Unusual gonad structure in the paedomorphic teleost
_Schindleria praematura_ (Teleostei: Gobioidei):
a comparison with other goboid fishes

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The gonads of eight gobioid species were examined histologically, including _Pandaka pygmaea_ and _Schindleria praematura_, in order to investigate the manifestations of miniaturization and paedomorphosis in the gonads. Rearrangements of reproductive structures were found only in _S. praematura_, and included only the gonad tissues, not the gametes. Both sexes of _S. praematura_ maintain basic germinal components: the spermatocyst composed of Sertoli cells and spermatogonia in the testis and the follicle and oocyte complex in the ovary. The stromal ovarian tissue and testicular interstitial tissue, however, is reduced compared to other gobies, and the number and location of gonial cells is restricted. This sequestered pattern of gonial cells is known as a restricted spermatogonial type in the testis, and has been reported only in atherinomorphs. The restriction of gonial cells in the ovary is extremely rare among teleosts, known only from one other species. These restricted gonial patterns in _S. praematura_ are probably related to the overall reduction of morphological complexity in this genus, due to its extreme paedomorphosis.

Key words: Gobiidae; Gobioidei; ovary; paedomorphosis; _Schindleria_; testis.

INTRODUCTION

Among gobiid fishes, morphological reduction is common but the specific manifestations of reduction vary. Reductive features in gobies range from simplifications and losses in the skeleton and other organ systems to the retention in the adult of larval features such as the pronephric kidney and the cartilaginous precursors of the skull (TeWinkel, 1935; Johnson & Brothers, 1993). The smallest vertebrates are goboids, both in terms of length (_Pandaka pygmaea_ Herre, females mature at 7–5 mm standard length, _L_s, and males at 10 mm _L_s, and _Trimmatom nanus_ Winterbottom & Emery mature at 8 mm _L_s) and mass [_Schindleria praematura_ (Schindler) and _Schindleria pietschmanni_ (Schindler), 2–8 mg] (Bruun, 1940; Miller, 1979, 1984). The genera _Pandaka_...
and *Schindleria* represent two different manifestations of reductive evolution. *Pandaka* is tiny but does not appear to be paedomorphic; no obvious ontogenetic reductions are seen in the skeletal elements or soft tissues. In contrast, *Schindleria* has been called ‘the most extreme example of progenetic developmental truncation known among fishes’ (Johnson & Brothers, 1993). In *Schindleria* every aspect of morphology is juvenilized: the body is transparent and scaleless, the heart is tubular with the atrium posterior to the ventricle, the kidney is pronephric, and the gills and gut are simplified. Many skeletal elements are absent and those that are present are simple and weakly ossified (Schindler, 1932; Johnson & Brothers, 1993). Some details of the ontogeny of *Schindleria* have been described, and it appears that this genus proceeds through typical early larval stages and then development ceases, with the exception of gonad maturation (Watson et al., 1984). This study was undertaken to determine whether the effects of miniaturization and reduction may be seen in the gonadal structures, and to compare the gonads of *Schindleria* to other gobiod gonads.

The general structural pattern of both the ovary and the testis of teleosts has been described. In both sexes, the gonad is derived from the cortex of the gonad primordium only, unlike other vertebrates in which the testis develops from the medulla (Dodd, 1977; Jones, 1978). The ovary is cystovarian, a hollow organ formed by the infolding of the gonad primordia into a sac. Ovaries may be paired or single (Dodd, 1977; Jones, 1978). Generally, the ovary is connected to the genital orifice by an oviduct which is derived from an extension of the gonad wall, in contrast to the condition in other vertebrates where the gonad ducts arise from renal duct primordia (Hoar, 1969). Most teleosts (including gobies) are oviparous and do not feature the extensive modifications that are present in the ovaries of livebearing fishes (Hoar, 1969; Dodd, 1977). Within the ovary, the tissue is thrown into ovigerous lamellae, consisting of connective tissue stroma, nerves and blood vessels. Within this stroma are the developing follicle and oocyte complexes. A basement membrane separates the germinal epithelium, containing oogonia and preprimary growth oocytes, from the stromal compartment of the ovary (Grier, 2000; Grier & LoNostro, 2000). Development of the oocyte within the follicle proceeds through meiosis and yolk deposition (Wallace & Selman, 1981, 1990; deVlaming, 1983; Selman & Wallace, 1989), and the oocyte is invested with a fibrous zona pellucida that may be sculpted or bear attachment structures. The micropyle (pore that permits sperm entry) is established by a specialized follicle cell that maintains contact with the oolemma and prohibits formation of the chorion over the pore (Nelsen, 1953; Wourms, 1976; Wallace & Selman, 1981; Nagahama, 1983). After the oocyte has reached the second meiotic metaphase, it undergoes hydration, is divested of its follicle layers, and ovulated into the ovarian lumen. Oocyte maturation in most teleosts occurs in batches, producing a clutch of mature eggs from the population of smaller oocytes repeatedly throughout the life of the fish (group synchronous pattern; Dodd, 1977).

