Institute of Parasitology, Biology Centre CAS
Folia Parasitologica 2025, 72: 014
doi: 10.14411/fp.2025.014

Folia Parasitologica
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Research Article OPEN ACCESS

Characterisation of eggs and larvae of *Lamellodiscus erythrini* (Monogenea: Diplectanidae) using light and scanning electron microscopy

Judith Revault[1,*], **Marie-Line Escande**[1], **Valentin Logeux**[2], **Yves Desdevises**[1] and **Élodie Magnanou**[1]

[1] Sorbonne Université, CNRS, Biologie intégrative des organismes marins, BIOM, Observatoire Océanologique, Banyuls-sur-Mer, France; [2] CNRS, Sorbonne Université, Service mutualisé d'aquariologie, Observatoire Océanologique, Banyuls-sur-Mer, France

Abstract: While the identification of adult monogeneans primarily relies on morphological criteria, the morphology of a number of monogenean larvae (oncomiracidia) is to this day scarcely described. Yet, oncomiracidium plays a crucial role in the life cycle of the parasite, being responsible for the detection and localisation of its host, as well as for its attachment to this host. Few studies investigated the external morphological structures related to these functions, especially in Monopisthocotylea. The present study focuses on the early life stages (egg and oncomiracidium) of *Lamellodiscus erythrini* Euzet et Oliver, 1967, which are accurately described for the first time by light and scanning electron microscopy. Eggs of *L. erythrini* are smooth, tetrahedral and extended by a long polar filament. Freshly laid, the egg is brown, opaque, impermeable and becomes transparent as it matures, revealing the larva and its eye spots. When the egg matures, the egg casing exhibits functional weak points all around the operculum through which the larva emerges. The larva of *L. erythrini* is elongated, cylindrical and has a highly developed ciliation covering three areas: an anterior zone, a pleural zone, and a posterior cone. The ciliated cells are contiguous and are organised in a structured mosaic of spherical droplets, each cilium inserted into one. The larval tegument presents microvilli as well as 9 pairs of dorsal sensilla. The haptor is a closed structure consisting of 14 sclerotised hooklets, 12 arranged in a circle, and one pair positioned at the centre of the haptor. The possible link between these morphological structures and larval behaviour is discussed.

Keywords: Monogenean, oncomiracidium, SEM, morphology, host-parasite interaction, micrographs.

This article contains supporting files (Figs. S1–S3, Video S1, S2) online at http://folia.paru.cas.cz/suppl/2025-72-014.pdf

Monogeneans form a paraphyletic group of highly diverse parasites regrouping the classes Monopisthocotyla and Polyopisthocotyla (Brabec et al. 2023), mainly including ectoparasites. They are widespread in all aquatic environments and are commonly found on teleost skin and gills. They have a direct life cycle, and require a single host. This characteristic, combined with their hermaphroditism, makes them harmful pathogens in aquaculture where high teleost densities favour the completion of the monogenean life cycle, and culture cages provide substrates for the entanglement of eggs (Hutson et al. 2018, Vaughan et al. 2018, Hoai 2020). While the traditional identification and classification of adult monogenean species rely on morphological criteria (Chisholm and Whittington 1998, Amine et al. 2006, 2007), comprehensive descriptions of the morphological structures of their early life stages of most species are lacking.

Adult oviparous monogeneans lay eggs in the water column, and are passively hooked to substrates. A free swimming oncomiracidium emerges from the egg and actively seeks out a suitable host over short period and distances to colonise its skin (Kearn 1967, Buchmann 2002). The larvae then lose their ciliature and typically migrate from the skin to the gills of their fish host (Tinsley and Owen 1975, Tinsley 1983, Kearn 1985). Therefore oncomiracidia play a crucial role as they are involved in the detection, localisation and attachment to their host.

In the literature, most studies focused on the taxonomic classification of adult monogeneans or factors enhancing success of the infection of hosts of monogeneans, particularly in aquaculture. Thus, monogeneans have been described to display particular egg-laying and hatching rhythms in response to environmental factors such as light (Shirakashi et al. 2021), mechanical disturbance (Whittington and Kearn 2011), photoperiodicity (Woo et al. 2024) and temperature (Zhang et al. 2015, Woo et al. 2024), and to host-related factors such as chemical cues emitted by their mucus (MacDonald 1974) to maximise opportunities to infect fish hosts. There is clear evidence that free living stages (i.e., eggs and larvae) display responses

Address for correspondence: Judith Revault, Sorbonne Université, CNRS, Oceanological observatory of Banyuls-sur-Mer, 1 avenue Pierre Fabre, 66650, France. E-mail: judith.revaultpicon@gmail.com. ORCID: 0009-0007-5443-4612.

