



Decomplicating and identifying species in the radiation of the Antarctic fish genus *Pogonophryne* (Arteidraconidae)

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Abstract

The 27 species of the genus *Pogonophryne* are a distinctive component of the radiation of cryonotothenioid fishes and commonly encountered during benthic trawling and commercial longlining for toothfish. They are difficult to identify because they are morphologically and ecologically similar and sympatric in their distributions. The genus has recently been the subject of a taxonomic consolidation that, on the basis of nuclear gene sequence data and morphometrics, has synonymized the 27 species to the five known species groups and detected an unnamed sixth clade, decreasing the diversity of *Pogonophryne* by $\approx 78\%$ and that of the radiation of cryonotothenioids by $\approx 16\%$. We clarify this situation by assigning each of the 27 species to a species group. We also provide an uncomplicated illustrated guide that requires no counting or measuring of characters and facilitates the placement of each of the species into one of three categories, five species groups, and three subgroups within the genus. These are the essential steps in identifying a species of *Pogonophryne* whether following the traditional or reduced view of diversity. With the exception of the details concerning the undescribed species, this is the heretofore elusive synopsis of the genus that should remain stable into the future.

Keywords Adaptive radiation · Biodiversity · Notothenioid · Species identification

Introduction

The 128 species of Antarctic cryonotothenioid fishes are one of the few well-documented examples of an adaptive radiation of fishes in the marine realm (Eastman and McCune 2000; Matschiner et al. 2015; Bowen et al. 2020). The genus *Pogonophryne* Regan 1914 (Arteidraconidae) is a component of that radiation, and the species are a ubiquitous benthic element of the shelf and upper slope waters of Antarctica (Eakin 1990; Hanchet et al. 2013; La Mesa et al. 2019). Over the past few decades the number of species has increased from 17 to 27, and *Pogonophryne* is now the most speciose genus of notothenioids (Eakin 1990; Eastman and Eakin 2021). They are medium-sized (predominantly 20–30 cm TL) sedentary benthic fishes found primarily at depths of 500–1600 m (Duhamel et al. 2014; Eastman 2017).

Unlike many other cryonotothenioids, they exhibit minimal ecomorphological disparity and are a non-adaptive element of the radiation. They do, however, possess a mental barbel of uncertain functional significance. This structure is subject to intraspecific variation in some species (Eakin et al. 2001). With an age estimate of < 1 Ma, *Pogonophryne* is also the most recently diverged cryonotothenioid lineage (Near et al. 2012) and, because they exhibit a relatively low degree of interspecific morphological variation, this makes the species of *Pogonophryne* the most difficult-to-identify cryonotothenioids.

To facilitate identification and based on similarities in external morphology, the 27 species are allocated among three categories and five species groups within the categories (Table 1), with one species group containing three subgroups (Balushkin and Eakin 1998). These divisions, based strictly on morphology, have no taxonomic status, although all five species groups are clades based on mitochondrial gene sequences (Eakin et al. 2009). This has been confirmed by more extensive DNA sequencing that involved genome-wide data (ddRADseq) and morphometric analyses of the body shape axis by Parker et al. (2022), who also identified a previously unrecognized sixth clade. Based on their sample

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of 18 of the 27 species, Parker et al. propose reducing the number of species of *Pogonophryne* from 27 to 6 by synonymizing the species in each of the five species groups into a single species bearing the name of the species group. This results in a 78% reduction in the number of species. The newly recognized sixth species from the Ross Sea has not been formally described and named, and there is insufficient information for us to consider it here.

