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Radular Anatomy and Systematics of the West American Conidae (Mollusca, Gastropoda)

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Representatives of the gastropod genus *Conus* that live in west American waters are a readily recognizable, uniform group. They are few in number and have been the subject of two recent and extensive systematic studies (Hanna and Strong, 1949; Hanna, 1963).

The systematics of this well-known group is not established. There has been continuing disagreement concerning the number of biologically recognizable species that live in the east Pacific (see Hanna, 1963; Wolfson, 1962). The disagreement is due partly to a lack of knowledge of the variability within the individual species and partly to the fact that the presently defined species are largely based on shell characters (Van Mol, Tursch, and Kempf, 1967).

The individual radula teeth of the Conidae are structurally the most complex of all mollusk radulae. They are asymmetrical and hence difficult to represent in two-dimensional drawings. The morphology of the individual teeth varies considerably between species (see Piele, 1939) and in some cases can be correlated with their diet (Endean and Rudkin, 1965; Nybakken, 1970).

The present investigation grew out of my ecological studies on the west American Conidae and was expanded when I discovered that there

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was some confusion in the literature concerning the identity of certain species. My ecological studies involve the examination of radulae in order to correlate radular structure with food preference. I also believe that a study of the radulae of all west American species of *Conus* might help effect a solution of the systematic problems.

The shells of the west American Conidae are well-known, and excellent black-and-white illustrations of all species are in Keen (1958) and in color in Hanna (1963). Hence, I do not think it necessary to figure the shells again in the present paper. For shell morphology and pattern see the above cited works.

I have chosen to organize the present paper so that the species with similar radula types are discussed together. The sequence of species found herein therefore will differ from that found in other systematic papers on this genus.

I want to thank the following people for lending me specimens: Mr. Allyn Smith of the California Academy of Sciences, Dr. James McLean of the Los Angeles County Museum, and Dr. Gilbert Voss of the University of Miami Marine Laboratory. Part of this work was financed by a grant from the local research committee of California State College at Hayward, for which I am grateful. I am also indebted to Stanford University and especially to Dr. Malvern Gilmartin for permitting me to participate in Cruise 16 of the "Te Vega" to the Gulf of California. During that cruise, a considerable number of *Conus* were collected and used in the present study. I owe considerable thanks to Dr. Alan Kohn of the University of Washington for his invaluable aid and advice on the study of *Conus* radula teeth. Finally, I should like to acknowledge National Science Foundation grant GB-5942X, which furnished the major support for this work during 1968–1969 while I was at the University of Washington.

LITERATURE REVIEW

The complex teeth of *Conus* have been known for a long time, but one of the first authors to describe and illustrate the radula teeth of 33 species was Bergh (1895). These illustrations are probably the finest ever produced in terms of detail. All of the species he illustrated, however, were Indo-Pacific or Atlantic in distribution.

Thiele (1931) illustrated the teeth of three species of Indo-Pacific *Conus* (excluding *Conorbis*), and Cotton (1945) gave a detailed description of the radula of *C. anemone,* and speculated on the purpose of the barbs. He also included photographs of the radula teeth of three other *Conus* species from Australia.

Piele (1939) reviewed the early literature on *Conus* radulae, illustrated 30 species, and made the first attempt to sort morphological variations into similar groups. He distinguished three well-defined groups and a fourth larger group, which he further subdivided into long-shafted and short-shafted subgroups. The fourth, ill-defined group comprised what we now know to be the vermivorous *Conus* species. Among the species drawn by Piele were two west American species, *C. purpurascens* and *C. californicus.* Piele suggested that the morphology of the teeth should be correlated with food habits and that the teeth would be as good a guide to classification as were the shell and operculum. His views on classification based on teeth have, however, never been utilized.

Other Indo-Pacific *Conus* radulae have been illustrated by Barnard (1958), who figured eight species from South Africa, and Endean and Rudkin (1965), who figured the teeth of three species. They also figured *C. tiaratus* from west America.

The radula teeth of seven Atlantic *Conus* species have been figured by Warmke (1960), who found that the teeth she studied fell into four distinct groups, and by Von Mol, Tursch, and Kempf (1967) who illustrated the radula dentition of six species.

Aside from the aforementioned three west American species, the only other illustrations of west American species appear to be outline drawings of the teeth of *C. princeps, C. ximenes, C. virgatus,* and *C. californicus* by Hanna (1963).

METHODS AND MATERIALS

Radula sheaths were dissected out of the preserved animals after the animal had been removed from the shell. The entire sheath was then placed in a depression on a spot plate and cleaned of extraneous adhering tissue. The clean radula sheath then was placed into a second depression on the plate into a few drops of Clorox. A few minutes in the Clorox usually sufficed to digest away most of the radula sheath material and free the radula ribbon. If possible the upper and ready arm portions of the sheath were separated at that time.

When the sheath had been sufficiently digested to begin to free the teeth, the separated upper and ready arm parts and the teeth were removed from the Clorox to a third, water-filled depression and rinsed.

The radula teeth were taken from the water and mounted on slides. Teeth from the ready arms and upper arm were mounted separately whenever possible. The mounting medium employed in most cases was PVA-K, a modification by Kohn of Weiss's polyvinyl lactophenol. This media is non-resinous. In a few cases the Turtox media CMC or CMC-S were used. After drying, the slides were ringed with Laktoseal to make the mounts permanent.

The slides were examined under a microscope; drawings were made with a camera lucida. Because *Conus* teeth are highly asymmetrical, it was attempted to draw for each species only a tooth with the orientation that would show the greatest number of features. It must be remembered that teeth in different positions have a slightly different appearance and that some of the structures visible in one position would be invisible in another.

The terminology used here in general follows that used by Warmke (1960) but is partly my own invention. Figure 1 illustrates a hypothetical *Conus* tooth and gives the terms for the tooth parts used in the present paper.

I have restricted the present paper to indigenous west American species of *Conus.* Hence I have not considered *C. ebraeus* and *C. tesselatus,* both Indo-Pacific species which are occasionally found in west America. The only west American species that I have not considered here is *C. emersoni,* the status of which is questionable (Hanna, 1963), and for which I was unable to obtain material.

Conus dalli Stearns, 1873

Figures 2, 3

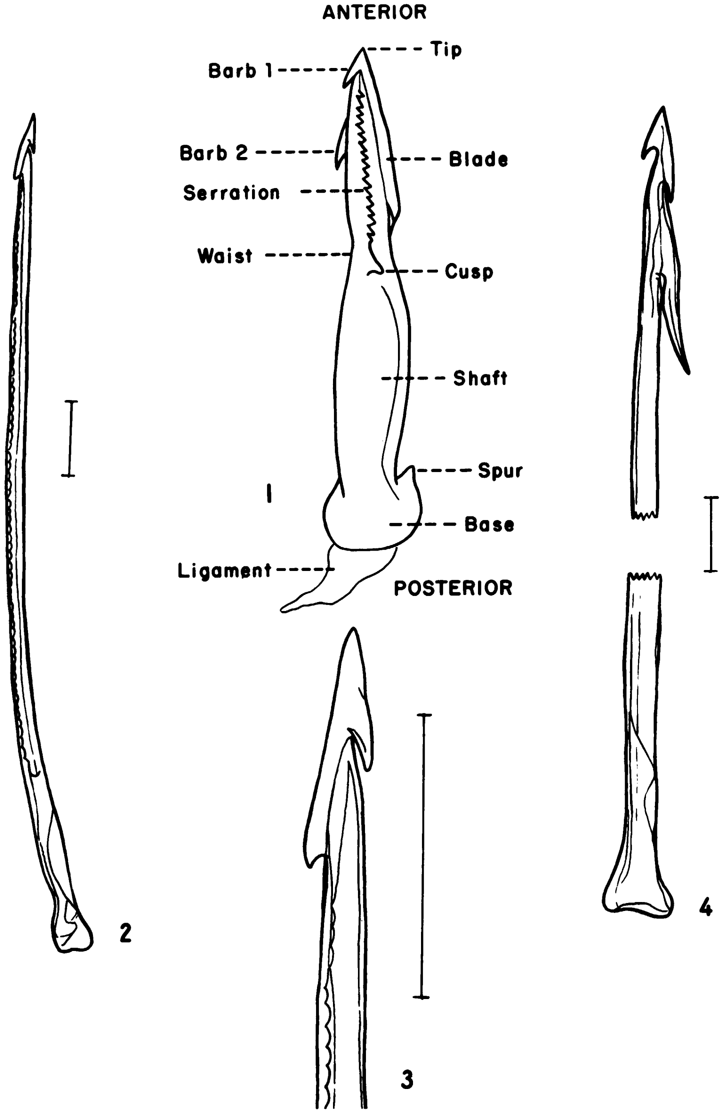
The radula teeth of this species are highly distinctive and cannot be confused with those of any other west American congener. *Conus dalli* is a mollusk-eating species (Nybakken, 1968) and the tooth is typical of other mollusk-eating species of the Indo-Pacific, such as *C. textile* and *C. pennaceus.*

