ACTA
PALAEONTOLOGICA
POLONICA

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Miocene cyclopid copepod from a saline paleolake in Mojave, California

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Hołyńska, M., Leggitt, L., and Kotov, A.A. 201X. Miocene cyclopid copepod from a saline paleolake in Mojave, California. *Acta Palaeontologica Polonica* XX (X): xxx-xxx. http://dx.doi.org/10.4202/app.00137.2014

There are remarkably few direct fossil records of Copepoda, which implies that current estimates of the lineage divergence times and inferences on the historical biogeography remain highly dubious for these small-sized crustaceans. The Cyclopidae, a predominantly freshwater copepod family with 1000+ species and distributed worldwide, has no fossil record at all. Recent collections from the middle Miocene Barstow Formation in Southern California resulted in ample material of finely preserved cyclopid fossils, including both adult and larval stages. To document the antennulary setation pattern in the adult and copepodid instars we used a coding system that is coherent between sexes and developmental stages. The majority of the cyclopid fossils, coming from saline lake environment, represent the modern genus *Apocyclops*, a euryhaline, thermophilic group occurring both in the New World and Old World. A new species *Apocyclops californicus* is described, based on the short medial spine and spiny ornamentation of the free segment of leg 5, spinule ornamentation of pediger 5, and well-developed protuberances of the intercoxal sclerite of leg 4. The presence of antennal allobasis and the features of the swimming legs unambiguously place the Miocene *Apocyclops* in the *panamensis*-clade, a predominantly amphi-Pacific group. The middle Miocene fossils with clear affinities to a subgroup of *Apocyclops* imply an early Miocene or Paleogene origin of the genus. Based on the geographic patterns of the species richness and morphology in *Apocyclops* and its presumed closest relative, genus *Metacyclops*, we hypothesize that: (i) the ancestor of *Apocyclops*, similar in morphology to some cave-dweller *Metacyclops* occurring today in the peri-Mediterranean region, might have arrived in North America from Europe via the Thulean North Atlantic bridge in the late Paleocene–Early Eocene; (ii) Eocene termination of the Thulean land connection might have resulted in the divergence of *Apocyclops* from the *Metacyclops* stock.

Key words: Copepoda, ontogeny, taxonomy, biogeography, saline lake, Barstow, Thulean, Miocene, amphi-Pacific.

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Received 10 November 2014, accepted 9 October 2015, available online 19 October 2016.

Introduction

Copepods are small crustaceans, most of them not larger than a few millimeters, with non-calcified cuticle. The "insects of the seas" occur in huge abundance not only in the world oceans but also in the continental waters (both surface and subterranean), and evolved an extraordinarily wide variety of the free-living and symbiotic life strategies. Still, there are very few direct fossil records of the Copepoda, which poses the most serious limitation on studies of copepod evolution.

Middle–Late Cambrian mandible fragments (cutting edge), similar in many details to those in modern copepods, were discovered from the Deadwood Formation (488−510 mya) in Saskatchewan (Canada) and from the Nolichucky Shale (495−500 mya) in Tennessee, USA (Harvey et al. 2012; Harvey and Pedder 2013). The relatively large mandibles could belong to a stem- or crown-group copepod of ~10 mm length (Harvey et al. 2012) living in shallow-marine environments. Evidence supporting a Paleozoic invasion of the continental waters by harpacticoid copepods were provided by the fossils (fragments of the cephalothoracic appendages) of late Carboniferous age (303 mya) in Oman (Selden et al. 2010). The harpacticoid assigned to the family Canthocamptidae could have inhabited a subglacial lake. A fish parasite (*Kabatarina pattersoni* Cressey and Boxshall, 1989; both sexes, entire body), belonging to the marine family Dichelesthiidae (order Siphonostomatoida) was described from the Early Cretaceous (110–120 mya) Santana Formation in Brazil (Cressey and Patterson 1973; Cressey and Boxshall 1989; Huys and Boxshall 1991). The oldest record of a modern copepod genus is that of *Cletocamptus* Schmankevitch, 1875 (Harpacticoida: Canthocamptidae) from the Miocene Barstow Formation in the Mojave Desert in Southern California (Palmer 1960). Later, Palmer (1969) designated (although with a question mark) the Miocene fossil to the extant species *Cletocamptus retrogressus* Schmankevitsch, 1875. From that same site three cyclopoid fossils were discovered as well, although the incomplete preservation of the specimens did not allow an accurate generic identification—none of the body appendages was described, and the identification at the order-level was based only on the body shape (Palmer 1960, 1969).

The early to middle Miocene Barstow Formation (from ~13.4 to 19.3 mya) became world-famous both for its terrestrial vertebrate fossils and the exceptionally preserved non-marine arthropod fauna (crustaceans, insects, water mites, and spiders) discovered in the middle and upper portions of the ca. 1000 m thick lacustrine and fluvial deposits (Park and Downing 2001). Mineralogy of the sediments, the composition of the arthropod fauna (e.g., fairy shrimps, biting midge *Dasyhelea*) and the presence of halophile diatoms indicated that Barstow lake was a shallow, poorly mixed, saline-alkaline lake in a warm temperate environment moister than today (Park 1995; Park and Downing 2001; Wilkinson et al. 2010). Concerning the zoogeographic affinities, Palmer (1957: 244) found that Barstow arthropods did not show “clear-cut resemblance” with the faunas of Central and South America, instead some forms seemed more related to groups now living in Europe, North Africa, Asia Minor and Central Asia (Turkestan), or to taxa distributed in SE Asia and tropical Americas. On the other hand, Belk and Schram (2001) found that the closest relative of the Miocene fairy shrimp *Branchinecta barstowensis* Belk and Schram, 2001 was the extant *B. pollicifera* Harding, 1940 known only from Peru and Bolivia (Volcanic Western Andes Cordillera). Rogers and Coronel (2011) hypothesized a very ancient Paleozoic–Mesozoic, or alternatively a recent (via the Isthmus of Panama) dispersal of the ancestor of these species in North- and South America.

All attempts so far made to reconstruct the biogeographic history of the freshwater copepods could only use indirect evidences on their evolution, such as phylogeny and the geographic distributional patterns of the modern species. Recent collections in Rainbow Canyon in the Mud Hills and at the Black Canyon have resulted in numerous well preserved copepod fossils (Cyclopoida and Harpacticoida) that may provide a large amount of information on copepod evolution in continental waters. This paper presents the results of the study of cyclopoid fossils belonging to the genus *Apocyclops* Lindberg, 1942. The silicified *Apocyclops* fossils, preserving even the finest microstructures, allowed us to make inferences about the taxonomic relationship of the Miocene form and yielded unexpected information on the evolution of the larval development of the antennule. Further, comparing the morphology and the geographic distribution of *Apocyclops* and its close relatives, we propose a hypothesis of the geographic origin and minimal divergence time of the genus.

Institutional abbreviations.—MIZ, Museum and Institute of Zoology Polish Academy of Sciences, Warsaw, Poland; OUMNH, University of Oxford Museum of Natural History, Oxford, UK; UMNH, Utah Museum of Natural History, Salt Lake City, USA.

Other abbreviations.—ae, aesthetasc; CIII−V, third to fifth copepodid instar; enp 1−3, first to third endopodal segment; exp 1−3, first to third exopodal segment; P1−P6, legs 1 to 6; sp, seta transformed to short spine. Caudal setae are coded according to Huys and Boxshall (1991): II, anterolateral; III, posterolateral; IV, outer terminal; V, inner terminal; VI, terminal accessory; VII, dorsal.

Geological setting

The three-dimensionally preserved copepod fossils were found in Rainbow Canyon in the Mud Hills, 17 km north of Barstow (southern California; 35.024 N, 117.041 W) along with cypridid ostracod fossils with soft anatomy described by Wilkinson et al. (2010).

The age of the copepods could be inferred from the age of the volcanic tuffs associated to the fossil-bearing sediments. The fossil-bearing calcareous concretions were collected in the middle member of the Barstow Formation about halfway between the Rak Tuff (16.3 +/- 0.3 mya) and the Oreodont Tuff (15.8 +/- 0.3 mya) (Wilkinson et al. 2010), the cyclopid fossils therefore likely date back to the latest Burdigalian (or earliest Langhian). The few centimeters large concretions, found over a horizontal distance of about 500 m, are early diagenetic carbonate formed within the lake sediments, i.e. each concretion is a cemented zone that crosses lake sediment bedding planes. Lake sediments in the concretion zone are microlaminated with alternating dark and light laminae. These might represent varves, in which a pair of light and dark laminae are deposited in a one-year time period. The fossil-bearing concretions formed around lake sediments that likely represent several years, i.e. fossils within the same concretion may have lived several years apart. The fossils were recovered without knowledge of their position within the concretion. Whole concretions were etched in a 10% formic acid bath and concretion residues were examined for the silicified fossils.

Material and methods

Approximately 290 scanning electron micrographs were made (by LL and AAK) on the fossils and analysed (by MH). In total, 55 specimens (adults and larvae, with very few exceptions with complete body) were examined from Rainbow Canyon in the Mud Hills, of which 40 could be unambiguously identified as *Apocyclops*, 12 specimens belonged to the genus *Acanthocyclops* and 3 specimens (1 male, 1 CII larva and a separated head part) remained Cyclopidae indet.

None of the specimens shows a full set of the armature elements on the limbs; therefore, unless indicated otherwise, the descriptions show a combined morphotype inferred from the morphologies of more than one specimen. In coding the antennulary segments we followed

Huys and Boxshall (1991) and Schutze et al. (2000). For coding the antennulary setae we developed a system that is coherent between sexes and developmental stages (Fig. 1). For this study, the male antennule of *Euryte robusta* Giesbrecht, 1900 was used as a reference point, because it shows the largest set of the setal elements known for the family Cyclopidae (see Huys and Boxshall 1991). It is important to note that the same setation pattern occurs in the males of the less-oligomerized eucyclopine and cyclopine taxa (e.g., *Macrocyclops* Claus, 1893 and *Mesocyclops* Sars, 1914). Setal homologies on the proximal and terminal compound segments were inferred from the antennule setation in some distantly related copepod taxa with ancestral multisegmented antennule (e.g., *Cyclopicina longifurcata* [Scott, 1901] [Cyclopoida]; *Exumella polyarthra* Fosshagen, 1970 [Calanoida]; and *Platycopia inornata* Fosshagen, 1972 [Platycopioida]); in the comparisons, we used the illustrations provided by Huys and Boxshall (1991). Our observations on the postnaupliar development of the antennule of both female and male of *Mesocyclops acanthoramus* Holyńska and Brown, 2003 (SOM 1, 2; Supplementary Online Material available at http://app.pan.pl/SOM/appXX-Holynska_etal_SOM.pdf) helped in setting homologies in the distal half of the male antennule, which bears highly modified elements in the adult. Antennulary setation of the fossils has also been compared to the pattern present in the extant species of *Apocyclops* (*A. panamensis* [Marsh, 1913], *A.* cf. *ramkhamhaengi* Chullasorn, Kangtia, Pinkaew, and Ferrari, 2008; collecting data are provided in SOM 3).

Concerning the armature of the first compound antennulary segment (ancestral segments I–V), we hypothesize that the three aesthetascs belong to the ancestral segments I, III, and V, and the two setae that fail to form in most Cyclopidae are the anteroproximal ones on ancestral segments I and IV. Identity of the ancestral segments with missing anteroproximal setae was inferred from the configuration of the setae as they appear from copepodid I to adult female (Schutze et al. 2000; this paper) and the unique occurrence of an extra seta (in total, 9 setae are present on segment [I–V]) between setae III_d and IV_d (Fig. 1) in the female of *Acanthocyclops michaelseni* (Mrázek, 1901) (see Iepure and Meleg 2011: fig. 4D).

We also assume that the distal plate-like element on the compound segment XXI–XXIII in male is homologous with the anterodistal seta of segment XXII. The short medial seta on the terminal compound segment (XXVI–XXVIII) is assumed to represent the anteroproximal seta of segment XXVI, while the anterodistal seta of segment XXVI failed to form. Four setal elements of segment XXVIII are indicated as XXVIII–1,2,3,4.

Systematic palaeontology

Family Cyclopidae Rafinesque, 1815

Genus *Apocyclops* Lindberg, 1942

Type species: *Apocyclops dengizicus* (Lepechkine, 1900), Lake Selety Tengiz (northern Kazakhstan), extant.

Apocyclops californicus sp. nov.

Figs. 2–9.

