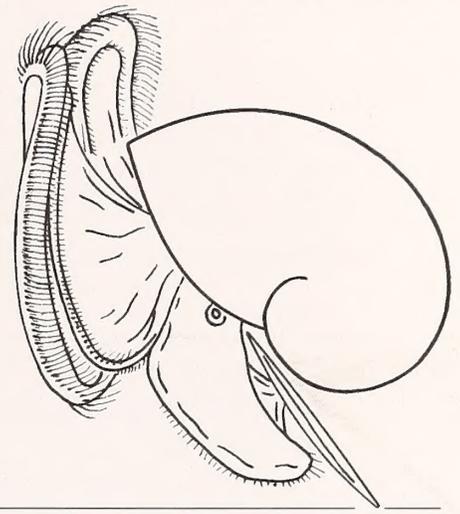


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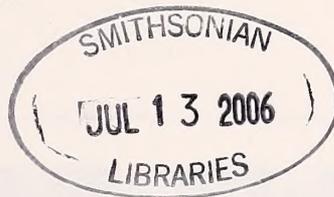
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A Preliminary Study on the Biology of the Predatory Terrestrial Mollusk *Rathouisia leonina*

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Abstract. A study about the natural history of the slug *Rathouisia leonina* Heude, 1882 was carried out both in the field and in the laboratory. The external morphology, distribution, habitat, food range and preference, predatory behavior and reproduction were studied. Adult slugs were up to 1.02 g in weight and 35 mm long when kept inactive. They always preyed upon eggs, juveniles and adults of snails, rather than those of slugs of other families. Smaller individuals (0.18–0.55 g) showed preferences for feeding on bradybaenid snails *Trichobrybaena submissa* with larger diameter and larger apertural opening, while larger slugs (0.63–1.02 g) showed no such preference. The slugs also showed a preference for the eggs of *Acusta ravidia* over those of *Bradybaena similaris* and *T. submissa*. The length of feeding scars on snail eggs made by infant slugs measured 0.24–0.47 mm, and those made by adult slugs 0.41–0.62 mm. After copulation adult slugs laid 10–49 eggs per clutch. The number of eggs was not correlated with their parent slugs' weight but the diameter of the eggs (1.88–3.09 mm) showed a positive correlation to the parent slugs' weight. It took 25–29 days for the eggs to hatch at 17.5–23.5°C, 86% ± 5% RH in the laboratory.

INTRODUCTION

Rathouisia leonina Heude, 1882 (Heude abbreviated as H. below) is a mollusk species that has not received attention since its original description. Among the approximately two thousand known species of land- and freshwater gastropods in China, rathouisiid slugs have received little attention. Soleolifera (*sensu* Solem, 1978) comprise two families: Rathouisiidae and Veronicellidae (= Vaginulidae). Along with these two terrestrial families, there is a marine family Onchidiidae (order Onchidiacea, *sensu* Solem, 1978) arranged in the superorder Systellommatophora Pilsbry, 1948. In China, six veronicellid species and three rathouisiids have been recognized: *Vaginulus carbonaria* H., 1882, *V. fargesiana* H., 1882, *V. chinensis* (Möllendorff, 1881), *V. lemonieriana* H., 1882, *V. patriatiana* H., 1882, *V. pictor* H., 1882,

Rathouisia tantherina H., 1882, *R. tigrina* H., 1882 and *R. leonina* H., 1882 (syn. *Vaginulus sinensis* H., 1882), distributed in Sichuan, Hubei, Jiangsu, Guangdong, Guangxi, Yunnan (Wu, unpublished report) and Hong Kong. The known northernmost limit of rathouisiids in China is the northern bank of lower Yangtze River (Heude, 1882–1890).

Heude's family Rathouisiidae was based on the lack of a jaw and the presence of a protrusile proboscis or suction trunk, as well as those characters shared with the related group Veronicellidae (= Vaginulidae). The uniqueness of the mouth structure corresponds with its predatory life. There are three species belonging to the genus *Rathouisia*. *R. tigrina* with the smallest body size is black when alive and purple when preserved in ethanol solution; its dorsal striation is elongatedly ovate, similar to that of *R.*



Figure 1. *R. leonina*.

leonina. *R. leonina* lives in the limestone hills of Chengkou county (31°54'N, 108°36'E), Sichuan. *R. tantherina* lives in the same habitat as *R. tigrina*, but has a lighter body color and a longer body; its dorsal striations are polygonal to amorphous spots. *R. leonina*, studied in the present work, has a larger body size than the previous two species and its body is elongatedly cylindrical in dor-

sal view. *R. leonina* colonizes the eastern valley of the Yangtze River. Besides the localities mentioned below, one specimen (ZMIZ00801) collected by the Zoological Museum (Institute of Zoology, Chinese Academy of Sciences) suggests another occurrence of *R. leonina* at Shaoguan (24°48'N, 113°36'E), Guangdong, in S. China (Wu, unpublished).

Heude (1882–1890) noticed that *R. leonina* is a predatory carnivore, preying upon land snails (*Helix sensu* Heude, 1882, which might belong to Bradybaenidae and families with similar shell shapes, according to the recent classification of land stylommatophoran shells). Heude also mentioned in the paper (1882–1890) that *R. leonina* lives in a similar habitat to the slug *Meghimatium bili-*

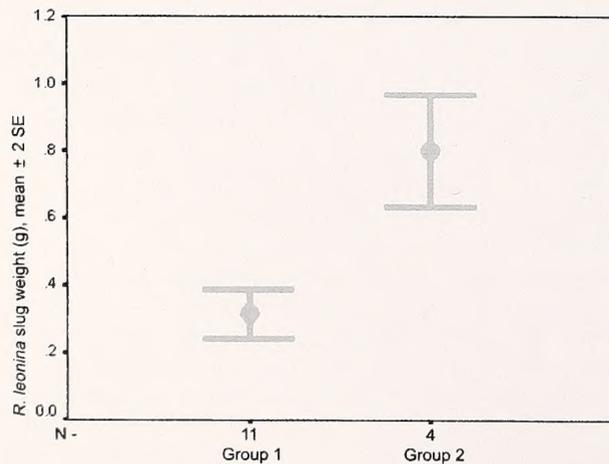


Figure 2. Mean weight \pm SE (g) of *R. leonina* Group 1 and Group 2 in the experiment on prey size choice.

Table 1

K-means Cluster Analysis for the investigated parameters of tested *T. submissa*, showing cluster centers.

Cluster center	Height (mm)	Diameter (mm)	Ratio of height/diameter	Apertural area (mm ²)
1	6.30	7.29	.51	10.32
2	5.40	11.48	.60	23.92
3	4.24	9.53	.55	17.33

Table 2

Preference records of the predatory slugs to different parameters of *T. submissa*, in Group 1 (slugs' weight 0.189–0.55 g) and Group 2 (slugs' weight 0.63–1.02 g). Abbreviations: J—juvenile, A—adult, H—shell height, D—shell diameter, RHD—ratio of height/diameter, Ap. A.—apertural area, Asymp. Sig.—Asymptotic significance. Asterisk “*” means statistically significant here.

Slug group	Prey maturity		Conchological parameters of preys												
	J	A	H1	H2	H3	D1	D2	D3	RHD 1	RHD 2	RHD 3	Ap. A. 1	Ap. A. 2	Ap. A. 3	
Group 1															
Sum of records	6	16	10	10	2	2	11	9	8	4	10	2	9	11	
Asymp. Sig.	0.033*		0.055			0.048*			0.280			0.048*			
Group 2															
Sum of records	5	3	3	1	4	3	3	2	3	2	3	2	3	3	
Asymp. Sig.	0.480		0.417			0.882			0.882			0.882			

neatum (Benson, 1842) (Philomycidae), although the former species is not observed commonly.

Although having a larger body size, *R. leonina* closely resembles *Incillaria* sp. (sensu Kurozumi, 1985; *Incillaria* Benson, 1842, a synonym of *Meghimatium* van Hasselt, 1823), which is distributed in Okinawa (26°13'N, 127°40'E), Japan, based on available information on morphological characters and biology (Kurozumi, 1985). Interestingly, *R. leonina* attacked all snails tested in the present work only through the shell aperture rather than both in this manner and drilling into the snails' shells, reported for *Incillaria* sp. (sensu Kurozumi, 1985). None of the two reports (Heude, 1882; Kurozumi, 1985) provides a picture or photograph of such drilled shells with feeding scars, although the photograph of the scars left on the calcareous egg shells, which is quite similar to those left by *R. leonina*, were shown from *Incillaria* sp. (sensu Kurozumi, 1985). Based on this point and the mor-

phological similarity, *Incillaria* sp. (sensu Kurozumi, 1985) might be more closely related to *R. leonina* than to herbivorous philomycid slugs. The eventual solution for this question will be based on the intensive comparative study of their morphology, habitats and other relevant ecological issues.

This paper is the preliminary part of a work dealing with several aspects of *R. leonina*, which originated from both the interest in this rarely seen predatory slug and using it as a potential bio-control agent. However, the latter idea has been postponed, because of both the lack of detailed biological data and the extremely powerful predatory capacity of this creature shown in the experiments which raised special bio-safety considerations. Other problems revealed during this work and others in progress will be discussed elsewhere.

MATERIALS AND METHODS

Field Survey

Field surveys were conducted respectively during May 2000 in Zhongshanling (32°00'N, 118°42'E), Nanjing, Jiangsu province, China, and during March 2001 in Yichang (30°36'N, 111°12'E), Hubei province, China.

Mollusk Collection and Rearing

***R. leonina* (Figure 1):** One living animal was collected from Zhongshanling, 2nd May 2000, two ones from Yichang on 30th Sept. 2000 and 49 (both adults and juveniles) from the same site in Yichang on 19th March 2001, respectively. In the meantime, the predatory behavior of *R. leonina* was observed both in the field (at Nanjing and Yichang) and in the laboratory. The *R. leonina* slugs used in the present experiments and non-experiment observation were more than 52 slugs from the field and their offspring cultured in the laboratory. Hatchlings were separated from their parents and were raised

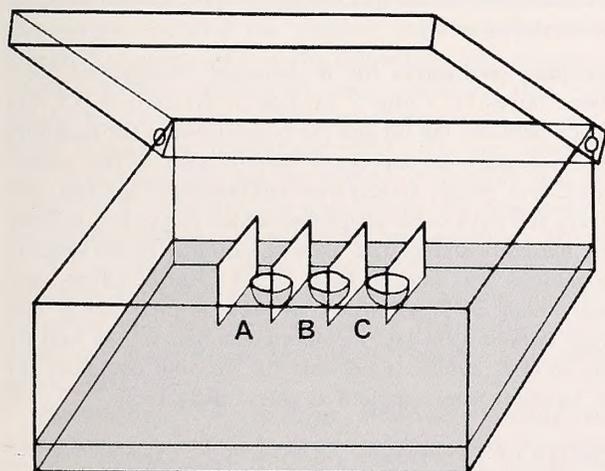


Figure 3. Experimental set used to detect the egg choice of *R. leonina*.

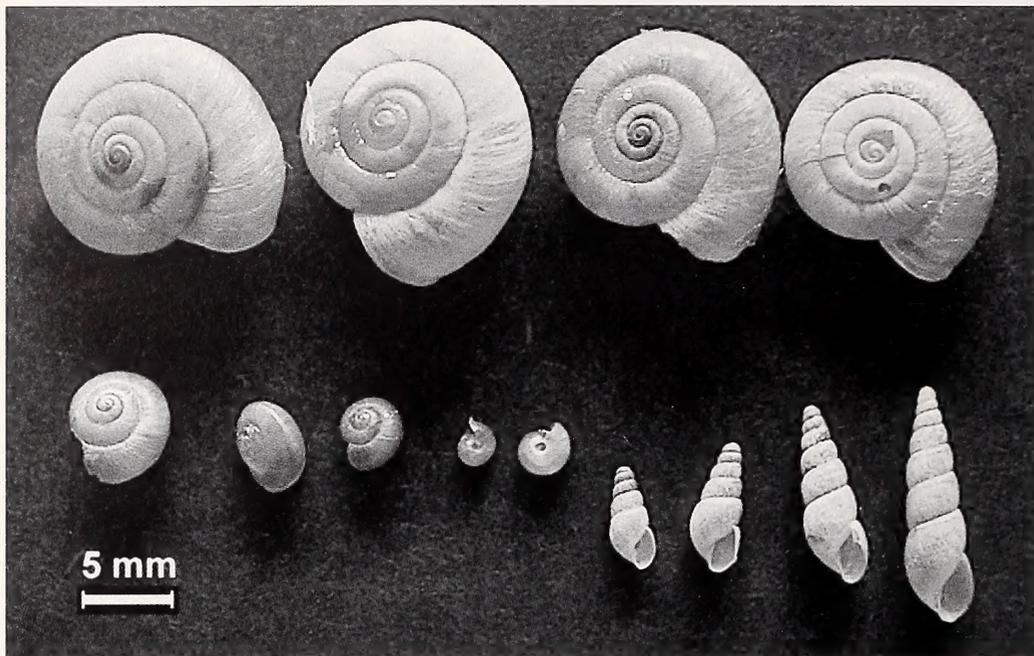


Figure 4. Empty shells of prey. Upper row and left five of lower row: *Trichobrybaena submissa*; right four of lower row: *Opeas arctispirale*.

together in the same container as the parents' (see below), with fresh eggs of *Trichobrybaena submissa* (Deshayes, 1873; generic position see Wu & Guo, 2003) as their daily food and with the empty snail egg shell not removed in this period. When they reached about 10 mm, they were separated and two non-experiment slugs were randomly picked out and raised together in one keeping container. All the slugs used in the experiments (see below) were adult individuals, whose maturity were proven by the fact that they began laying eggs. Each adult predatory slug used in the experiments and in non-experiment observation was given a unique code such as A, E2 or Q4.

Tested preys: Plenty of living slugs (both adults and juveniles) of Limacidae, *Lehmannia valentiana* (Férussac, 1823) and *Limax (Limacus) flavus* (Linnaeus, 1858), slugs of Philomycidae, *Meghimatium bilineatum*, snails of Bradybaenidae, *Bradybaena similaris* (Rang, 1831), *Acusta ravida* (Benson, 1842), and *Trichobrybaena submissa*, and snails (both adults and juveniles) of Subulinidae, *Opeas arctispirale* (Gredler, 1887), were collected in Yichang for this purpose. The snails not co-occurring with *R. leonina*: both adults and juveniles of *Cathaica fasciola* (Draparnaud, 1801) (Bradybaenidae), were collected in the outskirts of Beijing; *Helix (Cryptomphalus) aspersa* (O. F. Müller,) (Helicidae) and *Achatina fulica* (Bowdich) (Achatinidae), were taken from laboratory cultures. All above mentioned slugs and snails as well as their offspring, raised and used in the experiments, were kept in the laboratory located in Beijing. The

eggs of *B. similaris*, *A. ravida*, and *T. submissa*, laid in the keeping containers in the laboratory, were available all the time during the experiments.

Food for tested non *R. leonina* slugs and prey snails:

Snail's biscuit made of hen eggshell 6%, soybean 27%, food-pellets for egg-laying hens 16%, maize 50%, Vitamin C 1%, finely smashed and well mixed with an appropriate amount of water, molded into blocks of 1 cm³, dried in a microwave oven. The biscuit was soaked with water for 1 min before feeding. Lettuce was offered and changed every two days, and the keeping containers were cleaned frequently.

Keeping containers for *R. leonina*: Transparent polythene boxes (123 mm × 80 mm × 50 mm), a 0.5 mm space between the lid and the base ensuring the humidity and necessary air supply. A 10-mm layer of wet vermiculite was evenly spread over the bottom of the box, and every ten days some water was added to the box to keep the humidity stable. The relative humidity in the keeping containers was kept at 86% ± 5%. The different-sized individuals of *T. submissa*, as well as their newly laid eggs (which were laid in other containers and/or laid by the food *T. submissa* put into the keeping container for *R. leonina*) were supplied as slugs' daily food.

Design of Experiment on Prey Size Choice

Fifteen predatory slugs (from adults collected in Yichang in March 2001 and their mature offspring) were studied



Figure 5. Empty shells of prey. Upper row: *Cathaica fasciola*; left two of middle row: *Acusta ravidata*; right three of middle row: *Bradybaena similaris*; lower row: *Trichobrybaena submissa*.

to test whether or not their choice of prey snails depended upon the snails' size, shell shape or the different degree of maturity, from March 28th to May 11th, 2001. All the fifteen *R. leonina* individuals, which in size (estimated by the weight) included the smallest and the largest slug (Figure 2), were tested for the full period. In each experimental system (treatment), one predatory slug was placed into a keeping container together with six numbered *T. submissa* individuals, whose size and morphology were measured and the degree of maturity was recorded. If *T. submissa* laid eggs during the experimental period, the laid eggs were quickly moved away. After a kill by the slug, the empty snail shell was promptly removed and a healthy snail of similar size and maturity, numbered and measured, was added. During the experiment, the fifteen tested individuals' weights were measured every week.

The laboratory-kept predatory slugs were grouped into two groups according to their weights, using K-means Cluster Analysis. The slugs in Group 1 with the weight ranging from 0.18 to 0.55 g were represented by the final cluster center 0.31, and those of weights ranging from

0.63 to 1.02 g in Group 2 were represented by the final cluster center 0.80 (Table 1). Using the same method, all the tested snails of *T. submissa* were grouped into three groups by shell height, shell diameter, and relative apertural area approximately represented by the product of apertural length and apertural width (Wu & Chen, 1998). Then, if a snail was preyed on during the experiment period, its shell parameters and the degree of maturity were recorded as "1"; otherwise they were recorded as "0" (sum of the records see Table 2). Npar Analysis was employed to detect if any of these factors affected the slugs' predation.

Design of Experiment on Egg Choice

A food choice test of three kinds of snail eggs, to detect whether or not *R. leonina* prefers specific snail eggs (*T. submissa*, *B. similaris* and/or *A. ravidata*), was designed and the experimental set was depicted as Figure 3. This experiment lasted for ten days from April 18th to 27th, 2001. In each of thirteen tested predatory slugs (E1–E13, slugs from adults collected in Yichang in March 2001 and

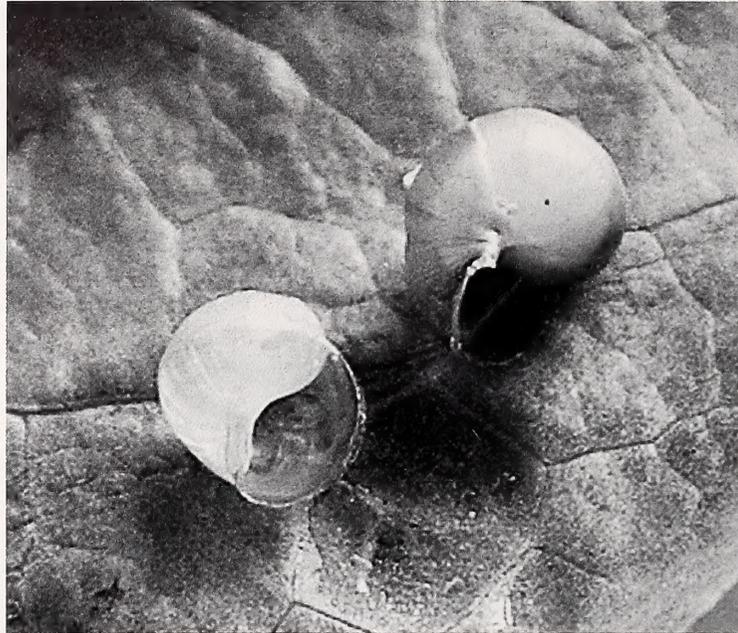


Figure 6. Shells of juvenile *Achatina fulica*, preyed upon by *R. leonina*.

their mature offspring cultured in the laboratory), 10 newly laid eggs each of *T. submissa*, *B. similaris*, and *A. ravidata* were added to pits A, B and C respectively (each pit was dug by 0.5 cm depth and partially separated by two pieces of thin glass (40 mm × 40 mm, thickness 0.5 mm); the distance between the centers of the two adjacent pits was 30 mm). In eight controls (C1–C8): each pit of C1–C3 contained 10 newly laid eggs of *T. submissa*, each pit of C4–C6 contained 10 newly laid eggs of *B. similaris*, and each pit of C7–C8 contained 10 newly laid eggs of *A. ravidata*. During the experiment the tested slugs re-

ceived no additional food. The number of eggs consumed was recorded at the end of the experiment.

Method of Weighing, Measuring and Data Analysis

The weight of slugs was measured with a calibrated digital electronic balance (accuracy ±1 mg, EX-200A, Mehcuhy), in the experiment on prey size choice. The length measurements of *T. submissa* were made with a calibrated electronic digital display caliper (accuracy ±0.01 mm). The maximum diameter of *R. leonina* eggs was obtained from digital photographs and measured by Photoshop 5.0. Statistical calculations were performed using SPSS for Windows 8.0.0 (SPSS Inc, 1989–1997, Standard Version). Bivariate correlation (2-tailed Pearson Correlation), non-parametric tests for several related samples (Kendall's W Test and Friedman Test) and K-means Cluster Analysis using for grouping numerical characters were employed.

Table 3

The predation by *R. leonina* in the field and/or in the laboratory. +: offered and preyed upon in the laboratory; ++: predation was observed in the field; -: offered but not preyed upon in the laboratory; ?: not tested in the present experiments.

Species	Eggs	Hatchlings	Elder juveniles	Adults
<i>Acusta ravidata</i>	+	+	+	+
<i>B. similaris</i>	+	+	+	+, ++
<i>T. submissa</i>	+	+	+	+
<i>C. fasciola</i>	?	+	+	+
<i>H. (C.) aspersa</i>	?	+	+	-
<i>O. arctispirale</i>	?	?	+	+
<i>Achatina fulica</i>	?	+	+	?
<i>M. bilineatum</i>	-	-	-	-
<i>Limax (Limacus) favus</i>	-	-	-	-
<i>Lehmannia valentiana</i>	-	-	-	-

RESULTS

Morphology of *R. leonina*

The weight of the adult slug ranges from 0.18 g to 1.02 g (Figure 2). The length is shorter than 35 mm when inactive. Its body contracts inconspicuously when preserved in 70% ethanol. The body color is light grayish brown to dark gray, sometimes reddish tinted, and the color fades in ethanol solution. It has numerous discontinuous short black longitudinal striations, which are shortened and turned into elliptic spots when the slug



Figure 7. *R. leonina* preying on a mature *T. submissa*.

contracts, distributed on its dorsal side. The sole of the animal is uniformly light reddish brown. The epidermis excretes a small amount of very sticky mucus. The optic tentacles are short and black, the lower pair of tentacles is somewhat shorter, lead-colored, bifurcate, and distally tapering when fully stretched (Figure 1).

Habitat

R. leonina is distributed from the middle to lower reaches of the Yangtze River, and is only known in Nanjing, Yichang and Shaoguan from our collection. It lives usually at foothills and adjoining land, sometimes also in city gardens. In field observation during the dry season in May 2000 at Nanjing, *R. leonina* inactively rested between the surface of sandy loam and thick litter layer, with co-occurring land mollusk species *Cyclophorus* sp. and *A. ravida* which were also inactive. In September 2000 and March 2001 at Yichang, in the fairly humid environment, this species actively moved on the litter-free laterite, with co-occurring mollusks *L. valentiana*, *L. (Limacus) flavus*, *M. bilineatum*, *B. similaris*, *A. ravida* and *O. arctispirale*. It prefers conditions of high humidity and shade, and usually rests on cool and smooth surfaces, such as on the underside of earth-free stones, bricks, and even on plastic pieces. Sometimes it retreats within the

crevices of moist clods or within earth tunnels produced by other organisms. In the field, they are known to be active in temperature ranges from 10.5°C (lowest temperature in May) to 35.5°C (highest temperature in May) in Nanjing, and from 4.0°C (lowest temperature in March) to 35.0°C (highest temperature in March or October) in Yichang.

Predation

In the field, several times one to three *R. leonina* were observed around an egg clutch of *M. bilineatum*. Some egg clutches with *R. leonina* resting nearby became milky and irregular in shape, and well distinguished from those in normal condition. However, we never observed *R. leonina* feeding on the eggs of *M. bilineatum* in the field or in the laboratory. In the laboratory, *R. leonina* was observed to prey on animals of *O. arctispirale*, *C. fasciola*, *A. fulica* and *H. (C.) aspersa*, and animals and eggs of *B. similaris*, *A. ravida* and *T. submissa* Deshayes (Figures 4–6; Table 3). None of the slugs tested were attacked or preyed upon. When preying on snails, they always attacked the body through the shell aperture. The prey snail contracted faster than normal, and secreted a large amount of foam or mucus. They then became quiescent and seemed to be insensitive to the predation by *R. leo-*



Figure 8. *R. leonina*, preying on a hatchling of *A. fulica*.

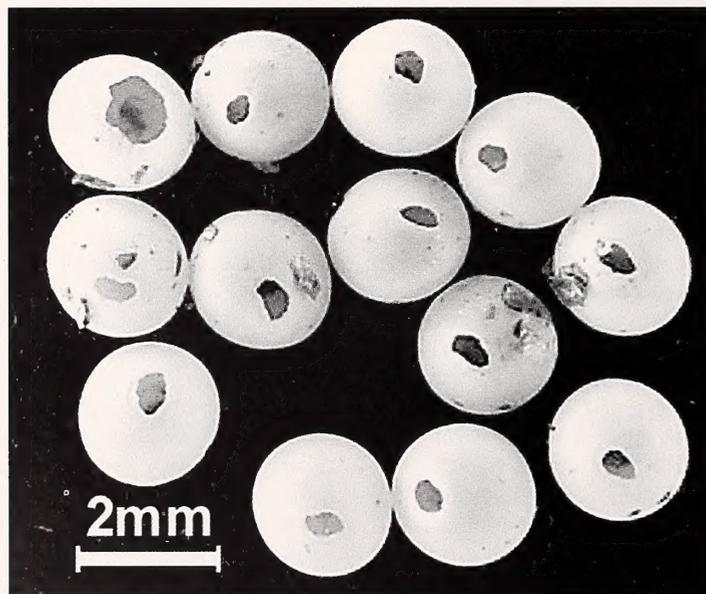


Figure 9. Empty egg shells of *T. submissa*, preyed upon by *R. leonina*.

