Memoirs of Museum Victoria 60(1): 63–70 (2003)

ISSN 1447-2546 (Print) 1447-2554 (On-line)
http://www.museum.vic.gov.au/memoirs

Endemic and enigmatic: the reproductive biology of *Aegla* (Crustacea: Anomura: Aeglidae) with observations on sperm structure

CHRISTOPHER C. TUDGE

Biology Department, American University, 4400 Massachusetts Ave. NW, Washington, DC 20016-8007, USA and Department of Systematic Biology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0163, USA (ctudge@american.edu and tudge.christopher@nmnh.si.edu)

Abstract Tudge, C.C., 2003. Endemic and enigmatic: the reproductive biology of *Aegla* (Crustacea: Anomura: Aeglidae) with observations on sperm structure. In: Lemaitre, R., and Tudge, C.C. (eds), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 63–70.

The endemic South American family of freshwater anomurans, Aeglidae, consists of three genera: the fossils *Haumuriaegla* Feldmann and *Protaegla* Feldmann et al., and the extant *Aegla* Leach. In *Aegla* there are >60 described species from Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay, between 20°S and 50°S. Very little is known about the reproductive biology of *Aegla*. This paper summarises this information based on study of the extensive preserved collections in the National Museum of Natural History, Smithsonian Institution, and on data from the literature. The data presented includes female reproductive cycles, mating behavior, external reproductive morphology of males and females, and internal reproductive morphology of males. Areas for future research in the reproductive biology of aeglids are indicated. The ultrastructure of spermatophore-like lobes and spermatozoa are described and illustrated for males of *Aegla longirostri* Bond-Buckup and Buckup and *Aegla rostrata* Jara. No distinctly structured spermatophores are present, and spherical sperm cells appear polymorphic. Both these characteristics are unusual, although not unique, for an anomuran crab.

Keywords Crustacea, Anomura, Aeglidae, *Aegla*, reproduction, sperm

Introduction

The anomuran family Aeglidae Dana, 1852 contains more than 60 species in the genus *Aegla* Leach, 1820 and two fossil species *Haumuriaegla glaessneri* Feldmann, 1984 and *Protaegla miniscula* Feldmann et al., 1998. The species of *Haumuriaegla* was found in late Cretaceous marine rocks at Cheviot, New Zealand (Feldmann, 1984), while *Protaegla* is from marine red limestone in quarries at Tepexi, Mexico (Feldmann et al., 1998). The fossil species are the only members of the family outside South America. Extant species of *Aegla* have a limited distribution across six countries in South America between latitudes 20°S and 50°S (see Bond-Buckup and Buckup, 1994, 1998, 1999 for reviews on aeglid taxonomy and biogeography). The restricted range of *Aegla* is very similar to the endemic South American parastacid freshwater crayfish genera, *Parastacus* Huxley 1878, *Samastacus* Riek, 1971, and *Virilastacus* Hobbs, 1991, and suggests a similar route of colonisation. In fact, their ranges overlap so extensively that Riek (1971) suggested that competitive exclusion by aeglids forced crayfish out of streams and rivers and into burrowing lifestyles along river banks and fields.

The discovery of the fossil *Haumuriaegla* in marine rocks in New Zealand (Feldmann, 1984) strengthened the arguments of Ortmann (1902) that aeglids invaded South America from the sea on the southern Pacific coast and then extended their range eastwards into freshwater systems, toward the Atlantic coast. Dispersal in the opposite direction (Atlantic to Pacific) has been suggested by others (Schmitt, 1942b; Ringuelet, 1949; Morrone and Lopretto, 1994, 1995) and is based on the premise that the least ornamented morphology, seen in the Atlantic species of *Aegla*, is the plesiomorphic condition. The fact that the Cretaceous fossil *Haumuriaegla* is heavily ornamented with spines and tubercles would seem to contradict this argument. The recent discovery of the fossil *Protaegla* in early Cretaceous marine rocks in Mexico, extends the stratigraphic and geographic range of the family, and adds further support to the marine origin of the family.

Crandall et al. (2000) have suggested that the sister-group to the parastacid crayfish of South America are Australian and New Zealand genera (based on the 16s mitochondrial gene). This result may suggest a similar dispersal and colonisation route for parastacids and Aeglidae.

The early confusion surrounding the taxonomy and systematics of the genus *Aegla* was discussed by Martin and Abele (1988) and Bond-Buckup and Buckup (1994, 1998, 1999) who listed described species, distributions, and references. The relationship of Aeglidae to the other anomuran families remains unresolved. Milne Edwards and Bouvier (1894: 243 and 311) derived the aeglids from marine hermit crabs and placed them on a direct lineage to the galatheids. Recently, Martin (1985, 1989) and Martin and Abele (1988) linked aeglids with hermit crabs (paguroids and coenobitoids) rather than with the galatheids, although a sister-group relationship with the Galatheoidea had been suggested earlier by Martin and Abele (1986). Representatives of the Aeglidae were included in some recent phylogenetic analyses of anomuran relationships (McLaughlin and Lemaitre, 1997; Pérez-Losada et al., 2001, 2002) but were absent from an analysis based on reproductive characters (Tudge, 1997). Further, some species of *Aegla* have been the subject of more focused studies of intrageneric relationships (Schuldt et al., 1988; D'Amato and Corach, 1997), biogeographic studies on areas of endemism (Morrone and Lopretto, 1994, 1995), and more recently phylogeny within the Chilean representatives of the family (Pérez-Losada et al., 2000).

This paper summarizes available information on reproduction in *Aegla* for the first time. Particular aspects of the reproductive biology of aeglids that still require investigation are highlighted. Novel data on the form of spermatophore-like lobes in the male reproductive system and light microscope and ultrastructural observations of spermatozoa of *A. longirostri* Bond-Buckup and Buckup, 1994 and *A. rostrata* Jara, 1977 are also presented.

