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Phylogenetics, development, and Cenozoic paleontology of Buccinidae (Mollusca:Gastropoda)

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Phylogenetics, Development, and Cenozoic Paleontology of Buccinidae (Mollusca: Gastropoda)

by

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requirements for the degree of

Doctor of Philosophy

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Dedication

To Gene Kwon, my beloved partner in life and sympathetic companion
in appreciating and exploring the natural world.

I cannot separate the aesthetic pleasure of seeing a butterfly and the scientific pleasure of knowing what it is. – Vladimir Nabokov, 1959

I gradually came to realize that these works of architecture are parts of living things that must make their way in a challenging world. Shells—the objects that I came to study most intensively—were no longer just things pleasing to the senses and hailing from lands and seas I dreamed of visiting someday, but in addition revealed a context in which organisms live and evolve. – Geerat Vermeij Nature: and Economic History, 2004

A biologist with a grounding in geology cannot help seeing the world differently from someone without that training because the dimension of time pervades what [they] see and adds interest and delight to it. They can see the past in the present.
–Norman Moore Bird of Time, 1987

Few of us, however, know what a million really means. Mr. Croll gives the following illustration: take a narrow strip of paper 83 feet by 4 inches in length, and stretch it along the wall of a large hall; then mark off at one end the tenth of an inch. This tenth of an inch will represent one hundred years, and the entire strip a million years.
– Charles Darwin On the Origin of Species 3rd Ed., 1861

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Acknowledgements

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The members of my qualifying exam committee: Kevin Padian, Bill Berry, Carol Tang, and chair Jere Lipps deserve special mention. They all devoted considerable time to conversations that expanded the breadth and depth of my knowledge of paleontology and natural history. For this I can not thank them enough.

Prior to my qualifying exam, Jere led an unforgettable tour of California Paleozoic and Mesozoic geology for UCMP graduate students that primed me for questions about fossil invertebrates and field geology. We covered the state from Mono Lake to Death Valley, hiked miles off trail, and pitched our tents by moonlight, all the while bering entertained by Jere's wisdom and stories. His uncanny sense of direction, affection for the field, and contagious enthusiasm are imprinted in my memory along with Crystal Springs stromatolites and the Johnnie Oolite.

Kevin Padian has been a remarkable mentor, confident, and sounding board throughout my graduate experience. His efforts to keep me on track were timely and his challenges to think broadly were vital to the development of my research. His famously rigorous and engaging Darwin and Gould seminars became fundamental components of my education at UC Berkeley. Alternatively, laid back Yale Avenue afternoons with Marty and Maggy allowed for reflection on research directions and life in general. Finally, Kevin's feedback on my written work was not only thorough but also entertaining. He called attention to awkward phrases, places for clarification, and punctuated stylistic suggestions by referencing Groucho Marx. I am deeply grateful to be included as a Padian Lab honorary member and am proud to share with Kevin our undergraduate alma mater.

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Thank you, Gene.

Introduction

The goal of this dissertation was to create complementary studies of extinct and extant buccinid lineages using a variety of methods. The family Buccinidae is rich in species and has an abundant fossil history that spans the Cenozoic. Although many extant buccinid whelks live in the intertidal and various deep water species have been (and still are) fished for human consumption around the world (e.g. England, Japan) myriad aspects of life history for most taxa are still undocumented. Furthermore, the phylogenetic relationships between subfamilies and putative members of the Buccinidae have only recently been investigated, mostly by Russian and Japanese malacologists (see Chapter 3).

Here, fossil investigations in the Buccinidae focused on *Bruclarkia,* an extinct whelk genus treated by Carole Hickman in faunal monographs of Paleogene formations in the Pacific Northwest (see Chapters 1 and 2). Taxa within this genus were initially of interest because they survived the dramatic Eocene/Oligocene extinctions that wiped out so many marine species in the Pacific Northwest. I was interested in the survivorship of taxa through this boundary and focused on *Bruclarkia* as a member of the molluscan the recovery fauna.

After initial investigations, it became obvious that species descriptions of *Bruclarkia* and identified material from museum collections (UCMP, CAS, etc.) were inconsistent. Also, few fossils were found of species described from taphonomically altered material and the range of morphological variation within species had not been thoroughly examined and reported. Therefore, a review of the genus was necessary. As part of this reviewa, nearly 800 fossil specimens identified by the author and by various collectors whose material was deposited in UCMP or CAS were examined and scored for a suite of morphological characters. These characters were used to identify species and one new taxon, *Bruclarkia ellenae*, was described. It is named for Ellen Moore, a paleontologist and geologist who treated *Bruclarkia* in monographs of Oligocene and Miocene strata in the Pacific Northwest.

The buccinid fauna of Japan is the richest and most diverse in the world (see Chapter 3) and therefore became the destination from which to collect taxa for phylogenetic analysis. Two dozen or so Japanese species, especially of large size, are fished by traul and baited trap and sold at local fish markets in Japan throughout the year. These markets became my field area for collecting species from the northwest Pacific and the Sea of Japan. Phylogenetic analyses were performed based on 28S and CO1 sequences that were evaluated independently and in conguntion. These genes were chosen because, (1) they were successful in resolving evolutionary relationships within a clade of muricid gastropods (see Ch. 3) and, (2) the genes used by other authors to reconstruct relationships within the buccinid clade (e.g. 18S and 16S) had produced disappointing results (see Ch. 3).

Kelletia kelletii, an eastern Pacific buccinid, became the taxon of focus for larval studies (Chapter 4) because of the suggestion (by Carole Hickman) to obersve it as a possible modern analogue for *Bruclarkia*. These taxa are similar in size, aggregated during eating and mating (a suggested behavior of *Bruclarkia*), and lived subtidally off the coast of California. *Kelletia* was amenable to laboratory conditions and successfully spawned many times—creating the opportunity to study its egg masses and larvae. Larvae of this species are unique among buccinids in that they have a planktonic phase that follows encapsulation. Most buccinids especially of cooler waters develop “directly” by metamorphosing within their capsule then emerging as crawling juveniles. One novel observation of *K. kelletii* larvae was that the morphology of veligers developes asymmetrically, a characteristic never before reported in the Buccinidae.

The method described for analyzing gastropod protoconchs—from casts rather than from original shell material was developed out of necessity (Chapter 5). While preparing for a research fellowship in Japan, I became interested in the morphology of protoconchs as a proxy for larval developmental mode. That is, the shape, ornamentation, and number of whorls of a protoconch can be used to infer development in many snails as either planktonic or non-planktonic. I would be visiting at least six museums in Japan, including some that exclusively housed and displayed mollusc shells, so I developed a way to copy the shell protoconch of museum specimens without damage. This method was inspired by Pat Holroyd’s (UCMP) application of the technique to micro-mammal teeth. An analysis of protoconch morphology from hundreds of casts from Japanese museums and the UMCP extant mollusc collection is in progress and is not presented in the following dissertation.

Abstract

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The buccinid gastropods (family Buccinidae) are a species-rich clade of mostly North Pacific taxa with an abundant fossil record that dates to the Cretaceous. Here, the evolution, systematics, and biology of fossil and extant members of this family are treated using a variety of analytical and methodological approaches. In chapter one, a new fossil species of *Bruclarkia*, an endemic eastern Pacific buccinid from the Eocene, Oligocene, and Miocene, is described from the Astoria Formation of the Pacific Northwest. This species, *B. ellenae*, was discovered among fossil material of the University of California Museum of Paleontology and California Academy of Sciences and had been either overlooked or identified incorrectly in previous reviews of Astoria fauna. Its novel morphology was characterized based on 11 shell traits and was compared to all other *Bruclarkia* species in a sample size of nearly 800 individuals. The challenges inherent to correlating Pacific Northwest and California Miocene sequences are also discussed.

In chapter two, all proposed *Bruclarkia* taxa are reviewed and re-described based on morphological characters determined from the largest examination of the genus to date. Intraspecific variation as well as autapomorphies and synapomorphies are characterized from hundreds of fossils that were measured and scored. Results suggest that of the twenty proposed *Bruclarkia* taxa, only seven are valid. The majority of remaining species are either synonymous with valid taxa or named from type material that is insufficient for suitable description. The value of *Bruclarkia acuminata, B. barkeriana,* and *B. gravida,* as index fossils is emphasized and the paleobiogeography of these and other *Bruclarkia* lineages throughout California, Oregon, Washington, Vanouver Island, Canada, and Alaska is reviewed.

In chapter three, the molecular phylogenetic systematics of 43 buccinid taxa mostly from Japanese waters is presented. Phylograms are based on Bayesian and maximum likelihood analyses of approximately 1500 base pairs from the mitochondrial gene CO1 and 625 base pairs from the nuclear gene 28S. These data suggest that: (1) Buccinidae is monophyletic, though the placement of several genera (e.g. *Lirabuccinuum, Microfusus*, and *Solenosteira*) is poorly resolved, (2) the genera *Busycon* and *Busycotypus*, which have often been classified in the family Melongenidae, belong within Buccinidae, (3) the subfamilies Beringiinae, Buccininae, Busyconinae, Neptuneinae, and Photinae are monophyletic, and (4) the genera *Neptunea*, *Buccinum,* and *Busycon* are also monophyletic. General characters of larval development in selected buccinids are presented in a cladistic framework, which reveals two species (*Kelletia kelletii* and *Volutharpa perryi*) from different subfamilies that both have planktonic larvae.

In chapter four, the early development of the California buccinid *Kelletia kelletii* is reviewed with new observations of larval asymmetries and feeding ability during incapsulation and after hatching. Larval shells and veligers were visualized under optical microscopy and SEM to observe fine-scale morphology at various ontogenetic stages. These observations reveal that: (1) intracapular veligers are capable of particle capture and transport but not ingestion, (2) hatching time varies between approximately 35 to 60 days depending on water conditions and temperature, (3) intracapsular larvae do not eat undeveloped eggs and/or embryos though they are present in all capsules, (4), pre-hatched veligers swim in the plankton if excapsulated at 27 days old and older, (5) within the capsule, veliger velar lobes are symmetrical but the right cephalic tentacles is larger than the left, (6) at 2.5 weeks in the plankton, both the right cephalic tentacle and right velar lobe are larger than those on the left, and (7) larval shells are brittle at emergence but calcify and grow apertural beaks and proto-siphonal canals by 2.5 weeks in the plankton.

Finally, in chapter five, a new method for replicating gastropod protoconchs (larval shells) is presented. It is based on protocols used in vertebrate paleontology for molding and casting micro-mammal and other small vertebrate teeth. Molding requires clean and periostracum-free shell apexes to be covered with a dental-grade polyvinylsiloxane impression material. Casts are made from molds using tinted epoxy resin and can be re-cast multiple times from the same mold without deterioration in cast quality. The practical applications of this technique to gastropods are substantial because for many snails, the protoconch indicates larval developmental mode as either planktonic or non-planktonic. Resulting casts can be examined in small SEM machines that could not accommodate the full gastropod shell, and can be made from specimens that would be otherwise be prohibited from such studies (e.g. living specimens, shells from protected land or private collections, type specimens, etc.).

Together these chapters tell the story of North Pacific buccinid evolution, speciation, and migration in selected fossil and extant lineages, early ontogeny in an unusual east Pacific buccinid, and practical methods for using protoconchs to answer questions about development in extant and extinct taxa. Future directions for research include expanding the sample size of buccinid taxa and the number of loci in molecular phylogenetic analyses, examining the shell characters and protoconchs of *Bruclarkia* taxa and their modern analogues to infer developmental mode and life history characteristics, and applying protoconchs replication methods (and subsequent analyses) to gastropods from diverse families- fossil and extant.

A new species of *Bruclarkia* (Mollusca: Gastropoda) from the Astoria Formation in Oregon and Washington and a review of Miocene congeners in the Pacific Northwest

Abstract

The Astoria Formation of the Pacific Northwest yields a well-documented early Neogene marine molluscan fauna of both endemic and cosmopolitan taxa. One of the endemics is the genus *Bruclarkia*— the largest whelk in the formation. Here, a new *Bruclarkia* species, *Bruclarkia ellenae,* is described and two other *Bruclarkia* species from the Astoria fauna are reviewed. They were compared with all proposed *Bruclarkia* taxa and scored for shell characters in the most inclusive examination of the genus to date. *Bruclarkia ellenae* occurs in Astoria strata of the Pacific Northwest, and appears to be restricted to the early Miocene. *Bruclarkia oregonensis* (Conrad) is the most common species of the genus in the Astoria Formation, and because of previous taxonomic ambiguity it is re-described and assigned a neotype and series of hypotypes. *Bruclarkia acuminata* (Anderson and Martin) is recognized for the first time from the Astoria Formation and (*Bruclarkia*) *Agasoma oregonense* Anderson and Martin is demoted to one of its junior synonyms. Lower Astoria sequences in which these species occur correlate with either the Pillarian or Newportian molluscan stage of the Pacific Northwest and most likely the "Temblor" molluscan zone of California. No *Bruclarkia* species is found in strata younger than the Astoria in the Pacific Northwest. All *Bruclarkia* taxa became extinct by the middle Miocene in Oregon and Washington. The cause of this extinction is unknown, but could be linked to either ocean warming during the Miocene Climatic Optimum or the climate cooling the followed. Fossil evidence suggests that unlike some Neogene gastropods (e.g. *Lirabuccinum* and *Nucella*), *Bruclarkia* remained confined to the eastern Pacific.

Introduction

The abundant shallow-water molluscs of the Miocene Astoria Formation have been used since the mid 1800s to correlate Neogene marine sediments throughout the Pacific Northwest (Conrad, 1865; Anderson, 1911; Arnold and Hannibal, 1913; Clark, 1918). With less success, this fauna has been a biostratigraphic benchmark for assessing coeval paleofaunas spanning Oregon, Washington, and California (Addicott, 1976). One characteristic genus of the Astoria fauna and its largest whelk is *Bruclarkia* Trask in Stewart, 1926. Members of this extinct clade occur in Paleogene and Neogene strata in Washington, Oregon, California, Vancouver Island, and Alaska (Smith, 1912; Arnold and Hannibal, 1913; Clark, 1918; Clark and Arnold, 1918; Trask, 1926; Durham, 1944; Addicott, 1972). Here, a new species, *Bruclarkia ellenae,* is described from museum specimens collected from Astoria outcrops in Washington and Oregon. Locality data suggest that *B. ellenae* was endemic to the Astoria Formation and restricted to the early Miocene to early middle Miocene (fig. 1). Two other species in this genus, *B. oregonensis* (Conrad) and *B. acuminata* (Anderson and Martin)*,* are also identified from the Astoria Fm. and re-described and evaluated for shell characters.

The first *Bruclarkia* species appears in Eocene rocks of the Keasey Formation in Oregon (Hickman, 1980). During the Oligocene and Miocene the lineage speciated into at least six taxa and migrated south into California and north into Alaska (Titova, 1994). In some Paleogene and Neogene west coast formations these taxa define stratigraphic beds or serve as index fossils

(Clark and Arnold, 1918; Clark, 1929; Davies, 1935; Shimer and Schrock, 1944; Addicott, 1970). Between 1926 and 1969, fifteen *Bruclarkia* species, subspecies, and forms have been proposed (Clark and Arnold, 1923; Durham, 1944; Moore, 1963; Hickman, 1969; Addicott, 1970; Armentrout, 1973; Moore, 1976; Hickman, 1980).

Morphological differences between *Bruclarkia* taxa are most obvious in body whorl ornamentation and spire sculpture. In general, shells are fusiform with an inflated body whorl and spiral threads and cords of varying prominence. Spire morphology ranges from smooth with an adpressed suture to stepped with a deeply impressed suture. The aperture is leaf-shaped and the siphonal canal is slightly recurved in most individuals, although it is often broken off. Species, subspecies, and forms are diagnosed based on the morphology of the spire, shoulder, spiral cords, axial growth lines, parietal lip, sutural collar, and whorl ornamentation (Tables 1 and 2).

The Astoria Formation

On the North American west coast, the Astoria Formation has long been known for its characteristic sequences of marine Cenozoic fossils (Dall, 1909). Astoria sequences are found in the Coast Range province of the Pacific Northwest and comprises Miocene marine sandstones, siltstones, and shales that alternate with layers of tuff and invasive basalts (Schenck, 1927; Snavely et al. 1973; Prothero et al., 2001). Fossil-rich sections crop out intermittently in sea cliffs from the Newport region to the city of Astoria in Oregon and in southwestern Washington within Grays Harbor and Wahkiakum Counties (Schenck, 1927; Etherington, 1931; Rau, 1948; Moore, 1963; Snavely et al., 1964; Addicott, 1976). Prior to the 1930s, Astoria shales and sandstones were referred to as the "Astoria beds" or the "Astoria series" (Hertlein and Crickmay, 1925; Etherington, 1931). Subsequent authors including Etherington (1931), Moore (1963), and others (Addicott, 1976; Prothero et al., 2001) referred to these sediments cumulatively as the Astoria Formation.

Near Newport, Oregon the Astoria Formation lies disconformably above the Nye Mudstone (Snavely et al., 1969; Prothero et al., 2001). At Coos Bay, unexposed Astoria sediments unconformably overlie the Tunnel Point Sandstone and underlie the Empire Formation (Moore, 1963; Armentrout, 1967; Prothero, 2001). In southwest Washington, the Astoria occurs above the Lincoln Creek Formation and below the late Miocene Montesano Fm. (Prothero et al., 2001). No exposures in Washington have been mapped directly to the type section in Oregon (Moore, 1963), so authors such as Moore (1963) and Addicott (1976) refer to them as the "Astoria(?) Fm."

Some of the first paleontological collections of the North American west coast came from lower Astoria Fm. sequences in Astoria, Oregon during the famous Wilkes Exploring Expedition of the 1830s-1840s (Weaver, 1942). Collections were also made by J.K. Townsend at Fort Astoria and along the nearby Columbia River at about the same time (Howe, 1926; Moore, 1963; Moore, 1994). Fossils collected by Townsend were described and figured by T.A. Conrad in 1848. The location of both collections later became the type section of the Astoria Fm., which today underlies the city of Astoria and is almost completely inaccessible (Howe, 1926; Moore, 1963; Prothero et al., 2001) (Fig. 1A).

Astoria Formation sediments were deposited in a warm-temperate sea at shallow to moderate depths of 10-100m (Moore, 1963). Sediment size ranges from silt to sand (Moore, 1963) and many soft-bottom benthic invertebrates were preserved *in situ* or with minimal transport (Moore, 1963; Prothero et al., 2001). The marine fauna of this formation includes fish, pinnepeds, a sea turtle, whale, desmostylid, and diverse invertebrates including 97 mollusc species (Packard, 1940; Moore, 1963; Prothero et al., 2001). Most of these were gastropods and bivalves that were adapted to temperate conditions (Moore, 1963; Addicott, 1976; 1977). Toward the Miocene Climatic Optimum as temperatures continued to warm, shallow-water thermophilic taxa migrated into the fauna from the south (Addicott, 1976; 1977).

Bruclarkia in the Astoria Formation

To date, faunal lists and descriptions of *Bruclarkia* from the Astoria Formation have included only *B. oregonensis* (Conrad) (Etherington, 1931; Moore, 1963; Addicott, 1976; Colbath, 1985; Moore, 1994; Moore, 2000). Early accounts of this species emphasized its highly variable shell morphology (Conrad, 1848; Anderson and Martin, 1914), which led subsequent authors to assign the name to distinctly different *Bruclarkia* morphotypes. Both *B. ellenae* and *B. acuminata* from Astoria Formation localities have been identified erroneously as *B. oregonensis* in the literature (Etherington, 1931) and in museum collections.

Abbreviations of Specimen Repositories

CAS: California Academy of Sciences, San Francisco, Invertebrate Paleontology collection.
SU NP: Stanford University (North Pacific Locality). Collection housed and incorporated into the California Academy of Sciences Invertebrate Paleontology collection.
UCMP: University of California Museum of Paleontology, UC Berkeley.
USGS: Unites States Geological Survey. Collection integrated into the UCMP collection.
USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. Specimens on loan to UCMP.
UW: University of Washington. Selected lots are incorporated into the UCMP collection.

SYSTEMATIC PALEONTOLOGY

Family BUCCINIDAE Rafinesque, 1815
Genus *Bruclarkia* Trask in Stewart, 1926
Type species: *Agasoma gravidum* Gabb, 1869
(By original description: *Clavella gravida* Gabb 1866, San Ramon Sandstone, CA)

Bruclarkia ellenae Vendetti, n. sp.

Plate 1. 2A-3C

Bruclarkia oregonensis (Conrad), Etherington, Univ. Calif. Pubs. Geo. Sci., v. 20, p. 48, pl. 11, fig. 5 (UCMP 31994, plesiotype), 1931.

Diagnosis: The following combination of characters distinguishes *B. ellenae* from all other *Bruclarkia* species. Spire tabulate; penultimate whorl with one row of evenly spaced nodes above the sutural collar; sutural collar slightly thickened and sometimes sinuous; one row of 11-13 evenly spaced nodes on body whorl; nodes are prominent and spinose in well-preserved specimens; nodes lie high on body whorl.

Description: The shell is stout and fusiform with a convex shoulder. The parietal lip extends across nearly ¾ of the body whorl in ventral (apertural) view. There are 5 whorls including the protoconch. Average shell width in adult specimens is 24 cm and average spire height is 9.25 cm. Axial growth lines are not prominent and twelve or more thin spiral cords of alternating thickness are evident on the body whorl in well-preserved specimens. The shell is ornamented by a single row of 11-13 evenly spaced and prominent nodes lying high on the body whorl. These spinose nodes often erode to rounded protrusions. Spire morphology is tabulate and the penultimate whorl has one row of evenly spaced nodes that is less prominent than on the body whorl. This single node row lies above the sutural collar, which is slightly thickened and sinuous in some specimens, but un-ornamented. The protoconch, though poorly preserved in most specimens, is small and paucispiral. The siphonal canal cannot be characterized because it is missing in all specimens.

Types: Holotype: UCMP 31994/loc. 9015 (pl. 1, fig. 1a-c), Paratypes: CAS SU45131/69261 (spec. NUMBER) (pl. 1, fig. 2a-c); UW 515 (spec. NUMBER) (pl. 1, fig 3a-3c). The holotype is deposited in the University of California Museum of Paleontology. Paratypes are curated in the invertebrate paleontology collections of the California Academy of Sciences.

The holotype (UCMP 31994) was chosen as one of the *B. oregonensis* hypotypes of Etherington, 1931 (plate 11, fig. 5). This specimen has distinctly different nodes than the other figured *B. oregonensis* specimens and can be differentiated easily from all other *Bruclarkia* species. It is likely that because *B. oregonensis* was described as "exceedingly variable" by both Etherington (1931) and Moore (1963) that the variant morphology of UCMP specimen 31994, which I propose as *B. ellenae*, was not noted by either author.

Type Dimensions: Holotype 31944: maximum width of body whorl: 27.06 mm, spire height (incomplete): 10.10 mm. Paratype NUMBER: max. width of body whorl: 26.45 mm, spire height: 9.79 mm. Paratype NUMBER: max. width of body whorl: 23.02, spire height (incomplete): 9.39 mm. Paratype (juvenile) NUMBER: max. width of body whorl: 17.57, spire height: 4.89 mm. All specimens are missing the lower body whorl and siphonal canal.

Type locality: Astoria Fm., Grays Harbor Co., WA (UMCP 9015, UW 418). The latitude and longitude coordinates provided in the UCMP type locality description (46.1° N, 123.1° W) maps to 4.5 miles east of Clatskanie, Oregon, not Washington. However, the public land survey data (T17N, R7W, sec23) provided by the University of Washington 418 locality (Weaver, 1942) maps to Grays Harbor Co., Washington. This Washington locality is here considered correct and its latitude and longitude should be 46.9° N, 123.5° W. *Bruclarkia* is rare at this locality, according to Etherington (1931).

Collected Material: Holotype material was collected by Thomas Etherington in 1925 while he was a student of Charles E. Weaver at the University of Washington.

Etymology: The species is named for Ellen Moore, a molluscan paleontologist and geologist, who has made substantial contributions to the stratigraphy of the Pacific Northwest. The name recognizes her treatment of *Bruclarkia* in monographs of the Astoria and Pittsburg Bluff Formations in Oregon in 1963 and 1976, respectively. Ms. Moore worked for the United States

Geological Survey in Washington D.C. and Menlo Park, California from 1950-1987. She has since published two books on the fossils of Oregon while a research associate at Oregon State University in Corvallis.

Occurrence and Age: *Bruclarkia ellenae* is known only from the lower Astoria Formation at the type locality in Astoria, Oregon and Astoria outcrops in southwestern Washington. Specimen localities are as follows: CAS/SU NP 45131/69261, Clatsop Co., City of Astoria, OR; CAS SU45173/69266, Southwestern WA; UCMP 9015/ UW 418, Grays Harbor Co., WA; UCMP D-294, Clatsop Co., City of Astoria, OR, at 4th and Commercial Streets; UW 515, Skamokawa, Wahkiakum Co., WA. The Astoria Fm. near Newport, Oregon is late early to middle Miocene in age (between 15.1-16 Ma and 19.2-21.1 Ma) (Prothero et al., 2001). The type section in the City of Astoria, Oregon however, is older than the Newport section (Prothero et al. 2001) and is probably of the early Miocene.

Similarity to other species: The shell morphology of *B. ellenae* is most similar to *B. acuminata* (Anderson and Martin, 1914). These taxa share a general body outline, stepped spire, well-developed parietal lip, and a node row on the penultimate and body whorl (Tables 1 and 2).

Outside the genus, *B. ellenae* most closely resembles *Cancellaria (Euclia) simplex* Anderson from the "Temblor" stage of California in its ornamentation and spire morphology. This species has unusually fine ornamentation and a weakly sculptured shell for a cancellarid. It occurs in the Temblor Fm., Topanga Fm., Olcese Sand, and Round Mountain Silt of the California Miocene (Addicott, 1970). A paratype of this species (UCMP33711/loc. B-1624) was examined and although it bears close resemblance to *B. ellenae*, its nodes, spire shape, and presence of columellar folds make it distinct and recognizable as a cancellarid.

Etherington (1931) figured four species of *Cancellaria* from the Astoria Formation, but according to Moore (1963), only *C. (Euclia) oregonensis* Conrad is valid. Neither this species nor any cancellarid figured in the Astoria Formation by Conrad (1848; 1865), Dall (1909), Weaver (1942), or Moore (1963) shares the morphology of *B. ellenae.* Therefore, it is unlikely that *B. ellenae* has been named for a species that has already been described.

Material examined: 38 *Bruclarkia ellenae* fossil specimens
CAS 69261/SU NP 45131, 17 specimens: 2 adults, 15 juveniles
CAS 69266/SU NP 45173, 3 specimens: 1 adult, 2 juveniles
UCMP 31994/loc. 9015 (UW 418), 1 specimen: 1 adult
UCMP D-294, 5 specimens: 2 adults, 3 juveniles
UW 515 (in UCMP Collections), 12 specimens: 2 adults, 10 juveniles

All proposed species, subspecies, and forms of *Bruclarkia* from the Eocene, Oligocene, and Miocene of California, Oregon, Washington, and Vancouver Island were compared to *Bruclarkia ellenae*. These included *Bruclarkia acuminatum (*Anderson and Martin, 1914)*, B. barkerianum* forma *santacruzanum* (Arnold, 1908)*, B. blakeleyensis* Durham, 1944*, B. chehalisensis* Armentrout, 1973 (unpublished Dissertation)*, B. chehalisensis nodulosa* Armentrout, 1973 (unpublished Dissertation), *B. columbianum (*Anderson and Martin, 1914)*, B. barkerianum* (Coooper, 1894)*, B. fulleri* Durham, 1944*, B. gravida* Trask in Stewart, 1926*, B. oregonensis*

(Conrad), *B. thor* Tegland, 1933, *B. seattlensis* Durham, 1944, *B. stanfordensis* (Arnold, 1908), *B. vokesi* Hickman, 1980, and *B. yaquinanum (*Anderson & Martin, 1914). A total of 797 *Bruclarkia* specimens were examined, 408 of which were measured and scored for shell characters. Their locality and specimen data are listed below as "State, Formation: Collection locality (number of specimens)." Locality numbers refer to UCMP material unless preceded by a collection abbreviation.

Oregon and Washington, Astoria Fm.: A-374 (3), D-294 (5), D-3225 (4), 3330 (23), 3334 (1), 3690 (2), 9069 (1), 10005 (2), 31994 (1), CAS 69260 (1), CAS 69264 (5), CAS 69265 (5), CAS 69261/SU NP 45131 (17), CAS 69266/SU NP 45173 (3); UW 515 (12); UW 54 (2); Blakeley Fm.: A-373 (2), A3707 (35390), A3708 (1), A3710 (1), A373/ UW 425 (3), A-6631 (1), no locality number (1); Butte Creek Volcanic Sandstone or Scotts Mills Formation (Scotts Mills Quadrangle): A-4011 (2), A-3852 (10), A-3877 (17), A-3878 (3); USGS 21347 (10); "Clatskanie beds": D-8281 (55), D-9045 (4), CAS, unidentified locality near Clatskanie: 69270 (7), 69271 (22); Clallam Fm.: A3692 (1), A3692 (1), A3692 (1); Eugene Fm.: CAS 69257/SU 3162 (1), CAS: 69253? (3), CAS 69254 (2), CAS 69272 (30), CAS 69256 (1), UCMP: 4084, 55105/USGS 152801 (1); USGS 15274 (1?), 15309 (1), 18798 (2), USNM: 15508, 251391/USGS 15282 (1), 251392/USGS 15282 (1); Lincoln Creek Fm.: A-9 (1), A-20 (4), A-364 (1); Pittsburg Bluff Fm.: A-194 (5), A-1599 (8), A-1601 (6), A-3669 (8), A-3782 (1), B-4288 (3), 3636 (2), 15264 (22), 69273 (3), 69259 (5), 7053 (1), 10001 (2), unidentified locality number (5); Quimper Sandstone: A-10 (2), A-1802 (3), A-3702 (1); Scappoose Fm.: CAS 168 (4), CAS 39; Schenck locality: NP 9 (2); Spencer Fm.: D9269; Tunnel Point Sandstone: A-1607 (99), A-1682 (1), B-7660 (3); British Columbia (Vancouver Is.), Sooke Fm.: collection of author (23), CAS 69267 (16), CAS 69268 (24), CAS 69269 (17), 69263 (1); California, Carquinez Qd.,?San Pablo Grp. (2); Hambre Sandstone of Monterey Group: A-4149 (3); Olcese Sand: B-1587 (9), B-1593 (17), B-1595 (5), B-1597 (7), B-1598 (2), B-1599 (11), B-1600 (6), B-1601 (16), B-1616 (3), B-1622 (28), B-1623 (6), B-1641 (6), B-1642 (3), (6), B-1657 (1), B-1660 (4); Kirker Tuff: A-4660 (3); Pleito Formation: 3199 (1), 3200 (4), 3203 (1), 3207 (1); Oursan Sandstone: A-4564 (5); San Ramon Sandstone: 14 (4) (5), 1310 (1), 1131 (1), 1203 (1), A-4661 (1), D-118 (19); San Emigdio Fm.: B-4573 (6); Sobrante Sandstone of Monterey Group: A4565 (1), 516 (20); Temblor: 1352 (2), A-506 (10), D-8808 (6), 1455 (1), 2298 (3), 2713 (1), 3688 (6), 3890 (1); Topanga Formation: B-7853 (3); Vaqueros: A-336 (1), A-585 (1); unknown locality: California Geological Survey Collection (3).

Remarks: No *B. ellenae* individuals were found in collections outside of the Astoria Fm. Of the five *B. ellenae* specimen lots, two were un-named (UCMP D-294 and UW 515) and three were identified as *Bruclarkia oregonensis* (CAS 69261, CAS 69266, and UCMP 31994/9015).

Preservation: The body whorls of all *B. ellenae* fossils are filled with a well-cemented dark gray mudstone. Taphonomic deformation is minimal although none of the specimens examined retain intact siphonal canals. Shell ornamentation ranges from slightly spinose nodes to eroded protrusions. In some specimens the stepped spire is worn to such a degree that it appears adpressed. Spiral threads and spire sculpture are present on half of the specimens examined. Shells from the locality CAS 45131 are altered to a chalky white texture.

Bruclarkia acuminata (Anderson and Martin, 1914)

?Un-named figs. 12, 12a, Dana, U.S. Expl. Exp. Geology, v. 10, altas, pl. 20, figs., 12, 12a, 1849.
?*Fusus corpulentus* (Conrad), Dana, U.S. Expl. Exp. Geology, v. 10, altas, pl. 20, fig. 4, 1849.
?*Priscofufus corpulentus* Conrad, Am. Jour. Conch., v. 1, p. 150, 1865.
?*Fusinus (Priscofusus) corpulentus* Conrad, Dall, USGS Prof. Paper 59, p. 39, 1909.
Agasoma acuminatum Anderson and Martin, Proc. Cal. Acad. Sci. v. 4, p. 73, 74, pl. 5, figs. 4a, 4b, 1914.
  Clark, Univ. Calif. Pubs. Geo. Sci., v. 11, p. 182, pl. 22, fig, 11, 1918;
  Clark and Arnold, Bull. Geol. Soc. Amer., v. 29, p. 304, 1918;
  Clark and Arnold, Univ. Calif. Pubs. Geo. Sci., v. 14, p. 130 (checklist), 131, 136, 160, pl. 29, figs. 1-3b, 1923;
  Hertein and Crickmay, Proc. Amer. Phil. Soc. v. 64(2): p. 252, 1925.
  Durham, Univ. Calif. Pubs. Geo. Sci., v. 27, p. 172, pl. 16, fig. 6, 1944.
Agasoma cf. *acuminata*, Hertein and Crickmay, Proc. Amer. Phil. Soc. v. 64(2): p. 254, 256, 1925.
Bruclarkia blakeleyensis Durham, Univ. Calif. Pubs. Geo. Sci., v. 27, p. 173, pl. 16, fig. 12, 13, 17, 1944.
Bruclarkia seattlensis Durham, Univ. Calif. Pubs. Geo. Sci., v. 27, p. 173, 174, pl. 16, fig. 15, 1944.
Bruclarkia oregonensis (Anderson and Martin), Addicott, USGS Prof. Paper 642, p. 89, 90, 91, pl. 10, figs. 15, 16, 1970;
  Moore, USGS Prof. Paper 419, p. 16, 18, 21, 22, 35, 36, pl. 3, figs. 2, 3, 8, 11, 1963;
  Addicott, USGS Prof. Paper 642, pl. 10, fig. 14-16?, 1970;
  Armentrout, Univ. Calif., Unpublished Dissertation, p. 165, pl. 4, fig. 21?, 1973.
Bruclarkia yaquinana (Anderson and Martin), Addicott, USGS Prof. Paper 642, p. 90, 91, pl. 10, figs. 8, 12, 13, 1970.
?*Bruclarkia yaquinana* (Anderson and Martin), Addicott, USGS Prof. Paper 642, pl. 10, figs. 8, 12, 13, 1970;
  Addicott, USGS Prof. Paper 976, p. 5, 14, 23, 24, pl. 2, figs. 5, 7, 8, 9, 1976a.
Bruclarkia acuminata (Anderson and Martin), Weaver, Univ. Wash. Pub. Geology, v. 5, p. 442, 740, pl. 87, figs. 1-4, 1942;
  Armentrout, Univ. Calif., Unpublished Dissertation, p. 66, 98, 108, 1973;
  Addicott, Neog. Sym. SEPM, p. 101, pl. 1, fig. 15, pl. 2, fig. 7, 1976;
  Addicott, Neog. Sym. SEPM, p. 101, pl. 1, fig. 15, 1976;
  Moore, J. Paleo. v. 58(3), p. 734, 1984;
  Johns and Cockburn, Fossils and geol. of the Cenozoic Carmanah Gp. SW Van. Is. (poster), 5th B.C. Paleo. Sym., 2003;
  Prothero et al., Can. J. Earth Sci. v. 45, p. 501, 2008.

Types: Holotype: CAS 157 and “co-type” (= paratype) 158 (Anderson and Martin, 1914). Hypotypes: UCMP 30083, 30084, and 30210 (Clark and Arnold, 1923).

Description: The shell is fusiform with six whorls including the protoconch. The shoulder is rounded and convex and a parietal lip extends across nearly ¾ of the body whorl in apertural view. Axial growth lines are sinuous and noticeable especially below (or anterior to) the sutural collar near the aperture. Thin spiral cords of unequal prominence are evident on the body whorl in well-preserved specimens. The shell has 1-3 rows of 17 evenly spaced and rounded nodes lying high on the body whorl. If there is more than one node row, the first and closest to the sutural collar is the most pronounced. Spire morphology is tabulate and the penultimate whorl has 1-2 node rows. In worn specimens these nodes often erode into fused bars instead of separate rows. The sutural collar is impressed and slightly thickened but un-ornamented. The protoconch, though poorly preserved in most of the specimens examined, is small and paucispiral. The siphonal canal is commonly recurved but straight in a few specimens.

<u>Type locality</u>: "Columbia Co., OR, 16 km northwest of Scappoose, OR" (Anderson and Martin, 1914) (= Scappoose Formation), (CAS locality 168: T4N, R3W, sec 36). Paratypes of Clark and Arnold (1923) are from the Sooke Fm., Vancouver Island, Canada (SU NP 129).

<u>Astoria Formation localities</u>: UCMP 3330, 3334, and A-3877.

<u>Material examined</u>: 9 specimens from the Astoria Formation. Fifty nine fossil specimens labeled *Bruclarkia acuminata, B. blakeleyensis, B. seattlensis, B. yaquinana*, and identified by the author as similar to *Agasoma acuminatum* Anderson and Martin (1914) were examined from museum collections and 55 were scored for shell characters.

<u>Remarks</u>: [Note: In 1926, the genus *Agasoma* was re-named *Bruclarkia* according to ICZN rules of nomenclature (see Stewart, 1926 and Opinion 121 ICZN, 1931)]. After inspecting the type material of Anderson and Martin (1914), it is the opinion of this author that the type and "co-type" (= paratype) of *Agasoma oregonense* are worn specimens of *B. acuminata*. The erosion of body whorl ornamentation is evident in the figure by Anderson and Martin (pl. 4, figs. 3a, 3b, 1914) and is unmistakable when handling the specimen. However, the spire of the specimen is well preserved and the node row on the penultimate whorl in intact, which suggest that this specimen *B. acuminata*. Because *B. acuminata* is described by Anderson and Martin (1914) prior to *A. oregonense*, the latter name becomes a junior synonym of *A. acuminatum*. California Academy of Science holotype 159, cotype 160, and cotype 160A of *A. oregonense* are renamed and designated as paratypes of *A. acuminatum* Anderson and Martin (1914).

Anderson and Martin (1914) described the ornamentation on *B. acuminatum* as, "quite variable as regards to the prominence of turbercules. On some specimens they are pronounced while on others they are almost obsolete" (p. 74). The distinguishing character of *B. acuminata,* as defined in this study, is the presence of an evenly spaced node row on the penultimate whorl. Specimens with small bead like nodes on the body whorl and the penultimate whorl should be classified as *B. oregonensis*. Likewise, if nodes are "almost obsolete" (Anderson and Martin, 1914) on a specimen, it should be classified as *B. oregonensis*, not *B. acuminatum*. *Bruclarkia oregonensis* specimens identified and figured by Moore (1963) from Coos Bay dredgings of the Astoria Fm./Tarheel Fm. were examined in the present study only from photographs, but they appear to have penultimate whorl ornamentation indicative of *B. acuminata*, not *B. oregonensis.*

Similarity between these species was noted by Lutz (1951) who stated in remarks about *B. oregonensis* (Conrad) from the Sobrante Sandstone of California that, "the impressed characters of the suture, the ribs on the body whorl, and posterior canal suggest *B. oregonensis* (Conrad)

1848, but nothing on this specimen seems to differ substantially from *B. acuminatum* (Anderson and Martin, 1914)." These two species should be considered distinct morphotypes of closely related taxa or perhaps the same taxon a different points along a morphological spectrum. Because *B. acuminata* and *B. oregonensis* co-occur in the same fossil lots and presumably in the same sedimentary sequences, it is likely that node ornamentation is a plastic character. Therefore, these species may represent morphological grades and not distinct evolutionary clades. This discussion is developed in the review of *B. oregonensis*.

Bruclarkia oregonensis (Conrad, 1848)

Referring to Conrad's type

Fusus oregonensis Conrad, Am. Jour. Sci. 2nd ser., v. 5, p. 433, fig. 13, 1848.
?Un-named figs. 12, 12a, Dana, U.S. Expl. Exp. Geology, v. 10, altas, pl. 20, figs., 12, 12a, 1849.
Sycotyphus (Fusus) oregonensis Conrad, Am. Jour. Conch., v. 1, p. 151, 1865.
Fusus (Priscofusus?) stanfordensis Arnold, Proc. Nat. Mus., v. 34, p. 383, pl. 35, fig. 7, 1908.
    Branner, Newson, and Arnold, Santa Cruz Folio, fig. 55, 1909.
Ficus (Trophosycon) oregonensis (Conrad), Dall, USGS Prof. Paper 59, p. 75, 1909.
Agasoma yaquinanum Anderson and Martin, Proc. Calif. Acad. Sci., v. 4, p. 75, pl. 4, figs. 5a, 5b, 1914.
Agasoma yaquinana Anderson and Martin, Proc. Calif. Acad. Sci., v. 4, p. 75, pl. 4, figs. 5a, 5b, 1914.
?*Agasoma acuminatum* Anderson and Martin, Clark, Univ. Calif. Pubs. Geo. Sci., v. 11, p. 230, pl. 22, fig. 11, 1918.
?*Agasoma gravida* Trask in Stewart, Clark, Univ. Calif. Pubs. Geo. Sci., v. 11, p. 230, pl. 22, fig. 19, 1918.
Bruclarkia oregonensis (Conrad), Etherington, Univ. Calif. Pubs. Geo. Sci., v. 20, p. 48 (checklist), 104, 105, 136, figs. 1, 3, 4, 7, 1931;
    Weaver, Univ. Wash. Pub. Geology, v. 5, p. 444, pl. 86, fig. 22, 1942 [not] fig. 21;
    Schenck and Keen, Cal. Fossils for the Field Geol., p. 43, fig. 5, 1950;
    Lutz, Univ. Calif. Pubs. Geo. Sci., v. 28, p. 379, 380, 382, 404, pl. 18, figs. 1, 6?, 1951;
    Moore, USGS Prof. Paper 419, p. 16, 18, 21, 22, 35, 36, pl. 3, fig. 13?, 1963;
    Addicott, USGS Prof. Paper 642, p. 26, 29, 36, 89, 90, 91, pl. 10, fig. 14?, 1970;
    Addicott, Pac. Coast Mio. Biostrat. Sym. SEPM, p. 11, 12, 13, pl.3, figs. 14, 15, 1972;
    Addicott, Neog. Sym. SEPM, p. 101, pl. 1, fig. 11, 1976, [not] p. 102, pl. 2, fig. 7.
    Addicott, USGS Prof. Paper 976, p. 5, 14, 23, 24, pl. 2, figs. 1-3, 1976a.
Bruclarkia yaquinana (Anderson and Martin), Weaver, Univ. Wash. Pub. Geology, v. 5, p. 444, pl. 87, fig. 6, 1942.
? *Bruclarkia yaquinana* (Anderson and Martin), Moore, Cont. Science, LACM, p. 13, 14, figs. 41, 44, 1984.
Bruclarkia seattlensis Durham, Addicott, Pac. Coast Mio. Biostrat. Sym. SEPM, p. 6, 7, pl.1, figs. 8, 13, 1972.
?*Bruclarkia* cf. *B. oregonensis* (Conrad), Addicott, USGS Prof. Paper 976, pl. 2, figs. 4, 6, 19, 1976a.

Incorrect identifications

[not] *Agasoma stanfordensis* Arnold, Proc. Nat. Mus., v. 34, p. 384, pl. 35, fig. 5, 1908;
    Branner, Newson, and Arnold, Santa Cruz Folio, fig. 54, 1909.

[not] *Agasoma oregonense* Anderson and Martin, Proc. Calif. Acad. Sci., v. 4, p. 74, pl. 4, figs. 3a, 3b, 1914.

[not] *Bruclarkia oregonensis* (Conrad), Etherington, Univ. Calif. Pubs. Geo. Sci., v. 20, p. 48 (checklist), 104, 105, 136, figs. 5, 1931;
Weaver, Univ. Wash. Pub. Geology, v. 5, p. 444, pl. 86, fig. 21, 1942;
Moore, USGS Prof. Paper 419, p. 16, 18, 21, 22, 35, 36, pl. 3, fig. 2, 3, 8, 11, 1963;
Addicott, USGS Prof. Paper 642, p. 26, 29, 36, 89, 90, 91, pl. 10, fig. 4, 15, 16, 1970;

<u>Of unknown affinity (without figured specimens)</u>

Agasoma oregonensis Conrad, Hertein and Crickmay, Proc. Amer. Phil. Soc. v. 64(2): p. 260, 282, 1925.

Agasoma oregonense Anderson and Martin, Hertein and Crickmay, Proc. Amer. Phil. Soc. v. 64(2): p. 252, 1925.

Agasoma oregonense Anderson and Martin, Wiedey, Trans. San Diego Soc. Nat. His., v. 5(10), p. 112, 115, 1928.

Agasoma andersoni Wiedey, Trans. San Diego Soc. Nat. His., v. 5(10), p. 115, 1928.

Bruclarkia oregonense (Conrad), Schenck, Univ. Calif. Pubs. Geo. Sci., v. 16, p. 456, 1927.

?*Bruclarkia* cf. *yaquinanum* (Anderson and Martin), Durham, Univ. Calif. Pubs. Geo. Sci., v. 27, p. 129, 1944.

Bruclarkia oregonensis (Conrad), Hall, GSA Special Paper 357, p. 26, 2002.

<u>Description</u>: The shell has 6 whorls including the protoconch and is fusiform with a rounded and convex shoulder. The parietal lip extends across nearly ¾ of the body whorl in apertural view. Axial growth lines are prominent and twelve or more thin spiral cords of alternating thickness are evident on the body whorl in well-preserved specimens. The body whorl is characterized by thickened spiral cords that in some specimens develop into small nodes that resemble beads on a string. The number and prominence of these cords and nodes varies greatly. If present, bead-like ornamentation is usually developed on no more than two spiral cords. The penultimate whorl is globose, has reticulated or cancellate ornamentation, and is without nodes. The sutural collar is impressed, slightly thickened, and un-ornamented. The protoconch, though poorly preserved in most specimens, is small and paucispiral. The siphonal canal is recurved is most specimens, but straight in others.

<u>Types</u>: Conrad’s holotype of *Fusus oregonensis* was lost and no neotype has been designated. Therefore, I propose the specimen lot CAS 69264/SU NP 269 as the type material for *Bruclarkia oregonensis*. The neotype is designated as specimen X and the remaining four specimens as hypotypes (A,B,C,D). The neotype has a primary and secondary node row on the body whorl and cancellate ornamentation on the penultimate whorl. This morphology closely matches the line drawing of *Fusus oregonensis* made by Conrad (1848) and a depiction of *Bruclarkia oregonensis* in Schenck and Keen (pl. 35, fig. 5, 1950).

Hypotype 1 (Specimen Y) is very similar to the neotype in body whorl ornamentation but has bead-like ornamentation on its penultimate whorl. Hypotype 2 lacks prominent spiral cords and nodes of any kind on the body whorl and penultimate whorl. Hypotype 3 shares the ornamentation morphology of the neotype and has a slightly recurved and nearly intact siphonal canal. The siphonal canal is missing in all specimens except hypotype 3. Hypotype 4 is the

largest specimen of the lot and has a more inflated body whorl than the other specimens. It has five thickened spiral cords on its body whorl and no node ornamentation.

Type locality: Astoria Fm., Grays Harbor Co., WA, near the Elkomin River, 19 km from Cathlamet, WA (CAS 69264/SU NP269).

Astoria Formation localities: UCMP 3330, 3690, 10005, A374, A3852, A3877, A3878, A4011, D3225, hypotypes of Etherington, (1931): 31992 and 31991, CAS 69260/SU 3132, 69264/SU NP269, 69265/SU NP 206; USGS 21347; UW 426.

Material examined: 48 specimens from the Astoria Formation. One hundred and fourteen fossil specimens labeled *Agasoma oregonense, Agasoma oregonensis, Bruclarkia oregonensis*, or identified as similar to *Fusus oregonensis* Conrad were examined from museum collections. Thirty specimens of *B. oregonensis* were scored for shell characters.

Remarks: *Bruclarkia oregonensis* was first described as *Fusus oregonensis* by Conrad (1848) from Astoria sediments in Oregon. It is unclear if the line drawing that accompanies this description was made from one or many individuals and unfortunately the type specimen was lost (Dall, 1909; Moore, 1963). It is evident from the drawing, however, that *F. oregonensis* likely represents *B. oregonensis* and not *B. ellenae* or *B. acuminata.* Specimens identified as *B. yaquinana* by Addicott (1976a) from the Clallam Fm. of Washington are likely *B. acuminata* or a variant of this morphotype that are not comparable to the *Agasoma yaquinana* type material of Anderson and Martin (1914).

In 1914, Anderson and Martin described and figured *Agasoma oregonense* from Oregon. They did not create a synonymy for this species or make any reference to *Fusus oregonensis* in their discussion of its morphology or occurrence. Therefore, the similarity in species name between *Agasoma oregonense* and *Agasoma oregonense* exists because both were described from Oregon, not because Anderson and Martin (1914) considered *A. oregonense* the same species as *F. oregonensis*. Subsequent authors disagreed on the placement, validity, and spelling of these taxa. Some synonymized them (e.g. Weidey, 1928; Weaver, 1942; Lutz, 1951; Addicott, 1970), others did not (e.g. Etherington, 1931; Moore, 1963), and one (Howe, 1926) created the name *Agasoma oregonensis* likely as an orthographic error. Further confusing matters, the name *Bruclarkia oregonense* (Conrad) was proposed by Schenck (1927). If Schenck meant this species to refer to *Fusus oregonensis* (Conrad) it should have ended in “ensis”, which would agree with the feminine suffix of the genus.

In the molluscan faunal monograph of the Washington Astoria by Etherington (1931) the name *Bruclarkia oregonensis* was used with reference to Conrad. Etherington (1931) synonymized it with *Agasoma oregonensis* from Howe (1926) and *Bruclarkia oregonense* in Schenck (1927) and Wiedey, all of which he spelled as *B. oregonensis.* Ever since, west coast molluscan paleontologists have used the name *Bruclarkia oregonensis* with reference to Conrad (1848) not Anderson and Martin (1914) (e.g. Weaver, 1942; Lutz, 1951; Schenck and Keen, 1950; Moore, 1963; Armentrout, 1973; Addicott, 1972; Addicott, 1976; Colbath, 1985; Moore, 1994; Moore, 2000). It is the view of this author that *Fusus oregonensis* Conrad and *Agasoma oregonense*

Anderson and Martin represent different morphotypes and separate species and therefore should not be synonymized. As described above, *A. oregonense* is a junior synonym of *A. acuminata*.

Discussion

Astoria Formation age

Magnetostratigraphic analyses by Prothero et al. (2001) date the Newport area Astoria Formation to between 19.2-21.1 and 15.1-16 Ma, between the late early to middle Miocene (Fig. 1B). A similar age was suggested by Howe (1926) whose opinion was considered "most extreme" by West Coast paleontologists who had established the rock units at Astoria as Oligocene (Schenck, 1927). *Bruclarkia ellenae* fossils occur in Astoria sections older than those from the Newport area. One of these is a fine-grained sandstone that Howe (1926) observed at the corner of Fifth St. and Commercial St. in the city of Astoria in 1921. Of the *B. ellenae* fossils examined in this study, one lot contained Astoria specimens from 4th and Commercial Streets (UCMP D-294), only 76 meters from the exposure Howe described. The precise date of these lower Astoria sequences has not been calculated because they now underlie the city and are inaccessible (Prothero, 2001).

Miocene outcrops in Washington are both some of the youngest and oldest Astoria strata (Addicott, 1976, Prothero et al., 2001). According to Moore (1963), 47 of the 97 species identified from the Astoria Formation in Oregon are found in the Astoria outcrops in Washington. In the present study, two specimen lots containing *B. ellenae* fossils were collected in localities in Oregon and three were collected from Washington. Unfortunately, the locality information from Washington sites does not specify how high or low in the Astoria section they were collected. Therefore, it is unknown whether *B. ellenae* spans the entire Astoria Formation or is restricted to its lowest and oldest horizons. The presence of *B. ellenae* in the Pacific Northwest, however, does support the hypothesis that the Oregon Astoria Formation and Washington Astoria sequences are coeval in time, if not contiguous in space.

Molluscan Zones in OR and WA

In 1976, Addicott chose the Astoria Formation of the Newport, Oregon embayment as the stratotype for the Newportian provincial molluscan stage of the middle Miocene in the Pacific Northwest. One of the characteristic molluscs of this stage was *Bruclarkia oregonensis* (Addicott, 1976; 1977). Dating based on benthic foraminifera places the Astoria of the Newport area in the upper Saucesian and Relizian Foraminiferal stages (Rau, 1948). Rare terrestrial mammal fossils from Astoria sequences suggest that it correlates with the lower Barstovian and most of the Hemingfordian North American land mammal stages (Armentrout, 1981).