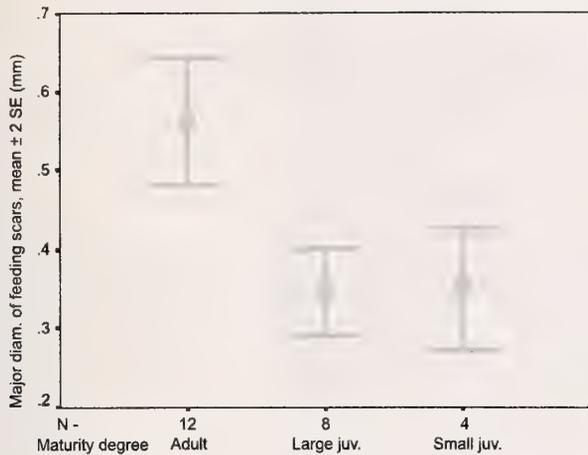


Figure 10. Mean major diameter \pm SE (mm) of feeding scars left on the eggshells of *T. submissa* made by *R. leonina* of different maturity degree.

nina. Two methods of feeding were used by this slug, inserting its head into the aperture (Figure 7), or just protruding the proboscis (termed 'suction trunk' by Heude, 1884) into the aperture (Figure 8), depending upon the aperture size of the prey.

The statistical results shown in Table 2 indicated that smaller slugs (from Group 1) preferred mature snails, which were generally those with a larger shell diameter and larger aperture (asymptotic significance <0.05), to juveniles. For larger slugs (from Group 2), no preference was detected (Table 2).

When *R. leonina* fed on snail eggs, it always kept a pose of curving its head and 'neck' in order to hold and fasten the egg, and bit into the egg a tiny hole, or feeding scar, which usually showed the shape of an elongated ellipse, a circle or rarely amorphous shapes. The edge of the hole was smooth or somewhat serrate (Figure 9). The laboratory observation on non-experiment predatory slugs showed: if they found eggs in the egg-laying pits dug by *T. submissa*, they sometimes stayed in the pits until all inside eggs had been consumed; the holes produced by the adults and the juveniles could be distinguished by the major diameter range, as for older or



Figure 11. *R. leonina* in copulation.

Table 4

R. leonina's preference for the eggs laid by three species. In experimental systems (treatments) E1–E13, pit A contained 10 *T. submissa* eggs, pit B contained 10 *B. similis* eggs, and pit C contained 10 *A. ravidia* eggs. In controls, each pit contained 10 eggs—in controls C1–3, pits A, B and C with *T. submissa* eggs; in controls C4–6, pits A, B and C with *B. similis* eggs; incontrols C7 and 8, pits A, B and C with *A. ravidia* eggs.

	Sum of consumed eggs in Pit A	Sum of consumed eggs in Pit B	Sum of consumed eggs in Pit C
E1–E13	11	7	28
C1–C3	8	8	7
C4–C6	13	6	6
C7, C8	8	3	10

younger juveniles the holes were smaller (Figure 10). The major diameter of feeding holes made by a mature individual of *R. leonina* ranged from 0.41 mm to 0.62 mm, and those made by elder or younger juveniles ranged from 0.24 mm to 0.47 mm.

R. leonina showed a significantly different preference for eggs laid by *T. submissa*, *B. similis* and *A. ravidia* (Table 4, Test for several related samples, Asymp. Sig. = 0.010; in controls, Asymp. Sig. = 0.267). The preference rank from high to low is: eggs of *A. ravidia* > eggs of *T. submissa* > eggs of *B. similis*.

Reproduction

Mature individuals: The mature slugs ranged from 0.18 g to 1.02 g. In the laboratory, only a few mating cases were observed in time. A copulating pair of *R. leonina* could be instantly distinguished from their connecting the right sides of the anterior parts (Figure 11).

Prior to egg laying, the slug dug a hole in the vermiculite layer. The hole was slightly broader than the slug itself and of ca. 5–10 mm depth. Then the animal inserted its anterior body into the hole and began to lay eggs. It seldom laid eggs on the surface of the vermiculite layer (Figure 12). The eggs of *R. leonina* were translucent, light smoke-blue to light pink, spherical or ellipsoidal (Figures 12, 13). In the field, the eggs of *R. leonina* could not be easily distinguished from those laid by *L. valentiana* (Figure 14). In the laboratory, recorded egg laying was observed 8 times in 5 different individuals, i.e., predatory



Figure 12. *R. leonina* laying eggs; eggs pink.



Figure 13. Eggs of *R. leonina*, eggs normal smoke-blue.



Figure 14. Eggs of *Lehmannia valentiana*, similar to those of *R. leonina*.

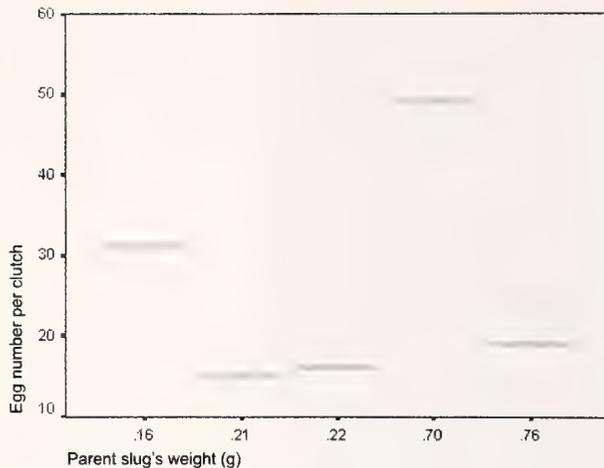


Figure 15. The relationship of parent *R. leonina* slug's weight (g) and the egg number per clutch.

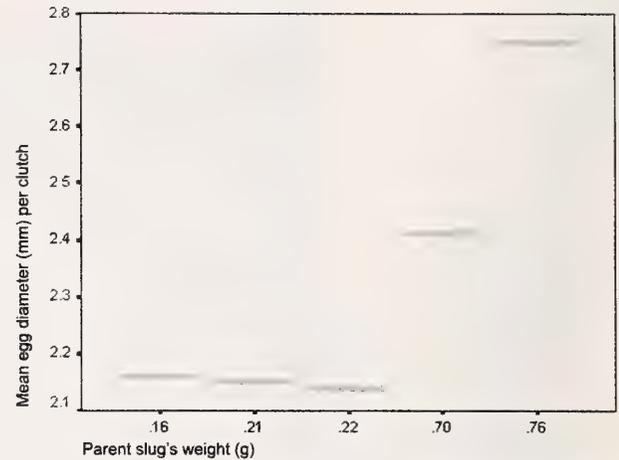


Figure 16. The relationship of parent *R. leonina* slug's weight (g) and the mean egg diameter (mm).

slug A laid 4 clutches during the experiment on prey size choice and during the daily culture. Most egg laying data from the slug daily culture were not recorded in order to avoid influencing the cultured slug maintenance. The predatory slug A laid its 4 clutches in the intervals of 6, 6 and 4 days respectively. Each one of the 8 clutches was made up of 10–49 eggs, the large diameter of the eggs ranged from 1.88 mm to 3.09 mm (mean 2.30 mm). The weight of the parent predatory slugs showed no correlation to the numbers of eggs of each clutch (Figure 15; 2-tailed Pearson Correlation, sig. = 0.508), but showed a positive correlation to the eggs' diameters (Figure 16; 2-tailed Pearson Correlation, sig. = 0.025).

Hatching

The embryos were visible by the naked eye when the eggs started to develop. In the condition of 17.5–23.5°C in the laboratory, it took 25–29 days for the eggs to hatch (Figure 17). In the first 1–3 days the hatchlings remained inside the egg-laying pit before they moved out of the pit and searched for food. Like their parents, the juveniles fed on calcareous snail eggs, hatchlings of snails and never fed on herbivorous slug's eggs.

DISCUSSION

Prey preference of the predatory land mollusks is always an important topic (Cowie, 2001). The present result showed that smaller individuals of the predatory slugs were particularly selective with respect to shell shape and size of prey, although larger individuals showed no preference. The Indian carnivorous shelled snail *Gulella bicolor* preferred the snails *Opeas gracile* of the size close to themselves (Raut & Shahbabu, 1986). Under natural conditions, compared with *Incillaria* sp. (sensu Kurozumi, 1985), *R. leonina* shows a more narrow prey range,

i.e., a less developed species preference. The former species was observed to consume the snails and eggs of helicoids such as *Satsuma mercatoria* (Camaenidae), *Bradybaena circulus* and *Aegista elegantissima* (Bradybaenidae), the animals and eggs of prosobranch snails such as *Georissa fukudai* (Hydrocenidae) and *Cyclophorus turgidus* (Cyclophoridae), and perhaps *Achatina fulica* (only inferred from the feeding scars left on the egg shells) (Kurozumi, 1985). For *R. leonina*, only species without operculum, such as bradybaenids, and perhaps subulinids (not directly observed in the field, only inferred from subulinids co-occurred in the habitats being predated in the laboratory).

The most interesting result of the present study is the prey preference of *R. leonina*, showed by the experiment based on the eggs of three species *T. submissa*, *B. similis* and *A. ravida*. However, limited by the food material for *R. leonina*, using eggs of *T. submissa* as the daily food of *R. leonina* might have influenced the results of the egg choice experiments: The slugs might have been "saturated" with *T. submissa* eggs, and preferred eggs of the other two snail species for a change (Heike Reise, reviewing comments, 2004). This consideration raised the subsequent work which will be of great interest and necessary.

In addition to the general interest in the natural history of predatory land mollusks, the idea for this study arose partly from the desire of choosing some 'beneficial' species with the purpose of controlling other harmful terrestrial snails such as the introduced *A. fulica*. For instance in Asia, *Gulella bicolor* (Hutton) that can prey on *A. fulica*, had been introduced into South Andamans in order to control the giant African snail before 1975 (Raut & Shahbabu, 1986). The present field observations show that *R. leonina* can occupy open habitats, such as at Yi-chang, and dry environments, such as at Nanjing. The



Figure 17. Hatchlings of *R. leonina*, making for the eggs of *T. submissa*; notice some eggs with regular feeding scars left on the egg shells.

present direct observations have enriched our knowledge of the habitat of this group, adding to data for related species described by Kurozumi (1985). The use of similar habitats by the dubious 'philomyxid' (*Incillaria* sp., sensu Kurozumi, 1985) and *A. fulica* implies that such species may be considered as a bio-control agent against *A. fulica* (Kurozumi, 1985). However, the present experiments challenge such consideration promptly, and at least two obvious problems exist. First, the experiments showed clearly that *R. leonina* preys on a wide variety of snail species and eggs. Although the experiments showed the preference for the eggs of agriculture pest snail *A. ravidia*, people know almost nothing about whether or not the predatory slugs will show a stronger preference to other snails untested in the present study, whether the preference is of high plasticity which might be revealed when adding the species of the tested snails, and so on. Second, presuming we know this predatory slug well in the laboratory, what the situation will be when the slugs are in the field? It is well known that usually the laboratory result is too weak to predict the relevant situation in the field. The well known examples here are the East African carnivorous snails *Gonaxis kibweziensis* (Smith) and *G. quadrilateralis* (Preston) (Streptaxidae), and the rosy wolf snail *Euglandina rosea* (Férussac) (Spiraxidae), once the

introduced 'bio-control agents' and eventually known as the dangerous invasive species, which in Hawaii and other places have been causing ecological calamities (Cowie, 2001). So the risk of their possible impact on the native biota should be adequately assessed before any consideration can be made on using them as so-called 'beneficial bio-control agent'. The effort of using predatory non-marine mollusks as bio-control agents, as well as the direct damage and potential danger, has been well reviewed by Cowie (2001). Because very little biological research has ever been carried out upon this species, and much more remains to be done prior to making any conclusion, especially in relation to biocontrol practices. Besides the biology of *R. leonina*, the impact on the population dynamics of different landsnail species should be emphasized in further work.

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The Genus *Offadesma* Iredale, 1930 (Bivalvia: Periplomatidae) in the Miocene of Patagonia

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Abstract. The periplomatid genus *Offadesma* Iredale, 1930 was known from a few species found from the middle Eocene to Recent in New Zealand and Australia. Two new records are added from southern South America in Argentina. *Offadesma* sp., represented by a sole specimen from the Monte León Formation (late Oligocene-early Miocene) exposed near Santa Cruz, in southern Patagonia, and *Offadesma isolatum* n. sp., collected at Punta Pardelas (northern Patagonia) in late Miocene rocks referred to the Puerto Madryn Formation. The relationships to other periplomatids from South America seem to be remote, and therefore the migration of *Offadesma* from Australasia to South America during Cenozoic times as a consequence of the onset of the Antarctic Circumpolar Current is proposed.

INTRODUCTION

The family Periplomatidae includes—among others—a number of species known from shelf environments along the Pacific and Atlantic coasts of America and in tropical West Africa. They are generally not very abundant and as fossils they have been recorded occasionally in rocks of different ages ranging from Jurassic to Recent (Harper et al., 2000). Their occurrence—whether living or fossil—is restricted to specialized environments (Morton, 1981b). In addition to their apparently low numbers, the aragonitic nature of their fragile shells conspires also against their preservation.

In southern South America, the family is represented by two extant species, i.e., *Periploma ovatum* d'Orbigny, 1846 and *Periploma compressum* d'Orbigny, 1846. Both species occur along the coast from southern Brazil to northern Patagonia (Ríos 1994). These two species belong in *Periploma* s.s., and are clearly different from our material and appear to be unrelated to it.

Periploma is represented by *Periploma topei* Zinsmeister (1984, p. 1525–1526, fig. 10F–G; Stilwell & Zinsmeister, 1992, p. 89, pl. 10, fig. e–i) in the Eocene La Meseta Formation just off the Antarctic Peninsula. The interior of this shell, however, is unavailable and the shape is reminiscent of the rather quadrate *Thracia meridionalis* E. A. Smith, 1885 (Dell, 1990, p. 63–65, fig. 109–111), an extant circum-Antarctic species. Shell interiors and conjoined specimens are necessary to ascer-

tain the correct generic placement of *Periploma topei*. Other records of fossil Periplomatidae in southern South America are restricted to only six species. *Periploma* (*Aelga*) *primaverensis* Griffin, 1991 (p. 141–142, fig. 10.3–10.6) appears very rarely in Eocene rocks exposed at the southernmost tip of the continent and has been referred to the subgenus *Aelga* Slodkewitsch, 1935 (type species *Tellina bessohensis* Yokoyama, 1924; p. 14, pl. 3, fig. 1–5; Makiyama, 1957, pl. 12, fig. 1–5) because of the sinuous character of its commissure in ventral view. The second record is a specimen illustrated herein—probably belonging in a new species—coming from the late Oligocene-early Miocene Monte León Formation exposed at Punta Beagle, a few kilometers upstream from the mouth of the Santa Cruz River, in southern Patagonia. The preservation of the sole specimen is too poor to warrant full description, but it apparently belongs in *Offadesma*, becoming thus the earliest representative of this subgenus in South America.

The third record—i.e., the new species described herein—is from Miocene rocks that outcrop along the coast of northern Patagonia and is the first one of the genus in Neogene deposits here, despite the fact that the faunas included in them are very diverse and well known. This testifies to the rarity of this taxon, which has obviously been overlooked during previous collecting in the area.

The other three nominal species referable to the Periplomatidae were described from Tertiary localities along

the Pacific coast of Chile. These are "*Anatina*" *suborbicularis* Philippi, 1887 (p. 154, pl. 33, fig. 2) from Mil-lanejo, "*Anatina*" *davilae* Philippi, 1887 (p. 155, pl. 33, fig. 1) from Levu and "*Anatina*" *arau-cana* Philippi, 1887 (p. 155, pl. 23, fig. 14) also from Levu. Only "*Anatina*" *suborbicularis* may be possibly referable to *Offadesma*. "*Anatina*" *davilae* is a closed shell with damaged edges and apparently lacks an umbonal slit. This seems to pre-clude its inclusion even in *Periploma*. "*Anatina*" *arau-cana* is represented by an internal mold with only frag-ments of the shell adhered to it, and it is practically un-identifiable.

GEOLOGY

In the area surrounding Punta Pardelas (Figure 10) there are numerous exposures of rocks referred to as the Puerto Madryn Formation (Haller, 1978), a marine unit that has yielded an abundant and diverse mollusk fauna known from the earliest years of the Twentieth Century (e.g., Ihering, 1907; Brunet, 1995, 1997; del Río & Martínez Chiappara, 1998 and references therein). The lithostrati-graphic unit comprises about 90 meters of sandstone and siltstone representing the widespread marine transgres-sion that occurred at the end of the Miocene covering large areas of southern South America (Frenguelli, 1920, 1926, 1947; Camacho, 1967; Aceñolaza, 1976; Irigoyen, 1969; Haller, 1978; Herbst & Zabert, 1987; del Río, 1992, 1994, 2000 and references therein). Previous paleoenvi-ronmental work by Scasso & del Río (1987) suggested a near-shore shelf environment for these deposits in the Puerto Madryn area. A sequence stratigraphic study by del Río et al. (2001), allowed discrimination of a number of different cycles representing diverse shell accumula-tions reflecting changes in sea level and environments. The age of the Puerto Madryn Formation was believed to be Late Miocene based on its fossil content (del Río, 1988, 1992), K/Ar dating (Zinsmeister et al., 1981) and Sr⁸⁷/Sr⁸⁶ dating (Scasso et al., 1999).

At Punta Pardelas, only about 20 meters of the total thickness of the Puerto Madryn Formation are exposed. They include a bottom bed of gray mudstone with an abundant and well preserved invertebrate fauna (6.5 m), overlain by very hard yellowish tuffaceous sandstones (3.5 m), a very fine gray sandstone with abundant mol-luscan shells and echinoids (4 m), a yellow fine sandstone with abundant mollusks and echinoids (1 m), yellowish laminated mudstones with intercalated gypsum beds (6 m) and cross-bedded light brown calcareous sandstone with abundant invertebrates. The material described here- in comes from the fine yellow sandstone at 15 meters above the base of the exposed section.

The specimen of *Offadesma* n. sp. illustrated in Figure 3 comes from the Monte Entrada Member of the Monte León Formation, exposed at Punta Beagle, about 15 km inland from the mouth of the Santa Cruz River, at its

junction with the Chico River, province of Santa Cruz, Argentina, southern Patagonia. The Monte León Forma-tion (Bertels, 1970, 1980) comprises about 200 m of sandstone, siltstone and tuffaceous sandstone with a very diverse, abundant and well preserved mollusk fauna (Ihering, 1897, 1907, 1914; Ortmann, 1902; del Río & Camacho, 1998, among others). The restricted outcrop at Punta Beagle includes only 10 to 12 meters of silty sand-stone, topped by a 60 cm oyster bank overlain by a hard and massive yellow sandstone from where the specimen was collected. The age of the Monte León Formation has been subject to controversy, but is generally accepted as latest Oligocene-earliest Miocene (Bertels, 1980; Náñez, 1990; Legarreta & Uliana, 1994; del Río & Camacho, 1998; Barreda & Palamarczuk, 2000).

All specimens described are housed in the Museo Pa-leontológico Egidio Feruglio (MEF-Pi), Trelew, Argenti-na and the University of La Pampa (GHUNPam), Santa Rosa, Argentina.

SYSTEMATICS

Class Bivalvia Linné, 1758

Subclass Anomalodesmata Dall, 1889

Order Pholadomyoida Newell, 1965

Superfamily THRACIOIDEA Yonge & Morton,
1980

Family PERIPLOMATIDAE Dall, 1895

Genus *Offadesma* Iredale, 1930

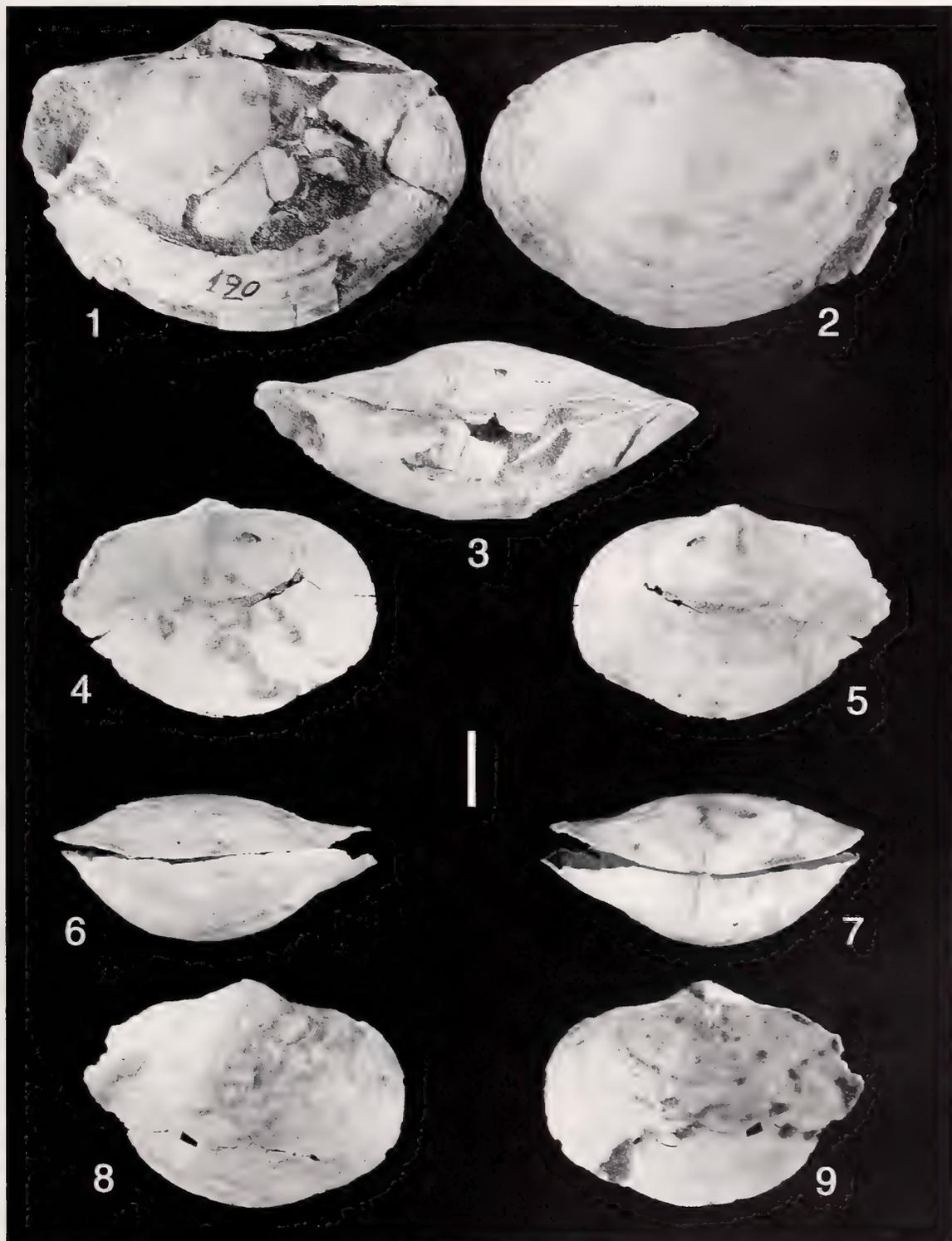
Type species: *Offadesma angasi* Crosse & Fischer, 1864.

Remarks: *Offadesma* has been considered a subgenus of *Periploma* Shumacher, 1817 by various authors (Keen, 1969), while others considered it a distinct genus within the family (Rosewater, 1968; Fleming, 1950). The much more pronouncedly inequivalve shells, the posteriorly in- clined chondrophore with poorly developed anterior and posterior outer ligaments, and the entirely missing litho- desma seem to warrant generic distinction (Fleming, 1950; Coan et al., 2000).

Offadesma isolatum Griffin & Pastorino sp. nov.
(Figures 1–9)

Diagnosis: Medium sized *Offadesma* (height about 40 mm, length about 60 mm) with chondrophore strongly directed postero-ventrally, anterior margin somewhat pro- duced, right valve inflated (about 25% more than left valve), posterior rostrum occupying 28–30% of total shell area.

Description: Shell strongly inequivalve, inequilateral, very thin, about 60 mm long and 40 mm high; right valve deeply cup-shaped; left valve gently convex; right umbo



Figures 1–9. *Offadesma isolatum* n. sp. Figures 1–3, holotype MPEF-PI 190, left, right and umbonal views, Punta Pardelas, Chubut, Argentina, Puerto Madryn Formation. Figures 4–9, paratype, MPEF-PI 191 Figure 4–5. Internal and external views of the left valve. Figures 6–7. Ventral and dorsal views of the same specimen. Figures 8–9. External and internal views of the right valve. Scale bar = 1 cm.

arched over left one; anterior margin rounded, narrowly gaping anteroventrally; posterior margin rostrate, truncated and slightly directed upwards and leftwards; rostrum slightly gaping; weak oblique ridge running from umbo to base of anterior margin; broader and slightly stronger ridge extending from umbo to base of posterior truncation; area between posterior ridge and dorsal border of shell apparently covered by fine sand grains which are impressed on the shell surface; transverse umbonal crack present, running perpendicular to dorsal antero-posterior axis of shell for about 10% of total height; anterior edge of crack overlying posterior edge; primary ligament in deep spoon-shaped chondrophore directed postero-ventrally; anterior outer lamellar ligament running in short moderately deep slit for about dorsal fourth of total height of inner fibrous ligament; posterior outer lamellar ligament in slightly wider and longer slit; chondrophores supported by clavicles extending from the posterior face of chondrophore in postero-ventral direction; chondrophores unequally aligned vertically, displaced to the right into the cup-shaped right valve; adductor muscle scars and pallial line unknown; external surface carrying weak and regularly spaced commarginal ribs and growth lines evident in the intercostal spaces.

Type locality: The material comes from Punta Pardelas in Península Valdés, northeastern Chubut, Patagonia, Argentina. All specimens come from rocks included in the late Miocene Puerto Madryn Formation.

Type material: Holotype, MEF-Pi-190a, a bivalved specimen (valves loose); paratype, MEF-Pi-190b a bivalved shell, partly broken.

Remarks: This species closely resembles *Offadesma marwicki* Fleming, 1950 (p. 246–247, pl. 24, fig. 10). The type specimens come from Black Point in the Waitaki Valley, New Zealand, where they were collected in late middle Eocene (Bortonian) rocks. Fleming also mentions this species from the Pahi Greensands in North Auckland, also Bortonian in age; these are the earliest record of *Offadesma*. As in the material from Punta Pardelas, the shell is not quite as strongly inequivalve as in the type species, which has a more inflated left valve. The New Zealand specimens seem to be slightly smaller and the umbos are more prominent than in our material.

