setae (1 unipinnate, 2 naked) and 1 strong, recurved claw; distal armature consisting of 2 long naked setae, 4 curved spines and short naked posterior seta; none of armature elements geniculate.

Labrum (Fig. 4A) double-walled, weakly bilobed. Anterior wall (Fig. 5A) with median concavity; bearing median patch of overlapping long spinules flanked by row of small denticles and one large dentiform process located close to spinular patch. Anterior face with some small spinules on either latero-lateral side (Fig. 5A) and a weakly developed median bulge (Fig. 4A). Posterior wall (Fig. 4B) also with median incision fringed with row of small denticles or spinules (median pair slightly larger than adjoining ones); lateral lobes with dentiform margin and set off from median concavity by large dentiform process. Posterior face with 4 secretory pores.

Mandible (Fig. 3C) with 2 setae and 2 blades. Dorsal element setiform and longest; multipinnate along its entire length. Blades fused basally along posterior surface. Dorsal blade strongly developed; spinulose along entire dorsal margin, bipinnate in distal half (additional spinules located anteriorly). Dorsal element longest, setiform, multipinnate.

Maxillule (Fig. 3D) weakly bilobate; no surface ornamentation discernible. Inner lobe (praecoxal arthrite) with 3 closely set elements: outermost element spiniform and bearing transverse spinule row, middle element short and sparsely pinnate, inner element setiform and bare. Outer lobe with 4 elements; 2 outer elements multipinnate, spiniform and with long setules along inner margin, innermost element unipinnate and setiform, second innermost with coarse spinules.

Maxilla (Fig. 3F) 2-segmented, allobasis shorter than syncoxa. Syncoxa unarmed, no surface ornamentation discernible. Allobasis produced distally into slightly curved claw with transverse surface suture marking original fusion plane, bearing cluster of strong spinules along proximal third of inner margin; outer margin with strong seta not extending to tip of allobasal claw; inner margin with slender pinnate seta and strong basally swollen spine bearing fine spinules.

Maxilliped (Fig. 3E) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa unarmed, with surface ornamentation consisting of setules on both anterior and posterior surfaces. Basis elongate; without ornamentation on posterior surface; anterior surface with few spinules; with hyaline serrate flap along most part of palmar margin and long setules distally; both palmar elements setiform and naked; distal seta slightly shorter than proximal one. Proximal endopod segment completely separated, unarmed. Distal endopod segment drawn out into slender, naked claw; accessory armature consisting of short,

naked seta on outer proximal margin and vestigial inner setule.

Swimming legs 1-4 biramous (Figs 4C-D; 5B-D), with 3-segmented exopods and distinctly 2 segmented endopods. Intercoxal sclerites well developed, with spinular pattern on posterior surface of legs 3-4 (Fig. 5B,D). Coxae with spinule rows as figured; with long plumose seta at inner distal corner in P1 (Fig. 4C). Bases with naked (P1-P2) or sparsely plumose (P3-P4) outer seta, arising from posterior surface. Inner portion of basis produced adaxially into rounded (P1) or angular process (P2-P4) bearing anterior patch of spinules increasing in size adaxially in P3-P4. Inner basal seta of P1 absent but cluster of three very long spinules present in this position.

Rami short in P1, slender and elongate in other legs. P1 exopod outer spines with subapical tubular extension, those of exp-3 with broad serrate flange. P2-P4 exopods with elongate distal segment, longer than exp-1 and -2 combined; outer margins of all segments minutely denticulate; outer spine of exp-2 and proximal outer spine of exp-3 short; terminal spines long, with broad outer serrate flange and second series of serrate outgrowths on posterior surface. Proximal endopod segment of P1-P2 with small denticles on anterior surface. P1 enp-2 short in comparison to other legs; outer distal spine with broad hyaline flange; distalmost inner seta shortest, pinnate and closely set to 5th inner seta which is pinnate along the distal inner margin. P2-P4 enp-2 slender, compound; fusion plane between original segments marked by small dentate process along outer margin, but not by surface sutures; P3-P4 outer spine lost, outer distal spine with reduced flanges, inner distal spine very long; without conical processes but pore present between distal spines of P2 and P3.