There are many teeth in the radula sheath. The ready arm of the sheath of the four specimens examined contains 22, 25, 15, and 18 teeth respectively. No counts were made of the teeth in the upper arm, but the large number in the ready arm contrasts with the smaller number in the ready arm of most west American *Conus* species.

The teeth are large, averaging about 3.0 mm., and the shell/tooth length ratio is low (averaging 11.74 for 16 teeth), indicating that the teeth are not only relatively large, but also absolutely large.

Each tooth has two barbs situated near the tip. The first is larger and has a straight point. The second is at the end of a short blade and slightly recurved at the tip to form the indication of a hook.

The remainder of the tooth consists of a long shaft that is without serrations and terminates in a slightly enlarged base which has no spur. The long shaft, if studied under high magnification, shows a long, con-



FIGS. 1–4. Composite hypothetical *Conus* radual tooth indicating areas referred to by terms used in text. 2. *C. dalli* tooth. 3. Detail of anterior portion of *C. dalli* tooth. 4. *C. purpurascens* tooth with central part of shaft omitted because of extreme length.

Length of scale bar is 0.5 mm. for all figures.

tinuous fine scalloping or fluting internally along one edge, which ends just above the base in a small, rounded cusp. A strong ligament is attached to the base of the tooth.

Conus purpurascens Broderip, 1833

Figure 4

Conus prupurascens is a fish-eating cone (Nybakken, 1967), and the teeth are typical of those found in all fish eaters examined. The tooth of *C. purpurascens* was drawn by Piele (1939, fig. 5) and is drawn here in more detail.

The teeth are very large. In the larger specimens they may reach a length of more than 7 mm. The shell/tooth ratio is therefore small (averaging 8.21 for 70 measured teeth).

The tip of the tooth has an armature consisting of two small opposing barbs followed by a very large third barb that protrudes outward distally, giving the whole tooth a harpoon-like appearance. In contrast to many other fish-eating cones, such as *C. striatus, C. consors,* and *C. achatinus,* the long third barb is not recurved or hooked at the distal end.

The remainder of the shaft is quite plain and uniformly cylindrical with neither serration nor cusp.

The base is rounded and only slightly larger than the shaft. No spur is present, but a large ligament is attached to the base.

Conus recurvus Broderip, 1833

Figure 5

In terms of tooth morphology *C. recurvus* resembles *C. arcuatus* (see below and fig. 6) with some slight differences.

The tooth is characterized by the presence of three barbs, one on one side nearest the tip, and two on the opposite side farther from the tip. The first two barbs back from the tip are pointed, but the third is in most cases more rounded. Barb 3 is somewhat closer to barb 2 in *C. recurvus* teeth than it is in *C. arcuatus* and serves to differentiate the teeth of these two species.

The narrowest part of the tooth occurs just posterior to the third barb, but the waist is not as pronounced as it is in *C. arcuatus.* The anterior portion is shorter than the anterior portion above the waist in *C. arcuatus.* Posterior to the waist the tooth reaches its maximum diameter then constricts slightly before expanding at the base.

The base is large and characterized by a large spur.

Conus arcuatus Broderip and Sowerby, 1829

Figure 6

The teeth in this species are similar in general form to those of *C. recurvus,* but are distinguished by the presence of a prominent blunt or rounded third barb, which is farther from the second barb than it is in *C. recurvus,* and by the position of the waist, which is near the center of the tooth rather than in the anterior third.

The teeth have two barbs near the tip, the second usually farther from the tip than is the case in *C. recurvus.* The barbs are not hooked or recurved. Both blade and cusp are absent.

A change in diameter of the tooth occurs about halfway down the shaft. From this waist area progressing toward the base, the tooth becomes convex at first then constricts immediately before the base is reached. The tooth does not expand in diameter anterior to the waist.

The base is wide and bears a prominent spur of a form similar to that in *C. recurvus.*

Conus lucidus Wood, 1828

Figure 7

The teeth in this species are similar in all major respects to the teeth in *C. perplexus* (see below and fig. 8). Shell morphology of *C. lucidus* and *C. perplexus* is very different, whereas the teeth are almost impossible to tell apart. Nothing is presently known concerning the diet of either *C. lucidus* or *C. perplexus,* but as there is a similar radula morphology, food preference would seem to be similar.

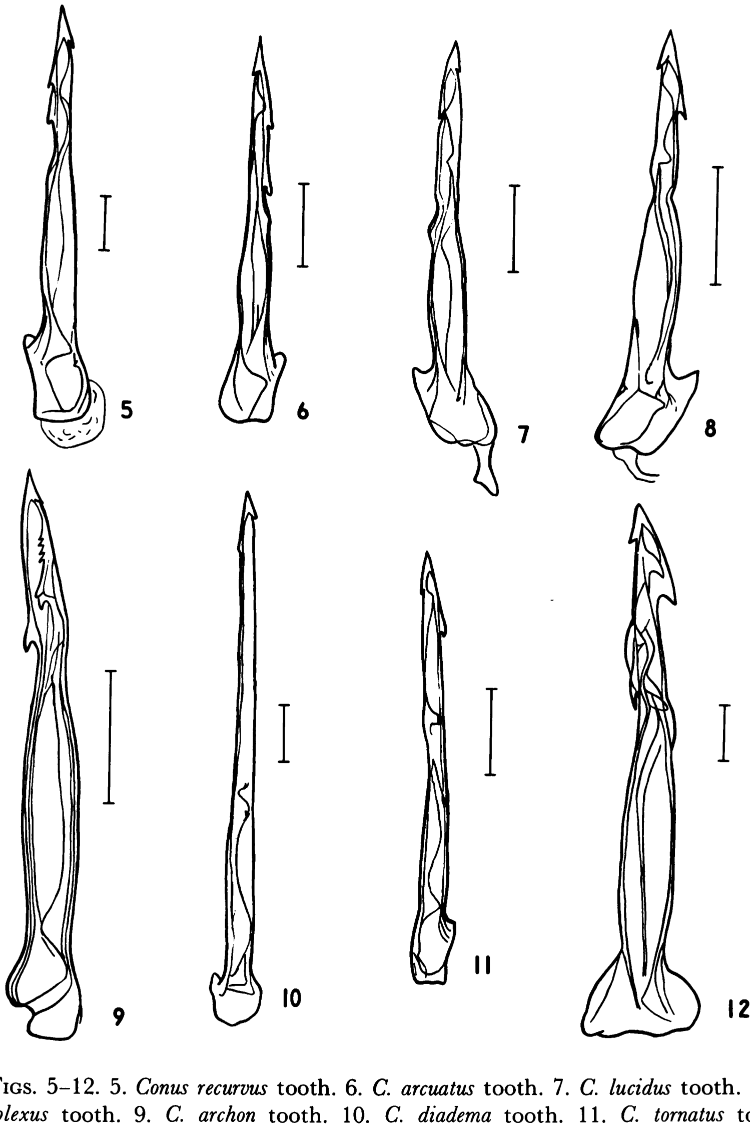
The teeth are characterized by the huge base and spur which together form the long axis of the base. This axis is set at an angle to the shaft of the tooth. Two barbs occur just back from the tip, but no serration nor cusp is present. A prominent waist occurs about one-third the distance from the tip to the base and is visible from any position where the long axis is perpendicular to the viewer.