Offadesma angasi (Crosse & Fischer, 1864) lives presently along the coast of southeastern, south and southwestern Australia and also in New Zealand (Rosewater, 1968; Morton 1981a). The only apparent difference with *Offadesma isolatum* n. sp. is that the shell in the type species is more strongly inequivalve and the anterior margin of the shell is more evenly rounded.

Offadesma sp. (Marwick, 1931, p. 83, fig. 110–111; Fleming, 1973, pl. 64, fig. 720–721) from the Kapitean (late Miocene) of New Zealand is very similar, except perhaps in that the shell is more strongly inequivalve.

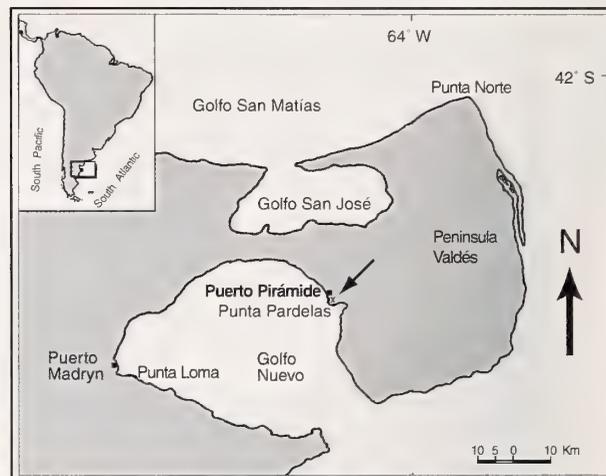


Figure 10. Location map of the fossil locality in the Valdés Peninsula area, Argentina.

Unfortunately, the interior of the material described by Marwick is not visible for further comparison.

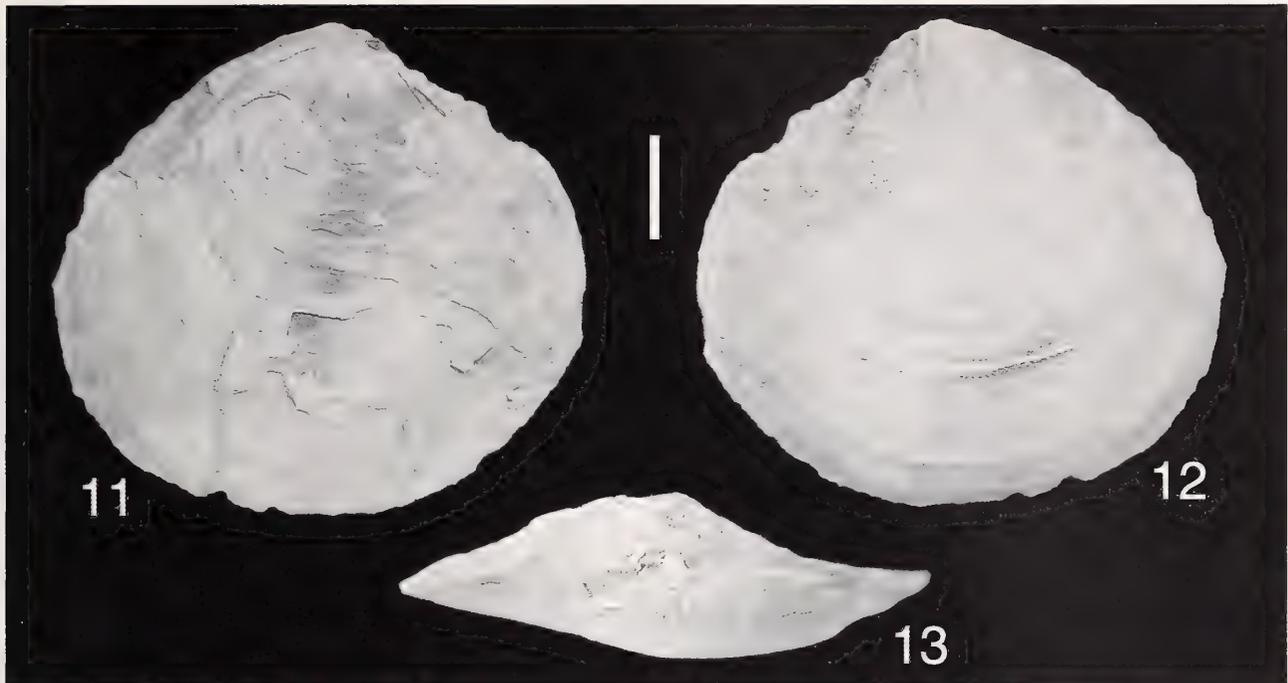
Of the three species of Periplomatidae described by Philippi (1887) from Tertiary rocks in Chile, none show the interior of the shells. Therefore their inclusion in *Offadesma* (and in two cases even in *Periploma*) is at present at least doubtful. The species that most closely resembles ours in shape is “*Anatina*” *suborbicularis* Philippi, 1887 (p. 154, pl. 33, fig. 2). However, it is much higher and apparently the posterior end of the shell is less clearly defined and the posterior gape is much narrower than in *Offadesma isolatum* n. sp.

Other species of Periplomatidae from South America can not be compared with our material. They all fall within *Periploma* s.s. and their differences with *Offadesma* are readily clear. Such is the case of the extant species from the Caribbean and northern South America *Periploma* (*Periploma*) *coseli* Ardila & Díaz, 1998 (p. 69–71, Fig. 1–2, 5) and *Periploma* (*Periploma*) *sanctamarthaensis* Ardila & Díaz, 1998 (p. 72, Fig. 3–4, 6). These are missing the distinctive backward pointing chondrophore and the posterior rostrum of *Offadesma*, which are clearly visible on our specimens. Likewise, the west African record of this genus, i.e. *Periploma camerunensis* Cosel, 1995 (p. 102–110, figs. 144–145) is also very different from *Offadesma*, while it appears to be quite close to the Caribbean species.

Etymology: From the Latin *isolatum* = detached, separate, in allusion to its isolate occurrence from other records of the genus.

Offadesma sp.
Figures 11–13

Material: One specimen, partly decorticated and somewhat crushed (GHUNLPam26300).



Figures 11–13. *Offadesma* sp. (GHUNLPam26300) from Punta Beagle, province of Santa Cruz, southern Patagonia, Argentina, Monte Entrada Member of the Monte León Formation. Scale bar = 1 cm.

Occurrence: Punta Beagle, province of Santa Cruz, southern Patagonia, Argentina (49°57'S 68°41'W). The specimen was found within the Monte Entrada Member of the Monte León Formation, at the top of the exposure of this unit in Punta Beagle.

Remarks: The only specimen available is somewhat deformed and the margins too broken to allow proper description or even accurate comparisons with other taxa. However, what is visible of its hinge shows a chondrophore that leaves no doubt it is an *Offadesma*. It is smaller and slightly more rounded than *Offadesma isolatum* n. sp. from the Puerto Madryn Formation. The significance of this material lies in that it is the earliest record of the genus in South America.

BIOGEOGRAPHIC HISTORY OF *OFFADESMA*

The living species of *Offadesma* are restricted to Australia and New Zealand, while *Periploma* s.s. is known to occur along both coasts of the American continent (including the coast along northern Patagonia) and along the western coast of tropical Africa (Cosel, 1995). The presence of *Periploma* in Africa can be easily explained through passive dispersal of larvae across the Atlantic in an eastwards direction by means of the Equatorial Undercurrent or the Equatorial Countercurrent. The role of these marine currents in passive dispersal of larvae of different groups of mollusks in the tropical Atlantic Ocean has been discussed by Scheltema (1995). Morton

(1981a) assumed a short planktonic period for the larvae of *Offadesma*, based on the size of the eggs and comparisons with other anomalodesmatans. He even suggested that the eggs may be incubated in the ctenidia, although admitting that there is no evidence for this. While the larval development of this genus remains obscure and further research is needed to assess its role in the geographic distribution of its species, the evidence provided by the fossil record suggests that it was far more widespread earlier in the Cenozoic than at present. No larval stages are known for fossil forms, but it could be possible that with increasing specialization and concomitant occupation of narrower niches, a shortening in the duration of larval stages would ensure the rapid development crucial to ensure rapid colonisation of difficult environments.

In Patagonia, the family is represented by *Periploma ovatum* d'Orbigny, 1846 (p. 514, pl. 81, fig. 10–12) and *Periploma compressum* d'Orbigny, 1846 (p. 514, pl. 78, fig. 19–20), both ranging from (northern?) Brazil to northernmost Patagonia. As already stated, although all these species undoubtedly belong in *Periploma*, their shell characters show that they are unrelated to the Indo-Pacific *Offadesma* and thus to *Offadesma isolatum* n. sp. from the Puerto Madryn Formation. The two extant species from the southwestern Atlantic seem to be closely allied to the Caribbean taxa mentioned above. This leads to the presumption that the origin of the two living taxa must lie in a southward migration of Caribbean fauna as proposed by del Río (1991) and Martínez Chiappara &

del Río (2002). This migration would have been responsible for the development of the Valdesian and Paranaian Malacological Provinces (Martínez Chiappara & del Río, 2002) along the coasts of the southernmost tip of South America during the late Miocene. Although the southward flowing Brazil current could have played a role in the dispersal of larvae along the coast of South America, it was probably far more important in the establishment of appropriate ecological conditions for the settlement of species from warmer water. These species could have extended or restricted their southward range merely by occupying or vacating progressively warmer or colder areas at the southernmost extreme of their distribution as the influence of the Brazil Current varied with the evolving circulation pattern in the South Atlantic during the Cenozoic. The warmer conditions that enabled the development of the provinces proposed by Martínez Chiappara & del Río (2002) would have been caused—according to them—by a temporary blocking of the Antarctic Circumpolar Current (ACC) due to the appearance of the Scotia volcanic arc. This, together with the fact that the cold northwards-flowing Malvinas Current (MC) was not fully developed yet, would have been the main cause of the warming of the surface water in northern Patagonia. Nevertheless, Martínez Chiappara & del Río (2002) suggested that a proto-MC may have been to some extent already influencing the conditions in the area during the late Miocene, as indicated by the fossil content of some of the shell bearing beds in the Puerto Madryn Formation.

At any rate, some elements of the Miocene fauna from the Puerto Madryn Formation could possibly have originated elsewhere. It is well known that the opening of Drake Passage was crucial in the development of the present marine circulation pattern in the southern oceans. This opening probably occurred at the end of the Oligocene (23.5 ± 2.5 Ma; Barker & Burrell, 1977, 1982), although it could have been a long process beginning as far back as 37 Ma (Crame, 1999). The consequent onset of the ACC—and its intensification with the beginning of glaciation in West Antarctica just before the end of the Miocene (Kennet et al., 1975; Kennet, 1977; Kennet & von der Broch, 1985)—provided a gateway for the migration of many mollusk genera from New Zealand eastwards to South America and from South America eastwards to Australasia. Examples of such migrations are many (Beu & Griffin, 1996; Beu et al., 1997) and taxonomic work on the Patagonian faunas may prove that there are even more cases that have been overlooked. One of these could be the case of *Offadesma isolatum* n. sp. The rarity of this species due to its fragile shells and restricted habitat (Morton, 1981b) could explain why it has not been previously mentioned in the Patagonian fossil record. The affinities of the new species described herein seem to lie with Indo-Pacific taxa ranging back into the Paleogene. While yet unclear and possibly subject to change with further collection, the fossil record

and present distribution of *Offadesma* point towards a southern Indo-Pacific origin. Although the fossil record of this genus is very poor, its appearance in New Zealand as early as the Bortonian (late middle Eocene) appears to be consistent with its present distribution and the only discordant records are the early and late Miocene South American occurrences. While acknowledging its poor chances of preservation, the absence of *Offadesma* from Cenozoic rocks anywhere in North, Central or elsewhere in South America suggests that its presence in the early Miocene Monte León Formation and the late Miocene Puerto Madryn Formation is unlikely to be caused by its southern migration from warmer water further north along the Atlantic coast. More plausible seems to be its arrival in southern South America as a consequence of dispersal by means of the ACC. The fact that it appears earlier in New Zealand is consistent with the postulated Indo-Pacific origin of the genus. The chances of passive dispersal of larvae in an eastwards direction from New Zealand to South America—rather than from South America to New Zealand—would be enhanced by the shorter distances involved and the increased speed of the ACC during the Miocene. The distribution of some mollusks common to South America and New Zealand/Australia is still poorly understood. However, it may be possible that migration between both areas occurred repeatedly throughout the Cenozoic in both directions, even as recently as the late Pleistocene, when the bivalve *Anadara trapezia* suddenly appeared in New Zealand (OIS11) and Australia (OIS7), probably descending from a South American ancestor (Beu & Griffin, 1995; Beu et al., 1997; Murray-Wallace et al., 2000).

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Cretaceous *Acila* (*Truncacila*) (Bivalvia: Nuculidae) from the Pacific Slope of North America

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Abstract. The Cretaceous record of the nuculid bivalve *Acila* (*Truncacila*) Grant & Gale, 1931, is established for the first time in the region extending from the Queen Charlotte Islands, British Columbia, southward to Baja California, Mexico. Its record is represented by three previously named species, three new species, and one possible new species. The previously named species are reviewed and refined. The cumulative geologic range of all these species is Early Cretaceous (late Aptian) to Late Cretaceous (early late Maastrichtian), with the highest diversity (four species) occurring in the latest Campanian to early Maastrichtian. *Acila* (*T.*) *allisoni*, sp. nov., known only from upper Aptian strata of northern Baja California, Mexico, is one of the earliest confirmed records of this subgenus. “Aptian” reports of *Truncacila* in Tunisia, Morocco, and possibly eastern Venzeula need confirmation.

Specimens of the study area *Acila* are most abundant in sandy, shallow-marine deposits that accumulated under warm-water conditions. Possible deeper water occurrences need critical evaluation.

INTRODUCTION

This is the first detailed study of the Cretaceous record of the nuculid bivalve *Acila* H. Adams & A. Adams, 1858, in the region extending from the Queen Charlotte Islands, British Columbia, Canada southward to the northern part of Baja California, Mexico (Figure 1). Schenck (1936) did a detailed study of Cretaceous to Recent specimens of *Acila* from the Pacific slope of North America, but his emphasis was on Cenozoic species because they had been better collected, both as to number of specimens and stratotype placement. Schenck (1943) added more information about some Cretaceous species. In the last 60 years, knowledge of Pacific slope of North America Cretaceous stratigraphy has increased significantly, and much more collecting has been done. This present investigation, which greatly expands on Schenck’s work, is based on collections borrowed from all the major museums having extensive collections of Cretaceous fossils from the study area. We detected 122 lots (72 = LACMIP, 26 = CAS, 15 = UCMP, 9 = other), containing a total of 868 specimens of *Acila*. Our work establishes a documentable paleontologic record of *Truncacila* from late Aptian to early late Maastrichtian on the Pacific slope of North America (Figure 2), with the highest diversity (four species) occurring during the latest Campanian to early Maastrichtian.

Acila lives today in the marine waters of the Pacific

and Indo-Pacific regions and is a shallow-burrowing deposit feeder. Like other nuculids, it lacks siphons but has an anterior-to-posterior water current (Coan et al., 2000). It is unusual among nuculids, however, in that it commonly inhabits sandy bottoms. Although it does not have a streamlined shell, it is a moderately rapid burrower because of its relatively large foot (Stanley, 1970). *Acila* has a very distinctive divaricate ornamentation, and, although this type of ornamentation is uncommon among bivalves, it “shows widespread taxonomic distribution, brought about through adaptive convergence” (Stanley, 1970:65).

Recent *Acila* has a considerable tolerance for temperature ranges, from cold to tropical waters, but the greatest number of specimens comes from temperate waters (Schenck, 1936). One example of having this eurythermal adaptability is *Acila* (*Truncacila*) *castrensis* (Hinds, 1843), known to range from the cold waters of Kamchatka and the northeastern Bering Sea into the tropical waters of the Golfo de California, Baja California Sur, Mexico (Coan et al., 2000). Cretaceous *Acila* in the study area lived mostly during warm-ocean periods. The Aptian fauna of the Alisitos Formation of northern Baja California is wholly tropical in aspect. Warm-temperate water conditions existed during the Albian to Turonian in the study area. Some cooling took place from the Coniacian to early Maastrichtian, but the faunas that lived during



Figure 1. Index map showing locales mentioned in text. 1 = Skidegate Inlet, Queen Charlotte Islands. 2 = Hornby and Denman islands. 3 = Nanaimo area. 4 = Chemainus River and Saltspring Island areas. 5 = Mitchell and Antone areas. 6 = Phoenix. 7 = Yreka. 8 = Ono. 9 = Redding area. 10 = Chico Creek. 11 = Pentz. 12 = Sites. 13 = Franklin Canyon. 14 =

this time also contain warm-water elements. There was a warming trend during the late Maastrichtian (Saul, 1986a).

Recent *Acila* also has a considerable depth range, from below the intertidal zone (5 m) into the bathyal zone (400 m) (Schenck, 1936:34, fig. 10; Coan et al., 2000). There are many shallow-water marine occurrences of Cretaceous *Acila* in the study area (e.g., Alisitos Formation, Pentz Road member of the Chico Formation, and Jalama Formation), but deeper water occurrences are equivocal, largely because of lack of detailed depositional-environment studies on beds containing *Acila* specimens. Based on a survey of the literature, it seems that the Moreno Formation (see Stratigraphy) has the best potential of containing relatively deep-water occurrences of *Acila*, but detailed studies are needed to confirm this assertion.

Sundberg (1980, 1982) defined an *Inoceramus-Acila* paleocommunity, which included the bivalves *Propeamusium* and "*Parallelodon*," as well as the scaphopod *Dentalium*, that occupied most of the Holz Shale Member of the Ladd Formation, Santa Ana Mountains, Orange County, southern California. He believed that this paleocommunity probably existed in restricted lagoonal waters, at depths between 0 and 100 m. Almgren (1973), on the basis of benthic foraminifera, however, reported that the major part of the Holz was deposited in slope depths. Saul (1982), on the basis of gastropods and bivalves, reported that the lower Holz was deposited in middle to outer shelf depths and that the upper Holz was deposited in outer to shallow shelf depths.

The earliest documented records of *Acila* are *Acila (Truncacila) schencki* Stoyanow, 1949 [not *Acila schencki* Kuroda in Kira, 1954:83, 155–156, pl. 41, fig. 6], from the upper Aptian Pacheta Member of the Lowell Formation, southeastern Arizona and *Acila (Truncacila) allisoni*, sp. nov. from the upper Aptian, lower part of the Alisitos Formation, Baja California, Mexico.

Acila (T.) bivirgata (J. de C. Sowerby, 1836) is the name that has been most commonly applied to Aptian-Albian specimens of *Acila* found anywhere in the world. The type locality of Sowerby's species is in southeastern England, in rocks correlative to the lower Albian ammonite *Douvilleiceras mammilatum* Zone (Casey, 1961: 605). Schenck's (1936:35, 47) reports of *Acila (T.) bivirgata* in the Aptian of Tunisia and Morocco, the Aptian-Albian of eastern Venezuela (also see Schenck, 1935a), and the Albian of France and Morocco all need confir-

←
 Mount Diablo and Corral Hollow Creek. 15 = Garzas Creek. 16 = Charleston School Quadrangle area. 17 = Panoche. 18 = Lake Nacimiento. 19 = North Shale Hills. 20 = Jalama Creek. 21 = Simi Hills. 22 = Santa Ana Mountains. 23 = Carlsbad. 24 = Punta Banda. 25 = Punta China and Punta San Jose. 26 = San Antonio del Mar. 27 = Arroyo Santa Catarina.

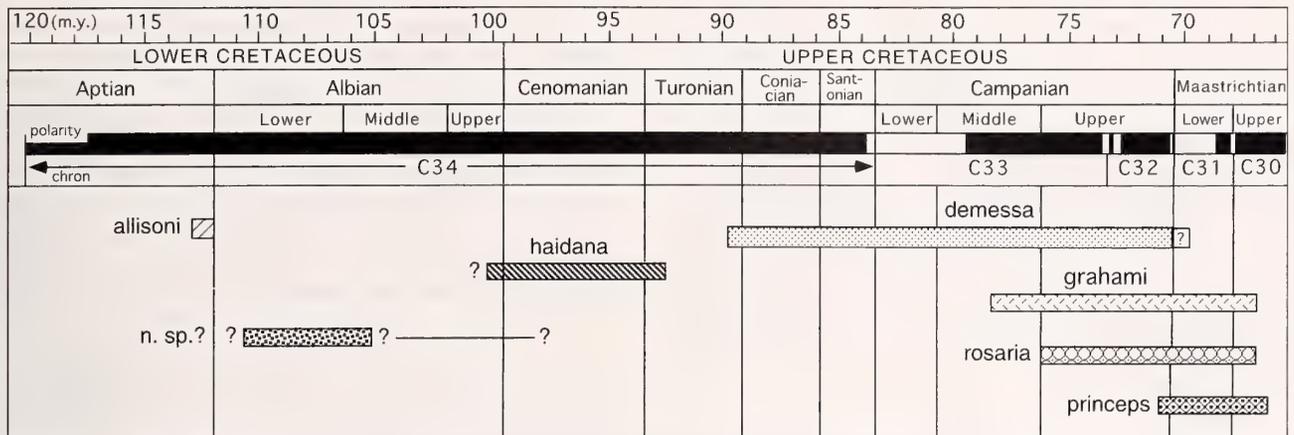


Figure 2. Chronostratigraphic positions of the new and restudied *Acila (Truncacila)* species. Geologic ages, geomagnetic polarities (black = normal, white = reversed), and chrons from Gradstein & Ogg (2004:fig. 2).

mation as to geologic age. Until this verification is done, global-migration routes of the earliest *Acila (Truncacila)* cannot be worked out.

Most of the study area specimens that have been mentioned in faunal lists or found in major museums have been identified as *Acila (Truncacila) demessa* Finlay, 1927, even though some of them belong to other species. Our study revealed that *A. (T.) demessa* ranges from late Turonian to late late Campanian and possibly early Maastrichtian, an interval of approximately 18 million years, thereby making it the longest ranging of the Cretaceous *Acila (Truncacila)* species in the study area. Such long ranges are not unusual for *Acila*; for example, *Acila (Truncacila) hokkaidoensis* (Nagao, 1932) from the Cretaceous Himenoura Group in Kyushu, Japan, ranges from Coniacian to Maastrichtian (Tashiro, 1976), an interval of approximately 19 million years.

Our study has refined also the geographic and stratigraphic ranges of the other two previously named study area species: *Acila (Truncacila) haidana* Packard in Schenck, 1936 and *Acila (Truncacila) princeps* Schenck, 1943. In addition, we discovered three new species and one possible new species.

Umbonal angle refers to the angle of divergence of the antero-umbonal and postero-umbonal surfaces, with the sides of the angle drawn to obtain maximum tangentiality with the valve surfaces. The umbonal-angle measurements were made from photographs of specimens. Although drawing the postero-umbonal part of the angle is easy because this surface is usually fairly straight, drawing the antero-umbonal part of the angle was usually subject to variation because this surface is usually convex. Chevron-angle measurements were also made using photographs of specimens, and measurements were taken near the point of divarication of the ribs, on approximately the medial part of the disk. It makes a significant difference where one measures this angle, because the

sides of the chevron angle becomes increasingly wider ventrally. In this study, the imaginary line bisecting the chevron angle is used as a reference point and referred to as a bisecting line.

In this study, shell size, rib width, and rib interspace width are all denoted by relative terms pertaining to subgenus *Truncacila* Grant & Gale, 1931. Rib width and rib interspace information, furthermore, pertain only to the area posterior to the line bisecting the chevrons on the disk area of adult specimens. Umbo and ventral margin areas posterior of the bisecting line are excluded. In the case of multiple chevrons, the rib-width and rib-interspace information pertain to the area posterior of the line bisecting the posteriormost chevron.

The suprageneric classification system used here follows that of Coan et al. (2000). Abbreviations used for catalog and locality numbers are: ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; GSC, Geological Society of Canada, Ottawa; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; LSJU, Stanford University, California (collections now housed at CAS); RBCM, Royal British Columbia Museum, Victoria; UCMP, University of California Museum of Paleontology, Berkeley; UO, University of Oregon, Eugene.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

The geologic ages and depositional environments of most of the formations and members cited in this paper have been summarized by Squires & Saul (2001, 2003a, b, c, d, 2004a, b). Stratigraphic and depositional-environment information mentioned below concerns those rock units not discussed in recent literature. The stratigraphic units are listed from oldest to youngest.

Hudspeth Formation

This formation crops out in the Mitchell area, Wheeler County, northeast-central Oregon (Figure 1, locale 5) and consists mainly of marine mudstone (Wilkinson & Oles, 1968). The type locality of *Acila (T.)* sp. nov.? plots on the geologic map of Wilkinson & Oles (1968:fig. 1) in the lower part of the "Main Mudstone member" of the Hudspeth Formation. Based on ammonites, Wilkinson & Oles (1968) reported the age of this part of the formation to be early or early middle Albian. There have been no detailed studies of the depositional environments of this formation.

Haida Formation

This formation crops out in the central part of the Queen Charlotte Islands, northern British Columbia (Figure 1, locale 1) and consists of two members, which accumulated as part of the same transgression event. The two members, a nearshore sandstone member and an overlying mostly outer shelf shale member, are laterally equivalent and interfinger. Storm deposits, which characterize the sandstone member, are also found in the shale member and are represented by fine- to medium-grained sandstone with associated shell lags (McLearn, 1972; Haggart, 1991a). The type locality of *Acila (Truncacila) haidana* Packard in Schenck, 1936, was reported to be a beach-cliff exposure of the Haida Formation, and utilizing the geologic map of Haggart (1991a:fig. 3), this exposure would seem to plot in the shale member. Schenck's (1936:51) description of the type locality "about 1 mile east of Queen Charlotte City," however, is not precise and could refer to outcrops in either the shale member or the sandstone member, depending on if one uses as a starting point the old hotel or the current post office in Queen Charlotte City, respectively (J. Haggart, personal communication). No *Acila* has been found by recent collecting in the sandstone member, and, consequently, Schenck's material probably came from the lower part of the shale member (J. Haggart, personal communication). The type specimens of *A. (T.) haidana* occur in fine-grained sandstone, and the holotype consists of conjoined valves. If these type specimens are part of a storm lag, then the amount of post-mortem transport was not great. All indications are that these specimens probably lived in a transitional nearshore to slightly deeper environment. This would be in keeping with the shallow-water environments of localities in the study area at which additional specimens of this species are found.

