

# The genus *Grimpoteuthis* (Octopoda: Grimpoteuthidae) in the north-east Atlantic, with descriptions of three new species

MARTIN A. COLLINS\*

Zoology Department, Aberdeen University, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

Received December 2001; accepted for publication April 2003

The systematics and distribution of the cirrate octopod genus *Grimpoteuthis* in the north-east Atlantic are reviewed. Three new species are described and *Grimpoteuthis wuelkeri* (Grimpe, 1920) is redescribed. A new generic diagnosis is proposed. Five species of *Grimpoteuthis* are recognized in the north-east Atlantic. The type species, *G. umbellata* (Fisher, 1883) is known only from the type specimen, which is in such poor condition that comparison with recently captured material was not possible. *G. wuelkeri* is a large, slope species, caught between 1600 m and 2200 m in the north-east and north-west Atlantic. Of the three new species, both *G. boylei* and *G. challengerii* are large abyssal species. *G. boylei* is found in the north-east Atlantic at the Porcupine Abyssal Plain (PAP) and the Madeira Abyssal Plain and may be found at abyssal depths throughout the north-east Atlantic. *G. challengerii* is known from the PAP, with a single specimen from the north-west Atlantic. *G. discoveryi* is a small, lower slope and abyssal species found in the north-east Atlantic. The *Grimpoteuthis* species can be separated based on shell form, presence of a radula and posterior salivary glands, arrangement of suckers and cirri and gill morphology. Two species, *G. megaptera* Verrill and *G. plena* Verrill, have been described from the north-west Atlantic, but the types are either lost (*G. megaptera*) or in poor condition (*G. plena*), hindering comparisons. Material examined from the north-west Atlantic included *G. wuelkeri*, *G. challengerii* and at least two other species. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, 139, 93–127.

ADDITIONAL KEYWORDS: Cirrata – deep-sea – Octopoda – Opisthoteuthidae.

## INTRODUCTION

The cirrate octopods are deep-sea cephalopods, possessing a semigelatinous body, paired fins, well developed webs, a large internal shell and paired cirri that straddle a single row of suckers. They are known from all oceans, usually inhabiting depths between 500 m and 7500 m (Voss, 1988a). The small numbers of cirrates captured in nets, coupled with their gelatinous, fragile nature and distortion during preservation has led to considerable confusion in the taxonomy of the group. Many species were described from material collected by the pioneering deep-sea expeditions of the late 19th and early 20th centuries (Fischer, 1883; Hoyle, 1886; Joubin, 1900, 1903; Chun, 1913), with

most described from single, badly damaged specimens, making comparison with new material very difficult. Recent years have seen renewed interest in this enigmatic group, with redescrptions of the Stauroteuthidae (Collins & Henriques, 2000), *Cirroteuthis magna* (Guerra *et al.*, 1998), a revision of the Atlantic species of the genus *Opisthoteuthis* (Villanueva *et al.*, 2002) and several new species described from New Zealand waters (O'Shea, 1999).

Sweeney & Roper (1998) separated the cirrates into three families (Opisthoteuthidae, Stauroteuthidae and Cirroteuthidae), but recent morphological (O'Shea, 1999) and molecular work (Piertney *et al.*, 2003) support a re-organization at the familial level. O'Shea (1999) proposed the splitting of Opisthoteuthidae, creating two new families (Grimpoteuthidae and Luteuthidae), with *Cirroctopus* included in Opisthoteuthidae. However molecular data indicate that *Luteuthis* should be included in

\*E-mail: macol@bas.ac.uk. Present address: British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge, CB3 0ET, UK.

Grimpoteuthidae, *Stauroteuthis* in Cirroteuthidae and a new family erected to include *Cirroctopus* (Piertney *et al.*, 2003). Cirroteuthids are distinguished from the other families in possessing a complex (secondary) web (see Vecchione & Young, 1997) and extremely long cirri. Grimpoteuthidae, Opisthoteuthidae and *Cirroctopus* are distinguished by the arrangement of the optic nerves, fin size and shell form.

In the present paper the north-east Atlantic species of the genus *Grimpoteuthis* are described in detail for the first time. This work is based largely on collections taken in the Porcupine Seabight and Porcupine Abyssal Plain by the Institute of Oceanographic Sciences in the late 1980s and 1990s but also includes a thorough examination of type material and other published records.

#### HISTORICAL RESUMÉ OF THE GENUS *GRIMPOTEUTHIS*

Fischer (1883) described *Cirroteuthis umbellata* from three specimens caught in the north-east Atlantic (Table 1). The larger specimen was caught at 2235 m depth near the Azores during the *Talisman* expedition with two smaller specimens caught at shallower depths (1139 and 1233 m) off the coasts of Morocco and the Canaries, respectively. The specimens were subsequently described in more detail by Fischer & Joubin (1907); the larger specimen and one of the smaller ones remain in the collections of MNHN in Paris.

Following the description of *umbellata*, Verrill (1885) described two new species of *Cirroteuthis* (sic) (*C. megaptera* and *C. plena*) from the north-west Atlantic. Later, Joubin (1903) described a new species, *Cirroteuthis richardi*, but subsequently considered this a junior synonym of Verrill's *C. megaptera* (see Joubin, 1920). Joubin (1900, 1920) reported three further specimens of *C. umbellata* from the North Atlantic. Six additional specimens of *C. umbellata* were reported by Chun (1913) from the *Michael Sars* expedition, but two of these were subsequently described as the types of *Stauroteuthis wulkeri* (Grimpe, 1920) and *Chunioteuthis ebersbachi* (Grimpe, 1916) (see Table 1). Voss (1955) described a gravid female from off Cuba.

Robson (1932) separated *Cirroteuthis* into two genera, with *Cirroteuthis* accommodating *C. muelleri* and a new genus *Grimpoteuthis* including some species previously in *Stauroteuthis* and *Cirroteuthis*. Following Robson's revision little taxonomic work was undertaken on the cirrates until the work of Voss and others in the 1980s. In recent years new *Grimpoteuthis* species have been described, such as *G. antarctica* (Kubodera & Okutani, 1986), *G. bruuni* (Voss, 1982) and *G. bathynectes* and *G. tuftsi* (Voss & Percy, 1990).

Voss (1988a) reviewed the world-wide distribution of *Grimpoteuthis* and included some new records,

whilst Voss (1988b) provided new generic diagnoses for the cirrates and moved *G. grimaldii* to the genus *Opisthoteuthis*. O'Shea (1999) proposed that *Grimpoteuthis* be removed from the Opisthoteuthidae and erected the new families, Grimpoteuthidae (to include *Grimpoteuthis* and his new genus *Enigmatiteuthis*) and Luteuthidae (to include the new genus *Luteuthis*). He further proposed that *G. glacialis* Robson and *G. mawsoni* (Berry) be removed from *Grimpoteuthis* and included in the re-instated genus *Cirroctopus* with a new species *C. hochbergi*. Collins *et al.* (2001) reported five putative species of *Grimpoteuthis* from south-west Ireland and west Scotland.

#### MATERIAL AND METHODS

Definitions of counts and measurements used here generally follow Guerra *et al.* (1998) and Voss & Percy (1990), and the basic measurements are defined in Figure 1. Indices (see below) were usually based on head width rather than mantle length as head width is less prone to variability under preservation and thus provides a stable base-line.

#### Abbreviations in text

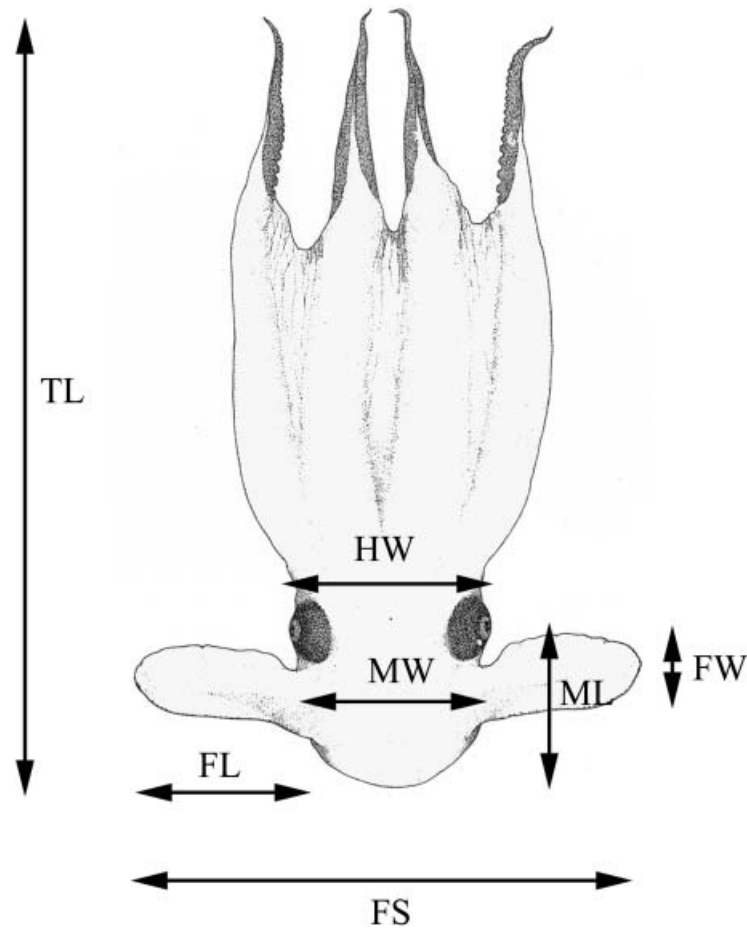
AL	arm length (dorsal arms)
ALI	arm length index
BN1.5	1.5 m benthic sledge
CLI	cirrus length index
ED	maximum eye diameter
EDI	eye diameter index
FL	fin length
FLI	fin length index
FuL	funnel length
FuLI	funnel length index
FS	fin span
FSI	fin span index
GD	gill diameter
GDI	gill diameter index
HW	head width
HWI	head width index
ML	mantle length
MCL	maximum cirrus length
MLI	mantle length index
MSD	maximum sucker diameter
OTSB	semiballoon otter trawl
SD	sucker diameter
SDI	sucker diameter index
TL	total length

#### Indices used

ALI	AL/TL*100
FSI	FS/TL*100
MLI	ML/TL*100

**Table 1.** Published records of specimens of *Grimpotoothis* from the North Atlantic Ocean. Asterisk indicates specimens not examined in present study

Original report	Location	Reported by	Catalogue No	Current status
<i>Cirrotoothis umbellata</i>	37°55'N, 20°22'W; 2235 m	Fischer (1883): large syntype	MNHN 3.6.698	Lectotype of <i>G. umbellata</i> . Very poor condition
<i>Cirrotoothis umbellata</i>	23°52'N, 19°37'W; 1250 m	Fischer (1883): medium syntype	Missing	Missing
<i>Cirrotoothis umbellata</i>	23°30'N, 19°37'W; 1139 m	Fischer (1883): small syntype	MNHN 3.6.699	<i>Opisthotoothis</i> sp. Small, poor condition
<i>Cirrotoothis umbellata</i>	42°59'N, 51°51'W; 1100 m	Chun (1913): <i>Michael Sars</i> 70	ZUB 36371	<i>Staurotoothis syrtensis</i> . Described as <i>Staurotoothis</i> by Ebersbach (1915) and <i>Chunioothis</i> by Grimpe (1920)
<i>Cirrotoothis umbellata</i>	35°46'N, 8°16'W; 2056 m	Chun (1913): <i>Michael Sars</i> 25	ZUB 36372	Type of <i>wuelkeri</i> (Grimpe, 1920). Shown in Ebersbach (1915: fig. 1) as <i>C. umbellata</i>
<i>Cirrotoothis umbellata</i>	34°59'N, 33°01'W; 2615 m	Chun (1913): <i>Michael Sars</i> 53	ZUB 36379	<i>G. discoveryi</i> . Good condition
<i>Cirrotoothis umbellata</i>	34°59'N, 33°01'W; 2615 m	Chun (1913): <i>Michael Sars</i> 53	ZUB 36379	<i>G. discoveryi</i> . Good condition
<i>Cirrotoothis umbellata</i> *	34°59'N, 33°01'W; 2615 m	Chun (1913): <i>Michael Sars</i> 53		Probably <i>G. discoveryi</i> . Dissected by Ebersbach (1915)
<i>Cirrotoothis umbellata</i> *	34°59'N, 33°01'W; 2615 m	Chun (1913): <i>Michael Sars</i> 53		Probably <i>G. discoveryi</i> . Dissected by Ebersbach (1915)
<i>Cirrhotoothis plena</i>	37°55'N, 71°18'W; 1963 m	Verrill (1885): 404, Pl. XLII, fig. 3	USNM 39908	<i>Grimpotoothis plena</i> . Poor condition
<i>Cirrhotoothis megaptera</i> *	39°43'N, 69°23'W; 1928 m	Verrill (1885): <i>Albatross</i> 2220	Missing	Lost
<i>Cirrhotoothis megaptera</i> *	36°16'N, 68°21'W; 4708 m	Verrill (1885): 405, Pl. XLIII, figs 1, 2; <i>Albatross</i> 2224	Missing	Lost ( <i>G. megaptera</i> ). Illustrated by Verrill (1885)
<i>Cirrhotoothis megaptera</i> *	36°16'N, 68°21'W; 4708 m	Verrill (1885): <i>Albatross</i> 2224	Missing	Lost
<i>Cirrhotoothis megaptera</i> *	36°05'N, 69°51'W; 4594 m	Verrill (1885): <i>Albatross</i> 2225	USNM 40131	<i>Cirrhothoona murrayi</i>
<i>Cirrhotoothis megaptera</i> *	36°05'N, 69°51'W; 4594 m	Verrill (1885): <i>Albatross</i> 2225	Missing	Lost
<i>Cirrotoothis umbellata</i>	39°54'N, 20°27'W; 4366 m	Joubin (1920): St 753	MOM 295091	<i>G. discoveryi</i>
<i>Cirrotoothis umbellata</i>	45°07'N, 7°06'W; 4870 m	Joubin (1920): St 2986	MOM 295344	<i>G. discoveryi</i>
<i>Cirrotoothis umbellata</i>	44°08'N, 10°44'W; 5000 m	Joubin (1920): St 2994	MOM 295245	<i>G. discoveryi</i>
<i>Cirrotoothis richardi</i>	16°12'N, 24°44'W; 3890 m	Joubin (1903): St 1150	MOM 295138	<i>Grimpotoothis</i> sp. Small specimen. Joubin (1920) revised ID to <i>C. megaptera</i>
<i>Grimpotoothis umbellata</i> *	19°43'N, 74°87'W; 2421–2780 m	Voss (1955)	MCZ 203986	Not examined
<i>Grimpotoothis</i> sp. A	Approx. 50°N, 13°W	Collins <i>et al.</i> (2001)	BMNH various	<i>G. wuelkeri</i>
<i>Grimpotoothis</i> sp. B	Approx. 48°30'N, 16°W	Collins <i>et al.</i> (2001)	BMNH various	<i>G. boylei</i>
<i>Grimpotoothis</i> sp. C	Approx. 48°30'N, 16°W	Collins <i>et al.</i> (2001)	BMNH various	<i>G. challengeri</i>
<i>Grimpotoothis</i> sp. D	Approx. 48–50°N, 14–16°W	Collins <i>et al.</i> (2001)	BMNH various	<i>G. discoveryi</i>
<i>Grimpotoothis</i> sp. E	Approx. 48–50°N, 14–16°W	Collins <i>et al.</i> (2001)	BMNH various	<i>G. discoveryi</i>



**Figure 1.** Diagrammatic view of a cirrate octopod, illustrating the basic measurements used in the present study.

HWI	$HW/TL*100$
FuLI	$FuL/HW*100$
EDI	$ED/HW*100$
FLI	$FiL/HW*100$
SDI	$MSD/HW*100$
CLI	$MCL/HW*100$

*Abbreviations in figures*

acg	accessory gland
asg	anterior salivary gland
bsp	basal plate
brh	branchial heart
cae	caecum
dgg	digestive gland
dod	distal oviduct
fun	funnel
gll	gill
int	intestine
ltw	lateral wing
oes	oesophagus

olf	olfactory organ
opn	optic nerve
opt	optic lobe
ovg	oviducal gland
ovy	ovary
pod	proximal oviduct
psg	posterior salivary gland
stm	stomach
svc	seminal vesicle complex
tes	testes
tmo	terminal organ
whb	white body
wsn	web supporting nodule.

*Institutional abbreviations*

BMNH	Natural History Museum (formerly British Museum), London, UK
MOM	Musée Océanographique, Monaco
MNHN	Muséum National d'Histoire Naturelle, Paris, France

DC-SOC	Discovery Collections, Southampton Oceanography Centre, UK
NMSZ	National Museums of Scotland, Edinburgh, UK
UMML	Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, USA
USNM	National Museum of Natural History, Washington, DC, USA
ZUB	Bergen University Museum, Bergen, Norway

## SYSTEMATICS

## FAMILY GRIMPOTEUTHIDAE O'SHEA, 1999

*New diagnosis*

Small to large octopods with bell-shaped, semigelatinous body; thick primary web, intermediate (secondary) web absent. White (areolar) spots absent. Fins medium to large, lateral, with distinct lobe near the anterior fin insertion. Eyes lateral. Gills of half-orange form. Optic lobe spherical; optic nerves pass through white body as a single bundle of fibres. Fin-supporting cartilage (shell) U-shaped, outer edges of lateral walls parallel, not tapered to single fine points. Radula present or absent. Posterior salivary glands present or absent. Digestive gland entire or bilobed.

*Remarks*

Diagnosis revised to include the genera *Grimpoteuthis*, *Luteuthis* and *Enigmatiteuthis*. There is little molecular (Piertney *et al.*, 2003) or morphological (see below) evidence to support the separation of the family Luteuthidae.

## GENUS GRIMPOTEUTHIS ROBSON, 1932

*New diagnosis*

Small to large octopods with semigelatinous body of bell-shaped form. Thick primary web, intermediate (secondary) web absent. White (areolar) spots absent. Fins medium to large, lateral, with distinct lobe near the anterior fin insertion. Eyes lateral. Gills half-orange in form. Optic lobe spherical; optic nerve passes through white body as a single bundle of fibres. Shell vestige U-shaped; lateral sides parallel, not tapered to fine points. Radula homodont or absent. Posterior salivary glands small or absent. Digestive gland entire (single lobe). Sucker sexual dimorphism present in some species, but with single enlarged field. Type species *Cirrotheuthis umbellata* by subsequent designation.

*Etymology*

Named in honour of the eminent cephalopod researcher Georg von Grimpé.

