Journal of
Molluscan Studies

The Malacological Society of London

Journal of Molluscan Studies (2013) **79**: 372–377. doi:10.1093/mollus/eyt029
Advance Access publication date: 23 August 2013

RESEARCH NOTE

EGG-HULL ULTRASTRUCTURE OF *ISCHNOCHITON STRAMINEUS* (SOWERBY, 1832), A SOUTH AMERICAN BROODING CHITON (CHITONINA: ISCHNOCHITONIDAE)

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Reproductive aspects of the life history of chitons have been relatively little studied in comparison with some morphological characters, such as valve morphology, girdle scales and radulae, which have historically been considered of taxonomic value. In recent times, however, some authors have pointed out that characters related to reproduction, such as egg-hull morphology, are also valuable for taxonomic purposes (Eernisse, 1988; Hodgson *et al*., 1988; Sirenko, 1993; Pashchenko & Drozdov, 1998; Okusu *et al*., 2003; Buckland-Nicks, 2006, 2008; Sirenko, 2006a; Buckland-Nicks & Schander, 2008; Buckland-Nicks & Reunov, 2009; Ituarte, Liuzzi & Centurión, 2010). Egg-hull morphology varies not only among different suborders (i.e. Chitonina, with spinose hull projections and narrow bases, *vs* Acanthochitonina, with large hull cupules and wide bases), but also when comparing species with different modes of development (i.e. free-spawning *vs* brooding species) (Eernisse, 1988; Sirenko, 1993; Buckland-Nicks, 2008). Despite the valuable information provided by this character, egg-hull morphology of southwestern Atlantic chitons remains poorly known. The only study dealing specifically with this issue is that by Ituarte *et al.* (2010) on *Plaxiphora aurata* and *Chaetopleura isabellei*.

Based on morphological characters, Sowerby (1832) described *Ischnochiton stramineus* (as *Chiton stramineus*) from Chiloé Island (Chile). Plate (1898) enlarged the description of this species (as *Ischnochiton imitator* (Smith), regarded as a synonym of *I. stramineus* by Kaas & Van Belle, 1990), providing novel information on its brooding behaviour and the general egg morphology (studied with light microscopy). More than a century later, Sirenko (2006b) reported for the second time the parental care in this species. The present contribution provides additional information on the reproductive characteristics of *I. stramineus*, focusing particularly on egg-hull ultrastructure.

The source of information for this study comes from three ethanol-preserved specimens (11.5 to 16.9 mm in length, brooding eggs or juveniles) in the collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia": 1 specimen (MACN–In 12483) with eggs from Puerto Harris, Isla Dawson, Magellan Strait (53°50.0′S–70°23.1′W); 1 specimen (MACN–In 22048) with juveniles from Puerto Olla, Isla Observatorio, Isla de los Estados Archipelago (54°39.4′S–64°08.7′W; 18–37 m); and 1 specimen (MACN–In 30695) with eggs from Celebroña (=Kidney) Island, Malvinas/Falkland Islands (51°37′S–57°45′W). Thirty-eight eggs were removed from the pallial groove, dehydrated in an ascending ethanol series (from 70 to 100%), dried in an EMS 850 critical-point dryer using liquid CO_2, coated with gold-palladium (40–60%) and photographed with a Phillips XL-30 scanning electron microscope. One juvenile was dehydrated and photographed in the same way as the eggs, but treated with hexamethyldisilazane and air dried instead of critical-point dried. The maximum length of the egg plate and micropore diameter, two characters of taxonomical value at suborder and family levels (Eernisse, 1988; Sirenko, 1993; Pashchenko & Drozdov, 1998; Buckland-Nicks, 2008), were measured, although the absolute values here provided should be considered with caution owing to the long time that these specimens had been preserved in ethanol since collection. Fifteen eggs were embedded in epoxy resin (Historesin Leica®). Sections (3.5–6 μm thick) were stained with haematoxylin-eosin.

