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The description of *Pseudobenedenia gunnari* sp. n. (Monopisthocotyla: Capsalidae) from the mackerel icefish (*Champsocephalus gunnari*) in South Georgia Island, South Atlantic

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Abstract. The mackerel icefish *Champsocephalus gunnari* (Channichthyidae) is a highly specialised Antarctic species inhabiting cold sub-Antarctic waters, particularly around South Georgia. Although the helminth fauna of this host is relatively well documented, only one representative of Monopisthocotyla collected in 1926 during the "Discovery" expedition, later prepared as a whole mount by D. I. Gibson in the 1970s and identified as *Pseudobenedenia notothenieae* Johnston, 1931, has been registered so far. The present study is based on a re-examination of a museum specimen preserved in the parasitological collection of the Natural History Museum in London, United Kingdom. Standard morphological techniques were used to examine and illustrate the specimen, including analysis of key reproductive, adhesive, and haptoral structures. The new species is diagnosed by a unique combination of features, including a bilobed terminal end of penis curved anteriorly; both male and female genital ducts opening into a shared genital orifice, but at distinctly separate positions within it, and vagina not adjacent to the vitelline reservoir. An additional unique feature is an exceptionally large body size (12 mm) and proportionally larger reproductive organs. A combination of these morphological features has not been previously reported in any other *Pseudobenedenia* Johnston, 1931 species. Reporting this unique form of *Pseudobenedenia* on a new host, ecologically isolated from all previously known hosts, emphasises the novelty of our discovery. The rarity of *Pseudobenedenia* records on *C. gunnari*, despite intensive examination of the host species, underscores the difficulty of obtaining fresh material for modern morphological analyses. Distinctive features of the genital system and marked size differences provide strong evidence of reproductive isolation and support the establishment of a new *Pseudobenedenia* species.

Keywords: Antarctic fish, Capsalidae, Monopisthocotyla, new species

1 Introduction

The mackerel icefish, *Champsocephalus gunnari* Lönnberg, 1905, is a member of the family Channichthyidae Gill, 1861, which belongs to the suborder Notothenioidei within Perciformes. This species inhabits cold marine environments of the Southern Ocean, including areas around South Georgia and the South Orkney Islands (Froese & Pauly, 2025; Fricke et al., 2025). *Champsocephalus gunnari* is known for its unique physiological adaptations to sub-zero environments. Like other channichthyids, it lacks hemoglobin but maintains oxygen transport through physiological adaptations and antifreeze glycoproteins that enable survival in freezing waters (Corliss et al., 2019; Shin et al., 2024). The parasitic community of *C. gunnari*, comprises representatives from multiple helminth and annelid taxa, primarily collected in the vicinity of South Geor-

gia, South Orkney, and other sub-Antarctic regions. In total, at least 14 species of digeneans, 2 cestodes, 15 nematodes, 2 acanthocephalans, 2 crustaceans and 4 annelids have been reported from *C. gunnari* over more than 50 years (Prudhoe & Bray, 1973; Parukhin & Lyadov, 1981; Zdzitowiecki, 1979; 1986; 1991; 2002; Beumer et al., 1983; Siegel, 1980; Wojciechowska et al., 1995; Utevsky, 2005; Rokicki et al., 2009; Kuhn et al., 2018; Parker et al., 2020; Kuzmina et al., 2022; Wang et al., 2024). Although the helminth and annelid fauna of this host is relatively well documented, its monopisthocotylan parasites have not been collected since 1926 (Gibson, 1976a).

2 Materials and methods

This study draws upon one whole-mounted specimen kindly provided by the Natural History Museum, London, United Kingdom. This slide was initially prepared by Dr. David Ian Gibson, whose work enabled the current investigation. As per Dr. Gibson's notes, the specimen was fixed using Bouin's solution and formalin. It was stained with Mayer's paracarmine, cleared in beechwood creosote, and mounted in Canada balsam (Gibson, 1976a). Drawings were prepared using a Ken-A-Vision micro projector from Ward's Biological Supply Co., Rochester, New York, and finalised in Adobe Illustrator (Adobe Systems, San Jose, CA). Microscopic images were captured using a Nomarski DIC Phase Contrast Trinocular Microscope (Munich, Germany) coupled with a Canon EOS 600D DSLR Camera (Melville, New York). Measurements were taken following the original description of *Pseudobenedenia* (Johnston, 1931). Unless otherwise specified, measurements are provided in millimeters.