## GRIMPOTEUTHIS UMBELLATA (FISCHER, 1883)

(FIGS 2, 17; TABLES 2, 11)

*Cirrotheuthis umbellata* Fischer, 1883: 404 (in part)  
*Cirrotheuthis umbellata* Fischer & Joubin, 1907: 318  
*Grimpoteuthis umbellata* (Robson, 1932: 137)  
*Grimpoteuthis umbellata* (O'Shea, 1999: 45)  
*Grimpoteuthis umbellata* (Voss, 1988, in part)  
*Grimpoteuthis umbellata* (Sweeney & Roper, 1998)  
 Non *Stauroteuthis umbellata* (Ebersbach, 1915: text fig. 1)  
 Non *Cirrotheuthis umbellata* (Massy, 1909: 4)  
 Non *Cirrotheuthis umbellata* (Joubin, 1920: 13)  
 Non *Cirrotheuthis umbellata* (Chun, 1913: 16)

*Material examined*

LECTOTYPE: MNHN 3.6.698: immature female, 25 mm ML; north-east Atlantic, Azores, between Fayal and San Miguel; 37°55'N, 20°22'W; 2235 m; *Talisman* 130; 16 August 1883.

*Type locality*

North-east Atlantic, Azores, between San Miguel and Fayal, 2235 m (37°55'N, 20°22'W)

**Table 2.** *Grimpoteuthis umbellata*. Details of the type series. Note the second specimen is herein removed from the type series and the larger specimen designated the lectotype. Here and in subsequent tables, all dimensions in mm; depth in m

	<i>Grimpoteuthis umbellata</i> Lectotype	<i>Opisthoteuthis</i> sp.
Cat. No.	3.6.698	3.6.699
Sex	Unknown	Unknown
Maturity	Unknown	Unknown
Date	16/8/1883	26/6/1883
Longitude	37°55'N	23°50'N
Latitude	29°22'W	19°37'W
Depth	2235	1255
Total length		35
Mantle length		16
Arm I length	100	33
Sucker count	65–68	42–47
MSD	2.2	0.4
MCL	2.7	1.0
Location of MSD	6–8	
Cirri start	4–5	1–2
Gill lamellae	8	8
Gill diameter	8.5	
Shell	Missing	Missing



**Figure 2.** Photograph of the lectotype of *Grimptoteuthis umbellata*.

#### *Distribution*

Known only from type locality.

#### *Remarks*

Known, with certainty, only from the type material, which is in poor condition, with the shell and reproductive system missing (Fig. 2). The species was first described by Fischer (1883), from three specimens caught at different depths and locations in the north-east Atlantic. A slightly more detailed description was subsequently published by Fischer & Joubin (1907). Despite a thorough search, only two of the specimens were traced in this study. Measurements of them are given in Table 2, with additional data from unpublished notes of the late Gilbert Voss. Voss & Percy (1990) suggested that the smaller syntype may be a different species and, although in poor condition, it is clearly an *Opisthoteuthis*, on the basis of body shape and sucker form. The larger specimen is herein designated the **lectotype** and the smaller specimen removed from the type series. The lectotype was dam-

aged upon capture and has subsequently been extensively dissected. Many specimens initially assigned to this species (Table 1) are unlikely to be *G. umbellata*, given the limited bathymetric distributions of individual species (see below). Despite a thorough search, no well-preserved specimens have been found from the type location. The only specimen from near the location is in poor condition (see Indeterminate Material below). It is possible that *G. wuelkeri* (see below) is a junior synonym of *G. umbellata*, but until new material is obtained from the type locality this will not be possible to evaluate. *G. wuelkeri* has similar sucker counts, but differs from *G. umbellata* in the gill lamellae count.

#### *GRIMPOTEUTHIS WUELKERI* (GRIMPE, 1920) (FIGS 3–7, 17; TABLES 3, 4, 11)

#### *Synonymy*

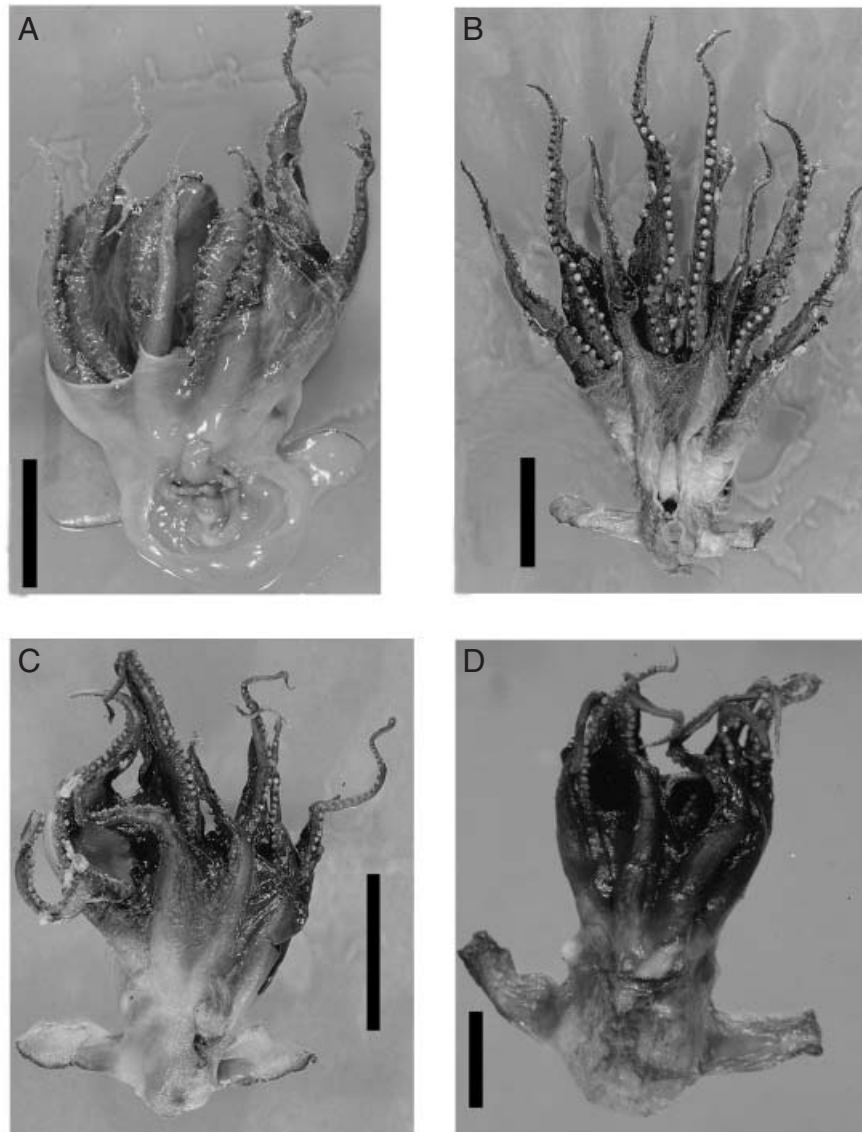
*Stauroteuthis wülkeri* Grimpe, 1920: 235  
*Cirroteuthis umbellata* (Chun, 1913: 16; in part)

**Table 3.** *Grimpot euthis wuelkeri*. Details of specimens examined

ID Number	Holotype ZMB 36372	DC-SOC <i>Discovery</i> 50510	BMNH 20030369	USNM 730896	NMSZ 1999.4128	Walther Herwig 836/74 (USNM)	BMNH 20030368
Sex	Female	Female	Female	Female	Female	Female	Male
Longitude	35°46'N	51°05'N	49°36'N	36°14'N	56°41'N	57°23'N	49°36'N
Latitude	8°16'W	13°04'W	12°37'W	74°30'W	09°47'W	11°29'W	12°37'W
Depth	2055	1924–1945	1857–1910	1550–1640	1775–1835	1900–1850	1857–1910
Total length	165	340	355	400	240	260	195
Mantle length	46	110	115	110	54	70	64
Head width	45	100	110	93	41	62	55
Fin span	134	215	240	230	130	185	150
Fin length	47	80	75	93	48	78	55
Fin width	19	32	36	40	18	31	21
Funnel length	17	28	34	33	27	22	24
Eye diameter	12	31	31	34	18	26	20
Arm I length	120	230	240	270	–	210	145
Sucker count	70	66	62	64	–	60	–
Arm formula	I.II.III.IV	I = II.III.IV	I = II.III.IV	I = II.III.IV	Damaged	I.II.III.IV	I = II.III.IV
Web formula	A.B.C = D.E	A.B.C.D.E	A.B.C.D.E	A.B.C.D.E	Damaged	A.B.C.D.E	A.B.C.D.E
MSD	2.0	3.5	4.0	5.5	2.8	4.1	2.2
MCL	2.9	5.0	6.5	4.6	Damaged	5.0	5.5
Location of MS	8–25	10th	10th	10th	Damaged	10th	10th
Cirri start	5th or 6th	6th or 7th	5th	6th	6th	5th or 6th	5th or 6th
Nodule locations: sucker no. on each arm	25–28	30,26,23,23	26,24,22,20	25,23,?,?	Damaged	Damaged	26,24,23,22
Gill lamellae	7	6/7	6/7	7/7	6/6	7/7	6/6
Gill diameter	7.7	14.0	16.0	17.5	11.0	12.5	9.0
Egg length (ovary)	–	12.0	12.2	13.0	–	–	–
Egg length (oviduct)	–	–	14.0 without shell	–	–	–	–

**Table 4.** *Grimpot euthis wuelkeri*. Indices of body proportions of examined specimens

	Male ( <i>n</i> = 1)	Female ( <i>n</i> = 5)		Combined ( <i>n</i> = 6)	
		Mean (SD)	Range	Mean (SD)	Range
ML	64	90.2 (30.7)	46–115	85.8 (29.4)	46–115
MLI	32.8	29.4 (2.7)	26.9–32.4	30 (2.8)	26.9–32.8
HWI	28.2	27.0 (3.4)	23.3–31	27.2 (3.1)	23.3–31
FSI	76.9	68.1 (8.9)	57.5–81.2	69.6 (8.7)	57.5–81.2
ALI	74.4	71.5 (5.6)	67.5–80.8	72.0 (5.1)	67.5–80.8
EDI	36.4	33.6 (6.7)	26.7–43.5	34.0 (6.1)	26.7–43.5
FuLI	43.6	33.5 (4.0)	28–37.8	35.2 (5.44)	28–43.6
FLI	100	96.0 (22.97)	68.2–127.4	96.6 (20.6)	68.2–127.4
SDI	4	4.9 (1.5)	3.5–6.6	4.77 (1.4)	3.5–6.6
CLI	10	6.1 (1.3)	5.0–8.1	6.73 (2.0)	5.0–10.0
GDI	16.4	17.2 (3.0)	14–21	17.1 (2.7)	14.0–21.0



**Figure 3.** Photographs of *Grimptoteuthis wuelkeri* (A), *G. boylei* sp. nov. (B), *G. challengerii* sp. nov. (C) and *G. discoveryi* sp. nov. (D). Scale bars = 100 mm (A–C); 40 mm (D).

*Stauroteuthis umbellata* (Ebersbach, 1915: text fig. 1)

*Grimptoteuthis wülkeri* (Robson, 1932: 152)

*Grimptoteuthis wuelkeri nomen dubium* (Voss, 1988a: 296)

*Grimptoteuthis wülkeri* (Sweeney & Roper, 1998: 577)

*Enigmatiteuthis wülkeri* (O'Shea, 1999: 50)

*Grimptoteuthis* sp. A. (Collins *et al.*, 2001)

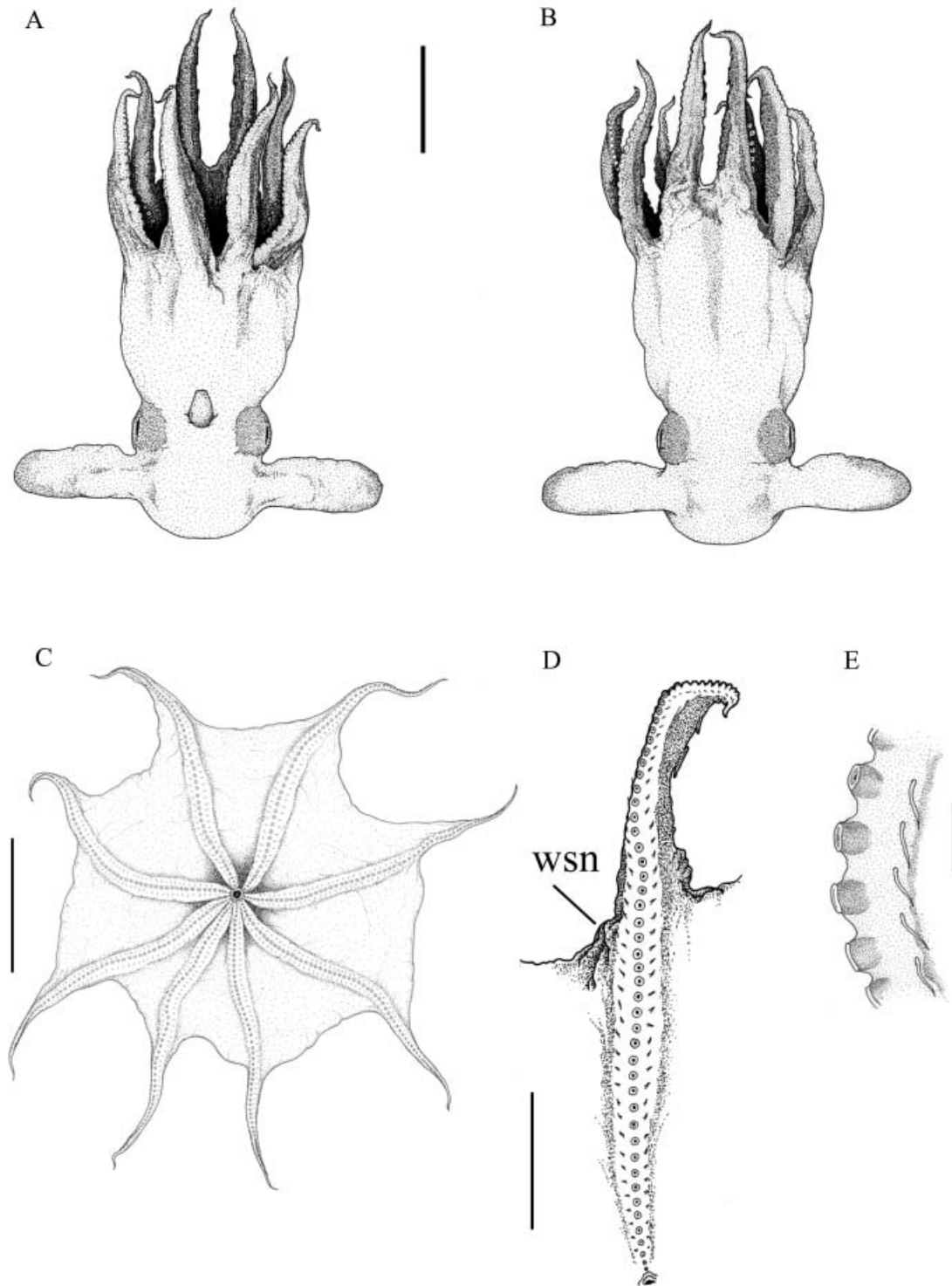
*Material examined*

HOLOTYPE: ZUB 36372; immature female 46 mm ML; 35°46'N, 8°16'W; 2056 m; 8 May 1910; RV *Michael Sars* Station 25.

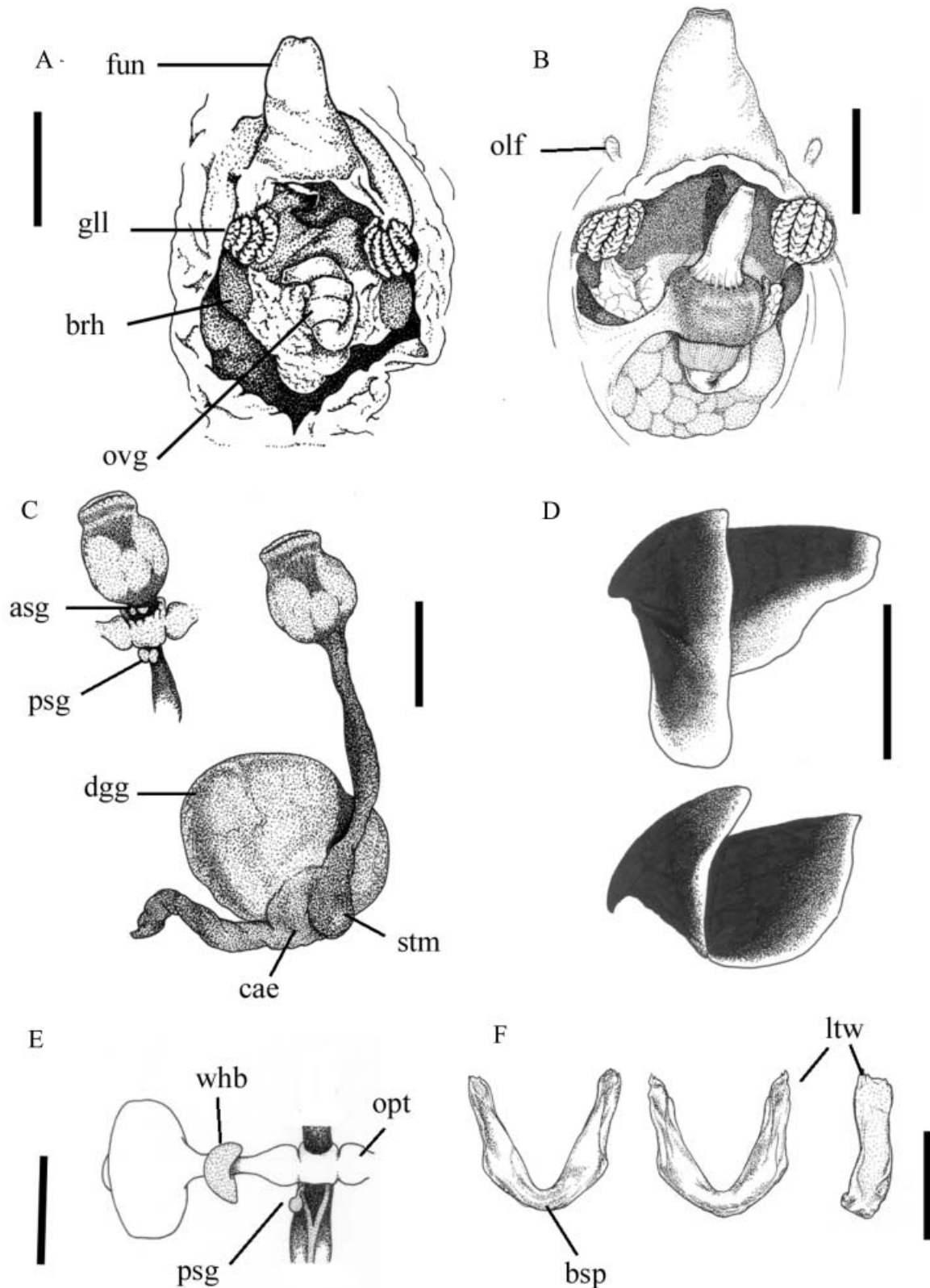
*Other material examined*

BMNH 20030368; 1 mature male; 49°36'N, 12°27'W; 1857–1910 m; OTSB; 30 May 1980; RRS *Discovery* 50802. BMNH 20030369; 1 mature female; 49°36'N, 12°27'W; 1857–1910 m; OTSB; 30 May 1980; RRS *Discovery* 50802. DC-SOC 50510; 1 mature female; 51°05'N, 13°04'W; 1924–45 m; OTSB; 3 June 1979; RRS *Discovery* 50510. USNM 730896; 1 female; 36°14'N, 74°30'W; 1550–1640 m; Trawl; 11 November 1974; RV *Gillis*. USNM; 1 female; 57°23'N, 11°29'W; 1850–1900 m; Trawl; 16 November 1974; *Walther Herwig* 836/74. NMSZ 1999.4128; 1 female; 56°41'N,