Materials and methods

A single male of *Aegla rostrata* was collected by Dr Carlos Jara from Lake Riñihue, Valdivia Provence, Chile on 13 Nov 1995. The gonads were removed and fixed in 3% glutaraldehyde in phosphate buffer. A squash of tissue was examined and photographed through a Leitz Orthoplan 2 microscope with Nomarski phase contrast, and attached Wild Photoautomat MPS 45 photomicrography system. Kodak T-Max 100 ASA black and white film was used. The remainder of the tissue was processed for transmission electron microscopy (TEM).

Gonads were dissected from three species of *Aegla*, collected by Mr Pérez-Losada on 30 Oct 2000, in Rio Grande do Sul, Brazil, and fixed in 3% glutaraldehyde in phosphate buffer. Specimens of *A. grisella* Bond-Buckup and Buckup, 1994 and *A. spinipalma* Bond-Buckup and Buckup, 1994 were collected in the Sangao River and the Capingui River, respectively, while a single *A. longirostri* was collected from the Carreiro River. Light microscope observations were made of the fixed tissues before they were processed for TEM (see Tudge et al., 2001).

Seven additional specimens of *Aegla* were collected by Mr Pérez-Losada in Chile and Argentina, 17–24 Feb 2000, fixed in 70% ETOH: *A. affinis* Schmitt, 1942, Maula River, Province of Taloa, Chile; *A. papudo* Schmitt, 1942, Rabuco River, Province of Quillota, Chile; *A. neuquensis* Schmitt, 1942, Chico River, Province of Mendoza, Argentina; *A. pewenchae* Jara, 1994, Lake Lialuia, Chile. External and internal reproductive morphology of all specimens was observed.

The identified aeglid collection (958 specimens from 22 species, including types) of the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) was examined, and sex ratio, date of collection, and presence of ovigerous females were recorded. Data for ovigerous females was supplemented from the literature.

Results and discussion

Sex ratio. The sex ratio (males to females) of an *Aegla* species was first reported as approximately 1:1 by Mouchet (1932, as *Aeglea laevis*). However, this species does not occur in Uruguay (G. Bond-Buckup and L. Buckup, pers. comm.) and therefore must be attributed to another taxon, possibly *A. uruguayana* Schmitt, 1942 or *A. platensis* Schmitt, 1942. Subsequent authors have stated that the sex ratio is usually 1:1 but may vary according to time of year, season, and where in the river specimens were collected (Bahamonde and López, 1961; Lopéz, 1965; Burns, 1972). More recently, Bueno and Bond-Buckup (2000) found a sex ratio of 1.08:1, in populations of *A. platensis* in the Mineiro River, Brazil and a ratio of 1:1 has been recorded for *A. castro* Schmitt, 1942 in Ponta Grossa, Brazil, by Swiech-Ayoub and Masunari (2001b).

Aeglids are gregarious animals known to congregate in large numbers at the river's edge, especially during the spawning season (Bahamonde and López, 1961; Burns, 1972; Martin and Abele, 1988). After mating, the number of females is greatest on the riverbanks, while the males return to the deeper water in the centre of the river. This sex-specific separation of habitat at this time may account for the observation by Mouchet (1932), that no males of *Aegla* sp. (as *Aeglea laevis*) were found at the end of winter (September–October) around Montevideo, Uruguay.

When investigating the sex ratio in the aeglid collection at USNM, the *Aegla* holdings were found to be biased toward male specimens (4:1). This under-representation of females across all 22 species in the collection further compounded the search for ovigerous females, of which there were only 40 specimens (4.2%). The paucity of female specimens in the USNM collections represents a collection bias favouring males, and enhanced by local cultural and ethical practices of not collecting ovigerous females (L. Buckup and G. Bond-Buckup, pers. comm.).

Mating. Aeglids are sexually dimorphic in a number of features. These include: the presence of abdominal pleopods in females over 12 mm carapace length (cl), a larger carapace (both length and width) in males, larger and unequal chelipeds in males, narrower abdomens in males, and difference in location of the ventral gonopores (Bahamonde and López, 1961; Burns, 1972). An ovigerous female of 9.87 mm cl was found by Bueno and Bond-Buckup (2000) for *A. platensis*, and appears to be the smallest female with eggs recorded to date. As far as can be ascertained, observations on mating behaviour have not previously been documented for any species of *Aegla*. No information appears to be available on whether pre- or post-copulatory mate guarding occurs or where mating occurs in the moult cycle. However, two instances (one in the wild and one in an aquarium) of finding male-female pairs in a sternum to sternum position, engaged in mating behavior, were recounted to me (J. W. Martin, pers. comm). On both occasions the animals separated upon being disturbed and no evidence of sperm transfer was seen. A ventral to ventral mating position would seem the most obvious for these crabs as has been commonly illustrated for other anomurans (e.g. Kamalaveni, 1949; Efford, 1967; Hazlett, 1968; Helfman, 1977; Wada et al., 1997; Hess and Bauer, 2002).

There is no published information about the size at sexual maturity for males of any *Aegla* species. Female size at sexual maturity has been recorded as a minimum of 12.5 mm cl (all mature by 20.5 mm) (Bahamonde and López, 1961; Burns, 1972) for female *A. laevis*, and between 9.8 mm and 17.7 mm cl (Bueno and Bond-Buckup, 2000) in female *A. platensis*.

