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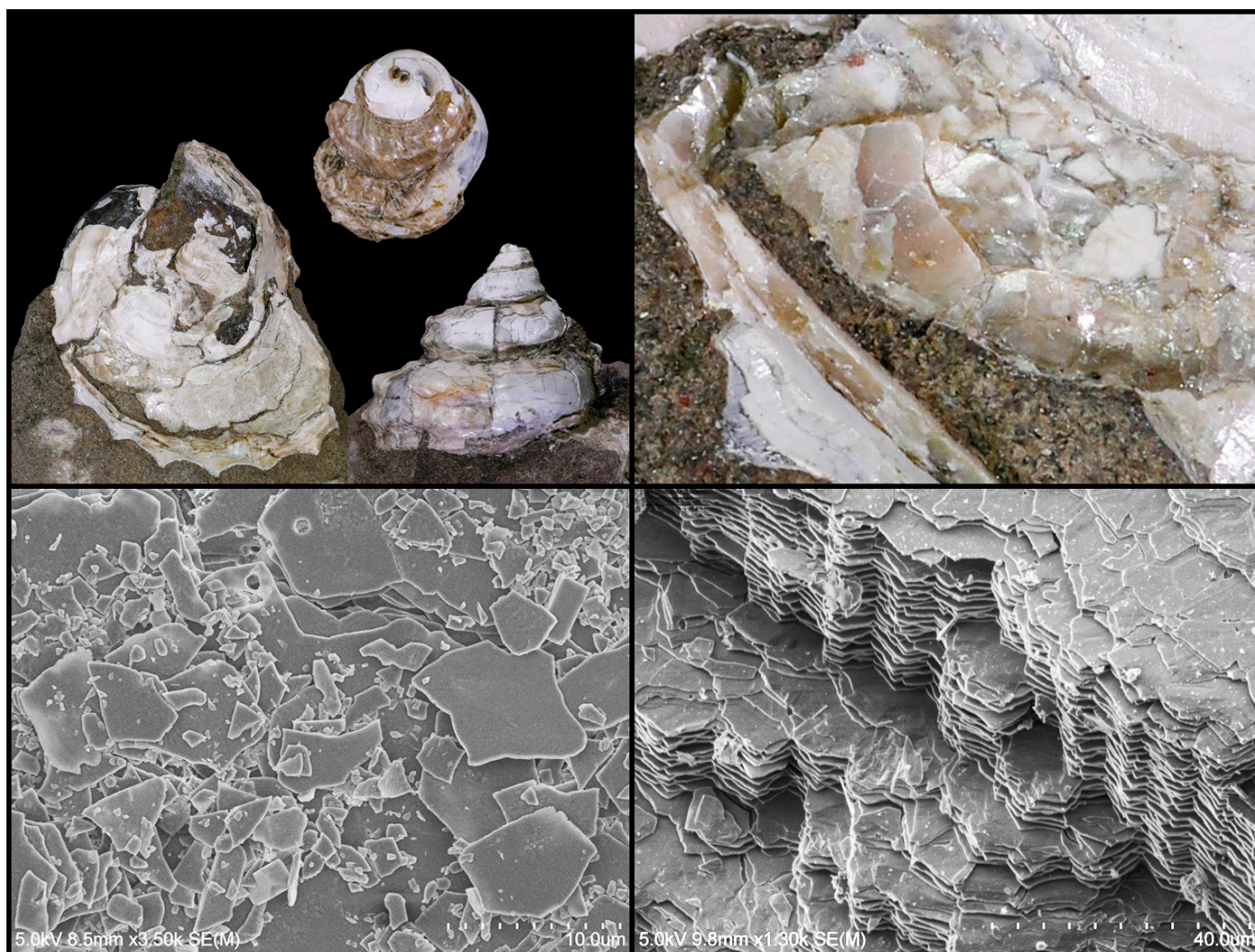
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Cover illustration: Nacreous shell fragments preserve original microstructure on individual growth surfaces, and transverse fractures preserve columns of successive aragonite tablets.

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A new *Calliovarica* species (Seguenzioidea: Chilodontidae) from the Eocene of Oregon, USA: Persistence of a relict Mesozoic gastropod group in a unique forearc tectonic setting

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A new, enigmatic chilodontid gastropod with distinctive periodic varices is described as *Calliovarica oregonensis*. It is based on ten specimens from slope deposits of the early late Eocene Nestucca Formation on the coastal Cascadia margin of present day Oregon, U.S.A. It is the last appearance of a Mesozoic group of epifaunal basal gastropods with periodic varices. It is the third species in a Cenozoic genus previously known only from the early Eocene Lodo Formation in California and the late Paleocene to early Eocene Red Bluff Tuff in New Zealand. The type species, *C. eocensis*, is refigured to clarify the nature of the axial varices as well as a terminal thickening and flaring of the apertural lip immediately following deposition of the final varix. Detailed preservation of microstructure in the nacreous layers of crushed and disintegrating shell fragments demonstrates the value of collecting material typically left behind in the field. *Calliovarica oregonensis* n. sp. is part of a poorly understood molluscan fauna that lived during an unusual paleoclimatic interval immediately prior to global cooling and extinctions in the late Eocene. It also thrived in an unusual volcano-sedimentary interval at the onset of subduction at the Cascadia margin. The tectonic setting provides a unique snapshot of a depositional environment receiving periodic influxes of ash from the young volcanic arc to the east and periodic basalt intrusions from the underlying asthenosphere into the forearc over a hotspot or through slab window emplacement. Links between biofacies and lithofacies demonstrate the ability of paleontology and geology to provide reciprocal illumination, especially in dynamic settings with no modern counterparts. The link between local persistence of relict Mesozoic taxa and localized tectonic events merits further integrative investigation.

