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A new species of *Crepipatella* (Gastropoda: Calyptraeidae) from northern Chile

DAVID VELIZ[1], FEDERICO M. WINKLER[2], CHITA GUISADO[3] & RACHEL COLLIN[4]

[1]Departamento de Ciencias Ecológicas and Instituto de Ecología y Biodiversidad (IEB), Universidad de Chile. Casilla 653, Santiago, Chile. E-mail: dveliz@uchile.cl (corresponding author)
[2] Departamento de Biología Marina, Universidad Católica del Norte, Sede Coquimbo. Casilla 117, Coquimbo, Chile. E-mail: fwinkler@ucn.cl
[3] Facultad de Ciencias del Mar y Recursos Naturales, Universidad de Valparaíso. Casilla 5080, Reñaca, Viña del Mar, Chile. E-mail: chita.guisado@uv.cl
[4] Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, República de Panamá. E-mail: CollinR@si.edu

Abstract

Crepipatella occulta n. sp. is described from the intertidal zone in northern Chile. This species is morphologically cryptic with two other *Crepipatella* species from Chile, *Crepipatella dilatata* (Lamarck, 1822) and *Crepipatella peruviana* (Lamarck, 1822) (a senior synonym of *C. fecunda*), with respect to adult shell morphology and anatomy. However, *Crepipatella occulta* is clearly distinguishable from both of them on the basis of embryonic development. It can be distinguished from *Crepipatella peruviana*, a planktotroph, and *Crepipatella dilatata*, a direct developer with uncleaved nurse eggs, because it has direct development with developing nurse embryos that are consumed before the juveniles hatch. Genetic data from DNA sequences also support the distinct status of this species, and show that the South African species *C. capensis* (Quoy & Gaimard, 1832–33) is more closely related to *C. dilatata* and *C. peruviana* than is *C. occulta*. In addition *Crepipatella occulta* displays diagnostic alleles in 14 allozyme loci when compared with the other two co-occuring Chilean species in northern Chile. Morphologically, *Crepipatella occulta* n. sp. does not attain the large size often observed in *C. peruviana*, and it typically has a shiny dark chestnut or chocolate shell interior.

Key words: cryptic species, *Crepipatella dilatata*, *Crepipatella fecunda*, Caenogastropoda

Introduction

Shell characters typically used in traditional molluscan taxonomy are frequently insufficient to delimit species of calyptraeid gastropods. This is primarily due to the sessile adult habit, which has led to simple shell morphologies that are prone to convergence (e.g. Collin 2003a; 2005a), which often show plasticity (Broderip 1835; Collin 2000; 2005b; Véliz et al. 2001), and which seldom retain the protoconch in adult shells. During the 20th Century this has resulted (e.g., Hoagland 1977) in the lumping together of many species that were originally described based only on their shells. However, examination of developmental characters starting with the work of Hoagland (1986), and subsequent application of molecular techniques, has resulted in the removal from synonymy of several genera and species of calyptraeids. For example, reproductive characters and soft body morphology have led to the recent redescription of several species of *Crepidula* Lamarck, 1799 (Gallado 1979; Brown and Olivares 1996; Cledón et al. 2004; Simone 2006). Mitochondrial DNA variation has been combined with morphological features (Collin 2003a,b; Collin 2005b) to remove the genera *Bostrycapulus* Olsson & Harbison, 1953, *Maoricrypta* Finlay, 1926 and *Crepipatella* Lesson, 1830 from synonymy with *Crepidula*, where they were placed by the last comprehensive taxonomic review of the genus (Hoagland 1977). Finally, Cytochrome Oxidase I (COI) sequence data have been combined with developmental and morphological features to describe morphologically cryptic species of *Crepidula* and *Bostrycapulus* (Collin 2000; 2005b).

The genus-group name *Crepipatella* Lesson, 1830 was first introduced as a subgenus of *Calyptraea* Lamarck, 1799 (Lesson 1830) and was subsequently used by that author as a subgenus of *Crepidula* (Lesson, 1832). The group is commonly distinguished from other calyptraeids based on a rounded convex shell with a somewhat cupped, internal septum showing a deep notch on the animal's left side. Extant *Crepipatella* occur in cold water in South Africa, along both coasts of South America, both coasts of the North Pacific, and a single tropical species is reported from Panama (Keen 1971). Unusually for his day, Lesson illustrated the external view of the body positioned inside the shell. The head, neck and foot are clearly those of a calyptraeid but the animals are depicted the wrong-way round in the shell, with the head pointing towards the apex of the shell, as first pointed out by Broderip (1835). The taxonomy of the genus in South America has a complicated history with at least 11 species described before 1900 (Table 1). Unfortunately, poor sampling, especially in the extreme south, and the smooth, featureless but variable shells, which usually lack a protoconch, make it very difficult to equate with any certainty the biological species with the original illustrations or type material.