3 Results

The proposed new species has the following taxonomy:

Class: Monopisthocotyla Brabec et al., 2023
Order: Capsalidea Lebedev, 1988
Family: Capsalidae Baird, 1853
Subfamily: Trochopodinae (Price, 1936) Sproston, 1946
Genus: *Pseudobenedenia* Johnston, 1931
Pseudobenedenia gunnari sp. n.

3.1 Description

Based on a single gravid specimen, the present material exhibits the diagnostic characteristics of the subfamily Trochopodinae and the genus *Pseudobenedenia*, as defined by Sproston (1946). Body ovally elongated. Length 12 mm and width 6 mm, body length-to-width ratio 2 (Fig. 1). Prohaptor with two glandular adhesive zones anterior to ventrally open suckers (Fig. 1b). Suckers 1.20 × 1.45 mm (Fig. 1). Two pairs of dorsal eyespots located at the level of mouth, anterior to well-developed muscular pharynx, which lies between suckers (Fig. 1). Pharynx 1.13 × 1.15 mm. Posterior end of body with roundish opisthaptor measuring 2.75 mm in length and 2.83 mm in width (Fig. 1). Outer margin of haptor with muscular rim, encircled by well-developed marginal valve (Fig. 1b). Body-length-to-haptor-length ratio 4.4. Haptor disc-like with central loculus surrounded by septum that radiates into six sections. Haptor armed with three pairs of large sclerotised structures: anterior and posterior hamuli and accessory sclerites (Fig. 2 a–c). Accessory sclerite (one missing) length 0.50, width 0.06 (Fig. 2a–c) with distinctly pigmented inner central region. Anterior hamulus 0.79 mm long (Fig. 2 a–c), also with distinctly pigmented inner central region. Posterior hamulus adjacent to anterior hamulus 0.21 mm long (Fig. 2d). Hooklets not seen. Common genital opening ventrally posterior to left sucker, on left ventral surface beneath midline of left sucker; its orifice diameter 0.56 mm (Fig. 4). Male and female genital canals terminate within common genital opening, their respective openings being well separated. Penis 1.38 × 0.20 mm (Fig. 1), its terminal end bilobed and curved anteriorly. Vagina on ventral side in anterior third of body, slightly to left of midline; not located adjacent to vitelline reservoir, its out-

