

The urocoptid closing device, rare and remarkable  
(Gastropoda, Pulmonata, Urocoptidae)

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The structure of the urocoptid closing device (UCD) was studied under the SEM in the only species in which it has been reported to occur. Over 40 urocoptid species were searched in vain for additional occurrences. When moistened, the UCD expands and may function in an analogous way to the clausiliid clausilium. The two devices are clearly not homologous.

Key words: Gastropoda, Pulmonata, Urocoptidae, Clausiliidae, shell aperture, urocoptid closing device, clausilium.

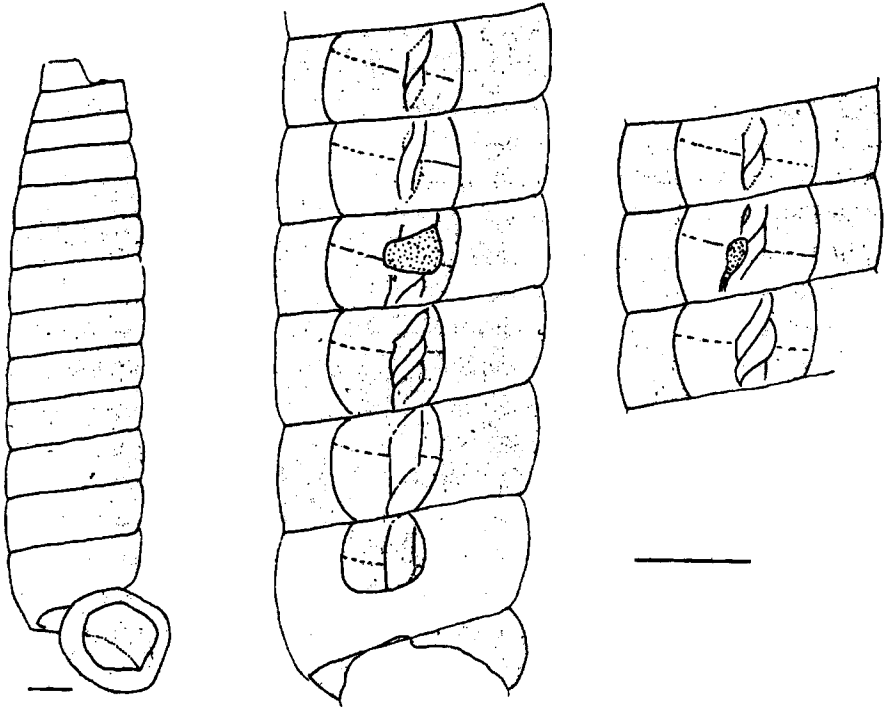
## INTRODUCTION

The wide variety of conchological elaborations of the urocoptid columella have been exhaustively illustrated by Pilsbry (1903, 1904), and some of these illustrations subsequently published by Zilch (1960). They typically take the form of one or more spiral lamellae, which may run the entire length of the shell or be confined to just one or two whorls. Sometimes these lamellae extend into ledges, the edges of which may become serrate or radially spinose. In the genera *Mychostoma* Albers, 1850, and *Apoma* Beck, 1837, as well as in several species of *Urocoptis* (*Spirocoptis*) Pilsbry, 1902, the columella is distinctly thickened. These thickenings may be single or double, and in some species may be beaded.

Axial lamellae in the lower whorls are postulated to have a protective function (Pilsbry, 1903: xvi; Gittenberger, 1996). The function of thickenings is uncertain but they certainly serve to strengthen the shell. It is noticeable that in the upper whorls of urocoptid shells which decollate, the columella is noticeably thinner. Spiral thickenings and lamellae may additionally provide channels to help align and support the free retractor muscles, principally the columellar muscle which supports the shell above the head-foot of the crawling snail (Paul, 1983); this is particularly important in groups as the Urocoptidae with elongate shells.

