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Gyratrix hermaphroditus Ehrenberg, 1831 (Platyhelminthes: Kalyptorhynchia) in the Strait of Magellan (Chile): Description and biogeographical insights

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ABSTRACT: *Gyratrix hermaphroditus* Ehrenberg, 1831 is a free-living aquatic microturbellarian, recognized as a species complex with a cosmopolitan distribution. In South America, *G. hermaphroditus* has only been reported from freshwater environments in Colombia, southern Brazil and Argentina. This study provides a comprehensive morphological description of marine specimens of *G. hermaphroditus* collected from the Strait of Magellan in Chile, and evaluates whether their morphology aligns with the morphological traits and well-established phenotypic stasis observed in other localities. Additionally, an updated key to the species of *Gyratrix* Ehrenberg, 1831 is given. The results indicate that the Chilean specimens are similar to populations found in European seas. This phenotypic similarity, in the context of the history of the Strait of Magellan, suggests potential human-assisted dispersal via maritime shipping routes. The study also highlights an intriguing biogeographic pattern found among certain putative species within *G. hermaphroditus*, consistent with vicariant processes associated with continental drift. Their distributions support the hypothesis of a long-term morphological stability within the species complex, potentially persisting for approximately 180 million years. This work contributes to the understanding of the distribution and evolutionary history of *G. hermaphroditus*, underscoring the plausibility of long-term morphological stasis in the species complex. The report herein is a new locality for the species complex, extends considerably the southern limit of the distribution of *G. hermaphroditus* in South America, and is the first marine record for the continent.

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KEY WORDS: Eukalyptorhynchia, Polycystididae, Gyratricinae, phenotypic stability, cosmopolitanism, cryptic species.

Gyratrix hermaphroditus Ehrenberg, 1831 (Platyhelminthes: Kalyptorhynchia) в проливе Магеллана (Чили): описание и биогеографические данные

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** Ответственный за переписку*

РЕЗЮМЕ: *Gyratrix hermaphroditus* Ehrenberg, 1831 — свободноживущая водная микротурбеллярия, признанная видовым комплексом с космополитическим распространением. В Южной Америке *G. hermaphroditus* был обнаружен только в пресноводных водоемах Колумбии, южной Бразилии и Аргентины. В данном исследовании представлено всестороннее морфологическое описание морских экземпляров *G. hermaphroditus*, собранных в проливе Магеллана в Чили. Проведена оценка соответствует ли их строение характерным морфологическим признакам и хорошо установленной фенотипической стабильности, наблюдаемой в других местах. Кроме того, приводится обновленный ключ для определения видов *Gyratrix* Ehrenberg, 1831. Результаты показывают, что чилийские экземпляры схожи с популяциями, обнаруженными в европейских морях. Это фенотипическое сходство в контексте истории пролива Магеллана предполагает потенциальное распространение с помощью человека по морским судоходным путям. Исследование также выявляет интригующую биогеографическую закономерность, обнаруженную среди некоторых предполагаемых видов *G. hermaphroditus*, которая согласуется с викариантными процессами, связанными с дрейфом континентов. Их распространение подтверждает гипотезу о долгосрочной морфологической стабильности внутри видового комплекса, потенциально сохраняющейся в течение приблизительно 180 миллионов лет. Эта работа способствует пониманию распространения и эволюционной истории *G. hermaphroditus*, подчеркивая правдоподобность долгосрочной морфологической стагнации в видовом комплексе. Представленное здесь сообщение описывает новое местонахождение видового комплекса, значительно расширяет южную границу распространения *G. hermaphroditus* в Южной Америке и является первой морской находкой на континенте.

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КЛЮЧЕВЫЕ СЛОВА: Eukalyptorhynchia, Polycystididae, Gyratricinae, фенотипическая стабильность, космополитизм, криптические виды.