Leg 5 (Fig. 1A-B, D) prominent; comprising basally defined exopod only (basal seta absent). Exopod slightly tapering distally, longer than wide; with 1 lateral and 2 distal bipinnate setae (inner one shortest); segment produced into short spinous process; spinules present around bases of setae and along inner margin.

Leg 6 (Fig. 2C, H) represented by operculum closing off each genital aperture; armed with a long spine and a short spinule.

Egg-sac not observed.

Male. Unknown.

Discussion

Archioncaea arabica displays a remarkable combination of primitive and advanced character states which clearly separates it morphologically from all other known oncaeids. Perhaps the most unusual character of *A. arabica* is the trisetose leg 5 exopod which is clearly exposed on the body and therefore allows for rapid identification of this species

without prior dissection. In all other oncaeids the exopod of leg 5 either has 2 setae (the majority of species), or 1 seta accompanied by a diminutive spinule (e.g. *O. englishi* Heron, 1977, *O. brodskii* Shmeleva, 1968), or only 1 seta (e.g. *O. tregoubovi* Shmeleva, 1968, most *Epicalymma* and *Conaea* species) or has been lost altogether (*Conaea rapax* Giesbrecht, 1891). Comparison with the bisetose condition of e.g. *O. damkaeri* Heron, 1977 indicates that it is the lateral element of *A. arabica* that has been lost in all other Oncaeidae. Conversely, despite the primitive condition of the exopod it is remarkable that the outer basal seta, usually arising from the dorsolateral surface of the somite, is lost in

Archioncaea. This seta has been retained in all other oncaeids including *O. atlantica* Shmeleva, 1967, whose reduced leg 5 was originally figured (Shmeleva, 1967) and subsequently redescribed (Boxshall & Böttger, 1987) with only one seta coming off from the surface.

A. arabica can be readily distinguished by the presence of a well developed inner coxal seta on leg 1. Recent re-examination of *O. brodskii* from material in the northern Arabian Sea has revealed the presence of a much shorter plumose seta in this position on leg 1 and of a vestigial naked seta on the coxa of leg 2. Boxshall (1977) reported the presence of a small spinule on the inner coxal corner of legs