Because explaining diversity is a major focus in organismal biology, it is of general interest when an issue arises involving species diversity within a radiation. This is exemplified by *Pogonophryne* given that Parker et al. (2022, p. 58) state that their analyses “result in a dramatic reduction in the number of distinct species within” an Antarctic adaptive radiation. We also recognize that there has been taxonomic inflation within *Pogonophryne*. In the aftermath of the revisions of Parker et al. there will be uncertainty among those confronted with understanding the amalgamations, specifically how species should be identified and assigned to one of the five known species groups. Whether the traditional or the new reduced approach to the taxonomy of *Pogonophryne* is employed, the placement of a species in a category and then in a species group is the essential step in the identification process. Here we provide a table and an uncomplicated pictorial identification guide for *Pogonophryne* that dispels confusion by (1) delineating multiple features of external morphology, unrelated to barbel morphology, that define the

categories and species groups and (2) identifying the species contained in each species group and subgroup.

Materials and methods

The initial step in the identification of an unknown species of *Pogonophryne* is the determination of its membership in a category and a species group (Table 1). This can be accomplished by utilizing features visible solely in the heads of species of each of the five groups. Although in Russian and not widely circulated, Figs. 2–5 in Andriashev’s (1967) review of the genus *Pogonophryne* are extremely useful for this purpose. The species groups were not yet recognized when he wrote the paper, but four of the five groups are represented in his figures. The fifth, or *P. albipinna* group, was subsequently recognized by Eakin (1981). It should also be noted that the *P. scotti* “group” consists of a single species.

Figures 2, 3, and 4 are scans of photographic copies of the original figures submitted for publication by Professor Anatole P. Andriashev (1967) for his paper reviewing the little-studied genus *Pogonophryne*. Andriashev gave photographic copies of his original illustrations to Professor Hugh DeWitt of the University of Maine who passed them on to his, then graduate student, Richard Eakin, and we are using them here. This is significant because these copies of the dorsal and lateral views of the head of *P. mentella* (Fig. 3c, d) show the large terminal expansion of the mental barbel as

Table 1 Distribution of the 27 species of *Pogonophryne* among the three categories, five species groups and, within the *P. mentella* group, three subgroups of species with either short (1), medium (2), or long (3) barbels

| Unspotted category | Dorsally spotted category | | | Dorsally unspotted category |
|---------------------------|---------------------------|---------------------------|---|-----------------------------|
| <i>P. albipinna</i> group | <i>P. barsukovi</i> group | <i>P. marmorata</i> group | <i>P. mentella</i> group | <i>P. scotti</i> group |
| <i>P. albipinna</i> | <i>P. barsukovi</i> | <i>P. maculiventrata</i> | { <i>P. bellingshausenensis</i> <i>P. brevibarbata</i> <i>P. neyelovi</i> <i>P. triono</i> <i>P. ventrimaculata</i> <i>P. fusca</i> Subgroups 2 { <i>P. platypogon</i> <i>P. squamibarbata</i> <i>P. cerebropogon</i> <i>P. eakini</i> <i>P. favosa</i> <i>P. lanceobarbata</i> 3 { <i>P. macropogon</i> <i>P. mentella</i> <i>P. orangeiensis</i> <i>P. pavlovi</i> <i>P. sarmentifera</i> | <i>P. scotti</i> |
| <i>P. dewitti</i> | <i>P. permitini</i> | <i>P. marmorata</i> | | |
| <i>P. immaculata</i> | | <i>P. skorai</i> | | |
| <i>P. stewarti</i> | | | | |

originally drawn by Andriashev's artist. All known reprints and reproductions of this article contain a printing error that omitted the terminal expansion.

We used photographs of a specimen of *P. immaculata* to represent the *P. albipinna* species group because the holotype and only known specimen of *P. albipinna* is a 37.5 mm SL juvenile (Eakin 1981). The photographed *P. immaculata* in Fig. 1 was a freshly caught 209 mm SL female now preserved and catalogued in the collections of the Museum of New Zealand Te Papa Tongarewa (NMNZ P.043715).