Keywords: Seguenzioidea, Chilodontidae, relict taxa, Nestucca Formation, Cascadia margin, northeastern Pacific

INTRODUCTION

During times of globally widespread warm thermal regimes and open low-latitude oceanic gateways, marine molluscan taxa have sometimes achieved unusually broad geographic distributions. The Paleocene-Eocene Thermal Maximum (PETM) is such a time, and is coincident with the broad geographic extent of the Tethyan Seaway and its westward-flowing currents. During the late Paleocene and early Eocene there was a low latitude influx of approximately 30 thermophilic genera from the European Tethys, Caribbean, and Gulf of Mexico into the Eastern Pacific (Squires 2003). The affinities of taxa in the Capay Formation in California with taxa in the Ypresian Stage of the Paris Basin were noted many years ago (Clark and Vokes 1936), and particular emphasis was placed on the neretid gastropod, *Velates perversus* (Gmelin, 1791),

as the arrival of a Paris Basin species in the Eastern Pacific (Vokes 1935, 1939).

It is notable that very few of the invading old-world thermophiles established lineages that survived the late Eocene–Oligocene Greenhouse-Icehouse transition and regional mass extinction of endemic genera and species (Hickman 2003). However, there was considerable Eocene diversification of thermophilic species in shallow-water faunas of the northeastern Pacific prior to the turnover. Diversification included the brief establishment of novel, endemic genus-group taxa.

One of the strangest brief appearances in the early Eocene fauna is the enigmatic genus *Calliovarica* Vokes, 1939. The novel defining feature of the type species is the presence of varices at 180° intervals on the spire whorls in addition to a thickened and reflected outer

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lip. True varices (periodic axial thickenings secreted at regular intervals, as opposed to axial growth checks) are otherwise unknown in Cenozoic vetigastropods. Confusion over the genus has arisen because the varices are not visible in the illustrations of the holotype and paratypes and were not clearly specified in original description of the type species. As a result, two Early Paleogene species described subsequently under *Calliovarica* lack true varices, although they both appear to have close affinities with Vokes' genus and provide some clues to their correct classification.

The purpose of this paper is to (1) provide a new differential diagnosis of the genus, (2) re-figure the type species to show the diagnostic features, (3) describe a new *Calliovarica* species from the early late Eocene of Oregon, (4) establish the unusual tectonic, stratigraphic, climatic and paleoceanographic setting of the Nestucca Formation, and (5) reevaluate the significance of varices in basal marine gastropods.

SYSTEMATIC PALEONTOLOGY

VETIGASTROPODA [SALVINI-PLAWEN, 1980](#)

SEGUENZIOIDEA [VERRILL, 1884](#)

EUCYCLOIDEA [KOKEN, 1897](#), UNRANKED

CHILODONTIDAE [WENZ, 1938](#)

Transfer of Chilodontidae and Calliotropidae [Hickman and McLean, 1990](#) from Trochoidea to Seguenzioidea, current status of the relationship between the two family groups, and revised treatment of chilodontid genera are reviewed by [Herbert \(2012\)](#). The classification of Calliotropidae is reviewed by [Hickman \(2016\)](#). There has been strong support for recognizing a third family group Eucyclidae [Koken, 1897](#) for extinct Mesozoic genera ([Hickman and McLean 1990](#), [Kiel and Bandel 2001](#)). However, [Bandel \(2010\)](#) has further proposed five additional family-group names for extinct genera as well as two new family-group names based on living genera. Bandel's new names and reallocation of living genera based on shell morphology are controversial where they are inconsistent with anatomical and radular data, and where molecular data are not available for testing putative relationships among genera.

A more conservative alternative proposal is that Calliotropidae is synonymous with Eucyclidae ([Kaim 2004](#)). This proposal is consistent with new well-preserved Jurassic material from Argentina and an argument for resolving a single long-ranging genus *Calliotropis* [Seguenza, 1903](#) into two temporal subgenera, *Calliotropis* s.s. for Cenozoic species and *Riselloidea* [Cossmann, 1909](#),

for Mesozoic species ([Ferrari et al. 2014](#)).

Comparable nomenclatural proposals to treat chilodontid genus-group taxa with robust shells and apertural elaborations as long ranging remain controversial. Recognition of living species of the Cretaceous genus *Agathodonta* [Cossmann, 1918](#) ([McLean 1984](#), [Hickman and McLean 1990](#)) has been rejected on the basis of detailed comparison of the type species with putative living members of the genus ([Herbert 2012](#)).