The sandstone member of the Haida Formation is Albian in age, based on a rich assemblage of ammonites (McLearn, 1972), and the shale member ranges from latest Albian to Cenomanian to early Turonian in age, based on scarce remains of inoceramid bivalves (McLearn, 1972; Haggart, 1987, 1991a). The exposures at the type locality of *A. (T.) haidana*, however, are probably latest

Albian to Cenomanian (J. Haggart, personal communication).

The Queen Charlotte Islands and Vancouver Island, which is mentioned later in this paper, are parts of an amalgamated sequence of tectonic terranes, collectively called the Insular Superterrane, whose accretional history is currently in dispute. Two mutually contradictory hypotheses deal with this accretionary history, and both have been summarized by Cowan et al. (1997) and Ward et al. (1997). One hypothesis suggests that the Insular Superterrane was already in place in its current position (more or less) relative to western North America by the Cretaceous and perhaps earlier. The second hypothesis, known as the "Baja BC hypotheses," suggests that the superterrane was situated 3000 km south of its present position. Kodama & Ward (2001), using paleomagnetic paleolatitudinal distribution of bivalve rudists, suggested that Baja BC was no farther south than 40°N (i.e., northern California) in the Late Cretaceous. The distribution of *Acila (T.) haidana* supports the contention that the Insular Superterrane was not any farther south than northern California during the Cretaceous, because besides being found in the Haida Formation, this species is only known elsewhere from southern Oregon and northern California.

Upper Cedar District Formation, West Shoreline of Denman Island

Both *A. (T.) demessa* and *A. (Truncacila) grahami*, sp. nov., occur in mudstone exposed in an intertidal bench at Locality 4 on the west-central shoreline of Denman Island, off the east coast of Vancouver Island, British Columbia (Figure 1, locale 2). The latest geologic map of this island shows these exposures to be part of the Cedar District Formation of the Nanaimo Group (Katnick & Mustard, 2001). Mustard et al. (2003) reported that this formation along the west side of Denman Island consists of proximal-turbidite deposits in lower and middle submarine-fan complexes. Mustard (1994:table A6) reported that megafossils found in these turbidite deposits include resedimented shallow-water taxa. All the acilid specimens collected from Locality 4 are single valves, and although this suggests that they might have been resedimented, taphonomic studies are needed.

Mustard et al. (2003:127) reported that molluscan fossils found locally in the Cedar District Formation on the west side of Denman Island indicate a late Campanian age. Mollusks found at Locality 4 include the ammonites *Metaplacenticeras* cf. *pacificum* (Smith, 1900) and *Desmophyllites diphyloides* (Forbes, 1846). The *Metaplacenticeras pacificum* biozone is of late middle to early late Campanian age (Elder & Saul, 1996:fig. 1), and the geologic range of *D. diphyloides* is "relatively long, covering most of the Campanian" (Matsumoto, 1959:10). The Cedar District Formation ranges in age from early to middle late Campanian (Jeletzky, 1970; Ward, 1978;

Haggart, 1991b), therefore, the strata at Locality 4 belong to the upper part of this formation. Enkin et al. (2001: figs. 3, 4) took paleomagnetic samples from the immediate vicinity of Locality 4 and determined that these samples represent sediments deposited sometime during the 33 N (normal) polarity interval, which is equivalent to the middle to early late Campanian (see Figure 2). Based on the molluscan and paleomagnetic data, therefore, the age of the fossils at Locality 4 can be assigned a late middle to early late Campanian age.

Moonlight Formation?

A few specimens of *Acila* spp. were detected in two collections made from muddy siltstones exposed in a small area on the north side of Shale Hills, southwest side of Antelope Valley, eastern Tumbler Range, Kern County, south-central California (Figure 1, locale 19). CAS loc. 1552 yielded a specimen of *Acila* (*Truncacila*) *rosaria*, sp. nov., and a specimen of *A. (T.) grahami*. CAS loc. 69095 yielded another specimen of *Acila (T.) rosaria*. These muddy siltstones were mapped by English (1921: pl. 1), who described them as being a soft clay shale. They are most likely correlative to the shallow-marine siltstone facies of the Moonlight Formation, which crops out on the other side of Antelope Valley (Marsh, 1960: pl. 1). This facies, which is soft and clayey, closely resembles the rocks described by English. Matsumoto (1959:11; 1960:63) noted that the ammonite *Baculites rex* Anderson, 1958, is found at CAS loc. 1552, and this biozone is early late Campanian in age (Elder & Saul, 1996: fig. 1).

Northumberland Formation at Collishaw Point, North End of Hornby Island

The type locality of *Acila (T.) grahami* occurs in mudstone exposed in an intertidal bench at Locality 3 at Collishaw Point, north end of Hornby Island, off the east coast of Vancouver Island, British Columbia (Figure 1, locale 2). The latest geologic work done on the Collishaw Point outcrops is that of Katnick & Mustard (2001, 2003) and Mustard et al. (2003). These workers assigned the mudstone in question to the Northumberland Formation of the Nanaimo Group. In Mustard et al. (2003:figs. 23, 24), Collishaw Point is also mentioned as a field-trip stop, and reports dealing with the fossils (including ammonites, inoceramids, and shark teeth) from this locale have been summarized by these authors. The beds there consist of silty mudstones intercalated with less common sandstone beds of turbidite origin. The *A. (T.) grahami* material is from a "thin lens of what appears to be a debris flow containing abundant shell fragments, numerous and diverse shark teeth, and rare bird bones" (R. Graham, personal commun.). No studies have been done yet on the depositional environment or of the taphonomy of the fossils found in this particular lens. All the specimens of *A.*

(*T.*) *grahami* are single valves, and they appear to be unabraded.

In spite of the presence of ammonites and inoceramids in the beds at Collishaw Point, there is no consensus on the age of these beds. As summarized by Mustard et al. (2003), the age has been variously reported as either latest Campanian or early Maastrichtian, and further work is needed to resolve this age disagreement.

As mentioned under the discussion of the Haida Formation, the amount of tectonic displacement that Vancouver Island (which is part of the Insular Superterrane) has undergone is controversial. As summarized by Enkin et al. (2001), sedimentologic and paleontological evidence, as well as some paleomagnetic studies (Kodama & Ward, 2001), indicate that the Nanaimo Group of Vancouver Island was deposited near its present northern position, whereas other paleomagnetic studies indicate that these sediments were deposited near the modern-day location of Baja California (Enkin et al., 2001).

Moreno Formation

This formation crops out along the western side of the San Joaquin Valley, central California (Figure 1, locales 15 and 16) and is a clastic sedimentary sequence that records the shoaling of the central San Joaquin basin from deep water to shelf depths. The formation, which is time-transgressive (Saul, 1983), consists of four members that span an interval from the Maastrichtian through early Danian (Paleocene) (McGuire, 1988). Members relevant to this report are the Tierra Loma and the supradjacent Marca Shale; both are discussed below.

Tierra Loma Member

This member, which crops out south of Los Banos, southwestern Merced County, California, consists mainly of muddy siltstones and turbidites containing irregularly interbedded, channelized sandstones (McGuire, 1988). One of these channelized sandstones, approximately in the middle of the Tierra Loma Member, was referred to by Schenck (1943) and Payne (1951) as the Mercy sandstone lentil. The type locality of *A. (T.) princeps* occurs within this lentil, and this locality was plotted on geologic maps by Schenck (1943:fig. 1) and by Payne (1951:fig. 2).

Acila (T.) rosaria also occurs in the Tierra Loma Member, and deposition of this member took place in an oxygen-deficient, lower to upper slope environment (McGuire, 1988). Specimens of this bivalve occur as a few single valves. Detailed work is needed to determine if these specimens are in situ or have undergone post-mortem transport from a shallower water environment.

Saul (1983) and Squires & Saul (2003a) discussed the geologic age of the Tierra Loma Member, which is late early to early late Maastrichtian age, based on turritelas, bivalves, and ammonites.

Marca Shale Member

This member crops out for a distance of approximately 20 km (in northwestern Fresno County) southward of where the Mercy sandstone lentil (see above) lenses out. The Marca Shale Member gradationally overlies the Tierra Loma Member and consists of 80 to 95 m of finely laminated siliceous shale and diatomaceous shale that accumulated in a gently inclined, upper slope environment under intense anoxic conditions associated with an upwelling system (McGuire, 1988). According to Payne (1951), at the top and bottom of this member, there are white, hard, calcareous concretions containing a few poorly preserved megafossils. A few specimens of *Acila* (*T.*) *grahami* have been collected from the Marca Shale Member. Only one specimen (Figure 32) is conjoined, and it is in a matrix of diatomaceous shale. It is unlikely that this specimen underwent any post-mortem transport by means of a turbidity current, because, according to McGuire (1988), there is a complete absence of any sandstone or other coarse terrigenous sediment in the Marca lentil. This absence indicates that the slope environment on which this unit accumulated was isolated from the source(s) of sands found in all other members of the Moreno Formation.

According to Saul (1983:fig. 10), the Marca Shale contains the ammonite *Trachybaulites columna* (Morton, 1834). This ammonite, which is an intracontinental zonal indicator of late early to early late Maastrichtian age (Cobban & Kennedy, 1995), also occurs in the underlying Tierra Loma Shale (see Squires & Saul, 2003b). Although the age of the Marca Shale is approximately the same age as that of the Tierra Loma Member, the Marca Shale is slightly younger because of its stratigraphic position.

Panoche Formation at Franklin Canyon

This formation crops out in Franklin Canyon in the Franklin Ridge area (Dibblee, 1980) just west of Martinez, Contra Costa County, northern California (Figure 1, locale 13). Weaver (1953) provided a faunal list of mollusks found in these rocks, and at a few localities he listed "*Acila* (*T.*) *demessa*" in association with the bivalve *Meekia sella* Gabb, 1864. Saul (1983:fig. 4) showed *Meekia sella* to range from early to late Maastrichtian (67 Ma), but not into the latest Maastrichtian. The only specimen of *Acila* we were able to find in any museum collection that was derived from this area was Schenck's (1943) specimen (hypotype CAS 69086.02) of *Acila* sp. D. This specimen is identified herein as *A. (T.) princeps* and is illustrated in Figure 46.

El Piojo Formation

This formation crops out in the vicinity of Lake Nacimiento, San Luis Obispo County, west-central California (Figure 1, locale 18) and consists mainly of sandstone

(Seiders, 1989). No detailed depositional-environment studies have been done on this formation. Although molluscan fossils are uncommon in this formation, Saul (1986b) studied the mollusks from LACMIP loc. 30141 and reported them to be of early late Maastrichtian age, including a single specimen of *Acila* sp. Additional cleaning of this specimen revealed it to be *Acila* (*Truncacila*) *princeps*.

Deer Valley Formation

Two specimens of *Acila* (*Truncacila*) *princeps* were detected in the LACMIP collection from very fine-grained sandstone in Deer Valley on the north flank of Mount Diablo, Contra Costa County, northern California (Figure 1, locale 14). This sandstone is in Colburn's (1964) informal Deer Valley formation, which, according to him, was deposited in a nearshore, above wave base, open-ocean environment. Colburn (1964) also mentioned the presence of *A. (T.) princeps* in this formation. Based on the presence of the bivalves *Meekia sella* Gabb, 1864, and *Calva* (*Calva*) *varians* (Gabb, 1864), this sandstone can be assigned to the upper Maastrichtian (Saul & Popenoe, 1962, 1992).

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Linnaeus, 1758

Class BIVALVIA Linnaeus, 1758

Order NUCULOIDEA Dall, 1889

Superfamily NUCULOIDEA J. E. Gray, 1824

Family NUCULIDAE J. E. Gray, 1824

Genus *Acila* H. Adams & A. Adams, 1858

Type species: *Nucula divaricata* Hinds, 1843, by subsequent designation (Stolickza, 1871); Recent, China.

Discussion: Like other nukulids, *Acila* has a posteriorly truncate, nacreous shell with opisthogyrate beaks, and an internal ligament in a resilifer. Three subgenera have been named: *Acila* sensu stricto, which ranges from Oligocene to Recent (Keen, 1969); *Lacia* Slodkevich, 1967, which ranges from late Eocene to late Pliocene (Slodkevich, 1967); and *Truncacila* Grant & Gale, 1931, which ranges from Early Cretaceous (late Aptian) to Recent (Schenck, 1936). *Acila* s.s. is characterized by large size, well-defined rostral sinus, a rostrate (protruding) posterior end, and strong divaricate ornamentation (Schenck, 1935b; Keen, 1969; Slodkevich, 1967; Addicott, 1976; Coan et al., 2000). *Lacia* is characterized by a very poorly defined rostral sinus. The characteristics of *Truncacila* are mentioned below.

Table 1

Check list of key morphologic characters used in differentiating the studied species.

Species	Shell size	#Ribs/ valve (approx.)	Divarication on venter	Other*
<i>allisoni</i>	small	55	central	roundly subquadrate; ribs very narrow, interspaces approximately $\frac{1}{3}$ as wide; escutcheonal ribs continuous with ribs on disk
n. sp.?	medium	55	anterior	quadrate; ribs narrow, interspaces approximately $\frac{1}{3}$ as wide
<i>haidana</i>	medium	40	usually central	usually subquadrate; ribs very narrow to narrow, interspaces $\frac{1}{3}$ approximately $\frac{1}{3}$ as wide to same width as ribs
<i>demessa</i>	medium	70	anterior	ribs flat and very narrow to moderately wide, interspaces approximately $\frac{1}{5}$ to $\frac{1}{2}$ as wide; escutcheonal area bounded by smooth groove
<i>grahami</i>	small	50	usually anterior	can be trigonal; ribs narrow to moderately wide, interspaces approximately $\frac{1}{3}$ to $\frac{1}{2}$ as wide; escutcheonal ribs continuous with ribs on disk
<i>rosaria</i>	medium	80	anterior	shell weakly rostrate postero-ventrally; ribs very narrow to narrow, interspaces approximately $\frac{1}{4}$ as wide to same width as ribs; escutcheon bounded by flattish to shallowly grooved area usually crossed by ribs not continuous with ribs on disk
<i>princeps</i>	large	85	anterior	subquadrate, rarely trigonal; ribs flat and narrow to wide, interspaces approximately $\frac{1}{5}$ to $\frac{1}{4}$ as wide

* Rib and interspace information pertains only to the area posterior to chevron-bisecting line on adult specimens; umbo and ventral-margin regions are excluded.

Subgenus *Truncacila* Grant & Gale, 1931

Type species: *Nucula castrensis* Hinds, 1843, by original designation; Pliocene to Recent, northeastern Pacific.

Discussion: *Truncacila* is characterized by small size, relative to other acilids, and an absence of a rostral sinus (Slodkevich, 1967; Coan et al., 2000). Although *Truncacila* has been reported as lacking a rostrate posterior end (Slodkevich, 1967; Coan et al., 2000), it can have a small rostration at the point of meeting of the ventral and posterior margins (Stoyanow, 1949:62). *Acila* (*T.*) *rosaria* has such a rostration. So do some of the subquadrate forms of *A.* (*T.*) *demessa* and *A.* (*T.*) *grahami*, as well as the best preserved specimens of *A.* (*T.*) *princeps*.

The key characters of the studied species are given in Table 1.

Acila (*Truncacila*) *allisoni* Squires & Saul, sp. nov.

(Figures 3–8)

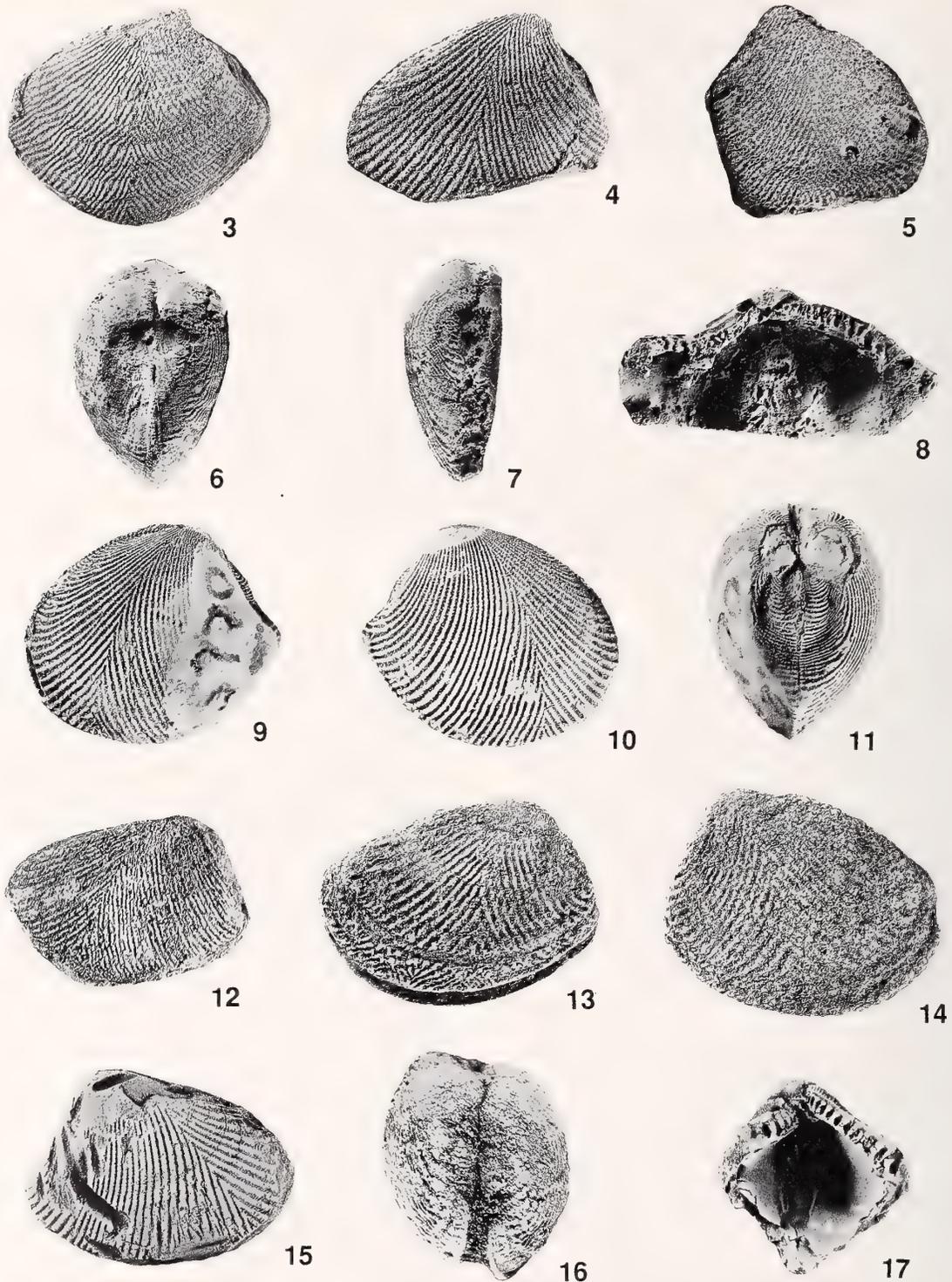
Acila (*Truncacila*) *bivirgata* (Sowerby). Allison, 1974: tables 4, 6, 7.

Not *Acila* (*Truncacila*) *bivirgata* (J. de C. Sowerby, 1836: 335, pl. 11, fig. 8).

Diagnosis: Shell small, roundly subquadrate. Chevrons bisected by line meeting center of ventral margin. Total number of ribs on disk of each valve approximately 55; ribs (posterior of chevron-bisecting line) very narrow, with interspaces approximately $\frac{1}{3}$ as wide. Escutcheonal ribs continuous with ribs on disk.

Description: Shell small for subgenus (up to 12.1 mm in height and 15.5 mm in length), longer than high, height/length ratio = 0.78. Roundly subquadrate, inequilateral, equivalved, valves moderately inflated. Anterior end broadly rounded. Antero-dorsal margin long and straight. Posterior margin truncate and set off from escutcheon by moderately strong rostration. Ventral margin convex. Umbones low, located posteriorly; umbonal angle 98 to 116°. Beaks pointed, incurved, opisthogyrate. Disk broad, ornamented with abundant ribs diverging from umbo area and forming chevron-shaped (divaricate) pattern. Chevron angle 38 to 47°. Chevrons bisected by line extending from slightly anterior of umbo to center of ventral margin; ribs anterior to bisecting line 23 to 34; ribs posterior to bisecting line 24 to 33 (excluding occasional short bifurcations near ventral margin). Total number of ribs on disk of each valve usually approximately 55; ribs very narrow with interspaces approximately $\frac{1}{3}$ as wide, except anterior of chevron-bisecting line, where ribs become slightly wider, occasionally wavy, and more widely spaced. Growth checks irregularly spaced from medial part of disk to ventral margin. Escutcheon moderately prominent, slightly sunken, and bounded by shallow groove crossed by very narrow ribs continuous with ribs on disk; ribs stronger (approximately same strength as those on disk) on elevated central part of escutcheonal area. Hinge with at least 14 anterior taxodont teeth and 11 posterior taxodont teeth. Resilifer opisthocline, narrow.

Dimensions of holotype: Conjoined valves (partial right



Explanation of Figures 3 to 17

Figures 3-8. *Acila (Truncacila) allisoni* Squires & Saul, sp. nov., rubber peels. Figure 3. Holotype UCMP 154232, UCMP loc. B-5665, left valve, $\times 2.8$. Figure 4. Paratype UCMP 154233, UCMP loc. B-5665, left valve, $\times 3.2$. Figure 5. Paratype UCMP 154234, UCMP loc. A-6275, right valve, $\times 2.8$. Figure 6. Holotype UCMP 154232, UCMP loc. B-5665, posterior view, $\times 3$. Figure 7. Paratype UCMP 154233, UCMP loc. B-5665, posterior view of

valve), height 12.1 mm, length 15.5 mm (incomplete), thickness 7.8 mm (approximate).

Holotype: UCMP 154232.

Type locality: UCMP B-5665, near Punta China, Baja California, Mexico, 31°30'N, 116°40'W.

Paratypes: UCMP 154233, 154234, 154235.

Geologic age: Late Aptian.

Distribution: Alisitos Formation, Baja California, Mexico.

Discussion: The above description of the new species is based on eight rubber peels: one left valve, three right valves, two with conjoined valves, and two partial hinges.

The new species is most similar to *Acila (Truncacila) bivirgata* (J. de C. Sowerby, 1836:335, pl. 11, fig. 8) from upper Aptian strata of England. The similarity is close enough for Allison (1974) to have identified as Sowerby's species specimens from the Alisitos Formation. Illustrations (Figures 9–11) of *A. (T.) bivirgata* are herein provided for comparison, and this is the same specimen used in Schenck (1936:47, pl. 2, figs. 1, 2). The new species differs from *A. (T.) bivirgata* by having the line bisecting the chevrons located nearer the center of the ventral margin, slightly wider ribs, narrower interspaces, and a less sunken escutcheon.

The new species differs from *Acila (T.) schencki* Stoyanow (1949:61–63, pl. 8, figs. 1–8), the only other Aptian acilid known from western North America, by having more numerous and narrower ribs (especially on the anterior half of the disk), no tendency for the line bisecting the chevrons to be slightly anterior of the center of the ventral margin, and an absence of strong curvature dorsally of the ribs near the anterior edge of the disk.

Etymology: Named for the late E. C. Allison, in recognition of his extensive collecting of mollusks from the Alisitos Formation.

Acila (Truncacila), sp. nov.?

(Figure 12)

Acila (Truncacila) sp. A. Schenck, 1936:51, pl. 2, fig. 13.

Diagnosis: Shell medium, quadrate. Chevrons bisected by line meeting ventral margin near meeting of anterior

end and ventral margin. Total number of ribs on disk of left valve approximately 55; ribs (posterior of chevron-bisecting line) narrow, with interspaces approximately $\frac{1}{3}$ as wide.

Description: Shell medium for subgenus (14.2 mm in height and 21.2 mm in length), longer than high, height/length ratio = 0.67. Quadrate, inequilateral, equivalved, valves moderately inflated. Anterior end broadly rounded. Antero-dorsal margin long and straight, generally parallel to ventral margin. Posterior end straight, truncate. Umbones low, located posteriorly; umbonal angle 100°. Disk broad, ornamented with abundant ribs diverging from umbo area and forming chevron-shaped (divaricate) pattern. Chevron angle 55°. Chevrons bisected by line extending from slightly anterior of umbo to point located near where anterior end and ventral margins meet; ribs anterior to bisecting line about 21; ribs posterior to bisecting line about 34 (excluding occasional short bifurcations near ventral margin). Total number of ribs on disk usually approximately 55; ribs narrow with interspaces approximately $\frac{1}{3}$ as wide, except anterior of chevron-bisecting line, where ribs become more widely spaced.

Geologic age: Early Albian or early middle Albian, possibly Cenomanian.

Distribution: POSSIBLY LOWER ALBIAN: Budden Canyon Formation, upper lower Chickabally Mudstone Member, Ono area, Shasta County, northern California. LOWER ALBIAN OR LOWER MIDDLE ALBIAN: Hudspeth Formation, lower part of "Main Mudstone member," near Mitchell, Wheeler County, northeast-central Oregon. POSSIBLY CENOMANIAN: Unnamed strata, near Antone, Wheeler County, northeast-central Oregon.

Discussion: The possible new species is known only from a single specimen (hypotype CAS 69097 = UO 6000), a left valve (height 14.2 mm, length 21.2 mm), the posterior end of which is not preserved. This hypotype is the only moderately well preserved specimen of *Acila* of Albian age known from the study area. It is likely that this species is new, but until more specimens are discovered, we are reluctant to name it.

