Marino Vacchi
Eva Pisano
Laura Ghigliotti   *Editors*

The Antarctic Silverfish: a Keystone Species in a Changing Ecosystem

Springer

Advances in Polar Ecology

Volume 3

Series editor
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Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany

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Marino Vacchi • Eva Pisano • Laura Ghigliotti
Editors

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Editors

Marino Vacchi
Institute of Marine
    Sciences (ISMAR) - CNR
Genoa, Italy

Laura Ghigliotti
Institute of Marine
    Sciences (ISMAR) - CNR
Genoa, Italy

Eva Pisano
Department of Earth, Environment
    and Life Sciences (DISTAV)
University of Genoa
Genoa, Italy

Institute of Marine
    Sciences (ISMAR) - CNR
Genoa, Italy

Foreword

Implementation of the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) ecosystem approach to the management of the marine living resources and environment of the Southern Ocean requires a thorough understanding of the biology and ecology of exploited, dependent and related species. CCAMLR came into force in 1982, primarily because of scientific, political and environmental concerns surrounding the potential detrimental impact of an expanding krill fishery upon the Southern Ocean ecosystem. Since the outset, a major scientific focus has been on Antarctic krill, *Euphausia superba*, and krill-dependent predators predominantly in the Atlantic sector of the Southern Ocean, a region where the krill fishery has traditionally operated.

However, in recent decades, the development of deep-water longline fisheries for toothfish (*Dissostichus* spp.) has led to an increasing scientific focus on other regions of the Southern Ocean where Antarctic krill are less abundant and play a reduced role in the ecosystem. In such regions, other macro zooplankton species or pelagic fish are important prey species in place of krill. Within the circum-Antarctic, high-latitude pelagic realm, the Antarctic silverfish, *Pleuragramma antarctica*, is a key prey species forming a significant part of the diet of a range of air-breathing and fish predators including the Antarctic toothfish (*Dissostichus mawsoni*). As the fishery for this species has developed at high latitudes in the Southern Ocean, there has been an increasing need to understand the ecology of the key species in the ecosystems within which the fishery operates.

The 13 chapters of this book provide, for the first time in a single volume, a comprehensive overview of the current state of knowledge of *P. antarctica*, a species that was once, itself, the target of a small exploratory fishery and until recently remained relatively poorly studied. The chapters cover a range of scientific disciplines including evolutionary adaptation, ecophysiology, trophic ecology and reproductive and population ecology, falling within three broad themes, namely, evolution and adaptations, ecology and life history and challenges and conservation perspectives. The broad circumpolar distribution of the Antarctic silverfish coupled with its key role in the Antarctic continental shelf pelagic ecosystem and physiological adaptation to living in a hostile environment makes understanding the species'

likely response to environmental change a key component in the future functioning of the regional ecosystem. Additionally, a detailed understanding of the abundance and trophic interactions of such a dominant keystone species is a vital element of informing the development of marine spatial planning and marine protected areas in the Antarctic continental shelf region.

The editors are to be congratulated for bringing together the impressive list of contributors who have provided such a broad diversity of expertise relating to the ecology of *P. antarctica*. This book will undoubtedly be a key publication not only for those interested in the ecology of this keystone species but also more broadly for those interested in the conservation of Antarctic marine living resources and the impacts of climate change upon them.

Chair of the CCAMLR Scientific Committee   Mark Belchier
British Antarctic Survey (BAS)
Cambridge, UK

Preface

Soon after the description of the species *Pleuragramma antarcticum* (Antarctic silverfish) by Boulenger in 1902, data collected during the first German and English South Polar expeditions in the early twentieth century (Pappenheim 1912, Regan 1916) suggested an important role for this small fish in the pelagic Antarctic system. The bulk of ecological information that has accumulated in subsequent years, especially in the 1970s and 1980s, confirmed the dominance of the Antarctic silverfish in the Antarctic shelf waters, where it plays a crucial role as the prevalent mid-trophic level fish species.

The ecological success of this pelagic swim-bladder-less teleost is the result of a long evolutionary journey shared with a handful of Antarctic fish relatives, an amazing story of organismal adaptive capability that attracted and still attracts the interest of a wide community of Antarctic researchers.

And yet, despite the increasing scientific interest toward the Antarctic silverfish, information on this species remains point and patchy, thus limiting our understanding of the potential of this Antarctic endemic fish to face climatic perturbations as individual species and limiting us from making sound predictions on the impact of the ongoing climate change on the Antarctic ecosystem. The need of filling gaps in the ecology and life history of the Antarctic silverfish, necessary to support regulation and protection initiatives in the Southern Ocean, emerged also from several reports by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and by the Antarctic Treaty Consultative Meeting (ATCM).

In accepting to edit this Springer volume, we thought the time was ripe to gather and organize the sparse information on Antarctic silverfish. This book was then conceived with the main aim to provide the large community of scientists and Institutions interested in Antarctic marine sciences and conservation with authoritative and comprehensive reviews useful to highlight current knowledge and gaps and hopefully to direct further research to specific and critical issues.

The book includes 13 thematic chapters arranged in the 3 subject areas (parts):

1. Evolution and adaptations
2. Ecology and life history
3. Challenges and conservation perspectives

Part I focuses on adaptive characteristics of the Antarctic silverfish including the astonishing evolutionary reshaping of its skeleton structure (Chap. 1), freezing avoidance capability (Chap. 2), peculiarities of the oxygen-transport system (Chap. 3) and antioxidant system responsiveness (Chap. 4).

Part II deals with fundamental ecological issues such as diet and trophic ecology in adults (Chap. 5) and early stages (Chap. 6), lipid accumulation (Chap. 7), bioenergetics and lifestyle (Chap. 8). The readers will also find information here on the species' reproduction (Chap. 9) as well as on the population structure and life history connectivity (Chap. 10).

A review on acoustic methods useful for improving the monitoring of the species (Chap. 11) is opening Part III, followed by a chapter approaching the potential vulnerability of the Antarctic silverfish using the Western Antarctic Peninsula (WAP) as a model system of warming shelf waters (Chap. 12). In the context of protection initiatives, Chap. 13, by underlining the role of this midtrophic fish as sentinel of changes in the Antarctic marine pelagic ecosystem, stresses the importance of conducting research and monitoring as well as preserving essential habitats of the species' sensitive ecophases.

The editing of the book took longer than expected due to several reasons, including the commitment in field activities of authors, editors and reviewers. However, as a bright side of the coin, this delay allowed the almost concurrent publication of the volume with the coming into force of the newly designated Ross Sea Region Marine Protected Area, a historical step toward the conservation of Antarctic marine ecosystems. Such a momentous decision rewards the efforts of researchers engaged in Antarctic research, including all contributors to the present volume, and encourages the thought that even greater environmental challenges may be addressed in the future.

