Beiträge zur Taxonomie und Biogeographie von Holothurien und Crinoiden (Echinodermata) der Südhemisphäre

Dissertation zur Erlangung des Doktorgrades der Fakultät für Biologie der Ludwig-Maximilians-Universität München

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Artikel

1. Altnöder, A., Bohn, J.M., Rückert, I. & Schwabe, E. (2007) The presumed shelled juvenile of the parasitic gastropod Entocolax schiemenzii Voigt, 1901 and its holothurian host Chiridota pisanii Ludwig, 1886 (Gastropoda, Entoconchidae - Holothuroidea, Chiridotidae). Spixiana, 30, 187–199.
2. Bohn, J.M. (2005) On two rare abyssal Myriotrochidae (Echinodermata: Holothuroidea: Apodida) new to the South Atlantic: Siniotrochus myriodontus Gage and Billett, 1986 and Neolepidotrochus parvidiscus angolensis subsp. nov.. Organisms, Diversity and Evolution, 5, 231–238.
3. Bohn, J.M. (2005) Myriotrochus (Oligotrochus) meteorensis spec. nov., a new myriotrochid holothurian from the deep-sea off NW Africa (Echinodermata: Holothuroidea: Myriotrochidae). Zootaxa, 1078, 33–40.
4. Bohn, J.M. (2006) The Crinoidea and Holothuroidea (Echinodermata) of the abyssal Angola Basin—Results of the DIVA-1 expedition of FS "Meteor" (Cruise M48/1). Zootaxa, 1276, 1–31.

Zusammenfassung

Bisher kaum untersuchte Tief- und Flachwasserbereiche des südlichen Atlantiks und des Südlichen Ozeans wurden im Verlauf der letzten Jahre von einer Reihe deutscher Expeditionen (EASIZ, DIVA I, LAMPOS, ANDEEP) mit verschiedenen Geräten systematisch beprobt. In diesem Rahmen wurde auch eine große Anzahl an Holothurien und einige Crinoiden gesammelt. Das Ziel dieser Dissertation ist die taxonomische Bearbeitung eines Teils dieses reichhaltigen Materials. Insgesamt 19 Holothurien und ein Crinoide werden dargestellt. Vier der Holothurien – *Myriotrochus* (*Oligotrochus*) *meteorensis* Bohn, 2005, *Pseudrotasfer microincubator* Bohn, 2007, *Neolepidotrochus parvidiscus angolensis* Bohn, 2005 und *Achlyonice longicornis* Bohn, 2006 – sind für die Wissenschaft neu und werden ausführlich beschrieben.

Ein Zentrales Thema dieser Arbeit stellen die im Verlauf der DIVA I Expedition im abyssalen Angola-Becken gesammelten Holothuroidea und Crinoidea dar. Zusammen neun Holothurien (inklusive *N. p. angolensis* und *A. longicornis*) und ein Crinoide werden beschrieben und ihre Verbreitung dargestellt. Darauf aufbauend wird eine Liste aller aus dem bathyalen und abyssalen Angola-Becken bekannten Arten dieser beiden Gruppen erstellt, anhand der dann die biogeographischen Beziehungen der Holothurien- und Crinoidenfauna dieses Beckens zu den entsprechenden Faunen der Nachbarbecken dargestellt und diskutiert wird.

Ein weiteres Thema dieser Dissertation beschäftigt sich mit einer Gruppe von sieben Arten antarktischer dendrochiroter Holothurien, die in einer ganzen Reihe von Merkmalen übereinstimmen: (1) Arten getrenntgeschlechtlich. (2) Sexualdimorphismus, Genitalpapille bei Männchen permanent fingerförmig, bei den Weibchen oft klein und unscheinbar. (3) Weibchen mit fünf interradialen anterioren Bruttaschen. (4) Charakteristische Spermatozoa. (5) Spermatozoa zu Spermatozeugmata gebündelt. Diese Merkmalskombination ist bisher einzigartig und spricht für einen monophyletischen Ursprung der Arten. Um diese Erkenntniss auch in der Taxonomie wiederzuspiegeln, werden die sieben Arten in der Gattung *Echinopsolus* Gutt, 1990 vereinigt. Die Spermatozoa und die Spermatozeugmata der sieben Arten werden mit licht- und elektronenmikroskopischen Methoden dargestellt und die Ergebnisse in Bezug auf Konsequenzen für die Taxonomie und Phylogenie dieser Gruppe diskutiert.

Abstract

A variety of German expeditions (EASIZ, DIVA I, LAMPOS, ANDEEP) sampled almost unexplored shallow-water and deep-sea areas of the South Atlantic and the Southern Ocean using different gear. In this context, a rich variety of holothurians and few crinoids were collected. To investigate the taxonomy of some of these holothurians and crinoids is the aim of this thesis. Altogether, one crinoid and 19 holothurian species are treated, four of which are new to science—*Myriotrochus* (*Oligotrochus*) *meteorensis* Bohn, 2005, *Pseudrotasfer microincubator* Bohn, 2007, *Neolepidotrochus parvidiscus angolensis* Bohn, 2005 and *Achlyonice longicornis* Bohn, 2006.

An important aim of this study is to investigate the taxonomy and zoogeography of the holothurians and crinoids sampled in the course of the DIVA I expedition to the Angola Basin. A single crinoid and nine holothurian species (including *N. p. angolensis* and *A. longicornis*), are described and their known distribution is summarized. Finally, a list of all hitherto known Holothuroidea and Crinoidea of the deeper Angola Basin is compiled, to evaluate and discuss possible zoogeographic relationships of its holothurian and crinoid fauna to faunas of deep--sea regions near by.

A further topic of this thesis is the taxonomy of a group of seven Antarctic dendrochirote holothurians, which share a variety of characteristics: (1) All gonochoric. (2) Sexual dimorphism, males with permanent digitiform genital papilla, females with inconspicuous small papilla. (3) Females brood offspring in five anterior interradial brood pouches. (4) Characteristic spermatozoa. (5) Multiple spermatozoa bundled to bunch-like spermatozeugmata. This combination of characters so far is unique, and indicates a close relationship based on common origin. As a consequence, all species sharing this set of synapomorphies are united in the genus *Echinopsolus* Gutt, 1990. The peculiar spermatozoa and spermatozeugmata of all *Echinopsolus* species are described using light- and electron-microscopical techniques and the results are evaluated and discussed concerning their taxonomy and phylogeny.

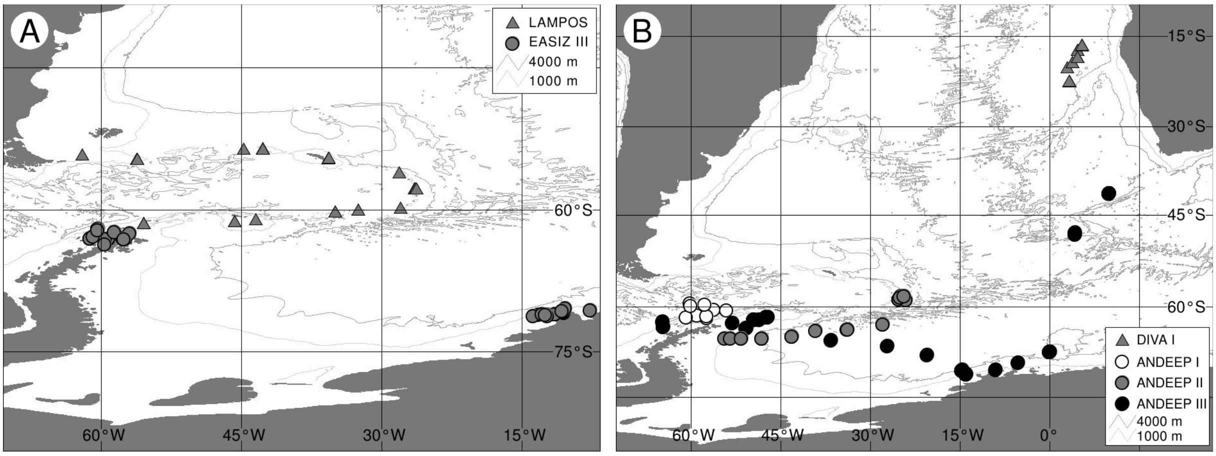

Abb. 1. Stationen an denen Holothuroidea auf verschiedenen Expeditionen in den südöstlichen Atlantik und den Südlichen Ozean gesammelt wurden. **A.** EASIZ III und LAMPOS Expedition mit FS "Polarstern". **B.** DIVA I Expedition mit FS „Meteor" und ANDEEP Expeditionen mit FS „Polarstern".

Einleitung

Holothuroidea[1], auch Seegurken oder Seewalzen genannt, gehören zu den Echinodermata (Stachelhäuter). Man kennt heute, je nach Autor, zwischen 1200 und 1400 Arten, die sich auf sechs Ordnungen, 25 Familien und etwa 200 Gattungen verteilen (Pawson 1982, Madsen & Hansen 1994, Rowe & Gates 1995).

Ihr Vorkommen ist rein marin und nur wenige Arten tolerieren einen geringeren Salzgehalt als für Meerwasser üblich (Madsen & Hansen 1994). Verbreitet sind sie weltweit und besiedeln dabei nahezu alle Bereiche, von der Gezeitenzone bis in hadale Tiefen (Pawson 1982). Beinahe alle Arten leben benthisch, entweder auf dem Substrat, oder in das Substrat eingegraben, nur die Arten der Familie Pelagothuriidae Ludwig, 1894 sind pelagisch und schwimmen (Miller & Pawson 1990, Billett 1991).

Nach der Art des Nahrungserwerbs unterscheidet man bei Holothurien Suspensions- und Substratfresser (Massin 1982), die verschieden gestaltete Tentakel besitzen. So lassen sich eine Reihe von Tentakeltypen unterscheiden, die für die Charakterisierung der sechs Holothurien-Ordnungen herangezogen werden (zusammengefasst nach Massin 1982, Pawson 1982, Madsen & Hansen 1994). Zu den passiv filtrierenden Suspensionsfressern gehören die Dendrochirotida, die mit ihren langen und reich verzweigten Tentakeln Nahrungspartikel aus der Wassersäule filtern. Einige Arten sitzen dabei auf Hartsubstrat, andere leben auf oder im Sedi-

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[1] In älterer Literatur auch häufig als Holothurioidea zu finden.

ment von Weichböden. Die zu den Substratfressern gehörenden Aspidochirotida und Elasipodida leben auf dem Sediment, haben kurze und oft schildförmige Tentakel, mit denen sie die oberste Sedimentschicht in den Mund schaufeln. Die fußlosen Molpadida und Apodida haben meist einfache fingerförmige bis gefiederte Tentakel und leben mit Ausnahme einiger Apodida in das Sediment eingegraben. Sie gehören ebenfalls zu den Substratfressern. Auch für die eingegraben lebenden Dactylochirotida mit ihren fingerförmigen bis gefingerten Tentakeln nimmt man an, dass sie Substratfresser sind, obwohl über deren Biologie praktisch nichts bekannt ist (Massin 1982).

Die einzelnen Ordnungen der Holothuroidea lassen sich zwar durch morphologische Merkmale relativ gut charakterisieren, ihre Verwandtschaftsverhältnisse zueinander sind aber umstritten. Einen Überblick über einige der konkurrierenden Hypothesen zur Phylogenie dieser Gruppe findet man bei Kerr & Kim (2001). Nur zwei moderne phylogenetische Analysen befassen sich mit dieser Problematik, davon ist eine morphologisch basiert (Kerr & Kim 2001), die andere molekular (Lacey et al. 2005). Beide stimmen in wichtigen Punkten überein und postulieren zum einen die basale Stellung der Apodida, zum anderen die Elasipodia als Schwestergruppe zu einer monophyletischen Gruppe aus Aspidochirotida, Dendrochirotida, Dactylochirotida und Molpadida. Die Verwandtschaftsverhältnisse innerhalb der letztgenannten Gruppe bleiben dabei unklar und bedürfen dringend weitere Untersuchungen.

Ihre höchste Diversität erreichen Holothurien in tropischen Flachwassergebieten (Pawson 1982), aber auch in extremeren marinen Lebensräumen, wie etwa der Tiefsee oder dem Südlichen Ozean findet man eine beachtliche Artenvielfalt (z.B. Hansen 1975, Gutt 1988, 1991a, Clarke & Johnston 2003). Aus der Tiefsee (>200–400 m) sind nach Hansen (1975) knapp 400 Holothurienarten bekannt. Das Gebiet des Südlichen Ozeans besiedeln etwas mehr als 100 Arten (Clarke & Johnston 2003), dieses beinhaltet sowohl Flach-, als auch Tiefwasserarten. Der relativ gut untersuchte Kontinentalschelf des Weddell Meeres birgt immerhin noch 36 verschiedene Holothuroidea (Gutt 1991a, Massin 1992, Massin & Hétérier 2004). Beide Lebensräume, sowohl die Tiefsee, als auch der Südliche Ozean erfordern von den dort lebenden Organismen Anpassungen an ähnliche Umweltbedingungen, wie etwa an niedrige Wassertemperaturen, oder an ein saisonal stark schwankendes Nahrungsangebot (Clarke 1996). Dennoch unterscheidet sich die Zusammensetzung der Holothurienfauna beider Gebiete beträchtlich. Die dominanten Taxa der Tiefsee sind die Elasipodida und die Synallactidae Ludwig, 1894 (Aspidochirotida), die alle zu den Substratfressern gehören (Hansen 1975). Der ant-

Tab. 1. In der Dissertation behandelte Crinoidea und Holothuroidea, mit Informationen zu nomenklatorischen Maßnahmen, wie Neubeschreibungen oder Neukombinationen.

Art	**Nomenklatorischer Akt**	**Quelle**
Crinoidea Miller, 1821		
Millericrinida Sieverts-Doreck, 1953		
Bathycrinidae Bather, 1899		
Bathycrinus aldrichianus Wyville Thomson, 1876		Bohn 2006a
Holothuroidea de Blainville, 1834		
Apodida Brandt, 1835		
Chiridotidae Østergren, 1898		
Chiridota pisanii Ludwig, 1886		Altnöder et al. 2007
Myriotrochidae Théel, 1877		
Myriotrochus (*Oligotrochus*) *meteorensis* Bohn, 2005	sp. nov.	Bohn 2005b
Neolepidotrochus parvidiscus angolensis Bohn, 2005	subsp. nov.	Bohn 2005a
Siniotrochus myriodontus Gage & Billett, 1986		Bohn 2005a
Synaptidae Burmeister, 1837		
Protankyra brychia (Verrill, 1885)		Bohn 2006
Aspidochirotida Grube, 1840		
Synallactidae Ludwig, 1894		
Molpadiodemas atlanticus (R. Perrier, 1898)		Bohn 2006
Dendrochirotida Grube, 1840		
Cucumariidae Ludwig, 1894		
Echinopsolus acutus (Massin, 1992)	comb. nov.	Bohn & Heß unveröff.
Echinopsolus acanthocola Gutt, 1990		Bohn & Heß unveröff.
Echinopsolus charcoti (Vaney, 1906)	comb. nov.	Bohn & Heß unveröff.
Echinopsolus koehleri (Vaney, 1914)	comb. nov.	Bohn & Heß unveröff.
Echinopsolus mollis (Ludwig & Heding, 1935)	comb. nov.	Bohn & Heß unveröff.
Echinopsolus parvipes Massin, 1992		Bohn & Heß unveröff.
Echinopsolus splendidus (Gutt, 1990)	comb. nov.	Bohn & Heß unveröff.
Pseudrotasfer microincubator Bohn, 2007	sp. nov.	Bohn 2007
Elasipodida Théel, 1882		
Deimatidae Théel, 1879		
Deima validum validum Théel, 1879		Bohn 2006
Elpidiidae Théel, 1882		
Achlyonice longicornis Bohn, 2006	sp. nov.	Bohn 2006
Peniagone purpurea (Théel, 1882)		Bohn 2006
Psychropotidae Théel, 1882		
Psychropotes semperiana Théel, 1882		Bohn 2006
Molpadida Haeckel, 1896		
Molpadiidae Müller, 1850		
Molpadia liska Pawson, 1977		Bohn 2006

arktische Schelf hingegen wird von dendrochiroten Holothurien dominiert, die sich als Suspensionsfresser betätigen (Gutt 1991a).

Das Interesse an der Erforschung der Biodiversität dieser beiden marinen Lebensräume hat in den letzten Jahren stark zugenommen. Die Grundvoraussetzung für das Verständnis der Vielfalt eines Lebensraumes ist immer erst einmal die Kenntnis der dort lebenden Arten. Erst dann können sinnvoll Fragen etwa zu historischen Prozessen gestellt werden, die zu der jetzigen Ausprägung eines Lebensraumes geführt haben könnten.

Vor diesem Hintergrund fanden einige deutsche Expeditionen statt, um bisher kaum untersuchte Flach- und Tiefwassergebiete des Südatlantiks und des Südlichen Ozeans zu beproben. Die Biodiversität des antarktischen und subantarktischen Schelfs stand im Mittelpunkt des Interesses zweier Expeditionen (EASIZ III, LAMPOS) in das Gebiet des östlichen Weddell Meeres, der Antarktischen Halbinsel und des Scotia-Bogens (Abb. 1A, Arntz 2001, 2003). Bis dato nahezu unerforschte Tiefseebereiche der abyssalen Becken und Ebenen des südöstlichen Atlantiks und des daran anschließenden Südlichen Ozeans waren das Ziel weiterer Expeditionen. Das Angola-Becken wurde dabei im Rahmen der DIVA I Expedition beprobt, im Verlauf der ANDEEP Expeditionen hingegen verschiedene Tiefseebereiche des südlichen Atlantiks und des Südlichen Ozeans (Abb. 1B, Brandt et al. 2006, Türkay 2006).

Auf diesen sechs Expeditionen wurden an etwa 160 Stationen Holothuroidea gefunden (an fünf Stationen auch Crinoidea), die sich auf über 1100 grob sortierte Proben verteilen, welche dem Autor zur Bearbeitung vorliegen. Da eine komplette Aufarbeitung dieses reichhaltigen Materials in absehbarer Zeit leider nicht zu erreichen ist, werden in dieser Arbeit beispielhaft verschiedene Aspekte zur Taxonomie und Zoogeographie einiger dieser Holothurien behandelt. Dieser Zweiteilung folgt auch die Gliederung der Arbeit. Zentrales Thema sind dabei die Holothuroidea und Crinoidea des abyssalen Angola-Beckens. Alle dort gefundenen Arten werden beschrieben, ihre Verbreitung wird dargestellt und darauf aufbauend werden dann die biogeographischen Beziehungen der Holothurien- und Crinoidenfauna dieses Beckens zu den Faunen benachbarter Tiefseebereiche diskutiert. In einem zweiten Block wird eine Gruppe brütender antarktischer Holothurien behandelt, die sich durch eine Reihe gemeinsamer morphologischer Merkmale von allen bekannten Holothurien unterscheiden. Diese morphologischen Merkmale werden beschrieben und mögliche taxonomische, phylogenetische und zoogeographische Konsequenzen erörtert.

Ergebnisse und Diskussion

In der vorliegenden Arbeit werden insgesamt ein Crinoide und 19 Holothurienarten behandelt (Tab. 1). Ausführlich beschrieben werden dabei alle neuen Arten, oder Arten, die bisher nur unzureichend bekannt sind, während für bekannte Arten meist eine kürzere zusammenfassende Darstellung gewählt wurde. Von den 19 Holothuroidea sind insgesamt drei Arten (*Myriotrochus* (*Oligotrochus*) *meteorensis* Bohn, 2005; *Achlyonice longicornis* Bohn, 2006; *Pseudrotasfer microincubator* Bohn, 2007) und eine Unterart (*Neolepidotrochus parvidiscus angolensis* Bohn, 2005) als neu beschrieben worden (Bohn 2005a, b, 2006a, 2007). Der Transfer von fünf Arten in die Gattung *Echinopsolus* Gutt, 1990 erfolgt, um die enge Verwandtschaft der nun insgesamt sieben Arten dieser Gattung zu reflektieren (Bohn & Heß unveröffentlicht). Sehr divers sind die Fundorte und Lebensräume der behandelten Arten. Fast alle stammen aus dem Südatlantischen- und dem angrenzenden Südlichen Ozean. Etwa die Hälfte der Arten (ein Crinoide, neun Holothurien) sind typische Tiefseeformen und wurden im Verlauf der DIVA I Expedition im abyssalen Angola-Becken gesammelt. Die übrigen Holothurien stammen von den Aufsammlungen der EASIZ und LAMPOS Expeditionen und sind Arten des antarktischen und subantarktischen Schelfs.

Die folgende Darstellung gliedert sich in einen taxonomischen und einen biogeographischen Abschnitt. Im ersten Teil werden verschiedene morphologische Merkmale von Holothurien vorgestellt und ihr Nutzen für taxonomische Fragestellungen aufgezeigt und diskutiert. Der zweite Teil stellt dann verschiedene Aspekte der Zoogeographie der Holothurien des abyssalen Angola-Beckens und des Südlichen Ozeans vor.

1. Taxonomie und Merkmale

Um Holothurien zu klassifizieren und zu beschreiben, und so gegen verwandte Taxa abzugrenzen, werden eine ganze Reihe verschiedener externer und interner morphologischer Merkmale herangezogen. Eine sehr ausführliche, dafür aber in Teilen veraltete Zusammenstellung der verschiedenen Merkmale findet man bei Ludwig (1892), eine modernere etwa bei Pawson (1970).

Wichtige externe Merkmale sind die generelle Form des Körpers, die Position von Mund und After, die Morphologie, Anzahl und Stellung der Tentakel, sowie die Form und Anordnung der Füßchen auf dem Körper. Wichtige interne Merkmale sind der Bau des Kalkringes, die Anhänge des Ambulacralgefäßsystems wie Polische Blasen oder Steinkanal und der generelle Verlauf und Bau des Verdauungstraktes und seiner Anhänge (Wasserlungen). Auch der Aufbau und die Lage der Gonaden kann als Merkmal eine Rolle spielen. Von ganz zentraler Bedeutung für die Taxonomie der Holothuroidea jedoch sind die subepidermalen Kalkkörper der Körperwand, der Füßchen und Tentakel. Die große Formenvielfalt der Kalkkörper wird intensiv zur Abgrenzung und Charakterisierung von Taxa innerhalb der Holothurien herangezogen.

Eine ausschließlich auf morphologischen Merkmalen basierende Taxonomie birgt gewisse Probleme in sich. Von Zentraler Bedeutung ist hier die unterschiedliche Interpretation und Wichtung eines Merkmals. Häufig ist es vom systematischen Niveau abhängig, ob sich ein bestimmtes Merkmal zur Klärung einer bestimmten Fragestellung eignet oder nicht. Probleme bereitet auch das Fehlen eines Merkmals, sei es durch schlechte Konservierung (saure Konservierungsflüssigkeit zerstört die Kalkkörper) oder weil dieses Merkmal wirklich nicht vorhanden ist. Die Auswahl der „richtigen“ Merkmale ist nicht immer einfach und die beste Vorgehensweise ist sicher, möglichst viele Merkmale zu untersuchen und in die systematischen Überlegungen einzubeziehen. Hilfreich wäre hier ein vermehrter Einsatz molekularphylogenetischer Analysen, der aber bisher in der taxonomischen Forschung an Holothuroidea kaum eine Rolle spielen.

1.1. Ossikel

Das Kalkskelett der Holothuroidea ist gegenüber anderer Klassen der Echinodermata reduziert und besteht aus mikroskopisch kleinen Kalkkörpern, meist als Sklerite oder Ossikel bezeichnet, die im Bindegewebe der Körperwand und der Anhänge des Ambulacralsystems (Füßchen und Tentakel) zu finden sind. Seltener finden sich Ossikel auch in der Wand einzelner innerer Organe, wie etwa der Gonaden oder des Ambulacralgefäßsystems. Die Formenvielfalt der Ossikel, die man innerhalb der Holothuroidea findet, ist groß. Abhängig von der Bauweise unterscheidet man daher verschiedenste Typen, wie etwa Stäbe, Platten, Türmchen, Körbchen, Anker und Ankerplatten oder auch Räder (Abb. 2). Typischerweise setzt sich das Kalkskelett einer bestimmten Art dabei aus einer ganzen Reihe verschiedener Ossikeltypen zusammen, die sich auch noch in verschiedenen Bereichen des Körpers, wie etwa Körperwand oder Tentakel, unterscheiden können.

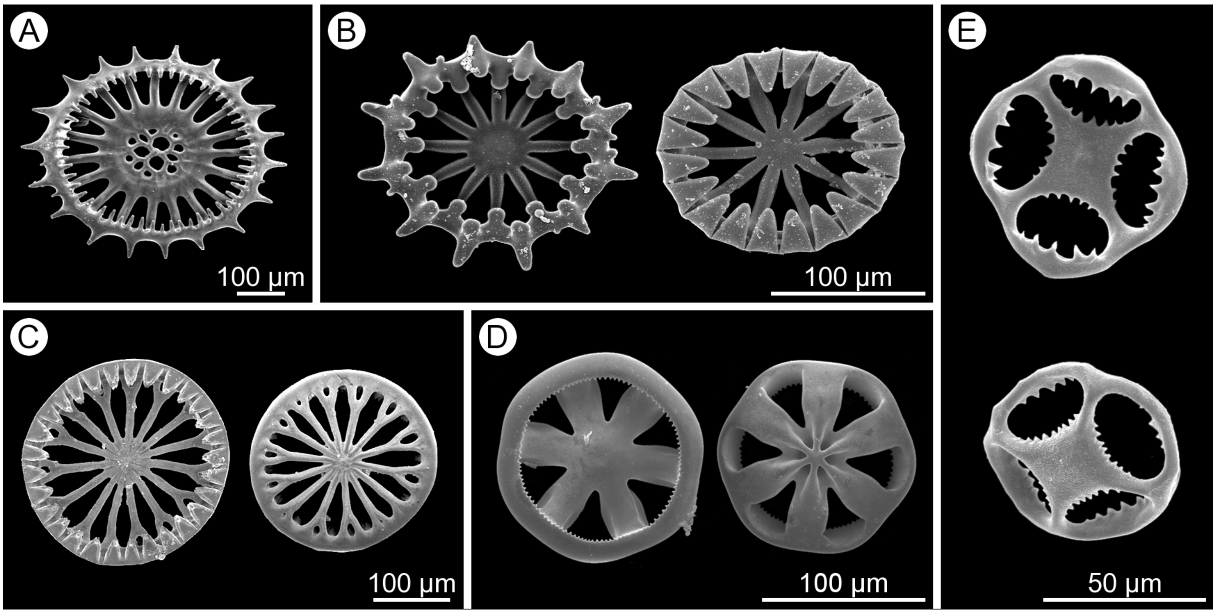

Abb. 2. Ossikel der Körperwand verschiedener Holothuroidea. **A.** Rad vom *Siniotrochus*-Typ, *Siniotrochus myriodontus* Gage & Billett 1986. **B.** Rad vom *Lepidotrochus*-Typ (links) und vom *Myriotrochus*-Typ (rechts), *Neolepidotrochus parvidiscus angolensis* Bohn, 2005. **C.** Räder von *Myriotrochus* (*Oligotrochus*) *meteorensis* Bohn, 2005. **D.** Räder von *Chiridota pisanii* Ludwig, 1886. **E.** „Körbchen" von *Pseudrotasfer microincubator* Bohn, 2007. (A, B verändert nach Bohn 2005a: Abb. 1B, D, E; C verändert nach Bohn 2005b: Abb. 1M; D verändert nach Altnöder et al. 2007: Abb. 10; E verändert nach Bohn 2007: Abb. 2G)

Die konsequente Berücksichtigung von Ossikeln in der Beschreibung von Holothurien erfolgte nach Ludwig (1892) erst durch Düben & Koren (1845, 1846). Seitdem werden die Kalkkörper als wichtiges Merkmal zur Abgrenzung von Arten, aber auch von Gattungen oder gar Familien innerhalb der Holothuroidea angesehen (z.B. Ludwig 1892, Hyman 1955, Hansen 1975, Gilliland 1993). So verwenden etwa Pawson & Fell (1965) in ihrer Neuordnung der dendrochiroten Holothurien, oder auch Smirnov (1998) in seiner Revision der Apodida die Ausbildung des Kalkskelettes als ein wichtiges Merkmal, um Familien zu charakterisieren. Ausführlich dargestellt werden die bekannten Ossikeltypen und ihre Ausprägung in den verschiedenen Taxa etwa von Ludwig (1892) oder Gilliland (1993).

Die Klassifizierung der Kalkkörper in bestimmte Typen hat einen großen Vorteil – die Beschreibungen und Charakterisierung des Kalkskelettes einer Art wird dadurch stark vereinfacht. Allerdings handelt es sich hierbei um eine mehr oder weniger künstliche Gruppierung. Der Besitz von Ossikeln, die dem gleichen Typus zugerechnet werden, bedeutet nicht automatisch eine nahe Verwandschaft der Taxa. Ein gutes Beispiel sind die Räder der Apodida und der Elasipodida, die oberflächlich betrachtet sehr ähnlich aussehen, ihrer Entwicklung nach wohl aber nichts miteinander zu tun haben (Hansen 1975).

Eine Klassifikation, die sich über weite Teile auf Unterschiede in der Zusammensetzung und im Bau der Kalkkörper innerhalb der einzelnen Taxa stützt, birgt weitere Probleme. Nicht alle Holothurien besitzen Ossikel, einigen Dendrochirotida, Apodida und Elasipodida fehlen sie komplett (z.B. Ludwig 1892, Pawson 1982, Smirnov 1998). Ebenso kommt es bei einigen Arten zu alters- und größenabhängigen Veränderungen des Kalkskelettes; dies wird als Kalkkörperwechsel und Kalkkörperschwund bezeichnet (siehe hierzu Massin 1994, Massin *et al.* 2000). Schließlich variieren Ossikel in ihrer Form und Größe sowohl innerhalb eines Individuums, als auch innerhalb einer Art. All diese Faktoren erschweren die Beschreibung, Bestimmung und Klassifizierung, und führen regelmäßig zur Neubeschreibung bereits bekannter Arten.

Gut abgrenzen lassen sich Taxa, wenn sie einen charakteristischen Ossikeltypus besitzen, der sich in dieser Form sonst nirgends findet. Die gerade erst beschriebene Art *Pseudrotasfer microincubator* Bohn, 2007 beispielsweise hat in der Körperwand in einer unteren Schicht große Platten mit vielen Löchern und in einer äußeren Schicht einzigartige, an Räder erinnernde „Körbchen“ (Abb. 2E, Bohn 2007). Das besondere an diesen „Körbchen“ ist das stark verbreiterte Primärkreuz im Zentrum, sowie die auffällige Bedornung im Bereich des Primärkreuzes und des umlaufenden Randes. Eine Reihe von Merkmalen, wie etwa der Bau des Kalkringes und der generelle Körperbau zeigen, dass dies Art zur Familie der Cucumariidae Ludwig, 1894 gehört, aber die Zuordnung zu einer bekannten Gattung fällt schwer. Zum einen sind vergleichbar gestaltete Kalkkörper bisher nicht bekannt, zum anderen gibt es auch sonst keine Hinweise auf eine nähere Verwandtschaft zu anderen Taxa innerhalb der Familie. Um diesem Umstand Rechnung zu tragen, wurde für die neue Art die ebenfalls neue Gattung *Pseudrotasfer* Bohn, 2007 geschaffen. Das Aufstellen solcher monotypischer Taxa ist durchaus kritisch zu bewerten, und sollte nur in besonderen Fällen geschehen. Höhere Taxa, wie etwa Gattungen oder Familien, dienen eigentlich dazu, erkannte monophyletische Gruppen gegen andere Gruppen abzugrenzen, monotypische Taxa sind hier nicht besonders hilfreich. Die Aufstellung der neuen Gattung war dennoch aus zwei Gründen erforderlich. Zum einen ist eine nähere Verwandtschaft von *P. microincubator* zu anderen Arten innerhalb der Cucumariidae nicht ersichtlich, zum anderen muss eine Art, um gültig beschrieben zu sein eindeu-

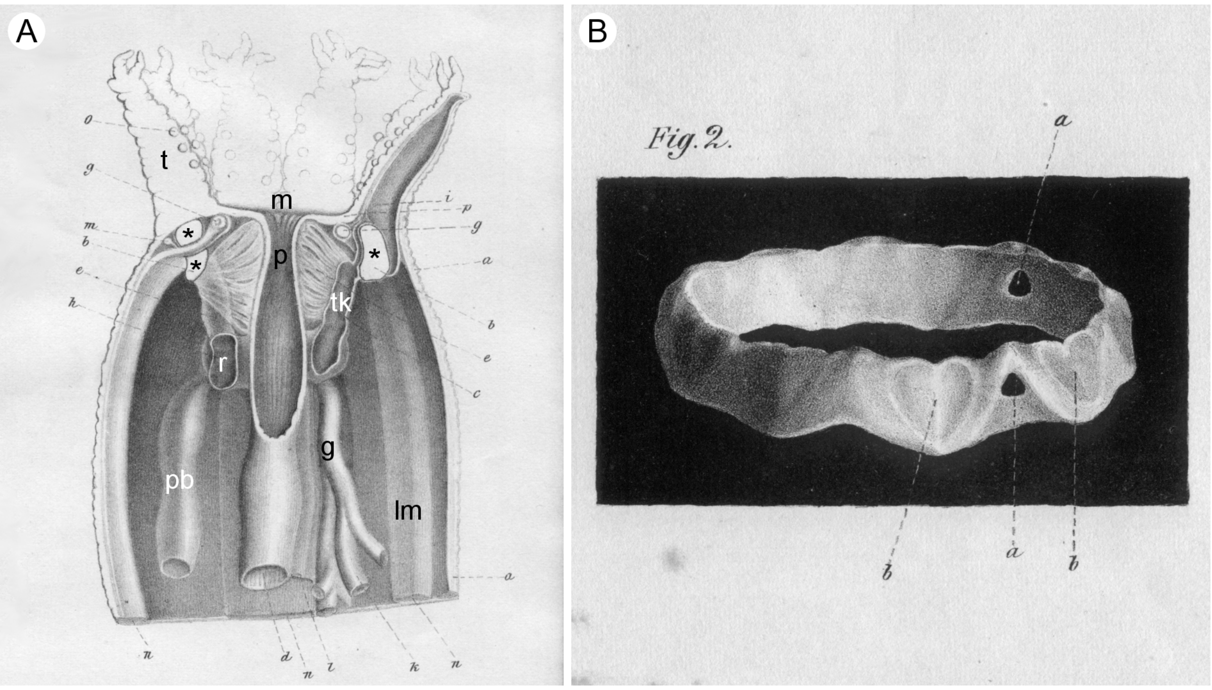

Abb. 3. Kalkring von *Oestergrenia digitata* (Montagu, 1815). **A.** Lage des Kalkringes (*) im Tier, schematische Darstellung. **B.** Kalkring in Lateralansicht, bei dieser Art sind nur die ventralen Radialia (a) durchbrochen. *g* Gonade, *lm* Längsmuskel, *m* Mund, *p* Pharynx, *pb* Polische Blase, *r* Ringkanal des Ambulacralsystems, *t* Tentakel, *tk* Tentakelkanal (A, B aus Baur 1864: Abb. 8, Abb. 2)

tig einer Gattung zugeordnet werden (ICZN 1999: Artikel 11.9.3), ein *incertae sedis* Status ist nicht erlaubt.

Auf einem höheren systematischen Niveau sind charakteristische Kalkkörpertypen zur Abgrenzung von Taxa sehr hilfreich. Ein schönes Beispiel hierfür sind die drei Familien der Apodida. Jede verfügt über einen einzigartigen Ossikeltypus, der nur innerhalb der jeweiligen Familie zu finden ist (Pawson 1982, Smirnov 1998). Die Synaptidae Burmeister, 1837 etwa besitzen Anker und Ankerplatten, die Chiridotidae Østergren, 1898 kompliziert gebaute Räder mit sechs Speichen (Abb. 2D) und die Myriotrochidae Théel, 1877 einfachere Räder mit mehr als sechs Speichen (Abb. 2A–C).

Auch die einzelnen Gattungen innerhalb der Myriotrochidae lassen sich anhand ihrer Räder gut charakterisieren. Man kennt momentan etwas über 40 Arten, die sich auf acht Gattungen verteilen (Gilliland 1993, Smirnov 1997, 1999, Smirnov & Bardsley 1997, Bohn 2005a, b, O'Loughlin & VandenSpiegel 2007). Eine Zuordnung der Arten zu den Gattungen ist trotz des sehr einheitlichen und damit merkmalsarmen Bauplan der Familie dabei meist unproblematisch. Merkmale der Tentakel (Anzahl und Bau), des Kalkringes und natürlich der vorhandenen Kalkkörper charakterisieren die acht Gattungen (Gage & Billett 1986, Smirnov 1998). Besonders hilfreich sind die insgesamt fünf verschiedenen Radtypen, die sich unterscheiden lassen (Gilliland 1993, Smirnov 1998). Schon die Namen der Radtypen zeigen an, für welche Gattung sie charakteristisch sind (*Acanthotrochus*-Typ; *Lepidotrochus*-Typ, Abb. 2B; *Myriotrochus*-Typ, Abb. 2B, C; *Siniotrochus*-Typ, Abb. 2A; *Trochoderma*-Typ). Einzige Ausnahme hiervon ist der *Myriotrochus*-Typ, der in fünf der acht Gattungen vorkommt (Gilliland 1993).

Viel schwieriger ist die Abgrenzung einzelner Arten innerhalb der Gattungen, denn hier kommen praktisch nur noch kleine Unterschiede im Bau und in der Größe der Räder zum tragen. Diese Problematik wurde schon relativ früh erkannt und es wurden einige Standardmessungen etabliert, die eine bessere Charakterisierung der Räder erlaubt (z.B. Østergren 1905, Heding 1935b). Doch erst Belyaev (1970) und Belyaev & Mironov (1977, 1978, 1980, 1981a, b, 1982) etablierten die heute verwendeten Radparameter und nutzten diese systematisch in ihren Beschreibungen neuer Myriotrochidae. Wichtige Parameter, die heute standardmäßig für die Beschreibung dieser Räder eingesetzt werden, sind der Raddurchmesser, der Durchmesser der Nabe, die Anzahl der Speichen und die Anzahl der Zähne auf dem Radkranz. Die Variationsbreite der Parameter wird dabei durch die Angabe der Minimal-, Maximal- und Mittelwerte, sowie der Standardabweichung verdeutlicht.

Statistische Methoden zur Auswertung diverser Radparameter werden erstmals von Gage & Billett (1986) in ihrer Aufarbeitung der Myriotrochidae des Rockall Trough eingesetzt. Auch die Beschreibung der drei Myriotrochidae (Siniotrochus myriodontus Gage & Billett 1986, Neolepidotrochus parvidiscus angolensis Bohn, 2005, Myriotrochus (Oligotrochus) meteorensis Bohn, 2005) im Rahmen dieser Arbeit folgt diesem neuen Standard (Bohn 2005a, b). Leider lagen von diesen Arten nur jeweils wenige Exemplare vor, so dass erhobenen Radparameter nur auf eine Abhängigkeit von der Größe der Räder getestet werden konnten (siehe Bohn 2005a, b). Weitergehende Aussagen, etwa zur Variabilität bestimmter Parameter innerhalb eines Individuums, innerhalb Individuen der selben Lokalität und innerhalb Individuen verschiedener Fundorte mit Hilfe der Varianzanalyse, wie sie von Gage & Billett (1986) für einige Arten durchgeführt werden konnten sind natürlich wünschenswert. Bei seltenen Tiefseearten ist das aber meist nicht praktikabel, da hierzu eine ausreichende Anzahl an Individuen von verschiedenen Fundorten nötig ist.

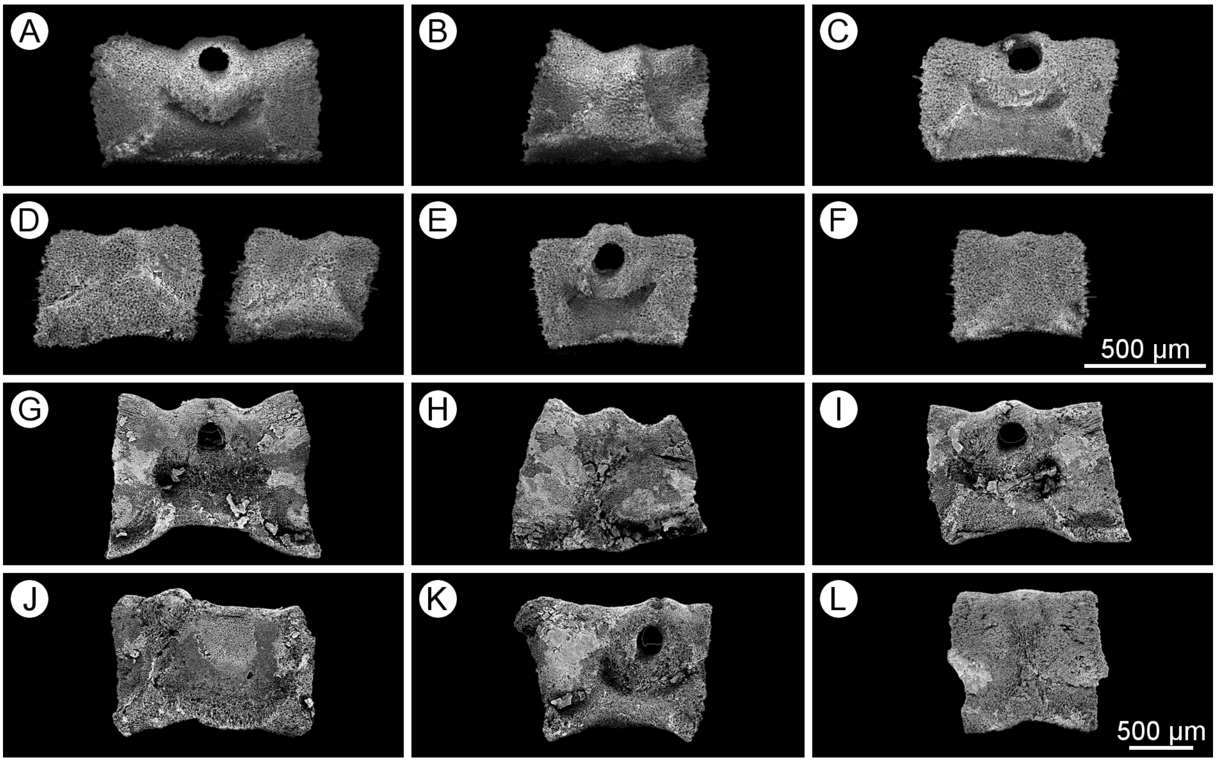

Abb. 4. Kalkringtypen der Gattung *Chiridota* Eschscholtz, 1829. **A–F.** Kalkring mit 12 Platten (alle gleiche Vergrößerung), *C. pisanii* Ludwig, 1886. **A.** Ventrales Radiale. **B.** Linkes ventrales Interradiale. **C.** Linkes ventrales Radiale. **D.** Linke laterale Interradialia. **E.** Linkes dorsales Radiale. **F.** Dorsales Interradiale. **G–L.** Kalkring mit 10 Platten (alle gleiche Vergrößerung), *C. laevis* (O. Fabricius, 1780). **G.** Ventrales Radiale. **H.** Linkes ventrales Interradiale. **I.** Linkes ventrales Radiale. **J.** Linkes laterales Interradiale. **K.** Linkes dorsales Radiale. **L.** Dorsales Interradiale. (A–F aus Altnöder *et al.* 2007: Abb. 3–8)

1.2. Der Kalkring

Üblicherweise besteht der Kalkring der Holothuroidea aus zehn, über Bindegewebe miteinander verbundenen Skelettelementen, die ringförmig das anteriore Ende des Verdauungstraktes umgeben (Abb. 3A, B). Fünf Kalkringglieder liegen radial (Radialia) und wechseln sich mit fünf interradial gelegenen Gliedern ab (Interradialia). Die Funktion des Kalkringes ist vor allem eine stützende – zum einen ist an seinem posterioren Ende der Ringkanal des Ambulacralgefäßsystems befestigt, zum anderen inserieren hier sowohl die Längsmuskeln der Körperwand, als auch die Rückziehmuskeln der Tentakel. Typischerweise sind die Vorderenden der Radialia für den Durchtritt des Radiärkanals und des Radiärnervs entweder eingeschnitten oder durchbohrt (nach Ludwig 1892, Hyman 1955, Gilliland 1993).

