Behaviour and ecology of the inter-tidal pulmonate mollusc, *Onchidium peronii*, in Kuwait

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ABSTRACT

The naked pulmonate mollusc, *Onchidium peronii*, is locally abundant on rocky shores in Kuwait. It lives in rock crevices or holes and, when uncovered by the tide, it may emerge and spend up to 3 hr feeding before it returns to its own home some time before the tide covers the rock. Emergence is correlated with the time of low tide and is less likely around midday. During feeding excursions a trail of faeces is laid, which provides a convenient way of monitoring the movements of animals. In homing, the animals sometimes retrace all or part of their outward path but on other occasions they home without contact with the outward trail. Descriptions are given of the size distribution of the population, and of feeding and reproductive behaviour.

INTRODUCTION

*Onchidium peronii* (Cuvier 1804) was the first described species of an interesting family of shell-less gastropods, the Onchidiidae. Family members are mostly inter-tidal; a few are marine. Cuvier recognized that *O. peronii* closely resembles terrestrial slugs. At present they are regarded as being pulmonates. At times in the past, however, they have been placed among the opisthobranchs. Like terrestrial pulmonates, they have a lung but here it is not part of the true mantle cavity. Fretter (1943) suggests that the pulmonates and the Onchidiidae are separate branches from the early opisthobranch stem.

Apart from their disputed taxonomic status the Onchidiidae have other claims to our attention. First, many have a large number of dorsal eyes, borne on papillae on the notum (Hirasaka 1922). These eyes have a complex structure, including an inverted retina, and a still unclear function. Secondly, *O. verruculatum* has photoexcitive neurones in its central ganglia that function to evoke raising of the mantle margin (Gotow *et al.* 1973). Thirdly, some species possess repugnatorial glands around the margin. In *O. floridanum* these produce a discharge which is ejected up to 15 cm (Arey 1937). Finally, some littoral species show a remarkable homing habit. This was first described for *O. floridanum* in Bermuda (Arey & Crozier 1918, 1921) where, when covered by water, the animals live within holes or crevices in the rock, often 12 or more to a 'nest'. Some time after the receding tide uncovers them, the animals emerge to crawl over the rocks and to feed off the algal covering. Arey & Crozier (1921) give a detailed description of the behaviour of *O. floridanum* but report few controlled
experiments. Apart from some ecological information in the work of Fretter (1943) on the functional morphology of Onchidella celtica, I am not aware of any detailed studies of the ecology and behaviour of these fascinating molluscs.

The present work is a preliminary study of the ecology and behaviour of Onchidium peronii in Kuwait. Clearly, littoral animals in Kuwait face extreme problems of temperature tolerance and resistance to desiccation, particularly those animals like O. peronii, that graze on rock surfaces during daylight hours. It will be shown that emergence behaviour is controlled to protect the animals from intense solar radiation. This work also shows that homing takes place in O. peronii: a detailed analysis of homing behaviour will be presented elsewhere.

MATERIALS AND METHODS

The study area was 1 km north of Messilah Beach Hotel, Kuwait. Here the upper shore is gently sloping sand, the middle shore is a more or less flat rock platform, and the lower shore is again sand. Onchidium peronii were found over the entire rock platform and on a few scattered rocks on the lower shore.

In most cases the animals' own faeces leave an accurate record of the feeding trail. Movements were timed by marking the tracks at intervals with small stones placed just behind the moving animals. For short tracks, photographs were taken from directly above and the track was later traced from projected slides. Longer tracks were mapped by triangulation. At night, observations were made with the aid of a torch shielded by a red filter.

