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## The first fossil isopod from Argentina: a new species of Cirolanidae (Crustacea: Peracarida) from the Miocene of Patagonia

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### ABSTRACT

*Cirolana centinelensis*, a new species of fossil cirolanid isopod from the early Miocene of Argentina is described, and the fossil record of South American isopods is briefly reviewed. Few fossil isopods are known from South America, and none were previously known from Argentina. The new taxon is represented by a single specimen collected from the Estancia 25 de Mayo Formation, formerly known as the Centinela Formation, in the Calafate region of southern Patagonia. It is preserved in a concretion that was formed in a glass-rich volcanic ash deposited into a shallow epicontinental seaway. The high reactivity of the enclosing volcanic ash set the stage for unique and variable taphonomic conditions with some skeletal elements being preserved in high resolution, whereas others were completely obliterated by the formation of large crystals of secondary zeolites. Because mouthparts that are usually used to make familial and generic assignments are not preserved, traditional systematic methods are combined with a multivariate principal coordinate analysis, as well as ecological and paleontological considerations to evaluate the most likely affinity of the fossil isopod.

**Key Words:** Centinela Formation, Estancia 25 de Mayo Formation, multivariate principal coordinate analysis, taphonomy, volcanic ash

### INTRODUCTION

The fossil record of isopod crustaceans is poor, despite being one of the most taxonomically diverse groups of modern crustaceans, with an estimated 10,000 or more known species that inhabit a cosmopolitan range of both terrestrial and marine environments (Poore & Bruce, 2012). While they have a fossil record dating back to the Carboniferous (Schram, 1970), such a record is frustratingly incomplete. Wieder & Feldmann (1992) did a comprehensive study of all Mesozoic and Cenozoic fossil isopods from North America and concluded that the group was represented by only nine species in five genera, which ranged in age from Cretaceous to Pleistocene. The fossil record of isopods is not appreciably more diverse in any other parts of the world, with relatively few specimens known from Europe (Brandt *et al.*, 1999; Pasini & Garassino, 2012; Hyžný *et al.*, 2013; Hyžný & Arpád, 2017), Asia (Karasawa *et al.*, 2008; Kato *et al.*, 2016; Park *et al.*, 2013), Australia and New Zealand (Feldmann & Rust, 2006;

Wilson *et al.*, 2011), and Africa and the Middle East (Morris, 1979; Feldmann & Goolaerts, 2005).

#### *Isopod taphonomy: why so few fossils?*

Isopods are known for their recalcitrant nature with respect to fossilization, and their poor representation in the fossil record is not likely due to a lack of numerical abundance or limited geographic distribution through geologic time. Rather, it is likely due to their physical and chemical composition as well as their behavior, which are not favorable for fossilization. Isopods have a generally lightly sclerotized, thin cuticle that rapidly disintegrates during their destructive biphasic molting behavior (Tait, 1917). Biphasic molting consists of two phases; during the first phase, the posterior cuticle (pleotelson, pleon, and the posterior pereon) is shed. The pereon and pleon sections may disarticulate, and become fragmented and unrecognizable. Although these posterior sections disarticulate readily, they are the most likely parts

to be preserved as fossils, and are often the only recognizable elements in fossil isopods. During the second phase, the anterior cuticle (anterior section of pereon and cephalon) is shed. These segments rapidly disarticulate and become fragmented (George, 1972) and are less likely to be preserved than the posterior elements. The amount of time between molt phases varies from minutes to days, and sometimes corresponds to receptive reproductive phases in females (Shuster, 1989). Arthropods that molt whole, or nearly whole, exoskeletons (e.g. crabs, lobsters, and horseshoe crabs) functionally increase the probability that identifiable remains will be preserved as fossils, as each molt, as well as the final corpse, has a chance to enter the fossil record. Because of their destructive molting behavior, isopods are not afforded this advantage, and thus remain drastically underrepresented in the fossil record.

Additionally, isopod cuticle is very thin when compared to that of other crustaceans that are seen with more frequency in the fossil record. Appendage cuticle tends to be the thinnest in many crustaceans, and the same is true for isopods. Taphonomic experiments with decapods have revealed that appendages are the least likely to be preserved (Stempien, 2005), excluding the chelipeds, which are hardened to resist damage caused by durophagy (Feldmann & Schweitzer, 2010). Appendages, particularly pereopods and mouthparts, are of great utility when diagnosing the higher affinities of isopods, and their very thin cuticle results in low fossilization potential. This is problematic, and presents great difficulties when attempting to classify fossil isopods. Nagler *et al.* (2017) recently used computed tomography (CT) scanning to uncover mouth parts and thoracopods (termed pereopods herein) in the fossil isopod *Urda rostrata* Kunth, 1870, which they used to infer a parasitic lifestyle. The use of modern techniques such as CT scanning will be integral to the future of systematic paleontology, and provides the means to access information preserved in fossil material that was previously inaccessible. Even with new methods available, however, classification of fossil isopods is difficult. The specimen examined by Nagler *et al.* (2017) was exceptionally well preserved, a rarity among the already rare fossil isopods. A similar CT scanning technique was repeated in this study, but revealed no more useful information. It appears that mouthparts are either truly not preserved, or the preservation is such that the density contrast is not sufficient to provide a useful CT image. Because of these many difficulties, fossil remains of isopods are likely underreported, and remain unclassified beyond the ordinal level. Additionally, there is a lack of fossil isopod workers, which leads to a collecting bias, which further amplifies the sparsity of the isopod fossil record.

Finally, the physical and chemical composition of isopod cuticle is not favorable for fossilization. Virtually all arthropod cuticle is composed of different proportions and variations of

calcium carbonate, calcium phosphate, organic polymers (e.g., chitin), as well as a variety of other organic components such as tanned and untanned lipids (Neville, 1975). In very rare circumstances, organic molecules are preserved in fossil arthropod cuticle (Briggs, 1999); however, only the crystalline and amorphous biomineral cuticle elements remain after preservation in most cases. Calcium carbonate and calcium phosphate can be either crystalline or amorphous, and their form varies among different arthropod groups. Calcium carbonate can also contain varying amounts of magnesium. High magnesium calcium carbonate is generally more soluble and less geologically stable than low magnesium varieties, as the presence of the magnesium ions forces disorder and instability in the crystal lattice (Bertram *et al.*, 1991). Isopod cuticle tends to incorporate high-magnesian crystalline calcium carbonate, amorphous calcium carbonate, amorphous calcium phosphate (hydroxyapatite), and a chitinous matrix (Neues *et al.*, 2007). The relative proportions of these components vary depending on the life style of the isopod (terrestrial *versus* marine; flexible *versus* hardened; hider *versus* roller, among several factors). Although variable, the ratio of amorphous and organic components to crystalline components in isopod cuticle tends to be high, a condition which is not favorable for fossilization (Neues *et al.*, 2007). Amorphous materials and organic biopolymers tend to be less stable over geologic time than crystalline materials. Amorphous mineraloids (e.g., hydroxyapatite) tend to devitrify over time, which can be destructive, obscuring or obliterating original structures. Organic materials (e.g., chitin) are also unstable over geologic time, and tend to rapidly decompose, even in dysoxic conditions.

