

FIRST RECORD OF A FOSSIL VERRUCID BARNACLE IN CALIFORNIA—  
*VERRUCA DIGITALI* SP. NOV. (CIRRIPEDIA: THORACICA) FROM THE  
LATE MIOCENE

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A B S T R A C T

A new cirripede (Verrucomorpha: Verrucidae) *Verruca digitali* Buckeridge sp. nov. is described from the late Miocene in Orange County, California. The discovery of dozens of specimens in siliceous shale of the upper Monterey Formation is remarkable because both living and fossil Verrucidae are rare in the Northeast Pacific and adjacent terranes and the stratigraphic sequence is characteristically bathyal in origin. We propose that these specimens of *V. digitali* were epiphytic, being attached to seaweed that was either planktic or uprooted and displaced downslope. This species is similar to *Verruca alaskana* Pilsbry, a Pliocene species from Alaska, and *Verruca laevigata* Sowerby, an extant species inhabiting shallow waters off the west coast of South America. *Verruca digitali* is a likely Miocene candidate for a “*Verruca laevigata* bioseries.”

GEOLOGICAL SETTING

Verrucid barnacles are rarely found as fossils, and on those occasions when they are recovered, they are generally preserved as isolated, disarticulated wall plates. This discovery is significant because it is only the second record of a fossil verrucid from the Pacific Northwest, and the remains are both relatively abundant and well preserved.

The discovery was made during monitoring of roadway excavations extending Antonio Parkway along the southwestern foothills of the Santa Ana Mountains, north of San Juan Capistrano, in Orange County, southern California (Fig. 1). The verrucids were recovered from localities MBAP–7061 and MBAP–7071, both within the Monterey Formation in SW  $\frac{1}{4}$  Sec. 28, T7S, R7W, Cañada Gobernadora Quadrangle (USGS 7.5 minute series topographic map, 1968, photorevised 1988).

The Monterey Formation is the most extensive stratigraphic unit mapped in the project area. As a source and reservoir rock for hydrocarbons elsewhere in California, the microfossils of the Monterey Formation have been studied intensively by palaeontologists in industry, academia, and government. Calcareous foraminiferans, siliceous diatoms, and radiolarians dominate the diverse and

abundant microbiota; in lesser abundance are silicoflagellates, ebridians, palynomorphs, and ostracodes. The macrobiota of the Monterey Formation includes filamentous algae, leaves and woody plant debris, bryozoans, gastropods, bivalves, crustaceans, polychaete worms, ichnofossils, fishes, aquatic birds, pinnipeds, sirenians, and cetaceans. The lower-middle bathyal floor of the Los Angeles depositional basin during “Monterey time” was a receptacle for fine-grained pelagic, hemipelagic, and distal turbidite fan sediments. Finely laminated muddy rhythmites common in the Monterey Formation represent seasonal variations in sedimentation, and their preservation indicates the exclusion of bioturbating benthic organisms due to low-oxygen waters (Bramlette, 1946; see Hülsemann and Emery, 1961). As a result, the larger palaeobiota of the Monterey Formation often lacks *in situ* benthic organisms. Instead, it is characterized by remnants of pelagic nekton (e.g., sharks, boney fish, seals, and whales) deposited post-mortem, and benthic organisms displaced downslope by turbidity currents.

Invertebrates other than molluscs are rarely encountered in the Monterey Formation. Hence, the association of barnacles and bryozoans in this formation is a most unusual find. Furthermore, the delicate nature of the cirripede remains described herein, and their spa-