However there is clear documentation that core Tethyan carbonate platform, hard-substrate chilodontids did not "wait" for the Cenozoic to expand over great distances into reefal facies of the Pacific. [Sohl \(1987\)](#) noted the presence of the Jurassic genus *Chilodonta* [Étallon, 1859](#) in Cretaceous carbonate facies on the now sunken guyots of the Mid-Pacific Mountains and hypothesized these as stepping stones for migration of "corallian facies" taxa during the Cretaceous ([Hamilton 1956](#), [Ladd et al. 1974](#)).

Strict maintenance of separate taxonomic names on either side of the Cretaceous-Tertiary boundary reinforces an unsupported conflation of the boundary between eras with a terminal mass-extinction event affecting all gastropods. In both Calliotropidae and Chilodontidae there is abundant evidence that prominent Cenozoic taxa originated deep in the Mesozoic, especially in the extra-tropical margins of the Tethyan realm. This was recognized perspicaciously by [Sohl \(1987, p. 1107\)](#) in his presidential address to the Paleontological Society when he noted: "... although (the) players may have new identities, their teams have remained the same."

It is appropriate to note here that the name Chilodontidae is preoccupied, and the case for emended spelling to resolve homonymy (ICZN Case 3555) is still listed as open. Accordingly, the name is retained here in accordance with ICZN Article 82.1 for maintenance of prevailing usage.

CALLIOVARICA [Vokes, 1939](#)

Type species—By monotypy. *Calliovarica eocensis* [Vokes, 1939](#). Early Eocene ("Capay stage"), Central California, Cerros Shale member of the Lodo Formation.

Stratigraphic occurrence—Restricted to the Paleocene and Eocene.

Differential diagnosis—Distinguished from all seguenzioid vetigastropods by axial varices at regular intervals of 180° on body whorl and spire whorls; terminal flaring of adult outer lip immediately following final varix; lacking reflected inner lip, expanded inductural

callus and apertural dentition in inner and outer lips.

Remarks—Three chilodontid genera that show some of the diagnostic features of *Calliovarica* are *Agathodonta* Cossmann, 1918, *Danilia* Brusina, 1865, and *Onkospira* Zittel, 1873.

Features of poorly known type species of *Agathodonta* [*Trochus dentigerus* d'Orbigny, 1843, from the Early Cretaceous (Neocomian) of France] have been clarified through designation of a lectotype (Kollmann 2005) and careful re-evaluation and illustration (Herbert 2012). Axial thickenings are clearly present on spire whorls of the lectotype. However, the outer lip is not reflected or thickened, there is no inductural callus, and there are well-developed apertural denticles. Clarification of the features of fossil *Agathodonta* led Herbert (2012) to consider it extinct and inappropriate to living taxa formerly allocated to the genus. He proposed *Clypeostoma* for a group of living Indo-Pacific species with strong inductural callus that is even farther removed morphologically from *Calliovarica*.

Danilia is similar to *Calliovarica* in developing a prominent subterminal thickening of the final aperture, but there are no varices on the spire whorls. *Danilia* also differs in the presence of a strong tooth and deep notch on the inner lip, and a prominent inductural callus. *Danilia* shares a Cretaceous origin with *Agathodonta*. It occurs throughout the Cenozoic, but never in large numbers and predominantly in deep water where it is often associated with hard substrate in sponge and coral thickets. For detailed nomenclatural history of *Danilia*, see Herbert (2012).

Onkospira is a Mesozoic high-spired genus that is similar to *Calliovarica* in having multiple synchronous varices that are closely aligned on successive whorls, with the final varix located immediately behind the outer lip. The outer, basal and inner lips are continuous, flared, relatively thin, and lack denticles. The type species is from the Late Jurassic (Oxfordian) of Germany, but species are also recognized as early as the Middle Jurassic (Bathonian) of India (Das et al. 1999) and the Late Cretaceous (Maastrichtian) of Siberia (Kaim et al. 2004).

This leaves *Calliovarica* as the least well-understood chilodontid genus with single or multiple variciform thickenings. Although Vokes (1939, p. 183) clearly stated that “no species similar to this has been previously described” and that it was distinguished by “numerous varices,” these features are not visible in the four inadequate photographs of the holotype and two paratypes (Pl. 22, figs. 20, 23, 25, 28). Stacked digital photographs of the types (Fig. 1A–F) illustrate characters in the new

differential diagnosis.

Two additional species, both from the late Paleocene–early Eocene have been described under *Calliovarica*. The species described as *C. pacifica* Squires and Goedert, 1994, is from the middle lower Eocene Crescent Formation in Washington. The assignment was based on thickening of the outer lip of the holotype, described as a “resting stage,” but there are no varices on the spire whorls. Although the shell has other clearly chilodontid features, notably prominent apertural denticles, it cannot be allocated to *Calliovarica* s.s. A second species of particular interest is from the Early Paleogene greenhouse interval in the Chatham Islands, eastern New Zealand. It was identified initially as *Bathybembix* (?) sp. nov. (Beu and Maxwell 1990) and subsequently as *Calliovarica* n. sp. (Beu and Raine 2009) prior to formal description as *C. rangiaotea* Stillwell, 2014.