Results and discussion

Categories, species groups, and subgroups of *Pogonophryne*

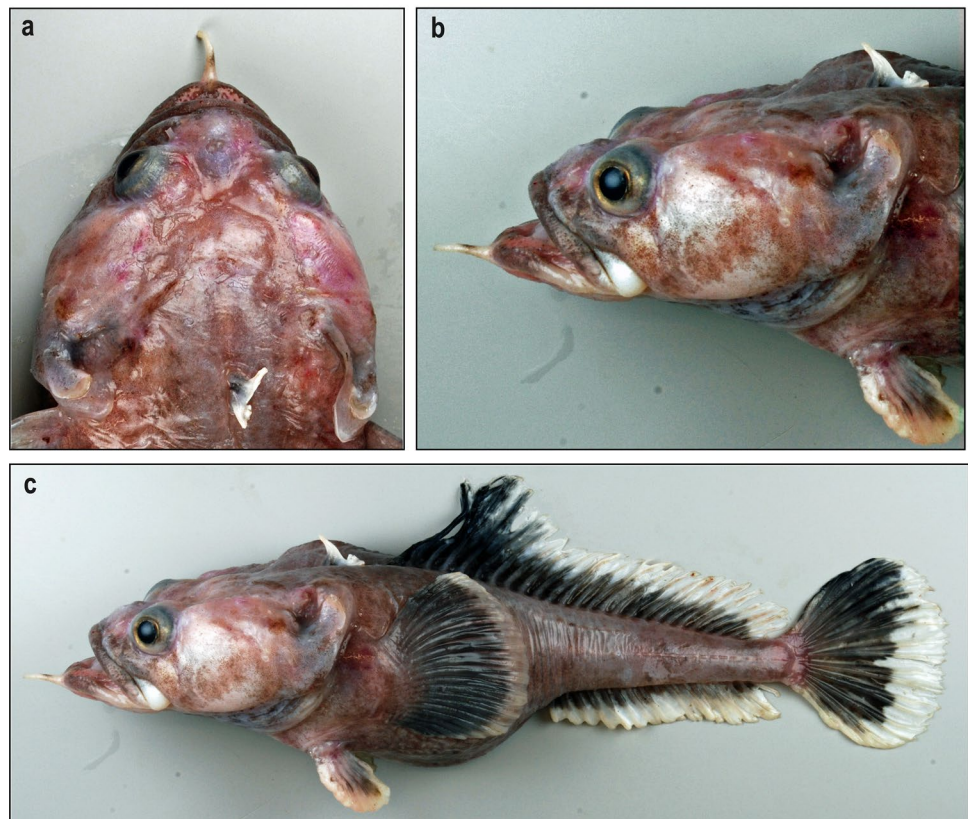
The guide is based on the pigmentation patterns, head shapes, and relative sizes of other features easily observed in dorsal or lateral views of the heads of *Pogonophryne*. The

figures show the key features that distinguish categories and species groups: (1) the color pattern of the integument of the dorsal head, (2) the shape of the head, (3) the degree of projection of the lower jaw, (4) the relative volume of the orbit occupied by the eye, and (5) the relative size and shape of the mental barbel.

Each species of *Pogonophryne* can be assigned to one of three distinct categories (Table 1) based on easily observed differences in spotting patterns of the skin and other less obvious characters not considered here (Eakin 1977; 1981; 1990; Balushkin and Eakin 1998). The species in each category are further separable into five morphologically well-defined species groups (Balushkin and Eakin 1998). The validity of the species groups reflects consistent differences in color patterns, head shapes, jaw prognathism, mental barbel features, and meristic counts that distinguish species in each group, for example, numbers of vertebrae, lateral-line pores or scales, and certain fin rays. There has probably been over reliance on the importance of barbel morphology in some recent descriptions of new species