Note on Taxonomy and Nomenclature

In this book, the taxonomic status of *Pleuragramma* follows the classification by Nelson (2006) with the genus included in the Antarctic notothenioid family Nototheniidae. The use of the specific name *antarctica* instead of the former *antarcticum* follows the change in specific nomenclature currently acknowledged (http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp) and adopted in the *Biogeographic Atlas of the Southern Ocean* (2014).

Genoa, Italy   Marino Vacchi
                                                                                                                         Eva Pisano
                                                                                                               Laura Ghigliotti

Acknowledgements

Contents

Contributors

R. Craig Albertson Department of Biology, University of Massachusetts Amherst, Amherst, MA, USA

Julian Ashford Department of Ocean, Earth and Atmospheric Sciences, Old Dominion University, Norfolk, VA, USA

Maura Benedetti Department of Life and Environmental Sciences, Università Politecnica delle Marche, Ancona, Italy

Andrea de Felice CNR-Consiglio Nazionale delle Ricerche, ISMAR Istituto di Scienze Marine, Ancona, Italy

H. William Detrich III Department of Marine and Environmental Sciences, Marine Science Center, Northeastern University, Nahant, MA, USA

Arthur L. DeVries Department of Animal Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA

Guido di Prisco Institute of Biosciences and BioResources (IBBR), National Research Council (CNR), Naples, Italy

Clive W. Evans School of Biological Sciences, University of Auckland, Auckland, New Zealand

Laura Ghigliotti Institute of Marine Sciences (ISMAR) - CNR, Genoa, Italy

Carolina Giraldo French Research Institute of the Sea - IFREMER, Channel and North Sea Fisheries, Research Unit, Boulogne-sur-Mer, France

Maria Elisa Giuliani Department of Life and Environmental Sciences, Università Politecnica delle Marche, Ancona, Italy

Susie Grant British Antarctic Survey, Natural Environment Research Council, Cambridge, UK

Wilhelm Hagen Marine Zoology, Bremen Marine Ecology (BreMarE), University of Bremen, Bremen, Germany

Volodymyr V. Herasymchuk Kyiv, Ukraine

Gerhard Kattner Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Ecological Chemistry, Bremerhaven, Germany

Karl-Hermann Kock Ammersbek, Germany

Philippe Koubbi Sorbonne Universités, MNHN, UPMC Univ Paris 06, UNICAEN, UA, CNRS, IRD, Biologie des Organismes et Ecosystèmes Aquatiques (BOREA, UMR 7208), Paris, France

Mario La Mesa Institute of Marine Sciences – National Research Council (ISMAR-CNR), Ancona, Italy

Iole Leonori CNR-Consiglio Nazionale delle Ricerche, ISMAR Istituto di Scienze Marine, Ancona, Italy

Gavin J. Macaulay Institute of Marine Research, Bergen, Norway

Eloy Martinez Department of Natural and Environmental Resources, Guánica Biosphere Reserve, Guánica, PR, USA

Katja Mintenbeck Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany

Richard L. O'Driscoll National Institute of Water and Atmospheric Research Limited, Wellington, New Zealand

Matthew H. Pinkerton National Institute of Water and Atmospheric Research Ltd (NIWA), Wellington, New Zealand

Eva Pisano Department of Earth, Environment and Life Sciences (DISTAV), University of Genoa, Genoa, Italy
Institute of Marine Sciences (ISMAR) - CNR, Genoa, Italy

John H. Postlethwait Institute of Neuroscience, University of Oregon, Eugene, OR, USA

David Ramm CCAMLR Secretariat, Hobart, Australia

Francesco Regoli Department of Life and Environmental Sciences, Università Politecnica delle Marche, Ancona, Italy

Alexander R. Simms Department of Earth Science, University of California Santa Barbara, Santa Barbara, CA, USA

Eric Tavernier Université Lille Nord de France, Lille, France
LOG, ULCO, Wimereux, France

Joseph J. Torres College of Marine Science, University of South Florida, Saint Petersburg, FL, USA

Marino Vacchi Institute of Marine Sciences (ISMAR) - CNR, Genoa, Italy

Cinzia Verde Institute of Biosciences and BioResources (IBBR), National Research Council (CNR), Naples, Italy

Department of Biology, University "Roma 3", Rome, Italy

Olga Voskoboinikova Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia

Lorenzo Zane Department of Biology, University of Padova, Padova, Italy

Part I
Evolution and Adaptations

Chapter 1
Evolution Reshaped Life for the Water Column: The Skeleton of the Antarctic Silverfish *Pleuragramma antarctica* Boulenger, 1902

Olga Voskoboinikova, H. William Detrich III, R. Craig Albertson, John H. Postlethwait, Laura Ghigliotti, and Eva Pisano

Abstract The Antarctic silverfish is a neutrally buoyant notothenioid fish that lives in resource-rich pelagic habitats through all life history stages. Given the ancestral benthic origin of notothenioids, the ability of this species to live in the water column required extensive evolutionary adjustments centered on buoyancy, a process referred to as secondary pelagization. Many of these adaptive changes are found in the silverfish skeleton, including partial or total reduction of bony elements, which reduces skeletal mass and body density. Other novel skeletal traits, such as lengthening of bones of the ethmoidal portion of the neurocranium and jaws, are related to foraging in the water column and planctophagia.

O. Voskoboinikova (✉)
Zoological Institute, Russian Academy of Sciences, Saint Petersburg 199034, Russia
e-mail: vosk@zin.ru

H.W. Detrich III
Department of Marine and Environmental Sciences, Marine Science Center, Northeastern University, Nahant, MA 01908, USA
e-mail: w.detrich@northeastern.edu

R.C. Albertson
Department of Biology, University of Massachusetts Amherst, Amherst, MA, USA
e-mail: albertson@bio.umass.edu

J.H. Postlethwait
Institute of Neuroscience, University of Oregon, Eugene, OR 97403, USA
e-mail: jpostle@uoneuro.uoregon.edu

L. Ghigliotti
Institute of Marine Sciences (ISMAR) - CNR, Via de Marini 6, Genoa 16149, Italy
e-mail: laura.ghigliotti@ge.ismar.cnr.it

E. Pisano
Department of Earth, Environment and Life Sciences (DISTAV), University of Genoa, Viale Benedetto XV 5, Genoa 16132, Italy

Institute of Marine Sciences (ISMAR) - CNR, Via de Marini 6, Genoa 16149, Italy
e-mail: pisano@unige.it; eva.pisano@ge.ismar.cnr.it

Reconfiguration of silverfish skeletal traits occurred via paedomorphosis (the retention of characters in adults that are juvenile traits in outgroup species) and reflects heterochronic shifts in gene expression during development.

In this chapter we describe the skeletal anatomy of silverfish larvae, juveniles and adults, including evidence for ontogenetic changes that relate to pelagic life. We then present the molecular basis of skeletal reduction as revealed by analysis of craniofacial gene expression during early skeletogenesis.