The two specimens containing eggs in the pallial groove were collected in June 1921 and August 1955 (austral winter), while the specimen bearing juveniles, with fully developed eight-valved shells, was collected in December 1933 (austral summer). Eggs (Fig. 1F) are packed in compact masses on both sides of the foot (Fig. 1A, B), up to 1600 eggs in one of the specimens (Fig. 1A). Egg hulls are formed of polygonal, perforated plates, about 30 μm in width (Fig. 1D). Micropores (0.2–0.5 μm; Fig. 1D) are randomly distributed over the entire surface of each plate, except for the area near the base of the projections (Fig. 1C). The periphery of the plates is raised, forming rounded, unperforated ridges (Fig. 1C, D). Each plate shows a small subcentral elevation, which is the base of a hollow and elongated projection with a spiral tip, the latter distally enlarged in a small ampoule (Fig. 1C, E–G). These curled projections (numbering approximately 204 per egg hull) interlock with those of other eggs and remain even in developing embryos (Fig. 1H). Seven fully metamorphosed young, of about 6 mm length, were found in one of the studied specimens (Fig. 1I). Our observations suggest that *I. stramineus* eggs (or at least some of them) are retained in the pallial grooves until completely developed.

The most frequent reproductive mode in chitons is the free spawning of gametes followed by indirect development, while