Female reproductive biology. Sexually mature females of *Aegla* can be distinguished from males primarily in the presence of four pairs of abdominal pleopods, and position of the gonopores (= genital pores) on the coxae of the third pereopods (P3) (Bahamonde and López, 1961; Burns, 1972; Martin and Abele, 1988). Illustrations of the gonopores and the pleopods in females of *A. platensis* can be found in Martin and Abele (1988, figs 10 and 16). The pleopods are used to carry fertilized eggs during the spawning period, and during this time eggs are groomed often to keep them aerated and clean of ectoparasites (Martin and Felgenhauer, 1986). Burns (1972) stated that females do not moult while brooding eggs, but no further information is available on the synchrony of the moult cycle and the reproductive cycle in *Aegla*. The eggs are spherical, small and have been described as pale yellow, orange, or reddish (Mouchet, 1932; Bahamonde and López, 1961; Lopéz, 1965; Burns, 1972; Jara, 1977). Measurements of aeglid egg diameter vary between species and have been recorded as 0.8–1.35 mm (Lopéz and Sawaya, 1960; Bahamonde and Lopéz, 1961; Lopéz, 1965) in *A. laevis*, 1.1–1.5 mm (Lopéz and Sawaya, 1960; Lopéz, 1965) in *A. paulensis* Schmitt, 1942 (as *A. odebrechtii paulensis*), 1.2 mm (Jara, 1977) in *A. rostrata*, 2.2 mm (Swiech-Ayoub and Masunari, 2001b) in *A. castro*. Bahamonde and López (1961: fig. 17) illustrated eggs attached to the female and further provide information on the range and frequency of egg size and numbers per female in *A. laevis*. The fecundity of females has been stated as 64–255 (Lopéz, 1965) eggs per female in *A. paulensis*, an average of 100 (Jara, 1977) in *A. rostrata*, and 90–204, average = 121 (Swiech-Ayoub and Masunari, 2001a) in *A. longirostri*.

The eggs have abundant yolk, direct development, no free-swimming larval forms and therefore hatch as juveniles, resembling adults (Mouchet, 1932; Martin, 1989; Bond-Buckup et al., 1996, 1998, 1999; Bueno and Bond-Buckup, 1996). The complete embryonic development of *Aegla platensis* has recently been documented as occurring in ten distinct, post-fertilisation, morphological stages (Lizardo-Daudt and Bond-Buckup, 2002).

The timing of spawning differs between species and between populations of the same species. Females of *Aegla castro* and *A. longirostri* live for about two years, and can reproduce in both years (Swiech-Ayoub and Masunari, 2001a, 2001b). A review of literature and examination of specimens in the USNM collections reveal that in 13 species of *Aegla*, ovigerous females have been found in every month except November and December (Fig. 1). However, in *A. platensis* some ovigerous females were collected in these months (Bueno and Bond-Buckup, 2000) making it the only species that potentially breeds all year round. Spawning times and/or collection of ovigerous females can be found in Swiech-Ayoub and Masunari (2001a, b) for *A. castro*, Jara (1989) for *A. denticulata* Nicolet, 1849, in Mouchet (1932), Bahamonde and López (1961) and Burns (1972) for *A. laevis*, in Lopéz (1965) for *A. paulensis*, in Rodrigues and Hebling (1978) for *A. perobae* Hebling and Rodrigues, 1977, in Bueno and Bond-Buckup (2000) for *A. platensis*, and in Jara (1977) for *A. rostrata*. The internal morphology of the female reproductive system has yet to be described or illustrated in the literature.

Male reproductive biology. Aeglid males have no easily observed abdominal pleopods, but some vestigial pleopodal remnants have been recorded (Martin and Abele, 1988) on abdominal segments 3 and 4 in *Aegla platensis*. The male gonopores are on the coxal segment of pereopod 5 (P5) (Burns, 1972; Martin and Abele, 1988), as with all decapods, but aeglids have an additional, tube-like extension. This tube was first illustrated in Aeglidae by Milne Edwards and Bouvier (1894: 240, fig. 30), and the taxonomic significance of the sexual tube morphology was recognised by Schmitt (1942a: 28). He stated that there "seem to be some differences in the relative proportions of the protruding sperm ducts on the reduced fifth legs" between *A. abtao* Schmitt, 1942 and *A. concepcionensis* Schmitt, 1942 and that the importance of this observation was being investigated.

As has been recorded in many freshwater crayfish, intersex males (exhibiting both male and female secondary sexual characteristics) have been observed in several species of *Aegla* (L. Buckup and G. Bond-Buckup, pers. comm.).

Lopretto (1978a) described the internal and external morphology of the fifth pereopod of 12 species of Argentine aeglids, including detailed drawings, and photographs, showing the fine structure of P5 and associated tube. Lopretto recognised the systematic and phylogenetic importance of this male sexual character, established a specific nomenclature for its structure, devised a key to these species based on P5 and tube morphology, and carefully documented tube diversity across these Argentine species. In doing so, she established several distinctive species groups based solely on P5 and tube characteristics (Lopretto, 1978a, 1978b, 1979, 1980a, 1980b, 1981).

Internal morphology of the reproductive system of male aeglids is virtually unknown. Mouchet (1932) stated that an *Aegla* species (as *Aeglea laevis*) males do not have spermatophores and recognised that this was exceptional among galatheoids. Lopretto (1978a: 288) vaguely described the male reproductive system as seen under the light microscope and noted small capsules with cellular elements and delicate intermediary connective threads. Lopretto's remarks could refer to spermatozoa with microtubular arms bundled into lobes within the testis and vas deferens, as observed in Tudge and Scheltinga (2002) and during this study (Fig. 2).

