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Morphological insights into the lobster genus *Uncina* Quenstedt, 1851 based on new material from the Ya Ha Tinda Konservat-Lagerstätte, Canada (Early Jurassic)

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ABSTRACT

It is rare to find Early Jurassic crustacean material outside of Europe but the discovery of the Ya Ha Tinda Konservat-Lagerstätte in Alberta, Canada, has significantly increased the number of crustacean specimens, specifically of the genus *Uncina*. New articulated specimens of *Uncina pacifica* and *Uncina ollerenshawi* preserve most of the cephalothorax and pleon, not just the chelae of the first pereiopod. This new material from Ya Ha Tinda permits revised morphologic descriptions as well as a quantitative analysis of the intra- and interspecific variability of *Uncina* claw morphology. Morphometric similarities and differences are noted between species, indicating that a notch at the distal end of the occlusal surface of the fixed finger is diagnostic for the genus. Our findings suggest that *Uncina* species are usually isochelous, with the exception of *Uncina pacifica*, which is heterochelous. The two co-occurring species of *Uncina* in the Ya Ha Tinda Formation, *Uncina pacifica* and *Uncina ollerenshawi,* likely occupied different niches, based upon differences in chela morphology.

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INTRODUCTION

Crustaceans are important components of benthic marine communities in both modern and ancient oceans. Decapod crustaceans have a well-documented fossil record through the Jurassic but are mostly known from European sites, such as the Toarcian Posidonia Shale in Germany, and Upper Jurassic lithographic limestones, like the Solnhofen Limestone in Germany (Schweigert et al., 2003; Klompmaker et al., 2013; Schweitzer and Feldmann, 2014). To date, there has been very little work on Jurassic crustaceans from sites outside of Europe (i.e., the Panthalassa Ocean).

The Jurassic lobster *Uncina* Quenstedt, 1851, belongs to the superfamily Enoplometopoidea de Saint Laurent, 1988, and the family Uncinidae Quenstedt, 1851 (Ahyong, 2006; Karasawa et al., 2013). Globally, *Uncina* is represented by four extinct species from the Early Jurassic (201 Ma to 174 Ma). Although uncinid lobsters have been found in deposits from the Panthalassa Ocean, namely Japan (Karasawa, 2002) and Canada (Feldmann and Copeland, 1988; Schweigert et al., 2003), most studied and articulated specimens are from Tethyan strata in Franconia, northwest and southwest Germany, as well as eastern France, and northern Italy (Schweigert et al., 2003) (Figure 1). In addition to the paucity of material from Panthalassa, *Uncina pacifica* Schweigert Garassino, Hall, Hauff, and Karasawa, 2003 (Canada and Japan) and *Uncina alpina* Schweigert, Garassino, Hall, Hauff, and Karasawa, 2003 (Germany) are only known from a few specimens of cheliped material. Moreover, *Uncina ollerenshawi* Feldmann and Copeland, 1988 (Canada) has, until recently, only been known from one molted specimen with poor sclerotization (Feldmann and Copeland, 1988). The diagnosis of *Uncina* originally was largely based on the type species, *Uncina posidoniae* Quenstedt, 1851 (Germany) and emended diagnoses have not benefitted from extensive studies of complete specimens (i.e., majority of the cephalothorax, pleon, and chelae) from the three other species (Schweigert et al., 2003). Recent discoveries at the Ya Ha Tinda Konservat-Lagerstätte in Alberta, Canada (Figure 1) (Martindale et al., 2017; Muscente et al., 2019), have substantially increased the number of *Uncina* specimens available for study including several articulated or mostly complete body fossils yielding new morphological information on the two Panthalassan species, *U. ollerenshawi* and *U. pacifica*. These new finds include 21 previously undescribed specimens of *U. pacifica* (two exhibiting carapace, chelae, uropods, and pleons, hereafter referred to as a "full body" specimen) and nine new specimens of *U. ollerenshawi* including two full body specimens. Herein, we provide emended diagnoses of the Panthalassan *Uncina* species as well as the

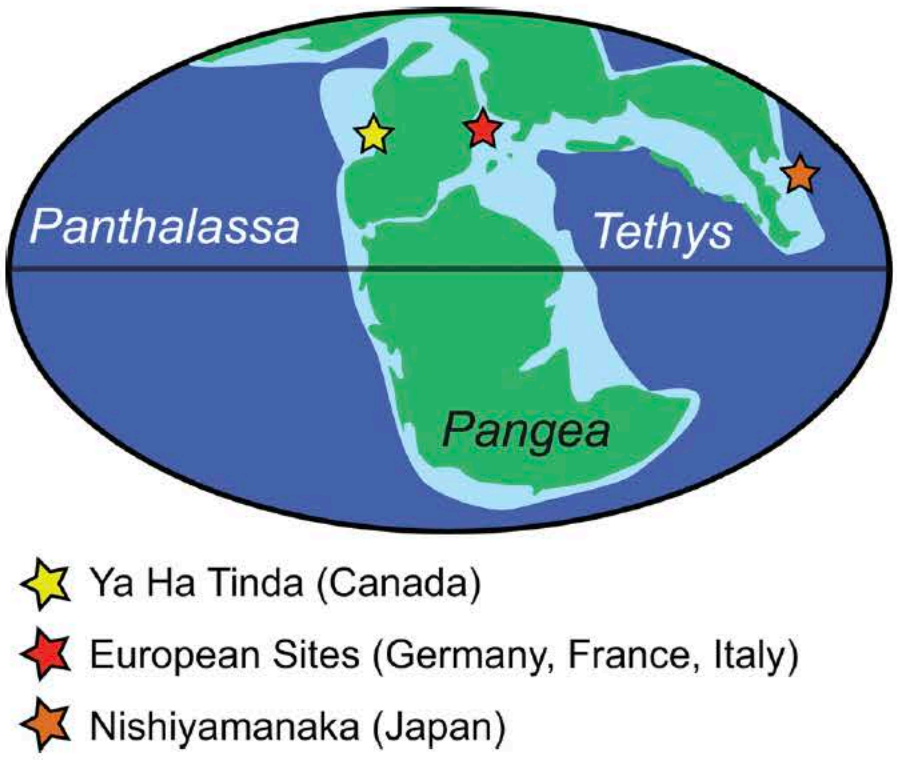


FIGURE 1. Paleogeographic map from the Early Jurassic indicating where *Uncina* lobsters have been found (Feldmann and Copeland, 1988; Karasawa, 2002; Schweigert et al., 2003; Martindale et al., 2017). The yellow star represents Ya Ha Tinda, Alberta, Canada, the red star represents the European sites bearing *Uncina alpina* and *U. posidoniae,* and the orange star represents the modern-day Japanese site bearing *Uncina pacifica* (Karasawa, 2002). Figure modified from Martindale et al. (2017).

genus, with emphasis on intraspecific variation of the first pereiopods as they are the most commonly and best-preserved part of the animal (Schweigert et al., 2003). This work also discusses the stratigraphic range and ecomorphology of species of this genus, with particular attention to the information yielded from the North American specimens.

GEOLOGICAL SETTINGS

Crustaceans from Ya Ha Tinda have been recovered from the Red Deer and Poker Chip Shale members of the Lower Jurassic Fernie Formation (Figure 2, Table 1) (Martindale et al., 2017). The Pliensbachian to early Toarcian Red Deer Member is composed of dark grey to black, platy, calcareous shale interbedded with fine siltstones and thin limestone shell beds, whereas the Toarcian Poker Chip Shale Member is chiefly black, calcareous shale, and mudstone that is fine-grained, poorly cemented, and fissile (Them et al., 2017, and references therein). These members are interpreted to have been deposited in periodically dysoxic conditions with regular intervals of oxygenation (Martindale and Aberhan, 2017; Muscente et al., 2019; Sinha et al., 2021). The chronostratigraphy of the site is best constrained by ammonite biostratigraphy and stable isotope chemostratigraphy, namely the carbon isotope excursion associated with the Toarcian Oceanic Anoxic Event (Figure 2) (Them et al., 2017). Both near-complete articulated specimens of *Uncina* and disarticulated material are abundant in strata prior to the Toarcian Oceanic Anoxic Event (Figure 2), but during the event and in the recovery from the event, lobster material is limited (Figure 2) (Martindale and Aberhan, 2017).

Decapod material was collected from Scalp Creek, Bighorn Creek, and the East Tributary of Bighorn Creek (referred to as “East Tributary”) sections at the Ya Ha Tinda Ranch, Alberta, Canada (Royal Tyrrell Museum of Palaeontology localities L2430, L2429, and L2428, respectively), but most of the material is from the East Tributary of Bighorn Creek. Many specimens were found in situ and thus can be assigned to a stratigraphic horizon and age; however, numerous significant finds were recovered from float material on the banks of the river (i.e., float) or were collected previously and stratigraphic information was not reported. In some cases, specific stratigraphic position is not known or was not recorded, but the ammonite zone was noted by the collector, the late Russell Hall, an ammonite biostratigrapher. In these cases, the age is assumed to be correct (denoted by dashed range in Figure 2). Recently collected specimens found in float material from East Tributary can be assigned a minimum age; the river cuts up-section, and so specimens that were not found in situ are interpreted to have originated from strata that are stratigraphically below the horizon in which they were found (denoted by the dashed arrow in Figure 2). Fernie Formation decapod material (Table 1) is predominantly preserved through secondary phosphatization and now consists of apatite minerals with some carbonaceous material, as well as minor auxiliary minerals (Muscente et al., 2019; Sinha et al., 2021).