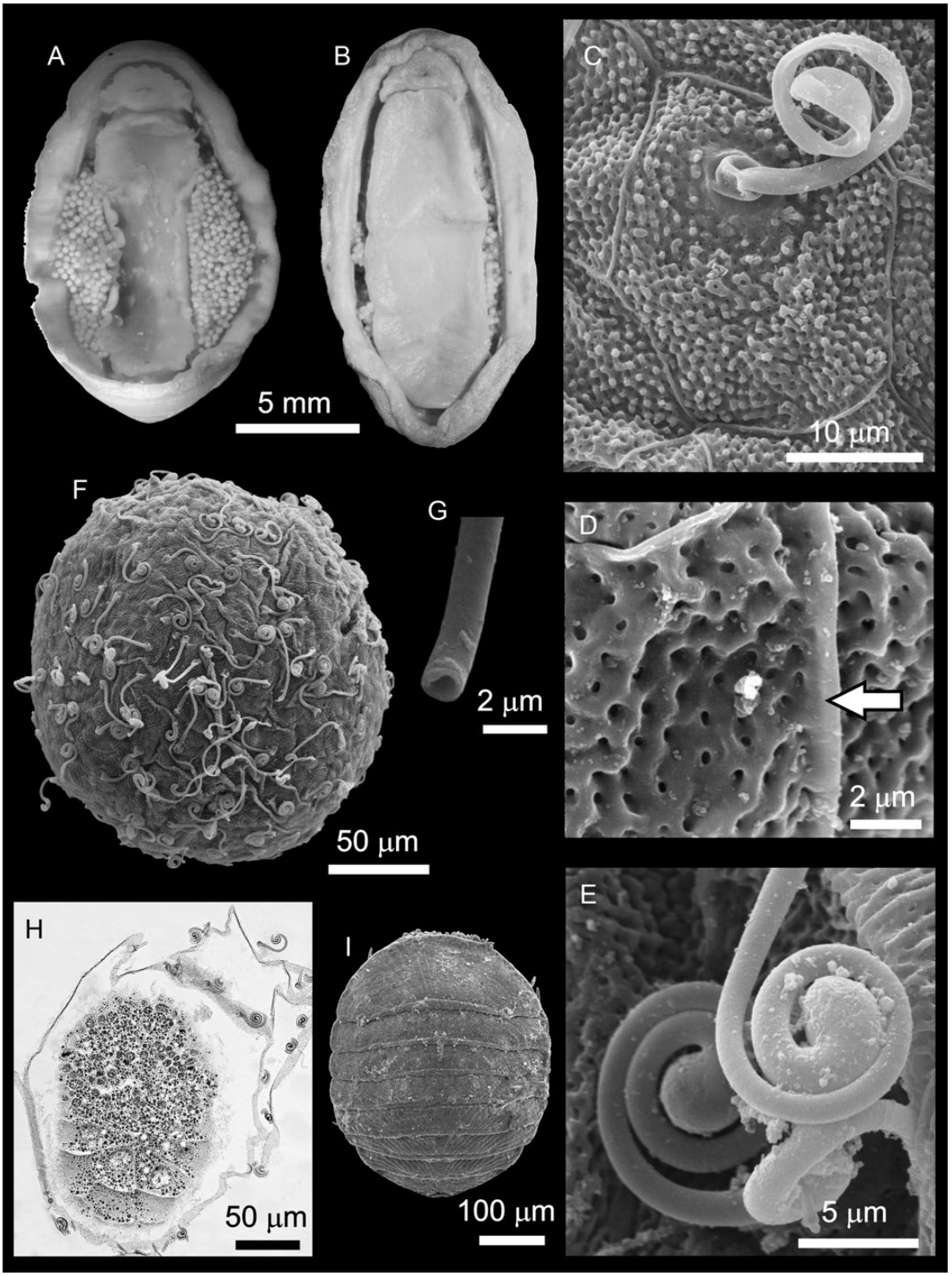

Figure 1. *Ischnochiton stramineus*. **A, C–H**. Specimen from Malvinas/Falkland Islands (MACN–In 30695). **B.** Specimen from Magellan Strait (MACN–In 12483). **I.** Specimen brooded in the pallial groove of the specimen from Isla de los Estados Archipelago (MACN-In 22048). **A, B.** Reflex images. **C–G, I.** SEM images. **H.** Optical microscope image. **A, B.** Ventral view of adult specimens with compact mass of eggs stored in the pallial groove. **C**. Detail of a polygonal egg plate. **D.** Detail of micropores and junction between plates; arrow points to the rounded ridge. **E.** Detail of the spiral egg hull projections. **F.** General view of an egg. **G.** Detail of a hollow broken projection. **H.** Histological section of a developing embryo showing curled egg hulls. **I.** One of the seven juveniles fully metamorphosed.

Table 1. Brooding chiton species and shape of egg-hull processes.

