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THE *BATHYPOLYPUS-BENTHOCTOPUS* PROBLEM OF THE NORTH ATLANTIC (OCTOPODIDAE, CEPHALOPODA)

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ABSTRACT

Profound confusion among deep-water octopods of the genera *Bathypolypus* and *Benthoctopus* stems from misidentifications of the Atlantic *Bathypolypus arcticus* (Prosch, 1849), which is here shown to consist of at least two allopatric species—the nominal form is a truly arctic species; the other, *Octopus bairdii* Verrill, 1873, is a boreal cold-water form, which is reinstated as a *Bathypolypus*. A third species, *Bathypolypus pugniger,* n. sp., of uncertain systematic position, occurs in a narrow belt along the southern limit of *B. arcticus.*

Synonyms are discussed, and evidence is advanced that all records of *Benthoctopus piscatorum* (Verrill, 1879) are erroneous and that the type specimen is identical with *B. bairdii.*

Using an amended generic diagnosis, a critical survey of all *Bathypolypus* species is given. Six species, all Atlantic, are recognized. Distribution and habitats are given, and a key and tables provided to facilitate identifications.

Key words: *Bathypolypus, Benthoctopus,* North Atlantic, Bathypolypodinae (Cephalopoda).

INTRODUCTION

The octopod genera *Bathypolypus* and *Benthoctopus* comprise deep-water species that have caused much taxonomic confusion since Victor Prosch described the first species, *Octopus arcticus,* from southwest Greenland waters in 1849.

The two genera were established in a rather casual way by Grimpe (1921), the respective type species being *Bathypolypus arcticus* (Prosch, 1849) and *Benthoctopus piscatorum* (Verrill, 1879). Robson (1924b, 1927) defined the two genera and then treated all known species in his monograph on octopods (1932).

From Robson's work on *B. arcticus,* supplemented by findings of Hoyle (1886), Pfeffer (1908), Joubin (1920), Grimpe (1933), Kondakov (1936), Adam (1939), Bruun (1945), Jaeckel (1958), Kumpf (1958), Macalaster (1976), Perez-Gandaras & Guerra (1978), Nesis (1987), and Voss (1988b), *B. arcticus* would appear to be a highly variable species with a huge geographic range in the North Atlantic. It seems in fact to be the most abundant bottom-living octopod on the upper half of the continental slopes from Florida to West Greenland, along both sides of the ridge between Greenland and Scotland and from the Bay of Biscay to the Barents Sea, Svalbard, and even the Kara Sea.

In a report on the cephalopods from the Danish Godthaab Expedition 1928 to Davis Strait and Baffin Bay (Muus, 1962), I discussed specimens of *B. arcticus* from near the type locality. This species was easily identified by means of the type material in ZMUC. However, I also described a new, rather abundant species, *Bathypolypus proschi,* which in spite of a superficial similarity diverged from *B. arcticus,* especially in eye size, ligula, radula, and spermatophores.

When years later I inspected the Norwegian collections, I was baffled to find *B. arcticus* only in the arctic material and *B. proschi,* along the Norwegian West coast, labelled as *B. arcticus*. It dawned upon me that there are still serious identification problems, not only with *B. arcticus* but, as I would learn, also with other species of the genera *Bathypolypus* and *Benthoctopus,* and that a revision was badly needed.

Robson (1932) expressed the need for much larger collections to settle the questions left by his revision. Fortunately, growing trawl and dredge activity along the continental slopes has procured substantial additional material from most parts of the North Atlantic. Thus, I have had over 600 specimens at my disposal and ample opportunity to inspect relevant type material and most of the specimens treated by previous authors to settle

what seemed to be a case of confusion among sibling species.

MATERIAL

The main revision concerns North Atlantic material deposited in various museums as species placed in one or the other of the genera *Bathypolypus* and *Benthoctopus*, supplemented with recently collected material from Faroese and Icelandic waters (the BIOFAR and BIOICE projects respectively) and from the deep-sea prawn fisheries off southwestern Greenland. The material is listed in Appendix I.

METHODS

Measurements, counts and calculation of indices were performed according to the standard for descriptive characters of octopods given by Roper & Voss (1983). The soft body and variable state of preservation, however, make many measurements of octopods subjective, and repeated measurements of the same specimens often gave results deviating 5–10%. If different persons perform the measurements, the deviation may be even greater, which I noticed when I remeasured specimens treated by other authors. Meristic characters, such as number of suckers and lamellae copulatoriae of the hectocotylus, were often more reliable. Also the eye lens was useful, being a solid structure, and supplementing the dorsal mantle length as a standard of size. The lens was extracted with tweezers through a slit cut horizontally in the lower part of the eyeball. Remnants of the darkish primary cornea suspending the lens at "equator" was removed, and the diameter was measured gently with a calipers, or under a microscope.

Due to the slightly subjective manner in which many measurements of octopods have to be conducted, all graphs and figures comparing species are based on my own figures to minimize bias. Only in Figure 9, a few meristic data from Macalaster (1976) are included.

For convenience, the standard measurements used in this work are presented below. In addition to conventional indices, I have added some new indices that might be useful in taxonomic work on other octopod genera.

Note that as a slight deviation from standards as given by Roper & Voss (1983), ligula and calamus length are measured from the center of last sucker, not from its rim. It is accurate and eases the use of calipers. Mantle length is always dorsal ML (midpoint between eyes to mantle apex).

Measurements		*Indices*
AL:	Arm length	ALI: % of ML
CaL:	Calamus length	CaLI: % of LigL
ED:	Diameter of eye ball	EDI: % of ML
HcL:	Hectocotylized arm length	HcLI: % of ML
HW:	Head width	HWI: % of ML
LD:	Lens diameter	LDEDI: LD % of ED (Muus)
LigL:	Ligula length	LigLI: % of HcL
ML:	Mantle length	MLTLI: % of TL
MW:	Mantle width	MWI: % of ML
		OAI: HcL % of 3. left AL
SD:	Sucker diameter (largest)	SDI: % of ML
		SDLDI: SD % of LD (Muus)
		SDEDI: SD % of ED (Muus)
SpL:	Spermatophore length	SpLI: % of ML
SpRL:	Sperm reservoir length	SpRI: % of SpL
SpW:	Spermatophore width	SpWI: % of SpL
TL:	Total length	
WD:	Web depth	WDI: % of longest armpair
	(web sectors: A,B,C,D,E)	WDMI: WD % of ML

Counts

LamC: Laminae copulatoriae LamCI: LamC % of SHcC (Muus)
SHcC: Suckers on hectocotylized arm

Acronyms of museum collections used:

BMNH British Museum of Natural History, London, England
IMNH Icelandic Museum of Natural History, Reykjavik, Iceland
IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MNHN Muséum National D'Histoire Naturelle, Paris, France
MNHT Museum of Natural History, Tórshavn, Faroe Islands, Denmark
TMDZ Tromsø Museum, Department of Zoology, Norway
USNM National Museum of Natural History, Washington, DC, USA
ZIASP Zoological Institute, Academy of Sciences, St. Petersburg, Russia
ZMUB Zoological Museum University of Bergen, Norway
ZMUC Zoological Museum University of Copenhagen, Denmark
ZMUO Zoological Museum University of Oslo, Norway

REDESCRIPTION OF *BATHYPOLYPUS ARCTICUS* (PROSCH, 1849)

The earliest recognition of octopodids in Greenland was by Fabricius (1780: 353). His *Sepia octopodia* is, however, at most a *nomen dubium*, because the meagre description fits any of the now known species, and no type material exists. *Sepia groenlandica* Dewhurst (1834: 263) is a *nomen nudum*, because no description was given, and *Octopus granula-*

tus Möller (1843: 77) is both a *nomen nudum* and a junior homonym of *O. granulatus* Lamarck, 1798.

The first direct reference to *B. arcticus* (under the name "*Octopus granulatus*") was in Reinhardt & Prosch's (1846) paper on the anatomy of *Cirroteuthis mülleri,* in which some specimens were used for anatomical comparison, and it was stated for the first time that both species are devoid of an ink sac. The authors mentioned that they had many specimens of the Greenland species at their disposal "different in sex, age and development" [my translation].

In 1849, Prosch described *Octopus arcticus* based on some of the specimens mentioned in 1846, which were sent from west Greenland in the early 1840s. He did not designate a type specimen, and the lectotype, and two paralectotypes described below were identified as prosch's original material and marked "types" about 1930 by the curator R. Spärck, among the specimens that were retained in the ZMUC.

Material Examined

ZMUC CEP-13: Lectotype of *Bathypolypus arcticus* (Prosch, 1849), called "holotype" in Kristensen & Knudsen (1983): Male, ML: 42 mm. Label: Greenland, K. M. Jörgensen, August 26, 1841; CEP-14, paralectotype: Female, ML: about 50 mm. Label: Greenland, K. M. Jörgensen, July 27, 1840; CEP-15, paralectotype: The dissected parts of a male used by Prosch (1849) for his drawings (his figs. 1–3). Depository: ZMUC.

Further 120 specimens from arctic and subarctic North Atlantic as listed in Appendix I.

Remarks on the Type Series

The lectotype has been dissected and some measurements are not reliable. The funnel organ is lost, but was formerly present and clearly VV-shaped. Measurements and indices are given in Table 1.

Paralectotype CEP-14: Female, ML about 50 mm. Has been dissected, and most measurements are unreliable. SD: 2–6 mm, ED: 12 mm. Crop diverticulum present containing polychete bristles and crustacean remains. Gonads filled with eggs.

Paralectotype CEP-15: The dissected parts of a male used by Prosch (1849) for his figs. 1–3. Hectocotylus abnormal: only left side of ligula developed, 14 laminae. Remnants of typical *B. arcticus* spermatophores (Fig. 2d).

Material seen by Steenstrup (1856a) and probably by Prosch (1849): Male, ML: 32 mm, ED: 9.5 mm, LD: 3.8 mm, SD: 2.7 mm. Ligula 9 mm with 9 laminae. Funnel organ lost. Too fragile and flabby for measurements. Label: Holböl and Möller, Julianehåb (southwestern Greenland, probably 1840).

Three females in a jar. They have all been dissected but agree in all recognizable characters with the lectotypes (sucker size, eyeballs, crop). I extracted the beak and radula from one of the specimens. (Fig. 5e) Label: *Octopus arcticus,* Greenland (probably 1840).

Synonymy

Octopus arcticus Prosch, 1849: 55, pl. 2, figs. 1–3
Octopus grönlandicus Dewhurst: Steenstrup 1856a: 17, pl. 2, fig. 2; 1856b: 234, pl. 11, fig. 2; 1857: 97, pl. 3, fig. 2
Octopus piscatorum Verrill: Hoyle, 1886: 91
Polypus piscatorum: Russell, 1922: 7, pl. 2, fig. 2
Polypus faeroensis Russell, 1909: 446; 1922: 5, pl. 1, fig. 1, pl. 2, figs. 4–6
Bathypolypus arcticus: Robson, 1927: 251, figs. 1a, 2A; 1932 [in part]: 286, pl. 6, figs. 1, 2, text-figs. 53–60; Kondakov, 1936: 61, figs. 1, 2; Adam, 1939 [in part]: 9, figs. 2–4; Bruun, 1945 [in part]: 6; Muus, 1959: 224, figs. 109A, C, 115; 1962: 10, figs. 1, 2, 4c

TABLE 1. Measurements (mm) of the *B. arcticus* Lectotype.

				AL:	I	II	III	IV
TL:	165			r	119	112	93	114
ML:	42	MLTLI:	25	l	120	113	112	110
HW:	27	HWI:	64					
MW:	(38)	MWI:	(90)					
ED:	9	EDI:	21					
LD:	5.6	SDLDI:	50			WD:		
SD:	2.8	SDI:	7	A	B	C	D	E
LigL:	19	LigLI:	20	33.5	33	30.5	32	29
LamC:	14	SHcC:	42		38	35	35	

Benthoctopus piscatorum: Robson, 1927: 254, figs. 2B, 3; 1932: 224, figs. 31, 34, 35
Benthoctopus sasakii Robson, 1927: 257, fig. 8.
Bathypolypus faeroensis: Toll, 1985: 598, figs. 1, 2

Diagnosis

Body egg-shaped, papillated with minute warts often in a stellate pattern on small light spots; head narrower than body; each eye with a verrucose supraocular cirrus; funnel organ double, a clear-cut VV; hectocotylus with about 40 suckers and a deeply excavated ligula with 10–16 laminae. Radula usually with irregularly multicuspid, seldom homodont rachidians. Esophagus with crop diverticulum. Total length rarely over 200 mm.

Description

Skin and Colors: In freshly caught specimens, the skin is violet to purple strewn with lighter yellowish subcircular spots with minute warts, often surrounding a central slightly bigger wart in concentric rings, as observed by Prosch (1849). Ventral side paler, with few or no warts. Over each eye is an erectile stout and verrucose cirrus often with adjacent smaller protuberances. The cirrus may be about 10 mm long but often more or less retracted in preserved specimens. Color and sculpture patterns of the skin vary with state of preservation. In some specimens, the skin is smooth with no evident sculpture. This is often the case with preserved juvenile specimens (ML: < 30 mm.)

Bodily Proportions: The mantle is ovoid in outline (MWI: 65–90) slightly constricted behind the eyes (Fig. 1). ML rarely over 60–70 mm., TL rarely over 200 mm. The head is narrower than the mantle. Due to allometric growth, HWI decreases from 60–85 at ML 10, to 40–70 at ML 60.

The eyeballs are not very prominent. They decrease in relative size with age, EDI being 28–40 at ML 10, 20–33 at ML 60 (Fig. 4). The lens measures about 35% of the ED (LDEDI: 30–40).

The mantle aperture is 40–50% of the circumference of the neck. The funnel is free of the mantle for about 50%.

The funnel organ is VV-shaped. Typically its limbs appear as narrow swollen "ropes" that are easily detached from the funnel wall. They may vary in form (Fig. 18).

The gills are reduced and have 6–7(8) gill filaments on each demibranch.

The brachial complex is stout, with the arm order I. II. III. IV. The ML constitutes 25–35% of the TL, which leaves 65–75% to the brachial complex. Arm length Index: I 231, II 218, III 202, IV 189 (mean of 12 specimens).

The web extends along the arms almost to the tips. The web sectors A, B, C and D are subequal in most specimens (WDI: 33–34 at an average), E usually slightly shallower (WDI: mean 30). In a beautifully preserved female with fully extended umbrella, the WDI was: A: 38, B: 46/46, C: 46/46, D: 46/43, E: 41 (ML: 24 mm, M/K "Asterias", Svalbard, ZMUO).

The suckers are biserial, rather small and well spaced, SDI: 6.5–7.3–8.4 depending on degree of expansion. They are of the same sizes on all arms, and there is no sexual dimorphism. They number 80–90 on the dorsal arms, 60–70 on the ventral.

The hectocotylized third right arm is somewhat shorter than the corresponding left arm (OAI: 75–86–100) and carries about 40 suckers (Fig. 8). The number is individually constant throughout life (Fig. 23). The ligula was not described by Prosch (1849) probably because he had only one male with an abnormal hectocotylus at his disposal when he finally described *B. arcticus* (paralectotype CEP-15). But Steenstrup (1856a, b, 1857) pictured a male with hectocotylized arm and, based on five specimens, he stated that the arm carries 41–43 suckers and ligula 13–17 transverse laminae. The ligula is a spoon-shaped pointed organ with inrolled curved sides (Fig. 1). The width is about 50–70% of the length. It has a central ridge and 11–16 (17) deep, well-separated laminae (variation shown in Fig. 9). The number of laminae is individually constant from the onset of maturity (Fig. 22). LigLI: 9–23, the observed variation also depending on state of sexual maturity (Fig. 3). Calamus is short and pointed, CaLI: approx. 20. Spermatophoral groove well developed, the strong membrane curling the arm inwards in preserved specimens. Already at ML 16 mm the ligula may be discernible as a 1.5 mm-long undifferentiated tip of the third right arm.

Female Organs: The ovary is large with big globular and heavily pigmented oviducal glands (Fig. 2c). Proximally, the united

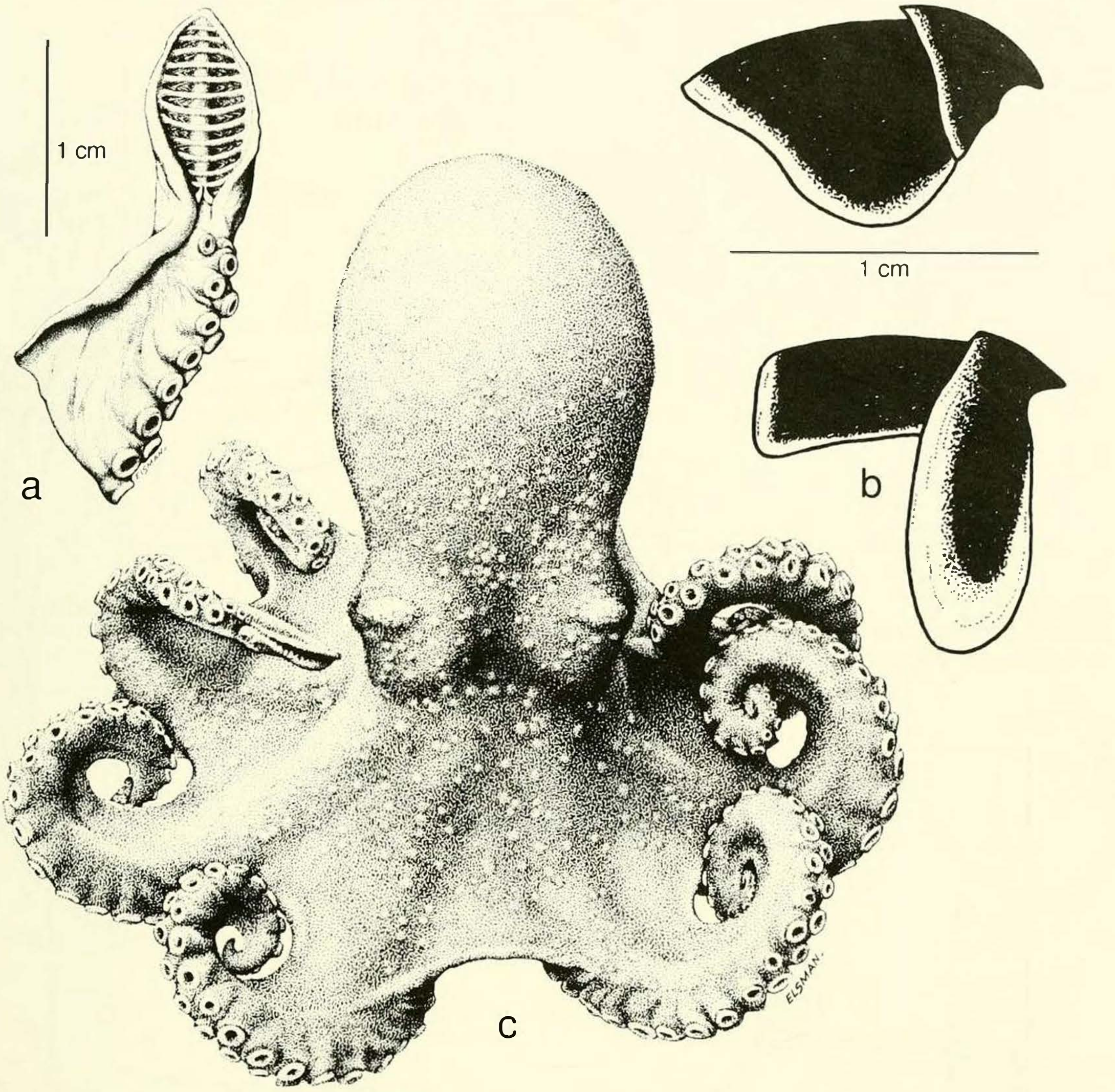

FIG. 1. *Bathypolypus arcticus* (Prosch, 1849). a: hectocotylus, ML: 40 mm; b: upper and lower beak, ♀ ML 46 mm, "Godthaab" Stn. 87, ZMUC; c: ♂ ML 54 mm, South Greenland, Just & Vibe Stn. 45, ZMUC.

oviducts are partly covered by the outer membrane of the ovary; distally they are short, very stout and leaving the oviducal glands forming a right angle. In ripe females, the gonad occupies 30–40% of the mantle cavity and is stuffed with 60–80 yellow or brownish eggs. Ripe eggs measure 16–18 mm in length. They are smooth, with fine longitudinal lines. The pointed end of each egg has a short stalk, and the stalks of all eggs are attached to the same small area of the ovary wall.

Male Organs: The penis has a well-developed diverticulum (Fig. 2b). Its size and shape very much depend on presence or absence of spermatophores, and it was not measured. Needham's sac was often distended by 3–6 spermatophores, as in Figure 2b. The large brownish spermatophores are very characteristic (Fig. 2d; Prosch 1849: fig. 2): the sperm reservoir occupies only about one third of the total length, and the oral end is a long, stout horn. The casing is very opaque, and details of the reservoir and middle piece could not be obtained. SpLI: 105–130, SpWI: approx. 18, SpRI: 26–32 (data from six males).

Beaks and Radula: The beaks do not have distinctive features. The radula seems to be very variable. In most cases, the central teeth

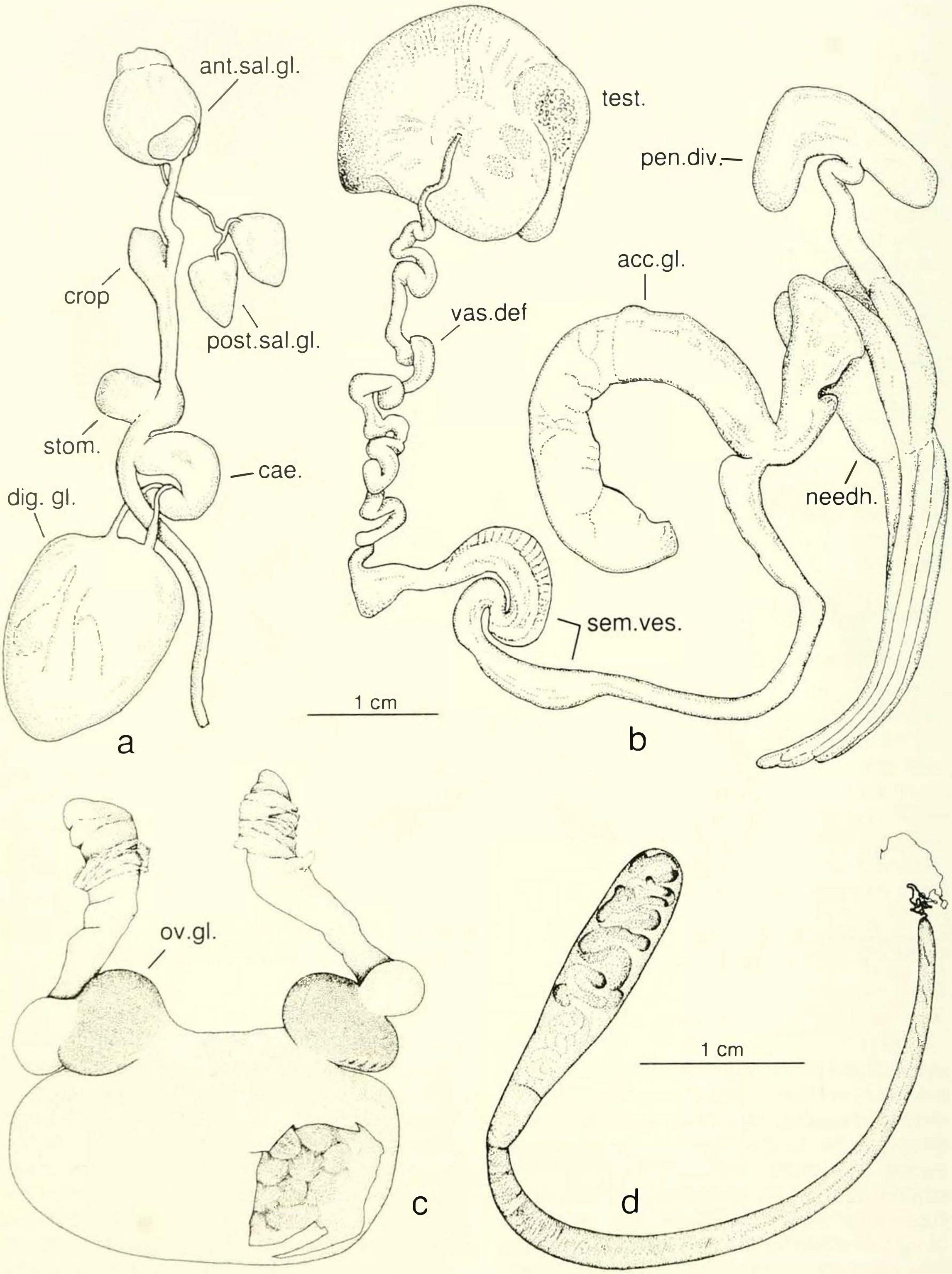

FIG. 2. *Bathypolypus arcticus*, a: digestive tract; ant.sal.gl.: anterior salivary glands; cae.: spiral caecum; dig.gl.: digestive or hepatic gland; post.sal.gl.: posterior salivary glands; stom.: stomach. b: male reproductive organs; acc.gl.: accessory gland; needh.: Needham's sac containing ripe spermatophores; pen.div.: penis diverticulum; sem.ves.: seminal vesicles; test.: testis; vas.def.: vas deferens. c: female reproductive organs; ov.gl.: oviducal gland; d: spermatophore. a,b and d from ♂ ML 43 mm, Ymer Island, East Greenland, 1932, ZMUC; c: ♀ ML 42 mm, BIOFAR Stn. 274, ZMUC.

