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ABSTRACT


The phylogeny of the genus *Udonella* has been disputed for quite some time, but recent phylogenetic analysis of molecular data confirms that the genus is a monopisthocotylean monogenean. Specimens of *Udonella myliobati* parasitizing the copepod *Lepeophtheirus natalensis*, an ectoparasite of the spotted ragged-tooth shark, (*Carcharias taurus*), were collected and studied. A total of 771 monogenean specimens were recovered from 54 infected copepods examined, with a mean intensity of 14.3 worms per copepod. Most of the monogeneans were found attached to the dorsal surface of the lateral and frontal marginal membranes of the copepod carapace. Eggs, with filaments and adhesive discs, were found ventrally on the host, mainly attached to the maxillae and maxillipeds, in clusters of 12–14. Observations on the morphology, distribution and behaviour of this monogenean are presented with the aid of light and scanning electron microscopy.

Keywords: *Carcharias taurus*, *Lepeophtheirus natalensis*, Monogenea, South Africa, *Udonella myliobati*

INTRODUCTION

All described species of the genus *Udonella* Johnston, 1835 are hypersymbionts found exclusively and commonly on caligid copepods parasitizing marine fish (Nichols 1975). In spite of their ubiquity, the phylogenetic position of *Udonella* has long been disputed and has kept many a systematist in discussion since the discovery of the type species. The type species, *Udonella caligorum* Johnson, 1835, was originally regarded as a leech, but was later moved to the Monogenea. However, because it possesses a non-ciliated larva and lacks hooks at any stage of development, some workers doubted its affinity to the Monogenea. The lack of hooks may be an evolutionary result of its copepod association, whose hard exoskeleton is in all likelihood not suitable for hook penetration (Littlewood, Rhode & Clough 1998). Notwithstanding this, *Udonella* has some similarities to a rhabdocoelian turbellarian, and this led Ivanov (1952) to erect a new class, Udonelloidea, to accommodate it. Ivanov & Mamkaev (1973) suggested that *Udonella* should be placed in a new order, Udonellida, which should be included with the neopochar Turbellaria. This proposal was accepted by some workers, but rejected by others. Littlewood et al. (1998) concluded, after phylogenetic analysis of molecular data (from complete 18S rRNA and partial 28S rRNA genes of a variety of plathyhelminths),

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that *U. caligorum* is a monopisthocotylean monogenean. They further suggested possible sister group status with the monogenean genus *Gyrodactylus*. This conclusion is also supported by previous ultrastructural studies of the tegument and some other structures, such as sensory receptors and spermatozoa (Aken’Ova & Lester 1996).

The discovery of a species of *Udonella*, later identified as *Udonella myliobati* (Guberlet, 1936), provided Aken’Ova & Lester (1996) with the opportunity to redescribe the species, elaborate on its behaviour and review the genus. The finding of this species in South African waters provided us with the chance of re-examining its morphological features and behaviour.

**MATERIALS AND METHODS**

Caligid copepods, later identified as *Lepeophtheirus natalensis* Kensley & Grindley, 1973, were observed infecting the skin of live spotted ragged-tooth sharks (*Carcharias taurus*) in captivity in the aquarium of the Oceanographic Research Institute (ORI) in Durban, South Africa. The copepods were collected using a device, made by a technician at ORI, which operates like a vacuum cleaner. This device was gently applied to the skin of the sharks during a cage dive in the tanks. Collected parasites were preserved and fixed in 70% ethanol. When the copepods were later examined in the laboratory, they were found to be infected by monogeneans of the genus *Udonella*. Some detached monogeneans, as well as some copepods with attached monogeneans, were stained in Horen’s trichrome stain, counterstained with alum carmine, mounted in Canada balsam and examined under a standard microscopy. Cleaning of copepod specimens for SEM studies was facilitated with the aid of a BRANSON 3200 ultrasonic cleaner after which the material (copepods and monogeneans) was dehydrated through graded ethanol (70–100% at 5–10 min. intervals), critical point dried (CPD) and sputter-coated with gold. Measurements were taken from 20 mature specimens. All measurements are given in millimeters.