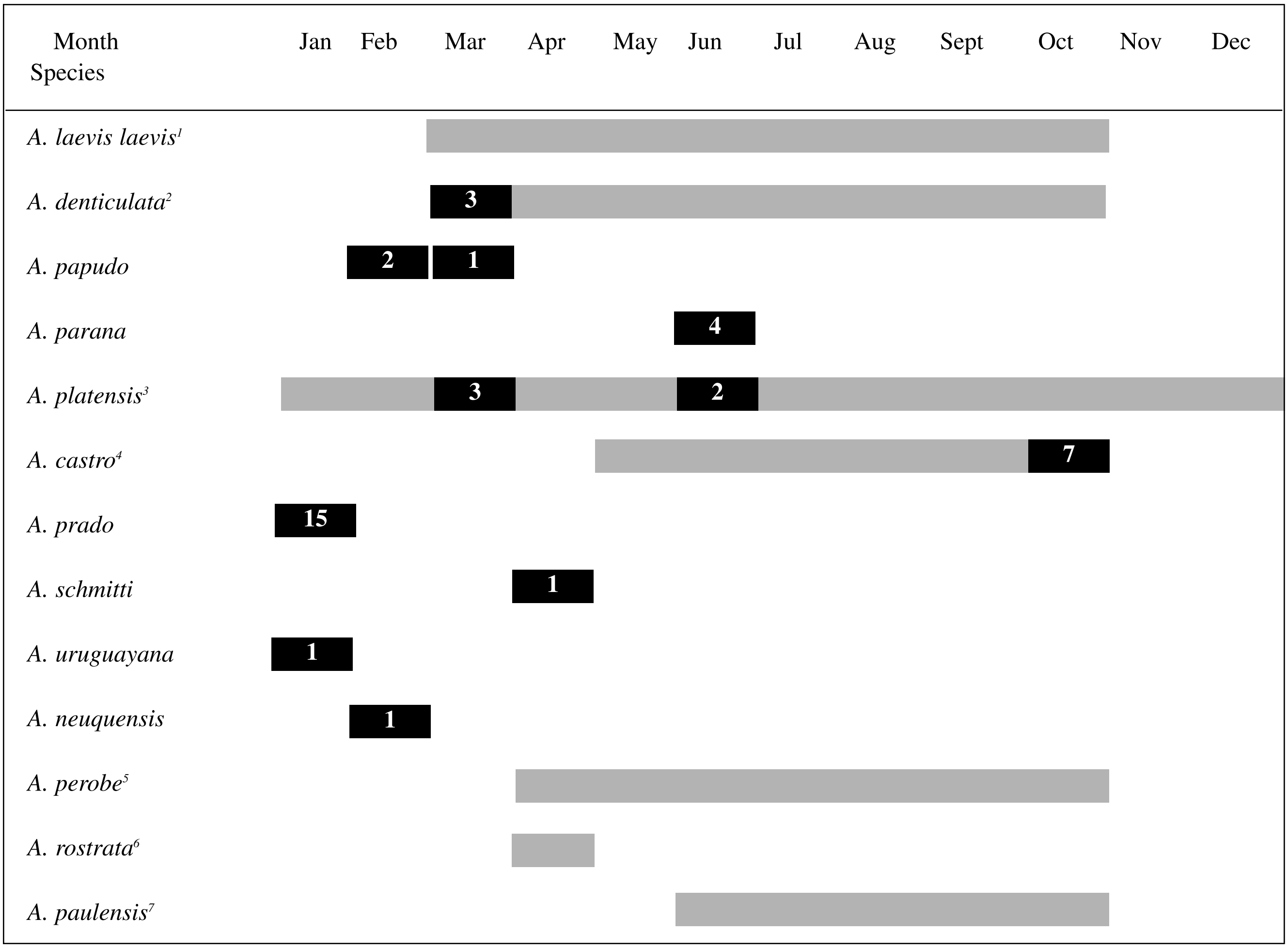

Figure 1. Occurrence of ovigerous females of *Aegla* species obtained from literature sources and USNM specimens. Total USNM specimens examined = 958 (40 ovigerous females). Symbols: [1] Bahamonde and López (1961); [2] Jara (1989); [3] Bueno and Bond-Buckup (2000); [4] Swiech-Ayoub and Masunari (2001a, 2001b); [5] Rodrigues and Hebling (1978); [6] Jara (1977); [7] Lopéz (1965). Shading = range from literature sources indicated. Solid black bar = number from USNM collection for that month.

Mouchet's (1932) statement on spermatophores is supported by observations presented herein of the male reproductive morphology (Fig. 2A) in *Aegla rostrata*. No distinct, encapsulated, spermatophores were observed in the vas deferens of *A. rostrata*, and instead there are only thin walled, spherical to oblong, lobes containing the sperm cells. These lobes were approximately 0.5–1 mm in size and bound by a thin, translucent membrane. Terminally, some exhibited a distinct line or fold, which may represent some sort of lumen. Presumably these blind-ending, spermatophoric lobes, empty into a common duct, or ducts, in the testis or vas deferens.

When a squash of these lobes was made on to a slide and observed using transmitted light microscopy, their contents revealed many different sized and shaped cells. Among this array of cells the spermatozoa were periodically scattered (Fig. 2B). Although themselves polymorphic, the sperm cells displayed a distinct suite of characteristics that identified them as decapod/anomuran sperm cells (Jamieson and Tudge, 2000; Tudge and Scheltinga, 2002). The roughly spherical to ovoid cells contained a smaller spherical vesicle (sometimes clearly ring-shaped) at one pole, and an adjacent coarse granular zone (Fig. 2B-G). These small vesicles represent the acrosome vesicles embedded in the cytoplasmic region. More obviously the spermatozoa were seen to have long, filamentous arms radiating from the central cell mass. The number and position of these arms is variable, from none being visible, to a maximum of three (Fig. 2E, G). Analysis at the electron microscope level (Tudge and Scheltinga, 2002; this study Fig. 3) revealed these filaments, or arms, to be the bundles of microtubules common to all anomuran spermatozoa recorded to date (Tudge, 1997; Jamieson and Tudge, 2000).