Calliovarica eocensis Vokes, 1939

FIG. 1A–F

Calliovarica eocensis Vokes, 1939. p. 183; pl. 22, figs. 20, 23, 25, 28.

Calliovarica eocensis (Vokes). Squires 1988. p. 206.

Remarks—The holotype (UCMP 15884) and one of the paratypes (UCMP 15885) are refigured here to illustrate the diagnostic features that are not visible in the original published figures.

The type locality (UCMP 1817-) in the Cerros Shale Member of the Lodo Formation has been known for more than 100 years, but the geographic location and stratigraphic position and geologic age have been reported differently in the literature, resulting in controversy that was resolved by rediscovery of the site and thorough documentation by Squires (1988). It is also the type locality of *Turritella andersoni* Dickerson, 1916, which has served as an important index fossil for correlating early Eocene strata on the Pacific coast. Because Vokes is the only person to have collected the distinctive varicate basal gastropod, it is significant to note that the glauconitic sandstone also contained abundant *T. andersoni*. Vokes published trimmed photographs of the holotype, but the apertural (Fig. 1A) and semiapertural views (Fig. 1B) shown here include not only the glauconitic matrix but also an imbedded specimen of *T. andersoni*.

Calliovarica oregonensis n. sp.

FIG. 2A–C

Calliovarica (?) n. sp. Snively and Vokes, 1949.