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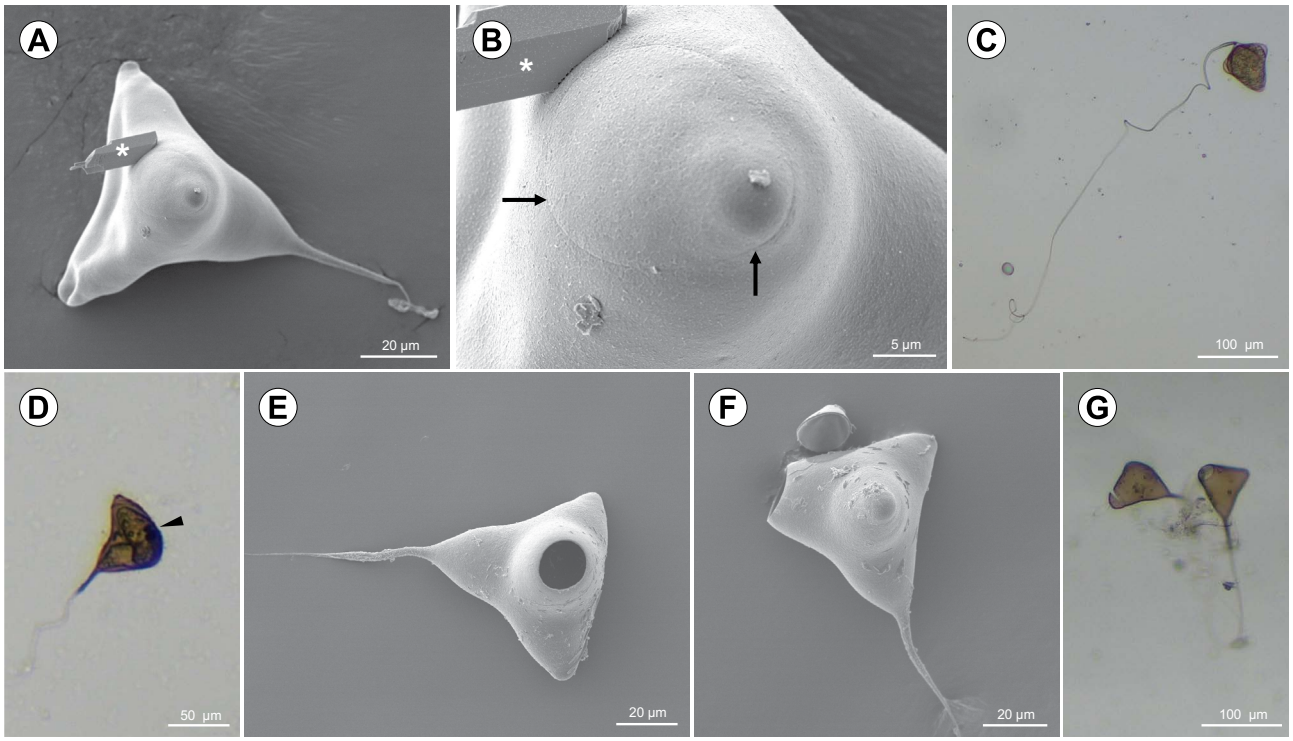

Fig. 1. Light and scanning electron micrographs of the eggs of *Lamellodiscus erythrini* Euzet et Oliver, 1967. **A**, **B** – scanning electron micrographs of a pre-operculated (arrows) egg with an artefact (star); **C** – embryonated egg with granular appearance and its polar filament; light microscopy; **D** – mature, transparent egg with a folded oncomiracidium visible (arrowhead) with its anterior part oriented toward the operculum; **E**–**G** – empty egg after hatching; operculum remains or is not attached.

to many stimuli, suggesting sensory-mediated actions, but little is known about the morphological structures involved in such mechanisms.

Working on oncomiracidia is challenging because they are nearly impossible to collect from wild hosts, they are fragile, very small and have a short life span (Hutson et al. 2018, Shirakashi et al. 2021). For that reason, the early-life stage of monogeneans is generally poorly characterised, especially in small-sized species.

The present study aims to characterise the larval stage of *Lamellodiscus erythrini* Euzet et Oliver, 1967, a monogenean belonging to the Diplectanidae (Monopistocotylea), and for which no image of larvae exists. Yet, these ectoparasites are particularly abundant on Mediterranean sparid hosts and have been studied for a long time, and their host ranges are considered as well-known (e.g., Euzet and Oliver 1966, 1967, Oliver 1974, Amine et al. 2006).

A specialist species, *L. erythrini*, was chosen for simplicity because it is the only species of *Lamellodiscus* Johnston et Tiegs, 1922 ever reported as parasitising *Pagellus erythrinus* (Linnaeus) in the study area (Desdevises et al. 2002, Kaci-Chaouch et al. 2008, Scheifler et al. 2022).

In this study, we focused on the description of the external morphology eggs and larvae of *L. erythrini* by combining light and scanning electron microscopy. Linked to the sensory structures identified from the morphological study, several behavioural traits of the oncomiracidia of *L. erythrini* were also observed using video recordings, following hatching.

MATERIALS AND METHODS

Fish were sampled in July 2023 in the Bay of Banyuls-sur-Mer (northwestern Mediterranean Sea, France). The Oceanological Observatory of Banyuls-sur-Mer holds the authorisation for fishing (Decision n°700/2023, Inter-regional direction of Mediterranean Sea), housing wild Mediterranean teleosts (66/070) and using animals for scientific purposes (A 06 918 012). Wild fish were caught and reared by a competent person and in accordance with European animal welfare regulations.