A possible record of *A. (T.)* sp. nov.? is a latex peel of a fragment from CAS loc. 69110 in the upper lower Chickabally Mudstone Member of the Budden Canyon

←

left valve, $\times 4$. Figure 8. Paratype UCMP 154235, UCMP loc. A-6275, right-valve hinge, $\times 3.7$. Figures 9–11. *Acila (Truncacila) bivirgata* (J. de C. Sowerby, 1836), CAS hypotype 5770, Gault Formation, Folkestone, England, $\times 3.7$. Figure 9. Left valve. Figure 10. Right valve. Figure 11. Posterior view. Figure 12. *Acila (Truncacila)* sp. nov.?, hypotype CAS 69087, UO loc. 461, left valve, $\times 1.8$. Figures 13–17. *Acila (Truncacila) haidana* Packard in Schenck, 1936, CAS loc. 69080. Figure 13. Holotype CAS 69081, left valve, $\times 3$. Figure 14. Paratype CAS 69080.01, left valve, $\times 2.8$. Figure 15. Hypotype LACMIP 13227, LACMIP loc. 24365, right valve, $\times 3.4$. Figure 16. Holotype CAS 69081, posterior view, $\times 3$. Figure 17. Hypotype CAS 69106.03, LACMIP loc. 23950, partial right-valve hinge, $\times 4.8$.

Formation in the Huling Creek area, southwest of Redding, Shasta County, northern California. Jones et al. (1965) assigned these rocks to the early Albian. Another possible record of *A. (T.)* sp. nov.? is a plastic replica of a partial specimen from unnamed strata at UCMP loc. 814 south of Antone, between Rock Creek and Spanish Gulch, Wheeler County, northeast-central Oregon. Popenoe et al., (1960:column 54 of chart 10e) assigned rocks from this area to the Cenomanian.

Acila (T.) sp. nov.? is similar to *A. (T.) rosaria* but differs by having a truncate posterior end, usually slightly wider ribs, and slightly wider spaced ribs. *Acila (T.)* sp. nov.? is somewhat similar to *A. (T.) allisoni* but differs by having a larger size, more widely spaced ribs that are never wavy, uniform-rib strength over the entire disk, and chevrons bisected by a line located anterior of center of ventral margin.

Acila (Truncacila) haidana Packard
in Schenck, 1936 .

(Figures 13–17)

Acila (Truncacila) demessa Finlay, var. *haidana* Packard in Schenck, 1936:50–51, pl. 2, figs. 3, 4, 6, 10.

?*Nucula (Acila) truncata* Gabb. Whiteaves, 1884:232.

Diagnosis: Shell small, subquadrate (usually) to elliptical. Chevrons bisected by line usually meeting center of ventral margin (rarely to anterior of center). Total number of ribs on disk of each valve approximately 40; ribs (posterior of chevron-bisecting line) very narrow to narrow, with interspaces $\frac{1}{2}$ as wide to same width as ribs.

Description: Shell small for subgenus (up 14.4 mm in height and 16.7 mm in length), longer than high, height/length ratio = 0.73 to 0.86. Subquadrate (usually) to elliptical, inequilateral, equivalved, valves moderately inflated. Antero-dorsal margin long, straight to lowly convex. Posterior end truncate and set off from escutcheon by weak rostration. Ventral margin convex. Umbones low, located posteriorly; umbonal angle 101 to 116°. Beaks pointed, opisthogyrate. Disk broad, ornamented with abundant ribs diverging from umbo area and forming chevron-shaped (divaricate) pattern. Chevron angle 46 to 59°. Chevrons bisected by line extending from slightly anterior of umbo to center (rarely anterior) of ventral margin; ribs anterior to bisecting line 18 to 20, ribs posterior to bisecting line about 20 to 28. Secondary divarication rare, only on specimens with anteriorly located divarication. Total number of ribs on disk of each valve usually approximately 40; ribs very narrow to narrow, with interspaces approximately $\frac{1}{2}$ as wide to same width as ribs, except anterior of chevron-bisecting line, where ribs become wider and more widely spaced. Growth checks near ventral margin or absent. Escutcheon moderately prominent, slightly sunken, and crossed by narrow ribs. Hinge with at least 18 anterior taxodont teeth

and, at least, six posterior taxodont teeth. Resilifer opisthocline, narrow.

Dimensions of holotype: Conjoined valves (partially open), height 11.5 mm, length 15.7 mm, thickness 9 mm (taking into account the partial opening).

Holotype: CAS 69081 [= CAS 5090].

Type locality: CAS 69080, just east of Queen Charlotte City, Bearskin Bay, Skidegate Inlet region, Queen Charlotte Islands, British Columbia.

Paratypes: CAS 69080.01 [= CAS 5091] and CAS 69080.02 [= CAS 5092].

Geologic age: Latest Albian (probably) to early Turonian.

Distribution: UPPERMOST ALBIAN (PROBABLY) TO CENOMANIAN: Haida Formation, just east of Queen Charlotte City, Bearskin Bay, Skidegate Inlet region, Queen Charlotte Islands, northern British Columbia. LOWER TURONIAN: Hornbrook Formation, Osburger Gulch Member, Jackson County, southern Oregon; Redding Formation, Frazier Siltstone, Shasta County, northern California; Cortina formation (informal), Venado Sandstone Member, near Sites, Colusa County, northern California; Panoche Formation, Garzas Creek, Stanislaus County, north-central California.

Discussion: The above description of this species is based on eight specimens: one left valve, six right valves, and one with conjoined valves. The escutcheon area is poorly preserved on all of these specimens.

Whiteaves (1884:232) reported one specimen of *Nucula (Acila) truncata* Gabb, 1864, from the type locality area of *A. (T.) haidana* and one specimen from the vicinity of Alliford Bay, also in the Skidegate Inlet region, Queen Charlotte Islands. Whiteaves, unfortunately, did not figure these specimens, nor could they be located by us in any museum collection. Based on their geographic occurrence, however, it is most likely that they are *A. (T.) haidana*.

Schenck (1936:50) included tentatively “?*Nucula (Acila) truncata* Gabb. Whiteaves, 1879:162; 1903:389–390,” in his synonymy of *A. (T.) haidana*, but Whiteaves reported that these specimens were collected at localities on 1) the northwest side of Hornby Island, 2) the southwest side of Denman Island, Vancouver Island, and 3) Sucia Island, Washington. All of these localities occur in the Nanaimo Group. Both *A. (T.) demessa* and *A. (T.) grahami* are herein recognized from this group, but *A. (T.) haidana* is not. It does not seem likely, therefore, that these Nanaimo Group specimens of Whiteaves (1879, 1903) should be identified as *A. (T.) haidana*. Whiteaves, furthermore, provided no type numbers and no illustrations of these specimens. In addition, Bolton (1965) did not list type numbers from them. Additionally, none of them is part of the GSC collection.

One specimen of *Acila (T.) haidana* is from USGS loc. M-175 near Sites, Colusa County, northern California. Although this locality is usually reported as being in the upper part of the Cenomanian Antelope Shale, Popenoe et al. (1987:79) reported that some of the fossils at this particular locality probably slumped from the overlying basal Venado Formation of early Turonian age. We concur, based on the presence of the following Turonian gastropods found with the *Acila (T.) haidana* specimen: *Gyrodes (?Sohlella) yolensis* Popenoe et al., 1987 and *Gyrodes (Gyrodes) dowelli* White, 1889.

Acila (Truncacila) demessa Finlay, 1927

(Figures 18–26)

Nucula truncata Gabb, 1864:198, pl. 26, figs. 184, 184a, 184b.

not *Nucula truncata* Nilsson, 1827:16, pl. 5, fig. 6.

Acila demessa Finlay, 1927:522 (new name for *Nucula truncata* Gabb, not Nilsson); Stewart, 1930:45, pl. 3, fig. 6.

Acila (Truncacila) demessa Finlay. Schenck, 1936:48–50, pl. 2, figs. 5, 7, 8, 9, text-fig. 7; 1943:pl. 8, fig. 5; pl. 9, figs. 1, 3, 7.

Acila shumardi Dall. Ludvigsen & Beard, 1994:90, fig. 54 (in part); 1997:110, fig. 65 (in part).

?*Nucula (Acila) truncata* Gabb. Whiteaves, 1879:162 (in part); 1903:389–390 (in part).

Diagnosis: Shell medium, subtrigonal to subquadrate. Chevrons bisected by line meeting ventral-margin anterior. Total number of ribs on disk of each valve approximately 70; ribs (posterior of chevron-bisecting line) flat and very narrow to moderately wide, with interspaces approximately $\frac{1}{5}$ to $\frac{1}{3}$ as wide. Escutcheon bounded by smooth area not crossed by ribs.

Description: Shell medium for subgenus (up to 20.4 mm in height and 26.5 mm in length, most specimens approximately 13 mm in height and 16 mm in length), longer than high, height/length ratio = 0.72 to 0.89. Subtrigonal to subquadrate; inequilateral, equivalved, valves moderately inflated. Anterior end broadly rounded. Antero-dorsal margin long, straight to convex. Posterior end straight, abruptly truncate and set off from escutcheon by weak rostration. Ventral margin convex. Umbones low, located posteriorly; umbonal angle 103 to 117°. Beaks pointed, incurved, opisthogyrate. Disk very broad, ornamented with abundant ribs diverging from umbo area and forming chevron-shaped (divaricate) pattern. Chevron angle approximately 30 to 34°. Secondary development of chevrons on few specimens. Chevrons bisected by line extending from slightly anterior of umbo to center of ventral margin; ribs anterior to bisecting line 22 to 39 (excluding occasional bifurcations near where anterior and ventral margins meet), ribs posterior to bisecting line 26 to 47. Total number of ribs on disk of each valve usually approximately 70; ribs flat and very narrow to moderately wide, with interspaces approximately $\frac{1}{5}$ to $\frac{1}{3}$ as wide,

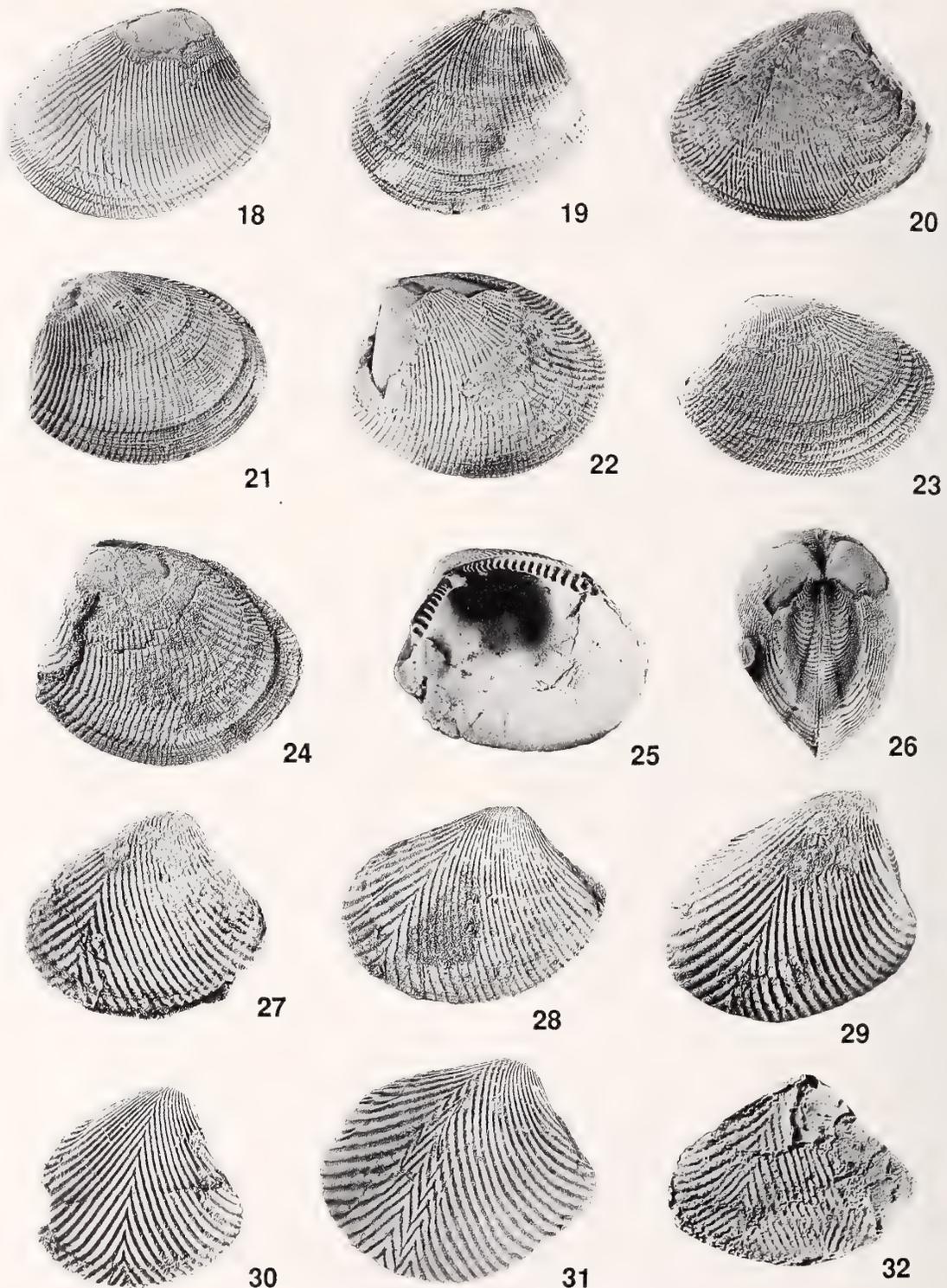
except anterior of chevron-bisecting line, where ribs become wider and more widely spaced. Growth checks near ventral margin common on some specimens and associated, from about $\frac{1}{3}$ of distance from posterior end to where anterior end meets ventral margin, with bifurcation of ribs into riblets and riblet insertion. Prominent growth checks, corresponding to same position on each valve, occasionally continue across escutcheon area to beaks. Ventral-margin edge and inner margin (for short distance) finely crenulate. Escutcheon prominent, sunken, and bounded by shallow groove not crossed by ribs; narrow ribs present on slightly inflated central part of escutcheon area. Interior nacreous. Adductor scars well delineated. Left-valve hinge with approximately 11 posterior taxodont teeth, similar in form, becoming stronger posteriorly; approximately 23 anterior taxodont teeth, similar in form, becoming stronger anteriorly. Resilifer narrow, opisthocline; bordered posteriorly by strong, high tooth.

Lectotype: ANSP 4417 (designated by Stewart, 1930:46).

Type locality: Pentz, Butte County, northern California.

Geologic age: Late Turonian to late late Campanian and possibly early Maastrichtian.

Distribution: UPPER TURONIAN: Budden Canyon Formation, Gas Point Member, Shasta County, northern California; Ladd Formation, Baker Canyon Member to Holz Shale Member transition, Santa Ana Mountains, Orange County, southern California. CONIACIAN: Redding Formation, Member V, upper part, Shasta County, northern California. LOWER SANTONIAN: Redding Formation, Member V, Shasta County, northern California. UPPER SANTONIAN: Haslam Formation, lower part, Chemanius River, near Nanaimo, Vancouver Island, British Columbia; Haslam Formation, lower part, Salt-spring Island, British Columbia; Redding Formation, Member VI?, Shasta County, northern California; Chico Formation, Musty Buck Member, Butte County, northern California. SANTONIAN UNDIFFERENTIATED: Panoche Formation, Merced County, north-central California. UPPER SANTONIAN/LOWERMOST CAMPANIAN: Haslam Formation, upper part, Brannen Lake, near Nanaimo, Vancouver Island, British Columbia. LOWER CAMPANIAN: Chico Formation, Ten Mile Member, Butte County, northern California; Chico Formation, Pentz Road member (informal), Butte County, northern California; Ladd Formation, upper Holz Shale member, Santa Ana Mountains, Orange County, southern California. LOWER MIDDLE CAMPANIAN: Ladd Formation, upper Holz Shale Member, Santa Ana Mountains, Orange County, southern California. UPPER MIDDLE TO LOWER UPPER CAMPANIAN: Cedar District Formation, upper part, west shoreline of Denman Island off east coast of Vancouver Island, British Columbia. Chatsworth Formation, Dayton and Bell canyons, Simi Hills, Ventura



Explanation of Figures 18 to 32

Figures 18–26. *Acila (Truncacila) demessa* Finlay, 1927. Figure 18. Hypotype LACMIP 13228, LACMIP loc. 10835, left valve, $\times 2.6$. Figure 19. Hypotype LACMIP 13229, LACMIP loc. 17611, left valve, $\times 2.6$. Figure 20. Hypotype RBCM.EH2003.009.0001, Locality 1, left valve, $\times 1.7$. Figure 21. Hypotype LACMIP 13229, LACMIP loc. 17611, right valve, $\times 2.6$. Figure 22. Hypotype LACMIP 13230, LACMIP loc. 10832, right valve, $\times 2.7$.

County, southern California; Williams Formation, Pleasants Sandstone Member, Santa Ana Mountains, Orange County, southern California. LOWER UPPER CAMPANIAN: Jalama Formation, Santa Barbara County, southern California. UPPER UPPER CAMPANIAN TO POSSIBLY LOWER MAASTRICHTAN: Rosario Formation at Punta San Jose and San Antonio del Mar, Baja California, Mexico.

Discussion: The above description is based on 847 specimens: 320 left valves, 356 right valves, and 171 with conjoined valves.

Our study revealed, for the first time, that on *A. (T.) demessa*, ribs commonly bifurcate into riblets near the ventral margin, the left-valve hinge has approximately 11 posterior teeth, and the right-valve hinge has approximately 18 anterior teeth.

Schenck (1936:48–50) reported *A. (T.) demessa* (from strata now referred to as the Rosario Formation) at Punta Banda and San Antonio del Mar, Baja California (Figure 1, locales 25 and 26, respectively). Only his San Antonio del Mar specimen is *A. (T.) demessa*. His Punta Banda specimen (hypotype CAS 6205) is *A. (T.) grahami*.

Whiteaves (1879, 1903) reported *Nucula (Acila) truncata* Gabb, 1864, from various localities, including the Nanaimo area, Vancouver Island, British Columbia, and Sucia Island, Washington. He provided no type numbers nor any illustrations of these specimens, and none is part of any known museum collection. Based on their geographic occurrences, however, it is possible that the Nanaimo area and Sucia Island specimens are *A. (T.) demessa*.

Page et al. (1951:1738–1739) mentioned that *Acila demessa* was found at four LSJU localities in beds in the Santa Ynez Mountains northeast of Santa Barbara, Santa Barbara County, southern California. These beds were later placed in the Espada Formation by Dibblee (1966:17), which ranges in range from latest Jurassic or Early Cretaceous to Late Cretaceous age (Dibblee, 1966). He also mentioned that these *Acila* specimens were found associated with the rudist *Coralliochama orcutti* White, 1885. This rudist is known to be of late Campanian to early Maastrichtian age (Marincovich, 1975). An attempt to find these *Acila* and rudist fossils in the CAS collection was unsuccessful. If the identification of the rudist is ac-

curate, these *Acila* specimens could be *A. (T.) demessa*, *A. (T.) grahami*, sp. nov., or *A. (T.) rosaria*, sp. nov.

Haggart & Higgs (1989) reported *Acila (Truncacila)* sp. from the upper Santonian in marine shales apparently overlying the Honna Formation in the area of Skidegate Inlet, Queen Charlotte Islands, British Columbia. Although the geologic age of this bivalve is within the range of *A. (T.) demessa*, closer investigation of this Queen Charlotte bivalve revealed that its preservation is too poor to even allow generic identification (J. Haggart, personal communication).

Acila (Truncacila) grahami Squires & Saul,
sp. nov.

(Figures 27–38)

Acila (Truncacila) cf. *demessa* Finlay, 1927. Schenck, 1936:50.

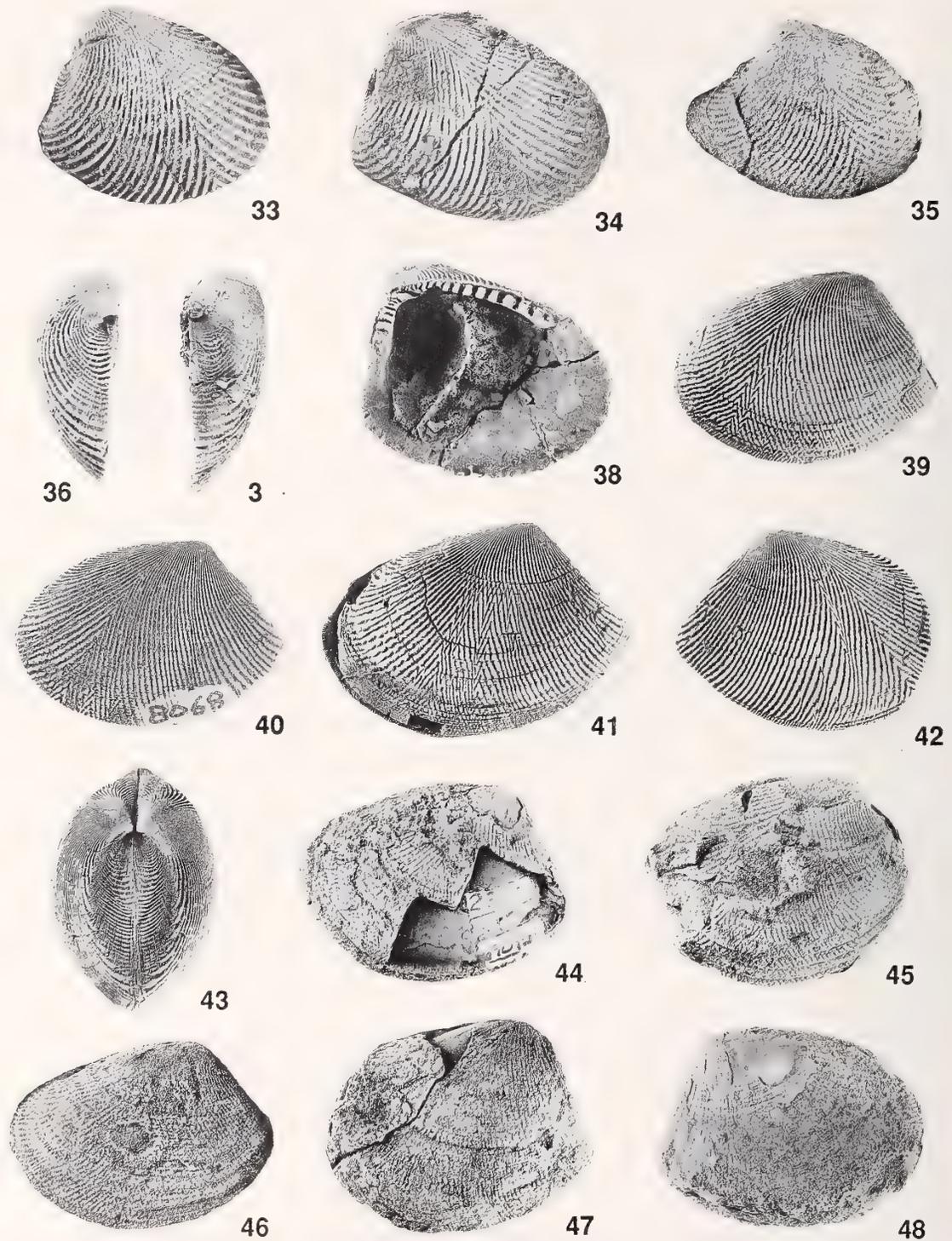
Acila (Truncacila) sp. E. Schenck, 1943:65–66, pl. 9, figs. 2, 4.

?*Nucula (Acila) truncata* Gabb. Whiteaves, 1879:162 (in part).

Diagnosis: Shell small, trigonal to subquadrate. Chevrons bisected by line usually meeting ventral-margin anterior (rarely center). Total number of ribs on disk of each valve approximately 50; ribs (posterior of chevron-bisecting line) narrow to moderately wide, with interspaces approximately $\frac{1}{3}$ to $\frac{1}{2}$ as wide. Escutcheonal ribs continuous with ribs on disk.

Description: Shell small for subgenus (up to 13.1 mm in height and 16.5 mm in length, most specimens approximately 8 mm in height and 9 mm in length), longer than high, height/length ratio = 0.75 to 0.92. Trigonal to subquadrate, inequilateral, equivalved, valves moderately inflated. Anterior end broadly rounded. Antero-dorsal margin long and straight. Posterior end truncate and set off from escutcheon by weak rostration. Ventral margin convex. Umbones moderately low, located posteriorly; umbonal angle varying from 86° (most trigonal shells) to 114° (most subquadrate shells). Beaks pointed, incurved, opisthogyrate. Disk very broad, ornamented with abundant ribs diverging from umbo area and forming chevron-shaped (divaricate) pattern. Chevron angle varying from 38° (most trigonal shells) to 56° (most subquadrate

Figure 23. Hypotype RBCM.EH2003.010.0001, Locality 2, right valve, $\times 1.8$. Figure 24. Hypotype LACMIP 13231, LACMIP loc. 22406, right valve, $\times 2.7$. Figure 25. Hypotype LACMIP 13232, LACMIP loc. 28780, left-valve hinge, $\times 3$. Figure 26. Hypotype LACMIP 13233, LACMIP loc. 10832, posterior view, $\times 1.4$. Figures 27–32. *Acila (Truncacila) grahami* Squires & Saul, sp. nov. Figure 27. Paratype RBCM.EH2003.012.0002, Locality 3, left valve, $\times 4.4$. Figure 28. Paratype RBCM.EH2003.014.0001, Locality 4, left valve, $\times 2.8$. Figure 29. Holotype RBCM.EH2003.011.0002, Locality 3, left valve, $\times 3.8$. Figure 30. Paratype RBCM.EH2003.012.0001, Locality 3, left valve, $\times 3.9$. Figure 31. Paratype RBCM.EH2003.013.0001, Locality 4, left valve, $\times 2.8$. Figure 32. Paratype CAS 69079, CAS loc. 69079, crushed specimen of left valve, $\times 2.4$.



Explanation of Figures 33 to 48

Figures 33–38. *Acila (Truncacila) grahami* Squires & Saul, sp. nov. Figure 33. Paratype RBCM.EH2003.012.0003, Locality 3, right valve, $\times 4.4$. Figure 34. Paratype RBCM.EH2003.011.0001, Locality 3, right valve, $\times 3.2$. Figure 35. Paratype CAS 69082.01, CAS loc. 69082, rubber peel of right valve, $\times 2.4$. Figure 36. Holotype RBCM.EH2003.011.0002, Locality 3, posterior view of left valve, $\times 4.2$. Figure 37. Paratype RBCM.EH2003.011.0003, Locality 3, posterior view of right valve, $\times 4$. Figure 38. Holotype RBCM.EH2003.011.0002, Locality 3,

shells). Chevrons bisected by line extending from slightly anterior of umbo to anterior part of ventral margin (rarely center); ribs anterior to bisecting line 12 to 30, ribs posterior to bisecting line 22 to 33. Total number of ribs on disk of each valve usually approximately 50; ribs narrow to moderately wide, with interspaces approximately $\frac{1}{3}$ to $\frac{1}{2}$ as wide, except anterior of chevron-bisecting line, where ribs become slightly wider and more widely spaced. Escutcheon moderately prominent, slightly sunken, and bounded by shallow groove crossed by ribs continuous with ribs on disk; ribs slightly stronger on inflated central part of escutcheon area. Anterior hinge with 16 teeth, posterior hinge with 9 teeth.

