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CONTENTS

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SOUND PRODUCTION AND OTHER BEHAVIOR OF SOUTHERN RIGHT WHALES, *EUBALENA GLACIALIS*

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ABSTRACT.—In late June and early July, 1971, we recorded underwater sounds from southern right whales in Golfo San José, Argentina. The most common sound, a *belch-like* utterance, averaged 1.4 sec in duration, with most of its energy appearing below 500 Hz. Levels of this strong signal ranged from 172 to 187 dB, re 1 $\mu N/m^2$ at 1 m. The whales also produced two kinds of low-frequency *moans*. Simple *moans* had a narrow band of frequencies (centered at about 160 Hz) without appreciable frequency shifts. Complex *moans* exhibited a wider band width (centered at about 235 Hz), extensive frequency shifts, and overtones. Other sounds were categorized as *pulses*, 0.06-sec bursts extending from 30 to 2100 Hz, and *miscellaneous* sounds, comprising numerous phonations below 1950 Hz that varied in length from 0.3 to 1.3 sec. There was no periodic occurrence of sound production other than that related to the appearance of whales in the recording area at low tide.

When presented underwater playbacks of killer whale sounds, a right whale exhibited a behavior pattern called "spyhopping," but there was no obvious avoidance. An attack by five killer whales on two other right whales ended after 25 min, apparently without serious harm to the right whales. A common behavior of these southern right whales, "headstanding," may be associated with bottom feeding. Patterns of breathing varied considerably depending upon associated activities.

Local citizens reported that right whales appear in Golfo San José and nearby Golfo Nuevo each year in late June. They are most numerous in late August and September, and they disappear in November. We saw several consorting pairs that appeared to be courting, but no copulations and no very young whales.

This report describes the underwater sounds and behavior of southern right whales in Golfo San José, Argentina, in June-July, 1971. A brief summary of some of this work was presented earlier (Cummings et al., 1971).

The right whale is virtually world-wide in distribution (Hershkovitz, 1966). Although three subspecies have been recognized (*australis:* Southern Hemisphere; *glacialis:* North Atlantic; and *japonica:* North Pacific), their validity is questionable (Rice and Scheffer, 1968). In this report we call this cetacean the "southern right whale" with no attempt to evaluate any subspecific rank.

Right whales, so named by whalers because these animals have a high oil content and float when dead, attain a maximum length of 18 m. They may be identified at sea by a characteristic V-shaped blow (Fig. 1A), light-colored horny protuberances on the upper snout which include the bonnet (see Ridewood, 1901, and Matthews, 1938, for detailed descriptions), and by the lack of both a dorsal fin and throat grooves. Compared with other species of great whales, right whales are very rotund (Figs. 1B, 2). Although killing of these animals has been prohibited for many years, the population remains exceedingly small in many regions (Ohsumi et al., 1971; Doi et al., 1971), and the species may be in danger of extinction through overharvesting.

Southern right whales have long been known to breed in bays and other sheltered waters (Scammon, 1874), and recent information indicates the same is true of northern animals (pers. comm. W. E. Schevill, Woods Hole Oceanogr. Inst.). In mid-July, 1969, Gilmore (1969) located 20 to 25 right whales that were courting and presumably mating in Golfo Nuevo, Argentina. On his advice, our attempts to record the vocalizations of this rare cetacean and to observe its behavior were concentrated in this region.

Little is known about vocalizations of the right whale. In discussing this whale's behavior after being harpooned, Scammon (1874) wrote that, "after going a short distance, it frequently stops, or 'brings to,' 'sweeping' as it is said, 'from eye to eye,' and at the same time making a terrific noise called 'bellowing,' this sound is compared to that of a mammoth bull, and adds much to the excitement of the chase and capture." Schevill and Watkins (1962) presented a description and a recording of low-frequency moaning sounds of northern right whales. Cummings and Philippi (1970) reported low-frequency (20-174 Hz)

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pulses and moans tentatively identified as being from northern right whales. These sounds, recorded off Newfoundland in December, 1965, appeared in repetitive, 11-min to 14-min stanzas that were separated by 8 to 10 min. Each stanza was composed of numerous signals appearing in a precise sequence that was repeated in the next stanza. Payne and McVay (1971) described a similar repetitive phenomenon, "songs," from the humpback whale, *Megaptera novaeangliae.*

MATERIAL AND METHODS

This research was largely carried out from the National Science Foundation's research ship, HERO, a 38-m vessel that is managed by the United States Antarctic Research Program. We left Punta Arenas, Chile, on 11 June and proceeded north along the coast as far as Bahía Blanca, Argentina (39°N), returning to Punta Arenas on 16 July. Although other marine mammals were sighted along the coast, we did not see right whales in areas other than Golfo San José, an enclosed bay, 44×20 km, on the north side of the Valdés Peninsula (Fig. 3). There, from 21-24 June and from 1-8 July, we observed about 10 southern right whales, this estimate based on searching the entire Gulf on each of several days.

The deepest area of the Gulf is about 82 m, but most of the whales were observed near shore in less than 37 m. Because the Gulf is protected and shallow, we generally experienced moderate or calm seas of State 2 or less. Air temperatures ranged from 6.1 to 8.3°C. We took bathythermographs in several areas of the Gulf and found isothermal conditions averaging 9.4°C. The ship's small boats occasionally were used for short excursions close to the whales, although we generally kept our distance so as not to intentionally crowd or molest them.

Underwater recordings were made with much the same system described by Calderon and Wenz (1967). Essentially, our recording system consisted of an acceleration-balanced hydrophone, flexible spar buoy, floating cable, calibrating device, sound-level meter, magnetic tape recorder, and monitoring equipment. Instruments used in playing sounds to right whales included a tape recorder (Uher 4200), preamplifier (Bogen BT-35A), high-power amplifier (Optimation PA 250 AC), and an underwater sound projector specially designed by Wesley L. Angeloff of the Naval Undersea Research and Development Center. The frequency response of the playback system was ±5dB from 650 to 3100 Hz, limited by the projector. Response of the receiving system was ±5 dB from 25 to 15000 Hz.

To obtain good recordings of low-frequency mysticete sounds, we have found it best to use a hydrophone that is relatively stationary in the water column and has a good low-frequency response, but not all the way down to 0 Hz. The response must be "rolled-off" in the low frequencies for use under normal sea conditions in order to prevent the reception of low frequency noise. Such a hydrophone is still unsuitable, however, for towing from a moving vessel.

A hydrophone is designed to respond to changing pressure. Pressure changes caused by towing a hydrophone, or those resulting from the vertical excursions so characteristic of moderate or greater sea states, will usually produce excessive low-frequency noise. Coupled with the high sound pressure of low-frequency ambient noise (Wenz, 1962), acceleration and flow noise of this type will easily mask a low-frequency mysticete signal. Experience has taught us that such recordings have very low signal-to-noise ratio. More often, they are rendered useless by intermittent or even continuous blocking of the hydrophone's preamplifier. The dynamic range of response of this preamplifier generally will not accommodate that of the electrical energy from sound pressures imposed on a hydrophone under the above circumstances. The blocking occurs when the preamplifier is overdriven by an input signal that greatly exceeds the maximum input level designed for the amplifier.

To reduce these vertical and horizontal movements, we use an inflatable buoy for flexibility and a 450-m buoyant cable that is let out as fast as the ship drifts. The cable floats by means of a buoyant sheath that is molded around the conductors. In combination with a good-quality hydrophone having low-frequency rolloff and acceleration

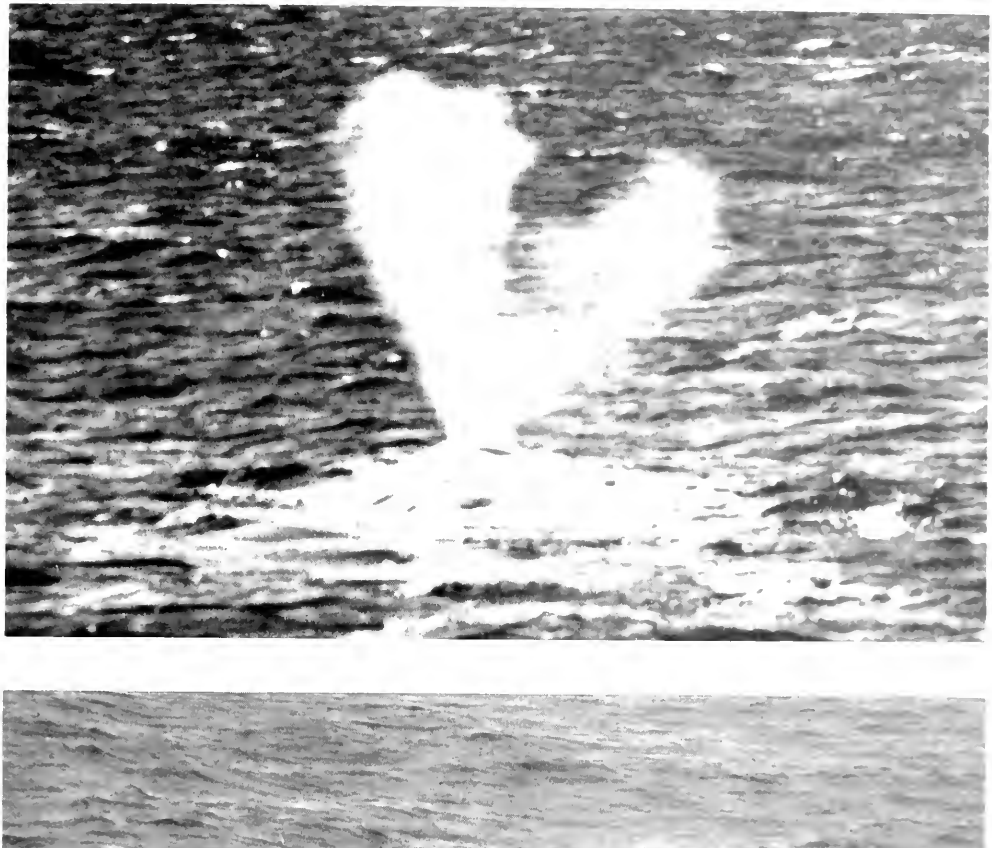

Figure 1. A, V-shaped blow (exhalation) of a southern right whale; B, quartering view.

balancing, this system works well for us most of the time. Other investigators have dealt with the problem in other effective ways (Watkins, 1966).

The right whale sounds were recorded under quiet conditions, with all engines shut off. However, the ship's generator was needed during playback experiments. Most of our recordings were made while the ship was quietly lying to, 0.2 to 1.5 km from the whales. Whenever possible, we kept an account of the whales' behavior during the recordings.

both in a written log and as verbal comments on magnetic tape. Recording times of contacts varied from 10 to 120 min, after which the whales either moved out of an area or we simply stopped the recording.

PHONATIONS AND SOUND PLAYBACK

Southern right whales made several different types of powerful, low-frequency sounds resembling belches, moans, and pulses (Fig. 4, A-D). They also produced a number of miscellaneous low-frequency sounds, too numerous to classify.

By far, the most common sound was a *belch-like* utterance that varied from 0.9 to 2.2 sec in duration and averaged 1.4 sec with principal energy centered at 235 Hz. Although the frequency ranged from 30 Hz to about 2200 Hz, the major portion fell below 500 Hz. *Belch-like* sounds often ended in about a 150-Hz upward frequency shift (Fig. 4A).

The first portion of the *belch-like* sound revealed two to four strong overtones with intervals of about 100 Hz. Sound pressure levels of the *belch-like* sounds were 172 to 187 dB, re 1 $\mu N/m^2$ (=72 to 87 dB, re 1 μbar) at 1 m from the source. Source levels were determined from measurements in a band from 25 to 2500 Hz, thus including all frequencies of *belch-like* sounds. These levels were derived from the absolute received sound pressure levels at the hydrophone (as measured in the laboratory from the calibrated recordings) and the estimated distances of the whales from the hydrophone. The calculations took into account an estimated spreading loss of 6 dB per distance doubled. Attenuation losses were regarded as negligible, because the whales were so close and their calls so low in frequency.

Southern right whales also made moaning sounds of several different kinds. Their moans were classified into two basic types, simple and complex (Fig. 4B). Simple *moans* had sound energy that was confined to a relatively narrow band without appreciable shifts in frequency. Simple *moans* lasted from 0.6 to 1.6 sec. The highest frequency noted was 320 Hz, the lowest was 70 Hz, and the region of principal energy was about 160 Hz. Complex *moans* exhibited a wider band of energy, extensive frequency shifts, overtones, and a longer duration compared to simple *moans.* The highest frequency observed among complex *moans* was 1250 Hz, the lowest was 30 Hz, and the region of principal energy was 235 Hz. The duration of complex *moans* ranged from 0.2 to 4.1 sec.

The third most common of the major types of right whale sounds were *pulses* (Fig. 4C). These sounds extended from 20 to 2100 Hz, and lasted only about 0.06 sec. The pulses frequently occurred in conjunction with a *moan.*

The remaining sounds consisted of numerous, *miscellaneous,* low-frequency sounds that varied in length from 0.3 to 1.3 sec (Fig. 4D). All of these were below 1950 Hz.

We were unable to associate sound production with any specific behavior. The sounds emanated from surfacing as well as from diving whales. They came from single whales or from small groups of two to three individuals. Although some of the right whales may have been feeding and others presumably were courting and perhaps mating, we were unable to associate any sounds with a particular activity. In one instance we were in a small rubber boat, close to a surfacing whale, when the whale produced a thunderous, cavernous, bellow between two exhalations. The sound was clearly audible in air and may have been the same type of sound described by Scammon (1874). This whale was one of two that were consorting near us, in very shallow water.

Extensive recordings were made in the southeast corner of Golfo San José to determine if there was any diurnal periodicity in sound production. These recordings were made for 15 min every 2 hrs, beginning at 1830 on 2 July and ending at 1030 on 4 July. We continued to listen for 10 to 20 min after each recording. Most of the right whale sounds on these recordings occurred close to the three low tides (Table 1), a phenomenon that may have been associated with the appearance of right whales in this area and not necessarily with any daily rhythm in sound production. At other times the whales moved along shore, either toward the west or north. There was no indication of a difference in daytime vs nighttime activity in sound production. In this general vicinity we doubt that whale sounds originating more than about 2 km away would have been detected, because of the limited propagation which could be expected in the presence of the coves, shallow water, and disrupted bottom.

Table 1. Occurrence of right whale sounds on nineteen 15-min recordings.

Time of Day	Date	No. of Sounds	Time of Low Tide
1830	2 July	0	
2030	2 July	0	
2230	2 July	4	
0030	3 July	3	0112
0230	3 July	30	
0430	3 July	0	
0630	3 July	3	
0830	3 July	1	
1040	3 July	0	
1245	3 July	28	1348
1515	3 July	1	
1945	3 July	4	
2150	3 July	0	
2345	3 July	10	
0145	4 July	11	0200
0345	4 July	1	
0545	4 July	6	
0830	4 July	0	
1030	4 July	6[1]	

[1] Five of these 6 sounds occurred in 9 sec and appeared to be a series of sounds from a single right whale.

Our earlier experiments had shown that certain marine mammals appeared to recognize underwater sounds of killer whales. Migrating gray whales, *Eschrichtius robustus*, off southern California, avoided underwater playbacks of killer whale "screams," (Cummings and Thompson, 1971); and playbacks prevented white whales, *Delphinapterus leucas*, from swimming up the Kvichak River in Alaska, where young salmon were migrating to the open sea (Fish and Vania, 1971). Thus, playback experiments provide a new source of information about the behavior of whales in their natural environment. For example, the escape reaction of the gray whale to killer whale sounds can be used to test the hearing capabilities of this species. Also, by playing tapes of certain segments of killer whale signals it may be possible to determine which parts of these signals induce an avoidance reaction.

We played back killer whale "screams" to a group of three southern right whales. HERO was 1.8 km from the beach, in 12 m of water, and all of the whales at first were less than 2 km away. The underwater sound was monitored with a hydrophone. We observed the whales for 15 min before playback. The first transmission consisted of 5 min of random noise, as a control. After 2 min of silence we transmitted a 5-min tone (described by Cummings and Thompson, 1971), also as a control. After 3 min of silence we played back 5 min of prerecorded killer whale sounds. Sound pressure levels of the playbacks, measured in situ with a calibrated system, varied from 159 to 163 dB, re 1 $\mu N/m^2$ at 1 m from the source. Generator noise from the ship measured 134 dB, over the effective bandwidth of the recording system, at the same location and time of the playback experiments.

Only one whale could be seen well enough to observe its reaction. For 15 min before, it had been moving slowly back and forth along the beach, blowing at irregular intervals. There was no obvious change in its behavior when confronted with either the random noise or the tone. When the killer whale "screams" were played back, the right whale appeared to behave as before, except that it frequently raised its head out of the water in a "spyhopping" posture. This behavior consisted of raising the head vertically out of the water with the eyes above the surface. In earlier experiments, Cummings and Thompson (1971) found that gray whales fled a sound source for an appreciable distance and then "spyhopped." They concluded, as did Gilmore (1958), that "spyhopping" was an investigative behavior.

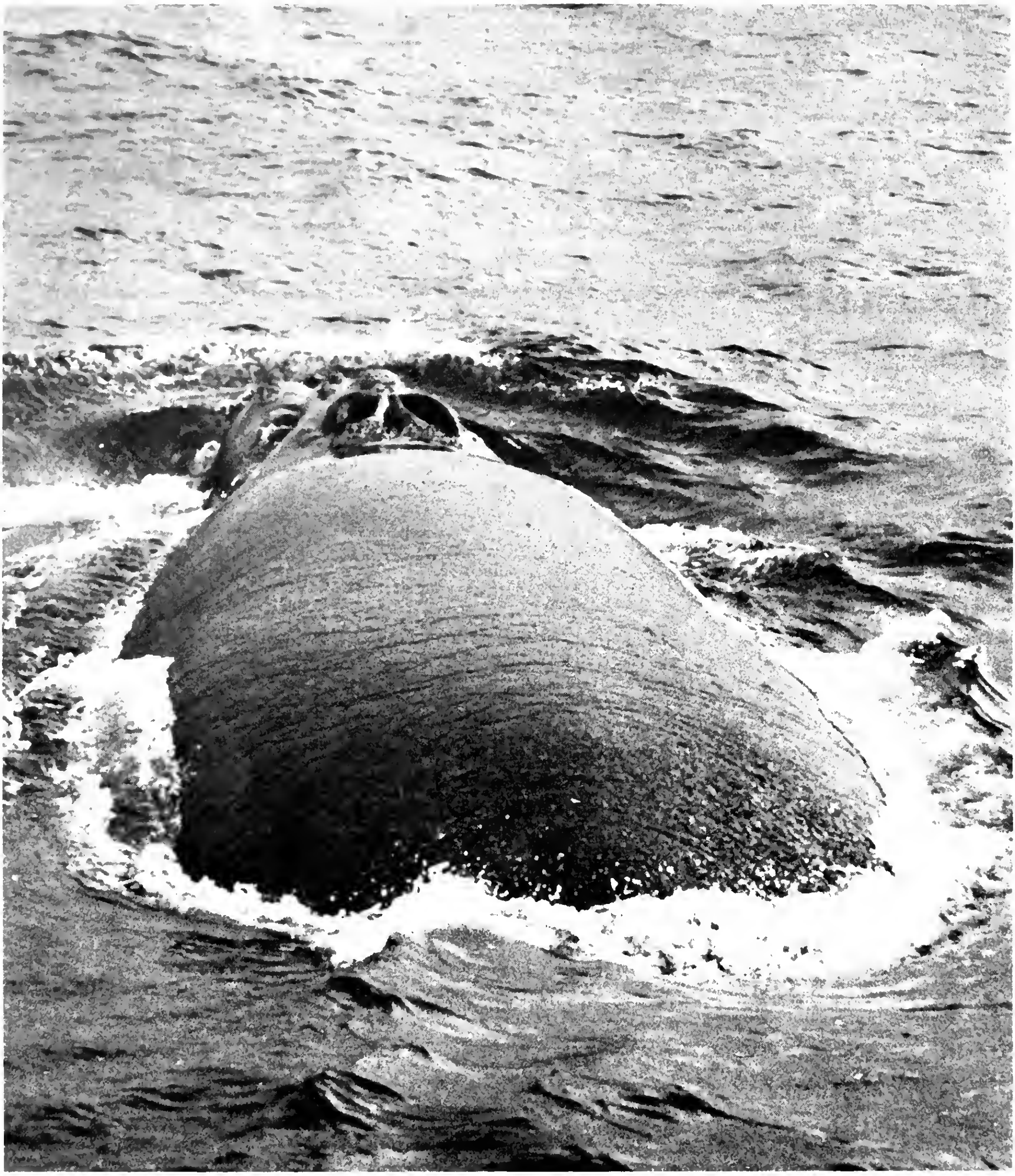

Figure 2. Dorsal view of a southern right whale heading away from the ship. Note the widely separated blow holes and the rotund form of this species.

OTHER BEHAVIOR

On 4 July, in order to make detailed photographs, we accompanied a pair of right whales that apparently had been courting. We had just finished our work at dusk, and they had resumed their rolling antics near the surface, when a group of killer whales appeared off HERO's stern. The killer whales were heading away from the right whales; then, suddenly, they whirled around and swam straight towards the two right whales which were separated by about 45 m.

When the killer whales were about 70 m away, the right whales came together so closely that they appeared to be touching one another. As soon as the killer whales had reached them, the right whales started slashing the water's surface with their flukes and flippers. The right whales were then blowing every 10 to 20 sec, twisting and turning in

Figure 3. Chart showing the Valdés Peninsula of Argentina.

the water as the killer whales swam around them.

We were too far away to see whether or not the killer whales were actually biting the right whales. However, in other respects it appeared to be a full-fledged attack. On at least three occasions, one or the other right whale was on its back, thrashing the water's surface with its flippers and flukes at the same time. At one point, the right whales were completely encircled by the killer whales. The most impressive of the large whales' defensive maneuvers was the way they kept together—rolling, turning, and slashing within such close quarters. In at least two instances, the attacked and the attackers all were below the surface with nothing showing but a slick of whirling water.

We moved to within 0.5 km to record any underwater sounds at short range. However, when the ship had stopped, and we had only been recording for a short time, the killer whales left their prey and swam toward the ship. We counted five killer whales, including one very young animal and apparently four females. The attack had lasted 25 min, and occurred in 30 m of water.

The right whales then moved into very shallow water (7-11 m) where they rolled at the surface, more slowly than before the attack, exhibiting a notable decrease in activity. There were no signs of blood or other evidence of physical harm in the vicinity of the attack.

We recorded for about 3 min before the attack ended and for 15 min afterward, but obtained no underwater sounds from either species, even though both were well within range of the hydrophone. Gray whales and white whales became significantly quieter when confronted with killer whale sounds (Cummings and Thompson, 1971; Fish and Vania, 1971). Nevertheless, even in a recording as short as ours, we expected some phonations from the loquacious killer whales or the right whales. However, under these circum-

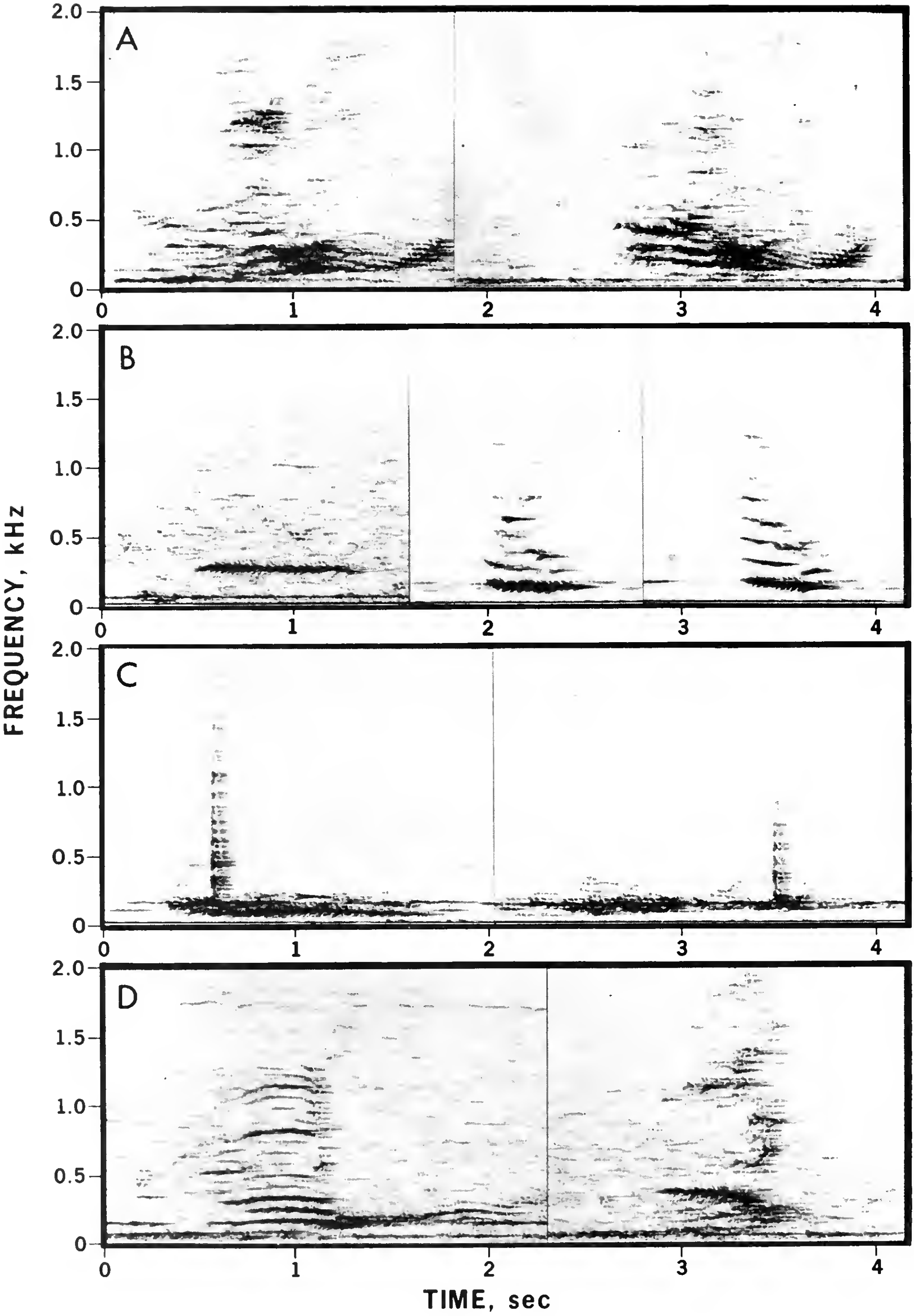

Figure 4. Sonagrams of sounds from southern right whales recorded in Golfo San José, Argentina. Row A, two *belch-like* sounds; Row B, one simple and two complex *moans;* Row C, *pulses* associated with simple *moans;* Row D, two examples of *miscellaneous* sounds. The effective bandwidth of the analyzing filter for these sonagrams was 10 Hz.

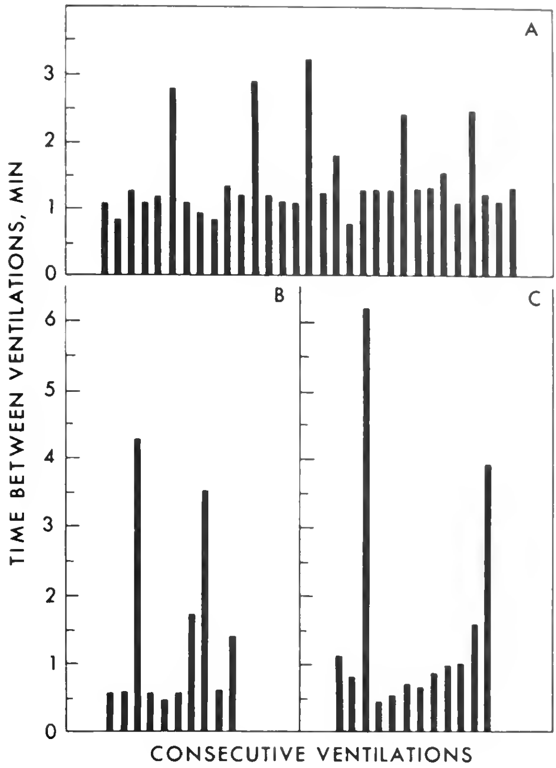

Figure 5. Histogram showing the time duration between consecutive ventilations of the southern right whale. Conditions A, B, and C explained in text.

stances neither may have profited from being noisy (see Schevill, 1964).

We saw killer whales on two other occasions in Golfo San José—a group of three on 1 July, in the mid Gulf, and another group, of six, on 8 July, near the east end. Evidently, these animals are common near Valdés Peninsula as several observers reported seeing them inside and outside of the two gulfs.

Two mussel fishermen, Jorge Enrique Ramirez and Jorge Raul Terenzi, related to us that their Captains, Roque Godio and Calixto Gerez, had also witnessed attacks of killer whales on right whales near the Valdés Peninsula. In one such attack they related that five killer whales "hammered" away at the head region until the right whale opened its mouth. The killer whales then started tearing away at the tongue. The area was colored with blood, the killer whales left, and the right whale was lying motionless at the surface, apparently dead.

Apparent pairs of right whales were seen on several occasions. They spent much time rolling at the water's surface, exposing bellies, backs, flukes and flippers, and occasionally "spyhopping." Members of a pair were often very close to each other, and at times they appeared to be in physical contact. Some of this behavior may have been associated with courtship, but we obtained no evidence of actual mating. Since we could not recognize individual whales, we could not determine if the association was prolonged for more than about half a day.

The "headstanding" posture consisted of holding the flukes upright and out of the water for periods up to 2 min. During this time, the flukes slowly rocked back and forth or from side to side, occasionally arching downward toward the water's surface. "Headstands" only occurred in very shallow depths, and the behavior was more frequent among single whales.

Right whales appeared to have little fear of the ship or the rubber boats. We once ventured as close as 9 m with a rubber boat, and neither one of a consorting pair showed any apprehension. Other observers have had the same experience (Matthews, 1938). Moreover, the two fishermen who were interviewed reported that they once were awakened at night by a right whale rubbing its head on the side of their boat.

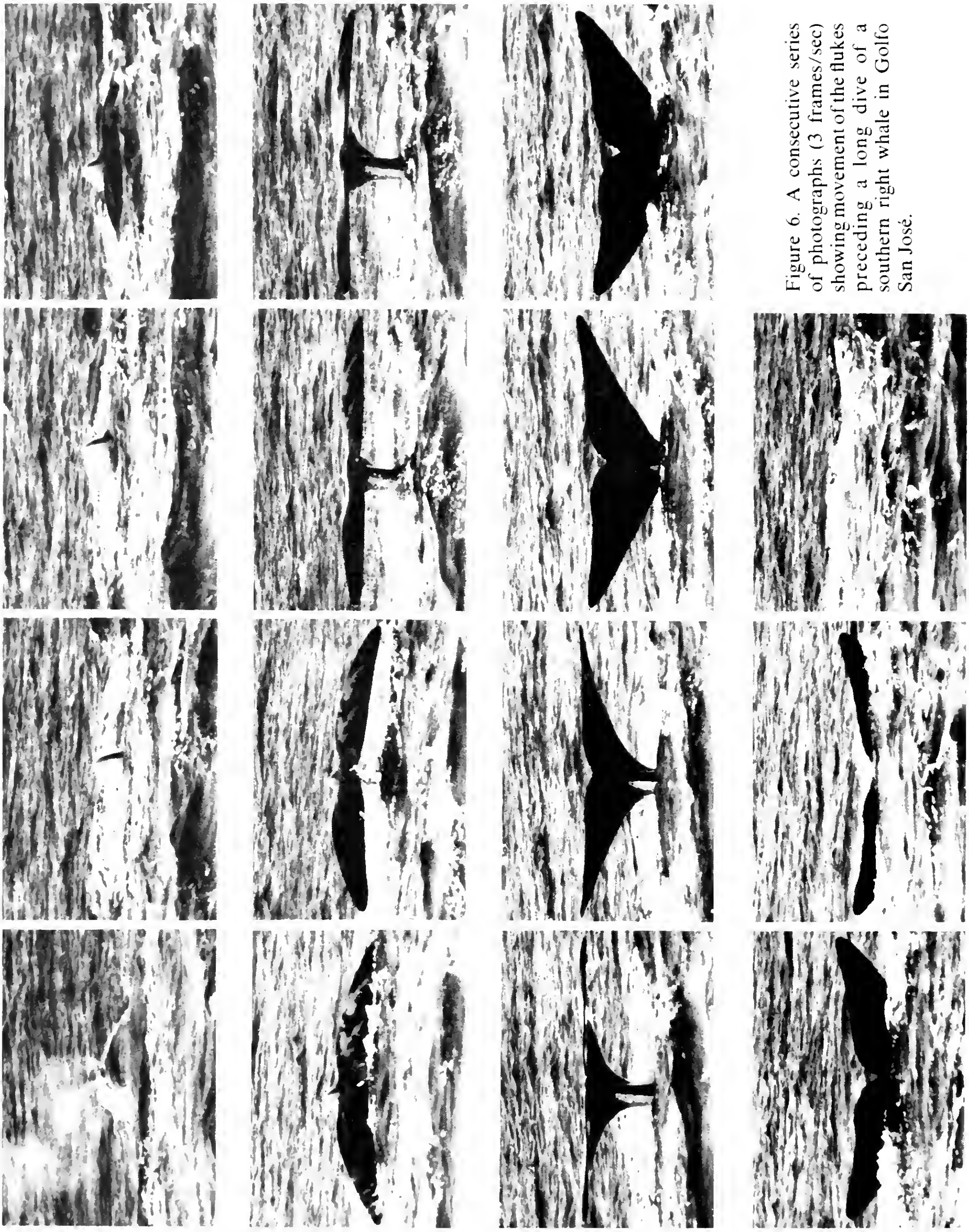

Figure 6. A consecutive series of photographs (3 frames/sec) showing movement of the flukes preceding a long dive of a southern right whale in Golfo San José.

Occasionally, kelp gulls, *Larus dominicanus*, and brown-headed gulls, *L. maculipennis*, landed and rode on whales at the surface. One gull that landed near the blowhole was blown off by the next expiration. The gulls actually pecked at the whales, and possibly were feeding on parasites.

The whales we studied were rather sluggish. Many swam very slowly at the surface for long distances—in one case about 4 km without diving. Apparently, the whales were incapable of speeds greater than about 14.8 km/hr (8 knots). HERO's top speed of 18.5 km/hr (10 knots) easily enabled us to overtake two whales, whereas at 14.8 km/hr the ship could only keep up with them. The two that we accompanied tired more quickly than other mysticete whales we have studied.

The whales' respiratory rate depended upon their activity. Whales swimming slowly at the surface ventilated about once a minute, or once every 2 to 3 min when performing "headstands" in the interim (Fig. 5A). A whale encountered in deeper water as it swam fairly rapidly and directly towards shore breathed irregularly, diving for periods that varied between 0.5 and 4.3 min (Fig. 5B). A whale we had been following stayed down for 6.2 min (Fig. 5C), and at another time its longest dive was 8 min.

Transiting right whales (those that moved along on a direct course without spending much time at the surface) usually displayed their flukes just before an extensive dive (Fig. 6). However, the next to last surfacing was sometimes accompanied by "false fluking," the flukes being drawn up close to but not above the surface.

Our brief stay in Golfo San José did not permit long-term observations of southern right whales, but the following information was obtained from local observers, particularly Santiago Ortega, Perez Macchi, and Carlos Oscar García:

1. Southern right whales occur in Golfo San José and nearby Golfo Nuevo each year. The whales come from the south and begin to show up at Golfo San José in late June, before they appear in Golfo Nuevo. They are most numerous in late August and September. Fewer are present in October, and all disappear during November.
2. The total number of right whales in the Valdés region is unknown, mainly because there is replacement, with some arriving and some departing throughout the season. Up to 30 may be seen at one time in Golfo San José during the peak of the season, and others can be found out to sea, just east of the peninsula. The reporters knew of no other place along the Argentine coast where this species enters bays each year.
3. All observers thought that right whales court and copulate in the two gulfs, but none thought that the young were born there. Small whales, seen in these gulfs, were judged too large to have been born there during a current "whale season."
4. Right whales reportedly have become more numerous in this area in recent years, as is true of elephant seals and sea lions of the region, possibly because the Valdés Peninsula has become a wildlife refuge for land and sea animals. It is illegal to kill marine mammals in either gulf and the area is heavily patrolled.

DISCUSSION

We have recorded underwater sounds from six of the ten species of mysticete whales, and all the sounds have been low-frequency utterances below 3000 Hz. Although there are a few reports of high-frequency phonations in the presence of mysticetes (Perkins, 1966; Poulter, 1968; Beamish and Mitchell, 1971), baleen and toothed whales are markedly different in that low frequency is more typical of the former and high frequency of the latter. A good single hydrophone can yield an acceptable recording of these strong low-frequency signals, when used in calm seas and not towed through the water .

(The single, omnidirectional hydrophone may eventually be replaced by an effective line array of several transducers that could be towed from a drifting or sailing ship. In theory, the advantage of a line array comes from increased signal-to-noise ratio accomplished through directivity toward the sound source. The means for attaining such directivity generally involves proper spacing of the individual hydrophones to phase out the input from directions other than those that are normal to the array's conformation. The extent of spacing is related to the wavelength involved and thus would be considerable in the case of low-frequency mysticete sounds where wavelengths are as long as 120 m or more. A 5-hydrophone array for this frequency would approximate 300 m in length. Unfortunately, present systems such as this are burdensome to use, and they involve complex signal processing. Moreover, the line array is not within the budget of most scientific investigations, nor is one yet available that is relatively noise-free with a high enough response across the entire frequency range of mysticete sounds.)

The *belch-like* sounds and complex *moans* of southern right whales reported here resemble some of the sounds of northern right whales presented by Schevill and Watkins (1962). However, we also found dissimilarities. Differences in behavior, in addition to possible regional differences resulting from evolutionary divergence, could account for such a disparity. Furthermore, our recordings had no evidence of repetitive stanzas that Cummings and Philippi (1970) suggested were from northern right whales. Their recordings were made in the open, deep sea, far from land in an area of the North Atlantic where breeding of northern right whales is unknown. The present recordings were made near shore in a protected, shallow embayment, where whales were courting.

Our earlier sound playback experiments were so successful in producing avoidances by gray whales and white whales that we expected the right whales to behave similarly, especially as they occur in an area where killer whales are known to attack them. Perhaps other playback attempts would produce a more decisive reaction. The source level of the sounds played was less than that used in experiments with gray whales and white whales. Also, the right whales were an appreciable distance from the ship, in very shallow water where we would not expect good propagation. Possibly the playback was not very audible to the whales in this location.

Right whales exhibited the "headstanding" posture mostly in the southeast corner of Golfo San José, in an area reported by fishermen to have dense populations of mussels. Local fishermen believe that this behavior is associated with feeding on mussels, and we support this idea. We observed the whales in water that was shallow enough to allow their heads to touch bottom and their tails to be exposed. In two instances of "headstanding," at a location where the water was only 6 to 8 m deep, the whales either had to be in contact with the bottom or had to arch their whole bodies. It is doubtful that they could have held their tails out of the water for such a long time, with the remainder of the body bent away from the bottom. Moreover, we did not observe "headstanding" in places known to be deeper than the estimated length of the whales. Right whales are positively buoyant, but holding their tails above the surface may make them just heavy enough in water to keep their heads against the bottom.

The idea of mysticetes feeding on mussels is not without precedent. Scammon (1874) reported that gray whales fed on mussels, based upon his having observed the mussels in the whales' "maws." In fact, he included the term "Mussel-digger" in his list of vernacular names for the gray whale.

The Valdés Peninsula area is well suited for studies of marine mammals. In addition to southern right whales and killer whales in Golfo San José, we observed southern sea lions (*Otaria flavescens*), elephant seals (*Mirounga leonina*), bottlenose porpoises (*Tursiops truncatus*), "white-sided" porpoises (*Lagenorhynchus* sp.), and common porpoises (*Delphinus* sp.). To the south, large numbers of sea lions haul out at points Leon, Loma, Pirámida, and Delgada (Fig. 3). There were about 800 sea lions at Punta Pirámida at the time of our visit, and we were told this number would increase to 3000 in December. Natural parks with facilities for visitors have been established at Punta Loma and Punta Pirámida. Some elephant seals occurred with the sea lions at Punta Leon. From our interviews, we learned that elephant seals are most numerous from September to December, especially at Punta Norte. It was in this area, in 1969, that Dr. Raymond M. Gilmore saw 150-200 elephant seals as early as 13 July (pers. comm.). The seals were in three scattered groups, some of them occurring with sea lions.

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EASTERN PACIFIC SNAKE-EELS OF THE GENUS *CALLECHELYS* (APODES: OPHICHTHIDAE)

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EASTERN PACIFIC SNAKE-EELS OF THE GENUS *CALLECHELYS* (APODES: OPHICHTHIDAE)

JOHN E. McCOSKER AND RICHARD H. ROSENBLATT

ABSTRACT.—Three species of *Callechelys* are recognized from the eastern tropical Pacific. Two, **C. eristigmus** and **C. galapagensis**, are described as new. *Callechelys cliffi* Böhlke and Briggs is redescribed from adults. The species differ in coloration, body proportions and vertebral number. *Callechelys cliffi* and **C. eristigmus** n. sp. range from Panama to the Gulf of California, and **C. galapagensis** is known only from the Galapagos Islands. Vertebral number and proportional tail length of the 15 species of *Callechelys* are given. Lineages within the genus are indicated by the presence or absence of a scapula and the condition of the urohyal.

Callechelys is one of the larger genera of the Ophichthidae with fifteen species, mainly limited to the tropics. The species are distinguished on the basis of coloration, vertebral number, and certain body proportions, mainly body depth and preanal distance. Like most snake-eels, members of the genus are sand dwelling and restricted to continental shelf depths. Some of the species attain lengths of one meter. It is not known whether they occupy burrows or wander extensively through the sand. Despite the sand-dwelling habit, many of the species are boldly marked. It is possible that they leave the sand at night, and the color pattern may have significance at these times. Occasional specimens have indeed been taken at the surface under lights at night.

When Storey (1939) published her revision of *Callechelys*, a single specimen, doubtfully referred to *C. marmoratus* or *C. luteus*, was known from the eastern tropical Pacific. Subsequently (Böhlke and Briggs, 1954) another specimen was taken and made the holotype of a new species. The collections at the Scripps Institution of Oceanography, the Department of Zoology, University of California, Los Angeles, and the University of Costa Rica now contain 55 eastern Pacific specimens of *Callechelys.* The recent collections of these eels are attributable to the development of synergized emulsified rotenone products. The use of these products has resulted in rich collections of ophichthid eels and other sand-dwelling fishes not obtainable with powdered derris root. Even with the use of powerful ichthyocides, the collection of these eels is not easy. Either because of a resistance to rotenone or the time involved in transport of rotenone down into the sand, they emerge long after most fishes are dead. Ophichthids may begin to appear after other fishes have been picked up and the station apparently completed.

Our material can be separated into three species, only one of which has been described. *Callechelys cliffi* Böhlke and Briggs, heretofore known only from the just-transformed holotype, can now be described on the basis of adult characters.

MATERIALS AND METHODS

Material used in this study is housed in the following institutions: University of California at Los Angeles, Department of Zoology (UCLA); National Museum of Natural History (USNM); California Academy of Sciences, material previously at Stanford University, (SU); Universidad de Costa Rica, Museo de Zoologia (UCR); and Scripps Institution of Oceanography (SIO). Paratypes of *Callechelys eristigmus* will be deposited at the Academy of Natural Sciences of Philadelphia and the USNM.

All measurements are straight-line measurements, made either with a 300 mm ruler with 0.5 mm gradations (for standard length, trunk length, and tail length) and recorded to the nearest 0.5 mm, or with dial calipers (all other measurements) and recorded to the nearest 0.1 mm. Head length is measured from the snout tip to the posterodorsal margin of the gill opening; trunk length is taken from the end of the head to mid-anus; body

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depth does not include the fin. Counts and proportions in Tables 2-4 include the mean, range, and 95% confidence limits of the mean. Fin ray and vertebral counts (which include the hypural) were made using radiographs or cleared and stained specimens.

Callechelys Kaup, 1856

The genus *Callechelys* may be distinguished from all other ophichthid genera on the basis of the following combination of characters: tip of tail a hard point; pectorals absent; anal fin present; dorsal fin originating on head; head and body laterally compressed; anterior nostrils tubular; a median groove on underside of snout; gill openings low-lateral and converging forward, the isthmus much narrower than the gill opening length; intermaxillary and vomerine teeth present, canine teeth absent.

Key to the Eastern Pacific Species of Callechelys

1a. Tail considerably shorter than head and trunk, 3.25-3.75 in total length. Greatest body depth of adults 3.3-3.5 times in head length. Color pattern of strongly contrasted round dark spots about as long as snout.
Vertebrae 154-163 . . . . *Callechelys eristigmus* n. sp.

1b. Tail almost equal to head and trunk, 2.2-2.4 in total length. Greatest body depth of adults 1.7-2.8 times in head length. Color pattern either solely of numerous small dark spots, or with larger dark oblongs as well, in which case the total vertebrae are 170-174 2

2a. Color pattern of numerous fine spots, not much larger than eye diameter, fins with a distinct white edge. Vertebrate 149-158 . . . . *Callechelys cliffi* Böhlke and Briggs

2b. Color pattern with oblong blotches varying in size between an eye diameter and a snout length along the major axis, fins without a white edging.
Vertebrae 170-174 . . . . *Callechelys galapagensis* n. sp.

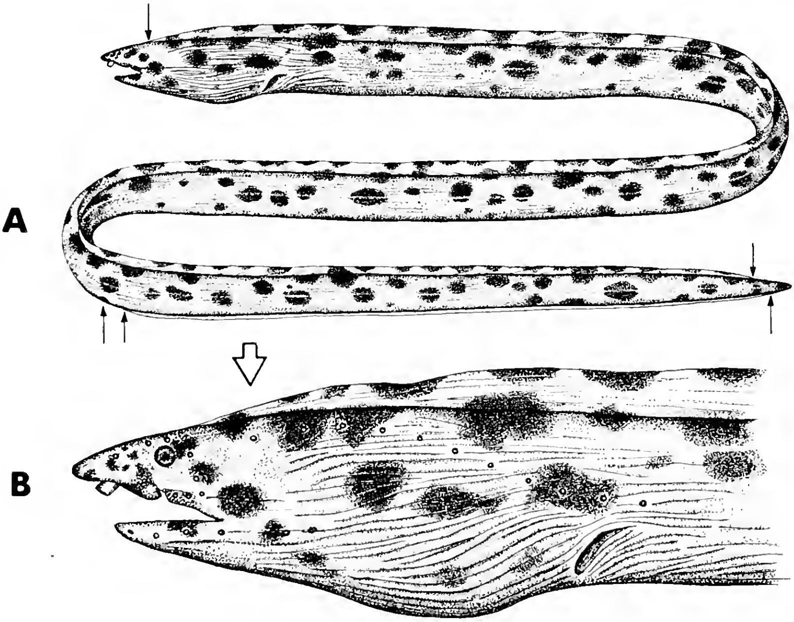

Figure 1a. *Callechelys eristigmus* n. sp., holotype, SIO 65-263, 503.5 mm total length. b. Head region of holotype of *Callechelys eristigmus* n. sp. Arrow indicates true dorsal fin origin.

Callechelys eristigmus n. sp.

Figs. 1, 2a, 5; Tables 1, 2, 5

Description of holotype.—Counts and proportions of the holotype are given in Table 1. Proportions of the holotype and 29 paratypes are given in Table 2.

Body laterally compressed throughout its length, tapering posteriorly to a hard fin-

Table 1. Counts, and proportions in thousandths, of the holotypes of the eastern Pacific species of *Callechelys*.

	C. cliffi	*C. eristigmus*	*C. galapagensis*
Total length (mm)	93.5	503.5	818.0
Total vertebrae	155	159	172
Preanal vertebrae		105	92
(thousandths of total length)			
Head	101	72	74
Trunk	467	628	483
Tail	433	300	444
(thousandths of head length)			
Dorsal fin origin	606	318	312
Snout	170	142	133
Upper jaw	340	285	262
Eye	74	41	46
Interorbital		132	108
Isthmus	74	55	119
Depth behind gill opening	351	345	464
Width behind gill opening		249	265
Depth at anus	330	258	365
Width at anus		195	249
Gill opening length		145	202

less point. Depth behind gill openings 40 times and at anus 51 times in total length; width behind gill openings 55 and at anus 71 in total length. Head and trunk 1.4, head 13.8 in total length. Snout acute, rounded at tip. Lower jaw included, its tip slightly before eye and midway between anterior and posterior nostrils. Eye small, about as long as tube of anterior nostril. Posterior nostrils open into mouth although their distal edges are open to the outer edge of lip, visible externally as a slit. Surface of head, trunk and tail markedly wrinkled (except top and sides of anterior portion of head smooth), with approximately 30 longitudinal grooves on each side of body. Tongue adnate. Branchial basket expanded, supported by 31 pairs of branchiostegals and jugostegalia which broadly overlap along ventral midline. Urohyal simple, a single slender filament posteriorly. Tip of lower jaw and lateral skin folds of upper jaw covered with numerous papillae (Fig. 2a).

Teeth small and pointed (Fig. 2a), uniserial in jaws. An anterior intermaxillary tooth-pair covered by skin folds for most of their length, followed by seven vomerine teeth that become biserial posteriorly.

Preoperculomandibular, temporal, postorbital, suborbital, and supraorbital series of pores present (Fig. 1b). Lateral line beginning on head with 10 pores before gill opening (lateral line canal and pores difficult to discern due to skin folds and waxy precipitate which forms on preserved specimens). Total right lateral line pores of the cleared and stained specimen 140, 92 before anus. Last pore ca. 0.15 head lengths before tail tip. Dorsal fin origin on head, above and slightly behind rictus; median fins end about a snout length before tail tip. Fin rays in dorsal 498, anal 143 (counted from the cleared and stained paratype).

Gill arches and hyoid apparatus of two paratypes removed and stained. First basibranchial ossified, second cartilaginous, third and fourth absent. Hypobranchials 1-2 ossified, third cartilaginous. Ceratobranchials 1-4 ossified, fifth absent. Infrapharyngobranchials 2-3 ossified. Lower pharyngeal teeth in elongate patches on fourth ceratobranchial and extend onto hypobranchial; upper pharyngeal tooth plate smaller, attached to distal ends of epibranchials 2-4 and second infrapharyngobranchial (I_3 of Nelson, 1966).

Color in alcohol mostly cream, overlain with numerous dark spots that extend onto the dorsal fin membrane. Chin, throat, and venter often spotted, but always less so than dorsum. Spots on nape and snout smaller (nearly as large as eye).

Etymology.—From the Greek ερι (eri), intensive participle, and στιγμα (stigma), spot, in reference to the distinctive coloration; regarded as an adjective.

Remarks.—Gulf of California specimens are inseparable on the basis of coloration and morphology from those from southern localities (Cocos Island, Costa Rica, and Panama). The mean vertebral number of specimens from these localities (158.3 for 29 Mexican specimens, 156.1 for 8 specimens from the south) are significantly different (P = .05 by t test); however, the degree of joint non-overlap is not sufficient to warrant taxonomic recognition.

Table 2. *Callechelys eristigmus* n. sp., counts, and proportions in thousandths, of holotype and 29 paratypes; mean, 95% confidence limits of the mean, and range.

	$\overline{X}$	*95% C. L.*	*range*
Total length (mm)			284-1126mm
Vertebrae (37 specimens)	157.9	157.2-158.5	154-163
		(thousandths of total length)	
Head	76	74-77	67-83
Trunk	628	624-632	610-662
Tail	295	291-299	268-309
		(thousandths of head length)	
Dorsal fin origin	327	316-337	250-379
Snout	152	149-155	135-167
Upper jaw	266	260-272	228-289
Eye	46	44-48	34-56
Interorbital	113	109-117	98-140
Left gill opening length	142	136-147	111-168
Isthmus	58	54-61	46-77
Depth behind gill opening	295	286-304	254-345
Depth at anus	250	237-262	172-338
Width behind gill opening	194	185-203	144-272
Width at anus	182	174-190	140-234

Material examined.—Holotype: SIO 65-263, a 503.5 mm adult from Isla San José, Gulf of California, Baja California Sur (24°52′15″N, 110°37′00″W). Taken with rotenone and SCUBA in depths of 20-25 m on a sand and boulder bottom by R. H. Rosenblatt and party on 7 July 1965. Paratypes: all collected using rotenone ichthyocides in relatively shallow water (5-25 m), generally over a sand and rock bottom. Panama-Islas Secas, Isla Cavada, SIO 70-136, 2(359-465); Islas Secas, Isla Seca, 70-140, 2(342-450). Costa Rica-Isla del Coco, UCLA 58-378, 1(361); Isla del Caño, UCR 423-126, 5(216-491). Gulf of California, Baja California Sur—Isla Carmen, UCLA 65-77, 3(325-420), SIO 65-299, 2(328-357); Isla Santa Catalina, SIO 65-337, 2(411-469); Isla Santa Cruz, SIO 65-342, 2(408-420), SIO 65-354, 2(431-498, the smaller specimen cleared and stained); Punta Nopolo, SIO 65-270, 1(564); Isla San José, SIO 65-263, 1(323, collected with the holotype), SIO 65-260, 1(372); Isla Espíritu Santo, SIO 61-277, 1(1126); Bahía de los Lobos, SIO 61-279, 1(418); Isla Ceralbo, SIO 61-256, 1(494), SIO 61-259, 2(399-493); Bahía de Palmas, UCLA 59-249, 1(285), UCLA 59-251, 2(284-538); Punta Pescadero, SIO 61-252, 2(317-557); Punta Los Frailes, SIO 61-239, 1(425); El Tule Ranch, east of Cabo San Lucas, SIO 65-185, 3(363-552).

Callechelys galapagensis, n. sp.

Figs. 2b, 3, 5; Tables 1, 3, 5

Callechelys marmoratus, nec Bleeker, Fowler, 1932: 3. Fowler, 1938: 251.
Callechelys luteus, nec Synder, Storey, 1939: 69.

Description of holotype.—Counts and proportions of the holotype are given in Table 1. Proportions of the holotype and 3 paratypes are given in Table 3.

Body laterally compressed throughout its length, tapering posteriorly to a hard finless point. Depth behind gill openings 29 times and at anus 37 in total length; width behind gill openings 51 and at anus 54.5 in total length. Head and trunk 1.8, head 13.5 in total length. Snout acute, rounded at tip. Lower jaw included, its tip closer to base of anterior nostrils than to a vertical from anterior margin of eye. Eye small, about equal in length to tube of anterior nostril. Posterior nostrils open into mouth, visible externally as a slit. Surface of head and trunk markedly wrinkled (except top and sides of anterior por-

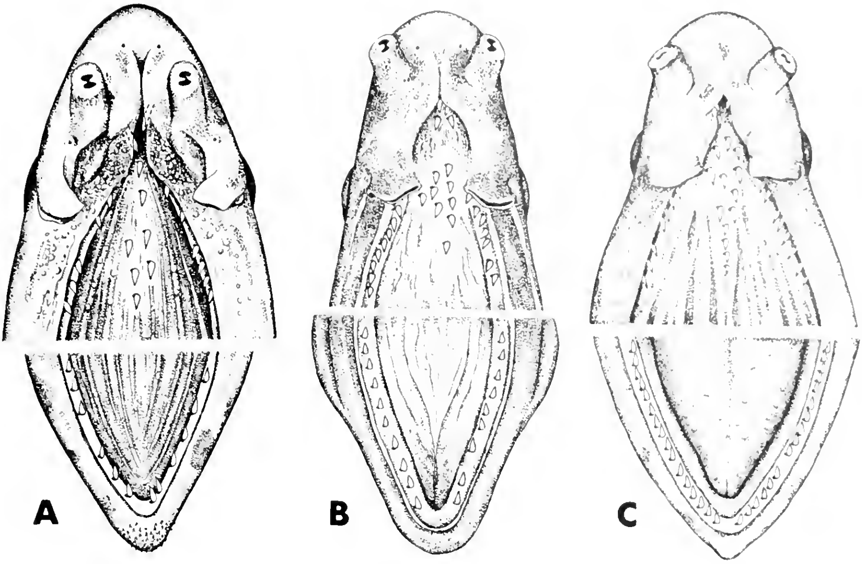

Figure 2a. Dentition of holotype of *Callechelys eristigmus*. b. *Callechelys galapagensis*, n. sp., a paratype, UCLA 67-33. c. *Callechelys cliffi*, SIO 62-42.

tion of head smooth) as in *C. eristigmus*, but becoming smoother posteriorly. Tongue adnate. Branchial basket expanded, supported by 26 pairs of branchiostegals and jugostegalia which broadly overlap along ventral midline. Urohyal split into two slender filaments for about 90% of its length. Tip of lower jaw and lateral skin folds of upper jaw papillose, as in *C. eristigmus.*

Teeth small and pointed (Fig. 2b). Intermaxillary teeth comprising two or three pairs partially covered by skin folds, largest anteriorly, followed by from four to six pairs of biserial vomerine teeth. Lower jaw teeth uniserial and small, about 10 to 15 on each side.

Preoperculomandibular, temporal, postorbital, suborbital, and supraorbital series of head pores present, not unlike those of *C. eristigmus* (Fig. 1b) in number and position. Lateral line (of the left side of holotype) beginning on head, with 10 pores before gill opening, 87 to anus, and 157 total pores ending 0.2 head lengths from tail tip. Dorsal fin origin on head, above and slightly behind rictus; median fins ending less than a snout

Table 3. ***Callechelys galapagensis*** n. sp., counts, and proportions in thousandths, of holotype and 3 paratypes; mean, and 95% confidence limits of the mean, and range.

	$\overline{X}$	*95% C. L.*	*range*
Total length (mm)			248-818 mm
Vertebrae	172	169.4-174.6	170-174
		(thousandths of total length)	
Head	76	67-85	69-82
Trunk	478	456-499	463-494
Tail	444	432-456	437-455
		(thousandths of head length)	
Dorsal fin origin	325	293-357	312-355
Snout	132	127-138	128-137
Upper jaw	248	194-302	197-269
Eye	55	42-68	46-66
Interorbital	103	80-126	81-112
Left gill opening length	178	115-240	127-214
Isthmus	109	71-148	76-133
Depth behind gill opening	418	293-544	349-506
Depth at anus	352	226-479	289-460
Width behind gill opening	252	170-334	203-319
Width at anus	226	158-293	178-272

length before tail tip. Fin rays in dorsal 520, anal 230 (counted from a radiograph of holotype).

Gill arches and hyoid apparatus of the largest paratype (UCLA 64-40) removed and stained. Configuration and condition of the gill arch members like that of *C. eristigmus* except that the upper and lower pharyngeal tooth plates are nearly equal in length, and oblong rather than elongate (the lower pharyngeal plate of *C. eristigmus* is larger and more slender than the upper).

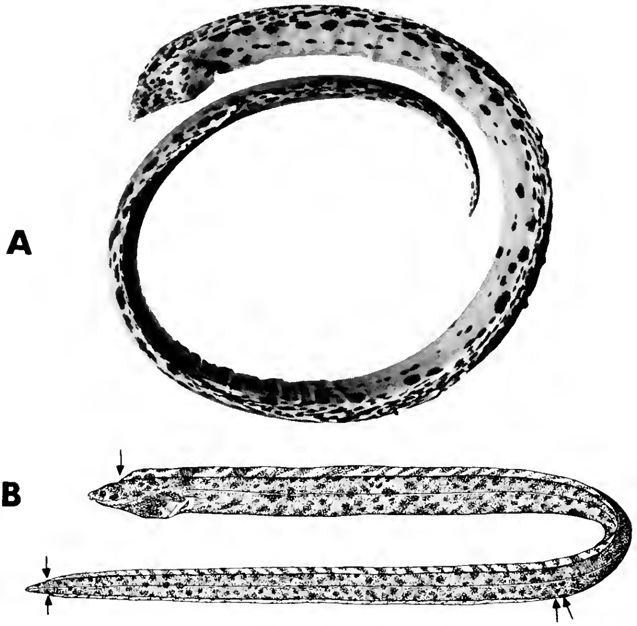

Figure 3a. *Callechelys galapagensis* n. sp., paratype, UCLA 64-40, 767 mm total length. b. *Callechelys galapagensis* n. sp., a darkly colored paratype, UCLA 67-33, 248 mm total length.

Color in alcohol mostly cream, overlain with numerous dark oblong markings that vary in length from the size of the eye to the length of the upper jaw. These spots extend onto median fins and become densely aggregated on chin and top and sides of head. Ventral and dorsal surfaces more spotted than flanks, which have a row of small spots unevenly distributed along midline. The smallest paratype (Fig. 3b) differs from the other types in having a chocolate brown background coloration, although the spotting is similar.

Etymology.—Named *galapagensis*, for the locality at which all known specimens were collected.

Material examined.—Holotype: SIO 72-1, formerly UCLA 64-39, an 818 mm adult from the Galapagos Islands, Isla Santa Cruz, north shore, off small cove. Taken with Chemfish and SCUBA over a sand, rock, and sparse coral bottom in ten meters by B. W. Walker and E. S. Hobson on 24 February 1964. Paratypes: all from the Galapagos Islands. USNM 89728, 1(312), Isla Santa Maria, Black Beach Anchorage. UCLA 64-40, 1(767), Isla Santa Cruz, North Coast. UCLA 67-33, 1(248), Isla San Salvador, James Bay.

Callechelys cliffi Böhlke and Briggs

Figs. 2c, 4, 5; Tables 1, 4, 5

Callechelys cliffi Böhlke and Briggs, 1954: 275. Fraile Bay (Los Frailes), Gulf of California.

Description.—Counts and proportions of the holotype are given in Table 1. Proportions of several juvenile and adult specimens are given in Table 4. The following description is based on the adult specimens.

Body laterally compressed throughout its length, tapering posteriorly to a point. Depth behind gill openings 23 times and at anus 27 in total length; width behind gill openings 43.5 and at anus 45 in total length. Head and trunk 1.7, head 10.7 in total length. Snout acute, rounded at tip. Lower jaw included, tip reaches level of anterior nostrils. Eye small, about as long as anterior nostril base. Posterior nostrils open into mouth, visible externally as a slit. Surface of head, trunk, and tail wrinkled (except top and sides of anterior portion of head smooth), becoming smoother on flanks posteriorly, as in *C. galapagensis*. Tongue adnate. Branchial basket expanded, supported by 26 pairs of branchiostegals and jugostegalia which broadly overlap along ventral midline. Urohyal split into two slender filaments for ca. 80% of its length. Tip of lower jaw and anterolateral skin folds of upper jaw lightly papillose (Fig. 2c).

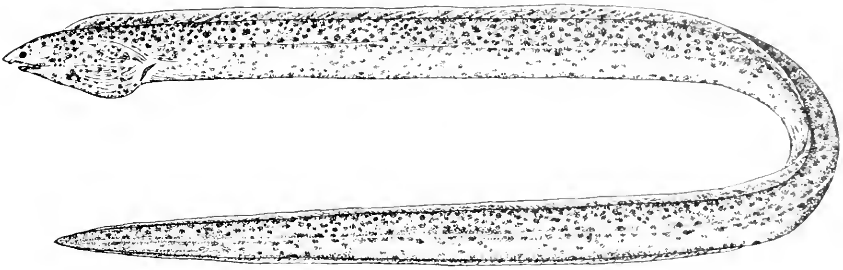

Figure 4. Adult of *Callechelys cliffi*, SIO 62-42, 455 mm total length.

Teeth small and pointed (Fig. 2c) uniserial in jaws. Two anterior pairs of intermaxillary teeth hidden by skin folds of underside of snout, followed by a patch of six to seven intermaxillary teeth joined posteriorly to uniserial vomerine row.

Preoperculomandibular, temporal, postorbital, and supraorbital pore series present. Lateral line beginning on head with ten pores before gill opening, 86 to anus, and 151 total pores, ending 0.3 head lengths from tail tip (SIO 62-42). Dorsal fin origin on head, above and slightly behind rictus; median fins end about a snout length before tail tip. Fin rays in dorsal 457, anal 205 (from radiograph of UCLA 63-45).

Gill arches and hyoid apparatus of two specimens (SIO 61-247, 65-281) removed and stained. The configuration and condition of the gill arch members is similar to that of *C. galapagensis* (see description) in that the upper and lower pharyngeal tooth plates are nearly equal in length and oblong, rather than elongate and unequal as in *C. eristigmus*.

Color in alcohol tan, overlain with numerous fine brown spots on body and fins. Median fins margined in white. Tips of snout, lower jaw, and tail cream-colored.

Table 4. *Callechelys cliffi* Böhlke and Briggs, counts, and proportions in thousandths, mean, 95% confidence limits of the mean, and range.

	$\overline{X}$	*95% C. L.*	*range*	*n*
Total length (mm)			97.5-455 mm	8
			154-455 mm	5
Vertebrae	154.9	153.4-156.5	149-158	14
	(thousandths of total length)			
Head	93	84-101	77-108	8
Trunk	474	459-488	441-496	8
Tail	434	426-442	418-450	8
	(thousandths of head length)			
Dorsal fin origin	413	351-474	363-480	5
Snout	142	123-161	121-170	5
Upper jaw	311	294-329	294-340	5
Eye	61	54-68	53-74	5
Isthmus	97	79-115	74-115	5
Depth behind gill opening	494	416-573	351-568	5
Depth at anus	429	370-488	330-502	5

Remarks.—Our material includes a single collection (SIO 67-40) which contains a series of individuals from newly settled juveniles to adults. This series displays the juvenile to adult color transformation and was compared with the holotype of *C. cliffi*. Smaller specimens in the series were identical with the type in coloration, pore pattern, and morphometry.

Material examined.—Mexico, Baja California Sur, Golfo de California—Bahía Los Frailes, SU 47521, 1(93.5 mm), the holotype. Punta Pulmo, SIO 61-247, 1(218). Punta San Telmo, SIO 65-281, 1(298). Buena Vista, UCLA 63-45, 1(382). Mexico, Nayarit, Bahía de Banderas, SIO 62-42, 1(455). Panama, Archipielago de las Perlas, Isla Saboga, SIO 67-40, 9(80-154).

DISCUSSION

We recognize 15 tropical and subtropical species in the genus *Callechelys. C. guichenoti* Kaup, the generic type, is considered by us to be a junior synonym of *C. marmoratus* (Bleeker, 1853). Kaup's (1856) description and Pellegrin's (1912) redescription of the type of *C. guichenoti*, a 475 mm specimen from Tahiti, do not separate it from adults of *C. marmoratus*. Furthermore, recent extensive collecting efforts in Tahiti and the Southern Caroline Archipelago (by the Vanderbilt Foundation, J. E. Randall, and others) using improved ichthyocides have obtained numerous specimens of *C. marmoratus* and *C. melanotaenius* Bleeker. It is highly unlikely that *C. guichenoti*, if indeed distinct, would not have been taken in the various habitats sampled. Smith (1957: 838; 1962) also suspected *C. guichenoti* to be a synonym of *C. marmoratus*, but was incorrect in considering *C. luteus* Snyder conspecific with *C. marmoratus*.

Table 5. Vertebral number and tail length of the species of *Callechelys.*

	Tail/SL	*Vertebrae*[1]	*Location*	*Source*
C. bilinearis Kanazawa	.364[2]	162	West Atlantic	Kanazawa, 1952; this study
C. bitaeniatus (Peters)	.385		E. Africa, Mombasa	Storey, 1939
C. cliffi Böhlke & Briggs	.434	155	Eastern Pacific	this study
C. eristigmus sp. nov.	.295	158	Eastern Pacific	this study
C. galapagensis sp. nov.	.444	172	Galapagos Is.	this study
C. holochromus (Ginsburg)	.333		Gulf of Mexico	Ginsburg, 1951
C. leucopterus (Cadenat)	.431-.475	164	Eastern Atlantic	Blache and Cadenat, 1971
C. luteus Snyder	.415	213	Hawaii	Gosline, 1951
C. marmoratus (Bleeker)	.345[2]	180	West Pacific	Storey, 1939; this study
C. melanotaenius Bleeker	.282[2]	203	West Pacific	Storey, 1939; this study
C. muraena Jordan & Evermann	.385[2]	141[2]	West Atlantic	Storey, 1939; this study
C. nebulosus Smith	.408	159	Red Sea	this study
C. perryae Storey	.328	178[2]	Gulf of Mexico	Storey, 1939; Blache and Cadenat, 1971
C. perryae Storey	.310	179	Eastern Atlantic	Blache and Cadenat, 1971
C. springeri (Ginsburg)	.350	170[2]	Gulf of Mexico	Ginsburg 1951
C. striatus Smith	.304	192	Red Sea	this study

[1] Rounded mean value

[2] Type specimen

Characters currently used for species separation in this genus include the coloration, body depth, preanal length, and vertebral number (Table 5). The angle of the gill opening, sometimes used as a character (Storey 1939), is of little use, because of variability. The species most closely related to the eastern Pacific species *C. cliffi* and *C. eristigmus* appear to be *C. muraena* Jordan and Evermann and *C. perryae* Storey, respectively. The remarkable similarity of each species pair is evidenced in the body depth and taper, coloration, preanal length, and certain osteological characters. The members of each pair are, however, separable by vertebral number. A preliminary osteological study of several species of *Callechelys* and closely related genera has revealed trenchant differences in the urohyal and pectoral girdle. The urohyal is either a simple slender filament (in *C. eristigmus, C. marmoratus*, and *C. melanotaenius*) or is split posteriorly into two slender diver-

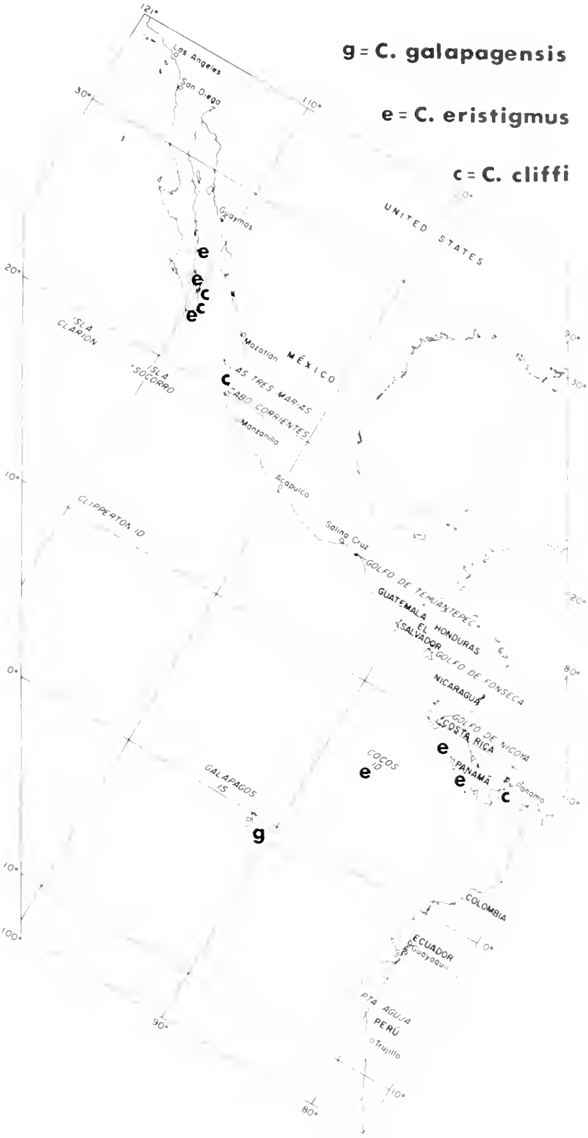

Figure 5. Distribution of the eastern Pacific species of *Callechelys*.

gent rays (in *C. cliffi*, *C. galapagensis*, and *C. muraena*). The pectoral girdle, as in most ophichthids that lack pectoral fins, is quite reduced, consisting of a slender cleithrum, supracleithrum, and small rodlike coracoid and scapula (?). Certain species of *Callechelys* (*C. eristigmus*, *C. marmoratus*, and *C. melanotaenius*) however, have lost the scapula, whereas others (*C. bilinearis*, *C. cliffi*, *C. galapagensis*, *C. luteus*, *C. muraena*, and *C. nebulosus*) have retained it. The retention of the scapula, along with the simple urohyal, may represent the generalized condition in *Callechelys*. The similarity of the New World forms, as well as their dissimilarity to other Indo-west Pacific species, strongly suggests a common ancestry prior to the closure of the middle American seaway. *C. galapagensis* appears most similar to the central Pacific *C. luteus* Snyder, but differs in having fewer vertebrae, a deeper body, and a spotted anal fin. (Snyder (1904: 517) described the type as having "fins colored like the body"; our specimen, SIO 68-497, 1038 mm, has an unspotted anal fin.) None of the three Atlantic species shows a close resemblance to *C. galapagensis*. On the basis of present evidence we therefore suggest that the three eastern

Pacific species of *Callechelys* have had two separate histories, with one species arising from a Pacific ancestor and the other two with a common New World ancestry.

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PALEONTOLOGY AND PALEOECOLOGY OF THE SAN DIEGO FORMATION IN NORTHWESTERN BAJA CALIFORNIA

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ROBERT W. ROWLAND

ABSTRACT—More than 100 species of invertebrate fossils were collected from gray sandstones of the San Diego Formation (Pliocene) exposed along the coast of northwestern Baja California. Paleoecologic evaluation of the extant species and associated sediments suggests that the fauna accumulated at shallow subtidal depths near a submarine bank or low rocky headland. This feature, which probably formed the southern flank of the Pliocene San Diego embayment, was composed of a Miocene volcanic formation which underlies the fossiliferous strata.

The light-colored sandstone underlying the southwestern portion of San Diego County, California, is known as the San Diego Formation (Arnold and Arnold, 1902). Extinct species indicate a Pliocene age for the formation and recent workers (Zullo, 1969; Wicander, 1970) regard it as late Pliocene. The formation extends into Baja California, where highway construction exposed a number of fossiliferous sites (Fig. 1). This paper describes the fauna of these beds and presents a paleoenvironmental reconstruction of the area using geological and paleontological evidence.

The geology of the Tijuana-Rosarito Beach area was mapped and described by Minch (1967). In this area the San Diego Formation is underlain by a thick sequence of basalt, tuff, sandstone and breccia. Minch named these rocks the Rosarito Beach Formation; their age is middle Miocene (Hawkins, 1970; Minch, et al., 1970). Minch (1967) recognized two members in the San Diego Formation. The lower unit is composed of light gray to light brown sandstone containing several discontinuous lenses of conglomeratic sand. The upper member is a yellowish brown coarse sandstone containing beds of cobble conglomerate. Overlying the San Diego Formation and capping the higher mesas is a reddish brown sandstone which Minch referred to the Lindavista Formation. Fossiliferous sand of Late Pleistocene age occurs on the low terraces along the coast (Valentine and Rowland, 1969).

Structurally the area consists of a series of elongate fault blocks which parallel the Pacific coast. These blocks are separated by high angle normal faults. Movement on the major faults has produced a west-tipped stepped structure and has separated the fossiliferous strata of the San Diego Formation into two belts. One lies within ¾ mile of the ocean, and the other, less clearly defined, more than 1¼ miles inland. The relationship between the two belts is not clear, for no stratum can be correlated in both deposits.

Three collections of fossils (A-239, A-241, A-249) were made from the inland belt. Locality A-252 is at the north end of the coastal belt, in the terrace which forms a base for the Pleistocene deposits of the Tijuana Playas area. The remaining localities are exposed in coastal bluffs and canyons from the International Border south to Rosarito Beach. Localities A-240, A-241, A-246, A-248, A-250 and A-251 are in basal conglomerates less than 20 feet above the base of the formation. Locality A-245 is 104 feet above locality A-240. The remaining localities are not in local superposition and their relative ages remain uncertain. Complete descriptions of the fossil localities have been presented elsewhere (Rowland, 1968).

METHODS

Thirteen localities were sampled semi-quantitatively. At each locality approximately 1.5 cubic feet of fossiliferous matrix was collected. The number of specimens of each species in this sample is recorded in Table 1. The matrix was used for grain size analysis. The weight of sediment remaining on each sieve (from -3ϕ to $+4\ 1/2\phi$) was calculated as a percent of

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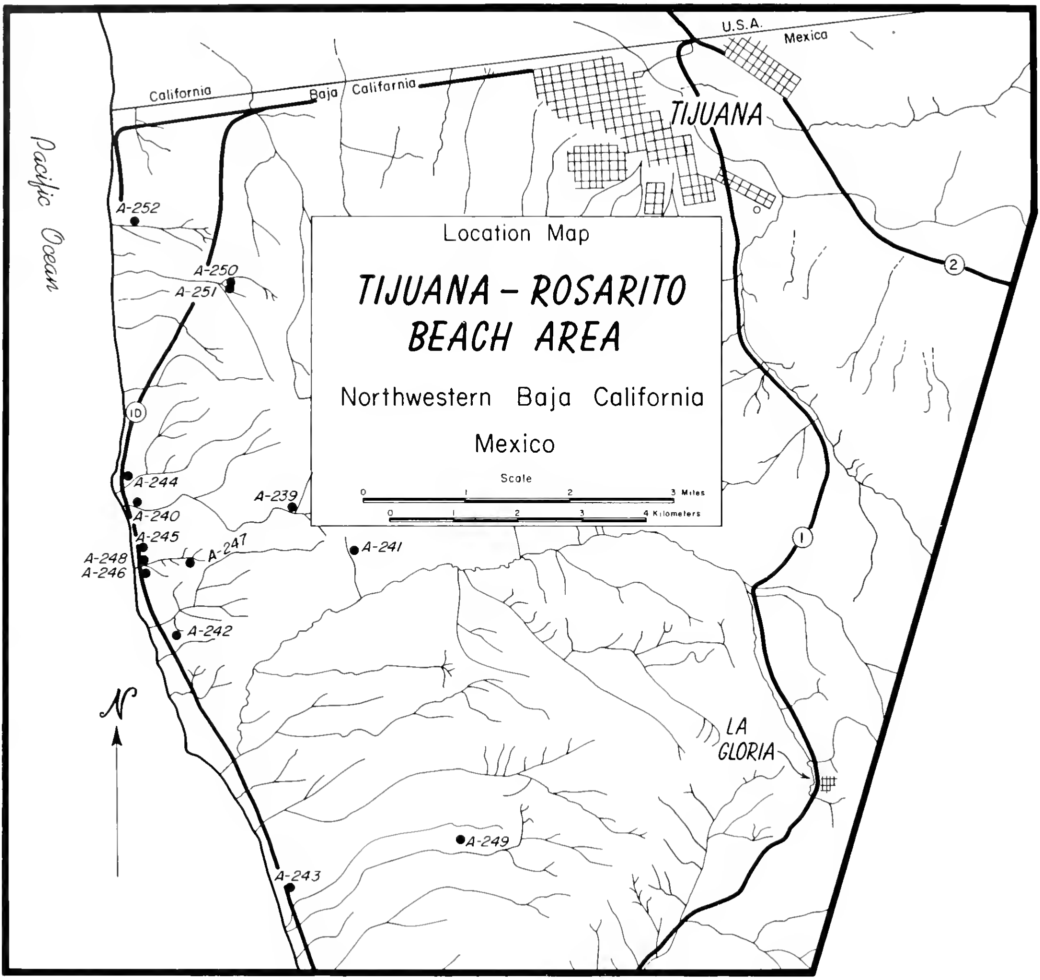

Figure 1. Map showing location of fossil localities sampled.

the total sample weight, then plotted against sieve size to produce size frequency histograms (Fig. 2). The collected material is deposited in the Geology Department, University of California, Davis.

Terminology for environmental parameters of wave exposure and water depth follows that of Valentine (1961: Fig. 2). The littoral zone is delineated by the high and low tide lines and the inner sublittoral zone by the low tide line and the 25 fathom contour line. Depth range, geographic range, and substrate requirements for the extant species were compiled from Grant and Gale (1931), Keen (1971), Morris (1966), Ricketts and Calvin (1968) and Valentine (1958).

RESULTS AND DISCUSSION

Megafossils collected are listed in Table 1. Extinct species form a significant portion of the fauna and are important in confirming the age of the strata. Common extinct species are: *Dendraster ashleyi* forma *ynezensis*, *Acanthina emersoni*, *Nassarius grammatus*, *Terebra martini*, *Ostrea erici*, *Anadara trilineata*, *Patinopecten dilleri*, *Patinopecten healyi*, and *Chlamys parmeleei*. These species are characteristic of Pliocene strata in the San Diego, Ventura, and Santa Maria areas of California. The exact age of the San Diego Formation, to which the deposits in northwestern Baja California are assigned, is not known. The uncertainty arises partly from problems associated with establishing the Pliocene-Pleistocene boundary in the marine strata of California (see Bandy and Wilcoxon, 1970) and from com-

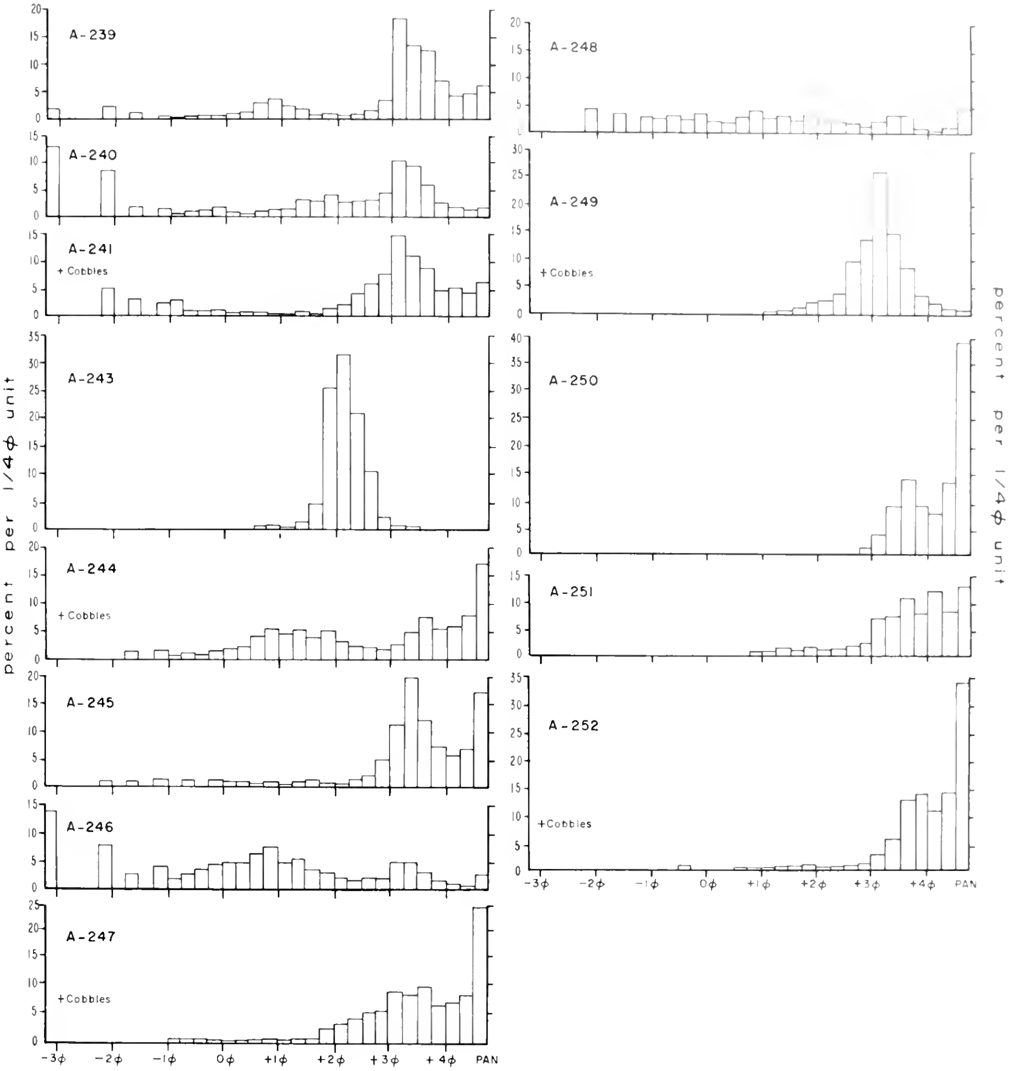

Figure 2. Size-frequency histograms of the sedimentary matrix at each fossil locality.

plexities within the formation itself. All the marine Pliocene deposits of western San Diego County are referred to the San Diego Formation, though the relationships between the strata of different areas are presently undeterminable. For example, Mission Valley and the Rose Canyon fault separate the San Diego Mesa with its Pliocene faunas from the Pliocene strata at Pacific Beach. These deposits may represent different times of deposition as discussed by Woodring and Bramlette (1950: 104-107), and surely they represent different depositional environments. The Pacific Beach fauna is indicative of a sand-cobble, open coast environment, whereas quiet water faunas characterize the San Diego Mesa deposits. The collections at hand contain faunas whose components show affiliation to both of these biostratigraphic zones.

The fauna contains species representative of three environments. *Calliostoma, Ocenebra, Acanthina, Tegula, Thais, Ostrea, Hinnites,* and *Architectonia* indicate a littoral-sublittoral rocky coast area. Representatives of this group occur at 11 localities (see Tables 1 and 2). *Tivela, Dentalium, Cadulus, Dendraster,* and certain lucinid bivalves suggest a sublittoral open coast environment with a sand substrate. This element is less abundant and occurs at four localities. Species of *Nuculana, Panope, Spisula, Tresus,* and *Nassarius* are predominant elements of a large fauna indicative of a fine mud or mud-sand substrate at

Table 1. Fossils from the San Diego formation in northwestern Baja California

Species	University of California Davis Fossil Localities A series												
	239	240	241	243	244	245	246	247	248	249	250	251	252
Anthozoa													
Astrangia cf. *A. insignificata* Nomland, 1916									4				
Balanophyllia elegans Verrill, 1846									1				
Gastropoda													
Haliotis fulgens Philippi, 1845				3									
Diodora aff. *D. inaequalis* (Sowerby, 1835)												1	
Calliostoma costatum (Martyn, 1784)					3	2	9		10			9	2
Calliostoma gemmulatum Carpenter, 1864							1		1			1	
Calliostoma kerri Arnold, 1910		3											
Tegula funebralis (A. Adams, 1854)		3	1										
Tegula gallina (Forbes, 1850)							1						
Astraea inaequalis (Martyn, 1874)										1			
Astraea undosa (Wood, 1828)													1
Eulima aff. *E. rutila* Carpenter, 1864												2	
Epitonium bellastriatum (Carpenter, 1864)							1					1	
Opalia varicostatum Stearns, 1875							2						
Tachyrhynchus erosus forma *major* Dall, 1919									1				
Turritella cooperi Carpenter, 1864	50				3		1	6	15			1	
Turritella gonostoma forma *hemphilli* Merriam, 1941									1				
Architectonica nobilis forma *discus* Grant and Gale, 1931												1	
Cerithidea californica (Haldeman, 1840)		1							1				
Calyptraea mamillaris Broderip, 1834		5											
Trochita radians Lamarck, 1822												6	
Crepidula onyx Sowerby, 1824					6		1	1				4	
Lunatia lewisii (Gould, 1847)							30		5			8	3
Polinices recluzianus (Deshayes, 1839)	10	1			25	2		20				25	3
Trivia sanguinea (Sowerby, 1832)							1					1	
Fusitriton oregonensis (Redfield, 1846)							1						5
Bursa californica Hinds, 1843													1
? *Ceratostoma foliata* (Gmelin, 1845)								1					
Jaton festiva (Hinds, 1844)									1			1	
Ocenebra aff. *O. fraseri* (Oldroyd, 1920)													1
Acanthina emersoni Hertlein and Allison, 1959		6	2	4						7			
Thais emarginata (Deshayes, 1839)		7	15			1	2						
Thais lamellosa (Gmelin, 1790)										4			
Cantharus aff. *C. ringens* (Reeve, 1846)												1	
Kelletia aff. *K. kelletii* (Forbes, 1850)												1	
Amphissa cf. *A. reticulata* Dall, 1916					1								
Mitrella gausapata (Gould, 1854)					5							15	
Nassarius californianus (Conrad, 1856)					10								
Nassarius grammatus (Dall, 1917)	1				c17		12	21	5			25	4
Nassarius mendicus forma *indisputabilis* (Oldroyd, 1927)												5	
Nassarius cf. *N. perpinguis* (Hinds, 1844)								3					
Barbarofusus barbarensis (Trask, 1855)					5		8	4					
Psephaea oregonensis (Dall, 1907)													1
Olivella biplicata (Sowerby, 1825)	6		48				1						
Olivella pedroana (Conrad, 1855)	3				9			1					
Cancellaria fugleri (Arnold, 1907)													1
Cancellaria tritonidea Gabb, 1866													2
Cancellaria rapa (Nomland, 1919)								c12				1	
Conus californicus (Hinds, 1844)								1					
Conus aff. *C. recurvus* Broderip, 1833					1								
Conus sp.								2					
Terebra martini English, 1914					7				1			4	2
Terebra sp.					1							1	
Clavus cf. *C. empyrosia* (Dall, 1899)					5			1				8	

sublittoral depths or in a semi-protected area; this fauna occurs at 11 localities. Because *Cerithidea californica*, *Bulla gouldiana*, and *Cryptomya californica* are rare or absent in these collections but are dominant species in modern coastal lagoons (Warme, 1971), I believe this last complex represents a sublittoral, open coast environment rather than a protected lagoon.

The hydrographic regime indicated by the fossil faunas is paradoxical. Commonly a locality contains representatives of extant species whose present geographic ranges along

Table 1 (continued)

Species	University of California, Davis, Fossil Localities, A-												
	239	240	241	243	244	245	246	4	45	[illegible]			
Turridae sp.					1		1						
Megasurcula carpenteriana (Gabb, 1865)					1		4	1					
Megasurcula tryoniana (Gabb, 1866)					2								
Volvulella cylindrica (Carpenter, 1864)													
Acteocina aff. *A. inculta* (Gould and Carpenter, 1857)													
Bivalvia													
Acila castrensis (Hinds, 1834)		4											3
Saccella taphria (Dall, 1896)		21			15		4		[illegible]				[illegible]
Anadara trilineata (Conrad, 1856)	1	4			[illegible]		[illegible]	1					
Glycymeris cf. *G. subobsoleta* (Carpenter, 1864)					1				1				
Mytilus cf. *coalingensis* Arnold, 1910									1				
Mytilus sp.										1			
Ostrea erici Hertlein, 1929			[illegible]						13				
Ostrea vespertina Conrad, 1854						[illegible]							
Ostrea sp.								1					
Chlamys (*Argopecten*) *circularis* (Sowerby, 1835)					(1)								
Chlamys hastata forma *hericia* (Gould, 1850)							11			[illegible]			
Chlamys parmeleei (Dall, 1898)		1					1	1	1	1			
Chlamys sp.			[illegible]										
Lyropecten cerrosensis (Gabb, 1866)									1				
Pecten bellus forma *hemphilli* Dall, 1879					4		1						
Pecten stearnsi Dall, 1879									[illegible]			[illegible]	
Pecten (*Patinopecten*) *dilleri* Dall, 1901									19			4	
Pecten (*Patinopecten*) *healeyi* Arnold, 1906	20	115				4		1					
Hinnites sp.													
Pododesmus cepio (Gray, 1850)												[illegible]	
Cyclocardia californica (Dall, 1903)					4		14	1					
Lucinoma annulata (Reeve, 1850)	2	6				[illegible]	1	1					[illegible]
Lucina excavata Carpenter, 1857					1		1						
Lucinisca nuttallii (Conrad, 1837)					[illegible]			4	6				1
Parvilucina tenuisculpta Carpenter, 1864					2							[illegible]	1
Thyasira bisecta (Conrad, 1849)		1											
Laevicardium quadragenarium (Conrad, 1837)					[illegible]				[illegible]				
Tivela stultorum (Mawe, 1823)	[illegible]								1				
Dosinia ponderosa (Gray, 1838) new form		19					[illegible]					[illegible]	
Chione cf. *elsmerensis* English, 1914		5											
Chione fernandoensis English, 1914													
Protothaca tenerrima (Carpenter, 1856)	1	8							1			1	
Spisula hemphilli (Dall, 1894)	2	11	1		6								
Mactra sp. #1		2											
Mactra sp. #2													
Mactra sp. #3					4								
Tresus nuttallii (Conrad, 1837)			12				4		[illegible]				
Gari edentula (Gabb, 1868-1869)													
Semele rubropicta Dall, 1871												1	
Siliqua lucida (Conrad, 1837)		4			1								
Corbula gibbiformis (Sowerby, 1833)					15		[illegible]						
Panope abrupta (Conrad, 1849)									[illegible]				
Scaphopoda													
Dentalium neohexagonum Sharp and Pilsbry, 1897							1		6				
Cadulus fusiformis Pilsbry and Sharp, 1897												[illegible]	
Arthropoda													
Balanus (*Balanus*) sp.	[illegible]	1				1	1						
Balanus (*Balanus*) *gregarius* (Conrad, 1856)													
Echinodermata													
Dendraster ashleyi forma *ynezensis* Kew, 1919													
Echinoid spines							[illegible]						
Eucidaris thouarsii (Valenciennes, 1846)													
Vertebrata													
Carcharodon arnoldi Jordan, 1909								[illegible]				[illegible]	

the western coast of North America do not overlap. For example, A-246 contains elements of all habitats as well as three *Trivia sanguinea*, which is living only in the Gulf of California and southward and a variety of *Dosinia ponderosa*. At present *Dosina* is not found north of Scammon's Lagoon, Baja California. The same locality also yielded *Calliostoma costatum*, *Parvilucina tenuisculpta* and *Chlamys hastata* forma *hericia*, which range from southern California to Alaska, as well as *Fusitriton oregonensis*, a submergent, stenothermal, frigiphilic species which lives intertidally north of Oregon and is not found at depths less than 80

Table 2: Correlation between faunal elements and preferred sediment type.
F – Faunal element present, S – Sediment peak developed

	Sediment coarser than -2.0ϕ	Sediment between -2.0ϕ and $+2.0\phi$	Sediment finer than $+2.0\phi$
Locality Number	Rocky substrate, Open coast fauna	Sand substrate, Open coast fauna	Fine sand or mud substrate, Offshore fauna
A-239		S F	S F
A-240	S F		S F
A-241	S F		S F
A-243	F (2 species)	S	
A-244	S F	S	S F
A-245	F		S F
A-246	S F	S F	S F
A-247	S F		S F
A-248	S F	S F	S F
A-249	S F		S F
A-250			S F (2 species)
A-251	S F	F	S F
A-252	S F		S F

fm. off southern California (Smith, 1970: 493). Depths of this magnitude are incompatible with environments indicated by the other species collected at this locality.

The concurrence of these northern and southern elements and the presence of *Fusitriton* is not readily explicable. Presumably nearshore upwelling of cool waters, perhaps into coastal waters warmer than presently found off southern California, was important in allowing these thermally anomalous species to coexist (Valentine and Emerson, 1961: 617-618).

Data from the sediment analysis can be used to clarify the paleoecological interpretations. Sediment samples from the center of the study area are poorly sorted (Fig. 2). The distinct size concentrations of coarse and fine material suggest that these sediment sizes were not transported together (see, for example, the curve for locality A-246). The coarse fraction of the sediment may represent either lag gravels of underlying volcanic rocks or cobbles transported by storm waves. Presumably the sand- and silt-size material infiltrated the coarser material. Samples with the best sorting (A-249, A-250, and A-252) are found on the margins of the area. The unimodal sand of A-249 implies sorting by beach transport. At most localities the sediment size indicated by the size-frequency-histograms is compatible with the substrate on which the extant species are commonly found. For example, the fauna of locality A-246 contains species indicative of the three environments described above. The size-frequency distribution curve for this locality has peaks (-3ϕ, $+1\phi$ and $+3.5\phi$), which correspond to the substrate of each of these environments. Interrelationships between fauna and sediment are shown in Table 2. There is significant accord between the fauna and the sediment in 23 of the 29 cases. The heterogeneous nature of the fauna and the poor sorting of the sediments suggests that the environments that contributed to the fossil beds were in close proximity to the site of burial.

In summary, the environment of deposition of the Pliocene strata of northwestern Baja California can be reconstructed as follows: the Rosarito Beach Formation does not extend northward into California; presumably it formed the southern flank of the San Diego embayment as a bank or headland. The faunas studied accumulated on this feature at subtidal, inner sublittoral depths in areas where patches of fine sand and mud were interposed between cobble beds and rocky exposures.

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SEISMIC RISK IN SAN DIEGO

ROBERT B. McEUEN AND CHARLES J. PINCKNEY

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SEISMIC RISK IN SAN DIEGO

ROBERT B. McEUEN AND CHARLES J. PINCKNEY

ABSTRACT.– Data from artificial earth satellites suggest that the regional shear stress responsible for earthquakes is relatively high in the San Diego region. The direction of this stress is related to the orientation of the East Pacific Rise and the Gorda Rise. The apparent nonequivalence of strain accumulation to release along active faults northeast of San Diego also suggests that shear stress is accumulating over a wide zone and that seismic activity may occur on adjoining but presently less active faults.

Maximum credible earthquake magnitudes for San Diego proper and for the San Clemente Island fault zone are 6.8 and 7.7, respectively. These events are highly unlikely but should be considered in designing critical structures such as nuclear power plants. Regarding probable earthquakes, San Diego falls in the second most active of six regional zones in the United States in terms of strain release and in the most active of three zones in terms of regional seismic risk. In the recent past, however, most of the regional strain energy has been released outside the immediate San Diego area. Our analysis of the mechanics of strain release indicates that San Diego proper will experience an acceleration of 0.2 g on worse ground approximately every 60 years. The area of worse ground is around the bays, where a two-fold amplification of bedrock acceleration could occur. The most likely source for this acceleration is the Elsinore fault.

A magnitude 6.3 or greater earthquake within the Continental Borderland could produce seismic sea waves capable of inundating San Diego's low lying coastal areas, but the occurrence of such an event is unlikely.

The purpose of this paper is to define seismic risk in San Diego, California. We have attempted to strike a balance between an "it couldn't happen here" attitude and one that states "it's only a matter of time." Most of the data on which our conclusions are based are available in the literature. Dr. Charles F. Richter's (1959) comment sets the stage for the discussion which follows:

> "There has been a general impression that earthquake risk does not exist at San Diego, historical records to the contrary being forgotten or ignored. Older structures were erected with no close attention to soundness. During and since World War II, population has increased enormously, and the city area has expanded at a pace hardly consistent with careful construction and inspection. Fortunately most of this expansion has been over the higher ground..."

SEISMOTECTONICS

The seismotectonic framework of the San Diego area can be best understood by analyzing seismotectonics on a global scale and by then studying in more detail those parts that have direct bearing on regional and local seismicity.

GLOBAL SEISMOTECTONICS

The seismic stresses responsible for earthquakes are thought to originate in the upwelling of hot light material of the earth's mantle. As this material convects it causes horizontal stresses in the earth's crust. The presence of such convection cells below the crust is indicated by slight changes in density of the material undergoing convection. These density variations in the earth cause deviations in the orbits of artificial satellites. Figure 1, shows satellite-deduced density variations for regions of high seismic activity (Schwiderski, 1968).

The Western Pacific (Fig. 1a) represents one of the most seismically active regions in the world. Here, zones of maximum seismic activity fall between low density areas presumably indicative of upwelling and high density areas indicative of convection downturn. Along the western coast of North and South America (Fig. 1b) the zone of seismic activity also lies between an area of convective upwelling and downturn. This effect is pronounced along the western coast of South America and we believe the western coast of North America is being influenced by similar convective stress. But, the magnitude of this stress appears to be less than in the high seismicity zones of the Western Pacific or along the western coast of South America. Note, particularly, that the zones of seismic activity, almost without exception, occur where the rate of change of density at the mantle surface is a maximum, that

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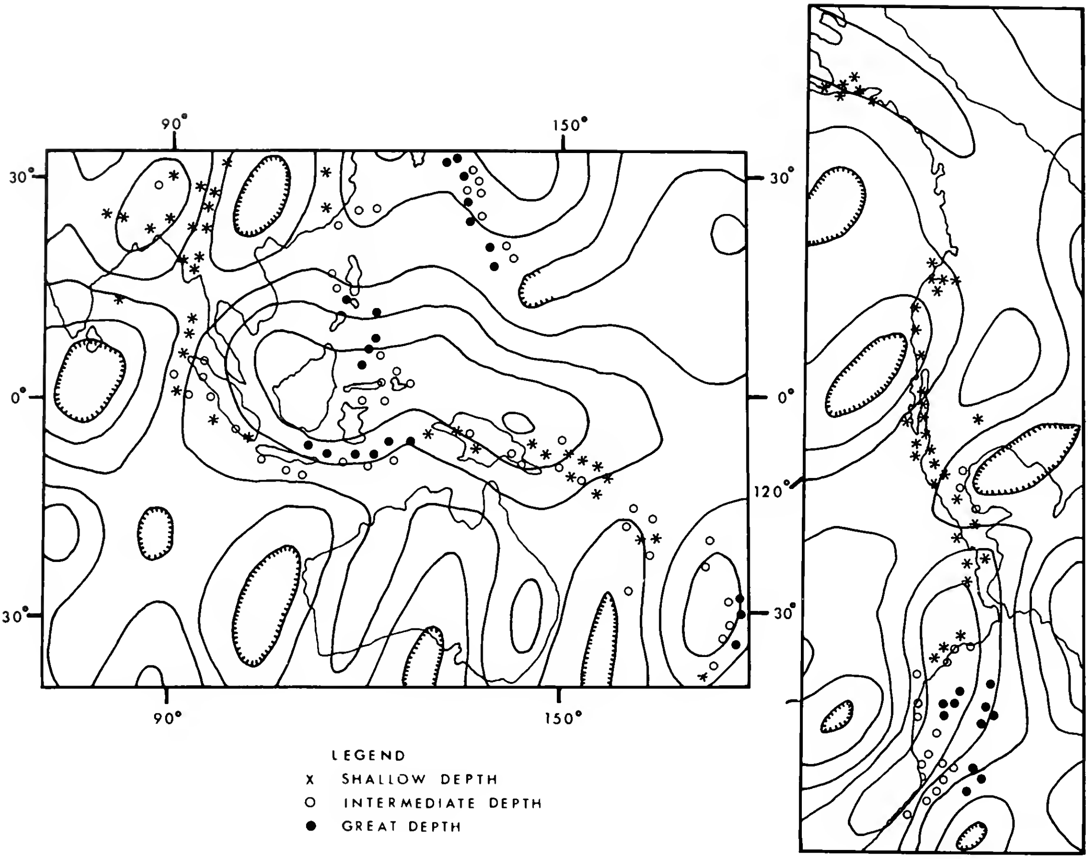


Figure 1. Contour map of density anomaly ρ' (in $g/(dm)^3$) at the surface of the mantle. Contour lines change by $\delta\rho' = 1.2$. Earthquakes after Gutenberg and Richter (1954). a, Western Pacific showing earthquake zones along unstable strips between low-density sources and high-density sinks. b, Eastern Pacific showing earthquake zones along unstable strip between low-density sources and high-density sinks.

is, where the contour lines in Figure 1 are most closely spaced. San Diego occurs in such an area.

REGIONAL SEISMOTECTONICS

Figure 2 shows regional tectonic features thought to have direct bearing on the seismicity of San Diego and adjoining areas. Figure 3 shows locations of earthquake epicenters for that portion of the area lying south of 34°N latitude. This area can be located on Figure 1b by noting where the 120°W longitude line intersects the western coast of North America.

Between the zone marked East Pacific Rise at the bottom of Figure 2 and the zone marked Gorda Rise at the top, there exists a series of en echelon faults extending from the Tamayo fracture zone to the San Andreas Fault Zone. All these faults have a right-lateral sense of displacement, with the eastern side moving southeast relative to the western side.

Ridge crests, such as the East Pacific Rise and the Gorda Rise, are areas in which new oceanic crust is being created. Molten material presumably wells up within these zones and in so doing shoulders aside older material. As this process is repeated the area on both sides of the ridge crest moves laterally. Records of seismic activity indicate that zones of shallow earthquakes are associated with ridge crests; these zones also tend to align between areas of mantle upwelling and downturning as delineated by upper-mantle density anomalies (Schwiderski, 1968). The apparent extension of the East Pacific Rise into the Basin and Range Province (Fig. 2) follows the zone of maximum upper-mantle density change (Fig. 1b).

The large arrows perpendicular to the strike of the East Pacific Rise and the Gorda

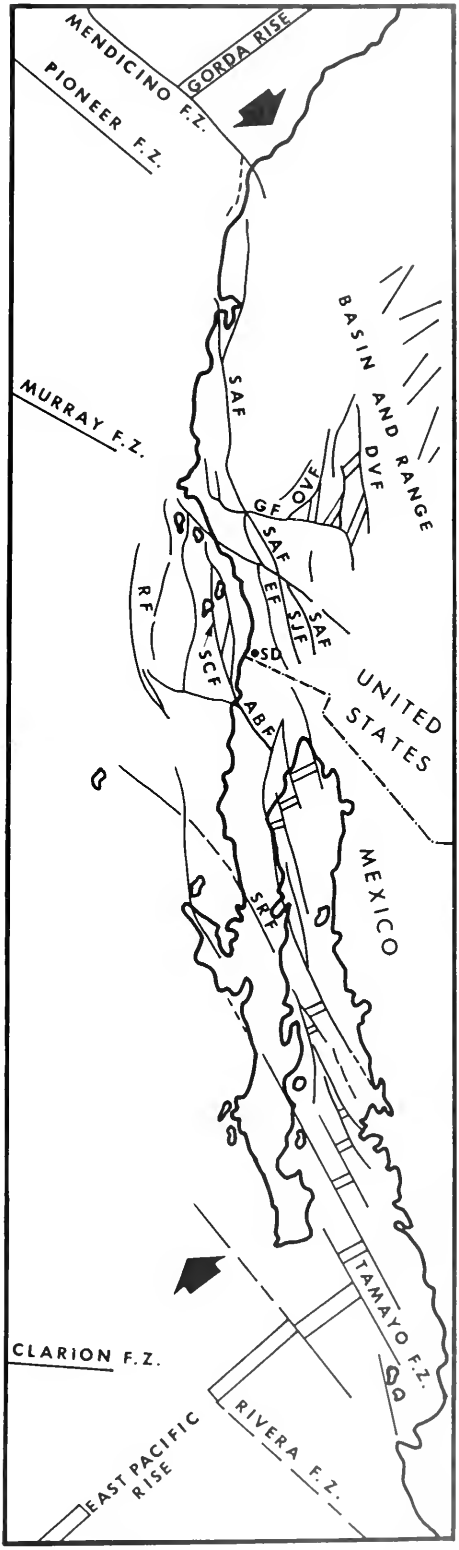


Figure 2. Fractures and spreading centers along part of the Pacific Coast of North America. S.D. marks the location of San Diego. Oceanic fracture zones (FZ) and continental faults (F) are solid black lines, dashed where uncertain. S.A.F.—San Andreas Fault; D.V.F.—Death Valley-Furnace Creek Wash Fault; O.V.F.—Owens Valley Fault; G.F.—Garlock Fault; E.F.—Elsinore Fault; S.J.F.—San Jose Fault; A.B.F.—Agua Blanca Fault; S.R.F.—Santa Rosalia Fault; S.C.F.—San Clemente Fault; R.F.—Rampart Fault. Postulated spreading centers along the crest of the East Pacific Rise and its possible continuation into the continent shown in gray. Representation of spreading centers in the Basin and Ranges is symbolic, indicating a region of crustal extension (Modified from Elders, et al., 1970).

Rise indicate the relative direction in which stress is applied due to forces produced along these spreading centers (Fig. 2). The right-lateral movement of the series of faults is accommodating this stress, and one is tempted to consider the whole zone of faulting as a shear set. Gastil et al. (in press) note, however, this simplistic view is not consistent with the right-stepping nature of the en echelon fault breaks.

In the San Diego region, the zone of possible stress accumulation reaches its widest extent in an area bounded on the east by the San Andreas fault and on the west by the Rampart fault, which marks the western limit of the California Continental Borderland.

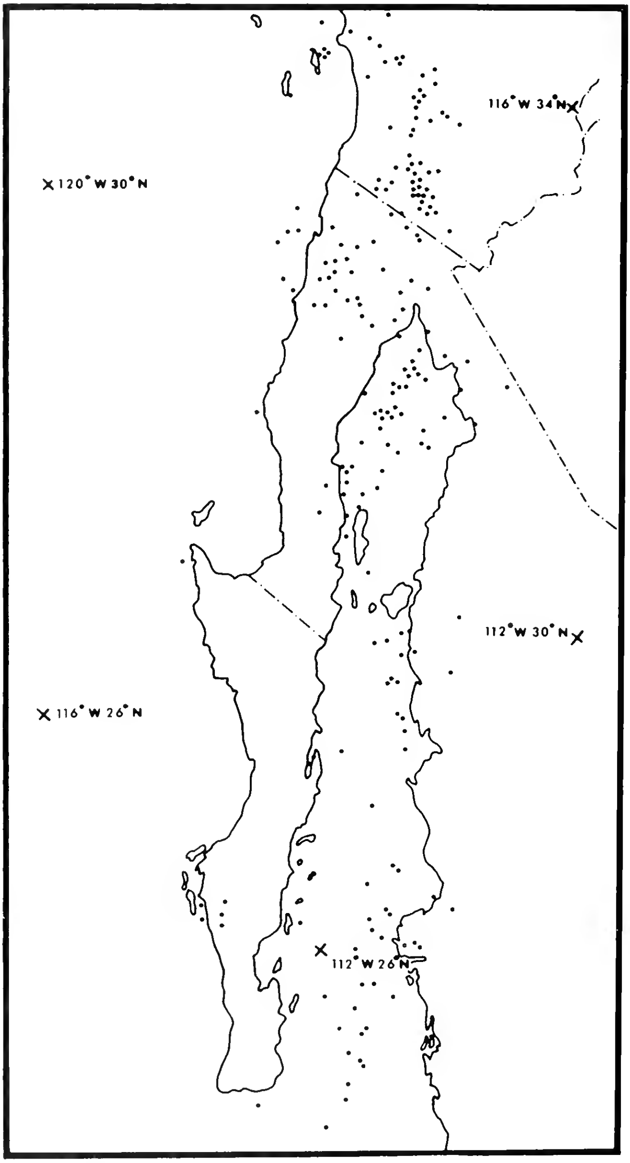


Figure 3. Earthquake epicenters with magnitudes of 4 or greater between 1958 and 1968 (from Gastil, Allison, and Phillips, in press).

Earthquakes occur in areas where differential stress exceeds the shearing resistance of the material in the area, and rupture occurs. If differential stress is applied across the broad zone of en echelon faults strain should be occurring throughout the zone. A necessary constraint to a surface rupture of considerable length is that the rate of surface strain accumulation must be a maximum in the immediate zone of faulting. If not, and large surficial plates are moving in opposite directions tangential to the fault (Fig. 2), the faulting must spread through time over a wide lateral area. With these thoughts in mind, let us examine the strain-accumulation and strain-release history of the onshore regions adjoining San Diego.

Onshore strain accumulation.—To determine strain accumulation, geodetic surveys should be carried out in intervals between earthquakes. Following the magnitude 7.1 Imperial Valley earthquake of 1940, the Imperial Valley triangulation network was resurveyed; a second resurvey was made in 1954, and a third in 1967. Scholz and Fitch (1969), summarized the data obtained in the area of the Imperial fault, which ruptured along 40 miles of its length in 1940, and therefore represents a zone along which strain accumulaton should attain a local maximum. They concluded that slip occurred along the Imperial fault between surveys, releasing about 15 per cent of the accumulated strain. Their slip-corrected data (Fig. 4) verifies that shear strain is accumulating at a higher rate near the fault. The data for the 1941-1954 period are shown in vector form in Figure 5a. The fact that the shear strain is appreciable at considerable distance from the fault zone led Scholz and Fitch (1969) to state that "the Elsinore, San Jacinto, and Mission Banning Creek faults... may, in fact, testify to a 'spreading' of the fault zone due to a nonequivalence of strain accumulation and release..."

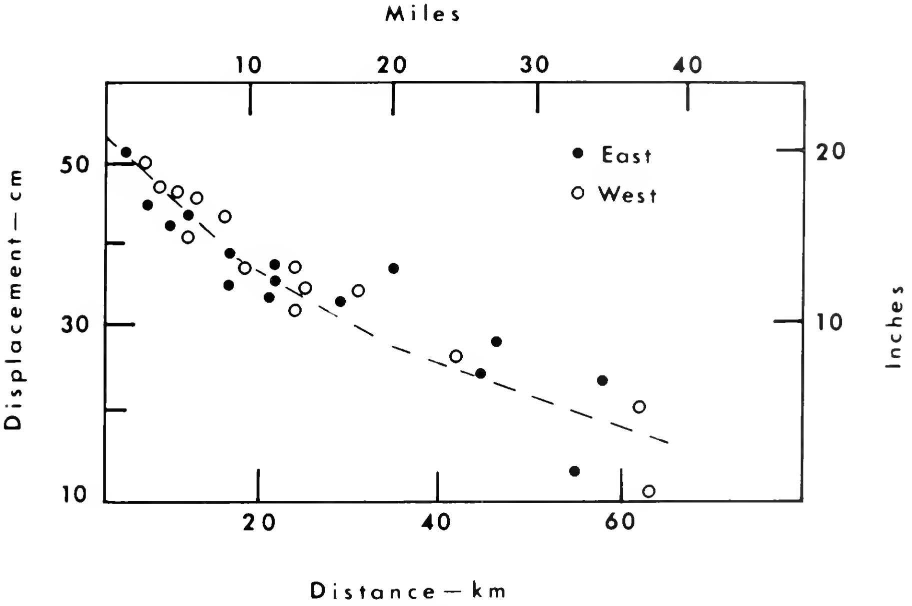


Figure 4. Strain accumulation parallel to the Imperial Fault versus distance from the fault for the period 1941-1954. The data has been corrected for the observed slip and superimposed on one side of the fault (Scholz and Fitch, 1969).

Savage (1970) shows that the strain that accumulated between 1941 and 1967 is approximately twice that accumulated between 1941 and 1954 and concludes that for the Imperial Valley triangulation network the strain rate is about $0.4 + 0.1\ \mu$ strain/yr over a zone 100 km (63 miles) wide.

Onshore strain release.—Strain release can be obtained by direct measurement if good geodetic control is available prior to the release of strain by an earthquake. Figure 5b shows retriangulation results obtained following the 1940 Imperial Valley earthquake. Such good geodetic control in the past has been the exception rather than the rule, and seismologists have had to rely on empirical relationships to establish probable strain release associated with earthquakes.

Figure 6 shows a strain-release map derived from a two year study of 28,000 earthquakes in the conterminous United States, including 16,000 in California. The map is useful in that it shows the relative rate of seismotectonic activity in various areas. Note that a zone of maximum seismotectonic activity lies just east of San Diego and that the San Diego area falls in the second most active of zones.

Offshore faulting.—Moore (1969) published a structural map of the California Continental Borderland based largely upon the interpretation of seismic reflection profiles. These profiles commonly show folded structure within strata and either directly or indirectly the location of faults. He concluded that the primary offshore structural pattern comprises two

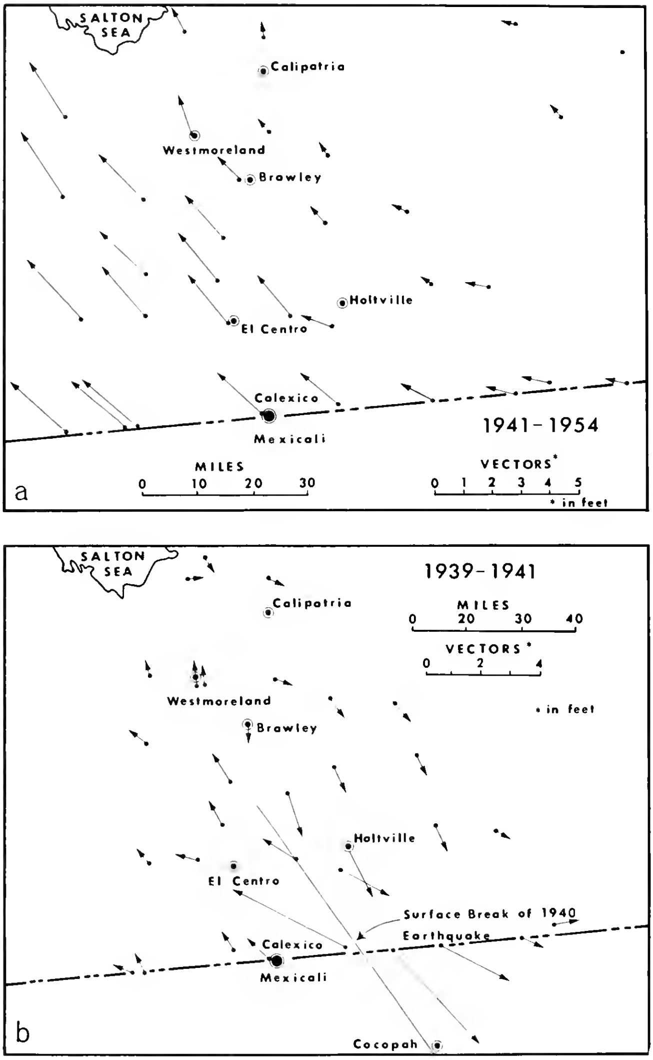


Figure 5. a, Retriangulation strain-accumulation results, U.S. Coast and Geodetic Survey, Imperial Valley, 1941-1954. b, Retriangulation strain-release results, U.S. Coast and Geodetic Survey, Imperial Valley, 1939-1941 [after Whitten by C. R. Allen] (Ritcher, 1958).

sets of faults, a set trending northwest and another east-northeast. The northwest trend so predominant onshore clearly carries through to most of the Borderland as the principal set and, where topographic offsets are well enough developed to be significant, movement appears to be right-lateral (Fig. 7). This conclusion is consistent with first-motion studies of earthquakes which, with one important exception, indicate right-lateral movement on northwest trending faults (Gutenberg, 1941; Allen, 1960). The exception is the 5.9 magnitude earthquake that occurred off the southeast tip of San Clemente Island in 1951. First motion for this earthquake can only be explained by assigning it a large component of dip-slip movement (Allen, 1960).

The dominant fault of the inner zone of major northwest trending faults is the San Clemente Island fault extending from the eastern side of San Clemente Island to the Cabo Colnett area of Baja California, Mexico. Another major fault forming the eastern face of Santa Catalina Island may be continuous with a fault along the western boundary of the San Diego Trough. Moore (1969) suggested, based on the sedimentation and structure of the Borderland and records of modern earthquake epicenters, that about 1 million years ago formation or rejuvenation of the Agua Blanca fault initiated strike-slip faulting in the inner zone of the Borderland, formed new inshore basins, and realigned drainage systems, forming centers of deposition for Pleistocene turbidity currents. This latest movement continues today, as shown by the modern seismic activity of the inner zone, but perhaps with abated intensity, inasmuch as deformation of Pleistocene sediment in the inner basis is uncommon.

Wiegand (1970) suggested that the Newport-Inglewood fault has an offshore extension of major proportion. Although there are faults observable offshore as far south as Encinitas that can be extrapolated northward in such a way as to merge with the Newport-Inglewood trend, there is insufficient evidence that these are continuous or that they involved offsets of the same order of magnitude as the major faults farther offshore.

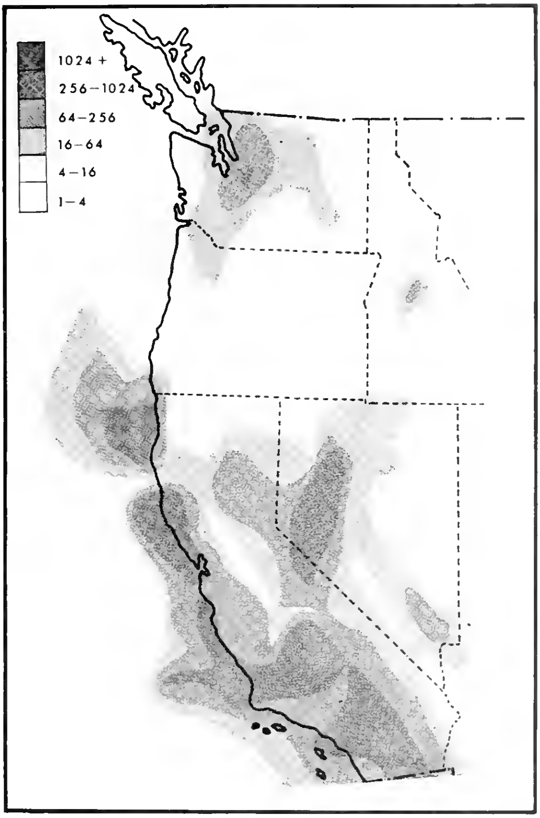


Figure 6. Strain release in the United States, 1900 to 1965, expressed as the equivalent number of magnitude 4 earthquakes/10,000 km^2/66 years (from Algermissen, 1969).

LOCAL SEISMOTECTONICS

Strain release—Earthquake epicenters recorded in the San Diego area are plotted on Figure 8. The data (Fig. 6) indicate that the energy associated with strain release in the San Diego area during the past 66 years should be equivalent to that produced by approximately 100 magnitude 4 earthquakes per 1,000 km^2 of surface area. Figure 9 gives a generalized relationship between the Richter Magnitude and Modified-Mercalli Intensity. Within a 1,000 km^2 circle centered on downtown San Diego, only 12 earthquakes have been reported during the past 66 years. The magnitudes of these average less than 4 and their intensities average about IV. We conclude that in the recent past most of the regional strain energy has been released outside the immediate San Diego area. Algermissen (1969) gives the average strain release per 1,000 km^2 for the entire Pacific Coast (west of 114°W longitude) as being equivalent to 12 magnitude 4 earthquakes per 66 year interval.

Surficial faulting.—The principal surficial faults in the San Diego area are shown on Figure 10. Many of these appear to be associated with past tectonic forces, but some of the northwest trending and north trending faults offset Holocene (less than 11,000 years old), as

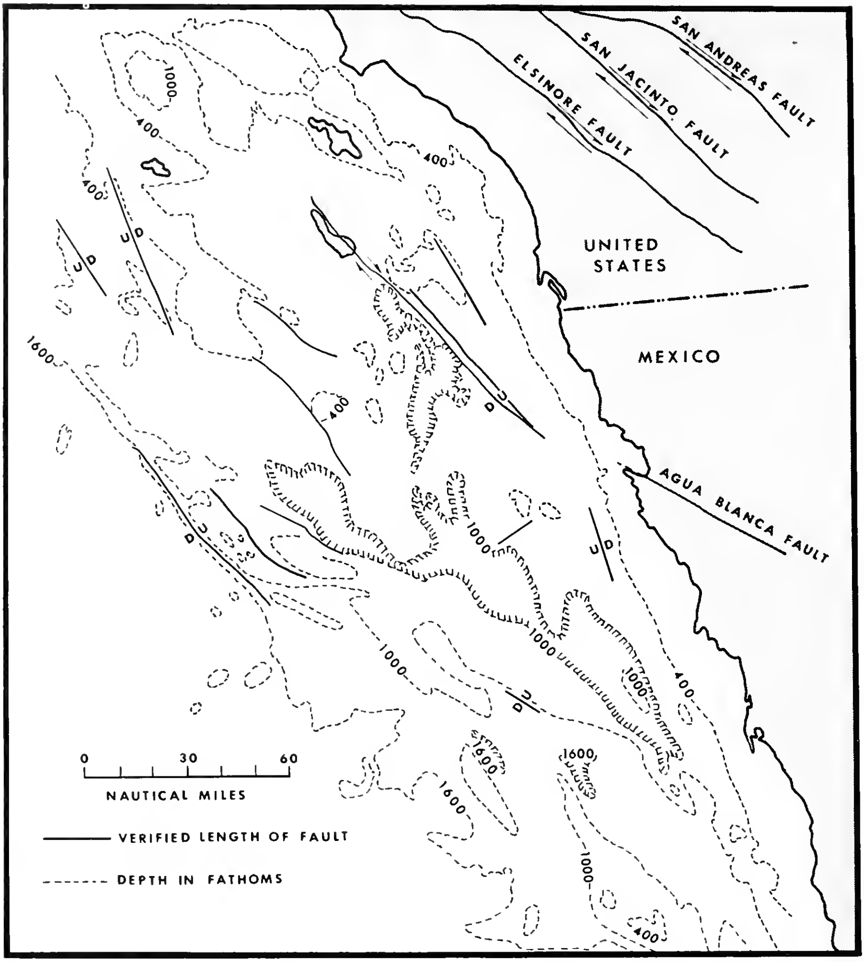


Figure 7. Structure of the Continental Borderland and adjacent regions (modified from Moore, 1969).

well as late Pleistocene (less than 400,000 years old) sediments. The north trending parallel series of faults on Point Loma, as well as faults in the Rose Canyon area, offset Pleistocene sediments. These faults can typically be mapped for at least a few miles (see Buffington, 1964; Kennedy, 1969). There is a series of normal faults east of San Diego Bay that offset Pleistocene sediments. One of these, the La Nacion fault, offsets Pliocene sediments by over 230 ft, Pleistocene sediments by over 200 ft, and Holocene materials a few feet.

Faulting in basement rock.—In areas covered by a veneer of sedimentary rock, changes in surface topography caused by faulting quickly become obscured by erosion or by deposition. For such areas, faulting is best delineated by changes in elevation of basement rock. In the parts of San Diego where batholithic rocks are absent, basement is represented by dense metavolcanic rocks of Jurassic age. Gravity data provide an excellent basis for predicting the elevation of this basement unit due to its high density relative to the overlying sediments (Elliott, 1970).

Location of probable basement faulting by analysis of gravity data is limited, since steep slopes on the basement surface produce gravity anomalies which differ only slightly from those produced by near-vertical faulting. The inferred regional stress pattern discussed earlier strongly suggests that primary basement faulting is responsible for the northwest trends evident in the gravity data in the San Diego Bay, Mission Bay, and Mount Soledad area.

