Zootaxa 3841 (4): 573–591
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3841.4.7
http://zoobank.org/urn:lsid:zoobank.org:pub:B07019EC-366E-4388-B744-88F6584E7F7D

The Antarctic holothurian genus *Echinopsolus* Gutt, 1990 (Dendrochirotida, Cucumariidae): brood pouches, spermatozoa, spermatozeugmata and taxonomic implications

JENS MICHAEL BOHN[1] & MARTIN HEß[2]

[1]*Bavarian State Collection of Zoology, Münchhausenstraße 21, D-81247 München, Germany. E-mail: jens.m.bohn@gmail.com*
[2]*Department Biologie II, Ludwig Maximilians-Universität München, Großhaderner Straße 2, D-82152 Planegg-Martinsried, Germany. E-mail: hess@bio.lmu.de*

Abstract

An examination of seven Antarctic brooding cucumariid and psolid holothurian species revealed a variety of characters all of them have in common: (1) All are gonochoric. (2) A genital papilla is present on the oral disc (permanent and digitiform in males). (3) Females brood their offspring in five anterior interradial brood pouches that are situated at the transition of body to introvert. (4) Multiple spermatozoa are always bundled to bunch-like spermato-zeugmata. (5) The spermatozoa have a fusiform head and a hollow cylinder-like mid-piece encircling the anterior end of the flagellum. This combination of characters so far is unique, and indicates a close relationship based on common origin. As a consequence, we unite all species sharing this set of synapomorphies in the genus *Echinopsolus* Gutt, 1990. The herewith included species are: *E. acanthocola* Gutt, 1990, *E. acutus* (Massin, 1992) comb. nov., *E. charcoti* (Vaney, 1906) comb. nov., *E. koehleri* (Vaney, 1914) comb. nov., *E. mollis* (Ludwig & Heding, 1935) comb. nov., *E. parvipes* Massin, 1992 and *E. splendidus* (Gutt, 1990) comb. nov.. Because the current assignment of *Echinopsolus* to the family Psolidae can not be retained, the genus is tranferred to the family Cucumariidae, as relationships to taxa within this family are obvious. The peculiar spermatozoa and spermato-zeugmata of all *Echinopsolus* species are described using light- and electron-microscopical techniques and the results are evaluated and discussed concerning their taxonomy and phylogeny.

Key words: Echinodermata, Antarctic radiation, sperm ultrastructure, Southern Ocean

Introduction

A considerable number of holothurian species of the dendrochirotid families Cucumariidae Ludwig, 1894 and Psolidae Burmeister, 1837 are known to protect their brood. Recent summaries list about 40 cucumariid (O'Loughlin 1994; O'Loughlin *et al.* 2009) and 11 psolid species (McEuen & Chia 1991). Various modes of brood-protection have been realized in both families (see McEuen & Chia 1991: tab. 2; O'Loughlin 1994: tab. 1): offspring may be brooded externally (e.g. held between tentacles; kept on substrate beneath ventral body, sometimes in folds or depressions), or internally (in variously shaped brood pouches, i.e. pocket-like inversions of the body wall with an opening to the exterior; in ovaries; in coelomic cavity or in coelomic brood sacs).

Interradial anterior brood pouches, situated at the transition of body to introvert, so far are only known from a variety of Antarctic Cucumariidae and Psolidae (Tab. 1). The number of brood pouches seems to be variable. The majority of species have five pouches, one in each interradius, while two cucumariid species possess two pouches and one species has three (see Tab. 1). Remarkable in this context is the common presence of a genital papilla on the oral disc, between or ventral to the mid-dorsal pair of tentacles (Tab. 1). Details for a variety of species are given by O'Loughlin (2001) and O'Loughlin *et al*. (2009). According to O'Loughlin *et al*. (2009: p. 217), these species have in common, that "males have a long genital papilla between the dorsal tentacle pair (...), and do not have marsupia; females have a short genital papilla between the dorsal tentacle pair (...), and have up to five anterior interradial marsupia with external pores.". Also the fact, that all species sharing this set of characters so far are restricted to Antarctica, was first stressed by these authors (O'Loughlin *et al.* 2009).