Addicott (1976) correlated the lower Miocene sections of the Astoria Fm. with the Pacific Northwest Pillarian provincial molluscan stage that lies below the Newportian. The Pillarian stage is based on a stratotype from the Clallam Formation in Washington and also includes the Hoh Formation and the Nye Mudstone (Addicott, 1976). It is characterized by a suite of molluscan taxa that also includes *Bruclarkia oregonensis* (Conrad) (Durham, 1944; Moore, 1963; Addicott, 1976; Moore, 1984).

Although the stratigraphic range of *B. ellenae* from the beginning to the end of the Astoria Formation is unknown, this species is almost certainly part of the Astoria fauna of the earliest

Miocene. According to the molluscan stage partitioning of Addicott (1976), if *B. ellenae* is restricted to the Astoria Formation of the early Miocene, it should be part of the Pillarian stage. However, the age of the Pillarian stage as early Miocene has been questioned by paleomagnetic evidence (Prothero and Burns, 2001). These data suggest that the Pillarian stratotype (the Clallam Fm.) spans only 0.4 Ma of the latest Oligocene (Prothero and Burns, 2001). Analysis of paleomagnetic data and planktonic foraminifera also suggest that the Pillarian stage Nye Mudstone dates from the late Oligocene to the Oligocene/Miocene boundary (28-23 Ma). In the view of Prothero (Prothero, 2001), the Pillarian stage correlates with the Clallam Formation and the lowest Nye Mudstone of the late Oligocene and earliest Miocene (0.4 Ma). It does not correlate with the Astoria Formation near Newport, the base of which is at least three million years younger based on biostratigraphy and magnetostratigraphy (Prothero, 2001) (Fig. 1).

Correlation with California

Correlating Miocene Pacific Northwest stages and formations with the molluscan zones of California has been problematic for West Coast paleontologists since the mid 1800s (Louderback, 1913; Prothero, 2001). This is because provincial molluscan communities of California and the Pacific Northwest during the early Miocene did not exchange many taxa and therefore have few that are useful for correlation (Addicott, 1977). Another reason is that Miocene molluscan zones of California, the “Vaqueros” and “Temblor”, were not named for faunas but for lithostratographic units (Louderback, 1913). These zones also include time-transgressive sequences that span nearly 10 million years, making them imprecise for fine-scale correlation (Prothero, 2001; Prothero et al., 2001a, Hall, 2002). Further confounding potential correlation, neither the Vaqueros nor the Temblor Formation corresponds exclusively to the “Vaqueros” and “Temblor” zones. In general, the “Vaqueros” zone includes most of the Vaqueros Formation (Prothero, 2001). The “Temblor” zone includes some but not all sections of the Temblor Formation, most of the Monterey Formation, and the Barker’s Ranch sequences of the Olcese Sand and Round Mountain Silt (Addicott, 1972; 1977).

Addicott (1976) correlated the Newportian and Pillarian stages of the Astoria Formation with the “Temblor” and “Vaqueros” zones, respectively (Addicott, 1970; 1976; 1977). He did acknowledge, however, that the Newportian stage was the only Neogene unit from the Pacific Northwest that could be correlated with confidence to a molluscan zone in California (Addicott, 1976; 1977). This view is consistent with most West Coast molluscan stratigraphers who correlated the Astoria Formation with the “Temblor” zone (e.g. Clark, 1921; Clark, 1929; Howe, 1926; Schenck, 1927; Etherington, 1931; Weaver, 1942; Weaver et al., 1944; Moore, 1963; Baldwin, 1964). Moore (1963) correlated the Astoria Formation in Oregon with the “Temblor” zone based on 20 shared species between molluscan faunas. Only four molluscan species were common between the Astoria and Vaqueros Formations (Moore, 1963). This correlation supports the stratigraphic hypothesis of Prothero (2001) and Addicott (1976) that the “Vaqueros” corresponds only to the very lowest Astoria Formation, if at all, and that most of the Astoria formation is of the Newportian stage and correlates with the “Temblor” of California.

Although *Bruclarkia ellenae* was not identified from the “Vaqueros” or “Temblor”, the *Bruclarkia* fauna of these zones is rich. The “Temblor” zone includes *B. gravida, B. oregonensis*, *B. barkeriana*, and *B. barkeriana forma santacruzana* (Arnold) (Smith, 1912; Howe, 1926; Schenck, 1927; Addicott, 1972). Faunal checklists of the “Vaqueros” zone include *B. gravida* and *B. barkeriana forma santacruzana* (Smith, 1912; Loel and Corey, 1932) and a survey of the Vaqueros Formation collections in the UCMP revealed three additional species, *B. oregonensis*, *B. acuminata*, and *B. barkeriana* (localities A585 and B6853).

Absence of B. ellenae* and *B. acuminata in Astoria Formation monographs
The molluscan fossil fauna of the Astoria Formation was studied by Conrad (1848), Dana (1849), Dall (1909), Etherington (1931), Weaver (1942), and Moore (1963). Given this attention, it is surprising that the morphology of *B. ellenae* had not already been described or that *B. acuminata* was not identified. I propose that the sampling of the Astoria Formation and the previous ambiguous description of *B. oregonensis* account for the omission of these species in faunal monographs.

In the Townsend collection described by Conrad (1848), *B. oregonensis* is figured as *Fusus oregonensis*, but a specimen like *B. ellenae* is not. It is possible that of the approximately 100 mollusc species in the Astoria Formation (Moore, 1963), Townsend simply did not collect *B. ellenae*. In the Wilkes Expedition collection described by Dana (1849), *B. ellenae* was also not included perhaps because it was rare and the sample size was too small at 43 taxa, or *B. ellenae* morphology could not be distinguished from molds and casts. It is notable that *B. oregonensis* and/or *B. acuminata* were likely part of this collection and are figured as either an un-named species (pl. 20, fig. 12, 12a, 1849) or as *Fusus corpulentus* (pl. 20, fig. 4, 1849). The specific identity of these specimens is difficult to determine because the figures were drawn from casts and otherwise diagnostic shell ornamentation is unclear.

The Astoria Formation monograph of Dall (1909) figures no specimens identifiable as *B. ellenae*, but its faunal review includes *Fusus oregonensis* renamed as *Ficus (Trophosycon) oregonensis*. Dall (1909) listed the two names as synonyms and included (but did not figure) the species as one of 63 molluscan taxa found in the Astoria Fm. The Astoria Fm. in Washington monographed by Etherington includes *B. ellenae* and *B. oregonensis*, but as mentioned earlier, Etherington (1931) did not treat the novel morphology of *B. ellenae* as a new taxon. It is probable the he followed the convention of Conrad (1848) and Anderson and Martin (1914) to consider *B. oregonensis* as highly variable.

Moore (1963) records *Bruclarkia oregonensis* as occurring throughout the Astoria Fm. from Newport, Oregon but figured it only from Coos Bay dredgings (loc. 187/USGS 18284) (Moore, 1963). Armentrout (1967) described these sediments as originating from the Tarheel Formation, a massive sandstone that lies below the Empire Formation and is considered coeval with Astoria sequences. The figured *Bruclarkia* specimens from the Tarheel deposits in Moore (1963) are characteristic of *B. acuminata* than *B. oregonensis* because a node row is present on their penultimate whorl (figs. 2, 3, 8, 11, 13, Moore, 1963). It is possible that less-noded *Bruclarkia* individuals identifiable as *B. oregonensis*, were collected from the Astoria Fm. type area and localities of Howe (1926) listed by Moore (e.g. loc. 1, 1a, 4/USGS 5403, 7/2263), but none of these specimens is figured. One reason for the absence of *B. ellenae* from the Tarheel Fm. dredgings may be because they were not collected low enough in the sequences to recover *B. ellenae*, if this species is indeed restricted to its lower strata. Alternately, the dredgings may not have included *B. ellenae* just by chance.

Endemism and Extinction
The occurrence of *B. ellenae* in only the Astoria Formation suggests that it is one of many Neogene taxa endemic to the eastern Pacific. Endemism, or provincialism, in marine molluscs began to increase after the close of the Eocene epoch, which was characterized by warm seas and cosmopolitan taxa (Addicott, 1976). During the early Miocene in California and the Pacific Northwest, warm-temperate faunas evolved locally into provincial faunas. This phenomenon was caused in part by an increase in latitudinal temperature gradients from the poles to the equator (Clark, 1921; Addicott, 1976; Hall, 2002). The duration of provincial faunas was interrupted by a commingling of taxa during the Climate Optimum of the late early and early middle Miocene (Addicott, 1972).

Despite the warming of the Miocene Climatic Optimum (MCO) and the cooling that followed it (Wolfe and Poore, 1982), relatively few molluscan taxa from the Astoria fauna went extinct (Moore, 1963). Of nearly 75 species comprising the Astoria fauna, only the *Bruclarkia* species presented here and six other taxa are not found in modern oceans or in the formations that overlie the Astoria (Moore, 1963). It is possible that *Bruclarkia*, which had evolved in a temperate to cool-water environment (Hickman, 2003), failed to adapt to the warmer oceans of the Miocene Climatic Optimum or the cooling that following it. If instead *B. ellenae* survived the MCO and went extinct in the upper Astoria Formation, then a generous estimate of its stratigraphic range is 9 Ma. If it was restricted to the lower Astoria Formation, it may have persisted for approximately 2.2 Ma.

It is evident from coeval Miocene fossil deposits in Kamchatka and Japan that no *Bruclarkia* species migrated westward to establish populations in the western Pacific (Oleinik and Marincovich, 2003). Trans Pacific migration was not uncommon for shallow water neogastropods (e.g. *Nucella* and *Lirabuccinum*) during peak Miocene warming (Amano and Vermeij, 2003). If the *Bruclarkia* fauna of the Astoria Formation survived the duration of the Miocene Climate Optimum, it is unclear why all members of this lineage remained endemic to the North American West Coast.

Conclusions

The Miocene Astoria Formation of the Pacific Northwest includes three species of the whelk genus *Bruclarkia: B. oregonensis, B. acuminata*, and *B. ellenae*. *Bruclarkia ellenae* is described for the first time and was likely unrecognized by previous workers because it was included as one of many morphotypes exhibited by *B. oregonensis*. The actual morphological spectrum of *B. oregonensis* includes variation only in the prominence of spiral cords and their ornamentation.

Paleomagnetic and stratigraphic data suggest that the *Bruclarkia* fauna of the Astoria Formation correlates with the Newportian Molluscan stage of the Pacific Northwest and the "Temblor" molluscan zone of California. It is possible that *B. ellenae* is only found in the oldest Astoria deposits and that it spans a small portion of the early Miocene Pillarian stage and Californian "Vaqueros" zone. This hypothesis is difficult to test because precise locality information for fossil lots and precise dates of lower Astoria Formation sequences are lacking.

The morphology of *B. ellenae* most closely resembles *B. acuminata* except in body whorl and spire ornamentation. Morphology between *B. acuminata* and *B. oregonensis* is even more similar, differing only in the presence or absence of ornamentation on the penultimate whorl. An examination of museum localities and published faunal lists suggests that *B. oregonensis* and *B. acuminata* occur in both the Astoria Formation and "Temblor" formations of California.

Locality data suggest that *B. ellenae* is endemic to the Astoria Formation and restricted to the early to early middle Miocene. Its presence in Oregon and Washington outcrops also suggests that the Astoria Formation in Oregon and Astoria outcrops in Washington are coeval and date to the early Miocene. The extinction of *B. ellenae* and its congeners could have been in response to ocean warming during the Miocene Climatic Optimum or the cold climate that followed it. It is unclear why *Bruclarkia* did not migrate to the west Pacific during the Miocene Climate Optimum like some other neogastropods.

The evaluation of shell characters and species variation in *Bruclarkia* was only possible by examining a large number of fossils (>600). Although the Astoria Formation fauna has been documented by several authors, *B. ellenae* was not identified until a large number of specimens from museum collections were examined. Therefore, the value of museums and paleontological collections as fossil repositories for the study of evolution and diversity cannot be overemphasized.

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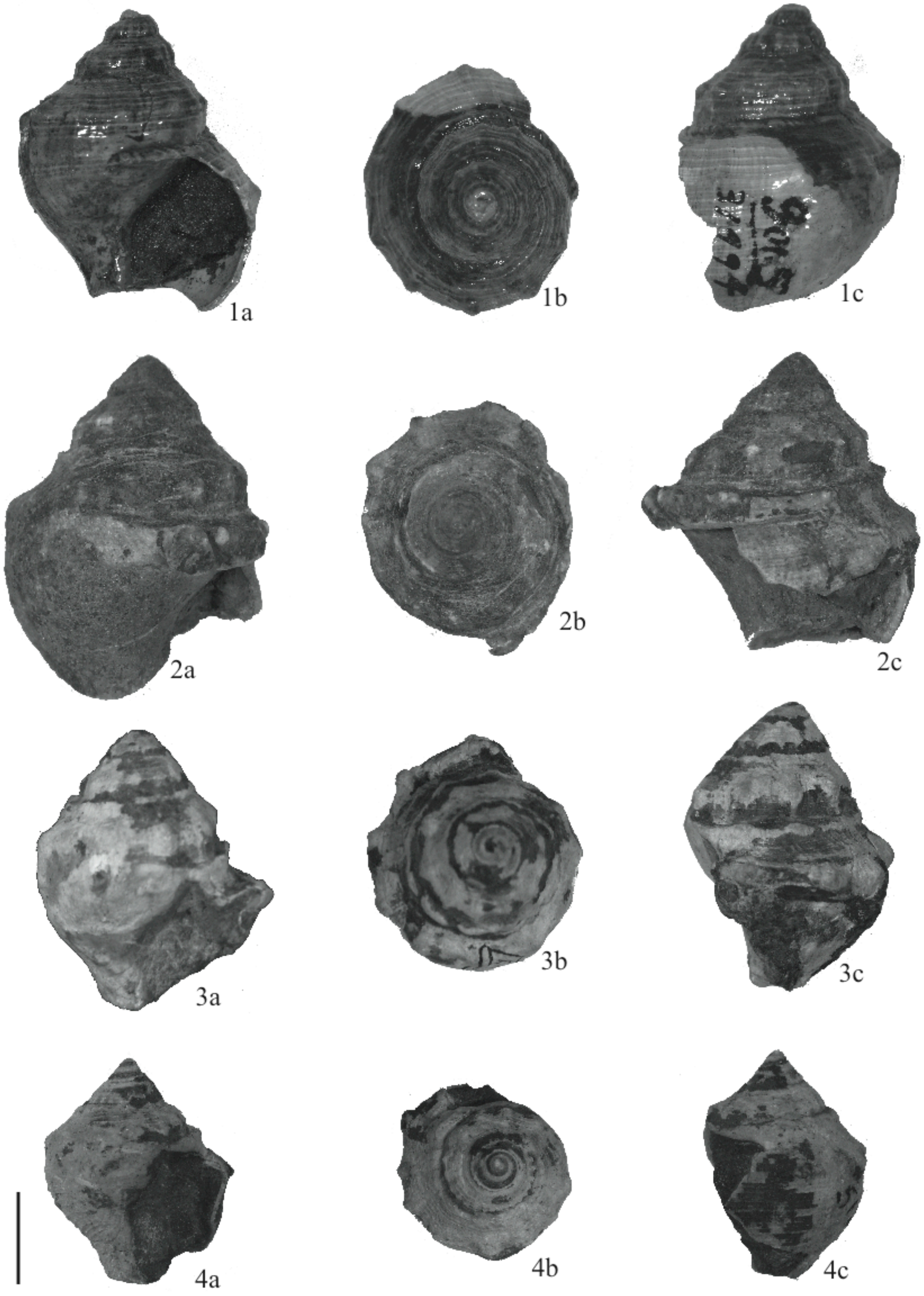

Plate 1. Holotype and paratype specimens of *Bruclarkia ellenae* n. sp. Apetural view, apical view, and adapertural view. 1a-c. Holotype specimen XXXX (UCMP 9015, Etherington, 1931 Hypotype), 2a-c. Paratype specimen XXXX (CAS SU 45131), 3a-c. Paratype specimen XXXX (UW 515), 4a-c. Paratype specimen XXXX (UW 515). Scale = 1cm.

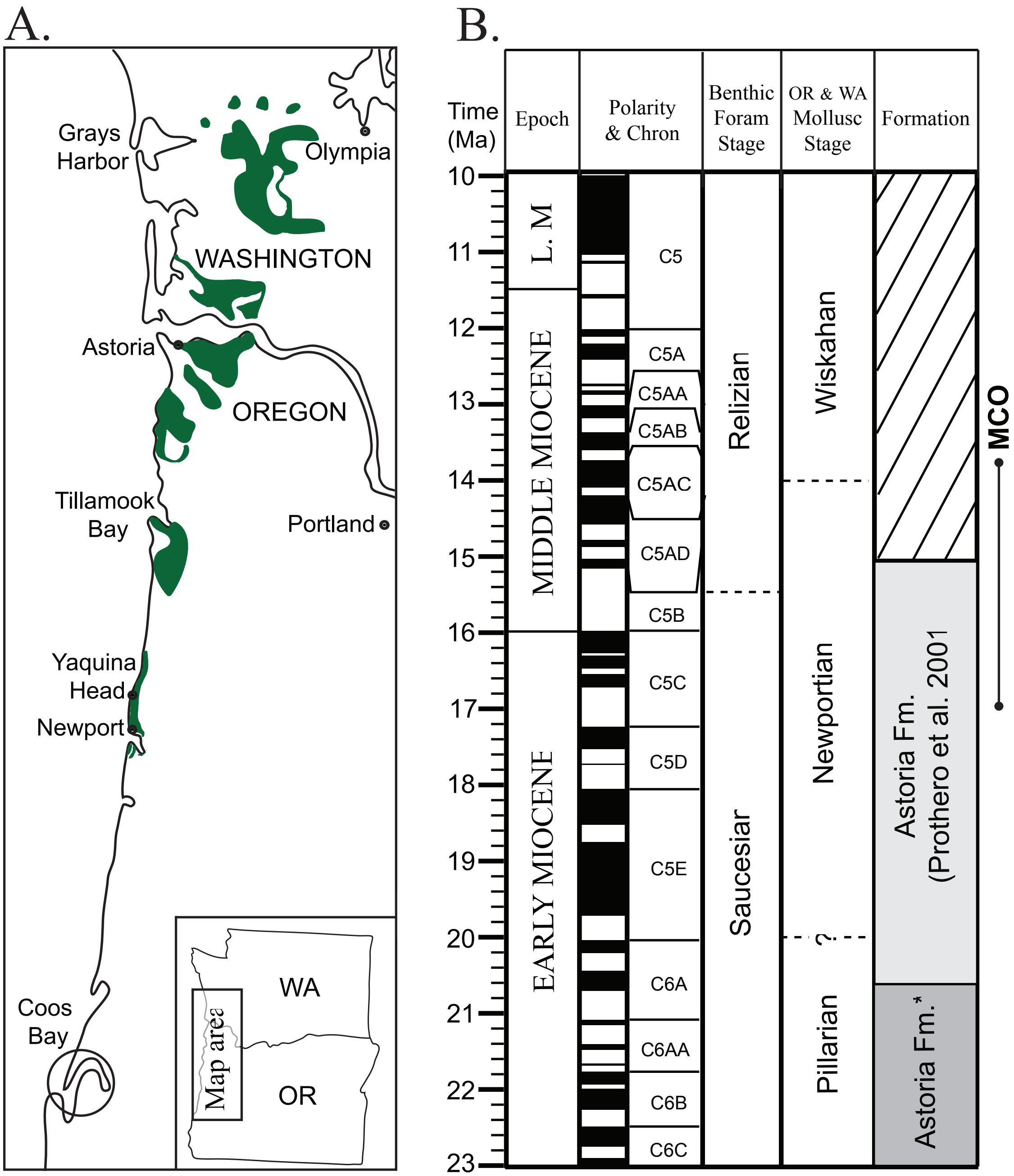

Figure 1. (A) Astoria Formation outcrops in Washington and Oregon based on maps of Moore (2000), Walker and Macleod (1991), and Walsh et al. (1987). The circle around Coos Bay approximates the area dredged for Tarheel Fm. deposits described in Moore (1963), (B) Neogene stratigraphic position and context of the Astoria Formation. Benthic Foram Stage and Pacific Northwest Molluscan Stages are based on Armentrout (1981). The Astoria Fm. represents the longest stratigraphic age from estimates of Prothero et al. (2001). The Lower Astoria Fm.* is shown correlating with the Pillarian Stage of Addicott (1976) and represents the type section in which *Bruclarkia ellenae* fossils are found. L.M.= the Late Miocene, "?" = the ambiguous upper Pillarian Stage boundary based on Prothero and Burns (2001), MCO = Miocene Climatic Optimum with a bar representing its duration. Time line was made with Time-Scale Creator, version 4.0.2 (Lugowski and Ogg, 2009).

Table 1. Shell width, spire height, and shell thickness in *B. ellenae* and six species and subspecies of the genus *Bruclarkia*. All measurements are in mm. M = mean; CV = coefficient of variation; N = sample size, n = total number of specimens examined. Table based on Kohn, 1980.

	B. ellenae (n=21)			*B. acuminata* (n=55)			*B. oregonensis* (n=30)			*B. barkeriana* (n=111)			*B. santacruzana* (n=19)			*B. gravida* (n=167)			*B. vokesi* (n=5)		
	M	CV	N	M	CV	N	M	CV	N	M	CV	N	M	CV	N	M	CV	N	M	CV	N
Shell width	24	9.6	4	32.7	19.1	18	23.9	26.6	13	29	18.6	89	27.6	23.5	18	27.0	22.9	128	23.7	4.9	4
Spire height	9.25	5.4	4	11.1	18.9	24	9.4	31.5	13	10.1	21.9	58	8.2	13.3	16	9.2	28.5	65	9.6	11.7	4
Shell thickness	0.90	13.1	8	0.9	26.1	20	1.1	27.6	45	1.1	27.7	45	1.1	28.3	13	1.0	30.5	43	1.6	21.9	3

Table 2. Morphologies and their character states in *B. ellenae* and other valid *Bruclarkia* taxa.

	Spiral cords		Axial growth line prominence	Parietal lip extent on body whorl	Spire whorl morphology	Shoulder morphology	Sutural collar	Penultimate whorl ornamentation	Body whorl nodes		
	Prominence	Thickness							# node rows	Node morphology	Nodes per whorl
B. ellenae n. sp.	major	unequal	minor	¾	tabulate	convex	un-adorned	1 node row	1	rounded	11-13
B. acuminata	major	unequal	obvious	¾	tabulate	convex	un-adorned	1-2 node rows	1-3	rounded	17
B. oregonensis	major	unequal	obvious	¾	globose	convex	un-adorned	N/A or small bead-like nodes	0-2	small, bead-like	variable
B. barkeriana	minor	equal	major, sinuous	> ¾	adpressed, globose	convex	noded, sinuous	absent	1-5	dashed	6-12
B. barkeriana santacruzana	minor	equal	major	> ¾	adpressed, globose	convex	noded, sinuous	absent	N/A	N/A	N/A
B. gravida	major	equal	major	≤ ¼	adpressed, flattened	straight concave	un-adorned	1 node row at the sutural collar	2-3	rounded	13-18
B. vokesi	minor	equal	major, sinuous	≤ ¼	adpressed, flattened	concave	un-adorned	1 node row at the sutural collar	3	spinose	15-18

A review of the neogastropod genus *Bruclarkia* (Trask in Stewart, 1926) from Paleogene and Neogene strata of the North American Pacific Coast

Abstract

The marine gastropod genus *Bruclarkia* is endemic to California and the Pacific Northwest and has been recognized for more than 100 years as stratigraphically valuable for dating and correlating Tertiary strata. Species in this genus define horizons and zones of the Oligocene and Miocene and are often among the largest neogastropods of their respective faunas. The stratigraphic range of *Bruclarkia* spans the Refugian to Luisian foram stages and Galvinian to Temblor/Newportian molluscan stages of the North American West Coast. Here, all members of *Bruclarkia* are reviewed and re-described based on an examination of 797 individuals. More than three hundred fossils were scored for eleven shell characters in the most extensive analysis of the genus to date. Of the twenty taxonomic names proposed for species of *Bruclarkia*, seven were determined to be valid and one individual had a unique morphotype that was previously unrecognized. Variable characters within some *Bruclarkia* species include siphonal canal length and shape, the number of node rows on the body whorl, the number of nodes per row, and the angle of the spire. Characters useful in diagnosing *Bruclarkia* taxa include penultimate whorl and sutural collar ornamentation, the extent of the parietal lip, and the overall ornamentation of the body whorl. Four of the seven *Bruclarkia* taxa identified in this review disappear during the early-middle Miocene. Extinctions of two other taxa, *B. vokesi* and *B. gravida*, occur in the early Oligocene and early Miocene, respectively. It is possible that the lack of *B. gravida* in the fossil record beyond the early Oligocene represents a pseudo-extinction. The cause of extinction for *B. gravida* by the early Oligocene and all *Bruclarkia* taxa by the middle Miocene in strata of the east Pacific is unknown, but could be linked to climatic changes during and following the Miocene Climatic Optimum.

Introduction

Cenozoic marine molluscan faunas of the eastern Pacific record dramatic changes in provinciality (Addicott, 1970; Tipton et al. 1973), responses to climate change (Oleinik and Marinkovich, 2003), and the influence of biotic invasions (Vermeij, 2001). The biostratigraphy of marine molluscan faunas through the Tertiary has formed the basis for correlation in sedimentary deposits of the West Coast (Prothero, 2003). Some Paleogene and early Neogene fossil marine gastropods from Alaska to southern California are so distinct that they characterize West Coast marine biostratigraphic stages. One of these genera is *Bruclarkia*, a neogastropod whelk. Its origin is in the late Eocene Galvinian molluscan stage and its last appearance is in the Temblor/Newportian stage of the middle Miocene.

Bruclarkia first appears as *B. vokesi* in the Eocene “turnover fauna” of Hickman (1969; 2003) in the Pacific Northwest. Here, it is rare in the subtropical Keasey Formation but abundant in the lower beds of the temperate Eugene Fm. (Hickman, 2003; Retallick et al., 2004). During the early Oligocene, a peak in global temperature followed by sea level regression and subsequent global cooling marks the extinction of foraminifera, echinoids, land plants, diverse terrestrial vertebrates, and more than 90 percent of marine mollusc species in the Pacific Northwest (Hickman, 2003). *Bruclarkia* survived this extinction as part of a cool-water recovery fauna that speciated in the Oligocene, and migrated into Alaska and California. All members of the genus went extinct by the middle Miocene with none giving rise to any extant taxon.

Provincialism in marine faunas intensified during the Oligocene. During this epoch, temperate faunas evolved into local endemics that were better adapted to a cooler marine environment than the tropical conditions of the Eocene. However, some *Bruclarkia* species spanned the west coast rather than remaining provincial during this period, making them particularly useful for correlation. No *Bruclarkia* species migrated across the Pacific to establish populations in the western Pacific, although other neogastropod taxa did during the Tertiary (Titova, 1994; Vermeij, 2001).

Bruclarkia species in West Coast strata have played a prominent role in efforts to correlate Tertiary formations of the eastern Pacific. Three species in the genus have defined horizons or zones in California, Oregon, and Washington where their fossils are locally abundant, and can occur in concentrated lenses (Fig. 1) (Louderback, 1913; Clark, 1918; Clark and Arnold, 1918; Stewart, 1926; Kleinpell and Weaver, 1963). In total, twenty species, forms, and subspecies of *Bruclarkia* have been proposed since the genus was first defined in the mid 1800s (Clark and Arnold, 1923; Durham, 1944; Moore, 1963; Hickman, 1969; Addicott, 1970; Moore, 1976; Armentrout, 1973; Hickman, 1980; Vendetti, 2009b). Some of these taxa, including *B. blakeleyensis* (Durham, 1944) and *B. seattlensis* (Durham, 1944) were described from one or few poorly preserved specimens. Here, the genus is revised based on an examination of the paleontological literature that treats *Bruclarkia* and an analysis of hundreds of *Bruclarkia* specimens available from museum collections.

Specimen examination

Although *Bruclarkia* has been included in more than 25 faunal reviews and monographs, the validity of some species and taxonomic names are questionable, as are the autapomorphic characteristics of species. Here, the first comprehensive review of members of the genus *Bruclarkia* is presented. It complements a recent species description of *B. ellenae* from the Astoria Formation in Oregon and Washington (Vendetti, 2009b).

The first step in this revision was to assemble material and evaluate types and locality records. Holotypes of some species were poorly preserved or inconsistent with the morphology of designated paratypes. Therefore, it was necessary to amass a large sample of *Bruclarkia* specimens to evaluate the plasticity of shell characters and determine the validity of proposed taxa. All published *Bruclarkia* species, subspecies, and forms were amassed from the paleontological collections of the University of California Museum of Paleontology, Burke Museum of Science and Culture at the University of Washington, California Academy of Sciences in San Francisco, and Smithsonian Paleontological collections. This sample constituted 797 *Bruclarkia* specimens from Paleogene and Neogene formations of California, Oregon, Washington, and Vancouver Island, Canada.

The next steps were to develop new characters and make quantitative measurements. Although morphological descriptions of *Bruclarkia* species are available from the literature (see references in “History of Study”), all characters included in this analysis were determined by the author

(Table 1). This methodology was chosen to gain familiarity with shell characters and score individuals without bias. Three hundred and forty-two specimens from the 797 specimen sample were scored for binary and multi-state shell characters and measured with digital calipers (Hausser Scientific # 100188) for shell height (maximum along axis of coiling), shell width (maximum at shoulder), spire height (maximum from suture to spiral apex in apertural view), and shell thickness. Taphonomic alteration and breakage of the siphonal canal and aperture, in particular, inhibited the scoring of hundreds of specimens. Spire characteristics, however, were generally well preserved enough to designate between species consistently.

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History of Study

The first reports of taxa later classified as *Bruclarkia* were from Conrad (1848) and the Geological Report of the Pacific Railroad Report by Blake (1856). The first definitive *Bruclarkia* species was described by Gabb in 1866 as *Clavella gravida* in Contra Costa County, California. In 1869, Gabb renamed this genus *Agasoma*, and in 1926 the genus name was changed to *Bruclarkia* (Trask in Stewart, 1926) in honor of Bruce Clark, a Professor in the UC Berkeley Paleontology Department and the first director of the University of California Museum of Paleontology (UCMP). A compilation of reports that make reference to *Bruclarkia* or taxa that would be latter classified in this genus are summarized below and keyed to specimens figured in plates 1-5. These references were chosen for their relevance to understanding the stratigraphy, paleobiogeography, and taxonomy of members of the genus.

Selected Reports of Bruclarkia with Notes and Comments

1848, Conrad. Describes and figures Fusus oregonensis (p. 433, fig. 13) from outcrops near Astoria, Oregon. The line drawing of this specimen depicts a straight siphonal canal, a distinct single row of evenly spaces nodes on the body whorl, and no ornamentation on the penultimate whorl. **Reference:** Conrad, T.A. 1848. Fossil shells from Tertiary deposits on the Columbia River, near Astoria. The American Journal of Science and Arts 5(15): 432-433. **Comment:** The holotype of this specimen has been lost. Most authors consider this species to be synonymous with Bruclarkia oregonensis (e.g. Etherington, 1931; Weaver, 1942; Lutz, 1951; Moore, 1963). **Figured:** Plate 1, fig. 1.

1856, Pacific Railroad Reports Un-named and un-described casts of gastropods in ad-apertural view are figured as drawings in "Appendix IV. Miocene Fossils from Ocoya Creek. Ocoya creek (Pose creek), from Mr. Blake, collected only as casts." The first of these (pl. 7, figs. 63) is drawn with a straight siphonal canal and no ornamentation and appears to be an internal mold. The second figure is smaller than the first and displays pronounced axial growth lines that connect to the sutural collar (pl. 7, fig. 68). **Reference:** Pacific Railroad Reports, 1856. United States. War Dept., Henry, Joseph, 1797-1878., Baird, Spencer Fullerton, 1823-1887., Report, by William P. Blake, Geologist and Mineralogist of the Expedition. Reports of explorations and surveys, to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean: Volume IV, Part 2. Routes in California, to Connect with the Routes near the Thirty-Fifth and Thirty-Second Parallels, Explored by Lieutenant R. S. Williamson, Corps of Topographical Engineers, in 1853. United States. Army., Washington: A. O. P. Nicholson, printer [etc.], 1855-60. **Comment:** This cast is considered to be *Agasoma gravida* Cooper (1894) by Gabb (1866), who remarks that it also resembles *Agasoma barkerianum*. **Figured:** Plate 1, fig. 2.

1866, **Gabb, W. M.** Describes and figures *Clavella gravida* from California as a synthetograph (pl 1, fig. 6). It is displayed in apertural view with two rows of nodes on the body whorl, an adpressed spire, and an aperture with a posterior notch. Gabb lists this fossil as having been collected "from the Miocene; abundant south of Martinez…by Dr. Fish and Dr. Mathewson." **Reference:** Gabb, W.M. 1869. Cretaceous and Tertiary fossils Palaeontology, Vol. II. California Geological Survey. 299 pp., 236 pls. **Figured:** Plate 1, fig. 3.

1869, **Gabb, W. M.** Renames *Clavella gravida* (1866) as *Agasoma gravida*. This genus is designated by Gabb from the material collected after the preparation of the first manuscript of Paleaontology, Vol. II. *Agasoma* differs from *Clavella* in having a shorter spire, slightly curved canal, and ornamentation of "revolving ribs and…tubercles." **Reference:** Gabb, W.M. 1866. Cretaceous and Tertiary fossils Palaeontology, Vol. II, Section 1, Part 1. California Geological Survey. 299 pp., 236 pls.

1894, Cooper, J. G. Describes, figures, and designates a holotype for *Agasoma barkerianum* (pl. 5, fig. 63) from Barker's Ranch in Kern County, California. **Reference:** Cooper, J.G. 1894. Catalogue of Californian Fossils (Parts II, III, IV, and V.) California State Mining Bureau, Bulletin 4: 36-65. pls. 6. **Comment:** The type specimen has been lost. This species was possibly identified as *Natica geniculata* Conrad in the Pacific Railroad reports, vol. 5, p. 328, pl. 7, fig. 67, 1856. It is mislabeled as *A. (Trophosycon) barkerianum* (pl. 3, fig. 52) and should be labeled as *A. barkerianum* (pl. 7, fig. 63). **Figured:** Plate 1, fig. 4.

1908, Arnold, R. Describes, figures, and designates holotypes for *Agasoma santacruzana* (pl. 34, fig. 7) and *A. stanfordensis* (pl. 35, fig. 7) from the Vaqueros and Monterey formations of

California, respectively. **Reference:** Arnold, R. 1908. Descriptions of new Cretaceous and Tertiary fossils from the Santa Cruz Mountains, California. Proceedings of the National Museum 34(1617): 345-384. **Comment:** The figured specimen and description for *A. stanfordensis* could be mislabeled as *Fusus stanfordensis* Arnold and may refer to the specimen in plate 35, fig. 7, not fig. 5. **Figured:** Plate 1, fig. 5.

1909, Dall, W.H. Proposes *Ficus (Trophosycon) oregonensis* (Conrad) for *Fusus oregonensis* of Conrad (1848) without having seen the type specimen because it was lost. **Reference:** Dall, W.H. 1909. Contributions to the Tertiary paleontology of the Pacific coast I. the Miocene of Astoria and Coos Bay, Oregon. Department of the Interior, United States Geological Survey, Prof. Paper 59, 278 pp.

1909, Branner, J.C., Newson, J.F. and R. Arnold. Figure *Agasoma santacruzana* (fig. 44) from the Vaqueros Sandstone as well as *A. stanfordensis* (fig. 55, not fig. 54) from the barnacle beds of the lowest Purisima Formation. **Reference:** Branner, J.C., Newson, J.F. and R. Arnold. 1909. Santa Cruz Folio. U.S. Geological Survey, Geol. Atlas, 163. **Comment:** The possible mislabeling of *A. stanfordensis* here is because of the mislabeling of the same specimens in Arnold, 1908. This species is also most likely erroneously attributed to the Purisima Formation. **Figured:** Plate 1, fig. 6.

1910, Arnold, R. and R. Anderson. Identify and figure *Agasoma santacruzana* from the top of the Vaqueros Sandstone in Coalinga, California, especially at locality 4633 where it is common. **Reference:** Arnold, R. and R. Anderson. 1910. Geology and Oil Resources of the Coalinga District California, U.S. Geological Survey, Bulletin 398, Washington. **Comment:** The species is misspelled as *A. sanctacruzana* Arnold on page 86. **Figured:** Plate 1, fig. 7.

1911, Anderson, F. A. Identifies *Agasoma gravidum* from Fossil zones A and B from the Kern River area of California. Anderson also notes that Ocoya Creek deposits have Barker's Ranch beds that yield *A. barkerianum* fossils. **Reference:** Anderson, F. 1911. The Neocene deposits of Kern River, California and the Temblor Basin. Proceedings of the California Academy of Sciences 3: 73-148. **Comment:** Anderson lists *A. gravidum* from the Pacific Railroad Reports (1866) collection of Blake as *A. gravidum* Garb (sic). He also changes the species name from the plural Latin neutral *gravida* to the singular neutral, *gravidum.*

1912, Smith, J. P. Proposes that *Agasoma barkerianum* and *A. gravidum* are confined to the Vaqueros and Monterey-Temblor faunas, and that *A. santacruzanum* is restricted to the Monterey-Temblor fauna. **Reference:** Smith, J.P. 1912. Geologic range of Miocene invertebrate fossils of California. Proceedings of the California Academy of Sciences 3: 161-182.

1914, Anderson, F. M. and B. Martin. Describe, figure, and designate holotypes for four new *Agasoma* species: *A. columbiana* (pl. 5, figs. 6a, 6b), *A. acuminata* (pl. 5, figs. 4a, 4b), *A. oregonense* (pl. 4, figs. 3a and 3b) and *A. yaquinanum* (pl. 4, figs. 5a, 5b). The authors also identify *A. barkerianum* and *A. sanctacruzanum* (sic) from the San Juan District in San Luis Obispo County and Kern River area of the Temblor Basin. **Reference:** Anderson, F. M. and Martin, B. 1914. Neocene record in the Temblor basin, California, and Neocene deposits of the

San Juan District, San Luis Obispo County. Proceedings of the California Academy of Sciences 4: 15-112. **Figured:** Plate 1, figs. 8-15.

1914, **English, W.A**. Describes *Agasoma barkerianum* Cooper, var. *clarki*. This variety is found above the *A. gravidum* zone of the Monterey Group in the Contra Costa Hills (UCMP Loc. 1352) in California. English also identifies *A. gravidum* and *A. barkerianum* from California. **Reference:** English, W.A. 1914. The *Agasoma*-like gastropods of the California Tertiary. University of California, Bulletin of the Department of Geology 8(10): 243-256, pls. 24-25. **Figured:** Plate 1, figs. 16-23.

1918, Clark, B.L. Describes and figures *Agasoma gravidum multinodosum* (pl. 23, fig. 8) from the San Lorenzo Series [Concord Fm., Kirker Tuff, and San Ramon Sandstone] in Contra Costa Co., California. This nodulose variety of *A. gravidum* is found within the "*Agasoma gravidum* fauna," "*Agasoma gravidum* zone," and "*Agasoma gravidum* beds" that Clark describes. He also lists *A. acuminatum* from the San Lorenzo Series, and notes that this fauna is distinct from that of the Temblor horizons where *A. barkerianum* occurs. **Reference:** Clark, B.L. 1918. The San Lorenzo Series of middle California. A stratigraphic and palaeontologic study of the San Lorenzo Oligocene Series of the general region of Mount Diablo, California. University of California, Bulletin of the Department of Geology 11(8): 45-234, pls. 3-24. **Figured:** Plate 2, figs. 24-29.

1918, Clark, B.L, and R. Arnold. Discuss the early Oligocene faunas of Oregon, Washington, and Vancouver Island as including beds of *Agasoma acuminatum*. The authors also define formations that yield this species as part of the San Lorenzo Series, which includes the Sooke Formation of Vancouver Island and the Lincoln, Porter, and Blakeley horizons described by Weaver (1942). **Reference:** Clark, B.L, and R. Arnold. 1918. Marine Oligocene of the west coast of North America. Bulletin of the Geological Society of America 29: 297-308.

1923, Clark, B. L. and R. Arnold. Identify and figure *Agasoma acuminatum* from the Sooke Fm. of Vancouver Island, British Columbia, Canada (pl. 29, figs. 1a, 1b, 2, 3a, 3b.). The authors list this species in the family Fusidae and note its range in variation. **Reference:** Clark, B.L and Arnold, A. 1923. Fauna of the Sooke Formation, Vancouver Island. University of California, Bulletin of the Department of Geology 14(5): 123-234. **Figured:** Plate 2, figs. 30-33.

1926, Howe, H.V. Identifies *Agasoma oregonensis* from the Astoria Formation in Oregon. Howe correlates this formation with the Barker's Ranch beds (Kern County) of the Monterey or Temblor in California, which includes *A. barkeriana* and *A. oregonense*. **Reference:** Howe, H.V. 1926. Astoria: mid-tertic type of Pacific coast. The Pan-American Geologist 45: 295-306. **Comment:** Howe is the first author to spell *A. oregonensis* as such and not as *Agasoma oregonense* as proposed by Anderson and Martin (1914). The former is probably a mistake because the author spells the species as *A. oregonense* in a correlation table of species from the Barker's Ranch fauna of California.

1926, Trask, P. D. Identifies *Agasoma barkerianum* from the Temblor near Pinon Peak, California. **Reference:** Trask, P. D. 1926. Geology of Point Sur quadrangle California. University of California Publications in Geological Sciences 16(6): 119-186.

1926, Schenck, H. G. Identifies *Agasoma columbianum* from the Pittsburg Bluff and *A. gravidum* from the Eugene Fm., Nye Shale, Tunnel Point beds, and Holmes Gap Fm. of Oregon. **Reference:** Schenck, H.G. 1926. Marine Oligocene of Oregon. Dissertation, University of California, Berkeley.

1926, Stewart, R. B. Renames *Agasoma* as *Bruclarkia* because the type specimen (*C. sinuata*) for the original genus *Clavella* does not belong within *Agasoma*. Stewart describes and figures the lectotype and another specimen of *B. gravida* (pl. 31, figs. 10, 11) from the material of Gabb. The new genus was proposed by Trask in honor of Dr. Bruce Clark the first Director of the Museum of Paleontology. **Reference:** Stewart, R.B. 1926. Gabb's California fossil type gastropods. Proc. Acad. Nat. Sci. Phila. 78: 287-447, pls. 13. **Figured:** Plate 2, figs. 34-35.

1927, Schenck, H.G. Lists *Bruclarkia oregonense* (Conrad) as common in the Miocene fossils above the Nye shale in Oregon. **Reference:** Schenck, H.G. 1927. Marine Oligocene of Oregon. University of California, Bulletin of the Department of Geology 16(12): 449-460.

1928, Wiedey, L. W. Proposes *Agasoma andersoni* as a new name for *A. oregonense* because the latter is synonymous with *"Fusus" oregonense* Conrad. *Agasoma andersoni* is named in honor of Frank M. Anderson. **Reference:** Wiedey, L. M. 1928. Notes on the Vaqueros and Temblor formations of the California Miocene with descriptions of new species. Transactions of the San Diego Society of Natural History 5(10): 95-182. **Comment:** Wiedey was unaware that the name *Agasoma* was changed to *Bruclarkia* (Trask in Stewart, 1926). *Agasoma andersoni* is an invalid name because the type material for *A. oregonense* should be considered paratypes of *A. acuminata* (Vendetti, 2009b).

1929, Clark, B.L. Identifies *Bruclarkia gravida* from the California San Ramon and cites *B. gravida columbiana* as common in strata of the San Emigdio Mountains, CA. **Reference:** Clark, B.L. 1929. <u>Stratigraphy and Faunal Horizons of the Coast Ranges of California</u> (Clark, self-published). **Figured:** Plate 2, figs. 36-39.

1931, Etherington, T. J. Identifies *Bruclarkia oregonensis* from the Astoria Formation of Southwest Washington (pl 11, figs. 1, 3, 4, 5, 7). **Reference:** Etherington, T. J. 1931. Stratigraphy and fauna of the Astoria Miocene of Southwest Washington. University of California, Bulletin of the Department of Geology 20(5): 31-142. **Figured:** Plate 2, figs. 40-43.

1932, Loel, W. and W.H. Corey. Identify and figure *Bruclarkia barkerianum* (Cooper) *santacruzanum* (Arnold) as the only *Bruclarkia* species from the Vaqueros horizon, CA. This species is small with no nodes on the body whorl, a low spire, and a strong corona. The authors also collected and identified *B. barkerianum* and *B. oregonensis* from the Temblor horizon of California. **Reference:** Loel, W. and W.H. Corey. 1932. The Vaqueros formation, lower Miocene of California I. Paleontology. University of California, Bulletin of the Department of Geology 22 (3): 31-410, pls. 61. **Figured:** Plate 2, figs. 44-45.

1933, Tegland, N. M. Describes, names, and figures *Bruclarkia thor* from the invertebrate marine fauna of the type Blakeley Shale of Bainbridge Island, Washington (pl. 12, figs. 9, 10, 11, 12.). **Reference:** Tegland, N.M. 1933. The Fauna of the type Blakeley Upper Oligocene of

Washington. University of California, Bulletin of the Department of Geology 23(3): 81-174. **Comment:** This species should be in the genus *Perse*. **Figured:** Plate 2, figs. 46-49.

1942, Weaver, C. E. Identifies and figures five *Bruclarkia* species from Oregon and Washington: *B. acuminata* (pl. 87, figs, 1, 2, 3, 4.), *B. columbiana* (pl. 87, figs. 7, 8), *B. oregonensis* (pl. 86, figs. 21, 22), *B. yaquinana* (pl. 87, fig. 6), and *B. thor* (pl. 87, figs. 5, 9). **Reference:** Weaver, C. E. 1942. Paleontology of the marine tertiary formations of Oregan and Washington University of Washington Publications in Geology vol. 5, University of Washington Press, Seattle: 789 pp. **Figured:** Plate 2, figs. 50-56, plate 3, figs. 57-60.

1944, Shimer, H.W. and R.R. Schrock. Include and figure *Bruclarkia gravida* as an index fossil of the middle Tertiary of California. **Reference:** Shimer, H.W. and R.R. Schrock. 1944. Index Fossils of North America MIT Press, 719 pp. **Figured:** Plate 3, fig. 61.

1944, Durham, J. W. Describes, names, and figures four new *Bruclarkia* species from northwestern Washington: *B. blakeleyensis* from the Blakeley Fm. (pl. 16, figs. 12, 13, 17), *B. fulleri* from the Quimper Sandstone (pl. 16, figs. 11, 14), and *B. seattlensis* from the Blakeley Fm. (pl. 16, fig. 15). Durham also identifies *B. acuminatum* from the Sooke Fm. near Seattle, *B. columbianum* from the Lincoln Fm., Pittsburg Bluffs, Quimper Sandstone, and Marrowstone Shale*, B. thor* from the Blakeley Fm.*,* and *B.* cf. *yaquinanum* from the Clallam Sandstone. **Reference:** Durham , J. W. 1944. Megafaunal zones of the Oligocene of Northwestern Washington, University of California Publications, Bulletin of the Department of Geological Sciences, 27(5): 101- 212. **Figured:** Plate 3, figs. 62-67.

1945, Vokes in Warren et al. Includes *Bruclarkia* among the fauna of northwestern Oregon. **Reference:** Warren, W.C., Grivetti, M., and H. Norbisrath. 1945. Geology of northwestern Oregon, west of Willamette River and north of latitude 45°15'. U.S. Geological Survey Oil and Gas Investigations Preliminary Map 42, geologic map and text.

1950, Schenck, H.G., and A. M. Keen. Figure *Bruclarkia oregonensis* from the "Temblor" Fm. (p. 43, fig. 5) and *B. columbiana* from the San Emigdio and Pleito formations in California (p. 37, fig. 5). **Reference:** Schenck, H.G., and Keen, A. M. 1950. California Fossils for the Field Geologist Stanford University Press, Stanford, 88 pp. **Figured:** Plate 3, figs. 68-69.

1951, Lutz, G. C. Identifies *Bruclarkia oregonensis* from the "Sobrante" Formation [not to be confused with the Sobrante Sandstone found elsewhere in California], but notes that he did not find *B. barkeriana* in the Sobrante or "Sobrante" sandstones, as Clark and Arnold (1918) did. Lutz also describes a rare and poorly preserved *Bruclarkia sp.* from the Pacheco syncline of the "Sobrante" Formation. **Reference:** Lutz, G. C. 1951. The Sobrante Sandstone. University of California, Bulletin of the Department of Geology 28(13): 367-406. **Figured:** Plate 3, figs. 70-71.

1963, Moore, E. J. Identifies and figures *Bruclarkia oregonensis* from the Astoria Fm. in Oregon (pl. 3, figs. 2, 3, 8, 11, 13). Moore discusses the variability of shell ornamentation in this species and identifies *B. yaquinana* as a highly sculptured variant of *B. oregonensis*. *Bruclarkia oregonensis* is also listed as occurring in the Astoria (?) Formation in Washington and the

Temblor and Sobrante Formations in California. **Reference:** Moore, E.J. 1963. Oligocene Marine Mollusks from the Pittsburg Bluff Formation in Oregon. United States Government Printing Office, Washington. Geological Survey Professional Paper 419. **Figured:** Plate 3, figs. 73-77.

1969, Hickman, C. S. Describes and figures *Bruclarkia vokesi* (pl. 13, figs. 6, 7, 8, 9, 10, 11) from the Eugene Formation in Oregon. Hickman also identifies *B. columbiana* from the youngest strata of the Eugene Fm., where it is a rare. **Reference:** Hickman, C.S. 1969. The Oligocene marine molluscan fauna of the Eugene Formation in Oregon. Mus. Nat. Hist. Univ. Oregon, Bulletin 16, 112 pp. **Figured:** Plate 3, figs. 78-80, pl. 4, figs. 81-85.

1970, Addicott, W. O. Identifies *Bruclarkia barkeriana* from the Jewett Sand and Olcese Sand, *B. oregonensis* from the Olcese Sand, and *B. yaquinana* from the Jewett Sand of the Kern River area, California. Addicott does not use the name *Bruclarkia (Agasoma) andersoni* proposed by Weidey (1926) in place of *A. oregonense*, but considers *B. oregonense* a high-spired variant of *B. oregonensis*. **Reference:** Addicott, W.O. 1970. Miocene gastropods and biostratigraphy of the Kern River area, California. United States Department of the Interior, Geological Survey Professional Paper 642. **Figured:** Plate 4, figs. 86-102.

1972, Addicott, W. O. Identifies *Bruclarkia columbiana, B. seattlensis, B. barkeriana,* and *B. oregonensis* within members of the Temblor Formation of California. **Reference:** Addicott, W.O. 1972. Provincial middle and late Tertiary molluscan stages, Temblor Range, California. SEPM Proceedings of the Pacific Coast Miocene Biostratigraphic Symposium 1-26. **Figured:** Plate 4, figs. 103-107.

1973, Armentrout, J. M. Describes, names, and figures *Bruclarkia chehalisensis* (pl. 4, fig. 22) and *B. chehalisensis nodulosa.* (pl. 4, fig. 27, 28) from the basal sandstones of the Lincoln Creek Formation in Washington. The species is named for the Chehalis River, WA. Armentrout notes that *B. chehalisensis nodulosa* might be a morphological variety of *B. chehalisensis* and not a separate species. **Reference:** Armentrout, J. M. 1973. Molluscan Paleontology and Biostratigraphy of the Lincoln Creek Formation Late Eocene-Oligocene Southwestern Washington. University of Washington, Dept. of Geology, Unpublished dissertation. **Figured:** Plate 5, figs. 108-111a

1976, Moore, E.J. Identifies *Bruclarkia columbiana* in the Pittsburg Bluff Fm. of Oregon. **Reference:** Moore, E.J. 1976. Oligocene Marine Mollusks from the Pittsburg Bluff Formation in Oregon. United States Government Printing Office, Washington. Geological Survey Professional Paper 922. **Figured:** Plate 5, figs. 112-117.

1976, Addicott, W.O. Identifies and figures *Bruclarkia oregonensis* (pl. 2, fig. 7) from the Newportian Molluscan Stage and both *B. oregonensis* and *B. acuminata* from the Juanian and Pillarian molluscan stages in Washington and Oregon. **Reference:** Addicott, W.O. 1976. Neogene molluscan stages of Oregon and Washington. Pp. 95-115 *in* Fritsche, A.E., Best, H.T., and W.W. Wornardt (eds) The Neogene Symposium, Annual Meeting Pacific Section SEPM, 160 pp. **Comment:** Figured specimen 7 on plate 2, p. 103 is the hypotype of Moore (1963) plate 3, fig. 2. **Figured:** Plate 5, figs. 118-119.

1980, Hickman, C. S. Identifies and figures *Bruclarkia vokesi* (pl. 7, figs. 8-12) and *Bruclarkia* n. sp. (pl. 7, fig. 13) from the Keasey Fm. of Oregon. **Reference:** Hickman, C.S. 1980. Paleogene Marine Gastropods of the Keasey Formation in Oregon. Paleontological Research Institution, Bulletins of American Paleontology 78(310), 112 pp. **Figured:** Plate 5, figs. 120-124.

1984, Moore, E.J. Lists the middle Tertiary molluscan stages and zones of the Pacific Northwest including *Bruclarkia blakeleyensis*, *B. seattlensis*, *B. thor*, *B. acuminata*, and *B. yaquinana.* **Reference:** Moore, E.J. 1984. Middle Tertiary molluscan zones of the Pacific Northwest. Journal of Paleontology 58(3): 718-737.