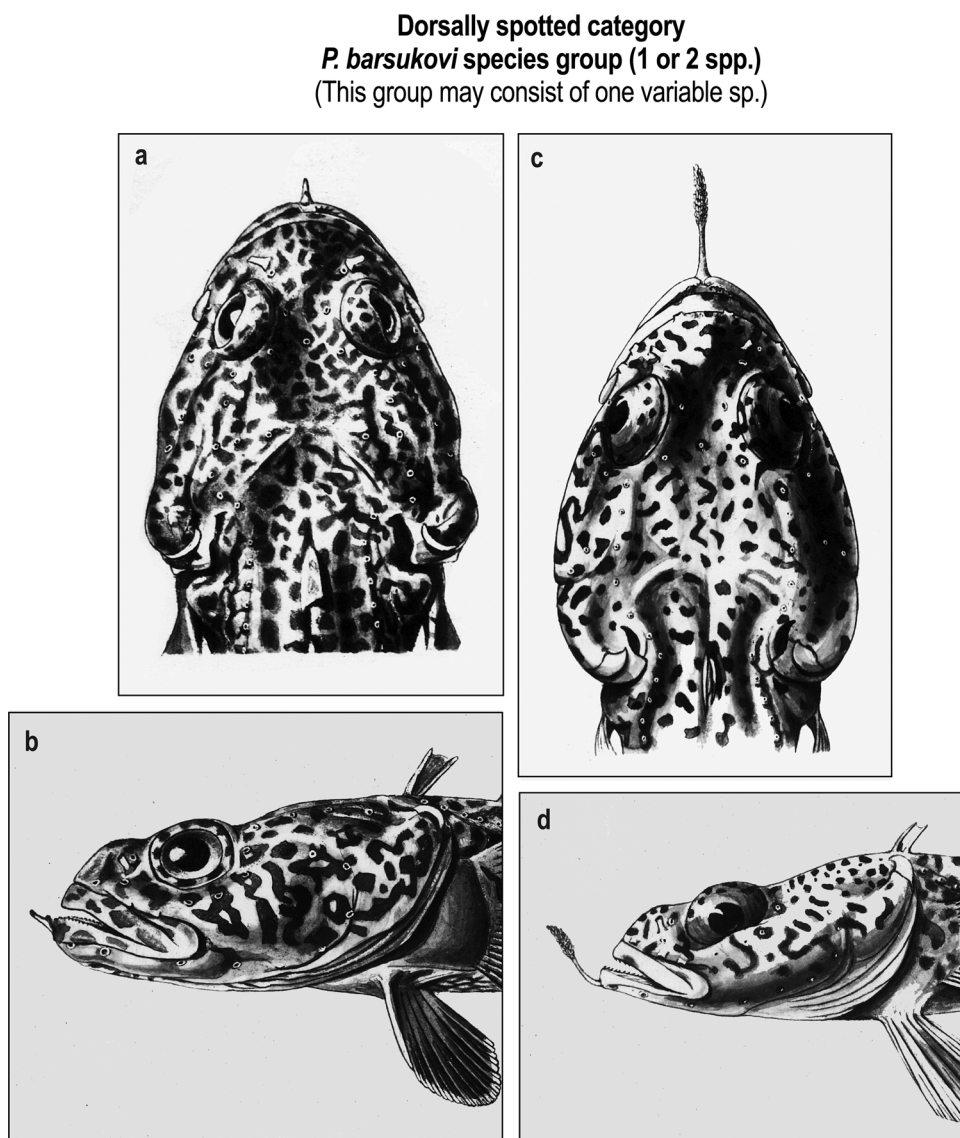
Fig. 1 The *P. albipinna* species group represented by *Pogonophryne immaculata*. Views of the head (**a**, **b**) and trunk (**c**) of a 209 mm SL female, NMNZ P.043715

Unspotted category *P. albipinna* species group (4 spp.) (represented by *P. immaculata*)



- No dark spots or markings on head or trunk
- Wide interorbital region, snout & jaws

Fig. 2 The *P. barsukovi* species group. Dorsal and lateral views of heads of *Pogonophryne barsukovi* (a, b), 217 mm and *P. permitini* (c, d), 126 mm. Both specimens are holotypes and females. From Andriashev (1967, Figs. 2, 3)



P. barsukovi

- Small densely distributed dark spots on dorsum of head
- Head heart-shaped in dorsal view
- Snout slopes steeply in lateral profile usually at $>45^\circ$ from horizontal
- Lower jaw does not or only slightly projects beyond upper
- Barbel short, tapered, lacks terminal expansion
- Adult males with tapered barbel have a darkly colored anterior lobe on second dorsal fin