Two species, *Crepipatella dilatata* and *Crepipatella peruviana* (commonly referred to by its junior synonym

Crepipatella fecunda (Gallardo, 1979)) are currently commonly recognized along the coast of Chile, and are among the most well-studied species of gastropods in the southern hemisphere (e.g., Gallardo 1976; 1977; 1979; Gallardo and Garrido 1987; Chaparro and Paschke 1990; Chaparro et al. 2001; 2002; 2005a; 2005b; 2008; 2009; Veliz et al. 2003; Montory et al. 2009; Schmidt et al. 2006; Guzman et al. 2011). The first of these names, *C. dilatata*, has been consistently applied to Chilean animals since it was proposed and is currently applied to a species with direct development where embryos consume uncleaved nurse eggs and hatch as crawling juveniles. *Crepipatella dilatata* is reported to range in Chile from San Marcos Bay (21º11'S) to Puerto Marín (43º47'S) (Gallardo 1979). *Crepipatella dilatata* is also often reported to occur in Peru, but this is based only on ambiguous shell material, and has yet to be verified by observations of development or genetics. This species is also reported from the coast of Argentina between Ushuaia (~55º S, Penchaszadeh et al. 2002) to Golfo Nuevo (~42º S) (Penchaszadeh et al. 2002; Collin et al. 2007) based on the presence of nurse eggs. The species identity of animals from Puerto Madryn has been verified with COI sequence data (Collin et al. 2007; Guzman et al. 2011), as has the identity of a population recently established on the northern coast of France (Collin et al. 2009). Aguirre (1993) designated a lectotype for *C. dilatata* from the material examined by Lamarck in the Mad. de Bandeville collection (MHNG 1090/70/1) and commented that Mermod (1950) considered the remaining specimen (MHNG 1090/70/2) to belong to a variety, probably synonymous with Broderip's *C. foliacea* (Broderip, 1834). It is unclear if *C. foliacea* represents an additional distinct species or a variant form of *C. dilatata*.

The second species in South America, *C. peruviana*, has been referred to as *Crepipatella fecunda* (Gallardo, 1979) in most recent publications. This species has planktotrophic development and is distributed from the vicinity of Lima, Peru (12º 0'S) (Collin 2003b) to Quintralco Fjord, Chile (45º43'S) (Gallardo 1979). This planktotrophic species reaches a greater maximum size than *C. dilatata*; large *C. dilatata* are usually 3–4 cm in shell length and large planktotrophs are generally 5–6 cm, although giants as large as 5 cm and 7 cm have been reported for the two species respectively (reviewed in Collin 2003c). The difference in development as well as the larger size and a paler shell were used to diagnose *C. fecunda* compared to the smaller shell and darker interior of *C. dilatata* (Gallardo 1979). This difference in shell color led Hoagland (1983) to suggest that *Crepipatella patula* (Deshayes, 1830) could be a senior synonym of *C. fecunda*. The published locality of Tahiti for *C. patula* is problematic, as *Crepipatella* have not otherwise been reported from Tahiti. An even older synonym is *Crepipatella peruviana* (Lamarck, 1822), whose locality of 'mer du Pérou', and large pale shell (described and shown in Figure 31a in Mermod 1950) provide convincing evidence that it is a synonym of *C. fecunda*. Despite the lack of protoconchs on the type of *C. peruviana*, direct developing *Crepipatella* have never been reported in Peru, and one of us (RC) found only planktotrophic *Crepipatella* in the vicinity of Lima, Peru. This further supports the synonymy of *C. peruviana* and *C. fecunda*.

Véliz et al. (2003) reported the existence of a third distinct *Crepipatella* species (as *Crepidula* sp.) sympatric with both *C. peruviana* and *C. dilatata* in northern Chile. This species was initially detected due to its unique development and allozymes, but DNA sequence data further supported its status as a species distinct from *C. dilatata* and *C. peruviana* (Collin 2003a, 2003b; Collin et al. 2007). Here we formally describe this species and name it *Crepipatella occulta* n. sp.

Materials & Methods

Material for this study was collected by hand in the low intertidal. Each female was carefully removed from the substrate along with egg capsules that were being brooded. Anatomical features were observed under a stereomicroscope following dissection. Radulae from 4–5 individuals were obtained by dissection and washed in 5% sodium hypochlorite in distilled water for 5 min to remove extraneous tissue. They were sputter coated with gold, observed and photographed using a JEOL T300 or Zeiss Evo 40 VP scanning electron microscopes. Protoconchs were prepared for SEM in a similar way. The size range of the different sexual phases and the developmental characters have already been reported (Véliz et al. 2003) and include sizes of the eggs, veliger larvae, and stage at hatching.

Systematics

Family **CALYPTRAEIDAE** Lamarck, 1809
Genus ***Crepipatella*** Lesson, 1830
Type species: *Crepipatella dilatata* by original designation

Crepipatella occulta n. sp.
(Figs 1–3)

Synonymy
Crepidula sp.—Véliz *et al.* 2003: 132, Fig. 2b
Crepidula n. sp.—Collin 2004: 1493, Fig. 2
Crepipatella sp.—Collin and Cipriani 2003: 2553, Fig.4; Collin *et al.* 2007: 85, Fig. 1E
'*Crepipatella* n. sp. Chile'—Collin 2003b: 625, Fig. 2

Type locality: Low intertidal, rocky shore, Totoralillo Beach, Coquimbo, Chile (30º 05' S; 71º22'W).