Tab. 2. Bau des Kalkringes in der Gattung *Chiridota* Eschscholtz, 1829, nach verschiedenen Autoren. (Verändert nach Altnöder *et al.* 2007: Tab. 4)

Art	**Quelle**	
	10 Platten	**12 Platten**
Chiridota albatrossii Edwards, 1907		Heding 1928
Chiridota aponocrita H.L. Clark, 1920		Heding 1928
Chiridota carnleyensis Mortensen, 1925		Mortensen 1925
Chiridota discolor Eschscholtz, 1829	Smirnov *et al.* 2000	
Chiridota fernandensis Ludwig, 1898		Ludwig 1898b
Chiridota gigas Dendy & Hindle, 1907		Hickman 1962
Chiridota hawaiiensis Fisher, 1907		Fisher 1907, Heding 1928
Chiridota heheva Pawson and Vance, 2004	Pawson & Vance 2004	
Chiridota hydrothermica Smirnov & Gebruk, 2000	Smirnov *et al.* 2000	
Chiridota laevis (O. Fabricius, 1780)	Smirnov *et al.* 2000, Altnöder *et al.* 2007	Heding 1935a
Chiridota marenzelleri R. Perrier, 1904	Perrier 1905	
Chiridota nigra Mortensen, 1925		Mortensen 1925, Pawson 1970
Chiridota ochotensis Saveljeva, 1941	Smirnov *et al.* 2000	
Chiridota orientalis Smirnov, 1981	Smirnov 1981	
Chiridota pacifica Heding, 1928		Heding 1928
Chiridota pisanii Ludwig, 1886		Théel 1886[1], Heding 1928, Altnöder *et al.* 2007
Chiridota rigida Semper, 1868		Heding 1929
Chiridota rotifera (Pourtalès, 1851)		Ludwig 1881, Heding 1928, Altnöder *et al.* 2007
Chiridota stuhlmanni Lampert, 1896		Heding 1928, Cherbonnier 1988
Chiridota tauiensis Saveljeva, 1941	Smirnov *et al.* 2000	

1 als *Chirodota purpurea* Lesson, 1830.

Die große Variabilität des Kalkringes innerhalb der Holothuroidea ist schon lange bekannt und wurde von Ludwig (1892) ausführlich dargestellt. Zum einen variiert natürlich die Gestalt und Größe der Kalkringelemente und somit auch die Form und Größe des Ringes selbst, zum anderen gibt es aber auch Abweichungen in der Anzahl der Glieder, die den Kalkring bilden. So kennt man eine Reihe Apodida, deren Kalkring durch eingeschobene Interradialia aus mehr als zehn (bis 18) Gliedern aufgebaut ist (Clark 1908). Häufig kommt es auch zu einer Reduktion von Teilen des Kalkringes. Bei einigen Dendrochirotida und Elasipodida besteht der Kalkring nur noch aus den fünf Radialia, die Interradialia fehlen (Ludwig 1892, Hansen 1975). Durch fehlende Verkalkung des Gewebes kann es auch zu einem gänzlichen Verlust des Kalkringes kommen, wie dies Hansen (1975) für einige Elasipodida nachwies.

Obwohl sich Ludwig (1892) der großen Variabilität des Kalkringes innerhalb der Holothuroidea bewusst war, maß er dem Kalkring als Merkmal für die Systematik dennoch eine geringe Bedeutung bei. Erst spätere Autoren, wie etwa Panning (1949), Heding & Panning (1954) oder Pawson & Fell (1965), räumen diesem Merkmal einen deutlich höheren Stellenwert ein. So basiert die noch heute akzeptierte Großgliederung (Ordnungen und Familien) der dendrochiroten Holothurien durch Pawson & Fell (1965) zu einem großen Teil auf morphologischen Unterschieden im Bau des Kalkringes in den verschiedenen Taxa. Auch auf Gattungs- und Artebene wird die Morphologie des Kalkringes regelmäßig herangezogen, um Taxa zu unterscheiden und einzuordnen (z.B. Heding 1928, Rowe 1969, Belyaev & Mironov 1977, Gage & Billett 1986).

Ein aus taxonomischer und phylogenetischer Sicht möglicherweise interessanter Punkt ist die bis dato kaum beachtete, aber schon lange bekannte Variabilität der Anzahl der Interradialia innerhalb der Apodida (z.B. Ludwig 1892, Clark 1908). Nach älteren Quellen besteht bei Apodida ein Zusammenhang zwischen der Anzahl der Tentakel und der Anzahl der Kalkringstücke (Ludwig 1892, Clark 1908). Synaptidae und Chiridotidae, mit mehr als zehn Tentakel, oft 12 oder 15, selten sogar 25 (Pawson 1982), sollten also dementsprechend viele Kalkringglieder besitzen. Eine Ausnahme hiervon bilden die Myriotrochidae mit 12 Tentakeln, von denen schon länger bekannt ist, dass sie nur zehn Kalkringstücke besitzen (Ludwig 1892). Diese Tatsache wurde auch durch zahlreiche weitere Untersuchungen bestätigt (Belyaev & Mironov 1982, Gage & Billett 1986, Smirnov 1999, Bohn 2005b).

In den letzten Jahren allerdings häufen sich die Hinweise, dass wohl auch eine ganze Reihe Synaptidae (z.B. Smirnov 1983, Gage 1985, eigene Beobachtungen) und Chiridotidae (z.B. Smirnov 1981, Smirnov *et al.* 2000) mit 12 Tentakeln einen aus 10 Platten aufgebauten Kalkring haben. Hierbei inserieren die beiden zusätzlichen Tentakel, unter Beibehaltung der Bilateralsymmetrie jeweils im rechten und linken dorsalen Interradius. Um den Tentakeln Raum zu geben, sind die entsprechenden Interradialia deshalb meist etwas breiter und besitzen für den zusätzlichen Tentakel eine weitere Insertionsstelle. Smirnov *et al.* (2000: S. 325) gehen sogar soweit, aus diesen Beobachtung eine Gesetzmäßigkeit abzuleiten: „Thus, accord-

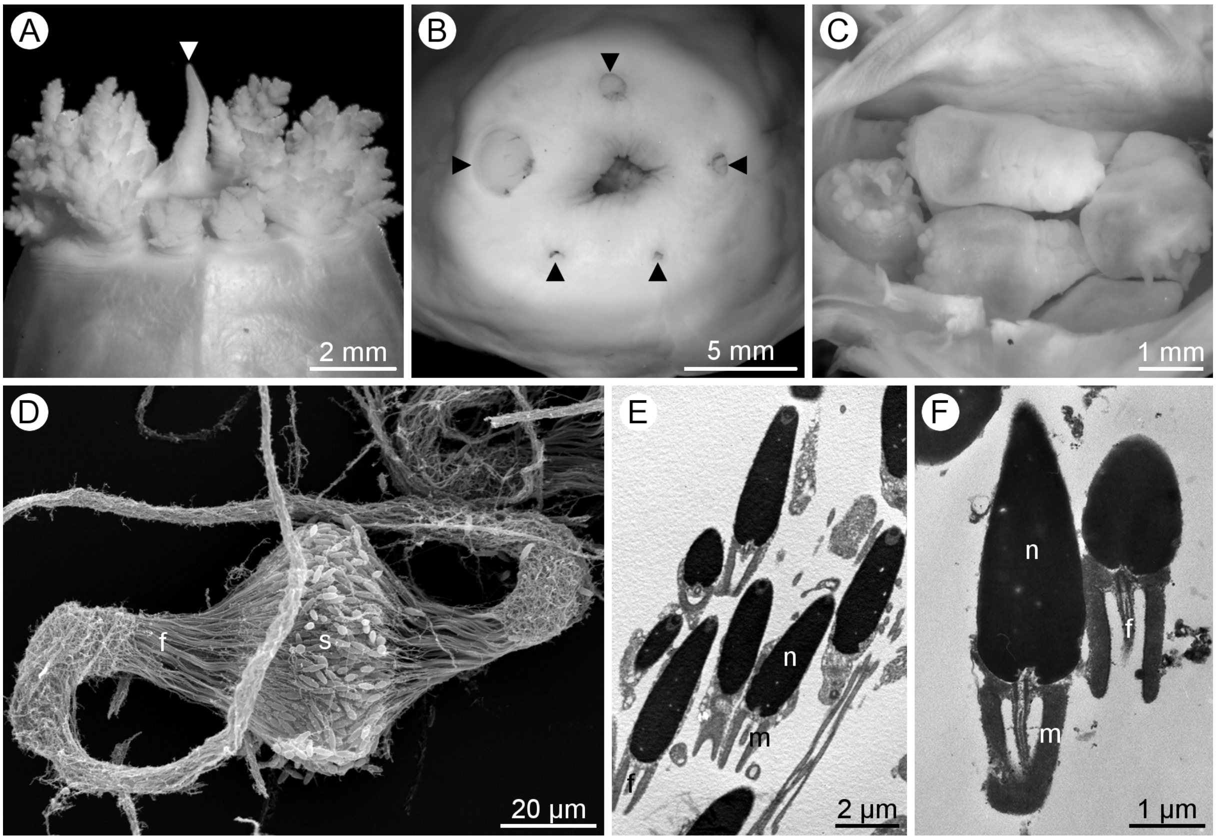

Abb. 5. Genitalpapille, Bruttaschen, Spermatozeugmata und Spermatozoa der Gattung *Echinopsolus*. **A.** Genitalpapille (▶) eines Männchens (*E. acutus*). **B.** Bruttaschen (▶) eines Weibchens mit zurückgezogenen Tentakeln in Frontalansicht (*E. splendidus*). **C.** Geöffnete Bruttasche mit mehreren Juvenilen (*E. splendidus*). **D.** Zwei Spermatozeugmata (*E. parvipes*). **E.** Längsschnitte (TEM) durch Spermatozoa (*E. acanthocola*). **F.** Längsschnitte (TEM) durch Spermatozoa (*E. splendidus*). *f* Spermienschwanz, *m* Mittelstück, *n* Nucleus, *s* Spermatozoa

ing to modern views, apodid species with 12 tentacles have ten pieces of calcareous ring with two dorsolateral pieces beeing bipartite, i.e. bearing two anterior processes…".

Es gibt aber Ausnahmen. Untersuchungen des Kalkringes einiger *Chiridota* Eschscholtz, 1829 zeigen klar, dass bei einigen Arten mit 12 Tentakeln ebenso viele Kalkringstücke vorhanden sind. Altnöder *et al.* (2007) konnten dies sowohl für *C. pisanii* Ludwig, 1886 (siehe Abb. 4A–F), als auch für *C. rotifera* (Pourtalès, 1851) nachweisen. Bei beiden Arten finden sich jeweils zwei Interradialia im linken und rechten dorsalen Interradius (Abb. 4D). *Chiridota laevis* (O. Fabricius, 1780) hingegen ist „regelkonform" und besitzt wirklich nur fünf Radialia und fünf Interradialia (Abb. 4G–L; Altnöder *et al.* 2007). Damit steht fest, dass es innerhalb der Gattung *Chiridota* zwei verschiedene Kalkringtypen gibt. Die sich dar-

Tab. 3. Literaturnachweise antarktischer Cucumariidae und „Psolidae“ mit anterioren interradialen Bruttaschen und einer Genitalpapille auf der Mundscheibe, durch eigene Daten ergänzt.

Art	Bt	Gp	Sze	Szo	Quelle	Benutzter Artname
Cucumariidae						
Cucumaria acuta Massin, 1992	5	+	+	+	Bohn & Heß unveröff.	*Echinopsolus acutus* (Massin, 1992)
		+			Massin 1992	
Cucumaria attenuata Vaney, 1906	5	+			Ekman 1925	?
Cucumaria coatsi [non Vaney, 1908]	5				Ekman 1925	?
Cucumaria ferrari (Bell, 1908)	3				McClintock *et al.* 1994	?
Semperia georgiana Lampert, 1886		+			Lampert 1886	?
Cucumaria georgiana (Lampert, 1886)	5				Ekman 1925	
“*Cucumaria georgiana*” Gruppe	5	+			O'Loughlin 1994, 2001	?
Cucumaria joubini Vaney, 1914	5	+			Vaney 1914, 1925	?
Cucumaria lateralis Vaney, 1906	2	+			Vaney 1906a, b	?
	2				Vaney 1908	
	2				Vaney 1925	
Cucumaria vaneyi Cherbonnier, 1949	2				Cherbonnier 1949	?
Microchoerus splendidus Gutt, 1990	5	+	+	+	Bohn & Heß unveröff.	*Echinopsolus splendidus* (Gutt, 1990)
		+			Gutt 1990	
	5	+			O'Loughlin 1994, 2001	
Pseudocolochirus mollis Ludwig & Heding, 1935	5	+	+	+	Bohn & Heß unveröff.	*Echinopsolus mollis* (Ludwig & Heding, 1935)
	5	+			Ludwig & Heding 1935	
“Psolidae”						
Echinopsolus acanthocola Gutt, 1990	5	+	+	+	Bohn & Heß unveröff.	*Echinopsolus acanthocola* Gutt, 1990
Echinopsolus parvipes Massin, 1992	5	+	+	+	Bohn & Heß unveröff.	*Echinopsolus parvipes* Massin, 1992
		+			Massin 1992	
Psolus charcoti Vaney, 1906	5	+	+	+	Bohn & Heß unveröff.	*Echinopsolus charcoti* (Vaney, 1906)
	5				Ekman 1925	
	5	+			O'Loughlin 2001	
Psolus koehleri Vaney, 1914	5	+	+	+	Bohn & Heß unveröff.	*Echinopsolus koehleri* (Vaney, 1914)
	5				Vaney 1914, 1925	
	5	+			Ekman 1925	

Bt Anzahl der Bruttaschen, *Gp* Genitalpapille, *Sze* Spermatozeugmata, *Szo* Spermatozoa vom “Echinopsolus”-typ, + vorhanden aus ergebenden taxonomischen und phylogenetischen Konflikte sind bisher unklar. Eine Durchsicht der Literatur offenbart, dass Daten zur Kalkringmorphologie bislang für 20 der etwa 30 bekannten *Chiridota* Arten vorliegen (Tab. 2). Von diesen 20 Arten sollen acht Arten einen Kalkring besitzen, der aus 10 Platten aufgebaut ist, und 13 Arten haben einen aus 12 Platten bestehenden Ring. Im Falle von *C. laevis* gibt es hier Überschneidungen (Tab. 2): während Heding (1935) für diese Art 12 Kalkringglieder angibt, fanden Smirnov *et al.* (2000) übereinstimmend mit Altnöder *et al.* (2007) nur 10 Platten. Die genaue Plattenzahl lässt sich nur durch Präparieren und Freilegen der einzelnen Kalkringglieder ermitteln; Literaturangaben dürfen deshalb nicht ohne Vorbehalte übernommen werden.

Die Merkmalskombination „12 Tentakel und ein Kalkring, der aus 10 Platten besteht", gibt es nur bei den Apodida. Die Myriotrochidae, der basalste Zweig der Apodida (Kerr 2001), zeigen sogar ausschließlich diese Merkmalskombination (siehe oben). Damit ist dieser Zustand für Arten der Gattung *Chiridota* eine Plesiomorphie. „Zwölf Tentakel und ein Kalkring der aus 12 Platten besteht" hingegen eine mögliche Synapomorphie einer noch nicht genau bekannten (und benannten) monophyletischen Untergruppe innerhalb der Gattung. Um diese Frage zu klären, braucht es aber noch weitergehende detaillierte Untersuchungen. Weitere vielversprechende Studienobjekte sind Arten der Synaptidae, denn unveröffentlichte Daten des Autors zeigen, dass auch innerhalb dieser Familie einzelne Arten mit 12 Tentakeln „entgegen der Regel" einen aus 12 Platten aufgebauten Kalkring haben.

1.3. Neue Merkmale – Spermatozoa, Spermatozeugmata und Brüten

Neue, oder bisher wenig beachtete Merkmale und Merkmalskombinationen bringen oft interessante und unerwartete Einsichten in taxonomische und phylogenetische Zusammenhänge. Beispielhaft kann dies an der antarktischen Gattung *Echinopsolus* Gutt, 1990 gezeigt werden (siehe hierzu auch Bohn & Heß unveröffentlicht). Eine ganze Reihe von Eigenarten, die alle mit der Art und Weise der Brutpflege dieser Gattung in Zusammenhang stehen, grenzen *Echinopsolus* von anderen Gattungen der Familie Cucumariidae ab.

Schon lange ist bekannt, dass nicht wenige dendrochirote Holothurien Brutpflege betreiben (McEuen & Chia 1991, O'Loughlin 1994), darunter auch viele antarktische Arten. Die Methoden, mit denen die Weibchen ihre Eier und Jungtiere beschützen, sind hierbei vielfältig und unterscheiden sich meist von Art zu Art (siehe McEuen & Chia 1991, O'Loughlin 1994). Auffallend ist, dass eine Reihe antarktischer Holothurien, die sich auf die Familien Cucumariidae und Psolidae verteilen, die Eier und den Nachwuchs in zwei bis fünf interradialen anterioren Bruttaschen austragen (Abb. 5B, C; Tab. 3). Eine weitere Gemeinsamkeit vieler dieser Arten ist die Präsenz einer Genitalpapille auf der Mundscheibe zwischen oder unterhalb des dorsalen Tentakelpaares (Abb. 5A; Tab. 3). Für einige dieser Arten wies O'Loughlin (2001) Sexualdimorphismus nach – Männchen haben eine fingerförmige, permanente Genitalpapille, Weibchen hingegen oft nur eine kleine und unauffällige, warzenförmige Papille.

Diese Merkmale fanden sich auch bei etwa 11 Arten, die dem vorliegenden reichhaltigen antarktischen Holothurien-Material entstammen. Nur sieben davon lassen sich gut definierten und gültigen Arten zuordnen und werden deshalb im weiteren Verlauf berücksichtigt (Tab. 3). Detaillierte morphologische und histologische Untersuchungen förderten weitere, bisher unbekannte Gemeinsamkeiten zutage: den Männchen dieser Arten sind charakteristische Spermatozoa gemein (Abb. 5E, F), die durch Verkleben der Schwänze zu ebenso charakteristischen Spermienbündeln (Spermatozeugmata) vereinigt sind (Abb. 5D).

Die Spermatozoa dieser sieben Arten weisen einen für Holothurien einzigartigen Bau auf und lassen sich wie folgt charakterisieren: Spermienkopf spindelförmig, daran anschließendes Mittelstück mit Mitochondrien-Derivat in der Form eines Hohlzylinders, der den proximalen Teil des Spermienschwanzes umgibt (Abb. 5E, F).

Bislang kennt man von Holothurien drei verschieden Typen von Spermien, die sich aber alle wesentlich von den hier gefundenen Spermien unterscheiden. Fast alle bislang untersuchten Holothurien (17 von 19 Arten) besitzen Spermien von einem einheitlichen Typus (Chia *et al.* 1975, Jamieson 1985, Hodgson & Bernard 1992), welcher sich durch seinen kugelförmigen Kopf und das flach schüsselförmige Mittelstück mit Mitochondrien-Derivat, das die beiden Centriolen, nicht aber den proximalen Spermienschwanz umschließt, von dem hier gefundenen Spermientyp abhebt.

Interessant an den beiden anderen Spermientypen ist, dass diese bei ebenfalls Brutpflege betreibenden Holothurien gefunden wurden (*Cucumaria lubrica* H.L. Clark, 1901 und *Cucumaria pseudocurata* Deichmann, 1938), allerdings werden hier die Eier von den Weibchen nicht in Bruttaschen, sondern zwischen dem Körper und dem Substrat aufbewahrt (Atwood & Chia 1974, Atwood 1975). *Cucumaria pseudocurata* hat aberrante Spermatozoa mit einem länglichen dorso-ventral abgeflachten Kopf, der auf der einen Seite das Acrosom und auf der gegenüberliegenden Seite, an der Basis des Nucleus, den Großteil des Mitochondrien-Derivates trägt (Atwood 1975). Die Spermatozoa von *C. lubrica* hingegen haben einen länglichen

Kopf und ein Mittelstück mit Mitochondrien-Derivat, welches ringförmig um den posterioren Teil des Nucleus liegt (Atwood & Chia 1974).

Obwohl sich die Spermien dieser zwei *Cucumaria* Arten in ihrem Aufbau deutlich von den Spermatozoa der Gattung *Echinopsolus* unterscheiden, so gibt es doch auch mehrere Gemeinsamkeiten. Zum einen haben alle längliche Spermienköpfe, zum anderen werden bei allen die Spermien in Form von größeren Einheiten in das Wasser abgegeben. *Cucumaria pseudocurata* produziert eine Art Spermatophore: es werden Stränge einer mukösen Substanz abgegeben, in die die Spermatozoa eingebettet sind (Atwood 1975, McEuen 1988). Die Spermatozoa von *C. lubrica* hingegen sind, ganz wie bei *Echinopsolus*, im Bereich der Schwänze zu Spermienbündeln (Spermatozeugmata) verbunden (Atwood & Chia 1974, McEuen 1988). Ähnliche Spermatozeugmata kennt man bei Holothurien sonst nur noch von einer weiteren brütenden Cucumariidae (*Pseudrotasfer microincubator* Bohn, 2007), die aber ihre Jungen in den Ovarien austrägt (Bohn 2007). Über den Bau der Spermatozoa dieser Art ist bislang nichts bekannt.

Einen engen Zusammenhang zwischen Brüten, der Verpackung der Spermatozoa zu größeren Einheiten und der länglichen Form der Spermien legen Lebendbeobachtungen an *C. pseudocurata* und *C. lubrica* nahe (z.B. Engstrom 1982, McEuen 1988). Bei diesen Arten sinkt das von den Männchen abgegebenen Sperma in Form von Strängen in der Nähe der Weibchen zu Boden und verbleibt dort eine ganze Weile, bevor sich die Stränge auflösen – genug Zeit, die Eier der Weibchen zu befruchten, die diese unter ihrem Körper ablegen. Die längliche Form der Spermienköpfe erlaubt dabei eine dichtere Packung der Spermien in den Spermatozeugmata und Spermatophoren (Atwood & Chia 1974, Atwood 1975) als dies mit kugeligen Köpfen möglich wäre.

Aus der bisherigen Darstellung geht hervor, dass Brutverhalten bei Holothurien möglicherweise gewisse evolutive Zwänge nach sich zieht, die zu ähnlichen Lösungen führen können, wie etwa die Verpackung von Spermatozoa zu größeren Einheiten und damit einhergehend eine Änderung der Spermienform. Im Detail aber sind die hier aufgezeigten Unterschiede im Bau der Spermien, oder in der Art und Weise des Brütens so groß, dass es sich sehr wahrscheinlich um parallele Entwicklungen handelt.

Damit lassen sich die Arten der Gattung *Echinopsolus* durch die folgende einmalige Merkmalskombination charakterisieren: (1) Arten getrenntgeschlechtlich. (2) Sexualdimorphismus, Genitalpapille bei Männchen permanent fingerförmig, bei den Weibchen oft klein

Tab. 4. Crinoidea und Holothuroidea des tieferen bathyalen und abyssalen Angola-Beckens (tiefer 1700 m) und benachbarter Bereiche, zusammengestellt nach verschiedenen Quellen. (Verändert nach Bohn 2006: Tab. 3)

Art	**Tiefe (m)**	**Quelle**
Bathycrinus aldrichianus Wyville Thomson, 1876	5415	Bohn 2006
Porphyrocrinus incrassatus (Gislén, 1933)	2400–2780	Gislén 1933
Deima validum validum Théel, 1879	4088–5426	Ifremer BIOCEAN, Bohn 2006
Psychropotes depressa (Théel, 1882)	2270	Hansen 1975
Psychropotes longicauda Théel, 1882	2475–3244	Ifremer BIOCEAN
Psychropotes semperiana Théel, 1882	3244–5126	Ifremer BIOCEAN, Bohn 2006
Peniagone diaphana (Théel, 1882)	3034	Ifremer BIOCEAN
Peniagone purpurea (Théel, 1882)	4660–5415	[1]Ifremer BIOCEAN, Bohn 2006
Achlyonice ecalcarea Théel, 1879	2400–2780	Hansen 1975
Achlyonice longicornis Bohn, 2006	5385–5387	Bohn 2006
Molpadiodemas atlanticus (R. Perrier, 1898)	4820–5415	[2]Ifremer BIOCEAN, Bohn 2006
Molpadiodemas depressus (Hérouard, 1902)	3034	[3]Ifremer BIOCEAN
Molpadiodemas involutus (Sluiter, 1901)	4613	[4]Ifremer BIOCEAN
Molpadiodemas villosus (Théel, 1886)	4550–4660	[5]Ifremer BIOCEAN
Mesothuria candelabra Hérouard, 1923	5220	Ifremer BIOCEAN
Paelopatides grisea R. Perrier, 1898	3035	Heding 1940
Paroriza pallens (Kœhler, 1896)	5124	Ifremer BIOCEAN
Molpadia musculus Risso, 1826	1756–4335	Ifremer BIOCEAN
[6]*Molpadia blakei* (Théel, 1886)	4335	Ifremer BIOCEAN
Molpadia liska Pawson, 1977	5385–5426	Bohn 2006
Protankyra brychia (Verrill, 1885)	2225–5426	[7]Ludwig & Heding 1935, [7]Ifremer BIOCEAN, Bohn 2006
Siniotrochus myriodontus Gage & Billett, 1986	5385–5389	Bohn 2005a, 2006a
Neolepidotrochus parvidiscus angolensis Bohn, 2005	5395	Bohn 2005a, 2006a

[1] als *Peniagone ferruginea* Grieg, 1921; [2] als *Pseudostichopus atlanticus* R. Perrier, 1898; [3] *Pseudostichopus depressus* Hérouard, 1902; [4] als *Pseudostichopus globigerinae* Hérouard, 1923; [5] als *Pseudostichopus villosus* Théel, 1886; [6] Bestimmung zweifelhaft, möglicherweise *M. liska* Pawson, 1977; [7] als *Protankyra abyssicola* (Théel, 1886)

und unscheinbar. (3) Weibchen mit fünf interradialen anterioren Bruttaschen. (4) Charakteristische Spermatozoa. (5) Spermatozoa zu Spermatozeugmata gebündelt.

In ihrer jetzigen Form umfasst die Gattung sieben antarktische Arten die sich in ihrer externen Morphologie (Anzahl, Form und Verteilung der Füßchen) als auch in der Ausprägung der Ossikel so stark unterscheiden, dass sie traditionell verschiedensten Gattungen in zwei verschiedenen Familien zugeordnet wurden (Psolidae und Cucumariidae, Tab. 3). Dem entgegen stehen aber die hier aufgezeigten Gemeinsamkeiten der sieben Arten, die in ihrer

Kombination so einmalig sind, dass kaum Zweifel an der Monophylie dieser Gruppe bestehen kann. Die Frage, warum sich diese Arten dennoch so stark unterscheiden, lässt sich relativ leicht mit Anpassungen an verschiedene ökologische Nischen erklären, vor allem das bevorzugte Substrat spielt hierbei ein große Rolle. Ein Teil der Arten beispielsweise lebt epizoisch auf Bryozoa- oder Hydrozoakolonien (Gutt 1988, 1991a, b), zwei Arten sogar ausschließlich auf den langen Primärstacheln von cidaroiden Seeigeln (Gutt 1988, 1991a, b, Massin 1992), was natürlich eine andere Morphologie bedingt, als eine aufsitzende Lebensweise auf Steinen oder Fels.

Noch nicht angesprochenen wurde die Tatsache, dass alle bisher beschriebenen dendrochiroten Holothurien mit interradialen anterioren Bruttaschen (siehe Tab. 3) ausschließlich im Südlichen Ozean verbreitet sind. Dazu gibt es deutliche Hinweise, dass auch die Arten, die bisher mit weniger als fünf Bruttaschen beschrieben wurden, in Wirklichkeit ebenfalls fünf Bruttaschen besitzen (siehe hierzu Bohn & Heß unveröffentlicht) und sehr wahrscheinlich ebenfalls der Gattung *Echinopsolus* zugerechnet werden müssen. Die Beschränkung dieser morphologisch variablen und möglicherweise artenreichen Gruppe auf den antarktischen Raum macht eine Diversifikation und Radiation im Südlichen Ozean wahrscheinlich. Damit eröffnen sich natürlich vollkommen neue und interessante Fragestellungen, wie etwa zur Phylogenie dieser Gruppe, denen baldmöglichst mit morphologischen und molekularen Methoden nachgegangen werden sollte.

Zusammenfassend lässt sich sagen, dass die Spermienmorphologie in bestimmten Fällen, trotz des vorherrschenden nahezu identischen Baus bei vielen Holothuroidea, ein nützliches Merkmal zur Beantwortung taxonomischer und phylogenetischer Fragestellungen sein kann. Auf Artebene reicht da schon die geringe morphologische Variabilität der „Standardspermien“ (Hodgson & Bernard 1992), allerdings nur ergänzend zu anderen Merkmalen. Aussichtsreicher und interessanter aber sind größere Abweichungen vom Standardbauplan, wie sie etwa im Falle von brütenden Arten zu erwarten sind (Atwood 1975).

Tab. 5. Schematische Verbreitung der Crinoidea und Holothuroidea des Angola-Beckens, die von mindestens zwei Fundorten bekannt sind. (Verändert nach Bohn 2006: Tab. 4)

Art	**Atlantischer Ozean**		**Indischer Ozean**		**Pazifischer Ozean**		**Südlicher Ozean**
	N	**S**	**N**	**S**	**N**	**S**	
Bathycrinus aldrichianus Wyville Thomson, 1876	+	+					
Porphyrocrinus incrassatus (Gislén, 1933)	+	+					
Deima validum validum Théel, 1879	+	+	+	+	+	+	
Psychropotes depressa (Théel, 1882)	+	+			+	+	
Psychropotes longicauda Théel, 1882	+	+		+	+	+	+
Psychropotes semperiana Théel, 1882	+	+	+	+			
Peniagone diaphana (Théel, 1882)	+	+		+	+	+	
Peniagone purpurea (Théel, 1882)	+	+		+	+		+
Achlyonice ecalcarea Théel, 1879	+	+		+	+	+	
Molpadiodemas atlanticus (R. Perrier, 1898)	+	+			+	+	
Molpadiodemas depressus (Hérouard, 1902)	+	+					
Molpadiodemas involutus (Sluiter, 1901)	+	+			+	+	+
Molpadiodemas villosus (Théel, 1886)	+	+		+	+	+	+
Mesothuria candelabra Hérouard, 1923	+	+					
Paelopatides grisea R. Perrier, 1898	+	+					
Paroriza pallens (Kœhler, 1896)	+	+					
Molpadia musculus Risso, 1826	+	+	+	+	+	+	+
Molpadia blakei (Théel, 1886)	+	+					
Molpadia liska Pawson, 1977		+				+	+
Protankyra brychia (Verrill, 1885)	+	+			+	+	
Siniotrochus myriodontus Gage & Billett, 1986	+	+					

N Nord; *S* Süd

2. Zoogeographie

2.1. Crinoiden und Holothurien des Angola Beckens

Das Angola-Becken liegt vor der Westküste Afrikas, auf Höhe von Angola und Namibia. Begrenzt wird es nach Osten durch die Küste Afrikas, nach Süden durch den Walfisch-Rücken und nach Westen durch den Mittelatlantischen-Rücken, eine klare Abgrenzung zum nördlicheren Guinea-Becken allerdings fehlt.

Aufsammlungen aus diesem Becken sind rar. Sowohl die Valdivia (Deutsche Tiefsee-Expedition, 1898–99) als auch die Galathea Expedition (Dänische Tiefsee-Expedition, 1950–52) beprobten bathyale und abyssale Bereiche nahe der Westküste Afrikas. Die vom Ifremer

(Institut français de recherche pour l'exploitation de la mer, Brest, Frankreich) mit NO „Jean Charcot“ durchgeführten Expeditionen Walda (05–08.1971) und Walvis (12.1978–01.1979) untersuchten unter anderem bathyale und abyssale Tiefen des Angola-Beckens nahe des Walfisch-Rückens und entlang der afrikanischen Küste. Hinzu kommt noch eine einzige Tiefseestation der Java-Südafrika Expedition von Dr. Mortensen vor St. Helena. Informationen zu den in diesem Rahmen gesammelten Crinoidea und Holthuroidea findet man bei Gislén (1933), Ludwig & Heding (1935), Heding (1940), Hansen (1975) und der Ifremer BIOCEAN Datenbank—bis dato sind eine Crinoiden Art und insgesamt 17 Holothurien Arten für dieses Becken nachgewiesen worden (siehe auch Tab. 4).

Ziel der DIVA I Expedition (Reise M 48/1 mit FS „Meteor“) war es, sechs geographisch voneinander getrennte Gebiete des bislang unbekannten zentralen Bereiches des abyssalen Angola-Beckens entlang eines etwa 700 km langen Transektes mit unterschiedlichem Gerät zu beproben (Türkay 2006).

Entlang dieses Transektes wurde an insgesamt 90 Stationen die benthische Fauna in einem Tiefenbereich zwischen 5120 m und 5450 m mit Agassiz-Trawl, Epibenthosschlitten, Kastengreifer und Multicorer beprobt. Dabei wurden an 12 Stationen insgesamt eine Crinoiden Art und neun Holothurien Arten gesammelt (Tab. 4). Zwei dieser Holothurien waren bis dato unbeschrieben (*Achlyonice longicornis* Bohn, 2006, *Neolepidotrochus parvidiscus angolensis* Bohn, 2005) und sowohl der Crinoide (*Bathycrinus aldrichianus* Wyville Thomson, 1876) als auch zwei weitere Holothurien (*Molpadia liska* Pawson, 1977 und *Siniotrochus myriodontus* Gage & Billett, 1986) sind Erstnachweise für das Angola-Becken, während alle anderen Holothurien bereits von früheren Aufsammlungen her bekannt waren (siehe Tab. 4).

Die einzige Art, die im Untersuchungsgebiet regelmäßig (auf sechs Stationen) und in höherer Stückzahl (bis zu sieben Exemplare) gefunden wurde, ist *Protankyra brychia* (Verrill, 1885), alle anderen Arten waren nur in ein oder zwei Proben vorhanden und dann auch meist nur mit ein oder zwei Exemplaren (siehe Bohn 2006).

Damit kennt man heute aus dem tieferen bathyalen und abyssalen Angola-Becken (tiefer 1700 m) insgesamt zwei Crinoidea aus der Ordnung Millericrinida und 21 Holothuroidea die sich auf die Elasipodida (8 Arten), Synallactidae (7 Arten), Molpadiidae (3 Arten) und die Apodida (3 Arten) verteilen (Tab. 4).

Abgesehen von den beiden Holothurienarten, deren Vorkommen bislang auf das Angola-Becken beschränkt ist (*A. longicornis, N. p. angolensis*), haben die meisten der verbleibenden Arten große Verbreitungsareale (Tab. 5). Offensichtlich ist auch die zoogeographische Nähe der Angola-Becken Crinoiden- und Holothurienfauna zu der der nordatlantischen Tiefseebecken – mit Ausnahme von *Molpadia liska* kommen alle bisher gefundenen Arten ebenfalls dort vor. Acht Arten sind momentan auf den Atlantik beschränkt, während alle anderen auch aus anderen Ozeanen bekannt sind. Der Einfluss einer „südlichen“ Tiefseefauna auf die Artenzusammensetzung der Angola-Becken Crinoidea und Holothuroidea scheint dagegen eher unbedeutend zu sein. Zwar kommen nicht weniger als sechs Arten auch im Südlichen Ozean vor, doch bis auf *M. liska* kann keine dieser als „südliche“ Art bezeichnet werden, da sie alle ein weites Verbreitungsgebiet im Atlantischen, Indischen und Pazifischen Ozean haben. *Molpadia liska* hingegen ist in ihrem Vorkommen nach jetzigem Wissensstand auf den südlichen Atlantik und Pazifik und den Südlichen Ozean beschränkt.

Zu sehr ähnlichen Ergebnissen kam Sibuet (1975) in ihrer Aufarbeitung der Tiefseeasteroiden des Guinea-, Angola- und Kap-Beckens, die im Rahmen der Walda Expedition gesammelt wurden. Von den 21 gefundenen Arten sind nur vier auf den Südatlantik beschränkt (zwei davon sind neue Arten), alle anderen kommen auch im Nordatlantik vor. Ebenso ist ein Einfluss einer subantarktischen abyssalen Asteroidenfauna auf die Asteroidenfauna des Kap- oder das Angola-Becken nicht ersichtlich. Sibuet (1975) schließt daraus, dass der Walfisch-Rücken keine effektive Barriere darstellt, die das Angola-Becken vom Kap-Becken trennt.

Die peracaride Krebsfauna des Angola-Beckens hingegen setzt sich aus vielen seltenen und wahrscheinlich neuen Arten, und nur wenigen Kosmopoliten und typischen atlantischen Arten zusammen (Brandt *et al.* 2005). Auch auf diese Fauna ist der Einfluss des Südlichen Ozeans zu vernachlässigen (Brandt *et al.* 2005).

Auffällig ist die Seltenheit kleiner, zur In- oder Epifauna gehörender Holothuroidea der Famile Myriotrochidae (Körperlänge bis wenige cm, normalerweise deutlich kleiner), welche in anderen Tiefseebecken regelmäßig mit dem Epibenthosschlitten oder dem Kastengreifer gesammelt werden. So fanden etwa Gage & Billett (1986) eine ganze Reihe verschiedener Arten dieser Gruppe im Gebiet des Rockall-Troges im NO Atlantik. Auch in den Tiefseeregionen des Südlichen Ozeanes, die im Rahmen der ANDEEP I–III Expeditionen besammelt wurden (Drake Passage, Weddell Tiefsee-Ebene, Süd-Sandwich-Graben), finden sich Myriotrochidae regelmäßig in den Proben aus dem Epibenthosschlitten und dem Kastengreifer (Gebruk *et al*. 2003, Bohn 2006). Obwohl die während der DIVA I Expedition eingesetzten Geräte fast baugleich mit denen der ANDEEP Expeditionen waren, konnte dennoch nur ein einziges Exemplar dieser kleinen Myriotrochidae (*N. p. angolensis*) erbeutet werden.

Ein ganz ähnliches Bild zeigen die Vergleiche der Tiefsee-Gastropodenfaunen des Guinea-, Angola- und Kap-Beckens mit denen der Weddell Sea durch Schrödl *et al*. (unveröffentlicht). Die Artenvielfalt der Gastropoda ist in den drei nördlichen Becken viel geringer als in den untersuchten Tiefseebecken des Südlichen Ozeans (Schrödl *et al*. unveröffentlicht). Dabei werden diese Tiefseegastropoda vorallem mit den gleichen Geräten gefangen, wie die kleinen Myriotrochidae.

2.2. Holothurien des Südlichen Ozeans – Anmerkung

Die Schelffauna des Südliche Ozeans (im biogeographischen Sinn alle Gebiete südliche der Polarfront z.B. Clarke & Johnston 2003, Clarke et al. 2007) hat sich über einen langen Zeitraum in Isolation entwickelt, denn der Austausch mit Faunen benachbarter Regionen wird durch umgebende Tiefseebecken und die Polarfront, die eine effektive natürliche Grenze darstellt (Crame 1999), erschwert. Charakteristisch für die Fauna des Südlichen Ozeans scheint ein hoher Anteil an Endemiten zu sein: in verschiedenen Gruppen variiert dieser Anteil auf Artebene zwischen 35 % und 90 % (Clarke & Johnston 2003). Auch für die Holothuroidea des Weddell Meeres konnte dies gezeigt werden. Nach Gutt (1991b) sind etwa 45 % der dort gefundenen Holothurienarten in ihrer Verbreitung auf den Südlichen Ozean beschränkt, und vernachlässigt man typische Tiefseeformen, so ist der Anteil der Endemiten sogar noch bedeutend höher (92 %). Auf einem höheren systematischen Niveau allerdings, wie etwa Gattung oder Familie, fand Gutt (1991b) keine Anzeichen einer ausgeprägten Radiation und Diversifikation im Südlichen Ozean.

Diese Aussage trifft so nicht mehr zu, denn zumindest die Gattung *Echinopsolus* hat in dieser Region eine bemerkenswerte Radiation erfahren hat. Die Gattung in ihrer jetzigen Form ist, ebenso wie die „potenziellen“ *Echinopsolus*-Arten (siehe Tab. 3), in ihrer Verbreitung auf den Südlichen Ozean beschränkt

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Artikel

1. Altnöder, A., Bohn, J.M., Rückert, I. & Schwabe, E. (2007) The presumed shelled juvenile of the parasitic gastropod *Entocolax schiemenzii* Voigt, 1901 and its holothurian host *Chiridota pisanii* Ludwig, 1886 (Gastropoda, Entoconchidae - Holothuroidea, Chiridotidae). *Spixiana*, 30, 187–199.

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The presumed shelled juvenile of the parasitic gastropod *Entocolax schiemenzii* Voigt, 1901 and its holothurian host *Chiridota pisanii* Ludwig, 1886*

(Gastropoda, Entoconchidae – Holothuroidea, Chiridotidae)

Andreas Altnöder, Jens Michael Bohn, Ina-Maria Rückert & Enrico Schwabe

Altnöder, A., J. M. Bohn, I.-M. Rückert & E. Schwabe (2007): The presumed shelled juvenile of the parasitic gastropod *Entocolax schiemenzii* Voigt, 1901 (Gastropoda, Entoconchidae) and its holothurian host *Chiridota pisanii* Ludwig, 1886 (Holothuroidea, Chiridotidae). – Spixiana **30/2:** 187-199

Four small shelled gastropods were found externally on the body wall of an apodid holothurian (*Chiridota pisanii* Ludwig, 1886), which was collected in the southern Chilean fjord region. Based on shell morphology and the host species we address these gastropods as the shelled juveniles of *Entocolax schiemenzii* Voigt, 1901, which as adult is a highly modified endoparasite in *Chiridota pisanii*. The holothurian host, as well as the juvenile parasites are thoroughly described, including a SEM study of the holothurian calcareous ring, the calcareous deposits and the juvenile gastropod shell. Furthermore, a detailed 3-D reconstruction of the juvenile for the first time allows a better understanding of its internal organisation.

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Introduction

Parasitic gastropods, in the majority eulimids, associated with Echinodermata as their hosts, are known from all major echinoderm taxa. All transitions, from simple ectoparasites to highly modified endoparasites occur. In his excellent review on the eulimid taxa associated with Echinodermata, Warén (1983) lists 33 species from 15 genera that parasitize on or in Holothuroidea, including the genus *Entocolax* Voigt, 1888 with altogether six described species (Tab. 1). As adults shell-less and highly modified, these endoparasites live in the coelomic cavity of apodid holothurians, where they are either attached to the body wall or to the intestine of their host (see Jangoux 1987: 220-222). Lützen (1968) outlined the morphology of the adults as follows: they are more or less vermiform, have a rudimentary intestine and a central cavity, called pseudopallial cavity, where the egg capsules are brooded; a visceral sac containing the ovary protrudes into the pseudopallial cavity which communicates via a small siphon with the exterior.

As opposed to the highly modified morphology of adult *Entocolax* specimens, the juveniles correspond to the usual gastropod bauplan (e.g. Schwanwitsch 1917, Heding 1934, Heding in Heding & Mandahl-Barth 1938, Iwanow 1945, Schwanwitsch 1946). In his elaborate study on the morphology of *E. schwanwitschi* Heding in Heding & Mandahl-

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Barth 1938 (= *E. ludwigi* sensu Schwanwitsch 1917), Schwanwitsch (1917) also describes the morphology of the juveniles of this species in detail. Shelled juveniles have been reported for all *Entocolax* species (see Tab. 1) except for *E. schiemenzii* Voigt, 1901 and *E. chiridotae* Skarlato, 1951, where the juveniles are unknown.

Herein, we present the juveniles of a gastropod found externally on the body wall of the apodid holothurian *Chiridota pisanii* Ludwig, 1886, which was collected in the southern Chilean fjord region. So far, parasitism on *C. pisanii* is known only from a single eulimid gastropod, *Entocolax schiemenzii*, to which we assign the four juveniles.

Records of *Chiridota pisanii* are not rare and the species has been described in detail (e.g. Ludwig 1886, 1898a, Ekman 1925, Heding 1928). The current knowledge on the morphology of the holothurian host is complemented by a detailed description and figures of the calcareous ring plates and figures and in-depth measurements of the calcareous deposits, which so far have been lacking.

Materials and methods

Host. Small pieces of body wall were macerated in a 12.5 % sodium hypochlorite solution to gain the calcareous deposits. These were rinsed several times in distilled water, then air-dried and finally mounted in Canada balsam on slides. The calcareous deposits were analysed with a Leitz microscope equipped with a video camera (380 USB 2.0 Spacec@m) and the software AxioVision LE. For SEM examinations (Scanning Electron Microscope) the calcareous deposits were transferred to aluminum stubs, sputtered with gold and studied in a LEO 1430 VP Scanning Electron Microscope.

Parasite. The juvenile gastropods were removed from the host's body wall with the aid of a scalpel. For SEM examinations of the shell, one specimen was handled as described in Schwabe and Ruthensteiner (2001). To enable thorough examination, the shell was attached to a needle, which was glued to a stub. For histology, one specimen was embedded in Spurr's medium according to the method of Spurr (1969) and serially sectioned in 1.5 µm steps. The 3-D reconstruction was done with the software Amira 3.1.1. Pictures of all slices were taken, combined to a stack and afterwards aligned with the "slice aligner". The organs on every third slice were marked manually, then connected with the "interpolate" tool and finally the surface of each organ was reconstructed using the "surface gen" and the "smooth surface" tool.