Detailed histological studies of oogenesis have been performed on only a few species. What is known of goby ovaries agrees with the general oviparous teleost patterns (Rajalakshmi, 1966; Shackley & King, 1977; Brummett et al., 1982; Selman & Wallace, 1986; Selman et al., 1991; Grier, 2000). The oocytes of...
gobies are unusual in that they are ellipsoid and adhesive rather than spherical, with a tuft of attachment filaments present around the oocyte micropyle. Gobies deposit eggs demersally in a nest or on some other substratum such as shells, rocks, algal filaments or the burrows of other animals. The eggs adhere to the substratum, and fertilization occurs as the eggs are deposited (Breder, 1943; Breder & Rosen, 1966; Takahashi, 1978; Ruple, 1984).

Patterns of testis structure and spermatogenesis in teleosts have also been documented. Like the ovary, the teleost testis is generally paired but may be single, and germ cells leave the body via ducts that are derived from the gonad epithelium, not the nephric duct system (Nagahama, 1983). Testis structure is classified based on the morphology of the seminiferous compartments and the distribution of spermatogenic units. In teleosts, testicular compartments are either blind ended (lobular) or form a network of passages (anastomosing tubular) (Grier, 1993). The lobular type is typical of perciform and atherinomorph fishes, and is further classified by the arrangement of spermatagonia within the lobules. The testis is of the restricted spermatogonial type when spermatagonia are present only at the distal ends of lobules, whereas testes in which spermatagonia are scattered throughout the lobule are termed unrestricted (Grier, 1993). Restricted spermatogonial testes are found in atherinomorphs and unrestricted testes are typical of other teleosts (Grier et al., 1980). The basic unit of spermatogenesis in teleosts is the spermatocyst, which is composed of a group of synchronously developing germ cells surrounded by a layer of protective Sertoli cells. Spermatogenesis, like oogenesis, begins in the germinal epithelium; spermatagonia begin development, are invested with a Sertoli cell layer, and are finally released from the spermatocyst into the testicular lumen when maturation is complete (Grier & Taylor, 1998). Surrounding the lobules or tubules are myoid connective tissue cells and steroidogenic Leydig cells. In areas where myoid cells are present at the lobule border, the Leydig cells lie outside them, but in the absence of myoid cells the Leydig cells may be in direct contact with the lobule border; blood vessels may also contact the lobule (Grier et al., 1980; Grier, 1993). Variation in morphology of the mature sperm varies with reproductive strategy, with sperm of internally fertilizing teleosts tending to have elongated heads and midpiece regions (Grier, 1981). Gobies possess spermatozoa with rounded or pointed heads and a mitochondrion present on one side of the nucleus where it meets the midpiece, such that the head appears bean-shaped or arrowhead-shaped in cross section (Jamieson, 1991).