RESULTS

Fig. 1 shows the appearance of O. peronii. The overall colour is brown-grey, often with irregular black patches. The brown-grey colour matches closely the colour of the rocks on which they are found. At the anterior end there are two stalked eyes and two oral lappets, the latter being in constant movement, touching and withdrawing from the substrate during locomotion. The dorsal surface (notum) is covered with many papillae, several of which bear between two and seven eyes. In the rear third of the notum the projections are longer, with many side branches, and give the appearance of the gills of dorid nudibranchs. These projections normally expand only when the animal is submerged and presumably they function to increase the area for pallial

![Image](image_url)

**Fig. 1.** Onchidium peronii preserved after magnesium anaesthetization. Note the head tentacles, oral lappets, dorsal papillae (some with eyes), and respiratory papillae (normally expanded only when under water). Length = 3.8 cm.
respiration. The opening to the lung lies at the posterior end of the body, just under the notal margin. The pneumostome opens only when the animals are out of water.

(a) Distribution, numbers, and sizes

*Onchidium peronii* is common in Kuwait and occurs on rock platforms, on large rocks embedded in sand, or associated with man-made structures such as jetties. It is not found in purely sandy areas. This species also occurs on the Arabian Gulf coast of Saudi Arabia (Basson et al. 1977). The rock is loosely aggregated sandstone and is often cracked into separate plates, 1–8 m across. The rocks contain a large cryptic fauna in internal cavities produced largely by the action of boring bivalves. In areas where *O. peronii* is found, the superficial sessile fauna is limited: limpets and barnacles are relatively rare. Large areas of rock surface are, however, often covered by the calcareous tubes of serpulid polychaetes (probably *Serpula vermicularis* L.). *Onchidium peronii* lives in ‘homes’ either under rocks, or in crevices between the rocks, or in holes in the rock platform. The animals are well concealed and a diligent search often fails to reveal their presence. Under certain conditions, however, they emerge in large numbers and feed on the exposed rock surface.

In some regions the population density may exceed 1·m$^{-2}$. No evidence was seen for territoriality: the feeding ranges of individuals often overlap and the animals were never seen to interact with each other (except in reproductive behaviour).

The lengths of animals were measured in April, October, and December 1978 (n = 130 in each case). The results are shown in Fig. 2. The normal maximum length seen was around 5 cm. The largest individual found (not shown in Fig. 2) was 12.8 cm.

![Histograms showing the distribution of body lengths during (a) April, (b) October, and (c) December 1978. In each case n = 130. There are few animals longer than 5.0 cm.](image-url)
long. These results may underestimate the numbers of small animals (less than 1.5 cm long) firstly because they are extremely difficult to detect and secondly because they appear to feed for a shorter time than larger animals and thus many may have already returned home when measurements were made. The increased number of small individuals seen in December is, however, probably a genuine phenomenon. The duration of development within egg capsules and the rate of growth subsequent to hatching are not known, so we cannot as yet say anything about the age structure of the population.

(b) Timing and control of emergence

Generally speaking, the pattern of tides in Kuwait is such that the lowest daytime tides occur in the cooler months. In the area studied the rock flat was exposed only by tides of less than 1.3 m above datum. During the hot months of May–September the majority of tides low enough to uncover the rocks occur during the hours of darkness. Onchidium peronii will emerge and feed in darkness. This differs from the behaviour of O. floridanum which has been reported to feed only during the day (Arey & Crozier 1921). During the main period of observation (October–December 1978) the animals were uncovered mainly during daylight hours but there were some tides a few hours before sunrise and a few hours after sunset.

The following description of the factors controlling emergence behaviour refers to observations made during October 1978 and may not be directly applicable to other months. Part of the study area (approximately 17 m × 12 m) was used for daily counts of the number of animals that emerged. The air temperature during this period ranged from 22–32°C. All counts were made within 10 min of the time of low tide. Fig. 3 plots the numbers seen against the time of low tide.