Dimensions of holotype: Left valve, height 9 mm, length 10.8 mm.

Holotype: RBCM.EH2003.011.0002.

Type locality: Loc. 3, north end of Hornby Island, British Columbia, 49°32'57"N, 124°41'40"W.

Paratypes: RBCM.EH2003.011.0001, RBCM.EH2003.011.0003, RBCM.EH2003.012.0001 to RBCM.EH2003.012.0003, RBCM.EH2003.013.0001, RBCM.EH2003.014.0001, and CAS 69082.01.

Geologic age: Late middle Campanian to early late Maastrichtian.

Distribution: UPPER MIDDLE TO LOWER UPPER CAMPANIAN: Cedar District Formation, upper part, west shoreline of Denman Island off east coast of Vancouver Island, British Columbia. LOWER UPPER CAMPANIAN: Jalama Formation, Santa Barbara County, southern California. UPPERMOST MIDDLE CAMPANIAN TO LOWERMOST UPPER CAMPANIAN: Moonlight Formation?, north end of Shale Hills, southwest side of Antelope Valley, eastern Tumbler Range, Kern County, south-central California. UPPERMOST CAMPANIAN OR LOWER MAASTRICHTIAN: Northumberland Formation, Collishaw Point, north end of Hornby Island, east coast of Vancouver, British Columbia. UPPER UPPER CAMPANIAN TO POSSIBLY LOWER MAASTRICHTIAN: Rosario Formation at Punta Banda, near Ensenada, Baja California. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Moreno Formation, Ortigalita Creek, Merced County and Ciervo Hills, Fresno County,

central California; Moreno Formation, Marca Shale Member, Fresno County, central California.

Discussion: This new species is based on 18 specimens: five left valves, 10 right valves, and three with conjoined valves. The best preserved ones are from the Northumberland Formation.

The new species is most similar to *Acila (Truncacila) haidana*, but the new species differs by having a more variable shape, narrower interspaces between the ribs, and having the line bisecting the chevrons located more anteriorly on the ventral margin.

Acila (Truncacila) grahami is similar to *Acila piura* Olsson (1931:35, pl. 2, figs. 9, 10, 14) from the upper Oligocene Heath Formation of northern Peru. The new species differs from *A. piura* by having a narrower chevron angle, more variability in the width of the interspaces between the ribs, and more ribs (22 to 33 versus 17) posterior to the bisecting line.

Whiteaves (1879:162) reported *Nucula (Acila) truncata* Gabb, 1864, from the northwest side of Hornby Island. He provided no type numbers nor any illustrations of any specimens, and none is part of any known museum collection. It is most likely, however, than any acilids found there would be *A. (T.) grahami*, because the type locality of this species is at the north end of Hornby Island.

Etymology: The species is named for Raymond Graham who collected many of the specimens and who informed the authors about them.

Acila (Truncacila) rosaria Squires & Saul,
sp. nov.

(Figures 39–43)

Diagnosis: Shell medium, elliptical-subquadrate. Chevrons bisected by line meeting ventral-margin anterior. Total number of ribs on disk of each valve approximately 80; ribs (posterior of chevron-bisecting line), very narrow to narrow, with interspaces approximately $\frac{1}{4}$ as wide to same width as ribs. Escutcheon bounded by flattish to grooved area usually crossed by ribs not continuous with ribs on disk.

Description: Shell medium for subgenus (up to 19.6 mm in height and 25.5 mm in length), longer than high, height/length ratio = 0.68 to 0.78. Elliptical-subquadrate,

←

left-valve hinge, $\times 3.8$. Figures 39–43. *Acila (Truncacila) rosaria* Squires & Saul, sp. nov. Figure 39. Holotype LACMIP 13234, LACMIP loc. 25431, left valve, $\times 1.8$. Figure 40. Paratype LACMIP 13235, LACMIP loc. 8068, left valve, $\times 2$. Figure 41. Paratype UCMP 155631, UCMP loc. B-5320, left valve, $\times 2$. Figure 42. Paratype LACMIP 13236, LACMIP loc. 25431, right valve, $\times 1.8$. Figure 43. Hypotype LACMIP 13234, LACMIP loc. 25431, oblique posterior view, $\times 2.3$. Figures 44–48. *Acila (Truncacila) princeps* Schenck, 1943. Figure 44. Holotype CAS 69075, CAS loc. 69075, left valve, $\times 1.3$. Figure 45. Hypotype LACMIP 13130, LACMIP loc. 23314, left valve, $\times 1.5$. Figure 46. Hypotype CAS 69086.02, CAS loc. 69086, rubber peel of left valve, $\times 2.1$. Figure 47. Paratype CAS 69078, CAS loc. 69075, left valve, $\times 1.5$. Figure 48. Paratype CAS 69076, CAS loc. 69075, right valve, $\times 1.5$.

inequilateral, equivalved, valves moderately inflated. Anterior end broadly rounded. Antero-dorsal margin long and straight. Posterior end straight, truncate and set off from escutcheon by weak rostration. Ventral margin convex. Lunule small, not very distinct, very slightly depressed, and crossed by ribs. Umbones low, located posteriorly; umbonal angle varying from 113 to 125°. Beaks pointed, incurved, opisthogyrate. Disk very broad, ornamented with abundant ribs diverging from umbo area and forming chevron-shaped (divaricate) pattern. Chevron angle 34 to 44°. Chevrons bisected by line extending from slightly anterior of umbo to anterior of ventral margin (rarely near center); ribs anterior to bisecting line 30 to 44 (excluding occasional bifurcations), ribs posterior to bisecting line 42 to 49. Secondary divarication common; tertiary divarication rare and only on those specimens where divarication is near center. Total number of ribs on disk of each valve usually approximately 80; ribs very narrow to narrow, with interspaces approximately $\frac{1}{4}$ as wide to same width as ribs, except anterior of chevron-bisecting line, where ribs become slightly wider, more widely spaced, and occasionally of irregular width. Ribs on juvenile specimens minutely tuberculate. Growth check(s) prominent on some adult specimens near ventral margin; growth check(s) commonly associated with riblet insertion near ventral-margin center and anterior of ventral-margin center. Ventral-margin edge and, for short distance, interior finely crenulate. Escutcheon prominent, sunken, bounded by flattish to shallowly grooved area usually crossed by ribs not continuous with ribs on disk, except on ventral part of escutcheon; flattish to shallowly grooved area occasionally smooth. Escutcheon area elevated centrally and with riblets more widely spaced than elsewhere on this area. Interior nacreous. Adductor scars well delineated. Right-valve hinge with at least 18 anterior teeth, similar in form, becoming stronger posteriorly. Resilifer narrow, oblique.

Dimensions of holotype: Conjoined valves, height 18.0 mm, length 25.4 mm, thickness 14.9 mm.

Holotype: LACMIP 13234.

Type locality: LACMIP loc. 25431, Punta San Jose, Baja California, Mexico, 31°26'30"N, 116°38'45"W.

Paratypes: LACMIP 13235 and 13236, and UCMP 155631.

Geologic age: Early late Campanian to early late Maastrichtian.

Distribution: LOWER UPPER CAMPANIAN: Moonlight Formation?, north end of Shale Hills, southwest side of Antelope Valley, eastern Temblor Range, Kern County, south-central California. UPPER UPPER CAMPANIAN TO POSSIBLY LOWER MAASTRICHTIAN: Point Loma Formation, near Carlsbad, San Diego County, southern California; Rosario Formation at Punta San Jose,

San Antonio del Mar, and Arroyo Santa Catarina, Baja California, Mexico. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Moreno Formation, Tierra Loma Member, Merced County, north-central California.

Discussion: This species is based on 40 specimens: 10 left valves, 11 right valves, and 19 with conjoined valves. Most show excellent preservation, although a few shells are partially decorticated. Most specimens are from the Rosario Formation, and most of these are from or near the vicinity of Punta San Jose.

The new species is most similar to *A. (T.) demessa*, but the new species differs by having a more oval shape, more projected anterior and posterior ends, generally more uniform sculpture over the entire valve surface, and usually a larger shell size. On the posterior part of the disk of the new species, the ribs have more prominent interspaces than those of *A. (T.) demessa*. In addition, large specimens of the new species have narrower ribs than large specimens of *A. (T.) demessa*. In addition, the ribs on the anterior part of the valves of the new species can be elevated and minutely tuberculate, whereas correspondingly, on *A. (T.) demessa* these ribs are flat-topped and smooth. The escutcheon area of the new species can be very similar to that of *A. (T.) demessa*, if the bounding shallow groove is smooth or smoothish, but most specimens of the new species have ribs across the entire escutcheon.

Acila (T.) rosaria is similar to *A. (T.)* sp. nov.? but differs by having a more elliptical shape, usually narrower ribs, and slightly narrower spaced ribs.

Etymology: The new species is named for the Rosario Formation, Baja California, Mexico.

Acila (Truncacila) princeps Schenck, 1943

(Figures 45–51)

Acila (Truncacila) princeps Schenck, 1943:63–66, pl. 8, figs. 1–4, 6–8.

Acila (Truncacila) sp. D. Schenck, 1943:65, pl. 9, fig. 5.

Acila (Truncacila) sp. F. Schenck, 1943:66, pl. 9, figs. 6, 8.

Acila sp. Saul, 1986b:26.

Diagnosis: Shell large, subquadrate, rarely trigonal. Chevrons bisected by line meeting ventral-margin anterior. Total number of ribs on disk of each valve approximately 85; ribs (posterior of chevron-bisecting line), flat and narrow to wide, with interspaces approximately $\frac{1}{5}$ to $\frac{1}{4}$ as wide.

Description: Shell large for subgenus (up to 25.8 mm in height and 34.4 mm in length), longer than high, height/length ratio = 0.71 to 0.85. Subquadrate, rarely trigonal; inequilateral, equivalved, and valves inflated. Anterior end broadly rounded. Antero-dorsal margin long and lowly convex. Posterior end straight, abruptly truncate and set off from escutcheon by weak rostration. Ventral mar-



Explanation of Figures 49 to 51

Figures 49–51. *Acila (Truncacila) princeps* Schenck, 1943. Figure 49. Holotype CAS 69075, CAS loc. 69075, right valve, $\times 1.3$. Figure 50. Hypotype CAS 950.01, CAS loc. 950, right valve, $\times 1.7$. Figure 51. Holotype CAS 69075, CAS loc. 69075, posterior view, $\times 1.3$.

gin convex. Lunule poorly developed, slightly depressed. Umbones low, located posteriorly; umbonal angle varying from 94 to 119°. Beaks pointed, incurved, opisthogyrate. Disk very broad, ornamented with abundant ribs diverging from umbo area and forming chevron-shaped (divaricate) pattern. Chevron angle 30 to 39°. Chevrons bisected by line extending from slightly anterior of umbo to anterior of ventral margin; ribs anterior to bisecting line 30 to 39, ribs posterior to bisecting line 45 to 54. Secondary divarication uncommon. Total number of ribs on disk of each valve usually approximately 85; ribs flat and narrow to wide, with interspaces approximately $\frac{1}{5}$ to $\frac{1}{4}$ as wide, except anterior of chevron-bisecting line, and to a lesser extent on extreme posterior part of disk, where ribs become round and slightly wider. Each rib commonly bifurcates into two riblets along ventral margin between approximately $\frac{1}{3}$ of distance from posterior end to meeting of anterior end and ventral margin. Growth check(s) near ventral margin often associated with appearance of these bifurcated riblets. Ventral-margin edge and interior, for short distance, finely crenulate. Escutcheon slightly? sunken, bounded by smooth? region; middle part of area crossed by numerous oblique ribs, becoming stronger ventrally. Interior nacreous. Simple pallial line. Adductor muscle scars well delineated. Approximately 21 anterior teeth and 11 posterior teeth.

Dimensions of holotype: Conjoined valves, height 26 mm, length 34.5 mm, thickness 18.7 mm.

Holotype: CAS 69075 [= LSJU 6960].

Type locality: CAS 69075 [= LSJU 2372], west side San Joaquin Valley, northern California.

Paratypes: CAS 69076 [= LSJU 6963]; CAS 69077 [= LSJU 6961], and CAS 69078 [= LSJU 6962].

Geologic age: Late late Campanian to early late Maastriichtian.

Distribution: UPPER UPPER CAMPANIAN TO POSSIBLY LOWER MAASTRICHTIAN: Point Loma For-

mation, La Jolla, San Diego County, southern California; Rosario Formation, San Antonio del Mar, Baja California, Mexico. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Tesla Formation, Alameda and San Joaquin counties, northern California; Moreno Formation, "Garzas Sand" member and also Mercy sandstone lentil, within middle part of Tierra Loma Member, Merced County, north-central California. LOWER UPPER MAASTRICHTIAN: El Piojo Formation, Lake Nacimiento, San Luis Obispo County, west-central California. UPPER MAASTRICHTIAN UNDIFFERENTIATED: Panoche Formation, Franklin Canyon, west of Martinez, Contra Costa County, northern California; Deer Valley formation (informal), north flank of Mount Diablo, Contra Costa County, northern California.

Discussion: The above description of this species is based on nine specimens: two left valves, one partial left valve, two right valves, three with conjoined valves, and one internal mold of a left valve. The lunule and escutcheon are both poorly preserved on every examined specimen.

Acila (T.) princeps is very closely similar to *A. (T.) demessa* in having, on some specimens, ribs that are flat-topped and very closely spaced. *Acila (T.) princeps* differs from *A. (T.) demessa* by having larger size, more uniform sculpture, and more numerous ribs. Schenck (1943:63) mentioned an area of obsolete radial ribbing on the holotype, but that is not the case (see Figures 44 and 49).

Schenck (1943:63) reported that the chevron angle, which he referred to as the angle of bifurcation, of *A. (T.) princeps* is 60 to 67°. In this present study, we measured the chevron angle of *A. (T.) princeps* near where the divarication begins, in the same manner as we measured this feature for all the other studied species. The only way we could obtain measurements of 60 to 67° is if we measured the along the ventral margin of the valve, where the ribs usually curve significantly.

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APPENDIX

LOCALITIES CITED

- Locality 1. Private shale quarry at 340 Blackburn Road, 6 km NW of Fulford Harbor, Saltspring Island, off southeast coast of Vancouver Island, British Columbia. Haslam Formation, lower part. Age: Late Santonian. Collector: Raymond Graham, September 29, 2000.
- Locality 2. Cliff on left bank of Chemainus River, 500 m downstream from the confluence with Banon Creek, 3.3 km SW of town of Chemainus, southeastern Vancouver Island, British Columbia. Haslam Formation, lower part. Age: Late Santonian. Collectors: Lois Walker and Raymond Graham, August 25, 2002.

- Locality 3. SE $\frac{1}{4}$ of an intertidal bench, 300 m seaward from the high-water mark at Collishaw Point, N end of Hornby Island, off east coast of Vancouver Island, British Columbia. Northumberland Formation. Age: Latest Campanian or early Maastrichtian. Collector: Raymond Graham, June 21, 1997.
- Locality 4. Intertidal bench 400 m N of Buckley Bay/Denman Island ferry terminal, west-central shoreline of Denman Island, off east coast of Vancouver Island, British Columbia. Cedar District Formation, upper part. Age: Late middle to early late Campanian. Collector: Raymond Graham, June 21, 2001.
- CAS 950. Hard lens about 0.3 m thick outcropping behind old distillery on Johnson Ranch at San Antonio del Mar, Baja California, Mexico. Rosario Formation. Age: Late Campanian to early Maastrichtian. Collectors: E. K. Jordan and L. G. Hertlein, January, 1926.
- CAS 1552. 152 m W of center of section 28, T. 26 S, R. 18 E., Sawtooth Ridge Quadrangle (7.5 minute, 1961), N end of Shale Hills, SW side of Antelope Valley, eastern Temblor Range, Kern County, south-central California. Moonlight Formation? Age: Latest middle Campanian to earliest late Campanian. Collector: G. D. Hanna and J. H. Snow, April, 1929.
- CAS 69075. [= SU 2372]. In second valley (with right turns), about 1.6 km N of Laguna Seca, on brow of hill on N side of valley, 366 m N and 503 m E of SW corner of section 12, T. 12 S, R. 10 E, Charleston School Quadrangle (7.5 minute, 1956), Merced County, north-central California. Moreno Formation, Mercy sand lentil within Tierra Loma Shale Member. Age: Late early to early late Maastrichtian. Collector: M. B. Payne, 1941.
- CAS 69079. [= LSJU 1274]. White concretionary limestone bed embedded in shale, just NE of town of Oil City, 305 m NE of center of section 17, T. 19 S, R. 15 E, Domengine Ranch Quadrangle (7.5 minute, 1956) Fresno County, north-central California. Moreno Formation, about 91 to 122 m below top of formation. Age: Late early to early late Maastrichtian. Collector: P. W. Reinhart, January 27, 1934.
- CAS 69080. About 1.6 km E of Queen Charlotte City, above beach, Bearskin Bay, Skidegate Inlet region, southern Graham Island, Queen Charlotte Islands, British Columbia, Canada. Haida Formation, probably Shale member. Age: Probably latest Albian to Cenomanian. Collector: unknown.
- CAS 69082. [= LSJU 2575]. Limestone concretion embedded in purple shale, NE corner of SE $\frac{1}{4}$ of section 23, T. 16 S, R. 12 E, Monocline Ridge Quadrangle (7.5 minute, 1955), Fresno County, northern California. Moreno Formation, Marca Shale Member. Age: Late early to early late Maastrichtian. Collector: D. C. Birch.
- CAS 69086. In railroad cut near Santa Fe Railroad tunnel above Franklin Canyon Inn, W of Martinez, Briones Valley Quadrangle (7.5 minute, 1959), Contra Costa County, northern California. Panoche Formation. Age: Late Maastrichtian. Collector: E. A. Watson.
- CAS 69095. In small area of Cretaceous siltstone in SW $\frac{1}{4}$ of section 21, T. 26 S, R. 18 E, Sawtooth Ridge Quadrangle (7.5 minute, 1961), N end of Shale Hills, W side of Antelope Valley, eastern Temblor Range, Kern County, south-central California. Moonlight Formation? Age: Latest middle Campanian or earliest late Campanian. Collector: G. Henny.
- CAS 69110. [= LACMIP 22874]. On E fork of Huling Creek, at edge of streambed in limestone bed, on S limb of hairpin meander, 1457 m N 25.5°E of confluence of Huling Creek and North Fork of Cottonwood Creek, Ono Quadrangle (15 minute, 1952), Shasta County, northern California. Budden Canyon Formation, Chickabally Mudstone Member. Age: Early Albian (*Leconteites lecontei* Zone). Collector: M. A. Murphy, summers 1951–1953.
- LACMIP 8068. Approximately 2.4 km S of Punta San Jose, Baja California, Mexico. Rosario Formation. Age: Late late Campanian to possibly early Maastrichtian. Collector: unknown.
- LACMIP 10832. In the field on both sides of the E-W highway connecting Pentz and Chico, about 1.3 km N86°W of Pentz, Cherokee Quadrangle (7.5 minute, 1949), Butte County, northern California. Chico Formation, Pentz Road member (informal). Age: Early Campanian. Collectors: W. P. Popenoe and D. W. Scharf, August 15, 1931.
- LACMIP 10835. Loose blocks in landslide, SW $\frac{1}{4}$ of SW $\frac{1}{4}$ of section 8, T. 22 N, R. 3 E, Paradise Quadrangle (15 minute, 1953), Butte Creek, Butte County, northern California. Chico Formation, Ten Mile Member. Age: Early Campanian. Collectors: W. P. Popenoe and W. Findlay, September 3, 1933.
- LACMIP 17611. Outcrop in streambed of Dry Creek, 472 m south and 152 m east of northwest corner of sec. 36, T. 21 N, R. 3 E, Cherokee Quadrangle (7.5 minute, 1970), Pentz area, Butte County, northern California. Chico Formation, Pentz Road member (informal). Age: Early Campanian. Collector: E. Göhre, 2000–2002.
- LACMIP 22406. Gullies on both sides of highway approximately 0.8 km straight W of Pentz, Cherokee Quadrangle (7.5 minute, 1970), Butte County, northern California. Chico Formation, Pentz Road member (informal). Age: Early Campanian. Collector: W. P. Popenoe, July 18, 1946.
- LACMIP 23314. On W slope of gully near gully bed, about 640 m S28°W of NE corner of section 24, T. 1 N, R. 1 E, of S side of Deer Valley, Antioch South Quadrangle (7.5 minute, 1973), Contra Costa County, northern California. Deer Valley formation (informal). Age: Late Maastrichtian Collector: W. P. Popenoe, August, 1944.
- LACMIP 23950 [= CAS 69106]. Gray mudstone in the

- N bank, 732 m W and 610 m N of SE corner of section 4, T. 29 N, R. 6 W, Ono Quadrangle (15 minute, 1952), Shasta County, northern California. Budden Canyon Formation, Gas Point Member. Age: Late Turonian. Collectors: W. P. Popenoe and W. A. Findley, 1933.
- LACMIP 24365. In fine-grained sandstone on left bank of French Creek [= Swede Creek], approximately 152 m N and W of SE corner of section 5, T. 32 N, R. 2 W, Millville Quadrangle (15 minute, 1953), Shasta County, northern California. Redding Formation, Frazier Siltstone Member. Age: Turonian. Collector: W. P. Popenoe, August 25, 1957.
- LACMIP 25431. Exposed in littoral zone and 3 to 6 m above high tide, S side of Punta San Jose, about 0.8 km E of the point and 48 km airline S of Ensenada, Pacific coast of Baja California, Mexico. Rosario Formation. Age: Late late Campanian to possibly early Maastrichtian. Collectors: W. P. Popenoe and W. Sliter, October, 1965.
- LACMIP 28780. Pentz, Butte County; northern California. Chico Formation, Pentz Road member (informal). Age: Early Campanian. Collector: P. W. Reinhart, year unknown.
- LACMIP 30141. Fossils in pebbly sandstone, about 1.6 km N of Nacimiento River on E side of road (?Bee Rock Road) near middle of northern-section line of section 18, T. 25 S, R. 10 E, Tierra Redonda Mountain Quadrangle (7.5 minute, 1949), San Luis Obispo County, west-central California. El Piojo Formation. Age: Early late Maastrichtian. Collector: unknown.
- UCMP 814. South of Antone, between Rock Creek and Spanish Gulch, in sections 12 and 13 and SE $\frac{1}{4}$ of section 11, T. 13 S, R. 24 E, Antone Quadrangle (7.5 minute, 1985), Wheeler County, Oregon. Unnamed Cretaceous strata. Age: Cenomanian. Collector: unknown.
- UCMP A-6275. Rio de Santo Tomás, Punta China area, northwest Baja California, Mexico. Alisitos Formation. Age: Late Aptian. Collector: E. C. Allison.
- UCMP B-5320. Sea cliff on S side of Punta San Jose, Baja California, Mexico. Rosario Formation. Age: Late late Campanian to possibly early Maastrichtian. Collectors: E. C. Allison and F. H. Kilmer, June 27, 1957.
- UCMP B-5665. In arenaceous bed 35 m stratigraphically below base of major volcanic-pyroclastic part of formation, upper Arroyo Ink, approximately 2 km due E of Punta China, Santo Tomás map (1:50,000, 1964), northwest Baja California, Mexico. Alisitos Formation. Age: Late Aptian. Collector: E. C. Allison.
- UO 461. Soft sandstone about 61 m above valley floor, NE side of Bridge Creek Valley, 0.8 km from and NW from Mitchell Rock, SE $\frac{1}{4}$, SW $\frac{1}{4}$ of section 26 and NE $\frac{1}{4}$, NW $\frac{1}{4}$ of section 35, T. 11 S, R. 21 E, Mitchell Quadrangle, Wheeler County, northeast-central Oregon. Hudspeth Formation, lower part of "Main Mudstone member." Age: Early Albian or early middle Albian. Collector: unknown.
- USGS M-175. 61 m E of the SW corner of sec. 33, T. 18 N, R. 4 W, 2012 m S of point "1009 ft" on Logan Ridge, Lodoga Quadrangle (15 minute, 1943), Colusa County, northern California. Probably float from lower Turonian Venado Sandstone Member of Cortina formation (informal). Collectors: R. D. Brown, Jr., and E. I. Rich, 1958.

Temporal and Spatial Recruitment Patterns in *Bankia martensi* Stempell (Bivalvia: Teredinidae)

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Abstract. Temporal and spatial variations in the recruitment of *Bankia martensi* Stempell, 1899 (Teredinidae: Bivalvia: Mollusca) were analysed in southern Chile.

B. martensi is the only species of shipworm inhabiting Chilean waters and the cause of severe damage to wooden structures in the sea. Two experiments were carried out over a period of approximately 20 years, in Codihué (41°54'S; 72°25'W) during 1979–1980 and Metri Bay (41°36'S; 72°42'W) during 2000–2001. Pine and oak panels were suspended at three depths and the density of recruits was determined based on the perforations or calcified cones produced when animals penetrate the wood.

Recruitment patterns were similar during both series of experiments. Average recruitment density did not differ statistically, neither did the incidence of attacks on pine and oak panels. Similarly, no differences were registered between the occurrence of attacks on the upper or underside of the panels. Seasonal differences did occur with regard to the period of maximum recruitment, although in both locations recruitment was significantly lower in winter. No differences were registered at depths of over 3 m, and lower recruitment was registered on superficial panels only in Codihué.

Results indicate continuous recruitment and low levels of temporal and spatial variability in spite of the different locations and periods when the data were collected. These patterns may be associated with the unpredictable presence of wood in the sea that is the specific substrate necessary for metamorphosis and adult development. *B. martensi* possesses reproductive characteristics that permit a constant supply of competent larvae, such as: reproduction throughout the year, early sexual maturity, alternative hermaphroditism and prolonged larval development, probably with teleplanic larvae. Low larval substrate selectivity also favours substrate colonization.