Gobioid males have a specialized testicular accessory organ, the sperm duct gland. This gland is located adjacent to the testis, connected to the sperm duct between the testis and the genital papilla. The duct is composed of lobules similar to the testicular lobules, but the tissue is secretory, not germinal, and interstitial Leydig cells are not present between the lobules. During mating, gobies may deposit a sperm trail or ribbon as the eggs are deposited (Wiesel, 1949; Miller, 1984, 1992). In the grass goby Zosterisessorophiocephalus (Pallas), the male deposits a mucus sperm-containing trail at the egg deposition site, both before and during spawning by the female. The sperm are released from the trail and activated by the water gradually, over a period as long as several hours (Mazzoldi et al., 2000); a similar sperm packaging occurs in mouthbrooding tilapiine fishes, where the fluid-suspended sperm are taken into the mouth of the female, where fertilization occurs (Grier & Fishelson, 1995). Additionally, goby
testes may include abundant interstitial tissue, sometimes aggregated into a testicular gland present in the dorsal portion of the testis near the mesorchium. In *Gobius paganellus* L. and *Gobius niger* L. this gland is present, but some Leydig cells are also found between the lobules in the main body of the testis (Stanley *et al.*, 1965; Colombo & Burighel, 1974).

This present study was undertaken in order to investigate the effects of miniaturization and paedomorphic reduction on the gonads. *Schindleriapraematura* and *P. pygmaea* were examined as representatives of paedomorphic and miniaturized species, respectively, and additional species *Neogobius fluviatilis* (Pallas), *Tridentiger bifasciatus* Steindachner, *Bathygobius lineatus* (Jenyns), *Cerdale floridana* Longley, *Microdesmus dorsipunctatus* Dawson and *Microdesmus bahianus* Dawson were examined. *Neogobius, Tridentiger* and *Pandaka* are included in the gobiid subfamily Gobionellinae (Pezold, 1993). *Bathygobius* is placed in the gobiid subfamily Gobiinae, which in a recent phylogenetic analysis (Thacker, 2003) was shown to be paraphyletic with respect to the families Microdesmidae (including *Microdesmus* and *Cerdale*) and Schindleriidae (including *Schindleria*). These species were chosen such that *P. pygmaea* and *S. praematura*, may each be compared to two typically-sized relatives, and each set of three species is representative of the two major clades (expanded monophyletic Gobiinae and expanded monophyletic Gobionellinae of Thacker, 2003) of higher gobioids (excluding Eleotridae, Xenisthmidae, Odontobutidae and Rhyacichthyidae).

**MATERIALS AND METHODS**

Both males and females of the species *N. fluviatilis, T. bifasciatus, B. lineatus, P. pygmaea* and *S. praematura* were examined. Different species of the family Microdesmidae were examined for each sex: a female of *C. floridana*, and males of *M. dorsipunctatus* and *M. bahianus*. *Cerdale* and *Microdesmus* are sister taxa (Thacker, 2000). One mature individual for each sex of each species was examined except in the case of *S. praematura*, in which two males and two females were sectioned. Gonads were removed from all specimens except *S. praematura*; for this genus the head and tail were removed and the entire portion of the body containing the gonads was embedded and sectioned. Specimens used were obtained from museum collections; they were initially fixed in formalin and transferred to 70% ethanol. It is not known how the tissues were treated, however, preservation was generally good. Some artifacts were noted similar to those described by Brown-Peterson *et al.* (2002). Gonads were embedded in glycol methacrylate using the Energy Beam Sciences Polaron H7000 Embedding Medium Kit (Agawam, MA, U.S.A.), following the kit directions. Blocks were trimmed and sectioned with glass knives at 2–3 μm on a BioRad JB-4 microtome. Sections were mounted on acid-cleaned glass slides and stained with haematoxylin and eosin (Humason, 1979), toluidine blue or thionin. Photographs were taken using Kodak Tungsten T160 film and the slides scanned into Adobe Photoshop for manipulation into the final figures. The species, catalogue number, sex and *Ls* length of the specimens examined are listed in Table I.

**RESULTS**

**OVARY**

Ovaries are paired and approximately of equal size to one another in all species examined. Ovaries join posteriorly into a single oviduct that exits via a...
genital papilla located posterior to the anus. Most of the species examined have similar ovarian morphology: the ovary is enclosed by a thin epithelium and the ovarian stroma consists of ovigerous lamellae containing several sizes of developing oocytes. There is a conspicuous lumen present unless the oocytes are so large it is occluded. Nests of oogonia are scattered throughout the germinal epithelia. Oocytes were observed in stages ranging from preprimary growth, primary growth and vitellogenesis (Grier, 2000). Final oocyte maturation (germinal vesicle migration and breakdown) was observed only in *S. praematura*. No sperm were found in any of the ovaries examined, nor is there any other evidence of internal fertilization. There is also no evidence of accessory gonadal structure primordia (AGS) on the ovaries which would indicate the potential for sex change (Cole, 1990; Cole *et al.*, 1994).