The number of O. peronii that emerge varies considerably at different times of day. There is a close correlation between time of low tide and numbers emerged: the numbers decrease before noon and increase again after noon. The results were ana-

![Fig. 3. Onchidium peronii tend not to emerge around midday. The graph plots the numbers seen feeding in a 12 m × 17 m study area against the time of low tide. The counts were made during the period 6–25 October, at every low tide which exposed the rock surface for more than 2 hr. The lines were fitted by regression analysis, the points before noon and those after noon being considered separately.](image-url)
lysed by calculating two regression lines, one for the points before noon and the other for points after noon. The slopes of the lines are the same\((-9.7, 9.7\). The correlation coefficients are 0.69 and 0.85, being significant \((p \leq 0.01)\) before noon and probably significant \((p \leq 0.05)\) after noon \((t\)-test). No significant correlation was found when the numbers emerged were plotted against air temperature, relative humidity, or wind speed.

Presumably the trigger for emergence is exposure as the tide recedes. The actual choice, whether or not to emerge, may be based on detection of light intensity, so that the animals avoid coming out when low tide is around midday. However, many of the animals have homes either under rocks or deep within rocks, so it is difficult to see how they could measure light intensity without first moving towards the entrance to their homes. In fact, on one occasion an animal was observed to emerge partially from its home, to stop, and then withdraw. Alternatively, the animals may have an internal clock for predicting tidal rhythm. The function of this behaviour is probably to avoid exposure to the drying conditions found in the middle of the day when generally temperatures are at their highest and relative humidity at its lowest. The few animals that do emerge around midday are normally in moist or shaded regions. In the study area there was one animal in particular that was seen out at almost every tide, regardless of the time of day. This was the only individual whose grazing area included shallow standing water.

On some days the animals may not emerge at all, on other days they may emerge at both tides. Marked individuals were observed to emerge at both morning and evening tides in April. On most days, however, there is only one tide low enough for emergence to occur. On usually 3 or 4 days a month neither tide is low enough.

\((c)\) Feeding behaviour

When an *Onchidium* leaves its home it moves across the rock surface, usually initially in a straight line, and as it crawls it feeds by scraping away the surface deposits with its radula.

The initial direction of travel is unrelated to the wind direction at the time of emergence (Fig. 4). This is important because Arey & Crozier (1921) suggested that *O.*

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**Fig. 4.** Direction of the outward path is not related to wind direction. When an *Onchidium* had moved at least 40 cm away from home the mean direction of the outward path was estimated. The figure shows the direction of the paths on two consecutive days for every individual which emerged in the study area. The arrows show the wind direction. Wind speed was between 2 and 5 m·sec\(^{-1}\). North is uppermost and the sea is due east. Each scale mark represents one animal.
*floridanum* finds its home again by olfactory cues from the home itself. Now, if this was true for *O. peronii*, one would expect the outward path to be downwind so that on return home the stimuli could be followed upwind. Clearly, however, if we consider the test sample, then we must conclude that there is no overall preferred orientation for the outward path. If, however, we study the directional preference of individuals, we find that an *Onchidium* may travel in more or less the same direction on several consecutive feeding excursions and then change to a completely different direction which may itself be followed for several consecutive excursions (Fig. 5). Such preferences might be learnt or might result from detection of some information, presumably chemical, remaining from previous expeditions. In any event it is clear that because the rock surface is not uniformly covered with food (the areas bearing calcareous polychaete tubes being obviously unsuitable for efficient feeding), it will be advantageous for the animals to locate preferred feeding grounds quickly and not to waste time grazing on areas with little food.

Feeding appears to start more or less immediately after emergence. During feeding, the rate of forward movement is slow and the head moves slowly from side to side, so that a zig-zag pattern of radula strokes is left on the rocks. It may occur continuously on the outward journey only and in this case the return home is usually rapid.

While moving over the rocks, the animals leave a trail of faeces that is useful as a reliable and accurate record of the course taken. Faeces begin to be deposited within a few minutes of emergence. At first the faeces are narrow and black for about 2 cm but then they become wide and sand-coloured. The faeces trail is continuous on short excursions but becomes discontinuous when the animals travel greater distances.