Figure 11 shows probable basement faulting superimposed on the gravity data recently published by Elliott. The two primary and presumably right-lateral faults, indicated

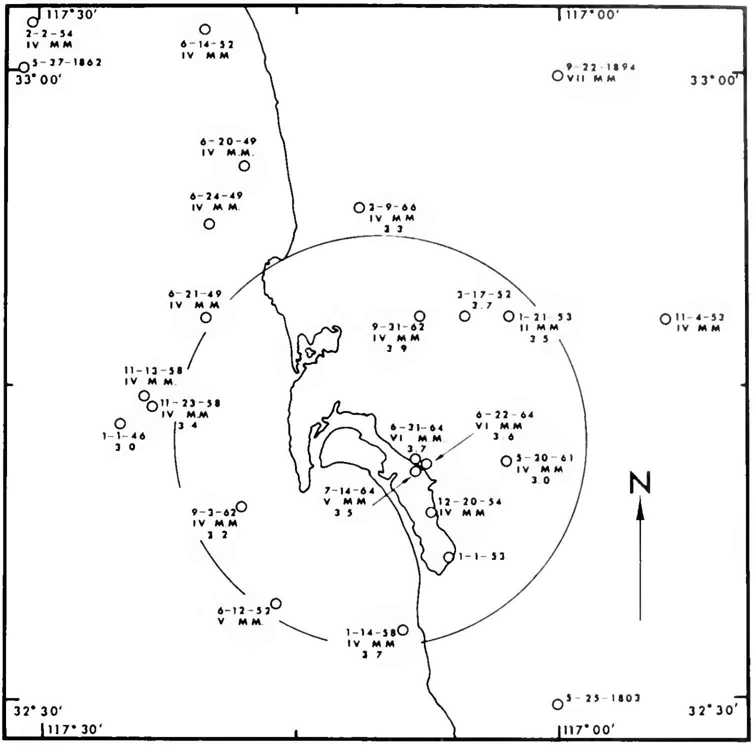


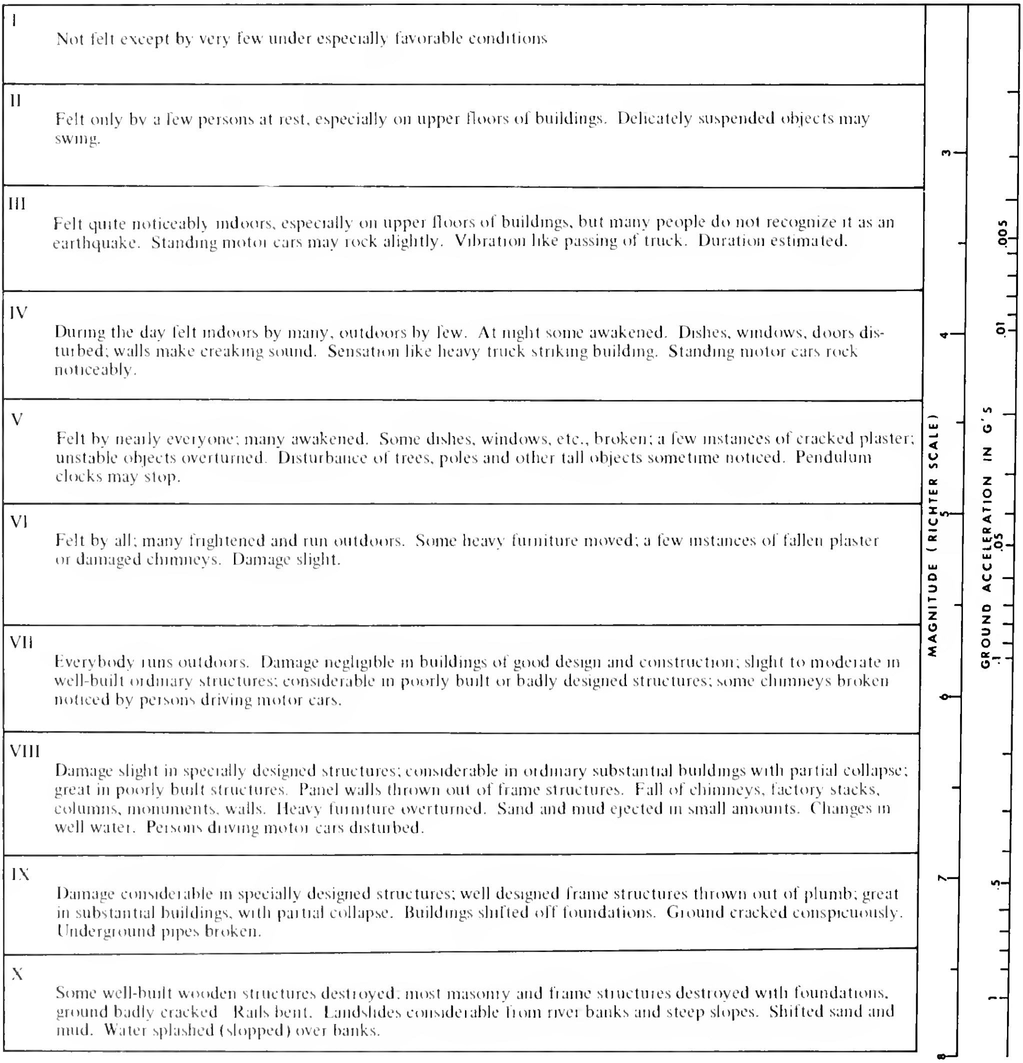
Figure 8. Epicenter map of the San Diego area giving date (e.g. 11-4-25), Modified-Mercalli Intensity (e.g. IV M.M.), and Richter Magnitude (e.g. 3.4) when known. Circle shown has area of 1,000 square kilometers.

by the dashed lines, form the edges of a zone which narrows to the northwest. Within this zone, secondary faulting, indicated by the dotted lines, may have occurred.

The right-lateral sense of the primary faults is suggested by the manner in which they offset the La Jolla Submarine Canyon (Buffington, 1964). The westernmost primary fault has some surface expression which has been mapped by Milow (see Buffington, 1964) and by Kennedy (1969). The right-lateral sense of this fault may be further indicated by offset topography along the eastern margin of Point Loma. Other geophysical data suggest that this fault continues to the south, where it parallels the western coast of Baja California (Allen et al., 1965). The easternmost of the primary faults has little surface expression, Rose Canyon notwithstanding. It can possibly be traced for a limited distance in the area northwest of Rose Canyon, and it may be correlated with faulting exposed east of Mission Bay. That motion along the primary fault set is not exclusively right-lateral is attested to by the pronounced gravity low in the region of San Diego Bay. This view is corroborated by the depths of basement rock in the area (Elliott, 1964). Vertical offset of basement rock in excess of a thousand feet is certainly consistent with geophysical and well data for the South Bay area.

Due to the convergence of the primary fault set, a zone of transitional stress occurs north of San Diego Bay. Compressional stress to the north may account for the anomalous elevation of Mount Soledad. It has been suggested that Mount Soledad represents the uptilted edge of a block which contains Mission Bay as the downtilted counterpart (Peterson, 1970). The secondary faults, indicated by dotted lines on Figure 11, allow for this possibility. The northernmost secondary fault is provided in order to allow for the possibility that Mount Soledad and Mission Bay represent a horst-graben set. These secondary faults are consistent with the gravity data and are placed along the strike of "positive" faults, as mapped by Milow (see Buffington, 1964). These "positive" faults have a direction of dip or relative vertical separation which is consistent with the gravity interpretation presented herein.

Wiegand (1970) analyzed selected geologic and geophysical data covering the area between the two suggested primary basement faults shown on Figure 11. He concluded that primary faulting has occurred along the axis of San Diego Bay and proposes this fault may be an extension of the Newport-Inglewood fault zone to the north and the San Miguel fault to the south. The gravity data of Figure 11 do not support such faulting through San Diego Bay.



I	Not felt except by very few under especially favorable conditions
II	Felt only by a few persons at rest, especially on upper floors of buildings. Delicately suspended objects may swing.
III	Felt quite noticeably indoors, especially on upper floors of buildings, but many people do not recognize it as an earthquake. Standing motor cars may rock slightly. Vibration like passing of truck. Duration estimated.
IV	During the day felt indoors by many, outdoors by few. At night some awakened. Dishes, windows, doors disturbed; walls make creaking sound. Sensation like heavy truck striking building. Standing motor cars rock noticeably.
V	Felt by nearly everyone; many awakened. Some dishes, windows, etc., broken; a few instances of cracked plaster; unstable objects overturned. Disturbance of trees, poles and other tall objects sometime noticed. Pendulum clocks may stop.
VI	Felt by all; many frightened and run outdoors. Some heavy furniture moved; a few instances of fallen plaster or damaged chimneys. Damage slight.
VII	Everybody runs outdoors. Damage negligible in buildings of good design and construction; slight to moderate in well-built ordinary structures; considerable in poorly built or badly designed structures; some chimneys broken noticed by persons driving motor cars.
VIII	Damage slight in specially designed structures; considerable in ordinary substantial buildings with partial collapse; great in poorly built structures. Panel walls thrown out of frame structures. Fall of chimneys, factory stacks, columns, monuments, walls. Heavy furniture overturned. Sand and mud ejected in small amounts. Changes in well water. Persons driving motor cars disturbed.
IX	Damage considerable in specially designed structures; well designed frame structures thrown out of plumb; great in substantial buildings, with partial collapse. Buildings shifted off foundations. Ground cracked conspicuously. Underground pipes broken.
X	Some well-built wooden structures destroyed; most masonry and frame structures destroyed with foundations, ground badly cracked. Rails bent. Landslides considerable from river banks and steep slopes. Shifted sand and mud. Water splashed (slopped) over banks.

Figure 9. Modified Mercalli Intensity scale showing approximate relationship with ground acceleration and magnitude of shallow local earthquakes (from Linehan 1970).

SEISMIC RISK

The determination of seismic risk is fraught with uncertainties. To quantify these uncertainties is beyond the scope of this paper, but we have attempted to estimate the maximum probable risk presented to the San Diego area by earthquake energy. An introduction to the probabilistic approach has been recently presented by Esteva (1970). Dr. Clarence Allen (1964) in a discussion of the engineering implications of seismic geology made the following comments:

> "Seismic zoning maps for engineering purposes have usually been constructed on the basis of the earthquake history of a region, sometimes in combination with the locations of so-called "active" faults and related seismo-tectonic features. Indeed, these are normally the only items of pertinent information available—however inadequate. It should be emphasized, however, that these data may be even far more inadequate than most people realize. The difficulties and dangers in interpreting a relatively short recorded earthquake history, as well as the problems in attempting to differentiate between active and inactive faults, have already been pointed out, together with the very widespread distribution of earthquake-induced effects during a great shock. In addition, major after-shocks of a great earthquake are distributed over a far wider area than has generally been appreciated, and they constitute a hazard that may seemingly be quite unrelated to the local fault pattern. Potentially damaging after-shocks of the 1960 Chilean earthquake, for example, blanketed an area almost the size of California. It is significant that those countries with the longest and most complete recorded earthquake histories are generally those in which the mapped zones of potential high seismic hazard are the broadest, and this lesson should be kept in mind by those persons attempting to construct new zoning maps or by engineers who are facing the same problems in regard to specific sites."

These comments apply to much of what follows.

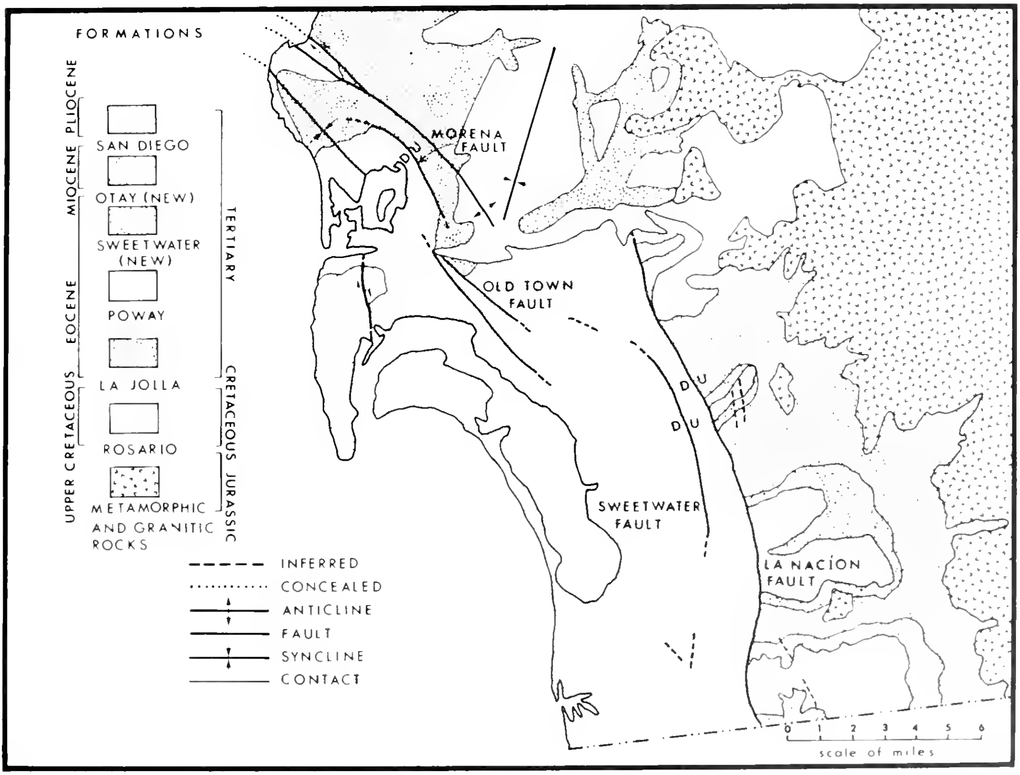


Figure 10. Principal surficial faults and related structures (from Artim and Pinckney, in press).

DEFINITIONS

It is of utmost importance to define the terminology used in ascertaining seismic risk.

Maximum credible earthquake.—This is the maximum earthquake that in our judgment appears capable of occurring. It is the maximum rational and believable event consistent with the known facts. While it is highly unlikely, it is still a believable event that could occur within the present geologic framework and present geologic epoch. No state-

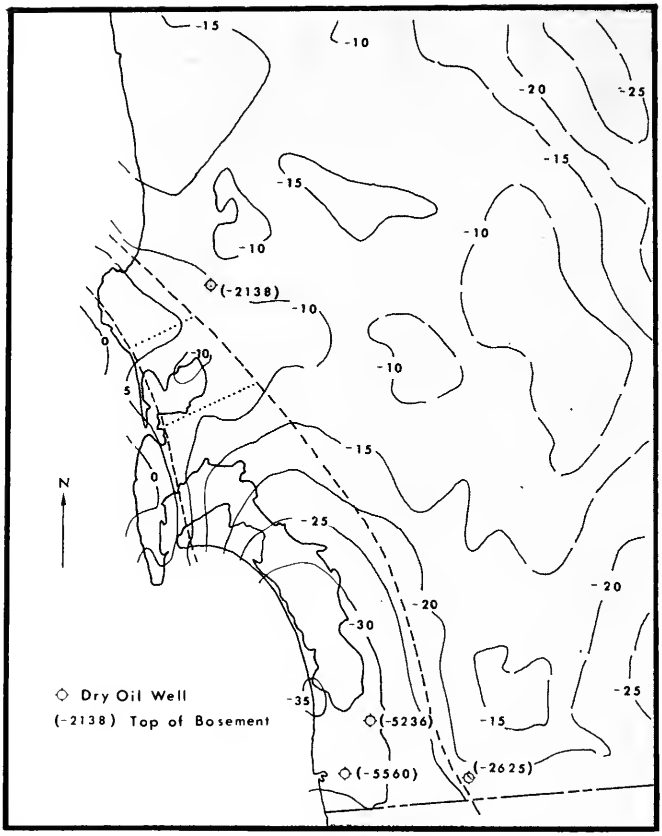


Figure 11. Probable basement faulting, Bouguer gravity map after Elliott (1970). — — — — Primary Basement Faulting; ······ Secondary Basement Faulting.

ment can be made with regard to its probability of occurrence, other than that it is finite (modified from Cluff et al., 1969).

Maximum probable earthquake.—This is the maximum earthquake that might occur with a fairly high probability. The tectonic forces which cause it are reasonably well understood. Statistical data allow the prediction of a recurrence interval for this earthquake. For all but the most critical considerations, it is the maximum "design" earthquake.

Active fault.—An active fault is one that has moved in historic time or along which offset of Holocene materials can be demonstrated. If Holocene materials are not offset, but numerous epicenters have been recorded in or in close proximity to the fault, a classification of active may be used.

Potentially active fault.—A potentially active fault is one that offsets Pleistocene materials, but for which offset of Holocene materials is lacking and for which seismic activity is nominal or absent.

REGIONAL RISK

Algermissen's regional risk map is reproduced in Figure 12. On this map San Diego is shown in the zone where "major destructive earthquakes may occur." This map is based on the following: the distribution of M.M. (Modified-Mercalli) intensities associated with the known seismic history of the United States; strain release in the United States since 1900; and the association of strain release patterns with large scale geologic features believed to be related to recent seismic activity. Since this map is based partly on maximum observed intensities, it is biased towards conditions expected on worse ground. The probable frequency of occurrence of damaging earthquakes in each zone was not considered in assigning ratings to the zones.

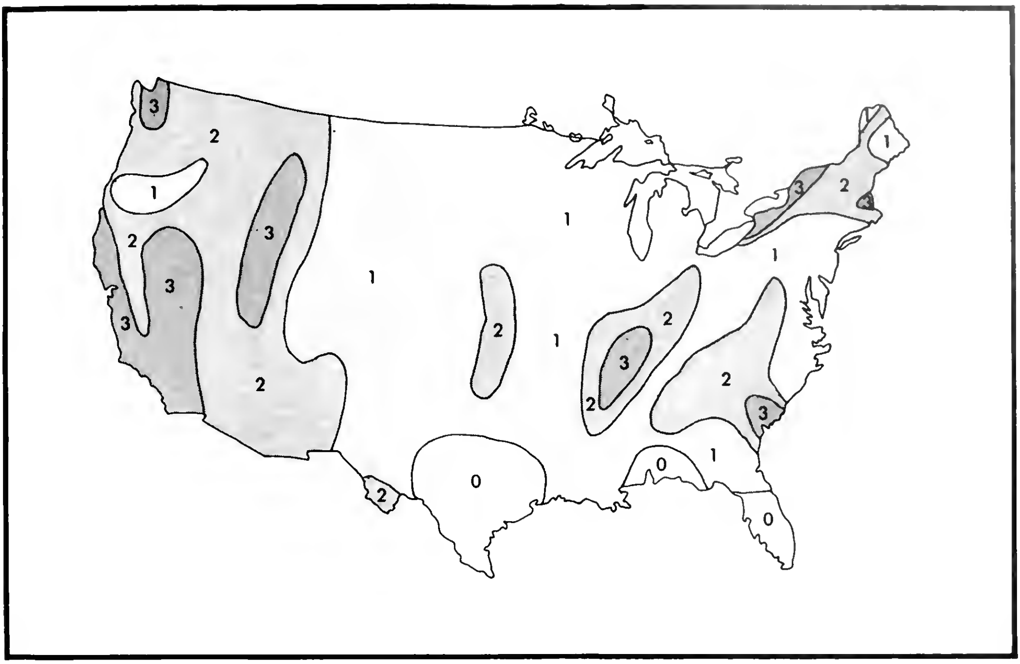


Figure 12. Seismic Risk (after Algermissen, 1969). Zone 0—No damage. Zone 1—Minor damage; distant earthquakes may cause damage to structures with fundamental periods greater than 1.0 seconds, corresponds to intensities V and VI of the M.M. Scale. Zone 2—Moderate damage; corresponds to intensity VII of the M.M. Scale. Zone 3—Major damage; corresponds to intensity VIII and higher of the M.M. Scale.

LOCAL RISK

Zone 3, which includes the San Diego area, corresponds to intensity VIII and higher on the M.M. scale. Assuming that San Diego falls in the intensity VIII portion of the zone leads to the conclusion that it will experience an acceleration on worse ground of approximately 0.2 g (Fig. 9).

An acceleration of 0.2 g exceeds by only a factor of four the acceleration which San Diego in all probability repeatedly experiences; the isoseismal maps shown in Figure 13 indicate probable ground accelerations in San Diego of 0.05 g. Events of this size (i.e. magnitude 6.3) originating in the same general 10,000 km^2 area as the earthquakes plotted on Figure 13 can be expected to occur approximately once every 15 years. Note that if for the earthquakes shown on Figure 13 one calculates the expected acceleration directly from magnitude and distance considerations using the most recent empirical relationships, considerably lower probable acceleration is obtained (Esteva, 1970; Seed, Idriss, and Kiefer, 1969). This deviation may be explained in terms of the shallow depth at which events in Southern California occur and local geology.

Seismic-input estimates.—The most difficult aspect of determining seismic risk is estimating the maximum energy which can be expected. Correlations between geological and seismological data must be used where statistically significant seismic data are lacking. Figure 14 shows an idealized relationship between the length of the surface fault breaks occurring at the time of earthquake (determined geologically) and earthquake magnitude (determined seismologically). The portion of the curve above magnitude 6.5 is based on a study of historic surface faulting in the continental United States and adjacent parts of Mexico carried out by Bonilla (1967). We have plotted on this figure the reported surface breaks and measured magnitudes of some important earthquakes. The size of the earthquakes plotted range from the great, magnitude 8.6, Chilean earthquake of 1960 where surface breakage occurred over a distance of 600 miles to the recent 6.6 magnitude San Fernando earthquake which had surface breakage of over 9 miles. This plot confirms that the stress drop across the slipped fault is the same for all large earthquakes; and therefore, that for a constant

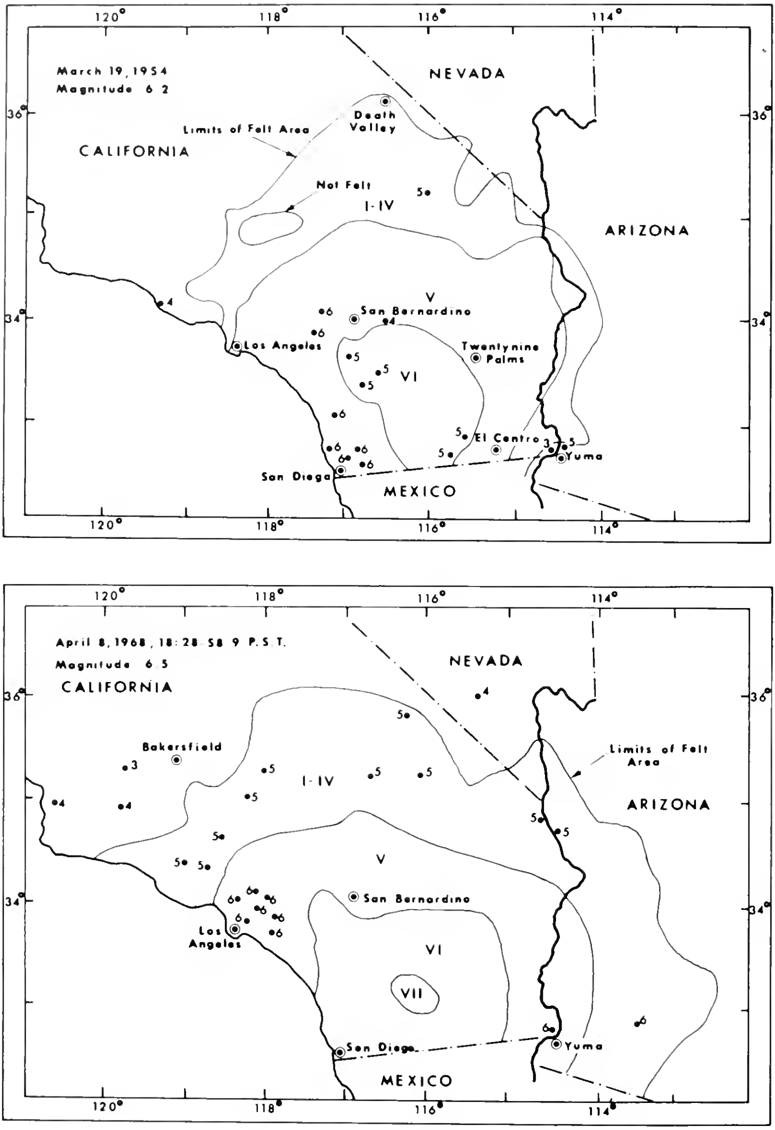


Figure 13. Borrego area earthquakes (Murphy and Cloud, 1956; Von Hake and Cloud, 1966). Stations reporting anomalously high intensity are indicated by black dots.

depth of faulting the total strain energy released is proportional to the length of surface breakage.

Maximum probable input from San Andreas system.—The work of Bonilla (1967) and Housner (1969) allows us to predict maximum probable earthquake magnitude for a given fault system by assuming a maximum probable length of surface breakage. For example, if one assumes for the Elsinore fault zone that surface breakage could occur along a zone 50 to 70 miles long, then the resultant magnitude would be 7.3. Such a surface break might be expected to have its southern limit near Vallecito Valley and its northern limit somewhere between Temecula and Lake Elsinore. Similarly, if one assumes for the San Jacinto fault zone that surface breakage could occur along a zone 150 to 190 miles long, then the resultant magnitude would be 7.8. Such a surface break might be expected to have its northern limit between Riverside and San Bernardino and its southern limit between Imperial and the known southern limit of the Imperial fault in Mexico. The above discussed approximations are plotted on Figure 14 and shown in map view on Figure 15.

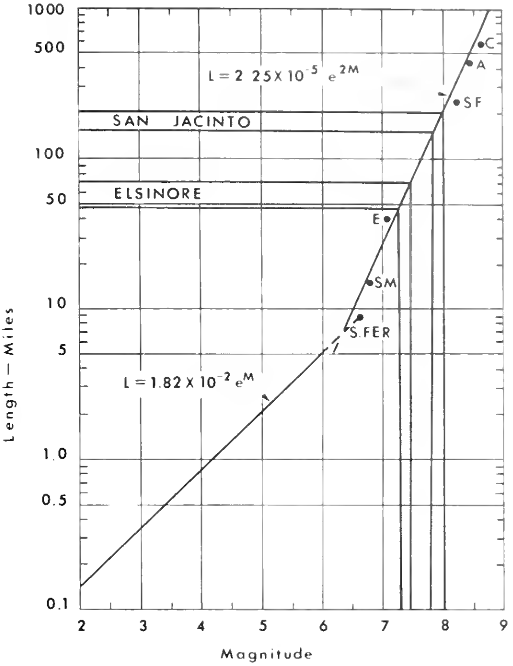


Figure 14. Idealized relation between length of surface breakage and magnitude of earthquake used for determination of maximum probable events on Elsinore and San Jacinto Faults. C = Chile (1960), A = Alaska (1964), S = San Francisco (1906), E = El Centro (1940), S.M. = San Miguel (1956), S.Fer. = San Fernando (1971) (Modified from Housner, 1969).

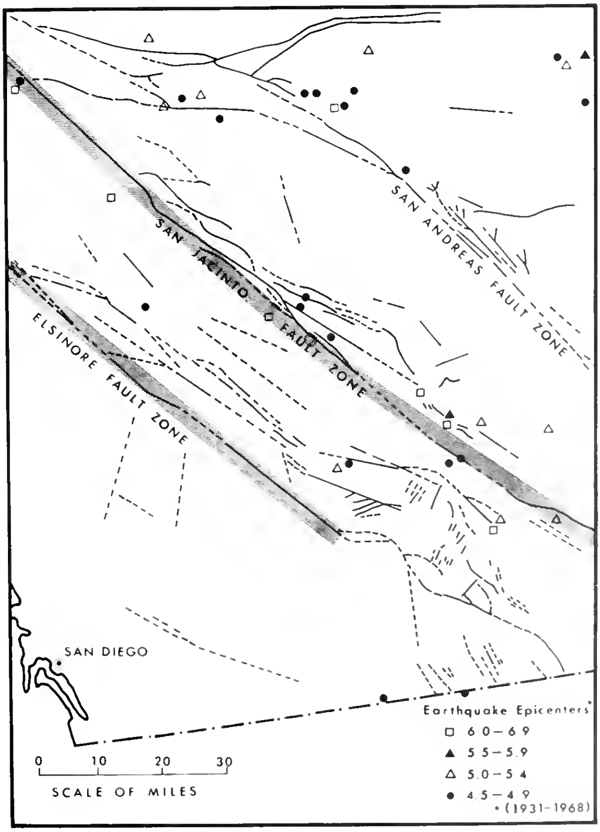


Figure 15. Maximum probably surface breakage—Epicenters and faults from California Dept. Water Res. Bull. 116-2. Cross-hatched zone = 10,000 km^2.

There is presently considerable debate as to the nature of the San Andreas fault in the area immediately south of the Salton Sea (see Fig. 16). Because the position of faults in that portion of the Imperial Valley is uncertain, estimates of maximum probable surface breakage along this part of the San Andreas fault are not presently feasible.

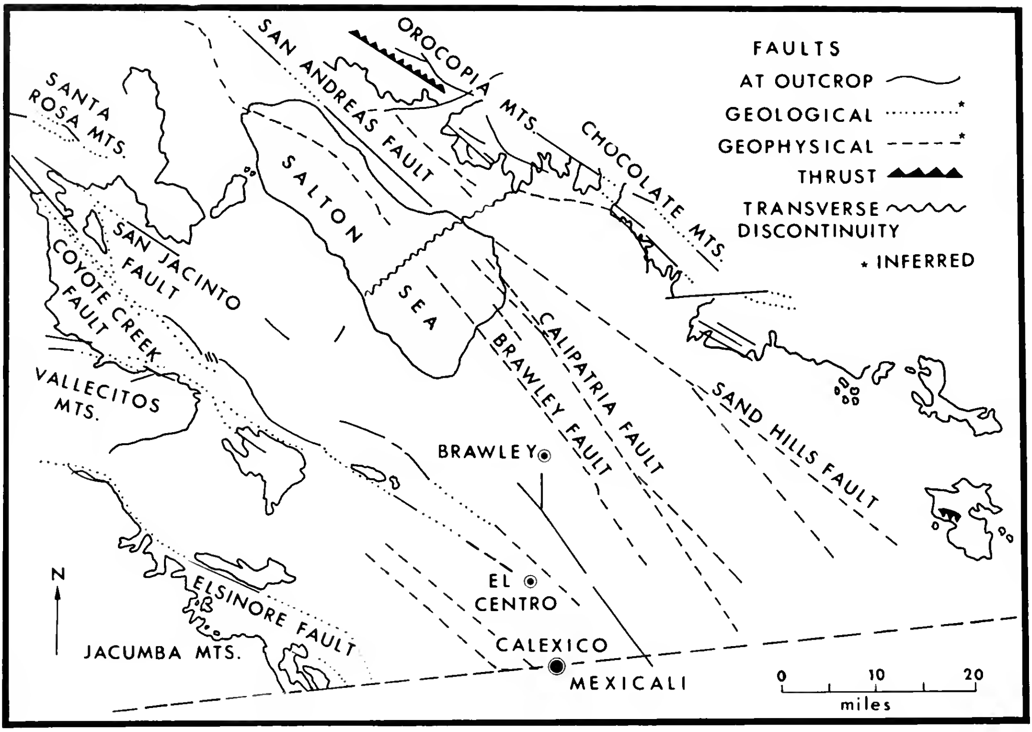


Figure 16. Faulting south of Salton Sea (from Elders et al., 1970).

Figure 17, which relates ground acceleration to epicentral distance, indicates that a magnitude 7.3 event on the Elsinore fault produces greater ground acceleration in San Diego than a magnitude 7.8 event on the San Jacinto fault. However, the duration of shaking for the magnitude 7.8 event can be expected to be 20 per cent greater than that produced by the magnitude 7.3 event (Steinburgge, 1966). These relative comparisons are valid, but the value of ground acceleration for a given site can range widely from the "intermediate ground" values given in Figure 17. An order of magnitude variation in acceleration is feasible (Esteva, 1970). At San Diego, the slightly longer duration of expected shaking produced by the larger San Jacinto fault event does not result in total delivered energy greater than that produced by the smaller event on the Elsinore fault.

The frequency of earthquakes in Imperial Valley has been graphed by Evernden (1970) in a form selected to reflect the repeat interval for earthquakes in a 10,000 km^2 area (Fig. 18). For comparative purposes Figure 15 shows a 10,000 km^2 zone 35 miles in width which extends southward from the town of San Jacinto to an area just west of the Laguna Salada in Baja California. From 1934-1971 this zone experienced five earthquakes having magnitudes greater than 6. This rate is consistent with the data of Figure 18, which can therefore be used to estimate repeat intervals for maximum probable events on the Elsinore and San Jacinto faults. Linear extrapolation to high magnitude, justified below magnitude 8, yields a repeat interval of approximately 60 years for the 7.3 event on the Elsinore and approximately 170 years for the 7.8 event on the San Jacinto.

Note that if the surface break on the Elsinore fault shown on Figure 15 is logical, and if the seismicity of the Imperial Valley can be applied to this area, then the Elsinore fault represents the source of maximum risk to the San Diego area. The maximum probable event for this fault occurs more often and delivers more energy to the San Diego area than does

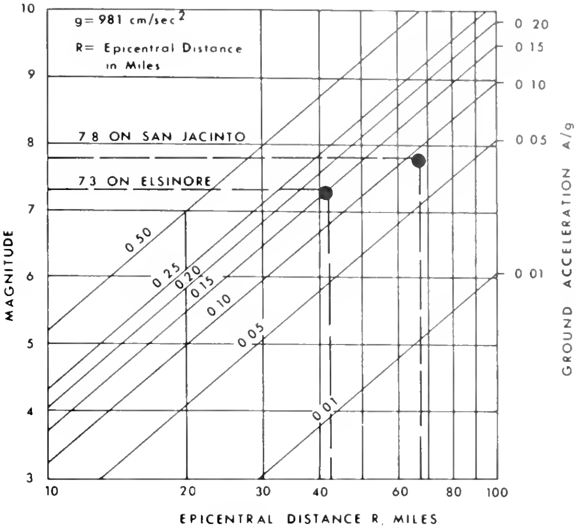


Figure 17. Acceleration on intermediate ground as a function of epicentral distance and magnitude (after Esteva et al., 1964).

the maximum probable event for the San Jacinto fault. The geologically short seismic history for this fault does not, so far, corroborate this view. The San Jacinto fault poses an equivalent threat in cases where the induced failure is extremely sensitive to the duration of shaking.

Maximum credible input from offshore.—On Figure 7, the maximum verified lengths of offshore faults are plotted. In order to be considered verified, two conditions must be met: the fault must have been positively identified on seismic profiles; and its extension between profiles must be consistent with submarine topography.

The largest fault within the California Borderland is the San Clemente Island fault, with a verified length of approximately 110 statute miles. The maximum credible earthquake for the Borderland, produced by breakage of this fault over its entire verified length, would have a magnitude of 7.7. Since this fault is approximately the same distance from San Diego as the Elsinore fault, we conclude that the maximum credible offshore event will produce approximately 50 per cent greater acceleration in San Diego then the maximum

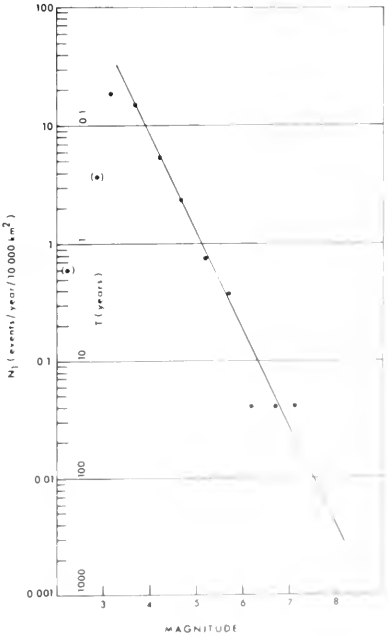


Figure 18. Regional seismicity, Imperial Valley, California, 1934-1963 (Everden, 1970).

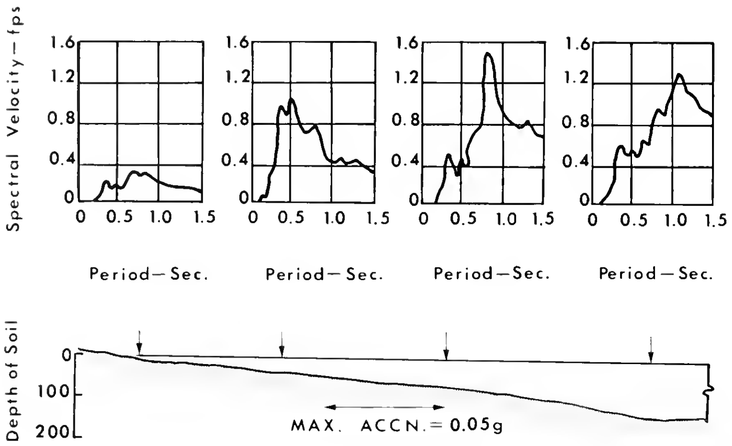


Figure 19. Computed response spectra for sand and gravel deposit (from Seed, 1969). Predominate period of bedrock motion = 0.35 seconds; equivalent damping = 5%.

probable event on the Elsinore. It would also cause a greater duration of shaking.

Tsunami (seismic sea wave) risk.—Joy (1968) discussed tsunamis and their occurrence along the San Diego County coast. He pointed out that the relatively wide Continental Borderland off the coast has historically acted as an effective diffuser and reflector of the energy which arrives from remotely generated tsunamis. Damage associated with remotely generated tsunamis, therefore, will be most likely confined to small craft in the harbor, although some waterfront structures may also be affected.

Locally generated tsunamis risk is difficult to assess. Tsunami generation requires a rapid dislocation of the sea surface or bed over a very large area (thousands of square miles). This size dislocation is not likely to occur if the source earthquake has magnitude less than 6.3 (Iida, 1970). Most major dislocations of the sea surface or bed are thought to be associated with fault movement of the "dip-slip" type. This type motion seems to have been associated with the 5.9 magnitude earthquake that occurred near San Clemente in 1951. Generation times for tsunami producing dislocations can be as large as several minutes. An earthquake could therefore initiate a large submarine landslide, which could then become a tsunami source.

Seven per cent of Southern California earthquakes have submarine epicenters (Clements and Emery, 1947), and yet only two or three locally generated tsunamis are known to have occurred off Southern California since 1800, none in the San Diego area. Joy (1968) points out that if the San Clemente Island fault and the Agua Blanca fault in Mexico (Fig. 2) "actually constitute a single larger feature, . . . it could represent a standing threat to San Diego County." He concluded, however, that "it is entirely speculative to suggest at this time that any significant threat exists. Certainly the nonoccurrence of tsunamis generated nearby, even if for the geologically short period of 170 years, cannot be ignored."

Whalin et al. (1970) have modeled the wave run-up which would occur at San Diego if a tsunami were to be generated locally. The period of the waves studied were intermediate, falling between values associated with the wind-wave and the typical tsunami-wave spectra; the longest studied was 186 seconds. Waves of this period are generated near tsunami sources, but become attenuated at great distance. They concluded that "the narrow, low-lying Silver Strand, the City of Coronado, California, and portions of North Island were completely inundated for most conditions tested. Wave heights in the restricted harbor entrance approached 26 feet . . . bores were observed in the smaller partially enclosed basins, bays, and creeks surrounding the harbor."

LOCAL RISK REGIONALIZATION

Subdivision of earthquake risk into local regions depends on knowledge of local faults and on the response of the surficial geology to shaking.

Risk due to surficial and basement faulting.—Surficial faults in the San Diego area present zones of increased risk due to the fact that the effects of shaking may be different on opposite sides of a fault. Where the fault zone itself is of considerable width, a third zone, possibly having a still different response, must be considered. Construction in zones of such variable response can result in earthquake-induced problems, such as differential settling, etc.

Figure 10 shows the faults in the San Diego area which are considered to be either "active" or "potentially active." The La Nacion fault has a verified length of approximately 15 miles. As this fault offsets Holocene materials at least locally and demonstrates repeated movement of late Pleistocene materials, it must be considered an active fault. The maximum credible event that could be expected would be of magnitude 6.8 with expected acceleration approaching 0.4 g.

Determining the maximum credible surface breakage for basement faults deduced from gravity data is not a reliable method of estimating maximum credible earthquake magnitudes. The approximate locations and sense of movement of these faults (Fig. 11) do, however, provide clues to the thickness of the less competent overlying sediment, to the location of zones along which aftershocks remote to large events are apt to occur, and to the location of zones along which local earthquakes are more apt to be centered.

Response of surficial materials.—Seed (1969) stated that "analysis of the effects of soil conditions on damage due primarily to the effects of ground shaking requires an understanding of the complex interrelationships between the effects of soil types, soil depth, the

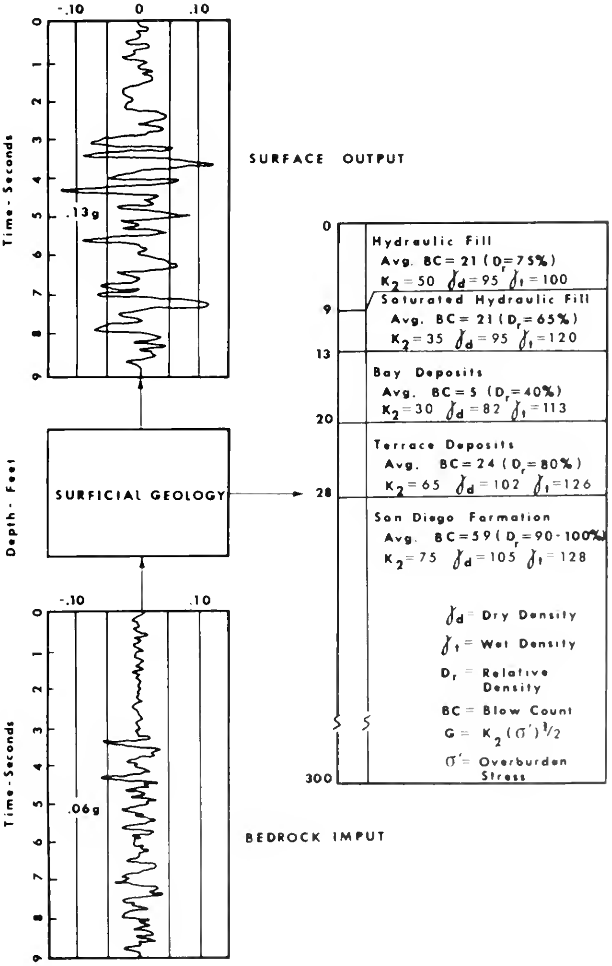


Figure 20. Input acceleration, surficial geology, and resulting surface acceleration output (Equivalent damping 7.8%).

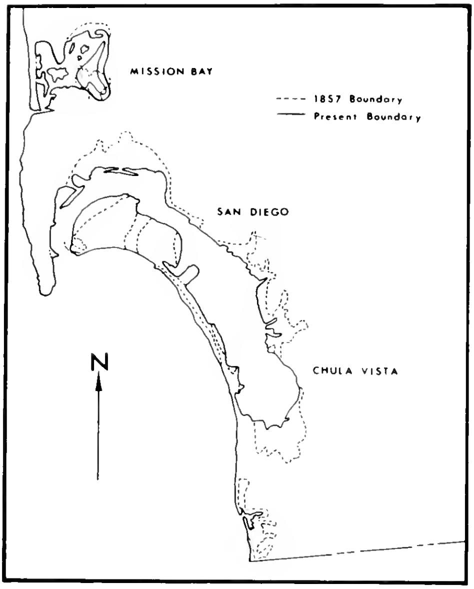


Figure 21. Areas which have been filled since 1857. (Sources: U.S.G.S. Water Supply Paper 446; San Diego Bay, 1859 Coast Survey Office; San Diego Union, June 29, 1971).

amplitude of ground motions, the frequency characteristics of ground motions, and the structural characteristics of buildings in order to analyze damage resulting from past earthquakes or prevent damage in future earthquakes."

From the standpoint of local zoning, a mappable parameter which reflects the maximum expected shaking is desired. One approach, illustrated in Figure 19, is to calculate the maximum probable shaking at the bedrock-soil interface and compute the theoretical response expected at the surface of the ground (see Seed, 1969). From these data one can compile a series of maps which allow rough reconstruction of the maximum expected shaking for any particular period of shaking. Housner (1952) suggested that the area under the particle velocity spectrum over a range of shaking rates be used to define the local intensity of shaking. This measure of intensity would be obtainable directly from such maps.

To calculate the theoretical response at the ground surface, values of the shear modulus, unit weight, and damping factor are needed as a function of depth from the surface to bedrock. Care must be taken in selecting these values due to the nonlinearity of some of these "constants" with increasing strain. The seismic input should be either an average smoothed response compiled from earthquakes having magnitude and epicentral distance similar to the maximum probable event expected to affect the San Diego area, or a "white" input. An advantage of using a "white" input is that it allows separation of effects due to surficial materials from those due to the transmission path; it also provides a mappable output from which the response for any input is readily calculable.

We have carried out recently a similar analysis to determine the response of the surficial materials to shaking and response of simple structures to the resultant velocity of surface shaking. Figure 20 shows the acceleration time history input at the top of the Cretaceous sediments, the assumed geologic column overlying these sediments, and the theoretically predicted acceleration time history which would result at the surface. For the geologic parameters and acceleration levels assumed, the maximum acceleration is increased by more than a factor of two (i.e. from 0.06 g to 0.13 g) in traversing the 300 foot column. Most of this amplification occurs in the upper 28 feet, which is assumed to be composed of loosely consolidated sediments. The stratagraphic column assumed is typical of much of the area surrounding the bays to which fill has been added (Fig. 21). These filled areas represent zones of maximum seismic risk.

The spectrum shown in Figure 22 approximates the particle velocity spectrum at the earth's surface for the conditions and assumptions described on Figure 20. If data of this

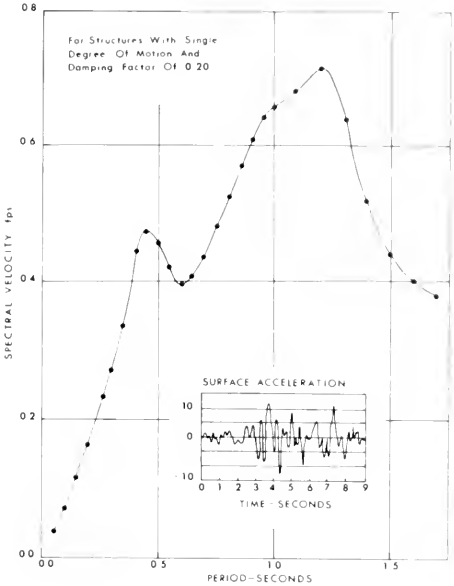


Figure 22. Spectral velocity derived from surface acceleration.

sort were available throughout areas of maximum expected seismic risk, considerable progress could be made toward rational seismic-risk zoning.

CONCLUSIONS AND RECOMMENDATIONS

In this paper we have consolidated the background information developed by various experts in the field of geology, seismology, and earthquake engineering with specific application to the San Diego area, and have formed the following conclusions and recommendations.

1. San Diego is in an active seismic area.
2. A Richter magnitude 7.3 earthquake on the Elsinore fault having a repeat interval of 60 years appears to be the "maximum probable" earthquake for San Diego. For most construction the "maximum probable" earthquake is recommended for design. In the case of structures such as hospitals which must remain operative during times of disaster and special installations such as nuclear reactors design should be based on the "maximum credible" earthquake.
3. Design studies should further consider the possible effects of a magnitude 7.8 "maximum probable" earthquake on the San Jacinto fault because of its longer expected duration of shaking.
4. Structures built on filled areas underlain by loose embayment type soils such as those found in San Diego and Mission bays are particularly susceptible to earthquake damage. Because of the numerous structures planned for such areas, a comprehensive study of the effects of earthquake-induced forces in embayment deposit areas is strongly recommended.
5. A seismic sea wave (tsunami) initiated within the offshore California Continental Borderland is possible. Such a wave could have a damaging effect on low-lying shoreline areas along the Pacific Ocean and in mouths of bays.

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APPENDIX
Important Earthquakes, Modified and Up-dated from Joy (1967).

Type, Date, and Time z indicates GMT * indicates PST	Generating region and epicenter, if known. Magnitude (Arabic) Modified Mercalli Intensity (Roman)	Remarks and References
Local earthquake April 11, 1769	San Diego (severe)	Diary of Miguel Costanso, Portola Expedition 1769-1770. Bancroft (Works, Vol. 18, p. 127); Wood (1916); Townley & Allen (1939).
Coastal earthquake November 22, 1800, 1330*	Southern California (VII)	The adobe walls of San Diego Presidio barracks were cracked. California Archives Provincial State Papers XXI, p. 135; Hittell (1898); Wood & Heck (1966); Trask (1864); Bancroft (1883) p. 86, 654, 658.
Local earthquake May 25, 1803 (no tsunami noted)	San Diego, near 32.5°N 117°W	Slightly Damaged San Diego Mission Church, Wood & Heck (1961); Bancroft (1883) p. 106, 114; Wood (1916).
Regional earthquakes May, 1812	Southern California	Southern California was subjected to nearly continuous shocks for 4 ½ months. The inhabitants abandoned their houses and lived out of doors. Townley & Allen (1939).
Local earthquakes October 12, 1812	San Diego	Shocks for 40 days. Townley & Allen (1939).
Coastal earthquake December 8, 1812 about 0700*	Coastal Southern California (VIII-IX)	*Mission San Juan Capistrano destroyed.* Strongly felt at San Diego, but no damage to San Diego Mission. Probably on Inglewood-Newport fault. Bancroft (1883) p. 347-348; Lounderback (1948); Heizer (1941) p. 221; *S. F. Bulletin,* March 5, 1864, March 19, 1864, p. 3, c. 4.
Local earthquake June 23, 1843, 1530*	San Diego (very severe) Baja California	Southern California to Mexico. Townley & Allen (1939); Wood & Heck (1966).
Local earthquake September 16, 1849	Santa Ysabel San Diego County	Probably on the Elsinore fault. Townley & Allen (1939).
Local earthquake September 22, 1849	Carrizo Creek San Diego County	Probably on Elsinore fault. Townley & Allen (1939).
Local earthquake April 12, 1852	San Diego	Townley & Allen (1939).
Local earthquakes October 26, 1852 November 27-30, 1852 (no tsunami noted)	San Diego (IX-November 29, 1852)	November 29 two minute shock in San Diego followed by light quakes for several days. Trask (1856); Wood, (1916); Townley & Allen (1939).
Possible remote tsunami November 1853	Kuril Islands	Reported to be a large tsunami. Small waves possibly recorded on newly installed San Diego gage. Solov'ev and Ferchev (1961); Iida, *et al.,* (1967); U.S. Coast Survey Report for 1855 (1856) p. 99.
Remote tsunami December 23, 1854, 0015z	Ansei, Tokkaido, Japan 34.1°N; 137.8°E (8.4)	*A very large tsunami.* Recorded at San Diego +12.6 hrs. later, 0.5 feet, 31 min. avg. period. Bache (1856); Iida, *et al.,* (1967); Shuck (1869).
December 24, 1854, 0800z	33.2°N; 135.6°E (8.4)	Two tsunamis, whose effects along this coast were more or less merged together.
Local earthquake September 20, 1856	San Diego County (VII)	Walls cracked, ceilings fell, and local Indians were terrified. Cattle stampeded at Santa Ysabel. Wood & Heck (Rev. 1966).
Several local earthquakes May 27, June 13-14, 1862 October 21, 1862 January 25, 1863, 0200* July 7, 1963, 1311*	All at San Diego	May 27, severe shock at San Diego, Temecula, Probably on Elsinore fault. Track (1864); Bancroft, MMs cited by Townley & Allen (1939).
Local earthquake April 19, 1865	San Diego	Severe shock. Townley & Allen (1939).
Remote tsunami April 2, 1868	S. E. Hawaii	Recorded at San Diego, 0.33 ft; 30 min. avg. period. *S. F. Bulletin,* June 13, 1868; Iida, *et al.,* (1967); Heck (1947); Townley & Allen (1939).

Type, Date, and Time z indicates GMT * indicates PST	Generating region and epicenter, if known. Magnitude (Arabic) Modified Mercalli Intensity (Roman)	Remarks and References
Remote Tsunami August 13, 1868, 1645z	N. Chile; So. Peru 18.5°S; 71°W	*Great Africa, Peru, Tsunami.* Recorded at San Diego 11.9 hrs. later, 1.0 ft, 16 min. avg. period. Noted at San Pedro and Wilmington, 6.0 ft, 20 min. avg. period. Proctor's article gives heights at San Pedro which are 10 times too great according to local newspaper accounts. *Alta California,* September 12, 1868; *L.A. Star,* August 14-19, 1868; Iida, *et al.,* (1967); von Hockstetter (1868); (1869); Berninghausen (1962); Proctor (1869).
Remote Tsunami August 23, 1872	Hawaii (?)	Iida, *et al.,* (1967), lists a tsunami noted in Hawaii on this date. Davidson (1872) gives August 24th as the date that a *tsunami was observed at Astoria, San Diego,* and *San Francisco.* No details.
Remote tsunami September 16-17, 1872	(?)	Davidson (1872) states that *tsunami activity was noted on these two dates on the San Diego, San Francisco, and Astoria Ore. tide gages.* No details or confirmation from other sources.
Remote tsunami November 22, 1878 Probably either that of May 10, 1877, or August 13, 1868, but misdated. (no local earthquakes reported)		Angel (1883) reports 6 ft. waves at Wilmington. Waves and damage done at San Luis Obispo, Point Sal, Avila, Port Harford, Surf, Pismo, Morro Bay, and Cayucos. *Not noticed in San Diego.* No reports from any other source for tsunamis of this date.
Offshore or coastal earthquake earthquakes and possible local tsunami August 10, 1879, 1315*	Los Angeles region (VI-V)	Sea wave noted in Santa Monica Bay. *Not reported in San Diego.* The sea wave was originally reported by Rockwood who was cited by Townley & Allen; no detail, small earthquake. No tsunami noticed elsewhere. Iida, *et al.,* (1967) cite Wood (1916) as authority for this event and accept it as a valid tsunami. Rockwood (1879); Wood (1916); Townley & Allen (1939); Iida, *et al.,* (1967).
Local earthquakes December 21, 1880 2300*	San Diego (V-strongest)	Townley & Allen (1939); Rockwood (1881).
Local earthquakes March 11, 1882, 1600* March 30, 1882, 2300* October 8, 1882, 0200* (no tsunamis)	San Diego (III-V)	Townley & Allen (1939).
Local inland earthquake February 9, 1890, 0406* (no tsunami)	San Jacinto fault (VI)	Felt in San Diego. Wood & Heck (Rev. 1966).
Offshore earthquakes February 23, 1892, 2320* Several aftershocks (no tsunamis)	Off coast N.W. of Ensenada, B.C., Mexico 31.5°N; 116.5°W (VII-IX)	*Considerable damage in San Diego.* Possibly Aqua Blanca fault. Wood & Heck (1966); Richter (1965); Holden (1898); Allen, Silver, & Stehli (1960); Townley & Allen (1934).
Local earthquake October 23, 1894	San Diego-Poway region 33°N; 117°W (VII)	Walls cracked, but no serious damage in San Diego. Wood & Heck (1966).
Local earthquake July 3, 1896, 2127* (no tsunami)	San Diego (Small)	Townley & Allen (1939).
Local inland earthquake December 23, 1899, 0425*	San Jacinto fault (IX)	Felt in San Diego. Wood & Heck (Rev. 1966).
Remote tsunami January 31, 1906, 1536z	Columbia - Ecuador 1°N; 81.5°W (8.6)	A major tsunami; *said to have been recorded in San Diego* although heights not given. Heck (1947); Iida, *et al.,* (1967).

Type, Date, and Time z indicates GMT * indicates PST	Generating region and epicenter, if known. Magnitude (Arabic) Modified Mercalli Intensity (Roman)	Remarks and References
Local inland earthquake May 15, 1910, 0747* (no tsunami)	Lake Elsinore (6.0)	Felt in San Diego. Probably Elsinore fault. Wood & Heck (1966).
Remote tsunami November 10, 1922 0433z	Atacama, No. Chile 25.5°S; 70°W (8.3)	At San Diego 13 hrs. later, 1.3 ft. max., 15 min. period. Willis, (1929); Berninghausen (1963); Iida, *et al.,* (1967).
Remote tsunami February 4, 1923 1602z	Kamchatka 54°N; 161°E (8.3)	At San Diego 10 hrs. later, 1.3 ft. max., 10 min. period. Iida, *et al.,* (1967); Miller (1964) RED in Honolulu.
Remote tsunami April 14, 1923, 1531z	Kamchatka 56.5°N; 162.5°E (7.2)	At San Diego 14.3 hrs. later, 0.75 ft. max., 43 min. period. Iida, *et al.,* (1967); Miller (1964) RED in Honolulu.
Offshore earthquakes *and local tsunami* November 4, 1927, 1351z 0551*	Off Cape Arguello 34.5°N; 121.5°W (7.3, IX-X)	*This is the only well documented locally generated tsunami in California history.* Byerly's paper reproduces marigrams. This was a very small tsunami; very small at La Jolla and San Diego, but was detected at Hilo, Hawaii 5.1 hrs. later where it produced water level excursions of about 8 in. Along this coast the max. heights nowhere exceed those attained by great tsunamis of distant origin. According to Wilson the earthquake was felt at sea by the *S.S. Socony* which at the time was at 34°54'34"N; 121°01'00"W. La Jolla +0.9 hrs., 0.02 ft. (6mm) Nr. Port San Luis 5 ft. Surf-Pismo 6 ft. San Diego 0.02 ft. San Francisco +1.2 hrs., 0.02 ft. (4mm) (15 min. period at La Jolla, 12 min. period at San Francisco) Byerly (1930); Wilson (1928); Miller (1964) RED; Wood & Heck (1961); Iida, *et al.,* (1967); Cox (1964).
Remote Tsunami March 3, 1933 March 2, 1933, 17:31z October 2, 1933, Aftershock	Sanriku, Japan Tuscarora Deep 39.1°N; 144.7°E	*Great Sanriku Tsunami.* Santa Monica 0.35 ft. San Pedro +11.5 hrs. 0.75 ft. La Jolla 0.25 ft. San Diego – probably recorded but very small. (14 min. period at San Pedro, 11 min. period at La Jolla). Neumann (1935) Heck (1947); Iida, *et al.,* (1967); Miller (1964) BLUE in Hawaiian Island.
Coastal earthquake March 10, 1933 1754*	Long Beach, California 33.6°N; 118°W (6.25, IX)	*Destructive Long Beach earthquake.* Newport-Inglewood fault. Tide gage records ground motion at Long Beach. Nothing noticed on San Diego tide gage record. Slight activity noticed at La Jolla; possible shelf seiche. The earthquake was felt aboard ships. Aftershock felt in San Diego. Emery (1960) p. 125; Wood (1933); Bittinger (1933); Wood & Heck (1961); Eaton (1933); Clements & Emery (1947); Buwalda (1933).
Local inland earthquake December 30-31, 1934	Imperial Valley in Mexico 32°N; 114.75°W (7.1, IX, X)	Strongly felt in Tiajuana and San Diego. Also felt in Arizona and Nevada. Wood & Heck (1966).
Large local earthquake May 18, 1940, 2036* (no tsunami)	S.E. of El Centro 32.7°N; 115.5°W (7.1, X)	The surface rupture produced during this earthquake was over 40 miles long. Shocks strongly felt throughout San Diego County with some damage. Wood & Heck (1966).
Possible remote tsunami February 9, 1941, 0144*	Cape Mendocino, California 40.9°N; 125.4°W (6.6)	From inspection of local tide records; not reported elsewhere. San Diego: +14 hrs., general increase in harbor seiching. La Jolla: no unusual activity noticed. Port Hueneme: +36 hrs., general increase in harbor seiching. San Francisco: +14 hrs., some harbor seiching.

Type, Date, and Time z indicates GMT * indicates PST	Generating region and epicenter, if known. Magnitude (Arabic) Modified Mercalli Intensity (Roman)	Remarks and References
Remote tsunami December 7, 1944, 0435z	Kii, Japan 33.75°N; 136°E (8.0)	San Diego, +13.9 hrs., 0.33 ft., 14 min. period. Terminal Island, Long Beach, 0.33 ft., 16 min. period. Iida, *et al.,* (1967); Heck (1947); Bodle (1946).
Local earthquake January 1, 1946,	32°43'N; 117°25'W (3.3)	Localized shock in the coastal area running from La Jolla through San Diego and National City "Buildings swayed."
Remote Tsunami April 1, 1946, 1229*	Aleutian Islands 53.5°N; 163°W (7.4)	*A great tsunami* San Diego 1.3 ft. La Jolla +6.2 hrs. 1.4 ft. Los Angeles 2.6 ft. Port Hueneme 5.5 ft. San Luis Obispo +5.6 hrs., 8.0 ft. Avila, Calif. 3.8 ft. Munk (1953); Green (1946); Bodle & Murphy (1948); Iida, *et al.,* (1967); Miller (1964) BLUE.
Local inland earthquake September 5, 1950, 1120* (no tsunami)	Anza Desert 33.7°N; 116.8°W (4.8)	Felt in San Diego. Wood & Heck (1966).
Offshore earthquake December 25, 1951, 1647*	San Clemente Island 32.8°N; 118.3°W (5.9, VI)	Slight damage in San Diego and northern parts of the county. No tsunami. Richter (1965); Wood & Heck (1966).
Remote tsunami March 4, 1952	Hokkaido, Japan 42.2°N; 143.8°E (8.1)	"There is some coherence between the two records, with similar phases occurring at Oceanside 2 to 3 min. after La Jolla." (Munk, 1953). Los Angeles, 2.6 ft: Oceanside, 1.5 in.; La Jolla, 1.0 in. (10 min. avg. period at Oceanside and La Jolla). Munk (1953); Miller (1964) RED; Murphy & Cloud (1954); Iida, *et al.,* (1967).
Remote tsunami November 5, 1952, 1658z	Kamchatka 57.75°N; 159.5°E (8.25)	*A great tsunami.* San Diego +9.6 hrs. 2.3 ft. La Jolla +9.6 hrs. 0.8 ft. L.A. (Berth 174) +9.6 hrs. 2.3 ft. San Pedro Bkwtr. +9.5 hrs. 1.7 ft. Santa Monica +9.6 hrs. 4.7 ft. Port Hueneme +9.0 hrs. 2.3 ft. Avila, Calif. +9.0 hrs. 3.3 ft. Iida, *et al.,* (1967); Zerbe (1953); Miller (1964) RED.
Local inland earthquake June 13, 1953, 2017*	Imperial Valley 32.8°N; 115.7°W (VII)	Felt from San Diego to Phoenix, Arizona. Wood & Heck (1966).
Local earthquake March 19, 1954, 0154*	Borrego Springs 33°17'N; 116°11'W (VI)	Intensity VI at La Jolla. Felt by and awakened many in La Jolla; frightened few. Cracked plaste and a few walls in La Jolla. Murphy & Cloud (1956).
Local inland earthquake March 22, 1954, 2015*	Santa Rosa Mountains 33.3°N; 116.2°W (5.1,VI)	Slight damage from Palm Springs to San Diego, Wood & Heck (1966).
Local inland earthquake October 17, 1954, 1457*	Baja California 31.5°N; 116.5°W (5.7)	Felt in San Diego County, Probably Agua Blanca fault. Murphy and Cloud (1956) Richter (1958).
Local inland earthquake October 24, 1954, 0144*	Baja California 31.5°N; 116°W (6.0)	Felt in San Diego County. Probably Agua Blanca fault, Murphy and Cloud (1956); Richter (1958).
Local inland earthquake November 12, 1954, 0427* Two aftershocks	Baja California 31.5°N; 116°W (6.3)	Extensive damage at El Alamo, Mexico. Felt in San Diego and much of southern California. Wood & Heck (1966).
Local earthquakes January 3, 1956 February 9, 1956, 0633*	Baja California both at 31.8°N; 115.9°W 1/3/56 (4.7) 2/9/56 (6.8, VI-VIII)	Tecate, B.C., Mexico to San Diego. Probably San Miguel fault. Richter (1965); Wood & Heck (1961).
Local earthquakes February 14, 1956, 1033* 1720*	Baja California 31.8°N; 115.9°W (V-VIII) 1033* = 6.3 1720* = 6.4	Probably on San Miguel fault. Richter (1965); Wood & Heck (1961).

Type, Date, and Time z indicates GMT * indicates PST	Generating region and epicenter, if known. Magnitude (Arabic) Modified Mercalli Intensity (Roman)	Remarks and References		
Remote tsunami March 9, 1957, 1422*	Aleutian Islands 51.3 N; 175.8°W (8.0-8.5)	*A great tsunami.*		
		Ensenada, B.C. Mexico	+6.8 hrs.	3.4 ft.
		San Diego	+6.9 hrs.	1.5 ft.
		La Jolla	+6.6 hrs.	2.0 ft.
		Newport Bay	+6.6 hrs.	0.9 ft.
		Anaheim Landing	+6.7 hrs.	2.6 ft.
		Long Beach	+6.6 hrs.	1.7 ft.
		San Pedro Bkwtr	+6.6 hrs.	1.2 ft.
		L.A. Harbor Term.I	+6.6 hrs.	0.6 ft.
		L.A. Harbor Berth 60	+7.0 hrs.	2.1 ft.
L.A. Harbor Berth		L.A. Harbor Berth 174	+6.9 hrs.	3.1 ft.
		Santa Monica	+6.6 hrs.	3.0 ft.
		Port Hueneme	+6.5 hrs.	3.5 ft.
		Avila, Calif.	+5.8 hrs.	3.5 ft.
		Iida, *et al.*,(1967); Salsman (1959); Miller (1964) BLUE.		
Remote tsunami May 22, 1960, 1911z	Southern Chile 41.0°S; 73.5°W (8.25-8.5)	*A great tsunami.*		
		Ensenada, B.C. Mexico	+13.6 hrs.	8.1 ft.
		San Diego	+14 hrs.	4.6 ft.
		La Jolla	+14 hrs.	3.3 ft.
		Wilson Cove, San Clemente Island	+14 hrs.	4.1 ft.
		Alamitos Bay, Long Beach	+14.5 hrs.	4.0 ft.
		L.B. Naval Ship Yard	+14.4 hrs.	5.7 ft.
		San Pedro Bkwtr.	+14.5 hrs.	3.0 ft.
		L.A. Harbor Berth 60	+14.5 hrs.	5.0 ft.
		Santa Monica	+14.4 hrs.	9.1 ft.
		Port Hueneme	+14.3 hrs.	8.8 ft.
		Berkman & Symons (1964); Iida, *et al.*, (1967); Miller (1964) RED.		
Remote tsunami March 27, 1964, 0336z	Prince William Sound & Gulf of Alaska (8.4)	*Great Alaska Earthquake and Tsunami.*		
		Ensenada, B.C. Mexico	+6.1 hrs.	7.8 ft.+
		San Diego	+6.2 hrs.	3.7 ft.
		La Jolla	+5.8 hrs.	2.2 ft.
		Newport Bay	+5.8 hrs.	1.3 ft.
		Alamitos Bay, Long Beach	+5.9 hrs.	2.8 ft.
		L.A. Harbor Berth 60	+5.8 hrs.	0.4 ft.
		Santa Monica	+5.7 hrs.	2.5 ft.
		Avila, Calif.	+5.4 hrs.	5.0 ft.
		Spaeth & Berkman (1965); Iida, *et al.*, (1967).		
Offshore earthquake December 22, 1964 (No tsunami noted)	N.W. of Ensenada, B.C. Mexico; 31.9°N; 117.1°W (5.5)	Possibly on submerged portion of Agua Blanca fault. Richter (1965).		
Remote tsunami October 17, 1966	Near coast of Peru 10.7°S; 78.7°W (7.5)	San Diego, +10.1 hrs., 0.25 ft. Berkman & Carrier (1967); Iida, *et al.*, (1967).		
Local inland earthquake April 8, 1968, 1828*	Ocotillo Wells, Calif. 33°10.5'N; 116°07.3'W (6.5, VII)	Felt by and frightened all in San Diego. Intensity VI in San Diego. Cracks opened on the west side of Sunset Cliffs Boulevard. Plaster cracked and fell in several San Diego buildings. A 9 ft. concrete retaining wall had 1/8-in. crack from top to bottom. von Hake & Cloud (1970).		
Local inland earthquake April 28, 1969, 1521*	Borrego Springs, Calif. 33°21'N; 116°21'W (5.9, VII)	Intensity V in San Diego.		

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THE FEEDING TECHNIQUES OF STILT SANDPIPERS AND DOWITCHERS

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P. J. K. BURTON

ABSTRACT.—This paper presents descriptive and quantitative observations of feeding behavior of Stilt Sandpipers (*Micropalama himantopus*) and dowitchers (*Limnodromus* spp.). Stilt Sandpipers make frequent use of "stitching"—a series of extremely rapid jabs into the mud surface, performed while pivoting the body or walking. This is probably a means of tactile foraging; visual searching behavior is also used. Dowitchers do not "stitch" but employ isolated (though frequent) deep jabs and probes, which are often prolonged and vigorous. They show little evidence of hunting by sight. The differences provide further evidence for assigning the Stilt Sandpiper and dowitchers to the Calidridinae and Scolopacinae, respectively. Significant differences in anatomy of the feeding apparatus are summarized.

The great diversity in bill shape and size among shorebirds leads one to expect a corresponding diversity in feeding techniques and methods; yet there have been few really detailed and quantitative studies of these techniques. One of the most thorough, concerning European shorebirds, is a little known study by Streefkerk (1960). Detailed descriptions of feeding methods in five species of shorebirds, with a summary of information available for others, are given by Burton (1969, and in press). The present paper concerns dowitchers (*Limnodromus* spp.) and the Stilt Sandpiper (*Micropalama himantopus*). Various descriptions in the literature suggest a close similarity between the feeding methods of these birds, and both are often stated to employ a "sewing-machine action" (e.g., by Peterson, 1947). The best accounts are those of Bent (1927) and Palmer (1967), but these include observations from a variety of sources and are insufficiently detailed for comparative purposes.

Dowitchers and Stilt Sandpipers have often been considered closely related, as indicated by their juxtaposition in many North American lists until recently. According to an alternative view (Lowe, 1931; Peters, 1934) the Stilt Sandpiper is closely related to *Calidris* (Scolopacidae, subfamily Calidridinae), while dowitchers are allied to the snipes, *Gallinago* spp. (subfamily Scolopacinae). This view is reinforced by recent work (Jehl, 1968; Burton, in press). As the Calidridinae and Scolopacinae differ extensively in feeding methods, the alleged similarity in this respect between dowitchers and the Stilt Sandpiper is surprising. Therefore, during the course of a visit to Texas during the latter half of April, 1969, I took the opportunity to make detailed observations on their feeding behavior.

METHODS

Stilt Sandpipers were watched principally at a brackish pool lying between agricultural land and mesquite brush near Alamo, lower Rio Grande valley, Texas. Dowitchers (mostly *L. griseus*) were watched at tidal pools on the mudflats of the west (Laguna Atascosa) shore of Padre Island, near Port Isabel, Texas. Observation was by telescope (30× to 60×). Quantitative aspects were studied by dictating running commentaries into a portable tape recorder. This provided data amenable to statistical treatment, and to timing of various items; some timed data were also obtained in the field, using a stop watch. Prolonged examination of qualitative aspects of behavior were also made, in addition to the taped recorded commentaries. The total observation time (about 20 hours for each species) is relatively brief but served to clarify considerably the similarities and differences between the two species in feeding methods.

STILT SANDPIPER

Three principal types of feeding action were distinguished:

a. *Pecks.*—These are extremely brief movements made into water, or at its surface, or

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into the surface of exposed mud.

b. *Probes.*—Longer movements in which the bill is thrust into the mud for some depth. As in the case of Dunlin (*Calidris alpina*) studied by Burton (in press), these are normally made with a very rapid up-and-down quivering action. This, and their distinctly longer duration, are the only means of distinguishing them from pecks when (as frequently happens) the insertion of the bill into the mud cannot be seen.

c. *Stitching.*—This term is used by Burton (in press) to refer to a feeding action which appears to be characteristic of the Calidridinae. It has previously been described from several members of the subfamily by Streefkerk (1960), Holmes (1966), and others. Basically, stitching consists of very rapid series of shallow jabs into the mud surface, made while on the move; Holmes (1966) refers to it simply as a "rapid series of jabs." Stitching and probes may appear closely similar, and in fact intergrade; probes are generally made in one spot, and usually deeper and more vigorously than stitching.

The Stilt Sandpipers invariably fed on mud covered by a layer of water, sometimes barely covering the feet, but usually to about tarsus length, and commonly to belly depth. A notable characteristic mentioned by several authors is their lack of mobility. This is especially striking by comparison with other species feeding near them in similar situations, in this case Lesser Yellowlegs (*Tringa flavipes*) and Wilson's Phalarope (*Phalaropus tricolor*). This lack of mobility is also a contrast to most other members of the Calidridinae, which, however, generally feed in shallower water or on exposed substrates.

Several accounts of the habits of the Stilt Sandpiper mentioned a characteristic attitude, with neck outstretched and bill pointed vertically down. This attitude is indeed well marked in this species, though a similar attitude is quite often assumed by other shorebirds (e.g. Redshank, *Tringa totanus*) wading in fairly deep water. It is restricted to spells of feeding by means of pecks; stitching series are carried out with the bill inclined at about 80° to the horizontal, as in other Calidridinae. The more perpendicular bill carriage where pecks predominate is probably related to the fact that these are used in hunting by sight; the perpendicular attitude may serve to minimize errors due to refraction. Stitching, on the other hand, appears to be a form of trial probing with the object of detecting prey by tactile means. The behavior of the birds while making pecks gave a strong impression that they were engaged in visual search. They would walk slowly about, on a zig-zag path or backwards and forwards, not covering a great amount of ground, but maintaining the outstretched neck and perpendicular attitude throughout.

Stitching usually involves even less mobility, and one bird may spend an hour or more in an area only a yard or so across; similar lethargy mentioned by Bent (1927) and Palmer (1967) probably refers to birds feeding in this way. By contrast with most *Calidris* species, which usually stitch while walking, Stilt Sandpipers generally carry this out while standing still, the only movement usually being a side to side pivoting at the pelvis combined with neck action, so that the stitching jabs are made around it in a semicircle. The tracks left by this process should have been highly characteristic if there were any, but the mud surface was much too soft to retain indentations. The bird seen swinging its immersed bill from side to side mentioned by Bent and Palmer was very probably stitching. Palmer's comparison with a side to side action seen in the Greater Yellowlegs (*Tringa melanoleuca*) is probably misleading. A side to side action is shown by a variety of Tringinae, especially Redshank (*T. totanus*) and Willet (*Catoptrophorus semipalmatus*), but close examination shows it to be accompanied by very rapid opening and shutting jaw movements, a feature never seen in the stitching of Calidridinae which it superficially resembles.

Stitching was usually performed in more shallow water than feeding by pecks, though some prolonged spells of stitching took place with the head completely immersed, only the quivering and slow pivoting of the body indicating what was happening. On the rare occasions when stitching was carried out on virtually exposed mud, it could be seen that the bill was very slightly open at the tip, as in Dunlin. The duration of 321 stitching sequences timed gave a mean of 2.3 secs with a maximum of 13.7 secs. This is somewhat shorter than that recorded for Dunlin (mean 3.9, maximum 25.7) on a tidal mudflat by Burton (in press) though it is pointless to pursue the comparison too closely.

Probes were relatively brief, the great majority lasting under one second. Since most were made under water (usually of belly depth), the depth to which the bill was inserted into the mud could not normally be seen; when visible, the amount of insertion appeared not less than half the bill length, and frequently its full length. No changes of bill orientation were seen during the course of a probe. The great majority of probes were isolated, but up to six have been observed in one spot, presumably in efforts to capture a particularly difficult prey animal. Most obvious captures (indicated by head jerking and swallowing movements) followed probes rather than pecks; probably the items acquired by pecking were mostly so small that their capture went unobserved.

The proportions of pecks, probes and stitching sequences in 52 minutes of timed observations were recorded (Table 1). Each stitching sequence was counted as a single movement. The mean number of feeding movements per minute was 40.2 (min. 10, max. 82). High rates were associated with a large proportion of pecks—not surprisingly, since pecks are the most rapid movements. Conversely, low rates are associated with a high proportion of spells of stitching, which are of longer duration than pecks or probes. Interestingly, highest probing rates occur around the middle of the range of total frequencies, and relatively few probes followed stitching sequences, contrasting with the Dunlin studied previously (Burton, in press). Evidently visual signs provided the clues leading to a probe in the majority of cases. Stitching thus appeared a relatively inefficient method of locating prey in this area, though it may have been more important near the edges of the pool, where prey were possibly deeper lying. In other situations, and especially at night, it may well be of much greater value.

Table 1. Summary of timed observations on feeding movements of individual Stilt Sandpipers.

Rate (Total movements per minute)	Number of minutes	Combined totals	Stitching	Pecks	Probes
10 to 19	5	79	77	2	0
20 to 29	8	192	123	32	37
30 to 39	14	483	8	197	278
40 to 49	13	598	19	273	306
50 to 59	6	317	34	269	14
60 to 69	3	190	3	151	36
70 to 79	2	145	6	126	13
80 to 89	1	82	0	44	38
Overall total	52	2086	270 (12.9%)	1094 (52.4%)	722 (34.5%)

DOWITCHER

Only two types of feeding action could be distinguished:

a. *Jabs.*—These are simple, brief movements in which the bill is thrust into the mud and immediately withdrawn.

b. *Probes.*—More prolonged movements in which the bill is thrust into the mud and held there for a short time, usually accompanied by a rapid up-and-down quivering action.

Probes are generally deeper than jabs, mostly between one third and the full length of the bill (where depth of insertion could be clearly seen), whereas most jabs were to less than half the bill length. However, the main distinction was the brevity of jabs, which were generally too rapid for accurate timing, though apparently under 0.5 seconds in duration. 103 probes timed averaged 1.7 seconds, with maxima of 4.1 and 7.3 seconds.

This classification is to some extent arbitrary, but probably most jabs are trials made in searching for prey by tactile means, while probes include most of the actions in which prey are actually captured. Probes were often grouped in one place. When this was the case, they were often made with obvious vigor, and frequently with the capture of a prey animal, as indicated by swallowing movements. Presumably, in such cases, prey had been located, but several attempts were needed to complete its extraction.

The dowitchers were nearly all feeding in tidal pools, frequently up to belly depth; a few were watched feeding on exposed mud. Though none ever showed the remarkable attachment to one spot displayed by some Stilt Sandpipers, their mobility was not great. Most commonly, a bird would concentrate on a small area for about 30 seconds, probing around itself with pivoting movements of the body and a leisurely step or two; then walk on more briskly for a few seconds, and pause to repeat the process. Long series of jabs were sometimes made while walking steadily forwards; however, these could not be confused with the stitching of Stilt Sandpipers and *Calidris* spp., as the frequency of jabs was far less rapid, and the bill was raised well clear of the mud between each.

Rates of feeding movements were generally high. The mean rate during 61 minutes of timed observations (Table 2) was 60.6 (min. 36, max. 110). Not surprisingly, high rates coincided with high proportions of jabs. Overall, there were slightly less (48%) jabs than probes. Highest rates were recorded from birds feeding on exposed mud, which employed a high proportion of jabs, and apparently met with little success. Birds feeding in this situation were occasionally seen to make short runs and sudden turns, suggesting pursuit of prey located by sight.

Between feeding actions, dowitchers held the bill inclined at about 70° or 80° to the horizontal. An attitude with neck outstretched and bill pointed vertically down, as in Stilt Sandpiper was never seen. The orientation of the bill was rarely altered to any significant extent during the course of a probe, though on one occasion the bird turned a full circle around its bill during a single probe. The probes themselves were sometimes made with considerable force and vigor, quite unlike anything seen in the Stilt Sandpiper.

No prey item was at any time seen. Several samples of mud in areas favored by dowitchers were dug up and carefully sifted, but the only animal species found was the small (5 to 9 mm.) bivalve *Lyonsia hyalina* Conrad. This mollusk is evidently abundant in the area, and may well have been the main prey of the dowitchers observed.

Table 2. Summary of timed observations on feeding movements of individual dowitchers.

Rate (Total movements per minute)	Number of minutes	Combined totals	Jabs	Probes
30 to 39	2	74	10	64
40 to 49	8	359	96	263
50 to 59	20	1099	455	644
60 to 69	18	1164	591	573
70 to 79	10	726	402	324
80 to 89	2	162	117	45
110	1	110	93	17
Overall total	61	3694	1764 (47.8%)	1930 (52.2%)

COMPARISON

Dowitchers and Stilt Sandpipers certainly show some similarities while feeding. Both forage largely in pools and show a generally high rate of feeding movements combined with low mobility. Their feeding actions are mostly simple, fairly regular movements, made more or less straight downwards. The impression of similarity is heightened by contrast with other waders feeding in the same situations, notably Greater and Lesser Yellowlegs, whose brisk actions include dashes and sudden turns.

Nevertheless, there are well marked and important differences. The most obvious of these is the absence of "stitching" in Dowitchers–notwithstanding the fact that the actions of both birds have been likened with some justice to a sewing machine. Despite the similarity of imagery, it must be remembered that the term "stitching" as used here and elsewhere (Burton 1971, and in press) applies specificially to an extremely rapid series of shallow jabs, made with minimum head movement. This action, seen in many calidridine sandpipers, including the Stilt Sandpiper, was never observed from dowitchers during the course of these observations. Conversely, Stilt Sandpipers rarely used deep test probes, whereas the jabs of dowitchers regularly penetrate to a third or more of their considerable bill length. Probes in both species are made with a similar quivering action, but Stilt Sandpipers never exhibit the vigor and forcefulness which is often shown by probing Dowitchers.

The attitude with neck outstretched and bill pointed perpendicularly down is characteristic of Stilt Sandpipers but is rarely shown by Dowitchers. As explained earlier, this attitude is probably connected with hunting by sight, and indicates the much greater importance of vision for feeding in the Stilt Sandpiper—a factor which underlies other differences between their feeding techniques. Stitching as a means of tactile foraging increases the chances of contact with prey lying near the surface in a given time, but must be relatively inefficient for detecting deeper lying prey. The individual jabs in a stitching series are shallow, and probably only penetrate the soft surface layer of water covered mud; they require relatively little anatomical specialization, and form part of a generally more versatile range of feeding techniques. The generally deeper jabs of dowitchers stand a greater chance of detecting deep lying prey, but there are many fewer in a given time. Also, since the head is fully raised and lowered between each one, and the deeper penetration involves entering a harder substrate, the amount of energy expended in proportion to the number of contacts with prey may well be greater in dowitchers. This is probably offset to some extent by greater tactile sensitivity in dowitchers. Moreover, dowitchers are capable of handling considerably larger prey than Stilt Sandpipers, and since these tend to be deeper lying dowitchers may be expected to encounter more of them. The feeding technique and anatomy of dowitchers thus probably depends on relatively infrequent contacts with larger prey.

Detailed information on anatomy of the feeding apparatus in shorebirds is given by Kozlova (1961-62) and Burton (in press). The points of difference between dowitchers and Stilt Sandpipers summarized below appear particularly relevant to a comparison of feeding methods.

a. The bill axis is considerably more downwardly directed relative to the cranium in dowitchers.
b. The dorsal bar of the upper jaw is greatly reinforced in dowitchers, and is almost in contact with the ventral bar. In the Stilt Sandpiper, both ventral and dorsal bars are thin and widely separated.
c. Hexagonal pits, indicating clusters of tactile receptors (Herbst's corpuscles) are much more numerous at the tips of the jaws in dowitchers.
d. M. protractor quadrati, which raises the tip of the upper jaw, is enormous in dowitchers by comparison with the Stilt Sandpiper.
e. M. adductor externus (of major importance for jaw closure and gripping prey) is relatively larger in dowitchers, and of more complex structure, with more pinnate fiber arrangements—a modification to increase the force of contraction over short distances.
f. M. rectus capitis superior, a flexor of the head and anterior part of the neck, lacks attachment to vertebra 4 in the Stilt Sandpiper. This curious feature, unique among shorebirds, is probably connected with its characteristic head attitude with bill pointed straight down, while feeding in water.

In most of these, and other anatomical features of head and neck, the Stilt Sandpiper is typical of the Calidridinae, whereas dowitchers closely approach the Scolopacinae, though showing some similarity to members of the Tringinae. Dowitchers have by some authors (e.g., Kozlova, 1961-2) been considered more closely allied to godwits, but Jehl (1968) has produced strong evidence for their close relationship to the Scolopacinae, first proposed by Lowe (1931). The results of this study bear out Jehl's view. The feeding technique of dowitchers closely resembles that of Snipe (*Gallinago gallinago*), described in detail by Burton (in press), in the great reliance of both on simple probing, and in the manner, timing, and disposition of probes. They certainly show little resemblance to the versatile techniques of the much more mobile godwits. Similarly, the feeding behavior of Stilt Sandpipers, with its frequent use of "stitching" is very similar to that of other Calidridinae, though with modifications for feeding in deeper water than most of the subfamily.

In any further study of feeding in dowitchers and Stilt Sandpipers, it would be desirable to observe them in an area where both forage together. I saw them in close proximity on various stretches of shore in the Laguna Atascosa Refuge, but was not able to prolong my observations there. Such a comparison might throw further light on the results obtained by Recher (1966) in a comparison of waders sharing a stretch of shore. It would be particularly interesting to know whether dowitchers (the larger species) take a narrower spectrum of prey, including more large items, than the Stilt Sandpiper. Such a difference might be expected from Recher's analysis of diets in relation to body size, though in the experience of Jehl (pers.comm.) the reverse seems to be the case at Churchill, Manitoba, where the two species often feed in close proximity.

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THORACIC CIRRIPEDIA FROM GUYOTS OF THE MID-PACIFIC MOUNTAINS

M. V. LAKSHMANA RAO AND WILLIAM A. NEWMAN

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ABSTRACT.—Knowledge of the fauna of oceanic seamounts is meager. To determine whether seamounts serve as stepping stones for the distribution and dispersal of sedentary faunas across oceanic barriers, and their role in the biogeography and speciation of deep-sea faunas, an expedition went to the Mid-Pacific Mountains in the summer of 1968. This paper reports on Thoracic Cirripedia from six guyots located there.

Nine species were identified, of which four are new. Three of the new species are allied to forms from the Indo-Pacific; the fourth is closely related to a Hawaiian species. Of the five previously known species, two are widely distributed in the Indo-Pacific, two are cosmopolitan and one is endemic to Hawaii. Thus, the affinities of the cirripeds are predominantly Indo-Pacific.

Virtually nothing is known of the faunas of submarine archipelagos. One would like to know specifically what role seamounts serve as stepping stones at bathyal depths, what importance they have in the evolution of deep-sea faunas, and to what degree these faunas tend to be endemic. In the summer of 1968, William A. Newman and Richard H. Rosenblatt, both of the Scripps Institution of Oceanography, John A. Allen of the Dove Marine Laboratory, England, and the late Edwin C. Allison of San Diego State College, and Harry S. Ladd of the U.S. Geological Survey staged an expedition (Styx-Leg 7) aboard the *R/V Alexander Agassiz* to investigate both recent and extinct faunas of the Mid-Pacific Mountains.

The Mid-Pacific Mountains are a chain of seamounts located between 17° and 23°N, with the main axis extending between 165°W and 170°E for some 2,780 km (Fig. 1). This chain of seamounts, part of the Marcus-Necker Ridge, forms the northeastern portion of the region designated as the Darwin Rise (Menard, 1964). Numerous flat-topped seamounts occur along this chain at depths ranging between approximately 1,000 and 1,700 m. Shallow water megafossils taken by dredging indicate that many flat-topped seamounts are guyots, land forms produced by subaerial erosion and marine planation at a time when they broke the sea surface. The fossils, particularly the rudist molluscs and associated organisms such as corals, indicate that the seamounts persisted as shallow water banks and reefs up to the mid-Cretaceous before subsiding more than a kilometer to their present depths (Hamilton, 1956). Prior to this time, the Mid-Pacific Mountains formed an extensive island chain, comparable to the present Hawaiian Archipelago. Since formation, the chain has migrated northwest some 25° to its present position (Lonsdale *et al.*, 1972). Consequently the chain has always been beneath tropical waters.

The tops of the guyots have been altered to varying degrees since they subsided (Karig *et al.*, 1970; Lonsdale *et al.*, 1972). Virtually all exposed hard surfaces, such as rudist reefs, limestone, exhumed chert and basalt outcrops are covered with ferromanganese oxides of varying thickness. For some reason fresh manganese-coated surfaces appear unfavorable for attachment of benthic organisms and the numerous large slabs and nodules dredged from the Mid-Pacific Mountains were devoid of them. Generally pieces of pumice, apparently of recent origin, and occasional small rocks (cherts) are free of manganese coatings. Otherwise, uncoated hard surfaces on which sedentary organisms might be expected to settle and attach are limited to the hard parts of living organisms such as spicules of siliceous sponges, shells of gastropods, barnacles and corals usually occurring on soft sediments. In the present collection cirripeds were taken from all these with the exception of the corals.

Sampling methods were varied. Pipe and chain-bag dredges were employed on hard bottoms and outcrops; otter and beam trawls over soft bottoms. A variety of benthic invertebrates was recovered and the present paper reports on the class Cirripedia. Only mem-

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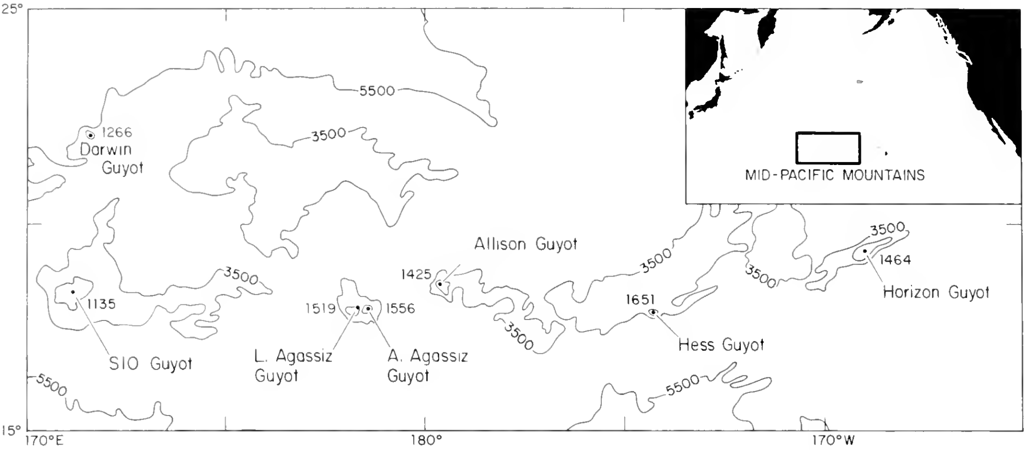

Figure 1. Chart indicating the location of the guyots sampled on the Mid-Pacific Mountains during the Styx-7 Expedition. Depths in meters. Numerous other guyots in the region not indicated. Of the guyots indicated, only Darwin, Hess and Horizon have been named previously.

bers of the order Thoracica were encountered on the six guyots sampled (Table 1). (Station numbers for this leg of the expedition were numerical: year, month, day, 1, 2 or 3 etc.).

Of the nine identifiable species found, four are new, the relative number of new species being comparable to that of the Antarctic (Newman and Ross, 1971). One cannot assume that all four new species from the Mid-Pacific Mountains are endemic to the region because knowledge of deep-sea cirripeds is meager (see Zevina, 1972). While one of the new species is most closely related to a species known previously only from Hawaii, the remaining three show close affinities with forms widely distributed in the Indo-Pacific. Of the five previously known species, two are known from the Indo-Pacific, one from Hawaii (and thus perhaps an Indo-West Pacific derivative endemic to Hawaii), and two are cosmopolitan. Thus, as one might have anticipated, the affinities of the cirriped fauna of the Mid-Pacific Mountains are primarily with the Indo-Pacific. The fishes show comparable affinities (R.H. Rosenblatt, pers. comm.).

While virtually nothing is known of the faunas of other submarine archipelagos, the fauna of Shoal Guyot, situated at approximately 25° S, 85° W, some 1,300 km west of South America at a depth of 288 m, is relatively well known and is of considerable biogeographic interest. Hubbs (1959) published on fishes, and information on echinoderms and barnacles was given by Zullo *et al.* (1964), Zullo and Newman (1964) and Allison *et al.* (1967). One might have expected the fauna of Shoal Guyot to be strongly Eastern Pacific in character since it is separated from the Indo-Pacific by the so-called East Pacific Barrier. To the contrary however, it proved to be primarily an eastward extension of the Indo-West Pacific and thus would appear to be the eastern terminus of a series of submarine stepping stones at bathyal depths across the East Pacific Barrier (Allison *et al.*, 1967). The situation is more complicated than this however, for there is apparently a peculiar extension of neretic plankton toward this region from the west (A. Fleminger, pers. comm.), and this indicates that the eastward extension of the Indo-Pacific fauna is not simply by way of submarine stepping stones in this region, as previously supposed.

SYSTEMATIC ACCOUNT

Order Thoracica Darwin, 1854

Suborder Lepadomorpha Pilsbry, 1916

Family Scalpellidae Pilsbry, 1916

Genus *Arcoscalpellum* Hoek, 1907

Arcoscalpellum alcockianum (Annandale), 1905

Figures 2 and 11G

Scalpellum alcockianum Annandale, 1905:82; 1906a:138; 1906b:392; 1913:229; 1916:129, pl. vi, fig. 5; Calman, 1918a:115; Nilsson-Cantell, 1928:6; 1931:2; 1938:7.

Table I. Cirripedia from guyots of the Mid-Pacific Mountains

Species	Horizon	Hess	Allison	Agassiz	Sio	Darwin	Previously known distributions	Sources
LEPADOMORPHA Family. Scalpellidae								
1. ?*Arcoscalpellum* sp.					1718m			Present report
2. *Arcoscalpellum alcockianum*			1418 1664m				Indian Ocean, Mozambique Channel, Gulf of Manaar; Bay of Bengal, Malay Archipelago, SW Pacific Ocean; (1098-1800m)	Annandale (1906); Calman (1918a); Nilsson-Cantell (1938)
3. *Arcoscalpellum elegantissimum* n. sp.	1652–1670m			1566m			Lukunor Atoll, Caroline Islands, (972m) (present report)	Present report
4. *Arcoscalpellum hawaiiense*			1415–1557m				Hawaii, (1460m)	Pilsbry (1907a)
5. *Arcoscalpellum michelottianum*	1584–1800m	1692–1735m	1413–1645m	1557m			Cosmopolitan – Atlantic, Indian, Pacific and Antarctic Oceans, (40-2900m)	Nilsson-Cantell (1938), Newman and Ross (1971)
6. *Arcoscalpellum radiatum*	1584–1800m		1413–1645m					Present report
7. *Arcoscalpellum rossi* n. sp.		1692–1735m	1413–1645m					Present report
8. *Mesoscalpellum gruvelii*			1429–1663m				Indian Ocean; Gulf of Aden, Laccadives; Gulf of Manaar; Andaman Sea; (794-2268m)	Nilsson-Cantell (1938)
Family Poecilasmatidae								
9. *Megalasma (Glyptelasma) pilsbryi*			1445–1557m				Indian Ocean, Malay Archipelago; Pacific and Atlantic Oceans; (1098-1647m)	Nilsson-Cantell (1938)
VERRUCOMORPHA								
10. *Verruca (Altiverruca) allisoni* n. sp.		1718–1770m	1413–1645m			1300–1353m		Present report

Material.—Styx-7, 680903-04 Sta. 1, Allison Guyot (18°31'N, 179°36'W), 1418-1664 m (otter trawl). One hermaphrodite on long glassy spicules of a siliceous sponge.

Supplementary description (hermaphrodite).—The capitular plates were adequately described by Annandale (1906b). Evidently the capitulum and the peduncle are subject to considerable variation (Annandale, 1913; Nilsson-Cantell, 1928). In the present specimen as compared to those shown by Annandale (1916), tergum is not as reduced, the scutal margin is hollowed out, and the carinal margin is angular and recedes from the carina both above and below. The scutum is not fully calcified, and the calcified portion is triangular, reaching to the lower extremity of the occludent margin of the tergum; the apex is terminal. A rostrum is present.

The peduncle is cylindrical, almost as high as the capitulum and armed with about 13 rows of transversely elongate plates. There is no basal disc in the present specimen, apparently reflecting the substrate to which the specimen is attached.

Of the arthropodal structures brief descriptions were given by Annandale and Nilsson-Cantell together with figures of the mandible, maxillae and caudal appendages. The following account and accompanying figures are supplementary.

Labrum bullate, very broad distally and mottled by pigment all over the surface; teeth very small; palp elongate, pointed at the tip and covered with plumose spines along the entire margin (Fig. 2D). Maxilla I having nearly straight cutting edge divided into two steps with about 13 strong spines above, and approximately 10 strong and 18 weaker spines of about equal length below (Fig. 2E). Maxilla II large, with superior margin long, supporting a continuous row of spines; a medial notch as noticed by Nilsson-Cantell (1928); maxillary lobe short, broad and truncate apically (Fig. 2F). Mandible with four teeth including inferior angle; first tooth well separated from second, third tooth nearer to inferior angle than to second (Fig. 2B); inferior angle supporting 30-31 short blunt subspatulate spines some of which are bifid (Fig. 2C).

Cirrus I widely separated from the rest; intermediate segments of the anterior ramus strongly protuberant, those of the posterior ramus cylindrical and 2/3 as wide; both rami prominently hairy (Fig. 2A). Cirrus II nearly 1½ times as long as cirrus I and cirrus III a little longer than the second. Cirri V and VI with terminal segments missing. Segment 18 of cirrus VI is figured (Fig. 2G); articular areas along greater curvature with 2-4 long and 1-2 short setae; lateral faces with a few short setae; interarticular areas devoid of setae and bristles. Setation ctenopod; four major pairs of setae along lesser curvature. Between each

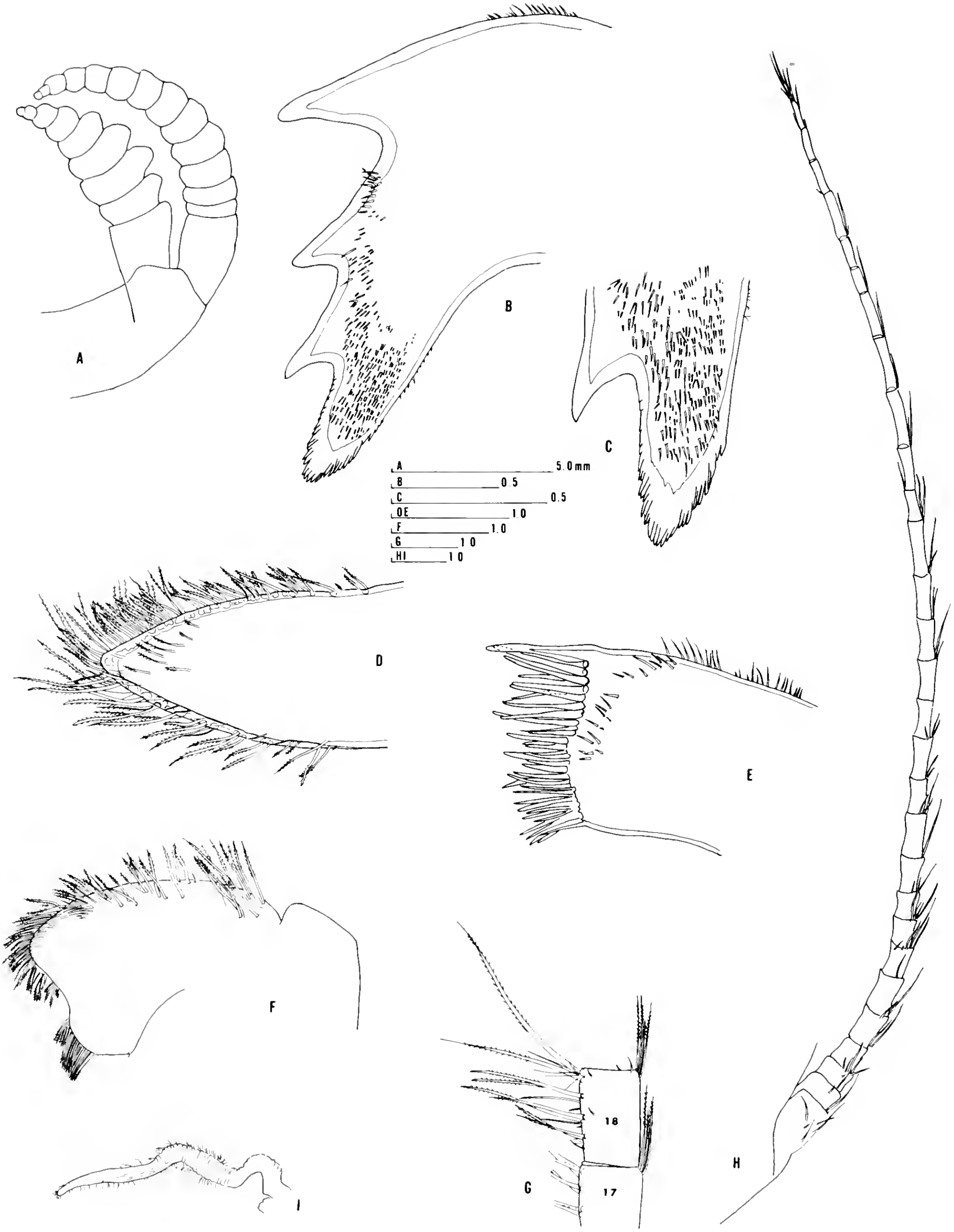

Figure 2. *Arcoscalpellum alcockianum* (Annandale), Styx-7, 680903-04 Sta. 1. A, cirrus I; B, mandible; C, third tooth and inferior angle of mandible; D, palp; E, maxilla I; F, maxilla II; G, intermediate articles of cirrus VI; H, caudal appendage; I, penis.

major pair there are 1-2 long bristles. Caudal appendage of 29 segments reaching to at least half the length of cirrus VI. Each segment with 1-5 setae along outer margin, terminal segment with a tuft of 5 short setae at tip (Fig. 2H).

Penis short, moderately stout, covered with small hairs and annulated in the proximal part; distal end narrow and covered with minute hairs (Fig. 2I).

Two complemental males were recovered, one from each pouch near the tip of the inside of each scutum. The male is sac-like, without traces of valves or cirri, but the mantle is covered with rows of spines and supports two prehensile antennae at the middle of the ventral margin.

Remarks.—This species is apparently distributed widely in the Indian Ocean, having been reported several times from the Bay of Bengal and Malay Archipelago. The only record outside of this area is in an unpublished report by Calman on specimens taken between Australia and New Zealand (Nilsson-Cantell, 1928). The present report extends its range far east into the Pacific.

Arcoscalpellum giganteum (Gruvel) from the Atlantic is closely related, but its tergum is much hollowed and the caudal appendage consists of only four segments.

Arcoscalpellum elegantissimum n. sp.

Figure 3

Material.—Styx-7, 680907 Sta. 1, Agassiz Guyot (17°50.6′ N, 178°25.0′ W), 1566 m (otter trawl) 1 spec.; 680829 Sta. 3, Horizon Guyot (19°28.0′ N, 168°52.3′ W), 1652-1670 m (rock dredge), 1 spec.; CARMARSEL Exped. Sta. 815 (off Lukunor Atoll, Caroline Islands, 10 March 1967), 972 m, 2 spec.

Depository.—U.S.N.M. no. 140943 (Holotype, Styx-7, 680907, Sta. 1) U.S.N.M. no. 140944 (Paratype, Styx-7, 680829, Sta. 3, 1 spec.) U.S.N.M. nos. 140945, 140946 (CARMARSEL Exped. Sta. 815, 2 spec.)

Diagnosis.—Capitulum with 14 fully calcified approximate plates ornamented with strong radial ridges. Carina broad basally; carinal roof traversed by longitudinal ridges; parietes well developed. Carinal latus as broad as high. Rostral latus wider than high. Rostrum ovotriangular and fully exposed. Inframedian latus higher than rostral latus but shorter than carinal latus. Mandible with 4 teeth including inferior angle. Maxilla I with straight cutting edge. Intermediate segments of cirrus VI with 2-3 major and 1 minor pair of setae. Caudal appendages with 4 partially fused segments reaching ¾ the length of first segment of pedicel of cirrus VI.

Description (female).—Capitulum globose, ovally elongate, apically pointed, hirsute especially on the carinal side; 14 fully calcified plates, white, with no indication of a persistent cuticle. Plates ornamented with prominent ridges, radiating from the umbones, intersected by faint growth lines (Fig. 3A).

Tergum nearly twice the area of the scutum, rhomboid, twice as long as wide; apex prominently acute; basicarinal angle reaching about ¾ the distance towards the base of the capitulum, nearly to the lower whorl of the plates; lateral margin partly overlapped by the upper latus. Scutum subquadrate, more than twice as long as broad; surface convex, appearing divided into halves by a diagonal angulation running from the umbo to the basilateral angle. Carina strongly bowed, broad basally, tapering towards apex; roof essentially flat, traversed by prominent longitudinal ridges; parietes well developed and also prominently ridged. Carinal latera meet for a short distance at base of carina forming a broad V-shaped margin (Fig.3B); each as broad as high, with an inwardly curved apex which projects slightly beyond the surface of the capitulum; basal and lateral margins irregular; two ledges running from umbo to base divide plate into two parts, a shallow wing-like expansion at base of upper latus and two triangular areas (one a raised carinal part adjoining the carina and the other a concave middle portion between this and the wing-like portion). Inframedian latus triangular, slightly higher than broad; apex raised above the surface of capitulum and curved inwards. Rostral latus twice as broad as high; scutal and basal margins subparallel; plate diagonally divided into halves by a faint ridge; apices of both sides partly overlapped by rostrum (Fig. 3C). Rostrum ovotriangular, broad at anterior end and narrow posteriorly (Fig. 3C). Peduncle short, ¼ height of capitulum and armored with 8-10 rows of 4-5 closely packed, narrow and elongate scales. Measurements (in mm) of the holotype follow: overall height, 16.5; height of capitulum, 13.0; height of peduncle, 4.0.

Labrum bullate, no soft setae present; crest armed with about 45 teeth. Palp elongate, triangular, somewhat rounded distally; proximal superior margin with short stiff bristles; distal border with long setae (Fig. 3H). Mandible with four teeth including inferior angle; second tooth well separated from first (Fig. 3D); inferior angle with 13-15 triangular to subspatulate teeth a few of which are bifid (Fig. 3E). Maxilla I with cutting edge feebly concave above and convex below; concave part supports 2 long, stout and 3-4 shorter, thinner spines (Fig. 3F). Maxilla II triangular in shape, lobes weakly developed; marginal setae dis-

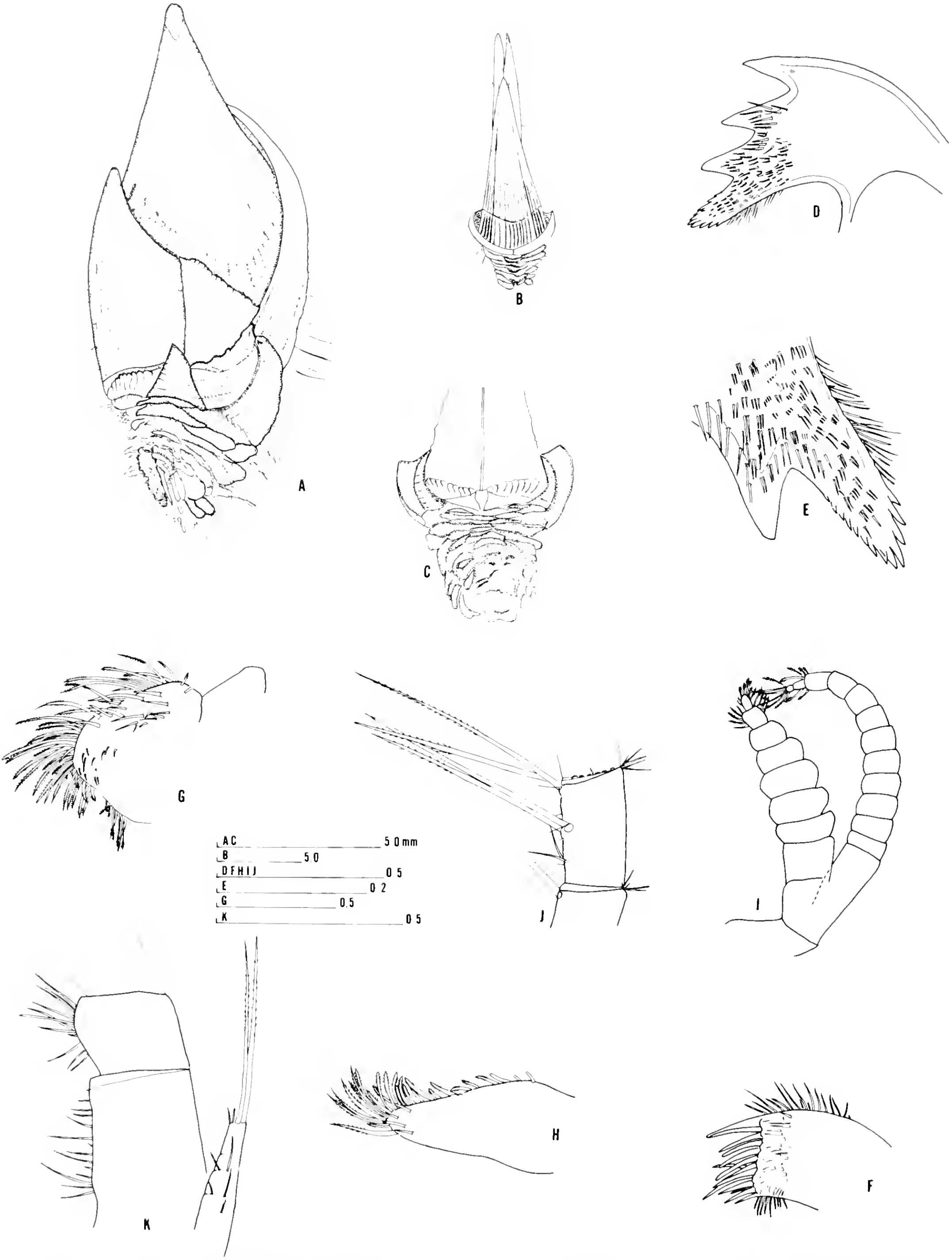

Figure 3. *Arcoscalpellum elegantissimum* n. sp., Holotype, Styx-7 680907 Sta. 1, Agassiz Guyot. A, side view of female; B, carinal view; C, rostral view; D, mandible; E, third tooth and inferior angle of mandible; F, maxilla I; G, maxilla II; H, palp; I, cirrus I; J, intermediate articles of cirrus VI; K, caudal appendage.

tributed in three clusters, but those of the superior and distal borders are contiguous; maxillary lobe short, broad and truncate apically (Fig. 3G).

Cirrus I well separated from the rest; anterior ramus shorter than posterior; intermediate segments of anterior ramus protuberant, those of posterior cylindrical and ¾ as wide; both rami clothed with long setae (Fig. 3I). Cirrus II normal. Cirri IV-VI nearly equal in length with equal or sub-equal rami. Each articulation along greater curvature of intermediate articles of Cirrus VI supporting 4-5 short slender setae. Interarticular areas along greater curvature and lateral faces free of setae. Setation ctenopod; 2-3 major pairs and 1 minor pair with 1-2 slender spines at bases of major setae (Fig. 3J). Caudal appendage composed of 4 stout, partially fused segments, extending about ¾ length of pedicel of Cirrus VI; distal article with tuft of 3-5 setae, 2 or 3 being longer than appendage (Fig. 3K). Cirral counts of the four specimens follow:

	I	II	III	IV	V	VI	Ca
Styx-7 680907 Sta. 1 Agassiz Guyot (Holotype)	$\frac{8}{12}$	$\frac{22}{20}$	$\frac{22}{21}$	$\frac{24}{25}$	$\frac{25}{17+}$	$\frac{25}{26}$	4
	$\frac{8}{13}$	$\frac{21}{22}$	$\frac{22}{24}$	$\frac{21}{25}$	$\frac{22}{24}$	$\frac{26}{26}$	4
Styx-7 680829 Sta. 3 (Paratype)	$\frac{7}{12}$	$\frac{20}{20}$	$\frac{23}{23}$	$\frac{25}{22}$	$\frac{15+}{23}$	$\frac{25}{23}$	3
	$\frac{7}{12}$	$\frac{20}{20}$	$\frac{22}{23}$	$\frac{13+}{23}$	$\frac{23}{23}$	$\frac{23}{23}$	3
CARMARSEL Sta. 815 (Paratype)	$\frac{8}{12}$	$\frac{20}{20}$	$\frac{22}{21}$	$\frac{22}{22}$	$\frac{24}{24}$	$\frac{25}{25}$	4
	$\frac{7}{12}$	$\frac{16+}{19}$	$\frac{21}{21}$	$\frac{22}{22}$	$\frac{16+}{23}$	$\frac{12+}{23}$	4
CARMARSEL Sta. 815 (Paratype)	$\frac{7}{9}$	$\frac{15}{15}$	$\frac{16}{15}$	$\frac{16}{15}$	$\frac{17}{17}$	$\frac{17}{17}$	2
	$\frac{7}{9}$	$\frac{14}{14}$	$\frac{15}{15}$	$\frac{16}{18}$	$\frac{15}{17}$	$\frac{17}{18}$	2

Remarks.—Arcoscalpellum elegantissimum is closely related to the *A. michelottianum* group of scalpellids (Newman and Ross, 1971). Important uniting characters are: a prominently hirsute capitulum, a triangular inframedian latus not exceeding the height of the carinal latus and with an apical umbo, carinal lateral plates not interdigitating where they meet below the carina, and a rostral latus almost twice as wide as high. The new species is closely allied to *A. hawaiiense* (Pilsbry) but differs in having: 1) apex of carinal latus curved inwards, not projecting beyond the base of the carina; 2) posterior ramus of cirrus I only slightly longer than the anterior ramus but with 1½ times as many segments; 3) caudal appendage with but four incompletely fused segments and less than the height of the first segment of the pedicel; 4) scales on the peduncle not overlapping or imbricating and 5) a much smaller size. In its small size and the general nature of the arthropodal structures *A. elegantissimum* shows some resemblance to *A. hirsutum* (Hoek). However, in the latter species the roof of the carina does not possess longitudinal ridges and the carinal latus is less elaborately developed.

The specific name refers to the elegant capitular ornamentation.

Arcoscalpellum hawaiiense (Pilsbry), 1907
Figures 4 and 11 C-D

Scalpellum hawaiiense Pilsbry 1907a: 181, pl. IV, fig. 1-2.

Material.—Styx-7, 680905 Sta. 2, Allison Guyot (179°37.1' W, 18°35.4' N) 1450-1557 m (otter trawl), 1 spec. attached to a small rock.

Supplementary description (female).—The capitular structure of this scalpellid agrees well with the description of the type from Kauai, Hawaii (Pilsbry, 1907a). The present specimen, larger than the type, has the following dimensions (in mm): overall height, 44; capitular height, 31; width of capitulum, 22; height of peduncle, 14.

The arthropodal structures were not described and are dealt with here. Labrum bullate, longer than broad, apex gently curving, surface mottled with pigment. Palp long and narrow, superior and anterior margins clothed with thick, short, slightly plumose setae; anterior margin and lateral faces naked (Fig. 4F). Mandible with 4 teeth including inferior angle; teeth more or less equidistantly spaced (Fig. 4B); inferior angle supporting about 14 teeth many of which are worn and blunt (Fig. 4C). Maxilla I with cutting edge nearly straight without evident notch; upper half supporting 7 spines, the uppermost 2 long and stout, the rest shorter and thinner; lower portion supporting 17-18 long and short spines (Fig. 4D). Maxilla II triangular, with 3 weakly developed lobes; marginal setae distributed in three clusters, those of superior and anterior margins being longer; lateral faces devoid of setae (Fig. 4E).

Cirrus I widely separated from the rest; posterior ramus 1½ times longer than anterior ramus; intermediate segments of anterior ramus strongly protuberant, those of posterior ramus cylindrical and ⅔ as wide (Fig. 4A). Cirrus II normal. Cirri III-IV about equal in length with equal or subequal rami. Each articulation along greater curvature of intermediate segments of cirrus VI with a cluster of 2-5 short setae. Setation ctenopod; 3 major pairs of setae along lesser curvature, a pair of long slender setae at base of distal pair and 2-3 short bristles at bases of all major pairs (Fig. 4G). Caudal appendage of six segments, each with 1-3 spines, reaching to about ½ length of second segment of pedicel of cirrus VI. Terminal segment with a tuft of 4 long and 2-3 short, slender setae (Fig. 4H). Cirral counts are as follows:

	I	II	III	IV	V	VI	Ca
Styx-7 680905 Sta. 2	$\frac{9}{17}$	$\frac{28}{27}$	$\frac{33}{32}$	$\frac{32}{32}$	$\frac{36}{34}$	$\frac{40}{40}$	6
	$\frac{9}{17}$	$\frac{28}{28}$	$\frac{30}{32}$	$\frac{33}{34}$	$\frac{34}{36}$	$\frac{40}{40}$	6

Eight dwarf males were recovered, four from each pouch on the inside of the distal end of the scutal plates. The males are sac-like, devoid of plates but covered with rows of spines.

Remarks.—This is the second report of *A. hawaiiense* which was originally dredged off Kauai, Hawaii at a depth of 1460 m. Though Pilsbry (1907a) did not describe the mouth parts and cirri, the capitular structure of our specimen agrees almost point for point with the description of the type specimen. The bathymetry also agrees. Pilsbry drew attention to the relationship between *A. hawaiiense*, *A. rubrum* (Hoek) and *A. hirsutum* (Hoek). In a later publication he (Pilsbry, 1911) included these species under the group of *Scalpellum velutinum*. With this we concur. However, a detailed comparison of *A. hawaiiense* from Allison Guyot with more complete descriptions of *A. rubrum* (Pilsbry, 1911) and *A. hirsutum* (Newman and Ross, 1971) shows that the resemblance is rather superficial, there being several differences in the capitular structure, mouth parts and cirri. *Arcoscalpellum hawaiiense* shows close resemblance to *A. elegantissimum* n. sp. While closely related, these can be distinguished from one another by the following characters; *A. hawaiiense* has 1) the apex of the carinal latus projecting, though slightly, away from the carina; 2) close and imbricating scales of the peduncle; 3) posterior ramus of cirrus I, 1½ times longer than the anterior and composed of nearly double the number of segments, 4) a caudal appendage composed of 6 segments and reaching to about ½ the length of second segment of the pedicel of cirrus VI, and 5) a much larger overall size.

Arcoscalpellum wyethi (Cornwall) from Guam appears to be a related form, but in this species the carinal latera project strongly beyond the base of carina, the scales on the peduncle do not overlap and are widely spaced, and the intermediate articles of cirrus VI support 5 pairs of setae instead of 3 pairs as in *A. hawaiiense*.

Arcoscalpellum michelottianum (Seguenza), 1876

Figures 5 and 11 A-B

Scalpellum michelottianum Seguenza, 1876:381, pl. 6, figs. 15-25: 464, pl. 10, fig. 26; *Arcoscalpellum michelottianum:* Newman and Ross, 1971: 71, pl. IXB, text-fig. 34 (see this reference for complete synonymy of this species).

Material.– Styx-7,680901 Sta. 3, Hess Guyot (174°24.8' W; 17°53.2' N), 1692-1735 m (Sigsbee beam trawl), 1 spec.; 680903-04 Sta. 1, Allison Guyot (179°36.0' W; 18°31.0' N); 1413-1645 m (otter trawl), 2 spec.; 680905 Sta. 2, Allison Guyot (179°37.1' W; 18°35.4' N), 1413-1449 m (otter trawl), several spec.; 680907 Sta. 4, Agassiz Guyot (178°14.2' W; 17°58.5' N), 1557 m (Sigsbee beam trawl), 1 spec.

Supplementary description (female).—The large series of specimens agree closely with

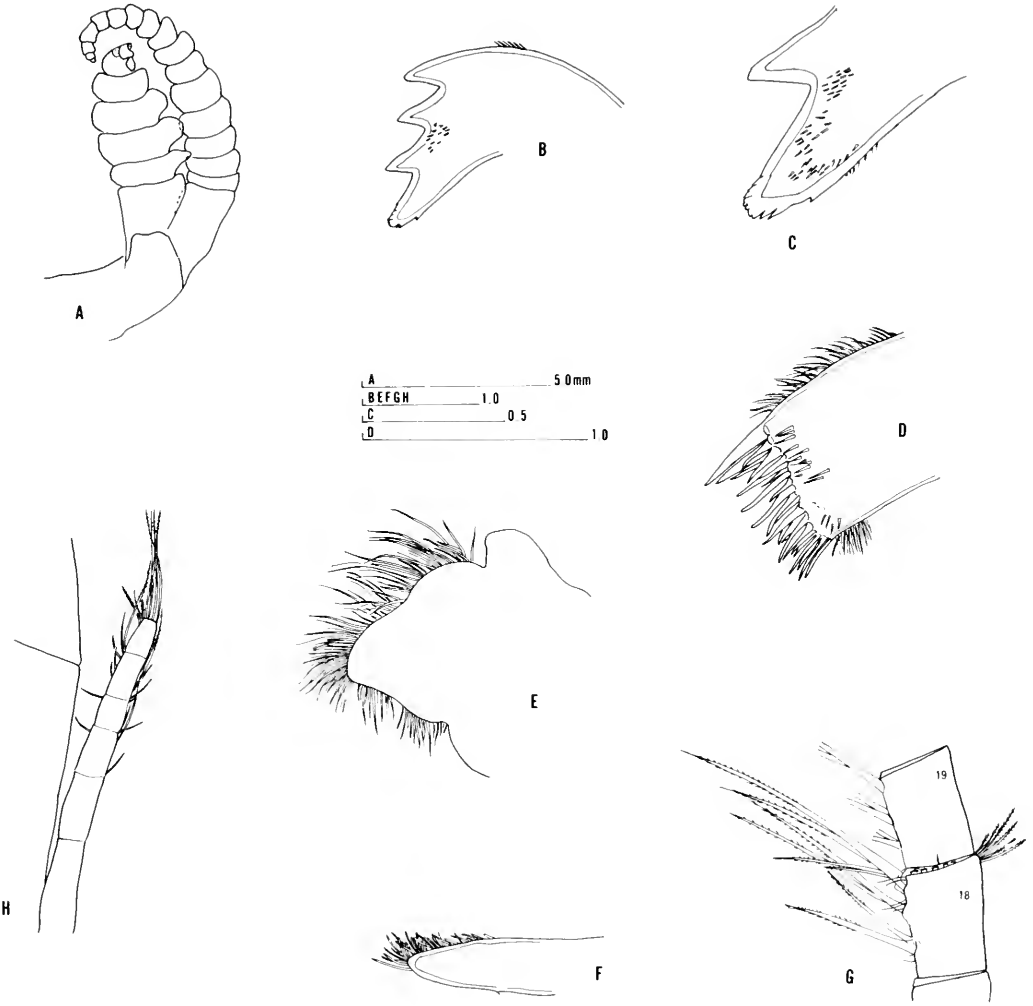

Figure 4. *Arcoscalpellum hawaiiense* (Pilsbry), Styx-7, 680905, Sta. 2, Allison Guyot. A, cirrus I; B, mandible; C, third tooth and inferior angle of mandible; D, maxilla I; E, maxilla II; F, palp; G, intermediate articles of cirrus VI; H, caudal appendage.

the descriptions of *Scalpellum eximium* Hoek (=*Arcoscalpellum michelottianum*). The lengthy synonymy under *A. michelottianum* (see Newman and Ross, 1971) indicates that this species is not only variable but that also several species were confused with and included in it. Because of this it is important that the specimens from the Mid-Pacific be carefully characterized, for the synonymy problem will undoubtedly continue.

Capitulum robust, thick near the peduncle and flatter towards the apex; surface covered by a yellow to olive colored cuticle, velvety to touch, prominently hairy in young individuals and sparsely so in older ones; 14 fully calcified plates usually fully approximate, but in some specimens carina separated from others by a narrow chitinous interspace (Fig. 11B). Scutum trapeziform; 1½-2 times as long as broad, divided into two parts by a faint diagonal ridge running from umbo to basilateral angle. Carina strongly bowed, narrow apically and gradually increasing in width towards base; roof gently convex and traversed by an indistinct longitudinal median ridge and marked by V-shaped growth lines; parietes well developed and sculptured with 4-6 distinct longitudinal ridges; base triangular and enters as a wedge between carinal latera (Fig. 11A). Carinal latus irregular; umbo at recurved apex which, in some specimens, is raised above surface of capitulum; plate divided into three parts by two ridges running from umbo to basal margin. Inframedian latus as high or slightly higher than wide; apex usually curved downwards. Form of plate

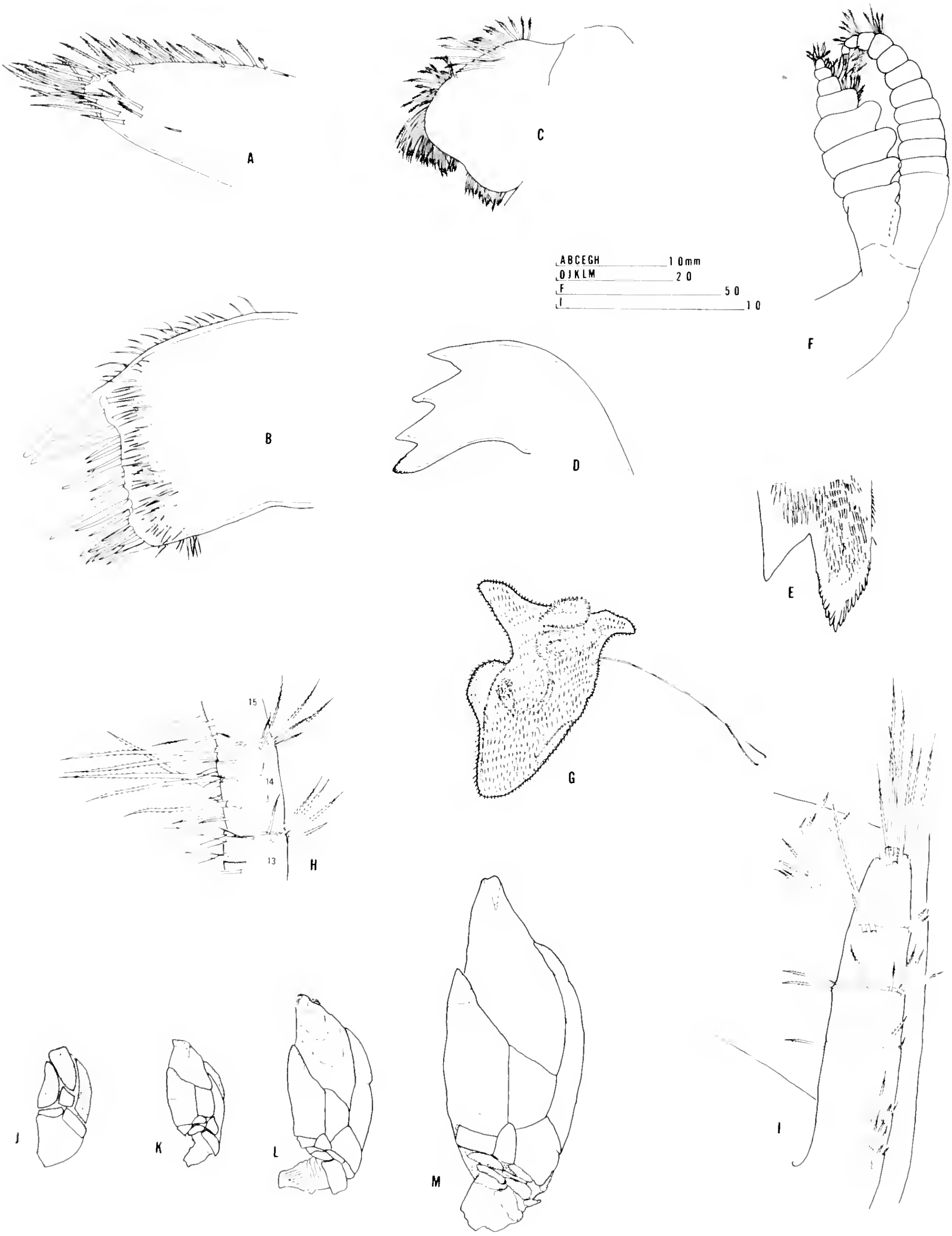

Figure 5. *Arcoscalpellum michelottianum* (Seguenza), Styx-7, 680901, Sta. 3, Hess Guyot. A, palp; B, maxilla I; C, maxilla II; D, mandible; E, inferior angle and third tooth of mandible; F, cirrus I; G, dwarf male; H, intermediate articles of cirrus VI; I, caudal appendage; J-M, side view of females.

changes considerably with growth (Fig. 5L-M). Rostral latus shorter than height of inframedian latus; broad and divided into two parts by a ridge running from umbo to lateral margin. Rostrum appearing externally in young individuals, lanceolate in shape; umbo apical. With growth, rostrum is overlapped by rostral latera of both sides and becomes hidden. Peduncle long; scales closely set or widely spaced, completely covered by a membrane or partly projecting through it.