Eight wild *Pagellus erythrinus* individuals were caught at night, dazzled by torchlight and caught in a net. Immediately after their capture, fish were carefully brought to the laboratory. They were placed into a 250 l closed circuit aerated aquarium for 10 weeks in which egg collectors were immersed. Egg collectors are simple leaded nylon threads placed in the water column on which eggs are passively hooked (Suppl. Fig. S1A), as we found this system to be very efficient for recovering monogenean eggs in our aquariums. Eggs were recovered by carefully lifting the nylon threads and were searched under a dissecting microscope. Other oviparous monogenean species parasitising *P. erythrinus* such as *Sparicotyle* sp. are bigger, and their eggs were easily distinguishable from those of *Lamellodiscus erythrini* (Supp. Fig. S1B, C).

The eggs of *L. erythrini* eggs were incubated *in vitro* at 18 °C in a Petri dish filled with filtred seawater (1 µm) complemented by streptomycin (20 mg/l) (Oliver 1987). Every day, this culture medium was changed and eggs were observed under a dissecting microscope until they hatched. Subsequently, larvae and hatched eggs were flattened between a glass slide and a coverslip and examined using light microscopy with oil immersion. Larvae and

eggs were fixed for scanning electron microscopy with 2.5% glutaraldehyde in a 0.4 M Na-cacodylate buffer prepared in filtred sea-water for 2 h at 18 °C and stored at 4 °C.

Thereafter, they were washed three times for 15 minutes in filtred seawater and 0.4 M Cacodylate. Successive EtOH baths (70%, 95%, and 100%) were used to dehydrate the specimens. An ascending series of increasing concentrations of hexamethyldisilazane (HMDS) was applied to the specimens to 100% ethanol. Petri dishes with specimens and pure HMDS were then placed under a vertical laminar flow hood and air-dried overnight. Specimens were mounted on an aluminum stub with the help of double-sided carbon tape and sputter-coated with an approximately 5 nm conductive layer of gold-palladium (60/40) before observation with a JEOL JSM 1T800 SHL scanning electron microscope. Observations were performed in high vacuum mode, using the in-chamber Everhart-Thornley secondary electron detector (SED).

All measurements in this manuscript are expressed as mean ± standard deviation, followed by range in parentheses. To confirm the affiliation of *Lamellodiscus* individuals to *L. erythrini*, at the end of the experiments two fish individuals were randomly chosen and euthanised with an overdose of buffered pharmaceutical grade MS-222 (tricaine) at a concentration of 400 mg/l. Their gill arches were dissected and observed under a stereomicroscope. The recovered *Lamellodiscus* individuals were confirmed to be *L. erythrini* based on the morphology of their haptor and male copulatory organ, observed under an optical microscope (Euzet and Oliver 1966, Oliver 1987).

Video recordings were carried out using a light microscope (Motic Panthera, Motic Europe, Barcelona, Spain) equipped with a digital camera (Motic, Moticam 1080).

RESULTS

A regular and easy collection of the eggs of *Lamellodiscus erythrini* was achieved using nine nylon threads (i.e., egg collectors, Suppl. Fig. S1) that were immersed in the aquarium containing eight *Pagellus erythrinus* individuals. After incubating the eggs, the larvae hatched between 1 and 5 days later depending on the maturity of the collected eggs. For this study, we examined 15 larvae under light microscopy, and 21 eggs and 19 larvae under scanning electron microscopy (SEM). Videos of the larvae hatching were recorded (Video S1).

Description of the eggs of *Lamellodiscus erythrini*

The eggs are tetrahedral with a smooth surface (Fig. 1A,B). Some eggs fixed for SEM were distorted (Suppl. Fig. S2) and their structure was better maintained when eggs were mature (Fig. 1A) or hatched (Fig. 1E,F). Eggs were 54 ± 5µm long (48–66 µm). One edge of the eggs was extended by a long polar filament about 320 µm long, i.e., more than 5 times the length of the egg (Fig. 1C). The shape of the end of the polar filament was interpreted as a slight sticky swelling (Suppl. Fig. S2).

Under light microscopy and just after the egg has been laid, the egg is brown and opaque. Over time, it becomes clearer and exhibits a granular appearance (Fig. 1C) under light microscopy, gradually revealing the pigmented eye spots of the larvae (Fig. 1D). The larvae are folded within the egg and the anterior part of the oncomiracidium is directed towards the operculum (Fig. 1D). During maturation, eggs exhibit functional weak points all around the operculum (Fig. 1B), which facilitates the emergence of the larva from the egg. Once the larva has emerged, the opening in the egg measures over 18 ± 3 µm (13–23 µm) and the opercula remain or not attached to the egg (Fig. 1E–G).

Hatching of the eggs

A few hours before hatching, the larva begins to move inside the egg, slowly rotating around the anteroposterior axis of its body (Fig. 2A, Video S1). Once the egg reaches maturity, hatching could be triggered by changing the culture medium or mimicking water current with a micropipette. A few seconds before hatching, the contraction movements of the oncomiracidium body, combined with ciliary activity, accelerate until the operculum opens, allowing the larva to be released from the egg (Fig. 2A, Video S1). Freshly hatched oncomiracidia seem to display a positive phototaxis.