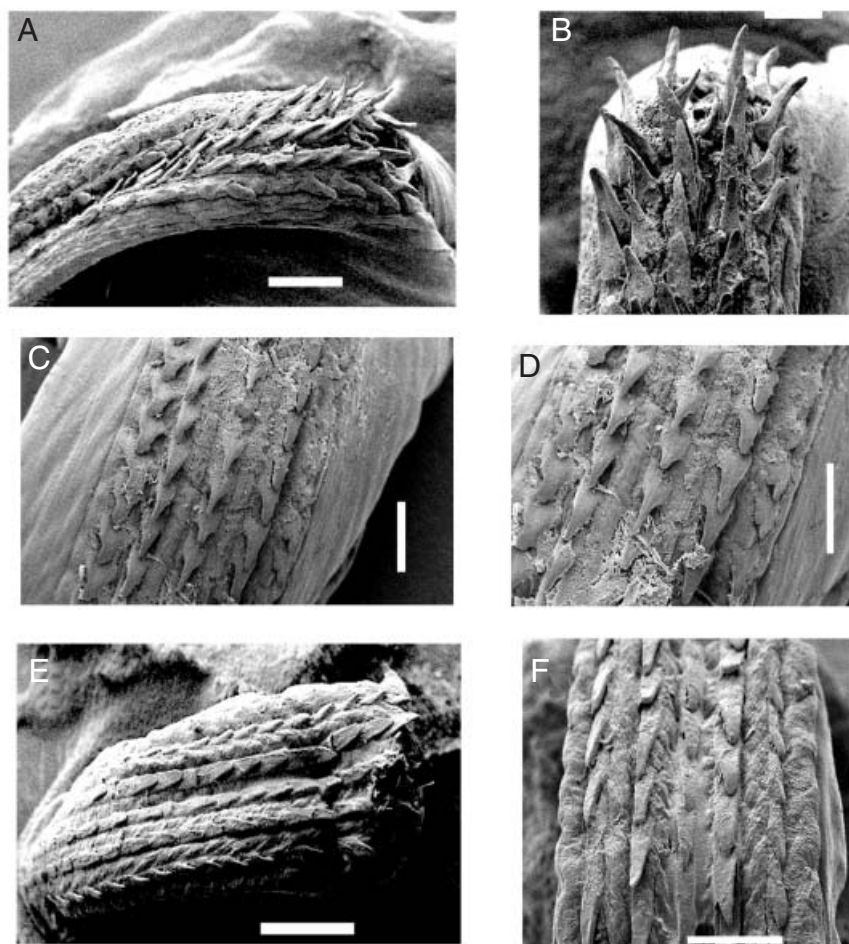




**Figure 4.** *Grimptoteuthis wuelkeri*: external anatomy. Ventral (A), dorsal (B) views of the holotype (ZUB 36372); oral view, orientated with dorsal arms up (C: BMNH???? (BMNH 20030369)); oral surface of first arm (D: holotype ZUB 36372), with detail of suckers and cirri (E: BMNH 20030369). Scale bars = 50 mm (A–C); 25 mm (D) and 5 mm (E).



**Figure 5.** *Grimptoteuthis wuelkeri*: internal anatomy. Ventral view of viscera of the holotype (A: ZUB 36372) and mature female (B: BMNH 20030369); digestive system (C); lower and upper beaks (D) optic nerve, white body and posterior salivary glands (E: all BMNH 20030369); dorsal ventral and lateral views of the shell of the holotype (F: ZUB 36372). Scale bars = 25 mm (A,B,F); 10 mm (C–E).



**Figure 6.** Scanning electron micrographs of the radulae of *Grimptoteuthis wuelkeri* (A,B), *G. boylei* sp. nov. (C,D) and *G. challengerii* sp. nov. (E,F).

09°47'W; 1775–1835 m; OTSB; 21 September 1993; RRS *Challenger*.

#### Diagnosis

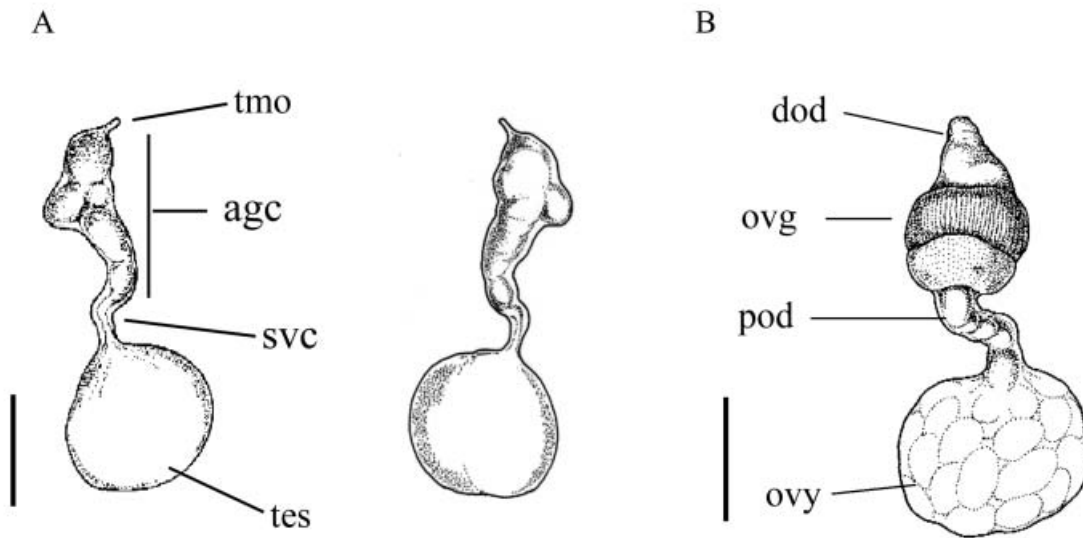
Large species. Cirri short; 60–70 suckers deeply embedded in each of the arms, with suckers of MSD present over broad range of arms. Radula present, all teeth homodont; posterior salivary glands small. Shell robust, with thickened basal portion and fin attachment area strengthened; lateral wings terminate in two lobes, one of which extends to a fine point. Gills large, with 6–7 broad lamellae.

#### Description

Large species, body semigelatinous, bell-shaped (Figs 3A, 4A,B). Eyes and fins lateral. Mantle length 30% TL, and broadly rounded posteriorly. Head slightly wider than mantle, with no discernible con-

striction between head and mantle. Eyes of moderate size (EDI 34). Pallial aperture small, closely surrounds funnel. Funnel moderately long (FuLI 35). Funnel organ V-shaped. Olfactory organs rounded, prominent; located just within mantle aperture, on either side of funnel. Fins large (mean FSI 69.6; mean FLI 96.6), positioned laterally with narrow muscular base, muscular area extending two-thirds of the fin length, tips rounded with slight point, anterior margin convex with distinct lobe.

Arms long (mean ALI 72.0), moderately stout, subequal in length, with arm formulae typically I.II.III.IV (Fig. 4C). Arms enveloped in single web, extending distally approximately 2/3 of arm length. Web extends distally further on the dorsal arms; formula A.B.C.D.E. Single web-supporting nodule present on the ventral side of each arm, usually located at level of sucker 28 on arm I, 26 on arm II, 24 on arm III and 22 on arm IV. Single row of suckers extends from mouth to arm tip (Fig. 4D). Suckers of moderate size (mean



**Figure 7.** *Grimpoteuthis wuelkeri*: internal anatomy. Dorsal and ventral view of the male reproductive system (A: BMNH 20030368); ventral view of female reproductive system (B: DC-SOC: *Discovery* 50510). Scale bars = 15 mm (A); 25 mm (B).

SDI 4.8), deeply set in semigelatinous tissue of all arms (Fig. 4E). Sucker count similar on all arms, range of 60–70. Suckers increase in size from mouth to 8th, then remain of similar size to approximately sucker 25, then decrease to arm tips. Cirri short (mean CLI 6.1 in females; 10.0 in single male), first appear between suckers 5 and 6 on most arms (occasionally between 4 and 5 or 6 and 7). Cirri extend to tips of arms; are longest on mid-portion of 1st arm.

Gills of half-orange (spherical) form (Fig. 5A,B), with 6–7 broad lamellae (6/6 in two specimens; 6/7 in two and 7/7 in three). Optic lobes slightly larger than semicircular brain, spherical, connected to the eye by single nerve bundle that passes through white body (Fig. 5E), which is a pink/grey colour in preserved specimens.

Entire outer surface of digestive tract deeply pigmented (Fig. 5C). Upper beak without special ridges, grooves or thickenings. Lower beak with rounded hood, raised above crest; broad wings with distinct ridge running diagonally across; lateral walls without ridge or fold (Fig. 5D). Radula (Fig. 6A,B) poorly developed with all teeth homodont. Anterior salivary glands small, attached to the base of the buccal mass, posterior salivary glands small, located posterior to brain and on the ventral surface of the oesophagus. Oesophagus twice length of intestine; crop absent. Caecum with single turn, connected to single-lobed digestive gland by two digestive gland ducts.

Fin-supporting cartilage (shell) robust, thickened U-shape, lateral wings with parallel outer edges

(Fig. 5F). Basal portion with outer and inner surfaces convex and with distinct ridge on the outer surface (not visible in illustration). Lateral wings terminate in two lobes, one of which has a small point.

Male reproductive tract (Fig. 7A) composed of large, oval testis located in median dorsal portion of mantle; vas deferens short; seminal vesicle complex large, convoluted; accessory gland complex consisting of three glands, with the distal gland largest and with a short-terminal organ (penis) projecting from it.

Female reproductive tract (Fig. 7B) simple, unpaired. Oviducal gland in two parts; proximal part cream in colour; distal section green/brown. Large eggs (12–13 mm in length) were found in the ovary of three specimens. Egg from oviducal gland of one specimen (BMNH 20030369) 14.0 mm in longest dimension.

Skin surface smooth, unpigmented on the oral and aboral surface in specimens preserved in Steadman's solution, except for the posterior margin of fins, which are purple.

#### *Type locality*

Off the coast of Morocco (35°46'N; 8°16'W), 2056 m.

#### *Distribution*

Known from depths of 1550–2056 m in the North Atlantic. One specimen from the north-west Atlantic, all others from north-east Atlantic.

*Etymology*

Named in honour of Gerhard Wülker.

*Remarks*

The type specimen was originally identified as *C. umbellata* by Chun (1913) and was the undissected specimen illustrated by Ebersbach (1915). Grimpe (1920) examined the *Michael Sars* material and designated the specimen as the holotype of his new species, *Stauroteuthis wülkeri*. The specimen from the north-west Atlantic (USNM 730896) was caught geographically and bathymetrically near to the type location of *G. plena* (Verrill, 1885). The type and only specimen of *G. plena* (see Tables 1, 12) is in poor condition and difficult to evaluate. Indices derived from Verrill's data and illustration indicate close similarity with the material described here, but fewer suckers were present on the *G. plena* specimen (55).

**GRIMPOTEUTHIS BOYLEI SP. NOV.**

(FIGS 3, 6, 8–10, 17; TABLES 5, 6, 11)

*Synonymy*

*Grimpoteuthis* sp. B (Collins *et al.*, 2001).

*Material examined*

HOLOTYPE: BMNH 20030370; 1 male 90 mm ML; 48°47'N, 16°30'W; OTSB; 4845–4847 m; 3 September 1989; RRS *Discovery* 11908#35.

PARATYPES: BMNH 20030371; 1 female 115 mm ML; 49°35'N, 14°01'W; OTSB; 4190–4255 m; 20 February 1982; RRS *Discovery* 51309. BMNH 20030372; 1 male 66 mm ML; 48°27'N, 15°40'W; OTSB; 4843–4840 m; 2 May 1999; RRS *Discovery* 54902#1. BMNH 20030373; male 65 mm ML; 48°53'N, 16°40'W; OTSB; 4848–4847 m; 10 July 1997; *Discovery* 13200#27. BMNH 20030374; male 63 mm ML; 48°53'N, 16°40'W; OTSB; 4848–4847 m; 10 July 1997; *Discovery* 13200#27. USNM 1013613; male 35 mm ML; 48°48'N, 16°16'W; OTSB; 4836–4839 m; 12 September 1996; *Discovery* 12930#64. DC-SOC; immature female 43 mm ML; 48°50'N, 16°29'W; OTSB; 4840 m; 18 March 1998; *Discovery* 13368#51.

*Other material examined*

*Discovery* 12600#23; 2 males, 1 female; 20°53'N, 31°14'W; OTSB; 4480–4565 m; 4 August 1993 (in BMNH Collections).

*Diagnosis*

Large species. Cirri long and suckers (52–58) large, cylindrical with MSD at web margin. Gills large with

7–8 broad lamellae. Radula present, teeth homodont; posterior salivary glands present. Fin-supporting cartilage (shell) U-shaped, smooth, with distinct depression in the posterior surface of the basal portion; outer edges of lateral walls parallel, with blunt termination.

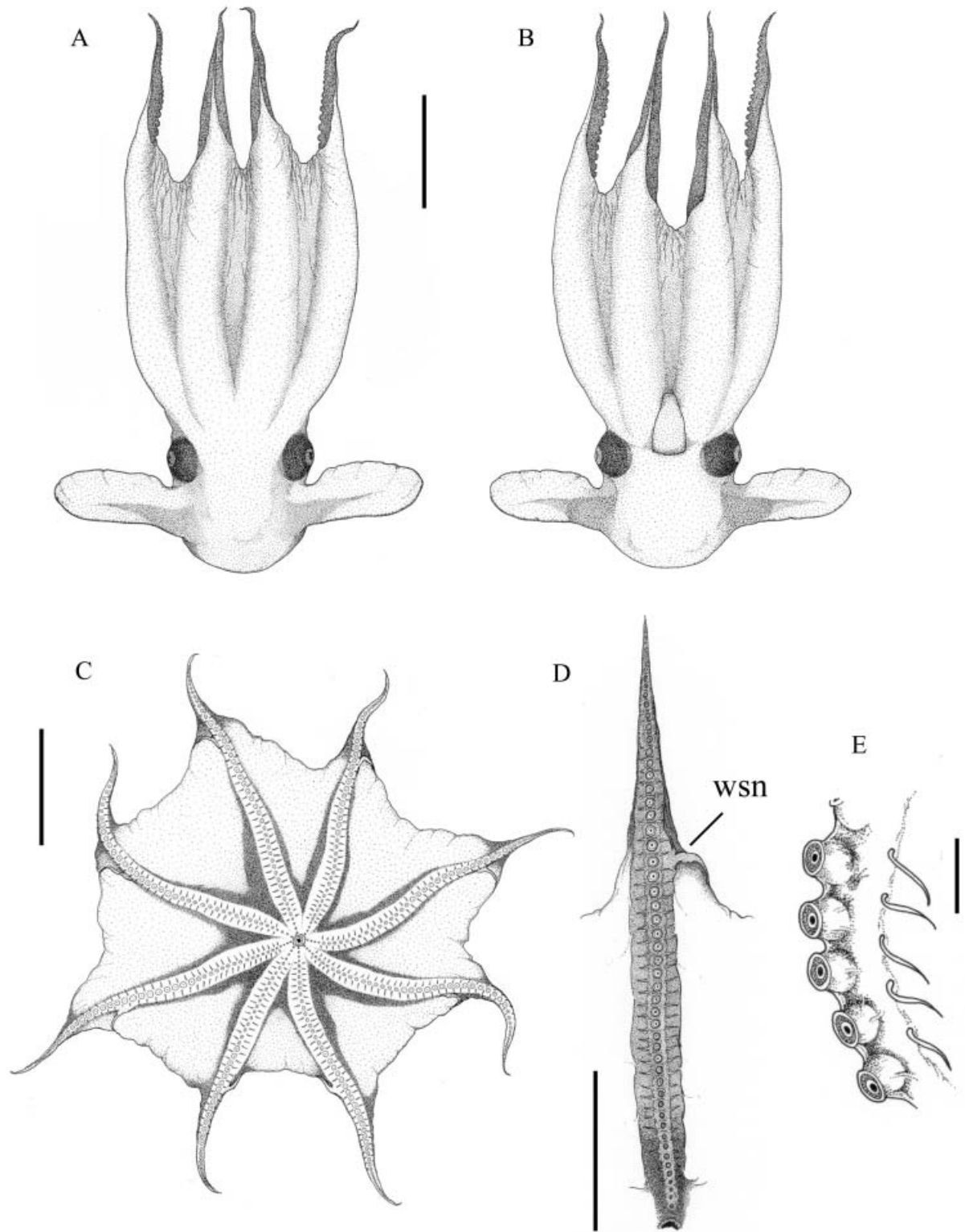
*Description*

Large species; body semigelatinous, bell-shaped (Figs 3B, 8A, B). Eyes and fins lateral. Mantle 20% TL, broadly rounded posteriorly. Head slightly wider than mantle, with no discernible constriction between head and mantle. Eyes of moderate size (mean EDI 33.9). Pallial aperture small, closely surrounds funnel. Funnel moderately long (mean FuLI 46.7). Funnel organ V-shaped. Olfactory organs (Fig. 9A) rounded, prominent, located just within mantle aperture on either side of funnel. Fins long (mean FSI 55.4; mean FLI 94.6), straight, tips rounded with slight point; anterior margin convex with distinct lobe. Fins with narrow muscular base, muscular area extending two-thirds of the fin length.