Type material. Holotype Totoralillo Beach, Coquimbo, Chile, coll. D. Véliz, 2009. Female in ethanol with egg capsules. Museo Nacional de Historia Natural, Chile MNHNC 5856 (Fig. 1a). Length = 3.3 cm, width = 2.8 cm; height = 1.1 cm. (MNHN 5856). Paratypes MNHNC 5857 (Fig. 1b) Female in ethanol with egg capsules from type locality (MNHNC 5858); Female from low intertidal, rocky shore La Herradura Bay, La Herradura Bay (29º 59' S; 71º21'W), Coquimbo, Chile, MNHNC 5859 (Fig. 1c) with egg capsules (MNHNC 5860); Female from La Herradura Bay, MNHNC 5861 (Fig. 1d) with egg capsules (MNHNC 5862).

Other material: Collin (2003a) - one specimen Totoralillo Beach, Field Museum, Chicago, USA (FMNH282280). One specimen, Academy of Natural Sciences, Philadelphia (ANSP 413606) (reported by Collin et al. 2007).

Description

Shell (Fig. 1): thick, convex, ovoid, round. Apex curves posterior right. Dorsal side creamy, numerous radial dark-brown lines often covering entire shell. Shell margin irregular. Inner surface nacreous brown. When infected by spionid polychaetes dull white (Fig 1c). Lunate muscle scar animal's left shell margin at juncture with septum. Septum concave in ventral view, attached along right and posterior edges. In juveniles attached symmetrically along both sides. Ridge runs anterior-posterior in central zone of septum.

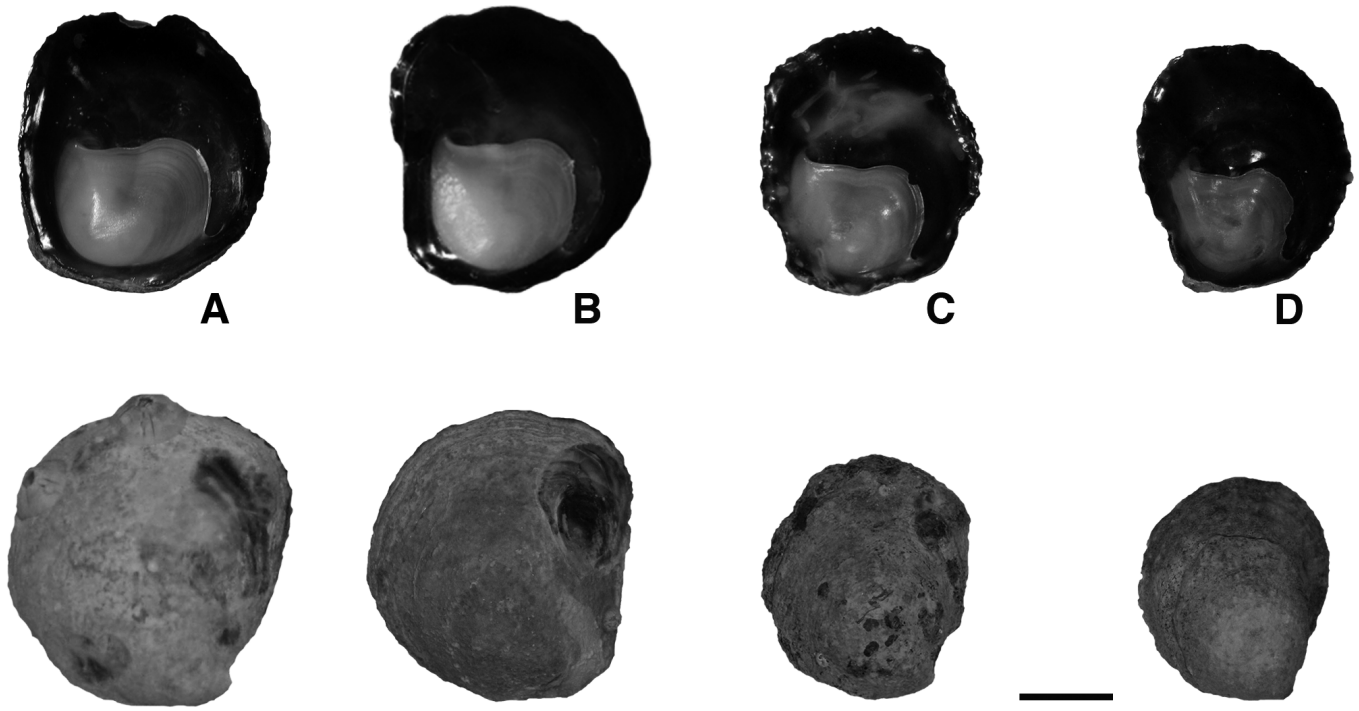

FIGURE 1: A–D. Shells of *Crepipatella occulta* n. sp. **A,** holotype, MNHN 5856. **B.** paratype from Totoralillo beach, Chile, MNHN 5857. **C, D.** paratypes from La Herradura bay, Chile, MNHN 5858 and MNHN 5859. Upper row ventral views, lower row dorsal views. Scale bar: 1 cm.