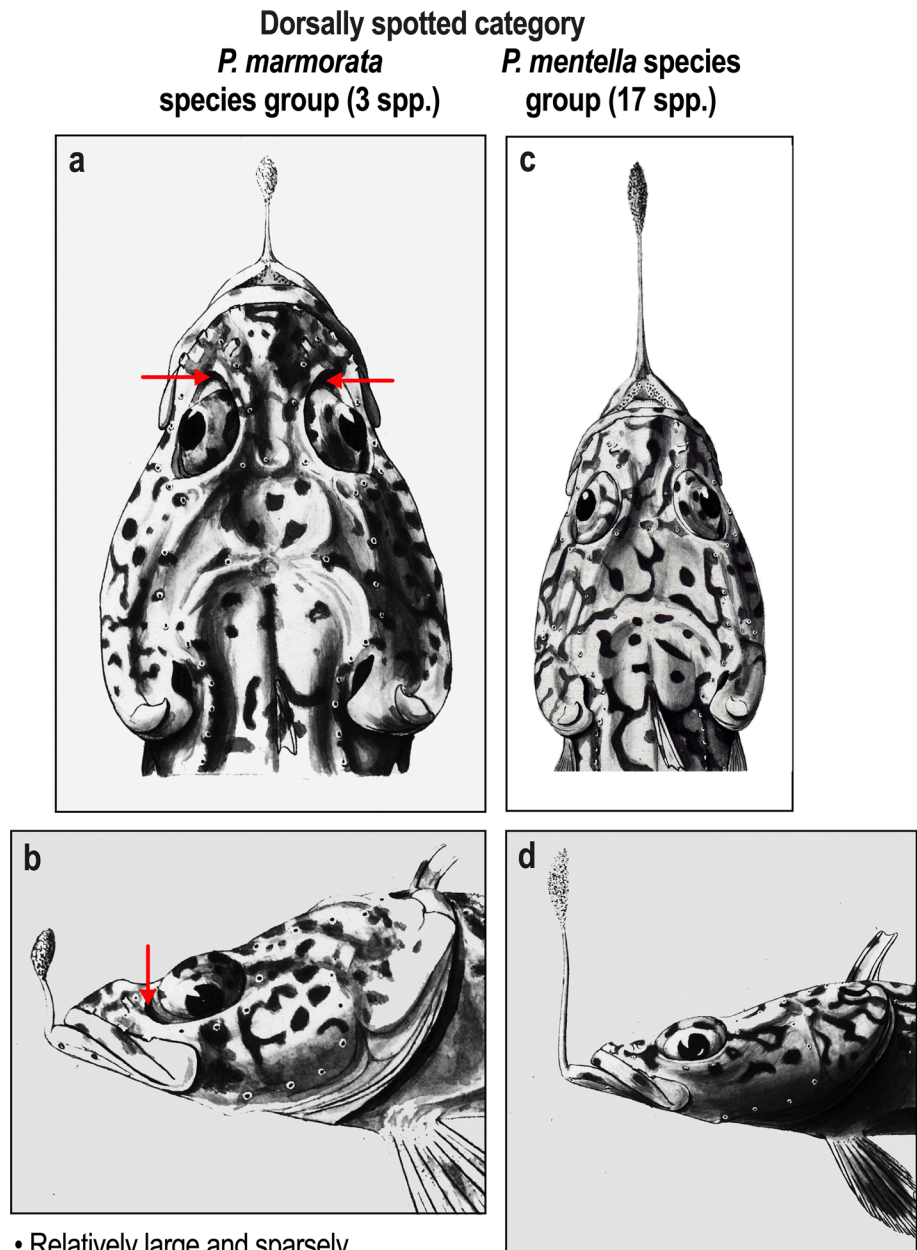
P. permitini

- Small less densely distributed dark spots on dorsum of head
- Head heart-shaped in dorsal view
- Snout slopes steeply in lateral profile usually at $>45^\circ$ from horizontal
- Lower jaw projects beyond upper
- Barbel usually has terminal expansion