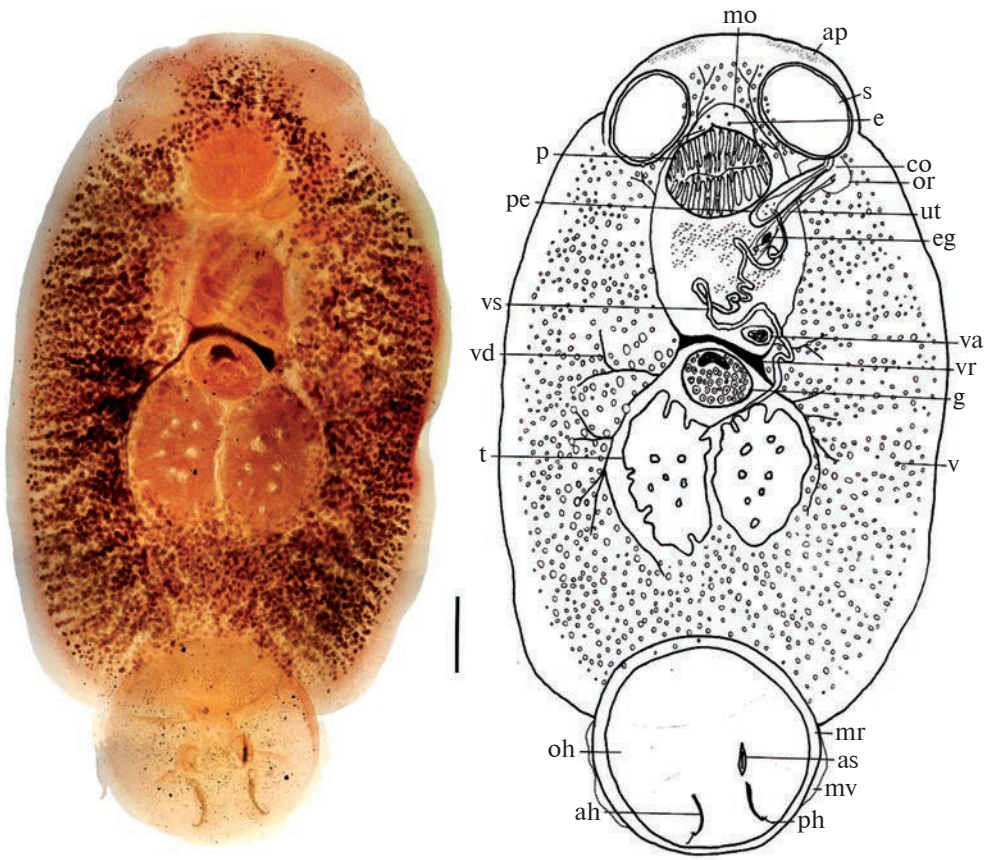

Figure 1. (a) Photomicrograph of an adult specimen of *Pseudobenedenia gunnari* sp. n. Scale bar 1 mm. (b) Ventral anatomy of *Pseudobenedenia gunnari* sp. n. Abbreviations: ah – anterior hamulus; ap – adhesive pad; as – accessory sclerite; co – common genital opening; e – eyespot; eg – egg; g – germarium; mo – mouth; mr – muscular ridge; mv – marginal valve; oh – opisthaptor; p – pharynx; pe – penis; ph – posterior hamulus; s – muscular oral sucker; t – testis; ut – uterus; v – vitellarium; va – vagina; vd – vitelline duct; vr – vitelline reservoir; vs – *vas deferens*. Scale bar 1 mm

er diameter 0.26 mm, inner diameter 0.15 mm. Germarium globular and median (0.84 × 1.05 mm) (Figs. 1b, 3b). Germarium chamber compact occupies approximately 1/7 of anterior part of germarium (Figs. 1b, 3b). Two testes adjacent to each other (Fig. 1), positioned posterior to germarium. Each testis measures 1.83 × 1.43 mm, with large perforations. Cortical tissue forms deep, jagged edges of testes.

Testes' length-to-width ratio 1.28. Vitelline reservoir very slender, vitelline glands highly developed, overlapping intestinal branches laterally and posteriorly, well visible throughout body. Vitellaria extend anterior to prohaptor between anterior suckers and posterior to opisthaptor level. Single egg with pointed anterior end and blunter posterior end 0.20 × × 0.14 mm, with long coiled filament (Figs. 1, 3a).

3.2 Remarks

This new species of *Pseudobenedenia,* with characteristics typical of the genus, was discovered on a host belonging to the family *Channichthyidae*, commonly known as crocodile icefishes or white-blooded fish. It differs from all known representatives of the genus by body size and proportion-