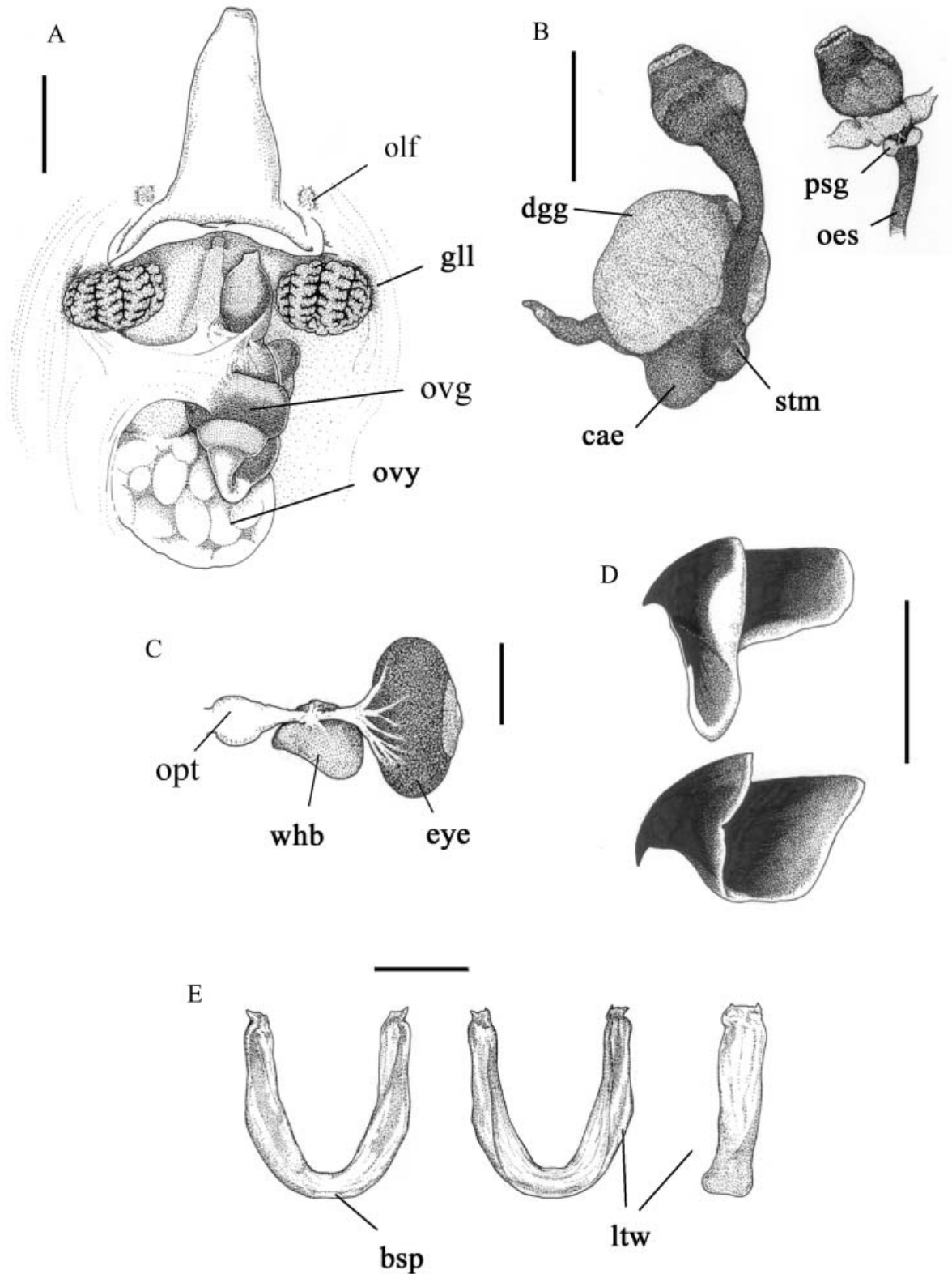
Arms long (mean ALI 75.5), moderately stout, subequal in length, arm formula typically I.II.III.IV. Arms enveloped in single web, extends distally 2/3 of arm length (Fig. 8C). Intermediate web absent. Web extends further on the dorsal arms; web formula typically A.B.C.D.E. Single web-supporting nodule prominent on the ventral side of each arm, usually located at the level of sucker 31 on arm I, 28 on arm II; 25 on arm III and 24 on arm IV. Single row of suckers extends from mouth to arm tip (Fig. 8D). Suckers broad (mean SDI 6.1), cylindrical with diameter greater than sucker height (Fig. 8E). Sucker count (52–58), approximately equal on all arms. Suckers increase in size from mouth to the web margin (MSD between suckers 25 and 35), then decline in size to arm tip. In some specimens there is a sharp decline in sucker diameter following sucker 35. Cirri long (mean CLI 12.2), first appear before the 5th, 6th or 7th sucker. Cirri extend to arm tips, longest on mid-portion of dorsal arms.

Gills large, of half-orange (spherical) form (Fig. 9A), with 7–8 broad lamellae (8/8 on six specimens; 8/7 on two and 7/7 on one). Optic lobes large, spherical, single bundle of optic nerves extend through the white body to each eye (Fig. 9C). White body, closely associated with eye, large, pale grey in preserved specimens.

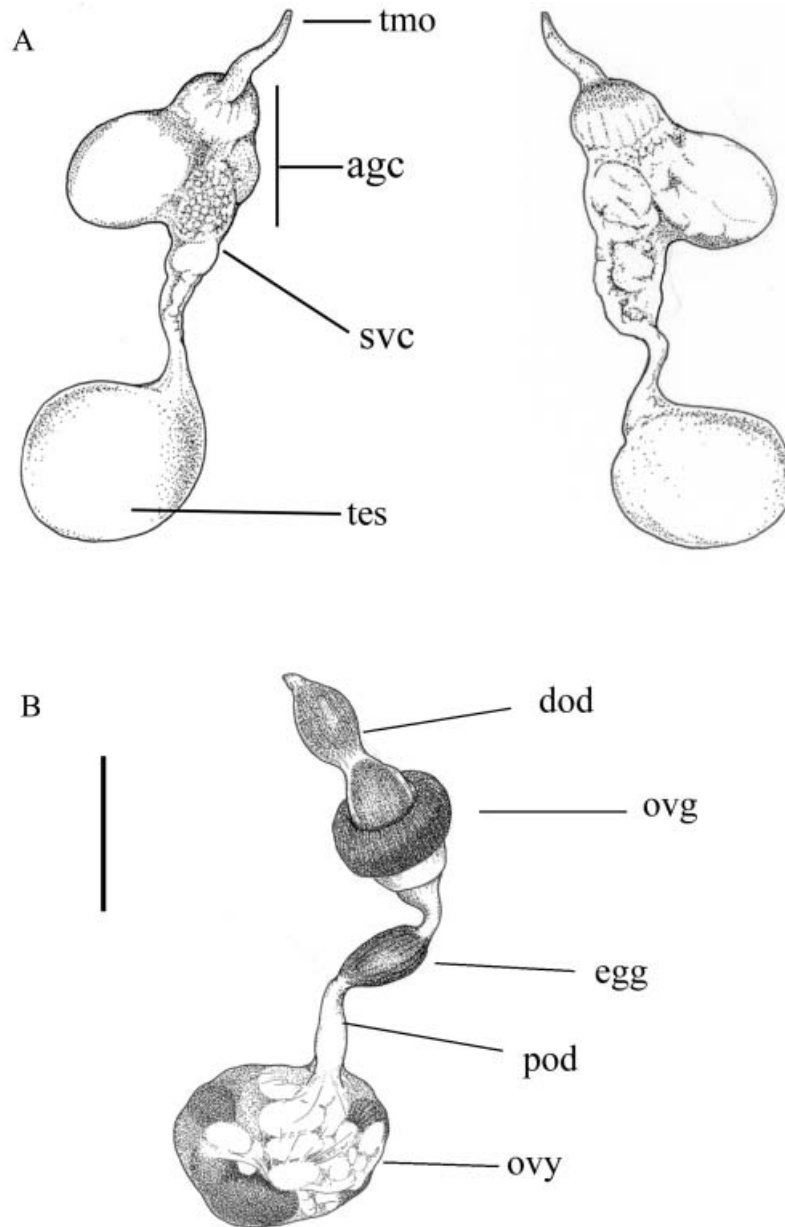
Entire outer surface of digestive tract deeply pigmented (Fig. 9B). Upper beak without special ridges or folds. Lower beak with rounded hood, raised above crest; broad wings with distinct flexure running diagonally across; lateral walls without ridge or fold (Fig. 9D). Radula poorly developed, all teeth homodont (Fig. 6C,D). Anterior salivary glands attached to the base of the buccal mass, posterior salivary glands small, connect into single duct, which passes through



**Figure 8.** *Grimpoteuthis boylei* sp. nov: external anatomy. Dorsal (A), ventral (B) and oral (C) views (all BMNH 20030371); oral view of first arm of male (D) with detail of suckers (E: both BMNH 20030370). Scale bars = 100 mm (A,B,C,D); 10 mm (E).



**Figure 9.** *Grimpoteuthis boylei* sp. nov.: internal anatomy. Ventral view of the viscera *in situ* (A: BMNH 20030371); the digestive system (B); optic nerve and white body (C); lower and upper beaks (D); dorsal, ventral and lateral view of shell (E: all BMNH 20030374). Scale bars = 20 mm (A,B,E); 10 mm (C,D).



**Figure 10.** *Grimpoteuthis boylei* sp. nov.: internal anatomy. Dorsal and ventral views of the male reproductive system (A: BMNH 20030373). Ventral view of the female reproductive system (B: BMNH 20030371). Scale bars = 15 mm (A); 30 mm (B).

the brain to the buccal mass. Oesophagus twice length of intestine; stomach small. Caecum with single turn, connected to single-lobed digestive gland by two digestive ducts. Intestine straight.

Fin supporting cartilage (shell) simple, broad, U-shape; smooth with distinct depression on the outer surface of the basal portion (Fig. 9E). Inner surface of basal portion convex. Lateral wings of shell with blunt termination.

Male reproductive tract (Fig. 10A) composed of large, oval testis located in the posterior median portion of mantle. Vas deferens short, seminal vesicle complex convoluted; accessory gland complex consisting of three glands. Terminal organ (penis) long, projecting from distal accessory gland.

Female reproductive tract (Fig. 10B) simple, unpaired. Oviducal gland large, in two parts, proximal third cream in colour, distal two-thirds green/



Table 5. *Grimpototeuthis boylei* sp. nov. Details of nine of the specimens

ID Number	Holotype BMNH 20030370	Paratype BMNH 20030373	Paratype BMNH 20030374	Paratype USNM 1013613	Paratype BMNH 20030372	Paratype DC-SOC 20030371	BMNH	BMNH
Station	Discovery 11908#35	Discovery 13200#27a	Discovery 13200#27b	Discovery 12930#64a	Discovery 54902#1a	Discovery 13368#51	Discovery 51309e	Discovery 12600#23
Sex	Male	Male	Male	Male	Male	Female	Female	Female-Imm
Date	3/9/89	10/7/97	10/7/97	12/9/96	2/5/99	18/3/98	20/2/82	4/8/93
Latitude	48°47'N	48°53'N	48°53'N	48°48'N	48°27'N	48°50'N	49°35'N	20°53'N
Longitude	16°30'W	16°40'W	16°40'W	16°16'W	15°40'W	16°29'W	14°01'W	31°14'W
Depth	4845–4847	4848–4839	4848–4839	4836–4839	4843–4840	4840	4190–4255	4480–4565
Total length	470	440	370	220	300	265	440	390
Mantle length	90	65	63	35	66	43	115	74
Head width	90	75	64	45	79	55	125	94
Fin span	230	205	180	120	200	155	270	200
Fin length	95	85	60	45	70	48	95	75
Fin width	42	23	17	17	28	13	45	27
Funnel length	48	47	38	18.5	40	26	51	36
Eye diameter	30	33	23	18	29	18	35	32
Arm I length	340	340	320	180	240	195	330	280
Arm formula	I.II.III.IV	I.I.III.IV	I.I.III.IV	I = II.III.IV	I = II.III.IV	I.I.III.IV	I.I.III.IV	I.I.III.IV
Web formula	A.B.C.D.E	A = B.C.D.E	A.B.C.D.E	A.B = C.D.E	Damaged	A = B.C.D.E	A.B = C.D.E	Damaged
Sucker count	55	56	56	58	55	58	55	Damaged
MSD	7.5	6.5	4.0	2.5	5.0	2.2	5.0	7.2
MCL	16	11	9.0	8.0	12	8.0	18	9.0
Location of MS	26–32	25–35	25–35	27–31	24–36	26–34	24–30	25–35
Cirri start	5th or 6th	5th or 6th	5th or 6th	5th	5th or 6th	6th or 7th	5th	7th
Nodule locations: sucker no. on each arm	29,25,23,23	31,28,26,26	30,26,24,24	30/27/24	? , 29, 26, 25	? , ? , 27	? , 27, 26, 24	Damaged
Gill lamellae	8/7	8/8	8/8	8/8	8/8	8/8	7/7	8/8
Gill diameter	13	14.0	10.0	6.5	12.0	9.0	17	14.5
Egg diameter	—	—	—	—	—	—	18	—

**Table 6.** *Grimpoteuthis boylei* sp. nov. Indices of body proportions of specimens examined

	Male ( <i>n</i> = 8)		Female ( <i>n</i> = 5)		Overall ( <i>n</i> = 13)	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
ML	54.8 (21.3)	28–90	56.6 (35.6)	25–115	55.4 (25.9)	25–115
MLI	19.6 (3.7)	15–26.9	21.8 (4.54)	16.2–26.3	20.4 (4.0)	15.0–26.9
HWI	22 (3.6)	17–26	22 (4)	18–28	21.9 (3.6)	17.0–28.4
FSI	55.2 (9.9)	43.2–69	55.8 (8.7)	42.9–61.4	55.4 (9.2)	42.9–69.0
ALI	77.4 (5.6)	71.8–86.5	71.1 (2.7)	68.2–73.6	75.5 (5.7)	68.2–86.5
EDI	36.2 (4.0)	30.6–44	29.8 (4.25)	25.7–35.5	33.9 (5.0)	25.7–44.0
FuLI	47.2 (9.3)	36.1–62.7	45.6 (4.8)	40.8–51.6	46.7 (8.0)	36.1–62.7
FLI	98.4 (12.9)	79.8–117	87.8 (16.4)	72.6–114	94.6 (14.6)	72.6–116.7
SDI	6.5 (1.6)	4–8.7	5.4 (2.2)	4–8.7	6.1 (1.8)	4.0–8.7
CLI	12.4 (5.2)	4.3–17.8	11.8 (4.6)	6.5–14.5	12.2 (4.8)	4.3–17.8
GDI	15.8 (1.7)	12.5–18.7	14.1 (2.2)	11.3–16.3	15.3 (2.0)	11.3–18.7

brown. Eggs large, capsules of mature ovarian eggs 18–20 mm in length (BMNH 20030371).

Skin surface smooth, deep red in fresh specimens, becoming reddish-brown with preservation. Pigmentation greatest on the oral and aboral surfaces of the arms and less on the mantle. Posterior margin of fin pigmented (purple).

#### *Type locality*

Porcupine Abyssal Plain, 48°47'N, 16°30'W, 4845–4847 m.

#### *Distribution*

Abyssal species, currently known from the type locality (Porcupine Abyssal Plain), from the Porcupine Seabight and the Madeira Abyssal Plain (Fig. 17). Probably distributed at abyssal depths from 20°N to 50°N in the north-east Atlantic.

#### *Remarks*

This species is similar to *G. challengerii* (see below), but can be distinguished by the shape of the shell, presence of posterior salivary glands, form of the gills, egg size and the number, form and arrangement of suckers. Stomach contents of single specimen (USNM 1013613) examined included remains of polychaetes (2–3 individuals), calanoid copepods, amphipods (*Rhachotropis* and *Octorama*) and isopods of the family Munnopsidae.

#### *Etymology*

Named in honour of Professor Peter Boyle in recognition of his contributions to cephalopod biology.

#### ***GRIMPOTEUTHIS CHALLENGERI* SP. NOV.**

(FIGS 3, 6, 11–13, 17; TABLES 7, 8, 11)

#### *Synonymy*

*Grimpoteuthis* sp. C. (Collins *et al.*, 2001).

#### *Material examined*

HOLOTYPE: BMNH 20030375; male 58 mm ML; 48°56'N, 15°45'W; OTSB; 4828–4838 m; 22 March 1998; RRS *Discovery* 13369#1.

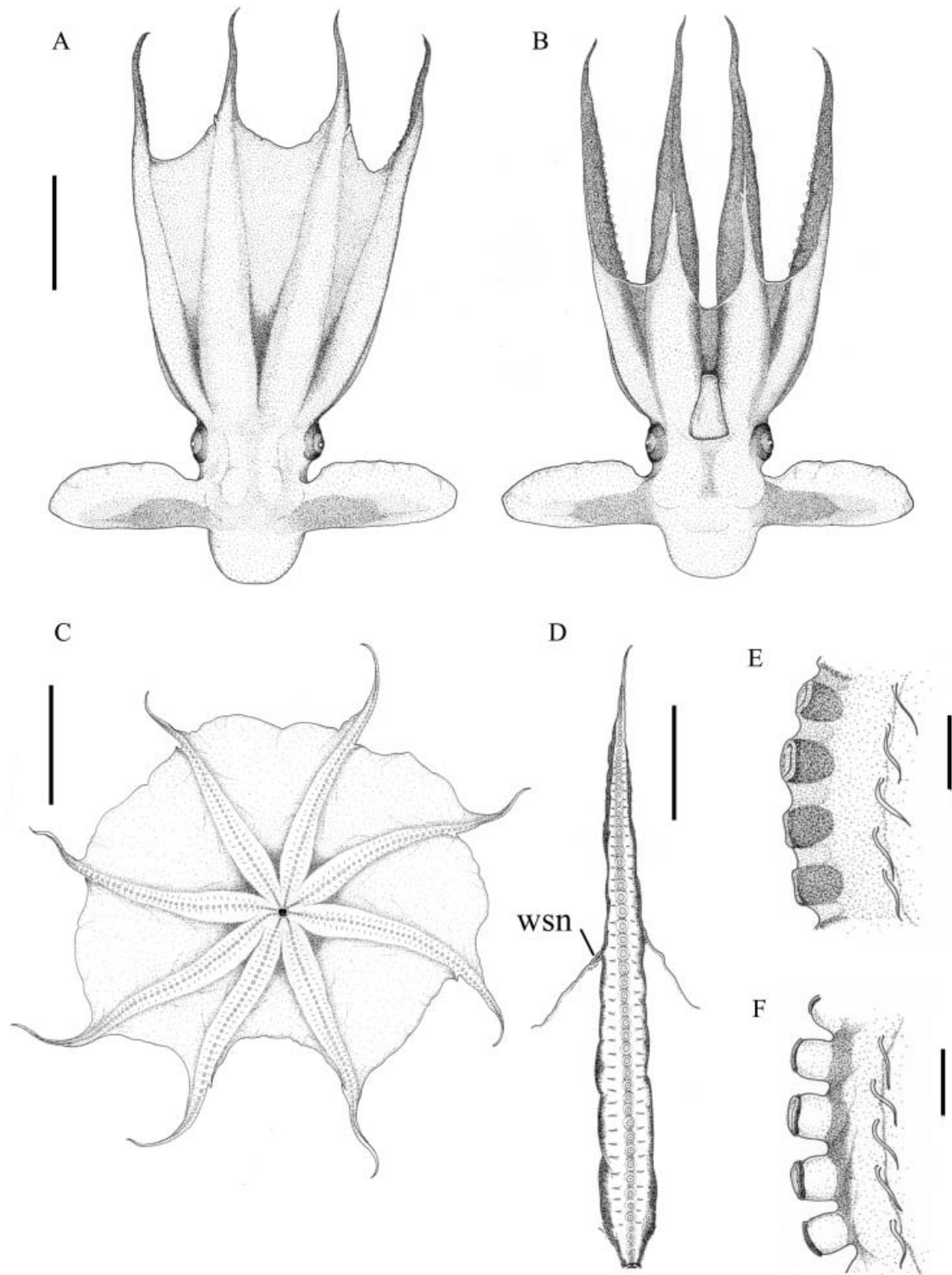
PARATYPES: USNM 1013614; male 75 mm ML; 48°47'N, 16°25'W; OTSB; 4853–4877 m; 12 September 1989; *Discovery* 11908#68. BMNH 20030376; male 55 mm ML; 48°27'N, 15°40'W; OTSB; 4843–4845 m; 2 May 1999; *Discovery* 54902#1. BMNH 20030377; female 70 mm ML; 48°48'N, 16°30'W; OTSB; 4843–4849 m; 5 September 1989; *Discovery* 11908#44. USNM 1013615; immature female 35 mm ML; 48°53'N, 16°31'W; OTSB; 4836–4840 m; 16 September 1996; *Discovery* 12930#77.