Order	Suborder	Species (alphabetically arranged within suborders)	Brood	Form of egg-hull processes	Source
Lepidopleurida	Lepidopleurina	*Leptochiton kerguelensis*	Eggs and juveniles	Unknown	Sirenko & Schrödl, 2001; Sirenko, 2006b
Lepidopleurida	Lepidopleurina	*Leptochiton algesirensis*	Eggs and juveniles	Unknown	Strack, 1987
Lepidopleurida	Lepidopleurina	*Hanleyella asiatica*	Eggs and juveniles	[Spinose projections with curled tip]	Sirenko, 1973; Sirenko, 1993
Chitonida	Acanthochitonina	*Cyanoplax caboverdensis*	Eggs and embryos**	Unknown	Strack, 1987 (as *Lepidochitona caboverdensis*)
Chitonida	Acanthochitonina	*Cyanoplax caverna*	Eggs and embryos**	Reduced cone-shaped cupules	Heath, 1905 (as *Trachydermon raymondi*); Eernisse, 1988 (as *Lepidochitona caverna*)
Chitonida	Acanthochitonina	*Cyanoplax cinerea*	Eggs and embryos*,**	Elongated cupules / short cupules[1]	Knorre, 1925 (*fide* Pearse, 1979 and Strack, 1987 as *Lepidochitona cinereus*); Matthews, 1956 (*fide* Pearse, 1979 as *L. cinereus*); Durfort *et al.*, 1982 (as *Trachydermon cinereus*); Richter, 1986 (as *L. cinerea*); Sirenko, 1993 (as *L. cinerea*); Okusu *et al.*, 2003 (as *L. cinerea*); Sirenko, 2006a (as *L. cinerea*)
Chitonida	Acanthochitonina	*Cyanoplax corrugata*	Eggs and embryos**	Unknown	Kowalevsky, 1883 (as *Chiton polii*); Strack, 1987 (as *Lepidochitona corrugata*)
Chitonida	Acanthochitonina	*Cyanoplax fernaldi*	Eggs and juveniles	Cupules reduced to flattened hexagonal plates	Eernisse, 1988 (as *Lepidochitona fernaldi*); Buckland-Nicks, 1993 (as *L. fernaldi*); Sirenko, 1993 (as *L. fernaldi*); Buckland-Nicks & Eernisse, 1993 (as *L. fernaldi*); Buckland-Nicks, 2008
Chitonida	Acanthochitonina	*Cyanoplax monterosatoi*	Eggs and embryos**	Unknown	Scuderi, RUSSO & DELL'ANGELO, 2004 (as *Lepidochitona monterosatoi*)
Chitonida	Acanthochitonina	*Cyanoplax stroemfelti*	Eggs and embryos**	Cone and cup-like cupules	Strack, 1987 (as *Lepidochitona stroemfelti*)
Chitonida	Acanthochitonina	*Cyanoplax thomasi*	Eggs and juveniles	Cupules reduced to flattened hexagonal plates	Heath, 1905 (as *Nuttallina thomasi*); Thorpe (in Smith, 1966 as *N. thomasi*); Eernisse, 1988 (as *Lepidochitona thomasi*)
Chitonida	Acanthochitonina	*Hemiarthrum setulosum*	Eggs and juveniles	Unknown	Martens & Pfeffer, 1886; Simpson, 1977
Chitonida	Acanthochitonina	*Placiphorella borealis*	Eggs	[Reduced peripheral skirt-like processes]	Sirenko, 1993
Chitonida	Acanthochitonina	*Plaxiphora australis*	Eggs and juveniles	Unknown	Dell, 1963 (*fide* Creese, 1986 and Murdoch, 1982); Creese (in Strack, 1987)
Chitonida	Acanthochitonina	*Schizoplax brandtii*	Eggs and juveniles	[spinose projections with curled tip distally enlarged in a ampoule]	Kussakin, 1960 (*fide* Smith, 1966); Sirenko, 1993
Chitonida	Chitonina	*Callistochiton asthenes*	Juveniles	Unknown	Smith, 1966 (as *Lepidozona asthenes*); Ferreira, 1979; Lindberg (in Pearse, 1979)
Chitonida	Chitonina	*Callistochiton leei*	Juveniles	Unknown	Ferreira, 1979
Chitonida	Chitonina	*Callochiton crocinus*	Eggs and embryos**	Unknown	Turner, 1978 (as *Paricoplax crocinus*); Hull (in Strack, 1987)
Chitonida	Chitonina	*Chaetopleura pomarium*	Eggs and juveniles	Unknown	Strack, 1987
Chitonida	Chitonina	*Chiton aorangi*	Eggs and juveniles	Unknown	Creese & O'Neill, 1987
Chitonida	Chitonina	*Chiton linsleyi*	Eggs and embryos**	Unknown	Strack, 1987 (as *C. perviridis*)
Chitonida	Chitonina	*Chiton rapaitiensis*	Eggs	[Apparently without projections]	Schwabe & Lozouet, 2006
Chitonida	Chitonina	*Chiton torri*	Eggs and juveniles	Unknown	Bullock (in Pearse, 1979)