Keywords Secondary pelagization • Skeletogenesis • Bone mineralization

1.1 Introduction

1.1.1 *Secondary Pelagization, a Major Step in the Evolutionary History of the Antarctic Silverfish*

The Antarctic silverfish, *Pleuragramma antarctica* Boulenger, 1902, is a species of great ecological success among the endemic fish inhabiting Antarctic waters, a conclusion supported by a substantial literature of ecological and morphological data (e.g. DeWitt 1962; Andriashev 1965, 1976, 1987; DeWitt and Hopkins 1977; DeVries and Eastman 1978; Eastman and DeVries 1981, 1982; Voskoboinikova 1982, 1993, 2010; Hubold 1985; Kellermann 1986; DeWitt et al. 1990; Eastman 1993, 1997, 2005; Voskoboinikova et al. 1994; Eastman and Lannoo 2011; Vacchi et al. 2004, 2012a, b; La Mesa and Eastman 2012). The silverfish has a circum-Antarctic distribution along the continental shelf (Duhamel et al. 2014), is abundant as shown by the high values reported for its biomass (DeWitt 1970; Hubold and Ekau 1987; Hubold 1990; La Mesa and Eastman 2012), and plays a major role in the Antarctic coastal ecosystem (Eastman 1985; La Mesa et al. 2004). There is little doubt that the ecological success of the Antarctic silverfish relates to its use of resource-rich pelagic habitats throughout its life cycle (Marshall 1953; Andriashev 1965; Eastman and DeVries 1982; Hubold and Ekau 1990; North 1991; Eastman 1993; Voskoboinikova 2001, 2007).

The ability of the silverfish to live primarily in the water column arose as part of the evolution of the perciform suborder Notothenioidei in the Southern Ocean (e.g. Anderson 1990; Eastman and Clarke 1998; Balushkin 2000; Eastman 2005; Voskoboinikova 2010). Acquisition of antifreeze glycoproteins (AFGPs), estimated by Near et al. (2012) as occurring between 42 and 22 million years ago (Ma), was an important innovation that enabled Antarctic notothenioids to survive in the cooling, and eventually icy, marine waters surrounding the Antarctic continent (Cheng and Detrich 2007). As near-shore fish taxa lacking AFGPs became locally extinct, numerous ecological niches opened to notothenioids, which share a negatively buoyant benthic ancestor (Eastman and Clarke 1998). Subsequently, the remarkable morphological and ecological disparity among Antarctic notothenioids as a whole (Hu et al. 2016), and within various subclades, was achieved during multiple, inde-

pendent diversification events after the onset of widespread sea ice in the Late Miocene (11.6–5.3 Ma) (Near et al. 2012). Along the buoyancy axis, species within several notothenioid subclades independently evolved to colonize benthic, epibenthic, semipelagic, cryopelagic and pelagic niches (Eastman 1993; Klingenberg and Ekau 1996; Near et al. 2012; Eastman et al. 2014).

Given the benthic origin of notothenioids, the presence of modern notothenioid species in niches throughout the water column must be based on evolutionary selection driving important morphological and physiological modifications during species diversification. Organismal re-shaping for life in the water column, occurring on an evolutionary timescale, is referred to as secondary pelagization (Nybelin 1947; Andriashev 1965, 1987; Klingenberg and Ekau 1996; Eastman 1997; Montgomery and Clements 2000). During secondary pelagization, natural selection favors reduction of body density to change buoyancy from negative values toward neutrality. Typically, fish enhance buoyancy by divergence in skeletal features, including reduction of bone mineralization (Eastman 1997; Eastman et al. 2014), and/or by corporeal lipid accumulation (e.g. Eastman 1993; DeVries and Eastman 1978).

Among notothenioids, the Antarctic silverfish can be placed at the pelagic extreme of the evolutionary/ecological axis from benthic to secondarily pelagic life style because it is neutrally buoyant (Eastman 1993, 1997; Eastman et al. 2014), a condition shared with four other notothenioid species (Near et al. 2007): *Aethotaxis mitopteryx*, *Dissostichus eleginoides, D. mawsoni,* and *Gvozdarus svetovidovi*. These five species belong to the subclade Pleuragrammatinae (Andersen and Hureau 1979; Balushkin 1992), consistent with the hypothesis that complete neutral buoyancy has a single evolutionary origin in the Notothenioidei (Near et al. 2007). The Antarctic silverfish is also unique among notothenioids as the only known holopelagic species, with all life history stages, from embryo through adult, living in the water column (e.g. DeWitt et al. 1990; Vacchi et al. 2012b). Distinctive characters of adult silverfish that have been associated with secondary pelagization include its haemoglobin system (reviewed in di Prisco and Verde 2017), its red-fibred lateralis superficialis muscle, its silver coloration and its laterally compressed body form [for details see Eastman (1997), Table 1; Montgomery and Clements (2000), Table 1]. Many of those characters are considered paedomorphic (Balushkin 1984; Voskoboinikova 1994, 2001; Clarke and Johnston 1996; Eastman 1997, Montgomery and Clements 2000).

Paedomorphosis (retention of ancestral juvenile traits by adults) is a major evolutionary process in notothenioids (Balushkin 1984, 1989, 2000; Voskoboinikova 1994, 2001, 2010; Albertson et al. 2010; Eastman et al. 2014) and implies heterochrony in the schedule of developmental events during ontogeny [for a review of terminology and concepts, see Klingenberg (1998)]. The Antarctic silverfish is among the few notothenioid fish in which heterochronic events leading to paedomorphic skeletal traits have been studied during early development through molecular analysis of gene expression (Albertson et al. 2010). In *Pleuragramma*, delayed branchial and cranial bone development results from heterochronic shifts in skeletal gene expression, leading to the prolongation of the chondrogenic developmental pathway compared to benthic Antarctic notothenioids (Albertson et al. 2010; Detrich and Amemiya 2010; Postlethwait et al. 2016).

In the following sections of this chapter, we provide: (a) an update of silverfish skeletal anatomy, based on published descriptions and on unpublished data (including larvae, juveniles and adults) prepared according to the bone and cartilage staining methods by Potthoff (1984), with an emphasis on paedomorphic skeletal traits; and (b) a summary of the molecular evidence for heterochrony during early skeletal development.

1.1.2 Note on Taxonomy and Nomenclature

In this review, the taxonomic status of Nototheniodei and *Pleuragramma* follows the classification by Nelson (2006) with the genus included in the Antarctic notothenioid family Nototheniidae. Within Nototheniidae, *Pleuragramma* is part of the subfamily Pleuragrammatinae (Andersen and Hureau 1979) along with *Aethotaxis*, *Dissostichus* spp. and *Gvozdarus* (Balushkin 1992). The use of the specific name *antarctica*, instead of the former *antarcticum*, follows Duhamel et al. (2014) and the currently acknowledged taxonomic nomenclature (http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp).