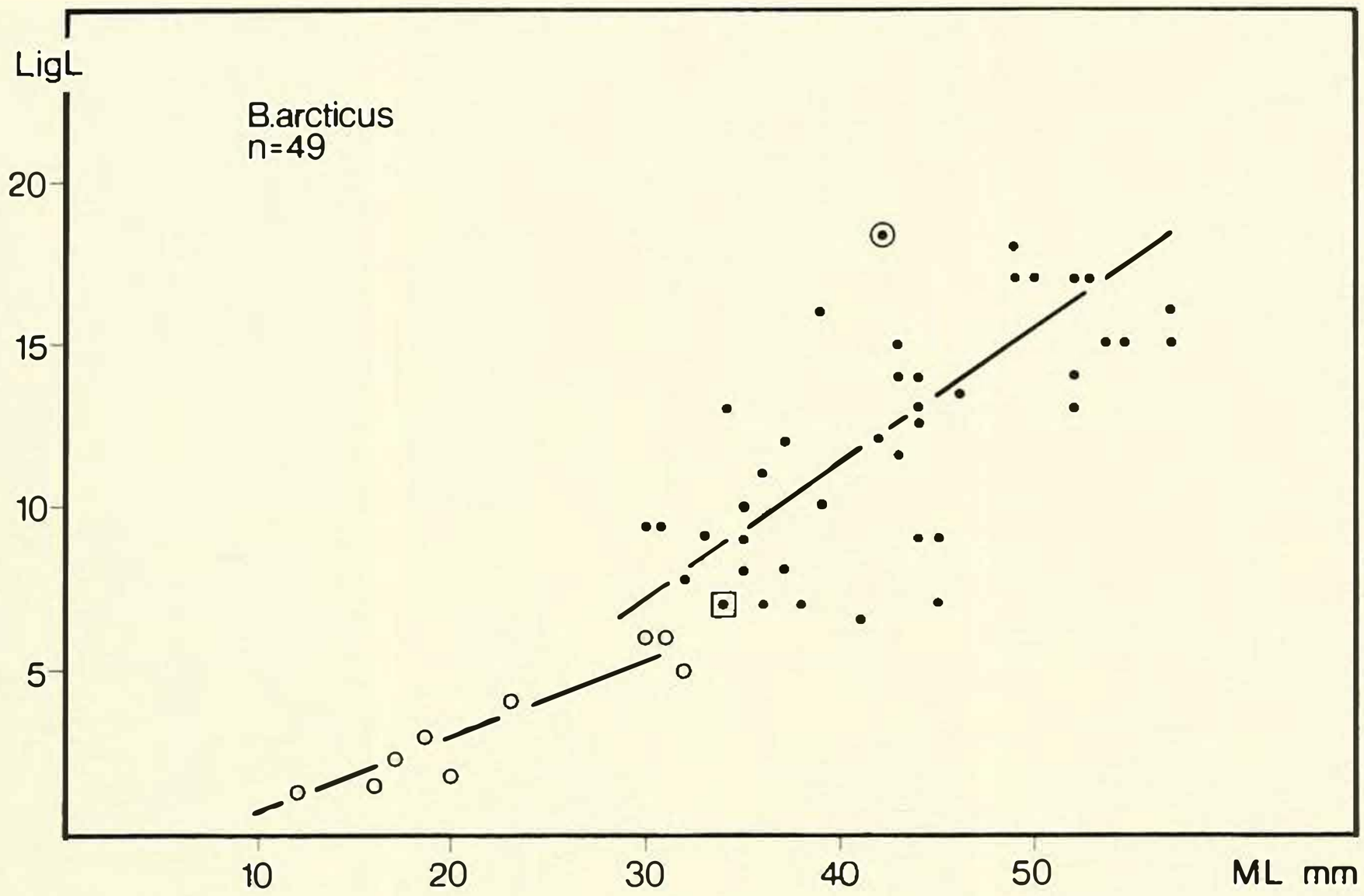

FIG. 3. Ligula length versus mantle length in *B. arcticus*. Open circles: juveniles. Maturity is reached at about ML 30 mm. Inserted lectotype of *B. arcticus* (encircled dot) and the "type" of *B. faeroensis* in ZMUC (dot in square). Juv.: $y = -1.90 + 0.225x$, $r^2 = 0.81$; ad.: $y = -3.9 + 0.340x$, $r^2 = 0.39$.

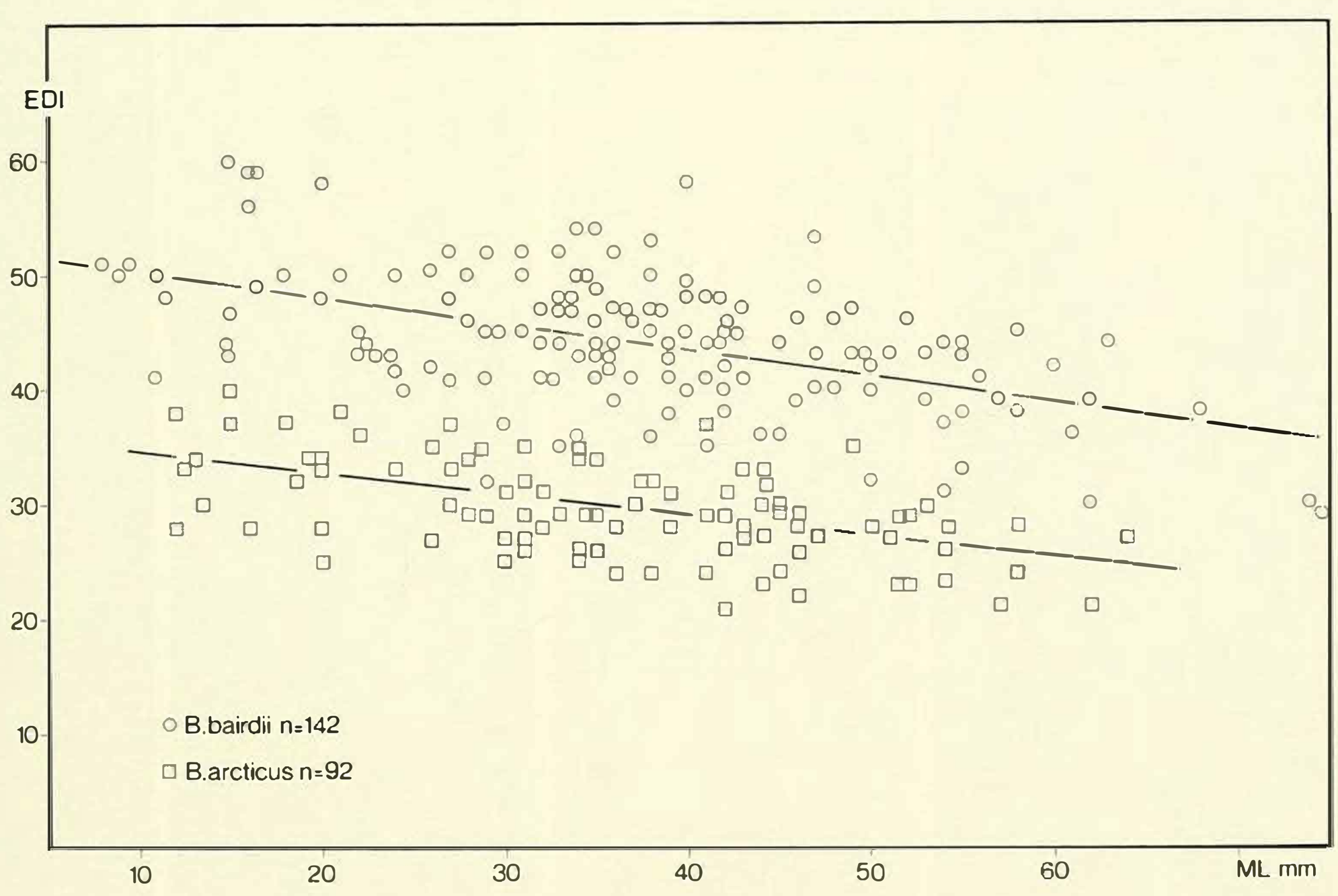

FIG. 4. Eye diameter index versus mantle length in *B. bairdii* and *B. arcticus*. No sex difference was found. Allometric growth is discernible, but correlation is weak; *bairdii:* $y = 52.68 - 0.2204x$, $r^2 = 0.249$; *arcticus:* $y = 36.7 - 0.199x$, $r^2 = 0.321$.

are clearly multicuspid (Fig. 5), with a seriation of 2–5 symmetrical (Fig. 5c) or asymmetrical teeth (Fig. 5b, d–f). In some specimens, the ectocones are rather delicate, uniform thorns (Fig. 5b); in others they form irregular rough knots. The ectocones may also be reduced to a certain lateral ruggedness of the rachis teeth even in presumed unworn parts of the radula. This may lead to quasi homodont rachidians, but completely homodont

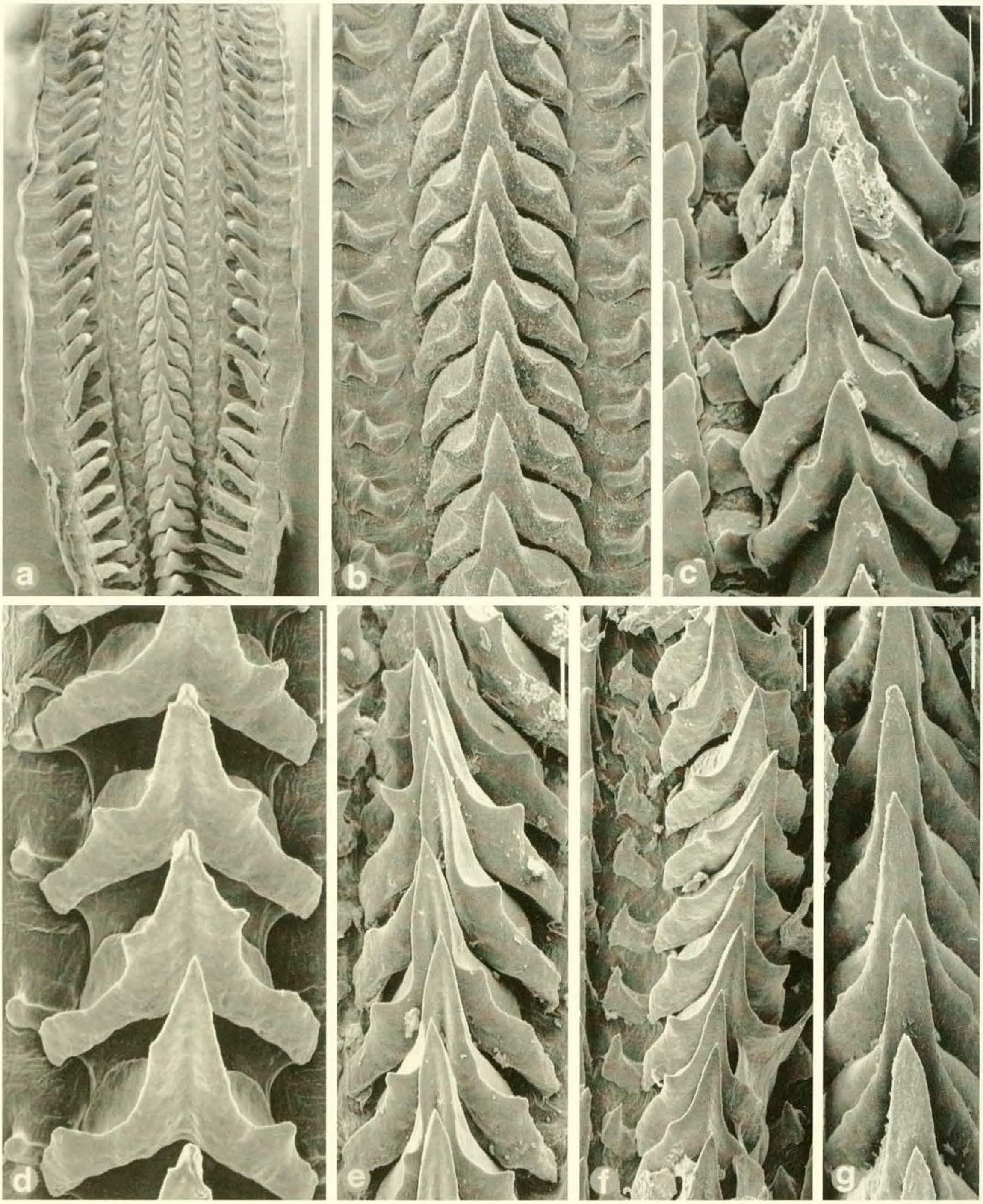

FIG. 5. Radula and rachidians of *B. arcticus;* a and b: ♀ ML 54 mm; c: ♀ ML 37 mm; d: ♀ ML 44 mm; e: ♀ ML approx. 50 mm; f and g: ♀♀ ML 33, 52 mm. Caught at various positions off northern Iceland, except e: southwestern Greenland, probably 1840. Scale: 100 µm.

rachidians are sometimes found. A striking example is demonstrated by two otherwise typical *arcticus* females (Fig. 5f, g) taken at BIOICE Stn. 2751. One has multicuspid, the other one homodont rachidians.

Digestive Tract: The esophagus has a well-developed crop diverticulum (Fig. 2a) on which the posterior salivary glands are loosely attached when in situ. The spiral caecum is reduced to at most one turn. The liver is large

and bulbous, about the same size as the testis. There is no ink sac.

Comparison with Prosch's Description

The material examined fits well with the types and Prosch's description, which is supplemented by Steenstrup's (1856a, b, 1857) remarks and illustrations of the species. One serious discrepancy, however, is the statement by Prosch that *arcticus* has no crop. This error of Prosch is hard to explain unless one of the specimens dissected during the study of the anatomy of *Cirroteuthis* (Reinhardt & Prosch, 1846) was *B. bairdii,* which is very common in West Greenland. I have however no evidence for this.

An important point that the present investigation confirms is that the rachidians are usually heterodont (Muus, 1962: 11, fig. 1A), though much more variable than I previously thought.

Junior Synonyms and Supposed Synonyms of *B. arcticus*

Three species which have contributed considerably to the prevailing taxonomic confusion are discussed below: *Bathypolypus faeroensis* (Russell, 1909), which was removed from the junior synonomy of *B. arcticus* by Toll (1985), and the two species that had been placed in *Benthoctopus*—*sasakii* (Robson, 1927) and *piscatorum* (Verrill, 1879).

Bathypolypus faeroensis (Russell, 1909)

Russell (1909) described *Polypus faeroensis* based on two males and a female trawled in the Faeroe Channel by the Fishery Cruiser "Goldseeker" Stn. 19a, 60°40′N, 4°50′W at 1030 m. August 24, 1908. In 1922, Russell repeated his earlier description based on the same three specimens, adding illustrations of radula, ligula, a papillary area of the skin, and a good photograph of the whole animal.

Russell stated that *faeroensis* is closely allied to the squat form that he knew as "*bairdii = arcticus*", from which it differs in certain well-defined ways: it has a better marked neck, a narrow head, and a shorter ligula, with more numerous laminae. The skin has a characteristic papillation with tiny warts arranged in a stellate pattern on light, circular spots.

Bathypolypus faeroensis has been considered a synonym of *B. arcticus* (Prosch, 1849) by Robson (1932, with hesitation), Jaeckel (1958), Kumpf (1958), Roper et al. (1984), and Nesis (1987). Toll (1985) redescribed *B. faeroensis* and reinstated it as a valid species based on a female specimen taken by FFS Walther Herwig in Denmark Strait, 67°21, 5′N, 23°30′W, 480–485 m, September 9, 1973. Because Toll was unable to trace the types of *B. faeroensis,* this specimen was designated neotype.

In ZMUC I found a misplaced jar labelled "*Polypus faeroensis,* Type, 61°27′N, 1°47′W, 1240 m, July 25, 1909. Russell det. Received from A. C. Stephen, the Fishery Board of Scotland, March 25, 1924." The specimen, a male with ML 34 mm, was caught a year after the specimens used for the description by Russell 1909 (and later 1922). I am inclined to believe it was received as a donation to ZMUC, but it is unknown whether Russell or the ZMUC curator (R. Spärck) is responsible for the "type" label. I found in BMNH a female specimen taken in the same haul as the above-mentioned male. Because it had been misplaced, the ZMUC-type is not recorded in the ZMUC type list (Kristensen & Knudsen, 1983).

The "type" in ZMUC might have been a better choice than the neotype designated by Toll, because it is a male, caught at the type locality and identified by the describer. Table 2 shows measurements of the specimen in ZMUC.

The ZMUC "type" has a VV-funnel organ. Hectocotylized arm with 39 suckers. The buccal mass has been removed, so the radula and beaks are missing. The esophagus has a

TABLE 2. Measurements (mm) of the *B. faeroensis* "type" in ZMUC.

TL:	105			AL:	I	II	III	IV
ML:	34			r	67	64	52	56
HW:	20	HWI:	59	l	70	62	59	57
MW:	27	MWI:	79					
ED:	12	EDI:	35					
LD:	3.7	SDLDI:	18.3			WD		
SD:	2.2	SDI:	6.5	A	B	C	D	E
LigL:	7	LigLI:	13.5	22	22	20	22	20
LamC:	11	SHcC:	42		?	25	21	

crop diverticulum. Needham's sac with four unripe spermatophores. SpL: 22 mm, SpRI 31, of the characteristic *arcticus* type (SpRI approx. 30; Fig. 2d).

In all measurable characters, the ZMUC specimen agrees with the general descriptions by Russell (1909, 1922) and Toll (1985).

Neither Russell nor Toll examined type material of *B. arcticus*. Both authors assumed that the "*bairdii*"-form is the true *B. arcticus*. Ironically, however, the species described by Russell and the *faeroensis* specimen in ZMUC is the genuine *Bathypolypus arcticus*, and all the data on *B. faeroensis* fit measurements and indices as indicated in the present redescription of that species. Toll's careful redescription of *faeroensis* might as well be a redescription of a female *arcticus*. The homodont rachidians pictured by Toll (his fig. 1b) are unusual but not unknown in *arcticus*. Homodont rachidians were found in one of two females (Fig. 5f, g) caught in the same haul at 68°00′N, 20°40′W (BIOICE Stn. 2751). In all aspects, Toll's specimen is indistinguishable from *B. arcticus*.

Benthoctopus sasakii Robson, 1927

Material examined: Types in BMNH: 89.1.24.33–34. A male and a female labelled: "*Benthoctopus sasakii* Robson, HMS 'Triton' Stn. 9, Faroe Channel, 60′5′N, 6′21′W, 608 fms. August 23, 1882".

Male: ML about 32 mm, distorted and dissected. Hectocotylized arm 59 mm with 44 suckers, LigL: 7.8 mm. Ligula with 12–15 indistinct lamellae. SD: 2.3 mm, ED: 10 mm, SpL: 34 mm, SpRL: 9 mm. Funnel organ VV with the outer limbs somewhat shorter than the median limbs. Skin smooth.

Female: TL: 100 mm, ML: 27, MW: 24, HW: 20, SD: 2.3 mm, ED: 10 mm. Funnel organ fragmented.

Robson (1927: 262, fig. 8) depicted the radula, which shows a more or less irregular seriation of multicuspid rachidians. Both specimens are typical of juvenile *B. arcticus*, as evidenced by the hectocotylus, the funnel organ and the indices: SDEDI: 23 and SpRI: 26 (Table 9). They were furthermore trawled in arctic water masses at the same depth and locality as *B. faeroensis* (= *B. arcticus*). Robson became doubtful about his *sasakii* and later (1932) treated it as a junior synonym of *Benthoctopus piscatorum* (Verrill, 1879), which prompted me to reexamination of the type of *piscatorum* in USNM.

Benthoctopus piscatorum (Verrill, 1879)

Material examined: Holotype USNM 574641. From western part of Le Have Bank off Nova Scotia, October 1879, 120 fms. (219 m). Female, ML: 39. Measurements are give in Table 3. The holotype was a unique specimen (Roper & Sweeney, 1978).

Description: The skin is smooth, with no evident sculpture. A much contracted cirrus detectable over the right eye, no trace over the left eye. The funnel organ partly missing but of *bairdii* type (Fig. 18). Esophagus without crop diverticulum, only with a slight swelling. Number of suckers on each arm 65–75. Radula and jaws not available.

Verrill's description (1879: 470) is not very exhaustive, as noted by Robson (1932). In Verrill's opinion, *piscatorum* was easily distinguished from *Octopus bairdii* "by a more elongated body, longer arms, shorter web, lack of supraocular cirrus and by its smoothness."

I believe that the type specimen of *Octopus piscatorum* is a somewhat aberrant specimen of *Bathypolypus bairdii* (Verrill, 1873), as is the case with his *O. lentus* and *O. obesus* (see below). None of the bodily proportions are distinctive. The only index that falls outside the natural variation of *bairdii* is SDEDI: 14 (Table 9), but this is compensated for by SDLDI: 28, which is a more reliable index, being based on the firm eye lense as standard for eye size (Fig. 16).

TABLE 3. Measurements of holotype of *Benthoctopus piscatorum*.

				AL:	I	II	III	IV
TL:	153			r	93	75	82+	78
ML:	39			l	98	102	77+	75+
HW:	28	HWI:	71			WD:		
MW:	33	MWI:	85					
ED:	15	EDI:	38	A	B	C	D	E
LD:	7.5	SDLDI:	28	25	16	27	24	12?
SD:	2.1	SDI:	5.4		32	32	25	

I believe that the smoothness of the body is due to contraction of all warts or flaccidity at the time of death, as seen in varying degrees in many preserved specimens of both *bairdii* and *arcticus*. Traces of a retracted cirrus over the right eye suggest that the smoothness over the left eye hides a potential cirrus.

The identity with *bairdii* is further substantiated by the lack of a crop diverticulum. This contrasts with Robson's statement that *piscatorum* has "a tolerably well-developed crop" (1932: 225) and his figure 31. However, Robson based this statement on dissections of *B. sasakii* (= *arcticus*).

In 1981, I discussed the *Bathypolypus-Benthoctopus* problems with Gilbert Voss, who also examined the type specimen of *piscatorum*. He concurred with my opinion that Verrill (1879) described a somewhat atypical specimen of *Bathypolypus* and consequently the genus *Benthoctopus* Grimpe, 1921, would be indistinguishable. (Voss & Pearcy 1990).

East Atlantic "*piscatorum*"

The true identity of *piscatorum* raises serious doubts as to the identity of the many specimens attributed to *piscatorum* from the East Atlantic by Hoyle (1886), Appellöf (1893), Pfeffer (1908), Massy (1909), Russell (1922), Robson (1932), Grieg (1933), and Grimpe (1933).

The first to record *piscatorum* from the Faroe Channel was Hoyle (1886). I examined his specimens in BMNH, and they are identical with the specimens later described as *Benthoctopus sasakii* by Robson (1927) and once again as *piscatorum* by Robson (1932). As argued above, the type specimens of *sasakii* are conspecific with *arcticus*.

Appellöf (1893), inspired by Hoyle (1886), identified three very juvenile specimens from 66°41′N, 6°59′E and 78°2′N, 9°25′E as *piscatorum*. He does not give particulars, except that the body is smooth and that mantle and head of the male measure 14 mm. One of the specimens was caught with a juvenile male "*Octopus lentus*" (junior synonym of *bairdii*), and later identified by Grieg (1933) as *piscatorum*. Because *piscatorum* specimens from the Svalbard-Barents Sea area are all caught in cold water (–0.9°–+0.8°C), I strongly suspect them to be smooth and partly juvenile specimens of *arcticus sensu stricto*. I dismiss the records as unreliable, although I have not seen the specimens.

Pfeffer (1908) merely repeated the American records of Verrill and the East Atlantic records of Hoyle (1886) and Appellöf (1893). He repeated Verrill's pictures of *piscatorum* and for unknown reasons synonymized *Benthoctopus ergasticus* with *piscatorum*. As shown below, *B. ergasticus* is a distinct species.

In conclusion, Pfeffer's records of *piscatorum* are unreliable.

Massy (1907) described *Polypus normani*, which she later, having consulted Pfeffer, decided was a *piscatorum* (Massy, 1909). It is a male, TL: 206 mm, trawled off Ireland at 51°15′N, 11°47′W, 707–710 fms., September 1907.

I have not examined the type, but Massy's measurements and drawings (1909: pl. II, figs. 3, 4) allow the conclusion that it is not conspecific with either the type of Verrill's *piscatorum* nor *bairdii* or *arcticus:* the hectocotylized arm has 64 suckers, far beyond the number found in *bairdii* (Fig. 8). OAI is 64.6, which is off the range of variation in *bairdii* and *arcticus*, in which OAI is about 80–90. SDI is 9.5, which means that the suckers are larger than in *bairdii* and *arcticus*. The smoothness of the skin and the bodily proportions given by Massy are not distinctive, but the shortness of the hectocotylized arm and its relatively high number of suckers reminiscent of *Benthoctopus ergasticus* (P. Fischer & H. Fischer, 1892). Two males and a female of this species were caught in the same haul as *normani*. Still, *B. normani* may be a valid species. Massy was advised by Pfeffer who, as mentioned above, considered *ergasticus* synonymous with *piscatorum*. The ligula and calamus of *normani* is clearly juvenile (Massy 1909: figs. 3, 4). Her figure was erroneously used by Nesis (1987: 318, fig. 84H) to illustrate the calamus and ligula of *piscatorum*.

