Notes on the ecology and behaviour of *Pseudamphithoides incurvaria* (Just) (Crustacea, Amphipoda, Amphithoidae)

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Notes on the ecology and behaviour of *Pseudamphithoides incurvaria* (Just) (Crustacea, Amphipoda, Ampithoidae)

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Introduction
The algal-inhabiting amphipod *Amphyllodomus incurvaria* (transferred by Karaman and Barnard (1979) to *Pseudamphithoides*) was first described by Just (1977) from one shallow water locality in the eastern Caribbean. Just (1977) mentioned the construction by this new species of an unusual bivalved domicile or 'pod', cut from the blades of a foliaceous brown alga, *Dictyopteris* sp. The range of *P. incurvaria* is herein extended to include the western Caribbean and the Bahamas, and as little has been reported concerning the natural history of this amphipod, it is of interest to record some details of its ecology and behaviour.

A number of amphithoid amphipods are known to be domiciliary, constructing stationary tubes of detritus and sediment in which they live. The algal-dwelling habit of *P. incurvaria* is unique in that portable pods are constructed from the primary food plant of these herbivorous amphipods. Observations on the habitat, population density, feeding habits, and pod construction behaviour of *P. incurvaria* are reported below.

Materials and methods
The study was conducted at the Smithsonian Institution's laboratory on Carrie Bow Cay, Belize, Central America (16°48'N, 80°05'W), from November 1979 to August 1980. A detailed description of the zonation of the barrier reef at this location is given by Rützler and MacIntyre (1982). Amphipods were collected in algae from a variety of reef zones, placed and sealed in plastic bags, and returned to the laboratory. Individual amphipods are quite cryptic while on their host plants, and for censusing were separated from their associated algae by gentle agitation of the plants in shallow trays. Amphipods were maintained for up to two weeks in the laboratory in aerated seawater, and kept in culture dishes with algae for behavioural observations. Algal biomass was determined using blotted wet weight.

Habitat and distribution
*Pseudamphithoides incurvaria* was found to inhabit and construct pods from the brown alga *Dictyota bartayresii* Lamouroux, in a wide range of habitats near Carrie Bow Cay. *Dictyota bartayresii* is abundant in many reef zones, and *P. incurvaria* was found in plants collected from shallow water back-reef areas (1-2 m depth), as well as
from the following areas of the fore-reef: upper spur and groove (6 m), outer coral ridge (14 m), and outer sand channel (27 m). *Pseudamphithoides incurvaria* was also collected by the first author at Andros Island, Bahamas (24°52'N, 77°54'W), in *Dictyota ciliolata* Kützing at a depth of 10 m on the fore-reef slope.

It would seem that *P. incurvaria* has specialized on particular brown algae in the family Dictyotaceae, perhaps on the basis of morphology. Many species of both *Dictyota* and *Dictyopteris* are characterized by narrow, flattened branches only three to four cell layers thick. Other members of the Dictyotaceae which were common in the study area, including *Stypopodium zonale*, *Padina sanctae-crucis*, and *Lobophora variegata*, were never found to contain *P. incurvaria*.

A large population of *P. incurvaria* occurring on *D. bartayresii* located in an area of back-reef (1-5 m depth) approximately 50 m north-west of Carrie Bow Cay was studied to determine population density and seasonal changes in size distributions. The substrate in this area is comprised primarily of coarse calcareous sediments, scattered small coral rubble, and patches of pavement rock. *Dictyota bartayresii* is the dominant component of a patchy algal cover (\( \bar{x} \pm s.d. = 11 \pm 9\% \) of total cover), which also includes algal turfs, crustose corallines, and scattered occurrences of *Halimeda opuntia* and *Padina sanctae-crucis*. This region is subject to strong tidal currents and wave action. Water temperatures in this area range annually from 25°C to 29°C. The fish fauna characteristic of the study area includes juvenile doctorfish, *Acanthurus chirurgus*, the beaugregory *Eupomacentrus leucostictus*, and two wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*.

The abundance of *P. incurvaria* on *D. bartayresii* was highly variable within the back-reef study area (see table), ranging from 1 to 64 individuals per 100 g of *Dictyota*. The extremely clumped local distribution of *P. incurvaria* on *D. bartayresii* plants, in conjunction with patchy algal distribution, suggests a high degree of spatial heterogeneity in the local distribution of *P. incurvaria*.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Abundance (Number of individuals)</th>
<th>Number of individuals per 100 g <em>Dictyota</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>B</td>
<td>35</td>
<td>30</td>
</tr>
<tr>
<td>C</td>
<td>23</td>
<td>64</td>
</tr>
<tr>
<td>D</td>
<td>15</td>
<td>1</td>
</tr>
<tr>
<td>E</td>
<td>18</td>
<td>15</td>
</tr>
</tbody>
</table>