Continued

Table 1. *Continued*

Order	Suborder	Species (alphabetically arranged within suborders)	Brood	Form of egg-hull processes	Source
Chitonida	Chitonina	*Eudoxochiton inornatus*	Eggs and embryos**	Unknown	Turner, 1978 (as *Eudoxoplax inornata*)
Chitonida	Chitonina	*Ischnochiton lentiginosus*	Eggs and juveniles	[Spinose projections split into two tips]	Penprase, 1981 (as *I. lentiginosa*); Sirenko, 1993
Chitonida	Chitonina	*Ischnochiton subviridis*	Eggs and juveniles	Unknown	Iredale & Hull, 1923 (as *Heterozona subviridis*); Turner, 1978 (as *H. subviridis*)
Chitonida	Chitonina	*Ischnochiton bergoti*	Eggs and juveniles	Unknown	Dell, 1962 (as *I. constanti*); Dell, 1964 (as *I. constanti*); Strack, 1987
Chitonida	Chitonina	*Ischnochiton circumvallatus*	Eggs	Unknown	Creese, 1986
Chitonida	Chitonina	*Ischnochiton mayi*	Eggs and juveniles	[Reduced auricular-like processes]	Turner, 1978; Cochran, 1986; Sirenko, 1993
Chitonida	Chitonina	*Ischnochiton* cf. *paessleri*	Juveniles	Unknown	Strack, 1987
Chitonida	Chitonina	*Ischnochiton stramineus*	Eggs and juveniles	Spinose projections with spiral tip distally enlarged in an ampoule	Plate, 1898 (as *I. imitator*); Sirenko, 1993 (as *I. inca*); Sirenko, 2006b (as *I. stramineus*); this study
Chitonida	Chitonina	*Ischnochiton virgatus*	Eggs	Unknown	Burn, 1984 (*fide* Cochran, 1986 and Eernisse, 1988)
Chitonida	Chitonina	*Onithochiton neglectus*	Eggs and embryos**	Short, blunt processes	O'Neill, 1984; Creese, 1986
Chitonida	Chitonina	*Radsia barnesii*	Eggs and embryos**	Unknown	Plate, 1898 (as *Chiton barnesi*)
Chitonida	Chitonina	*Radsia nigrovirescens*	Eggs and juveniles	Spinose projections with hooked tip	Thiele, 1910 (as *Ischnochiton nigrovirens*); Dell, 1962 (as *Sypharochiton nigrovirens*); Dell, 1964 (as *S. nigrovirens*); Smith, 1966 (as *S. nigrovirens*); Strack, 1987 (as *Chiton nigrovirescens*); Buckland-Nicks, 2006 (as *C. nigrovirescens*); Buckland-Nicks, 2008; Buckland-Nicks & Brothers, 2008
Chitonida	Chitonina	*Tonicia lebruni*	Eggs and juveniles	Unknown	Sirenko, 2006b; Ituarte & Arellano (in prep.)

Forms of egg-hull processes in brackets denote that they were characterized based on illustrations in the sources. Underlined sources correspond to papers that figured the egg-hull processes.

[1]Some authors have reported elongated egg-hull projections while others have observed short processes. With the exception of species of the genus *Lepidochitona*, which are referred to as *Cyanoplax* following Buckland-Nicks (2008), valid status and synonymies of species are based on the *World Register of Marine Species* (http://www.marinespecies.org/index.php, accessed June 2013).

Annotations: *, rarely broods eggs; **, embryos kept until released as trochophores.

some degree of parental care is another, less common, alternative. At present, the number of known species that brood eggs/juveniles in the pallial groove is 36 (Table 1), *I. stramineus* being one of them (Plate, 1898; Sirenko, 1993; Sirenko, 2006b; this study). Plate (1898) and Sirenko (2006b) found brooding individuals of this species collected between May and July. Based on the absence of brooding specimens in other months of the year, Plate (1898) concluded that brooding only occurs during the winter. The finding of a specimen brooding eggs in August, and another carrying juveniles in December (this study) reveals that the brooding period is longer than previously assumed.