Russell (1922) recorded three male and four female *Polypus piscatorum* taken in the Faeroe Channel in the same haul as his *P. faeroensis* ("Goldseeker" Stn. 19a). All seven specimens are juvenile. His measurements do not allow the species to be even tentatively identified. But if his measure "Posterior end to eye" is accepted as expression of the ML, the SDI of the largest female (ML: 32 mm) and the largest male (ML: 27 mm) is 9.4 and 7.4 respectively, beyond the sucker size of *bairdii*, but compatible with *arcticus*. The large female *faeroensis* (= *arcticus*) taken in the same haul (Russell, 1922: 6) has SDI: 8.3. The ligula of the largest male is depicted and shows a 6.5-mm-long typical juvenile *arcticus* ligula with

"half a dozen indistinct transverse ridges" (Russell, 1922: fig. 7).

Like many of the earlier writers, Russell has attached undue weight to the smoothness of the skin of his "*piscatorum*" specimens. I consider it indubitable that they are juvenile *arcticus,* as all the other specimens I have examined from the arctic water masses in the depth of the Faeroe Channel (Fig. 19).

Robson (1932) did not examine the type of *piscatorum.* He based his revision on three specimens, two of which are the specimens originally described as *piscatorum* by Hoyle (1886), later as *sasakii* by Robson (1927). As argued above, *sasakii* is a junior synonym of *arcticus.*

The only other specimen seen by Robson is a female (Robson's C30) surprisingly caught in the same haul as the "type" of *faeroensis* found in ZMUC: Faroe Channel 61°27′N, 1°47′W, 681 fms., July 25, 1909. I have examined the specimen at BMNH: the body is ovoid, the skin smooth with no trace of warts. The funnel organ is not well preserved but shows VV, the inner limbs are however weakly joined anteriorly. Measurements are given in Table 4.

Robson (1932: 225, fig. 35) shows the radula of this specimen. The rachidians are heterodont, showing irregular lateral cusps and a seriation of about four teeth. The esophagus has a well-developed crop diverticulum.

The multicuspid rachis teeth, the presence of a crop diverticulum, as well as the measurements and indices in Table 4 show that Robson's *piscatorum* is really the smooth-skinned specimen of *B. arcticus.*

In conclusion, *Benthoctopus piscatorum sensu* Verrill, 1879, is a junior synonym of *Bathypolypus bairdii,* whereas *B. piscatorum sensu* Hoyle (1886), Russell (1922), and Robson (1932) is smooth-skinned and often juvenile *Bathypolypus arcticus.*

A large female octopod caught 1967 at a depth of 60 fathoms in Placenta Bay, Newfoundland, and identified as *Benthoctopus piscatorum* by Aldrich & Lu (1968: table 1, figs. 1, 2) is undoubtedly misidentified and should be reexamined. With a TL of 362 mm, ML 89 mm and HWI of only 35, the specimen deviates considerably from both *B. bairdii* and *B. arcticus*. The authors were aware of the inconsistency with Robson's description of *piscatorum* but put it down to its poor state of preservation. Nixon (1991), studied the eggs of this specimen (as "*piscatorum*" eggs).

Revision of *B. arcticus* by Robson (1932)

Robson (1932) was very uncertain about the large number of forms ascribed to the *arcticus-bairdii* complex. Though with hesitation, he concluded that *faeroensis* with the ovoid body and narrow head at the one extreme and the *bairdii* form with the saccular body and large ligula at the other were one and the same species, *B. arcticus.*

Robson presented two excellent photos of the two forms (1932: pl. VI, figs. 1, 2), one of which is a "type"-specimen of *B. arcticus* from Greenland on loan from ZMUC. I have tried in vain to identify the specimen in the Copenhagen collections, but the photo is easily recognizable as *B. arcticus, sensu stricto.* The other photo depicts a typical *B. bairdii,* the square-bodied boreal form, which is reinstated as a distinct species below.

Because the two species were confounded, Robson's text is of limited use. Besides the photo, he provided (1932: 290–291) three figures of a *B. arcticus, sensu stricto,* from the Barents Sea: outline of mantle (fig. 54), an ocular cirrus (fig. 55), and a funnel organ (fig. 56). The radulae (fig. 58) are from *B. bairdii* specimens.

Robson (1932) enforced the prevailing taxonomic confusion by his erroneous identification of smooth skinned and juvenile *B. arcticus* as *Benthoctopus piscatorum.*

Records of *B. arcticus* by Adam (1939)

Adam (1939: 6, table, figs. 2–4) records six juvenile specimens of *B. arcticus* from

TABLE 4. Measurements of Robson's *Benthoctopus piscatorum.*

TL:	185			AL:	I	II	III	IV
ML	43			r	133	130	131	130
HW:	34	HWI:	79	l	129	136	?	134
MW:	48	MWI:	112			WD:		
ED:	14	EDI:	33	A	B	C	D	E
SD:	3.3	SDI:	7.6	30	33	38	38	30
		SDEDI:	24		35	36	39	

the Iceland-Faroe area (about 66°25′N, 12°30′W). I reinspected the material on loan from IRSNB and found, that four of the specimens (Adam's specimens b and c) were identical with *arcticus* as here redescribed. They all have the typical VV funnel organ and the diagnostic index SDLDI is: 53, 53, 53 and 59, respectively, which distinguishes *arcticus* from *B. bairdii* and *B. pugniger,* n. sp. (with SDLDI < 40). Two of the specimens are erroneously identified as females (specimens b: ML 14 and 16 mm). They are juvenile male *arcticus* with undifferentiated ligulae of 1.5 and 1.9 mm. Adam's drawing of the radula of a female *arcticus* (p. 12, fig. 4, specimen c) shows a homodont rachidian reminiscent of the radula from "*B. faeroensis*" pictured by Toll (1985: 600, fig. 1) and my Figure 5g. It underlines the fact that *B. arcticus* has a very variable radula.

The remaining two specimens of the material treated by Adam (1939: specimens a, figs. 2, 3), I consider to be *B. pugniger*, n. sp., and are discussed below.

REINSTATEMENT AND REDESCRIPTION OF *BATHYPOLYPUS BAIRDII* (VERRILL, 1873)

Material examined: about 500 specimens from boreal parts of the North Atlantic as listed in Appendix I. Types examined: *Octopus bairdii* Verrill, 1873 (syntype, USNM 574638) *Octopus piscatorum* Verrill, 1879 (holotype, USNM 574641) *Octopus lentus* Verrill, 1880 (holotype, USNM 34223) *Octopus obesus* Verrill, 1880 (holotype, USNM 382469).

Synonymy

Octopus bairdii Verrill, 1873a: 5; 1873b: 394, figs. 76, 77; 1881: 107, pl. 2, fig. 4, pl. 4, fig. 1; 1882: 368, pl. 33, fig. 1, 1a, pl. 34, figs. 5, 6, pl. 36, fig. 10, pl. 38, fig. 8, pl. 49, fig. 4, 4a, pl. 51, fig. 1, 1a; Sars, 1878: 339, pl. 17, fig. 8, pl. 33, figs. 1–10; Kumpf, 1958 (passim)

Octopus piscatorum Verrill, 1879: 470; 1882: 377, pl. 36, figs. 1, 2

Octopus obesus Verrill, 1880: 137; 1882: 379, pl. 36, figs. 3, 4; Robson, 1932: 299; Kumpf, 1958 (passim).

Octopus lentus Verrill, 1880: 138; 1881: 108, pl. 4, fig. 2; 1882: 351, 375, pl. 35, figs. 1, 2, pl. 51, fig. 2; Robson, 1932: 297; Kumpf, 1958 (passim)

Octopus arcticus: Norman, 1890: 466; Joubin 1920: 32, pl. 7, figs. 4, 5

Polypus arcticus: Pfeffer, 1908: 16, fig. 6

Polypus lentus: Pfeffer, 1908: 17, figs. 7, 8

Bathypolypus arcticus: Robson, 1932 [in part]: 286, figs. 53–60, pl. 6, figs. 1, 2; Thiele, 1935: 992, fig. 890; Boone, 1938: 360, pl. 152; Bruun, 1945 [in part]: 6; Kumpf, 1958: 1–135; Jaeckel, 1958: 563: Cairns, 1976: 261; Macalaster, 1976; Perez-Gandaras & Guerra, 1978: 201, figs. 6–8; O'Dor & Macalaster, 1983: 401, fig. 24.1, 24.2; Roper et al., 1984: 222; Nesis, 1987: 315, fig. 83B–E; Guerra, 1992: 251, fig. 89

Bathypolypus proschi Muus, 1962: 13, figs. 2–4

Diagnosis

Square-bodied, with papillated skin; arms short; head broad, with large eyeballs, each with a supraocular cirrus; funnel organ double, pad-like; hectocotylized arm with about 40 suckers; ligula very large deeply excavated with 8–12 prominent laminae. Radula with homodont central teeth. Esophagus without crop diverticulum. Total length rarely over 200 mm.

Description

Skin and Colors: In newly caught specimens, the skin is violet to purple, often without any conspicuous spots or patterns, but sometimes speckled with small greyish spots. In preserved specimens, the skin may be smooth, but more often the dorsal surface is papillated, especially in the antero-dorsal region. Single warts or aggregations occur, the latter sometimes in a stellate pattern, a number of small warts encircling a larger one, similar to *B. arcticus.* Over each eye is an erectile pointed cirrus with adjacent smaller protuberances. Erected it measures 5–10 mm.

Bodily Proportions: Square-bodied, with broad head and huge eyeballs. HWI decreases from 80–100 at ML 10 to 60–90 at ML 60 mm. TL rarely over 200 mm.

The eyeballs are very prominent. They decrease in relative size from EDI 40–60 at ML 10, to 30–45 at ML 60 (Fig. 4). The lens measures on an average 41% of the ED (LDEDI: 35–46).

The mantle aperture is 36–42% of the cir-

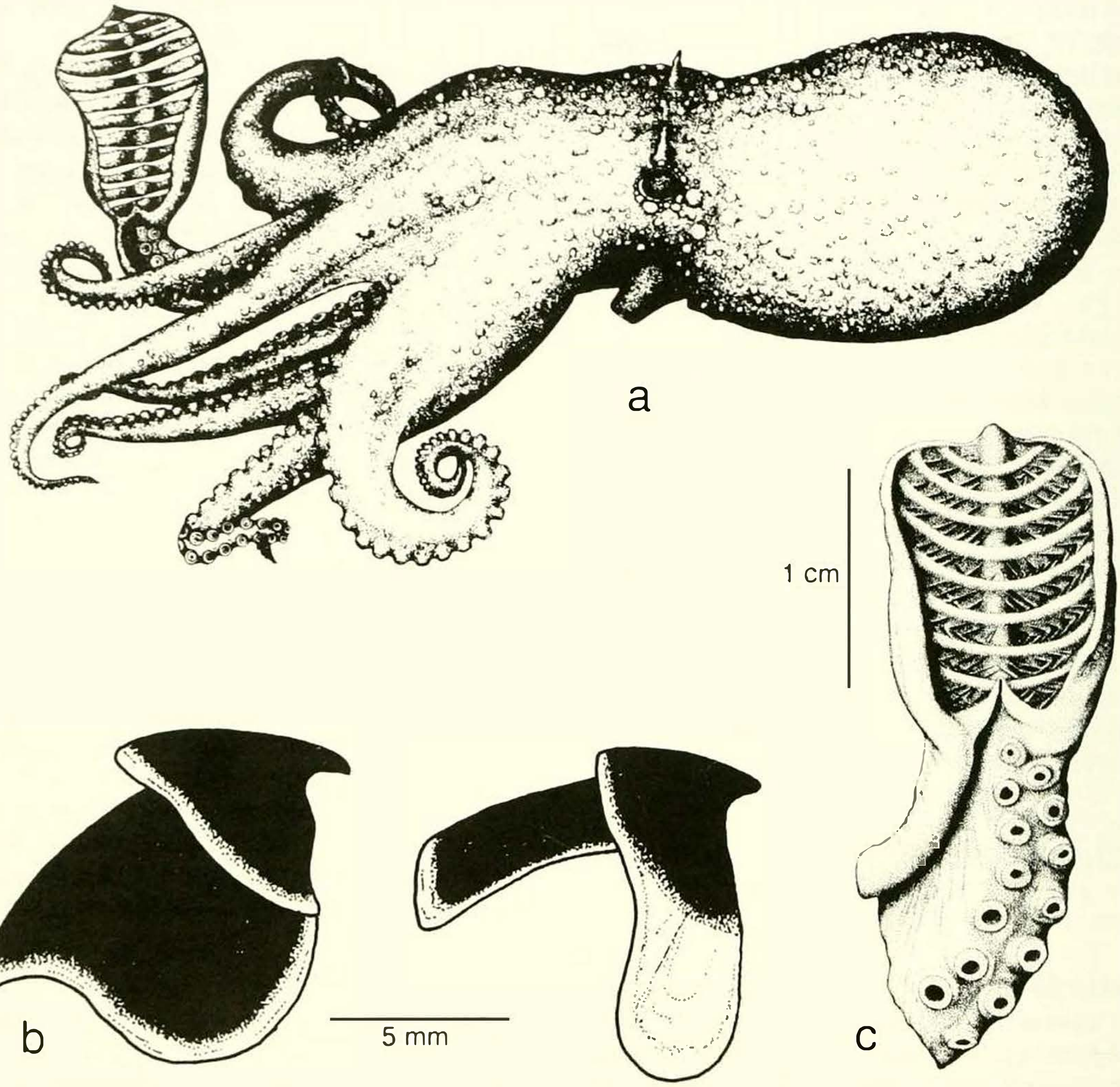

FIG. 6. *Bathypolypus bairdii* (Verrill, 1873). a: habitus (after Vecchione et al., 1989); b: upper and lower beak; c: hectocotylus of ♂ ML 42 mm, Greenl. Fish. Invest. Stn. 5047, ZMUC.

cumference of the mantle. The funnel is free of the mantle for about 50%.

The funnel organ consists typically of two pad-like structures with a very variable appearance (Fig. 18). They are never strictly VV-shaped, but may have an anterior indentation like a heart or be broken up into bars, suggesting an evolutionary past as VV-shaped organs. They are rather loosely connected with the funnel wall and easily lost.

The gills are reduced and have 6–8 gill filaments on each demibranch.

The arm order is I.II.III.IV. The ML constitutes 28–38% of the TL, which leaves 62–73% to the brachial complex. ALI: I 201, II 184, III 174, IV 168 (mean of 21 specimens).

The web extends along the arms. The web sectors B, C and D are subequal. WDI: A 32, B 35, C 36, D 35, E 27. WDMI: A: 54, B: 59, C: 60, D: 59, E: 46 (mean of 21 specimens).

The suckers are biserial, small and well spaced. SDI: 2.9–3.9–4.8 depending on degree of expansion. They are similar in size on all arms, and there is no sexual dimorphism.

The hectocotylized third right arm is shorter than the left (OAI: mean, 88). Spermatophoral groove well developed. The number of suckers on the hectocotylized arm shows geographical variation: the east American population (S of 45°N) has 26–40 suckers, whereas specimens from western Greenland and the eastern Atlantic have 35–49 (Fig. 8). The number is individually constant throughout life (Fig. 23).

The ligula is a large spoon-shaped organ, which in ripe animals (ML > 30 mm) is often

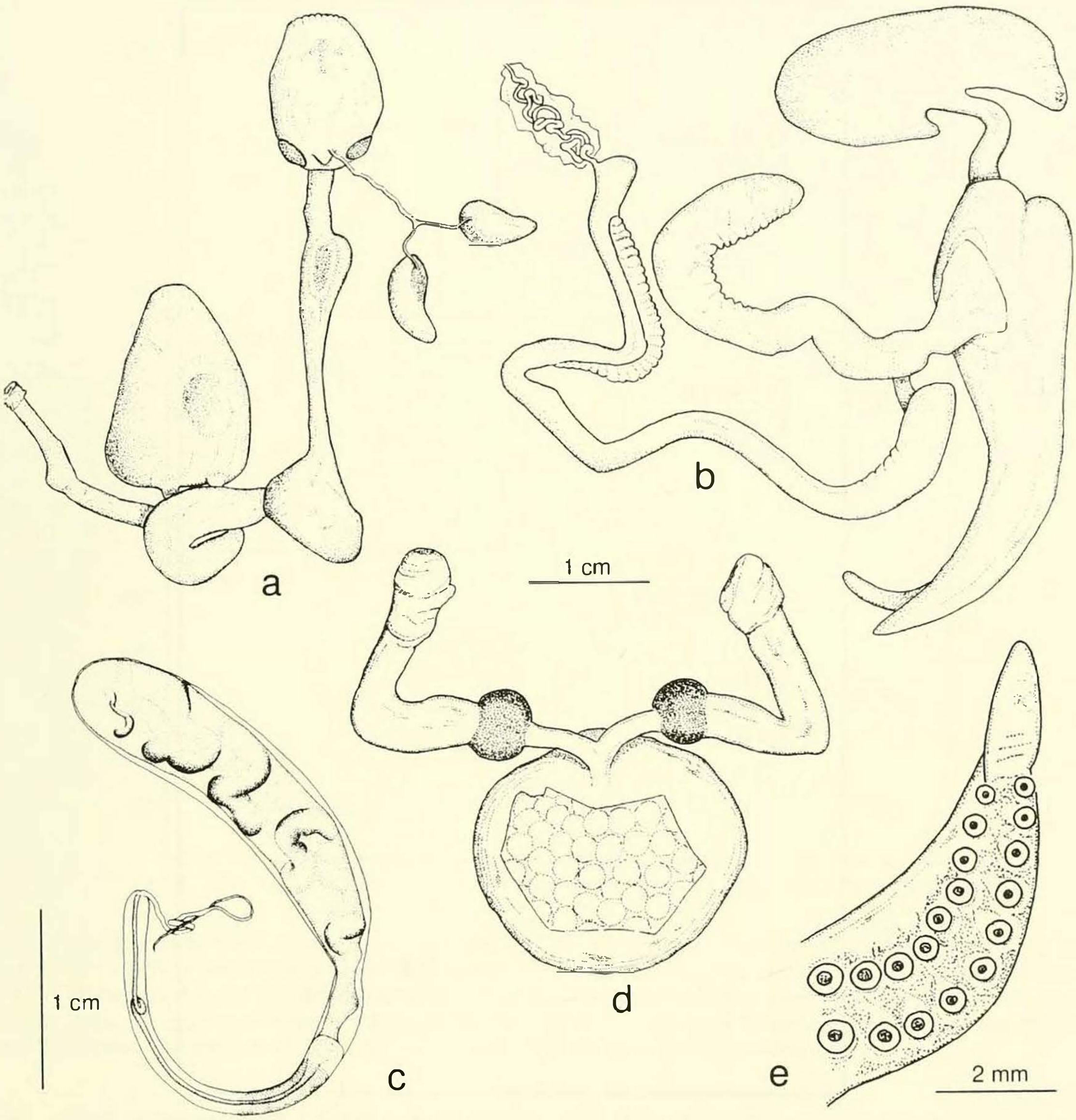

FIG. 7. *B. bairdii.* a: digestive tract; b: reproductive organs; c: spermatophore of ♂ ML 41 mm, Dana Stn. 11648, ZMUC; d: female reproductive organs, ML 41 mm, Greenl. Fish. Invest. Stn. 5112; e: hectocotylus of juvenile ♂ ML 23 mm, Dana Stn. 2346, ZMUC.

rather square, with almost parallel sides distally ending with rounded flaps and a small pointed tip (Fig. 6). The width is 50–75% of the length. It has a central ridge and a number of deep and well-separated laminae. The number is individually constant from the onset of maturity. It has a total range of 7–13, but shows a geographical variation that is very apparent in the western Atlantic, the Newfoundland waters being a transitional area between the American population and the populations off Labrador and western Greenland (Fig. 9). Also, the size of the ligula in ripe animals shows geographical variation: at a ML > 30 mm, LigLI in the eastern American population is 24–44, whereas in western Greenland and the rest of the North Atlantic, it is 18–38. The American population apparently reaches maturity at a ML of 25–35 mm, whereas in the rest of the Atlantic maturity is generally reached at ML 30–40 (Fig. 10).

Calamus is short and pointed (CaLI approx.

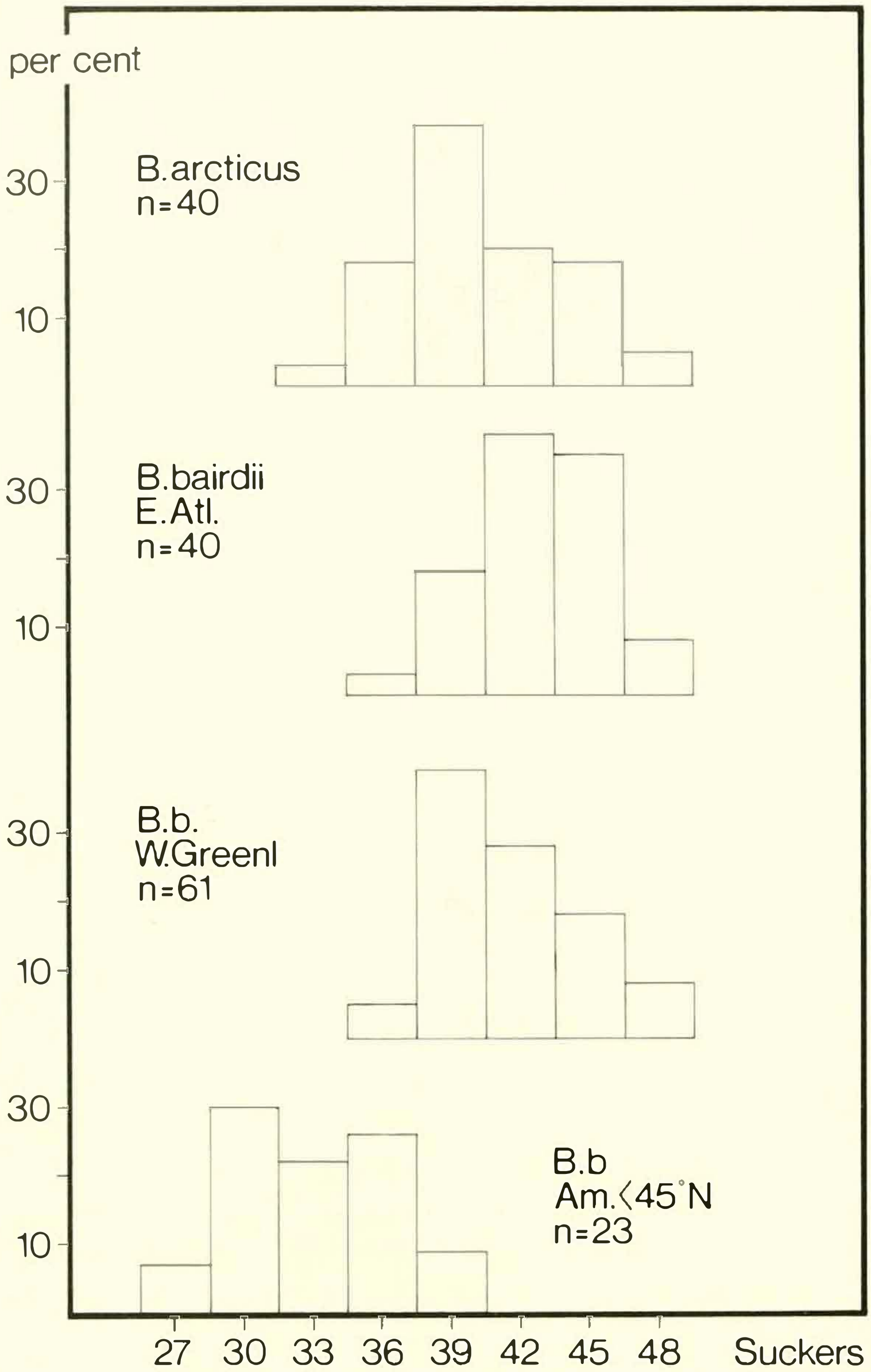

FIG. 8. The American population of *B. bairdii* (< 45°N) deviates in mean number of suckers on the hectocotylus from the western Greenland population (P = 0.95); mean: 32.6, SE 2.6 versus 41.4, SE 3.4. The eastern Atlantic population differs only slightly from Greenland (mean: 42.7, SE 3.1). Inserted: *arcticus,* mean: 39.7, SE 3.1.

20). Already at ML 11 mm the ligula may be identified as a 1.2-mm-long undifferentiated tip of the third right arm.

Female Organs: The ovary is large, with conspicuous globular blackish oviducal glands (Fig. 7d). Ripe females with 60–85 yellowish eggs measuring 15–18 mm in length. The eggs are smooth with fine longitudinal lines.

Male Organs: The penis with well-developed diverticulum (Fig. 7b). In Needham's sac was found up to six spermatophores. The sausage-shaped sperm reservoir of the spermatophore occupies about half of the total length, and the oral end is a slim, rather stiff and curved tube (Fig. 7c; Verrill, 1882: pl. 36, fig. 10). The spermatophore is glossy and opaque; the interior details are difficult to make out. SpLI: 60-90-115, SpWI about 19, SpRI 50–60.