Protoconch (Fig. 2): Smooth, globose, three quarters of a whorl. Protoconch-teleoconch boundary marked by initiation of growth lines at 900–1000 µm.

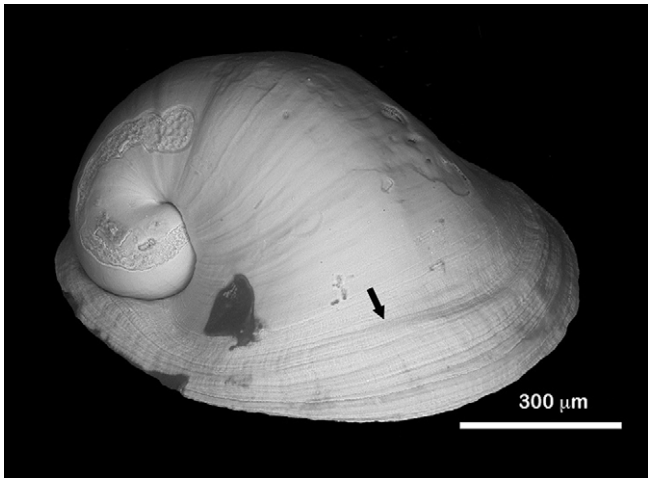

FIGURE 2: Protoconch of juvenile *C. occulta* n. sp. from Totoralillo and raised in the laboratory. Arrow indicates protoconch-teleoconch boundary.

Radula (Fig. 3): Taenioglossate; rachidian 2–5 (mean 3.3, sd = 0.67, n = 35) cusps on each side. Lateral tooth 5–11 (mean = 7.8, sd = 1.45, n=41) cusps outer side, 1–3 (mean = 1.3, sd = 0.53, n = 29) cusps inner side. Inner marginal tooth, 5-12 (mean = 7.34, sd = 1.9; n 23) cusps internal, 3–6 (mean = 4.3, sd = 1.1; n =17) external cusps. Outer marginal tooth 3–5 (mean = 3.8, sd = 0.53; n = 17) cusps internal side, external side lacks cusps.

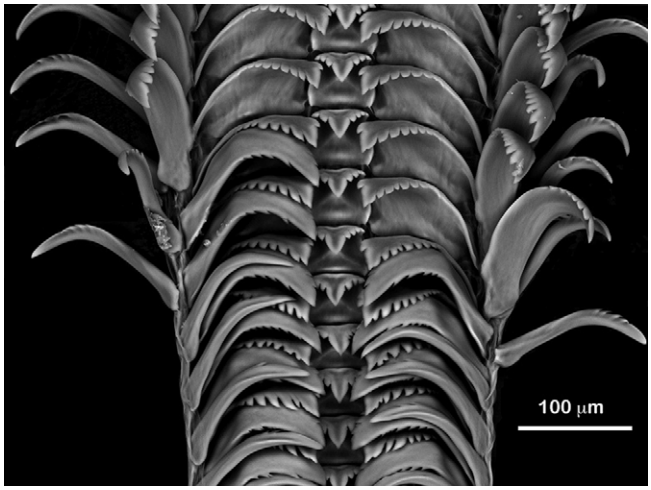

FIGURE 3: Part of the radular ribbon of *Crepipatella occulta* n. sp. from Totorallilo.

Anatomy: Features similar to other *Crepipatella* (see Collin 2003a). Foot: round, rectangular propodium, no mesopodial flaps, no black pigment. Neck: dorsoventrally flattened, lappets on each side, narrow food groove dorsal on right side. Tentacles: stubby, narrow suddenly before simple black eye laterally. Food pouch anterior on mantle margin. Mantle and neck with white and yellow pigment blotches and white pigment granules. Some black pigment on tentacles, head. Osphradium: brownish, bipectinate, anterior row of leaflets reduced. Salivary glands, tubular, extend halfway down neck. Neck filled with dense connective tissue.

Visceral mass: covers left 2/3 of foot, does not extend to posterior margin of foot. Gill extends on left side to posterior visceral margin. Stomach located about 1/3 from posterior margin on right side of viscera. Style sac runs laterally between stomach and gill in dorsal viscera, short compared to *Crepidula*, entirely surrounded by digestive gland and gonad. Intestine runs posterior from style sac to posterior margin of viscera before looping ventrally. Heart and kidney between the 1st and 2nd descending loops of the intestine. Digestive gland visible anterior and posterior to stomach in dorsal view. Gonad below mantle cavity, extending dorsally on posterior margin of viscera. Shell muscle runs from foot to dorsal shell at anterior right corner of viscera, lateral to the capsule gland. Dorsal attachment: muscle visible superficial to intestine anteriocentral. Capsule gland and albumin gland medial to shell muscle and slightly in front. Narrow, grooved female genital papilla, free of mantle, blunt end. Penis: flattened, ventral sperm groove, evenly tapered but with short distal papilla.

Reproduction: Protandrous (Veliz et al. 2003). Juvenile shell length: 1.2–8.1 mm; Male shell length: 7.0–20.0 mm; Transitional shell length 14.1–26.3 mm; Female shell length: 22.8–34.0 mm from La Herradura Bay, Chile. Females usually paired with single male, occasionally with multiple juveniles. No multiple stacks. Brooded egg capsules, globose, stalk tapered.