of *Pogonophryne*, although among all species only the barbels of *P. scotti* exhibit documented intraspecific variation (Eakin et al. 2001). Parker et al. (2022, p. 71) indicate that their “results provide no genomic or phenotypic support for differentiation among species of *Pogonophryne*

that are diagnosed exclusively using barbel morphology.” However the barbel has not been the sole character used in describing species. For example, six species of the *P. mentella* group (*P. macropogon*, *P. cerebropogon*, *P. ventrimaculata*, *P. orangiensis*, *P. squamibarbata*, and *P.*

Fig. 3 The *P. marmorata* and *P. mentella* species groups. Dorsal and lateral views of the heads of *Pogonophryne marmorata* (a, b), 176 mm and *P. mentella* (c, d), 132 mm, holotype. Red arrows (a, b) indicate anterior area or gap within the orbit not filled by eye of *P. marmorata*. Both specimens are females. From Andriashev (1967, Figs. 2, 5)



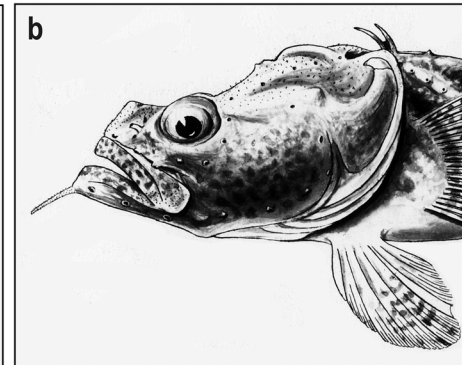
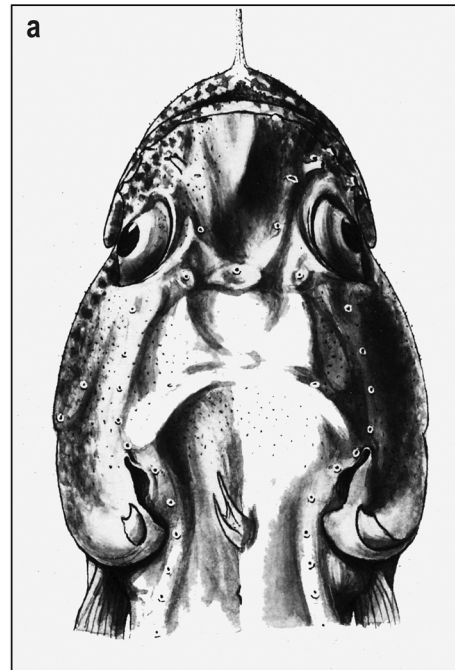
- Relatively large and sparsely distributed dark spots and vermiculations on dorsum of head
- Head pear-shaped in dorsal view
- Interorbital width narrow
- Lower jaw projects slightly
- In most the eye does not occupy orbit anteriorly leaving gap (arrows)¹
- Post-temporal ridges well developed
- Pectoral rays 17–20 versus 18–22 present in other species groups

¹ This is a space in the orbital cavity, not a bony feature

- Various sized and distributed dark spots and vermiculations on dorsum of head
- Head narrowly triangular in dorsal view
- Interorbital width wide
- Lower jaw projects greatly
- Post-temporal ridges not well developed