#### *Fossil Record of Isopods in South America*

Fossil isopods are rare worldwide, and few are known from South America. To our knowledge, eight fossil isopod species in four genera had been reported from South America prior to this study, all from Brazil (Table 1). Lindoso *et al.* (2013) suggested one other possible isopod, *Saucrolus silvai* Santos, 1971 from Brazil; however, many aspects of its morphology are inconsistent with Isopoda, making its placement therein dubious. It has no identifiable pleotelson, or pleon, and seems to have only 8 body segments at most. Santos (1971) originally placed *Saucrolus silvai* in Saucrolidae, which Popov & Bechly (2007) considered a subjective synonym to Naucoridae, a family heteropteran insects.

The specimen reported herein was collected during the austral summer of 1995 along with representatives of a diverse decapod fauna, including seven families of brachyuran crabs, and one anomuran (Table 2). The fauna is contained within the Quién Sabe (lower) member of the Estancia 25 de Mayo Formation in the Santa Cruz Province of Argentina (Fig. 1).

**Table 1.** List of all known fossil isopods from South America.

Family	Species	Formation/Location	Age
Cirolanidae	<i>Pseudopalaega granulifer</i> Mezzalira & Martins-Neto (1992)	Tatuí, Brazil	Permian
	<i>Pseudopalaega microcelata</i> Mezzalira & Martins-Neto (1992)	Tatuí, Brazil	Permian
	<i>Protourda tupiensis</i> Mezzalira & Martins-Neto (1992)	Tatuí, Brazil	Permian
	<i>Protourda circumscripta</i> Mezzalira & Martins-Neto (1992)	Tatuí, Brazil	Permian
	<i>Pseudopalaega iratiensis</i> Martins-Neto (2001)	Irati, Brazil	Permian
	<i>Palaega tremembeensis</i> Martins-Neto (2001)	Tremembé, Brazil	Oligocene
	<i>Cirolana centinelensis</i> n. sp.	Estancia 25 de Mayo, Argentina	Miocene (Burdigalian)
Sphaeromatidae	<i>Unusuropode castroi</i> Duarte & Santos (1962)	Açú, Brazil	Cretaceous (Upper)
Archaeoniscidae	<i>Codoisopus brejensis</i> Lindoso, de Souza Carvalho & Mendes (2013)	Codó, Brazil	Cretaceous (Aptian)

**Table 2.** Crustacean taxa collected by S. Casadio and R.M. Feldmann from the Estancia 25 de Mayo Formation, Argentina during 1995. Table modified and updated from [Casadio \*et al.\*, 2000](#).

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Order Isopoda Latreille, 1817
Family Cirolanidae Dana, 1852
<i>Cirolana centinelensis</i> n. sp.
Order Decapoda Latreille, 1802
Infraorder Anomura H. Milne Edwards, 1832
Family Galatheididae Samouelle, 1819
<i>Munida</i> <a href="#">Leach, 1820</a>
Infraorder Brachyura Latreille, 1802
Family Raninidae de Haan, 1839
<i>Raninoides</i> sp.
Family Cancridae Latreille, 1802
<i>Metacarcinus</i> ? Sp.
<i>Notocarcinus sulcatus</i> <a href="#">Schweitzer &amp; Feldmann, 2000</a>
Family Macropidae Stephenson & Campbell, 1960
<i>Archaeogeryon latus</i> <a href="#">Glaessner, 1933</a>
Family Carpillidae Ortman, 1893
<i>Carpilius</i> ? sp.
Family Geryonidae Colosi, 1923
<i>Chaceon peruvianus</i> <a href="#">d'Orbigny, 1842</a>
Family Varunidae H. Milne Edwards, 1853
<i>Asthenognathus urreta</i> <a href="#">Schweitzer &amp; Feldmann, 2001</a>
Family Majidae Samouelle, 1819
<i>Rochinia cf. R. hystrix</i> <a href="#">Stimpson, 1871</a>
Genus indeterminate

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## GEOLOGIC SETTING

The Estancia 25 de Mayo Formation, formerly known as the Centinela Formation ([Furque & Camacho, 1972](#)), consists of marine and estuarine to fluvial sediments which were deposited in a foreland basin on the eastern flank of the Andes Mountains during the early Miocene. It represents one of a series of several transgressive-regressive events that occurred in the latest Mesozoic through Cenozoic in South America ([Malumián & Nández, 2011](#)). Shallow epicontinental seaways covered large portions of the South American continent during this time. The early Miocene transgression (also called the Patagoniense) was one of the most extensive, covering much of southern Patagonia, and extending as far north as modern-day Buenos Aires Province. At the same time as the Patagoniense transgression, intense Andean volcanism periodically deposited large quantities of volcanic ash in the shallow epeiric seas. The Estancia 25 de Mayo Formation records numerous volcanic events, one of which is responsible for a mass mortality event that killed, buried, and ultimately preserved the isopod reported herein. These volcanic events are noteworthy because the rapid deposition of volcanic ash buries and preserves marine communities, which typically would not be preserved with much frequency. The very fine-grained nature of the ash also enhances the quality of preservation by restricting the amount of oxygen that can move through sediment post-burial ([Orr \*et al.\*, 2000](#); [Crawford \*et al.\*, 2008](#); [Maguire \*et al.\*, 2016](#)).