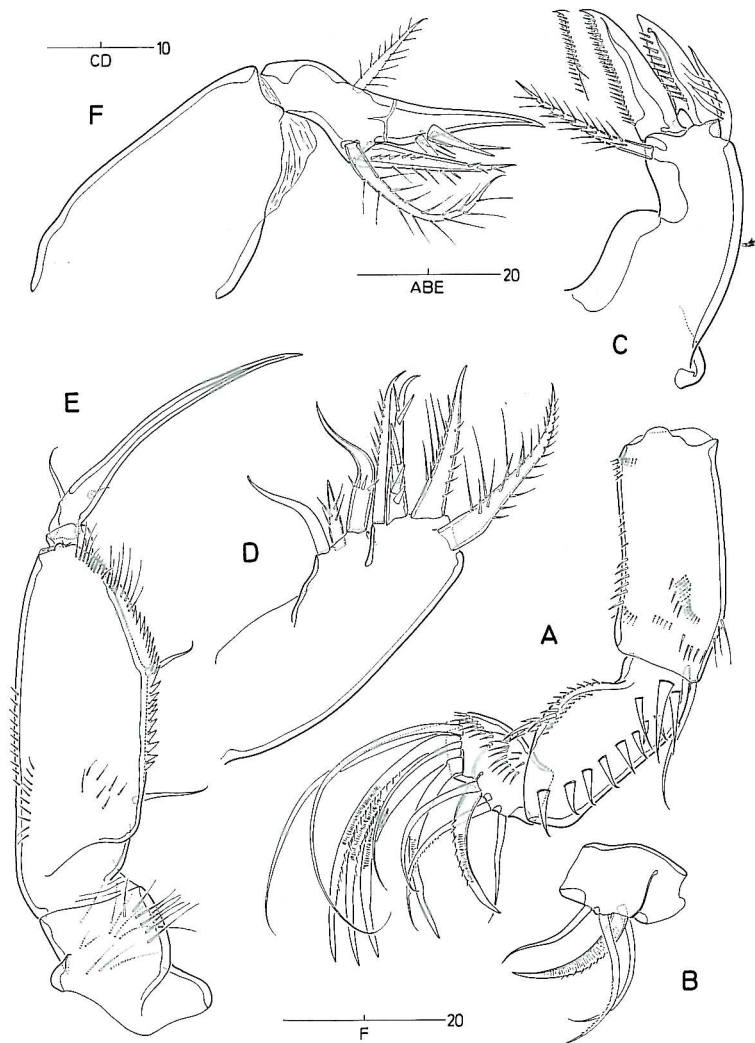


Figure 3. *Archioncaea arabica* gen. et sp. nov. (♀). A, antenna, posterior; B, antennary distal endopod segment, anterior; C, mandible, posterior (inset showing anterior view of dorsal blade); D, maxillule; E, maxilliped, anterior; F, maxilla.

Figure 3. *Archioncaea arabica* gen. et sp. nov. (♀). A, antenne, vue postérieure; B, article distal de l'endopodite antennaire, vue antérieure; C, mandibule, vue postérieure (encart : vue antérieure de l'épine dorsale); D, maxillule; E, maxillipède, vue antérieure; F, maxille.

1-4 in *O. notopus* Giesbrecht, 1891 and of legs 1 and 2 in *O. ornata* Giesbrecht, 1891. Boxshall's observations would require confirmation since no such spinules have been reported by Heron (1977) in the closely related species *O. damkaeri* and *O. englishi*. The loss of the inner coxal seta on P1-P4 has been regarded as a diagnostic family character separating the Oncaeidae from the Lubbockiidae (Huys & Böttger-Schnack, 1997), however its discovery in *A. arabica* and *O. brodskii* indicates that this loss happened secondarily in the evolution of the family.

The antennule of the new genus displays the most ancestral setal formula found thus far in the Oncaeidae. An unpublished survey of the various *Oncaea* species revealed that antennular armature is remarkably conservative in the family with the majority of species sharing the following setal formula: 3 [3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[6+(1+ae)]. *A. arabica* possesses two additional elements on segment 2, and an additional seta on segments 3 and 4.

The primitive position of *Archioncaea* is also revealed by the detailed morphology of the antenna, maxilla and maxilliped. Unlike certain Lubbockiidae (Huys & Böttger-Schnack, 1997) oncaeids invariably have a 3-segmented antenna, comprising a coxobasis and a 2-segmented endopod. The distal segment is a compound one derived by fusion of the second and third endopod segments which are expressed in many other poecilostomatoid families. *A. arabica* is the only oncaeid where this original segmentation is still discernible in the form of a transverse surface suture running across most of the anterior surface. It has been generally assumed that the maxillary allobasis in poecilostomatoids primitively has 3 free elements associated with the spinous outgrowth or process. The condition in *A. arabica* strongly suggests that the allobasal "claw" is homologous to an incorporated armature element since a distinct transverse suture is found around the basis of the claw probably marking the original articulation. The endopodal claw of the female maxilliped in oncaeids is usually accompanied by 2 accessory elements: an outer vestigial seta and an inner pinnate element. The latter is always fused basally to the claw and in some species it is even further incorporated leaving behind the ornamentation along its axis. In *A. arabica* the inner element is still discrete albeit strongly reduced compared to most other oncaeids.

A. arabica possesses an unusual swimming leg setal formula not found in any other extant oncaeid. The identical [II,I,5] exopodal armature pattern displayed on legs 2-4 (resulting from the loss of one outer spine on P2 exp-3) is found only in *O. brodskii* and *O. longipes* Shmeleva, 1968, however these species differ considerably in the endopodal armature. The endopodal pattern of *A. arabica* is characterized by the loss of the outer spine on the distal endopod segment of legs 3-4 but not of leg 2. This unique combination is not found anywhere else in the family since

in the various lineages of *Oncaea* showing reduced setation patterns (e.g. *O. englishi* and *O. platysetosa* species groups), such reductions are invariably expressed as a general pattern affecting all legs (i.e. legs 2-4).

Archioncaea displays a number of distinct autapomorphies:

(1) Antenna with short naked coxobasal seta and strongly abbreviated distal endopod segment; the coxobasal seta is remarkably reduced in *A. arabica* and unlike all other members of the family it lacks ornamentation; the distal endopod segment is unusually short and is reminiscent of the condition found in *O. walleni* Heron, 1977, a species belonging to the *O. notopus* group.