Under the transmission electron microscope the spermatozoa of *Aegla rostrata*, although slightly irregular in shape, were found to have a consistent ultrastructure. The spherical to ovoid sperm cells are approximately 5 μm wide and 4 μm in height (through the acrosomal axis), with the acrosome vesicle being 1.5 μm in diameter. The entire sperm cell can be divided into two hemispheres; the upper (or acrosomal) one containing the

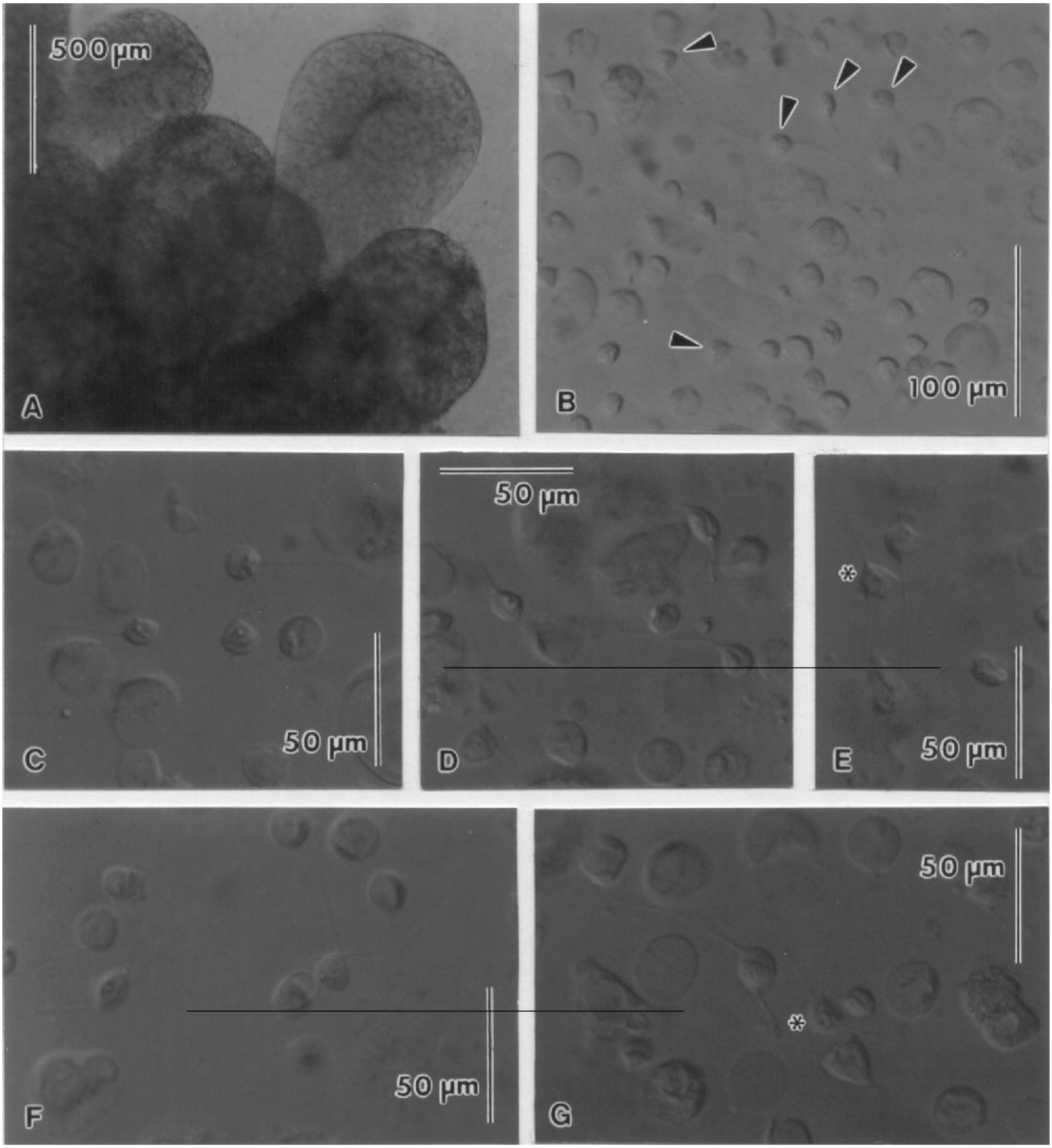

Figure 2. Light micrographs of *Aegla rostrata* Jara, 1977. A, Spermatophoric lobes; B–G, Squash of spermatophoric lobe contents showing spermatozoa (arrowheads) scattered amongst assorted cells (Asterisk in E and G indicate individual spermatozoa with three microtubular arms).

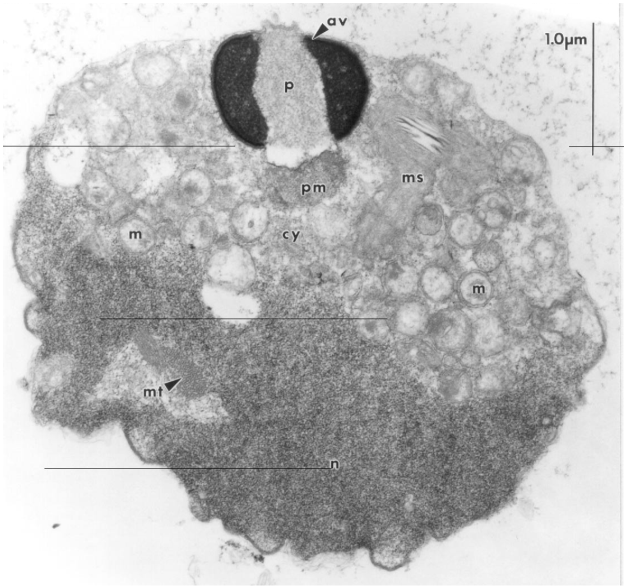

Figure 3. Transmission electron micrograph of spermatozoon of *Aegla longirostri* Bond-Buckup and Buckup, 1994 in longitudinal section. Abbreviations: av, acrosome vesicle; cy, cytoplasm; m, mitochondrion; ms, membrane system; mt, microtubular bundle; n, nucleus; p, perforatorial column; pm, periacrosomal material.