Accepted by M. Eleaume: 25 Jun. 2014; published: 29 Jul. 2014

would allow the inclusion of this monophyletic Antarctic clade without getting para- or even polyphyletic, except for *Microchoerus* and *Echinopsolus*. Both were established by Gutt (1990) for new Antarctic dendrochirote holothurians which are included in the current study. Due to the fact, that *Microchoerus* Gutt, 1990 is an unavailable name—it is a junior homonym of *Microchoerus* Wood, 1844, which was established by Wood (1844) for the extinct primate *Microchoerus erinaceus* Wood, 1844—all species dealt with are assigned to the genus *Echinopsolus*.

The morphological diversity in mind, it is obvious, that the current assignment of *Echinopsolus* to the family Psolidae can not be retained. This family is characterised by a test of imbricating and often macroscopic dorsal plates, the (usual) presence of a well defined ventral sole and a dorsally turned mouth and anus (e.g. Pawson & Fell 1965; Pawson 1982). On the other hand, relationships to taxa within the Cucumariidae are very likely and therefore *Echinopsolus* is transferred to this family. Characteristic for Cucumariidae are a simple calcareous ring without posterior processes, small inconspicuous calcareous deposits and tube feet often restricted to the radii, either scattered or arranged in regular rows (e.g. Pawson & Fell 1965; Pawson 1982). *Echinopsolus* species like *E. acutus* and *E. mollis* agree very well with this diagnosis and display at least some of the characters, which may be plesiomorphic for this genus. Most probably, plesiomorphic features are cylindrical tube feet restricted to the radii, in few radial rows on the ventral side and more irregularly scattered on the dorsal side and scattered simple perforated plates in the body wall. Conical tube feet, a loss of dorsal tube feet and a restriction of tube feet to a ventral sole along with a reduction of the mid-ventral tube feet to the anterior and posterior end of the sole are probably derived characters. This is also true for calcareous deposits of the body wall which are thickened or multi-layered and test-like arranged.

So far, these ideas have not been tested in any phylogenetic analysis and thus are somewhat speculative. Recently, O'Loughlin *et al.* (2011) were able to demonstrate in their molecular study on antarctic holothurian diversity a close relationship of *Echinopsolus koehleri* and *E. charcoti,* an obvious radiation of species belonging to the "*Cucumaria georgiana*" group, and possible cryptic species closely related to *E. mollis.* These results do not contradict our conclusions about a probable radiation of the species investigated here, subsumed within the genus *Echinopsolus*. Hopefully further investigations will provide sufficient data, preferably on morphological as well as on molecular level, to allow a clarification of the phylogenetic history of this highly interesting case of an Antarctic radiation of a rather diverse and speciose holothurian group.

Acknowledgements

First of all, we want to thank Prof. Dr. Wolf Arntz (AWI) for providing the great opportunity to participate in the EASIZ III and LAMPOS expeditions, and we are also very grateful to the crew of FS "Polarstern" and all participants of the expeditions for their fruitful cooperation aboard. Furthermore, we are indebted to Heidemarie Gensler for her invaluable technical assistance.

References

Atwood, D.G. (1975) Fine structure of an elongated dorso-ventrally compressed echinoderm (Holothuroidea) spermatozoon. *Journal of Morphology*, 145, 189–208.
http://dx.doi.org/10.1002/jmor.1051450206

Atwood, D.G. & Chia, F.-S. (1974) Fine structure of an unusual spermatozoon of a brooding sea cucumber, *Cucumaria lubrica*. *Canadian Journal of Zoology*, 52, 519–523.
http://dx.doi.org/10.1139/z74-064

Bohn, J.M. (2007) *Pseudrotasfer microincubator* gen. et spec. nov., a brooding cucumariid holothurian (Echinodermata: Holothuroidea: Dendrochirotida) from the Burdwood Bank (south-western Atlantic Ocean). *Zootaxa*, 1662, 61–68.

Cherbonnier, G. (1949) Primera expedicion antarctica Chilena: Une nouvelle holothurie incubatrice de l'antarctique chilien: *Cucumaria Vaneyi* n. sp. *Revista de Biología Marina*, 1, 229–232.

Chia, F.-S., Atwood, D.G. & Crawford, B. (1975) Comparative morphology of echinoderm sperm and possible phylogenetic implications. *American Zoologist*, 15, 553–565.
http://dx.doi.org/10.1093/icb/15.3.553

Clarke, A., Griffiths, H.J., Linse, K., Barnes, D.K.A. & Crame, J.A. (2007) How well do we know the Antarctic marine fauna?

A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs. *Diversity and Distributions*, 13, 620–632.
http://dx.doi.org/10.1111/j.1472-4642.2007.00380.x

Clarke, A. & Johnston, N.M. (2003) Antarctic marine benthic diversity. *Oceanography and Marine Biology: an Annual Review*, 41, 47–114.