(2) The mandible with only 4 elements is shared with *Conaea rapax* (Huys & Böttger-Schnack, unpubl.); the missing element can be identified as the small seta which is usually present between the dorsal multipinnate seta and the dorsal blade.

(3) Female maxilliped with naked palmar setae and endopodal claw; in all other oncaeids the endopodal claw is pinnate in the distal half or along its entire length; at least one (usually the distal) of the palmar setae/spines is ornate in other Oncaeidae, except for the unrelated *O. tenuimana* Giesbrecht, 1891, in which both palmar setae are also naked.

(4) P1-P4 with 2-segmented endopods. *A. arabica* is the only oncaeid with distinctly 2-segmented endopods on all swimming legs. Heron (1977) described legs 3 and 4 of *Epicalymma schmitti* Heron as 2-segmented and Heron *et al.* (1984) pointed out that the segmentation of the endopods was often obscure in *E. brittoni* Heron, English & Damkaer, 1984. Re-examination of *O. atlantica* and *O. platysetosa* Boxshall & Böttger revealed that the P1 endopod is incompletely 2-segmented due to partial fusion of the middle and distal segments. Similar incomplete fusions have been observed for the leg 2 endopod of *O. subtilis* Giesbrecht, 1892 and the leg 4 endopod of *O. brodskii*.

(5) P5 ♀ without basal seta.

On account of the unique plesiomorphies discussed above, the genus *Archioncaea* can be considered the earliest known offshoot in the evolution of the Oncaeidae. Its discovery is of major significance in assessing the phylogenetic relationships within the family, particularly in determining the polarity of character state changes in ornamentation and integumental structures. For example, within the genus *Oncaea* it is difficult to interpret the evolutionary sequence of changes in the form and shape of the dorsal blade of the mandible. In our preliminary analysis in-group comparison had already given some indication that the dentate and cuspidate blade types (as found in e.g. *O. venusta* Philippi, 1843 and *O. conifera* Giesbrecht, 1891) had evolved from a setulose or spinulose condition. The presence of the latter state in *Archioncaea* appears to