Jaws and Radula: The beaks do not present distinctive features. The radula is homodont, the rachidians having smooth concave sides

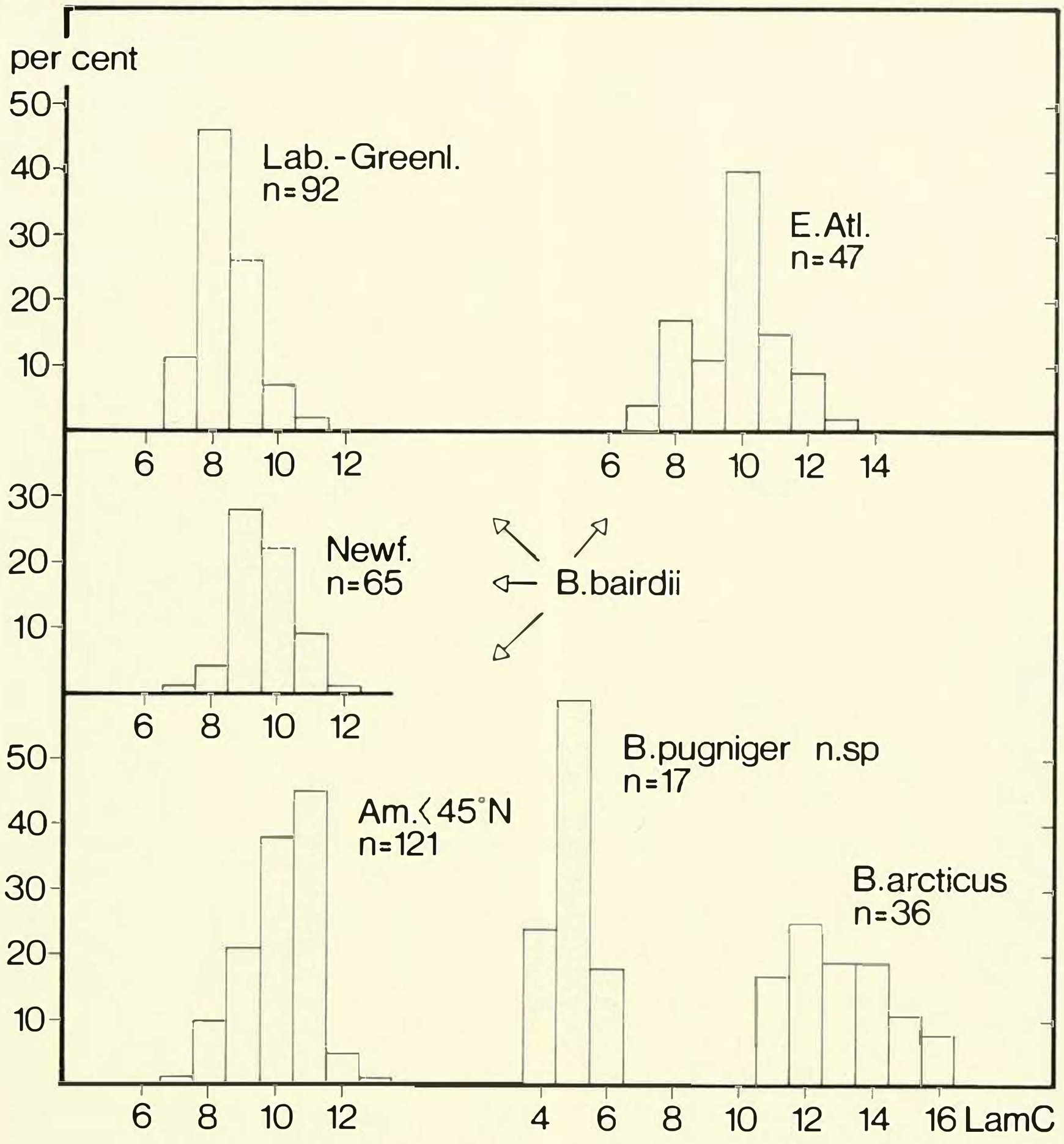

FIG. 9. Number of laminae copulatoriae. *B. bairdii* shows geographic variation with a highly significant difference (P: > 0.99, z-test) in mean number between the American (< 45°N) and the western Greenland population (mean: 10.12, SE 0.109 versus 8.38, SE 0.3). The Newfoundland area forms a transitional zone (mean: 9.56, SE 0.2). East Atlantic (mean: 9.89, SE 0.2) versus western Greenland shows a similar significant difference. Variation in *B. pugniger*, n. sp., and *B. arcticus* inserted for comparison.

and never showing any sign of ectocones (Fig. 11; Verrill, 1882: pl. 49, fig. 4).

Digestive Tract: The esophagus has no crop diverticulum, only a slight swelling where the posterior salivary glands are fastened when in situ (Fig. 7a). The spiral caecum is reduced to less than one turn. The liver is large, about the same size as the testis.

Junior Synonyms of *B. bairdii*.

Robson (1932) strongly suspected that *Octopus lentus* Verrill, 1880, and *O. obesus* Verrill, 1880, were conspecific with the typical *bairdii* form, because he was not able to find critical differences. Not having seen the type specimens, however, he hesitated to place them in synonomy.

In a master's thesis, Kumpf (1958) tried to sort out the *Bathypolypus arcticus-bairdii-lentus-obesus* complex. He had a large amount of material, 178 specimens, caught off the eastern American coast, including the types of Verrill's *Octopus bairdii, O. lentus* and *O. obesus*. In addition, he used measurements of seven "*B. arcticus*" specimens examined by Gilbert Voss in the BMNH.

Kumpf applied the standard of measurements of Robson (1927, 1932) and amplified by Pickford (1945, 1949). He thoroughly compared his material with the types of *bairdii, lentus* and *obesus* and concluded that these species are conspecific and that in spite of all variation, only one *Bathypolypus* species is represented in his material.

I can confirm this part of his conclusion. The bulk of Kumpf's material stems from between

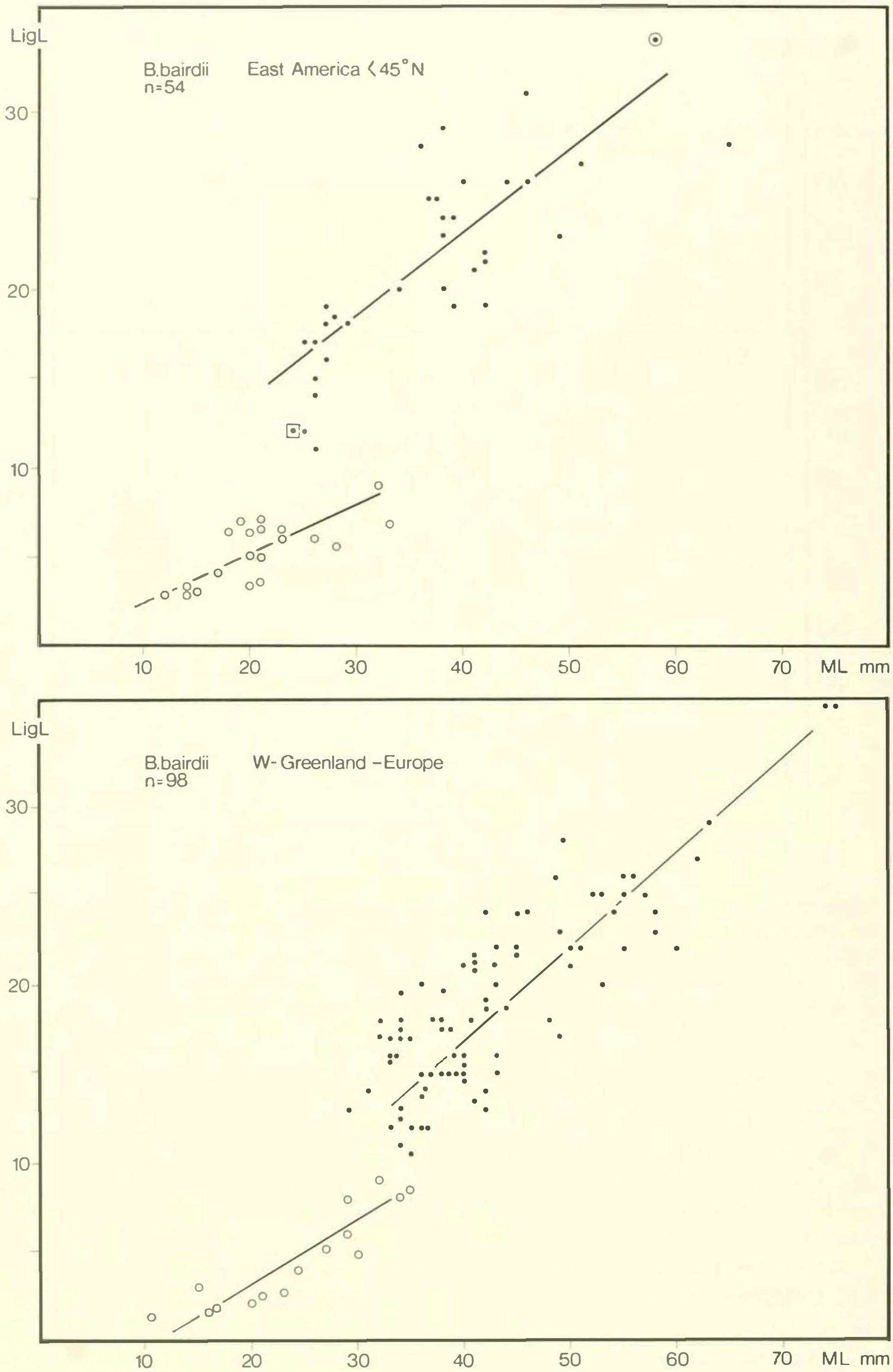

FIG. 10. Ligula length versus mantle length in *B. bairdii*. Open circles: juveniles. Lower figure: pooled data for western Greenland and NE Atlantic (juv.: $y = -3.34 + 0.333x$, $r^2 = 0.58$; ad.: $y = -3.20 + 0.505x$, $r^2 = 0.66$).

Upper figure: Eastern America < 45°N (juv.: $y = -0.49 + 0.248x$, $r^2 = 0.39$; ad.: $y = 4.90 + 0.452x$, $r^2 = 0.58$).

In eastern America, maturity is often reached already at ML 25 mm and ligula grows larger than in the North Atlantic. Dot in circle: syntype of *bairdii* (USNM 574638). Dot in square: holotype of *B. obesus* (Verrill, 1882) (USNM 382469).

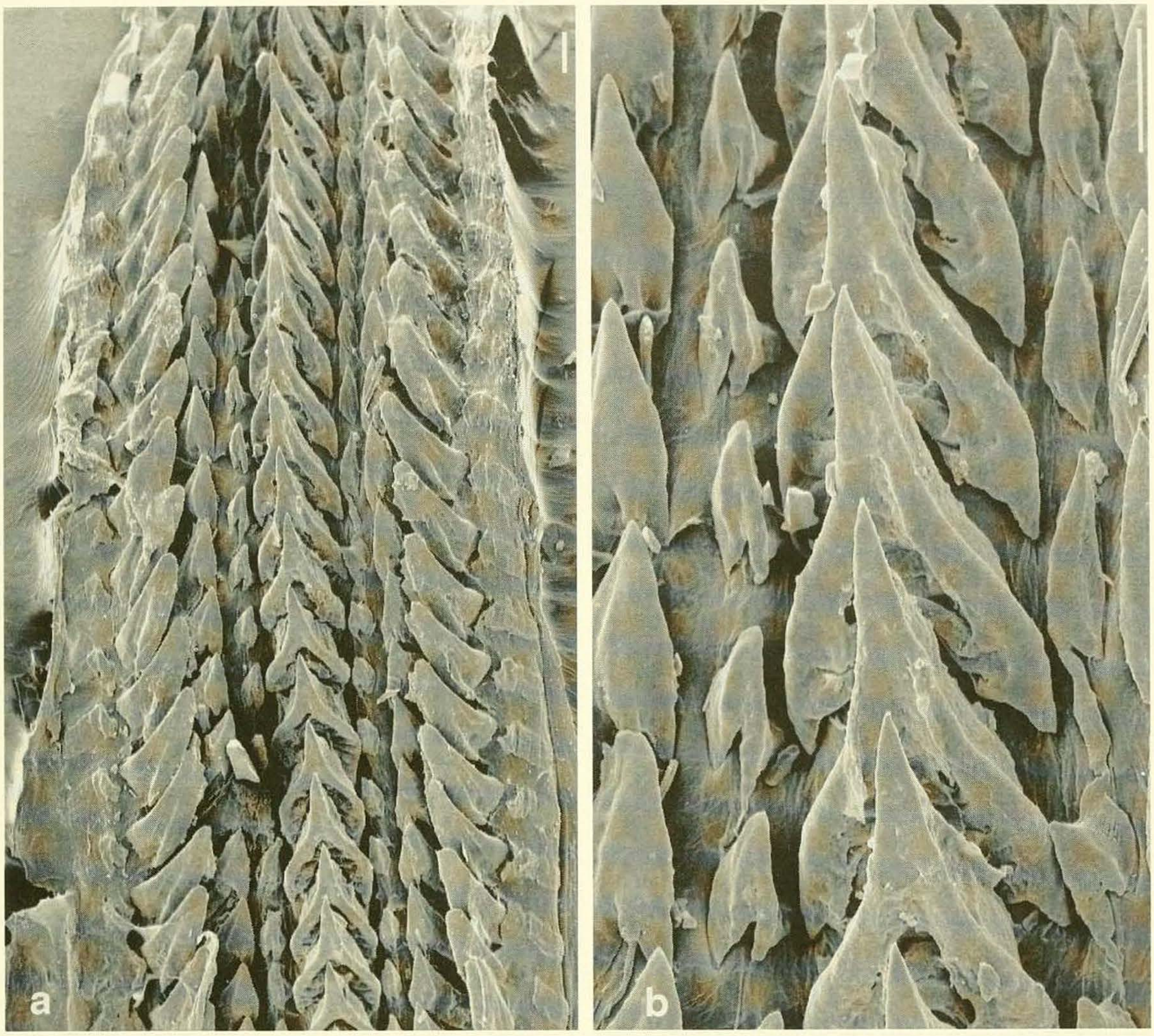

FIG. 11. Radula and central teeth of *B. bairdii.* ♂ ML 55 mm., Davis Strait 65°12′N, 56°21′W. Scale: 100 μm.

30°N and 45°N, and I examined and remeasured most of it, including the types of *bairdii, obesus* and *lentus*, during a visit to USNM in 1975. The data are included in the present revision.

Kumpf's main conclusion, however, that Verrill's species are junior synonyms of *arcticus*, is erroneous. The genuine *arcticus* is a more northerly species, not found off the east coast of USA (Fig. 20). Paradoxically, Kumpf never saw the species he purports to revise. To understand *B. arcticus*, he had to rely on the literature, especially on Robson's (1932) revision, with all its ambiguities and errors. Kumpf focused on the squat "*bairdii*-type" as being the typical *arcticus*, thus missing the point that Verrill's *bairdii* is a separate species.

Kumpf (1958) was incorrect in stating that Verrill did not know of Prosch's *arcticus*. In a footnote describing *bairdii,* Verrill (1873a: 5) wrote that his species differed from *O. groenlandicus* Dewhurst, which has a smaller hectocotylus "with more numerous folds, and the basal part bears 41–43 suckers". This is a citation from Steenstrup's then well-known paper (1856a, or the translations of it: 1856b, 1857), in which *O. groenlandicus* is synonymized with *arcticus* and in which the species and its hectocotylized arm are figured (see also Verrill, 1880: 138, footnote).

The knowledge of West Atlantic *Bathypolypus* was much extended and elaborated upon by Macalaster (1976), who studied no less than 750 *Bathypolypus* specimens collected in Canadian waters from Georges Bank to the Labrador Sea. Macalaster was warned by me that "*arcticus*" covered more than one species, but through morphometric analyses

she showed convincingly that only one species occurs in Canadian waters and that it is identical with Kumpf's "*B. arcticus*". Leaning on Kumpf's revision, she excusably put the wrong species in the title of her otherwise valuable contribution, instead of *B. bairdii*. This mistake was repeated by O'Dor & Macalaster (1983) and by Wood et al. (1998), which are in fact accounts of life cycle and breeding ecology, respectively, of *B. bairdii*, not of *B. arcticus*, as indicated in the titles.

Macalaster's primary interest was not taxonomy but the opportunity to study the life cycle, growth, and reproduction of *Bathypolypus*, including observations of live animals kept in aquaria. Of principal interest to the present revision, however, is Macalaster's comprehensive measurements, which supplement Kumpf's (1958) and my own American data and which show that *B. bairdii* is commonly distributed along the upper part of the slopes from Florida to the Labrador Sea and that the genuine *B. arcticus* seems to be absent. I included some of her data as a supplement to my own to demonstrate morphological differences between the southern and northern populations of *B. bairdii*.

Octopus piscatorum Verrill, 1879

A full account of this nominal species and description of the holotype is given above under the synonymy of *B. arcticus*, which has been the species most often mistaken for *piscatorum*. It is here shown beyond reasonable doubt that *O. piscatorum* is a junior synonym of *O. bairdii* Verrill, 1873. It is also shown that Robson's concept of *piscatorum* was based upon misidentified *arcticus* specimens from the Faroe Channel and that consequently characters of *B. arcticus*, for example, presence of crop diverticulum, multicuspid radula, have crept into his diagnosis of *piscatorum*. This of course has repercussions on the concept of the genus *Benthoctopus*, of which *piscatorum* is the type species.

Bathypolypus proschi Muus, 1962

Holotype: Male TL 115 mm, "Dana" Stn. 10018, 65°02′5″N, 56°00′W, Davis Strait, 730–740 m, trawl, July 19, 1956. Depository: ZMUC.

The unanimous claim among earlier authors (exception: Sars, 1878) that *bairdii* is synonymous with *arcticus* led me to describe *proschi* as a new species, because it was obviously distinct from the type material of *B. arcticus* (Muus 1962: 18, table III).

The large amount of material now available and examination of Verrill's types of *bairdii* made it evident that *proschi* is identical with the here-reinstated *bairdii* and is a junior synonym of that species. It should however be pointed out that there are (subspecific?) morphological differences between the American and West Greenland populations (see below).

Bathypolypus Species Recorded from Northwestern Spain

A paper by Perez-Gandaras & Guerra (1978) recorded for the first time *Bathypolypus* from 120–439 m off the Galician coast. Of 22 specimens, 14 were identified as *B sponsalis*, three as *B arcticus*, another three (type A) with hesitation as *B. proschi*, while two defective specimens could not be assigned to any known species.

The present revision shows that it is highly improbable that *arcticus*, a true arctic species (Fig. 20), would be found off Spain. The boreal *bairdii*, formerly confused with *arcticus*, is a more likely candidate and could be expected to have its southern East Atlantic limit somewhere in the Biscayan neighbourhood.

The data for "*arcticus*" given by Perez-Gandaras & Guerra (Table 5) seem to support this expectation. The specimens concerned are two males, ML: 27–39 mm, and a female, ML: 37 mm.

With few probably insignificant deviations, the index values lie within the range of variation of *bairdii* (Table 9) and exclude the other here recognized *Bathypolypus* species. Such important meristic characters as number of laminae copulatoriae (8–10) and suckers on the hectocotylized arm (31–35) confirm affinity to *bairdii*. One male specimen figured by Guerra (1992: 252, fig. 89) shows a typical *bairdii* form, apart from the ligula, which has a pointed tip different from the broad-tipped norm for *bairdii* known from eastern America and the Scotland-Greenland Ridge (Fig. 6).

Some other characters described by Perez-Gandaras & Guerra (1992) are ambiguous. The rachidian (their fig. 7) is described as multicuspid on account of two very small cusps at the base. This is unusual in the northern populations of *bairdii*, which have smooth bases (Fig. 11). Further the sper-

TABLE 5. Measurements (mm), indices and counts of three dubious "*arcticus*" from the Galican coast extracted from data of Perez-Gandaras & Guerra (1978).

Sex	male	male	female
TL:	78	102	113
ML:	27	39	42
MLTLI:	35	33	37
HWI:	85	62	62
EDI:	44	36	31
SDI:	5.2	4.4	5.7
SDEDI:	12	12	18
ALI:			
I	178	179	150
II	174	179	152
III	174	179	136
IV	167	167	131
HcLI:	130	115	—
OAI:	74	64	—
LigLI:	20	18	—
LamC:	9–10	8–9	—
SHcC:	31	35	—
SpLI:	—	144	—
SpRI:	—	31	—

matophore (their fig. 8) has a reservoir occupying only 31% of the spermatophore length, which among the *Bathypolypus* species is a value known only from *arcticus* (Table 9). Apart from the longer oral end, the spermatophore has proportions similar to what is found in *bairdii*, for example, the characteristic light swelling seen in the cement gland portion. In *arcticus*, the oral end of the spermatophore is a thick, opaque tube with no swelling where the cement gland is located (Fig. 2d).

Unfortunately, funnel organ and digestive tract were not described. Until further material can be studied, I think the three specimens should be assigned to *B. bairdii*, but with reservation.

"Type A", described by Perez-Gandaras & Guerra (1978: figs. 9–11) includes one female and two males, ML: 34–40 mm, that could not be assigned to a known species with any certainty. The authors suggest *B. proschi*, but that species is now shown to be synonymous with *bairdii*. The specimens possess a peculiar supraocular cirrus, which is smooth, cylindrical and raised at the anterior edge of a hemispherical wart (their fig. 9). The ligula (their fig. 10) is a simple spoon-shaped organ with midrib and 9–12 low laminae and a small pointed calamus, LigLI: 16–18. Compared with *bairdii*, it looks juvenile. Proportions of body, spermatophore and most indices (their table 4) are compatible with *bairdii*. The rachidians have two small denticles at their bases like the "*arcticus*" specimens described above, and one radula is abnormal, having nine rows of teeth (their fig. 11). One male (Guerra, 1992: 254, fig. 90) has much smaller eyeballs (EDI: approx. 27, measured on the drawing) than indicated by Perez-Gandaras & Guerra (1978: table 4), in which EDI is given as 35-41, compatible with *bairdii*.

I think "type A" has to retain its dubious position until a larger series of specimens becomes available.

Bathypolypus pugniger, n. sp.

Material examined: 31 specimens from the Iceland-Faroe area as listed in Appendix I.

Holotype: Male, ML 32 mm, Icelandic Fishery Investigations, haul B5-78-44, 64°58′N, 27°44′W, 860–870 m, March 14, 1978. Measurements: Table 5, specimen 470. Depository: IMNH 19990971.

Paratypes: 9 males, 10 females as listed and measured in Tables 6 and 7.

Synonymy

Bathypolypus arcticus: Adam, 1939 [in part]: 9, figs. 2, 3

Diagnosis

Ovoid or square-bodied with papillated skin; arms very short, arm order III:IV:II:I or of subequal length; head broad, with large eyes, each with a supraocular erectile cirrus; hectocotylized arm with about 35 suckers; ligula globular fleshy and deeply excavated, with 4–6 laminae; funnel organ double and pad-like. Radula with broad homodont central teeth; esophagus without crop diverticulum. Total length rarely over 150 mm.

Description

Skin and Colors: Freshly preserved, the skin is violet to purple dorsally, ventrally lighter and yellowish or brownish. The antero-dorsal region more or less equally strewn with numerous small warts. Over each eye is a 3–7 mm-long single verrucose cirrus, which may be bifurcated, the anterior branch being shortest, or there are two closely set cirri.

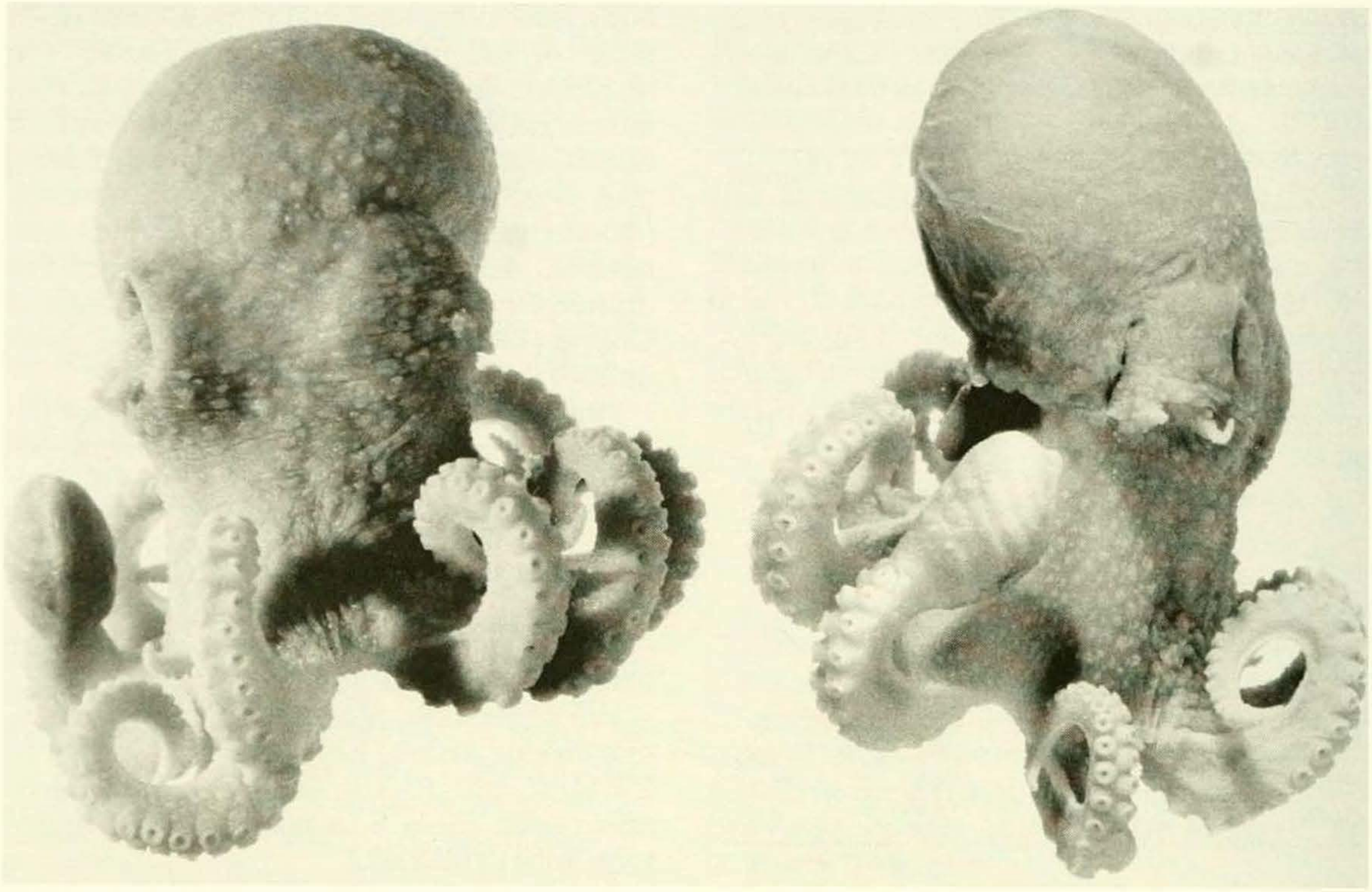

FIG. 12. Holotype of *Bathypolypus pugniger*, n. sp., ♂ ML 32 mm. Depository: IMNH 19990971.