Conus perplexus Sowerby, 1857

Figure 8

The teeth of this species closely resemble the teeth of *C. lucidus. Conus perplexus* teeth have two barbs set back from the tip and neither is recurved nor hooked. The barbs tend to be larger and better developed than those in *C. lucidus.* No blade nor serration is present.

A waist occurs about one-third of the distance from the tip to the base, and is a prominent feature of the tooth. A cusp is absent, although



FIGS. 5–12. 5. *Conus recurvus* tooth. 6. *C. arcuatus* tooth. 7. *C. lucidus* tooth. 8. *C. perplexus* tooth. 9. *C. archon* tooth. 10. *C. diadema* tooth. 11. *C. tornatus* tooth. 12. *C. californicus* tooth.

Length of scale bar is 0.1 mm. for all figures.

a peculiar rounded part of the inrolled tooth may be observed just posterior to the second barb halfway between it and the waist.

The base is enlarged and bears a very large spur. The poison duct opens via a wide aperture between the two barbs.

Conus archon Broderip, 1833

Figure 9

This rare species has unique teeth. To my knowledge there are no other species of *Conus* from other areas whose teeth look like those of this west American *Conus*.

The unique feature of the tooth is a barb (barb 2) between barb 1 and the barb terminating the narrow blade which itself has an accessory barb. This barb also has a short serration that immediately precedes the small accessory barb, which may be pointed or rounded.

There is a slight waist posterior to the barb terminating the blade. No cusp is present, and there is no major serration on the shaft.

The remainder of the shaft is unornamented and runs in a smooth curve to the base. There is a slight constriction in shaft diameter where it joins the base. The base is rounded, relatively large, and bears a single spur on one side (absent in the present figure).

Conus diadema Sowerby, 1834

Figure 10

Another of the species that has characteristic teeth, *C. diadema,* is readily recognizable by the long cylindrical shaft which is without evidence of serration or waist and which bears a single short barb and blade at the tip.

The barb is pointed, but the blade is beveled at its end. A small rounded cusp occurs on the shaft about one-third the distance from the base to the tip. The shaft shows little change in diameter throughout.

The base is rounded and bears a single prominent spur.

Conus tornatus Broderip, 1833

Figure 11

This is another species with a characteristic tooth morphology that is difficult to confuse with that of any other species.

The tooth has a long, narrow shaft surmounted at the tip by a small sharp-pointed barb on one side and a longer blade on the other. The blade terminates in a pointed barb. No serration nor cusp is present.

A slight waist occurs about halfway down the shaft. Just anterior to the waist a peculiar circular aperture occurs in the structure of the tooth which appears to open from the inside of the tooth to the outside. This type of structure has never been observed in other *Conus* teeth from west

America. Perhaps it is the opening of the venom canal, but its actual function is not known.

The base of the tooth is only slightly enlarged and bears a large spur on one side.

Conus californicus Hinds, 1844

Figure 12

The teeth of *C. californicus* have been illustrated and described previously by Piele (1939) and Hanna (1963) and are also included here.

The teeth are readily distinguishable from all other congeners in west America by the presence of five barbs, one of which may be considered to terminate in a short blade.

No serration is present, but a conspicuous groove extends from the barbed anterior portion through the posterior portion of the shaft to the base. No cusp is present, and the base is large and rectangular without evidence of a spur.

Saunders and Wolfson (1961) have reported on the diet of this species, and Kohn (1966) has shown that it has the most catholic diet of any *Conus*. It may be that species with wide food preferences can be associated with this tooth type. At any rate, the tooth type is rare (Piele, 1939).

Conus gladiator Broderip, 1833

Figure 13

The teeth of *C. gladiator* are characterized by the presence of a strongly developed, large serration. The serration length is about one-half the length of the tooth and terminates in a prominent posterior pointing cusp. The individual teeth of the serration are larger and more rounded than are similar serration teeth in other species.

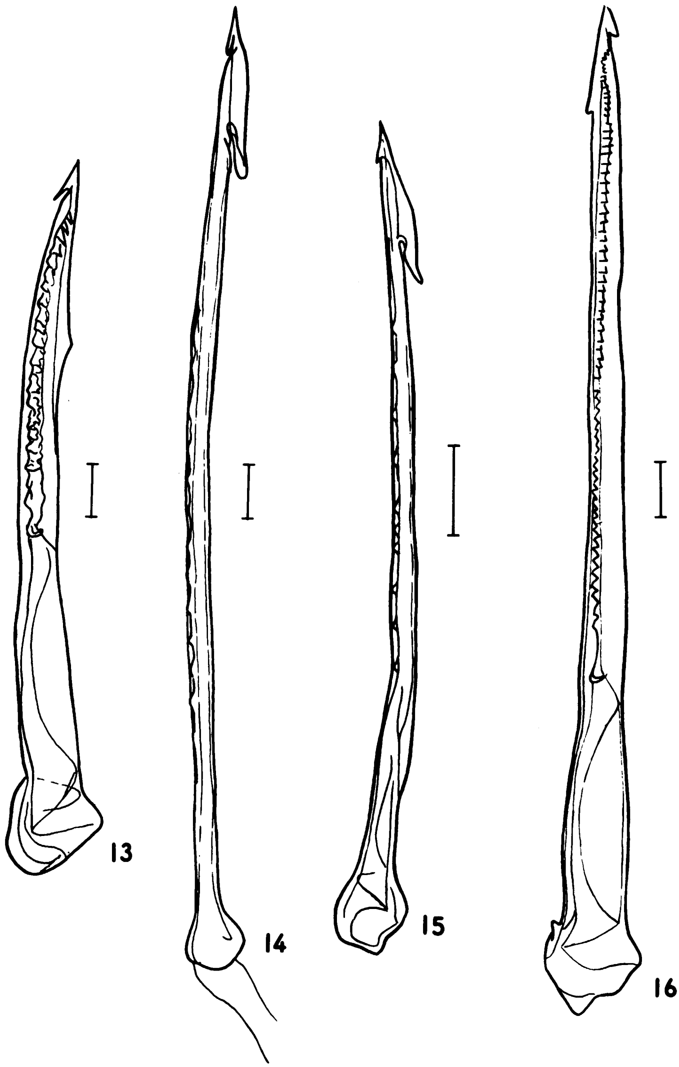
Each tooth has a single barb just posterior to the tip. A prominent blade runs posteriorly from the tip reaching a maximum width at a point halfway between the tip and the cusp. It then tapers off abruptly. No barb is present.

No prominent waist divides the tooth into regions, but a slight waist occurs just posterior to the cusp. This is followed by an enlargement and then another more prominent constriction where the shaft joins the base. The base is rounded and slightly enlarged. It bears a small spur on one side (not visible in the present illustration).