The investigated material is deposited in the Zoologische Staatssammlung München (ZSM). Individual numbers (JMB-) are assigned to holothurian specimens, to allow confident recognition of specimens within a lot.

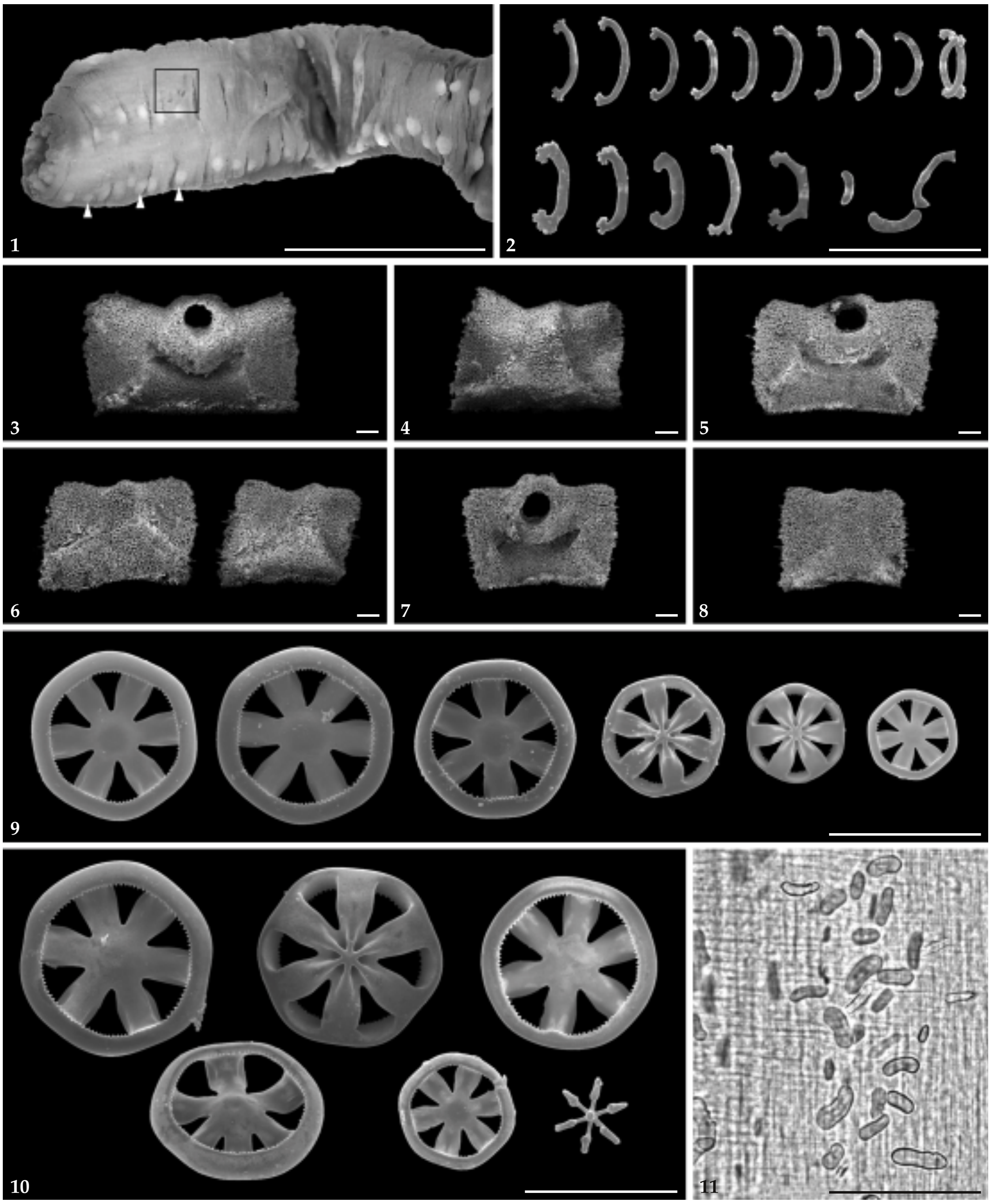
Results and Discussion

Host

Class Holothuroidea de Blainville, 1834, Order Apodida Brandt, 1835, Family Chiridotidae Østergren, 1898, Genus *Chiridota* Eschscholtz, 1829.

Tab. 1. *Entocolax* Voigt, 1888 species, their holothurian hosts, their distribution and reports of juvenile shells.

Species	Host	Distribution	Juvenile shells
E. chiridotae Skarlato, 1951	*Chiridota pellucida* (Vahl, 1806)	Sea of Japan	no juveniles reported
E. ludwigii Voigt, 1888	*Myriotrochus rinkii* Steenstrup, 1851	Greenland	Heding & Mandahl-Barth (1938: 15, figs 16-18)
E. rimskykorsakovi Iwanow, 1945	*Myriotrochus mitsukurii* Ohshima, 1915	Sea of Japan	juveniles only sparsely described, shell mentioned
E. schiemenzii Voigt, 1901	*Chiridota pisanii* Ludwig, 1886	SE Pacific (Chile)	**herein**
E. schwanwitschi Heding in Heding & Mandahl-Barth, 1938	*Myriotrochus eurycyclus* Heding, 1935	Kara Sea	Schwanwitsch (1917: 39, pl. 2, figs 32-33); Heding & Mandahl-Barth (1938: 15, figs 16a-18a)
E. trochodotae Heding, 1934	*Trochodota purpurea* (Lesson, 1830)	Southern South America or Falkland Islands	Heding (1934: 213, fig. 14); Heding & Mandahl-Barth (1938: 9)



Figs 1-11. *Chiridota pisanii* Ludwig, 1886. **1.** Anterior third of specimen infested with *Entocolax schiemenzii* Voigt, 1901, box indicates position of four parasites (see also Fig. 19), arrowheads point on wheel papillae. **2.** Tentacular rods. **3-7.** Plates of calcareous ring. **3.** Mid-ventral radial plate. **4**. Left ventral interradial plate. **5.** Left ventral radial plate. **6.** Left lateral interradial plates. **7.** Left dorsal radial plate. **8.** Mid-dorsal interradial plate. **9.** Wheel deposits from anterior body wall. **10.** Wheel deposits from posterior body wall. Star-shaped structure on lower right is a developing wheel. **11.** Miliary granules of longitudinal muscles. Scale bars: Fig. 1: 10 mm, Figs 2-11: 100 µm.

Chiridota pisanii Ludwig, 1886
Figs 1-12

Chirodota pisanii [sic!] Ludwig, 1886: 29, pl. 2 (fig. 14). – Lampert 1889: 851.

Chiridota pisanii, Ludwig 1892a: 359; 1892b: 350, pl. 16 (figs 1-9); 1898a: 71; 1898b: 445; Perrier 1905: 79; Clark 1908: 29, 118; Ekman 1925: 143, fig. 37; Heding 1928: 297, fig. 62 (1-9); 1931: 682, fig. 14; Deichmann 1947: 347; Pawson 1964: 464; 1969: 140; O'Loughlin 2002: 298 [partim: Tierra del Fuego specimens].

Chirodota purpurea [sic!] Théel, 1886: 15, pl. 2 (fig. 1). – Lampert, 1889: 851 [non *Holothuria purpurea* Lesson, 1830].

Chiridota purpurea, Ludwig, 1892a: 359, pl. 1 (fig. 5) [non *Holothuria purpurea* Lesson, 1830].

Anapta fallax Ludwig, 1898a: 70 [non *Anapta fallax* Lampert, 1889].

Type material. Chile, De Los Chonos, Puerto Lagunas, [45°17'S 73°43'W], coll. G. Chierchia, Dec. 1882, in sand and under stones (whereabouts unknown, 8 syntypes).

Material examined. Chile, Los Lagos, Caleta Gonzalo, 42°33'S 72°36'W, 15-25 m, coll. V. Häussermann and G. Försterra, 17 Jan. 2000 (ZSM Ev20043114, 1 specimen infested with *Entocolax schiemenzii*). Chile, Magallanes y Antartica Chilena, Cabo Direccion, 52°20.98'S 69°29.13'W, intertidal zone: coll. J. M. Bohn and M. Schrödl, 26 Feb. 2002, in tide puddles under stones on a muddy bottom (ZSM Ev20043115, 10 specimens without parasites); coll. J. M. Bohn and E. Schwabe, 09 Apr. 2005, same habitat (ZSM Ev20043137, 3 specimens without parasites).

Description

Investigated specimens up to 68 mm long (-130 mm Ludwig 1898b), width close to calcareous ring 6.3 mm (Fig. 1). Preserved specimens dirty white to pinkish. Alive, specimens dark red ("crimson" Ludwig 1898b, "carmine" Ekman 1925, "purplish" Deichmann 1947), shallow water specimens may lack reddish pigment (Deichmann 1947).

Tentacles 12, with 4-7 pairs of lateral digits, which get continuously longer from proximal to distal. Calcareous deposits of tentacles bracket-shaped rods with more or less branched ends (Fig. 2), sometimes with knob like swelling close to middle. On average rods are 45.8 µm long and range from 16 to 69 µm (Tabs 2, 3).

Calcareous ring (Figs 3-8) consists of 5 radial and 7 interradial plates. Left and right dorsal interradius each with two interradial plates (Fig. 6). All radial plates perforated for passage of nerve (Figs 3, 5, 7). According to Heding (1928, 1931), mid-ventral radial plate somewhat variable, sometimes perforated for passage of nerve, sometimes only with anterior notch.

Gonad consists of tuft of few, thick, long, sometimes branching tubules on both sides of dorsal mesentery. Sexes separate (Ludwig 1898a, Heding 1928). Polian vesicles 4-11 (-16, Théel 1886). Stone canal single. Intestine with large loop, bending close to anterior and posterior end of specimen. Single ciliated urns at base of mesenteries, numerous in mid-dorsal and left dorsal interradius, scarce in right ventral interradius.

Calcareous deposits of body wall chiridotid type wheels, gathered together in papillae, arranged in single interradial rows (Fig. 1: arrowheads). Papillae usually distinct in dorsal interradii (at least in mid-dorsal interradius), inconspicuous or lacking in ventral interradii. Some specimens only have one distinct row in mid-dorsal interradius, while others have distinct rows in all three dorsal interradii. Ekman (1925) even reported on specimens with two rows of papillae in mid-dorsal interradius. Size of papillae variable, according to Heding (1928) up to

Tab. 2. *Chiridota pisanii* Ludwig, 1886. Measurements of tentacular rods and wheel deposits from anterior and posterior parts of body of four specimens: means, standard deviations (in parentheses) and range. **n**, number of measurements; **tr_l, µm**, length of tentacular rods; **w_d, µm**, diameter of wheels; **w_s, n**, number of spokes per wheel.

Parameter	Specimen			
	ZSM Ev20043114	ZSM Ev20043115		
		JMB-01326	JMB-01632	JMB-01633
tr_l, µm	49.1 (±9.7) 34-69 [n = 50]	42.1 (±6.6) 27-60 [n = 50]	43.9 (±11.0) 16-63 [n = 50]	47.9 (±9.5) 26-67 [n = 50]
w_d, µm (anterior) w_s, n (anterior)	86.7 (±18.6) 43-121 6.0 (±0) 6 [n = 50]	101.9 (±6.8) 82-115 6.5 (±0.6) 6-8 [n = 27]	90.0 (±10.0) 65-109 6.3 (±0.5) 6-8 [n = 50]	98.3 (±8.7) 76-117 6.1 (±0.4) 5-7 [n = 50]
w_d, µm (posterior) ws, n (posterior)	107.3 (±20.5) 65-147 6.0 (±0.2) 6-7 [n = 50]	115.5 (±7.0) 104-134 6.3 (±0.5) 6-8 [n = 27]	94.4 (±9.0) 70-110 6.1 (±0.2) 6-7 [n = 50]	105.0 (±8.1) 90-125 6.1 (±0.4) 6-8 [n = 50]

2.3 mm in diameter, but papillae may also merge to form longitudinal band up to 11 mm long (Ekman 1925).

Wheel deposits (Figs 9-10) mean diameter of about 100 µm and range from 43 to 147 µm. Wheels from anterior end of body on average somewhat smaller than wheels from posterior end. Spokes usually 6, only few wheels with 7 or 8. Serration on inner side of wheel continuous. For details of wheel measurements see Tabs 2 and 3.

Calcareous deposits of longitudinal muscles oval to elongated, sometimes curved, often rod-like miliary granules (Fig. 11), 14-49 µm long (Tab. 3).

Distribution (Fig. 12). Pacific and Atlantic coast of southern South America (south of 42°S), Falkland Islands; intertidal zone to 102 m.

Habitat. Prefers sediment bottoms, primarily muddy or sandy, rarely also on seaweeds: *Macrocystis* fronds and holdfasts (Pawson 1964). These sediment bottoms are often covered with stones or boulders: gravel and clay, mixed with mud and covered with boulders or sand gravel and muddy clay covered with boulders or boulders and stones on sand (all from Pawson 1969), underneath which the animals seem to live: in sand under stones (Ludwig 1898a, Ekman 1925) or on a muddy bottom under stones (this study).

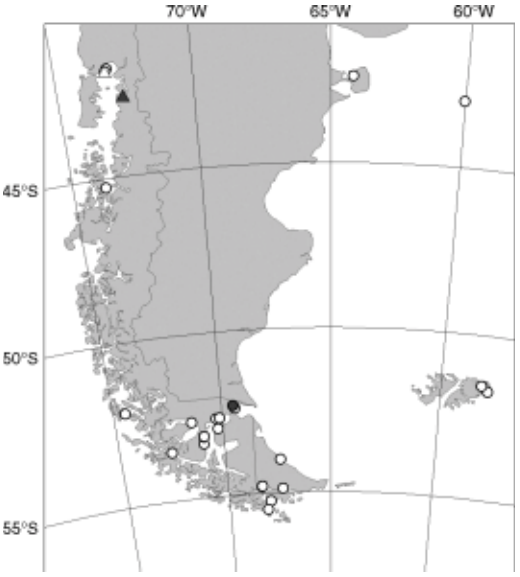


Fig. 12. Distribution of *Chiridota pisanii* Ludwig, 1886 (○,●) and its parasite *Entocolax schiemenzii* Voigt, 1901 (△,▲). Filled labels indicate investigated material, all other records are from literature. (Distribution data have been compiled from several sources, see references in synonymy of *C. pisanii*)

Remarks. The specimens from both localities (Caleta Gonzalo and Cabo Direccion) in most details correspond to the descriptions given by earlier authors. Though records of this species are not rare, figures and measurements of the calcareous deposits are scarce (see Tab. 3). The size range given by Ekman (1925) for wheel deposits fit very well with our measurements (Tab. 3). The same is true for the sizes of wheel deposits, tentacular rods and miliary granules as presented by Heding (1928) or of the tentacular rods as given by Pawson (1964).

Contrary, wheel deposits of the Falkland Island specimens collected by the Challenger Expedition (Théel 1886) are conspicuously larger (140-160 µm, see Tab. 3). In the current specimens, only three out of 354 wheels have a diameter larger than 140 µm. Such striking differences in size ranges of wheel deposits usually are thought to indicate different species. On the other hand, there can be little doubt that *Chiridota pisanii* does also occur at the Falkland Islands, since some of the specimens investigated by Ekman (1925) originated there, and the measurements presented by Ekman for wheel deposits are very close to ours.

Tab. 3. *Chiridota pisanii* Ludwig, 1886. Measurements of tentacular rods, wheel deposits and miliary granules of the investigated specimens compared to published measurements compiled from different sources: means, standard deviations (in parentheses) and range. **mg_l, µm**, length of miliary granules; **n**, number of measurements; **tr_l, µm**, length of tentacular rods; **w_d, µm**, diameter of wheels; ^{1}, length of tentacular deposits (fig. 62.8-9) and miliary granules (fig. 62.3-4) calculated from Heding's fig. 62; ^{2}, Tierra del Fuego specimens described in O'Loughlin (2002).

Parameter	Source										
	Present study	(1886)		(1925)		(1928)		(1964)		(pers. comm.)^2	
tr_l, µm	45.8 (±9.7) 16-69 [n=200]	–	–	–	–	–	32-63^1	50	–	–	32-48
w_d, µm	98.7 (±15.3) 43-147 [n=354]	–	140-160	–	80-140	–	70-130	–	–	–	72-104
mgl, µm	29.5 (±7.3) 14-49 [n=100]	–	–	–	–	–	24-44^1	–	–	–	24-32

The measurements given by O'Loughlin (2002) for specimens from Tierra del Fuego and Heard Island also differ to some extent from our own. This is mainly based on the fact that measurements from both localities are presented as a mix (O'Loughlin pers. comm.). If measurements of calcareous deposits from each locality are considered apart, it becomes evident that the Heard Island specimens may represent a different species, closely related to *Chiridota pisanii*, which will be described by O'Loughlin in near future (pers. comm.). The Tierra del Fuego specimens on the other hand seem to be conspecific with our specimens. Sizes of calcareous deposits are very similar to our own (see Tab. 3).

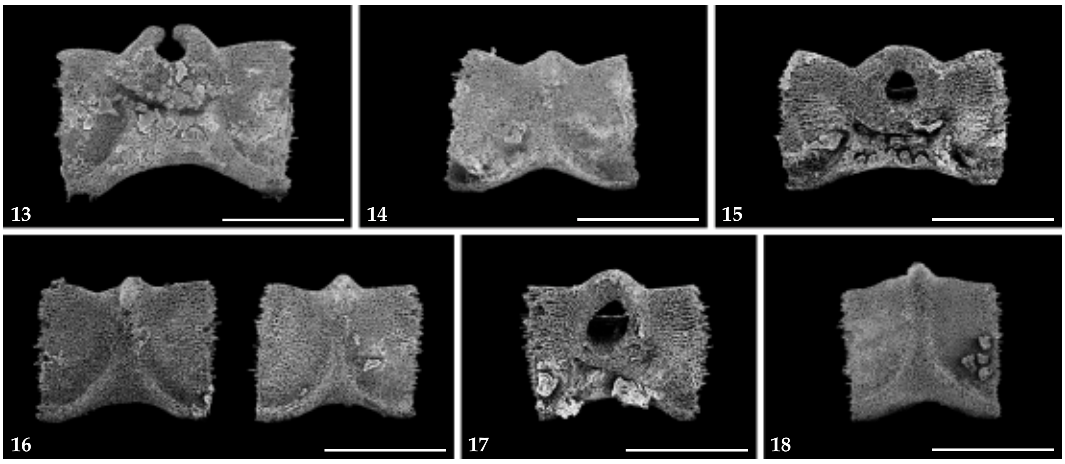
The afore mentioned differences in calcareous deposit sizes usually are thought to indicate the presence of more than a single species under the name *Chiridota pisanii*. But until now, knowledge on the variability of deposit sizes within chiridotid species is scarce. Smirnov et al. (2000) for example relate an increase in wheel size in *Chiridota hydrothermica* Smirnov & Gebruk, 2000 with somatic growth, smaller specimens have considerably smaller wheels than larger specimens. Whether this is also true for *C. pisanii* is unknown. Wheel deposit measurements are derived from specimens with a diameter close to the calcareous ring ranging from 3.8 to 5.5 mm, which is close to the total size range (3.3 to 6.3 mm) of specimens at hand. There seem to be no differences in wheel sizes between the smallest (Tab. 2: JMB-01633) and the larger specimens.

Chiridotid and synaptid holothurians have long been thought to possess a calcareous ring composed of as many pieces as there are tentacles, that is 12 tentacles should result in 12 calcareous ring plates, five radialia and seven interradialia (e.g. Clark 1908). This traditional view has changed considerably during the last years. Nowadays many of the Apodida with 12 tentacles have been shown to possess only 10 plates in the calcareous ring, with the two dorsolateral radial plates being bipartite, to allow the insertion of the additional tentacles. This has been demonstrated for all Myriotrochidae investigated hereupon (e.g. Belyaev & Mironov 1982, Gage & Billett 1986, Smirnov 1999, Bohn 2005), for some Synaptidae (e.g. Smirnov 1983, Gage 1985, Bohn unpublished data) and also for some Chiridotidae (e.g. Smirnov 1981, Smirnov et al. 2000). "Thus, according to modern views, apodid species with 12 tentacles have ten pieces of calcareous ring with two dorsolateral pieces being bipartite, i.e. bearing two anterior processes ..." (Smirnov et al. 2000: 325), but nature seems not to adhere so strictly to this "modern view".

Concerning the genus *Chiridota*, Heding (1928: 281) states that the "... calcareous ring consists in all species examined of twelve pieces". According to various authors, at least 13 of about 30 known

Tab. 4. Morphology of the calcareous ring in the genus *Chiridota* Eschscholtz, 1829 compiled from several sources. [1], as *Chirodota purpurea* Lesson, 1830.

Species	Source	
	10 plates	12 plates
Chiridota albatrossii Edwards, 1907		Heding 1928
Chiridota aponocrita H. L. Clark, 1920		Heding 1928
Chiridota carnleyensis Mortensen, 1925		Mortensen 1925
Chiridota discolor Eschscholtz, 1829	Smirnov et al. 2000	
Chiridota fernandensis Ludwig, 1898		Ludwig 1898b
Chiridota gigas Dendy & Hindle, 1907		Hickman 1962
Chiridota hawaiiensis Fisher, 1907		Fisher 1907, Heding 1928
Chiridota heheva Pawson & Vance, 2004	Pawson & Vance 2004	
Chiridota hydrothermica A. V. Smirnov & Gebruk, 2000	Smirnov et al. 2000	
Chiridota laevis (O. Fabricius, 1780)	Smirnov et al. 2000, **herein**	Heding 1935
Chiridota marenzelleri R. Perrier, 1904	Perrier 1905	
Chiridota nigra Mortensen, 1925		Mortensen 1925, Pawson 1970
Chiridota ochotensis Saveljeva, 1941	Smirnov et al. 2000	
Chiridota orientalis A. V. Smirnov, 1981	Smirnov 1981	
Chiridota pacifica Heding, 1928		Heding 1928
Chiridota pisanii Ludwig, 1886		Théel 1886[1], Heding 1928, **herein**
Chiridota rigida Semper, 1868		Heding 1929
Chiridota rotifera (Pourtalès, 1851)		Ludwig 1881, Heding 1928, **herein**
Chiridota stuhlmanni Lampert, 1896		Heding 1928, Cherbonnier 1988
Chiridota tauiensis Saveljeva, 1941	Smirnov et al. 2000	



Figs 13-18. *Chiridota rotifera* (Pourtalès, 1851), plates of calcareous ring. **13.** Mid-ventral radial plate. **14.** Left ventral interradial plate. **15.** Left ventral radial plate. **16.** Left lateral interradial plates. **17.** Left dorsal radial plate. **18.** Mid-dorsal interradial plate. Scale bars: Figs 13-18: 500 µm.

species (see Tab. 4) have been described to possess a calcareous ring with 12 pieces (e.g. Cherbonnier 1988, Fisher 1907, Heding 1928, 1929, 1935, Hickman 1962, Ludwig 1881, 1898b, Mortensen 1925, Pawson 1970, Théel 1886). On the other hand, there are currently eight species said (Tab. 4) to have a calcareous ring composed of 10 plates (Pawson & Vance 2004, Perrier 1905, Smirnov 1981, Smirnov et al. 2000), among them one of the species stated by Heding (1935) to possess 12 calcareous ring plates.

Based on own experience, the exact number of pieces constituting a calcareous ring can only be identified by dissecting, as borders separating adjoining pieces usually are concealed, and thus impossible to make out in an entire ring. To unravel these to some extent conflicting data, a detailed reexamination of *Chiridota* calcareous rings would be appropriate. To make a first move, two further species, represented in the Bavarian State Collection of Zoology, were investigated – *Chiridota laevis* (O. Fabricius, 1780) and *Chiridota rotifera* (Pourtalès, 1851).

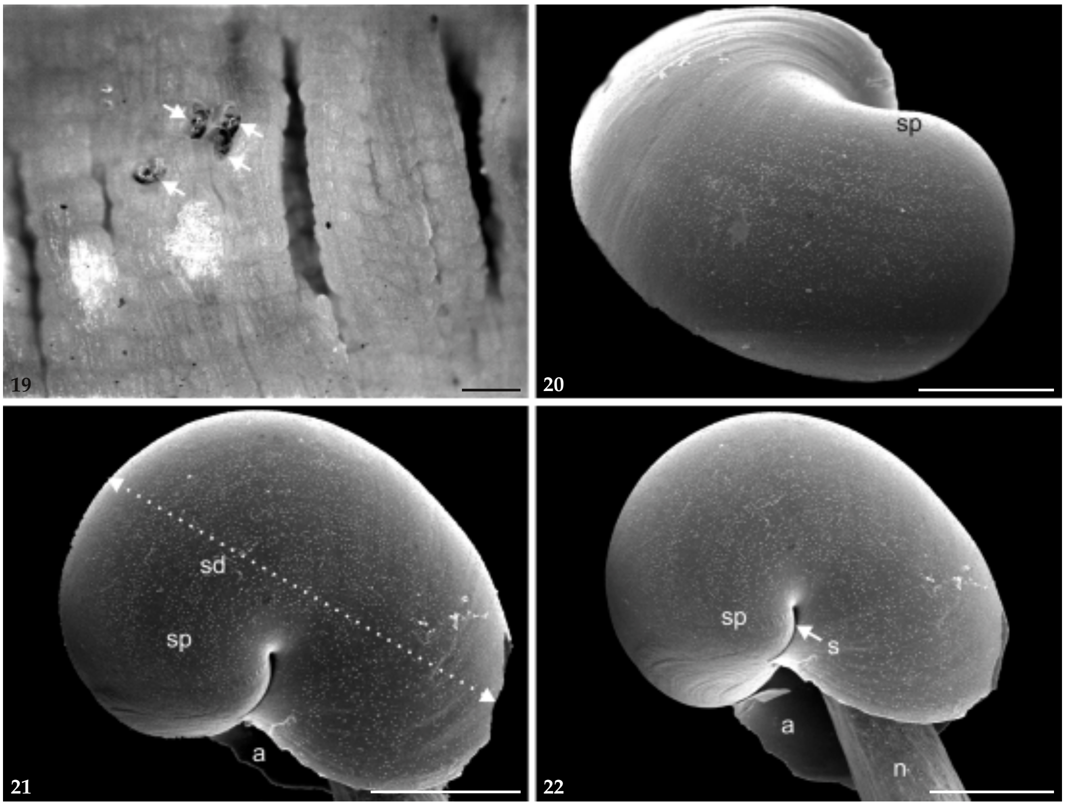
Chiridota laevis (O. Fabricius, 1780), specimen from Svalbard, Brandalpynten, 78°56.8'N 11°51.5'E, 15 m, coll. M. Hermann, 11 Jun. 2003. Calcareous ring composed of 10 pieces, five perforated radialia and five interradialia. This result is in accordance with the information given by Smirnov et al. (2000) for this species, while it refutes Heding (1935), who described the presence of 12 plates (see Tab. 4).

Chiridota rotifera (Pourtalès, 1851), specimen from Brazil, Rio de Janeiro, Búzios, Ilha do Cabloco, 0-3 m, coll. M. Schrödl, Nov. 2002. Calcareous ring composed of five radialia and seven interradialia, with two interradialia present in each lateral interradius (Figs 13-18). All radialia perforated, except for the mid-ventral one, which instead is anteriorly notched. This coincides with the data presented by Ludwig (1881) and Heding (1928).

The interpretation of these two types of calcareous ring morphologies with regard to taxonomy and phylogeny of the genus *Chiridota* is far from clear. A combination of 12 tentacles and a calcareous ring composed of 10 pieces, with the two dorsolateral radial plates beeing bipartite, probably is a synapomorphic feature for Apodida (see above; Myriotrochidae are thought to be the most basal apodid taxon, e.g. Kerr 2001), and thus is plesiomorphic for *Chiridota*. A calcareous ring composed of 12 pieces, with two interradialia in each lateral interradius, on the other hand, seems to be a synapomorphic feature of a subgroup within the genus *Chiridota* (so far demonstrated for *C. pisanii* and *C. rotifera*), that may provide useful information to reconstruct their phylogeny. But today, knowledge on the structure of the calcareous ring and its variability within the genus *Chiridota* is still too scarce, to draw any conclusions, and more reliable data are urgently needed.

Parasite

Class Gastropoda Cuvier, 1795, Superorder Caenogastropoda Cox, 1960, Order Sorbeoconcha Ponder & Lindberg, 1997, Superfamily Eulimoidea Philippi, 1853, Family Entoconchidae Gill, 1871, Genus *Entocolax* Voigt, 1888, *Entocolax* Voigt, 1888: 658. Type species (by monotypy): *Entocolax ludwigii* Voigt, 1888; recent.



Figs 19-22. *Entocolax schiemenzii* Voigt, 1901. **19.** Four juvenile specimens in their natural position on the host (arrows). **20-22.** Larval shell in different views. **a**, aperture; **n**, needle (to fix specimen on stub); **s**, suture; **sd**, shell diameter; **sp**, spire. Scale bars: Fig. 19: 500 µm, Figs 20-22: 100 µm.

Entocolax schiemenzii Voigt, 1901

Figs 12, 19-31

Entocolax sp. Ludwig, 1897: 248; 1898b: 446.

Entocolax schiemenzii Voigt, 1901: 286. Tikasingh & Pratt 1961: 65; Lützen 1979: 40.

Entocolax schiemenzi, Schwanwitsch 1917: 104; Thiele 1931: 231; Heding & Mandahl-Barth 1938: 5; Iwanow 1945: 534; 1947: 4; Skarlato 1951: 362; Warén 1983: 41.

Entocolax schimenzi [sic!], Heding 1934: 214.

Type material. Chile, Los Lagos, Calbuco, [41°45'S 73°08'W], coll. L. Plate, Nov.-Dec. 1894, in *Chiridota pisanii* specimens burried in the sand of the beach (whereabouts unknown, 2 syntypes).

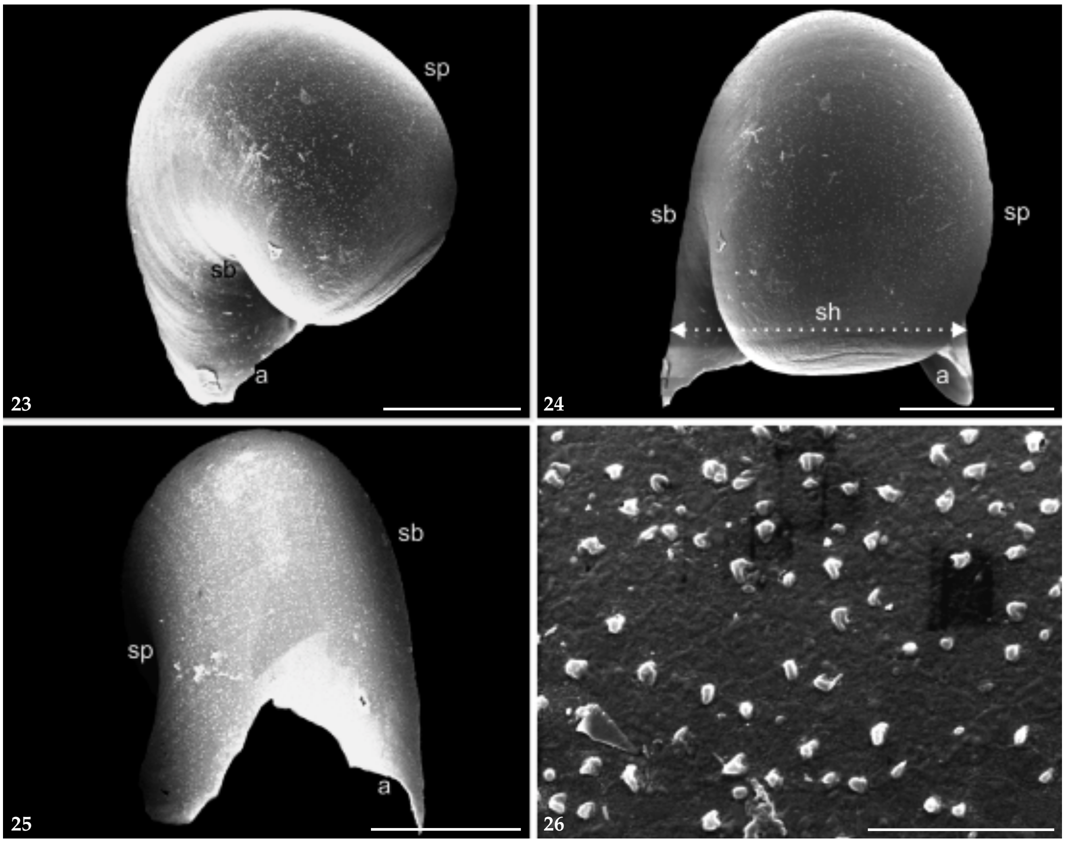
Material examined. Chile, Los Lagos, Caleta Gonzalo, [42°33'S 72°36'W], 15-25 m, coll. V. Häussermann and G. Försterra, 17 Jan. 2000, externally on a *Chiridota pisanii* specimen (ZSM Moll20051307, 4 juveniles).

Description

Four specimens attached to body wall of holothurian host (with proboscis or foot?), close to its anterior end in right dorsal interradius (Figs 1, 19), somewhat embedded in skin.

Glossy, transparent, orthostrophic, paucispiral, dextral shell smooth, thin, consists of 1.5 protoconch whorls only (Figs 21-22). Shell depressed, aperture nearly elliptical. Suture (Fig. 22) clearly indicated, umbilicus absent. Shell with microsculpture of very fine spiral threads of irregularly formed (mainly hook-like) and arranged calcareous splits (Figs 20-21, 26). Spiral bands have higher density at top of shell, become less distinct to absent towards base. Maximum shell hight may attain 200 µm (close to youngest aperture edge, Fig. 24), maximum shell diameter 308 µm (Fig. 21).

Histologically examined specimen (Figs 27-31) bent and about 282 µm long. Soft part of body, completely covered by shell, clearly differentiated into head and fleshy, elongated foot which is poste-



Figs 23-26. *Entocolax schiemenzii* Voigt, 1901. **23-25.** Larval shell in different views. **26.** Detail of the micro "sculpture" of the shell. **a**, aperture; **sb**, shell base; **sh**, shell hight; **sp**, spire. Scale bars: Figs 23-25: 100 µm, Fig. 26: 10 µm.

riorly covered by operculum, about 68 µm in diameter. Ventral mouth opens into large oesophagus, which leads into simple, sac-like stomach. Gastric shield situated on right side of stomach (Fig. 29: *gs*). Dorsally, stomach connects to intestine, which forms three loops (Fig. 27: *i*) and ends in short rectum. Anus missing. Large midgut gland situated on ventral side of stomach, consisting of two lobes, of which right one is considerably smaller. Yolk scattered throughout whole body, especially around midgut gland (Fig. 29: *y*). Foot gland (detailed structure unknown) situated in body cavity above foot anterior of operculum.

Pair of statocysts (Fig. 28: *st*) of about 21 µm in diameter situated ventrally of oesophagus. Each with single globular statolith. Dorsally, pair of eyes present (Figs 28, 31: *e*), situated at base of large cephalic tentacles (Figs 27-28, 31: *t*). Eyes smaller than statocysts, with well developed round lenses in black pigmented cup. Due to state of preservation, no other parts of nervous system could be detected.

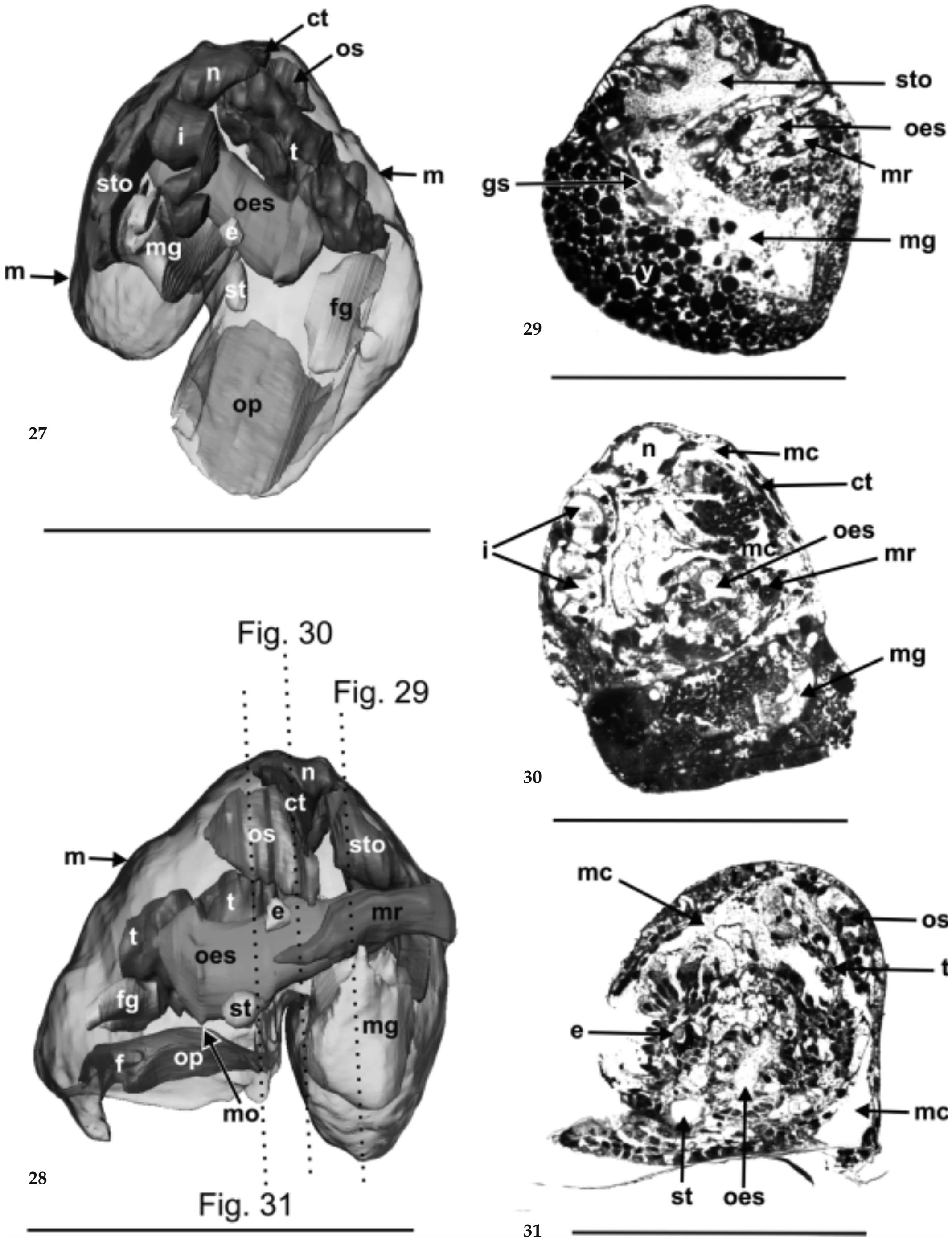
Dorsal nephridium well developed (Figs 27-28, 30: *n*), with connection to mantle cavity. No heart. Ctenidium small, on dorsal left side of body, extending into mantle cavity (Figs 28, 30: *ct*). Osphradial organ well developed, located in front of ctenidium (Figs 27-28, 31: *os*).

Retractor muscle (Figs 28-30: *mr*) attached to shell on posterior side of specimen, attains nearly half length of body.

Distribution (Fig. 12)**.** Chile, Los Lagos: Calbuco (type locality) and Caleta Gonzalo; intertidal zone to 25 m.

Remarks. In accordance with article 33.4 of the fourth edition of the International Code for Zoological Nomenclature (1999) we consider the subsequent spellings of *schiemenzii* as incorrect and use the original spelling.

There are several reasons that corroborate our belief, to address these gastropods as the juveniles



Figs 27-31. *Entocolax schiemenzii* Voigt, 1901. **27-28.** 3-D reconstruction of a juvenile. **27.** Dorso-lateral view from right side (anterior end to the right). **28.** Lateral view from left side (anterior end to the left). **29-31.** Transverse sections (1.5 µm thick). **ct**, ctenidium; **e**, eye; **f**, foot; **fg**, foot gland; **gs**, gut shield; **i**, intestine; **m**, mantle; **mc**, mantle cavity; **mg**, midgut gland; **mo**, mouth; **mr**, retractor muscle; **n**, nephridium; **oes**, oesophagus; **op**, operculum; **os**, osphradium; **st**, statocyst; **sto**, stomach; **t**, tentacle; **y**, yolk. Scale bars: Figs 27-31: 200 µm.

of the endoparasitic *Entocolax schiemenzii* which yet are undescribed.

There are only three eulimid genera known to be associated with apodid holothurians, viz. *Entocolax* with altogether six described species, and *Entoconcha* Müller, 1852 and *Mucronalia* A. Adams, 1860 with one species each (Warén 1983, Jangoux 1987). *Mucronalia variabilis* Schepman, 1914 is shelled and lives as an ecto- or endoparasite (Jangoux 1987) associated with the synaptid holothurian *Patinapta ooplax* (Marenzeller, 1881), whereas the species of the other genera are highly modified and as adults shell-less endoparasites (Warén 1983, Jangoux 1987). The larval shell morphology of our specimens fits very well with that known from species of the afore mentioned genera *Entocolax* and *Entoconcha* (see Schwanwitsch 1917, Heding 1934, Heding & Mandahl-Barth 1938). Furthermore, the only gastropod species known so far to be associated with *Chiridota pisanii* is *Entocolax schiemenzii*. Less than 100 km beeline separate the type locality (Chile: Calbuco) from the locality where our specimens have been collected.

The morphology of the juveniles too, does not contradict our assumption, that the present juvenile gastropod specimens represent *E. schiemenzii*, although knowledge so far is quite scarce. Young *E. schiemenzii* specimens have never been described nor figured in detail, but four of the six species of *Entocolax* are known to have a larval shell (see Tab. 1). Until now, the most detailed description of *Entocolax*-larvae was given by Schwanwitsch (1917), who conscientiously investigated the juveniles of *Entocolax schwanwitschi* Heding in Heding & Mandahl-Barth, 1938 (under the name *Entocolax ludwigi*). They have a velum, a simple digestive tract consisting of a pharynx and a bipartite intestine, a paired foot gland, a gonad, 3 pairs of fused ganglia and an unpaired ganglion, a retractor muscle, a pair of statocysts, yolk and an operculum. Schwanwitsch does neither mention the occurrence of eyes, an osphradium, a ctenidium nor a nephridium. Heding (1934) states the presence of a distinct velum and probably an operculum for juveniles of *E. trochodotae* Heding, 1934. Larvae of *E. rimskykorsakovi* Iwanow, 1945 posses "… a shell, a mantle, a cephalic lobe, a foot with pedal glands, and an operculum. Nervous ganglia, statocysts and a sex rudiment …" (Iwanow 1945: 536). Later on, Schwanwitsch (1946) confirmed his previous results while studying the larval metamorphosis of *Entocolax schwanwitschi*.

Except for a velum, a sex rudiment and details concerning the nervous system (ganglia) that could not be reconstructed in our specimen, due to the state of preservation, all organs found by Schwanwitsch (1917, 1946) and Iwanow (1945) are also existent in juvenile *E. schiemenzii*. Additionally, the presence of eyes, an osphradium, a nephridium, a ctenidium and a more complex digestive system could be demonstrated.

The attachment of the adult parasites in their host, viz. to the body wall or to the intestinal tract of the host, strongly depends on the mode of live of the latter (Heding & Mandahl-Barth 1938). Holothurians, only partly buried in the sediment may become infected externally via the skin, whereas species living entirely buried in the sediment only may become penetrated via the mouth of the host, while feeding. *Chiridota pisanii* usually lives in sediment bottoms, often under stones in shallow water (see habitat paragraph of host). This corresponds well to the first scenario, that is, settlement of the juvenile parasites externally on the host. The position of the four juvenile *E. schiemenzii* specimens (exteriorly in right dorsal interradius, close to the anterior end of the host) and the position of the adult *E. schiemenzii* (within the coelomic cavity, attached to dorsal body wall, close to anterior end of host; Ludwig 1898b) both support this assumption.

A hypothetical development from a shelled juvenile, that externally settles on the skin of the holothurian, to the adult endoparasitic specimen is presented by Mandahl-Barth in Heding & Mandahl-Barth based on his examinations of *E. ludwigii*.

The presence of a well developed osphradial organ, usually serving as a chemosensory organ (Kay et al. 1998), may support the juvenile in locating a suitable host.

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2. Bohn, J.M. (2005) On two rare abyssal Myriotrochidae (Echinodermata: Holothuroidea: Apodida) new to the South Atlantic: *Siniotrochus myriodontus* Gage and Billett, 1986 and *Neolepidotrochus parvidiscus angolensis* subsp. nov.. *Organisms, Diversity and Evolution*, 5, 231–238.