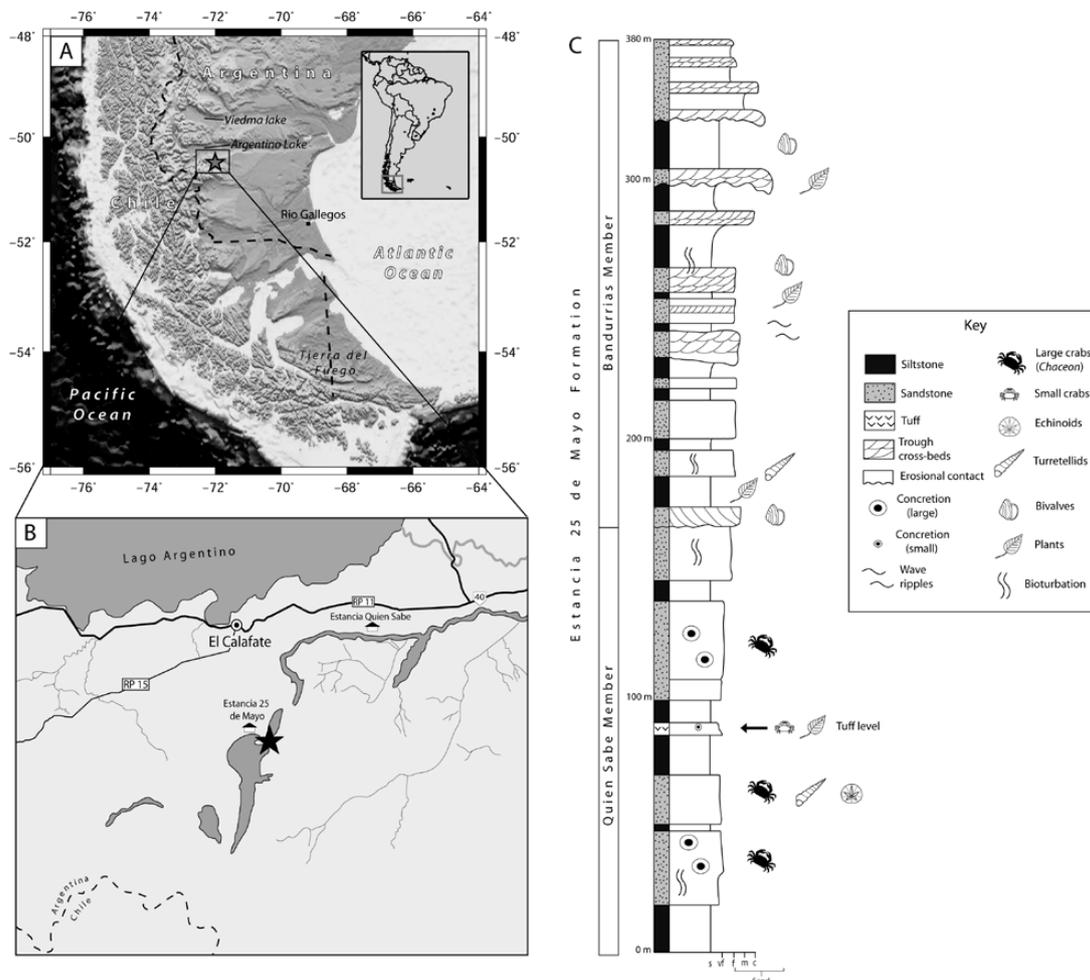
The age of the Estancia 25 de Mayo Formation has been variously assigned from Eocene to Miocene, but most recently [Cuitiño \*et al.\*, 2012](#) assigned U-Pb and  $^{87}\text{Sr}/^{86}\text{Sr}$  ages of 19.14 and 18.85 Ma (Burdigalian age), respectively. The marine sediments record a major transgressive event, referred to as the Patagoniense, which affected much of Patagonia, and lesser parts of northern Argentina. The unit is approximately 180 m thick, and contains two members: the lower Quién Sabe and the upper Bandurrias.

The two members are separated by an unconformable contact, and are distinguished on the basis of distinct lithologies. The Quién Sabe Member is composed largely of medium to fine-grained sandstones with abundant marine fossils, whereas the Bandurrias Member is dominated by coarser, cross-bedded sand. The Estancia 25 de Mayo Formation is bounded unconformably below by the Rio Leona Formation, and above by the Santa Cruz Formation. The tidal marine to estuarine deposits of the Estancia 25 de Mayo Formation give way to the fluvial and terrestrial deposits of the Santa Cruz Formation via a gradational contact, and no sharp boundary exists. The boundary between the two formations is variously drawn, but is usually based on the first appearance of distinctly terrestrial fossils, which varies with locality. The Santa Cruz Formation is noteworthy because of its abundant and taxonomically diverse fossil mammal assemblages, which have been used to define some of the South American land mammal ages for the Miocene. [Casadio \*et al.\* \(2000\)](#) extracted stable oxygen isotopes from oysters in the Estancia 25 de Mayo Formation, and used  $\delta^{18}\text{O}$  ratios to reconstruct paleotemperature. They reported an annual temperature fluctuation of 15–21 °C, which is much warmer than the current temperatures in that region, which range from approximately 5–15 °C on average, estimated using data from the Columbia University International Research Institute for Climate and Society monthly ocean temperature mapper [Barnston \*et al.\* \(2010\)](#). The record of the Patagoniense transgression also suggests different climatic conditions, as it correlates with high eustatic sea level in other parts of the world; however, the rise in sea level was also likely amplified by local tectonic subsidence ([Malumián, 1999](#)). The Cretaceous also saw high sea levels and the establishment of epicontinental seas on the South American continent. These high sea levels during the Mesozoic and early Cenozoic were likely important times for the colonization by isopods of the interior South American continent, which are now known in abundance in both freshwater and marine systems.

## MATERIALS AND METHODS

The new isopod taxon herein is known from a single specimen contained within a concretion composed entirely of volcanic ash. Both part and counterpart are preserved but the anterior section of the counterpart is lost. The anterior is preserved on the part; however, limited information is preserved.

Multivariate analysis to compare multiple characters across different genera was carried out using the character matrix of [Hansen & Hansen \(2010\)](#). Characters chosen were those that are commonly preserved on fossil isopods, including the pleotelson, pleon, and posterior pereonites (see [Fig. 4](#)). It contains 12 unique, binary character states, and 130 taxa including the new taxon. The matrix of [Hansen & Hansen \(2010\)](#) was used because the set of characters they selected were all present in the taxon herein, and the taxa selected are representatives of genera that closely match the morphology of *C. centinelensis* and could not be eliminated as generic assignments based on available features. Other groups that bear a superficial resemblance, but can be eliminated based on available features are discussed below. Various species of *Aega* [Leach, 1815](#), *Cirolana* [Leach, 1818](#), *Natatolana* [Bruce, 1981](#), and *Nerocila* [Leach, 1818](#) are included to represent the intrageneric morphologic variation which occurs across those groups. The morphospace of each genus was bounded by connecting the data points of the group's outliers to create polygons which represent the range of morphologic variation of the selected characters within each group, following the methodology of [Hansen & Hansen \(2010\)](#). As expected, there is significant overlap of the groups, especially among *Aega*, *Cirolana*, and *Natatolana*. A unique morphospace is, however, visible for each group. Principal



**Figure 1.** Locality maps and generalized stratigraphic section of the region where the crustacean fauna was collected. Map of South America created using Generic Mapping Tools (GMT) (A). Inset geologic map showing outcrops of the Estancia 25 de Mayo Formation in dark gray (the star indicates locality of new taxon). Modified from Cuitiño & Scasso (2013) (B). Generalized stratigraphic section of the Estancia 25 de Mayo Formation near where the isopod was collected, modified from Casadío *et al.* (2000) and Cuitiño & Scasso (2013). The specimen was collected from the “tuff level”, indicated by arrow (C).

coordinate analysis was carried out using both PAST and MVSP. In order to compare morphology of available characters, two different distance measures were used: Mean Character Distance (MCD), and Jaccard Similarity Index. The MCD measure was first proposed for phenetic taxonomy by Cain & Harrison (1958), who used it as a tool to quantitatively evaluate taxonomic affinities. When using the MCD method, axes were extracted using Kaiser’s rule, which eliminates axes with an eigenvalue of less than 1. In this way, the maximum amount of variance can be evaluated using only two axes. The Jaccard Similarity Index was used by Hansen & Hansen (2010) and is repeated herein for comparability between the two studies. The Jaccard index is useful for binary character sets, usually as presence-absence states of ecological data (Hammer & Harper, 2006). This method, however, ignores “double zero” cases, making comparisons only for characters which are present, and does not maximize character distances.