**DESCRIPTION**

*Udonella myliobati* (Guberlet, 1936); Aken’Ova & Lester, 1996

Synonym: *Calinella myliobati* Guberlet, 1936

The total length of the elongated, sub-cylindrical body (Fig. 1 and 2), including the posterior haptor, is 1–1.24 with a maximum width of 0.24–0.42 at midbody. The terminal posterior haptor is more or less rounded, 0.22–0.232 x 0.24–0.248, and lacks hooks or any other structures (Fig. 3). The anterior
end of the body is notched to form two lateral lobes
where the cephalic glands open into the head organs
(Fig. 1). The glands are situated laterally in the an­
terior quarter of the body. The mouth opening (Fig.
4) is subterminal, situated behind the indentation on
the ventral surface at the anterior end of the body.
The mouth opening leads to a well-developed, elon­
gated, eversible pharynx, measuring 0.14–0.16 ×
0.096–0.1. The intestinal caecum is large and sack­
like, extending to near the posterior end of the body.
Occasionally, the contents of the intestinal caecum
are dark in colour and dark granules are seen to be
expelled via the pharynx and mouth opening.

The male reproductive system (Fig. 1) is represented
by a single large, roughly round testis, measuring
0.108–0.12 in diameter, situated posterior to the
ovary in the middle of the body. No cirrus or cirrus­
sac is seen, but in some specimens a small seminal
vesicle, the size of which varies from specimen to
specimen, is seen near the genital pore. The genital
pore is situated ventrally in the anterior quarter of the
body (Fig. 4). The female genital system comprises
a single large, round ovary, 0.14–0.156 × 0.064–0.07
in diameter. The vitellarium consists of large follicles,
extending roughly from the level of the genital pore
to the posterior end of the body (Fig. 11). In the re­
gion anterior to the testis, the follicles are restricted
to the lateral margins, but posterior to the testis the
follicles fill the space on the dorsal side of the body.
The pyriform-shaped egg (Fig. 5, 6 and 8), 0.17–0.19
long with a maximum width of 0.064–0.070, is at­
tached by a thin filament, 0.054–0.066 long, to a
round adhesive disc, 0.052–0.06 in diameter.

**DISTRIBUTION AND OTHER OBSERVATIONS**

Very few male copepods were recovered and none
of these harboured any monogeneans. The per­
centage of infected female copepods, randomly selected
for inspection, was 100%. A total of 771 monogene­
anans of different stages of development were seen
attached to 54 copepods, with a mean intensity of
14.3 specimens per copepod. The range of infection
varied from one to 46 worms per copepod.

Most of the worms, both mature and immature, were
found on the dorsal surface of the carapace, attached
to the lateral and frontal marginal membranes. Very
few of them were attached to other parts of the cope­
pod body (e.g. the genital complex), and even fewer
were attached to the copepod egg sacs.

Most of the eggs were encountered on the ventral
surface of the copepod (Fig. 7), and were attached
in clusters (Fig. 6) primarily to the maxillae and maxil­
lipeds (Fig. 8). Very few eggs were attached to the
first thoracic leg and occasionally single eggs were
observed on other parts of the copepod body. The
number of eggs in each cluster varied from 12–14.

Some of the eggs had hatched and only their empty
capsules remained. Eggs have no operculum, and
observations on the hatched eggs suggested that
there possibly is a weak point in the structure of the

**Abbreviations:** m = mouth opening, g = genital pore
Observations on lesser-known monogeneans, *Udonella myliobati*

The anterior end of the egg capsule, which breaks as a result of pressure from the worm immediately before hatching. In the majority of hatched eggs, the anterior part of the capsule was very neatly detached, but only in a few cases the cut surface was torn (Fig. 6).

**DISCUSSION**

Guberlet (1936) described *Calinella myliobati* attached to *Trebius latifurcatus* Wilson, 1921 which parasitizes the stingray *Myliobatis californica* from Monterey Bay, California. Although Price (1938) synonymized the genus *Calinella* Monticelli, 1910 with *Udonella*, he did not discuss the taxonomic status of *C. myliobati*. Aken'Ova & Lester (1996) found some monogeneans attached to the copepod *Caligus epidemericus* parasitizing the yellow-fin bream, *Acanthopagrus australis* from Moreton Bay and other localities in Australia. Their specimens closely resemble those of Guberlet (1936) and they suggested that *C. myliobati* be placed in the genus *Udonella* in a new combination. The five known species of *Udonella* (*U. caligorum* Johnston, 1835, *U. myliobati* (Guberlet, 1936), *U. ophiodontis* Kay, 1945, *U. papillifera* Van der Land, 1967 and *U. murmanica* Kornakova & Timofeeva, 1981) have all been collected from the caligid copepod genera *Caligus*, *Trebius* and *Lepeophtheirus*, all known to parasitize marine fish.