Development: All eggs cleave; nutritive embryos consumed by veliger stage embryos via slow depletion of yolk inside embryoid. Approximately 7% of eggs per capsule develop to hatching. Hatching size: 900–1100 µm. Egg size: 190–230 µm

Distribution and habitat

La Herradura Bay (29º 59’ S; 71º21’W) and Totoralillo beach (30º 05’ S; 71º 22’W), Chile, in rocky intertidal and shallow subtidal (to at least 2 m), attached to the upper sides of rocks.

Etymology

occulta—adjective referring to cryptic morphology, previously unrecognized status of this species.

Available genetic data

COI and 16S sequences from a voucher at the Field Museum (FMNH282280) from Totoralillo beach (Genbank AF550491, and AF550461 respectively; www.ncbi.nlm.nih.gov; Collin 2003b). Additional COI sequence from Totoralillo (DQ811129) and La Herradura Bay (DQ811129 from voucher ANSP 413606) (Collin et al. 2007). Allozymes were described in Véliz et al. (2003).

Remarks

Shell color is variable within *Crepipatella* (Fig. 4) but large pale shells belong to *C. peruviana* and small pale shells often do as well. The interior of the shells of *C. dilatata* usually reflect the external color and can range from creamy white to purplish brown. The interior of virtually all healthy shells of *C. occulta* n. sp. are shiny chestnut brown. We did not observe pale shell interiors from the two populations described here unless they were infested with shell borers. However, animals reared from hatchlings in incubators in the laboratory were completely white, a shell colour that we have never observed in field samples from the two known locations. The possibility of environmentally-induced variation in shell color should be further explored to verify its utility as a taxonomic character in *Crepipatella*. Caution should be used when assigning *Crepipatella* to species based exclusively on shell characters, as is also the case with *Bostrycapulus*, and the flat white species of *Crepidula*, among other calyptraeids. This is especially true since we have been unable to detect any other consistent anatomical or morphological differences between these three species. Observation of the embryonic stages remains the most effective way to distinguish these species from live material.

The geographic distribution of the three Chilean *Crepipatella* species needs to be examined in more detail. The occurrence of *C. dilatata* and *C. peruviana* is well documented between Chiloé and Coquimbo, but the northern and southern range end points of these species are unknown. It is also likely that the known range of *C. occulta* will expand once its existence is more widely known. The continued application of the name *C. dilatata* to *Crepipatella* shells for which no developmental or genetic data are available without the discussion of the possible identity with *C. peruviana* or *C. occulta* will further obfuscate the ranges of these species (e.g., Paredes and Cardoso 2007).

There are a number of available names for species of *Crepipatella* in Chile (Table 1). However none of them provide a good fit with *C. occulta*. Because shell morphology is not unambiguously diagnostic, these previous names should be associated with any of the three known species with caution unless other information is available. None of the species descriptions mention a shiny dark chestnut or chocolate shell interior, which is the most common morphology observed in the new species. In most cases the types are pale or have light chestnut or reddish markings.

The localities associated with the names and types (see Table 1; Fig 5) make it unlikely that most of the named species are synonymous with *C. occulta*. These localities represent central Chile in the vicinity of Concepción or Valparaiso, as well as Argentina and Peru. None are from the known range of the new species (between Totoralillo and La Herradura Bay near Coquimbo, Chile). All of these other

TABLE 1. Species names for Recent South American *Crepipatella*.