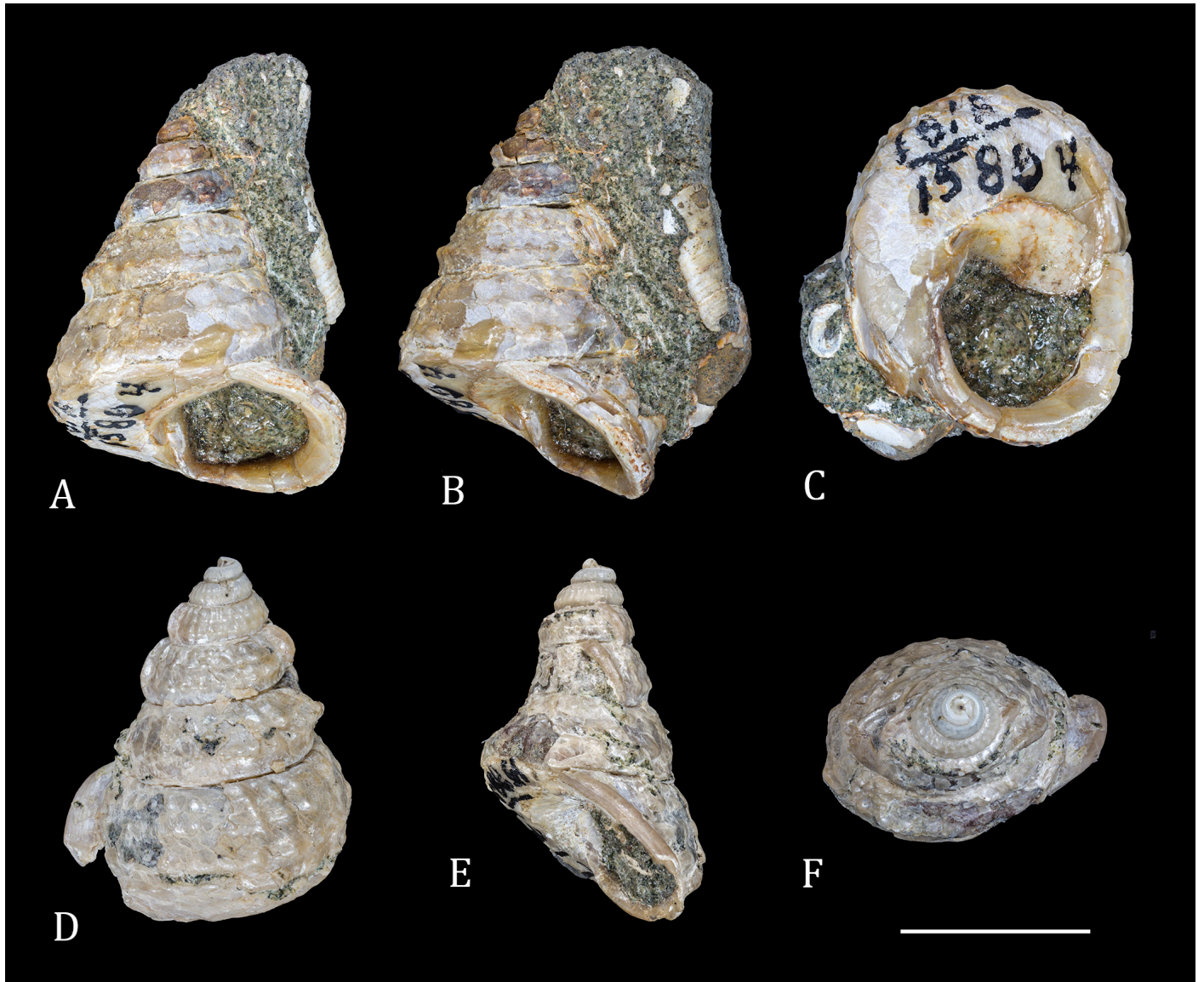


Figure 1A-F. Re-photographed types of *Calliovarica eocensis* Vokes. **A, B.** Apertural and semiapertural views of holotype, UCMP 15884. UCMP Locality 1817-, with specimen of *Turritella andersoni* embedded in attached matrix. **C.** Basal view of holotype. **D, E.** Adapertural and semiapertural views of paratype, UCMP 15885, UCMP Locality 1817-. **F.** Apical view of the paratype, showing lateral compression of the specimen. Scale bar = 1 cm.

Holotype—Part and counterpart in matrix. UCMP 110715a (positive) and 110715b (negative); height (incomplete) 30.0 mm; width (incomplete) 21 mm.

Figured paratype—UCMP 110716, in matrix; height (incomplete) 23 mm; width (estimated) 15 mm.

Unfigured paratypes—UCMP 110717, 110718, 110719, 110720, 110721, 110722, 10723, 110724.

Material examined—10 specimens in the type lot.

Type locality—UCMP IP6496 (=USGS 16981). Cliffs on the south side of the mouth of the Nestucca River at Point Porter, Nestucca Bay Quad., Oregon, USA.

Stratigraphic occurrence—Nestucca Formation,

early late Eocene (late Narizian and early Refugian benthic foraminiferal stages and CP 15a-15b calcareous nannoplankton zones of [Bukry and Snavely \(1988\)](#)).

Etymology—Named to emphasize the Oregon occurrence of the species.

Diagnosis—Shell high spired (height exceeds width), larger than that of type species (ht=28 mm); spiral angle greater (estimated 50–60°); spire whorls slightly biangulate, with three rows of distinct tubercles; varices deviating very slightly from 180° apart, forming successively later during growth; Outer lip prominently thickened immediately following final varix; outer shell layers well