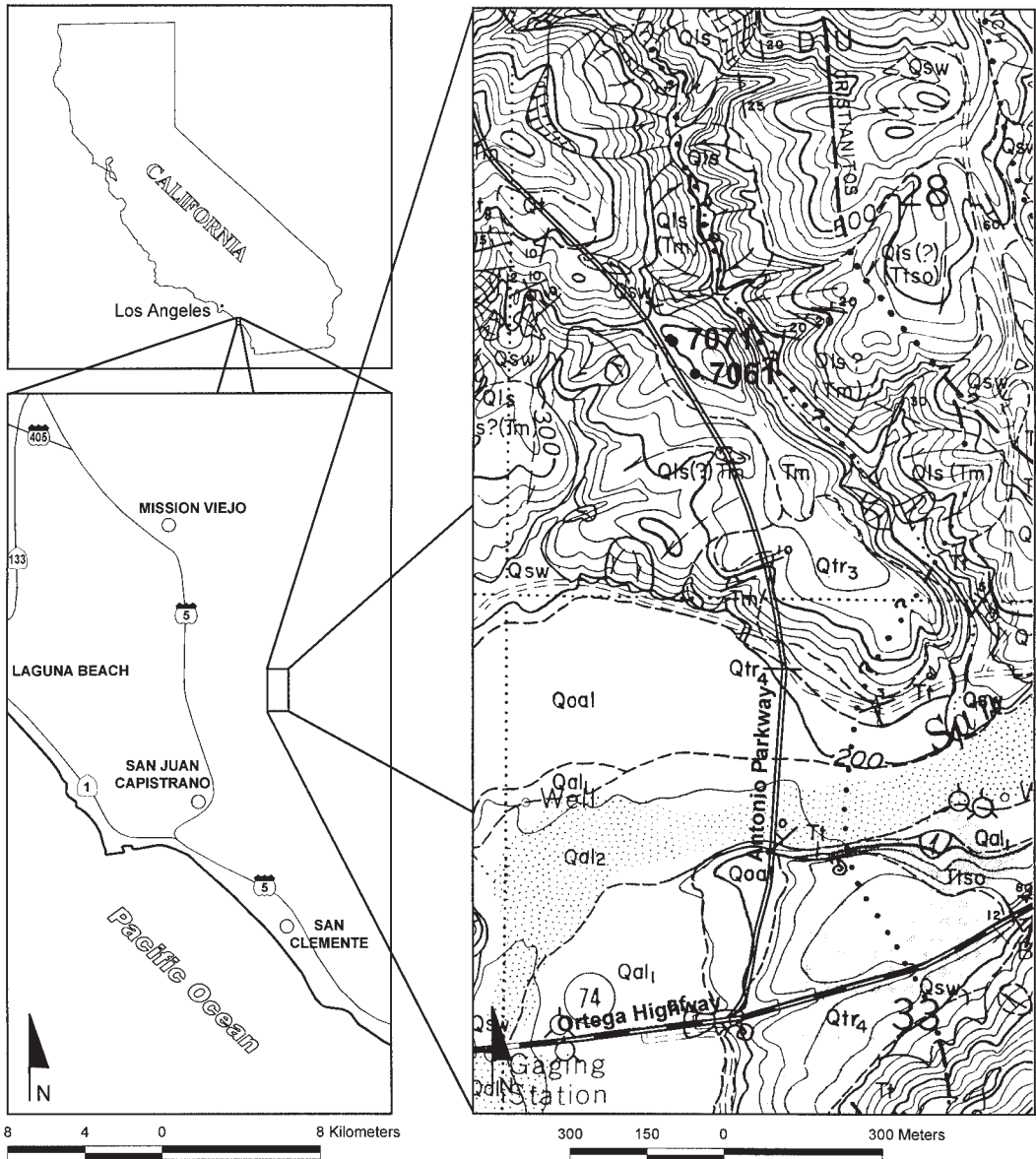


Fig. 1. Locality diagram showing collection sites 7061 and 7071, on the west side of the Antonio Parkway, Orange County, California.

tial disposition, suggest that they neither represent a biocoenosis, nor were derived from shallower rocky benthic environments (as are related species of *Verruca*).

Local biostratigraphic and lithostratigraphic correlations indicate this part of the formation is within the interval of 8.2–11.3 my, approximating the early late Miocene. Thus, the verrucid-bearing rocks correlate the Clarendonian mammal age, and California's "Margaritan" molluscan and Mohnian foram stages.

#### SYSTEMATICS

Order Thoracica Darwin, 1854  
 Suborder Verrucomorpha Pilsbry, 1916  
 Family Verrucidae Darwin, 1854  
 (amend. Newman and Hessler, 1989)

*Diagnosis.*—Verrucomorpha with four primary wall plates (carina, rostrum, fixed scutum, fixed tergum) in contact with the substratum; latera absent.

Table 1. Stratigraphic and geographic distribution of genus *Verruca*.