Etymology: In reference to its origin from the state California in USA.

Holotype: UMNH IP 4824, adult female, ventral aspect showing nine body segments and caudal rami, caudal setae II–VI (VI intact, other setae are partly injured), antennule except for three terminal segments, antennal endopodite (allobasis cannot be verified), maxilla, P1–P4 (medial spine on P1 basipodite cannot be verified), spinule ornamentation on free segment of P5 and spinule ornamentation of pediger 5 anteriorly to P5.

Type locality: Mud Hills, 17 km north of Barstow, Southern California, USA.

Type horizon: Latest Burdigalian or earliest Langhian in the middle member of the Barstow Formation, Miocene.

Material.—Thirty eight specimens including adult (both sexes) and copepodid III−V instars; see SOM 3.

Description.—*Female*: Body length excluding caudal setae 730–945 µm (holotype 775 µm; mean 862 µm; n=13). Body nine-segmented (Fig. 2A$_1$, SOM 4: A). Prosome length/urosome length 1.1–1.4 (n=10); cephalothorax length/width 1.05 (UMNHIP 4834) to 1.20 (UMNH IP 4852); width of cephalothorax/width of genital double-somite 2.1 (UMNH IP 4852) to 2.3 (UMNHIP 4834). Body surface smooth, without rows of pits. Posterolateral corner of pediger 4 weakly produced. Genital double-somite as long as wide, with two low medial humps dorsally in anterior half of segment (SOM 4: B). In one female (Fig. 2B) two spermatophores ~43 µm long, forming nearly right angle, attached next to copulatory pore on ventral surface of genital double-somite, and an extra pair attached near anterior margin of double-somite. Anal operculum with straight posterior margin. Two medial hair-sensilla present (insertion sites verified in UMNH IP 4846) anterior to anal operculum. Posterior margin of anal somite bearing tiny spinules on ventral surface (Fig. 2A$_2$), spinules absent (or very tiny) on dorsal surface (SOM 4: C). Caudal rami (Fig. 2A$_2$, SOM 4: C) 4.2–4.8 times as long as wide (n=11) (holotype: 4.4; mean: 4.48), with lateral crest more distinct near insertion of posterolateral (III) seta. Tiny spinules present on dorsal surface of rami, no hairs on medial margin. Caudal ramus bearing six setae. Anterolateral (II) seta inserted at distance of 0.43–0.46 (n=9) ramus length measured from posterior end (Fig. 2A$_2$, SOM 4: C). No spinules present at insertion of antero- (II) and posterolateral (III) setae. Relatively large gap between insertion sites of posterolateral and outer terminal (IV) setae (Fig. 2A$_2$, D). Dorsal (VII) and posterolateral setae inserted nearly the same distance from posterior end of ramus (Fig. 2D). Seta III 1.9 (UMNH IP 4852; Fig. 2D) to 2.1 (UMNH IP 4839) times as long as terminal accessory seta (VI). Outer (IV) and inner terminal (V) setae thick at their base. Seta V (SOM 4C) ~1.5 and 4.0 times as long as seta IV and III, respectively, and about half as long as urosome length (UMNH IP 4852).

Antennule (Fig. 2C$_1$, see Fig. 9C) reaching posterior fourth of cephalothorax to middle of pediger 2, and composed of 11 segments: I–V, VI–VII, VIII–XI, XII–XIII, XIV, XV–XVI, XVII–XX, XXI–XXIII, XXIV, XXV, XXVI–XXVIII. Setation formula (Arabic numerals mean the number of setae on each segment): 8, 4, 6, 2, 2, 2, 3, 2+ae, 2, 2(+ae?), 6(?)+ae (UMNH IP 4824 [holotype], 4829, 4834, 4836, 4844 and OUMNH NT.233). Setae I$_\mathrm{d}$, II$_\mathrm{p–d}$, IV$_\mathrm{d}$, V$_\mathrm{d}$, VI$_\mathrm{p–d}$, VII$_\mathrm{p–d}$, VIII$_\mathrm{d}$, X$_\mathrm{d}$, XI$_\mathrm{p–d}$, XII$_\mathrm{d}$, XIII$_\mathrm{d}$, XIV$_\mathrm{p–d}$, XV$_\mathrm{d}$, XVII$_\mathrm{d}$, XVIII$_\mathrm{d}$, XX$_\mathrm{d}$, XXI$_\mathrm{d}$, XXIII$_\mathrm{d}$, XXIV$_\mathrm{p–d}$, XXV$_\mathrm{p–d}$, XXVI$_\mathrm{p}$, XXVII$_\mathrm{p–d}$, XXVIII-2, 3, 4, and aesthetascs Ae$_\mathrm{XXI}$ and Ae$_\mathrm{XXVIII}$ present (Figs. 2C$_1$, 3A$_1$, see Fig. 1); presence of setae III$_\mathrm{p–d}$, V$_\mathrm{p}$, IX$_\mathrm{p–d}$, and XVI$_\mathrm{d}$ was inferred from the positions of integumental holes indicating insertion sites of these setae. Seta XXVIII-1 and aesthetasc Ae$_\mathrm{XXV}$, present in extant *Apocyclops*, could not be verified in fossils. Setae VIII$_\mathrm{p}$, X$_\mathrm{p}$, XII$_\mathrm{p}$, and XIII$_\mathrm{p}$, missing in extant *Apocyclops*, were not found in the fossils either.

Antenna (Fig. 2C$_1$, C$_2$) with allobasis and two free endopodal segments (UMNH IP 4824 [holotype], OUMNH NT.233 and UMNH IP 4844). Presumptive coxobasis bearing exopodal seta and two medial setae, presumptive enp1 with one medial seta; enp2 (second free segment) with six setae on medial margin and four setae at mediodistal angle (Fig. 3A$_1$).

Mandibular palp reduced to two long and one short setae verified in copepodid V (UMNH IP 4832).

Maxillule (Fig. 2C$_2$) praecoxal arthrite bearing three mediodistal claws, one seta on ventral (or posterior) surface and one robust seta on medial margin next to mediodistal claws

(OUMNH NT.233 and UMNH IP 4845). Close to base of arthrite one long (feathered?) and one short seta as proximalmost element; other setae present in extant species could not be verified. Palp bearing one proximal seta, and at least two setae inserted on lateral lobe (three setae present in extant species). Robust spinous seta inserted on apical margin of the maxillulary palp, other elements (two more slender setae present in extant species) could not be verified.

Maxilla (Figs. $2C_2$, $3A_1$) composed of praecoxopodite, coxopodite, basipodite, and two-segmented endopodite (UMNH IP 4824 [holotype] and OUMNH NT.233). Arthrodial membrane between praecoxopodite and coxopodite failed to form on frontal surface; praecoxopodite bearing one endite with two setae, coxopodite with proximal and distal endite bearing one and two setae, respectively. Claw-like medial attenuation of basipodite with many fine spinules on concave margin. One robust seta inserted proximal to medial attenuation, and one shorter seta inserted on caudal surface near base of medial attenuation. Proximal endopodal segment bearing two setae, and distal endopodal segment bearing one large and two distinctly smaller setae (Fig. $3A_1$). Arthrodial membrane between distal endopodal segment and large terminal seta failed to form on frontal surface, but discernible on caudal surface.

Maxilliped is covered by other structures therefore the armature could not be verified.

Leg 1–4 rami (Fig. 3B, SOM 4: D) two-segmented. Setation (UMNH IP 4824 [holotype], 4826, 4829, 4844, 4845, 4860 and OUMNH NT.233) is shown in Table 1. Transverse row(s) of small spinules present on caudal surface of P1 (Fig. $2C_2$) and P4 intercoxal sclerites. Distal margin of P1 intercoxal sclerite (Fig. $2C_2$) with large and obtuse protuberances bearing small spinules; protuberances on P4 intercoxal sclerite reaching well beyond distal margin of sclerite and likely spinulose (inferred from the presence of spinules in male). P4 coxopodite (Fig. 3B) bearing many small, equal-sized spinules arranged in one row along distal margin, transverse medial row of small spinules near proximal margin, and tiny spinules arranged in group laterally to medial row on caudal surface (UMNH IP 4845). P1, P3 and P4 basipodite with rounded medial expansion (P2 not verified).

Lateral spine of exp1 distinctly oblique to exp2 spines in P1ï P4 (Fig. 2C$_2$, SOM 4: E). On terminal exopodal segments of P2–P4, spines conspicuously increasing in length from proximal to distal: length proportion of distalmost and proximalmost spines ~2.8 in P2 (UMNH IP 4826), 3.4–3.8 in P3 (UMNH IP 4826, 4860; see SOM 4: E) and 3.5 in P4 (UMNH IP 4826).

P4 enp2 (45 µm) apically bearing one lateral spine (25 µm) and one medial seta (70 µm) (measured on UMNH IP 4826).

P5 with one wide (width/length 1.6–2.1) free segment (Table 2, Fig. 3A$_2$, C), whole surface covered with small spinules (UMNH IP 4824 [holotype], 4826, 4829, 4846, 4852). Free segment bearing medial spine shorter than segment and one lateral seta inserted far from medial spine, near laterodistal corner of segment. Lateral seta of presumptive first segment of cyclopine P5 (Fig. 3C) inserted on laterodorsal surface of pediger 5. Pediger 5 ornamented with many small spinules arranged in field rather than row on dorsal surface next to insertion of lateral seta (Fig. 3C) and on ventral surface anterior to free segment (Fig. 3A$_2$). Presence of spinules could not be verified on ventral surface of pediger 5, medially to P5.

Male: Body length 590–765 µm (mean 709 µm; n=9). Body 10-segmented (Fig. 3D, E). Prosome length/urosome length 1.07–1.17 (Fig. 3D, E). Cephalothorax length/width 1.06—the cephalothorax dorsoventrally is slightly compressed therefore true proportion may be higher (UMNH IP 4856; Fig. 3E); cephalothorax width/genital segment width 2.5—true proportion may be lower as the cephalothorax is dorsoventrally compressed. Somites devoid of surface ornamentation formed by cuticular pits. Medial hair-sensilla(?), inferred from insertion sites, present on dorsal surface of pediger 5 (UMNH IP 4856). Anal operculum with straight posterior margin. Caudal rami 3.9–4.8 (mean 4.3; n=8) times as long as wide, no hairs on medial margin. Anterolateral (II) seta inserted at distance of 0.45–0.46 ramus length measured from posterior end (UMNH IP 4828, 4856). Large gap between insertion sites of posterolateral (III) and outer terminal (IV) setae. Dorsal (VII) and posterolateral (III) setae inserted nearly the same distance from posterior end of ramus. Seta III ~1.5 times as long as terminal accessory (VI) seta (OUMNH NT.234). Inner (V) and outer (IV) terminal caudal setae thick at their base.

Antennule (Figs. 4, 5) 16-segmented: I–V, VI–VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII, XIX–XX, XXI–XXIII, XXIV–XXVIII. In one male (UMNH IP 4858) the antennule is 17(or 18)-segmented (Fig. 3D, SOM 5: A), segments XXIV and XXV (segments 9 and 10 in female) remained separated instead of being fused, and segment XXV at least partly, also separated from segment XXVI–XXVIII. Fused condition of segments XXIV and XXV in the male is widely distributed in Cyclopoida (Huys and Boxshall 1991), and is also common, likely representing the plesiomorphic state in male Cyclopidae (Fig. 9B, D), therefore the separated state of these segments is considered here as a developmental aberration (an atavism?). The following setal elements and aesthetascs were identified (UMNH IP 4830, 4850, Figs. 4, 5, see also Figs. 1, 9, SOM 2): I_{d}, $\mathrm{II}_{p\text{–}d}$, $\mathrm{III}_{p\text{–}d}$, IV_{d}, $\mathrm{V}_{p\text{–}d}$, $\mathrm{VI}_{p\text{–}d}$, VII_{d}, VIII_{d}, IX_{d}, $\mathrm{Ae}_{\mathrm{IX}}$, X_{d}, $\mathrm{XI}_{p\text{–}d}$, XIV_{p}(?), XIV_{d}, XV_{p}, XVI_{d}, $\mathrm{XVII}_{p\text{–}d}$, XVIII_{p}, $\mathrm{Ae}_{\mathrm{XVIII}}$(?), $\mathrm{XIX}_{p\text{–}d}$, XX_{d}, XXI_{d}, $\mathrm{Ae}_{\mathrm{XXI}}$, XXII_{d}, XXIII_{d}, $\mathrm{XXIV}_{p\text{–}d}$, XXV_{p}, XXVI_{p}, $\mathrm{XXVII}_{p\text{–}d}$. Presence of setae I_{d}, and IV_{d} was inferred from the position of integumental holes indicating insertion sites of these setae. Setae XIX_{d}, XXI_{d}, and XXII_{d} transformed to striated plate-like structures on segment 14 (XIX–XX) and segment 15 (XXI–XXIII). One large oval pore (SOM 5: A) with longer diameter ~2 μm on proximal plate (modified seta XXI_{d}) of segment 15 (UMNH IP 4858).