The measurements (in mm) of four dissected individuals are given below:

Station (Styx-7)	680901 Sta. 3	680903-04 Sta. 1	680903-04 Sta. 1	680907 Sta. 4
Overall height	53	58	22	50
Height of capitulum	30	36	16	32
Height of peduncle	25	25	8	20

Labrum bullate; palp triangular, rather broad and short, superior and distal margins covered with long plumose spines, inferior margin naked (Fig. 5A). Maxilla I with cutting edge nearly straight; spines distributed in three indistinct sets; upper margin supporting 2 long stout and 5 short spines; intermediate set consisting of 1 long and 2 short spines; lower margin with a set of 1 long and 9-11 short spines (Fig. 5B). Mandible with four teeth including inferior angle; teeth spaced nearly equidistant from one another (Fig. 5D); inferior angle supporting 22-25 bluntly pointed teeth (Fig. 5E). Maxilla II broadly triangular, setae distributed in three clusters, those of superior and distal lobes contiguous; maxillary lobe broad, short and truncate apically (Fig. 5C).

Cirrus I widely separated from others; intermediate segments of anterior ramus strongly protuberant, those of posterior ramus moniliform and ⅔ as wide (Fig. 5F). Cirrus II normal, almost twice length of cirrus I. Cirri III-VI subequal with equal or subequal rami; articular areas along greater curvature have 3-4 long plumose setae; lateral faces with 2-5 rows of setae; setation ctenopod, three major pairs and one minor pair along lesser curvature; 2-3 short setae between major pairs (Fig. 5H). Caudal appendage of 4 incompletely fused segments, less than height of first segment of pedicel of cirrus VI; distally, articular areas with 2-4 spines on the outer margin; third segment with one long and one short seta on distal margin; distal segment with a tuft of 7-8 long plumose setae (Fig. 5I). Cirral counts of four dissected specimens follow:

	I	II	III	IV	V	VI	Ca
Styx-7 680901 Sta. 3	8/13	26/29	31/30	35/25+	18+/20+	17+/16+	4
	8/13	28/27+	30/31	35/26+	18+/18+	18+/19+	4
Styx-7 680903-04 Sta. 1 (spec. 1)	8/13	26/30	30/31	35/25+	19+/22+	18+/18+	4
	8/13	28/31	30/31	35/36	36/40	15+/13+	3
Styx-7 680903-04 Sta. 1 (spec. 2)	8/11	18/21	23/22	25/24	25/23	25/23	2
	8/11	19/19	23/22	20/21	24/25	25/24	2
Styx-7 680907 Sta. 4	7/13	28/27	35/28	36/32	34/35	35/33	4
	7/13	29/27	32/32	31/34	37/35	35/35	4

Dwarf males recovered from three large specimens; as many as 5-9 in a pouch on the inner sides of the scuta (Fig. 5G). They resemble those figured for *S. eximium* by Hoek (1883, pl. 9, fig. 10).

Remarks.—The Mid-Pacific specimens agree closely with Hoek's description of *Scalpellum eximium* and the resemblance is particularly striking with regard to the characteristic shape of the dwarf males.

The specimens from the Mid-Pacific differ from the examples of Newman and Ross (1971). The latter have a supramedian notch in the cutting edge of Maxilla I where as none is apparent in the present specimens; the intermediate segments of cirrus VI have 4 pairs of setae in Pacific specimens as opposed to 3 pairs in the North Atlantic individuals. The *Elta-*

nin specimens, which are relatively small, came from depths exceeding 3000 meters while the specimens from the Mid-Pacific were dredged at nearly half that depth and are large. However, while it is possible that allometry and bathymetry account for the observed differences, it is also possible that the differences are genetic. There are presently insufficient data to resolve this problem.

Arcoscalpellum radiatum n. sp.

Figure 6

Material.—Styx-7, 680903 Sta. 1 Allison Guyot (179°36.0' W, 18°31.0' N), 1413-1645 m (otter trawl), 2 spec.

Depository.—U.S.N.M. no. 140947 (Holotype, Styx-7, 680903 Sta. 1); U.S.N.M. no. 140948 (Paratype, Styx-7, 680903, Sta. 1).

Diagnosis.—Capitulum with 14 fully calcified approximate plates sculptured with prominent radial ribs emanating from the umbones. Carinal latera interdigitate at base of carina. Carinal roof flat, parietes well developed. Rostrum exposed, elongate triangular. Mandible with 4 teeth including a strongly denticulate inferior angle. Maxilla I with a deep medial notch in cutting edge. Caudal appendage uniarticulate and much shorter than first segment of pedicel of cirrus VI.

Description (female).—Capitulum elongate, oval, almost twice as long as broad; occludent and carinal margins moderately arched, covered with long hairs; 14 fully calcified approximate plates sculptured with prominent, evenly spaced ribs which extend from umbones to basal margins; ribs intercepted by feeble lines of growth (Fig. 6A). Scutum subquadrate; twice as long as broad and broadest in the middle; occludent and carinal margins subparallel, the latter ⅔ as long; surface slightly convex and traversed by ribs emanating from region of umbo; ribs more conspicuous in lower half of plate; apical umbo partly overlapping occludent margin of tergum. Tergum triangular, sculptured with longitudinal ribs except for a narrow carinal portion. Upper latus appears triangular but is four sided; a faint diagonal angulation runs from umbo to carinolateral angle. Carina with broad base enclosed between carinal latera; roof flat and marked with broad 'U' shaped lines of growth; parietes well developed, smooth (Fig. 6B). Carinal latus higher than wide, lateral margin long and partly overlapped by inframedian latus; ribs radiate from umbo; while not shown in figure, carinal margins broadly interdigitating (Fig. 6B-C). Inframedian latus more than 4 times as long as broad; traversed by transverse striae; umbo at truncate apex. Rostral latus trapeziform; divided into two unequal triangular areas by a faint ridge that runs from umbo to basilateral angle. Rostrum well developed, triangular, broad above and pointed below (Fig. 6D). Peduncle short, covered with 6 rows of strong scales with projecting edges.

Labrum bullate; crest armed with 21 V-shaped pointed teeth (Fig. 6H). Palp long and narrow; proximal superior and distal margins covered with spines (Fig. 6I). Mandible with 4 teeth including the inferior angle; first tooth well separated from second (Fig. 6E); inferior angle strongly denticulate and armed with 8 pointed teeth (Fig. 6F). Maxilla I with a deep notch in middle of cutting edge; 2 long and 2 short spines above notch and 2 long and 2-3 short spines below notch; surface covered with long setae (Fig. 6G). Maxilla II triangular and covered with a few marginal setae on superior, distal and inferior margins.

Cirrus I separated from remaining cirri; posterior ramus slightly longer; segments moniliform; covered with long plumose setae (Fig. 6J). Cirrus II not modified. Cirri III-VI essentially equal in length with subequal rami. Articular areas along greater curvature with 1-2 long thin setae; interarticular areas and lateral faces naked; setation ctenopod; 2 major and 1 minor pair of setae along lesser curvature; a few short bristles at bases of these (Fig. 6K). Caudal appendage uniarticulate; shorter than first segment of pedicel of cirrus VI; anterior and posterior borders free of setae; 4-5 setae distally. Cirral counts of the holotype follow:

	I	II	III	IV	V	VI	Ca
Styx-7 680903 Sta. 1 (Holotype)	$\frac{7}{8}$	$\frac{11}{12}$	$\frac{14}{13}$	$\frac{15}{15}$	$\frac{16}{16}$	$\frac{17}{16}$	1
	$\frac{7}{8}$	$\frac{12}{10}$	$\frac{14}{14}$	$\frac{15}{14}$	$\frac{15}{16}$	$\frac{15}{17}$	1

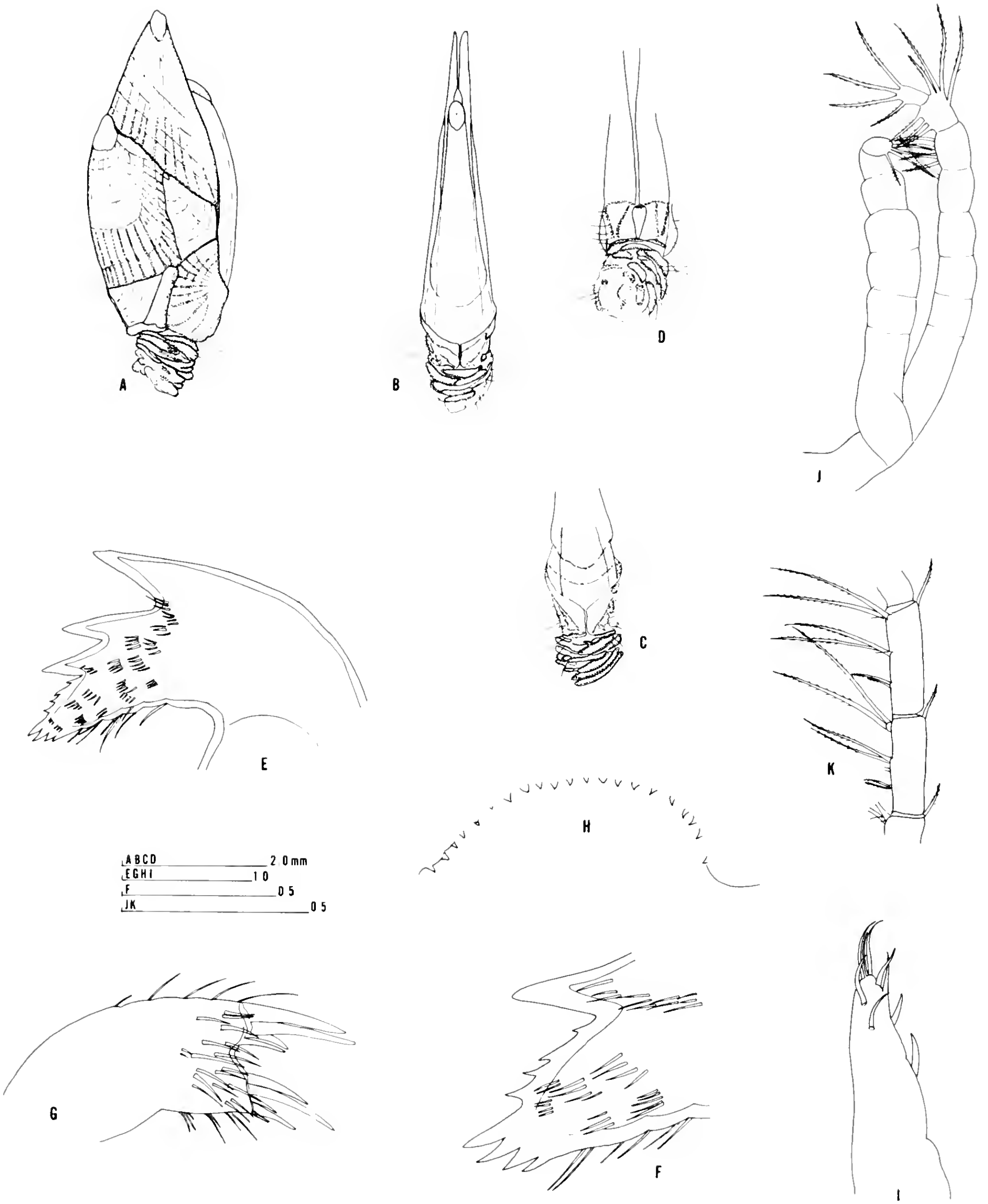

Figure 6. *Arcoscalpellum radiatum* n. sp., Holotype, Styx-7, 680903, Sta. 1, Allison Guyot. A, side views of female; B, carinal view; C, base of carina and abutment of carinal latera; D, rostrum and adjoining plates; E, mandible; F, third tooth and inferior angle of mandible; G, maxilla I; H, crest of labrum; I, palp; J, cirrus I; K, intermediate articles of cirrus VI.

Remarks.—Arcoscalpellum radiatum is related most closely to *A. pacificum* (Pilsbry), *A. chiliense* (Pilsbry) (new name for *A. gracile* (Pilsbry) and *A. semisculptum* (Pilsbry). Characters in common are an elongate capitulum, a narrow and elongate inframedian latus with an apical umbo and shorter than the carinal latus, the presence of a narrow and elongate rostrum and the possession of carinal latera which are higher than wide and interdigitating where they meet. The ornamentation of the capitular plates of *A. radiatum* recalls the condition in *A. pacificum.* However, the rostral latera of *A. pacificum* are wider than high, the umbones of the carinal latera are at the lower ¼ of the carinal margin (Pilsbry, 1907a), the cutting edge of maxilla I is nearly straight and the caudal appendage is five-segmented (Annandale, 1913). *Arcoscalpellum radiatum* differs from *A. pacificum* in all these characters. It differs from *A. chiliense* in the possession of longitudinal ribs on the terga and scuta, in the carinal roof being flat rather than convex, and in the inframedian latus which is proportionately much wider and decidedly higher than the adjoining rostral latus. *Arcoscalpellum semisculptum* also has an inframedian latus which is much narrower than in *A. radiatum*, but in this species the umbones of the carinal latera are placed at the lower ⅓ of the carinal margin as opposed to their distinctly medial position in the new species. The type of *A. semisculptum* came from a depth of 512 meters which is nearly one-third the depth from which the Mid-Pacific specimens were taken. Broch (1953) recorded one specimen from a depth of 1484 meters, comparable to the Pacific station. Unfortunately neither Pilsbry (1907c) nor Broch gave any details of the arthropodal structures of this species.

Also present at the same station is a small individual which has not yet developed the radial sculpture, but is in all other respects similar to the one described above.

Arcoscalpellum rossi n. sp.

Figure 7

Material.—Styx-7, 680901 Sta. 3, Hess Guyot (174°24.8' W, 17°53.2' N), 1692-1735 m (Sigsbee beam trawl), 1 spec. Styx-7, 680903-04 Sta. 1, Allison Guyot (179°36.0' W, 18°31.0' N), 1413-1645 m (otter trawl), 2 spec.

Depository.—U.S.N.M. no. 140949 (Holotype, Styx-7, 680901, Sta. 1) U.S.N.M. no. 140950 (Paratypes, Styx-7, 680903-04 Sta. 1, 2 spec).

Diagnosis (female).—Capitulum long and narrow, composed of 14 fully calcified plates. Roof of carina flat, parietes well developed, especially towards distal half of plate. Rostrum large, ovotriangular and fully exposed. Maxilla I with notch in middle of cutting edge. Mandible with four teeth including inferior angle; upper margin of third tooth serrated. Caudal appendage of 4 segments and reaching to ¾ height of first segment of pedicel of cirrus VI.

Description (female).—Capitulum long and narrow, composed of 14 fully calcified plates and sparsely covered with hairs. Plates separated by narrow chitinous interspaces and marked with faint lines of growth. Occludent margin strongly convex; carinal margin irregularly straight; apex slightly retroverted towards the carinal side (Fig. 7A).

Tergum triangular, occludent margin short and convex, scutal and basal margins almost straight, carinal margin concave for ⅔ the distance towards the carinal angle and straight thereafter. Scutum more than twice as long as broad; lateral margin sinuate just below tergolateral angle; apex of upper latus projects towards this sinuous part; umbo apical, overlapping occludent margin of tergum. Upper latus appearing triangular but five sided. Carinal latus fully twice as long as broad; carinal margin curving out at base of carina, beyond which umbones bluntly project. Carinal latera meet and surround base of carina in form of a broad 'V' and do not interdigitate (Fig. 7C). Carina long and simply bowed; roof flat; parietes well developed towards distal half of plate (Fig. 7B). Inframedian latus rectangular, more than four times as long as broad, umbo submedial in position, slightly displaced towards distal half and slightly raised above surface of plate. Rostral latus nearly rectangular in outline, with parallel but unequal scutal and basal margins and sub-parallel lateral margins. Rostrum large, fully exposed, elongate triangular, broad above and pointed below (Fig. 7D). Peduncle short, bent at right angles to capitulum and covered with 6-8 rows of narrow elongate plates with chitinous interspaces.

Labrum bullate; crest armed with 22 teeth. Palp narrow and elongate; superior and anterior margins armed with a few spines; inferior margin with proximal short stout spine (Fig. 7E). Maxilla I with a well defined notch in middle of cutting edge, 2 long and 1-2 short stout spines above and one long and 3-5 short spines below notch (Figs. 7H, I). Maxilla II with 3 well defined lobes; marginal setae long and setulose; setae distributed in 3 clusters, those of inferior margin being segregated; lateral margins sparsely setose; maxillary lobe moderately long and cylindrical (Fig. 7J). Mandible with 4 teeth including inferior angle; second tooth twice the distance from the first than from the third tooth; upper margin of third tooth serrate (Fig. 7F); inferior angle supporting 8 long, narrow and pointed teeth (Fig. 7G).

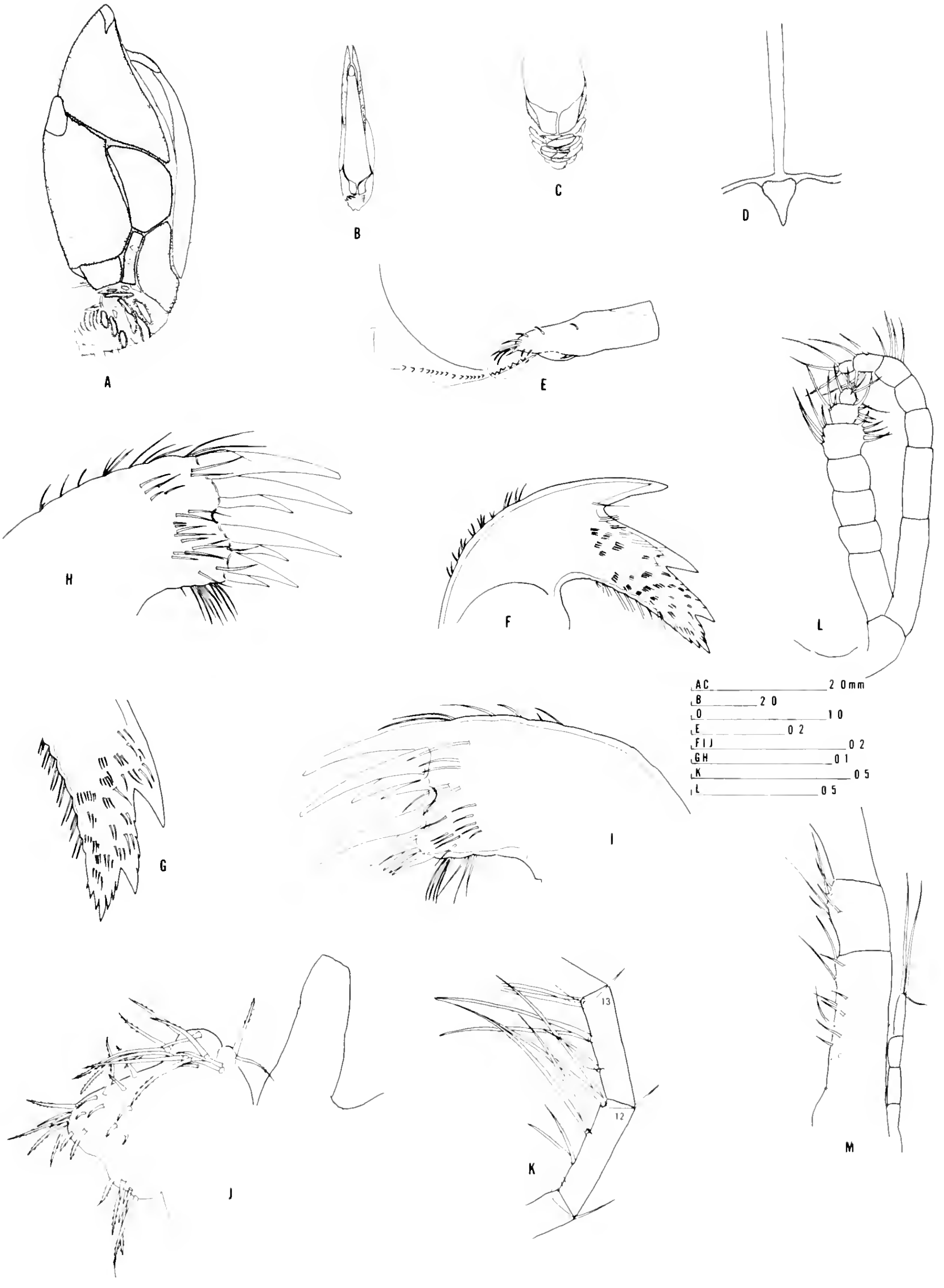

Figure 7. *Arcoscalpellum rossi* n. sp., Holotype, Styx-7, 680901, Sta. 3, Hess Guyot. A, right side view of female; B, carinal view; C, carinal latera; D, rostrum; E, crest of labrum and left palp; F, mandible; G, third tooth and inferior angle of mandible; H-I, maxillae I; J, maxilla II; K, intermediate articles of cirrus VI; L, cirrus I; M, caudal appendage.

Cirrus I (Fig. 7L) separated from the rest; cirrus II normal; articular areas along greater curvature of cirrus VI with one sharp spine; interarticular areas faintly serrated with 5-6 spines; lateral faces devoid of setae. Setation ctenopod; 2 major and 1 minor pair along lesser curvature. Caudal appendage composed of 4 segments; reaching to ¾ length of first segment of pedicel of cirrus VI; distal segment with 2 long and 1 short setae (Fig. 7M). Cirral counts follow:

	I	II	III	IV	V	VI	Ca
Styx-7, 680901 Sta. 3 (Holotype)	$\frac{7}{8}$	$\frac{12}{13}$	$\frac{15}{18}$	$\frac{18}{18}$	$\frac{18}{19}$	$\frac{18}{19}$	4
	$\frac{1+}{8}$	$\frac{12}{14}$	$\frac{17}{15}$	$\frac{19}{17}$	$\frac{19}{19}$	$\frac{20}{18+}$	4

Remarks.—Arcoscalpellum rossi is related to *A. flavum* (Hoek, 1883:127), *A. novae-Zealandeae* (Hoek, 1883:124), *A. abyssicola* (Hoek, 1883:114), *A. minutum* (Hoek, 1883:113), *A. perlongum* (Pilsbry, 1907b:198), *A. albatrossianum* (Pilsbry, 1907c:54). Characters that unite all these species are: 1) the capitulum is elongate and narrow, the lower whorl of latera contributing in part to its lengthening; 2) a long and narrow inframedian latus with an umbo that is medial to basal.

With the exception of *A. rossi* all these species have an inframedian latus which is either hour-glass shaped or has at least a narrow constriction in the middle. *Arcoscalpellum rossi* can be separated readily from these by its rectangular inframedian latus which is not at all constricted. Further, it has a well developed rostrum that is fully exposed whereas in the others a rostrum has not been described or, if present, is of a smaller size.

In the relative proportions of the capitular plates and in the general nature of the arthropodal structures *A. rossi* shows a close resemblance to *A. albatrossianum* and *A. perlongum.* All three species have a mandible in which the upper margin of the third tooth is serrate and maxilla I has a deep notch in the middle of the cutting edge (Nilsson-Cantell, 1925; MacDonald, 1929). However, in *A. albatrossianum* and *A. perlongum* the caudal appendages reach beyond the pedicel of cirrus VI and respectively have 8 and 6 segments whereas in *A. rossi* the caudal appendage is shorter than the first segment of the pedicel of cirrus VI and has 4 segments.

The species is named for Arnold Ross, Natural History Museum, San Diego, student of barnacles, and friend.

?*Arcoscalpellum* sp.
Figure 11E-F

Material.—Styx-7, 680910 Sta. 5, Sio Guyot (171°05.7' E, 18°17.7' N). 1692 m (pipe dredge), broken shells.

The shell fragments from Sio Guyot, while undoubtedly belonging to a scalpellid, are too incomplete to allow positive identification and are tentatively assigned to *Arcoscalpellum* on the basis of a carina (Fig. 11F) and a scutum (Fig. 11E).

Genus *Mesoscalpellum* Hoek, 1907
Mesoscalpellum gruvelii (Annandale), 1906
Figures 8 and 11H-I

Scalpellum gruvelii Annandale 1906b:390; 1906a:141, text-fig. 4; 1907-1908, pl. 1, fig. 1, pl. II, figs. 1, 1a, 3; 1913:232; *Scalpellum gruvelii* var. *quadratum* Annandale, 1906b:391; 1907, pl. II, fig. 3; *Annandaleum gruvelii;* Newman and Ross, 1971:122; *Scalpellum chitinosum* Hoek, 1907:73 pl. VII, fig. 4; *Scalpellum imperfectum* Pilsbry, 1907c:75, pl. IV, figs. 15-18, text-fig. 30; Barnard, 1924:46; 1925:3; MacDonald, 1929:537, pl. 2, fig. 3; Broch, 1953:9; Stubbings, 1961:11, fig. 2; Zevina; 1969:67; *Mesoscalpellum imperfectum:* Newman and Ross, 1971:119; fig. 62.

Material.—Styx-7, 680903-04 Sta. 1, Allison Guyot (179°36.0' W, 18°31.0' N), 1429-1663 m (otter trawl), 1 spec.; 680905, Allison Guyot (179°37.1' W, 18°35.4' N), 1449-1557 m (otter trawl), several spec.

Supplementary description (female).—There is considerable variation in the external morphology of the large series of specimens from the Mid-Pacific (see fig. 8A-C, 11H-I). However, specimens comparable in size to Annandale's types appear identical with his descriptions. Some clarification is needed as regards the vase-shaped nature of the inframedian latus, supposedly characteristic of the genus *Annandaleum* (Newman and Ross, 1971). In *A. gruvelii,* both in the original description and in several of the specimens in the present collection the outline of this plate has the shape of an hourglass. A club-shaped ridge, with its expanded extremity, projects outwards, and it is this ridge that gives the plate its vase-like appearance, especially when seen through the semi-transparent membrane.

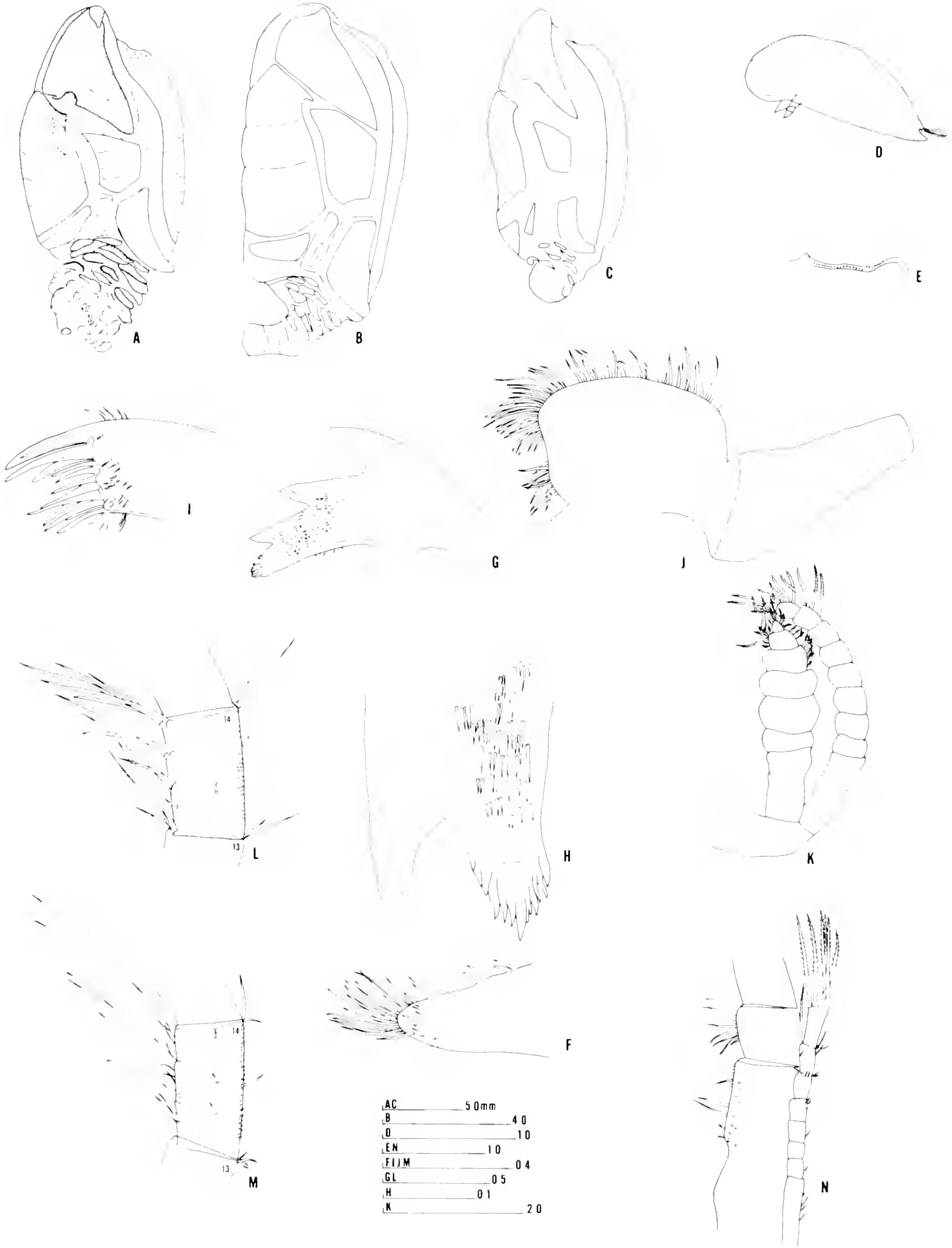

Figure 8. *Mesoscalpellum gruvelii* (Annandale), Styx-7, 680903-04 Sta. 1, Allison Guyot (A and D-N); Styx-7, 680905, Sta. 2, Allison Guyot (B-C). A-C, side views of females; D, male cyprid; E, crest of labrum; F, palp; G, mandible; H, third tooth and inferior angle of mandible; I, maxilla I; J, maxilla II; K, cirrus I; L, intermediate article of outer ramus of cirrus VI; M, intermediate article of inner ramus of cirrus VI; N, caudal appendage.

The bearing this problem has on the distribution of the genus will be taken up below, under remarks.

Annandale's descriptions of mouth parts and cirri are incomplete and are elaborated on as follows. Labrum long, triangular rather than bullate; crest armed with 40-50 bluntly pointed teeth (Fig. 8E). Palp elongate, bluntly triangular distally; superior proximal margin with a few stout spines; distal extremity strongly spinose, lateral faces with a few spines (Fig. 8F). Maxilla I with straight cutting edge; upper margin with 1 short and 2 long spines; lower margin supporting 2 long and 4 short, stout spines (Fig. 8I). Mandible with 4 teeth including a slightly receding inferior angle; first tooth well separated from second; third tooth proximal to inferior angle (Fig. 8G); inferior angle supporting 12-13 moderately long, somewhat pointed teeth (Fig. 8H). Maxilla II triangular, lobes feebly developed; marginal setae distributed in 3 clusters; lateral faces setose; maxillary lobe elongate, broad near the base and narrow apically (Fig. 8J).

The cirri, as noted by Annandale, are devoid of pigment. Cirrus I widely separated from the rest; intermediate segments of anterior ramus protuberant, those of posterior ramus cylindrical and ¾ as wide (Fig. 8K). Cirri II-VI increasing progressively in length and with equal or subequal rami. Greater curvatures of cirri II-VI with 2-3 rows of stiff bristles; lateral faces with 1-4 rows of setae; articular areas with a cluster of 3-5 setae; interarticular areas with 1-4 setae. Distal cluster of setae along lesser curvature of intermediate segments hypolasiopod in outer ramus and ctenopod (3 major pairs and 1 minor pair) in inner ramus; 2-3 pairs at bases of all major setae (Figs. 8L, M). Caudal appendages as long as pedicels of cirrus VI; each consisting of 8 segments; distal segment supporting 6 long setae of equal length (Fig. 8N). Cirral counts of one specimen are:

	I	II	III	IV	V	VI	Ca
Styx-7, 680903-04 Sta. 1	$\frac{8}{11}$	$\frac{19}{22}$	$\frac{23}{24}$	$\frac{27}{28}$	$\frac{28}{26}$	$\frac{30}{28}$	8
	$\frac{8}{10}$	$\frac{20}{22}$	$\frac{24}{26}$	$\frac{26}{26}$	$\frac{28}{28}$	$\frac{29}{29}$	8

A male cyprid was found in a pouch on the inner side of the right scutum of one specimen. It resembles (Fig.8D) the male cyprid of *S. gruvelii (=M. gruvelii)* by Stewart (1911).

Remarks.—Several authors expressed concern over the similarities between *Annandaleum gruvelii* (Annandale), *Mesoscalpellum imperfectum* (Pilsbry), and *M. sanctaebarbarae* (Pilsbry), (see Pilsbry 1907c; Annandale, 1913; Barnard, 1924; Stubbings, 1961; Newman and Ross, 1971). This and related problems need clarification here. The first is with regard to the inclusion of *gruvelii*, in the genus *Annandaleum* proposed by Newman and Ross (1971) for the reception of this and three other Indo-West Pacific species. The most diagnostic characteristic of *Annandaleum* is the large and vase-shaped inframedian latus, which as far as can be judged from published figures, is present in *A. japonicum*, *A. lambda* and *A. flavum*. In *A. gruvelii*, it is not well developed and the inclusion of this species in *Annandaleum* greatly weakens the definition of this genus. Actually *A. gruvelii* has a facies similarity with members of the genus *Mesoscalpellum* and we propose that it be transferred to this genus. This greatly sharpens the distinction between the two genera.

The second problem concerns *M. gruvelii* and *M. imperfectum*. Several specimens from the Mid-Pacific collection show a point to point similarity with the description of *M. gruvelii* (Annandale, 1906b) and there is no doubt that the specimens before us belong to this species. However, the arthropodal structures of the Mid-Pacific specimens are almost identical with those of the paratypes of *M. imperfectum* figured by Newman and Ross (1971, text-fig. 62). Therefore we believe that *imperfectum* and *gruvelii* are the same species, a synonymy that has been suggested before.

This leaves us the question as to the status of *M. sanctaebarbarae*. Newman and Ross pointed out several differences in the anatomy of *M. imperfectum (=M. gruvelii)* and *M. sanctaebarbarae*. We have had the opportunity to examine closely the soft parts of the latter species from the San Diego Trough, which confirm that the differences are consistent, with one exception. The setation of the distal cluster of the intermediate articles of the outer rami of cirrus VI is said to be ctenopod in the paratypes whereas it is distinctly hypolasiopod in the specimen from the San Diego Trough. The importance of this difference remains to be determined and in the light of other differences we are inclined to continue to recognize the two species.

With the transfer of *gruvelii* to *Mesoscalpellum* and the recognition of *M. imperfectum* as a synonym of *M. gruvelii,* the genus and the species take on a world wide distribution (Indian, Atlantic and Pacific oceans).

Family Poecilasmatidae Annandale, 1909
Genus *Megalasma* Pilsbry, 1907c
Subgenus *Glyptelasma* Pilsbry, 1907c
Megalasma (Glyptelasma) pilsbryi Calman, 1919
Figure 9

Megalasma (Glyptelasma) pilsbryi Calman, 1919:363, fig. 1A-C, fig. 2; Nilsson-Cantell, 1928:20, fig. 9A-E; 1938:10.

Material.—Styx-7, 680905 Sta. 2, Allison Guyot (179°37.1′ W, 18°35.4′ N), 1445-1557 m (otter trawl), 10 spec., all attached to *Arcoscalpellum michelottianum* and *Mesoscalpellum gruvelii.*.

Supplementary description.—The external morphology of our specimens agrees with the description given by Calman (1919). The base of the carina is produced into two teeth on the inner side (Fig. 9C). In the present specimens the basal margin of the scutum and carina meet at an angle of more than 90° whereas in Calman's specimens these are shown to meet at right angles. This character varies with growth.

Nilsson-Cantell (1928) gave brief descriptions of the mouth parts. More detail of the trophi and cirri is in order. Labrum bullate, slightly broader than long and bluntly triangular anteriorly; anterior margin and surface covered with tufts of 2-6 fine, short hairs; crest armed with 35 small, stout and somewhat pointed teeth (Fig. 9F). Palp broad proximally and bluntly conical distally; superior margin free of setae; inferior and distal margins bordered by long plumose setae; lateral faces setose (Fig. 9F). Mandible with 5 teeth including inferior angle; upper margin of fourth tooth serrate; surface profusely covered with long thin spinules some of which cross the cutting edge; superior and inferior margins bordered by short, thin hairs along the entire length (Fig. 9G); inferior angle tridentate, the teeth being short and pointed (Fig. 9H). Maxilla I with cutting edge concave above and strongly convex below, without a well defined notch, 2 long and 1 short spine above; the convex lower portion supports a set of 14-15 short and long spines, and superior and inferior margins as well as surface covered with short hairs (Fig. 9I). Maxilla II triangular, higher than wide; superior lobe well developed, distal and inferior lobes feebly so; marginal setae distributed in three clusters, those of superior and distal lobes separated by a naked superior margin (Fig. 9J).

Cirrus I widely separated from cirrus II; anterior and posterior rami equal in length and composed of 9 and 10 segments respectively; segments of anterior ramus 1¼-1½ times broader than those of posterior (Fig. 9E). Cirrus II, 1½ times longer than cirrus I; cirri III-VI equal in length with equal rami and composed of a rather constant number of segments. Articular areas along greater curvatures with 2-3 long and 1-2 short setae; interarticular areas and lateral faces devoid of setae; setation ctenopod; 3 major pairs and 1 minor pair along lesser curvature; 1-3 short bristles at bases of major pairs (Fig. 9K). Caudal appendage uniarticulate, short, about ⅓ height of first segment of pedicel of cirrus VI; anterior and posterior margins bordered with small and inconspicuous spinules; distal end broad, with 8 short to long plumose setae (Fig. 9L). Penis large, proximally broad, gradually tapering to a blunt apex; surface covered with long thin setae which are sparsely distributed for a greater length of the organ but are more profuse and conspicuous towards the distal end. A single pair of rather short, slender filamentary appendages are present on dorsum of prosoma near its posterior margin (Fig. 9M), as described and figured by Calman (1919). Cirral counts of the dissected specimen follow:

	I	II	III	IV	V	VI	Ca
Styx-7, 680905 Sta. 2	$\frac{9}{10}$	$\frac{15}{16}$	$\frac{19}{19}$	$\frac{18}{19}$	$\frac{19}{19}$	$\frac{19}{20}$	1
	$\frac{9}{10}$	$\frac{17}{16}$	$\frac{19}{19}$	$\frac{19}{19}$	$\frac{19}{19}$	$\frac{20}{18}$	1

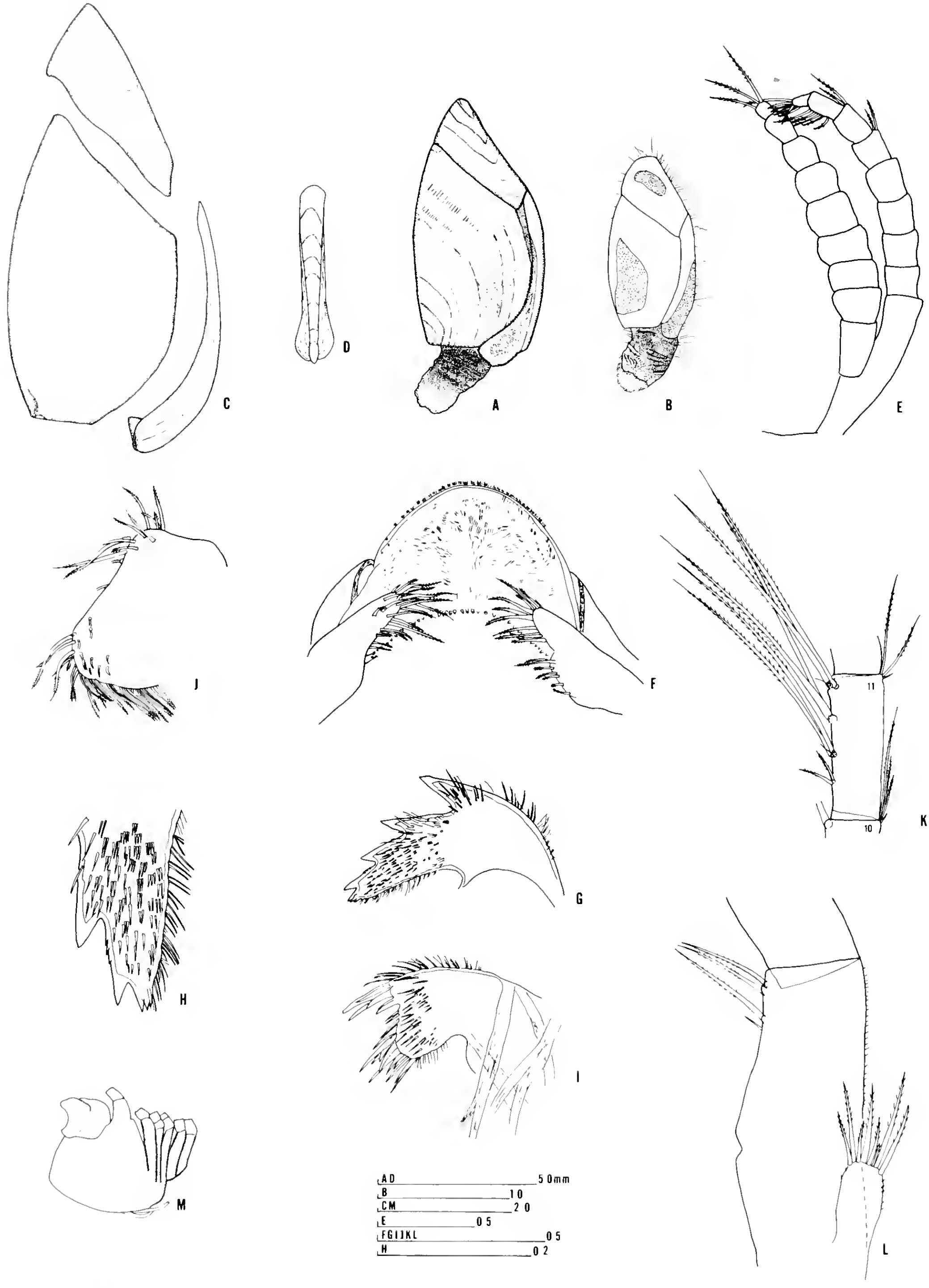

Figure 9. *Megalasma (Glyptelasma) pilsbryi* Calman, Styx-7, 680905, Sta. 2, Allison Guyot. A-B, right side view of hermaphrodites; C, inner view of disarticulated shells; D, outer view of carina; E, cirrus I; F, labrum and palps; G, mandible; H, third and fourth teeth and inferior angle of mandible; I, maxilla I; J, maxilla II; K, intermediate articles of cirrus VI; L, caudal appendage; M, prosoma and filamentary appendages.

Remarks.—Pilsbry (1907c,d) and Calman (1918b, 1919) discussed the status and definitions of the genus *Megalasma* and its subgenera *Megalasma* s.s. and *Glyptelasma.* The specimens from the Mid-Pacific are clearly referable to *Glyptelasma* because the basal margin of the scutum forms a distinct angle with the occludent margin, and also by the weak sculpture of the plates. The configuration and relative proportions of the capitular plates and the general structure of the trophi and cirri are in agreement with the description of *Megalasma (Glyptelasma) pilsbryi.* The bathymetry is also similar. The figures and descriptions given by Nilsson-Cantell show that the crest of the labrum has about 50 teeth, the rami of cirrus I have 9 and 11 segments and the posterior cirri have 23-24 segments. In contrast, the crest of the labrum of the Mid-Pacific specimen supports 35 teeth, the rami of cirrus I have 9 and 10 segments respectively and the posterior cirri are composed of 18-20 segments. It is likely that allometry may account for these differences, Nilsson-Cantell's specimens being larger (capitular height: 20 mm) than the Mid-Pacific example (capitular height: 11 mm).

Megalasma pilsbryi is closely related to *M. annandalei* Pilsbry. Calman (1919) and Barnard (1925) recognized this, but both authors advocated their retention as good species. Calman stated that *M. pilsbryi* differs from *M. annandalei* "in having no sudden widening of the sides of the carina and no excavation of the adjacent sides of the scutum, as well as in the thick cuticle covering the valves . . . " Furthermore the intermediate segments of cirrus VI of *M. pilsbryi* support 3 major pairs and one minor pair of setae along the lesser curvature whereas in *M. annandalei* there are 4 major pairs and 1 minor pair (Pilsbry, 1907, pl. V, Fig. 14).

The Mid-Pacific specimens were found attached to *Arcoscalpellum michelottianum* and *Mesoscalpellum gruvelii.* Nilsson-Cantell (1928) collected this species from *Scalpellum velutinum (=A. michelottianum)* and *S. alcockianum (=A. alcockianum).*

Suborder Verrucomorpha Pilsbry, 1916
Family Verrucidae Darwin, 1854
Genus *Verruca* Schumacher, 1817
Subgenus *Altiverruca* Pilsbry, 1916
Verruca (Altiverruca) allisoni n. sp.
Figure 10

Material.—Styx-7, 680901, Hess Guyot (174°24.8' W, 17°53.2' N), 1,718-1,770 m (Sigsbee beam trawl), 3 spec., on trochid gastropods; Styx-7 680915 Sta. 1, Darwin Guyot, (171°16.5' E, 21°53.3' N), 1,300-1,353 m (rock dredge), 2 spec., on manganese fragment.

Depository.—Holotype U.S.N.M. no. 140951 (Styx-7, 680915); Paratypes U.S.N.M. no. 140952 (Styx-7, 680901).

Diagnosis.—Distinguished from all other *Altiverruca* in having 7 rather than 3 or 4 interlocking teeth forming the suture between the carina and rostrum.

Description.—Shell white, without persistent yellow cuticle. Suture between rostrum and carina formed by numerous interdigitating ribs (Fig. 10H). It can be deduced from successive growth lines that the number of ribs increases throughout life. In the holotype this number has increased from as few as 3 or 4 to 7. Sutures formed by rostrum overlapping fixed scutum and by carina overlapping fixed tergum; sutures simple except carinal margin of fixed tergum is ala-like. Suture between fixed tergum and fixed scutum formed by an ala-like margin on former and radius-like margin on latter (Fig. 10G). Parietal portion of fixed tergum interdigitates between radius-like and parietal portions of fixed scutum.

Movable tergum and scutum articulated by the interdigitation of proximal portions of their apico-basal ridges (Fig. 10H). Supplemental ridges parallel main ridges on scutal side of the movable tergum, and the rostral portion of the movable scutum is ornamented by longitudinal lines (Figs. 10K, L).

Crest of labrum supports numerous teeth, nearly 80 in the paratype; palps pointed, sparsely covered with short strong setae (Fig. 10A). Mandible with 3 teeth, not including lower cutting edge and inferior angle; upper margin of third tooth and lower cutting edge serrate; inferior angle of several stout spines (Fig. 10B). First maxilla with group of long strong spines above and below well developed notch; inferior angle supporting few short, bifid spines (Fig. 10C). Second maxilla notched and sparsely covered with setae (Fig. 10D).

Second cirri resemble more the first than the succeeding pairs. Their rami are relatively short, subequal and uncoiled. Intermediate articles of posterior pairs ctenopod, each supporting 1 long plumose and 1 short simple pair of setae, and often 1 minute simple seta, along the lesser curvature (Fig. 10F). Caudal appendages of 6 to 8 segments and less than

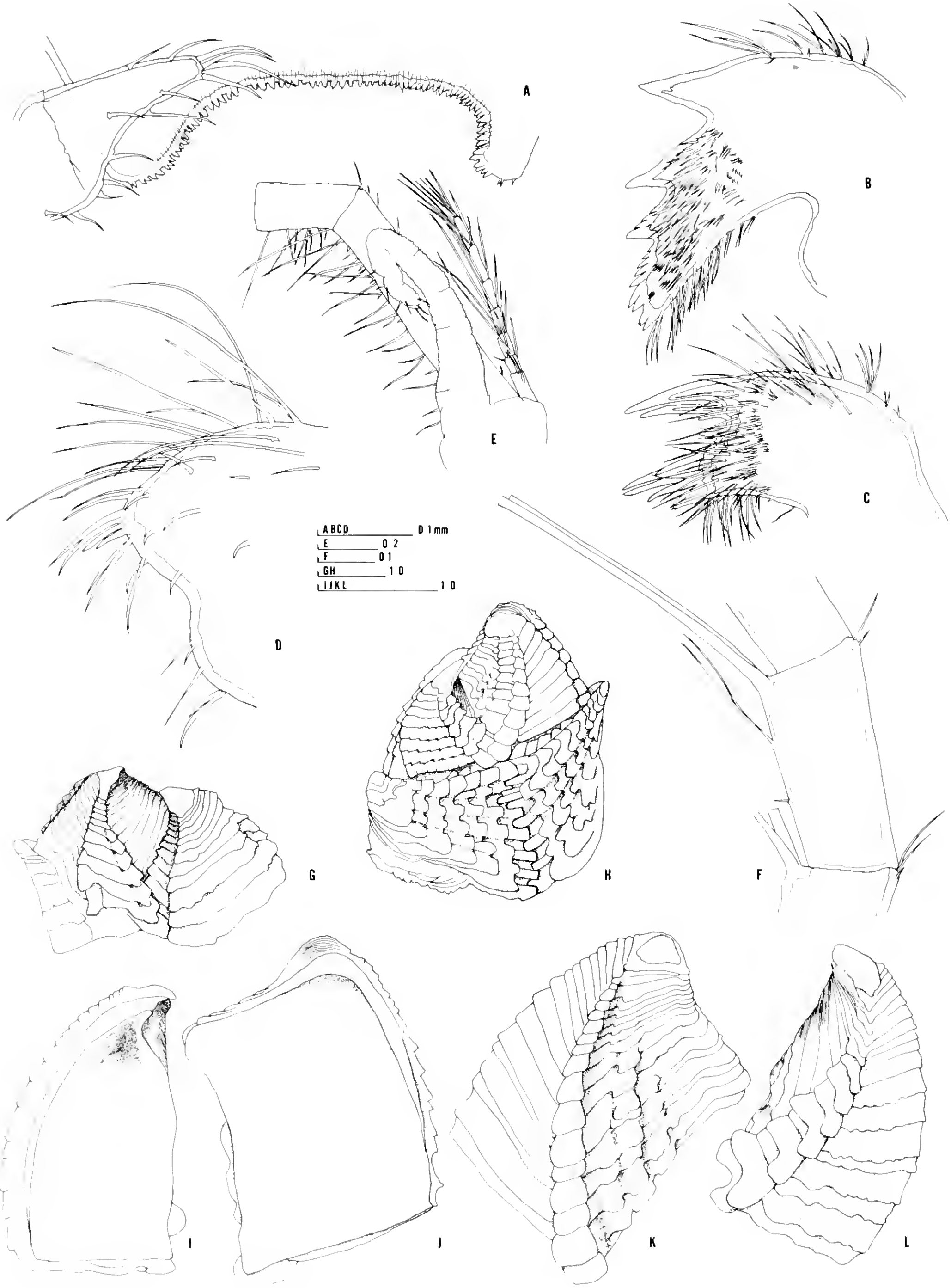

Figure 10. *Verruca (Altiverruca) allisoni* n. sp. A-F and I-L, Holotype. A, labrum and palp, left palp removed; B, mandible; C, maxilla I; D, maxilla II; E, pedicle of cirrus VI supporting penis and caudal appendage; F, intermediate article of cirrus VI; G, lateral view of entire specimen illustrating relationship of carina, fixed tergum and fixed scutum; H, lateral view of entire specimen illustrating relationship of movable terga and scuta with the carina and rostrum; I and L, interior and exterior views of the movable scutum respectively; J and K, interior and exterior views of the movable tergum respectively.

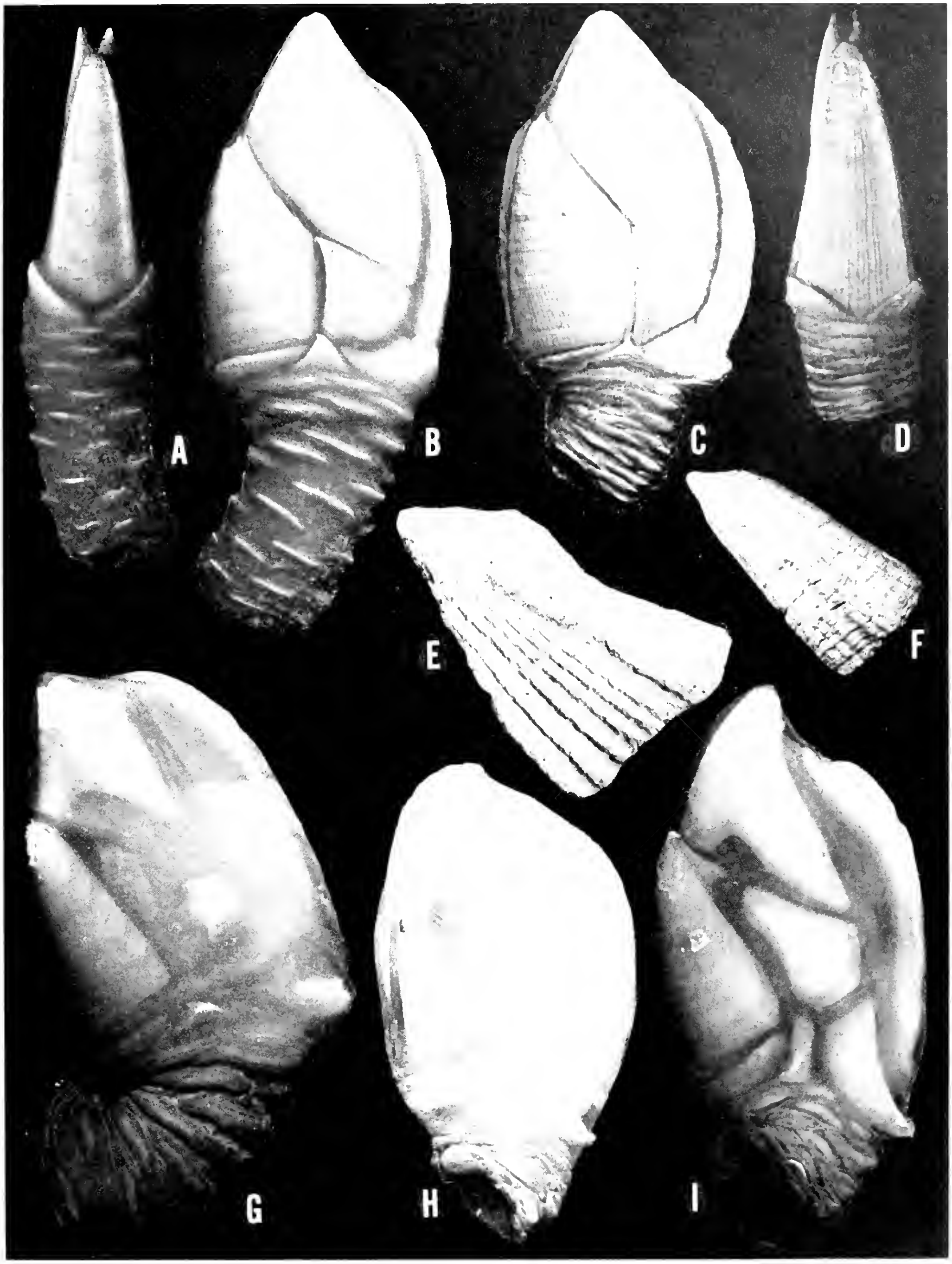

Figure 11. A. *Arcoscalpellum michelottianum* (Seguenza), carinal view of female X 1.42; B, right side view of the same individual X 1.6; C, *A. hawaiiense* (Pilsbry), right side view of female X 1.7; D, carinal view of the same individual X 1.4; E, ? *Arcoscalpellum* sp. scutum X 4.2; F, ? *Arcoscalpellum* sp., carina X 3.4; G, *A. alcockianum* (Annandale), right side view of hermaphrodite X 1.57; H, *Mesoscalpellum gruvelii* (Annandale), right side view of female X 1.4; *Mesoscalpellum gruvelii* (Annandale), right side view of female X 3.9 (A-D and H from Styx-7, 680905 Sta. 2, Allison Guyot; E-F from Styx-7, 680910 Sta. 5, Sio Guyot; G and I from Styx-7, 680903-04 Sta. 1, Allison Guyot).

the length of the basal segment of the pedicel of cirrus VI; the penis relatively short, provided distally with a few short seta (Fig. 10E). Cirral counts for three specimens follow:

	I	II	III	IV	V	VI	
Hess Guyot Styx-7, 680901 (Paratype)	9/8	7/8	13/16	22/23	22/–	24/26	7
Hess Guyot Styx-7, 680901 (Paratype)	11/9	9/11	13/16	17/21	20/15	17/19	8
Darwin Guyot Styx-7, 680915 Sta. 7 (Paratype)	6/6	9/10	13/14	17/16	17/–	19/–	6

Remarks.—*Verruca (Altiverruca) allisoni* is similar to *V. (A.) cristallina* Gruvel, 1907 from the East Indies, *V. (A.) gibbosa* Hoek, 1883 which is nearly cosmopolitan, and *V. (A.) regularis* Nilsson-Cantell 1929 from the Nicobar Islands. It differs from the first in having 7 rather than 3 or 4 interlocking teeth between the rostrum and carina, in lacking multiple interlocking ridges between the suture of the fixed tergum and scutum and in lacking the small beaded ridges along the scutal margin of the rostrum. It differs from the second and third in having 7 rather than 4 interlocking teeth between the rostrum and the carina, in having the movable scutum with longitudinal markings and in having a fixed scutum lacking an ala-like rostral margin.

The major difference between this and other species of *Altiverruca* is the large number of interlocking teeth between the rostrum and carina. In fact this same difference separates this species from all other *Verruca* except *V. (?Rostratoverruca) dens* Broch 1931, *V. (R.) intexta* Pilsbry 1912, *V. (?R.) koehleri* Gruvel 1907, *V. (?R.) nexa* Darwin 1854 and *V. (Verruca) scrippsae* Zullo 1964. Broch's illustration indicates there are about 6 interlocking teeth between the rostrum and carina, essentially as in the present species. Pilsbry (1907c), discussing Darwin's species, says that there are 7 ribs on the carina interlocking with the rostrum. It is curious that the new *Altiverruca* should be so similar in this regard to these members of *Rostratoverruca.* One might suspect that the subgeneric diagnosis was wrong. However there is no question that the apex of the rostrum is not separated from the scutal margin of the plate, as it is in *Rostratoverruca.* The similarity to *V. (V.) scrippsae* is only with regard to the carino-rostral suture; the complex interlocking sutures between the fixed scutum and the rostrum and the fixed tergum and the carina are wholly lacking in *V. (A.) allisoni.*

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A NEW MITRID FROM THE WESTERN ATLANTIC

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A NEW MITRID FROM THE WESTERN ATLANTIC

GEORGE E. RADWIN AND LOYAL J. BIBBEY

ABSTRACT.—**Mitra helenae** n. sp. from Cay Sal Bank, between the Florida Keys and Cuba, is assigned to the subgenus *Pleioptygma* Conrad, 1863, which was previously known to contain only species of Miocene and Pliocene age. The large size of this gastropod, its distinctive clouded color pattern and its threaded sculpture are unique among Recent western Atlantic mitrids. Although assigned to the Mitridae, the true familial affinities of *Pleioptygma* and this new species must await study of the radular dentition.

Malacology has long benefitted from the cooperation of commercial fishermen whose constant searching of the ocean for the objects of their commerce has led them to discover many new forms of marine life.

Recently, through the kindness of Mr. Ivan Thompson of El Cajon, California, we examined two specimens of a remarkable and apparently undescribed mitrid. Mr. Thompson received these gastropods from Captain Jack Casey of Marathon, Florida, who reported collecting them in lobster pots set at a depth of 21.5 m on Cay Sal Bank, between the Florida Keys and Cuba, in December, 1971. Both shells were inhabited by hermit crabs whose well-known carnivorous and scavenging feeding habits almost certainly account for their presence in the pots.

Family Mitridae Swainson, 1831
Genus *Mitra* Lamarck, 1798
Subgenus *Pleioptygma* Conrad, 1863

Type species.—Voluta carolinensis Conrad, 1840, by monotypy; Miocene; North Carolina.

Definition.—Shell large, up to 125 mm in length, fusiform, elongate, inflated, and moderately light in weight; protoconch of 2 or 2½ smooth whorls, teloconch of 6 to 8 slightly convex whorls. Sculpture consisting of moderate to very sharp spiral threads or cords, spaced irregularly and becoming obsolete medially on the whorl. Aperture elongate, slightly longer than spire, smooth within, lip edge thin, with or without a slight swelling anteriorly just below the shoulder slope on the inner surface of the lip; columella with 6-9 irregular, moderately thin, simple folds. Siphonal notch weak to moderately strong; a thin columellar callus extends along the entire inner margin. (Modified after Cernohorsky, 1970:60).

Remarks.—Cernohorsky (1970) indicated that *Pleioptygma* probably belongs in the Volutidae. He based his opinion on "large size, inflated and light shell, large columellar callus, absence of a siphonal notch and thin, irregular, often intercalate columellar folds."

We disagree with this placement for several reasons, but primarily as a result of our examination of two Recent specimens of a species referable to *Pleioptygma.* It seems to us that the extremely diverse nature of mitrid and volutid shell form greatly weakens Cernohorsky's arguments. Although volutids average larger than mitrids, the existence of such species as *Mitra swainsoni, M. belcheri* and *M. mitra,* all of which reach 120-150mm, clearly shows the potential for large size in this family. Cernohorsky's other arguments are equally difficult to accept as criteria for excluding *Pleioptygma* from the Mitridae. A siphonal notch is apparent on our specimens of the type species and on our new species. Irregularities in the plication and extent of callus development are certainly no greater here than in *Dibaphus* Philippi, 1847, an unquestioned mitrid with no plaits or callus.

Our contention for a mitrid assignment is based on the general form of the shell and, in particular, on the unusual clouded color pattern and the threaded sculpture. Also, the protoconchs of both fossil and Recent species (Figs. 7, 8) are different from any known type of volutid protoconch (see Pilsbry and Olsson, 1954). We are thus tentatively placing the subgenus *Pleioptygma* in the Mitridae, pending examination of the radular dentition of *M. (P.)*

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helenae.

As Cernohorsky noted, no Recent representatives have been found.

Mitra (Pleioptygma) helenae n. sp.

Type locality.—Cay Sal Bank (between the Florida Keys and Cuba), ca. 23°45′N., 80°20′W., 21.5 m, Captain Jack Casey coll., December, 1971 (holotype: Figs. 2, 5).

Type depository.—Holotype, San Diego Soc. Nat. Hist., Mar. Invert. no. 61863; paratype, collection of Ivan Thompson.

Diagnosis.—*Mitra helenae* is comparable to two fossil species from the southeastern United States. It is similar in size and shape to *M. carolinensis* (Conrad, 1840), a species that is probably identical to *M. heilprini* Cossmann, 1899 (=*M. lineolata* Heilprin, 1887, not Bellardi, 1885). It differs from *M. carolinensis* in its more poorly marked columellar callus, its less sharp-crested more closely spaced spiral threads, its broader more inflated penultimate nuclear whorl, its more strongly impressed suture, its more apparent siphonal fasciole, its slopingly shouldered body whorl and its possession of small intermediate plaits between the anterior columellar plaits.

The other fossil species, *M. prodroma* Gardner, is probably the ancestor of *M. heilprini* (see Gardner, 1937:406). It is generally much smaller than *M. helenae* (avg. length 69mm. vs. 112mm.), has fewer (3-5) columellar plaits, which are of regularly increasing prominence, and has a proportionately smaller body whorl that makes up about three-fifths of the total shell length compared to two-thirds or more of the total shell length in *M. helenae.*

Chronologically, *M. prodroma* was the first to appear, followed by *M. carolinensis* and then by *M. helenae.* Morphologically, as well as chronologically, *M. carolinensis* apparently is closer to *M. helenae.*

No other western Atlantic mitrid has been reported to reach the size of *M. helenae.* Another Floridian member of the family, *M. (Dibaphimitra) florida* Gould, 1856, reaches a relatively large size (38-50mm) but has a more convex whorl profile, a shorter spire, a more ventricose body whorl and a white shell with spiral rows of brown dots and some nebulous brown blotches.

Species to which *M. helenae* could be compared in its color pattern and sculpture include *M. versicolor* Reeve, 1844, *M. nebulosa* Reeve, 1844, *M. lamarcki* Reeve, 1844 and *M. serpentina* Lamarck, 1822. None of these reach the size of *M. helenae,* none have its almost volute-like form and all are apparently limited to the Indo-west Pacific.

Description.—The shell is large for the genus (98-123mm in length). It is moderately heavy, fusiform, and has a moderately high spire (about 2/5 of total shell length). The shell surface is smooth and polished. The spire whorls are demarcated by an impressed suture. The spire consists of 2¼ smooth, polished, tightly wound nuclear whorls and 7 or 8 weakly convex postnuclear whorls.

The body whorl is large (about 3/5 of total shell length) and fusoid; it is weakly shouldered a short distance anterior to the suture and tapers gradually toward the anterior end. The aperture is long, moderately narrow, and almost rectangular, except at its posterior end. The outer apertural lip is thin and even in a mature specimen. Just below the shoulder margin, on the inner surface of the outer apertural lip, there is a slight swelling extending anteriorly for about 25 mm. The inner lip is oblique and is coated with a thin callus of minor extent. The inner lip bears a series of 9 plaits of various strengths. The two posterior-most are strongest and of these the first is stronger and thicker than the second. These are followed anteriorly by 1 weak and 6 moderately weak plaits that diminish in strength and extent of projection from the aperture proceeding anteriorly. The siphonal fasciole is well-defined, originating as a white raised ridge at the fifth plait from the upper end of the series. The siphonal notch is well-defined and moderately deep.

Axial sculpture is lacking except for fine growth lines, and erratically occurring stronger lines representing major growth stoppages. Spiral sculpture on the spire whorls consists of numerous fine erratically spaced cords; 2 or 3 immediately below the suture are bunched more closely than the others. The stronger primary cords are sharply raised and bear an interrupted brown and white spotted color pattern that is distinct from the background. Weaker secondary cords are ephemeral and, as such, are not visible uniformly over

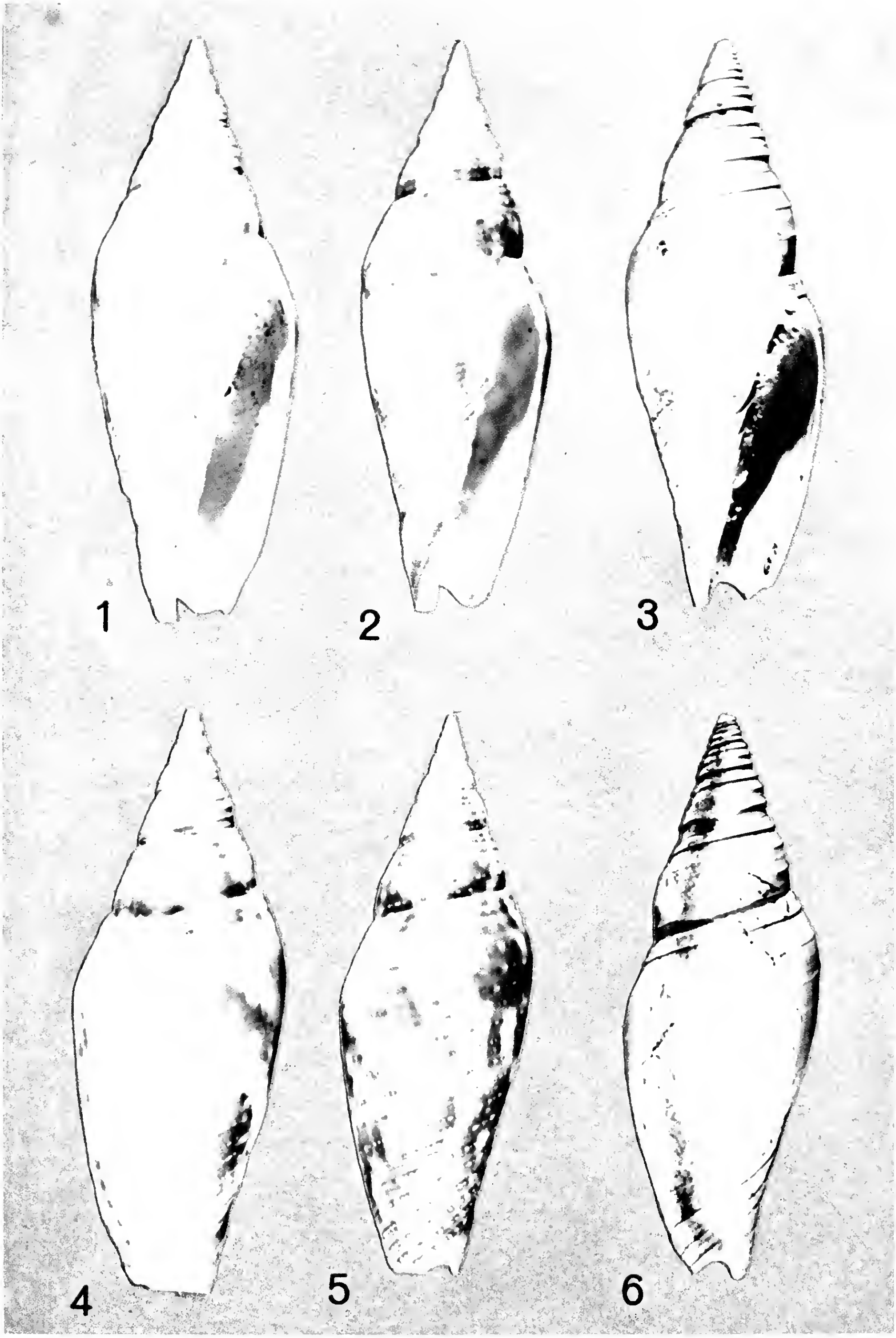

Figure 1, 4. *Mitra (Pleioptygma) helenae* n. sp., paratype, Cay Sal Bank, 21.5 m, in lobster pots, length—123 mm, maximum diameter—41.1 mm, collection of Ivan Thompson. 2, 5, *M. (P.) helenae* n.sp., holotype, Cay Sal Bank, 21.5 m, in lobster pots, length—98.4 mm, maximum diameter—32.1 mm, SDSNH Mar. Invert. no. 61863. 3, 6, *M. (P.) carolinensis* (Conrad, 1840), Pliocene, Clewiston, Florida, length—103 mm, maximum diameter—34.8 mm, SDSNH Paleo. no. 07248.

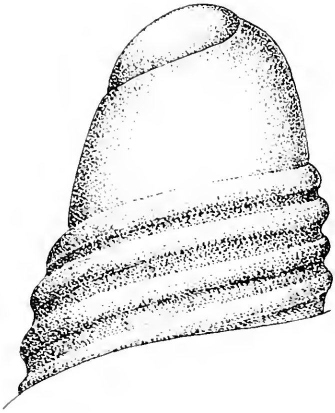

Figure 7. *Mitra (P.) carolinensis* (Conrad, 1840), protoconch, locality data as in Figure 3.

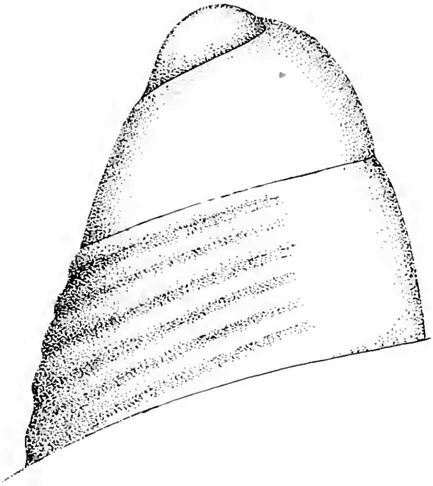

Figure 8. *Mitra (P.) helenae* n.sp., protoconch, locality data as in Figure 2.

the shell. This spiral sculpture becomes partially obsolete on the periphery of the body whorl.

The shell is white with numerous irregular diffuse flammules of reddish chestnut brown. The interior of the aperture is porcellaneous white.

Measurements.—Holotype—length, 98.4mm; greatest diameter, 32.1mm; paratype—length, 123mm (lacking protoconch); greatest diameter, 41.1mm.

Remarks.—The holotype and the single paratype were inhabited by hermit crabs at the time they were collected. The holotype is in fresh condition and apparently is not full-grown; it has a thin, immature, outer apertural lip. The paratype has apparently attained full size but it lacks a protoconch; its surface is more worn and the color pattern is comparatively faded.

Mitra helenae is here considered a living representative of *Pleioptygma,* a genus that is known otherwise only from Miocene and Pliocene species. Other species previously assigned to this group include *M. carolinensis, M. heilprini* and *M. prodroma.*

Etymology.—This patronym honors the late Mrs. Helen Thompson of El Cajon, California.

ACKNOWLEDGMENTS

We thank Captain Jack Casey and Mr. Ivan Thompson for their interest and courtesy in providing us with the only known specimens of *M. helenae.* Mr. David K. Mulliner photographed the specimens and Mr. Clifton Martin supplied references. Mr. Anthony D'Attilio illustrated the protoconchs.

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DIAGNOSES OF NEW CYPRINID FISHES OF ISOLATED WATERS IN THE GREAT BASIN OF WESTERN NORTH AMERICA

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CARL L. HUBBS AND ROBERT RUSH MILLER

ABSTRACT.—One new genus, two new species, and six new subspecies are diagnosed from highly restricted endorheic basins of the western United States—**Relictus solitarius** n. gen. and n. sp., from the basins of pluvial lakes Gale, Franklin, Steptoe, and Waring; **Gila alvordensis** n. sp., from the basin of Lake Alvord; and the following new subspecies: **Gila bicolor newarkensis** and **G. b. euchila** (Lake Newark), and **G. b. isolata** (Lake Clover), **Rhinichthys osculus reliquus** (Lake Gilbert), **R. o. oligoporus** and **R. o. lethoporus** (Lake Clover).

In amplification of our general summary (Hubbs and Miller, 1948), we are now documenting in detail the correlations between the hydrographic history of the endorheic waters of the Great Basin and the differentiation of the remnant fish fauna that somehow has managed to survive in the pitiful remnants of the pluvial lakes and streams that in late Pleistocene time covered about one-fifth of the now arid area. One of the species described herein, and the post-Pleistocene desiccation of the Alvord basin to which it is rigidly confined, are under intensive study; all of the other taxa are integral parts of a major treatise now in final processing (Hubbs and Miller, in press).

The type specimens are deposited in the University of Michigan Museum of Zoology (UMMZ).

Relictus n. gen.

Type species.—Relictus solitarius.

A cyprinid of moderate size (larger than *Rhinichthys*), with some distinctive osteological characters: dorsal crest of maxilla greatly expanded upward and backward; cleithrum slender; supraethmoid elongate, slender medially but notably expanded laterally at front (resembling that of *Rhinichthys*); urohyal long and narrow. Vertebrae 35-39. Pharyngeal arch moderately strong and heavy, but rather thin and somewhat lacy on the strongly expanded median section; not strongly elevated at the posterior end of the tooth row; without a flattened shelf on which a second tooth row might develop; teeth 4—4 (rarely 5—4 or 4—3). Gill-rakers small and few (7-12, usually 8-11, on first arch). Mouth oblique and terminal, completely lacking horny cutting edges; no frenum or barbel. Lateral line obsolescent, rarely extending to below origin of dorsal fin, commonly disrupted; total pores 3-29. Supratemporal canal seldom complete (only 4 of 76 specimens have the commissure closed), with usually 3 or 4 (0-5) pores in each lateral segment; preoperculomandibular pores 11-19; mandibular pores 3-8. Scales rather small (50-70 transverse rows), poorly imbricated and markedly irregular; each usually vertically oval but sometimes becoming rectangular with age; with numerous radii on all fields (much as in *Rhinichthys* and some other Western genera). Fins small and strongly rounded; the pelvic especially and uniquely paddlelike; dorsal and pelvic both displaced backward, and both beginning at approximately the same vertical (as in the subgenus *Siphateles* of the genus *Gila* and in many species of the typical subgenus *Gila*); dorsal and pelvic rays typically 8, anal 7. Nuptial tubercles form a highly distinctive pattern on head; the largest uniserially line the infraorbital sensory canal and suborbital margin; large uniserial caducous cones (much stronger than in *Gila*) line the upper edge of the first pectoral ray; smaller cones, also strictly uniserial (not forking once as they do in *Rhinichthys*) occur along one to several following rays; in high males some tubercles develop along outer pelvic rays and along first anal rays. Head and body turgid. Coloration much as in *Siphateles*, rather even, and often with large melanophores on lower side; lacking the two lateral bands, the head stripe, the paired light spots at caudal base, and

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other features characteristic of *Rhinichthys*. Intestine forming a single, simple, compressed-S loop, as in *Rhinichthys* and many other American cyprinids. Karyotype distinguished by a relatively large number (2 large and 8 small) of acrocentric chromosomes but many (12) metacentrics; remaining 28 are subtelocentric and submetocentric (total 50 as in other American cyprinids examined).

Relictus solitarius n. sp.

Holotype.—UMMZ 186904, a nuptial male 60.3 mm in standard length, from upper, hillside spring on Kirkpatrick Ranch (earlier called "Atwood Ranch," later called "Don Phalan Ranch") on east side of Butte Valley north of the narrows, in east part of T.29 N., R.62 E., Elko County, Nevada, 21 km northwest of Currie; collected by the Hubbs family June 27, 1942 (collection H42-47).

The characters of the species are essentially those of the genus. Counts for the holotype and the paratypes (UMMZ 141518) from the same collection follow. Rays: dorsal 7-8 (mean 7.40), anal 6-7 (6.95), caudal 18-21 (19.17), pectoral 13-16 (14.17), pelvic 7-9 (7.95). Vertebrae: 35-37 (36.05). Scale-row counts: lateral-line 50-57 (54.6), predorsal 30-33 (31.4), dorsal to anal origins 21-23 (22.4), around body 55-58 (55.8), around peduncle 30-31 (30.2). Pores: lateral-line 13-26 (18.4), supratemporal 2-4 (3.0), mandibular 4-7 (5.33). Gill-rakers 7-11 (8.90). Measurements of holotype in thousandths of standard length: predorsal length 579, anal origin to caudal base 318, body depth 295, caudal-peduncle depth 158, head length 282, head depth 207, head width 170, snout length 76, orbit length 59, upper-jaw length 82, mandible length 102, interorbital width 88, suborbital width 41, depressed-dorsal length 223, caudal length 238, pectoral length 208, pelvic length 160.

Gila alvordensis n. sp.

Holotype.—UMMZ 130495, an adult female 70.7 mm in standard length,from Trout Creek, tributary to Alvord Desert, in Harney County, Oregon; just below the canyon and just below bridge where roads to Denio, Jordan Valley, and Fields meet, in southeast part of T.39 S., R.36 E.; collected by the Hubbs family July 26, 1934 (collection M34-87).

A chub of moderate size (though usually greatly dwarfed in Borax Lake), agreeing most closely with *Siphateles* (now regarded as a subgenus of *Gila*), but with scales much reduced in size and more embedded, and with radii all around, much as in *Rhinichthys* and *Relictus*. Pharyngeal teeth uniserial, normally 5—4 (rarely 5—5, 4—5, 4—4, or 4—3), with the first tooth on a moderately elevated base. Nuptial tubercles strong on the flattened and moderately twisted pectoral fin of nuptial males; developed on the outer half (by number) of the rays, over at least two-thirds of the width of the fin, covering nearly the full length of each thickened ray; uniserial and small on the only moderately thickened outermost ray; the row branching once on each of the following rays: very strong on rays 2 and 3 (on the ridge of the distorted fin), then decreasing inward in number and size; each tubercle set on a single ray segment and rising from a large rounded base to end in a rather narrow and sharply pointed, essentially erect, tip (with only a slight cant basad); in high males similar but weaker tubercles discernible on the pelvic fin, but not on other fins; minute excrescences, simulating tubercles, over the top and sides of head in high males. General color dusky with a continuous file of large melanophores, usually uniserial or nearly so, aligned on either side of the back.

Fin rays: dorsal 7-10 (normally 7), anal 6-9 (normally 7), caudal 17-20 (normally 19), pectoral 12-17, pelvic 7-9 (normally 8). Gill-rakers: 16-22, usually short, especially forward. Measurements of holotype in thousandths of standard length: predorsal length 568, anal origin to caudal base 312, body depth 250, caudal-peduncle depth 129, head length 267, head depth 163, head width 139, snout length 77, orbit length 48, upper-jaw length 72, mandible length 100, interorbital width 85, suborbital width 33, depressed-dorsal length 204, caudal length 238, pectoral length 191, pelvic length 141, pelvic insertion to anal origin 185.

Gila bicolor newarkensis n. subsp.

Holotype.—UMMZ 188893, a nuptial male 68.0 mm in standard length, from spring in

Newark Valley on west side near Diamond Peak (called South Peak in 1934), on alluvial slope about opposite south end of Newark Dry Lake, near middle of T.10 N., R.55 E., in northwestern White Pine County, Nevada; collected by the Hubbs family September 11, 1934 (collection M34-206).

A medium to rather small-sized chub (largest of many specimens 97 mm long). General color tone darker and more uniform than in *G. b. obesa,* not closely approaching the bicolored pattern of that subspecies; dark pigmentation of sides less uniform than in other forms, because of the thick and broad concentration of melanophores around margins of scale pockets, leaving the rounded central area of pockets largely clear, to form rather conspicuous stripes along the horizontal scale rows; the dark pigment extending farther down, usually more or less completely rounding caudal peduncle; basicaudal spot replaced by a thin blackish streak along curving posterior border of squamation. Head and body strongly turgid, rounded in all aspects. Muzzle broadly rounded; mouth generally low, curved, and less oblique than usual, becoming more nearly horizontal forward; mandible slightly included at tip. Nuchal region more humped than in most forms; dorsal contour scarcely elevated at front of dorsal fin. Fins distinctively rounded, without any falcation; unusually large; sexual dimorphism in fin lengths extreme. Anal-ray count averaging low, modally 7; pelvic rays averaging 8.10 and 8.66 in two races. Vertebral and scale counts averaging low (scale counts around body averaging fewer than 47; those around peduncle fewer than 27). Gill-rakers outstandingly few (modally 12), short, soft, and swollen. Pharyngeal teeth usually 5—4.

Gila bicolor euchila n. subsp.

Holotype.—UMMZ 124938, an adult female 141 mm in standard length, from Fish Creek Springs in northwestern part of Fish Creek (Little Smoky) Valley, in main ditch about 0.5 km below junction of two main spring-fed branches, in Sec. 8, T.16 N., R.53 E.; near southwest corner of Eureka County, Nevada; collected by the Hubbs family August 17, 1938 (collection M38-134).

An outstandingly large chub (for an isolated population), males reaching 114 mm and females 149 mm; the distinction in bulk is even more striking than in length. Agreeing with *G. b. newarkensis* in color pattern (as described above), but differing in color: females deep moss-green on back, with scale borders tending to converge backward, with sides usually mottled or speckled on individual scales, with lower fins deep-olive, grading to blackish on rays and to yellowish on membranes, and with dorsal and caudal fins very dark olive; adult males with much more gilt than females on cheeks, opercles, and sides, and with gilt on body somewhat rosy, with blue reflections rather strong on lower sides, with scale margins ventrally orange-red,with a considerable wash of lemon-orange on dorsal and caudal fins, with axils of paired fins rather bright orange, with this color rather strong on interradial membranes, and with rays of lower fins deep-olive. Body contours typically much less turgid than in *G. b. newarkensis*, and head much more pointed in side view, with the tip much nearer horizontal midline of head; anterodorsal profile much straighter and less decurved; head much larger; suborbital and muzzle wide and flat; mouth much larger, straighter, and more oblique, with particularly massive lips and mandible (yet tip of mandible is also slightly included). Fins hardly falcate, but less rounded than in *G. b. newarkensis.* Supratemporal canal, as also only in *G. b. newarkensis*, but in contrast with other forms of *G. bicolor*, more often complete than incomplete. Dorsal fin more posteriorly inserted than in other subspecies, even more than in *G. b. newarkensis.* Paired fins in males larger than in nearly all other populations studied. Scale-row counts, as in *G. b. newarkensis*, average lower than in other forms, with little overlap in most categories. Gill-rakers average few and generally shorter and less hard than usual in *G. b. obesa.*

Gila bicolor isolata n. subsp.

Holotype.—UMMZ 186906, an adult female 85.8 mm in standard length, from Warm Springs of Independence Valley (also known as Ralph's Warm Springs), just off base of Pequop Mountains, approximately on edge of bed of pluvial Lake Clover, on either side of

T.35-36 line near middle of R.66 E., in east-central Elko County, Nevada; collected by Miller and Hubbs August 25, 1965 (collection M65-33).

A somewhat dwarfed chub (largest male 73 mm and largest female 91 mm long). Unpigmented ventral band wider than in *G. b. newarkensis* and *G. b. euchila*; the pigment almost never rounding peduncle below; however, almost all specimens have a highly distinctive black speck on midventral line at the very outset of the lower procurrent caudal rays. Anterodorsal profile less rounded and decurved than usual in *G. b. newarkensis*. As in *G. b. obesa*, contrasting with *G. b. newarkensis* and *G. b. euchila* front tips of mandible and upper lip about even; in contrast with *G. b. newarkensis*, mouth nearly straight, and sufficiently oblique to rise nearly to lateral midline of head. Lateral line, even in larger adults, usually incomplete posteriorly, lacking at least on peduncle, usually throughout that region and in some farther forward, where it may be either lacking or interrupted. Supratemporal canal regularly complete, as in none of the other subspecies studied. Dorsal fin, with little overlap, farther back than in any of the other forms considered except *G. b. newarkensis* and *G. b. euchila*. Distance from anal origin to caudal base averaging shorter than in the other subspecies considered, including *G. b. newarkensis* but not *G. b. euchila.* Mandible averaging larger than in other forms considered, except *G. b. euchila* and the variant form of *G. b. obesa* in Sulphur Spring (Diamond Valley). Sexual dimorphism of pectoral fin about as in *G. b. obesa*, much less than in *G. b. newarkensis* and *G. b. euchila*. Anal rays predominantly 7 rather than 8—as also in *G. b. euchila* and two of the three populations of *G. b. newarkensis* studied. Pelvic rays predominantly 8 instead of 9 (as in two *G. b. newarkensis* populations). Numbers of vertebrae and scale rows low. Gill-rakers also few (8-14, averaging 11.14). Rakers essentially like those of *G. b. obesa.*

Rhinichthys osculus reliquus n. subsp.

Holotype.—UMMZ 124906, an adult female 67 mm in standard length, from spring-fed creek in a grassy meadow in the partly enclosed southwestern arm of Grass Valley, 13 km east of Mt. Callaghan, in course of Callaghan (Woodward) Creek, on Grass Valley Ranch, in SW 1/4, Sec. 10, T.21 N., R.46 E., in eastern Lander County, Nevada; collected by Hubbs family and Miller, August 9, 1938 (collection M38-116).

A relatively large dace, despite its occurrence (now apparently extinct) in a restricted habitat; largest size 82 mm. Quite different in appearance from *R. o. robustus:* body less speckled; blackened regenerated scales rather fewer and less emphasized; underlying main dark lateral band generally broader, more solid, more even-edged. Pattern further intensified by more definitely lightened ground color between this lateral band and the dark, broad predorsal stripe. Deep-lying giant melanophores often formed on the lower sides, especially posteriorly, much more conspicuous than in *R. o. robustus*, forming puncticulations somewhat similar to those on this region in subgenus *Siphateles* of *Gila.* Lower dark lateral line, usually rather well developed in *R. o. robustus*, obsolescent. A very distinctive dark streak or wedge developed along lower border of caudal peduncle. Head characteristically darkened from the dark area of the suborbital region, and from front of mouth, upward and backward over front and top of head: horizontal dark stripe on snout, characteristic of *R. o. robustus*, barely even suggested. Vertical fins also more uniformly darkened, and less speckled, than in *R. o. robustus*, with hardly a trace of the especial blackening at the bifurcation of the rays. Lower lip, even in specimens with lower surface of head elsewhere devoid of pigment, heavily punctate all around. Red color often apparent in *Rhinichthys osculus*, in axils of paired fins, about mouth, and on preopercle, scarcely evident in life. Body more turgid in nuchal region, and snout more rounded, more declivous, and broader (overall width of mouth, in consequence, approximately equally as long as, rather than shorter than, the snout). Mouth as seen from below broadly U-shaped, instead of being narrower approaching a V. Barbel almost invariably absent. Lateral line on both body and head greatly reduced; supratemporal canal commissure consistently interrupted medially, typically very widely. Body averaging slenderer than in other forms; caudal-peduncle depth is less than in *R. o. lethoporus*, with slight overlap. Pelvic-fin insertion more posterior than in any other form considered. Sexual dimorphism in pectoral-fin length most extreme. Dorsal fin more posteriorly inserted in males than in females, on the average, contrary to findings for other forms of *Rhinichthys* (and for cyprinids in general). Pectoral-ray counts on the average lower than in other subspecies treated. Caudal vertebrae definitely averaging fewer. Scale counts averaging consistently higher than in the two forms described below.

Rhinichthys osculus oligoporus n. subsp.

Holotype.—UMMZ 186902, an adult female 55.2 mm in standard length, from Warm Springs in Clover Valley, at Warm Creek (formerly Clover) Ranch, near southeastern corner of Clover Valley, near foot of bajada just above the ancient bed of Lake Clover, in Sec. 7, T.33 N., R.61 E., in southeastern Elko County, Nevada; collected by James E. Deacon and Mary Beth Rheuben September 14, 1964.

A dace of about average size. Body more extensively speckled with black than in *R. o. robustus;* lower lateral band as a rule much less or not at all evident; dark pigmentation around snout generally diffused, with no evidence of the usual horizontal black streak in front of eye, but retaining a tendency for its continuation across opercle. Jet-black basicaudal wedge much reduced in size and intensity, more disrupted, occasionally hardly evident. Dusky dashes on dorsal and caudal fins tending to be more numerous, but barely evident on anal fin (where often evident in *R. o. robustus*); these marks much less apt to form in, and to be largely restricted to, the crotches of the bifurcating rays. Main lateral band bordered above by a light streak, barely evident in *R. o. robustus.* Life color on back bright-olive or golden-green and below silvery, with an intervening bright-gilt stripe and with dusky mottling. Axils of paired fins and base of anal in adult male clear red (contrasting with males of *R. o. reliquus*). Differing from *R. o. robustus* in general form: outlines of body, and especially of head, more curved; head in particular more rounded, in both dorsal and lateral aspects. Mouth tending to be more definitely lower than lower border of eye, and generally more curved; whole aspect bulkier. Barbel invariably absent (51 specimens). Reduction of lateral line on body extreme (as in *R. o. reliquus* and *R. o. lethoporus*). Suborbital averaging slightly narrower than in other forms studied, *R. o. lethoporus* excepted. Pelvic-fin insertion averaging farther back than in typical *R. o. robustus* or in *R. o. lethoporus*, but farther forward than in *R. o. reliquus.* Number of rays in paired fins somewhat reduced in average number. Scale counts averaging definitely lower than in *R. o. reliquus*, about the same or not quite so low as in *R. o. lethoporus*, and somewhat lower than in more typical races of *R. o. robustus.*

Rhinichthys osculus lethoporus n. subsp.

Holotype.—UMMZ 186905, an adult female 35.3 mm in standard length, from Warm Springs in Independence Valley (the same collection from which the type of *Gila bicolor isolata* was taken; see above).

Apparently the most dwarfed dace of any in the general area under consideration: the largest male measures 34 mm and the largest female 39 mm in standard length, among the 101 specimens collected (not much larger than young-of-the-year of some of the other forms). Dark speckling usually very fine, and tending to extend downward across the caudal peduncle; lower edge of peduncle often with a blackish wedge or streak. Horizontal stripe on head restricted largely to snout and upper part of opercle, usually developed, at least as a trace (much as in *R. o. robustus*, contrasting with *R. o. oligoporus*). Blackening of crotches at bifurcation of dorsal and caudal rays, and occasionally of anal rays, more as in *R. o. robustus* than in *R. o. oligoporus.* Light streak above main lateral band, frequent in *R. o. oligoporus*, obvious in only a few of the preserved specimens. Form particularly distinctive, unusually compressed for a *Rhinichthys:* greatest body width steps over the curve of the sides about 2.0 times, rather than about 1.5 times in *R. o. robustus* (*R. o. oligoporus* approximately intermediate). Anterior profile less flattened than in *R. o. robustus* and less arched than in *R. o. oligoporus.* Anterior part of head more foreshortened than in *R. o. robustus*, but rather more pointed (less rounded) than in *R. o. oligoporus.* Mouth definitely straighter than in *R. o. oligoporus*, but more oblique, rising forward to a horizontal through the lower edge of the eye. Barbel almost invariably absent, as in the two other subspecies here named. As in the other two, development of lateral line greatly reduced—even more than in *R. o. oligoporus*, less extreme than in *R. o. reliquus*. The body proper, and more strikingly the caudal peduncle, averaging deeper than in the two other forms here described. Dorsal and anal fins are inserted farther back than in *R. o. robustus*. The mouth, strikingly, is strongly oblique and nearly straight, the upper jaw rising to about level with middle of eye. Pectoral rays average few (12.72). Vertebrae and scale rows somewhat reduced in number.

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PATTERNS OF LARVAL DEVELOPMENT IN STENOGLOSSAN GASTROPODS

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ABSTRACT.—Studies of egg capsules and the mode of development in certain species of stenoglossan prosobranchs from the northeastern Gulf of Mexico revealed an apparent disproportionate number of species with non-pelagic larval development. Thorson (1950) suggested that among shallow-water marine invertebrates incidence of pelagic development increased from the arctic to the tropics and predominated in the subtropics and tropics. His conclusions were based largely on prosobranch mollusks. We suggest that the mode of early development in the Stenoglossa tends to follow phyletic lines, regardless of latitude or climatic conditions.

Many prosobranch gastropods lay their eggs in parchment-like capsules, separately or in clusters, attached to firm substrata. Unequivocal species identification is possible when the capsules are deposited in an aquarium containing individuals of a single species or when observations on ovipositing snails are made. The young of most higher prosobranchs pass the veliger stage within the capsule and may be sufficiently developed before emergence to be identifiable either by the sculpture of the early teloconch sculpture or by the radular dentition. In other groups the young are released as veligers and are carried in the plankton until they settle and metamorphose. Pearse (1969) described a third mode of development which seems to be intermediate between these two. In this type a modified veliger (called by some authors a veliconcha) emerges from the egg capsule and swims feebly for a short time in the bottom-most layer of water before settling. He has called this a demersal mode of development. The only stenoglossan species we know to exhibit this kind of development is *Olivella verreauxi* (Duclos).

Identification of capsules of marine gastropod species can contribute to distributional data which may be useful in zoogeographic studies and may serve as an ecological tool in determining the reproductive range of a species. In addition, their use as taxonomic characters at the generic level should be considered.

In this paper the spawning conditions and egg capsules of nine species of stenoglossan mollusks from the northeastern Gulf of Mexico are described. These observations were made from March 1963 to July 1964. The species treated are: *Phyllonotus pomum* (Gmelin), *Muricanthus fulvescens* (Sowerby), *Calotrophon ostrearum* (Conrad), *Urosalpinx tampaensis* (Conrad), *Urosalpinx perrugata* (Conrad), *Thais floridana* (Conrad), *Cantharus cancellarius* (Conrad), *Cantharus multangulus* (Philippi), and *Pollia tincta* (Conrad).

SPAWNING SITES, EGG CAPSULES, AND LARVAL DEVELOPMENT

Phyllonotus pomum (Gmelin, 1791) (Fig. 1, 1a). Localities: St. Teresa and Bay Mouth Bar, Franklin Co., Fla., attached to large, empty bivalve shells. Period: May-July. The capsules are deposited in irregular compact masses up to 30 cm across; individual capsules are superficially similar to those of *Buccinum* and *Neptunea*. From two to five larvae develop in each.

Tryon (1880), Webb (1942), and Perry and Schwengel (1955) described and figured the capsule mass of *P. pomum*, and Webb reported communal spawning by as many as twenty-five females. This egg mass is similar to that reported for *Murex senegalensis* (see Knudsen, 1950). D'Asaro (1970b) reported non-pelagic development for *P. pomum*.

Muricanthus fulvescens (Sowerby, 1834) (Fig. 5). Locality: St. Andrews State Park, Bay Co., Fla., attached to rocks of the breakwater. Period: June-August. Capsules deposited in clusters with their bases fused. Each capsule is a flattened cylinder about 25 mm high, with the top broader than the base. All were empty when collected. Identification was made on the basis of a laying female and an egg mass (catalogue no. 599643) in the collection of the Division of Mollusks, U.S. National Museum of Natural History. Moore (1961: 26) figured a similar capsule collected off Mississippi as *M. fulvescens*. He gave the height of "one typical specimen" as 14 mm which, from the examples we have seen, seems to be too small. He also reported that there are over one hundred eggs in each capsule.

Calotrophon ostrearum (Conrad, 1846) (Fig. 7,7a). Localities: 1) St. Teresa, Franklin Co., Fla., on the blades of turtle grass; 2) dredged in 13 m off Dog Island, Franklin Co., Fla., attached to the sides of egg capsules of *Ficus communis* (Röding); and 3) attached to the walls of aquaria in which specimens of *C. ostrearum* were isolated (see Radwin and Wells, 1968). Period: early May to mid-June. Numerous capsules are laid individually, their bases separated; they are roughly semicircular, average about 4 mm high, and when first deposited usually contain 3 to 5 large, spherical, reddish eggs. Emergence is in the crawling stage (pelagic stage absent). Egg capsules apparently of this species were attributed by Perry and Schwengel (1955) to both *Urosalpinx perrugata* and *Cantharus floridanus*.

Urosalpinx perrugata (Conrad, 1846) (Fig. 2). Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla., attached to empty mollusk shells; 2) attached to the sides and bottoms of aquaria in which adults were isolated (see Radwin and Wells, 1968). Period: late April to mid-June. Numerous erect capsules, with fused bases, are deposited in a mat; the capsules, about 10 mm high, are inversely pyramidal and have two lateral alae and apical protuberances. An egg mass may contain as many as 200 capsules. A large but undetermined number of eggs is initially deposited; the majority are apparently nurse-eggs, since only 5 to 15 larvae develop fully. Larvae emerge in the crawling stage (pelagic stage absent). Egg capsules of this species are misidentified in Perry and Schwengel (1955) as the product of *Nassarius vibex*.

Urosalpinx tampaensis (Conrad, 1846) (Fig. 3). Locality: Attached to the floor of an aquarium in which individuals of this species were isolated (see Radwin and Wells, 1968). Period: March (in aquarium). The erect egg capsules, about 8 mm high, are deposited singly. They resemble plump fingers on stalks and are more similar to those of *Eupleura sulcidentata* (see Perry and Schwengel, 1955) than to those of the other two western Atlantic species of *Urosalpinx* (*cinerea* and *perrugata*). Each capsule contains numerous eggs which, in our material, did not develop.

Thais floridana (Conrad, 1837) (Fig. 4,4a). (For characters distinguishing this species from *T. haemastoma*, see Radwin and Wells, 1968.) Locality: St. Andrews State Park, Bay Co., Fla., attached to empty bivalve shells and rocks of the breakwater. Period: July-August. The elongate, trough-shaped capsules are about 12 mm high, have apical escape pores, and are deposited in large masses. The capsules at the base of a mass tend to be nearly erect and are attached side by side to the substratum, with their bases fused. Other capsules are attached to those beneath in an arborescent pattern.

Burkenroad (1931) figured a capsule mass and commented on the hatching process. D'Asaro (1966), who figured the capsule and described the spawning and embryology in detail, reported communal spawning occurring from February through November at Miami, Fla. He suggested that spawning "probably occurs also in December and January when the temperature is above average." A shorter spawning season in the northeastern Gulf of Mexico is consistent with the shorter period of warm water temperature there. Large numbers of veligers emerge and have a prolonged pelagic development (D'Asaro, 1966). This mode of development (also reported by other workers for this species in North American waters) contrasts with that of most stenoglossans treated in this paper.

Thorson (1946, 1950) cited *T. floridana* as having pelagic development in some parts of its range and direct, non-pelagic development in others. This may be correct, but his evidence is apparently inferred from Lamy (1928), who referred, in turn, to Korschelt and Heider (1900), which reference we have not seen. Lamy reported only that many of the larvae die after cleavage and are then eaten by the others in the capsule. Although this "nurse-egg" type of feeding is usually associated with non-pelagic larval development, it

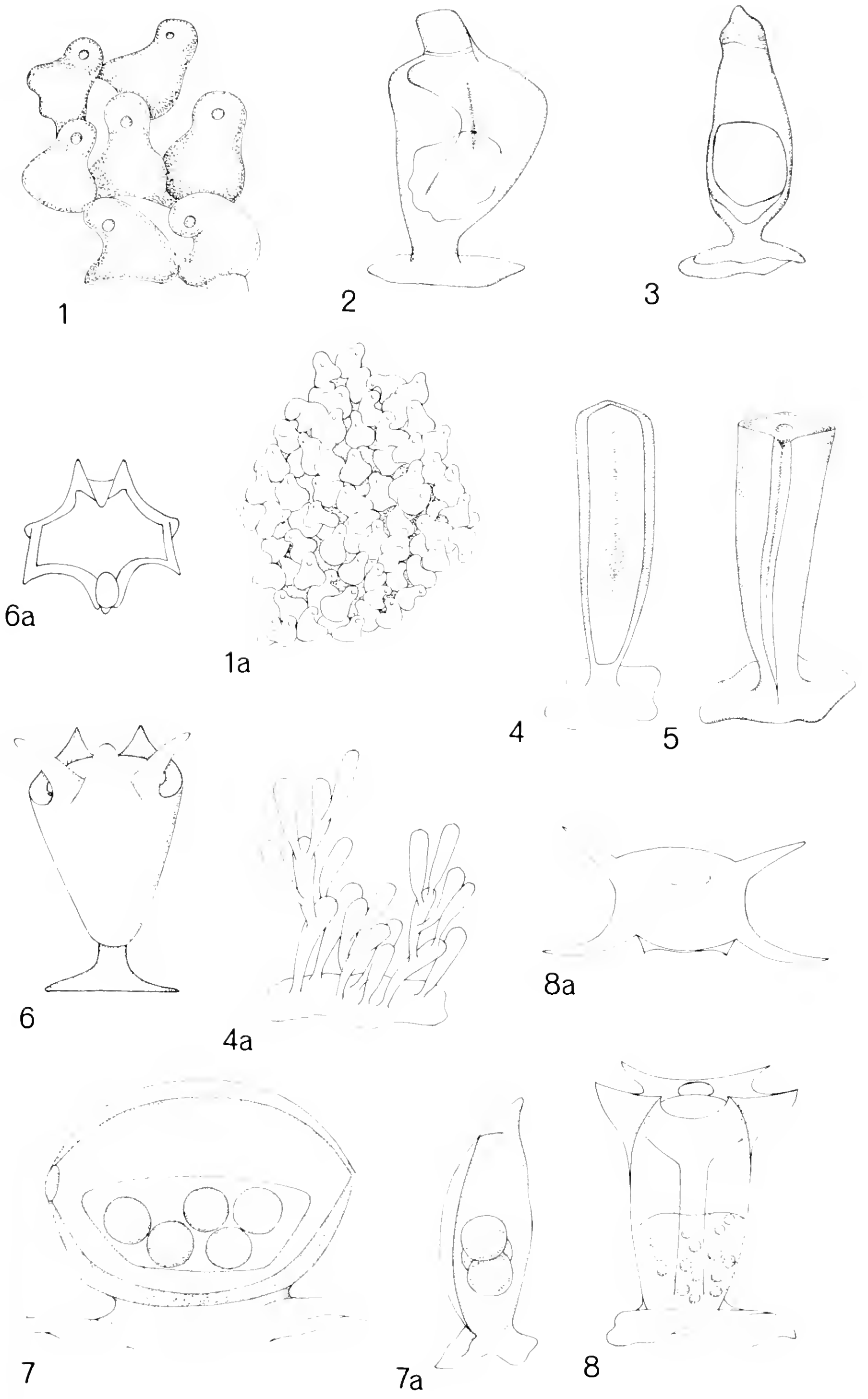

Figure 1. *Phyllonotus pomum*—seven capsules from an egg mass. 1a. *P. pomum*—small egg mass. 2. *Urosalpinx perrugata*—single egg capsule. 3. *Urosalpinx tampaensis*—single egg capsule. 4. *Thais floridana*—single egg capsule. 4a. *Thais floridana*—portion of an egg mass. 5. *Muricanthus fulvescens*—single egg capsule. 6. *Cantharus multangulus*—single egg capsule. 6a. *Cantharus multangulus*—top view of a single egg capsule. 7. *Calotrophon ostrearum*—single egg capsule. 7a. *Calotrophon ostrearum*—side view of a single egg capsule. 8. *Cantharus cancellarius*—single egg capsule. 8a. *Cantharus cancellarius*—top view of a single egg capsule.

is not proof of such development, as Thorson (1950) pointed out for *Natica catena*.

Cantharus cancellarius (Conrad, 1846) (Fig. 8, 8a). Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla., on empty mollusk shells; 2) Seahorse Key, Cedar Keys, Levy Co., Fla., on stones and empty mollusk shells; and 3) attached to the sides of aquaria in which adults were isolated (Radwin and Wells, 1968). Period: early May to late June. The erect capsules are deposited in a mat with their bases confluent. In nature the mats contained 15-20 capsules; the number of capsules laid in aquaria was smaller. Individual capsules are roughly rectangular, have four distinctive spinose projections at the top, and are about 4 mm high. In each capsule approximately 10-20 larvae develop to the crawling stage.

Moore (1961:26) figured a capsule of this species as *Cantharus reticulatus*. He also noted that on the Mississippi coast "these capsules are rather common objects during March, April, and May," and that from one capsule "a dozen or more eggs hatch out while still in the veliger stage." We have seen no other report of pelagic development in this species or elsewhere in the entire family Buccinidae.

Cantharus multangulus (Philippi, 1849) (Fig. 6, 6a). Capsules illustrated in Perry and Schwengel (1955), fig. 340. Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla.; 2) St. Teresa, Franklin Co., Fla.; and 3) deposited on the floor of aquaria. The capsules collected in the field were on shells and turtle grass. Period: May-July. Each capsule is inversely pyramidal and about 4 mm high; the top surface bears four spine-like projections. The capsule mass is a mat formed by the confluent bases of the capsules. When first deposited each capsule contains 8-20 flesh-colored eggs, a number of which apparently serve as nurse-eggs, as only a few crawling-stage larvae eventually emerge from each capsule.

Pollia tincta (Conrad, 1846) (see Perry and Schwengel, 1955; Lebour, 1945). Localities: St. Teresa, Franklin Co., Fla., and Seahorse Key, Cedar Keys, Levy Co., Fla., on shells and small rocks. Period: June-July. Clusters of several capsules are deposited, each about 5 mm high, broadly goblet-shaped and basally pedunculate. Each capsule contains 5 to 15 eggs, which, in our material, did not hatch. Lebour (1945) described the larval development as non-pelagic. Generic distinction of *Cantharus* and *Pollia* (as *Pisania*), based on radular dentition (see Troschel, 1866), is corroborated by differences in egg capsule morphology. *Cantharus* capsules are four-sided and rectangular or inversely pyramidal, with a flat top. *Pollia* capsules are goblet-shaped.

DISCUSSION

The nine species studied belong in either the family Muricidae (six species) or the Buccinidae (three species), and constitute a majority of these families reported to live in the area of field work (Perry and Schwengel, 1955). The two families are both in the suborder Stenoglossa, order Neogastropoda.

Among shallow-water, benthic, marine invertebrates, Thorson (1950) found that species with pelagic larval stages were rare in polar regions but increased, and indeed predominated toward the tropics. This conclusion was based primarily on samples of prosobranch mollusks from several widely separated areas. However, our data and those of D'Asaro (1970) indicate that at least in the stenoglossans, non-pelagic forms of development may be more common in tropical waters than is generally recognized. Thorson's data demonstrate a substantial increase in the percentage of species with pelagic development from arctic to temperate waters (0% in East Greenland to 63.5% in southern England) but they show a much smaller increase in percentage from temperate to tropical waters (e.g. southern England to a) Canary Islands, 4.5%; b) Persian Gulf, 11.5%; c) Bermuda, 21.5%). These facts have led us to question whether the proportional increase implied by Thorson (1950) is demonstrable in lower latitudes.

A review of the literature on modes of larval development among marine prosobranchs shows that in the Archaeogastropoda there is no clear predominance of either pelagic or non-pelagic development. In the Mesogastropoda, however, pelagic development predominates. Within the Neogastropoda the suborder Toxoglossa exhibits pelagic larval development, whereas the suborder Stenoglossa is the only major prosobranch group in which non-pelagic larval development seems to clearly predominate (Table I).

The apparent predominance of non-pelagic development in the Stenoglossa, regardless of latitude, as well as the abundance of species of this suborder in lower latitudes suggests that the Stenoglossa were under-represented in at least some of the areas discussed by Thorson. The Bermudas, the Canaries, and the Persian Gulf are not typical of the main tropical and subtropical shelf regions of the world. The first two are small island groups, separated from the adjacent mainland by deep water (over 1,000 m), and the third is a hypersaline body of water with excessively high water temperatures (Mohr, 1929) and a restricted outlet to the Indian Ocean.

Bermuda.—Lebour's (1945) data, on which Thorson (1950) based his estimate of 85% of Bermudan species having pelagic development, are biased toward species with pelagic development, as her study was based principally on plankton samples. Only 29 of her prosobranch species were sufficiently identified to be used in a calculation. Of these, only three (10%) are stenoglossans; two have non-pelagic development. All 26 of the non-stenoglossans have pelagic development.

The actual percentage of Bermudan prosobranchs with pelagic development, though apparently less than 85% may, nevertheless, be higher than is typical of tropical and subtropical western Atlantic areas. Evidence for this supposition stems from the fact that stenoglossans make up a smaller percentage of total prosobranchs at Bermuda than is typical of other similar areas. Peile (1927) listed 215 Bermudan species of marine prosobranchs, excluding abyssal species, of which 21% are stenoglossans. In comparison, faunal lists for the adjacent mainland and Caribbean island areas give the following percentages of stenoglossans: western Florida, 28% (Perry and Schwengel, 1955); West Indies, 29-32% (Arango, 1878; Dall and Simpson, 1901; Mörch, 1878); Brazil, 32% (Lange de Morretes, 1949).

Canary Islands.—Thorson (1950) reported that 68% of the Canary Islands marine prosobranchs exhibit pelagic development. Faunal lists for these islands and for the adjacent coast of western Africa indicate a situation parallel to that in Bermuda, with fewer stenoglossans among marine prosobranchs at the islands than at the mainland areas: Canaries, 30% (Dautzenberg, 1890, 1891); western Africa, 37% (Nicklés, 1950). São Thomé, in a more tropical position off the western coast of Africa, has an essentially similar situation; 28% of the marine prosobranchs are stenoglossan (Tomlin and Shakleford, 1923).

Evidence of a lower percentage of prosobranchs with non-pelagic larval development at Bermuda, the Canaries, and São Thomé is, in itself, of biogeographical and ecological interest. The faunal lists cited above show that the marine mollusks of these islands include few endemics. Such low endemism is evidence of recent faunal origin by immigration. The marine molluscan fauna of Bermuda is considered a depauperate Antillean fauna (Warmke and Abbott, 1961), and the prosobranchs of the Canaries and São Thomé are just as clearly depauperate western African. The colonization of these islands largely by species with pelagic larvae could be attributed to their ability, as larvae, to traverse the geographical and bathymetric barriers isolating the islands from the mainland.

Persian Gulf.—Thorson (1940a, 1950) found that 75% of the prosobranch species studied from the Persian Gulf had pelagic development. His data seems moderately biased toward such species as only 24% of them (5 of 21 species) were stenoglossans. Melvill and Standen (1901) and Melvill (1928) indicate that just over 30% of the marine prosobranchs from this area are stenoglossans.

In view of Thorson's original data showing only a small increase in the percentages of prosobranch species with pelagic larval development from temperate to tropical waters the question arises whether any significant increase exists. Regardless of the answer to this question—and our evidence is not enough to resolve it—there remains the question of why a steep gradient exists in higher latitudes but only a weak one (if, indeed, any exists) in lower latitudes. Of course, data on larval ecology and distribution must include other invertebrate groups as well.

After a draft of this paper was sent to Thorson in 1968, he informed us (in litt.) that the data he had compiled on stenoglossan early development, more extensive than the data in Table I, suggest an appreciably lower percentage of species with non-pelagic de-

TABLE I

OCCURRENCE OF PELAGIC AND NON-PELAGIC LARVAL DEVELOPMENT WITHIN THE STENOGLOSSA

Superfamily Family Genus	No. Species With Pelagic Larvae	No. Species With Non-pelagic Larvae	Reference
Muricacea			
Rapanidae			
Rapana	3		18,37,83
Muricidae			
Murex	4	5	15,43,63,75,83
Chicoreus		3	26,62,76
Phyllonotus	3	1	26,83
Boreotrophon		6	30,50,55,85
Calotrophon		1	xx
Bedevina	1		61
Bedeva		1	7
Favartia		1	74
Vitularia	1		25
Ceratostoma		1	6
Ocenebra		1	30
Urosalpinx		3	11,34,xx
Eupleura		1	11
Thaididae			
Purpura	1		49
Neptunea		4	6,30,40
Siphonalia		1	81
Pollia		1	48
"Cantharus"		2	xx
Buccinum		8	30,84
Volutharpa		1	30
Macron		1	14
Chauvetia		1	30
Melongenidae			
Melongena		1	35,45,71
Syrinx		1	36,61
Busycon		3	45,71,xx
Hemifusus		1	6
Fasciolariidae			
Leucozonia		2	26,49,75
Peristernia		1	x
Fasciolaria		3	26,45,xx
Pleuroploca		2	45,75
Fusinus		2	6,14,43
Troschelia		1	30
Volutacea			
Volutidae			
Voluta		2	45,80
Thais	9	1	6,15,24,26,43,45,49,63,83
Nucella		3	30,39,47
Buccinacea			
Columbellidae			
Pyrene		2	72
Mitrella	1	1	6,63
Anachis	5	1	6,25,54,78
Zafrona	1		4,6
Astyris		1	82,85
Amphissa	1		70
Columbella	2	1	43,72
Nassariidae			
Nassarius	11	3	3,17,30,41,42,45,63,79,83,92,93
Tritia	2	2	3,5
Ilyanassa	1		79
Buccinidae			
Beringius (Jumala)		4	21,30,50,82
Volutopsius		1	30,85
Pyrulofusus		2	22,32
Colus		9	30,82,84,xx
Plicifusus		1	50
Alcithoe		1	33
Melo		3	6,20,38,88
Cymba		1	51
Cymbiola		2	9,45
Marginellidae			
Persicula		1	43
Marginella		7	43
Prunum		1	26
Cancellariidae			
Cancellaria		1	43
Admete		1	82
Vasidae			
Vasum		1	26
Mitridae			
Strigatella	3		26,66
Atrimitra	1		16
Turbinellidae			
Turbinella (Xancus)		1	26
Olividae			
Ancilla		1	63
Olivella		4	6,30,53,67
Oliva	1		65

x E. Allison Kay, personal communication
xx – this paper

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Strigatella	3		26,66
Atrimitra	1		16
Turbinellidae			
Turbinella (Xancus)		1	26
Olividae			
Ancilla		1	63
Olivella		4	6,30,53,67
Oliva	1		65

x — E. Allison Kay, personal communication

velopment (62% compared to our 72%). Thorson's reasons for believing "that the species with a non-pelagic development predominate more in available data than they do in nature" are 1) these species have egg capsules which are large, conspicuous, and easy to discover; 2) they tend to be discovered more often with their capsules than do species with pelagic development because they have a longer spawning season; 3) the capsules are easier to identify to species and 4) his experience at the Canary Islands and in Thailand indicates "that most species with pelagic development there will reproduce in the hottest season of the year," whereas "biologists tend to make expeditions to such places at the cooler times of the year." Correction for these biases would lower Thorson's entire gradient of pelagic vs. non-pelagic development, except for the Arctic, where we have seen no evidence to indicate the existence of pelagic development among stenoglossans; thus the slope of the gradient probably would be increased from high to mid-latitudes. We would not, however, expect the slope to be changed much from mid- to low latitudes by corrections for any of the sources of bias suggested by Thorson, except his last one, which would, in theory, result in some steepening.

SELECTIVE ADVANTAGE OF NON-PELAGIC LARVAL DEVELOPMENT

The apparent predominance of non-pelagic development in the Stenoglossa has necessitated a more detailed review of early development in this group (Table 1). The mode of larval development in the Stenoglossa seems generally to follow phyletic lines, regardless of latitude or climatic conditions (beginning with the Buccinidae pelagic development is almost unknown). Exceptions include the Nassariidae, in which pelagic development is clearly predominant and the Mitridae, whose wide distribution in the Indo-west Pacific (Cernohorsky, 1965) suggests that the pelagic mode of development predominates. We cannot explain these apparent inconsistencies on the basis of our data.

Thorson (1950) argued that pelagic development is disadvantageous in the Arctic because the period of rich plankton production on which most pelagic larvae depend for food is too short. For the lower latitudes, where both modes of development are practical, the problem remains.

Garstang (1928) and Thorson (1950) showed that pelagic development permits rapid dispersal, repopulation of depleted areas, and establishment of dense populations when the larvae encounter optimal conditions. By contrast, non-pelagic larvae tend to remain in established optimal situations, are not as numerous as pelagic larvae, and are provided with protection and a large food supply by parental brooding. This mode inhibits rapid dispersal, repopulation of depleted areas, and short-term establishment of dense populations.

There is little information on the advantages of the various modes of larval development to marine prosobranchs and other marine invertebrates of shallow waters. Thus, the selective advantage of non-pelagic larval development in the stenoglossans is not clearly understood. However, most stenoglossans are carnivorous and, therefore, occupy relatively high trophic levels in their ecosystems. It seems reasonable to suggest that these animals are probably food-limited. Thus, it may be more advantageous for stenoglossans to use their energy in producing relatively few, non-pelagic young that can utilize "proved" local food resources, than to adopt the alternative strategy of producing vast numbers of highly vagile young that must find suitable conditions to insure survival.

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A MARINE INVERTEBRATE FAUNULE FROM THE LINDAVISTA FORMATION, SAN DIEGO, CALIFORNIA

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ABSTRACT.—A small mainly molluscan invertebrate fauna, dominated by the Pismo clam *Tivela stultorum* (Mawe), occurs in the reportedly unfossiliferous Lindavista Formation on the Linda Vista Terrace (at an altitude of 130-140 m) east of Murphy Canyon, city of San Diego, San Diego County, California. The faunule is suggestive of two habitats, an exposed open coast sandy beach, and a cobble or rocky-bottom, both at littoral or shallow adlittoral depths. The age of the Lindavista Formation may either be late Pliocene or early Pleistocene on the basis of the fauna, which contains the extinct species *Arca sisquocensis* Reinhart and *Pecten bellus* (Conrad). Because of the fewer tectonic-related events experienced by the Lindavista Formation than by the unconformably underlying late Pliocene sediments, the formation may actually be early Pleistocene in age.

The presence of late Pleistocene marine fossils from the San Diego area has been well documented by numerous authors (see references in Kern, 1971; also Ellis, *in* Ellis and Lee, 1919; Berry, 1922; Valentine and Meade, 1961; Moore, 1968; Kern, Stump, and Dowlen, 1971; Bishop and Bishop, 1972). Fossils from the older Pleistocene(?) Lindavista Formation (called the Sweitzer Formation by some authors) are unknown from the San Diego area, although Minch (1967: 1170) has reported finding "poorly preserved casts" at one locality in the Lindavista Formation in the Tijuana-Rosarito Beach area of northwesternmost Baja California, Mexico. In August, 1971, Richard C. Schwenkmeyer of San Diego Mesa College located an exposure of fossiliferous beach sand containing numerous fragments and a few complete single valves of the Pismo clam *Tivela stultorum* (Mawe) in a new housing development east of Murphy Canyon in San Diego (Fig. 1). Mr. Schwenkmeyer kindly brought this discovery to my attention, and the results of the ensuing investigation form the basis for this note.

THE LINDAVISTA FORMATION

The Lindavista Formation, named for exposures near the Lindavista railroad siding (Hanna, 1926: 218), consists of several meters of iron-red, moderately indurated dirty sand and pebble-cobble conglomerate. Along the eastward extent of the formation, the sandy facies interfingers with terrestrial gravels which are probably deltaic in origin. In addition, the formation is commonly characterized by pea-sized hematitic concretions on weathered surfaces (Hanna, 1926: pl. 23; Emery, 1950). The lithology at the fossil localities (see also Register of Localities) varies from a very modern-looking clean gray laminated beach sand to a fossiliferous conglomerate rich in heavy minerals (Fig. 2).

The Lindavista Formation blankets the Linda Vista Terrace, a broad and essentially planar, slightly westward sloping wave-cut surface extending from the present coastline nearly fifteen kilometers inland, where it terminates at the base of the foothills. Remnants of this formation are exposed on terraces from northernmost Baja California (Minch, 1967: 1157, 1170) to areas near Oceanside in San Diego County (Emery, 1950: 214, and pl. 29). The most prominent features of the Linda Vista Terrace are the three ancient beach ridges which approximately parallel the present coastline. These have been interpreted as stillstands during the marine regression which followed cutting of the terrace (Peterson, 1970: 122). Marine sediment along the eastern margin of this wave-cut surface was deposited earlier than that toward the coast.

The history of Pliocene and Pleistocene sedimentation of the San Diego coastal plain has been summarized by Hertlein and Grant (1944) and by Peterson (1970). Two possible sea level stands have been postulated for the events in the formation of the Linda Vista

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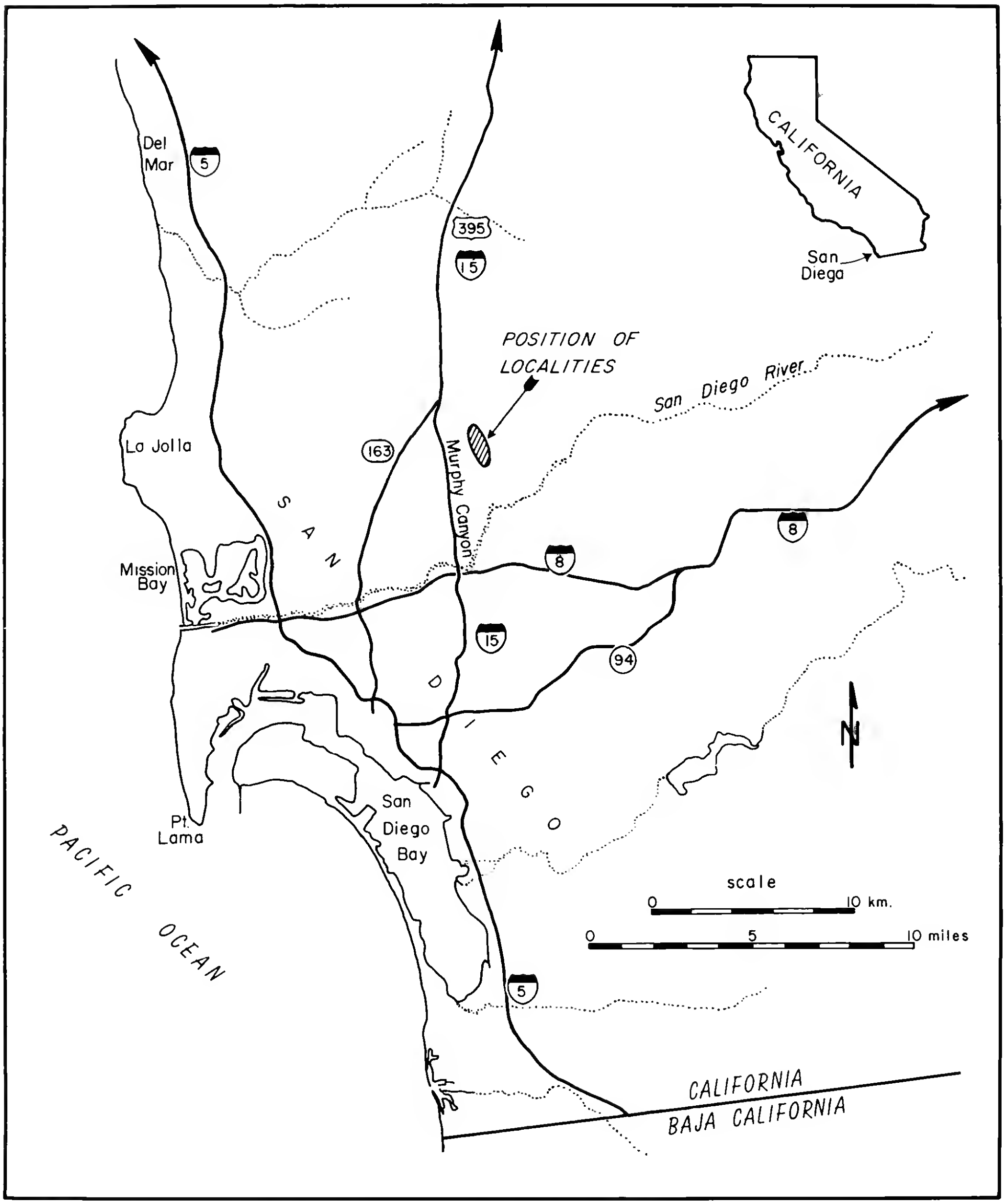

Figure 1. Index map of San Diego area showing general position of fossil localities on east side of Murphy Canyon.