1985, Colbath, S.L. Identifies *Bruclarkia oregonensis* from the Astoria Fm. at Beverly Beach State Park, Oregon and hypothesizes that it could have been a eurytopic species that occurred in relatively low numbers. Colbath also mentions that *B. oregonensis* could be an extinct genus in the family Muricidae. **Reference:** Colbath, S.L. 1985. Gastropod predation and depositional environments of two molluscan communities from the Miocene Astoria Formation at Beverly Beach State Park, Oregon. Journal of Paleontology 59(4): 849-869. **Comment:** Colbath references Moore (1963) when hypothesizing that *B. oregonensis* could be an extinct genus in the family Muricidae, however, Moore (1963) classifies this species as a neptuneid, now considered a clade within the Buccinidae.

1994, Titova, L. V. Lists *Bruclarkia* as a putative member of the buccinid subfamily Siphonaliidae that originates in the late Oligocene and goes extinct by the early middle Miocene in Washington, Oregon, and California. **Reference:** Titova, L.V. 1994. Cenozoic history of Turritelloidea and Buccinoidea (Mollusca: Gastropoda) in the North Pacific. Palaeogeography, Palaeoclimatology, Palaeoecology 108: 319-334.

1994, Ludvigsen, R. and G. Beard. Figures and identifies whelks from the Sooke Fm. on Vancouver Island as *Levifusus acuminatum.* **Reference.** Ludvigsen, R. and G. Beard. 1994. West Coast Fossils: a Guide to the Ancient Life of Vancouver Island Whitecap Books, Vancouver, 193 pp. **Comment:** The fossils figured are identical to *Bruclarkia acuminatum* and are erroneously identified as the genus *Levifusus*. **Figured:** Plate 5, fig. 126-127.

1999, Orr, E. and W. Orr. Identify and figure *Bruclarkia* from the Miocene of Oregon (p. 153, 168). **Reference:** Orr, E.L. and W.N. Orr. 1999. Oregon Fossils. Kendall/Hunt Publishing: Iowa, 381 pp. **Comment:** The figured *Bruclarkia* on page 153 is *Muricidea paucivaricata* Gabb (pl. 14, fig. 1) from the Geological Survey of California, v. 2, by Gabb (1869). The figured *Bruclarkia* on page 168 of Orr and Orr (1999) also appears to be mis-identified. **Figured:** Plate 5, fig. 128.

2003, Johns, M., and T. Cockburn. Figure two *Bruclarkia acuminata* specimens from the Sooke Fm. on Vancouver Island. **Reference:** Johns, M., and T. Cockburn. 2003. Fossils and geology of the Cenozoic Carmanah Group, southwestern Vancouver Island. Poster presented at the Fifth British Columbia Paleontological Symposium, Malaspina University College, Nanaimo, B.C., May 2-5, 2003. **Figured:** Plate 5, fig. 129-130.

Figured Bruclarkia specimens not reproduced in plates 1-5

Bruclarkia barkeriana (Davies, 1935, p. 285, 286, fig. 422, a synthetograph)
Bruclarkia (Orr et al. 1992, p. 178). Specimen is most similar to *B. columbiana*.
Bruclarkia (Orr and Orr, 1999, p. 168). Specimen is has plateaus on the body whorl and penultimate whorl that are uncharacteristic of *Bruclarkia*.
Bruclarkia acuminata (Moore, 2000, p. 61)
Bruclarkia columbiana (Oleinik and Marincovich, 2003, p. 44, fig. 3.3, number 14). Specimen appears to be *B. vokesi*.
Bruclarkia columbiana (Addicott, 1972, pl. 1, fig. 12)
Bruclarkia oregonensis, B. cf. *B. oregonensis*, and *B. yaquinana* (Addicott, 1976a, pl. 2, figs. 1-9)

All proposed names for Bruclarkia taxa
Fusus oregonensis Conrad, 1848
Agasoma gravidum Gabb, 1869
Agasoma barkerianum Cooper, 1894
Agasoma santacruzana Arnold, 1908
Agasoma stanfordensis Arnold, 1908
Agasoma acuminatum Anderson & Martin, 1914
Agasoma barkerianum var. clarki English, 1914
Agasoma barkerianum var. santacruzanum English, 1914
Agasoma columbianum Anderson & Martin, 1914
Agasoma oregonense Anderson & Martin, 1914
Agasoma yaquinanum Anderson & Martin, 1914
Agasoma gravidum multinodosum Clark, 1918
Bruclarkia gravida (Gabb), (Trask in Stewart, 1926)
Agasoma andersoni Weidey, 1928
Bruclarkia oregonensis (Conrad) in Etherington, 1931
Bruclarkia thor Tegland, 1933
Bruclarkia blakeleyensis Durham, 1944
Bruclarkia fulleri Durham, 1944
Bruclarkia seattlensis Durham, 1944
Bruclarkia chehalisensis Armentrout, 1973 (unpublished dissertation)
Bruclarkia chehalisensis nodulosa Armentrout, 1973 (unpublished dissertation)
Bruclarkia vokesi Hickman, 1980
Bruclarkia ellenae Vendetti, 2009

Stratigraphic and geographic distribution

Bruclarkia acuminata, B. gravida, and *B. oregonensis* range from California to the Pacific Northwest and are the most geographically widespread species of the genus (Fig. 2). During the Oligocene and Miocene these taxa overlapped stratigraphically, with *B. acuminata* and *B. oregonensis* persisting from approximately 35-15 Ma and *B. gravida* spanning from 35-21 Ma. Molluscs of the Oligocene Zemorrian stage and Matlockian, Juanian, and Pillarian molluscan stages reached marked degrees of provincialism as faunas adapted to a cooler temperate marine environment (Tipton et al., 1973). Therefore, the occurrence of *Bruclarkia acuminata, B.*

gravida, and *B. oregonensis* taxa in Oligocene sediments from California to Washington during a period of provinciality requires explanation.

Stratigraphic data suggest that *B. gravida* migrated from the Pacific Northwest and reached Alaska by the early Oligocene (Oleinik and Marincovich, 2003). Without precise ages for some California stratigraphic sequences such as the San Ramon Fm., it is difficult to assess when *B. gravida* expanded into California. Fossil evidence suggests, however, that the extinction of this species near the Oligocene/Miocene boundary was coincident in California and the Pacific Northwest.

Bruclarkia barkeriana and *B. santacruzana* are California endemics found within the boundaries of the Oligocene-Miocene San Joaquin/Temblor basin of California (Nilsen, 1987). These species co-occur in many of the same localities, but stratigraphic data suggest that *B. santacruzana* (23-16.3 Ma) precedes as well as outlasts *B. barkeriana* (25?-15 Ma). It is curious that *B. barkeriana* and *B. santacruzana* do not occur outside of California because they were abundant during a period of decreased provinciality and increased migration of molluscs that happened during the Climate Optimum of early middle Miocene (Addicott, 1972). These taxa would be expected to have migrated north as temperatures warmed and more habitat was available and amenable to survival. It is possible that physical boundaries of the inland San Joaquin basin restricted the range of these taxa (Arnold, 1909).

Bruclarkia ellenae appears to be endemic to Oregon and Washington. Locality information suggests that it is restricted to the Astoria Formation and persists from 23-15? Ma or 23-20 Ma (see Vendetti, 2009b).

Systematic Descriptions

Shell shape in this genus is generally fusiform with species-specific patterns of node rows and spiral cords on the body whorl. Here, the examination of more than 700 *Bruclarkia* individuals suggests a suite of intraspecific characters including siphonal canal length and shape in *B. acuminata*, body whorl ornamentation (number of node rows) in *B. barkeriana*, *B. acuminata*, and *B. oregonensis,* and spire angle in *B. gravida.* The number of nodes per whorl was also found to be highly variable in *B. barkeriana* and *B. oregonensis.*

Characters that are informative in diagnosing *Bruclarkia* species and therefore are consistent within species include the ornamentation of the penultimate whorl, ornamentation of the sutural collar, and the extent of the parietal lip. Shell measurements of continuous characters are summarized in Table 2. As a result of character coding, seven valid *Bruclarkia* species and one unique morphotype were recognized (Table 3) out of all specimens scored (Table 4). These results were possible because a large number of specimens of each species were examined.

Taxonomic Reassignments

The list below summarizes the taxonomic reassignments of proposed *Bruclarkia* taxa that are provided in the synonymies of each taxon under “Systematic Paleontology”.

Previous Assignment	**Preferred Assignment**

Agasoma andersoni Weidey, 1928……….………………...invalid

Agasoma acuminatum Anderson & Martin, 1914
Agasoma oregonense Anderson & Martin, 1914
Agasoma yaquinanum Anderson & Martin, 1914
Bruclarkia blakeleyensis Durham, 1944
Bruclarkia seattlensis Durham, 1944………………………*Bruclarkia acuminata* (Anderson & Martin)

Agasoma barkerianum Cooper, 1894
Agasoma barkerianum var. clarki English, 1914………….*Bruclarkia barkeriana* (Cooper)

Bruclarkia ellenae Vendetti, 2009…………………………*Bruclarkia ellenae* Vendetti, 2009

Agasoma gravidum Gabb, 1869
Agasoma columbianum Anderson & Martin, 1914
Agasoma gravidum multinodosum Clark, 1918
Bruclarkia fulleri Durham, 1944
Bruclarkia chehalisensis Armentrout, 1973
Bruclarkia chehalisensis nodulosa Armentrout, 1973 ……..*Bruclarkia gravida* (Gabb)

Fusus oregonensis Conrad, 1848
Agasoma stanfordensis Arnold, 1908…….……………....*Bruclarkia oregonensis* (Conrad)

Agasoma barkerianum var. santacruzanum English, 1914
Agasoma santacruzana Arnold, 1908……………………...*Bruclarkia santacruzana* (Arnold)

Bruclarkia vokesi Hickman, 1980…………………………*Bruclarkia vokesi* Hickman

Abbreviations of Specimen Repositories
ANSP: Academy of Natural Sciences of Philadelphia
BMUW or UW: Burke Museum of Science and Culture, University of Washington, Seattle
CAS: California Academy of Sciences, San Francisco, Invertebrate Paleontology collection.
LSJU or **SU**: Leland Stanford Junior University (Stanford University). Collection housed and incorporated into the California Academy of Sciences Invertebrate Paleontology collection.
UCMP: University of California Museum of Paleontology, UC Berkeley.
UO: University of Oregon
USGS: Unites States Geological Survey. Some fossils integrated into the UCMP collection.
USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. Specimens on loan to UCMP.
UW: University of Washington. Selected lots are incorporated into the UCMP collection.

In the synonymies listed below, a question mark precedes a species name when its identification or affinity to the species being reviewed is doubtful.

SYSTEMATIC PALEONTOLOGY

Family BUCCINIDAE Rafinesque, 1815
Genus *Bruclarkia* Trask in Stewart, 1926
Type species: *Agasoma gravidum* Gabb, 1869
(By original description: *Clavella gravida* Gabb 1866, San Ramon Sandstone, CA)

Bruclarkia acuminata (Anderson and Martin, 1914)

Plate 6, figs. 1-4
(For synonymy, description, and further remarks see Vendetti, 2009b)

Occurrence and Age: California, Oregon, Washington and Vancouver Island, British Columbia, Canada from the late Eocene/early Oligocene to early middle Miocene, approximately 35-15 Ma.

Localities (in literature): Oregon and Washington: Scappoose, CAS 168 (Anderson and Martin, 1914); Astoria Fm., USNM 563138, 18284 (Moore, 1963); Blakeley Fm., A-3692, A-3710, A-3708, A-3707, A-1803, A-1804, A-1807 (Durham, 1944); UCMP 1310; Vancouver Island, British Columbia: Sooke Fm., USNM 240153, M4060 (Addicott, 1976); California, 1310 (Clark, 1918).

Material examined: 112 specimens. State, Formation: Collection Locality (number of specimens). Oregon and Washington, Blakeley Fm.: A3707 (1, hypotype 35390, Durham, 1944), A3708 (1), A3710 (1, hypotype 35391, Durham, 1944), A373/ UW 425 (3), A-6631 (1), no locality number (1); Scappoose: CAS 168 (3); Astoria Fm.: 3334 (1), 3330 (12), British Columbia (Vancouver Is.), Sooke Fm.: collection of author (23), CAS 69267 (16), CAS 69268 (24), CAS 69269 (17), 69263 (1); California, San Ramon Fm.: 1310 (1, hypotype 11239, Clark, 1918); San Emigdio Fm.: B-4573 (6). Localities are UMCP unless prefaced by a collection abbreviation.

Remarks: *Bruclarkia acuminata* is relatively rare in strata of the California Oligocene (e.g. San Ramon and San Emidgio Fms.) but abundant in coeval deposits in Oregon, Washington, and the Sooke Fm. of the southern coast of Vancouver Island.

Bruclarkia barkeriana (Cooper, 1894)

Plate 6, figs. 5-8

Un-named, Conrad, Pacific Railroad Reports v. 5, pl. 7, figs. 63, 68, 1856.
?*Natica geniculata* Conrad, Pacific Railroad Reports v. 5, pl. 7, figs. 67, 1856, [nomen dubium].
Agasoma barkerianum Cooper, Calif. Min. Bureau 4, p. 53, 65 pl. 5., fig. 63, 1894 (not fig. 52 or subgenus *Trophosycon* as listed on pg. 64);
    Anderson, Proc. Cal. Acad. Sci., v. 3, (table), 1911;
    Smith, Proc. Cal. Acad. Sci., v. 3, p. 165, 174, 1912;
    English, Univ. Calif. Pubs. Geo., p. 252, pl. 25, figs. 3, 13, 14, 1914;
    Anderson and Martin, Proc. Cal. Acad. Sci., v. 4, p. 42, 1914;
    Clark, Univ. Calif. Pubs. Geo. Sci., v. 11, p. 82 [*A. barkernianum* (sic)], pl. 19, figs. 1, 3 , 5, 1918;

Clark, Journal Geol. Sci., v. 29, table, 1921;
Howe, The Pan-Am. Geol., v. 45, p. 304, 1926;
Trask, Univ. Calif. Pubs. Geo. Sci., v. 16(6), p. 151, 1926;
Wiedey, Trans. San Diego Soc. Nat. His., v. 5(10), p. 112, 1928;
Davies, Tertiary Faunas v. 1, p. 286, 287, fig. 422 (a synthetograph), 1935.
Agasoma gravidum Gabb, Anderson, Proc. Cal. Acad. Sci., v. 3, p. 100, 1911.
Agasoma barkerianum Cooper *clarki* English, Univ. Calif. Pubs. Geo., p. 253 pl. 25, figs. 9, 10, 1914;
Wiedey, Trans. San Diego Soc. Nat. History, v. 5(10), p. 112, 1928.
Bruclarkia barkeriana (Cooper), Clark, (self-published) Strat. and Faunal Horiz. Coast Range Cal., pl. 18, figs. 1, 2, 1929;
Loel and Corey, Univ. Calif. Pubs. Geo. Sci., v. 22(3), p. 148, 1932;
Lutz, Univ. Calif. Pubs. Geo. Sci., v. 28, p. 378, 380, 1951;
Addicott, USGS Prof. Paper 642, p. 26, 28, 29, 31, 88, pl. 9, figs. 13?, 23-25, 27, 28, pl. 10, figs. 3, 5, 7, 10, 1970;
Hall, GSA Special Paper 357, p. 24, 83, 376, 2002;
[not] Hall, GSA Special Paper 357, p. 376, 2002 [Here Hall equates *Agasoma gravidum* Gabb with *Bruclarkia barkeriana* (Cooper)].
Bruclarkia geniculata (Conrad), Keen, Trans. San Diego Soc. Nat. History v. 10(2), p.36, 1943.
Bruclarkia ("*Agasoma*") *barkeriana*, Kleinpell and Weaver, Univ. Calif. Pubs. Geo. Sci., v. 43, p.12, 113, 21, fig. 5 (a correlation chart), 1963.

Diagnosis: Sutural collar prominent, noded, and sinuous with an overlap of the lower penultimate whorl; parietal lip thickened and extensive covering ≥ ¾ of the body whorl in apertural view; penultimate whorl smooth and adpressed; posterior whorls globose; body whorl with one to five rows of 6-12 horizontally elongated "dashed" nodes that can be developed into cords.

Description: The shell is fusiform with an inflated body whorl and a convex shoulder. There are 5-6 whorls including the protoconch. The parietal lip is thickened and extends across more than ¾ of the body whorl in ventral (apertural) view. It often covers and obscures node rows on the body whorl. Average shell width of adult specimens is 29 cm and average spire height is 10.1 cm. Axial growth lines are prominent especially toward the aperture where they can be pronounced and connect to the sutural collar in folds that stand out in relief. The sutural collar is prominent, thickened, and often noded. It overlaps onto the lower penultimate whorl and is often interrupted by sinuous growth lines. The penultimate whorl is straight or convex, generally adpressed, and either lacks node rows or has one row of small, closely spaced nodes near the sutural collar. Apical whorls are globose and have minor spiral cords or cancellate ornamentation. A noded and/or sinuous sutural collar can exist between the penultimate whorl and apical whorls in large specimens. Node rows are not present on the penultimate whorl. The body whorl is ornamented by thin spiral cords of equal thickness and 1-5 rows of 6-12 horizontally elongated nodes that vary from raised dashes to thickened cords. Of these rows, the first (posterior) is the most prominent. The siphonal canal is recurved and the protoconch is small and paucispiral.

Similarity to other species: *Bruclarkia barkeriana* shares most of its shell characters with *B. santacruzana*. These similarities include the morphology of the shell in profile, body whorl, spire, shoulder, sutural collar, and parietal lip. The extensive parietal lip is common only to *B. barkeriana* and *B. santacruzana.* Body whorl ornamentation is the only pronounced difference between these taxa and is present as node rows in *B. barkeriana* but absent in B. *santacruzana*. A sinuous and thickened sutural collar found in *B. barkeriana* and *B. santacruzana* that overlaps onto the penultimate whorl also occurs in the California Miocene taxon *Agasoma sinuatum* (Conrad), the type species of *Agasoma*.

Type: Original type lost. Lectotype designated by Addicott (1970) as CAS 2860, locality CAS 64, Olcese Sand, California, figured by English, pl. 25, figs. 13, 14, 1914.

Type Dimensions: Lectotype height: 55 mm, maximum diameter: 32 mm.

Etymology: The species was named by Cooper (1894) after fossiliferous strata at John Barker's Ranch in Kern County, California, where it is abundant. The so-called "Barker's Ranch fauna" is considered typical of lower Miocene Temblor strata in California (Addicott, 1972).

Occurrence and Age: California from the early to middle Miocene, approximately 23-16.3 Ma.

Localities (in literature): California: Temblor (San Juan and Kern districts), Kern River Formation: Barker's Ranch, Kern County, San Luis Co., Raymond Hills, LA Co.; "Ocoya Creek Beds/Poso Creek beds", Temblor of Coalinga; "Vaqueros" with *Turritella ocoyana*; Sobrante Sandstone, "Sobrante" Formation (Lutz, 1951); Jewett Sand; Lower part of Olcese Sand; Round Mountain Silt; "Vaqueros" of San Juan and Santa Cruz regions; Temblor horizon (Loel and Corey, 1932).

Material examined: 149 specimens. State, Formation: Collection Locality (number of specimens). California, Olcese Sand: B-1587 (2), B-1593 (17), B-1595 (5), B-1597 (7), B-1598 (1, Addicott hypotype pl. 9, figs. 25, 1970), B-1599 (11), B-1600 (6), B-1601 (16), B-1622 (28), B-1623 (6), B-1641 (6), B-1642 (2), B-1642 (1, Addicott hypotype pl. 10, figs. 3, 7, 1970), Temblor: 1352 (2, English holotype pl. 25, fig. 9 and paratype pl. 25, fig. 10, 1914), A-506 (10), D-8808 (6), 2298 (3), 3688 (6), 3890 (1), Topanga Formation: B-7853 (3); unknown locality: California Geological Survey Collection (3). Localities are UMCP unless prefaced by a collection abbreviation.

Remarks: *Bruclarkia barkeriana* is so common in marine Miocene sedimentary rocks of the Kern River area that it defines the *Agasoma zone* of Merriam (Arnold, 1908; Hall and Grinnell, 1919), which is also known as the "*Bruclarkia ('Agasoma') barkeriana* fauna of Kleinpell and Weaver (1963). Hall (2002) like many authors, considered *B. santacruzana* as a subspecies of *B. barkeriana* and assigned them to stratigraphic ranges of 27-17 and 27-13, respectively. However, according to Addicott (1970), *B. santacruzana* occurs earlier in the fossil record than *B. barkeriana*.

Bruclarkia ellenae Vendetti, 2009

Plate 6, figs. 9-12

(For synonymy, description, etymology, and further remarks see Vendetti, 2009b)

Occurrence and Age: Astoria Formation, Washington and Oregon, early Miocene from 23-15?, or restricted to 23-20 Ma.

Localities (in literature): All Astoria Formation localities: UCMP 31994 (1), UCMP D-294 (5); CAS 69261/SU NP 45131 (17), CAS 69266/SU NP 45173 (3); UW 515 (12).

Material examined: 38 specimens. See above.

Remarks: This species occurs in the Astoria Fm. in Washington and Oregon and possibly is restricted to the lowest sections of the formation.

Bruclarkia gravida (Gabb, 1866)

Plate 7. 13-19

Clavella gravida Gabb, Palae. Calif. Cret. and Tert. Fossils, v. 2, pl. 1, fig. 6, 1866.
Agasoma gravida Gabb, Palae. Calif. Cret. and Tert. Fossils, v. 3, p. 46, 1869;
  {Note: the following authors use the species name *gravida* or *gravidum*}
  Tryon, Man. Couch., v. 3. 1881, p. 105, pl. 31, fig. 75, 1881;
  Anderson, Proc. Cal. Acad. Sci., v. 3, p. 101 [Gabb misspelled as "Garb"], 1911;
  Smith, Proc. Cal. Acad. Sci., v. 3, p. 165, 175, 1912;
  English, Univ. Calif. Pubs. Geo. Sci., v. 8, p. 245, 251, pl. 25, figs 7, 8, 1914;
  Clark, Univ. Calif. Pubs. Geo. Sci., v. 11, p. 73, 76, 79, 80, 81, 82, 91, 95, 97, 101, 107, 182, 183, 224, pl. 19, figs. 3, 5, pl.22, fig. 19?, 1918;
  Schenck, Univ. Calif. Dissertation (unpublished), p. 66, 98, 108, 1927;
  Opinion 121, Smithsonian Misc. Coll. v. 73(7), p. 31, 32, 1931.
Agasoma columbianum Anderson and Martin, Proc. Cal. Acad. Sci., v. 4, p. 73, pl, 5, figs. 6a, 6b, 1914;
  Schenck, Univ. Calif. Dissertation (unpublished), p. 55, 129, 1927.
Agasoma gravidum multinodosum Clark, Univ. Calif. Pubs. Geo. Sci., v. 11, p. 97, 183, 232, pl. 22, fig. 5, 1918 (An interesting variety, but only one specimen was identified thus it is probably not of taxonomic importance (Stewart, 1926)).
Bruclarkia gravida (Gabb), Stewart, Proc. Nat. Sci. Phil., v. 78, p. 308, 397, 398, pl. 31, figs. 10, 11, 1926;
  Clark, (self-published) Strat. and Faunal Horiz. Coast Range Cal., p. 17, 1929;
  Hertlein, Cal. Div. Mines, Bull. 154, p. 189, 190, 191, fig. 2, No. 6, 1951;
  Tipton, Kleinpell, and Weaver, Univ. Calif. Pubs. Geo. Sci., v. 105, fig. 5 (stratigraphic correlation table), 1973.
Bruclarkia gravida columbiana Anderson and Martin, Clark, (self-published) Strat. and Faunal Horiz. Coast Range Cal., p. 18, pl. 18, figs. 17, 18, 1929.
Bruclarkia columbiana (Anderson and Martin), Schenck and Kleinpell, Bull. AAPG, v. 20(2), p. 221, 1936;
  Weaver, Univ. Wash. Pub. Geology, v. 5, p. 443, pl. 87, fig. 7, 8, 1942;
  Durham, Univ. Calif. Pubs. Geo. Sci., v. 27, p. 116, 120, 121, 1944;
  Schenck and Keen, Calif. Fossils for the Field Geol., p. 37, fig. 5, 1950;

Hickman, Bulletin 16, Mus. Nat. His., Univ. Ore., p. 13, 92, 94, pl. 13, figs. 12, 13, 1969;
Addicott, Pac. Coast Mio. Biostrat. Sym. SEPM, p. 5, 6, pl. 1, fig. 12, 1972;
Armentrout, Univ. Calif. Dissertation (unpublished), p. 165, 278, 279, pl. 4, fig. 15, 1973;
Tipton, Kleinpell, and Weaver, Univ. Calif. Pubs. Geo. Sci., v. 105, p. 27, 28, 1973;
Moore, USGS Prof. Paper 922, p. 1, 2, 5, 9, 11, 14, 15, 21, 23, 24, 26, 28, 34, pl. 3, figs. 1-5, 21-23, 1976;
Squires, From Greenhouse to Icehouse, Ch. 2, pgs. 19, 23, 25, 27, 29, 2003.

Bruclarkia fulleri Durham, Univ. Calif. Pubs. Geo. Sci., v. 27, p. 173, pl. 16, fig. 11 (UCMP 35396), 14 (UCMP 35395), 1944.

Brucklarkia (sic) ("*Agasoma*") *gravida*, Kleinpell and Weaver, Univ. Calif. Pubs. Geo. Sci., v. 43, fig. 8 (a stratigraphic column), 1963.

Bruclarkia ("*Agasoma*") *gravida*, Kleinpell and Weaver, Univ. Calif. Pubs. Geo. Sci., v. 43, p. 38, 113, 1963.

Bruclarkia n. sp.? Hickman, Bull. Of Am. Paleo., v. 78(310), p. 96, pl. 7, fig. 13, 1980 [very subtly noded variant of *B. gravida*].

Bruclarkia chehalisensis nodulosa Armentrout, Univ. Wash. Dissertation (unpublished), p. 154, 277, 278, pl. 4, fig. 27, 28, 1973.

?*Bruclarkia chehalisensis* Armentrout, Univ. Wash. Dissertation (unpublished), p. 154, 276, 277, pl. 4, fig. 22, 1973.

Diagnosis: Shell ornamented by 2-3 rows of 13-18 evenly spaced nodes; when three node rows are present, the two anterior rows are closer to each other than to the most posterior row; spire adpressed often (but not always) at a nearly 80° angle; parietal lip extends no more than ¼ of the body whorl in apertural view; penultimate whorl has one row of evenly spaced nodes bordered or partially covered by the sutural collar; sutural collar is unornamented and thickened; axial growth lines often sinuous and noticeable; siphonal canal recurved.

Description: The shell has an inflated body whorl and fusiform shape with a straight or concave shoulder. The parietal lip is often thickened and extends across ¼ (or less) of the body whorl in apertural view. Axial growth lines are sinuous and noticeable in most specimens especially between the sutural collar and the first node row on the body whorl. Spiral cords of equal thickness characterize the body whorl between node rows particularly toward the anterior of the body whorl and siphonal canal, in well-preserved specimens. The shell has 2-3 rows of 13-18 evenly spaced rounded nodes on the middle to anterior body whorl. If three node rows are present, the two most anterior rows are spaced close to each other with a gap separating them from the most posterior row. Nodes are spinose or rounded in well preserved specimens, and erode to rounded protrusions in worn specimens. The spire is adpressed and the lower penultimate whorl has one row of evenly spaced nodes that is bordered or partially covered by the sutural collar. The height of the spire is highly variable, though in most specimens it is relatively low at approximately ¼ of the length of the shell and often at an angle between 65°-80°. The sutural collar is unornamented but thickened in most species such that it is noticeable in shell profile. The protoconch is poorly preserved in most specimens and is paucispiral. The siphonal canal is recurved and varies greatly from approximately 8-18% of total shell length.

Similarity to other species: See the description of similarity between *Bruclarkia vokesi* and this species.

Types: The lectotype was chosen by Stewart (1926) as ANSP 4345 from the San Ramon Sandstone, California, pl. 31, fig. 10. Stewart (1926) considers this specimen to be the one used predominantly by Gabb (1869) to make a synthetograph of *Agasoma gravida*. A better preserved specimen is figured as 4345a, pl. 31, fig. 11. The *Agasoma columbianum* types of Anderson and Martin (1914) are CAS specimens 155 (holotype) and 156 (co-type/paratype) from the Pittsburg Buff Fm, Oregon, (pl. 5, figs. 6a and 6b).

Type Dimensions: Lectotype height (incomplete): 32 mm, maximum diameter: 21 mm. Specimen 4545a of Stewart (1926), height (incomplete): 42 mm, max. diameter: 29 mm. Anderson and Martin holotype of *Agasoma columbiana*: CAS 155, height: 56 mm, max. diameter: 40 mm.

Etymology: The origin of *gravida* as a species name is not stated by Gabb (1866) but may refer to the stout and inflated appearance of the body whorl.

Occurrence and Age: Southern California through Oregon, Washington, and into Alaska from the late Eocene (Lincoln Creek Fm. and Quimper Sandstone) to the latest Oligocene or earliest Miocene (San Ramon Sandstone and Kirker Tuff), approximately 35-21 Ma.

Localities (in literature): Oregon and Washington: UO 12, 28, 46, 47, 27415, 27416, Washington: Quimper Sandstone, Marrowstone Shale; USGS 2415, 2714, 2715, 2721, 5394, 15264, 15264a, 15310, 15310a-c, e, f, j, 15312, 15316, 15499, 15532, 15586, 15588, 18638, M3858, M3871, M3872, M3877, M3878 (Moore, 1976), Toledo Formation, Lincoln Creek Formation, Pittsburg Bluff Formation, Tunnel Point Sandstone, ; California: Ocoya Creek, Pleito Formation (UCMP 3203, 3206, 3216, 3220), San Ramon Sandstone, Temblor Formation; Alaska: Split Creek Sandstone and Basin Creek Members of the Poul Creek Formation (Oleinik and Marincovich, 2003), Standard Oil localities: 443, 444, 448.

Material examined: 352 specimens. State, Formation: Collection Locality (number of specimens). California, San Ramon Sandstone: 14 (4) (5, hypotypes 11239, 11245, 11247, 11283, 11266, Clark, 1918), 1131 (1), 1203 (1, hypotype 11908, English, 1914), A-4661 (1, hypotype 32426, Hertlein, 1951), D-118 (19); Kirker Tuff: A-4660 (3); Pleito Formation: 3199 (1), 3200 (4), 3207 (1); Oregon, unidentified locality near Clatskanie: CAS 69270 (7), CAS 69271 (22); Tunnel Point Sandstone: A-1607 (99), A-1682 (1), B-7660 (3); Butte Creek Volcanic Sandstone or Scotts Mills Formation (Marion Co., Mollalla Qd., Scotts Mills Quadrangle, not Astoria Formation as identified by specimen labels and UCMP online database): A-4011 (2), A-3852 (10), A-3877 (17), A-3878 (3); USGS 21347 (10); "Clatskanie beds": D-8281 (55), D-9045 (4); Pittsburg Bluff Formation: USGS 15264 (22), A-194 (5), A-1599 (8), A-1601 (6), A-3669 (8), A-3782 (1), B-4288 (3), 3636 (2), 7053 (1), 10001 (2), unidentified locality number (3); Lincoln Creek Formation: A-9 (1, hypotype pl. 87, fig. 8, mislabeled, Weaver, 1942), A-20 (4), A-364 (1, hypotype 14492, Armentrout ,1973, unpublished dissertation); Washington: Quimper Sandstone: A-10 (2, hypotypes *B. fulleri*, paratype 35396, holotype 35395, Durham, 1944), A-1802 (3), A-3702 (1, Durham hypotype, un-figured); Schenck locality: NP 9 (2); Pittsburg Bluff Formation: without locality number (Anderson and

Martin holotype pl. 5, fig. 6a and paratype pl. 5, 6b), 69273 (3), 69259 (5). Localities are UMCP unless prefaced by a collection abbreviation.

Remarks: This review synonymizes *B. columbiana* with *B. gravida* and therefore renames the *Agasoma columbianum* type material of Anderson and Martin (1914) and the hypotypes from Weaver (1944), Hickman (1969), and Moore (1976). It appears that Anderson and Martin (1914) described *Agasoma columbiana* from the Pittsburg Bluff Formation in Oregon without recognizing that virtually the same morphology had already been described by in California by Gabb as *Agasoma gravida*. Neither Hickman (1969) nor Moore (1976) included *Agasoma* or *Bruclarkia gravida* within their treatments of *Bruclarkia columbiana* in monographs of the Oregon Eugene and Pittsburg Bluff formations, respectively. Likewise, Hall (2002) overlooked *B. gravida* in his extensive review of the Paleogene and Neogene molluscan faunas of California.

The description of *A. columbianum* by Anderson and Martin (1914) includes five of the shell features also described by Gabb (1866) for *A. gravida*. These characteristics are: five shell whorls, three node rows, a shell surface ornamented with revolving threads, an incrusted inner lip (= parietal lip), and a curved or twisted siphonal canal. *Agasoma gravida,* as depicted in the synthetograph by Gabb and lectotype figured in Stewart (1926), can be matched to specimens identified as *B. columbiana* from the Keasey, Pittsburg Bluff, and Tunnel Point Sandstone formations in Oregon, the Quimper Sanstone, Lincoln Creek, and Skookumchuck Fm. in Washington, and the Kirker Tuff, San Ramon Sandstone, and Pleito Fm. in California.

Uniting *B. columbiana* with *B. gravida* extends the stratigraphic range of the species and has considerable implications for understanding its paleobiogeography. First, it is evident from the examination of fossils, collection localities, and geologic ages, that *B. gravida* originated in the Pacific Northwest and spread south into California and north into Alaska during the Oligocene and Miocene. In California, it was commonly named *B. gravida*, whereas in Oregon, Washington, and Alaska it was more often refered to as *B. columbiana*. For example, Kleinpell and Weaver (1963) discuss the well-known *Bruclarkia ("Agasoma") gravida* zone of the early Oligocene and lower Zemorrian stage in California. They describe it as coeval with the Poule Creek beds in Alaska, which yield *Bruclarkia columbiana* fossils, but do not mention the similarities between these taxa (Kleinpell and Weaver, 1963; Oleinik and Marincovich, 2003).

Second, the extended stratigraphic range of *B. gravida* spans the Refugian, Zemorrian, and Saucesian benthic foram stages. Anderson and Martin (1914) and Schenck and Kleinpell, 1936 considered that in Oregon the uppermost Refugian marked the last appearance *B. columbiana*. However, in 1972, Addicott reported a range extension of *B. columbiana* into the Zemorrian. He identified *B. columbiana* from the California Cymric Shale (= "Salt Creek Shale," the oldest member of the lower Temblor Shale), which is Zemorrian in age at 33-32 Ma (Prothero and Resseguie, 2001). In an alternative explanation, Tipton et al. (1973) suggest that the *B. columbiana* fossils identified by Addicott (1972) could have been collected from the lowest beds of the "Salt Creek Shale", which correspond to the Refugian stage. Although they object to the range extension reported by Addicott (1972), Tipton et al. (1973) nonetheless emphasize that range extensions of Tertiary molluscan species in California should be expected as "the rule rather than the exception in biostratigraphy".

It is appropriate that these authors, (Tipton et al., 1973 and Kleinpell and Weaver, 1963), report *B. gravida* from the California Pleito Fm., which they correlate to the lower Zemorrian. Because *B. columbiana* is the same species as *B. gravida*, a range extension of this taxon into the Zemorrian is credible. The species also extends into the younger Saucesian stage based on reports of *B. gravida* from the Kirker Tuffs and San Ramon Fm. in California. It should be noted, however, that stratigraphers disagree on the age of the San Ramon Sandstone and Kirker Tuff as either Oligocene or Miocene in age based on microfossils and molluscs (Graymer et al., 2002). Here, these formations are considered to span the latest Oligocene to earliest Miocene following the estimations of Graymer (2000) and Collins et al. (1996).

Although the majority of paleontologists who have treated *B. gravida* or *B. columbiana* restricted them to California or the Pacific Northwest, respectively, some authors identified these species as spanning both regions. Most found *B. columbiana* in California rather than reporting *B. gravida* in the Pacific Northwest. For example, Schenck and Keen (1950) figured *B. columbiana* from the California San Emidgio Formation and Addicott (1972; 1976), Weaver (1944), and Tipton et al. (1973) all reported *B. columbiana* from various localities in California. Of the authors who treated this genus, only Clark (1918) and Schenck (1926) reported *A. gravida* from Oregon, in the Nye Shale, Eugene, Pittsburg Bluff, and Tunnel Point formations. Clark (1918) also explicitly discussed the similarity between *B. gravida* and *B. columbiana* and gave priority to *A. gravidum*, considering the former a subspecies of the latter (Clark, 1918). He reiterated this interpretation in 1929 but in one case reversed the names creating *Bruclarkia columbiana gravida* (Clark, 1929).

Size differences among *Bruclarkia gravida* individuals may be one reason for the designation of *B. gravida* and *B. oregonensis* as separate taxa. Gabb (1866) described *Agasoma gravida* as "short" whereas Anderson and Martin (1914) and Moore (1976) referred to *Agasoma* (or *Bruclarkia) columbiana* as large for the genus. The size range in maximum length is striking, with juveniles at under 15 mm, mature specimens from California (e.g. figured by Stewart, 1926) measuring nearly 40 mm in length, and some individuals from Oregon localities reaching 65 mm. Size tends to decrease in this species through the Tertiary, with Paleogene (Eocene/early Oligocene) *B. gravida* specimens from the Pacific Northwest (described as *B. columbiana*) measuring larger than *B. gravida* individuals from the Neogene. For example, *B. gravida* specimens of 55 mm or greater in shell height occur in the Scotts Mills Quadrangle and Pittsburg Bluff Fm. of Oregon, whereas specimens at approximately 35 mm in height are common to the "*Bruclarkia (Agasoma) gravida* zone" of California.

The preservation of *B. gravida* fossils varies greatly. Several localities within the "Clatskanie beds" in Oregon yield *B. gravida* individuals with loosely cemented matrix, intact siphonal canals, and excellent preservation. At the Butte Creek Beds of the Scotts Mills Quadrangle large *B. gravida* fossils are preserved as taphonomically altered steinkerns that are flattened along multiple axes (pl. 7, figs. 17-19). Despite this distortion, most of these individuals can be identified to species because of intact body whorl node rows and spire morphology.

Bruclarkia oregonensis (Conrad, 1848)

Plate 7. 20-23

(For synonymy, description, and further remarks see Vendetti, 2009b)

Occurrence and Age: California, Oregon, and Washington, from the early Oligocene to the early middle Miocene, approximately ?34-15.1 Ma (fig. 2).

Localities (in literature): California: Temblor Fm., Monterey Shale, Oursan Sandstone of Monterey Group? (Moore, 1963), Sobrante Sandstone of Monterey Group, "Temblor" Formation (Vallecitos area) (Schenck and Keen, 1950), Buttonbed Shale and Gould Shale of Temblor Formation, Olcese Sand; Oregon and Washington: Clallam Fm., USNM 215950, M4678; Lincoln Creek Fm?; Astoria Fm., Hoh Formation.

Material examined: 73 specimens. State, Formation: Collection Locality (number of specimens). California: Carquinez Qd.,?San Pablo Grp. (2); Pleito Fm.: 3203 (1); Oursan Sandstone: A-4564 (5); Hambre Sandstone of Monterey Group: A-4149 (3); Sobrante Sandstone of Monterey Group: A4565 (1), 516 (20); Washington: UCMP, Blakeley: A-373 (2), Clallam Fm.: A3692 (1), A3692 (1), A3692 (1), Scappoose Fm.: CAS 168, CAS 39; Oregon and Washington: Astoria Fm.: 10005 (2), 3330 (1), D-3225 (4), A-374 (3), 3330 (10), 3690 (2), 9069 (1), CAS 69260 (1), CAS 69264 (5), CAS 69265 (5), UW 54 (2). Localities are UMCP unless prefaced by a collection abbreviation.

Remarks: *Bruclarkia oregonensis* was first described as *Fusus oregonensis* by Conrad (1848) from the Astoria sediments in Oregon. *Fusus oregonensis* and *Agasoma oregonense* represent different morphotypes and separate species and therefore should not be synonymized.

Bruclarkia santacruzana (Arnold, 1908)
Plate 8. 24-27

Agasoma santacruzana Arnold, Proc. Nat. Mus., v. 34, p. 350, 379, 380, pl. 34, fig. 7, 1908;
    Arnold, U.S. Geol. Survey Bull. 398, p. 18, pl. 8, fig. 5, 1909;
    Branner, Newson, and Arnold, USGS Santa Cruz Folio, pg. 163, fig. 44, 1909;
    Arnold and Anderson, U.S. Geol. Survey Bull. 398, p. 85, 86
Agasoma sanctacruzana (sic), 87, 294, pl. 30, fig. 5, 1910;
    Smith, Proc. Cal. Acad. Sci., v. 3, p. 166, 1912.
Agasoma sanctacruzanum (sic) Arnold, Anderson and Martin, Proc. Cal. Acad. Sci., v. 4, p. 42, 1914.
Agasoma barkerianum Cooper, var. *santacruzanum* Arnold, English, Univ. Calif. Pubs. Geo., p. 252, pl. 25, figs. 11, 12, 1914.
Bruclarkia barkerianum (Cooper) *santacruzanum* (Arnold), Loel and Corey, Univ. Calif. Pubs. Geo. Sci., v. 22(3), p. 110, 124, 130, 148, 171, 250, 376, pl. 48, figs. 10, 11, 12, 1932.
Bruclarkia barkeriana forma *santacruzana* (Arnold) Addicott, USGS Prof. Paper 642, p. 89, 28, 37, pl. 10, figs. 1, 2, 5, 9, 1970.

Diagnosis: Sutural collar prominent, noded, and sinuous with an overlap of the penultimate whorl; parietal lip thickened and extensive covering ≥ ¾ of the body whorl in apertural view; penultimate whorl smooth and adpressed; posterior whorls globose; body whorl generally smooth, ornamented by fine spiral cords and axial growth lines.

Description: The shell has an inflated body whorl and is fusiform with a convex shoulder. The parietal lip is thickened and extends across more than ¾ of the body whorl in ventral (apertural) view. It often covers and obscures node rows on the body whorl. There are 5-6 whorls including the protoconch. Average shell width in adult specimens is 27.6 cm and average spire height is 8.2 cm. Axial growth lines are prominent especially toward the aperture where they can become pronounced and connect to the sutural collar in folds that stand out in relief. The sutural collar is prominent, thickened, and often noded. It connects to the lower penultimate whorl and is often interrupted with sinuous growth lines. The penultimate whorl is straight or convex, generally adpressed and lacks node rows. Apical whorls posterior to the penultimate whorl (toward the apex) are globose and has minor spiral cords and sometimes cancellate ornamentation. The noded and/or sinuous ornamentation of the sutural collar is sometimes found between the penultimate whorl and nuclear whorls in large specimens. Node row ornamentation is not found on the penultimate whorl or body whorls. The siphonal canal is recurved, never straight. The protoconch is small and paucispiral.

Similarity to other species: See the description of similarity between *Bruclarkia barkeriana* and this species.

Type: LSJU 5369, Locality SU C301, one mile north-northeast of the north end of Searsville lake, San Mateo Co., CA.

Type Dimensions: Holotype height: 26 mm, maximum diameter: 16 mm.

Etymology: Arnold (1908) described this species from the Santa Cruz quadrangle.

Occurrence and Age: California from the lower to middle Miocene, approximately 25?-15 Ma (fig. 2).

Localities (in literature): California: Vaqueros sandstone and "Vaqueros": San Joanquin Hills, San Luis Obispo Co., Monterey Co., Santa Cruz region, San Emigdio district, Kern River zone, Fresno Co.; Monterey-Temblor.

Material examined: 29 specimens. State, Formation: Collection Locality (number of specimens). California, Olcese Sand: B-1616 (3), B-1587 (7), B-1598 (1, Addicott hypotype pl. 10, fig. 12, 1970), (6), B-1657 (1), B-1660 (4), Vaqueros: A-336 (1, Loel and Corey hypotype pl. 48, fig. 12, 1932), A-585 (1, Loel and Corey hypotypes pl. 48, fig. 10, 11, 1932), Temblor: 2713 (1), Kern Co.: 1455 (1), unknown locality: California Geological Survey Collection (3). Localities are UMCP unless prefaced by a collection abbreviation.

Remarks: This species occurs with *B. barkeriana* throughout much of its range (Addicott, 1970) and spans the Saucesian, Relizian, and part of the Luisian foram stages. It could be an un-noded form of *B. barkeriana* and not a distinct species, however, it appears prior to *B. barkeriana* in the lower Miocene and extends into younger strata than *B. barkeriana*. If this stratigraphic occurrence reflects phylogeny, then *B. santacruzana* could be an ancestral to *B. barkeriana* and therefore should not be named as a form or subspecies of *B. barkeriana*.

Bruclarkia vokesi

Plate 8. 28-31

Bruclarkia n. sp. Vokes, U.S. Geol. Survey. Oil and Gas Invest. Prelim Map 42, (checklist), 1945.

Bruclarkia vokesi Hickman, Mus. Nat. Hist. Univ. Oregon Bull. 16, p. 18, 91, 94, pl. 13, figs. 6-11, 1969;

Hickman, Bull. Of Am. Paleo., v. 78(310), p. 10a (figure), 11, 57, 58, pl. 7, figs. 8-12, 1980.

Diagnosis: Shell ornamented by 3 rows of 15-18 evenly spaced nodes; when three node rows are present, the two anterior rows are closer to each other than to the most posterior row; spire adpressed; parietal lip extends no more than ¼ of the body whorl in apertural view; penultimate whorl has one row of evenly spaced nodes bordered by the sutural collar; sutural collar is unornamented and thickened; axial growth lines often sinuous and noticeable; siphonal canal recurved.

Description: The shell is fusiform with a concave shoulder. The parietal lip is very thinly callused and extends up to ¼ of the body whorl in ventral (apertural) view. There are 5-6 whorls including the protoconch. Spiral cords of equal thickness characterize the body whorl between node rows particularly toward the anterior body whorl and siphonal canal, in well-preserved specimens. Axial growth lines are sinuous and prominent especially toward the aperture and between the sutural collar and the first row of nodes on the body whorl. The sutural collar is thickened but un-ornamented and is noticeable in shell profile. The body whorl has three rows of 15-18 evenly spaced spinose nodes on the middle to anterior body whorl. The two most anterior rows are spaced close to each other with a gap separating them from the most posterior row. The spire is adpressed and the lower penultimate whorl has one row of evenly spaced nodes that borders the sutural collar. The siphonal canal is recurved and the protoconch is small and paucispiral.

Similarity to other species: *Bruclarkia vokesi* is most similar to *B. gravida* as noted by Hickman (1969; 1980) in her comparison of the taxon to *B. columbiana*. They share the prominence and thickness of spiral cords, visibility of axial growth lines, extent of the parietal lip, spire ornamentation, thickening of the sutural collar, and node ornamentation of the penultimate whorl. Morphological differences between these taxa are more subtle than between other *Bruclarkia* species. In general, the *B. vokesi* spire has a more acute angle than in *B. gravida*, though not all. The morphology of the shoulder, which is generally straight in *B. gravida*, is always concave in *B. vokesi*. There are two or three node rows on the body whorl in *B. gravida*, but always three in *B. vokesi*, which also averages more nodes per row than *B. gravida*.

Type: Holotype is UO 27400 (pl. 13, fig. 6) and paratypes are UO 27401, 27402, 27403 (pl. 13, figs, 7-11), designated by Hickman (1969).

Type Dimensions: Holotype height (incomplete): 40.5 mm, maximum diameter 24 mm. Paratype 27401, height (incomplete): 32 mm, max. diameter: 22 mm. Paratype 27402, height (incomplete): 36 mm, max. diameter 24.5 mm. Paratype 27403, height (incomplete): 30 mm, max. diameter: 21.5 mm.

Etymology: The species was named by Hickman (1969) after the late Dr. Harold E. Vokes, a paleontologist and geologist whose work focused on fossil and recent molluscs of the North American east and west coasts.

Occurrence and Age: Oregon from the late Eocene (lower Keasey Formation) to the early Oligocene (Eugene Fm.), approximately 36-29 Ma (fig. 2).

Localities (in literature): Locality, Formation. Oregon, Eugene Fm.: 3, 5, 9, 10, 11, 15-27, 28, 29, 30, 31, 34, 35, 37-40, 27400-2714; Keasey Fm., USGS 15265, 15307, 15309, 15277, 15280, 15281, 15282, 15508, 25030, 25039, 25918. Localities are UMCP unless prefaced by a collection abbreviation.

Material examined: 44 specimens. Collection, Formation: Locality (number of specimens). Eugene Fm., Oregon: CAS 69257/SU 3162 (1), CAS: 69253? (3), 69254 (2), 69272 (30), 69256 (1), UCMP: 4084, 55105/USGS 152801 (1); USGS 15274 (1?), 15309 (1), 18798 (2); USNM: 15508, 251391/USGS 15282 (1, Hickman hypotype pl. 7, fig. 11, 1980), 251392/USGS 15282 (1, Hickman hypotype pl. 7, fig. 12, 1980); Spencer Fm.: UCMP D9269.

Remarks: *Bruclarkia vokesi* is the oldest species of the genus. In Oregon, it is abundant in the Eugene Formation but rare in the older Keasey Formation.

Bruclarkia sp. aff. ***Bruclarkia barkeriana*** (Cooper, 1894)

Plate 8, figs. 32

Bruclarkia oregonensis (Conrad), Addicott, USGS Prof. Paper 642, pl. 10, fig. 4, 1970.

Description: The shell is fusiform with an inflated body whorl and a convex shoulder. There are six whorls including the protoconch. The parietal lip is thickened and extends across more than ¾ of the body whorl in ventral (apertural) view. It obscures four major spiral cords on the body whorl in apertural view. The sutural collar is thickened and noded with sinuous connections to the penultimate whorl. The penultimate whorl is tabulate with two rows of horizontally elongated nodes that are not obscured by the sutural collar. Apical whorls are globose and are ornamented by minor nodes and varicies. The body whorl is ornamented by 2 rows of 10 horizontally elongated nodes, 4 thickened cords, and thin spiral cords of equal thickness. The noded rows are posterior to the thickened cords. The siphonal canal is recurved. The protoconch is small and paucispiral.

Similarity to other species: *Bruclarkia sp.* aff. *Bruclarkia barkeriana* shares body whorl node morphology, shell profile, thickening of the sutural collar, and an extended parietal callus with *B. barkeriana*. The node ornamentation of the penultimate whorl, however, is unique to this specimen.

Type: UCMP specimen 32832, pl. 10, fig. 4 in Addicott (1970).

Type Dimensions: Height (incomplete): 37 mm, maximum diameter 24 mm.

Occurrence and Age: California from the early Miocene (Olcese Sand), approximately 16.6-17.8 Ma (fig. 2).

Localities (in literature): California: UCMP B-1593, Olcese Sand (Addicott, 1970).

Material examined: 1 specimen, see above.

Remarks: Although Addicott (1970) identified this specimen as *Bruclarkia oregonensis*, its morphology is almost identical to that of *B. barkeriana*. Because only one individual was found with the unique penultimate whorl ornamentation described above, it is likely that it is a variant of *B. barkeriana*.

Summary

The *Bruclarkia* fauna of the Paleogene and Neogene from California to Alaska comprises seven species: *B. acuminata, B. barkeriana, B. ellenae, B. gravida, B. oregonensis, B. santacruzana,* and *B. vokesi.* These and all proposed taxa in the genus were evaluated based on eleven shell characters including spiral cords, extent of the parietal lip, spire morphology, ornamentation of the sutural collar and penultimate whorl, and node rows (or absence of) on the body whorl. The set of *Bruclarkia* individual scored for shell characters and measured for height, diameter (width), and shell thickness was 342. The total set of *Bruclarkia* fossils identified to species was over 750.

Variable shell characters within *Bruclarkia* species include siphonal canal length and shape in *B. acuminata*, the number of node rows on the body whorl in *B. barkeriana*, *B. acuminata*, and *B. oregonensis,* and spire angle in *B. gravida.* The number of nodes per node row was also highly variable in *B. barkeriana* and *B. oregonensis.* Proposed *Bruclarkia* species that were considered invalid included *B. fulleri, B. seattlensis*, and *B. blakeleyensis* and were either placed in synonymy with another species, left out of synonymies, or tentatively grouped with another species because their type material was poorly preserved or of dubious affinity. Collapsing the number of *Bruclarkia* taxa from more than a dozen to seven suggests that the genus was not as species-rich as previously thought. Furthermore, a greater spectrum of variation exists within members of this genus than had been recognized by previous authors.

The stratigraphic range of *Bruclarkia* begins in the late Eocene and ends during the middle Miocene based on paleomagnetic dates of formations that yield *Bruclarkia* fossils and correlations using benthic foraminifera and other molluscs. Corresponding foram stages span the Refugian to the Luisian and the Galvinian to Temblor/Newportian mollusc stages of Armentrout (1981). It is difficult to date the well-known *B. gravida* zone from the San Ramon Fm. and Kirker Tuff in California because microfossils and molluscs from these strata do not yield precise ages. Here they are considered latest Oligocene to earliest Miocene in age.