The relationship between the size of the animal and the length of the feeding trail has not been studied quantitatively. It was observed, however, that small individuals (less than 2 cm long) were rarely found more than 20 cm away from home whereas larger animals (5 cm or longer) may be found 150 cm or more from home and often travel to that point by a circuitous route. The longest path seen was 630 cm, covered in
Fig. 6. On a given day, the total excursion time for individuals of similar size tends to be fairly constant, regardless of the time spent on the outward part of the movement. In other words the longer the time spent moving away from home, the faster the return home. The graph plots duration of return home against duration of outward part of the journey for 10 individuals within the size range 4.5–5.0 cm.

A time of 191 min. The distance travelled varies considerably between excursions. One individual, followed for nine consecutive trips, moved the following distances from home (outward and return paths were more or less straight): 110, 83, 55, 100, 105, 30, 115, 80, and 150 cm. The outward path length showed no significant correlation with air temperature, relative humidity, or time of low tide (factors considered separately).

Fig. 7. Feeding trail of an individual that appeared to home by following its outward trail. The stippled area is the region that had obviously been scraped by the radula. The faeces trail is a clear indication of where the animal has been moving over the rock. This is the track of a small animal (less than 2 cm long). The drawing was made from a photograph. Scale = 1 cm.
(d) Return home

The first animals to emerge do so about 100 min before low tide and the last ones to return home do so about 100 min after low tide. Emergence begins some time after the rock surface has been exposed and all animals have returned home well before the incoming tide covers the rock. The actual duration of the time away from home is generally around 150–200 min. The smallest individuals (less than 2 cm long) return home well before larger animals. The duration of the time away from home is not significantly correlated with time of low tide, air temperature, relative humidity, or wind speed (factors considered separately). The only correlation found was that the longer the time spent on the outward portion of the trip, the faster was the return home (Fig. 6). The line was fitted by regression analysis: \( r = -0.64 \), \( t = 2.3 \) (probably significant, \( p \leq 0.05 \)). On the particular day that these results were obtained the mean total excursion time was 170 min (range 148–207 min).

If we consider the actual route taken during a feeding trip then there are two extremes. Sometimes the outward route is very closely followed on the way home (Fig. 7). At other times the return home is obviously by a different route (Fig. 8). Most examples fall somewhere within these extremes, with different degrees of contact with the outward track. Individuals have never been seen to return to anywhere except the home from which they emerged (in some cases, however, homes have more than one entrance and return may not be to the same hole that the animal emerged from). The behavioural basis of homing will be considered elsewhere.

(e) Reproductive behaviour

Copulatory behaviour has been seen elsewhere during June 1978 (D. Clayton, personal communication) and in the study area from 17–22 October 1978. The animals are hermaphrodite and pairing takes place during a feeding excursion. Individuals involved in reproduction were never less than 4 cm long. In the part of the study area where daily counts were made, the number of mating pairs were 2, 5, 2, 0, 2, and 1 for the morning tides over the period 17–22 October. The estimated total population in this area is 90–100, so about 25% of the population were observed to mate. The actual percentage may have been somewhat higher since observations were not made at the two evening tides during this period that were low enough to expose the rock surface. The relative humidity was generally low (50–65%) during this period, except for the 18th when it reached 92°. The 18th was the day when the maximum number of mating pairs was seen.

An animal may find a mate by following the mucus trail of another individual. Location of a mate has, however, only been observed on two occasions, so random searching cannot be eliminated as a possible method. Normally, individuals show no response to the trails of others.

The male organ is situated anteriorly and the female opening is at the posterior of the body. The mating pair align themselves head to tail during copulation and they continue to crawl, but as they are linked together they just circle in one position. Circling is always in a clockwise direction because the male organ is on the right side of the head and the body must bend to the right for coupling. Occasionally three animals were seen linked together in a mating group.

Mating groups appeared to stay on the surface for longer than animals that were
not mating. Eventually the animals separated and headed for their own homes. Egg capsules have not been found: presumably they are laid within the homes.

**DISCUSSION**

In terms of biomass, *O. peronii* can be regarded as the dominant grazing animal on
uncovered littoral rock surfaces in Kuwait. They are particularly abundant in areas where there are plenty of crevices and cavities to act as homes.