Antenna (Figs. 4A, 5A) composed of allobasis and two free endopodal segments. Exopodal seta present on presumptive coxobasis. Second endopodal segment (second free segment of antenna) bearing 8 setae (4 on medial margin and 4 at mediodistal angle). The antennal setation was verified in one specimen only (UMNH IP 4850). The nine-setae state of the second endopodal segment presumably is also present in the adult male, because one male copepodid V (UMNH IP 4825) had nine setae on this segment.

Endopodite of maxilla: arthrodial membrane formed on caudal surface between distal endopodal segment and large terminal seta.

P2–P4 rami 2-segmented, setation pattern as in Table 3 (UMNH IP 4828, 4840, 4850, 4856, 4858). P3 and P4 intercoxal sclerites (Fig. 6A_1, A_2) with transverse rows of spinules in middle line and near distal margin on caudal surface; large obtuse protuberances on distal margin, those of P4 bearing spinules. P4 coxopodite (Fig. 6A_2) bearing many small equal-sized spinules arranged in single row along distal margin, small spinules present at proximolateral and distalolateral angle. Medial expansion of P4 basipodite (Fig. 6A_1, A_2) rounded and bearing spinules. Spines on P2 exp1 and P3 exp1 distinctly oblique (Fig. 3D), and to less extent the proximalmost spine of P2 exp2 also oblique to other spines of P2 exp2; P2 exp1 spine with fine setules (UMNH IP 4828, 4858). On terminal exopodal segments of P2−P4, spines conspicuously increasing in length from proximal to distal: length proportions of distalmost and proximalmost spines 3.2, 3.8, and 2.9 in P2, P3, and P4, respectively (P2−P3, UMNH IP 4840; P4, UMNH IP 4850). P4 enp2 (length 42 μm) ~2 times as long as wide (UMNH IP 4850).

P5 free segment 1.2–1.6 times as wide as long (Fig. 6A_1, B, SOM 4: F, SOM 5: B), likely covered with spinules (UMNH IP 4850, 4856, 4858). Free segment with medial spine 1.4–2.7 times longer than segment (UMNH IP 4850, 4856) and lateral seta inserted at laterodistal corner, far from medial spine. Lateral seta of presumptive first segment of cyclopine P5 inserted on laterodorsal surface of pediger 5 (Fig. 6B). Anteriorly to P5 free segment, pediger 5 ornamented with small spinules arranged in field rather than single row (Fig. 6A$_1$, A$_3$); medially to P5 spinules arranged in triangular pattern on ventral surface of somite (UMNH IP 4850).

P6 bearing three elements (Fig. 6C), medial (13 µm) and middle (12 µm) setae subequal in length, and long lateral seta (40µm) (UMNH IP 4828; body length:765 µm). P6 flap with transverse rows of spinules (UMNH IP 4850).

Copepodid V (female and male): Body length 620 µm (UMNH IP 4854) to 875 µm (UMNH IP 4841); mean 748 µm; n=10. In one female (UMNH IP 4857; Fig. 8A, SOM 5: C) and one male (UMNH IP 4825; Figs. 7A, 8B), in which the sex could be identified by the laterodorsal and ventral position of P6, respectively, the body size significantly differed: female ~780 µm, and male 640 µm. Body composed of nine somites, anal somite longer than wide. Prosome length/urosome length 1.20–1.35 (UMNH IP 4825, 4832, 4835, 4841, 4851). In one CV larva (UMNH IP 4841) two spermatophores attached ventrally, next to posterior margin of genital somite (SOM 5: D); length of spermatophore 43 µm. Caudal rami 3.4–3.7 times as long as wide (mean: 3.5; n=6), bearing six setae (SOM 5: E). Anterolateral (II) seta inserted at distance of 0.42 ramus length measured from posterior end (UMNH IP 4851). Large gap between insertion sites of posterolateral (III) and outer terminal (IV) setae. Seta III ~1.6 times as long as terminal accessory (VI) seta (UMNH IP 4851, body length 770 µm). Inner (V) and outer (IV) terminal setae thick at their base. Dorsal (VII) seta 1.3 times as long as seta III (UMNH IP 4851).

Antennule (Fig. 7B, SOM 6: A) as in adult female 11-segmented, and reaching to or slightly beyond posterior margin of cephalothorax (UMNH IP 4825, 4832, 4848, 4857). The following setae and aesthetascs were identified: $\mathrm{I_d}$, $\mathrm{II_d}$, $\mathrm{III_{p-d}}$, $\mathrm{IV_d}$, $\mathrm{V_{p-d}}$, $\mathrm{VI_p}$(?) in UMNH IP

4848, VI_d(?) in UMNH IP 4848, $VII_{p–d}$, $VIII_d$, IX_d, X_d, $XI_{p–d}$, XII_d, $XIV_{p–d}$, XV_d, $XVII_d$, $XVIII_d$, XX_d, XXI_d, Ae_{XXI}, $XXIV_{p–d}$, $XXV_{p–d}$, Ae_{XXV}, $XXVI_p$(?) in UMNH IP 4857, $XXVII_{p–d}$, XXVIII-2,3,4, Ae_{XXVIII} (UMNH IP 4825, 4848, 4851, 4857). Presence of seta $XXIV_d$ and aesthetasc Ae_{XXI} were inferred from the insertion sites of these elements. Setae XII_p and $XIII_p$ absent in adult female, were not found in CV female either (UMNH IP 4857; Fig. 7B); presence of setae XII_p and $XIII_p$ could not be verified in CV male (UMNH IP 4825; SOM 6: A). Setae $VIII_p$ and X_p (missing in both adult female and male), which might be inserted on ventral surface of the compound segment 3 (VIII–XI) could not be verified, as the copepodids (UMNH IP 4825, 4848, 4851, 4857) showed the dorsal surface of the antennule. At least one of the CV larvae is a male (UMNH IP 4825), yet none of the additional armature elements, typical of the male, could be verified on the antennule (SOM 6: A).

Antenna (Fig. 7C) with allobasis, setation of allobasis as in adults (UMNH IP 4825, 4854). Enp2 with five setae on medial margin and four setae at mediodistal corner.

Mandibular palp (Fig. 7D) bearing two long and one short setae (UMNH IP 4832).

P1–P4 rami (Fig. 7E) two-segmented (P3 endopodite was not verified), armature formula shown in Table 4 (UMNH IP 4825, 4832, 4854, 4857). Transverse row of spinules present near distal margin on caudal surface of P4 intercoxal sclerite (Fig. 8B), and a second row likely also present at the middle of sclerite. Two obtuse protuberances on distal margin of intercoxal sclerite with relatively large spinules (UMNH IP 4825). P4 basipodite (Fig. 8B) with rounded medial expansion (UMNH IP 4825, 4854). On terminal exopodal segments of P2–P4 distalmost spines significantly longer than proximalmost spines (exact measurements were not possible).

P5 (UMNH IP 4825, 4832, 4841, 4857) appearing in female copepodid as a lateroventral lobe (UMNH IP 4857; Fig. 8A) rather than separated segment, with slight cuticular invagination between presumptive free segment and pediger 5, while separation of P5 segment rather distinct in the male (UMNH IP 4825; Fig. 8B). P5 segment (or lobe) bearing two setae (UMNH IP 4857, medial seta/lateral seta = 21 µm/17 µm, body length 780 µm; UMNH IP 4832, medial seta/lateral seta = 24 µm/23 µm, body length 840 µm; UMNH IP 4841, medial seta/lateral seta = 24 µm/23 µm, body length 875 µm), with wide gap between setae. Lateral seta (UMNH IP 4857, 19 µm) of presumptive first segment of cyclopine P5 similar in length to lobe setae, and inserted on laterodorsal surface of pediger 5 (Fig. 8A). Presence of spinules on P5 lobe could not be confirmed unambiguously, but few spinule-like structures were observed in UMNH IP 4825, 4841, and 4857. Medially to P5, row of longer spinules present on ventral surface of pediger 5 (UMNH IP 4841; SOM 5: D).

P6 sexually dimorphic: in female (Fig. 8A) low hump likely bearing three elements on laterodorsal surface near posterior margin of genital segment − posteriormost element unambiguously confirmed, two more anterior setae injured (UMNH IP 4857); in male one thick (medial spine) and one slender element (supposed to be one of the two lateral setae, see Fig. 8B) were confirmed on ventral surface next to posterior margin of genital segment (UMNH IP 4825).

Copepodid IV: Body length 575 µm (UMNH IP 4835); prosome length/urosome length 1.2. Body (Fig. $8C_2$) composed of eight segments, anal somite longer than wide. No spinules present on posterior margin of anal somite (lateral view). Caudal rami measured across its widest part 3.2 times as long as wide, and bearing six setae. Anterolateral (II) seta inserted at distance of 0.44 ramus length measured from posterior end. Large gap between insertions of posterolateral (III) and outer terminal (IV) setae. Spinules absent at insertion of seta II and III. Seta III ~1.8 times as long as terminal accessory seta (VI). Outer (IV) and inner (V) terminal setae thick at their base. Dorsal (VII) seta (42 µm) 1.6 times as long as seta III.

Antennule not reaching posterior margin of cephalothorax. More proximal segments are covered with sediments, only five terminal articles (XVII–XX, XXI–XXIII, XXIV, XXV and XXVI–XXVIII) could be confirmed.

P1–P4 exopodites two-segmented (endopodites not verified). Presence of lateral basipodite setae was confirmed in P1 and P3 (Fig. 8C$_1$, C$_2$). Proximal exopodal segment with one spine in P1–P4, distal exopodal segments of P1–P4 with 3, 4, 4, 3 spines. Distalmost spines significantly longer than proximalmost ones on terminal exopodal segments of P2–P4. P5 (Fig. 8C$_1$) lobe-like, not separated from pediger 5 with arthrodial membrane, and bearing medial (15 µm) and lateral (14 µm) setae. Lateral seta (14 µm) of presumptive first segment of cyclopine P5 inserted on laterodorsal surface of pediger 5. P6 (Fig. 8C$_1$) composed of two setae (medial ~12 µm, lateral 10 µm) inserted ventrally on posterior margin of genital segment (urosomite 2).

Copepodid III: Body length 560 µm (UMNH IP 4849), prosome length/urosome length: 1.6. Body (Fig. 8D$_1$, SOM 6: C) composed of 7 segments, anal somite 1.4 times as long as wide. Anal operculum with straight posterior margin. Caudal rami (SOM 6: C) 2.8 times as long as wide (true proportion may be higher, as the specimen is dorsoventrally compressed), bearing six setae. Anterolateral (II) seta (13 µm) inserted at distance of 0.44 ramus length measured from posterior end. Wide gap between insertions of posterolateral (III) and outer terminal (IV) setae. Outer (IV) and inner (V) terminal setae thick at their base. Length of terminal accesory seta (VI), and setae V, IV and III, 18 µm, 148 µm, 123 µm and 28 µm, respectively. Dorsal (VII) seta 1.4 times as long as seta III. Conspicuous lateral keel present on caudal rami posteriorly to insertion of seta II.

Antennule (Fig. 8D$_2$) reaching about posterior third of cephalothorax, 9-segmented: I–V, VI–XI, XII–XIV, XV–XVI, XVII–XX, XXI–XXIII, XXIV, XXV, XXVI–XXVIII. The following setal elements were confirmed (dorsal view): III_d(?), VII_d, XI_d, XIV_p, XV_d, $XVII_d$, $XVIII_d$, XXI_d, $XXIII_d$, $XXIV_{p–d}$, $XXV_{p–d}$, $XXVI_p$, and at least four apical elements on terminal segment (XXVI–XXVIII).

P5 covered with sediment, yet two elements, a robust seta (or spine) and more dorsally a slender seta were confirmed. Insertion site of slender seta (on P5 lobe, or laterodorsally on pediger 5) could not be verified.