The morphology of *B. ellenae* is unique among *Bruclarkia* species in having a stratigraphic range that is restricted to one formation, the Astoria in Oregon and Washington. It is also the only *Bruclarkia* taxon to have only one node row lying high on the body whorl. *Bruclarkia* *barkeriana* and *B. santacruzana* are endemic to California and have nearly identical shell sculpture except for body whorl ornamentation, which is present in *B. barkeriana* but absent in *B. santacruzana*. These two taxa can be readily distinguished from other members of the genus by their extensive parietal lip and flared sutural collar. *Bruclarkia acuminata* and *B. oregonensis* have the longest duration of all *Bruclarkia* species, spanning the early Oligocene to middle Miocene in the Pacific Northwest and California. They are more similar to each other than to any other *Bruclarkia* species and differ only in the presence of well developed ornamentation on the penultimate whorl. *Bruclarkia gravida* is ornamented by three rows of nodes on its body whorl and has an adpressed spire. These characters are also common to *B. vokesi*, which may be sister or ancestral to *B. gravida.* Stratigraphically, these taxa are the oldest of the genus and become extinct by the early Miocene. *Bruclarkia gravida* has the most expansive geographic range, occurring from Alaska to California. In contrast, *B. vokesi* is endemic to the Pacific Northwest.

The synonymy of *B. columbiana* with *B. gravida* extends the range of *B. gravida* from the Refugian to the Zemorrian and Saucesian benthic foram stages, and Galvinian, Matlockian, Juanian, and Pillarian/Vaqueros mollusc stages. The unification of these taxa also expands the geographic range of *B. gravida* to include California, Oregon, Washington, and Alaska. It is interesting that this species covered such a broad area during the Oligocene when the proportion of cosmopolitan taxa within faunas decreased as provinciality, or endemism, increased. This species and its conspecifics, despite their range in the northeastern Pacific and occurrence in large numbers in some formations, did not migrate across the Pacific like many other neogastropod taxa during the Paleogene and Neogene. The extinction of *Bruclarkia* in the middle Miocene could have been influenced by ocean warming during the Miocene Climatic Optimum or the cooler climate that followed it.

The evaluation of *Bruclarkia* species based on shell characters was possible only by examining a large number of fossils (>700). Although this genus has been reviewed and documented in more than 25 publications, many of the features described here and used as criteria for synonymizing taxa were not identified until many specimens from museum collections were examined. This study, like so many in which fossil invertebrates are treated in detail, underscores the value of museums and paleontological collections.

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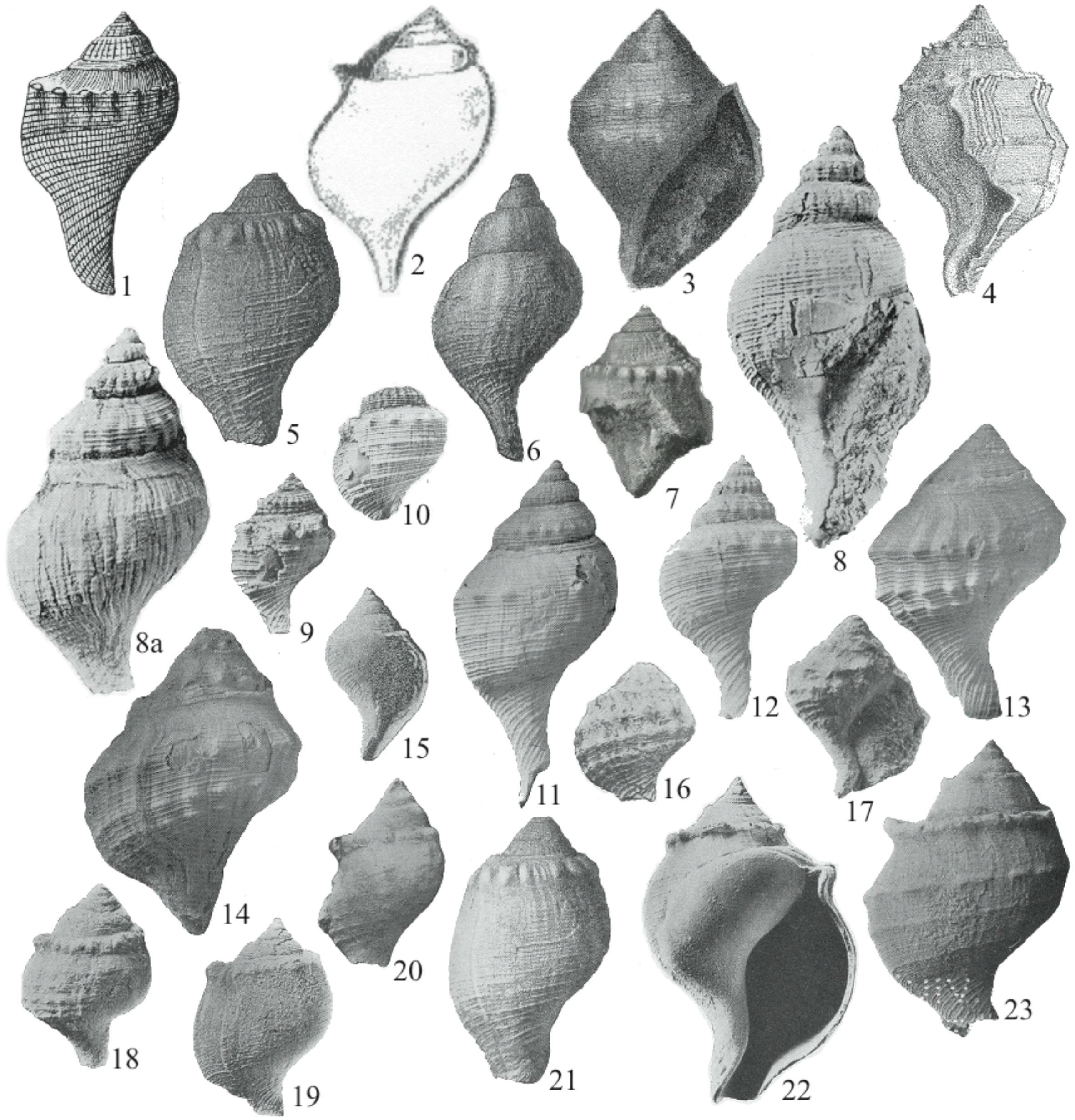

Plate 1. 1. *Fusus oregonensis* Conrad (1848), 2. W.P. Blake cast, Pacific Railroad Report Vol. II, (1866) 3. *Agasoma gravida* Gabb (1869) (= *Clavella gravida* Gabb,1866) and *A. gravida* Gabb (Tryon, 1881). 4. *Agasoma barkerianum* Cooper (1894), 5. *Agasoma santacruzana* Arnold (1908), 6. *Agasoma stanfordensis* Arnold (1908), 7. *Agasoma santacruzana* Arnold (Arnold and Anderson, 1910), 8-8a. *Agasoma oregonense* Anderson & Martin (1918), 9-10. *Agasoma yaquinanum* Anderson and Martin (1914), 11-12. *Agasoma acuminatum* Anderson & Martin (1914), 13-14. *Agasoma columbianum* Anderson & Martin (1914), 15. *Agasoma barkerianum* Cooper (English, 1914), 16-17. *Agasoma gravidum* (Gabb) (English, 1914), 18. *Agasoma barkerianum* Cooper *var. clarki* English (1914), 19. *Agasoma barkerianum* Cooper *var. santacruzanum* Arnold (English, 1914), 20. *Agasoma barkerianum* Cooper *var. clarki* English (1914), 21. *Agasoma barkerianum* Cooper *var. santacruzanum* Arnold (English, 1914), 22-23. *Agasoma barkerianum* Cooper (English, 1914).

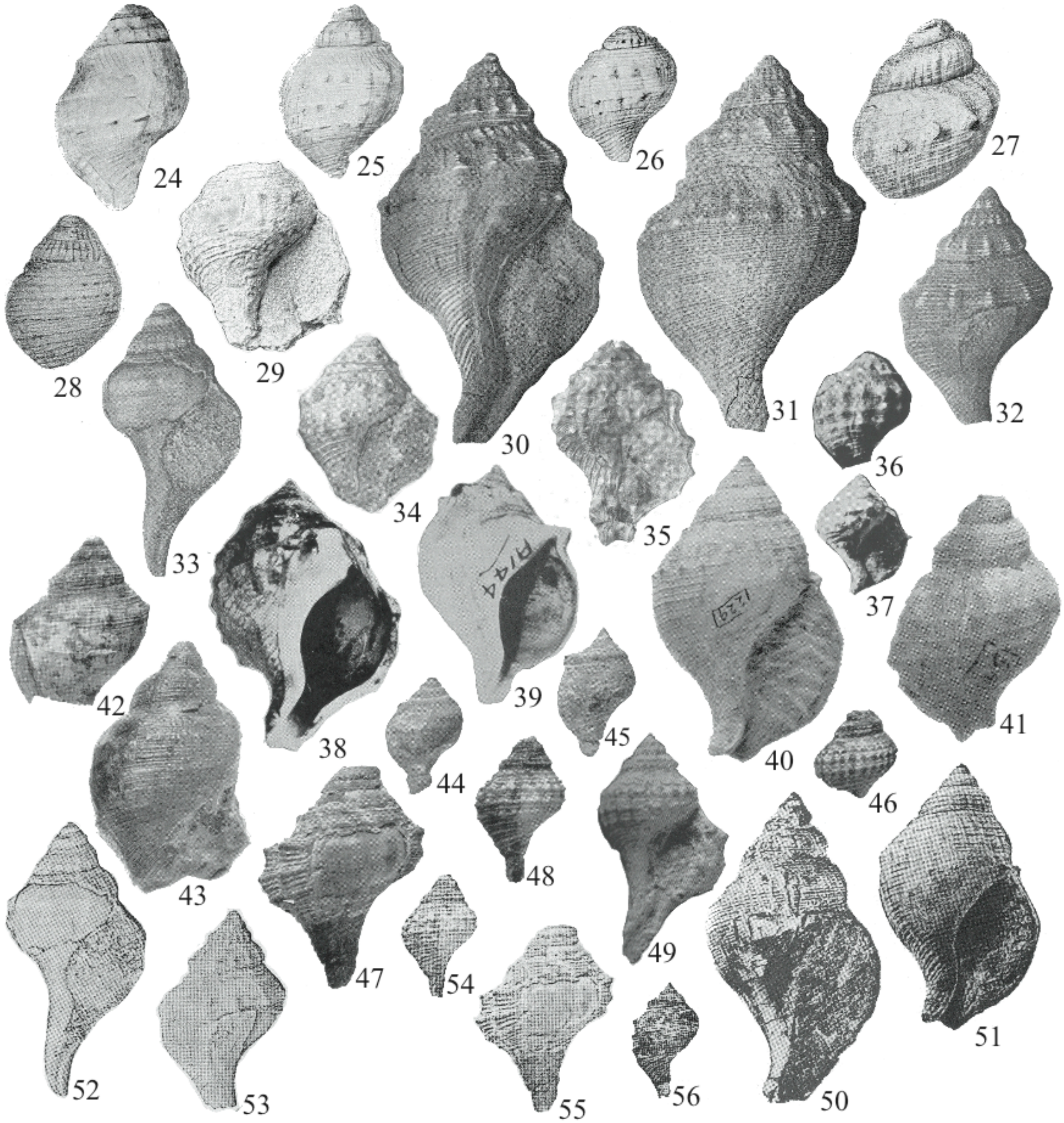

Plate 2. 24-26. *Agasoma gravidum* Gabb (Clark, 1918), 27. *Agasoma acuminatum* Anderson & Martin (Clark, 1918), 28. *Agasoma gravidum* Gabb [not Anderson & Martin] (Clark, 1918), 29. *Agasoma gravidum multinodosum* Clark (Clark, 1918), 30-33. *Agasoma acuminatum* Anderson & Martin (Clark & Arnold, 1923), 34-35. *Bruclarkia gravida* (Gabb) (Stewart, 1926), 36-37. *Bruclarkia gravida* (Gabb) (Clark, 1929), 38. *Bruclarkia gravida columbiana* Anderson & Martin (Clark, 1929), specimen in adapertural view not shown. 39. *Bruclarkia barkerianum* (Cooper) (Clark, 1929), specimen in adapertural view not shown, 40-43. *Bruclarkia oregonensis* (Conrad) (Etherington, 1931), specimen in adapertural view not shown, 44-46. *Bruclarkia barkerianum* (Cooper) *santacruzana* (Arnold) (Loel & Corey, 1932), partial specimen not shown, 46-49. *Bruclarkia thor* Tegland (Tegland, 1933), 50-51. *Bruclarkia oregonensis* (Conrad) (Weaver, 1942), 52-53. *Bruclarkia acuminata* Anderson & Martin (Weaver, 1942), 54-55. *Bruclarkia thor* Tegland (Weaver, 1942), 56. *Bruclarkia yaquinana* (Anderson & Martin) (Weaver, 1942).

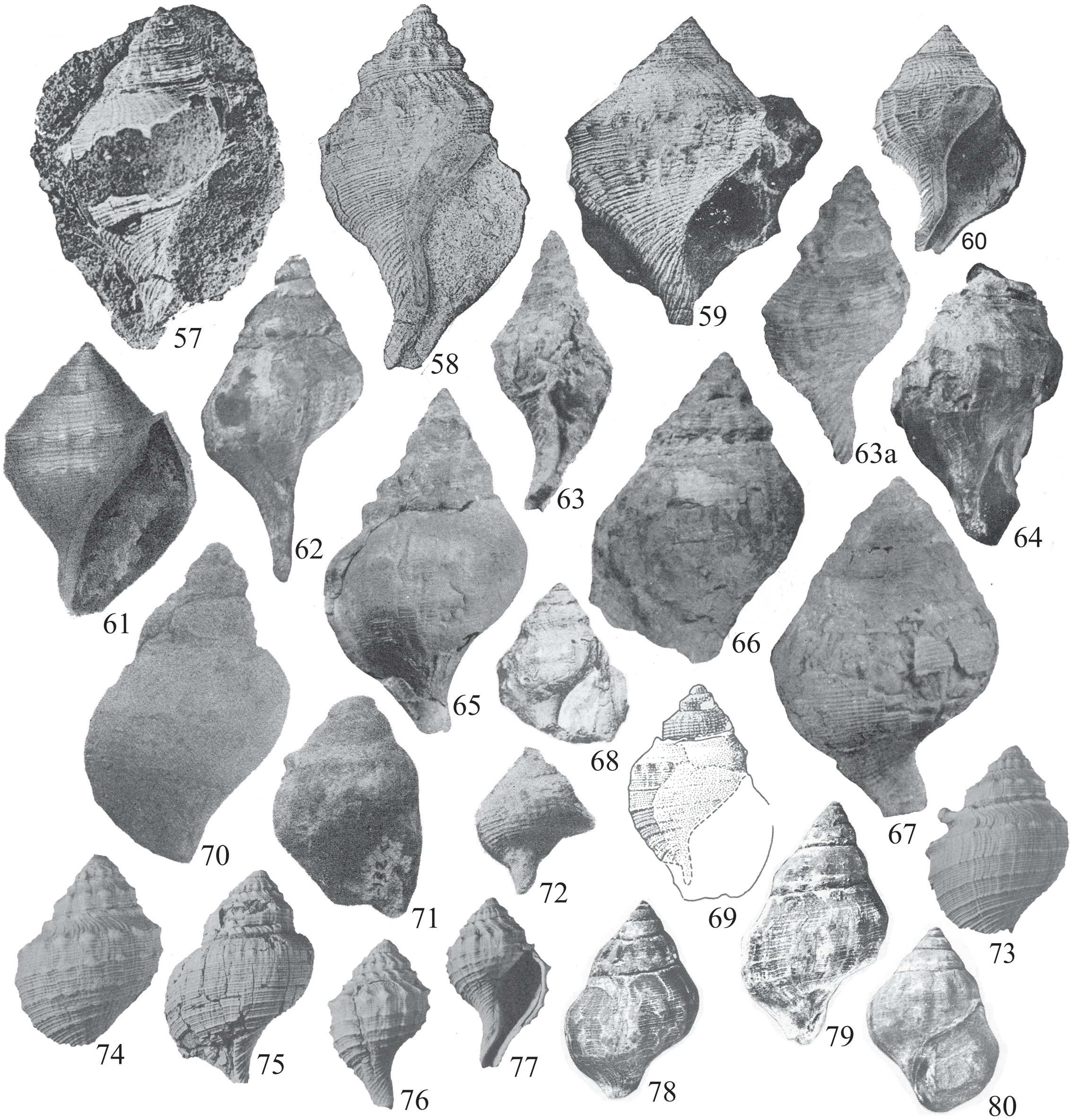

Plate 3. 57-58. *Bruclarkia acuminata* (Anderson & Martin) (Weaver, 1942) [58 also figured in Moore, 2000], 59-60. *Bruclarkia columbiana* (Anderson & Martin) (Weaver, 1942), 61. *Bruclarkia gravida* (Gabb) (Shimer & Schrock, 1944), 62. *Bruclarkia fulleri* Durham (1944), 63-63a. *Bruclarkia blakeleyensis* Durham (1944), 64. *Bruclarkia fulleri* Durham (1944), 65. *Bruclarkia acuminatum* (Anderson & Martin) (Durham, 1944), 66. *Bruclarkia seattlensis* Durham (1944), 67. *Bruclarkia blakeleyensis* Durham (1944), 68. *Bruclarkia oregonensis* (Schenck & Keen, 1950), 69. *Bruclarkia columbiana* (Schenck & Keen, 1955), 70-71. *Bruclarkia oregonensis* (Conrad) (Lutz, 1951), 72. *Bruclarkia sp*. (Lutz, 1951), 73. *Bruclarkia oregonensis* (Conrad) [beaded form] (Moore, 1963), also figured by Addicott, 1976, (Plate 2, fig. 7), 74. *Bruclarkia oregonensis* (Conrad) [noded form] (Moore, 1963), 75. *Bruclarkia oregonensis* (Conrad) [smooth form] (Moore, 1963) [73 and 74 also figured in Moore, 2000], 76-77. *Bruclarkia oregonensis* (Conrad) [spinose form] (Moore, 1963), 78-80. *Bruclarkia vokesi* (Hickman, 1969).

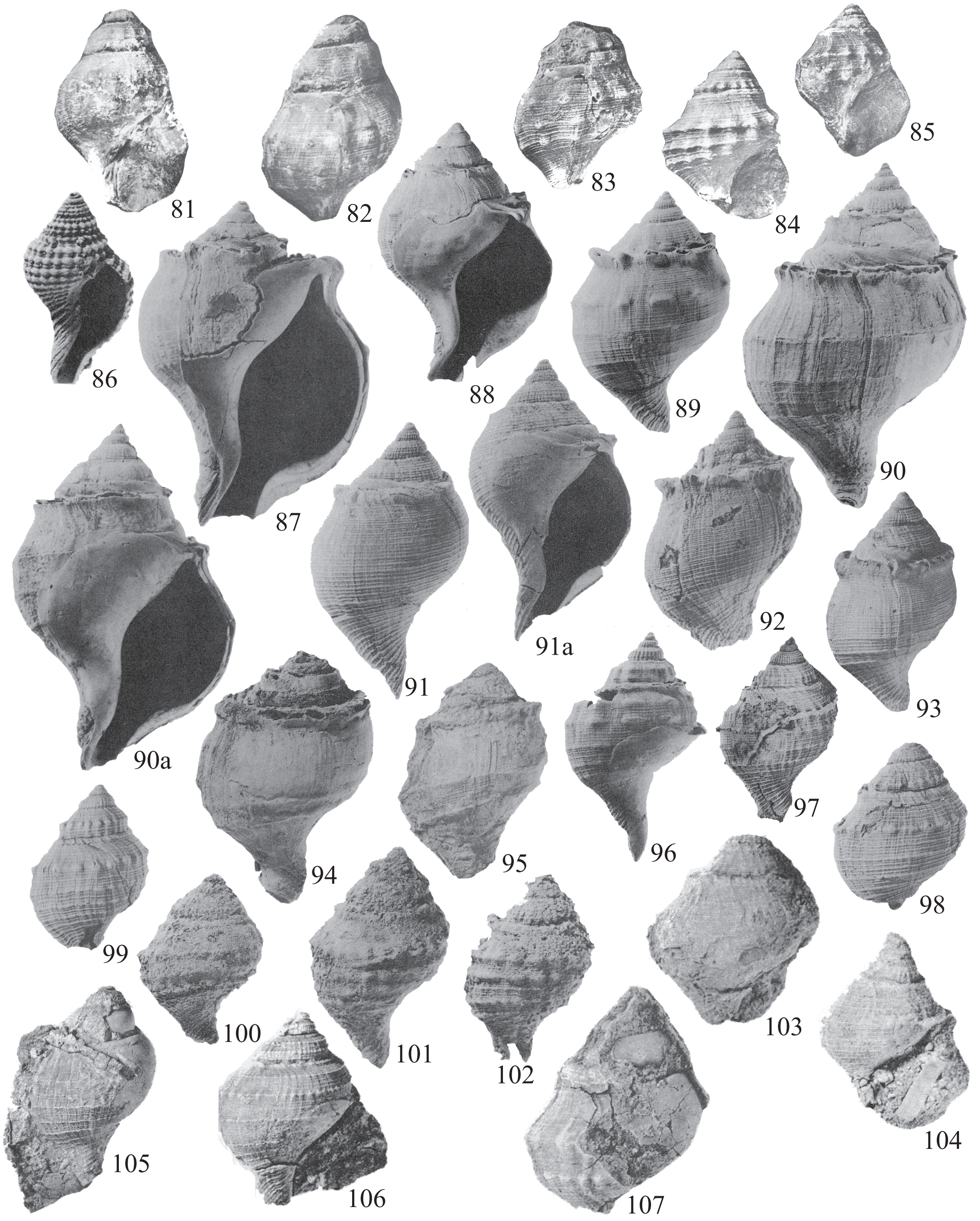

Plate 4. 81-83. *Bruclarkia vokesi* (Hickman, 1969), 84-85. *Bruclarkia columbianum* (Anderson & Martin) (Hickman, 1969), 86-90a. *Bruclarkia barkeriana* (Cooper) (Addicott, 1970), 91-93. *Bruclarkia barkeriana forma santacruzana* (Arnold) (Addicott, 1970), 94-95. *Bruclarkia barkeriana* (Cooper) (Addicott, 1970), 96-99. *Bruclarkia oregonensis* (Conrad) (Addicott, 1970), 100-102. *Bruclarkia yaquinana* (Anderson & Martin) (Addicott, 1970), 103-104. *Bruclarkia seattlensis* Durham (Addicott, 1972), 105-106. *Bruclarkia oregonensis* (Conrad) (Addicott, 1972), 107. *Bruclarkia columbiana* (Anderson & Martin) (Addicott, 1972).

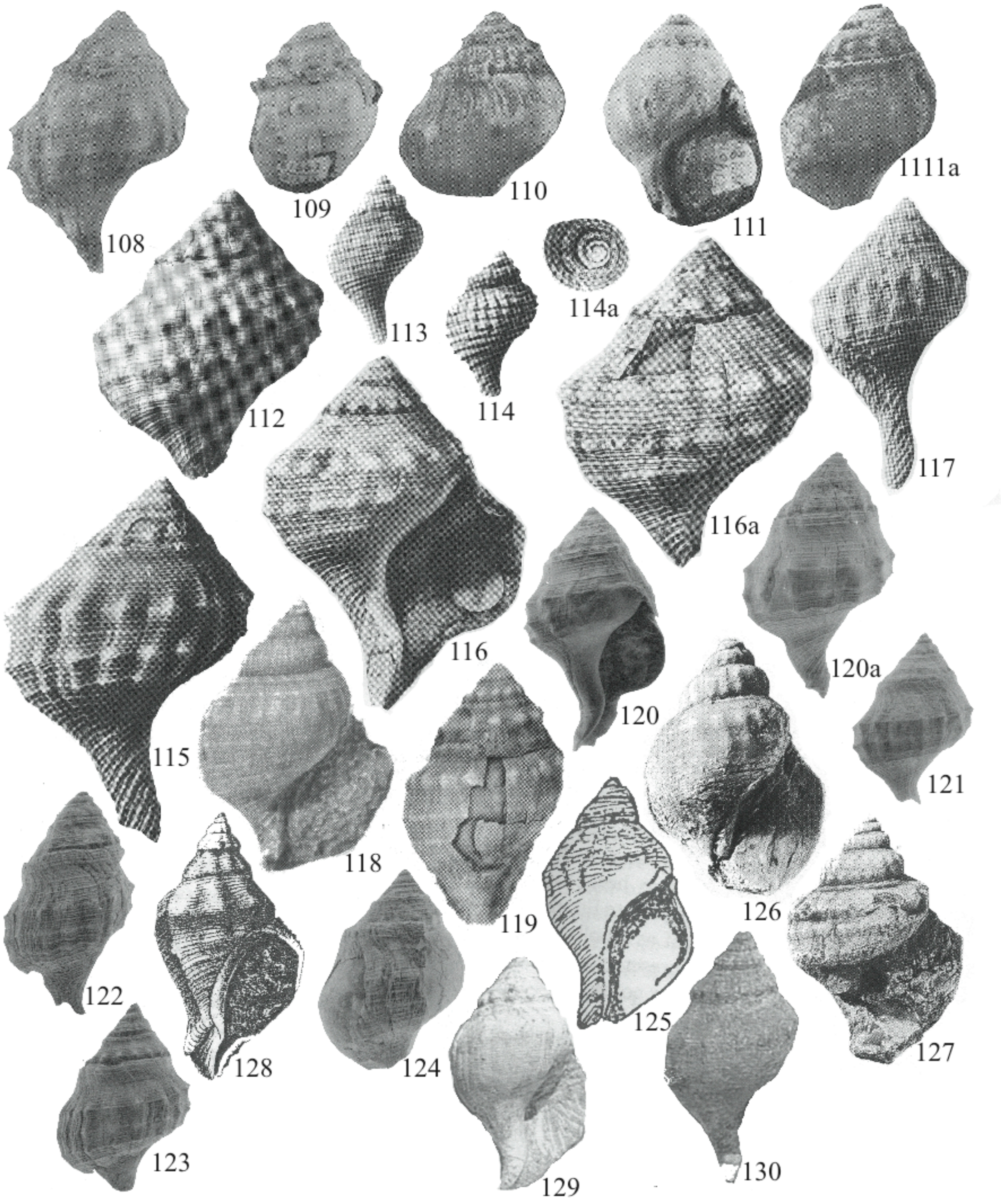

Plate 5. 108. *Bruclarkia columbiana* (Anderson & Martin) (Armentrout, 1973), 109. *Bruclarkia oregonensis* (Conrad) (Armentrout, 1973), 110. *Bruclarkia chehalisensis* Armentrout (1973), 111-111a. *Bruclarkia chehalisensis nodulusa* Armentrout (1973), 112-117. *Bruclarkia columbiana* (Anderson & Martin) (Moore, 1976), 118**.** *B. oregonensis* (Conrad) (Addicott, 1976), 119. *B. acuminata* (Anderson and Martin), 120-123. *Bruclarkia vokesi* (Hickman, 1980), 124. *Bruclarkia sp.* (Hickman, 1980), 125. *Bruclarkia sp.* (Orr and Orr, 1981), 126-127. *Levifusus acuminatum* (Ludvigsen and Beard, 1994), specimens in adapertural view not shown, 128. *Bruclarkia* (Orr and Orr, 1999), 129-130. *Bruclarkia acuminata* (Anderson & Martin) (Johns and Cockburn, 2003).

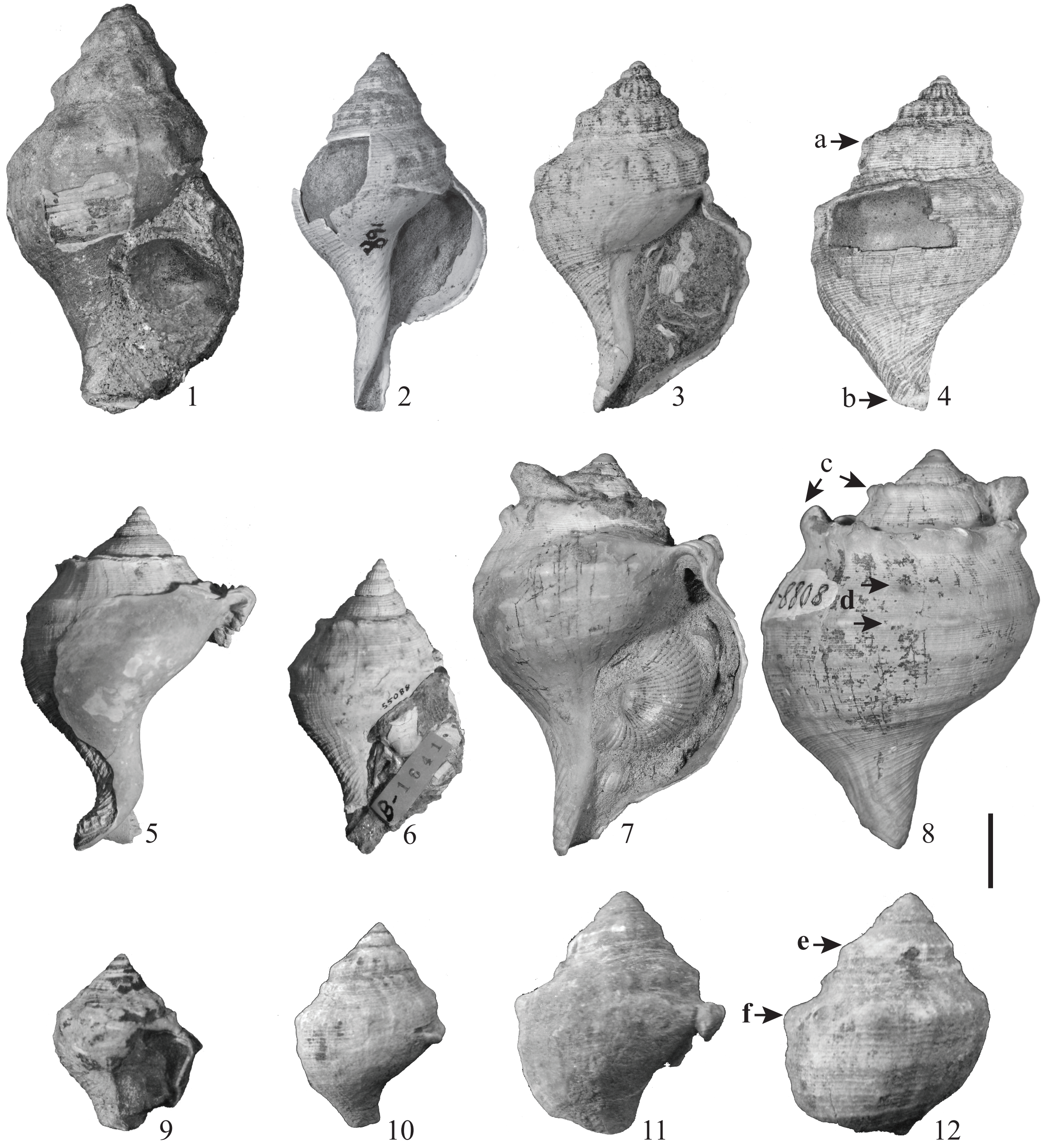

Plate 6. *Bruclarkia* specimens with descriptions of selected morphological features (a-f). 1-4. *Bruclarkia acuminata*, (1. CAS 69267, 2. CAS 69269, 3-4. UCMP xxxx/xxxx), a.one or two node rows on the penultimate whorl. b. the siphonal canal is usually recurved as in this specimen but can be straight as in specimen 2. 5-8. *Bruclarkia barkeriana*, (5. UCMP B-1623/xxxx, 6. UCMP B-1641/xxxx, 7-8. UCMP D-8808/xxxx), c. noded sutural collar present at the boundary of the penultimate whorl and the nuclear whorls. d. node rows with elongated node morphology. 9-12. *Bruclarkia ellenae*, (9. UCMP D-294/xxxx, 10. UCMP B-1641/xxxx, 11-12. UCMP D-8808/xxxx), e. one row of nodes on a tabulate spire. f. one node row on the body whorl. Scale = 1cm.

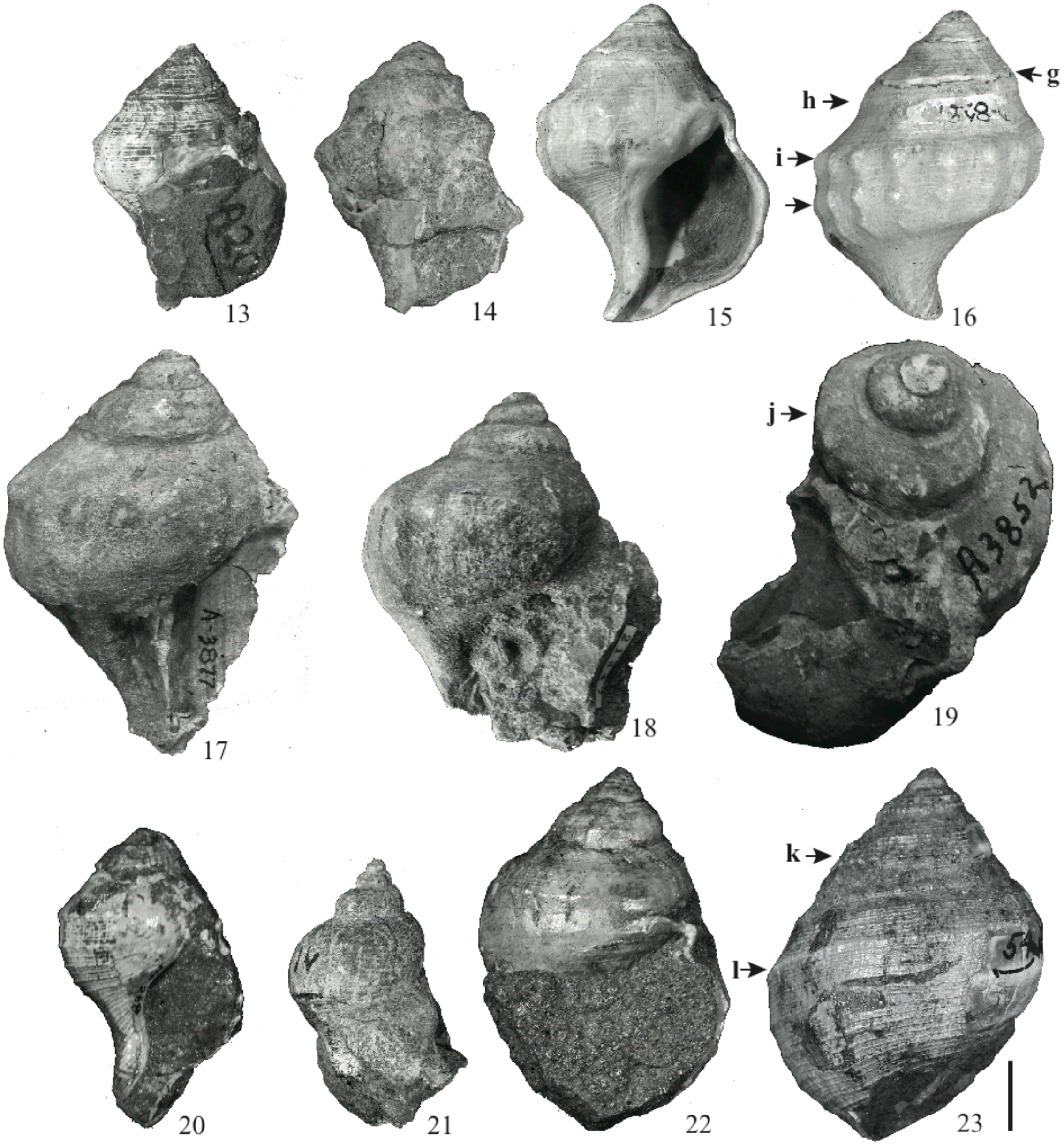

Plate 7. *Bruclarkia* specimens with descriptions of selected morphological features (g-l). 13-16. *Bruclarkia gravida*, (13. UCMP A-20/xxxx, 14. UCMP 3200/xxxx, 15-16. UCMP D-8281/55093, 17, UCMP A-3877/xxxx, 18. USGS 21347/xxxx, 19. UCMP A-3852/xxxx), g. one row of nodes partially covered at the sutural collar of the adpressed spire. h. a slightly concave shoulder. i. node rows on the body whorl. Here, the two indicated with arrows are more prominent then the third node row toward the anterior of the shell. j. the shell is taphonically altered and flattened most dramatically in this specimen, but also in specimens 17 and 18. 20-23. *Bruclarkia oregonensis* (20. CAS 69264, 21. UCMP 516/xxxx, 22-23. UW 54), k. the penultimate whorl has one minor row of nodes that are numerous and small. l. the node row of the body whorl like that of the penultimate whorl. Scale = 1cm.

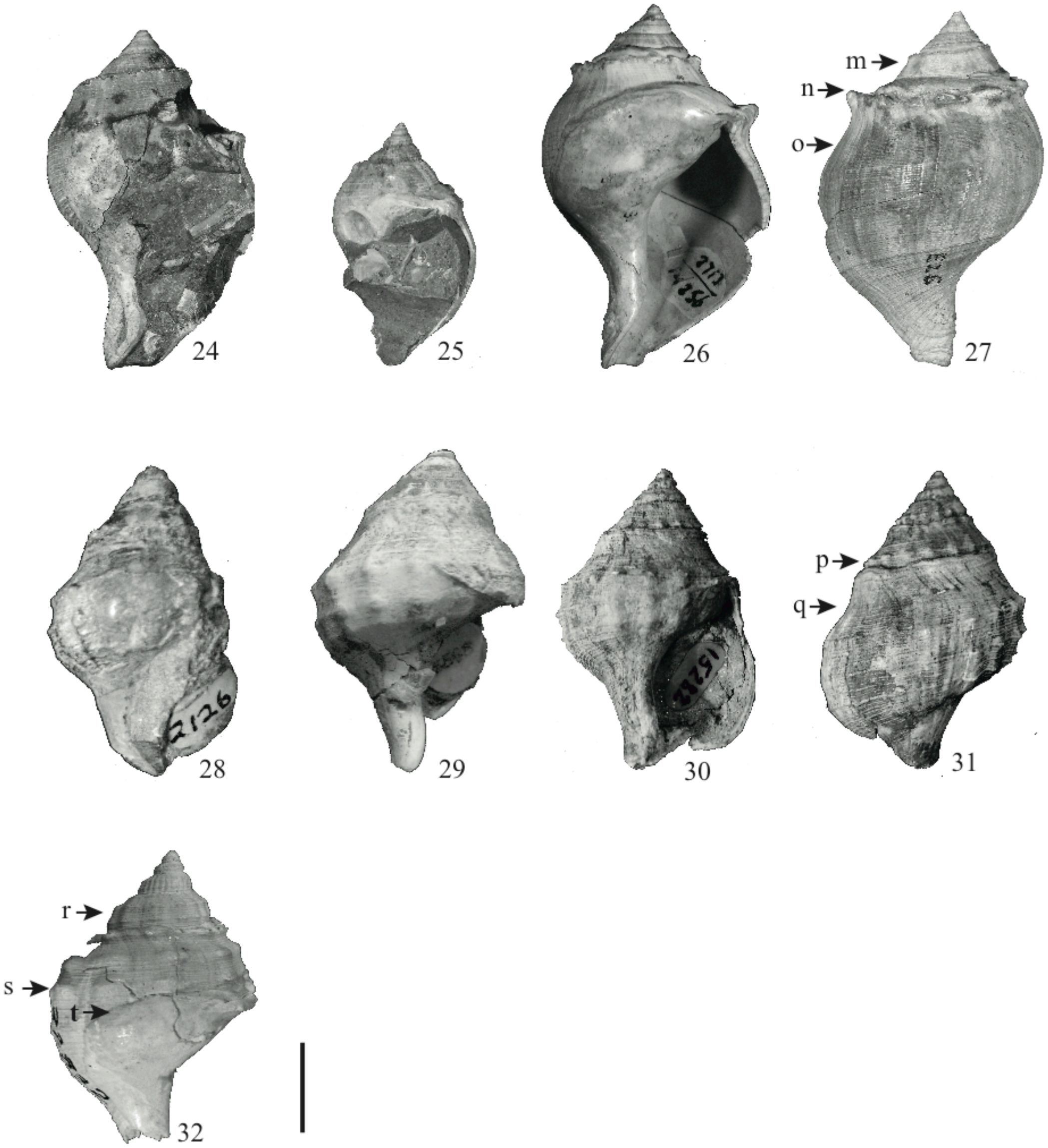

Plate 8. *Bruclarkia* specimens with descriptions of selected morphological features (m-t). 24-27. *Bruclarkia santacruzana*, (24. UCMP xxxx, California State Geological Survey specimens in UCMP, collected by J. G. Cooper in the 1860s-1890s, 25. UCMP xxxx, 26-27. UCMP 2713/xxxx), m. penultimate whorl. n. ornamented and thickened sutural collar. o. body whorl absent of node rows, 28-31. *Bruclarkia vokesi*, (28. CAS 69254, 29. USNM 15508, 30-31. USGS 15282), p. the nearly covered row of nodes on the penultimate whorl. q. a concave shoulder common in this species. 32. *Bruclarkia* aff. *barkeriana* (UCMP B-1593/32832, in Addicott, 1970), r. two rows of elongated nodes on the penultimate whorl. s. node rows on the body whorl. t. extensive parietal callus/lip. Scale = 1cm.

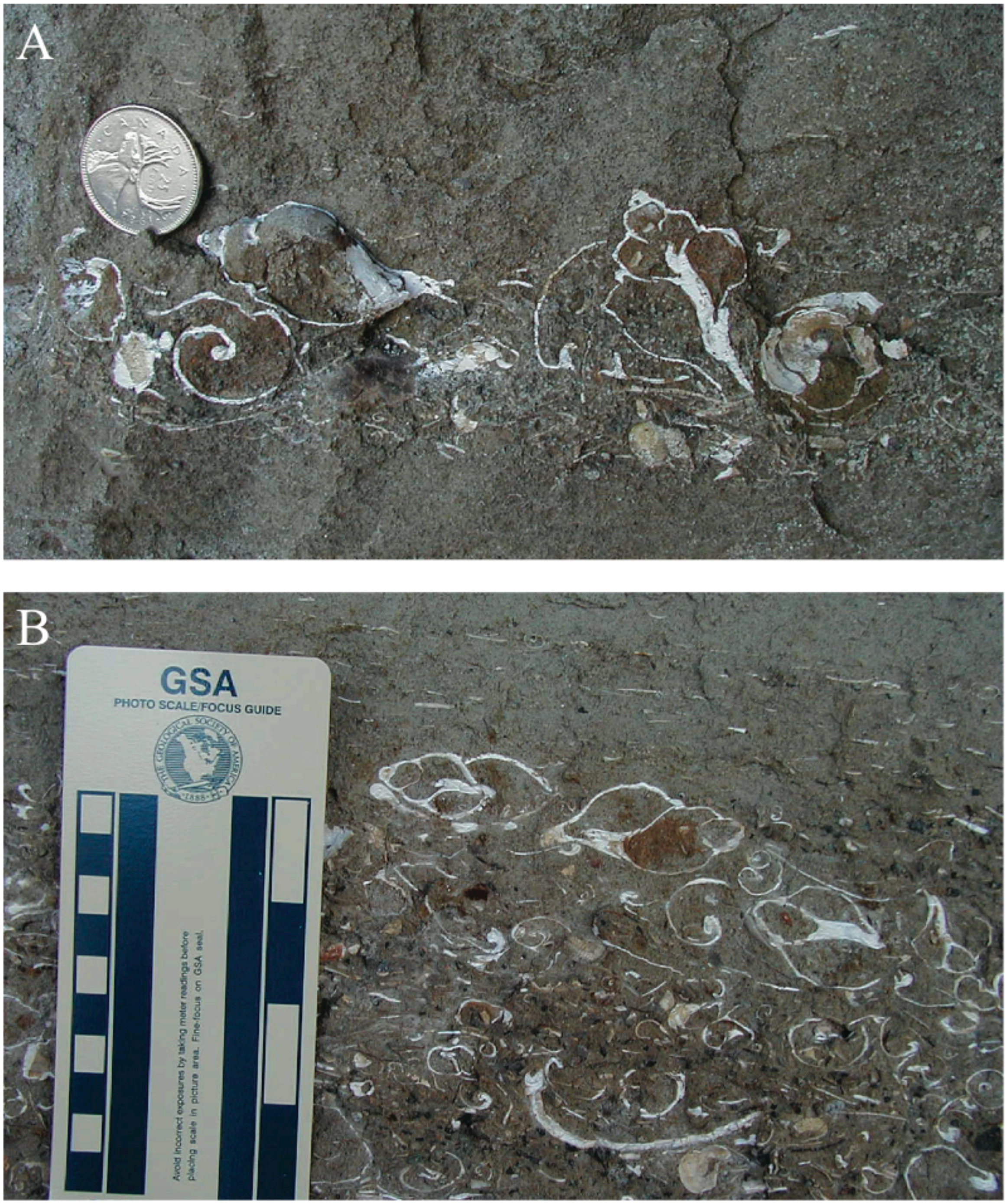

Figure 1 (A, B). Folliliferous lenses of *Bruclarkia acuminata* from the Sooke Fm. on the southwest coast of Vancouver Island, B.C. These accumulations are the *Agasoma acuminatum* beds of Clark and Arnold (1918).

Table 1. Discrete morphological characters and character states for *Bruclarkia* taxa.

A. **Spiral cord prominence**	0= minor. 1= major (12+)
B. **Spiral cord thickness**.	0= unequal. 1= equal.
C. **Axial growth line prominence**.	0= minor. 1= obvious. 2= major: sinuous and noticeable.
D. **Parietal lip**.	0= covering less than or equal to ¼ of the body whorl in ventral view, can be thickened. 1= extends ¾ of the body whorl in ventral view. 2= covers more than ¾ of the body whorl in ventral view.
E. **Spire whorl morphology**.	0= apical whorls globose. 1= tabulate or stepped. 2= an adpressed penultimate whorl and globose apical whorls. 3= adpressed and flattened.
F. **Shoulder morphology**.	0= concave. 1= convex/rounded.
G. **Sutural collar type**.	0= Unornamented. 1= Noded or flared subsutural collar with suture collar developed onto lower portion of penultimate whorl interrupted by twisted growth lines.
H. **Penultimate whorl ornamentation**.	0= absent. 1= one row of evenly spaced nodes partially covered by or bordering sutural collar. 2= nodes closely spaced in a "beaded" row not bordering sutural collar in ad-apertural view. 3= one or two evenly spaced node rows not bordering the sutural collar. 4= one evenly spaced node rows not bordering the sutural collar.
I. **Body whorl, # node rows**.	0= none. 1= one row. 2= primary threads with no significant nodes to 2 rows of bead-like nodes. 3=one to three rows of evenly spaced nodes. 4= one to five rows of nodes. 5= two to three node rows with two more prominent than the third, if present. 6= three node rows.
J. **Body whorl node morphology**.	0= Not applicable, no nodes. 1= rounded. 2= dashed or horizontally elongated. 3= spinose. 4= small and bead-like.
K. **Body whorl nodes per whorl.**	0= Not applicable, no nodes. 1= six to twelve nodes. 2= eleven to thirteen nodes. 3= thirteen to eighteen nodes. 4= fourteen to eighteen nodes. 5= seventeen nodes. 6= variable.

Table 2. Shell width, spire height, and shell thickness in *Bruclarkia*. All measurements are in mm. M = mean; CV = coefficient of variation; N = sample size, n = total number of specimens examined. Table based on Kohn, 1980 and reproduced from Vendetti, 2009b.

	B. ellenae (n=21)			*B. acuminata* (n=55)			*B. oregonensis* (n=30)			*B. barkeriana* (n=111)			*B. santacruzana* (n=19)			*B. gravida* (n=167)			*B. vokesi* (n=5)		
	M	CV	N	M	CV	N	M	CV	N	M	CV	N	M	CV	N	M	CV	N	M	CV	N
Shell width	24	9.6	4	32.7	19.1	18	23.9	26.6	13	29	18.6	89	27.6	23.5	18	27.0	22.9	128	23.7	4.9	4
Spire height	9.25	5.4	4	11.1	18.9	24	9.4	31.5	13	10.1	21.9	58	8.2	13.3	16	9.2	28.5	65	9.6	11.7	4
Shell thickness	0.90	13.1	8	0.9	26.1	20	1.1	27.6	45	1.1	27.7	45	1.1	28.3	13	1.0	30.5	43	1.6	21.9	3

Table 3. Morphological characters and their character states for valid *Bruclarkia* species.

	Spiral cords								Body whorl nodes		
	A. Prominence	B. Thickness	C. Axial growth lines	D. Parietal lip extent	E. Spire whorl morphology	F. Shoulder morphology	G. Sutural collar	H. Penultimate whorl ornamentation	I. # node rows	J. Node morphology	K. Nodes per whorl
B. acuminata	1	0	3	2	1	1	0	3	3	1	5
B. barkeriana	0	1	1	0	2	1	1	0	4	2	1
B. ellenae	1	0	1	2	1	1	0	4	1	1	2
B. gravida	1	1	2	1	3	0	0	1	5	1	3
B. oregonensis	1	0	3	2	0	1	0	2	2	1	6
B. santacruzana	0	1	1	0	2	1	1	0	0	0	0
B. vokesi	0	1	2	1	3	0	0	1	6	3	4

Table 4. Species designations with those determined by this study in bold, the number of specimens examined (no. spec.), specimen and locality numbers, formation and location, and reference for figured specimens. Type specimens are abbreviated as follows: H= holotype, HP= hypotype, CT=cotype, PT= paratype, LT= lectotype, PL= plesiotype.