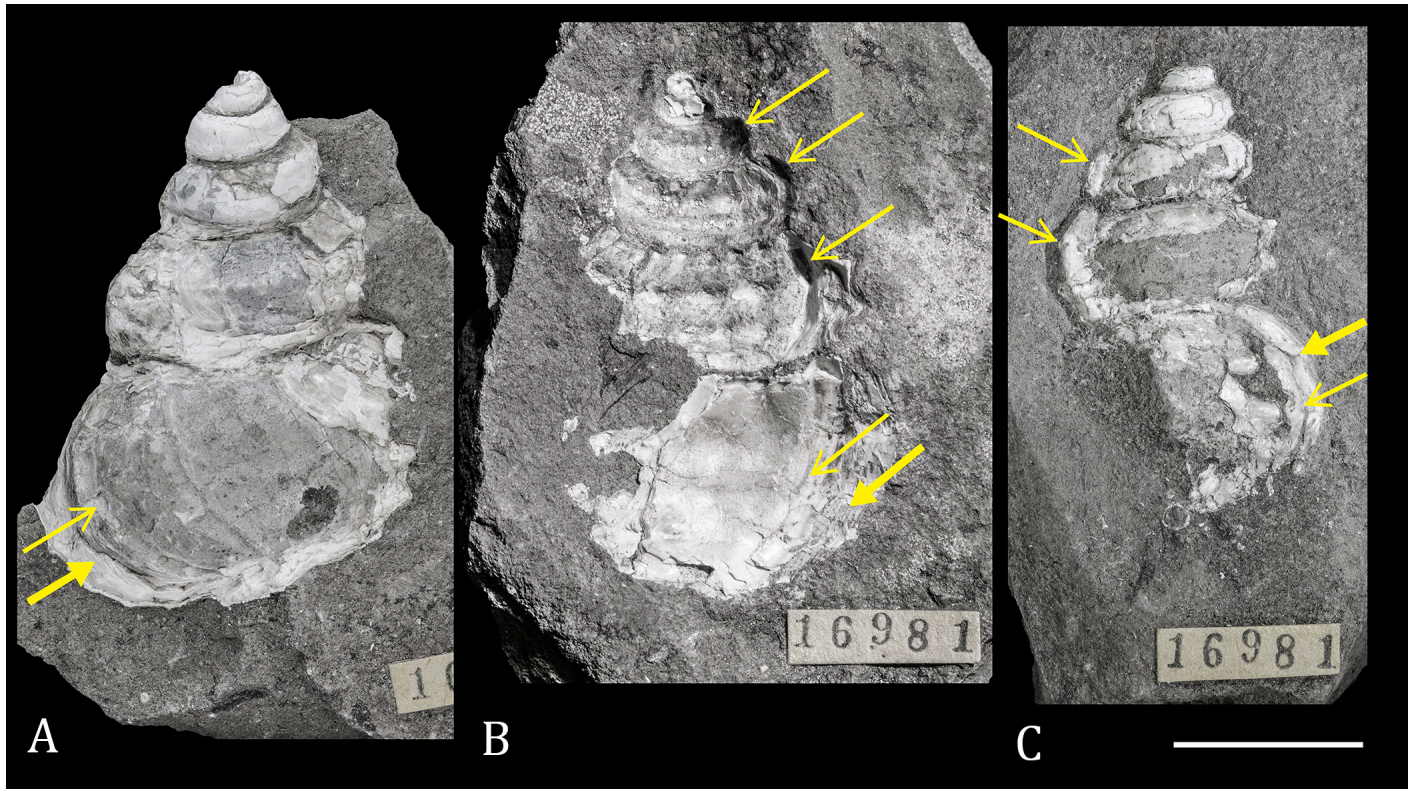


Figure 2A–C. *Calliovarica oregonensis* Hickman, n. sp. **A, B.** Part counterpart of holotype, UCMP 110715a (positive) and 110715b (negative) in matrix, UCMP Locality IP6496. **C.** Paratype, UCMP 110716 in matrix, UCMP Locality IP6496. Yellow solid tipped arrows denote shell material of final aperture; yellow open tipped arrows indicate shell material of varices on spire and body whorls. Scale bar = 1 cm.

developed and thicker than interior nacre.

Description—Shell material is strongly altered and partially exfoliated on all specimens. Protoconchs are broken or worn. The suture appears to be slightly impressed where shell material on adjacent whorls is most intact. There is no evidence of denticulation of either the inner or outer lip. The shape of the peristome and apertural inclination cannot be determined. The varices are robust, but shell material is too degraded to determine thickness. The base of the shell has at least five spiral ribs with fine nodes, although the base is known from two incomplete fragments. Nodes on the spire are most prominent and least numerous on the adapical spiral cord and finer and more numerous on the two abapical cords.

Specimen preservation—Although specimens are incomplete two fortuitous aspects of preservation enhance the information. The coarsely-tuffaceous matrix of the Nestucca Formation does not record fine detail in exterior molds, but it has cleaved in the plane of bedding to produce negative and positive counterparts that have separated with shell material on each half. In the case of the holotype, nacre is present primarily on a portion of

the body whorl of the internal mold (Fig. 2B). The final varix and terminal apertural thickening are partially preserved on both part and counterpart (Fig. 2A, B). Reconstruction of other features of the shell also requires observation of both part and counterpart. Exfoliation of altered shell material clearly occurred during collecting, but fragments provide evidence of original shell structure that are not available in the more stable, but highly altered, shells of the type species of *Calliovarica* (Fig. 1A–F). The type lot of the new species was not subjected to stabilizing coatings or excessive preparation. No further preparation was attempted during study, and specimens were not coated for photography in order to illustrate the state of preservation. Each fragmental specimen has been assigned a separate paratype number.

Remarks—The new Oregon species is distinguished from the type species, *C. eocensis*, by its larger size, and proportionately broader shell with a greater spiral angle and more rapidly expanding body whorl. In size and proportions, the shell is closer to the southern hemisphere species *C. rangiaotea* [Stillwell, 2014](#) from the Red Bluff Tuff in the Chatham Islands Archipelago. Although the Chatham Islands species lacks multiple well-developed

synchronized varices, [Stillwell \(2014\)](#) noted evidence of “indistinct” varices on spire whorls. For this reason, *C. rangiaotea* is here retained as a species of *Calliovarica*.

The species described as *Calliovarica pacifica* by [Squires and Goedert \(1994\)](#), from middle lower Eocene beds in the Crescent Formation in Washington, cannot be included in the genus because the shell lacks multiple varices, although it does have a thickened terminal lip. It is a low-spired turbiniform shell that is most remarkable in the interior elaboration of the outer lip, which is thickened within by strongly-developed denticles that are continuous with denticles on the basal and columellar lips. The apertural elaborations place it clearly in Chilodontidae, but it lacks the expanded parietal callus shield characteristic of *Clypeostoma* [Herbert, 2012](#) and the subterminal varix behind the prominently expanded outer lip of *Danilia* [Brusina, 1925](#), a distinctive genus of smaller and more elevated shells that originated in the Mesozoic and persists in modern deep-water faunas associated with carbonate substrates.

It is noteworthy that the Crescent Formation chilodontid species also is part of an Early Paleogene incursion of taxa of Tethyan origin into the northeastern Pacific. As noted by [Squires and Goedert \(1994\)](#), the Crescent fauna has received little study. In this sense it is similar to the Nestucca fossils. Both faunas occur in volcanogenic sedimentary facies, although the Crescent taxa are indicative of a shallow bathymetric setting.