Conus ximenes Gray, 1839

Figure 14

When contrasted with the radula teeth of other west American *Conus*,



FIGS. 13–16. 13. *Conus gladiator* tooth. 14. *C. ximenes* tooth. 15. *C. mahogani* tooth. 16. *C. princeps* tooth.
Length of scale bar is 0.1 mm. for all figures.

the teeth of *C. ximenes,* and *C. mahogani* (below and fig. 15) are much less rigid than any of the others. In many cases when transferring the teeth to the mounting medium they would bend as when any attempt was made to move them in either water or the mounting medium. They also tended to have the same refractive index as the medium and hence became invisible after a few days or weeks and could only be observed under phase contrast optics. These observations caused me to wonder how the teeth can be used for any sort of piercing as they are in other species. The diet of the species is presently unknown.

The tooth morphology is also very different from that in other *Conus* species, except *C. mahogani.* The tooth has a long, unornamented shaft surmounted by two barbs. A small barb occurs near the tip and a much larger barb opposes it. The large barb is blunt-ended but protrudes in a manner similar to that of the large barbs of the fish-eating species (see fig. 4).

The shaft is characterized by the presence of rounded bumps spaced evenly along one side. No serration nor cusp is present, and the shaft shows no sign of a waist. The shaft ends in a rounded base, which is only slightly expanded in diameter beyond that of the shaft. No spur is present.

Conus mahogani Reeve, 1843

Figure 15

The teeth in this species are similar in all respects to the teeth of *C. ximenes.* They also show the same lack of rigidity in structure as do those in *C. ximenes.*

The only difference I was able to observe between the teeth of *C. mahogani* and *C. ximenes* was that the second barb is somewhat more pointed in *C. mahogani.* This, however, was not a constant feature.

Conus princeps Linnaeus, 1758

Figure 16

The teeth of *C. princeps* are characterized by a long serration that extends more than half the length of the tooth. In this respect and in general shape it resembles the teeth of *C. fergusoni* (below and fig. 18) and *C. patricius* (below and fig. 17).

The shaft is straight and of maximum diameter near the base. It has a nearly uniform diameter along the length of the serration. The tip of the shaft bears a small barb on one side and a short blade on the opposite side that ends in a truncated point. The serration is terminated by a prominent rounded cusp. There is a slight indication of a waist just posterior to the cusp. The shaft terminates in a rounded base bearing a small, acute spur on one side.

Conus fergusoni Sowerby, 1873

Figures 18–20

Although differing in shell morphology, the adult *C. fergusoni* has teeth similar in most features to those of the adult *C. patricius* (below).

The teeth of the adult are characterized by the presence of a long serration that greatly exceeds the length of the barbs, and approximates half the length of the entire tooth. The serration terminates in a small-pointed cusp in contrast to the larger, rounded cusp of *C. patricius.*

The head of the shaft bears two barbs, the most anterior of which has a more acute point. The posterior barb terminates a short blade.

Some of the specimens that have the juvenile shell pattern (see Hanna, 1963 for a discussion of the juvenile color pattern) have quite different types of teeth than those of the adult and similar to the type of tooth seen in the *C. regularis* group (compare figs. 20, 22). Others (fig. 19) show an intermediate type of tooth between the adult (fig. 18) and the *C. regularis* type, exemplified in figure 20. The implications of these differences are discussed in a later section.

Conus patricius Hinds, 1843

Figures 17, 21

As in *C. fergusoni,* the teeth of the adults of *C. patricius* are characterized by a structure in which the serration is long relative to the lengths of barb and blade. The serration approaches half the length of the entire tooth and ends in a prominent rounded cusp that protrudes from the smooth line of the shaft.

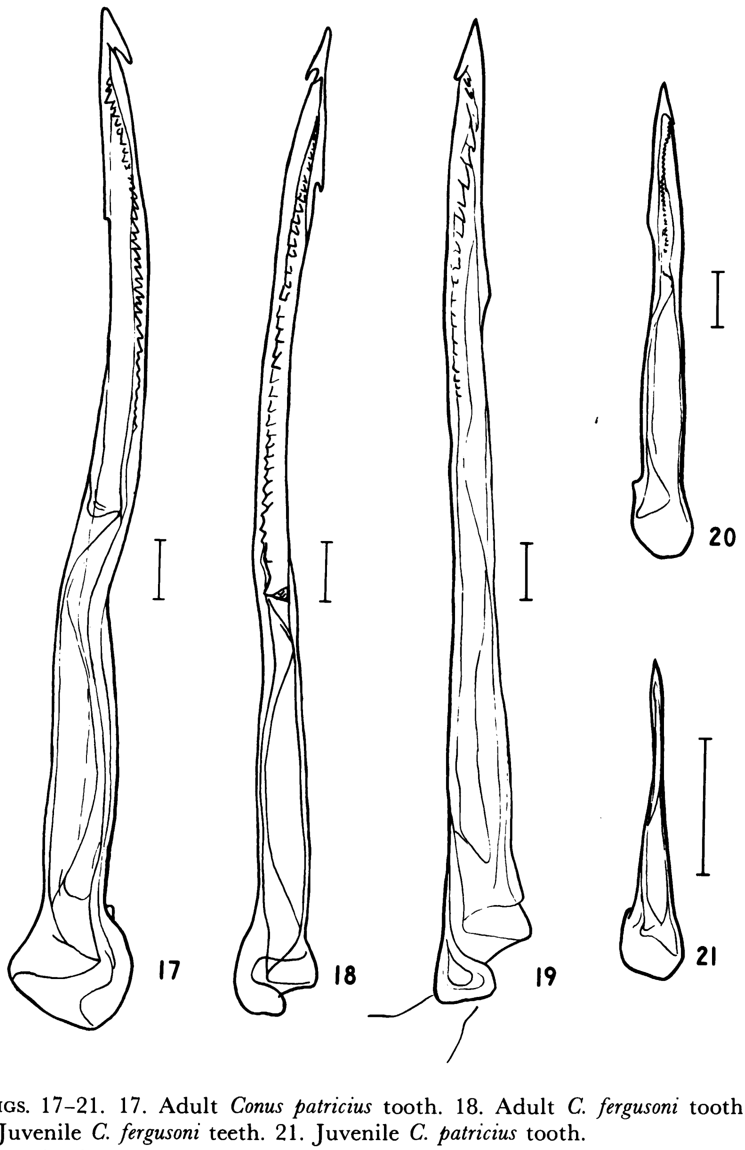
Each adult tooth is surmounted by a short, pointed barb on one side opposed by a short blade on the other. The blade is truncated at the end in contrast to the pointed end of the blade in *C. fergusoni.*

The tooth shaft is of a uniform diameter in the anterior half and only slightly enlarged in the posterior half. A slight hint of a waist occurs at the level of the cusp.

The base is slightly expanded and bears a small spur which is visible only in certain views of the tooth.

The teeth of young or juvenile specimens of *C. patricius* are strikingly different from those of the adult. The tooth of a young specimen 27.1 mm. in length is illustrated in figure 21 and shows this difference.

The young specimens have a very small tooth with no indication of barb, blade, or serration. The opening to the poison canal gaps widely near the tip, and the base is large relative to the rest of the tooth. The shaft is very short and narrow toward the anterior end.



FIGS. 17–21. 17. Adult *Conus patricius* tooth. 18. Adult *C. fergusoni* tooth. 19, 20. Juvenile *C. fergusoni* teeth. 21. Juvenile *C. patricius* tooth.
Length of scale bar is 0.1 mm. for all figures.

Conus regularis Sowerby, 1833

Figure 22

The tooth morphology of *C. regularis* is the basic *Conus* type to which I have referred all others that appear similar (i.e. to the *C. regularis* type). It is a type of tooth morphology that is virtually indistinguishable among several species, some of which show quite different and others very similar shell characteristics.

The teeth of *C. regularis* have a single pointed barb near the tip. Opposite the barb is a weakly developed blade which extends about one-third the length of the shaft. The blade has a rounded or truncated end. Another prominent feature of the tooth is the presence of a serration approximately equal in length to that of the blade. The serration ends before the cusp leaving a gap or diastema between them. The cusp is rounded and not as prominent as it is in other species. The cusp is followed by a slight waist. Posterior to the waist the tooth is unornamented and only slightly expanded.