Scanning electron microscopy and petrographic microscopy were used to analyze lithology, taphonomy, and mode of preservation. A Hitachi 3030 (Hitachi, Tokyo, Japan) equipped with a Quantax Energy Dispersive Spectrometer (Bruker, Billerica, MA, USA) was used for electron microscopy, and a Leica DMPEP (Leica, Wetzlar, Germany) petrographic microscope was used for thin section analysis.

## SYSTEMATIC PALEONTOLOGY

**Isopoda** Latreille, 1817

**Cymothoida** Wägele, 1989

**Cirolanidae** Dana, 1852

**Cirolana** Leach, 1818

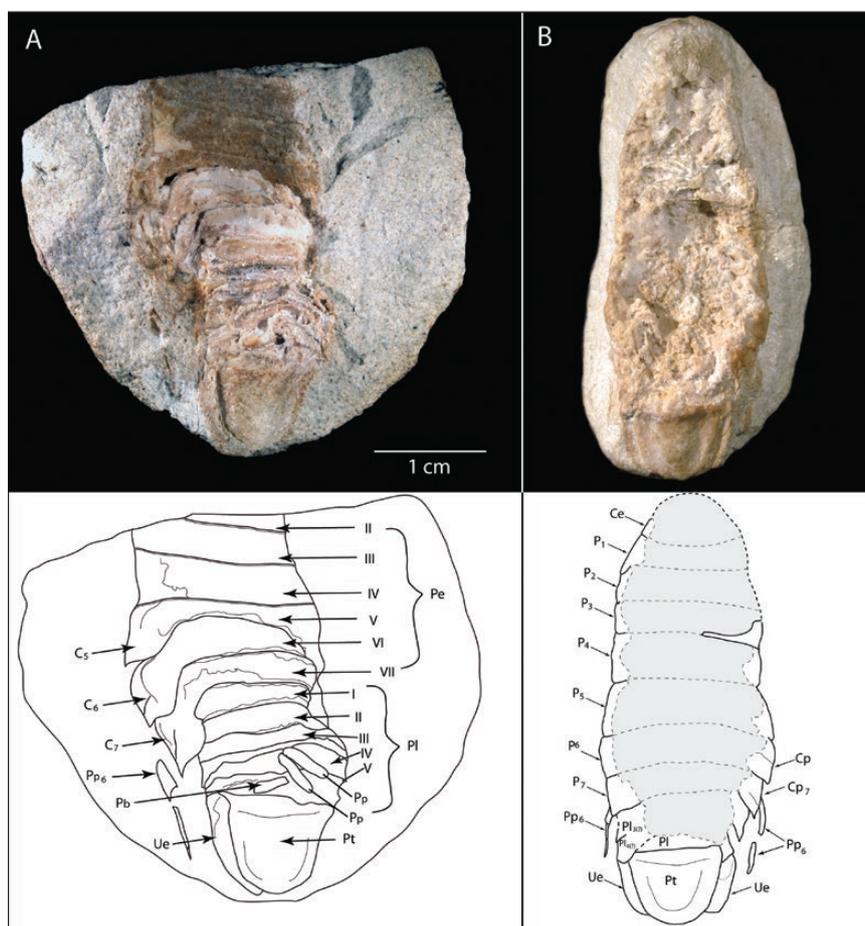
***Cirolana centinellensis* Maguire n. sp.**

(Figs. 2, 3)

**Holotype:** Assigned catalog number MPEF-PI 6131a (part, Fig. 2B) and MPEF-PI 6131b (counterpart, Fig. 2A), Museo Egidio Feruglio, Trelew, Argentina.

**Diagnosis:** Pereiopods V–VII ambulatory. Coxal plates IV–VII deltidoid with tips slightly deflected posteriorly, distinct longitudinal groove anterior to tip. Pleotelson margin entire, parabolic with flattened margins becoming moderately vaulted axially. Pleon enveloped by pereonite VII. Pleonite IV overlaps margins of pleonite V. Pleon, pleotelson roughly equal in length. Pleonite I partially covered by pereonite VII.

**Description:** Specimen measures 40.10 mm length, 16.10 mm maximum width (L:W = 2.18). Body dorsoventrally compressed, moderately vaulted, ovoid with maximum width occurring at



**Figure 2.** Part (B) and counterpart (A) of the holotype of *Cirolana centinelensis* n. sp. Cn = coxal plate corresponding to pereonite number *n*; Pp = pereopod; Pb = pleopod base; Ue = uropodal endopod; P = pereonite; Pl = pleonite; Pt = pleotelson, Ce = posterolateral corner of cephalon. This figure is available in color at *Journal of Crustacean Biology* online.

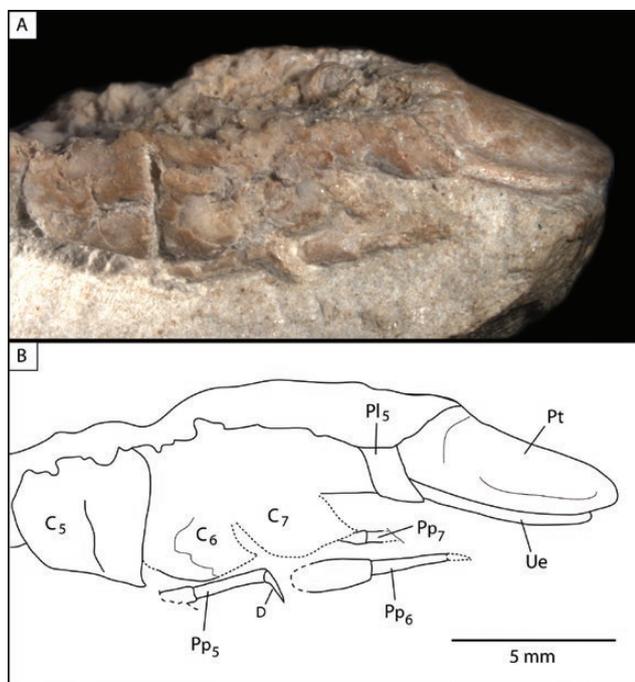
approximately 2/5 total length from distal end of pleotelson, at pereonite VI. Cephalon poorly preserved, convex in outline, likely partially enveloped by pereonite I. Tergites of pereonite I, II not preserved. Lateral margin of pereonite I more than twice as broad as pereonite II. Coxal plates II–IV increasing in size, with pereonite II smallest, pereonite IV largest. Coxal plates IV–VII roughly equal in size. Posterolateral angle of coxal plate I obtuse, rounded with groove subparallel to margin, diverging axially toward anterior. Posterolateral angle of coxal plate on pereonite II rounded, obtuse. Posterolateral angle of coxal plate III weakly acute. Pereonite III weakly concave anteriorly, posterolateral angle of coxal plate acute, deltoid. Pereonite IV weakly convex anteriorly, coxal plate deltoid with distinct longitudinal groove terminating anterior to posterolateral angle. Pereonite V anteriorly convex, coxal plate strongly deltoid with distinct groove terminating anterior to posterolateral angle, ~15% larger than pereonite IV, but identical in shape. Pereonite VI anteriorly convex, coxal plate identical to pereonites IV, V, approximately equal in size to pereonite V. Pereonite VII poorly preserved.