Discussion

The morphology of leg 5 (single wide segment bearing two elements inserted far from each other), the presence of the antennal allobasis and ten setae on the penultimate endopodal segment of the antenna, a 11-segmented antennule, the segmentation and setation of the swimming legs, and the presence of one seta and one spine on the distal endopodal segment of leg 4 leave no doubt that Barstow copepods here examined belong to the extant cyclopid genus, *Apocyclops*.

The genus with eight nominal (+ two unpublished; Arnofsky 1996 and Botelho 2000) extant species occurs in the warm temperate and tropical regions, from about 50° North (Central Asia) to ~30° South in Australia and South America (Bayly 1976; Timms 1993; Botelho 2000; Menu-Marque 2000-2001; Karanovic 2004; Gusakov 2011). The United States is distinguished by its relatively rich fauna, with the exception of *A. procerus* (Herbst, 1955) (southern Brazil and Argentina), all the taxa reported from the Americas occur in this country (Reid et al. 2002; Dussart and Defaye 2006): *Apocyclops dimorphus* (Kiefer, 1934), *A. panamensis* (Marsh, 1913), *A. panamensis tannica* (Davis, 1948), *A. spartinus* (Ruber, 1968), one unpublished species from California (Arnofsky 1996) and another unpublished one from Louisiana (USA) and San Salvador Island (Bahamas) (Botelho 2000). Three species, *A. royi*

(Lindberg, 1940), *A. borneoensis* Lindberg, 1954, and *A. ramkhamhaengi* Chullasorn, Kangtia, Pinkaew, and Ferrari, 2008, are known from East and Southeast Asia (Dussart and Defaye 2006; Chullasorn et al. 2008; Yoon and Chang 2008). At least two species, *A. dengizicus* (Lepechkine, 1900) (Karanovic 2004; Dussart and Defaye 2006) and *A.* cf. *ramkhamhaengi* (new record reported herein, see SOM: 3), occur in Australia, and one, *A.* cf. *borneoensis*, was recorded from the Southern Pacific (Fiji) (Yeatman 1983). Two or three taxa, *A. dengizicus*, *A. dengizicus elamicus* (Lindberg, 1940) and *A. royi*, occur from India to North Africa (Kiefer 1948, 1978; Dussart and Defaye 2006; Turki and Turki 2010). In contrast, very few species (none is perhaps native) are known from tropical Africa, south of the Sahara. *Apocyclops panamensis* has been found in a few places in the Ivory Coast (Dumont and Maas 1988) and Egypt (Nile Delta and Lake Qarun region) (El Shabrawy and Belmonte 2004; El Shabrawy 2013), but the wide distribution of the species in the eastern United States and Middle America and the reports on fish restocking in Lake Qarun from the coastal waters of Egypt (El Shabrawy and Belmonte 2004) suggest that *A. panamensis* could be introduced via ballast waters and fishery to African waterbodies. An *Apocyclops* reported as *A.* cf. *dengizicus*, whose correct identity and origin needs to be verified, lives in the hypersaline St. Lucia Estuary on the east coast of South Africa (Carrasco and Perissinotto 2012).

A specific ecological character of *Apocyclops* is its wide spectrum of salinity tolerance (0−~100 gl^{-1}), which supposedly is an evolutionarily ancient adaptation present in several lineages of the Cyclopidae to drastically changing water chemistry of the ephemeral continental waters (Löffler 1961; Hammer 1986; Dexter 1993; Timms 1993; Reid et al. 2002; Pinder et al. 2005; Carrasco and Perissinotto 2012). *Apocyclops* species have been found sometimes in extreme high density in inland saline lakes and coastal lagoons, pools, salt marshes, and phytotelmata (Yeatman 1983; Reid et al. 2002). Fresh or oligohaline environments can be suboptimal for *Apocyclops*, as evidenced by the fact that there are no (or very few) records of the genus from true freshwater habitats, not having even temporary connection with salt water (Reid et al. 2002). Experiments (Dexter 1993) testing survivorship of both larvae and adults of "*Apocyclops dengizicus*" (=*Apocyclops dimorphus*) from the Salton Sea in southern California at various salinities showed that low salinity (0.5−1.0 gl^{-1}) resulted in worse survival of the nauplii, decrease of the body size of the gravid females and lower densities in long-term cultures. Though euryhalinity is observed in some species belonging to different genera of the Eucyclopinae–Cyclopinae lineage (e.g., *Cyclops*, *Diacyclops*, *Acanthocyclops*, *Metacyclops*, *Eucyclops*) (Löffler 1961; Hammer 1986; Di Lorenzo and Galassi 2013), *Apocyclops* as a whole is adapted to saline environment, suggesting that the ancestor of the genus could have lived in saline waters. Hence the Miocene finding of *Apocyclops* in the saline Barstow lake in southern California is in good agreement with what is known about the ecology and zoogeography of the extant species of the genus.

Apocyclops californicus is a member of the *panamensis*-group comprising *A. panamensis*, *A. panamensis tannica*, *A. spartinus*, *A. procerus*, *A. borneoensis*, *A. royi*, *A. ramkhamhaengi*, and two unpublished species from California, Louisiana, and Bahamas (Arnofsky 1996; Botelho 2000; Reid et al. 2002; Chullasorn et al. 2008). The group can be defined by at least one synapomorphy, i.e. the fusion of the antennal coxobasis and first endopodal segment (allobasis). Antennal allobasis frequently occurs in the freshwater Harpacticoida and is typical of the cyclopoid Oithonidae, but it is a rare feature in Cyclopidae. We know only two other cyclopid taxa, the genus *Orthocyclops* Forbes, 1897 and *Diacyclops incolotaenia* (Mazepova, 1950), in which the antennal allobasis is present. There are also other characters that distinguish the *panamensis*-clade from rest of the genus (i.e., *dengizicus*-group: *A. dengizicus*, *A. dengizicus elamicus*, and *A. dimorphus*) (Arnofsky 1996; Botelho

2000; Reid et al. 2002; Chullasorn et al. 2008), such as the rounded medial expansion of the basipodite of the swimming legs, the short medial spine on leg 1 basipodite (not reaching the distal margin of the terminal endopodal segment), the short lateral spine on the terminal endopodal segment of leg 4 (lateral spine 0.5−0.8 times as long as segment), and the presence of spinules on the ventral surface of pediger 5, the polarity of which is yet difficult to infer without a rigorous phylogenetic analysis. In an inspiring work Schutze et al. (2000) examined the postnaupliar development of the antennule in the family Cyclopidae, and proposed another alleged apomorphy of the *panamensis*-clade. The adult female has 11-segmented antennule in all *Apocyclops* species, but the number of the antennulary segments in the CIV and CV instars varies within the genus. In *A. dengizicus* (the specimen from Coahuila, Mexico was likely conspecific with *A. dimorphus*; see Reid et al. 2002: 10) the antennule is 10-segmented in the CIV and 11-segmented in CV instar (the ancestral developmental pattern in Cyclopidae), while in *A. procerus* (a member of the *panamensis*-clade) the antennule is 9-segmented in the CIV and 10-segmented in the CV instars. This delayed developmental pattern has been reported also for an Indian representative of the *panamensis*-group, supporting the hypothesis of Schutze et al. (2000). The Indian population (from Bandra Creek, Bombay) was identified by Valderhaug and Kewalramani (1979) as *A. dengizicus*, but the antennal allobasis and the rounded medial expansions of P1–P4 basipodites, figured by the authors, unambiguously place the Indian *Apocyclops* (*A. royi*?) into the *panamensis*-clade rather than in the *dengizicus*-group. The Miocene fossils somewhat modify this evolutionary scenario, because the fifth copepodid instar of *A. californicus* already shows the 11-segmented state, which suggests that the delayed development of the antennule was not a character present in the ancestor of the *panamensis*-group, it appeared later in the course of the evolution of the group. Concerning the setation pattern of the female antennule in the extant *Apocyclops*, there are some discrepancies between the authors (e.g., Mirabdullayev and

Stuge 1998; Schutze et al. 2000; Reid et al. 2002; Chullasorn et al. 2008; Yoon and Chang 2008), and possibly only partially corresponding to real intrageneric variation. The setation 8, 4, 6, 2, 2, 2, 3, 2+ae, 2, 2+ae, 7+ae was found in *A. ramkhamhaengi* (Chullasorn et al. 2008) and in both extant species (*A. panamensis* and *A.* cf. *ramkhamhaengi*) here compared and belonging to the *panamensis*-clade (Fig. 9). The antennule setation in the Miocene form is almost fully congruent with the pattern known in the *panamensis*-group. We failed to find the aesthetasc on segment 10 (ancestral segment XXV) and the small terminal seta (XXVIII-1) on segment 11, but this is very likely due to the injury of these structures. The same setation pattern (though segmentation can be different) is present in the less derived *Metacyclops* taxa (e.g., *M. oraemaris* Rocha, 1994 and *M. hirsutus* Rocha, 1994; see Rocha 1994), and other genera more or less closely related to *Metacyclops*, such as *Fierscyclops* Karanovic, 2004 (De Laurentiis et al. 2001; Boonyanusith et al. 2013), *Allocyclops* Kiefer, 1932 (sensu Fiers 2012), *Hypocyclops* Fiers, 2012, which suggests that this setation pattern could be a plesiomorphy shared by the ancestor of *Apocyclops*, and then retained by the members of the *panamensis*-clade. On the other hand, additional setal elements have been reported on the antennule in the *dengizicus*-group. Mirabdullayev and Stuge (1998) showed three setae inserted on the fourth antennulary segment (XII−XIII) in the adult female of *A. dengizicus*, but only two setae were figured by Reid et al. (2002). Also, three elements are shown on this segment in the CV instar of *A. dengizicus* (= *A. dimorphus*; see Reid et al. 2002) from Mexico (Schutze et al. 2000). The extra element is the anteroproximal seta XII_p, that fails to form in the *panamensis*-group. (see Figs. 1 and 9). We are not aware of any similar case in the Cyclopidae, where the anteroproximal seta XII_p (and $XIII_p$?) is present while setae $VIII_p$ and X_p are absent in the female, which seems to be the case of the *dengizicus*-group. In general, higher number of setae is considered ancestral if compared to a reduced setation pattern, as in the Crustacea (incl. Copepoda) evolution seemed to have proceeded towards character’s losses and fusion

(Huys and Boxshall 1991; Adamowicz and Purvis 2006). Yet, the unusual pattern in the *dengizicus*-group suggests that presence of seta XII_p might be an apomorphy or a developmental aberration rather than the plesiomorphic state in *Apocyclops*. Another extra seta (XVI_p) was also figured on segment 6 (XV−XVI) in *A. dengizicus* (Mirabdullayev and Stuge 1998; Reid et al. 2002). This element appears in the male of the Cyclopidae, but it is (almost) never expressed in the cyclopid female (neither is it present in the female of the basal Euryteinae), which again indicates that seta XVI_p in the female is likely an autapomorphy or an aberration in *A. dengizicus*. Numerous developmental abnormalities were observed on the maxilla and swimming legs in a culture of *A. ramkhamhaengi* (Chullasorn et al. 2008) in Thailand, and even among the Miocene fossils one male had unusual segmentation of the antennule (SOM 5: A), which suggest that morphological abnormalities may be not so rare in *Apocyclops*.

While the evidences are strong about the group affiliation of *A. californicus*, it is difficult to infer the relationships within the *panamensis*-clade, because the morphology (the mouthparts in particular) is still insufficiently known in some species. If the delayed development of the antennule segmentation would be present in all extant representatives of the *panamensis*-group, then none of them could be the sister of *A. californicus*—but we know the antennular development just in three of the ten taxa (including *A. californicus* and two unpublished species in the Ph.D. theses of Arnofsky [1996] and Botelho [2000]) of the *panamensis*-group. Nonetheless it can be stated with certainty that the Miocene fossils are not conspecific with any known representative of the group. *Apocyclops californicus* can be distinguished from other members of the *panamensis*-clade by the: (i) spinule ornamentation of the free segment of P5 (spinules absent in *A. borneoensis*, *A. panamensis*, *A. procerus*, and *A. royi*); (ii) short medial spine of P5 (medial spine at least as long as free segment in *A. borneoensis*, *A. panamensis*, *A. procerus*, *A. ramkhamhaengi*, *A. royi*, and *A. spartinus*); (iii) small spinules arranged in scattered pattern rather than single row on the ventral surface of pediger 5 anterior to P5 (spinules are longer and arranged in row in *A. borneoensis*, *A. panamensis*, *A. procerus*, *A. ramkhamhaengi*, *A. royi*, and *A. spartinus*); (iv) and the relatively large protuberances of P4 intercoxal sclerite (protuberances slightly reaching beyond the distal margin of P4 intercoxal sclerite in *A. borneoensis*, *A. panamensis*, *A. procerus*, *A. ramkhamhaengi* and *A. royi*,) (Lim and Fernando 1985; Arnofsky 1996; Botelho 2000; Chullasorn et al. 2008).