	Type Locality	**Comments**	**Current status**
Crepidula dilatata Lamarck, 1822	Barbary?	Lectotype designated by Aguirre 1993. MHNG 1090/70/1. Figured in Mermod 1950.	Valid
Crepidula peruviana Lamarck, 1822	Peru	Senior synonym of *C. fecunda* and also *C. patula*, Figured in Mermod 1950. protoconch eroded. Shell pale, large, robust.	Valid
Crepidula subspirata Blainville, 1825	None	Type lost, *C. subspirata* Blainville, 1824 is *nonem nudum* as no figure or type material cited. The same text includes a reference to a figure in Blainville (1825) which appears to be a *Crepipatella.* The illustrated shell appears to be thin, convex and is clearly curved to the right. The shell is completely white inside and out and shows strong foliations, both characteristic of *Crepidula lessoni* (Broderip, 1834) and not a combination typical of *Crepipatella*, although *C. lessoni* is not typically convex.	*Nomen dubium*
Crepidula patula Deshayes, 1830	Tahiti	Locality (Tahiti) almost certainly in error. Synonymized with *C. dilatata* in Hoagland (1977), but Hoagland (1983) concluded this species is the senior synonym of *C. fecunda* (Hoagland 1983). Shell apex and protoconch eroded. Shell large, robust and pale interior.	Junior synonym of *C. peruviana*
Calyptraea (Crepipatella) adolphei Lesson, 1830	'Perou' or Talcahuano, Conception, Chile	Synonymized with *C. dilatata* in Hoagland (1977), but described as 'conspecific with' *C. fecunda* (Hoagland 1983: 1, 6). The types are very large and Lesson (1830) describes the species as having a white and shiny shell interior. This is all consistent with *C. peruviana*. Lesson claims that it is clearly distinct from *C. peruviana* but does not specify how.	Junior synonym of *C. peruviana*
Calyptraea (Crepipatella) chiliensis Lesson, 1830	Concepcion, Chile	Type lost; not figured.	*Nomen nudum*
Calyptraea (Crepipatella) depressa Lesson, 1830	Peru and/or Talcahuano, Conception	Synonymized with *C. dilatata* in Hoagland (1977; 1983). Shell apex eroded. Types thin and brown but some larger and robust. The location of Peru is not consistent with the documented distribution of *C. dilatata* or *C. occulta*, and both *C. peruviana* and *C. dilatata* are known to occur in Conception so these are most probably a mixed lot of *C. peruviana* and *C. dilatata*.	*Nomen dubium*
Crepidula (Crepipatella) nautiloides Lesson, 1832	Pacific ocean? (sic)	Types lost; illustration with type description looks very similar to the figure of *C. subspirata* in Blainville 1825. The foliations suggest that the animal was growing on a small substrate that limited its growth. Inside of shell dark purple. Illustration shows pale medial stripe, both typical of *C. dilatata*.	Junior synonym of *C. dilatata*
Calyptraea strigata Broderip, 1834	Valparaiso, Chile	NHMUK Reg.no. 1977100; 2 syntypes; pale with light chestnut brown stripes, shell interior white, thin, protoconch detail indistinct.	Status unclear, possibly a valid species, certainly not a synonym of *C. occult*a.
Calyptraea pallida Broderip, 1834	Falkland Islands	Very pale shell	Status unclear
Calyptraea foliacea Broderip, 1834	Arica, Peru [now Chile]	NHMUK Reg. no. 196633-34; 6 syntypes; Shells pale outside and in with some light reddish markings. Rugose or laminated shell; protoconch somewhat more coiled than *C. occulta* n. sp.	Probably valid on the basis of unusual shell sculpture.
Crepidula patagonica d'Orbigny, 1841	Patagonia south of Rio Negro	Types in British Museum d'Orbigny collection, reg no. NHMUK 1854.12.4.572. Shell brownish or purplish with medial white stripe. D'Orbigny 1847 states that it can be distinguished from *C. dilatata* by the red spots on the animal and that the species is rare. We have not encountered animals with this pigmentation but live animals have not been widely sampled in Patagonia.	Probably valid, on the basis of distinct body pigmentation
Crepidula fissurata Sowerby, 1883	None	Most likely *C. lingulata* from the Pacific Northwest.	Synonym of *C. lingulata* Gould 1846
Crepidula fecunda Gallardo, 1979	Bahía Chinquihue	Pale and large. Species described on the basis of planktotrophic development.	Junior synonym of *C. peruviana*

type localities represent locations where either *C. peruviana* (in Peru and northern Chile) or both *C. peruviana* and *C. dilatata* (most of Chile) are known to occur. In most of central and southern Chile, *Crepipatella* are extremely abundant and well-studied with respect to genetics and development. Since morphological evidence does not suggest otherwise it is prudent to assume that these types belong to one of the species of *Crepipatella* known to exist in the locations from which they were collected and not to a newly discovered species that occurs 400–1400 km away.

The geographically closest two species that have not already been synonymized with *C. dilatata* or *C. peruviana* (Table 1) are *C. strigata* (Broderip, 1834) reported from Valparaiso (and possibly Peru), approximately 400 km from Coquimbo and *C. foliacea* (Broderip, 1834) from Arica, 1300 km from Coquimbo. *Crepipatella occulta* is unlikely to be synonymous with either of these species as they are both clearly very pale (Fig 6). *Crepipatella foliacea* shows a unique shell sculpture, which appears to be endogenous, and not purely the result of having grown on a ridged substrate, as occasionally occurs with many calyptraeids.