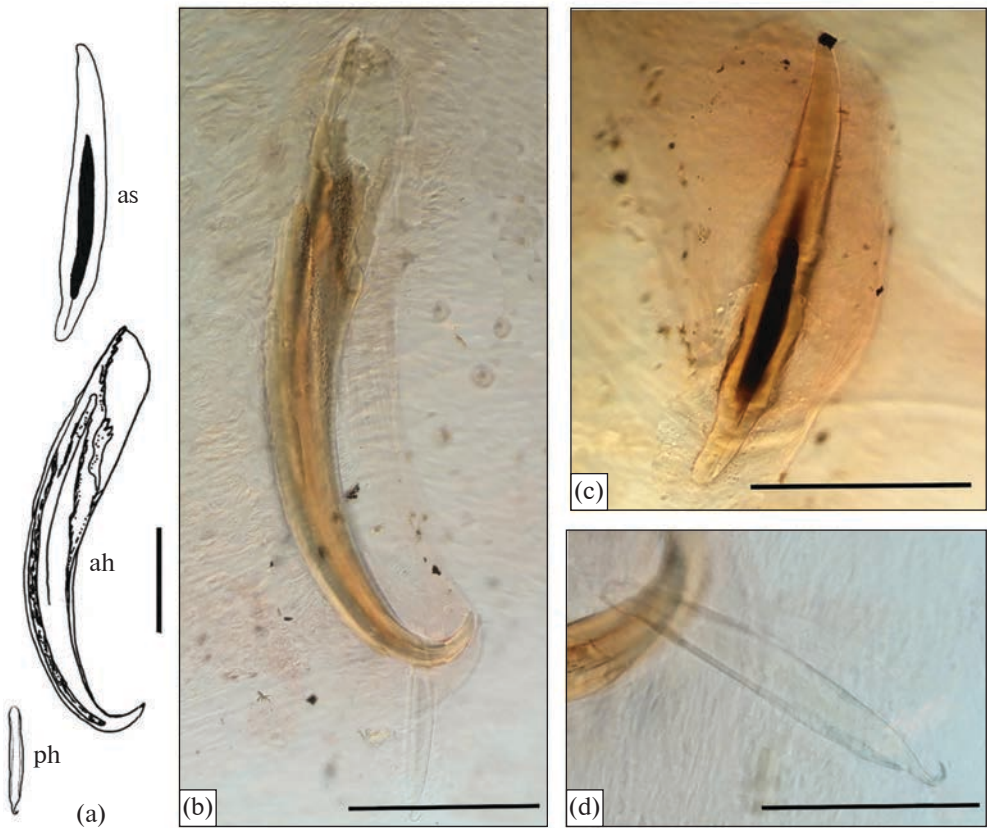

Figure 2. Haptoral structures of *Pseudobenedenia gunnari* sp. n. (a) Morphology of sclerotized structures of *Pseudobenedenia gunnari* sp. n.: ah – anterior hamulus; as – accessory sclerite; ph – posterior hamulus. Scale bar 200 μm. (b) Anterior hamulus. Scale bar 200 μm. (c) Accessory sclerite. Scale bar 250 μm. (d) Posterior hamulus. Scale bar 100 μm

ally larger body organs. It exhibits the largest dimensions of the anterior suckers, pharynx, germarium, testes, penis, and opisthaptor among all described species of *Pseudobenedenia* (Johnston, 1931; 1937; Szidat, 1965; Timofeeva et al., 1987; Rubtsova et al., 2023; Rubtsova & Marcotegui, 2024). Due to the limited amount of material, it was impossible to illustrate the accessory sclerite in profile, and one accessory sclerite was missing. *Pseudobenedenia gunnari* sp. n. has an unusually slender vitellaria reservoir, unlike all other described *Pseudobenedenia* species (Figs. 1, 3b). Its vagina is not closely adjacent to the vitellaria reservoir like in all other *Pseudobenedenia* species, though it generally keeps the exact location in the body. It possesses a unique penis morphology, characterised by a bilobed, anteriorly curved terminal end. The position of the genital openings also distinguishes this species from all other known *Pseudobenedenia*, as both male and female ducts open into a common genital aperture, yet at distinctly separate positions within it. The uniqueness of this newly described species is further emphasised by its association with a host that exhibits markedly distinctive biological, physiological, and ecological traits compared to all previously known hosts of *Pseudobenedenia*.