As in other members of the Chitonina, the egg hull of *I. stramineus* is formed by numerous, polygonal, perforated plates, with spinose projections. This condition is similar to that reported for instance in *Radsia nigrovirescens*, *Chaetopleura apiculata*, *C. isabellei*, *Stenosemus albus* and *I. hakodadensis* (Buckland-Nicks, 2008; Buckland-Nicks & Brothers, 2008; Ituarte *et al*., 2010). Within the Ischnochitonidae, species such as *S. exaratus*, *S. golikovi*, *I. acomphus*, *I. comptus*, *I. elongates*, *I. hakodadensis*, *I. interstinctus*, *I. luticolens*, *I. petaloides*, *I. rissoi* and *I. smaragdinus* show the hull projections distally split into two or more tips (Hull & Risbec, 1930; Sirenko, 1993, 2006a), while other species, such as *S. albus* and *Ischnoplax pectinata* (Sowerby) show 'simple' (in the sense of Buckland-Nicks & Brothers, 2008), rounded or tapered spines (Sirenko, 2006a; Buckland-Nicks & Schander, 2008). In this, *I. stramineus* appears similar to the species included in the second group, except for the fact that the projected processes are coiled. This peculiar projection morphology, which broadly agrees with illustrations given by Plate (1898) and Sirenko (1993), may be an adaptation to retain larger numbers of eggs in the pallial grooves. When comparing the shape of egg-hull processes among closely-related species with different mode of development, the reduction of projections, as well as their curled distal tips, has been noted for most brooding chitons (Eernisse, 1988; Sirenko, 1993; Buckland-Nicks, 2008).

ACKNOWLEDGEMENTS

We express our gratitude to C. Ituarte for providing some specific literature, histological support and helpful comments on an earlier version of this manuscript; to J. López Gappa for language suggestions that helped us to improve this manuscript and to A. Tablado for allowing the study of the specimens housed at the collection of the Museo Argentino de Ciencias Naturales. We also thank two anonymous referees for their valuable comments.

REFERENCES

BUCKLAND-NICKS, J. 1993. Hull cupules of chiton eggs: parachute structures and sperm focusing devices?. *Biological Bulletin*, **184**: 269–276.

BUCKLAND-NICKS, J. 2006. Fertilization in chitons: morphological clues to phylogeny. *Venus*, **51**: 51–70.

BUCKLAND-NICKS, J. 2008. Fertilization biology and the evolution of chitons. *American Malacological Bulletin*, **25**: 97–111.

BUCKLAND-NICKS, J. & BROTHERS, E. 2008. On fertilization in *Chaetopleura apiculata* and selected Chitonida. *Biological Bulletin*, **214**: 184–193.

BUCKLAND-NICKS, J. & EERNISSE, D.J. 1993. Ultrastructure of mature sperm and eggs of the brooding hermaphroditic chiton, *Lepidochitona fernaldi* Eernisse 1986, with special reference to the mechanism of fertilization. *Journal of Experimental Zoology*, **265**: 567–574.

BUCKLAND-NICKS, J. & REUNOV, A. 2009. Ultrastructure of hull formation during oogenesis in *Rhyssoplax tulipa* (=*Chiton tulipa*) (Chitonidae: Chitoninae). *Invertebrate Reproduction and Development*, **53**: 165–174.

BUCKLAND-NICKS, J. & SCHANDER, C. 2008. Fertilization in the white chiton, *Stenosemus albus*, with implications for its phylogenetic position. *Canadian Journal of Zoology*, **86**: 1024–1030.

BURN, R. 1984. Brooding in *Ischnochiton v*irgatus. Malacological Society of Australasia. *Victoria Branch Bulletin*, **114**: 3.

COCHRAN, T.G. 1986. Brooding in southern Australia's chitons. *Hawaiian Shell News*, **35**: 5.

CREESE, R.G. 1986. Brooding behaviour and larval development in the New Zealand chiton, *Onithochiton neglectus* de Rochebrune (Mollusca: Polyplacophora). *New Zealand Journal of Zoology*, **13**: 83–91.

CREESE, R.G. & O'NEILL, M.H.B. 1987. *Chiton aorangi* n. sp., a brooding chiton (Mollusca: Polyplacophora) from northern New Zealand. *New Zealand Journal of Zoology*, **14**: 89–93.

DELL, R.K. 1962. Stages in the development of viviparity in the Amphineura. *Nature*, **195**: 512–513.

DELL, R.K. 1963. The littoral marine Mollusca of the Snares Islands. *Records of the Dominion Museum*, **4**: 221–229.