Description of the oncomiracidium

The oncomiracidium of *L. erythrini* is elongated and cylindrical (Figs. 2B,C, 3A) and measures 91 ± 5 µm in length (83–100 µm) and 21 ± 2 µm in width (17–24 µm) when measured under light microscopy. Note that when measured under SEM, these measurements were 61 ± 4.8 µm in length (54–71 µm) and 14 ± 3 µm in width (10–19 µm), but they are likely influenced by the sample preparation used for this technique.

Larvae have highly developed cilia covering four distinct areas: one area on the anterior part of the body, two areas on each lateral part and more extensively on the ventral side than on the dorsal side, and one as a fully ciliated posterior cone (Figs. 2C, 3A,B). Non-ciliated parts of the oncomiracidium tegument displays a corrugated aspect with microvilli (Fig. 3C). Ciliated cells are joined together, spherical and contain a mosaic of organised spherical droplets onto which each cilium is implanted (Fig. 3D,E).

On their anterodorsal part, oncomiracidia possess two pairs of well-defined eyespots with two pairs of crystalline lenses that are only visible in light microscopy (Fig. 2B,C). The most anterior eyespots are smaller and their crystalline lenses are oriented posterolaterally. In contrast, the posterior eyespots are larger and the crystalline lenses are oriented anterolaterally. The ventromedial and cylindrical pharynx is barely visible in light microscopy (Fig. 2D), and imperceptible under scanning electron microscopy due to its location between the two extensively ciliated pleural areas on the ventral surface.

The haptor of the larva (Fig. 2C–E) is located on the ventral side just in front of the ciliated cone. It consists of 14 sclerotised hooklets, 12 arranged in a circle and one pair positioned at the centre of the haptor. Sclerified parts of the haptor are visible under light microscopy (Fig. 2C– E). Most larvae prepared for scanning electron microscopy exhibited a folded haptor (Fig. 4A). However, one larva with an unfolded haptor was observed, though the 14 hooklets were not visible (Fig. 4B,C).