The ovarian morphology in *N. fluviatilis*, *B. lineatus* and *P. pygmaea* is shown in Fig. 1(a), (b), (c). In these samples, the oocytes are large, and the ovarian lumen is mostly obscured. Smaller oogonia, preprimary growth oocytes and primary oocytes may be seen at the lamellar borders. In *C. floridana*, ovigerous lamellae extend into the ovarian lumen but do not occlude it, and several stages of oocyte maturation were seen [Fig. 1(d)]. A closeup of the *C. floridana* ovary [Fig. 1(e)] shows the germinal epithelium, containing preprimary growth oocytes. Patterns in *T. bifasciatus* are similar to those in the other species; Fig. 1(f) shows a closeup of the germinal epithelium, with both oogonia and preprimary growth oocytes indicated.

The ovaries of *S. praematura* differ in many respects from the other gobiod species. The ovary has a much smaller absolute size, but is proportionally larger than in larger fishes, and the oocytes are not absolutely smaller. Because the oocytes are disproportionately large compared to the ovary that contains them, the observed clutch size is much smaller, generally 25–30 oocytes. A range of oocyte stages is present in the two individuals sectioned. In an ovary containing a clutch of immature oocytes, the nuclei are prominent and contain nucleoli at their periphery, and the cytoplasm is uniform and darkly staining [Fig. 1(g), (h)]. Larger oocytes are observed with accumulation of yolk globules (vitellogenic stage) and also in final maturation stages, during which the germinal vesicle migrates and breaks down, the yolk coalesces and hydration occurs [Fig. 1(i); Wallace & Selman, 1981; Selman & Wallace, 1989]. In these preovulatory oocytes, the zona pellucida is thick and

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**Table I.** Species, catalogue number, standard length and sex of gobiod fishes examined. Institutional abbreviations follow Leviton *et al.* (1985)

<table>
<thead>
<tr>
<th>Species</th>
<th>Catalogue number</th>
<th>$L_S$ (mm)</th>
<th>Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Neogobius fluviatilis</em></td>
<td>LACM 44708-1</td>
<td>68.7–70.6</td>
<td>F and M</td>
</tr>
<tr>
<td><em>Tridentiger bifasciatus</em></td>
<td>LACM 45686-1</td>
<td>53.7–56.0</td>
<td>F and M</td>
</tr>
<tr>
<td><em>Bathygobius lineatus</em></td>
<td>LACM 43690-27</td>
<td>73.1–75.6</td>
<td>F and M</td>
</tr>
<tr>
<td><em>Cerda floridana</em></td>
<td>ANSP119203</td>
<td>70.4</td>
<td>F</td>
</tr>
<tr>
<td><em>Microdesmus dorsipectatus</em></td>
<td>GCRL2311</td>
<td>53.1</td>
<td>M</td>
</tr>
<tr>
<td><em>Microdesmus bahianus</em></td>
<td>MZUSP 9852</td>
<td>38.9</td>
<td>M</td>
</tr>
<tr>
<td><em>Pandaka pygmaea</em></td>
<td>UMMZ 174664</td>
<td>10.2–11.2</td>
<td>F and M</td>
</tr>
<tr>
<td><em>Schindleria praematura</em></td>
<td>UMMZ 196857</td>
<td>13.5–16.1</td>
<td>F and M</td>
</tr>
</tbody>
</table>
Fig. 1. Thin sections of ovaries of (a) *Neogobius fluviatilis*, (b) *Bathygobius lineatus*, (c) *Pandaka pygmaea*, (d), (e) *Cerdale floridana*, preprimary growth oocytes (OOC), (f) *Tridentiger bifasciatus*, preprimary growth oocytes (OOC) and oogonium surrounded by prefollicle cells (OOG) in the germinal epithelium, (g), (h), (i) *Schindleria praematura* (the band of small cells in the lower portion is the germinal ridge; the oocyte cap (CAP) and micropyle (MP) are indicated. Scale bars: (a), (b) 500 μm; (c) 1 mm; (d), (g), (i) 100 μm; (e), (f), (h) 10 μm.
darkly staining, and distinctive cap structures can be seen forming around the micropyle at one pole [Fig.1(i)]. These caps have been described previously in *S. praematura* eggs, and are evidence that *S. praematura* is a gobioid (Johnson & Brothers, 1993); goby oocytes generally have tufts of adhesive filaments surrounding the micropyle (Breder, 1943; Ruple, 1984). The caps are elaborate, composed of a thick collar at one pole of the oocyte into which a narrow column of cytoplasm intrudes. The micropyle is present at the centre of the cap, delimited by a cluster of elongate micropylar cells [Fig.1(i)].