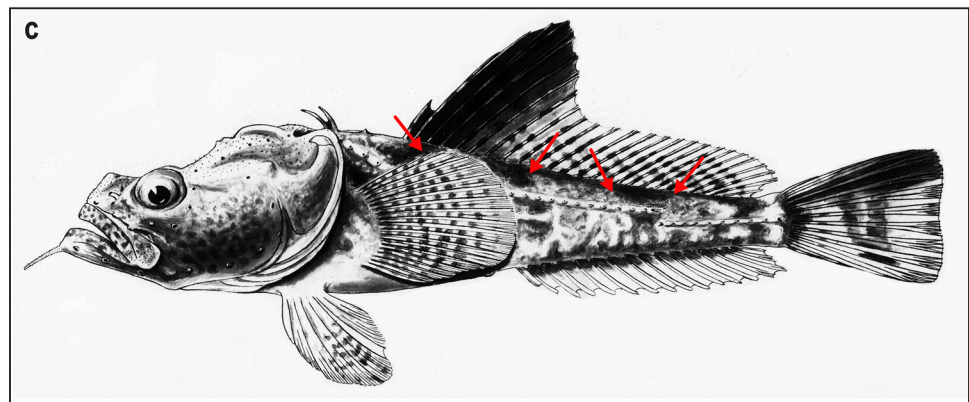
Fig. 4 The *P. scotti* species group. Dorsal and lateral views of the head (**a**, **b**) and trunk (**c**) of *Pogonophryne scotti*, 248 mm, male. From Andriashv (1967, Fig. 4)

Dorsally unspotted category
***P. scotti* species group (1 sp.)**



P. scotti

- No dark spots on dorsal aspect of head
- All ridges on dorsum of head well developed
- In lateral view red arrows delimit two dark saddle-shaped patches extending from base of second dorsal fin to upper lateral line, a characteristic feature of this species



bellingshausenensis) are each defined by a unique combination of at least four characters: barbel length, terminal expansion morphology, spotting patterns, and vertebral counts (Eakin 1981, 1987; Eakin and Balushkin 1998, 2000; Eakin and Eastman 1998; Eakin et al. 2008).

Within the diverse *P. mentella* group there are three subgroups (Table 1) that contain 63% (17/27) of the species of *Pogonophryne*. These subgroups have no phylogenetic basis and are arbitrarily recognized based on the relative length of the mental barbels. However, arranging and categorizing the 17 species in this group by their barbel lengths facilitates their identifications as species.

This does not imply that barbel morphology is the sole diagnostic character for these species, but rather that relative barbel lengths are useful in, for example, taxonomic key couplets (Eakin 1990, pp. 339–340). These subgroups are the focus of much of the consolidation suggested by Parker et al. (2022). Finally, we do not doubt the existence of a sixth lineage identified by Parker et al. and we urge future restraint in the description of new species of *Pogonophryne* without supporting nucleotide sequence data.

Faunal surveys of Antarctic fishes are now increasingly conducted using images obtained from towed high-resolution

camera systems rather than by benthic trawling with its habitat-altering consequences. Although only a dorsal image of the fish is obtained in most survey photographs, it can usually be identified at the species level (Eastman et al. 2013; La Mesa et al. 2019). In addition to presence/absence data, these images also provide insight into other aspects of biology including reproductive behavior and have documented the universality of nesting and nest guarding behavior in cryonotothenioids, including *Pogonophryne* spp. (La Mesa et al. 2021). Although species identifications are difficult in *Pogonophryne*, our identification guide makes it possible to determine the species group membership using easily visible features in a dorsal image.

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Author contributions Both authors participated in the analysis, writing, and final approval of this paper. RRE was responsible for recognizing, defining, and determining the species composition of the categories, species groups, and subgroups of *Pogonophryne* and also for supplying the original photographic prints for Figs. 2–4.

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Data availability Some specimens and data are deposited in the ichthyology collections of the Peabody Museum of Natural History, Yale University, New Haven, CT USA.

Code availability NA.

Declarations

Conflict of interest The authors declare that they have no conflicting or competing interests.

Consent to participate Both authors have given consent to participate.

Consent for publication Both authors have given consent for publication.

Ethical approval Ethics approval was not needed for this particular study but, in a broader perspective, both authors followed all applicable national and institutional guidelines for the collection, care, and ethical use of research organisms and material in the conduct of the research, specifically those under protocol L01-14 as approved by the Institutional Animal Care and Use Committee of Ohio University.

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