The *Apocyclops* body plan basically conforms to that of a *Metacyclops* with one seta and one spine on the distal endopodal segment of P4, and wide P5 segment with large gap between setae. A world-scale phylogenetic analysis has not been attempted in *Metacyclops* yet, but the recent studies (Fiers 2001, 2012; Karanovic 2004; Karanovic et al. 2011) on *Metacyclops*-related taxa suggest that the genus might be paraphyletic rather than monophyletic, giving rise to a few more derived genera (e.g., South America, *Hesperocyclops* Herbst, 1984, *Virbiocyclops* Fiers, 2012; Africa, likely *Allocyclops* Kiefer, 1932; Australia, *Meridiecyclops* Fiers 2001, *Fierscyclops* Karanovic, 2004, *Pescecyclops* Karanovic, Eberhard, and Murdoch 2011). The very close relationships of *Apocyclops* and *Metacyclops* are reflected in the fact that almost all the *Apocyclops* taxa have been formerly allocated to the genus *Metacyclops* (or to *Cyclops* [*Metacyclops*]). The two genera show an intriguing contrast in the geographic patterns of the species richness. *Metacyclops* (65 [sub]species), a predominantly tropical group, shows highest diversity in South America (19) and Africa (15). The further we are from these continents the lower species richness can be observed: ten species live in the Western Palearctic, nine in Middle America, seven in Australia (five of those are recently moved to the genus *Pescecyclops* erected by Karanovic et al. 2011), five in the Oriental region (India+SE Asia), three in East Asia (two of which are shared with the

Oriental), two in Siberia (shared with western Palearctic), two in North America, and one in Madagascar (shared with Africa) (Dussart and Defaye 2006; Defaye and Por 2010; Mercado-Salas et al. 2013). In contrast *Apocyclops* has five species (*A. panamensis*, *A. spartinus*, *A. dimorphus* and two unpublished species (Ph.D. theses of Arnofsky [1996] and Botelho [2000]) in North America, two (*A. panamensis* and *A. dimorphus*) in Middle America and two (*A. panamensis* and *A. procerus*) in South America, four (*A. borneoensis*, *A. ramkhamhaengi*, *A. royi* and *A. dengizicus*) in the Oriental region, at least two species (*A. dengizicus* and *A.* cf. *ramkhamhaengi*) live in Australia, while Africa harbors two native species (*A.* cf. *royi* and *A. dengizicus*) in North and one (*A.* cf. *dengizicus*, likely shared with North Africa) in South Africa. Competitive exclusion between these genera is unlikely, because both *Metacyclops* and *Apocyclops* live in a wide variety of habitats including benthic/semiterrestrial and limnetic ones in epigean and subterranean systems. Both genera are thermophilic, therefore the underlying causes of the contrasting geographic pattern of the species richness in these genera can be historical.

The disjunct distribution of the extant *Apocyclops* between warm temperate and (sub)tropical Americas and Asia (*panamensis*-clade: eastern US, Middle- and South America, East Asia [as far as Honshu], Southeast Asia, Australia and southern Pacific, India; *dengizicus*-group: southern part of USA [California, Texas, Florida], Mexico and Antilles, Western- and Central Asia, India, Australia) with few outliers (*A. royi* and *A. dengizicus*) in North and South Africa, suggests an early Cenozoic origin of the genus in the northern hemisphere. Similar, tropical amphi-Pacific disjunctions in the aquatic invertebrates (e.g., Trichoptera, Ostracoda, Copepoda, and Cladocera in particular) have recently been overviewed by Van Damme and Sinev (2013). According to this scenario, the ancestor of *Apocyclops* could have originated in North America and/or Eastern Palearctic in the Paleocene–Eocene, when a much warmer climate allowed dispersal of the warm-temperate–

tropical fauna between Siberia and Alaska across Beringia (Sanmartín et al. 2001; Brikiatis 2014). In the early Cenozoic the Beringian land bridge was exposed in the early (66–65 mya) and late Paleocene (in a short period between 59 and 58 mya). Intermittent connections could also exist between Alaska and Siberia in the Eocene until the late Miocene (Tiffney 1985; Brikiatis 2014). Climate cooling that started in the late Eocene caused gradual southward shifts of the geographic range on both sides of the Pacific ocean. The middle Miocene (~16 mya) age of the *Apocyclops* fossils with unambiguous affinity to a subgroup of the genus (the *panamensis*-clade) also supports an early Miocene or Paleogene origin of the genus. Concerning *Metacyclops*, the large taxonomic and morphological diversification (including less-oligomerized ancestral morphology) of the genus in South America and Africa suggest an older, Gondwanan origin. The scarcity of *Metacyclops* in subtropical eastern Asia and in the United States does not seem to be consistent with a very ancient Pangean age and distribution, as it was suggested by Defaye and Por (2010). This implies that the ancestor of *Apocyclops* should have arrived in North America–East Palearctic from the southern hemisphere. Significant pre-Miocene trans-Tethyan dispersal of the land vertebrates has been documented between South and North America in Campanian (Late Cretaceous)–Paleocene, between Africa and Europe in Campanian (Late Cretaceous)–late Eocene, and between India and Eurasia since the Maastrichtian (Late Cretaceous) (Rage 1997; Ezcurra and Agnolín 2012). The most obvious hypothesis might be that *Apocyclops* originated from a *Metacyclops*-like ancestor that lived in South America. Interestingly, however, it is not the Neotropics but Europe (the peri-Mediterranean region) where the “seta+spine” armature of the terminal endopodal segment of P4, a character state present in all *Apocyclops*, appears in two cave-dwelling *Metacyclops* (*M. stammeri* Kiefer, 1938 from Apulia, Italy and Montenegro, and *M. longimaxillis* Defaye and Por, 2010 from Israel) (Kiefer 1938; Karanovic 1999; Defaye and Por 2010). Among the extant *Metacyclops* these species are the only ones with this character state. In fact the swimming legs in *M. longimaxillis* show stunning similarity to those in the *Apocyclops panamensis* group. There are also other similarities between *Apocyclops* and *M. stammeri* and *M. longimaxillis*, such as the anterior positon of the anterolateral (II) caudal seta, swollen base of the inner terminal (V) caudal seta (in *Apocyclops* both terminal setae are thick), relatively large gap between the insertions of posterolateral (III) and outer terminal (IV) caudal setae, and lack of breaking plane of the terminal setae (IV and V). Both *M. stammeri* (from an anchialine cave) and *M. longimaxillis* (from a groundwater pool in cave) live in saline/brackish waters. Nonetheless, *M. stammeri* and *M. longimaxillis* display the *Metacyclops*-state of the fifth leg (segment longer than wide, setae on free segment inserted close to each other) rather than the *Apocyclops* state. The “seta+spine” armature of the P4 endopodite is also present in the highly derived *Pilbaracyclops* Karanovic, 2006 (Western Australia) and *Yansacyclops* Reid, 1988 (South America). There is no shared apomorphic character that would support sister relationship between *Apocyclops* and *Pilbaracyclops* (Karanovic et al. 2011), though these groups might have a common *Metacyclops*-like ancestor (also shared by other lineages) that once lived on Gondwana. *Yansacyclops* differs from *Apocyclops* in several characters (segmentation and setation of the antennule, shape of seminal receptacle, morphology of P5 and caudal setae) which indicate even more distant relationships between these genera.

The spinulose surface ornamentation of pediger 5 anteriorly to the P5 free segment and/or next to the insertion of the remnant seta of the presumptive proximal segment of P5, is another character widely distributed in *Apocyclops* and rare but present in *Metacyclops*. The character is expressed in *M. mendocinus* (Wierzejski, 1892) (observed in populations from Cuba and Puerto Rico), *M. leptopus mucubajiensis* Kiefer, 1956 (Venezuela), *M. superincidentis* Karanovic, 2004 (Western Australia) and in the European(!) *Metacyclops problematicus* Dumont, 1973 (Belgium) (Kiefer 1956; Dumont 1973; Smith and Fernando

1978; Pesce 1985; Karanovic 2004). Geographically disjunct occurrence of the spinulose pediger 5 character state and its association with some ancestral traits (e.g., two spines instead of just one spine, or seta+spine on the terminal endopodal segment of P4; three elements instead of two on the sixth leg in the male—no data on the sixth leg in *M. superincidentis*) can be explained with an old, Gondwanan origin of this feature that has been retained in the ancestor of *Apocyclops*. The surface ornamentation of pediger 5 in the Miocene *A. californicus*, with a field of tiny spinules anteriorly to P5 is much reminiscent of what can be found in the recent *Metacyclops* mentioned above.

In the Paleocene−Eocene epochs the European archipelago could harbor a *Metacyclops* fauna coming from Africa, some descendants of which survived in the Mediterranean region. In the Late Paleocene–Early Eocene (57 and 56 mya) the North Atlantic (Thulean) bridge (Fig. 10) connecting southern Europe, the British Isles, central Greenland and Eastern North America might have acted as the shortest dispersal route for the ancestor of *Apocyclops* from Europe to North America (Tiffney 1985; Brikiatis 2014). A dispersal via the northern Bering Strait (between Siberia and Alaska) or the De-Geer Bridge (connecting Fennoscandia, Svalbard, Greenland and Canadian Arctic Archipelago, 63–71 mya) would be much longer and/or could impose a climate burden on the thermophilic *Apocyclops*. The Thulean bridge that allowed the exchange of the warm temperate/subtropical fauna between North America and Europe was broken in the early Eocene, which would imply an Eocene divergence between *Apocyclops* and *Metacyclops*.

Conclusions

Recent fossil finds of Cyclopidae (adult and copepodid instars) in the middle Miocene Barstow Formation in Southern California have yielded a large amount of morphological information on a copepod group that did not have any fossil record so far. The good preservation of the limbs (including setation of the antennule both in female and male) allowed us to infer the evolutionary relationships of the Miocene species. Most of the fossils belong to a single species of the modern genus *Apocyclops*, a euryhaline group, giving further support for the saline character of the Barstow paleolake. *Apocyclops californicus* sp. nov. can unambiguously be allocated in the *panamensis*-clade (eight extant species), implying a minimum age estimate of ~16 mya for the divergence of the *panamensis*-clade. The predominantly amphi-Pacific distribution of the thermophilic *Apocyclops* suggests a Paleogene origin of the genus in the northern hemisphere. The geographic pattern of the species richness in *Metacyclops*, the presumed closest relative of *Apocyclops*, and the occurrence of some *Metacyclops* species with "*Apocyclops*-like" morphology in the peri-Mediterranean region, hint that the ancestor of *Apocyclops* arrived in North America from Europe via the North Atlantic (Thulean) bridge in the Late Paleocene–Early Eocene. The Eocene termination of the Thulean dispersal route implies an Eocene divergence between *Apocyclops* and *Metacyclops*—it would be highly interesting to test whether molecular divergence data also support an (Early?) Eocene origin of *Apocyclops*. *Apocyclops* and *Metacyclops* belong to the oligomerized, more derived lineages of the Cyclopidae. If our hypotheses about the Eocene divergence of *Apocyclops* and the Gondwanan (Mesozoic) origin of *Metacyclops* are correct it would mean also that Cyclopidae are very likely an ancient (Palaeozoic?) group.

Acknowledgements.—We are very much obliged to Janet W. Reid (Virginia Museum of Natural History, Martinsville, USA) who kindly helped us to get access to the precious Ph.D. dissertations of Pamela Arnofsky and Marcia J.C. Botelho. The *Apocyclops panamensis* material was placed at our disposal by Gamal El-Shabrawy (National Institute of

Oceanography and Fisheries, Cairo, Egypt). The first author wishes to thank Frank D. Ferrari and T. Chad Walter (both Smithsonian Institution, Washington D.C., USA) for helping her to join the fascinating studies on the Barstow copepods. We gratefully acknowledge the helpful comments of two anonymous reviewers. AAK was supported by the Russian Government Program of Competitive Growth of Kazan Federal University. We thank the copyright owners, John Wiley & Sons, for granting us permission to use a figure (Fig. 10 here) from the article Brikiatis 2014 published in Journal of Biogeography. Bureau of Land Management is acknowledged for scientific paleontological collecting permit, CA-04-00-001P.