In addition to these modifications of the columella, at least one species of urocoptid possesses a closing device. This urocoptid closing device (= UCD) was initially observed by G. H. Clapp of Pittsburgh, Pennsylvania, but a description was first published by Pilsbry (1903: 97-98, pl. 1 figs 14-15) for the Jamaican *Mychostoma album* (C. B. Adams, 1849) var. *occidentalis* Pilsbry, 1903, for which the type locality is the Great Valley estate,

Hanover, and var. *minima* Pilsbry, 1903, from Swift River. Pilsbry stated that the UCD resembles the clausilium of the Clausiliidae; he described it as a tongue-shaped, whitish process continuous with the solid axis of the shell, situated in the fifth whorl from the base. Paul (1983: fig. 4B, C [our figs 2, 3]) also illustrated the UCD, which he found in only a single population. He referred this population to a complex comprising the dextral forms of *Mychostoma*, which includes *M. album*, but for which he considered the epithet *alabastrina* L. Pfeiffer, 1845 (fig. 1) to have priority. This UCD was situated in whorls 4-5 where, in this species, the columella has become markedly thickened.



Figs 1-3. *Mychostoma alabastrina* (L. Pfeiffer, 1845), Jamaica. 1, shell shape of a syntype from an unknown locality; 2, 3, details of shells from Great Valley Estate, Hanover, showing the location of the UCD, stippled, on the columella. Scale bars 1 mm. After Paul, 1983: figs 2A, 4B, 4C.

## SURVEY

Using a scanning electron microscope we studied the structure of the UCD in a dry shell of *Mychostoma alabastrina* (L. Pfeiffer, 1845) from Jamaica, Great Valley Estate, Hanover (fig. 4), in the collection of the National Museum of Natural History, Leiden. The strongly wrinkled UCD (fig. 4B, C) is connected to the smooth columella by a broad zone in which the two extremely different surface types are connected without any clear boundary (fig. 4A).