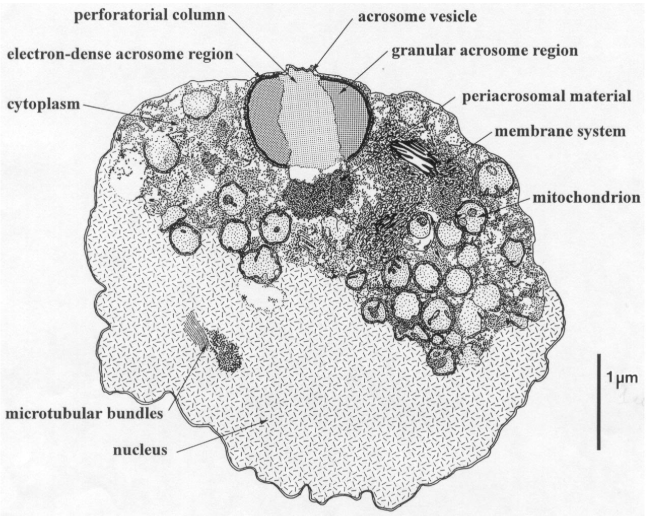

Figure 4. Semidiagrammatic representation of longitudinal section of spermatozoon of *Aegla longirostri* Bond-Buckup and Buckup, 1994, based on a micrograph (Fig. 3).

acrosome and cytoplasmic elements, the lower (or nuclear) one the nucleus (Tudge and Scheltinga, 2002; this study Figs 3, 4). The acrosome vesicle is irregular in shape and is composed of an electron-dense outer ring with an electron-pale central area. This central column can be posteriorly penetrated by irregular intrusions. Cytoplasmic elements include many circular mitochondria, membrane bundles or arrays, and sometimes a centriole is visible immediately posterior to the acrosome. The nucleus is coarsely granular, more electron-dense than the cytoplasm, and is penetrated by the bases of the microtubular arms, which are mostly evident as short bundles of microtubules in oblique section (Tudge and Scheltinga, 2002; this study Figs 3, 4). All the spermatozoa observed exhibited the above ultrastructural characteristics, with differences between sperm cells being in their overall shape, and in the irregular, often crenulated, dense region of the acrosome.

In summary, it can be clearly seen that much research is still needed to gather basic information on reproductive cycles and morphology in aeglids. Areas of future research that would be fruitful include, but are not restricted to, observations on mating behaviour, timing of mating during the moult cycle, sperm transfer mechanisms, male sexual tube(?) morphology and microstructure, male and female reproductive system gross morphology, egg ultrastructure, and further spermatophore and sperm cell ultrastructure. The latter is needed to confirm that the novel observations provided above, and in Tudge and Scheltinga (2002), are representative for the genus and family.

Acknowledgements

The author wishes to thank Carlos Jara (Universidad Austral de Chile, Chile), Ludwig Buckup, Georgina Bond-Buckup (Universidade Federale do Rio Grande do Sul, Porto Alegre, Brazil), and Marcos Pérez-Losada (Brigham Young University, Utah, USA) for collecting specimens of aeglids from various localities in Chile, Argentina, and Brazil. Alexandre Almeida (Universidade Estadual de Santa Cruz, Brazil) and Alessandra Bueno (Universidade Federale do Rio Grande do Sul, Porto Alegre, Brazil) are thanked for providing important literature. Dave Scheltinga and Lina Daddow (Department of Zoology and Entomology, University of Queensland, Australia) provided expert assistance with the fixation and processing for transmission electron microscopy of the aeglid reproductive material. This research was started when the author was a Smithsonian Institution Postdoctoral Fellow (1995-1996) in the then Department, and now section, of Invertebrate Zoology, NMNH, Washington DC, and was completed while a research associate (1999–2002) at the same institution. Kristian Fauchald and Rafael Lemaitre are thanked for access to facilities within that Department.

References

Bahamonde, N.N., and López, M.T. 1961. Estudios biologicos en la poblacion de *Aegla laevis laevis* (Latreille) de el Monte (Crustacea, Decapoda, Anomura). *Investigaciones Zoológicas Chilenas* 7: 19–58.

Bond-Buckup, G., and Buckup, L. 1994. A família Aeglidae (Crustacea, Decapoda, Anomura). *Arquivos de Zoologia, São Paulo* 32(4): 159–346.

Bond-Buckup, G., and Buckup, L. 1998. Malacostraca – Eucarida. Aeglidae. Pp. 431–437 in: Young, P.S. (ed), *Catalogue of Crustacea of Brazil.* Museu Nacional: Rio de Janeiro.

Bond-Buckup, G., and Buckup, L. 1999. Família Aeglidae (caranguejos anomuros de água doce). Pp. 362–382 in: Buckup, L., and

Bond-Buckup, G. (eds), *Os crustáceos do Rio Grande do Sul.* Universidade/UFRGS: Porto Alegre.

Bond-Buckup, G., Bueno, A.P., and Keunecke, K.A. 1996. Primeiro estágio juvenil de *Aegla prado* Schmitt (Crustacea, Decapoda, Anomura, Aeglidae). *Revista Brasileira Zoologia* 13(14): 1049–1061.

Bond-Buckup, G., Bueno, A.P., and Keunecke, K.A. 1998. Morphological characteristics of juvenile specimens of *Aegla* (Anomura: Aeglidae). *Proceedings and Abstracts, Fourth International Crustacean Congress, Amsterdam* 20–24 July, 1998: 130.

Bond-Buckup, G., Bueno, A.P., and Keunecke, K.A. 1999. Morphological characteristics of juvenile specimens of *Aegla* (Decapoda, Anomura: Aeglidae). Pp. 371–381 in: Schram, F.R., and von Vaupel Klein, J.C. (eds), *Crustaceans and the biodiversity crisis.* Brill: Leiden.

Bueno, A.P., and Bond-Buckup, G. 1996. Os estágios juvenis iniciais de *Aegla violacea* Bond-Buckup and Buckup (Crustacea, Anomura, Aeglidae). *Nauplius, Rio Grande* 4: 39–47.

Bueno, A.P., and Bond-Buckup, G. 2000. Dinâmica populacional de *Aegla platensis* Schmitt (Crustacea, Decapoda, Aeglidae). *Revista Brasileira Zoologia* 17(1): 43–49.

