DISTRIBUTION AND FEEDING BEHAVIOUR OF *CHLAMYDEPHORUS GIBBONSI* IN THE WESTERN CAPE PROVINCE OF SOUTH AFRICA

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Abstract *The purpose of this study was to investigate the distribution and feeding behaviour of the South African predatory slug,* Chlamydephorus gibbonsi *Binney, 1879 (Mollusca: Gastropoda), which is endemic to the eastern region, but has now spread to the Western Cape province (WCP). A total of 210* C. gibbonsi *specimens were collected from the WCP between January 2012 and December 2015. Slug numbers were found to steadily increase from nine specimens collected in 2012, to 111 specimens collected in 2015, indicating establishment of* C. gibbonsi *in its new habitat. Of the sample sites studied, 13.7% were found to be positive for* C. gibbonsi*, including sites in George, Knysna, Swellendam, Hermanus and Stellenbosch. The habitats of positive sample sites were all commercial nurseries. Feeding behaviour of* C. gibbonsi *is described using an earthworm of the genus* Amynthas*.*

Key words *Chlamydephoridae; Distribution; Feeding; Invasion; Earthworms*

INTRODUCTION

Terrestrial pulmonate molluscs (both snails and slugs) are commonly herbivores feeding on algae, fungi and plant material, hence their interest as economically significant pests. However, occasionally species that are primarily herbivorous will feed on living invertebrates, or decaying flesh of dead animals, and under extreme conditions, can resort to cannibalism (South, 1992). Obligate carnivory occurs in several slug families e.g. Chlamydephoridae, Papillodermidae, Plutoniidae, Rathouisiidae, Testacellidae, as well as some snail species (Herbert, 2000).

The families Rhytididae, Streptaxidae and Chlamydephoridae are all carnivorous terrestrial molluscs indigenous to South Africa, the latter of the three the sole slug representative. Chlamydephoridae are typically narrow, firm and dry to the touch and have a characteristic postero-dorsally positioned pneumostome. Additionally, the dorsal surface is marked with well-defined grooves radiating from the pneumostome. An anatomical review of the family was conducted by Watson (1915), and taxonomy and biogeography was examined by Forcart (1967), van Bruggen (1969, 1978) and Herbert (1997). Like many carnivorous slugs Chlamydephoridae are secretive, well camouflaged, and are subterranean, so little is known of their behaviour and distribution.

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Chlamydephoridae are represented by nine species in South Africa, and five are from the Eastern region, with *Chlamydephorus gibbonsi* Binney, 1879, *Chlamydephorus burnupi* (Smith, 1892) and *Chlamydephorus dimidius* (Watson, 1915) thought to be endemic to the area. *Chlamydephorus gibbonsi* occurs in a wide range of habitats, spanning open thornveld to indigenous forests. Initial distribution was thought to range from eastern Zimbabwe, through to the Eastern Cape of South Africa (Herbert, 1997). Herbert & Kilburn (2004) noted that *C. gibbonsi* had been found in KwaZulu-Natal at the Ngome Forest, Lake Sibaya, Colenso and Pietermaritzburg, and in the Eastern Cape from Transkei and East London. Herbert (1997), however, also found a single outlying specimen in the Western Cape, as did Ross *et al*. (2012), indicating that the species has invaded the WCP. To date, very little is known of the distribution or the invasive behaviour of *C. gibbonsi*.

The feeding habits of chlamydephorids are poorly understood, and their proposed prey of earthworms and other molluscs, is based on distinctive anatomical features such as dagger-like teeth and a short digestive system. Herbert

(2000) reported observations of *C. dimidius* feeding on snails, and *C. burnupi, Chlamydephorus bruggeni* (Forcart, 1967) and *Chlamydephorus sexangulus* (Watson, 1915) have been reported feeding on pill millipedes (Herbert 2000). However, the feeding habits of *C. gibbonsi* have yet to be fully elucidated. Watson (1915) proposed that they feed on earthworms, but gave no details of observations, and Herbert (2000) supported this proposal based on the fact that the slug has subterranean habitats.

During fieldwork in George (33°59'27''S 22°30'54''E), a specimen of *C. gibbonsi* was observed feeding on an earthworm (*Amynthas* sp.). The two invertebrates had been placed in the same sample box, and although the killing process had not been observed, the earthworm was alive when collected. This observation confirmed the proposal of Watson (1915) and Herbert (2000), but provided little information regarding the killing process. Therefore, additional samples of *C. gibbonsi* were brought back to the laboratory in order to explore this behaviour further. This study details observations on the distribution and feeding behaviour of *C. gibbonsi* in the Western Cape of South Africa.