The present material closely resembles Aken'Ova & Lester's (1996) description of *U. myliobati*, although the specimens are much larger in size with slight variation in the measurements of the various organs. In spite of this, we have no hesitation in identifying our specimens as *U. myliobati*. The present specimens were found attached to *L. natalensis* parasitizing spotted ragged-tooth sharks (*C. taurus*), and both represent new host records for *U. myliobati*. Moreover, this is the first geographical record of a species of the genus *Udonella* from the African seas.

The four sharks examined, were in the shark tank at ORI. They were caught off the coast of Natal and had been in captivity for about 18 years. Other parasitological investigations of several shark species, including *C. taurus*, done at the facilities of the Natal Sharks Board, revealed *L. natalensis* from *C. taurus*. A few unidentified egg capsules were found on one of these copepods, but none haboured any adult udonellids.

Our average burden of 14.3 worms per infected female copepod was much higher than that of 5.8 found by Kabata (1973) for *U. caligorum* on *Caligus elongatus*, but less than the 38.7 found by Aken'Ova & Lester (1996). Minchin & Jackson (1993) found the infection rates of *U. caligorum* on *Lepeophtheirus salmonis* highly variable, with the highest being 111 immature and nine adults on a single female copepod. It is, however, considered that the infection rate we recorded is much less than the actual rate. The vacuum-like device used to collect the copepods might have removed some but not all of the worms as many detached monogeneans were observed after preservation of the copepods. A similar observation was made by Minchin & Jackson (1993) who noted some unattached specimens of *U. caligorum* from *Lepeophtheirus salmonis* and *C. elongatus*.

The distribution of species of *Udonella* and their eggs on the copepod host varies considerably, and depends on both the species of *Udonella* and the copepod host species. Aken'Ova & Lester (1996) found that adult *U. myliobati* are more prevalent on the posterior half of the copepod *C. epidemericus* than on the anterior part. Kabata (1973) and Aken'Ova & Lester (1996) further reported a high prevalence of adult worms on the genital complex, but no worms were...
found attached to the ventral side of the copepod. Nichols (1975) found that adult worms of *U. caligorum* are more prevalent on the egg sacs of *Lepeophtheirus longipes* than on the carapace. In the present study adult and juvenile worms were more prevalent on the anterior part of the copepod than the posterior part, and no worms were attached to the genital complex. Minchin & Jackson (1993) found adult worms on *L. salmonis* predominantly on the dorsal posterior regions of the carapace, less frequently on the ventral surfaces and rarely on egg sacs. Adult and immature worms were also present predominantly on the dorsal carapace for *U. caligorum* collected from *C. elongatus*. Schram & Haug (1988) also observed a distribution of adult worms on *L. hippocoglossi* very similar to that of the present study.

Kabata (1973) found most of the eggs attached posteriorly on the genital complex and abdomen. Aken’Ova & Lester (1996) found 75% of unhatched eggs on the ventral and marginal parts of the genital complex. Our observation of egg distribution resembled that of Schram & Haug (1988) on *Lepeophtheirus hippocoglossi* who found that the eggs are attached to the underside of the copepod’s carapace at the base of the appendages, particularly the maxillae, but not the genital complex. Minchin & Jackson (1993) found eggs to be distributed mainly on the dorsal and ventral surfaces of the three posterior tagma of the copepod (fourth free thoracic segment, genital complex and abdomen). No eggs were reported attached to any of the cephalic appendages.

Sproston (1946) suggested that species of *Udonella* are detritus feeders, taking mucus and gill epithelium of the fish “kicked” back by the copepod. It has also been suggested that the mainly marginal distribution of the monogeneans on the carapace of the copepod enables feeding on superficial fish tissues (Kabata 1973). We believe that, in the present case, *U. myliobati* feeds directly on the epithelial cells of the skin of the shark. The dark colouration seen in the gut of the worms (Fig. 9) is possibly due to melanin from the shark epithelial cells in the diet. *Udonella* species, in common with other monopisthocotylean monogeneans, are epithelial browsers. This is very similar to the case of the monogenean *Macrogyrodactylus polypteri* parasitic on the skin of the fish *Polypterus senegalus*, in which Cable, Harris & Tinsley (1997) have clearly demonstrated, using histochemical techniques, that the dark colouration of the gut is due to the presence of melanin. Some of our specimens of *U. myliobati* were seen expelling dark granules via the pharynx and mouth opening, similar to those described for *M. polypteri*, as noted by Khalil (1970).

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REFERENCES