Bodily Proportions: Ovoid (Fig. 12) or more square-bodied, like *bairdii* (Fig. 13), with large eyeballs. MWI: males 67-92-106, females 73-96-118. HWI: males 73-85-100, females 48-79-96. TL rarely 150 mm, ML rarely over 50 mm. MLTLI: 33-37.5-42. EDI for both sexes 30-44-50, highest for young specimens. The lens measures on an average 37% of the eye diameter. The rough diagnostic index SDEDI, useful to discriminate *arcticus* and *bairdii,* shows *pugniger* to lie between the two species (Table 9). The corresponding relation between SD and LD is supposed to be more accurate, but still shows some overlap with young specimens of *bairdii* (Fig. 16).

The mantle aperture is about 40% of the mantle circumference, and the funnel is free for about 50%.

The funnel organ is a couple of pad-like structures sometimes heart-shaped but variable as in *B. bairdii* (Fig. 18).

The gills are reduced and have 6–7 gill filaments on each demibranch.

The arm length order is III:IV:II:I or subequal (Tables 6, 7). This is reverse from arm order of *B. arcticus* and *B. bairdii.* The ML constitutes 33–42% of the TL making *B. pugniger* the most short-armed of the three species. ALI: I 145, II 150, III 155, IV 154 (means in Tables 6, 7).

The web extends along the arms. WDMI: A 53, B 56, C 59, D 60, E 51 (mean of 18 specimens). In well-preserved specimens, web sectors C and D tend to be subequal.

The suckers are biserial, small, and well spaced. Each arm with 65–75 suckers. They are of the same order of size on all arms, and there is no sexual dimorphism. SDI: 4.7-5.8-7.6.

The hectocotylized third right arm is usually slightly shorter than the left opposite arm. OAI: 83-91-106. It has 31-35-45 suckers. Spermatophoral groove well developed.

The ligula is fleshy, short, and broad, with firmly inrolled borders, giving it a globular appearance as a clenched fist (Figs. 12, 13c). LigLI: 22-27-34 in 11 specimens > 25 mm ML. The ligula has a tiny pointed tip between the broadly rounded anterior flaps (Fig. 13a). The width is 80–100% of the length. The spoon has a central ridge and 4–6 deep, well-separated laminae (Figs. 9, 13a). Calamus is stout, CLI: 26-38-51. Already at a ML of 6 mm, the nectocotylized arm may be identified by the

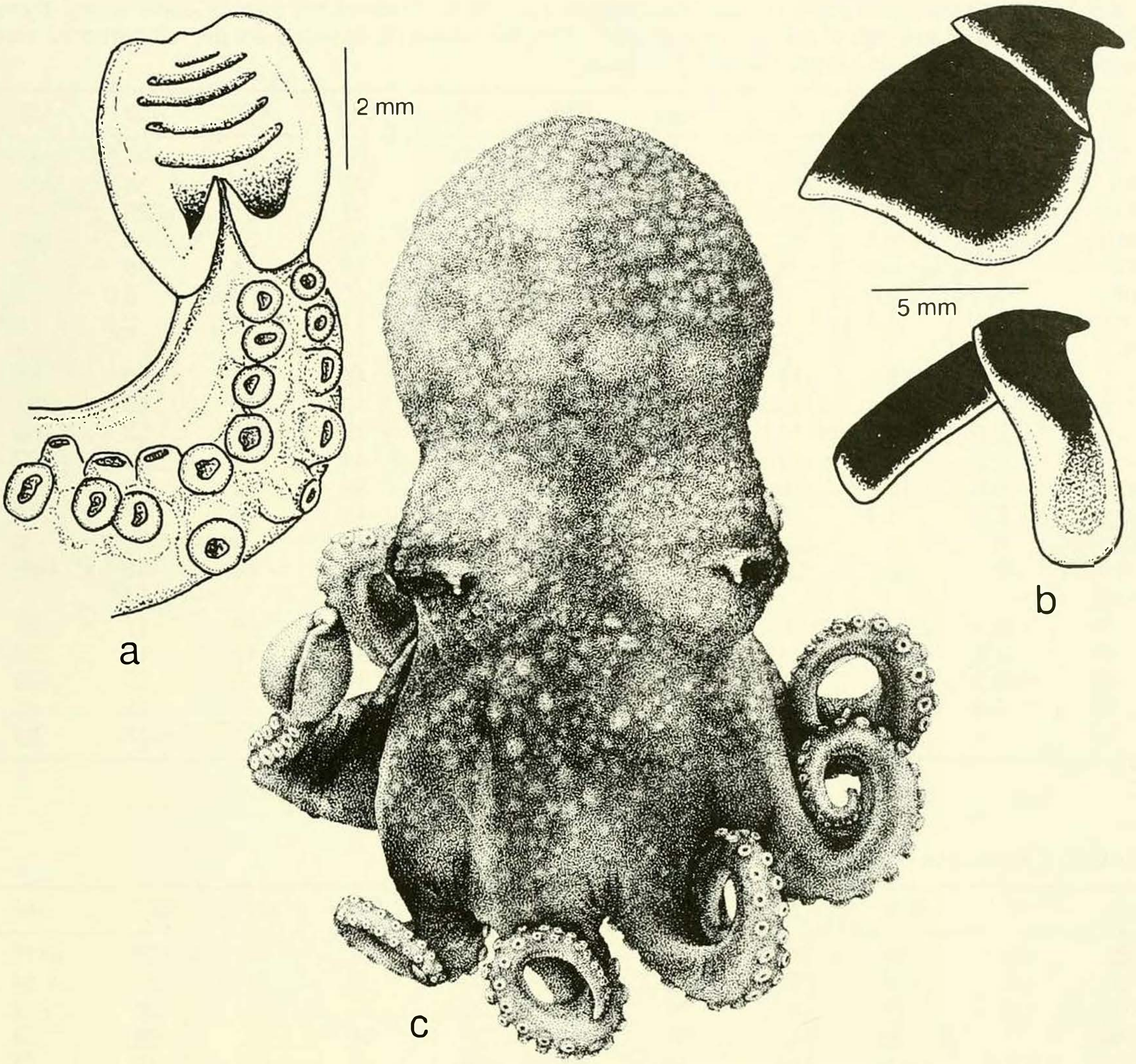

FIG. 13. *Bathypolypus pugniger*, n. sp. a: distal hectocotylus of young ♂ ML 18 mm. The "clenched" ligula was forced open to show the laminae; b: upper and lower beak of ♂ ML: 33 mm; c: paratype ZMUC CEP-17, ♂ ML 54 mm. Dana Stn. 16437, southwestern Greenland.

0.8-mm-long, as-yet undifferentiated ligula (Table 6: no. 77).

Female Organs: The ovary is large with blackish globular oviducal glands (Fig. 14a, b). Proximally the oviducts are joined, distally they are short, stout, leaving the oviducal glands forming right angles. Supposedly ripe eggs measure about 10 mm. They are smooth, with fine longitudinal lines.

Male Organs: The penis with well-developed diverticulum (Fig. 14f). The spermatophores are of *bairdii* type, with sausage-shaped sperm reservoir occupying about 55% of the total length. SpLI: 60-100.

Beaks and Radula: The beaks do not present distinctive features. Only four radulae have been investigated. The rachidians deviate considerably from both *arcticus* and *bairdii* (Fig. 15), whereas the lateral teeth show no distinct features. Basically, the rachidians are homodont, but they may be very broad with highly set or drooping shoulders (Fig. 15b, e, respectively) or just stocky and pointed homodont, with almost straight sides (Fig. 15c, f), but different from the slim, slightly concave homodont teeth of *bairdii*.

Digestive Tract

The esophagus has no crop diverticulum, but swells to double diameter from the point

TABLE 6. Measurements (mm) of male *Bathypolypus pugniger*, n. sp. (Note that in Tables 6 and 7 arm length is given as average of paired arms, except for males, where AL III represent the left arm only. Web depth for sectors B, C and D are likewise averages.)

No	77	76	75	659	653	463	648	470	453	122
TL:	11	30	38	51	67	76	88	90	91	146
ML:	6.2	11	15	18	25	30	33	32	36	54
HW:	5.9	10	12	15	25	22	27	31	29	45
MW:	5.5	9.3	12	19	28	20	34	32	33	45
ED:	2.0	4.5	6.2	10	13	11	13	16	16	22
LD:	1.0	2.0	—	3.7	5.0	4.2	5.5	5.8	6.0	7.4
SD:	0.4	0.7	0.8	1,2	1.9	1.5	1.8	2.0	2.0	2.5
AL:										
I	8.5	15	17	26	36	39	40	55	50	85
II	8.5	15	19	26	37	41	48	55	55	87
III	8.5	14	19	29	37	42	45	56	53	89
IV	9.0	—	19	28	40	43	44	55	55	87
HcL:	9.0	13	16	24	34	37	38	52	50	83
LigL:	0.8	2.4	3.1	3.5	10	8.3	13	15	13	18
LamC:	0	4	4	5	6	5	5	6	5	6
SHcC:	35	31	32	34	31	42	34	40	40	45
WD:										
A:	3.8	—	—	9.5	14	14	14	20	17	33
B:	3.8	—	—	11	14	15	16	19	19	35
C:	3.9	—	—	10	15	15	16	20	20	38
D:	3.4	—	—	10	16	15	16	20	23	40
E:	3.0	—	—	7.8	14	14	10	15	18	29

TABLE 7. Measures of females attributed to *B. pugniger*, n. sp.

No	74	649	71	455	461	466	465	456	457	464
TL:	38	46	55	83	c 90	100	97	99	103	c115
ML:	15	18	23	27	c 32	33	36	39	40	c 44
HW:	12	16	19	26	—	30	30	33	30	21
MW:	11	17	21	31	—	39	34	35	35	34
ED:	6.6	11	10	13	15	14	14	16	16	13
LD:	—	4.0	3.6	5.5	5.3	—	—	5.8	5.8	5.0
SD:	0.8	1.1	1.1	2.1	2.0	1.9	1.9	2.0	2.2	2.1
AL:										
I	18	26	29	47	53	60	58	50	58	64
II	19	25	32	52	56	60	66	50	55	69
III	22	28	33	55	58	68	62	50	59	64
iv	19	26	32	55	59	60	61	52	56	65
WD:										
A:	7	10	12	19	17	19	17	21	14	21
B:	6.5	11	13	16	20	18	18	23	21	21
C:	7.5	10	13	19	22	24	22	26	20	22
D:	8.5	8.5	12	19	23	23	22	22	23	24
E:	8	8	11	20	19	19	19	17	16	20

where the leaf-like second salivary glands are fastened and down to the stomach (Fig. 14c). The two ducts from the posterior salivary glands are separate for more than half of the distance to the buccal mass (Fig. 14c–e). In *arcticus* and *bairdii*, the united excretory canal is relatively longer (Figs. 2a, 7a). When in situ, the very large stomach rests in a deep groove of the liver, which is almost bilobed. The spiral caecum is scarcely coiled. There is no ink sac.

Etymology

pugniger, derived from the Latin *pugnus*, a fist, alludes to the characteristic boxing glove appearance of ligula.

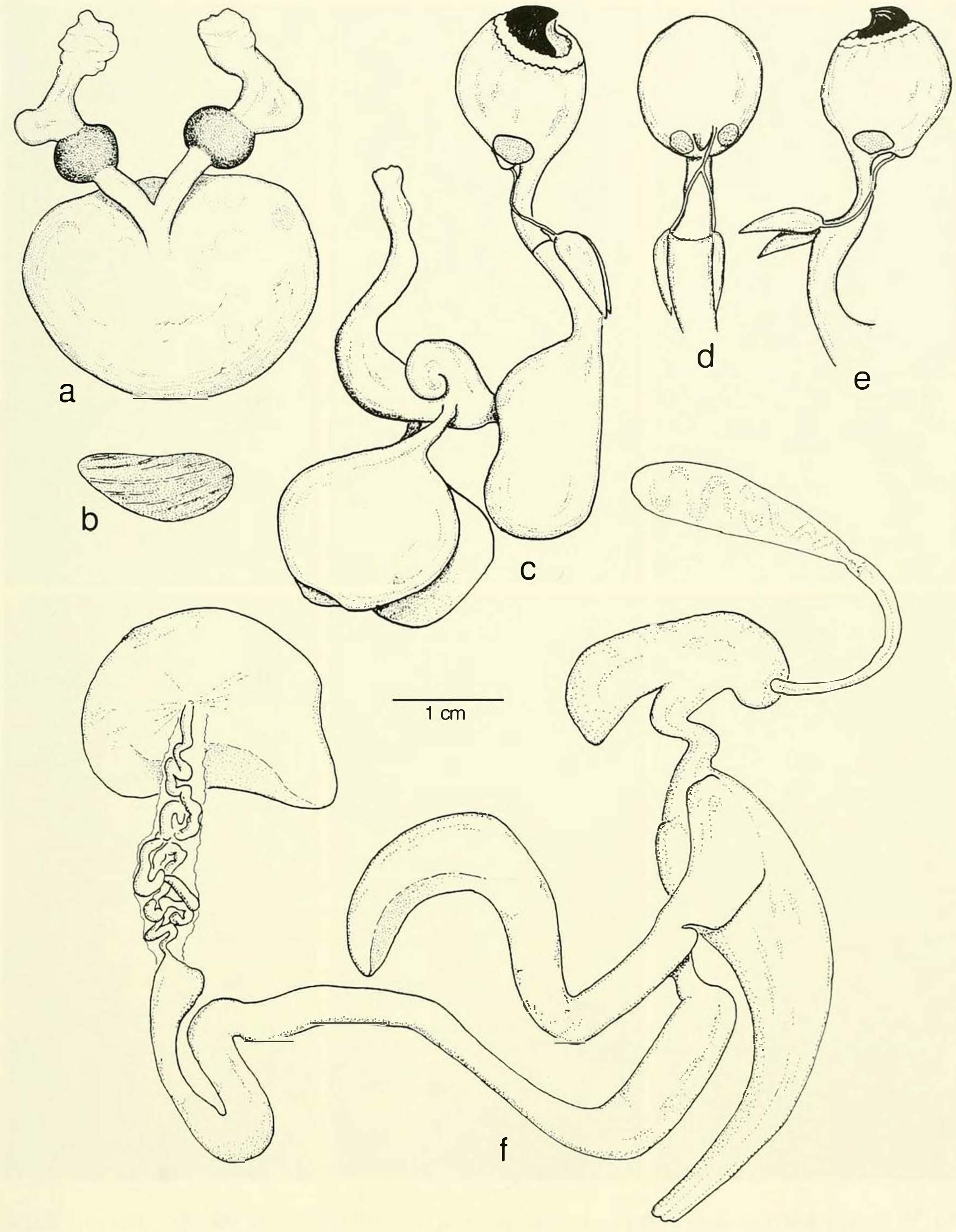

FIG. 14. *Bathypolypus pugniger*, n. sp. a: reproductive organs of ♀ ML 40 mm; b: egg from same specimen, Stn. B5-77-46, IMNH; c-e: digestive tract; f: reproductive organs of ♂ ML 38 mm. A spermatophore is attached to the penis. MNHT, haul 25, July 19, 1979, now ZMUC.

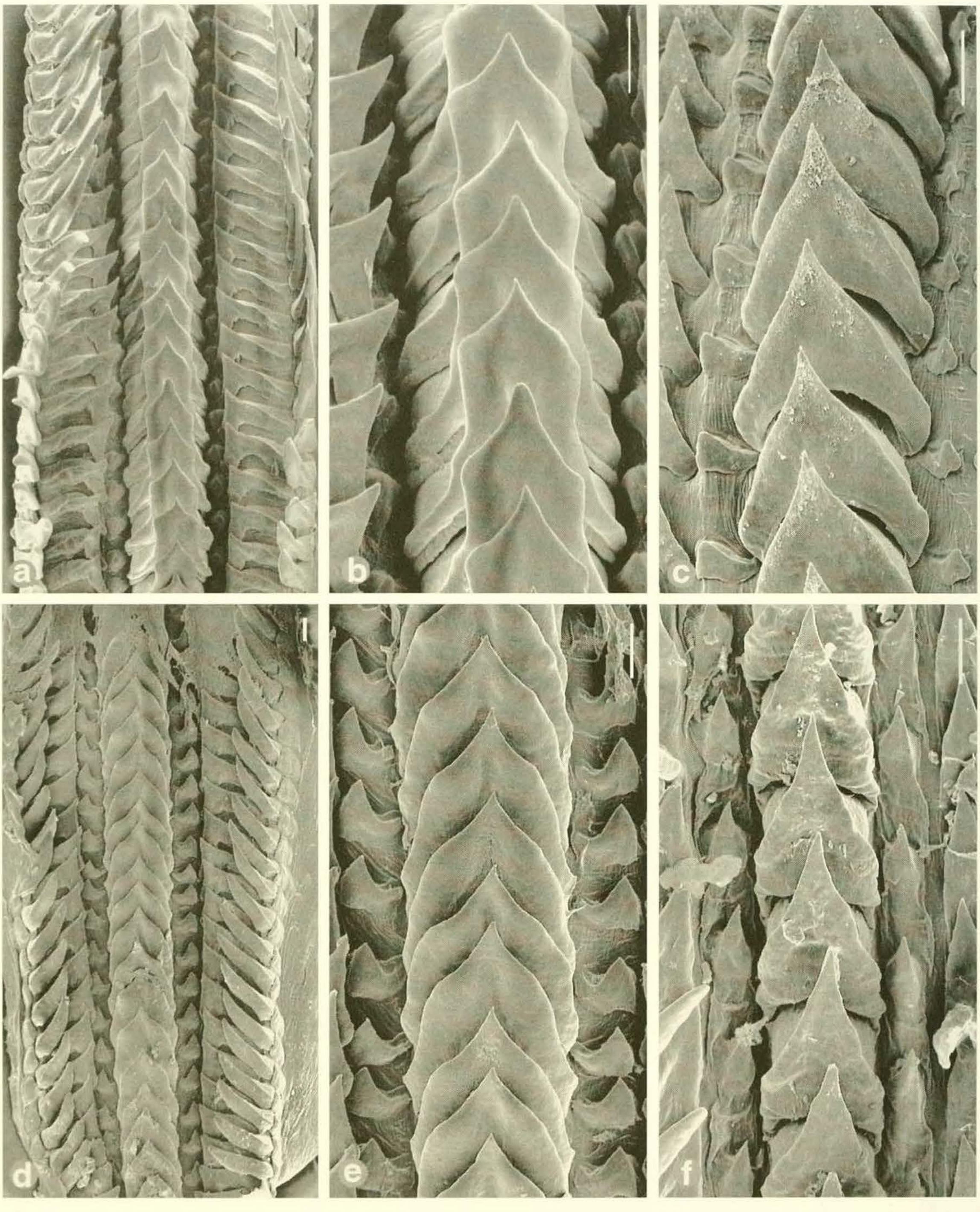

FIG. 15. Radula and rachidians of *B. pugniger*, n. sp. a and b: ♂ ML 31 mm., BIOFAR Stn. 269; c: ♂ ML 36 mm, Iceland Fish. Invest., haul B5-77-46; d and e: ♂ ML 33 mm, BIOFAR Stn. 269; f: ♀ ML 33 mm, Iceland Fish. Invest., haul B5-77-48. Scale: 100 μm.

Synonyms of *B. pugniger*, n. sp.

A revision of specimens identified by Adam (1939) as *B. arcticus* showed two specimens to be identical to *B. pugniger*, n. sp. They are juvenile, a male (ML: 22 mm) and a female (ML: 18 mm) caught in 1938 off the east coast of Iceland (66°23′N, 12°53′W) in 200–250 m. Adam (1939: 10, specimens a, figs. 2, 3) figures the reproduction organs of the male and the globose ligula with five distinct laminae typical of *B. pugniger*.

TABLE 8. Measurements (mm) of a male *B. pugniger*, n. sp., identified as *B. arcticus* by Adam (1939). Adam's 60-year-old measurements in parenthesis.

			Indices			Arm Length			
						right		left	
TL:	59	(–)							
ML:	22	(25)	MLTLI:	37	(–)				
HW:	17	(19)	HWI:	77	(73)	I	32 (33)	34	(36)
MW:	20	(18.5)	MWI:	91	(71)	II	30 (33)	35	(36)
ED:	9.0	(–)	EDI:	40	(–)	III	28 (32)	33	(34)
SD:	1,3	(1.3)	SDI:	5.9	(5)	IV	— (–)	—	(28+)
LigL:	6.2	(6.5)	LigLI:	22	(20)				

Table 8 shows measurements and indices of the male specimen. Comparison with Adam's measurements, which were done while the material was fresh, show considerable preservational shrinkage.

Recognition of *B. pugniger* as a New Species

The first specimens seen were in fact identified as slightly abnormal *B. bairdii.* The globose ligula of the males at first believed to be an accidental deformity or a regeneration phenomenon turned out to be a regularly occurring stable structure with 4–6 laminae, thus deviating significantly from North and East Atlantic *B. bairdii* (Fig. 9). This character, in combination with a reverse arm order as compared with *bairdii* and *arcticus*, deviating rachidians (Fig. 15), and sucker and eye sizes (Fig. 16) justified establishment of a new species.

As is usual in octopods, the hectocotylized males offer the best distinguishing characters. The females were only recognized after renewed inspection of all material from the Faroe-Iceland area that I had previously identified as *B. bairdii.*

The search for females of *pugniger* was based on the assumption that, like in other *Bathypolypus* species, there would be no sexual dimorphism. This means that bodily proportions, arm order and size of eyes and suckers should match *pugniger* males of similar sizes. In this way, 12 females could be attributed to *B. pugniger.* A circumstantial evidence for the plausibility of the result is the sex ratio of 39% females, close to the sex ratio found in *bairdii* (38% females; n = 235).

Morphologically *pugniger* is very close to *bairdii.* As yet few characters distinguishing these species have been found. Among juveniles and females mistaken identity between *pugniger* and *bairdii* is possible, because the state of preservation can blur the differences in arm order and size of suckers and eyes.

The rough diagnostic index SDEDI useful to discriminate between *arcticus* and *bairdii,* shows *pugniger* to lie between the two species (Table 9). The corresponding relation between SD and LD should be more accu-

TABLE 9. Range of distinctive indices and counts of the *Bathypolypus* species based on material examined. The sparse data for *valdiviae* are extracted from text and drawings of Chun & Thiele (1915), Robson (1924b), and Sanchez & Moli (1984). Data for *sponsalis* from the Mediterranean population.

	arcticus	*bairdii*	*ergasticus*	*pugniger*	*sponsalis*	*valdiviae*
CaLI	15–25	15–25	30–40	26–38–51	33–42	28–38
EDI	20–35	30–55	31–41–47	30–44–50	30–41–47	40
LamC	11–16	7–12	7 (n = 4)	4–5–6	4–6–7	4–5
LigLI	9–23	18–44	6–9–12	22–27–32	10–12–15	15–18
MLTLI	24–29–35	27–33–38	13–17–23	33–38–42	16–22–26	30
OAI	83–89–100	71–88–104	53–60–70	83–91–106	47–63–73	75
SDEDI	18–26–34	6–9–13	9–11–13	11–13–16	4–6.5–8.5	13
SDI	6–7–8.4	3–4–5	3.5–4–5.5	4.7–5.1–6	2.1–3–3.7	5
SDLDI	50–70–100	19–25–36	22–25 (n = 2)	32–35–40	15–19–22	—
SHcC	32–49	36–49	73–77–83	31–35–45	52–57–61	45
SpLI	105–130	60–90–115	110–150	90 (n = 3)	50–70	100
SpRI	26–32	50–60	50–60	50–60	50–60	50
Eye cirri	present	present	absent	present	absent	present
Crop divert.	present	absent	present	absent	absent	?

rate, but still shows some overlap with *bairdii*, especially with younger specimens (Fig. 16)

In bodily proportions and hectocotylus, *B. pugniger* has a striking resemblance to the South African *Bathypolypus valdiviae* (Chun & Thiele, 1915), known from the Agulhas Bank and off the Namibian coast.