There is a slight constriction at the end of the shaft where it joins the base. The base is rounded and not greatly expanded. It bears a small spur on one side.

Conus gradatus Mawe, 1823

Figure 23

Only two specimens assignable to this species were available for dissection. One was furnished by James McLean of the Los Angeles County Museum (L.A.C.M. No. 65–23), the other came from the Pillsbury Expedition to the Gulf of Panama. The shell of L.A.C.M. No. 65–23 was similar to those of the many *C. regularis* in my collection and, indeed, the teeth were indistinguishable from those of the typical *C. regularis.*

The second specimen, from which figure 23 was drawn, had a different shell morphology than that of the typical *C. regularis,* but the teeth were similar to typical *C. regularis* teeth.

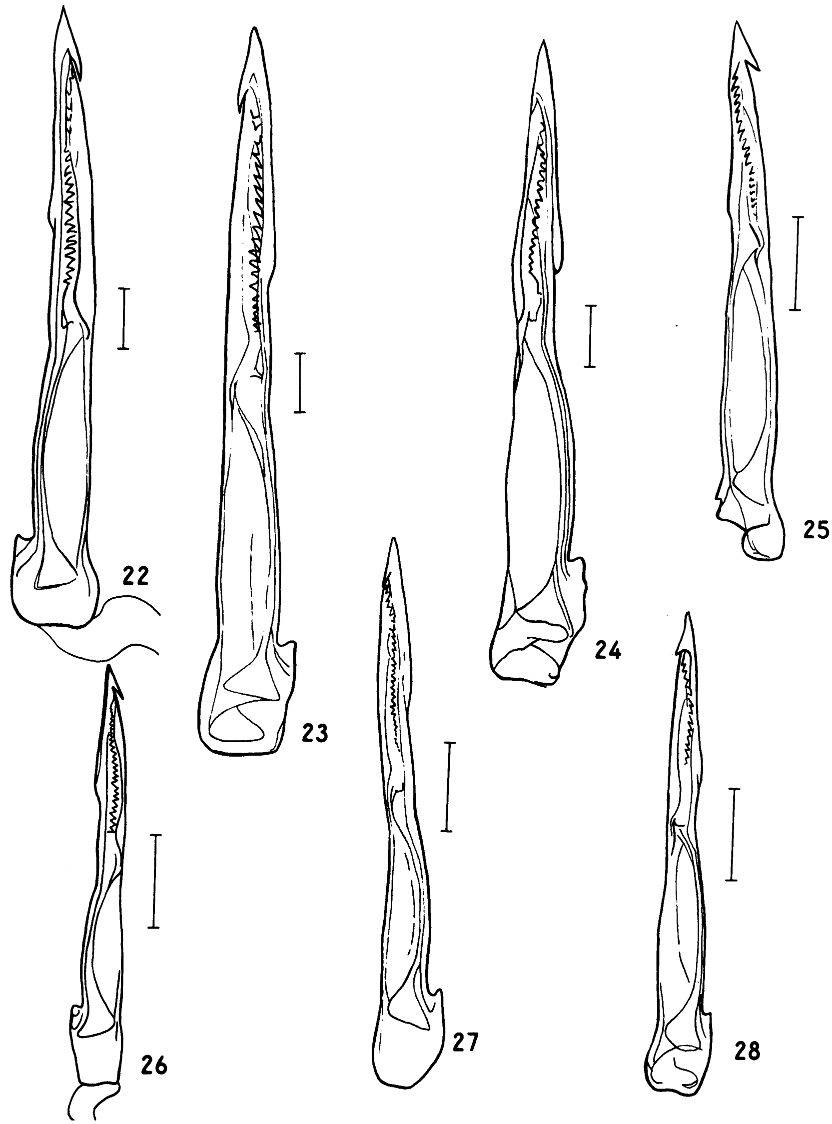
There is no single feature of the morphology of the teeth that is different from that of the teeth of *C. regularis* described above, hence no description of the tooth is necessary here. With additional material it is possible that certain differences in proportions could be quantified, but it is not possible with the present limited material.

Conus scalaris Valenciennes, 1832

Figure 24

The teeth of this species fall into the *C. regularis* complex. They appear to be almost indistinguishable morphologically from the other species in the complex.

The teeth are slender and surmounted by a single barb on one side opposed by a weakly developed blade. The blade extends about one-third the length of the tooth.



FIGS. 22–28. 22. *Conus regularis* tooth. 23. *C. gradatus* tooth. 24. *C. scalaris* tooth. 25. *C. dispar* tooth. 26. *C. poormani* tooth (view 1). 27. *C. poormani* tooth (view 2). 28. *C. virgatus* tooth.
Length of scale bar is 0.1 mm. for all figures.

A prominent serration extends from near the tip to between one-third and one-half the length of the shaft. The serration and blade end at approximately the same level on the tooth. A cusp terminates the serration. The waist occurs immediately posterior to the cusp. The posterior half of the tooth is unornamented and there is a slight constriction in the shaft before it joins the base. The base is large and rounded and bears a single spur.

The only differences between the teeth of *C. scalaris* and *C. regularis* are the relatively weaker barb and blade in *C. scalaris,* but these may be eliminated when a large number of specimens are examined, in which case there may be no morphological differences between the two.

Conus dispar Sowerby, 1833

Figure 25

This cone is one of the rarest of the west American species, and only two specimens were available for dissection.

The teeth of this species are virtually indistinguishable from those in the other species in the *C. regularis* complex, thus supporting Hanna (1963) who noted that its shell morphology placed it in this group.

The teeth have the usual single barb just back of the tip and an indistinct blade that runs about one-third the length of the tooth terminates in a smooth transition to the main outline of the tooth. A conspicuous serration extends from the base of the barb to the end of the blade and terminates in a rounded cusp. Posterior to the cusp is an indistinct waist. Posterior to the waist the tooth is unornamented.

The base of the tooth is swollen and bears a single small spur on one side (absent in the present illustration).

Conus poormani Berry, 1968

Figures 26, 27

This is the most recently described west American *Conus* species and appears, on the basis of shell morphology and periostracum, to be valid. It was originally described without a figure, but figure 5 in Emerson and Old (1962) is the species (as a color form of *C. recurvus*). All specimens on which tooth descriptions and figures are here based were taken in the Gulf of Panama by the Pillsbury Expedition of the University of Miami Institute of Marine Sciences. A rather large series of material that was collected alive was available. It is puzzling to me that such a large *Conus* species had remained undescribed for so long.

The teeth are typical of the *C. regularis* complex, armed at the tip with a single pointed barb. The single barb is opposed by a strong blade that extends almost one-third the length of the tooth. It terminates in a rounded edge.

A long serration is also a prominent feature and extends posteriorly beyond the end of the blade. This feature serves to distinguish the tooth from some in the *C. regularis* complex in which blade and serration are about equal length. There is a slight gap following the end of the serration before the cusp is reached. The cusp is rounded and not prominent.

Posterior to the cusp is a slight hint of a waist followed by the expansion of the shaft to its maximum diameter in the posterior third of the tooth. There is then another slight constriction where the shaft meets the base. The base is enlarged and rounded and bears a single spur on one side.

Conus virgatus Reeve, 1849

Figure 28

The teeth of *C. virgatus* are also typical of the *C. regularis* complex.

Each tooth is surmounted by a single pointed barb on one side. This barb is opposed by a blunt-ended blade which extends about one-third the length of the shaft. A serration is also present and approximates the length of the blade; it ends before the cusp is reached leaving a diastema between the two.

Immediately posterior to the cusp there is a very slight waist after which the shaft expands to a maximum diameter before narrowing again as the shaft joins the base. The base is expanded only slightly, is rounded, and bears a small spur on one side.