MATERIALS AND METHODS

Fifty-one sample sites around the Western Cape were examined for slugs between January 2012 and December 2015. Habitats included domestic gardens, nurseries, agricultural land, forest areas and road side verges. A total of one hour was spent at each location, focusing on as many different vegetation and microhabitat types as possible. Collected slugs were stored in sealed containers at one hundred percent humidity, and transported to the laboratory where they were identified using morphological analysis and dissection of genitalia.

Under laboratory conditions, single specimens of *C. gibbonsi* were placed in plastic containers lined with moist paper towels. Slugs were kept in isolation for three days to allow for starvation. Individual earthworms (*Amynthas* sp.) were then added to the experimental arena. Feeding behaviour was recorded and photographed.

RESULTS

A total of 2876 slugs were collected in the WCP between 2012 and 2015 and of these, 7.3% were

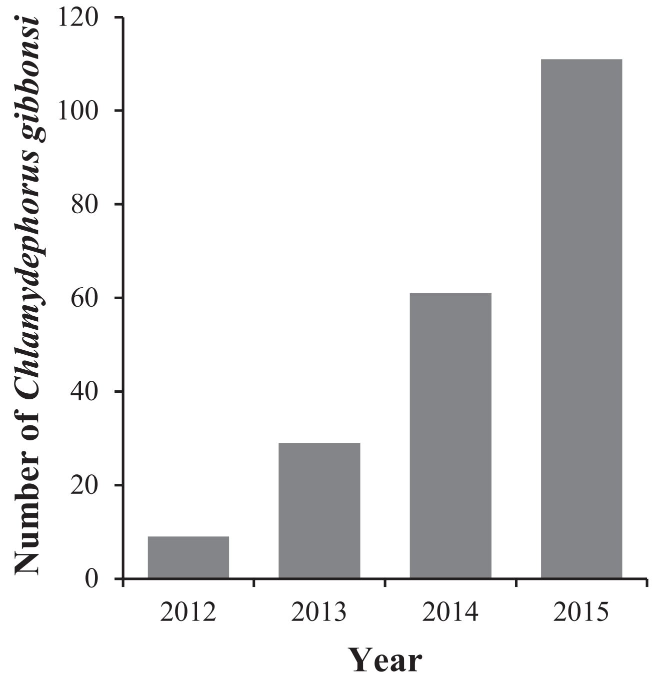

Figure 1 Number of *Chlamydephorus gibbonsi* specimens collected in the Western Cape between 2012 and 2015

C. gibbonsi. Numbers of *C. gibbonsi* were found to steadily increase, from nine specimens collected in 2012, to 111 specimens collected in 2015 (Fig. 1). Seven sample sites, all commercial nurseries, were positive for *C. gibbonsi*: three sites in George (33°59'27''S 22°30'54''E; 33°59'40''S 22°32'19''E; 33°59'38''S 22°23'35''E) and single sites in Knysna (34°01'57''S 22°59'22''E), Swellendam (34°02'21''S 20°32'49''E), Hermanus (34°24'41''S 19°12'01''E) and Stellenbosch (33°54'24''S 18°50'38''E).

On encountering prey *C gibbonsi* spends an extended time exploring the surface of the earthworm with its inferior tentacles (Fig. 2A). It then slowly evaginates the anterior part of the buccal chamber through the mouth (Fig. 2B). By doing so, the odontophore covered by the radula is carried forward, but initially does not protrude from the buccal cavity. The odontophore is then rapidly thrust forward to collide with the prey, followed by a rapid retraction in a piston-like action. During this action, radular teeth are lodged into the body wall of the prey, resulting in the prey being partly drawn into the slug's mouth. Simultaneously, the evaginated part of the buccal cavity is also invaginated.

The finer details of the effective capturing and swallowing process can be understood by examining the morphology of the concerned structures.