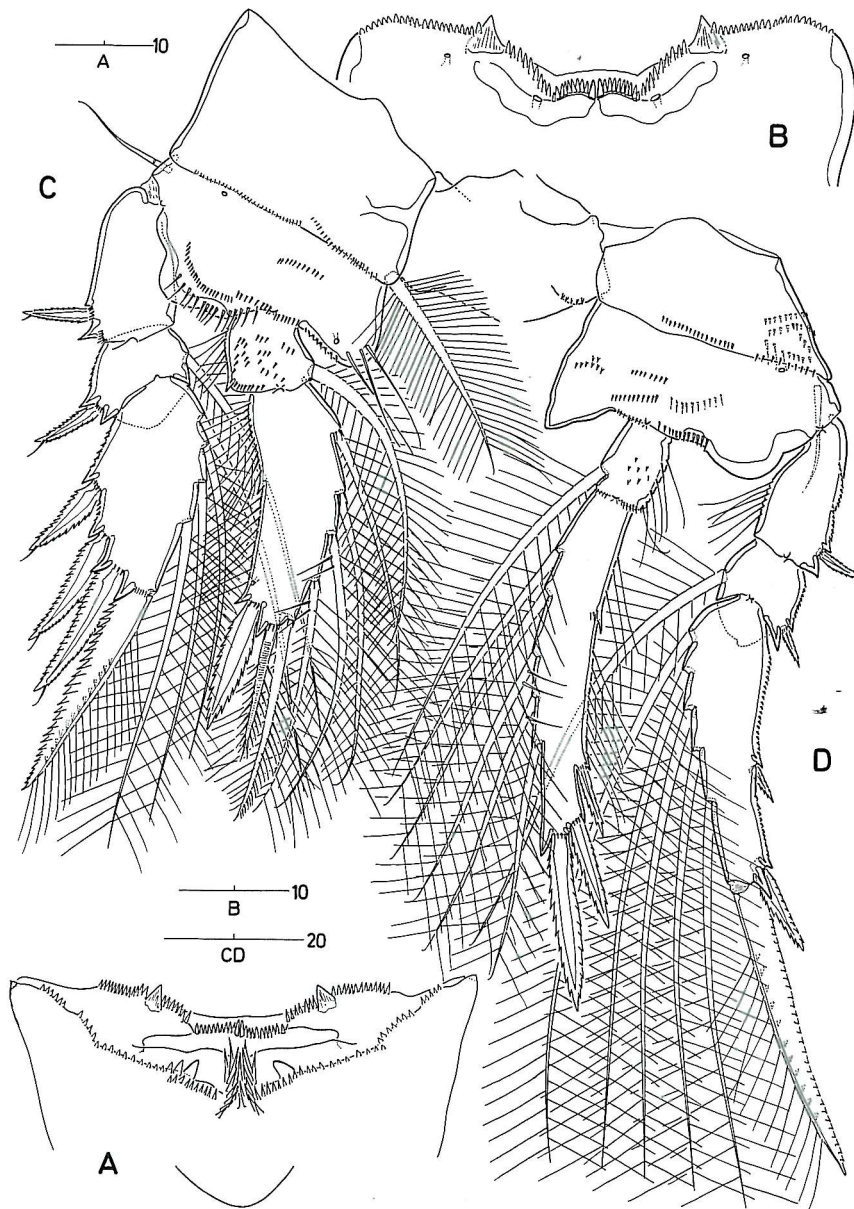


Figure 4. *Archioncaea arabica* gen. et sp. nov. (♀). A, labrum, ventral; B, labrum, posterior; C, P1, anterior; D, P2, anterior.

Figure 4. *Archioncaea arabica* gen. et sp. nov. (♀). A, labre, vue ventrale ; B, labre, vue postérieure ; C, P1, vue antérieure ; D, P2, vue antérieure.

support that hypothesis. Secondly, the absence of conical processes on the distal endopod segments of legs 2-4 in *A. arabica* is highly informative. In the great majority of species, legs 2-3 possess a conical or rounded projection arising from the distal margin between the inner and outer distal spines/setae. However, the presence of a serially homologous structure on leg 4 in the *O. conifera/similis* group, in conjunction with the complete absence of these structures on all swimming legs in a small number of species, make assessment of the evolutionary polarity of this character difficult. This essentially leads to the question

whether or not the oncaeid ancestor had conical processes on legs 2-4 which then persisted only in the species of the *O. conifera/similis* group but were lost on leg 4 in the majority of species and disappeared altogether in a minor group including *O. brodskii*, *O. subtilis*, *O. ivlevi* and a few others. The alternative hypothesis, assuming a secondary evolution of conical processes in the family, gains more credence with the discovery of the primitive *A. arabica*. The small pores located between the distal spines of legs 2-3 of *Archioncaea*, and which are also present in *O. brodskii*, *O. ivlevi* Shmeleva, 1966 and *O. subtilis*, can be regarded as

the morphological precursors of the conical or rounded processes which typically have an apical or slightly subapical pore. A process can therefore be regarded as an excessively raised pore which initially evolved only in legs 2-3 and subsequently also in leg 4.

Ecological data

The family Oncaeidae shows a remarkable diversity in the Arabian Sea (Böttger-Schnack, 1996). A total of 69 species (including 44 provisionally classified species) were recorded from the two stations (stations 347 and 496) where

A. arabica occurred. The vertical distribution of the oncaeid fauna in the Arabian Sea is strongly influenced by the extended oxygen minimum zone (OMZ) occurring between ca 150 m and at least 1000 m depth. The majority of the 69 species found at the type locality display one of two main unimodal patterns of vertical distribution: (i) about 18 species (14 identified and 4 putative) showed maximum concentrations in the epipelagic zone (0-100m), and (ii) 4 identified species and 44 provisionally classified forms showed maximum concentrations in the bathypelagic zone below 900(1050) m depth. The vertical distribution of