Introduction

Morphological stasis has been described as the lack of trait divergence over time, regardless of the time scale. This concept applies to both microevolutionary and fossil time series data, which appear to form a continuum (Arnold, 2014). Under a stasis scenario, cladogenesis is not followed by significant morphological changes, even in species-specific traits. As a result, different evolving lineages — a group of cryptic species — maintain a single species identity. These new taxa can remain unmodified over long spans of time, ranging from several thousand to millions of years. Many causes may contribute to the lack of morphological divergence, such as stabilising selection, large populations, developmental constraints, or niche conservatism. These causes are not mutually exclusive, and may in fact act together (Struck, Cerca, 2022). Morphological stasis is not, however, the only evolutionary process that may give rise to cryptic species. Recent divergence, parallelism, convergence, and introgression may also result in species that are morphologically indistinguishable or have only minor differences (Struck *et al*., 2018; Monro, 2022). Research focused on cryptic species is therefore a rich ground for evolutionary studies and a relevant source of discussion at the level of macro- and microevolution (Cerca *et al*., 2019; Monro, 2022).

Gyratrix hermaphroditus Ehrenberg, 1831 (Rhabdocoela: Eukalyptorhynchia) is a free-living aquatic microturbellarian, originally thought to be a single species with surprising phenotypic stasis in the context of: (i) a cosmopolitan distribution (Africa, Antarctica, Australia, Eurasia, South and North America) (Heitkamp, 1978; Tessens *et al*., 2021), (ii) an exceptionally broad range of environmental adaptability (marine, estuarine, and freshwater environments, sometimes located hundreds of kilometers from the nearest sea) (Heitkamp, 1978; Gamo, Noreña-Janssen, 1998; Tessens *et al*., 2021), and (iii) the existence of different diploid numbers of chromosomes in relation to the environment: six chromosomes known only from marine and estuarine specimens and four from freshwater forms (note that freshwater polyploid forms — 3n = 6, 4n = 8 — were also recorded at Roscoff, France) (Reuter, 1961; L'Hardy, 1986; Puccinelli *et al*., 1990, Curini-Galletti, Puccinelli, 1998).

However, more than a century after the species' description, the long-standing notion of an ubiquitous, morphologically conserved species would change: Heitkamp (1978) provided morphological and karyological evidence for the existence of at least five reproductively isolated sibling species in Germany, and suggested that more might exist, first referring to *G. hermaphroditus* as a species complex. L'Hardy (1986), studying specimens from France, increased the number of sibling species to seven or eight and found evidence that the ecological differentiation between marine and freshwater forms could be explained by aneuploidy. Curini-Galletti and Puccinelli (1998), using karyological and morphological data, identified eight sibling species in eastern Australia, confirming the status of *G. hermaphroditus* as a species complex. More recently, Tessens *et al*. (2021), studying specimens from several localities worldwide, distinguished 14 morphotypes of the sclerotised parts of the male copulatory organ, based on subtle variations in their shape and size. The molecular species delimitation methods used in the latter study revealed the existence of approximately 80 putative species, with most morphotypes encompassing between two and 12 cryptic species (Tessens *et al*., 2021).

In South America, *G. hermaphroditus* has only been reported from freshwater environments in Colombia (Fuhrmann, 1914), southern Brazil (Marcus, 1946, 1948; Reyes *et al*., 2021, 2022) and Argentina (Noreña-Janssen, 1995). In the latest systematic review (Tessens *et al*., 2021), many specimens from multiple locations across the species complex distribution range were studied, but South America was only represented by freshwater forms from Brazil.

The main goals of this article are to provide a comprehensive morphological description of marine specimens of *G. hermaphroditus* collected from the Strait of Magellan, Chile, and to evaluate whether their morphology aligns with the morphological traits and well-established phenotypic stasis observed in other localities. An updated key to the species of *Gyratrix* Ehrenberg, 1831 is also given. The study contributes to the understanding of the distribution and history of the species complex; our new report extends considerably the southern limit of the distribution of *G. hermaphroditus* in South America, and is the first marine record from the continent.

Material and methods

Collection data

Specimens were collected from a dissipative sandy coast on the Strait of Magellan, Magellan Province, Chile (53.016667° S, 70.816667° W), on 19 December 2009, and 20 February 2010 (collector: R. Ponce de León).