In addition to these unique features, morphometric analysis differentiates *P. gunnari* sp. n. from other members of the genus by a combination of different characteristics. The new species is distinguished from *P. nototheniae* Johnston, 1931 by

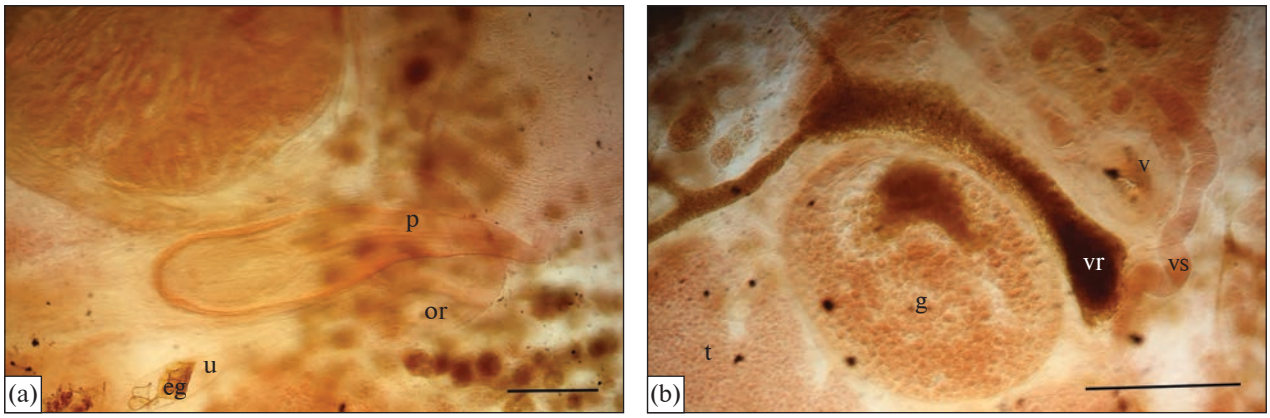

Figure 3. Details of the reproductive system of *Pseudobenedenia gunnari* sp. n.: (a) p – penis, eg – egg in uterus (u); orifice (or) of common genital opening. Scale bar 200 μm; (b) germarium (g) and vitelline reservoir (vr), *vas deferens* (vs), testes (t), vagina (v). Scale bar 250 μm

its 12 mm body length and a larger body-length-to-haptor-length ratio of 4.36, compared to 2.35–2.91 in *P. nototheniae*. It possesses larger hamuli (anterior and posterior), accessory sclerites, a larger vagina, and exhibits different host specificity. The anterior hamulus length-to-accessory-sclerite-length ratio is 1.58 (*vs.* 2.1 in *P. nototheniae*). *Pseudobenedenia gunnari* sp. n. also lacks cuticular fibers and has a testes-length-to-width ratio of 1.28 (*vs.* 1.5–1.6 in *P. nototheniae*) (Johnston, 1931; 1937; Rubtsova et al., 2023).

Pseudobenedenia gunnari sp. n. is further distinguished from *P. lauriei* Szidat, 1965 by the presence of lobulated, separated by a distinct gap between testes; body-length-to-opisthohaptor-length ratio of 4.36 (*versus* 2.6 in *P. lauriei*); significantly larger anterior and posterior hamuli and accessory sclerites; and by its occurrence on a different host species (Szidat, 1965; Rubtsova & Marcotegui, 2024).

Pseudobenedenia gunnari sp. n. is further distinguished from *P. dissostichi* Timofeeva, Gaevsakja & Kovaliova, 1987 by possessing larger, lobulated testes separated by a distinct gap, a larger vagina, smaller anterior and posterior hamuli and accessory sclerites, as well as by its occurrence on a different host species (Timofeeva et al., 1987).

The new species is further distinguished from *Pseudobenedenia gibberifrons* Timofeeva, Gaevskaja & Kovaliova, 1987 by a larger vagina, larger anterior hamuli and accessory sclerites, smaller posterior hamuli, and a smaller egg, as well as by differences in infection sites and host specificity (Timofeeva et al., 1987).