With one exception from West Greenland (Fig. 13c, Table 6: no. 122), all specimens of *pugniger* are caught on the Faroe-Iceland plateau in warm Atlantic water. The zoogeographical and ecological perspectives are discussed below.

HISTORICAL REVIEW AND PRESENT STATUS OF *BATHYPOLYPUS* AND *BENTHOCTOPUS*.

In 1921, Grimpe erected two new genera in the subfamily Octopodinae to accommodate some characteristic octopods without ink sac: *Octopus arcticus* Prosch, 1849, was designated type species of *Bathypolypus*, and *O. piscatorum* Verrill, 1879, type species of *Benthoctopus*. Grimpe just stated that the two species "erheblich verschieden" [differ considerably], but he did not otherwise define the genera.

To accommodate two new species (*Bathypolypus grimpei* and *Benthoctopus berryi*), Robson (1924a, b) defined the genera this way:

"*Bathypolypus* Grimpe: Deepwater polypods with broad and long hectocotylus and unicuspidate rhachidian teeth. The skin is usually covered with warts and may be gelatinous. There is no ink sac. Type: *B. arcticus*."

"*Benthoctopus* Grimpe: Abyssal polypods with small hectocotylus, multicuspid rhachidian teeth and smooth skin. There is no ink sac. Type: *B. piscatorum*."

Without discussing details, Grimpe (1925: 100, footnote) declared himself in complete agreement with Robson's generic definitions.

With small modifications these definitions have persisted (for example, Thiele, 1935; Mangold & Portmann, 1989). Robson (1927) amended the generic definitions slightly and later (1928) erected a new subfamily, Bathypolypodinae, comprising the two genera and simply defined as: "Octopods mainly abyssal in habitat and devoid of an ink sac".

In his monograph, however, Robson (1929, 1932) moved *Benthoctopus* with 14 nominal species back to the subfamily Octopodinae, while *Bathypolypus* with six nominal species was retained in Bathypolypodinae. With the characters of the subfamily (Robson, 1932: 286), *Bathypolypus* was now defined as: "Abyssal octopodids devoid of an ink sac and in which the crop is usually reduced and sometimes absent. Eggs and vaginae are large and spermatophores large and few in number. The mantle aperture is very narrow and the general habit squat and short armed."

Robson removed *Benthoctopus* to Octopodinae because he felt that some of the species resembled ordinary forms of *Octopus* and that "were it not for the lack of the ink-sac one would place them in that genus" (Robson, 1932: 51). On the other hand, Robson realized that some species have traits of both genera.

The latter problem has caused some taxonomic confusion. After a redescription of *Bathypolypus sponsalis*, it prompted Wirz (1955: 146) to declare that the strict distinction between the genera *Benthoctopus* and *Bathypolypus* made by Robson was unjustified considering the small number of differences. Thiele (1935) reunited the two genera in Bathypolypodinae.

As presented by Robson, the two genera represent an array of species that in varying degrees demonstrate traits believed to reflect adaptation to benthic life in deep water-absence of ink sac; reduction of gills, radula, and crop; increasing size of eggs and spermatophores; elaboration of ligula; shortening of the arm complex; and funnel organ tending to be double.

In general, the least specialized species, that is, those most similar to *Octopus*, seem to be accommodated in *Benthoctopus*, the most divergent in *Bathypolypus*.

The present revision shows that most of the existing confusion derives from misidentifications that have led to errors in the concept of the two type species and subsequent misunderstandings in the generic definitions of *Bathypolypus* and *Benthoctopus*.

The choice by Grimpe (1921) of *Octopus piscatorum* as type for *Benthoctopus* was especially unlucky, because an examination of the type shows it to be identical with the here-reinstated *Bathypolypus bairdii* (Verrill, 1873).

Aware of this fact and in connection with the description of five new species of *Benthoctopus* from the Pacific, Voss & Pearcy (1990) plead for the preservation of the name *Benthoctopus*, which now includes 20 species worldwide (Sweeney & Roper, 1998).

Voss (1988a, b) restricted the subfamily Ba-

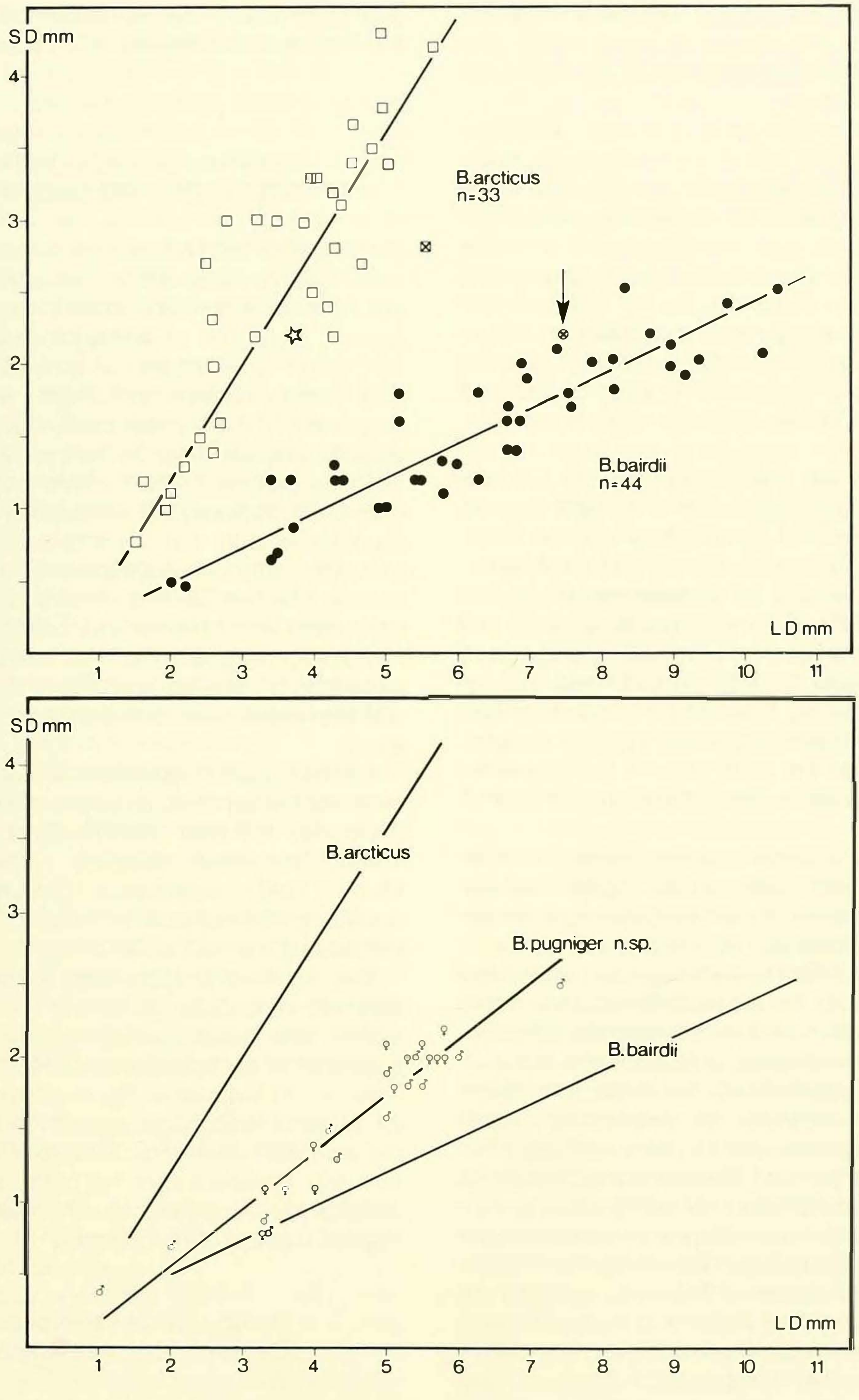

FIG. 16. Sucker diameter versus lens diameter in *arcticus, pugniger*, n. sp., and *bairdii*. Reduced major axis regressions show that the relation differs among *arcticus* and *bairdii* and among *arcticus* and *pugniger* at the P = 0.01 level of significance. Among *pugniger* and *bairdii* at P = > 0.1 < 0.05. Regression slopes with 95% confidence intervals and coefficient of determination: 0.8372 (0.7177–0.9766; 0.9766) for *arcticus;* 0.4112 (0.3541–0.4774; 0.9025) for *pugniger*, and 0.2643 (0.2294–9.3045; 0.7921) for *bairdii*. The regression intercepts are 0.1614, 0.0641, and 0.0592 respectively and not considered different in pairwise comparison among species.

Inserted in upper figure: data for the type of *B. arcticus* (crossed square), the "type" of *B. faeroensis* found in ZMUC (star) and the holotype of *Benthoctopus piscatorum* (cross in circle).

thypolypodinae to benthic octopods with biserial suckers and devoid of ink sac and proposed the following definition of *Benthoctopus* Grimpe, 1921:

"Deepwater octopods of normal *Octopus*-like appearance with short to long arms, suckers biserial; hectocotylus *Octopus*-like, ligula slightly to moderately excavated with indistinct midrib, smooth or bearing low, often indistinct rugae, never laminate; crop present, usually with diverticulum; ink sac absent; radula with strongly, seldom weakly, multicuspid rachidian; body entirely smooth, papillae or ocular cirri absent. Type species *Octopus piscatorum* Verrill, 1879, by original designation."

If the genus *Benthoctopus* is to be preserved, it would need a different type species to be designated by the International Commission on Zoological Nomenclature. A sensible choice would be *Benthoctopus januarii* (Hoyle, 1885). This species is revised and thoroughly redescribed by Toll (1981) based on a series of recently caught male and female specimens. It conforms to the diagnosis of *Benthoctopus* suggested by Voss and furthermore has the advantage of being a widespread species in the Gulf of Mexico and off Brazil.

The final decision and the plea to the International Commission on Zoological Nomenclature, however, should be made by a reviser of the *Benthoctopus* species.

The genus *Bathypolypus* should under any circumstances be preserved. Robson, being the first revisor of the two genera, acknowledged *Octopus arcticus* as type of a group of species characterized by large lamellated ligulae, as opposed to another group of species characterized by small *Octopus*-like ligulae, the present *Benthoctopus* group. To uphold the distinction between the two groups and to match the definition of *Benthoctopus* by Voss & Pearcy (1990). I propose the following modification of Robson's definition of *Bathypolypus* in an attempt to make an operational distinction between the two genera:

Bathypolypus Grimpe, 1921. Type species: *Octopus arcticus* Prosch, 1849, by original designation.

Deepwater octopods of normal *Octopus*-like appearance, with stout body and generally with short arms; suckers biserial; hectocotylus with deeply excavated ligula bearing a number of well-defined laminae; crop, if present, seldom with diverticulum; ink sac absent; radula with homodont or weakly and irregularly multicuspid rachidians; skin usually with papillae; supraocular cirri often present.

GENERAL SURVEY OF THE *BATHYPOLYPUS* SPECIES

The elaborated hectocotylus, with a prominent, deeply excavated, laminated ligula, is the most distinctive character in the amended generic definition of *Bathypolypus*. In addition, there are reductions in digestive tract, gills, radula, relative arm length, and the enlargement of eyes exhibited by the species in varying degrees. A tendency to develop some of these traits is found in *Benthoctopus*. The difference between the hectocotyli of the *Bathypolypus* and the *Benthoctopus* species provides sufficient substance to justify preserving the two genera, if only as a preliminary measure. For the time being, our ignorance regarding evolutionary sequence and weighting of derived characters in Octopodidae precludes serious phylogenetic considerations.

Bathypolypus comprises six species in the most recent list of accepted cephalopod taxa (Sweeney & Roper, 1998): *arcticus* (Prosch, 1849); *faeroensis* (Russell, 1909); *proschi* Muus, 1962; *salebrosus* (Sasaki, 1920); *sponsalis* (P. Fischer & H. Fischer, 1892); and *valdiviae* (Chun & Thiele, 1915).

The species *proschi* and *faeroensis* are here shown to be synonyms of the reinstated *bairdii* and *arcticus* respectively, whereas *pugniger* is recognized as new. It remains, however, to reconsider the remaining three of the hitherto recognized species in the light of the amended generic definitions of *Bathypolypus* and *Benthoctopus*. Also, the position of *Benthoctopus ergasticus* (P. Fisher & H. Fischer, 1892) is reconsidered.

Benthoctopus salebrosus (Sasaki, 1920), new comb.

Polypus salebrosus Sasaki, 1920: 182; 1929: 99, text-fig. 54, pl. 6, figs. 5, 6.

Bathypolypus salebrosus: Robson, 1929: 41; 1932: 302; Akimushkin, 1965: 134, fig. 34; Nesis, 1987: 315, fig. 83A.

Type and paratype: two females, USNM 332969, TL: 153 mm, ML: 45 mm; USNM 332970, TL: 77 mm, ML: 23 mm (not examined).

A characteristic, though not well-known species from the Okhotsk Sea and off the Japanese Pacific coast in 212–1070 m.

Based on the female types, Robson (1929, 1932) assigned *salebrosus* to *Bathypolypus* with hesitation, mostly on account of its short arms, rather deep web (33%), and because it is sculptured with closely set, well-defined, roundish warts. He found that the rachidians were weakly multicuspid, with at most one denticle on each side, and he established the absence of an ink sac.

The hectocotylus was later described by Akimushkin (1965: fig. 34) and Nesis (1987: fig. 83A). The ligula is narrow, conical and pointed, LigLI about 14. The central groove is shallow and transversely striated with numerous indistinct rugae. Calamus is short and pointed.

Benthoctopus salebrosus has no supraocular cirri. The funnel organ is figured by Sasaki (1929: text-fig. 54) as a single W, the outer legs being the shortest. Gills not much reduced, each demibranch with 9–10 filaments, the mantle aperture correspondingly moderate (B-C in Robson's terminology).

The slim, striated ligula unknown to Robson is of a type seen in some *Benthoctopus* species but very different from the highly specialized ligulae of *Bathypolypus arcticus* and *B. bairdii*.

I conclude that *salebrosus* is best placed in the genus *Benthoctopus* due to the simple non-laminated ligula and the single funnel organ, irrespective of its warty skin, which is unusual among other species of that genus. No other character contradicts this opinion.

Bathypolypus sponsalis
(P. Fischer & H. Fischer, 1892).

Octopus sponsalis P. Fischer & H. Fischer, 1892: 297, fig. A; Fischer & Joubin 1907: 322, pl. 22, figs. 5–11

Bathypolypus sponsalis: Robson, 1927: 252; 1932: 300, figs. 61–63; Wirz, 1954: 139, figs. 1–5; 1955: 129, figs. 1–12; Adam, 1960: 504, fig. 2; Mangold-Wirz, 1963: 49; Perez-Gandaras & Guerra, 1978: 195, figs. 2–5; Nesis, 1987: 315, fig. 83I; Guerra, 1992: 249, figs. 88, 91.

Material examined: Syntypes of *Octopus sponsalis* P. Fischer & H. Fischer, 1892, MNHN 571097: 4 males ML: 27–41 mm, Exp. du "Talisman", 332–1250 m, NW-Africa; in ZMUC, 8 males, ML: 33–49 mm and 3 females ML: 27–38 mm, Catalan Sea, western Mediterranean, June–September 1954 and June–September 1955, 200–500 m; in BMNH: one female, ML: 36 mm, Exp. du "Talisman", July 12, 1885.

This species was originally caught off western Sahara (22°N, 19°46′E) at the same locality as *B. ergasticus*. It has since been reported as a common mesobenthic species in the western Mediterranean (Wirz, 1954, 1955), the Aegean Sea (D'Onghia et al., 1993), and off Portugal and Galicia (Perez-Gandaras & Guerra, 1978).

Good pictures of the whole animal and the hectocotylus are presented by Fischer & Joubin (1907: pl. 22), radula and internal organs by Robson (1932: figs. 61–63), and Wirz (1954: figs. 3–5; 1955: figs. 5–12).

Robson (1927, 1932) placed *sponsalis* in *Bathypolypus* because of its apparent affinities to the *arcticus*-group: a squat, relatively short-armed body with huge eyes, small suckers, double funnel organ, a reduced radula with homodont rhachidians, lack of crop, and a ligula that is deeply excavated, with 6–7 laminae.

The morphometrics and major features of the life cycle of the Mediterranean population of *sponsalis* are well known (Wirz, 1955; Mangold-Wirz, 1963) based on about 600 specimens caught at all times of the year. Table 9 gives the main distinctive indices based on my own measurements of specimens from the Catalan Sea.

There are, however, some discrepancies between these data and descriptions of specimens from the type locality (Cape Verde Islands). Examination of the syntypes (MNHN 571097) shows that the Mediterranean population deviates in several important traits:

Two spermatophores extracted from one of the syntypes confirmed Robson's observation (1932) that the sperm reservoir is long, SpRI: 65–70 (versus 50–60 in the Mediterranean). The short oral end has a distinct swelling in the middle, making it spindle-shaped, unlike any other spermatophores of the genus (Fig. 17). The apical end is swollen compared with the smaller and more cylindrical reservoir in Mediterranean specimens.

Calamus is very large and fleshy (Fischer & Joubin, 1907: pl. 22, fig. 6). In four syntypes, I found CaLI: 57–71 (Medit.: 33–42). The difference was noted by Wirz (1955).

The ligula is larger in the type series, LigLI: 14–22 (n = 5) (Medit.: 10–15), and the num-

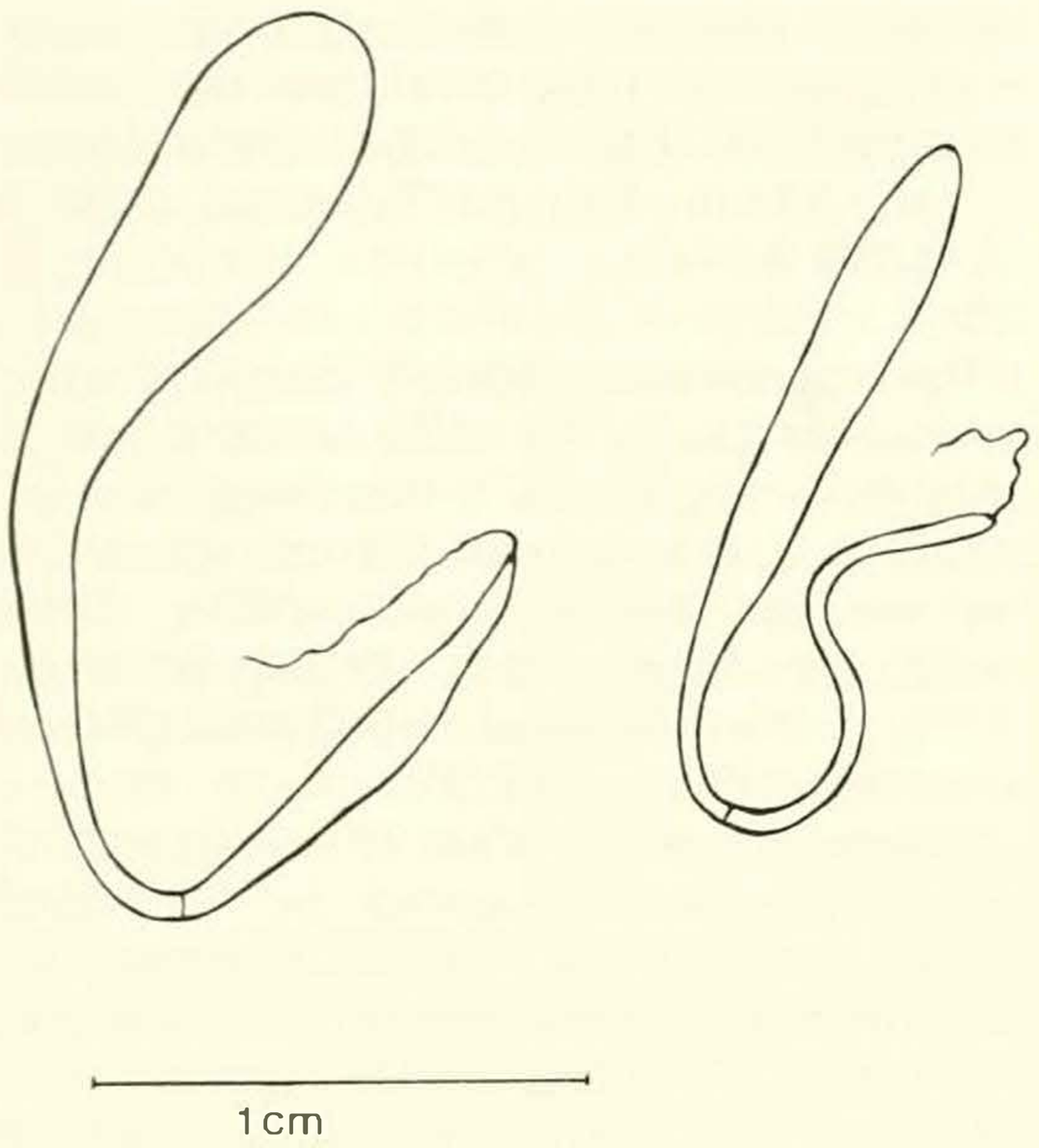

FIG. 17. Spermatophores of *B. sponsalis*. Left: syntype, ML 41 mm., Cape Verde. Right: specimen from the Catalan Sea, western Mediterranean, ML 44 mm.

ber of suckers on the hectocotylus is low, SHcC: 44–50 (n = 4) (Medit.: 57–61).

The type specimens have warts or pustules over the eyes and often on the antero-dorsal region. Adam (1960: fig. 2) found supraocular cirri, as well as a mixture of multifid and simple warts sprinkled dorsally on two specimens from the Cape Verde Plateau. In contrast, the Mediterranean and Galician specimens have smooth skin without traces of warts.

I conclude that the morphological deviations between populations may be rooted in subspecific variation or even represent unrecognized sibling species. Not least, the morphology of hectocotylus and spermatophores speak for the latter possibility. The Mediterranean population is well documented, but more specimens from the Cape Verde Plateau are needed. Regardless, the specimens hitherto identified as *sponsalis* clearly belong to the genus *Bathypolypus*.

Bathypolypus valdiviae
(Chun & Thiele, 1915)

Polypus valdiviae Chun & Thiele, 1915: 485, text-figs 52, 53, pl. 80, figs. 1–5
Bathypolypus grimpei Robson, 1924a: 208; 1924b: 663, text-figs. 37–41, pl. 2, fig. 10
Bathypolypus valdiviae: Massy, 1927: 165; Robson, 1932: 303, figs. 64–68; Sanchez & Moli, 1984: 19, fig. 18; Nesis, 1987: 315, fig. 83F-H
Type: Z. M. Humboldt Univ. Berlin. Male, ML: approx. 30 mm (not examined).

This species is known from the South African Agulhas Bank and off the Namibian coast.

Bathypolypus valdiviae has a remarkable resemblance to *B. pugniger*, n. sp, being a short-armed, big-eyed, warty species usually with supraocular cirri and having the same kind of characteristic hectocotylus. Ligula is globular and deeply excavated with 4–5 well developed laminae. LigLl: 15–18. The hectocotylized arm bears about 45 suckers. HcLl: approx. 75. The arms are of subequal length (Chun & Thiele, 1915: pl. 1, fig. 4; Robson, 1924b: fig. 37, as "*B. grimpei*").

Also in other characters *valdiviae* shows affinity to *pugniger* and *bairdii.* The funnel organ is a pair of widely separated V-shaped pads (Robson, 1932: text-fig. 66); the rhachidians are homodont, but more pointed than the broad teeth in *pugniger;* the spermatophore is a true copy of *bairdii* and *pugniger* spermatophores (Robson 1924b: text-figs. 39, 41).

I conclude that placement of *valdiviae* in *Bathypolypus* is justified.

Bathypolypus ergasticus
(P. Fischer & H. Fischer, 1892), new comb.

Octopus ergasticus P. Fischer & H. Fischer, 1892: 298, fig. B; Fischer & Joubin, 1907: 325, fig. 2A, pl. 22, figs. 1–4
Octopus profundicola Massy, 1907: 277.
Polypus ergasticus: Massy, 1909: 7, pl. 1, figs. 1–3, pl. 2, fig. 1; 1913: 1; Robson, 1924b: 668
Benthoctopus ergasticus: Grimpe, 1921: 300; Robson, 1927: 255, figs. 4–6, 9; 1932: 244, figs. 44, 45; Nesis, 1987: 320, fig. 84E, F.
Material examined: Syntypes of *Octopus ergasticus* P. Fischer & H. Fischer 1892, MNHN 5811: 3 juv. males ML: approx. 17–35 mm, Exp. du "Talisman" 1883, 830 m, NW-Africa; in BMNH: syntypes of *Polypus profundicola* Massy, 1907: 3 males, ML: 50–80 mm; 3 females, ML: 57–61 mm. "Helga" stations 363, 365, 369, 400, 477 and 489, approx. 51°25′N, 11–12°W, 385–720 fath. One male *er-*

gasticus, ML: 45 mm, NW-Africa (gift from Prof. Joubin).

This characteristic species originally caught off western Sahara (22°24′N, 19°46′E, 860 m) is well described by Fischer & Joubin (1907: pl. 22) and by Massy (1907, as *O. profundicola;* 1909: pls. 1, 2) based on specimens caught off western Ireland. Robson has described reproductive organs, radula (1927: figs. 4–6, 9), and the digestive tract (1932: figs. 44, 45).

The main indices of *ergasticus* are given in Table 9 based on my own measurements. Additional data in Massy (1909).