DISCUSSION

Unusual relict taxa and anomalous faunal assemblages in the Nestucca Formation are inextricably linked with an unusual period of global climate and paleogeography at the end of the PETM as well as a unique interval of local syndepositional volcanic and tectonic activity on the Cascadia margin of present day Oregon. Detailed discussion of this interval in terms of extensional tectonics, driven by change in the rate and direction of convergence of the Farallon and North American plates, is beyond the scope of this discussion. However, geologic history and marine faunal history of the Cascadia margin, typically pursued in isolation from one another, are more productively reconstructed through integration. Accordingly, this paper departs from normal format to include further exploration of links between and among the following components: geologic age and correlation, tectonic setting, volcanology, bathymetric setting, stratigraphy, molluscan faunal assemblages, and global paleobiogeography. A final consideration of the significance of varices in basal seguenzioid gastropods places *Calliovarica* in a

broader context of life and earth history.

Geologic age, correlation and tectonic setting

Early late Eocene age of the Nestucca Formation of the central Oregon coast is established both on the basis of planktonic foraminifera ([McKeel and Lipps 1975](#)) and calcareous nannoplankton ([Bukry and Snively 1988](#)). This is consistent with radiometric dates for intercalated basalt units (e.g., [Parker et al. 2010](#)). It falls roughly within the late Narizian and early Refugian Stage of [Schenck and Klempell \(1936\)](#), recognizing that this stage is time transgressive. It is roughly correlative with parts of the San Lorenzo Formation in California and the Bastendorff Formation on the southern Oregon coast ([Warren and Newell 1981](#)) as well as beds assigned to the Cowlitz Formation in the Oregon Coast Range ([Snively and Vokes. 1949](#)).

It is not surprising that the unusual molluscan assemblages in the Nestucca Formation cannot be assigned to a provincial molluscan stage, even as amended by [Armentrout \(1981\)](#). It is likewise unsurprising that [Nesbitt \(2018\)](#) reports no new information on the Nestucca in her excellent summary of new data on marine formations of similar age in Washington and Oregon.

The new Oregon species of *Calliovarica* is younger than the California type species (early Eocene, Domengine stage) and occurs in a macrofaunal assemblage indicative of a deeper facies. Nestucca sedimentary rocks rest unconformably on the Yamhill Formation as well as on underlying oceanic basaltic crust of the massive accreted volcanic province of Siletzia that underlies coastal western Oregon ([Wells et al. 2014](#)) and Washington ([Eddy et al. 2016, 2017](#)). The formation consists of up to 2,000 m of thinly-bedded, fine-grained forearc sediment and arc-derived andesitic ash ([Snively et al. 1969, 1976](#)) and interfingers with extrusive and intrusive igneous rocks of the Yachats Basalt and Cascade Head Basalt ([Snively and MacLeod 1974, Parker et al. 2010](#)). The unusual facies and depositional environment of the Yachats Basalt and associated volcanoclastic sediments are described by [Shroba and Orr \(1995\)](#).

Bathymetric setting

Bathymetrically the Nestucca Formation is a relatively deep-water (slope) accumulation in a young forearc setting on accreted oceanic crust undergoing extension during a major tectonic reorganization during the late Eocene. At this time the rate and direction of plate convergence between the Farallon and North American plates was changing dramatically. Geochemical analyses

of the intercalated basalts are consistent with a source in the mantle beneath the subducting slab (Barnes and Barnes 1992). The basalts have been interpreted alternatively as slab window emplacements (e.g., Hole et al. 1991) or as a consequence of hotspot volcanism (e.g., Duncan et al. 1982). However, a mantle plume source is not incompatible with the slab window model of emplacement (e.g., Chan et al. 2012). The importance for slope faunas in the marginal forearc basins of Cascadia in the late Eocene is the amount and diversity of volcanic input. Although chilodontid gastropods are typically associated with hard substrata, they can cling tentaciously to hard objects in habitats dominated by soft substrata (Herbert 2012). Sediment heterogeneity, including lenses of conglomerate derived from interbedded basalts, was noted in the original description of the Nestucca Formation (Snively and Vokes 1949).

Stratigraphy

The physical stratigraphy of the Nestucca Formation is complex and poorly documented. Variably thick fine clastic layers alternate with thin layers of arc-derived andesitic ash and basaltic sands and grits, in addition to extrusive and intrusive basalt from within the forearc. Rocks are poorly exposed in widely-separated outcrops, and the formation has not been subdivided into mappable units.

Molluscan biostratigraphy is likewise unresolved. The fossil assemblages reported by Vokes (Snively and Vokes 1949) represent different facies with few species in common. None of the nine reported assemblages has a clear relationship to any well documented west coast Eocene fauna.

Faunal assemblages

The specimens described herein were collected by Harold E. Vokes in the course of mapping the geology of the Oregon coastal area between Cape Kiwanda and Cape Foulweather (Snively and Vokes 1949). Although the assemblage of 27 species from this locality (USGS 16981, now at the University of California Museum of Paleontology, UCMP IP6496) does not have a clear deep-water taxonomic structure as defined by Hickman (1984), it does include higher taxa characteristic of depths greater than 200 m. It is consistent with the fine-grained siltstone matrices in which the fossils occur. Only six mollusks in the checklist are positively identified species. Of the remaining 21, assignments are in open nomenclature, in part because of poor preservation. However there are two bivalves (a mud pecten and a giant limid) that appear

to be new. Both would have been epifaunal, requiring hard objects for byssal attachment.