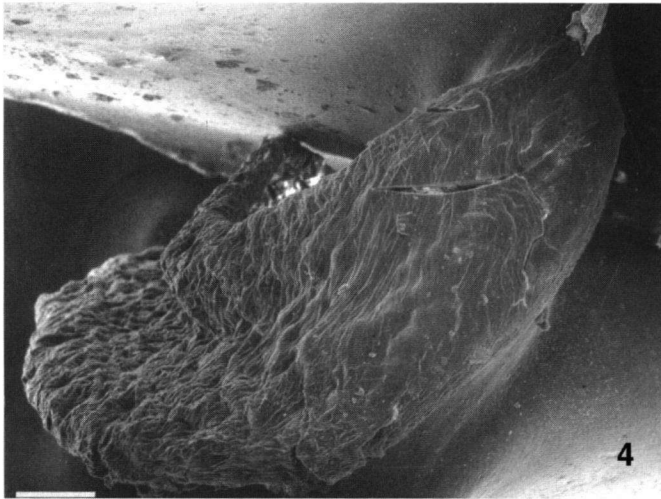


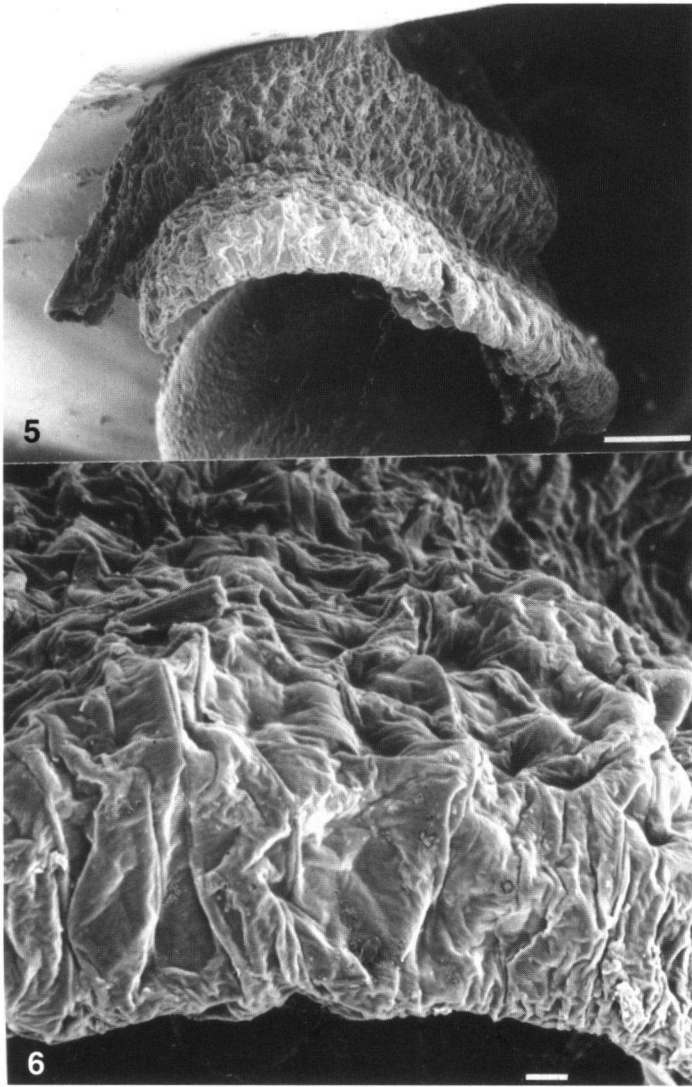
Fig. 4. The UCD in a dry shell of *Mychostoma alabastrina* (L. Pfeiffer, 1845); the connection to the columella. Jamaica, Great Valley Estate, Hanover; Colln National Museum of Natural History, Leiden. Scale bar 100  $\mu\text{m}$ . SEM photograph by J. Goud (Leiden).

We have also undertaken a broad survey of the Urocoptidae searching for any further occurrence of the UCD. This included over 40 species in 14 genera from the three sub-families Urocoptinae, Eucalodinae and Microceraminae in the collections of the British Museum (Natural History) (Table 1). Most were dry shells, but it is possible to examine these for presence of a UCD in a non-destructive way by using very strong transmitted light, as recommended by G. H. Clapp, the original finder, in a letter to E. R. Sykes dated 1902 and housed in the BM (NH); this was followed where necessary by internal examination of the shell. The small number of alcohol-preserved shells were dissected.

UCDs were recorded only in *M. alabastrina*. A total of 14 lots of *M. alabastrina*, all dry, were examined; of a total of 114 individual shells, 51 (45%) contained the UCD. In all cases the UCD occupied the 5th or 6th whorl. Pilsbry (1903: 97-98) stated that the UCD becomes flexible when wet, though it is not sufficiently large to occlude the entire cavity of the shell whorl. We were able to confirm the first part of this statement, but observed that when moistened the UCD expanded slightly, the wrinkles on its surface disappeared, and it was in fact able to occlude the whole cavity. Pilsbry also described the structure as being made of "conchiolin covered with an unconsolidated layer of lime crystals"; again, the first part of the statement appears to be true, but the crystals are clearly situated within the conchiolin matrix of the device.

## DISCUSSION

Paul (1983) has undertaken a phylogenetic analysis of Jamaican urocoptid genera, in which *Mychostoma* emerges as an advanced group of Apominae. There is no reason to believe that the UCD is anything more than an autapomorphy of a single species, or possibly species complex, of this genus.



Figs 5, 6. *Mycostoma alabastrina* (L. Pfeiffer, 1845), the structure of the UCD, close to the end of the process. Jamaica, Great Valley Estate, Hanover; Colln National Museum of Natural History, Leiden. 6, detail of 5. Scale bars 100  $\mu\text{m}$  (5) and 10  $\mu\text{m}$  (6). SEM photographs by J. Goud (Leiden).

The UCD is attached to the columella distally from the aperture, and the animal withdraws above the level of it. The function of the UCD is therefore most probably protective as it would tend to oppose any entry from the aperture direction. It is uncertain why the UCD is missing in slightly more than half the specimens that were investigated, but post-mortem loss seems the most likely explanation although there was no attachment scar visible on the columella.