DELL, R.K. 1964. Antarctic and subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. *Discovery Reports*, **33**: 93–250.

DURFORT, M., BARGALLÓ, B., BOZZO, M.G., FONTARNAU, R. & LóPEZ-CAMPS, J. 1982. Relationship between follicular cells and oocytes of *Trachydermon cinereus* Thiele (Mollusca, Polyplacophora). *Malacologia*, **22**: 211–217.

EERNISSE, D.J. 1988. Reproductive patterns in six species of *Lepidochitona* (Mollusca: Polyplacophora) from the Pacific Coast of North America. *Biological Bulletin*, **174**: 287–302.

FERREIRA, A.J. 1979. The genus *Callistochiton* Dall, 1879 (Mollusca: Polyplacophora) in the Eastern Pacific, with the description of a new species. *Veliger*, **21**: 444–465.

HEATH, H. 1905. The breeding habits of chitons of the Californian coast. *Zoologischer Anzeiger*, **29**: 390–393.

HODGSON, A.N., BAXTER, J.M., STURROCK, M.G. & BERNARD, R.T.F. 1988. Comparative spermatology of 11 species of Polyplacophora (Mollusca) from the suborders Lepidopleurina, Chitonina and Acanthochitonina. *Proceedings of the Royal Society of London, Biological Series*, **235**: 161–177.

HULL, A.F.B. & RISBEC, J. 1930. The loricates of the New Caledonian region (class Mollusca – order Loricata). *Australian Zoologist*, **6**: 277–286.

IREDALE, T. & HULL, A.F.B. 1923. A monograph of the Australian Loricates (phylum Mollusca: order Loricata). Vol 1. Systematics and Structure. *Australian Zoologist*, **3**: 186–194.

ITUARTE, C., LIUZZI, M.G. & CENTURIÓN, R. 2010. Egg hull morphology in two chitons (Polyplacophora) from the Southwestern Atlantic Ocean. *Malacologia*, **53**: 167–174.

KAAS, P. & VAN BELLE, R.A. 1990. Monograph of living chitons (Mollusca: Polyplacophora). *Vol. 4*, Suborder Ischnochitonina: Ischnochitonidae: Ischnochitoninae (continued), Additions to vols. 1, 2 and 3. E.J. Brill, Leiden.

KNORRE, H. VON 1925. Die Schale und die Rückensinnesorgane von *Trachydermon (Chiton) cinereus* L. und die ceylonischen Chitonen der Sammlung Plate. *Jenaische Zeitschrift für Naturwissenschaft herausgegeben von der medizinisch-naturwissenschaftlicken Gessellschaft zu Jena*, **61**: 469–632.

KOWALEVSKY, M.A. 1883. Embryogénie du *Chiton polii* (Philippi) avec quelques remarques sur le développement des autres chitons. *Annales du Musée D'Histoire Naturelle de Marseille, Zoologie*, **1**: 1–46.

KUSSAKIN, O.G. 1960. Biological peculiarities of the Far Eastern mollusk *Schizoplax brandtii* (Middendorff). *Zoological Journal of the Academy of Natural History of the U.S.S.R.*, **39**: 1145–1150.

MARTENS, E. VON & PFEFFER, G. 1886. Die Mollusken von Süd-Georgien nach der Ausbeute der Deutschen Station 1882–83. *Jahrbuch der Hamburgischen wissenschaftlichen Anstalten*, **3**: 63–135.

MATTHEWS, F.G.C. 1956. *The breeding behavior, embryology and larval ecology of* Lepidochitona cinereus *(L.)*. PhD thesis, University of London.

MURDOCH, R.C. 1982. A new species of *Plaxiphora* (Mollusca: Polyplacophora) from southern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **16**: 175–178.

OKUSU, A., SCHWABE, E., EERNISSE, D.J. & GIRIBET, G. 2003. Towards a phylogeny of chitons (Mollusca, Polyplacophora) based on combined analysis of five molecular loci. *Organisms, Diversity & Evolution*, **3**: 281–302.