<i>Verruca</i> species	Stratigraphic range	Location
† <i>V. alaskana</i> Pilsbry, 1943	Pliocene	Alaska
<i>V. cookei</i> Pilsbry, 1927	Recent	Hawaii, Tuamotu, Reunion
† <i>V. digitali</i> sp. nov.	Late Miocene	California
<i>V. jago</i> Buckeridge, 1997	Recent	Comoro Islands
<i>V. laevigata</i> Sowerby, 1827	Recent	Peru, Chile
† <i>V. prisca</i> Bosquet, 1854	Late Cretaceous	Western Europe
† <i>V. pusilla</i> Bosquet, 1857	Late Cretaceous	Western Europe
† <i>V. nuciformis</i> Buckeridge, 1983	Early Eocene-Early Miocene	New Zealand
† <i>V. rocana</i> Steinmann, 1921	Late Cretaceous	Argentina
<i>V. spengleri</i> Darwin, 1854	Recent	Madeira
<i>V. stroemia</i> (Müller, 1776)	Pliocene-Recent	North Atlantic, Northern Europe
† <i>V. tasmanica chatheca</i> Buckeridge, 1983	Late Palaeocene-Early Eocene	Chatham Islands
† <i>V. tasmanica tasmanica</i> Buckeridge, 1983	Late Cretaceous-Early Oligocene	Australia, New Zealand

*Distribution*.—Upper Cretaceous to Recent.

*Remarks*.—The Verrucidae was revised by Young (1998), who proposed splitting *Verruca sensu lato* into three genera (*Verruca sensu stricto*, *Newmaniverruca*, and *Costatoverruca*). In light of this, there are now eight verrucid genera recognised, and a key to these is available in Young (1998). Only two genera are currently known to have a fossil record: *Metaverruca* Pilsbry, 1916, and *Verruca* Schumacher, 1817; Buckeridge (1997) listed their respective species. By excluding fossil taxa from his revision, Young (1998) effectively avoided the placement of (fossil) species that are transitional—this is important, as he acknowledges that two transformation series exist within the verrucids, one based upon shell shape, the other on the morphology of rostral and carinal ridges. If these transformations represent a time-transgressive bioseries, then we should anticipate that some fossil taxa are transitional between Young's new genera. Fortunately, the new species described here clearly falls within *Verruca* s.s.

Pilsbry (1916) carried out one of the first comprehensive modern works on the Verrucidae, in which he discussed the global distribution of extant verrucids. At that time, there were no records of either living verrucids in the Northeast Pacific or fossil verrucids in western North America. Subsequently, extensive collecting of the regional marine biota revealed its remarkably low diversity of verrucids. Pilsbry (1943) described disarticulated verrucid plates from shallow-water deposits near Nome, Alaska, as *Verruca alaskana*. More recently, Zevina (1987) proposed three new verrucid species (*Altiverruca angustiterga*, *A. sculpturata*, and *A. sublima*)

from the North Pacific. These are known only from depths between 3,000–4,700 m, and they are the only living verrucids collected from the region.

Genus *Verruca* Schumacher, 1817

*Diagnosis*.—Small verrucids with shell form depressed, umbones of rostrum and carina marginal, operculum parallel to base, myophore well developed, parallel to base.

*Distribution*.—Upper Cretaceous to Recent.

*Remarks*.—With this new record, there will be 13 taxa within the genus *Verruca*, of which nine, including this species, possess a fossil record. As Young (1998) did not consider fossil taxa in his revision, the eight *Verruca* known to be extinct are prefixed by a “†” in Table 1.

*Verruca digitali* Buckeridge, sp. nov.  
Figs. 2a, b, 3a, b

*Diagnosis*.—*Verruca* having quadrangular movable tergum with prominent apico-basal rib, which articulates basally with narrow, movable scutum and two secondary articulating ribs; all plates penetrated by fine circular punctae arranged along exterior growth lines; external ribbing weak.

*Material*.—MBAP-7061 (specimen numbers 2, 3A, 3B) numerous casts of complete shells embedded in a light-grey siliceous shale of the Monterey Formation. Associated fauna includes Plantae (woody plant fragment), Bryozoa (cheilostomes), Bivalvia (?*Diplothyra* sp.), Gastropoda (*Serpulorbis* sp., *Vitrinella* sp.), Pisces (Clupeidae, ?*Ganolytes cameo* Jordan, *Lompoquia* sp., *Xyne grex* Jordan and Gilbert). Field Station 121, (33°31'54"N, 117°37'11"W); collection and identification of non-cirripede taxa by D. M. Pelletier and K. L. Finger on 24 September 1997; MBAP-7071, two more-or-less complete shells (calcified but partially decorticated), embedded in