#### *Other material examined*

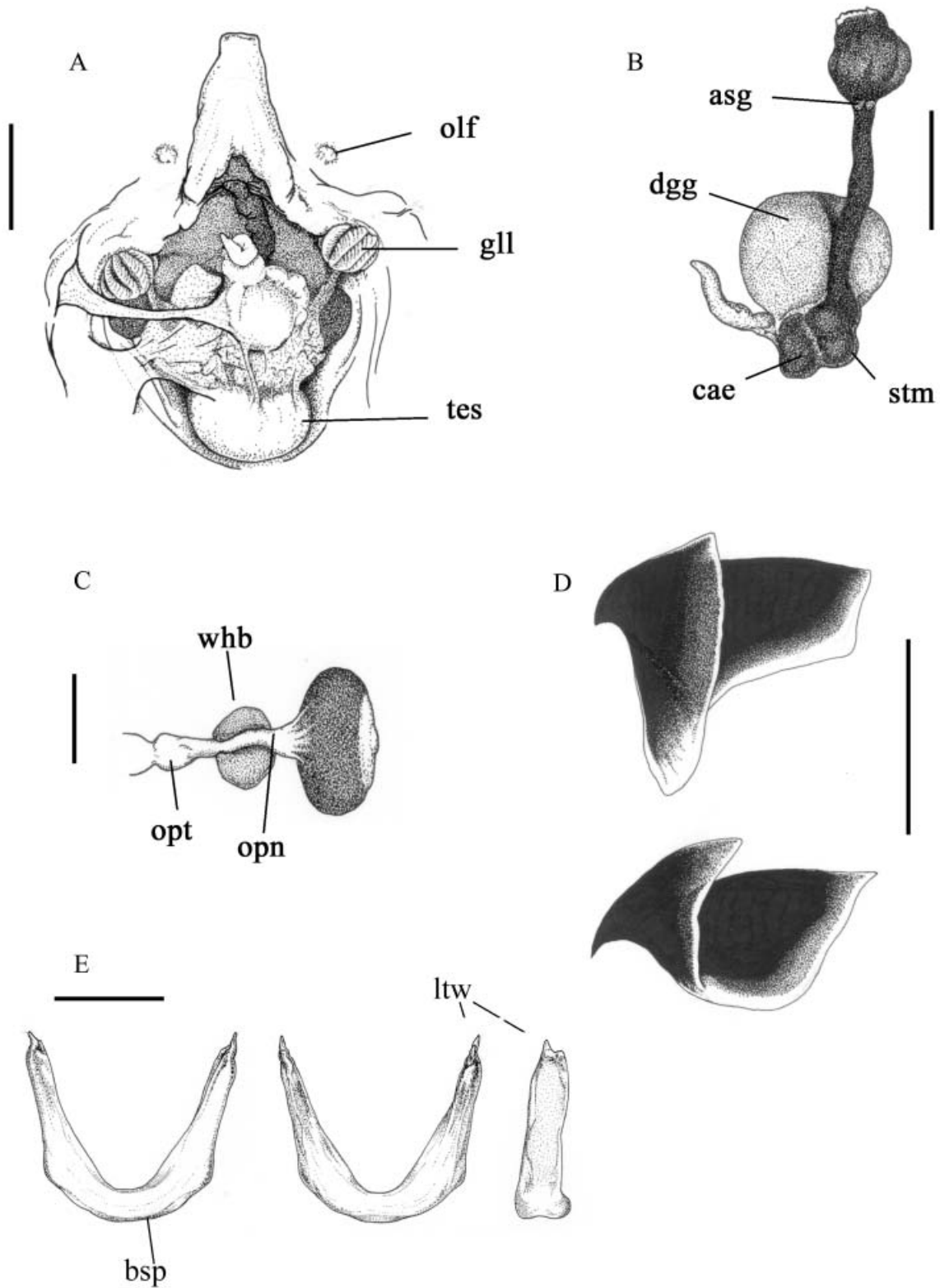
*Discovery* 13369#2; male; 48°55'N, 15°40'W; OTSB; 4832–4836 m; 23 March 1998 (DC-SOC). *Discovery* 54901#2; male; 48°42'N, 16°52'W; OTSB; 4811–4837 m; 26 April 1999 (DC-SOC). *Discovery* 12930#64; female; 48°48'N, 16°16'W; OTSB; 4836–4839 m; 12 September 1996 (DC-SOC). UMML31.2890; female; RV *Gillis* St. 144; no record of locality.

#### *Diagnosis*

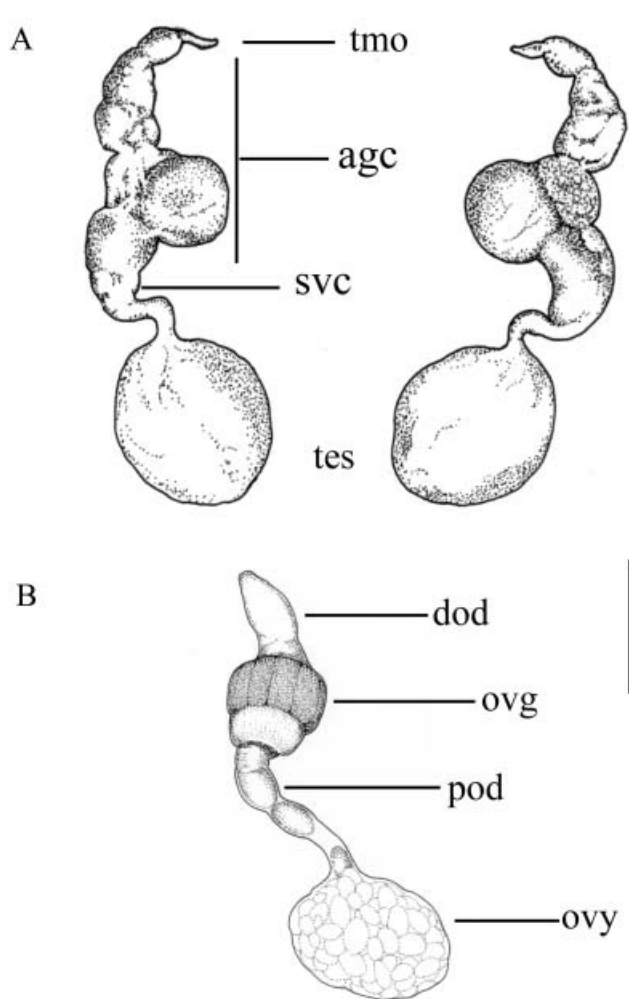
Large species. Cirri long and suckers (63–72) moderate with MSD at web margin. Gills with eight narrow lamellae. Fin-supporting cartilage (shell) robust



**Figure 11.** *Grimpoteuthis challengerii* sp. nov: external anatomy. Dorsal (A), ventral (B) and oral (C) views (all BMNH 20030375); oral view of first arm (D: BMNH 20030375), with detail of female (E: BMNH 20030377) and male suckers (F: BMNH 20030375). Scale bars = 50 mm (A,B,D); 100 mm (C); 5 mm (E,F).



**Figure 12.** *Grimpoteuthis challengeri* sp. nov.: internal anatomy. Ventral view of the viscera *in situ* (A); detail of the digestive system (B); optic nerve and white body (C) lower and upper beaks (D); dorsal, ventral and lateral view of shell (E: all BMNH 20030376). Scale bars = 15 mm (A); 20 mm (B,E); 10 mm (C,D).



**Figure 13.** *Grimpoteuthis challengerii* sp. nov.: internal anatomy. Dorsal and ventral views of the male reproductive system (BMNH 20030376) (A). Ventral view of the female reproductive system (BMNH 20030377) (B). Scale bars = 10 mm.

U-shape; lateral wings well developed, each terminating in two lobes. Radula present; posterior salivary glands absent.

#### Description

Large species; body semigelatinous, bell-shaped (Figs 3C, 11A,B). Mantle 22% TL, and broadly rounded posteriorly. Head slightly wider than mantle, no discernible constriction between head and mantle. Eyes of moderate size (mean EDI 32.7). Pallial aperture small, closely surrounding funnel. Funnel, moderately long (mean FuLI 50.7). Funnel organ V-shaped. Olfactory organs rounded, prominent, located just within mantle aperture on either side of funnel. Fins very long (mean FSI 59.0; mean FLI 113.8), tips rounded with slight point, anterior margin convex

with distinct lobe. Fins with narrow muscular base, muscular area extending two-thirds of the fin length.

Arms long (mean ALI 74.3), moderately stout, subequal in length, with arm formulae typically I.II.III.IV. Web single, occupying approximately 2/3 of arm length (Fig. 11C). Intermediate (secondary) web absent. Web extends further on dorsal arms, and generally of the formula A.B.C.D.E. Single web-supporting nodule on the ventral side of each arm, typically located at level of sucker 34 on arm I, 30 on arm II; 28 on arm III and 27 on arm IV (Fig. 11C,D). Suckers in single row, count similar on all arms (range 63–72), extend from mouth to arm tip. Suckers cylindrical (Fig. 11E,F) with sucker diameter similar to sucker height (mean SDI 4.6), increase in size from mouth to the web margin (MSD between suckers 30 and 38), then decline in size to the arm tip. MSD similar in

Table 7. *Grimpot euthis challengeri* sp. nov. Details of specimens examined

ID Number	Holotype BMNH 20030375	Paratype USNM 1013614	Paratype BMNH 20030376	DC-SOC	Paratype BMNH 20030377	USNM 1013615	DC-SOC	DC-SOC
Station	Discovery 13369#1	Discovery 11908#68	Discovery 54902#1	Discovery 13369#2	Discovery 11908#44	Discovery 12930#77	Discovery 12930#64	Discovery 13078#31
Sex	Male	Male	Male	Male	Female	Female	Female	Female
Date	22/3/98	12/9/89	2/5/99	23/3/98	5/9/89	16/9/96	12/9/96	5/4/97
Longitude	48°56'N	48°47'N	48°27'N	48°55'N	48°47'N	48°53'N	48°48'N	48°53'N
Latitude	15°45'W	16°25'W	15°40'W	15°40'W	16°0'W	16°31'W	16°16'W	16°22'W
Depth	4828–4838	4853–4877	4843–4845	4828–4836	4843–4849	4836–4840	4836–4839	4850–4844
Total length	295	370	290	245	285	150	170	150
Mantle length	58	75	55	55	70	35	40	42
Head width	66	80	58	63	59	27	35	34
Fin span	160	195	160	150	170	105	115	95
Fin length	62	80	58	51	68	41	45	42
Fin width	27	32	17	23	32	18	17	16
Funnel length	34	35	27	27	25	16	15	19
Eye diameter	22	27	17	19	18	10	11	11
Arm I length	225	275	205	180	200	110	135	110
Arm formula	I.II.III.IV	I.II.III.IV	I.II.III.IV	I.II.IV.III	I.II.III.IV	I.II.III.IV	I.II.III.IV	I.II.III = IV
Web formula	A.B.C = D.E	A.B.C.D.E	Damaged	A.B.C.D.E	A.B.C.D.E	A.B.C.D = E	A.B.C.D.E	A.B.C.D.E
Sucker count	71	72	Damaged	71	72	67	–	63
MSD	2.9	3.3	3.0	2.3	2.4	1.3	1.2	1.3
MCL	7.2	8.0	–	7.0	8.0	4.5	6.5	4.0
Location of MSD	30–37	30–38	–	30–38	24–36	26–	28–34	28–35
Cirri start	5th	5th	5th or 6th	5th or 6th	7th	5th or 6th	6th or 7th	5th or 6th
Nodule locations: sucker no. on each arm	32,29,27,27	? , 31, 27, 25	–	34, 30	33, 30, 28, 26	34, 31, 28, 26	33, ?, 28, 27	34, 32, 27, 28
Gill lamellae	8	8	8	8	8	8	8	8
Gill diameter	9.0	10	7.5	7.5	7.5	4.7	5.0	5.5
Egg diameter	–	–	–	–	13.0	–	–	–

**Table 8.** *Grimpot euthis challenger* sp. nov. Indices of body proportions of specimens examined

	Male ( <i>n</i> = 5)		Female ( <i>n</i> = 5)		Combined ( <i>n</i> = 10)	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
ML	62.6 (9.3)	55–75	46.6 (13.9)	35–70	54.6 (14.0)	35.0–75.0
MLI	20.2 (1.4)	19–22.4	24.2 (1.5)	23.3–26.7	22.2 (2.5)	19.0–26.7
HWI	21 (3.6)	16–26	19.9 (2.1)	17.6–22.7	20.4 (2.8)	15.9–25.7
FSI	53.5 (5.5)	46.4–61.2	64.5 (4.2)	59.6–70	59.0 (7.4)	42.4–70.3
ALI	73 (2.5)	70.7–76.3	75.4 (4.6)	70.2–81.0	74.3 (3.8)	70.2–81.0
EDI	32.2 (2.4)	29.3–34.8	33.3 (2.7)	30.5–37	32.7 (2.5)	29.3–37.0
FuLI	46.5 (3.2)	42.9–51.5	54.9 (12.3)	42.4–70.2	50.7 (9.5)	42.4–63.0
FLI	100 (15)	81–124	131 (17)	115–156	113.8 (22.1)	81.0–155.6
SDI	4.8 (1.1)	3.7–6.6	4.3 (0.9)	3.4–5.7	4.6 (1.0)	3.4–6.5
CLI	12 (2.7)	10–16	15.0 (2.7)	11.8–18.6	13.7 (3.0)	10.0–18.6
GDI	13.6 (1.2)	12.5–15.5	15.7 (2.8)	12.5–18.5	15.1 (2.7)	12.5–19.7

males and females; but suckers deeply embedded in arms in females (Fig. 11E,F). Cirri long (mean CLI 13.7), first appear before the 5th, 6th or 7th sucker. Cirri extend to the tips of the arms, longest on mid-portion of dorsal arms.

Gills moderate, of half-orange (spherical) form (Fig. 12A), normally with eight narrow lamellae (8/8 on eight specimens; 8/7 on one). Optic lobes large, spherical, with a single bundle of optic nerves running through white body to each eye (Fig. 12C). White body, closely associated with eye, large, pale grey in preserved specimens.

Outer surface of oesophagus and stomach deeply pigmented (Fig. 12B). Upper beak without well defined ridges or grooves. Lower beak with rounded hood, distinctly raised above crest; broad wings with distinct flexure running diagonally across; lateral walls without ridge or fold (Fig. 12D). Radula present (Fig. 6E,F), poorly developed, all teeth homodont. Anterior salivary glands small, attached to the base of the buccal mass; posterior salivary glands absent. Oesophagus twice the length of intestine. Stomach small, simple, appears as a swelling of the oesophagus. Caecum with single turn, connected to single-lobed digestive gland by two digestive ducts.

Fin supporting cartilage (shell) robust, thickened U-shape, with the outer walls of the lateral wings parallel. Inner surface of the basal portion convex; outer surface concave. Lateral wings each terminate in two lobes (Fig. 12E).

Male reproductive tract (Fig. 13A) composed of large, oval testis located in the posterior median portion of the mantle. Vas deferens short, seminal vesicle complex convoluted. Accessory organ complex consists of three glands, with proximal gland the largest. A long-terminal organ (penis) projects from the distal accessory gland.

Female reproductive tract (Fig. 13B) simple, unpaired. Oviducal gland in two parts, proximal third cream in colour, distal two-thirds green/brown. Eggs of moderate size, 13 mm in length in oviduct of specimen BMNH 20030377.

Skin surface smooth, reddish-brown following preservation. Pigmentation greatest on the oral and aboral surfaces of the arms and less on the mantle. Posterior margin of fins pigmented (purple).

#### *Type locality*

Porcupine Abyssal Plain, 48°56'N, 15°45'W; 4828–4838 m.

#### *Distribution*

Abyssal species, known from the type locality, caught at depths of 4800–4850 m (Fig. 17). The capture location for the single specimen in the UMML collection is not known, but is from the north-west Atlantic.

#### *Remarks*

This species is similar to *Grimpot euthis tuftsi*, which Voss & Pearcy (1990) described from abyssal depths in the North Pacific, but can easily be distinguished from the other north-east Atlantic species by the narrow lamellae of the gills.

#### *Etymology*

Named after RRS *Challenger*, which, together with RRS *Discovery*, was the vessel responsible for catching many of the specimens reported in the present study.

**GRIMPOTEUTHIS DISCOVERYI SP. NOV.**

(FIGS 3, 14–17; TABLES 9–11)

*Synonymy*

*Grimpoteuthis* spp. D & E (Collins *et al.*, 2001)  
*Cirroteuthis umbellata* (Chun, 1913: 16, in part)  
*Cirroteuthis umbellata* (Joubin, 1920: 13)  
*Grimpoteuthis* s.sp. D (Piertney *et al.*, 2003)

*Material examined*

HOLOTYPE: BMNH 20030378; male 50 mm ML; 49°35'N, 14°01'W; 4190–4255 m; OTSB; 20 February 1982; *Discovery* 51309.

PARATYPES: BMNH 20030379; male 45 mm ML; 49°35'N, 14°01'W; 4190–4255 m; OTSB; 20 February 1982; *Discovery* 51309. USNM 1012988; male 42 mm ML; 49°35'N, 14°01'W; 4190–4255 m; OTSB; 20 February 1982; *Discovery* 51309. USNM 1012989; female 35 mm ML; 49°35'N, 14°01'W; 4190–4255 m; OTSB; 20 February 1982; *Discovery* 51309. BMNH 20030380; female 55 mm ML; 50°00'N, 14°07'W; 4180–4310 m; OTSB; 30 March 82; *Discovery* 51414. BMNH 20030381; female 51 mm ML; 50°00'N, 14°07'W; OTSB; 4180–4310 m; 30 March 82; *Discovery* 51414. UMML 31.3166; 1 male 36 mm ML; 1 female 46 mm ML; 50°03'N, 13°51'W; 3749–3757 m; OTSB; 12 June 1977; *Discovery* 9640#1.