*Onchidium peronii* has no known predators. Semper (1881) suggested that the dorsal eyes enable the animal to respond to attacks by the air-breathing fish *Perioptalmus*. No evidence was presented to support this belief and such an interaction is unlikely here as in Kuwait *Perioptalmus* occurs only on mud flats. The only inter-specific interaction seen was that the crabs which are active on the rock surface would occasionally nip any *Onchidium* which tried to enter the holes where the crabs were sitting. The only response by the *Onchidium* was to stop moving for a few minutes. Some other species have repugnatorial glands which are believed to protect the animals when exposed to air, but not when under water (Arey 1937). Arey suggested that the most important factor was to prevent detachment from the rock. *Onchidium peronii* apparently lacks repugnatorial glands; possibly its large size protects it from dislodgement.

Predation is unlikely when the animals are covered by water as they are usually well hidden and the entrances to their homes are often very small: sometimes less than half the diameter of the animal's body.

Environmental factors, particularly high temperatures, may be considered of major importance to *O. peronii* in Kuwait. The highest midsummer temperatures are avoided because low tides then occur in morning and evening. In October midday air temperatures exceed 30°C, but it was shown that emergence is much reduced at low tides around midday. Possibly the dorsal eyes function to monitor the light intensity and thus control emergence. It is unfortunate that more information is not available regarding emergence patterns in *O. floridanum* as this species lacks dorsal eyes. Arey & Crozier (1921) report only that it is less likely to emerge on windy days than on calm days, and they claim that the head tentacles act as wind detectors. There is another possible function for the dorsal eyes in *O. peronii*: they may detect the light falling on the body in the place of concealment and cause the animal to move so that no part of the body is left exposed to direct sunlight. If only the tentacular eyes were used, the animal might sit with its head in the shade but its body exposed to the sun.

Are *O. peronii* of any ecological significance? Grazing probably removes many things from the rock surface—not only sand and algae, but also newly settled larvae of sessile organisms. As reported above, barnacles are rarely found on rock surfaces with a large population of *Onchidium*. They are, however, locally abundant in regions with few or no *Onchidium*. Possibly this is because in some areas rapid deposition of sediment prevents larval settlement but as a basis for future studies it may be suggested that the scarcity of barnacles results from the settled larvae being eaten by grazing *Onchidium*. If this is true, then one must also ask how it is that serpulid polychaetes manage to gain a foothold on the rocks.

**REFERENCES**


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دراسة بينية وسلوكية للأونكيديوم بيرونياي (الرخويات، عارية الرتين) على شواطئ الكويت

ابن دوجلان ماكرلين
قسم علم الحيوان بجامعة الكويت

خلاصة

كثر انتشار اونكيديوم بيرونياي وهو من الرخويات عارية الرتين على شواطئ الكويت الصخرية. يتخذ هذا الحيوان من الشفوف الصخرية والجروح منازل له، وعندما ينحسر المد ويصبح الحيوان عرضا للهواء الجوئ فإنه غالباً ما يخرج ويقضي فترة قد تصل إلى 3 ساعات في الغذخ قبل أن يعود إلى منزله الخاص مستقباً المد الذي قد يغطي الصخر فذ بذ. ويعتمد ظهور الحيوان اعتياداً كلياً على فترات النزول، وقيلما يخرج في منتصف النهار. وعادة ما يترك الحيوان خلفه مساراً من المواد الاجزاجية أثناء مساراته الغذائية. وتتوفر هذه المسارات وسيلة ملائمة جداً لتنبض الحركات الأونكيديوم. وقد يهتدى الحيوان إلى بعض هذه المسارات أثناء رحلة العودة إلى البحر فيبعها، والأفانفس يسركط طريعاً جديدًا. ويعطى البحث وصفاً لكثافة توزيع الحيوانات على الشواطئ بالإضافة إلى شرح لسلوك التغذى وسلوك التكاثر.