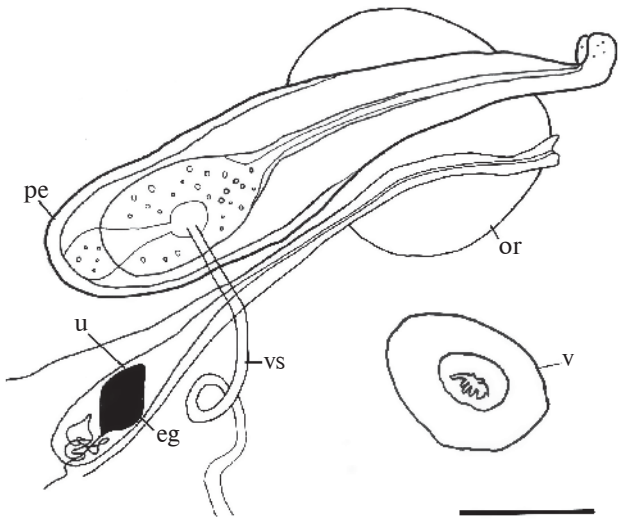

Figure 4. Schematic representation of part of the reproductive system of *Pseudobenedenia gunnari* sp. n. Abbreviations: eg – egg; or – orifice of common genital opening; pe – penis; v – vagina; vs – *vas deferens*; u – uterus. Scale bar 200 μm

Pseudobenedenia gunnari sp. n. is also distinguished from *P. coriicepsi* Rubtsova, Chaudhary, Salganskiy & Kuzmina, 2023 by the presence of a gap between the testes, larger anterior and pos-

terior hamuli and accessory sclerites, smaller eggs, and by its association with a different host species (Rubtsova et al., 2023).

3.3 Taxonomic summary

Type locality: coastal waters near Georgia Island; South Atlantic Ocean 54°24′S, 36°42′W.

Type host: the mackerel icefish, *Champsocephalus gunnari* Lönnberg, 1905.

Site of infection: body surface.

Material examined: one specimen stained with Mayer's paracarmine.

Type material: catalogued in the Natural History Museum, London, United Kingdom (BMNH-1975.3.17.103).

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Etymology: the species name *gunnari* refers to its type host species name.

4 Discussion

The genus *Pseudobenedenia* (Capsalidae) currently comprises four recognised species, which occur in Antarctic and sub-Antarctic regions. These are *P. lauriei*, from *Notothenia neglecta* Nybelin, 1951; *P. gibberifrons*, from *Gobionotothen gibberifrons* (Lönnberg, 1905); *P. dissostichii*, from *Dissostichus eleginoides* Smitt, 1898; and the recently described *P. coriicepsi*, from *Notothenia coriiceps* Richardson, 1844 (Szidat, 1965; Timofeeva et al., 1987; Rubtsova et al., 2023; Rubtsova & Marcotegui, 2024; Fricke et al., 2025).

Several taxa once placed in *Pseudobenedenia* have since been reassigned to other genera. For example, *Pseudobenedenia shorti* Hargis & Dillon, 1968 (Hargis & Dillon, 1968), was transferred to *Pseudobenedenoides* Szidat, 1967, by Gibson (1976a). Likewise, four species described from Hawaiian waters (*Pseudobenedenia noblei* Menzies, 1946; *Pseudobenedenia elongata* Yamaguti, 1968; *Pseudobenedenia merinthe* Yamaguti, 1968; and *Pseudobenedenia ovalis* Yamaguti, 1968 (Yamaguti, 1968) were moved to the newly erected genus *Menziesia* by Gibson (1976a, b) (Menzies, 1946; Gibson, 1976a, b).

The type species, *P. nototheniae*, is now regarded as a species complex rather than a single broadly host-specific taxon (Johnston, 1931; Whittington, 2004; Rubtsova et al., 2023; Rubtsova & Marcotegui, 2024).