It is unlikely that this peculiar device would have a simple, single-gene background. There is no obvious homologue structure known from closely related species. Therefore, its evolutionary origin is unclear.

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Table 1. The urocoptid species searched. Nomenclature after Richardson (1991).

<i>acus</i> (L. Pfeiffer, 1841), <i>Tomelasmus</i>	<i>humboldtii</i> (L. Pfeiffer, 1840), <i>Pychnoptychia</i>
<i>album</i> (C. B. Adams, 1849), <i>Mychostoma</i>	<i>insuflatus</i> Jaume & Torre, 1972, <i>Tetrentodon</i>
[= <i>M. alabastrina</i> (L. Pfeiffer, 1845)]	<i>intermedium</i> Sowerby, 1875, <i>Spirostemma</i>
<i>albocrenata</i> (L. Pfeiffer, 1863), <i>Paracallonia</i>	<i>interruptum</i> (L. Pfeiffer, 1857), <i>Idiostemma</i>
<i>angustior</i> (L. Pfeiffer, 1864), <i>Capillacea</i>	<i>irroratus</i> (Gundlach, 1856), <i>Tomelasmus</i>
<i>apiostoma</i> (L. Pfeiffer, 1856), <i>Epirobia</i>	<i>ipswichensis</i> Pilsbry, 1903, <i>Spirostemma</i>
<i>caymanensis</i> (Pilsbry, 1930), <i>Brachypodiella</i>	<i>keineri</i> (L. Pfeiffer, 1846), <i>Microceramus</i>
<i>chemnitzianum</i> (Férussac, 1821), <i>Apoma</i>	<i>lescallei</i> Jaume & Torre, 1972, <i>Brachypodella</i>
<i>chordata</i> (L. Pfeiffer, 1855), <i>Brachypodiella</i>	<i>menkeana</i> (L. Pfeiffer, 1853), <i>Urocoptis</i>
<i>clara</i> (L. Pfeiffer, 1865), <i>Liocallonia</i>	<i>microstoma</i> (L. Pfeiffer, 1861), <i>Coelostemma</i>
<i>collaris</i> (Férussac, 1821), <i>Brachypodiella</i>	<i>palmeri</i> Bartsch, 1906, <i>Holospira</i>
<i>costata</i> (Guilting, 1828), <i>Brachypodiella</i>	<i>plumbea</i> (L. Pfeiffer, 1864), <i>Badiofaux</i>
<i>cuestai</i> Torre, 1930, <i>Liocallonia</i>	<i>poeana</i> (Orbigny, 1841), <i>Cochlocinella</i>
<i>diminutum</i> (C.B. Adams, 1851), <i>Apoma</i>	<i>princeps</i> (C.B. Adams, 1851), <i>Spirostemma</i>
<i>dautzenbergiana</i> (Crosse, 1890), <i>Callonia</i>	<i>procera</i> (C.B. Adams, 1850), <i>Urocoptis</i>
<i>dunkeri</i> (L. Pfeiffer, 1845), <i>Spirostemma</i>	<i>prunosa</i> (Morelet, 1849), <i>Necocoptis</i>
<i>elatior</i> C.B. Adams, 1851), <i>Spirostemma</i>	<i>pupaeformis</i> (C.B. Adams, 1850), <i>Urocoptis</i>
<i>elegans</i> (L. Pfeiffer, 1863), <i>Microceramus</i>	<i>shuttleworthiana</i> L. Pfeiffer, 1856), <i>Pychnoptychia</i>
<i>gossei</i> (L. Pfeiffer, 1845), <i>Microceramus</i>	<i>simplex</i> (C.B. Adams, 1849), <i>Simplicervix</i>
<i>gracilis</i> (Adams, 1851), <i>Anoma</i>	<i>truncatula</i> (Lamarck, 1822), <i>Amphicosmia</i>
<i>guitarti</i> Jaume & Torre, 1972, <i>Heterocoptis</i>	<i>variabilis</i> (L. Pfeiffer, 1863), <i>Macroceramus</i>