SPECIES DESIGNATION (**THIS STUDY**) with the species assignments from previous studies listed below	NO. SPEC..	SPECIMEN & LOCALITY NUMBERS	FORMATION & LOCATION	AUTHOR(S) FIGURED BY
Bruclarkia acuminatum				
?	15	CAS 69267/ 231	Sooke Fm., Canada	-
?	9	CAS 69268/ 232	Sooke Fm., Canada	-
Agasoma acuminatum	9	CAS 69269/ 168	Sooke Fm., Canada	-
?	20	UCMP XXXX	Sooke Fm., Canada	This study
B. acuminatum[1] **HP**	1	UCMP 35390/ A3707	“Blakeley” Fm.?	Durham, 1944
B. acuminatum **HP**	1	UCMP 35391/ A3710	Sooke Fm., Canada	Durham, 1944
?Bruclarkia columbianum	5	UCMP B4573	San Emigdio Fm., CA	-
unidentified	1	UCMP A6631	Blakeley Fm., WA	-
Bruclarkia seattlensis **H**	1	UCMP 35397/ A1803	Blakeley Fm., WA	Durham, 1944
Agasoma acuminatum n. sp.[2] **H**	1	CAS 157/ 168	NW of Scappoose, OR	Anderson & Martin, 1914
Agasoma acuminatum n. sp.[2] **CT**	1	CAS 158/ 168	NW of Scappoose, OR	Anderson & Martin, 1914
Agasoma oregonense **H**	1	CAS 159/ 168	NW of Scappoose, OR	Anderson & Martin, 1914
Agasoma oregonense **CT**	1	CAS 160/ 168	NW of Scappoose, OR	Anderson & Martin, 1914
Bruclarkia seattlensis **H**	1	UCMP 35397/A1803	Blakeley Fm., WA	Durham, 1944
Bruclarkia blakeleyensis **H**	1	UCMP 35392/A1807	Blakeley Fm., WA	Durham, 1944
Bruclarkia blakeleyensis n. sp. **PT**	1	UCMP 35393/A1807	Blakeley Fm., WA	Durham, 1944
Bruclarkia acuminatum	1	UCMP 3203	Pleito Fm., CA	-
Unidentified	1	UCMP A373	Blakeley Fm., WA	-
B. acuminata	2	UCMP A3708	Blakeley Fm., WA	-
Agasoma yaquinanum **PT**	1	CAS 162/ 39	Near Yaquina Bay, WA	Anderson & Martin, 1914
Bruclarkia yaquinanum **H**	1	CAS 161/ 39	Near Yaquina Bay, OR	Anderson & Martin, 1914
Bruclarkia cf. yaquinanum **HP**	1	UCMP 35400/ A3692	Clallam Fm., WA	-
Bruclarkia cf. yaquinanum **HP**	1	UCMP 35401/ A3692	Clallam Fm., WA	-
Bruclarkia cf. yaquinanum **HP**	1	UCMP 35402/ A3692	Clallam Fm., WA	-
B. oregonensis	5	CAS 69264/ NP269	Astoria Fm., WA	-
Bruclarkia cf. oregonensis	1	UCMP A4149	Hambre Fm., CA	-
Bruclarkia oregonensis **HP**	1	UCMP 31993/ A373	Astoria Fm., WA	Etherington, 1931
Bruclarkia oregonensis	1	CAS 69263/ NP45	Astoria Fm., WA	-
Bruclarkia oregonensis **HP**	1	UCMP 31992/ 54	Astoria Fm., WA	Etherington, 1931
Bruclarkia oregonensis **HP**	1	UCMP 31991/ 9069	Astoria Fm., WA	Etherington, 1931

Bruclarkia acuminatum	1	UCMP 3203	Pleito Fm., CA	-
Bruclarkia oregonensis	2	UCMP A4564	Oursan Fm., CA	-
Bruclarkia oregonensis	1	CAS 69260/ 3132	Astoria Fm., WA	-
Bruclarkia oregonensis	4	CAS 69265/ NP306	Astoria Fm., WA	-
unidentified	1	UCMP 1218	?San Pablo Group, CA	-
Bruclarkia stanfordensis	9	UCMP 516	Sobrante Fm., CA	-
Bruclarkia cf. yaquinanum	1	UCMP 35400/ A3692	Clallam Fm., WA	-
Bruclarkia cf. yaquinanum	1	UCMP 35401/ A3692	Clallam Fm., WA	-
Bruclarkia cf. yaquinanum	1	UCMP 35402/ A3692	Clallam Fm., WA	-
Bruclarkia oregonensis				
Bruclarkia oregonensis HP	1	UCMP 34162/ A4565	Sobrante Fm., CA	Lutz, 1951
Bruclarkia oregonensis **HP 5**	1	UCMP 34163/ A4565	Sobrante Fm., CA	Lutz, 1951
Bruclarkia barkeriana				
B. barkeriana **HP**	1	UCMP 32776/ B1598	Olcese Sand, CA	Addicott, 1970
Bruclarkia oregonensis[3] **HP**	1	UCMP 32832/ B1593	Olcese Sand, CA	Addicott, 1970
B. barkeriana **HP**	1	UCMP 32807/B1646	Olcese Sand, CA	Addicott, 1970
B. barkeriana **HP**	1	UCMP 32775/ B1587	Olcese Sand, CA	Addicott, 1970
Bruclarkia barkerianum	2	UCMP 3688	Near Kern River, CA	-
unidentified	1	UCMP 3890	Temblor Fm., CA	-
unidentified	7	UCMP A506	Temblor Fm., CA	-
unidentified	5	UCMP D8808	Temblor Fm., CA	-
unidentified	4	UCMP B1614	Olcese Sand, CA	-
unidentified	3	UCMP B1621	Olcese Sand, CA	-
unidentified	5	UCMP B1597	Olcese Sand, CA	-
unidentified	1	UCMP B1642	Olcese Sand, CA	-
Bruclarkia barkerianum	3	UCMP B7853	Topanga Fm., CA	-
B. stanfordensis	1	UCMP 516	Monterey/Sobrante Fm., CA	-
B. barkeriana	1	UCMP 55082/ B1601	Olcese Sand, CA	-
B. barkeriana	1	UCMP 55083/ B1601	Olcese Sand, CA	-
B. barkeriana	1	UCMP 55084/ B1601	Olcese Sand, CA	-
B. barkeriana	10	UCMP B1601	Olcese Sand, CA	-
B. barkeriana	9	UCMP B1622	Olcese Sand, CA	-
B. barkeriana	6	UCMP B1600	Olcese Sand, CA	-
B. barkeriana	16	UCMP B1593	Olcese Sand, CA	-
B. barkeriana	4	UCMP B1599	Olcese Sand, CA	-
B. barkeriana	3	UCMP B1587	Olcese Sand, CA	-
B. barkeriana	7	UCMP B1623	Olcese Sand, CA	-

B. barkeriana	4	UCMP B1599	Olcese Sand, CA	-
B. barkeriana	4	UCMP B1595	Olcese Sand, CA	-
Bruclarkia santacruzana				
Agasoma barkerianum	8	California Geol.Survey Coll.	Barker Ranch, CA	-
Agasoma barkerianum	2	California Geol.Survey Coll.	Barker Ranch, CA	-
Bruclarkia barkerianum	2	UCMP 3688	Near Kern River, CA	-
Bruclarkia barkeriana	1	UCMP 2713/ E26	Temblor Fm., CA	-
Bruclarkia barkeriana santacruzanum **HP, PL**	1	UCMP 31593/ A585	Vaqueors Fm., CA	Loel & Corey, 1932
??	1	UCMP 32806/ B1598	Olcese Sand, CA	Addicott, 1970
Bruclarkia barkeriana	1	UCMP B1657	Olcese Sand, CA	-
Bruclarkia barkeriana var. santacruzanum	3	UCMP B1616	Olcese Sand, CA	-
Bruclarkia barkeriana forma. santacruzana	2	UCMP B1660	Freeman-Jewett Silt, CA	-
Bruclarkia gravida				
Bruclarkia columbiana **H**	1	CAS 155	Pittsburg Bluff, OR	Anderson & Martin, 1914
Bruclarkia columbiana **CT**	1	CAS 156	Pittsburg Bluff, OR	Anderson & Martin, 1914
Bruclarkia columbiana **HP**	1	UCMP 32442/ A9	Pittsburg Bluff, OR	Weaver, 1942
Bruclarkia chehalisensis n. sp. **H**	4	UWBM 27726/ A413	Lincoln Fm., WA	Armentrout, 1973
Bruclarkia columbiana **HP**	1	UCMP 35394/ A3702	Pittsburg Bluff, OR	Durham, 1944
Bruclarkia fulleri **PT**	1	UCMP 35396/ A10	Quimper Fm., OR	Durham, 1944
Bruclarkia fulleri **H**	1	UCMP 35395/ A10	Quimper Fm., OR	Durham, 1944
Bruclarkia chehalisensis nodulosa	1	UWBM	Lincoln Creek Fm., WA	
Bruclarkia cf. acuminata	4	UWBM 43658/ WA313	Shookumchuck Fm?, WA	
Bruclarkia columbiana	10	CAS 69271/ 167	(near Claskanie), OR	-
Bruclarkia columbiana	2	CAS 69270/ 4	(near Claskanie), OR	
Bruclarkia columbiana	18	UCMP 55093/ D8281	Clatskanie Beds, OR	-
Bruclarkia columbiana	4	UCMP D9045	Clatskanie Beds, OR	-
Bruclarkia columbiana	5	UCMP A3669	Pittsburg Bluff, OR	-
Bruclarkia columbiana	3	UCMP A1601	Pittsburg Bluff, OR	-
Bruclarkia columbiana	1	UCMP A3782	Pittsburg Bluff, OR	-
Bruclarkia columbiana	2	UCMP/USGS 15264/ 55085	Pittsburg Bluff, OR	-
Bruclarkia columbiana	2	UCMP Ellen Moore Material	Pittsburg Bluff "Gries Ranch", OR	-
Bruclarkia columbiana	1	UCMP 3636	Pittsburg Bluff, OR	-
Bruclarkia columbiana	3	UCMP A194	Pittsburg Bluff, OR	-
Bruclarkia columbiana	14	UCMP 15264	Pittsburg Bluff, OR	-
Bruclarkia columbiana	3	CAS 69273/NP5/ 473	Pittsburg Bluff, OR	-
Bruclarkia columbiana	1	UCMP 1001	Pittsburg Bluff, OR	-

Bruclarkia columbiana	2	UCMP A3702	Quimper Fm., OR	-
Bruclarkia fulleri	1	UCMP A1802	Quimper Fm., OR	-
unidentified	56	UCMP A1607	Tunnel Point Ss, OR	-
unidentified	1	UCMP A1682	Tunnel Point Ss, OR	-
Bruclarkia columbiana	1	UCMP B7660	Tunnel Point Ss, OR	-
Bruclarkia columbiana	2	UCMP A4660	Tunnel Point Ss, OR	-
Bruclarkia columbiana	4	UCMP 3200	Pleito Fm., CA	-
Bruclarkia columbiana	1	UCMP 3207	Pleito Fm., CA	-
Bruclarkia columbiana	1	UCMP 14492/ A364	Lincoln Creek Fm., WA	Armentrout, 1973
Bruclarkia columbiana	4	UCMP A20	Lincoln Creek Fm., WA	
Bruclarkia columbiana	2	UCMP 69274/ NP9	Schenck Loc. NP 9	-
Bruclarkia n. sp.	1	USGS ??	Loc. 15298, OR	-
Bruclarkia gravida	4	UCMP D118	San Ramon Fm., CA	-
Bruclarkia acuminata	2	UWBM 65790/ A42	Lincoln Fm., WA	-
Bruclarkia columbiana	1	UCMP/USGS 15298	Scappoose, OR	-
Bruclarkia columbiana	4	UCMP D8218	Clatskanie Beds, OR	-
Bruclarkia columbiana	2	CAS 69271	Clatskanie Beds, OR	-
Bruclarkia gravida	3	UCMP 14	San Ramon Fm., CA	-
Bruclarkia gravida	2	UCMP A4661	San Ramon Fm., CA	-
Bruclarkia gravida	2	UCMP D118	San Ramon Fm., CA	-
Bruclarkia gravidum	1	UCMP 3199	Pleito Fm., CA	-
Bruclarkia gravida	1	UCMP 55080/ 1131	San Ramon Fm., CA	-
Bruclarkia gravida **HP**	2	UCMP 32426/ A4661	San Ramon Fm., CA	Hertlein, 1951
Bruclarkia gravida **LT**	1	CAS 4345	San Ramon Fm., CA	Stewart, 1926
Bruclarkia gravida	1	CAS 4345a	San Ramon Fm., CA	Stewart, 1926
Bruclarkia vokesi				
unidentified	3	CAS 69272/ 217	Unknown, WA	-
unidentified	1	CAS 69257/ 3162	Eugene Fm., OR	-
Bruclarkia vokesi **HP,** *Bruclarkia precursor* **H**	1	USNM 251391/ USGS 15282	Keasey Fm., OR	Hickman, 1980
Bruclarkia vokesi **HP,** *B. precursor* **PT**	1	USNM 251392/ USGS 15282	Keasey Fm., OR	Hickman, 1980
unidentified	2	CAS 69254/ 2126	Eugene Fm., OR	-
unidentified	1	CAS 69256/ 3133	Eugene Fm., OR	-
unidentified	3	USGS 18798	Eugene Fm., OR	-
unidentified	2	UCMP 4084	Eugene Fm., OR	-
Bruclarkia precursor Vokes	1	USGS 15274	Keasey Fm., OR	-
Bruclarkia precursor Vokes	1	USGS 15277	Keasey Fm., OR	-
Bruclarkia precursor Vokes	2	USGS 15280	Keasey Fm., OR	-
Bruclarkia precursor Vokes	1	USGS 15281	Keasey Fm., OR	-

Bruclarkia precursor Vokes	1	USGS 15282	Keasey Fm., OR	-
Bruclarkia precursor Vokes	1	USGS 15307	Keasey Fm., OR	-
Bruclarkia precursor Vokes	1	USGS 15309	Keasey Fm., OR	-
Bruclarkia precursor Vokes	1	USGS 15508	Keasey Fm., OR	-
Bruclarkia ellenae				
Bruclarkia oregonensis **HP**	1	UCMP 31994/ 9015	Astoria Fm., WA	Etherington, 1931
Bruclarkia oregonensis	1	UCMP 69266/ 45173	Astoria Fm., WA	-
Bruclarkia oregonensis	10	UCMP 69261/ 45131	Astoria Fm., WA	-
Bruclarkia barkeriana	1	UCMP 908/ A4961	Temblor Fm., CA	-

Footnotes

1. The specimen label for this Hypotype (external mold and cast) erroneously describes it as figured in Durham, 1944 as figure 16, Plate 16. The specimen figured in Durham, 144, Plate 16, Fig. 16 is *B. acuminata*, UCMP Hypotype no. 35391. Loc. 3710.
2. The CAS holotype and cotype specimens are worn and damaged compared to their pictures in Anderson and Martin, 1914.
3. This specimen has characters unlike other *B. barkerianum* specimens, for example, it has two rows of horizontal nodes on its penultimate whorl. This is more like *B. acuminatum*, but has clear characters that unite it with the other *B. barkerianum* species.
4. The specimen label for these fossils lists "U.C. Vol. 8, No. 10, p. 253, Pl. 25", which is English, 1914. However, these fossils are not figured in English, 1914.
5. This specimen has the characteristics of *B. oregonensis* AND the sinuous suture collar developed onto lower portion of penultimate whorl common in *B. barkeriana*.

Molecular systematics of Buccinidae (Neogastropoda) of the North Pacific: relationships of some major genera and subfamilies

Abstract

Marine whelks in the Family Buccinidae make up one of the most diverse, commercially important, and widespread clades of carnivorous marine gastropods. The fauna of Japan alone includes 344 buccinid species within ten putative subfamilies. Most phylogenetic relationships among genera in this family are unresolved and neither the extent nor composition of subfamilies has been rigorously tested using molecular data. To contribute to the resolution of buccinid relationships, taxa from the North Pacific (n=22) and western Atlantic (n=1) were collected and sequenced for the mitochondrial gene CO1 and the nuclear gene 28S. Analyses included these 23 taxa and 20 additional buccinids and outgroup species whose sequences were retrieved from GenBank. Phylograms were created using maximum likelihood criteria in PhyML and Bayesian inference in MrBayes. Combined (CO1 + 28S) and single gene analyses were performed with the inclusion of putative buccinid genera *Busycon* and *Busycotypus* (Melongenidea *sensu* Wade, 1917, and Buccinidae *sensu* Bouchet and Rocroi, 2005). Resulting phylogenies suggest that: (1) Buccinidae is monophyletic, (2) *Busycon* and *Busycotypus* belong within Buccinidae; (3) Beringiinae, Buccininae, Busyconinae, Neptuneinae, and Photinae are monophyletic subfamilies; and (4) *Neptunea*, *Buccinum,* and *Busycon* are monophyletic genera. Several genera including *Lirabuccinuum, Microfusus*, and *Solenosteira* either fell outside of the family in some analyses or were based in polytomies. Buccinid characteristics during larval development are presented in a cladistic framework, which reveals two distantly related species with planktonic larvae. Though preliminary, these data suggest considerable evolutionary diversification of early development in the family.

Introduction

Phylogenetic studies of major extant marine gastropod clades have focused largely on tropical and/or shallow water taxa such as the calyptraeid limpets (Collin, 2003), cerithoideans (Lydeard et al., 2002), columbellids (deMaintenon, 1999), cypraeids (Meyer, 2003), littorinids (Reid, 1989; Reid, 1990b; Reid, 1990a; Winnepenninckx et al., 1998;Williams et al., 2003), conoideans (Puillandre et al., 2008), muricids (Vermeij and Carlson, 2000; Claremont et al., 2008), opithsobranchs (Grande et al., 2004; Vonnemann et al., 2005), patellid limpets (Koufopanou et al., 1999), and trochids and turbinids (Williams and Ozawa, 2006). Less research has attempted to understand the phylogenetic relationships within families of cooler-water gastropods, particularly those in the high-latitude North Pacific. The few groups of such inquiry include the Japanese cerithids (Ozawa et al., 2009) and selected buccinids from the North Pacific and Sea of Japan (e.g. Hayashi 2005; Iguchi et al. 2008). Buccinid gastropods at high latitudes are uniquely suited to studies of evolution, speciation, phylogeography, and larval development because the family is species-rich, diverse in life history strategies, and has a rich fossil record. Although recent efforts have begun to elucidate the phylogenetic relationships within the Buccinidae, many sublittoral and deep water (>350 m) taxa remain unresolved (Warén and Smith, 2006).

The buccinid whelks comprise a predominantly cold-temperate and polar marine clade with a global distribution that peaks in species diversity in the high-latitude North Pacific (Borulya and Bregman, 2002; Martell et al., 2002; Nesbitt, 2003; Kos'yan and Kantor, 2007). The neogastropod clade, of which buccinids are part, originated during the Cretaceous in temperate oceanic provinces outside of the tropical Tethys (Sohl, 1987). By the early Oligocene, buccinids had experienced a rapid evolutionary radiation in the North Pacific in response to late Eocene/early Oligocene global cooling (Nesbitt, 2003). This proliferation was followed by Neogene migrations of various clades into the Oregonian and Californian Provinces of the east Pacific and subarctic and cool-temperate zones of the west Pacific (Oleinik and Marincovich, 2003). Rapid speciation in these clades occurred during the Miocene and Pliocene, when it outpaced even the Conidae (Crame, 1997).

All buccinids are dioecious and many species aggregate during mating (Ilano et al., 2004). Females lay egg capsules on benthic substrates in clutches, egg towers, or in *Busycon* and *Busycotypus* as capsule strings anchored in the sand (Harasewych, 1982). In some taxa it is common for females to deposit egg clutches onto the shells of conspecifics (e.g. *Solenosteira, Neptunea,* and *Kelletia*) (Habe, 1960; Power and Keegan, 2001). Although egg capsule structure has not be formally reviewed in the Buccinidae, a preliminary examination (Vendetti, unpublished) reveals that capsule morphology is diverse across the family and can be vasiform, discoidal, lenticular, or lingulate.

Buccinid larval development begins within benthic egg capsules that contain few to hundreds of individuals. Larvae either pass through metamorphosis within the capsule, (non-planktonic development) or swim away as veligers and complete metamorphosis in the plankton (planktonic development). These developmental modes are not known to vary within buccinid species (Miloslavich and Dufresne, 1994; Tan and Morton, 1998). Many buccinids, especially those with non-planktonic development, have evolved specialized nutritive modes during encapsulation. These include the absorption of albumen (the proteinaceous fluid that fills the capsule), the ingestion of nurse eggs (developmentally arrested embryos), and the consumption of sibling larvae (adelphaphagy/cannibalism). Some buccinids, like *Neptunea antiqua,* encapsulate thousands of nurse eggs to feed one surviving hatchling (Thorson, 1949). Other species have no nutritive intracapsular eggs or embryos and develop non-planktonically (e.g. *Pareuthria plumbea*) or planktonically (*Kelletia kelletii*) (Rosenthal, 1970; Pastorino and Penchaszadeh, 2002).

As adults, whelks live on a variety of rocky and unconsolidated sediments from the upper intertidal to abyssal zone (Ota and Tokeshi, 2002). At depth they occur at hydrothermal vents, cold seeps, whale falls, and wood falls (Harasewych, 1998; Kantor and Harasewych, 1998; Okutani and Iwasaki, 2003; Amano and Little, 2005; Kiel and Goedert, 2006; Kiel and Goedert, 2007). Most feed as predators or opportunist scavengers and their dietary preferences range from polychaetes and bivalves to vertebrate carrion (Taylor et al., 1980; Shimek, 1984; Britton and Morton, 1993). Their predation strategies include shell wedging and marginal chipping of bivalves as well as engulfment of small prey items including other gastropods (Shimek, 1984; Power et al., 2002). Notably, members of the buccinid genus *Neptunea* sequester tetramine toxin in their salivary glands, presumably to be used in prey capture, though its role is unclear (Kawashima et al., 2002; Barceloux, 2008;). Tetramine is a neurotoxin that is also used by carnivorous turrids, terebrides, and conids to subdue prey (Shindo et al., 2000; Halstead, 2001; Power et al., 2002).

The buccinid fauna in Japanese waters is the most diverse in the world, comprising 344 species within ten putative subfamilies (Higo et al., 1999). It includes intertidal to deep water taxa from subtropical to subarctic latitudes that span fifteen degrees in the northwest Pacific and Sea of Japan (fig. 1A, B). Here, tropical and boreal ocean currents (the Kuroshio, Oyashio, and Tsushima) flow along the coasts of the Japanese islands extending the typical ranges of warm-water and cold-water buccinid taxa (Kuroda and Habe, 1952) (fig. 1A, B).

In the Bering Sea, Sea of Okhotsk, West Pacific, and Sea of Japan, many whelk species from the continental shelf and slope (fig. 1B-D, Table 1) are harvested by trawl and baited trap for a lucrative Japanese fishery (MacIntosh and Somerton, 1981; Okutani et al., 1988; Fujinaga et al., 2006; Iguchi et al., 2007; Iguchi et al., 2008). Whelk harvesting by trawling occurs in the fall, winter, and spring and baited trapping is done in the summer months (T. Haga, personal communication). At least 22 buccinid species in the greater North Pacific and Sea of Japan, predominantly of the genera *Buccinum* and *Neptunea*, are commonly harvested and sold year-round as "tsubu gai" [Japanese for whelk] in seafood markets throughout Japan (personal observation and T. Haga personal communication) (fig. 2).

Recent studies of the Buccinidae have addressed life history strategies (Ota and Tokesi, 2002; Pasterino and Penchaszadeh, 2002; Valentinsson, 2002; Nasution, 2003; Son, 2003; Ilano et al., 2004; Miranda et al., 2008), imposex in response to tributyltin (TBT) compounds (Power and Keegan, 2001; ten Hallers-Tjabbes et al., 2003; Fujinaga et al., 2006), internal anatomy (Harasewych and Kantor, 2002a; Kos'yan and Kantor, 2004; Kos'yan and Kantor, 2007; Kos'yan, 2007), and phylogenetic relationships using morphological (Kos'yan and Kantor, 2007) and molecular data (Harasewych et al., 1997; Hayashi, 2005; Iguchi et al., 2007; Dong et al., 2008; Iguchi et al., 2008; Hayes and Karl 2009). Despite these important efforts, most buccinid workers emphasize the need for further resolution of phylogenetic relationships and hierarchical systematics (e.g. subfamilies) in the clade (Vermeij, 1991; Harasewych, 1998; Amano and Vermeij, 2003; Hayashi, 2005) (Table 2). To contribute to this effort, I generated molecular phylogenies based on two genes and 35 novel molecular sequences from 23 putative buccinid species in a total dataset of 43 taxa. This is the largest sample size for a molecular phylogenetic analysis of buccinids to date. Phylogenies were produced using Bayesian inference and maximum likelihood approaches and were used to test Buccinidae monophyly, identify buccinid subfamilies, determine the phylogenetic affinity of the genera *Busycon* and *Busycotypus* (previously classified in the Melongenidae), and map the distribution of larval developmental modes.

Materials and Methods

Taxon collection and identification

Ten of the 23 buccinid species sequenced for this study were purchased live from seafood markets in the Japanese cities of Nagoya, Joetsu, Tokyo, and Sendai in July and August of 2008 (Table 3). Specimens were frozen on site and transported on ice (e.g. Yamato Transport) to the laboratory where they were stored at -80°C. Ten additional buccinid species from Japan were generously given to the author from the personal collections of T. Haga (University of Tokyo), Mr. Higuchi of Sendai, M. Kumagai (Museum of Sea and Shells, Rikuzen-Takata, Japan), and S. Hayashi (Nagoya University). Three North American taxa, *Solenosteira macrospira, Kelletia* *kelletii,* and *Busycotypus canaliculatus (= Busycon canaliculatum)*, were acquired from R. Grosberg (UC Davis), T. Herrlinger (UC Berkeley), and the author from the 99 Ranch Market in Richmond, California, respectively. Shells of voucher and representative specimens are figured in Plates 1 and 2. Museum abbreviations for figured specimens are: NSMN = Nishinomiya Shell Museum, Nishinomiya (Japan), UCMP = University of California, Museum of Paleontology, UKM = Museum of Sea and Shells, Rikuzen-Takata (Japan), UMUT = The University Museum, The University of Tokyo (Japan). Digital images of voucher shells are available at Cal Photos (http://calphotos.berkeley.edu).

Gastropod tissue was sampled by excising approximately 1 cm^3 of un-mottled or un-pigmented frozen foot muscle and placing it into 95% ETOH. After DNA extraction, the remainder of this tissue was retained as a specimen voucher in the Invertebrate Tissue Collection at the University of California Museum of Paleontology (UCMP) at -80°C. In total, thirteen putative buccinid genera and 23 species were sampled. The majority of these species were in the genera *Buccinum* and *Neptunea* (15/23, 65%), the most species-rich buccinid clades in the western North Pacific and the Sea of Japan. Collected specimens were identified from shell morphology using four guides to Japanese molluscs: Higo et al. (1999), Okutani (2000), Okutani et al. (1988), and Kira (1972). Additional sequence data from taxa in the Buccinidae and neogastropod families Babyloniidae, Melongenidae, Conidae, and Muricidae were accessed from GenBank.

DNA extraction, amplification, and sequencing

Extraction

DNA was extracted from 25 mg tissue samples following the Spin-Column Protocol in the Qiagen DNeasy® Blood and Tissue Kit. All tissue samples were lysed in proteinase K and ATL buffer overnight (>8 hrs). Portions of the rapidly evolving mitochondrial CO1 (cytochrome oxidase subunit 1) gene and the more slowly evolving nuclear 28S (large subunit ribosome RNA) gene were sequenced. Used together, CO1 and 28S have been effective in resolving phylogenetic relationships within another neogastropod family, the Muricidae (Claremont et al., 2008).

Amplification and sequencing

The following primers were used to amplify approximately 1500 base pairs (bp) of 28S: LSU50F (forward) 5' TAG GTC GAC CCG CTG AAY TTA AGC A 3' and LSU1600R (reverse) 5' AGC GCC ATC CAT TTT CAG G 3' (Claremont, 2008). Primers for CO1 amplification of approximately 625 bp were: LCO1490 (forward): 5' GGT CAA CAA ATC ATA AAG ATA TTG G 3' and HCO2198 (reverse) 5' TAA ACT TCA GGG TGA CCA AAA AAT CA 3' (Folmer et al., 1994). The polymerase chain reaction (PCR) protocol for 28S followed the method of Williams and Ozawa (2006). To amplify partial CO1 sequence, the 16S protocol from Iguchi et al. (2004) was modified slightly resulting in the following steps: 35 cycles at 94°C for 5 minutes, 94°C for 30 seconds (denaturation), 50°C for 60 seconds (annealing), 72°C for 90 seconds (extension), 5 minutes at 72°C (extension), then 4°C until samples were removed from the PCR machine. PRC reactions of both CO1 and 28S were made in 25µl of total volume containing 0.5µM of forward and reverse primers, 0.5 U of AmpliTaq Gold® DNA Polymerase, 1x AmpliTaq Gold® Buffer 1 (Applied Biosystems), and 200µM dNTP. DNA template dilutions from 10x -100x were necessary to amplify some specimens. Multiple individuals of *Buccinum* and *Neptune*a were sequenced for CO1 to calculate intraspecific variation. Sequence length and quantity were evaluated using 1% agarose gel electrophoresis. PCR products were cleaned with ExoSAP-IT® (Affymetrix, Inc.) and partial gene segments were sequenced by a 96 capillary 3730xl DNA Analyzer (Applied Biosystems). Primers for amplification and sequencing were identical, and 28S data were sequenced in both forward and reverse directions. A list of all species included in this study and their accession numbers in GenBank are provided in Table 3.

Molecular Sequence Datasets

Partial sequence data from putative buccinids and outgroup taxa were analyzed in six sets: (A) CO1 (n=37), (A_1) CO1 dataset A with the exclusion of *Busycotypus canaliculatus* (GenBank accession #: BCU86325, Harasewych et al., 1997) (n=36), (B) CO1 of taxa in dataset A excluding three *Conus* species (n=35), (B_1) CO1 dataset B with the exclusion of *Busycotypus canaliculatus* (n=33), (C) 28S (n=26), and (D) combined 28S + CO1 (n=21). The muricid *Trophon plicatus* was set as the outgroup in all analyses.

Sequence Analysis and Alignment

Partial CO1 sequence data from *Busycotypus canaliculatus* (BCU86325) were included in datasets A and B, because this sequence was part of the neogastropod dataset analyzed by Harasewych et al. (1997) and it was desirable to compare their results to those in this study. This sequence was the only CO1 data available for *B. canaliculatus* because sequencing UCMP specimen 557055 was unsuccessful. However, the GenBank sequence of *B. canaliculatus* (BCU86325) is described as a pseudogene, so datasets A and B were also analyzed excluding it.

Partial 28S sequences were assembled from overlapping forward (410 bp) and reverse (835 bp) strands in the program Geneious 4.5.5 (Drummond et al., 2008). CO1 and 28S sequences were combined into dataset D for all taxa with available sequences. To account for insufficient genetic data from the same specimens, composite chimeras of CO1 and 28S were created from different individuals of *Buccinum tsubai* and *Buccinum undatum* and from closely related genera for *Busycon/Busycotypus sp.* (*Busycotypus canaliculatus* (28S) and *Busycon carica* (CO1)). The latter sequence was created because the available CO1 data for *Busycotypus canaliculatus* (BCU86325) as described above is a pseudogene and therefore is not orthologous to other CO1 sequences in this analysis. Although *Busycotypus canaliculatus* (28S) and *Busycon carica* (CO1) are not of the same genus or species, they are closely related and were considered justifiable compliments to each other. These taxa were analyzed together in dataset D as the chimera taxon, *Busycon/Busycotypus sp*.

After trimming, all sequences were globally aligned with free end gaps in Geneious Align (Drummond et al., 2008) using the following default settings: 65% cost matrix, gap penalty of 12, and gap extension penalty of 3. Alignments were checked by eye and poorly aligned sections were either manually corrected or removed. All CO1 sequences were translated to check for gastropod stop codons. Pairwise genetic distances, the proportion of phylogenetically informative nucleotide sites, and estimates of divergence between sequences were calculated using MEGA 4 (Tamura et al., 2007) and DAMBE 5.0.80 (Xia, 2001; Xia and Xie, 2001). Models of sequence evolution were estimated by Modeltest in PAUP* 4.0b 10 (Swofford, 2003) using Akaike Information Criterion (AIC) in a stepwise, heuristic search.

Tree Construction

Phylograms were constructed using maximum likelihood (ML) criteria in PhyML (Guidon and Gascuel, 2003) and Bayesian inference with Markov Chain Monte Carlo (MCMC) in MrBayes (Ronquist and Huelsenbeck, 2003). These programs were run within Geneious 4.5.5 (Drummond et al., 2008). Resulting phylograms were manipulated in FigTree v1.2.2 (Rambaut, 2009) and edited in Adobe Illustrator CS4.

Bayesian Analyses

Four separate analyses of datasets A-D were performed in MrBayes. The first, for datasets A, A_1, B, and B_1 used the sequence evolution model (General Time Reversible) GTR+I+Γ and included: an MCMC chain length of 1,100,000 generations, four heated chains, a burn-in length of 110,000, a subsample frequency of 200, and unconstrained branch lengths. In the second analysis, the same parameters were applied to dataset C with the exception of chain length and subsampling, which were increased to 2,000,000 and 350, respectively. The third analysis partitioned dataset D (28S + CO1) by gene and by codon position for CO1 only, and used the sequence evolution model GTR+SS+Γ. This model maximally unlinks parameters allowing them to vary independently and account for saturated codon positions, if present. The fourth analysis also partitioned dataset D, but used the Chunky method of non-parametric Bayesian inference (Huelsenbeck, 2009). This method employed a E(K)=2 model with a Dirichlet process prior and "Chinese restaurant process" of distribution over all parameters, which explored potential linkages and considered partitioning schemes themselves as variables (Huelsenbeck, personal communication).

All MrBayes analyses were performed twice for each dataset and the average standard deviation of split frequencies was compared between runs. The second and third Bayesian analyses described above included an MCMC chain length of 1,000,000, a subsample frequency of 100, and a burn-in fraction of 0.25. The Bayesian Chunky method cladogram was a 50% majority-rule consensus tree of 10,000 trees. No codon positions were excluded from any MrBayes analysis. Phylograms and corresponding posterior probability values generated by MrBayes are figured in this paper with bootstrap values from PhyML analyses included at nodes if they are greater than or equal to 70/100.

PhyML Analyses

Maximum likelihood analyses were performed in PhyML for datasets A-D. For each analysis, 1,000 bootstraps were run and tree topology, branch lengths, and rate parameters were optimized. Because PhyML does not distinguish ingroup versus outgroup taxa in its algorithm, two analyses of each dataset were performed, as suggested by the program designers: one of putative ingroup taxa and another of all taxa (Guindon and Gascuel, 2003). Bootstrap values between these sets were compared and ingroup support values were only included on phylograms if they were greater than 70 and existed for nodes that were unsupported in the analysis of all taxa. Log likelihood scores for resulting phylograms are presented for the analysis of the full taxon set. The ingroup for datasets A and A_1 comprised all buccinids in the monophyletic subgroup created by the MrBayes analysis of 28S, with the addition of *Busycon carica* and *Busycon sinistrum* and the exclusion of *Busycotypus canaliculatus* for dataset A_1. Dataset B included the ingroup taxa chosen for dataset A and dataset B_1 excluded *B.*

canaliculatus. Ingroup taxa for datasets C and D included all putative buccinids that formed a monophyletic clade when all taxa were analyzed in MrBayes.

Analysis of CO1 and 28S Combinability

To analyze the combinability of 28S and CO1 sequences, a partition homogeneity test, or incongruence length difference (ILD) test, was performed in PAUP*. Five hundred replicates were analyzed with the maxtrees option set to 1,000, and excluding invariant sites and autapomorphic characters, following the procedure of Collin (2003).

Analysis of CO1 Saturation

To examine the phylogenetic information and potential saturation in each codon position of CO1, four analyses were performed: (1) six parsimony cladograms (50% majority-rule consensus) generated in MEGA 4 from each codon position separately and in combination (sites 1+2, 2+3, and 1+3) with all gaps and missing data removed from the dataset, (2) three maximum likelihood phylograms generated in DAMBE from the complete CO1 sequence, position one, and position two using the "quick add" tree-making option, (3) three graphs (for all codon positions, position 1, and position 3) created in DAMBE that plotted the estimated number of transitions and transversions in CO1 against genetic distance, and (4) the evolutionary divergence percentages between sequences estimated in MEGA 4 based on a pairwise analysis of taxa for each codon position, using a maximum composite likelihood method. The rate variation among sites was also calculated in MEGA 4 using a gamma distribution (shape parameter = 1) with all gaps and missing data eliminated from the dataset.

Results

DNA amplification & Babylonia japonica

Taxa did not amplify with equal success for CO1 and 28S. The genus *Buccinum* amplified more easily for CO1 than for 28S, whereas *Neptunea* amplified almost equally well for both genes. *Babylonia japonica* (Reeve, 1842), until recently classified as a buccinid, was collected from a seafood market in Japan and sampled for DNA, but did not amplify successfully for either CO1 or 28S. A Bayesian analysis of CO1 in buccinids including a *B. japonica* sequence acquired from GenBank (accession #: AF37388, Harasewych and Kantor, 2002a) revealed that this taxon falls outside of the Buccinidae (Appendix, fig. 1). The log likelihood score for this phylogram is -5661.728 in MrBayes and -5645.00 in PhyML. These results corroborate other molecular (16S, 28S, and CO1) and morphological analyses that suggest *Babylonia* is likely a neogastropod but not a buccinid (Harasewych and Kantor, 2002a; Kantor, 2003; Hayashi, 2005; Dong et al., 2008).

Sequence Analysis and Models of Evolution

Sequences of CO1 and 28S aligned unambiguously in single gene alignments and contained poorly aligned sections only in the combined gene dataset. Poorly aligned sections were manually corrected and a small segment was removed. Translated CO1 sequences revealed no gastropod stop codons. CO1 sequences were more phylogenetically informative than 28S sequences. Parsimony informative characters comprised 37% of CO1 and 6.11% of 28S. Parsimony informative sites were evenly distributed throughout CO1, whereas in 28S they were concentrated in "hot spots" between bases 94-113 (7 parsimony informative sites) and 381-729 (50 parsimony informative sites). Modeltest in PAUP* chose the sequence evolution model

GTR+I+Γ for datasets A, B, and D, and (Tamura Nei) TrN+I+Γ for dataset C (Table 3). The Tamura Nei model was used for dataset C when it was analyzed in PhyML.

Saturation in CO1: parsimony and maximum likelihood methods

Parsimony cladograms generated in MEGA 4 revealed that (trees not shown): (1) codon position 1 when analyzed alone created a polytomy for all taxa except the three *Conus* species, (2) codon position 2 generated well-resolved and monophyletic clades for *Buccinum, Busycon, Neptunea* and *Melongena* and *Conus*, though *Conus* (considered an outgroup) nested within the Buccinidae and sister to *Clinopegma,* (3) codon position 3 resolved a monophyletic *Buccinum, Melongena*, and *Busycon*, but revealed *Conus* as polyphyletic. The DAMBE maximum likelihood phylograms (not shown) resolved *Conus, Buccinum, Busycon, Melongena,* and *Neptunea* as monophyletic in analyses of all codon positions and codon position two. In the phylogram for position 3, all genera were monophyletic except *Conus*, which split into *C. nux* + *C. ammiralis* and *C. wakayamaensis*, the latter species nesting within *Buccinum* and sister to *Fasciolaria tulipa*.

Saturation in CO1: genetic distance methods

Graphs of CO1 transitions and transversions versus genetic distance (model K80) revealed that codon position 3 is likely saturated (fig. 3). This result is confirmed by an analysis of estimates of pairwise distance between sequences, which identified the greatest genetic distance of all taxa between *Conus wakayamaensis* and other taxa (0.049 base substitutions per site) at position 1, between *Conus nux* and *Favartia alveata* (14.08) at position 2, and between *Conus wakayamaensis* and *Hexaplex trunculus* (0.27) at position 3. The likelihood estimates of nucleotide substitutions within CO1 are presented in Table 4. Results of the saturation analyses described above and the long branches of *Conus* species evident on each phylogram produced in PhyML and MrBayes were used to justify removing *Conus* from dataset B, while retaining all codon positions of other taxa.

Partition Homogeneity Test

Combined 28S and CO1 sequences had 279/2055 parsimony information sites and 401/2055 variable sites. The partition homogeneity/incongruence-length difference test for CO1 and 28S indicated conflict between the data sets (P=0.02). This conflict was resolved when the outgroup taxon *Favartia alveata* was removed. Therefore, dataset D excludes this species.

Nucleotide frequency and genetic distance

The nucleotide frequencies in CO1, estimated by MEGA, are 0.256 (A), 0.366 (T), 0.179 (C), and 0.2 (G). The transition/transversion rate ratios are $k_1 = 4.196$ for purines, $k_2 = 4.351$ for pyrimidines, and the overall transition/transversion bias is $R = 1.815$. The nucleotide frequency of CO1 (all codon positions) and CO1 position 3 estimated by DAMBE are summarized in Appendix Tables 1, and 2, respectively.

For *Buccinum* and *Neptunea*, genetic distance was calculated between species for 28S, and between and within species for CO1. Sequence data from 28S suggest that there is greater maximum genetic distance between *Buccinum* species (n=5) than between *Neptunea* species (n=7), at approximately 1.1% vs. 0.8%, respectively. For CO1, genetic distance is also greater overall within *Buccinum* than within Neptunea. However, genetic distance was detected within three species of *Neptunea*: *N. arthritica* (n=2)*, N. constricta* (n=3), and *N. cumingii* (n=3). Zero genetic distance was found within the *Buccinum* species *B. bayani* and *B. middendorffi*. These results are summarized in Table 5.

MrBayes analysis of CO1 in *Neptunea* (n=15) and *Buccinum* (n=11) found *N. arthritica* and *N. constricta* to be paraphyletic (fig. 4**)**. This topology may indicate that the CO1 gene evolves too fast for phylogenetic resolution of some species, but that it is informative at the genus level and could also be at the population level. Although *N. arthritica* is paraphyletic, its position relative to *N. cumingii* is not entirely inconsistent with current classification, which often considers *N. cumingii* a subspecies of *N. arthritica* (Okutani et al., 1988; Okutani, 2000).

Phylogenetic Hypotheses: Bayesian and maximum likelihood analyses

In MrBayes analyses of CO1, the Buccinidae is an unresolved, polyphyletic clade (figs. 5A, 5B), but is monophyletic when analyzed for 28S and 28S + CO1 (figs. 5C, 5D). Phylograms produced in PhyML support this topology and the majority of phylogenetic relationships illustrated in Figure 5, with the exception of dataset D (CO1 + 28S). Phylograms created from datasets A_1 and B_1, which exclude *B. canaliculatus*, also support the phylogenetic relationships and topologies of phylograms 5A, 5B, and Appendix fig. 2. All analyses support the inclusion of *Busycon* and *Busycotypus* within the Buccinidae, and all but phylogram D have high confidence values for this topology. Log likelihood scores for MrBayes and PhyML analyses as well as other characteristics of datasets A-D are presented in Table 6.

Phylogenetic Hypotheses: datasets A and B

Bayesian and maximum likelihood analyses of CO1 data (figs. 5A, 5B**)** reveal a polyphyletic Buccinidae in which *Microfusus magnifica* falls outside of the family and nests sister to the muricid *Favartia alveata*. In dataset B, the Buccinidae clade excluding *M. magnifica* is supported by a Bayesian posterior probability of 78%. In the PhyML analysis of this dataset, *M. magnifica* also nests sister to *Favartia alveata* and the polytomy at the base of the Buccinidae includes *Fasciolaria tulipa* and the *Melongena* species, though with a bootstrap values less than 50 (phylogram not shown).

In all analyses of datasets A and B, *Buccinum, Busycon*, and *Neptunea* are monophyletic and *Busycon* and *Busycotypus* form a well-supported clade within the Buccinidae (disregarding *Microfusus magnifica*) (figs. 5A, 5B). The Melongenidae genus *Melongena* falls outside of the Buccinidae (excluding *M. magnifica*) and nests sister to *Fasciolaria tulipa* in both analyses. The topology and support values of phylograms 5A and 5B are congruent with those from datasets A_1 and B_1 (Appendix, fig. 2). The log likelihood scores for the latter phylograms are -6054.54 ± 177 (A_1) and -5298.96 ± 0.485 (B_1) in MrBayes and -6039.074 (A_1) and -5278.244 (B_1) in PhyML.

Unresolved or poorly supported taxa in phylograms from datasets A and B include *Lirabuccinum fuscolabiatum, Nassaria sp*., and *Solenosteira macrospira*. The placement of *Clinopegma*, though clearly within the Buccinidae, is also dubious with respect to other buccinids. It either creates a polytomy with the *Neptunea* and *Busycon + Beringion + Buccinum* clades (fig. 5A) or is sister to the *Neptunea* and *Busycon + Beringion + Buccinum* clades, but with low support (67% posterior probability, 20.3 bootstrap support) (fig. 5B).

Phylogenetic Hypotheses: dataset C

Bayesian and maximum likelihood phylograms derived from 28s data (fig. 5C**)** support a monophyletic Buccinidae with a posterior probability of 100% and a bootstrap support value of 63.1. Like their resolution in CO1 analyses, *Buccinum* and *Neptunea* are monophyletic and *Busycotypus* nests within the Buccinidae in all MrBayes and PhyML phylograms. The genus *Clinopegma* nests sister to the *Beringion* + *Japelion* clade with 80% posterior probability but a bootstrap support value of only 24.5.

Three sister relationships between genera are also strongly supported by analyses of dataset C: *Buccinum* + *Volutharpa*, *Beringion* + *Japelion*, and *Kelletia* + *Nassaria*. A close phylogenetic association is also shown between *Busycotypus* and *Microfusus*, but this relationship is not supported in the PhyML analysis of all taxa, and is only recovered by relatively poor support in MrBayes (posterior probability 57%) and the ingroup PhyML analysis (bootstrap support value 71.3).

Phylogenetic Hypotheses: dataset D

The combined 28S + CO1 dataset analyzed using MrBayes resolves a monophyletic Buccinidae with a posterior probability of 61%. When analyzed in PhyML this monophyly is violated by *Conus*, which nests within it (phylogram not shown). Like the singe gene trees of fig. 5A-C, phylogram D also recovers *Neptunea* and *Buccinum* as monophyletic and includes *Busycon/Busycotypus sp.* within the Buccinidae. The latter taxon has an unresolved position within the family, creating a polytomy with *Microfusus magnifica* and the remaining buccinid clades (fig. 5D).

When analyzed in MrBayes using the sequence evolution model GTR+SS+Γ, dataset D also supports the monophyly of the Buccinidae with nearly the same topology as in fig. 5D, but with 100% posterior probability (Appendix fig. 2). The Chunky method (Huelsenbeck, 2009) also resolves a monophyletic Buccinidae with 92% posterior probability, but because this analysis does not exclude any taxa (e.g. *Favartia alveata*) the species *Nassaria sp.* nests sister to the clade uniting *Beringion, Buccinum,* and *Clinopegma* (fig. 6).

Discussion

Buccinid Subfamilies

This study provides some of the first molecular evidence for valid subfamilies in the Buccinidae and confirms the inclusion of the Busyconinae within the family as suggested by previous morphological and molecular analyses (Kos'yan and Kantor, 2004; Bouchet and Rocroi, 2005; Hayes and Karl, 2009). Resulting phylograms recover five subfamilies with confidence values of at least 95 posterior probability or bootstrap support. They are the: (1) Beringiinae Golikov and Starobogatov, 1975 (*Beringion* + *Japelion*), (2) Buccininae Rafinesque, 1815 (*Buccinum* + *Volutharpa*), (3) Busyconinae Wade, 1917 (*Busycon* + *Busycotypus*), (4) Neptuneinae Stimpson, 1865 (*Neptunea*), and (5) Photinae Gray, 1857 (*Kelletia* + *Nassaria*) (fig. 7). These clades are consistent with the subfamily designations made by authors Higo et al. (1999) for the Beringiinae, and Habe and Sato (1973) and Sakada and Tanaka (1999) when the subfamily was named Liomesusinae; Kuroda et al. (1971), Habe and Sato (1973), Titova (1994), and Higo et al. (1999) for the Buccininae; Akers and Akers (1997), Kos'yan and Kantor (2004), Bouchet and

Rocroi (2005), and Hayes and Karl (2009) for the Busyconinae; many authors including Higo et al. (1999) and Habe and Sato (1973) for the Neptuneinae; and Kuroda et al. (1971) for the Photinae (see Table 2). A scenario for the tree topology of these confirmed subfamilies is depicted in fig. 8.

This scenario supports as well as challenges a variety of hypotheses of buccinid systematics proposed since the late 1990s. For example, in 1997, Harasewych et al. included *Neptunea*, *Buccinum*, *Busycon*, and *Busycotypus* in an analysis of the Neogastropoda using 18S rDNA and CO1 data. Their results identified CO1 but not 18S as a useful gene for revealing relationships between these genera in maximum parsimony (MP), maximum likelihood (ML), and neighbor-joining (NJ) analyses. Hayashi's (2005) treatment of the Buccinidae included 17 putative buccinid species in MP and ML analyses of the complete 16S rRNA gene. Resulting phylograms did not support a monophyletic Buccinidae, but did recover sister relationships between *Buccinum* + *Neptunea* and *Penion* + *Kelletia*. In 2007, Iguchi et al. also analyzed 16S sequence data and used Bayesian and NJ approaches to elucidate relationships within *Buccinum* species (n=8) from the Sea of Japan. Dong et al. (2008) analyzed *Buccinum, Neptunea, Japelion,* and *Siphonalia* for partial 28S gene sequences in distance-based (NJ) and minimum evolution (ME) analyses. Their results revealed a paraphyletic *Neptunea* and *Siphonalia*, but a monophyletic *Buccinum*. Most recently, an analysis of CO1 and 16S from the Melongenidae and Buccinidae by Hayes and Karl (2009) suggested that the Busyconinae subfamily belongs within the Buccinidae. The Busyconinae and other subfamilies of the Buccinidae suggested by the CO1 and 28S analyses presented here are reviewed below.

Subfamily Ancistrolepidinae

Though not supported directly by the analyses of this study, the Ancistrolepidinae is included in fig. 8 as *Clinopegma unicum* and *Ancistrolepis sp*. The genus *Ancistrolepis* originated in the middle Miocene and is often considered a subgenus of *Clinopegma* (Kantor, 1988 in Titova, 1993; Titova, 1994). Fossil evidence suggests that the Ancistrolepidinae originated in northern Japan and the Kamchatka Peninsula during the late Eocene and migrated across the North Pacific reaching North American by the early Oligocene (Titova, 1993). In contrast to many boreal buccinids, it did not migrate into the Artic and North Atlantic during the Pliocene (Titova, 1993). The modern distribution of this clade in the Pacific extends northward from Sagami Bay, Japan to the Gulf of Alaska and the Aleutian Islands. This subfamily has been proposed as a close relative of the Neptuneinae (Amano, 1997; Titova, 1993), although phylogenetic results from this study (figs. 5C, 5D) suggest that Ancistrolepidinae is more closely related to the subfamilies Beringiinae and Buccininae (fig. 5).

Subfamily Beringiinae

The genera *Beringion* and *Japelion* originated in the early middle Miocene in the northwest Pacific (Titova, 1993), possibly in response to global cooling that followed the climate optimum of the early middle Miocene (Titova, 1993). Species of *Beringion* migrated across the Pacific reaching the Gulf of Alaska by the late Oligocene, whereas *Japelion* remained endemic to Japan (Amano, 2005). Today, *Beringius* is found across the boreal North Pacific from Japan to California (Titova, 1993) as well as in the North Atlantic (Warén and Smith, 2006). The appearance of the Beringiinae after the origin of the Ancistrolepidinae (middle Miocene v. late Eocene) is consistent with molecular results from 28S analysis in this study, which suggest that the Beringiinae may branch off from the Ancistrolepidinae (fig. 7C, Ancistrolepidinae is represented by *Clinopegma*). The placement of *Japelion* in the 28S cladograms of Dong et al. (2008) does not support the phylogenetic relationships suggested in this paper. That is, instead of resolving *Japelion* as ancestral to a *Neptunea* + *Siphonalia* clade (Dong et al., 2008), results from this study suggest that *Japelion* + *Beringion* (+ *Clinopegma*) as sister to *Buccinum*, with *Neptunea* as ancestral (fig. 7).

Subfamily Buccininae

The Buccininae is a strictly boreal clade with a late Eocene origin in the North Pacific (Harasewych and Kantor, 1988; Titova, 1993). Paleontological evidence suggests that *Buccinum* appears in the late Eocene and *Volutharpa* by the late Pliocene (Titova, 1993; Titova, 1994). Between the late Miocene and early Pliocene, the Buccininae expanded their boreal range into the Arctic and North Atlantic through the Bering Strait (Titova, 1993; Amano and Watanabe, 2001). Fossils of both genera are found from Japan and California, which coincides with their modern distribution (Higo et al., 1999; Ruiz et al., 2006).

Contrary to paleontological data, the 28S phylograms presented in this study do not support a derived position of *Volutharpa* (fig. 5C). However, the union of these genera into a monophyletic clade is the first time that this relationship has been suggested by molecular data. In the analyses of Hayashi (2005) there is a strongly supported sister relationship between *Buccinum* and *Neptunea*, which would have been replicated in this study if a smaller or different taxon sample were analyzed (i.e. excluding *Clinopegma, Beringion, Japelion, Busycon, Busycotypus*, and *Volutharpa*). Data from 16S (Iguchi et al., 2007) reveals genetic similarity between *B. bayani* and *B. tenuissimum*, though CO1 phylograms in this study support a sister relationship between *B. bayani* and *B. striatissimum*. The latter relationship is supported, at least provisionally, by similarities in shell morphology (Okutani, 2000; Iguchi et al., 2007). Also, like Dong et al. (2008) and Iguchi et al. (2007), this study recovered a monophyletic *Buccinum.*

Subfamily Busyconinae

The genera *Busycon* and *Busycotypus* are shallow water taxa that have lived along the coasts of the North American Atlantic Ocean and Gulf of Mexico since the early Miocene (Kent, 1983; Dietl, 2004). Fossil evidence suggests that they comprise an endemic American clade with a northern range limit in New England and a southern limit in the Yucatan and Gulf of Mexico (Hollister, 1958). Unlike all other buccinid subfamilies described here, Busyconinae has a sparse fossil record in the North Pacific. A modern population of *Busycotypus canaliculatus* lives in the San Francisco Bay, but it was accidentally introduced there from the North American east coast in the 1930s (Hollister, 1958).

In 1997, Harasewych et al. reported that *Busycon carica* and *Busycotypus canaliculatus* had identical partial 18S rDNA sequences and nested sister to one another in analyses of CO1. In 2004, Wise et al. demonstrated similar results with molecular evidence that *Busycotypus canaliculatus* was sister to *Busycon*. Morphological evidence from the proboscis, salivary duct, and stomach also suggest that the Busyconinae should be classified within the Buccinidae and not the Melongenidae (Kantor, 2003; Kos'yan and Kantor, 2004; Bouchet and Rocroi, 2005). Molecular evidence from partial 16S rRNA and CO1 sequences suggest this as well (Hayes and Karl, 2009). Results of the study presented here confirm both of these outcomes; that *Busycon* and *Busycotypus* form a subfamily clade, and that this clade nests within the Buccinidae. This conclusion further challenges the validity of the Melongeninae as a Buccinidae subfamily (Ponder and Warén, 1988), because although the Busyconinae nest within the family, members of the Melongeninae (e.g. *Melongena*) do not.

The paleobiogeography and migratory histories of the Busyconinae between the Atlantic and Pacific are enigmatic. Although the Busyconinae has an excellent fossil record throughout the Carolinas, Florida, and the northeastern Gulf of Mexico from the Miocene to the Pleistocene (Petuch, 1982; Petuch, 2004; Dietl, 2006), few fossils of this lineage appear in the Pacific. If the Busyconinae originated at the same time as most of the Buccinidae, and especially if it appeared before the Buccininae, as suggested by CO1 data, it would have had to originate in the North Pacific in the Paleocene or early to middle Eocene. However, there is no fossil evidence to support this scenario. In fact, one of the oldest potential relatives of the Busyconinae in the Pacific, *Protobusycon judithae* Saul (1988), is found in Paleocene rocks of the "Martinez" Formation of central California. Allied taxa of this genus come from Gulf Coast deposits of the latest Cretaceous Ripley Formation in Tennessee (Saul, 1988).

If *Protobusycon* is a member of the Busyconinae lineage, it would make Busyconinae one of the oldest living buccinid clades. Busyconinae would have originated off the North American coast in the extra-Tethyan Atlantic during the Maastrichtian, migrated to the Pacific through the proto-Caribbean Sea by the Paleocene, become extinct in the Pacific in the Paleocene or Eocene, but continued to diversify in the Atlantic and Gulf of Mexico. The lack of a fossil record for this history was explained by Paine (1962), who proposed that the earliest Busyconinae had thin shells that did not fossilize well. By the middle Miocene these shells had evolved to be much thicker (Paine, 1962), which may explain the rich Pliocene and Pleistocene busyconine fossil deposits of the northwest Atlantic. Molecular CO1 data do not support fossil evidence and therefore the position of *Busycotypus canaliculatus* at the base of the Buccinidae in the 28S and combined gene phylograms (Fig. 5C and 5D) is a more likely evolutionary scenario given the probable age of this subfamily.