Terrace (Hertlein and Grant, 1944: 64-65). One is that after deposition of the uppermost San Diego beds, the region was elevated but remained sufficiently below wave base for wave erosion or sea floor scour to truncate the marine Pliocene and Eocene beds. The Lindavista Formation therefore represents distribution by ocean waves and near-shore currents of coarse material derived from the local clastic formations, or by stream erosion on older rocks in the mountainous areas to the east. The second possibility is that parts of the San Diego Formation were elevated slightly above sea level at the close of the diastrophic movements which "inaugurated Sweitzer time." The soft nature of the San Diego beds resulted in their quick destruction by waves and subsequent reduction to a shallow submarine platform. However, formation of the Linda Vista Terrace may also have been the result of a relative subsidence of the coastal plain (or rise in sea level) with concomitant transgression of a shallow sea, then followed by submarine erosion. Subsequent retreat of the sea (as evidenced by the beach ridges) and deposition of the offlap facies (deltaic and terrestrial clastic sediments) to the east culminated deposition of the terrace material.

Despite problems of reconstructing these earlier events, at least 150 meters of relative sea-level change and only minor deformation has occurred during and since the creation of the Linda Vista platform (Peterson, 1970: 122). West of the Rose Canyon Fault considerable tilting and uplift has occurred, although not to the extent as affects the late Pliocene San Diego Formation underlying it (Moore, 1972: 116, fig. 3 [Structure contours on the base of the Lindavista Formation]). The Lindavista Formation to the south on San Diego Mesa is flat-lying and in slight angular unconformity with the underlying San Diego Formation which dips 6° to 8° to the south-southwest (Hertlein and Grant, 1944: 63 [as the Sweitzer Formation]).

AGE OF THE LINDAVISTA FORMATION

The age of the Lindavista Formation has been variously interpreted as late Pliocene to late Pleistocene. Originally Hanna (1926: 218) simply assigned his "Lindavista terrace material" to the Quaternary. Hertlein and Grant (1939: 71) considered their Sweitzer Formation (which equals the Lindavista Formation) to be younger than the Pliocene San Diego Formation and to be either late Pliocene or early Pleistocene in age. Milow and Ennis (1961: 28) called the "Lindavista Formation" upper Pleistocene, but they were referring instead to deposits of topographically lower and younger terraces than the Linda Vista Terrace. Their combined Sweitzer Formation and an overlying unnamed Sandstone comprise the Lindavista Formation of current usage. Most recently Peterson (1970: 122) has assigned the Lindavista Formation to the middle Pleistocene because of its medial position between the "Early Pleistocene?" higher greatly dissected Poway Terrace and the late Pleistocene lower terrace associated with the Bay Point Formation. Fossils collected from the Linda Vista Terrace (see below; also Fig. 3) indicate either a late Pliocene or early Pleistocene age for the formation. Because of the greater number of tectonic-related events experienced by the late Pliocene San Diego Formation (see above), the Lindavista Formation may actually be early Pleistocene in age, although further evidence is needed before any age determination can be substantiated.

FAUNA OF THE LINDAVISTA FORMATION

The fauna of the Lindavista Formation is essentially a modern one, with a few exceptions. Two of these, *Arca sisquocensis* Reinhart and *Pecten bellus* (Conrad), are known only from Pliocene and lower Pleistocene strata in California. *Turritella gonostoma hemphilli* Merriam, only questionably found in the Lindavista Formation, also occurs in upper Pliocene rocks in California. *Tegula hemphilli* Oldroyd occurs in both the upper Pliocene San Diego Formation, and the upper Pleistocene of Pacific Beach, San Diego. The remaining molluscan species are all extant, but range back into the Pliocene. The barnacle *Balanus pacificus* Pilsbry, also only doubtfully identified, is not positively known to occur in Pliocene or older rocks (Zullo, 1969: 10). These fossils indicate either a late Pliocene or early Pleistocene age for the fauna.

The possibility that the fossils have been reworked from the Pliocene San Diego Formation is slight, but cannot be discounted entirely. The Lindavista Formation in the vicinity of the fossil exposures unconformably overlies the Eocene Friars Formation and Stadium Conglomerate (Kennedy and Moore, 1971). Field investigations have revealed no outcrops of the San Diego Formation anywhere in the area (G. W. Moore, pers. commun.; Hertlein and Grant, 1944: 50). The closest exposures of Pliocene strata are all several kilometers distant, to the south on the south side of Mission Valley, and to the west in the vicinity of Mission Bay and on Mt. Soledad.

The following species were found in exposures of the Lindavista Formation on the east side of Murphy Canyon in San Diego. Nearly all the species are from one locality (SDSNH loc. 0325); numbers following the species name are the number of specimens (fragments in parentheses) collected from this locality, unless otherwise noted. For local-

Figure 2. SDSNH locality 0329: Fossiliferous exposure on Santo Road, San Diego, showing heavy-mineral sand, cobble conglomerate, and fragmented valves of *Tivela stultorum*. Meterstick for scale.

ity data see Register of Localities.

Mollusca, Gastropoda: *Diodora arnoldi* McLean, 1966–3; *Calliostoma spp.*–(11); *Tegula hemphilli* Oldroyd, 1921–3(4); *Tegula funebralis* (Adams, 1855)–2(6); *Turritella* sp. cf. *T. gonostoma hemphilli* Merriam, 1941–(6); *Turritella* sp.–1(1); *Crepidula* spp.–(2); *Crucibulum spinosum*? (Sowerby, 1824)–(1); *Polinices recluzianus* (Deshayes, 1839)–1(?12); *Acanthina spirata* (Blainville, 1832)–(21); unidentified fragments–(3). Mollusca, Bivalvia: *Yoldia cooperi* Gabb, 1865–(1); *Arca sisquocensis* Reinhart, 1937–(1); *Ostrea* sp.–(1); *Pecten bellus* (Conrad, 1857)–1; "*Pecten*" spp.–(16); *Anomia*? sp.–1; *Pododesmus* sp.– (2); *Cardita* sp. aff. *C. affinis* Sowerby, 1833–1 at loc. 0329; *Lucinisca nuttalli* (Conrad, 1837)–2(15); *Tivela stultorum* (Mawe, 1823)–12, 1(15) at loc. 0321, (6) at loc. 0322, fragments not collected at locs. 0323 and 0324, (1) at loc. 0326, 3(10) at loc. 0329; *Protothaca*? sp.–(1) at loc. 0329; *Petricola carditoides* (Conrad, 1837)–(1); *Spisula hemphilli* (Dall, 1894)–(2); *Tellina*? sp.–(2); *Macoma nasuta*? (Conrad, 1837)–(1); *Zirfaea pilsbryi* Lowe, 1931–(6, ?2); *Penitella* sp.–(?1), (4) at loc. 0326; unidentified fragments–(9). Annelida, Polychaeta: spionid worm burrows–15 [in single *Tegula funebralis*]. Echinodermata, Echinoidea: echinoid spines–8. Arthropoda, Crustacea (Cirripedia): *Balanus* sp. cf. *B. pacificus* Pilsbry, 1916–1; *Megabalanus* sp.–2; unidentified barnacle wall plates–75 +.

PALEOECOLOGY

The fauna collected does not represent the remains of any single biotic community, but rather is a detrital death assemblage from several near shore marine habitats. Specimens have been derived mainly from two habitats: sandy beach and cobble or rocky-bottom.

An exposed open coast sandy beach habitat at littoral or adlittoral depths is strongly suggested by the great abundance of the Pismo clam *Tivela stultorum*, as well as by the presence of *Spisula hemphilli. Donax gouldi*, a common member of this habitat group was unexpectedly absent. Many specimens are quite fragmented (most post depositionally), but their association with the cobble conglomerate indicates either local transport before deposition, or mixing with an offlap regressive facies.

A cobble or rocky-bottom habitat is suggested by many of the species in the fauna, including those in the genera *Diodora, Calliostoma, Tegula, Acanthina, Arca, Cardita, Protothaca, Petricola, Penitella, Balanus,* and *Megabalanus*. Most of the specimens are fragmentary and while the conglomeratic nature of the outcrop may have been similar to the paleosubstrate (see above), mixing and local transport are indicated here.

In addition to the above habitats, there are representatives of soft-bottom (sand and mud) habitats which could have occurred in shallow protected bays or offshore below the level of effective wave action. These include species of *Turritella, Polinices, Yoldia, Pecten, Lucinisca, Tellina, Macoma,* and *Zirfaea.*

Most species are largely represented by only a relatively few fragments, and indicate at least local transport and mixing. The high degree of breakage may well be a consequence of the conglomeratic substrate and proximity to surf action.

Of the extant species represented in the fauna, only *Cardita* sp. aff. *C. affinis* does not occur today in the vicinity of San Diego. *Cardita affinis* occurs from Bahía de Pequeña (26° 12′ N) on the outer coast of southern Baja California, throughout the Gulf of California, and south to northern Peru. *Turritella* sp. cf. *T. gonostoma hemphilli*, a relative of the living *T. gonostoma s.s.*, which occurs today from the Gulf of California southward to Ecuador, also suggests warmer water. The remainder of the fauna suggests a water temperature comparable with that of the present Californian Province. There are no cold-water or strictly northern species in the fauna. The occurrence in Pleistocene sediments of both cooler water (Californian) and warmer water (Panamic) species cannot yet be satisfactorily explained.

Reconnaissance geology of the area of outcrop by George W. Moore (pers. comm.) indicates that the Lindavista Formation lies on the Eocene Friars Formation (soft sandstone) directly north of the eroded edge of the overlying Eocene Stadium Conglomerate, the contact between the two Eocene formations trending northeasterly. A ridge of the more resistant southward dipping conglomerate seems to have stood slightly in relief during erosion of the wave-cut platform. The fossiliferous deposits of the Lindavista Formation lie in an embayment etched into the poorly cemented Friars Formation directly north of a Pleistocene rocky headland of Stadium Conglomerate. This physiographic configuration may have been responsible for the accumulation of different habitat forms in the fauna. Subsequent deposition of an offlap facies (conglomerate and tight deltaic sandy claystone, never deposited to the west), protected the deposits from weathering and erosion which probably accounts for the general lack of fossils in the formation as a whole.

SYSTEMATIC NOTES

Mollusca: Gastropoda

Diodora arnoldi McLean, 1966

Fig. 3c

Range.—Crescent City, Del Norte County, California, to Isla San Martín, Baja California (McLean, 1966:6).

Remarks.—This small keyhole limpet occurs exclusively in the sublittoral zone and is not uncommon on the undersides of rocks below a depth of 9 m (McLean, 1969: 13). *Diodora arnoldi* is also known from the upper Pliocene San Diego Formation from southwesternmost San Diego County (LACMIP loc. 305A).

Tegula hemphilli Oldroyd, 1921

Fig. 3 a,b

Remarks.—This extinct low spired *Tegula* was described from upper Pleistocene deposits on the La Jolla Terrace at Pacific Beach, San Diego (Oldroyd, 1921: 115). It is also known to occur in the upper Pliocene San Diego Formation, where it is exposed on Telegraph Canyon Road, east of the city of Chula Vista.

Tegula funebralis (Adams, 1855)

Fig. 3d

Range.—Vancouver Island, British Columbia, to central Baja California (McLean, 1969: 22).

Remarks.—This species occurs strictly intertidally and is abundant in rocky areas at

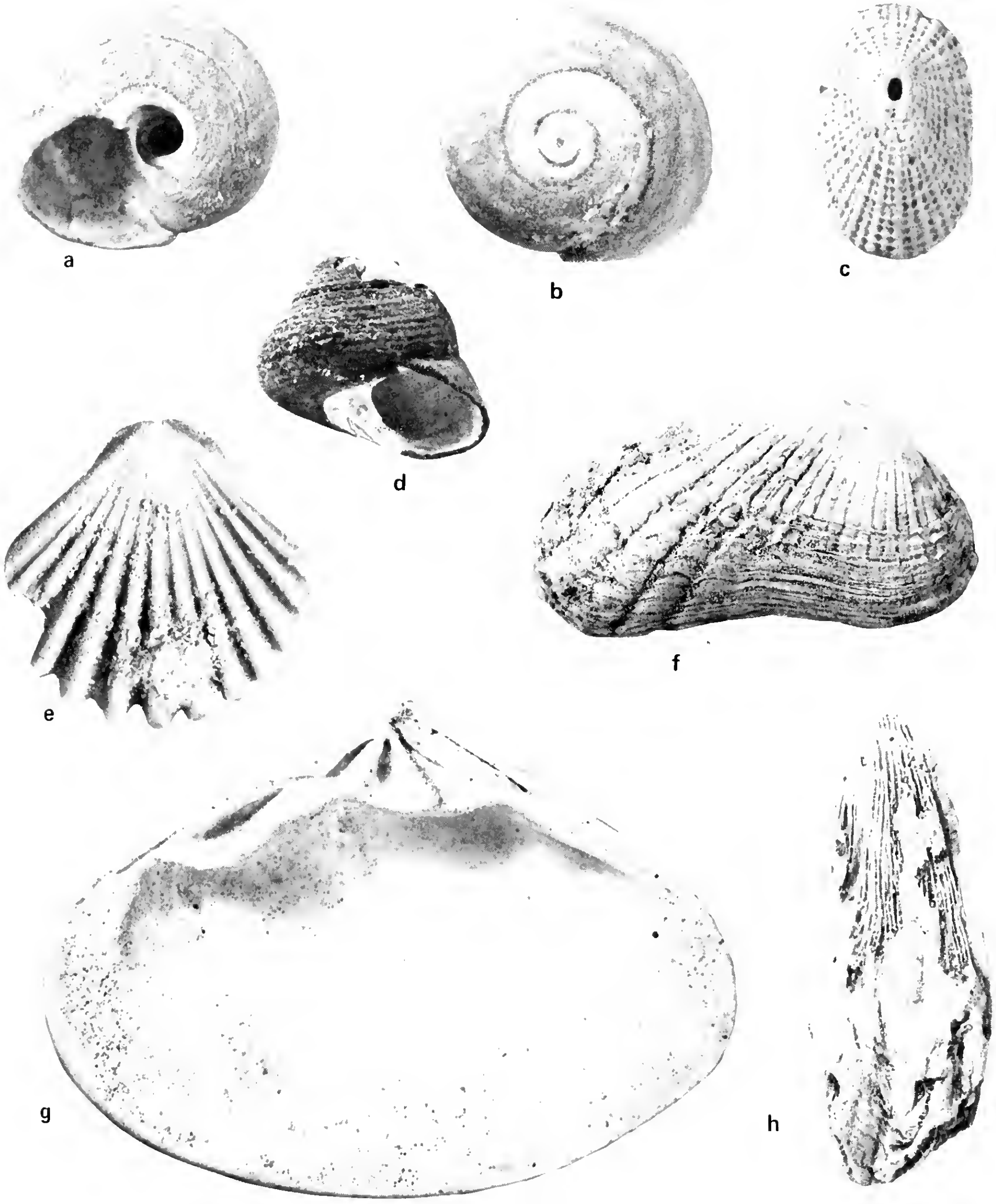

Figure 3. Fossils from the Lindavista Formation. a, b, *Tegula hemphilli*, SDSNH 15581, width 16.2 mm; c, *Diodora arnoldi*, SDSNH 14886, length 9.1 mm; d, *Tegula funebralis*, SDSNH 14889, width 27.2 mm; e, *Pecten bellus*, SDSNH 13117, height 22 mm; f, *Cardita* sp. aff. *C. affinis*, SDSNH 16678, length 59 mm; g, *Tivela stultorum*, SDSNH 14887, length 78.7 mm; h, *Megabalanus* sp., SDSNH 14888, height 60 mm.

the midtide level (McLean, 1969: 22). Dead shells are retained in the intertidal zone by hermit crabs, which use them for their own protection. The columella of one specimen has been extensively bored by spionid worms.

Mollusca: Bivalvia

Arca sisquocensis Reinhart, 1937

Remarks.—One fragment of this distinctive Pliocene and lower Pleistocene *Arca* was found. This species, described from the Pliocene Careaga Formation, also occurs in the lower Pleistocene Santa Barbara Formation (Reinhart, 1943: 25), as well as in the upper

Pliocene San Diego Formation exposed in southwesternmost San Diego County (LACMIP locs. 305 and 305A).

Pecten bellus (Conrad, 1857)

Fig. 3e

Remarks.—One small flat left valve referable to *Pecten bellus* has the apical angle, number of ribs, and muscle scar typical of the species. This characteristic middle to late Pliocene species also occurs in the lower Pleistocene Santa Barbara Formation (J. W. Valentine, pers. commun.). Sixteen additional pectinid fragments remain unidentified.

Cardita sp. aff. *C. affinis* Sowerby, 1833

Fig. 3f

Range.—[of *C. affinis*] Bahía de Pequeña, and the Gulf of California south to northern Peru (Keen, 1958: 85; Olsson, 1961: 190).

Remarks.—One complete right valve differs from Recent specimens examined by its more central umbo, rounded anterior and posterior margins, and greater thickness, although these differences may only be phenotypic. *Cardita affinis* occurs under rocks or in crevices intertidally and offshore to a depth of 27 meters (Keen, 1971: 107). This is the only living species in the fauna of the Lindavista Formation that does not presently occur along the San Diego coastline.

Fossil occurrences of *C. affinis* are known only from the upper Pliocene and Pleistocene of the southern part of the Gulf of California (Durham, 1950: 72; Hertlein, 1957: 62; Emerson and Hertlein, 1964: 341).

Tivela stultorum (Mawe, 1823)

Fig. 3g

Range.—Halfmoon Bay, San Mateo County, California, to Bahía Magdalena, Baja California (Fitch, 1953: 60).

Remarks.—This is the most abundant of any species found, and fragments and occasional complete valves were present at every locality in the area which produced fossils. No paired valves were found, and all appear to be detrital. A few specimens still exhibit faint coloration patterns. Many of the valves have been post-depositionally fragmented. *Tivela stultorum* usually occurs in the intertidal zone on flat sandy beaches on the open coast (exposed to the full force of the surf), or in channels leading into bays and estuaries (Fitch, 1953: 60).

Penitella sp. indet.

Remarks.—Several small specimens of a poorly preserved *Penitella* were removed from sandstone cobbles at two localities. The umbonal regions of all the specimens are too damaged for specific identification. Species of *Penitella* are commonly found in cobbles in molluscan death assemblages, and usually represent intertidal or high inner sublittoral zones on the open coast where wave action is strong and fine sedimentation does not occlude the siphonal openings.

Arthropoda: Crustacea

Cirripedia

Remarks.—Over 75 fragments of barnacle wall plates were found at one locality. These, although mostly unidentified, represent several species belonging to both *Balanus s.s.* and *Megabalanus* (Fig. 3h). Numerous fragments were recovered from the conglomeratic sandstone, but none were found attached to cobbles, nor were any bases found on any of the cobbles. A single opercular plate has been tentatively identified as *Balanus* sp. cf. *B. pacificus* Pilsbry, a species not positively known from Pliocene or older rocks (Zullo, 1969: 10). *Balanus pacificus* occurs today from San Francisco, California, to northern Peru, and is common in Pleistocene deposits of California and northern Baja California (Zullo, 1969: 10).

REGISTER OF LOCALITIES

All of the following localities are from the lower Pleistocene (?) Lindavista Formation from exposures on the Linda Vista Terrace east of Murphy Canyon in the city of San Diego, San Diego County, California. Most of the specimens were collected by me in September (locs. 0321-0326) and late November (loc. 0329), 1971. These localities are now mostly on private residential property. Specimens have been deposited in the Department of Invertebrate Paleontology in the San Diego Natural History Museum and bear its locality numbers.

Loc. 0321. Northwest trending bank facing southwest on east (back) side of residence at 5349 Jazmin Court, San Diego. Unconsolidated sand. Altitude 142 m. Approximate coordinates: 32° 49.7′ N., 117° 5.6′ W. Locality found by R. C. Schwenkmeyer.

Loc. 0322. West-facing bank at the northeast corner of the intersection of Sandia Place and Gabacho Drive (10810 Gabacho Drive), San Diego. Fossil fragments in gray laminated and cross-bedded non-indurated beach sand with occasional scattered pebbles. Approximate coordinates: 32° 49.8′ N., 117° 5.8′ W.

Loc. 0323. North-facing bank on south side of lot at 10805 Gabacho Drive (in cul-de-sac opposite Sandia Place), San Diego. Laminated gray unconsolidated beach sand overlain by well-indurated fossiliferous conglomeratic sandstone, which in turn is overlain by a terrestrial conglomeratic facies. Approximate coordinates: 32° 49.8′ N., 117° 5.8′ W.

Loc. 0324. East-west trending utilities ditch in south side of street along north side of 10825 Gabacho Drive, San Diego. Approximate coordinates: 32° 49.8′ N., 117° 5.8′ W.

Loc. 0325. North-facing bank on south side of residence at 10735 Montego Drive (in southeast corner of first cul-de-sac on Montego Drive west of El Noche Way), San Diego. Unconsolidated fossiliferous conglomeratic sandstone. Altitude 131 m. Approximate coordinates: 32° 49.7′ N., 117° 5.8′ W. Locality found by G. W. Moore.

Loc. 0326. West-facing bank on east side of residence at 10735 Montego Drive (in southeast corner of first cul-de-sac on Montego Drive west of El Noche Way), San Diego. Approximate coordinates: 32° 49.7′ N., 117° 5.8′ W.

Loc. 0329. Ninety-meter stretch along west-facing roadcut on east side of Santo Road, beginning approximately 35-40 meters north of intersection of Santo Road and Monte Negro Drive, San Diego. Fossiliferous lenses mixed with black heavy-mineral sand and cobble conglomerate. Locality found by G. W. Moore.

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POST-BATHOLITHIC GEOLOGY OF THE JACUMBA AREA, SOUTHEASTERN SAN DIEGO COUNTY, CALIFORNIA

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POST-BATHOLITHIC GEOLOGY OF THE JACUMBA AREA, SOUTHEASTERN SAN DIEGO COUNTY, CALIFORNIA

JOHN A. MINCH AND PATRICK L. ABBOTT

ABSTRACT.—The post-batholithic history of the Peninsular Range is documented by sparse exposures of fluvial and volcanic rocks in widely separated areas. The Jacumba Valley outcrops present one of the most complete stratigraphic records in the range.

The intial erosion surface upon the Southern California Batholith probably formed in the Late Cretaceous. This surface was fairly deeply weathered as was the earliest granitic gravel deposited upon it. Clasts resembling those of the Table Mountain Gravels were transported across the Jacumba area to the Pacific Coastal region, where they appear in the Cabrillo Formation of Late Cretaceous age. Eocene "Poway-type" gravel was transported across an essentially parallel surface just south of Jacumba Valley near La Rumorosa. Erosion partially removed and reworked the gravel until Early Miocene outpourings of basalt and pyroclastic debris filled in much of the Jacumba Valley area. The first basalt flows from eruptive centers within the valley were followed by faulting and the deposition of andesitic pyroclastic and lahar deposits. The source of this andesite may have been the plug-like masses at Round Mountain and Jade Benchmark. Continued faulting offset the volcanic rocks before the eruption of a second series of basalt flows which covered the andesite in the northeast and east portions of the valley. Intermittent erosion within the volcanic sequence is evidenced by fluvial and eolian volcaniclastic deposits. Post-volcanic faulting elevated the Peninsular Range and accelerated erosion to produce the present topography.

The Jacumba Valley area is located at the crest of the Peninsular Range and straddles the Mexico-United States boundary. Interstate 8 and the San Diego and Arizona Eastern Railroad pass through the valley between San Diego and the Imperial Valley. Rainfall is light resulting in sparse vegetation and excellent outcrops. Field work for this report was accomplished in the fall of 1971 and spring of 1972 in conjunction with a field geology class at California State University, San Diego.

The first account of the post-batholithic geology of Jacumba Valley was by Fairbanks (1893), who indicated the presence of the gravels and volcanics at the crest of the Peninsular Range. Miller (1935a) followed with a brief description of the rocks and included speculations on their former widespread extent, exotic origin, and Miocene age.

In the late 1940s and early 1950s field classes from San Diego State College used the area for reconnaissance mapping exercises. These were compiled as map sheet 23 (Brooks and Roberts, 1954) in Bulletin 170 of the California Division of Mines and Geology. Jacumba Valley remains an excellent area for students to map in a terrane exposing a variety of eruptive features resting on sedimentary, plutonic, and metamorphic rocks.

Gastil and Bushee (1961) and Weber (1963) briefly mention the valley. Hawkins (1970) provided a detailed analysis of the chemistry of the volcanic rocks in the valley and tied them into the over-all picture of sea-floor spreading in Southern California. Minch (1971) described the Table Mountain Formation and indicated its nonlocal origin.

BASEMENT ROCKS

The crystalline rocks flooring the valley have been mapped as two separate units (Weber, 1963). The older mass is comprised of metamorphic rocks mixed with granodiorite, diorite, and pegmatites. These metasedimentary rocks are dominated by the quartz- and mica-rich Julian Schist, with minor amounts of gneiss and quartzite and occasional pods of marble. These are cut by abundant pegmatites and plutonic bodies.

The younger plutonics of the Southern California Batholith are here composed mostly of quartz diorite along with granodiorite and minor pods of gabbro.

TABLE MOUNTAIN GRAVELS

The Table Mountain Gravels are light yellow-brown, moderately bedded, fairly well-sorted, very friable, medium to coarse-grained sandstones and conglomeratic sandstones which crop out in and near Jacumba Valley. In addition to local granitic clasts they contain clasts of low-grade green metavolcanic and metasedimentary rocks and quartzites that are not found locally.

Miller (1935a: 138) defined the Table Mountain Formation from exposures at Table Mountain 7 km northeast of Jacumba as: "Moderately consolidated deposits of yellowish to reddish-brown gravels and sands. Various kinds of pre-Cretaceous crystalline rock fragments occur in the formation . . . These sediments are rather variable in character, crudely stratified, and gently dipping."

Several authors have indicated the exotic nature of these gravels found high in the Peninsular Range (Fairbanks, 1893; Brooks and Roberts, 1954; Weber, 1963). Brooks and Roberts (1954) compare the clasts to the Santiago Peak Volcanics of western San Diego County: "They contain fragments of dacites and other aphanitic rocks that show strong similarities to the Jurassic?Santiago Peak Volcanics of western San Diego County. These gravels are partially interbedded with and principally overlain by other volcanic rocks."

DISTRIBUTION.—The Table Mountain Gravels crop out on the erosion surface in a belt about 10 km wide and 25 km long that lies roughly parallel to the axis of the Peninsular Range. They are the remnants of an extensive fluvial deposit. In the Jacumba area they stretch another 5 km down the frontal scarp of the range. The principal outcrops are in and around Jacumba Valley and in the area just west of La Rumorosa in Baja California. The small isolated patches of the gravels which occur at lower elevations on the frontal scarp of the range are the easternmost exposures.

The best exposures of the Table Mountain Gravels are in the area of Jacumba Valley where the Jacumba Volcanics form a resistant cap above the gravels (Fig. 1). A typical section measured on a flat-topped hill just north of Jacumba in the northwest corner of Sec. 5, T 18 S, R 8 E consists of 75 m of interbedded light yellow-brown, moderately to thickly bedded, very friable, medium- to coarse-grained sandstone and ½ to 1 m thick beds of conglomeratic sandstone. The sandstones within the Table Mountain Formation are sheet-wash to fluvially deposited, plutonic lithic arkose. The framework grains are very angular, poorly to very poorly sorted, mineralogically immature, and are cemented by poikilotopic, very coarsely crystalline calcite where unleached. Common grains include both fresh and heavily sericitized plagioclase and orthoclase, polycrystalline quartz, schist and plutonic rock fragments along with hornblende, biotite, muscovite, and other accessory minerals.

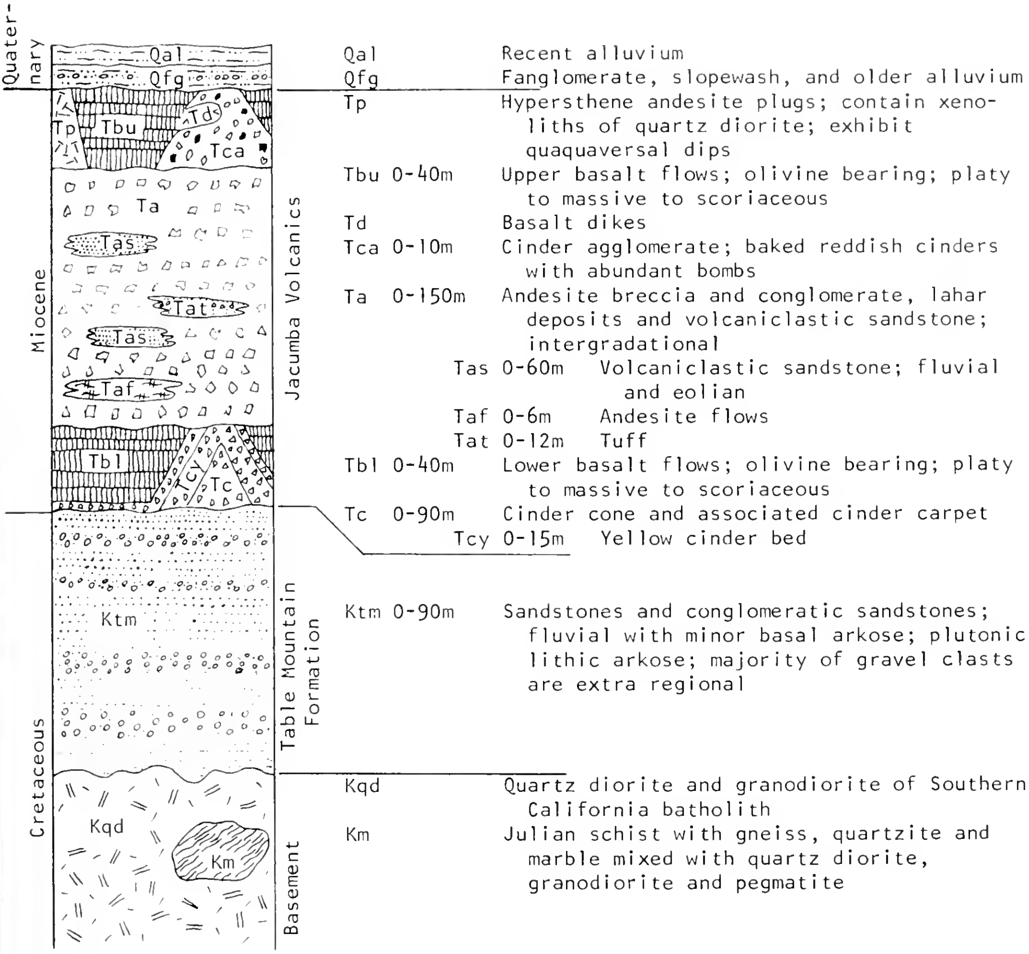
The gravel-sized clasts are subangular to subrounded and average 2.5 to 5 cm in diameter with clasts commonly to 10 cm and rarely to 30 cm. Fifty percent of the clasts are extraregional, low-grade, green metavolcanic and metasedimentary rocks. Other significant components of these gravels are quartzites and resistant sandstones (25%), and local granitic and gneissic basement rocks (12%). The thickness of the gravels is quite variable, ranging from a thin mantle on the surface to greater than 75 m. Most exposures are less than 30 m in thickness.

Other good exposures of these gravels occur on the northeast side of Jacumba Peak (N. Center Sec. 7, T 18 S, R 8 E), on Table Mountain (T 17 S, R 8 E), and in Myer Valley (NE ¼, Sec. 26, T 17 S, R 19 E) about halfway down the frontal scarp.

In the Jacumba area the Table Mountain Gravels seem to have been highly eroded before the deposition of the Jacumba Volcanics. This is evident because the basalts and breccias have an irregular basal contact which, in one case, rests on 75 m of gravel at one end of a hill but sits on the granitic erosion surface 120 m lower in altitude at the other end of the hill.

AGE.—The Table Mountain Gravels are certainly older than the 18.5 m.y. Jacumba Volcanics which overlie them, and they are younger than the rocks of the Peninsular Range Batholith upon which they rest (90-105 m.y., Bushee et al., 1963; cooling age of 65-80 m.y., R. G. Gastil, pers. comm.). They were deeply eroded before the deposition of the Jacumba Volcanics, suggesting that they may be significantly older than the Miocene volcanics.

In the San Diego coastal area the conglomerate of the Upper Cretaceous Cabrillo



Qal		Recent alluvium
Qfg		Fanglomerate, slopewash, and older alluvium
Tp		Hypersthene andesite plugs; contain xenoliths of quartz diorite; exhibit quaquaversal dips
Tbu	0-40m	Upper basalt flows; olivine bearing; platy to massive to scoriaceous
Td		Basalt dikes
Tca	0-10m	Cinder agglomerate; baked reddish cinders with abundant bombs
Ta	0-150m	Andesite breccia and conglomerate, lahar deposits and volcaniclastic sandstone; intergradational
Tas	0-60m	Volcaniclastic sandstone; fluvial and eolian
Taf	0-6m	Andesite flows
Tat	0-12m	Tuff
Tbl	0-40m	Lower basalt flows; olivine bearing; platy to massive to scoriaceous
Tc	0-90m	Cinder cone and associated cinder carpet
Tcy	0-15m	Yellow cinder bed
Ktm	0-90m	Sandstones and conglomeratic sandstones; fluvial with minor basal arkose; plutonic lithic arkose; majority of gravel clasts are extra regional
Kqd		Quartz diorite and granodiorite of Southern California batholith
Km		Julian schist with gneiss, quartzite and marble mixed with quartz diorite, granodiorite and pegmatite

Figure 1. GENERALIZED COLUMNAR SECTION

Formation (Kennedy and Moore, 1971) contains a small percentage of black to blue-gray quartzite, light colored quartzite, and chert pebbles, and several types of metavolcanic clasts not associated with the local basement. These clasts are not found in the locally derived gravel of the underlying Lusardi Formation, indicating that they are extra-regionally derived clasts. These exotic clast types are also found in the Table Mountain Formation.

The presence of the extra-regional clasts in the Cabrillo Formation, which has been dated as Maestrichtian (Kennedy and Moore, 1971), suggests a relation to the Table Mountain Gravels, which in turn suggests that the two formations might be the same age. If so, this would place the initial deposition of the gravels in the Late Cretaceous.

JACUMBA VOLCANICS

The Jacumba Volcanics were defined by Miller (1935a: 138-139) for "...the extensive rocks which are excellently exposed in the several areas north to east of Jacumba . . . Some volcanic breccias or pyroclastics here occur toward the bottom of the lava beds." In the present report the Jacumba Volcanics are subdivided into three basic units. They are: (1) basalt flows and cinder-cone deposits, (2) basaltic-andesite plugs, and (3) andesite breccia, lahar deposits, conglomerate, and volcaniclastic sandstone.

The same authors who discussed the Table Mountain Gravels also generally discussed the Jacumba Volcanics (Fairbanks, 1893; Miller, 1935a, b; Brooks and Roberts, 1954; Gastil and Bushee, 1961; and Weber, 1963). In addition, Hawkins (1970) discussed the petrochemistry of the volcanics and cited a K/Ar whole rock date of 18.7±1.3 m.y. for the lower part of the basalt sequence.

The Jacumba Volcanics form a 20 by 55 km belt of outcrops parallel to the axis of the Peninsular Range. However, the principal areas of outcrop are in a narrow belt 5 to 10 km wide by 55 km long on and along the frontal scarp of the range, with the majority of the outcrops near the base of the scarp. The Jacumba Volcanics also crop out in and around Jacumba Valley.

The basalt flows are the most extensive part of this unit, with outcrops over most of the valley. The andesite breccia, lahar deposits, and volcaniclastic sandstone are as extensive but more limited in outcrop. Remnants of at least five cinder cones and two prominent hypersthene andesite plugs are exposed in the valley.

FLOWS.–The lavas consist of up to 40 meters of gray to dark gray, platy to massive, vesicular olivine basalt and basaltic andesite. The basalt flows crop out at the base and at the top of the volcanic sequence. As many as five or six flow units may be represented in any given outcrop. These flow units tend to be massive in their upper portions but exhibit platy jointing due to flow shearing at their bases or where they abut other rocks (see Hawkins, 1970, for detailed chemical description).

DIKES AND CINDER CONES.–Squaw Tit is an excellent example of one of several prominent dikes exposed on Table Mountain (Map-Fig.2). This dike system appears to have partially followed a northwest-trending fracture system. The basalt in these dikes ranges from a dense gray-green to dark gray, well-jointed olivine basalt to a scoriaceous olivine basalt which appears to have been close to the surface of a vent represented by the spine of Squaw Tit. These dikes cut the lower basalt unit and may be the source for the upper basalt unit.

Associated with these dikes are at least two cinder cones. The oldest cinder cone is at the base of the section east of a fault on the southern side of Table Mountain. It is 75 to 90 m high and is well exposed as a result of quarrying operations. The cinders comprising the cone are red- to purple-brown, well sorted, thinly bedded, and tend to be lapilli to dust size with a small percentage of blocks and very few bombs. The upper 15 m of the cone has been altered by gasses to a yellow-brown color. Also deposited during this pyroclastic episode is a thinly bedded cinder carpet up to 4.5 m thick, which appears to be thicker to the east and southeast of the cone, suggesting a paleowind direction similar to the present prevailing wind pattern. This cone may have been the source for the earlier basalt flows. A fault truncates its west side and moves the western portion right-laterally about 90-150 m.

Transitional lithologies occur where the first pyroclastic eruptives are mingled with the granitic wash mantling the Table Mountain Formation. Commonly found here are volcanic glass-cemented, spherical concretions of slightly granular, bimodal, very coarse- and very fine-grained, volcanic lithic arkose. The coarser mode contains numerous plutonic rock fragments along with microcline, orthoclase, and perthite from the surrounding highlands. The finer mode comprises idiomorphic volcanic plagioclase, relict shards, lamprobolite, zircon, biotite, and apatite. The non-concretionary arenite in places contains montmorillonite formed from altered pyroclastics.

West of the major fault and interlayered with but partially overlying the earlier flows is a series of agglomerate and cinder deposits. These pyroclastics are distinguished from the earlier cone materials because they overlie the lower basalt, are coarser, lack sorting, and contain a large percentage of bombs and agglutinate material. Some of the bombs and blocks in this younger cone are up to 1.3 m in diameter, although most average 3 to 5 cm. Several basalt flow units appear to have issued from the base of the younger cone along the west and northwest side of Table Mountain. The cone morphology is not obvious as it has largely been destroyed or obscured by later deposits. Cinder and scoria deposits suggestive of smaller eruptive centers are found on the east side of the border hill (VABM 3572), in a pit along Carrizo Gorge road just north of old Highway 80, in a pit east of Round Mountain and south of Interstate 8, and in the low hills north of the freeway and west of the Jacumba turnoff. All have an abundance of calcite cement, and in the eruptive center just south of the freeway the calcite percentage is so high that the cinders initially appear to lack a supporting framework.

ANDESITE PLUGS.–Round Mountain and the hill at Jade Benchmark (Map-Fig. 2) are plugs whose chemistry differs significantly from the other volcanic rocks in the valley (Hawkins, 1970). They contain significant percentages of hypersthene in place of the hornblende typical of the basalt flows. These plugs are largely intact and have typical onion-skin jointing and a bulbous dome-like structure. Both plugs contain xenoliths of granodiorite, quartz diorite, and schist from the basement rock.

The plugs are younger than at least that part of the andesite breccia sequence which they rest upon. No clear-cut evidence can be presented for their minimum age and they could be much younger than the lavas and andesites. Similar appearing plugs of Pliocene age (R. G. Gastil, pers. comm.) occur in other parts of the Peninsular Range near the international boundary.

ANDESITE BRECCIA, LAHAR DEPOSITS, CONGLOMERATE, AND SANDSTONE.–A heterogeneous sequence of andesitic lahar deposits, breccia, conglomerate and sandstone form a significant portion of the Jacumba Volcanics. The andesites are up to 150 m thick in some localities and generally average 90 m thick over much of the area. The breccia appears to be the dominant form of the andesite, but other forms are more common locally. The intergradation of the component rock types and the presence of a heavy lag gravel over the andesite prevented the mapping of the individual andesitic rock units.

The best exposure of the andesite breccia is just east of the Table Mountain quarry in NE ¼, Sec. 35, T 17 S, R 8 E (Map-Fig. 2). There the breccia consists of red-brown to brown to gray massive hornblende andesite which has been intensely sheared, broken, and comminuted to form a flow breccia. No bedding or stratification can be discerned at the outcrop.

The andesite breccias grade into lahars (mudflows of volcanic detritus). In the vicinity of the Table Mountain quarry an approximately 9 m thick lahar deposit consists of a red-brown to brown, massive andesitic breccia with andesite and cinder particles ranging from dust to small boulder size. The complete lack of bedding and sorting coupled with monolithologic andesite fragments are characteristic of a lahar deposit. Intermittent fluvial action has reworked the breccia and lahar deposits producing volcaniclastic conglomerate and sandstone which occur throughout the section. These fluvial units resemble the breccia in clast composition, and they are distinguished by the presence of bedding and of increased sorting of the clasts. A typical sandstone exposed above the quarry on Hill 4089 (SW ¼, Sec. 26, T 17 S, R 8 E) is a very poorly sorted, very angular to subangular, pebbly medium sandstone. This and similar sandstone beds are lithic arkoses and are loaded with volcanic rock fragments and extrusive euhedral minerals, while plutonic-derived sediment is usually absent.

Mixed plutonic-volcanic lithic arkoses are found between tuffs (below) and volcanic mudflows (above) on the south side of Round Mountain. This mixed-provenance lithology illustrates the intermittent nature of volcanic sedimentation that allowed inworking of granitic-derived debris.

Intercalated within the volcanic sequence west of Gray Mountain is a volcanic lithic arkose mass exhibiting 0.6 to 1.3 m thick planar-wedge sets of cross-laminae. These fine sandstone grains are mostly plagioclase, volcanic-rock fragments, hypersthene, hornblende, and biotite that are moderately sorted, skewed toward the fines, and subrounded to subangular. The sedimentary structures, presence of abrasion, fine grain size, and best sorting in the valley all indicate an episode of reworking of volcanic sediment into eolian dunes.

The various units of the Jacumba Volcanics are considered to be of Early Miocene age. The K/Ar whole rock age date of 18.7 ±1.3 m.y. (Hawkins, 1970) for a basalt on Jacumba Peak corresponds with concordant hornblende and plagioclase dates of 18.5 ±0.9 m.y. and 18.6 ±0.8 m.y., respectively, obtained from a clast in the andesite breccia on Table Mountain (K/Ar laboratory CSUSD). Thus, the bulk of the Jacumba Volcanics were erupted in the Early Miocene.

STRUCTURE

The structure of the Jacumba area is dominated by a series of northwest-trending normal and reverse faults. Two east-trending faults bound the area on the north and south. Only a few northwest-trending faults could be traced beyond the east-trending faults.

The northwest-trending set of faults produces a horst and graben effect within the valley. Throws of up to 300 m are necessary to produce some of the observed features. The fault which bisects Table Mountain has approximately 90 to 150 m of right-lateral separation and 30 to 60 m of vertical separation. In many cases a fault which can be traced for some distance with certainty in the volcanic rocks is lost within a few feet in the granitic rocks. In other cases a single fault in the volcanic rocks splits into several segments as it enters the granitic rocks.

An interesting feature noted along several large faults is the inclusion of a thin sliver of Table Mountain Formation in the fault zone. In a number of cases the presence of a fault was recognized by the thin strip of conglomerate between the granitic and the volcanic rocks.

The two east-trending faults are primarily in granitic rocks and have helped erosion produce long linear valleys. The northern fault exhibits a 0.6 to 1.5 m shear zone along the north side of Table Mountain.

The structure in the Jacumba Valley closely parallels the regional structure of the northwest side of the Peninsular Range. The valley itself is directly along the projected trend of the Elsinore fault zone as it passes out of the main mountain mass near Banner Grade. The right-lateral separation on at least one fault in the Jacumba area may suggest that some of the displacement on the Elsinore is taken up by movement along its projected trend in the Jacumba Valley area.

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REVISION OF THE CORAL-INHABITING BARNACLES (CIRRIPEDIA: BALANIDAE)

ARNOLD ROSS AND WILLIAM A. NEWMAN

TRANSACTIONS

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Figure 1. *Boscia anglicum* on *Caryophyllia smithii* Stokes and Broderip; Eddystone, South Devon, England; British Museum (Nat. Hist.) 1904.6.27.13. British Museum photograph.

REVISION OF THE CORAL-INHABITING BARNACLES (CIRRIPEDIA: BALANIDAE)

ARNOLD ROSS AND WILLIAM A. NEWMAN

ABSTRACT.—The biogeography, growth, morphology and host specificity of all known taxa of coral-inhabiting barnacles in the Pyrgomatinae are reviewed. In addition to *Pyrgoma* and *Creusia*, among which all of the species were previously divided, we resurrect five genera and propose **Hoekia, Hiroa** and **Cantellius**. These 10 genera fall into three groups: *Boscia* (cosmopolitan), *Ceratoconcha* (Pliocene in the eastern Pacific, Mio-Pliocene in the Mediterranean Basin, and as Miocene relicts in the western Atlantic), and *Cantellius* and its derivatives (Miocene to Recent in the Indo-west Pacific). The Pyrgomatinae are apparently polyphyletic; *Cantellius* and possibly *Boscia* arose from different armatobalanid stocks, while *Ceratoconcha* arose from an indeterminate balanoid stock. *Cantellius* and *Ceratoconcha* first appeared in the Miocene during the break up of the Tethyan Sea and the initiation of faunal provincialism.

The reef coral community has been characterized by Cloud (1959: 387) as essentially a steady-state oasis of high population density, intense calcium metabolism, and complex nutrient cycling, generally surrounded by waters of relatively low nutrient and plankton content. Aside from interesting parallels with tropical rain forests and man-made megalopolises, Newell (1971: 2) argued that the organisms comprising the coral reef community are "superlatively coadapted." One of the remarkably coadapted animal groups is the coralliophilic pyrgomatines.

Barnacles comprising the Pyrgomatinae are obligatory symbionts or parasites primarily of scleractinian corals. They occur in all regions of the world that support major growths of hermatypic corals, and they have been found in sediments dating from the early Miocene. Modern pyrgomatines were probably recognized by naturalists in the 18th century, but the group did not receive serious attention until the middle of the 19th century. The present study is the first general revision on a world-wide basis.

HISTORICAL ACCOUNT

Studies on pyrgomatine cirripeds may be grouped into three periods. The work of Leach (1817, 1818, 1825), Sowerby (1823), Gray (1825, 1831), and many other conchologists characterize the earliest period as one of describing new taxa and grouping these into a hierarchy.

The second period, covering about 70 years, began with the publication of Darwin's (1854) monograph of the Balanidae and Veruccidae. Darwin attempted to embody the best features of earlier studies; however, he chose not to follow the generic divisions proposed by Leach and Gray, and retained only *Pyrgoma* and *Creusia*, and the latter he assigned subgeneric status. Leach and Gray had attempted to group a seemingly meager number of species into a maximum number of poorly defined genera. Consequently, Darwin's conservative approach was generally accepted; and such caution has proved a deterrent to unraveling the systematics of this group.

The third period began with the work of Annandale (1924), followed by Withers (1926, 1929), Hiro (1935, 1938), and Nilsson-Cantell (1938), and more recently, by Brooks and Ross (1960), Utinomi (1962, 1967), Baluk and Radwański (1967a, 1967b, 1967c), and Ross and Newman (1969). Annandale, Hiro, and Nilsson-Cantell provided names for the majority of Darwinian numerical varieties, and they added considerably to our knowledge of the Indo-Pacific members of the subfamily.

Of the many classifications proposed for this group, the earliest were taxonomic rather than phylogenetic, except that of Gray (1825: 102), which was based on an ecological concept. The most promising classification was proposed recently by Baluk and Radwański (1967c) who resurrected the generic groupings initiated by Leach, Gray and

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Sowerby, and proposed several new names. The present study somewhat revises and greatly extends their classification.

BIOGEOGRAPHY

Modern pyrgomatines occur in all regions of the world that support major growths of hermatypic corals. Fossils occur predominantly in the Tertiary and Pleistocene of the western Atlantic and the Mediterranean Basin (Withers, 1929: 2; Brooks and Ross, 1961: 326; Baluk and Radwański, 1967c; Newman and Ladd, in press). The western Atlantic contains but a few morphologically primitive pyrgomatines, while the Indo-west Pacific has the greatest variety and abundance and the morphologically most advanced species. The disparity between these faunal realms may relate to the greater number of reef corals available as hosts in the Indo-Pacific, of which there are 80 genera and 500 species as compared to 20 genera and 65 species in the western Atlantic (Newell, 1971: 26), but the latter has also witnessed a general decline in the biota dating from the Miocene (Newell, 1971: 23).

Three major morphological groups of Pyrgomatinae are recognized in this paper (*Ceratoconcha*, *Boscia* and *Cantellius* and its derivatives), and these have interesting implications. The first and most generalized is the creusioid *Ceratoconcha*, which first appears in sediments of lower Miocene age. Based on studies by Brooks and Ross (1961: 362), Baluk and Radwański (1967c), and Newman and Ladd (in press), it is evident that during the Miocene *Ceratoconcha* was not only more diverse in terms of species than it is today, but also ranged throughout the tropical Atlantic and its eastern Pacific outpost, while it survives as a Miocene relict in the western Atlantic (Fig. 2). *Ceratoconcha* apparently never ranged into the Indo-Pacific, probably because communications between the Indian Ocean and the Mediterranean had ceased in early Miocene times (Ruggieri, 1967: 284) with the northward movement of the African land mass.

The Pliocene fauna in the Mediterranean Basin includes only *C. costata* (see Baluk and Radwański, 1967c: 483; Moroni, 1967: 17); apparently no Pleistocene ceratoconchoids are found there. The short stratigraphic range of *Ceratoconcha* in the Mediterranean Basin is not surprising, because climatic cooling which had already begun in the Oligocene (Wells, 1956; Ekman, 1953), coupled with isolation (Ruggieri, 1967: 284), resulted in a decline in, if not total destruction of, the hermatypic corals and other tropical elements of the fauna.

The Mediterranean ceratoconchoids are probably western Atlantic derivatives despite the great distance separating these two regions. Numerous other invertebrates presently have trans-Atlantic distribution patterns (Briggs, 1970), and apparently many of these animals have larvae that were transported eastward from the western Atlantic (Robertson, 1964: 21; Scheltema, 1971: 284).

Ceratoconcha was represented by at least five species in the western Atlantic in the early Miocene (Newman and Ladd, in press), and some time thereafter by a few species in the eastern Pacific. At least two species are found in Pliocene corals of the Imperial Formation of the Carrizo Creek and Coyote Mt. areas of southern California (Ross, unpubl.). There are no Pleistocene or living ceratoconchoids in the eastern Pacific. The western Atlantic Pliocene fauna contains only *prefloridanum*; the Pleistocene fauna contains *barbadensis*, possibly *prefloridanum*, and several undescribed species (Brooks and Ross, 1960: 362). The Recent western Atlantic contains two or possibly three species.

The second group, containing only the primitive pyrgomoid *Boscia* (Fig. 2), has been found in sediments of Pliocene age in the Mediterranean Basin (Baluk and Radwański, 1967c: 483) and England (Darwin, 1854b; Withers, 1926). Pleistocene occurrences include Italy (Alessandri, 1906) and Japan (Sakakura, 1938). Although Sakakura reported the individuals he found on an ahermatypic coral as *anglicum*, restudy of these may reveal that they represent either a new species or *oulastreae* (see Utinomi, 1967: 232), since *anglicum* appears to be restricted to the western Mediterranean and eastern Atlantic (Moyse, 1961: 384; Utinomi, 1967: 231; cf. Rees, 1962: 412). *Boscia* occurs on hermatypic corals in the western Atlantic (*madreporarum*) and western Pacific (*oulastreae*), whereas in the eastern Atlantic and Mediterranean (*anglicum*) it settles only on ahermatypic corals. There are no records of *Boscia* in the eastern Pacific.

The third group is wholly Indo-west Pacific with species ranging from the Red Sea to the Great Barrier Reef and to the Line Islands (Fig. 2 and 3). There are but two Miocene records for the eight genera in this group, but the specimens have not yet been identified (Newman and Ladd, in prep.). *Nobia*, *Cantellius*, and *Savignium* are found throughout the Indo-Pacific, but only *Savignium* ranges as far south as the Great Barrier Reef and as far east as the Line Islands. *Pyrgoma*, *Creusia*, and *Hoekia* range from eastern India to Japan, although *Hoekia* has been reported from Mauritius (Ross and Newman, 1969). There is only one record for *Hiroa*, in the Caroline Islands.

From the foregoing, two provincial coral-barnacle faunas can be recognized, one centering in the Caribbean portion of the western Atlantic and the other in the Australasian portion of the Indo-Pacific. Comparable biogeographic patterns have long been recognized in other invertebrates and in fishes (see Briggs, 1970). The coral barnacles were evolving when the continuity of the Tethyan Sea was being destroyed, ultimately leading to faunal provincialism. In light of the geological history of these regions and considering the morphological features of these two groups, it is apparent that they developed independently in the two regions from different balanoid ancestors. *Boscia*, which appears to be a third independent group, may owe its widespread distribution to its ability to settle on deep-water ahermatypic corals.

GROWTH AND FORM

The early growth stages of pyrgomatines look much like those of ordinary balanids. It is in the later stages that their adaptations to an intracoralline life become evident. Knowledge of the larval stages is limited: Kolosváry (1950: 293) described typically balanoid nauplii of *Savignium milleporae* and Moyse (1961: 371) described all larval stages of *Boscia anglicum*. Duerden (1904: 39) suggested that the cyprid bores through the living tissue of the polyp and that in the process of growth the skeletons of the two become fused.

Utinomi (1943: 16) followed the ontogeny of the earliest juveniles of *Creusia indicum* Annandale, and found that the juvenile does not initially attach to the coral skeleton but remains imbedded in the coral tissue. While the four plates making up the wall and the opercular valves are calcified, the cup-shaped basis of the juvenile is wholly membranous. Even after the basis calcifies there is a period when the juvenile remains free in the coral tissue before the basis and corallites come into contact and fuse. Moyse (1971: 127) noted similar relationships in *Boscia anglicum*.

Subsequent growth is rapid, especially laterally, so that the shell reaches essentially maximum diameter early in life. This is well illustrated by Hiro (1938, fig. 11 and 12). In general, the wall becomes proportionately less conical as its diameter and basal height increase, the aperture enlarging by diametric growth in four-plated forms, or by corrosion and cirral rasping in single-plated forms. In the scatter diagram plotted by Hiro (1938, fig. 12) for *Creusia indicum*, after the period when the basal height and shell width increase uniformly, width stabilizes while basal height continues to increase, as it must throughout the life of the barnacle. During the early period of rapid increase in width, the barnacle may rotate its position by as much as 90° (Baluk and Radwański, 1967b, fig. 2, 1; Newman and Ladd, in press, pl. 2h).

Creusioids with well developed radii are commonly overgrown to some extent by the coral, and enlargment in both basal height and shell diameter requires breaking the overgrowth along the sutures. Creusioids with radii indicated by simple sutures, and pyrgomoids in general (except *Boscia*, see Moyse, 1971), have the ability to suppress coral skeleton deposition around the margin of the shell so that vertical growth can proceed without mechanical breakage. In some cases, the coral may lay down skeletal elements on the wall of the barnacle suggestive of normal septa, and the barnacle then takes on the appearance of a corallite (Duerden, 1904: 39); this is an unusual form of mimicry to say the least. In other cases, only coral tissue grows over the wall of the barnacle, and in *Hoekia* this tissue proliferates over the aperture where it is fed upon by the barnacle (Ross and Newman, 1969).

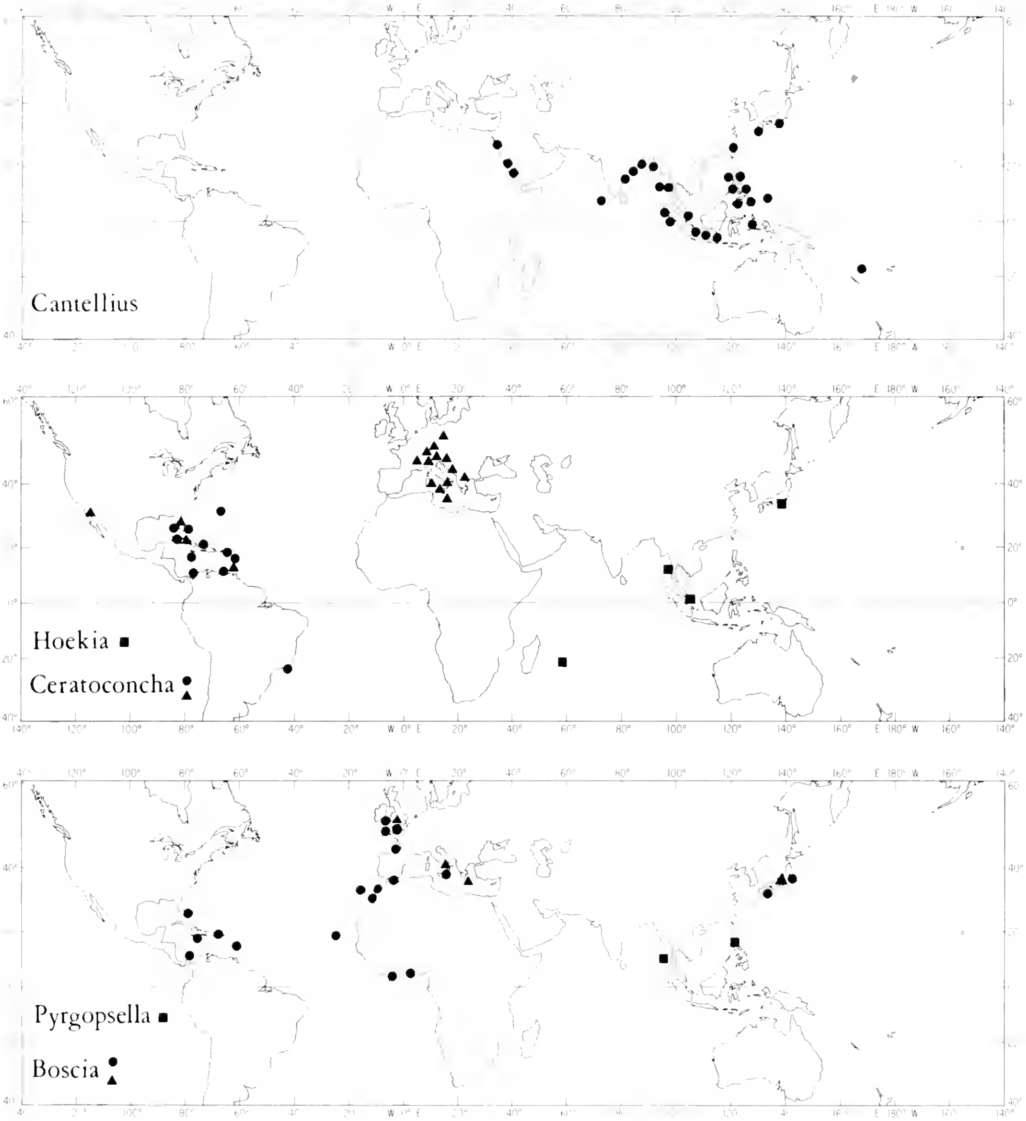

Figure 2. Distributional records for *Nobia, Pyrgoma, Hiroa, Savignium,* and *Creusia.* Data from same sources as Figure 3.

In specimens of *Savignium crenatum* that we have observed growing between low branches of the surface of *Merulina ampliata*, the rate of growth of the barnacle exceeds that of the coral so that the barnacle extends well above the general surface of the corallum. In most cases a thin layer of coral skeleton grows up onto the surface of the basis of the rapidly advancing barnacle, aiding in its support, but in some a fair proportion of the basis stands free of the coral. While it might appear that the barnacle's growth rate is simply out of phase with that of the coral, there is adaptive value in growing in this manner. The barnacles are growing up between branches of the coral which will eventually fuse laterally at higher levels. If the barnacles simply kept pace with the growth of the surface, they would more than likely be buried.

Boscia anglicum grows in a similar manner, but on solitary ahermatypic corals, along the margin of the corallite (Fig. 1). In this position there is relatively little interference with the normal feeding mechanism of the coral. Established individuals frequently serve as sites for subsequent generations. Cloud (1959: 392) suggested that the barnacles replace the coral polyps, and although this is certainly not true here, it may more frequently

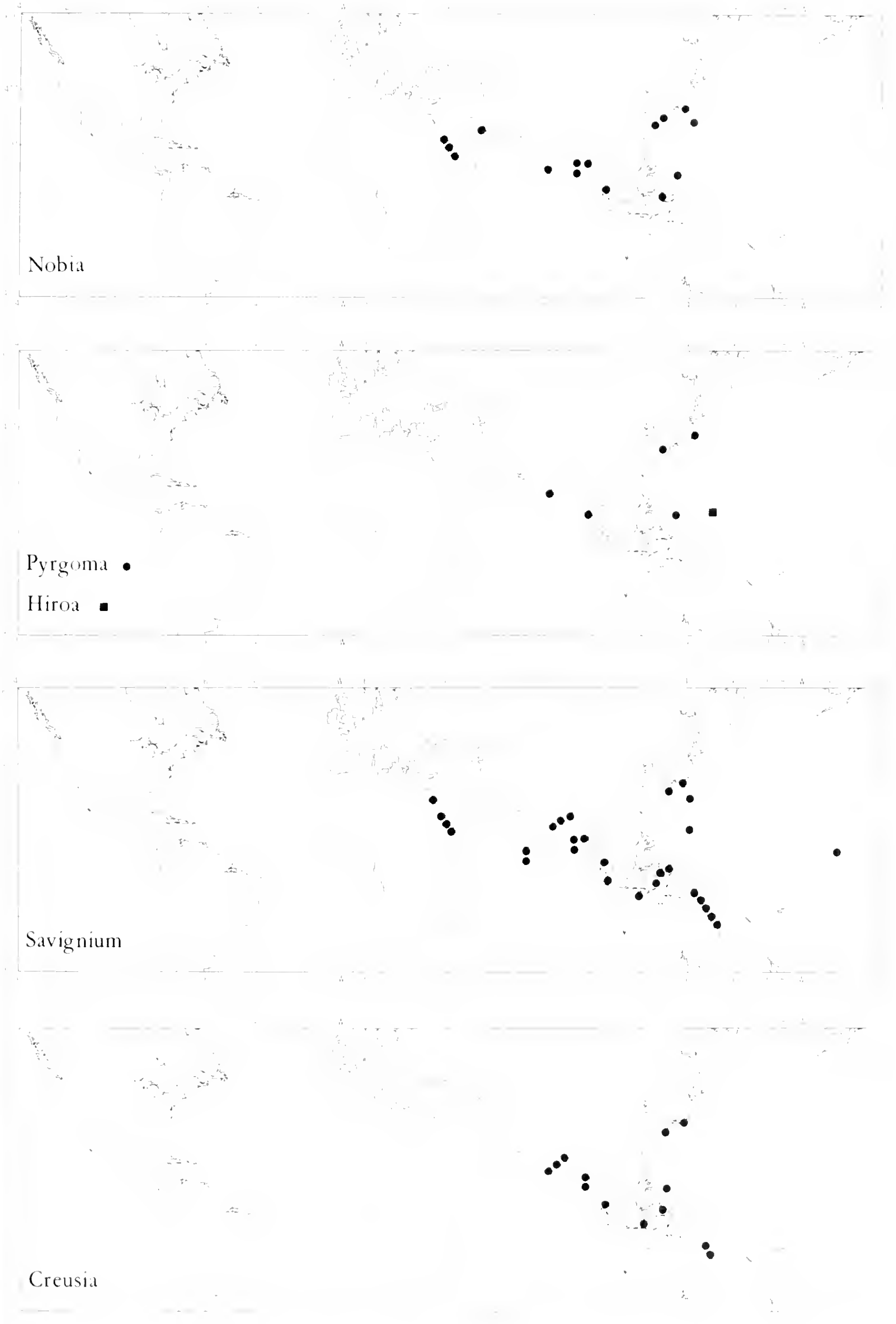

Figure 3. Distributional records for *Cantellius*, *Hoekia*, *Ceratoconcha*, *Pyrgopsella*, and *Boscia*. Circles and squares represent Recent records, triangles fossil records. Data based on specimens in the American Museum, San Diego Natural History Museum, Scripps Institution of Oceanography, Florida State Museum, British Museum (Natural History), Museum of Comparative Zoology, Harvard University, and available literature.

be true in those corals having smaller calices. Duerden (1904: 39) found that in *Siderastrea radians*, *Ceratoconcha* fixes itself in the calicinal cavity, never on the ridges connecting two calices and that the presence of the barnacle results in imperfections in the surrounding polyps.

The only pyrgromatine growing on the stinging hydrocoral *Millepora* is *Savignium milleporae*. It is not uncommon to find a thick-walled chimney of the host skeleton elevated about 5 mm above the general surface of the coral supporting the barnacle. The basis of the barnacle occupies the whole chimney, with the initial point of attachment essentially at the level of the surrounding colony. The top of the chimney is flush with the flat top of the barnacle. Evidently the general surface of the coral does not grow fast enough to accommodate the rapidly growing body chamber of the barnacle. Whether the barnacle is able to regulate the growth rate of the coral, so that the supporting chimney is formed, or the coral is simply reacting to the presence of a foreign object and attempting to bury it, has not been determined. Interestingly, *Balanus stultus*, the only other barnacle occurring on *Millepora*, likewise extends well above the general surface of the coral. It is also covered by a layer of coral skeleton, but it appears to be simply encrusted, rather than contained within a thick-walled chimney as is *S. milleporae*. *Balanus stultus* continues to grow diametrically by fracturing the coral skeleton along the sutures in the wall. Thus in both cases the coral is reacting in ways that favor the different growth habits of the barnacles, and this suggests that these barnacles are exercising some control over the growth habits and defense mechanisms of the coral.

In general, shell color in the pyrgomatines is white. *Boscia* juveniles have a white shell, but with later growth the shell takes on a pinkish or pinkish-purple hue. *Hoekia* has a pinkish-purple shell, while that of *Nobia* is white and splotched with pink or purple. In *Cantellius* some species are all white, whereas in others the apical portion of the opercular plates is tinted purple. The shell in *Savignium* is commonly pinkish red, and in *Pyrgoma* it is a pale pink. *Ceratoconcha* is invariably white. While the basis is never pigmented, the exposed shell of most genera is. Consequently, there must be some adaptive or functional significance to these colors. Since the colors do not match those of their hosts, they apparently do not serve as protective coloration.

Generalized creusioids have well developed radii, and undergo diametric growth during the better part of their lives. The radii range in form from triangular to rectangular, or they may be indicated externally simply by sutures. When the radii are triangular, the base of the isosceles triangle forms part of the apertural margin and indicates that the aperture has enlarged disproportionately to the total diameter of the shell. Rectangular radii indicate proportionate increments. Where radii are evidenced simply by sutures, diametric growth has all but terminated, and the total diameter of the wall can increase only by marginal increments. The aperture either remains the same or is enlarged by corrosion and (or) by the rasping effect of cirral movement; such forms have effectively reached the pyrgomoid level of organization.

The surface of the basis is commonly marked by longitudinal ribs, corresponding to the internal radiating ribs of the wall, and by transverse growth lines. The growth lines are generally very fine, ranging between 4 and 24 per mm (Newman and Ladd, in press), and are interrupted by discontinuities at more or less regular intervals (Baluk and Radwański, 1967a, fig. 2; Newman and Ladd, in press, pl. 1,b). The interruptions are frequently at intervals of 5 mm or so and probably correspond to the annual density bands in coral described by Knutson et al (1972: 270). This suggests that coral barnacles live for several years, which agrees with the age estimate given by Hiro (1938: 410). Unfortunately, the barnacles in which these bands have been observed are fossil forms that have been leached out of the coral so that the host species is unknown. With intact specimens, agreement between the bands in the coral and the barnacle probably could be determined by the x-ray techniques employed by Knutson et al (1972), but such work remains to be done.

Coral barnacles do not live as long as their hosts, and eventually they become entombed. In some cases the opercular parts of the entombed barnacles are cemented in the position they occupied in life, while in others they have fallen into the body chamber. In the first case the coral undoubtedly overwhelmed the barnacle while alive. This could be true in the second case, although it may be that the barnacle died before the coral overgrew it. In any event, the coral usually forms a "stopper," growing into the aperture a short distance, before attaining a normal growth pattern over the barnacle (Baluk and Radwański, 1967c: 490).

To the best of our knowledge all pyrgomatines have solid walls, at least fundamentally. Some species develop parietal tubes where the longitudinal ribs on the interior of the wall become fused with the sheath, while others form tubes between external longitudinal ribs. In still others, where the sheath becomes fully fused to a much thickened wall, several rows of more or less regularly spaced tubes develop. In none of these cases are the tubes formed in the same way as in the tubiferous balanids (subgenera *Balanus* and *Megabalanus*) where interlaminate figures can be observed in the longitudinal septa separating the inner and outer laminae of the wall.

The ontogenetic and phylogenetic development of tubiferous walls has been analyzed in a number of cases (Costlow, 1956; Newman et al, 1967; Ross and Newman, 1967), but their function has only been a point of speculation. A few systematists have suggested applying the general engineering principle that, for a given amount of material, a properly designed tubiferous structure would be mechanically stronger than a solid one. If it were necessary for a barnacle to be economical in its use of calcium carbonate, then a tubiferous wall should be advantageous in high energy environments. Barnes et al (1972) tested the resistence of certain species to impaction and found that breakage occurred not in the plates themselves but at the sutures between them. They concluded that the strength of the plates generally exceeded the strength of the articulating joints. The nature of the articulation between the wall and calcareous basis is also of great importance (Newman et al, 1967: 170). These structural features are well developed in the pyrgomatines. However, wall strength in coral barnacles can hardly be related to withstanding impaction as in many free-living forms, but rather is related to the pressures required to sustain growth in an intracoralline habitat.

Considering the array and independent occurrences of tubiferous walls, and the secondary modifications found in them, e.g. sealing off into chambers, secondarily filling with calcareous material, or filling with chitin during construction, one might look for some adaptive value other than simply strength. Ross (1970: 9) and Newman and Ross (1971) suggested that such adaptations might include defensive mechanisms against borers, specifically against the drilling of gastropods. In this regard, Orton (1927: 653) noted that "oysters are frequently attacked and abandoned (by gastropods) . . . if either a chamber or loose horny layer is encountered . . ." It would be expected that free-living barnacles, which are frequently attacked by gastropods, would also have developed defense mechanisms against them. However, in the pyrgomatines predation by borers has not been reported. Their tubiferous walls, then, developing in different ways in different members of the group, undoubtedly have some other function. Strength is probably the important one, but it is also likely that these tubes allow for physiological interactions between the barnacle and its host. In many species the tubes are arranged so as to leave gaps around the margin of the shell, which appear to allow the uncalcified integument of the barnacle to come into intimate contact with the tissue of the coral. Moyse (1971) suggested that the barnacle may receive metabolic substances from the host by this route. However, we believe it more likely or important that these are the sites where physiological control of coral growth are initiated.

The opercular valves function to guard the aperture and range in form from wholly balanoid to highly modified. In *Cantellius* and *Ceratoconcha*, the two most generalized genera, the four-plated wall varies from high conic to virtually flat. Yet the valves are always tall and typically balanoid. The same can be said of *Boscia*, except that it has a concrescent shell. In these three genera the terga as well as the scuta occlude the aperture.

In the *Savignium* line (Fig. 5), the opercular valves are generally thin and fragile, and the wall is totally concrescent. The scuta are relatively elongate and the reduced terga become completely fused to them. Likewise, the aperture is elongate, and it is guarded primarily by the scuta. The epitome of modified valves is seen in *Hoekia*. However, it has a minute orifice and this is related to its wholly parasitic way of life (Ross and Newman, 1969).

In the *Hiroa* lineage the opercular valves tend to remain balanoid, although the scuta alone occlude the aperture. Modifications within the lineage include elongation and narrowing of the terga and reduction of articular margins on one hand (*Hiroa*, *Pyrgoma*), and broadening and concrescence on the other (*Nobia*, *Creusia*). In *Hiroa-Pyrgoma* the opercular plates are relatively thin and fragile while in *Nobia-Creusia* they are thick and massive. This disparity correlates to some extent with size, but the difference probably also relates to the amount of protection each requires from predators. Baluk and Radwański (1967c: 463), with reference to Darwin's plate 13, fig. 1d,(Fig.12, c herein), misunderstood the anatomical relationships between the opercular valves and the wall in *Nobia*, and concluded that the valves no longer guard the aperture. Apparently, they were not distinguishing between the scutal and tergal portions of the concrescent valves and thought that the occludent margins of the scutal portions were fused together and no longer functional.

In summary, cyprids of coral barnacles apparently first settle on coral tissue where they metamorphose into juveniles. A juvenile doesn't attach to the coral skeleton until after the cup-shaped basis has become calcified. During this period, and to some extent after attachment, the juvenile may undergo reorientation in relation to the host of as much as 90°. Unlike ordinary barnacles, subsequent growth is primarily through elongation of the basis rather than the wall. Species with radii generally undergo diametric growth and, in the process, frequently fracture the coral skeleton overgrowing them. Advanced species apparently gain a degree of control over coral tissue, and its ability to lay down new skeleton. While barnacles live for several years, they eventually become entombed.

HOST SPECIFICITY

Gray (1825: 102) proposed the Pyrgomatidae to accommodate several balanoid genera peculiar to certain zoophytes; *Pyrgoma* and *Creusia* imbedded in scleractinian corals, *Conopea* in gorgonians and *Acasta* in sponges. The unification of these genera under one family was based primarily on comparable habitats.

Figure 4 summarizes available data on distribution of the various genera of Pyrgomatinae among the scleractinian suborders. Of the ten genera all, except *Pyrgopsella* in sponges (not included in the figure) and *Savignium milleporae* on nine species of *Millepora*, occur exclusively on hermatypic and ahermatypic corals. Of these, seven genera occur on Faviina, five on Fungiina, five on Astrocoeniina, four on Dendrophylliina, and two on Caryophylliina. Faviina then, with the greatest diversity of genera, supports the greatest diversity of coral barnacles. Caryophylliina, while nearly equal to Faviina in numbers of genera, supports the least. This is no doubt because Faviina, Fungiina, and Astrocoeniina are hermatypic, while Dendrophylliina and Caryophylliina are ahermatypic with representatives ranging into deep water. Balanoids in general are shallow water organisms.

Only the cosmopolitan genus *Boscia* is known to inhabit all five scleractinian suborders and it is, as far as opercular valves are concerned, among the most generalized of the Pyrgomatinae. *Hoekia*, *Pyrgoma*, and *Hiroa* are each limited to but one scleractinian suborder, and each is monotypic. Of these, the first two are among the more specialized members of the subfamily, *Hoekia* being the most specialized balanoid known. *Hiroa* on the other hand resides at the stem of the other higher forms (*Creusia*, *Nobia*, and *Pyrgoma*) which, between themselves share all five scleractinian suborders, with *Nobia*, a relatively highly modified form, occurring on four of them.

Ceratoconcha is one of the most generalized forms, yet it inhabits but two of the scleractinian suborders. In being an Atlantic genus, it has survived in a situation where coral diversity has declined since the Oligocene or Miocene (see Biogeography). The remaining generalized genus, *Cantellius*, stands at the stem of the Indo-Pacific members of the subfamily and is well represented on the three principal shallow water suborders, Faviina, Fungiina, and Astrocoeniina.

From the foregoing, what can be said of host specificity among Pyrgomatinae at the

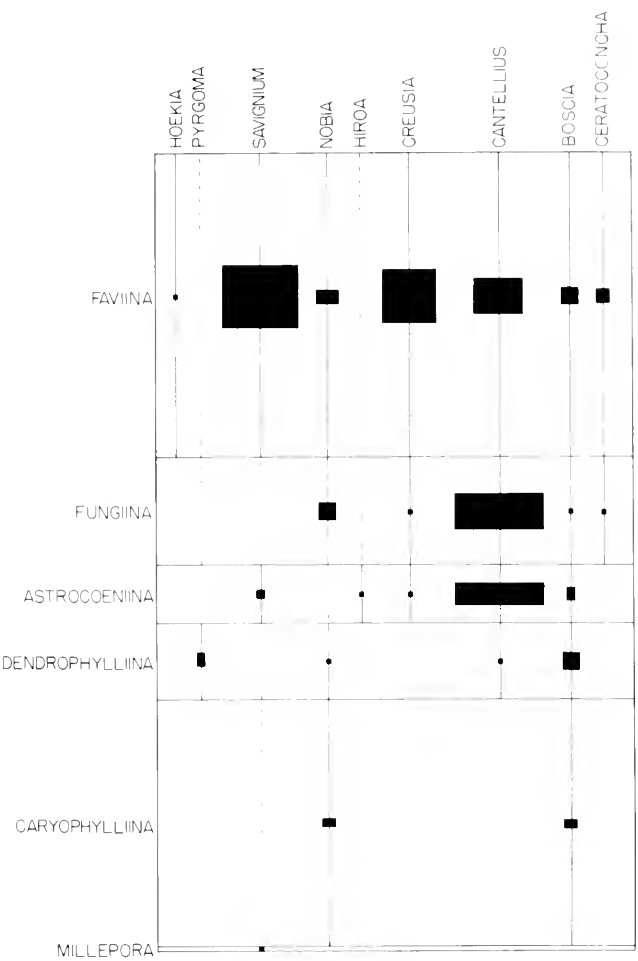

Figure 4. Distribution of genera of Pyrgomatinae among scleractinian coral suborders derived from the literature. Space for each coral suborder is proportional to the total number of coral genera within each suborder; bar width indicates number of occurrences of barnacles within each suborder; bar height represents the number of coral genera on which the barnacles are known to occur.

scleractinian subordinal level? One might expect highly modified forms to be highly host specific, and for such extremes as *Hoekia* this is indeed the case. However, *Nobia* is among the most modified forms, yet it occurs on all scleractinian suborders except Astrocoeniina, while *Hiroa*, an intermediate in the transition between *Cantellius* and *Creusia*, has been found only on Astrocoeniina. *Savignium* and *Creusia* exploit mainly Faviina while *Cantellius* exploits mainly Fungiina and Astrocoeniina, but the division is not precise as there is considerable overlap among the three.

What then seems to be the situation as regards host specificity at the specific level? Hiro (1935: 23) found that in Tanabe Bay, Japan, "A given species of *Pyrgoma* is practically confined to a single species of coral, whereas the same variety of *Creusia* may be found on various kinds of coral." In 1938 he reported on his findings in the more tropical Palau Islands. While expanding the number of corals playing host to species of *Pyrgoma* (1938: 404), he again came to the same general conclusion (1938: 392). Presently, his statement holds best for the monotypic genera.

The suborder Faviina plays host to most of the genera of Pyrgomatinae. Of the Faviina, *Porites* apparently has been selected most frequently as a host. Other balanids also have invaded *Porites*, the Recent armatobalanid *Balanus allium*, the Pliocene to Recent armatobalanid *Balanus durhami* and the Miocene balanid *Balanus duvergieri* are notable. Growth on *Porites* is independent of the growth of individual coral polyps and consequently requires little specialization. This appears to us to be the reason why *Porites* plays host to a variety of barnacles. *Millepora*, on the other hand, does not, and one might suspect that this is due to its stinging ability.

In summary then—1) the greatest diversity of Pyrgomatinae in terms of numbers of genera is found among hermatypic suborders, particularly Faviina and this is probably because balanids in general are shallow water organisms; 2) there are no marked differences between the occurrences of pyrgomoids and creusioids as a whole on the various suborders of scleractinian corals—in both groups Faviina is preferred, with scattered occurrences between the other scleractinian suborders; and 3) the rule (Hiro 1938: 408), that the more peculiar the morphological characteristics of species, the more rigid their host specificity, holds in a general way. The same rule holds only weakly when applied to barnacle genera and scleractinian suborders, for some relatively specialized genera, such as *Nobia* and *Boscia*, occur on a wide variety of corals and are notable exceptions.

ORIGIN AND EVOLUTION

The Pyrgomatinae are a well defined group (Baluk and Radwański, 1967b: 465), but to what lineage of the Balaninae the subfamily owes its origin has not been resolved. Although the consensus is that the Pyrgomatinae are polyphyletic, only the broader outlines of their evolution have been elucidated (Withers, 1929: 564; 1935: 38; Hiro, 1938: 402, 412; Zullo, 1961: 72; 1967: 127; Baluk and Radwański, 1967c: 500). Existing problems stem from a lack of critical data on fossil and Recent forms, as well as from Darwin's (1854) conservative handling of genera and species. His treatment of *Creusia* as a subgenus of *Pyrgoma* has not been accepted by later workers. Also, his reluctance to recognize geographic populations of *Creusia* as species, even though a sample from a given locality showed markedly uniform characteristics (Darwin, 1854: 376), and the failure of subsequent workers to rectify this, resulted in a plethora of subspecific and infrasubspecific taxa that make little sense biologically. Therefore, before looking into the origins of these barnacles relationships within the subfamily are discussed.

Pyrgoma, in the broad sense, contains the most highly evolved members of the Pyrgomatinae (Darwin, 1854: 355, 375; Hiro, 1938: 402). Baluk and Radwański (1967b: 691; 1967c: 486) revised *Pyrgoma*, dividing it into *Pyrgomina* (=*Megatrema* of Utinomi, 1967: 232) and *Pyrgoma* with its subgenera *Nobia* and *Daracia*. We recognize somewhat similar groupings, with minor differences in the arrangement of species, but all at the generic level. The relationships of the genera are indicated in Figure 5.

Pyrgoma s. s., *Nobia*, *Savignium*, *Hoekia*, and *Pyrgopsella* are Indo-Pacific shallow-water pyrgomoids. *Boscia* is a cosmopolitan pyrgomoid, having both shallow and deep-water representatives. The Indo-Pacific pyrgomoids differ morphologically from *Boscia* in having highly modified opercular valves and in lacking paired fissures ('sutures') in the sheath; they can be derived readily from Indo-Pacific creusioids (*Cantellius*, *Creusia*, *Hiroa*), as will be discussed, but they cannot be derived readily from *Boscia*. We infer that *Boscia* has had a separate origin—that is, that the Pyrgomatinae are at the least diphyletic. In contrast, the Indo-Pacific pyrgomoids apparently are related through two major lines derived from different creusioid lineages. Hence, we infer that the pyrgomoid level of organization has been achieved at least four times (Fig. 5).

Creusia, in the broad sense, contains the most generalized members of the Pyrgomatinae. Baluk and Radwański (1967c: 484) attempted a modest revision of *Creusia*, which they divided into the nominate subgenus and a new subgenus, *Withersia*. Their revision was based mainly on fossil forms, thereby considering only the Atlantic fauna and thus failed to come to grips with the Indo-Pacific *Creusia spinulosa* complex; and the natural groupings that exist within *Creusia* were overlooked. All of the Atlantic species, both living and fossil, form a natural unit for which the name *Ceratoconcha* is available. *Ceratoconcha* has relatively unmodified balanoid opercular valves of a characteristic type that differ markedly in form from what would be considered generalized balanoid valves of the Indo-Pacific forms contained within our newly proposed genus *Cantellius*. This indicates that the generalized or primitive creusioids are not closely related and if the creusioids descended from a common balanoid stock, they did so independently in the

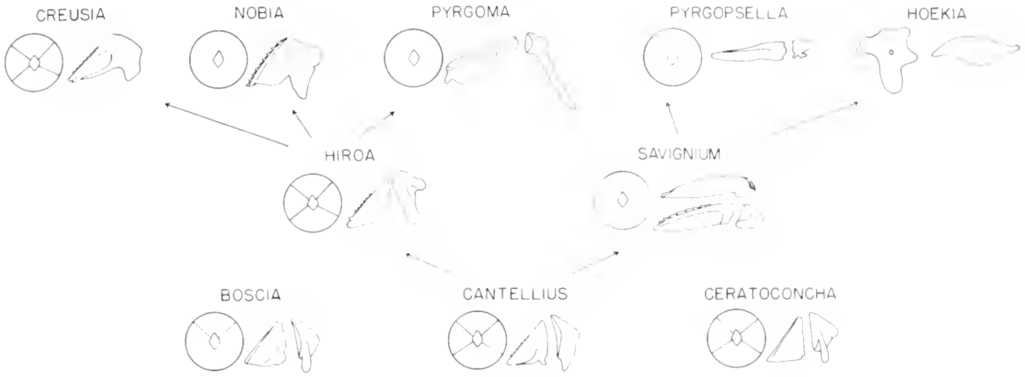

Figure 5. Diagram depicting inferred phylogenetic relationships within the Pyrgomatinae. The group or groups from which *Boscia*, *Ceratoconcha*, and *Cantellius* evolved remain unknown. The solid lines radiating from the orifice of the shell, shown in plan view, indicate relative position of the sutures separating the compartments; the dotted lines in *Boscia* indicate the position of the pseudoalae. Dotted lines on the opercular plates indicate a structures present in only a few species of that group.

Atlantic and the Indo-Pacific. Thus we set *Ceratoconcha* from the Atlantic apart and independent from the Indo-Pacific creusioid genus *Cantellius*, and consider the subfamily to be triphyletic (see Fig. 5).

Although *Ceratoconcha* has remained much the same throughout its history, the Indo-Pacific creusioids have undergone marked diversification. There is no fossil record to document the lineages leading to contemporary forms, but among Recent representatives there are sufficient forms upon which to draw inferences. First, there presently appears to be no reason to suggest that the Indo-Pacific creusioids are other than a natural group since they can be derived readily from one another. *Cantellius* is the most generalized and is envisaged as the stem from which the remaining genera evolved. Secondly, there are apparently two major lineages, one stemming from *Hiroa*, the other from *Savignium*;—that is, two parallel lines, each leading independently from *Cantellius* to pyrgomoid forms (Fig. 5). *Pyrgopsella*, occurring in sponges, appears to be an offshoot of the *Savignium-Hoekia* line. The modifications that ensue in each line concern alterations in the form of the opercular valves and concrescence of the wall plates, presumably better adapting the barnacles to different host corals. Interestingly, the most modified form, *Hoekia*, has the most reduced wall plate, aperture, and opercular valves of any pyrgomoid. It has also modified its nutritional source, shifting from setose feeding to feeding directly on the tissues of the host coral (Ross and Newman, 1969: 255).

Baluk and Radwański (1967c: 465) believed that *Pyrgopsis annandalei* Gruvel (=*Pyrogopsella* nom. nov., Zullo, 1967), dredged from 90m off the Andaman Islands, should not be assigned to the Pyrgomatinae because the basis is membranous. Gruvel (1907: 8) had three specimens, but the habitat and (or) actual relationship of the barnacle to the substratum were unknown. He inferred that the membranous elongate basis functioned as a peduncle or stalk, analogous to the fleshy stalk of *Xenobalanus*, by which the animal attached to the substratum. Indeed, Zullo (1967: 123) referred to *Pyrgopsella* as an "unusual pedunculate balanid." Recently, however, Rosell (pers. comm., 1971) reported finding a new species of *Pyrgopsella* imbedded in a sponge from the Philippines, and we believe that this explains the peculiar anatomical structure of the genus. The membranous stalk is not a "peduncle" in the sense used by Gruvel, but rather it is an elongate basis comparable to and serving the same function as the elongate basis of other Pyrgomatinae. In inhabiting sponges, rather than a coral, the basis is membranous rather than calcareous, analogous to the situation seen in *Membranobalanus* also inhabiting sponges. The single plate making up the wall and the pyrgomoid valves suggest that *Pyrgopsella* is an off-shoot of the coral-inhabiting pyrgomatines. Indeed the valves are similar to those of *Savignium*, and it is from this genus that we infer it has evolved.

In summary then, the Pyrgomatinae are a diverse group of coral-inhabiting balanids, dominated by a central group of eight wholly Indo-Pacific genera stemming from *Can-*

tellius, and flanked by the cosmopolitan genus *Boscia* and the Atlantic genus *Ceratoconcha*. *Cantellius*, *Boscia*, and *Ceratoconcha* have rather generalized balanoid opercular valves, but there is no indication that one gave rise to the other. Rather it is inferred that they descended independently from balanoid ancestors, and therefore the subfamily is considered triphyletic. We can now ask from which balanines these three lines may have evolved.

There is ample evidence that the Pyrogomatinae have been derived from balanines; the rostrum overlaps the laterals, the opercular plates are balanoid, the labrum is notched, and the intromittant organ bears a basidorsal point. While the most primitive living balanid (*Chelonibia*) has eight plates making up the wall, it is apparently a specialized survivor of an ancient stock that presumably gave rise to the more typical balanines. The vast majority of typical balanines have six plates making up the wall, and it has generally been assumed that the Pyrgomatinae descended from some six-plated ancestor (Withers, 1929: 564; 1935: 38; Hiro, 1938: 402; Zullo, 1967: 127; Baluk and Radwański, 1967c: 504). Withers (1935: 38) suggested that *Balanus* (*Balanus*) *duvergieri* (Alessandri) might be such a form, and Zullo (1961: 72) proposed the subgeneric name *Hexacreusia* for *Balanus durhami*, a species he thought also likely to be such a form.

Balanus duvergieri, with its tubiferous wall and basis, appears to belong to the subgenus *Balanus*, where Withers placed it. The wall of all known pyrgomatines is solid; while tubes may be found in some species, they are formed between the sheath and the internal ribs or between external ribs of the wall and therefore are not homologous with the tubes of *Balanus*. All generalized pyrgomatines, except *Boscia anglicum*, have a solid basis. The opercular valves of *B. duvergieri* are generalized, resembling those of *Cantellius* more than those of *Boscia* and *Ceratoconcha*, but this is no doubt simply because *Cantellius* has the most generalized valves of any of the pyrgomatines. In light of the differences in the wall between *B. duvergieri* and the Pyrgomatinae, and in light of the evidence indicating that the Pyrgomatinae had a solid-walled ancestry, we must agree with Baluk and Radwański (1967c: 504) that *B. duvergieri* is not an ancestor of the Pyrgomatinae as Withers suggested, nor is it closely related to the stock from which the Pyrgomatinae must have been derived.

Balanus durhami appears closer than *B. duvergieri* to the stem line of the Pyrgomatinae since it has a solid wall and basis, and since the opercular valves are superficially comparable. If *B. durhami* had but four wall plates rather than six, would it then belong to the Pyrgomatinae, and if so, to which of the three major groups would it be assigned? It would belong to the Pyrgomatinae as presently defined, but it is not readily assignable to any one of the three existing divisions. The tergum, with broad spur and strongly developed depressor muscle crests, and the scutum, with a broadly developed adductor ridge descending from the occludent margin, differ markedly from the generalized types seen in the subfamily, so that *B. durhami* would have to be placed as a fourth and independent line. Although for different reasons, we agree with Baluk and Radwański (1967c: 504) that *B. durhami* is not a surviving ancestor of the Pyrgomatinae. Yet it is much closer to what must have been the balanine stock from which one or more of the Pyrgomatinae lines were derived, and it is therefore necessary to look closely at the affinities of *B. durhami*.

Zullo (1961: 75) stated that *B. durhami* resembles species of the subgenus *Armatobalanus* but differs from them in having the anterior margin of cirrus III toothed rather than only cirrus IV, and he placed it in a new subgenus, *Hexacreusia*.[1] However, when Zullo (1963: 590) described *B.* (*Armatobalanus*) *nefrens* from California, he noted that this species lacks hooks or spines on cirrus IV, as does *B.* (*A.*) *oryza* Broch from the southwest Pacific. Zullo (1967: 127) later noted that Darwin (1854) confused specimens of *B. durhami* with *B.* (*A.*) *allium* from the southwest Pacific. He stated that such species of *Armatobalanus*, as *terebratus* Darwin are so similar to *B. durhami* that it appears reasonable to assume that the armatobalanids were the ancestral stock from which the coral barnacles

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[1] We wholly concur that *Hexacreusia* and *Armatobalanus* are similar, and in fact, except for the development of the scutal adductor ridge in the former, there are no diagnostic differences between them. Rather than elevate *Hexacreusia* to generic rank as did Zullo, et al (1972: 72), we consider it synonymous with *Armatobalanus*. If *Armatobalanus* were raised to generic rank, it would be reasonable to consider *Hexacreusia* subgenerically distinct.

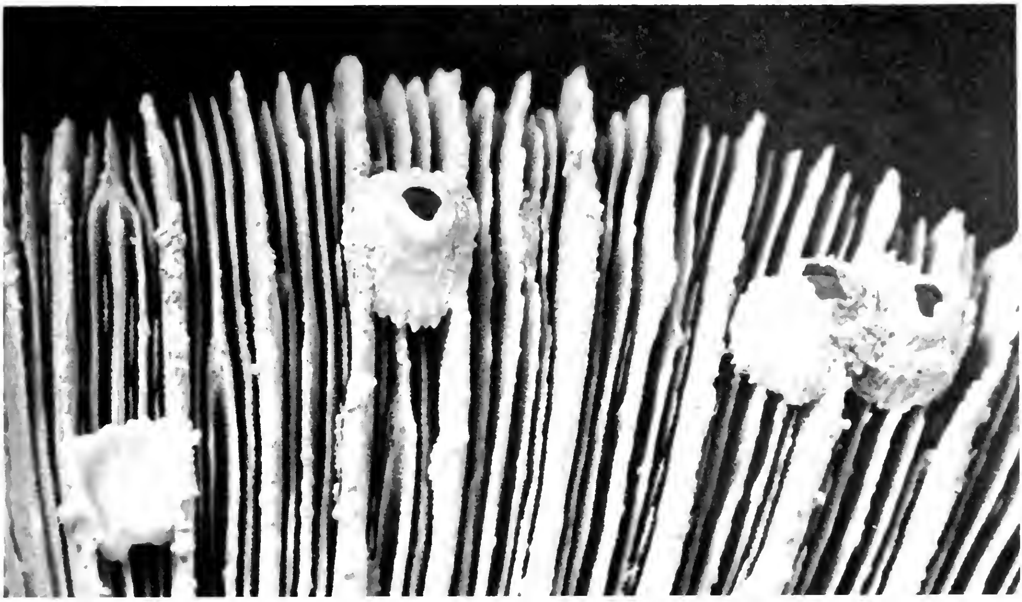

Figure 6. *Cantellius pallidus* on *Fungia fungites* (Linnaeus). Indo-west Pacific. Zoologisk Museum, Copenhagen.

were derived.

Darwin (1854: 282), Hiro (1938: 402), and Zullo (1967: 127) looked to *Armatobalanus* as the stem line from which the Pyrgomatinae evolved. Members of the subgenus are found in both the Atlantic and the Indo-Pacific, some occur exclusively on corals, and one is known from the late Miocene of the United States (Ross, 1965: 337). There is a fair diversity of opercular valves, and in general these bear a closer resemblance to those of *Cantellius* than to those of *Boscia* or *Ceratoconcha*.. If the lines within the Pyrgomatinae have in fact evolved three times, it seems likely that at least the Indo-Pacific *Cantellius* and its derivatives and perhaps *Boscia* have an *Armatobalanus* ancestry. The affinities of *Ceratoconcha* are still too obscure to conjecture (see Newman and Ladd, in press).

SYSTEMATICS

Descriptions of the 54 or more species in this subfamily are not included here, because many require redescription and adequately preserved material is unavailable. To obviate the problem of deciding on the author's intent in relegating subspecific or infrasubspecific rank to a taxon (ICZN, Art. 45), we have blanketly endorsed all known nominal taxa, and accordingly assigned them appropriate rank. Our reasons for placing a nominal species or genus in synonymy are given in the remarks section under the respective taxon. For each species, following citation of the author and date of publication, we cite type locality and host-coral. A list of species incertae sedis follows the systematics section.

Family Balanidae, Leach, 1817

Subfamily Pyrgomatinae Gray, 1825

Balanidae Leach, 1817: 68, in part; Darwin, 1854a: 33, in part.
Pyrgomatidae Gray, 1825: 102, in part; Reichenbach, 1828: 89, in part.
Bifora Latreille, 1825: 234, in part.
Pyrgomacea Menke, 1830: 92, in part; Philippi, 1853: 424, in part.
Sessilia: Philippi, 1836: 247, in part.
Tetrameridae Gruvel, 1903: 159, in part; Alessandri, 1922: 226, in part.
Creusiinae Baluk and Radwański, 1967c: 468.

Definition.—Shell of four parietal plates with radii and alae, or totally concrescent, with or without carinal "pseudoalae" discernible in sheath; walls solid or tubiferous, the tubes occurring in one or more rows either between the sheath and internal ribs or between external ribs of wall; scutum and tergum either separate, cemented, or calcified together; basis membranous or calcareous, when calcareous cup-shaped and shallow or cylindrical and deep; labrum with deeply incised notch; intromittant organ with basi-dorsal point. Obligatory symbionts or parasites primarily of scleractinian corals. (One species occurs on a hydrocoral, another on a sponge.) Type genus: *Pyrgoma* Leach, 1817.

Key to Genera of Pyrgomatinae

1.	Basis membranous (1 sp.)	*Pyrgopsella*
1.	Basis calcareous	2
2.	Shell concrescent	3
2.	Shell separable into 4 plates	7
3.	Scutum at least twice as long as high	4
3.	Scutum as long as high	5
4.	Tergal spur well developed (1 sp.)	*Pyrgoma*
4.	Tergal spur rudimentary	6
5.	Opercular plates balanoid, separable; tergum triangular (4 spp.)	*Boscia*
5.	Opercular plates modified, fused together; tergum quadrate (6 spp.)	*Nobia*
6.	Shell irregular in outline; aperture minute (1 sp.)	*Hoekia* n. gen.
6.	Shell regular in outline; aperture large (4 spp.)	*Savignium*
7.	Opercular valves fused (3 spp.)	*Creusia*
7.	Opercular valves not fused	8
8.	Opercular valves highly modified (1 sp.)	*Hiroa* n. gen.
8.	Opercular valves balanoid	9
9.	Scutum with basal margin entire, depressor muscle pit present, but no rostral tooth; tergum with broad pad in area normally occupied by depressor muscle crests (16 spp.)	*Ceratoconcha*
9.	Scutum with basal margin notched near basi-tergal angle, commonly with depressor muscle pit, and a rostral tooth; tergum without broad pad (17 spp.)	*Cantellius* n. gen.

Cantellius n. gen.

Definition.—Wall of four plates, conical to flat; compartments separated by well defined radii; scutum varies from high triangular to transversely elongated, and bearing prominent adductor ridge and lateral depressor muscle depression; scutum commonly with rostral tooth and notch in basal margin near basitergal angle; spur of tergum essentially confluent with scutal margin, and about ½ width of basal margin; crests for tergal depressor muscles feebly developed or wanting.

Type species.—*Cantellius transversalis* (Nilsson-Cantell), 1938; Recent, Andaman Islands.

Etymology.—Named in honor of Carl August Nilsson-Cantell.

Species assigned to genus:

Cantellius acutum (Hiro), 1938: 398 (syn.: *Creusia spinulosa* var. 6 subvar. 2 Darwin, 1854: 379); Palao Islands, Caroline Islands; on *Acropora formosa*.

Cantellius arcuatum (Hiro), 1938: 395; Palao Islands, Caroline Islands; on *Porites capricornis*.

Cantellius brevitergum (Hiro), 1938: 397; Palao Islands, Caroline Islands; on *Acropora* sp.

Cantellius euspinulosum (Broch), 1931: 118 (syn.: *Creusia spinulosa* var. 1 Darwin, 1854: 377); Amboina, Molucca Islands; on *Herpetolitha* sp.

Cantellius gregarea (Sowerby), 1823 [no pagination] (syn.: *Creuisa spinulosa* var. 3 Darwin, 1854: 378; *Creusia spinulosa pseudoseptima* Kolosváry, 1948: 362; *Creuisa spinulosa paeudoseptima* [sic]: Kolosváry, 1951 lb: 292); near Kei Islands (5°31′S., 132°47′E.); on *Acropora cytherea*, type host here designated.

Cantellius iwayama (Hiro), 1938, p. 393; Palao Islands, Caroline Islands; on *Porites iwayamaensis*.

Cantellius madreporae (Borradaile), 1903: 443 (syn.: *Pyrgoma madrepoarae* [sic]: Nilsson-Cantell, 1938: 65); Hulule, Male Atoll, Maldive Islands; on *Madrepora* sp.

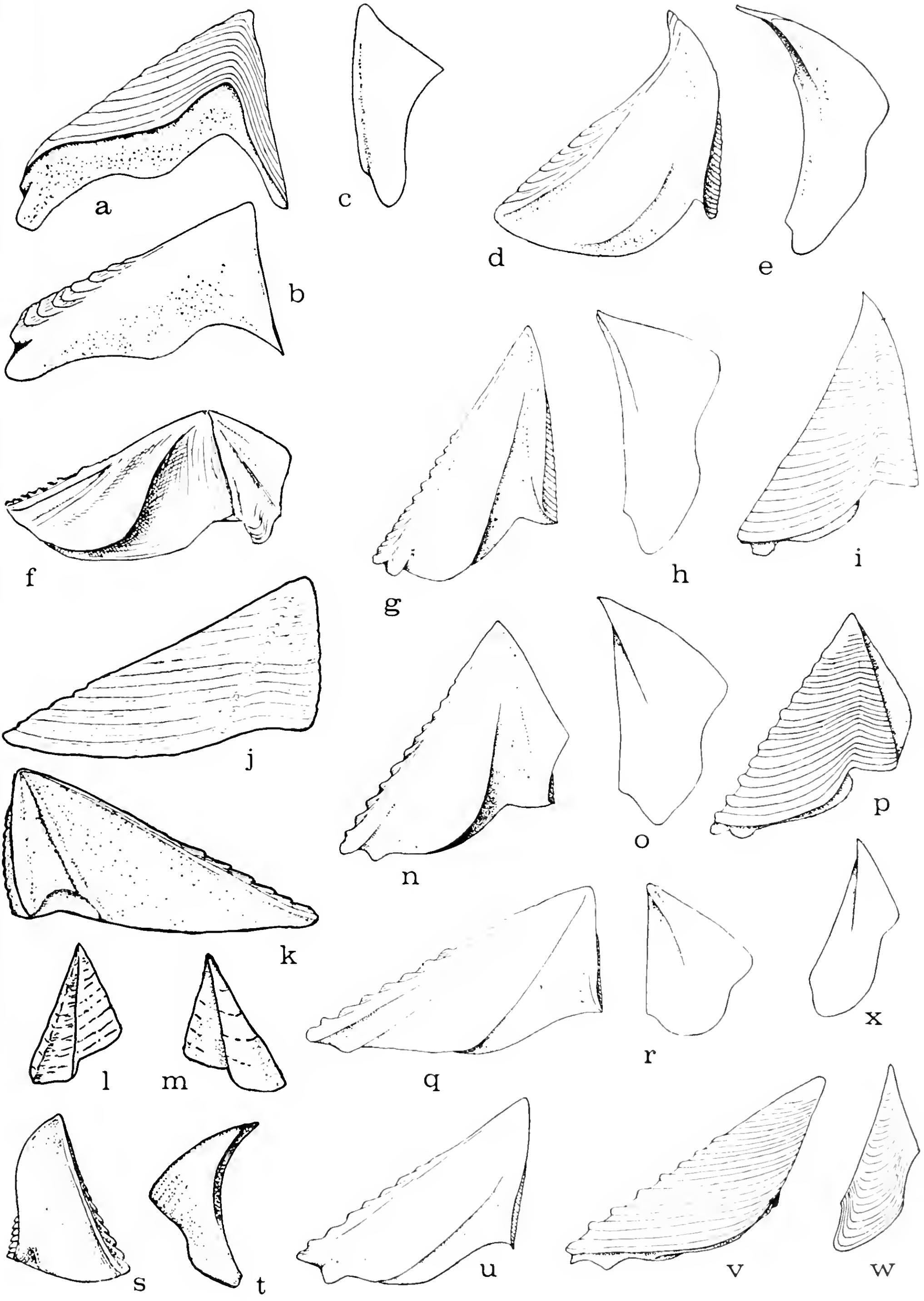

Figure 7. Opercular plates of *Cantellius*. a-c, *C. sextus*, after Hiro, 1938; d, e, *C. arcuatus*, after Hiro, 1938; f, *C. madreporarae*, after Borradaile, 1903; g-i, *C. euspinulosum*, after Hiro, 1938; j-m, *C. transversalis*, after Nilsson-Cantell, 1938; n-i, *C. iwayama*, after Hiro, 1938; q, r, *C. brevitergum*, after Hiro, 1938; s, t, *C. tredecimus*, after Kolosváry, 1947; u-x, *C. acutum*, after Hiro, 1938.

Cantellius octavus Ross and Newman, n. sp. (syn.: *Creusia spinulosa* var. 8 Darwin, 1854a: 380); type locality, distribution and host coral not known.

Cantellius pallidus (Broch), 1931: 118; Banda Sea (5°32′S., 132°37′E.); on *Pocillopora damicornis*, type host here designated.

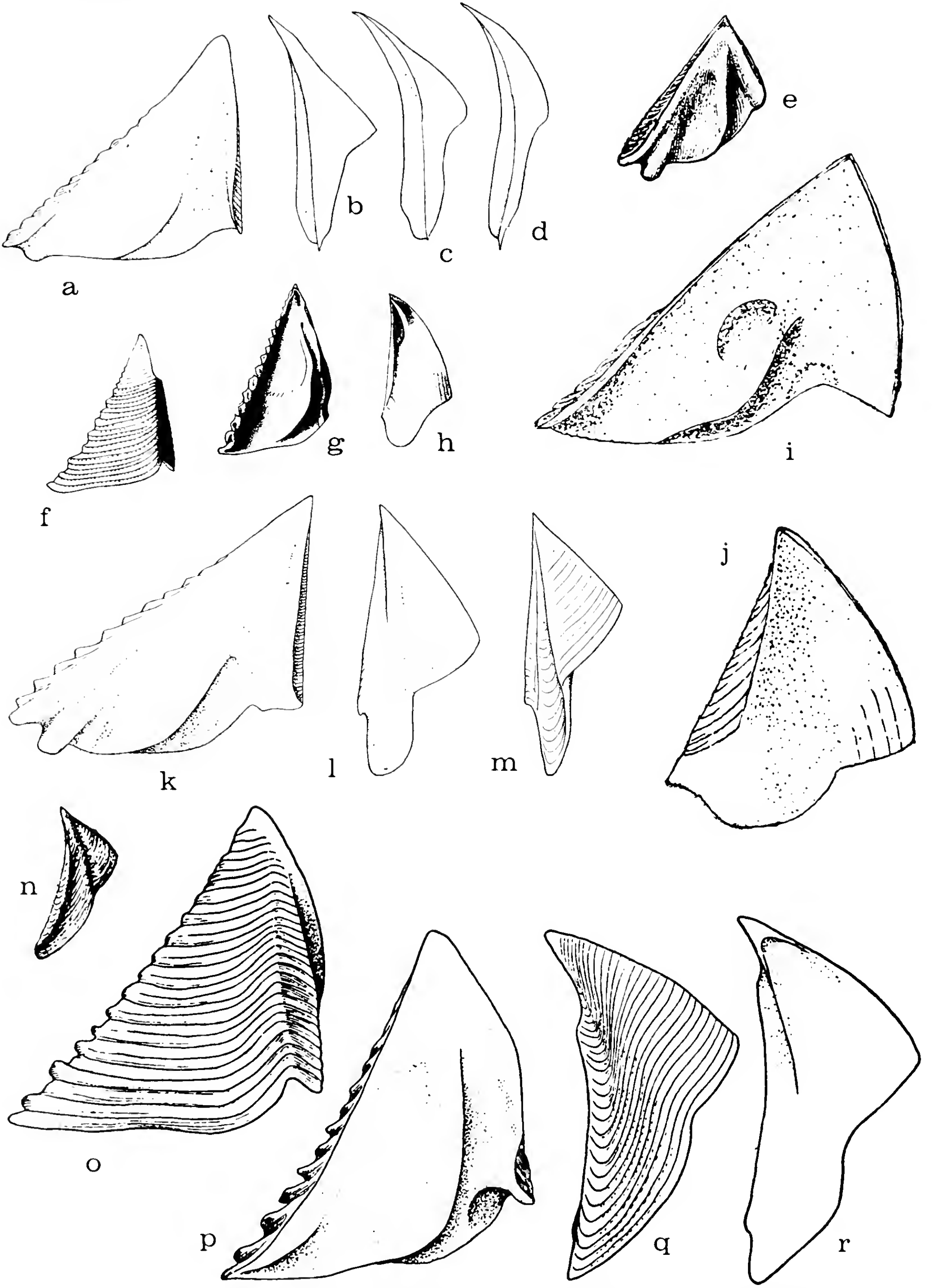

Figure 8. Opercular plates of *Cantellius*. a-d, *C. secundus*, after Hiro, 1938; e, *C. septimus*, after Darwin, 1854; f-h, *C. sumbawae*, after Hoek, 1913; i, j, *C. gregarea*, after Nilsson-Cantell, 1938; k-m, *C. septimus*, after Hiro, 1938; n, *C. quintus*, after Darwin, 1854; o-r, *C. pallidus*, after Hiro, 1935.

Cantellius quintus Ross and Newman, n. sp. (syn.: *Creusia spinulosa* var. 5 Darwin, 1854a: 379); type locality, distribution and host coral not known.

Cantellius pseudopallidum (Kolosváry), 1948: 362; Pacific area; on *Pavona varians*.

Cantellius secundus (Broch), 1931: 118 (syn.: *Creusia spinulosa* var. 2 Darwin, 1854: 378); off Naira, Banda Islands; on *Pavonia* sp.

Cantellius septimus (Hiro), 1938: 395 (syn.: *Creusia spinulosa* var. 7 Darwin, 1854: 380; *Creusia spinulosa duodecima* Kolosváry and Wagner, 1941: 9); Palao Islands, Caroline Islands; *Montipora* sp.
cf. *M. cacutus*.

Cantellius sextus (Hiro), 1938 (syn.: *Creusia spinulosa* var. 6 subvar. 3 Darwin, 1854: 379); Palao Islands, Caroline Islands; on *Pachyseris rugosa*.

Cantellius sumbawae (Hoek), 1913: 265; east of Dangar Besar, Saleh Bay; on *Heteropsammia* sp.

Cantellius transversalis (Nilsson-Cantell), 1938: 61 (syn.: *Creusia spinulosa* var. 6 subvar. 1 Darwin, 1854: 379); North Bay, Port Blair, Andaman Islands; on *Madrepora* sp.

Cantellius tredecimus (Kolosváry), 1947: 426; Island of Singapore; on *Tridacophyllia lactuca*.

Remarks.—Cantellius is proposed for those Indo-Pacific creusoids with unfused opercular valves of which the scutum commonly possesses a notch in the basal margin near the basi-tergal angle, a rostral tooth, an adductor ridge, and a lateral depressor muscle pit. The tergum has either feebly developed crests for the depressor muscles, or no crests.

In critically comparing the illustrations and brief description of *Creusia spinulosa duodecima* Kolosváry (1941: 9) with that of *Cantellius septima*, the authors find no differences that warrant continued rocognition of *duodecima*. We also find, for the same reasons, that *C. spinulosa pseudoseptima* is synonymous with *C. gregarea*.

Hiroa n. gen.

*Definition.—*Wall of four plates, small, flat or low conical; parietal tubes present; sheath occupying whole inner wall; basis cylindrical and deep; triangular scutum high and elongated transversely; adductor ridge projecting below basal margin of valve; tergum narrow, with spur about ½ or less height of valve, lacking crests for depressor muscles; overall height of tergum greater than that of scutum and about equal in bulk to scutum.

Type species.—Hiroa stubbingsi, new species.

*Etymology.—*Named in honor of Dr. Fijio Hiro (= Huzio Utinomi), in appreciation of his numerous studies on the Pyrgomatinae.

Remarks.—Hiroa bridges the gap between *Cantellius* and the morphologically advanced Indo-Pacific creusoids and pyrgomids. In having a shell with four distinct plates, it is readily separable from *Nobia* and *Pyrgoma*. The bizarre development of the opercular plates, which are separate, distinguishes it from *Cantellius* on one hand, and from *Creusia* on the other.

Hiroa stubbingsi n. sp.

*Diagnosis.—*Because there is but a single known species, the diagnosis is the same as that for the genus.

*Material.—*Numerous specimens in *Stylophora* sp., type host: Ollan Island, Truk Islands, 7°14′N, 151°38′E, type locality; CARMARSEL Exped. sample CRS 811; 25 February 1967; coral blasted from base of seaward reef front at 8 m; c^{14} dating indicates age of less than 500 BP.

*Description.—*Specimens were entombed in coral so that the external surfaces of the wall could not be observed; wall of four plates, flat or low conic; outline ovate; rostrocarinal diameter less than 5 mm, lateral diameter less than 3 mm; parietes non-tubiferous and thickened marginally, thinning toward aperture; sutural surfaces of radii strongly denticulate; sheath extending to basal margin of wall with basal edge depending freely.

Basis deep (greater than 26 mm); cylindrical; strongly ribbed internally; non-tubiferous; gradually expanding from point of initial growth.

Scutum high and transversely elongated (1.7 mm high x 1.6 mm wide); exterior surface sculptured with irregular, high, growth ridges; tergal margin about ½ length of basal; occludent margin coarsely toothed; internal surface smooth; slight indication of adductor muscle depression; adductor plate extends well below basal margin of valve proper; rostral angle of adductor plate slightly produced.

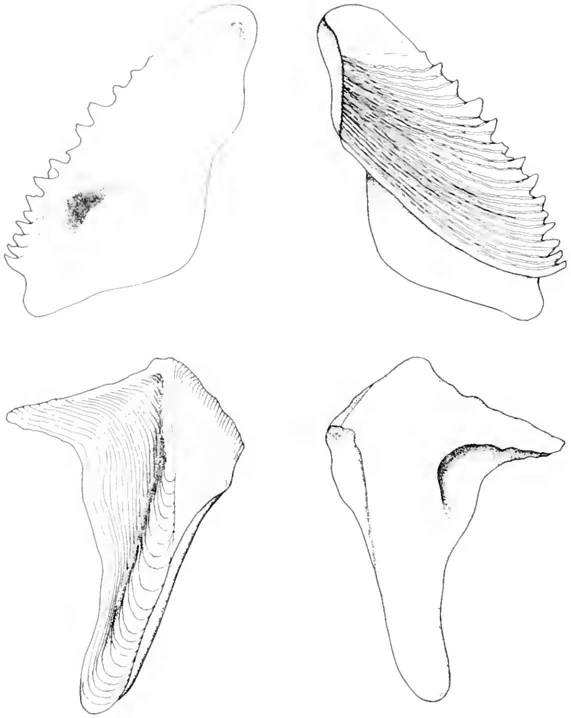

Figure 9. Opercular plates of *Hiroa stubbingsi* n. gen., n. sp.

Tergum T-shaped or narrowly triangular (2.3 mm high x 1.6 mm wide); external surface ornamented with irregular low growth ridges; external longitudinal furrow deep, steep-walled and open throughout its length; internal surface smooth, lacking crests for depressor muscles, deep depression present in area bordering basi-carinal angle.

Disposition of types.—The holotype and two paratypes are deposited in the collections of the National Museum of Natural History. The remaining paratypes are housed in the collections of Scripps Institution of Oceanography.

Etymology.—Named in honor of H. G. Stubbings, long-time student of the Cirripedia, on the occasion of his retirement.

Genus *Creusia* Leach

Creusia Leach, 1817: 68. Genus without originally included nominal species; first species assigned to genus: *Creusia spinulosa* Leach, 1818, Recent, type locality unknown, *ipso facto* type species by subsequent monotypy (Leach, 1818: 171).

Cerusia (error for *Creusia* Leach, 1817): Ranzani, 1818: 92; Ranzani, 1820: 56.

Creusa (error for *Creusia* Leach, 1817): Catlow, 1843: 39.

Definition.—Shell flat, ribbed, compartments separated by narrow radii; parietal tubes absent in small species, rarely present in larger ones; scutum and tergum calcified together without visible indication of line of juncture; adductor "plate" commonly extending below basal margin of valve; where plate extends below margin it is produced as basi-rostral tooth; no distinct lateral depressor muscle depression on scutum; tergal portion of valve somewhat quadrate, occupying ½ or more of total area; basis oval, or nearly circular in outline and commonly deep.

Species assigned to genus:

Creusia decima Ross and Newman, n. sp. (syn.: *Creusia spinulosa* var. 10 Darwin, 1854: 381); type locality, distribution, and host coral not known.

Creusia indicum (Annandale), 1924: 64 (syn.: *Creusia spinulosa* var. 11 Darwin, 1854: 381: *Pyrgoma indicum* phase *merulinae* Annandale, 1924: 65; *Pyrgoma indicum* phase *symphylliae* Annandale, 1924: 65; *Creusia spinulosa angustiradiata* Broch, 1931: 118; *Creusia spinulosa angustiterga* [sic]: Nilsson-Cantell, 1938: 63); Padaw Bay, King-Island, Mergui Archipelago; on *Favia valenciennesii*.

Creusia spinulosa Leach, 1818: 171 (syn.: *Creusia spinulosa* var. 9 Darwin, 1854: 380); type locality, distribution, and host coral not known.

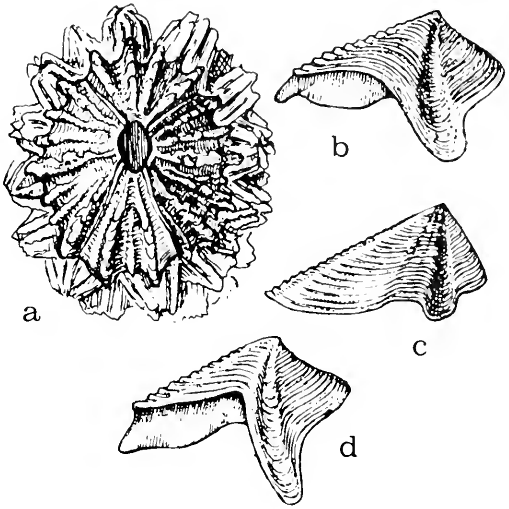

Figure 10. *Creusia.* a, b, shell and opercular plate of *C. indicum*; c, opercular plate of *C. spinulosa*; opercular plate of *C. decima*; all figures after Darwin, 1854.

Remarks.—The original definition of *Creusia* follows: "Testa quadripartita; operculum valvis unipartitis" (Leach, 1817: 68). This was later given by Leach (1818: 171) as: "Shell quadripartite; parts equal. Valves of the operculum unipartite. Base infundibuliformis." In reference to Leach's statement that the opercular valves are fused, Gray (1825: 103) stated, in his discussion of *C. spinulosa*, "Dr. Leach describes the valves of the operculum as soldered two and two, but they are not so in the Museum specimens." Probably the opercular valves of the specimens in question, which are not necessarily a species of *Creusia* (*sensu stricto*), are only cemented together, rather than calcified together, and this would account for the discrepancy between the two descriptions.

Of the 13 numbered varieties and sub-varieties of *C. spinulosa* described by Darwin (1854a), three have not been redescribed nor assigned formal names. For "variety 5" we propose the name *Cantellius quintus;* for "*C. spinulosa* var. 8," the name *Cantellius octavus*; for "*C. spinulosa* var. 10," the name *Creusia decima.*

Nilsson-Cantell (1938: 63) considered Annandale's phase *merulinae* and phase *symphylliae* to be synonymous with Creusia *spinulosa angustiradiata.* This taxon is a junior subjective synonym of *C. indica*, as noted by Utinomi (1962: 227), who also followed Nilsson-Cantell's suggestion in synonymizing Annandale's several "phases."

Genus *Nobia* Sowerby

Nobia Sowerby (*ex* Leach), 1839: 71. Type species: *N.* [*obia*] *grandis* Sowerby, Recent, Island of Singapore (type locality here designated), by monotypy.

Definition.—Shell flat or conical, ribbed or smooth, composed of one piece lacking all evidence of radii and alae; shell perched on basis; sheath applied directly to wall, extending to, or nearly to basis; opercular valves nearly of equal size and fused, with line of fusion invisible, or visible either externally, internally, or both; scutal portion of valve quadrate to subquadrate in outline; basis deep, cylindrical, and either exserted or flush with corallum.

Species assigned to genus:

Nobia conjugatum (Darwin), 1854: 364; Red Sea; on *Cyphastraea chalcidicum.*
Nobia grandis Sowerby, 1839: 71; Singapore; on *Galaxea musicalis.*
Nobia halomitrae (Kolosváry), 1948: 363; type locality and distribution unknown; on *Halomitra* sp.
Nobia kuri (Hoek), 1913: 259; near Kei Islands (5°28.4'S., 132°0.2'E.,); on *Caryophyllia* sp.
Nobia orbicellae (Hiro), 1934: 367; Tanabe Bay, Japan; on *Goniopora* sp.
Nobia projectum (Nilsson-Cantell), 1938: 70; Persian Gulf; on *Caryophyllia* sp.

Remarks.—Sowerby's (1839: 71) original definition of *Nobia* is: "This genus resembles Pyrgoma, Auct. consisting of a conical paries supported upon a funnel-shaped cavity in the madrepore, but differs in its operculum, which consists of two valves; whereas that of Pyrgoma has four."

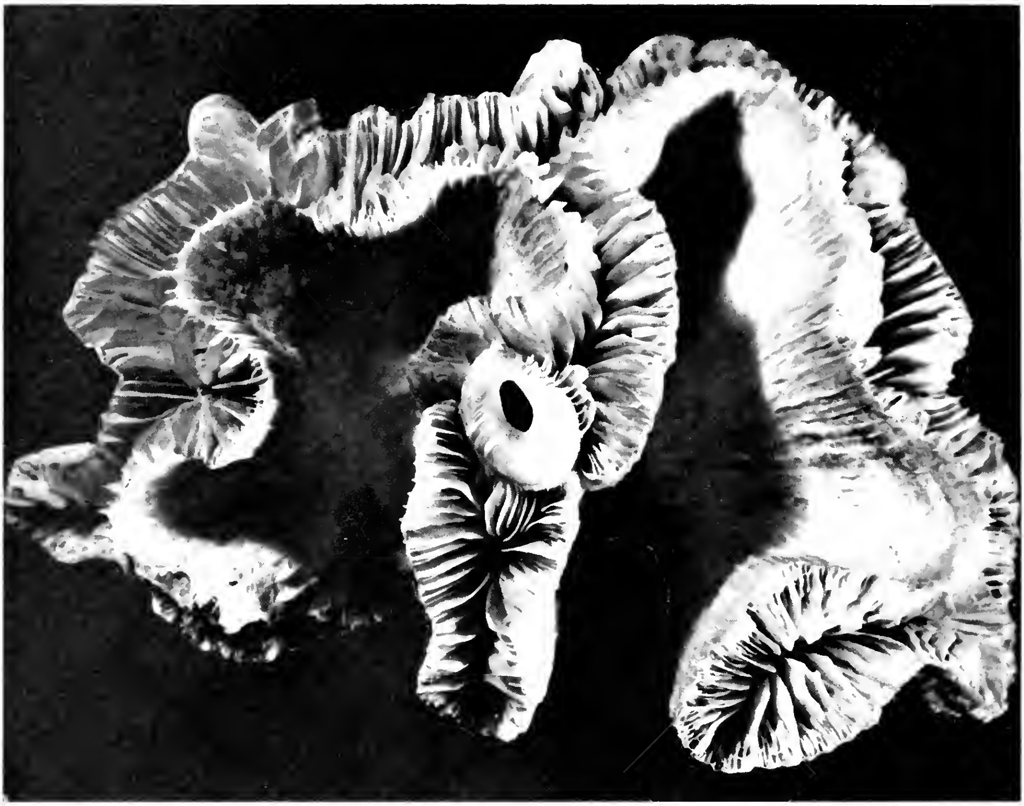

Figure 11. *Nobia grandis* on *Euphyllia fimbriata* (Spengler); Warrior Reef, Torres Straits, Australia; Museum Comparative Zoology coral 5685.

Genus *Pyrgoma* Leach

Pyrgoma Leach (*ex* Savigny MS), 1817: Genus without originally included nominal species; first species assigned to genus: *Pyrgoma cancellata* Leach, 1818, Recent, Indo-Pacific, *ipso facto* type species by subsequent monotypy (Leach, 1818, 171; and by subsequent designation of Brooks and Ross, 1960: 354).

Pyrgone (error for *Pyrgoma* Leach, 1817): Ferrusac, 1822: 144.

Pyrgona (error for *Pyrgoma* Leach, 1817): Catlow, 1843: 39.

Pyrgomum (error for *Pyrgoma* Leach, 1817): Darwin, 1854: 364 (footnote).

Pyrogoma (error for *Pyrgoma* Leach, 1817): Kolosváry and Wagner, 1941: 12; Kolosváry, 1943: 95.

Pytgoma (error for *Pyrgoma* Leach, 1817): Johnson, 1963: 95.

Definition.—Shell large, flat to sub-conical, plates totally fused; short adpressed sheath covers about 1/5 height of inner wall; parietal tubes present; triangular scutum high and elongated transversely; adductor ridge projecting below basal margin of valve; tergum extremely narrow, with spur ⅔ to ¾ height of valve; lacking crests for depressor muscles; overall height of tergum greater than that of scutum, but about ½ bulk of scutum.

Species assigned to genus:

Pyrgoma cancellata Leach, 1818: 171 (syn.: *Pyrgoma lobata* Gray, 1825: 102; *Pyrgoma cancellatum* var. *japonica* Weltner, 1897: 255); Sirahama, Honshu Island, Japan, type locality here designated; on *Turbinaria contorta*.

Remarks.—Leach's (1817: 68) original definition of *Pyrgoma* is: "Testa unipartita; operculum valvis bipartitis." In subsequent publications Leach (1818, 1825) neither enlarged nor amplified this description.

Pyrgoma cancellata is the only species assigned to this genus. The unusual development of the opercular valves, especially the tergum, and the concrescent shell, serve to distinguish it from those species previously referred to *Pyrgoma*.