Morphological study methods and repository

Specimens were first observed alive. Two were whole mounted in Faure's medium (Langeron, 1949). Two additional specimens were fixed in hot Bouin's solution (Langeron, 1949) for 12 hours and later washed with 70% ethanol. They were then dehydrated via an ascending series of ethanol, cleared in xylene, and embedded in paraffin. Series of sagittal and transversal sections were cut at 3 µm, stained with hematoxylin (Langeron, 1949), and mounted in Canada balsam. Drawings were made with the aid of a drawing tube. Averages and sample sizes follow the ranges between parentheses. Terminology of the atrial organs follows Artois & Shockaert (2003, 2005). The whole mounts and slides with sectioned specimens are deposited in the Colección Helmintológica de la Sección Zoología de Invertebrados, Facultad de Ciencias, Universidad de la República, Uruguay (CHFC 12870–12873).

Measurements

All measurements are provided in micrometers and are presented in the format: mean (sample size, standard deviation).

Ethics statement

All work was performed according to and within the regulations enforced by the Chilean Authorities. No specific permissions were required for the field studies as the locality is a public area, and *Gyratrix hermaphroditus* is neither an endangered nor a protected species.

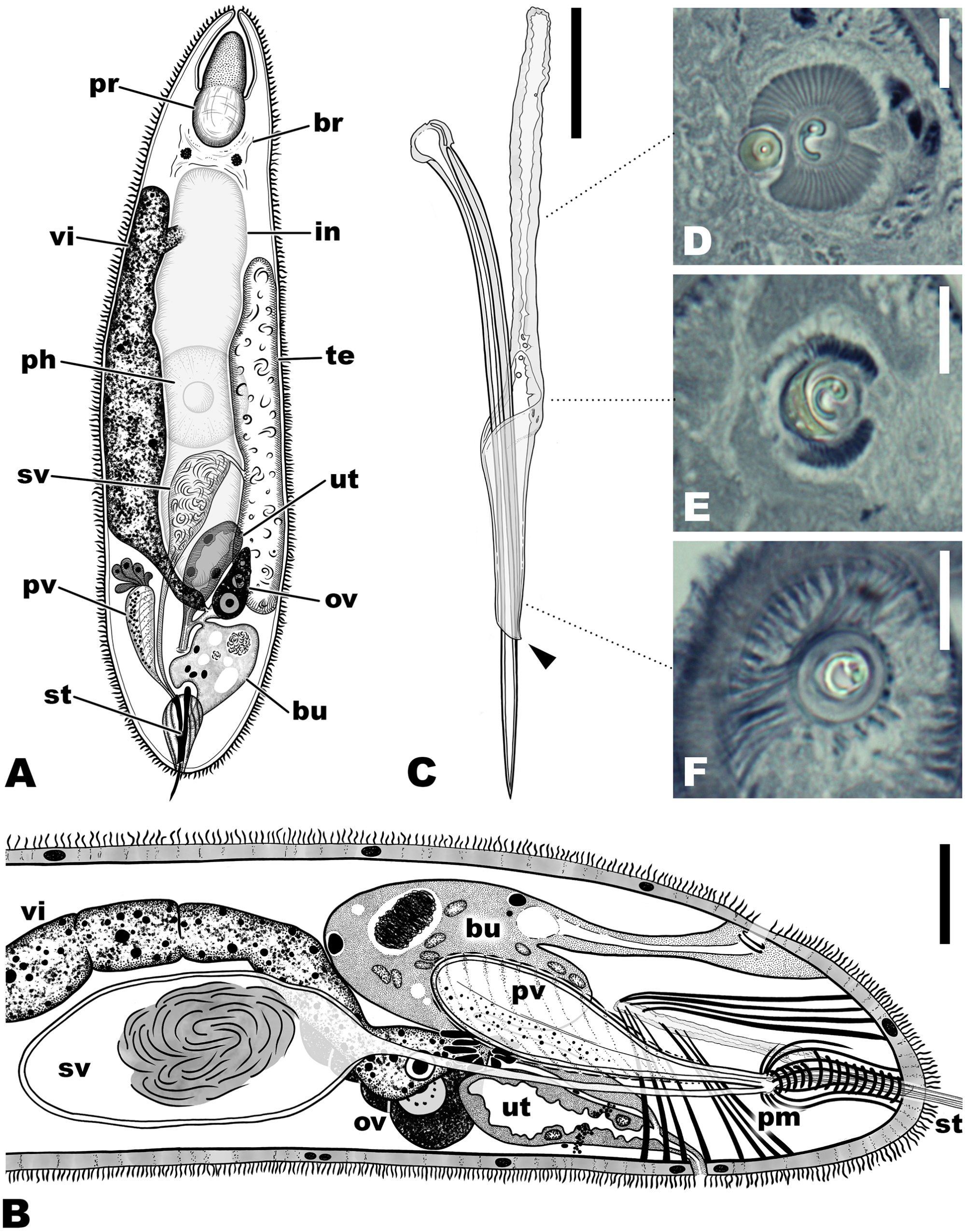

Fig. 1. Details of anatomy in *Gyratrix hermaphroditus* from the Strait of Magellan. A — freehand drawing of a live specimen; B — reproductive system, reconstructed from a series of sagittal sections; C — prostate stylets type II and III. Arrow, distal expansion of the sheath of prostate stylet type III; D–F — cross sections of prostate stylets type II and III; the dotted lines indicate the levels of these sections in part C of the figure. Abbreviations: br — brain; bu — bursa; in — intestine; ov — ovary; ph — pharynx; pm — protractor muscles; pr — proboscis; pv — prostatic vesicle; st — prostatic stylets; sv — seminal vesicle; te — testis; ut — uterus; vi — vitellaria. Scale bars: B — 25 µm; C — 25 µm; D — 10 µm; E — 10 µm; F — 10 µm.