Burns, J.W. 1972. The distribution and life history of South American freshwater crabs (*Aegla*) and their role in trout streams and lakes. *Transactions of the American Fisheries Society* 101(4): 595–607.

Crandall, K.A., Fetzner, J.W., Jara, C.G., and Buckup, L. 2000. On the phylogenetic positioning of the South American freshwater crayfish genera (Decapoda: Parastacidae). *Journal of Crustacean Biology* 20(3): 530–540.

D'Amato, M.E., and Corach, D. 1997. Highly repetitive DNA sequences unique to Aeglidae (Anomura). *Journal of Crustacean Biology* 17(1): 184–191.

Efford, I.E. 1967. Neotony in sand crabs of the genus *Emerita* (Anomura, Hippidae). *Crustaceana* 13: 81–93.

Feldmann, R.M. 1984. *Haumuriaegla glaessneri* n. gen., and sp. (Decapoda; Anomura; Aeglidae) from Haumurian (Late Cretaceous) rocks near Cheviot, New Zealand. *New Zealand Journal of Geology and Geophysics* 27: 379–385.

Feldmann, R.M. 1986. Paleobiogeography of two decapod crustacean taxa in the southern hemisphere: global conclusions with sparse data. Pp. 5–19 in: Gore, R.H., and Heck, K.L. (eds), *Crustacean biogeography, Crustacean Issues* 4. Balkema: Rotterdam.

Feldmann, R.M., Vega, F.J., Applegate, S.P., and Bishop, G.A. 1998. Early Cretaceous arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, México. *Journal of Paleontology* 72(1): 79–90.

Hazlett, B.A. 1968. The sexual behavior of some European hermit crabs (Anomura: Paguridae). *Pubblicazioni della Stazione Zoologica di Napoli* 36: 238–252.

Helfman, G.S. 1977. Copulatory behavior of the coconut or robber crab *Birgus latro* (L.) (Decapoda Anomura Paguridea Coenobitidae). *Crustaceana* 33(2): 198–202.

Hess, G.S., and Bauer, R.T. 2002. Spermatophore transfer in the hermit crab *Clibanarius vittatus* (Crustacea, Anomura, Diogenidae). *Journal of Morphology* 253(2): 166–175.

Jamieson, B.G.M., and Tudge, C.C. 2000. Crustacea-Decapoda. Pp. 1–95 in: Jamieson, B.G.M. (ed), *Progress in male gamete ultrastructure and phylogeny*, Vol. 9, part C in: Adiyodi, K.G., and Adiyodi, R.G. (eds), *Reproductive biology of invertebrates.* John Wiley and Sons: Chichester.

Jara, C.G. 1977. *Aegla rostrata* n. sp., (Decapoda, Aeglidae), nuevo crustáceo dulceacuícola del Sur de Chile. *Studies on Neotropical Fauna and Environment* 12: 165–176.

Jara, C.G. 1989. *Aegla denticulata lacustris,* new subspecies, from Lake Rupanco, Chile (Crustacea: Decapoda: Anomura: Aeglidae). *Proceedings of the Biological Society of Washington* 102(2): 385–393.

Kamalaveni, S. 1949. On the ovaries, copulation and egg-formation in the hermit-crab, *Clibanarius olivaceous* Henderson (Crustacea, Decapoda). *Journal of the Zoological Society of India* 1(2): 120–128.

Lizardo-Daudt, H.M., and Bond-Buckup, G. 2002. The embryonic development of *Aegla platensis* (Crustacea, Decapoda, Aeglidae). *Invertebrate Zoology* (In press).

Lopéz, M.T. 1965. Estudios biologicas en *Aegla odebrechtii paulensis*, Schmitt (Crustacea, Decapoda, Anomura). *Zoologia* 25: 301–314.

Lopéz, M.T., and Sawaya, P. 1960. Observaciones biologicas en la población de *Aegla odebrechtii paulensis*, Schmitt de Alto da Serra, São Paulo (Crust. Decapoda Anomura). *Anais da Academia Brasileira de Ciências* 32(3/4): 37–38.

Lopretto, E.C. 1978a. Estructura exoesqueletaria y miológica del quinto par de pereiópodos del macho de la familia Aeglidae (Crustacea Anomura). *Limnobios* 1(8): 284–298.

Lopretto, E.C. 1978b. Las especies de *Aegla* Leach del centro-oeste Argentino en base a la morfología comparada del quinto par de pereiópodos (Crustacea, Anomura, Aeglidae). *Neotrópica* 24(71): 57–68.

Lopretto, E.C. 1979. Estudio comparativo del quinto par de pereiópodos en los representantes del género *Aegla* de la Patagonia Argentina (Crustacea Anomura). *Neotrópica* 25(73): 9–22.

Lopretto, E.C. 1980a. Análisis de las características del quinto pereiópodo en las especies de *Aegla* del grupo "*platensis*" (Crustacea Anomura Aeglidae). *Physis (Buenos Aires)* (B) 39(96): 37–56.

Lopretto, E.C. 1980b. Clave para la determinación de las especies del género *Aegla* de la República Argentina en base al estudio comparativo del quinto par de pereiópodos masculinos (Crustacea Anomura Aeglidae). *Limnobios* 1(10): 431–436.

Lopretto, E.C. 1981. Consideraciones sobre la estructura apendicular vinculada al dimorfismo sexual en los machos de las especies de *Aegla* del noroeste Argentino (Crustacea, Anomura, Aeglidae). *Acta Zoológica Lilloana* 36(2): 15–35.

Martin, J.W. 1985. Phylogenetic relationships of the genus *Aegla* (Decapoda, Anomura, Aeglidae). *American Zoologist* 25(4): 127A (Abstract).

Martin, J.W. 1989. Almost a crab. *Terra* 27(5–6): 17–19.