In contrast to the other species examined, in which oogonia are present in clusters throughout the germinal epithelium in the ovary and do not all mature synchronously, the oogonia in *S. praematura* are restricted to a germinal ridge, running ventrally along the length of the ovary [Fig.1(g), (h), (i)]. The stroma of the ovary is extremely reduced compared to the other species, and there are no ovigerous lamellae. Each ovary has a single continuous lumen, and as oocytes mature they become so large that the ovarian wall is compressed to a squamous epithelium.

**TESTIS**

In males of all species except *S. praematura*, the paired, elongate testes extend posteriad to a common sperm duct exiting through a genital papilla. Testicular lobules (Grier, 1992, 1993) are large, with wide lumina that become confluent in the posterior portion of the testis. An accessory sperm duct gland is present at the posterior end of the testis in all the species examined. All of the species examined exhibit the unrestricted spermatogonial testis type typical of perciforms, with a germinal epithelium, containing scattered spermatogonia, along the walls of the testicular lobules [Fig.2(a), (b), (c), (d)] rather than being restricted to the distal termini of the lobules [Fig.2(e), (f)]. In most of the gobioïds examined, the spermatogonia are small and present in nests along the walls of the lobules. In these individuals, spermatogenesis is actively proceeding, and the germinal epithelium appears discontinuous, with spaces between maturing spermatocytes where spermatozoa have already been released (Grier & Taylor, 1998). As the lobules continue in a posterior direction, their walls transform from a thick germinal epithelium with embedded cysts to the thinner, columnar epithelium of the sperm duct gland. In section, the lobule chambers are round or irregular and embedded in thick interstitial tissue. The chambers seen in sections of the sperm duct gland are similar in shape to the lobular chambers; a few spermatozoa and acellular material were observed in the testicular lumen but there was no visible secretion present. The sperm duct gland chambers in the posterior part of the testis are thin-walled and no secretions were evident. The lobule lumina are packed with mature spermatozoa with rounded heads and prominent tails. The testis in *P. pygmaea* is small, with few lobule chambers entering a central lumen, and sparse interstitial tissue. Spermatogenic cysts, however, were observed throughout the testis, in different stages of maturation [Fig.2(d)].

In contrast, the testis of *S. praematura* differs greatly from the typical perciform testis and from the other gobioïds examined. The testis of *S. praematura* is a single, slender and elongate organ with paired extensions continuing from both
Fig. 2. Thin sections of testes of (a) *Tridentiger bifasciatus*, (b) *Neogobius fluviatilis*, (c) *Microdesmus dorsipunctatus*, (d) *Pandaka pygmaea* and (e), (f) *Schindleria praematura*. In (a), (b), (c) and (d) the typical teleost lobular testis structure is evident, with spermatocysts lining the lobule walls, and spermiation taking place into the lobule lumen. The *S. praematura* testes in (e) and (f) feature no lumen, just spermatocysts packed into lobules. Testes of *Bathygobius lineatus* resembled patterns seen in (a) and (b), and those of *Microdesmus bahianus* were similar to (e), and are not illustrated. Scale bars: (a), (d) 100 µm; (b), (c), (f) 200 µm; (e) 1 mm.

the anterior and posterior ends (Schindler, 1932). Within a testis, lobules can be traced from anterior to posterior; these lobules do not have lumina and are instead packed with thin-walled spermatocysts, containing spermatocytes in various stages of development. The spermatocysts are so large that a single spermatocyst fills the lobule in which it is located [Fig. 2(e), (f)]. Earlier stages are concentrated at the anterior portion of the testis and later stage spermatocytes and mature spermatozoa occur in the posterior portion. Spermatogonia are only observed within lobule termini at the anterior end of the testis. It is hypothesized that maturing spermatocysts progress down the lobule from anterior to posterior and are released at the posterior terminus of the testis only. Scant interstitial tissue is present between the lobules.