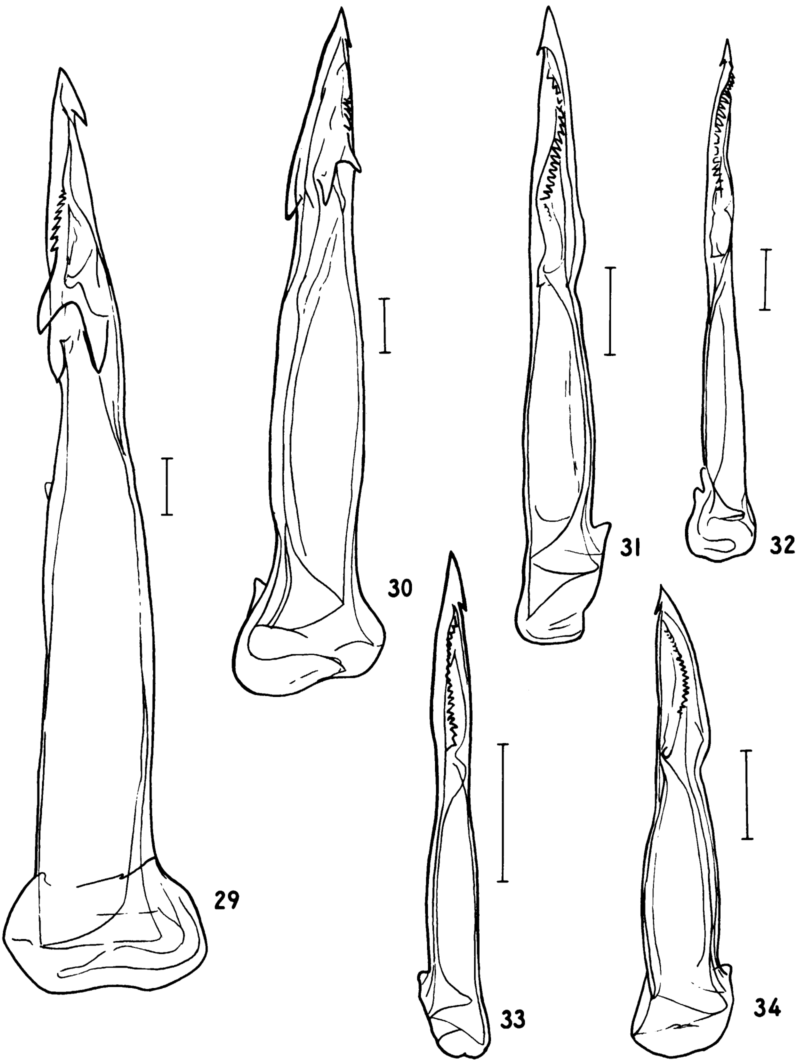
Conus tiaratus Broderip, 1833

Figure 31

The teeth of *C. tiaratus* can be placed in the *C. regularis* group. They do not appear to show any distinctive morphological features that would separate them from other teeth in the same group.

Each tooth is surmounted by a single barb. A narrow blade opposes this barb and extends posteriorly from one-third to one-half the length of the tooth. It terminates in a rounded edge just anterior to the waist. It is the very long length of the blade that serves to separate this tooth from many others in the *C. regularis* group. Further, it is always longer than the serration, a feature not seen in most of the teeth of the *C. regularis* group.

A well-developed serration extends from just posterior to the barb to about one-third the distance down the shaft. A gap separates the end of the serration from the cusp which occurs immediately anterior to the waist.



FIGS. 29–34. 29. *Conus brunneus* tooth. 30. *C. bartschi* tooth. 31. *C. tiaratus* tooth. 32. *C. vittatus* tooth. 33. *C. orion* tooth. 34. *C. nux* tooth.
Length of scale bar is 0.1 mm. for all figures.

The remainder of the tooth is unornamented and only a slight constriction occurs in the shaft before it joins the base. The base is rounded and bears a single spur on one side.

Conus vittatus Hwass in Bruguiere, 1792

Figure 32

The teeth of *C. vittatus* are characterized by the absence of a blade. Otherwise they closely resemble the typical teeth of the *C. regularis* complex.

Each tooth is surmounted by a single pointed barb, followed by a strong serration which extends posteriorly about one-third the length of the tooth. The serration ends leaving a short gap before the cusp, which is prominent.

Posterior to the cusp there is a very slight waist, followed by a gradual increase in the diameter of the shaft until it reaches a maximum in the posterior third of the tooth. There is then a slight constriction before the shaft joins the base. The base is only slightly expanded and bears a small spur on one side.

Conus orion Broderip, 1833

Figure 33

The teeth in this species are similar to those of *C. vittatus,* with which the species has been placed as a color variant, but differ from them by having a weakly developed blade apparently absent from *C. vittatus.* In fact the teeth resemble the typical teeth of the *C. regularis* complex to such a degree that it would be difficult to differentiate them. However, I dissected only a single specimen of this species so I do not have an appreciation for the variation which might occur among the teeth of different individuals.

Each tooth has a single barb on one side of the tip and a blade on the other. The blade extends back about one-third the length of the tooth and is rounded at the end.

A conspicuous serration extends from the base of the barb as far posterior as the blade. The serration is terminated, after a gap, by a rounded cusp which is not as prominent as that in *C. vittatus.*

There is a slight waist posterior to the cusp and the remainder of the shaft is unornamented and only slightly expanded between it and the base. The base is large and rounded and bears a small spur.

Conus brunneus Wood, 1828

Figure 29

The teeth of *C. brunneus* and *C. bartschi* are similar, and so highly distinctive that it is impossible to confuse them with any other west American species. The tooth type is correlated with a specialized food organism (Nybakken, 1970).

The number of teeth in the radula sheath is small; the ready arm usually has only four. This small number of teeth bears a correlation to their large size. They are not particularly long, but are very wide. One is impressed by their stout, massive appearance.

Characteristic of the teeth is the presence of four barbs near the anterior end. One of these barbs juts out from the tooth in such a way that in some views it forms a prominent angle with the shaft. This barb also bears a serration along its outer surface. The presence of a serration on a barb is seen in only one other west American *Conus, C. archon.*

In most views of the teeth, the most prominent barb is the one that has the greatest length and terminates in a very large blade. All the barbs are pointed, but none is recurved or hooked. Three terminate at nearly the same level, but are spread in an arc around the tooth.

Posterior to the barbs is a slight waist. Posterior to the waist, the shaft expands to its maximum diameter narrowing only slightly before joining the base. No cusp is present.

The base is massive, almost rectangular in outline, and bears a single large spur (absent in the present figure).

Conus bartschi Hanna and Strong, 1949
Figure 30

The radula teeth of *C. bartschi* are similar to the teeth of *C. brunneus* in all respects.

The teeth are large, and the radula sheath contains few of them The ready arms of the two specimens dissected contain four teeth each.

The teeth have the usual four barbs, one of which bears a serration. The shaft is thick and unornamented posterior to the barbs, and the base is stout, rectangular, and bears a single spur.

Conus nux Broderip, 1833
Figure 34

In this species the teeth are short and stout and distinguishable by their general over-all shape.

The anterior portion of the shaft is dominated by the presence of a strong blade which extends from the tip to the waist. A small barb is also found just back from the tip.

A prominent serration extends through the central part of the anterior third of the tooth and terminates before the cusp is reached, leaving a gap. The cusp is not prominent, and observable only as a slightly rounded protuberance.

Posterior to the waist, the shaft broadens to its maximum width and then constricts slightly before terminating in a very large base. The base is large relative to the tooth, elliptical in shape, and bears a very large spur on one side.