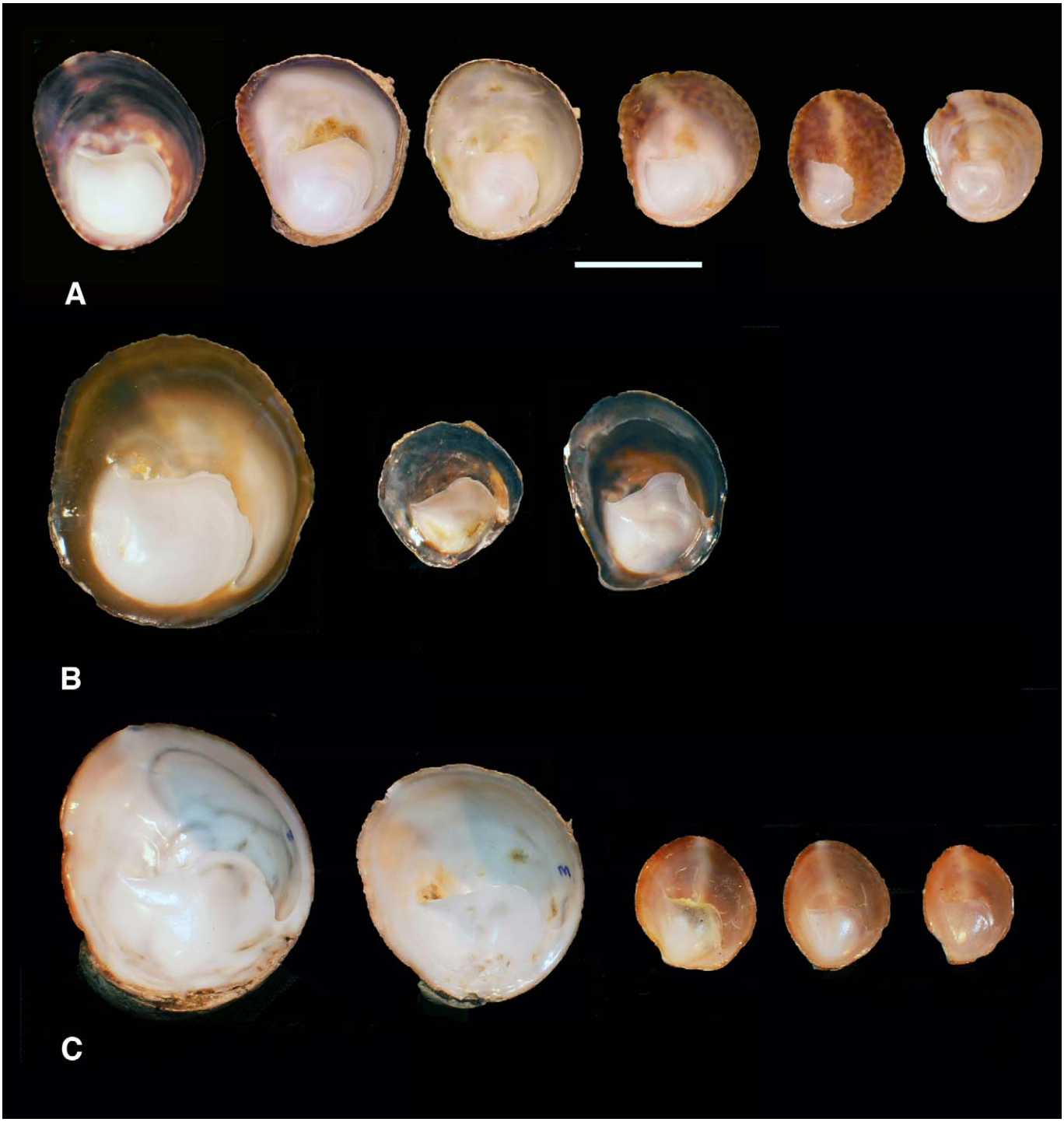

FIGURE 4: Examples of shells of South American species of *Crepipatella*. **A,** *Crepipatella fecunda* from Peru; **B**, *Crepipatella dilatata* from Argentina; **C,** *Crepipatella occulta* n. sp. from Totoralillo beach. Scale = 2 cm.