Systematics

Order Rhabdocoela Ehrenberg, 1831
Suborder Kalyptorhynchia Graff, 1905
Infraorder Eukalyptorhynchia Meixner, 1928
Family Polycystididae Graff, 1905
Subfamily Gyratricinae Graff, 1905
Gyratrix Ehrenberg, 1831
Gyratrix hermaphroditus Ehrenberg, 1831
Fig. 1.

MATERIAL EXAMINED. CHFC 12870, one specimen, whole mounted. CHFC 12871, one specimen, squashed. CHFC 12872, one specimen on three slides, transversal sections. CHFC 12873, one specimen on one slide, sagittal sections. All specimens from the northern coast of the Strait of Magellan, Magellan Province, Chile (53.016667° S, 70.816667° W), collected on 19.12.2009 except for CHFC 12870, collected on 20.02.2010; coll. R. Ponce de León.

EXTERNAL MORPHOLOGY. Cylindrical, elongated body, tapering anteriad and rounded posteriorly (Fig. 1A), approximately 1 mm in length. Maximum width corresponding to roughly 1/3 of the total length, at about 2/3 from the anterior end.

COLOURATION. Translucent to whitish, except for the contents of the intestinal sac, which may appear yellowish to brown.

ANATOMY. Syncytial, ciliated epidermis, 3–4 µm in height, with the higher values towards the anterior and posterior ends of the body; cilia as tall as or taller than the syncytial cell bodies; large nuclei, displaced towards the base of the cells. Conspicuous basal membrane. Body wall with external circular, and internal longitudinal muscle fibers. Parenchyma is sparse due to the extensive development of the internal organs, which occupy most of the body.

No sphincter surrounding the opening of the proboscis sheath. Proboscis approximately 80 µm long, width about half that value. Distal region conical when extended, with abundant glandular secretions; rounded muscular base (Fig. 1A). Fixator, protractor and retractor muscles are present. Abundant gland cells surrounding the muscular base.

Large brain, posterior to the base of the proboscis (Fig. 1A). Paired eyes, cup-shaped, with brown pigment granules.