1.2 Anatomical Features of the Silverfish Skeleton

The skeletal anatomy of *P. antarctica* has been analyzed as part of systematic studies of the notothenioids (DeVries and Eastman 1981; Eastman and DeVries 1982; Voskoboinikova 1982, 1993, 2001, 2010; Andersen 1984; Balushkin 1989; DeWitt et al. 1990; Miller 1993). Many of these studies were targeted at assessing the taxonomic position of the species within the family Nototheniidae and at evaluating skeletal features related to life in the water column (Regan 1913; Norman 1938; Andersen and Hureau, 1979; Andersen 1984; Balushkin 1984, 1989; Voskoboinikova 1982, 1993). Overall, coverage of skeletal elements in adult nototheniids is incomplete. For example, the structure of the neurocranium has been described only for members of the subfamily Nototheniinae (Balushkin 1984, 1989), and little information (Eastman et al. 2014) has been provided for *Pleuragramma* prior to this report.

1.2.1 The Neurocranium

The neurocranium of adult *P. antarctica* (Fig. 1.1) is elongated compared to other nototheniids, especially compared to benthic species (Balushkin 1989, Figs. 6–14). Elongation is mainly due to lengthening of bones of the ethmoid region (i.e. the mesethmoid, lateral ethmoid, and vomer) and the elongation of bones that form the interorbital region (the frontals and parasphenoid) on the anterior/posterior (AP)
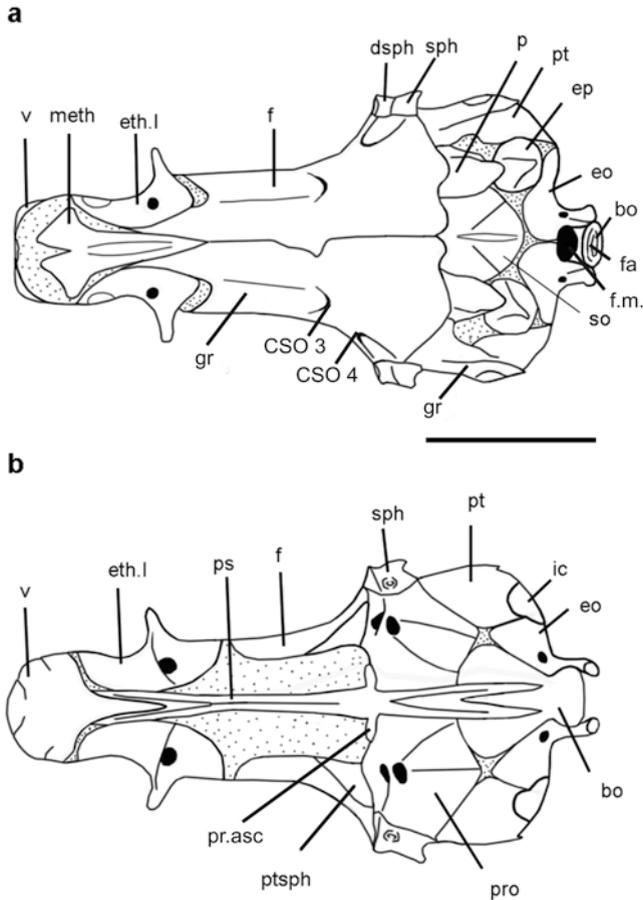
Fig. 1.1 The neurocranium of adult *P. antarctica* (specimen of SL 147.8 mm). (**a**) Dorsal view, (**b**) ventral view. *bo* basioccipital, *CSO3, CSO4* supraorbital canal pores, *sph* dermosphenoid, *eth.l* lateral ethmoid, *eo* exoccipital, *ep* epiotic, *f* frontal, *fa* articulating facet, *fm* foramen magnum, *gr* groove, *ic* intercalary, *meth* mesethmoid, *p* parietal, *pr.asc* ascending process of the parasphenoid, *ps* parasphenoid, *pro* prootic, *pt* pterotic, *ptsph* pterosphenoid, *so* supraoccipital, *sph* sphenotic, *v* vomer. Cartilage stippled. Scale bar = 10 mm

axis. The preponderance of cartilage in the ethmoid region and the skull, the thin lateral ethmoid, and the modest width of the interorbital space are also notable traits. Several features of other bones are noteworthy, including the unusual two-bladed shape of the anterior end of the mesethmoid that covers the upper surface of the ethmoidal region dorsally (probably with a protective function) and the elongated projections of the lateral ethmoid (Fig. 1.1a). The rectangular vomer has an extended anterior/posterior arm that reaches the middle of the lateral ethmoid (Fig. 1.1). The canals of the seismosensory system on the frontal, sphenotic and pterotic are almost completely lost but the longitudinal grooves on these bones

indicate their antecedent location during development. The exception is the nasal, which forms a small tube through which an anterior segment of the supraorbital canal passes, as well as a small portion of the channel between the pores CSO3 and CSO4 on the frontal (Fig. 1.1a).

Ventrally, the slender parasphenoid (Fig. 1.1b) is situated within an elongated anterior region. Posteriorly, the parasphenoid forms a shortened ascending process and a posterior branch rostral to the basioccipital. The shape of bones forming the base of the skull – the basioccipitals and exoccipitals – differ from those of other nototheniids (see Balushkin 1989, Figs. 6–14) due to a laterally elongated exoccipital and the large size of the articular facet and foramen magnum. The infraorbital ring in silverfish adults includes the lacrimal, the infraorbital 4 and dermosphenotic similar to those of other nototheniids. In contrast to most other nototheniids (Jakubowski 1971; Andersen 1984), infraorbitals 2 and 3 are absent (see Fig. 1.3a), leaving a gap in the corresponding seismosensory canal.