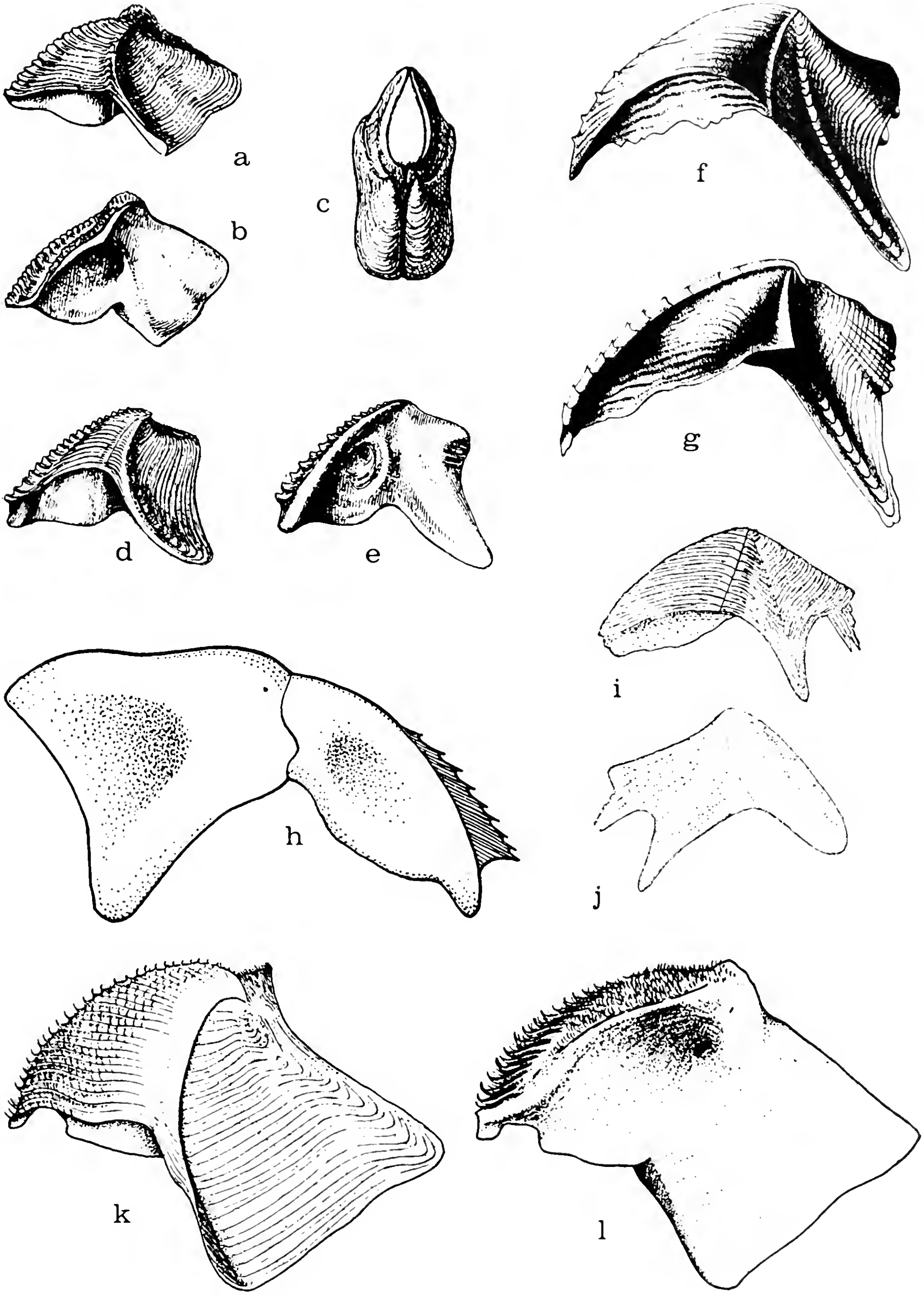

Figure 12. Opercular plates of *Nobia*. a-c, *N. grandis*, after Darwin, 1854; d, e, *N. conjugatum*, after Darwin, 1854; f, g, *N. kuri*, after Hoek, 1913; h, *N. halomitrae*, after Kolosváry, 1948; i, j, *N. projectum*, after Nilsson-Cantell, 1938; k, l, *N. orbicellae*, after Hiro, 1935.

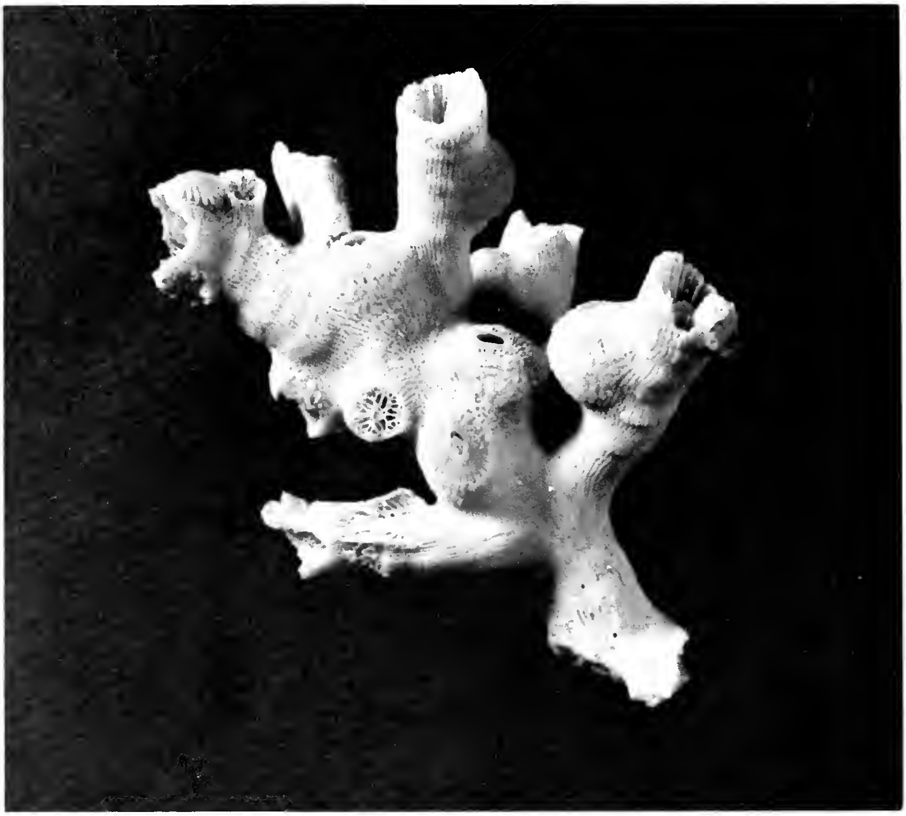

Figure 13. *Pyrgoma cancellata* Leach on *Dendrophyllia micranthus grandis* Crossland; Great Barrier Reef, Australia; Zoologisk Museum, Copenhagen.

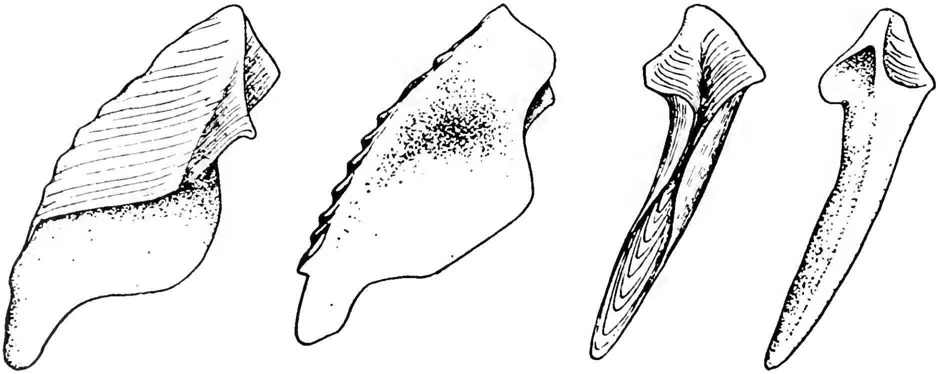

Figure 14. Opercular plates of *Pyrgoma cancellata*, after Hiro, 1935.

Genus *Savignium* Leach

Savignium Leach, 1825 (not Sowerby, 1823, *nomen nudum*): 210. Genus without originally included nominal species; first species assigned to genus: *D.* [*aracia*] *linnaei* Gray, 1825 [= *Savignium crenatum* Sowerby, 1823], Recent, Island of Singapore (type locality here designated), *ipso facto* type species by subsequent monotypy (Gray, 1825: 102).

Daracia Gray, 1825: 102. Type species: *D.* [*aracia*] *linnaei* [= *Savignium linnaei* = *Savignium crenatum* Sowerby, 1823], Recent, Philippine Archipelago, by monotypy.

Doracia (error for *Daracia* Gray, 1825): Weltner, 1897: 278.

Definition.—Shell totally fused, flat, oval in outline; lower margin of sheath free, extending nearly to basal edge of wall; opercular valves separate, cemented, or fused to-

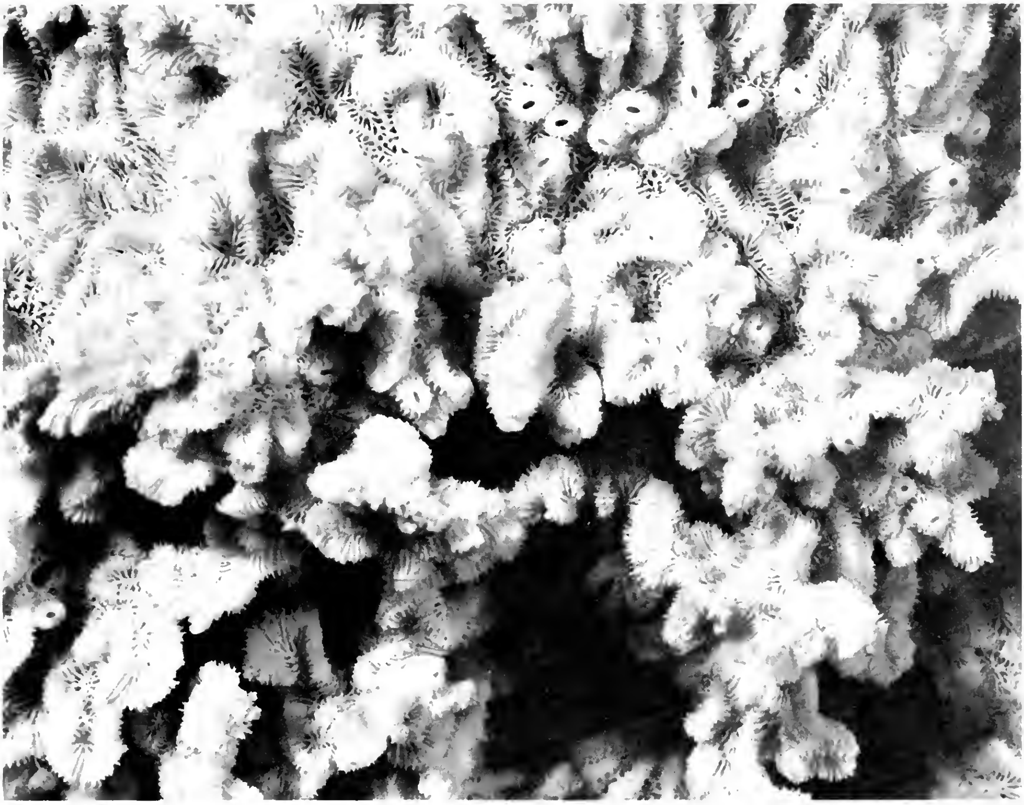

Figure 15. *Savignium crenatum* on *Merulina ampliata* Ellis and Solander; Singapore; American Museum coral 1868.

gether; scutum transversely elongated, its overall length exceeding that of tergum; tergum variable, commonly lacking definitive spur and lacking crests for depressor muscles; scutum comprising bulk of operculum; basis commonly deep and cylindrical.

Species assigned to genus:

Savignium crenatum Sowerby, 1823, no pagination (syn.: *Pyrgoma crenatum* phase *tridacophylliae* Annandale, 1924: 66; *Pyrgoma crenatiformis* Kolosváry, 1951: 287); Singapore, type locality here designated; on *Tridacophyllia lactuca*.

Savignium dentatum Darwin, 1854: 369; Red Sea; on *Meandrina spongiosa*.

Savignium elongatum Hiro, 1931: 154; Sirahama, Honshu Island, Japan; on *Madrepora* sp.

Savignium milleporae Darwin, 1854: 367 (syn.: *Pyrgoma millepora* [sic]: Nilsson-Cantell, 1938: 65; *Pyrgoma milleporae* forma *typica* Kolosváry, 1950: 292; *Pyrgoma milleporae* forma *snelliusi* Kolosváry, 1950: 292); Mindoro Island, Philippine Archipelago; on *Millepora complanata*.

Remarks.—After Leach (1817, 1818) published his first two studies on the Cirripedia he subdivided *Pyrgoma* and proposed the genera *Savignium*, *Megatrema*, and *Adna*. Although he did not publish these names until 1825, he did leave labeled specimens in the British Museum (Natural History) collections (see Sowerby, 1823; Gray, 1825: 107). Sowerby (1823) found "... upon examining the collection of Cirripedes, in the British Museum, as it now remains arranged by Leach himself, that since the publication of the 'Supplement to the Encyclopedia Britannica,' where the characters of the genus [*Pyrgoma*] first appear in print, he [Leach] had divided into four; upon what grounds we must acknowledge ourselves entirely ignorant, except it be from some differences in the form of the shell, and the valves of the operculum ... We do not consider ... these four genera ... sufficiently distinct to constitute several genera ... wherefore we still include all above enumerated [*Megatrema*, *Savignium*, and *Adna*] under the denomination of *Pyrgoma*."

Sowerby is not considered the author of *Megatrema*, *Savignium*, or *Adna*, although his publication has priority, because, "A name first published as a synonym is not thereby

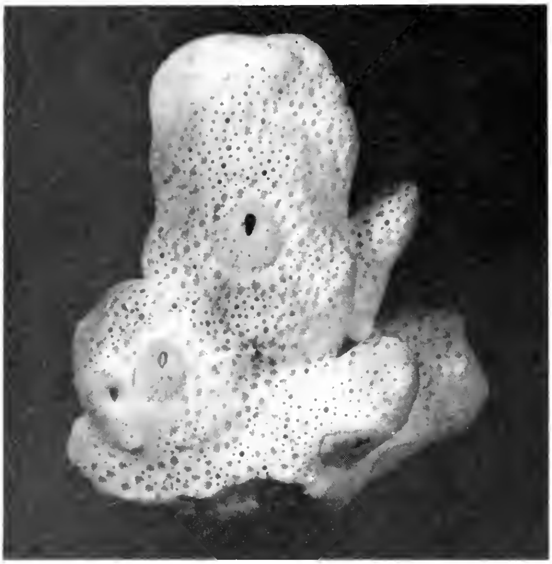

Figure 16. *Savignium milleporae* on *Millepora* sp.; Heron Island, Great Barrier Reef, Australia.

made available unless prior to 1961 it has been treated as an available name with its original date and authorship, and either adopted as the name of a taxon or used as a senior homonym" (Article 11 (d), ICZN). Sowerby's use of the specific names, *Savignium crenatum* and *Adna anglica*, suggested by Leach, on the other hand, entitles him to the authorship of these.

Leach's second synopsis of the Cirripedia, published in July of 1825, contained brief descriptions of *Savignium*, *Megatrema*, and *Adna*. At the same time Leach was working on his manuscript, Gray (1825) was also preparing a synopsis of the Cirripedia, which was published in the August issue of the *Annals of Philosophy*. In his synopsis, Gray (1825: 102) described the genus *Daracia* as follows: "*Daracia*, Gray, *Savignium*, Leach, without character. Valves of the body of the shell, four, soldered together." This description compares favorably with Leach's abbreviated description of *Savignium*: "Testa indivisa: basis immersa, valvae indivisae" (1825: 210). The only species mentioned by Gray in connection with the definition of *Daracia* is *linnaei*, which is not described. In the discussion of *Pyrgoma*, Sowerby (1823) made reference to *Savignium crenatum*, which he attributed to the authorship of Leach. That Gray referred to the same specimens as did Sowerby, who figured them, seems probable at this time, and Gray more than likely based his concept of *D. linnaei* on these specimens. Therefore, we believe that Gray's *D. linnaei* is actually a junior objective synonym of *Savignium crenatum*. It should also be noted that Gray, proposed *Daracia* as a replacement name for *Savignium* (see Gray 1825: 102, footnote).

Based on the general aspects of barnacles overgrown by a milleporine, Darwin (1854: 366) suspected Chenu's (1843) *Creusia madreporarum* to be synonymous with his *Pyrgoma milleporae*. Chenu, questionably, ascribed this taxon to the authorship of Leach, and his illustration speaks favorably of its being the same as Darwin's taxon. So far as we have been able to determine, the only pyrgomatid reported from a milleporine is *P. milleporae*. In the interests of stability, although recognizing that *C. madreporarum* has priority, Darwin's name is used here.

Two forms of *Pyrgoma milleporae* were designated by Kolosváry (1951: 292), *typica* (= *P. milleporae milleporae*) and *snelliusi*. These are not recognized here because the morphological variations recorded fall within the limits of variation assumed to correlate with different infrageneric milleporine associations.

In the coral collections of the American Museum there are two large specimens of *Merulina ampliata* (cat. no. 1868 and 3214) from the Island of Singapore infested with pyrgomatids. Our study of these indicated that they are conspecific with *Pyrgoma crenatum*. In 1951 Kolosváry described *P. crenatiformis* from the coral *Merulina ampliata*, col-

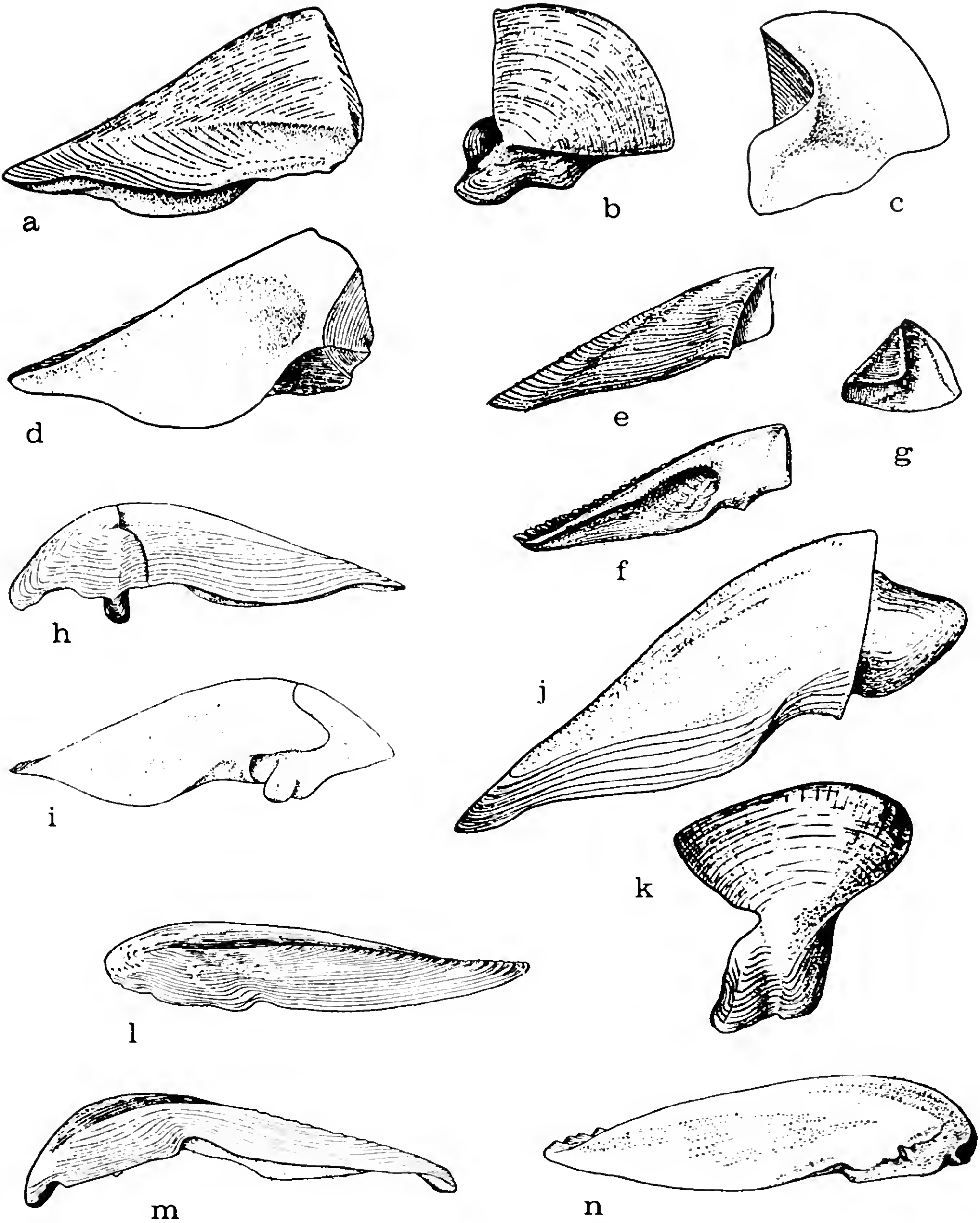

Figure 17. Opercular plates of *Savignium*. a-d, *S. crenatum*, after Hiro, 1935; e-g, *S. milleporae*, after Darwin, 1854; h-k, *S. dentatum*, after Hiro, 1935 and 1938; l-n, *S. elongatum*, after Hiro, 1938.

lected in the vicinity of the Island of Singapore. Comparison of our specimens with Kolosváry's illustrations and brief description does not reveal differences that enable one to separate these two species.

Hoekia n. gen.

Definition.—Shell totally concrescent, irregularly lobate in outline, and exhibiting no definitive peripheral shape; region surrounding minute ovate orifice elevated above externally flat or undulatory surface of shell; sheath short, adpressed, basal margin not depending freely; irregularly scattered wall tubes occur at varying distances from shell

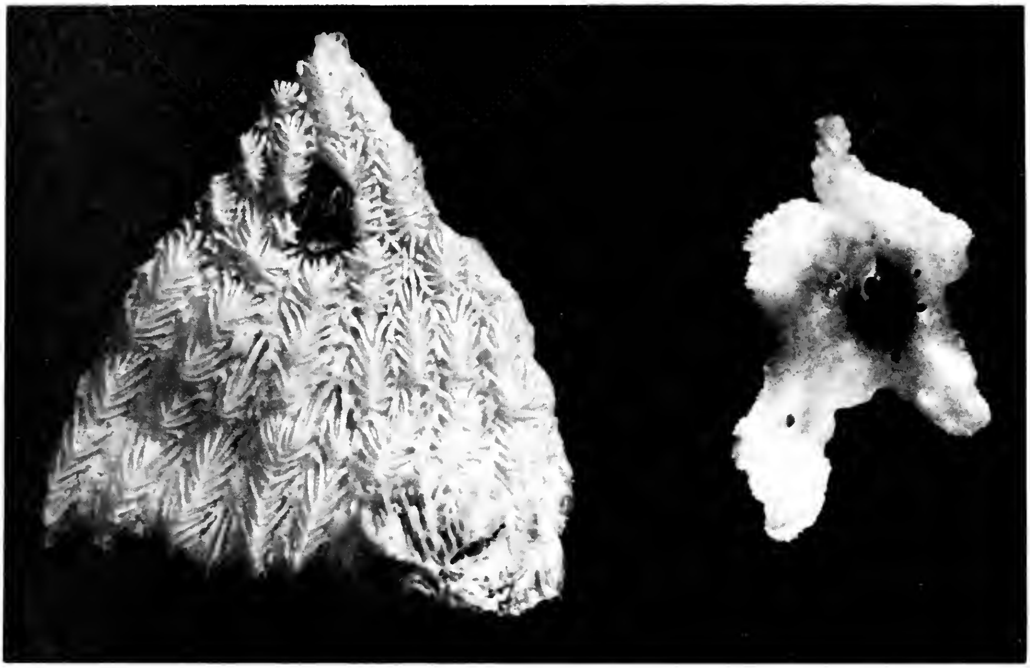

Figure 18. *Hoekia monticulariae*. Left, on *Hydnophora exesa* (Pallas); Mortensen Java-South Africa Expedition 1929-30; Station 44, Flat Island, Mauritius; Zoologisk Museum, Copenhagen. Right, internal view of shell from *Hydnophora exesa*; Singapore; American Museum coral 1883.

margin; operculum minute; scutum and tergum fused without evidence of suture, forming elongate valve with broad occludent ledge; tergal end of valve lacking spur.

Etymology.—This taxon honors the late Dutch cirripedologist Paulus Peronius Cato Hoek (1851-1914).

Type species.—*Pyrgoma monticulariae* Gray, 1831, Recent, Island of Singapore.

Species assigned to genus:

Hoekia monticulariae (Gray), 1831: 6; Singapore; on *Hydnophora exesa*.

Remarks.—The gross differences between the shell and opercular valves of *monticulariae* and those of other Pyrgomatinae are of sufficient magnitude to warrant its separation as a distinct genus (see Ross and Newman, 1969).

Although Baluk and Radwański (1967b: 487) resurrected the name *Daracia* to include *Pyrgoma monticulariae* and *P. elongatum*, it is readily apparent that not only was *Daracia* proposed as a replacement name for *Savignium* (see Gray, 1825: 102, footnote), but also the type species *D. linnaei* appears to be a junior objective synonym of *S. crenatum*. Consequently, we feel justified in proposing a new taxon.

Hoekia is allied morphologically to *Savignium* in that the fused opercular valves show some affinity to those of *S. crenatum*, *S. dentatum*, and less so to *S. milleporae*, as pointed out by Darwin (1854a: 374). But, in these species the valves are separate or only cemented together.

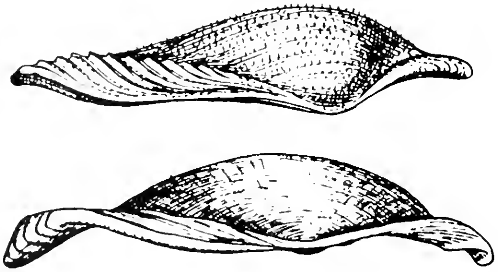

Figure 19. Opercular plate of *Hoekia monticulariae*; top, after Darwin, 1854; bottom, after Hiro, 1935.

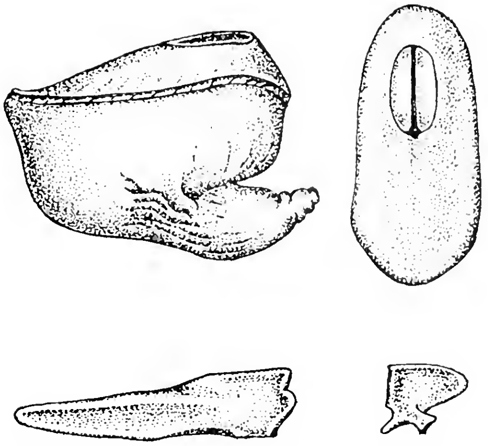

Figure 20. Shell and opercular plates of *Pyrgopsella annandalei*, redrawn after Gruvel, 1907.

Aside from the fact that *H. monticulariae* is the only known wholly parasitic balanid, the trophi of this species depart radically from those of other pyrgomatines (Ross and Newman, 1969: 255). Apparently, critical study of the mouth field should provide additional and independent criteria for recognition of pyrgomatine generic groups. Our preliminary studies of species having morphologically primitive shells indicate that the trophi of these depart little from that of many primitive balanids (see Broch, 1924, fig. 10).

Genus *Pyrgopsella* Zullo

Pyrgopsis Gruvel, 1907: 8. Type species: *Pyrgopsis annandalei* Gruvel, Recent, Andaman Islands, by monotypy.

Pyrgopsella Zullo, 1967: 109 (substitute name for *Pyrgopsis* Gruvel, 1907, not Rochebrune, 1884).

Definition.—Wall subconical, rostro-carinally elongate, smooth, composed of numerous calcareous rods contained in a chitinous envelope continuous with basis; basis elongate and membranous; opercular plates separate, well calcified, scutum transversely elongated; tergum triangular with short irregular spur; living in sponges.

Species assigned to genus:

Pyrgopsella annandalei (Gruvel), 1907: 8; Andaman Islands; host unknown.

Remarks.—The remarkable feature in *Pyrgopsella* is the membranous basis that Gruvel (1907: 9) thought served as a peduncle. Rosell (pers. comm.) recently discovered a new species of *Pyrgopsella* living in a sponge in the Philippines, and from this it is clear that the function of the elongate membranous basis is comparable to that of the elongate calcareous basis of the other pyrgomatines, and that being membranous is simply a secondary adaptation to living in sponges as opposed to corals.

Utinomi (1943: 16) studied the post larval settlement stages in *Creusia indicum*, and found the basis to be initially cup-like and wholly membranous. It is evident that calcification of the basis is delayed, at least in *C. indicum*, and hence it is not difficult to envisage that in *Pyrgopsella* ontogenetic suppression of calcium deposition would result in a membranous basis.

The general shape of the shell and the opercular plates of *Pyrgopsella* are similar to those found in *Savignium dentatum*. From the morphology of the hard parts it is apparent that *Pyrgopsella* was derived from *Savignium*.

Genus *Boscia* Ferussac

Boscia Ferussac, 1822: 145. Type species: *Balanus madreporarum* Bosc, 1812 [=*Boscia madreporarum* (Bosc)], Recent, Caribbean-western Atlantic, by monotypy.

Megatrema Leach, 1825 (not Sowerby, 1823, *nomen nudum*): 210. Genus without originally included nominal species; first species assigned to genus: *M.* [*egatrema*] *stokesii* Gray, 1825 [=*Boscia madreporarum* (Bosc), 1812], Recent, Caribbean-western Atlantic; *ipso facto* type species by subsequent monotypy (Gray, 1825: 102), and subsequent designation of Philippi (1853: 424).

Adna Leach, 1825 (not Sowerby, 1823, *nomen nudum*): 210. Genus without originally included nominal spe-

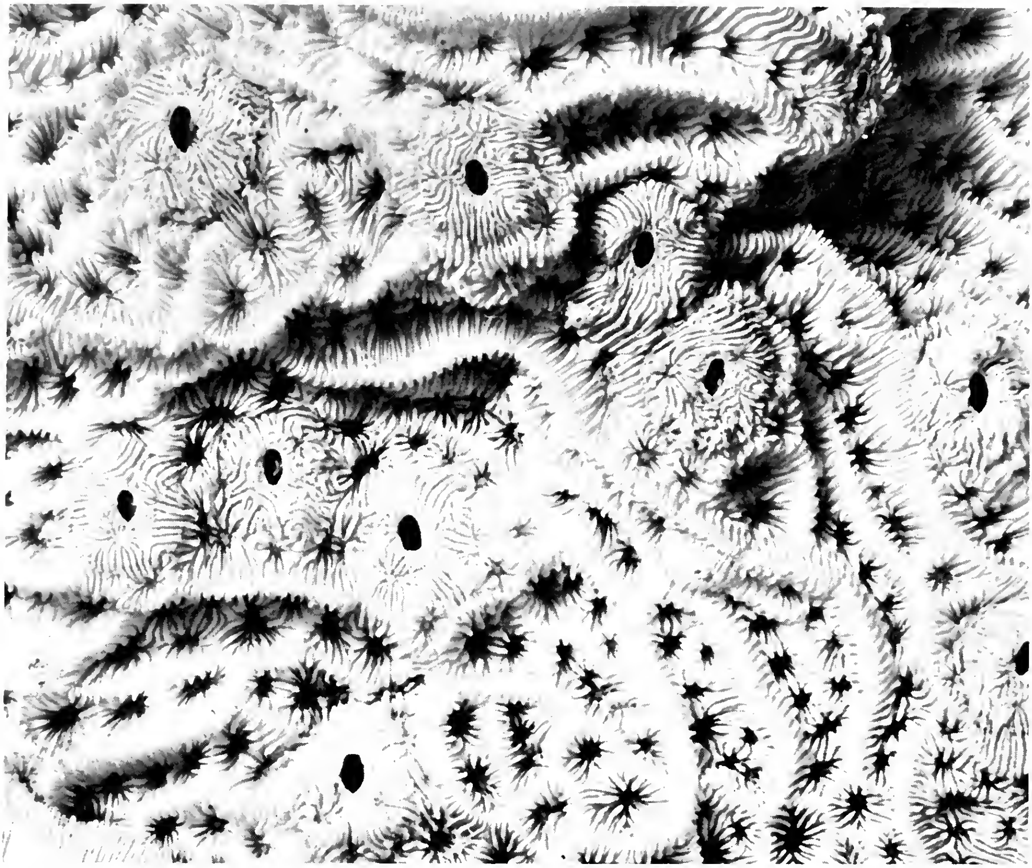

Figure 21. *Boscia madreporarum* on *Agaricia agaricites* (Linnaeus); Dry Rocks, off Key West, Florida.

cies; first species assigned to genus: *M.* [*egatrema*] (*A.* [*dna*]) *anglica* Gray, 1825 [=*Boscia anglicum* Sowerby, 1823], Recent, coast of Devonshire, England; *ipso facto* type species by subsequent designation of Philippi (1853: 424).

Pyrgominia Baluk and Radwański, 1967b: 691. Type species: *Pyrgominia seguenzai* Baluk and Radwański, 1967 [=*Boscia seguenzai* Baluk and Radwański], by original designation, Pliocene, Island of Crete, Greece.

Definition.—Shell conical in juveniles and commonly flat or low conical in later stages; shell plates totally fused externally; pseudo-alae may be present; sheath adpressed and covering ⅔ to entire inner wall; opercular valves typically balanoid; terga lacking depressor muscle crests; basis cup-shaped or sub-cylindrical, exserted or flush with corallum.

Species assigned to genus:

Boscia anglicum Sowerby, 1823 [no pagination] (syn.: *Pyrgoma sulcatum* Philippi, 1836, pl. 12, fig. 24; *Pyrgoma undatum* Michelotti, 1839: 140-141); coast of Devonshire, England; on *Caryophyllia smithii.*

Boscia madreporarum (Bosc), 1812: 66 (syn.: *Creusia boscii* DeBlainville, 1824: 378; *Pyrgoma stokesii* Gray, 1825: 103; *Creusia decorata* Chenu, 1843 [no pagination]; *Pyrgoma stockesi* [sic]: Kruger, 1940: 382); "Amerique" [=Caribbean western-Atlantic]; on *Agaricia agaricites.*

Boscia oulastreae (Utinomi), 1962: 83; Nomosaki, Kyushu Island, Japan; on *Oulastrea crispata.*

Boscia seguenzai (Baluk and Radwański), 1967b: 691; Gournes, Island of Crete, Greece; Pliocene.

Remarks.—Ferussac's (1822: 14) original description of *Boscia* follows: "*Test univalve en cones tres-surbaisse, a parois tubuleuses; articule avec la base. Celle-ci, plus grande, enforme de godet ou de cupule.*"

In the year following the publication of *Boscia*, Sowerby (1823) published two manuscript names of Leach: *Megatrema* and *Adna*. When Sowerby described *Megatrema* he failed to mention any nominal species. Subsequently, *stokesii* was assigned to the genus (Gray, 1825: 103). However, it appears that *Megatrema stokesii* is a junior subjective syn-

Figure 22. *Boscia madreporarum* (= *Pyrgoma stokesii*). Top, slab with several shells and opercular valves mounted and identified by Darwin; bottom right, external view of shell shown at top center of slab; bottom left, internal view of shell shown at top left of slab. British Museum (Nat. Hist.) 1962. 12.7.1.

onym of *Boscia madreporarum*, because there are no differentiating morphological features, and because it occurs on the same host coral, *Agaricia agaricites* (Linnaeus), in the same geographical region.

Adna was described by Sowerby (1823) as a subjective synonym of *Pyrgoma*. However, Sowerby is regarded as the author only of the specific name *anglica* (see Article 11(d), ICZN). Leach, who originally proposed *Adna*, did not publish the name until 1825. At that time no nominal species was assigned to the genus. Gray (1825: 103) included only one species, *Adna anglica*.

The manner is which Gray (1825: 103) cited the taxon *Adna* suggests that it was to be recognized as a subgenus of *Megatrema*. He did not state why this, rather than a generic assignment was made, nor did Darwin (1854: 360) who also cited *Adna* as a subgenus.

Leach's original definition of *Megatrema* is "Testa indivisa: basis immersa, valvae Balani," while that of *Adna* is: "Testa indivisa: basis exserta, valvae Balani" (1825: 210). The only difference between the two, as proposed by Leach, is in the basis, which in *Adna* is not flush with the surface of the corallum.

Of the pyrgomatids known to Darwin (1854a: 355), only *Pyrgoma stokesii* (= *Boscia madreporarum*) and *P. anglicum* (= *B. anglicum*), ". . . have some claims to be generically separated from the other species of Pyrgoma . . ." This opinion was based on the similarity of the operculum, and the conical shells which internally exhibit carinal pseudoalae. The authors have adopted Darwin's suggestion and maintain these two species, in addition to *Boscia oulastreae* and *B. seguenzai* in a distinct genus.

What have been interpreted as carinal sutures are a pair of lines where the arthrodial

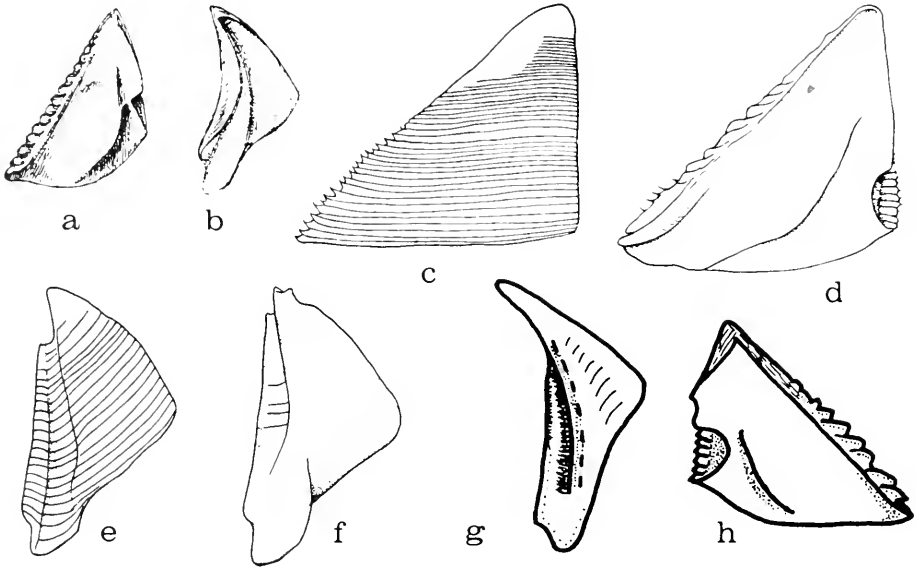

Figure 23. Opercular plates of *Boscia*. a, b, *B. anglicum*, after Darwin, 1854; c-f, *B. oulastreae*, after Utinomi, 1962; g, h, *B. madreporarum*.

membranes of the scuta and terga attach to the sheath. As the operculum is carried basally with growth of the sheath, the lines remain marking the points of earlier attachment. These lines could represent vestiges of the suture, but they appear only in the sheath and not the wall. When the shell is ground transversely, the area beneath the lines has a folded appearance; the overlapping portion being termed a pseudoala.

Genus *Ceratoconcha* Kramberger-Gorjanovic

Ceratoconcha Kramberger-Gorjanovic, 1889: 50. Type species: *Ceratoconcha costata* Kramberger-Gorjanovic [= *Creusia krambergeri* nom. nov. = *Ceratoconcha krambergi* (Baluk and Radwański), 1967: 145], Miocene, Yugoslavia, by monotypy.

Paracreusia Abel, 1927: 101. Type species: *Paracreusia trolli* Abel [= *Ceratoconcha trolli* (Abel)], Miocene, Italy, by monotypy.

Andromacheia Kolosváry, 1949: 4. Type species: *Andromacheia noszkyi* Kolosváry [= *Ceratoconcha noszkyi* (Kolosváry)], Upper Miocene, southern Hungary, by monotypy.

Withersia Baluk and Radwański, 1967c: 485. Type species: *Creusia barbadensis* Withers, Pleistocene, Barbados by original designation.

Definition.—Shell of four compartments separated by radii and alae, the latter trending toward reduction in size; shell ribbed, ranging from conical to nearly flat; sheath approximately ½ height of wall, with basal margin depending freely; well developed ribs may occur on inner surface of shell and extend from base to sheath; opercular valves typically balanoid; rostral tooth of scutum either inconspicuous or wanting; well developed lateral depressor muscle pit present; tergum commonly bears a prominent ridge or plate on carinal segment, rather than depressor muscle crests; basis commonly deep and cylindrical.

Species assigned to genus:

†*Ceratoconcha barbadensis* (Withers), 1926: 2 (syn.: *Creusia barndensis* [sic]: Nilsson-Cantell, 1938: 63); Barbados, West Indies; Pleistocene.

†*Ceratoconcha costata* (Sequenza), 1876, p. 316 (syn: *Creusia costata elargata* (Sequenza), 1876: 317; *Creusia moravica* Prochazka, 1893: 20; *Creusia spinulosa* forma *praespinulosa* Kolosváry, 1949: 1, fig. 5 only; *Creusia spinulosa* forma *kojumdgievae* Kolosváry, 1962: 86); Messina, Italy; Pliocene (Astian).

†*Ceratoconcha darwiniana* (Prochazka), 1893: 23; Leibnitz, Australia; Miocene.

†*Ceratoconcha diploconus* (Seguenza), 1876: 322; Messina, Italy; Pliocene (Astian).

Ceratoconcha domingensis (Des Moulins), 1867: 307; Port-au-Prince, Haiti; on *Porites astreoides.*

Ceratoconcha floridanum (Pilsbry), 1931: 81; Gulf of Mexico; on *Maeandra sp. cf. M. areolata.*

†*Ceratoconcha krambergeri* (Baluk and Radwański), 1967a: 145 (see Kramberger-Gorjanovic, 1889: 50); Podsused, Yugoslavia; Miocene.

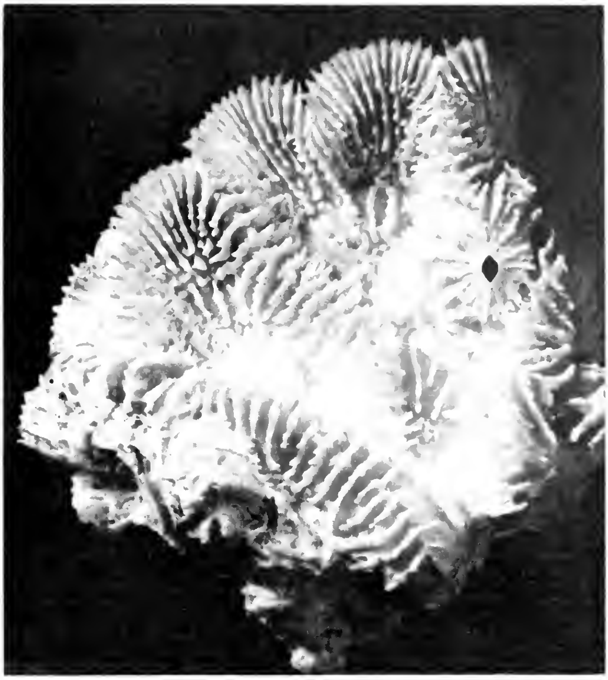

Figure 24. *Ceratoconcha floridanum* on *Mycetophyllia lamarckana* Milne-Edwards and Haime; Recent, Florida Keys.

†*Ceratoconcha miocaenica* (Prochazka), 1893: 22; Wollersdorf, Austria; Miocene.

†*Ceratoconcha noszkyi* (Kolosváry), 1949: 4; Magyarszek, Hungary; Miocene.

†*Ceratoconcha prefloridana* (Brooks and Ross), 1960: 355 (syn.: *Creusia neogenica* weisbord, 1972: 60); Florida, U.S.A.; Pliocene; on *Manicina mayori*.

Ceratoconcha quarta (Kolosváry), 1947: 426 (syn.: *Creusia spinulosa* var. 4 Darwin, 1854: 378); West Indies; West Indies; on *Colpophyllia natans*.

†*Ceratoconcha rangi rangi* (Des Moulins), 1867: 302 (syn.: *Pyrgoma multicostatum* Seguenza, 1873: 319; *Creusia fuchsi* Prochazka, 1893: 18; *Creusia spinulosa* forma *caldangiae* Kolosváry, 1949: 1; *Creusia spinulosa* forma *praespinulosa* Kolosváry, 1949: 1, figs. 2-3 only); Bazas, France; Miocene (Aquitanian).

†*Ceratoconcha rangi latum* (Seguenza), 1876: 321; Rometta, Italy; Miocene (Tortonian).

†*Ceratoconcha sanctacrucensis* Baluk and Radwański, 1967c: 468; Korytnica, Poland; Miocene (Tortonian); on *Tarbellastraea reussiana*.

†*Ceratoconcha sturi* (Prochazka), 1893: 15; Sudic, Czechoslovakia; Miocene.

†*Ceratoconcha trolli* (Abel), 1927: 101; Voslau, Austria; Miocene; on *Siderastraea crenulata*.

Remarks.—In view of the allocation of the coral-inhabiting barnacles to different genera, the specific name *Ceratoconcha costata*, proposed by Kramberger-Gorjanovic (1889: 50), becomes a junior homonym of *Creusia costatum* (Sequenza, 1876: 316). As a replacement for this preoccupied name, Baluk and Radwański (1967a: 145) proposed *Creusia krambergeri*.

The validity of *Paracreusia* has long been questioned (Withers, 1929: 565; Hiro, 1938: 414; Krüger, 1940: 452), because no apparent differences allowing separation from *Ceratoconcha* were noted by Abel (1927, 1928), or subsequent workers. Baluk and Radwański (1967c: 482) suggested merging *Paracreusia*, a proposal we have adopted here.

Kolosváry (1949: 4) proposed *Andromacheia* on the basis of one poorly preserved specimen with visible and irregularly developed squamate compartments. The shell surface was said to bear three rows of scales. These are probably the result of weathering inasmuch as the same feature was noted in *Ceratoconcha cladangiae* (Kolosváry, 1949: 2); therefore they are not considered to be of major taxonomic significance. The poor demarcation of the parietal plates and poor development of radii and alae, as noted by Kolosváry, is often encountered in fossil material. Baluk and Radwański (1967c: 476) questioned whether *Andromacheia* was even a barnacle.

Many fossil Pyrgomatines have been described from specimens lacking morphologically important details (Baluk and Radwański, 1967c: 482). Many of these are based on unique specimens, and many of them have not been reported or described since their in-

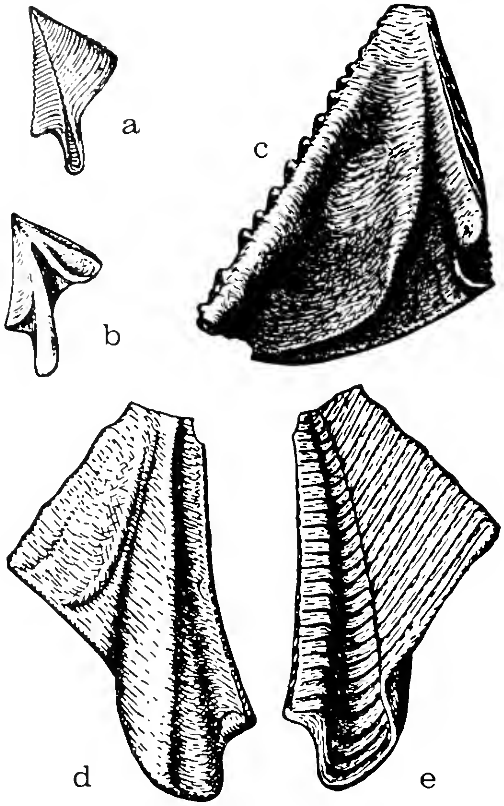

Figure 25. Opercular plates of *Ceratoconcha*. a, b, *C. quarta*, after Darwin, 1854; c-e, *C. prefloridanum*, after Brooks and Ross, 1960.

itial publication. Over half of the species assigned to *Ceratoconcha* were originally based on incomplete specimens and still are known to us solely on the basis of an abbreviated, incomplete description. Invariably these descriptions omit the morphology of the operculum, which is perhaps the most diagnostic feature of this genus. Therefore, the assignment of many of the species must remain tentative until well preserved and more complete material becomes available.

Baluk and Radwański (1967c: 485) proposed the subgenus *Withersia* for two species, one of which, *Creusia barbadensis*, is here referred to *Ceratoconcha*, and the other, *C. oulastreae*, to *Boscia*. The reason for proposing *Withersia* was that the radial sutures are "indistinct or even disappearing." In *barbadensis* sutures are present, but poorly discernible or obscure largely due to secondary calcification, whereas in *oulastreae* radial sutures are never present in the adult stage.

Incertae Sedis

The following taxa cannot be assigned to any of the genera defined herein: *Creusia childreni* Gray, 1825; *Balanus duploconus* Lamarck, 1818; *Megatrema semicostata* Sowerby, 1839; *Pyrgoma stellata* Chenu, 1843; *Pyrgoma spongiarum* Chenu, 1843; *Pyrgoma corymbosa* "Valenciennes" Chenu, 1843; *Creusia radiata* Chenu, 1843; *Creusia multistriata* Chenu, 1843; *Creusia madreporarum* "Leach?," Chenu, 1843; *Creusia striata* Chenu, 1843; *Pyrgoma undata* Michelotti, 1839.

Darwin (1854: 365, footnote) noted that *Balanus duploconus* Lamarck may be synonymous with *Nobia grandis* Sowerby. Lamarck's (1818: 394) description, "*B. testae parte suprema univalvi, indivisa, convexa; inferiore turbinata, non clausa; apertura elliptica,*" may also apply to other species here included in the genera *Nobia*, *Pyrgoma*, or *Boscia*. The uncertainty that surrounds the nature of *B. duploconus*, which Lamy and Andre (1932) failed to clarify, stems from the lack of a more complete description.

Schluter (1838: 38) considered Lamarck's *Balanus duploconus* to represent a distinct genus, for which he proposed *Duplocona*, with *D. laevigata* Schluter (=*Balanus duploconus* Lamarck, 1818) as the sole nominal species. Although *D. laevigata* is accompanied by a reference to Lamarck's work, no description or illustrations are given, the section on barnacles being for the most part a list of names. Pilsbry (1916: 261), without any comment, placed Schluter's taxon in the synonymy of *Pyrgoma* as then recognized. Because of the dubious nature of *Balanus duploconus, Duplocona* cannot be defined.

Both *Creusia childreni* and *Megatrema semicostata* are presented without description or locality. Sowerby's illustration of the external surface of *M. semicostata* is too small and generalized to be of any taxonomic value. *Creusia childreni* was not figured.

In his "Illustrations Conchyliologiques" Chenu (1843) figured seven species of *Creusia* and five species of *Pyrgoma*. Of these, only *Creusia grandis*, *C. decorata*, *C. madreporarum*, *Pyrgoma cancellatum*, and *P. crenatum* can be identified with any certainty. The lack of text, figure explanations, or locality data, precludes identification of the remaining seven species.

The illustration of *Creusia striata* presented by Chenu shows only the internal surface of the shell *in situ*. Close inspection reveals six lines marking the interior surface of the sheath, indicating that the wall is composed of six plates. Therefore, Chenu's form is either a species of *Balanus* or *Hexacreusia*.

Darwin (1854: 364 footnote) stated that J. E. Gray thought *Pyrgoma stellata* Chenu was a synonym of *P. conjugatum* Darwin. However, Darwin commented that, ". . . it may be so; but the figure given of the shell will do equally well or rather better for the *Pyrgomum* [sic] *dentatum* of this work, and for some varieties of *P. crenatum*." The uncertainty regarding the identity of *P. stellata* stems from the lack of illustrations of the opercular plates.

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BIOLOGY, GEOGRAPHICAL DISTRIBUTION, AND STATUS OF *ATTEVA EXQUISITA* (LEPIDOPTERA: YPONOMEUTIDAE)

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ABSTRACT.—Moths of the genus *Atteva* are colorful insects that are often encountered at flowers during daytime. Taxonomic relationships among the ten described New World species are poorly known. Three species occur in Nearctic North America: the widespread *punctella* Cramer, the quite similar *exquisita* Busck which was formerly known only from northern Mexico, and a dissimilar endemic in Florida, *floridana* Neumoegen. The geographical distribution and status of *exquisita* in relation to *punctella* are analyzed. The two are allopatric with a meeting and possible blend zone near the Rio Grande. The northward spread of *punctella* following the distribution of adventive *Ailanthus* trees is documented. The biology and behavior of *exquisita*, based primarily on a recently discovered colony in southeastern California, and the relationship of the distribution of this moth to various Simaroubaceae are examined. After a long premating period, mating takes place at the onset of the light phase of the diel cycle; oviposition occurs at the end of the light phase, on fibrous substrates, probably mainly in the larval webbing in the field; larvae feed gregariously in a tent-like shelter, using flowers and seed of *Castela emoryi* and also foliage of more leafy host plants, reaching maturity in about 50 days at laboratory temperatures; pupation occurs in a frail cocoon within the larval tent; the pupa remains in place at emergence of the moth. The species is multivoltine, apparently without a diapause period. The egg, larva, and pupa are described.

Members of *Atteva* are colorful, rather conspicuous moths that are encountered during the daytime at flowers but apparently are essentially crepuscular and nocturnal in behavior. The genus is primarily Pan-Tropical in distribution, consisting of some 50 species, half of which are described from the Indo-Malayan area. About ten New World species have been described, and these are concentrated in the Antillean and circum-Caribbean region. There are three species represented in the Nearctic: the widespread *punctella* (Cramer) (= *aurea* Fitch), *floridana* Neumoegen in Florida and *exquisita* Busck, previously known only from northern Mexico. Despite the relatively large size of the individuals compared to most so-called Microlepidoptera, and their conspicuousness, no satisfactory taxonomic treatment exists for New World species. Most of the described Neotropical species have been inadequately sampled to enable firm conclusions on geographical variation and relationships.

In 1966 our attention was called to the occurrence of an *Atteva* near Coyote Wells, Imperial County, in the Colorado Desert area of southern California, when larvae were collected by R. V. Moran. Records at the California Department of Agriculture, Sacramento, showed that this moth had been discovered in California by R. A. Flock of the University of California, Riverside, who collected larvae "near Seeley," Imperial County in November, 1964. Probably the actual source was the same colony from which our collections were made. Moths reared from the Moran collection were determined as *Atteva exquisita* Busck (1912), described from Mobano, Coahuila, Mexico. This species has received little notice since its original description, and apparently it was not collected again until recently.

The California population, which is located in an isolated grove of *Castela (Holacantha) emoryi* Gray (Simarubaceae) seven airline miles southeast of Coyote Wells, Imperial County, was used as the principal source of material in our biological study. The locality was revisited by Calvert Norland and Powell in June, 1966; by Harbison in December, 1966; and by Powell in October, 1967, and June, 1968, to obtain additional information on the habits of this moth. Our observations, together with data based on scattered collections made in Baja California, Mexico, should prove of value in assessment of comparative biology when a comprehensive study of relationships in American *Atteva* is realized. Various aspects of the bionomics of *Atteva punctella* have been recorded from the eastern United States, and that species recently has been extensively studied in Connecticut (Taylor, 1966, 1967). Nothing has been reported previously on the biology of *exquisita*.

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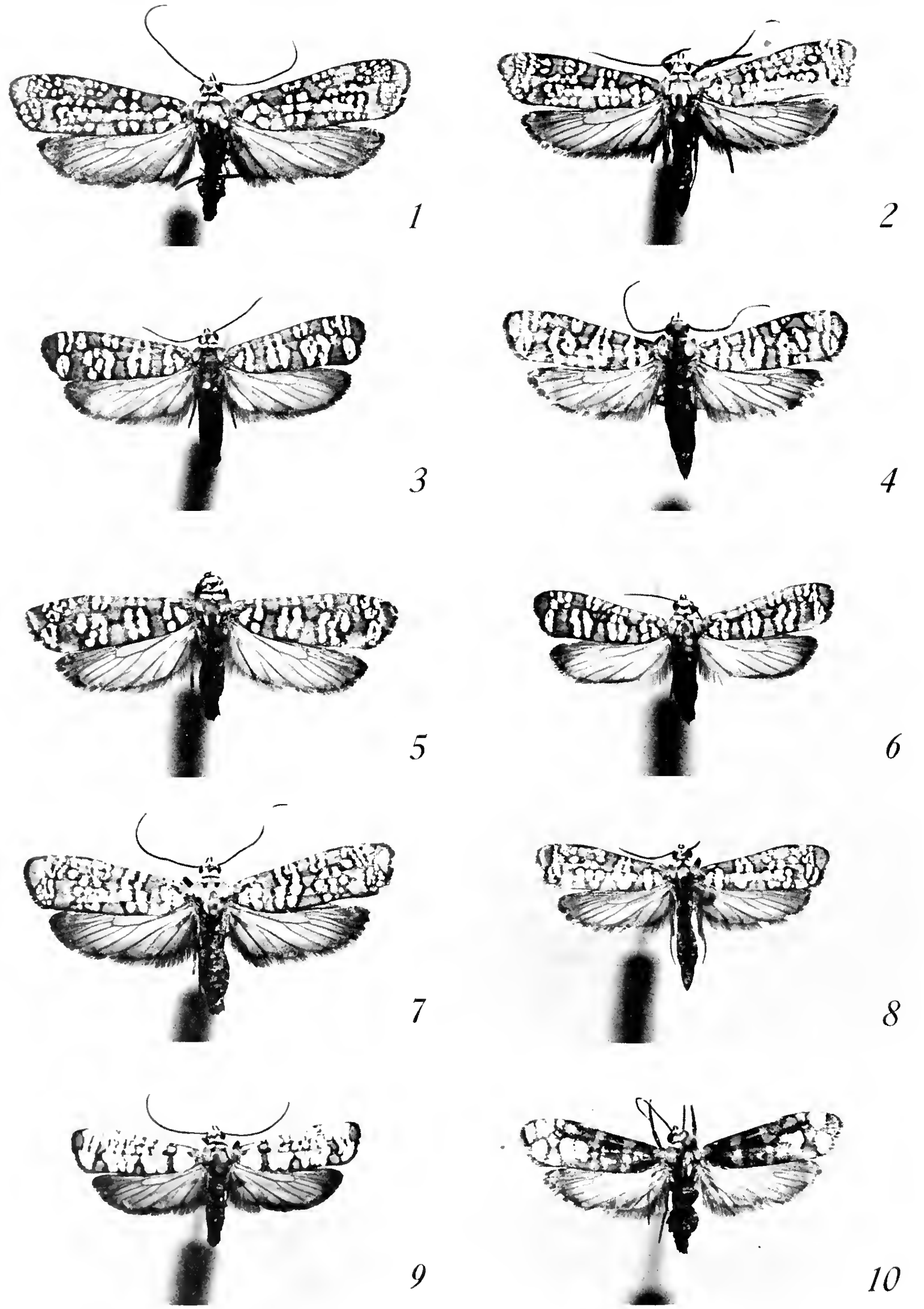


Figures 1-10. Adults of *Atteva*: 1, *punctella* female, 5 mi. W. Cave City, Ky. VIII-3/4-71 (J. Powell) 2, *punctella* male, Alexandria, Va. IX-17-70 (J. Powell). 3, *exquisita* female, 3 mi. E. Galeana, N.L., Mex. VIII-7/9-63 (Duckworth & Davis). 4, *exquisita* male, 7 mi. SE. Coyote Wells, Calif. VI-25-66, r. f. *Holacantha emoryi* (J. Powell No. 66F13) 5, *exquisita* female, Isla San Francisco, Golfo de California, Mex. IV-17-62 (Harbison). 6, *exquisita* female, 21 mi. W La Paz, Baja, Calif., Mex. VII-9-66 (J. A. Chemsak). 7, 8, *punctella* × *exquisita* (putative blend zone population) female and male, 20 mi. S. Sabinas Hidalgo, N.L., Mex. VII-7-66 (Buckett & Gardner). 9, aberrant female same data. 10, *exquisita* aberrant female, same data as fig. 4.

PHENOTYPIC VARIATION

Atteva exquisita differs from *A. punctella*, a widespread Neotropical species originally described from Surinam, and other similar described species (Walsingham, 1914) by having the yellow transverse bands of the orange forewing paler and relatively unbroken by dark lines. In particular, the submedian band is composed of about 4 to 7 separate pale spots in *punctella* and 2 to 4 in *exquisita;* the postmedian band is a granulated-appearing patch of 12 to 16 more or less distinct spots in *punctella,* whereas in *exquisita* these spots are partially confluent, numbering about 6 to 8 (Figs. 1-6). Although both *punctella* and *exquisita* are variable in details of forewing markings, neither varies to an extent that field collected series of one include individuals with the wing pattern characteristic of the other.

To what degree these differences reflect different environmental effects acting directly on individuals rather than expression of genetic characteristics of the populations is unknown. O. R. Taylor (in litt.) has shown extreme variability in laboratory stocks and believes there are many temperature labile genes in *punctella.* Color features, including the quality of orange, amount of melanic reticulation on the transverse yellow areas of the forewing, and paleness of the yellow vary with temperature. Taylor stated, for example, that the melanic reticulations all but disappear in the two proximal bands at high temperatures. The existence of reduced melanic lines in *exquisita* in widespread desert areas would seem to corroborate this correlation, although this feature may be genetically fixed. In addition, frequent occurrence of striking aberrations (Figs. 9, 10) both in the field and in moths reared from field collected larvae suggests caution should be exercised in forming conclusions about genetic relationships reflected by the various phenotypic expressions.

California *exquisita* adults vary in color, both in the quality of the orange and in the markings, which range from whitish to yellowish. The individuals that exhibit the palest markings, and therefore approach most closely the type of *exquisita*, are those reared in January. Those emerging in both spring and fall have pale yellow transverse bands, indistinguishable from field collected specimens from various localities, including northern Mexico.

During this study no morphological differences could be discovered among several collections of *Atteva punctella* from southern Mexico and the eastern United States. This supports the opinion that *aurea* (Fitch, 1857) is a synonym of *punctella*, as was indicated by Zeller (1871), Walsingham (1897), and Forbes (1923). Evidently the persistent use of the name *aurea* for Nearctic populations of this species by textbooks and most lepidopterists is due to their reliance on Holland's *Moth Book* and McDunnough's *Check List.* We concur with Taylor (1967) in treating *aurea* as a synonym.

The separation of *exquisita* as a species is also suspect, because it is an allopatric counterpart in western arid regions and is also very similar in morphological details (including genitalia). Probably *exquisita* should be treated as a subspecies of *punctella* pending investigation of the nature of the color differences.

GEOGRAPHICAL DISTRIBUTION

Atteva exquisita is widespread in desert and thorn forest areas of northern Mexico and southwestern United States (Appendix; Fig. 11). In addition to the type locality, this species has been taken in Nuevo Leon in Northeastern Mexico, while westward, it has been collected in the plateau region in southern Chihuahua, and at a number of stations in southern Baja California and along the Gulf of California. It ranges thence northward into southern California and Arizona.

Available information indicates that *exquisita*, like related species, is restricted to Simarubaceae for larval foodplants. The species is more widespread than any genus of Simarubaceae in this part of the continent (Standley, 1923), but a complex of essentially allopatric members of the family comprise a distributional pattern corresponding to that of *exquisita.* Thus the host in Coahuila and Nuevo Leon presumably is *Castela (C.) texana* (Torrey and Gray), while *Alvaradoa amorphoides* Liebm. is available in southern Chihuahua; the moths have been associated with *Castela (C.) peninsularis* Rose in southern Baja California, with *Castela (Eremacantha) polyandra* Moran and Felger (1968) in the cen-

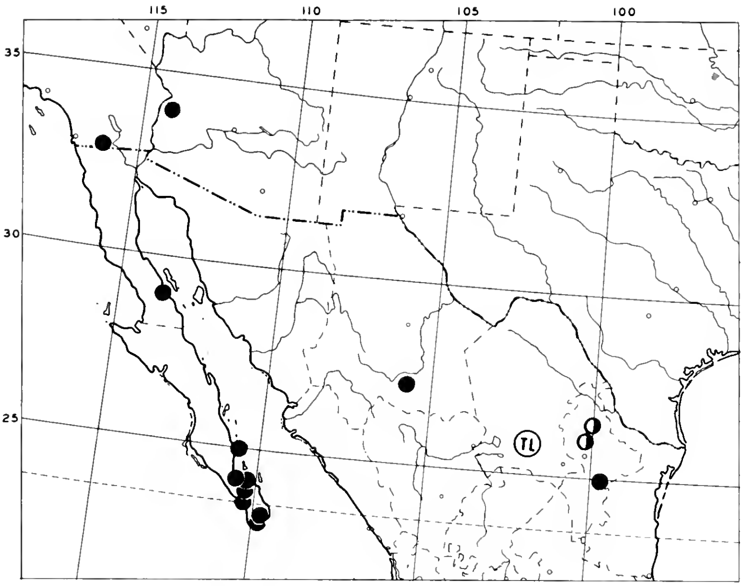


Figure 11. Geographical distribution of *Atteva exquisita* Busck, according to material cited in the Appendix. Half-closed circles indicating localities where the phenotype of samples suggests a possible blend zone with *A. punctella* to the north. The type locality (TL) of *A. exquisita*, Mobano, Coahuila, is indicated, but this place has not been located on maps we examined.

tral Gulf of California region, and with *Castela (Holacantha) emoryi* in southern California. This last plant presumably also serves as the foodplant in Arizona.

The most commonly encountered and best known species of American *Atteva, punctella (= aurea),* is widespread in the eastern United States. The species is assumed to be adventitious from some Neotropical area because its host plant, *Ailanthus altissima* (Mill.) (Simarubaceae) is an introduced ornamental tree from Asia. The plant was brought to North America by way of Europe about 1784 (Davies, 1941), and it adapted and voluntarily spread so that by the middle of the nineteenth century, when the *Atteva* was first formally noticed, it was widespread in the eastern United States.

Atteva aurea was described by Fitch (1857), who received specimens from a correspondent in Savannah, Georgia. Clemens (1861) redescribed the moth (as *compta*) based on specimens from Texas. The species was found to be common on *Ailanthus* in Missouri by Riley (1869), and general statements in the literature listed *A. punctella* (as *aurea*) from the Gulf States and thence southwestward. No reports of its presence in the Washington, D.C.—Pennsylvania areas were made by Clemens, Riley, or other early entomologists of the region. Later, occurrence of the species was recorded at Raleigh, North Carolina (Brimley, 1909), at Philadelphia, Pa. (Ilg, 1911), and at Baltimore, Maryland, and in Illinois (Gibson, 1920). The distribution was summarized as New York to Illinois and southward by Forbes (1923). Thus the fragmentary record suggests that the extension to approximately 42° N latitude was the result of spread during the half century between 1870 and 1920. The range may not have expanded much subsequently, but Taylor (in litt.) has seen specimens from Minnesota (St. Paul) and southeastern South Dakota (Yankton). We have specimens from northern Wisconsin (Lake Katherine, Oneida County, H. M. Bower) collected in 1961, which represent the northern record we have seen, about 46° N.

Although *Ailanthus* is the only host over most of eastern North America, in southern regions three native species of Simarubaceae are available (Small, 1903). In southern Texas *Castela texana* (Torrey and Gray) is native, while in Florida both *Picrannia pentantra* Sw. and *Simarubra glauca* DC. may serve as hosts. The latter is used by a related species, *Atteva floridana* Neumoegen, but is not known to be a host plant of *punctella* (Dyar, 1897; Kimball, 1965).

Thus it seems likely that *punctella* was not introduced into the United States by man but merely represents a northern component of populations that were native in the West Indies, or Florida and (or) southern Texas. A spread northward, as *Ailanthus* became sufficiently abundant to support populations, presumably occurred from the nearest geographical areas in which the species lived.

As noted, the close similarity and allopatry of *punctella* and *exquisita* suggest that they are geographical components of a single species. The blend zone between the two, or possible sympatric occurrence, is to be expected in southern Texas or areas of Mexico near the Rio Grande. Material for study from this region has been limited. A series from the vicinity of Galeana in southern Nuevo Leon shows a phenotype similar to the type of *exquisita* in reduction of dark lines in the forewing pattern. However, a single, worn specimen from Vallecillo, and a good series from 20 miles south of Sabinas Hidalgo in northern Nuevo Leon are less similar. The submedian band is relatively unbroken, as in *exquisita,* while the postmedian band has more extensive dark lines, differentiating about 9 to 13 pale spots, an intermediate condition between *exquisita* and *punctella* (Figs. 7, 8). These specimens lend credence to the supposition that the populations here treated as *exquisita* represent a western, arid country subspecies of *punctella.*

BIOLOGY AND BEHAVIOR

Observations were made on plant associations of the moths at the Imperial County, California, site and in two areas of Baja California, on Isla San Francisco in the Gulf of California, and in the vicinity of La Paz. Behavior of the adults was studied in the laboratory, using reared moths from Coyote Wells and employing glass jar breeding cages with a screen ceiling of nylon (Powell, 1964) or a portable type consisting primarily of a plastic cylinder 17 x 30cm. Larval and pupal habits in the field were recorded only at the Imperial County locality.

Adult.—During the daytime adults of both sexes were found on the host plant, as well as at flowers of other plants. Diurnal visitation of various flowers has also been recorded for *Atteva punctella* (Brimley, 1909; Ilg, 1911; Riley, 1869). At Isla San Francisco *A. exquisita* was taken in association with *Castela peninsularis,* a presumed foodplant; at Coyote Wells a few were found on the larval webs and flowers of *Castela emoryi;* while in the La Paz area adults were visiting flowers of *Wislizenia refracta* Englem. (Capparidaceae) and two unidentified shrubs. The moths were observed at midday but were not witnessed flying. Several individuals were taken at light. The species was attracted in numbers to fluorescent blacklight at two localities in Nuevo Leon. *Atteva punctella* is also commonly collected at lights.

Under laboratory conditions, several groups of adults (totaling about 80 individuals) were caged during a sequence of nine weeks in the summer of 1966 and in January, 1967. Cages were stored in one of three conditions: a) at outdoor temperatures (which in inland Contra Costa County, California, are lower, especially the nightly minima, than would be expected at the Coyote Wells site); b) at variable room temperature (15-20 C.); and c) in a temperature controlled laboratory at 20 ±1 C. *Atteva exquisita* proved to be a hardy moth, relative to many Microlepidoptera, and successful mating and oviposition were obtained in all three situations. Individual moths lived 4 to 36 days and averaged about 15 days. Mating and oviposition took place primarily during the first few days after caging and neither occurred after the tenth day. Females survived in dry vials up to four days, but the moths were observed to take water readily, even during midday, especially after periods when none had been available.

The moths appear to be primarily crepuscular in activity, but some phases of behavior, notably mating, apparently consistently occur at other times in the diel rhythm. Under natural lighting conditions the period of greatest activity of caged adults was about 1730 to 2000 PST, from about 1.5 hours before sunset to 1 hour or more after sunset. Possibly temperature was a critical factor in masking normal activity periods, since evenings were cool, usually below 15 C. by nightfall or shortly afterwards. During the late afternoon and dusk period, most individuals actively crawled about the screen ceiling of the cage and occasionally flew. At other times of day only occasional moths moved; a reaction to the observer appeared to be a factor. Artificial, overhead lighting affected diurnal activity of *exquisita.*

Individuals exposed to this light condition (in a temperature controlled laboratory) sporadically moved about without apparent external stimulus, but neither mating nor oviposition was observed under these circumstances. With the lights off, the same moths became less active during mid afternoon than they had been while exposed to artificial lighting.

Pronounced activity at the side of the cage towards lights was also noted at night. Therefore, nocturnal observations were made by means of a red-covered flashlight, which did not seem to affect the moths. In outdoor temperature conditions they became inactive by 2030 and 2130, with the temperature at 16 and 13 C. on different evenings, while once when the temperature remained at 19 C. at 2130, the moths were still slowly crawling. At 2300 with the temperature 13 C. there was no activity, even when a flashlight was directed onto the moths.

Mating by six pairs was observed, at least once in each of the three cage situations. Pairs copulated on the second to seventh day following emergence (average 4.8 days). Under controlled conditions of regular photoperiod and constant temperature (about 22 and 28 C.), Taylor (1967) found a long premating period also characteristic in *punctella*: isolated pairs of virgin moths usually did not mate until the third to sixth day after eclosion. In each case our *exquisita* pair was witnessed at the onset of morning observations, usually at 0700, but once at 0510 (after daybreak), and the moths remained apparently inactive, *in copulo* during the morning hours. Separation usually occurred between 1000 and 1100. In once instance the pair was first observed at 1054, and they separated at 1148. In at least three examples the moths were known to have been not *in copulo* late the previous evening, after apparent activity had ceased. Mating did not take place during the crepuscular height of individual movement, and no copulation was observed in the field.

Taylor (1967) found that *punctella* males' responsiveness and mating occurred chiefly during the first 30 minutes of the light period. Evidently a similar diel rhythm obtains in the mating behavior of *exquisita*.

Oviposition by *exquisita* took place in late afternoon. Females engaged in a characteristic behavior pattern, walking slowly, with the abdomen extended and curved ventrad. The extended ovipositor could be seen to press against the twig or protrude through the nylon mesh of the cage ceiling. Oviposition was a slow process, often requiring two to three minutes at one egg site, and no female was observed to deposit a second egg without moving. Our observations corroborate those of Taylor (1967) on *punctella* in a controlled environment. He reported that oviposition generally began 1 to 3 hours before the end of the light period and continued into the dark period.

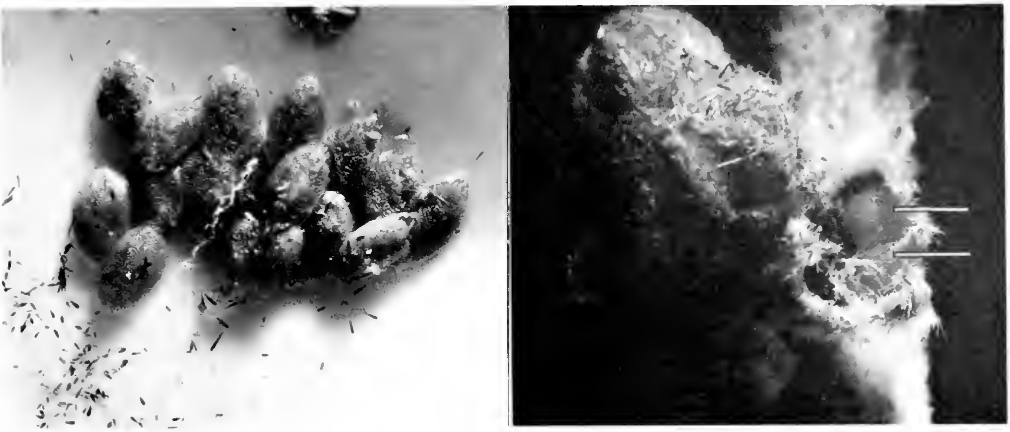
Females of *exquisita* consistently selected fibrous or pitted surfaces for egg laying. Counts were not made of the various substrates used for oviposition in the cages, but nearly all eggs were deposited on the screen, on the foodplant, especially in partially eaten flowers (Figs. 12, 13), or on the cotton used to hold the foodplant bouquet. A few were placed on the rough wooden floor of the cylinder cage. None were laid on the smooth walls of the breeding cages, where the moths spent most of their time crawling.

Ilg (1911) stated that eggs of *Atteva punctella* (= *aurea*) were distributed through the communal web. We provided females with *Castela emoryi* which had been cleaned of nearly all the silk webbing. Selection of the cotton and nylon fibers for oviposition suggests that *A. exquisita* uses the larval webbing in the field.

Riley (1881) reported that the egg of *A. punctella* was sometimes laid on the web, but generally was attached to the side of the mid-rib of the new leaves of *Ailanthus*, where it caused a well defined swelling of the leaf vein. Riley attributed this to a toxic substance which he supposed was secreted during oviposition.

Egg.—Eggs of *exquisita* required 8 to 9 days for development at 20 ±1 C. Groups of eggs were stored in a refrigerator at 4 C five or six days (third to eighth day and about fifth to eleventh day) and their development took 15 to 16 days. Eggs stored in a dry refrigerator for several weeks did not survive.

Larva.—A tendency for larvae of various ages to live gregariously and occupy a common web is characteristic for *Atteva* (e.g., *punctella*, (Ilg, 1911) and *fabriciella* (Swed.) in India (Fletcher, 1920)). Larvae of *exquisita* produce copious amounts of silk, even in the early instars, and at the Coyote Wells site large inflorescences of the host plant were enmeshed in



Figures 12, 13. Eggs of *Atteva exquisita* Busck. 12, (left) eggs deposited on flat, plastic surface. 13, (right) eggs deposited in the laboratory in partially eaten *Holacantha* flowers.

fine webbing. Larvae of various sizes were present in the same web in June. Since *Castela emoryi* is essentially leafless, most of the feeding took place on the flowers and developing seed. Both male and female flowers of the dioecious plant were used, but in late June larvae were more abundant on the staminate inflorescences. Later in the season, after the flowers had dried, overwintering individuals were found only among the seed-bearing inflorescences, where they fed primarily on the seed covers. Moran and Felger (1968) found a similar situation with *Castela polyandra* in Baja California, where at each of their localities at flowering time, larvae of *exquisita* "festoon the flowering branches with spidery webs." They noted that larvae also ate the leaves and bark.

In the laboratory newly hatched larvae were able to establish and survive on 25 to 40 day old *Castela* stems with remnants of flowers eaten by preceding generation larvae. The bark was skeletonized and at times whole twigs were girdled. Similar feeding behavior was reported for *Atteva punctella* on *Ailanthus*, a leafy plant, by Riley (1869). Although the *Castela* branches were kept in water, they appeared dry by the time the first instar larvae began hatching during our study. When first and second instar larvae were placed in vials containing *Castela* twigs and fresh terminal leaflets of *Rhus typhina* (Anacardiaceae) from the University of California, Berkeley, campus, only the *Castela* was accepted. A small amount of feeding occurred on the *Rhus*, but no larvae successfully established on it. A few larvae survived to the penultimate instar on the dry, skeletonized *Castela* branches, but none reached maturity.

Other first instar larvae were offered only fresh leaflets of *Ailanthus altissima* from the University of California, Berkeley, Botanical Garden. Development on *Ailanthus* was only partially successful, with a small percentage of first instar establishment. Once established, growth occurred at about the same rate as in larvae feeding on *Castela* stems. The few surviving individuals on *Ailanthus* did not reach maturity, but rearing conditions other than the food may have been critical. Larvae died in the penultimate and antepenultimate instars, when 15 to 20 days old.

Larger larvae taken from *Castela* in May accepted *Ailanthus* foliage from San Diego and development proceeded successfully. However, penultimate and final instar larvae collected in December failed to accept seeds of *Ailanthus* from Contra Costa County even when these were sliced longitudinally, exposing the soft, inner tissue.

An attempt was made to determine the number of instars through head capsule measurements. However, data are inconclusive, owing to lack of material representing the intermediate instars. Probably five or six instars are normal, and it is likely that the number differs depending upon circumstances. Larvae subjected to adverse conditions, such as during winter, may undergo an additional moult. The largest head capsule measurements originate from larvae collected in October and December. There is considerable overlap in the size of the final two instars when individuals representing various seasons are considered

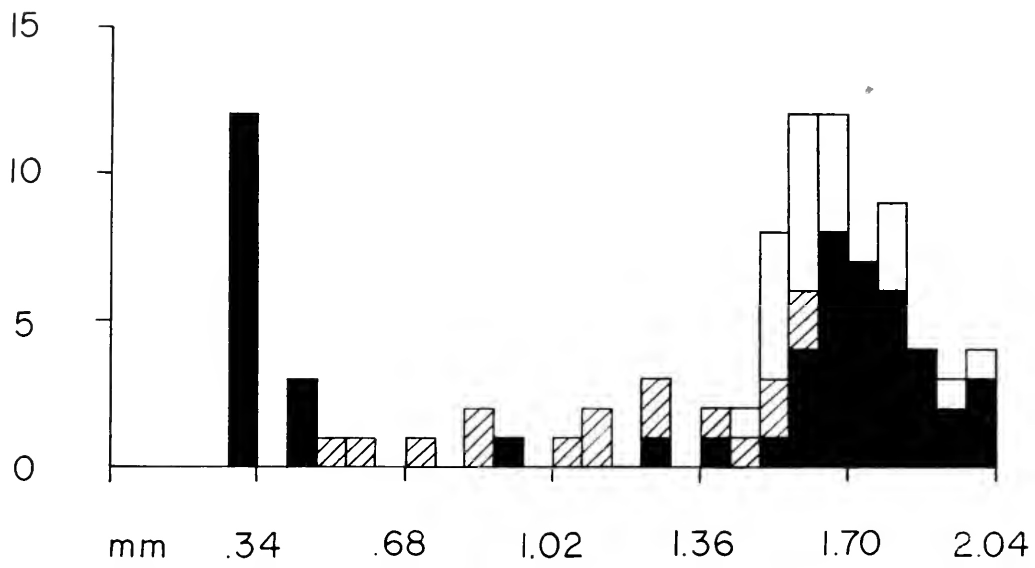


Figure 14. Distribution of measurements of head capsule width in larval *Atteva exquisita* Busck; based on samples taken in various seasons from one site near Coyote Wells, California. Filled squares indicate head capsules of preserved larvae; cross-hatched squares indicate head capsules shed by pre-final instar larvae; open squares indicate head capsule widths of final instar exuviae (estimated by conversion from measurements of frontal triangle).

together (Fig. 14).

Pupa.—At maturity larvae construct a frail silken network in which they suspend for pupation. In the field pupae were found within the inflorescence, particularly in lower portions of the webbing which the larval colony inhabited. The extremely thin cocoon appears to be a biological feature associated with a behavioral tendency to remain in the communal shelter, and a tendency to wander in the laboratory probably is abnormal. Cocoons also occur in the larval webs in *punctella* (Ilg, 1911) and *Atteva floridana* (Dyar, 1897).

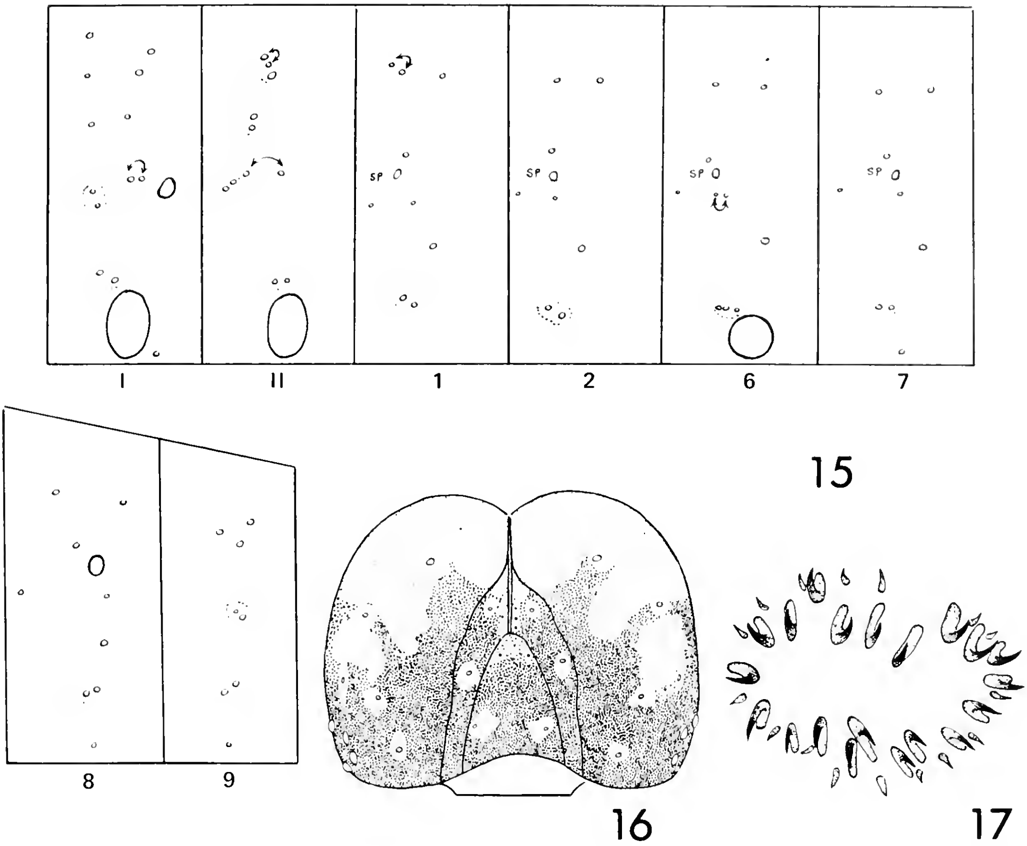
Construction of the cocoon, a quiescent prepupal period, and transformation to the pupa required about 48 hours. Cocoons spun in isolation from other larval webbing were so thin as to be almost invisible. They were rather flat, roughly oval, measuring about 25 × 35mm in outline, with an irregular interior network and a slightly heavier inner cocoon some 15mm in length in which the pupae was suspended, held about 2mm from the substrate.

Metamorphosis in the pupa required nine days at room temperatures (approximately 18 to 22 C. daily range).

LIFE HISTORY

There was no indication in the laboratory of either obligate or facultative diapause. Evidently there are at least two or three annual generations, with emergence of adults in late May or June, again in July, and probably at least once more in late summer. Probably extreme summer conditions reduce longevity of adults compared to that in confinement, but, even so, flight periods of generations overlap. By mid-June all stages were present at the Coyote Wells site, and well-defined generations probably are not exhibited from that time on through the season.

Our observations indicate a developmental period of about 40 to 50 days. Thus adults emerging in May could produce a third generation by late August or early September. Survey in October and in late December revealed only larger larvae. No adults, eggs, or pupae could be located. When brought into laboratory temperatures these larvae continued development, feeding on nearly dry seed covers, and produced adults within a month. Apparently individuals resulting from eggs deposited in fall begin feeding and enter a quiescent state, possibly growing slowly by feeding during warm spells in winter, and reach maturity by the time *Castela* blooms again in spring.



Figures 15-17. Structures of last instar larva of *Atteva exquisita* Busck. 15, setal arrangements on segments I and II of thorax, and 1, 2, 6, 7, 8, and 9 of abdomen; SP = spiracle, arrows indicate variable loci. 16, frontal view of head capsule, showing color pattern, black ventral, red-brown median, and orange dorsal. 17, crotchets of abdominal proleg.

Riley (1869) believed that adults of *Atteva punctella* overwintered, because he was unable to obtain oviposition from moths emerging in September and October. Taylor (in litt.) has no data indicating appreciable cold-hardiness in any stage of *punctella* and believes that the species does not overwinter in the northern part of its range.

DESCRIPTION OF EARLY STAGES

Egg[1].—Appearing whitish when first deposited, turning pale yellow within 48 hours and gradually deeper yellow prior to darkening of the embryo. Pliable when deposited and assuming variable shapes depending in part upon substrate; on flat surfaces, oval, flattened, somewhat produced towards micropylar end (Fig. 12), varying from about 1.05 × 0.60mm to 1.15 × 0.65mm; on fibrous and other irregular surfaces, usually somewhat thickened and less regular in outline (Fig. 13). Dorsal surface more or less regularly sculptured with round, shallow pits.

Riley (1881) mentioned the variable form of the eggs in *punctella* and indicated that one end frequently was produced into a "short neck." Riley gave the length as 0.9mm, and Peterson (1967), who published a photograph of eggs of *A. punctella* (= *aurea*), gave 0.9 × 0.5mm, slightly smaller than any observed in our study.

Larva[2].—First Instar: Head capsule, width 0.27 to 0.31mm; pale when teneral, becoming dark brown, slightly paler towards frontal triangle. Body, length about 2.3 mm when teneral, 3.0 to 3.4 mm when fully fed; integument unpigmented at first, becoming lightly mottled with reddish gray specks, without a distinct pattern. Thoracic shield scarcely discernible; anal shield unpigmented. Setae and pinacula minute and colorless; arrangement apparently very similar to that of final instar. Abdominal proleg crotchets, 6, in an irregular circle; anal proleg crotchets, 8 or 9.

Second Instar: Head capsule, width 0.41 to 0.58mm (possibly to 0.68mm), dark brown with well defined pale spots on front and crown, corresponding to, but proportionately larger than, those of last instar. Body, length about 3.4 to 4.1 mm; integument heavily mottled with brownish gray, tending to form dorsolateral bands which contrast with the relatively large, unpigmented DL pinacula. Thoracic shield brown, well defined. Setae relatively elongate, unpigmented, apparently arranged as in final instar. Abdominal proleg crotchets, 10 to 12, uniordinal, in a regular circle; anal proleg crotchets, about 14, irregularly biordinal.

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[1] Description based on specimens from La Paz area of Baja California; females collected in August, 1966.

[2] Based on specimens from the Coyote Wells site in California; distended in K.A.A.D.; first two instars from eggs deposited by females reared in July; late instars from larvae collected in May, June, and December.

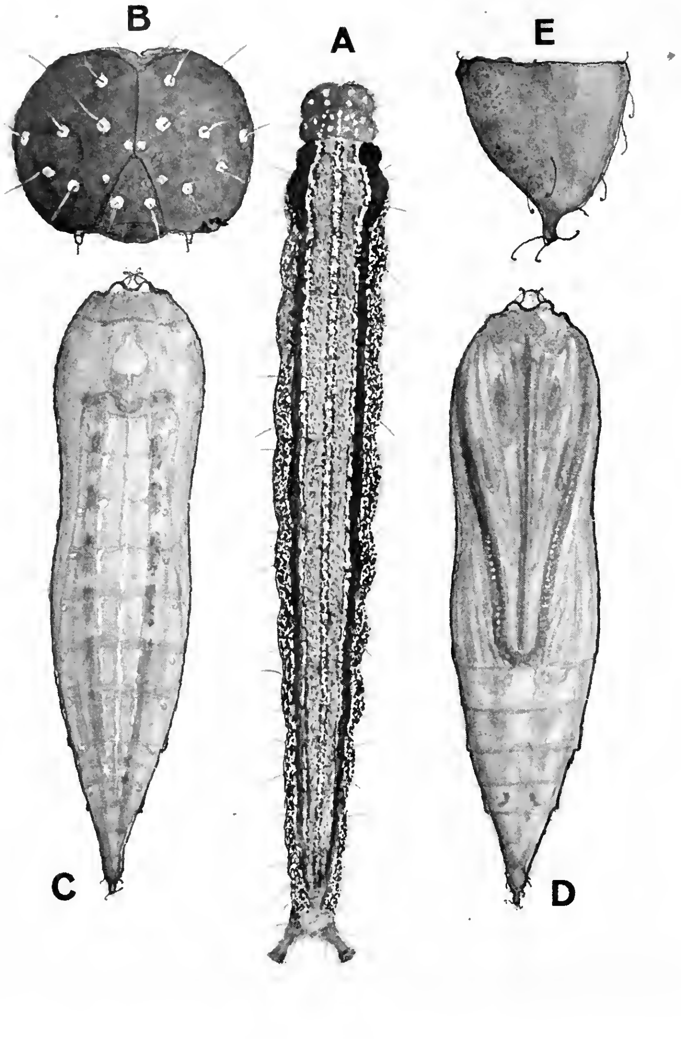

Figure 18. Larva and pupa of *Atteva exquisita* Busck. A, Penultimate instar, dorsal aspect. B, penultimate instar, head capsule, anterior aspect. C, pupa, dorsal aspect. D, pupa, ventral aspect. E, pupa, caudal area, showing cremaster structure.

Penultimate Instar: (Figs. 18A, B). Head capsule, width (possibly from 1.05 mm) 1.20 to 1.60 mm; nearly unicolorous, black, at times deep red-brown at crown; round unpigmented spots surrounding setal bases, appearing white on the living larva. Body, length about 11 to 19 mm; longitudinally striped with orange, black, and white, color pattern variable, consisting of small spots, blotches and irrorations; a broad dorsal band of orange or ochreous-orange (absent on prothorax), sprinkled with white and dark orange spots, enclosing a thin, mid-dorsal whitish line, margined by a fine, broken, black edging; an irregular dorsolateral band of black, subtended by a lateral band of blackish which is heavily sprinkled with white dots and irregular spots; a narrow spiracular band of orange running the length of abdomen, lacking on thorax, venter mottled, black and white. The relatively small prolegs banded yellowish and black. Setal arrangement not differing from final instar. Thoracic legs heavily sclerotized, black. Abdominal proleg crotchets, about 26 to 34, in an irregular biordinal to triordinal circle; anal proleg crotchets, about 24 to 28, more or less evenly biordinal.

FINAL INSTAR: Head capsule, width 1.43 to 2.00 mm; black below middle, red-brown to orange at crown, the pattern and extent of black-to-brown marking variable (Fig. 16), spots surrounding setal bases unpigmented, appearing white on the living larva. Body, length about 16 to 25 mm; color pattern variable, similar to penultimate instar, generally less black pigment, with corresponding brighter orange and paler dark bands. Spiracles on abdominal segments 1 to 7 very small, scarcely larger than base of DL seta. Setal arrangements as in Figure 15; pinaculi moderately strongly upraised, whitish; setae unpigmented, mostly elongate, L setae on abdominal segments very small. Abdominal proleg crotchets, about 36 to 40, an irregular arrangement of 18 to 20 large inside a peripheral circle of 18 to 19 small (Fig. 17); anal proleg crotchets, about 32 to 35, a marginal row of 14 to 16 small spurs followed posteriorly by irregularly scattered large crotchets.

Setal characteristics of *exquisita* do not differ appreciably from those given by Mathur (1960) in his excellent description of the larva of *fabriciella* (Swed.). This and the partial description of *punctella* given by Peterson (1956) indicate a close similarity in larvae of various species in this genus. The abdominal proleg crotchets apparently are more irregularly arranged in *fabriciella*, and the anal crotchets are more numerous (±43) in that species. Although variable in placement and number to some extent, the abdominal proleg crotchets are more numerous than those of the anal proleg in all instars of *exquisita*, whereas the reverse is true in *fabriciella* according to Mathur.

Pupa.–(Figs. 18C-E) Length about 12 mm; greatest width 3 mm. Subfusiform, head round anteriorly, cauda regularly tapering. Front and sides of head with a number of hooked anchor setae; front with two small, whitish nodules, each with two hooked setae. Antennae and maxillae reaching wing tips, darker than other appendages. General color light brown, with darker shading on several structures, as illustrated; wings with several veins darker than ground color. Dorsum with the longitudinal white lines of larva, considerably obscured; a black longitudinal line lateral to each white line, discontinuous on anterior portion of abdomen, unbroken on caudal segments. Cremaster (Fig. 18E) with numerous, fragile, hooked anchor setae, easily broken; apparently showing no regularity in placement.

Details of the pupal structure of *punctella* have been illustrated by Mosher (1916).

ACKNOWLEDGMENTS

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Photographs of the eggs were made by A. A. Blaker, Scientific Photographic Laboratory, University of California, Berkeley.

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APPENDIX

Data from specimens examined representing *Atteva exquisita* and populations of possible blend with *A. punctella*.

MEXICO

Baja California, Norte: Bahia de Los Angeles, VII-2-66, on *Castela polyandra* (R. P. Phillips).

Baja California, Territorio Sur: Isla San Francisco, Golfo de California, IV-17-62 (C. F. Harbison). 9 mi. SW La Paz, VIII-10-66, at fls. *Wislizenia refracta* (J. T. Doyen, J. Powell); VIII-14-66 (J. Powell). 21 mi. W La Paz, VIII-9-66, at fls. legume shrub (J. A. Chemsak). 26 mi. W. La Paz, VIII-10-66 (J. A. Chemsak). 7 mi. S San Pedro, VIII-10-66, at light (J. Powell). Todos Santos, VII-14-57 (D. Spencer, R., J. & A. Ryckman). 1 mi. SW Punta Palmilla, IX-14-67, at Bl. & white lights (J. A. Chemsak). 3 mi. N San Jose del Cabo, IX-10, 11-67 (J. A. Chemsak).

Chihuahua: 8 mi. NE Hidalgo del Parral, VII-13-64, at light (J. A. Chemsak, J. Powell).

Coahuila: Mobano (R. Muller). Vallecillo, VI-2-51 (P. D. Hurd).

Nuevo Leon: 20 mi. S Sabinas Hidalgo, VII-7-66 (J. S. Buckett, M. Gardner). 3 mi. E Galeana, VIII-7/9-63 (Duckworth & Davis).

UNITED STATES

Arizona: 24 mi. SE Parker, Yuma Co., IX-5-64 (J. Haddock).

California: Hiway 98, 7 airline mi. SE Coyote Wells, Imperial Co., V-22-66, reared from *Holacantha emoryi* (R. V. Moran); VI-11-66, reared from *H. emoryi* (C. E. & B. Norland); VI-25-66, on *H. emoryi* (J. Powell); reared from *H. emoryi*, emgd. VI-29 to VII-13-66 (J. Powell-66F13); XII-25-66, reared from *H. emoryi*, emgd. I-18, 19-67 (C. F. Harbison; JAP-67A6); X-5-67, reared from *H. emoryi*, emgd. X-11-67 (P. A. Opler, J. Powell, P. A. Rude; JAP-67K68).

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Powell: Department of Entomological Sciences, University of California, Berkeley 94720. Comstock: Deceased subsequent to the writing of the original draft. Harbison: Natural History Museum, San Diego, California 92112.

LIFE HISTORY OF THE WESTERN NORTH AMERICAN GOBY, *CORYPHOPTERUS NICHOLSII* (BEAN)

JAMES W. WILEY

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JAMES W. WILEY

ABSTRACT.–The life history of *Coryphopterus nicholsii* was investigated by field and laboratory studies based primarily on a population at Laguna Beach, California. The species occurs in depths of 6m to more than 60m on rock reefs, where it utilizes holes and undercuts in the rock for shelter. Crustaceans (amphipods and copepods) are the major food item; mollusks are also taken in significant numbers. Echinoderms, annelids, mollusks, bryozoans and various eggs are more important food items during fall and winter seasons. Pelagic prejuveniles feed only on copepods. In the study area the sex ratio is 1.7 females : 1 male. Juveniles were first observed on the reefs in February 1967. Length-frequencies and observed scale age groups show 4 to 5 age groups. *Paralabrax nebulifer* and *Lythrypnus dalli* prey on *C. nicholsii.* Sexual dimorphism occurs in the genital papilla, size, length of dorsal and anal fins, and nuptial color of pelvic fins. Breeding extended from mid-February to late August in 1967. Males became ripe at 55 mm, in age-group II and III. Females became ripe at about 47 mm, in age-group II. Ripe ovaries contain two egg groups: ripe and unripe. The total number of ripe eggs in 4 individuals ranged from 3274 to 4788. The spindle-shaped fertilized eggs are attached directly to the overhanging rock surface of the nest. The larvae are pelagic and prejuveniles have been taken far from shore. Juveniles as small as 21.8 mm were found on the reefs from February through August, 1967. The male prepares and guards the nest. In courtship the male rushes at the female and also rises off the bottom a few centimeters with the fins spread, before it settles back down. This species is territorial. A hierarchy is established in the laboratory aquarium.

The gobies constitute a widely divergent group of fishes, the suborder Gobioidei. They occur in the tropical, temperate, and subboreal zones throughout the world, avoiding only the polar regions. Most gobioids are marine, but some inhabit fresh water, including a few in torrential streams.

Gobies of the New World genus *Coryphopterus* are common in the inshore waters of both the tropical western Atlantic and eastern Pacific, inhabiting holes in shallow water coral reefs or rocks. Nine species have been described in the tropical and subtropical western Atlantic. Of the two eastern Pacific species, *C. urospilus* is tropical, but *C. nicholsii* (Bean), the subject of this paper, ranges widely from subtropical to subboreal waters.

STUDY AREA

An intensive field study of *Coryphopterus nicholsii* was conducted at Laguna Beach, Orange Co., California from September 1966 through January 1968. The study area consisted of two rock reefs: one a shallow, breaking reef which extends down to 10m is approximately 90m offshore; the other varies from 15 to 25m in depth, and is approximately 1200m from the shallow reef, and 800m offshore. Each is approximately 45m long, and is surrounded by sand bottom.

METHODS AND MATERIALS EXAMINED

The population at Laguna was sampled at weekly or biweekly intervals with the use of SCUBA. Most specimens were collected with a slurp gun, although some were taken with "Chem-Fish." Other collections were made in California at Malibu and Palos Verdes, Los Angeles Co.; at Cameo Shores and Aliso Creek, Orange Co.; and at La Jolla, San Diego Co.; and in Baja California, Mexico, at Punta Banda (SW side).

Methods of counting serial parts and taking measurements follow those of Hubbs and Lagler (1958), except that the caudal ray counts follow the methodology of Ginsburg (1945). The last two ray bases of the dorsal and anal fins were counted as one ray. All measurements were taken with dial calipers to the nearest 0.1 mm. Proportions, obtained arithmetically, are presented as ranges and means. All measurements of body length are standard lengths (S.L.).

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Museum specimens examined were from the following collections: Stanford University (SU); California Academy of Sciences (CAS); Scripps Institution of Oceanography (SIO); University of California, Los Angeles (UCLA); Los Angeles County Museum of Natural History (LACM); and California State College, Long Beach (CSCLB).

BLUESPOT GOBY
Coryphopterus nicholsii (Bean)

Gobius nicholsii.—Bean, 1881: 469 (original description; type locality, Departure Bay, British Columbia; 20 fm.). Jordan and Evermann, 1898: 2218 (specimens recorded from coast of British Columbia). Halkett, 1913: 30, 95 (listed; coast of British Columbia). Fowler, 1923: 293,300 (Malibu Cove, Point Firmin, Newport, Catalina, Isthmus Harbor, Cataling Harbor, Avalon, Santa Cruz, and La Jolla, California). Clemens and Wilby, 1946: 168 (description of type).

Gobius nicholsi.—Jordan and Gilbert, 1882: 946 (coast of British Columbia; description). Jordan and Eigenmann, 1886: 489, 494, 516, 517 (coast of British Columbia; analysis; listed). Jordan, 1885: 893 (105) (listed). Eigenmann and Eigenmann, 1888: 59 (California; listed). Eigenmann and Eigenmann, 1892: 354 (San Diego, California). Eigenmann, 1892: 130, 159 (Point Loma, California). Jordan and Starks, 1895: 838 (Vancouver Island, British Columbia; listed). Jordan and Evermann, 1896: 456 (coast of British Columbia; listed). Gilbert and Starks, 1904: 176 (mentions *Gobius nicholsi* in comparing dermal fold of *Microgobius emblematicus*). Starks, 1911: 211 (listed; San Juan Islands, Washington). Bean and Weed, 1919: 79 (3 specimens – 33, 43, and 47 mm long; taken at Ucluelet, Vancouver Island, British Columbia, during low tide; June-July, 1909).

Gobius nicholsoni (sic).—Eigenmann, 1890: 66 (taken in deep water by the Albatross off Point Loma, California). Eigenmann, 1909: 65 (off Point Loma, California).

Rhinogobius nicholsii.—Starks and Morris, 1907: 223 (San Pedro, California). Starks and Mann, 1911: 16 (San Diego, California; 50 fm.).

Rhinogobius nicholsi.—Snyder, 1913: 459 (Pacific Grove, California; description; taken from 10-15 fm.). Gilbert, 1915: 359 (abundant in harbor at Avalon, Catalina Island; taken in shallow water at Monterey, California). Kincaid, 1919: 40 (San Juan Islands, Washington).

Rhinogobiops nicholsii.—Hubbs, 1926: 2 (type of genus; description; Santa Barbara Channel and southwest of Newport, California). Hubbs, 1928: 15 (listed). Ulrey and Greeley, 1928: 20 (Catalina Island, Huntington Beach, Malibu, Newport, Point Firmin, and Santa Cruz, California). Jordan, Evermann, and Clark, 1928: 440 (coast of British Columbia, south to southern California). Ulrey, 1929: 10 (listed). Wismer and Swanson, 1935: 343; Table 19 (San Juan Channel, Washington; depth 8-12m; estimate of numbers of *R. nicholsii* at 17 fish/2000m^2 on dredge and trawl catches). Schultz, 1936: 122, 191; fig. 16 (key; figure showing ventral side; British Columbia to southern California). Barnhart, 1936: 81; fig. 245 (description; San Clemente Island to British Columbia; sometimes taken in more than 2100 feet). Schultz and DeLacy, 1936: 137, 213 (British Columbia to southern California; Hood's Canal near Holly, Washington; marine; not rare; San Juan Island, Washington). Clemens and Wilby, 1946: 5, 29, 167-168; fig. 103 (key; listed; range, English and Nanoose bays, Barkley Sound at Ucluelet, Esperanza Inlet on west coast of Vancouver Island, Skidegate Channel, Queen Charlotte Islands; 20 fm. or more; description). Limbaugh, 1962: 552 (La Jolla, California; colonizing newly exposed reefs).

Coryphopterus nicholsii.—Ginsburg, 1938: 113 (no locality; differences from *Coryphopterus urospilus*). Ginsburg, 1945: 136, 137 (*C. nicholsii* used in study of fin-ray count methodology). McAllister, 1960: 38 (listed). Miller and Lea, 1972: 186 (figure; description; key; range – south of Point Rompiente, Baja California, to Skidegate Channel, Queen Charlotte Island, British Columbia; depth 5 to 80 feet).

Coryphopterus nicholsi.—Hubbs and Follett, 1953: 34 (listed). Limbaugh, 1955: 26, 35, 120 (southern California; observed in "sand-bottom holdfast biotope" and "kelp rock-bottom biotope"; preferred southern California habitat sand near rocks; 1-180 feet; description; observed at following localities – Pacific Grove, Yankee Point, Goleta, Point Dume, El Segundo, Rocky Cove, Newport Beach, San Clemente, and La Jolla; and at San Miguel, Santa Rosa, Santa Cruz, Anacapa, Santa Catalina, Los Coronados, and San Martín islands). Böhlke and Robins, 1960: 103, 105 (key; characteristics; discussion of genus). Ebert and Turner, 1962: 249-252 (ecology; breeding habits; behavior; description of eggs and embryos). Pequegnat, 1964: 272 (Corona del Mar, California; abundance on reef). Carlisle, Turner and Ebert, 1964: 15, 28, 73, 77 (listed; observed on artificial reefs and offshore oil installations, and in Santa Monica Bay, California; spawned on Redondo Beach, California artificial reef; listed – Seal Beach, Rincon, Summerland, Redondo Beach, and Paradise Cove, California). Best and Oliphant, 1965: 101 (listed; Point Arguello, California). Turner, Ebert and Given, 1965: 109, 112 (listed, San Elijo Lagoon, San Diego County, California). Berry and Perkins, 1966: 676 (distribution of pelagic prejuveniles). Turner, Ebert and Given, 1966a: 16, 17, 18, 19, 26-27, 29; tables 1-4 (abundance; distribution on benthic quadrats; listed as abundant; Point Loma, California). Turner, Ebert and Given, 1966b: 40, 47 (distribution around Orange Co., California sewer outfall pipeline; relative abundance of goby in vicinity of outfall). McCart, 1967: 433-434 (scale regeneration). Fitch, 1967: 4, 16; fig. 3 (lower Pleistocene otoliths). Fitch, 1968: 2, 21-22; fig. 2s (early Pleistocene otoliths). Turner, Ebert and Given, 1969: 185 (habits on southern California artificial reefs). Macdonald, 1972: 91 (cephalic-lateralis system). Quast, no date (a): 4, 6; table 1 (listed among species ranging from boreal into temperate waters; British Columbia through north temperate; 0-130 feet; listed as member of southern California rocky-inshore zone fauna).

Bohlke and Robins (1960) referred to this species as *Coryphopterus nicholsi.* Although it stands alone in the group, Bohlke and Robins accept it in *Coryphopterus.* They indicated that should *C. nicholsii* be treated as subgenerically distinct, the name *Rhinogobiops* Hubbs would apply.

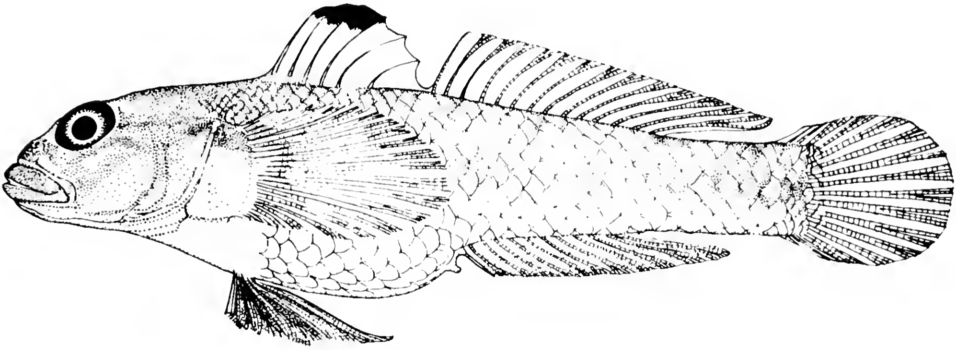

Figure 1. *Coryphopterus nicholsii.* Adult male, 86.5 mm in standard length, from Laguna Beach, Orange Co., California.

Diagnosis.–Coryphopterus nicholsii (Fig. 1) is easily distinguished from all other species of *Coryphopterus* by having more soft dorsal, anal, and pectoral rays, more scales, and in having a narrow wedge of scales reaching a point above the anterior margin of the opercle.

Description.–It has an elongate, moderately stout body. Greatest body depth 4.1-6.1 (5.17) in standard length. Body slightly compressed, width 5.7-10.6 (7.26) in standard length. Head moderate, wider than deep; head width 1.2-2.1 (1.50) in head length; head length 3.0-4.2 (3.56) in standard length. Cheeks not tumid. Mouth small and terminal. Lower jaw projecting. Maxilla not reaching to point below anterior margin of eye, 1.9-3.2 (2.58) in head length. Jaw teeth conical, in bands, enlarged in both an outer and inner row. Tongue truncate at tip. Eye directed superolaterally and large (diameter 2.5-4.3 (3.42) in head length). Bony interorbital very narrow. A high, thin and nearly vertical crest on top of head from behind eyes to origin of spinous dorsal fin. Rows of papillae on sides of head moderately developed. No barbels (Fig. 12). Slit behind fourth gill-arch reduced; pseudobranchiae exposed. Branchiostegals 5 (1 on epihyal). Pelvic fins fully united, free from belly, each with I, 4 rays. Pectoral fins with 21-24 (22.3) rays, none silky. Dorsal fins barely separated, VI-I, 12-15 (13.8). Caudal fin broadly rounded, 17: 12 segmented, branched rays and a variable number of segmented, unbranched rays and simple (procurrent) rays. Some specimens with 2 above and 1 below segmented, unbranched rays, plus 2 simple rays below occur about as frequently as those with 2 above and none below segmented, unbranched rays, plus 3 simple rays – 1 above, 2 below. Rarely the caudal elements composed of 12 branched, segmented rays with above and below 1 unbranched, segmented ray, plus 1 above and 2 below simple rays. Anal I, 11-14 (12.1). Body completely scaled except in predorsal midline. Head scaleless. Scales of sides each with a comb-like row of marginal spines, a submarginal focus, and basal radii. Scales in oblique rows, 23-28 (25.6) at midline. No lateral line. Shoulder girdle without papillae. Color: pale orange-olive or light yellow, with irregular vertical purplish brown streaks developed at time of death or in social interaction. Body irregularly flecked with metallic blue-green. Iridescent stripe below eye, giving rise to vernacular name – bluespot goby. Tip of first dorsal jet black. Pelvic fin of breeding male black.

OCCURRENCE

Coryphopterus nicholsii ranges from Point Rompiente (27°N), Baja California to Skidegate Channel (53°N), Queen Charlotte Island, British Columbia (Miller and Lea, 1972; McCart, 1967). It is common in this area and its range may be more extensive than is currently realized.

Otoliths of *C. nicholsii* have been found in many southern California Pliocene and Pleistocene deposits. More than 1,700 have been recovered from the Lomita marl (Pliocene) at San Pedro, and others have come from Timms Point silt, San Pedro sand (Lower Pleistocene) and Baldwin Hills, Los Angeles (Upper Pleistocene) (Fitch, 1967, 1968).

GENERAL ECOLOGY AND NATURAL HISTORY

Coryphopterus nicholsii inhabits shallow water, from 6m to more than 60m. After a pelagic oceanic existence as larvae and early juveniles, individuals assume a benthic habit. The preferred habitat appears to be a rock-reef area, but small groups of rocks on the open sand are also inhabited. The greatest concentrations occur near the periphery and in the channels of the reef, where the rock meets the surrounding sand bottom; in these areas there are numerous undercuts and holes, into which this goby can find safety. It is seldom found more than 25 cm from protective cover, but is common on the open sand or rubble bottom in front of its shelter. The open area around the hole serves as a feeding and display site.

Coryphopterus nicholsii is also found over the tops of reefs, particularly in areas having many holes, ledges, or thick gorgonian cover. Using the protective cover of the gorgonian canopy, individuals may venture more than a meter from their home shelter.

MORPHOMETRICS

The meristics of *C. nicholsii* from the sampled areas are rather uniform (Table 1). However, pectoral ray counts from British Columbia are lower than those from the southernmost locality (Isla San Martín).

Pelagic prejuveniles were sampled in southern California from San Pedro Basin, San Juan Seamount, and between Anacapa and Santa Cruz Islands. Variation in the pelagic prejuveniles was similar to that in the juvenile-adult sample with the exception of the first dorsal spines and scale counts. For the scales the explanation is one of delayed development. Variation in dorsal spines between the age groups may be the result of delayed development or perhaps some spines were overlooked.

Morphological data for three localities were considered in size groups in Table 2. Although adequate samples were not available from Baja California or British Columbia, no notable trend of morphological variation was evident. Differences in proportions were observed in fin ray lengths. As *C. nicholsii* exhibits sexual dimorphism of some body parts (particularly fins) morphological comparisons should be made on the basis of individual sex, but sample sizes were inadequate for such analyses.

FOOD HABITS

Food studies were conducted to identify the major foods, to determine if differences in seasonal utilization occurred, and to disclose any variation in the foods taken by fish of different sizes. Three methods of analysis were used: numerical, volumetric, and frequency-of-occurrence. Of the 106 stomachs examined, two were empty, and were not included in the calculations.

It appears that crustaceans are the principal food item of *C. nicholsii* (Fig. 2); they were found in nearly all stomachs examined, generally in the greatest numbers, and formed the bulk of the volume. Numerically crustaceans comprised 90.9% of the food items; mollusks (4.8%) were second. Other food items, such as annelids, echinoderms, etc., were usually found in small numbers.

By volume crustaceans made up 79.0% of the diet; mollusks again were second (4.6%). Other foods composed a small portion of the diet.

Crustaceans occurred in 97.0% of the stomachs analyzed (Fig. 2). Although found in small quantities numerically and volumetrically, mollusks occurred in 63% of stomachs examined. Bryozoans, which accounted for only 0.4% of total food volume, were found in 37% of stomachs examined. As this goby was not observed to selectively bite off pieces of bryozoans on the reefs it is possible that these organisms were picked up incidentally along with the preferred bottom-dwelling food items. Bryozoans are relatively indigestible and are probably retained in the gut for some time, which may account for their apparent abundance.

Table 1. Meristic variation in juveniles to adults and in pelagic prejuveniles of *Coryphopterus nicholsii*

Locality	First dorsal spines			Second dorsal rays (total)				Anal rays (total)				Pectoral rays (each side)				Scales along midline							
juveniles to adults	4	5	6	12	13	14	15	11	12	13	14	21	22	23	24	21	22	23	24	25	26	27	28
Baja California, Mexico																							
Isla San Martín.			3		2	2			2	2				4	4					2	2		
Punta Colnett			1			1			1			1	1								1		
Punta Banda (SW).			41		9	21	11		32	6	2		35	41	4				4	13	13	15	1
Islas Los Coronados.			3		1	2			3				1	3	2					1	3	1	1
Southern California																							
Laguna Beach			196		41	144	15	7	166	24	1	15	171	175	31			5	7	80	88	33	5
Santa Catalina Island		1	24		8	16			21	2			45	27	4				5	13	10	1	
Santa Rosa Island			46	1	15	30			42	4			21	43	26				6	25	28	12	
San Nicholas Island			8		2	7			7	2			2	11	3					4	8		
British Columbia																							
Hunt Island			20		14	6		4	13	3		4	32	4					7	8	17	4	
Southern California (totals)																							
Pelagic prejuveniles[1]	1	4	19	1	5	17		1	19	4		7	13	16	2	3	1	3	2	6	2	5	
Juveniles to adults		1	274	1	66	197	15	7	236	32	1	15	239	256	64			5	18	122	134	46	5

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[1] Pelagic prejuveniles from San Pedro Basin, San Juan Seamount, and between Anacapa and Santa Cruz islands, all off southern California.

Table 2. Comparison of morphometrics among populations of *Coryphopterus nicholsii*

		Punta Banda, Baja California			Laguna Beach, California			Hunt Island, British Columbia		
Proportions	S.L.	N	Range	Mean	N	Range	Mean	N	Range	Mean
$\frac{\text{standard length}}{\text{head length}}$	22-39mm	11	3.0-3.4	(3.30)	39	3.0-3.6	(3.30)			
	40-55	17	3.1-3.8	(3.39)	56	3.1-3.7	(3.40)			
	56-75	18	3.2-4.0	(3.60)	86	3.3-3.9	(3.46)	9	3.6-3.9	(3.75)
	76-92				26	3.3-4.2	(3.65)	17	3.3-4.0	(3.76)
$\frac{\text{standard length}}{\text{body width}}$	22-39mm	11	5.7-8.4	(7.46)	37	7.0-10.6	(8.48)			
	40-55	9	6.7-7.8	(7.33)	45	6.1-8.7	(7.25)			
	56-75	17	6.6-8.1	(7.35)	51	5.9-8.5	(6.60)			
	76-92				28	5.9-8.8	(7.28)			
$\frac{\text{standard length}}{\text{length base 1st dorsal}}$	22-39mm	11	5.7-6.4	(6.17)	39	5.3-7.2	(6.28)			
	40-55	14	4.7-5.8	(5.30)	51	4.9-7.1	(5.67)			
	56-75	18	5.1-6.1	(5.59)	75	4.9-6.2	(5.41)	10	5.0-6.0	(5.50)
	76-92				23	4.6-6.1	(5.20)	17	4.8-6.1	(5.25)
$\frac{\text{standard length}}{\text{length base 2nd dorsal}}$	22-39mm	11	3.4-4.0	(3.80)	39	3.4-4.1	(3.82)			
	40-55	15	3.4-3.8	(3.58)	54	3.0-3.8	(3.56)			
	56-75	18	3.4-4.2	(3.74)	76	3.3-3.9	(3.51)	10	3.5-3.8	(3.64)
	76-92				23	3.2-4.0	(3.54)	17	3.3-4.2	(3.67)
$\frac{\text{standard length}}{\text{length base anal}}$	22-39mm	11	3.9-4.9	(4.69)	38	3.4-4.8	(4.78)			
	40-55	13	4.3-4.9	(4.54)	49	3.9-5.1	(4.61)			
	56-75	18	4.4-4.8	(4.56)	79	4.1-5.0	(4.69)	10	4.4-4.8	(4.56)
	76-92				24	4.0-4.9	(4.52)	17	4.2-5.0	(4.54)
$\frac{\text{standard length}}{\text{length of longest pectoral ray}}$	22-39mm	11	3.0-3.6	(3.40)	38	3.1-3.9	(3.51)			
	40-55	16	3.3-3.9	(3.46)	52	3.1-4.3	(3.60)			
	56-75	18	3.1-4.0	(3.51)	70	3.1-4.0	(3.69)	3	3.1-3.2	(3.17)
	76-92				21	3.2-3.9	(3.55)	17	2.8-3.5	(3.22)
$\frac{\text{standard length}}{\text{length of longest 2nd dorsal ray}}$	22-39mm	11	2.4-2.8	(2.53)	28	2.4-2.5	(2.45)			
	40-55	16	3.2-3.7	(2.74)	11	2.1-2.5	(2.32)			
	56-75	18	2.0-2.2	(2.15)	34	1.9-2.4	(2.23)	3	2.0-2.1	(2.03)
	76-92				18	1.9-2.3	(2.10)	17	1.7-2.0	(1.89)
$\frac{\text{standard length}}{\text{body depth}}$	22-39mm	11	4.4-5.4	(4.97)	39	4.5-5.9	(5.18)			
	40-55	16	4.5-5.5	(4.98)	50	4.4-5.9	(5.35)			
	56-75	18	4.6-5.6	(5.00)	73	4.1-6.1	(5.05)	3	4.9-5.3	(5.10)
	76-92				23	4.5-6.1	(5.27)	17	4.8-5.9	(5.39)
$\frac{\text{standard length}}{\text{length of longest pelvic ray}}$	22-39mm	11	4.0-4.4	(4.21)	39	4.1-4.7	(4.40)			
	40-55	3	4.3-4.5	(4.37)	11	4.1-5.1	(4.48)			
	56-75	4	3.9-4.6	(4.38)	28	3.5-5.1	(4.55)	3	4.2-4.8	(4.44)
	76-92				19	4.3-4.8	(4.66)	17	3.9-4.5	(4.25)
$\frac{\text{standard length}}{\text{length of longest anal ray}}$	22-39mm	3	2.8-3.4	(3.03)	35	2.9-3.0	(2.97)			
	40-55	3	2.6-2.8	(2.74)	12	2.7-3.4	(2.89)			
	56-75	4	2.6-2.8	(2.75)	28	2.4-3.0	(2.74)	3	2.5-2.7	(2.56)
	76-92				17	2.3-2.9	(2.56)	16	2.1-2.7	(2.18)
$\frac{\text{head length}}{\text{length upper jaw}}$	22-39mm	4	2.5-3.2	(2.65)	35	2.4-3.2	(2.82)			
	40-55	16	2.3-3.1	(2.66)	56	2.3-3.2	(2.86)			
	56-75	7	2.4-2.9	(2.64)	77	2.1-3.2	(2.55)	3	1.9-2.8	(2.40)
	76-92				22	2.2-2.7	(2.44)	16	2.3-2.7	(2.45)
$\frac{\text{head length}}{\text{head width}}$	22-39mm	4	1.6-1.7	(1.62)	36	1.5-2.1	(1.75)			
	40-55	16	1.3-1.7	(1.49)	59	1.4-1.8	(1.51)			
	56-75	7	1.3-1.5	(1.43)	77	1.2-1.8	(1.42)	3	1.4-1.5	(1.43)
	76-92				24	1.2-1.6	(1.37)	17	1.3-1.7	(1.54)
$\frac{\text{head length}}{\text{snout length}}$	22-39mm	4	3.5-4.9	(4.06)	36	3.3-4.5	(3.84)			
	40-55	15	3.2-4.0	(3.51)	56	3.2-3.9	(3.42)			
	56-75	7	3.1-3.9	(3.34)	78	2.9-4.0	(3.57)	3	2.9-4.5	(3.63)
	76-92				22	3.1-4.0	(3.45)	17	3.5-4.4	(3.99)
$\frac{\text{head length}}{\text{length of eye}}$	22-39mm	4	3.2-4.3	(3.52)	35	3.1-3.8	(3.30)			
	40-55	15	2.9-3.8	(3.04)	54	2.9-3.9	(3.36)			
	56-75	7	3.1-3.9	(3.46)	78	2.9-4.2	(3.52)	3	2.5-3.3	(2.97)
	76-92				24	3.3-4.0	(3.61)	17	3.1-3.6	(3.45)

Echinoderms (mainly sea urchin spines and tests) were also found in relatively high frequency (26%), probably for the reasons discussed for bryozoans. The nutritional importance of bryozoans and echinoderms is seemingly small.

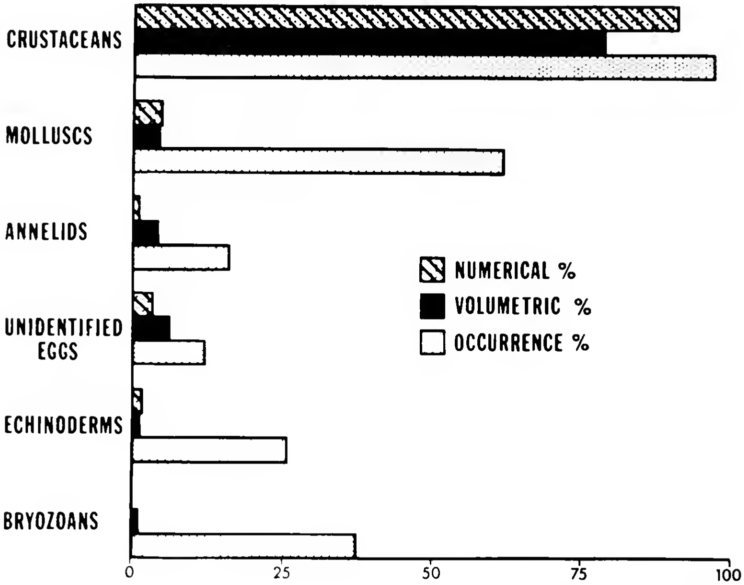

Figure 2. Analysis of 106 stomach contents of *Coryphopterus nicholsii* taken at Laguna Beach, California, from October 1966 to September 1967.

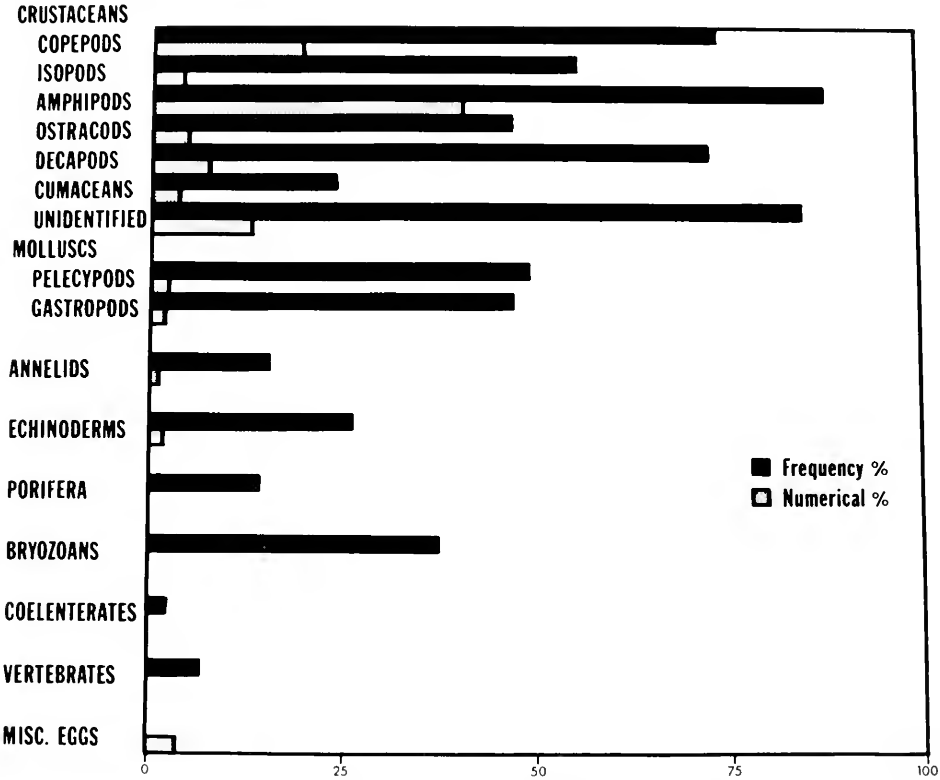

Figure 3. Further analysis of the stomach contents of *Coryphopterus nicholsii* expressed as numerical and frequency-of-occurrence percentages.