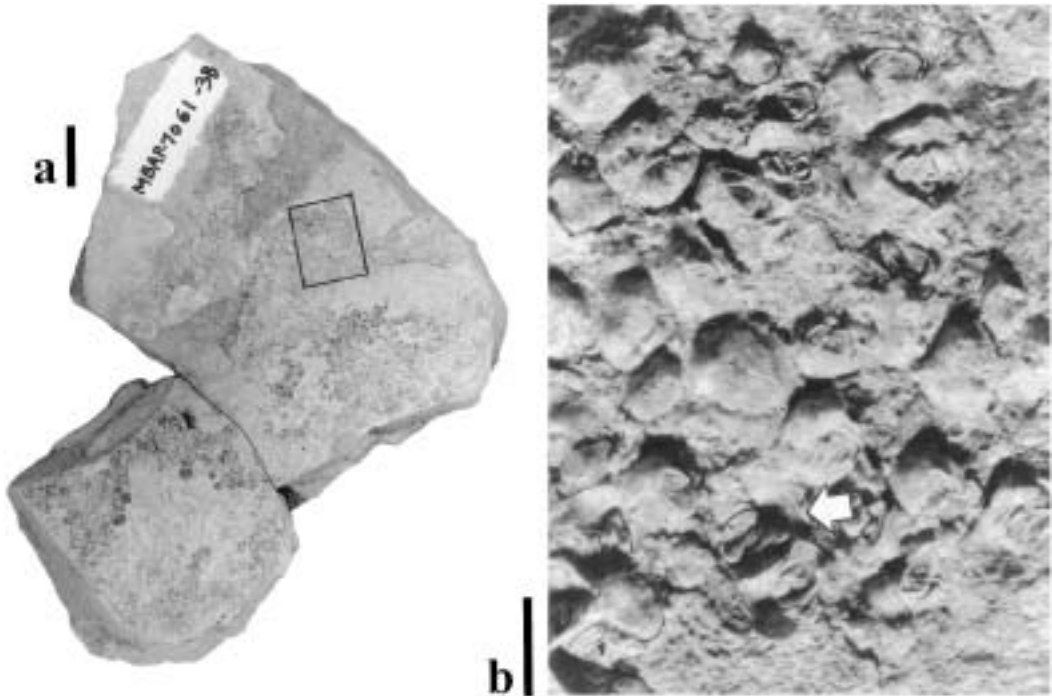


Fig. 2. a, b: *Verruca digitali* sp. nov. a, Specimen MBAP-7061-3B, containing the holotype, C-10129 (the 2 mm diameter depression at arrow in b), the remainder comprising the paratype collection C-10130; b, Detail of rectangular area in Fig. a, showing both inverted and "correct orientation" casts. Note: Figure b is rotated clockwise by about 15 degrees with respect to its noted position on a. Bar scale in a is 10 mm, in b is 2 mm.

a light-grey laminated shale of the Monterey Formation, Field Station 124, (33°31'58"N, 117°37'15"W); collected by K. L. Finger and F. D. Bigony on 8 August 1997.

*Age*.—Late Miocene (Margaritan Molluscan Stage).

*Type Material*.—Holotype: C-10129, an external cast of a complete specimen (interior perspective, from base), from MBAP-7061-3B. Basal diameter 1.9 mm. Paratypes: C-10130, the remaining 250+ specimens attached to the same rock as the holotype. AUT 113, a rock fragment with 190+ specimens of varying degree of preservation, from MBAP-7061-2. Types with the prefix "C" are held in the Benthic Invertebrate Collection, Scripps Institution of Oceanography, California; that with the prefix "AUT" in the type collection of the Auckland University of Technology, Auckland, New Zealand.

*Description*.—A small *Verruca* with weak external ribbing developed basally on fixed plates, all plates, including opercula, with fine, circular perforations arranged along well-formed, transverse growth lines; rostro-

carinal side of shell slightly elevated, such that "D-shaped" operculum is subparallel to base; rostrum relatively broad, semiconic, interlocking with carina by up to five ribs; carina interlocking with fixed tergum by one primary and one secondary rib, fixed tergal margin almost vertical; fixed tergum interlocking with fixed scutum by one weak rib; fixed scutum narrow, with moderately developed alar extension; movable scutum triangular, relatively wide, with one primary, and two secondary apico-basal ribs; movable tergum quadrangular, with strong primary apico-basal rib and two weaker apico-basal ribs abutting scutal margin; lower rib broadly rounded, slightly vaulted, upper rib flat. Interior of larger plates with short, fine longitudinal ribs developed near basal margin.