Pleon as wide as pleotelson, narrower than posterior pereon. Pleon partially enveloped by pereonite VII, pleonite I partially covered by pereonite VII. Pleon with 6 free, unfused pleonites, I–VI approximately equal in length, VI slightly reduced. Pleotelson parabolic, entire. Length approximately equal to width. Margins flattened, becoming axially vaulted. Uropods articulate anterolaterally on pleotelson. Uropodal endopod flat, approximately equal in length to pleotelson. Uropodal endopods lie partially beneath pleotelson. Uropodal exopods not preserved.

Pereopods I–IV not preserved. Pereopods V–VII ambulatory, slender, with straight dactyl (Fig. 3). Dactyl of pereopods VI, VII not preserved, but inferred as similar in nature to pereopod V. Although there are often differences between anterior, posterior pereopods in isopods, it is assumed that pereopods V, VI, VII are functionally the same, as in majority of other cirolanids.

**Etymology:** The trivial name is derived from the Centinela River, which flows past the outcrop from which the specimen was collected.

**Remarks:** Many higher classifications of isopods rely on the morphology of appendages and mouthparts (Kensley, 1978; Poore, 2002), features which are rarely preserved in fossils. This has led many authors to attempt to use other more commonly preserved characters to correctly place fossil taxa, with varying results (Feldmann & Rust, 2006; Hansen & Hansen, 2010; Jones et al., 2014). Hyžný et al. (2013) noted that the posterior parts (pleon, pleotelson, and others) are most commonly preserved, and created a dichotomous key to fossil cirolanid isopods using only those parts. Hansen & Hansen (2010) also used posterior morphology to classify fossil flabelliferans, constructing a character matrix that they used to perform principal coordinate analysis (PCO) to analyze morphologies. Without appendages preserved, however, placing fossil taxa in families such as Cirolanidae is dubious. Isopods display a wide range of diversity, and similarities in gross morphology are common among families. Because of these similarities, taxonomic placement may be difficult, and misclassification common. Great care must be taken, then, to classify fossil isopods using a preponderance of characters,



**Figure 3.** Photograph of the left lateral side of the holotype of *Cirolana centinelensis* n. sp. (A). Line drawing of A showing the posterior three pereopods (PP<sub>5-7</sub>) corresponding to pereonites 6, 7, and 8, with the dactyl (D) preserved on PP<sub>5-6</sub> (B). Other notations as explained in Figure 2. This figure is available in color at *Journal of Crustacean Biology* online.

rather than any one character.

The early Miocene age of the taxon makes it unlikely that it belongs to any extant species. Estimates of average species duration for marine invertebrates vary, but most fall within the range of 1–10 Ma (Valentine, 1970; Raup, 1991). The probability of a species living for greater than 20 million years without any morphological changes is unlikely. Although species durations of longer than 20 million years have been documented, these cases are the exception, rather than the rule. It is therefore most parsimonious that the new taxon herein is not a member of an extant species. It is, however, perfectly reasonable to consider extant genera for placement, as generic survival time ranges are much higher than those of species.

**Nomenclatural statement:** A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:DFBED920-EB0A-4F65-9E1F-8A914B86EA66.

## RESULTS AND DISCUSSION

The affinities of fossil isopods to higher taxa are notoriously difficult to diagnose. A high degree of intrageneric and even intra-specific variation sometimes exists, especially in the posterior parts such as the pleotelson, which sometimes vary significantly among different genera in the same family and among different species within the same genus. Consequently, deductive reasoning, and correlations between particular characters must sometimes be used to place fossil isopods. Jones *et al.* (2014), for example, used a preponderance of morphological characters such as presence of free pereonites, epimeres on pereonites IV–VII, and configuration of the uropods and pleotelson to argue a cirolanid affinity for a fossil isopod from Italy. Hansen & Hansen (2010) used principal coordinate analysis (PCO) to argue an aegid affinity for a fossil isopod from the Miocene of Denmark, a methodology which is repeated herein. We can eliminate many isopod families based on

gross morphology, but others are not so easily dismissed, because the taxon bears features that are possessed by multiple families.

Several families were initially considered because of superficial resemblance to the new taxon: Cirolanidae, Corallanidae, Tridentellidae, Aegidae, Sphaeromatidae (as suggested by Casadio *et al.*, 2000), and Cymothoidae. Cymothoids are obligate parasites (Nagler *et al.*, 2016, 2017) and possess a complete set of prehensile pereopods. Our fossil isopod bears at least three pairs of ambulatory posterior pereopods, so Cymothoidae is excluded. Sphaeromatids bear fused anterior pleonites which are often defined only by lateral furrows, whereas the new taxon bears five free pleonites. Tridentellids are more difficult to differentiate, but there are some key features that set them apart. The family is monogeneric, and represented by 17 species (Bruce, 2008) across which a fair amount of morphological disparity is displayed. They have a global distribution, and no clear preference for substrate, with habitats ranging from carbonate hardgrounds to soft subtidal zones, and even abyssal plains (Delaney & Brusca, 1985). Most tridentellids have a high degree of dorsal ornamentation, but a few species, such as *Tridentella memikat* and *T. tanimbar* lack ornamentation. Tridentellids also tends to be small, with the largest-size species (*T. memikat*) reaching a maximum size of approximately 40 mm. The new taxon, at 40 mm long, is therefore as large as the largest modern tridentellid, substantially larger than most tridentellids. Tridentellids also tend to have large, well developed eyes that are placed at the posterolateral corner of the cephalon (Delaney & Brusca, 1985). While the cephalon is very poorly preserved, the posterolateral corner preserves no evidence of an eye. The Tridentellidae has no fossil record, whereas other groups like the Cirolanidae have a relatively robust fossil record. Each of these deductions may not be conclusive in eliminating tridentellids as a possible placement for the new taxon, but, taken in conjunction, a tridentellid affinity is unlikely. The distinction between cirolanids, corallanids, and aegids lies chiefly in the morphology of mouth parts (see Bruce *et al.*, 1982), which are not preserved on the fossil specimen. Corallanids bear a distally narrowed mandible, a prominent lacinia mobilis, and a reduced molar; cirolanids bear a tridentate incisor, and a mandible with a fleshy lobe bearing a spine row, and aegids have a maxillipedal palp tipped with spines or hooks (Kensley, 1978; Brandt & Poore, 2003). These features are either not preserved, or too poorly preserved to differentiate on the fossil specimen. Unlike cymothoidids, corallanids, aegids, and cirolanids often bear ambulatory posterior pereopods in combination with prehensile anterior pereopods (Bruce *et al.*, 1982), which is consistent with the fossil specimen. The anterior pereopods of the fossil taxon are not visibly preserved, so none of these families can be eliminated based solely on pereopod morphology. Like tridentellids, aegids usually have large, well developed eyes, which take up most of the cephalon. As in tridentellids, aegid eyes often begin at the posterolateral corner of the cephalon, a condition that is not present in the fossil specimen.