*Other material examined*

ZUB 36379; 1 male, 1 female; 34°59'N; 33°01'W; 2615 m; *Michael Sars* 53; 8 June 1910. MOM 295091; female; 39°54'N, 20°27'W; 4360 m; Trawl; 18 August 1896; *Princesse Alice* 753. MOM 295245; male; 44°08'N, 10°44'W; 5000 m; Trawl; 19 August 1910; *Princesse Alice* 2994. MOM 295344; male; 45°07'N, 7°06'W; 4870 m; Trawl; 17 August 1910; *Princesse Alice* 2986. NMSZ 1994128.45603; male; 54°42'N, 12°16'W; 2875–2900 m; OTSB; 21 October 1987; *Challenger* 20/87/3. NMSZ 1999158.158; female; 49°50'N, 14°18'W; 4143 m; OTSB; 9 August 1997; *Challenger* 134/6. NMSZ 1999158.160; female; 49°50'N, 14°18'W; 4143 m; OTSB; 9 August 1997; *Challenger* 134/6. NMSZ 1999158.159; male; 49°58'N, 14°29'W; 4139 m; OTSB; 17 August 1997; *Challenger* 134/24. NMSZ 1999158.161; male; 49°58'N, 14°29'W; 4139 m; OTSB; 17 August 1997; *Challenger* 134/24. *Discovery* 9756#3; 1 male, 1 female, 49°48'N, 14°15'W; 4080–4156 m; OTSB; 11 April 1978. *Discovery* 9756#5; female; 49°49'N, 14°05'W; 4012–4020 m; OTSB; 12 May 1978. *Discovery* 51012; 1 male, 2 females; 49°51'N, 13°58'W; 3880–3920 m; OTSB; 5 May 1981. *Discovery* 50512; female; 50°14'N, 13°42'W; 3022–3110 m; OTSB; 4 June 1979. *Discovery* 50811; 2 males; 49°39'N, 14°32'W; 4400–4350 m; OTSB; 2 August 1980. *Discov-*

*ery* 50910; male; 49°50'N, 14°40'W; 4265–4320 m; OTSB; 10 November 1980. *Discovery* 51216#4; 1 male, 1 female; 49°49'N, 14°07'W; 4000–3970; OTSB; 29 September 1981. *Discovery* 51803; female; 49°37'N, 13°49'W; 3990–3920 m; OTSB; 29 September 1983. *Discovery* 9638#2; 1 female, 1 male; 49°50'N, 14°07'W; 4043–4104; OTSB; 8 June 1977. *Discovery* 9640#1; male; 50°03'N, 13°51'W; 3749–3757 m; OTSB; 12 June 1977. *Discovery* 13369#1; female; 48°56'N, 15°45'W; 4828–4838 m; OTSB; 22 March 1998. *Discovery* 13369#2; female; 48°54'N, 15°40'W; 4828–4836 m; OTSB; 23 March 1998. *Discovery* 50514; male; 49°44'N, 14°02'W; 4017–4095 m; OTSB; 5 June 1979. *Discovery* 54301#6; male; 48°47'N, 16°50'W; 4837–4846 m; OTSB; 20 October 1997. *Discovery* 52403#13; 2 males; 48°52'N, 15°57'W; 4805–4810 m; OTSB; 5 December 1986. *Discovery* 52403#14; female; 49°02'N; 16°00'W; 4850–4860 m; BN1.5; 5 December 1986. *Discovery* 11908#7; male; 49°04'N, 16°04'W; 4847–4789 m; OTSB; 24 August 1989. *Discovery* 11908#51; female; 48°46'N, 16°32'W; 4839–4856 m; OTSB; 7 September 1989. *Discovery* 11908#68; 1 female, 2 males; 48°47'N, 16°25'W; 4853–4877 m; OTSB; 12 September 1989. *Discovery* 12930#26; male; 48°53'N, 16°43'W; 4836–4843 m; OTSB; 4 September 1996. *Discovery* 12930#64; female; 48°48'N; 16°16'W; 4836–4839 m; OTSB; 12 September 1996. *Discovery* 51608#1; male; 49°36'N, 14°30'W; 4370–4270 m; OTSB; 19 August 1982. *Discovery* 54901#2; female; 48°42'N, 16°52'W; 4811–4837 m; OTSB; 26 April 99. *Discovery* 54902#1; female; 48°27'N, 15°40'W; 4843–4845 m; OTSB; 2 May 99. *Discovery* 13906#1; male; 50°12'N, 14°40'W; 3972–4003 m; OTSB; 18 September 2000. *Discovery* 13925; 3 males; 48°57'N, 16°55'W; 4835–4845 m; OTSB; 7 October 2000.

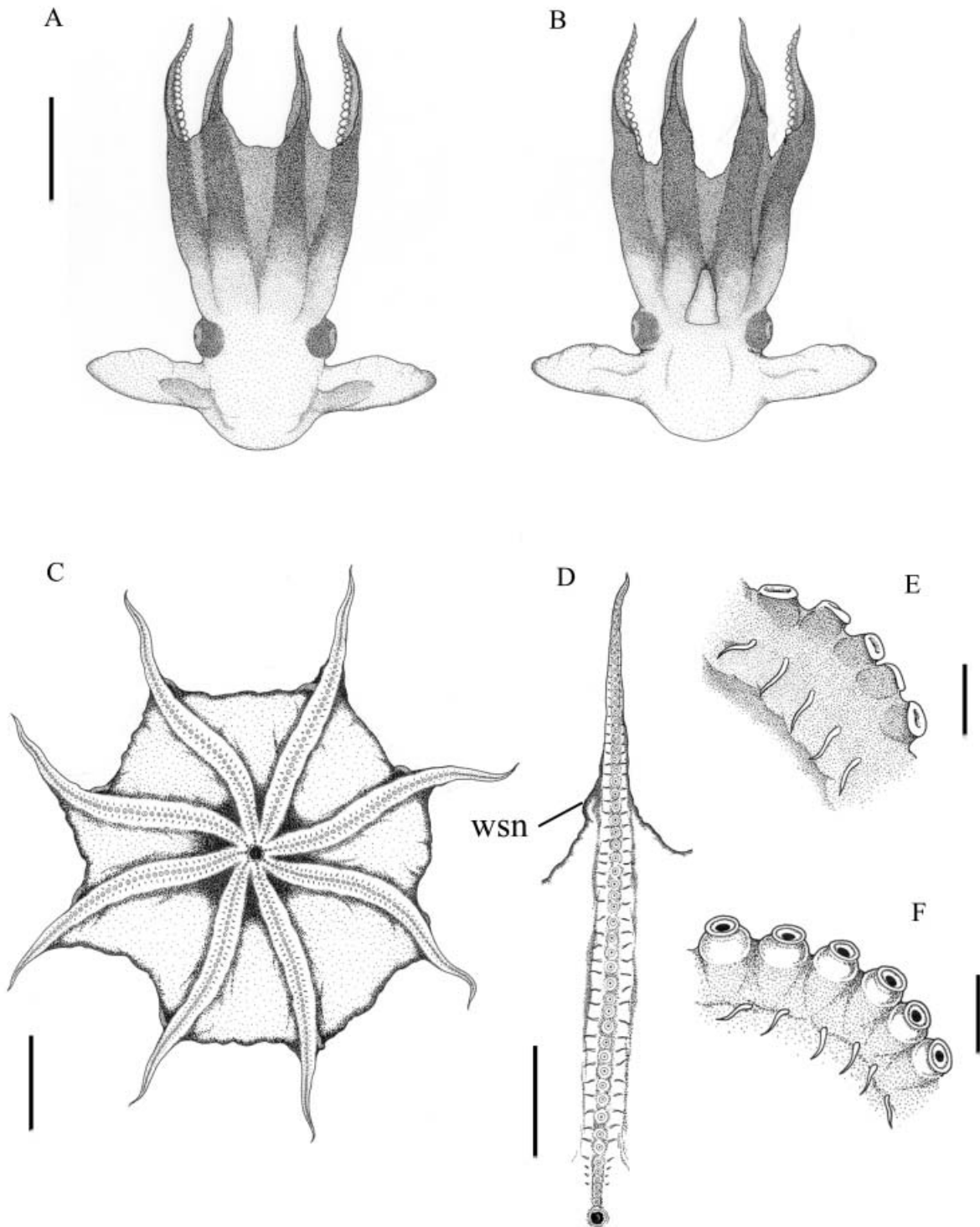
*Diagnosis*

Small to medium sized species. Gills with seven (occasionally six or eight) broad lamellae. Radula and posterior salivary glands absent. Fin-supporting cartilage (shell) U-shaped, with outer edges of lateral wings parallel, terminating in two lobes. Eggs 10–11 mm. Oral suckers (1–4) small with distinct increase in size at sucker 6. Suckers of MSD present over broad range of arms; sexually dimorphic, larger in males. Cirri of moderate length.

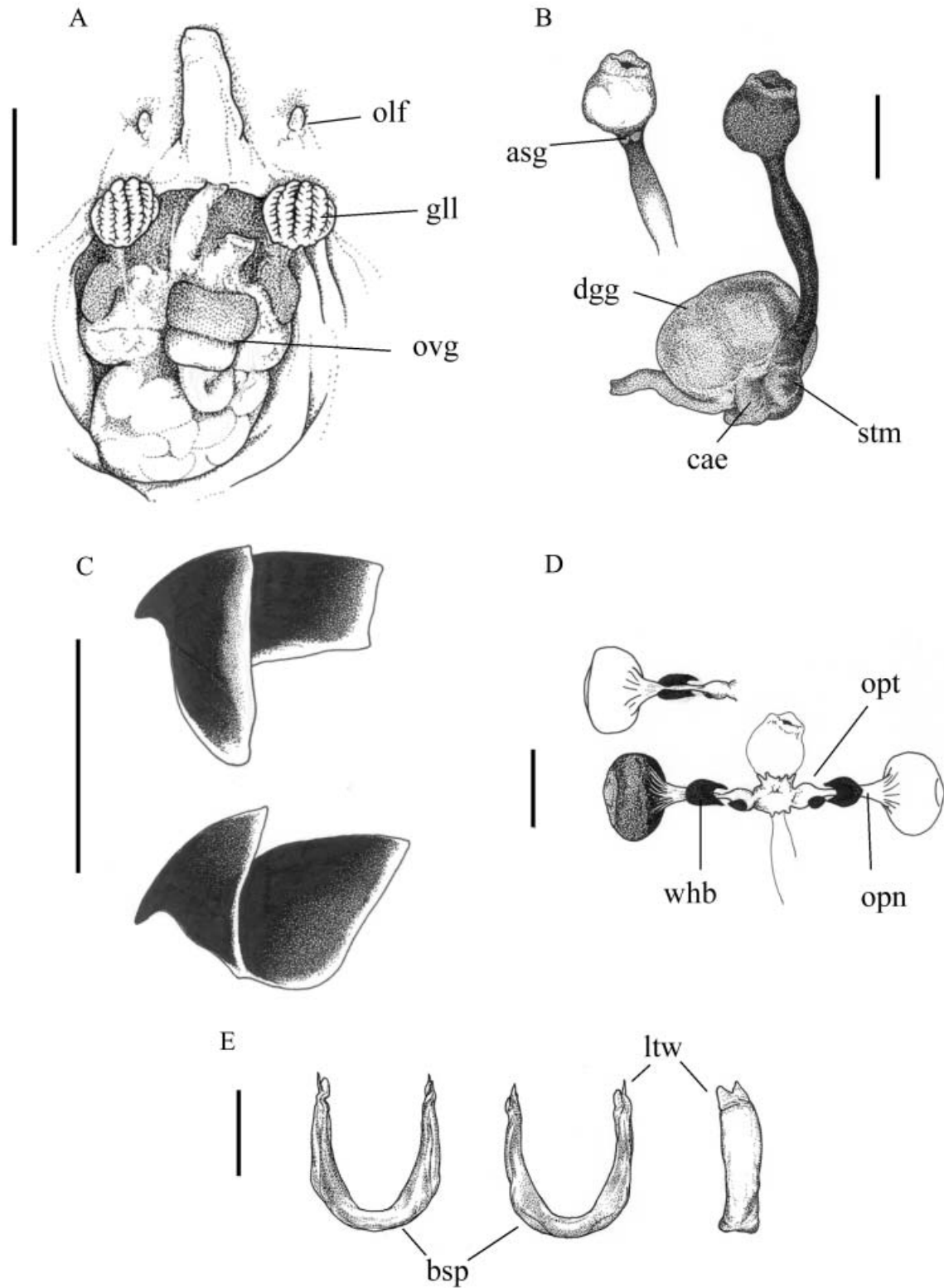
*Description*

Small to medium species; body semigelatinous, bell-shaped (Figs 3D, 14A,B). Mantle 25% TL, and broadly rounded posteriorly. Head slightly wider than mantle, with no discernible constriction between head and mantle. Pallial aperture small, closely surrounding funnel. Funnel, moderately long (mean FuLI 45.4).

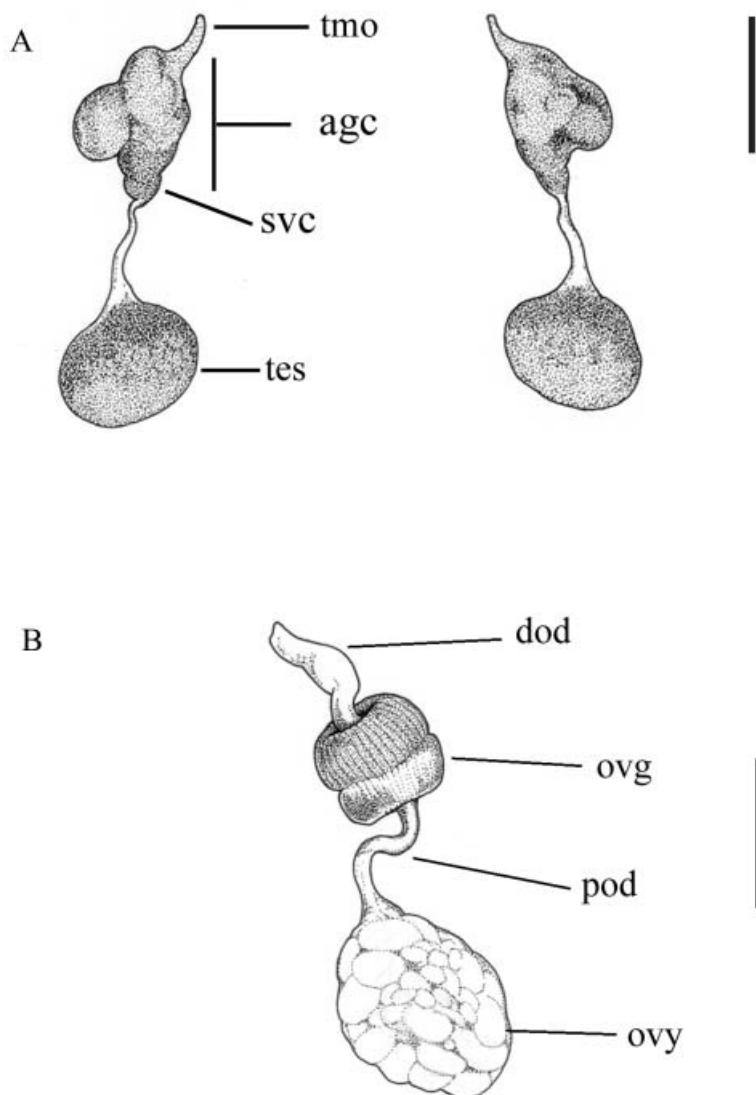




**Figure 14.** *Grimpoteuthis discoveryi* sp. nov.: external anatomy. Dorsal (A), ventral (B) and oral (C: all BMNH 20030380) views; oral view of first arm (D), with detail of female (E: BMNH 20030380) and male (F: BMNH 20030378) suckers and cirri. Scale bars = 50 mm (A–C); 25 mm (D); 5 mm (E,F).



**Figure 15.** *Grimpoteuthis discoveryi* sp. nov: internal anatomy. Ventral view of the viscera *in situ* (A: BMNH 20030380): note pallial adductor has been cut and is not illustrated; detail of the digestive system (B); lower and upper beaks (C); optic nerve and white body (D: all BMNH 20030381); dorsal, ventral and lateral view of shell (E: BMNH 20030380). Scale bars = 20 mm (A); 10 mm (B–D); 15 mm (E).

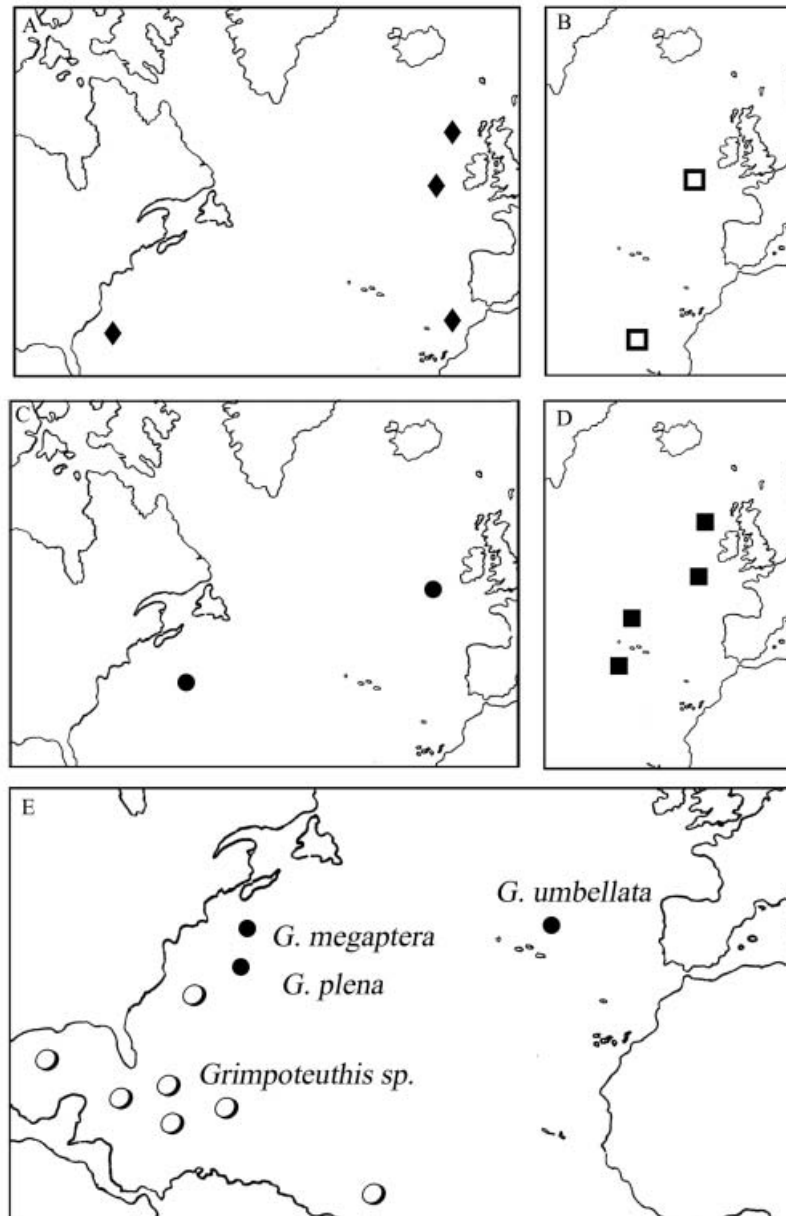


**Figure 16.** *Grimpoteuthis discoveryi* sp. nov.: internal anatomy. Dorsal and ventral views of the male reproductive system (A: BMNH 20030378). Ventral view of the female reproductive system (B: BMNH 20030381). Scale bars = 20 mm.