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RESULTS OF THE DIVA-1 EXPEDITION OF RV "METEOR" (CRUISE M48/1)

On two rare abyssal Myriotrochidae (Echinodermata: Holothuroidea: Apodida) new to the South Atlantic: *Siniotrochus myriodontus* Gage and Billett, 1986 and *Neolepidotrochus parvidiscus angolensis* subsp. nov.

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Abstract

In the course of the DIVA 1 expedition (RV "Meteor", cruise M48/1) to the Angola Basin (South Atlantic) two myriotrochid holothurians were collected at abyssal depths – *Neolepidotrochus parvidiscus angolensis* subsp. nov. and *Siniotrochus myriodontus* Gage and Billett, 1986. The latter, until now, was known only from few specimens from the north-eastern Atlantic Ocean. This new record of *S. myriodontus* for the South Atlantic Ocean indicates a wide geographical distribution. Both species are described in detail, including parameters for the wheel deposits.

Keywords: Angola basin; Apodida; Holothuroidea; *Lepidotrochus*; Myriotrochidae; *Siniotrochus*; *Neolepidotrochus* nom. nov.; South atlantic ocean; Taxonomy

Introduction

The aim of the DIVA 1 expedition with RV "Meteor" (cruise M48/1) to the Angola Basin (south-eastern Atlantic Ocean) was to investigate the biodiversity of this abyssal plain. At several stations along a transect of about 700 km, a rich variety of abyssal Holothuroidea was collected with an Agassiz trawl and an epibenthic sledge. Among these were two species of Myriotrochidae. The knowledge on this family in the southern Atlantic Ocean is fragmentary. Only five species are known, one from the equatorial mid-Atlantic Ocean and four from the Scotia Sea area (Belyaev and Mironov 1978, 1980, 1982). There are no published records of Myriotrochidae for the area between. *Siniotrochus myriodontus* Gage and Billett, 1986 is hitherto known only from few specimens from the type locality and its immediate vicinity in the north-eastern Atlantic Ocean (Gage and Billett 1986). The second species belongs to the genus *Neolepidotrochus* nom. nov. and has close affinities to *N. parvidiscus* (Belyaev and Mironov, 1980) known from the southern Indian Ocean (Belyaev and Mironov 1980).

Material and methods

Specimens were collected with an Agassiz trawl and an epibenthic sledge. The Agassiz trawl material was fixed in buffered formalin while the epibenthic sledge material was fixed in cold ethanol.

For examination of calcareous deposits small pieces of the body wall were macerated in a 12.5% Natrium-hypochlorite solution, then rinsed several times in distilled water and air-dried. The calcareous deposits were mounted on slides and analysed with a Zeiss Axioplan microscope equipped with a Sanyo CCD video camera (VCB-3512R) and the software analySiS (version 2.1). For SEM examinations the calcareous deposits were transferred to aluminum stubs, sputtered

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with gold and studied in an Philips XL 20 Scanning Electron Microscope.

Important diagnosic features for Myriotrochidae are their wheel-like deposits in the body wall. A number of measurements and counts have been established that are used to characterize species (e.g. Belyaev, 1970; Belyaev and Mironov, 1982; Gage and Billett, 1986). Wheels are described in terms of the wheel diameter (D, µm), the hub diameter (d_h, µm), often expressed as a percentage of the total wheel diameter (d_h, %), the number of spokes (n_s) and the number of teeth, which can be inward-pointing (n_{it}) or outward-pointing (n_{ot}). If there are two size classes of inward- or outward-pointing teeth, the larger ones are called primary teeth (n_{ipt}: number of primary inward-pointing teeth, n_{opt}: number of primary outward-pointing teeth), whereas the smaller ones are referred to as secondary teeth (n_{ist}: number of secondary inward-pointing teeth, n_{ost}: number of secondary outward-pointing teeth). Also the numerical proportion between spokes and inward-pointing teeth expressed as a percentage (s/it, %) is used. In case of a perforated hub the number of hub perforations (n_p) is also counted. The abbreviations used in this study follow Gage and Billett (1986).

The investigated material is deposited in the Zoologische Staatssammlung München (ZSM). The registration numbers, together with specimen numbers (JMB-) are given in the descriptions below.

Taxonomy

Family Myriotrochidae Théel, 1877

Siniotrochus **Pawson, 1971**

Siniotrochus Pawson, 1971: 232 – Belyaev and Mironov, 1982: 109.

Siniotrochus myriodontus **Gage and Billett, 1986 (Figs. 1A, B and 2)**

Siniotrochus myriodontus Gage and Billett, 1986: 266–272, Figs. 28C–E, 29–31 – Bohn (in press).

Material. 1 posterior fragment (ZSM 20020016 [JMB-00692]), station M 48/1-347, 28 July 2000, Agassiz trawl, 16°14.0′S, 5°26.7′E–16°23.1′S, 5°27.0′E, 5389–5388 m. 2 posterior fragments (ZSM 20020015 [JMB-01112, JMB-01113]), station M 48/1-351, 30 July 2000, Agassiz trawl, 16°25.2′S, 5°27.1′E–16°33.2′S, 5°27.3′E, 5387–5385 m.

Description. All three specimens are posterior fragments of more or less cylindrical outline, and range from 17 to 31 mm in length and 6–7 mm in width.

The body wall has a single layer of wheel deposits, closely packed on the dorsal side and at the posterior end, getting scarce towards the ventral side and being almost absent in the median body region of the mid-ventral radius. The extreme posterior end around the anus is devoid of wheel deposits, instead there are simple rods.

All internal organs, including gonads, stone canal, and polian vesicles are missing. Only remnants of the digestive tract with a loop are present.

The rod deposits (Fig. 1A) are about 100–250 µm long, simple, often slightly curved, sometimes with knob like swellings and in few cases bifurcated. They are mainly restricted to the extreme posterior end of the body around the anus, where they are quite numerous. Single rods also occur in the median region of the body close to the longitudinal muscles.

The wheel deposits are all of one type (Fig. 1B), all details of measurements of wheel parameters are summarized in Table 1. The wheels are circular or oval and range from 284 to 560 µm in diameter. The hub is about half the diameter of the wheel and perforated centrally by a variable number of holes. Three series of teeth, two outward-pointing and one inward-pointing, project from rim. The primary outward-pointing teeth (Fig. 1B: opt) are prominent, often equal in number to the spokes and alternating with these. The secondary outward-pointing teeth (Fig. 1B: ost) vary much in size and number and are usually much smaller than the preceeding ones. In their position they correspond to the spokes. The inward-pointing teeth are slender and pointed and usually more than twice the number of the spokes.

There is a significant linear relationship between the number of spokes ($p<0.0001$), the number of inward-pointing teeth ($p<0.0001$), the hub diameter ($p<0.0001$) and the diameter of the wheels (Fig. 2). With increasing size of the wheel, the number of spokes and inward-pointing teeth as well as the size of the hub increase.

Remarks. Currently three species are included in the genus *Siniotrochus* – *S. phoxus* Pawson, 1971 (north-western Atlantic Ocean), *S. spiculifer* Belyaev and Mironov, 1981 (northern Pacific Ocean) and *S. myriodontus* Gage and Billett, 1986 (north-eastern Atlantic Ocean). *S. spiculifer* differs from its congeners by the frequent presence of simple rods together with wheel deposits in the body wall. In addition, wheel deposits lack outward-pointing teeth that are characteristic for both other species (Belyaev and Mironov 1981). According to Gage and Billett (1986) *S. myriodontus* differs from *S. phoxus* by the presence of secondary outward-pointing teeth, resulting also in a higher total number of outward-pointing teeth. All other wheel parameters are quite similar in both species (Gage and Billett 1986).

With regard to the wheel parameters the specimens from the Angola Basin resemble *S. myriodontus* and *S. phoxus* (see Gage and Billett 1986; Pawson 1971). Owing to the presence of secondary outward-pointing teeth the Angola Basin specimens fit with the diagnosis given for *S. myriodontus*.

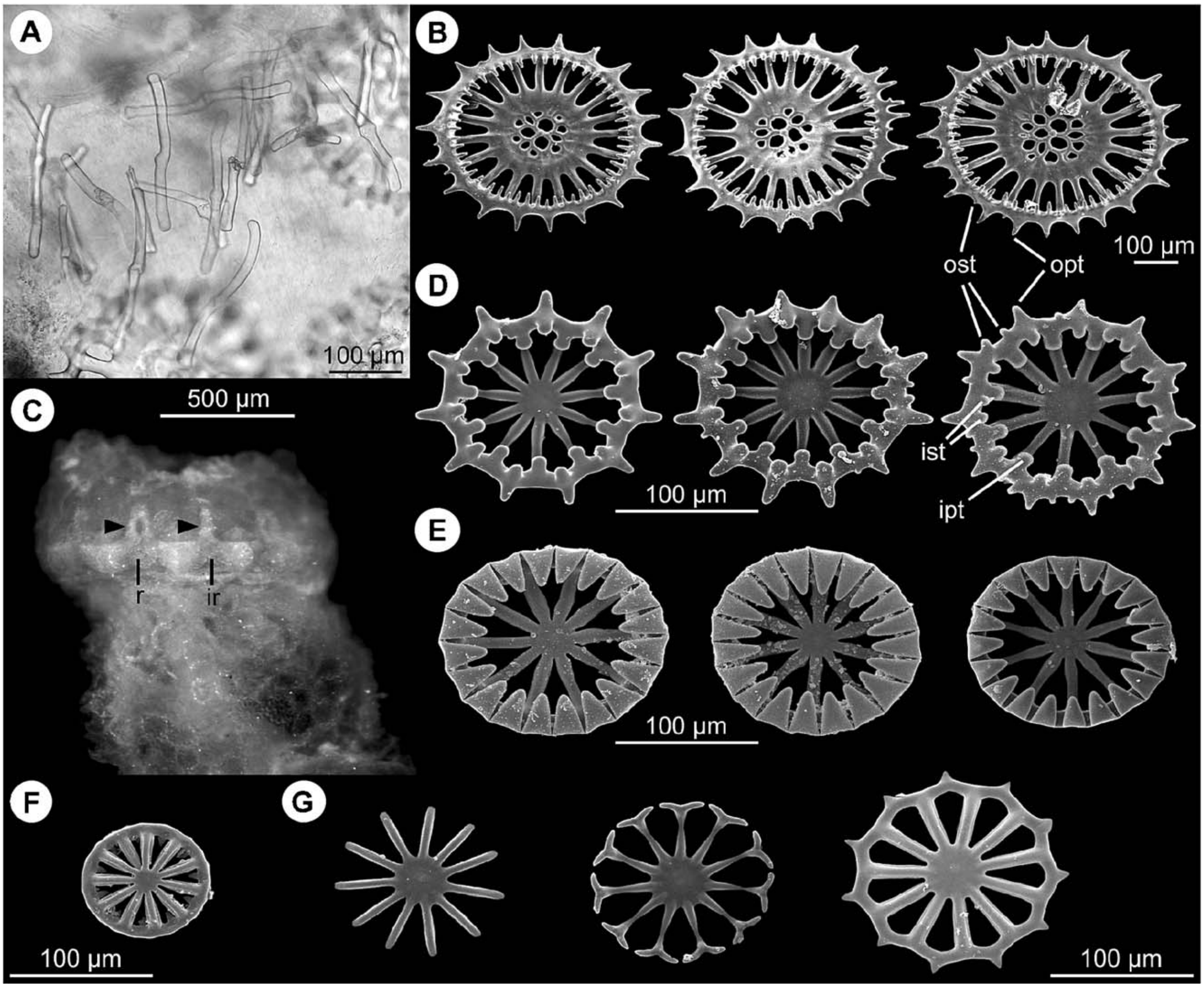

Fig. 1. (**A**–**B**) *Siniotrochus myriodontus*, deposits of the body wall. (**A**) Simple rods from the extreme posterior end of the body around the anus. (**B**) Wheel deposits. (**C**–**G**) *Neolepidotrochus parvidiscus angolensis* subsp. nov. (**C**) Tentacle region of the holotype, with plates of the calcareous ring visible through the body wall (r: radial plate, ir: interradial plate, arrowhead: anterior process). (**D**) Wheel deposits of the lepidotrochid type. (**E**) Wheel deposits of the myriotrochid type, outer surface. (**F**) Wheel deposit of the myriotrochid type, inner surface. (**G**) Developing wheels, early and later stages (from left to right; constriction on spokes of middle wheel artificial, due to adhering glue from stub). Abbreviations: opt: primary outward-pointing teeth, ost: secondary outward-pointing teeth, ipt: primary inward-pointing teeth, ist: secondary inward-pointing teeth.

The number of secondary outward-pointing teeth on the wheels in the South Atlantic specimens is a variable feature (Table 1). Out of 179 wheels 25 had no secondary outward-pointing teeth at all (9 wheels in JMB-00692, 16 wheels in JMB-01113). Gage and Billett (1986) found only 6 wheels out of 170 devoid of secondary outward-pointing teeth. Also the mean values of secondary outward-pointing teeth in their specimens were higher (7.2, 8.5 and 14.0) than in the current material (only specimen JMB-01112 is within this range, see Table 1). The frequency of wheels with 6 or more secondary teeth was also much higher in the material from the north-eastern Atlantic (65%, 80% and 95% in three specimens, Gage and Billett 1986) than in the South Atlantic specimens (JMB-01113 7.27%, JMB-00692 40.54%, JMB-01112 94%).

The presence or absence as well as the number of secondary outward-pointing teeth are variable features Until now too few specimens of both species are known to assess the taxonomic value of this character, i.e., whether or not it may be useful to distinguish *S. myriodontus* and *S. phoxus*. It is possible that future investigations will prove *S. myriodontus* to be a junior synonym of *S. phoxus* and that secondary outward-pointing teeth are a feature present in some individuals, while lacking in others.

Table 1. Measurements of wheel parameters: *Siniotrochus myriodontus*

Parameter	Specimen		
	JMB-00692 ($n = 74$)	JMB-01112 ($n = 50$)	JMB-01113 ($n = 55$)
D (µm)	425 (±42.7) 340–546	388 (±40.2) 284–494	432 (±43.0) 358–560
d_h (%)	53.1 (±3.3) 47.3–63.7	53.1 (±1.9) 48.2–56.9	53.5 (±1.6) 50.6–57.8
n_s	15.6 (±2.5) 12–25	16.6 (±2.3) 13–22	19.5 (±2.4) 16–25
n_{it}	42.0 (±5.1) 33–54	39.2 (±5.8) 30–54	46.0 (±4.9) 40–67
s/it (%)	37.2 (±4.7) 28.9–50.0	42.6 (±3.9) 34.2–50.0	42.5 (±3.0) 36.2–50.0
n_{opt}	17.1 (±3.4) 11–31	16.7 (±2.2) 13–22	19.5 (±2.7) 16–28
n_{ost}	5.1 (±4.1) 0–17	12.5 (±4.6) 4–29	2.1 (±2.1) 0–8
n_{ot}	22.2 (±5.8) 14–36	29.2 (±4.6) 21–47	21.6 (±3.6) 16–31
n_p	6.5 (±2.0) 4–13	9.0 (±2.7) 5–16	13.1 (±3.1) 8–22

Means, standard deviations (in parentheses) and range of wheel parameters for three specimens. D, µm: diameter of wheel, d_h, %: diameter of hub expressed as a percentage of total wheel diameter, n_s: number of spokes, n_{it}: number of inward-pointing teeth, s/it, %: ratio of spokes to inward-pointing teeth, n_{opt}: number of primary outward-pointing teeth, n_{ost}: number of secondary outward-pointing teeth, n_{ot}: total number of outward-pointing teeth, n_p: number of hub perforations.

Distribution. Porcupine Seabight (type locality), north-eastern Atlantic Ocean, 3490–4000 m; Angola Basin, south-eastern Atlantic Ocean, 5385–5389 m.

This new record for the south Atlantic Ocean indicates a wide geographical distribution. Also its depth range has been considerably extended by the new material. However, too few records of *Siniotrochus* species exist so far, to draw any conclusions concerning geographical distibution or zoogeographical relationships.

Neolepidotrochus nom. nov.

Lepidotrochus Belyaev and Mironov, 1980: 1811–1812 – Belyaev and Mironov, 1982: 108–109.

Remarks. *Neolepidotrochus* nom. nov. is a replacement name for *Lepidotrochus* Belyaev and Mironov, 1980, which is a junior homonym of *Lepidotrochus* Koken, 1894. This genus was established by Koken (1894) for the triassic trochid gastropod *Lepidotrochus bittneri* Koken, 1894. For diagnosis and type species see Belyaev and Mironov (1980).

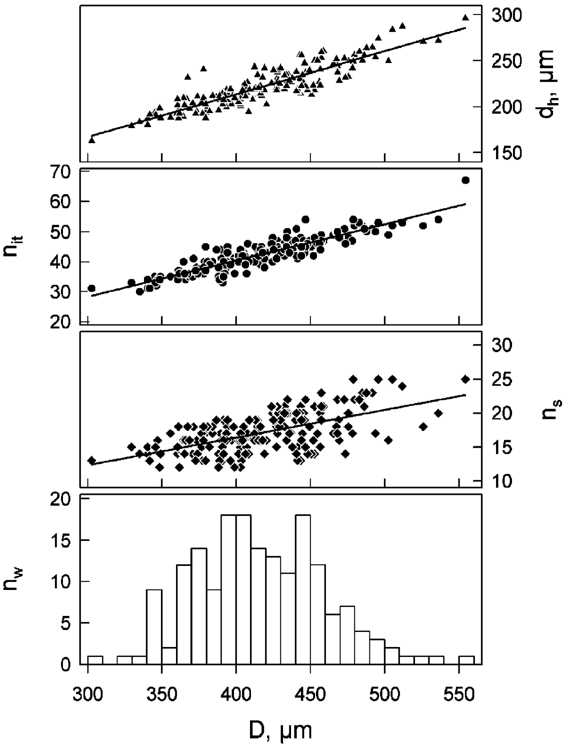

Fig. 2. *S. myriodontus*: wheel parameters and size distribution of wheel diameters (D, µm; n_w: number of wheels), with plots of the number of spokes (n_s: rhombus), number of inward-pointing teeth (n_{it}: circle), and the diameter of the hub (d_h, µm: triangle) in relation to the wheel diameter. Linear regression of n_s, n_{it} and d_h (µm) on D (µm) are shown, where $n_s = 0.0930 + (0.0408 \times D$, µm), $r^2 = 0.3642$, $p < 0.0001$; $n_{it} = -7.9416 + (0.1210 \times \text{D}$, µm), $r^2 = 0.8189$, $p < 0.0001$; d_h, µm $= 27.1451 + (0.4664 \times D$, µm), $r^2 = 0.7978$, $p < 0.0001$. (Wheel diameter size classes: 10 µm.)

***Neolepidotrochus parvidiscus angolensis* subsp. nov. (Figs. 1C–G, 3 and 4)**

Lepidotrochus cf. *parvidiscus* Belyaev and Mironov, 1980 – Bohn (in press).

Material. Holotype (ZSM 20020017), station M 48/1-340, 23 July 2000, epibenthic sledge (epinet), 18°18.3′S, 4°41.3′E–18°19.4′S, 4°41.9′E, 5395–5395 m.

Description. The holotype is cylindrical in outline, 7.2 mm long and 1.1 mm wide (at calcareous ring).

There are 12 tentacles with digits, but owing to the contraction of the tentacles it is not possible to confirm the number of digits per tentacle.

At the tentacle bases and in the body wall there is a single layer of closely packed wheel deposits of two types – lepidotrochid type wheels (Fig. 1D) and myriotrochid type wheels (Fig. 1E, F). The lepidotrochid type wheels dominate in the anterior (98% lepidotrochid type wheels, 3% myriotrochid type wheels) and median regions of the body, while the myriotrochid type wheels dominate in the posterior end

Table 2. Measurements of wheel parameters: *Neolepidotrochus parvidiscus angolensis* subsp. nov

Parameter	Myriotrochid type wheels			Lepidotrochid type wheels		
	N. parvidiscus angolensis subsp. nov.		*N. parvidiscus parvidiscus*	*N. parvidiscus angolensis* subsp. nov.		*N. parvidiscus parvidiscus*
	Anterior ($n = 2$)	Posterior ($n = 50$)	($n = 6$)	Anterior ($n = 49$)	Posterior ($n = 49$)	($n = 31$)
D (μm)	97 (±2.9) 94–100	131 (±19.9) 75–166	121 93–134	111 (±8.5) 95–129	140 (±6.0) 127–158	119 110–132
d_h (%)	24.8 (±1.2) 23.6–26.0	20.8 (±1.7) 17.7–25.9	17.7 16–20	40.0 (±4.0) 29.7–47.2	28.4 (±2.9) 21.7–36.1	26.3 22–31
n_s	10.5 (±0.5) 10–11	10.2 (±1.0) 8–14	9.7 9–11	12.3 (±1.1) 10–16	11.0 (±0.9) 9–13	11.1 9–13
n_{ipt}	—	—	—		Same as spokes	
n_{ist}	—	—	—	12.3 (±1.2) 10–16	12.7 (±2.5) 10–24	10.5 6–12
n_{it}	21.5 (±0.5) 21–22	20.7 (±1.4) 18–27	20.5 20–22	—	—	—
S/it (%)	48.8 (±1.2) 47.6–50.0	49.0 (±3.4) 38.1–55.0	47 43–50	49.9 (±0.5) 46.4–50.0	46.8 (±4.9) 29.4–50.0	—
n_{opt}	—	—	—		Same as spokes	
n_{ost}	—	—	—	2.1 (±3.3) 0–14	5.3 (±4.1) 0–16	—

Means, standard deviations (in parentheses) and range of wheel parameters for the myriotrochid and lepidotrochid type wheels from the anterior and posterior body wall of the holotype, compared to the wheel parameters of *N. parvidiscus parvidiscus* (data from Belyaev and Mironov, 1980). D, μm: diameter of wheel, d_h, %: diameter of hub expressed as a percentage of total wheel diameter, n_s: number of spokes, n_{ipt}: number of primary inward-pointing teeth, n_{ist}: number of secondary inward-pointing teeth, n_{it}: total number of inward-pointing teeth, s/it, %: ratio of spokes to inward-pointing teeth, n_{opt}: number of primary outward-pointing teeth, n_{ost}: number of secondary outward-pointing teeth.

of the body (39% lepidotrochid type wheels, 61% myriotrochid type wheels).

The radial as well as the interadial plates of the calcareous ring have anterior processes (Fig. 1C, arrowheads). The radial canal pore of the radial plate is placed higher than the base of the anterior process. No further details of the morphology of the calcareous ring can be stated without the mutilation of the specimen.

All internal organs, except for the gonads (juvenile?) are well developed. There is one polian vesicle and the digestive tract has a loop.

The lepidotrochid type wheels are of characteristic shape (Fig. 1D). They are circular or oval and range from 95 to 158 μm in diameter. The hub is about one-fifth to nearly half the size of the wheel diameter. There are four types of teeth series projecting from the rim, two inward-pointing and two outward-pointing series. Primary inward-pointing teeth (Fig. 1D: ipt) are large, scale like and always correspond in position to the spokes. Secondary inward-pointing teeth (Fig. 1D: ist) are smaller, also scale like and correspond in position to spaces between the spokes. Primary outward-pointing teeth are prominent (Fig. 1D: opt) and have a blunt or rounded tip. They alternate in position with the spokes. The edge of the rim between two primary outward-pointing is often roughly straight (Fig. 1D), although there are also wheels with a more or less curved edge. The knob-like secondary outward-pointing teeth (Fig. 1D: ost) are much smaller, very variable in number and correspond in position to spaces between primary outward-pointing teeth. Primary outward-pointing and inward-pointing teeth are always equal in number to the spokes, while the number of secondary inward-pointing teeth is more variable. Often they are equal in number to the spokes, but sometimes the tooth number exceeds the number of spokes (Fig. 1D, wheel on the right side). All details concerning measurements of wheel parameters are summarized in Table 2.

The lepidotrochid type wheels from the anterior and posterior end of the body differ in some details (see Table 2 and Fig. 3). The wheels from the anterior end of the body are smaller and there is a significant linear relationship between the number of spokes ($p < 0.0001$), the hub diameter ($p < 0.0001$) and the wheel diameter (Fig. 3). With increasing size of the wheel, the number of spokes and the size of the hub increase as well. No such linear relationship exists for wheels from the posterior end of the body (Fig. 3). Also the mean value of the hub diameter expressed as a percentage of the total wheel diameter (d_h, %) is higher in wheels from the anterior end of the body than in those from the posterior end (Table 2).

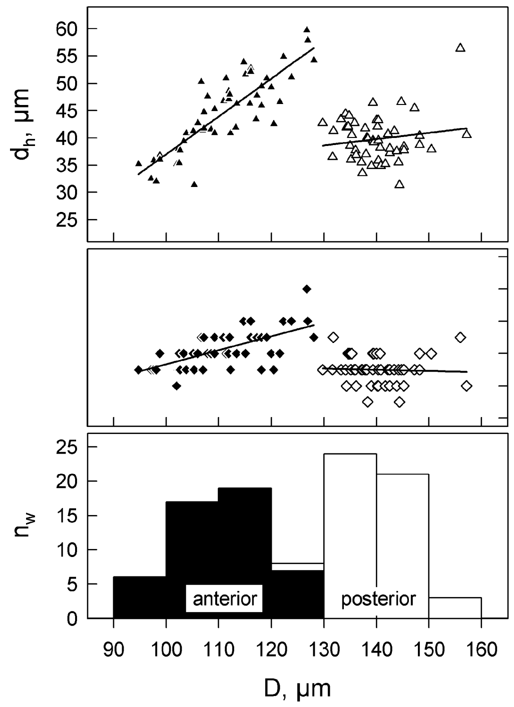

Fig. 3. *N. parvidiscus angolensis* subsp. nov: Lepidotrochid type wheel parameters and size distribution of wheel diameters (D, μm; n_w: number of wheels), from the anterior (solid symbols) and posterior (outlined symbols) end of the body, with plots of the number of spokes (n_s: rhombus), and the diameter of the hub (d_h, μm: triangle) in relation to the wheel diameter. Linear regression of n_s and d_h (μm) on D (μm) are shown for wheels from the anterior end of the body ($n_s = 2.7278 + (0.0861 \times D,\ \mu m)$, $r^2 = 0.4100$, $p<0.0001$; d_h, $\mu m = -32.4473 + (0.6944 \times D,\ \mu m)$, $r^2 = 0.7152$, $p<0.0001$) and wheels from the posterior end of the body ($n_s = 12.0959 + (-0.0078 \times D,\ \mu m)$, $r^2 = 0.0027$, $p = 0.7228$; d_h, $\mu m = 23.6860 + (0.1149 \times D,\ \mu m)$, $r^2 = 0.0252$, $p = 0.2757$). (Wheel diameter size classes: 10 μm.)

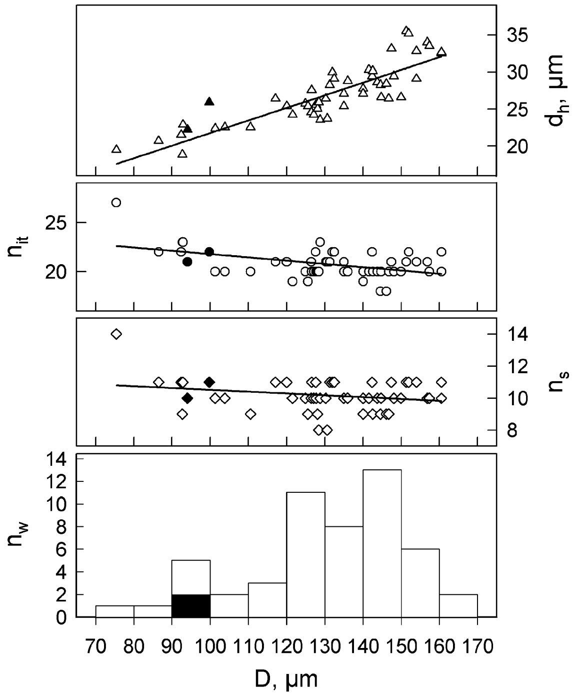

Fig. 4. *N. parvidiscus angolensis* subsp. nov: Myriotrochid type wheel parameters and size distribution of wheel diameters (D, μm; n_w: number of wheels), from the anterior (solid symbols) and posterior (outlined symbols) end of the body, with plots of the number of spokes (n_s: rhombus), number of inward-pointing teeth (n_{it}: circle), and the diameter of the hub (d_h, μm: triangle) in relation to the wheel diameter. Linear regression of n_s, n_{it} and d_h, μm on D, μm for wheels from posterior end of body are shown, where $n_s = 11.6639 + (-0.0114 \times D,\ \mu m)$, $r^2 = 0.0527$, $p = 0.1087$; $n_{it} = 25.1286 + (-0.0334 \times D,\ \mu m)$, $r^2 = 0.2111$, $p = 0.0008$; d_h, $\mu m = 4.7636 + (0.1702 \times D,\ \mu m)$, $r^2 = 0.7495$, $p<0.0001$. (Wheel diameter size classes: 10 μm.)

The myriotrochid type wheels (Fig. 1E, F) are circular or oval and range from 75 to 166 μm in diameter. The hub is usually smaller than one quarter the size of the wheel diameter. A central knob on the hub seems to be missing. One series of large inward-pointing teeth projects from the rim. They are triangular in outline, have a more or less rounded tip and are about twice the number of spokes. All details concerning measurements of wheel parameters are summarized in Table 2.

Significant linear relationships between the number of teeth ($p = 0.0008$), the hub diameter ($p<0.0001$) and the diameter of the wheels from the posterior end of the body exist (Fig. 4). With increasing size of the wheel, the size of the hub increases as well, while the number of teeth decreases. There is no linear relationship between the number of spokes and the size of the wheels (Fig. 4).

Developing wheels of different stages (Fig. 1G) are present throughout the body wall. Wheels of the lepidotrochid type as well as of the myriotrochid type can be found among them.

Remarks. The genus *Neolepidotrochus* is characterized mainly by the presence of lepidotrochid type wheels and by the morphology of the calcareous ring (Belyaev and Mironov, 1980). Currently there are five species included – *N. variodentatus* (Belyaev and Mironov, 1978), *N. kermadecensis* (Belyaev, 1970), *N. novaeguinensis* (Belyaev and Mironov, 1980), *N. parvidiscus* (Belyaev and Mironov, 1980) and *N. pawsoni* (Belyaev and Mironov, 1980).

N. novaeguinensis differs from all its congeners by the lack of myriotrochid type wheels. The myriotrochid type wheels of *N. pawsoni* stand owing to their large size with a diameter ranging from 139 to 196 μm (mean 172 μm), while all other species have myriotrochid type wheels with mean diameters less than 150 μm (140 μm in current specimen). *N. kermadecensis* and *N. variodentatus* differ from the described specimen by the absence of wheel deposits at the base of the tentacles (present in the latter). Furthermore the mean value of the ratio hub diameter to wheel diameter (d_h, %) in lepidotrochid type wheels of both species is more or less constant for all wheels throughout the body (*N. kermadecensis*, d_h, % = 45%; *N. variodentatus*, d_h, % = 41%). This is not the case for the current specimen where the ratio hub diameter to wheel diameter differs considerably between lepidotrochid type wheels from the anterior (d_h, % = 40.02%) and the posterior body (d_h, % = 28.42%, Table 2).

N. parvidiscus is the only species that the current specimen possesses closer affinities to. *N. parvidiscus* is known only from a posterior end found in the southern Indian Ocean. According to Belyaev and Mironov (1980) this species is mainly characterized by the presence of three types of wheels in the body wall (lepidotrochid type, myriotrochid type and acanthotrochid type wheels) and by lepidotrochid type wheels which have a small-sized hub, resulting in a low mean ratio of hub diameter to wheel diameter (d_h, % = 26.3%). Additionally, the edge of the rim between two primary outward-pointing teeth is roughly straight, instead of curved. This specimen is referred to as *N. parvidiscus parvidiscus* below.

The lepidotrochid type wheels from the posterior end of the body of *N. parvidiscus angolensis* subsp. nov. have small sized hubs (Table 2) as in *N. p. parvidiscus*. In addition, the edge of the rim between two neighbouring teeth is often straight, although not always.

However, there are also several differences between the two subspecies of *N. parvidiscus*. The lepidotrochid type wheels of *N. p. parvidiscus* are smaller than those of *N. p. angolensis* (Table 2). *N. p. parvidiscus* has lepidotrochid type wheels with fewer secondary inward-pointing teeth in comparison to *N. p. angolensis* although the number of spokes in both subspecies are the same (Table 2). The most obvious difference is the presence of secondary outward-pointing teeth in lepidotrochid type wheels of *N. p. angolensis* (Fig. 1D: ost). This character is less distinct in wheels from the anterior end of the body with a mean number of about two teeth per wheel compared to about five teeth for wheels from the posterior end of the body (Table 2). One or more secondary outward-pointing teeth are present in 55% of the wheels from the anterior end of the body, while more than 80% of the wheels from the posterior end have at least one tooth. A distinct series of secondary outward-pointing teeth has not been noted by Belyaev and Mironov (1980) for *N. p. parvidiscus* and seems to be missing.

The myriotrochid type wheels of both subspecies also differ to some extent (see Table 2). The wheels of *N. p. parvidiscus* are smaller and have a smaller ratio of hub diameter to wheel diameter (d_h, %). The number of inward-pointing teeth is about the same, but there are fewer spokes in *N. p. parvidiscus* resulting in a lower ratio number of spokes to number of teeth (Table 2).

A third type of wheel, the so-called acanthotrochid type wheels, which are thought to be characteristic of *N. p. parvidiscus* (see Belyaev and Mironov, 1980) are also present in *N. p. angolensis*. However, these wheels are only a development stage of lepidotrochid type wheels (Fig. 1 G, wheel on right side). In the current specimen many intermediate stages between both types of wheels were observed.

In conclusion, *N. p. angolensis,* though similar to *N. p. parvidiscus*, differs in several features and may be distinguished from the latter on the basis of features of the lepidotrochid type wheels. In *N. p. angolensis*, these wheels are of a larger size and have, at least the majority of them, secondary outward-pointing teeth projecting from the rim.

Etymology. The name, *angolensis*, refers to the type locality (Angola Basin) of this subspecies.

Distribution. Only known from type locality, Angola Basin, south-eastern Atlantic Ocean, 5395 m.

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Myriotrochus (*Oligotrochus*) *meteorensis* spec. nov., a new myriotrochid holothurian from the deep-sea off NW Africa (Echinodermata: Holothuroidea: Myriotrochidae)

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Abstract

A new myriotrochid holothurian, *Myriotrochus* (*Oligotrochus*) *meteorensis* spec. nov., has been discovered in a deep-sea sample taken during an expedition with FS 'Meteor' (M 36) off north-west Africa, together with specimens of *Molpadia musculus* Risso, 1826, *Hedingia albicans* (Théel, 1886) and *Protankyra* cf. *brychia* (Verrill, 1885). The new species is similar to *M*. (*O*.) *vitreus* (M. Sars, 1866) and *M*. (*O*.) *clarki* Gage and Billett, 1986; it is thoroughly described and detailed measurements of wheel parameters are presented. This is the first record of a myriotrochid holothurian for the NE Atlantic Ocean south of 40°N.

Key words: Holothuroidea; Myriotrochidae; *Myriotrochus*; *Oligotrochus*; *M*. (*O*.) *meteorensis* spec. nov.; taxonomy; systematics

Introduction

The benthos of the north-western Africa upwelling area from Cape Blanc to off northern Morocco has been sampled during four cruises (M 26, M 36, M 44 and M 53) with the German research vessel 'Meteor' (Thiel 1981) by the means of eight depth transects.

A hitherto unsorted holothurian sample from a deep station taken during cruise M 36 off Cape Blanc in 1975, held at the Zoologische Staatssammlung München (ZSM), contained in addition to *Molpadia musculus* Risso, 1826 (10 specimens, ZSM 20043111), *Hedingia albicans* (Théel, 1886) (3 specimens, ZSM 20043110) and *Protankyra* cf. *brychia* (Verrill, 1885) (35 fragments, ZSM 20043109) several fragments of a yet undescribed myriotrochid holothurian.

The Myriotrochidae Théel, 1877 are a family of apodous, usually infaunal holothurians that are worldwide distributed in the deep-sea, though few species are also known

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from shallow waters. Albeit the bathyal and abyssal north Atlantic Ocean may be one of the best sampled deep-sea regions concerning myriotrochid holothurians (Belyaev & Mironov 1982, Gage & Billett 1986), knowledge of this family there is still scarce. The specimens collected during the cruise M 36 with FS 'Meteor' off Cape Blanc are the first record of a myriotrochid holothurian from the NE Atlantic Ocean south of 40°N.

Material and Methods

For examination of calcareous deposits small pieces of the body wall were macerated in a 12.5 % Natriumhypochlorite solution, then rinsed several times in distilled water and air-dried. The calcareous deposits were mounted on slides and analyzed with a Leitz microscope equipped with a video camera (380 USB 2.0 Spacec@m) and the software AxioVision LE. For SEM examinations the calcareous deposits were transferred to aluminum stubs, sputtered with gold and studied in a LEO 1430 VP Scanning Electron Microscope.

The wheel-like deposits in the body wall of the Myriotrochidae are an important diagnostic feature and a number of measurements and counts have been established to describe and characterize species (see Belyaev 1970, Belyaev & Mironov 1982, Gage & Billett 1986, Bohn 2005).

Taxonomy

Family Myriotrochidae Théel, 1877
Genus *Myriotrochus* Steenstrup, 1851
Subgenus *Oligotrochus* M. Sars, 1866

Myriotrochus (*Oligotrochus*) *meteorensis* spec. nov.

(Figs 1A–M, 2)

Material. Holotype (♀ anterior fragment, ZSM 20043112), 8 paratypes (2 ♂ anterior fragments, 2 ♀ anterior fragments, 2 juv. [?] anterior fragments, 2 posterior fragments, ZSM 20043108), FS "Meteor", station M 36/99, Agassiz trawl 151, 21°36.2' N, 18°40.6' W, 2786–2843 m, 26.II.1975.

Description. The seven anterior fragments are only few millimeters long and 6.0–9.2 mm wide (close to the calcareous ring). The larger of the two posterior fragments is about 25 mm long. The anterior fragments are circular to slightly oval in cross-section, the posterior fragments have a slightly tapering posterior end.

There are 12 conical tentacles with 4–5 pairs of lateral digits. Both, the left and right lateral interradius have three tentacles, while all other interradii only have two. The tentacles lack calcareous deposits.

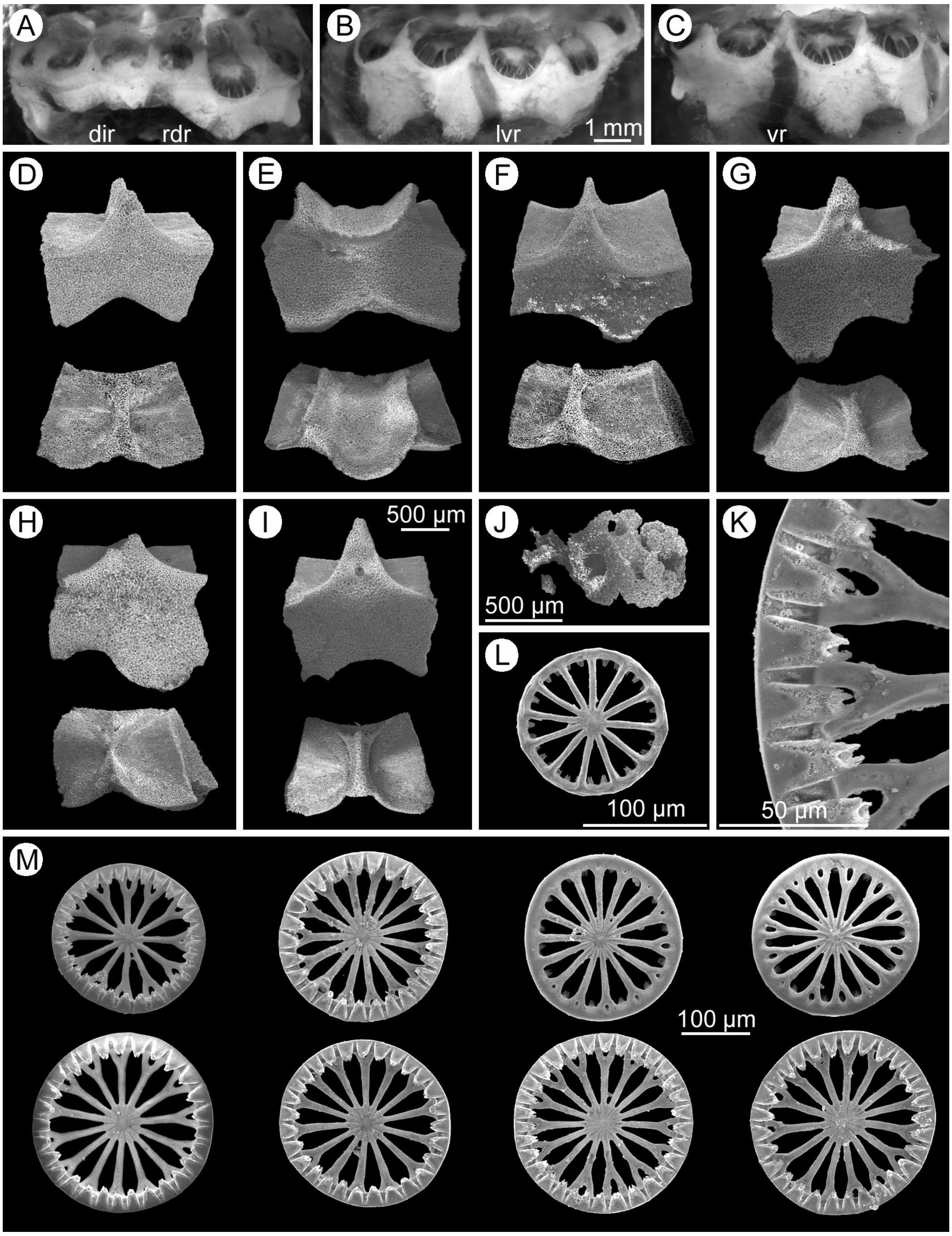

FIGURE 1. *Myriotrochus* (*Oligotrochus*) *meteorensis* spec. nov. **(A–C)** Calcareous ring of holotype (all to the same scale). **(A)** Dorsal view (dir: dorsal interradial plate, rdr: right dorso-lateral radial plate). **(B)** Left lateral view (lvr: left ventro-lateral radial plate). **(C)** Ventral view (vr: ventral radial plate). **(D–I)** Individual plates of calcareous ring of a paratype, outer (top) and anterior (bottom) view (all to the same scale). **(D)** Dorsal interradial plate. **(E)** Right dorso-lateral radial plate. **(F)** Right lateral interradial plate. **(G)** Left ventro-lateral radial plate. **(H)** Right ventral interradial plate (anterior process damaged). **(I)** Ventral radial plate. **(J)** Madreporite body (small basal piece broken off). **(K–M)** Wheel deposits of body wall from paratypes. **(K)** Detail of a wheel, rim with bifid teeth. **(L)** Small wheel lacking branched spokes. **(M)** Common large wheels with branched spokes.

Body wall deposits are myriotrochid type wheels (Fig. 1L, M), which are scattered in the anterior part of the body and get scarce towards the median body region. The posterior end of the body lacks wheel deposits.

The calcareous ring is stout (Fig. 1 A–C), and ventrally much higher than dorsally. The posterior margin of the ring is undulating, in particular on the lateral and ventral side, due to flat posterior processes on the plates (Fig. 1F–H). Five radial and five interradial plates build up the calcareous ring. The two dorso-lateral radial plates each have two anterior processes (Fig. 1E), while all other plates only have one anterior process (Fig. 1D, F–I), which are all of about the same height. The radial plates are perforated for the passage of the nerve.

The gonad consists of two tufts of few branching tubules. There is a single tubular polian vesicle. The stone canal, which is in close contact to the dorsal interradial plate, consists of a short convoluted tube embedded in a prominent calcareous madreporite body (Fig. 1J). The intestine has a large loop.

The myriotrochid type wheels are circular or oval and range from 111 to 316 µm in diameter. The hub is due to the fusion of proximal parts of adjacent spokes of variable outline (Fig. 1M) and size and reaches from about one-sixth to more than one-third the size of the wheel diameter. There are 10 to 18 spokes per wheel, fused in their proximal part with their neighbors, thus enlarging the hub. They are more or less straight in their free part, and close to the rim the majority of the spokes branche into two (Fig. 1M, see also Tab. 1). The mean ratio of branched spokes to spokes varies in the seven investigated specimens between 75.8–100 % (Tab. 1). Usually, there are about twice as much teeth projecting from the rim of the wheel as there are spokes. The teeth are triangular in outline and have a bifid tip (Fig. 1K). Detailed measurements of wheel parameters for seven specimens are given in Table 1 and are summarized in Table 2.