The shape of the neurocranium in *Pleuragramma* differs from those of other nototheniids even in early stages of development (Voskoboinikova et al. 1994; Voskoboinikova and Kellermann 1997; Voskoboinikova 2010). As shown in Fig. 1.2,
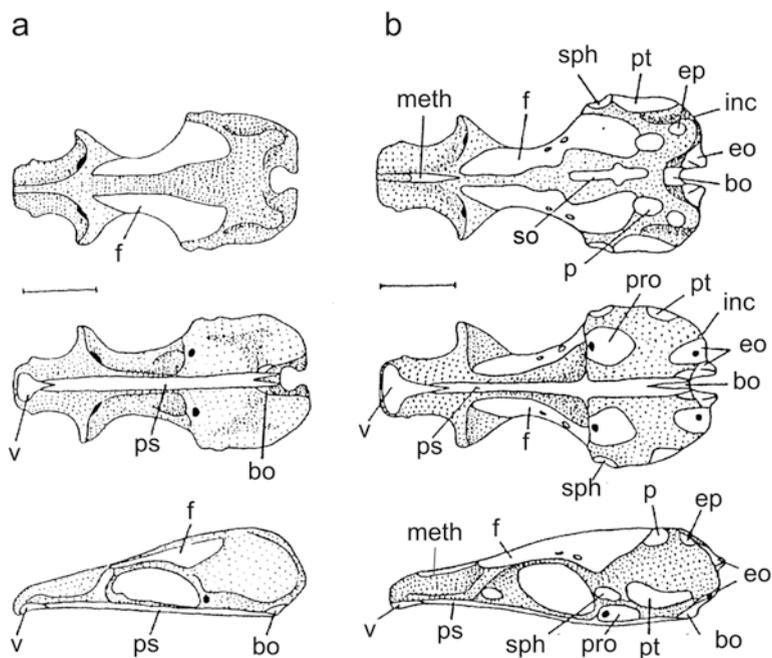
Fig. 1.2 Development of the neurocranium of *P. antarctica* showing dorsal (*upper*), ventral (*middle*) and left lateral (*bottom*) views. (**a**) specimen of SL 33.0 mm, (**b**) specimen of SL 44.9 mm. *bo* basioccipital, *eo* exoccipital, *ep* epiotic, *f* frontal, *inc* intercalar, *meth* mesethmoid, *p* parietal, *ps* parasphenoid, *pro* prootic, *pt* pterotic, *so* supraoccipital, *sph* sphenotic, *v* vomer. Cartilage stipped, ossifying white. Scale bars = 1 mm

the neurocranium of a young silverfish of 33 mm SL (approximately 9–10 months old) is already rather elongated, with a long and low ethmoidal region, a broad interorbital space, and convex dorsal profile of the skull (Fig. 1.2a). In a specimen of SL 44.9 mm (approximately 2 years old), the relative length and height of the ethmoidal region and the width of the interorbital space remain constant, the dorsal profile of the skull is straightened and the ventral profile becomes strongly bent (Fig. 1.2b), as also occurs in *A. mitopteryx* (Voskoboinikova and Kellermann 1997).

Later in development (from specimens at SL 72.1 mm), the longitudinal ridge along the mesethmoideum is formed which later develops two small lateral plates anteriorly divided by a narrow notch. In adults, such plates spread and touch laterally the margins of the ethmoidal region and the notch becomes deeper (Voskoboinikova et al. 1994). The most notable ontogenetic changes occur in the basioccipital and exoccipital. In the basioccipital, an articular facet of unusually large size compared to other nototheniids begins to form in specimens of 30 mm SL (Fig. 1.2a; see also Voskoboinikova et al. (1994)). In specimens of SL ≥ 40.0 mm, the exoccipital occurs as a small ossification lateral to the foramen magnum and closer to the upper than the temporal edge of the endocranium (not shown). From 44.0 mm, SL the exoccipital forms the well-developed condyle for the first vertebra (Fig. 1.2b). Later in development the condyle descends to the level of the temporal edge of the skull and its articular surface turns downward. In adults, the structure of these bones become similar to those of other nototheniids. Thus, their early features and changes during development are related to the large dimensions of the larval vertebral centra, which become relatively much smaller in adults.

1.2.2   The Splanchnocranium

In *P. antarctica* adults, elongation of the jaws, bones of the palatoquadrate, hyoid and gill arches and opercular bones are pronounced (Figs. 1.3 b, b′, b″ and 1.4). Most of these bony elements have structural features unique to nototheniids (Voskoboinikova 1982, 1993). Small and villiform teeth are arranged in 1–2 rows on the premaxillae and dentary (Fig. 1.3b). One tooth from the inner row at the symphysis of the premaxillae and 1–2 teeth in the middle of the first row of the dentary appear significantly enlarged relative to the teeth in other nototheniids. The mouth is slightly protractile because the ascending process of the premaxillae constitutes about one-third of the bone and the postmaxillar process is large. The posterior end of the maxillae forms an incisure, a common trait in Pleuragrammatinae.

The suspensorium (Fig 1.3b′) shows a number of prominent specific characters (Voskoboinikova 1993). The bones of this skeletal part are much thinner with respect to those of other nototheniids, and the elongate palatine directs forward and up, covering only a quarter to a third of the anterior edge of the pterygoid. The mesopterygoid does not lean on the quadrate medially. The posterior process of the quadrate is longer and higher than in other nototheniids. On the hyomandibulae, the channel of the facial nerve on the outer surface is sharply reduced and a foramen for
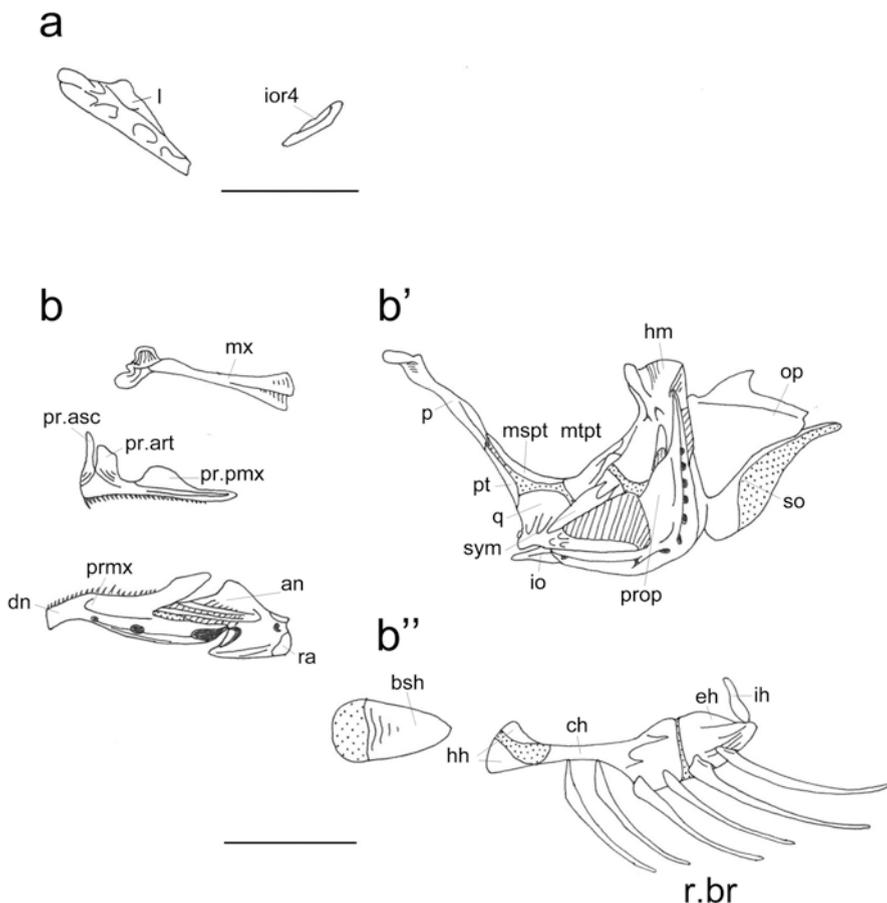
Fig. 1.3 The circumorbital ring (**a**) and the splanchnocranium (**b**, **b′**, **b″**) of adult *P. antarctica*. Specimen of SL 147.8 mm. (**a**) Circumorbital ring: *l* lacrimal, *ior4* interorbital; (**b**) Jaws: *an* angu-loarticular, *dn* dentary, *mx* maxillae, *pr.art* articular process, *pr.asc* ascending process, *pr.pmx* postmaxillar process, *prmx* premaxillae, *ra* retroarticulare; (**b′**) Suspensorium: *hm* hyomandibu-lar, *io* interopercle, *mspt* mesopterygoid, *mtpt* metapterygoid, *op* opercle, *p* palatine, *prop* pre-opercle, *pt* pterygoid, *q* quadratum, *so* subopercle, *sym* symplecticum; (**b″**) Hyoid arch, ventral part: *bsh* basihyal, *ch* ceratohyal, *eh* epihyal, *hh* hypohyals, *ih* interhyal, *r.br* radii branchiostegi. Scale bars = 10 mm