TAXONOMIC AND MORPHOMETRIC METHODS OF ANALYSIS

Rock slabs of curated specimens were trimmed and reconsolidated with Paraloid B-72 (a thermoplastic resin) if fractured, and overlying matrix was removed. Then, each specimen was photographed in plain light and angled light with a Canon EOS Rebel SL2 Digital SLR camera with an EFS 18-55 mm lens; specimens were also photographed under UV light and polarized light with limited success. Particularly informative specimens were whitened with ammonium chloride (see Feldmann, 1989, for details on this methodology) and photographed with low-angle light using a Nikon D3100 camera with AF-S micro Nikkor 60 mm lens. Images of the fossil specimens were enhanced in Adobe Photoshop to increase contrast and assist identification of features.

The most consistently preserved elements of uncinid lobsters are the chelipeds. Since these elements are not only abundant but diagnostic for each species, they are ideal for morphological assessments of cheliped variation among and between *Uncina* species. Numerous measurements were taken for each cheliped (Appendix 1, Appendix 2). For specimens measured physically, digital calipers were used; measurements taken from photographed specimens figured in Schweigert et al. (2003) were calculated using the measuring tool in ImageJ (Schneider et al., 2012). All statistical and morphometric analyses were performed in R studio (R Core Team, 2008). R code used for box plots and Wilcoxon (1945) Ranked-Sum tests can be found in Appendix 3. The Wilcoxon Ranked-Sum tests were employed to test the statistical similarity of measurements taken on the chelae of each species. The null hypothesis is that the median difference between the observations is zero. The confidence interval used was

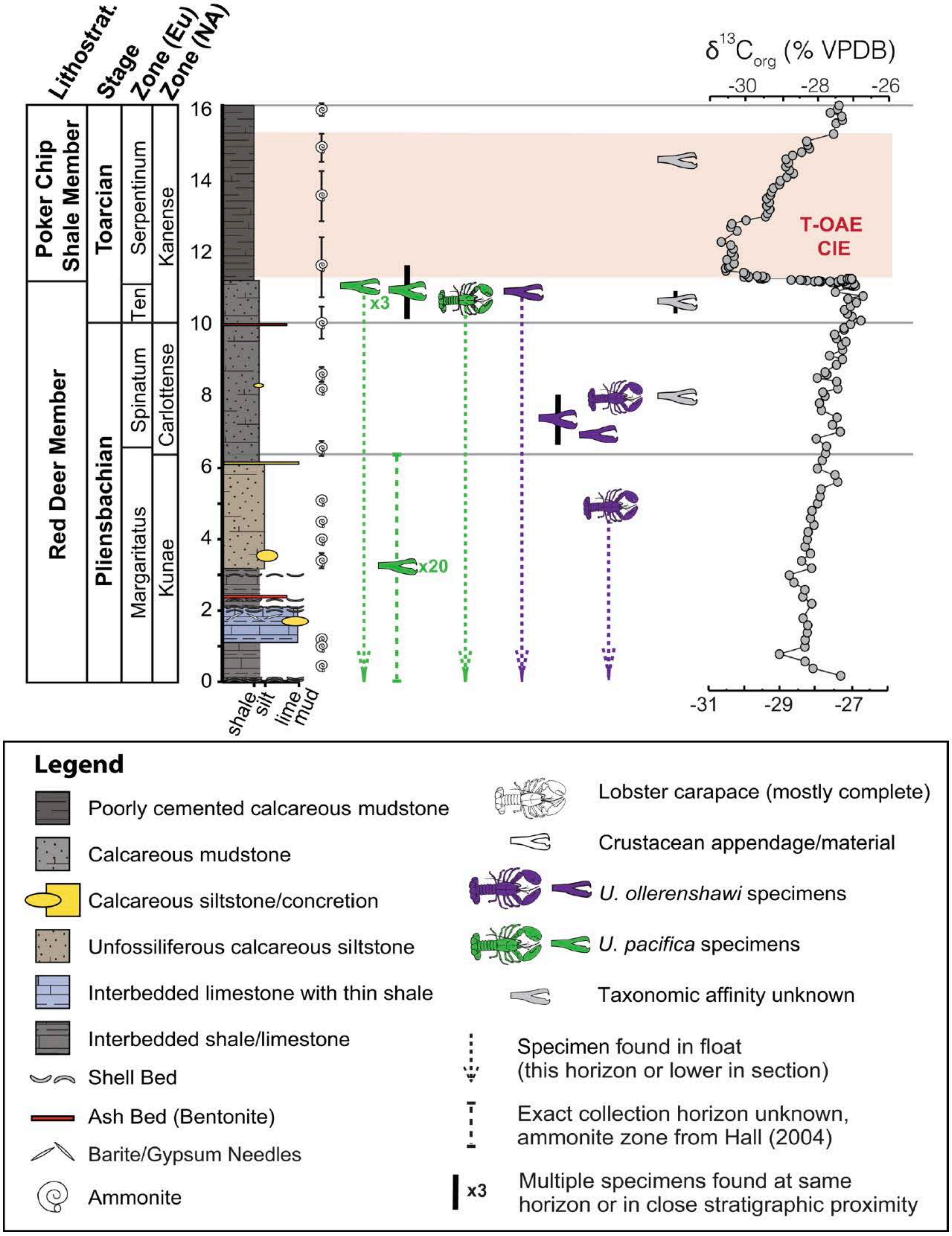


FIGURE 2. Stratigraphic column of the East Tributary of Bighorn Creek section, Ya Ha Tinda Ranch, Alberta, Canada. Symbols denote the stratigraphic heights at which crustacean material was found as well as the elements and species (if applicable). Sepent. = Serpentinum, Falcif. = Falciferum, Eu = Europe, NA = North America. Lithostratigraphy and carbon isotope curve from Them et al. (2017) and fossil heights from Martindale et al. (2017). Some specimens are not reported from a particular horizon; instead, the collector Russell Hall (an ammonite biostratigrapher) noted the ammonite zone and so the age is assumed to be correct (dashed range). Specimens found in float from East Tributary can be assigned a minimum age; the river cuts up-section and so specimens not found in situ are interpreted to have originated from strata that are stratigraphically below the horizon in which they were found (dashed arrow).

TABLE 1. The *Uncina* specimens use in this study with their locality, formation, stratigraphic height, when known, and age.

Species	Specimen Number	Locality	Formation, Member	Ammonite Zone - Stratigraphic Height (Figure 2) included for East Tributary Specimens		Age
U. pacifica	TMP 2018.024.0005	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone (or older) -	Float at 11m	Toarcian or older
	TMP 2018.024.0035	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone (or older) -	Float at 11m	Toarcian or older
	TMP 2018.024.0004	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone (or older) -	Float at 11m	Toarcian or older
	TMP 2018.024.0003	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone (or older) -	Float at 11m	Toarcian or older
	TMP 2017.015.0007	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Unknown		Unknown
	TMP 2017.015.0005	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone-	11.1m	Toarcian
	TMP 2017.015.0003	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Unknown		Unknown
	TMP 2017.015.0001 a & b	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Unknown		Unknown
	TMP 2016.027.0003	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Unknown		Unknown
	TMP 2015.050.0069	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone (or older) -	Float at 11m	Toarcian or older
	TMP 2015.050.0039	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone (or older) -	Float at 11m	Toarcian or older
	TMP 2014.021.0023	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Unknown		Unknown
	TMP 2015.050.0038	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone-	10.45m	Toarcian
	TMP 2014.021.0033	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone-	11.18m	Toarcian
	TMP 2014.021.0034	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone-	11.15m	Toarcian
	TMP 2014.021.0007	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone-	11.5m	Toarcian
	TMP 2002.043.0012	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)		Pliensbachian
	TMP 2002 043.0019 a & b	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)		Pliensbachian
	TMP 2014.021.0003	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone-	10.2m	Toarcian
	TMP 2002.043.0008	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)		Pliensbachian
	TMP 2002.043.0015	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)		Pliensbachian
	TMP 2002.043.0007	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)		Pliensbachian
	TMP 2002.043.0003 a & b	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)		Pliensbachian
	TMP 2002.043.0006	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)		Pliensbachian
	TMP 2002.043.0002	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)		Pliensbachian
	TMP 2014.021.0008	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone-	11.5m	Toarcian

TABLE 1 (continued).