Ventral mouth, at about the middle of the body (Fig. 1A). Prepharyngeal cavity short, with a low epithelium. Rosulate pharynx, about 150 µm in diameter, with a narrow lumen; with circular, longitudinal and radial muscles, and abundant glands with a coarse secretion, opening into the lumen. An intestinal sac extends anteriorly up to the level of the posterior part of the brain, and posteriorly up to the level of the reproductive complex.

Male reproductive organs

Long testis, about 400 µm long, extending from midway between the brain and the pharynx to approximately the level between the third and fourth quarters of the body (Fig. 1A). It gives rise to a short vas deferens that opens into a large, piriform to oval seminal vesicle, situated ventrally and posteriorly to the pharynx. The seminal vesicle is about 85 µm long, and is lined by a low, nucleated epithelium and oblique muscle fibers. The posterior wall of the seminal vesicle continues into a long and narrow ejaculatory duct that extends posteriorly and opens into the male atrium, close to the proximal end of the prostate stylet type II.

Prostatic vesicle type II elongated, pyriform, about 90 µm long, surrounded by a conspicuous sheath composed of strong oblique muscles (Fig. 1A, B). The stylet type II (Fig. 1C) is 119 µm (2, 14.1) in length and 6 µm (2, 0.0) in maximum width; somewhat curved proximally, straight and pointed distally, with its proximal rim turned outward, making the proximal end 9 µm (2, 0.0) wide. In cross section, the stylet has a secretory duct that receives the secretion of the type II prostatic vesicle, and a seminal groove (Fig. 1D–F). The proximal part of the stylet is inside a male atrium, surrounded by a thick layer of inner circular muscles up to the proximal rim of the sheath of the type III stylet, and outer protractor muscles (Fig. 1D, E). The distal part of the stylet glides inside the sheath (Fig. 1F).

The prostate stylet type III is composed of a proximal stalk, 74 µm (2, 3.5) long and 7 µm (2, 0.7) wide, and a distal sheath, 34 µm (2, 9.2) long, 11 µm (2, 0.0) in proximal width and 4 µm (2, 1.4) in distal width (Fig. 1C). The stalk runs parallel to the male atrium; attached to its proximal end there are bundles of protractor muscle fibers that extend to the posterodorsal and posteroventral body wall, including a few fibers that attach to the body wall anteriorly to the female gonopore (Fig. 1B). The distal end of the sheath bears a barely visible spine (Fig. 1C, arrow).

A genital atrium surrounded by circular muscles opens into the terminal male gonopore (Fig. 1B).

Female reproductive organs

Vitelline glands are situated dorsolaterally opposite the testis, arranged either in a single mass (Fig. 1A) or in a somewhat reticulate pattern, spanning from the level of the brain to the level of the ovary. The single ovary lies in the posterior third of the body; it is about 50 µm long; the short oviduct and the vitelline duct open next to each other into a female duct type II.

Large bursa, anterior to the male atrium, in a dorsal position. It is lined with a chitinous epithelium, contains large cavities with sperm, and several large nuclei in a syncytial mass. Its dorsal wall extends posteriorly as a vaginal duct; the latter opens into a vaginal pore on the posterodorsal body wall, at, or posteriorly to, the level of the female gonopore (Fig. 1B). A small sphincter surrounds the distal part of the vaginal duct, just below the epidermis (Fig. 1B). The anterior, ventral wall of the bursa gives off a common oviduct, which leads into the proximal part of the female duct from the dorsal side.

Uterus lined with a high, nucleated epithelium, about 70 µm long, at, or overlapping, the level of the prostatic vesicle. It extends posteriorly and opens into the distal, rostral wall of the female duct, giving a very short *ductus utero-communis* that ends in the female genital pore on the ventral body wall (Fig. 1B). Two large clusters of shell glands are present on both sides of the uterus, discharging their secretion through the epithelium at approximately the midpoint of its length. A small, inconspicuous sphincter is present proximally to the entrance of the shell glands.

GEOGRAPHIC RANGE. Cosmopolitan species complex (Tessens *et al*., 2021); Strait of Magellan, Chile (new report, present work).

BIOLOGY. The specimens were found on algae debris, on a dissipative sandy coast.