Robson found it difficult to accommodate *ergasticus* in either *Bathypolypus* or *Benthoctopus*. He decided on the latter genus, however, mainly because he, in contrast to Massy, found that the rachidians are multicuspid and because the esophagus has a crop diverticulum. As mentioned earlier, Robson confused the type species of the genus, *Benthoctopus piscatorum*, with specimens of *Bathypolypus arcticus* from the Faroe Channel. Multicuspid rhachidians and a crop diverticulum are found in the latter species and are thus not unique to *Benthoctopus*.

Robson (1932: 247) admits that the hectocotylus of *ergasticus* is unlike those of other *Benthoctopus* species. The hectocotylized arm is short (OAI: 60) with a well-developed, deep, spoon-shaped ligula with about 7 strong laminae (LigLI: 9). Calamus prominent (CaLI: 30–40). The hectocotylus has a strong likeness to that of *sponsalis.* Chun & Thiele (1915: 485) consider it obvious that *ergasticus, sponsalis*, and *valdiviae* are related due to the form of the hectocotylus.

Another character showing affinities to the *Bathypolypus* species is the enormous spermatophore. One specimen with a total length of 111 mm, had a sperm reservoir of 51 mm in length and 8 mm in width. Apart from the size, the proportions are very much like the spermatophores of *bairdii* and *pugniger* (Robson, 1927: 255, fig. 4).

The funnel organ is double, and in the specimens from Ireland consists of two very characteristic subquadratic or pentagonal pads (Fig. 18), a type unknown in *Benthoctopus*, but not far from the structures in *bairdii* and *pugniger*. In the specimen from West Africa, the funnel organs each had a slight indentation anteriorly, making them more heart-shaped.

In the light of the amended generic diagnoses given, *ergasticus* is best accommodated in genus *Bathypolypus*.

The genus *Bathypolypus,* as here recognized, thus includes only the following six Atlantic species: *arcticus* (Prosch, 1849), *bairdii* (Verrill, 1873), *pugniger,* n. sp., *sponsalis* (P. Fischer & H. Fischer, 1892), *valdiviae* (Chun & Thiele, 1915), and *ergasticus* (P. Fischer & H. Fischer, 1892). The species *salebrosus* (Sasaki, 1920) is moved to *Benthoctopus* on account of the simple, non-laminated hectocotylus and single funnel organ.

DISTRIBUTION OF *BATHYPOLYPUS*

Bathypolypus arcticus, s. str., are confined to Norwegian Sea Deep Water (NSW), whereas the squat, broad-headed species (*B. bairdii, B. pugniger*, n. sp.) are found in the warmer Atlantic water south of, or on top of, the Greenland-Scotland Ridge.

This is brought out in Figure 19, which is based on the updated hydrographic and topographic rewiew papers by Hansen (1985) and Westerberg (1990) in connection with the BIOFAR benthic projects. It is seen that subzero NSW fills the trough of the Faroe-Shetland Canal 500–700 m under the north-going warm Atlantic Current. Almost barred in the south by the Wyville Thomson Ridge, the main flow of NSW is forced to make a bend round the southern end of the Faroe Plateau and flows through the Faroe Bank Canal to reach, and eventually slide down, the southern slopes of the Iceland-Faroe Ridge mixed with Atlantic water.

Northern species – *B. arcticus, B. bairdii, B. pugniger,* n. sp.

Bathypolypus arcticus

Horizontal Distribution: Figure 19 clearly demonstrates the stenothermal arctic affinity of arcticus. Specimens caught outside NSW are invariably in places intermittently exposed to overflow of cold water, which on the Faroe-Iceland Ridge often is a mixture of NSW and Arctic Intermediate Water (AI) generated in the Iceland and Greenland seas.

The arctic affinity of *arcticus* is confirmed by its wider distribution in the cold parts of the Barents Sea, off eastern Greenland, and in the cold threshold fiords of southwestern

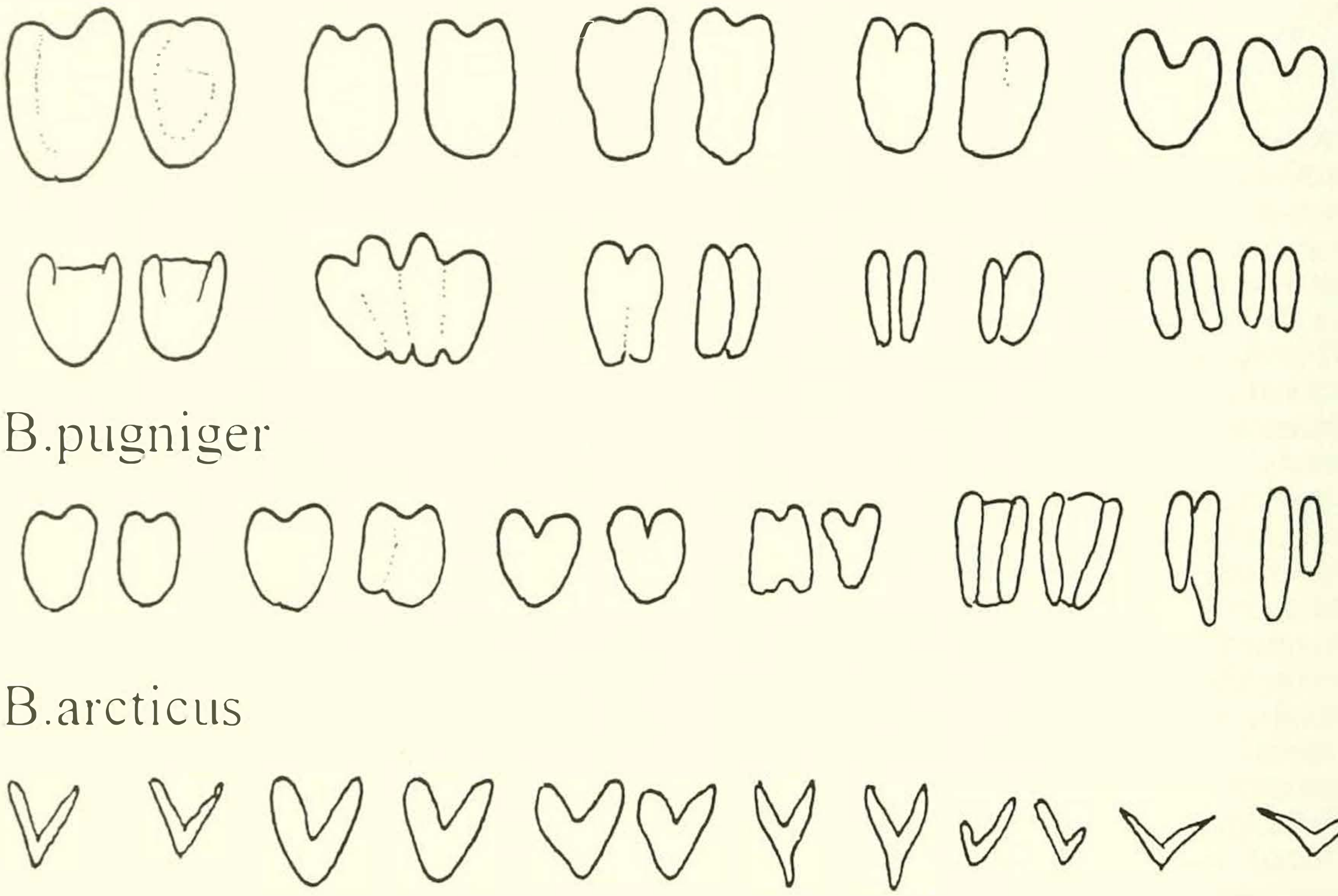

FIG. 18. Variability of funnel organ in five North Atlantic *Bathypolypus* species. The left pair in each row is considered typical of the species.

Greenland, not influenced by the warm Irminger Current (Fig. 20). According to Kondakov (1936), *arcticus* occurs in the Kara Sea (78°01′N, 105°27′W, 175 m, –0.64°C). I have not had the opportunity to verify this identification, but Kondakov's drawing looks convincing.

Bruun (1945: 8) in his treatise of Icelandic cephalopods, though following Robson's *sensu lato* concept of *arcticus,* is the only author who noticed that the narrow-headed specimens occur off northern Iceland, whereas the "*bairdii* form" is found off the south and southeast coast of Iceland, that is south of the North Atlantic Ridge.

The material of adult *arcticus* are too few to disclose possible geographic variation in meristic characters.

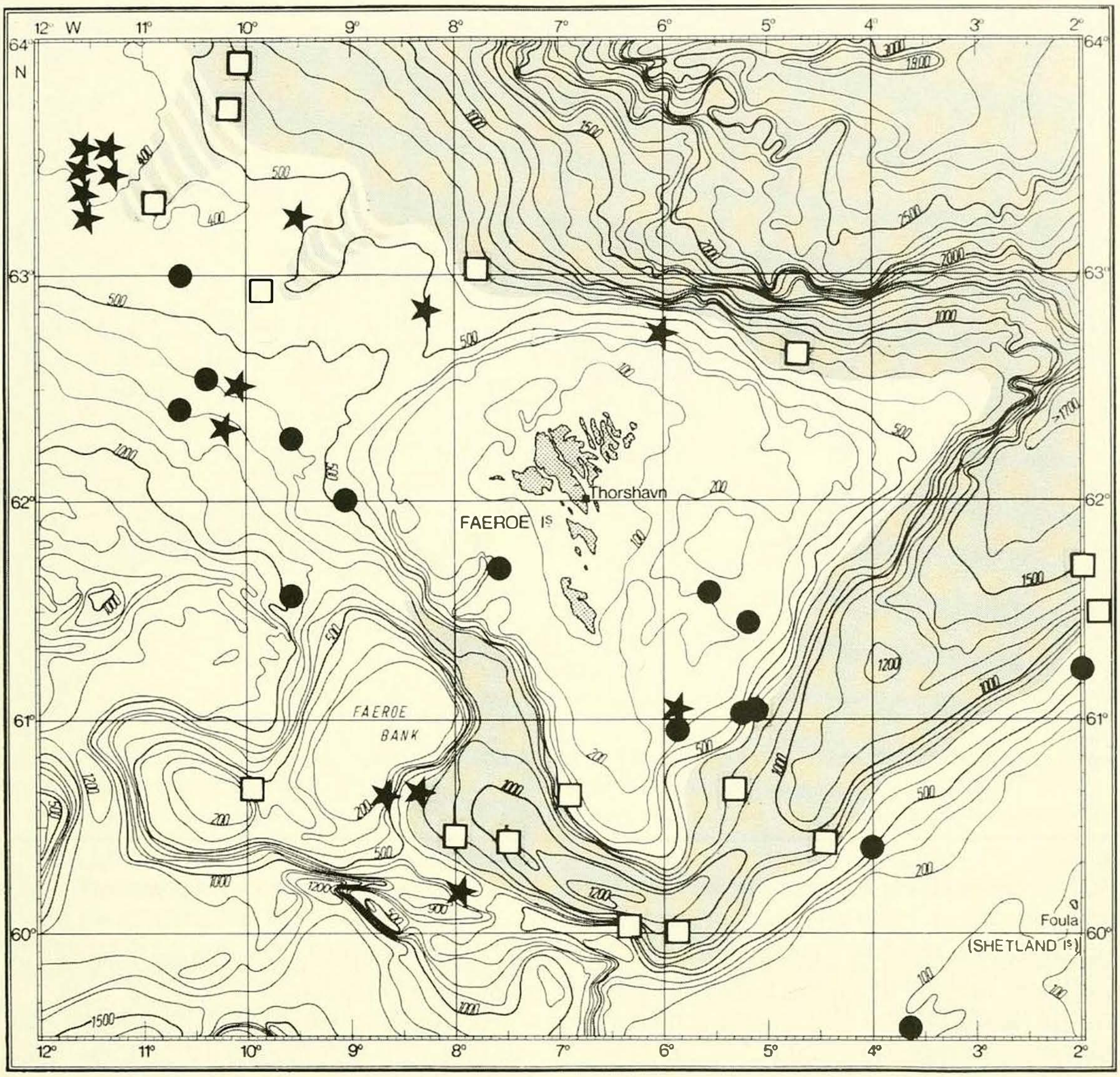

FIG. 19. Distribution in Faroese waters of *B. arcticus* (squares), *B. bairdii* (dots) and *B. pugniger*, n. sp. (stars). Arctic deep water with negative temperatures darkly screened. In northwest occasional overflow of arctic water is indicated.

Bathymetrical Distribution: Based on the present material, the depth range of *arcticus* is 37–565–1210 m. Only in the northernmost localities is the species caught in less than 100 m. In the south, optimal low temperatures are found at greater depth, usually over 400 m. Juveniles and sexually mature animals are evenly scattered at all depths.

Bathypolypus bairdii

Horizontal Distribution: This species seems to prefer Atlantic water masses with temperatures in the range of 2–8°C (Figs. 19, 21). Due to the warm Norwegian Current, *bairdii* ranges from the northern North Sea and Skagerrak along the Norwegian Coast to the southern parts of the Barents Sea. It is common on the southern slopes of the Iceland-Greenland Ridge, but is probably barred from southern Greenland by the eastern Greenland Polar Current. The southeastern Atlantic limit for bairdii seems to be northwestern Iberian waters (Perez-Gandaras & Guerra 1978).

In western Greenland, *bairdii* is found in water tempered by the warm Irminger Current, and it is common on the prawn trawling grounds and fishing banks south of the ridge

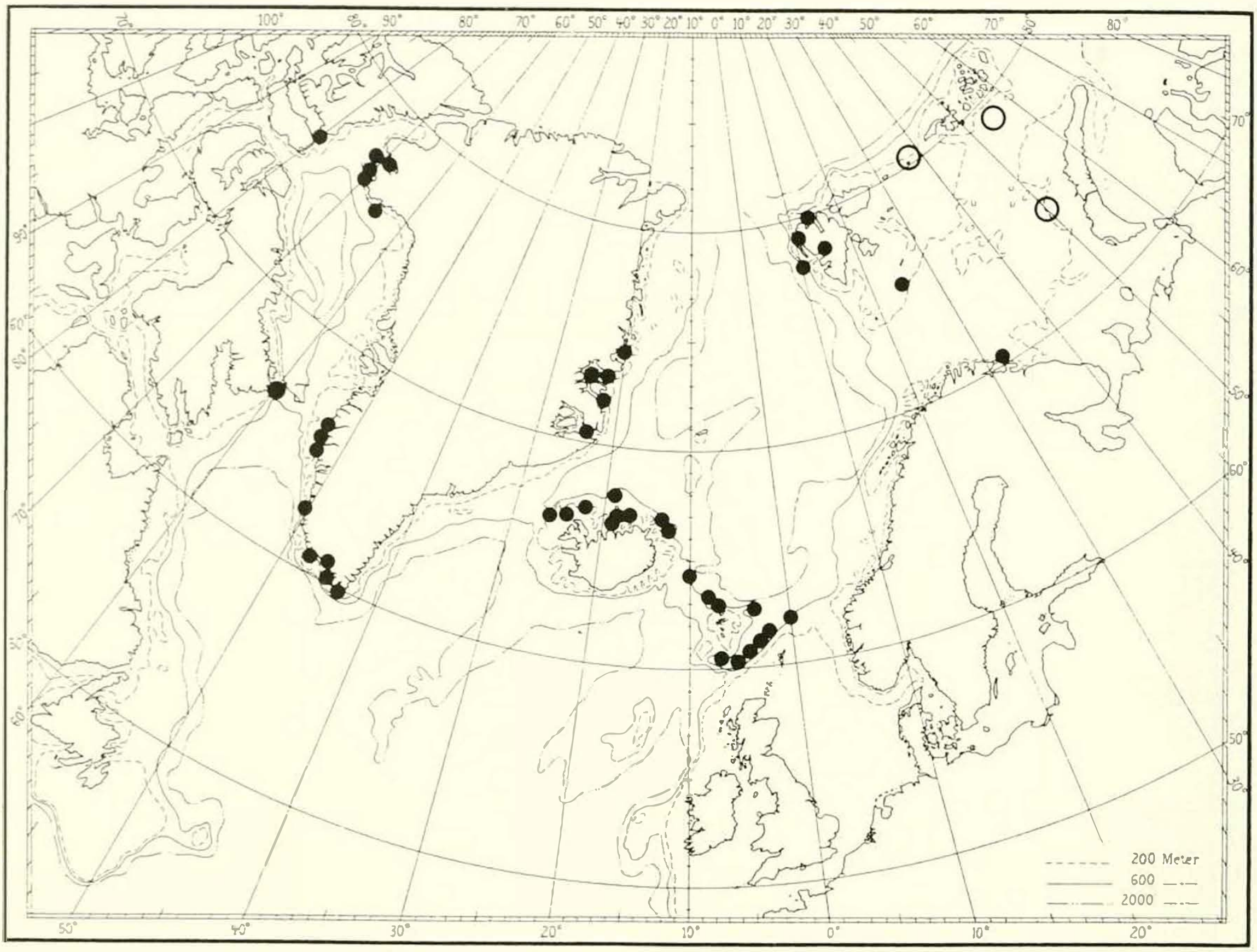

FIG. 20. Distribution of *Bathypolypus arcticus* (Prosch, 1849). Open circles: positions not precisely known.

separating Davis Strait and Baffin Bay. There are fewer records along the Labrador coast, but the Newfoundland area seems to offer the species excellent conditions. The Labrador Current, with admixture of warmer Atlantic water, fills the deeper parts (> 100–200 m) of the Laurentian Channel with water that rather constantly holds 2–5°C (Brunel et al., 1998). Macalaster (1976, as "*B. arcticus*") records an average temperature of 4.3°C (SD: 1.7°C) for stations where the species was caught.

The species was reported as far south as Fowey Rocks, Miami (Boone, 1938). Cairns (1976) showed *bairdii* to be the most abundant cephalopod in the Straits of Florida.

Geographic variation: Bathypolypus bairdii is distributed in a many thousand km long, narrow band largely following the upper 180–1000 m of the continental slopes of the North Atlantic (Fig. 21). As it probably is a rather stationary animal and having non-pelagic young, a certain clinal geographic variation could be expected. In bodily proportions, there does not seem to be variation. But characters of the hectocotylus show statistically significant geographic variation.

Populations south of 45°N have larger ligulae (Fig. 10), with more laminae (Fig. 9) but fewer suckers on the hectocotylized arms (Fig. 8) than populations from Labrador and western Greenland. As regards the number of laminae, the Newfoundland area acts as a transitionary zone (Fig. 9). The clinal variation may be due to genetic differencies, or it may be a response to different ecological or hydrographic regimes.

Small but perceptible geographic variation exists between the population from Labrador and western Greenland and their eastern Atlantic fellows. The Cape Farewell area at the southern tip of Greenland seems to form a distributional gap (Fig. 21). The occurrence of *B. arcticus* in this area (Fig. 20) suggests that the eastern Greenland Polar Current, which sweeps the slopes causes the absence of *bairdii*. In the eastern Atlantic, the ligula has more laminae (Fig. 9) and the hectocotylus slightly fewer suckers than found in Labrador and western Greenland. The relative size of

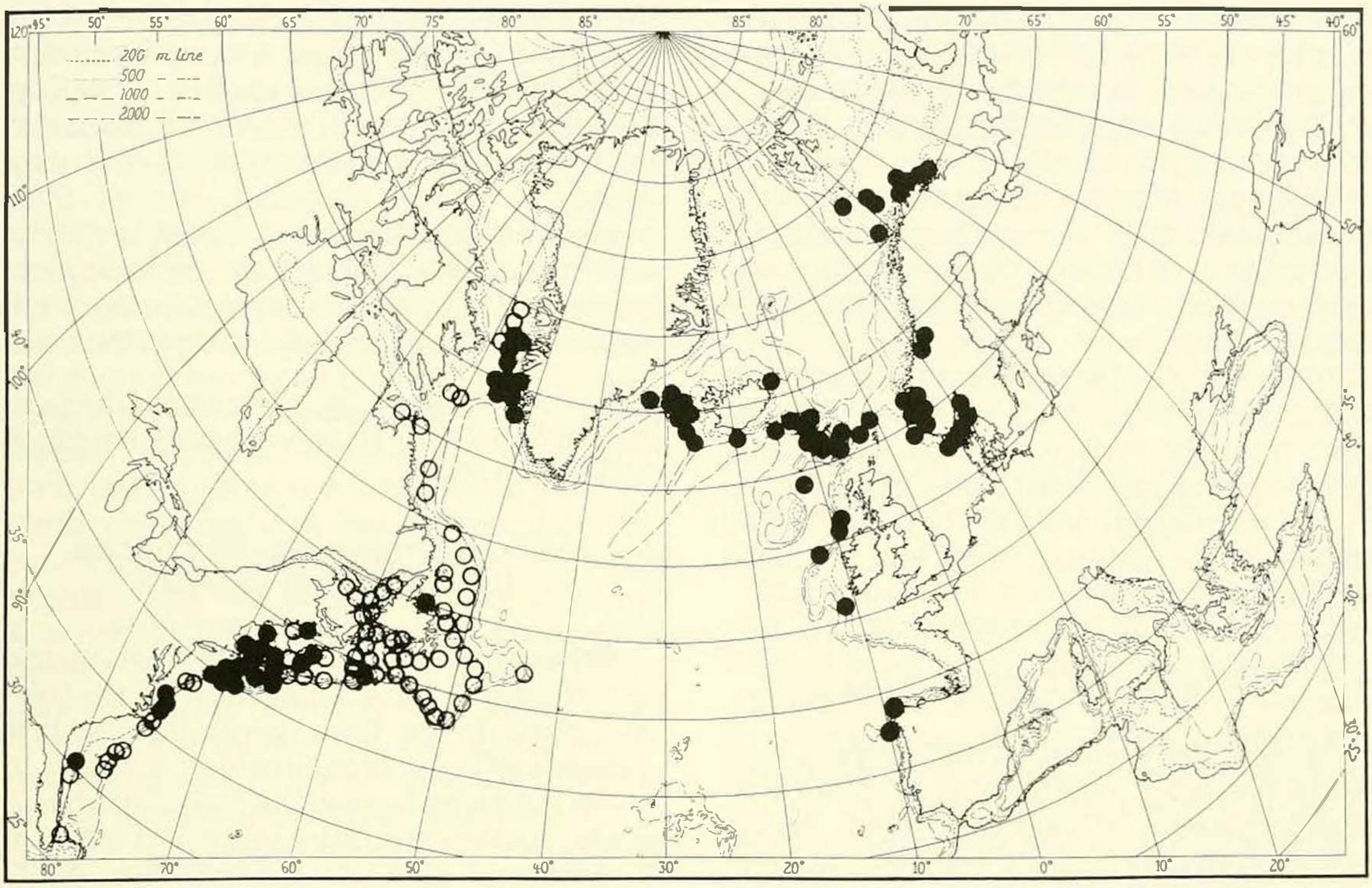

FIG. 21. Distribution of *Bathypolypus bairdii* (Verrill, 1873). Dots: specimens examined by the author, open circles: specimens treated by Kumpf (1958) or Macalaster (1976), but not examined by the author.

ligula (LigLI) is the same for both populations (Fig. 10).

The geographic variation is established for the males only, and it is most distinct in the western Atlantic population south of Newfoundland. At the present state of knowledge I do not think a subspecific division is advisable. The two major dividing areas, Newfoundland and Cape Farewell, southern Greenland, have led to three slightly different populations.

Bathymetric Distribution: Kumpf (1958) states the depth range of his large western Atlantic material of *bairdii* to be 20–350–1545 m. In the Strait of Florida, Cairns (1976) found the depth range to be 190–365–674 m. The southernmost record (29°45′N, 30°09′W) was also the deepest. Similar depth ranges were found off Greenland (maximum 1100 m) and in the East Atlantic (maximum 910 m).

Juveniles and sexually mature animals are found at all depths, and there are no evidence of vertical migrations.

Habitat and Biology: The vast majority of specimens are caught in trawling grounds on muddy or sand-mixed bottoms, which seem to be its natural habitat. The catches suggest a rather even dispersion. Underwater photos from the western Greenland prawn grounds showed *bairdii* in its natural surroundings. The animal was seen resting unprotected in an evidently self-made shallow depression with the arms neatly curled along its sides. The stomach contents of simultaneously caught specimens showed a variety of polychete bristles and crustacean remains, including *Pandalus*.

Based on aquaria observations, O'Dor & Macalaster (1983) suggest that *bairdii* practises a sit-and-wait feeding strategy, and they list food items demonstrating its omnivorous nature.

Underwater photos confirm the supposed feeding strategy. In the prawn trawling grounds, *bairdii* is surrounded by a rich food supply of roaming crustaceans, polychetes, and molluscs.

Mortality must be very low. O'Dor & Macalaster (1983) show that a three-year lifespan, including one reproduction period, is probable, but that a longer life cannot be ruled out. They estimate that due to the few eggs (at most 100) and even fewer hatchlings, about 4% of the latter have to survive to replace the parents.

To deposit and guard the eggs, the females

need a firm substratum. This may explain why I found a skewed sex ratio on the level trawling grounds poor in shelters (38% females, n = 235). Hiding egg-guarding females are less apt to be caught in a trawl.

Brooding females may be found in rocks (Macalaster, 1976) or in cans and containers discharged from ships (my observation) and even in plastic bags (Bergstrom, *fide* Macalaster, 1976).

Wood et al. (1998) observed mating behaviour and brooding of *B. bairdii* (called "*B. arcticus*") from Fundy Bay, Canada. In aquaria, brooding of eggs lasted over 400 days (at 6–10°C) or roughly one-third of the stipulated lifetime of *bairdii.* Hatchlings had a mantle length of 6 mm.