Species	Specimen Number	Locality	Formation, Member	Ammonite Zone - Stratigraphic Height (Figure 2) included for East Tributary Specimens	Age
	TMP 2014.021.0002	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone- 10.25m	Toarcian
	TMP 2002.043.0004	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)	Pliensbachian
	TMP 2002.043.0005	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Margaritatus zone (Hall 2004)	Pliensbachian
	KMNH IvP 300,027	Northwestern coast of Ainoshima Island, Kokurakita-ku, Kitakyushu City, Fukuoka Prefecture.	Yamaga Formation, Ashiya Group	Not attributed to a zone	Toarcian
U. ollerenshawi	TMP 2018.024.0009	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone (or older) - Float at 11m	Toarcian or older
	TMP 2018.024.0006	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kanense Zone (or older) - Float at 11m	Toarcian or older
	TMP 2016.027.0008	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Material in Float	Unknown
	TMP 2015.051.0063	Ya Ha Tinda Ranch- Scalp Creek, AB, Canada	Fernie Formation, Red Deer Member	Not Applicable/Material in Float	Unknown
	TMP 2014.0021.0052 A & B	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Carlottense Zone 7.75m	Pliensbachian
	TMP 2015.050.0011	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Carlottense Zone 6.55m	Pliensbachian
	TMP 2013.036.0002	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Carlottense Zone 7.4m	Pliensbachian
	TMP 2005.028.0004 (pt & cpt)	Ya Ha Tinda Ranch- East Tributary, AB, Canada	Fernie Formation, Red Deer Member	Kunae Zone (estimated, material in float)	Pliensbachian
	GSC 80067 A & B (HOLOTYPE)	GSC locality 75402 on Bighorn Creek, above a small waterfall	Fernie Formation	Margaritatus zone	Pliensbachian
U. posidoniae	MB.A.3826 (2 claws)	Holzmaden, Baden-Württemberg, SW Germany	Lias epsilon	Not Applicable	Toarcian
	Posidoniae1A	SW Germany	unknown	Unknown	Unknown
	Posidoniae1B	SW Germany	unknown	Unknown	Unknown
	Posidoniae2	SW Germany	unknown	Unknown	Unknown
	Poidoniae (LECTOTYPE)	Metzingen, "Bierkeller", SW Germany (Schweigert et al., 2003, Plate 1)	Posidonia Shale Formation, Fleins Bed	Tenuicostatum Zone, Semicelatum Subzone	Early Toarcian
	SMNS no. 29150 (2 claws)	Holzmaden, Baden-Württemberg, SW Germany (Schweigert et al., 2003, Plate 2)	Posidonia Shale Formation, Unterer Schiefer Bed	Tenuicostatum-Falciferum Zone, Semicelatum or Exaratum Subzone	Early Toarcian
	No ID "Plate 4" (2 claws)	Holzmaden, Baden-Württemberg, SW Germany (Schweigert et al., 2003, Plate 4)	Posidonia Shale Formation, Unterer Schiefer Bed	Tenuicostatum-Falciferum Zone, Semicelatum or Exaratum Subzone	Early Toarcian
	SMNS no. 62815	Holzmaden, Baden-Württemberg, SW Germany (Schweigert et al., 2003, Plate 8)	Posidonia Shale Formation, Unterer Schiefer Bed	Tenuicostatum-Falciferum Zone, Semicelatum or Exaratum Subzone	Early Toarcian

TABLE 1 (continued).

Species	Specimen Number	Locality	Formation, Member	Ammonite Zone - Stratigraphic Height (Figure 2) included for East Tributary Specimens	Age
U. alpina	MSNM no. i10864 (2 claws)	Monte Brughetto near Sogno, Southern Alps, N Italy (Schweigert et al., 2003, Plate 10, Figure 2)	Basal beds of Sogno Formation	Tenuicostatum or Falciferum Zone	Early Toarcian
	MNSM no. i10863	Monte Brughetto near Sogno, Southern Alps, N Italy (Schweigert et al., 2003, Plate 10, Figure 3)	Basal beds of Sogno Formation	Tenuicostatum or Falciferum Zone	Early Toarcian
	MNSM no. i10851	Kreuzwirtzbach gorge near Pfronten-Grau, Bavaria, S Germany (Schweigert et al., 2003, Plate 10, Figure 5)	Allgau-Schichten Formation, Manganschiefer Member	Tenuicostatum or Falciferum Zone	Early Toarcian

0.99 and the Alpha Value was 0.05. Images of all new specimens are included in Appendix 4.

Institutional Abbreviations

TMP, The Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; KMNH, Kitakyushu Museum of Natural History, Kitakyushu, Japan; GSC, Geological Survey of Canada, Ottawa, Ontario, Canada.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder ASTACIDEA Latreille, 1802
Superfamily ENOPLOMETOPOIDEA de Saint Laurent, 1988
Family UNCINIDAE Beurlen, 1928
Genus *UNCINA* Quenstedt, 1851
(syn.: *LEPTOCHIRUS* Krause, 1891)

Type species. *Uncina posidoniae* Quenstedt, 1851, by monotypy.

Diagnosis. Astacidean with weakly sclerotized carapace, median suture present; strong, serrate rostrum; granulated carapace; first pereiopods chelate, enlarged, bearing marginal, distally-directed spines with robust, elongate merus; propodus with distally curved fingers; line of highly sclerotized nodes present across manus; manus with concave inner margin and convex outer margin; first pereiopods heterochelous or isochelous; occlusal surface of fixed finger and dactylus dentate; distal part of the fixed finger deeply incised with a notch; second and third pereiopods chelate; fourth and fifth pereiopods achelate, terminating in triangular dactylus; exopod of uropod with straight diaeresis.

Remarks. With the discovery of the two full body specimens of *Uncina pacifica* and two new full body specimens of *U. ollerenshawi* described herein, many genus-level traits are confirmed. The straight diaeresis of the exopod of the uropods is present in all specimens that exhibit pleons (TMP 2018.024.0001, species unknown, telson, uropods, and pleon only; TMP 2005.028.0004, *U. ollerenshawi* full body specimen; GSC 80067, *U. ollerenshawi* full body specimen; TMP 2014.021.0002, *U. pacifica* full body specimen; TMP 2017.015.0001, *U. pacifica* full body specimen; TMP 2014.021.0052, *U. ollerenshawi* full body specimen; see Figure 3, Figure 4, and Appendix 4) so we confirm this trait as a generic characteristic. The new specimen of *U. pacifica* with both chelipeds articulated (TMP 2017.015.0001, Figure 4B) is found to be heterochelous, a previously unknown condition for uncinids; however, the three full body *U. ollerenshawi* specimens studied (GSC 80067, TMP 2005.028.0004, and TMP 2014.021.0002) are isochelous and fit the original genus description. No new *U. alpina* or *U. posidoniae* specimens were collected; examinations focused mainly on published material.

Uncina ollerenshawi (Feldmann and Copeland, 1988)
Figure 3

1988 ?*Eryma ollerenshawi* Feldmann and Copeland, p. 93., fig. 4.2; pls. 4.1-4.2.
2003 *Uncina ollerenshawi* (Feldmann and Copeland); Schweigert et al., p. 10., pl. 11.
2010 *Uncina ollerenshawi* (Feldmann and Copeland); Schweitzer et al., p. 27.
2019 *Uncina ollerenshawi* (Feldmann and Copeland); Muscente et al., p. 522.