Discussion

Taxonomic and biogeographic remarks

Although originally described as a single species, today we know that the cosmopolitan *Gyratrix hermaphroditus* is a species complex potentially comprising up to about 80 putative species, a large proportion of which seem to be endemic. A few, however, seem to have wide distributions, with a handful being present in more than one continent (Tessens *et al*., 2021).

In South America, the *G. hermaphroditus* complex has been reported from latitude 4°S in Colombia (Fuhrmann, 1914), to latitude 32°S in Brazil (Reyes *et al*., 2021). The current report from the Strait of Magellan in Chile, at a latitude of 53°S, extends the range of distribution in the South American continent 2,700 km to the south. The southernmost record of the species complex, however, is from the coast of Queen Maud Land, Antarctica, at a latitude of 71°S (Artois *et al*., 2000).

The remarkable morphological stasis within this species complex, combined with the lack of detailed descriptions for many populations, hinder an accurate comparison of the Chilean material with specimens from many regions, but some interesting observations can be made.

In a comprehensive study of the hard parts of specimens of *G. hermaphroditus* from Eurasian lakes that also considered available data from the bibliography, Timoshkin *et al*. (2004) highlighted the importance of including certain measurements and proportions of the sclerotised structures of the male copulatory system in the descriptions: total length of the prostate stylet types II and III, and of the sheath and stalk of the latter; the ratios of the lengths of stylets type II/III and of the stalk/sheath of the stylet type III, as well as detailed descriptions of the fine structure of the sheath. Subsequently, Tessens *et al*. (2021), in a morphometric study of more than 400 specimens from several localities worldwide, found that measurements of the sheath and stalk of the stylet type III relative to the length of the stylet type II, and of the sheath relative to the stalk, were moderately correlated. Based on all these measurements and proportions, as well as on existing data from the literature, the material from Chile falls within the expected ranges for the species complex.

Tessens *et al*. (2021) identified 14 distinct morphotypes of the sclerotised copulatory organs. Unfortunately, they were not assigned to the measured specimens, which prevent us from making a direct comparison between the qualitative characters of these specimens and the ones from Chile. However, based on the proportions of the morphotypes in Figure 1 of the aforementioned work, and on the presence of a slight, dorsal spine in the distal part of the sheath, the Chilean material can be ascribed to morphotype M.

Specimens from the nearest South American locality, in Brazil (Reyes *et al*., 2021), also show some similarity, but differ in the stalk length, the ratio of stylets II/III, and the ratio stylet II/stalk; furthermore, they were reported from a freshwater environment.

Comprehensive descriptions of the soft reproductive organs in *G. hermaphroditus* are very limited, but notable variation has been observed (Artois, Schockaert, 2001; Reyes *et al*., 2021). In this respect, however, other than the length of the vaginal duct, our material is strikingly similar to that of Meixner (1929) from Kiel Bay (Baltic Sea), with which it shares even details such as the insertion of a few protractor muscle fibers of stylet III anteriorly to the female gonopore (Meixner, 1929, fig. 15). This result, however, is not surprising if we consider shipping routes as a means of human-assisted dispersal. The Strait of Magellan has long been a strategic gateway between the Atlantic and Pacific Oceans, and several European countries have used it, from historic exploration voyages to more recent commerce. Until late 1870s, having no cargo on the outbound leg, vessels sailed "in ballast" — carrying sand, stone, or other heavy material for stability; since then, ballast water tanks came into regular use (Davidson, Simkanin, 2012). Both ballast water and ship hull fouling are well-documented vectors for the anthropogenic translocation of marine organisms across biogeographic boundaries (Hewitt *et al*., 2009). Furthermore, as a result of the maritime shipping connectivity, allochthonous species are known to have been introduced from the Northern Hemisphere into the Strait of Magellan, such as a northern lineage of *Mytilus galloprovincialis*, recently found in areas within the strait directly associated with the presence of foreign ships (Oyarzún *et al*., 2016). Human-assisted dispersal of *G. hermaphroditus* to, or from, the Strait of Magellan, is therefore a realistic hypothesis.