Funnel organ V-shaped. Olfactory organs rounded, prominent, located just within mantle aperture on either side of funnel. Fins lateral, moderately long (mean FSI 63.9; mean FLI 104.8); posterior margin straight; tips rounded with slight point, anterior margin convex with distinct lobe. Fins with narrow muscular base, muscular area extending two-thirds of the fin length.

Arms long (mean ALI 72.5), moderately stout, subequal in length, with arm formulae generally I.II.III.IV. Arms enveloped in single web, occupying approximately 2/3 of arm length (Fig. 14C). Intermediate (secondary) web absent. Web extends further on dorsal arms, generally of formula A.B.C.D.E. Single,

prominent, web supporting nodule on the ventral side of each arm, located at approximately sucker 31 on arm I, 29 on arm II; 27 on arm III and 25 on arm IV (Fig. 14C,D). Suckers in single row from mouth to arm tip, approximately equal numbers on all arms (range 56–61). Suckers barrel-shaped and show distinct sexual dimorphism (Fig. 14E,F). In mature females sucker height approximately equal to SD (mean SDI 4.4). In mature males sucker height (distance from sucker base to tip) greatly exceeds SD. SD is significantly greater in males (mean SDI 6.4) than females. In both sexes the first 4 or 5 (oral) suckers are very small, and there is a distinct increase in SD at sucker 5 or 6; this increase is greatest in mature males. From



**Figure 17.** Distribution of the genus *Grimptoteuthis* in the North Atlantic. *Grimptoteuthis wuelkeri* (A), *G. boylei* sp. nov. (B), *G. challengeri* sp. nov. (C), *G. discoveryi* sp. nov. (D), *G. umbellata*, *G. plena* and *G. megaptera* (E).

sucker 6 to approximately sucker 40 the sucker size is constant. Terminal 15–20 suckers decrease rapidly in size. Cirri moderate (mean CLI 7.3), first appear before the 4th or 5th sucker. Cirri extend to the tips of the arms, longest on mid-portion of dorsal arms.

Gills large, of half-orange (spherical) form (Fig. 15A), normally with seven broad lamellae (7/7 on 29 specimens; 8/7 on 10; 8/8 on four, 7/6 on 2 and 6/6 on one). Eyes of moderate size (mean EDI 32.5). Optic lobes large and spherical, with a single bundle of optic nerves running through the white body to each eye

(Fig. 15D). White body of characteristic shape, closely associated with eye, large, dark grey in preserved specimens.

Entire outer surface of digestive tract deeply pigmented (Fig. 15B). Upper beak lacking distinct ridges or grooves. Lower beak with rounded hood, slightly raised above crest; broad wings with distinct ridge running diagonally across; lateral walls without ridge or fold (Fig. 15C). Radula absent. Anterior salivary glands attached to the base of the buccal mass, posterior salivary glands absent. Oesophagus twice the

Table 9. *Grimpot euthis discoveryi* sp. nov. Details of specimens in the type series

ID Number	Holotype BMNH 20030378	Paratype BMNH 20030379	Paratype USNM 1012988	Paratype USNM 1012989	Paratype BMNH 20030380	Paratype BMNH 20030381	Paratype UMML 31.3166	Paratype UMML 31.3166
Station	Discovery 51309	Discovery 51309	Discovery 51309	Discovery 51309	Discovery 51414#1	Discovery 51414#1	Discovery 9640#1	Discovery 9640#1
Sex	Male	Male	Male	Female	Female	Female	Male	Female
Date	20/2/82	20/2/82	20/2/82	20/2/82	30/3/82	30/3/82	13/11/77	13/11/77
Longitude	49°35'N	49°35'N	49°35'N	49°35'N	50°00'N	50°00'N	50°03'N	50°03'N
Latitude	14°01'W	14°01'W	14°01'W	14°01'W	14°07'W	14°07'W	13°51'W	13°51'W
Depth	4190–4255	4190–4255	4190–4255	4190–4255	4180–4310	4180–4310	3749–3757	3749–3757
Total length	210	210	180	155	210	195	145	152
Mantle length	50	45	42	35	55	51	36	46
Head width	47	60	52	38	52	40	32	39
Fin span	138	145	130	110	125	125	91	115
Fin length	55	55	50	40	45	45	37	48
Fin width	21	25	22	18	22	22	16	20
Funnel length	26	27	21	17	24	18	18	22
Eye diameter	19	19	16	11	15	12	11	12
Arm I length	165	160	140	100	130	130	105	105
Arm formula	I.II.III.IV	I.II.III.IV	I.II.III.IV	I.I.III.IV	I.II.III.IV	I.II.III.IV	I.I.III.IV	I.I.III.IV
Web formula	Damaged	Damaged	A.B.C.D.E	A.B.C.D.E	A.B.C.D.E	Damaged	A.B.C.D.E	A.B.C.D.E
Sucker count	58	59	58	58	58	58	57	61
MSD	3.4	3.0	2.8	1.5	2.2	2.0	2.2	2.0
MCL	4.5	3.0	3.5	3.0	4.1	3.8	2.5	2.2
Location of MS	8–40	7–40	7–36	8–36	6–30	6–	7–35	7–35
Curri start before	4th or 5th	4th	4th or 5th	4th or 5th	4th	5th	5th	5th
Nodule locations: sucker no. on each arm	? , 29, 27, ?	Damaged	? , ? , 24, ?	? , 26, 26, ?	? , 24, 22, ?	31, 29, ?, ?	?	30, 29, 29, ?
Gill lamellae	7/7	7/8	7/8	7/7	7/7	8/7	7/7	6/6
Gill diameter	8.5	7.2	7.2	6.0	7.5	7.5	6.0	8.0
Egg diameter	–	–	–	–	11.0	10.5	–	10.5

**Table 10.** *Grimpoteuthis discoveryi* sp. nov. Indices of body proportions of specimens examined

	Male ( <i>n</i> = 28)		Female ( <i>n</i> = 20)		Overall ( <i>n</i> = 48)	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
ML	39.3 (7.6)	25–52	44.1 (7.4)	32–58	41.4 (7.8)	25–58
MLI	23.4 (2.6)	18–30	26.8 (2.9)	21.2–33.7	24.8 (3.2)	18.0–33.7
HWI	23.0 (3.2)	16.7–28.9	24.2 (2.1)	20.5–27.8	23.5 (2.8)	16.7–28.9
FSI	63.1 (6.0)	52.4–76	65.0 (6.5)	54.8–75.6	63.9 (6.2)	52.4–76.0
ALI	74.1 (4.4)	65.1–80.6	70.2 (5.3)	61.9–80.7	72.5 (5.1)	61.9–80.7
EDI	33.4 (4.5)	24.3–43.2	31.2 (4.8)	24.4–46.2	32.5 (4.7)	24.3–46.2
FuLI	46.3 (8.1)	30.8–66.7	44.2 (7.3)	30.8–56.4	45.4 (7.8)	30.8–66.7
FLI	107.0 (16.9)	80.9–140	101.9 (11.6)	80.8–120.5	104.8 (14.9)	80.8–140.0
SDI	6.4 (1.4)	4.4–10.6	4.43 (0.65)	3.33–5.56	5.6 (1.5)	3.3–10.6
CLI	7.5 (2.4)	3.6–13.8	7.01 (1.92)	3.57–11.1	7.3 (2.2)	3.6–13.8
GDI	17.5 (3.2)	12.0–27.9	17.0 (2.0)	12.8–20.5	17.2 (2.8)	12.0–27.9

length of the intestine; stomach small, a simple swelling of the distal oesophagus. Caecum with single turn, connected to single-lobed digestive gland by two digestive ducts.

Fin-supporting cartilage (shell) robust, thickened U-shape (Fig. 15E). Outer edge of lateral wings parallel, terminating in two lobes. Inner and outer surfaces of the basal portion convex.

Male reproductive tract (Fig. 16A) with large, oval testis located in the posterior median portion of the mantle. Vas deferens short; seminal vesicle complex convoluted; accessory gland complex comprising three glands; terminal organ (penis) of moderate length, projecting from distal accessory gland.

Female reproductive tract simple, unpaired (Fig. 16B). Oviducal gland in two parts, proximal third cream in colour, distal two-thirds either green or red-brown, depending on preservative. Oviducal eggs of maximum length 10–11 mm.

Skin surface smooth, oral and aboral surfaces of arms deeply pigmented (purple). Mantle with less pigmentation. Posterior margin of fins pigmented (purple).

#### *Type locality*

Porcupine Seabight; 49°35'N, 14°01'W; 4190–4255 m.

#### *Distribution*

Caught at depths of 2600–4870 m in the north-east Atlantic (Fig. 17).

#### *Remarks*

*Grimpoteuthis discoveryi* is a variable form occupying a broad depth range and Collins *et al.* (2001) thought

it may be two distinct species. Variability was noted in the cirrus length and shell form. Cirri length varied from 1.5 to 5.0 mm (CLI 3.6–13.8), but this may be due to fixation. The form of the shell varied, but this may be attributable to sexual dimorphism and size (maturity). It is possible that the material examined represents more than one species but further detailed morphological, and perhaps molecular, work is required. In view of this the type series was selected from close proximity (50°N, 40°W) at a similar depth (~4000 m). The size of the suckers is highly dimorphic in mature animals, with males possessing large barrel-shaped suckers. The enlargement of suckers differs from that found in *Opisthoteuthis* in that there is only one, extended field of enlargement.

#### *Etymology*

Named after RRS *Discovery*, which was responsible for collecting most of the specimens.

#### INDETERMINATE SPECIES

#### *Grimpoteuthis* sp.

#### *Material examined*

UMML 31.2481; unsexed; 19°01'N, 85°40'W; 4418–4416 m; 41' Trawl; 25 July 1972; RV *Gillis* 27. UMML 31.2470; male; 20°45'N, 65°00'W; 5175–5221 m; 41' Trawl; 3 July 1971; RV *Pillsbury* 1376. UMML 31.2469; unsexed; 19°48'N, 85°30'W; 4413 m; 40' Trawl; 22 May 1969; RV *Pillsbury* 577. UMML 31.2476; unsexed; 22°30'N, 75°01'W; 2577 m; 41' Trawl; 2 September 1975; RV *Iselin*-399. UMML 31.2477; unsexed; 22°05'N, 75°01'W; 2681 m; 41' Trawl; 6 September 1975; RV *Iselin* – 400. UMML

Table 11. Summary of Atlantic species of *Grimpoteuthis*

	<i>G. umbellata</i>	<i>G. wuelkeri</i>	<i>G. boylei</i>	<i>G. challengerii</i>	<i>G. discoveryi</i>	<i>G. megaptera</i>	<i>G. plena</i>
ML Range		46–115	25–115	35–75	25–58	25	57
Sucker size	Large	Medium	Large	Medium	Large	Small	Medium
Cirri length	Moderate	Short	Long	Long	Moderate	Long	Short
Sucker count	65–68	60–70	55–58	63–72	54–60	-	55
Lamellae form	Broad	Broad	Broad	Fine	Broad	-	Broad
Gill lamellae	8/9	6 or 7	8	8	7	Unknown	Unknown
Size at maturity	Unknown	Large	Large	Large	Small	Unknown	Unknown
Shell form	Unknown	Robust, thick lateral wings	Simple U; depression on basal plate	Robust, thick lateral wings	Slightly robust lateral wings end in two lobes	Unknown	Unknown
Egg size	Unknown	14 mm	18–20	13	8–11	Unknown	Unknown
Radula	Unknown	Present	Present	Present	Absent	Unknown	Unknown
Posterior salivary glands	Unknown	Small	Present	Absent	Absent	Unknown	Unknown
Depth	2233	1550–2055	4190–4800	4400–4800	2900–4800	4560	1948

31.2468; unsexed; 24°37'N, 65°16'W; 5404–5508 m; 41' Trawl; 30 June 1971; RV *Pillsbury* 1370. UMML 31.2492; female; 25°21'N, 91°02'W; 3203–3157 m; 30' Trawl; 25 July 1959; RV *Oregon*, 2567. UMML 1679; unsexed; 19°08'N, 79°53'W; 7279 m; 41' Trawl; 23 July 1975; RV *Gillis* 127. UMML 31.2523; unsexed; 13°17'N, 64°36'W; 3422–3464 m; 45' Trawl; 26 November 1981; RV *Norda*. UMML 31.2525; 3 unsexed; 15°08'N, 69°13'W; 3993–4065 m; 45' Trawl; 28 October 1981; RV *Norda*. UMML 31.2462; unsexed; 23°07'N, 64°57'W; 5614–5651 m; 41' Trawl; 26 November 1981; RV *Pillsbury* 1372. UMML 31.2483; unsexed; 17°54'N, 64°46'W; 4596 m; 41' Trawl; 17 July 1975; RV *Gillis* 117. UMML 31.2482; unsexed; 2°04'N, 40°32'W; 4416–4422 m; 41' Trawl; 10 August 1973; RV *Gillis* 77. UMML 31.2480; unsexed; 23°52'N, 77°18'W; 1378 m; 40' Trawl; 4 February 1974; RV *Iselin* 149. UMML 31.2522; unsexed; 13°50'N, 67°35'W; 5050–5055 m; 45' Trawl; 7 November 1981; RV *Norda*. UMML 31.2527; unsexed; 14°51'N, 67°29'W; 4956–5005 m; 45' Trawl; 3 December 1981; RV *Norda*. USNM 1013983; unsexed; 38°43'N, 72°30'W; 2366 m; 40' Trawl; 17 January 1974 RV *Delaware* D-74-2. *Discovery* 50910; 2 unsexed; 51°05'N, 13°05'W; OTSB; 4283–4341 m; 10 November 1980. *Discovery* 50515; unsexed; 49°44'N; 15°05'W; OTSB; 4180–4310 m; 06 June 1979. *Discovery* 51414#1; unsexed; 49°44'N, 14°10'W; 4180–4310 m; OTSB; 30 March 1982. *Discovery* 13078#37; female; 48°53'N, 16°22'W; OTSB; 4842–4844 m; 7 April 1997. *Discovery* 13200#9; unsexed; 48°52'N, 16°25'W; 4844–4850 m; OTSB; 6 July 1997. *Discovery* 54301#6; unsexed; 48°47'N, 16°50'W; OTSB; 4837–4846 m; 20 October 1997. *Discovery* 54301#8; unsexed; 48°49'N, 16°38'W; OTSB; 4839–4844 m; 22 October 1997. *Discovery* 13368#51; female; 48°50'N, 16°29'W; OTSB; 4840 m; 18 March 1998. *Discovery* 13627#10; unsexed; 48°53'N, 16°42'W; OTSB; 4837–4835 m; 30 October 1998. *Discovery* 52216#8; male; BN1.5; 4900–4930 m; 25 June 1985. *Discovery* 11908#68; female; 48°47'N, 16°25'W; OTSB; 4853–4877 m; 12 September 1989. *Discovery* 53201#1; 2 males; 48°52'N, 16°41'W; OTSB; 4834–4836 m; 7 April 1994. *Discovery* 12930#60; male; 48°50'N, 16°33'W; OTSB; 4838–4841 m; 12 September 1996. *Discovery* 12930#64; 2 females; 48°48'N, 16°16'W; OTSB; 4836–4839 m; 12 September 1996. *Discovery* 53201#28; male; 48°56'N, 17°00'W; OTSB; 4845–4846 m; 15 April 1994. *Discovery* 12930#46; 48°47'N, 16°43'W; male; OTSB; 4837–4841 m; 9 September 1996. *Discovery* 51608#1; 2 unsexed; 49°36'N, 14°30'W; OTSB; 4370–4270 m; 19 August 1982. *Discovery* 54901#9; 2 females; 48°47'N, 16°42'W; OTSB; 4837–4841 m; 30 April 1999. *Discovery* 54901#5; unsexed; 48°45'N, 16°41'W; OTSB; 4825–4828 m; 28 April 1999. *Discovery* 54901#2; female; 48°42'N, 16°52'W; OTSB; 4811–4837 m; 10

September 1990. *Discovery* 11908#35; male; 48°53'N, 16°18'W; OTSB; 4843–4847 m; 3 September 1989. *Discovery* 54902#1; male; 48°26'N, 15°40'W; OTSB; 4843–4845 m; 2 May 1999. *Discovery* 13906#1; unsexed; 50°12'N, 14°40'W; OTSB; 3972–4003 m; 18 September 2000. *Discovery* 13925#1; 2 unsexed; 48°54'N; 16°46'W; OTSB; 4835–4845 m; 7 October 2000. *Discovery* 51608; 2 unsexed; 49°36'N; 14°30'W; OTSB; 4390–4270 m; 19 August 1992. *Discovery* 9021; male; 30°07'N; 11°36'W; OTSB; 2173–2122 m; 19 August 1976. *Discovery* 50811; female; 49°39'N, 14°32'W; OTSB; 4400–4350 m; 2 August 1980. *Challenger* 8/80; 1 male, 1 unsexed; 49°47'N, 14°21'W; AT; 3910 m; 19 May 1980. NMSZ 1994128.45606; female; 55°37'N; 10°25'W; OTSB; 10 September 1990; RRS *Challenger* 72/90/13. MOM 295348; male; 39°56'N, 56°20'W; 5270 m; 9 August 1913; *Princesse Alice* Stn 3412. MOM 295138; unsexed; 16°12'N, 24°44'W; 3890 m; 25 September 1901; *Princesse Alice* Stn 1150.

#### Remarks

The *Discovery* specimens included here were mostly small, immature animals that could not be identified to the species level, but probably belong to one of the above described species. Two larger specimens are of particular interest. *Discovery* 50811 is an immature female (45 mm ML), similar to *G. boylei*, but with up to 64 suckers on each arm, and nine lamellae on each gill. *Discovery* 9021 was caught on the Madeira Abyssal Plain, relatively close in location and depth to the type of *G. umbellata*. However, it is in poor condition and differs from the type of *G. umbellata* in the gill lamellae count. Both these specimens appear different from those described above, and until additional specimens are caught they cannot be fully described.