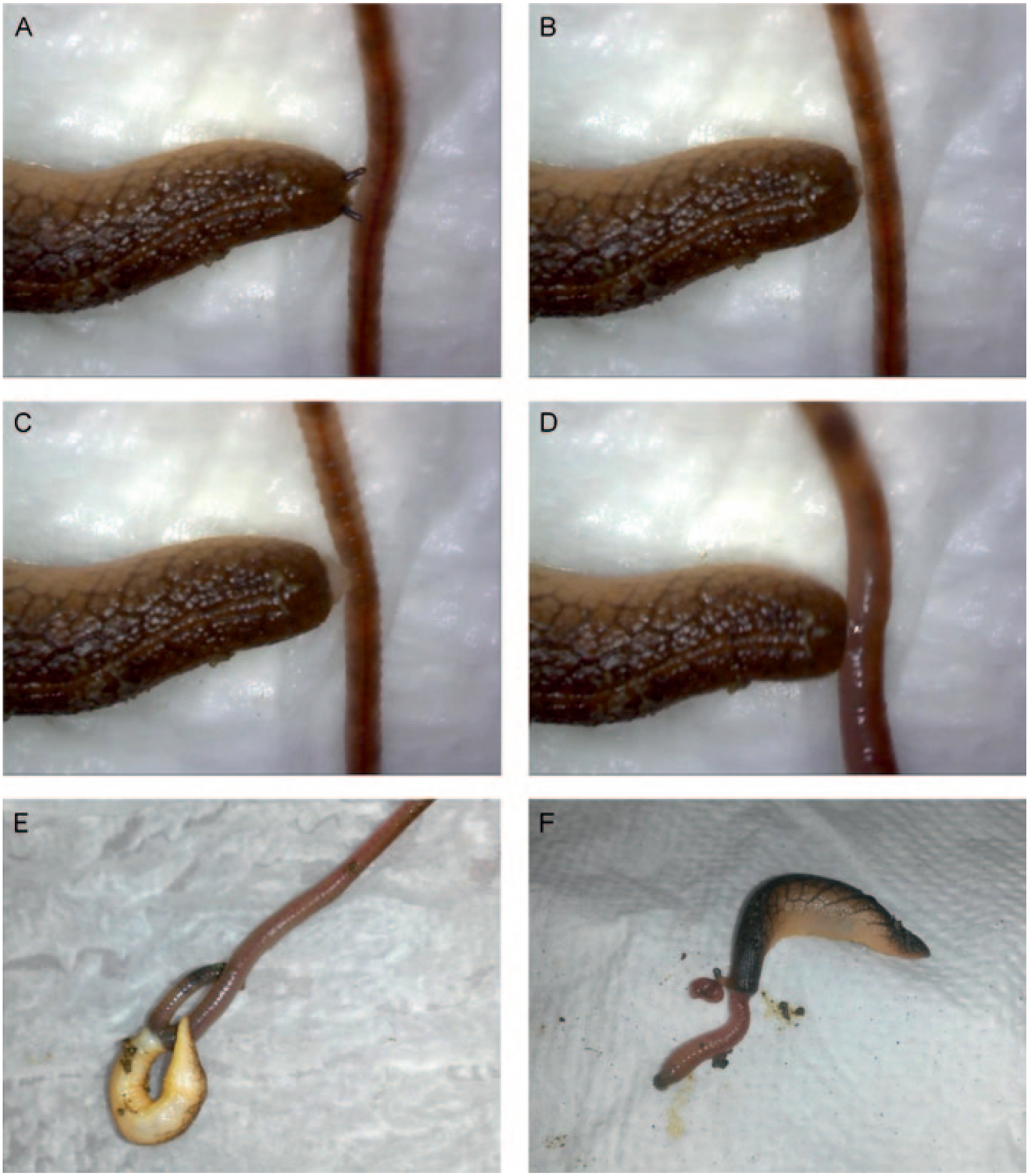

Figure 2 *Chlamydephorus gibbonsi* capturing and killing the *Amynthas* sp. A, *Chlamydephorus gibbonsi* exploring the surface of the worm with its inferior tentacles. B, Evagination of the anterior section of the buccal cavity. C, D, Ejection of odontophore and hooking the hapless annelid on long radular teeth. E, F, Feeding and swallowing of the worm through a combination of suction and movement of the odontophore.