Size-frequency distributions for *P. incurvaria* collected during November 1979, March 1980, and August 1980, are given in fig. 1. Pod size (length of the major axis) is used as an estimate of amphipod size as observations indicate that the two measures are highly correlated. Only pods inhabited by amphipods at the time of collection have been included. Pod sizes range from 1-0 mm (juveniles) to 3-5 mm (ovigerous females). Mean pod size in the March collection (1-4 mm) was considerably lower than that of the November and August collections (2-3 mm); the March population contained many newly released juveniles, and a single ovigerous female. The distribution of brood sizes for 13 ovigerous females is given in fig. 2, ranging from two to five eggs per marsupium.
Ecology and behaviour of *Pseudamphithoides incurvaria*

Feeding behaviour

*Pseudamphithoides incurvaria* appear to be entirely herbivorous, and in the study area are found only on *D. bartayresii*. In the laboratory, individuals which were offered *Paddina sanctae-crucis*, *Thalassia testudinum*, or *Halimeda* sp. were never observed to feed on these species. Individuals offered *D. bartayresii* ate voraciously, and amphipods were maintained on a diet of *D. bartayresii* for two weeks. Animals...
feeding on *D. bartayresii* were most often observed taking bites out of the margin of the thallus, but occasionally ate epiphytes and algal hairs removed from the flat surface of the thallus by the gnathopods. Individuals also feed both on their own and on others’ pods. Amphipods grazing their own pods remove a strip along the dorsal/ventral seam, rolling it neatly towards the pod entrance with gnathopods 1 and 2, and then pass the parcel to the mouthparts. Aggressive interactions between individuals were observed which often included one animal climbing onto and eating portions of the others’ pod. Faecal material accumulating in the pod is either expelled by the gnathopods or carried away in a ventilating current set up by the pleopods.

**Pod construction**

Although the relationship of pod size to amphipod size suggests that pods may be replaced as animals moult, adult *P. incurvaria* appear rarely to leave their algal pods. While walking or swimming, pereopods 5–7 remain anchored inside the pod, which is thus carried about with the animal. Individuals are able to retract entirely into their pods, but are most often found with the first and second antennae protruding from the entrance. Individuals can be induced to leave their pods only when extreme pressure is applied along the pod margin, at which point the animal forcibly ejects itself. Agitated and apparently randomly directed swimming ensues until the animal encounters a suitable alga. When *D. bartayresii* is available, pod construction is initiated almost immediately. Individuals offered other algal species (*Padina sanctae-crucis, Lobophora variegata*) do not construct pods.

Observations were made of the sequence of pod construction (fig. 3) using several amphipods which had been removed from their pods. Animals encountering a blade of *D. bartayresii* first crawl along the thallus to the growing tip of a branch. Pod construction is initiated by the animal positioning itself laterally across the width of the blade, seemingly checking dimensions with the first and second antennae, and occasionally repositioning itself for a suitable fit. The surface of this portion of the blade is then cleared of algal filaments and epiphytes using pereopods 1–4, while hanging onto the thallus with the posterior three pairs of pereopods. A curvilinear cut is started at the blade margin with the mouthparts (fig. 3 A), and continued across the thallus to the opposite margin (fig. 3 B), forming the first valve of the pod. A small notch is frequently made in the opposite margin, about midway in the cutting, which apparently serves as a marker. The process of cutting across the flat surface of the algal blade is done in two steps. A cut is first made through the upper
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Fig. 3. Sequence of algal pod construction by *Pseudamphithoides incurvaria* on *Dictyota bartayresii*: A, Initiation of cut and notch; branch tip will form first valve; B, Continuation of cut across algal thallus; C, Measuring and clearing algal hairs off second branch tip; D, Second valve being cut; E, Completed pod with valves attached along margins by threadlike secretions.

Layer of cortical cells and through part of the single medullary cell layer; working from the same side of the blade, the lower layer of cortical cells is then severed. As the algal piece is separated from the plant, it is held alongside the amphipod with pereopods 5–7 in the manner of a shield. With the first valve held thus in place, the individual crawls down the branch and up another, eventually taking up a new position at another branch apex (fig. 3 C). A similar process of measuring and clearing the blade surface is carried out. After the second cut is initiated, the two valves, one still incompletely cut, are attached along their interchangeable dorsal/ventral margins by threadlike secretions of pereopods 3 and 4. The second curvilinear cut is then completed to match the shape of the first valve (fig. 3 D).

The completed pod (fig. 3 E) is comprised of two ovate valves, each containing one or two apical cells from the algal branch tip. The pod has an opening at each end.
Fig. 4. SEM micrographs of *Pseudamphithoide incrivia* pods: A, Anterior view of pod entrance with three cell layers of *Dictyota* thallus evident; B, Lateral view of pod with valve formed from portions of two blades joined together; first and second antennae protruding from pod entrance to right.