Most of the UMML specimens included here were small and in poor condition, and were tentatively identified as *G. megaptera* by Gil Voss. However there are at least two species and, in the absence of the type of *G. megaptera*, it is difficult to assign them to any species.

The USNM (RV *Delaware*) specimen is from close to the type locality of *G. megaptera*, but from considerably shallower depth. A brief examination of this specimen confirmed that it differs from any of the north-east Atlantic species described above, notably in possessing approximately 90 suckers on each arm (ML 120 mm; MSD 3.9 mm; MCL 4 mm).

#### Comparative material

*Grimptoteuthis pacifica* (Hoyle, 1885): BMNH 1890.1.24.3 (holotype); 13°50'S, 151°49'W; 4538 m; 25 August 1874; HMS *Challenger* 181. *Grimptoteuthis meangensis* (Hoyle, 1885): BMNH 1890.1.24.4 (holo-

type); 4°33'N, 127°06'E; 4930 m; 10 February 1875; HMS *Challenger* 21. *Grimptoteuthis plena* (Verrill, 1885): USNM 39908 (holotype); 39°35'N, 71°19'W; 1073 fathoms; 20 August 1884; RV *Albatross*. *Grimptoteuthis bathynectes* Voss & Percy, 1990; USNM 730715; male; 45°01'N; 135°12'W; 3932 m; 1 October 1972; RV *Yaquina*. *Grimptoteuthis bathynectes*; USNM 817582 (paratype); male; 45°05'N; 134°43'W; 3932 m; 9 October 1972; RV *Yaquina*. *Grimptoteuthis brunni* Voss, 1982; USNM 730617 (paratypes); 13 specimens; 41°S; 70°35'W; 250–360 m; 17 August 1966; RV *Anton Brunn*. *Grimptoteuthis tuftsi* Voss & Percy, 1990; USNM 730714; male; 45°05'N, 134°43'W; 3900 m; 9 October 1972; RV *Yaquina*. *Grimptoteuthis albatrossi*; USNM 332949 (holotype); 38°11'N, 142°08'E; 266 fathoms; 10 October 1906; RV *Albatross*.

## DISCUSSION

The present study attempts to resolve some of the taxonomic problems of the genus *Grimptoteuthis* in the North Atlantic. However, the poor condition of the types of *G. umbellata* and *G. plena* and the loss of the type of *G. megaptera* have prevented a full evaluation. Four species of *Grimptoteuthis* are described or redescribed in this paper, which together with *G. umbellata*, *G. plena* and *G. megaptera* increase the number of recognized species in the North Atlantic to seven (see Table 11). *Grimptoteuthis wuelkeri* or *G. discoveryi* may be a junior synonym of *G. umbellata*, but new material is needed from the type locality (Azores) to determine this.

A detailed study of the north-west Atlantic material is required in order to redescribe *G. megaptera* and *G. plena* and determine how they relate to north-east Atlantic species. *Grimptoteuthis wuelkeri* may be a junior synonym of *G. plena*, but there are differences in sucker counts between the type of *G. plena* and *G. wuelkeri*. The type of *G. megaptera* is lost, but the original description indicates that it differs from the species described here. A specimen examined at the USNM (RV *Delaware*) is from close to the type location and may be attributable to this species. Details of the types of *G. megaptera* and *G. plena* are reproduced from Verrill (1885) in Table 12.

The species described here can be separated based on characters such as the morphology of the shell, gills and suckers, presence or absence of a radula and posterior salivary glands, length of cirri and sucker count (see Table 11). However, the appearance of animals of the same species differs according to the preservative (e.g. ethanol, formalin, Steadman's), which can easily lead to confusion. Although shell morphology can be used to separate the species, caution should be taken with frozen specimens as freezing causes distortion in the shell. The presence of posterior salivary glands,



**Table 12.** *Grimpoteuthis plena* and *G. megaptera*. Measurements taken from (Verrill, 1885). # indicates estimated from Verrill's figure

Species ID Number	<i>G. plena</i> USNM 39908	<i>G. megaptera</i> Lost
Sex	Unknown	Unknown
Date	20/8/1880	9/9/1884
Latitude	37°35'N	36°05'N
Longitude	71°18'W	69°52'W
Depth	1948	4560
Total length	185	107
Mantle length	57	25
Head width	70#	27
Fin span	130	68
Fin length	32	24
Fin width	22#	9
Funnel length	14	8
Eye diameter	12	9
Arm I length	125	95
Arm formula	I.II.III.IV	I.II.III.IV
Web formula	A.B.C.D.E	A.B.C.D.E
Sucker count	55–60	–
MSD	2.5	1.0
MCL	4.0	2.0
Location of MSD	10–28	
Web nodule	Not determined	Present

albeit very small, is interesting, as they were previously thought to be absent in cirrates (Voss, 1988b). The glands may have been overlooked in previous studies but are not found on Atlantic species of *Opisthoteuthis* (Villanueva *et al.*, 2002) or *Stauroteuthis* (Collins & Henriques, 2000). Aldred, Nixon & Young (1983) and Collins & Henriques (2000) did report salivary glands on the buccal mass of *Stauroteuthis* and *Cirrothauma*, respectively, but these are not true posterior salivary glands.

The definition of the genus *Grimpoteuthis* has been problematic since it was first proposed by Robson (1932). Cirrate species have variously been placed in *Opisthoteuthis*, *Stauroteuthis* and *Grimpoteuthis*. O'Shea (1999) recently proposed two new genera (*Luteuthis* and *Enigmatiteuthis*) to accommodate new Pacific species and moved some species from *Grimpoteuthis* to these genera (see Table 13). O'Shea (1999) based his description of *Grimpoteuthis s. s.* on a specimen from the Lord Howe Rise, west of New Zealand, which had a gill structure similar to that described for *G. umbellata* by Ebersbach (1915) and Robson (1932), although neither Ebersbach or Robson were actually referring to the type of *G. umbellata*. It will not be possible to define *Grimpoteuthis s. s.* without knowledge of the form of the type species.

O'Shea (1999) proposed the new family Luteuthidae from a single specimen (*Luteuthis dentatus*), on the basis of a W-shaped shell, the presence of a radula, a bilobed digestive gland and cirri commencing between suckers 1 & 2. A second species (*Luteuthis shuishi*) has recently been added to the genus (O'Shea & Lu, 2002). The presence of a radula is fairly common amongst *Grimpoteuthis*, the shape of the shell is not greatly different from *G. wuelkeri* and *G. challengerii* (in the *L. dentatus* specimen the shell may have been distorted by freezing) and single and bilobed digestive glands are found in the *Opisthoteuthis* genus (Villanueva *et al.*, 2002). Neither of the *Luteuthis* specimens were examined in the present study, but tissue was included in a molecular phylogenetic study (Piertney *et al.*, 2003), which placed it close to *G. discoveryi*, which lacks a radula, has a U-shaped shell and an entire digestive gland. It is therefore questionable whether the *Luteuthis* species should remain in a distinct genus, but clear that it should be allied with *Grimpoteuthis* in Grimpoteuthidae, particularly as *Grimpoteuthis s. s.* has yet to be established. O'Shea (1999) considered that *G. tuftsi* may also belong in *Luteuthis*, but examination of the type in the present study showed it to be similar to *G. challengerii*; it should therefore remain in *Grimpoteuthis*.

O'Shea (1999) included *G. wuelkeri* and *G. bathynectes* in his new genus, *Enigmatiteuthis*, along with *E. inominata*. *Enigmatiteuthis* mainly differs from *Grimpoteuthis* in the form of the shell; however, following examination of the *G. wuelkeri* holotype and specimens of *G. bathynectes*, I suggest they all remain in *Grimpoteuthis*. *Enigmatiteuthis inominata* should be *Grimpoteuthis inominata comb. nov.*

The Atlantic species of both *Opisthoteuthis* and *Stauroteuthis* have recently been redescribed (Collins & Henriques, 2000; Villanueva *et al.*, 2002) and the new generic diagnoses from these studies and the present one should permit the correct generic placement of most of the recognized species (see Table 13). The Cirroteuthidae (*Cirroteuthis*, *Cirrothauma* and *Stauroteuthis*) are easily separated from the Opisthoteuthidae and Grimpoteuthidae in possessing a secondary web and extremely long cirri on the mid sections of the arms. Grimpoteuthidae and Opisthoteuthidae can be separated on the form of the shell, fins, optic nerve and the presence of two enlarged sucker fields in mature males of *Opisthoteuthis* (see Table 14). According to the new diagnoses, *Grimpoteuthis bruuni* should be *Opisthoteuthis bruuni comb. nov.*, as it possesses three bundles in the optic nerve complex, lateral wings of the shell that taper to fine points and two fields of enlarged suckers in the males. When Voss (1982) described *bruuni*, there was consid-

**Table 13.** Generic placement of species previously or currently considered included in the genus *Grimpoteuthis*

Originally described as	Sweeney & Roper (1998)	O'Shea (1999)	Proposed
<i>Cirroteuthis umbellata</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>
<i>Cirrhoteuthis plena</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>
<i>Cirrhoteuthis megaptera</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>
<i>Stauroteuthis wuelkeri</i>	<i>Grimpoteuthis</i>	<i>Enigmatiteuthis</i>	<i>Grimpoteuthis</i>
<i>Cirroteuthis pacifica</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>
<i>Grimpoteuthis glacialis</i>	<i>Grimpoteuthis</i>	<i>Cirroctopus</i>	<i>Cirroctopus</i>
<i>Grimpoteuthis tuftsi</i>	<i>Grimpoteuthis</i>	<i>Luteuthis</i>	<i>Grimpoteuthis</i>
<i>Grimpoteuthis antarctica</i>	<i>Grimpoteuthis</i>	Junior synonym of <i>glacialis</i>	Not reviewed
<i>Grimpoteuthis bathynectes</i>	<i>Grimpoteuthis</i>	<i>Enigmatiteuthis</i>	<i>Grimpoteuthis</i>
<i>Grimpoteuthis abyssicola</i>	–	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>
<i>Enigmatiteuthis inominata</i>	–	<i>Enigmatiteuthis</i>	<i>Grimpoteuthis</i>
<i>Stauroteuthis mawsoni</i>	<i>Grimpoteuthis</i>	<i>Cirroctopus</i>	<i>Cirroctopus</i>
<i>Stauroteuthis albatrossi</i>	<i>Opisthoteuthis</i>	<i>Opisthoteuthis</i>	<i>Opisthoteuthis</i>
<i>Cirroctopus hochbergi</i>	–	<i>Cirroctopus</i>	<i>Cirroctopus</i>
<i>Grimpoteuthis hippocrepium</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>	<i>Grimpoteuthis</i>
<i>Grimpoteuthis meangensis</i>	–	<i>Enigmatiteuthis</i>	<i>Grimpoteuthis</i>
<i>Grimpoteuthis bruuni</i>	<i>Grimpoteuthis</i>	–	<i>Opisthoteuthis</i>
<i>Luteuthis dentata</i>	–	<i>Luteuthis</i>	<i>Luteuthis</i>
<i>Luteuthis shuishi</i>	–	–	<i>Luteuthis</i>

**Table 14.** Characters of the families Grimpoteuthidae O'Shea and Opisthoteuthidae Verrill

	Grimpoteuthidae	Opisthoteuthidae
Shell	U-shaped with outer lateral walls parallel, not tapering to fine points	Broad U-shape, with flaring lateral walls tapering to fine points
Fins	Large, lateral, with distinct lobe on anterior margin	Small to medium sized, posterolateral, distinct lobe on anterior margin absent
Optic nerve	Single bundle passing through white body	Three bundles pass through white body
Optic lobe	Spherical	Kidney shaped
Suckers	Single medial field of slightly enlarged suckers in both sexes	Proximal and distal fields of enlarged suckers in mature males; proximal field only in females
Radula	Present or absent	Absent
Posterior salivary glands	Present or absent	Absent
Digestive gland	Entire or bilobed	Entire or bilobed

erable confusion surrounding the diagnoses of *Grimpoteuthis* and *Opisthoteuthis*. He suggested that *bruuni* was allied to *Grimpoteuthis grimaldii*, which he (Voss, 1988b) subsequently moved to *Opisthoteuthis*; it too has recently been redescribed by Villanueva *et al.* (2002).

#### ACKNOWLEDGEMENTS

Thanks to the following for sending specimens and their help and hospitality during various museum visits: Mike Thurston, Dave Billet (SOC); Clyde Roper, Mike Vecchione and Mike Sweeney (USNM);

Michele Bruni (MOM); Louise Allcock (NMSZ); Fred Naggs & Richard Williams (BMNH); Philippe Bouchet (MNHN); Jon Kongsrud (ZUB). The project was funded by NERC Grant GR8/04443. Ian Rendall was responsible for all the artwork, which was funded by a grant from the Linnean Society. Oliver Yates, Heather Daly, Louise Allcock, Cynthia Yau, Mary O'Dea, Jasmine Hagqvist and Iona McPhee assisted with the examination of specimens at various times. Eric Hochberg and Nancy Voss provided very helpful comments on early versions of the manuscript. Thanks to Kevin Mackenzie and Brian Stewart for technical support.

## REFERENCES

- Aldred RG, Nixon M, Young JZ. 1983.** *Cirrothauma murrayi*, a finned octopod. *Philosophical Transactions of the Royal Society of London B* **301**: 1–54.
- Chun C. 1913.** Cephalopoda from the 'Michael Sars' north Atlantic deep-sea expedition 1910. In: Murray J, Hjort J, eds. *Report of the scientific results of the 'Michael Sars' north Atlantic deep-sea expedition 1910*, Zoology. Bergen, 1–28.
- Collins MA, Henriques C. 2000.** A revision of the family Stauroteuthidae (Octopoda: Cirrata) with redescription of *Stauroteuthis syrtensis* and *S. gilchristi*. *Journal of the Marine Biological Association of the United Kingdom* **80**: 685–697.
- Collins MA, Yau C, Allcock LA, Thurston MH. 2001.** Distribution of deep water benthic and benthopelagic cephalopods from the NE Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **81**: 105–117.
- Ebersbach A. 1915.** Zur anatomie von *Cirroteuthis umbellata* Fischer und *Stauroteuthis* sp. *Zeitschrift Wissenschaftliche Zoologie* **113**: 361–483.
- Fischer P. 1883.** Note préliminaire sur une nouvelle espèce du genre *Cirroteuthis*. *Journal de Conchologie* **31**: 402–404.
- Fischer H, Joubin L. 1907.** Cephalopodes. *Expéditions Scientifiques du Travailleur et du Talisman* **8**: 313–353.
- Grimpe G. 1916.** *Chunioteuthis* – Eine neue Cephalopoden-gattung. *Zoologische Anzeiger* **46**: 349–359.
- Grimpe G. 1920.** Teuthologische Mitteilungen V. Zwei neue Cirraten-Arten. *Zoologischer Anzeiger* **51**: 230–243.
- Guerra A, Villanueva R, Nesis KN, Bedoya J. 1998.** Redescription of the deep-sea cirrate octopod *Cirroteuthis magna* Hoyle 1885, and considerations on the genus *Cirroteuthis* (Mollusca: Cephalopoda). *Bulletin of Marine Science* **63**: 51–81.
- Hoyle WE. 1886.** Report on cephalopods collected by HMS Challenger during the years 1873–1876. *Report of the scientific results of the voyage of HMS Challenger during the years 1873–76 (Zoology)* **16**: 1–245.
- Joubin L. 1900.** Cephalopodes provenant des campagnes de la Princesse Alice (1891–1897). *Resultats des campagnes scientifiques accomplies sur son yacht par Albert I Prince Souverain de Monaco* **17**: 1–135.
- Joubin L. 1903.** Sur quelques Cephalopodes recueillies pendant les dernières campagnes de S.A.S. le Prince de Monaco (1901–03). *Comptes Rendus des Séances de l'Académie des Sciences, Paris* **136**: 100–102.
- Joubin L. 1920.** Cephalopodes provenant des campagnes de la Princesse-Alice (1898–1910). *Resultats des campagnes scientifiques accomplies sur son yacht par Albert I Prince Souverain de Monaco* **54**: 1–95.
- Kubodera T, Okutani T. 1986.** New and rare cephalopods from the Antarctic waters. *Memoirs of the National Institute of Polar Research Special Edition* **44**: 129–143.
- Massy AL. 1909.** The Cephalopoda Dibranchiata of the coasts of Ireland. *Fisheries, Ireland Scientific Investigations* **1907**: I: 1–39.
- O'Shea S. 1999.** *The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda)*. Wellington: NIWA Research.
- O'Shea S, Lu CC. 2002.** A new species of *Luteuthis* (Mollusca: Cephalopoda: Octopoda: Cirrata) from the South China Sea. *Zoological Studies* **41**: 119–126.
- Piertney SB, Huedelot C, Hochberg FH, Collins MA. 2003.** Phylogenetic relationships among cirrate octopods (Mollusca: Cephalopoda) resolved using mitochondrial 16S ribosomal DNA sequences. *Molecular Phylogenetics and Evolution*. **27**: 348–353.
- Robson GC. 1932.** *A monograph of Recent Cephalopoda. Part II. The Octopoda (excluding the Octopodinae)*. London: British Museum.
- Sweeney MJ, Roper CFE. 1998.** Classification, type localities and type repositories of recent Cephalopoda. In: Voss NA, Vecchione M, Toll RB, Sweeney MJ, eds. *Systematics and biogeography of cephalopods*. Washington DC: Smithsonian Institution Press, 561–599.
- Vecchione M, Young RE. 1997.** Aspects of the functional morphology of cirrate octopods: Locomotion and feeding. *Vie et Milieu* **47**: 101–110.
- Verrill AE. 1885.** Third catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species with notes on others previously recorded. *Transactions of the Connecticut Academy of Science* **6**: 395–452.
- Villanueva R, Collins MA, Sanchez P, Voss NA. 2002.** Systematics and distribution in the Atlantic Ocean of the cirrate octopods of the genus *Opisthoteuthis* (Mollusca, Cephalopoda), with description of two new species. *Bulletin of Marine Science* **71**: 933–985.
- Voss GL. 1955.** The Cephalopoda obtained by the Harvard-Havana expedition off the coast of Cuba in 1938–39. *Bulletin of Marine Science* **5**: 81–115.
- Voss GL. 1982.** *Grimpoteuthis bruuni*, a new species of finned octopod (Octopoda: Cirrata) from the southern Pacific. *Bulletin of Marine Science* **32**: 426–433.
- Voss GL. 1988a.** The biogeography of the deep-sea Octopoda. *Malacologia* **29**: 295–307.
- Voss GL. 1988b.** Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). In: Clarke MR, Trueman ER, eds. *The Mollusca, Vol. 12. Paleontology and neontology of cephalopods*. San Diego: Academic Press, 253–276.
- Voss GL, Percy WG. 1990.** Deep-water octopods (Mollusca: Cephalopoda) of the northeastern Pacific. *Proceedings of the California Academy of Sciences* **47**: 47–94.