INTRODUCTION

There is only one species of wood-boring teredinid in Chile, *Bankia martensi* Stempell, 1899, which is the principal cause of attacks on wood in the sea (Stuardo et al., 1970; Campos & Ramorino, 1990). Recruitment occurs throughout the year (Campos & Ramorino, 1990), although factors operating at different spatial and temporal scales can generate variations in recruitment intensity. Antecedents do exist with regard to seasonal variations (Stuardo et al., 1970) as well as differential attacks according to the particular physical characteristics of different types of wood (Almuna et al., 1999).

Teleplanic larvae, common among teredinids (Scheltema, 1971), not only recruit on substrates at a distance from the breeders, but can also adjust their position in the water column in response to different environmental factors. In particular, reactions to light and depth are common in competent larvae of bivalve molluscs (Jackson, 1986). For this reason, the recruitment of *B. martensi* could vary seasonally according to the supply of larvae which is influenced by maturity periods and spawning factors, in addition to the degree of larval permanence and dispersion. It has been established that water circu-

lation patterns (Varotto y Barreto, 1998) and the physical effect of water conditions on larval mobility (Gara et al., 1997) can influence colonization in teredinids. Spatial variations in recruitment can be attributed to substrate characteristics and the position of larvae in the water column (Turner, 1984; Baker & Mann, 2003).

Recruitment of sessile or semi-sessile invertebrates can vary both spatially and temporally (Underwood & Keough, 2001), producing significant effects on populations. Recruitment variations may determine the number of individuals that reach maturity, since they affect the survival (Bertness, 1989). Recruitment variations can also determine the reproductive potential and functional condition of individuals that reach maturity (Sutherland, 1990). Evidence indicates that recruitment patterns account for fluctuations in population size throughout the year and between years, as well as the age structure of open populations (Roughgarden et al., 1985). Nevertheless, little is known about these aspects in teredinids.

This study aims to establish the recruitment patterns of the shipworm *Bankia martensi* by determining the effect of season, substrate location and type of wood in studies carried out during different periods and in different locations.

MATERIALS AND METHODS

Experiments were undertaken in two locations in southern Chile, with an interval of around 20 years between study periods. Experiments were initially carried out between October 1979 and October 1980 in the inlet of Codihué (41°45'S; 73°25'W) and then replicated in Metri Bay (41°36'S; 72°42'W) between November 2000 and November 2001. The sites are separated by a distance of 21.15 km, direct route. Both sites are located in the northern border of the Ancud Golf; Metri to the east of Reloncavi Bay and Codihué to the west. Oceanographic and climatic conditions are similar in both sites. Surface water temperature followed a clearly seasonal pattern in both locations, with average maximum tides of 7 m. Average monthly temperatures in Codihué ranged from 9.5°C to 16.8°C and in Metri Bay from 9.9°C to 17.5°C. Salinity in Codihué varied between 31‰ and 35‰ and in Metri Bay between 34‰ and 35‰.

Wood panels measuring approximately 20 × 10 × 5 cm were suspended from long lines at three depths: superficial, between 0.5 and 1 m; middle, between 3 and 4 m; and deep, between 6 and 8 m. Each group of 3 panels was placed at random, in triplicate. The panels were removed at monthly intervals and observed under a stereoscopic microscope in order to determine the number and density of recruits, based on the perforations or calcified cones produced when animals bore into the wood (Turner & Johnson, 1971).

Monthly registers for both locations and study periods were grouped seasonally, in order to establish temporal variability; spatial variability was determined by comparing recruitment at different depths on the upper and lower surface of each panel. Three-way variance analysis was used: season, depth and panel surface, following root transformation of data (Sokal & Rolph, 1969). The Tukey test was used for *a posteriori* analysis (Steel & Torrie, 1985).

Parallel to the above-mentioned experiments, degree of substrate selectivity was evaluated in both locations and study periods. For this purpose, panels of two types of wood were used: pine (*Pinus radiata*) and oak (*Nothofagus* sp.), and recruitment monitored over a two month

period. The wood was selected according to antecedents presented by Almuna et al. (1999), establishing that pine is more susceptible to attacks by *Bankia martensi* than oak. Data were compared with a two way and single variance analysis following root transformation. Similarly, we established whether recruitment was at random, using χ^2 according to Poisson.

RESULTS

Bankia martensi recruitment did not differ statistically either according to depth or between two closely located sites in southern Chile, where evaluations spanning a period of around 20 years were undertaken (Table 1); average density of recruits in Codihué during 1980, was $0.57 \pm \text{SE}: 0.09$ individuals-cm⁻² and in Metri during 2000, $0.69 \pm \text{SE}: 0.07$ individuals-cm⁻².

Recruit density on pine and oak panels did not differ either in Codihué ($F = 0.93$; $df = 1;42$; $P < 0.001$) or Metri ($F = 0.78$; $df = 1;11$; $P > 0.001$).

Spatial distribution of recruits on pine and oak panels submerged in Metri Bay was at random, following the Poisson rule ($\chi^2 = 14.38$; $df = 13$; $P > 0.05$).

B. martensi recruitment occurred throughout the year in both locations (Figure 1) and at all depths (Figure 2). Nevertheless, it was possible to differentiate periods of maximum recruitment. In Codihué (1980), highest levels were reached in spring/summer, with a drop in winter, when lowest recruitment levels were recorded ($F = 12.65$; $df = 3;29$; $P < 0.001$). In Metri Bay, on the other hand, highest recruitment occurred during summer/autumn, with significant differences compared to the winter period ($F = 14.5$; $df = 3;77$; $P < 0.001$).

Recruitment on the upper and lower surfaces of the panels did not vary, either in Codihué ($F = 0.29$; $df = 1;29$; $P = 0.10$) or in Metri ($F = 1.72$; $df = 1;77$; $P = 0.19$) (Figure 3).

Table 1

Two-way ANOVA of the number of *Bankia martensi* recruits in Codihué 1979–1980 and Metri Bay, 2000–2001, according to depth.

Source of variation	MS	df	F	P
Locality	0.006	1	0.46	0.49
Depth	0.026	2	1.98	0.14
Interaction	0.017	2	1.28	0.28
Error	0.013	84		

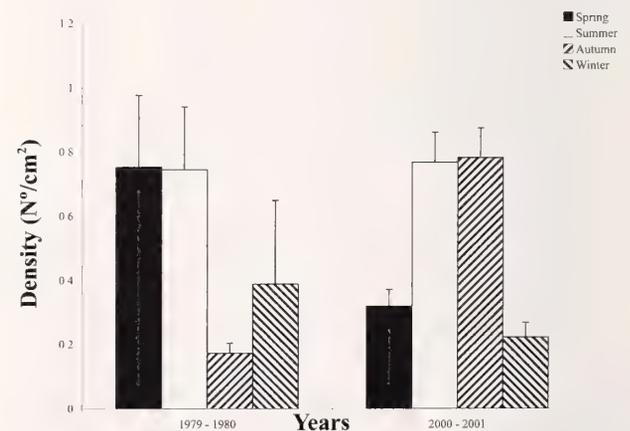


Figure 1. Average seasonal density \pm SE of *Bankia martensi* recruits in Codihué, 1979–1980 and Metri Bay, 2000–2001.

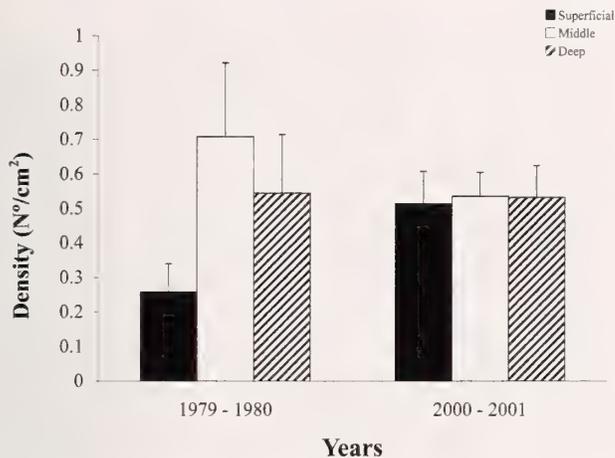


Figure 2. Average density \pm SE of *Bankia martensi* recruits at three depths, in Codihué, 1979–1980 and Metri Bay, 2000–2001.

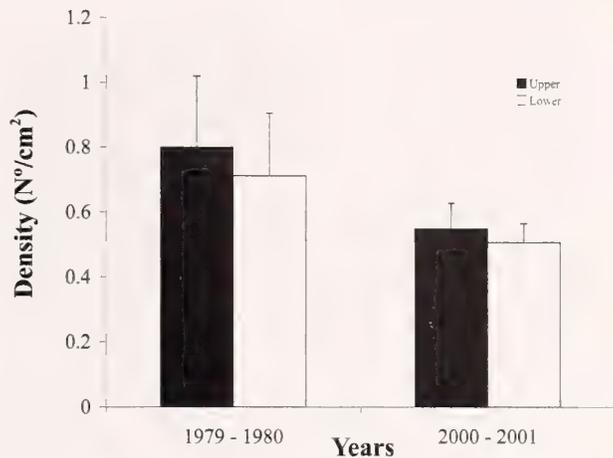


Figure 3. Average density \pm SE of *Bankia martensi* recruits on the upper and lower surface of panels, in Codihué, 1979–1980 and Metri Bay, 2000–2001.

DISCUSSION

Recruitment experiments were carried out on *Bankia martensi* in two sites in southern Chile, located close by, separated by an interval of around 20 years; results revealed low temporal variability. Recruitment occurred throughout the year in both locations, as recorded by Campos & Ramorino (1990), in studies undertaken in the area of Valparaíso, approximately 1000 km further north; this suggests that species reproduction-type is continuous, with successive gametogenic cycles during the year, which would account for the low degree of synchronisation between individual specimens.

Seasonal variations between study sites can produce local variations during periods of maximum recruitment. However, lowest recruitment levels always coincided with lower temperatures (winter). In studies carried out along the coast of Concepción, 600 km north of the sites being studied, Stuardo et al. (1970) recorded attacks on wood from the end of winter to the beginning of spring, suggesting that spawning would occur in spring and at the beginning of autumn. On occasions, *B. martensi* recruitment could occur considerably later than the spawning periods, since planktonic larvae may be highly dispersed, as generally occurs with veligers of the Teredinidae family (Scheltema, 1971). Thus competent larvae could colonize areas at a distance from the parental population. Furthermore, it has been established that recruitment and metamorphosis could be delayed in the absence of the substrate necessary for settlement (wood). Under laboratory conditions, pedivelifer larvae swam actively for more than 100 days after fertilisation when wood was not available and metamorphosised around 60 days after fertilisation in the presence of wood (Campos & Ramorino, 1990). Various morphological changes occur during metamorphosis; among others the disoconch develops initially along the anterior margin of the shell, creating a

denticulated external border which permits wood boring. If this does not occur, recruitment is not possible (Campos & Ramorino, 1990).

In *Bankia martensis*, as with other species of shipworm, a selective adjustment of reproductive processes can be expected in response to the availability of wood in the sea. Larvae only settle and grow on this particular type of substrate, whose temporal availability is estocastic. Thus, reproductive success should be substrate-dependent to a greater extent than in other species of sessile invertebrates. Reproductive processes should also tend to maximise colonisation of the substrate, both spatially and temporally. In the case of *Bankia martensis*, in addition to the capacity to recruit and grow on various types of wood, this is expressed in year-round recruitment and larval settlement with no significant spatial and temporal variations. These characteristics are the result of reproductive factors, such as early sexual maturity, successive gametogenic cycles, development of teleplanic larvae and hermaphroditism with autofertility, not necessarily protandric (Turner, 1973; Spormann, 2004).

Planktonic larvae of many species of bivalves can adjust their position in the water column in response to different factors, such as light, depth, temperature, salinity and current. This affects substrate colonisation (Jackson, 1986). The combined effect of light and pressure can determine variations in substrates located at different depths. Other factors such as the relative quantity of sediments and organic film on the upper and underside of substrates, could also cause recruitment levels to vary (Keough & Raimondi, 1995; Gara et al., 1997). In *Bankia martensis*, the only variations detected between study sites related to quantity of recruits on superficial panels. No variations were detected at greater depths, or between the different surfaces of the panels, confirming a low level of spatial variability in recruitment.

In *Bankia martensi* the presence of mature specimens all year round has been verified, including smaller sizes. Similarly, hermaphroditism, although non-protandric, has been confirmed (Spormann, 2004). Studies of sexual phases revealed that all the teredinid species are protandric hermaphrodites (Nair, 1962; Turner, 1966; McKoy, 1980; Hiroki et al., 1994). Hoagland (1978) has reported that due to the opportunist and sedentary nature of these species and the discontinuous availability of the substrate in the environment, they adopt protandry and minimise age of first reproduction, thus increasing reproductive potential. Nevertheless, non-protandric hermaphroditism is even more favourable to an opportunist strategy. Reproductive maturity in females is reached early. Campos & Ramorino (1990) have reported specimens with a shell length of 2.5 mm emitting gametes; this size is reached on wood panels maintained for 2.5 months in the water.

The larval development period in *B. martensi* plankton appears to be prolonged. Under laboratory conditions, wood boring starts 65 days after fertilization, and at 74 days larvae have already bored into the wood (Campos & Ramorino, 1990). The length of the development process is similar to that of other species of this genus such as *Bankia setacea* (Townsend et al., 1966). Although data obtained under controlled conditions cannot be extrapolated to the natural environment, they do suggest a high capacity for larval dispersion. The length of the larval period and current velocity determine the distance between recruits and parental population (Scheltema, 1971). The duration of the larval period has also been associated to population size (Jablonski, 1986) as well as to genetic continuity among populations (Scheltema, 1971).

All these reproductive characteristics tend to maximise colonisation on unpredictable substrates (Tuente et al., 2002), given that longevity depends on the size and perishable characteristics of the substrate where larvae recruit and grow. For this reason, difficulties have been encountered in controlling attacks on wood.

Efforts have been made to control shipworm wood attacks using chemical compounds that can operate at three levels: preventing larval settlement, increasing mortality prior to total settlement or provoking mortality after settlement (Giúdice, 1999). Copper compounds and organometallic compounds such as tributyltin fluoride (TBTF), triphenyltin fluoride (TPTF) and tributyltin oxide (TBTO) have been used in antifouling paints (Giúdice, 1999). However, antecedents indicate that they pollute the environment, in particular the latter compounds (Huggett et al., 1992). The need to settle on a specific type of substrate would limit the selectivity of competent larvae with respect to other substrate characteristics, as a result of which attacks on a wide variety of wood are to be expected. Although antecedents of differential attacks by teredinids do exist (Nair, 1962; Turner, 1984) including *B. martensi* (Stuardo et al., 1970; Almuna et al., 1999), it has been established that this species can attack all

types of wood, although with greater intensity on soft as opposed to hard woods (Stuardo et al., 1970). Nevertheless, a high degree of variability in attacks on panels of the same type of wood has been recorded (Stuardo et al., 1970; Almuna et al., 1999), which indicates stochastic processes associated with a complex group of factors that determine physical contact between larvae and substrates. Results obtained in the present study indicate that frequency of attacks on pine is similar to that of attacks on oak and that recruitment was at random.

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Two Introduced Pest Slugs: *Tandonia budapestensis* New to the Americas, and *Deroceras panormitanum* New to the Eastern USA

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Abstract. This paper reports new findings in North America of two pest slugs from Europe. *Tandonia budapestensis*, previously unknown from America, was found in Washington DC and near Philadelphia. *Deroceras panormitanum*, unreported from the Eastern United States and from Eastern North America outside of greenhouses, was found in Washington DC. We describe how to recognize these species and briefly summarize knowledge of their distribution and ecology.

INTRODUCTION

Since the classic monograph of Pilsbry (1939–1948), a number of papers have dealt further with introduced terrestrial mollusks in North America (e.g., Hanna, 1966; Chichester & Getz, 1969; Dundee, 1974, 1977; Rollo & Wellington, 1975; Roth & Pearce, 1984; Forsyth, 1999). However, in the last twenty years rather little has been published on this topic. This is surprising as the introduced species tend to dominate the malacofauna in disturbed habitats, and consequently are economically the most important pests. They are often also significant pests in their countries of origin (Godan, 1979, 1983). Without knowing the present distribution of an introduced species, or even if it is present in North America, the US Department of Agriculture's Animal and Plant Health Inspection Service's Plant Protection and Quarantine division (USDA APHIS PPQ) lacks the basis to determine whether a mollusk species intercepted on an imported commodity represents a potential novel agricultural or environmental threat.

In Europe the spread of some recent introductions has been followed in detail (e.g., De Wilde et al., 1986; von Proschwitz, 1996; Reise et al., 2000). In contrast, in North America the density of recording of terrestrial mollusks has been much lower. Consequently with novel records there must often be uncertainty about how long ago the introduction had occurred. Nevertheless such initial

reports are important in providing a baseline for later studies that follow up the subsequent survival and spread. Introductions of some species started long ago and have occurred repeatedly (e.g., *Arion subfuscus* (Draparnaud, 1805); Chichester & Getz, 1969; probably also *Arion silvaticus* Lohmander, 1937; Geenen et al., 2003). However, other species might well have been introduced only very recently, as seems very probable with *Boettgerilla pallens* Simroth, 1912, since it has spread from the Caucasus through Europe only within the last few decades (Reise et al., 2000). Species currently unknown in North America are frequently reported on incoming cargo (Robinson, 1999).

Species not yet reported for North America are liable to be overlooked because of the difficulties of identification when the North American literature does not deal with them. The problem is worse for slugs, because the lack of shell deprives them of many more obvious identification characters. For unfamiliar species often the clearest characters require dissection, which is always necessary for some species. To further complicate the matter, ongoing research among malacologists in Europe has shown that several of the Palearctic taxa actually represent complexes of closely related or superficially similar species: e.g., *Arion hortensis* Férussac, 1819 s.l. (Davies, 1979; Backeljau, 1987); *A. subfuscus* s.l. (Pinceel et al., 2004); *Arion fasciatus* (Nilsson, 1823) s.l. (Backeljau

et al., 1987; but see Jordaens et al., 2000). More anatomical evidence, perhaps coupled with molecular data, needs to be used to determine which members of these species complexes are present on the North American continent.

This paper reports occurrences that considerably extend the range of two pest slugs from Europe: *Tandonia budapestensis* (Hazay, 1881), previously unreported from America, and *Deroceras panormitanum* (Lesson & Polonera, 1882), unreported from the Eastern United States and from Eastern North America outside of greenhouses. Because of its greater novelty, we give more details on identification and ecology of *T. budapestensis* than of *D. panormitanum*.

COLLECTION DETAILS

H.R. and J.M.C.H. found three juvenile specimens of *T. budapestensis* on 28 July 1998 along Rock Creek in Washington DC (38°54.48'N, 77°03.24'W). The habitat was broad-leaved woodland along the slope above the creek, without much ground flora, but with garbage and flood debris. The specimens were raised in the laboratory for differing periods and then dissected to confirm identification. Two specimens are stored in the collection of the State Museum of Natural History Görlitz, Germany (p13048 and p13049).

Two adult specimens of *T. budapestensis* were collected on 29 May 1999 by Richard Horowitz (of the Academy of Natural Sciences, Philadelphia) from under a decaying log in Carroll Park, north bank of Cobbs Creek, south of Old Manor Road, Havertown, a suburban parkland area in Delaware County, just west of Philadelphia, Pennsylvania (39°58.78'N, 75°16.95'W). One specimen has been deposited in the collection of the Academy of Natural Sciences, Philadelphia (ANSP A 19999), the other in the USDA National Mollusk Collection (USDA 10294). In addition to the anatomical evidence, the identity of the latter specimen was confirmed by matching DNA sequencing data from conspecific specimens from the United Kingdom and Belgium, by Douglas Prasher of the USDA APHIS PPQ Center for Plant Health, Science and Technology.

H.R. and J.M.C.H. found two specimens of *D. panormitanum* on 29 July 1998 outside the National Museum of Natural History on Constitution Avenue, Washington DC (38°53.50'N, 77°01.57'W). They were collected in litter under rhododendron bushes, surrounded by a sparse lawn; this was shaded by the museum building, and periodically watered. Determination was based on genital anatomy. They are stored in the State Museum of Natural History Görlitz, Germany (p13050).

TANDONIA BUDAPESTENSIS

Taxonomy and Appearance

Tandonia budapestensis (the Budapest slug) is a member of the Milacidae, a family of less than 50 species,

with a center of distribution in the Balkans (Wiktor, 1981). Until Wiktor's taxonomic review of 1981, *T. budapestensis* was usually included in the other genus of the family, *Milax*. *Milax gracilis* (Leydig, 1876) is a synonym. In Britain it was not distinguished from *Tandonia sowerbyi* (Férussac, 1823) until Phillips & Watson's paper of 1930.

Like other milacids, *T. budapestensis* has a prominent keel running from the tail to the rear of the mantle, the pneumostome is at the rear half of the mantle, and a horseshoe-shaped groove runs around the central part of the mantle. *T. sowerbyi*, *Milax gagates* (Draparnaud, 1801), and *Milax nigricans* (Philippi, 1836) are the other widespread synanthropic Milacidae in Western Europe (and *M. gagates* is known from North America), but *T. budapestensis* is slenderer and when resting often curls round into a C shape (Figure 1a), whereas these others hunch up into a bilaterally symmetrical dome (Kerney & Cameron, 1979). *Boettgerilla pallens* is another species known from North America with a long keel, but it is much paler, smaller, and wormlike (Reise et al., 2000). In color *T. budapestensis* is somewhat polymorphic, but usually of a dark dirty appearance due to dense dark speckling on a dull cream or orange background (Figure 1b); the keel stands out owing to its lighter olive or dull orange color. However, in alcohol it is only the black pigment that remains prominent. The length when crawling is 50–70 mm. For other characters, including anatomy, see Phillips & Watson (1930), Wiktor (1987) and Barker (1999).

Ecology and Distribution

The original range of this European species is probably the southern Alps and northern Balkans (Wiktor, 1987). However, it is now known from Turkey to northernmost Great Britain and Iceland, and in much of this range is clearly a still-spreading introduction, as it is in New Zealand (Waldén, 1966; Wiktor, 1987; Barker, 1999; Kerney, 1999). Waldén's collection from Iceland was not restricted to greenhouses (*contra* Kerney & Cameron, 1979; T. von Proschwitz, personal communication). Previous reports from America seem unreliable. Godan (1979:63) refers to occurrences in America, Hawaii and Australia, but this must have been a misprint (these localities are listed for *M. gagates* earlier in the book; we can find no such records for *T. budapestensis* before or since). She elsewhere refers to interceptions of *T. budapestensis* on shipments to the USA based on the "Lists of intercepted plant pests" of the "Plant Protection and Quarantine Programs, Animal and Plant Health Inspection Service, US Department of Agriculture." These lists record incidents of pests being discovered, at which point the plants would be fumigated, incinerated or returned to the country of origin, so they are not cases of introductions. Moreover, D.G.R.'s redetermination of a sample of such records of a variety

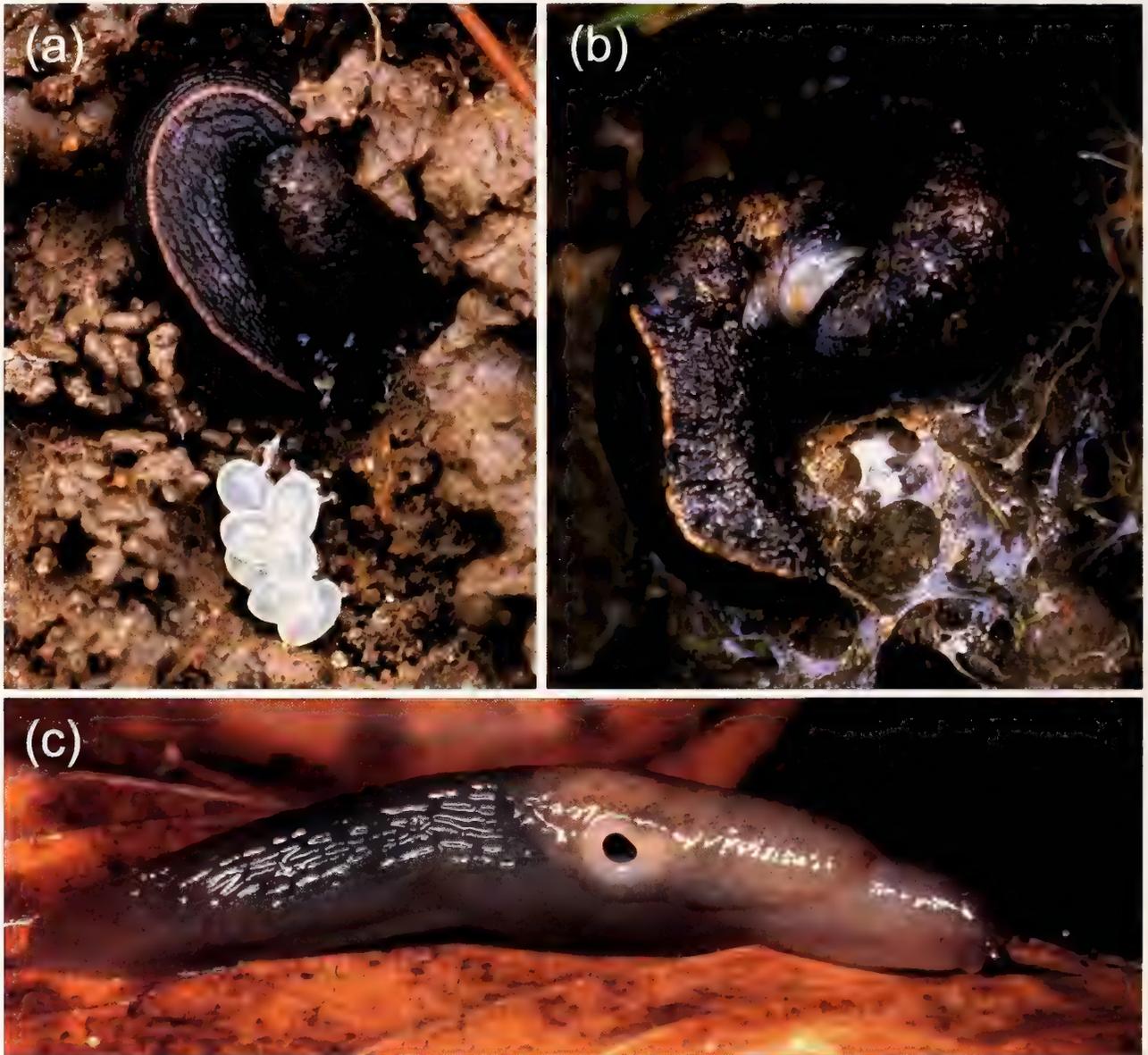


Figure 1. (a) *Tandonia budapestensis* in its typical C-shape resting position within a soil cavity that was topped by a board. The eggs could well be from this specimen. (b) A pair of mating *T. budapestensis*, as the species is commonly encountered because of its prolonged copulation (typically from evening to midday: Quick, 1960). Both pictures from Nork Park allotments, Banstead, Surrey, England. (c) *Deroceras panormitanum*, from England.

of species has shown that the lists prior to 1993 are frequently based on faulty identification. Based on later records, Robinson (1999) reported *T. budapestensis* as occurring in <0.1% of interceptions, but this was based on a single juvenile specimen tentatively identified as this species, whereas other intercepted *Tandonia* from the same country of origin have all been *T. sowerbyi*. Thus, despite the enormous volumes of imported commodities from Europe over the years, *T. budapestensis* has not been definitively identified among the many slug specimens intercepted by the USDA.