Subfamily Neptuneinae

The Neptuneinae is a monotypic subfamily that originated between the late Eocene and early Oligocene in the North Pacific near Japan (Oyama et al., 1960). It migrated throughout the high latitude Pacific in the late Oligocene, reaching Alaska and the Oregonian Province by the middle Miocene (Nelson, 1986). One of the first fossil species of *Neptunea* in the North Pacific, *Neptunea ezoana*, occurs in upper Eocene rocks of Honshu and Hokkaido (Gladenkov and Sinel'nikova, 2009). During the Pliocene, the Neptuneinae dispersed into the Arctic, North Atlantic, and Japan Sea after the opening of the Bering Strait (Amano, 1997). The monophyly of *Neptunea* was recovered in every analysis of CO1 and 28S data in this study, which contrasts the polyphyletic position of *Neptunea* reported by Dong et al. (2008) in 28S NJ and ME analyses. One of the taxonomic subdivisions of Goryachev (Goryachev, 1987 in Amano, 1997), *N. arthritica* + *N. cumingii,* is also supported by the molecular results presented here.

Subfamily Photinae

The Photinae includes *Kelletia* and *Nassaria* in this analysis, and although this clade was supported by a high Bayesian posterior probability, it was only recovered once, so should be considered a tentative phylogenetic group. The earliest known *Kelletia* fossil, *Siphonalia (Kelletia) merriami* Wagner and Schilling 1923, occurs in the Oligocene San Emigdio Formation of California (Ruth, 1942). Although the identity of *Siphonalia (Kelletia) merriami* as a valid *Kelletia* congener has been questioned (L. Groves in Hayashi, 2005), an examination of *S. (Kelletia) merriami* types (UCMP #: 11427 and 11428) reveal that while they are smaller than the modern Californian *Kelletia kelletii* (45 mm v. 85-105mm), they share a similar shell profile, leaf-shaped aperture, knobbed ornamentation, siphonal fasciole, and recurved siphonal canal. Miocene species in California include *K. posoensis* (Anderson and Martin, 1914) and *K. lorata* Addicott, 1970 (Addicott, 1970). The first record of *Kelletia* in Japan is from the Miocene (Tomida in Hayahsi, 2005), which suggests that *Kelletia* migrated from the east to west Pacific (Hayashi, 2005) and had a continuous distribution across the Pacific until the late Miocene (Vermeij et al, 1990). The only extant *Kelletia* species in Japanese waters, *Kelletia lischkei*, ranges no further north than Honshu Island and the present distribution of the Californian species of *Kelletia, K. kelletii*, reaches its northern limit at Monterey Bay (Ruth, 1942; Zacherl et al., 2003). Because neither *Kelletia* extends further north, they are a discontinuous species pair restricted to either coast of the coast (Kuroda, 1938).

The genus *Nassaria* is characterized by a relatively small (1.5-4 cm), thick shell, and lives in the shallow tropics from East Asia to the Indo-West Pacific (Fraussen, 2004). In Japan it ranges from central Honshu south to the tropics (Okutani, 2000). *Nassaria* is also a taxonomically labile genus, having been re-named *Hindsia, Benthindsia*, and most recently, *Microfusus* (Koen, 2007). However, the *Nassaria.*and *Microfusus* species included in this study do not form a clade in any analysis. Although the buccinid affinity of *Nassaria* has been questioned by Kantor (2003), it was recovered within the Buccinidae in all analyses of this study, albeit with poor resolution.

It is worth noting that *Kelletia* and *Nassaria* both possess lirae, or sculptured ridges, on the inner side of the outer lip of their shells. Vermeij (1991) notes that lirae are also present in the buccinid genera *Buccinulum, Siphonalia, Penion*, and *Lirabuccinum*. Lirate sculpture may be a characteristic of a number of closely related buccinid subfamilies (e.g. Pisania or Photinae), a synapomorphy of the genera in one family (suggested by Vermeij, 1991), or an independently evolved character in these genera.

Unresolved Buccinid Taxa

The genus *Lirabuccinum* originated in the Northeastern Pacific during the Oligocene and spread to the western Pacific, reaching the Kamchatka Peninsula and Japan by the early Miocene (Amano and Vermeij, 2003). In the present study, *Lirabuccinum* nests within the Buccinidae in CO1 analyses but creates a basal polytomy for the family (figs. 5A, 5B). It and the unresolved genera *Microfusus* and *Solenosteira* all possess a lirate shell lip (Amano and Vermeij, 2003). *Microfusus* has also been alternately named *Hindsia* and *Benthindsia* as well as *Nassaria* (Habe et al., 1999; Okutani, 2000). Because *Microfusus* lies outside of the Buccinidae in both CO1 phylograms, unlike any other taxon in this study, it is considered by the author to be of dubious buccinid affinity.

The genus *Solenosteira* is found in shallow warm-temperate/tropical waters of the east Pacific and is considered closely allied to *Cantharus* (Keen, 1958). The geographic range for modern and extinct *Solenosteira* taxa is confined to the east Pacific where its evolutionary history begins at least by the Pliocene (Kidwell and Gyllenhaal, 1998). Its fossils occur in lower Oligocene deposits along the modern coasts of Florida, Georgia, and the tropical Atlantic (Petuch, 2005). During the Pliocene and Pleistocene, two marine extinction events contributed to the demise of this genus in the Atlantic, but not in the Pacific (Petuch, 2005).

The appearance of *Solenosteira* in the Atlantic and Gulf of Mexico before it is found in the Pacific suggests that it followed a migration route similar to the Busyconinae. That is, *Solenosteira* could have originated in the extra-Tethyan North Atlantic during the Late Cretaceous and migrated to the Pacific through the proto-Caribbean Sea at or before the early Miocene. By the middle Miocene, it had reached Colombia (Petters and Sarmiento, 1956). The placement of *Solenosteira* as a basal buccinid in phylograms of dataset B provides preliminary and provisional support for this hypothesis of evolution and migration. Additional studies of molecular and paleontological data would improve the phylogenetic resolution of *Solenosteira, Microfusus*, and *Lirabuccinum*, further test their placement within buccinid subfamilies, and aid in elucidating their paleobiogeography and evolutionary histories.

Developmental Mode

Larval developmental mode, defined here by the location of metamorphosis from veliger to juvenile, can be either planktonic or non-planktonic in the Buccinidae. Although life history data are not available for most species, those that are known are sufficient to indicate a remarkable range of life history evolution within the family. Of the species included in this study, two are known to have a planktonic developmental mode; *Kelletia kelletii* and *Volutharpa perryi* (Hirai, 1963; Rosenthal, 1970). Twenty-two of the remaining taxa develop non-planktonically and for five taxa developmental mode is unknown or undocumented (fig. 8, Table 7).

It is interesting that at least one subfamily recovered in this study, the Buccininae, comprises taxa of both developmental types. It is not uncommon, however, for generalizations of larval mode to be applied to entire buccinid subfamilies or genera (e.g. Amano, 1997 for the Ancistrolepinae, and Iguchi et al., 2004 for *Buccinum*). Although it is possible that members of each of these clades share a planktonic or non-planktonic developmental mode, this phenomenon has been under-explored. Relatively few direct observations of larval mode have been made of North Pacific taxa and differing reports of early development in buccinids seem to suggest that larval modes are not necessarily shared by all members of a subfamily, genus, or even species.

For example, in fossils of *Penion*, a buccinid genus found off Australia and New Zealand (Abbott and Dance, 1982), different species have been recorded as developing planktonically and non-planktonically (Hansen, 1982). In the tropical buccinid, *Pisania pusio*, development is planktonic but its congener, *Pisania maculosa*, develops non-planktonically (Shuto, 1974). The North Pacific taxon *Volutharpa perryi* has planktonic larvae (Hirai, 1963), but the larvae of another species in the genus, *V. ampullacea*, are described as non-planktonic (Vermeij et al., 1990). Finally, all extant *Neptunea* species have been called non-planktonic developers (Nelson, 1986), but protoconch size, one indicator of larval mode, varies greatly within the genus (Tiba and Kosuge, 1988), and the larvae of *Neptunea (Golikovia) smirnia* have been reported as planktonic (Stafford, 1986). Varying accounts of larval development reveal either inconsistencies in observations or cryptic diversity in the early ontogenetic modes within a single gastropod family. Expanding the body of descriptive data in a phylogenetic context will contribute to broader understanding of the evolution of development in gastropods and the plasticity of the biphasic lifestyle.

Relevance of systematics and taxonomy

A robust phylogenetic framework for the Buccinidae has substantial implications for improving the identification and classification of new extant and fossil taxa. For example, a Cretaceous fossil genus from California, *Deussenia* Stephenson, 1941, is described as a buccinid within the Melongeninae subfamily based on a classification scheme that assigns the Melongeninae to the Buccinidae (Akers and Akers, 1997; Squires and Saul, 2000). Another fossil genus, a Pliocene-Pleistocene gastropod called *Pyruella* Petuch, 1982, from the Pinecrest beds of Florida, is considered a busyconine melongenid. This classification reflects the inclusion of the Busyconinae within the Melongenidae and not the Buccinidae. However, it is clear from the molecular data presented in this and other studies that (for *Deussenia*) the Melongeninae should not be considered a subfamily of the Buccinidae, and (for *Pyruella*) the busyconine gastropods should be classified within the Buccinidae, not the Melongenidae. These data are necessary to elucidate the evolutionary history of *Deussenia* and *Pyruella* and their relationship to Tertiary buccinid genera.

Finally, extant buccinid species that are new to science are being described frequently from submersible and ROV explorations of marine abyssal depths, hot vents, and cold seeps (Okutani and Iwasaki, 2003). These taxa are of both new and familiar genera and include *Colliloncha, Bayeriusthese, Manaria, Buccinum* and *Neptunea* (Harasewych and Kantor, 2002b; Okutani and Iwasaki, 2003; Fraussen, 2004). The placement of these genera within verified subfamilies of the buccinid family tree is crucial to assessing the diversity of the Buccinidae and its subclades.

Conclusions

The present study had four objectives, to: (1) test the monophly of the North Pacific Buccinidae, (2) resolve the subfamilies within the clade, (3) determine the placement of the Busyconinae within or outside of the family, and (4) note the pattern of larval evolution in the clade. The conclusions derived from CO1 and 28S molecular phylogenetic analysis are discussed below.

(1) Monophyly of the Buccinidae was supported by molecular analyses (28S and 28S+CO1) of a sample of more than 20 mostly North Pacific taxa. Further phylogenetic resolution and a broader scope of the family could be achieved by adding the North Pacific genera: *Colus, Engina, Harpofusus, Helicofusus, Japeuthria, Mohnia, Plicifusus, Siphonalia, and Volutopsius* to future molecular analyses. The present study did not sample species from the Southern oceans or the Indo-West Pacific, and included only one taxon from the Atlantic. The addition of taxa from these localities would help to clarify the global relationships among Buccinidae, their post-Cretaceous migration routes, and their patterns of extinction and diversification.

(2) The genus *Babylonia*, formerly considered a buccinid but removed from the family in recent classifications was confirmed by CO1 data to fall outside of the Buccinidae.

(3) The Atlantic Busyconinae taxa *Busycon* and *Busyconinae* nest within the Buccinidae. Their phylogenetic position is derived when analyzed for CO1, but is basal and rooted in a polytomy when analyzed for 28S. Paleontological evidence supports the latter scenario, because it allows the clade to be older, which accommodates the lack of Busyconinae fossils found in the Pacific. The migration route of this lineage to the Pacific after its extra-Tethyan origination in the Late Cretaceous is poorly understood.

(4) The following five buccinid subfamilies are strongly supported in the phylogenetic analyses of this study: (1) Beringiinae Golikov and Starobogatov, 1975 (*Beringion* + *Japelion*), (2) Buccininae Rafinesque, 1815 (*Buccinum* + *Volutharpa*), (3) Busyconinae Wade, 1917 (*Busycon* + *Busycotypus*), (4) Neptuneinae Stimpson, 1865 (*Neptunea*), and (5) Photinae Gray, 1857 (*Kelletia* + *Nassaria*). Predictably, all buccinid genera represented by more than one species in this analysis (i.e. *Buccinum, Busycon,* and *Neptunea*) resolve as monophyletic.

(5) Preliminary analyses of larval development in Buccinidae reveal multiple origins of planktonic development within the family. In future studies, it would be useful to characterize developmental mode (planktonic and non-planktonic) and the allocation of nutritive intracapsular eggs and embryos in the taxa for which these developmental characteristics are not known. To further evaluate the number of times planktonic development has evolved in this family, future phylogenetic analyses should include putative buccinid genera with planktonic development, e.g. *Engina* (Tan and Morton, 1998), *Cantharus* (Miloslavich and Penchaszadeh, 1994), *Hinia* (Stroben et al., 1992), *Pollia* (D'Asaro, 1970), *Pisania* (Shuto, 1974).

(6) Representatives from the genera *Lirabuccinum, Microfusus,* and *Solenosteira* were generally poorly resolved in CO1 and 28S analyses and therefore cannot be assigned to a buccinid subfamily. Their phylogenetic position was either based in a polytomy or resolved with low support as sister to gastropod species outside of the Buccinidae. However, *Microfusus* was the only taxon of the three that fell outside of the family. Further study of these genera and their putative allies using molecular and morphological characters could clarify their position within the Neogastropoda.

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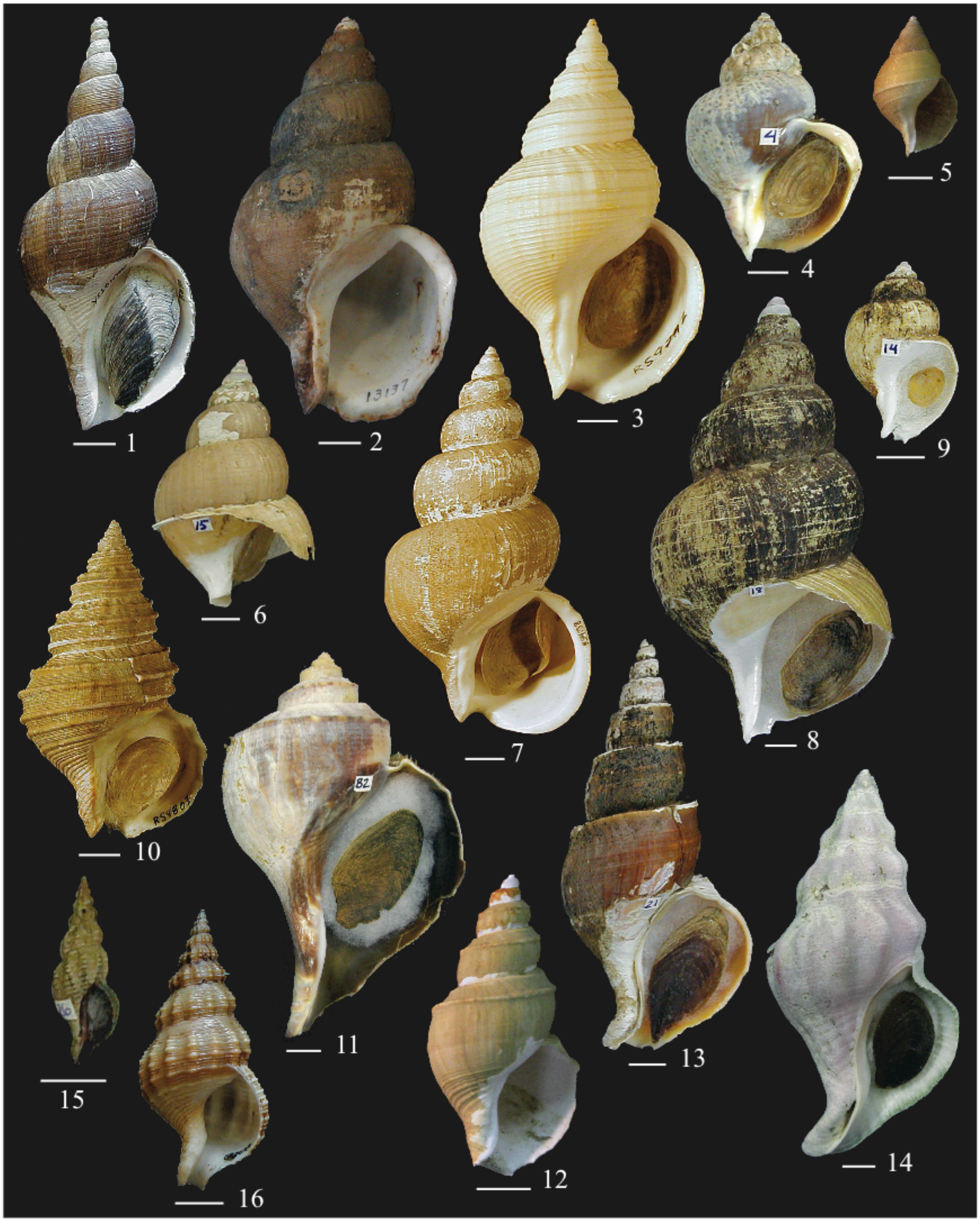


Plate 1. 1. *Beringion polynematicus** (UKM), 2. *Buccinum bayani** (NSMN), 3. *B. leucostoma** (UCMP 170792), 4. *B. middendorffi* (UCMP 556105), 5. *B. pemphigus** (UMUT Tsuchida Collection), *B. senshumaruae* (UCMP 556095), 7. *B. striatissimum** (UCMP RS4158), 8. *B. tenuissimum* (UCMP 556096), 9. *B. tsubai* (UCMP 556097), 10. *B. verkrüzeni** (UCMP RS9803), 11. *Busycotypus canaliculatus* (UCMP 557055), 12. *Clinopegma unicum** (UMUT Tsuchida Collection), 13. *Japelion pericochlion* (UCMP 556111), 14. *Kelletia kelletii* (UCMP 557057), 15. *Lirabuccinum fuscolabiatum* (UCMP 556102), 16. *Microfusus magnifica** (UKM *Benthindsia magnifica*). Species marked (*) are representatives of the species from which tissue samples were collected, not voucher specimens. Scale = 1cm

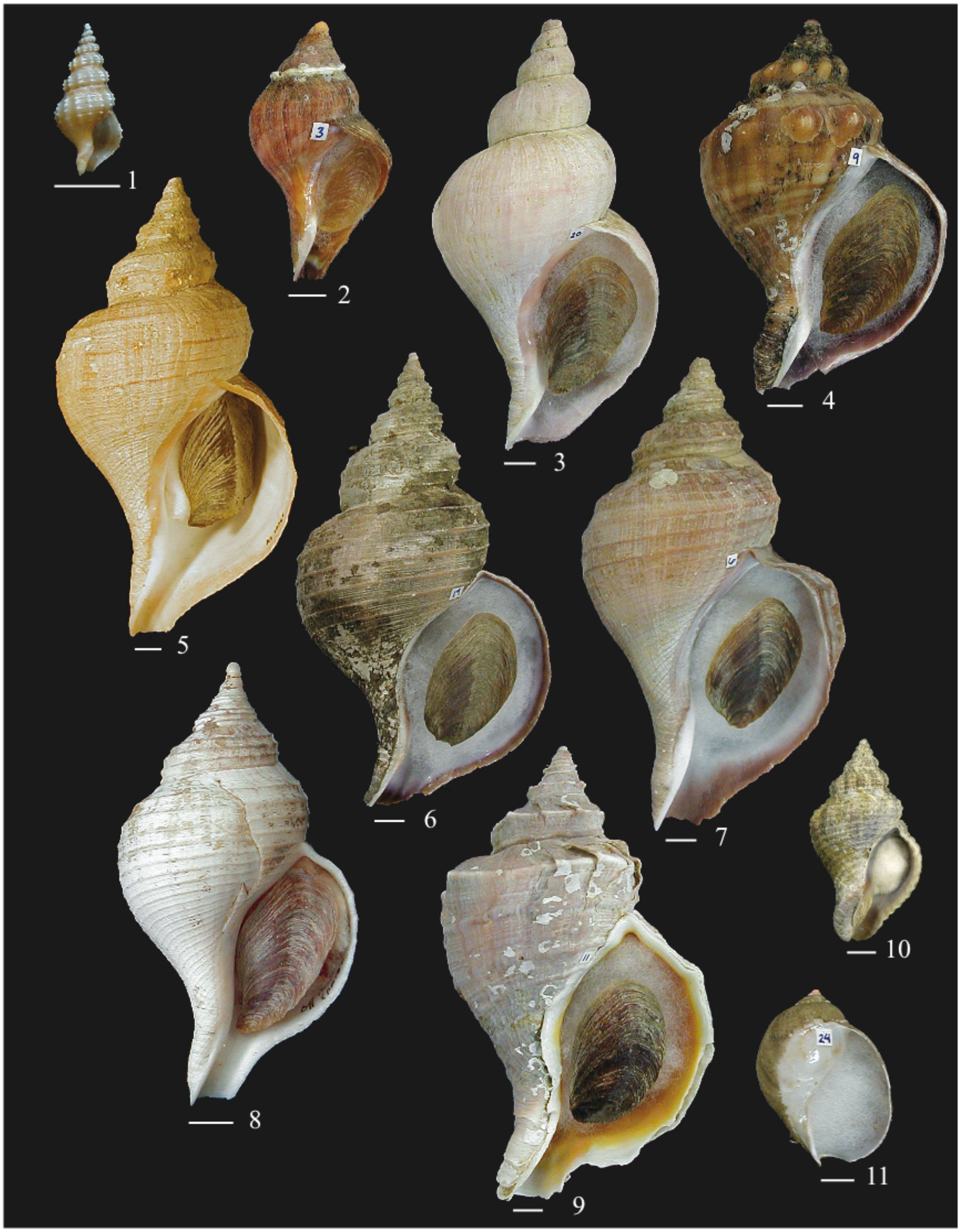


Plate 2. 1. *Nassaria sp.** (UKM *Benthindsia sinensis*), 2. *Neptunea arthritica* (UCMP 556104), 3. *N. constricta* (UCMP 556094), 4. *N. cumingii* (UCMP 556107), 5. *N. eulimata** (UCMP 556098), 6. *N. frater* (UCMP 556110), 7. *N. intersculpta* (UCMP 556106), 8. *N. kuroshio** (NSMN), 9. *N. polycostata* (UCMP 556108), 10. *Solenosteira macrospira** (UCMP 557058), 11. *Volutharpa perryi* (UCMP 556109). Species marked (*) are representatives of the species from which tissue samples were collected, not voucher specimens. Scale = 1cm

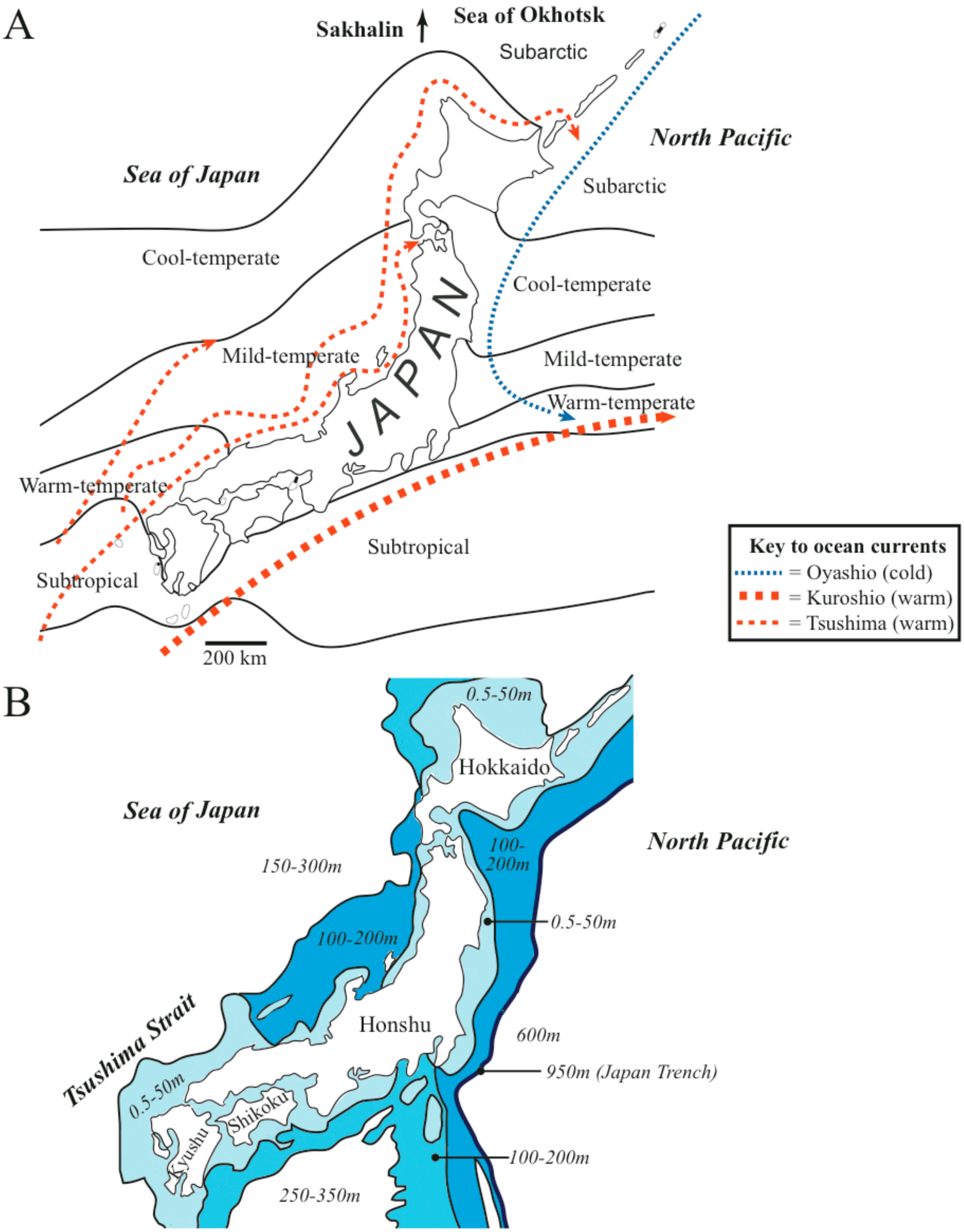


Figure 1 (A, B). Oceanic and bathymetic characteristics of coastal Japan. (A) zoogeographic divisions based on Ogasawa, 1994 (from Nishimura 1981) with oceanic currents from Hase et al., 1999, (B) ocean floor bathymetry based on maps by the Japan Coast Guard's Hydrographic and Oceanographic Department (http://www1.kaiho.mlit.go.jp/KAIYO/sokuryo/japan_all.jpg).

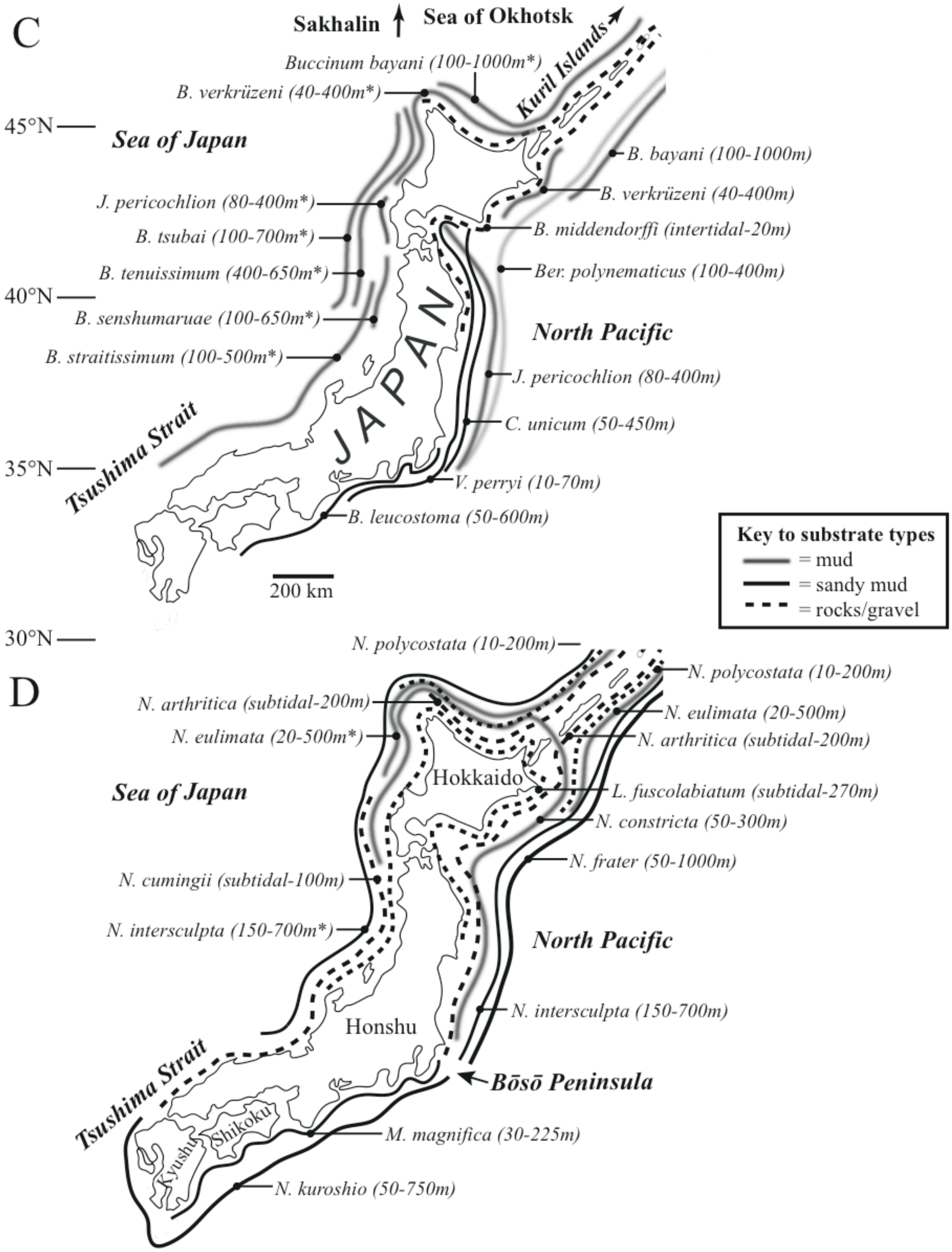


Figure 1 (C, D). Species ranges, depths, and substrate preferences of selected buccinids in Japanese waters. (C) includes the genera *Beringion, Buccinum, Clinopegma, Japelion*, and *Volutharpa*, (D) includes *Lirabuccinum, Microfusus*, and *Neptunea*. Maximum depths marked * indicate that the maximum depth for that species exceeds the depth indicated.

Figure 2 (A-C). Three buccinid species from summer seafood markets in two cities in Japan. (A) *Neptunena polycostata* Scarlato,1955 from Sendai, (B) *Neptunea cumingii* (Crosse, 1862) from Sendai, and (C) *Buccinum bayani* (Jousseaume, 1883) from Joetsu.

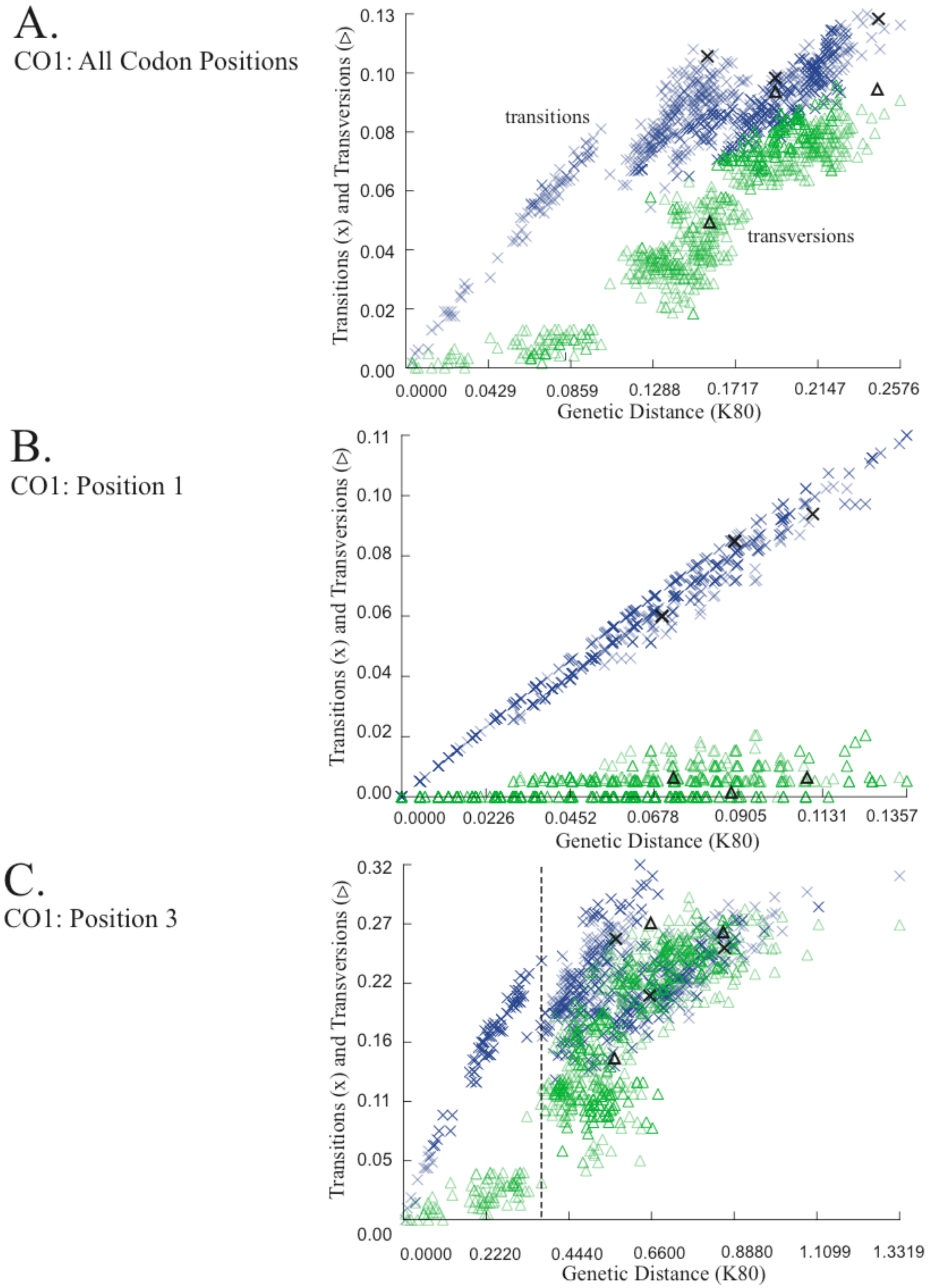


Figure 3 (A-C). Graphs of the estimated transitions (x) and transversions (△) in mtCO1 plotted against genetic distance determined by the Kimura, 1980 model (K80). Transitions and transversions in bold indicate values from the three *Conus* species included in this analysis. Taxa with genetic distance estimates greater than 0.335 (to the right of the dotted line) in (C) likely have a saturated third codon position. Graphs were created in DAMBE, 5.0.80 (Xia and Xie, 2001).

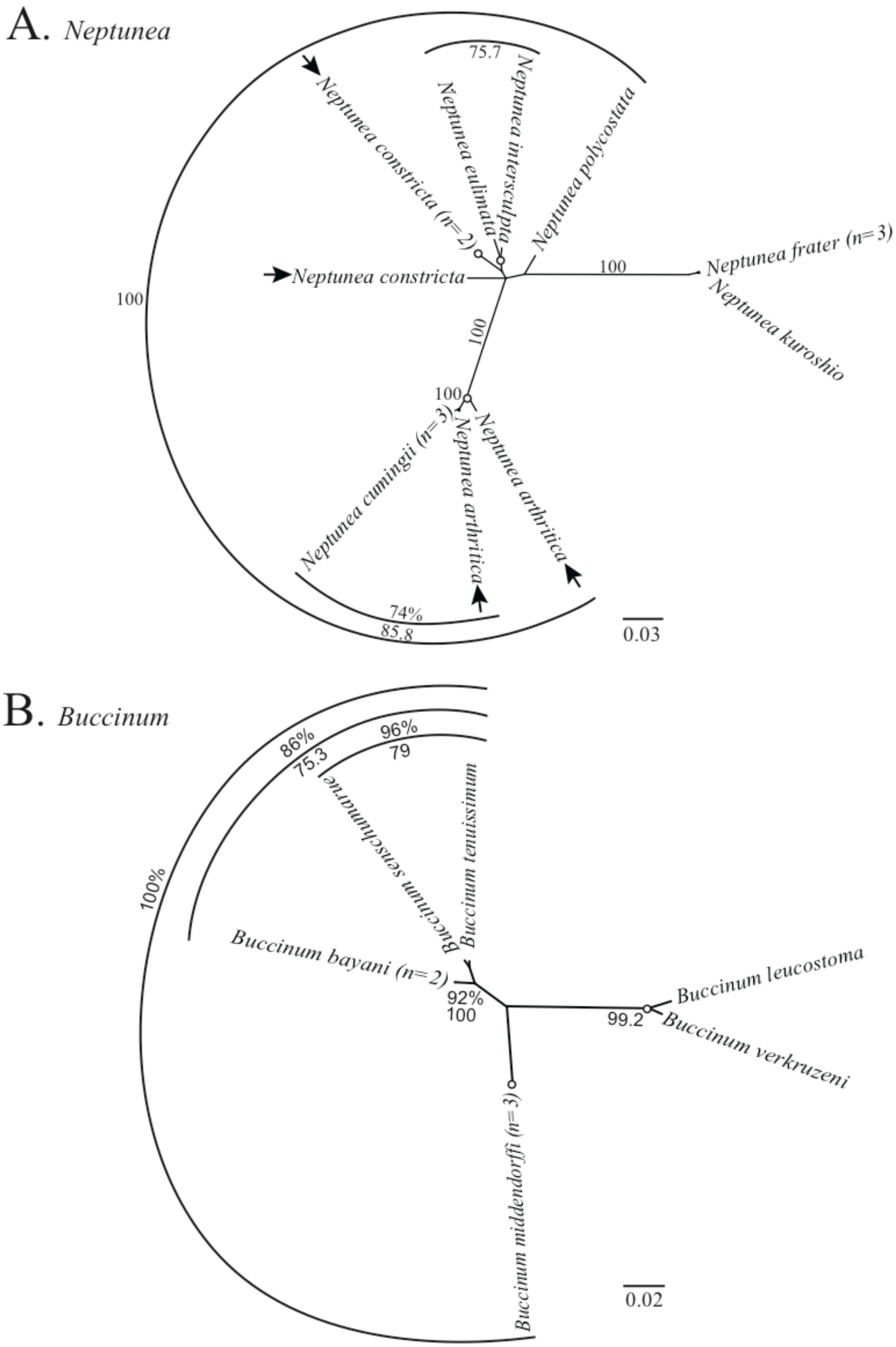


Figure 4 (A, B). Unrooted partial CO1 Bayesian trees with support values >70 for (A) *Neptunea* and (B) *Buccinum*. Posterior probabilities from 99%-100% are indicated at nodes by a "○". Posterior probabilities < 99 are shown as percents. Maximum likelihood bootstrap support values are indicated as decimals. Arrows point to polyphyletic taxa.

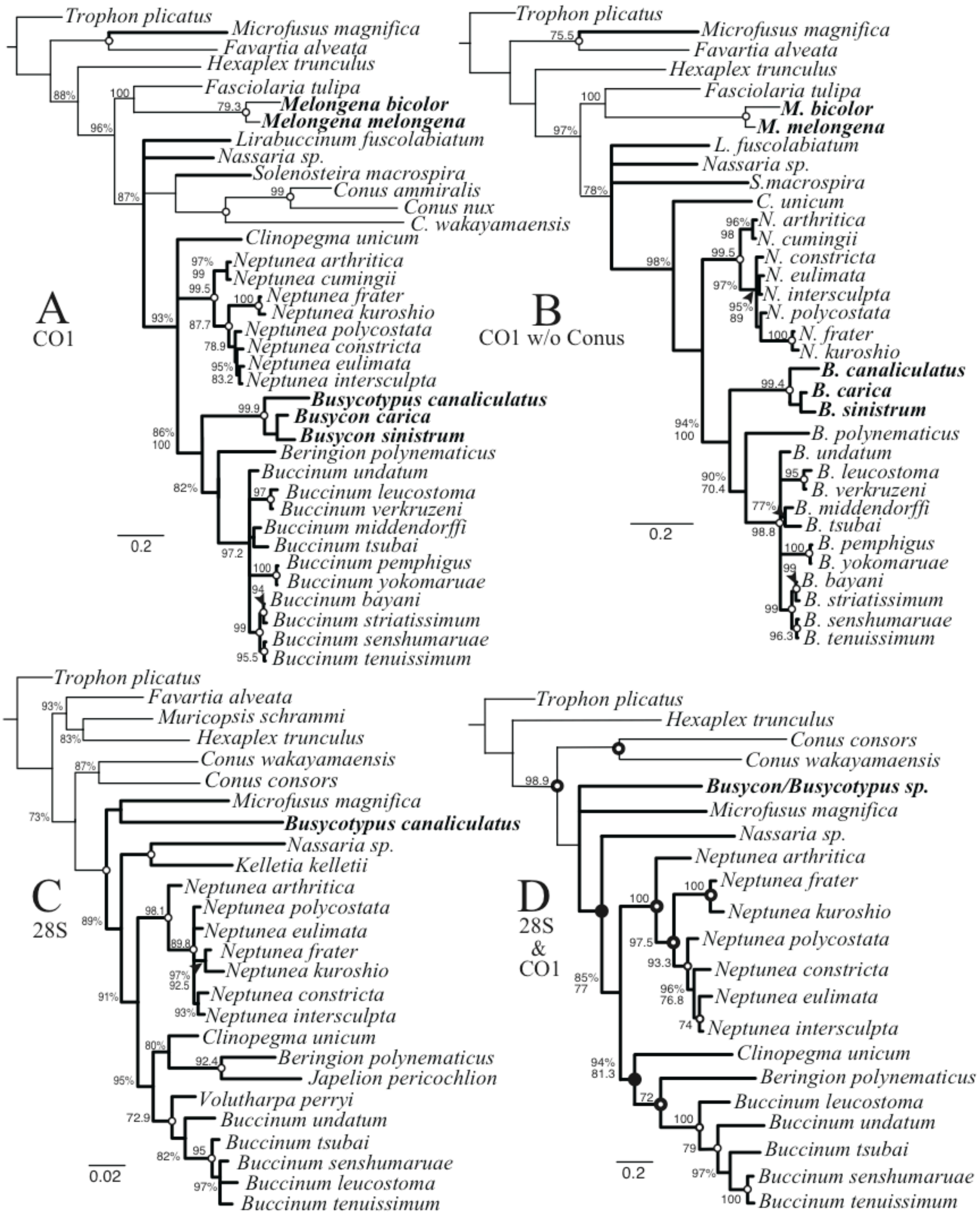


Figure 5 (A-D). Consensus Bayesian phylograms of partial 28S and mtCO1 sequences. (A) CO1, (B) CO1 without *Conus* taxa, (C) 28S, (D) combined 28S + CO1. Posterior probabilities >70% are shown. Values 99%-100% are indicated at nodes by a "ᵒ". Bootstrap support values (ML) are shown as whole numbers or decimals. Nodes with a posterior probability or boostrap value < 50 have been collapsed into polytomies. Buccinid taxa *sensu* Bouchet and Rocroi, 2005 are indicated by branches in bold. Melongenidae taxa *sensu* Gill, 1871 are indicated by taxononic names in bold. A black circle, "●" indicates posterior probabilities of 99%-100% from a MrBayes analysis using model GTR+SS+Γ.

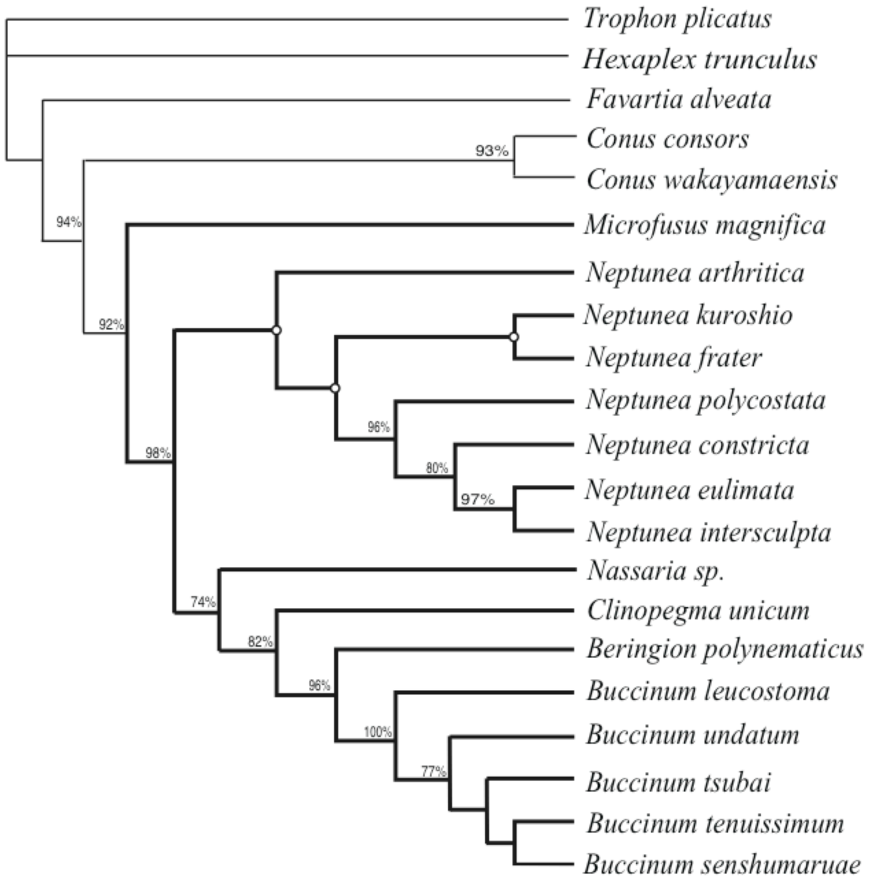


Figure 6. Consensus MrBayes cladogram of 28S + CO1 (50% majority-rule consensus of 10,000 trees) produced using the bayseian Chunky method (Hulsenbeck, 2009). Posterior probabilities >70% are shown. Values 99%-100% are indicated at nodes by a "∘". Branches in told indicated buccinid taxa *sensu* Bouchet and Rocroi, 2005.

Table 1. Depth range, substrate preference (abbreviated "Sub."), and geographic range of selected buccinids included in this study from the northwest Pacific and Sea of Japan.

Taxon	Depth	Sub.	Geographic Range	Source
Beringion polynematicus	100-400m	mud	Central Honshu to Aleutian islands, Alaska	1, 3
Buccinum bayani	100-1000m	mud	Okhotsk sea and Japan Sea to NE Hokkaido and Sakhalin, Bering Sea	1, 2, 3
Buccinum leucostoma	50-600m	sand, mud	Sagami Bay, central Honshu to Boso peninsula	1, 2, 3
Buccinum middendorffi	intertidal - 20m	rocks	Iwate to Hokkaido to Kuril Islands and Sakhalin	2, 3
Buccinum senshumaruae	100-650m	mud	Northern Honshu, Japan Sea	1, 2, 3
Buccinum striatissimum	200-500m	mud	Japan Sea	1, 2, 3
Buccinum tenuissimum	400-650m	mud	Middle to northern Japan Sea	1, 2, 3
Buccinum tsubai	100-700m	mud	Japan Sea (Yamaguchi Prefecture) and northwards	1, 2, 3
Buccinum verkrüzeni	40-400m	mud	Eastern Hokkaido north to Japan Sea, northwestern Hokkaido	1, 3
Clinopegma unicum	50-450m	sandy mud	Eastern Honshu north to southern coast of Hokkaido	1, 2, 3
Japelion pericochlion	80-400m	mud	Central Honshu north to eastern Hokkaido	1, 2, 3
Lirabuccinum fuscolabiatum	subtidal - 270m	rocks, gravel	Northeast Honshu to Hokkaido to Noto Peninsula, Japan Sea	1, 2, 3
Microfusus magnifica	30-225m	sand, mud	Shikoku and Kyushu to Boso peninsula, Honshu	1, 2, 3
Neptunea arthritica	subtidal - 200m	rocks, gravel	Eastern central Honshu (Chiba) north to Japan sea and Kuril Islands	1, 2, 3
Neptunea constricta	50-300m	mud?	Eastern central Honshu north to Hokkaido and Japan sea	1, 2, 3
Neptunea cumingii	subtidal - 100m	rocks, gravel	Tsushima strait north to Japan sea	1, 2, 3
Neptunea eulimata	20-500m	sand, mud	Hokkaido, Bering sea, Kuril Islands	1, 2, 3, 4
Neptunea frater	50-1000m	sand	Eastern central Honshu (Chiba) north to Northeastern Hokkaido	1, 2, 3, 4
Neptunea intersculpta	150-700m	sandy mud	Eastern central Honshu to Kuril Islands, Japan Sea to Toyama Bay	1, 2, 3
Neptunea kuroshio	50-750m	sandy mud	Eastern central Honshu south to Kyushu	1, 2, 3
Neptunea polycostata	10-200m	rocks, gravel	NE Hokkaido north to Kuril Islands, Okhotsk sea, Bering sea, and Japan	1, 2, 3, 4
Volutharpa perryi	10-70m	sandy mud	Eastern central Honshu to Hokkaido, and Japan Sea	1, 2, 3

1= Okutani et al., 1988, 2= Okutani, 2000, 3= Higo et al., 1999, 4= UCMP locality for extant shells

Table 2. Systematic position of selected putative buccinid genera within families and subfamilies. Names are as they were found in the literature. Capitalized fonts indicate subfamily authors. Familial designations outside of the Buccinidae are in bold.

Buccinum LINNAEUS, 1758	Buccininae RAFINESQUE, 1815 (Wenz, 1938-1944)
	Buccininae RAFINESQUE, 1815 (Kuroda et al., 1971)
	Buccininae (Habe and Sato, 1973)
	Buccininae (Golikov and Sirenko, 1988)
	Buccininae RAFINESQUE, 1815 (Vaught, 1989)
	Buccininae RAFINESQUE, 1815 (Titova, 1994)
	Buccininae (Sakada and Tanaka, 1999)
	Buccininae RAFINESQUE, 1815 (Higo et al., 1999)
	Buccininae (Riedel, 2000)
	Buccininae RAFINESQUE, 1815 (Bouchet and Rocroi, 2005)
Busycon RÖDING, 1798 and/or *Busycotypus* WENZ, 1943	**Busyconidae** (Fagerstrom, 1961)
	Melongenidae, Busyconinae WADE, 1917 (Harasewych, 1982)
	Melongeninae GILL, 1871 (=Busyconidae) (Ponder and Warén, 1988)
	Busyconinae WADE, 1917 (Akers and Akers, 1997)
	Melongenidae GILL, 1871 (Higo et al., 1999)
	Melongenidae GILL, 1871 (Riedel, 2000)
	Busyconinae WADE, 1917 (Kos'yan and Kantor, 2004)
	Busyconinae WADE, 1917 (Bouchet and Rocroi, 2005)
	Busyconinae (Hayes and Karl, 2009)
Clinopegma GRANT & GALE, 1931	Ancistrolepisinae (Habe and Sato, 1973)
	Ancistrolepidinae HABE & SATO, 1972 (Titova, 1994)
	Ancistrolepidinae HABE & SATO, 1972 (Amano et al., 1996)
	Neptuneidae (MacIntosh and Somerton, 1981)
	Ancistrolepisinae (Sakada and Tanaka, 1999)
	Ancistrolepisinae HABE & SATO, 1973 (Higo et al., 1999)
Japelion DALL, 1916	Liomesusinae HABE & SATO, 1973 (Habe and Sato, 1973)
	Beringiidae, Japelioninae GORYACHEV, 1987 (Titova, 1994)
	Neptuneinae (Kuroda et al., 1971)
	Ancistrolepidinae HABE & SATO, 1972 (Goryachev, 1987 *fide* Amano, 1996)
	Liomesusinae (Sakada and Tanaka, 1999)
	Beringiinae GOLIKOV & STAROBOGATOV, 1975 (Higo et al., 1999)
Kelletia FISCHER, 1884	**Chrysodomidae** (Dall, 1921)
	Buccinulinae FINLAY, 1928 (Wenz, 1938-1944)
	Neptuneidae (Addicott, 1970)
	Photinae (Kuroda et al., 1971)
	Siphonaliinae (Sakada and Tanaka, 1999)
	Siphonaliinae FINLAY, 1928 (Higo et al., 1999)
Lirabuccinum VERMEIJ, 1991 or *Searlesia* HARMER, 1915	**Chrysodomidae** (Dall, 1921)
	Cominellinae GRAY, 1857 (Wenz, 1938-1944)
	?Siphonaliidae GORYACHEV, 1987 (Titova, 1994)
	Pisaniinae GRAY, 1857 (Higo et al., 1999)
	Buccininae (Riedel, 2000)
	Photinae GRAY, 1857 (Amano and Vermeij, 2003)
Microfusus Dall, 1916	Photinae (Kuroda et al., 1971)
	Photinae (Sakada and Tanaka, 1999)
	Photinae GRAY, 1857 (Higo et al., 1999

Nassaria LINK, 1807 or *Benthindsia* IREDALE, 1936	Photinae (Kuroda et al., 1971) Photinae (Sakada and Tanaka, 1999) Photinae GRAY, 1857 (Higo et al., 1999)
Neptunea RÖDING, 1798	**Muricidae** (Dall, 1921) Neptuneinae STIMPSON, 1865 (Wenz, 1938-1944) Neptuneinae (Kuroda et al., 1971) Neptuneinae STIMPSON, 1865 (Habe and Sato, 1973) **Neptuneidae** (MacIntosh and Somerton, 1981) Neptuneinae TROSCHEL, 1869 (Titova, 1994) Neptuneinae TROSCHEL, 1869 (Amano, 1997) Neptuneinae (Sakada and Tanaka, 1999) Neptuneinae STIMPSON, 1865 (Higo et al., 1999) Neptuninae (Haasl, 2000) Buccininae (Riedel, 2000) Buccininae (Skoglund, 2002) Colinae (Kos'yan, 2007)
Solenosteira DALL, 1890 or *Cantharus* RÖDING, 1798	Cantharinae (Sakada and Tanaka, 1999) [not Cantharinae IMHOFF, 1856; a beetle] Pisaniinae GRAY, 1857 (Higo et al., 1999) Pisaniinae GRAY, 1857 (Vermeij, 2001)
Volutharpa FISCHER, 1856	Buccininae (Kuroda et al., 1971) Buccininae RAFINESQUE, 1815 (Habe and Sato, 1973) Buccininae (Golikov and Sirenko, 1988) Buccininae RAFINESQUE, 1815 (Titova, 1994) Volutharpinae (Sakada and Tanaka, 1999) Buccininae RAFINESQUE, 1815 (Higo et al., 1999)

Table 3. Gastropods included in this study followed by their locality data, UCMP voucher number, GenBank accession number(s), and references. An asterisk indicates that a specimen came from a fish market. A circle signifies that it was obtained without detailed locality data.