Nevertheless, future studies on the Chilean population should adopt an integrative taxonomic approach — combining detailed morphological assessments with molecular analyses — to test whether the South American and other populations genuinely represent the same evolutionary lineage.

Key to the species of *Gyratrix*

Currently, *Gyratrix* Ehrenberg, 1831 comprises five nominal taxa: the cosmopolitan species complex *G. hermaphroditus* Ehrenberg, 1831, *Gyratrix proavus* Meixner, 1929, from the North Sea and nearby areas, *Gyratrix proaviformis* Karling et Schockaert, 1977, only known from the United States (Oregon), and *Gyratrix sinensis* Wang et Li, 2005, from Southern China. *Gyratrix attemsi* Graff, 1896 was transferred to *Gyratricella* when the genus was erected by Karling (1955), and *Gyratrix arenarius* Evdonin, 1971 from Sea of Japan (Peter the Great Gul), which was considered a synonym of *G. hermaphroditus* by Karling et Schockaert, 1977.

In the latter work, Karling & Schockaert (1977) correctly pointed out that the soft body characteristics used by Evdonin (1971, 1977) to diagnose *G. arenarius* were unreliable, and that the proportions and shape of the cuticular pieces fell within the those expected for *G. hermaphroditus*. Evdonin's description and diagnosis of *G. arenarius*, however, includes a character that was not explicitly mentioned. In his 1977 work, when describing *G. hermaphroditus*, he correctly describes the prostatic stylet type II as being *прямой или слегка изогнут, с секреторной трубкой и наружным желобом* — "straight or slightly curved, with a secretory tube and an external groove". Then, describing *G. arenarius*, he also writes that *Простатический стилет слабо изогнут, с секреторным каналом внутри и семенным желобом* — "the prostatic stylet is slightly curved, with a secretory duct inside and a seminal groove", but adds that *Стилет на противоположной желобу стороне несет продольный гребень* — "the stylet on the opposite side of the groove has a longitudinal ridge". Furthermore, the sheath of the type III stylet is described and depicted as *острое* — "sharp" distally, unlike that of *G. hermaphroditus*. Because of these characters, and the fact that other authors have considered *G. arenarius* as a valid species (Curini-Galletti, Puccinelli, 1990; Wang, Li, 2005), we find it more conservative to include it in the present key, pending further taxonomic analysis.

We have decided to exclude soft-body characters such as testis, seminal vesicle, or vitelline glands from the key, as these features are highly variable depending on the maturity of the specimens. In addition, we find that the morphology of the stylet of *G. sinensis* (Wang, Li, 2005) falls within the variations that were found in freshwater *G. hermaphroditus* by Timoshkin *et al.* (2004) in specimens from Eurasia. The two characters that seem unique to *G. sinensis* are the ventral opening of the proboscis and the very long egg stalk, so these have been used.

Karling (1955), Schockaert (1973) and Evdonin (1977) created keys for the identification of species of *Gyratrix*, but these do not include *G. proaviformis* and *G. sinensis*. Therefore, we present a key to the five species of *Gyratrix*:

1a. Prostatic stylet type III without or with a short cuticular stalk, only slightly extended dorsally.2

1b. Prostatic stylet type III with a long cuticular stalk...3

2a. Proximal part of the sheath rounded-pointed; distal end narrowed and sharp, with a small tooth-like appendage. Stylet type II about three times as long as the sheath, or more. Eyes absent. .... *Gyratrix proavus* Meixner, 1929

2b. Proximal part of the sheath square; distal end truncated, without a tooth-like appendage. Stylet type II about twice as long as the sheath. Eyes present. .... *Gyratrix proaviformis* Karling et Schockaert, 1977

3a. Anterior proboscis opening. Egg stalk short (generally shorter than the length of the egg) or absent. 4

3b. Ventral proboscis opening. Egg stalk long (400–500 µm, much longer than the length of the egg). Eyes present. ....*Gyratrix sinensis* Wang & Li, 2005