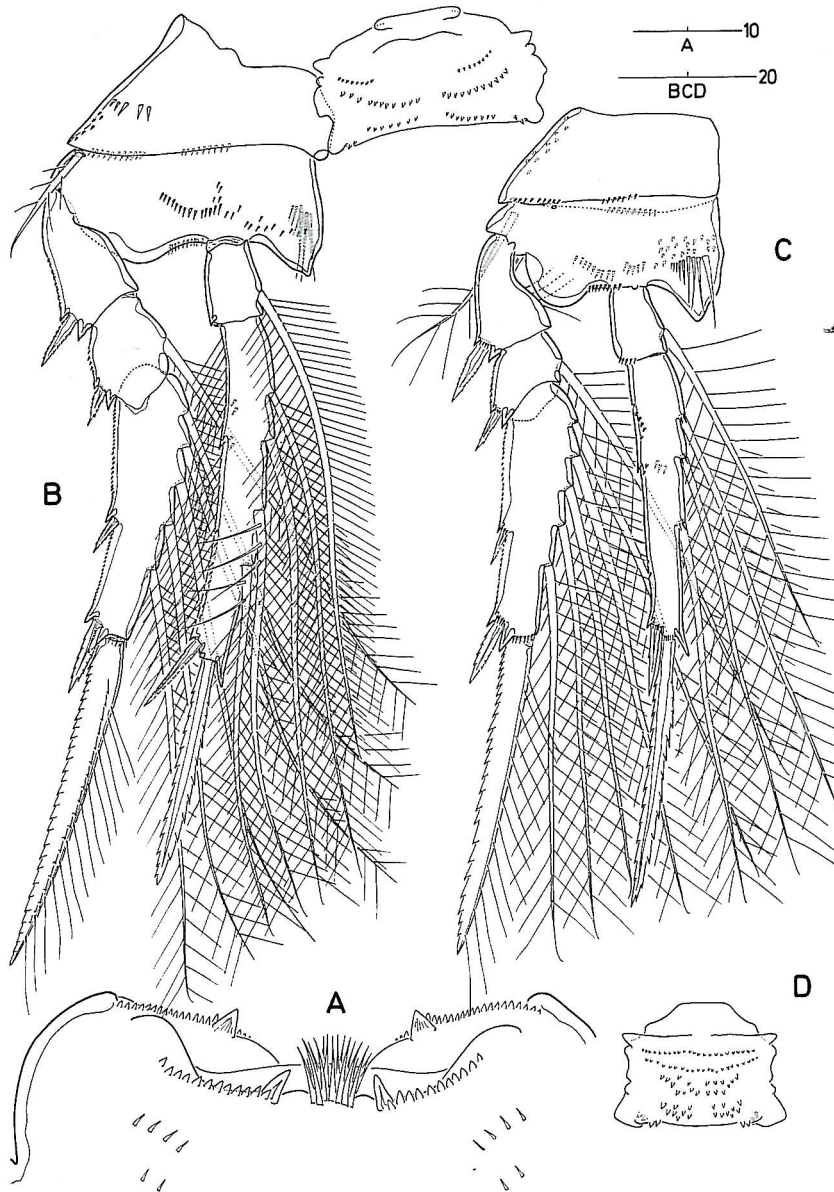


Figure 5. *Archioncaea arabica* gen. et sp. nov. (♀). A, labrum, anterior; B, P3, posterior; C, P4, anterior; D, intercoxal sclerite of P4, posterior.

Figure 5. *Archioncaea arabica* gen. et sp. nov. (♀). A, labre, vue antérieure ; B, P3, vue postérieure ; C, P4, vue antérieure ; D, P4, sclérite intercoxal, vue postérieure.

another four species differed from these patterns as they appeared to be concentrated within the OMZ but did not occur above or below it.

A. arabica is quite exceptional in showing a bimodal distribution pattern, occurring both within the OMZ and in the deeper layers below it. At both stations, the shallower part of the population coincided with an intermediate plankton maximum within the OMZ (expressed in total plankton biomass and abundance of copepods, appendicularians, polychaetes and ostracods), which was situated at 250-350(400) m near Oman and somewhat deeper, at 450-(600)750 m, in the central area. The dominant copepod species within these peaks was *Oncaea* sp. C, a small unidentified species possibly related to *O. ovalis* Shmeleva, 1966 (Böttger-Schnack, 1996: Tables IV, V).

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