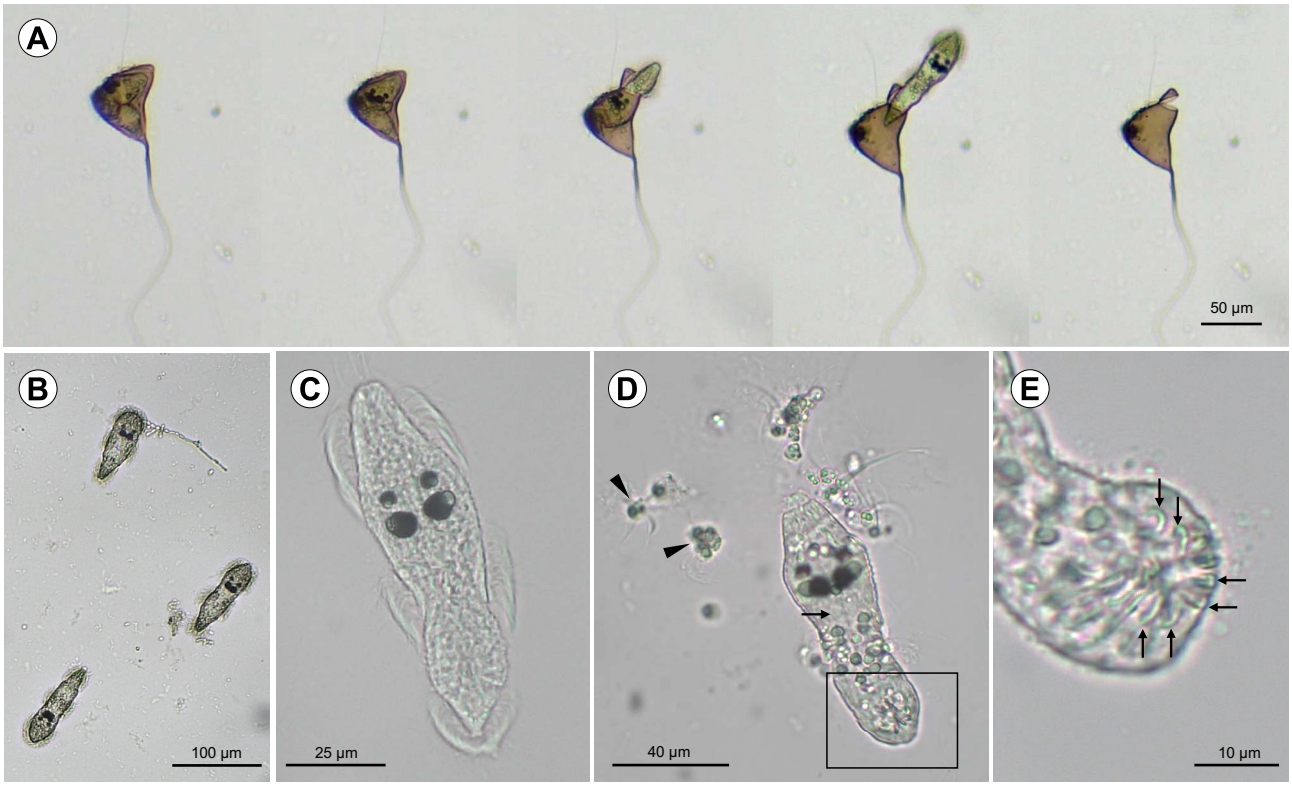

Fig. 2. Light micrographs of the egg and oncomiracidia of *Lamellodiscus erythrini* Euzet et Oliver, 1967. **A** – snapshots of video of hatching (see Video S1 for the full video); **B**, **C** – freshly hatched larvae; **D** – oncomiracidium rejecting its ciliated cells (arrowheads), pharynx (arrow), haptor (frame) (see Video S2 for the full video); **E** – detail of a deciliated larva, sclerified parts of the haptor (arrows).

SEM micrographs revealed ciliated sensory organs or sensilla on the dorsal surface of hatched oncomiracidia, structures not visible under light microscopy (Figs. 3C, 5A–C). These sensilla consist of a single cilium that emerges through a pit in the epidermis bordered by a crown of microvilli (Figs. 3C, 5A–C). In all oncomiracidia examined under SEM, we identified nine pairs of mid-dorsal sensilla forming a longitudinal row like a buttonhole, and two pairs of sensilla on either side of the fourth and fifth pair of mid-dorsal sensilla starting from the anterior part of the larva (detailed in yellow on Fig. 5D). In some of these oncomiracidia, supplementary dorsal sensilla were identified (detailed in pink on Fig. 5D). No sensilla were observed on the ventral part because the majority of the larvae were dorsally oriented and as in the case of the pharynx, the cilia are more developed than on the dorsal side and could hide it (Fig. 3B).

A few hours after hatching, some larvae slow down their movements until they either settle at the base of the Petri dish to die or to shed their ciliated cells through contraction (Fig. 2D, Video S2).

DISCUSSION

To our knowledge, we present here the first micrographs of any species of *Lamellodiscus* which until now have only been schematically represented (Oliver 1987, Bychowsky 1957). The experimental set-up we developed to collect eggs and obtain larvae was based on an egg collection system that is cheap and easy to install in any aquarium and provides an effective and non-invasive proxy for determining if oviparous monogenean species are present on fish hosts. The size of oncomiracidia measured by light microscopy differed by 33 % from those measured by scanning electron microscopy. This difference has already been reported by Oliver (1987) in another species of diplectanids and may be due to the elongation caused by the pressure of the coverslip, or to contraction caused by the fixation in glutaraldehyde, or both causes simultaneously.

The presence of a long polar filament and a slight sticky swelling on the eggs of *Lamellodiscus erythrini* allows them to adhere to substrates once laid, as observed in many other monogenean species (Kearn 1986a). This prevents the eggs from being carried away by water currents and maintains them close to the host habitat (Kearn 2004). In *Dawestrema cycloancistrium* Price et Nowling, 1967 and *Dionchus remorae* MacCallum, 1916 the eggs attach directly to the gill filaments of the host fish (Maciel et al. 2017, Whittington 1990). However, the majority of monogenean eggs are shed by gill ventilation or directly transported into the environment by currents after laying (Hutson et al. 2018).

Since a suitable host species is not usually nearby eggs, different factors have the effect to maximise host colonisation success. For example, we observed that mechanical disturbance elicits egg hatching, as previously reported (Ktari and Maillard 1972, Kearn 1986a, Whittington and Kearn 1988, Glennon et al. 2006). Turbulence has been suggested to be a signal for hatching as this mechanical disturbance mimics the host passage close to the egg (MacDonald 1974, Whittington and Kearn 1988, 2011).