There is a significant linear relationship between the number of spokes ($p < 0.0001$), the number of teeth ($p < 0.0001$), the hub diameter ($p < 0.0001$) and the diameter of the wheels (Fig. 2). With increasing size of the wheel, the number of spokes and teeth as well as the size of the hub increase.

Remarks. Based on the shape of the calcareous ring (stout, with undulating posterior margin) and the morphology of the tentacles (conical, with 4–5 pairs of lateral digits) this new species has to be placed in the subgenus *Oligotrochus* sensu Heding (1935). Currently there are five species included in *Oligotrochus* (see Smirnov 1999)—*Myriotrochus* (*Oligotrochus*) *vitreus* (M. Sars, 1866), *M.* (*O.*) *bathybius* H. L. Clark, 1920, *M.* (*O.*) *clarki* Gage and Billett, 1986, *M.* (*O.*) *neocaledonicus* Smirnov, 1999 and *M.* (*O.*) *rotulus* Smirnov, 1999.

Good characters separating the new species together with *M.* (*O.*) *vitreus* and *M.* (*O.*) *clarki* from *M.* (*O.*) *bathybius*, *M.* (*O.*) *neocaledonicus* and *M.* (*O.*) *rotulus* are the morphology of the wheels and the calcareous ring.

According to Smirnov (1999), the last-mentioned three species have wheel deposits with a hub perforated by a more or less complete circle of holes and a calcareous ring where the ventral pieces are less than two times as high as the dorsal pieces (not known in *M.* (*O.*) *rotulus*). In contrast, *M.* (*O.*) *meteorensis*, *M.* (*O.*) *vitreus* and *M.* (*O.*) *clarki* have wheels without perforations on the hub and the ventral pieces of the calcareous ring are about two times higher than the dorsal pieces (see Heding 1935, Gage & Billett 1986, Smirnov 1999). Though quite similar, the new species also differs in several characters from *M.* (*O.*) *vitreus* and *M.* (*O.*) *clarki*.

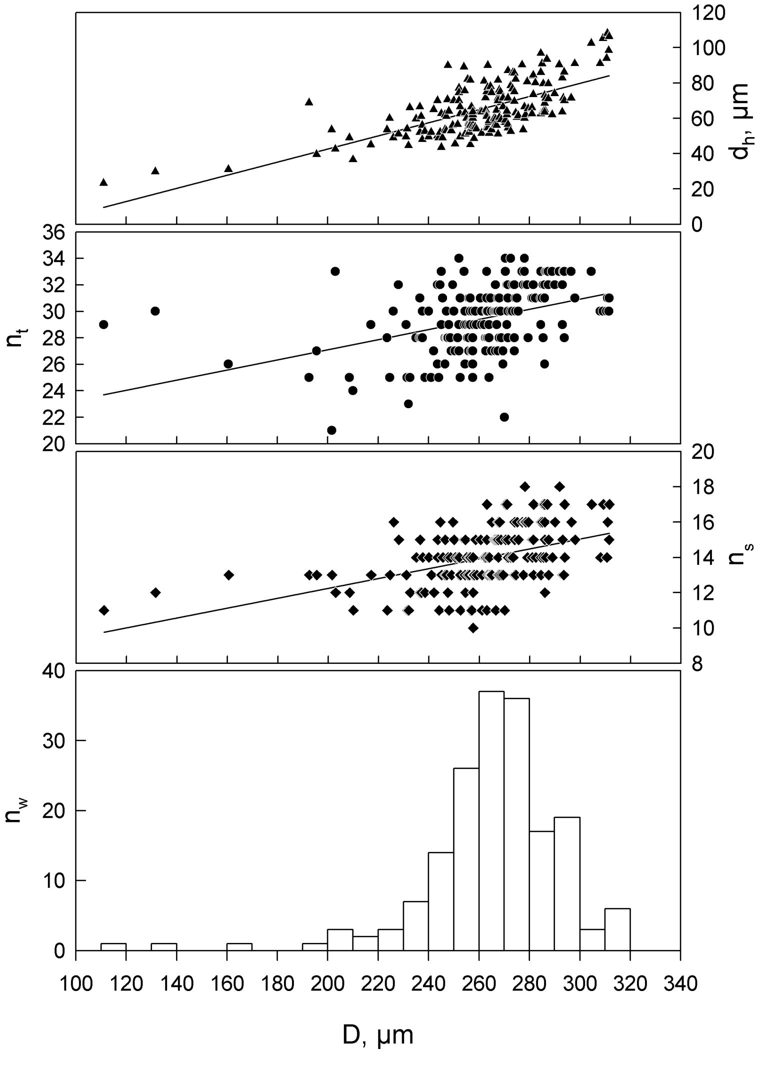

FIGURE 2. *Myriotrochus* (*Oligotrochus*) *meteorensis* spec. nov. Wheel parameters and size distribution of wheel diameters (D, µm; n_w: number of wheels), with plots of the number of spokes (n_s: rhombus), number of teeth (n_t: circle), and the diameter of the hub (d_h, µm: triangle) in relation to the wheel diameter. Linear regression of n_s, n_t and d_h, µm on D, µm are shown, where $n_s = 6.65 + (0.03 \times D, \mu m)$, $r^2 = 0.22$, $p < 0.0001$; $n_t = 19.44 + (0.04 \times D, \mu m)$, $r^2 = 0.17$, $p < 0.0001$; $d_h, \mu m = -31.81 + (0.37 \times D, \mu m)$, $r^2 = 0.47$, $p < 0.0001$. (Wheel diameter size classes: 10 µm.)

TABLE 1. *Myriotrochus* (*Oligotrochus*) *meteorensis* spec. nov. Means, standard deviations (in parentheses) and range of wheel parameters for seven specimens. D, µm: diameter of wheel, d_h, %: diameter of hub expressed as a percentage of total wheel diameter, n_s: number of spokes, n_{sb}/n_s, %: ratio of branched spokes to spokes, n_t: number of teeth, lt, %: length of teeth expressed as a percentage of total wheel diameter, s/t, %: ratio of spokes to teeth.

Parameter	Specimen						
	ZSM 20043112	ZSM 20043108					
	JMB–01314 (n=31)	JMB-01317 (n=31)	JMB-01319 (n=31)	JMB-01309 (n=11)	JMB-01313 (n=30)	JMB-01318 (n=21)	JMB-01316 (n=22)
D, µm	253.9 (±27.9) 157–299	272.6 (±38.5) 111–315	262.0 (±28.0) 131–298	244.5 (±21.1) 201–275	256.8 (±16.4) 208–293	256.1 (±17.5) 222–294	269.0 (±24.0) 182–316
dh, %	21.8 (±1.4) 19.3–25.0	24.8 (±4.6) 19.3–34.8	22.0 (±2.0) 17.5–26.1	20.5 (±2.6) 17.4–26.6	25.3 (±2.2) 20.2–28.7	28.9 (±2.4) 23.9–35.0	31.1 (±2.7) 25.4–36.3
n_s	14.6 (±1.2) 13–17	14.6 (±1.6) 11–18	13.7 (±1.5) 11–17	12.1 (±1.3) 10–14	13.3 (±1.8) 11–17	13.5 (±1.3) 11–16	14.6 (±1.4) 13–18
n_{sb}/n_s, %	91.5 (±18.4) 0.0–100	95.2 (±17.6) 0.0–100	95.0 (±17.8) 0.0–100	92.4 (±22.0) 23.1-100	100	94.2 (±11.5) 61.5-100	75.8 (±31.6) 0.0-100
n_t	30.6 (±2.0) 26–34	30.2 (±1.9) 25–34	29.1 (±2.3) 25–33	25.2 (±2.4) 21–29	28.2 (±2.1) 25–33	30.0 (±2.2) 25–34	30.4 (±2.1) 25–33
lt, %	10.4 (±0.7) 9.1–12.1	11.7 (±0.8) 9.8–13.1	13.1 (±0.8) 11.5–15.2	11.3 (±1.4) 9.5–14.3	12.4 (±0.6) 11.4–13.5	11.3 (±0.7) 9.5–12.4	9.3 (±0.6) 8.3–10.3
s/t, %	47.8 (±3.3) 39.4–53.3	48.4 (±4.4) 36.4-56.7	47.3 (±4.9) 34.4–57.1	48.3 (±5.5) 38.5–61.9	47.2 (±4.8) 35.5–53.8	45.2 (±3.6) 39.3–52.0	48.5 (±3.4) 41.9–54.8

The wheels of *M.* (*O.*) *vitreus* are considerably smaller, with a diameter ranging from 55 to 95 µm (Østergren 1902, Heding 1935) compared to those found in *M.* (*O.*) *meteorensis* which have a mean diameter of 260.6 µm (range: 111–316 µm, see Tab. 2). Other wheel parameter separating both species are the number of teeth, which usually is lower in *M.* (*O.*) *vitreus* and the ratio of spokes to teeth, which is considerably higher in *M.* (*O.*) *vitreus* (see Tab. 2). A character, both species have in common are their tentacles with four to five pairs of lateral digits.

Myriotrochus (*O.*) *clarki* differs by several wheel parameters from the new species (see Tab. 2). Most obvious is the smaller size of the wheel deposits, which have a mean diameter of 121.7 µm and range from 56 to 244 µm (Gage & Billett 1986) compared to those found in *M.* (*O.*) *meteorensis* (mean: 260.6 µm, range: 111–316 µm). Also the mean number of spokes and teeth per wheel are lower in *M.* (*O.*) *clarki* (see Tab. 2). The size differences observed in the wheels of both species cannot be ascribed to size differences of the investigated material, because the current specimens (calcareous ring diameter: 6.0–9.2 mm) are within the range of the specimens described by Gage & Billett (calcareous ring diameter: 1.6–9.2 mm). Furthermore, both species differ in their tentacle morphology: *Myriotrochus* (*O.*) *clarki* has two pairs of lateral digits per tentacle (Gage & Billett 1986), while the new species has four to five pairs.

TABLE 2. *Myriotrochus* (*Oligotrochus*) *meteorensis* spec. nov. Means, standard deviations (in parentheses) and range of wheel parameters of the new species compared to the wheel parameters of *M.* (*O.*) *clarki* (data from Gage & Billett 1986) and *M.* (*O.*) *vitreus* (data from Østergren 1902). D, µm: diameter of wheel, d_h, %: diameter of hub expressed as a percentage of total wheel diameter, n_s: number of spokes, n_{sb}/n_s, %: ratio of branched spokes to spokes, n_t: number of teeth, lt, %: length of teeth expressed as a percentage of total wheel diameter, s/t, %: ratio of spokes to teeth.

Parameter	Species		
	M. (*O.*) *meteorensis* (n=177)	*M.* (*O.*) *clarki*	*M.* (*O.*) *vitreus*
D, µm	260.6 (±27.9)	121.7	70-80
	111–316	56–244	55–95
d_h, %	24.9 (±4.3)		
	17.4–36.3		
n_s	13.9 (±1.6)	12.8	
	10–18	10–18	11–16
n_{sb}/n_s, %	92.8 (±19.5)		
	0.0–100		
n_t	29.4 (±2.5)	27.4	
	21–34	21–34	17–26
lt, %	11.5 (±1.4)		
	8.3–15.2		
s/t, %	47.5 (±4.4)	49.4	
	34.4–61.9	37.9–75.0	55–60

There can be little doubt, that both species are closely related. Some presumable synapomorphic features are their unique wheel deposits. (1) Spokes are fused in their proximal part with their neighbors, thus enlarging the hub. (2) Close to the rim spokes branche into two. (3) The teeth projecting from the rim of the wheel often are bifid. According to Gage & Billett (1986) these characters are only present in the larger wheels of *M.* (*O.*) *clarki*, while they are found in nearly all wheels of *M.* (*O.*) *meteorensis* with a diameter larger than 210 µm. Out of 177 wheels measured, there were only 4 wheels which had no branched spokes, and each one, with only 1, 2 or 3 branched spokes. Five of these seven wheels have a diameter of less than 210 µm. Similar to small wheels in *M.* (*O.*) *clarki*, small wheels in *M.* (*O*). *meteorensis* may lack this character, though all of them have bifid teeth projecting from the rim.

Myriotrochus (*O.*) *clarki* has been found off NW Ireland and off NW United Kingdom at depths between 1040 and 2907 m (Gage & Billett 1986, Harvey *et al.* 1988). Recently, it also has been described from off NW Spain, at a depth of 480–520 m (Smirnov 1999).

In conclusion, *M.* (*O.*) *meteorensis* may be distinguished from the closely related *M.* (*O.*) *clarki* by its tentacles, which bear four to five pairs of lateral digits, instead of only two in the latter species, and by its considerably larger wheels.

Distribution. Only known from the type locality, off NW Africa, NE Atlantic Ocean, 2786–2843 m.

Etymology. The name, *meteorensis,* refers to the German research vessel FS "Meteor" the service of which contributed much to our current knowledge on marine biodiversity.

Acknowledgements

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Crinoidea and Holothuroidea (Echinodermata) of the abyssal Angola Basin—Results of the DIVA-1 expedition of FS "Meteor" (Cruise M48/1)

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Abstract

Agassiz trawl and epibenthic sledge samples taken at abyssal depths in the Angola Basin (south-eastern Atlantic Ocean) during the expedition DIVA-1 with FS "Meteor" in July 2000 yielded a rich variety of Echinodermata: inter alia one stalked crinoid (*Bathycrinus* cf. *aldrichianus* Wyville Thomson, 1876) and altogether nine holothurian species, two of which are subspecies. One of these, *Achlyonice longicornis* **spec. nov.**, is new to science, while all others have been described earlier: *Deima validum validum* Théel, 1879, *Psychropotes semperiana* Théel, 1882, *Peniagone purpurea* (Théel, 1882), *Molpadiodemas atlanticus* (R. Perrier, 1898), *Molpadia liska* Pawson, 1977, *Protankyra brychia* (Verrill, 1885), *Siniotrochus myriodontus* Gage & Billett, 1986 and *Neolepidotrochus parvidiscus angolensis* Bohn, 2005. All species collected are described and their known distributions are given. Finally, two crinoids and 21 holothurian species, so far known from the abyssal Angola Basin, are listed and their zoogeographical relationships are discussed.

Key words: Echinodermata; Crinoidea; Holothuroidea; South Atlantic Ocean; Angola Basin; deep-sea; taxonomy

Introduction

For a long time, the south-eastern Atlantic deep-sea remained almost unexplored (Fig. 1). The Valdivia expedition took samples in the Gulf of Guinea and along the western coast of Africa and information on the Holothuroidea collected there have been published by Ludwig & Heding (1935) and Heding (1940). Similarly to the Valdivia expedition, the Danish Deep-Sea Expedition (Galathea) explored bathyal and abyssal depths in the Gulf of Guinea and off the western coast of Africa. So far, only the elasipodid holothurians collected have been published in an excellent monograph on this group (Hansen 1975). Extensive sampling in the Cape Basin, the Angola Basin and the Guinea Basin was conducted by the French Research Institute for Exploitation of the Sea (IFREMER, Brest, France) in the course of the Walda (05–08.1971) and the Walvis (12.1978–01.1979) cruises with NO "Jean Charcot". Even though only the Asteroidea of the Walda cruise have been published so far (Sibuet 1975), data for the Holothuroidea collected are nowadays available in the IFREMER BIOCEAN Database, which is part of the Ocean Biogeographic Information System (OBIS) at www.iobis.org.

The aim of the DIVA-1 expedition with FS "Meteor" (cruise M48/1) to the Angola Basin (south-eastern Atlantic Ocean) was to investigate the biodiversity of this abyssal plain. At several stations along a transect of about 700 km samples were taken with an Agassiz trawl and an epibenthic sledge (Fig. 1).

The objective of this paper is to describe and document the Crinoidea and Holothuroidea collected in the course of the DIVA-1 expedition (other Echinodermata collected will be the subject of another publication). Based on these results and by incorporating all available other sources, a list of the hitherto known species of this deep-sea basin is compiled. Finally, zoogeographical relationships of the holothurian and crinoid fauna with other deep-sea regions are discussed.

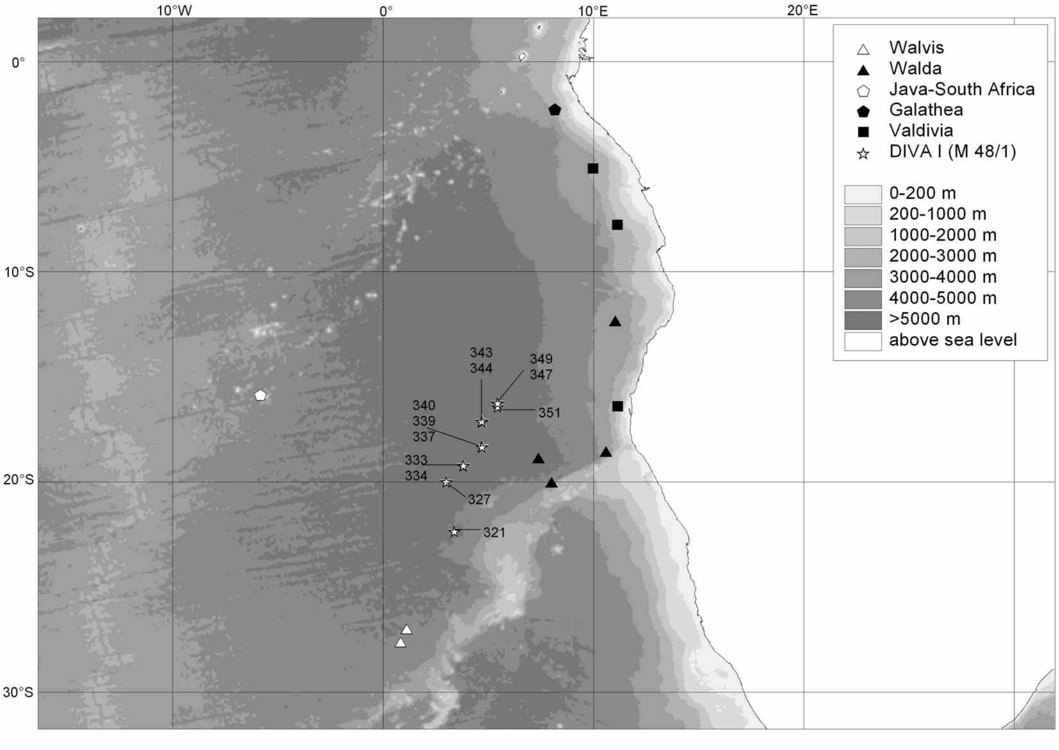

FIGURE 1. Records of Crinoidea and Holothuroidea in the Angola Basin and vicinity by the Valdivia expedition (Ludwig & Heding 1935; Heding 1940), Dr Mortensen's Java—South Africa expedition and the Galathea expedition (Hansen 1975), the Walda and Walvis cruises (IFREMER BIOCEAN) and the DIVA-1 expedition.

Material and methods

The crinoid and holothurian specimens investigated were sampled at 12 stations, deploying an Agassiz trawl or an epibenthic sledge (station details are summarized in table 1). The material from the Agassiz trawl was first fixed in buffered formalin and then transferred to ethanol for long term storage, while the epibenthic sledge samples were fixed in cold ethanol. The investigated material is deposited in the Bavarian State Collection of Zoology in Munich (ZSM).

TABLE 1. Stations, collection methods and species collected in the course of the DIVA-1 expedition with FS "Meteor" (M 48/1) to the Angola abyssal plain. *AGT*—Agassiz trawl; *EBS*—epibenthic sledge; +— fragments.

Station	Details	Species	Number of specimens
M 48/1-321	22°20.6' S, 3°23.6' E, 5126 m to 22°27.6' S, 3°27.9' E, 5121 m, AGT, 10 Jul, 2000	*Psychropotes semperiana* Théel, 1882	2
M 48/1-327	19°59.2' S, 3°00.9' E, 5448 m to 20°07.5' S, 3°07.9' E, 5439 m, AGT, 15 Jul, 2000	Bathycrinidae gen. sp.	+
M 48/1-333	19°12.9' S, 3°48.6' E, 5426 m to 19°17.4' S, 3°52.2' E, 5424 m, AGT, 19 Jul, 2000	*Deima validum validum* Théel, 1879	1
		Molpadia liska Pawson, 1977	2
M 48/1-334	19°12.5' S, 3°49.0' E, 5426 m to 19°19.8' S, 3°55.6' E, 5425 m, AGT, 19 Jul, 2000	Bathycrinidae gen. sp.	+
		Protankyra brychia (Verrill, 1885)	3
M 48/1-337	18°18.9' S, 4°42.7' E, 5393 m to 18°24.6' S, 4°45.1' E, 5392 m, AGT, 21 Jul, 2000	Bathycrinidae gen. sp.	+
		Protankyra brychia (Verrill, 1885)	1
M 48/1-339	18°19.4' S, 4°42.1' E, 5395 m to 18°25.3' S, 4°44.0' E, 5392 m, AGT, 22 Jul, 2000	Bathycrinidae gen. sp.	+
		Deima validum validum Théel, 1879	1
M 48/1-340	18°18.3' S, 4°41.3' E, 5395 m to 18°19.4' S, 4°41.9' E, 5395 m, AGT, 23 Jul, 2000	*Neolepidotrochus parvidiscus angolensis* Bohn, 2005	1

.... *to be continued*

Table 1 (continued)

Station	Details	Species	Number of specimens
M 48/1-343	17°07.5' S, 4°42.9' E, 5415 m to 17°11.6' S, 4°45.9' E, 5415 m, AGT, 25 Jul, 2000	*Deima validum validum* Théel, 1879	1
		Peniagone purpurea (Théel, 1882)	2
		Molpadiodemas atlanticus (R. Perrier, 1898)	1
		Protankyra brychia (Verrill, 1885)	1
M 48/1-344	17°06.2' S, 4°41.7' E, 5415 m to 17°07.5' S, 4°42.3' E, 5415 m, EBS, 25 Jul, 2000	Bathycrinidae gen. sp.	+
		Bathycrinus cf. *aldrichianus* Wyville Thomson, 1876	1
M 48/1-347	16°14.0' S, 5°26.7' E, 5389 m to 16°23.1' S, 5°27.0' E, 5388 m, AGT, 28 Jul, 2000	*Molpadiodemas atlanticus* (R. Perrier, 1898)	1
		Protankyra brychia (Verrill, 1885)	5
		Siniotrochus myriodontus Gage & Billett, 1986	1
M 48/1-349	16°14.8' S, 5°26.5' E, 5389 m to 16°24.7' S, 5°26.2' E, 5388 m, AGT, 29 Jul, 2000	*Molpadia liska* Pawson, 1977	4
		Protankyra brychia (Verrill, 1885)	4
M 48/1-351	16°25.2' S, 5°27.1' E, 5387 m to 16°33.2' S, 5°27.3' E, 5385 m, AGT, 30 Jul, 2000	*Achlyonice longicornis* **sp. nov.**	1
		Molpadia liska Pawson, 1977	5
		Protankyra brychia (Verrill, 1885)	7
		Siniotrochus myriodontus Gage & Billett, 1986	2

To examine the diagnostically important calcareous deposits, pieces of the body wall were macerated in 12.5 % sodium hypochlorite solution. The remaining calcareous deposits were rinsed several times in distilled water and finally air-dried. One part of the deposits was mounted in Canada Balsam on slides, to be analyzed with a Leitz microscope equipped with a video camera (380 USB 2.0 Spacec@m) and the software AxioVision LE. For SEM examinations, the other part of the deposits was transferred to aluminium stubs, sputtered with gold and studied in a LEO 1430 VP Scanning Electron Microscope.

This paper does not aim to provide a complete synonymy of the species treated; instead only the original combination and source of the name as well as its junior synonyms are given. Further details are available from the references indicating the current use of a name, including a more complete synonymy.

The data for the species distributions are based on geo-referenced localities extracted from literature (mainly expedition reports) and the IFREMER BIOCEAN database, including distribution records of species nowadays treated as junior synonyms of the species in question. Records from the IFREMER BIOCEAN database were only included when identifications were made by experienced echinoderm taxonomists like Myriam Sibuet (IFREMER, France) or Michel Roux (University of Reims, France).

Symbols used to describe crinoid ossicles and series of ossicles of arms, pinnules and the stalk conform with the abbreviations used by Roux *et al.* (2002) for stalked crinoids, which differ slightly from the symbols sometimes used to describe "stalk-less" comatulid crinoids (Roux *et al.* 2002).

Taxonomy

Class Crinoidea Miller, 1821

Family Bathycrinidae Bather, 1899

Bathycrinidae gen. sp.

Material. M 48/1-327: 1 stalk fragment (ZSM 20043082). 48/1-334: 3 stalk fragments (ZSM 20043081). M 48/1-337: 8 stalk fragments (ZSM 20043085), 1 stalk fragment (ZSM 20020069). M 48/1-339: 7 stalk fragments (ZSM 20043083). M 48/1-344: 1 stalk fragment (ZSM 20043084).

Remarks. The available stalk fragments only allowed identification to family level.

Genus *Bathycrinus* Wyville Thomson, 1872

Bathycrinus cf. *aldrichianus* Wyville Thomson, 1876
(Figs 2A, 3)

Bathycrinus aldrichianus Wyville Thomson, 1876: 47–51, fig. 1; Clark, 1977: 159–162, fig. 1 (g) [synonymy]
Bathycrinus campbellianus P.H. Carpenter, 1884: 238–240, fig. 15
Bathycrinus serratus A.H. Clark, 1908: 205–207, fig. 1

Material. M 48/1-344: 1 calyx (ZSM 20043086).

Description. The specimen is small and damaged, only the radials and arms (up to Br_{10}) are preserved, the basals and the stalk are missing (Fig. 2A). The calyx is about 1.7 mm wide. The five radials are smooth, about 0.7 mm high, have a proximal width of 0.5 mm and a distal width of 0.8 mm. Sharp-edged lateral flanges and a prominent crest-like keel characterise the first brachitaxis (IBr_1 and IBr_2) and the proximal brachials. On the axillaries (IBr_2) the keel is Y-shaped. In distal brachials the lateral flanges disappear and the crest-like keel is less prominent. The first brachitaxis is about 1.8 mm long and at the joint of IBr_1 and IBr_2 0.9 mm wide. Though indistinct, the first non-muscular joints are between brachials 1+2, 4+5 and 7+8. No pinnules were found (not developed yet?).

Remarks. Currently, there are two Atlantic *Bathycrinus* species recognized, viz *B. aldrichianus* Wyville Thomson, 1876 and *B. gracilis* Wyville Thomson, 1872 which both are similar in being "very serrated in profile" in contrast to the remaining Atlantic species which have "smooth and rounded ossicles and profiles" (Clark 1977: p. 167). The current specimen corresponds with both species in the ornamentation of the first brachitaxis and the proximal brachials, with a central keel and lateral flanges (Clark 1977, 1980; Macurda & Meyer 1976). Slight differences in the specificity of the ornamentation may be correlated with size (Clark 1977) and thus not sufficient to separate both species. The only character known to distinguish both species seems to be the position of the first pinnule on the arm. *Bathycrinus gracilis* has the first pinnule on brachials 10 to 12, while *B. aldrichianus* has the first pinnule on brachials 8 to 11 (Clark 1980). Due to the fact that the current specimen lacks pinnules, a reliable determination is not possible and the specimen is tentatively assigned to *B. aldrichianus* because of the geographical vicinity to other records of this species.

Distribution. *Bathycrinus aldrichianus* has been described from the north-western, the central and the southern Atlantic Ocean (Fig. 3), 3305–5860 m (Carpenter 1884; Clark 1908; Clark 1977; Gislén 1951; Macurda & Meyer 1976; herein), whereas *B. gracilis* seems to be restricted to the north-eastern Atlantic Ocean (Fig. 3), 2880–5330 m (Carpenter 1884; Clark 1977, 1980; Harvey et al. 1988; IFREMER BIOCEAN; Kœhler 1909).

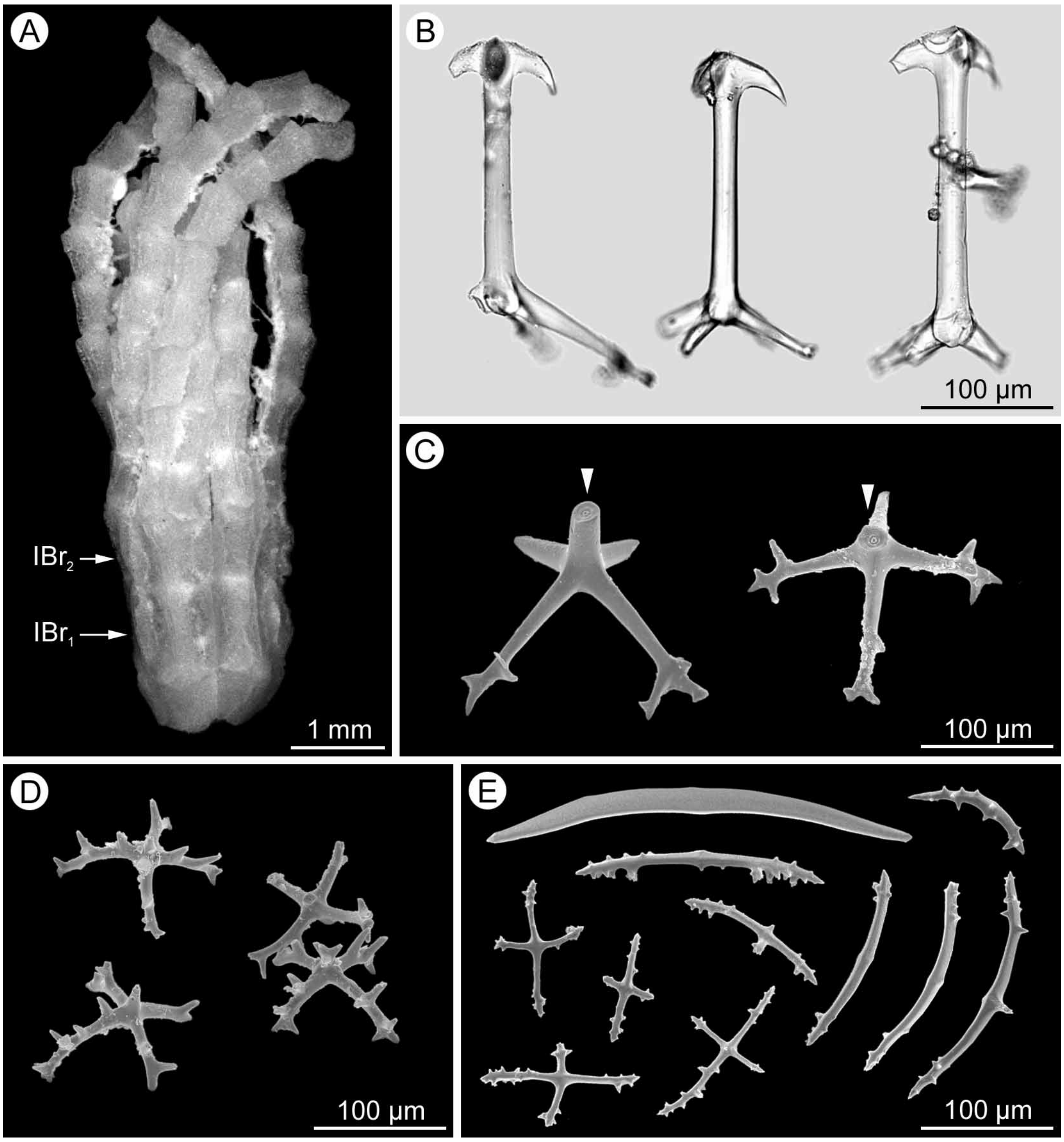

FIGURE 2. (A) *Bathycrinus* cf. *aldrichianus* Wyville Thomson, 1876. Distal part of calyx with arms, basals and stalk missing (*IBr*$_1$, *IBr*$_2$—first and second brachials of first brachitaxis). **(B–E)** *Psychropotes semperiana* Théel, 1882. Calcareous deposits. **(B)** Large crosses (damaged) from dorsal body wall, with four arms, central apophysis and downwardly bent hooks. **(C)** Large crosses (damaged) from dorsal body wall, with four arms and central apophysis (*arrowheads*). **(D)** Small crosses from dorsal body wall. **(E)** Rods and crosses from ventral body wall.

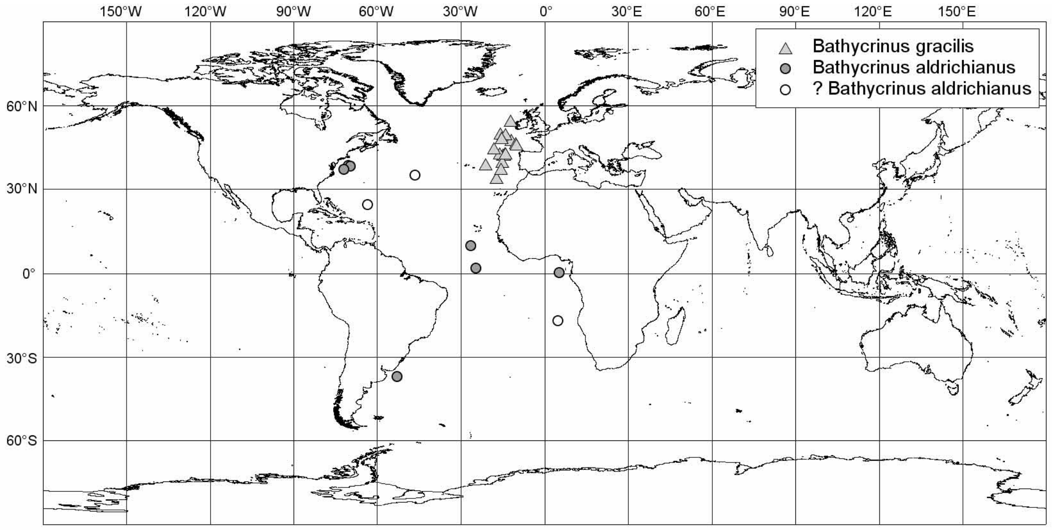

FIGURE 3. Distribution of *Bathycrinus aldrichianus* Wyville Thomson, 1876 and the closely related *B. gracilis* Wyville Thomson, 1872. Questionable records for *B. aldrichianus*, often based on stalk fragments solely, are indicated as blank circles.

Class Holothuroidea de Blainville, 1834

Family Deimatidae Théel, 1879

Genus *Deima* Théel, 1879

Deima validum validum Théel, 1879
(Fig. 4)

Deima validum Théel, 1879: 5, figs 36–38
Deima validum validum. Hansen, 1975: 17–23, fig. 1, pls 11 (fig. 1), 13 (figs 1–2), [synonymy]
Deima fastosum Théel, 1879: 5–6, figs 1–3
Deima blakei Théel, 1886b: 1–2, figs 1–2
Deima atlanticum Hérouard, 1898: 88–89, figs 1–2
Deima mosaicum Ohshima, 1915: 233–234

Material. M 48/1-333: 1 specimen (ZSM 20043072). M 48/1-339: 1 specimen (ZSM 20020018). M 48/1-343: 1 specimen (ZSM 20043071).

Remarks. The taxonomy, morphology and distribution of this subspecies has been described in detail by Hansen (1975). It is characterised by: 10–13 pairs of ventro-lateral tube feet in single rows; mid-ventral tube feet absent or rarely represented by a reduced pre-anal pair; dorsal papillae 5–10 pairs; ventro-lateral papillae 3–7 pairs; calcareous deposits are perforated plates, usually large and multilayered; dorsal plates 1.5–7.0 mm in diameter, ventral plates 0.5–4.0 mm. The investigated specimens fit with this diagnosis. The largest specimen (86 mm in length) has a single (?) small pre-anal tube foot, while there are no pre-anal tube feet present in the other specimens. This is the second record of this species for the South Atlantic Ocean and the known depth-range is increased from 4820 m to more than 5400 m.

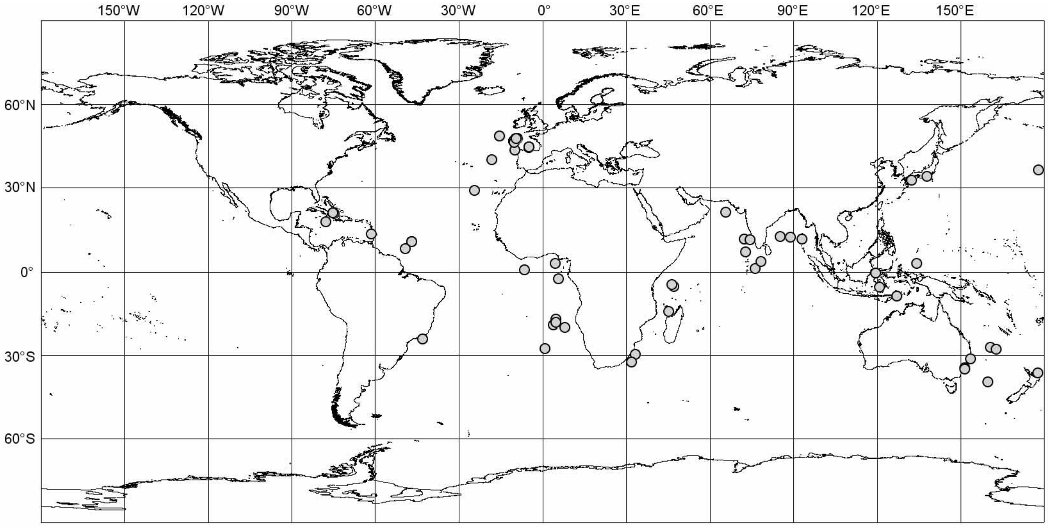

FIGURE 4. Distribution of *Deima validum validum* Théel, 1879.

Distribution. (Fig. 4) This subspecies probably has a cosmopolitan distribution, except for the Arctic and Southern Ocean, 724–5426 m (Deichmann 1940; Grieg 1921; Hansen 1975; Hérouard 1902, 1923; IFREMER BIOCEAN; Kœhler & Vaney 1905; Ohshima 1915; O'Loughlin 1998; Sibuet 1977; Sluiter 1901; Théel 1882, 1886b; herein).

Family Psychropotidae Théel, 1882

Genus *Psychropotes* Théel, 1882

Psychropotes semperiana Théel, 1882
(Figs 2B–E, 5)

Psychropotes semperiana Théel, 1882: 100–101, pl. 34 (figs 10–11); Hansen, 1975: 102–105, figs 41–42 [synonymy]
Psychropotes kerhervei Hérouard, 1902: 27–30, pl. 4 (figs 1–9)
Euphronides anchora Hérouard, 1912: 6–7, fig. 5

Material. M 48/1-321: 2 specimens (ZSM 20043075).

Description. Anteriorly, the specimens are more or less flat, while the posterior part of the body is elevated and gives rise to the unpaired dorsal appendage. The larger specimen is 79 mm long and 22 mm wide (across ventral sole), while the smaller specimen measures 53 mm in length and 17 mm across the ventral sole. Both are of a purple colour (preserved). The mouth and the anus are ventral and confined to the anterior and the posterior end of the body. There are 16 tentacles, with conspicuous, rounded discs. The ventral sole is delimited on both sides by a narrow brim (damaged for the most part), formed by basally fused tube feet. Mid-ventral tube feet are conical and restricted to a double row, which seems to be present (partly damaged) throughout the length of the ventral sole. The unpaired dorsal appendage arises from a dorsal bulge, which is situated one-seventh body length in the large specimen and one-fourth body length in the small specimen from the posterior end of the body. In both specimens, the dorsal appendage is more or less contracted and thus nothing can be said about the original size. The almost complete dorsal appendage of the large specimen ends in two long slender papillae, each about 18 mm long. Anterior to the dorsal bulge of the small specimen, are three pairs of short conical papillae (indistinct in the larger specimen).

Calcareous deposits of the dorsal body wall are crosses of two types (Figs 2B–D). The four arms of the larger type are smooth in their proximal parts and are equipped with irregularly placed spines close to their distal ends (Fig. 2C). The high central apophysis is smooth and ends in three or four downwardly bent hooks (Fig. 2B). Crosses of the second type are considerably smaller, have irregularly placed spines along the arms and a low and also spinous central apophysis (Fig. 2D). The calcareous deposits of the ventral body wall are rods and crosses with irregularly placed spines (Fig. 2E).

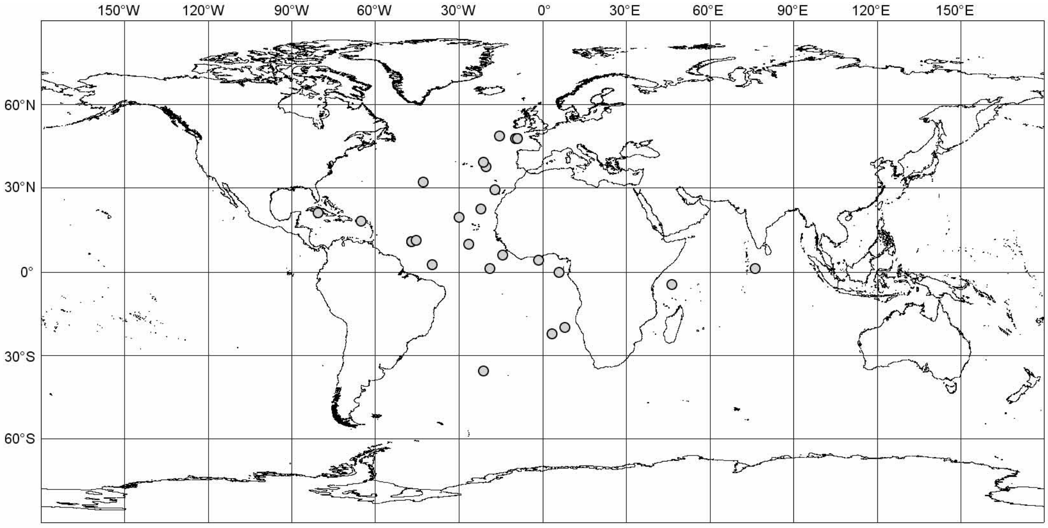

FIGURE 5. Distribution of *Psychropotes semperiana* Théel, 1882.

Remarks. The two specimens described herein conform to the detailed description given by Hansen (1975) for this species. Very characteristic are the large cross-shaped deposits of the dorsal body wall with a high and smooth central apophysis, ending in three or four downwardly bent hooks, which are unique within the genus (Hansen 1975).

Distribution. (Fig. 5) Northern and southern Atlantic Ocean, northern and western Indian Ocean, 2695–5610 m (Deichmann 1930, 1940; Hansen 1975; Hérouard 1902, 1923; IFREMER BIOCEAN; Madsen 1953; Sibuet 1977; Théel 1882; herein).

Family Elpidiidae Théel, 1879

Genus *Peniagone* Théel, 1882

Peniagone purpurea (Théel, 1882)

(Figs 6A–D, 7)

Elpidia purpurea Théel, 1882: 21–23, pls 7 (figs 4–6), 33 (figs 13–14), 44 (fig. 6)
Elpidia ambigua Théel, 1882: 27–28, pl. 33 (fig. 6)
Peniagone vexillum R. Perrier, 1900: 118
Peniagone ferruginea Grieg, 1921: 7–8, fig. 3, pl. 1 (figs 4–6)
Peniagone lacinora Agatep, 1967: 53–55, pl. 3 (figs 1–9)
Peniagone lugubris Théel, 1882. Madsen, 1953: 153–155, figs 2–3
Peniagone purpurea. Gebruk, 1990: 111–113, fig. 46 [synonymy]

Material. M 48/1-343: 2 specimens (ZSM 20043074).

Description. The body is more or less flat, with a distinct brim along the lateral edges of the body, continuous with the velum (Fig. 6A). The two specimens are 37 and 55 mm long and 12 and 24 mm wide. Preserved they are purple to dark purple (tentacle discs and around mouth). The ventral mouth is situated on an anterior bulge-like enhancement, while the posterior anus opens dorsally above the posterior tube feet. Ten conspicuous tentacles encircle the mouth (larger specimen: 7 preserved, smaller specimen: 1 preserved). The tentacle discs are large, almost circular in outline, and have an irregular margin, due to several retractile lobes. The posterior three-fifths of the ventral sole are bordered by 7–8 pairs of conspicuous conical tube feet. From anterior to posterior, they continuously decrease somewhat in size and become closer to each other. The anterior tube feet are well separated and situated on the ventral side of the specimen, while the posterior ones are in contact and are contiguous with the lateral brim. The most posterior pair of tube feet is considerably smaller than the preceding ones. The dorsal velum, continuous with the lateral brim, is conspicuous and composed of four basally fused papillae. The papillae are long and slender and the anterior pair is about twice as long as the posterior pair. A short distance from the velum there is a variable number of pairs of free papillae (1–3).