Martin, J.W., and Abele, L.G. 1986. Phylogenetic relationships of the genus *Aegla* (Decapoda: Anomura: Aeglidae), with comments on anomuran phylogeny. *Journal of Crustacean Biology* 6(3): 576–616.

Martin, J.W., and Abele, L.G. 1988. External morphology of the genus *Aegla* (Crustacea: Anomura: Aeglidae). *Smithsonian Contributions to Zoology* 453: 1–46.

Martin, J.W., and Felgenhauer, B.E. 1986. Grooming behaviour and the morphology of grooming appendages in the endemic South American crab genus *Aegla* (Decapoda, Anomura, Aeglidae). *Journal of Zoology, London* (A) 209: 213–224.

McLaughlin, P.A., and Lemaitre, R. 1997. Carcinization in the Anomura – fact or fiction? I. Evidence from adult morphology. *Contributions to Zoology* 67(2): 79–123.

Milne Edwards, A., and Bouvier, E.-L. 1894. Considérations générales sur la famille des Galathéidés. *Annales des Sciences Naturelles Zoologie* (7) 16: 191–327.

Morrone, J.J., and Lopretto, E.C. 1994. Distribution patterns of freshwater Decapoda (Crustacea: Malacostraca) in southern South America: a pangeographic approach. *Journal of Biogeography* 21: 97–109.

Morrone, J.J., and Lopretto, E.C. 1995. Parsimony analysis of endemicity of freshwater Decapoda (Crustacea: Malacostraca) from southern South America. *Neotrópica* 41(105–106): 3–8.

Mouchet, S. 1932. Notes sur la biologie du galathéide *Aeglea laevis* (Latr.). *Bulletin de la Société zoologique de France* 57: 316–340.

Ortmann, A.E. 1902. The geographical distribution of freshwater decapods and its bearing upon ancient geography. *Proceedings of the American Philosophical Society, Philadelphia* 41: 267–400.

Pérez-Losada, M., Jara, C., Bond-Buckup, G., and Crandall, K. 2000. Phylogeny of the Chilean freshwater crabs Aeglidae (Decapoda, Anomura): Implications for conservation. *I Congresso Brasileiro sobre Crustáceos, 2000, São Pedro, São Paulo, Brasil. Resumos ICBC, Sociedade Brasileira de Carcinologia*, Resumos vol. 1. p.181 (abstract).

Pérez-Losada, M., Jara, C.G., Bond-Buckup, G., Porter, M.L., and Crandall, K.A. 2001. Anomuran phylogenetic relationships: on the taxonomic positioning of Aeglidae freshwater crabs (Crustacea, Anomura). *Abstracts, Fifth International Crustacean Congress, 9–13 July, 2001, Melbourne, Australia*: 120–121(abstract).

Pérez-Losada, M., Jara, C.G., Bond-Buckup, G., Porter, M.L., and Crandall, K.A. 2002. Phylogenetic position of the freshwater anomuran family Aeglidae. *Journal of Crustacean Biology* 22(3): 670–676.

Riek, E.F. 1971. The freshwater crayfishes of South America. *Proceedings of the Biological Society of Washington* 84(16): 129–136.

Ringuelet, R.A. 1949. La prioridad en el estudio biométrico de los decápodos anomuros del género *Aegla* Leach. *Notas del Museo de La Plata, Zoológica* 14: 119–121.

Rodrigues, W., and Hebling, N.J. 1978. Estudos biológicos em *Aegla perobae* Hebling and Rodrigues, 1977 (Decapoda, Anomura). *Revista Brasiliera Biologica* 38(2): 383–390.

Schmitt, W.L. 1942a. Two new species of *Aeglea* from Chile. *Revista Chilena de Historia Natural* 44(1940): 25–31.

Schmitt, W.L. 1942b. The species of *Aegla*, endemic South American fresh-water crustaceans. *Proceedings of the United States National Museum* 91: 431–520.

Schuldt, M., Nuñez, P., Mersing, W., Del Valle, A., and Manceñido, M.O. 1988. *Aegla* (Crustacea Anomura) en el Lago Huechulafquen (Neuquen, Argentina) y algunas implicancias filogenéticas para Aeglidae del centro-oeste de Argentina. *Anales de la Sociedad Científica Argentina* 217: 27–37.

Swiech-Ayoub, B.P., and Masunari, S. 2001a. Flutuações temporal e espacial de abundância e composição de tamanho de *Aegla castro* Schmitt (Crustacea, Anomura, Aeglidae) no Buraco do Padre, Ponta Grossa, Paraná, Brasil. *Revista Brasileira Zoologia* 18(3): 1003–1017.

Swiech-Ayoub, B.P., and Masunari, S. 2001b. Biologia reprodutiva de *Aegla castro* Schmitt (Crustacea, Anomura, Aeglidae) no Buraco do Padre, Ponta Grossa, Paraná, Brasil. *Revista Brasileira Zoologia* 18(3): 1019–1030.

Tudge, C.C. 1997. Phylogeny of the Anomura (Decapoda, Crustacea): Spermatozoa and spermatophore morphological evidence. *Contributions to Zoology* 67(2): 125–141.

Tudge, C.C., and Scheltinga, D.M. 2002. Spermatozoal morphology of the freshwater anomuran *Aegla longirostri* Bond-Buckup & Buckup, 1994 (Crustacea: Decapoda: Aeglidae) from South America. *Proceedings of the Biological Society of Washington* 115(1): 118–128.

Tudge, C.C., Scheltinga, D.M., and Jamieson, B.G.M. 2001. Spermatozoal morphology in the "symmetrical" hermit crab, *Pylocheles (Bathycheles)* sp. (Crustacea, Decapoda, Anomura, Paguroidea, Pylochelidae). *Zoosystema* 23(1): 117–130.

Wada, S., Ashidate, M., and Goshima, S. 1997. Observations on the reproductive behavior of the spiny king crab *Paralithodes brevipes* (Anomura: Lithodidae). *Crustacean Research* 26: 56–61.