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Table 1. Armature of leg 1–4 in the adult female of *Apocyclops californicus* sp. nov. Spines are denoted by Roman, setae by Arabic numerals. The armature on the lateral margin of any segment is given first, followed by the elements on the apical and medial margins. ?: element could not be verified; *: presence of the medial spine on P1 basipodite was inferred from the presence of this spine in the adult male and copepodid V.

	Coxopodite	Basipodite	Exopodite	Endopodite
Leg 1	0-1	1-I*	I-1; III-2-3	0-1; 1-I,?-?
Leg 2	0-?	1-?	I-1; III-I,1-4	?-1; 1-I,1-4
Leg 3	0-?	1-?	I-1; III-I,1-4	?-1; ?-?-?
Leg 4	0-?	1-0	I-0; II-I,1-4	?-1; 1-I,1-3

Table 2. Morphometric characters of leg 5 in the adult female of *Apocyclops californicus* sp. nov. (absolute values are rounded).

Females	leg 5 (P5)					Body length (µm)
	segment length (µm)	segment width (µm)	segment length/width	medial spine length (µm)	medial spine /segment length	
UMNH IP 4826	9	19	0.48	7	0.80	730
UMNH IP 4829	12	19	0.65	11	0.92	745
UMNH IP 4852	18	29	0.61	12.5	0.70	945

Table 3. Armature of leg 1–4 in the adult male of *Apocyclops californicus* sp. nov. Coding system as in Table 1; 1?: seta is likely present.

	Coxopodite	Basipodite	Exopodite	Endopodite
Leg 1	0-1	?-I	I-?; III-?	0-1; 1-I,1-3
Leg 2	0-1?	1-0	I-1; III-I,1-4	0-1; 1-I,1-4
Leg 3	0-?	1-0	I-1?; III-I,1-4	?-?; ?-?-?
Leg 4	0-1	1-0	I-0; II-I,1-4	0-1; 1-?,1-?

Table 4. Armature of leg 1–4 in copepodid V of *Apocyclops californicus* sp. nov. Coding system as in Table 1.

	Coxopodite	Basipodite	Exopodite	Endopodite
Leg 1	0-1	1-I	I-?; III-2-?	?-?; 1-I,1-?
Leg 2	0-?	1-?	I-?; III-I,1-?	?-1; 1-I,1-?
Leg 3	0-?	1-?	I-?; III-I,1-?	?-?; ?-?-?
Leg 4	0-1	1-0	I-0; II-I,1-4	0-1; ?-?,1-3

Captions to figures:

Fig. 1. Coding of the antennulary setae, shown on the female of cyclopid copepod *Apocyclops* cf. *ramkhamhaengi* (MIZ 2/2015/9) from Townsville (Australia), extant species. **A**. Segments 1−5 (I−XIV); **B**. Segments 6−8 (XV−XXIII). **C**. Segments 9−11 (XXIV−XXVIII). Setal elements denoted by black and grey codes are present in the male of *Euryte robusta*; codes in black denote setae present in female in the *Apocyclops panamensis* group; Roman numeral refers to the ancestral segment on which the seta is inserted; p or d means anteroproximal- or anterodistal seta; Ae with Roman numeral in subscript means an aesthetasc inserted on the ancestral segment given in the subscript.

Fig. 2. Adult female of cyclopid copepod *Apocyclops californicus* sp. nov. from Mud Hills (Southern California), Burdigalian/Langhian (Miocene). **A**. UMNH IP 4824 holotype, habitus (A_1) and anal somite and caudal rami (A_2) in ventral view. **B**. UMNH IP 4833, pediger 5 and genital double-somite with two pairs of spermatophores (arrowed) in ventral view. **C**. OUMNH NT.233, 11-segmented antennule and antenna with allobasis in ventral view (C_1), cephalothoracic appendages (arrow shows oblique spine on the first exopodal segment of leg 1) in ventral view (C_2). **D**. UMNH IP 4852, caudal setae with setules on setae IV and V in dorsal view. A1, antennule; A2, antenna; Md, mandible; Mxl, maxillule; Mx,: maxilla; P1, leg 1.

Fig. 3. Cyclopid copepod *Apocyclops californicus* sp. nov, from Mud Hills (Southern California), Burdigalian/Langhian (Miocene). **A**−**C**. Adult female. **A**. UMNH IP 4824 holotype, median section of the antennule showing some setae coded on segments 2−5 (VII−XIV) and antennal endopodite in anterior view (A_1), spinulose surface ornamentation of pediger 5 and free segment of leg 5 in ventral view (A_2); p or d means anteroproximal- or anterodistal seta, arrows point to ten setae on the second (penultimate) endopodal segment of the antenna, and two short setae on the distal endopodal segment of the maxilla (Mx). **B**. UMNH IP 4845, prosome with four pairs of the swimming legs in lateroventral view. **C**. UMNH IP 4852, spinulose surface ornamentation of pediger 5 and free segment of leg 5 in dorsal view. **D**−**E**. Adult male habitus. **D**. UMNH IP 4858, in lateroventral view. **E**. UMNH IP 4856, in dorsal view.

Fig. 4. Cyclopid copepod *Apocyclops californicus* sp. nov. (UMNH IP 4850) from Mud Hills (Southern California), Burdigalian/Langhian (Miocene), adult male antennule in ventral view. **A**. Segments 1−8 (I− XIII) and antenna with allobasis. **B**. Segments 1−11 (I−XVI). **C**. Segments 10−14 (XV−XX). **D**. segments 15−16 (XXI−XXVIII).

Fig. 5. Cyclopid copepod *Apocyclops californicus* sp. nov. (UMNH IP 4850) from Mud Hills (Southern California), Burdigalian/Langhian (Miocene), adult male antennule in ventral view. The line drawings based on the scanning electron micrographs (see Fig. 4A–D) show some setal elements or their insertion sites (coding as in Fig. 1). **A**. segments 1−2 (I−VII). **B**. segments 2−11 (VI−XVI). **C**. segments 11−14 (XVI−XX). **D**. segments 15−16 (XXI−XXVIII).

Fig. 6. Adult male of cyclopid copepod *Apocyclops californicus* sp. nov. from Mud Hills (Southern California), Burdigalian/Langhian (Miocene). **A**. UMNH IP 4850. Protopodite and

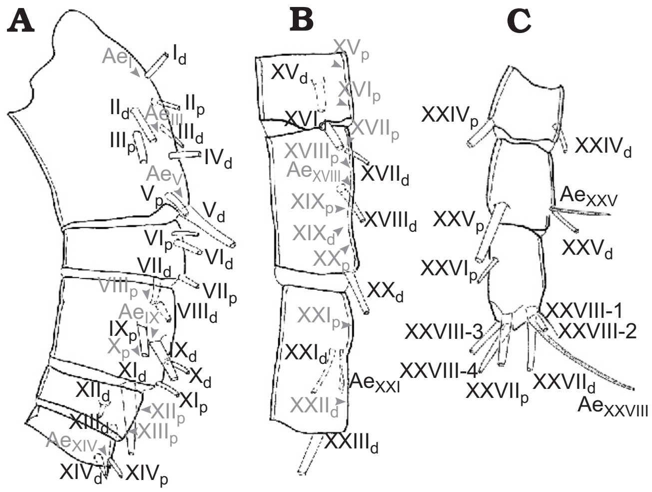
proximal segments of the exo- and endopodite of leg 4 (caudal view), and pediger 5 in ventral view (A_1). Drawings of protopodite and proximal segments of the exo- and endopodite of leg 4, and intercoxal sclerite of leg 3 in caudal view (A_2) and pediger 5 with leg 5 in ventral view (A_3). **B**. UMNH IP 4856, pediger 5 with leg 5 in dorsal view; lateral seta of presumptive proximal segment of leg 5 is inserted on pediger 5. **C**. UMNH IP 4828, leg 6 in lateral view; arrowheads show the three setal elements, whole length of the lateralmost seta is indicated by bracket.

Fig. 7. Copepodid V of cyclopid copepod *Apocyclops californicus* sp. nov. from Mud Hills (Southern California), Burdigalian/Langhian (Miocene). **A**. UMNH IP 4825, male, habitus in ventral view. **B**. UMNH IP 4857, female, 11-segmented antennule. **C**. UMNH IP 4854, sex cannot be determined, antenna with allobasis in ventral view; arrows show the insertion sites of five setae on the medial margin of the penultimate segment of the antennal endopodite. **D**. UMNH IP 4832, sex cannot be determined. Antennule (segments 1−8), coxopodite of the mandible (Md) with palp bearing two long and one short setae, maxillulary arthrite and maxilla (D_1). Swimming legs 1 to 4 in lateral view (D_2), arrow points to the medial spine of leg 1 basipodite.

Fig. 8. Cyclopid copepod *Apocyclops californicus* sp. nov. from Mud Hills (Southern California), Burdigalian/Langhian (Miocene). **A**, **B**. Copepodid V. **A**. UMNH IP 4857, female, swimming legs 3−4, leg 5 and leg 6, in lateral view; arrowheads point to lobe setae and lateral seta of leg 5, and posteriormost seta of leg 6. **B**. UMNH IP 4825, male, leg 4 protopodite in caudal view, urosomites 1−3 in ventral view; arrowheads point to setae of leg 6. **C**. Copepodid IV, UMNH IP 4835, coxopodite, basipodite, and first exopodal segment of leg 3 and 4, and leg 5 and leg 6 (C_1) and habitus (C_2) in lateral views. **D**. Copepodid III, UMNH IP 4849, habitus (D_1) and nine-segmented antennule (D_2) in dorsal views.

Fig. 9. Schematic representation of the antennule segmentation and setation in Cyclopidae. **A**, **B**. *Euryte robusta*. **A**. Female. **B**. Male. **C**, **D**. *Apocyclops panamensis*. **C**. Female. **D**. Male. Symbols: short line, anteroproximal seta; long line, anterodistal seta; ellipse, aesthetasc; filled black triangle, spinous seta on segment XIV; trapezoids, modified setae. Structures indicated with thick lines are present in the male but not expressed in the conspecific female. Roman numerals denote the ancestral segment homologies in the male of *A. panamensis*.