Measurements and counts from the mollusks were taken with the shell intact. However, for accurate evaluation, only the digestible parts should be considered. This was not possible, because of the small size of the food items. Because mollusk shells are relatively undigestible, and they may be retained in the stomach, data for this element are probably biased. Some shells may have been picked up incidentally along with the substrate as the goby grabbed for a desired bottom-dwelling organism. Empty gastropod shells could also be the shelter of hermit crabs, an important part of the decapod element of the diet. The crabs are presumably digested rapidly, whereas the shells may accumulate in the gut. These emptied hermit crab shelters would then be categorized as a mollusk element even though the food item selected by the goby was a crustacean.

Amphipods (39.9% numerically) and copepods (19.6% numerically) were the most abundant crustaceans taken by *C. nicholsii* (Fig. 3). One stomach contained 256 amphipods. Isopods (3.6%) and decapods (6.8%) also made up an important part of the diet.

Amphipods were found in 88% of the stomachs examined. Copepods (74%), decapods (73%) and isopods (55%) were also found in most stomachs (Fig. 3). Although pelecypods and gastropods composed only 2.5% and 2.3% of the total number of food items respectively, pelecypods were found in 49% and gastropods in 47% of all stomachs examined (Fig. 3).

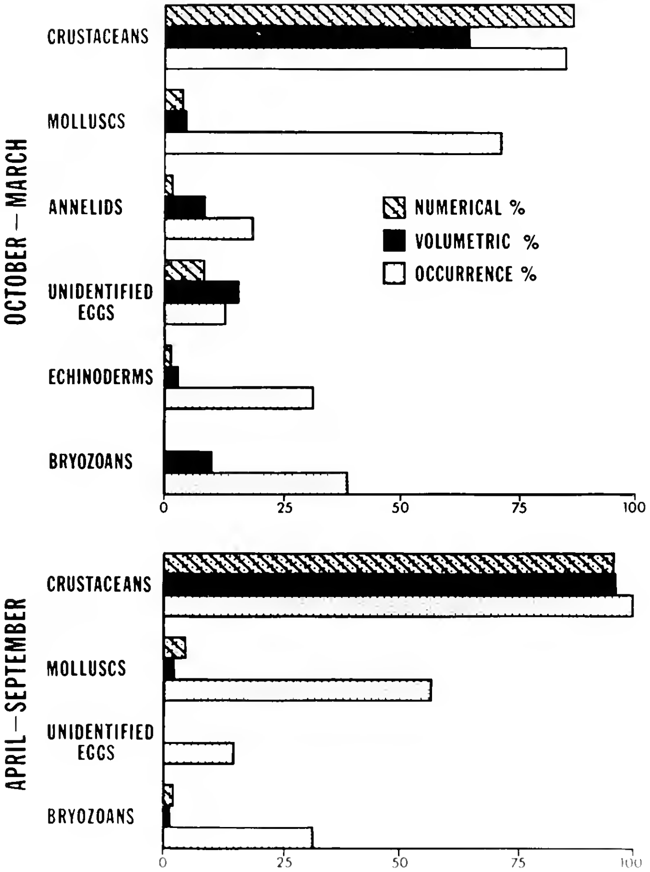

Figure 4. Seasonal analysis of the stomach contents of *Coryphopterus nicholsii.*

Coryphopterus nicholsii exhibited seasonal variation in food utilization (Fig. 4). Crustaceans were the major food item in both the October-March sample (numerical: 87.7%; volumetric: 66.0%) and the April-September sample (numerical: 94.0%; volumetric: 95.5%). Mollusks apparently became more important in October-March (numerical: 4.5%; volumetric: 4.6%) as compared to April-September (numerical: 5.3%; volumetric: 1.5%). The other food classes, e.g., echinoderms, annelids, etc., also became more important during the Fall and Winter.

The frequency analysis also showed a similar pattern of seasonal food use (Fig. 4). Crustaceans were found in 86% of the October-March stomachs and 98% of the April-September stomachs. Mollusks were found in 70% of the October-March samples, but in only 58% of the April-September samples. Thirty-two percent of the October-March stomachs contained echinoderms, but only 18% of the April-September stomachs contained this food.

Benthic organisms, such as mollusks, echinoderms, annelids and bryozoans, were found more frequently in the October-March period. Also in the October-March sample the crustacean element shifted somewhat to more benthic forms such as decapods, cumaceans, and ostracods, with concomitant decreases in copepods and other swimming and planktonic forms. This shift in diet perhaps reflected changes in populations of the latter groups.

Copepods composed 100% (N = 47) of the food of four pelagic postlarvae (18.7-21.1 mm) from the San Juan Seamount, California. One stomach contained a single scale. No gross differences in diet were noted between size classes or sexes once the gobies had assumed a benthic existence.

POPULATION STRUCTURE

The Laguna population showed a sex ratio of 1.7 females to 1 male (165 females and 96 males). The sex ratio seemingly fluctuated somewhat, but the paucity of data for some months precluded a complete analysis.

Scales provided satisfactory material for aging *C. nicholsii*, and scale analysis demonstrated the relation between age and size (Fig. 5). Modes in the length-frequency distributions agree well with the observed ages, although overlap occurs due to the differential growth and prolonged spawning period.

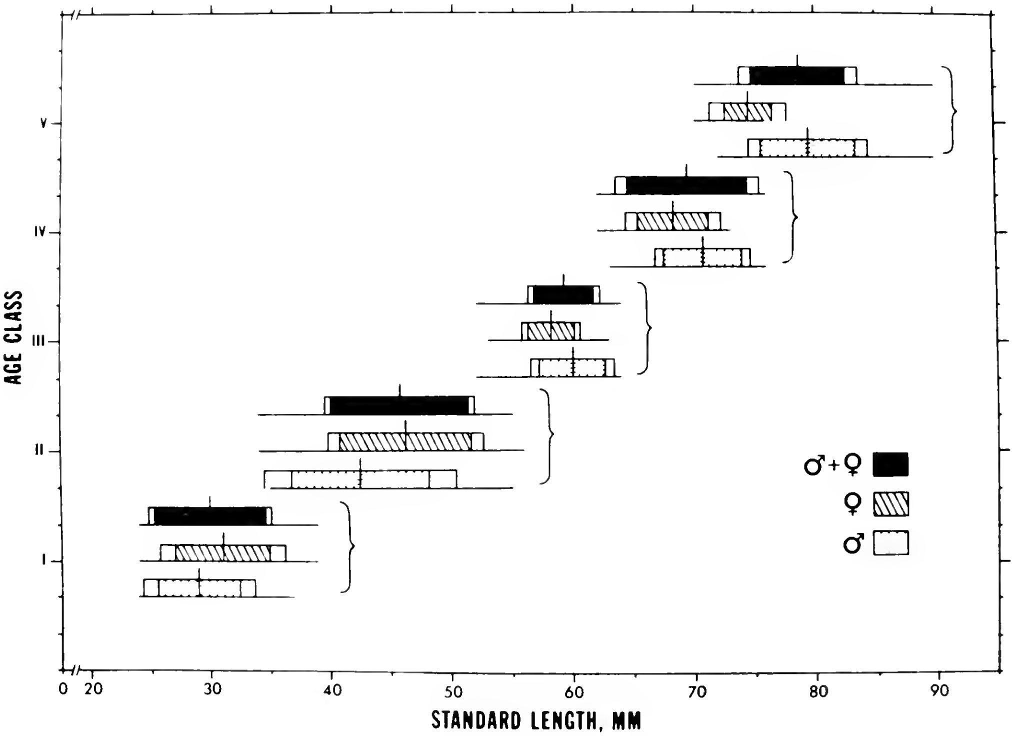

Figure 5. Empirical growth rate of *Coryphopterus nicholsii* from Laguna Beach, California, based on scale analysis of 134 specimens collected from October 1966 through January 1968. Vertical line represents mean; horizontal line, the range of variation; longer rectangle, one standard deviation on either side of the mean; shorter rectangle, 2 standard errors on either side of the mean.

Young gobies were first observed on the Laguna reefs in February. These individuals, which ranged from 21.8 to 26.2 mm in standard length, were probably ones that had hatched the previous year. Growth during the pelagic period is considerable as the newly-hatched larvae measure under 3.0 mm in total length.

Scales of *C. nicholsii* form during the pelagic period. One specimen showed some well developed scales at 19.5 mm on 28 December 1966. However, the majority of specimens did not show scales until they had attained a length of 21.1 mm or greater. This is the approximate size at which *C. nicholsii* settled on the reefs in 1967. The first annulus is not laid down until the following winter.

The observed length-frequencies of *C. nicholsii* collected at Laguna Beach (Fig. 6) usually corresponded with the observed age-groups indicated by scales in that five (sometimes four) frequency groups were represented in the samples. Males of any frequency group were relatively larger (as indicated by mean standard length) than females of the same group.

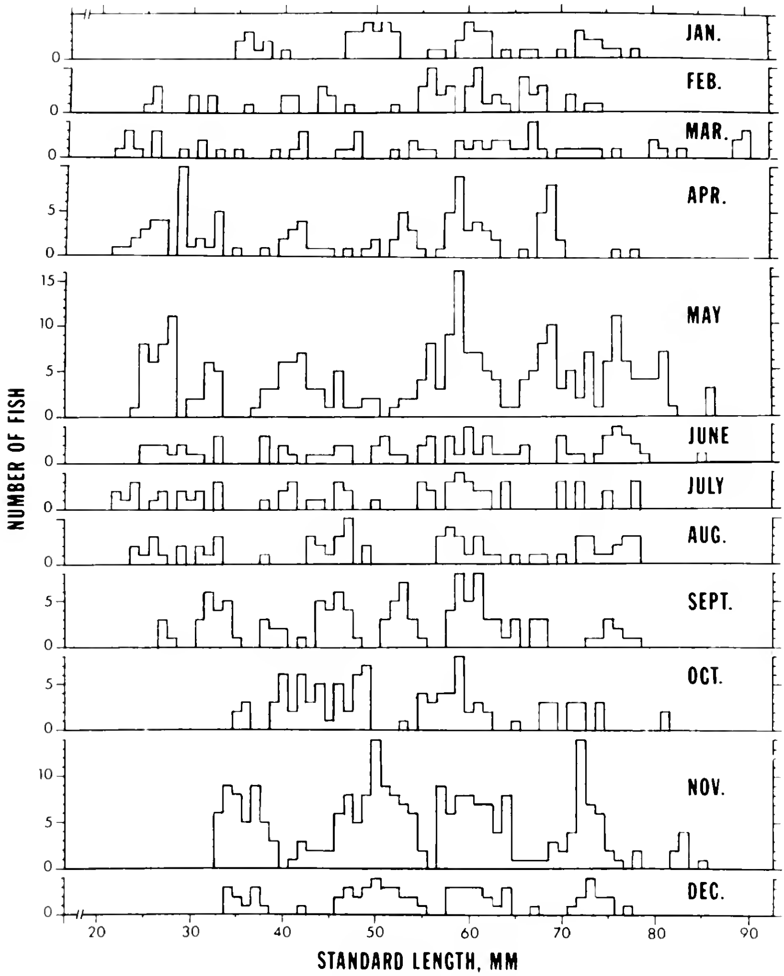

Figure 6. Length-frequency measurements of 1325 specimens of *Coryphopterus nicholsii* taken at Laguna Beach, California, from October 1966 through September 1967.

PREDATION

One incident of predation on *C. nicholsii* was observed on the shallow Laguna reef. A small sand bass (*Paralabrax nebulifer*) caught and ate a *Coryphopterus* after I flushed the goby away from the shelter of the reef onto the surrounding open sand. Subsequent collections of

22 sand bass on the reef revealed that 7 (32%) had fed on *C. nicholsii.* Turner, Ebert and Given (1969) did not find *C. nicholsii* in the stomach of large predaceous fish collected on reefs between 1960 and 1963, although this goby was abundant and appeared to be a suitable food item. Smith (1970) and Quast (n.d.b.) list Gobiidae as a food of kelp bass (*Paralabrax clathratus*).

Stomach analyses of bluebanded gobies, *Lythrypnus dalli,* another common inhabitant of the southern California rock reef, revealed larval *C. nicholsii* in 2 of 42 (4.8%) stomachs. Investigations were not made on the food habits of other possible predators on the reefs inhabited by *C. nicholsii.*

Turner, Ebert and Given (1969) observed a 3 mm larval *C. nicholsii* entrapped in the hydranth of an *Obelia* on an artificial reef off southern California.

SEXUAL DIMORPHISM

Sexual dimorphism of the genital papilla, is usually evident in the Gobiidae (Dôtu, 1957a, 1958a, 1961a; Miller, 1963; Springer and McErlean, 1961; Tavolga, 1954; Smith, 1964; Weisel, 1947). Dimorphism has also been noted in fin size (Hildebrand and Cable, 1938; Baird, 1965; Dôtu, 1958b, 1959, 1961b), pigmentation (Heincke, 1880; Tavolga, 1954; Ninni, 1938; Dôtu, 1958c, 1961c), shape of mouth (Baird, 1965), and size and shape of the body (Breder and Rosen, 1966; Baird, 1965; Dôtu, 1957b, 1958c, 1961c).

Four hundred specimens of *C. nicholsii* from 9.6 to 88.0 mm in standard length were examined for external sex identification. The genital papilla was found to be sexually dimorphic (Fig. 7). Specimens shorter than 25 mm standard length could not be accurately sexed externally, but those larger than 25 mm were correctly sexed by examination of the papilla, which is elongate and pointed in the male and is broad and truncate in the female.

During the breeding season the males of *C. nicholsii* are easily distinguished from the females by their black pelvic fins. These fins remain light grey throughout the year in the females.

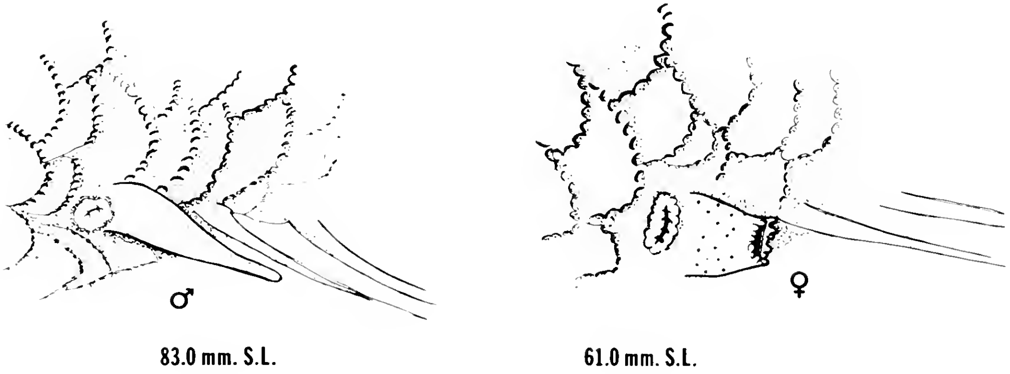

Figure 7. Sexual dimorphism in the genital papilla of *Coryphopterus nicholsii.*

Dimorphism is also discernable in the maximum sizes of the sexes. Males attain a greater length than females. The largest male examined was 90.0 mm in standard length, whereas the largest female was 76.0 mm. Larger size may accord the nest-guarding male greater success in the protection of the eggs.

Examination of the length of the second dorsal and anal fins of mature gobies also revealed sexual dimorphism. Both fins were found to be relatively longer in the male (Fig. 8). Measurement was from the front of the base of the first element to the distal end of the last ray. This dimorphism was not expressed in meristic differences.

REPRODUCTION

The Laguna population was sampled at weekly or biweekly intervals from October 1966 to September 1967 to determine the length of the breeding season. The presence of eggs and individuals of both sexes in breeding condition was used as evidence of reproductive activity.

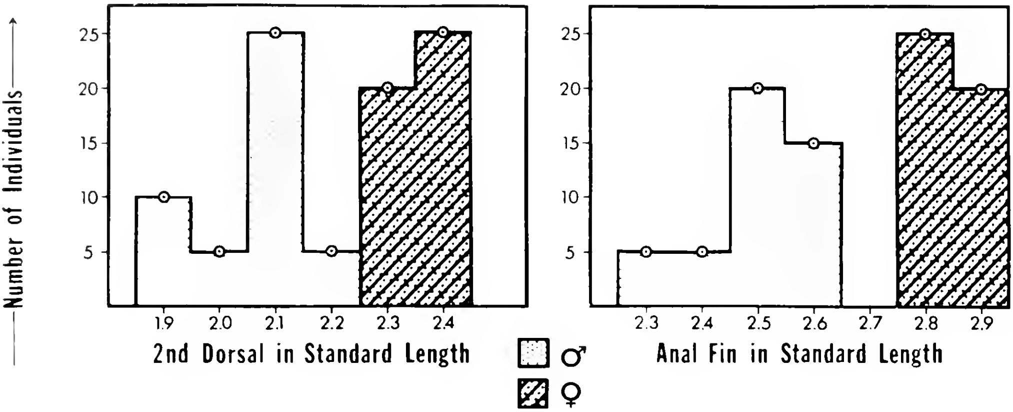

Figure 8. Sexual dimorphism in length of the second dorsal and anal fins of *Coryphopterus nicholsii*, from anterior of base to posterior tip of last ray; expressed as ratio of length of fin into standard length.

Females of *C. nicholsii* were found to be mature at 47.3 mm or larger (Fig. 9). This size corresponds to age-group II as observed from scale and length-frequency analysis. Mature males shorter than 55 mm were not found. This size corresponds with the last of age-group III. However, mature males were found with two or more annuli (age-groups III through V). Ripe females were found in age-groups II through V.

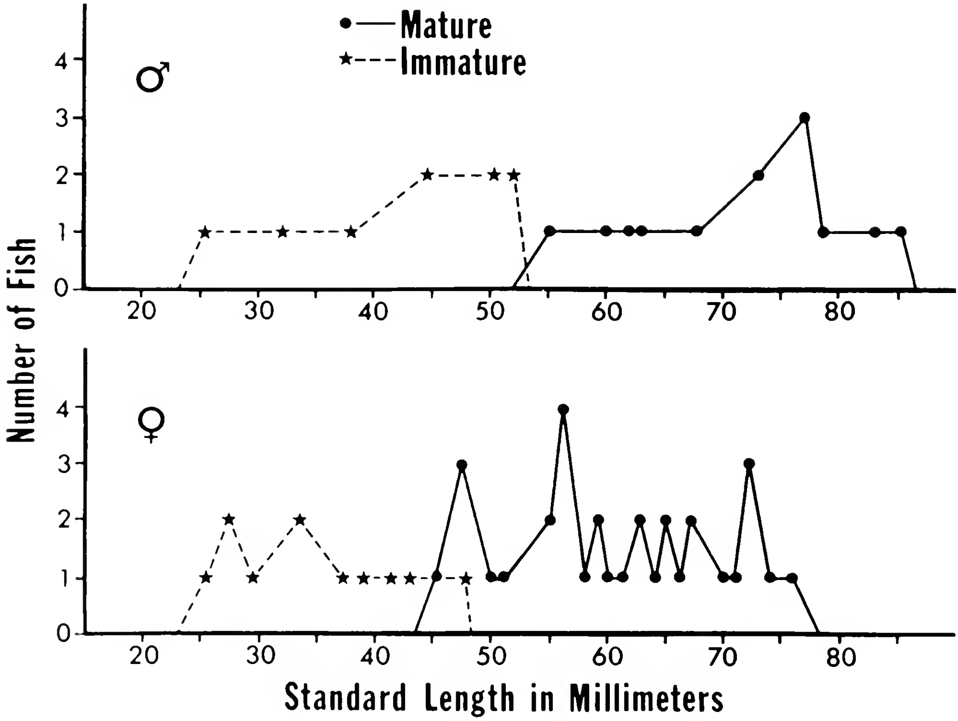

Figure 9. Standard lengths of *Coryphopterus nicholsii* at sexual maturity based on gonad development of 22 males and 43 females from Laguna Beach, California.

The first ripe females, measuring 47.3 to 73.5 mm in standard length, were taken on 10 February 1967. The first ripe males appeared slightly earlier on 2 February 1967; they ranged from 72.1 to 83.0 mm in standard length. No ripe gobies of either sex were found after 26 August 1967 (Fig. 10).

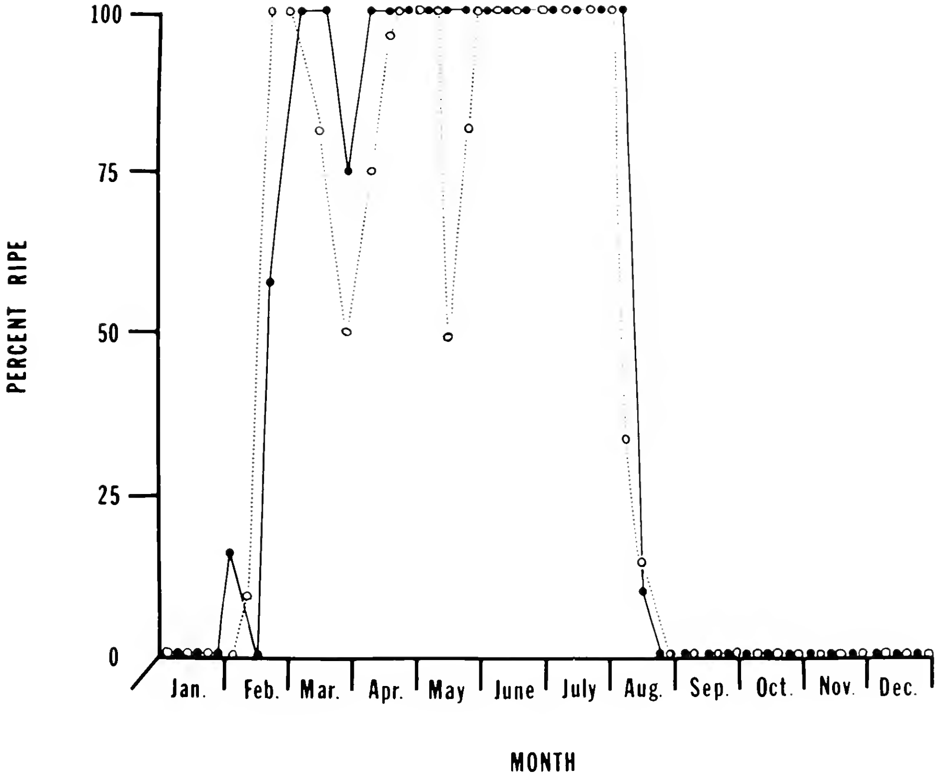

Figure 10. Monthly percentages of ripe *Coryphopterus nicholsii* from Laguna Beach, California. Based on 1134 specimens taken from Laguna Beach, California from October 1966 through September 1967. Solid dots (solid line) represent males, circles (broken line) represent females.

The mature ovaries contained two egg groups, one ripe and one unripe. The ripe egg group seemed to be spawned at one time. The number of ripe ovarian eggs (in both ovaries) was found in four individuals to range from 3274 to 4788. However, the assessment of fecundity in a species which may spawn several times over an extended period, has little biological value per se. I could not determine how many times this species spawned in a season.

Ripe ovarian eggs are orange and round, and measure 0.4 to 0.7 mm. Unripe eggs range in diameter from 0.05 to 0.2 mm.

Eggs were found on the Laguna reefs from 11 April to 5 August 1967. However, because it is difficult to locate the nests, I do not think that these dates wholly encompass the spawning period. Ebert and Turner (1962) observed nests off Hermosa Beach and Santa Monica, California, from April through October.

Fertilized eggs (Fig. 11) have the spindle shape characteristic of gobies. They are attached directly to the rock surface but have no adhesive threads. Ebert and Turner (1962) found that mature eggs averaged 2.10 mm long by 0.48 mm wide. The embryo within each mature egg averages 2.97 mm in length and its head is directed opposite (downward from) the pole of attachment on the lower surface of the nest. Ebert and Turner described the developing embryo.

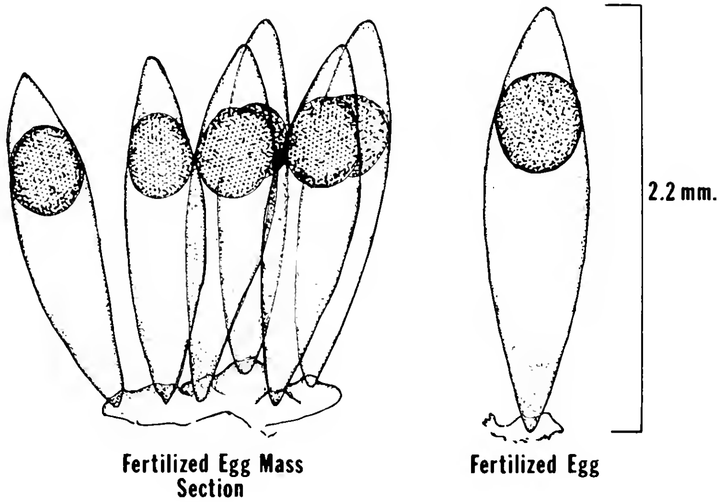

Figure 11. Fertilized eggs of *Coryphopterus nicholsii.*

The prejuvenile of *C. nicholsii* (Fig. 12) is pelagic. Specimens ranging in size from 15.5 to 29.0 mm standard length have been taken 560 km off San Francisco and 260 km off Santa Barbara. One individual was taken on Davidson Seamount, 97 km southwest of Point Sur, California (Berry and Perkins, 1966). These individuals have been described by Berry and Perkins as pelagic, oceanic, protracted prejuvenile stages. Specimens from the vicinity of San Diego ranging from 9.6 to 22.6 mm in standard length, have been examined. These were distinct from the adults in having vertical bars which are burnt orange in life. These bars become light brown in alcohol.

Juveniles of *C. nicholsii* were found to assume a benthic habit on the Laguna study reefs at 21.8 mm standard length. Specimens as short as 24.0 mm were found on other reefs. Fish of this size were found on the Laguna reefs in February through August 1967.

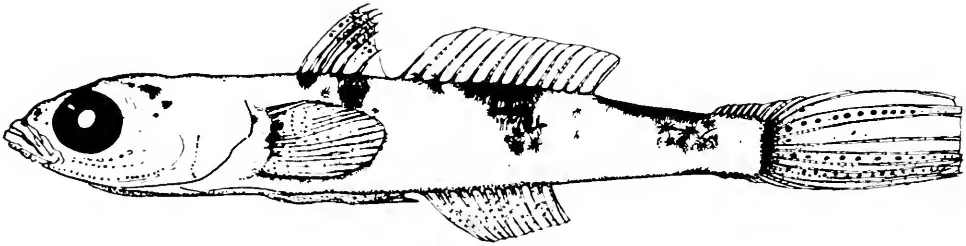

Figure 12. Pelagic prejuvenile of *Coryphopterus nicholsii,* 19.4 mm in standard length, from San Pedro Basin, California.

FEEDING BEHAVIOR

Coryphopterus nicholsii has three feeding-behavior patterns. The most frequent was swimming off the bottom for a distance of about 8 cm, grabbing a small crustacean and then settling. Another pattern involved picking a benthic organism from the substrate. The third involved picking up a mouthful of the loose bottom, spitting it out, and then selecting the desired food as it fell through the water. By the latter two methods such items as decapods, annelids, and echinoderms were taken. These items were probably detected visually, although this species does have moderately developed papillae (Macdonald, 1972) which may function in sensing burrowing organisms.

I noted one exception to the general benthic habit on the southwest coast of Punta Banda, Mexico, where there are many narrow canyons through which strong upwelling currents flow. Gobies there hovered 0.5 to 1.0m off the bottom, using their pectoral fins as the means to counter the current, as they fed on the plankton that drifted up the canyons.

In the aquarium, *C. nicholsii* was fed on frozen brine shrimp. Usually the gobies grabbed the shrimp in midwater, and swallowed them whole. If the shrimp was picked off the bottom the goby would spit it out with the associated rubble and then once again grab the shrimp as it drifted downward. When fed on chunks of frozen smelt, which were too large to be swallowed whole, the gobies, which have moderately developed teeth, bit off large pieces.

BREEDING BEHAVIOR

Gobies and species of various other groups endowed with adherent eggs generally seek some rocky crevice, shell, or other hard object suitable for egg attachment. As is typical of gobioid fishes, and most territorial fishes, the male *C. nicholsii* selects and prepares the nest (Tavolga, 1954; Dôtu, 1958a; Guitel, 1893). Nest building is intermittent, alternating with courtship and other phases of social behavior. The male enters and leaves his shelter frequently. The duration of the stay within the shelter is highly variable.

Nest preparation consists of several cleaning movements, similar to those described by Tavolga (1954) for *Bathygobius soporator:* fanning, rubbing, scooping, and nibbling. Fanning the most frequent act, consists of the vigorous waving of the body and pectoral fins, sending up a cloud of sand for several seconds. This appears to be the most efficient type of digging activity for this fish. Rubbing consists of brushing the body against the algae-covered surface of the nest, apparently to dislodge this material. Scooping is accomplished by taking mouthfuls of sand, small shells, or other debris and carrying it away from the nest. Nibbling may occur if the shelter has algae or other material clinging to its surface. Nest cleaning is not thorough and the adhesive algae and other organisms are not cleaned off completely.

Essentially the same nest-preparation movements observed in *C. nicholsii* have been described for other species of gobies, as well as for most teleosts that construct any sort of hollow in sand substrates. The fanning method of nest formation is probably the most widespread of the nesting behaviors in fishes and has been described for the *Centrarchidae* (Breder and Rosen, 1966), certain cichlids (Baerends and Baerends-Van Roon, 1950), and *Clinocottus* and other cottids (Breder and Rosen, 1966).

When courting, each male rose a few centimeters off the bottom, spread his fins fully, and settled back to the substrate. After one to several of these displays, he swam back to his nest, where he continued nest construction for a short time, and then resumed his courting.

Intermittently the male swam swiftly toward the female and then quickly returned to his starting place, apparently in an attempt to stimulate the female and to attract her to his nest site. If the female reacted negatively, the male followed and continued courting, often nipping and chasing her. Early in courtship the female simply darted away into other shelters. Prior to spawning the female often took shelter in the male's nest, from which she was chased. However, the male, upon seeing the female within the nest, approached with courting movements before entry and chasing. Apparently the male faced a conflict situation between defense of his nest and enticing the female to remain and spawn. Occasionally a female approached a male that was courting her. The female then slowly undulated the body, gaped, and spread the fins.

Some form of courtship behavior is exhibited by males of most nesting species of fishes. There is considerable interspecific variation in the details of this behavior within gobiids. The courting male of *Gobius minutus* exhibits body tremors and rapid breathing movements while approaching the female with short hops, his fins bristling, head raised, throat puffed, and mouth agape (Guitel, 1892). Males of *Gobiosoma* approach the female with short darts, with fins widely spread (Breder, 1942). Courting males of *Brachygobius xanthozonus* swim back and forth in front of the female (Field, 1945). The courtship display of a male *Elacatinus oceanops* consists of violent swimming while he clings to the substrate with the pelvic cup; he then butts the female in the head and genital regions with his nose, and slaps her on the head with his caudal fin (Feddern, 1967). The male of *Bathygobius soporator* slowly approaches the female and positions himself beside or in front of her; he then waves his body, tail, and pectorals in a manner similar to that involved in nest cleaning; if the female moves away, the male follows and continues courting, often chasing and nipping her (Tavolga, 1954).

A change in the color of the pelvic fin of *Coryphopterus nicholsii* males during the breeding season presumably stimulates courtship response by the female. Color changes have been noted in various fins of other gobiid fishes during the breeding season (Dôtu, 1956; Kinzer, 1960). Tavolga (1954) showed that *Bathygobius soporator* females can at times "recognize" males by coloration, in the absence of any courtship activity. That the male's black pelvic fin may provide adequate stimulus for sexual recognition was suggested in an experiment wherein an adult female with artificially blackened pelvic fins was approached by a ripe female showing definite courtship behavior.

The female *C. nicholsii* attaches her eggs to the underside of the nest. The deposited egg masses average 10 cm in diameter, are roughly circular and are made up of a single layer of eggs. The male is intermittently present in the nest at the time of oviposition, where he frequently circles the female, butting and bitting her. He often passes his turgid genital papilla over the surface of the eggs. Fertilization apparently takes place during and immediately after oviposition.

Among the gobies whose nesting habits have been described, oviposition on the underside of shelters is quite common. Fishes that hide and nest under shelters are likely to be confronted with a nest floor which consists of sand, mud, rubble, or other irregular surfaces, whereas the ceiling will probably present a hard surface more suitable for the adherence of eggs. Also such shelters offer a degree of safety against egg predators.

Tavolga (1950) found that unless artificially fertilized eggs of *Bathygobius soporator* are placed in a hanging position many of the embryos do not rotate properly within their elongate egg cases. Such individuals develop with their heads pointed toward the attached end of the shell and are thus unable to hatch.

Spawning completed, the male of *C. nicholsii* defends, cleans, and fans the eggs until they hatch. He fans the eggs by intermittently waving his body and pectoral fins. This movement resembles that of nest preparation, and produces a strong current of water over the eggs. The residing male rushes out to chase away any goby or other organism that approaches the nest, as well as a slurp gun placed in front of the nest.

The male guards the eggs in the majority of nesting fishes (Breder and Rosen, 1966). Among the gobies, only *Typhlogobius* is reported as an exception, in that both sexes guard and fan the spawn (MacGinitie, 1939). Brood care by the male of *C. nicholsii* consists almost exclusively of fanning with some or all of the fins. Brood care is practiced by most nesting fishes. The function of the brooding is three-fold: circulation of water for respiration, prevention of bacterial and fungal growth, and defense of the eggs. Tavolga (1954) proposed another function in that the fanning activity of the male in some way prevents the abnormal positioning of the embryos within the eggs.

SOCIAL BEHAVIOR

Coryphopterus nicholsii is a bottom dweller. Its swimming activity is confined to short, quick spurts for feeding, for territory defense, and for escape to shelter. Although it is able to change color and pattern according to the habitat, its light color is generally retained even in dark, rocky areas. This light color blends well with the sand bottom, which appears to be the preferred substrate type of this goby. The black eyes and tip of the first dorsal, although conspicuous to the human observer, may serve as disruptive markings, breaking up the shape of the goby before a predator.

Like many other gobies (Stebbins and Kalk, 1961; Tavolga, 1954), *C. nicholsii* exhibits territorial behavior. It is a solitary species that sets up a territory that includes a shelter and a feeding-display area in front of it. The juxtaposition of the territories, which may be spaced less than 25 cm between shelter centers, induces numerous encounters between neighboring individuals. In the aquarium any available shelter, including a tank corner, was utilized and fought over. The species was quite aggressive in a tank containing several fish; there was almost continuous nipping and chasing.

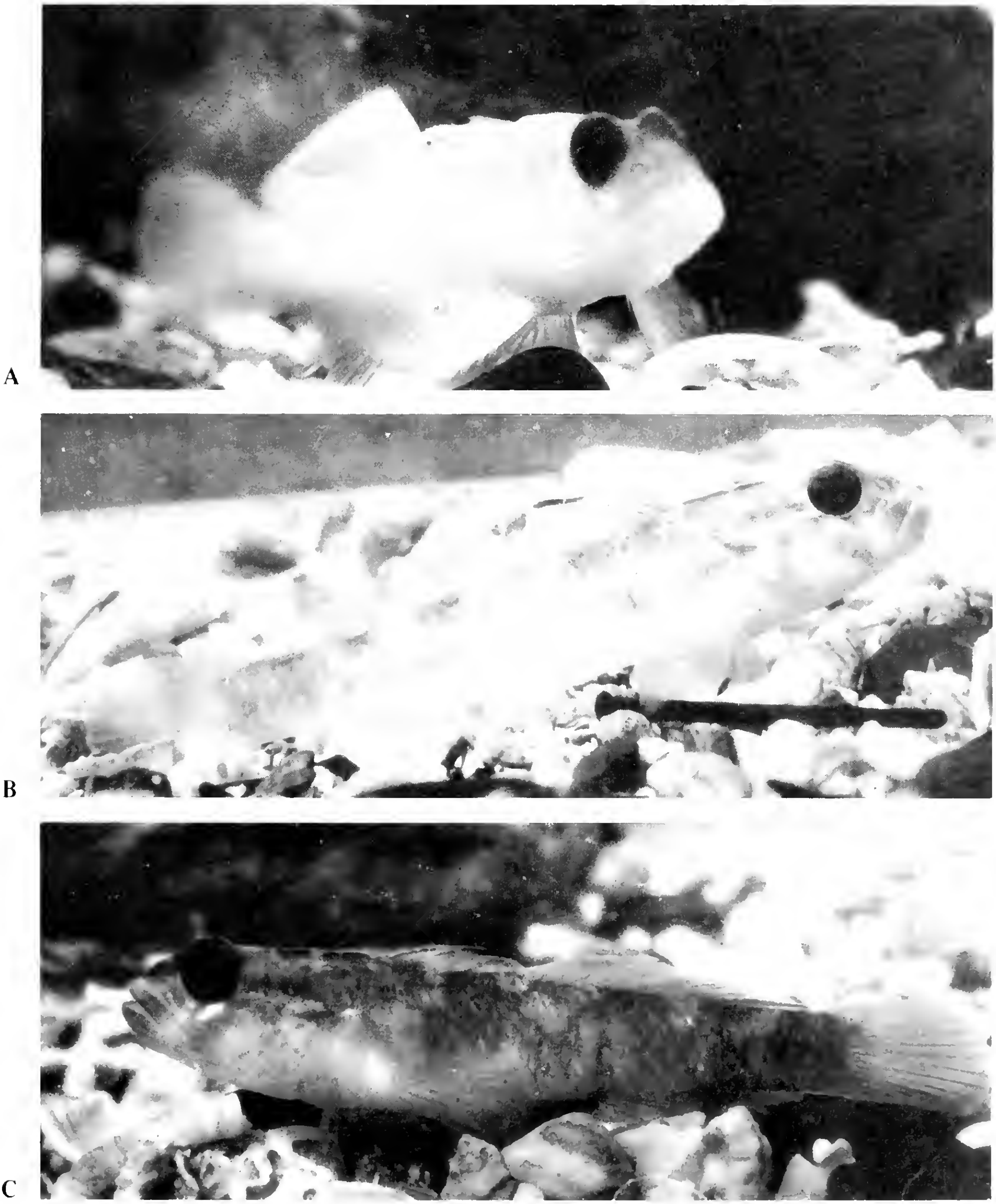

Figure 13. Changes in coloration of *Coryphopterus nicholsii* during social interaction. A. Normal light coloration of undisturbed or dominant individual. B. Intermediate darkening of submissive goby. C. Final darkened coloration of submissive goby. Note light spot under eye. This spot is blue in life and gives rise to the vernacular name, bluespot goby.

A variable nip order was established which was somewhat, but not absolutely, correlated with size (see also Bopp, 1957; Tavolga, 1954). Social orders were established very quickly. During the breeding season, spawning males, which were the largest individuals, appeared to be dominant. Subdominant members retreated to higher levels of the aquarium, hanging on the tank walls and corners by means of continuous swimming movements of the fins and by the suction of their fused pelvic fins. Some attempted to jump out of the tank.

The fundamental color of *C. nicholsii* is uniform pale yellow, but the coloration is variable, changing rapidly in response to different social situations. During social interactions the subordinate animal usually becomes much darker, and is mottled (Fig. 13). One subordinate individual which had been displaced from the bottom of the tank took up a position three-fourths of the way up the tank wall next to the filter siphon which had evenly spaced holes with growths of dark algae. The color pattern of the fish quickly matched that of the siphon holes. This individual held this position and retained this color pattern for several days.

Figure 14. Combat-threat posturing behavior of adult males of *Coryphopterus nicholsii* in aquarium.

The highest degree of aggressive behavior was observed in encounters between mature fish of about equal size. The two gobies approached each other with slow undulations of the body, and with all fins stiffly erected. They positioned themselves next to one another, directly head on (Fig. 14), or head to tail. The mouth was then widely gaped, with the throat expanded and the head elevated. The two gobies displayed either alternately or simultaneously. The "loser" assumed the mottled color pattern and dashed to the safety of shelter.

Interactions between fish of different sizes, or after a hierarchy has been established, usually involve a quick dash by one of the fish, the more dominant one, with the other fish retreating. The more dominant fish nips the fins and scales of the retreating individual. In the laboratory, the fish of the higher rank continually attacked the subordinate intruders if the tank was not large enough to provide adequate territories for the gobies present.

Pugnacity, a feature common to gobies and most territorial fishes, is expressed in *C. nicholsii* as a simple type of biting and pursuit behavior between combatants. Guitel (1892) described similar darkening, throat puffing, gaping, and fin stiffening in *Gobius minutus.* Breder (1942) reported that males of *Gobiosoma robustum* exhibit darkening and fin spreading as intimidation mechanisms. Tavolga (1954) found *Bathygobius sporator* also exhibits color changes correlated with fighting and with reproductive behavior, especially in males, and that extreme darkening is characteristic of fighting males; this occurs together with throat puffing, gaping, quivering, butting, and biting movements. Weisel (1947) found that intimidation behavior of *Gillichthys mirabilis* consists almost entirely of the display of its huge gape.

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A NEW *PLATYDORIS* (GASTROPODA: NUDIBRANCHIA) FROM THE GALÁPAGOS ISLANDS

DAVID K. MULLINER AND GALE G. SPHON

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A NEW *PLATYDORIS* (GASTROPODA; NUDIBRANCHIA) FROM THE GALÁPAGOS ISLANDS

DAVID K. MULLINER AND GALE G. SPHON

ABSTRACT.—**Platydoris carolynae** n. sp. is described from the Galápagos Islands and compared with the two eastern Pacific species of *Platydoris* and with *P. scabra*, the only member of this genus with wide distributional limits. Platydorids are rasping sponge feeders that live in tropical and temperate oceans. The distribution and nomenclature of the 36 known species is reviewed briefly.

The nudibranch fauna of the Galápagos Islands has been neglected by previous workers. Apparently, only two species, *Doris peruviana* Orbigny 1837 and *Onchidium lesliei* Stearns 1893, have been reported (Pilsbry and Vanatta, 1902: 556; Stearns, 1893: 383). Yet, in March 1971 members of the Ameripagos Expedition to the Galápagos Islands collected at least 15 species of nudibranchs, some of them fairly common, at various localities in the islands (Sphon and Mulliner, 1972). Included among these was a previously undescribed species of *Platydoris* that was found at several localities, and which may be endemic to these islands. In this paper, we describe this new species, and briefly review the distribution and nomenclature of *Platydoris.*

BIOGEOGRAPHY

Members of the genus *Platydoris* are sluggish, retiring invertebrates that cling tightly to crevices on the underside of rocks and coral heads. They are found in tropical and temperate waters from 40° N latitude to 32° S latitude. All but one of the thirty-six known species have limited ranges, usually consisting of one shoreline, one island chain, or one location (Fig. 1). *Platydoris scabra* (Cuvier, 1804) is the exception, ranging in tropical waters from 38° E longitude to 155° W longitude.

The majority of the platydorids are found in the Indo-Pacific. They are rasping sponge-feeders, and the great abundance and diversity of sponges may account for the large number of platydorids found in these seas as compared to the Atlantic or Eastern Pacific.

SYSTEMATICS

Order Nudibranchia

Family Dorididae

Genus *Platydoris* Bergh, 1877

Definition.—The body is leathery, flattened, and oval with a coarse to smoothly granular mantle. The foot is notched anteriorly. The branchial aperture is oval and six-lobed. There is no labial armature, and the radula consists of numerous hamate teeth. The stomach is large; the penis is armed with small spines, and the vagina has a thick cuticular lining (translated and modified after Bergh, 1877).

Type species.—*Platydoris argo* (Linnaeus, 1758), by original designation.

Platydoris carolynae n. sp.

Type locality.—Docking area, Charles Darwin Research Station, Santa Cruz Island, Galápagos Islands, Ecuador, (0° 45' 05" S, 90° 15' 38" W).

Description.—The ground color of the animal is cream, the entire dorsum mottled with black or brown blotches. The ventral side of the mantle is also cream with black or brown spotting, each spot made up of multiple fine cross-hatched lines. The rhinophores are tan-colored with dark brown spots. The branchiae are translucent with dark brown or

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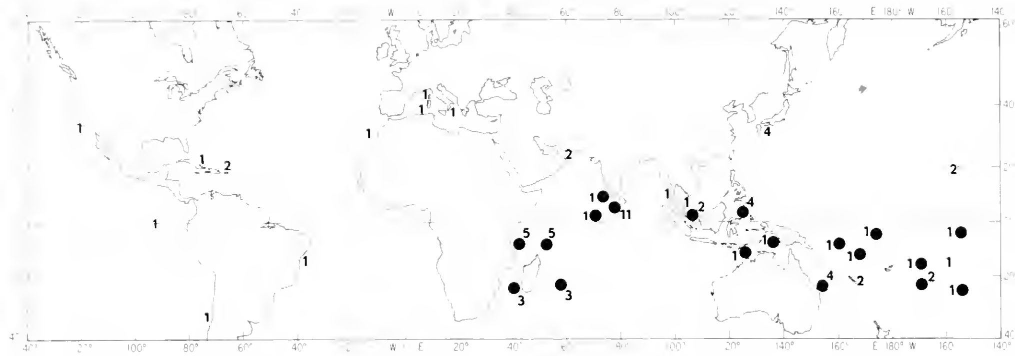

Figure 1. Distributional records for *Platydoris scabra* are indicated by the solid dots. Numerals represent the number of *Platydoris* species found at each locality.

black specks (Fig. 2).

The rhinophores are perfoliate with twenty-four leaves. They are completely retractable and set in a rhinophoral pit with a seven-lobed margin. The branchiae are completely retractable, tripinnate, six in number and divided into two groups of three. The anterior end of the branchial opening forms a crenulate lobule. The pharynx extends for approximately half the distance from the anterior end of the foot to the edge of the dorsum.

Two small head tentacles are attached to the head between the mantle and the body. No eyespots are visible. The foot is bilabiate anteriorly to just behind the foot corner, notched medially. The radula is approximately heart-shaped with 76 longitudinal rows of hamate teeth. No rachidian teeth are present. The radula formula is 76 x 70.0.70 (Figs. 3, 4). In the reproductive system the spermatocyst is elongated, connecting directly into the mucus and albumen gland. A short convoluted tube connects to the oval spermatheca. The prostate is large and globular. The penis is armed with erect, slightly curved spines. The vagina is lined with thick cuticle-bearing folds (Fig. 5).

Etymology.—This species is named for Carolyn Stover, a member of the Ameripagos Expedition.

Type material.—Holotype, California Academy of Sciences, Invertebrate Zoology Type Series No. 303. Photographs of the living animal are deposited in the CASIZ slide collection as Nos. 153-155. The specimen, which is 46.4 mm long and 32.5 mm wide was collected by Andre DeRoy on 13 February 1964, intertidally at the Charles Darwin Research Station dock.

Paratypes (7).—One specimen deposited at the Charles Darwin Research Station, collected intertidally in shallow pools on Santa Cruz Island. One specimen deposited at the Los Angeles County Museum of Natural History, Invertebrate Zoology. Type Collection No. 1619, collected intertidally at Duncan Island, by the Ameripagos Expedition on 26 March 1971. Two specimens deposited at the San Diego Natural History Museum, Department of Marine Invertebrates: SDSNH No. 62826, collected from 10m at Jervis Island by the Ameripagos Expedition on 24 March 1971; Radula slide and dissected animal SDSNH No. 62827, collected from 6m off Punta Alfaro, Isabella Island, by the Ameripagos Expedition on 25 March 1971. One specimen deposited at the American Museum of Natural History, Department of Living Invertebrates, AMNH No. 173729, collected from 10m, off Jervis Island, by the Ameripagos Expedition on 24 March 1971. One specimen deposited at the United States National Museum of Natural History, type Collection No. 735349, collected from 6m off Punta Alfaro, Isabella Island, by the Ameripagos Expedition on 26 March 1971. One specimen deposited at the Delaware Museum of Natural History, No. 64524, collected at Long Beach on the northern coast of Santa Cruz Island by Sue Andrews on 21 December 1972. The paratypes range in size from 19.5 mm long and 14.2 mm wide to 42.3 mm long and 28.0 mm wide.

Discussion.—The only species of *Platydoris* known from the eastern Pacific are *P. macfarlandi* Hanna, 1951, and *P. punctatella* Bergh, 1898. The three species are separ-

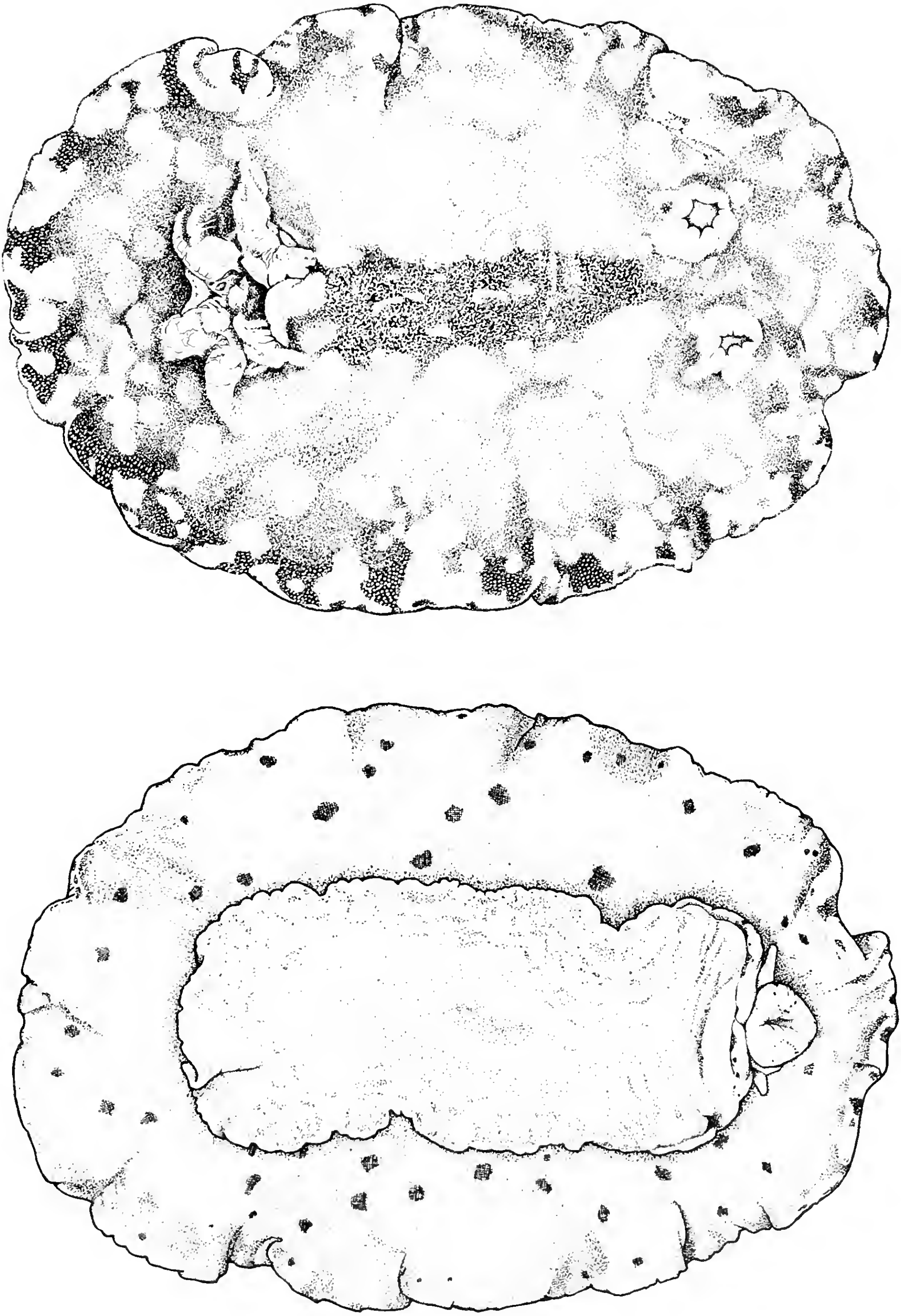

Figure 2. *Platydoris carolynae*, dorsal (top) and ventral (bottom) views.

able by external appearance and geographical range. *Platydoris macfarlandi* is known only from the type lot of four specimens dredged from 172m off Pismo Beach, San Luis Obispo County, California. It is dark red, velvety smooth, with no spots or markings on the surface. The foot tapers to a point posteriorly. *Platydoris punctatella* is from "Isla de Pajargo", Chile (?=Isla de Pajaros, Chile, ca. 26° S. lat.). It is pale yellow. The rhinophores and the anterior margin of the foot are bright yellow. The back has a few scattered

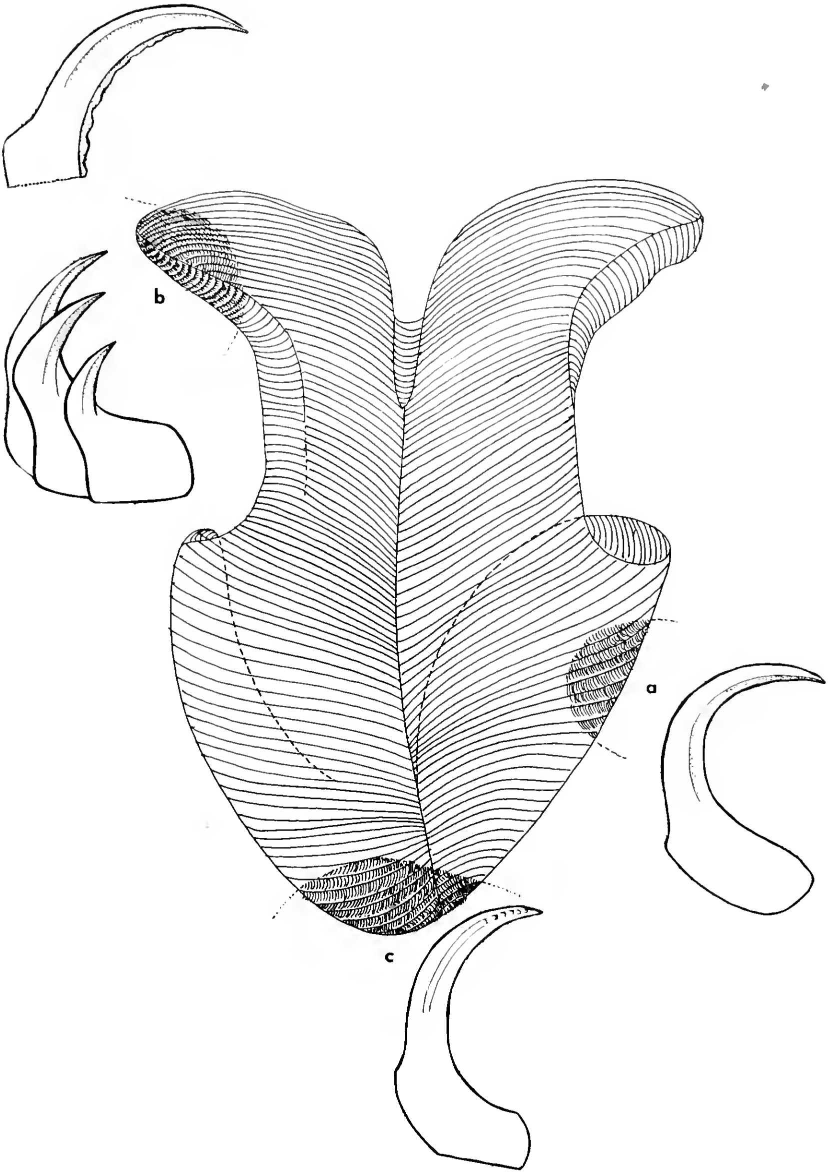

Figure 3. Radula with offset drawings of individual teeth.

light brown spots and flecks. The underside of the mantle is smooth and faint yellow with no markings.

Platydoris carolynae is known only from the Galápagos Islands. The foot is round posteriorly in contrast to *P. macfarlandi.* The color is cream or white with brown or black mottling on the dorsum. Each of the spots on the ventral side of the mantle is made up of fine cross-hatched lines. *Platydoris punctatella* has no ventral markings.

Internal differences were noted in *P. carolynae.* The radula formula is 76 x 70.0.70 for a 46 mm animal, whereas the radula of a 50 mm *P. scabra* is less elongated, 49 x 103.0.103. The vas deferens in *P. scabra* is long and coiled, whereas it is short and straight in *P. carolynae.*

THE SPECIES OF *PLATYDORIS*

We have been able to find 46 specific names described as, or later assigned to *Platy-*

doris in the literature. Of these, one (*P. variolata*) has been shifted to *Anisodoris*; eight are currently considered synonyms; and two are *nomina nuda*. The remaining names are listed alphabetically in Table 1. Synonyms are cited chronologically under the currently accepted name. We have also indicated the distribution of each species and have added the two *nomina nuda* at the end of the list, as they both appear to be undescribed species.

TABLE 1. Currently recognized species of *Platydoris* and their distributions.

SPECIES	**DISTRIBUTION**
P. angustipes (Mörch, 1863)	Southern Florida, through Caribbean, and south to Bahía, Brazil.
Synonyms:	
P. angustipes alaleta (Bergh, 1877a)	
P. rubra White, 1952	
P. argo (Linnaeus, 1767) (Type species of the genus)	Mediterranean Sea. Also, a questionable report from the East Indies.
P. canariensis (Orbigny, 1839)	Canary Islands.
P. capricornensis Allan, 1932	Capricorn Group, Queensland, Australia.
P. carinata Risbec, 1928	New Caledonia.
P. cruenta (Quoy and Gaimard, 1832)	Western Pacific, Japan, Philippine Islands, and East Indies.
Synonym:	
P. arrogans Bergh, 1877a	
P. dura Pruvot-Fol, 1951	Mediterranean Sea.
P. ellioti (Alder and Hancock, 1864)	Indian Ocean and southeast coast of India.
P. flammulata Bergh, 1905	East Indies.
P. formosa (Alder and Hancock, 1864)	Eastern Indian Ocean; also, reported from Hawaii.
P. galbanus Burn, 1958	Southern Australia.
P. hepatica (Abraham, 1877)	Riciniola[1] (Pacific Ocean).
P. herdmani Farran, 1905	Ceylon.
P. immonda Risbec, 1928	New Caledonia.
P. incerta Eliot, 1904	Zanzibar.
P. inframaculata (Abraham, 1877)	Ceylon and East Indies.
P. infrapicta (Smith, 1884)	Queensland, Australia.
P. laminea Risbec, 1928	New Caledonia.
P. macfarlandi Hanna, 1951	Central California.
P. murrea (Abraham, 1877)	Mauritius, Indian Ocean.
P. noumeae Risbec, 1928	New Caledonia.
P. papillata Eliot, 1904	Eastern Africa.
P. philippi Bergh, 1877a	Mediterranean Sea.
P. pulchra Eliot, 1904	Eastern Africa.
P. punctata (Orbigny, 1839)	Canary Islands.
P. punctatella Bergh, 1898	Isla de Pajaros, Chile.
P. sanguinea Bergh, 1905	East Indies.
P. scabra (Cuvier, 1804)	Indian and western Pacific Oceans.
Synonyms:	
P. coelestis (Kelaart, 1858)	
P. eurychlamys Bergh, 1877a	
P. coriacea (Abraham, 1877)	
P. vicina Bergh, 1880	
P. iredalei Allan, 1932	
P. sordida (Quoy and Gaimard, 1832)	Mauritius, Indian Ocean.
P. speciosa (Abraham, 1877)	Western Pacific Ocean.
P. spinulosa Farran, 1905	Ceylon.
P. spongilla Risbec, 1928	New Caledonia.
P. striata (Kelaart, 1858)	India and Japan.
P. townsendi Eliot, 1905	India.
P. variolata (Orbigney, 1837)	Central Chile.
See: *Anisodoris variolata* (Bergh, 1898)	
P. variegata Bergh, 1880	Tahiti.
NOMINA NUDA	
P. brunnea Bergh, 1877a	
P. marmorata Bergh, 1877b	

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[1] Although this is the type locality of *P. hepatica*, as given by Abraham (1877), we have been unable to locate such a locality from available gazetteers.

Figure 4. Scanning electron micrographs from a section of the radula at 3a. Left, X400; right, X900.

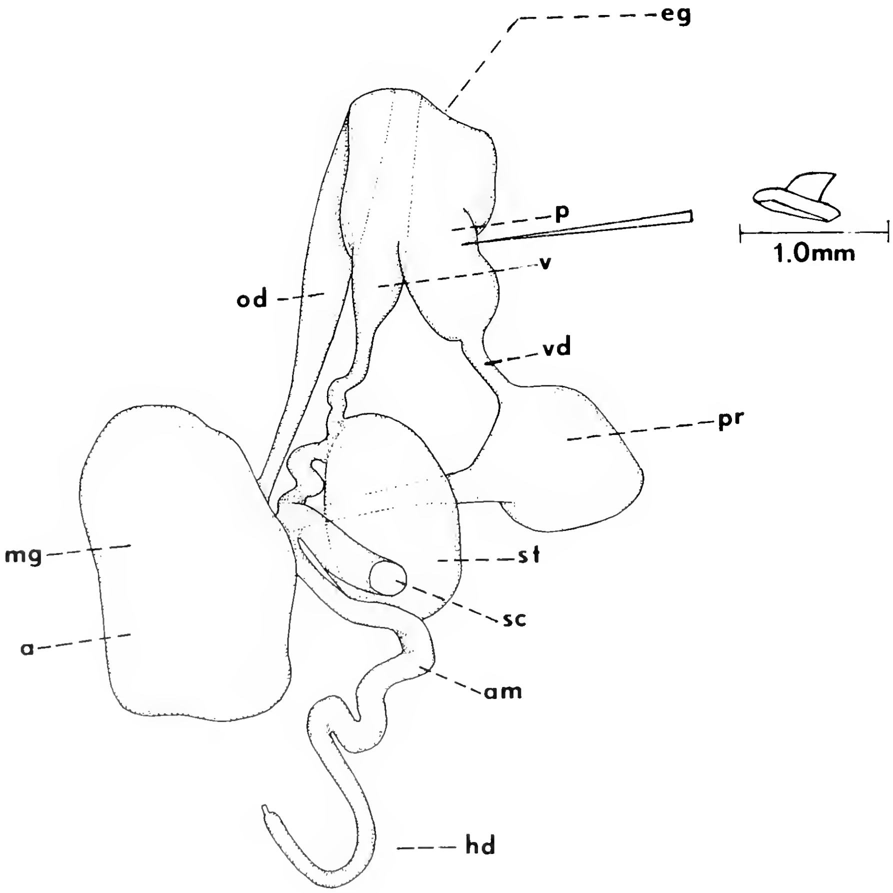

Figure 5. Camera-lucida drawing of reproductive organs with offset of a cirral hook. hd-hermaphrodite duct, sc-spermatocyst, st-spermatheca, pr-prostate, vd-vas deferens, v-vagina, p-penis, od-oviduct, mg-mucus gland, a-albumen gland, am-ampulla, eg-external genital opening.

ACKNOWLEDGEMENTS

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We also wish to thank Allyn G. Smith, Department of Invertebrate Zoology, California Academy of Sciences for lending specimens and photographs.

Joe Nakanishi of the Los Angeles County Museum of Natural History prepared the illustrations of the dorsal and the ventral views of the holotype; Anthony D'Attilio of the San Diego Natural History Museum drew the reproductive organs and the radula; Michael Featherby made the SEM photographs. James Lance helped with the literature search and offered technical advice. George E. Radwin read the manuscript, offered technical advice, and extracted and mounted the radula. Thanks are also due to the Ameripagos Expedition members for their collecting help and companionship.

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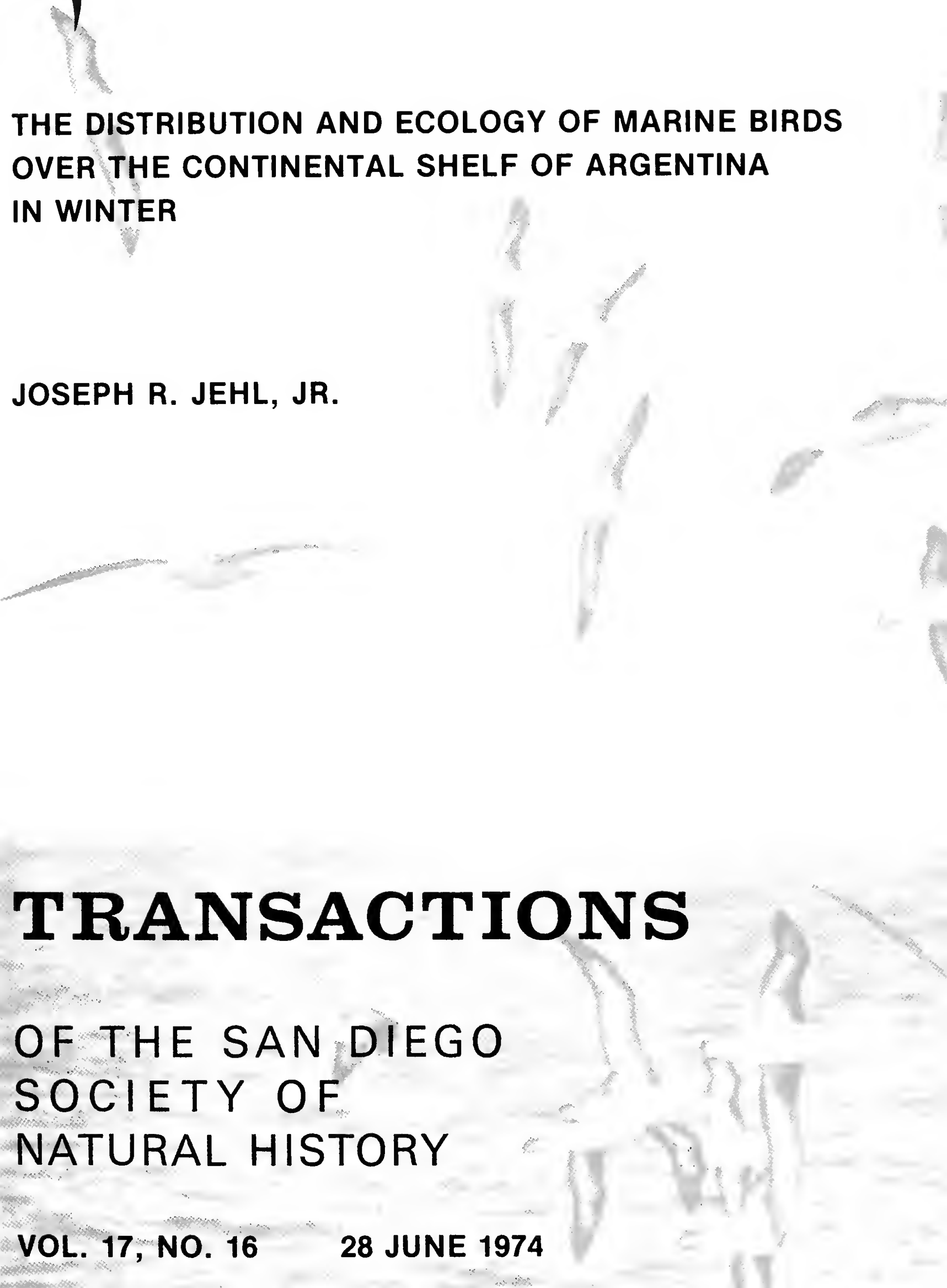
THE DISTRIBUTION AND ECOLOGY OF MARINE BIRDS OVER THE CONTINENTAL SHELF OF ARGENTINA IN WINTER

JOSEPH R. JEHL, JR.



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THE DISTRIBUTION AND ECOLOGY OF MARINE BIRDS OVER THE CONTINENTAL SHELF OF ARGENTINA IN WINTER

JOSEPH R. JEHL, JR.

ABSTRACT.—Quantitative data on the distribution and abundance of marine birds in winter were obtained on three transects of the coastal shelf of Argentina in 1971 and 1972. On the basis of avifaunal assemblages, the shelf waters can be divided into two zones, the boundary occurring near the southern edge of Golfo San Jorge (47°S). *Spheniscus magellanicus*, *Puffinus griseus*, and *Sterna hirundinacea* were characteristic of the northern zone; *Fulmarus glacialoides*, *Eudyptes crestatus*, *Pelecanoides magellani*, *Diomedea exulans/epomophora*, and *Pachyptila* sp. of the southern zone. Beyond the continental shelf off northern Argentina the avifauna was similar to that over the southern shelf, but included several additional species: *Garroidia nereis*, *Procellaria cinereus*, and *Pelecanoides urinatrix*.

Winter sea bird populations along the coast of Argentina appear to be established by mid-June and to remain stable through the winter. In general, abundances seemed low and concentrations were found mainly in areas of strong mixing or upwelling. The winter census data are compared with those from a brief summer transect. Despite pronounced shifts in the ranges of individual species, there was little seasonal difference in total sea bird abundance. A preliminary ecological study indicated that the bulk of the sea bird biomass through the entire year is contributed by large species that obtain their food from the upper meter of the sea, mainly by surface seizing. However, marked seasonal and latitudinal differences in patterns of resource utilization appear among divers, plungers, and filter feeders.

Circumstantial evidence suggests that oil pollution is a major cause of sea bird mortality, particularly over the northern shelf.

Although sea birds are among the most conspicuous inhabitants of the ocean, their role in marine ecosystems has received little attention (Ashmole, 1971). Basic information such as population sizes at different seasons, species composition of sea bird flocks, and periods of migration are prerequisites for ecological analysis. While such data are slowly beginning to accumulate (e.g., King, 1970), they are inadequate if not entirely lacking for most parts of the world.

In the austral winters of 1971 and 1972, the R/V Hero, a research vessel of the National Science Foundation was engaged in oceanographic research along the coast of Argentina (Cummings et al., 1971; Jehl, 1973b). One objective was to obtain data on the distribution, abundance, and ecology of sea birds over the continental shelf. General patterns of sea bird distribution in this area have been presented by Murphy (1936), Escalante (1970), and others (references in Cooke and Mills, 1972). Watson et al. (1971) have mapped the distribution of those antarctic and subantarctic species that occur there. Yet, detailed data are scarce and pertain mostly to observations made in spring, summer, or autumn. With the exception of Cooke and Mills' (1972) report on a brief summer transect between Buenos Aires and Tierra del Fuego there seem to be no precise quantitative data for shelf waters at any season. Tickell and Woods (1972) discussed sea bird abundance between Montevideo, Uruguay, and the Falkland Islands on the basis of 17 transects in the period November-May 1954-64; however, their transect route was largely beyond the continental shelf and their quantitative data are too simplified for detailed analysis.

This paper deals mainly with quantitative data obtained on three transects of the Argentine coastal shelf: one in June 1971 between the Strait of Magellan and Bahía Blanca; the second in July 1971 on the return voyage; and the third in July-August 1972 between Buenos Aires and the Strait of Magellan. The dates of the several transect periods were far enough apart that distributional changes through the austral winter could be determined. The present data with those of Cooke and Mills (1972) also allow a preliminary comparison of summer and winter differences in abundance, distribution, and

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ecological impact of the sea bird fauna.

The survey area.—The coast of Argentina is bordered by a broad, shallow continental shelf, which extends offshore for about 180 km at the latitude of Mar del Plata, 500 km near Bahía Blanca, and 800 km, to the Falkland Islands, off the Strait of Magellan. Over most of the shelf depths are less than 60 fathoms, and along the transect routes depths over 40 fathoms were uncommon.

The shelf waters are derived from the subantarctic waters of the Falkland (Malvinas) Current, which flows northward along the edge of the continental slope. They can be separated into two zones. South of Golfo San Jorge (ca. 47° S) strong westerly winds prevail for most of the year, forcing surface waters seaward, and causing upwelling. In that area surface waters are cold and rich in dissolved oxygen, nitrates, and phosphates. North of Golfo San Jorge, surface waters are warmer and levels of dissolved nutrients are much lower. Beyond the continental shelf off northern Argentina, the Falkland Current brings subantarctic waters into sharp juxtaposition with the warmer shelf water. Although conditions there are similar to those prevailing over the southern shelf, it is useful to recognize a third zone beginning about 30 km landward of the continental slope.

The northern terminus of the Falkland Current varies seasonally. In August-September waters beyond the continental slope retain a subantarctic character to about 36°30' S. There they meet and mix with warmer waters moving northeastward off the continental shelf and with subtropical waters of the southward-flowing Brazil Current. This area of confluence, which is often realized near the mouth of the Rio de la Plata, creates rich feeding conditions for a wide variety of sea birds (Murphy, 1936; Escalante, 1970; Cooke and Mills, 1972). There is a pronounced faunal shift there, with warm water species reaching their southern limits and cold water species their northern limits over the shelf.

Detailed oceanographic information on the region may be obtained in the extensive series of "Pesqueria" reports (Aragno, 1968; Valdez, 1969; Villanueva, 1969-1971). Cooke and Mills have summarized some of these data that pertain to the summer months.

CRUISE TRACKS AND METHODS

In 1971 the Hero departed Punta Arenas, Chile, on 11 June and proceeded northward over the continental shelf of Argentina to Bahía Blanca, arriving on 25 June (Fig. 1). In general the transect route lay 16 to 40 km offshore, although we cruised within several km of the beach in Golfo San Jorge and Golfo Nuevo. Observations were made in Golfo San José on 22 and 23 June. We left Bahía Blanca on 28 June for Golfo San José, remaining inside the gulf until 8 July. After a port call in Puerto Madryn we proceeded southward on 12 July along a route similar to that of the northward transect, except for crossing Golfo San Jorge near its mouth. The cruise terminated in Punta Arenas on 16 July.

In 1972 the Hero left Buenos Aires, Argentina, on 26 July. Between 28 and 30 July we cruised slowly southwestward between 37°07' S and 41°40' S, mostly over deep water beyond the continental shelf but occasionally zigzagging over the edge of the shelf. Late on 30 July we re-entered shelf waters and headed to Puerto Madryn, arriving on 1 August. Late on 3 August we departed for Golfo San José, where we spent the period 4 to 19 August. Following a port call in Bahía Blanca, we departed for Punta Arenas on 22 August, arriving there on 30 August. The route was similar to that of the southward transect in 1971, except that most of 25 August was spent in Bahía Concepción and 27 August in Bahía de los Nodales.

In 1971 I made censuses as often as possible, except when the ship was at anchor. The duration of the observations depended upon weather conditions and ship's activities, and varied from 2 to 7 hours per day. In 1972, with the assistance of Jon P. Winter, it was possible to monitor bird populations almost continously. Most observations were made from a flying bridge 7 m above the waterline, affording good visibility in all directions. All birds were counted, but for ship-following species the maximum numbers were estimated hourly. In 1971, daily counts were totalled, whereas in 1972, for increased precision, they were divided into morning and afternoon components. Surface water temperatures were taken regularly except when sea conditions precluded work on deck. Quantitative data,

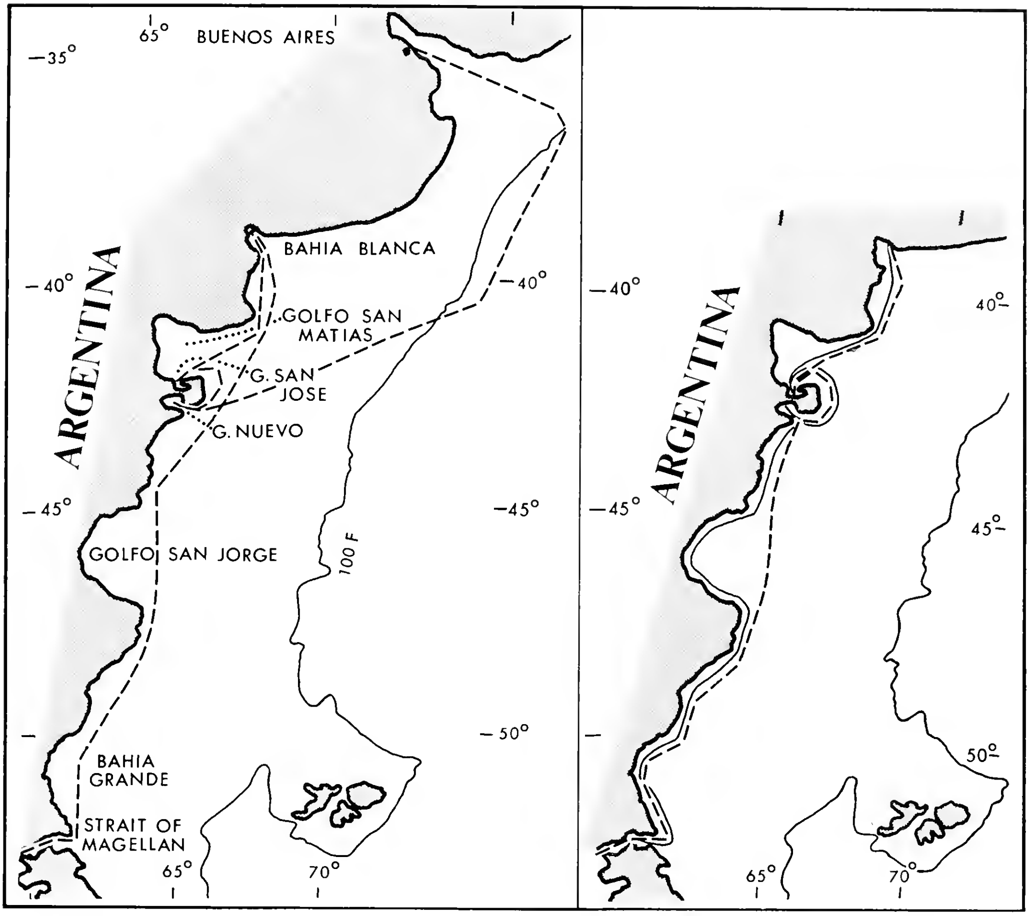

Figure 1. Cruise track of the R/V Hero along the coast of Argentina during transects reported in this study: 1972 (left), 1971 (right).

precise localities, and sea surface temperatures are given in Tables 1 and 2.

In this paper I consider only those species that regularly occur over the open ocean, or more than about 5 km from shore. Information on Golfo San José is presented elsewhere (Jehl, Rumboll, and Winter, 1973). Specimens obtained in these studies are deposited in the Natural History Museum, San Diego.

In the following species accounts I follow the generic classification of Procellariiformes of Alexander et al. (1965). Otherwise, classification and common names largely follow Meyer de Schauensee (1966). The exceptions involve my strong preference for retaining the traditional whalers' names for certain species. In my opinion the use of such prosaic names as Gray Petrel for Pediunker and White-chinned Petrel for Shoemaker has little, if anything, to recommend it.

ANNOTATED LIST OF SPECIES

Rockhopper Penguin (*Eudyptes crestatus*).—Rockhopper Penguins follow the Falkland Current north to Uruguay in winter (Escalante, 1970). They seem restricted to the cold, deep waters beyond the continental shelf, and may be much commoner off northern Argentina than the literature suggests. Groups of up to 15, mostly adults, were common between 36-40° S in late July 1972; the maximum concentration was 79/hour. Over the continental shelf, however, Rockhoppers were rare or absent. The only sighting in 1971 was of a single bird near 40° S on 15 July. In 1972 a few appeared at the southern edge of Golfo San Jorge, where surface temperatures dropped sharply to 4.4° C, but none were seen in colder waters farther south. In summer Cooke and Mills (1972) recorded only one Rockhopper over the shelf near 52°40'S.

Magellanic Penguin (*Spheniscus magellanicus*).—In summer Magellanic Penguins are common in the vicinity of nesting colonies in southern Argentina (i.e., south of 44° S); in winter they largely abandon these areas and move northward as far as Uruguay and southern Brazil. We found them fairly common between Buenos Aires and the Valdes Peninsula, uncommon to rare southward; in all areas their local abundance was markedly reduced by turbid water. All sightings were made in shelf waters, mostly within 30 km of shore in areas where surface temperatures exceeded 9° C. On all three transects we found concentrations 15 km off the Valdes Peninsula; maximum densities were 27/hour. The largest concentration, 300 birds, 150 km east of the peninsula on 31 July 1972, was near the area where Cooke and Mills found large flocks in summer. Penguin flocks were usually accompanied by South American Terns (*Sterna hirundinacea*) and Sooty Shearwaters (*Puffinus griseus*), which feed on fish that penguins drive to the surface. This penguin-tern-shearwater assemblage is the most conspicuous and characteristic avian grouping over northern shelf waters.

Wandering Albatross (*Diomedea exulans*), Royal Albatross (*D. epomophora*).—Rare over the northern shelf but slightly commoner farther south. In 1971 we saw occasional great albatrosses as far north as the Valdes Peninsula but the only concentration, 20 birds, was in Bahía Grande on 15 July. Small numbers near the Valdes Peninsula and in Golfo San Matías in late August 1972 indicate a northward shift of the population later in winter. Beyond the continental shelf great albatrosses were fairly common from 36-40° S. They appeared as soon as the ship crossed into deep water and often outnumbered the Black-brows. Their abundance declined immediately as we re-entered the shelf waters and en route to Puerto Madryn none was seen closer to land than 200 km.

On 29 July 1972 we saw over 110 great albatrosses, 3 of which were color banded; 30 were with a large flock of Black-brows at 39°22' S; 50 more along with other seabirds fed on scraps from a fishing trawler; and another 30 were scattered along the route. Most of the birds in the first group of 30 were photographed; of these, at least 4 were Royals (dark line on tomium visible) and 20 were Wanderers. Sight records suggest a similar species composition in the other groups. No Royals were identified over shelf waters in 1972, although two birds in 1971 were thought to be *epomophora* (Cabo Danoso, 15 July; Bahía Engano, 18 June).

Robertson and Kinsky (1972) showed that large numbers of Royal Albatrosses use the southwestern Atlantic as a major feeding area, particularly in winter. However, their suggestion (following Dabbene, *in* Murphy, 1936) that it is the common species of great albatross there is questionable. The present data indicate that Wanderers greatly outnumber Royals throughout the winter, in coastal as well as offshore waters. Robertson and Kinsky (1972) also found that about 55 per cent of the Royals wintering in the southwestern Atlantic are three years old or less and about 70 per cent are four or less. Wandering Albatrosses of those ages retain considerable brown in their plumage and should be distinguishable in the field (see Tickell, 1968: fig. 12). Yet, only one of over 145 great albatrosses observed in this study was in the brown juvenile plumage of *exulans*; four were in the adult "*chionoptera*" stage of *exulans*; and the rest were in plumages in which the two species are usually indistinguishable. If my estimates of relative abundance are accurate, it would appear that Wanderers wintering off Argentina average several years older than Royals in the same are. This is a potentially important biological difference between these similar species that requires confirmation. Furthermore, since mottled immatures of *exulans* were fairly common along the coast of Chile in the winter of 1970 (pers. obs.), the average age of Argentine Wanderers may be greater than that of birds wintering off the Pacific coast of South America.

Black-browed Albatross (*Diomedea melanophris*).—Common to abundant along the entire coast, except where waters are excessively turbid. In both years it was rather regularly distributed over the shelf north to Bahía Blanca, and concentrations were found off the Valdes Peninsula and in Golfo San Jorge, although in 1971 the largest numbers (150/hour) were seen in Bahía Grande. No important seasonal or yearly differences in

Figure 2. Part of a flock of 10,000 Black-browed Albatrosses and other sea birds. Coast of Argentina, 39°22'S, 55°22'W, 29 July 1972.

distribution were evident. Tickell and Woods (1972) did not observe seasonal differences in abundance on transects between Montevideo and the Falkland Islands.

The species was also common — and once spectacularly abundant — near the edge of the continental shelf. On the morning of 29 July 1972 an estimated 10,000 were feeding with other sea birds and a large pod of Pilot Whales (*Globicephala melaena*) near 39°22' S, 55°22' W at the edge of the shelf (Fig. 2). That afternoon an additional 10,000 were feeding on scraps from a large trawler. Over the entire route it appeared that adults outnumbered immatures by about 5 to 1, although immatures seemed more likely to occur in near-shore waters and mouths of bays. Many birds near Buenos Aires were heavily oiled.

Giant Petrel (*Macronectes giganteus*).—Widespread and remarkably uniformly distributed in shelf and offshore waters through the year, though commoner in winter. Usually three or four followed in our wake. Over 500 were scavenging offal near a fishing ship at 39°40' S on 29 July 1972.

In 1971 approximately 70 per cent of the birds seen were immatures, whereas in 1972 adults slightly outnumbered immatures over the continental shelf. This age distribution suggests a possible influx of adults later in the winter. Beyond the continental shelf immatures composed over 70 per cent of the flocks, and in harbors and waters very close to shore they predominated strongly. Only 3 white-phased birds were encountered, one with a huge flock of sea birds at 39°22' S in 1972, and two well inside Golfo Nuevo in 1971. No birds suspected of being *Macronectes halli* were among the giant petrels flying near the ship (see Bourne and Warham, 1966, for characters that may allow these similar species to be identified under field conditions).

Southern Fulmar (*Fulmarus glacialoides*).—Common to abundant over southern shelf waters in winter, in waters colder than 7° C. In June and July 1971, Southern Fulmars were common to about 49° S, but disappeared abruptly in warmer waters to the north. On the southward transect in August 1972 a few appeared at 44° S, where temperatures dropped under 7° C, but none was seen again until 47°24' (4.4° C). Fulmars were uncommon but regular beyond the continental shelf at 36-40° S; surface temperatures there were less than 6.7° C. Cooke and Mills did not record this species on their summer transect.

Cape Pigeon (*Daption capense*).— Cooke and Mills did not observe this species during their cruise. In June 1971 it was widely distributed but uncommon; in July 1971 it was seemingly commoner, especially in the south; and in August 1972 it was common over much of the shelf and in offshore waters. These data suggest a shift northward as the winter progresses. It occurred in greatest abundance beyond the continental shelf on 29 July 1972, where flocks of 4000 and 6000 were in association with albatross flocks.

Whale-birds or Prions (*Pachyptila* spp.).— In 1971 scattered prion flocks were seen between San Julián and the Valdes Peninsula, and in Golfo San José. The largest concentration (up to 150/hr.) occurred off Río Chico on 15 July. In August 1972 they were uncommon to rare over shelf waters, except inside Golfo San José (Jehl et al., 1973). Prions were somewhat commoner offshore, especially near 41°40' S, where we found scattered flocks of 10-15 birds. Although *P. desolata* and *P. belcheri* are said to occur in this general area (Escalante, 1970), the only specimens we obtained were *belcheri* (♂, 109 g, 37°22' S, 54°24' W; ♂, 41°38' S, 56°43" W; ♀?, Golfo San José). In summer Cooke and Mills observed prions only south of 50° S, near presumed breeding grounds.

Pediunker (*Procellaria cinereus*).— A single bird made several passes near the ship on 30 July 1972, when we set out a chum slick well offshore. This was our only observation of the species, which appears to avoid shelf waters at all seasons. Not recorded by Cooke and Mills.

Shoemaker (*Procellaria aequinoctialis*).— In June 1971, Shoemakers were widespread though generally uncommon along the entire coast, whereas a month later they were virtually absent south of 43° S. In August 1972, too, they were uncommon in coastal waters north of 44° S. and much rarer to the south. In both years concentrations occurred in waters adjacent to the Valdes Peninsula.

Beyond the continental shelf Shoemakers replaced Sooty Shearwaters as the dominant, and usually only, species of shearwater, though they appeared to be no commoner there than in coastal waters. The limited data hint that this species may be more abundant in summer than in winter.

Greater Shearwater (*Puffinus gravis*).— Common to abundant in summer but rare or absent in winter, when the species occurs in the North Atlantic. Our only winter observations were in mid-June 1971: four between 43°40' S and 42°00', and several in Golfo San José. These were apparently late stragglers on the northward migration.

Sooty Shearwater (*Puffinus griseus*).— In winter Sooties are largely restricted to shelf waters north of 45° S; their distribution seems to be strongly affected by surface temperatures for they are rare in waters cooler than 9° C. On the northward transect in June 1971 none were seen south of 43°40' S (9.5° C), but farther north they were common to abundant, particularly near the Valdes Peninsula (maximum, 375/hr.). On the southward transect in July they seemed rarer. Only scattered individuals were seen between the Valdes Peninsula and Golfo San Jorge and the only bird seen farther south (47°35' S) was sick and emaciated (specimen, weight 563 g).

A similar distribution was observed in August 1972, with concentrations off the Valdes Peninsula and the northeastern corner of Golfo San Matías (maximum 800/hr.), and in the mouths of the larger bays. Although some birds occurred as far south as the Strait of Magellan, they were uncommon south of 45° S. One hundred and fifty km off the Valdes Peninsula we observed 600 with large flocks of South American Terns and Magellanic Penguins. Sooties were virtually absent from waters beyond the continental shelf.

Manx Shearwater (*Puffinus puffinus*).— This northern-hemisphere migrant winters commonly off the northern coast of Argentina (Cooke and Mills, 1972), but leaves the area in the austral winter. Our only sightings were in 1972; one, 50 km S. of the coast of Uruguay, 27 July; and two in Golfo San Matías, 23 August.

Wilson's Storm-Petrel (*Oceanites oceanicus*).— In both years Wilson's Storm-Petrels were rare over the continental shelf between the Strait of Magellan and Bahía Blanca, and the only area of local abundance (maximum 23/hr) was off the Valdes Peninsula. Nearly all of our observations were made north of 44° S, where surface temperatures exceeded 9° C. The similar distribution patterns found in all three transects indicate that migration is largely completed by June. These petrels were widespread but still uncommon in colder waters (<6° C) beyond the continental slope, Twenty-five, in a small area 225 km SE of Mar del Plata on 29 July 9172, comprised the only significant concentration. Surprisingly, Wilson's Storm-Petrel seems even rarer in shelf waters in summer. Cooke and Mills saw only a single storm-petrel (sp.?) during their transect.

Gray-backed Storm-Petrel (*Garrodia nereis*).— This species was not observed by Cooke and Mills (1971), and Escalante (1970) does not include it in his compilation. We saw only one bird over shelf waters, 37 km offshore at 48°59' S on 15 June 1971. Beyond the shelf, on 30 July 1972, we saw five birds and collected one (♂, wt. 33 g) near 41°38' S, 56°43' W. They were associated with a flock of six Wilson's Storm-Petrels. These appear to represent the northernmost records of the species (cf. Watson et al., 1971; Olrog, 1958), which nests on the Falkland Islands.

Megallanic Diving-Petrel (*Pelecanoides magellani*).— This was the only species of diving-petrel that could be identified in the shelf waters of southern Argentina, and all observations there are referred to it. In each year it occurred to Golfo San Jorge, which is farther north than the range given by Meyer de Schauensee (1966), though it was regular only south of 49° S and common to abundant only between the mouth of the Rio Chico and the Strait of Magellan. The largest concentration (85/hr.) was found in Bahía Grande on 15 July 1971. Although these diving-petrels seem to prefer waters colder than 7° C, we found no seasonal or yearly differences in distribution even though quite different water temperatures prevailed in the two years. In summer Cooke and Mills saw a few diving-petrels, presumably *magellani*, near Bahía Grande.

Subantarctic Diving-Petrel (*Pelecanoides urinatrix*).— This species, which nests on the Falkland Islands, ranges north to Uruguay in winter (Escalante, 1970). Apparently, it follows the Falkland Current, for we saw scattered diving-petrels, all presumably *urinatrix*, well offshore in late July 1972. Our first records were made on the night of 27 July, when 7 flew aboard; all had fed on small crustaceans 8 to 10 mm long. Other sightings were made between 35-42° S, mostly near the edge of the continental shelf; one bird was as close as 160 km from shore. Weights: 2♀: 148, 160 g; 4♂: 120, 144, 145, 145 g.

Great Skua (*Catharacta skua*).— Skuas are rare off Argentina in summer (Cooke and Mills, 1972) and in winter. Our few sightings in 1971 were made within a mile or so of land, generally in the vicinity of bays and harbors, and the only concentration included several flocks on the beach at San Julián on 14 June. Only 9 skuas were seen in 1972: five off Mar del Plata on 27 July, one well offshore on 30 July, and three in near-shore waters between the Valdes Peninsula and Golfo San Jorge. All were referable to *C. s. chilensis* except for one near Mar del Plata which was probably *C. s. antarctica.* In each year several skuas wintered in Golfo San Jose; some of these did not appear to be *chilensis* and may have been *antarctica.*

Parasitic Jaeger (*Stercorarius parasiticus*).— One record, a dark-phased bird near Golfo Nuevo on 18 June 1971.

Kelp Gull (*Larus dominicanus*).— In winter Kelp Gulls disperse widely along the Argentine coast. Apparently their post-breeding movements are largely completed by June, because we noted no important distributional differences in the three transects. Except for local concentrations in bays and near centers of human habitations, this gull was uncommon within 30 km of the coast, and was virtually absent farther offshore. None were seen beyond the continental shelf. Well over 90 per cent of the birds were adults. Cooke and Mills encountered the species rarely, and only near land. Weights: 6♂, 850-1130 (952) g; 8♀, 430 (starved), 680-1040 (865) g.

Brown-hooded Gull (*Larus maculipennis*).— Not seen at sea, except for three in mid-Golfo San Matías in 1971. Fairly common in large harbors north to Buenos Aires.

TABLE 1. Summary of daily censuses, coast of Argentina. June – July 1971. Abundance indicated is number of birds per hour of observation.

	Strait of Magellan to Bahía Blanca									Bahía Blanca to Strait of Magellan					
Species	June 12	13	15	16	17	18	19	21	24	29	30	July 8	13	14	15
Eudyptes crestatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3
Spheniscus magellanicus	+	–	0.2	0.5	–	7.7	1.5	11.0	13.0	1.7	1.0	14.3	2.0	0.5	1.5
Diomedea exulans/ epomophora	1.5	–	0.4	–	–	0.6	–	0.5	–	–	–	–	0.3	–	3.2
Diomedea melanophris	2.5	1.5	6.8	5.5	1.8	2.7	3.0	1.0	7.0	0.7	0.6	0.3	0.7	3.3	49
Macronectes giganteus	4.0	6.5	7.6	0.5	2.5	6.8	2.5	5.0	3.9	3.3	4.8	1.3	2.0	4.3	18.5
Fulmarus glacialoides	17.5	2.5	2.4	–	–	–	–	–	–	–	–	–	–	–	22.2
Daption capensis	1.5	–	2.0	–	0.2	1.8	0.2	5.0	2.7	–	–	0.7	2.0	2.0	7.5
Pachyptila sp.	1.0	–	2.5	5.2	2.2	0.7	–	–	0.4	–	1.6	–	–	4.7	23.5
Procellaria aequinoctialis	14.5	0.5	3.8	5.0	5.2	6.4	2.2	40	1.7	0.3	0.4	3.3	–	0.8	–
Puffinus griseus	–	–	–	–	–	16.0	66	199	32	–	1.8	43	7.0	0.2	–
Puffinus gravis	–	–	–	–	–	0.1	0.2	1.0	–	–	–	–	–	–	–
Oceanites oceanicus	–	–	0.6	–	0.8	1.8	–	1.5	2.2	–	–	8.3	–	0.2	0.5
Garrodia nereis	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–
Pelecanoides sp.	3.5	0.5	3.4	–	1.2	–	–	–	–	–	–	–	–	0.2	0.5
Larus dominicanus	0.5	1.5	0.4	5.0	5.2	2.1	13.5	–	0.4	7.7	0.6	8	0.3	2.2	–
Larus maculipennis	–	–	–	–	–	–	0.5	–	1.3	–	–	–	–	–	–
Sterna hirundinacea	0.5	0.5	0.4	5.0	–	58	100	27	41	9.7	6.4	22.3	4.0	2.5	0.2
Catharacta skua	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–
Hours	2	2	5	4	4	7	4	2	2.3	3	5	3	3	4	4
Latitude °S	52 16	49 20	49 02	47 00	45 17	43 22	43 00	42 00	41 34	40 57	42 03	42 01	43 52	47 10	49 52
Longitude °W	68 33	67 34	66 50	65 44	66 42	64 24	65 15	63 42	63 22	62 20	64 05	64 20	65 15	65 27	67 47
Sea Temperature °C	6.5	6.8	7.0	7.8	9.0	9.5	9.5	11.5	11.5	9.1	9.5	10.0	9.1	6.6	4.5

TABLE 2. Summary of daily censuses, coast of Argentina. July – August 1972. Abundance indicated is number of birds per hour of observation. Species seen on fewer than three days are omitted.

	Buenos Aires to Puerto Madryn											Golfo San José to Bahía Blanca to Strait of Magellan											
Species	July 27A[1]	27P[1]	28A	28P	29A	29P	30A	30P	31A	31P	August 1A	20A	20P	23A	23P	24A	24P	25P	26A	26P	28A	28P	29A
Eudyptes crestatus	—	—	2.8	23.2	10.0	6.2	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.8	—	—	—
Spheniscus magellanicus	0.2	3.2	0.2	—	—	—	—	—	—	27.2	20.0	1.2	6.7	4.2	19.0	0.2	1.2	5.0	—	1.2	—	0.2	—
Diomedea exulans/ epomophora	—	—	0.8	0.8	8.0	20.0	1.5	3.0	1.5	0.2	—	—	—	0.8	2.4	0.2	—	—	0.2	—	—	+[2]	0.3
Diomedea melanophris	7.7	3.2	5.2	9.4	2500	2625	2.8	1.5	2.8	4.5	3.0	1.0	2.8	4.8	15.0	8.0	3.9	1.8	5.8	27.0	0.3	6.0	2.0
Macronectes giganteus	3.0	2.0	0.2	0.6	75	131	3.0	3.8	3.2	3.6	4.0	2.2	3.5	1.8	3.6	4.2	0.4	3.2	0.7	4.0	2.2	2.0	3.3
Fulmarus glacialoides	—	—	1.0	1.3	0.5	4.0	1.7	4.2	—	—	—	—	—	—	—	2.5	0.6	—	—	0.7	2.3	6.2	2.6
Daption capensis	4.0	13.0	4.8	3.8	1000	1565	3.8	11.2	3.2	10.0	4.0	1.8	0.4	3.5	10.2	3.2	1.7	1.2	2.0	1.5	0.7	0.8	7.8
Pachyptila spp.	—	—	1.2	4.4	—	0.5	6.8	0.2	21.0	0.4	0.2	—	—	4.2	—	—	0.3	0.5	—	—	—	—	3.6
Procellaria aequinoctialis	0.8	19.0	1.2	—	0.8	2.8	0.5	1.0	1.2	7.3	7.0	0.2	1.3	3.8	11.0	4.8	0.3	0.5	1.2	0.8	—	0.5	1.0
Puffinus griseus	5.0	36	1.0	0.4	0.2	—	—	—	3.2	7.2	580	0.8	—	271	53	5.4	38	13.0	0.7	6.5	2.3	6.2	6.0
Oceanites oceanicus	—	0.8	0.2	0.4	0.8	7.0	1.5	0.5	0.5	1.8	—	—	—	1.2	8.8	1.2	—	—	—	—	—	0.2	—
Pelecanoides spp.	—	—	0.2	0.2	—	—	—	—	9.5	0.7	—	—	—	—	—	—	—	—	0.5	—	2.0	1.0	18.0
Larus dominicanus	—	—	—	—	—	—	—	—	—	—	12.0	—	1.2	3.5	5.4	2.7	4.2	7.5	1.0	8.8	9.0	0.2	0.6
Sterna hirundinacea	5.4	29.0	—	—	—	—	—	—	—	270	25.0	5.2	12.0	28.0	60	1.5	21.0	2.8	2.8	9.8	—	—	—
Catharacta skua	—	1.2	—	—	—	—	0.2	—	—	—	—	—	—	0.5	—	0.2	—	—	—	—	—	—	—
Hours	4	4	4	5	4	4	4	4	4	5.5	2	4	4.5	4	5	4	6.5	4	4	4	3	4	3
Latitude °S	35 26	35 26	36 22	38 00	39 22	39 50	41 38	41 42	41 56	42 11	42 50	41 00	41 45	41 37	42 24	43 49	44 24	44 55	47 24	48 00	49 21	49 48	52 19
Longitude °W	55 25	54 21	54 24	55 12	55 22	55 40	56 42	57 33	59 33	61 45	64 20	62 25	62 02	62 11	62 58	65 03	65 10	65 25	65 24	65 35	67 34	67 39	68 15
Sea temperature °C	8.9	10.6	5.6	6.1	5.6	5.6	5.6	5.6	8.9	8.9	8.9	9.5	9.2	9.5	9.5	6.7	6.7	6.7	4.4	3.3	2.2	2.8	2.2

[1] A = A.M. P = P.M.

[2] Recorded, but not in timed census periods

South American Tern (*Sterna hirundinacea*).— After the nesting season South American Terns leave southern Argentina and migrate north to Brazil. They were rare or absent south of 40° S, and uncommon south of Golfo San Jorge. Farther north they were common to abundant, particularly near the mouth of bays and near the Valdes Peninsula, where large flocks were present each year (maximum 375/hr.). We saw no terns beyond the continental shelf, although on 31 July 1972 we observed scattered terns up to 190 km offshore, and 140 km offshore 1500 were feeding with Sooty Shearwaters and Magellanic Penguins. All seemed to be *hirundinacea*, but other species could have been overlooked. Most sighting were made within 30 km of shore.

ZONATION, CONCENTRATIONS

Each of the three oceanographic zones in the survey area contains a distinct faunal assemblage. *Spheniscus magellanicus, Puffinus griseus, Oceanites oceanicus,* and *Sterna hirundinacea* were largely restricted to the continental shelf north of Golfo San Jorge; surface temperatures there were greater than 7° C. Farther south, particularly south of 49° S, sea temperatures were lower and those species were rare or absent. *Fulmarus glacialoides, Eudyptes crestatus, Pelecanoides magellani* appeared and *Diomedea exulans/epomophora* and *Pachyptila* spp. became commoner. In cool waters beyond the continental shelf off northern Argentina the avifauna was similar to that of the southern shelf. Immediately as we passed beyond the shelf *Puffinus griseus, Spheniscus magellanicus,* and *Sterna hirundinacea* dropped out and the following species appeared or occurred in greatly increased numbers: *Diomedea exulans/epomophora, Fulmarus glacialoides, Eudyptes crestatus, Pachyptila* spp., *Garrodia nereis, Procellaria cinereus,* and *Pelecanoides urinatrix*. Note that the diving-petrel of deep waters (*urinatrix*) is not that of the southern shelf (*magellani*).

Precise patterns of distribution within these zones are strongly affected by local conditions, especially turbidity. Waters in many near-shore areas (e.g., the mouth of the Rio de la Plata nearly to Punta del Este; much of the north shore of Golfo San Matías and northward within 15 km of shore to Bahía Blanca; the mouth of the estuary near San Julián) are heavily laden with sediment. This reduces underwater visibility and precludes the presence of divers such as penguins; it also reduces feeding opportunities for plungers such as terns and some shearwaters. Even scavengers are scarce, presumably because increased turbidity also reduces the size of fish populations.

Concentrations of sea birds were found in few localities, and indeed the general sparseness of sea birds over shelf waters was impressive. Concentrations seemed to occur mainly in areas of upwelling or strong tidal currents, where vertical mixing could enrich surface waters. For example, in each year flocks of Magellanic Penguins, Sooty Shearwaters, and South American Terns were at the mouth of Golfo Nuevo and Golfo San José as well as 8-15 km of the northeastern corner of the Valdes Peninsula. On 23 August 1972 large numbers of sea birds were distributed across the mouth of Golfo San Matías, but greatest abundances were realized east of Punta Rasa and near the tip of the Valdes Peninsula. Strong tidal currents prevail in all of these areas. The only other significant concentration over shelf waters consisted largely of great albatrosses, Black-browed Albatrosses, Magellanic Diving-Petrels, Southern Fulmars, and prions in Bahía Grande on 15 July 1971. Surface temperatures there were anamalously cold (4.5° C), suggesting a strong, local upwelling.

Farther offshore, large flocks of terns, penguins, and shearwaters were feeding 150 km east of the Valdes Peninsula on 31 July 1972. Cooke and Mills (1972) also found sea bird concentrations there and pointed out that the area is rich in dissolved nutrients.

The largest concentrations were at the edge of the continental shelf. On the morning of 29 July at 39°22' S, 55°22' W, we estimated 10,000 Black-browed Albatrosses, 30 Royal/Wandering Albatrosses, 4,000 Cape Pigeons, 300 Giant Petrels, 2 Shoemakers, 2 Southern Fulmars, and 1 Sooty Shearwater, all in association with a pod of Pilot Whales. As we passed through the flock we were accompanied by ranks of 50 to 100 Black-brows sailing by in formation, and this sight was repeated in all directions over an area of perhaps eight km^2. Many of the birds, particularly the great albatrosses, were feeding on white wormlike masses approximately 20 cm long, and on dead reddish fish (presumably *Sebastes* or *Helicolenus*, Scorpaenidae). That afternoon we found an even larger concentration, also at the edge of the shelf, near 39°40' S, 55°35' W. There, 10,000-12,000 Black-browed Albatrosses, 50 Royal/Wandering Albatrosses, 6,000 Cape Pigeons, and 500 Giant Petrels were feeding on offal from a large trawler. In each area sonar tracings revealed the presence of large schools of fish.

SEASONAL DIFFERENCES

Census data indicate few pronounced differences in the distribution and abundance of most species over the Argentine coastal shelf in winter. Apparently wintering populations are established by mid-June and remain largely stable through August. To obtain a more representative picture of average winter conditions, I pooled the data from all three transects. This procedure reduces bias from inadequate sampling on individual transects and minimizes differences caused by minor variations in routes. In Table 3 the combined data are compared with those gathered by Cooke and Mills in a rapid transect between Buenos Aires and Tierra del Fuego in summer. For convenience the data are grouped by 2° increments of latitude. The data from each season are not so complete as to inspire any great confidence as to their general applicability; however, they are the only available quantitative data and can be used to make preliminary comparisons of summer and winter patterns.

Differences between the summer and winter surveys are largely interpretable in terms of the breeding biology of particular species. For example, the high density of *Speniscus magellanicus* south of 44° S in summer is attributable to concentrations in the vicinity of nesting colonies; winter densities are lower because the species disperses widely over the northern shelf waters. A similar pattern of increased density near known or presumed southern nesting grounds in summer followed by northward dispersal in winter is shown by *Pachyptila* ssp. (presumably *P. belcheri* from the Falkland Islands), *Eudyptes crestatus*, and *Pelecanoides magellani*.

Albatrosses and Giant Petrels occupy the shelf waters year-round, with few differences in distribution or abundance. These species have long deferred maturity. If populations of great albatrosses in the area consist largely of pre-breeding-age individuals, as seems to be the case for *D. epomophora*, the lack of large seasonal differences would not be unexpected. However, the higher density of *Macronectes* in winter may reflect a post-nesting influx of adults. This is suggested by the apparent increase in adults in August 1972 as compared with earlier censuses. Large concentrations of *Diomedea melanophris* between 42-48° S in summer suggest locally rich feeding conditions that do not persist into the winter months.

Though not as pronounced, deferred maturity is also characteristic of smaller Procellariiformes (Ashmole, 1971: Table 2), and one would expect some non-breeders of most species to occur in the area throughout the year. The absence of fulmarine petrels (*Fulmarus glacialoides*, *Daption capensis*) in summer is probably attributable to their breeding biology: young birds tend to search for nesting sites at colonies several years in advance of active breeding (G. E. Watson, pers, comm.).

Procellaria aequinoctialis is resident in the southern hemisphere, nesting in the austral summer (Murphy, 1936: 644;. Its apparent predominance in summer seems unusual and may be due to concentrations of non-breeders near 44° S; the situation may be similar to that shown by *D. melanophris*. *Puffinus gravis* was virtually absent in winter, having migrated to the northern hemisphere; its abundance far from any known nesting grounds in summer presumably indicates a large population of non-breeding individuals (see also Watson, 1971; Tickell and Woods, 1972). Most *Puffinus griseus* winter in the northern hemisphere, but large numbers occur over the Argentine shelf all year. The limited data do not suggest any important differences in abundance between wintering and summering populations in the area, but there is an obvious shift northward in winter. However, much greater abundances are expected during periods of migration.

TABLE 3. A comparison of winter (W) and summer (S) seabird densities over the continental shelf of Argentina. Winter data are pooled from three transects (see text); summer data are from one transect (Cooke and Mills, 1972). Abundance indicated is number of birds per hour of observation. Species seen on fewer than five days are omitted from the winter sample.

		Latitude °S						
Species		40-42	42-44	44-46	46-48	48-50	50-52	52-54
Eudyptes crestatus	W	—	—	—	0.5	—	0.4	—
	S		—	—	—	—	—	0.5
Spheniscus magellanicus	W	5.4	5.4	1.7	0.5	0.5	0.8	—
	S		—	19.5	10.0	3.0	0.8	0.5
Diomedea exulans/ epomophora	W	0.3	0.6	—	0.1	0.1	6.0	0.4
	S		0.5	0.7	1.7	0.3	0.8	—
Diomedea melanophris	W	3.0	5.3	2.9	10.8	9.7	66	2.4
	S		9.2	32	13.2	5.5	0.8	3.5
Macronectes giganteus	W	2.8	3.1	3.6	2.8	6.8	8.0	3.1
	S		2.7	2.2	3.1	2.1	1.6	1.0
Fulmarus glacialoides	W	—	0.3	0.2	0.5	7.5	41	6.0
	S		—	—	—	—	—	—
Daption capensis	W	2.0	2.6	1.4	1.6	1.3	13.2	5.4
	S		—	—	—	—	—	—
Pachyptila spp.	W	2.5	2.5	0.8	2.1	8.0	78	4.4
	S		—	—	—	—	16.3	19.0
Procellaria aequinoctialis	W	2.1	7.5	0.8	2.1	0.7	6.8	5.6
	S		15.1	60	4.8	1.5	0.8	0.5
Puffinus gravis	W	—	—	—	—	—	—	—
	S		36	284	67	8.3	0.8	0.5
Puffinus griseus	W	120	36	18.0	1.7	2.4	—	3.6
	S		5.6	51	0.8	—	—	1.0
Puffinus puffinus	W	—	—	—	—	—	—	—
	S		—	—	—	4.4	—	—
Oceanites oceanicus (incl. petrel sp.)	W	1.1	2.5	0.5	0.2	0.2	—	—
	S		0.5	—	—	—	—	—
Pelecanoides magellani (and Pelecanoides sp.)	W	—	—	0.4	0.9	1.9	0.8	11.8
	S		—	—	—	—	27.6	2.5
Catharacta skua	W	0.5	0.1	0.2	—	—	—	—
	S		0.4	—	—	0.9	—	—
Stercorarius parasiticus (and Stercorarius sp.)	W	—	—	—	—	—	—	—
	S		0.6	0.7	3.5	40	0.8	—
Larus dominicanus	W	2.2	4.3	6.6	3.9	2.4	0.4	0.4
	S		—	—	—	—	—	0.5
Sterna hirundinacea	W	24.8	39.6	9.2	4.8	0.2	0.4	—
	S		—	—	—	—	—	2.0
Hours of observation	W	9.3	31.0	16.5	17.0	13.5	2.5	5.0
	S		6.2	2.7	2.3	3.2	1.2	2.0

Oceanites oceanicus and *Catharacta skua* were uncommon at both seasons, though more widespread and northerly in winter. Post-breeding northward dispersal in *Larus dominicanus* and *Sterna hirundinacea* is largely responsible for their predominance in the winter censuses, although the virtual absence of *L. dominicanus* in summer is partly attributable to the fact that Cooke and Mills' route was farther offshore than the normal range of this gull.

Two migrants from the northern hemisphere, *Puffinus puffinus* and *Stercorarius parasiticus*, occurred almost exclusively in their non-breeding season, the austral summer; at the latitudes under consideration the shearwater is very uncommon.

In all three winter transects the transition between the northern and southern shelf avifaunas occurred near 47° S. Cooke and Mills suggested that the transition zone was nearer 50°S in summer, but it seems to occur near Golfo San Jorge area in that season as well (Table 3, Fig. 5).

ECOLOGICAL CONSIDERATIONS

Despite their limitations, the quantitative data are useful in suggesting questions for future research. For example, do latitudinal or seasonal distributional patterns of sea birds suggest corresponding differences in the productivity of shelf waters. Neither the winter nor the summer data show any consistent relationship between latitude and sea bird abundance (Fig. 3), although in both seasons the highest concentrations were recorded in the northern half of the census area. Seasonal differences in abundance also seem minor, as the summer and winter curves correspond fairly closely over most of the range. (North of 40° S the winter data were largely gathered beyond the continental shelf.) Biomass is a more useful index to productivity, for it indicates the total mass of

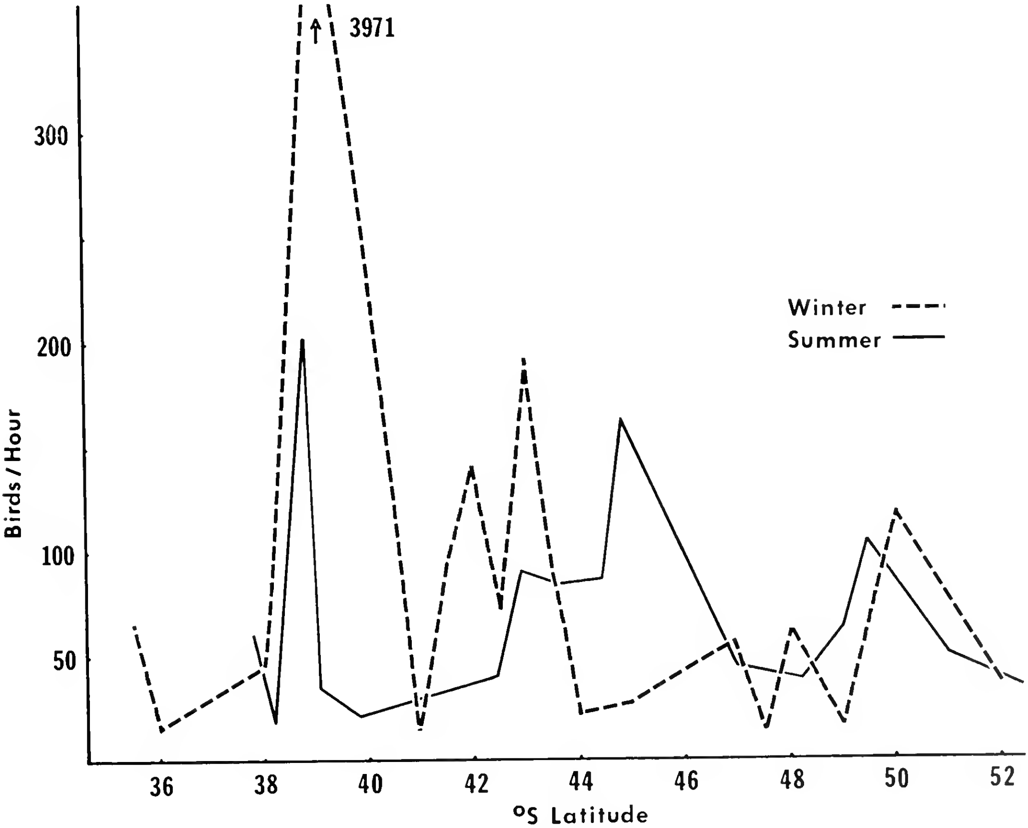

Figure 3. Sea bird abundance along the coast of Argentina, plotted to nearest 0° 30' of latitude. Winter data are pooled from three transects; summer data are from Cooke and Mills (1972).

organisms that is being maintained in an area. To obtain this statistic, the density of each species in Table 3 was multiplied by its average weight (Appendix) and the results were summed, giving grams/hours/2° increment of latitude. The data hint at increased biomass to the north (Fig. 4), but they are strongly biased by inadequate sampling, particularly at the higher latitudes. The winter peak at 50-52° S is especially suspect, being based on only 2-1/2 hours of observations on a single day. In summary, present data on sea bird abundance and biomass do not indicate marked seasonal or latitudinal differences in the productivity of the Argentine coastal waters. This conclusion is tentative and requires additional study.

A more interesting question is how seasonal and latitudinal differences in species composition may affect patterns of resource utilization. Table 4 presents a simplified ecological classification of sea birds modified after Ashmole (1971), which should be consulted for details. In this table, I have grouped the avifauna into nine categories based on size of bird, major feeding behaviors, and food preferences. The Shoemaker is separated from the other shearwaters partly because of its greater size and different feeding behavior, but mainly because it is resident in the southern hemisphere and therefore its ecological impact is expected to be more constant. Since total biomass at any latitude is variable (Fig. 4) and is strongly affected by census errors, the data have been converted to a percentage basis for each category. When these data are presented graphically (Fig. 5) the marked change in the ecological composition of the sea bird community at 46-48° S is emphasized.

In summer, north of this area, virtually the entire biomass is made up of large species that obtain their food from the upper meter of the sea, mainly by surface seizing or pursuit plunging (albatrosses, large and small shearwaters). The remainder consists largely of divers (penguins) that feed on fish. Groups that feed at least in part by filtering small organisms (fulmarine petrels, prions and storm-petrels) are absent. South of 46-48° S large surface feeders compose only 50-60 per cent of the biomass, and there is a sharp increase in the biomass of divers and filter feeders. The high percentage of gulls and skuas at 48-50° S is based on a concentration of Parasitic Jaegers. Jaegers typically derive much of their food by piracy; however, since likely prey species were rare or absent they may have been feeding by surface seizing or scavenging.

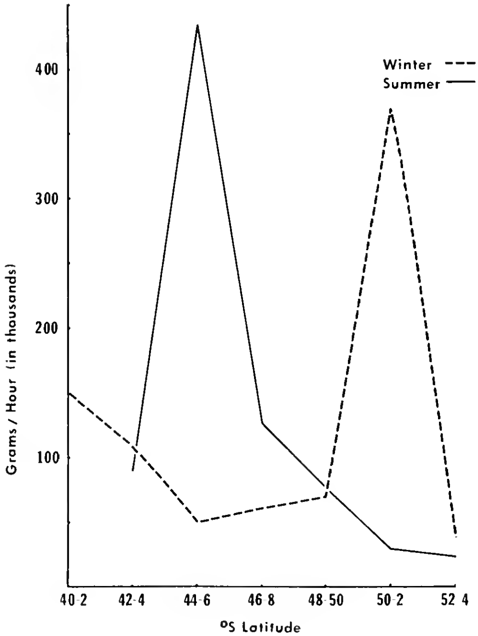

Figure 4. Seasonal relationship between biomass (grams/hour) and latitude along the coast of Argentina, plotted by 2° increments of latitude. Winter data are pooled from three transects, summer data are from Cooke and Mills (1972).

TABLE 4. A simplified ecological classification of seabirds (modified from Ashmole, 1971).

Group	Species	Weight	Major Food	Foraging Behavior
A. Albatrosses and giant petrels	Diomedea exulans D. epomophora D. melanophris Macronectes giganteus	Larger than 3000g	Fish, carrion, cephalopods	Surface seizing, scavenging
B. Fulmarine petrels	Fulmarus glacialoides Daption capensis	350-700g	Crustaceans, cephalopods, carrion	Surface seizing, filtering, scavenging
C. Gulls and skuas	Larus dominicanus Catharacta skua Stercorarius parasiticus	500-1500g	Varied	Scavenging, surface seizing, piracy
D. Prions and storm-petrels	Pachyptila spp. Oceanites oceanicus Garrodia nereis	30-130g	Small fish, plankton	Filtering, pattering
E. Large shearwaters	Procellaria aequinoctialis	1250g	Cephalopods, fish, crustaceans	Surface seizing, pursuit plunging
F. Smaller shearwaters	Puffinus gravis Puffinus griseus Puffinus puffinus	400-750g	Fish, cephalopods crustaceans	Surface seizing, pursuit plunging
G. Terns	Sterna hirundinacea	200g	Small fish	Plunging
H. Penguins	Spheniscus magellanicus Eudyptes crestatus	2500-4900g	Fish, cephalopods, crustaceans	Pursuit diving
I. Diving-petrels	Pelecanoides magellani Pelecanoides urinatrix	150-160g	Crustaceans, small fish	Pursuit diving

In winter the transition zone persists at 46-48° S, but biomass relationships are more complex. The proportion of surface feeders increases from about 75 per cent in the north to 90 per cent in the south. In the north this is divided among albatrosses, large and small shearwaters, and gulls; the remainder consists of diver (penguins) and plungers (terns). In the south albatrosses alone make up approximately 75 per cent of the biomass, the remainder being contributed by smaller surface feeders and filter feeders; the percentage of divers is much reduced, and plungers are absent.

Through the year the biomass contributed by some ecological groups remains fairly constant. Surface feeders dominate the shelf waters all year, and piratical feeders make up a fairly consistent though small proportion of the biomass. It is interesting, however, that major seasonal shifts in distribution shown by many species are not accompanied by a compensatory movement into the vacated area by taxa that utilize the similar foods. For example, penguins vacate the southern shelf in winter, and fulmarine petrels, prions, and diving-petrels shift northward. The biomass they contributed to southern waters is not replaced by other divers, small scavengers, or filter feeders but by large surface feeders. Also, terns congregate over the northern shelf in winter, an area that contained no plungers in summer. These shifts may indicate an increase in the spectrum of available food in winter. More likely, however, a wide variety of foods is present all year but cannot be exploited in summer because this area is too distant from nesting colonies.

Marine bird populations beyond the continental shelf.— The marine avifauna beyond the continental shelf differs importantly both in species composition and in relative abundance of species from that nearer shore. The major differences noted in winter have been discussed (p. 226). Tickell and Woods (1972) reported several species on transects between Montevideo, Uruguay, and the Falkland Islands from late spring to late autumn that we did not find over the shelf in winter. These included *Phoebetria palpebrata*, *Pterodroma macroptera*, *Pt. lessoni*, *Pt. incerta*, *Pt. mollis*, *Halobaena caerulea*, *Fregetta tropica*, *Fregetta grallaria*, *Stercorarius pomarinus*, and *S.*

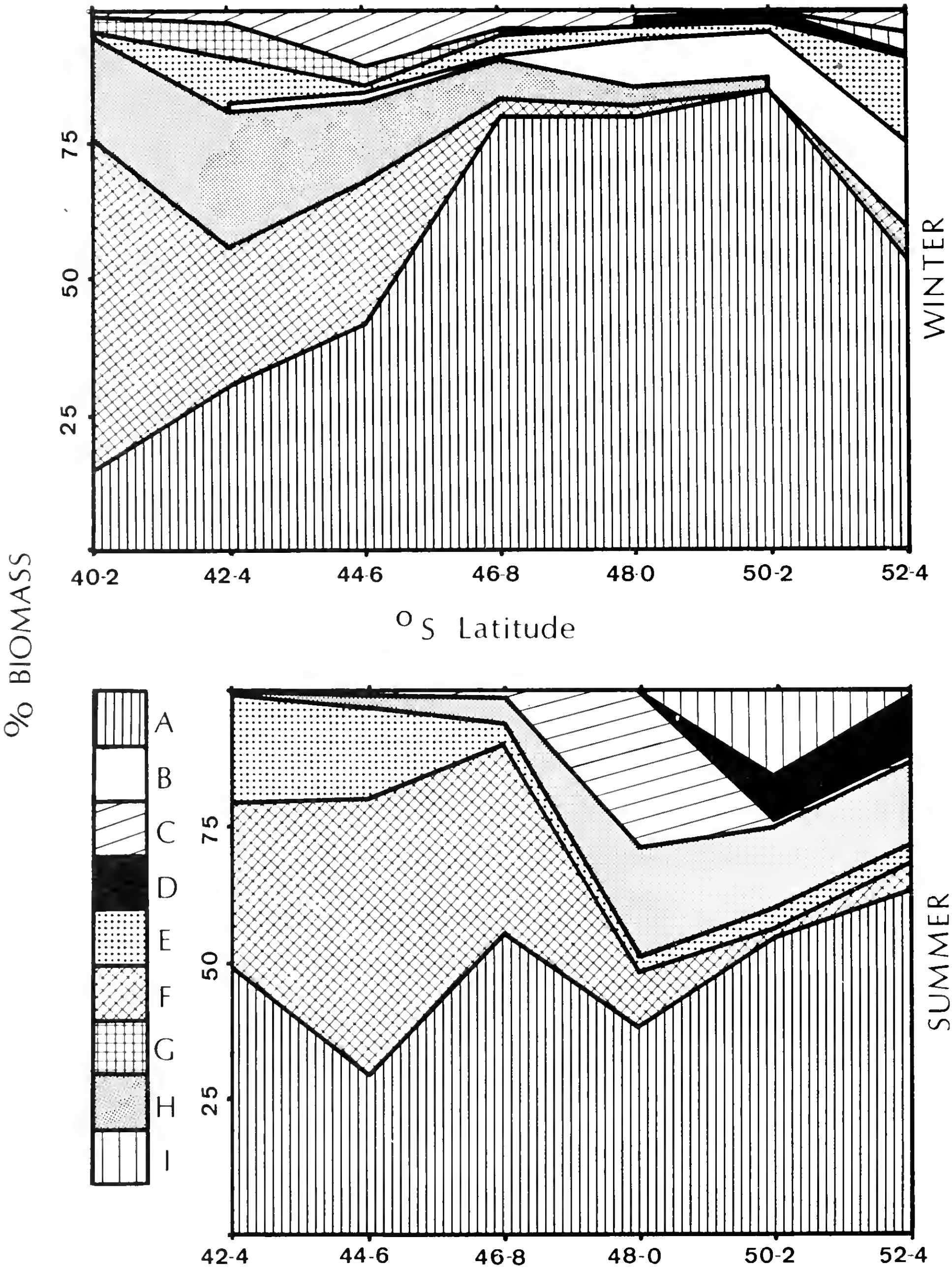

Figure 5. Biomass relationships of seabirds by feeding types, along the coast of Argentina in winter (upper) and summer (lower). Groupings comprising less than 1 per cent of the biomass for any period are not plotted. A. Albatrosses and giant petrels. B. Fulmarine petrels. C. Gulls and skuas. D. Prions and storm-petrels. E. Large shearwaters. F. Smaller shearwaters. G. Terns. H. Penguins. I. Diving-petrels.

longicaudus. Several other species e.g., (*Procellaria cinereus, Puffinus gravis, Garrodia nereis*) seemed to be far commoner in deep waters than near shore. Almost certainly, sea bird density, latitudinal patterns of abundance and distribution, and ecological patterns of resource utilization also differ significantly between these areas, but the only semi-quantitative data (Tickell and Woods, 1972) are insufficient to permit even preliminary comparison and analysis.