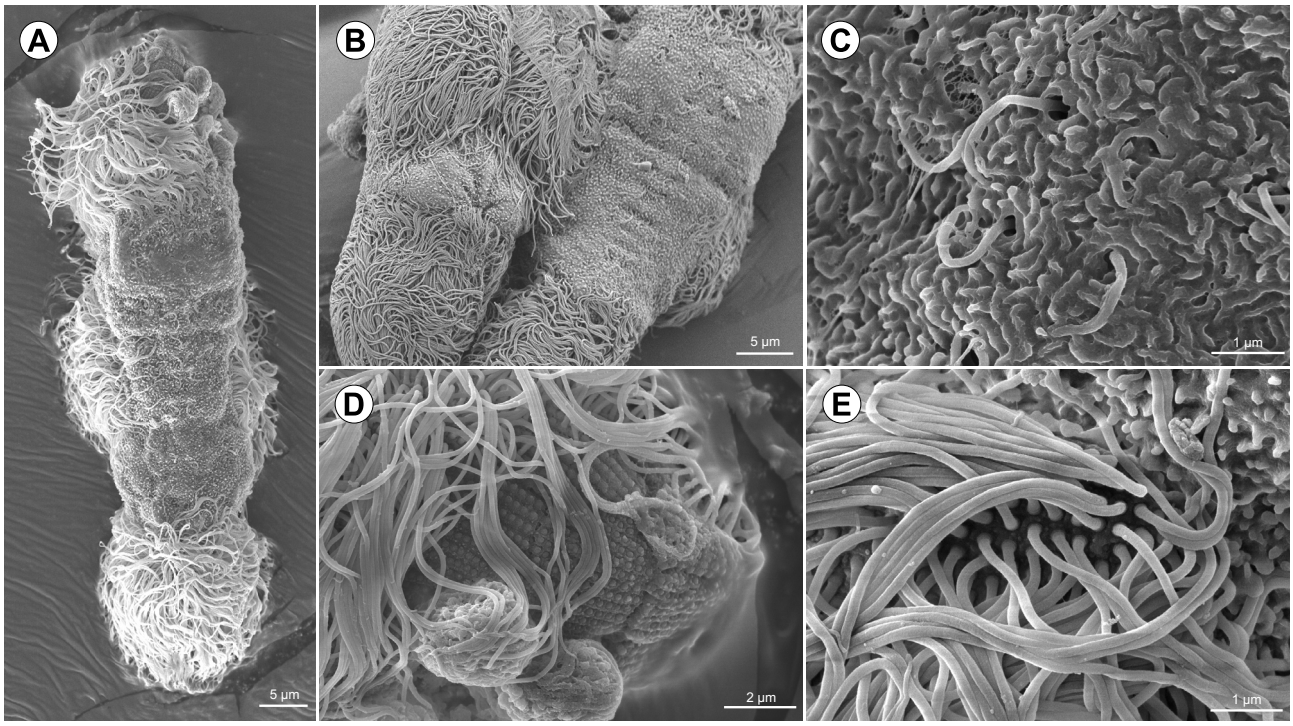

Fig. 3. Scanning electron micrographs of oncomiracidia of *Lamellodiscus erythrini* Euzet et Oliver, 1967. **A** – oncomiracidium, dorsal view; **B** – two oncomiracidia, left: ventral view, right: dorsal view; **C** – detail of the non-ciliated part of the tegument and the insertion of the dorsal sensilla; **D** – detail of ciliated cells from the anterior ciliated zone that have lost some of their cilia; **E** – detail of cilia.

We observed that fixation of immature eggs in glutaraldehyde results in a distortion of their structure, except when they were pre-operculated or hatched. This suggests that immature eggs are hermetic, a well-known characteristic contributing to recurring reinfections in aquaculture linked to their resistance to chemical treatments (Shirakashi et al. 2010, Vaughan et al. 2018).

Interestingly, the presence of mucus stimulates egg hatching in some monogenean species such as *Acanthocotyle lobianchi* Monticelli, 1888 (MacDonald 1974) and *Discocotyle sagittata* (Leuckart, 1842) (Gannicott and Tinsley 1998). While this has not been experimentally tested here, the mechanisms by which mucus penetrates the eggshell and promotes egg hatching could be linked to this pre-opening observed in mature eggs. This could also explain why glutaraldehyde better preserves the overall structure of pre-cut eggs by penetrating the eggshell through this opening.

Once the egg hatches, the oncomiracidium of *L. erythrini* must quickly find and reach its host to transition from a free-living to a parasitic lifestyle. We observed that freshly hatched *L. erythrini* larvae exhibit a positive phototaxis, as larvae of many other monogenean species (Whittington et al. 1999, Hendrix 2004, Maciel et al. 2017, Shirakashi et al. 2021, Wan Sajiri et al. 2023) and photoreceptors could be used to orient the larvae in the water column (Randel and Jékely 2016). Positive phototaxis would help the larvae to move toward the surface, likely increasing the chance of encountering a suitable fish host leading to higher probability of infection (Shirakashi et al. 2021). Even if the unique host of *L. erythrini* in the study area, *Pagellus erythrinus*, is a bottom-dwelling, semipelagic and dem-

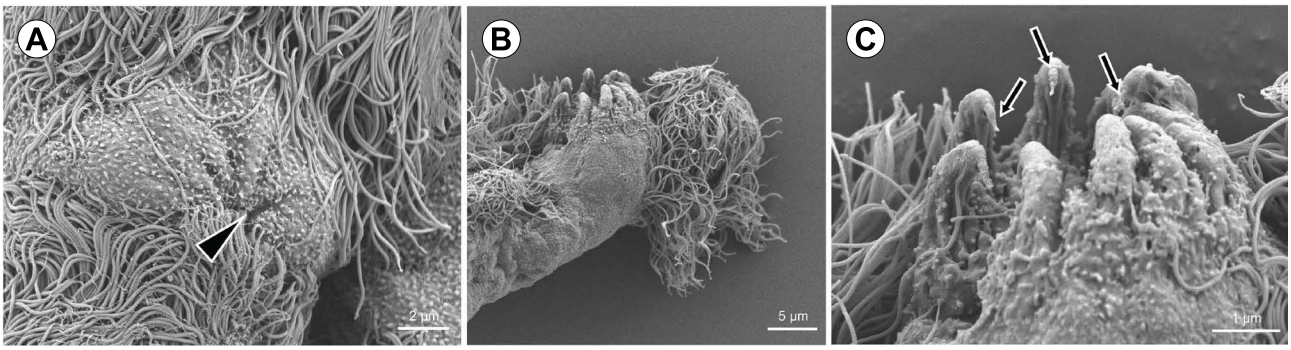

Fig. 4. Scanning electron micrographs of detailed parts of the haptor of the oncomiracidia of *Lamellodiscus erythrini* Euzet et Oliver, 1967. **A** – folded haptor (arrowhead), ventral view; **B**, **C** – unfolded haptor with some apparent hooklets (arrows).