Posterior to the testis is a hollow structure composed of a thin dorsal wall and a thick, densely staining ventral wall with several prominent vacuoles in the epithelial cells. The entire structure is surrounded by several layers of filmy epithelium and is present in males with mature spermatozoa as well as those with immature spermatocytes only. No secretion is evident in the lumen. Except for the lack of secretory products, this structure agrees well with Schindler’s (1932) description of the ‘appendage organ of the male reproductive system’. It differs in some respects from the thin-walled, multi-chambered sperm duct glands observed in the other species, but is found in the same position and also has a secretory tissue structure.

DISCUSSION

Gobioid species examined in this study represent a range of sizes and reductive morphologies. The reproductive morphology observed in the miniaturized species (*P. pygmaea*) is similar to other gobioids examined and without evidence of any morphological reduction or simplification (except in overall size) in either the gonad tissues or the gametes and their immediate supportive structures (follicle cells in the females and Sertoli cells in the males). Only the paedomorph *S. praematura* exhibits deviations from the pattern of complex, robust gonads with a complement of supportive tissues in association with the developing spermatogonia and oogonia. In all species examined except *S. praematura*, the ovary is composed of thick stromal lamellae, bounded by germinal epithelia. Nests of oogonia are embedded in the germinal epithelia; as an oocyte develops it is invested with a follicle layer, forming a follicle (Grier, 2000; Grier & LoNostro, 2000) that supports the oocyte as it develops and contributes to the outer egg envelope. The presence of several oocyte stages in the ovaries examined indicates that these species are iteroparous. The testes of gobioids examined, except *S. praematura*, feature lobules in which spermatogonia and associated Sertoli cells are present along the lobule wall, composed of a germinal epithelium. The sperm duct gland typical of gobioids is present as a chambered structure posterior to the testis, the walls of which are composed of a thin columnar epithelium.

*Schindleria praematura* gonad structure is a significant departure from the other species. In *S. praematura*, the paedomorphic morphology includes changes in the gonads and accessory structures of both males and females. In the ovary, the stromal tissue is reduced, there is a single chamber rather than a series of...
ovigerous folds, and the oogonia are restricted to a germinal ridge at the ventral margin of the ovary. Reduction to this degree is unknown among teleosts, but a germinal ridge has previously been observed in the seahorse *Hippocampus erectus* Perry (Selman et al., 1991). In *H. erectus*, rather than oogonia being scattered throughout the germinal epithelium, they are restricted to the innermost fold of a spiral of tissue that forms the ovary. In *S. praematura* the location of the gonial cells is similarly restricted, but the ovary is even more simplified, with the germinal ridge present at the ventral margin of a tubular ovary, lacking any additional tissue folds or spirals. Schindler (1932) in his original description of *S. praematura* and description of its anatomy, also described a distribution of oocyte sizes and maturation stages consistent with a ventral germinal ridge.

Observed simplifications in the *S. praematura* testis include a drastic reduction in the amount of interstitial tissue, reduction in the extent of secretory tissue in the sperm duct gland, and compression and reduction in number of the spermatogenic lobules. The testicular units are lobules, rather than tubules, as indicated by the lack of anastomoses and termination of the lobules at the testis periphery. The lobules in *S. praematura* are unusual in that they are so tightly packed in the testis that there is no lumen present. The Sertoli cells forming borders of the spermatocysts extend processes that bridge the diameter of the lobule, and there is no central lumen. Lacking a central lumen, the criteria for an epithelium (Grier, 2000; Grier & LoNostro, 2000) are not fulfilled. Therefore, the lobules possess an epithelioid arrangement of germ cells and Sertoli cells, as in the epithelioid cords of germ cells and Sertoli cells that grow from the distal termini of the lobules in cobia *Rachycentron canadum* (L.) at the end of the breeding season (Brown-Peterson et al., 2002). Spermatogonia are present only at the end of the lobules, much like the restricted testis type found in atherinomorphs (Grier et al., 1980; Grier, 1993). The presence of an atherinomorph-like testis structure in a perciform is unusual, but there are other examples. The embiotocid *Cymatogaster aggregata* Gibbons has a similar epithelioid arrangement of spermatocysts packed into lobules, to the exclusion of a lumen (Wiebe, 1968; Gardiner, 1978). This condition was interpreted by Grier et al. (1980) as a modified restricted testis, with spermatogonia restricted to the distal termini of the lobules.