MORTALITY

In 1972 we found the desiccated remains of Magellanic Penguins every 30 m or so along the beaches of Golfo San José (Jehl et al., 1973); extensive mortality was also noted at Punta Norte and elsewhere on the Valdes Peninsula. Most of the birds had been dead for a long time, and although there was no evidence that the mortality had been caused by a single event, the majority of the carcasses were oiled. At sea it was not uncommon to observe oiled albatrosses, Giant Petrels, and Cape Pigeons. I made no quantitative estimates, but the incidence of oiling was greatest off northern Argentina, particularly in the vicinity of the Rio de la Plata. This heavily-trafficked area is close to one of the most important feeding grounds for sea birds in the South Atlantic (Murphy, 1936; Robertson and Kinsky, 1962; Cooke and Mills, 1972). In many miles of beachcombing in Golfo San José, I found the remains of few pelagic birds other than penguins, and none that were oiled. Flying birds are less likely than penguins to amass lethal doses of oil at one sitting, but even small amounts can break down the insulation of the feather coat and lead to death far from the area of contamination. Further, the pelts of Procellariiformes are less durable than the tough hides of penguins, and their bodies seem more likely to be devoured by Giant Petrels and other scavengers before they can drift ashore. I suspect that the incidence of sea bird mortality from oil pollution, even in the remote reaches of the South Atlantic, is more insidious and pervasive than the present documentary evidence indicates (see also Jehl, 1975).

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APPENDIX I
Weights of seabirds[1]

Eudyptes crestatus, 2500 (L). *Spheniscus magellanicus*, 4900 (L). *Diomedea exulans/epomophora*, 8500 (L, SSW, SD). *Diomedea melanophris*, 3600 (SD). *Macronectes giganteus*, 3000 (SSW, SD). *Fulmarus glacialoides*, 700 (J). *Daption capensis*, 350 (J). *Pachyptila* spp., 130 (J). *Procellaria aequinoctialis*, 1250 (SD). *Puffinus griseus*, 750 (J). *Puffinus gravis*, 650 (E). *Puffinus puffinus*, 400 (L). *Oceanites oceanicus*, 30 (L, J). *Pelecanoides magellani*, 160 (J). *Pelecanoides urinatrix*, 150 (SD, this paper). *Catharacta skua*, 1400 (SD). *Stercorarius parasiticus*, 500 (L). *Larus dominicanus*, 910 (SD). *Sterna hirundinacea*, 200 (SD).

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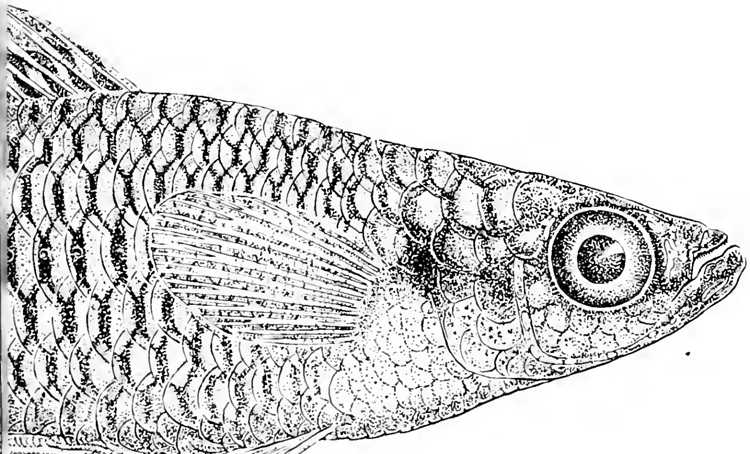
[1] References: L = Lack, 1968, appendix 17. J = Jehl, 1973a. SSW = Serventy, Serventy, and Warham, 1971. SD = specimens in San Diego Natural History Museum. E = estimate.

MEXICAN SPECIES OF THE GENUS *HETERANDRIA*, SUBGENUS *PSEUDOXIPHOPHORUS* (PISCES: POECILIIDAE)

ROBERT RUSH MILLER



TRANSACTIONS

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MEXICAN SPECIES OF THE GENUS *HETERANDRIA*, SUBGENUS *PSEUDOXIPHOPHORUS* (PISCES: POECILIIDAE)

ROBERT RUSH MILLER

ABSTRACT.— The subgenus *Pseudoxiphophorus* is currently regarded as monotypic, with a single widespread species, *Heterandria bimaculata*, inhabiting the Atlantic slope of Middle America. Actually, the taxon includes two sharply distinct species in México, the more primitive being *H. jonesi*; other species of *Pseudoxiphophorus* occur in Guatemala. The basis for recognizing subgenera of *Heterandria* is presented as well as a detailed comparison between *H. bimaculata* and *H. jonesi*, including illustrations of gonopodia, gonopodial suspensoria, and the whole fish. *Heterandria jonesi*, which occurs at elevations up to 2,385 meters, is close to the ancestral stock of the genus.

RESUMEN.— El subgénero *Pseudoxiphophorus*, de acuerdo a la literatura corriente, es considerado como monotipico, con una sola especie de amplia distribución, *Heterandria bimaculata*, que habita la vertiente Atlantica de México y America Central. Como se muestra aqui, en México hay dos especies claramente distintas, la mas primitiva siendo *H. jonesi*; otras especies de *Pseudoxiphophorus* existen en Guatemala. La base para reconocer subgéneros de *Heterandria* se presenta asi como una comparacion detallada entre *H. bimaculata* y *H. jonesi*, incluyendo ilustraciones de gonopodios, suspensores de gonopodio, y ademas de el pez completo. *Heterandria jonesi*, que occure a alturas hasta 2,385 metros, es cercano a el tronco ancestral de el género.

Until the recent general review of the Poeciliidae by Rosen and Bailey (1963), *Heterandria* and *Pseudoxiphophorus* were regarded as monotypic genera represented, respectively, by *H. formosa* Agassiz in Florida and adjacent coastal lowlands, and by *P. bimaculatus* (Heckel) from northeastern México southward and eastward into Nicaragua. Among ichthyologists publishing on *Pseudoxiphophorus* during this century, only Regan (1904-1913) consistently maintained that this subgenus comprises two fully distinct species, although Hubbs (1924-1936) divided *P. bimaculatus* into four subspecies, including the one that is here restored to full specific status. Rosen and Bailey (1963: 131), commenting on Hubbs' action, indicated that the characters distinguishing these forms "are apparently clinal and grade imperceptibly from one race to another." In attempting to distinguish forms of *Pseudoxiphophorus*, overemphasis has been placed on the dorsal-ray number which varies widely in the two species of this group in México. As usual in poeciliids, the detailed architecture of the gonopodium proves to have far more important systematic value, although the size and position of the dorsal fin is also highly useful. Color pattern helps to distinguish the Mexican species (*Pseudoxiphophorus*) but it is too variable for complete reliance.

Regan was correct in concluding that *P. jonesi* (restricted to east-central México) and *P. bimaculatus* are distinct species, even though the male of *jonesi* was unknown to him. As here shown for the first time, the gonopodium of *Heterandria jonesi* is consistently and sharply distinct from that of *H. bimaculata*. Although these species have overlapping ranges they are rarely taken together, as in central Veracruz (see below). My paper on the zoogeography of Middle American freshwater fishes (Miller, 1966) did not include the extralimital *H. jonesi*, but recognition of more than one species of *Pseudoxiphophorus* in México was implied in the range statement for *Heterandria bimaculata*, since the subgenus *Pseudoxiphophorus* ranges northward into southeastern Tamaulipas.

This paper presents a detailed comparison between *H. jonesi* and H. *bimaculata* in México, illustrates their distinctive gonopodia and suspensoria as well as the general form and appearance of each species, and discusses variation in coloration, body proportions, and meristic characters. The distribution of the two species is also treated and support is presented for the view that *H. jonesi* is closest to the common ancestor of the genus.

SAN DIEGO SOC. NAT. HIST., TRANS 17(17): 235-250, 28 JUNE 1974

MATERIALS AND METHODS

Specimens examined came from the following museum collections: BMNH, British Museum (Natural History), P, Instituto Politecnico Nacional (México), UMMZ, University of Michigan Museum of Zoology, USNM, United States National Museum. I am grateful to P.H. Greenwood for making a syntype of *Mollienisia jonesii* available, to José Alvarez for the loan of topotypes of that species, to William M. McLane and Brandon McNair for information regarding the sympatric occurrence of *H. bimaculata* and *H. jonesi*, to Royal D. Suttkus for the loan and exchange of specimens, to the staff of the National Museum of Natural History (USNM) for facilities and working space, and to the John Simon Guggenheim Memorial Foundation for support as a Guggenheim Fellow while preparing this manuscript. Appreciation is also extended to Martha B. Lackey, former staff artist of the Museum of Zoology, for the accompanying illustrations, except Figure 4, drawn by Patricia J. Wynne, current staff artist. I am grateful to Mexican officials for permission to collect fishes in their country.

Table 1. Distinguishing characters of the subgenera of *Heterandria*.

Character	*Heterandria*	*Pseudoxiphophorus*
Gonopodium (Fig. 2):		
Serrae on posterior margin of ray 4p	7-9	9-18
Segments beyond distalmost serrae of ray 4p	5 or fewer	5 or more
Tip of ray 5a	Extends beyond tip of ray 4p	Extends to or falls short of of tip of ray 4p
Distal part of ray 3	Widely separated from ray 4	Closely adjoining ray 4
Gonopodial suspensorium (Fig. 3):		
Ligastyle	Reduced to an oval remnant below 10th vertebra	An elongate bone lying below 11th vertebra
Tip of gonapophysis I	Extends ventrally about 1/3 way from vertebral column to insertion of pelvic fin	Extends ventrally more than 1/3 to 1/2 way from vertebral column to insertion of pelvic fin
Reproductive biology:		
Superfetation	Strongly developed[1]	Absent as far as known
Egg size at fertilization, in mm[2]	0.37-0.40	2.08-2.56
Brood interval[3]	Averaging 5-6 days (small broods)	35-40 days (large broods)
Size	Minute; largest mature male ca. 14 mm S.L.	Moderate; smallest mature male (*jonesi*) ca. 22 mm S.L.
Dorsal fin of female	About equal in size to anal, its origin behind anal origin, over 16th or 17th vertebra	Much larger than anal, its origin usually farther forward (behind in one species), over 12th to 15th vertebra[4]
Dorsal rays	6-8	9-18
Vertebral number	Sexually dimorphic; males 32-34, females 30-33 (Table 4)	No sexual dimorphism; total variation, 30-34

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[1] As many as 6 stages of developing embryos in a single ovary (Turner, 1937).

[2] From Scrimshaw, 1946; based on *H. formosa* and *H. bimaculata* only.

[3] At height of reproductive season (Turner, 1937).

[4] Over 16th in one form in Alta Verapaz, Guatemala (D.E. Rosen, pers. comm.)

Counts and measurements were made as prescribed by Hubbs and Lagler (1958: 19-26). Measurements are expressed as permillages of the standard length; they were taken with dial calipers reading to the nearest tenth of a millimeter. One ratio (length of depressed dorsal into predorsal length) was stepped off with a pair of dividers and estimated to the nearest tenth. A second ratio (base of dorsal fin into predorsal length) was measured with calipers, converted into permillages, and mathematically calculated—a more accurate and objective means of obtaining the required figures. The vertebral count includes the hypural plate as the terminal vertebra; the second vertebra is the first rib-bearing one in all cyprinodontoids.

CHARACTERS OF THE TWO SUBGENERA

When only two species were assigned to *Heterandria*, the need for subgeneric recognition was minimal. Now that *Pseudoxiphophorus* is polytypic (probably containing three or more species—Miller, 1966, and Rosen and Bailey, MS), it is helpful to employ the subgenus when discussing the Middle American forms. Consequently I have drawn up a comparison (Table 1) which provides a biological as well as a structural basis for recognizing two subgenera of *Heterandria;* some may feel the differences are sufficient for generic recognition. Characters that indicate a close relationship between *Pseudoxiphophorus* and *Heterandria* involve the morphology of the reproductive system and the breeding behavior as well as the osteology of the skull (as pointed out by Rosen and Bailey, 1963: 128-129). Another interesting common feature discovered in the present study is the marked sexual dimorphism in the length of the snout: *H. jonesi*—43 males, 78-96; 47 females, 92-111. *H. bimaculata*—30 males, 82-100; 30 females, 94-111. (Figures are permillage of standard length; see Table 3.) *H. formosa*—10 males, 58-75; 10 females, 76-89. Another interesting aspect of the comparison is the sexual dimorphism in vertebral number in subgenus *Heterandria* only: males, 32 (8), 33 (26), 34 (3); females, 30 (1), 31 (13), 32 (18), 33 (1)—Table 4. The tiny egg of the subgenus *Heterandria* is correlated with the high degree of dependence on the mother for nourishment by the developing embryo. Such virtual elimination of yolk is paralleled in certain species of *Poeciliopsis* (e.g., *Poeciliopsis elongata* [Günther] and *P. prolifica* Miller—see Schultz and Thibault, MS), in which superfetation is also strongly developed. Presumably superfetation is not developed in subgenus *Pseudoxiphophorus* (checked only in *H. bimaculata* and *H. jonesi*).

THE MEXICAN SPECIES

Heterandria jonesi (Gunther)
(Figs. 1-3)

Mollienisia jonesii.— Günther, 1874: 371 (original description, based on females only; Lago Alcuhuaca, México = Lago de Aljojuca — see Alvarez, 1950).

Gambusia jonesii.— Regan, 1907: 260 (name; comparisons). Regan, 1906-08: 94, 97-98, pl. 12, fig. 8 (key; description; synonymy; female syntype figured; distribution).

Pseudoxiphophorus jonesii.— Regan, 1913: 993 (synonymy; description; range).

Pseudoxiphophorus bimaculatus jonesii.— Hubbs, 1924: 17-18 (characters; synonymy). Alvarez, 1950: 88-91 (redescription of topotypes; correction of type locality to Lago de Aljojuca, 15 km NE of Ciudad Cerdán, Puebla; comparison with sample from Tepeaca, Puebla, in Río Balsas basin).

Pseudoxiphophorus bimaculatus (misidentification).— Woolman, 1894: 55-56 (description; Río Blanco at Orizaba). Jordan and Evermann, 1896: 678 (description, based on Orizaba specimens). Meek, 1904: 127 (in part; Orizaba records only).

Heterandria bimaculata (misidentification).— Rosen and Bailey, 1963: 131 (in part; references to *jonesi* and *pauciradiatus*).

Pseudoxiphophorus reticulatus (misidentification).— Jordan and Evermann, 1896: 678, footnote (description of specimens from Río Blanco at Orizaba, where only *H. jonesi* occurs).

Pseudoxiphophorus pauciradiatus.— Regan, 1904: 256 (original description, based on 8 of Woolman's specimens from Orizaba). Regan, 1905: 362-363 (validity of species; comparison with *bimaculatus*). Regan, 1907: 260 (listed as synonym of *Mollienisia jonesii*).

Diagnosis.—A species of the subgenus *Pseudoxiphophorus* (Table 1) distinguished from *H. bimaculata* as follows (see also Table 5): Terminal segment of ray 4a of gono-

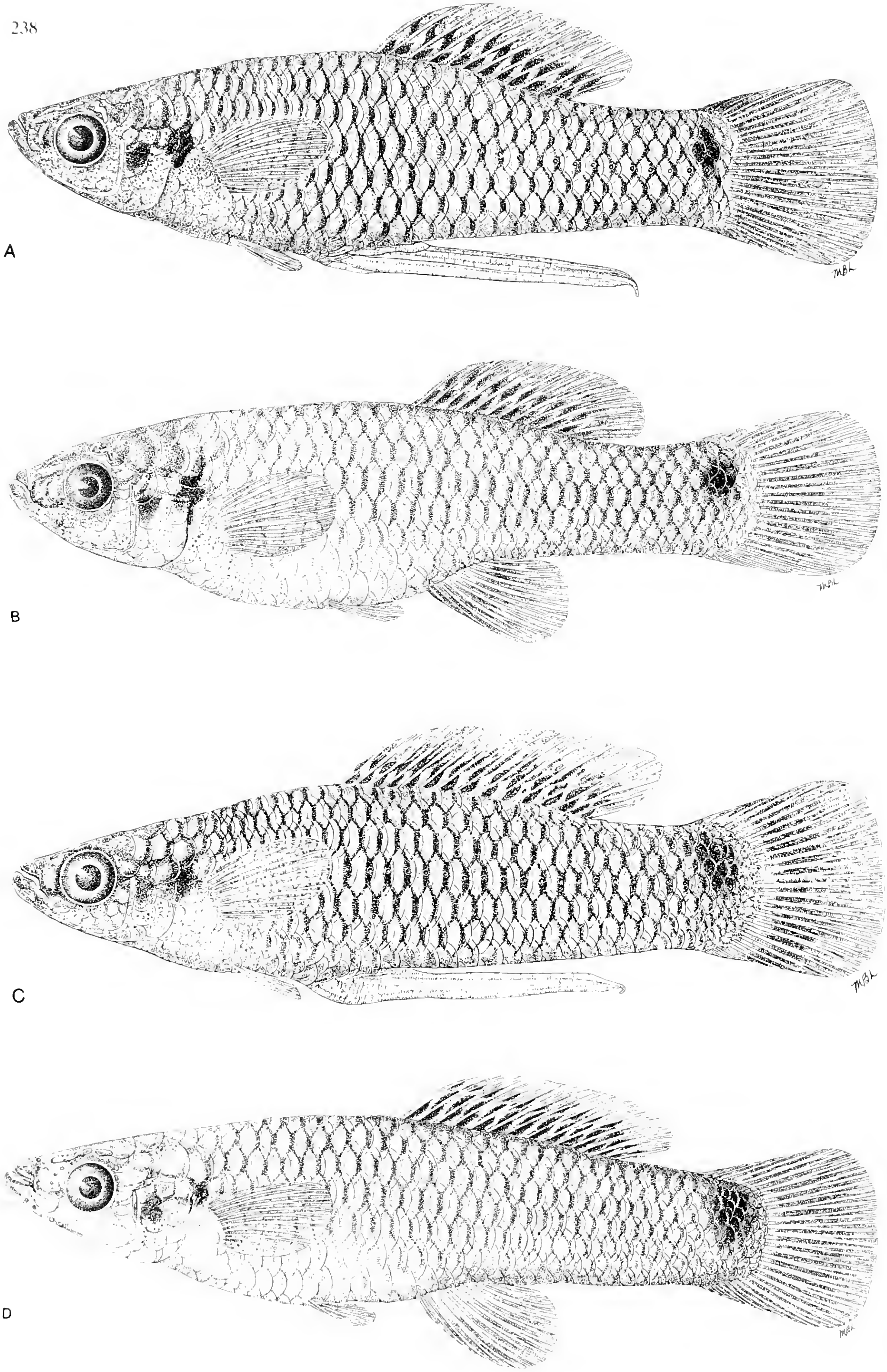

Figure 1. Top to bottom: *Heterandria jonesi*, adult male, 37 mm, Rancho Sierra de Agua, Orizaba Valley (UMMZ 183894); *Heterandria jonesi*, adult female, 43.5 mm, from same collection (topotypes of *P. pauciradiatus* Regan); *Heterandria bimaculata*, adult male, 35.5 mm, Nacimiento de Cosolapa (UMMZ 183902); *Heterandria bimaculata*, adult female, 50 mm, from same collection.

podium short (not longer than 2-3 subdistal segments and often barely exceeding penultimate one), slightly recurved, not reaching tip of enclosing membrane; anterior margin of subdistal segments of ray 4a smooth; ray 4p forming part of curved tip of gonopod (Fig. 2). Base of dorsal fin enters predorsal length 1.6 to 2.4 times in males, and 2.0 to 2.9 times in females; depressed dorsal fin enters same distance 1.2 to 1.6 (rarely 1.1) times in males, and 1.4 to 2.0 times in females. Origin of dorsal fin more posterior (Table 3). Basicaudal spot generally smaller, lower, and more anterior, lying mostly on caudal peduncle.

Type locality.—This species was described from Lago de Aljojuca, a crater lake or *axalapazco* (Tamayo, 1964: 113) in the endorheic part of the high Puebla Plateau (Llanos de El Salado), 15 km northeast of Ciudad Cerdán, Puebla, and west of the great volcano Pico de Orizaba (5,750 m) at an elevation of 2,385 m (Alvarez, 1950, 1972). Apparently it is the only fish native to this lake, although three other similar lakes to the north each

Table 2. Variation in number of dorsal fin rays in two species of *Heterandria* from México.

Cat. no. and/or authority and locality[1]	Number of dorsal rays									No.	Avg.
	9	10	11	12	13	14	15	16	17		
H. jonesi											
P 203, Alvarez, 1950 (topotypes)[2], Lago de Aljojuca, Puebla	—	—	70	34	—	—	—	—	—	104	11.33
P 184, Tepeaca, Puebla (Balsas basin)	—	—	6	13	1	—	—	—	—	20	11.75
183986, Acosac, Puebla (Balsas basin)	—	—	17	13	—	—	—	—	—	30	11.43
186675, Tehuacán, Puebla (Papaloapan basin)	—	—	1	22	7	—	—	—	—	30	12.20
183894, Hubbs, 1924, 1926, Orizaba Valley	—	—	38	149	14	7	3	—	—	211	12.00
162143, Río Atoyac, Veracruz[3]	1	3	48	43	1	—	—	—	—	96	11.42
183896, Río Atoyac, Veracruz	—	—	96	29	—	—	—	—	—	125	11.23
124304, Río Necaxa, Puebla (Tecolutla basin)	—	—	—	24	20	3	—	—	—	47	12.55
193493, 42 km WSW Poza Rica, Veracruz (Cazones basin)	—	—	1	12	5	1	—	—	—	19	12.32
124330, 162141, Palitla, S.L. Potosí (Pánuco basin)	—	—	—	19	54	3	—	—	—	76	12.79
183887, Jaumave, Tamaulipas (Tamesí basin)	—	—	—	—	8	24	3	—	—	35	13.86
H. bimaculata											
Hubbs, 1924, 1926, Jico and Jalapa, Veracruz (Chachalacas basin)	—	—	—	2	30	11	2	—	—	45	13.29
USNM 31023, 45489, Mirador, Veracruz (Chachalacas basin)	—	—	—	—	6	23	4	—	—	33	13.94
162144, Río Atoyac, Veracruz[4]	—	—	—	—	8	26	4	—	—	38	13.89
181309, Hubbs, 1924, 1926, Córdoba, Veracruz (subtopotypes)	—	—	—	1	7	30	13	—	—	51	14.08
Regan, 1905, Río Tonto, Veracruz (Papaloapan basin)	—	—	—	—	—	5	7	3	—	15	14.87
183902, Cosolapa, Oaxaca (Papaloapan basin)	—	—	—	3	12	32	13	—	—	60	13.92
124234, 4 km E El Hule, Veracruz (Papaloapan basin)	—	—	—	3	21	28	1	—	—	53	13.51
Regan, 1905, in Hubbs, 1924, Sto. Domingo Petapa, Oaxaca (Coatzacoalcos basin)	—	—	—	—	—	1	3	1	1	6	15.33
178533, Río Sarabia, Oaxaca (Coatzacoalcos basin)	—	—	—	—	—	12	23	16	—	51	15.08

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[1] Catalog numbers are those of UMMZ unless otherwise stated.

[2] In 28 loaned from this series I counted 11 (22), 12 (6). Also included is a count of 12 on a syntype, BMNH 1873.1.13.1 (illustrated by Regan, 1906-08: Pl. 12, Fig. 8).

[3] Sympatric with *bimaculata* (162144).

[4] Sympatric with *jonesi* (162143).

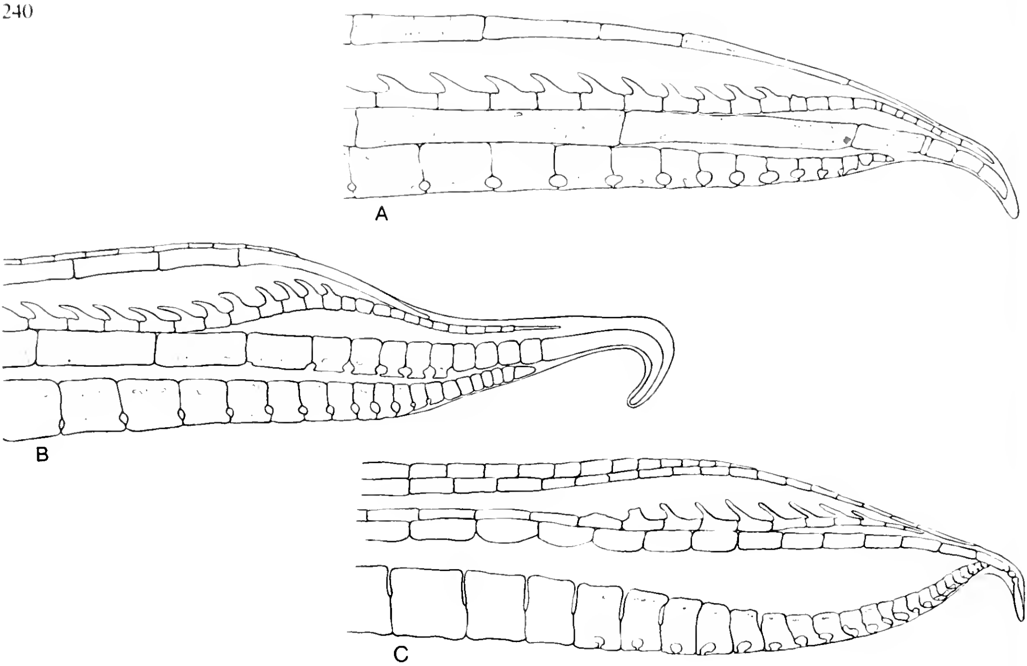

Figure 2. Gonopodia of: A. *Heterandria jonesi*; B. *Heterandria bimaculata*; C. *Heterandria formosa.*

contain an atherinid of the genus *Poblana* (=*Chirostoma;* see Bolland and Barbour, MS). The fish was named for its discoverer, T.M. Rymer Jones.

Variation.—The gonopodium (Figs. 2, 3) provides the major criterion for distinguishing *H. jonesi* from its relatives. It is therefore important to know how much it varies. The three characteristics given in the diagnosis include the variation known for the populations examined. Other features follow. Ray 3 terminates near the proximal end of segments 3 to 6 of ray 4a. There is sharp transition between the several elongate proximal segments of ray 4a and the short subterminal segments. There is always a rather abrupt change in height and size between the most proximal serra-bearing segment of ray 4p and the next succeeding segments of this ray. These shorter segments, which precede the last one of ray 4a, vary from 2 to 5. Ray 4p has from 12 to 18 strong, retrorse serrae. Ray 5a ends about 2 to 4 segments from the tip of ray 4a.

Ten measurements were made on males and females of four populations of *H. jonesi* (Table 3) representing: (1) the type locality of the species (Aljojuca), at 2,385 m; (2) the type locality of *P. pauciradiatus* (Orizaba), at 1,240 m; a locality (Palitla) in the southern part of the Río Pánuco basin, at about 120 m; and the northernmost known population (Jaumave), in the headwaters of the Río Guayalejo, at about 330 m. These data show that: (1) Aljojuca and Orizaba specimens have the shortest dorsal-fin base, Jaumave the longest, with Palitla intermediate; (2) Jaumave females have the longest anal fin, Orizaba and Aljojuca the shortest, with Palitla somewhat intermediate; (3) the caudal fin is longest at Jaumave, generally shortest at Orizaba and Aljojuca, and again somewhat intermediate at Palitla, although the measurements do not overlap those at Jaumave; (4) body depth varies greatly, in part because of the reproductive condition of the female, as at Aljojuca (see below); (5) head length shows little or no sexual dimorphism at Aljojuca, Orizaba, or in the Río Atoyac at Atoyac (10 males, 269-283, ave. 273, 10 females, 260-280, ave. 269), but is dimorphic at Palitla and Jaumave (and might be found to be so in populations at lower elevations between Atoyac and Palitla); (6) snout length is sharply dimorphic between the sexes at all four localities, as are predorsal length and distance between dorsal origin and base of caudal fin; but that (7) the distance from anal origin to caudal base is neither sexually dimorphic nor significantly different in the four samples.

The number of dorsal-fin rays is highest at Jaumave, among the lowest at Aljojuca, and intermediate at Palitla (Table 2).

Vertebral number is rather consistently 32, varying from 31 to 33, in Puebla and adjoining parts of Veracruz, but shows a decrease toward the north (southwest of Poza

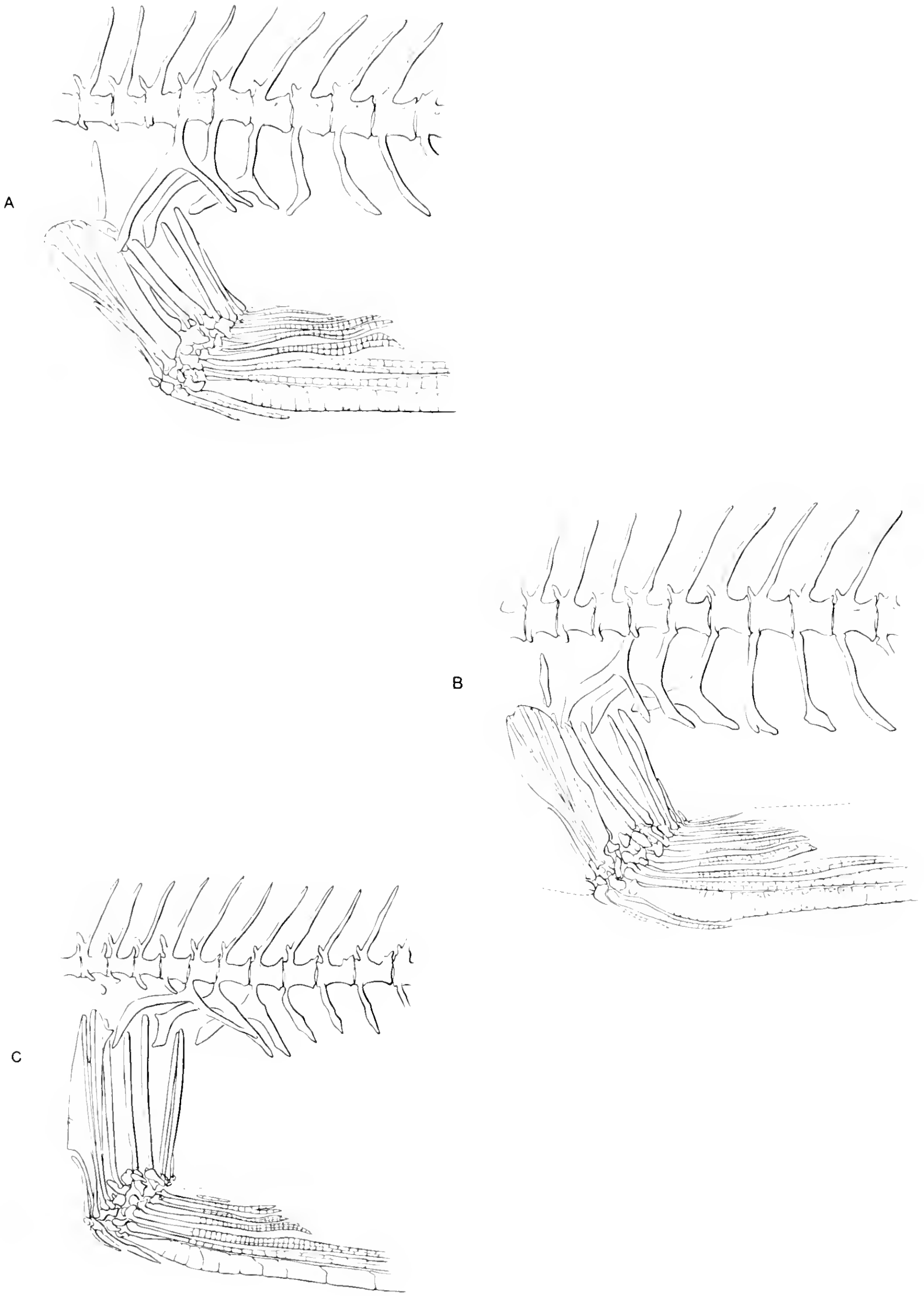

Figure 3. Gonopodial suspensoria of: A. *Heterandria jonesi*; B. *Heterandria bimaculata*; C. *Heterandria formosa*. (From same specimens illustrated in Fig. 2.)

Rica, in the Río Cazones basin), especially at Jaumave, where the mode is 31 and the range 30 to 32 (Table 4).

Color pattern is rather consistent for the populations from the Puebla Plateau (Alojojuca, Tepeaca, Acosac), the Orizaba Valley, and the Río Atoyac. They are moderately to strongly barred, with 3 to 11 rather narrow and usually short, vertical bars confined to the midside from just behind the base of the pectoral fin to just before the basicaudal spot. Generally, the larger fish have the most bars. These vary from 5 to 9 in the

Table 3. Proportional measurements of *Heterandria jonesi* and *H. bimaculata* (in permillage of standard length).

	Heterandria jonesi				*H. bimaculata*	
	Aljojuca P 203	Orizaba 183894	Palitla 162141	Jaumave 183887	Córdoba 108614+ 181309	Cosolapa 183902
Standard length, Range (mean) No.						
Males	23.0-36.1 (27.2) 7	23.6-36.1 (30.9) 15	24.4-37.1 (30.1) 14	22.8-27.1 (25.4) 7	30.1-48.4 (38.9) 15	25.5-51.9 (39.2) 15
Females	31.1-41.6 (38.2) 4	29.9-55.5 (41.5) 15	30.1-55.0 (38.9) 13	26.0-47.1 (36.7) 15	32.7-68.4 (50.0) 15	43.1-76.2 (55.9) 15
Body depth						
Males	267-290 (282)	264-295 (280)	264-297 (281)	266-306 (293)	253-290 (270)	249-288 (267)
Females	255-283 (267)	274-333 (299)	271-296 (282)	296-323 (310)	240-281 (261)	248-281 (265)
Predorsal length						
Males	516-534 (525)	500-538 (516)	489-532 (519)	498-522 (510)	453-494 (470)	452-486 (470)
Females	575-593 (587)	568-597 (582)	553-573 (563)	561-589 (576)	496-536 (520)	516-546 (528)
D. Origin to C. base						
Males	490-518 (500)	495-520 (507)	492-531 (515)	515-533 (523)	540-583 (563)	539-571 (554)
Females	421-430 (426)	427-461 (445)	456-483 (466)	450-476 (462)	477-514 (500)	479-508 (493)
A. origin to C. base						
Females	437-453 (445)	413-452 (437)	431-448 (439)	422-450 (437)	431-470 (455)	438-460 (449)
Head length						
Males	270-287 (279)	263-280 (269)	263-296 (278)	266-276 (270)	266-287 (276)	250-275 (261)
Females	270-286 (279)	263-293 (277)	276-308 (295)	272-300 (284)	252-306 (281)	252-282 (267)
Snout length						
Males	78-89 (83)	78-87 (82)	86-96 (92)	79-82 (81)	85-100 (92)	82-96 (89)
Females	93-97 (95)	92-105 (98)	99-111 (105)	92-103 (98)	89-108 (102)	94-107 (101)
C. peduncle depth						
Males	163-177 (170)	158-176 (168)	148-186 (169)	166-193 (184)	165-186 (178)	157-190 (178)
Females	147-151 (150)	144-161 (151)	160-171 (164)	172-183 (176)	155-178 (162)	153-168 (161)
D., basal length						
Males	235-255 (244)	225-256 (245)	268-299 (284)	302-325 (309)	326-369 (348)	329-358 (342)
Females	205-210 (207)	202-226 (213)	242-267 (253)	264-290 (274)	284-310 (300)	273-315 (302)
A., depressed length						
Females	190-203 (196)	182-211 (196)	203-225 (213)	234-252 (244)	193-239 (212)	199-243 (220)
C., length middle rays						
Males	238-258 (248)	221-245 (232)	237-275 (258)	279-289 (283)	227-260 (239)	231-275 (248)
Females	220-227 (223)	206-231 (215)	225-256 (246)	257-284 (271)	203-239 (218)	201-230 (216)

material examined from Aljojuca, although large females (such as the syntype figured by Regan, 1906-08: pl. 12, fig. 8, 65 mm S.L., examined by me) may show no trace of bars. At Acosac, adults of both sexes have from 3 to 8 bars, although a 63-mm female lacks them. In the Orizaba Valley, 45 fish (30 males, 15 females) have from 4 to 10 bars. Vertical bars are most strongly developed in the two samples from Río Atoyac, wherein all fish (including young only 11 mm long) are barred, and the number of bars varies in 53 adults from 6 to 11, usually 8 to 10. In the Río Cazones drainage (42 km WSW of Poza Rica), the bars on males are weakly developed (1-7 in 14) and are apparently lacking in females and juveniles. At Palitla, bars are also weakly developed in males (from none to 7) and none is evident in females or juveniles. The extreme variation is attained at Jaumave, where none of the fish collected show vertical bars. The basicaudal spot, also quite uniform from the Puebla Plateau to Río Atoyac, is rather small, generally oval, and lies mostly on the base of the caudal peduncle not far above the body axis (Fig. 1). In the Río Cazones collection, the spot is larger, higher, and almost as much of it lies on the caudal fin as on the peduncle, thus more closely approaching the basicaudal spot typical of *H. bimaculata.* At Palitla, the spot is more like that at Río Atoyac except that it lies higher above the body axis. At Jaumave, the basicaudal spot is similar to that at Palitla but tends to become obsolete in large females.

Biology.—As suggested above, body depth in females is strongly influenced by pregnancy. In the four mature females measured from Aljojuca (Table 3), collected 21 May 1949, there were large mature eggs but no embryos. Permillage values for body depth are from 255 to 283 (avg. 267), whereas in 43 females from the three other localities (with mean standard lengths not greatly different from those of the females from Aljojuca) these values are from 271 to 333 (avg. 282, 299, 310). Clearly the reproductive season is much shorter at Aljojuca (2,385 m) than it is at the lower elevations. For example, in the 10 largest and fattest females, collected 18 March 1968 from Acosac (UMMZ 183986, ca. 1,830 m), one had advanced embryos, one had early embryos, and eight were packed with large eggs—demonstrating that at this lower elevation the reproductive season was well under way, even though the fish were taken earlier in the year. At still lower elevations production probably occurs over a long time span as suggested by the two collections made during the latter half of December from Atoyac (UMMZ 162143) and Palitla (UMMZ 162141), each of which contains individuals as small as 11 mm.

It is a general observation for poeciliids (but not for all viviparous cyprinodontoids—e.g., goodeids, Fitzsimons, 1972: 730) that males have determinate growth and attain maturity at widely different sizes. This is abundantly supported for *H. jonesi* by the following data giving the frequencies for each standard length measurement (rounded to nearest whole number) followed by number of specimens and mean value: Orizaba Valley (UMMZ 183894), 24 (7), 25 (16), 26 (9), 27 (9), 28 (11), 29 (8), 30 (2), 31 (4), 32 (3), 34 (6), 35 (3), 36 (2), in 80, range 23.6-36.1 mm, mean 28.1 mm; Rio Atoyac at Atoyac (UMMZ 183896), 27 (1), 29 (1), 30 (1), 31 (2), 32 (1), 35 (1), 36 (2), 37 (7), 38 (3), 39 (2), 41 (1), 42 (1), 45 (1), 46 (1), 25, 37.5 (range 27.5-45.7 mm). The Orizaba collection is from a spring-fed, roadside ditch, whereas the Atoyac collection is from a large river.

At only one locality and at only one time were *H. jonesi* and H. *bimaculata* taken together and then the circumstances were unusual although the data on number of dorsal rays suggest that sympatry may be normal in this area. The collection was made by W. McLane and B. Schultz on 23 December 1940 in the Río Atoyac (then in flood), 6.5 km north of Hacienda Potrero Viejo (E of Córdoba and N of Hwy 150) and contains 96 specimens of *H. jonesi* (11-53 mm, UMMZ 162143), including one transforming male, and 38 of *H. bimaculata* (10-40 mm, UMMZ 162144), including one mature male. The dorsal rays (Table 2) show an overlap only at 13 rays; the 8 specimens of *H. bimaculata* with that number are discussed under Variation in the account of that species.

Range.—The northern limit of this species (Fig. 4) is the Río Guayalejo of southeastern Tamaulipas, the major tributary of the Río Tamesí, where it must be scarce. Darnell (1962) failed to take *Heterandria* in the 66 collections (totaling over 11,000 fishes) made during 1950-53 in the Tamesí basin, and that only two collections are known from that drainage: 2 specimens from near the bridge just west of Nuevo Morelos, Tamaulipas, Rosen and Gordon, 18 January 1957 (specimens lost), and 94 from Jaumave, discussed herein. The species is probably widespread in suitable habitats throughout the Río Pánuco basin (up to elevations near 2,000 m—e.g., Tula, Hidalgo) southward to the Río

Table 4. Number of vertebrae in three species of *Heterandria* from México and Florida.

Species, cat. no.[1], locality	Number of vertebrae					No.	Avg.
	30	31	32	33	34		
H. jonesi (México)[1]							
P 203, L. Aljojuca, Puebla (topotypes)	—	—	12	2	—	14	32.14
P 184, Tepeaca, Puebla (Balsas basin)	—	2	8	—	—	10	31.80
183986, Acosac, Puebla (Balsas basin)	—	—	13	—	—	13	32.00
187718, Orizaba Valley, Veracruz	—	—	19	6	—	25	32.24
183896, Río Atoyac, Atoyac, Veracruz	—	4	24	1	—	29	31.90
193493, WSW Poza Rica, Veracruz (Cazones basin)	—	11	6	1	—	18	31.44
162141, Palitla, S.L. Potosí (Pánuco basin)	—	4	22	—	—	26	31.85
183887, Jaumave, Tamaulipas (Tamesí basin)	5	24	1	—	—	30	30.87
H. bimaculata (México)[1]							
USNM 31023, 45489, Mirador, Veracruz (Chachalacas basin)	—	1	13	—	—	14	31.93
108614, 181309, Córdoba, Veracruz (subtopotypes)	—	—	13	17	—	30	32.73
183902, Cosolapa, Oaxaca (Papaloapan basin)	—	—	12	7	1	20	32.45
124234, near El Hule, Veracruz (Papaloapan basin)	—	8	8	—	—	16	31.50
178533, Río Sarabia (Coatzacoalcos basin)	—	3	20	1	—	24	31.92
H. formosa (Florida)							
USNM 133265, Crows Bluff, Deland, males	—	—	2	12	1	15	32.93
females	1	7	9	—	—	17	31.47
USNM 210703, Monroe Station, Tamiami Trail, males	—	—	6	14	2	22	32.82
females	—	6	9	1	—	16	31.69

[1] All catalogue numbers are UMMZ, except as noted. Localities under *H. jonesi* are arranged from high to low elevations (Aljojuca to Atoyac) and from south to north (Poza Rica to Jaumave); under *H. bimaculata*, they are arranged from north to south.

Nautla. The species reappears in the Río Atoyac, southwest of Veracruz (City), and is the only *Heterandria* of the Orizaba Valley and the streams, irrigation ditches, and crater lakes (Aljojuca only) of the Puebla Plateau, where it occurs as high as 2,385 m. In this elevated region it lives in tributaries of the Río Balsas and Río Papaloapan as well as in waters without exit to the sea. Its distribution south of the latitude of Tehuacán (1,649 m) is unknown, but it has not been found in the lowlands of the Papaloapan basin or anywhere in the Río Coatzacoalcos system, the next major drainage to the south.

Zoogeography.—The occurrence of *Heterandria jonesi* in a high-elevation crater lake (Aljojuca) in the endorheic, semidesert basin (area ca. 8,000 km^2) occupied by the Llanos de Puebla or San Juan (Tamayo, 1964: 113, Fig. 4) calls for explanation. The remnant native fish fauna (*Chirostoma*, *"Poblana"*, and *Heterandria*) in this area indicates that the interior basin they now occupy was connected with at least three different major drainages during late Cenozoic time. Barbour (1973) has presented convincing biological evidence to tie the area in with the Río Lerma basin via the Valle de México. The occurrence of the cyprinid *"Aztecula vittata* (Girard)" in Pleistocene lake deposits and an adjacent Recent tributary of the Balsas basin just south of the city of Puebla (Miller and Uyeno, MS) demonstrates a former connection between the Valle de México, Llanos de San Juan, and the Río Balsas drainage. Finally, the occurrence of the otherwise exclusively Atlantic (in México) subgenus *Pseudoxiphophorus* in both Lago de Aljojuca and in Río Balsas tributaries proclaims a former connection between the Llanos de San Juan, the Atlantic slope, and the Balsas system.

Why does not *Heterandria jonesi* also occur in the three other fish-inhabited crater lakes and in Laguna de El Carmen (the large marsh-like, shallow lake just west of the crater lakes)? Probably because those lakes contain species of atherinids that either prey on the newborn young of the poeciliid or outcompete *Heterandria* in other ways. Lago de Aljojuca contains only *Heterandria* which elsewhere in this plateau region occurs only in spring-fed ditches and ponds that contain no other fishes.

Alvarez (1972) has presented the following hypothesis to explain the distribution of the fishes of the Llanos. Prior to the Pleistocene this plateau region contained an enormous shallow lake that was connected to the Valle de México by way of Apizaco and Apam (Barbour, 1973: Fig. 5). The crater lakes in question were formed much later by volcanic explosion, and their cavities were filled with water because they all lay below the highest level of the Plio-Pleistocene lake. Because of their different altitudes, the crater lakes were isolated from each other at varying times as the level of the hypothetical lake fell below 2,440 meters.

Lago de Aljojuca is the highest of these fish-supporting crater lakes and some particular aspect of the history of its colonization, as yet undetermined, must account for the fact that it alone contains *Heterandria.* Very likely other species of fishes became extinct in the area following virtual desiccation of the original lake.

Specimens examined (All in México).— Hidalgo: M74-48, in UMMZ, ditch near Tula; Puebla: BMNH 1873.1.13.1 (syntype), Lago de Aljojuca; P 184 (10), Tepeaca; P 203 (20 topotypes), Lago de Aljojuca; UMMZ 124304 (47), Río Necaxa; UMMZ 183986 (50), trib. Río Balsas at Acosac; UMMZ 186675 (57), trib. Río Papaloapan, Tehuacán; UMMZ 193493 (19), trib. Río San Marcos, 42 km WSW of Poza Rica. San Luis Potosí: UMMZ 124330 (48), 162141 (45), Palitla; Tamaulipas: UMMZ 183887 (94), Jaumave. Veracruz: UMMZ 162143 (96), Río Atoyac, 6.5 km N Potrero Viejo; UMMZ 183894 (500), Orizaba Valley; UMMZ 183896 (869), Rio Atoyac at Atoyac; UMMZ 187718 (476), Orizaba Valley.

Heterandria bimaculata (Heckel)
(Figs. 1-3)

Xiphophorus bimaculatus.— Heckel, 1848: 297-299, pl. 9, figs. 1-2 (original description; a clear brook of the Orizaba Mountains, México).

Poecilioides bimaculatus.— Steindachner, 1863: 176 (original description; Teapa, Tabasco, México — see Rosen and Bailey, 1963).

Pseudoxiphophorus bimaculatus.— Garman, 1895: 81-82, pl. 3, fig. 6, pl. 8, fig. 9 (in part; synonymy; description). Meek, 1902: 98 (brief description; maximum adult size; notes on eggs, embryos, time of birth). Meek, 1904: 127-128 (in part; synonymy, excluding *P. pauciradiatus* Regan; description; range). Regan, 1904: 256 (comparison with *P. pauciradiatus*; *P. reticulatus* Troschel in synonymy). Regan, 1913: 993-994, fig. 170C (synonymy; description; gonopodium figured). Scrimshaw, 1946 (size of ova and ovisac). Rosen and Gordon, 1953: 26, Fig. 32C (gonopodium). Rosen and Mendelson, 1960: fig. 4M (hypothetical correlation between sensory canals of head and feeding habits). Rosen and Tucker, 1961: fig. 2 (secondary sex characters and sexual behavior).

Heterandria bimaculata.— Rosen and Bailey, 1963: 131, figs. 49B, 51D, 55B (in part; synonymy, excluding references to *jonesi* and *pauciradiatus*; range; skeleton and gonopodial suspensorium of male figured). Miller, 1966: 790 (range).

Gambusia bimaculata.— Regan, 1906-08: 98, pl. 14, fig. 4 (synonymy; description; range, excluding Orizaba).

Gambusia (Pseudoxiphophorus) bimaculata.— Regan, 1907: 260 (listed in comparison with *G. annectens*).

Pseudoxiphophorus bimaculatus bimaculatus.— Hubbs, 1924: 18 (synonymy; distribution; dorsal-ray counts).

Pseudoxiphophorus bimaculatus taeniatus.— Regan, 1905: 363 (original description; San Domingo de Guzman, Oaxaca, México; this locality, now called Petapa, is on a tributary of the Río Coatzacoalcos SW of Matías Romero).

Pseudoxiphophorus bimaculatus peninsulae.— Hubbs, 1936: 230-232, pl. 8, fig. 1 (original description; vicinity or Progreso, Yucatán, México).

Pseudoxiphophorus reticulatus.— Troschel in von Müller, 1865: 638-639 (original description; México).

Diagnosis.—A species of the subgenus *Pseudoxiphophorus* (Table 1) distinguished from *H. jonesi* as follows (see also Table 5): Terminal segment of ray 4a of gonopodium greatly elongate (as long as 4-8 subdistal segments), its tip strongly hooked forward (J-shaped), reaching tip of enclosing membrance; anterior margin of 4 to 6 subdistal segments of ray 4a with keel-like prominences; ray 4p not entering into curved tip of gonopod (Fig. 2). Base of dorsal fin enters predorsal length 1.2 to 1.5 times in males, and 1.6 to 1.9 times in females. Origin of dorsal fin more anterior (Table 3). Basicaudal spot generally larger, higher, and more posterior, lying mostly on caudal fin.

Type Locality.—Confusion has resulted from the common misinterpretation of Heckel's type locality as "Orizaba". In the same paper in which *H. bimaculata* is described, Heckel (1848) also described *Xiphophorus helleri* and *Poeciliopsis gracilis* (see

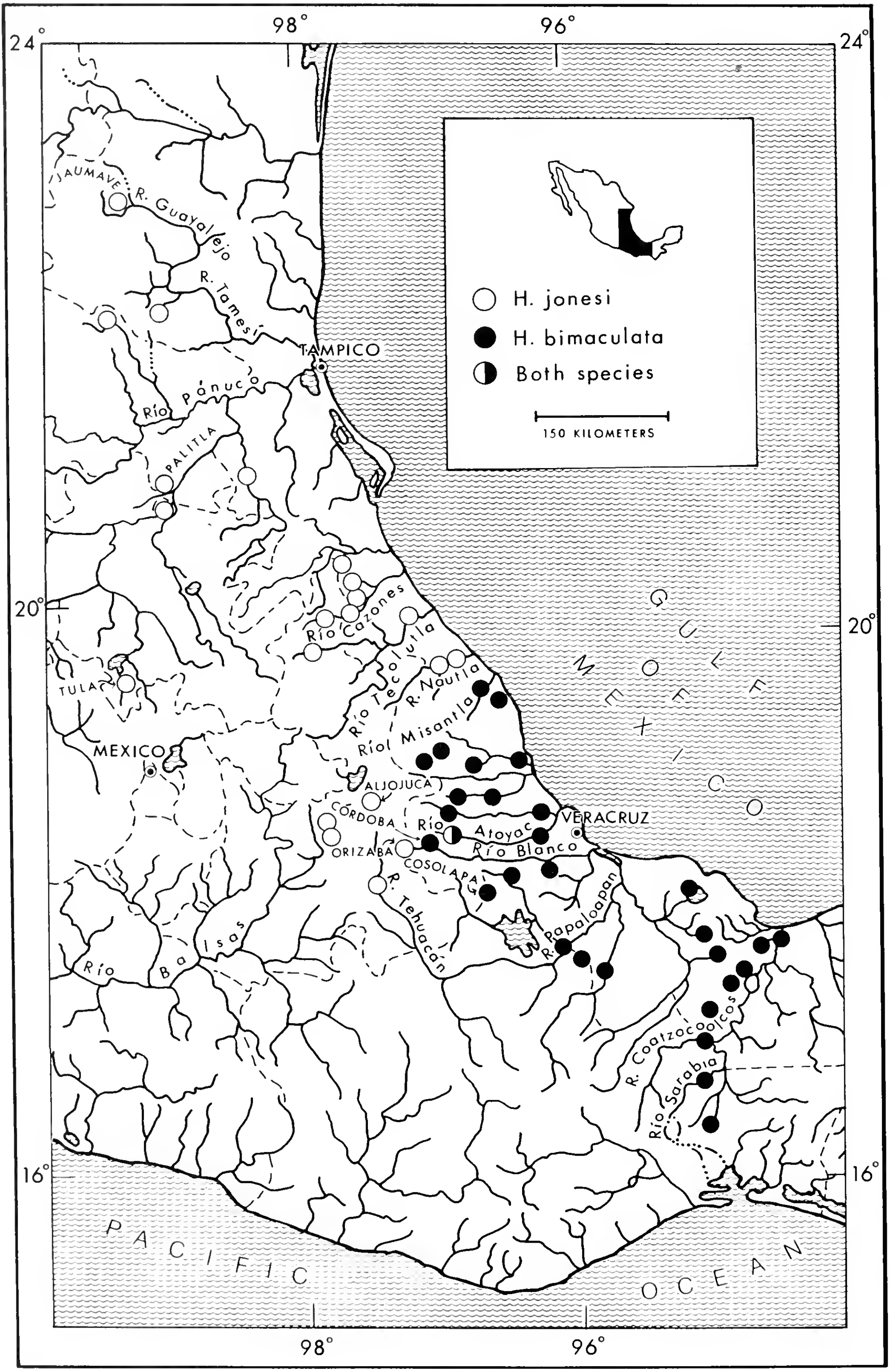

Figure 4. Distribution of two species of *Heterandria* in México. For *H. bimaculata* (which ranges eastward and southward into Nicaragua) only the records from the Río Coatzacoalcos basin northward are included. Stations are from UMMZ records and Meek's (1904: 128) localities (except Sanborn, not found).

Table 5. Comparison between two species of *Heterandria* inhabiting México.

Character	*H. jonesi*[1]	*H. bimaculata*[2]
Gonopodium (Fig. 2):		
Terminal segment of ray 4a	Short, slightly curved forward, not reaching tip of enclosing membrane; not longer than 2-3 subdistal segments, often only exceeding penultimate one	Greatly elongate, tip strongly hooked forward (J-shaped), extending to end of enclosing membrane; as long as 4-8 subdistal segments
Anterior margin of subdistal segments of ray 4a	Evenly smooth on all	With keel-like prominences on 4-6 segments
Ray 4p	Extending far beyond tip of ray 3 to form part of curved tip of gonopod	Extending just beyond tip of ray 3, not entering into curved tip of gonopod
Ray 5a	Distal part curves evenly toward tip of gonopod; ray 4p is only slightly elevated in this region	Distal part descends abruptly to ray 4p which is strongly elevated in this region
Gonopodial suspensorium (Fig. 3)	Angle of gonactinosts about 45° from vertical. Ligastyle as long as or longer than basal stem of gonapophysis III	Angle of gonactinosts about 33° from vertical. Ligastyle shorter than basal stem of gonapophysis III
Dorsal origin to caudal base	Shorter. In permillage of S.L., males 490-533; females 421-483 (Table 3)	Longer. In permillage of S.L., males 539-575; females 479-508 (Table 3)
Predorsal length[3] / Base of dorsal fin	Males 1.6-2.4; females 2.0-2.9	Males 1.2-1.5; females 1.6-1.9
Predorsal length / Depressed dorsal-fin length	Males 1.1-1.6[4]; females 1.4-2.0	Males 0.9-1.1; females 1.2-1.4
Basicaudal spot (Fig. 1)	Generally smaller, its position lower and more anterior (weakest in females from Jaumave)	Generally larger, its position usually higher and more posterior
Cross-hatching on sides	Well developed and generally extending ventrally around caudal peduncle	Well developed above body axis but fading ventrally; none on venter of caudal peduncle

[1] Ratios and proportions based on specimens from 5 populations (including topotypes of *M. jonesii* and *P. pauciradiatus*) as follows: UMMZ 162141 (Palitla), 183887 (Jaumave), 183894 (Orizaba Valley), 183896 (Atoyac), and P 203 (Aljojuca).

[2] Ratios and proportions based on specimens from 2 populations (3 collections, including subtopotypes of *X. bimaculatus*) as follows: UMMZ 108614 and 181309 (Córdoba), and 183902 (Cosolapa).

[3] This ratio was determined mathematically by dividing the measurement of the base of the dorsal fin into that of the predorsal length for each fish.

[4] The ratio of 1.1 in *H. jonesi* occurred in only 1 male from Jaumave; otherwise the range was 1.2-1.6.

Rosen and Bailey, 1963: 131-133) and stated that all three species live together "in einem klaren Bache des Gebirges Orizaba". Although *X. helleri* inhabits streams of the Orizaba Valley, neither *H. bimaculata* nor *P. gracilis* live there (the only other known fish is *H. jonesi*). Therefore, apparently none of Heckel's species came from any tributary of or stream in the trough-like Orizaba Valley, which lies at an elevation of about 1,240 m. Menzel and Darnell (1973: 232), in discussing the type locality of *Poecilia mexicana* Steindachner, also said to be from Orizaba, concluded that the types came from a much lower elevation in either the Río Jamapa or Río Blanco drainages. Most likely *X. helleri* and *H. bimaculata* (if not *P. gracilis*) came from the vicinity of Córdoba at an elevation of about 870 m. Woolman (1894: 65) described the rapids and barrier falls in the Río Blanco, the drainage system of the Orizaba Valley, which prevent the ascent of fishes into this valley from lower elevations to the east of Orizaba.

Variation.—The salient characters distinctive of the gonopodium of this species have been given in the Diagnosis and also appear in Table 5. Additional traits follow. Ray 3 extends to the base of the penultimate segment or to that of the terminal one (the J-shaped hook) of ray 4a. Distal to the elevated flange or keel of ray 3 are from 6 to 9 small segments. Ray 4a bears from 2 to 4 squarish segments between the terminal one and the last keeled segment, and from 6 to 9 segments distal to the terminal serra on ray 4p. There are 6 to 12 segments distal to the last serra of ray 4p, and this ray bears 10 to 14 strong, retrorse serrae. Ray 5a ends several segments of ray 4a short of the base of the J-shaped hook.

Ten measurements (Table 3) were made on 30 males and 30 females sampled from two places in Veracruz and Oaxaca—Córdoba (approximate type locality of the species) and Cosolapa, approximately 50 airline km SE of Córdoba. These data show very close agreement except in head length, which is longer at Cosolapa. Sexual dimorphism is strongly marked in dorsal origin (as shown by predorsal length, and dorsal origin to caudal base) and basal length of dorsal fin; it is less striking in caudal peduncle depth and length of middle caudal rays.

The number of dorsal fin rays, lowest in the highlands (Jico-Jalapa) near the northern limit of the range, appears to show an increase southward and toward lower elevations. The extreme range for this species is from 11 to 18 (11 in one specimen from Honduras, UMMZ 173305, and 18 in three from Belize, formerly British Honduras—specimens taken by David W. Greenfield at Sta. G70-139).

Vertebral number shows modes of 32 or 33 in samples from five populations in México (Table 4).

Color pattern is generally more consistent in *bimaculata* than in *jonesi.* Cross-hatching is well developed on the upper and mid-sides but begins to pale ventrally and fades out entirely over the ventral surface of the caudal peduncle. Vertical bars are rare although Hubbs (1936: 231) stated that *H. b. peninsulae* from Yucatán has 2 to 4 such bars, "like narrow parr marks", behind the shoulder spot. Among 35 young to juvenile individuals from the Río Atoyac (UMMZ 162144) are 8 with 2 to 5 faint bars anteriorly; 7 of these have 13 dorsal rays, the number that overlaps that of *H. jonesi* at this same locality. However, in no other features do these specimens resemble *jonesi*; measurements of the basal length of the dorsal fin and predorsal length yielded calculated ratios of less than 1.0 in all eight specimens (see Table 5). Bars thus appear to be only rarely developed in *H. bimaculata.* The basicudal spot is somewhat variable in size and position. Typically it is large, roundish, more or less equal to the diameter of the eye, set higher than in *jonesi* and mostly on the caudal fin. However, in a collection from the Río Coatzacoalcos basin (Río Sarabia, Oaxaca, UMMZ 178533), the spot lies almost entirely on the base of the caudal fin, generally only slightly above the body axis, and varies from round to triangular with the apex of the triangle (often drawn out) directed posteriorly. This population (corresponding to *H. b. taeniata* of Regan) also shows a well-developed midlateral stripe that is disrupted in young specimens.

Biology.—Meek (1902: 98) reported that this species probably gives birth "near the first to the middle of June" (at Jalapa, Veracruz, 1,427 m). Possibly this is true but if so, successful fertilization and development take place later in the year than it does in *H. jonesi.* A collection (UMMZ 108614) made on 22 March from Córdoba (872 m) contains individuals as small as 14 mm standard length, indicating that brood production had been under way for some time. As already indicated (see Biology, *H. jonesi*), both species had produced young in the Río Atoyac (about 600 m) by late December.

Mature males of *H. bimaculata,* like those of *H. jonesi,* vary greatly in size: 25 (1), 27 (1), 29 (2), 30 (1), 31 (1), 32 (3), 33 (6), 34 (2), 35 (3), 37 (1), 38 (2), 39 (2), 40 (2), 43 (1), 44 (3), 45 (5), 46 (1), 47 (2), 48 (3), 49 (3), 50 (1), 51 (1), 52 (1), 48, avg. 39.4 mm (UMMZ 183902, Cosolapa). The largest of 20 immature males in this collection was 51, the smallest 40, and 16 were 41 or more mm long (all these males had the gonopodium elongated but undifferentiated at the tip). The 74 mature females in this collection, varying from 43 to 76 mm long, averaged 58.1 mm.

Sympatry between *H. bimaculata* and *H. jonesi* has already been discussed (see Biology, *H. jonesi*).

Range.—The precise northern limit of *H. bimaculata* on the Atlantic coastal plain is uncertain, but it evidently does not extend to the Río Nautla basin, which as far as known contains only *H. jonesi.* The northernmost collection known to me is from the Río Misantla (M74-6, in UMMZ; Fig. 4), an independent tributary to the Gulf of Mexico lying just southeast of the Río Nautla, Veracruz; this stream is north of Jalapa, which lies near the northernmost inland limit of *H. bimaculata.* In México the species occurs at elevations from near sea level to at least 1,430 m (Jalapa).

Specimens examined (All in México).— Oaxaca: UMMZ 178533 (52), Río Sarabia on Trans-Isthmian Hwy; UMMZ 183902 (757), Cosolapa. Veracruz: USNM 31023 (5) and 45489 (27), Mirador; UMMZ 108614 (207), Río Chico, Córdoba; UMMZ 124234 (69), 4 km E of Papaloapan (=El Hule); UMMZ 162144 (38), Río Atoyac, 6.5 km N of Potrero Viejo; UMMZ 181309 (35), Córdoba; UMMZ 184512 (94), 32.5 km N of José Cardel.

PHYLOGENY

In considering the relationships of phyletic lines within the subgenus *Pseudoxiphophorus*, it is clear from Table 5 and Figures 2 and 3 that *H. jonesi* is less specialized than *H. bimaculata.* The gonopodium, especially, is of simpler construction in *jonesi.* Although several species of this subgenus are yet to be described from Guatemala, I have examined all of them and conclude that none is more primitive than *H. jonesi.* In body form and proportions, position and size of the dorsal fin, head shape, length of mandible, and detailed architecture of the gonopodium, each of the Guatemalan species shows some features that indicate a less generalized condition than is found in *H. jonesi.* The species represented by UMMZ 193893 (Alta Verapaz, Guatemala) is perhaps as close to *jonesi* as is any of the Guatemalan species, but it shows certain modifications about the distal end of the gonopodium (e.g., thickening of ray 3, increased number of small segments in ray 4a) that, to me, mark it as more specialized.

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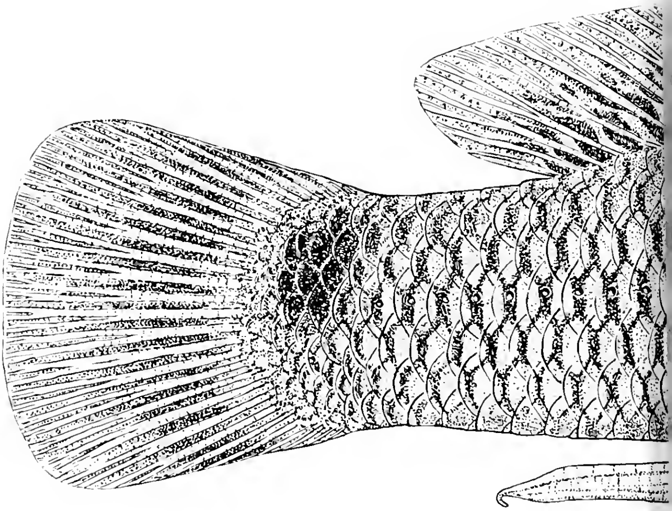

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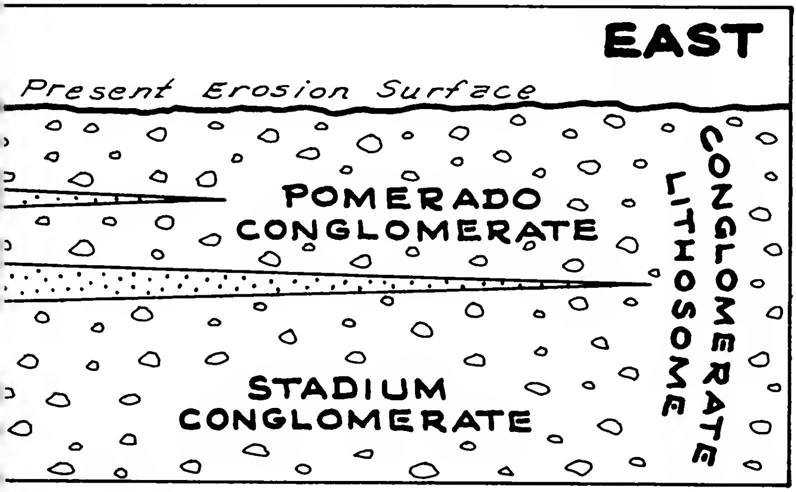

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LITHOSTRATIGRAPHIC VARIATIONS IN THE POWAY GROUP NEAR SAN DIEGO, CALIFORNIA

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ABSTRACT.—The Eocene Poway Group consists of two mutually intertongued bodies of rock, or lithosomes. One consists predominantly of coarse conglomerate of fluvial origin and is located principally in the eastern San Diego area. The other consists of sandstone and siltstone and lies predominantly west of the conglomerate lithosome. Tongues of the conglomerate lithosome extend toward the west and include the Stadium Conglomerate and the herein named Pomerado Conglomerate (Upper Eocene). Tongues of the sandstone lithosome extend toward the east and pinch out within the conglomerate. Lower sandstone tongues constitute the Mission Valley Formation, and an upper tongue is herein named the Miramar Sandstone Member of the Pomerado Conglomerate (Upper Eocene). The sandstone lithosome is partly of nearshore-marine and partly of nonmarine origin, whereas the conglomerate is of fluviatile origin. The conglomerate was deposited as a delta at the site where a large Eocene river emerged onto a low-lying coastal plain.

One of the most distinctive and widespread stratal units in the San Diego area is referred to in the older literature as the "Poway Conglomerate" (Ellis and Lee, 1919; Hanna, 1926; Bellemin and Merriam, 1958; and many others). More recently, Kennedy and Moore (1971) recognized that this Eocene stratal unit is composed not only of conglomerate, but also contains at least one widespread mappable sandstone unit. They revised the nomenclature accordingly and raised the rank of the "Poway Conglomerate" to the Poway Group. Within the Poway Group, Kennedy and Moore (1971) recognized a lower rock unit designated the Stadium Conglomerate, a middle unit dominated by fine-grained sandstone designated the Mission Valley Formation, and a third unnamed conglomerate, herein designated the Pomerado Conglomerate.

A geologic map of part of San Diego, and adjacent areas, now completed at a scale of 1:24,000 (Kennedy and Peterson, 1974), shows the distribution of these formations and their relationships to one another. A small portion of that map is included here as Figure 1. The purpose of this paper is to name, briefly describe, and establish type sections for new rock units, as well as to describe the vertical and lateral variations in lithologic character within the Poway Group.

The lateral distribution of rock types within the Poway Group is best illustrated and explained by utilizing the lithosome concept of Wheeler and Mallory (1956), rather than more traditional lithostratigraphic units (formations and members). Briefly, a lithosome is a rock body of uniform character that intertongues with one or more other rock bodies of uniform but differing character. The individual tongues of the lithosome are referred to by Wheeler and Mallory as lithostromes, and are here what we have mapped as formations and members (Fig. 1).

The lithostratigraphic variation in the Poway Group is most pronounced in an east-west direction (Fig. 2). The Poway Group is subdivided into two mutually intertongued lithosomes, each representing a different depositional environment. One lithosome is dominated by conglomerate and is herein informally referred to as the conglomerate lithosome. The other is dominated by soft, friable sandstone and is hereafter referred to as the sandstone lithosome.

The basically simple lithosomal relations that we illustrate in Figure 2 are in part interpretational, since the Poway Group is only partially preserved. The principal complicating factor is the presence of the Lindavista Terrace, a Pleistocene wave-cut platform capped by a thin veneer of reddish-brown sandstone and conglomerate (the Lindavista Formation). Because of this later erosional episode, the Poway Group has a large notch removed, and the variations within this missing portion of the group are no longer evident. This erosional notch affects the western part of the Poway Group, or that

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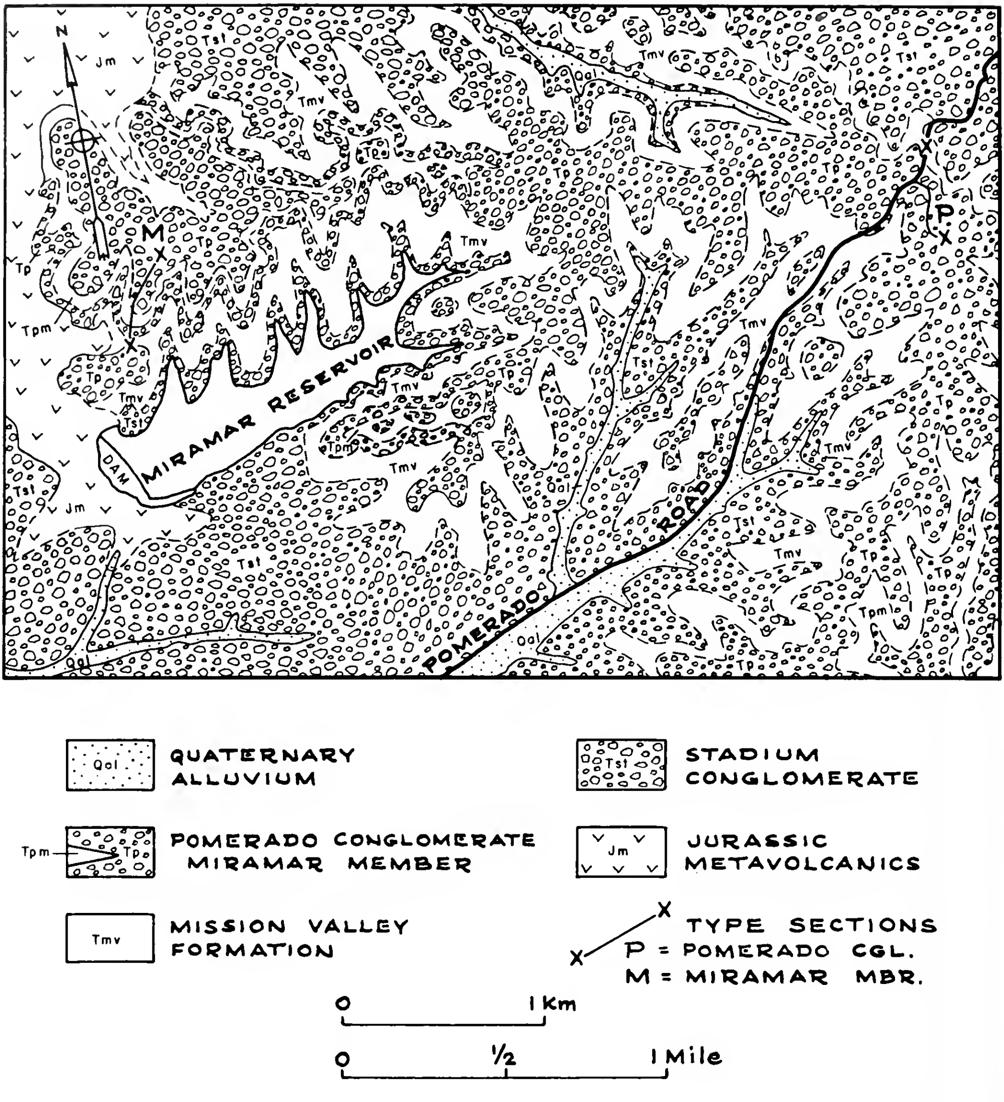

Figure 1. Geologic map of the Miramar Reservoir area showing locations of type sections of the Late Eocene Pomerado Conglomerate and Miramar Sandstone Member.

portion which we interpret to be dominated by the sandstone lithosome. We have reconstructed within this missing portion what we consider to be the most reasonable lithostratigraphic variation to account for the relations observed and mapped within the preserved portion of the section.

The lithosomes, together with their lithostromes, which are mappable rock units of member and formational rank, are briefly described below. A discussion of the regional genetic significance follows in the last section.

CONGLOMERATE LITHOSOME

The conglomerate lithosome is composed of one of the most distinctive rock types in the San Diego area. The clasts range in size from pebbles to small boulders, and locally are up to nearly a meter in diameter. Clasts over 30 cm in diameter are rare. The clasts are subrounded to rounded and are set in a medium- to coarse-grained sandstone matrix.

In general field appearance the conglomerate is so distinctive that with only some minor exceptions involving reworking, it can be readily distinguished from the older and younger conglomerates of the area (Peterson, 1970). Thin beds and lenses of cross-stratified sandstone lithologically similar to the conglomerate matrix occur throughout the section and increase in persistence toward the west. The conglomerate is chiefly nonmarine, and we interpret the interstratified sandstone to be partly marginal marine but predominantly of fluvial origin.

The conglomerate is characterized by the Poway suite of clasts (Bellemin and Merriam, 1958; DeLisle *et al.*, 1965; Woodford *et al.*, 1968; Peterson, 1971), an exotic assemblage consisting predominantly of rhyolitic to dacitic volcanic and volcaniclastic rocks with a smaller but significant proportion of quartzite. This assemblage of clasts first appears in the stratigraphic succession at San Diego in the Eocene (Peterson and Nordstrom, 1970), is extensively reworked into post-Eocene rock units, and in most places is the dominant clast suite found in the modern stream and beach gravels. The Poway clasts are exceedingly durable, having travelled an exceptionally long distance to the site of deposition. Their probable area of origin seems to be on the Sonoran side of the Gulf of California (Bellemin and Merriam, 1958; DeLisle *et al.*, 1965; Woodford *et al.*, 1968; Minch, 1970, 1972).

The character of the conglomerate lithosome is surprisingly uniform throughout the San Diego area. It varies little either geographically or stratigraphically. Thus the Stadium Conglomerate is lithologically nearly identical to the Pomerado Conglomerate. These conglomerates can be differentiated only because they are separated by the Mission Valley Formation.

Stadium Conglomerate.—The lower conglomerate lithostrome was designated the Stadium Conglomerate, with a type section near San Diego Stadium in Mission Valley. This rock unit is very widespread and has been recognized throughout the San Diego region (Kennedy and Moore, 1971; Peterson, 1971). Its thickness is highly variable and ranges from a few meters to perhaps 75 m. In general it is thickest and most typically developed in the central San Diego area and becomes progressively thinner to the north and west. The Stadium Conglomerate is overlain by the finer-grained Mission Valley Formation. The contact between the two units is gradational, and locally the two units are intertongued.

Pomerado Conglomerate.—The upper conglomerate lithostrome is here named the Pomerado Conglomerate. A well-exposed section, here designated the type section, is located along the roadcuts of Pomerado Road and Sycamore Canyon access road between San Diego and Poway (location P in Figure 1).

At the type section, the Pomerado Conglomerate gradationally overlies the Mission Valley Formation, a unit consisting of gray to light brown sandstone containing a small amount of whitish caliche, scattered pebbles, and small cobbles of rhyolitic rock. The basal Pomerado contact is placed at the base of a 7 m massive conglomerate of typical Poway type. Overlying the conglomerate is a 7 m thick medium-grained, soft, friable sandstone resembling the underlying Mission Valley Formation but interpreted here as a lens of sandstone within the Pomerado Conglomerate.

Overlying the sandstone lens is a 14 m thick massive cobble conglomerate with the typical Poway suite of clasts, many of which are fractured *in situ*. This conglomerate grades upward into a sandstone containing small scattered pebbles and a thin bed of pebble conglomerate. Thickness of the sandstone is 7 m. It is overlain by 5 m of cobble conglomerate with some clasts up to 30 cm diameter. Overlying this conglomerate is a 2 m thick sandstone lens which is in turn overlain by a 1 m massive cobble conglomerate bed. Overlying the conglomerate is a 3 m bed of soft, friable, medium-grained sandstone containing some Poway-type pebbles. The highest exposed unit of the Pomerado Conglomerate is a 10 m thick bed of cobble to boulder conglomerate. Some of the boulders are up to 30 cm in diamter and many are fractured *in situ*. Some thin, mostly discontinuous beds and lenses of sandstone are present in this otherwise massive conglomerate bed.

The top of the type section of the Pomerado Conglomerate ends at the crest of the

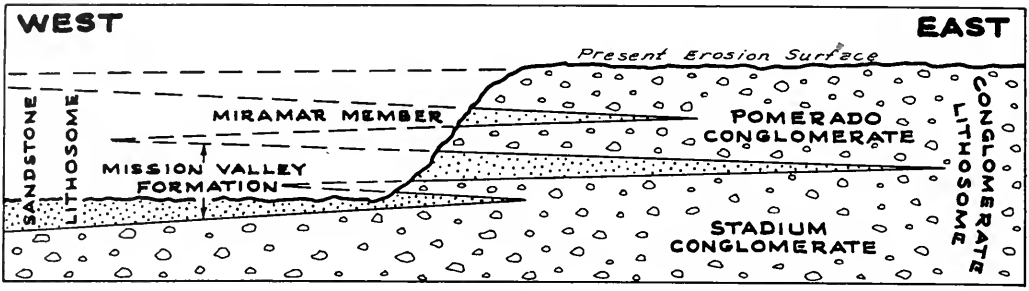

Figure 2. Generalized diagram of relationship between sandstone lithosome (Mission Valley Formation and Miramar Sandstone Member of Pomerado Conglomerate) and conglomerate lithosome (Stadium Conglomerate and Pomerado Conglomerate).

hill. In this area no further units overlie the Pomerado. Farther to the south, the Pliocene San Diego Formation unconformably overlies the Pomerado Conglomerate.

The Pomerado Conglomerate is gradational with the underlying Mission Valley Formation throughout the map area (Fig. 1) and much of the San Diego region. To the east, however, the Mission Valley Formation becomes thinner and finally pinches out between the Pomerado Conglomerate and Stadium Conglomerate.

No fossils have been found in the Pomerado Conglomerate; it is here considered to be Late Eocene in age, as it is gradational with and overlies the Mission Valley Formation, which is Late Eocene (Kennedy, 1973).

The Pomerado Conglomerate is not nearly as widespread as the Stadium Conglomerate, but the difference in distribution is at least in part a matter of preservation. The Stadium Conglomerate extends beneath the Lindavista wave-cut platform and is present in much of the western part of the San Diego area. The Pomerado Conglomerate, for the most part, terminates at the old sea cliff associated with the Lindavista Terrace (Fig. 2).

Within part of the Pomerado Conglomerate is a moderately widespread sandstone and siltstone unit here designated the Miramar Sandstone Member. We interpret this as a tongue of the sandstone lithosome (Fig. 2) described below.

SANDSTONE LITHOSOME

The sandstone lithosome is composed primarily of soft white, gray, yellow, and light brown friable sandstone with interbedded soft gray to green-gray siltstone. In general, this rock type crops out much more poorly and is not nearly as obvious as the conglomerate. In addition, the sandstone and siltstone rock units tend to be covered with slopewash derived from the overlying conglomerate. However, exposures are present at road cuts and because of a distinctive topographic expression their distribution can be mapped with some degree of certainty.

In addition to the dominant lithology, the sandstone lithosome contains random thin beds and lenses of conglomerate. The conglomerate is similar in all respects to that of the conglomerate lithosome and is considered to represent minor tongues of that unit. The conglomerate beds and lenses locally constitute up to about 20 per cent of the sandstone lithosome, which is also equivalent to the maximum per cent of sandstone beds and lenses locally present in the conglomerate lithosome.

A marginal marine and nonmarine environment of deposition for the sandstone lithosome is based on the presence of fossil mammals, fish, lagoonal oysters, and nearshore-marine mollusks (Kennedy, 1973).

Mission Valley Formation.—The Mission Valley Formation is a rock unit named by Kennedy and Moore (1971), with a type section along the south side of Mission Valley near State Highway 163 (old U.S. 395). From that locality the Mission Valley Formation extends over a wide area that includes parts of the La Mesa, La Jolla, Del Mar, and

Poway 7½ minute quadrange. The Mission Valley Formation is thickest in its westernmost exposures near Mission Valley. To the east, within the upper Mission Gorge area, the lower part of the formation intertongues with the upper part of the Stadium Conglomerate (Fig. 2). An upper tongue of the Mission Valley Formation can be seen in upper Murphy Canyon but pinches out rapidly toward the eastern boundary of the Poway and La Mesa quadrangles. Beyond this line, the Pomerado and Stadium Conglomerates are in contact. A Late Eocene age has been assigned to the Mission Valley Formation based on the presence of Tejon mollusks in the nearshore-marine part of the section and Uinta C mammals in the nonmarine part (Kennedy, 1973).

Miramar Sandstone Member of Pomerado Conglomerate.—The uppermost tongue of the sandstone lithosome is found entirely within the Pomerado Conglomerate in the general vicinity of Miramar Reservoir. Lithologically, it is identical to the Mission Valley Formation, and its outcropping characteristics are similar. However, because this unit is wholly within the Pomerado Conglomerate, and because it is nowhere in contact with the Mission Valley Formation, we are here designating it the Miramar Sandstone Member of the Pomerado Conglomerate. We interpret the Miramar Member as well as the Mission Valley Formation to be tongues of the sandstone lithosome, but this interpretation depends on evidence within that part of the Poway Group that has been erosionally removed by the cutting of the Lindavista Terrace (Fig. 2).

The type section for the Miramar Sandstone Member is here designated to be along the fire road extending along the ridge at the northern margin of Miramar Reservoir (see Fig. 1). At the type section, the Pomerado overlies the Mission Valley Formation which consists of soft, friable, red to brown weathering sandstone. The lower part of the Pomerado consists of 17 m of pebble to cobble conglomerate composed of the Poway suite of clasts.

Overlying the lower conglomerate is 20 m of soft medium- to coarse-grained, gray to gray-brown, red-brown weathering sandstone here designated the Miramar Sandstone Member. The sandstone is best exposed in gullies at the edge of the fire road. Locally it is pebbly, containing the Poway suite of clasts, and locally it is fractured with the fractures filled with caliche. In all respects, the Miramar Member strongly resembles the Mission Valley Formation.

The Miramar Member is overlain by 32 m of massive cobble conglomerate, the upper unit of the Pomerado Conglomerate in this section. The conglomerate is dominated by cobbles and small boulders with some of the clasts ranging up to 30 cm in diameter.

From the type section, the Miramar Member can be traced around the hills surrounding Miramar Reservoir. Where traced to the east it pinches out within the Pomerado Conglomerate (Figs. 1, 2).

No fossils were found within the Miramar Member, although the general lithologic similarity to the Mission Valley Formation suggests a similar environment of deposition. The fact that it is within the Pomerado Conglomerate, which is gradational with the underlying Mission Valley Formation, suggests an age of late Eocene.

REGIONAL IMPLICATIONS

In the Late Eocene in the San Diego area a large river valley emerged along the Pacific Coast. This ancient valley, called the Ballena Channel by Minch (1970, 1972), is traceable eastward almost to the Elsinore Fault. It enters the San Diego area in the vicinity of San Vicente Reservoir. There are narrowly distributed channel deposit, (the "Ballena Gravel") rapidly fans out and grades westwardly into the Late Eocene stratal units of the San Diego area (Kennedy and Moore, 1971; Peterson, 1971).

Apparently the Ballena Channel carried much of the coarse sediment, especially that of the coarse conglomerate characterized by "Poway" clasts, which is now so abundant in the Eocene succession of the San Diego area. The Ballena River entered the San Diego embayment from the east, apparently dropping much of its coarsest load in the area of lowering gradient as it entered the coastal plain of San Diego. The conglomerate lithosome represents predominantly fluvial deposits. These conglomerate beds grade laterally and intertongue westward (also to an extend northward and southward) with the sandstone lithosome.

The sandstone lithosome is at least partially marine. Thus a significant portion of the fine detritus may have been derived via longshore transport or roughly at right angles to the westward paleoslope indicated by the Ballena Channel. In addition , much of the fine detritus appears to be supplied by local minor drainage channels (Peterson, 1971).

Generally continuous submergence was necessary to preserve the rocks of the Poway Group. The large scale intertonguing of the two distinctive lithosomes can be interpreted in several ways. First, the eastward extensions of the partially marine sandstone-siltstone lithosome indicate eastward transgression of the strand line. The maximum transgression would be represented by the Mission Valley Formation. The regressive phases would be represented by the fluvial conglomerate lithosome, with the maximum regressions represented by the Stadium and Pomerado Conglomerates. The transgressive-regressive fluctuations could have been caused by interacting eustatic sea-level changes and local tectonic subsidence. Such fluctuations fit well with earlier transgressive-regressive episodes represented within the underlying La Jolla Group (Kennedy and Moore, 1971).

A second possible interpretation is that the size and position of the conglomerate lithosome may be due to variations in the amount of coarse fluvial detritus being transported into the San Diego area. That is, in times of voluminous supply, such as during the deposition of the Stadium and Pomerado conglomerates, a conglomeratic fan-delta could have built westward at the expense of the marine environment. During times of less fluvial sediment supply during the subsidence, the marine environment might again have encroached eastward.

A third possibility is that the intertonguing lithosomes indicate a combination both of changes in rate of submergence and of changes in rate of sediment influx. We consider this possiblity the most plausible.

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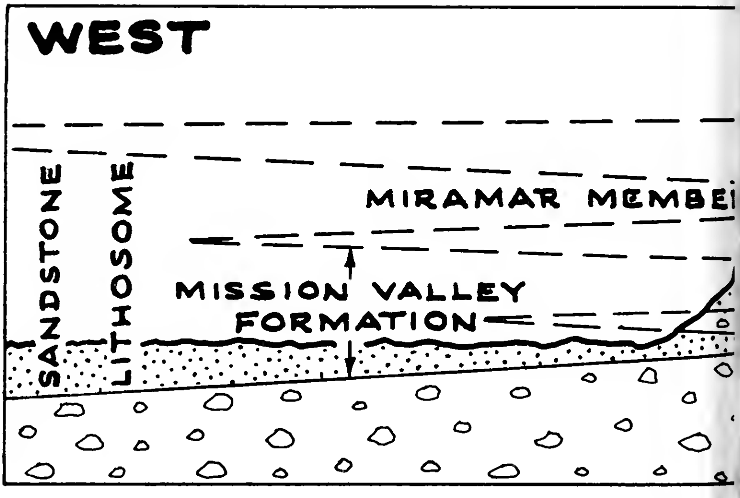
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FORMATION

THE AUTECOLOGY OF *XANTUSIA HENSHAWI HENSHAWI* (SAURIA: XANTUSIIDAE)

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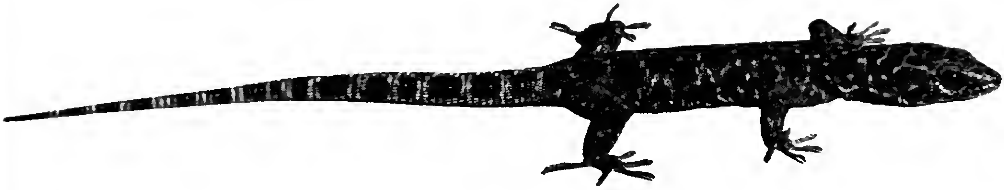

TRANSACTIONS

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THE AUTECOLOGY OF *XANTUSIA HENSHAWI HENSHAWI* (SAURIA: XANTUSIIDAE)

JULIAN C. LEE

ABSTRACT.—*Xantusia henshawi henshawi* is a secretive, crevice-dwelling lizard confined to southern California and adjacent Baja California, Mexico. Field studies during portions of four years at two sites in western San Diego Co. and studies of musuem specimens revealed that the distribution of this saxicolous species is correlated with the presence of granitic rocks. The availability of suitable rock crevices is an important factor limiting both population size and geographic distribution. Brush fires may generate additional crevices by accelerating the exfoliation of boulders.

This species is slow-growing, late-maturing, long-lived, and has the lowest reproductive potential yet reported for any lizard. Males probably first breed at about 2.5 years; females breed first at 3.5 years, and produce one brood (mean size 1.46) per season. Head and tail length exhibit allometric growth relative to snout-vent length; linear growth is determinant. The frequency of caudal autotomy is high among adults and probably results from intra-specific fighting rather than predation. The mortality rate from all causes is low.

Xantusia h. henshawi occupies a thermally buffered microhabitat, and in summer maintains body temperatures within approximately the same limits day and night. This species is eurythermic, showing no distinct temperature preference. Body temperature is highly dependent on substrate temperature.

The life history of this lizard is similar to that of *Xantusia vigilis.*

Of the approximately 3,000 living species of lizards, the life histories of perhaps no more than 50 have been studied thoroughly (Fitch, 1970). Because of its limited and highly disjunct distribution, the family Xantusiidae is of particular interest. Yet the only general life history for any xantusiid, is Miller's (1951) study of *Xantusia vigilis.* The present study, designed to fill partially this gap in our knowledge of lizard ecologies, presents an analysis of the life history of *Xantusia henshawi.*

Possibly because of its limited distribution, secretive habits, and specialized microhabitat, little information has been published on this species since its discovery in 1893. Authors who have discussed aspects of the biology of *X. henshawi* — often in casual or anecdotal fashion — include: Atsatt (1925), Brattstrom (1951, 1952, 1965), Grinnell and Camp (1917), Klauber (1926, 1931, 1939), Lee (1974), Mautz and Case (1974), Scott (1971), Shaw (1949), and Stephens (1921).

Description.—Xantusia henshawi is a small lizard. Adult males average 56 mm SVL and weigh about 2.9 g. Adult non-gravid females average 62 mm and 3.3 g. These lizards are dorso-ventrally compressed (Fig. 1), a feature associated with their crevice dwelling habits. The limbs are well developed, pentadactyl, and the digits bear small, strongly recurved claws. The head is covered with enlarged, symmetrical shields; the dorsal and lateral body surfaces and throat are covered with granular scales; the venter bears 14 longitudinal rows of enlarged rectangular plates; and the tail is covered with whorls of smooth, rectangular scales. Femoral pores are present in both sexes. As in all xantusiids, eyelids are lacking, the eye being covered by a transparent spectacle. The pupil is vertically elliptical. This species exhibits a daily rhythmic color change (Atsatt, 1939): during the day, the animal is dark gray or black with a fine yellowish reticulum; at night the yellowish network expands, and the animal becomes grayish with dark spots.

Distribution.—Prior to 1970, *X. henshawi* was known only from "Rocky areas on both sides of the mountains from northern Riverside Co., California, to the San Pedro Martir Mountains, Lower California" (Stejneger and Barbour, 1943; see also maps in Stebbins, 1954, 1966). Webb (1970) described a disjunct population which he named *Xantusia henshawi bolsonae,* from a single locality in eastern Durango, Mexico, 1280 km

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Figure 1. Adult male *Xantusia henshawi henshawi*, 56 mm snout-vent length.

southeast of the nearest population of the nominate race. Figure 2 presents the distribution of *X. h. henshawi* based upon published localities, museum records, and data from this study.

Webb (1970) summarized variation in *X. h. henshawi* based upon an examination of 108 specimens from throughout its geographic range. Comparison with Webb's data indicated that the Mt. Woodson and Lee Valley populations sampled in this study are referable to *X. h. henshawi* (Table 1).

Habitat.—*X. henshawi* is saxicolous and is rarely found far from crevices, especially those formed by the exfoliation of granitic boulders (Fig. 3). Such rocks are a requirement for this species, and their absence is probably a factor limiting both distribution and population density.

Chaparral is the principal plant community in the range of the nominate race, although ecotonal chaparral-coastal sage scrub situations are inhabited in western San Diego Co., as is the chaparral-creosote bush scrub ecotone in eastern San Diego Co., southwestern Imperial Co., and portions of Riverside Co.

Summers are generally hot and dry throughout the range of this subspecies. However, the rock-crevice microhabitat occupied by *Xantusia henshawi henshawi* protects

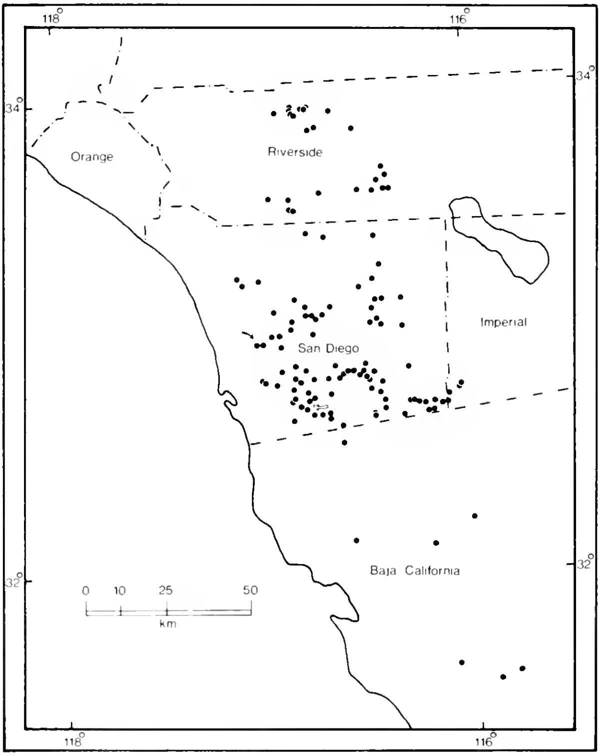

Figure 2. Distribution of *Xantusia henshawi henshawi*. Open arrow indicates study site 1, solid arrow indicates study site 2.

TABLE 1. Comparison of taxonomic characters in 20 adult *Xantusia henshawi henshawi* from Mount Woodson, San Diego County, California, 20 adults from Lee Valley, San Diego County, and 108 specimens of the subspecies from throughout its range (Webb, 1970). The first figure is the mean; the figures in parentheses, the range.

Character	Webb, 1970	Mount Woodson	Lee Valley
Number of infralabials	5.1 (4-7)	5.8 (5-6)	6.4 (5-7)
Number of supralabials	6.2 (5-8)	6.7 (6-9)	7.0 (6-8)
Head width/body length	0.18 (0.16-0.28)	0.17 (0.16-0.18)	0.17 (0.16-0.19)
Number of dorsal granules at midbody	62.8 (56-71)	61.3 (55-66)	63.4 (57-69)
Number of transverse rows of ventral scales	32.7 (30-36)	34.1 (32-36)	33.0 (31-34)
Number of enlarged scales on gular fold	10.3 (7-14)	11.2 (9-13)	11.8 (7-14)
Number of temporal scales	5.6 (4-8)	5.6 (5-7)	5.6 (4-8)
Number of femoral pores	10.7 (7-16)	11.0 (10-13)	11.3 (10-14)

them from temperature extremes. This thermal buffering effect is illustrated in Figure 4. The meager rainfall (often less than 36 cm per year) is mostly restricted to the cooler fall, winter, and spring months (Fig. 5).

The possible ecological relationships of vertebrates known to coexist with *X. h. henshawi* are indicated in Table 2.

MATERIALS AND METHODS

Field work at two sites was conducted intermittently in 1968, 1970, and 1971, and systematically from April through October, 1972. Site 1, in Lee Valley, San Diego Co., California (Fig. 2) is described elsewhere (Lee, 1974). Site 2 is located 4.8 km north and 4.8 km east of Poway, San Diego Co., California (Fig. 2). The site includes portions of Warren Canyon and the south and southwest slopes of Mount Woodson. Elevation ranges from 430 m at the bottom of Warren Canyon to 890 m at the top of Mount Woodson. The steep flanks of Warren Canyon and the slopes of Mount Woodson are strewn with exfoliating granitic boulders and covered with chaparral (Fig. 6). Portions of the area were burned in 1967.

In this investigation 735 living lizards and 171 preserved specimens from the San Diego Society of Natural History (SDSNH) were examined. Locality data were obtained from collections in the San Diego Society of Natural History, Museum of Vertebrate Zoology, Los Angeles County Museum of Natural History, and the California Academy of Sciences.

Population structure.—From late April to mid October, 1972, samples were taken at approximately monthly intervals from contiguous areas at site 2. Specimens were captured by removing granitic flakes with a crowbar (see Klauber, 1926). Weights and measurements were taken in the laboratory within 24 hours of capture. Weights were taken on a Mettler balance and read to the nearest 0.01 g. Snout-vent, tail, and axilla-groin lengths were measured with a plastic millimeter rule and read to the nearest mm. Head length (anterior margin of auditory meatus to tip of rostrum) and head width (greatest width anterior to auditory meatus) were measured with vernier calipers to the nearest 0.1 mm. Caudal autotomy was noted for each lizard, as was the number of femoral pores and the sex of each adult. All lizards were released unharmed in the approximate area of capture. The same data, with the exception of weight, were obtained from specimens in the San Diego Society of Natural History.

Reproduction.—Testes of preserved specimens were measured to the nearest 0.01 mm with an ocular micrometer. Testicular volume was calculated using the formula for the volume of an ellipsoid. Copulatory activity in recently captured lizards was recorded, and gravid females were held in captivity until parturition to provide information on brood size, characteristics of the newborn, and timing of parturition.

TABLE 2. Vertebrate associates of *Xantusia henshawi henshawi.*

Group	Potential Competitors For Food	Potential Predators	Relationship Unknown
Amphibians	Hyla regilla Bufo boreas		
Lizards	Sceloporus occidentalis Sceloporus orcutti Uta stansburiana Urosaurus microscutatus Phrynosoma coronatum Cnemidophorus tigris C. hyperythrus Coleonyx variegatus Phyllodactylus xanti	Sceloporus orcutti	
Snakes		Lichanura trivergata Lampropeltis getulus Masticophis lateralis Salvadora hexalepis Hypsiglena torquata Trimorphodon vandenburghi Crotalus ruber Crotalus mitchelli	Pituophis melanoleucas
Birds	Numerous insectivorous passerines	Falco sparverius Buteo jamaicensis Tyto alba Otus asio Bubo virginianus Geococcyx californianus Corvus corax Aphelocoma coerulescens	Numerous granivorous passerines
Mammals		Neotoma sp. Canis latrans	Dipodomys agilis Perognathus sp. Peromyscus sp. Sylvilagus sp. Myotis subulatus Odocoileus hemionus

Radiographic examination.—Following the technique described by Etheridge (1962), 15 preserved specimens were x-rayed to determine the presence or absence of epiphysial-diaphysial fusion and to verify caudal autotomy in certain specimens.

Thermal biology.—From 14 June through 19 October, 1972, lizards were captured at night at site 1 and the following data were recorded: date and time of capture, sex, cloacal temperature, air temperature (1 cm above substrate), and substrate temperature. Temperatures were taken with a Schultheis rapid equilibrium thermometer and read to the nearest 0.1 C. Cloacal temperatures were read within 10 seconds of capture, and were taken only from lizards which were abroad on boulders.

RESULTS

Sexual dimorphism.—Adult females average 6 mm longer in SVL than adult males (62 mm vs. 56 mm; Fig. 7), and weigh more (3.3 g vs. 2.9 g), but at any given length, males and non-gravid females weigh the same. I found no sexual dichromatism or intersexual differences in relative head length, head width, axilla-groin length, or tail length of adults.

As in many species of lizards, *X. h. henshawi* has a row of femoral pores along the postero-ventral margin of the thighs. In males they are large and produce an obvious secretion; in females they are small and inconspicuous (Fig. 8). Dissection of preserved specimens confirms that these secondary sex characters permit accurate sexing of adult

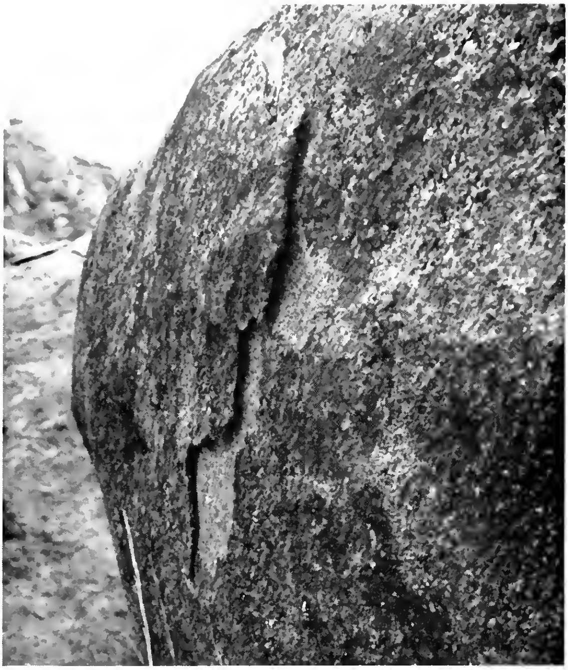

Figure 3. Crevice formed by the exfoliation of a granitic boulder. Photographed at site 1.

lizards. I interpreted the presence of a waxy plug within the pore as evidence of active secretion. In preserved lizards and in living material, a secretory plug was first evident in males at a SVL of 42 mm and 43 mm respectively. The number of pores ranges from six to 14 per thigh; often the number on one thigh exceeds that on the other by two or three. I found no significant intersexual difference in mean number of femoral pores on the right thigh (males = 11.0, females = 11.2, N = 100 and 97 respectively, t = 1.36, P> 0.2).

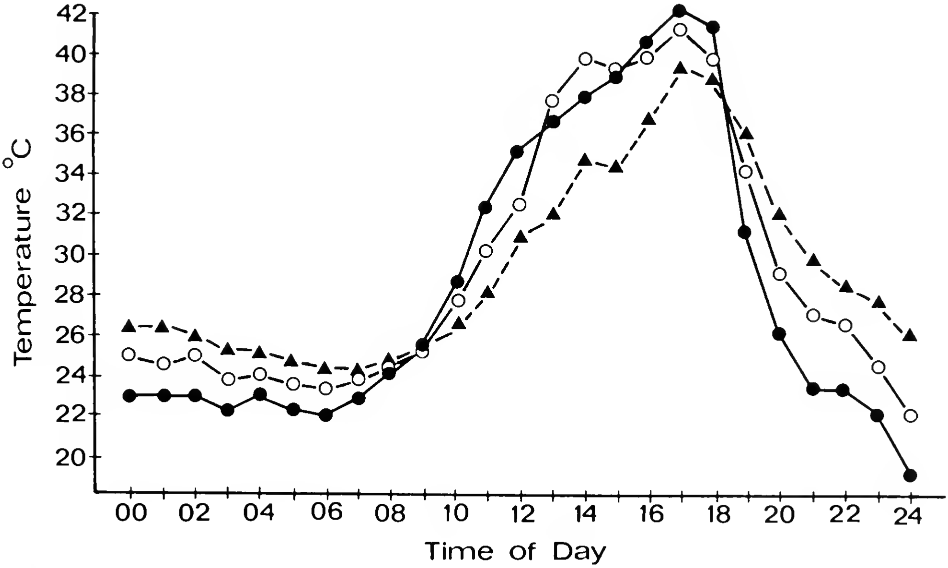

Figure 4. Twenty-four hour temperature cycles on a granitic boulder. Solid circles indicate temperature on outer surface of exfoliating flake; open circles indicate temperature at edge of crevice; triangles indicate temperature 25 cm inside crevice. Recorded 22 September 1972 at site 1.

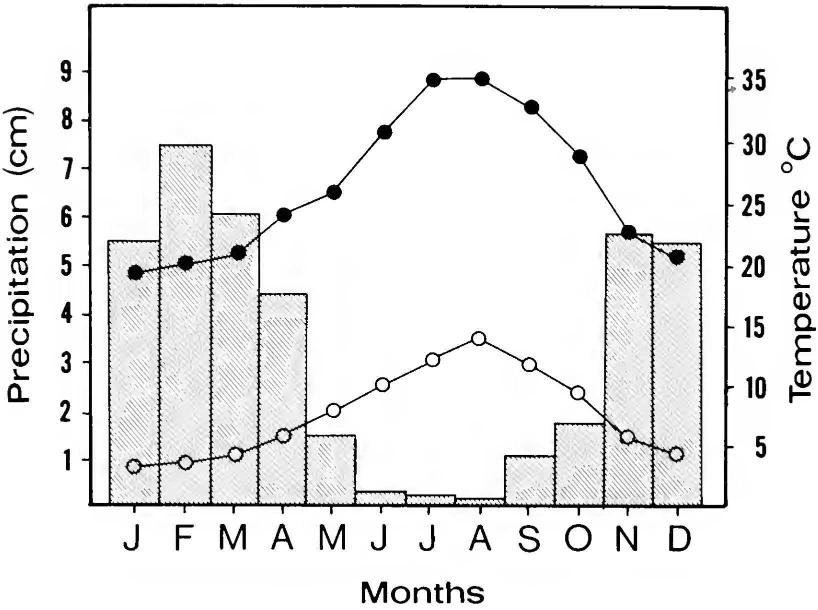

Figure 5. Ten year mean monthly maximum (solid circles) and minimum (open circles) temperatures and mean precipitation for the period 1957-1966 from Ramona, San Diego Co., California, 13.5 km from study site 2. Data from U.S. Weather Bureau, Ramona-Spalding station.

Population structure.—No significant deviation from a 1 : 1 sex ratio exists in adults from site 2 ($X^2 = 2.81$, $P > 0.05$), or in specimens of first year (21 males, 23 females), second year (12 males, 11 females), or adult lizards ($X^2 = 2.34$, $P > 0.10$) in the SDSNH collected throughout San Diego Co. Figure 7 presents frequency distributions of SVL for six successive monthly samples from site 2. For lizards which produce only one brood per season and in which parturition occurs over a short period, a SVL frequency distribution

Figure 6. Study site 2, Mount Woodson, San Diego Co., California.

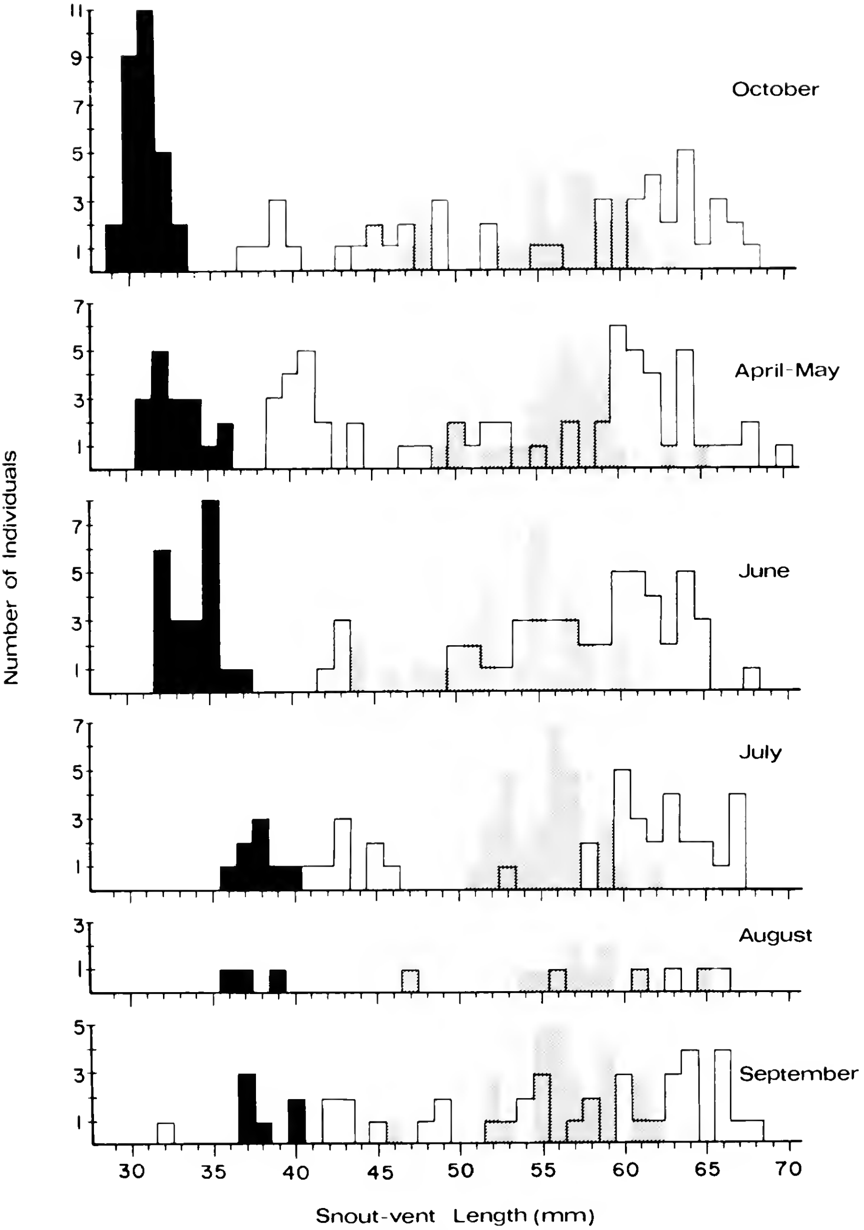

Figure 7. Population structure of *Xantusia henshawi henshawi*. For lizards 44 mm or above, open bars are females, shaded bars are males. Lizards below 44 mm were not sexed. Black bars indicate lizards in the first year of life. October sample is inverted to facilitate comparison of age classes.

will be polymodal, with the modes representing size classes, which in turn represent age classes. Thus in the October sample, lizards 29 to 33 mm SVL are deemed newborn (see reprodution, below), those 37 to 40 mm are one year old, those 43 to 49 mm two years old, and those 52 mm and above are three years or older. Designation of age class boundaries is sometimes arbitrary, especially for older lizards where growth rates are slower, causing size classes to overlap. Thus in the July sample I consider as first year lizards those with a SVL of 40 mm or less. To the extent that age classes can be inferred from size classes, Figure 7 indicates that in each month lizards three years or older comprised over 50 per cent of the sample. Over the entire six months, lizards in the first year of life comprised 18.2 per cent, second year lizards 9.3 per cent, and lizards in the third year or older, 72.5 per cent of the total sample.

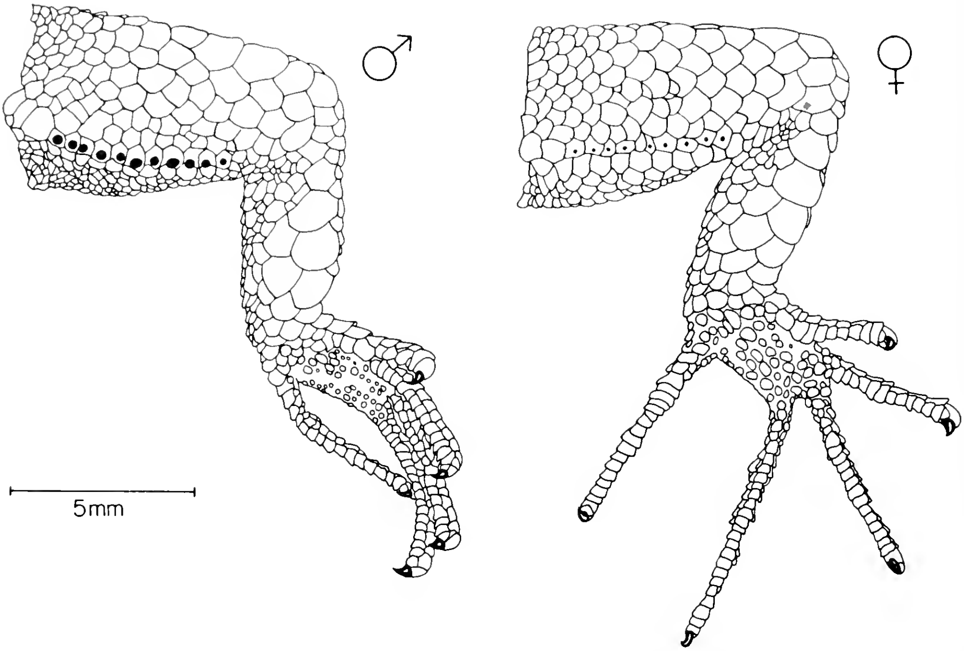

Figure 8. Femoral pores of adult male and female *Xantusia henshawi henshawi*. Pores are darkened for emphasis.

Growth.—A statistical approximation of growth is obtained by plotting the mean SVL for each size class against time. Results (Fig. 9, based upon data in Fig. 7) are only as accurate as the age class designations, which are somewhat arbitrary. At birth mean SVL is 31 mm and mean weight is 0.44 g; at one year, 39 mm and 0.89 g; at two years, 47 mm and 1.51 g; and by June of the third year, when lizards are approximately 32 months old, mean SVL is 51 mm and mean weight is 1.96 g.

Growth in *X. h. henshawi*, as in most vertebrates, is allometric (Figs. 10, 11). Relative to SVL, small lizards have short tails and long heads. A possible deviation from simple allometry is suggested in Figure 11. Lizards above 60 mm apparently have relatively shorter tails than lizards of intermediate sizes; possibly I failed to detect caudal autotomy in some of the larger lizards.

Contrary to the situation among turtles and crocodilians, some lizards exhibit determinate growth which results from fusion of the primary centers of ossification (diaphyses) with the secondary centers (epiphyses) of the endochondral bones (Haines, 1969). Such epiphysial-diaphysial union is illustrated for *X. h. henshawi* in Figure 12. Of 15 lizards examined by radiography, the smallest male showing such union was 52 mm SVL; the smallest female, 58 mm. These are close to the sizes at which I estimate reproductive maturity is attained. The approximately normal size distribution of adults from site 2 (Fig. 7) and the lack of extraordinarily large individuals also suggests determinant growth for this species.

Mortality.—Available life table data for *X. h. henshawi* are inadequate for calculation of mortality rates, but an approximation of mortality can be inferred from the relative abundance of age classes. Newborn lizards in the October sample from site 2 comprise 28 per cent of that month's sample. If the population is at equilibrium, annual mortality approximates 28 per cent. The abundance, in each sample, of lizards in the third year or older indicates that large numbers of lizards survive the first two years — convincing evidence that mortality is low.

In October, 1970, in the vicinity of Jamul, San Diego Co., lizards were collected in areas devastated two days previously by the Laguna Fire. Lizards were frequently removed from beneath flakes that had been blackened by fire, yet no dead or injured lizards were found, nor did lizards seem less abundant than in contiguous unburned situations. Samples from a burned area and an adjacent unburned area, collected approximately three months after the fire, showed little length-specific weight difference (Fig. 13),

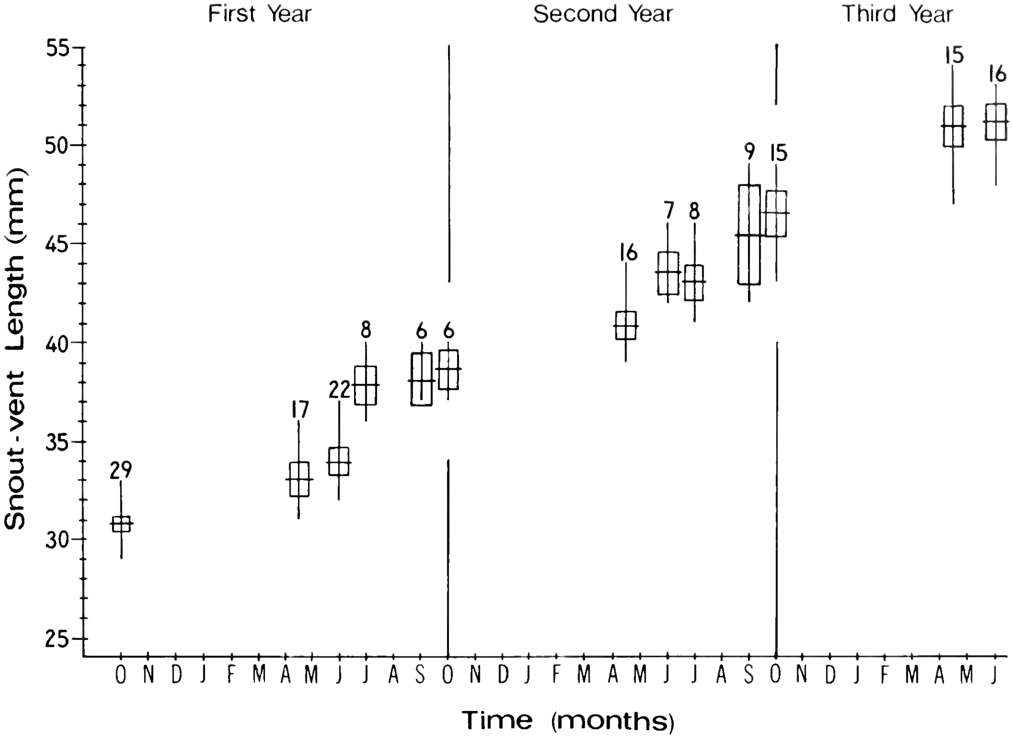

Figure 9. Growth rate in *Xantusia henshawi henshawi* during the first three years of life. For each sample, vertical line indicates range, horizontal line indicates mean. Rectangles encompass 95% confidence limits for the parametric means. Number above vertical line indicates sample size.

indicating that lizards from burned and unburned areas are equally well nourished.

No incidents of predation on *X. h. henshawi* were observed during this study, but potential predators (Table 2) were encountered frequently. Murray (1955) recorded a *Sceloporus orcutti* with the hind portion of a *X. h. henshawi* protruding from its mouth. *Petrosaurus mearnsi* eats *X. h. henshawi* in captivity (Cozens, pers. comm.); *Petrosaurus* is widely sympatric with *X. h. henshawi*, and occupies a similar microhabitat. In this study, *Hypsiglena torquata* was twice oberved at night resting about one and a half meters above ground between the leaves of a shrub and the side of a boulder. In both cases the snakes were within a meter of individual *X. h. henshawi*. In captivity this species readily devours *X. h. henshawi*, as do *Masticophis lateralis, Trimorphodon vandenburghi, Salvadora hexalepis*, and *Lampropeltis getulus*, all of which are sympatric with *X. h. henshawi*.

Potential diurnal avian predators include *Falco sparverius, Buteo jamaicensis, Geococcyx californianus, Aphelocoma coerulescens*, and *Corvus corax*. Due to its secretive habits, *X. h. henshawi* probably rarely falls prey to these birds. Nocturnal birds such as *Bubo virginianus, Tyto alba*, and *Otus asio* may occasionally capture these lizards, but *Xantusia* are probably below the usual size range of prey items for the former two species.

Many rodents are omnivorous (Landry, 1970), and I consider *Neotoma* a potential predator, particularly because of its size, its propensity for rocky situations, and its nocturnality which undoubtedly brings it into contact with *X. h. henshawi*.

Caudal autotomy.—Like many lizards, *X. h. henshawi* can lose and subsequently regenerate portions of the tail. It is frequently assumed that regenerated tails can be distinguished on the basis of size, color, and scutellation. Yet, Zweifel and Lowe (1966) were sometimes unable to distinguish regenerated tails in *Xantusia vigilis* without the aid of radiographs. Of 15 *X. h. henshawi* examined in this study by radiography, however, regeneration was invariably associated with one or more of the above criteria. Nonetheless, some autotomy may have gone undetected. Thus data concerning the frequency of autotomy are minimal estimates. Of 257 sexable lizards from site 2, 159 (61.4%) have experienced caudal autotomy at least once, with larger (presumably older) lizards showing the highest frequency (Fig. 14). The incidence of autotomy was the same in males (74 of 122, 60.0%) and females (85 of 135, 62.5%).

Reproduction.—Of 75 preserved males in the SDSNH, the smallest exhibiting testicular enlargement were 47 mm SVL. Because slight shrinkage occurs in preservative, I infer that sexual maturity in males is attained at about 50 mm SVL, when lizards are in their third year. Testicular volume varies considerably through the year (Table 3). Testicular volume is low during winter, maximizes in late spring and early summer, then apparently declines in late summer and fall.

TABLE 3. Seasonal variation in testicular volume in *Xantusia henshawi henshawi*. N indicates number of testes examined.

Month	N	$\overline{X}$	SD
January	13	3.83	2.17
March	5	7.53	2.64
April	10	17.01	10.49
May	3	30.30	7.14
June	5	19.49	7.61
July	3	23.18	5.13
November	2	11.20	0.01

The smallest gravid female I encountered was 56 mm SVL, suggesting that sexual maturity is attained at about that length. Moreover, females above 54 mm SVL undergo pronounced seasonal weight change, whereas those below 54 mm do not (Fig. 15). Above 54 mm, April-May females are significantly heavier than January females, and June females are significantly heavier than the April-May sample. By October weights have regressed to slightly below January levels. This weight change is probably the result of fat deposition necessary to carry gravid females through the hot dry period of gestation. Males do not exhibit this seasonal weight change. I therefore infer that females are sexually mature at about 54-56 mm SVL, a length attained late in the third, or early in the fourth year of life.

I observed attempted copulation among recently captured lizards on 18 June, 6 July, and 7 July. The attempts were similar to the general saurian pattern, and presumably reflected the timing of copulatory activity in the population from which they came. Thus breeding extends from at least mid June through early July.

Like other xantusiids, *X. h. henshawi* is viviparous. Parturition usually occurs from mid September through mid October. Parturition dates for 28 broods born to recently captured females spanned the period 17 September to 19 October, but a newborn lizard collected at site 2 on 3 September shows that parturition occasionally occurs earlier. Assuming that fertilization occurs shortly after copulation, gestation requires about 90 days.

Population structure, timing of seasonal weight increase, and timing of copulation and parturition indicate that females at site 2 produce one brood per year. Because most sexually mature females exhibit a pronounced weight increase in spring, I assume that females are able to breed each year.

Of 28 broods, 13 contained two offspring and 15 contained one ($\overline{X} = 1.46$). For broods consisting of two offspring, a strong positive correlation exists between the SVL of the female and the combined weight of her offspring ($r = 0.915$, $P < 0.01$).

Thermal biology.—Sixty-eight cloacal temperatures ranging from 18.1 to 31.8 C were obtained from lizards abroad at night at site 2. Mean temperatures for males and females do not differ significantly (25.6 and 25.2 respectively). Cloacal temperatures are strongly

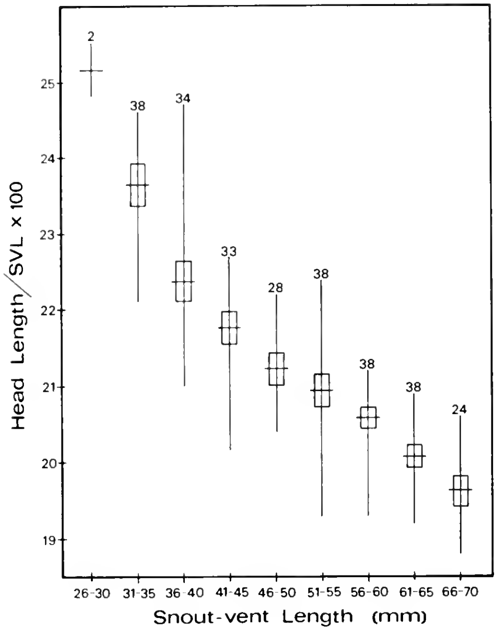

Figure 10. Allometric growth in the head of *Xantusia henshawi henshawi*. Symbols as in Figure 9.

correlated with both substrate and air temperatures (Figs. 16 and 17 respectively), but the higher coefficient of determination indicates that lizards are more closely coupled to substrate temperatures than to air temperatures.

DISCUSSION AND CONCLUSIONS

Sexual dimorphism.—Like many species of lizards, *X. h. henshawi* exhibits sexual size dimorphism, with females larger than males. Because larger female *X. h. henshawi* produce heavier, presumably more fit offspring, this may be an adaptation to accommodate relatively large embryos.

Among lizards, sexual dichromatism is widespread and often assumed to have a social function. Dichromatism therefore implies color vision, and the absence of color vision should preclude the evolution of social sexual dichromatism. *Xantusia vigilis* and *Klauberina riversiana* possess retinas adapted to conditions of low light intensity (Walls, 1942), conditions under which visual information in terms of color would be difficult to perceive, and color vision would be unlikely to evolve. Both are sexually monochromatic. Similarly, the secretive crepuscular-nocturnal habits of *X. h. henshawi* suggest the absence of color vision and probably account for the monochromatism of this species.

Males of many species of lizards, including *X. h. henshawi,* possess enlarged femoral pores, whereas those of the females are rudimentary. Pores and their secretions may somehow be associated with sexual activity (Atland, 1941; Bellairs, 1970; Bostic, 1964; Cole, 1966), but in *X. h. henshawi* femoral pore secretion is first evident in males at a SVL of about 44 mm and thus preceeds the acquisition of sexual maturity.

Population structure.—Many investigators have found unbalanced sex ratios among reptiles (Fitch, 1961). Among lizards such deviations usually favor females and are interpreted as the result of differential predation acting against the more conspicuous territorial males. The expected 1:1 sex ratio in *X. h. henshawi* for all age classes indicates that no such differential mortality is operating on this species. This is reasonable, for in this secretive monochromatic species, males are no more conspicuous than females.

A remarkable feature of the age class structure of the *X. h. henshawi* population is the high proportion of adults, implying a low rate of turnover. In this *X. h. henshawi* is similar to *Xantusia vigilis* in which 51 per cent of a winter population consisted of mature

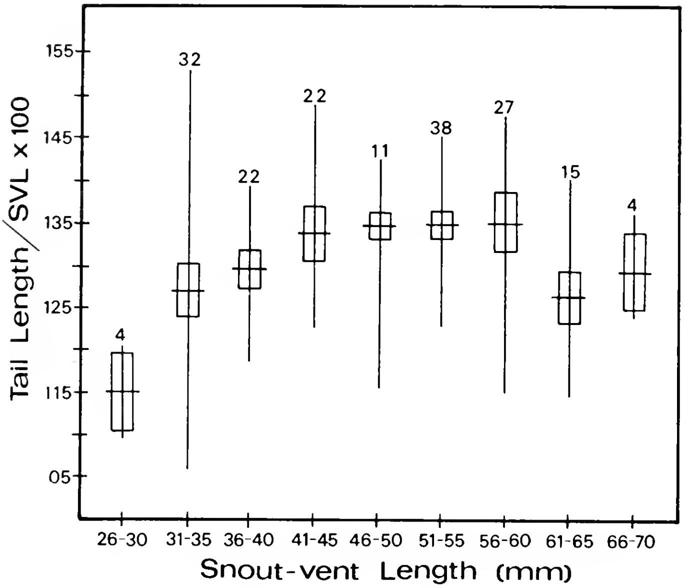

Figure 11. Allometric growth in the tail of *Xantusia henshawi henshawi.* Symbols as in Figure 9.

individuals (Zweifel and Lowe, 1966). Such age class structure is not unique to *Xantusia,* but it is in sharp contrast with the situation in many iguanids where high reproductive potential and high mortality combine to produce populations in which rates of turnover are high and immature lizards are abundant relative to adults. The iguanid lizard *Uta stansburiana* in west Texas is an extreme example in which life expectancy is little more than a year, and annual turnover approaches 100 per cent (Tinkle, 1965).