The process of hauling the prey into the alimentary system is permitted by adaptations of the radular apparatus. Firstly, the odontophore is gutter shaped, and its inner surface and anterior edge is covered by the radular membrane. The latter carries numerous transverse rows of radular

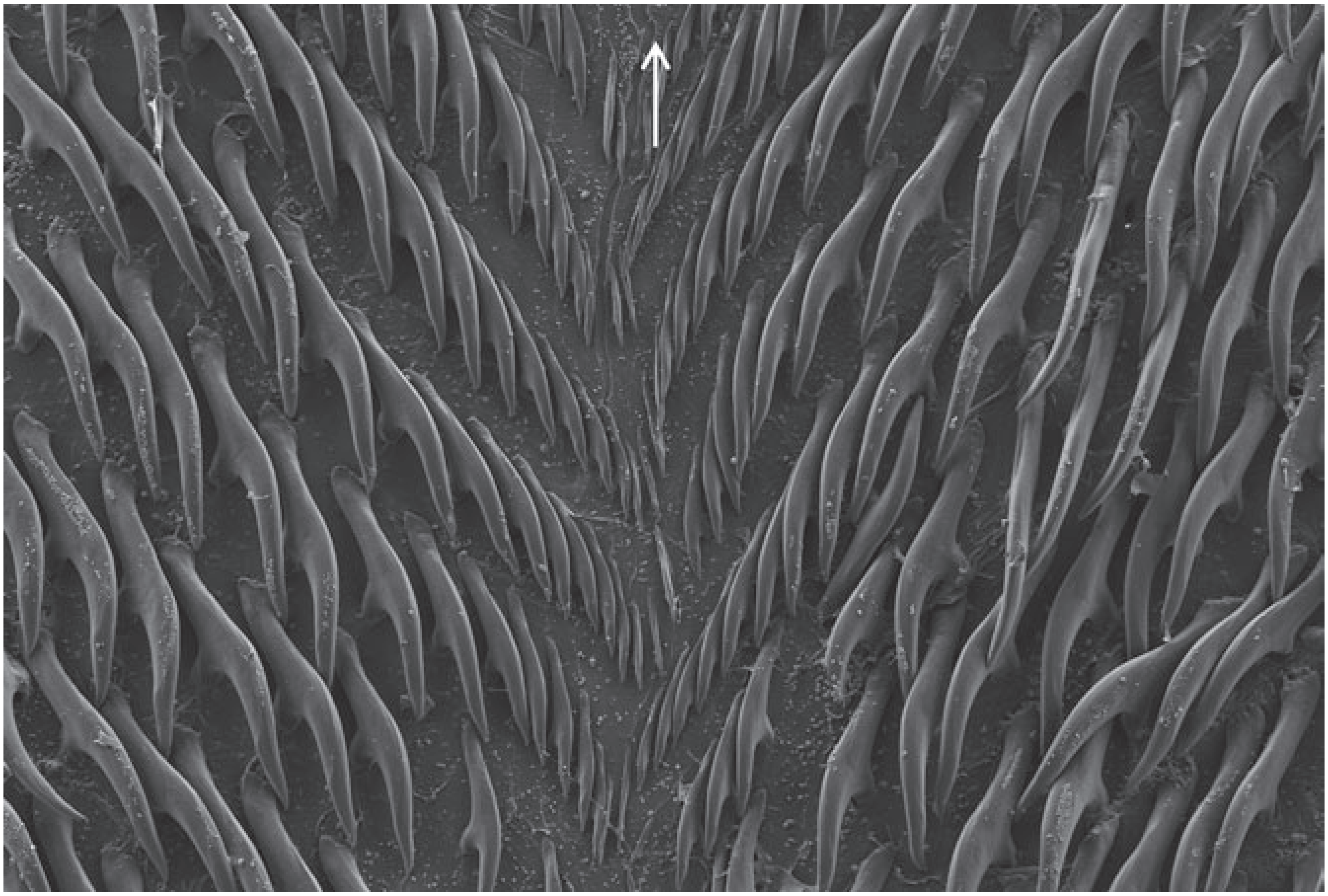

Figure 3 Radula of *Chlamydephorus gibbonsi* (magnification approximately 101x), showing the under developed centrally located teeth, as well as the more lateral, more developed teeth. Arrow indicating the direction of the mouth opening

teeth. Secondly, these teeth are long, sharp, dagger shaped and project posteriorly within the buccal mass. The central (median) tooth of each transverse row, as well as a few admenian teeth on either side, are small and under developed. Following each row laterally, the teeth gradually enlarge, and from approximately the tenth lateral tooth onwards, appear fully developed (Fig. 3). Each fully developed lateral tooth has the shape of a long curved thorn, and consists of a cusp and a basal plate, which are carried on the radular membrane. The cusp consists of an apical and basal portion. The sharply pointed apical portion (Fig. 4A) is slightly flattened on its ventral side, and extends posteriorly within the buccal bulb. At its base, it passes over into the cylindrical basal portion, which gradually, but strongly, enlarges towards its base, especially in the antero-posterior plane (Fig. 4B). Near its base, this portion is also strongly curved ventrally to form an angle of approximately ninety degrees, where it transmits into the basal plate. The latter is an elongated disc-shaped structure implanted, and longitudinally orientated, on the radular membrane. It is important to note that this base plate is deeply concave as seen from its ventral side (Fig. 4C). The concavity gives the impression that it could function like an articulation socket. At the same time, the elongated basal plate would enable the cusp of each tooth to maintain its posterior orientation, even when traction is exerted on it during the process of inhauling of the prey. The anterior margin of the radular membrane is fused to the ventral and lateral walls of the buccal cavity ventrally, and laterally to the anterior margin of the odontophore.