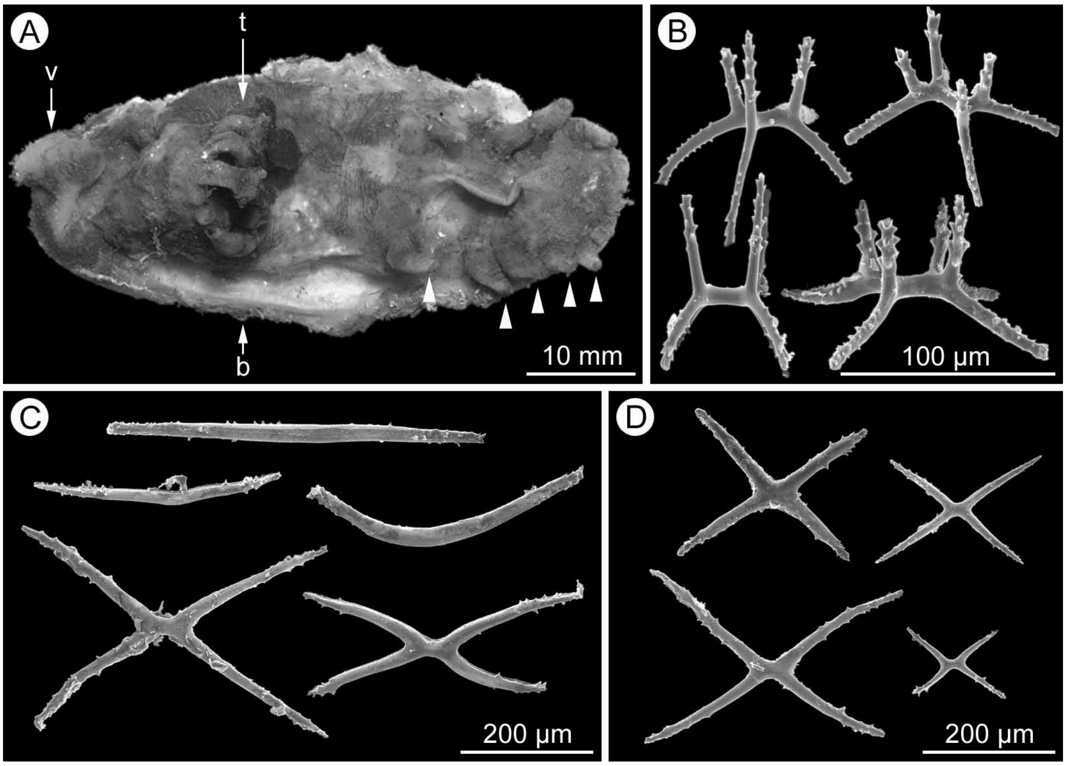

FIGURE 6. *Peniagone purpurea* (Théel, 1882). **(A)** Ventral view of a specimen, anterior end to the left (*b*—brim, *t*—tentacles, *v*—velum, *arrowheads*—tube feet). **(B)** Primary crosses from body wall. **(C)** Large crosses and rods from tentacles. **(D)** Large crosses from tube feet.

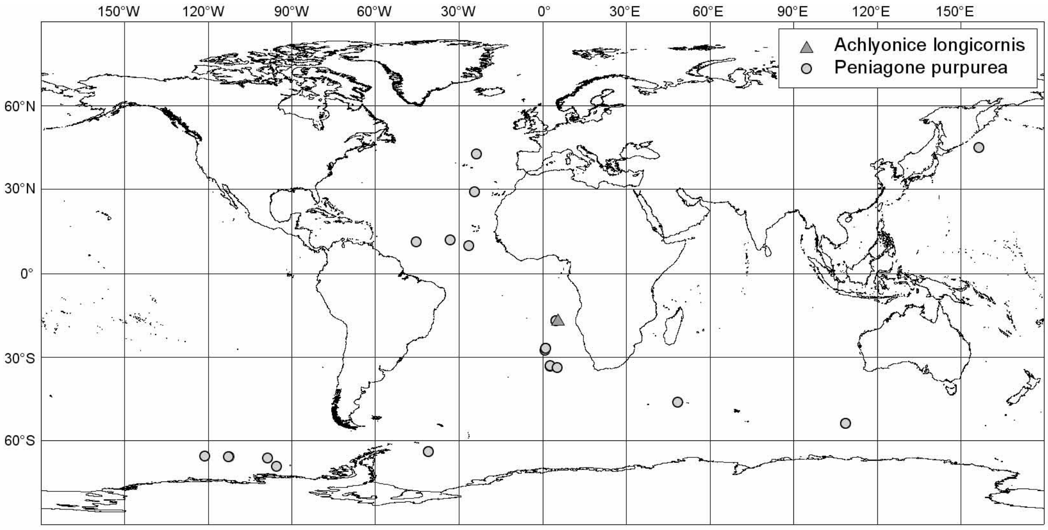

FIGURE 7. Distribution of *Peniagone purpurea* (Théel, 1882) and *Achlyonice longicornis* **spec. nov.**

Calcareous deposits of the body wall are primary crosses with a well developed stem, more or less bent arms and four high apophyses, one on each arm (Fig. 6B). The arms and apophyses of the primary crosses are irregularly equipped with small spines. Usually, the apophyses are shorter than the arms, but not always. In addition to the common primary crosses, in the tentacles also large spinous crosses and rods are present (Fig. 6C). Similar spinous crosses also do occur in the tube feet (Fig. 6D).

Remarks. In his revision of the family Elpidiidae, Gebruk (1990) synonymised the two species *P. purpurea* and *P. ferruginea*, till then recognised as valid (e.g. Hansen 1975). According to Gebruk, *P. purpurea* is characterised by the following features: calcareous deposits of dorsal body wall primary crosses of two types, both with four apophyses, which are usually shorter than arms, in one type arms are bent, while in the other type arms are about horizontal; dorsal velum large, papillae of velum free in their distal part. The current specimens fit with this diagnosis regarding the morphology of the dorsal velum, which is formed by four basally fused papillae. However, with reference to the supposed two types of primary crosses in the dorsal body wall, the current specimens differ somewhat. There are primary crosses with conspicuously bent arms as well as crosses with almost horizontal arms, but there are also intermediate forms with more or less bent arms. Likewise variable primary crosses are also present in the ventral body wall of both specimens investigated. It seems, that in reality these two "types" represent the extremes of a continuous range.

Distribution. (Fig. 7) Northern and southern Atlantic Ocean, southern Indian Ocean, northern Pacific Ocean and Southern Ocean, 2800–5880 m (Agatep 1967; Gebruk 1990; Grieg 1921; IFREMER BIOCEAN; Madsen 1953; Perrier 1902; Théel 1882; herein).

Genus *Achlyonice* Théel, 1879

Achlyonice longicornis spec. nov.

(Figs 7, 8A–E)

Material. Holotype (ZSM 20043073), FS "Meteor", DIVA-1, station M 48/1-351, 16°25.2' S, 5°27.1' E, 5387 m to 16°33.2' S, 5°27.3' E, 5385 m, Agassiz trawl, 30 Jul, 2000.

Description. The holotype is more or less ovoid (Figs 8A–B), 35 mm long, about 10 mm wide (across ventral sole), and of a dirty-white colour (preserved). The mouth is ventral and the anus is terminal, dorsally of the ventral sole. Ten tentacles encompass the mouth, eight (?) of which are connected by a membrane, while at least the two posteriormost tentacles are free. Terminal discs of tentacles with numerous minute processes. Nine pairs of tube feet border the posterior two-thirds of the ventral sole (Figs 8A–B). The anterior five pairs are conical and bear a terminal disc consisting of four lobes (Fig. 8D). They are well separated from each other and slightly decrease in size from anterior to posterior. The remaining four pairs, all of about equal size, are clustered brim-like at the posterior end of the ventral sole. A conspicuous dorsal velum, about as long as the body, is situated close to the anterior end of the specimen (Figs 8A, C). It is composed of four papillae, of which the long median pair are fully fused along their length, while the outer papillae are much shorter and separate in their distal part, forming small lateral lobes. A third pair of small and free papillae is present close to the base of the velum.

A calcareous ring seems to be missing. The single polian vesicle is large. The unpaired left gonad consists of richly branched short tubules opening into a well developed common duct. The anterior part of the intestine is straight, while the posterior forms a loop.

Calcareous deposits are straight or slightly curved spinous rods (Fig. 8E), up to 470 µm long, which are present in the tentacles the dorsal papillae and the tube feet; but none were found in the body wall (some of the deposits are in the process of dissolving, due to acidic fixation fluid).

Remarks. *Achlyonice longicornis* differs from all other known elpidiid species by the combined occurrence of the following two characteristics: the peculiar triangular velum with two small lateral lobes and the large spinous rods present in the tentacles, the dorsal papillae and the tube feet.

Only one species is known to possess a somewhat similar velum, the single specimen of *Peniagone stabilis* Kœhler and Vaney, 1905 collected in the Bay of Bengal. It is characterised by a triangular velum consisting of one large and two small papillae and a posterior lobated border of fused tube feet (Kœhler & Vaney 1905). It differs from *Achlyonice longicornis* by the much shorter velum, which is only 5 mm high (with both specimens being of similar size) and by its calcareous deposits, which are four-armed and have one central apophysis and one apophysis on each arm.

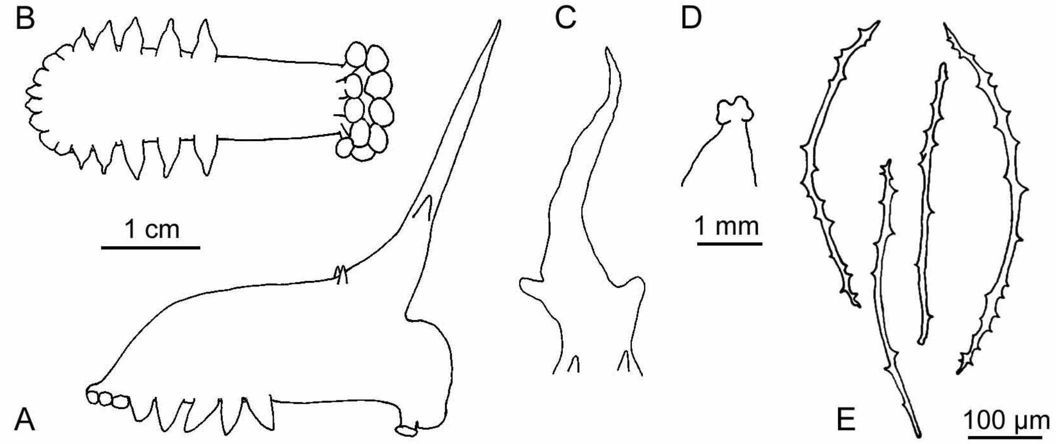

FIGURE 8. *Achlyonice longicornis* **spec. nov.** **(A)** Right lateral view (schematic). **(B)** Ventral view (schematic). **(C)** Velum. **(D)** Distal end of tubefoot. **(E)** Rods from dorsal papillae. Figs A–C to the same scale.

The generic assignment of the new species is somewhat ambiguous. Three out of five species of the genus *Achlyonice* Théel, 1879 and all species of the genus *Ellipinion* Hérouard, 1923 are known to possess rod-shaped, often spinous deposits and a velum. *Ellipinion* species differ from *Achlyonice* by the additional presence of small C-shaped deposits and constantly 10 tentacles. Hansen (1975) characterises *Achlyonice* as follows: tentacles 10–12; deposits tripartite, rod-shaped or absent; calcareous ring consisting of five isolated pieces, each having a varying number of arms. Absence of C-shaped deposits assigns the new species to *Achlyonice* rather than to *Ellipinion*.

Within this genus there are two species, *Achlyonice monactinica* Ohshima, 1915 and *Achlyonice myriamae* Gebruk, 1997, which share some similarities with *A. longicornis*. All three have the anterior tentacles connected by a membrane and the calcareous deposits are rods (Ohshima 1915; Gebruk 1997). Most obviously, *A. longicornis* differs from *A. myriamae* and *A. monactinica* by: different tentacle numbers, both species have 12 tentacles as opposed to *A. longicornis*, which has only ten; its peculiar dominant triangular velum; the restriction of rod deposits to the tentacles, the dorsal papillae and the tube feet, which are present throughout the body wall in the other species. Furthermore, *A. myriamae* has in addition to rod deposits also tripartite deposits, which are lacking in *A. monactinica* as well as in *A. longicornis*.

Distribution. (Fig. 7) So far, this species is only known from the type locality, Atlantic Ocean, Angola Basin, 5385–5387 m.

Etymology. The name, *longicornis*, refers to the characteristic, horn-like shape of the dorsal velum.

Family Synallactidae Ludwig, 1894

Genus *Molpadiodemas* Heding, 1935

Molpadiodemas atlanticus (R. Perrier, 1898)

(Figs 9A, 10)

Pseudostichopus atlanticus R. Perrier, 1898: 1665
Molpadiodemas acaudum Heding, 1935: 78–80, pl. 6 (figs 1–2)
Molpadiodemas atlanticus. O'Loughlin & Ahearn, 2005: 153, figs 3(a–b), 4(a–d), 6(a–b) [synonymy]

Material. M 48/1-343: 1 ♀ (ZSM 20020019). M 48/1-347: 1 ♂ (ZSM 20043076).

Additional Material. 1 ♀ (ZSM 20043140), FS "Meteor", station M 3/24, Agassiz trawl 2, 42°26.8' N, 14°49.0' W to 42°40.9' N, 14°49.2' W, 5270 m, Agassiz trawl, 11 Mar, 1966, det. C.G. Ahearn (USNM), 2004.

Description. The specimens range from 76 to 100 mm in length and 24 to 54 mm in width. The body is more or less cylindrical with rounded anterior and posterior ends, of a dirty-white colour (preserved) and without encrusting foreign bodies. Mouth ventral, encompassed by 20 prominent brown tentacles, which often are retracted and thus difficult to make out. The anus is ventral in position, enclosed in an inconspicuous pygal furrow. Filiform tube feet, lacking a sucking disc, are found sparsely scattered on the ventral side (often visible as small brown spots) but could not be detected dorsally. The body wall is thick and rugose.

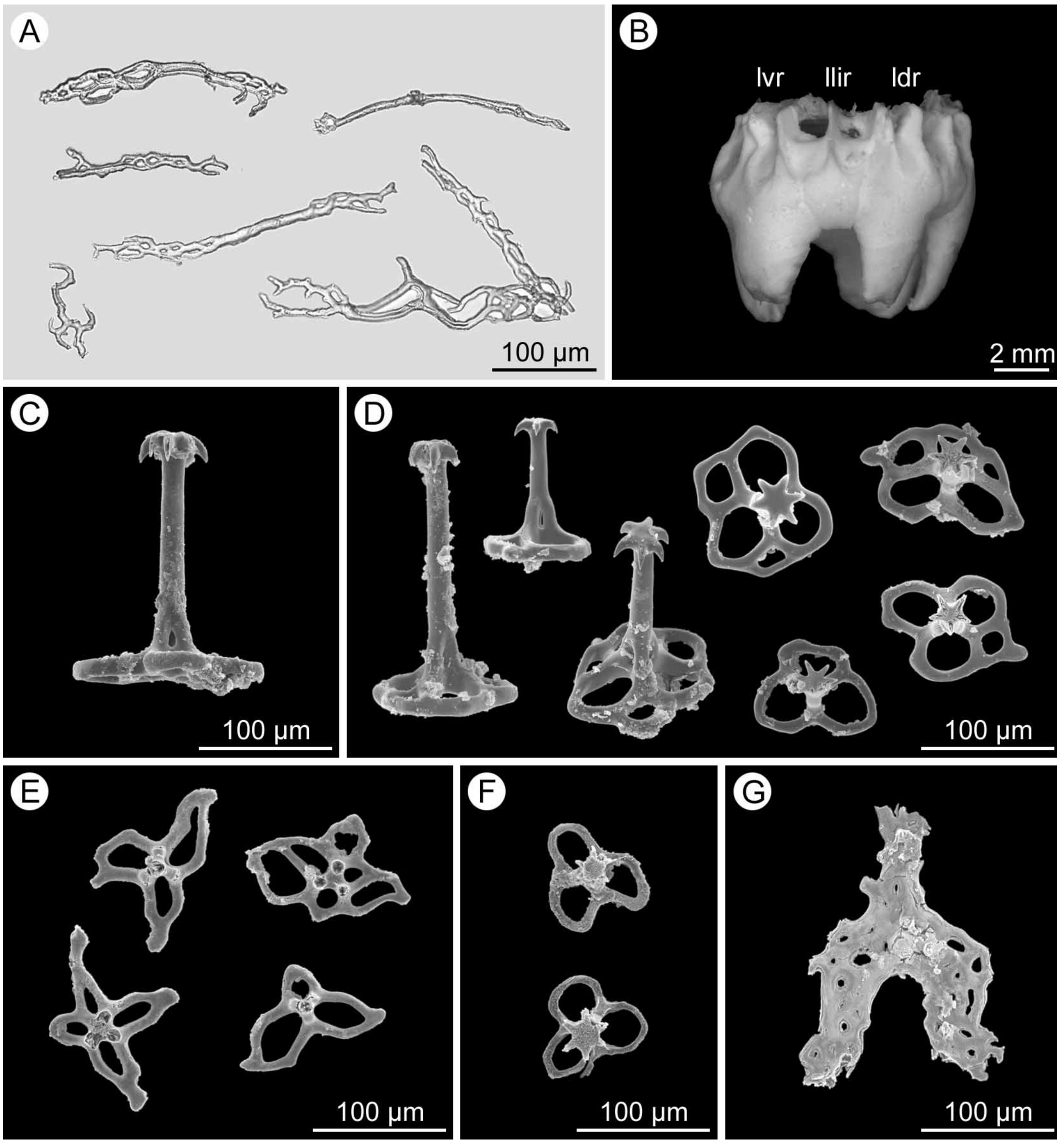

FIGURE 9. (A) *Molpadiodemas atlanticus* (R. Perrier, 1898). Rod-like deposits from tentacles. **(B–G)** *Molpadia liska* Pawson, 1977. **(B)** Calcareous ring, left lateral view (*ldr*— left dorso-lateral radial plate, *llir*—left lateral interradial plate, *lvr*—left ventro-lateral radial plate). **(C)** Table from body wall (JMB-01141). **(D)** Tables from body wall (JMB-01646). **(E)** Tables from tail (JMB-01141). **(F)** Tables from tail (JMB-01646). **(G)** Anal tooth (JMB-01646).

The calcareous ring is prominent. Longitudinal muscles are flat and wide. There is a single ventral polian vesicle. The gonad consists of a tuft of branching tubules on both sides of the dorsal mesentery. The intestine forms a large loop, and the respiratory trees originate with a common trunk from the right side of the cloaca.

Calcareous deposits are scarce. Isolated deposits are present in the tentacles, which are irregularly rod-like, sometimes bent, often branching and with a tendency to form an irregular network, resulting in few to several perforations (Fig. 9A). No deposits could be detected in the body wall, in the tube feet, in the gonads nor in the respiratory trees.

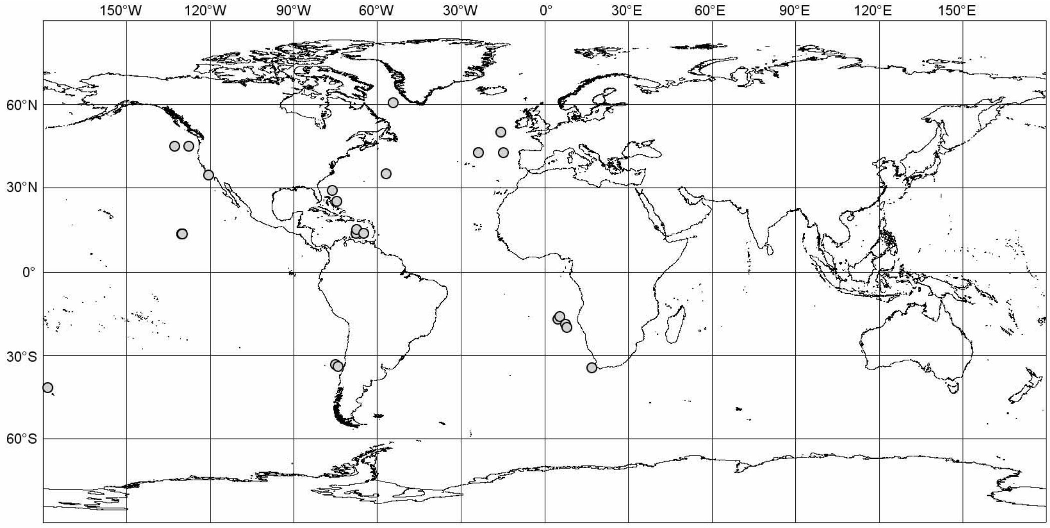

FIGURE 10. Distribution of *Molpadiodemas atlanticus* (R. Perrier, 1898).

Remarks. In an long-needed and extensive review of the pygal-furrowed Synallactidae (O'Loughlin & Ahearn 2005) all hitherto known species as well as several new species are described, and detailed information is presented, including their synonymy and distribution.

Molpadiodemas atlanticus differs from its congeners by a combination of the following characters (O'Loughlin & Ahearn 2005): body large and sac-like; even cover of tube feet, frequently inconspicuous; frequent presence of large, irregular, open mesh-like gonad ossicles. The two Angola Basin specimens are assigned to *M. atlanticus*, although they lack the characteristic calcareous deposits in the gonad. Also the third specimen investigated (see additional material), which was determined by C.G. Ahearn in 2004 as belonging to this species, lacks calcareous deposits in the gonad. According to O'Loughlin and Ahearn (2005: p. 153) the lack of calcareous deposits in tentacles or gonads is not uncommon: "…ossicles frequently abundant in tentacles and gonads, sometimes rare or absent;…". But based on the body form (large and sac-like), the inconspicuous tube feet and the overall resemblance of the Angola Basin specimens with the specimen determined by C.G. Ahearn, the author is convinced, that the specimens are conspecific.

Distribution. (Fig. 10) Northern and south-eastern Atlantic Ocean, northern and southern Pacific Ocean, 2610–5415 m (Heding 1935; IFREMER BIOCEAN; O'Loughlin & Ahearn 2005; Perrier 1902; Thandar 1999; herein).

Family Molpadiidae Müller, 1850

Genus *Molpadia* Risso, 1826

Molpadia liska Pawson, 1977

(Figs 9B–G, 11)

Molpadia liska Pawson, 1977: 115–116, figs 6 (a–g, i), 7 (a–b, d)

Material. M 48/1-333: 1 specimen (ZSM 20043068), 1 specimen (ZSM 20043069). M 48/1-349: 4 specimens (ZSM 20020025). M 48/1-351: 5 specimens (ZSM 20020028).

Description. The specimens range from 24 to 63 mm in length, and 6 to 13 mm in width (at calcareous ring). The body is approximately cylindrical, with a tapering posterior end, resulting in a very short tail (only few millimetres long). Preserved specimens are dirty-white with a tinge of pink. Fifteen retracted tentacles encompass the terminal mouth. Likewise, the anus is terminal and in each radius there are few short anal papillae.

The calcareous ring is solid, smooth and composed of five radial plates (Fig. 9B: *ldr*, *lvr*), with prominent posterior projections and five much smaller interradial plates (Fig. 9B: *llir*).

The tentacle ampullae are short. Longitudinal muscle bands are undivided. There is one tubular polian vesicle in the left ventral radius. The single stone canal is long and embedded in the dorsal mesentery and has a large oval madreporite body close to the dorsal body wall. The gonad consists of tufts of branching, tubules on both sides of the dorsal mesentery. The intestine forms a large loop (as long as body) and the respiratory trees are conspicuous.

The calcareous deposits of the body wall (Figs 9C–D) and the tail (Figs 9E–F) are exclusively tables with 3–9 holes and a large solid spire, derived from three fused pillars, with 4–6 terminal hooklets. The tables of the body wall in the current specimens on average range from 95 to 121 µm (Tab. 2) and usually have 4 or 5 holes, while the tables from the tail are smaller, on average 86 to 105 µm in diameter (Tab. 2) and have fewer holes (3 or 4). There are no phosphatic deposits, but anal teeth are present (Fig. 9G).

Remarks. The current specimens agree in all details with *Molpadia liska* as characterised by Pawson (1977): body wall and tail deposits similar, exclusively tables with solid spires composed of three fused pillars, with usually three perforations but often with more up to a maximum of eight. Table deposit diameters of the current specimens are also in accordance with the table sizes as presented by Pawson (Tab. 2). There is only one other species known to possess similar table deposits in the body wall and in the tail: *Molpadia discors* Pawson, 1977. This species differs from *Molpadia liska* by its invariable number of three holes per table, which in *Molpadia liska* may be up to eight or nine (Pawson 1977). Another closely related species, which may result in misidentifications, is *Molpadia blakei* (Théel, 1886), which with certainty is known from the northern Atlantic deep-sea (Pawson *et al.* 2001). This species differs from *M. liska* by the presence of fusiform rods (mean length: 256 µm) in the tail, which are perforated by large holes and have a low spire (Pawson *et al.* 2001).

TABLE 2. *Molpadia liska* Pawson, 1977. Means, standard deviations (in parentheses) and range of diameter of tables from body wall (D_{bw}, µm) and from tail (D_t, µm) compared to range of mean values as presented by Pawson (1977) for the type specimens. *n*—number of measurements.

Parameter	Specimen			Pawson (1977)
	ZSM 20020028 JMB-01144	ZSM 20020025 JMB-01141	ZSM 20043069 JMB-01233	
	(n=50)	(n=50)	(n=50)	
D_{bw}, µm	120.5 (±16.6)	120.8 (±18.4)	94.6 (±14.0)	80 to 168
	75–144	83–160	66–129	
	(n=50)	(n=50)	(n=41)	
D_t, µm	81.6 (±20.1)	103.5 (±27.5)	85.3 (±20.6)	75 to 144
	46–136	67–165	49–132	

This is the first record of this species for the Atlantic Ocean, and the known depth range is considerably increased from 4740 to more than 5420 m.

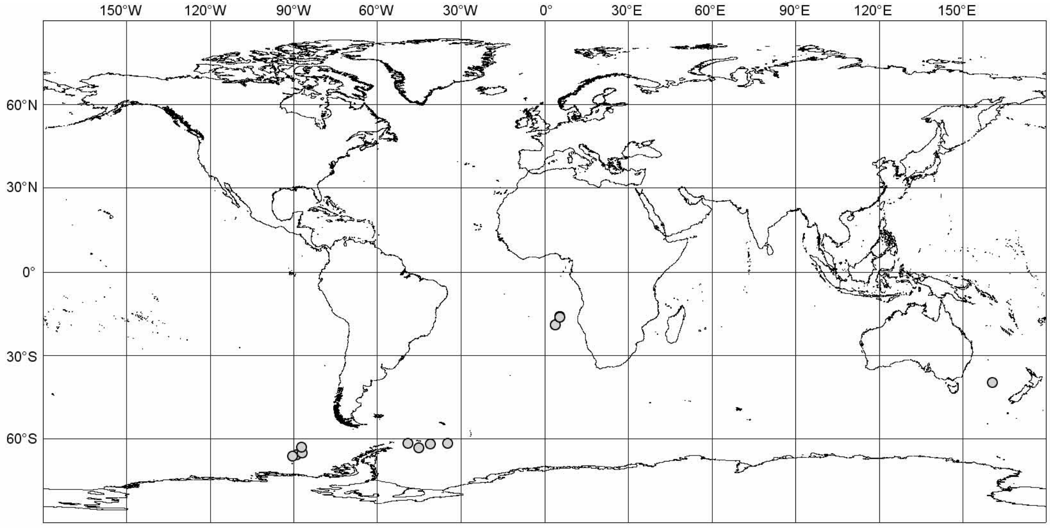

FIGURE 11. Distribution of *Molpadia liska* Pawson, 1977.

Distribution. (Fig. 11) South-eastern Atlantic Ocean, south-western Pacific Ocean and Southern Ocean, 3111–5426 m (Pawson 1977; herein).

Family Synaptidae Burmeister, 1837

Genus *Protankyra* Østergren, 1898

Protankyra brychia (Verrill, 1885)

(Fig. 12)

Synapta brychia Verrill, 1885: 539
Synapta abyssicola Théel, 1886a: 14–15, pl. 1 (fig. 11)
Synapta abyssicola var. *pacifica* Ludwig, 1894: 174–178, pl. 18 (figs 13–19)
Protankyra brychia. Pawson *et al*., 2003: 160–171, figs 1–3, 8–11 [synonymy]

Material. M 48/1-334: 1 specimen, 2 anterior fragments, 2 posterior fragments (ZSM 20043077). M 48/1-337: 1 posterior fragment (ZSM 20043079). M 48/1-343: 1 specimen, 2 posterior fragments (ZSM 20043070). M 48/1-347: 2 specimens, 1 anterior fragment, 3 posterior fragments (ZSM 20020023), 2 anterior fragments, 1 posterior fragment (ZSM 20043078). M 48/1-349: 4 specimens, 2 median fragments, 7 posterior fragments (ZSM 20020021). M 48/1-351: 4 specimens, 8 posterior fragments (ZSM 20020027), 3 anterior fragments, 1 median fragment (ZSM 20043080).

Additional Material. 1 specimen (ZSM 20043139), FS "Polarstern", ANDEEP III, station PS 67/016-5, 41°07.5' S, 9°56.3' E, 4723 m, giant box corer, 25 Jan, 2005. 6 specimens, 2 anterior fragments, 1 posterior fragment (ZSM 20043138), FS "Polarstern", ANDEEP III, station PS 67/016-11, 41°07.7' S, 9°56.3' E, 4727 m to 41°07.4' S, 9°54.8' E, 4694 m, Agassiz trawl, 26 Jan, 2005.

Remarks. This species has been excellently reviewed by Pawson *et al.* (2003) including its synonymy, morphology and distribution. A quite characteristic feature of this species are the large calcareous deposits (after Pawson *et al.* 2003): anchors usually less than 700 µm long, but sometimes up to 1000 µm, with branched stock and flukes with about six teeth; anchor plates up to 700 µm long, with 50–70 dentate holes. Pawson and his co-authors are convinced, that the giant pelagic larva, the so called *Auricularia nudibranchiata* Chun, 1896 is the larva of *P. brychia.* The specimens reported herein considerably enlarge the known distributional area of the species in the Atlantic Ocean (from about 16°S to 41°S), as well as the depth-range (from about 5000 m to more than 5400 m).

Distribution. (Fig. 12) This species probably has a cosmopolitan distribution, Atlantic Ocean, eastern and western Pacific Ocean, 869–5426 m (H.L. Clark 1908, 1920, 1924; Deichmann 1940; Gage *et al.* 1985; Harvey *et al.* 1988; Hérouard 1923; IFREMER BIOCEAN; Ludwig & Heding 1935; Madsen 1953; Pawson *et al.* 2003; Perrier 1902; Sibuet 1977; Théel 1886a; herein).

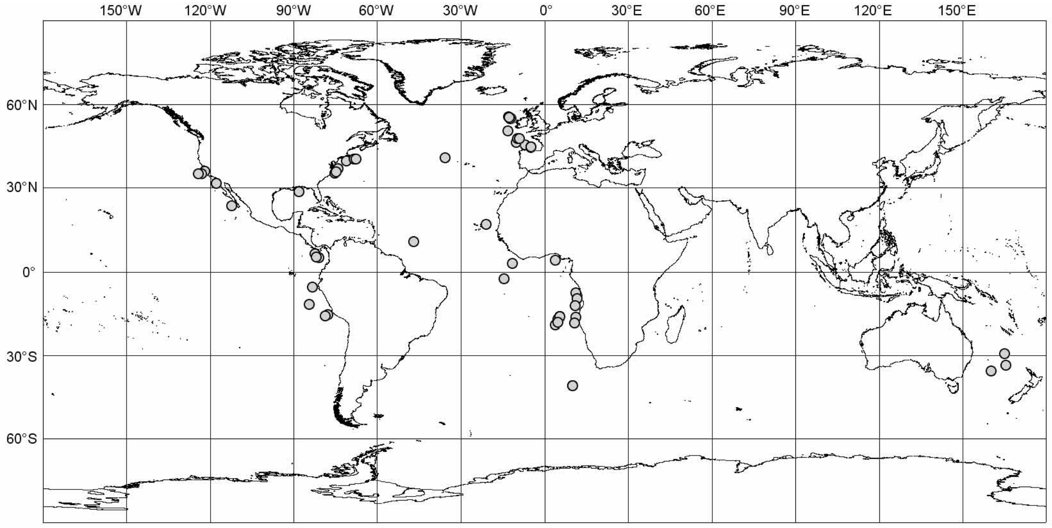

FIGURE 12. Distribution of *Protankyra brychia* (Verrill, 1885).

Family Myriotrochidae Théel, 1877

Genus *Siniotrochus* Pawson, 1971

Siniotrochus myriodontus Gage & Billett, 1986

(Figs 13A, 14)

Siniotrochus myriodontus Gage & Billett, 1986: 266–272, figs 28(C–E), 29–31; Bohn, 2005: 232–234, figs 1(A–B), 2

Material. M 48/1-347: 1 posterior fragment (ZSM 20020016). M 48/1-351: 2 posterior fragments (ZSM 20020015).

Remarks. Gage and Billett (1986) provide an excellent description of this species, including detailed information on a variety of taxonomically important wheel parameters. Given that the current specimens have already been treated in more detail (Bohn 2005) the species is only shortly outlined: body about cylindrical, up to 31 mm long and 7 mm wide; tentacles 12, with four pairs of lateral digits; calcareous ring with 5 radial and 5 interradial plates; body wall with single layer of wheel deposits of the so-called siniotrochid type (Fig. 13A); wheel diameter 414 µm (284–560 µm); hub about half the diameter of the wheel, perforated by several holes; spokes 17 (12–25); inward-pointing teeth 42 (30–67); outward-pointing primary teeth 18 (11–31); outward-pointing secondary teeth 6 (0–29) (*arrowheads* in Fig. 13A); simple rod deposits present in tentacles and around anus.

Siniotrochus myriodontus closely resembles the north-western Atlantic Ocean *S. phoxus* Pawson, 1971 from which it differs by the presence of outward-pointing secondary teeth on the wheels.

Distribution. (Fig. 14) North-eastern Atlantic Ocean (Porcupine Seabight) and south-eastern Atlantic Ocean, 3490–5389 m (Bohn 2005; Gage & Billett 1986).

TABLE 3. List of deeper bathyal and abyssal crinoids and holothurians of the Angola Basin and its vicinity, collected by the Valdivia expedition (Ludwig & Heding 1935; Heding 1940), the Java—South Africa expedition (Gislén 1933; Hansen 1975), the Galathea expedition (Hansen 1975), the Walda and Walvis cruises (IFREMER BIOCEAN) and the DIVA-1 expedition. *1*—as *Peniagone ferruginea* Grieg, 1921; *2*—as *Pseudostichopus atlanticus* R. Perrier, 1898; *3*—*Pseudostichopus depressus* Hérouard, 1902; *4*—as *Pseudostichopus globigerinae* Hérouard, 1923; *5*—as *Pseudostichopus villosus* Théel, 1886; *6*—determination doubtful, may be the closely related *M. liska* Pawson, 1977; *7*—as *Protankyra abyssicola* (Théel, 1886).

Species	Depth (m)	Source
Bathycrinus aldrichianus Wyville Thomson, 1876	5415	herein
Porphyrocrinus incrassatus (Gislén, 1933)	2400–2780	Gislén 1933
Deima validum validum Théel, 1879	4088–5426	IFREMER BIOCEAN; herein
Psychropotes depressa (Théel, 1882)	2270	Hansen 1975
Psychropotes longicauda Théel, 1882	2475–3244	IFREMER BIOCEAN
Psychropotes semperiana Théel, 1882	3244–5126	IFREMER BIOCEAN; herein
Peniagone diaphana (Théel, 1882)	3034	IFREMER BIOCEAN
Peniagone purpurea (Théel, 1882)	4660–5415	[1]IFREMER BIOCEAN; herein
Achlyonice ecalcarea Théel, 1879	2400–2780	Hansen 1975
Achlyonice longicornis spec. nov.	5385–5387	herein
Molpadiodemas atlanticus (R. Perrier, 1898)	4820–5415	[2]IFREMER BIOCEAN; herein
Molpadiodemas depressus (Hérouard, 1902)	3034	[3]IFREMER BIOCEAN
Molpadiodemas involutus (Sluiter, 1901)	4613	[4]IFREMER BIOCEAN
Molpadiodemas villosus (Théel, 1886)	4550–4660	[5]IFREMER BIOCEAN
Mesothuria candelabra Hérouard, 1923	5220	IFREMER BIOCEAN
Paelopatides grisea R. Perrier, 1898	3035	Heding 1940
Paroriza pallens (Kœhler, 1896)	5124	IFREMER BIOCEAN
Molpadia musculus Risso, 1826	1756–4335	IFREMER BIOCEAN
[6]*Molpadia blakei* (Théel, 1886)	4335	IFREMER BIOCEAN
Molpadia liska Pawson, 1977	5385–5426	herein
Protankyra brychia (Verrill, 1885)	2225–5426	[7]Ludwig & Heding 1935; [7]IFREMER BIOCEAN; herein
Siniotrochus myriodontus Gage & Billett, 1986	5385–5389	herein
Neolepidotrochus parvidiscus angolensis Bohn, 2005	5395	herein

Genus *Neolepidotrochus* Bohn, 2005

Neolepidotrochus parvidiscus angolensis Bohn, 2005
(Figs 13B–C, 14)

Neolepidotrochus parvidiscus angolensis Bohn, 2005: 234–237, figs 1(C–G), 3, 4

Material. M 48/1-340: Holotype (ZSM 20020017).

Remarks. This subspecies has been recently described in more detail (Bohn 2005) and is characterised by: body wall and tentacle bases with two types of wheel deposits, neolepidotrochid type wheels (Fig. 13B) and myriotrochid type wheels (Fig. 13C). Neolepidotrochid type wheels with variable number (up to 16) of outward-pointing secondary teeth (Fig. 12B: *arrowheads*), not present in all wheels, but in the majority; edge of rim between two outward-pointing primary teeth roughly straight; neolepidotrochid type wheels from anterior body smaller (mean diameter: 111 µm, range: 95–129 µm), than wheels from posterior body (mean diameter: 140 µm, range: 127–158 µm) and with higher ratio of hub diameter to wheel diameter (mean: 40 %, range: 30–47 %) compared to wheels from posterior body (mean: 29 %, range: 22–36 %). Myriotrochid type wheels have a diameter of 130 µm (75–166 µm), ratio of hub diameter to wheel diameter 21 % (18–26 %), spokes 10 (8–14).

Distribution. (Fig. 14) Angola Basin in the south-eastern Atlantic Ocean, 5395 m.

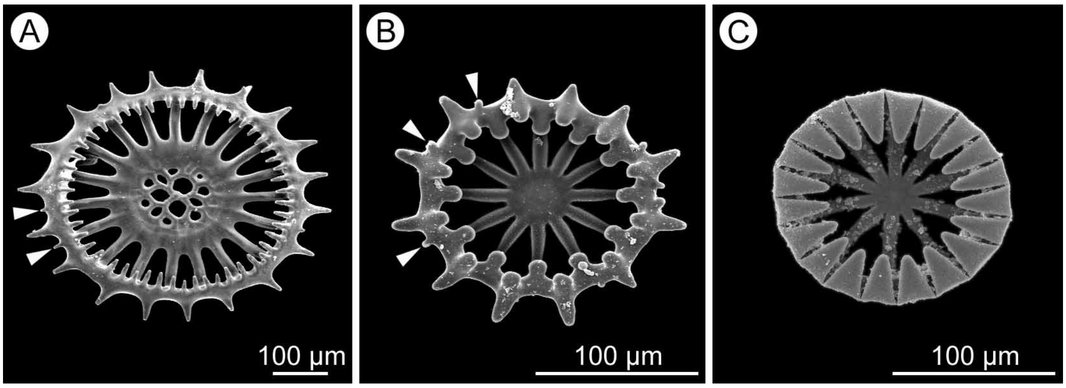

FIGURE 13. **(A)** *Siniotrochus myriodontus* Gage & Billett, 1986. Wheel deposit of body wall. **(B–C)** *Neolepidotrochus parvidiscus angolensis* Bohn, 2005. Wheel deposits of body wall. **(B)** Neolepidotrochid type wheel. **(C)** Myriotrochid type wheel. *Arrowheads* – outward-pointing secondary teeth.

TABLE 4. Schematic distribution of Crinoidea and Holothuroidea collected in the Angola Basin, that are known from at least two localities. *N*—North; *S*—South.

Species	Atlantic Ocean		Indian Ocean		Pacific Ocean		Southern Ocean
	N	S	N	S	N	S	
Bathycrinus aldrichianus Wyville Thomson, 1876	+	+					
Porphyrocrinus incrassatus (Gislén, 1933)	+	+					
Deima validum validum Théel, 1879	+	+	+	+	+	+	
Psychropotes depressa (Théel, 1882)	+	+			+	+	
Psychropotes longicauda Théel, 1882	+	+		+	+	+	+
Psychropotes semperiana Théel, 1882	+	+	+	+			
Peniagone diaphana (Théel, 1882)	+	+		+	+	+	
Peniagone purpurea (Théel, 1882)	+	+		+	+		+
Achlyonice ecalcarea Théel, 1879	+	+		+	+	+	
Molpadiodemas atlanticus (R. Perrier, 1898)	+	+			+	+	
Molpadiodemas depressus (Hérouard, 1902)	+	+					
Molpadiodemas involutus (Sluiter, 1901)	+	+			+	+	+
Molpadiodemas villosus (Théel, 1886)	+	+		+	+	+	+
Mesothuria candelabra Hérouard, 1923	+	+					
Paelopatides grisea R. Perrier, 1898	+	+					
Paroriza pallens (Kœhler, 1896)	+	+					
Molpadia musculus Risso, 1826	+	+	+	+	+	+	+
Molpadia blakei (Théel, 1886)	+	+					
Molpadia liska Pawson, 1977		+				+	+
Protankyra brychia (Verrill, 1885)	+	+			+	+	
Siniotrochus myriodontus Gage & Billett, 1986	+	+					

Discussion

The sampling activities of the DIVA-1 expedition focussed on the central abyssal plain of the Angola Basin. Along a transect of about 700 km, six areas were sampled, at each deploying the same variety of gears. These areas were all of a comparable depth, ranging between 5120 and 5450 m. Altogether one crinoid and nine holothurian species have been collected at 12 stations (Tab. 1), mainly with the Agassiz trawl (10 stations), and to a lesser extent also with the epibenthic sledge (two stations). Most of the species were only present at one or two stations and usually as one or two specimens. *Protankyra brychia* (Verrill, 1885) is the only species, that has been collected regularly (in 6 out of 12 stations) and also in higher specimen numbers (up to 7).

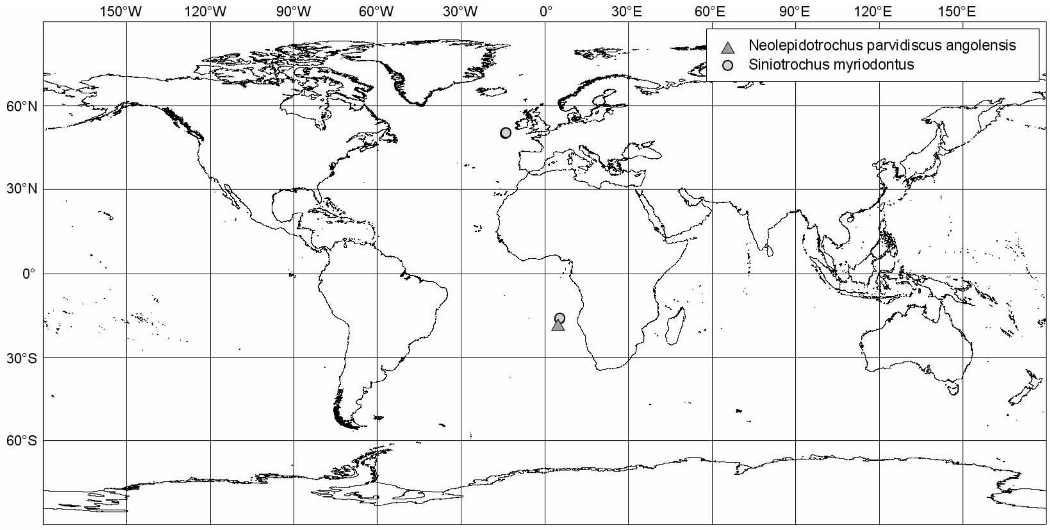

FIGURE 14. Distribution of *Siniotrochus myriodontus* Gage & Billett, 1986 and *Neolepidotrochus parvidiscus angolensis* Bohn, 2005.

Five species present in the current material are new records for the Angola Basin (Tab. 3; *Bathycrinus aldrichianus* Wyville Thomson, 1876; *Achlyonice longicornis* **spec. nov.**; *Molpadia liska* Pawson, 1977; *Siniotrochus myriodontus* Gage & Billett, 1986; *Neolepidotrochus parvidiscus angolensis* Bohn, 2005), while the five others have been found previously.