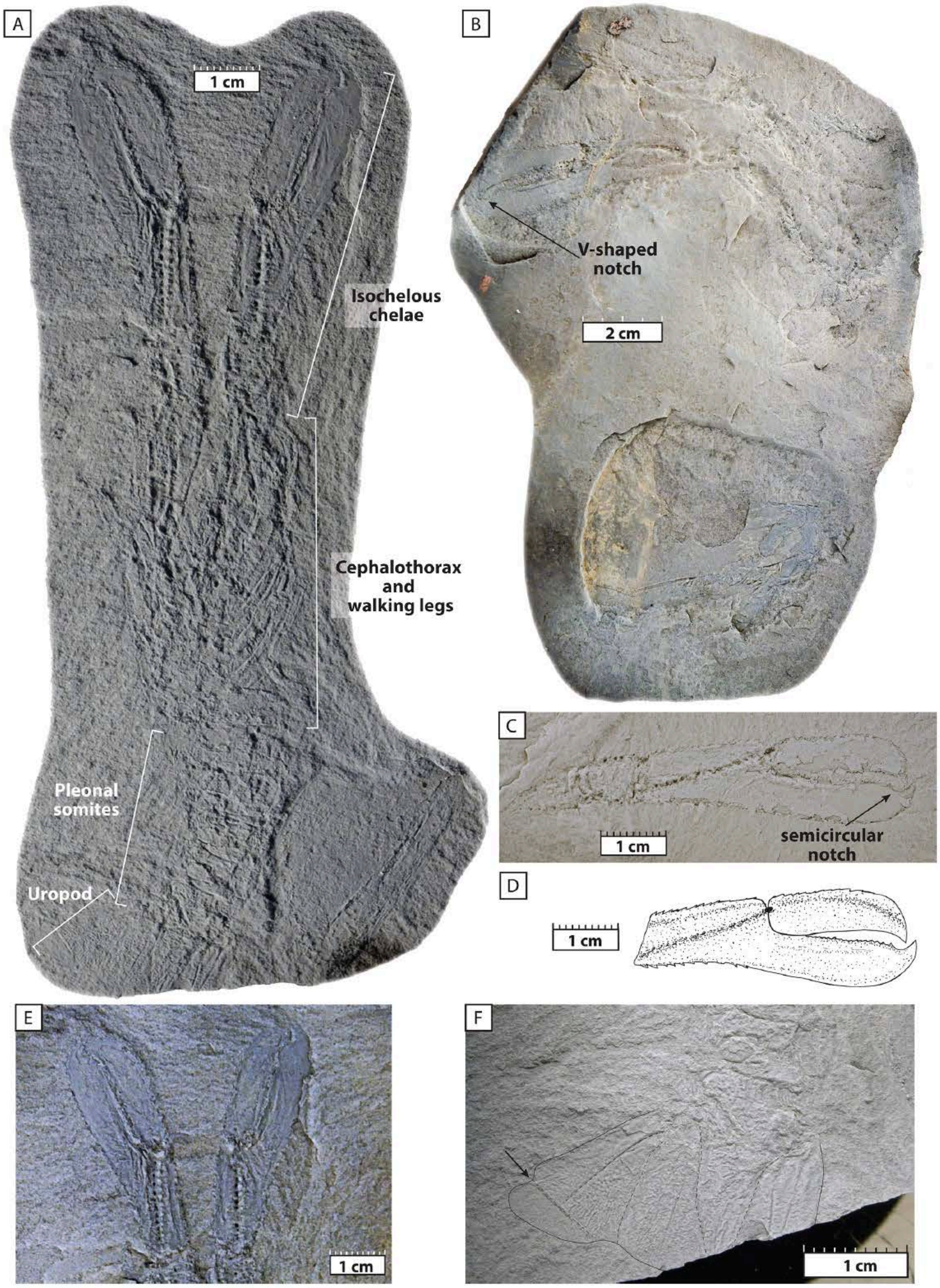


FIGURE 3. Selected specimens of *Uncina ollerenshawi*; all whitened with ammonium chloride. A) Holotype specimen of *U. ollerenshawi* (GSC 80067). Specimen is a molt (Feldmann and Copeland, 1988) found at GSC locality 75402, above a small waterfall on Bighorn Creek, Fernie Formation, Pliensbachian age. B) Nearly complete molt specimen of *U. ollerenshawi* (TMP 2014.021.0052). Late Pliensbachian in age, collected from the Red Deer Member of the Fernie Formation at the East Tributary of Bighorn Creek locality at Ya Ha Tinda Ranch, Alberta, Canada. C) Claw of the first pereiopod of *U. ollerenshawi* (TMP 2015.051.0063). Ya Ha Tinda Ranch of Alberta, Canada, Fernie Formation, Red Deer Member, Exact age unknown, collected from the Red Deer Member of the Fernie Formation at the Scalp Creek locality at Ya Ha Tinda Ranch, Alberta, Canada. D) Sketch of TMP 2015.051.0063 to scale. E) Close up of the chelae from the holotype of *U. ollerenshawi* (GSC 80067). F) Close up of the tail from the holotype of *U. ollerenshawi* (GSC 80067), faint outlines of the uropods and telson annotated, arrow identifies the straight diaeresis on the exopod.

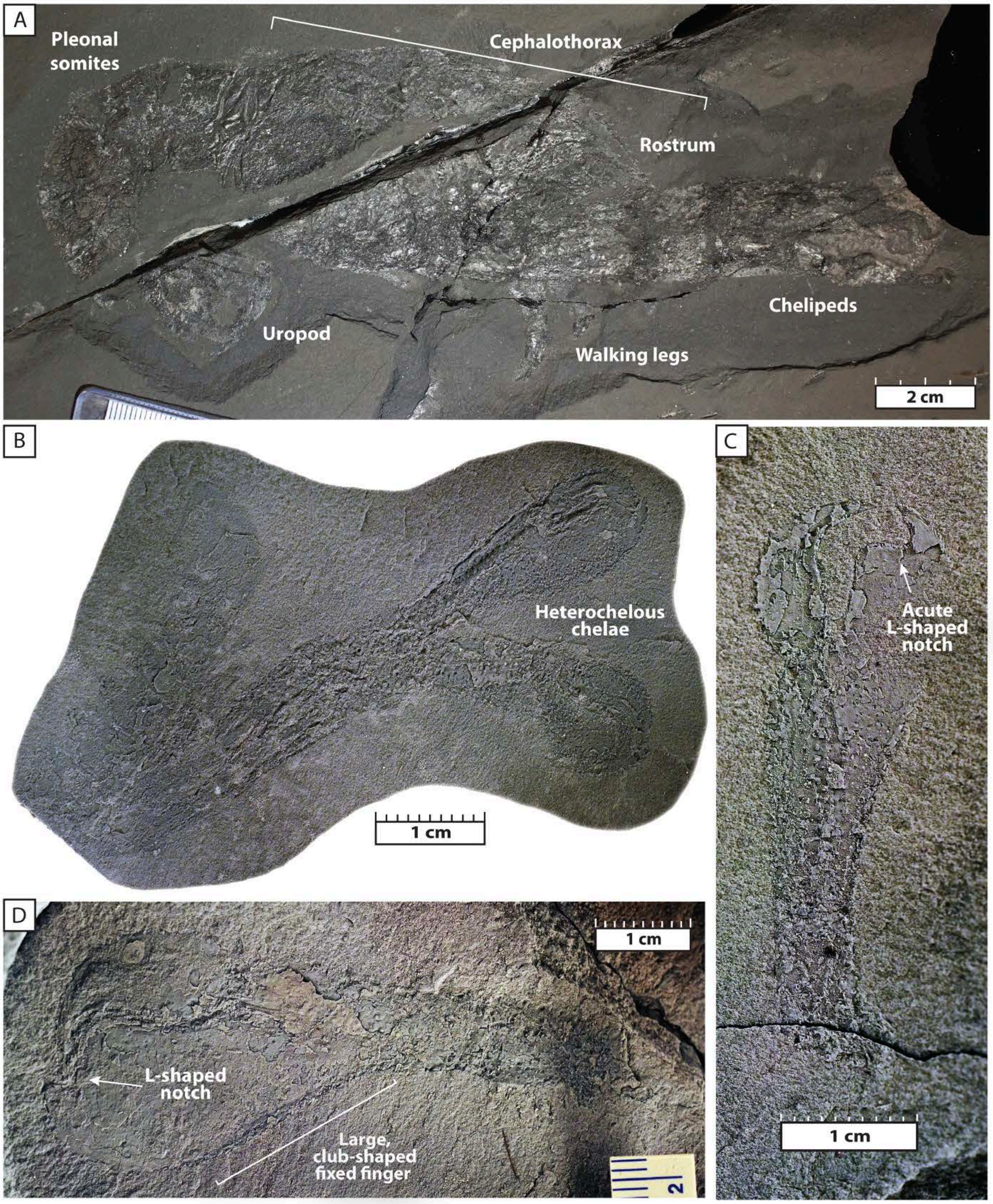


FIGURE 4. Selected specimens of *Uncina pacifica* (all whitened with ammonium chloride unless otherwise noted). All specimens are Toarcian in age and were collected from the Red Deer Member of the Fernie Formation at the East Tributary of Bighorn Creek locality at Ya Ha Tinda Ranch, Alberta, Canada. A) Near complete specimen of *U. pacifica* (TMP 2014.021.0002), imaged in polarized light. B) Full body specimen of *U. pacifica* (TMP 2017.015.00001), possible molt, otherwise poorly preserved. Specimen has both chelae of the first pereiopod preserved and demonstrates that *U. pacifica* is heterochelous. C) Isolated minor chela of the first pereiopod of *U. pacifica* (TMP 2017.015.0005). D) Isolated major chela of the first pereiopod of *U. pacifica* (TMP 2014.021.0003).

Holotype. GSC 80067.

Type locality. GSC locality 75402 on Bighorn Creek (see Frebold 1957: 85-86), SW Alberta, Canada (RTMP Locality L2429).

Type horizon. Fernie Formation, Red Deer Member (Upper Pliensbachian, Margaritatus Zone).

Studied material. GSC 80067, TMP 2005.028.0004, TMP 2013.036.0002, TMP 2014.021.0052 (both pereiopods), TMP 2015.050.0011, TMP 2015.051.0063, TMP 2016.027.0008, TMP 2018.024.0006 and TMP 2018.024.0009 (Table 1).

Occurrence. Pliensbachian of Canada.

Diagnosis. Isochelous species of *Uncina* in which pleonal pleura are rectangular; fixed finger of first pereiopod almost equal in length with the manus; maximum width of fixed finger and dactylus nearly equal; semicircular to V-shaped notch in distal part of fixed finger; diagonal row of nodes from top of manus attachment to dactylus attachment; dorsal and ventral margins of chelae of first pereiopods covered with distally-directed spines.

Remarks. Previously, only the holotype of *Uncina ollerenshawi* was described. In this study, eight new specimens were evaluated, including two other full body specimens; these additional specimens verify traits described in Feldmann and Copeland (1988) and Schweigert et al. (2003). The holotype represents a molt of the animal (Feldmann and Copeland, 1988), so the addition of new specimens, specifically those representing corpses, were useful in confirming that the original holotype observations were not modified by the molting process. Molt specimens are recognizable by their often weaker sclerotization and wrinkled appearance. The new *U. ollerenshawi* specimens were used to confirm the following generic traits: serrate rostrum, ridged claws, long occlusal surface of fingers, and diaeresis on exopods of uropods.

Comparisons. The chelae of *Uncina ollerenshawi* appear similar to those of *U. posidoniae* with the key difference being the length of the fixed finger and dactylus when compared to that of the rest of the cheliped. In *U. ollerenshawi*, there is a nearly 1:1 ratio between the lengths of the fixed finger and the manus, whereas in *U. posidoniae*, the hand is much longer than the fixed finger. *Uncina pacifica* and *U. ollerenshawi*, the two species found in North America, are most notably different when considering the height of the fixed finger compared to the hand. In *U. pacifica* the fixed finger is much larger and more club-like when compared to the manus, whereas in *U. ollerenshawi* the hand and fixed finger are nearly equal in width. *Uncina ollerenshawi* also differs from *U. alpina* in this way. The pleonal pleura of *U. ollerenshawi* are rectangular and more pointed on their distal corners while specimens of *U. posidoniae* have rounded pleurae. *Uncina pacifica* has much more pointed corners than those of the pleurae of *U. ollerenshawi*. In addition, all pleurae of *U. ollerenshawi* are nearly equal in size, which differs strongly from *U. pacifica* and *U. posidoniae.*

Uncina pacifica (Schweigert, Garassino, Hall, Hauff, and Karasawa, 2003)
Figure 4

2002	*Uncina* sp., Karasawa, p. 13, pl. 2, fig. 1.
2003	*Uncina pacifica* Schweigert, Garassino, Hall, Hauff, and Karasawa, p. 12, figs. 4, 5b, pl. 12, figs. 1-4.
2010	*Uncina pacifica* Schweigert, Garassino, Hall, Hauff, and Karasawa; Schweitzer et al., p. 27.
2017	*Uncina pacifica* Schweigert, Garassino, Hall, Hauff, and Karasawa; Martindale et al., p. 257, fig. 3.
2019	*Uncina pacifica* Schweigert, Garassino, Hall, Hauff, and Karasawa; Muscente et al., p. 519, fig. 3N [unnamed] and 3O.