All previously described *Pseudobenedenia* species are associated with hosts from Nototheniidae, whereas *C. gunnari* belongs to Channichthyidae — a phylogenetically and ecologically isolated lineage characterised by the absence of hemoglobin and distinctive life-history traits. The discovery of *P. gunnari* sp. n. on *C. gunnari* from this hemoglobinless channichthyid fish expands both the known host range and biogeographic distribution of the genus *Pseudobenedenia*. Monogeneans are widely recognised for their high host specificity, often infecting a single host species or a narrow group of closely related hosts (Whittington, 2004; Poulin & Morand, 2000). This specificity is typically driven by the combined effects of host phylogeny, ecological niche, microhabitat preference on the host body, and the precise compatibility between parasite attachment and reproductive structures and host integumentary traits (Chisholm & Whittington, 2007). For capsalids in particular, host specificity can be pronounced, as their life cycles rely heavily on direct transmission and intimate epidermal contact, making successful colonisation contingent upon fine-scale physiological and behavioral matching between parasite and host (Whittington, 2004; Chisholm & Whittington, 2007).

Antarctic notothenioid fishes evolved within the chronically cold-stable and oxygen-rich waters of the Southern Ocean, where long-term environmental stability and geographical isolation promoted a well-resolved adaptive radiation and strong phylogenetic structuring of fish lineages (Clarke & Johnston, 1996; Cheng & Detrich, 2011; Bilyk et al., 2018; Eastman, 2024). In parallel, Antarctic monogeneans exhibit a high degree of host specificity, with most monopisthocotylean line-

ages restricted to notothenioid hosts or even particular host families (Klapper et al., 2017; Heglasová et al., 2018). In combination with general models of host–parasite diversification under stable conditions (Hoberg & Brooks, 2008), these patterns are consistent with long-term coevolutionary associations between Antarctic monogeneans and their notothenioid hosts. All previously known *Pseudobenedenia* species conform to this pattern, occurring on representatives of Nototheniidae. The presence of *P. gunnari* sp. n. on a member of Channichthyidae therefore represents a notable deviation from the established host-specificity spectrum of the genus. This observation may indicate either a historically broader host range in ancestral *Pseudobenedenia* lineages or, more plausibly, a highly specialised host shift followed by prolonged isolation on *C. gunnari*.

Given the pronounced genetic and physiological differentiation of channichthyids – most notably their hemoglobinless condition and distinct epidermal microstructure (Beers & Sidell, 2011) – successful colonisation by a monogenean adapted to notothenioid hosts would require substantial evolutionary accommodation. The unique morphological attributes of the reproductive system in *P. gunnari* sp. n. may reflect such specialisation, supporting the hypothesis that this species evolved under strong host-driven selection pressures. The extreme rarity of this parasite further aligns with expectations for a monogenean exhibiting strict host specificity on a pelagic, low-contact fish species, where opportunities for reinfection and host-to-host transmission are intrinsically limited.

As mentioned above, previous parasitological surveys of *C. gunnari* have consistently documented a diverse assemblage of helminths – yet Monopisthocotyla have been notably absent from published records (Prudhoe & Bray, 1973; Beumer et al., 1983; Parukhin & Lyadov, 1981; Zdzitowiecki, 1979; 1986; 1991; 2002; Rokicki et al., 2009). Given that such large ectoparasites on the host's external surface are unlikely to be overlooked in the numerous studies conducted on these well-examined fish species, this scarcity suggests the parasite's possible extinction. This observation underscores the rarity of available material and highlights the considerable difficulty in obtaining fresh specimens suitable for the detailed analyses required today.

Two major morphological characteristics of the genital system point to a pronounced degree of reproductive isolation in this taxon. Historically, distinctions between Mono- and Polyopisthocotyla (formerly Monogenea) have relied on the morphology of the genital apparatus (Gussev, 1985). In this context, the combined evidence of extreme material scarcity, substantial differences in the configuration of the reproductive system, and marked divergence in body size strongly supports reproductive isolation from all described species of *Pseudobenedenia* and convincingly justifies the recognition of a new species.

The predominantly pelagic lifestyle of *C. gunnari* in cold, well-oxygenated waters may reduce opportunities for direct parasite transmission compared with benthic or reef-associated teleosts, where close contact and high habitat fidelity favor monogenean life cycles. The rarity of Monopisthocotyla in pelagic Antarctic fish, as noted by Kuhn et al. (2018), suggests that the host's life history imposes ecological barriers to infestation, making this single record especially significant.