Although many useful morphological characters are preserved on the fossil taxon, the available characters are not sufficient to make a confident taxonomic assignment. Modern corallanids are ectoparasites and micropredators of fishes, worms, and crustaceans, and are currently restricted to tropical and subtropical environments, with a preference for carbonate environments (Delaney, 1989), with the family named for their preference to coral reef environments. The Estancia 25 de Mayo Formation was deposited at high latitude, outside the current range of the majority of corallanids; however, owing to the much warmer climate in the early Miocene, it is feasible that their range could have extended to higher latitudes at that time. The formation represents a largely siliciclastic environment, with brief intervals of fluvial influence, and so would be an unusual environment for a corallanid, given their preference for carbonate environments. While corallanids prefer carbonate environments, some estuarine and freshwater forms are known (Poore, 2002). Modern

corallanids are usually found together with fishes and other crustaceans (Brusca & Gilligan, 1983; Bunkley-Williams and Williams, 1998). Abundant crustacean fossils are present within the Estancia 25 de Mayo Formation, as well as a diverse array of mollusks, however, fish and crustaceans are not found associated with one another. This may be a preservation bias caused by lower abundances of fishes, whose deaths rarely correlated with burial events, but some fish fossils would be expected if fishes were a major part of the ecosystem. Fish bones typically have a higher preservation potential than arthropod cuticle, so taphonomic bias cannot be an explanation for the absence of fishes in the formation. The Estancia 25 de Mayo fauna is comprised almost entirely of benthic animals, so it is possible that nektonic animals were able to escape burial during depositional events, either floods or volcanic eruptions, by swimming away. Corallanids cannot be eliminated based on morphology alone, but given their preferred ecological conditions, as well as their relatively small size, a corallanid affinity for this taxon is unlikely. The Cirolanidae and Aegidae also cannot be differentiated based on the available morphology, so other considerations must be made in order to evaluate the most likely taxonomic affinity of the fossil taxon. Because of this, other clues, such as ecological preferences (both biotic and abiotic), are used to evaluate the placement. Additionally, the nature of the fossil record for each group is considered. Like corallanids, aegids have a strong preference for a parasitic lifestyle, and are very commonly associated with fishes. The fossil isopod is not associated with fishes, but with other crustaceans. While some isopods are known parasites of other crustaceans (e.g., Bopyridae), aegids are not common parasites of crustaceans. There is only one possible fossil aegid (Hansen & Hansen, 2010), cirolanids, however, have a robust fossil record, with multiple genera dating to the Mesozoic. Cirolanids are not obligate parasites, nor are they strongly associated with any other taxa. They occupy a number of ecological niches, and are often found as scavengers or predators, and are common in different environments, including rocky shores and beaches, coral reefs, and continental slopes and shelves (Poore, 2002). The ecological and environmental preferences of cirolanids are more consistent with the fossil isopod than those of aegids. A more objective approach to analyzing the available morphological characters, however, is still warranted.