the facial nerve is located at the base of the anterior upper process of this bone. The front edge of the hyomandibulae and an intermediate portion of the preopercle are greatly reduced, and the latter does not reach the symplectic. Although the interme-diate portion of the preopercle is reduced, this bone as a whole is unusually wide with very large pores of the seismosensory canal. The opercle has an elongated posterior end. The upper process of the opercle forms a small triangle that differs from the higher processes present in other nototheniids. Reduction compensatory ridges are located on the opercle, symplectic, epi- and ceratohyals. Other opercular

Fig. 1.4 Gill arches of *P. antarctica,* specimen of SL 83.1 mm. *bbh* basibranchials, *hbh* hypobranchials, *cbh* ceratobranchials, *ebh* epibranchials, *pbh* pharyngobranchials. Scale bar = 1 mm
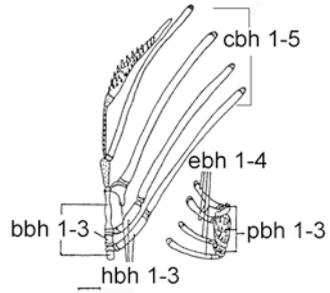
bones are smooth. The presence, in the hyoid arch (Fig. 1.3b″), of a large basihyal of almost oval shape and of truncated branchiostegal rays with relatively enlarged heads is also unusual for the nototheniids. The bones of the gill arches (Fig. 1.4) are lengthened and considerably thinned. Pharyngeal teeth on pharyngobranchials 2–4 and ceratobranchial 5 are sharp, conical, and much larger than the maxillary teeth. Gill rakers on the cerato-, hypo-, and epibranchials of the first gill arch are greatly elongated compared to other nototheniids.

As for the neurocranium, ontogeny of the splanchnocranium of *P. antarctica* differs with respect to other nototheniids. Like other Pleuragrammatinae, many facial bones of larvae and juveniles are elongated (e.g., jaws, the palatine, etc.), and most of them are reduced (e.g. upper process of the opercle, radii branchiostegi), and comparison of juveniles and adults shows that many specific cranial traits persist relatively unchanged throughout the *Pleuragramma* life cycle (see for details Voskoboinikova et al. 1994; Voskoboinikova and Kellermann 1997).

1.2.3   The Shoulder Girdle Skeleton

The shoulder girdle of adult silverfish shares general basic features with other nototheniids (see Balushkin 1989, Figs. 18, 19). Specific characteristics include the elongated anterior process of the coracoid and the striking extension of the upper end of the cleithrum, which is considerably higher than the dorsal edge of the scapula (Fig. 1.5a). In other nototheniids, in contrast, the posterior portion of the upper lobe of the cleithrum occurs at the same level as the dorsal edge of the scapula. The presence of small compensatory longitudinal ridges on the cleithrum is another characteristic trait, possibly related to reduction of the pectoral fin skeleton. A deep notch is situated between the anterior process of the coracoid and the main part of this bone. The posttemporal and supracleithrum are elongated but otherwise similar to those of other nototheniids.

Enhancement of the upper cleithral extension is observed during early silverfish development (Fig. 1.5b, c). In other Pleuragrammatinae, including *Aethotaxis,* similar extensions occur, but they are not preserved in adults. The presence of three radials in the shoulder girdle is a diagnostic character for the suborder Notothenioidei
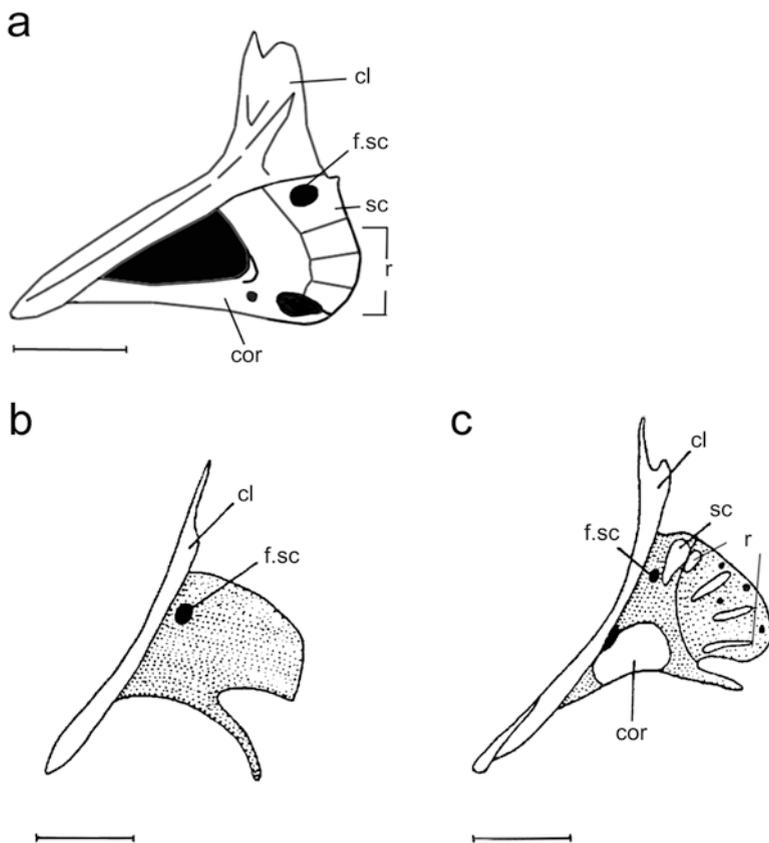
Fig. 1.5 The pectoral girdle of *P. antarctica*. (**a**) Adult specimen of SL 147.8 mm; (**b**) specimen of SL 33.0 mm; (**c**) specimen of SL 44.0 mm. *cl* cleithrum, *cor* coracoid; *f.sc* scapular foramen, *r* radials, *sc* scapula. *Black spots*: foramina; *stippled areas*: cartilaginous tissue. Scale bars: **a** = 10 mm; **b**, **c** = 1 mm

(e.g. Regan 1913, 1914; Norman 1938) and *P. antarctica* adults (Fig. 1.5a) share this feature with the other nototheniids. The three adult radials arise from four radial bone anlagen in the radial cartilage plate of the shoulder girdle of juveniles (Fig. 1.5c), the uppermost radial anlage fuses with the scapula as development proceeds (Andriashev 1987; Voskoboinikova et al. 1994; Voskoboinikova and Kellermann 1997).