DISCUSSION

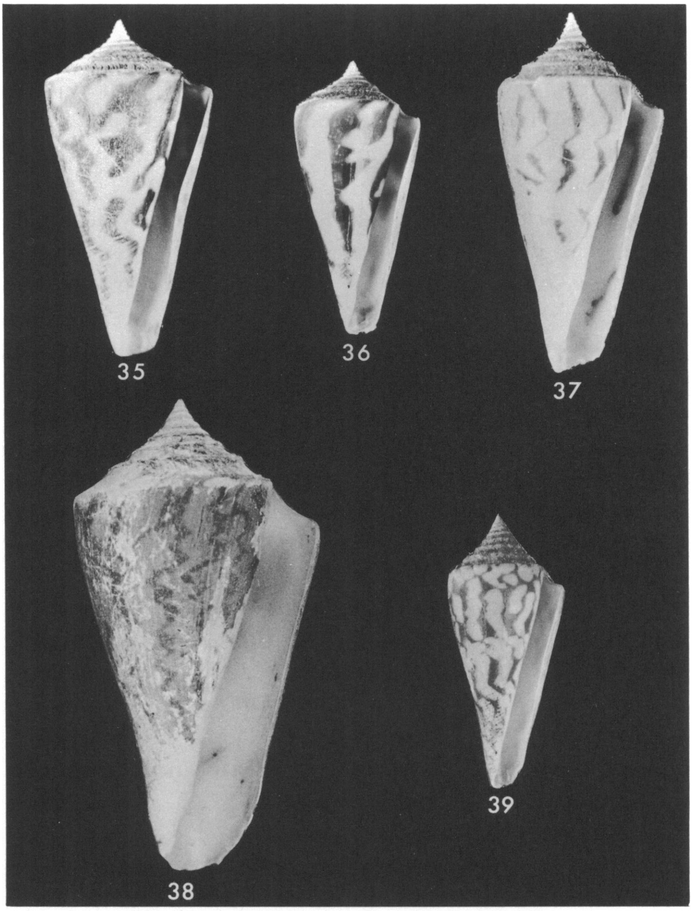
The present study has resolved some of the previous problems that existed in relation to the identification of certain west American species.

Two of the most difficult species to distinguish on the basis of shell morphology are *C. perplexus* and *C. ximenes.* As Wolfson (1962) pointed out the shell pattern and color are virtually identical, and conchologists have relied on relative differences in size and shell proportions to distinguish between them. Wolfson (1962) was able to distinguish between them by using a discriminant function derived from a multiple regression analysis of shell characters. That is a tedious method, and, if these are good species, one would hope that a more simple method might be found to determine species on an individual basis. The present study of radula morphology has produced further convincing proof of the validity of the two species by illustrating the striking differences in the teeth of the two species. The teeth of *C. ximenes* resemble only the teeth of *C. mahogani,* whereas *C. perplexus* teeth are more similar to those of *C. lucidus* than to any other species. In no case is there any evidence of a change in tooth morphology with increase in size of the animal. I do not believe that it is possible to consider one as a juvenile tooth and the other an adult. It might be noted that, except for *C. patricius* and *C. fergusoni,* radula teeth were not found to change in structure with a change in size (age) of the animal. Hence the radula tooth is a most useful character in identification.

Difficulties in distinguishing between *C. brunneus* and *C. diadema* have also been encountered by malacologists for the shells often appear indistinguishable (Keen, 1958). Hanna (1963) noted that many authors have included *C. diadema* in the synonymy of *C. brunneus* although he believes that it is a good species. As the figures of the teeth illustrate, the two have entirely different teeth which are impossible to confuse (figs. 10, 29). This difference further serves to validate them as good species and to suggest, as with *C. perplexus* and *C. ximenes,* that they are not closely related despite shell similarity.

It is also possible to differentiate live members of *C. diadema* from *C. brunneus* on the basis of color; the former is orange, the latter a deep purple-red or wine color.

Although *C. brunneus* has been considered common in shallow water



FIGS. 35–39. *Conus recurvus* shells. 35. Length, 50.2 mm. 36. Length, 47.5 mm. 37. Length, 54.2 mm. 38. Length, 68.6 mm. 39. Length, 50.0 mm.

in west America and *C. diadema* rare except on the offshore islands, I found the opposite to be true in two and one-half months of collecting in the Gulf of California in 1967. I also found *C. diadema* to dominate the habitats (rocky ledges) which Keen (1958) indicated were the habitats of *C. brunneus.* It is possible that this distribution anomaly is due to misidentification of *C. diadema* by collectors in the past.

Conus recurvus is another problem species of which Hanna (1963) has said: "the shells of this group comprise a maze of variations, exceedingly difficult to understand." Most authors have considered this species to be close to the *C. regularis* complex of species based on similarity of color pattern and shape of shell. When a radula study is done on this species, however, it becomes a simple task to separate true *C. recurvus* from other members of the *C. regularis* complex. The radula is entirely different in morphology from the radula type characteristic of the *C. regularis* complex (compare figs. 5 and 22) and resembles the radula of *C. arcuatus,* another deep-water species.

Conus recurvus varies in shell coloration from the typical pattern of bold flammules of reddish brown to almost white. I have figured here a series of shells all of which have the typical *C. recurvus* radula tooth but which differ in color pattern (figs. 35–39). In this case the tooth is a much more conservative character and more reliable in identifying the species than is the shell pattern.

The fact that the tooth of *C. recurvus* resembles *C. arcuatus* and no other shallow-water species, and that both species are almost always collected alive only by dredging, suggests that the shape of the tooth is in some way related to a prey organism present in deep and not shallow waters. At present no data on food preferences are available for either of these species.

The teeth of *C. brunneus* and *C. bartschi* appear to me to be indistinguishable. Their similarity may not be apparent from the figures because the few teeth available to me from two individuals of *C. bartschi* necessitated drawing the *C. bartschi* tooth in a different orientation from that of *C. brunneus.* As the teeth of *C. brunneus* and *C. bartschi* are so different from any other west American species and apparently indistinguishable from each other, I believe that it is most likely that *C. bartschi* is only a deep-water color variant of *C. brunneus.*

The *C. vittatus—C. orion* problem cannot be resolved from the present study. The radula teeth of the two are similar, but do not appear identical. However, only a single specimen of *C. orion* was available for dissection, hence I have no real appreciation for the variability that might occur in this form, especially since, in the specimen examined, the teeth are close to those in *C. vittatus.* I have not seen a live animal of *C. orion* so I do not know what the animal is like in terms of color. It seems reasonable, on the basis of present evidence of shell differences, to retain them as separate species.

Conus mahogani has been considered a separate species by some authors (Hanna, 1963), and only as a subspecies of *C. ximenes* by others (Keen, 1958). The results of the present study indicate no demonstrable differences between the radula teeth of the two taxa. As for *C. brunneus* and *C. bartschi,* these two species have teeth entirely different from any other congeners in west America. The similarity of the teeth and the shell lead me to conclude that it is best to consider *C. mahogani* a color variant of *C. ximenes.*