*Remarks*.—All specimens studied, with the exception of the two from MBAP-7071 are preserved as casts. This has permitted a better understanding of shell structure than is often the case with fossils (e.g., *Verruca tasmanica*), for fine perforations within the

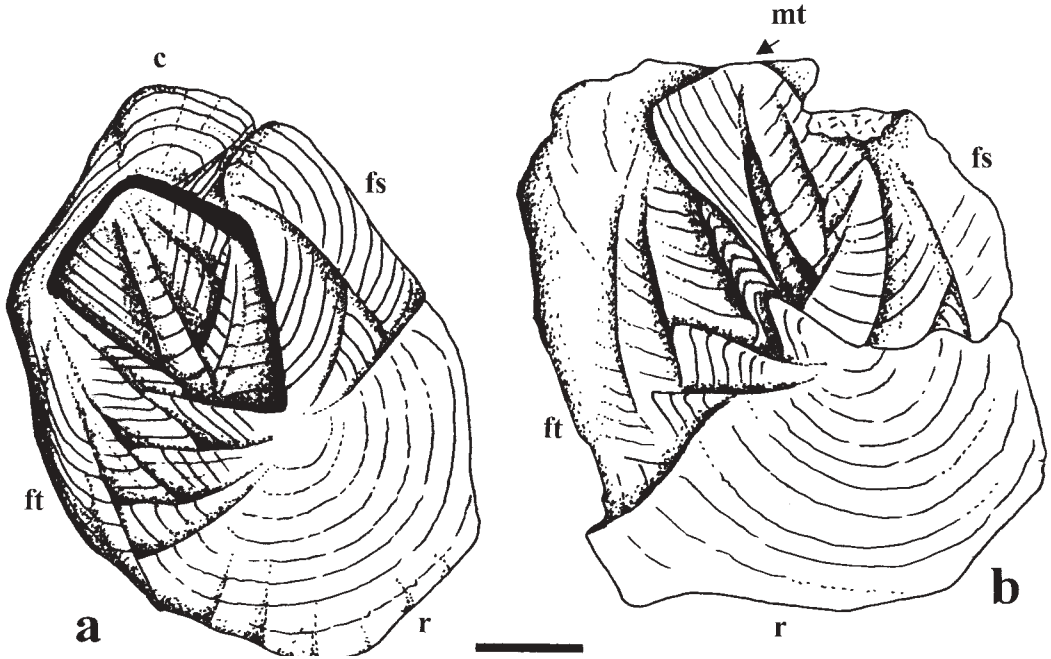


Fig. 3. *Verruca digitali* sp. nov. a, Reconstructed shell of single individual from rock specimen MBAP-7061-3A. Drawing based on a latex cast of the original. The movable tergum abuts the fixed tergum and carina, the movable scutum abuts the fixed scutum and rostrum. The operculum (lying in the modified "d-shaped" area in left centre) has dropped slightly, likely during early diagenesis. b, C-10129 (Holotype) from MBAP-7061-3B. Internal view of the exterior surface; i.e., the drawing shows the cast of the inner surface of the operculum and the shell wall as it appears after dissolution of the shell's calcite during diagenesis. Most of the carina is absent, as such the movable tergum extends to the edge of the specimen (arrow). The shell is arranged similarly to that in a, although as a cast it is reversed, with the operculum being elevated. (c = carina, fs = fixed scutum, ft = fixed tergum, mt = movable tergum, r = rostrum). Bar scale 2 mm.

plates are often preserved, particularly well in internal views of casts of the external surface. As casts, these "perforations" now appear as delicate needles, many of which possess a bulbous terminus; from this it may be inferred that the original perforations had a spherical basal cavity of approximately twice the diameter of the tube leading to the surface.

On the basis of the gaps between inner and outer cast surfaces, it appears that the shell was approximately 0.1–0.2 mm thick.