5 Conclusions

The present study documents *P. gunnari* sp. n., a previously unrecognised member of the Capsalidae discovered on the mackerel icefish *C. gunnari*. This species is established on the basis of a uniquely preserved museum specimen collected in 1926, which remains the only monopisthocotylan ever recovered from this host despite nearly a century of intensive parasitological research across the Southern Ocean. The exceptional scarcity of material underscores both the rarity of this parasite and the scientific value of historical collections.

A combination of distinctive morphological features – including a bilobed, anteriorly curved pe-

nis; distinctly separated male and female genital duct openings within a shared aperture; vagina not adjacent to the vitelline reservoir; and proportionally enlarged reproductive structures – clearly distinguishes *P. gunnari sp. n.* from all currently recognised congeners. These traits, together with significant morphometric differences and the unique host association, support the conclusion that this taxon represents a morphologically and reproductively isolated lineage within *Pseudobenedenia*.

The discovery of *P. gunnari* sp. n. highlights the continued relevance of museum collections for unveiling hidden components of Antarctic biodiversity and emphasises the need for renewed parasitological attention to channichthyid fishes. This study contributes to a more complete understanding of Southern Ocean parasite diversity and underscores the importance of preserving and re-examining historical material for modern taxonomic and evolutionary research.

As *C. gunnari* is a commercially harvested species throughout parts of the Southern Ocean, improved knowledge of its parasitic fauna – including rare monogeneans – is essential for broader ecological assessments, providing valuable indicators of host population structure, trophic interactions, and environmental change.

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Conflict of Interest. The author declares no conflicts of interest.

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Опис *Pseudobenedenia gunnari* sp. n. (Monopisthocotyla: Capsalidae) від щуковидної білокрівки (*Champsocephalus gunnari*), Південна Джорджія, Південна Атлантика

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Реферат. Щуковидна білокрівка *Champsocephalus gunnari* (Channichthyidae) є високоспеціалізованим антарктичним видом, який населяє холодні субантарктичні води, зокрема район навколо острова Південна Джорджія. Хоча гельмінтофауна цього хазяїна загалом добре вивчена, донині був зареєстрований лише один представник Monopisthocotyla, зібраний у 1926 році під час експедиції «Discovery», пізніше змонтований Д. І. Гібсоном у 1970-х роках та ідентифікований як *Pseudobenedenia nototheniae* Johnston, 1931. Представлене дослідження ґрунтується на повторному аналізі цього музейного зразка, збереженого у паразитологічній колекції Музею природознавства в Лондоні. В роботі застосовано стандартні морфологічні методи, включно з аналізом ключових структур репродуктивної системи, адгезивного апарату та гаптору, а також детальним ілюструванням. Новий вид діагностується за унікальною комбінацією ознак: дволопатевим термінальним кінцем пеніса, зігнутим допереду; відкриттям чоловічої та жіночої статевих проток у спільний генітальний отвір, але у чітко розділених позиціях; а також розташуванням вагіни, яка не межує з жовтковим резервуаром. Додатковою діагностичною особливістю є винятково великий розмір тіла (12 мм) та пропорційно збільшені репродуктивні органи. Таке поєднання морфологічних характеристик раніше не було описане ні для одного з видів *Pseudobenedenia* Johnston, 1931. Реєстрація цього унікального представника *Pseudobenedenia* на новому хазяїні, який є екологічно ізольованим від усіх попередньо відомих хазяїв роду, підкреслює новизну знахідки. Рідкісність виявлень *Pseudobenedenia* на *C. gunnari*, попри інтенсивне вивчення цього виду риб, свідчить про складність отримання свіжого матеріалу для сучасних морфологічних досліджень. Виразні унікальні морфологічні особливості будови статевої системи та значні розбіжності у розмірах тіла в порівнянні з іншими відомими представниками роду становлять переконливі докази репродуктивної ізоляції та підтверджують встановлення нового виду *Pseudobenedenia*.

Ключові слова: Capsalidae, Monopisthocotyla, антарктична риба, новий вид