Holotype. TMP 2002.043.0005.

Studied material. TMP 2002.043.0002 to TMP 2002.043.0008, TMP 2002.043.0012, TMP 2002.043.0015, TMP 2014.021.0002 (note: specimen split across two samples, TMP 2013.036.0004 and TMP 2014.021.0002, hereafter specimen is referred to as TMP 2014.021.0002), TMP 2014.021.0003, TMP 2014.021.0005, TMP 2014.021.0007, TMP 2014.021.0008, TMP 2015.050.0039, TMP 2016.027.0003, TMP 2017.015.0001, TMP 2017.015.0003, TMP 2017.015.0005, and TMP 2018.024.0004 (Table 1).

Type locality. Tributary NE of Bighorn Creek (see Hall et al. 1998, fig. 2.9), Alberta, Canada; RTMP locality L2428 (East Tributary of Bighorn Creek).

Type horizon. Fernie Formation, Red Deer Member (Upper Pliensbachian, Margaritatus Zone).

Occurrence. Toarcian of SW Japan (Locality: Nishiyamanaka, Kikukawacho, Toyouragun, Yamaguchi Prefecture) and Pliensbachian to Toarcian of East Tributary of Bighorn Creek, Alberta, Canada (RTMP locality L2428).

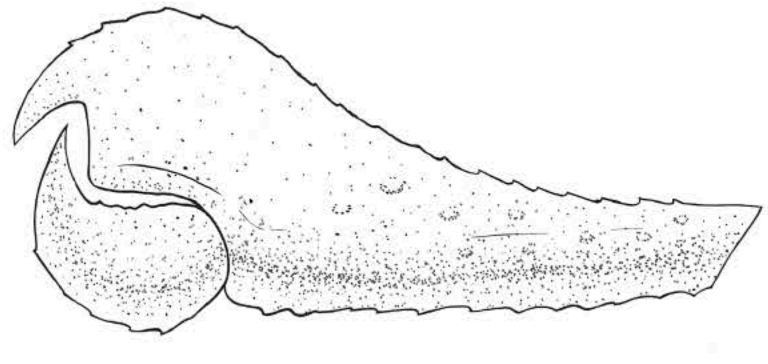
Diagnosis. Heterochelous species of *Uncina*; postcervical groove arcuate, carapace of cephalothorax rounded at posterior margins, pleonal pleura rounded at proximal margins and acutely pointed at distal margins; overall shape of chelae of first pereiopod similar in both claws, but fixed finger height and notch height are greater in major claw; chelae of first pereiopod widen distally; manus almost double the length of the dactylus; diagonal row of nodes extends from the manus attachment to the dactylus attachment; strong L-shaped (right angle) notch in the distal margin of the fixed finger; dactylus narrows distally; upper and lower margins covered with forwardly-directed spines.

Remarks. The diagnosis of Schweigert et al. (2003) can be expanded. Our study of 18 new specimens of *Uncina pacifica*, including two mostly complete corpses and multiple specimens with both first chelipeds of a single individual intact, provides a more complete characterization of the species. Specimen TMP 2017.015.001 (Figure 4B) clearly shows the two different sizes of the claws of the first pereiopods, with the key areas that differ being the L-shaped notch and the height of the fixed finger. This specimen shows the two different shapes of the chelae of the first pereiopod. *Uncina pacifica* specimens also greatly differ in size and represent some of the smallest uncinid fossils known, suggesting that the initial "large" descriptor should be abandoned.

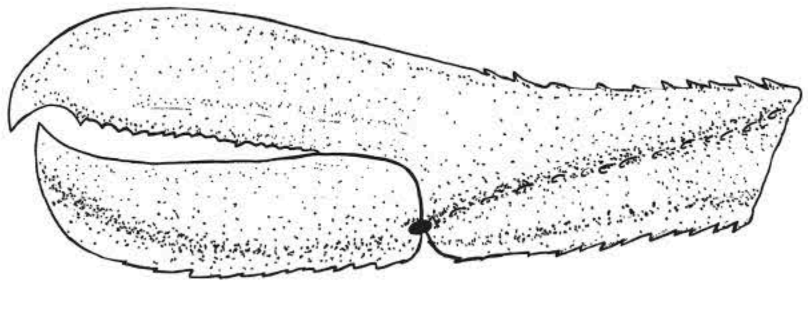
RESULTS OF MORPHOMETRIC ANALYSES OF *UNCINA* SPECIES CHELAE

With the addition of multiple new articulated specimens of *Uncina* (Table 1), several with both first chelipeds from a single individual preserved, morphometric analyses of these elements were undertaken. Cheliped morphometric measurements were used to determine the variability between left and right claws as well as intraspecific and interspecific variability of shape (e.g., Figure 5). Plots of chosen morphometric ratios are displayed in Figure 6. To statistically compare the ratios from Figure 6 and Table 2, Wilcoxon Ranked-Sum tests were employed to distinguish significant variation between characters among the *Uncina* species (Table 3, Table 4, Table 5, Table 6, Table 7). It should be noted that there were often a low number of measurements for *U. alpina*, so statistical analyses were not always conclusive.

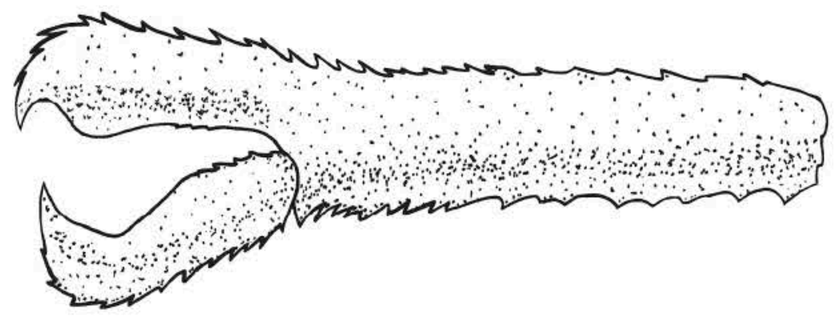
A. *Uncina pacifica (minor)*



B. *Uncina ollerenshawi*



C. *Uncina posidoniae*



D. *Uncina alpina*

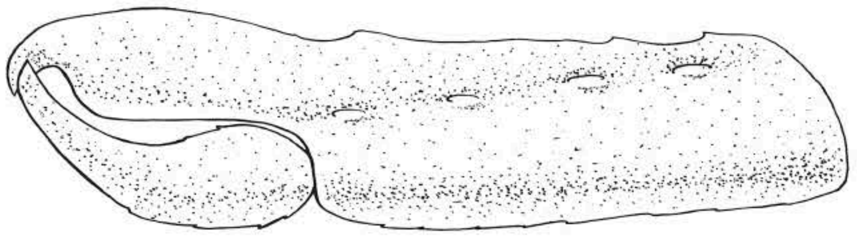


FIGURE 5. Morphological variation of the chelae of the first pereiopod in the four *Uncina* species. All sketches are based on real specimens but are shown at approximately the same size to facilitate comparison of morphologies between species (i.e., sketches were either enlarged or reduced proportionally). A) *Uncina pacifica*, minor claw, specimen TMP 2014.021.0003, B) *Uncina ollerenshawi*, specimen TMP 2015.051.0063. C) *Uncina posidoniae*, specimen from the Hauff collection, D) *Uncina alpina*, redrawn from Schweigert et al. (2003, pl. 10, fig. 4).

In the Wilcoxon Ranked-Sum tests, *Uncina pacifica* and *U. alpina* tested as statistically different only in the dactylus thickness to index height ratio (*p*-value = 0.006216, Table 3). The claws are morphologically very similar, except in breadth of the distal end of the claw (Figure 6); the two species are not statistically different in the ratio of the length of the fingers to the length of the manus, the notch shape, index shape, or the maximum to minimum manus heights. *Uncina alpina*, however, is underrepresented by measurable specimens, so results may change with the introduction of new specimens for study.

Uncina ollerenshawi and *U. pacifica* are statistically different in all areas except the manus length to index length (*p*-value = 0.3097, Table 6,