Crame, J.A. (1999) An evolutionary perspective on marine faunal connections between southernmost South America and Antarctica. *In*: Arntz, W.E. & Ríos, C. (Eds.), *Maggelan-Antarctic: Ecosystems that drifted apart. Scientia Marina*, 63, pp. 1–14.

Ekman, S. (1925) Holothurien. *In*: Odhner, T. (Ed.), *Further Zoological Results of the Swedish Antarctic Expedition 1901-1903. Under the Direction of Dr. Otto Nordenskjöld. Vol. 1*. P.A. Norstedt & Söner, Stockholm, Sweden, pp. 1–194.

Engstrom, N.A. (1982) Brooding behavior and reproductive biology of a subtidal Puget Sound sea cucumber, *Cucumaria lubrica* (Clark, 1901) (Echinodermata: Holothuroidea). *In*: Lawrence, J.M. (Ed.), *Echinoderms: Proceedings of the International Conference, Tampa Bay, September 14-17, 1981.*, 447–450.

Gutt, J. (1988) Zur Verbreitung und Ökologie der Seegurken (Holothuroidea, Echinodermata) im Weddellmeer (Antarktis). *Reports on Polar Research*, 41, 1–87.

Gutt, J. (1990) New Antarctic holothurians (Echinodermata)—I. Five new species with four new genera of the order Dendrochirotida. *Zoologica Scripta*, 19, 101–117.
http://dx.doi.org/10.1111/j.1463-6409.1990.tb00243.x

Gutt, J. (1991) Are Weddell Sea holothurians typical representatives of the Antarctic benthos? *Meeresforschung*, 33, 312–329.

Hadley, A. (2008) CombineZM, image stacking software. Available from: http://www.hadleyweb.pwp.blueyonder.co.uk/CZM/combinezm.htm (accessed 18 April 2008)

Hodgson, A.N. & Bernard, R.T.F. (1992) Spermatozoon structure of eight species of South African holothurians (Echinodermata). *Journal of Morphology*, 211, 179–186.
http://dx.doi.org/10.1002/jmor.1052110206

Jamieson, B.G.M. (1985) The spermatozoa of the Holothuroidea (Echinodermata): an ultrastructural review with data on two Australian species and phylogenetic discussion. *Zoologica Scripta*, 14, 123–135.
http://dx.doi.org/10.1111/j.1463-6409.1985.tb00183.x

Jörger, K.M., Heß, M., Neusser, T.P. & Schrödl, M. (2009) Sex in the beach—spermatophores, dermal insemination, and 3D sperm ultrastructure of the aphallic, acochlid *Pontohedyle milaschewitchii* (Acochlidia, Opistobranchia, Gastropoda). *Marine Biology*, 156, 1159–1170.
http://dx.doi.org/10.1007/s00227-009-1158-5

Lampert, K. (1886) Die Holothurien von Süd-Georgien, nach der Ausbeute der deutschen Polarstation in 1882 und 1883. *Jahrbuch der wissenschaftlichen Anstalten zu Hamburg*, 3, 11–21.

Ludwig, H. & Heding, S.G. (1935) Die Holothurien der deutschen Tiefsee-Expedition. I. Fußlose und dendrochirote Formen. *In*: Chun, C., Brauer, A., Vanhöffen, E. & Apstein, C. (Eds.), *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899*. *Vol. 24*. Verlag von Gustav Fischer, Jena, Germany, pp. 123–214.

Massin, C. (1992) Three new species of Dendrochirotida (Holothuroidea, Echinodermata) from the Weddell Sea (Antarctica). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, 62, 179–191.

Massin, C. (2010) On a small collection of Antarctic sea cucumbers (Echinodermata; Holothuroidea) from Léopold III Bay and vicinity. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, 80, 261–275.

McClintock, J.B., Slattery, M., Gaschen, B. & Heine, J. (1994) Reproductive mode and population characteristics of the antarctic sea cucumber *Cucumaria ferrari*. *In*: David, B., Guille, A., Féral, J.-P. & Roux, M. (Eds.), *Echinoderms through time*, 530.