Comparisons with other species.—*Verruca digitali* sp. nov. has similarities with *V. laevigata*, with which it and *V. alaskana* may well form a bioseries. The lack of strong regular external ribbing distinguishes it from *V. stroemia*, *V. pusilla*, and *V. rocana*. A quadrangular (rather than triangular) movable tergum distinguishes *V. digitali* sp. nov. from *V. cookei*. The movable scutum in *V. digitali* sp. nov. is comparatively much narrower than in

*V. laevigata*, *V. prisca*, and *V. spengleri*. The overall shell morphology and smaller diameter shell perforations distinguishes it from the very flattened *V. jago*. It may be distinguished from *V. alaskana* by the rostrum, which in *V. alaskana* is comparatively narrow, has a produced, somewhat curved apex, and internally a deep apical cavity. The finely perforate shell wall is a characteristic of this species, although *V. jago*, *V. laevigata*, and *V. stroemia* are also perforate. Perforations are, however, unknown in *V. tasmanica* and *V. nuciformis*; Pilsbry (1943) makes no reference to them in *V. alaskana*, nor does Withers (1935) in his descriptions of *V. prisca*, *V. pusilla*, and *V. rocana*.

*Etymology*.—Named for Kenneth L. Finger, who collected the specimens and brought them to the attention of JSB. The name also reinforces the characteristic interdigitating nature of the wall plates of this species.

## PALAEOECOLOGY

The material available is unusual for fossil verrucids in that it includes a very high proportion of complete shells. The shells are very numerous and in most cases are arranged in sheets. At their most dense packing, individual specimens have adopted the hexagonal cross-section also found with close-packed intertidal cirripedes such as *Chamaesiphon columna* Moore. What is more unusual about the remains is their spatial disposition; groups of approximately several dozen specimens are inverted, but alongside other groups that are in "correct" orientation (Fig. 2a). Further, there is no evidence of an attachment substrate, and this is perhaps unusual, as most *Verruca* species typically inhabit relatively shallow-water conditions adhering to hard surfaces.

If one considers the delicate nature of the complete verrucid shell, and the fact that very few specimens of *V. digitalis* sp. nov. appear to have been damaged before preservation, it is reasonable to conclude that burial was rapid. This is not inconsistent with a depositional environment fed by turbidity currents (Hülsemann and Emery, 1961). The absence of any identifiable attachment substrate is best explained by proposing that this species settled on material that was unlikely to be preserved in the fossil record. The most likely candidate for its substrate is benthic seaweed, with settlement probably occurring on the "firmer" sections of the algal stipe near the holdfast. Encrusting organisms, including balanomorph cirripedes, can be seen in this position on living species such as the widespread Southern Hemisphere brown seaweed *Durvillaea*.

Study of the alignment of encrusting individuals may be carried out with the holotype-paratype group (Fig. 2b). Because the barnacles are of similar size, it is highly probable that they originated in the same settlement phase. The fragility and disposition of many of the specimens confirms that they are preserved in much the same relationship with each other as they were when alive. If a vertical axis through the rostral-carinal suture is considered for each specimen in discrete groups (e.g., on MBAP 7061-3B), there is no consistent orientation or alignment of the shells (and therefore of feeding structures). Shell alignment is typical in barnacles that

settle where there is a strong current from a single vector. Barnacles that grow in conditions of high turbulence (e.g., around the base of algae in turbulent waters of the upper subtidal zone) do not show this alignment, thus supporting the hypothesis that these specimens were attached low on an algal stipe.

We believe that the associated fauna and the nature of these *Verruca digitalis* sp. nov. remains confirm a relatively shallow-water habitat, possibly upper subtidal. This analysis is not inconsistent with the associated fauna of nekton, woody plant fragments, bryozoans, and molluscs. The latter two groups include cheilostome bryozoans and *Serpulorbis* sp., respectively, taxa commonly found encrusting the basal stipe of large seaweeds.

## BIOGEOGRAPHY

Of all the species of *Verruca*, *V. digitalis* sp. nov. is most like the Recent *V. laevigata*, which is known as intertidal on the Pacific coast from Tierra del Fuego to Peru.

Insights into the amphitropical distribution patterns of invertebrates are provided by Newman and Foster (1987) and Newman (1991). The Cainozoic distribution of *Verruca* in the Americas is certainly amphitropical and is characterised by moderately high endemism. A bioseries is proposed here, represented in the north by the late Miocene *Verruca digitalis*. Later in the Cainozoic, a southern group (*V. laevigata*) became isolated, with *V. alaskana* evolving from *Verruca digitalis* during the Pliocene. General morphology of the three species would support the brief, but unsuccessful, excursion to the north, as of the three species, *V. alaskana* the most distinct. This pattern supports the hypothesis that southern endemism is due to the extinction of Northern Hemisphere counterparts rather than having evolved there (Eskov and Golovatch, 1986; Newman and Foster, 1987).

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