To compile a list of the known crinoid and holothurian species of the Angola Basin, first of all, the area of interested has to be circumscribed. In the east, the Angola Basin is delimited by the coast of Africa, in the south by the Walvis Ridge and in the west by the Mid-Atlantic Ridge, but a clear delimitation towards the Guinea Basin in the north is missing (see Fig. 1). So far, only few expeditions have sampled the deep-sea in this area. The sampling activities of the Valdivia and the Galathea expeditions and to a lesser extent also of the Walda cruise were limited to bathyal and abyssal areas close to the African west coast (Fig. 1). The Walvis cruise investigated bathyal and abyssal depths in the southern Angola Basin close to the Walvis Ridge, and Dr Mortensen's Java—South Africa expedition deployed one deep-sea dredge of interest off St. Helena. Finally, the DIVA-1 expedition focused on sampling the central Angola Basin.

Altogether 2 stalked crinoid species of the suborder Bourgueticrinina (Tab. 3) and 21 holothurian species (Tab. 3), belonging to the Elasipodida (8 species), the Synallactidae (7 species), the Molpadiidae (3 species) and the Apodida (3 species) have been recorded so far. These came from 24 stations, covering a depth range from 1700 m close to the African coast, to more than 5000 m in the central abyssal Angola Basin (Fig. 1, Tab. 3).

When discussing zoogeographical relationships of different deep-sea regions, it always has to be kept in mind, that current knowledge of species distribution is very limited, considering the restricted number of deep-sea samples taken so far, as well as disparate sampling activities in different geographical regions (e.g. North Atlantic compared to the South Atlantic or central Indian Ocean; see Hansen 1975: figs 108 and 109). Thus "endemism" may just be the result of these causes.

Except for the two holothurians so far restricted to the Angola Basin (Achlyonice longicornis spec. nov.; *Neolepidotrochus parvidiscus angolensis* Bohn, 2005), most of the crinoid and holothurian species of the Angola Basin have large distributional areas (Tab. 4). A close relationship to the crinoid and holothurian fauna of the northern Atlantic Basins is evident, as all species known so far, except for *Molpadia liska* Pawson, 1977 also have been found there. Currently, eight of these are restricted to the Atlantic Ocean, while all others are known from other Oceans as well. The influence of a "southern" (Subantarctic) deep-sea fauna, on the other hand seems to be negligible. Though several of the recorded species are also known from the Southern Ocean (altogether six species) only one of them might be called a "southern" species: *Molpadia liska*, which so far is restricted to the Southern Ocean, the southern Atlantic and the southern Pacific (Fig. 11), while the others are widely distributed in the Atlantic, the Indian and the Pacific Ocean.

Concerning the deep-sea Asteroidea of the Angola, the Guinea and the Cape Basins taken in the course of the Walda expedition, Sibuet (1975) found a similar situation: out of 21 Asteroidea only four species (two of them new to science) are restricted to the South Atlantic, while all others are also known from the North Atlantic Ocean. Furthermore, there seems to be no influence of the Subantarctic abyssal asteroid fauna on the asteroid fauna of the Cape Basin or the Angola Basin, which prompts Sibuet (1975) to doubt the Walvis Ridge being an effective barrier for Asteroidea, separating the Angola and the Cape Basin.

Remarkable is the almost complete absence of small (up to few cm, usually smaller) in- or epifaunal holothurians of the family Myriotrochidae that are quite abundant in other deep-sea basins. These tiny and fragile organisms are usually caught with an epibenthic sledge or a box corer. A rich variety of species has been described by Gage & Billett (1986) from the Rockall Trough area (NE Atlantic Ocean), and recent expeditions (ANDEEP I and II) to the Weddell Sea, the Scotia Sea and the Drake Passage proved the presence of several myriotrochid species in the Antarctic and subantarctic deep-sea (Gebruk *et al*. 2003). The DIVA-1 expedition only yielded one small myriotrochid specimen (*Neolepidotrochus parvidiscus angolensis* Bohn, 2005), though almost the same gears were used in the DIVA-1 and the ANDEEP expeditions.

Concluding, the crinoid and holothurian fauna of the Angola Basin is very similar to that of deep-sea basins in the North Atlantic Ocean, with a high percentage of species with a much wider distributional range including the Southern, the Indian and Pacific Ocean.

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5. 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.

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Pseudrotasfer microincubator gen. et spec. nov., a brooding cucumariid holothurian (Echinodermata: Holothuroidea: Dendrochirotida) from the Burdwood Bank (south-western Atlantic Ocean)

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Abstract

A new brooding cucumariid holothurian, *Pseudrotasfer microincubator* **gen. et sp. nov.** has been discovered in samples taken by the LAMPOS expedition with FS "Polarstern" at Burdwood Bank in the south-western Atlantic Ocean. This species is characterised by peculiar wheel-like baskets in its outer body wall and a deeper layer of simple large perforated plates, that require the establishment of a new genus. The new genus and species are characterised, and a description is provided of its external and internal morphology, including a SEM study of its ossicles.

Key words. Echinodermata, Cucumariidae, taxonomy, south-western Atlantic Ocean, spermatozeugmata, ovarian brooder

Introduction

The aim of the LAMPOS expedition with FS "Polarstern" (cruise ANT XIX/5, Apr. 2002) was to study the "biogeographic and evolutionary links between the Magellan region (South America) and the Antarctic continent" (Arntz 2003: p. 1). In particular, a study was made of the shallows and islands of the Scotia Arc connecting the Magellan and the Antarctic region, to determine whether or not they serve as stepping stones supporting faunal dispersal, and if so, what is the direction of faunal migration (Arntz 2003)? To address these questions, 13 areas along the Scotia Arc, ranging from 200 to 650 m depth, were sampled, using a variety of gear, including Agassiz trawl, bottom trawl and box corer.

During this cruise, the eastern and western extensions of the Burdwood Bank were also sampled. The Burdwood Bank represents the north-western most part of the Scotia Ridge towards South America (Fig. 1). This part of the ridge has a depth as shallow as about 75 m, and is a flat-topped area measuring about 350 km by 100 km at the 200 m isobath (Davey 1972, GEBCO Digital Atlas 2003). The holothurian fauna of this area is poorly known. Previous expeditions (Scottish National Antarctic Expedition, station 346; Swedish Antarctic Expedition, station 59) gathered a total of six holothurian species (Tab. 1), described by Vaney (1908) and Ekman (1925).

Current investigations of samples taken in the course of the LAMPOS expedition in the Burdwood Bank area, revealed the presence of a seventh, new, small brooding dendrochirote holothurian. A striking character of this new species is an outer layer of wheel-like baskets in the body wall, which have not been reported before and necessitate the erection of a new genus.

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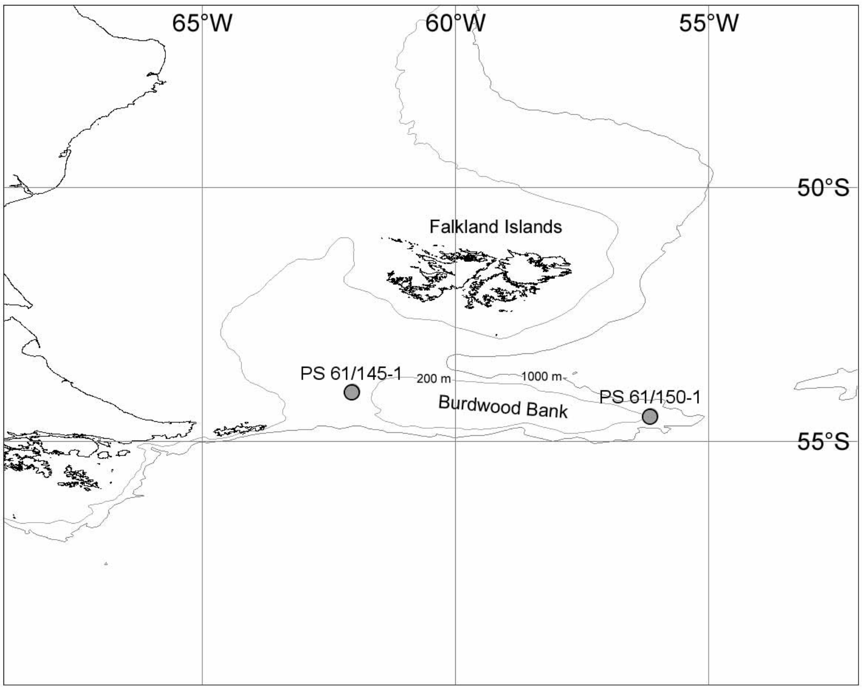

FIGURE 1. Agassiz trawl samples taken at the Burdwood Bank in the course of the LAMPOS expedition (FS "Polarstern", ANT XIX/5), containing *Pseudrotasfer microincubator* **spec. nov.**

TABLE 1. Previously recorded holothurian species from the Burdwood Bank.

Current name	Vaney (1908)	Ekman (1925)
Cladodactyla crocea croceoides (Vaney, 1908)	*Cucumaria croceoida*	*C. crocea croceoides*
Heterocucumis steineni (Ludwig, 1898)		*Cucumaria steineni*
Pseudocnus perrieri (Ekman, 1927)	*Cucumaria laevigata* [non Verrill, 1876]	*C. laevigata*
Psolus squamatus (Koren, 1844)		*P. squamatus* var. *segregatus* R. Perrier, 1905
Psolidium dorsipes Ludwig, 1886		*P. dorsipes*
Taeniogyrus contortus (Ludwig, 1874)		*T. contortus*

Material and methods

The holothurians collected in the course of the LAMPOS expedition (station PS 61/145-1, PS 61/150-1, Fig. 1) at Burdwood Bank were sorted to morpho-species and subsequently fixed in 96 % ethanol. The material is deposited in the Bavarian State Collection of Zoology in Munich (ZSM).

To investigate spermatozoa with a scanning electron microscope (SEM), single male gonad tubules were removed from the specimens and dehydrated according to the AXA method of Kees van Achterberg (Naturalis, Leiden, the Netherlands), a modified version of the alcohol-ethyl acetate method established by Vockeroth (1966), where ethyl acetate is replaced by amyl acetate. The gonad tubules were placed for 24 h in a mixture of 40 % xylene and 60 % ethanol (96 %), then transferred to amyl acetate and dried for 24 h. Finally, the dry gonad tubules were transferred to aluminium stubs, and opened up with a fine pin to spread the spermatozoa on the stub.

For SEM examinations of ossicles, small pieces of the body wall were macerated in a 12.5 % sodium hypochlorite solution, then rinsed several times in distilled water and air-dried. The ossicles were transferred to aluminium stubs. The SEM specimens were sputtered with gold and studied with a LEO 1430 VP scanning electron microscope.

Taxonomy

Order Dendrochirotida Grube, 1840

Family Cucumariidae Ludwig, 1894

Genus *Pseudrotasfer* gen. nov.

Diagnosis. Tentacles dendritic, 10, two ventral considerably smaller. Tube feet restricted to radii; dorsal radii devoid of tube feet except for a single small tube foot close to tentacles and next to anus; ventrolateral radii likewise with a single small tube foot close to tentacles; large tube feet demarcate ventral sole, in single radial rows in ventrolateral radii and in double row in midventral radius. Calcareous ring simple, without posterior processes. Ossicles of body wall of two types, scattered large smooth perforated plates in deeper layer and shallow baskets in a dense upper layer; baskets resemble four-spoked wheels with centrally broadened “hub” armed with outward-pointing teeth, undulating rim connecting “spokes” armed with inward-pointing teeth.

Type species. *Pseudrotasfer microincubator* **sp. nov.**

Etymology. The epithet *Pseudrotasfer* (gender male) refers to the wheel-like baskets of the body wall, characteristic of this genus.

Pseudrotasfer microincubator spec. nov.
(Fig. 2A–J)

Material examined. Holotype. FS “Polarstern”, LAMPOS, station PS 61/150-1, 54°30.22' S, 56°08.20' W, 286 m to 54°29.64' S, 56°08.13' W, 290 m, Agassiz trawl, 06 Apr. 2002 (ZSM 20070012, 1 ♂).
Paratypes. FS “Polarstern”, LAMPOS, station PS 61/145-1, 54°01.58' S, 62°01.03' W, 271 m to 54°01.11' S, 62°01.63' W, 272 m, Agassiz trawl, 05 Apr. 2002 (ZSM 20070011, 1 ♀); station PS 61/150-1 [for details see holotype] (ZSM 20070013, 1 ♂).

Description. Although three specimens are available (holotype: ♂, body length 7 mm; paratypes: 1 ♂, body length 6 mm; 1 ♀, body length 5 mm), the description of the new species is mainly based on the holotype and the male paratype, due to the fact that the female paratype is in a defective state of preservation. Although the specimens are small, all of them are mature. Preserved, the specimens are of a whitish colour. The body is subcylindrical (Fig. 2A–B), but with a flattened ventral sole, and rounded posterior end. Mouth terminal, anus subdorsal above ventral sole (Fig. 2A: *arrowhead*). Tentacles 10, dendritic, two ventral considerably smaller than others.

The dorsal radii are almost devoid of tube feet, each radius with single radial tube foot present close to anterior end of body, and next to anus. These are cylindrical and considerably smaller than those on the sole. Likewise, a single tube foot is also present in each of the ventrolateral radii close to anterior end of body. Somewhat distanced from anterior end (1.6–1.7 mm in the current specimens), ventral sole extends to posterior end of body (Fig. 2B). Tube feet defining sole conspicuous, cylindrical, with distinct terminal discs. Feet restricted to radii, a single row in each ventrolateral radius (♂ paratype: 8 tube feet, holotype: 11 tube feet), and a double row in a zig-zag arrangement in mid-ventral radius (♂ paratype: 8 tube feet, holotype: 13 tube feet).

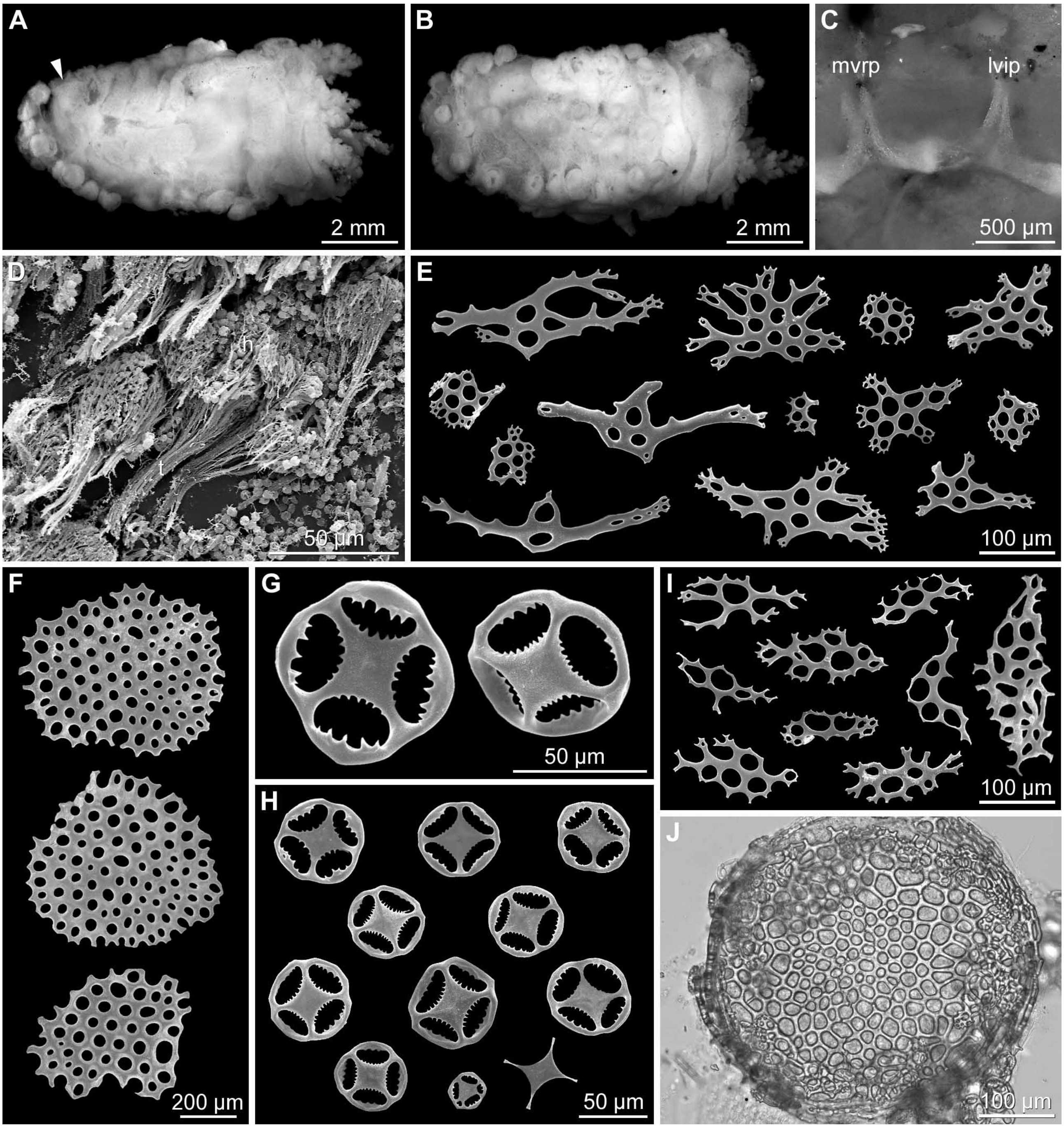

FIGURE 2. *Pseudrotasfer microincubator* spec. nov. **A–B.** Holotype (ZSM 20070012). **A.** Lateral view (*arrowhead*: anus). **B.** Ventral view. **C.** Calcareous ring plates (*mvrp*: midventral radial plate, *lvip*: left ventral interradial plate) of a paratype (ZSM 20070013). **D.** Potential spermatozeugmata consisting of various bunch-like bundled spermatozoa (*h*: heads of spermatozoa, *t*: bundled tails) (ZSM 20070013). **E–J.** Ossicles. **E.** Plates of tentacles (ZSM 20070011). **F.** Large perforated plates of deeper layer of body wall (ZSM 20070011). **G–H.** Wheel-like baskets of upper layer of body wall (ZSM 20070011). **I.** Plates of deeper layer of terminal tube foot region (ZSM 20070011). **J.** Terminal plate of a tube foot (ZSM 20070013).

Calcareous ring simple (Fig. 2C), with no posterior processes. Anterior processes of all 10 plates about same height. They are oblong rectangular, incised anteriorly in radial plates. Interradial plates oblong triangular, except for middorsal interradial plate, which has a deeply incised V-shaped anterior process. Posterior margin of plates emarginated, more pronounced in radial plates than in interradials.

Retractor muscles arise from longitudinal muscles about one third body length from anterior end. A single tubular polian vesicle present in left lateral interradius (stone canal and madreporite not investigated due to delicate state of specimens). Intestinal tract consists of a short oesophagus, followed by an intestine with a long loop, and terminates in a short cloaca. Anterior descending intestine suspended on midventral mesentery, ascending anterior intestine on a mesentery fixed to left lateral interradius, and descending posterior intestine on a mesentery attached to right side of midventral longitudinal muscle. Right and left respiratory trees arise with a short common trunk from anterior dorsal side of cloaca. Both trees simple short tubules, which may have few short side branches.

Sexes are separate. Due to delicate state of specimens, position of gonopore could not be ascertained. Gonad consists of left and right bunch of few simple unbranched tubules attached to middorsal mesentery immediately posterior to middorsal interradial plate of calcareous ring. In males, each bunch is composed of 3–6 long tubules, as well as few short and probably developing tubules. Long tubules are densely filled with so-called spermatozeugmata (Fig. 2D), bunch-like structures composed of numerous spermatozoa with agglutinated tails (Fig. 2D: *t*). Female paratype with a bunch of simple balloon-shaped tubules on both sides of middorsal mesentery (two on left and about four on right side), filled with embryos (all of about same developmental stage). In addition, single small tubules filled with eggs present.

Tentacles supported by very variable rod- to plate-like ossicles (Fig. 2E), up to 350 µm long, in outline elongated to rounded. Ossicles smooth, with holes of variable size, central holes usually larger than peripheral, often with irregular branching marginal outgrowths.

Body wall ossicles of two types, a deeper layer of scattered large plates and an upper layer of densely distributed wheel-like baskets. Plates of deeper body wall (Fig. 2F) large (up to 700 µm in diameter), smooth, irregularly circular in outline, with holes of varying sizes. Baskets of upper body wall (Fig. 2G–H) small (30–75 µm in diameter), shallow, resembling four-spoked wheels, with hub-like broadened central primary cross and undulating rim connecting its four arms (“spokes”). While outer margin of hub is armed with several small outward-pointing teeth, inner surface of rim between spokes is equipped with fewer, usually larger, inward-pointing teeth.

Tube feet covered by a dense outer layer of wheel-like baskets, absent only from terminal disc. Baskets overlie a layer of smooth, usually slightly curved plates (Fig. 2I), similar to those in tentacles, with irregular elongated outline, perforated by larger and smaller holes, and often with various marginal outgrowths. These plates restricted to distal ends of tube feet, adjacent to terminal plates. Terminal disc supported by single terminal plate (exceptionally by few smaller plates), up to 400 µm in diameter, smooth, roundish in outline, with irregular marginal outgrowths; central holes of plates smaller than peripheral (Fig. 2J).

Reproduction and development. Brooding period includes at least the beginning of April. The only known female has its gonad tubules filled with juveniles, which are all at about the same developmental stage. The juveniles are about 1.2 mm long. The body is cylindrical to deformed due to packing within the gonad tubules. There are at least eight tentacles of about the same size, all retracted. No tube feet were detected and the body wall is covered by a layer of wheel-like baskets, which are also present in the adults.

Distribution. (Fig. 1) So far, *Pseudrotasfer microincubator* is only known from the Burdwood Bank in the south-western Atlantic Ocean, depth range 271 to 290 m.

Etymology. A small breeder (*microincubator*).

Discussion

Referral of *Pseudrotasfer* to a family is somewhat difficult, as there are feasible relationships with at least two families. Based on 10 dendritic tentacles, a simple calcareous ring without posterior processes and the presence of baskets (although modified) in the body wall, the new genus can be assigned to the Cucumariidae or the Psolidae. Characteristic of the latter are a test of imbricating (often macroscopic) dorsal plates, the (usual) presence of a well defined ventral sole and a dorsally turned mouth and anus, while in cucumariids body wall deposits are diverse, usually small and inconspicuous and do not from a dorsal test of imbricating plates (e.g. Pawson & Fell 1965, Pawson 1982, Rowe & Gates 1995).

Although the presence of a ventral sole and large macroscopic plates in the body wall of *Pseudrotasfer* seems to indicate a closer affinity to the Psolidae than to the Cucumariidae, there are also substantial arguments to assign the new genus to the Cucumariidae. First of all, the large plates present in the body wall are scattered dorsally as well as ventrally, and do not form a test of imbricating plates. Also the ventral sole of *Pseudrotasfer* differs from that of a “typical” psolid holothurian. Psolidae usually have a soft, often thin-walled ventral sole, lacking large plates, which is clearly demarcated from the remaining body (Pawson 1982), whereas the impression of a ventral sole in *Pseudrotasfer* results from the arrangement of the tube feet on the ventral radii—they are lacking in an anterior area, whereas they are arranged more or less crowded around the posterior end of the body. Furthermore, the body wall of the ventral sole does not differ from that of the remaining body, it is not thin-walled, and large smooth perforated plates are also present ventrally. Based on these facts, the author is convinced that *Pseudrotasfer* has to be assigned to the Cucumariidae, and not to the Psolidae. Within the Cucumariidae, there is also a variety of genera known to possess a kind of ventral sole, like *Apsolidium* O'Loughlin & O'Hara, 1992, *Microchoerus* Gutt, 1990, *Neocnus* Cherbonnier, 1972 or *Psolidiella* Mortensen, 1925 (for details see Cherbonnier 1972, Gutt 1990, O'Loughlin & O'Hara 1992, O'Loughlin 2000).

The wheel-like baskets, found in the outer body wall of the new species, so far are unique. There are no cucumariid (or psolid) genera known to possess comparable baskets, so the erection of a new monotypic genus is justified.

Bowl-shaped ossicles, somewhat similar in appearance to the wheel-like baskets found in the new species are only present in the cucumariid holothurian *Staurocucumis liouvillei* (Vaney, 1914). This species has an outer layer of flat, bowl-shaped ossicles, which are subcircular to suboval in outline, perforated by holes armed with marginal teeth; four central holes usually large, surrounded by variable number of smaller holes (e.g. Ekman 1925, 1927, Massin 1994, O'Loughlin 2002, own observations). Although the ossicles of both species concur in two features—both are bowl-shaped and have holes armed with teeth, there are also considerable differences. The bowl-shaped ossicles of *S. liouvillei* invariably have a greater number of holes and they lack the broadened central primary crosses, which are present in baskets of *P. microincubator*. Furthermore, *S. liouvillei* has 10 subequal tentacles (e.g. Ekman 1925, 1927, O'Loughlin 2002, own observations), while in the new species, the two ventral tentacles are considerably smaller than the remaining. Both species do not seem to be closely related.

Although the list of holothurian taxa known to occur in the Burdwood Bank area so far is quite short (see Tab. 1), it is obvious, that there are close relationships to the holothurian fauna of southern South America and the Falkland Islands. Basically, the Burdwood Bank area can be regarded as the south-eastern most extension of the South American continental shelf in terms of its holothurian fauna. All Burdwood Bank species (except for *P. microincubator)* are also known from the Falkland Islands and five of the seven species have also been recorded off southern South America (not *P. microincubator* and *Heterocucumis steineni)* (e.g. Ekman 1925, 1927, Pawson 1969). According to Ekman (1925, 1927), three of the Burdwood Bank holothurians are also present off South Georgia (*Pseudocnus perrieri*, *H. steineni* and *Taeniogyrus contortus*). Two of these (*H. steineni* and *T. contortus*) have also been recorded from several localities off the Antarctic continent (e.g. Ekman 1925, 1927, Cherbonnier 1974, Gutt 1988, O'Loughlin 2002), although some authors doubt the conspecifity of the South American and Antarctic specimens and treat them as separate species (e.g. Cherbonnier 1974: *H. steineni* and *H. antarctica* (Vaney, 1908) or Heding 1931: *T. contortus* and *T. antarcticus* Heding, 1931).

Packaging of sperms to spermatophore- or spermatozeugmata-like structures is uncommon for holothurians. According to literature, all but two species have simple free sperm of a uniform type, similar to spermatozoa found in other echinoderm classes (e.g. Chia *et al*. 1975, Jamieson 1985, Hodgson & Bernard 1992). Two brooding holothurians are exceptional: *Cucumaria pseudocurata* Deichmann, 1938 releases sperm in the form of a modified spermatophore—the spermatozoa are tightly packed into dense strands of mucus that are quite resistant to dilution (Atwood 1975, McEuen 1988: fig. 5C), while in *C. lubrica* Clark, 1901 spermatozoa are bundled and after spawning remain together for an extended length of time before dispersing in the water (Atwood & Chia 1974, Engstrom 1982, McEuen 1988). These bunch-like bundles consist of numerous spermatozoa with their tails intertwined (McEuen 1988: fig. 4D), very similar in appearance to the apparent spermatozeugmata found in *Pseudrotasfer microincubator.* Although the state of preservation of spermatozoa in both male specimens is deficient, both were found to possess sperm that is bundled into bunch-like structures by agglutinated tails. Similar bunch-like spermatozeugmata are also present in a variety of brooding Antarctic Cucumariidae of the so-called "*Cucumaria georgiana*"-group (author's unpublished observations). All aforementioned species are probably not closely related to the current species.

For brooding holothurians, packaging of sperms to spermatophore- or spermatozeugmata-like structures seems to be advantageous. So far, similar structures have only been observed in combination with brood protection. *Cucumaria lubrica* and *C. pseudocurata* brood their young between the ventral body and the substrate (Atwood & Chia 1974, Atwood 1975, Engstrom 1982, McEuen 1988), while species of the "*Cucumaria georgiana*"-group keep their young in brood pouches (e.g. O'Loughlin 1994, 2001, own observations) and *P. microincubator* is an ovarian brooder.

Although there are reports of pseudocopulation in holothurians (see McEuen 1988), and a kind of copulatory behaviour has been assumed for some brooding dendrochirotids (see O'Loughlin 2001), there is no proof of copulation in holothurians so far (McEuen 1988, O'Loughlin 2001). Free-spawning—the release of gametes into the water column, where fertilization takes place, seems to be prevailing. A sufficient way to transfer sperm from a male to a female that keeps their eggs, instead of releasing them into the water column, is to pack large number of spermatozoa in a way, that they sink, are not dispersed into the water and even may stick on the surface of the female, until the eggs are extruded, to guarantee fertilization (Engstrom 1982).

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6. Bohn, J.M. & Heß, M. (unveröffentlicht) The brooding Antarctic holothurian genus *Echinopsolus* Gutt, 1990 (Dendrochirotida, Cucumariidae): spermatozoa, spermatozeugmata and taxonomic implications.

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

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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 spermatozeugmata. (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 spermatozeugmata of all *Echinopsolus* species are described using light- and electron-microscopical techniques and the results are evaluated and discussed concerning their taxonomy and phylogeny.

Keywords: Echinodermata, Antarctic radiation, sperm ultratructure, Southern Ocean

Introduction

A considerable number of holothurian species of the dendrochirotid families Cucumariidae Ludwig, 1894 and Psolidae R. Perrier, 1902 are known to protect their brood. Recent summaries list 30 cucumariid (O'Loughlin 1994) 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 (Table I). The number of brood pouches seems to be variable. The majority of the species (six Cucumariidae and two Psolidae), have five pouches, one in each interradius, while there are only two cucumariid species known to possess two pouches and one species which has three (see Table I). Remarkable in this context is the common presence of a genital papilla on the oral disc, between or ventrally of the mid-dorsal pair of tentacles in a variety of the species (Table I). Detailed information for three species, determined as “*Cucumaria georgiana*” group species, *Microchoerus splendidus* Gutt, 1990 and *Psolus charcoti* Vaney, 1906 is given by O'Loughlin (2001): these species are gonochoric, males have a large permanent digitiform genital papilla (2–4 mm long), while in females, a genital papilla may be absent, small lump-shaped or rarely digitiform and up to 1 mm in length.

The “*Cucumaria georgiana*” group was first established by Gutt (1988) and further specified by Massin (1992). Included are 11 Antarctic *Cucumaria* species (see Massin 1992), which are of a more or less dubious taxonomic status. Five of these are known to brood their offspring in interradial anterior brood pouches (Table I). According to Massin (1992: p. 187)

"*Cucumaria georgiana*" group species are "...small Antarctic dendrochirote holothurians, with the tube feet on 1–3 rows in each ventral radius and more randomly scattered dorsally..." their calcareous deposits "..., abundant in young specimens and often rare or absent in adults, are knobbed or spiny perforated plates, which show great variability...".

An examination of the rich holothurian samples collected in recent years by a variety of Antarctic expeditions with FS "Polarstern" in the Weddell Sea and the Antarctic Peninsula area (EASIZ I to III, BENDEX), revealed the presence of about 11 different species, which are brooders with five anterior interradial brood pouches and which have distinct genital papillae present on the oral disc in both sexes (although smaller in females). Detailed investigations of male specimens of these species revealed a further, so far unknown feature, all of them have in common: peculiarly modified spermatozoa, which are bundled to bunch-like spermatozeugmata.

The vast majority of holothurian spermatozoa investigated so far are of a uniform type (e.g. Chia *et al.* 1975, Jamieson 1985, Hodgson & Bernard 1992), similar to spermatozoa found in other echinoderm classes like Crinoidea, Asteroidea and Ophiuroidea (Chia *et al.* 1975, Jamieson 1985). This type has been denoted as "echinosperm" by Jamieson (1985), and Chia *et al.* (1975: p. 554) characterize it as follows: "…the head is essentially spherical with the acrosome positioned at the anterior end of the nucleus in a depression, while the mitochondrial middle piece takes the form of an annular band at the posterior end of the nucleus…".

The only holothurian species known to depart from the "echinosperm" type are *Cucumaria lubrica* H.L. Clark, 1901 and *Cucumaria pseudocurata* Deichmann, 1938 which both brood their young between the ventral surface and the substrate (e.g. Atwood & Chia 1974, Atwood 1975). *Cucumaria pseudocurata* has tabloid spermatozoa, that have their acrosome located on the side of the nucleus, and the majority of the mitochondrial mass on the opposite side (Atwood 1975, Chia *et al*. 1975). Sperm is released in the form of a modified spermatophore, where the spermatozoa are tightly packed into dense strands of mucus, hence quite resistant to dilution (Atwood 1975, McEuen 1988). The spermatozoa of *C. lubrica* are cylindrical or cigar-shaped (Atwood & Chia 1974, Chia *et al*. 1975) and numerous spermatozoa are bunch-like bundled by interwined tails (McEuen 1988). After spawning these spermatozoan bundles remain together for an extended length of time before dispersing in the water (Atwood & Chia 1974, Engstrom 1982, McEuen 1988).

Quite recently, comparable spermatozoan bundles have been described for males of the cucumariid holothurian *Pseudrotasfer microincubator* Bohn 2007, which is also a brooder. Contrary to the aforementioned species, females of *P. microincubator* hatch their brood in the ovaries (Bohn 2007).

The aim of the this study is to describe in detail the peculiar spermatozoa and spermatozeugmata of seven Antarctic Cucumariidae, using light- and electron-microscopical techniques and to evaluate and discuss the results concerning their taxonomy and phylogeny.

Material and Methods

The holothurians investigated in the current study were collected in the course of various Antarctic expeditions with FS "Polarstern" to the Weddell Sea and the Antarctic Peninsula area using Agassiz and bottom trawls (Table II). On board, specimens were sorted to morpho-species and afterwards either fixed in buffered formalin or 75 % ethanol. The material is deposited in the Bavarian State Collection of Zoology in Munich.

Extended depth of field images of holothurian specimens were generated with the software CombineZM (Hadley 2008) from a series of partially focused digital images take with a digicam on a standard stereo microscope.

To investigate spermatozoa and spermatozeugmata with a scanning electron microscope

(SEM) single gonad tubules were removed from male specimens and dehydrated according to the AXA method (for details see Bohn 2007). The dry gonad tubules were placed on aluminum stubs with adhesive carbon tabs and opened up with a fine pin to spread the speramtozeugmata on the stub. Finally, the SEM specimens were sputtered with gold in a Biorad Polaron SEM coating system (2.4 kV, 120") and studied with a LEO 1430 VP scanning electron microscope at 25 kV.

For histology and fine structure investigations short pieces of the tubules (preferably cut out at a swelling) were dehydrated in a graded acetone series and embedded in epoxy resin (Epon 100, Roth Company). Semithin sections (0.5–1 µm) were cut with glass knives on a RMC MT-XL 7000 ultramicrotome, stained with Richardson's reagent (Richardson *et al.* 1960) and documented with a digicam on a standard widefield light microscope. Thin sections (80 nm) were cut with a 45° diamond knife, mounted on formvar coated copper grids, stained with lead citrate and uranylacetate and inspected with a Zeiss EM10 at 80 kV and a FEI Technai Spirit transmission electron microscope at 120 kV.

Results

The rich Antarctic holothurian samples at hand, collected in recent years in the Weddell Sea and the Antarctic Peninsula area, contain about 11 discernible species, which share a variety of characters. So far only seven of these holothurians can be assigned to well-defined species and therefore are included in this investigation (*Cucumaria acuta* Massin, 1992; *Echinopsolus acanthocola* Gutt, 1990; *Echinopsolus parvipes* Massin, 1992; *Microchoerus splendidus* Gutt, 1990; *Pseudocolochirus mollis* Ludwig & Heding, 1935; *Psolus charcoti* Vaney, 1906; *Psolus koehleri* Vaney, 1914). For now omitted, but to be clarified and described later on, are species which have a dubious taxonomical status ("*Cucumaria georgiana*" group) or are new to science.

The species investigated agree in the following characters (see also Table I). (1) All are gonochoric. (2) A genital papilla is present on the oral disc, between or ventrally of the dorsal pair of tentacles. In males these papillae are permanent, large (up to 4 mm in length) and digitiform (Figs 1a–b). In females, the genital papilla is sometimes absent, but usually small (up to 1 mm in length), wide conical to digitiform (Fig. 1c). (3) Females brood their offspring in five anterior interradial brood pouches, that are situated at the transition of body to introvert (Figs 1d–f) and open via a small interradial slit.

Histological and fine structural investigations of the spermatozoa of these species revealed some further features shared by all.

Morphology of spermatozoa and spermatozeugmata

The seminiferous gonad tubules of the inspected male specimens vary widely in length and diameter between species. The tubules have a circular to oval smooth outer cross section profile (Fig. 3a) and marked longitudinal tissue-folds defining the inner surface (Figs 2d, 3a). The lumina are filled with densely packed sperm cell bundles (i.e. spermatozeugmata, Figs 2a, 3a). Each spermatozeugma is composed of several hundred, prevailingly mature sperm cells (e.g. approximately 1100 in *E. acutus*) aligned in the same orientation, united to a bunch with the sperm heads forming a compact knob or “bobble” and the flagella, which stick together by some amorphous material, form a rotund shaft tapering towards the end. With few exceptions, spermatozeugmata are found in a paired constellation with their heads in tight contact and the flagella pointing in opposite directions (Figs 2b, d, e).

Mature and almost mature sperm cells of the seven species investigated in this study all have the same general structure, subdivided into a head, a mid-piece and a tail (flagellum), with some species-specific variation in detail (Figs 2–4, Table V).

The head always has a circular cross section and an elongate spindle-shaped profile in any axial cutting plane (Figs 2f–g, 3c, e, 4a–b, e–f). With a maximum diameter in the basal quarter, it tapers to a rounded tip containing the globular acrosome (Figs 4c, f, g). The overall shape of the head is markedly similar in *E. acanthocola*, *E. acutus*, *E. mollis*, *E. parvipes* and *E. splendidus*, the latter especially pointed, the first one extra slender (length-to-max. diameter ratios see Table V). The head of *E. koehleri* is less pointed (torpedo-shaped, Figs 2g, 4f), that of *E. charcoti* comparatively stocky (acorn-shaped, Fig. 2c). At the basis, i.e. the anchoring site of the ciliary tail, the head shows a small, somewhat folded invagination, the centriolar fossa (Fig. 5a). After standard TEM preparation the head has a very electron dense appearance with several bright plaques (nuclear "vacuoles") of up to 70 nm (Figs 4b, f, 5a, d). The cell membrane envelopes the nuclear material tightly, small residues of the cytoplasm are found only between the basal head curvature and the mitochondrial ring of the mid-piece.

The membrane-bound acrosomal vesicle is positioned at the tip of the sperm head, emerging more (e.g. in *E. charcoti* and *E. koehleri*, Figs 2g, 4f) or less over the head-tip curvature. It is embedded and anchored in an apical cup-shaped recess (Figs 4g, 5a), filled with periacrosomal material of medium electron density. The vesicle has a diameter of about 400 nm (*E. acutus*, *E. acanthocola*), 500 nm (*E. charcoti*, *E. splendidus*, *E. koehleri*, *E. mollis*), or even 600 nm (*E. parvipes*) and contains a heterogeneous matrix of intermediate electron density with darker granules in the center (Fig. 4g). In addition, a small circumscribed globular structure (diameter ca. 200 nm) of decreased electron density is found in the centre or shifted apically (Figs 5a, b).

The mid-piece has the shape of a hollow cylinder, tightly connected with the head basis and centred around the first 1.5 µm of the flagellum. With a diameter of a little less than the maximum head diameter, it is set off against the head only by a slight ring-shaped contraction. This is best seen in *E. parvipes* (Fig. 4h) and *E. koehleri* (Figs 2g, 4f). In *E. acanthocola* the transition between mid-piece and head appears rather smooth (Figs 2f, 4e), due to some cytoplasmatic residues (premature state?). As a rule, the diameter of the "cylinder" slightly decreases towards its caudal end, proving itself a truncated hollow cone in the strict sense. The thickness of this structure amounts to 220–300 nm (in *E. koehleri* up to 400 nm) and slightly tapers caudally. Ultrastructurally it turns out to be a combination of a ring-shaped mitochondrial derivative in front, tightly connected to a roughly hollow cylinder-shaped mitochondrial derivative behind (Fig. 5a). The inner wall of the latter is somehow reinforced, indicated by a membrane of increased electron density. In cross sections this mitochondrial derivative shows stacks of parallel membranes at an angle with respect to the outer and inner walls (good structural preservation provided, Figs 4i, k).

The flagellum has the typical 9 x 2 + 2 microtubuli structure, a length of up to 150 µm (e.g. *E. parvipes*, Fig. 2e) or even 250 µm (*E. mollis*, Fig. 2d) at an average diameter between 170 and 185 nm. The first 250 nm, situated within the mid-piece cylinder, have a slightly enlarged diameter (230–280 nm) with a 9 x 2 + 0 microtubuli structure. Directly inside the insertion point and reaching a few nm into the centriolar fossa of the head, the ciliary body, with its 9 x 3 + 0 microtubuli structure, is found in axial alignment with the flagellum. The second component of the diplosome, the proximal centriole, is located in proximate neighbourhood, but paraxial and turned 90° (Figs 4j, 5a). A rather complex ultrastructural feature of the ciliary root is the so called "satellite complex": nine electron dense branches radially emerge from the caudal half of the distal centriole in a plane normal to the sperm cells long axis (Figs 4d, i–k, 5e) leading to a ring-shaped structure in the notch, between the mitochondrial ring and the mitochondrial cylinder. Half the way, the branches dilate to bifurcations, resulting in altogether 18 tiny spokes.

Taxonomy

To the characters shared by these species, which have already been mentioned (gonochorism;

sexual dimorphism, large digitiform genitalpapilla in males, usually inconspicuous in females; brood protection in five anterior interradial brood pouches), two further have to be added: (1) Multiple spermatozoa are bundled by somehow agglutinating tails to bunch-like spermatozeugmata. (2) The spermatozoa are unique in having 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 in our opinion indicates a close relationship based on common origin, which should also be reflected in terms of taxonomy. As a consequence, we propose to unite all species sharing this set of synapomorphies in the cucumariid genus *Echinopsolus* Gutt, 1990 (see also Table I).

Echinopsolus Gutt, 1990

Echinopsolus Gutt, 1990: 112. Type species: *E. acanthocola* Gutt, 1990, by original designation.

Microchoerus Gutt, 1990 [non Wood, 1844]: 105. Type species: *M. splendidus* Gutt, 1990, by original designation. [*Microchoerus* Gutt, 1990 is a junior homonym of *Microchoerus* Wood, 1844]

Echinopsolus acanthocola Gutt, 1990 (Figs 1e, 2b, f, 4e, 6a).

Echinopsolus acanthocola Gutt 1990: 113, figs 17–20.

Echinopsolus acutus (Massin, 1992) **comb. nov.** (Figs 1a, 3a–c, 6b)

Cucumaria acuta Massin, 1992: 184, figs 6–8.

Echinopsolus charcoti (Vaney, 1906) **comb. nov.** (Figs 2c, 4j, 6c)

Psolus charcoti Vaney, 1906a: 406.

Echinopsolus koehleri (Vaney, 1914) **comb. nov.** (Figs 2a, g, 4f, k, 6d)

Psolus koehleri Vaney, 1914: 24, pls 1 (figs 2, 5–6), 5 (figs 1–10).

Echinopsolus mollis (Ludwig & Heding, 1935) **comb. nov.** (Figs 2d, 3f–g, 6e)

Pseudocolochirus mollis Ludwig & Heding, 1935: 204, figs 62–65, pl. 2 (figs 21–38).

Echinopsolus parvipes Massin, 1992 (Figs 2e, 4g–i, 6f)

Echinopsolus parvipes Massin, 1992: 179, figs 1–5.

Echinopsolus splendidus (Gutt, 1990) **comb. nov.** (Figs 1b–d, f, 3d–e, 4a–d, 6g).

Microchoerus splendidus Gutt, 1990: 107, figs 9–11.

Albeit the striking similarities shared by these species, there are also considerable differences separating them. This applies first of all to the arrangement and shape of the tube feet (for details see Figs 6a–g and Table III). Dorsal tube feet are either restricted to radial rows, or are irregularly scattered or lack almost entirely. Also the shape of the dorsal tube feet is variable, in some species they are cylindrical and have a well developed terminal sucking disc, while in others they are conical and lack a terminal disc. The ventral tube feet usually are restricted to distinct radial rows. Noticeable is a distinct tendency to form a ventral sole, which may be delimited from the remaining body either by the arrangement of the tube feet or by a distinct bulge. A concomitant phenomenon is the reduction of the number of the mid-ventral tube feet to few at the anterior and posterior end of the ventral sole.