McEuen, F.S. (1988) Spawning behaviors of northeast Pacific sea cucumbers (Holothuroidea: Echinodermata). *Marine Biology*, 98, 565–585.
http://dx.doi.org/10.1007/bf00391548

McEuen, F.S. & Chia, F.-S. (1991) Development and metamorphosis of two psolid sea cucumbers, *Psolus chitonoides* and *Psolidium bullatum*, with a review of reproductive patterns in the family Psolidae (Holothuroidea: Echinodermata). *Marine Biology*, 109, 267–279.
http://dx.doi.org/10.1007/bf01319395

Neusser, T.P., Heß, M., Haszprunar, G. & Schrödl, M. (2007) Sperm ultrastructure of *Microhedyle remanei*, an interstitial acochlidian gastropod with dermal fertilization. *Journal of the Marine Biological Association of the UK*, 87, 747–754.
http://dx.doi.org/10.1017/s0025315407055750

O'Loughlin, P.M. (1994) Brood-protection and fissiparous cucumariids (Echinodermata, Holothurioidea). *In*: David, B., Guille, A., Féral, J.-P. & Roux, M. (Eds.), *Echinoderms through time. Proceedings of the Eighth International Echinoderm Conference, Dijon, France, September 6-10, 1993*, 539–547.

O'Loughlin, P.M. (2001) The occourrence and role of a digitate genital papilla in holothurian reproduction. *In*: Barker, M. (Ed.), *Echinoderms 2000. Proceedings of the 10th International Echinoderm Conference, Dunedin, 31 January - 4 February 2000*, 363–368.

O'Loughlin, P.M., Eichler, J., Altoff, L., Mackenzie, M., Whitfield, E. & Rowley, C. (2009) Observations of reproductive strategies for some dendrochirotid holothuroids (Echinodermata: Holothuroidea: Dendrochirotida). *Memoirs of Museum*

Victoria, 66, 215–220.
O'Loughlin, P.M., Paulay, G., Davey, N. & Michonneau, F. (2011) The Antarctic Region as a marine biodiversity hotspot for echinoderms: Diversity and diversification of sea cucumbers. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 58, 264–275.
http://dx.doi.org/10.1016/j.dsr2.2010.10.011
Pawson, D.L. (1982) Holothuroidea. *In*: Parker, S.P. (Ed.), *Synopsis and classification of living organisms*. *Vol. 2*. McGraw-Hill Book Company, New York, USA, pp. 813–818.
Pawson, D.L. & Fell, H.B. (1965) A revised classification of the dendrochirote holothurians. *Breviora*, 214, 1–7.
Richardson, K.C., Jarett, L. & Finke, E.H. (1960) Embedding in epoxy resins for ultrathin sectioning in electron microscopy. *Stain Technology*, 35, 313–323.
http://dx.doi.org/10.3109/10520296009114754
Ridder, C. De, David, B., Hétérier, V. & Massin, C. (2005) A new case of brooding in an Antarctic holothuroid. *Evolution and Biodiversity in Antarctica. Abstract book.*, 127.
Tyurin, S.A. & Drozdov, A.L. (2003) Spermatozoa ultrastructure of five sea cucumber species (Holothuroidea, Echinodermata). *Zoologicheskii Zhurnal*, 82, 382–387.
Vaney, M.C. (1906a) Note préliminaire sur les holothuries recueillies par l'Expédition Antarctique Française du Dr Charcot. *Bulletin du Muséum d'Histoire naturelle, Paris*, 12, 402–407.
Vaney, M.C. (1906b) Holothuries. *In*: Joubin, L. (Ed.), *Expédition Antarctique Française (1903-1905) commandée par le Dr Jean Charcot. Sciences Naturelles: Documents Scientifique*. Masson et Cie, Paris, France, pp. 1–30.
Vaney, M.C. (1908) XVIII.—Les Holothuries de l'Expédition Antarctique Nationale Écossaise. *Transactions of the Royal Society of Edinburgh*, 46, 405–441.
http://dx.doi.org/10.1017/s0080456800002829
Vaney, M.C. (1914) Holothuries. *In*: Joubin, L. (Ed.), *Deuxième Expédition Antarctique Française (1908-1910) commandée par le Dr Jean Charcot. Sciences Naturelles: Documents Scientifique*. Masson et Cie, Paris, France, pp. 1–54.
Vaney, M.C. (1925) L'incubation chez les holothuries. *Travaux de la Station Zoologique de Wimereux*, 9, 254–274.
Wood, S.V. (1844) Record of the discovery of an *Alligator* with several new Mammalia in the freshwater strata at Hordwell. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology*, 14, 349–351.
http://dx.doi.org/10.1080/037454809495192