The presence of a scapular foramen in the scapula is considered as an apomorphic feature in nototheniids (Voskoboinikova and Kellermann 1997). Many authors (Regan 1913, 1914; Pappenheim 1914; Norman 1937, 1938; Andriashev 1965; Balushkin 1984, 1992, 2000) assign considerable significance to the position of the scapular foramen, which currently serves as a diagnostic character for the subfamilies Nototheniinae and Trematominae. In *P. antarctica*, the foramen is in the scapula (Fig. 1.5a), as in Trematominae, but it forms in a different manner during ontogeny.

In all nototheniids, the anlage of the scapula initially grow down, creating a cavity between the anterior and posterior portions of the bone. In the trematomins (Voskoboinikova and Kellermann 1997), the posterior portion of the scapula grows and bends down and anteriorly, producing an edge below the cavity. This extension then fuses with the anterior upper portion of the bone, thus closing the cavity as the scapular foramen. In contrast, in *P. antarctica*, downward growth of the anterior and posterior portions of the scapula leads to closing at the bottom of the cavity to form the scapular foramen.

As shown by Balushkin (1984, 1989) for nototheniins, the number of small inter-radial foramina in nototheniids tends to decrease during evolution. Various developmental patterns lead to the establishment of the specific final number of these structures (Voskoboinikova and Kellermann 1997). *Pleuragramma* larvae initially have five interradial foramina (Fig. 1.5c); later in ontogeny the foramina between the scapula and radial 1, between radials 1 and 2, and between radials 2 and 3 sequentially close. In adults (Fig. 1.5a), only the lowermost hole remains, or it may be absent.

1.2.4 The Axial Skeleton

According to Norman (1938), the axial skeleton of the Antarctic silverfish is formed by 53 vertebrae (19 precaudal + 34 caudal), whereas DeWitt et al. (1990) reported 52–56. Recent counts indicate 17–20 precaudal + 34–37 caudal = 53–55 vertebrae (Balushkin, personal communication).

One of the most striking features of adults is the vertebral centrum (DeVries and Eastman 1978; Eastman and DeVries 1981, 1982; DeWitt et al. 1990; Eastman et al. 2014). Each centrum (Fig. 1.6a) appears as a thin bony collar surrounding a large hole, the notochordal canal, which is filled, *in vivo*, by a persistent notochord. Comparison of the relative diameter of the notochordal canal (diameter of notochordal canal/diameter of vertebral centrum × 100) in 38 species spanning the notothenioid phylogeny showed that the Antarctic silverfish possesses the relative largest canal (Eastman et al. 2014). The next largest was found in the close relative *A. mitopteryx*. Maintenance into adulthood of wide vertebral canals (and consequent reduction of axial bone mass), coupled with persistence of the low-density notochord, contributes substantially to the neutral buoyancy of the Antarctic silverfish.

The appearance of ossified vertebrae occurs late, during juvenile stages from 40.0 to 89.0 mm SL (Voskoboinikova et al. 1994), with consequent underdevelopment of the centra and persistence of the notochord in adults. Moreover, given the limited bone growth, the notochord canal remains large, and the vertebral centra do not become completely amphicoelous (Totton 1914; Eastman and DeVries 1981, 1982; DeWitt et al. 1990; Voskoboinikova et al. 1994; Voskoboinikova 2001; Eastman et al. 2014). The vertebral centra form from two small oval ossified plates lateral to the notochord (Fig. 1.7). The bony plates lie usually two by two lateral to the notochord dorsally and ventrally and join medially. Then the plates of both sides
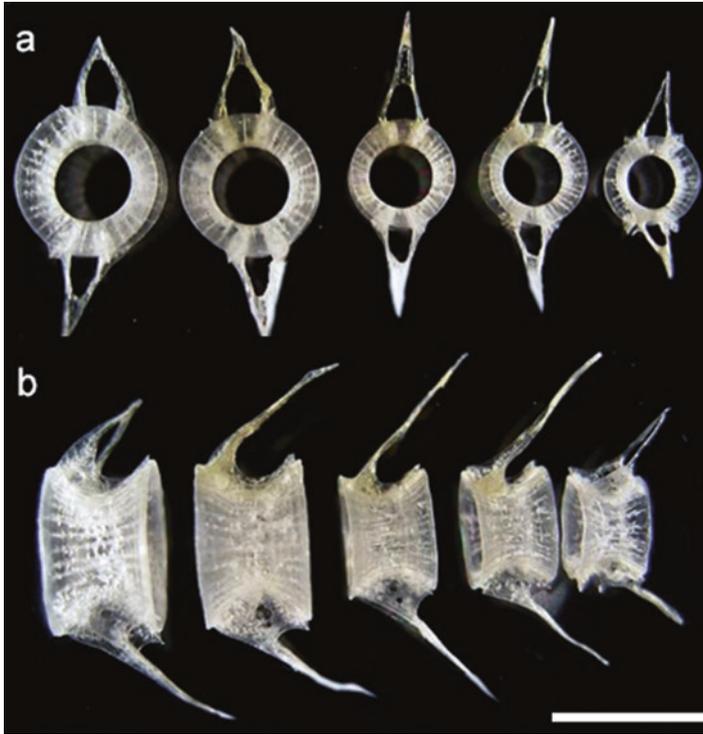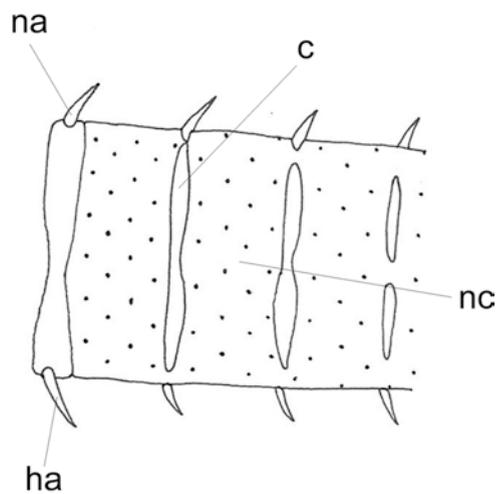
Fig. 1.6 Vertebrae of *P. antarctica,* adult specimen of SL 184.6 mm. (**a**) Superior view, (**b**) lateral view. Scale bar = 5 mm (Modified from Busekist et al. 2007, ANFIBO Base)