Fig. 10. Palaeogeography of the North Atlantic (Thulean) bridge during the sea-level lowstand in the Late Paleocene. The subaerial land connection (Davis Strait) between Baffin Island and central Greenland is under discussion. The much warmer climate and more southern position of the British Isles and Greenland facilitated dispersal of the thermophilic taxa between Europe and North America (modified from Brikiatis 2014).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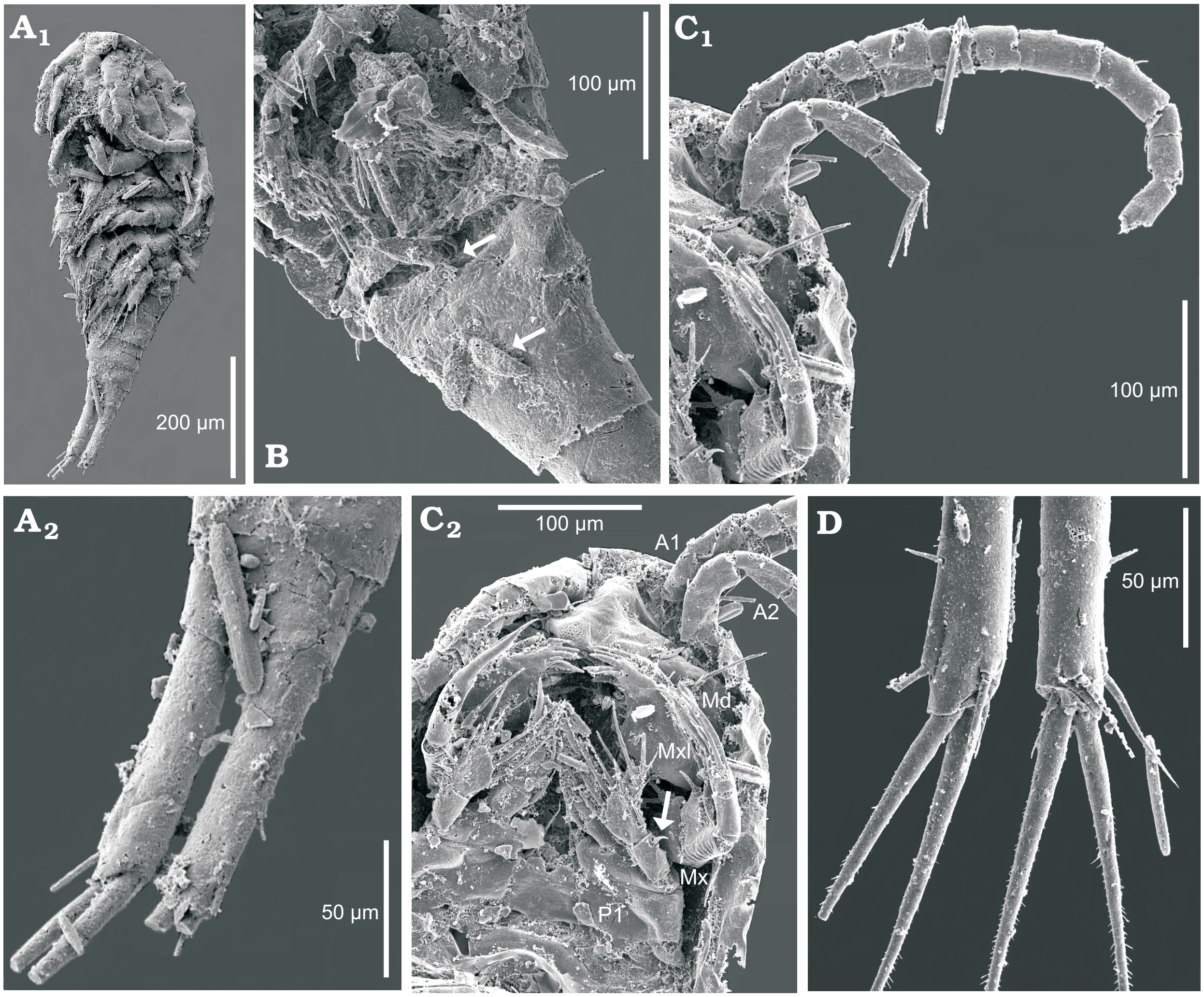
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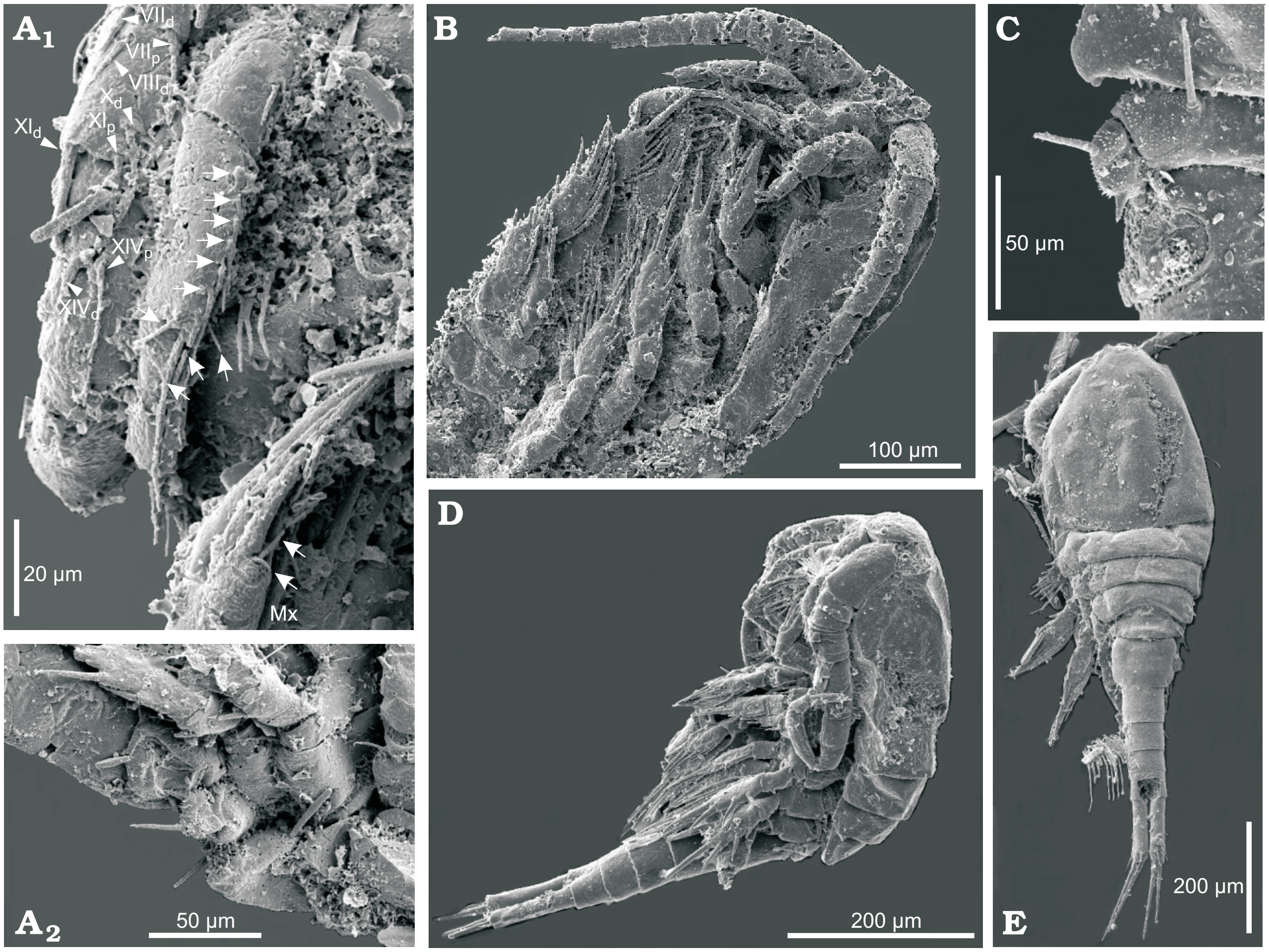
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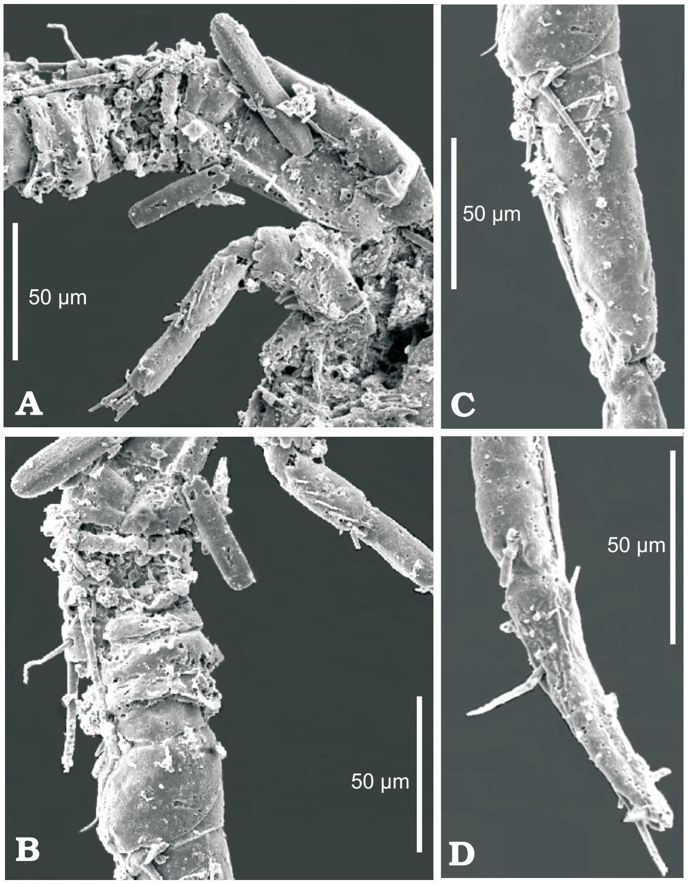