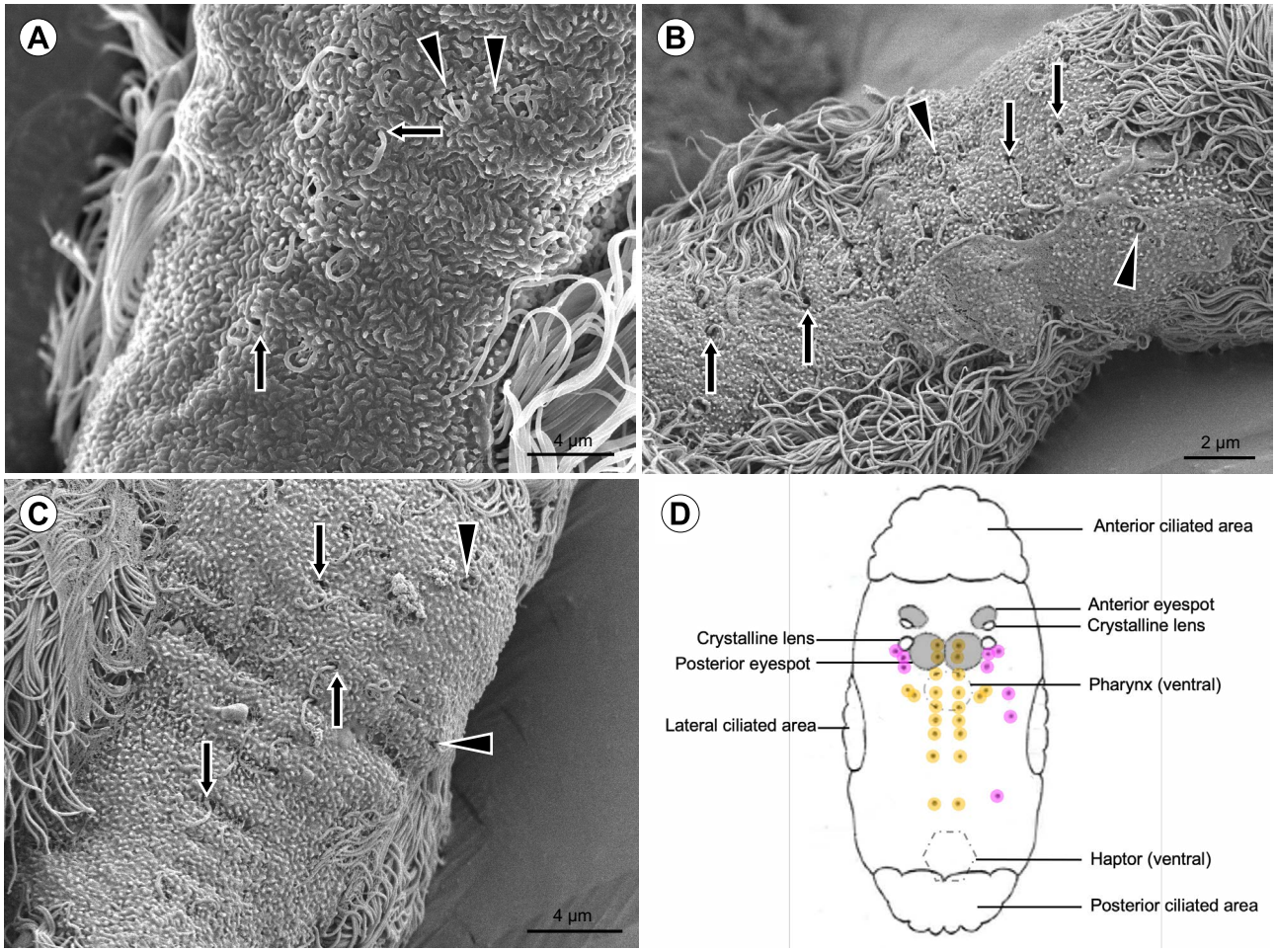

Fig. 5. Scanning electron micrographs of *Lamellodiscus erythrini* Euzet et Oliver, 1967 oncomiracidia, dorsal views. **A**–**C** – middle pair sensilla (arrows), supplementary sensilla (arrowhead); **D** – schematic representation of a freshly hatched oncomiracidium of *L. erythrini*, dorsal view; adapted from the scheme of *Furnestinia echeneis* (Wagener, 1857) drawn by Oliver (1987). Sensilla observed in all oncomiracidium of *L. erythrini* are highlighted in yellow; sensilla observed in some oncomiracidia of *L. erythrini* are highlighted in pink.