O'NEILL, M.H.B. 1984. Morphological changes in *Onithochiton neglectus* Rochebrune, 1881 (Mollusca: Chitonidae), and their taxonomic significance. *New Zealand Journal of Zoology*, **11**: 43–48.

PASHCHENKO, S.V. & DROZDOV, A.L. 1998. Morphology of gametes in five species of far-eastern chitons. *Invertebrate Reproduction and Development*, **33**: 47–56.

PEARSE, J.S. 1979. Polyplacophora. In: *Reproduction of marine invertebrates*, Vol. 5 (A.C. Giese & J.S. Pearse, eds), pp. 27–85. Academic Press, London.

PENPRASE, J.R. 1987. Brooding of *Ischnochiton (Haploplax) lentiginosa* (Sowerby, 1840) in New South Wales. *Journal of the Malacological Society of Australia*, **5**: 65–66.

PLATE, L.H. 1898. Die Anatomie und Phylogenie der Chitonen. *Zoologische Jahrbücher. Fauna Chilensis*, 2(Suppl 5), pp. 15–216.

RICHTER, H.P. 1986. Ultrastructure of follicular epithelia in the ovary of *Lepidochitona cinerea* (L.) (Mollusca: Polyplacophora). *Development Growth and Differentiation*, **28**: 7–16.

SCHWABE, E. & LOZOUET, P. 2006. Chitons (Mollusca, Polyplacophora) from Rapa, the southernmost island of Polynesia. *Zoosystema*, **28**: 617–633.

SCUDERI, D., RUSSO, G.F. & DELL'ANGELO, B. 2004. Polyplacophora taxocoene of Ognina and Acitrezza (bay of Catania, Sicily), with some notes on early development of *Lepidochitona monterosatoi* Kaas & Van Belle, 1981. *Bollettino Malacologico, Roma*, **5**: 105–110.

SIMPSON, R.D. 1977. The reproduction of some littoral molluscs from Macquarie Island (Sub-Antarctic). *Marine Biology*, **44**: 125–142.

SIRENKO, B.I. 1973. A new genus of the family Lepidopleuridae (Neoloricata). *Zoologicheskii Zhurnal*, **52**: 1569–1571.

SIRENKO, B.I. 1993. Revision of the system of the order Chitonida (Mollusca: Polyplacophora) on the basis of correlation between the type of gills arrangement and the shape of the chorion processes. *Ruthenica*, **3**: 93–117.

SIRENKO, B.I. 2006a. New outlook on the system of chitons (Mollusca: Polyplacophora). *Venus*, **65**: 27–49.

SIRENKO, B.I. 2006b. Report on the present state of our knowledge with regard to the chitons (Mollusca: Polyplacophora) of the Magellan Strait and Falkland Islands. *Venus*, **65**: 81–89.

SIRENKO, B.I. & SCHRÖDL, M. 2001. Mollusc biodiversity and ecology. *Berichte zur Polar – und Meeresforschung*, **402**: 85–95.

SMITH, A.G. 1966. The larval development of chitons (Amphineura). *Proceedings of the California Academy of Sciences*, **32**: 433–446.

SOWERBY, G.B. 1832. [Characters of new shells from the collection formed by Mr. Cuming]. Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II, 104–105.

STRACK, H.L. 1987. The Polyplacophora of Gran Canaria, including a worldwide survey of the brooding species. *Iberus*, **7**: 179–187.

THIELE, J. 1910. Polyplacophora, Gastropoda marina, Bivalvia. In: Zoologische und Anthropologische Ergebnisse einer Forschungsreise im Westlichen und Zentralen Südafrika ausgeführt in den Jahren 1903–1905. *Vol. 4*. Systematik und Tiergeographie. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena*. (L. Schultze, ed.), pp. 269–270.

TURNER, E. 1978. Brooding of chitons in Tasmania. *Journal of the Malacological Society of Australia*, **4**: 43–47.