4a. Prostatic stylet type II without a longitudinal ridge. Distal end of the sheath narrow, with two, one, or no noticeable tooth-like appendage. Female genital and vaginal pore far apart from the male pore; male pore terminal. Eyes present or absent. .... *Gyratrix hermaphroditus* Ehrenberg, 1831

4b. Prostatic stylet type II with a longitudinal ridge. Distal end of the sheath narrow and sharp, without a tooth-like appendage. Eyes present. .... *Gyratrix arenarius* Evdonin, 1971

An intriguing distribution pattern

In theory, *G. hermaphroditus* should encounter significant barriers to long-distance dispersal across continents due to its small body size, meiobenthic lifestyle in the marine environment, and its lack of a planktonic larval stage. Nevertheless, beyond the human-assisted dispersion mentioned above, the intercontinental distribution observed in a few putative species within the species complex (Tessens *et al*., 2021) could hypothetically be explained by passive natural dispersal mechanisms, such as rafting on macroalgae or phoresis (Artois *et al*., 2011). More speculatively, vicariant events associated with continental drift could have separated ancestral populations, leading to their present-day distribution. On a global scale, it is highly likely that multiple mechanisms have played a role in the biogeographic history of the group.

In this context, four of the 62 putative species identified by Tessens *et al*. (2021) with the Automatic Barcode Gap Discovery method are of particular interest: freshwater species D1 (found in South Africa and India) and D2 (present in South Africa, India, Australia and Hawai‘i), and the marine species M1 (India and Australia) and N1 (India, Australia, Qatar and Hawai‘i). Clade M is also interesting: out of the three putative species it encompasses, M1 is, as stated above, in India and Australia; M2 is in Australia, and, in the present work, a species belonging to morphotype M is being reported from South America. The recurrence of shared species between different combinations of South Africa, India, and Australia, plus a new link to South America, is suggestive of a historical distribution potentially linked to the fragmentation of Gondwana, a hypothesis that has also been proposed for other flatworms, such as temnocephalans (Cannon, Joffe, 2001).

This interpretation is highly speculative and circumstantial in the absence of definitive phylogenetic evidence, but it is, however, compelling. It would mean that the common ancestor of these putative species would have existed before the breakup of Gondwana, and that their remarkable morphological stasis might have persisted for about 180 million years (McLoughlin, 2001).

Although such long-term stasis is extremely rare, it is not without precedent. Recently, Kolesnikov *et al*. (2025) found fossil evidence of stasis for about 99 million years in a mite belonging to *Paralycus* Womersley, 1944 (Acari: Oribatida: Pediculochelidae), recovered from Middle Cretaceous amber. An even more striking example is given by Cerca *et al*. (2019), who found evidence of morphological stasis lasting between 75-205 million years in a morphotype belonging to the interstitial *Stygocapitella* species complex (Annelida: Orbiniida: Parergodrilidae). Such a long-term morphological stability in *G. hermaphroditus* is, therefore, not impossible. In fact, Tessens *et al*. (2021, 2025) recently proposed that selective pressures arising from the dual function of the sclerotised parts of the male copulatory system, in both mating and feeding, might constrain morphological modification, thereby accounting for the high similarity among variants and the prevalence of cryptic species within the complex. Because these functions are essential and conserved across generations, such selective pressures are likely to persist over evolutionary timescales, reinforcing the possibility of long-term morphological stasis. Calibrated molecular clock analyses are essential to test this hypothesis, as they can provide robust estimates of divergence times and help determine whether the observed biogeographic patterns align with ancient vicariant events.

Nearly two centuries ago, Christian Gottfried Ehrenberg (1831) recognized the exceptional nature of this organism, remarking: *Haec forma inter eas est, quae Planariarum naturam quam optime develant* — “This form is among those which most excellently reveal the nature of the planarians.” Today, *G. hermaphroditus* remains as enigmatic as it was at the time of its discovery — an organism whose apparent simplicity conceals a fascinating evolutionary history.

Compliance with ethical standards

CONFLICT OF INTEREST**:** The authors declare that they have no conflicts of interest.

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