A great diversity exists also in the shape, size and arrangement of the calcareous deposits of the body wall of the species involved (see Table IV), although all of these deposits can be derived from simple multi-perforate plates. These perforated plates are very variable in size, are of an irregular, elongated or rounded outline and have a smooth, spiny or knobbed surface. In some species, these plates are strengthened, either by secondary thickening of the plate (*E. splendidus*), or by adding a three-dimensional calcareous network resulting in multi-layered plates (*E. acanthocola*, *E. charcoti*, *E. koehleri*, *E. parvipes*). Two types of plates in two layers—an outer layer of small flat to deep basket-like plates and a deeper layer of very large plates—is found in two species only (*E. charcoti*, *E. koehleri*), all others have plates of one type present in the body wall, although there may be considerable differences between plates from different parts of the body. Also the arrangement of the calcareous deposits in the body wall is variable and ranges from very scattered to a test composed of multiple layers of plates. In four species, the arrangement of the plates is size dependent, an increasing body size is accompanied by a decrease in number or size of plates, or both.

Discussion

At first glance, it may not seem convincing, that species so diverse in their external morphology, that they even have been classified in two different families, are so closely related, to justify a unification in one genus. But in our opinion, the morphological features shared by these species are so striking, that a common origin and close relationship can hardly be negated. It is true, that all morphological similarities presented, are somehow linked to brooding, and that the one or the other character has also been realized by other brooding holothurians, but the combination of characters so far is unique.

Out of 23 holothurian species known to possess genital papillae, only seven display sexual dimorphism, where males have large papillae, while papillae in females are smaller or even are lacking (O'Loughlin 2001). Significantly, two of these species, *Microchoerus splendidus* and *Psolus charcoti*, are covered herein and a third, determined as "*Cucumaria* *georgiana*” group species by O'Loughlin (2001), most probably also should be transferred to *Echinopsolus*. The remaining species differ from *Echinopsolus* species in the mode of brooding—*Pseudocnus laevigatus* (Verrill, 1876) has two ventral mid-body brood pouches, *Psolidocnus sacculus* (Pawson, 1983) has three dorsal internal coelomic brood sacs, *Cucumaria pseudocurata* is an external brooder and *Gephyrothuria alcocki* Kœhler & Vaney 1905 is not known to brood at all (O'Loughlin 2001).

Brood pouches, pocket-like inversions of the body wall with an opening to the exterior are regularly found in brood protecting cucumariid holothurians, and they vary in number and arrangement in different species (see O'Loughlin 1991). So far, five anterior interradial brood pouches are only known from species inhabiting Antarctic waters (O'Loughlin 1991, herein). Three Antarctic species, *Cucumaria lateralis*, *C. vaneyi* and *C. ferrari*, which also have anterior interradial brood pouches, differ from the remaining species in having only two or three pouches (Vaney 1906a, b, Vaney 1908, Cherbonnier 1949, McClintock *et al.* 1985) instead of five. Based on the descriptions and specimens at hand, it is very likely, that all three also belong to *Echinpsolus* and reports on deviating numbers of brood pouches are erroneous. This view is also supported by the fact, that brood pouches usually are arranged in a way, that the bilateral symmetry of the body is retained, but this is not the case in *C. lateralis* and *C. vaneyi* (see Vaney 1906a, b, Vaney 1908, Cherbonnier 1949; Table I).

Comparable holothurian spermatozeugmata, composed of various bunch-like bundled spermatozoa, so far are only known from two other Cucumariidae, namely *Cucumaria lubrica* (see McEuen 1988: fig. 4D) and *Pseudrotasfer microincubator* (see Bohn 2007: fig. 2D). Both are brooders, but neither of them has five anterior interradial brood pouches. *Cucumaria lubrica* broods the young between the substrate and the ventral surface (e.g. Atwood & Chia 1974, Engstrom 1982, McEuen 1988), while *P. microincubator* is an ovarian brooder (Bohn 2007). Both are probably not closer related to the current species.

The spermatozoa of the seven *Echinopsolus* species investigated are of a unique type and deviate from all other holothurian sperm cells known so far. Nevertheless, there is also morphological variation within *Echinopsolus* spermatozoa, which may turn out to be species specific. Conspicuous unifying features of *Echinopsolus* spermatozoa are the fusiform elongated head and the hollow cylinder-like mid-piece containing the mitochondrial derivative, ensheathing the anterior end of the flagellum.

In contrast, sperm cells of the "echinosperm" type, the usual type of spermatozoa found in holothurians differ from the former by their subspherical to ellipsoid head and the shallow bowl-shaped mid-piece with the mitochondrion forming a postnuclear annular band surrounding the two centriols (e.g. Chia *et al.* 1975, Jamieson 1985, Hodgson & Bernard 1992), but not the proximal end of the flagellum. Two other holothurian species, namely *Cucumaria lubrica* and *C. pseudocurata*, are also known to possess sperm cells, deviating from the "echinosperm" type. Apart form the elongated heads, there are conspicuous differences, separating the spermatozoa found in *Echinopsolus* from the latter. Sperm cells of *C. pseudocurata* are unique, they are tabloid in shape (elongated and dorso-ventrally compressed), have the acrosome located on one side of the nucleus and the majority of the mitochondrial derivative at the base of the nucleus on the opposite side (Atwood 1975). Somewhat similar in external appearance to spermatozoa of *Echinopsolus* are the cylindrical or cigar-shaped sperm cells of *C. lubrica*, which differ from all other holothurian spermatozoa in the arrangement of the mid-piece—the mitochondrial derivative surrounds the posterior quarter of the elongated nucleus (Atwood & Chia 1974).

In situ observations of spawning *C. lubrica* specimens (Engstrom 1983, McEuen 1988) indicate, that bundled spermatozoa may have an advantage for brooding species, which do not release their eggs freely into the water column nor have any kind of copulatory behaviour: to ease fertilization of eggs, extruded sperm sinks to the bottom, preferably in the immediate vicinity of a female, and remains clumped for a longer time, rather than rapidly dispersing into the water (Atwood & Chia 1974, Engstrom 1983, McEuen 1988). The elongate genital papilla of the males is thought to be of help in forming these sperm stands or strings (McEuen 1988). According to Atwood & Chia (1975), elongated sperm heads may reflect a specific adaptation to facilitate the packaging of spermatozoa to spermatozeugmata.

This scenario somewhat contradicts the idea of O'Loughlin (2001), at least in the case of *E. splendidus* and species of the "*Cucumaria georgiana*" group. He supposed copulatory behaviour for species in which the male genital papilla is permanently digitiform and the female shows externally opening brood pouches harbouring juveniles all in the same stage of development. Albeit not observed so far, as a modification of external fertilization and brooding it would seem natural that eggs, from the bottom or directly from the genital opening, are transferred into the brood pouches with the (female's) tentacles and subsequently fertilized directly by injection of spermatozeugmata via the male genital papilla. In addition there is ultrastructural indication for poor swimming endurance of single spermatozoa: the small mid-piece volume argues for limited energy reserves and the restricted area of contact between the mitochondrial derivatives and the flagellum for a limited flow of metabolites (contrary e.g. to sperm cells, that have to drill actively through the female body wall as in the gastropod acochlidians; Neusser *et al*. 2007). The big and prominent acrosomal vesicle on the other hand should mediate a fast penetration of the egg integument.

The limited distribution of *Echinopsolus* is noteworthy—all species investigated so far are restricted to waters south of the Polar Front, thus endemic to the Southern Ocean (in a biogeographic sense, e.g. Clarke & Johnston 2003, Clarke *et al*. 2007). This is also true for all "potential" *Echinopsolus* species, which are not included in the current investigation (see Table I and sources therein). Such a limited distribution of a presumably speciose monophyletic and morphologically diverse group implies a radiation and diversification in place.

The Southern Ocean shelf fauna has evolved for a long time in isolation; surrounding deep-sea basins and the Polar Front, which constitutes an effective natural boundary (Crame 1999), make faunal exchange with adjacent faunas difficult. Thus, a high degree of endemism is thought to be characteristic for the Southern Ocean fauna, and values for different groups at species level range from about 35 % to 90 % (Clarke & Johnston 2003). This could also be demonstrated for Weddell Sea holothurians (Gutt 1991b): 45 % of the holothurian species found in the Weddell Sea area are restricted to the Southern Ocean, and if typical deep-sea species are omitted, the percentage of endemism even is much higher (92 %). But concerning higher taxonomic levels like genus or family, there is no indication for a high degree of radiation in the Southern Ocean (Gutt 1991b). The current investigations clearly refute this view, there is at least one group of holothurians, that experienced a remarkable radiation within this area.

The morphological diversity found within the genus *Echinopsolus* can be explained with an adaptation to different ecological niches, related (at least in part) to substrate preferences in combination with feeding and food availability. Dendrochirote holothurians (including *Echinopsolus*) are suspension feeders, which live either on hard substrates or on soft bottoms and collect food by extending their richly branched tentacles into the water column (Massin 1982). Due to the fact, that suspension feeding is passive (no water flow is produced), at least some denrochirote holothurians exhibit a rheophilic (orientate tentacles towards current) and acrophilic (sit in elevated positions to increase exposure to current) behaviour (Massin 1982). Although the knowledge of the ecology of *Echinopsolus* species is scarce, an acrophilic behaviour is obvious for a variety of species and the preferred substrate without a doubt has an influence on the external morphology of these species.

According to Gutt (1988, 1991a, b) "*Cucumaria georgiana*" group species, which lack a ventral sole and have cylindrical tube feet present in all five radii, live epizoic between branched bryozoans or hydroid stalks. This tube feet arrangement is interpreted by Gutt (1988) as an adaptation to a small structured three-dimensional substrate, that facilitates a proper attachment with different parts of the body. The species subsumed as "*Cucumaria georgiana*" group sensu Gutt (1988), most probably also contained *E. acutus*, which is not uncommon in the eastern Weddell Sea area (Massin 1992, own observations) investigated by Gutt (1988).

Species with a well developed ventral sole probably prefer other substrates. The broad ventral sole and the stout tube feet of *E. charcoti* are suited to rest against structures on the sediment (stones, bryozoans, hydroids or poriferans), while the body is erected vertically to feed (Gutt 1988, 1991a, b). Outstanding are *E. acanthocola* and *E. parvipes*, which both have a slender ventral sole, very well adapted to cling to an elongated rod-shaped substrate like the large primary spines of cidaroid echinoids, where both of them are regularly found (Gutt 1988, 1991a, b, Massin 1992, own observations, Fig. 2f).

The arrangement of the calcareous deposits in the body wall also can be explained to some extent with habitat preferences. To facilitate climbing in epizoic species (e.g. *E. acutus*), it may be favourable to reduce specific gravity via a thin body wall, with few ossicles loosely scattered, which in addition may decrease in size and number with increasing body size (Gutt 1988). Thickened or multi-layered calcareous deposits arranged test-like in multiple layers however are usually found in species favouring a more or less sedentary live on solid substrates like boulders or stones (e.g. various species of the family Psolidae).

Based on their external morphology and their calcareous deposits, the species treated herein, up to now have been classified in a variety of different genera in the families Cucumariidae and Psolidae. Non of these genera 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. But 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.

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Table I. Literature records of Antarctic Cucumariidae and "Psolidae" with anterior interradial brood pouches and a genital papilla on oral disc complemented by data from the current investigation.

Species	number of brood pouches	genital papilla	spermaot-zeugmata	*"Echinopsolus"* spermatozoa	Source	Name used herein
Cucumariidae						
**Cucumaria acuta* Massin, 1992	5	+	+	+	**herein**	*Echinopsolus acutus* (Massin, 1992)
		+			Massin 1992	
**Cucumaria attenuata* Vaney, 1906	5	+			Ekman 1925	?
Cucumaria coatsi [non Vaney, 1908]	5				Ekman 1925	?
Cucumaria ferrari (Bell, 1908)	3				McClintock *et al*. 1994	?
**Semperia georgiana* Lampert, 1886		+			Lampert 1886	?
**Cucumaria georgiana* (Lampert, 1886)	5				Ekman 1925	
"*Cucumaria georgiana*" group species	5	+			O'Loughlin 1994, 2001	?
**Cucumaria joubini* Vaney, 1914	5	+			Vaney 1914, 1925	?
**Cucumaria lateralis* Vaney, 1906	2 (mdi, rli)	+			Vaney 1906a, b	?
	2 (rli, rvi)				Vaney 1908	
	2				Vaney 1925	
**Cucumaria vaneyi* Cherbonnier, 1949	2 (lli, mdi)				Cherbonnier 1949	?
Microchoerus splendidus Gutt, 1990	5	+	+	+	**herein**	*Echinopsolus splendidus* (Gutt, 1990)
		+			Gutt 1990	
	5	+			O'Loughlin 1994, 2001	
Pseudocolochirus mollis Ludwig & Heding, 1935	5	+	+	+	**herein**	*Echinopsolus mollis* (Ludwig & Heding, 1935)
	5	+			Ludwig & Heding 1935	
"Psolidae"						
Echinopsolus acanthocola Gutt, 1990	5	+	+	+	**herein**	*Echinopsolus acanthocola* Gutt, 1990

Table 1. continued

Species	**number of brood pouches**	**genital papilla**	**spermaot-zeugmata**	***"Echinopsolus"* spermatozoa**	**Source**	**Name used herein**
Echinopsolus parvipes Massin, 1992	5	+	+	+	**herein**	*Echinopsolus parvipes* Massin, 1992
		+			Massin 1992	
Psolus charcoti Vaney, 1906	5	+	+	+	**herein**	*Echinopsolus charcoti* (Vaney, 1906)
	5				Ekman 1925	
	5	+			O'Loughlin 2001	
Psolus koehleri Vaney, 1914	5	+	+	+	**herein**	*Echinopsolus koehleri* (Vaney, 1914)
	5				Vaney 1914, 1925	
	5	+			Ekman 1925	

lli: left lateral interradius, mdi: mid-dorsal interradius, rli: right lateral interradius, rvi: right ventral interradius, +: present, *: "*Cucumaria georgiana*" group species sensu Massin (1992)

Table II. Locality data of *Echinopsolus* specimens pictured herein for specimen details, scanning electron microscopy, histology or fine structure.

Species	**Specimen**	**Expedition**	**Station**	**Latitude**	**Longitude**	**Depth (m)**
E. acanthocola	JMB-00090, JMB-01779	EASIZ III	PS 56/109-1	71°11.3' S	12°18.5' W	311–316
	JMB-01760	BENDEX	PS 65/090-1	70°56.1' S	10°31.7' W	274–288
E. acutus	JMB-01731	EASIZ I	PS 39/06 AGT 1	71°31.8 'S	13°34.5 'W	254–261
	JMB-01712	EASIZ II	EASIZ II	71°09.7' S	12°28.7' W	341–360
E. charcoti	JMB-01832, JMB-01837	EASIZ III	PS 56/065-1	71°17.6' S	13°48.0' W	615–648
E. koehleri	JMB-01833, JMB-01836	EASIZ III	PS 56/085-1	71°11.3' S	12°15.4' W	309–318
E. mollis	JMB-01680		PS 39/11 GSN 4	73°22.6' S	21°10.6' W	333–338
	JMB-01831	BENDEX	PS 65/336-1	70°50.7' S	10°28.3' W	276–281
E. parvipes	JMB-01825, JMB-01826	EASIZ III	PS 56/065-1	71°17.6' S	13°48.0' W	615–648
E. splendidus	JMB-01696, JMB-01698	EASIZ II	PS 48/077	71°09.7' S	12°28.7' W	341–360
	JMB-00122	EASIZ III	PS 56/085-1	71°11.3' S	12°15.4' W	309–318
	JMB-00088, JMB-01702	EASIZ III	PS 56/109-1	71°11.3' S	12°18.5' W	311–316

Table III. Morphological variability of tube feet arrangement of *Echinopsolus* species, own observations supplemented by data from literature.

<table>
<tr><th>Species</th><th colspan="7"><i>Echinopsolus</i></th></tr>
<tr><th></th><th><i>acutus</i></th><th><i>mollis</i></th><th><i>acanthocola</i></th><th><i>parvipes</i></th><th><i>splendidus</i></th><th><i>charcoti</i></th><th><i>koehleri</i></th></tr>
<tr><td>Dorsal tube feet</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Shape</td><td>cylindrical</td><td>cylindrical to conical</td><td colspan="2">--------large conical-------</td><td colspan="3">------------small cylindrical-----------</td></tr>
<tr><td>Arrangement</td><td>single radial rows</td><td colspan="3">------------------scattered-----------------</td><td colspan="3">single tube feet close to anterior end and around anus</td></tr>
<tr><td>Ventral tube feet</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Distinct sole</td><td colspan="2">-----------indistinct---------</td><td colspan="4">---------------delimited by tube feet----------------</td><td>delimited by bulge of body wall</td></tr>
<tr><td>Lateral radii</td><td>single row</td><td>single to double row</td><td colspan="4">--------------------single row-------------------------</td><td>double row</td></tr>
<tr><td>Mid-ventral radius</td><td colspan="2">---------double row----------</td><td colspan="4">double row restricted to anterior and posterior end of sole</td><td>double row, often scattered in middle part of sole</td></tr>
<tr><td>Sources</td><td>Massin 1992</td><td>Ludwig & Heding 1935</td><td>Gutt 1990</td><td>Massin 1992</td><td>Gutt 1990</td><td>Ekman 1925</td><td>Ekman 1925</td></tr>
</table>

Table IV. Morphological variability of calcareous deposits of the body wall of *Echinopsolus* species, own observations supplemented by data from literature.

Species	***Echinopsolus***						
	acutus	***mollis***	***acanthocola***	***parvipes***	***splendidus***	***charcoti***	***koehleri***
Calcareous deposits	only plates					outer layer of basket-like plates, deeper layer of plates	
Variation in deposit number and size with increasing body size	decrease in number	decrease in number and size	no changes	decrease in size	decrease in number and size	no changes	
Dorsal plate arrangement	scattered	scattered	partly overlapping	partly overlapping	dense to scattered	dense to scattered	multiple layeres
Outline	irregular	rounded to elongated, one end often spiny	irregular to rounded	rounded	rounded	rounded	rounded
Surface	spiny	smooth	knobbed	knobbed	knobbed	smooth	smooth
Structure	simple	simple	multi-layered, tower-like central bump	multi-layered	simple to thickened	multi-layered	multi-layered, often tower-like bump
Maximum size (µm)	400	700	1500	600	500	1220	3300
Ventral plate arrangement	*	*	partly overlapping	partly overlapping	*	partly overlapping	multiple layers
Outline			rounded	irregular to rounded		rounded to elongated	rounded
Surface			knobbed	spiny or knobbed		smooth	smooth
Structure			often multi-layered	simple		thickened to multi-layered	simple to multi-layered
Maximum size (µm)			800	375		700	530
Sources	Massin 1992	Ludwig & Heding 1935	Gutt 1990	Massin 1992	Gutt 1990	Ekman 1925	Ekman 1925

*: Ventral plates similar to dorsal plates

Table V. Morphometric data of *Echinopsolus* sperm cells (values in µm).

Species	***Echinopsolus***						
	acutus	***mollis***	***acanthocola***	***parvipes***	***splendidus***	***charcoti***	***koehleri***
Head length	4.1	4.1	5.0	4.1	4.2	2.9	4.6
Head diameter	1.5	1.4	1.3	1.3	1.5	1.4	1.6
Head length / diameter	2.7	2.9	3.85	3.15	2.8	2.1	2.9
Mid-piece length	1.4	n.d.	1.8	1.6	1.6	1.4	1.6
Mid-piece diameter	1.2	n.d.	1.3	1.2	1.3	1.4	1.5
Thickness of mid-piece wall	0.3	n.d.	0.25	0.25	0.3	0.25–0.3	0.4

Diameters measured on cross sections or on oblique sections (smallest diameter). Longimetry was performed on cutting profiles that show the distal centriole and the acrosomal vesicle simultaneously. The bad structural conservation of sperm mid-pieces in *E. mollis* (no aldehyde fixation) did not allow any reliable measurement.

Figure 1. Genital papillae and brood pouches of *Echinopsolus* spp. **a.** Male genital papilla (*arrowhead*) of *E. acutus*. **b–d.** *E. splendidus*. **b.** Male genital papilla. **c.** Female genital papilla (*arrowhead*). **d.** Brood pouch openings (*arrowheads*) of a female with retracted tentacles. **e.** *E. acanthocola*, brood pouch opening of a female (*arrowhead*). **f.** *E. splendidus*, brood pouch (opened up) with developing juveniles.

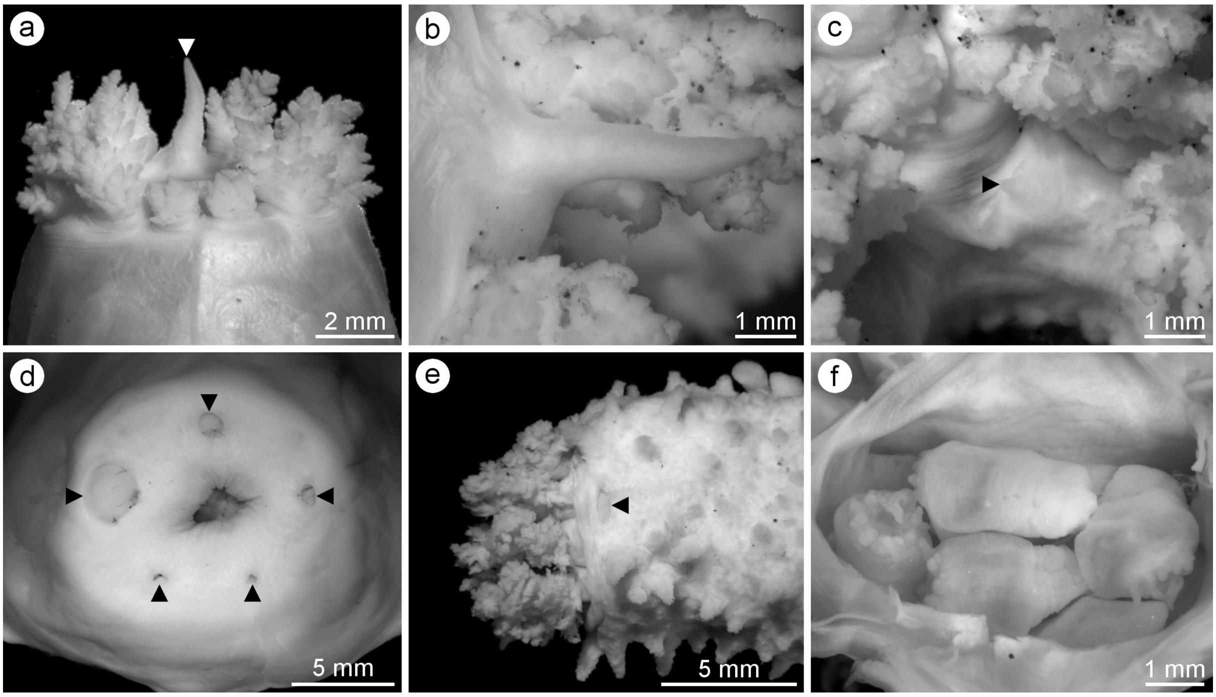


Figure 2. Ultrastructure (SEM) of spermatozeugmata and sperm cells of *Echinopsolus* spp. **a.** Mass of sperm bundles in gonad tubule (opened up) of *E. koehleri*. **b–e.** Spermatozeugmata. **b.** *E. acanthocola*. **c.** *E. charcoti*. **d.** *E. mollis*. **e.** *E. parvipes*. **f–g.** Spermatozoa. **f.** *E. acanthocola*. **g.** *E. koehleri*. (arrows: acrosomes, arrowheads: cylinder shaped mid-pieces)

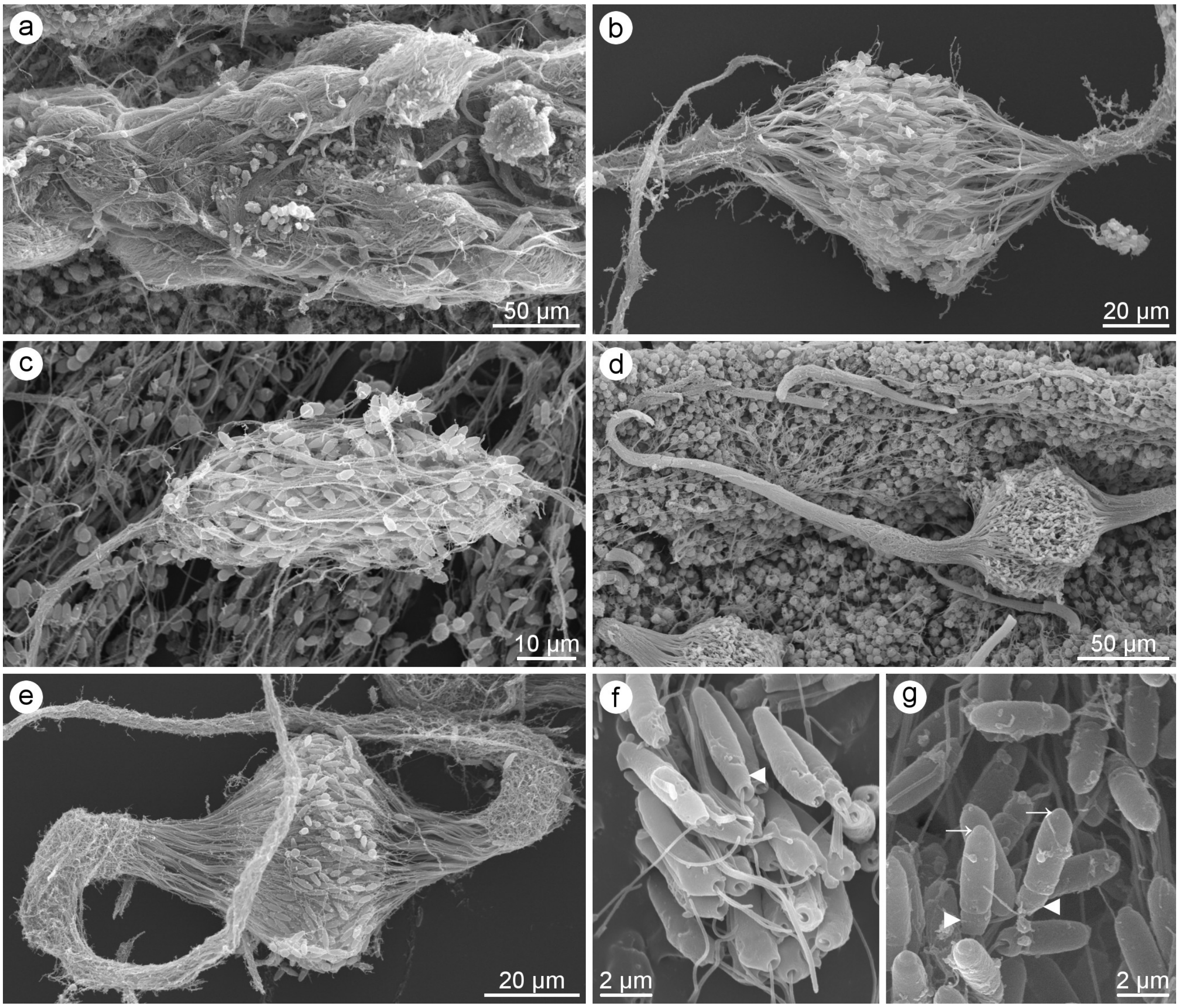


Figure 3. Histology of spermatozeugmata and sperm cells of *Echinopsolus* spp. **a–c.** *E. acutus*. **a.** Semithin cross section in centre of seminiferous tubule. **b.** Sperm bundles fill central space of seminiferous tubule. **c.** Longitudinal section through spermatozeugma showing sperm heads, mid-pieces and flagella. **d–e.** *E. splendidus*. **d.** Mass of sperm bundles. **e.** Longitudinal section through spermatozeugma. **f–g.** *E. mollis*. **f.** Mass of sperm bundles. **g.** Longitudinal section through spermatozeugma with poor structure preservation (alcohol conservation, no aldehyde fixation). (f: flagellum, m: mid-piece, n: nucleus)

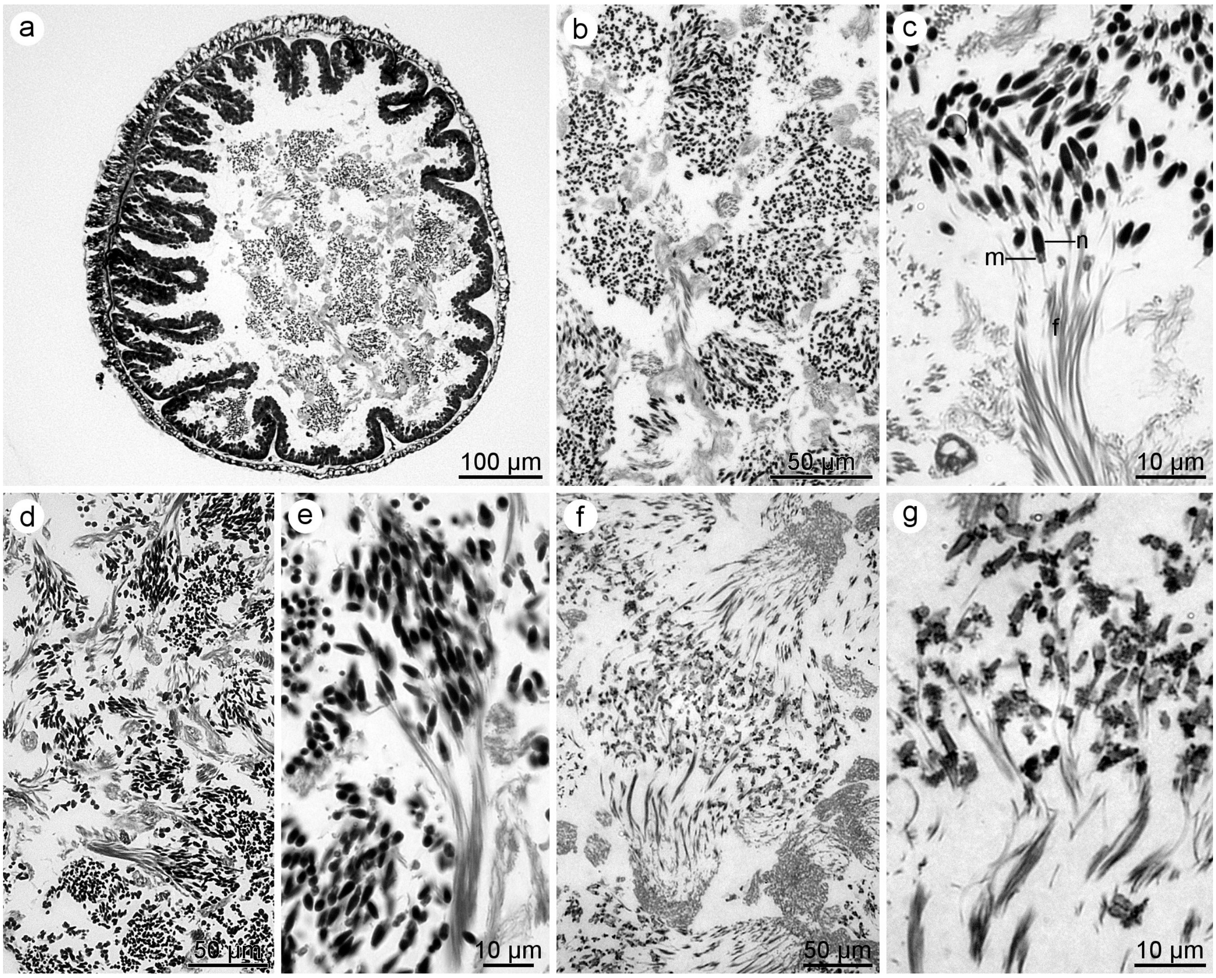


Figure 4. Ultrastructure (TEM) of spermatozeugmata and sperm cells of *Echinopsolus* spp. **a–d.** E. *splendidus*. **a.** Overview of ripe sperm cells and spermiogenesis-stages. **b.** Different regions of sperm cells in oblique cutting planes. **c.** Nuclear apex with cup-shaped indentation containing acrosomal complex. **d.** Cross section through mid-piece at level of centriolar satellite complex. **e.** *E. acanthocola*, longitudinal sections through sperm-cell head and mid-piece. **f.** *E. koehleri* longitudinal section through sperm-cell head and mid-piece. **g–i.** *E. parvipes*. **g.** Close up of nuclear apex with acrosomal vesicle anchored by actomere and subacrosomal plate (*arrowheads*) in periachrosomal material. **h.** Close up of the mid-piece region in axial section plane. **i–k.** Cross sections through mid-pieces at level of centriolar satellite complex. **i.** *E. parvipes.* **j.** *E. charcoti.* **k.** *E. koehleri* (premature). (a: acrosomal vesicle, dc: distal centriole, f: flagellum, m: mid-piece, n: nucleus, p: periacrosomal material, pc: proximal centriole, s: spermiogenesis-stages, sc: centriolar satellite complex)

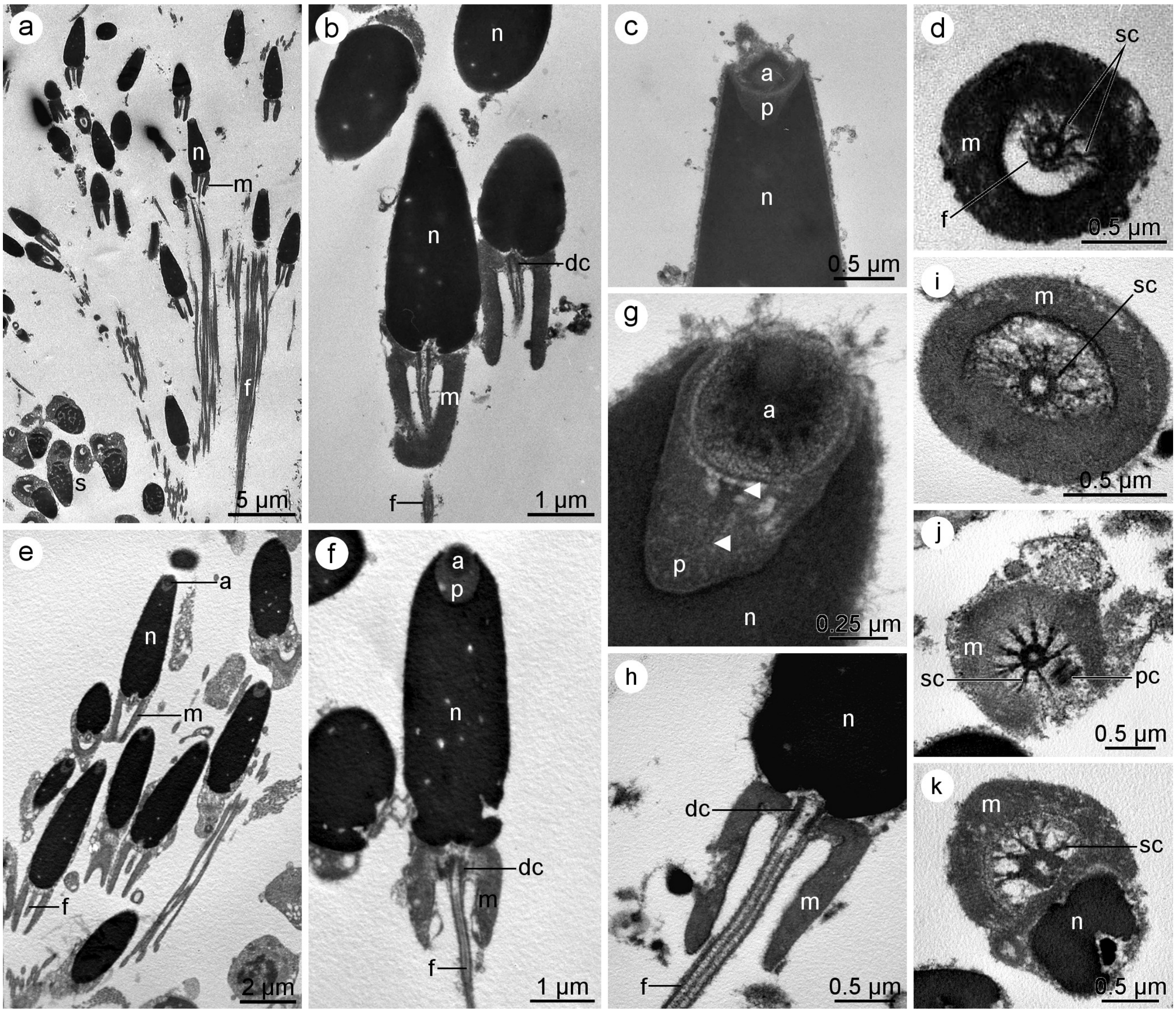


Figure 5. Schematic reconstruction of sperm ultrastructure of *Echinopsolus splendidus*. **a.** Longitudinal section of sperm head with acrosomal complex, diplosome with satellite complex and cylindrical mid-piece with mitochondrial ring and mitochondrial cylinder wraping basis of flagellar sperm-tail. **b–g.** Cross sections. **b.** Rim of the anterior nuclear depression with embedded acrosomal vesicle. **c.** Periacrosomal mass. **d.** Electron dense nucleus with small electron light "vacuole". **e.** Distal centriole (9 x 3 + 0 tubular arrangement) with satellite complex and subnuclear mitochondrial ring. **f.** Jacket-shaped mitochondrial derivative encircling flagellar tail-base. **g.** Flagellar tail. (a: acrosomal vesicle, cf: centriolar fossa, cm: cell membrane, dc: distal centriole, f: flagellum, mc: mitochondrial cylinder, mr: mitochondrial ring, n: nucleus, p: periacrosomal material, pc: proximal centriole with fibrous arm, sc: satellite complex, v: nuclear vacuole, x: extracellular space within the mitochondrial cylinder)

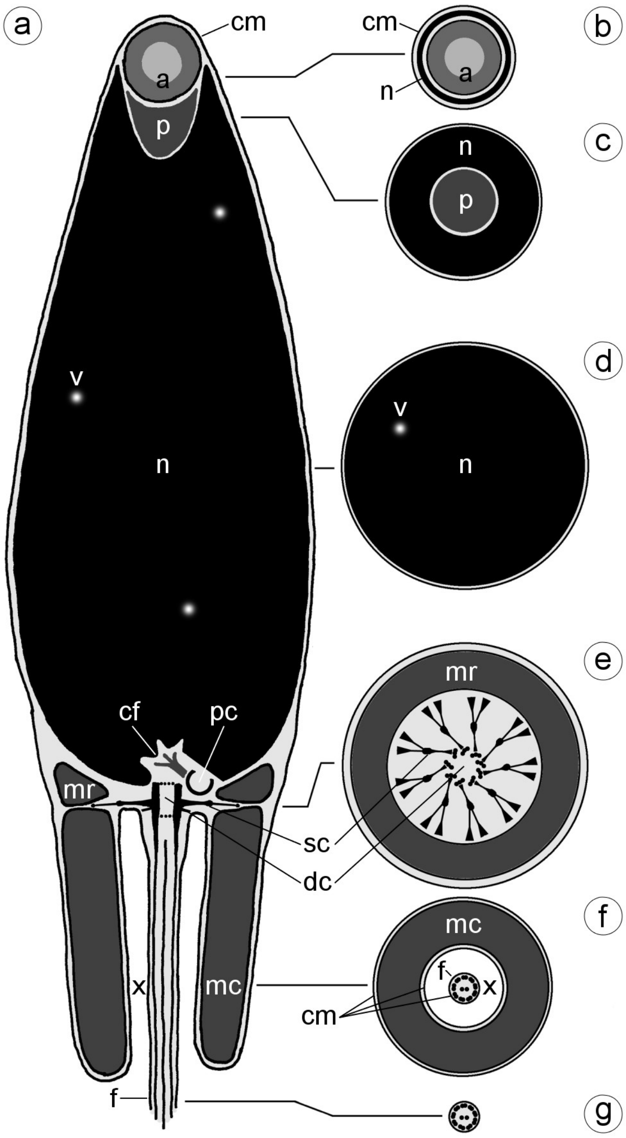
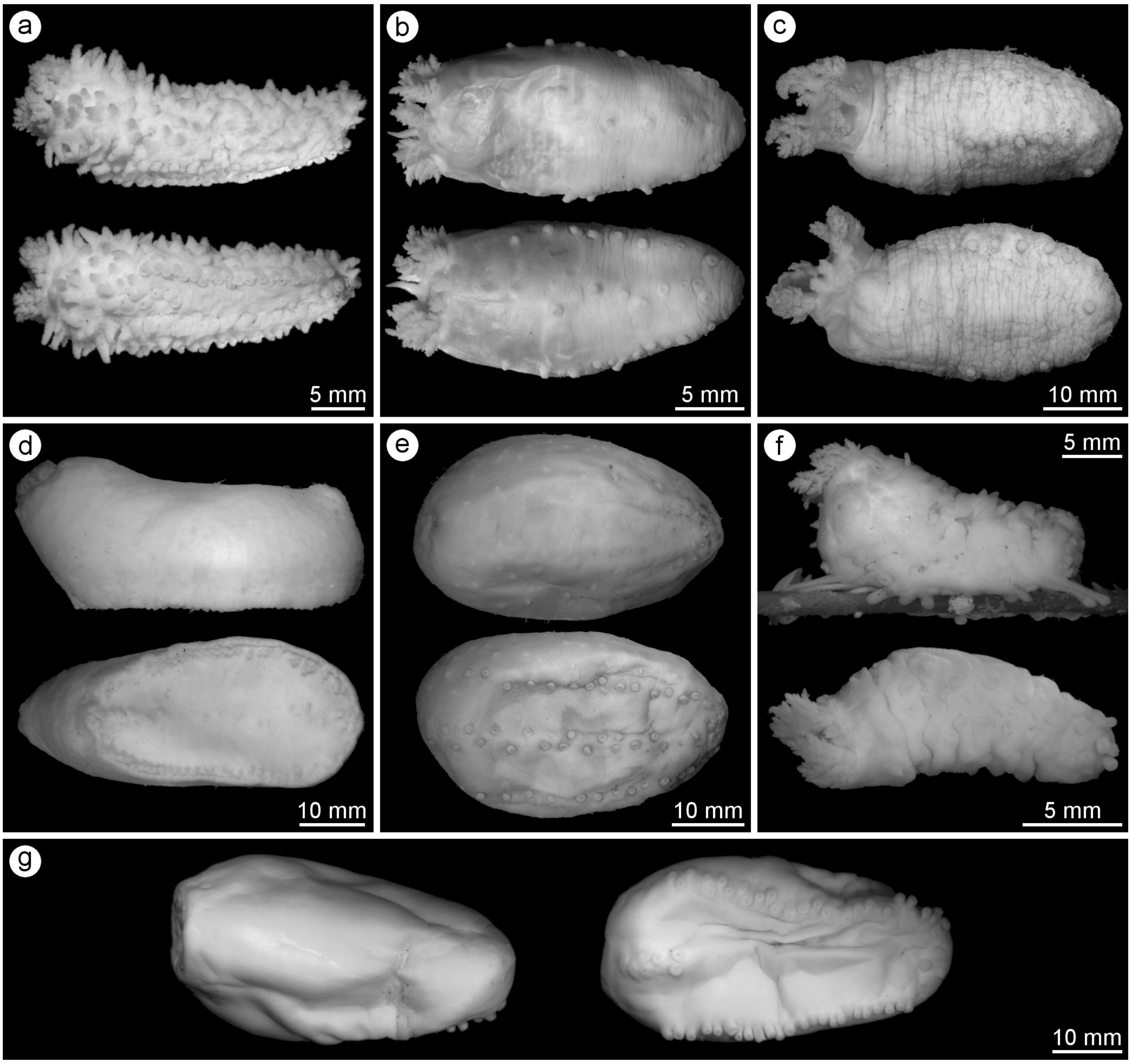


Figure 6. Variability of tube feet arrangement of *Echinopsolus* spp. **a.** *E. acanthocola*, lateral and ventral view. **b.** *E. acutus*, dorsal and ventral view. **c.** *E. charcoti*, lateral and ventral view. **d.** *E. koehleri*, lateral and ventral view. **e.** *E. mollis*, dorsal and ventral view (tentacles retracted, mouth to the left). **f.** *E. parvipes*, lateral and ventral view. **g.** *E. splendidus*, lateral and ventral view (tentacles retracted, mouth to the left).



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Eingeworbene Drittmittel

DFG Projekt (RU-895/1-1) "Taxonomy and zoogeography of the Echinodermata collected during the DIVA I expedition with RV "Meteor" to the Angola basin", im Rahmen des Programms 516 (Auswertung der Meteor-Expeditionen) von mir gestellter Projektantrag unter der Leitung von Dr. Bernhard Ruthensteiner (ZSM)

Anstellungen

Wissenschaftlicher Angestellter im DFG Projekt "Taxonomy and zoogeography of the Echinodermata collected during the DIVA I expedition with RV "Meteor" to the Angola basin" an der Zoologischen Staatssammlung München (ZSM)	09.2002–08.2003
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Publikationsliste

Altnöder, A., Bohn, J. M., Rückert, I. & Schwabe, E. (2007) The presumed shelled juvenile of the parasitic gastropod *Entocolax schiemenzii* Voigt, 1901 and its holothurian host *Chiridota pisanii* Ludwig, 1886 (Gastropoda, Entoconchidae – Holothuroidea, Chiridotidae). *Spixiana,* **30**, 187–199.

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