Bearing the above mentioned morphology of the radula in mind, the capturing and hauling of the prey can further be elaborated on. During the final stages, when the odontophore is rapidly thrust towards the prey, it is clear that the inextensible radular membrane has to slide

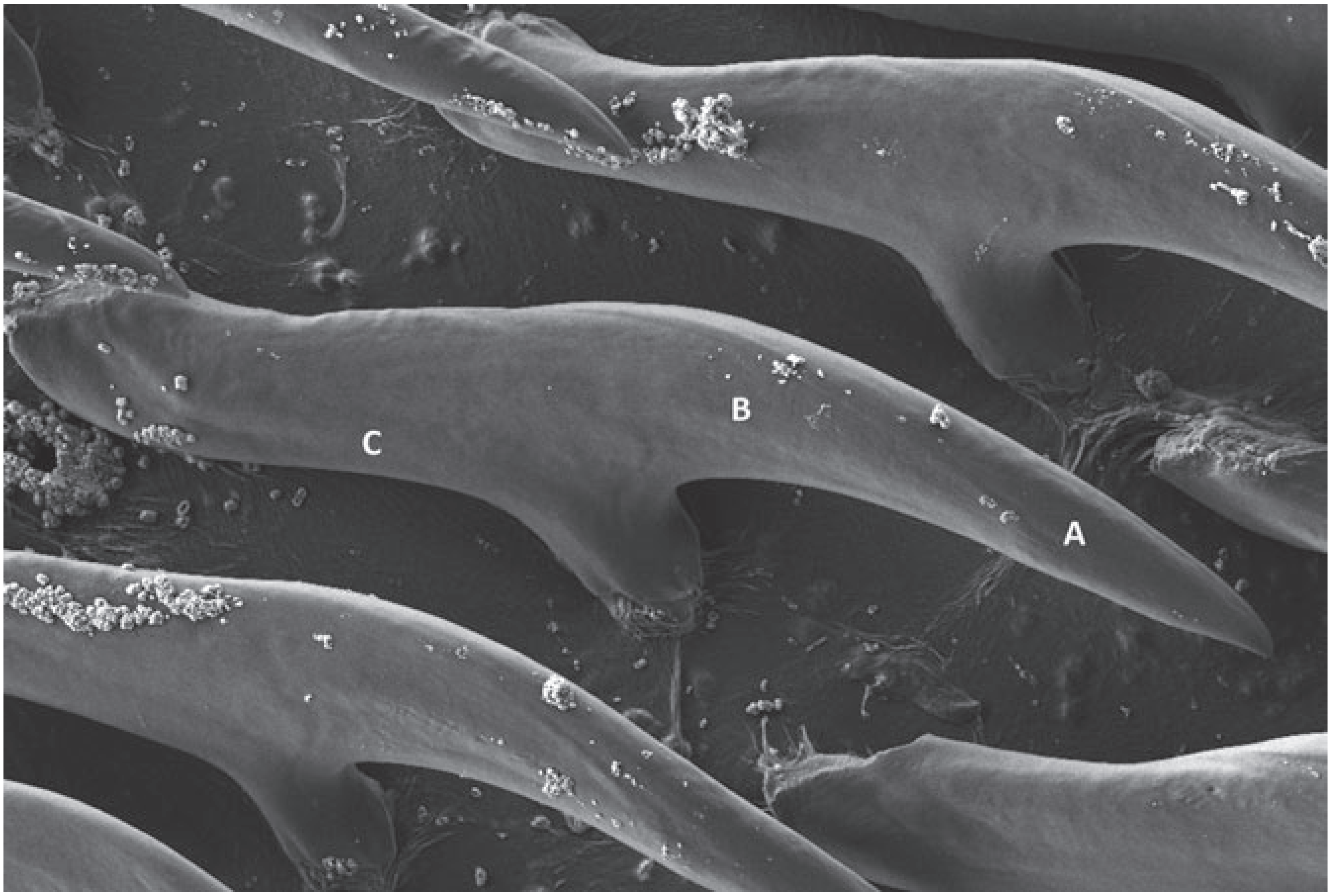

Figure 4 Dorso-lateral view of a well-developed lateral tooth of *Chlamydephorus gibbonsi* (magnification approximately 450x) displaying; A, the apical portion with a sharp tip, orientated posteriorly; B, basal portion; and C, the deeply concave basal plate implanted on the radular membrane.