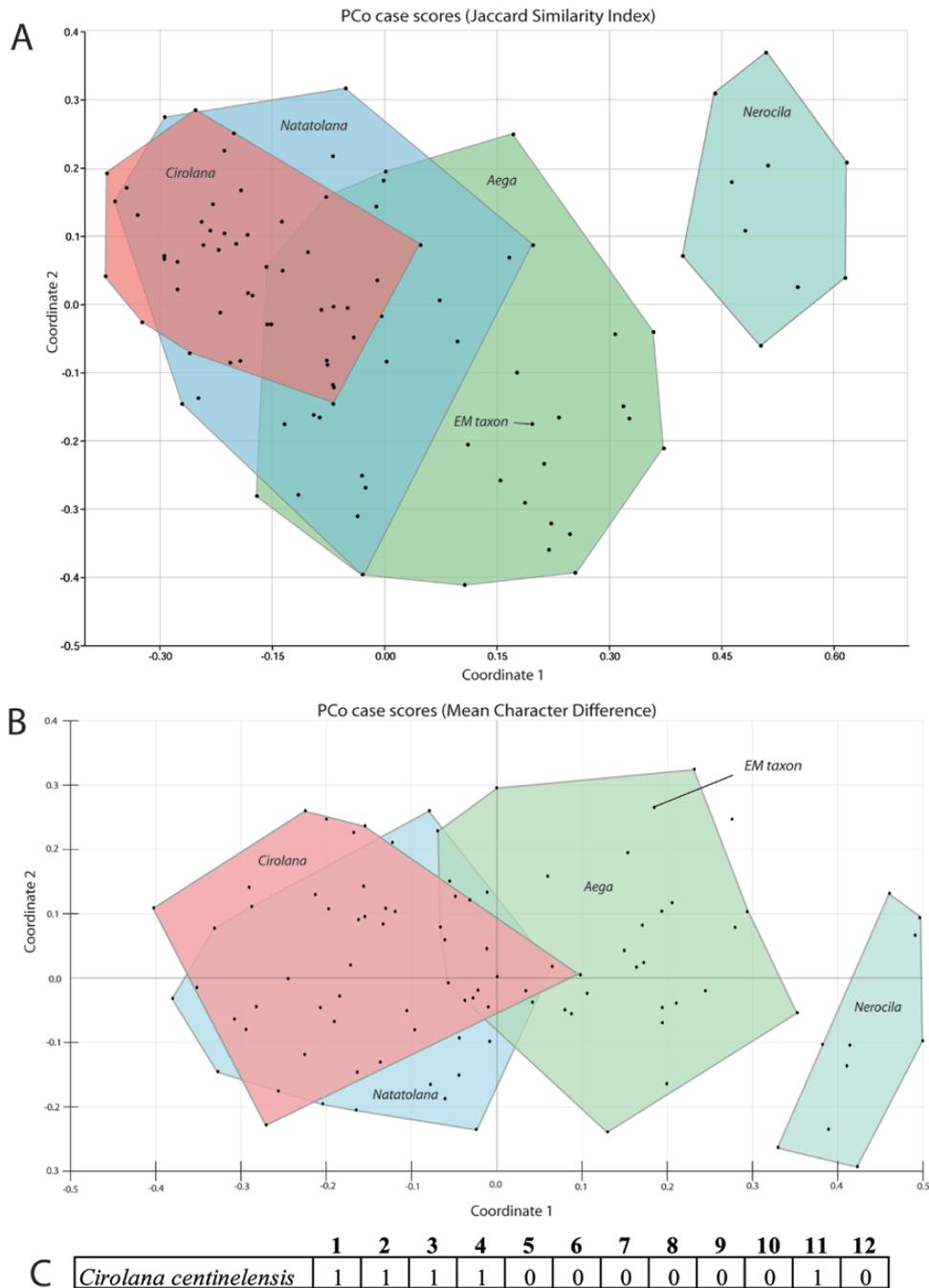
#### Principal coordinate analysis

All evidence considered, the most probable familial placement for the new fossil taxon is either in Aegidae or Cirolanidae. Because no one character can be used to place the taxon in either family, a multivariate principle coordinate analysis (PCO) was performed to evaluate trends in characters across representatives of the two families. The purpose of the analysis was to evaluate morphologic trends in available characters without imparting an *a priori* bias onto the dataset. The character matrix of Hansen & Hansen (2010) was chosen because the fossil taxon they evaluated is very similar to the new taxon herein, and many of the same parts are preserved. The matrix is composed of 12 binary (presence-absence) characters, which are focused primarily on posterior morphology. *Cirolana* and *Natatolana* represented Cirolanidae and *Aega* Aegidae. Because the overall goal of the analysis was to find familial, not generic, placement, the genera included are limited to those that we considered to be representatives of the typical morphology of their respective families. Hansen & Hansen (2010) included *Nerocila*, a cymothoid, because its posterior morphology is similar to that of aegids and cirolanids; however, they did not have any posterior pereopods preserved on their fossil taxon. The presence of ambulatory posterior pereopods on our taxon eliminated Cymothoidae as a possible familial placement, but *Nerocila* is included as an “outgroup.” Members of this genus plot clustered closely together, and do not overlap any other generic

morphospace, which demonstrates that the PCO accurately tracks variation across different families.

To ensure that the particular distance measure used did not change the outcome, two different PCO methods were used: the Jaccard Similarity Index (JSI; Fig. 4a), which was also used by Hansen & Hansen (2010), and the Mean Character Difference method (MCD; Fig. 4b). Cain & Harrison (1958) first proposed the MCD as a tool for phenetic taxonomy, and it was further discussed by Panchen (1992). The JSI method was carried out using the Paleontological Statistics program (PAST) (Hammer & Harper, 2006), and the MCD method using the Multivariate Statistics Package (MVSP) (Kovach, 2007). Both methods yielded similar results, and both are appropriate for binary data. Although the distribution of data points in each method was different, their relative positions remained largely the same, and each method placed the new taxon in the *Aega* morphospace. Using the Jaccard Similarity Index, the eigenvalue of Axis 1 was 9.8586 and explained 24.78% of the variation in the data, and the eigenvalue of Axis 2 was 4.5899, and explained 11.53% of the variation. Using the Mean Character Difference Method, Kaiser’s rule was used to extract two axes; Axis 1 has an eigenvalue of 6.8 and explains 52% of the variation in the dataset, and Axis 2 has an eigenvalue of 2.46 and explains 19.2% of the variation. Together, the two axes explain 72% of the variation in the dataset. By examining the groupings of taxa on the PCO scatter plots, it is possible to discern which characters account for certain groupings. While each group cannot be conclusively eliminated based on the characters analyzed, we evaluated trends among groups of characters that indicated the morphological tendencies of the genera considered. For example, members of *Nerocila* plot closely together, and do not overlap any of the other genera in the plot. This shows that the analysis accurately tracks morphologic variation, and there must be a character, or set of characters, that are unique to *Nerocila* and control its placement. A review of the data matrix reveals that character 12, pleonites with posterolateral process, is present in all members of *Nerocila*, but very rarely present in any other taxon examined. The far-right end of axis 1 (Fig. 4) is thus controlled by the presence of that character, and taxa with that character present load on that end of the scatter plot. The character groups that place the taxon with aegids and not the other genera tested can be similarly deduced by examining the dataset. The cirolanids in our dataset have a strong tendency to have the presence of multiple ornamentation character states on the posterolateral margin of their pleotelson, whereas aegids tend to have an absence, or single presence, of pleotelson modifications, favoring a smooth, entire posterolateral margin. This tendency is explained by characters 4–7, which score for various modifications of a simple pleotelson margin. Additionally, all but one aegid (*Aega ventrosa* Sars, 1859), lacks an oblique furrow on the anterolateral part of the pleotelson, whereas the presence or absence of this character is more variable in the cirolanids. Almost all *Cirolana* and *Natatolana* taxa do not have a distinctly acute posterolateral corner on pereonite VII, a character that is variable in the species of *Aega* and present in our new taxon.

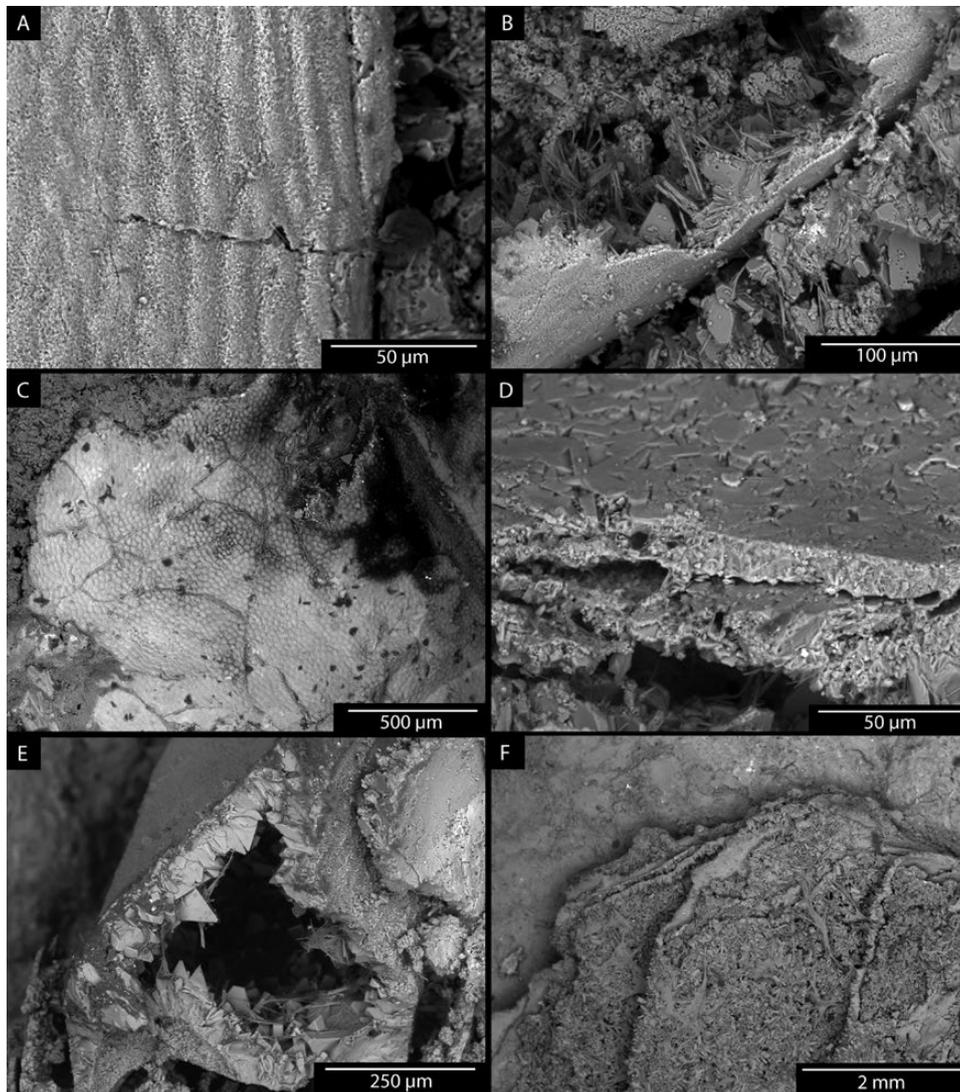
Despite our taxon plotting in the *Aega* morphospace in this analysis, we do not consider Aegidae the best placement for it. Because of paleontological and ecological considerations (see above), it is more likely that Cirolanidae is the best familial placement for the new taxon. It is our judgement that while the multivariate analysis is a useful tool for visualizing morphologic trends in available characters, its results do not outweigh paleontological and ecological considerations in this study. Once a diagnosis of a cirolanid affinity is made, a generic placement within the family is less difficult. Hyžný et al. (2013) reviewed the fossil record of the Cirolanidae, and identified six genera which have fossil representatives therein: *Urda* Münster, 1840, *Brunnaega* Polz, 2005, *Cirolana*, *Palaega* Woodward, 1870, *Bathynomus* Milne-Edwards, 1879, and