For *X. h. henshawi*, a species of narrow ecological tolerance, limited geographical distribution, existing in an area of low and unpredictable rainfall, a high proportion of long-lived breeding adults is adaptive in that it permits the population to survive several successive seasons of reproductive failure. The probability of such failure may be high, for the correlation between reproductive failure and inadequate mositure has been

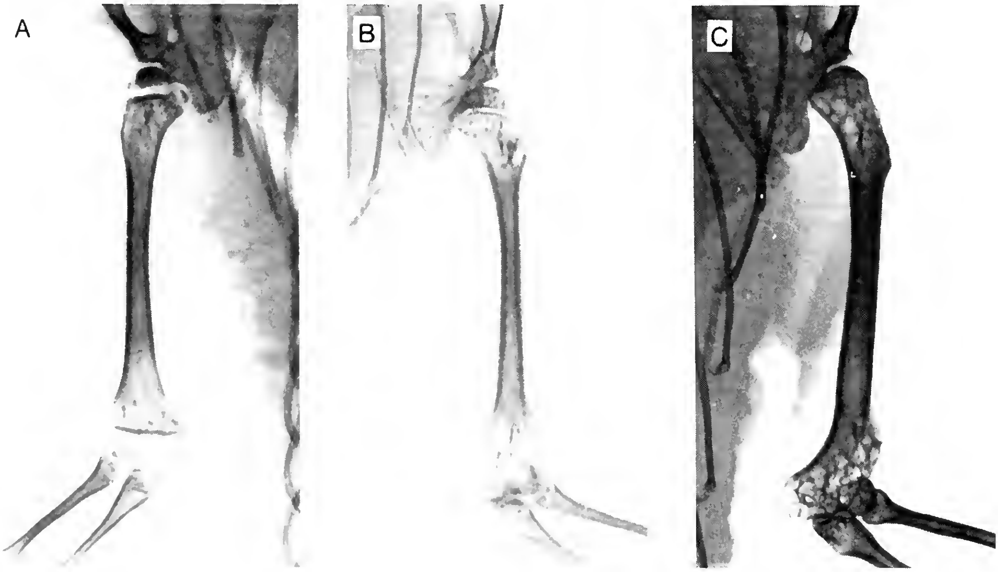

Figure 12. Epiphyseal-diaphyseal fusion in the humerus of *Xantusia henshawi henshawi.* A. 46 mm SVL B. 49 mm SVL C. 62 mm SVL.

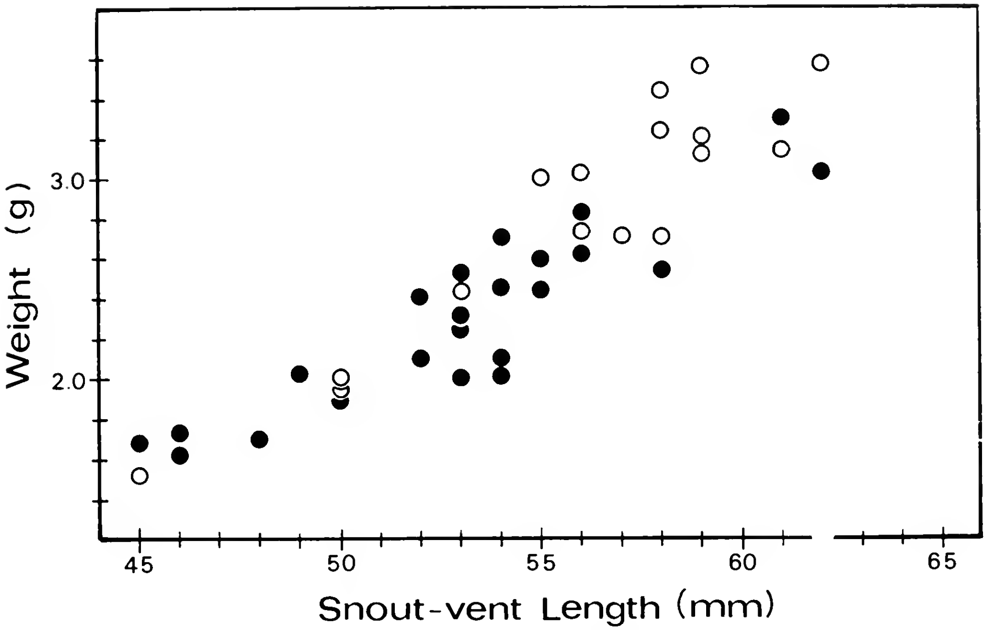

Figure 13. Comparison of the relationship between weight and snout-vent length in samples of *Xantusia henshawi henshawi* from burned (solid circles) and unburned (open circles) areas.

documented for some lizards (Mayhew, 1965; Nagy, 1973), including *X. vigilis* (Zweifel and Lowe, 1966).

Growth.—For its size, *X. h. henshawi* is an unusually slow growing, late maturing species; males first breed at about two and a half years, females at three and a half years. In this respect *X. h. henshawi* is identical to *X. vigilis* (Miller, 1951).

Like most vertebrates, *X. h. henshawi* has a relatively larger head at birth than at adulthood. This presumably results from the concentration of sense organs and nerve tissue in that area. Once ossified, the numerous complex, interlocking cranial elements preclude very much expansion in the head region. The biological significance of allometric growth in tail length of *X. h. henshawi* is obscure. It might reflect an ontogenetic change in the importance of the tail as an organ for fat storage, or changing demands on the tail as an organ of balance during locomotion. Fitch (1954) found similar allometric growth in the tail of the skink, *Eumeces fasciatus*.

Mortality.—Available evidence indicates that in *X. h. henshawi* mortality from all causes is low, as it must be for a species with low reproductive potential. This is so despite the fact that coexisting with *X. h. henshawi* are numerous potential predators. These lizards are probably most vulnerable when abroad at night, but their light nocturnal color phase closely approximates their granitic background, rendering them difficult to detect visually. *Hypsiglena torquata* and *Trimorphodon vandenburghi*, both nocturnal, perhaps occasionally prey on *X. h. henshawi*, but since neither species is numerous they may not make serious inroads in the lizard population. Nonetheless, the precise background matching coloration indicates that selection in the form of visually oriented predation has been a significant factor in the ecology of this species.

Brush fires might be a source of mortality in *X. h. henshawi*, as suggested by Klauber (1939). His conclusion that *X. h. henshawi*, in contrast to *Uta* and *Sceloporus*, was little affected by fires agrees with my observations that these lizards not only survive fires, but remain well nourished after living several months in a burned area.

Most chaparral fires in southern California occur during late summer and early fall during periods of high temperature, a time when *X. h. henshawi* seeks refuge deep within rock crevices from unfavorable temperatures. So situated, they are protected from fires

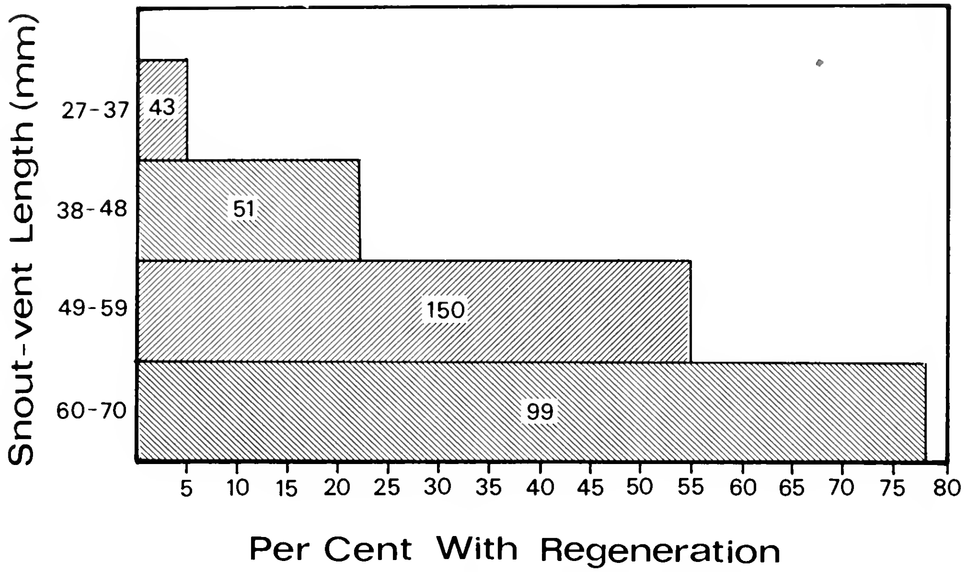

Figure 14. Frequency of caudal autotomy in *Xantusia henshawi henshawi* by size class. Numbers inside bars indicate sample size.

which, although generating high temperatures, are of short duration.

Because the presence of granitic exfoliations is important for the existance of this species, fires, rather than being detrimental, may be an asset; the rapid expansion of boulders caused by the heat of brush fires accelerates exfoliation, thereby generating more habitat.

I have no evidence that food shortage contributes to mortality in post-partum lizards, although it might lower reprodutive success. Of 735 lizards collected in this investigation, only two were obviously malnourished; this could have been the result of pathology unrelated to the availability of food.

Of those species which are potential competitors for food (Table 2), most are either temporally or spatially separated from *X. h. henshawi. Coleonyx, Phyllodactylus, Urosaurus, Uta, Sceloporus,* and *Petrosaurus* are likely to share the same boulder-crevice microhabitat, but only the activity of the first two overlaps both temporally and spatially with that of *X. h. henshawi,* which tend to be active within crevices during late afternoon and early evening and quiescent while abroad on boulders at night (Lee, 1974). In the area of sympatry between *X. h. henshawi* and *Coleonyx,* the latter is nowhere numerous, and *Phyllodactylus* overlaps *X. h. henshawi* geographically only on the desert slopes of mountains. Thus, although potential competitors for food are numerous, actual interspecific competition — if in fact food is limiting — is rare.

Caudal autotomy.—A high frequency of caudal autotomy suggests heavy predation pressure, but such a conclusion is inconsistent with the ecology of *X. h. henshawi,* for actual predator species are few, and individuals never abundant. Observations by Heimlich and Heimlich (1947), Lowe (1948), and Brattstrom (1952) provide an alternative explanation. Both Heimlich and Heimlich, and Brattstrom found tails of conspecifics in the stomachs of *Xantusia vigilis;* Lowe reported agonistic interactions among captive *X. vigilis* involving biting; and Zweifel and Lowe (1966) concluded that intraspecific fighting accounted for most of the autotomy observed by them during their nine year study of *X. vigilis* in the Mojave Desert. My observations on captive *X. h. henshawi* agree closely with those of Lowe (1948) for *X. vigilis.* Among captive *X. h. henshawi,* fights were common and involved twitching of the tail and biting, with the bites often directed toward the base of the tail. Several lizards exhibiting recent autotomy undoubtedly lost their tails in this manner. The high incidence of caudal autotomy in *X. h. henshawi* probably is more a reflection of intraspecific fighting than a high rate of attempted predation.

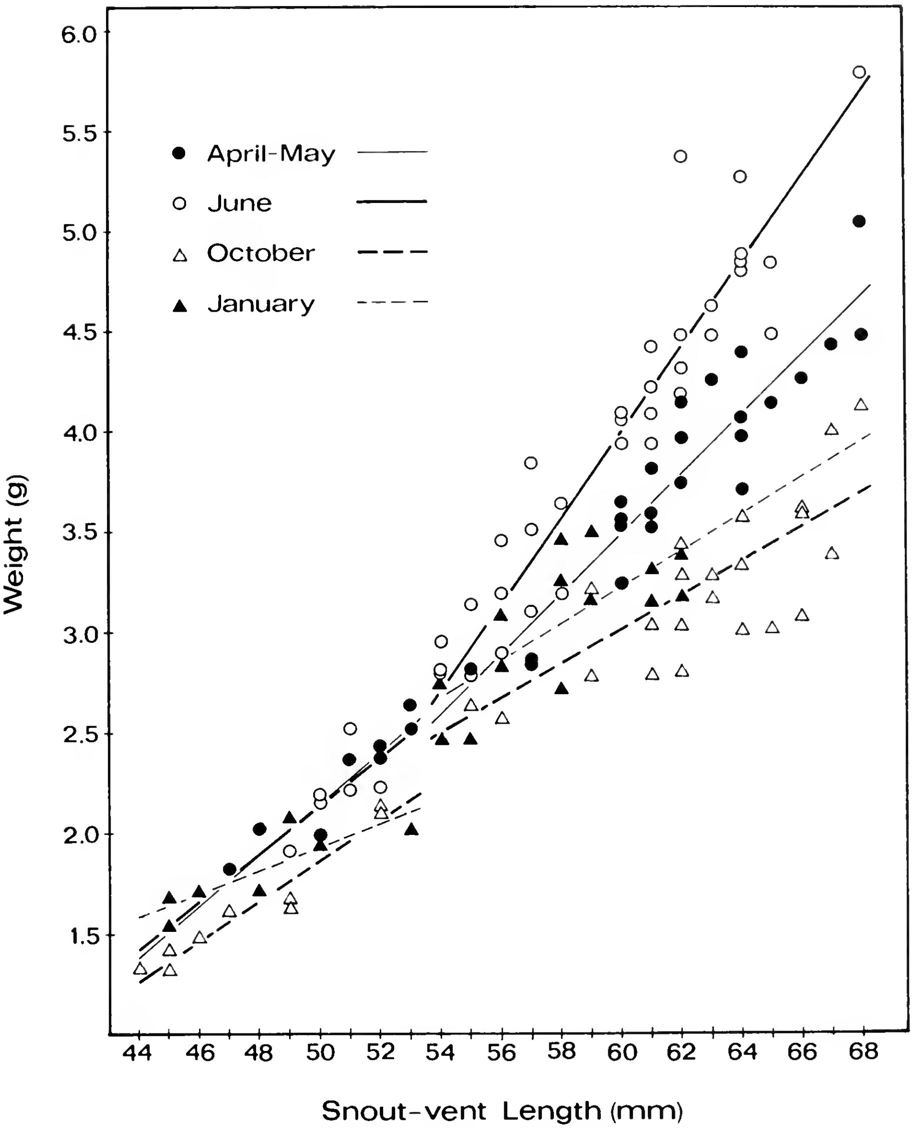

Figure 15. Relationship between weight and snout-vent length for female *Xantusia henshawi henshawi* collected at different times of the year. Below 54 mm 95% confidence limits for all regressions broadly overlap. Above 61 mm confidence limits for January entirely overlap October and slightly overlap April-May.

Reproduction.—Mean brood size for *X. h. henshawi* is lower than that reported for *Xantusia vigilis* by Zweifel and Lowe (1966) (1.46 and 1.87 respectively). Because female *X. h. henshawi* probably require three years to reach reproductive maturity, produce only a single brood per season, and average 1.46 offspring per brood, this species has the lowest reproductive potential (in the sense of Ballinger, 1973) reported for any lizard. However, the difference in brood size between *X. h. henshawi* and *X. vigilis* may not be significant, because Zweifel and Lowe (1966) demonstrated a strong positive correlation between brood size and amount of winter precipitation. If a similar relationship exists for *X. h. henshawi,* my estimate of brood size, based upon lizards collected in 1972, is a minimal one. Precipitation for the winter of 1971-72 in San Diego Co. was well below normal.

The low reproductive potential of *X. h. henshawi* may be contrasted with that of *Sceloporus olivaceous,* a species with perhaps the highest known reproductive potential of

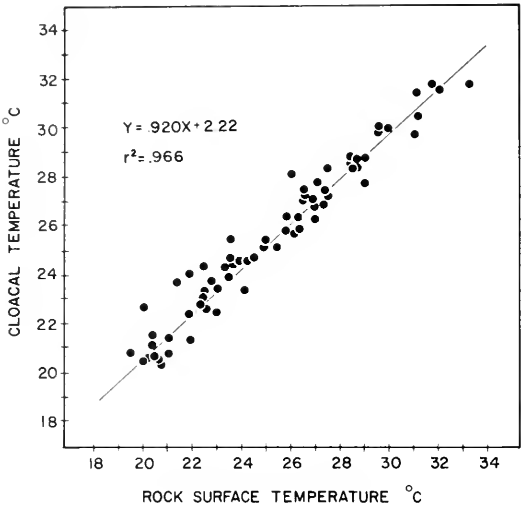

Figure 16. Regression of cloacal temperature of *Xantusia henshawi henshawi* against rock surface temperature.

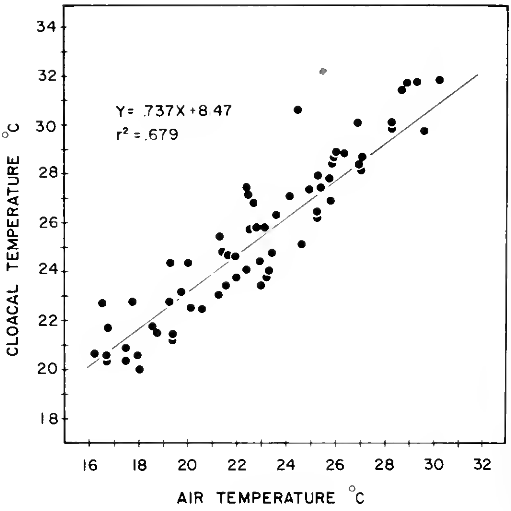

Figure 17. Regression of cloacal temperature of *Xantusia henshawi henshawi* against air temperature.

any lizard. In that species, yearling females may produce four clutches of eggs per season with a mean clutch size of 11.3 eggs. Clutch size increases to 18.4 in two-year-olds, and 24.5 in lizards three years of age (Blair, 1960). Theoretically, a female *Sceloporus olivaceous* surviving through the third breeding season could produce about 217 offspring in the time it would take *X. h. henshawi* to produce one or two. Mortality, of course, is very different in these two species. An average of 75 per cent of *Sceloporus olivaceous* eggs fail to hatch, and mean life expectancy at hatching is about three months (Blair, 1960). In the viviparous *X. h. henshawi,* developing embryos are protected, reducing mortality during development, and post-partum mortality is low, allowing females a protracted breeding life.

On the basis of reproductive strategy and attendant life history characteristics, Tinkle (1969) and Tinkle *et al.,* (1970) have identified two categories of lizards. One contains small species that are early-maturing, short-lived, and highly fecund (e.g., *Sceloporus olivaceous*); the other contains larger species that are late-maturing, have long life expectancy, and produce few offspring per season. Members of the former category are relatively *r*-selected (Pianka, 1970); they allocate large amounts of energy for reproduction, produce many offspring, but apportion little energy per individual offspring. Members of the latter category are relatively *K*-selected, channeling energy into production of a few highly fit offspring. Except for size, *X. h. henshawi* typifies the latter category and is a highly *K*-selected species.

Thermal biology.—In previous studies dealing with the thermal biology of *X. h. henshawi* (Brattstrom 1965; Mautz and Case, 1974; Scott, 1971) cloacal temperatures obtained from lizards in the field were apparently taken only during daylight hours, and from lizards that had been removed from crevices. In the present study, cloacal temperatures obtained at night from lizards abroad on boulders indicate that *X. h. henshawi* is highly dependent on rock surface temperatures; thus, Brattstrom's (1965) designation of this species as a thigmotherm is appropriate.

Cowles and Bogert (1944) define the normal activity range of temperatures in reptiles as ". . . the thermal range extending from the resumption of ordinary routine (after the animal has ceased basking, in the case of diurnal forms) and terminates at a point just below the level at which high temperatures drive the animal to shelter." Elsewhere (Lee, 1974) I show that maximum activity in this species occurs before lizards issue forth from their crevices at night. Therefore, the range of temperatures recorded for these lizards abroad at night may not reflect the normal activity range, but rather the range over which a relatively quiescent portion of the activity cycle occurs. Thus, my data cannot be directly compared with published data on normal activity ranges of lizards. It is of interest, however, to compare them with the range of temperatures tolerated voluntarily during the day as determined by Scott (1971). The close correspondence between Scott's data (18.6 to 33.0 C, $\overline{X} = 26.0$) and mine (18.1 to 31.8 C, $\overline{X} = 25.3$) indicates that in general, during the warmer part of the year, lizards maintain body temperatures within about the same limits both day and night. This species is clearly eurythermic, tolerating a wide range of body temperatures and with no clearly defined preferred temperature.

The biology of Xantusia henshawi *compared with that of other xantusiids.*—The Xantusiidae are a small, apparently ancient family of unknown origin (Bezy, 1972). Savage (1963) recognized four living genera: *Cricosaura,* monotypic and known only from Cabo Cruz, Oriente Province, Cuba; *Klauberina,* also monotypic and restricted to the Channel Islands off the coast of southern California; *Lepidophyma,* with perhaps 12 species, confined to southern Mexico and Central America; and *Xantusia,* with two species, restricted to northeastern Mexico and the southwestern United States.

Ecologically, the family is relatively homogeneous. Xantusiids tend to be small, secretive, and terrestrial. So far as known, all are viviparous and most have low reproductive potential (Goldberg and Bezy, 1974). As a group they are relatively *K*-selected. *Xantusia henshawi henshawi* and *Xantusia vigilis* are especially similar in reproductive biology, population structure, growth (Miller, 1951), and thermal biology (Kour and Hutchinson, 1970).

Xantusiids exhibit highly disjunct, frequently relictual distributions, and often have specialized microhabitat requirements (rock crevices, fallen yuccas, decomposing logs in humid tropical forests). Bezy (1972) views this as a response to increasing aridity during the Tertiary. Perhaps an additional factor has been competition with other lizards. If xantusiids are competitively inferior, the few existing species are those that have survived the Tertiary radiations of other lizard groups by avoiding competition, either by increased specialization (e.g., *Xantusia henshawi henshawi*) or by fortuitous establishment on (or restriction to) islands (e.g., *Klauberina*).

ACKNOWLEDGEMENTS

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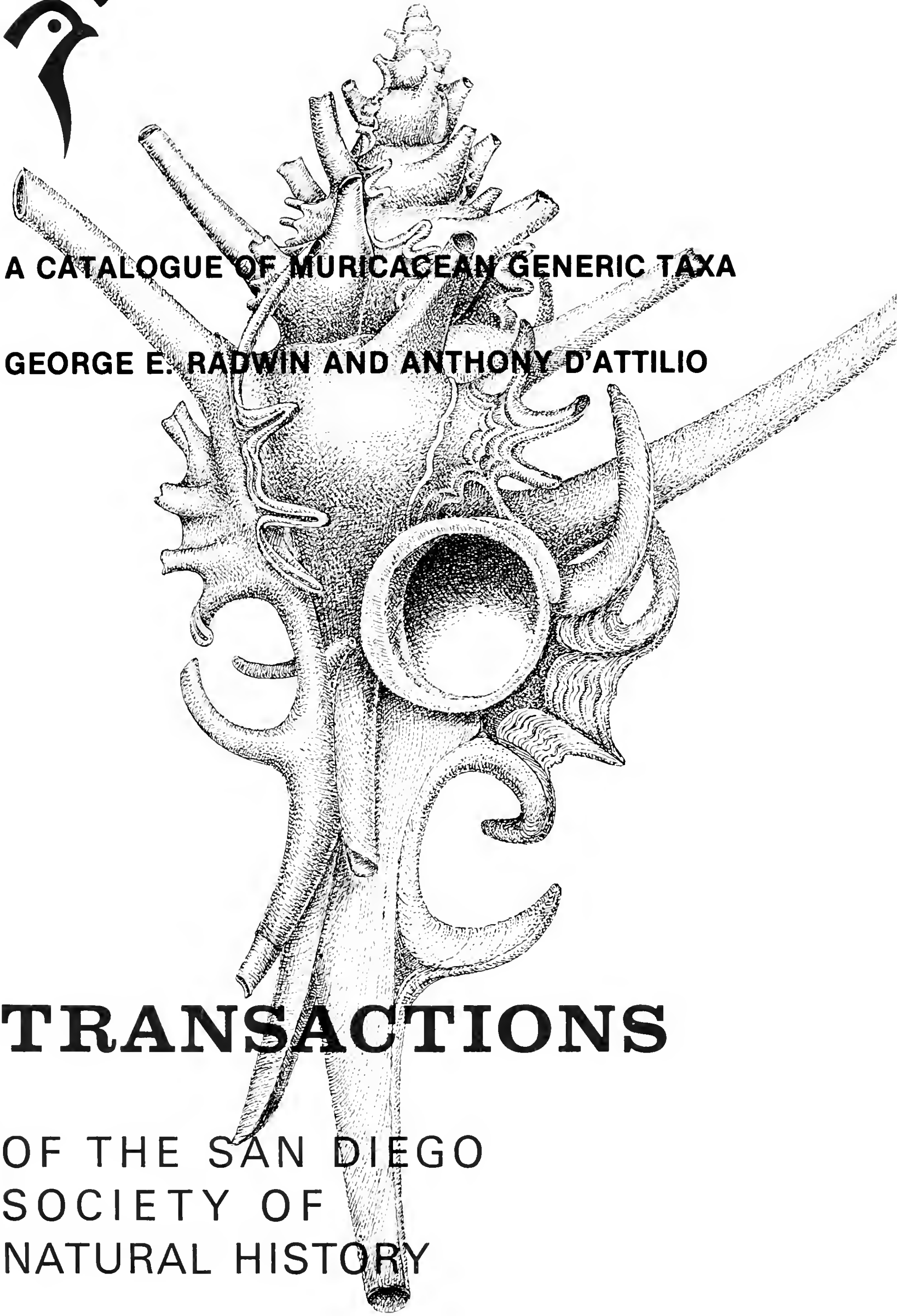
A CATALOGUE OF MURICACEAN GENERIC TAXA

GEORGE E. RADWIN AND ANTHONY D'ATTILIO



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A CATALOGUE OF MURICACEAN GENERIC TAXA

ERRATA

p. 279, last line - should read -- monotypy; - -extinct genus
p. 281, right column, immediately after line 52 insert --
CYMIA Morch, 1860: 97, 98
Type sp. (M.): *Cuma sulcata*
Swainson, 1840, A Treatise on
Malacology, p. 87, fig. 4
(= *Buccinum tectum* Wood, 1828)
p. 283, right column, line 34 - should read -- LYROTYPHIS.
p. 284. left column, line 35 -- delete whole line
left column, line 44 -- acute accent over "e" in Linne.
right column, line 59 -- "Jousseaume" instead of "Jousseaum".
p. 286, left column, line 43 -- should read -- Meth. pl. 436, fig. 1,
Liste, p. 8.
right column, line 1 -- should read -- figs. 1a, 1b, Liste, p. 1.
right column, line 10 -- "non-bionominal" should be - "non-binominal"
p. 288, right column, line 53 -- "Collected" should begin with a lower
case letter.
p. 289, right column, line 59 -- "recent" should begin with an upper case
letter.

SAN DIEGO SOC. NAT. HIST., TRANS. 17(20): 279-292, 16 MAY 1975.

A CATALOGUE OF MURICACEAN GENERIC TAXA

GEORGE E. RADWIN AND ANTHONY D'ATTILIO

ABSTRACT.—A compilation of genus-level taxa and their type-species is provided, including the mode of type designation and references to the original descriptions of the genera and the type-species.

Despite long-standing and recently intensified interest in muricacean mollusks, no compilation of generic taxa is currently available. The most complete listing (Wenz, 1941) lacks the depth needed by taxonomists and other workers. Wenz listed only 223 taxa and he treats half of these as synonyms, for which he does not supply type-species; where he does note type-species he rarely cites the mode of type designation or gives references to these type-species. Vokes (1971) presented a more complete listing, at the species level, for several subfamilies of the Muricidae, and Keen (1944) catalogued the Typhinae at the specific and generic levels.

In preparing a guide to the Muricidae, we compiled nomenclatural data on genera in that and other muricacean families. They are catalogued below. In the first section we list nominal generic and subgeneric muricacean taxa, most cited from primary sources, arranged alphabetically, including type-species designations and original references. The list is essentially complete through 1974. In the second section we present a bibliography of works in which muricacean generic taxa have been introduced. We have supplied complete citations to generic references, abbreviated references of type-species and subsequent type designations. As this catalogue is intended to serve as a reference work, rather than as a vehicle for our taxonomic opinions, we have avoided all but the most essential comments on synonymy. The following abbreviations are used: O. D.—type species by original designation; S. D.—type species by subsequent designation; M.—type species by monotypy; T.—type species by tautonymy; S. M.—type species by subsequent monotypy;—extinct genus.

SAN DIEGO SOC. NAT. HIST., TRANS. 17(20): 279-292, 16 MAY 1975.

GENERIC AND SUBGENERIC TAXA OF THE MURICACEA

AARONIA A. H. Verrill, 1950: 4
Type sp. (O. D.): *Murex (Aaronia) strausi* Verrill, 1950, Min. Conch. Club S. California 103: 4.

ACANTHINA Fischer de Waldheim, 1807: 174
Type sp. (S. D., Gray, 1847b): *Buccinum monoceros* Chemnitz, 1788 (= *Buccinum monodon* Pallas, 1774), Neues Systematisches Conchylien-Cabinet 10: 197, pl. 154, figs. 1469, 1470).

†ACANTHINELLA Shuto, 1969: 109
Type sp. (O. D.): *Acantina* (sic.) *javana* Martin, 1899, Samml. Geol. Mus. Leiden, N. F. 1: 109.

ACANTHINUCELLA Cooke, 1918: 8
Type sp. (O. D.): *Acanthina punctulata* (Sowerby, 1835), Proc. Zool. Soc. London 3: 50.

†ACANTHOLABIA Olsson & Harbison, 1953: 252
Type sp. (O. D.): *Acantholabia floridana* Olsson & Harbison, 1953, Acad. Nat. Sci. Phila. Monogr. 8: 251, pl. 33, fig. 10.

ACANTHOTROPHON Hertlein & Strong, 1951: 86
Type sp. (O. D.): *Trophon (Acanthotrophon) sorensoni* Hertlein & Strong, 1951, pt. X, Zoologica 36(2): 86, p. 2, fig. 1.

ACTINOTROPHON Dall, 1902: 534
Type sp. (M.): *Trophon (Boreotrophon) actinophorus* Dall, 1889, Mus. Comp. Zool. Harvard 18: 206.

ACUPURPURA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex tenuispina* Lam., 1822, (= *M. pecten* Lightfoot, 1786) Hist. Nat. Anim. s. Vert. 7: 158.

ADAMSIA Dunker, 1857: 357 (Not Forbes, 1840)
Type sp. (O. D.): *Adamsia typica* Dunker, 1857 (= *Purpura tritoniformis* Blainville, 1832), Proc. Zool. Soc. London 25: 357.

AFRITROPHON Tomlin, 1947: 271
Type sp. (O. D.): *Trophon kowieensis* Sowerby, 1901, Proc. Malac. Soc. London 4: 213, pl. 22, fig. 16.

AGNEWIA Tenison-Woods, 1878: 29
New name for *Adamsia* Dunker, 1857, not Forbes 1840.

†ALDRICHIA K. Palmer, 1937: 262
Type sp. (O. D.): *Murex cancellaroides* Meyer & Aldrich, 1886 (= *Muricopsis aldrichi* Cossmann, 1903, new name for *M. cancellaroides* Meyer & Aldrich, 1886, not Grateloup, 1833), J. Cinn. Soc. Nat. Hist. 9: 44, pl. 2 fig. 15.

ALIPURPURA P. Fischer, 1884: 641
Type sp. (O. D.): *Murex acanthopterus* Lamarck, 1822, Hist. Nat. Anim. s. Vert. 7: 165.

ANATROPHON Iredale, 1929a: 186
Type sp. (O. D.): *Trophon sarmentosa* Hedley & May, 1908, Rec. Australian Mus. 7: 121.

ANTIMUREX Cossmann, 1903: 12
New name for *Crassilabrum* Jousseaume, 1880, not Megerle von Muhlfeld (Ms) in Scudder, 1882. (This unnecessary replacement name was introduced by Cossmann on the assumption that Megerle's manuscript genus *Crassilabrum* preoccupied *Crassilabrum* Jousseaume. In actuality Megerle's (Ms) name was not validated until Scudder (1882), thus making it junior to Jousseaume's taxon.)

APIXYSTUS Iredale, 1929a: 185
Type sp. (O. D.): *Trophon stimuleus* Hedley, 1907, Rec. Australian Mus. 6: 293, pl. 55, fig. 19.

ARADOMUREX Coen, 1929: 1281
Type sp. (O. D.): *Murex sophiae* Aradas & Benoit, 1870, Conch. Viv. Mar. Sicil. p. 270-271, pl. 5, fig. 7.

ARANEA Perry, 1810: 225 (not *Aranea* Linné, 1758)
Type sp. (M.): *Aranea gracilis* Perry, 1810, The Arcana, p. 225, pl. 47.

ASPELLA Mörch, 1877: 24
Type sp. (M.): *Ranella anceps* Lamarck, 1822, Hist. Nat. Anim. s. Vert. 7: 154.

ATTILIOSA Emerson, 1968a: 380
Type sp. (O. D.): *Coralliophila incompta* Berry, 1960, Leaflets in Malacology 1(19): 119-120.

AUSTROTROPHON Dall, 1902: 534, 548
Type sp. (S. D. Grant & Gale, 1931): *Trophon cerrosensis* Dall, 1891, Proc. U. S. Natl. Mus. 14: 181, pl. 5, figs. 5, 7.

AXYMENE Finlay, 1927: 426
Type sp. (O. D.): *Trophon (A.) turbator* Finlay, 1927, Trans. Proc. New Zealand Inst. 57: 426, pl. 23, figs. 127, 128.

AZUMAMORULA Emerson, 1968b: 380
New name for *Morulina* Dall, 1923, not Börner, 1906.

BABELOMUREX Coen, 1922: 68
Type sp. (O. D.): *Fusus babelis* Requien, 1848, Cat. des Coquilles de l'île de Corse, pt. 49 p. 76, sp. 549.

BASSIA Jousseaume, 1880: 335 (not Quoy & Gaimard, 1830)
Type sp. (O. D.): *Murex stainforthi* Reeve, 1842, Proc. Zool. Soc. London 9: 104.

BASSIELLA Wenz, 1941: 1089
New name for *Bassia* Jousseaume, 1880, not Quoy & Gaimard, 1830.

BATHYMUREX Clench & Pérez Farfante, 1945: 41
Type sp. (O. D.): *Bathymurex atlantis* Clench & Pérez Farfante, 1945, Johnsonia 17: 41, pl. 21, figs. 3-5.

BEDEVA Iredale, 1924: 183
Type sp. (O. D.): *Trophon hanleyi* Angas, 1867 (= *Trophon paivae* Crosse, 1864), Proc. Zool. Soc. London 31: 110, pl. 13, fig. 1.

BEDEVINA Habe, 1946: 198
Type sp. (O. D.): *Trophon birileffi* Lischke, 1871, Malak. Bl. 18: 39.

BENTHOXYSTUS Iredale, 1929a: 185
Type sp. (O. D.): *Trophon columnarius* Hedley & May, 1908, Rec. Australian Mus. 7: 121, pl. 24, fig. 22.

BIZETIELLA Radwin & D'Attilio, 1972: 341
Type sp. (O. D.): *Tritonalia carmen* Lowe, 1935, Trans. San Diego Soc. Nat. Hist. 8(6): 20, pl. 2 fig. 6.

BOLINUS Pusch, 1837: 134
Type sp. (O. D.): *Murex brandaris* Linné, 1758, Syst. Nat., Ed. 10, p. 747, no. 446.

BOREOTROPHON P. Fischer, 1884: 640
Type sp. (M.): *Murex clathrata* Linné, 1767, Syst. Nat., Ed. 12, p. 1223, no. 563.

BRONTA Pusch, 1837: 130
New name for *Brontes* Montfort, 1810, not Fabricius, 1801.

BRONTES Montfort, 1810: 623 (not Fabricius, 1801)
Type sp. (O. D.): *Brontes haustellum* Montfort,

1810, (= *Murex haustellum* Linné, 1758) Conch. Syst. 2: 623, pl. 622.

BRONTESIA Reichenbach, 1828: 91

New name for *Brontes* Montfort, 1810, not Fabricius, 1801.

CALCITRAPESSA Berry, 1959: 13

Type sp. (O. D.): *Murex leeanus* Dall, 1890, Proc. U. S. Nat. Mus. 12: 329, pl. 7, fig. 1.

CALOTROPHON Hertlein and Strong, 1951: 87

Type sp. (M.): *Calotrophon bristolae* Hertlein & Strong, 1951 (= *Tritonalia turrita* Dall, 1919), Zoologica 36(2): 87, pl. 2, fig. 2.

CANRENA Link, 1807: 126

Type sp. (O. D.): *Murex neritoideus* Gmelin, 1791, Syst. Nat. Ed. 13, p. 3537, no. 43.

CARIBIELLA Perrilliat, 1972: 82

Type sp. (O. D.): *Murex intermedius* C. B. Adams, 1850, Contrib. to Conch. 1(4): 60.

CENTRIFUGA Grant and Gale, 1931: 706-707

Type sp. (O. D.): *Murex centrifuga* Hinds, 1844, Mollusca, pl. 1, p. 8, pl. 3, figs. 7, 8.

CENTRONOTUS Swainson, 1833: 100 (not *Centronotus* Schneider 1801)

Type sp. (O. D.): *Murex eurystomus* Swainson, 1833 (= ?*M. duplex* Röding, 1798), Zool. Illust. (2)3: 100, pl. 3.

Type sp. (S. D., ICZN, 1970): *Murex radix* Gmelin, 1791, Syst. Nat., Ed. 13, p. 3527. (see ICZN opinion 911, 1970, Bull. Zool. Nomencl. 27: 20, wherein *M. radix* was designated as type to supersede all others).

CERASTOMA Conrad, 1837: 264

Type sp. (M.): *Murex* (*Cerastoma*) *nuttalli*, Conrad, 1837: J. Acad. Nat. Sci. Philadelphia 7: 264, pl. 20, fig. 22.

CERATOSTOMA Hermannsen, 1846: 206

New name for *Cerastoma* Conrad, 1837, not Latreille, 1802.

CHALMON de Gregorio, 1885: 28

Type sp. (O. D.): *Trophon* (*Chalmon*) *muricatus* Montagu, 1802, Test. Brit. 1: 262, pl. 9, fig. 2.

CHATHAMIDEA Dell, 1956: 118

Type sp. (O. D.): *C. expeditionis* Dell, 1956, Dominion Mus. Bull. 18: 118, figs. 159, 160.

CHICOMUREX Arakawa, 1964: 361

Type sp. (O. D.): *Murex superbus* Sowerby, 1889, Proc. Zool. Soc. London 1889: 565, pl. 28, figs. 10, 11.

CHICOREUS Montfort, 1810: 610

Type sp. (fixed by ICZN opin. 911, 1970, Bull. Zool. Nomencl. 27: 20): *Murex ramosus* Linné, 1758, Syst. Nat. Ed. 10, p. 747, no. 448.

CHOREOTYPHIS Iredale, 1936: 324

Type sp. (O. D.): *Typhina pavlova* Iredale, 1936, Rec. Australian Mus. 19(5): 324, pl. 24, fig. 12.

CHORUS Gray, 1847b: 136

Type sp. (O. D.): *Monoceros giganteus* Lesson, 1831, Zool. 11(1): 403.

CINCLIDOTYPHIS DuShane, 1969: 343

Type sp. (O. D.): *C. myrae* DuShane, 1969, The Veliger, 11(4): 343, p. 54, figs. 1-3.

COLUMBARIUM von Martens, 1881: 105

Type sp. (O. D.): *Pleurotoma* (*Columbarium*) *spinicinctum* Martens, 1881; Conchologische Mitteilungen, 2: 105, pl. 21, fig. 1-4.

COLUZEA Finlay 1927: 407

Type sp. (O. D.): *Fusus spiralis* A. Adams, 1856, Proc. Zool. Soc. London 23: 221. (For comments see Keen, A. M., 1969, Bull. Zool. Nomencl. 26: 184.)

COMPTELLA Finlay, 1927: 424

Type sp. (O. D.): *Trophon curtus* Murdoch, 1905, Trans. New Zealand Inst. 37: 228.

CONCHOLEPAS "Klein" Bruguière, 1792: 535

Type sp. (S. D. Lamarck, 1801): *Concholepas peruvianus* Lamarck, 1801 (= *Buccinum concholepas* Bruguière, 1789), Syst. Anim. s. Vert. p. 70.

CONCHOPATELLA Herrmannsen, 1847: 291

Listed as synonym of *Concholepas* Lamarck, 1801 (= *Concholepas* Bruguière, 1792).

CONCHULUS Rafinesque, 1815: 142

Introduced as a synonym of *Concholepas* Lamarck, 1801 (= *Concholepas* Bruguière, 1792).

CONOTHAIS Kuroda, 1930: 1

Type sp. (M.): *Conothais citrina* Kuroda, 1930, Venus, 2(1): 1.

CORALLINIA Bucquoy & Dautzenberg (*in*, Bucquoy, Dautzenberg, & Dollfus), 1882: 24

Type sp. (O. D.): *Murex aciculatus* Lamarck, 1822, Hist. Nat. Anim. s. Vert. 7: 176.

CORALLIOBIA H. & A. Adams, 1853: 138

Type sp. (M.): *Leptoconchus* (*Coralliobia*) *fimbriata* H. & A. Adams, 1853 (nomen nudem) (= *Concholepas* [*Coralliobia*] *fimbriata* A. Adams, 1854), Proc. Zool. Soc. London 19: 93.

CORALLIOFUSUS Kuroda, 1953: 119

Type sp. (O. D.): *Coralliofusus acus* Kuroda, 1953, Venus 17: 119, figs. 3, 4.

CORALLIOPHILA H. & A. Adams, 1853: 135

Type sp. (S. D. Iredale, 1912): *Murex neritoideus* Chemnitz (non-binominal) (= *Fusus neritoideus* Lamarck, 1816), Neues Systematisches Conchylien-Cabinet 10: 280, pl. 165, figs. 1577, 1578.

CRASPEDOTRITON Dall, 1904: 119

Type sp. (O. D.): *Triton convolutus* Broderip, 1833, Proc. Zool. Soc. London 1: 7.

CRASSILABRUM Jousseaume, 1880: 335

Type sp. (O. D.): *Murex crassilabrum* Sowerby, 1834, Conch. Illust. *Murex*, pl. 59, fig. 14.

CRONIA H. & A. Adams, 1853: 128

Type sp. (M.): *Purpura amygdala* Kiener, 1835, Spec. Gen. Icon. Coq. Viv. . . . Pourpre, p. 39, pl. 10, fig. 26.

CUMA Swainson, 1840: 87, 307

Type sp. (O. D.): *Buccinum tectum* Wood, 1828, Index Testaceologicus . . . A catalog of shells, Suppl. p. 12, no. 13, pl. 4, fig. 13.

CUMOPSIS Rovereto, 1899: 105

New name for *Cuma* Swainson, 1840, not Milne-Edwards, 1828-see *Cymia* Mörch, 1860.

CYTHAROMORULA Kuroda, 1953: 183

Type sp. (M.): *Cytharomorula vexillum* Kuroda, 1953, Venus 17: 183.

DALLIMUREX Rehder, 1946: 142

Type sp. (O. D.): *Murex nuttingi* Dall, 1896 (= *Murex pazi* Crosse, 1869), Bull. Lab. Nat. Hist., State Univ. Iowa 4(1): 13, pl. 1, fig. 1.

DENTOCENEBRA Monterosato, 1917: 21

Type sp. (O. D.): *Ocenebra corallinus* Scacchi, 1836 (= *O. aciculata* Lamarck, 1822), Cat. Conch. Regni Neap., p. 11, fig. 15.

DERMOMUREX Monterosato, 1890: 181

New name for *Poweria* Monterosato, 1884, not Bonaparte, 1841.

DICATHAIS Iredale, 1936: 325

Type sp. (O. D.): *Buccinum orbita* Gmelin, 1791, Syst. Nat. Ed. 13, Vermes, p. 3490, no. 183.

DISTICHOTYPHIS Keen & Campbell, 1964: 56
Type sp. (O. D.): *Distichotyphis vemae* Keen & Campbell, 1964, The Veliger 7(1): 56-57, pl. 11, figs. 45-47.

DRUPA Röding, 1798: 55
Type sp. (S. D. Rovereto, 1899): *Drupa morum* Röding, 1798, Museum Boltenianum p. 55, no. 694.

DRUPELLA Thiele, 1925: 137
Type sp. (S. D. Wenz, 1941): *Drupa* (*Drupella*) *ochrostoma* (Blainville, 1832), Nouv. Ann. Mus. Hist. Nat. Paris ser. 3, 1: 205.

DRUPINA Dall, 1923: 303
Type sp. (O. D.): *Ricinula digitata* Lamarck, 1816 (= *Drupa grossularia* Röding, 1798), Tableau Encycl. Mèth. pl. 395, fig. 7a, 7b, Liste, p. 2.

†ECPHORA Conrad, 1843: 310
Type sp. (O. D.): *Fusus quadricostatus* Say, 1824, J. Acad. Nat. Sci. Philadelphia 4: 127.

EMOZAMIA Iredale, 1929a: 185
Type sp. (O. D.): *Murex licinus* Hedley and Petterd, 1906, Rec. Australian Mus. 6: 219, pl. 37, fig. 6.

ENATIMENE Iredale, 1929a: 185
Type sp. (O. D.): *Trophon simplex* Hedley, 1903, Mem. Australian Mus. 4(1): 380.

ENIXOTROPHON Iredale, 1929a: 185
Type sp. (O. D.): *Trophon carduelis* Watson, 1882, Mollusca of H. M. S. Challenger Expedition, pt. 14, p. 388.

†ENTACANTHUS Ihering, 1907: 183
Type sp. (M.): *Trophon monoceros* Ihering, 1907, Anal. Mus. Nac. Buenos Aires 14: 183.

†EOTYPHIS Tembrock, 1963: 322
Type sp. (O. D.): *Typhis sejunctus* Semper, 1861, Arch. Verens. Freunde Naturg. Mecklen. 15: 161.

ERGALATAX Iredale, 1931: 231
Type sp. (O. D.): *Ergalatax recurrens* Iredale, 1931 (= *Buccinum contractum* Reeve, 1846), Rec. Australian Mus. 18: 231.

EUPHYLLON Jousseaume, 1880: 335
Type sp. (O. D.): *Murex monodon* Sowerby, 1825 (= *Murex cornucervi* Röding, 1798), Cat. Shells Tankerville, App., p. 19, sp. 1703.

EVOKESIA Radwin & D'Attilio, 1972: 335
Type sp. (O. D.): *Sistrum rufonotatum* Carpenter, 1864, Ann. Mag. Nat. Hist., ser. 3, 14:.48.

EUPLEURA H. & A. Adams, 1853: 107
Type sp. (S. D., F. C. Baker, 1895): *Ranella caudata* Say, 1822, J. Acad. Nat. Sci. Philadelphia 2: 236.

FAVARTIA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex breviculus* Sowerby, 1834, Conch. Illust., pl. 63, fig. 37.

†FLEXOPTERON Shuto, 1969: 112
Type sp. (O. D.): *Flexopteron philippinensis* Shuto, 1969, Mem. Fac. Sci. Kyushu Univ. (ser. Geol.) 19: 112.

FORRERIA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex belcheri* Hinds 1844, Proc. Zool. Soc. London 11: 128.

FRONDOSARIA Schlüter, 1838: 20
Type sp. (S. D., E. H. Vokes, 1964): *Frondosaria inflata* (Lamarck, 1822) (= *Murex ramosus* Linné, 1758), Hist. Nat. Anim. s. Vert. 7: 160.

FUEGOTROPHON Powell, 1951: 157
Type sp. (O. D.): *Fusus crispus* Gould, 1849 (= *Murex pallidus* Broderip, 1833), Proc. Boston Soc. Nat. Hist. 3: 141.

†FULGUROFUSUS Grabau, 1904: 86
Type sp. (O. D.): *Fusus quercollis* Harris, 1896, Bull. Amer. Paleo. 1: 200, pl. 18, fig. 9.

FUSOMUREX Coen, 1922: 69
Type sp. (O. D.): *Purpura alucoides* Blainville, 1829, Faune Française, p. 128, pl. 5b, fig. 1.

†GALEROPSIS Hupé, 1860: 127
Type sp. (O. D.): *Galeropsis lavenayana* Hupé, 1860, Rev. Mag. Zool. 12: 127.

GALFRIDUS Iredale, 1924: 271
Type sp. (O. D.): *Triton* (*Cumia*) *speciosum* Angas, 1871, Proc. Zool. Soc. London, 89: 13, pl. 1, fig. 1.

GEMIXYSTUS Iredale, 1929a: 185
Type sp. (O. D.): *Trophon laminatus* Petterd, 1884, J. Conch., 4: 136, pl. 22, fig. 3.

GENKAIMUREX Kuroda, 1953: 120
Type sp. (O. D.): *Coralliophila* (*Genkaimurex*) *varicosa* Kuroda, 1953 (= *Murex fimbriatulum* A. Adams, 1863), Venus 17: 120.

GRACILIMUREX Thiele, 1929: 289
Type sp. (O. D.): *Gracilimurex bicolor* Thiele, 1929, Handbuch Syst. Weichtier., p. 289.

GRACILIPURPURA Jousseaume, 1880: 335
Type sp. (O. D.): *Fusus strigosus* Lamarck, 1822, Hist. Nat. Anim. s. Vert. 7: 130.

HADRIANIA Bucquoy & Dautzenberg, 1882: 16, 33
Type sp. (O. D.): *Murex craticulatus* Brocchi, 1814 (not Linné, 1758) (= *Hadriania craticuloides* E. H. Vokes, 1964), Conch. Foss. Subapp., 2: 406, pl. 7, fig. 14.

HANETIA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex haneti* Petit, 1856, J. Conchyl. 5: 90.

†HARMATIA Noszky, 1940: 28
Type sp. (O. D.): *Murex* (*Harmatia*) *stephani* Noszky, 1940, Ann. Hist. Nat. Mus. Hung. Min. Geol. 33: 1-80.

HAUSTELLARIA Swainson, 1833: pl. 100
Type sp. (O. D.): *Haustellaria haustellum* Linné, 1758, Syst. Nat., Ed. 10, p. 746, no. 493.

HAUSTELLOTYPHIS Jousseaume, 1880: 335
Type sp. (O. D.): *Typhis cumingi* Broderip, 1833, Proc. Comm. Sci. Corr. Zool. Soc. London 2: 177.

HAUSTELLUM "Klein" Bruguière, 1792: 533
Type sp. (S. M., Schumacher, 1817), *Murex haustellum* Linné, 1758, p. 746, no. 213.

HAUSTRUM Perry, 1811: pl. 44
Type sp. (S. D. Iredale, 1915): *Buccinum haustrum* Martyn, 1788 (non-binominal) (= *Buccinum haustorium* Gmelin, 1791), Univ. Conch., vol. 2, fig. 9c.

HERTLEINELLA Berry, 1958: 95
Type sp. (O. D.): *Hertleinella leucostephes* Berry, 1958, 1(16): 95.

†HETEROPURPURA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex polymorphus* Brocchi, 1814, Conch. Foss. Subapp. 2: 415, pl. 8, figs. 4a, 4b.

†HEXACHORDA Cossmann, 1903: 47
Type sp. (O. D.): *Murex tenellus* Mayer-Eymar, 1869, J. Conchyl. 17: 82, pl. 3 fig. 5.

HEXAPLEX Perry, 1811: pl. 8
Type sp. (S. D. Jousseaume, 1880): *Murex cichoreum* Gmelin, 1791, Syst. Nat., Ed. 13, 1: 3530.

†HIPPOCAMPOIDES Wade, 1916: 466
Type sp. (O. D.): *Hippocampoides serratus*

Wade, 1916, Proc. Acad. Nat. Sci. Philadelphia 68: 466, pl. 24, figs. 11-13.

HIRTOMUREX Coen, 1922: 69
Type sp. (O. D.): *Fusus lamellosa* Philippi, 1836, Enum. Moll. Sicil., p. 204.

†HIRTOTYPHIS Jousseaume, 1880: 336
Type sp. (O. D.): *Murex horridus* Brocchi, 1814, Conch. Foss. Subapp., 2: 405, pl. 7, fig. 17.

†HISPIDOFUSUS Darragh, 1969: 67
Type sp. (O. D.): *Fusus senticosus* Tate, 1888, Trans. Roy. Soc. S. Austr., 10: 135, pl. 7, fig. 3.

HISTRICOSCEPTRUM Darragh, 1969: 87
Type sp. (O. D.): *Columbarium atlantis* Clench & Aguayo, 1938, Mem. Soc. Cuba Hist. Nat. vol. 12(5): 382, pl. 28, fig. 1.

HOMALOCANTHA Mörch, 1852: 95
Type sp. (M.): *Murex scorpio* Linné, 1758, Syst. Nat. Ed. 10, p. 747, no. 449.

†INDOTYPHIS Keen, 1944: 59
Type sp. (O. D.): *Laevityphis* (*Indotyphis*) *bantamensis* (Oostingh, 1933), De Mijningenieur, Jaarg. 14, p. 193.

INERMICOSTA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex fasciatus* Sowerby, 1841, Proc. Zool. Soc. London 8: 144.

IOPAS H. & A. Adams, 1853: 128
Type sp. (S. D. Dall, 1909): *Purpura sertum* Lamarck, 1816 (= *Buccinum sertum* Bruguière, 1789), Tableau Encycl. Mèth., pl. 397, fig. 2, Liste p. 2.

JANIA Cossmann, 1892: 68
Type sp. (O. D.): *Murex blainvillei* Payraudeau, 1826, Cat. Moll. Corse, p. 149.

JATON Pusch, 1837: 135
Type sp. (O. D.): *Murex decussatus* Gmelin, 1791, Syst. Nat. Ed. 13, p. 3527, no. 7.

JATOVA Jousseaume, 1880: 335
Type sp. (O. D.): *Purpura jatou* Adanson, 1757 (non-binominal) (= *Murex decussatus* Gmelin, 1791), Hist. Nat. du Sénégal. Coquillages, p. 129, pl. 9, fig. 21.

KALYDON Hutton, 1884: 220 (not to be confused with *Calydon* J. Thomson, 1864) (*Kalydon* suppressed — ICZN Opin. 911, 1970, Bull. Zool. Nomencl. 27: 20).
Type sp. (O. D.): *Fusus plebeius* Hutton, 1873, Cat. Mar. Moll. New Zealand p. 9.

LAEVITYPHIS Cossmann, 1903: 59
Type sp. (O. D.): *Typhis coronarius* Deshayes, 1865 (= *Typhis muticus* J. Sowerby, 1834), Descr. Anim. s. Vert. decouv. Bassin de Paris. p. 335, pl. 88, figs. 11-13.

LAMELLATIAXIS Habe & Kosuge, 1970: 182
Type sp. (O. D.): *Latiaxis* (*Lamellatiaxis*) *marumai* Habe & Kosuge, 1970, Venus 24(4): 182.

LATAXIENA Jousseaume, 1883: 187
Type sp. (T.): *Lataxiena lataxiena* Jousseaume, 1883 (= *Trophon fimbriatus* Hinds, 1844), Bull. Soc. Zool. Franc. 8: 187.

LATIAXIS Swainson, 1840: 82, 306
Type sp. (M.): *Pyrula mawae* "Gray" Griffith & Pidgeon, 1834, (*in*, Cuvier, Regne Animal) Mollusca & Radiata, p. 599, pl. 25, figs. 3, 4.

LATIMUREX Coen, 1922: 70
Type sp. (O. D.): *Murex meyendorffi* Calcara, 1845, Cenne Moll. Sicil., p. 38.

LENITROPHON Finlay, 1927: 424
Type sp. (O. D.): *Trophon convexus* Suter, 1909, Rec. Canterbury Mus. 1(2): 126, pl. 12, fig. 4.

LEPADOMUREX Coen, 1922: 70
Type sp. (O. D.): *Purpura brevis* Blainville, 1832, Nouv. Ann. Mus. Hist. Nat. Paris, vol. 1(2): 233.

LEPSIA Hutton, 1884: 223
Type sp. (O. D.): *Purpura haustrum* Martyn, 1788 (= *Buccinum haustorium* Gmelin, 1791), Univ. Conch., vol. 2, fig. 9c.

LEPSIELLA Iredale, 1912: 223
Type sp. (O. D.): *Purpura scobina* Quoy & Gaimard, 1833, Voyage of the "Astrolabe," Zool. II, p. 567.

LEPSITHAIS Finaly, 1928: 258
Type sp. (O. D.): *Polytropa squamata* Hutton, 1878, J. Conchyl. 26: 19.

LEPTOCONCHUS Rüppell, 1834: 105
Type sp. (S. D Gray, 1847): *Leptoconchus peroni* Lamarck, 1818, Hist. Nat. Anim. s. Vert. 5: 374.

LINIAXIS Laseron, 1955: 72
Type sp. (O. D.): *Liniaxis elongata* Laseron, 1955, Proc. Roy. Zool. Soc. New South Wales 1953-54: 72.

LITOZAMIA Iredale, 1929a: 185
Type sp. (O. D.): *Peristernia rudolphi* Henn & Brazier, 1894, Proc. Linn. Soc. New South Wales 19: 166, pl. 14, fig. 1.

†LOWENSTAMIA Sohl, 1964a: 182
Type sp. (O. D.): *Lowenstamia funiculus* Sohl, 1964, U.S. Geol. Surv. Prof. Paper 331b: 182, pl. 21, figs. 23, 26.

†LYROPURPURA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex crassicostata* (Deshayes, 1835, Descrip. Coq. Foss. Environ. de Paris 2: 601, pl. 82, figs. 13, 14.

†LYROTHYPHIS Jousseaume, 1880: 336
Type sp. (O. D.): *Typhis cuniculosus* Duchâtel, (in Bronn), 1848 (= *Murex cuniculosus* Nyst, 1836), Mess. Sci. Arts Belg. 4: 176.

MACULOTRITON Dall, 1904: 136
Type sp. (O. D.): *Triton bracteata* Hinds, 1844, Proc. Zool. Soc. London, 12: 132.

MAGILOPSIS Sowerby, 1919: 77
Type sp. (O. D.): *Leptoconchus lamarcki* Deshayes, 1863, Cat. Moll. Conchyl. L'île de la Réunion (Bourbon), p. 127, pl. 12, figs. 1-3.

MAGILUS Montfort, 1810: 42
Type sp. (O. D.): *Magilus antiquus* Montfort, 1810, 2: 42.

MANCINELLA Link, 1807: 115
Type sp. (T.): *Murex mancinella* Linné, 1758 (= *Mancinella aculeata* Link, 1807), Syst. Nat. Ed. 10, p. 751, no. 469.

MARCHIA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex clavus* Kiener, 1843 (= *Murex elongata* Lightfoot, 1786), Spec. Gen. Icon. Coq. Viv. 7: 111, pl. 37, fig. 2.

MAXWELLIA Baily, 1950: 9
Type sp. (O. D.): *Murex gemma* Sowerby, 1879, Thes. Conch., vol. 4, *Murex*, p. 32, fig. 214.

MENATHAIS Iredale, 1937: 256
Type sp. (O. D.): *Purpura pica* Blainville, 1832, Nouv. Ann. Mus. Hist. Nat. Paris, ser. 3, 1: 213.

†MICRORHYTIS Emerson, 1959: 6
Type sp. (O. D.): *Pterorytis* (*Microrhytis*) *pecki* Emerson, 1959, Amer. Mus. Novitates 1974.

MICROTOMA Swainson, 1840: 301
Type sp. (S. D. Gray, 1847 [as *Microstoma*]): *Microtoma persica* (Lamarck, 1799), Mem. Soc. Hist. Nat. Paris, p. 71.

MINNIMUREX Woolacott, 1957: 115

Type sp. (O. D.): *Minnimurex phantom* Woolacott, 1957, Proc. Roy. Soc. New South Wales, 1955-56, p. 115.

MINORTROPHON Finlay, 1927: 425
Type sp. (O. D.): *Daphnella crassilirata* Suter, 1908, Trans. Proc. New Zealand Inst. 57: 425.

†MIOCENEBRA E. H. Vokes, 1963: 162
Type sp. (O. D.): *Tritonalia* (*Miocenebra*) *silverdalense* E. H. Vokes, 1963, Tulane Stud. Geol. 1(4): 162, pl. 2, figs. 6a, 6b, 7a, 7b.

MIPUS De Gregorio, 1885: 28
Type sp. (O. D.): *Trophon gyratum* Hinds, 1844, Voy. H. M. S. Sulphur, Zoology, 2: 14, pl. 1, figs. 14-15.

MONOCEROS Lamarck, 1822: 250 (not Bloch & Schneider, 1801)
Type sp. (S. D., herein): *Monoceros imbricatum* Lamarck, 1816 (= *Buccinum monodon* Pallas, 1774), Tabl. Encycl. Meth., pl. 396, figs. 1a, 1b, Liste, p. 2.

MONSTROTYPHIS Habe, 1961: 19 (appendix)
Type sp. (O. D.): *Typhis* (*Typhinellus*) *tosaensis* Azuma, 1960, Cat. Shell-bearing Mollusca Okinoshima, Kashiwajima . . . (Tosa Province), Shikoku, Japan., p. 99, pl. 2, fig. 8.

†MOREA Conrad, 1860: 290
Type sp. (M.): *Morea cancellaria* Conrad, 1860, J. Acad. Nat. Sci., Philadelphia 4: 290.

MORULA Schumacher, 1817: 68, 227
Type sp. (M.): *Morula papillosa* Schumacher, 1817 (= *Drupa uva* Röding, 1798), Ess. Vers. Test., pp. 68, 227.

MORULINA Dall, 1923: 303 (not Borner, 1906)
Type sp. (O. D.): *Ricinula mutica* Lamarck, 1816, Tabl. Encycl.
Tabl. Encycl. Meth., pl. 395, figs. 2a, 2b, Liste, p. 1.

MORUNELLA Emerson & Hertlein, 1964: 361
Type sp. (O. D.): *Buccinum lugubre* C. B. Adams, 1852, Cat. Shells coll. Panama . . ., p. 69.

MUREX Linné, 1758: 746
Type sp. (S. D., Montfort, 1810): *Murex pecten* Montfort, 1810, (not Lightfoot, 1786), (= *Murex tribulus* Linne, 1758), Conch. Syst. 2: 619.

MUREXIELLA Clench & Pérez Farfante, 1945: 49
Type sp. (O. D.): *Murex hidalgoi* Crosse, 1869, J. Conchyl. 17: 408.

MUREXSUL Iredale, 1915: 471
Type sp. (O. D.): *Murex octogonus* Quoy & Gaimard, 1832, Voyage . . . l'Astrolabe . . . Paris, Zool., Mollusca, 2: 531, pl. 36, figs. 8, 9.

MURICANTHUS Swainson, 1840: 296
New name for *Centronotus* Swainson, 1833, not Schneider, 1801.

MURICIDEA Swainson, 1840: 64
Type sp. (O. D.): *Murex magellanicus* Lamarck, 1816 (= *Buccinum geversianum* Pallas, 1774), Tabl. Encycl. Meth., pl. 419, figs. 4a, 4b, Liste, p. 5.

MURICODRUPA Iredale, 1918: 38
Type sp. (O. D.): *Purpura fenestrata* Blainville, 1832 (= *Murex funiculus* Wood, 1828), Nouv. Ann. Mus. Hist. Nat. Paris 1: 221.

MURICOPSIS Bucquoy & Dautzenberg, 1882: 16, 19
Type sp. (O. D.): *Murex blainvillei* Payraudeau, 1826, Cat. Descr. Meth. Annel. Moll. Île de Corse, p. 149.

MURITHAIS Grant & Gale, 1931: 729
Type sp. (O. D.): *Murex trunculus* Linné, 1758, Syst. Nat. Ed. 10, p. 747, no. 447.

†MUROTRITON de Gregorio, 1890: 97
Type sp. (O. D.): *Triton grassator* de Gregorio, 1890, Ann. Geol. Paleo. 7: 97.

NAQUETIA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex triqueter* Born, 1778, Index Mus. Caes. Vindobon., p. 288.

NAMAMUREX Carrington & Kensley, 1969: 197
Type sp. (O. D.): *Namamurex odontostoma* Carrington & Kensley, 1969, Ann. S. Afr. Mus. 52: 197.

NASSA Röding, 1798: 132
Type sp. (S. D., Dall 1909): *Nassa picta* Röding, 1798 (= *Buccinum sertum* Bruguière, 1789), Museum Boltenianum, p. 132.

NEMOFUSUS Cossmann, 1903: 195
Type sp. (O. D.): *Murex fusulus* Brocchi, 1814, Conch. Foss. Subapp. 2: 409, pl. 8, fig. 9.

NEORAPANA Cooke, 1918: 7, 11
Type sp. (O. D.): *Purpura muricata* Broderip, 1832, Proc. Comm. Sci. Zool. Soc. London, 2: 125, 126.

NEOTHIAS Iredale, 1912: 223
Type sp. (O. D.): *Purpura smithi* Brazier, 1889, Mem. Australian Mus. 2: pl. 4, figs. 1-4, 7-12, 21, 22.

†NEOTYPHIS Vella, 1961: 385
Type sp. (O. D.): *Typhis tepunga* Fleming, 1943, Trans. Roy. Soc. New Zealand 73(3): 205, pl. 30, fig. 21.

†NEURARHYTIS Olsson & Harbison, 1953: 252
Type sp. (O. D.): *Purpura* (*Pterorhytis*) *fluviana* (Dall, 1903), Trans. Wagner Free Inst. Sci. 3(6): 1633, pl. 60, figs. 20, 21.

NIPPONOTROPHON Kuroda & Habe, 1971: 233 (Japanese), 152 (English)
Type sp. (O. D.): *Boreotrophon echinus* Dall, 1920, Proc. U.S. Natl. Mus. 54: 232.

NODULOTROPHON Habe & Ito, 1965: 32-33
Type sp. (O. D.): *Trophon dalli,* Kobelt, 1878 (in Küster) Martini & Chemnitz Conchylien-Cabinet, pt. 275, p. 289, pl. 74, figs. 1, 2.

NOTHOTYPHIS Fleming, 1962: 109, 119
Type sp. (O.D.): *Pterynotus* (*Nothotyphis*) *norfolkensis* Fleming, 1962, Trans. Roy. Soc. New Zealand 2(14): 109, 119.

NUCELLA Röding, 1798: 131
Type sp. (S. D. Winckworth, 1945): *Nucella theobromus* Röding, 1798 (= *Buccinum lapillus* Linné, 1758), Mus. Bolten. p. 131.

OCINEBRELLUS Jousseaume, 1880: 335
Type sp. (O. D.): *Murex eurypteron* Reeve, 1845, Conch. Icon., vol. 3, *Murex,* sp. 176, pl. 34, fig. 176a, 176b.

OCENEBRA Gray, 1847a: 269
Type sp. (M.): *Murex erinaceus* Linné, 1758, Syst. Nat. Ed. 10, p. 748, no. 451.

OCINEBRINA Jousseaum, 1880: 335
Type sp. (O. D.): *Fusus corallinus* Scacchi, 1836 (= *Murex aciculatus* Lamarck, 1822), Cat. Conch. Neap., p. 11.

OLLAPHON Iredale, 1929a: 186
Type sp. (O. D.): *Trophon molorthus* Hedley & May, 1908, Rec. Australian Mus. 7: 122.

OPPOMORUS Iredale, 1937: 258
Type sp. (O. D.): *Morula nodulifera* Menke, 1829, Conch. Samml. Malsburg, p. 33.

ORANIA Pallary, 1900: 285

Type sp. (O. D.): *Pseudomurex spadae* Libassi, 1859, Atti Acad. Palermo, 3: 43, fig. 29.

PAGODULA Monterosato, 1884: 116
Type sp. (O. D.): *Murex vaginata* Cristofori & Jan, 1832, Cat. . . . rerum Nat. Mus. Extant. Josephi de Cristofori, Sect. II(1), Conch. Fossili, p. 11.

†PANAMUREX Woodring, 1959: 217
Type sp. (O. D.): *Murex gatunensis* Brown & Pilsbry, 1911, Proc. Acad. Nat. Sci. Philadelphia 63: 354, pl. 26, fig. 2.

PARATROPHON Finlay, 1927: 424
Type sp. (O. D.): *Polytropa cheesemani* Hutton, 1882, New Zealand J. Sci. 1: 69.

PASCULA Dall, 1908: 311, 312
Type sp. (O. D.): *Trophon* (*Pascula*) *citricus* Dall, 1908, Bull. Mus. Comp. Zool. 43(6): 312.

PATELLIPURPURA Dall, 1909: 50
Type sp. (O. D.): *Buccinum patulum* Linné, 1758, Syst. Nat., Ed. 10, p. 739, no. 402.

PAZIELLA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex pazi* Crosse, 1869, J. Conchyl., 17: 183.

PAZINOTUS E. H. Vokes, 1970b: 27
Type sp. (O. D.): *Eupleura stimpsoni* Dall, 1889, Bull. Mus. Comp. Zool. 18: 204.

PENTADACTYLUS "Klein" Bruguière, 1792: 520 (not Schultze, 1760)
Type sp. (S. D., F. C. Baker, 1895): *Pentadactylus ricinus* Lamarck (= *Murex ricinus* Linné, 1758, Syst. Nat., Ed. 10, p. 750, no. 464.)

†PERITROPHON Marwick, 1931: 119
Type sp. (O.D.): *Peritrophon decoratus* Marwick, 1931, Paleont. Bull. New Zealand no. 13: 119.

PEROTYPHIS Jousseaume, 1880: 336 (error for *Pterotyphis* — q.v.)
Type sp. (O.D.): *Typhis pinnatus* Broderip, 1833, Proc. Comm. Sci. Corr. Zool. Soc. London 2: 178.

PHYLLOCOMA Tapparone-Canefri, 1881: 44
Type sp. (O. D.): *Triton convolutus* Broderip, 1833, Proc. Zool. Soc. London 1: 7.

PHYLLONOTUS Swainson, 1833: pl. 100
Type sp. (S. D. Swainson, 1833 — pl. 109): *Murex imperialis* (var.a) Swainson, 1833 (= *Murex imperialis,* Swainson, 1831) (not Fischer de Waldheim, 1807), (= *Murex margaritensis* Abbott, 1958), Zool. Illust., ser. 2, 3: pl. 100.

PHRYGIOMUREX Dall, 1904: 137
Type sp. (O. D.): *Triton sculptilis* Reeve, 1844, Proc. Zool. Soc. London 12: 118-119.

†PILSBRYTYPHIS Woodring, 1959: 220
Type sp. (O. D.): *Typhis gabbi* Brown & Pilsbry, 1911, Proc. Acad. Nat. Sci. Philadelphia 63: 354, pl. 26, fig. 6.

PINAXIA H. & A. Adams, 1853: 132
Type sp. (M.): *Pinaxia coronata* H. & A. Adams, 1853 (nomen nudem) (= *Pinaxia coronata* A. Adams, 1853, Proc. Zool. Soc. London 19: 185).

PINON de Gregorio, 1885: 28
Type sp. (O. D.): *Trophon* (*Pinon*) *vaginatus* Cristofori & Jan, 1832, Cat. rerum Nat. Mus. Sect. II(1), Conch. Foss., p. 11.

†PIRGOS de Gregorio, 1885: 28
Type sp. (S. D., Cossmann, 1904): *Fusus alveolatus* J. Sowerby, 1823, Min. Conch. 5: 9.

PIRTUS de Gregorio, 1884: 257
Type sp. (O. D.): *Murex* (*Pirtus*) *fiatus* de Gregorio, 1884, Bull. Soc. Malac. Ital. 10: 257.

PLANITHAIS "Bayle" Fischer, 1884: 645
Type sp. (O. D.): *Purpura planospira* Lamarck, 1822, Hist. Nat. Anim. s. Vert. 7: 240.

PLICOPURPURA Cossmann, 1903: 69
New name for *Purpurella* Dall, 1871, not Robineau-Desvoidy, 1853.

POIRIERIA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex zelandicus* Quoy & Gaimard, 1833, Voy. Astrolabe, Zool. 2: 529, pl. 36, figs. 5-7.

POLYPLEX Perry, 1811: pl. 9
Type sp. (S. D., ICZN Opinion 911, 1969 — see Bull. Zool. Nomencl., 27: 20): *Polyplex bulbosa* Perry, 1811, Conchology, pl. 9.

POLYTROPA Swainson, 1840: 305
Type sp. (S. D., Gray, 1847): *Buccinum lapillus* Linné, 1758, Syst. Nat., Ed. 10, p. 739, no. 403.

POROPTERON Jousseaume, 1880: 335
Type sp. (O. D.): *Murex tubifer* Bruguière, 1972, (an apparent error as Jousseaume also designated this species as type of *Typhis* Montfort)
Type sp. (S. D. Jousseaume, 1881): *Murex uncinarius* Lamarck, 1822, Hist. Nat. Anim. s. Vert. 7: 166.

POWERIA Monterosato, 1884: 113 (not Bonaparte, 1841)
Type sp. (M.): *Poweria scalarina* Bivona, 1832 (= *Murex scalaroides* Blainville, 1826), Effem. Lett. Sicil., p. 22.

PROTOTYPHIS Ponder, 1972: 221
Type sp. (O. D.): *Typhis angasi* Crosse, 1863, J Conchyl. 11: 86, pl. 1, fig. 2.

PROVEXILLUM Hedley, 1918: 79
New name for *Vexilla* Swainson, 1840, not *Vexillum* Röding, 1798.

†PSEUDOMOREA Cossmann, 1925: 265
Type sp. (M.): *Morea marylandica* Gardner, 1916, Maryland Geol. Survey, Upper Cretaceous, Syst. Paleo. Mollusca, p. 371.

PSEUDOMUREX Monterosato, 1872: 15, 33
Type sp. (O. D.): *Murex bracteata* Brocchi, 1814, Moll. Foss. Subapp., p. 409, pl. 9, fig. 3.

†PSEUDORAPA Holzapfel, 1888: 111
Type sp. (O. D.): *Murex pleurotomoides* Muller, 1851, vol. 1, Mon. 2, p. 24, pl. 3, fig. 31.

PSEUDOSALPINX Olsson & Harbison, et al., 1953: 254
Type sp. (O. D.): *Urosalpinx floridana* (Conrad, 1837) (= *Murex ostrearum* Conrad, 1846), J. Acad. Nat. Sci. Philadelphia 7: 265.

PTEROCHELUS Jousseaume, 1880: 335
Type sp. (O. D.): *Murex acanthopterus* Lamarck, 1816, Tabl. Encycl. Mèth. pl. 417, figs. 2a, 2b, Liste, p. 5.

PTEROPURPURA Jousseaume, 1880: 335
Type sp. (O. D.): *Murex macropterus* Deshayes, 1839, Rev. Zool. Soc. Cuv. 2: 360.

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PTEROTYPHIS Jousseaume, 1881: 338 (Emendation for *Perotyphis* Jousseaume, 1880)

PTERYMUREX Rovereto, 1899: 105
New name for *Pteronotus* Swainson, 1833, not Rafinesque, 1815.

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Type sp. (O. D.): *Pterynopsis prosopeion* E. H. Vokes, 1972 (= *Murex nysti* von Koenen, 1867, not Rouault, 1850), Bull. Inst. R. Sci. Nat. Belg.

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PURPURA Bruguière, 1789: xv
Type sp. (S. D., Montfort, 1810): *Buccinum persicum* Linné, 1758, Syst. Nat., Ed. 10, p. 738, no. 401.

PURPURELLA Dall, 1871: 110 (not Bellardi, 1882, nor Robineau-Desvoidy, 1853)
Type sp. (O. D.): *Purpura columellaris* Lamarck, 1816, Tabl. Encycl. Mèth., pl. 398, figs. 3a, 3b, Liste, p. 2.

†PURPURELLA Bellardi, 1882: 193 (not Dall, 1871, nor Robineau-Desvoidy, 1853)
Type sp. (M.): *Purpurella canaliculata* Bellardi, 1882, Moll. Terr. Terz. Piem. Ligur. pt. 3, p. 193, pl. 11, fig. 35.

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Type sp. (O. D.): *Murex gambiensis* Reeve, 1845, Conch. Icon. vol. 3, *Murex*, pl. 16, sp. 65.

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QUOYULA Iredale, 1912: 221
Type sp. (O. D): *Purpura monodonta* Quoy & Gaimard, 1833, Voy. Astrolabe, Zool. 2, p. 561, pl. 37, figs. 9, 11.

RAPA "Klein" Bruguière, 1792: 533
Type sp. (S. D., Herrmannsen, 1848): *Bulla rapa* (Linné, 1767) (= *Murex rapa* Linné, 1758, not Gmelin, 1791), Syst. Nat. Ed. 12, p. 1184, no. 384.

RAPANA Schumacher, 1817: 214
Type sp. (M.): *Rapana foliacea* Schumacher, 1817 (= *Buccinum bezoar* Linné, 1758), Ess. Vers. Test., p. 214.

RAPANUS "Schum." Sowerby, 1839: 92
Type sp. (M.): *Pyrula papyracea* [Lamarck, 1816] (= *Rapa rapa* Bruguière, 1792), Tabl. Encycl. Mèth. pl. 436, fig. 1.

RAPELLA Swainson, 1840: 82, 307
Type sp. (M.): *Rapella papracia* (sic) (Lamarck, 1816), Tabl. Encycl. Mèth. pl. 436, fig. 1, Liste, p. 8.

RHINOCANTHA H. & A. Adams, 1853: 72
Type sp. (S. D., E. H. Vokes, 1964): *Murex brandaris* Linné, 1758, Syst. Nat., Ed. 10, p. 747, no. 446.

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Type sp. (S. D., Children, 1823): *Ricinula horida* (sic) Lamarck, 1816, Tabl. Encycl. Mèth., pl. 395, figs. 1a, 1b.

RISOMUREX Olsson & McGinty, 1958: 40
Type sp. (O. D.): *Engina schrammi* Crosse, 1863, J. Conchyl. 11: 86, pl. 1, fig. 2.

ROPERIA Dall, 1898: 5
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Type sp. (O. D.): *Buccinum monoceros* Chemnitz, 1788 (non-bionominal) (= *Buccinum monodon* Pallas, 1774), Neues Systematisches Conchylien-Cabinet 10: 197, pl. 154, figs. 1469, 1470.

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Type sp. (M.): *Fusus strumosa* Conrad, 1862, Proc. Acad. Nat. Sci. Philadelphia 14: 560.

SEMIRICINULA von Martens, 1903: 95
Type sp. (M.): *Purpura muricina* Blainville, 1832, Nouv. Ann. Mus. Hist. Nat. Paris 1: 218.

†SEMITYPHIS K. Martin, 1931: 31
Type sp. (M.): *Semityphis incisus* K. Martin, 1931, Wetens. Meded. 18: 31, pl. 5; figs. 1a, 1b.

†SERRATIFUSUS Darragh, 1969: 89
Type sp. (O. D.): *Fusus crasspedotus* Tate, 1888, Trans. Roy. Soc. South Australia 10: 134, pl. 8, fig. 4.

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SISTRUM Montfort, 1810: 595
Type sp. (M.): *Sistrum album* Montfort, 1810, Conch. Syst. 2: 595.

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Type sp. (O. D.): *Murex euracantha* A. Adams, 1851, Proc. Zool. Soc. London 18: 268.

SPINOSTOMA Coen, 1943: 90
Type sp. (S. D. herein): *Murex nuttalli* Conrad, 1837, J. Acad. Nat. Sci. Philadelphia 7: 264, pl. 20, fig. 22.

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STRAMONITROPHON Powell, 1951: 156
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TAKIA Kuroda, 1953: 190
Type sp. (O. D.): *Murex inermis* Sowerby, 1841 (not Philippi, 1836) (= *Dermomurex* [*Takia*] *infrons* E. H. Vokes, 1974), Venus 17(4): 190.

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†TAURASIA Bellardi, 1882: 194
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THAIS Röding, 1798: 54
Type sp. (S. D. Stewart, 1926): *Thais lena* Röding, 1798 (= *Nerita nodosa* Linné, 1758, p. 777.)

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Type sp. (O. D.): *Purpura trinitatensis* Guppy, 1869, Proc. Sci. Assoc. Trinidad 1: 366.

THALESSA H. & A. Adams, 1853: 127
Type sp. (S. D., Cossmann, 1903): *Purpura hypocastaneum* "Linné," Cossmann, 1903 (= *Murex hippocastanum* "Linné" Auct.) (= *Murex hippocastanum* Gmelin, 1791, p. 3539.)

†TIMBELLUS de Gregorio, 1885: 275
Type sp. (O. D.): *Murex latifolius* Bellardi, 1872, Moll. Terr. Terz. Piem. Ligur. pt. 1, p. 54, pl. 4, fig. 5.

†TIMOTHIA Palmer, 1938: 3
New name for *Aldrichia* Palmer, 1937, not Coquillet, 1894, nor Vaughan, 1900.

TOLEMA Iredale, 1929a: 186
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Type sp. (O. D.): *Trachypollia sclera* Woodring, 1928, Carnegie Inst. Wash. Publ. 385: 269, pl. 16, figs. 7, 8.

TRANSTRAFER Iredale, 1929b: 290
Type sp. (O. D.): *Transtrafer longmani* Iredale, 1929, Mem. Queensland Mus. 9: 290.

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TRIPLEX Perry, 1810: M7
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Type sp. (M.): *Trochia sulcata* "Lamarck," Swainson, 1840 (= *Buccinum cingulatum* Linné, 1771), Treat. Malac. p. 302.

TROMINA Dall, 1918a: 137
Type sp. (O. D.): *Fusus unicarinatus* Philippi, 1868, Malak. Bl. 15: 223.

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Type sp. (O. D.): *Murex muricatus* Montagu, 1803, Test. Brit., 1: 262, pl. 9, fig. 2.

TRUBATSA Dall, 1889: 215
Type sp. (S. D., Keen, 1944): *Typhis (Trubatsa) longicornis* Dall (*in*, Agassiz), 1888, The Three Cruises of the "Blake," 2: 70, fig. 294.

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New name for *Truncularia* Monterosato, 1917, not Wiegmann, 1832.

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Type sp. (O. D.): *Murex brevispina* Lamarck, 1822, Hist. Nat. Anim. s. Vert. 7: 159.

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Type sp. (O. D.): *Typhis grandis* A. Adams, 1855, Proc. Zool. Soc. London 22: 41.

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†VESANULA Finlay, 1926: 245
Type sp. (M.): *Trophon chaskanon* Finlay, 1926,

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Type sp. (M.): *Vexilla picta* Swainson, 1840 (= *Murex vexillum* Gmelin, 1791), Treat. Malac., p. 300.

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BLOOD CIRCULATION IN FOUR SPECIES OF BARNACLES (*LEPAS, CONCHODERMA:* LEPADIDAE)

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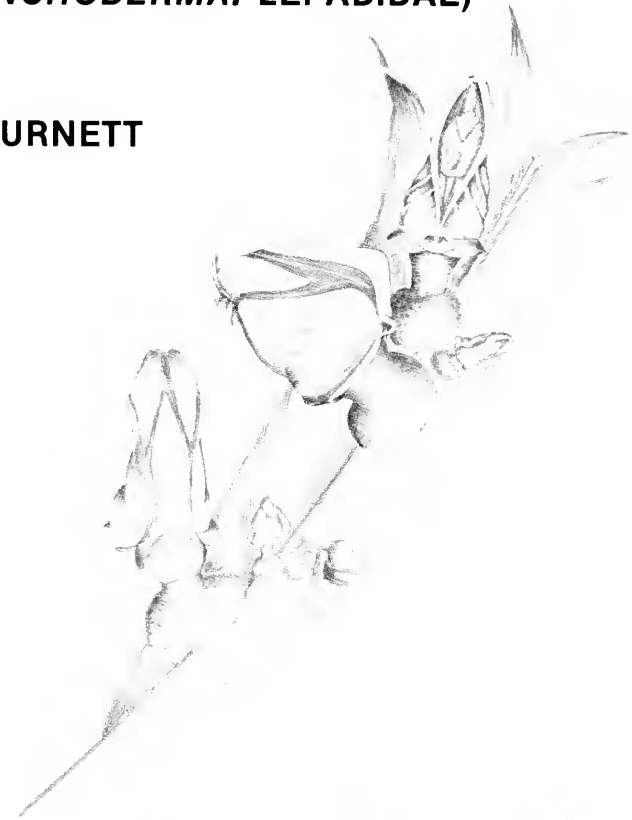

TRANSACTIONS

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BLOOD CIRCULATION IN FOUR SPECIES OF BARNACLES (*LEPAS, CONCHODERMA:* LEPADIDAE)

BRYAN R. BURNETT

ABSTRACT.—Circulatory morphologies of the primitive lepadomorphans *Lepas anatifera, L. pectinata pacifica, L. fasicularis* and *Conchoderma virgatum* are similar, but major differences appear in vessel caliber and refinement of the basic system. The smaller species (*L. fasicularis* and *L. pectinata pacifica*) have larger vessels for their body size than the larger species (*L. anatifera* and *C. virgatum*). Circulatory organization of the lepadids is simpler than that of *Pollicipes polymerus* (Scalpellidae) and *Balanus tintinnabulum* (Balanidae). The lepadid rostral vessel, which is morphologically similar to that of *P. polymerus*, is interpreted as a vestige of the heart. Pump function can be attributed to the rostral sinus (the blood pump), which is apparently a remnant of the pericardial sinus. Transfer of hemolymph pumping from the heart to the rostral sinus probably occurred with the development of the peduncle.

Detailed accounts of cirriped circulation may be found in Cannon (1947) and Burnett (1972). The circulatory systems of *Lithotrya valentiana* and *Pollicipes polymerus* (Cannon, 1947) had been considered to represent the general condition for thoracican Cirripedia (e.g. Maynard, 1960). However, Burnett (1972) showed that the circulatory system of the pedunculate barnacle *Pollicipes polymerus* was unlike that of other Crustacea. In order to obtain a more complete understanding of circulatory relationships in the Cirripedia, I studied the circulatory systems of four species of Lepadidae: *Lepas anatifera, L. pectinata pacifica, L. fasicularis* and *Conchoderma virgatum.*

MATERIALS AND METHODS

The three species of *Lepas* were collected from debris that washed ashore at Scripps Institution of Oceanography, La Jolla, California in the summers of 1972 and 1973. The *Conchoderma virgatum* were collected from a Pacific Ridley sea turtle (*Lepidochelys olivacea*) captured off La Jolla. Living specimens were injected with yellow (MV-122) or maroon (MV-118) Microfil (Canton Bio-Medical Products, Inc. P.O. Box 2017, Boulder, Colorado 80302), either into the peduncle or through the adductor scutorum into the rostral sinus, following techniques developed in an earlier study (Burnett, 1972). The amount injected ranged from 0.5 to 2.0 ml based on the size of the animal. In each species, the rostral valve at the posterior-most part of the peduncular vessel usually did not hold under the pressure exerted from the Microfil injections into the peduncle; almost always a significant amount of Microfil entered the body via the peduncular vessel. The rostral valve in the lepadids is more delicate than that of *P. polymerus;* consequently their vessels are more prone to rupture and distort, which makes it difficult to trace circulatory pathways, especially with the peripheral-collecting circulation. In order to determine vessel wall structure, portions of the gut vessels were removed (while they still had solidified Microfil in the vessel lumina) and embedded in Spurr (Polysciences, Inc. Paul Valley Industrial Park, Warrington, Penna. 18976). Sections, 2 μm thick, were made with a glass knife on a Porter-Blum JB-4 microtome.

Body movements of *L. fasicularis* were observed through a dissection microscope by shining a light through the thin walled capitulum.

CIRCULATORY MORPHOLOGY

Basically, I shall follow Burnett (1972) in dividing the barnacle circulatory system into three arbitrary divisions: 1) the circulation of the peduncle and mantle, 2) the distributive circulation and 3) the peripheral-collecting circulation.

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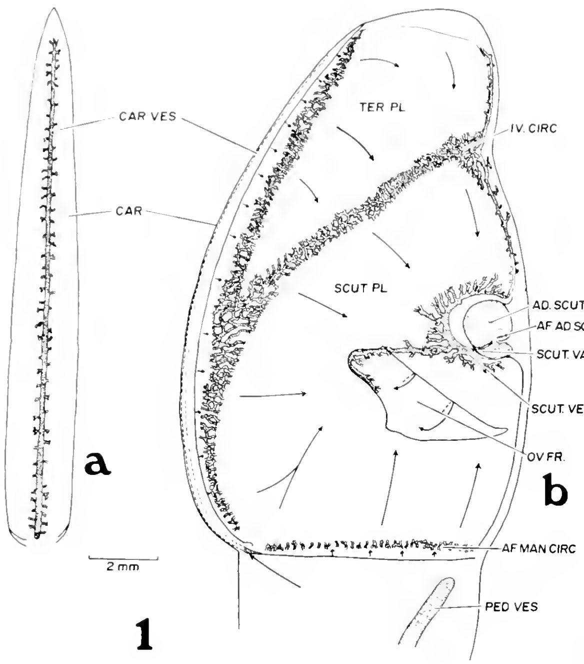
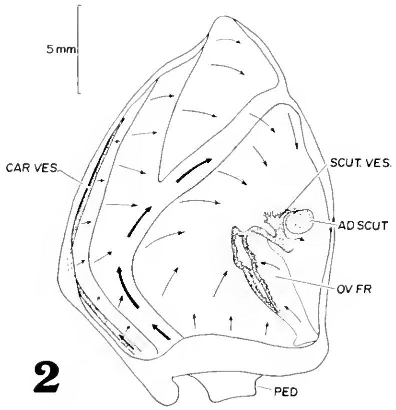
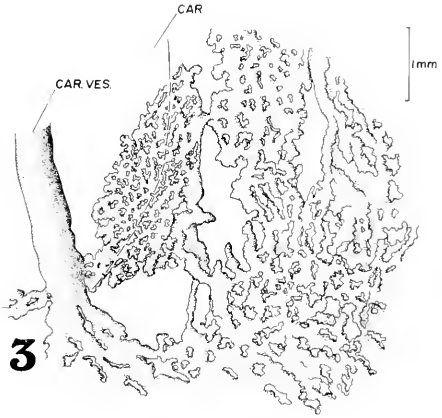
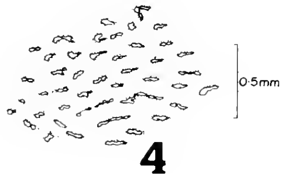
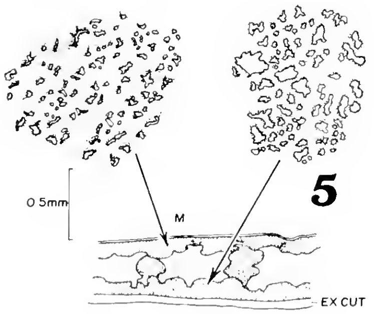










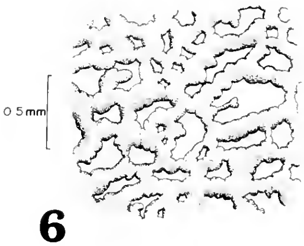


Figure 1. Mantle circulation in *L. anatifera.* a. View of the carina with the carinal vessel situated along the midline of the valve. b. View of the right side of the mantle and a portion of the peduncle. Only the intervalve circulation is shown, with the arrows representing the direction of hemolymph flow. Basically, this pattern of circulation is present in *L. pectinata pacifica* and *C. virgatum.* Abbrevations are explained in the Appendix.

Figure 2. Mantle circulation (right side) in *L. fasicularis.* Arrows show the direction of flow with the heavier arrows indicating major hemolymph flow.

Figure 3. The origin and associated circulation of the carinal vessel in *L. fasicularis.*

Figure 4. A portion of the tergal plexus from *L. pectinata pacifica.*

Figure 5. The double circulation of the mantle in *C. virgatum.*

Figure 6. A portion of the tergal plexus from *L. anatifera.*

Circulation of the peduncle and mantle.—The peduncular vessel extends the full length of the peduncle without giving off any branches, and ends with a gradual enlargement at the basal disc. From the basal disc, the hemolymph percolates towards the mantle, and it appears that the entire peduncle is a single sinus.

Hemolymph from the peduncle enters the mantle circulation by two pathways (Fig. 1). In one route, blood is directed into the mantle circulation from the posterior-most part of the peduncle by a series of short parallel vessels (Fig. 1b). From these vessels the blood moves through a plexus toward the ovigerous frena and eventually into the paired scutal vessels. *Lepas fasicularis* has enlarged vessels entering the mantle in the area between the scutal and carinal regions (Figs. 2, 3).

The other pathway by which the blood enters the mantle is through the carinal vessel (Figs. 1-3). In *Lithotrya valentiana,* Cannon (1947) described a pair of vessels in the mantle region between the terga and carina, but I doubt these are homologous to the carinal vessel of the Lepadidae, which is unpaired. The carinal vessel extends the full length of the carina, and gives off smaller vessels along its entire length. Almost all of the tergal area and a good portion of the scutal area of the mantle is supplied by this vessel.

In lepadids, the ovigerous frena (Figs. 1, 2) are highly vascularized with a circulation similar to the rest of the mantle. A vessel, connecting the scutal vessel on each side of the mantle, borders the distal margin of each ovigerous frenum. In *L. fasicularis,* the ovigerous frena are bilobate (Fig. 2), with a large vessel extending along the distal margin of each lobe. These vessels join and the resulting vessel connects to the scutal vessels, which in turn enter the body. In contrast to the situation in *P. polymerus,* the mantle knobs and the circulation associated with the mantle muscles are not present in the lepadids.

The paired scutal vessels partially circle the adductor scutorum at the muscle's insertion on the two scutal plates (Figs. 1, 2) in a manner similar to that found in *P. polymerus.* The scutal valve (Fig. 1) lies just inside the entrance of the scutal vessel into the body.

The circulation of the mantle varies between species (Figs. 3-6), with the plexuses appearing random in *L. anatifera* (Fig. 6) to fairly organized in *L. pectinate pacifica* (Fig. 4). The mantle circulation of *C. virgatum* (Fig. 5) differs from *Lepas* in being essentially a double system in which plexuses are associated with both the external and internal cuticles of the capitulum. Scattered connections exist between these two plexuses.

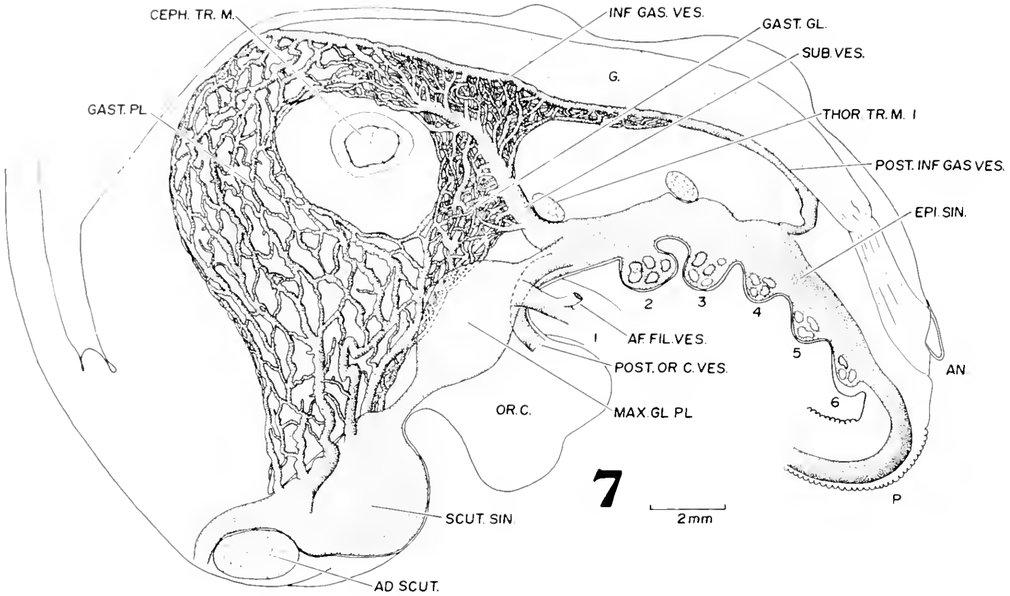
In *L. anatifera,* the vessels between the capitular plates enlarge somewhat; in *C. virgatum* the plexal vessels appear uniform throughout the mantle, but enlarge as they approach the scutal vessels.

Distributive circulation.—Near the points where the adductor scutorum inserts on the scuta, the two scutal vessels enter the body from the mantle and enlarge to form the paired scutal sinuses (Figs. 7-10). In all four species, as in *P. polymerus,* the scutal sinuses are located on each side of the rostral sinus, in close proximity to the adductor scutorum. The precise position of the scutal sinuses varies from species to species: in *L. anatifera* they are mostly posterior to the adductor scutorum; in *L. fasicularis* they are anterior; and in *L. pectinata pacifica* and *C. virgatum* they are dorsal. Their shape and extent also varies.

The adductor scutorum receives blood from the scutal sinuses in all species. The afferent circulation to this muscle is located immediately posterior to the scutal valves. From the scutal sinuses hemolymph enters the vessels of the gut, gastric gland, and the maxillary gland.

On the gut, the gastric plexus continues around most of the cephalic portion of the gut with little variation in vessel caliber (Figs. 7-10). In the posterior part of the cephalic gut, the paired inferior gastric vessels continue from vessels of the gastric plexus. As this pair of vessels continues posteriorly, branches of the gastric gland plexus also combine with the inferior gastric vessels.

The paired inferior gastric vessels join on the ventral surface of the thoracic gut above the first pair of cirri. This combined vessel (the posterior inferior gastric vessel) continues posteriorly and descends to contact the epineural sinus by one or more



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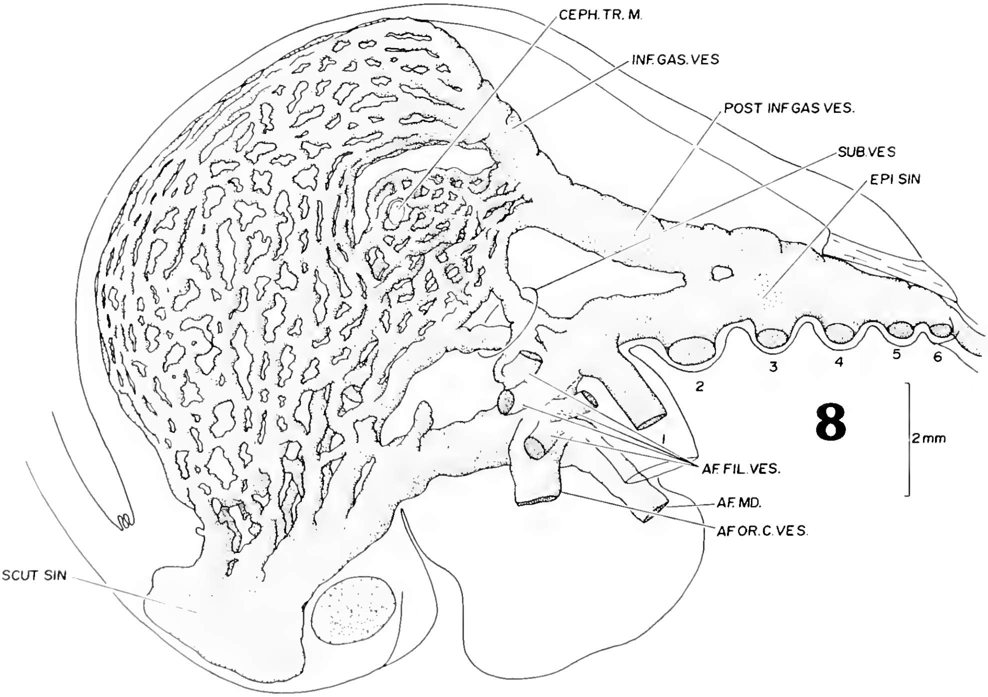

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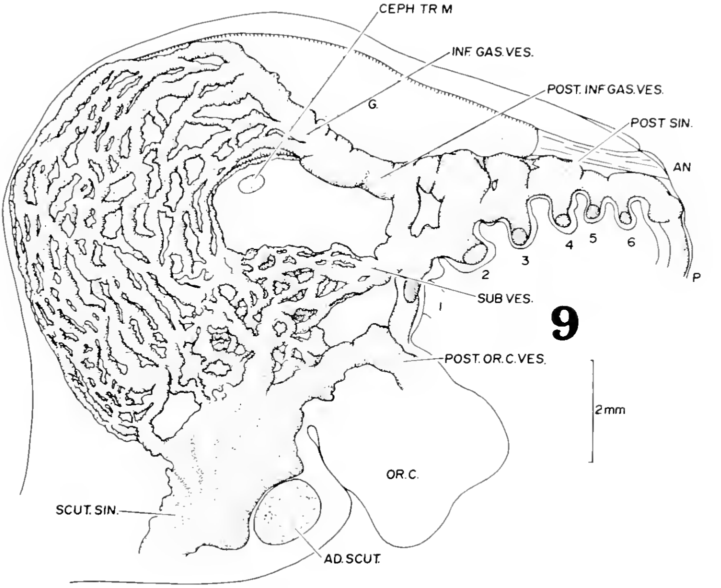
Figure 7. Distributive circulation as seen from the left side of the body in *L. anatifera.* Numbers 1-6 refer to the positions of the respective cirri.

Figure 8. Distributive circulation in *L. fasicularis.*

branches. In *L. anatifera,* the posterior inferior gastric vessel is reduced and has only one contact with the epineural sinus. In all lepadids, the epineural sinus, which surrounds the nerve cord at the base of the cirri, receives blood from two additional sources: 1) the scutal sinuses through the maxillary gland, to connect to the anterior part of the epineural sinus, and 2) a connection by the subintestinal vessel from the gastric gland



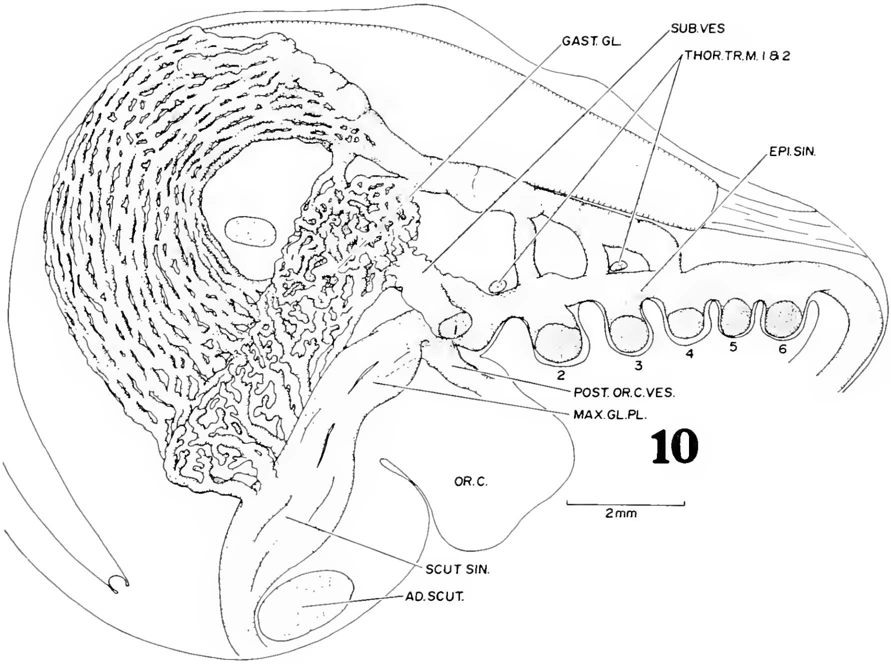


Figure 9. Distributive circulation in *L. pectinata pacifica*.
Figure 10. Distributive circulation in *C. virgatum*.

plexus. Blood from the epineural sinus goes to the cirri, penis and oral cone.

In *L. anatifera* the subintestinal vessel originates as a pair of vessels among the plexus surrounding the gastric gland. These two vessels collect blood from the gastric gland plexus and enlarge as they descend toward the epineural sinus. The subintestinal vessel is then formed by the combining of the two vessels just anterior to the first thoracic transverse muscle. On the anterior part of the epineural sinus, the subintestinal vessel enters slightly dorsal to the maxillary gland connections. In the other three species the subintestinal vessel consists of one or two short vessels connecting the gastric gland plexus to the epineural sinus.

The distributive circulation of *L. fasicularis* is more grossly constructed in contrast to *L. anatifera.* The posterior inferior gastric vessel unites with the epineural sinus to form a large posterior sinus. The afferents to the oral cone, which originate from the epineural sinus, are divided into two vessels, the afferent mandibular vessel going directly to the mandibles, and the afferent oral cone vessel to the rest of the oral cone. The afferent filamentary vessels to the four filamentary appendages at the base of each first cirrus originate on the anterior-most part of the epineural sinus.

Circulatory morphology in *L. pectinata pacifica* appears most similar to that of *L. fasicularis.* The union of the posterior inferior gastric vessel to the epineural sinus is so extensive that the two make up a single sinus (the posterior sinus) posterior to the second thoracic segment. The gastric gland plexus does not extend directly around the cephalic transverse muscle and the large sinus at the base of the first cirrus is not present as it is in *L. fasicularis.*

The distributive system of *C. virgatum* is similar to that of *Lepas* (Fig. 10). The gut plexus is strongly directionally oriented. The connection of the posterior inferior gastric vessel to the epineural sinus is by two or three large caliber vessels. Plexal circulation of the gastric gland appears more haphazard than in *L. anatifera.* The dorsal part of the gastric circulation is connected to the inferior gastric vessels by a varying number of short vessels.

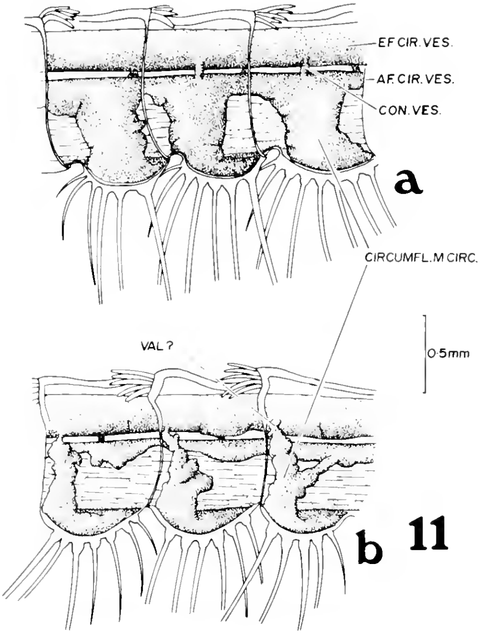
In *P. polymerus,* the cirri are too darkly pigmented to observe their circulatory morphology, but the opposite holds with the lepadids. Figure 11 shows the circulation of three segments of a ramus from *L. anatifera,* which is similar to that of the other species being considered here.

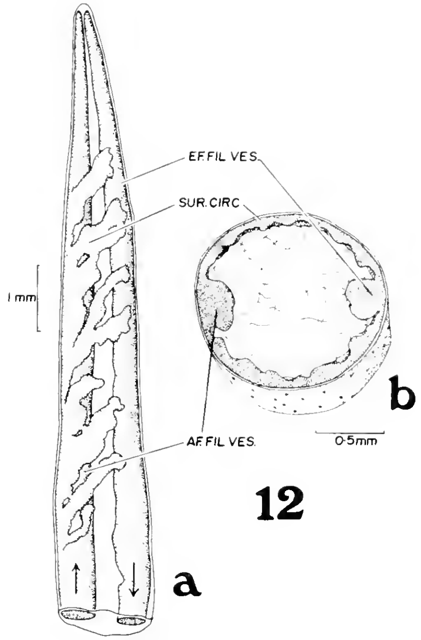
The afferent circulation in a ramus of a cirrus continues distally from the epineural sinus and is in close contact with the flexor muscle. In each segment of a ramus, the circumflexor muscle circulation originates from the afferent vessel and surrounds the flexor muscle in a sheet-like sinus. This circulation connects to the efferent circulation of the ramus by a steadily constricting sinus. There may be a valve at the contact point with the efferent cirral vessel. The efferent cirral vessel progresses down the outside margin of the ramus to eventually connect with the peripheral-collecting circulation.

The general morphology of circulation in the lepadid filamentary appendage is similar to that of *P. polymerus* (Burnett, 1972). There are two vessels (the filamentary vessels) on opposite sides of the filamentary appendage that parallel the main axis of the appendage (Fig. 12). From the afferent filamentary vessel, a sheet-like sinus arises on each side of the vessel, and each extends in a semicircle around the filamentary appendage to connect the efferent filamentary vessel.

The Lepadidae have two types of filamentary appendages: type I receives hemolymph from the afferent circulation to the cirri; type II receives blood from the peripheral circulation and will be discussed below. Each species shows a different arrangement and number of type I filamentary appendages. *Lepas anatifera* has a type I appendage at the base of the first cirrus. *Lepas pectinata pacifica* also has one in the same location, but it is reduced. There are four such appendages in *L. fasicularis,* which form a star pattern where they originate at the base of first cirrus. *Conchoderma virgatum* has filamentary appendages of the first type at the base of the first, third, fourth and fifth cirri. Interestingly, *C. virgatum* has an additional filamentary appendage at the base of the first cirrus that receives blood from the efferent circulation of that cirrus (a type II filamentary appendage). This is the only case where a type II filamentary appendage occurs on a cirral base.

Peripheral-collecting circulation. (Figs. 13-18).—In *P. polymerus,* I described three circulations of the body: distributive, peripheral and collecting. The lepadids, however, have only two distinctive circulations of the body, the distributive and the return. In order to maintain uniformity in nomenclature, I shall call the return circulation of the lepadids the peripheral-collecting circulation. Cannon (1947) also described the return circulation





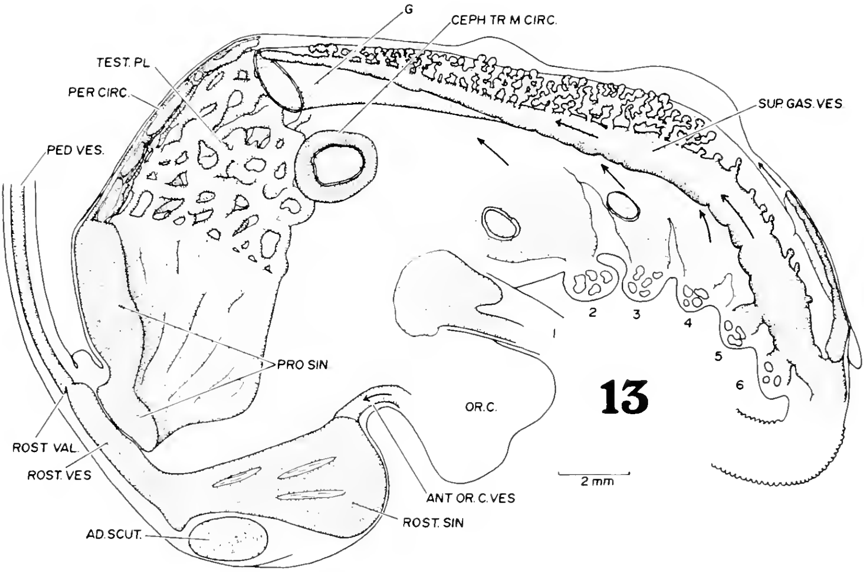
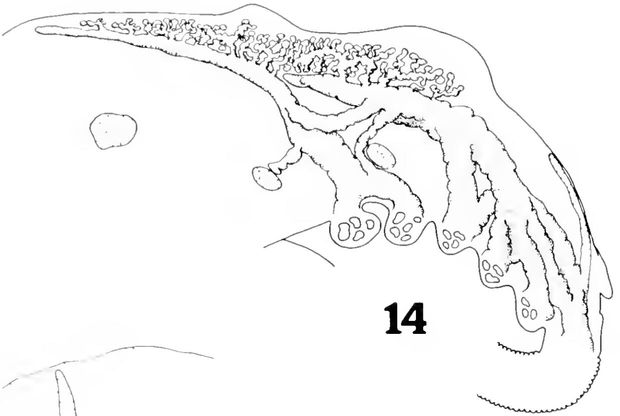


Figure 11. Circulation of three segments of a ramus in *L. anatifera*. a. View of the posteriorly facing side of the ramus, b. anteriorly facing side.

Figure 12. A filamentary appendage from the base of the first cirrus in *L. anatifera* showing the circulatory pattern. This arrangement is basic to all filamentary appendages thus far observed. a. Longitudinal view, b. cross section.

Figure 13. The peripheral-collecting circulation of *L. anatifera* in an illustration similar to Fig. 7. The superior gastric vessel along most of its length abutts directly against the inferior gastric vessel (see Fig. 7).



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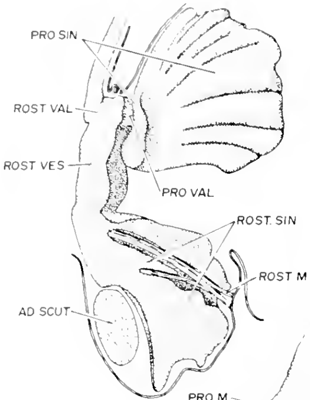

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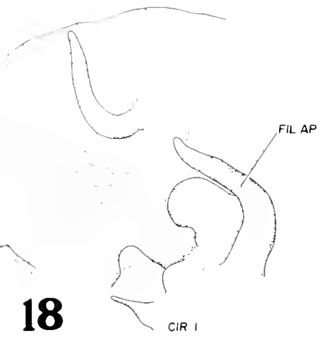

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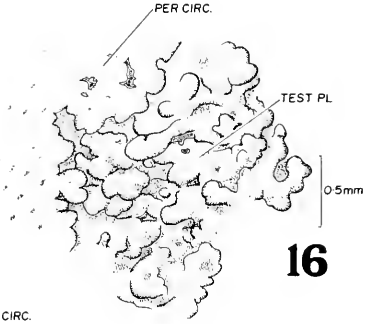

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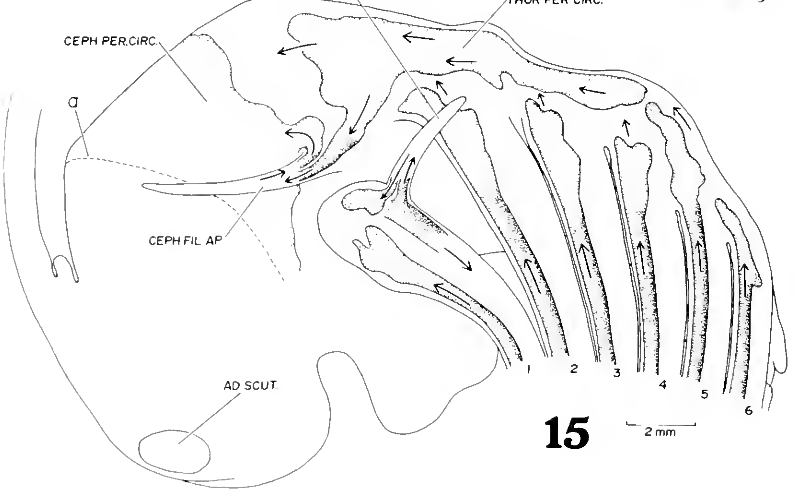

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Figure 14. Variation in the superior gastric vessel of *L. anatifera.* See text for description.

Figure 15. The peripheral-collecting circulation as seen from the left side of the body of *L. anatifera,* a. the border of the prosomal sinus.

Figure 16. Close-up of the peripheral-collecting circulation of the cephalic region in *L* fasicularis showing the thin layer of the peripheral circulation along with the testicular plexus.

Figure 17. The rostral vessel and its associated sinuses in *L. anatifera.*

Figure 18. The distribution of the thin layer of muscle surrounding the prosomal sinus in *C. virgatum.*

in *Lithotrya valentiana* as essentially a peripheral-collecting system.

The peripheral-collecting circulation in the Lepadidae was much more difficult to trace due to the weakness of the rostral valve and a consequent filling of the prosoma with Microfil. However, in a few *L. anatifera* I was able to trace this circulation, although fine details were usually obscurred.

The major source of hemolymph to the peripheral-collecting circulation comes from the efferent cirral vessels and the return flow from the penis. There are two possible routes for this hemolymph after it leaves the cirri. In one pathway, vessels from the posterior cirri (5 and 6) and penis join to form the paired superior gastric vessels (Fig. 13). These vessels occupy a ventrolateral position on each side of the thoracic gut and decrease in caliber from their posterior origin. The superior gastric vessels give rise to a plexus covering almost the entire thoracic gut. Essentially the same pattern is shown in *P. polymerus* (Burnett, 1972). In one individual (of five *L. anatifera*) the efferent circulations from the left side of cirri 2 through 6 contributed to the superior gastric vessel (which in this case was divided into two vessels; Fig. 14). On the right side, the morphology was as described above.

The efferent cirral circulation also contributes to the peripheral circulation of the thoracic region (Fig. 15). In the dorsal part of the thorax the peripheral circulation is derived from the plexus of the thoracic gut circulation. The two peripheral circulations combine and their hemolymph flows anteriorly. At the cephalic-thoracic border, a vessel emanating from the thoracic peripheral circulation enters the cephalic filamentary appendage.

There is a peripheral connection between the thoracic and cephalic peripheral circulations, but as this area is remote from the site of injection, the Microfil rarely formed a continuous band from the thoracic to the cephalic peripheral-collecting circulations. The cephalic filamentary appendage (a type II filamentary appendage), however, serves as a less resistant connection between the two halves of the peripheral-collecting circulations. The cephalic transverse muscle, in contrast to that of *P. polymerus,* is surrounded by hemolymph from the cephalic peripheral circulation (Fig. 13).

The peripheral-collecting system of the prosoma has two regions. In the posterior part, the circulation is divided into a plexus that surrounds the testes (the testicular plexus). This is similar to the peripheral-collecting circulation of the thoracic region. In *L. fasicularis,* this plexus is more grossly constructed than in *L. anatifera* and in both a thin peripheral circulation arises from connections with the testicular plexus.

The testicular plexus and peripheral circulation connect anteriorly to the prosomal sinus (Figs. 13, 17), which is a half bowl-shaped sinus occupying the anterodorsal part of the body. This sinus is completely covered by a thin blanket of muscle (Fig. 18) that is sandwiched between the sinus and the cuticle of the prosoma.

As in *P. polymerus,* the prosomal sinus is connected by a pair of round openings (the prosomal valves, Fig. 17) to the rostral vessel. The morphology of the region appears to be as in *P. polymerus,* except the valve flaps of the rostral vessel do not appear to be present (this is probably due to vessel distortion so frequently observed in the injections of the lepadids).

The rostral sinus (Figs. 13, 17) also has a morphology similar to that of *P. polymerus.* This sinus receives blood from the oral cone, the adductor scutorum, and perhaps the prosomal sinus via the rostral vessel.

By shining a light through *L. fasicularis,* I observed that the cuticle between the adductor scutorum and the oral cone pulsates every 3-4 seconds at 22°C. Such movements probably result from the contraction of the rostral sinus muscles. However, for the rostral sinus to operate as a pump, a valve should be located between the rostral sinus and the anterior oral cone; none was found.

It appears that the rostral sinus pumps hemolymph through the rostral vessel and into the peduncle. The direction of flow is deduced from the position of the valves, partial injections of Microfil, and from my studies with *P. polymerus* (Burnett, 1972).

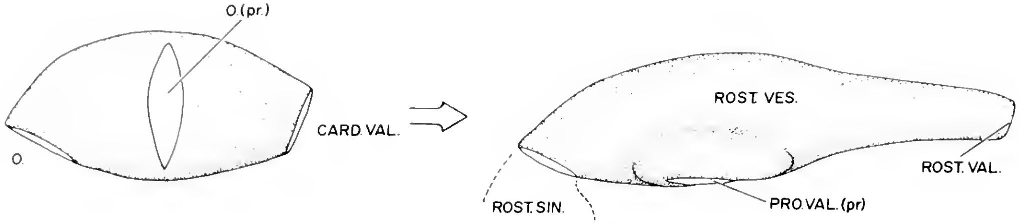

Figure 19. Comparison of the rostral vessel (right) with the heart of *Calanus finmarchicus* (left — redrawn from Lowe, 1935).

The structure of the vessel wall of the cephalic gut is like that of the midsagittal vessels in *P. polymerus.* Light microscopy shows an intima containing large branching fibers that become more diffuse a short distance from the intima. The spaces with no apparent circulation ventral to the gut are occupied by the seminal vesicles. These organs appear to have little circulation associated with them.

The distributive circulation of the four species differs in vessel number and caliber: the smaller species (*L. fasicularis* and *L. pectinata pacifica*) have fewer, larger caliber vessels than the larger species, suggesting that small barnacles have less complex circulation. *Conchoderma virgatum* and *L. fasicularis* are of similar size, but the former has more complex circulation.

The blood pump.—The location of the hemolymph pump in barnacles has been in dispute (Fyhn et al., 1973). From a study of serial sections of *Lithotrya valentiana,* Cannon (1947), placed it between the adductor scutorum and the base of the oral cone (the rostral sinus). He called this sinus the "blood pump" instead of a heart because the muscles are located within the sinus rather than encircling it. In *Balanus balanoides,* Gutmann (1960) argued that circulation takes place as a result of muscular activity or during cirral extension and retraction: during periods of inactivity contraction of muscles in the prosoma propel the blood. However, in inactive barnacles Blatchford (1970) observed movements in the region of the rostral sinus that he ascribed to circulatory movements.

I found by my observations on *L. fasicularis* that the rostral sinus probably acts as a blood pump for this species and for the other lepadid species.

DISCUSSION

Newman et al. (1969) postulated that the thoracican Cirripedial were derived from an ascothoracican-like maxillopodian ancestor and therefore are closely allied to the Copepoda. I noted (1972) the similarity of the heart of the copepod *Calanus finmarchicus* to the rostral vessel of *P. polymerus* (Fig. 19). The lepadid rostral vessel with its connection to the prosomal sinus has the same arrangement as in *P. polymerus.* The argument supporting the rostral vessel as being a vestigial heart is 1) the rostral vessel is essentially in a dorsal position and is properly oriented, 2) the openings into the rostral vessel correspond to the positions of the ostia in the copepod *Calanus finmarchicus* (Lowe, 1935), and 3) the rostral valve is homologous to the cardioarterial valve in the copepod heart.

Since the rostral vessel lacks musculature, I infer that during the evolution of the Cirripedia, heart function was shifted from the heart (rostral vessel) to the rostral sinus (an original part of the pericardial sinus). Why would there be a shift of heart function in the barnacles? In pedunculate barnacles contraction of the peduncle forces a large pulse of hemolymph into the body. Apparently, the only large sinus positioned to receive and store this extra hemolymph is the prosomal sinus. The prosomal sinus probably not only acts as the main venous sinus for the body, but also is involved in maintaining equilibrium between the peduncle and the body.

In the primitive thoracic cirriped, the heart was suspended in a sinus that was subject to increasingly high pressures as the peduncle became more dynamic. The net effect of these increasingly high pressures would be collapse of the heart. A shift of blood pumping from the heart to a sinus where the muscles are intrinsically located would solve the problem of collapse.

The reason for splitting the primitive pericardial sinus into the prosomal and rostral sinuses is difficult to postulate. Perhaps this separation was present prior to the development of a peduncle and the consequent loss of heart musculature. Such a separation would be necessary if part of the pericardial sinus was to act as a reservoir and part as a pumping organ.

Regardless of the state of the peduncle, it must always receive oxygenated blood. This is accomplished by a continuous beating of the rostral sinus in which, no matter what the length of the peduncle, a constant volume of blood is pumped into the peduncle from the rostral sinus. Peduncular extension is probably mostly mediated by hemolymph from the prosomal sinus that was originally squeezed out of this sinus by contraction of the prosomal muscles.

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APPENDIX
ABBREVIATIONS

AD. SCUT.	adductor scutorum
AF. AD. SCUT.	afferent of the adductor scutorum
AF. CIR. VES.	afferent cirral vessel
AF. FIL. VES.	afferent filamentary vessel
AF. MAN. CIRC.	afferent mantle circulation
AF. MD.	afferent mandible circulation
AF. OR. C. VES.	afferent oral cone vessel
AN.	anus
ANT. OR. C. VES.	anterior oral cone vessel

CAR.	carina
CAR. VES.	carinal vessel
CARD. VAL.	cardioarterial valve
CEPH. FIL. AP.	cephalic filamentary appendage
CEPH. PER. CIRC.	cephalic peripheral circulation
CEPH. TR. M.	cephalic transverse muscle
CEPH. TR. M. CIRC.	cephalic transverse muscle circulation
CIR. 1	cirrus I
CIRCUM. FL. M. CIRC.	circumflexor muscle circulation
CON. VES.	connective muscle
EF. CIR. VES.	efferent cirral vessel
EF. FIL. VES.	efferent filamentary vessel
EPI. SIN.	epineural sinus
EX. CUT.	exterior cuticle
FIL. AP.	filamentary appendage
G.	gut
GAST. GL.	gastric gland
GAST. PL.	gastric plexus
INF. GAS. VES.	inferior gastric vessel
IV. CIRC.	intervalve circulation
M.	mantle
MAX. GL. PL.	maxillary gland plexus
O.	ostium
O. (pr)	ostium (paired)
OR. C.	oral cone
OV. FR.	ovigerous frenum
P.	penis
PED.	peduncle
PED. VES.	peduncular vessel
PER. CIRC.	peripheral circulation
POST. INF. GAS. VES.	posterior inferior gastric vessel
POST. OR. C. VES.	posterior oral cone vessel
POST. SIN.	posterior sinus
PRO. M.	prosomal muscle
PRO. SIN.	prosomal sinus
PRO. VAL.	prosomal valve
PRO. VAL. (pr)	prosomal valve (paired)
ROST. M.	rostral muscle
ROST. SIN.	rostral sinus
ROST. VAL.	rostral valve
ROST. VES.	rostral vessel
SCUT. PL.	scutal plexus
SCUT. SIN.	scutal sinus
SCUT. VAL.	scutal valve
SCUT. VES	scutal vessel
SUB. VES.	subintestinal vessel
SUP. GAS. VES.	superior gastric vessel
SUR. CIRC.	surface circulation
TER. PL.	tergal plexus
TEST. PL.	testicular plexus
THOR. FIL. AP.	thoracic filamentary appendage
THOR. PER. CIRC.	thoracic peripheral circulation
THOR. TR. M.	thoracic transverse muscle
VAL.	valve