Taxon	Locality	UCMP Voucher	GenBank Accession Numbers (28S)	(CO1)	Source
Buccinidae Rafinesque, 1815 (*sensu* Bouchet & Rocroi, 2005)					
Beringion polynematicus (Pilsbry, 1907)	Hokkaido, Japan°	556099	FJ710093	FJ710067	This study
Buccinum bayani (Jousseaume, 1883)	Tokyo, Japan*	556091		FJ710068	This study
Buccinum leucostoma Lischke, 1872	Awa-gun, Japan	556092	FJ710094	FJ710070	This study
Buccinum middendorffi Verkruzen, 1882	Nagoya, Japan*	556105		FJ710071	This study
Buccinum pemphigus Dall, 1907	China			EU883628	Dong et al., 2008
Buccinum senshumaruae Kosuge & Ishiyama, 1971	Joetsu, Japan*	556095	FJ710095	FJ710074	This study
Buccinum striatissimum Sowerby, 1899	Sea of Japan			AB183328	Iguchi et al., 2007
Buccinum tenuissimum Kuroda, 1933	Joetsu, Japan*	556096	FJ710096	FJ710075	This study
Buccinum tsubai Kuroda, 1933	Joetsu, Japan*	556097	FJ712705		This study
	Sea of Japan			AB183327	Iguchi et al., 2007
Buccinum undatum (Linnaeus, 1758)	Reykjanes, Iceland		EU391567		Claremont et al., 2008
	Gullmarsfjord, Sweden			F528303	
Buccinum verkrüzeni Kobelt, 1883	Hokkaido, Japan°	556100		FJ710076	This study
Buccinum yokomaruae Yamashita & Habe, 1965	China			EU883631	Dong et al., 2008
Busycon carica (Gmelin, 1791)	Woods Hole, MA			AY194560	Wise et al., 2004
Busycon sinistrum Hollister, 1958	Fort DeSoto Park, FL			AY464677	Hayes & Karl, 2009
Busycotypus canaliculatus (Linnaeus, 1758)	Richmond, CA* °	557055	GQ850522		This study
	Cape Henlopen, DE			BCU86325	Harasewych et al., 1997
Clinopegma unicum (Pilsbry, 1905)	Hokkaido, Japan°	556101	FJ710097	FJ710077	This study
Japelion pericochlion (Schrenck, 1862)	Port of Soma, Japan°	556111	FJ710098		This study
Kelletia kelletii (Forbes, 1850)	Monterey Bay, CA	557057	FJ710099		This study
Lirabuccinum fuscolabiatum (Smith, 1875)	Rikuzen-Takata, Japan	556102		FJ712704	This study
Microfusus magnifica (Lischke, 1871)	Miura City, Japan	556103	FJ710100	FJ712703	This study
Nassaria sp.	New Caledonia		EU01555	EU015666	Puillandre et al., 2008
Neptunea arthritica (Bernardi, 1857)	Nagoya, Japan*	556104	FJ710101	FJ710078	This study

Neptunea constricta (Dall, 1907)	Joetsu, Japan*	556094	FJ710102	FJ710080	This study
Neptunea cumingii (Crosse, 1862)	Sendai, Japan*	556107		FJ710083	This study
Neptunea eulimata (Dall, 1907)	Wakkanai, Japan	556098	FJ710103	FJ710086	This study
Neptunea frater (Pilsbry, 1901)	Port of Soma, Japan°	556110	FJ710104	FJ710087	This study
Neptunea intersculpta (Sowerby, 1899)	Nagoya, Japan*	556106	FJ710105	FJ710090	This study
Neptunea kuroshio Oyama in Kira, 1959	Awa-gun, Japan	556093	FJ710106	FJ710091	This study
Neptunea polycostata Scarlato, 1955	Sendai, Japan*	556108	FJ710107	FJ710092	This study
Solenosteira macrospira Berry, 1937	Baja, Mexico	557058		No Acc. #	Grosberg, unpublished
Volutharpa perryi (Jay, 1856)	Port of Soma, Japan°	556109	FJ710108		This study
Babyloniidae Kuroda, Habe, and Oyama, 1971					
Babylonia japonica (Reeve, 1842)	Unknown			AF373888	Harasewych & Kantor 2002
Melongenidae Gill, 1871					
Melongena bicolor (Say, 1826)	Barnes Sound, FL			AY464678	Hayes & Karl, 2008
Melongena melongena (Linnaeus, 1758)	Celestun, Mexico			AY194558	Wise et al., 2004
Muricidae Da Costa, 1776					
Trophon plicatus (Lightfoot, 1786)	Golfo Elephantes, Chile		EU391547	EU391578	Claremont et al., 2008
Favartia alveata (Kiener, 1842)	Bocas del Toro, Panama		EU391569	EU391588	Claremont et al., 2008
Hexaplex trunculus (Linnaeus, 1758)	Ria del Alvor, Algarve, Portugal		EU391563	EU391577	Claremont et al., 2008
Muricopsis schrammi (Crosse, 1863)	Bocas del Toro, Panama		EU391544		Claremont et al., 2008
Conidae Rafinesque, 1815					
Conus ammiralis Linnaeus, 1758	Unknown			EU812755	Nam et al., 2009
Conus nux Broderip, 1833	Panama			EU423428	Duda et al., 2008
Conus consors Sowerby, 1833	Vanuatu		EU015636	EU015751	Puillandre et al., 2008
Conus wakayamaensis (Kuroda, 1956)	Philippines		EU015619	EU015734	Puillandre et al., 2008
Fasciolariidae Gray, 1853					
Fasciolaria tulipa (Linnaeus, 1758)	Unknown			AF373884	Harasewych & Kantor, 2002a

Table 4. Maximum Composite Likelihood Estimate of Nucleotide Substitutions in CO1

	A	**T**	**C**	**G**
A	-	*5.83*	*2.84*	**13.33**
T	*4.07*	-	**12.38**	*3.18*
C	*4.07*	**25.36**	-	*3.18*
G	**17.08**	*5.83*	*2.84*	-

Entries show the probability of substitution from one base (row) to another (column). Only entries with-in a row should be compared. Rates of transitions are in bold and transversions are in italics. Values were calculated in MEGA 4 (Tamura et al., 2007).

Table 5. Genetic Distances of 28S and CO1 Sequences in *Buccinum* and *Neptunea.*

Percent Pairwise Genetic Distance Percentage ± SE		
	28S	**CO1**
Buccinum species	0.0-1.1 ± 0.4 (n=5)	0.0-9.4 ± 1.5 (n=11)
Buccinum bayani		0.0 (n=2)
Buccinum middendorffi		0.0 (n=3)
Neptunea species	0.0-0.8 ± 0.3 (n=7)	0.9 ± 0.4 - 8.9 ± 1.4 (n=8)
Neptunea arthritica		1.5 ± 0.5 (n=2)
Neptunea constricta		4.0 ± 0.8 (n=3)
Neptunea cumingii		0.0-0.2 ± 0.1 (n=3)
Neptunea frater		0.0 (n=3)

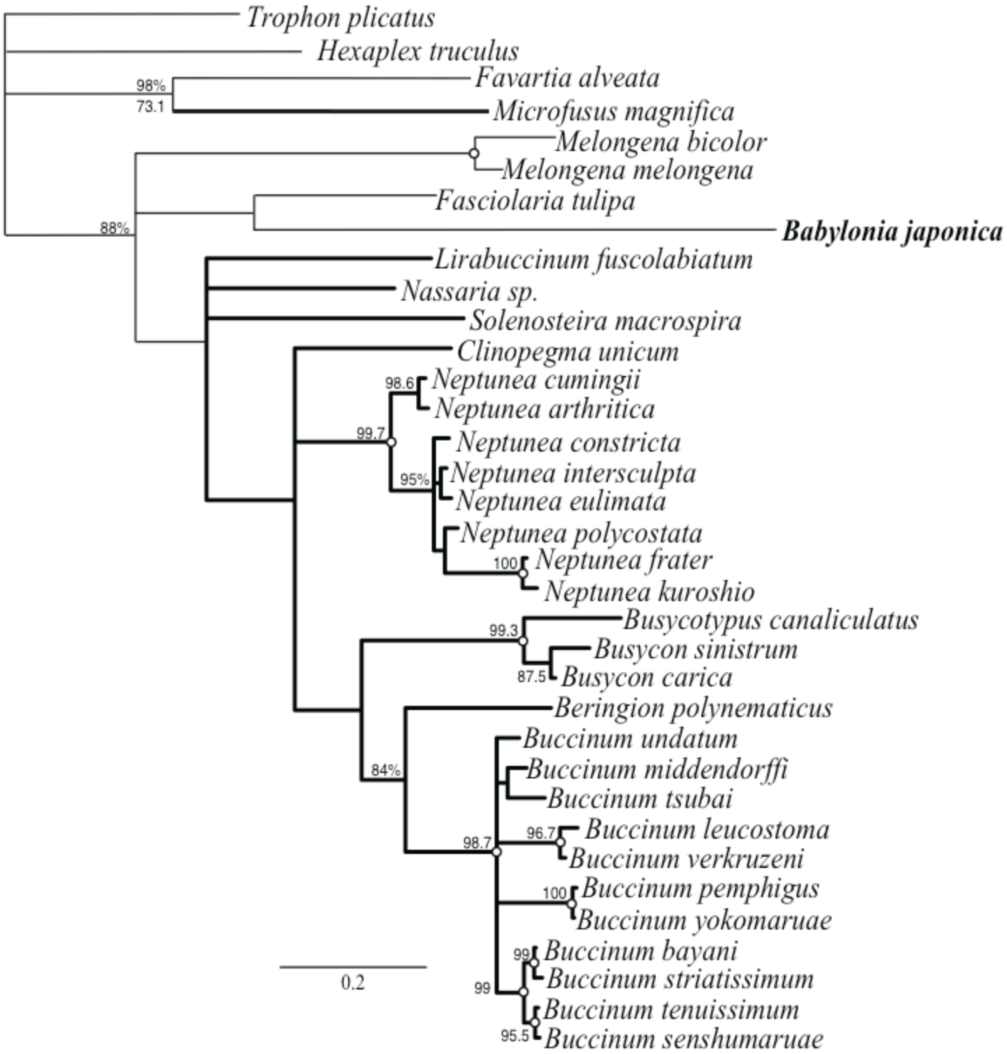
Values and their standard error calculated using the Kimura 2-parameter method with default parameters and 500 bootstraps in MEGA 4 (Tamura et al., 2007).

Table 6. Characteristics of CO1 and 28S Sequence Data and Analysis

	Dataset A CO1	**Dataset B CO1 w/o *Conus***	**Dataset C 28S**	**Dataset D 28S + CO1**	**Dataset D 28S + CO1 MrBayes unlinked**	**Dataset D 28S + CO1 MrBayes "Chunky"**
Number of taxa	37	35	26	21	21	20
No. Of base pairs sequenced	629	629	1422	2055	2055	2055
No. of parsimony informative sites	245	229	87	279	279	279
Model of sequence evolution	GTR+I+Γ	GTR+I+Γ	TrN+I+Γ	GTR+I+Γ	GTR+SS+Γ	-
Chain length for MrBayes	1,100,000	1,100,000	2,000,000	1,100,000	1,000,000	1,000,000
Log likelihood score for MrBayes	-6179.758 ± 0.338	-5432.66 ± 0.2695	-3990.066 ± 0.0566	-8040.746 ± 0.0155	-8071.22 ± 0.25	-
No. of bootstraps for PhyML	1,000	1,000	1,000	1,000	-	-
Log likelihood score for PhyML	-6202.519	-5412.138	-3799.12	-8018.041	-	-

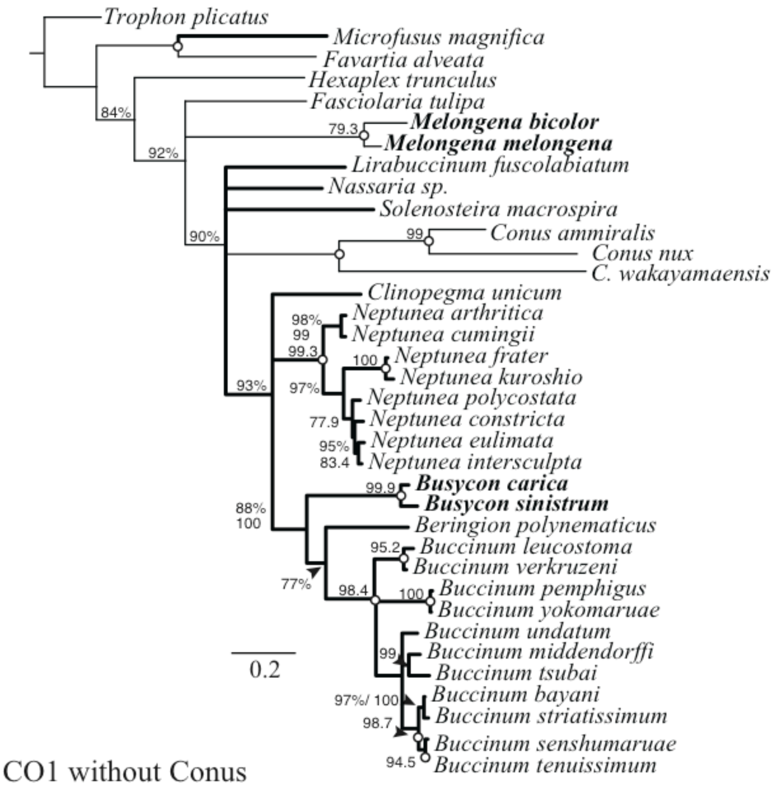
Table 7. Developmental strategies of selected buccinids and neogastropod outgroups included in this study. Post-intracapsular developmental mode and the presence or absence of nurse eggs are listed. Taxa in bold are included in figure 8.

Taxa	Mode of Development	Nurse eggs?	Source
Beringion polynematicus	?	?	-
Buccinum bayani	non-planktonic	Yes	Seto and Doi, 1999
Buccinum leucostoma	non-planktonic	?	Iguchi et al., 2004
Buccinum middendorffi	non-planktonic	?	Iguchi et al., 2004
Buccinum senshumaruae	non-planktonic	?	Iguchi et al., 2004
Buccinum tenuissimum	non-planktonic	?	Iguchi et al., 2004
Buccinum tsubai	non-planktonic	?	Iguchi et al., 2004
Buccinum undatum	non-planktonic	Yes	Jablonski & Lutz, 1983
Buccinum verkrüzeni	non-planktonic	?	Iguchi et al., 2004
Busycon carica	non-planktonic	Yes	Johnson & Allen, 2005
Busycon sinistrum	non-planktonic	?	Johnson & Allen, 2005
Busycotypus canaliculatus	non-planktonic	?	Wise et al., 2004
Clinopegma unicum	non-planktonic	?	Amano et al., 1996
Japelion pericochlion	?	?	-
Kelletia kelletii	planktonic	No	Rosenthal, 1970
Kelletia lischkei	planktonic	?	(Inferred from *K. kelletii*)
Lirabuccinum fuscolabiatum	non-planktonic	Yes	Rivest, 1992 (Based on *L. dira*)
Microfusus magnifica	?	?	-
Nassaria sp.	?	?	-
Neptunea arthritica	non-planktonic	Yes	Miranda et al., 2009, Fujinaga, 2003
Neptunea constricta	non-planktonic	Yes	Son, 2003
Neptunea cumingii	non-planktonic	?	Amio, 1963
Neptunea eulimata	non-planktonic	?	Nelson, 1986
Neptunea frater	non-planktonic	?	Nelson, 1986
Neptunea intersculpta	non-planktonic	Yes	Amio, 1963, Spight, 1976
Neptunea kuroshio	non-planktonic	?	Nelson, 1986
Neptunea polycostata	non-planktonic	?	Nelson, 1986
Solenosteira macrospira	non-planktonic	Yes	Houston, 1971, Grosberg, pers. com.
Volutharpa perryi	planktonic	-	Hirai, 1963
Outgroup taxa			
Conus ammiralis	?	?	-
Conus consors	planktonic	?	Duda & Palumbi, 1999
Conus nux	?	?	-
Conus wakayamaensis	?	?	-
Fasciolaria tulipa	non-planktonic	Yes	Penchaszadeh & Paredes, 1996
Favartia alveata	non-planktonic	?	-
Hexaplex trunculus	non-planktonic	Yes	Vasconcelos et al., 2004
Melongena melongena	non-planktonic	?	Hayes & Karl, 2009
Trophon plicatus	non-planktonic	?	Gallardo & Penchaszadeh, 2001

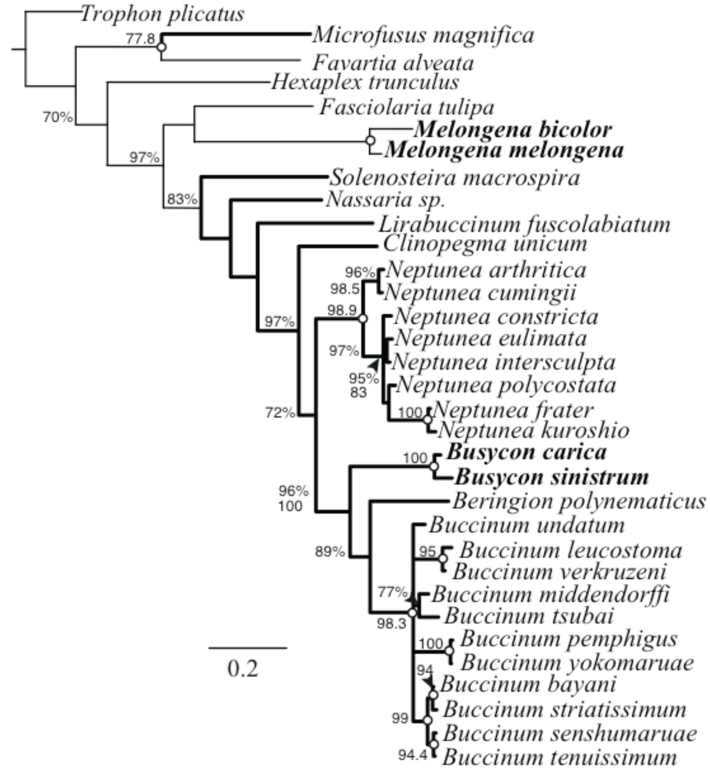


Appendix Figure 1. Consensus MrBayes phylogram of partial mtCO1 including *Babylonia japonica* (shown in bold italics) and taxa from dataset B. Posterior probabilities >70% are shown. Values 99%-100% are indicated at nodes by a "∘". Bootstrap support values (ML) are shown as whole numbers or decimals. Nodes with a posterior probability or boostrap value < 50 have been collapsed into polytomies. Buccinid taxa *sensu* Bouchet and Rocroi, 2005 are indicated by branches in bold. The log likelihood of this phylogram is -5661.728.

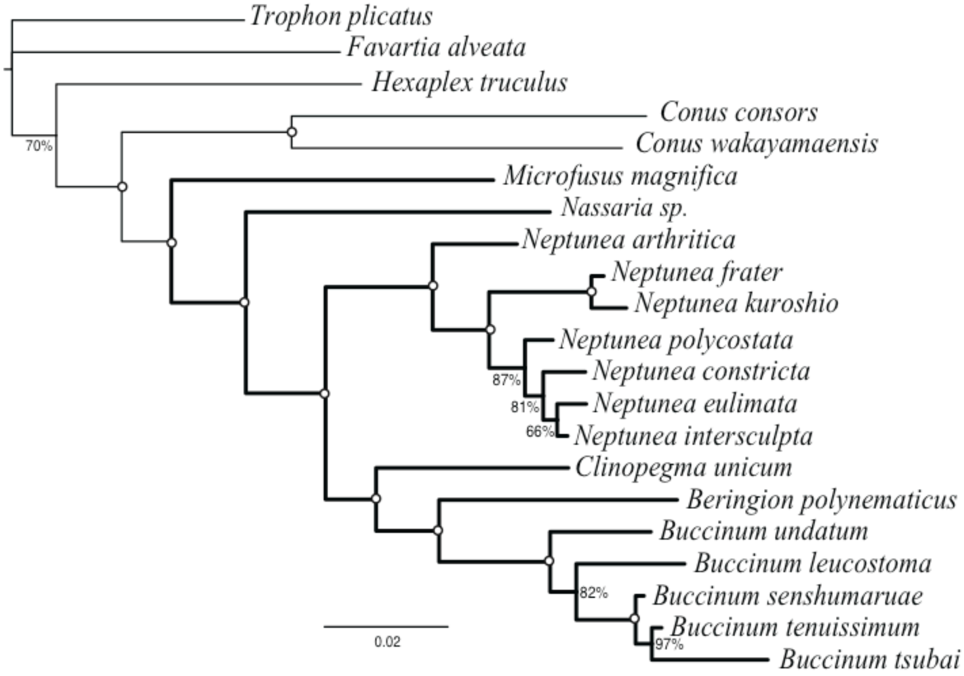
A. CO1



B. CO1 without Conus



Appendix 1. Fig. 2 (5A1 and 5B1). Consensus Bayesian phylograms of partial 28S and mtCO1 sequences exlcuding *Busycotypus canaliculatus*. (A) CO1, (B) CO1 without *Conus* taxa. Posterior probabilities >70% are shown and values of 99%-100% are indicated at nodes by a “ ”. ML bootstrap support values are indicate as whole numbers or decimals. Nodes with a posterior probability or boostrap value less than 50 have been collapsed into polytomies. Buccinid taxa *sensu* Bouchet and Rocroi, 2005 are indicated by branches in bold and Melongenidae taxa *sensu* Gill, 1871 are indicated by taxonomic names in bold.



Appendix Figure 3. Consensus MrBayes phylogram produced from model GTR+SS+Γ. Posterior probabilities >70% are shown. Values 99%-100% are indicated at nodes by a "∘". Buccinid taxa *sensu* Bouchet and Rocroi, 2005 are indicated by branches in bold.

Appendix Table 1. Nucleotide frequencies of all codon positions in CO1.

Taxon	Base Pairs	A	C	G	T
Beringion polynematicus	625	0.2480	0.1824	0.2048	0.3648
Buccinum bayani	625	0.2432	0.1888	0.2016	0.3664
Buccinum leucostoma	625	0.2624	0.1744	0.1840	0.3792
Buccinum middendorffi	625	0.2544	0.1840	0.1856	0.3760
Buccinum pemphigus	612	0.2549	0.1748	0.1961	0.3742
Buccinum senshumaruae	625	0.2496	0.1856	0.1952	0.3696
Buccinum striatissimum	490	0.2531	0.1898	0.2000	0.3571
Buccinum tenuissimum	624	0.2500	0.1891	0.1955	0.3654
Buccinum tsubai	490	0.2714	0.1837	0.1898	0.3551
Buccinum undatum	588	0.2483	0.1905	0.1922	0.3690
Buccinum verkruzeni	625	0.2576	0.1744	0.1888	0.3792
Buccinum yokomaruae	612	0.2549	0.1748	0.1977	0.3725
Busycon carica	592	0.2635	0.1757	0.1892	0.3716
Busycon sinistrum	524	0.2538	0.1737	0.2023	0.3702
Clinopegma unicum	625	0.2464	0.1936	0.2000	0.3600
Conus ammiralis	625	0.2384	0.1632	0.2192	0.3792
Conus nux	625	0.2336	0.1760	0.2112	0.3792
Conus wakayamaensis	625	0.2400	0.1744	0.1984	0.3872
Fasciolaria tulipa	591	0.2470	0.1709	0.1878	0.3942
Favartia alveata	625	0.2336	0.1728	0.2112	0.3824
Hexaplex trunculus	624	0.2260	0.1683	0.2115	0.3942
Lirabuccinum fuscolabiatum	610	0.2475	0.1852	0.1918	0.3754
Melongena bicolor	524	0.2290	0.1985	0.2099	0.3626
Melongena melongena	624	0.2244	0.2003	0.2179	0.3574
Microfusus magnifica	625	0.2480	0.1648	0.1920	0.3952
Nassaria sp.	625	0.2432	0.1840	0.1872	0.3856
Neptunea arthritica	625	0.2656	0.1824	0.1824	0.3696
Neptunea constricta	625	0.2576	0.1856	0.1920	0.3648
Neptunea cumingii	625	0.2656	0.1808	0.1824	0.3712
Neptunea eulimata	625	0.2592	0.1792	0.1920	0.3696
Neptunea frater	623	0.2616	0.1862	0.1878	0.3644
Neptunea intersculpta	625	0.2624	0.1760	0.1904	0.3712
Neptunea kuroshio	622	0.2621	0.1849	0.1913	0.3617
Neptunea polycostata	625	0.2656	0.1840	0.1840	0.3664
Solenosteira macrospira	568	0.2588	0.1673	0.1901	0.3838
Trophon plicatus	625	0.2448	0.1824	0.1968	0.3760

Appendix Table 2. Nucleotide frequencies of the third codon position of CO1.

Taxon	Base Pairs	%A	%C	%G	%T
Beringion polynematicus	208	0.3654	0.1058	0.1202	0.4087
Buccinum bayani	208	0.3558	0.1058	0.1202	0.4183
Buccinum leucostoma	208	0.4087	0.0673	0.0721	0.4519
Buccinum middendorffi	208	0.3846	0.0817	0.0769	0.4567
Buccinum pemphigus	204	0.3971	0.0490	0.0931	0.4608
Buccinum senshumaruae	208	0.3750	0.1010	0.1010	0.4231
Buccinum striatissimum	164	0.3963	0.1098	0.1159	0.3780
Buccinum tenuissimum	207	0.3768	0.1063	0.1014	0.4155
Buccinum tsubai	164	0.4512	0.0854	0.0854	0.3780
Buccinum undatum	195	0.3692	0.0872	0.1026	0.4410
Buccinum verkruzeni	208	0.3942	0.0673	0.0865	0.4519
Buccinum yokomaruae	203	0.3941	0.0493	0.0985	0.4581
Busycon carica	197	0.4213	0.0914	0.0761	0.4112
Busycon sinistrum	174	0.4023	0.0862	0.1149	0.3966
Clinopegma unicum	208	0.3654	0.1202	0.1154	0.3990
Conus ammiralis	208	0.3365	0.0481	0.1683	0.4471
Conus nux	208	0.3173	0.0769	0.1538	0.4519
Conus wakayamaensis	208	0.3462	0.0721	0.1058	0.4760
Fasciolaria tulipa	197	0.3706	0.0660	0.0761	0.4873
Favartia alveata	208	0.3269	0.0673	0.1490	0.4567
Hexaplex trunculus	102	0.3092	0.0531	0.1449	0.4928
Lirabuccinum fuscolabiatum	195	0.3744	0.0872	0.0872	0.4513
Melongena bicolor	174	0.3276	0.1034	0.1437	0.4253
Melongena melongena	207	0.3043	0.1304	0.1594	0.4058
Microfusus magnifica	208	0.3702	0.0481	0.0817	0.5000
Nassaria sp.	208	0.3558	0.0962	0.0721	0.4760
Neptunea arthritica	208	0.4183	0.0769	0.0625	0.4423
Neptunea constricta	208	0.3942	0.0865	0.0913	0.4279
Neptunea cumingii	208	0.4183	0.0673	0.0625	0.4519
Neptunea eulimata	208	0.3990	0.0721	0.0913	0.4375
Neptunea frater	207	0.4058	0.1014	0.0773	0.4155
Neptunea intersculpta	208	0.4087	0.0673	0.0865	0.4375
Neptunea kuroshio	206	0.4078	0.0971	0.0874	0.4078
Neptunea polycostata	208	0.4183	0.0865	0.0673	0.4279
Solenosteira macrospira	189	0.3968	0.0582	0.0847	0.4603
Trophon plicatus	208	0.3654	0.0673	0.1010	0.4663

Early development in *Kelletia kelletii* (Forbes, 1850), a buccinid gastropod with a planktonic veligers

Abstract

Kelletia kelletii (Forbes, 1850) is a marine buccinid gastropod from California with a "mixed" developmental mode. Characteristics of its mating behavior and general life history are known, although details about its larval lifestyle, from morphology to behavior, are lacking. Here, aspects of its spawning and in particular, larval development and behavior are chronicled. They include: oviposition, capsule morphology, intracapsular feeding, undeveloped eggs, velar form and function, asymmetrical development, particle ingestion, larval yolk reserves, and larval shell morphology. Snails were observed in aquaria and egg capsules were selected and dissected at different stages of development to observe the characteristics listed above. Larval shells were also isolated and mounted for SEM analysis at early to late veliger stages.

Egg capsules all contained undeveloped and arrested eggs and embryos but intracapsular *K. kelletii* larvae never ate them. Endogenous yolk stores were present in most veligers at emergence, although hatching time varied between approximately 35 to 60 days depending on water conditions and temperature. Pre-hatching veligers could swim in the plankton if excapsulated at 27 days and older. Their velar lobes were symmetrical but their cephalic tentacles were not. At 2.5 weeks in the plankton, both cephalic tentacles and velar lobes were asymmetrical with those on the right markedly more developed than those on the left. Larval shells were brittle and poorly calcified at emergence (at 39 days) but calcified and displayed an apertural beak and proto-siphonal canal by 2.5 weeks in the plankton. Particle capture and transport through the velar lobes to the mouth was possible in pre-hatching veligers, but ingestion only occurred in emerged veligers when yolk stores were depleted. Larval asymmetries and shell morphology have not been reported for the majority of buccinid taxa. With increased study of larvae in buccinid taxa, early ontogenetic data could be mapped onto existing molecular phylogenies of this family to assess the evolution of development mode in a buccinid neogastropods.

Introduction

The evolution of development in marine invertebrates has been most famously studied within the echinoderms (Strathmann, 1970; 1975; Smith, 1997; Wray and Bely, 1994; Jefferey, 2003) and the neogastropod genus *Conus* (Perron, 1981; Kohn and Perron, 1994; Duda and Palumbi, 1999). Knowledge of species-specific characteristics during early ontogeny makes such studies possible, but these data are lacking for taxa in many other developmentally diverse clades. The neogastropod family Buccinidae is one such group. Here, the larval behavior, morphology, and early ontogenetic shell traits of the buccinid gastropod, *Kelletia kelletii* (Forbes, 1850) are characterized, many for the first time.

Kelletia kelletii is a subtidal whelk from Monterey, California to Baja California, Mexico (Herrlinger, 1981) where it is a predator and scavenger common to kelp forests. It is tentatively placed in the buccinid subfamily Photinae along with the genus *Nassaria* (Vendetti, 2009c). Its general life history characteristics including many aspects of mating and spawning were described by Rosenthal in 1970. More recently, its range extension northward in California and trace element absorption by larvae have been studied by Zacherl and colleagues (2003; 2003a). General life history traits are presented in Table 1.

Unlike most members of the Buccinidae in California and the North Pacific, development in *Kelletia kelletii* is "mixed" (Rosenthal, 1970; Pechenik, 1979). Mixed development requires that the earliest stages of ontogeny, including the trochophore, develop inside an egg capsule after which larvae emerge as planktonic veligers (Buckland-Nicks et al., 2002). This developmental mode is defined by the location of development, not the nutritive mode of larvae (for a discussion of terms and their use see Havenhand, 1995; Bouchet, 1989, and Moran, 1999). For convenience, *K. kelletii* development will be referred to here as planktonic.

All buccinid development begins within an egg capsule (Pastarino and Penchaszadeh, 2002). Intracapsular embryos develop in one of the following modes; (1) as non-planktonic larvae (often called "direct-developers") that crawl out of their capsule as metamorphosed juveniles (Romero and Gallardo, 2004), (2) as veliger larvae that swim out of their capsule, feed in the water column, then metamorphose into benthic adults, or (3) as planktonic non-feeding veligers that swim out of their capsule and metamorphose and settle without feeding (Pearce and Thorson, 1967). During development, buccinid larvae can derive nourishment from their own yolk, intracapsular fluid, and/or by ingesting eggs (nurse eggs) or young embryos and sibling larvae within their capsule. Benthic egg capsules can house a single embryo or more than one thousand (Thorson, 1950).

I observed *Kelletia kelletii* larvae at various stages of development and recorded pre and post hatching endogenous yolk stores, ability to feed, and symmetry or asymmetry in veliger morphology. Selected veligers were fixed, critical point dried, and visualized with Scanning electron microscopy (SEM) to observe fine-scale morphology. Veligers were also tested for particle capture, transport, and ingestion in the plankton. Larval shells were isolated and examined for morphological traits and calcification during development from SEM digital photomicrographs.

Materials and Methods

Voucher material including adult shells, preserved egg capsules, and mounted larval shells have been deposited into the University of California, Museum of Paleontology extant shell collections and wet collections, respectively.

Kelletia kelletii adults, capsules, and larvae

Twelve adult specimens of *Kelletia kelletii* were collected by hand from subtidal kelp forests near Santa Barbara (n=5) and Monterey (n=7), California by Tim Herrlinger (UC Berkeley) and Shane Anderson (UC Santa Barbara) using SCUBA in January of 2006 and June of 2007. Specimens were maintained in a re-circulating and aerated saltwater aquarium at 13-16°C. One third of the water in the tank was replaced with natural seawater or artificial seawater once per month. Snails were fed shrimp or bivalves approximately every three to four weeks. Their mating and oviposition behaviors were recorded from January 2005 through October 2009.

Embryos and larvae were excapsulated by hand with forceps and dissecting scissors to allow different stages of development to be sampled, drawn, and photographed. The morphology of egg capsules and shells, the number of eggs per capsule, and the onset of velar structures, organs, larval pigment, and larval shell calcification were observed and recorded. Intracapsular behavior was also observed through transparent capsules laid by one female collected from Santa Barbara. Capsules and veligers were observed at magnification with a Wild Heerbrugg M-series stereomicroscope. Digital photographs were taken through this microscope using an optical coupler (Optem) and Coolpix (Nikon) 995 camera.

Larval feeding

Larvae that naturally emerged from their capsules and those that were excapsulated by hand were transferred by glass pipette to watch glasses filled with micro-filtered seawater. To test for feeding, a solution of seawater and red or blue non-toxic micro-particles (DayGlo fluorescent pigment, DayGlo Color Corporation, Cleveland, Ohio) was introduced into the water. Larvae were left undisturbed for 10 minutes before checking for ingested particles, which would be visible in the gut through the translucent shell.

Larval Shells: preparation for ESEM

Several ontogenetic series of larval shells were prepared from 35 samples of both intracapsular and emerged veligers. Isolated larval shells were prepared for microscopic analysis following a modified protocol of Pedersen and Page (2000): veligers were gently removed from beakers using a pipette and anaesthetized in MgCl2 for two hours, then bathed in a 3:10 (bleach: water) solution for up to 18 hours. Larval shells were rinsed with DI water and allowed to dry on link-free paper. They were then transferred into glass vials of acetone with a fine sable brush prior to mounting.

Cleaned larval shells were mounted with a sable brush onto aluminum stubs that were each affixed with a conductive carbon adhesive pad. Shells were repositioned when necessary using a human or Dalmatian dog hair mounted on a wooden stirring stick. Mounted specimens were sputter coated with iridium on a Medo20 Sputter Coater to a thickness of 0.014 kÅ (kiloangstrums) and visualized with a Philips XL-30 ESEM. Specimens were viewed at an accelerating voltage of 10-15kV and at a working distance of 15 mm. Image quality and magnification were controlled using Philips XL-30 imaging software and micrographs were saved as digital .tif files. Contrast and brightness were adjusted in Adobe Photoshop CS4. From these images, characteristics of larval shell ornamentation, microstructure, and shape were observed and recorded. Measurements were made using ImageJ digitizing and imaging software (v.1.36b National Institutes of Heath).

Larvae: preparation for ESEM

Larvae were relaxed in calcium-free seawater (Page, personal communication), fixed in a 2% glutaraldehyde solution, rinsed in an osmium tetroxide and sodium cacodylate buffer, and dehydrated in a 7 step ethanol series from 35-100% ETOH. Fixed specimens were then critical point dried and visualized uncoated using a Hitachi TM-1000 SEM at an accelerating voltage of 15-20 kv.

Results

Oviposition and capsule morphology

Capsules were laid in benthic clutches numbering 3 to 82 and were attached to each other at their bases. In most capsules, the escape aperture and mucoid plug were at the top, although in one clutch of abnormal capsules the escape aperture was on the side (fig. 1A). Capsule walls were translucent white to transparent and in the specimens examined here enclosed rarely zero, but most often between 477-966 eggs and embryos per capsule. Eggs were bright yellow/orange and capsules averaged 8.09 mm from their base to escape aperture and 6.60 mm in maximum width (n=15). Capsule shape is lingulate, slightly convex/concave, and lacks sutures.

Nineteen instances of egg laying were recorded between May and October from 2006 to 2008. Oviposition while mating was observed twice and females had a tendency to lay capsules next to clutches already laid by other females. Under laboratory conditions, capsules were deposited on the sides of the glass aquarium, on rocks, and in one case, on the shell of another adult (fig. 1B-D). Females were only slightly larger than males at an average maximum length (from apex to siphonal canal) of 88.91 mm versus 87.08 mm for males. Specimens collected off the coast of Santa Barbara were significantly larger than those from Monterey, at an average of 92.48 mm versus 71.33 mm long, respectively.

Intracapsular feeding and undeveloped eggs

Undeveloped or arrested eggs and embryos comprised 2.5%-38% of intracapsular individuals. In all dissected capsules (n=65) there was a proportion of eggs/embryos that did not match the developmental stage of the majority of individuals in the capsule. This was true as early as the 4-8 cell stage as well as at veliger hatching. In healthy capsules, undeveloped eggs were not damaged or in any stage of disintegration, indicating that they had not been perturbed or eaten by developing larvae. Observations through transparent capsules confirmed that trochophore and veliger larvae did not eat or disturb undeveloped eggs and embryos as they would have if these were nutritive material such as nurse eggs. Intracapsular embryos and veligers were fed by endogenous egg stores and possibly albumen.

Developmental characteristics

Development was observed from uncleaved fertilized eggs to trochophores (fig. 2) prior to differentiation into veligers. Black pigment developed on veligers prior to their emergence and this color change made the translucent capsules appear gray. A chronology of characteristics observed during *Kelletia kelletii* development is presented below and is summarized in Table 2.

Day 0: uncleaved eggs
2-3: cleavage: four to eight cell stage
4: cleaved ball stage
5: gastrulation stage
9-11: trochophore: early to late stages. At the late stage, embryos slowly rotate in the capsule
18-19: eye spots present, some larvae with black pigment, some without
19-21: early veliger stage: larvae closely packed, presence of larval shell, velum, and red organ (larval kidney), ciliary movement, black pigment developed in ring around shell margin
23-25: veligers actively swimming inside capsule with small velar lobes

27: Excapsulated: veligers competent swimmers, 2 endogenous yolk balls in shell
29: Excapsulated: veligers competent swimmers, 1 or 2 endogenous yolk balls in shell, phototaxic
30: black pigment in veligers well developed, constant movement in capsule
32: operculum obvious
33: cephalic tentacles present, some yolk in shell, grainy exudate from veligers or in albumen?
36-37: small yolk balls to no yolk in shells, fragile larval shells not fully calcified (e.g. with holes), if excapsulated veligers do no eat
38: some veligers without yolk, most with yolk, many veligers nearly breaking through capsular plug
39-61: hatching: veligers emerged from capsule as planktonic veligers
39-40: veligers competent swimmers, small amount of yolk in shell, phototaxic, some holes in shells, foot is pigmented
45: asymmetrical cephalic tentacles obvious
49: no yolk balls in shell
68: (8 days as veliger) velar lob asymmetry obvious
69: (9 days as veliger) veligers began to die
78: particles ingested by veligers
82: (21 days as veliger): few veligers alive

The substantial range in age of veligers at hatching—from 39 to 61days—can be attributed to low disturbance in the water and/or plugging of the capsule escape aperture with masses of undeveloped eggs. Water disturbance or aeration in aquaria assisted in the release of veligers by agitating the capsules. In still seawater, it was not uncommon for veligers to hatch after 45 days or more and for many intracapsular veligers to die inside the capsule.

Velar form and function

Feeding experiments suggest that opposed band cilia on velar lobes of *Kelletia kelletii* are capable of particle capture and transport in addition to swimming. At pre and post hatching, particles could be pulled from the water into the food groove of either velar lobe and travel toward the mouth (fig. 3). Before veligers naturally hatched from their capsules they used the velum to “swim” within the albumen of the capsule. If excapsulated, veligers of approximately 20-23 days old and older could swim outside the capsule in seawater. All veligers that could swim outside the capsule whether naturally hatched or excapsulated by hand were phototaxic.

Asymmetrical development

Prior to hatching, velar lobes were of equal size but cephalic tentacles were not (fig. 4A, B). In all observed veligers, the right tentacle was longer than its counterpart on the left. By 68 days old or 2.5 weeks in the plankton, depending on the date of hatching, velar lobes were also asymmetrical (fig. 4C, D).

Particle ingestion and yolk reserves

Prior to hatching, bright yellow yolk reserves filled most of the veliger larval shell (fig. 5A, B). Yolk was distributed into one or two balls that were visible through the translucent shell. If veligers were excapsulated while yolk reserves were abundant, they would not ingest planktonic particles. If micro-particles were introduced into the environment of an excapsulated pre-hatchling, they would get caught in the velar lobes, settle in the food groove, and move toward the mouth where they would be expelled down the ciliated foot. Veligers did not ingest particles unless their yolk stores were depleted (fig. 5C, D), which in the present study was at 18 days in the plankton. Ingestion of micro-particles was confirmed when the bright color of the particles was visible within the gut (fig. 5E).

Larval shell morphology
Shells of late pre-hatchlings (intracapsular) veligers were thin, brittle, and often had holes indicating poor calcification (fig. 6, 7). Shells had a granulated texture consisting of bead-like micro-protuberances. Shells of early emergent veligers were similar to those of pre-hatchlings, but were slightly more calcified and not as brittle. Between day 13 and 15 as a veliger, larval shells were fully calcified and growth lines were evident. Late stage veligers at or near 19 days in the water column had an apertural beak and the beginnings of a siphonal canal. At this stage, beaded micro-protuberances on the shell were evident up to the apertural margin. The maximum diameter of *K. kelletii* larval shells was 0.407 mm (N=10) in apical view. However, overall size was variable within capsules and cohorts were not always at the same stage of shell development and calcification, especially as pre-hatchlings and early stage emerged veligers.

Discussion

Kelletia kelletii larvae experience two phases of developmental in terms of location and feeding. First, larvae are non-feeding (lecithotrophic) within their egg capsules, which always include arrested or non-fertilized eggs. After emergence, developmental continues in the plankton where veligers feed only after their endogenous yolk stores are absorbed (Table 3). This planktonic developmental mode is generally expected in tropical buccinids including *Pisania pusio* (Linnaeus, 1758) and *Cantharus tinctus* (Conrad, 1846) (Miloslavich and Penchaszadeh, 1994), but is less common in buccinids from the California coast, especially one with a range that is expanding north (Herrlinger, 1981; Zacherl et al., 2003).

The buccinid clade is an excellent candidate for studies of early development. It has been the focus of recent molecular analyses that strongly support monophyletic subfamilies (Vendetti, 2009c). Some developmental modes of buccinid taxa are know, so it is clear that early ontogeny varies within the family. Furthermore, the family is species-rich (>700 taxa), found world-wide, and many taxa with poorly described larval biology are easily accessible for examination (see Vendetti, 2009c).

Although developmental mode (as planktonic or non-planktonic) and the presence of intracapsular nutritive eggs within capsules has been described for some species within major buccinid genera (e.g. *Buccinum undatum* Linnaeus, 1758 and *Neptunea antiqua* (Linnaeus, 1758)) detailed studies of development in most other buccinids are lacking, especially for taxa with planktonic larvae. In a literature search of 500 species of endemic North Pacific buccinids, less than one fourth had accompanying developmental data and many of these data were generalizations based on observations of larval development in one species of a genus (Vendetti, unpublished).

Without greater documentation of larval development in the buccinid clade, important characteristics like developmental asymmetries and larval shell morphology can not be integrated into phylogenetic analyses of development. For example, the asymmetrical development of velar lobes and cephalic tentacles shown here for *Kelletia kelletii* is the first time these traits has been reported for any buccinid, although this phenomenon has been recorded in the muricid, *Thais chocolate* (Duclos, 1832) (Romero et al., 2004). For future phylogenetic analyses of development, it would be necessary to know if these early ontogenetic characteristics are shared by other taxa in the Photinae (e.g. *Nassaria*) or in species elsewhere in the buccinid family tree.

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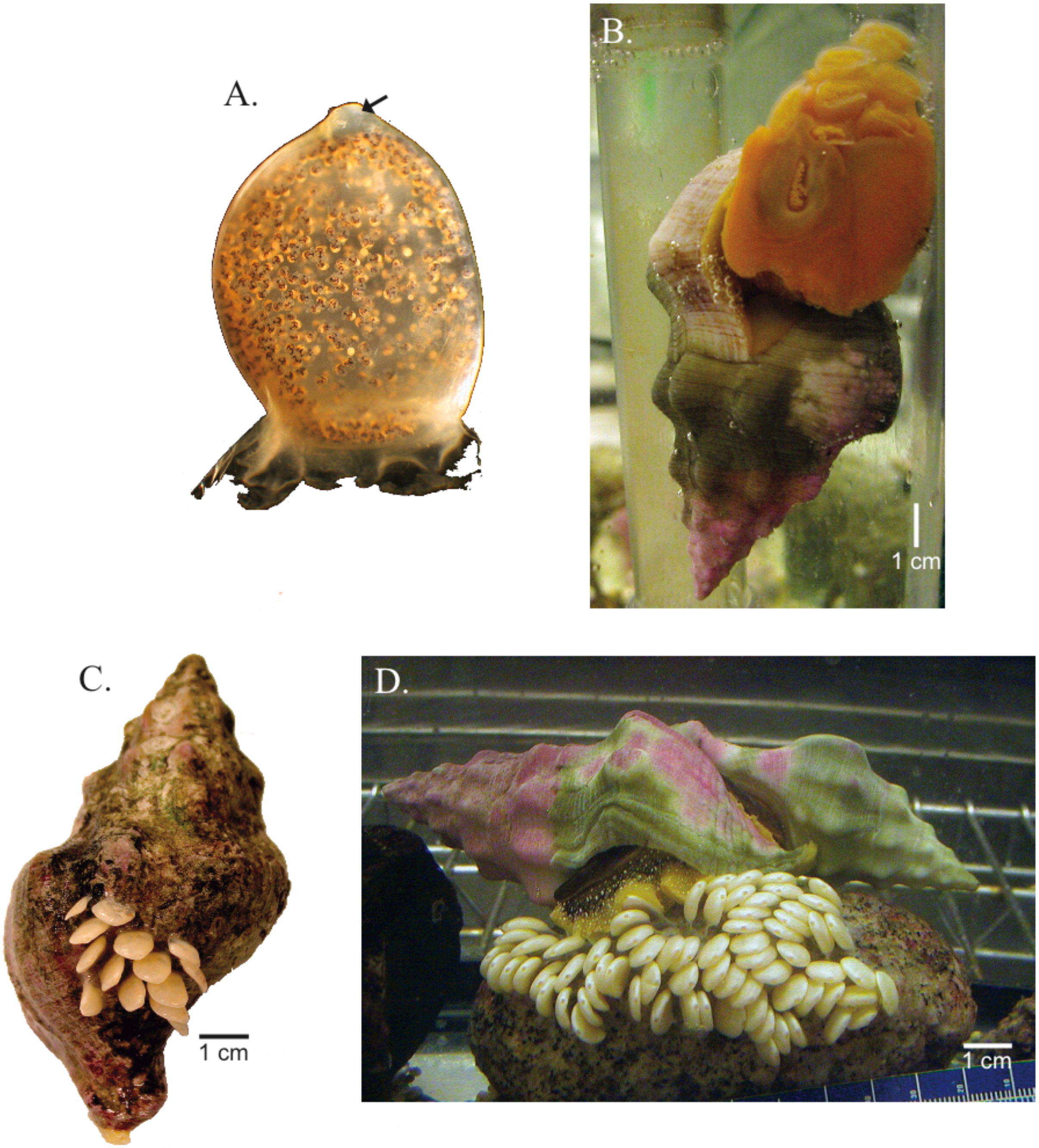


Figure 1 (A-D). *Kelletia kelletii* egg capsules and adults. (A) egg capsule with larvae almost competent to emerge. Escape aperture is indicated by arrow. Lenght from escape aperture to base is 9 cm, (B) ovipositing female in captivity, (C) *K. kelletii* individual with egg capsules laid on its shell, (D) female from Monterey, California laying egg capsules in captivity for three days in late spring.

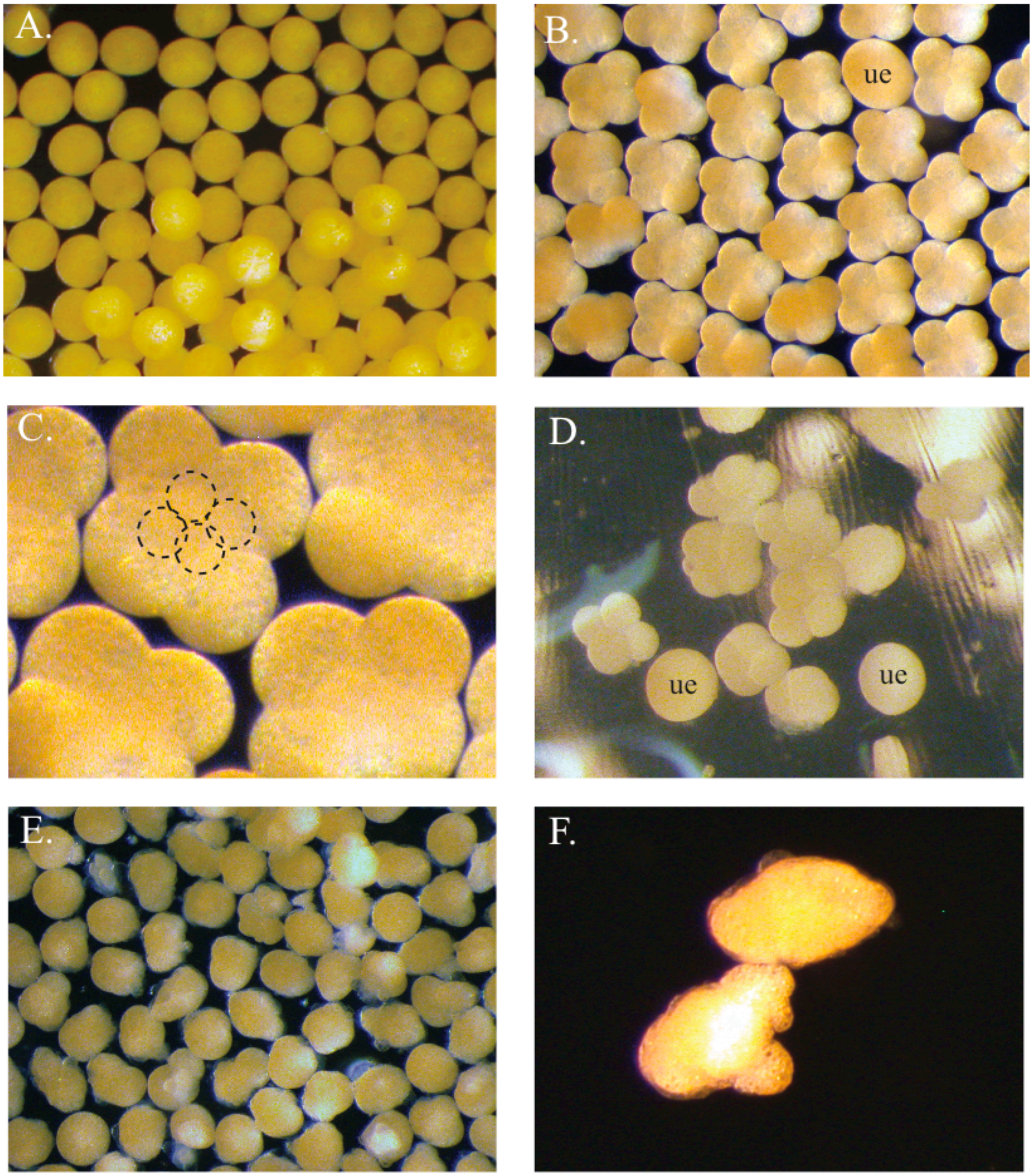


Figure 2 (A-F). *Kelletia kelletii* intracapsular developmental stages. (A) uncleaved egg, (B and C) 4-8 cell stage at two days. Dashed circles outline the first micromere quadrant, ue: undeveloped egg or embryo, (D) embryos and undeveloped eggs photographed inside a transparent capsule, (E and F) trochophore stage.