**Figure 4.** PCo scatter plots of the results of principal coordinate analysis using Jaccard Similarity Index, **(A)** and Mean Character Distance measure **(B)**. Polygons represent variability of characters within the character matrix. Character states of *Cirolana centinelensis* **(C)**. Characters scored are taken as follows: 1) pleonite 1 partly covered by pereonite VII; 2) pleonites equal in width; 3) pleonite 4 overlapping lateral parts of pleonite 5; 4) pleotelson with evenly curved posterolateral margin; 5) posterior margin of pleotelson angular pointed; 6) posterolateral margin of pleotelson serrated; 7) pleotelson with marginal teeth; 8) pleotelson with circum-lateral furrow; 9) oblique furrow on anterolateral part of pleotelson; 10) pleotelson widening abruptly at anterolateral corners; 11) posterolateral corner of pereon VII distinctly acute; 12) pleonites with posterolateral process. Characters from Hansen & Hansen (2010). This figure is available in color at *Journal of Crustacean Biology* online.

*Pseudopalaega Mezzalira & Martins-Neto, 1992.* They created a dichotomous key, which when applied to this taxon, resulted in a diagnosis of *Cirolana*. The features which lead to this diagnosis are as follows: 1) Pleotelson without distinct spines or denticulation on posterior margin; 2) Pleotelson longer than pleon, ovate to subtriangular, without median dorsal ridge; 3) Pleonite 5 laterally overlapped by pleonite 4.

The PCo analysis demonstrates its potential utility for evaluating trends in available characters in fossil material that are not necessarily the most taxonomically informative, but nonetheless must be considered. Multivariate analyses are a viable way to objectively view morphological trends in presence-absence datasets. Because of the incomplete nature of fossil specimens, however, paleontologists are faced with making taxonomic assignments



**Figure 5.** Scanning electron micrographs showing different taphonomic features of *Cirolana centinelensis* **n. sp.**: micro-scale cuticle architecture preserved on a pereiopod (A); cross-section of a broken pereiopod, showing very thin cuticle and altered minerals (B); coarse cuticle ornamentation preserved on dorsal cuticle (C); moldic surface of zeolites which abutted the pleotelson (D); zeolites growing inside a broken coxal plate (E); clinoptilolite and erionite encrusting and replicating the surface of pereonites (F).

using considerations outside pure morphology. It is also important to note, that although the PCO analysis placed our new taxon in the *Aega* morphospace, none of the 12 characters used preclude a generic assignment of any other genera considered. Furthermore, the dataset does not include all members of each family or genus considered, which would more accurately display the full range of morphologic variability in the selected characters therein, and expand each morphospace. The addition of other similar genera such as *Rocinela* Leach, 1818, *Politolana* Bruce, 1981, or *Booralana* Bruce, 1986, would more accurately show the full range of variation of forms within the Cirolanidae, but this is outside the scope of this study.

### TAPHONOMY

*Cirolana centinelensis* **n. sp.** displays various modes and qualities of preservation. Fine-scale cuticle microarchitecture is preserved in some areas (Fig. 5A, C), whereas the formation of secondary ash alteration products (largely zeolites) has obliterated all or most structure in others (Fig. 5B, D, F), most notably the dorsal tergites. The specimen of the new taxon is preserved in volcanic ash,

which presents unique early diagenetic conditions favorable for preservation. The rapid deposition of very fine-grained volcanic ash creates optimal conditions for fossil preservation. Volcanic ash can rapidly kill and bury benthic faunas (Crawford *et al.*, 2008; Maguire *et al.*, 2016), and its very fine grain size may restrict oxygen diffusion through sediment during early diagenesis, a crucial criterion for preservation of recalcitrant tissues. The high reactivity of the ash, however, makes it unstable over geologic time, and secondary alteration products rapidly form during the devitrification of the volcanic glass, a process that can be destructive. The production of early diagenetic clay minerals may also play a role in enhancing preservation by creating surficial molds, and adding to the cohesive strength of the ash, as suggested by Orr *et al.*, 2000, in their taphonomic model for the Herefordshire Lagerstätte (England). The alteration products of the ash enclosing *Cirolana centinelensis* **n. sp.** are dominated by the zeolite minerals clinoptilolite and erionite, which were identified based on crystal morphology and elemental composition. Clinoptilolite is a microporous zeolite mineral which forms tabular, triangular or “coffin-shaped” monoclinic crystals (Fig. 5B, D, E, F). Erionite is also a zeolite mineral formed by ash devitrification; it forms fibrous, acicular, and

hexagonal crystals (Fig. 5B, E, F). These zeolites are products of the devitrification of originally amorphous volcanic glass shards. Amorphous allophones are also present as void-filling growths. When present, cuticle material is variously composed of aluminosilicate minerals and calcium phosphate, likely in the form of hydroxyapatite ( $\text{Ca}_3(\text{PO}_4)_3(\text{OH})$ ), identified through the use of energy dispersive spectroscopy (EDS). When cuticle is absent, parts of the fossil are preserved as moldic surfaces created when growing zeolite minerals abutted the fossil (Fig. 2D). The presence of zeolitic molds in areas where cuticle is missing indicates that the cuticle was preserved at least until the formation of the zeolites. The cuticle was likely destroyed contemporaneously with, or sometime after, zeolite formation, likely due to the movement of ground water through the sediment.

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