over the surface of the odontophore, and this will carry the teeth of at least the anterior part of the radula to glide over the anterior edge of the odontophore. As each of these curved teeth transgress the anterior edge of the odontophore, they naturally splay and flip over to then point anteriorly and laterally. This "flipping-over" action of each tooth could be facilitated by the concavity on the ventral side of the basal plate of each tooth. On impact with the surface of the prey, these now anteriorly directed sharp teeth thrust into the body wall of the prey. The odontophore then rapidly retracts and the teeth crossing the anterior edge of the odontophore during this return stroke will flip back to restore their original, posteriorly directed position thus performing. a grabbing action on the prey, and hauling it into the buccal cavity of the slugs (Fig. 2C, D). As mentioned above, the anterior section of the buccal cavity is simultaneously invaginated during the retraction of the odontophore. This exerts suction on the prey, thus aiding its intake. The swallowing process of the prey (Fig. 2E, F) involves the radula repeatedly moving anteriorly and posteriorly within the buccal cavity. With each anterior movement, the teeth will be withdrawn from the prey only to hook further onto its body, when the next posterior movement commences. The entire capturing and swallowing process takes approximately one hour.

DISCUSSION

Interest in the science and management of biological invasions has expanded in recent years due to the sharp increase in the introduction of invasive species in virtually all major habitats on Earth (Mack *et al*., 2000). An organism is considered invasive when it successfully establishes and thrives outside its natural range. Successful invasions arise from the transportation of alien species from one location to another, by activities of man, either intentionally or unintentionally, resulting in the establishment of these species in a new geographical region (Perrings *et al*., 2010). Invasions are occurring at an extraordinary rate due to the expansion of trade and the economical ease of travel. The introduction of alien species can have severe consequences on agricultural and horticultural industries, as well as having a direct impact on the economy, natural environments, biodiversity and human health (Mack *et al*., 2000).

The observations of this study indicate that *C. gibbonsi* has successfully invaded the WCP and is now widespread, as far west as Stellenbosch. Previous studies by Herbert (1997) and Ross *et al*., (2012) found only a single specimen of *C. gibbonsi* in the Western Cape, however, this study demonstrates that slug numbers have increased in recent years. In order to regulate this process, it is important to have an increased understanding of the causes and mechanisms of the spread of these species. Reports from around the world suggest that the horticultural industry acts as a vector for invasive species (Cowie *et al*., 2008). This can be confirmed in this instance, with positive sample sites being commercial nurseries. We propose that the slug has been spread to the WCP through transportation of plant material.

We herewith confirm that *C. gibbonsi* feeds on earthworms and this process is documented in figure. 2. This procedure is very similar to the feeding habits of the carnivorous family Testacellidae, which also prey on earthworms, as well as other molluscs (Webb, 1893; Quick, 1960). Crampton (1975) provides a comprehensive study of the feeding process of *Testacella*, detailing a two phased process involving an initial stage of seizing the worm and drawing the first part of the body through the mouth; and then a second phase whereby the remainder of the worm is ingested. This process was previously observed by Stokes (1958) and further described and photographed by Liberto *et al*. (2011), who observed that feeding generally takes up to one hour.

The introduction of *C. gibbonsi* to the WCP may have an impact on earthworm abundance, now that it has been confirmed that they play a role in the diet of *C. gibbonsi*. Future work should monitor the impact of *C. gibbonsi* on earthworm populations, as earthworms are important to the soil biota (Lavelle *et al*. 1997), nutrient dynamics (Schmidt & Curry, 1999), decomposition processes (Bonkowski *et al*., 2001), soil microorganisms (Clapperton *et al*., 2001), microarthropods (McLean & Parkinson, 1998), seed germination (Grant, 1983) and plant growth (Brussaard, 1999). Furthermore, they also play a substantial part of the diet of aboveground invertebrate (Guillemain, Loreau & Daufresne, 1997) and vertebrate predators (Ferrari & Weber, 1995).

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