It is noteworthy that the only other new and endemic species described from the Nestucca Formation is *Nucella oregona* Vokes, 1956. It is the only known Pacific Coast Eocene occurrence of an entire family of minute bivalves of Early Jurassic origin and a modern representation extending into the deep sea. The hinge characters are well preserved, and there is no doubt as to its assignment, adding to the enigmatic nature of the Nestucca fauna.

A lithofacies link between *Calliovarica* and a volcanic setting is noted by Stillwell (2014) in his description of *Calliovarica rangiaotea* from the Red Bluff Tuff in the Chatham Islands of Paleogene Zealandia. The relationship between fauna and volcanic lithofacies may be more than coincidental. These kinds of links should not be ignored when attempting to understand rare and unusual taxa in settings that lack modern analogs.

Paleobiogeography and the PETM

The disjunct high latitude occurrences of *Calliovarica* (approximately 44°S in Paleogene Zealandia and 44°N in Paleogene Cascadia) is unlikely to be entirely a matter of coincidence.

However the link to active margin volcanic setting is not sufficient to explain the paleogeographic expansion out the old world Tethys and Paratethys. Living chilodontid gastropods, along with sister families of Seguenzioid basal gastropods, have short-lived planktonic larval stages or hatch directly from benthic egg masses. Developmentally they do not have good potential for long-distance dispersal. While the expansion of *Calliovarica* is difficult to reconcile with its poor dispersal capability, the potential for rafting and rare chance events is correlated with oceanic gateway events. Gateway events have played a major role in global climatic change (Berggren 1982). While the Tethyan gateway was open to the spread of taxa into the Pacific during the PETM, it was the lack of thermal stratification of the Pacific Ocean that permitted subsequent expansion to high latitudes. This interval ended in the late Eocene with gateway opening of the Drake Passage, thermal isolation of Antarctica, formation of a cold bottom layer, a thermally stratified ocean and onset of an increasingly steep latitudinal gradient.

Significance of varices in vetigastropods

Calliovarica is the only Cenozoic vetigastropod genus that produced true varices, defined here as multiple, rounded, synchronous thickenings at regular intervals on the shell. There are a few vetigastropods, both living

and fossil, that secrete a single terminal thickening of the apertural lip or that secrete minor thickenings of the shell referred to as “growth checks.” Terminal thickenings are rare in vetigastropods and are associated with determinate growth in the seguenzioid families Gazidae [Hickman and McLean, 1990](#) and Calliotopidae [Hickman and McLean, 1990](#). In both groups the thickened lip occurs because secretion at the shell margin continues after spiral coiling has ceased ([Hickman 2012, 2016](#)). It is not clear whether this is a genetically programmed feature indicative of maturity (adult stage) or if it represents a dramatic gerontic (senescent) slowing of spiral growth. Growth checks, on the other hand may be multiple and occur most commonly during a brief interval of shell repair in response to non-lethal damage to the growing margin during an unsuccessful predation attempt.

A review of the distribution of varices and their evolution in gastropods ([Webster and Vermeij 2017](#)) recognizes 41 independent origins of the feature. They conclude that varices are phylogenetically clumped and most common in higher gastropods in warm shallow water and environments in which predation is intense. They note that in basal gastropods multiple varices occur only in seguenziodeans and in no extant taxa. In addition to *Calliovarica*, varices have been noted in the extinct Cretaceous genus *Agathodonta* [Cossmann, 1918](#) and the extinct Jurassic-Cretaceous genus *Onkospira* [Zittel, 1873](#). Two extant species have been assigned to *Agathodonta* by some authors (e.g., [McLean 1984](#)). However, [Herbert \(2012\)](#) has examined and figured the Cretaceous type species and shown that the putative extant species lack synchronous varices on spire whorls and differ significantly in several apertural features.

The Mesozoic *Onkospira* definitely has synchronous varices and merits additional discussion. Multiple species are represented by well-preserved European material and excellent figures in the literature (e.g., [Gründel et al. 2017](#)), and cosmopolitan distribution has become apparent in new species described from India ([Das et al. 1999](#)) and Siberia and the Tinman region of Russia ([Kaim et al. 2004](#)). Two consistent features of the varices are also present in *Calliovarica*: (1) placement is not strictly synchronous at 180° intervals and occurs slightly later on each successive whorl and (2) the final varix on the body whorl is not at the apertural margin but immediately preceding a terminal expansion or flaring of the aperture. There are effectively two terminal axial structures. A similar subterminal axial thickening occurs in another chilodontid genus, *Danilia* [Brusina, 1865](#) (Cretaceous–Recent). Although this has been referred

to as a “subterminal varix” ([Herbert 2012](#)), there are no periodic thickenings on the spire whorls.

The evidence is increasingly strong that *Calliovarica* is the last gasp of the Mesozoic varicate chilodontids, which persisted into the Eocene before exiting the evolutionary stage.

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