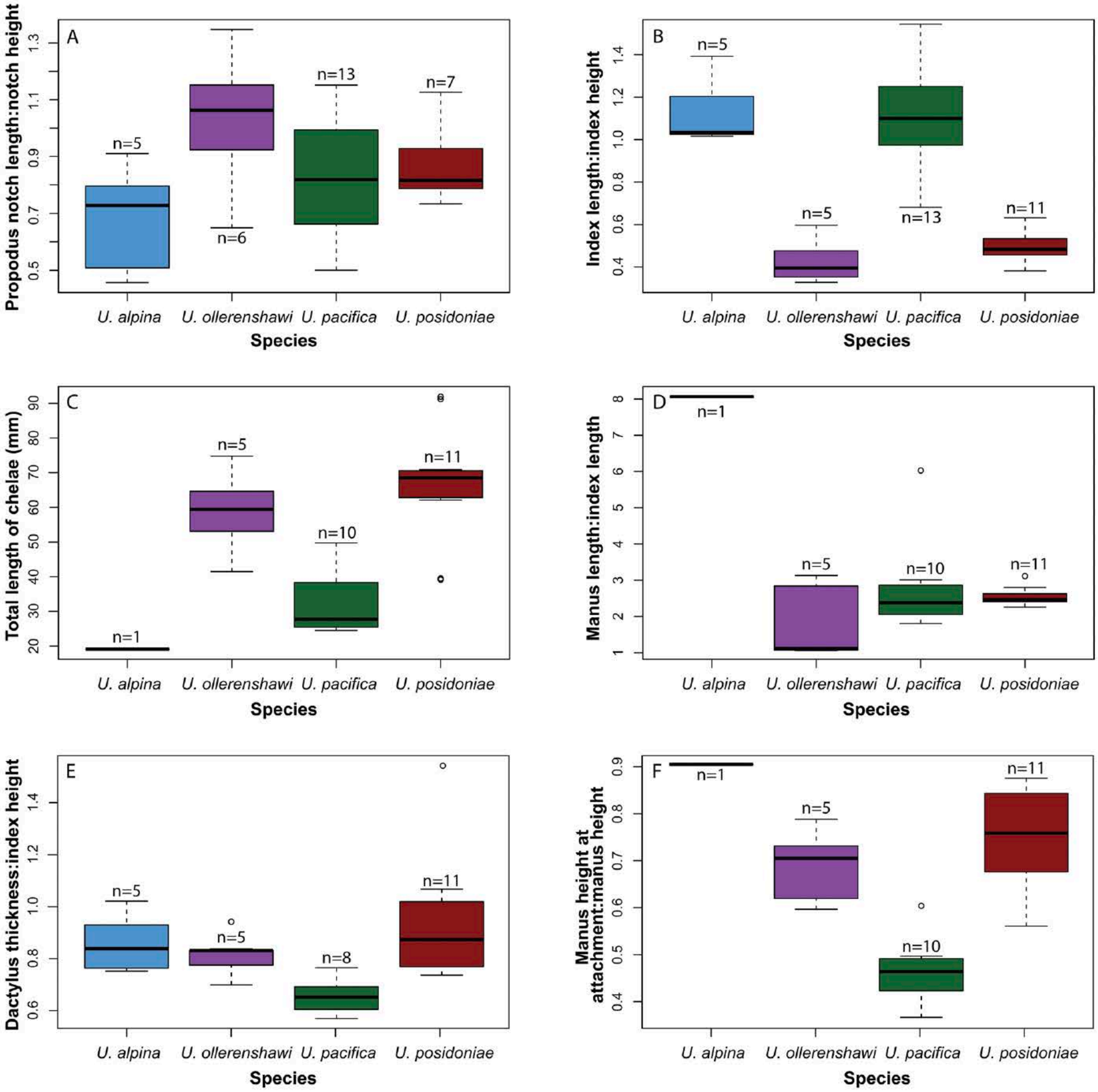


FIGURE 6. Box plots of morphometric measurements from *Uncina* species; the tops and bottoms of the colored boxes indicate the first and third quartile respectively and the solid black lines within represent medians. The whiskers outside of the boxes represent the lowest and highest datum (within 1.5 times the interquartile range), open circles outside of the whiskers indicate outliers; "n" refers to number of specimens (per species) with which that variable could be measured. A) Ratio of the propodus notch length to notch height in different species of *Uncina*. B) Ratio of the index length to index height in different species of *Uncina*. C) Total length of chelae in different species of *Uncina*. D) Ratio of manus length to index length in different species of *Uncina*. E) Ratio of the dactylus thickness to index height in different species of *Uncina*. F) Ratio of manus height at its minimum to manus height maximum for each uncinid species.

Figure 6) and notch length to notch height ratios (*p*-value = 0.1274, Table 7, Figure 6). These ratios appear to occur consistently among all species in the genus *Uncina*. These two species are differentiated by their respective manus height minimum to maximum measurements (Table 5) and the index length to index height ratios (Table 4).

Uncina posidoniae and *U. ollerenshawi* exhibit no statistical differences in any of the Wilcoxon Ranked-Sum tests performed on measured vari-

TABLE 2. Morphometric measurements of the uncinid claws used in Wilcoxon Ranked-Sum tests and box plots (Tables 3-6, Figure 6). If blank (dash), the specimen was fragmentary, making measurements impossible.

Species	Specimen Number	Manus Length (mm)	Manus Height (mm)	Propodus Length (mm)	Dactylus Length (mm)	Dactylus Thickness (mm)	Dactylus Height (mm)	Manus Height at Attachment (mm)	Index Length (mm)	Notch Length (mm)	Notch Height (mm)	Index Height (mm)
U. pacifica	TMP 2018.024.0005	-	-	-	23.01	11.28	16.92	-	-	-	-	-
	TMP 2018.024.0004	-	10.60	-	-	-	-	-	7.83	2.81	3.88	6.18
	TMP 2017.015.0005	27.04	11.85	38.33	12.61	4.64	8.61	5.61	11.29	3.2	3.28	7.32
	TMP 2017.015.0003	14.17	8.99	25.46	11.15	4.28	7.46	-	-	-	-	-
	TMP 2017.015.0001a	16.92	9.59	24.5	9.81	4.01	7.26	4.76	6.46	2.39	2.91	6.69
	TMP 2017.015.0001b	15.21	10.22	24.69	10.42	4.53	6.47	5.02	5.05	2.42	3.65	7.38
	TMP 2016.027.0003	34.87	22.91	-	-	-	-	9.81	-	-	-	16.53
	TMP 2015.050.0039	27.63	17.38		15.7	7.36	9.45	7.36	11.6	-	-	9.6
	TMP 2014.021.0023	26.82	19.62	45.43	21.83	9.99	13.89	7.92	14.84	3.39	6.74	14.94
	TMP 2014.021.0007	31.05	15.67	49.76	15.75	6.95	7.47	5.74	10.79	-	4.91	12.16
	TMP 2002.043.0012				12.11	5.56	7.74	-	-	-	-	-
	TMP 2002 043.0019a	14.91	8.28	27.7	11.2	4.47	8.04	4.98	7.02	2.78	2.71	6.37
	TMP 2002 043.0019b	-	-	-	11.8	4.24	8.67	-	-	-	-	-
	TMP 2002.043.0008	18.02	9.5	27.7	-	-	-	4.35	8.77	3.26	2.84	6.98
	TMP 2002.043.0015	-	-	-	-	-	-	-	7.4	-	-	6.97
	TMP 2002.043.0007	-	-	-	10.75	4.48	7.8	-	-	-	-	-
	TMP 2002.043.0003a	-	9.63	-	-	-	-	-	8.38	4.07	4.1	8.59
	TMP 2002.043.0003b	-	-	-	-	-	-	-	7.96	2.69	4.12	7.19
	TMP 2002.043.0006	-	8.79	-	-	-	-	-	6.35	2.68	3.25	-
	TMP 2002.043.0002	-	-	-	16.56	6.9	10.78	-	-	-	-	-
	TMP 2014.021.0008	-	-	-	15.33	7.32	11.51	-	-	-	-	-
	TMP 2002.043.0004	16.63	11.34	27.68	13.15	4.76	7.21	4.78	8.69	3.55	3.35	6.9
	TMP 2002.043.0005	-	19.94	-	18.22	8.32	12.68	-	10.73	4.34	6.44	-
	TMP 2014.021.0004	-	-	-	-	-	-	-	-	-	-	-
	KMNH IvP 300,027	26.43	-	29.98	11.08	28.073	-	20.89	4.4	4.54	7.9	-
U. ollerenshawi	TMP 2018.024.0009	-	-	-	25.6	7.38	10.75	-	-	-	-	-
	TMP 2018.024.0006	-	-	-	-	-	-	-	-	4.75	3.53	9.07
	TMP 2016.027.0008	-	-	-	41.54	8.95	15.99	-	-	-	-	-
	TMP 2015.051.0063	19.54	10.71	41.46	21.04	5.9	8.24	7.54	17.84	2.03	3.14	7.05
	TMP 2015.050.0011	24.77	11.5	53.09	29.16	5.84	8.86	9.06	21.4	6.65	7.22	7.02
	TMP 2013.036.0002	35.2	17.13	74.76	37.94	8.7	13.04	10.63	31.66	5.35	4.69	11.18
	GSC 80067 A * HOLOTYPE	43.67	12.05	64.61	22.11	5.84	11.31	8.81	13.95	4.84	4.959	8.33
	GSC 80067 B * HOLOTYPE	40.54	14.49	59.41	22.01	6.4	11.1	8.65	14.27	5.18	4.5	6.8

TABLE 2 (continued).

Species	Specimen Number	Manus Length (mm)	Manus Height (mm)	Propodus Length (mm)	Dactylus Length (mm)	Dactylus Thickness (mm)	Dactylus Height (mm)	Manus Height at Attachment (mm)	Index Length (mm)	Notch Length (mm)	Notch Height (mm)	Index Height (mm)
U. posidoniae	MB.A.3826 top claw	24.73	7.67	39.16	14.77	4.08	7.06	5.03	9.9	2.43	3.06	4.07
	MB.A.3826 bottom claw	24.52	7.99	39.51	13.27	3.56	6.61	5.24	9.8	2.39	2.94	4.74
	Posidoniae1A	46.58	16.731	70.275	27.12	7.46	9.846	14.098	20.376	-	-	7.797
	Posidoniae1B	44.228	17.3	70.89	28.049	14.77	9.45	14.6	19.608	5.61	4.98	9.57
	Posidoniae2	54.74	19.62	91.92	32.16	10.82	17.72	11.009	22.61	5.18	7.06	13.7
	Poidoniae LECTOTYPE	57.96	20.167	91.18	32.404	10.77	16.064	13.971	23.506	-	-	12.278
	SMNS no. 29150 top claw	45.81	16.12	69.31	27.496	9.573	14.533	14.134	19.006	-	-	8.967
	SMNS no. 29150 bottom claw	45.66	16.26	68.54	26.419	9.451	14.22	13.802	18.971	-	-	9.097
	No ID "Plate 4" top claw	40.495	11.034	63.584	22.9	5.935	10.932	8.661	14.718	4.754	4.566	8.038
	No ID "Plate 4" bottom claw	41.204	12.804	62.095	21.799	5.517	12.36	8.96	14.705	3.799	4.857	6.503
	SMNS no. 62815	45.135	14.623	67.417	23.006	6.774	11.284	11.065	14.493	4.549	5.562	9.162
U. alpina	MSNM no. i10864 left claw	13.31	3.15	19.08	5.12	2.03	2.74	2.84	1.65	0.79	1.72	1.99
	MSNM no. i10864 right claw	-	3.69	-	4.69	1.80	2.93	-	1.71	0.82	1.61	2.38
	MNSM no. i10863	-	5.29	-	5.40	2.46	4.06	-	2.83	1.44	1.97	2.92
	MNSM no. i10851 part	-	4.20	-	6.00	2.70	4.16	-	2.82	1.24	1.56	2.89
	MNSM no. i10851 counterpart	-	4.30	-	6.50	2.31	4.28	-	2.97	1.21	1.33	3.02

TABLE 3. *p*-value results of the Wilcoxon Ranked-Sum tests comparing dactylus thickness to index height of each uncinid species. This test was employed to distinguish the differences in the depth of the index of each species. Alpha value = 0.05; see Table 2 for measurements and Appendix 3 for R code.