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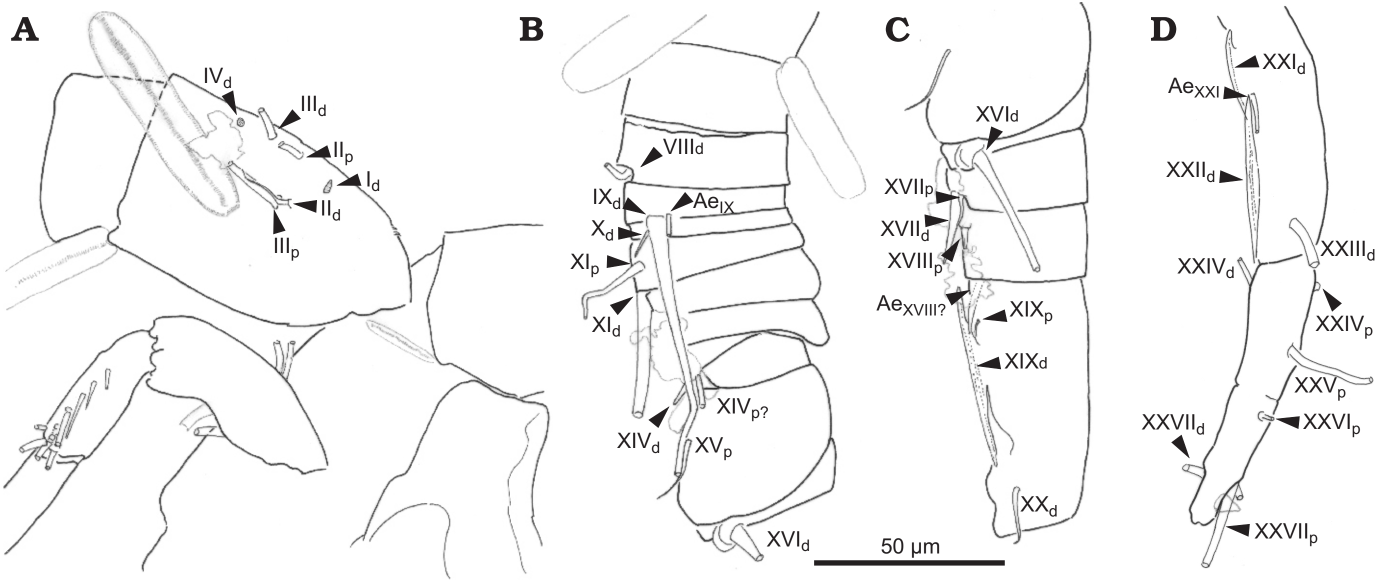
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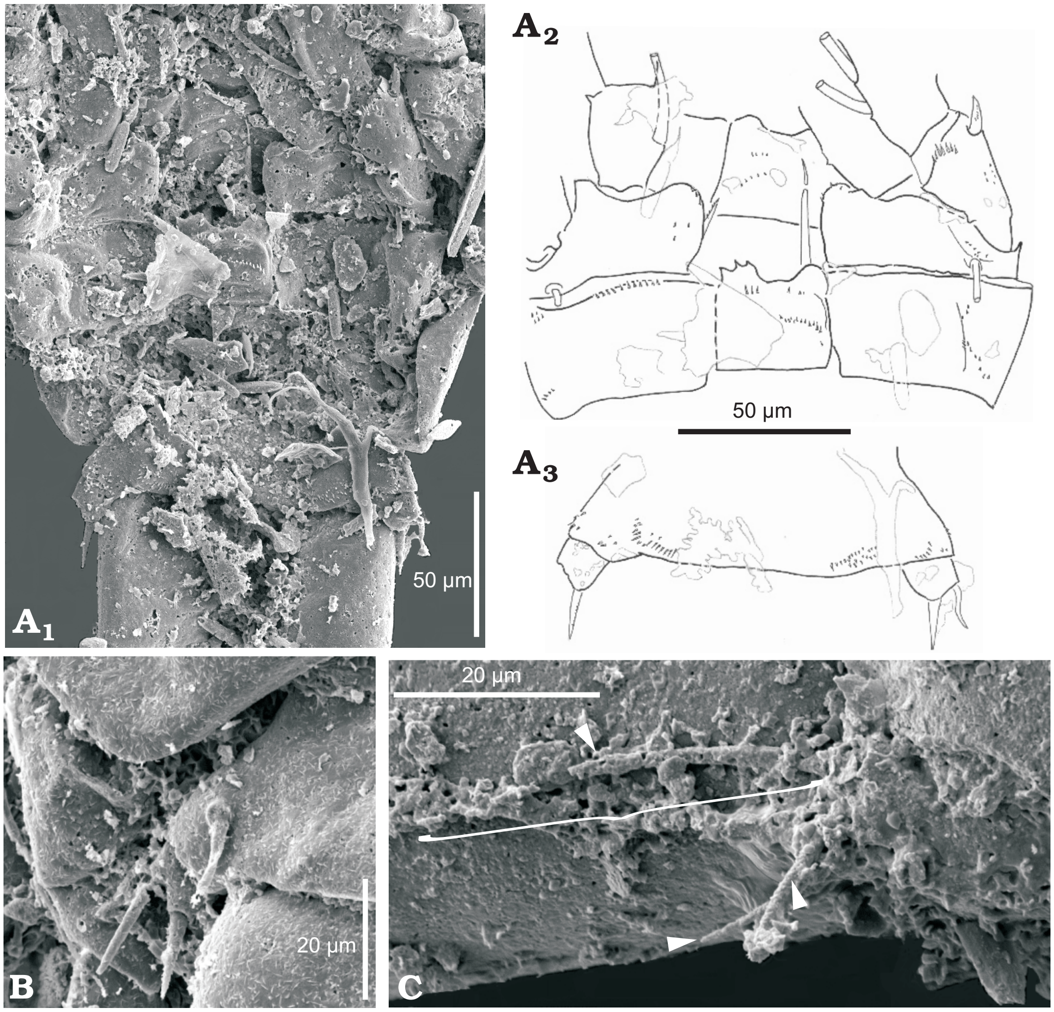
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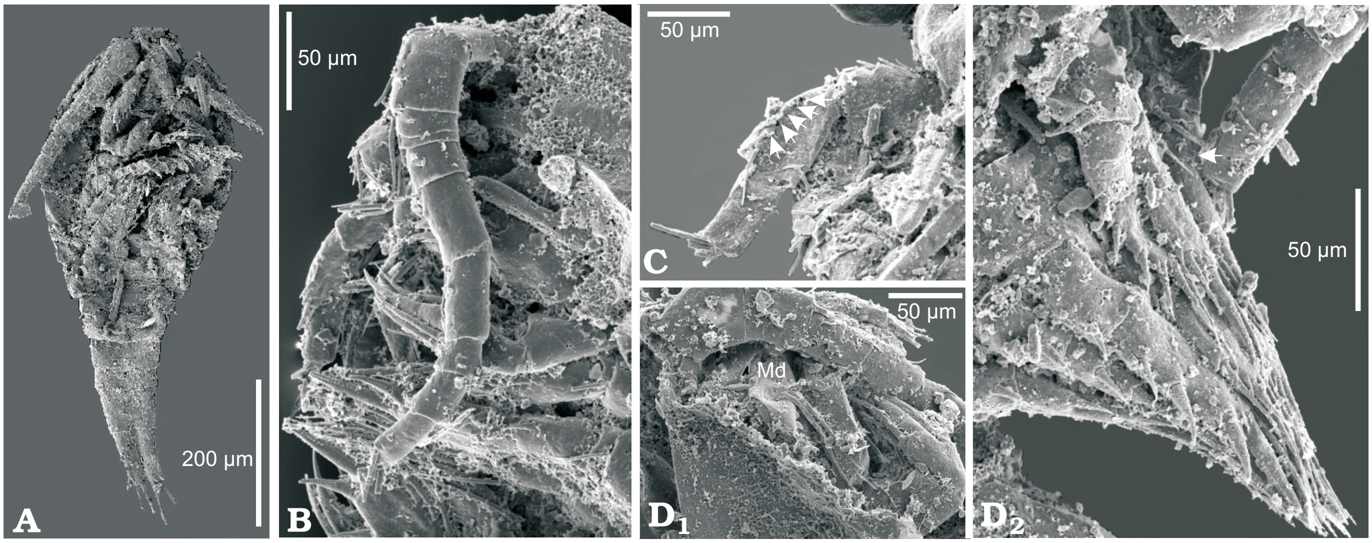
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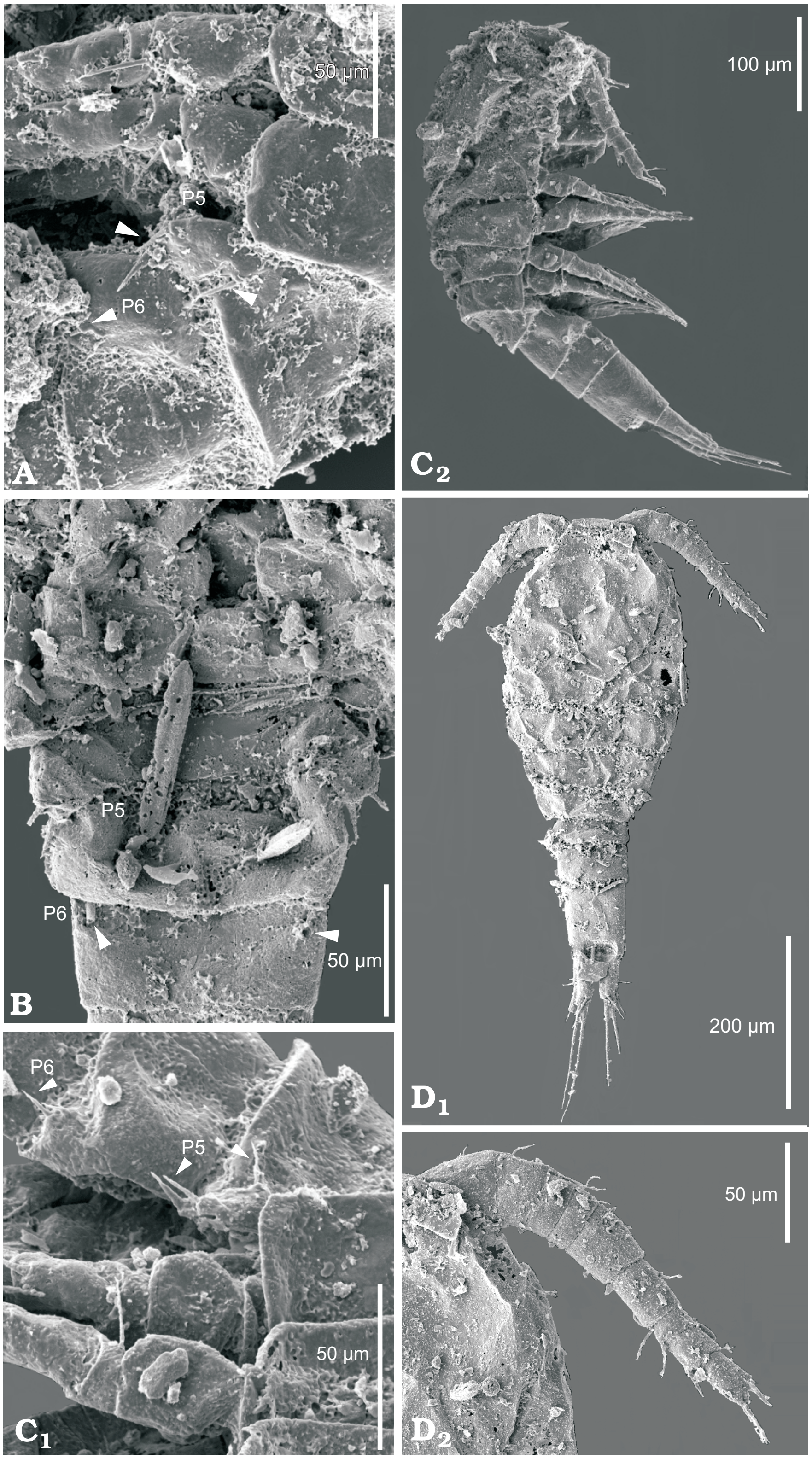
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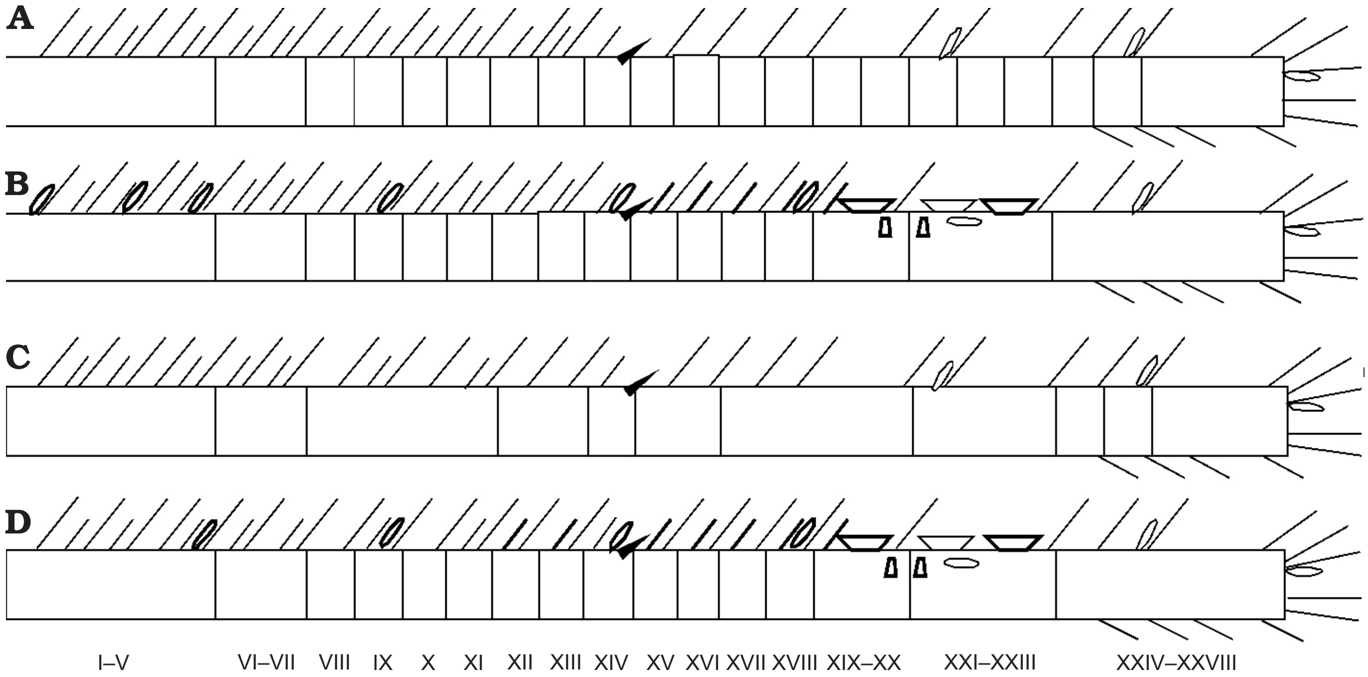
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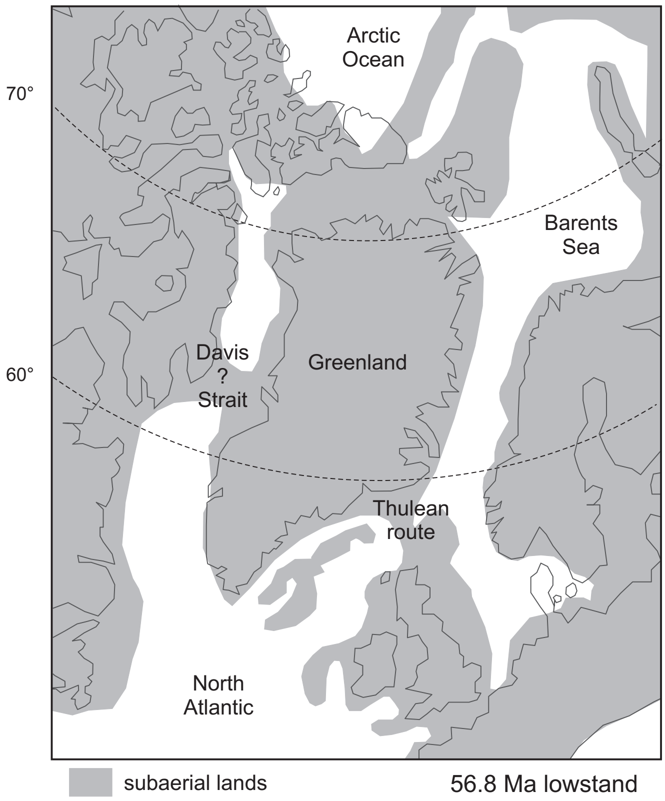
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