The reduced gonad morphology seen in *S. praematura* does not appear to have any effect on its ability to produce gametes; the oocytes and spermatozoa observed were not absolutely smaller or more reduced in complexity than those in other goby species. Males have a simplified form of the gobiod sperm duct gland. In this study, secretions in this gland were not observed, but Schindler (1932) reports that in fresher specimens the sperm duct gland is full of a darkly staining secretion. In some other gobies (Wiesel, 1949; Miller, 1984, 1992; Mazzoldi et al., 2000), this secretion functions to adhere spermatozoa to a substratum on which the eggs are laid, achieving fertilization via the micropyle before the eggs adhere to the substratum and the micropyle is blocked. *Schindleria praematura* is unusual among gobies in that it is planktonic; not only does it retain a larval morphology, it also exhibits a larval ecology, never settling out of the plankton as do most gobies (Watson et al., 1984). *Schindleria praematura* populations are found near islands in the tropical Pacific and Indian oceans, not in open waters, and perform the diel migrations typical of plankton,
rising to the surface at night and returning to the bottom during the day. The spawning behaviour is not known, but oocytes are rarely found in plankton tows even when large numbers of adults are captured (Watson et al., 1984). Schindleria praematura males have a genital papillae and sperm duct gland like those used by other goby species for demersal deposition of sperm, and females produce eggs with complex cap structures that could function in attachment of the oocyte to the substratum. These structure, however, could simply be indicative of the phylogenetic history of S. praematura rather than current ecology; until spawning is observed it will remain unclear whether or not the drastic changes in both morphology and ecology have also affected breeding behaviour and patterns.

Only the gonads of the paedomorphic species (S. praematura) are rearranged; gonad structure in the miniaturized species (P. pygmaea) is similar to that seen in the other gobioids examined. The rearrangements in S. praematura primarily affect the supportive and interstitial tissues of the gonad. The functional units of gamete production and the gametes themselves do not appear to be significantly changed, although the germinal epithelium is reduced in females and incomplete in males. In males, the Sertoli cell and spermatocyte cyst are preserved and spermatozoa are not reduced in size or complexity. Since a lumen is not present, however, the criteria for a germinal epithelium are not fulfilled and instead, the S. praematura testis features an epithelioid arrangement of spermatogonia. In other gobioids, the testicular interstitial tissue is composed of round cells with small dense nuclei. No such tissue is seen in S. praematura, rather, few small interstitial cells are visible between the thin-walled lobules packed with cysts. The sperm duct gland is present in S. praematura but is also reduced; a thick secretory epithelium is still present but only in the ventral portion of the gland, and the gland consists of a single chamber rather than an arrangement of lobules similar to those in the spermatogenic portion of the testis.

Reductions of the interstitial gonad tissue are also seen in the S. praematura ovary. Lamellae are absent, and the ovary consists of a thin-walled tube. A germinal epithelium is present, but it is restricted to a ridge along the ventral wall of the ovary. Follicle and oocyte complexes are reduced in number but not in size. The few oocytes that are produced possess a complex fibrous cap surrounding the micropyle that is arguably more complex than the filamentous attachment structures normally seen in gobioids. The basic gonad morphology is preserved even in the most extreme example of vertebrate paedormorphosis known; reductions have occurred only in the supportive gonad tissues and in a restriction of the distribution of gonial cells. The restricted distributions of gonial cells in the ovary and testis of S. praematura are extremely rare among percomorphs. Both these reductions in gonad morphology are probably related to the drastic overall size reduction in S. praematura caused by paedomorphosis, particularly since these patterns are not seen in a smaller species (P. pygmaea), which does not show evidence of ontogentic truncation.

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