(fig. 4 A), either of which serves as an entrance, the animal being able to execute deft somersaults inside the pod. When the length of the amphipod exceeded the width of the available alga, individuals were observed to join together two narrow portions of the blade by glandular secretions to form one valve of the pod (fig. 4 B). The entire sequence of pod construction was essentially identical for all adults observed, with pods being completed within one-half to two hours.

Newly-hatched juveniles are retained within the pod of the female for a period of time before they are released. Observations were made of pod construction by about 20 newly released juveniles. These individuals, about 0.8 mm body length, make a single cut along the flat part of the algal blade through the upper cortical layer, and insinuate themselves between the cortical and medullary layers. These juveniles were observed to leave their pods for brief feeding excursions to the margin of the blade.

Discussion

Many amphithoid amphipods construct domiciles composed of detritus, algal fragments, and sediment bound together with glandular secretions. These domiciles are most often stationary, but in some species are carried about by the animal. Although the domiciliary habit has traditionally been viewed as serving a protective function (e.g. Schmitt 1965, Kaestner 1970), Nelson (1979) provided the first experimental evidence of increased mortality from fish predation on individuals of two species of tubiculous amphipods which had been prevented from constructing tubes.

Only three species of herbivorous amphipods, including *P. incurvaria*, appear to have been reported to construct domiciles from portions of their primary food plant. *Ampithoe humeralis* (Stimpson), the kelp curler, constructs a large tubular colonial chamber from the blades of *Macrocystis* (Jones 1971) or *Ecklonia* (Griffiths 1979) plants, or in *Macrocystis* holdfasts (Barnard 1969). These chambers remain attached
to the kelp plant, and the interior walls of the chambers serve as food for the inhabitants (Griffiths 1979). Similarly, the amphipod *Amphitholina curvata* (Stebbing) has been noted (Myers 1974) to burrow into the stipes of the kelp *Alaria esculenta*, feeding exclusively on its host plant. The domiciles of these kelp-inhabiting amphipods appear to provide proximity to the food source while affording protection against the occupants' being dislodged from their host plants by wave-generated turbulence.

The pod constructed by *P. incurvaria* is believed to be a unique instance of a portable algal domicile. There is no mention in the literature of a domiciliary habit in the second species of *Pseud amphithoides*, viz. *P. bacesci* Ortiz. The nature of the selective pressure which may be involved in the maintenance of this unusual and complex behaviour is of some interest.

The extremely cryptic appearance of podded *P. incurvaria in situ* on a host plant suggests that this pod-construction behaviour may have evolved in response to strong selective pressure from visually hunting predators. Indeed, in the areas studied in the present investigation, the carnivorous wrasses *Halichoeres bivittatus* and *Thalassoma bifasciatum* are a dominant component of the fish fauna. Both of these species are diurnally active and have been reported to consume a variety of benthic invertebrates (Randall 1967). Examination of the stomachs of ten *H. bivittatus* collected from the back-reef study area revealed *P. incurvaria* pods in two individuals. The possibility of differential predation on podded and unpodded *P. incurvaria* as a mechanism for maintaining pod construction behaviour remains to be investigated.

This same crypticity may, however, entail an associated risk of accidental ingestion by herbivores feeding on the host plant. Although potentially toxic secondary compounds have been isolated from *Dictyota bartayresii* (Norris and Fenical 1982), a number of herbivorous fish have been reported to feed on *Dictyota* species in other areas of the Caribbean (Randall 1967, Earle 1972). The importance of such incidental ingestion as a source of *P. incurvaria* mortality remains unknown.

Finally, the possession of a portable food reserve may be of some advantage to *P. incurvaria*, particularly if individuals are periodically separated from their primary food plants. In shallow water habitats, *P. incurvaria* may be easily detached from its host plant by high current flow or wave action, and thus carrying an algal box-lunch may be essential.

**Summary**

The algal-dwelling habit of the herbivorous amphipod *Pseud amphithoides incurvaria* is a unique instance of a portable domicile constructed from a primary food plant. The range of *P. incurvaria* is extended to include the western Caribbean and the Bahamas. The occurrence of these amphipods on two new brown algal hosts in the Dictyotaceae, *Dictyota bartayresii* and *D. ciliolata*, is reported. *Pseud amphithoides incurvaria* occurs on *D. bartayresii* from 1.5–27 m depths in the vicinity of Carrie Bow Cay, Belize. Habitat and local distribution are described for *P. incurvaria* population in a shallow water back-reef location. Observations of feeding behaviour and the sequence of pod construction are reported.

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