	U. pacifica	***U. ollerenshawi***	***U. alpina***
U. posidoniae	**<0.001***	0.267	0.743
U. alpina	**0.006***	0.691	-
U. ollerenshawi	**0.006***	-	-

* = Statistically significant difference via Wilcoxon ranked-sum testing (bold).

TABLE 4. *p*-value results of the Wilcoxon Ranked-Sum tests comparing the index length to index height of each uncinid species. This test was employed to determine the differences in the shape of the index between species. Alpha value = 0.05; see Table 2 for measurements and Appendix 3 for R code.

	U. pacifica	***U. ollerenshawi***	***U. alpina***
U. posidoniae	**<0.001***	0.145	**<0.001***
U. alpina	0.849	0.008*	-
U. ollerenshawi	**<0.001***	-	-

* = Statistically significant difference via Wilcoxon ranked-sum testing (bold).

TABLE 5. *p*-value results of the Wilcoxon Ranked-Sum tests comparing the manus height at its minimum and its maximum for each uncinid species. This test was employed to determine the differences in the overall shape of the claw between species. Alpha value = 0.05; see Table 2 for measurements and Appendix 3 for R code.

	U. pacifica	***U. ollerenshawi***	***U. alpina***
U. posidoniae	**<0.001***	0.377	0.167
U. alpina	0.182	0.333	-
U. ollerenshawi	**0.001***	-	-

* = Statistically significant difference via Wilcoxon ranked-sum testing (bold).

TABLE 6. *p*-value results of the Wilcoxon Ranked-Sum tests comparing the manus length to index length of each uncinid species. This test was employed to determine the differences in the relative length of the fingers between species. Alpha value = 0.05; see Table 2 for measurements and Appendix 3 for R code.

	U. pacifica	***U. ollerenshawi***	***U. alpina***
U. posidoniae	0.426	0.510	0.167
U. alpina	0.182	0.333	-
U. ollerenshawi	0.310	-	-

* = Statistically significant difference via Wilcoxon ranked-sum testing (bold).

TABLE 7. *p*-value results of the Wilcoxon Ranked-Sum tests comparing the notch length to the notch height of each uncinid species. Alpha value = 0.05; see Table 2 for measurements and Appendix 3 for R code. Note that this test does not take roundness of the hook into account. This test was employed to determine the differences in the shape of the notch between species, which ultimately appears to be a trait that may be shared by all uncinids. It should be noted that these comparisons are difficult for *U. alpina* and *U. ollerenshawi,* as there is a paucity of measurements (low number) and a notably different curvature of *U. alpina*.

	U. pacifica	***U. ollerenshawi***	***U. alpina***
U. posidoniae	0.588	0.181	0.106
U. alpina	0.289	**0.030***	-
U. ollerenshawi	0.127	-	-

* = Statistically significant difference via Wilcoxon ranked-sum testing (bold).

ables; all morphological measurements are within the same range (Figure 6, Table 3, Table 4, Table 5, Table 6, Table 7). The claws are not statistically different in height, ratio of the length of the fingers to the length of the manus, ratio of the manus height minimum to the maximum, or the index shape. The chelae can be differentiated by the amount of ornamentation present on the outer layer of the cuticle, the shape of the dactylus, and the length of the fixed finger and dactylus when compared to that of the rest of the cheliped (Figure 5B-5C).

Uncina pacifica and *U. posidoniae* are statistically different in all areas except the manus length to the index length (*p*-value = 0.4262, Table 6) and notch length to notch height ratios (*p*-value = 0.588, Table 7). These ratios appear to not be statistically different when comparing all species in the genus *Uncina* against each other. These two species can also be differentiated by their manus height minimum to maximum measurements (*p*-value = 0.00001134, Table 5) and the index length to index height ratio (*p*-value = 0.0000008012, Table 4).

In the Wilcoxon Ranked-Sum tests, *Uncina posidoniae* and *U. alpina* were only statistically different in the index shape ratio (*p*-value = 0.0004579, Table 4). The claws are visually very different, but the ratios used in these tests are not statistically different. Likewise, *U. ollerenshawi* and *U. alpina* are not statistically different in any areas, even though the shapes are visually quite distinct. Herein, this is attributed to the paucity of *Uncina alpina* specimens available for measurements; this result may change with the discovery and inclusion of more specimens.

DISCUSSION

The Spatiotemporal Range of *Uncina* Species

The Early Jurassic *Uncina* species are relatively short-lived since they are only known to occur in the late Pliensbachian and early Toarcian stages of the Early Jurassic (Figure 7). The Canadian species *U. ollerenshawi* has only been recovered from upper Pliensbachian strata (Spinatum Zone) or float, so it may persist to the early Toarcian, but as of now, we can only confirm that it existed during the late Pliensbachian, which is consistent with Feldmann and Copeland (1988) and Schweigert et al. (2003). *Uncina pacifica* specimens have been recovered from both upper Pliensbachian (Margaritatus zone) and lower Toarcian (Tenuicostatum zone) strata as well as the

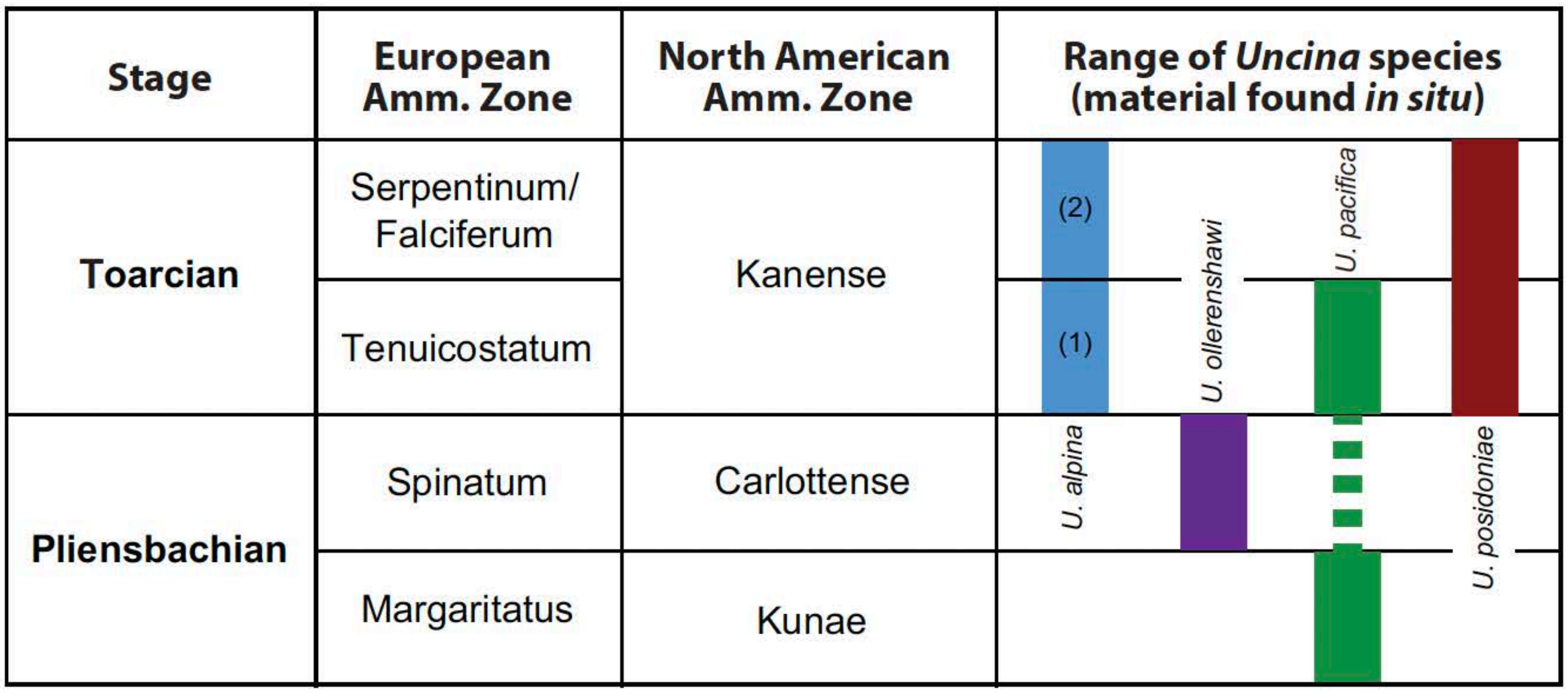


FIGURE 7. Known age ranges of the four *Uncina* species confirmed based on in situ fossil collections (note that the occurrence is not resolved below ammonite zones). Range through data are denoted with dashed lines (assumed). Age ranges for *U. alpina* (1 = Garassino and Teruzzi, 2001; 2 = Jenkyns et al., 1985) and *U. posidoniae* from Hauff and Hauff (1981), Schweigert et al. (2003); ages of *U. pacifica* from Karasawa (2002), Schweigert et al. (2003), Nakada and Matsuoka (2009), Martindale et al. (2017), and this work (including Hall's collection notes at the Royal Tyrrell Museum of Palaeontology); and ages of *Uncina ollerenshawi* from Feldmann and Copeland (1988), Schweigert et al. (2003), Martindale et al. (2017), and this work. Amm. Zone = Ammonite Zone.