ersal fish, positive phototaxis may help larvae emerging from eggs resting on the sea floor to reach their hosts. Oncomiracidia of other monogenean species of benthic fish have been documented to also exhibit positive phototactic responses such, as *Benedenia epinepheli* (Yamaguti, 1937) (Shirakashi et al. 2021) or *Entobdella soleae* (Van Beneden and Hesse, 1863) (Kearn 1980). In *E. soleae* and in two monogenean species from the genus *Kuhnia* Sproston, 1945, it has been observed that responses to light evolve with the age of larvae and their maturation (Kearn 1980, Whittington and Kearn 1990). Finally, light intensity has been reported as a factor influencing egg hatching as it can maximise opportunities to co-occur with an easily accessible host (Kearn 1986b, Whittington and Kearn 1989, Gannicott and Tinsley 1997, Hoai and Hutson 2014); as the eggshell becomes clearer and transparent along larvae maturation, photoreceptors may play a role for determining the right time of hatching.

External morphological features, such as microvilli and ciliation pattern of the oncomiracidia of *L. erythrini* observed in the present study, are consistent with those reported for *Lamellodiscus echeneis* (Wagener, 1857) (reported as *Furnestinia echeneis* – see Desdevises 2001) (Lambert 1980, Oliver 1987, Strona et al. 2010, Farjallah et al. 2024) or for other diplectanid species (Oliver 1987). The larval haptor structure we have observed using SEM, and the sclerotised parts visible in light microscopy, looked like a closed structure folded inside the larva's body until its deployment and not an "open cup" structure as described by Oliver (1987) in *L. echeneis* and the larvae of *Diplectanum aequans* (Wagener, 1857).

We also observed the presence of several pairs of dorsal sensilla in *L. erythrini* oncomiracidia, but we could not identify any sensilla on their ventral part as it was already reported in *F. echeneis* by Oliver (1987) or other monogenean species (Lambert 1980, Chisholm 1998, Cribb et al. 2003). Easily identifiable sensilla described in the larvae of *F. echeneis* by Oliver (1987), such as the third pair located against the ciliated pleural areas, do not appear to be present in *L. erythrini*.

Although the existence of sensilla on monogenean oncomiracidia is known, the exact role of these structures remains unclear. Hypotheses on the possible functions of sensilla for host location can, however, be proposed as some of these structures disappear when the larva attaches to its host. For example, Cribb et al. (2003) has shown that

24 hours after host invasion, the post-oncomiracidia of *Merizocotyle icopae* Beverley-Burton et William, 1989 lost their 8 pairs of mid-dorsal sensilla, and the authors suggested that these sensilla act as chemoreceptors, involved in recognising chemical signals emitted by the host.

It has been proposed that sensilla play a role as mechanoreceptors or georeceptors (Buchmann 2002). Villar-Torres et al. (2018) showed that the larvae of *Sparicotyle chrysophrii* (Van Beneden et Hesse, 1863) display upward and downward behaviour in the water column, as also to the larvae of *Entobdella hippoglossi* (Müller, 1776) (Yoon 1998), which could be interpreted as a geotactic response.

Furthermore, as proposed by other authors (Whittington 1987, Hodová et al. 2010), the dorsal sensilla of monogenean larvae might act as rheoreceptors. However, evidence of the involvement of the sensilla as sensory receptors is missing. Nevertheless, the absence of sensilla in certain unciliated monogenean larvae, such as *Udonella caligorum* Johnston, 1835 (Lambert 1980), supports the hypothesis that dorsal sensilla play a significant role during the free-swimming stage.

Additional work is needed to characterise monogenean eggs and larvae, and the combination of various microscopy technics should help to provide a comprehensive view of their structures such as the haptor or their sensillae. Finally, the sparid-*Lamellodiscus* association emerges as a promising biological model to study the morphological structures of early monogenean life stage. Indeed, exploring the morphological adaptation to host-specific biological and ecological traits (i.e., lifestyle, social behaviour, position in the water column, diet, life cycle), such as in Mediterranean sparids and their various specificity profiles, undoubtedly represents compelling research directions.

Acknowledgements. We would like to thank the EnRMAT platform (https://enrmat.univ-perp.fr/) and Yonko Gorand for the access to the instrumentation and the advices provided to carry out this project, as well as Pascal Romans, Rémi Pillot, the "Service des Moyens à la Mer" and the "Service Mutualisé d'Aquariologie de l'Observatoire Océanologique de Banyuls-sur-Mer" (FR3724) for fish sampling and for the help in maintaining fish. This study was funded by the National Centre for Scientific Research (CNRS).

Authors' contribution statement. All authors contributed to the study conception and design. VL contributed to capture and maintain the fish. MLE and JR contributed to the methodology, material preparation and data collection. JR conducted the morphological analysis and writing of the original manuscript. JR, YD and EM contributed to reviewing and editing of the manuscript. All authors read and approved the final manuscript.

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Received 29 November 2024 Accepted 12 February 2025 Published online 15 May 2025

Cite this article as: Revault J., Escande M.-L., Logeux V., Desdevises Y., Magnanou É. 2025: Characterisation of eggs and larvae of *Lamellodiscus erythrini* (Monogenea: Diplectanidae) using light and scanning electron microscopy. Folia Parasitol. 72: 014.