Fig. 1.7 Vertebral centra in formation in *P. antarctica* (specimen of SL 48.6 mm), middle region of the vertebral column. *c* centrum, *na* neural arch, *ha* haemal arch, *nc* notochord

join dorsally and ventrally and form the bony ring around the notochord (Voskoboinikova et al. 1994). The vertebrae form from the urostyle forward by spreading of two preurostilar centra; then the centra appear from the basioccipital and spread in a caudal direction. In other nototheniids, by contrast, the centra begin with the appearance of saddle plates at the base of the haemal arches (nototheniins) or the haemal and neural arches (trematomins and *A. mitopteryx*). The centra of the nototheniins, trematomins, and *A. mitopteryx* form simultaneously from the basioccipital caudally and from the urostyle rostrally.

Other vertebral features provide additional anatomical characters specific to the Antarctic silverfish. The neural and haemal arches are poorly developed, with corresponding spines greatly shortened (Fig. 1.6) (Norman 1938; Balushkin 1984, 1989; DeWitt et al. 1990; Voskoboinikova et al. 1994). According to available studies, epipleural ribs attached to the centra of the first eight vertebrae are first found in specimens of 51 mm SL; these increase to 10 ribs in adults. At 51.7 mm, six pleural ribs are attached to the parapophyses of vertebrae 4–9. Subsequently, their number gradually increases to 9–12 in adult fish, but the last 3–4 ribs are not attached to parapophyses and lie freely in myosepta. The presence of floating ribs is a diagnostic feature of the suborder Notothenioidei (Balushkin 1992, 2000; Hastings 1993; Near et al. 2015). As is typical for Pleuragrammatinae, the first pleural rib attaches to centrum 4, rather than to the third centrum (Balushkin 1992; Voskoboinikova et al. 1994). Such a variation of the attachment position of the first pleural rib could have functional implications by increasing head mobility during feeding.

1.2.5   Unpaired Fins and the Caudal Fin

The skeleton supporting the unpaired fins consists of the serial pterygiofores, including proximal and dorsal elements. The proximal pterygiofores develop a special dorsal articular surface for the attachment of the distal pterygiofores, which remain almost entirely cartilaginous except for a small pair of bony plates on their lateral surfaces. The first appearance of the proximal pterygiofores occurs in the middle of the second dorsal fin in specimens of 43.7 mm and in the middle of the anal fin in specimens of 40 mm. Subsequently, ossification of the pterygiofores extends forward and backward. Ossification of the pterygiofores of the first dorsal fin occurs later. Full development of the pterygiofores is observed in specimens of 62.1 mm LS. The sequence of appearance of unpaired fin pterygiofores in *P. antarctica* is similar to that of other nototheniids (Voskoboinikova and Kellermann 1997).

With respect to the caudal fin, *P. antarctica* (Fig. 1.8a), together with *Gobionotothen gibberifrons* (Nototheniinae), possesses the greatest number of apomorphic features within Nototheniidae (Totton 1914; Balushkin 1984, 1989; Voskoboinikova et al. 1994; Voskoboinikova and Kellermann 1997; Voskoboinikova 2010). During development, one hypaxial hypural 1 + 2 cartilage generates one hypural 1 + 2 bone (Fig. 1.8b, c); two cartilaginous epaxial hypurals fuse (cartilaginous hypural 3 + 4), and then produce hypural bones 3 and 4; these later fuse to
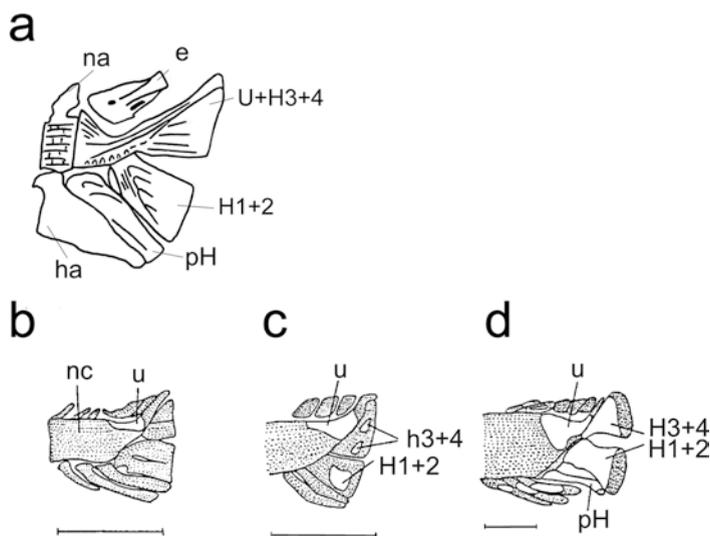
Fig. 1.8 Major steps in the development of the skeleton of the caudal fin of *P. antarctica*. (**a**) Specimen of SL 48.6 mm; (**b**–**d**) specimens of SL 18.9 mm, 33.0 mm, and 44.9 mm, respectively. *ha* haemal arch, *na* neural arch, *e* epural, *h* hypural, *H* complex hypural, *nc* notochord, *pH* parhypural, *u* ural center, *U + H* ural center + complex hypural. Scale bars = 1 mm

form one bone (hypural 3 + 4; Fig. 1.8c, d). As in trematomins, the epaxial hypural plate 3 + 4 is fused with the ural center. Hypural 5 is absent, as is the uronrural, which is present in all other nototheniids. Due to the loss of a number of early stages of development of the caudal fin skeleton the later stages in *P. antarctica* begin earlier than in other nototheniids, resulting in the most advanced structure of the caudal fin skeleton of the *P. antarctica* (Eakin 1981; Balushkin 1984; Voskoboinikova 2010).

1.3 Antarctic Silverfish Skeletal Characteristics and Pelagic Life

Studies of specimens at different developmental stages (Voskoboinikova et al. 1994; Voskoboinikova and Kellermann 1997; Voskoboinikova 2010, present work) indicate that silverfish develop almost all elements of the nototheniod bony skeleton. However, most skeletal elements are thin and have smooth surfaces, and many of them are reduced in size, compared to other nototheniods and to species of the same family Nototheniidae. Thinning and reduction in size of bony elements, together with low bone mineral density, result in reduced skeletal mass, as documented by the low weights of ashed silverfish skeletons (DeVries and Eastman 1978). The bone reduction, combined with the persistence of low-density tissues (cartilage and notochord), are major skeletal changes contributing to the acquisition