Toarcian of Japan (not attributed to a zone) so this lobster species may have been longer lived than the others (Figure 7). Although partial crustacean specimens have been found after the Toarcian Oceanic Anoxic Event at Ya Ha Tinda, they are not identifiable as uncinids (Martindale et al., 2017). In contrast, the European species are only recovered from lower Toarcian strata, with *U. posidoniae* found in the Tenuicostatum and Falciferum zones and *U. alpina* found in either the Tenuicostatum or Falciferum zone. Specimens from Japan are from the Toarcian Period, but no other age information has been published. All species, including those found in Europe, seem to disappear after the Toarcian Oceanic Anoxic Event (Falciferum zone) based on the specimens currently known (Hauff and Hauff, 1981; Schweigert et al., 2003).

It is also interesting to note the geographic ranges of the Early Jurassic *Uncina* species. As Schweigert et al. (2003) previously noted, of the four *Uncina* taxa, two are exclusively from the Panthalassa Ocean *(U. ollerenshawi* and *U. pacifica),* whereas two are exclusively from the Tethys Ocean *(U. posidoniae* and *U. alpina).* Moreover, *U. alpina* and *U. posidoniae* are recovered from different regions of the Tethys and, to our knowledge, have not been recovered from the same formations. To date, the only uncinids that occur within the same localities (and at the same horizons) are *U. ollerenshawi* and *U. pacifica* (e.g., TMP 2002.043.0003, Appendix 4).

Morphology of *Uncina* Species

Through the statistical analysis of the morphologies of the chelae of the first pereiopod (Figure 5), a new genus-level trait emerged. In all cases, the notch ratio (Table 7) and the ratio between the manus length and length of the fixed finger (Table 6; Appendix 2) are not statistically different between *Uncina* species. Our data confirms that, at the genus level, uncinids share a similar ratio between the length of the fingers to the length of the manus as well as overall notch shape ratio, which is one of the defining traits of the genus.

Uncina alpina and *U. pacifica* (Figure 4) appear very similar (Figure 5) but through statistical analysis, an important distinction arose: the dactylus thickness to index height ratios are different (Table 5). Although the dataset for *U. alpina* is small, *Uncina pacifica* and *U. alpina* share a right-angled notch (sometimes more curved, notch shape varies per specimen), which is a trait unique to these two species.

Uncina ollerenshawi and *U. posidoniae* are similar visually (Figure 5) so it was not surprising that their morphological measurements were often not statistically different. Nevertheless, they are distinguishable by the shape of the dactylus, which was not considered in the Wilcoxon Ranked-Sum tests. *Uncina posidoniae* has a very strongly hooked dactylus shape with the spine facing the notch in normal position. The spine of the dactylus of *U. ollerenshawi* faces the notch and is very lightly hooked in comparison to the other *Uncina* species (Figure 5).

Uncina pacifica and *U. ollerenshawi* are distinctive, which is reflected in the morphological results (Table 3, Table 4, Table 5, Table 6, Table 7, Figure 5, Figure 6). This applies to *U. pacifica* and *U. posidoniae* as well since *U. posidoniae* and *U. ollerenshawi* are so similar. The most significant morphological differences are the manus height (maximum to minimum) ratio (Table 5) and index length to index height ratio (Table 4).

Uncina alpina differs from *U. ollerenshawi* and *U. posidoniae* in much the same way. *Uncina alpina* is significantly similar to both taxa with the exception of the index ratio, and notch ration in *Uncina alpina* and *U. ollerenshawi* (Table 3, Table 4, Table 5, Table 6, Table 7). *Uncina alpina* has very little gradient between the maximum and minimum height (Table 5), an almost square-shaped index and a smaller fixed finger than hand (Figure 5). The overall shape of the claw is very different from *U. ollerenshawi* and *U. posidoniae* in several areas (Figure 5); *Uncina alpina* has an L-shaped notch between the hand and fixed finger (although some specimens do exhibit a more curved V), a unique trait to this species but not obvious in every specimen. *Uncina alpina* also has a comma-shaped (i.e., ",") dactylus like *U. pacifica* (see Figure 5). There is also a limited dataset for *U. alpina*, so the statistical tests based on these measurements should be viewed cautiously.

Ecology of *Uncina* Species

As the claws of the first pereiopods of lobsters are their primary food-processing and food-capturing devices, they provide a picture of the life of the animal (Schweitzer and Feldman, 2010). Broadly, *Uncina alpina, U. ollerenshawi,* and *U. posidoniae* have similarly shaped claws, with the main difference between each of them being the shape of the dactylus. The dactyli of *U. pacifica* and *U. alpina* are both more comma-shaped while the dactyli of *U. ollerenshawi* and *U. posidoniae* are much less curved with an overall even width until the tip. *Uncina ollerenshawi, U. posidoniae*, and *U. alpina* exhibits isochelous chelae of the first pereiopod and so each hand likely had a similar crushing power as well, a trait directly correlated to claw morphology (Alexander, 1968). Therefore, it is likely that *U. ollerenshawi, U. posidoniae*, and possibly also *U. alpina*, occupied similar niches and fed on similar foods. *Uncina pacifica* is unique in that it is the only *Uncina* species that exhibits heterochelous chelae of the first pereiopod, a common trait in extant lobsters (Figure 4).

Compared to the other species of uncinids, *Uncina pacifica* has a broad and club-like claw shape with an exaggerated index height. This height is exaggerated further in one of the chelae of the first pereiopods of the animal (Figure 5). We posit that *U. pacifica* had a different lifestyle than the other lobsters of this genus based on this unique trait, possibly with one claw having a greater crushing power than the other (Alexander, 1968). The chelae of *U. pacifica*, while heterochelous, do not differ enough for them to be considered distinct crusher and cutter (Figure 5); instead, they are referred to as major and minor. This adaptation is strongly associated with predation but also can arise by other means such as sexual selection (Schweitzer and Feldmann, 2010).

The diet of extant lobsters can be analyzed to give some clarity into the possible diets of the extinct *Uncina* species. The Mesozoic adaptations of the chelae of the first pereiopods in nephropid lobsters give them access to a varied diet; they are predominantly durophagous but can also consume other organisms, such as fish and other crustaceans (Schweitzer and Feldmann, 2010). Bivalves are one of the most abundant animals at Ya Ha Tinda, although the fossil record is inevitably skewed towards hard-bodied animals (Muscente et al., 2019). The abundance of bivalves at Ya Ha Tinda indicates that they were a common benthic organism during this time interval and thus were a likely food source for uncinids. That said, lobsters have a varied diet and so without physical evidence of predation from this locality, it is impossible to be certain upon what organisms they were preying.

Although *U. alpina* and *U. posidoniae* occur in the same time interval (the early Toarcian; Schweigert et al., 2003), they are found in different formations and countries and so are unlikely to have lived together in the same habitat. In contrast, *U. pacifica* and *U. ollerenshawi* occur within the same Pliensbachian-aged member of the Fernie Formation at Ya Ha Tinda and in some cases, are even found on the same bedding plane. TMP 2002.043.0003 (Appendix 4) contains 3 chelae: both chelae of a single specimen of *U. pacifica* and a specimen of *U. ollerenshawi* together suggesting that these two species likely lived in the same (or at least a similar habitat) during the late Pliensbachian. This observation does not confirm that the species interacted frequently, if at all, as the carcasses may have accumulated by other means, such as winnowing, or condensation of the section. TMP 2002.043.0003 sample supports the notion that *Uncina pacifica* and *U. ollerenshawi* were occupying different niches in the late Pliensbachian, as crustaceans of the same genus rarely occupy the same niche in the same area as they are very aggressive and competitive (Huber et al., 1997). This difference in niche may have allowed *U. pacifica* to survive into the Toarcian whereas *U. ollerenshawi* may have gone extinct at the stage boundary.

CONCLUSIONS

Through the morphometric reanalysis of specimens of *Uncina* species and with the addition of numerous new specimens, we confirm the presence of a diaeresis on the uropods but also observe that this genus is more morphologically variable than previously described in the following ways: a) *U. pacifica* is heterochelous, and b) chelae shape varies more than previously noted, both within and between species, *U. ollerenshawi* exhibits proportionally larger fingers when compared with other members of the genus. Understanding the paleoecology of these animals is important for reconstructions of Early Jurassic benthic ecosystems and how these communities were influenced by biotic crises, such as the Toarcian Oceanic Anoxic Event. Important new findings about the evolution and natural history of Early Jurassic astacideans, especially the superfamily Enoplometopoidea, are indicated by the observation that *U. ollerenshawi* and *U. pacifica* occupied different ecological niches in the Early Jurassic. This differentiation may have altered their ability to survive the paleoenvironmental perturbations through this interval.

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