Tandonia budapestensis is the commonest milacid in Britain, where its habitat includes gardens, ploughed fields, waste ground and woods that have been subject to some disturbance (Kerney, 1999). In Central Europe it has been observed to be associated with lowland plains rather than hilly areas (Dvořák et al., 2003). It occurs amongst litter, and is often easiest to find under wood and stones, but it also burrows up to 37 cm underground (Stephenson, 1966) and over summer the entire population in potato fields can temporarily disappear deeper than 15 cm (Wareing & Bailey, 1989). In Western Europe it can be

a serious pest on arable land, particularly of potatoes and other root crops, and some ornamental flowers (Van den Bruel & Moens, 1958; Godan, 1979, 1983; South, 1992), and in captivity at least it also eats grain seeds and seedlings (Duthoit, 1964). Its underground habits make it less susceptible to control both by poison bait and cultivation (Symondson, 1997), but it is not so consistently a problem as some other slug pests (South, 1992).

In England the eggs hatch in spring and summer. The rate of development of both eggs and young is strongly dependent on temperature, being very slow at 5°C (Hunter, 1966a; Stephenson, 1966). Adults mature and mate in late autumn and winter, but this is usually their second winter, and they die off by August (Bett, 1960; Hunter, 1966a). However, in the more continental climate of the Czech Republic and Slovakia, mating slugs are found mostly in summer (Hudec, 1963).

For other aspects of its biology see Hunter (1966b) and literature cited in South (1992) and Symondson (1997).

DEROCERAS PANORMITANUM

This species has formerly been referred to as *D. caruanae* (Pollonera, 1991), which is now generally considered as a synonym (Wiktor, 2000). It is believed to originate from the Mediterranean, where there are several similar forms whose taxonomic status is still controversial (Wiktor, 2000).

In appearance it has a watery thin transparent skin (Figure 1c). Individuals vary from light grayish brown to chocolate brown, to almost black, and this is fairly uniform over the body; the fine dark spotting usually present is only obvious under magnification. In North America it is most readily confused with *Deroceras laeve* (O. F. Müller, 1774), some morphs of which resemble *D. panormitanum* much more closely, especially in size, than do specimens from Europe. In fact at the same site in Washington DC where we collected the two *D. panormitanum* we collected 12 other specimens which we considered to be conspecific, but which upon dissection turned out to be aphyallic or hemiphallic and thus were presumably *D. laeve*. Barker (1999) gives the pale rim to the pneumostome of *D. panormitanum* as a character distinguishing these species, but our examination of European and North American material has shown that it is sometimes not pale in *D. panormitanum* and it is often pale in *D. laeve*. A considerably more reliable character, although not clear in all specimens, is the shape of the tail (de Winter, 1988): seen in profile, the tail of *D. panormitanum* rises up from the sole vertically, or even curves backwards, whereas in *D. laeve* it slopes forward. The difference may exist because in *D. panormitanum* a flattening and enlargement of the tail accompanies its use in courtship (H.R., personal observation; Barker, 1999), but the character is still visible in non-courting individuals, especially if gently irritated. The difference is also usually apparent in alco-

hol-preserved specimens. In Europe there are other externally very similar species such as *Deroceras sturanyi* (Simroth, 1894).

Deroceras panormitanum has colonized large areas of Europe away from the Mediterranean and is still spreading (e.g., only recently reported for Poland (Wiktor, 2001)). It occurs mainly in disturbed sites but in Britain, for instance, is also found in wilder habitats such as woods and sea cliffs (Kerney & Cameron, 1979; Kerney, 1999). In Fennoscandia it occurs only in greenhouses (Waldén, 1966; von Proschwitz, 1993). It has also been introduced to the Canary Islands, South Africa, Colombia, Australia, New Zealand, Tristan da Cunha and even Marion Island 47°S (Smith, 1992; Barker, 1999; Preece, 2001; Hausdorf, 2002). The first report in North America is from California where it was already widespread in the Bay Area by 1940 (Pilsbry, 1939–1948). The next report was from two greenhouses in Quebec (Chichester & Getz, 1969), and it is now widespread in synanthropic habitats in the Pacific Northwest, both in the USA and Canada (Rollo & Wellington, 1975; H.R. & J.M.C.H., personal observation). But we know of no outdoor records from the East, nor any records from the Eastern United States. This is surprising as the USDA regularly intercepts the species on a wide variety of commodities, particularly on cut flowers and fresh fruits and vegetables from Colombia, Panamá, the Netherlands, and New Zealand (D.G.R., personal observation). Earlier records of interceptions into the USA cited by Godan (1979, 1983) and Dundee (1974) suffer from the same unreliability of the USDA lists as discussed above for *T. budapestensis*.

Deroceras panormitanum can be important as a pest in pastures, nurseries, greenhouses, gardens and commercial crops such as asparagus and lettuce (Castillejo et al., 1996; Barker, 1999), but seems not to be mentioned as a significant pest of cereals or root crops. In a 1988 survey of 372 gardens in Manchester, England, it was found in 258 of them, more than any other slug (North & Bailey, 1989).

It may be helpful to note that Quick (1960) rightly questioned Gregg's (1944) interpretation of the life cycle of *D. panormitanum* in California: probably the study population was mixed with *D. laeve*.

CONCLUSION

As mentioned above, the sparse recording of introduced slugs in North America makes it likely that *T. budapestensis* and *D. panormitanum* are already more widely distributed there than these three new records indicate. In an effort to collect slug data from throughout the United States and Canada, and map the distributions of all introduced species, the USDA APHIS PPQ initiated in 1998 the North American Slug Project (NASP), encouraging any interested malacological workers to collect and submit slug specimens for identification. Most submitted

slugs have been dissected to confirm identity, and samples have been DNA sequenced to add to the national database. A number of individual State Departments of Agriculture have also participated in NASP over the last five years, and slug surveys have been conducted in a number of states under the Cooperative Agriculture Pest Survey (CAPS) program, producing vast amounts of data that is still being collated and analyzed. Although our understanding of the distribution of a large number of Palearctic species is now far better than before, NASP has not turned up additional records of *T. budapestensis* or *D. panormitanum* other than the latter from regions where it was already known.

However, since the original submission of this manuscript, one of us (J.M.C.H.) spent one week in summer 2004 surveying synanthropic habitats in the Denver region of Colorado. *D. panormitanum* was widespread and common in garden centers, often together with externally very similar *D. laeve*, but it also turned up in a park-like habitat along the unkempt grassy bank of a drainage ditch. This confirms our suspicion that it might occur more widely east of the Rocky Mountains.

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Larval and Early Juvenile Development in *Tegula funebris* (Adams, 1855) (Gastropoda: Trochidae) in Baja California Sur, México

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Abstract. Larval and early juvenile development in *Tegula funebris* was observed for 63 days under static culture conditions at temperatures ranging from 19°C–20°C. The post-larvae were fed *Phaeodactylum trichorhotum* microalgae. Embryonic development from fertilized egg *in vitro* to competent larval stage lasted 8 days. Teleoconch secretion occurred on day 11. Very fine longitudinal striations, appearing on the anterior edge of the teleoconch on day 14, became parallel ribs extending from the teleoconch to the protoconch in juvenile stages. The shell aperture acquired a fanlike shape and the dextrally coiled spire rose, becoming conical on day 48.

INTRODUCTION

Along the central Pacific coast Baja California, the community associated with abalone (*Haliotis* spp.) banks includes a variety of gastropod species. Most common, in terms of frequency and abundance, are *Megastraea* (= *Astraea*) *undosa* (Wood, 1828), *Megathura crenulata* (Sowerby, 1825), and species of the genus *Tegula* (Guzmán del Prío et al., 1991). *Tegula funebris* is widely distributed in the intertidal zone of the Pacific coast of the Baja California Peninsula (Guzmán del Prío et al., 1991). Other species of this genus, *T. aureotincta* (Forbes, 1850), *T. eiseni* (Jordan, 1936), and *T. regina* (Stearns, 1892), share the habitat of *H. fulgens* in the subtidal zone of Bahía Tortugas (Carreón-Palau, 2000).

From recent studies on microhabitat and recruitment in juvenile *Haliotis* spp. (Carreón-Palau, 2000; Carreón-Palau et al., 2003) and some preliminary experiments on settlement of post-larval abalone in artificial collectors (Ponce-Díaz, 2004) in this area, the need to identify post-larval and early juvenile stages of the gastropods associated with the abalone rocky reefs has emerged. These species share a habitat and overlap in their spawning season, September to November (Belmar et al., 1991; Belmar & Guzmán del Prío, 1992; Guzmán del Prío, unpublished data).

Identification of these early life history stages has proved difficult because there is a dearth of literature on reproduction and development of members of the Trochidae (C. S. Hickman, quoted in Kulikova &

Omel'yanenko, 2000). Consequently, in the laboratory, the authors have been culturing the major gastropods sharing the habitat of *Haliotis* spp. to obtain reference collections that will assist in identifying larval and early juvenile stages of these gastropods.

Larval development in *T. funebris* (Adams, 1855) was described by Hewatt (1934) and later by Moran (1997) for a population in Oregon. This study presents results from a population in Baja California Sur, about 2500 km to the south. Here, females were induced to spawn. Detailed drawings of the development, which complements available information, will facilitate future identification of the early stages of this species in all of its range.

MATERIALS AND METHODS

Collection and Maintenance of Specimens

We collected 60 adult specimens of *T. funebris* (basal diameters 22–26 mm, shell height 15–20 mm, and total weight 5.17–8.04 g). The specimens were collected in the rocky intertidal zone of Bahía Tortugas, B.C.S. (27.7°N, 114.9°W) in January 2002. The specimens were transported in a cooler, maintaining humid conditions by layering the specimens between folds of giant kelp (*Macrocystis pyrifera*) leaves with an interior temperature of 10°C.

In the CIBNOR laboratory, the specimens were placed in 40-L plastic aquariums. Seawater in the aquariums was kept between 18°C–20°C with constant aeration. The specimens were fed rehydrated giant kelp (*M. pyrifera*) leaves. Water and food were replaced every other day.

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Gonad Conditioning

To attain maximum gonad development, specimens were fed *ad libitum* and the water kept between 18°C–20°C. Five snails were sacrificed weekly to monitor the stage of gonadal maturation by microscopic observations of gametes. Color of gonads (cream in males and moss green in females) provided determination of gender.

Induction of Spawning

After 60 days of gonadal conditioning, spawning was induced. Fifteen snails were removed from the aquarium (about 20°C) and were exposed to air for 30 min at 19°C in the shade and for 15 min at 29°C in the sunlight. They were then subjected to abrupt temperature shifts in seawater: the snails were returned to an aquarium at 16°C, then to an aquarium at 25°C. The cold and warm treatment was done twice, holding the specimens in each aquarium for 30 min. The snails were then returned to the 40-L aquarium. About 24 hr after thermal stimulation, only unfertilized eggs were found on the bottom of the aquarium. These eggs were fertilized with sperm extracted from dissected males (1 oocyte/15 sperm).

Sieving of Embryos and Larvae

Embryos were cultured in 16-L tanks and benthic phase specimens in 20 × 30 × 5 cm trays. Seawater was passed through a filter (1 μm pore size). Larvae were sieved through Nytex mesh (236, 160, 140, and 100 μm pore size) to remove organic waste. Sieving was done every 48 hr throughout the experiment. Benthic post-larvae were fed *Phaeodactylum tricornutum* (Bohlin, 1974) microalga. A video monitor attached to a microscope was used to observe and record morphological changes associated with larval and early juvenile development through day 63. Drawings were made from video images by tracing the outline and the main features of each stage directly from the TV screen. Mean (±SD) length of all stages was based on a sample of five individuals at each stage. From the veliger stage onward, size refers to the long axis of the shell. Seawater in the aquariums was kept at 19°C–20°C during growth phases through day 63.

RESULTS

Removal and maintenance of adult *T. funebris* in coolers with a humid environment proved effective. No deaths occurred following 14 hr of transport. In the laboratory, the specimens ate the food supplied (rehydrated *M. pyrifera*) as their regular diet throughout the experiment.

Induced spawning had positive results in females, while males failed to spawn. *In vitro* fertilization was successful, allowing subsequent observation of larval development. Observations were made from the time of fertilization through the early juvenile phase. The following

descriptions identify the stages and more prominent features during early development of the species (Figure 1).

Embryonic Development

Day 1. Fertilized eggs range in diameter, $145 \pm 5 \mu\text{m}$. Eggs are enclosed in a membrane with outside diameter $175 \pm 5 \mu\text{m}$, with a thick, additional gelatinous cover 140–320 μm thick (1). Eggs are bright green, remaining so throughout larval development. First cleavage occurs at 35–45 min, resulting in two same-sized cells (2). Second cleavage occurs at 55–65 min, forming four cells (3). Third cleavage occurs at 1–2 hr, forming eight cells. Subsequent cleavages occur after 2 hr (4). The ciliated gastrula (5–6 hr) remain enclosed in the egg membrane, attaining a diameter of $155 \pm 15 \mu\text{m}$ diameter (5). Invagination of the posterior end occurs (6), which corresponds to the shell gland. Trochophore forms at 9–10 hr, reaching a length of $160 \pm 10 \mu\text{m}$ (7). After elongation, prototrochal girdle begins to develop at one end (8) and two lateral tufts of cilia appear on its base (9). Early veligers form at 21–22 hr and are $200 \pm 10 \mu\text{m}$ long (10). Velum (11) and primordium of the foot (12) are present. Shell covers the entire body (13) except the velum.

Day 2. Veliger larvae after torsion, $223 \pm 16 \mu\text{m}$ long (14). Cephalo-pedal mass (15) with operculum (16). The velum branches into two sections (17) and lengthens posteriorly to form cephalic tentacles. Foot displays retractile movements and larvae swim with irregular motions.

Days 4–7. Late veligers are $226 \pm 10 \mu\text{m}$ long (18). Larvae withdraw into shell. Formation of the first whorl occurs. Eye spots are apparent (19). Shedding of cilia begins (20). Larvae exhibit exploratory movements in search of attachment substrates.

Benthic Phase

Day 8. Post-larvae are $240 \pm 12 \mu\text{m}$ (21a). Cephalic tentacles (22) and mouth (23) appear, and operculum becomes prominent (24). A few remnants of cilia tufts remain but with little motility (25). All larvae have settled.

Day 11. Post-larvae are $255 \pm 10 \mu\text{m}$ long (21b). When the first suture forms, it separates the protoconch from the teleoconch, which now begins to develop (26).

Juveniles

Day 14. Juveniles are $271 \pm 10 \mu\text{m}$ long (27a). Very fine longitudinal striations start to form on the anterior edge of the teleoconch (28).

Day 22. Juveniles are $290 \pm 20 \mu\text{m}$ long (27b). Longitudinal striations become more conspicuous and take the shape of ribs running the length of the shell (29). Transverse sutures in the teleoconch increase (30). Shell spiral

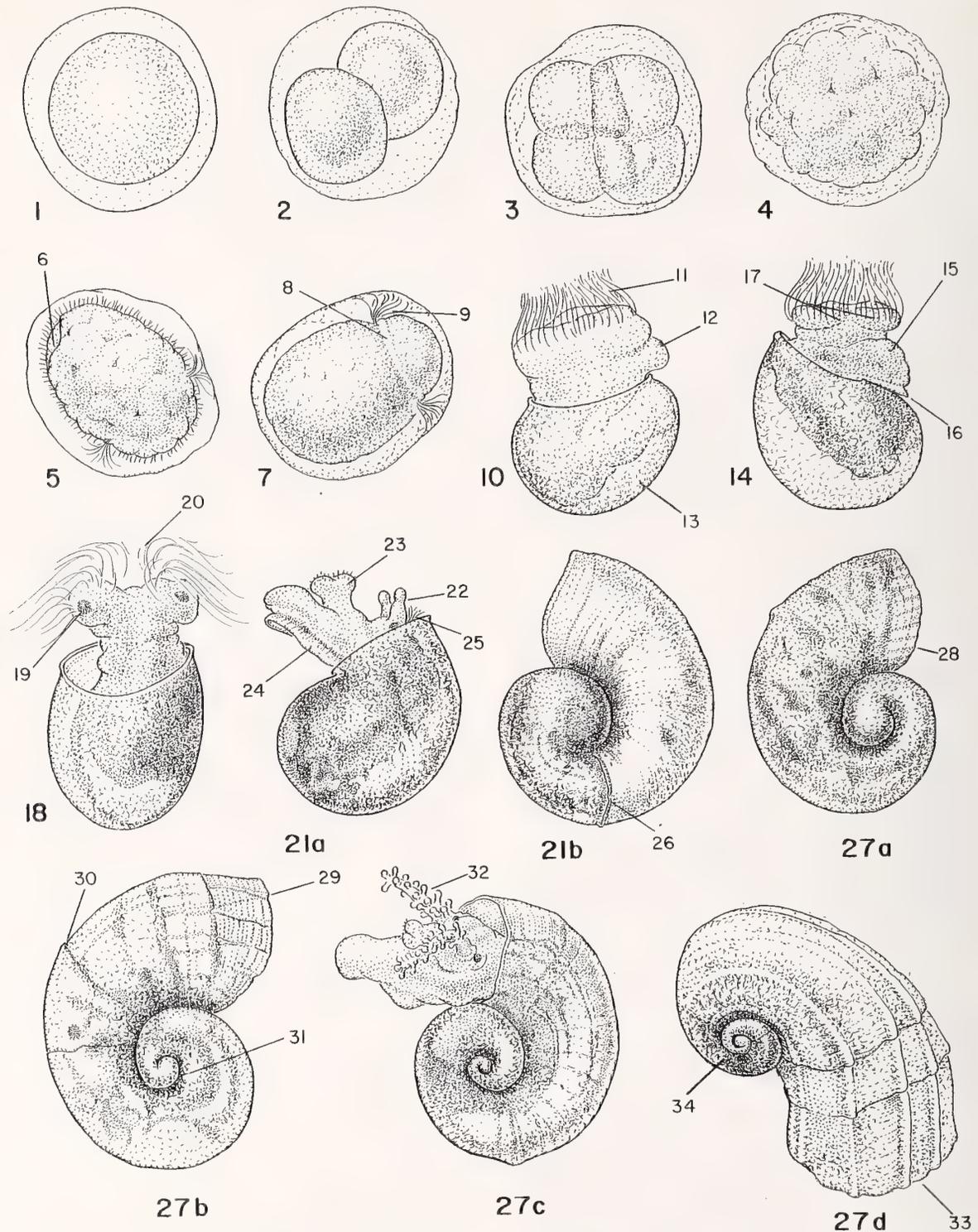


Figure 1. Developmental stages of *Tegula funebris* from egg to 48 days. (1) Fertilized egg. (2) First cleavage. (3) Second cleavage. (4) Morula. (5) Gastrula. (6) Shell gland. (7) Embryonic trochophore. (8) Proto-trochal girdle. (9) Lateral cilia. (10) Early veliger. (11) Velum. (12) Foot primordium. (13) Shell. (14) Veliger after torsion. (15) Cephalo-pedal mass. (16) Operculum. (17) Branching of velum. (18) Late veliger. (19) Eye spots. (20) Shedding of velum. (21a,b) Post-larvae. (22) Cephalic tentacles. (23) Mouth. (24) Operculum. (25) Remnant cilia. (26) First suture. (27a,b,c,d) Juvenile. (28) Longitudinal striations. (29) Ribs. (30) Transverse sutures. (31) Spire. (32) Cephalic tentacles. (33) Shell aperture. (34) Dextrally coiled shell. Bold numbers = different stages, normal numbers = morphological characters.

Table 1.

Development time in *Tegula funebris* from embryo to juvenile under laboratory conditions with temperature range of 19°C–20°C.

Stage	Time
First cleavage (two cells)	35–45 min
Second cleavage (four cells)	55–65 min
Third cleavage (eight cells)	1–2 h
Ciliated gastrula	5–6 h
Trochophore	9–10 h
Early veliger	21–22 h
Veliger	2 days
Late veliger	4–7 days
Settlement (benthic phase), two cephalic tentacles	8 days
Postlarva: suture separates proto-conch from teleoconch	11 days
Juvenile: fine longitudinal striations	14 days
Juvenile: ribs running the length of the shell, cephalic tentacles with 12 papillae	22 days
Juvenile: Cephalic tentacles with 18 papillae	34 days
Juvenile: Cephalic tentacles with 21 papillae	43 days
Conical shell	48 days

is more evident (31). Cephalic tentacles have 12 papillae each.

Day 34. Juveniles are $380 \pm 60 \mu\text{m}$ long (27c). Longitudinal ribs and transverse sutures become very evident. Cephalic tentacles have 18 papillae (32).

Day 43. Juveniles attain length of $455 \pm 30 \mu\text{m}$; cephalic tentacles have 21 papillae each.

Day 48. Juveniles are $463 \pm 9 \mu\text{m}$ long (27d). Shell aperture is now fan-shaped (33); dextrally coiled spire rises, becoming conical (34). Juvenile appearance remains unchanged from this day through day 63, when the experiment ended. Table 1 and Figure 1 summarize the stages of development. Figure 2 summarizes growth during the experiment. The rate of growth was about $5.6 \mu\text{m day}^{-1}$.

DISCUSSION

Maintenance of *T. funebris* under laboratory conditions posed no problems. Specimens adapted easily to feeding on rehydrated *M. pyrifera* foliage. The induction to spawn through different methods (thermal shock, desiccation, hydrogen peroxide, UV-radiation of seawater, etc.) has been used in gastropods (Kikuchi & Uki, 1974; Holyoak, 1988; González et al., 1999; Leighton, 2000). In this study, although different temperatures and times to spawning induction were assayed, it was possible to obtain the spawning of females only. This species is naturally adapted to drastic thermal changes in their environment, the intertidal zone, which may be related to its limited response to changes in temperature.

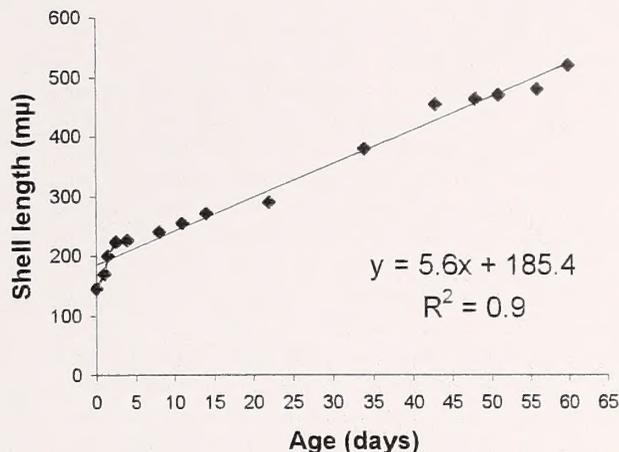


Figure 2. Post-larval and juvenile growth of *Tegula funebris*. Day 0 corresponding to veliger stage. ◆ = average of 5 measurements.

Release of oocytes was an important factor for the success of the experiment because of attempts to obtain oocytes through gonadal dissections failed. Female gametes have very fragile membranes that break when manipulated for artificial fertilization. Oocytes released into the water suggest that fertilization is external, agreeing with observations by Moran (1997), who rejected a process of internal fertilization reported years ago by Hewatt (1934).

Embryonic development up to the formation of the trochophore took 9–10 hr. Moran (1997) reported 25 hr for this species. Kulikova & Omel'yanenko (2000) reported 16–17 hr for *T. rustica*. From veliger larvae to the onset of the benthic phase, development time was similar to the report of Moran (1997), the larvae attaching between days 6–8. Moran noted longitudinal striations on the shell on day 21, while our observations placed this feature at day 14. Another important difference is the absence of pigmentation in the foot and head in our specimens, compared to Moran's finding of pigmentation in juveniles at 2 months' development.

Such variations in *T. funebris* may be a consequence of temperature conditions during the experiment: 18–20°C in our study and 13–15°C in Moran's investigation. For *T. rustica*, differences could be related to species characteristics, since early development in this species took place at temperatures similar to those used in our study.

From day 14 onward, some events and features, such as transverse sutures in the teleoconch, number of papillae, shell-aperture shape, spire-raising, and time of adult characteristics, cannot be compared with Moran's study because they were not described in his work.

We found that larval development among the species that we studied is very similar until the veliger stage. To distinguish conspicuous differences, experiments need to be undertaken beyond that stage, preferably to the early

juvenile stages, where teleoconch development begins to show different morphological characteristics. For example, in early juvenile *T. funebris*, very fine longitudinal striations are formed on the anterior edge of the teleoconch. These become longitudinal ribs in juveniles. In *Megastraea undosa*, early juveniles develop a crenulated ornamentation and brown spots at the edge of the teleoconch (Guzmán del Prío et al., 2003).

The recognition of these differences among early juvenile stages of gastropods living in rocky habitats, in association with abalone (*Haliotis* spp.), will provide important information about intensity of reproductive activity and settlement patterns shared by these species and the dynamics of interaction within the rocky communities of the central Pacific coast of Baja California.

Understanding reproductive interactions and strategies that these species have developed for resource allocation may help improve management of heavily exploited species, such as *Haliotis* spp. and *M. undosa*, as well as of other species associated with this benthic community that may come under future management by reason of their commercial value.

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