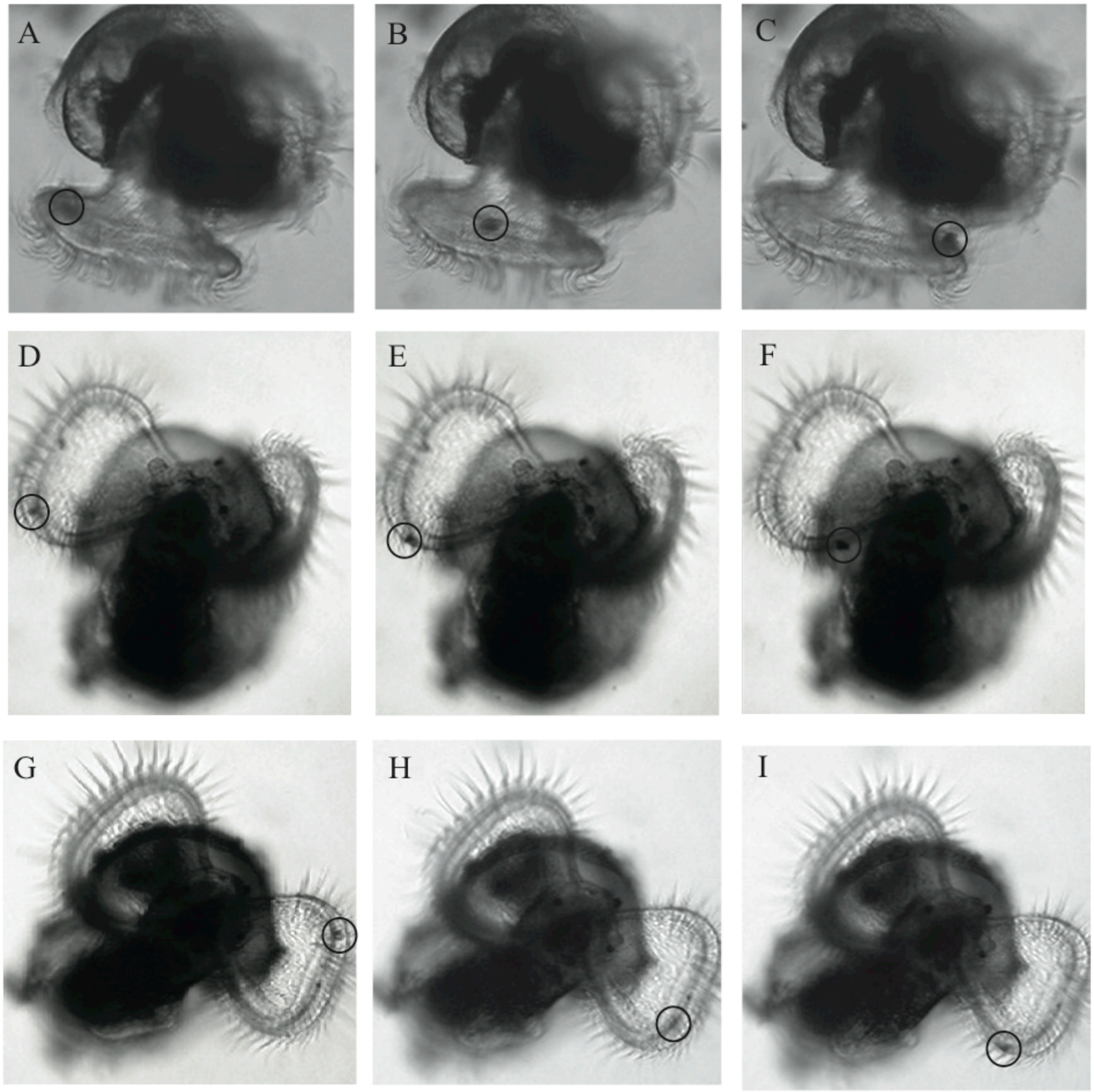
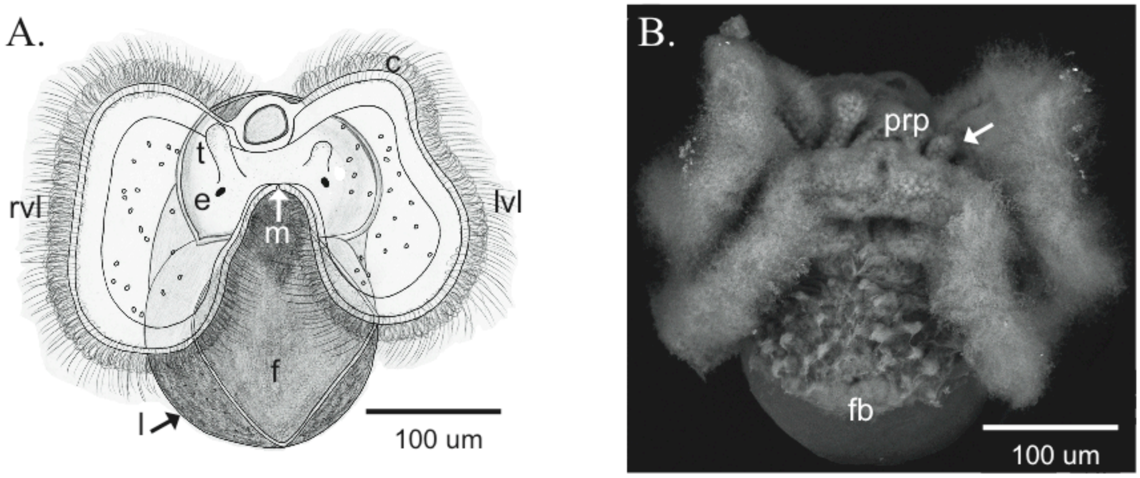


Figure 3 (A-I). Particle capture and transport through the velar food groove in Kelletia kelletii veligers. Images were isolated from video footage. A-C, D-F, particle capture and counter- clockwise movement in the right velar lobe of a post-hatched veliger. G-I, particle capture and clockwise movement in the left velar lobe of a post-hatched veliger.

2 weeks prior to hatching



2.5 weeks after hatching

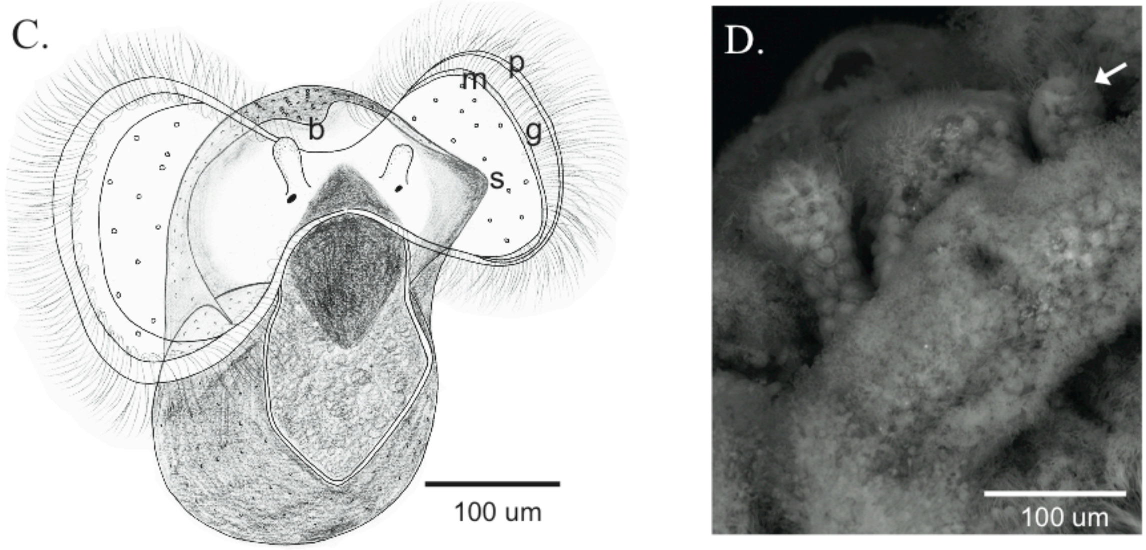
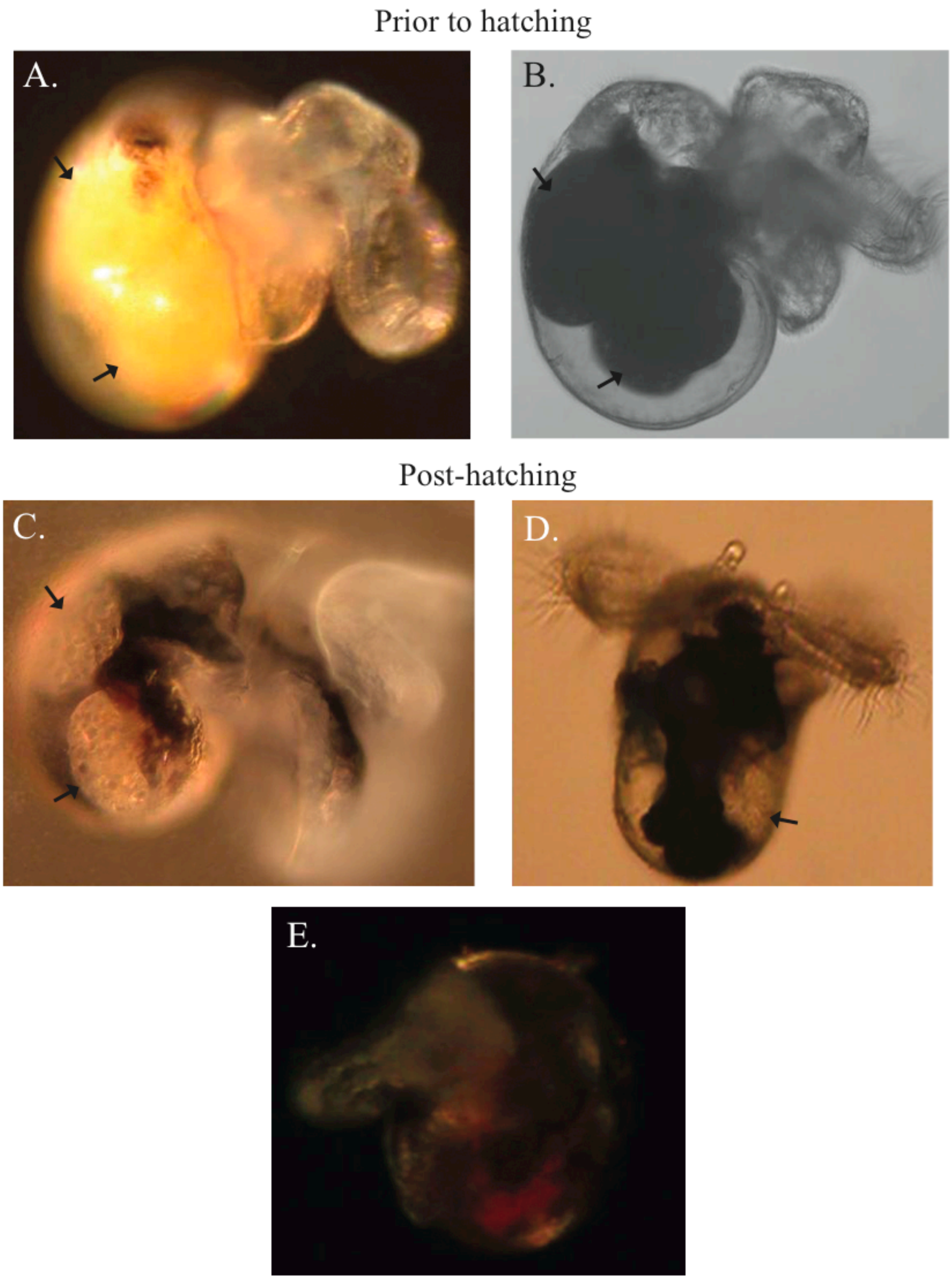


Figure 4 (A-D). *Kelletia kelletii* veliger larvae at two weeks prior to and post hatching. (A) Larva showing symmetrical velar lobes but assymetrical cephalic tentacles; c: velar cilia, rvl: right velar lobe, lvl: left velar lobe,t: tentacle, e: eye, m: mouth, f: ciliated foot, l: larval shell, (B) SEM image taken of a critical point dried specimens using a Hitachi TM-1000. Arrow indicates smaller left cephalic tentacles; prp: post-oral ciliary patch, fb: foot bristles, (C) larva showing assymetrical velar lobes and cephalic tentacles as well as development of the shell into the siphonal canal and beak. b: beak, g: food grove, s: siphonal canal, p: prototroch, m: metatroch, (D) SEM image taken of a critical point dried specimens using a Hitachi TM-1000. Smaller of the assymetical cephalic tentacles indicated by arrow.


Prior to hatching

Post-hatching

Figure 5 (A-E). *Kelletia kelletii* veliger larvae showing endogenous yolk reserves pre and post hatching as well as evidence of particle ingestion. (A and B) larval yolk reserves prior to hatching, (C) first day post-hatching. Two yolk stores fill much of the larval shell, (D) post-hatching day 10, yolk stores are nearly depleated as indicated by arrows, (E) post-hatching veliger with ingested flourescent particles visible (red) in the gut.

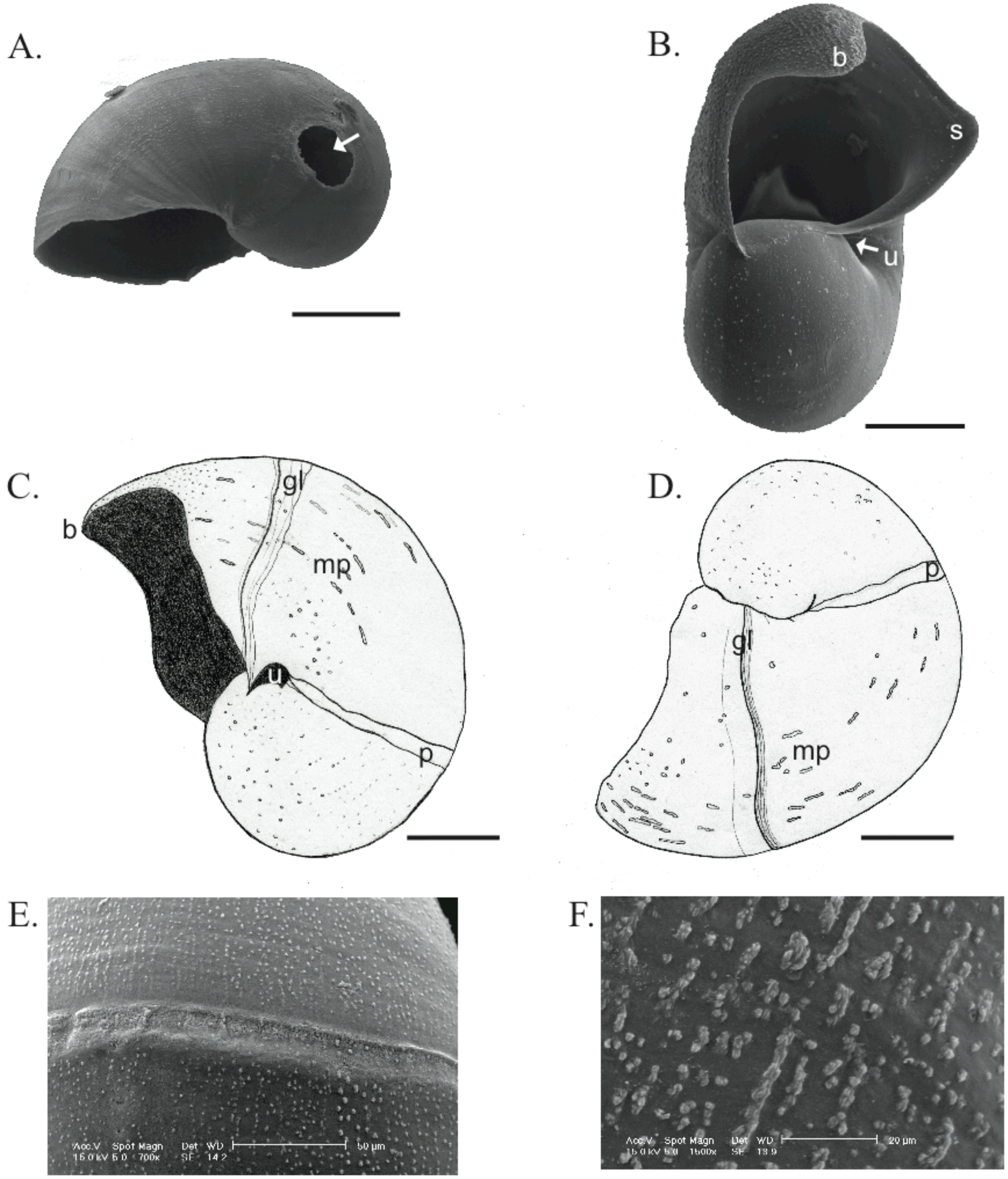


Figure 6 (A-F). Characteristics of *Kelletia kelletii* veliger larval shells. (A) ESEM larval shell of late pre-hatchling shells are thin, brittle, and have holes, an indicated by an arrow, (B) ESEM larval shell and two weeks post hatching, (C and D) line drawings of late-stage veliger shells with characteristics: b: apertural beak, gl: growth lines/boundary indicating shell size at hatchings, mp: bead-like microprotuberances, p: boundary/break in growth of protoconch 1, u: umbilicus, s: proto-siphonal canal, (E) close-up of the boundary of protoconch 1, (F) close-up of larval shell microprotuberances.
Scale = 100 um

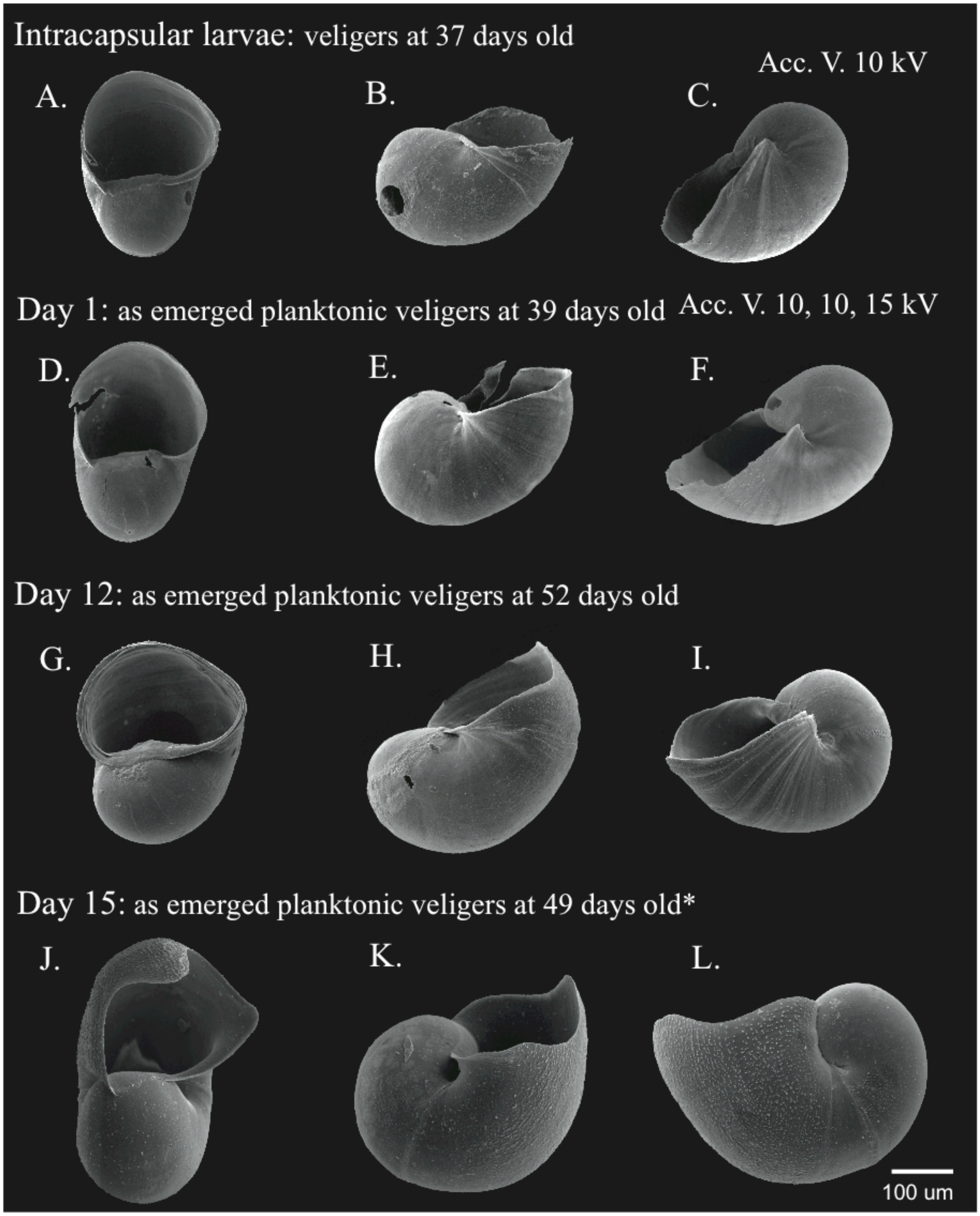


Figure 7 (A-L). ESEM micrographs of *Kelletia kelletii* larval shells. (A-C) larvae were excapsulated prior to natural emergence and shells were visualized at an accelerating voltage (acc. v.) of 10 kV, (D-F) larval shells at day one of emergence and visualized at an acc. v. of 10 kV, 10kV, and 15 kV, respectively, (G-I) larval shells at day 12 as planktonic veligers and visualized at an acc. v. of 15 kV, (J-L) larval shells at day 15 as planktonic veligers and visualized at an acc. v. of 15 kV. * This sample was excapsulated at day 34 and displays the morphology of larval shells near metamorphosis.

Table 1**.** Life history characteristics of *Kelletia kelletii*

Adult Range	• Point Conception, CA - Baja California, Mexico (Morris, 1980) • Central CA. to Baja California, Mexico (Zacherl, 2003)
Depth	• Subtidal to 70 m and among kelp (Morris, 1980) • 2m-70 m (Zacherl, 2003)
Substrate	• Rocky reefs, pebbles and sand in kelp forests (Zacherl, 2003)
Mating	• March, April and May (Rosenthal, 1970) • March & April (Morris, 1980)
Aggregations	• 200-300 individuals during spawning and other times (Rosenthal, 1970) • Up to 200 individuals (Morris, 1980)
Adult size	• 2.5-3 inches at 7 or 8 years old (MacGinitie and MacGinitie. 1949) • Females larger on average: males: 62-120 mm, females: 71-121 mm (Rosenthal, 1970) • 170 mm (Morris, 1980)
Capsule laying period	• (mostly) April –May (Rosenthal, 1970)
Oviposition sites	• Hard substrate, aquaria glass (in lab), *K. kelletii* shells, substrate w/ *K. kelletii* capsules already laid (Rosenthal, 1970).
No. of capsules laid per female	• One female laid 4x over 30 days: 85 capsules (Rosenthal, 1970)
Capsule morphology	• smooth, white and laid without much order (MacGinitie and MacGinitie, 1949) • Ovate, deflated with one face slightly convex translucent then darkens because of larvae inside (Rosenthal, 1970)
Capsule clutches	• 20-80 capsules in a "brood" (Zacherl, 2005)
Eggs/embryos per capsule	• 2,182 eggs in one capsule (MacGinitie and MacGinitie. 1949) • 400-1022 eggs, though capsules can also be empty! Eggs are yellow, 200-300 microns in diameter (Rosenthal, 1970) • Up to 1000 eggs (Morris, 1980) • 400-2000 larvae/capsule (Zacherl, 2003)
Larval shell	• Made of aragonite (Zacherl, 2003; 2005)
Larval development	• Hatching @ 30-34 days @ 14.5-17.5 °C (Rosenthal, 1970; Morris, 1980; Zacherl, 2003)
Post-hatching veligers	• Begin a planktonic existence until settlement is achieved (Rosenthal, 1970) • Pelagic, time before metamorphosis unknown (Zacherl, 2003)
Other	• Drilled by <u>*Polinices lewisii*</u> (MacGinitie and MacGinitie. 1949) • Feeds with <u>*Pisaster giganteus*</u> (Morris, 1980)

Table 2. Characteristics of pre and post hatching *Kelletia kelletii* larvae.

Pre-hatching

- No intracapsular feeding: no nutritive eggs or embryos
- Endogenous yolk reserves
- Veligers capture and move particles through both velar lobes, but do not ingest them
- Veligers could swim
- Cephalilic tentacles asymmetric, right one larger
- Velar lobes were of equal size
- Veligers phototaxic
- Larval shells growing, ornamented with micro-protuberances, poorly calcified

Post-hatching

- Veligers capture and move small particles through the food grooves of both velar lobes and ingest them
- Endogenous yolk stores were present in most larvae at hatching. Yolk depleted when veligers were 1.5-2 weeks old in the plankton.
- Cephalilic tentacles asymmetric, right one larger
- Velar lobes asymmetric, right one larger
- Veligers phototaxic
- Larval shells growing, well calcified, apertural beak and siphonal canal

Table 3. Larval developmental characteristics in buccinid gastropods

Site of larval development (developmental mode)	**Nutritive Mode**	**Source of Nutrition**	**Representative Buccinid**
Egg capsule[1] and plankton[2] (mixed)	Lecithotrophic (non-feeding) in capsule and plankton	endogenous yolk stores	None described
	Intracapsular feeding + lecithotrophic in plankton	nurse-eggs or sibling larvae (adelphaphagy)	None described
	Intracapsular feeding + planktotrophic	nurse-eggs or sibling larvae (adelphaphagy) and plankton in the water column	None described
	Lecithotrophic in capsule + planktotrophic	endogenous yolk stores and plankton in the water column	***Kelletia kelletii***
Egg capsule only (non-planktonic)[1]	Lecithotrophic	non-feeding, growth from endogenous yolk stores)	*Pareuthria plumbea*
	Intracapsular feeding	nurse-eggs or sibling larvae (adelphaphagy)	*Neptunea arthritica*

Development is intra-capsular = [1], Development is in the plankton = [2], [1] + [2] = mixed development (Pechenik, 1979)

A method for replicating gastropod protoconchs for morphological analysis

Abstract

In many gastropod taxa the protoconch, or first whorls at the apex of the shell, is an indicator of larval developmental mode. Because of their small size, the examination, analysis, and quantitative measurement of protoconch morphology often requires scanning electron microscopy (SEM) or other object digitizing techniques. Limitations of such studies include access and cost of microscopic time and the capacity of specimen chambers in SEM and other imaging machines to accommodate the gastropod specimens of choice. In this paper, a novel method is described to replicate gastropod protoconchs by molding and casting. This technique was tested successfully with more than 100 fossil and extant shell specimens from the neogastropod family Buccinidae. Casts were imaged using a Hitachi TM-1000 SEM. Resulting protoconch casts can be examined in lieu of original and fossil shells in SEM and other imaging analyses. Casts are durable, versatile, and molds can be made successfully from museum and type specimens, shells that are too large for available SEM machines or digitizing scanners, live gastropods, shells from protected land or private collections, and specimens from museums that do not have on-site imaging facilities. This approach has potentially diverse applications for morphological studies of invertebrates within biology and paleontology.

Introduction

This paper introduces a technique of molding and casting fossil and extant marine gastropod protoconchs (or larval shells) for comparative analysis. In 1946, Thorson proposed that protoconchs of many taxa can indicate larval developmental mode as either planktonic or non-planktonic (Thorson, 1946). Since then protoconch morphology have been used in biology and paleontology to infer early ontogeny in extant and extinct gastropods (Shuto, 1974; Hansen, 1980; Hansen, 1982; Jablonski and Lutz, 1983; Bandel, 1988; Lima and Lutz, 1990; Scheltema, 1994; Jablonski and Hunt, 2006). The maximum diameter and number of volutions of the protoconch are especially important for determining larval mode (Shuto 1974). For example, a bulbous protoconch with a wide diameter and few volutions suggests non-planktonic development. Alternatively, a high-spired protoconch with a narrow diameter and multiple whorls indicates development that took place, at least in part, in the plankton.

For many gastropod species and well-preserved fossils with protoconchs greater than 5 mm in diameter, developmentally informative morphology can be examined from photographs, directly from shells, or with a hand lens or light microscope (Weedon, 2007). Smaller protoconchs and fine shell detail, however, require analysis by alternative techniques such high-vacuum scanning electron microscopy (SEM) (Robertson, 1971; Bandel, 1988), or more recent technologies such as variable pressure environmental scanning electron microscopy (VP-ESEM), computed tomography (CT) scanning, or z-stacking digital elevation models. The objective of this paper is not to compare these imaging or analytical methods, but to propose protoconch casts as a viable and convenient alternative to using original shells in such analyses.

Most comparative studies of protoconchs have focused on larval shells (Hurst, 1967; Robertson, 1971; Hickman, 2005; Kowalke, 2006) and early post-metamorphic individuals (Hickman, 1992; Nützel and Frýda, 2003; Nützel and Pan, 2005; Parkhaev, 2006). To date, less research has assessed protoconch morphology in taxonomically diverse adult shells (Reid, 1989; Solsona and Martinell, 1999). The practicality and success of such studies may be impeded by the limitations and cost of microscopy and other imaging equipment, access to gastropod specimens, and the capacity of imaging machines.

Specimen capacity of Scanning Electron Microscopes can often be too small to accommodate gastropods of interest. For example, a compact SEM with a 2 by 2 stage (e.g., Quanta 200 FEG ESEM) can hold objects up to 28mm^3. The FE1/Philips XL30 ESEM FEG allows examination of specimens no larger than 50 mm^3. Although convenient for most small samples, specimen chambers like these preclude the study of entire gastropod families in which adults typically exceed these dimensions. Also, for small shells that fit into a traditional high-vacuum SEM, the altering effects of heavy metal sputter-coating and conductive tab mounting may prohibit the visualization and analysis of museum and type specimens. For even larger capacity SEMs (e.g., JEOL 5800LV) or high-resolution digitizers, establishing a consistent and stable orientation of the shell in the microscope or scanner may be difficult and prohibitively time consuming, especially for specimens that are broken, have a long or thin siphonal canal, or are otherwise difficult to mount with putty or on conductive tabs. Living snails and those preserved in museum wet collections are also precluded from use in many SEM and digital scanners.

Acquiring shell specimens for high resolution imaging may also present unique challenges to the researcher. Many museum collections rarely loan museum types or un-catalogued specimens. Likewise, shells from marine protected areas, fossils from State or National Parks, or endangered living gastropods would not be available for this or any such analyses. Even when specimens are accessible, imaging equipment and facilities might not be. University or other collections may not host in-house imaging facilities, or these might be accessible only to trained faculty, staff, or students— not the short-term visitor. If such facilities are available for visiting scientists, it could compromise the consistency of technique to use different imaging machines at each institution visited. Also, the cost of imaging or scanning may be prohibitive depending on the institution and the technology used. A conservative estimate of the cost of SEM beam time based on eight U.S. university electron microscope laboratories ranges from $26-$90 per hour. Imaging bulk samples at these rates could make such studies unfeasible especially if samples need to be stabilized, corrected, and repositioned while at the microscope.

The molding and casting method described here precisely replicates intact gastropod protoconchs for SEM and other analyses. Its advantages include speed, portability of molding equipment, durability of casts, and the ability to mold shells in the field or in collections with minimal equipment. Casts can also be prepared and mounted prior to valuable beam time, saving the researcher time and money.

Molding and casting materials

Molding material is a quick-setting (180 seconds), dimensionally stable polyvinylsiloxane that is harmless to most gastropod shells and faithfully captures fine details of shell surface morphology (Galbany et al., 2006). The molding technique described here is a modification of a common procedure in dentistry that has been adopted by anthropologists and paleontologists to mold the teeth of hominids and other primates (Hlusko et al., 2002; Guatelli-Steinberg et al., 2005). This is the first study to apply this technique to mollusc shells. It was tested with excellent results on

113 gastropod protoconchs of dry, wet, and fossil shells with varied surface finishes and microstructures (i.e., polished, chalky, smooth, and finely ornamented).

Protoconch casting requires limited materials and can be performed at the home institution or preparatory laboratory of the researcher. The casting material is epoxy resin, which makes highly accurate and detailed casts from silicone molds (Purnell, 2003). The casting protocol described here was modified from a technique used in paleontology to replicate microvertebrate fossils (Waters and Savage, 1971; Reser, 1981; Goodwin and Chaney, 1994). It has been used by anthropologists and paleontologists to reproduce vertebrate teeth and bone for SEM and other analyses (Rose, 1983; Beynon, 1987; Ungar and Williamson, 2000).

Methods

Molding

1. Shells were stabilized vertically and their apexes pulsed 2-3 times with canned compressed air (e.g., Falcon Dust-Off™) to remove dust and other debris. Shell surface and overall durability were examined carefully at this step, because molding material will remove periostracum and can damage very fragile shells.

2. Clean protoconchs (fig. 1.1.) were covered with a 3-5 mm layer of polyvinylsiloxane (e.g., Coltène/Whaledent Affinis® fast light body) (fig. 1.2). This is a low-viscosity dental-grade silicone elastomer that dispenses from 50 ml cartridges into a detachable applicator tip (e.g., Coltène/Whaledent Affinis® Dispenser 50/75 ml). Because polyvinylsiloxane hardens in the applicator tip in 3 minutes, shell apexes were molded in sets of ten or more, rather than one at a time. This approach allowed for efficiency in mold-making with a minimal waste of applicators. An attempt was also made to mold protoconchs with a medium-viscosity silicone elastomer (e.g. Coltène President Plus® medium body). This material set well but tore more often than the low-viscosity material when casts were removed from molds.

3. After molding material was applied directly to shell apexes it was pulsed with compressed air to drive out air bubbles from between the shell surface and the polyvinylsiloxane. Bubbles in the mold make minor, but undesirable, convex artifacts in the cast. At this step, care was taken to ensure that sufficient molding material coated each shell apex. If the molding material was so thin that the protoconch was visible through it, another layer of polyvinylsiloxane was applied.

4. Coated shell apexes were left to set for three minutes. Dried but flexible molds were then removed from shells and glued to paper labels with a silicone-based adhesive (e.g., ACE Siliconized Acrylic Caulk™).

Casting

1. For casting, an epoxy resin (e.g., TAP™ Four-to-One Super Hard Epoxy Resin) was tinted with a pigment (TAP™ Pigment) until opaque. It was then mixed with its catalyst in a 4:1 ratio by volume (e.g., 1 teaspoon epoxy to ¼ teaspoon catalyst) following the instructions of the manufacturer. The 4:1 mixture was painted onto the interior of the mold with a small paintbrush (size 0-2), then added in drops until the mold was almost filled (Goodwin and Chaney, 1994). No mold release was used. The approximate working time of this casting

material is one half hour (Reser, 1981). Safety protocol for using this epoxy resin should be followed carefully, (e.g. wearing protective gloves and mixing and pouring the product while in a well-ventilated room) (see MSDS Jeffco 3120, 2006).

2. To de-bubble the epoxy, filled molds were placed in a vacuum chamber and exposed to six cycles of pressure at 30 inHg (0.1016 Mpa) for ten seconds followed by 15 inHg (0.0508 Mpa) for five seconds (Reser, 1981; Umstead, 2006). Although not tested in this study, a hand-crank centrifuge is a possible alternative to a vacuum chamber (see Reser, 1981),. De-bubbled casts were allowed to set at room temperature overnight (>12 hrs) in a fume hood or well-ventilated space.

3. Hardened casts were freed from molds by peeling off the flexible polyvinylsiloxane in one piece. This material regained its shape quickly and rarely tore. In this study, casts of small specimens (<5 mm) were then prepared for imaging by SEM.

Cast Preparation for Imaging

1. To prepare casts for mounting, the base of each was leveled and smoothed with damp sandpaper (≤ grade 80) or a nail file while the specimen was immersed in water. This technique eliminated airborne and potentially carcinogenic epoxy dust (DHS Fact Sheet, 1989). Leveled casts were dried and pulsed with compressed air while under a fume hood until they were free of dust

2. Casts were mounted onto SEM specimen stubs with double-sided carbon conductive adhesive tabs (e.g., PELCO Tabs™ Double Coated) (fig. 1.3). Prepared stubs were placed in an SEM storage box and kept in a desiccator until ready to image (fig. 1.4).

3. Mounted casts were left uncoated, though they can be sputter-coated if necessary. Casts were imaged with a back-scattered electron detector (BSE) scanning electron microscope (Hitachi TM-1000 SEM) (fig. 2). Image brightness and contrast were adjusted with SEM controls and altered in Adobe Photoshop CSR®, when necessary.

4. Protoconch morphology was examined from SEM images. Quantitative measurements could be made using one of many image processing programs (e.g., ImageJ® or SPSS Sigma Scan® Aspire Software International).

Conclusions

The novel method of protoconch molding and casting described here is intended to improve the feasibility of studies of early ontogeny in extant and extinct gastropods. Its practical advantages include rapid molding, a relatively simple casting procedure, and ease in transporting casts, molds, and molding equipment. The analysis of protoconch casts instead of original shells allows the researcher to: 1) examine the morphology of valuable gastropod specimens outside their repository, 2) amass morphological data from bulk samples relatively easily; 3) replicate the apexes of live or preserved snails from wet collections, 4) replace molds if lost or damaged by making a mold from an existing cast (Waters and Savage, 1971), 5) collect detailed morphological data from protected species and specimens from fossil sites, marine reserves, or private collections; 6) prepare a standard orientation of casts before magnification, and; 7) save time and money by preparing and mounting casts before imaging.

Because this method is non-destructive for most lithified fossils and calcified hard parts, it has broad potential applications for fossil and living invertebrates. Molding and casting or the molding procedure alone merit testing with other morphologies of the molluscan shell such as micr-ornamentation, shell breakage and repair surfaces, micro-rasping marks, and drill holes. In other invertebrates this method could be applied to ornamented exoskeletons or epibiont encrusted surfaces. These and other applications provide exciting possibilities for future research.

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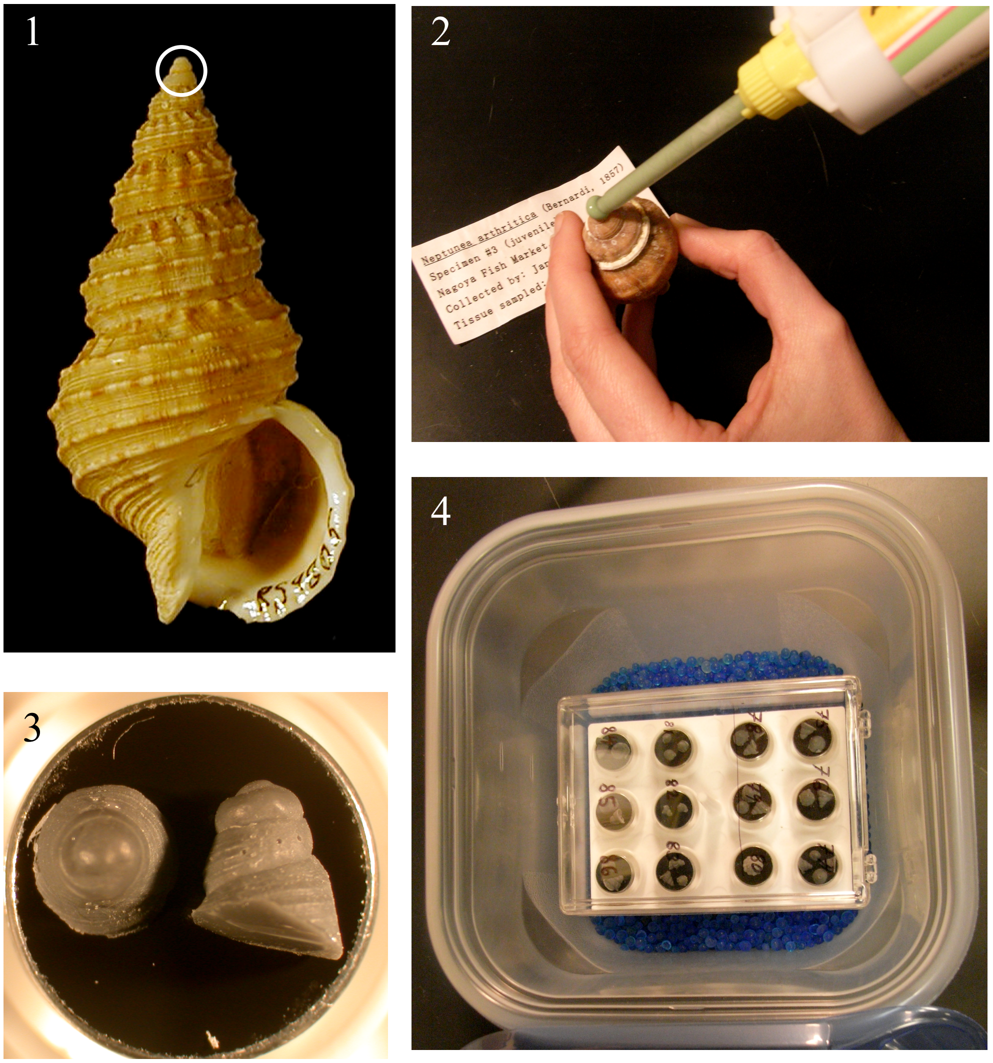

Figure 1. (1) Protoconch circled at the apex of *Buccinum zelotes* Dall, 1907. Length of specimen = 52 mm, (2) application of polyvinylsiloxane molding material to a gastropod shell apex, (3) epoxy resin casts of *Neptunea sp.* in apical and lateral view mounted on a specimen stub (12.7 mm in diameter) with a carbon conductive adhesive tab, (4) an SEM storage box inside a simple desiccator: a plastic storage container with desiccant beads.

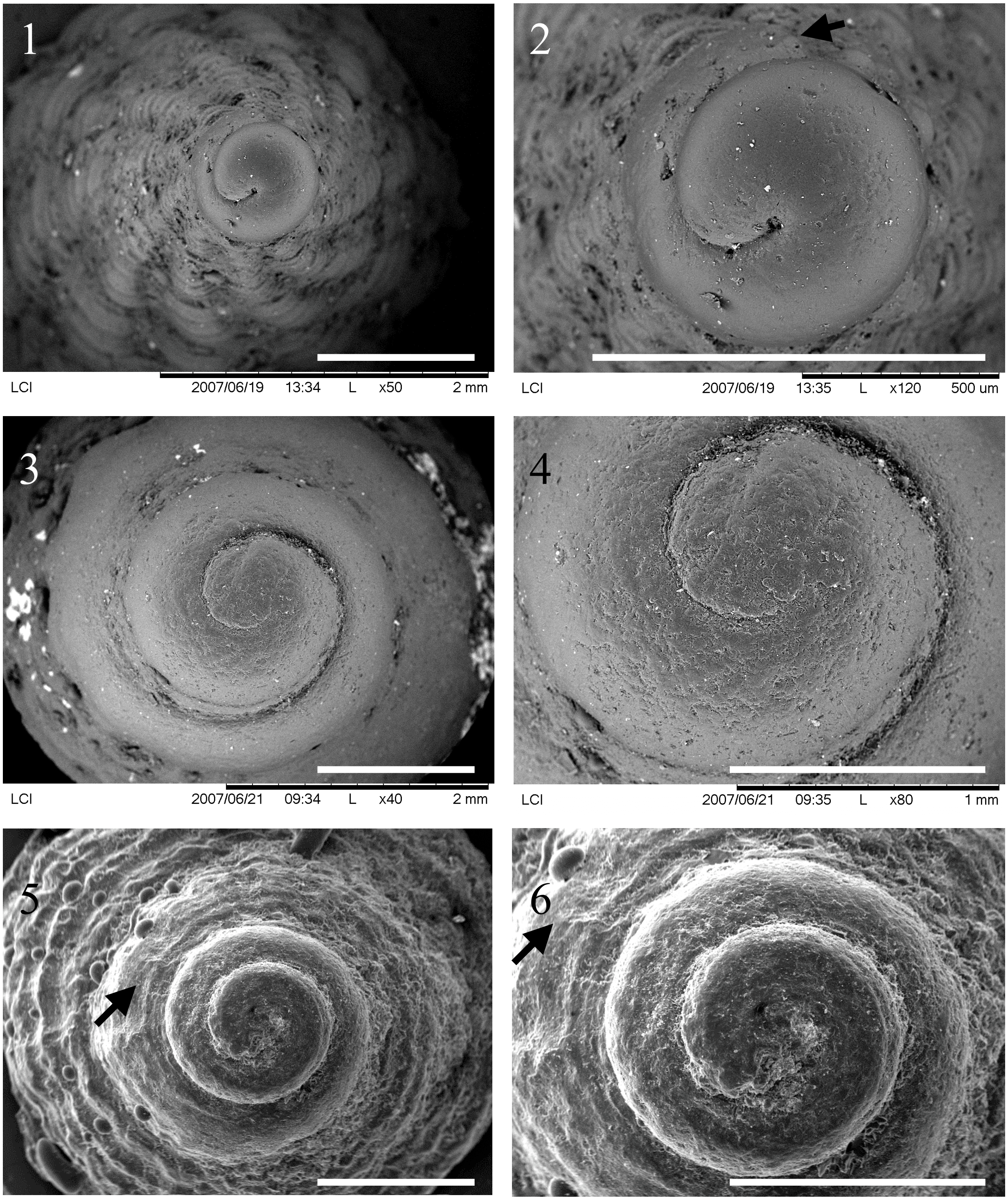

Figure 2. Scanning electron micrographs (at 15 kV) of gastropod protoconch casts made of 4:1 epoxy resin (1, 2) *Cantharus undosa* Linnaeus, 1758, uncoated modern shell. Arrow indicates the protoconch/teleoconch boundary, (3, 4) *Bruclarkia columbianum* (Anderson and Martin, 1914), uncoated fossil shell, (5, 6) *Bruclarkia acuminatum* (Anderson and Martin, 1914), sputter-coated (with Pt) fossil shell. Arrows indicate convex artifacts from air bubbles in the mold. Scale bar = 1 mm.

Summary

The following statements summarize the major conclusions and data reviewed in each chapter.

Ch. 1: A new species of *Bruclarkia* (Mollusca: Gastropoda) from the Astoria Formation in Oregon and Washington and a review of Miocene congeners in the Pacific Northwest

- The Miocene Astoria Formation of the Pacific Northwest includes three species of the whelk genus *Bruclarkia: B. oregonensis, B. acuminata*, and *B. ellenae*.
- *Bruclarkia ellenae* is described for the first time and was originally included as one of many morphotypes of *B. oregonensis*.
- *Bruclarkia ellenae* is endemic to the Astoria Formation and restricted to the early to early middle Miocene.
- Paleomagnetic and stratigraphic data suggest that most of Astoria Formation correlates with the Newportian molluscan stage of the Pacific Northwest and the "Temblor" molluscan zone of California.
- *Bruclarkia ellenae* is found only in the oldest Astoria deposits and possily spans a small portion of the early Miocene Pillarian stage and Californian "Vaqueros" zone.
- The morphology of *B. ellenae* most closely resembles *B. acuminata*
- It is unclear why *Bruclarkia* did not migrate to the west Pacific during the Miocene Climate Optimum like some other neogastropods.
- An examination of many specimens (>700) from museum collections was necessary to identify *B. ellenae* as a separate species.

Ch. 2: A review of the neogastropod genus *Bruclarkia* (Trask in Stewart, 1926) from Paleogene and Neogene strata of the North American Pacific Coast

- All proposed taxa in the genus were evaluated for eleven shell characters including spiral cords, extent of the parietal lip, spire morphology, ornamentation of the sutural collar and penultimate whorl, and node rows (or absence of) on the body whorl.
- 797 *Bruclarkia* fossils were identified to species in this study.
- Of twenty proposed *Bruclarkia* taxa, seven are valid species: *B. acuminata, B. barkeriana, B. ellenae, B. gravida, B. oregonensis, B. santacruzana,* and *B. vokesi.*
- *Bruclarkia* span the Paleogene and Neogene from California to Alaska.
- Variable shell characters include siphonal canal length and shape, the number of node rows on the body whor*l,* the number of nodes per row, and the angle of the spir*e.*
- Invalid *Bruclarkia* species include *B. fulleri, B. seattlensis*, and *B. blakeleyensis.*
- Results suggests that the genus was not as species-rich as previously thought.
- The stratigraphic range of *Bruclarkia* spans the Refugian to Luisian and the Galvinian to Temblor/Newportian mollusc stages of Armentrout (1981).
- The morphology of *B. ellenae* is unique among *Bruclarkia* species in having a stratigraphic range that is restricted to one formation, the Astoria Fm. in Oregon.
- *Bruclarkia barkeriana* and *B. santacruzana* are endemic to California and have nearly identical shell sculpture except for body whorl ornamentation, which is present in *B. barkeriana* but absent in *B. santacruzana*.
- *Bruclarkia vokesi* may be sister or ancestral to *B. gravida* and stratigraphically, these taxa are the oldest of the genus and become extinct by the early Miocene.

- *Bruclarkia gravida* has the most expansive geographic range, occurring from Alaska to California.

Ch. 3: Molecular systematics of Buccinidae (Neogastropoda) of the North Pacific: relationships of some major genera and subfamilies

- Monophyly of the Buccinidae is supported by molecular analyses (28S and 28S+CO1) in a sample of more than 20 species, most from the northwest Pacific.
- The genus *Babylonia*, formerly considered a buccinid but removed from the family in recent classifications, was confirmed by CO1 data to fall outside of the Buccinidae.
- The Atlantic Busyconinae taxa *Busycon* and *Busyconinae* nest within the Buccinidae.
- Five buccinid subfamilies are strongly supported by molecular data: (1) Beringiinae Golikov and Starobogatov, 1975 (*Beringion* + *Japelion*), (2) Buccininae Rafinesque, 1815 (*Buccinum* + *Volutharpa*), (3) Busyconinae Wade, 1917 (*Busycon* + *Busycotypus*), (4) Neptuneinae Stimpson, 1865 (*Neptunea*), and (5) Photinae Gray, 1857 (*Kelletia* + *Nassaria*).
- All buccinid genera represented by more than one species in this analysis (i.e. *Buccinum, Busycon,* and *Neptunea*) resolve as monophyletic.
- Preliminary analyses of larval development in Buccinidae reveal multiple origins of planktonic development within the family.
- Members of the genera *Lirabuccinum, Microfusus,* and *Solenosteira* resolve poorly in CO1 and 28S analyses and can not be assigned to a buccinid subfamily.

Ch. 4: Early development and feeding mode in *Kelletia kelletii* (Forbes, 1850)*,* a buccinid gastropod with a veliger larva

- Twelve *K. kelletii* specimens from Santa Barbara and Monterey, Calfornia were kept in a circulated seawater aquarium at UC Berkeley and successfully spawned periodically over three years.
- *Kelletia kelletii* larvae are non-feeding (lecithotrophic) within their egg capsules, but feed as swimming veligers.
- Larval shells and veligers were visualized with optical microscopy and SEM.
- Observations, SEM photomicrographs, and tests of larval feeding reveal that:
    - (1) intracapular veligers are capable of particle capture and transport but not particle ingestion,
    - (2) hatching time varies between approximately 35 to 60 days depending on water conditions and temperature,
    - (3) intracapsular larvae do not eat undeveloped eggs and/or embryos though they are present in all capsules,
    - (4) pre-hatched veligers swim in the plankton if excapsulated at 27 days old and older,
    - (5) within the capsule, veliger velar lobes are symmetrical but the right cephalic tentacles is larger than the left,
    - (6) at 2.5 weeks in the plankton, both the right cephalic tentacle and right velar lobe are larger than those on the left,

(7) larval shells are brittle at emergence but calcify and grow apertural beaks and proto-siphonal canals by 2.5 weeks in the plankton.

Ch. 5: A method for replicating gastropod protoconchs for morphological analysis

- Method is based on protocols used in vertebrate paleontology for molding and casting micro-mammal and other small vertebrate teeth.
- Molding requires clean and periostracum-free shell apexes to be covered with a dental-grade polyvinylsiloxane impression material.
- Casts are made from molds using tinted epoxy resin and can be re-cast multiple times from the same mold without deterioration in cast quality.
- Casts can be made from specimens that would be otherwise be prohibited from microscopic and SEM analysis (e.g. living specimens, shells from protected land or private collections, type specimens, etc.).
- Casts can be examined in small SEM machine chambers that can not accommodate an adult gastropod shell.