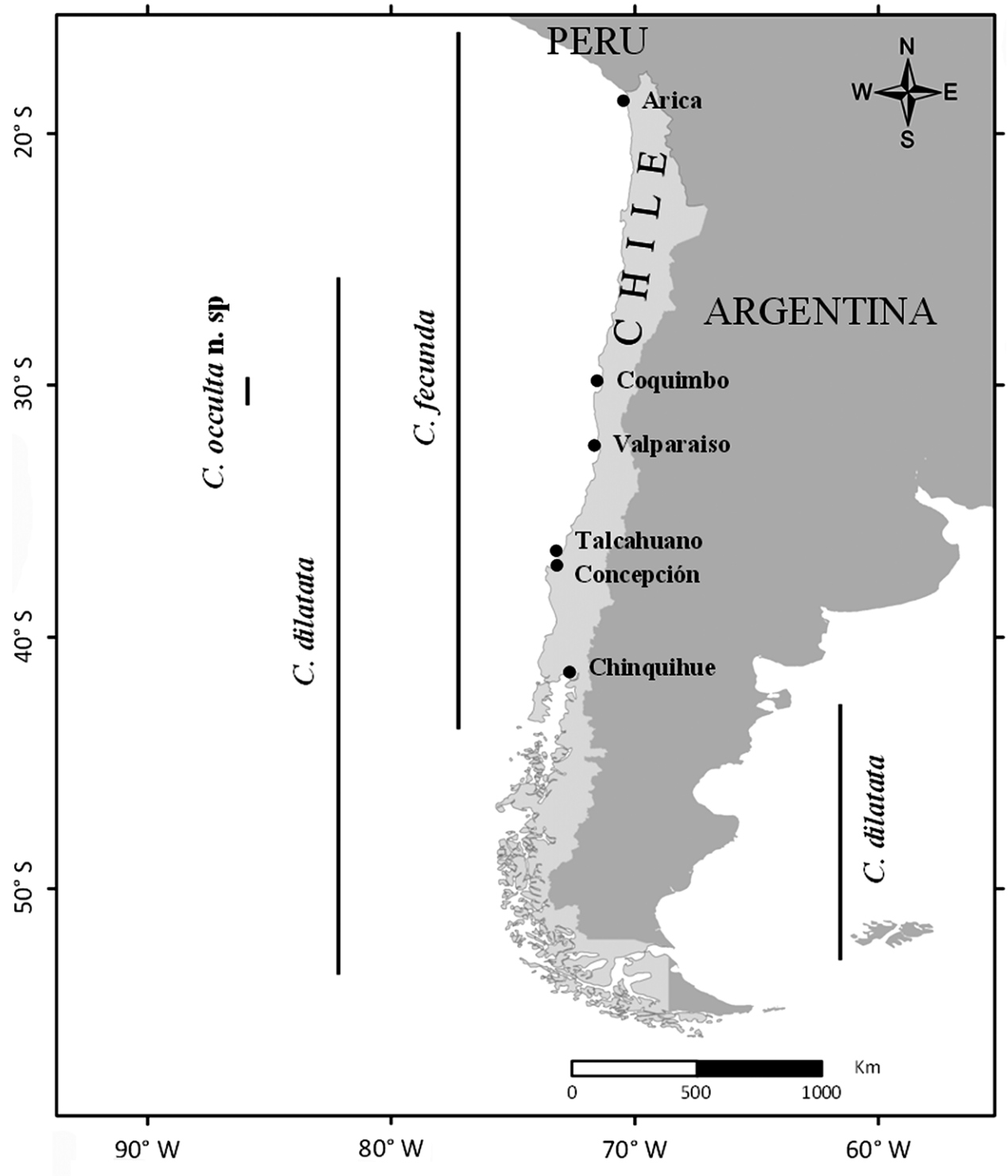

FIGURE 5: Map of Chile showing the range of *Crepipatella dilatata*, *Crepipatella fecunda* and *Crepipatella occulta* n. sp. Possible type localities for other *Crepipatella* species listed in Table 1 are indicated on the map.

Discussion

A diverse array of evidence is available to support the distinct status of the three sympatic species that co-occur in central Chile, despite the ambiguity of the morphology. The three species show different allozyme frequencies, and diagnostic alleles where they co-occur in Bahia Herradura. *Crepipatella occulta* has unique alleles at 14 allozyme loci when compared to *C. peruviana* and *C. dilatata* from the

same region (Véliz et al. 2003). COI mtDNA sequences from *C. occulta* show more than 15% divergence from those of *C. peruviana* and *C. dilatata* (Collin et al. 2007) and that *C. capensis* from South Africa is more closely related to *C. peruviana* and *C. dilatata* than is *C. occulta*. Finally *C. occulta* differ from the other two in possessing direct development in which nurse embryos cleave and begin development before being consumed by their siblings. So, although *Crepipatella* fall short in exhibiting the diagnostic features in the shell characters traditionally used for taxonomy (as noted by Broderip 1835), there is a wealth of information supporting their status as a distinct species.

Small radiations of calyptraeids composed of species that do not appear to be of particularly recent origin based on COI divergences, but nevertheless show few if any diagnostic morphological differences, are common among the calyptreaids (Collin 2001; 2005b). They can often, however, be distinguished on the basis of differences in development, which suggests that divergence in development could play a role in species divergence, as suggested by Krug (2011). The three sympatric Chilean *Crepipatella* with differing development offer an ideal system with which to test these ideas.

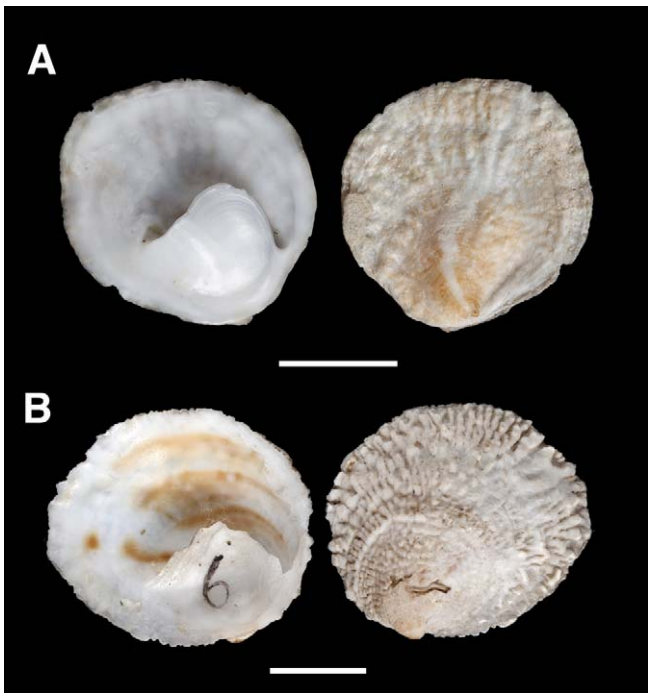

FIGURE 6: A, one of the two syntypes of *Crepipatella strigata* (Broderip) Reg. No. 1977100. Scale = 1 cm; **B**, The figured syntype of *Crepipatella foliacea* (Broderip) Reg. No. 1966633-34. Images courtesy of H. Taylor, NHMUK Photographic Unit.

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