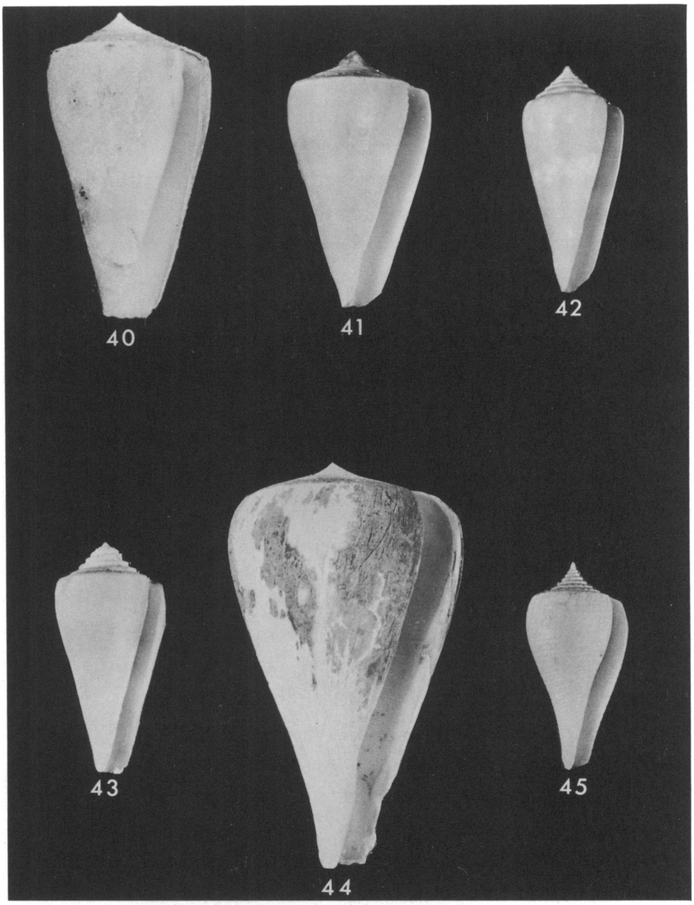
Conus fergusoni has created a problem that was not anticipated when the present study was begun. Hanna (1963) has shown that the young of *C. fergusoni* have a different color pattern from that of the adults and were originally described as a separate species (*C. xanthicus* Dall, 1910). He was able to show this by laying out a series of growth stages in this species which showed the transition in color pattern from young to adult.

When radula mounts were made of young and adults of *C. fergusoni,* a curious anomaly became apparent. Whereas all the adult animals showed the typical *C. fergusoni* radula tooth as illustrated in figure 18, some of the juveniles showed this same tooth but others had a radula tooth of an entirely different morphology, approaching the *C. regularis* type of tooth (fig. 20), and in one case the tooth was intermediate (fig. 19). The shell morphology and color pattern appeared similar in most cases. In one instance two juveniles with differing shell morphologies had the same type of teeth. Whereas two other juveniles, which had similar shells that matched the shell of a specimen possessing the typical adult *C. fergusoni* teeth, were found to have teeth of the *C. regularis* type. Illustrated here (figs. 40–43) are the shells of specimens showing the different types of teeth to demonstrate the variations in shell morphology.

There are three possible explanations for this anomaly. One is that *C. fergusoni* exists in two dimorphic forms with regard to the radula teeth. That this is possible is given credence by the fact that such a dimorphic situation exists in the radula teeth of *C. rattus* (Kohn, personal commun.). In the case of *C. rattus* however, the differences are not as great between the extremes and seem to be more a matter of proportion than a complete change in tooth morphology.

Another possibility is that there really are two species of *Conus* involved; one is the young of *C. fergusoni* that has a radula tooth as seen in figures 18 and 19, and the other, which appears very similar in shell characteristics to young *C. fergusoni,* is a species that does not get very large. If this latter possibility is true, then it seems that this species should be identified as *C. xanthicus* Dall, as it looks like the holotype figured by Hanna (1963 pl. 5, fig. 5) and appears to be the earliest name available pending a literature search.

The final possibility, and the one that appears to be most likely, based on evidence from *C. patricius* as discussed below, is that radula structure changes with the age of the animal. This, however, does not explain the curious anomaly of two shells of the same length having different teeth.



FIGS. 40–45. 40. *Conus fergusoni,* shell length, 51.9 mm.; tooth type as in figure 18. 41. *C. fergusoni,* shell length, 43.5 mm.; tooth type as in figure 18. 42. *C. fergusoni,* shell length, 39.1 mm.; tooth type as in figure 19. 43. *C. fergusoni,* shell length, 36.7 mm.; tooth type as in figure 20. 44. *C. patricius,* adult, shell length, 80.0 mm. 45. *C. patricius,* juvenile, shell length, 27.1 mm.

A similar anomaly was observed in the specimens of *C. patricius* examined. As I noted in the descriptions given above, the teeth of the juvenile specimens of *C. patricius* are different from those of the adult specimens. There appears to be no taxonomic problem with *C. patricius,* therefore it seems certain that the young specimens are *C. patricius.* This is the first case recorded in *Conus* where a definite change in tooth structure occurs with age of the animal. Since the teeth of *C. fergusoni* and *C. patricius* are very similar as adults, this suggests that the anomaly observed in the teeth of *C. fergusoni* from specimens of different shell lengths and morphology reflects differences in the ages of the specimens.

If this is the case in both of the above species, it is of interest to inquire whether this phenomenon is widespread in *Conus.* If widespread, it could potentially invalidate some of the differences here established between species. In an attempt to obtain some evidence to answer the question, I examined the teeth from a series of different shell sizes of *C. arcuatus, C. nux, C. princeps,* and *C. virgatus.* These species were chosen because they were the only species available to me which had a series of different shell sizes. In all cases there was no change in the tooth morphology with increase in size. This is especially interesting in the case of *C. princeps* which has a tooth type similar to adult *C. fergusoni* and *C. patricius* (compare figs. 16, 17, 18). The results suggest that this is not a widespread phenomenon in west American *Conus* but is restricted to a few, the reasons for which are not yet known.

I also have seen three specimens representing the taxon that Berry (1968) described as *C. chrysocestus;* similar specimens have been illustrated by Emerson and Old (1962, figs. 15, 16), as deep-water ecotypes of *C. fergusoni.* Unfortunately, these shells were without animals, but the shell morphology and coloration indicate they should be considered young *C. fergusoni,* at least until animals are available for radula analysis.

I have included in this study the newly described species of *Conus, C. Poormani* Berry, 1968, for which a series of 25 animals was available from the Gulf of Panama. The radula of this species is similar to the radulae of the *C. regularis* complex, but the shell and periostracum are quite different. It thus seems more reasonable to treat *C. poormani* as a separate species than some of the taxa now referred to the *C. regularis* complex.

The *C. regularis-gradatus-scalaris* group of species has presented a problem to systematists for many years (see Hanna, 1963; Keen, 1958, for discussions), and, unfortunately, is not resolved by the present study. The teeth of *C. regularis, C. gradatus, C. scalaris, C. dispar, C. virgatus, C. tiaratus, C. poormani, C. vittatus,* and *C. orion* are all essentially similar in general structure, so that it is difficult, and in some cases impossible, to tell them apart. Fortunately, *C. virgatus, C. tiaratus, C. vittatus, C. orion,* and *C. poormani* are all readily recognizable from shell structure and color pattern and do not seem to intergrade. Hence it is not necessary to consider them in a discussion of the *C. regularis* complex which is best reserved for *C. regularis, C. gradatus, C. scalaris,* and *C. dispar.* It is not possible to separate these four species on the basis of differences in the radula morphology, though differences in proportions might become apparent in a statistical analysis which I propose to do in another paper.

It further does not seem possible to me to separate *C. regularis, C. scalaris,* or *C. gradatus* on any objective basis, as the shells form a continuous series. It may be best to consider these species as color variants of single species of which *C. gradatus* Mawe, 1823 is the oldest available name.

Finally, it should be noted that in the remaining species of *Conus* the structure of the radula substantiates the species identifications. It is not necessary to discuss them further here except to note that, in general, similar radula teeth do not occur in *Conus* species that have been considered closely related based on shell characteristics. This in turn suggests that subgeneric classification of *Conus* based on shell morphology may not reflect the true phylogenetic relationships among the species. The apparent plasticity of many of the shell characters seems to have contributed most to the confused situation in the *C. regularis* complex. Except for the odd case of *C. fergusoni* and *C. patricius,* the radula anatomy seems to be a more conservative character and, in many cases, a more reliable indicator of the species, and perhaps also of the relationships among the species. In the future the radula should be studied before positive identification is made of several species, notably *C. perplexus, C. ximenes, C. brunneus, C. diadema,* and *C. recurvus.*

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