Bathypolypus pugniger, n. sp.

Horizontal Distribution: While *arcticus* and *bairdii* present a neat picture as distinct allopatric species, *B. pugniger,* n. sp., brings new problems through its enigmatic systematic position and peculiar distribution. The single find from western Greenland (Table 6: no. 122) and the specimens from the Faroe-Iceland Ridge are all caught in waters with positive temperatures but in localities episodically exposed to overflow of arctic water from the realm of arcticus. I find this distribution suggestive and propose three different speculative explanations:

(1) *B. pugniger* is a stunted form of *B. bairdii.*

Adult *bairdii* living on the Faroe-Iceland Ridge may endure periods of overflow with arctic water. Brooding females probably stay on. Is it possible that negative temperatures during embryonic development result in stunted development? If this is the case, why are there not transitional stages between *bairdii* and *pugniger?*

(2) *B. pugniger* is a hybrid between *bairdii* and *arcticus.*

The similarity in lifestyle, habitat, and morphology of the two species suggests that mating behaviour may also be similar. Is it possible that male *arcticus* in places with episodic overflow of arctic water extend their territory and seduce (rape?) female *bairdii* left behind and perhaps less resistant, chilled as they are? This and the previous suggestion could explain the peculiar distribution of *pugniger* in a narrow zone bordering the *arcticus* habitat.

(3) *B. pugniger* is a valid species.

It has been overlooked and confused with *bairdii.* The *Bathypolypus* species of the East Atlantic are not yet well known and more material will show a wider distribution of *pugniger.*

The question can best be solved by molecular approaches, such as protein electrophoresis or DNA-sequencing using fresh material not previously preserved in formalin.

Bathymetric Distribution: The depth range of 20 stations where *B. pugniger* was caught is 200–610–1000 m.

The Southern Species–*B. sponsalis, B. ergasticus, B. valdiviae*

Bathypolypus sponsalis is an East Atlantic species, which replaces *bairdii* from the Galician coast to the Cape Verde Islands. It is widespread in the Mediterranean. It seems to prefer the same habitats as *bairdii* and has a similar bathymetric distribution: 170–1250 m (P. Fischer & H. Fischer, 1892; Wirz, 1955; Perez-Gandaras & Guerra, 1978). Some evidence of upslope ontogenetic migration was found in the eastern Mediterranean by Villanueva (1992).

Bathypolypus ergasticus occurs off southwestern Ireland and the Cape Verde Islands but is not known from the Mediterranean. In its northern distribution, it overlaps *bairdii* and further south *sponsalis.* However, *ergasticus* prefers deeper water than its congeners: 704–1350 m off Ireland (Massy, 1909), 932–1139 m off Cape Verde Islands (P. Fischer & H. Fischer, 1892). The three species are parapatric.

Bathypolypus valdiviae is the only representative of the genus known from the southern hemisphere. Off the Namibian coast and on the Agulhas Bank, the species does not seem to be rare on soft bottoms. Bathymetric range: 500–900 m (Chun & Thiele, 1915; Massy, 1927; Roeleveld, 1974; Sanchez & Moli, 1984).

REMARKS ON THE IDENTIFICATION OF SPECIES

The application of bivariate ratios (indices) in multivariate statistical analysis is inadvisable (Atchley et al., 1976), but ratios are useful in taxonomic work, such as in keys. They are also used here for comparison with earlier

published data. Ratios based on variables with isometric or approximately isometric growth (e.g., SDI, LDI, OAI) are acceptable tools for identification of species and of course so are indices based on size-independent meristic characters. Allometric growth, which may impair the usefulness of indices, is not prominent in the *Bathypolypus* species within the relevant size range of adolescent and adult animals (ML 20–60 mm). It is modest even where it can best be demonstrated (EDI, Fig. 8, HWI), and generally intraspecific inherent variability and artifacts far exceed and mask variation due to allometric growth in these phenetically similar species. For purposes of species identification, the allometric variation was less than overall variation and was not calculated. Regrettably, interspecific overlap is often unavoidable (Table 9). The parameters are normally or approximately normally distributed, and the application of several indices tends to obliterate marginal values and leads to clearer discrimination of species, supplementing other, more tangible distinctive characters (funnel organ, crop, radula, sculpture, meristic characters).

An important point that the present revision brought out is that the number of suckers on the hectocotylus is individually constant, even from the juvenile stage, and that the number of laminae is constant from the onset of maturity, irrespective of later increase in size (Figs. 22, 23) Counts of suckers and laminae are good size-independent meristic characters to use in concert with other characters, even if cases of overlap exist (Fig. 9, Table 9). The relative constancy of SHcC was also demonstrated by Toll (1988), who used differences in SHcC as additional argument for taxonomic separation of Atlantic and Pacific *Scaeurgus*.

In the radula, only the rachidians are distinctive in the *Bathypolypus* species. They may be very uniform (*bairdii, sponsalis*), in others very variable (*arcticus*, *pugniger,* n. sp.). A striking example of similar variability is seen in *Graneledone pacifica,* in which the rachidians range from heterodont B8 seriation to simple homodont or even degenerate condition (Voss & Pearcy, 1990: 87, fig. 19).

KEY TO THE NORTH ATLANTIC *BATHYPOLYPUS* SPECIES

The majority of specimens may be identified by outer distinctive features, supplemented by inspection of the funnel organ (Fig. 18). Additional help may be gained from Table 9, which shows ranges of essential indices and counts. For juveniles, females, aberrant males, and less well-preserved specimens, however, inspection of radula, digestive tract, and spermatophores may be necessary.

1a. Mantle length usually more than 25% of total length. Arms with fewer than 100 suckers. Length of hectocotylus at least 70% of opposite (3, left) arm and with fewer than 50 suckers. Skin often warty and with a pointed cirrus over each eye .2

1b. Mantle length usually less than 25% of total length. Arms with over 140 suckers. Length of hectocotylus at most 70% of opposite arm and with over 50 suckers. Skin smooth, supraocular cirri absent 4

2a. Body egg-shaped, with a constriction behind the head. Diameter of eyes less than 33% of ML. Largest sucker diameter

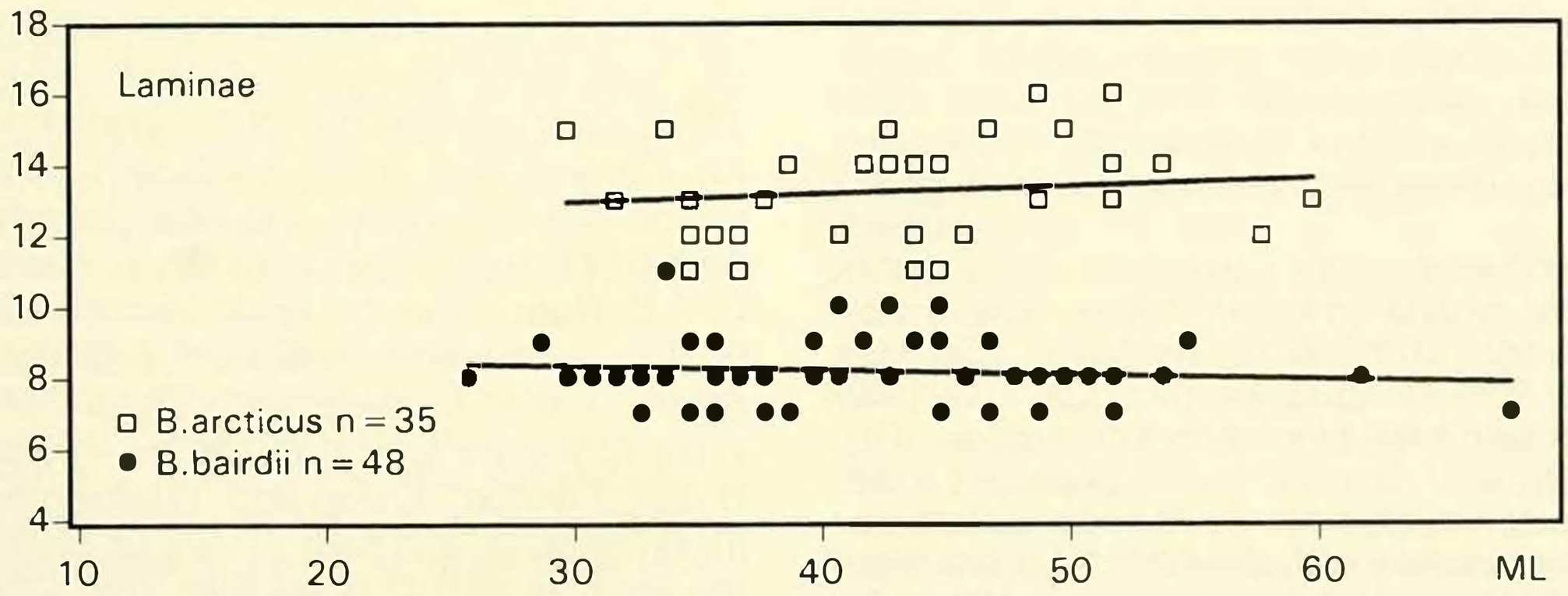

FIG. 22. In *Bathypolypus* species the number of laminae on ligula seems to be individually constant from the onset of maturity. Regress. slopes: < +/– 0.023, r^2: < 0.015 (data for *bairdii* from western Greenland).

FIG. 23. In *Bathypolypus* species, the number of suckers on the hectocotylized arm seems to be constant throughout life. Regress. slopes: < +/– 0.03, r^2 < 0.02.

6.5–8.5% of ML and 18–33% of eye diameter. Ligula with 11–16 laminae; funnel organ a clear-cut VV (Fig. 18); esophagus with prominent crop diverticulum; radula usually with heterodont rachidians (Fig. 5); seminal reservoir occupying only 30% of the spermatophore length . . . .*arcticus*

2b. Body squat; diameter of eye-balls 30–45% of ML; largest sucker diameter less than 6.5% of ML and at most 6–16% of eye diameter. Funnel organ pad-like, never a clear-cut VV. Ligula with less than 13 laminae. Esophagus without crop diverticulum; radula homodont; seminal reservoir occupying about 50% of spermatophore length 3

3a. Arm length order usually: 1.2.3.4. Ligula large, oblong, with 7–12 laminae; calamus 15–25% of ligula length; radula with long, slim homodont rachidians (Fig. 11) . . . . . .*bairdii*

3b. Arm length order usually 3.4.2.1 or subequal. Ligula globular, fleshy, deeply hollowed, with 4–6 laminae; calamus 26–51% of ligula length; radula variable but with broad homodont rachidians (Fig. 15). . . . . .*pugniger*, n. sp.

4a. Hectocotylus with 70–85 suckers; other arms usually with over 200 suckers. Funnel organ almost square pads (Fig. 18). Esophagus with crop diverticulum. Spermatophore very large, longer than ML .*ergasticus*

4b. Hectocotylus with 50–65 suckers; other arms with 140–200 suckers. Funnel organ VV (Fig. 18); esophagus without crop diverticulum. Spermatophore shorter than ML . . . . . .*sponsalis*

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APPENDIX I

Collection localities and specimens examined in this study. Sex and mantel length are stated.

Bathypolypus bairdii (Verrill) East Atlantic

BMNH:

W of Ireland, May 9, 1896, 610–680 fms., ♀ ML: 55.—Off S Ireland, May 21, 1898, Norman coll., 2 ♀♀ ML: 47, one distorted.—60°57′N, 05°47′W, June 26, 1909, 348 m, juv. ML: 8.—61°16′N, 02°08′W, July 9, 1913, 630 m, juv. ML: 8.—Udsire Hole, 58°58′N, 03°37′E, May 15, 1912, ♀ ML: 35.—71°50′N, 28°10′E, May 1, 1975, 180 fms., ♀ ML: approx. 50.

MNHT:

Haul 46, 61°25′N, 05°13′W, July 7, 1979, 481 m, ♂ ML: 23.—BIOFAR project: Stn. 117, 62°00.7′N, 09°4.63′W, July 25, 1987, 481 m, ♀ ML: 16.—Stn. 124, 62°16.94′N, 09°38.93′W, July 26, 1987, 600 m, ♂ ML: 35.—Stn. 158, 61°38′N, 05°38′W, May 7, 1988, 322 m, ♂ ML: 36.—Stn. 419, 62°25′N, 10°38.17′W, June, 1, 1989, 702 m, 2 ♂♂ ML: 40, 42.—Stn. 420, 62°32′81N 10°27.57′W, June 1, 1989, 597 m, ♂ ML: 33.—Stn. 482, 61°01.94′N, 05°13.94′W, July 22, 1989, 509 m, ♀ ML: 24.

IMNH:

B5-77-?, 65°42′N, 27°53′W, February 24, 1977, 750–820 m, 2 ♀♀ ML: 23, 33.—B5-77-48, 65°38′N, 29°27′W, March 23, 1977, 450 m, ♂ ML: 41, ♀ ML: 33.—B5-77-49, 65°37′N, 29°32′W, March 23,

1977, 420–430 m, ♂ ML: 41, ♀♀ ML: 21, 50.—B5-77-50, 63°38′N, 29°27′W, March 23, 1977, 450–460 m, 2 ♂♂ ML: 35, 45, 2 ♀♀ ML: 24, 36.—B5-77-73, 63°38′N, 26°14′W, March 27, 1977, 575 m, ♀ ML: 35.—B5-78-07, 63°48′N, 27°00′W, March 10, 1978, 1110–1095 m, ♂ ML: 63.—B5-78-22, 64°56′N, 27°59′W, March 14, 1978, 970–1030 m, ♀ ML: 47.—DALB-1-80-13, 66°39′N, 28°43′W, October 21, 1980, 415 m, ♀ ML: approx. 64.—B3-81-34, 65°22′N, 32°37′W, February 25, 1981, 910 m, ♂ ML: 75.—BIOICE project: Stn. 2299, 63°00′10N, 22°39′61W, September 10, 1992, 775 m, juv. ML: 28.—Stn. 2346, 63°23′N 12°88′W, May 6, 1993, 501 m, ♂ ML: 39, ♀ ML: 18.

ZIASP:

Nr. 25, near Spitsbergen, 215 m, ♂ ML: 35.

ZMUB:

Norwegian North-Atl. Exp. Stn. 290, 72°27′N, 20°51′E, July 7, 1878, 349 m, ♂ ML: 26, ♀ ML: 18.—Outer part of Laksefjord, Finmark (approx. 71°N, 27°E), August 27, 1900, 280 m, ♂ ML: 24, ♀ ML: 39.—R.V. "Michael Sars": Stn. 56, 70°09′N, 31°00′E, May 21, 1901, 200 m, juv. ♂ ML: 23.—Stn. 108, 70°32′N, 18°17′E, June 18, 1909, 300 m, juv. ♂ ML: 11.—Stn. 5, 70°07′N, 30°53′E, June 4, 1914, ♀ ML: approx. 44.—Stn. 28, 70°16′N, 32°20′E, June 24, 1914, ♀ ML: approx. 30.—MS "Armauer Hansen" Stn. 2, outer part of Sognefjord (N of Bergen), March 10, 1917, juv. ♂ ML: 15.—Salhus (N of Bergen), July 17, 1916, 400–500 m, ♂ ML: 55.—42837, Salhusfjord (N of Bergen), July 12, 1934, 2 ♂♂ ML: 40, 42.—Mangerfjord (N of Bergen), March 18, 1931, 300–400 m, 2 ♂♂ ML: 36, 38.—53336, Kvinnheradsfjord, 59°59′50″N, 05°54′E, December 7, 1956, 687–672 m, 3 ♂♂ ML: 34–42, 3 ♀♀ ML: 22–36.—Hardangerfjord, NE of Varaldsøy, Stn. F 103, November 8, 1957, 690 m, ♂ ML: 40.—50281, Sognefjord, 61°03′N, 06°25′E, May 3, 1966, 1238–1228 m, ♂ ML: 56, 3 ♀♀ ML: 28–47.—R.V. "G.O. Sars", S of Bear Island (Björnöya), August 4, 1974, 500 m, ♂ ML: 74.

ZMUC:

Trondhjemsfjord, Norway, March 4, 1891, Storm leg., ♀ ML: 26.—Trondhjemsfjord, September 19, 1934, 180–220 m, ♀ ML: 16.—Skager-rak, NNW of Skagen, July 28, 1897, 210 fms., 2 ♂♂ ML: 29, 49.—Skagerrak, July 28, 1897, C. G. Joh. Petersen leg., 275 fms., 2 juv. ML: 7, 7.—Skagerrak, about 14 n.m. NW of Hirtshals, June 21, 1911, 313 m, ♂ ML: 41.—Trondhjemsfjord, Norway, N of Tatra, September 19, 1934, 180–220 m, Stephensen leg., ♀ ML: 15.—"Thor": Stn. 167, 63°05′N, 20°07′W, July 14, 1903, 557 m, ♀ juv. ML: 9.—Stn. 223, 64°30′N, 12°25′W, March 17, 1904, 535 m, ♂ ML: 60.—Stn. 99, 61°35′N, 9°35′W, May 22, 1904, 900 m, ♂ ML: 38.—Stn. 274, Skagerrak, NW of Hirtshals, October 9, 1904, 660 m, ♂ juv. ML: 23.—Stn. 1074, Skagerrak, 4.5 n.m. S of Oksø lighthouse, May 28, 1907, 480 m, ♂ ML: 43, ♀ ML: 45.—Stn. 1570, Skagerrak, 53 n.m. N of Hanstholm, June 23, 1911, 525–550 m, ♂ ML: 58, juv. 11.—"Dana": Stn. 6001, 63°33′N, 11°25′W, July 24, 1938, 322 m, ♂ ML: 33.—Stn. 6004, 63°06′N, 10°40′W, July 24, 1938, 437 m, ♂ ML: 43.—Stn. 11643, 57°44′N, 07°40′W, April 17, 1961, 440 m, 2 ♂♂ ML: 50, 55.—Stn. 13320, 58°10′N, 04°22′E, March 12, 1965, 270 m, ♂ ML: 42.—Stn. 15194, 57°35′N, 08°08′E, September 19, 1969, 210 m, 2 ♂♂ ML: 27, 29.—Stn. ?, 61°03′N, 05°04′W, April 20, 1988, 800–600 m, ♂ ML: 38.

ZMUO:

Oslofjord, off Filtvet lighthouse, April 26, 1910, 100 fms., juv. ML: 13.—Oslofjord, Filtvet, May 3, 1966, 150–280 m, ♀ ML: 61.—32291, Oslofjord, Torbjørnskær lighthouse, ♂ ML: 39.—Oslofjord, Drøbak, ♂ ML: 43, ♀ ML: 31.—Oslofjord, Vestmedet, August 14, 1937

Greenland

ZMUC:

"Ingolf": Stn. 28, 65°14′N, 55°42′W, July 1, 1895, 420 fms., ♂ ML: 37.—Stn. 32, 66°35′N, 56°38′W, July 11, 1895, 2 ♀♀ ML: 18, 62 + 4 juv.—Stn. 35, 65°16′N,

55°05′W, July 18, 1895, 682 m, 2 juv. ML: 8, 9.—"Tjalfe": Stn. 337, 64°05′N, 55°20′W, May 8, 1909, 1100 m, ♀ ML: 54.—Stn. 428, 63°54′N, 53°15′W, June 8, 1909, 988 m, ♂ ML: 21.—"Rink": Stn. 45, Bredefjord, SW Greenl. (approx. 60°49′N, 46°45′W), July 18, 1912, 430–450 m, ♂ ML: 52.—"Dana": Stn. 2346, 66°37′N, 56°37′W, June 22, 1925, 450 m, 6 ♂♂ ML: 16–68, 2 ♀♀ ML: 32, 44, 3 juv.—Stn. 2361, 68°08′N, 57°30′W, June 26, 1925, 398 m, 3 ♂♂ ML: 46–55, ♀ ML: 54.—Stn. 10018, 65°02′N, 56°00′W, July 19, 1957, 730–740 m, ♂ ML: 45 (type of *B. proschi* Muus, 1962).—Stn. 13662, 64°24′N, 52°57′W, July 27, 1966, 450–510 m, ♂ ML: 32.—Greenl. Fish. Invest.: Stn. 4539, 64°19′N, 52°55′W, June 4, 1971, 470–570 m, 29 ♂♂ ML: 26–50, 10 ♀♀ ML: 25–54.—Stn. 5043, 63°57′N, 52°21′W, June 18, 1975, 300 m, ♂ ML: 33 + juv.—Stn. 5047, 64°21′N, 52°58′W, June 24, 1975, 550–580 m, 8 ♂♂ ML: 15–49, 8 ♀♀ ML: 24–42.—Stn. 5101, 66°34′N, 54°15′W, August 10, 1975, 335–340 m, ♂ ML: 20.—St. 5112, 64°23′N, 52°58′W, August 21, 1975, 450–510 m, 5 ♂♂ ML: 32–41, ♀ ML: 41.—Stn. 5206, 63°58′N, 52°21′W, June 3, 1976, 300–310 m, ♂ ML: 38.—Stn. 5209, 63°58′N, 52°21′W, June 8, 1976, 300–308 m, ♂ ML: 34, ♀ ML: 46.—Stn. 5215, 64°21′N, 52°59′W, June 10, 1976, 510–520 m, 4 ♂♂ ML: 29–45, 5 ♀♀ ML: 37–41.—Stn. 5384, 64°21′N, 52°59′W, April 22, 1977, 485–510 m, ♂ ML: 44.—"Elias Kleist": Stn. 791010/3, 67°57′N, 57°10′W, October 10, 1979, 310–100 m, ♀ ML: 47.

American East Coast

BMNH:

Off Marthas Vineyard, Massachusetts, May 21, 1898, 200–388 fms., ♂ ML: 35 (labelled *Octopus bairdii*).

USNM:

34223, Le Have Bank, Nova Scotia, 120 fms., holotype of *Octopus lentus* Verrill, 1880.—382469, fishing banks off Massachusetts, 36 miles E of NE Light, Sable Island, from halibut stomach, holotype of *Octopus obesus* Verrill, 1880, ♂ ML: 44.—39943, off New Jersey, 39°49′30N, 71°10′W, August 3, 1884, 420 fms., ♀ ML: 51.—52979, off New Jersey, 39°50′N, 71°43′W, September 18, 1885, 137 fms., ♂ ML: approx. 41.—574638, Bay of Fundy, paratype of *Octopus bairdii* Verrill, 1873, ♂ ML: 24. 575271, 43° 38′N, 69°13′W, August 2, 1912, 60 fms., ♀ ML 20.—575274, Gulf of Maine, August 16, 1878, 75 fms., 3 ♂♂ ML: 21–26.—575275, off Cape Cod, August–September 1878, 70–94 fms., 6 ♂♂ ML: 12–26, 4 ♀♀ ML: 10–18.—575276, off Salem, 41°58′30N, 69°44′W, September 18, 1879, 4 ♂♂ ML: 20–27, ♀ ML: 39.—575277, off Salem, August 1877, 49 fms., 2 ♂♂ ML: 27, 39, 1 ♀ ML: 10.—575278, 42°31′N, 70°20′W, September 2, 1878, 98 fms., 3 specimens.—575279, off Martha's Vineyard, 39°46′N, 71°05′W, February 10, 1880, 487 fms., ♀ ML: 39, juv. ML: 9.—575280, 40°02′N, 70°23′6W, September 4, 1880, 192 fms., ♂ ML: 14, ♀ ML: 35.—575281, 37°24′N, 74°17′W, November 16, 1880, 300 fms., 2 ♂♂ ML: 26, 23, 3 ♀♀ ML: 17–27.—575282, 39°49′N, 70°54′W, September 13, 1880, 225–252 fms., 2 ♂♂ ML: 20, 38.—575285, 37°07′50N, 74°34′20W, November 18, 1884, 167 fms., ♂ ML: 37.—575288, off Martha's Vineyard, 39°53′30N, 71°13′30W, August 9, 1881, 319 fms., 2 ♂♂ ML: 50, one damaged, ♀ ML: 50.—575289, 40°04′N, 69°29′ 30W, September 28, 1884, 58 fms., ♂ ML: 39.—575293, 39°52′20N, 70°58′W, October 2, 1880, 372 fms., ♂ ML: 28.—575294, 39°53′N, 70°58′30W, October 2, 1880, 365 fms., 3 ♂♂ ML: 38–46.—575306, off Gay Head, Martha's Vineyard, 39°57′N, 70°31′30W, August 23, 1881, 225–396 fms., ♂ ML: 40, 3 ♀♀ ML: 21–49.—575971, 39°57′N, 70°58′W, August 25, 1879, 175–200 fms., ♂ ML: 44.—RV "Oregon": Stn. 6800, 29°48′N, 80°09′05W, July 20, 1967, 183 fms., 2 ♂♂.—Gosnold cruise: Stn. 105, 39° 51′N, 70°56′W, August 10, 1972, 875–880 m, ♂ ML: 51.—Stn. 120, 39°50′N, 70°32′W, August 16, 1972, 750–775 m, ♂ ML: 65.—RV "Chain": Stn. 243, 39°30′N, 72°20′W, February 28, 1973, 474–529 m, ♂ ML: 21, ♀ ML: 27.—Stn. 244, 39°28′N, 72°18′W, February 28, 1973, 260–342 m, ♀ ML: 44.—Stn. 254,

39°51′N, 70°47′W, March 2, 1973, 768–947 m, ♂ ML: 49, ♀ ML: 56.—Stn.?, 39°31′N, 78°18′W, February 26, 1973, 810–900 m, ♀ ML: 41.—Stn.?, 39°31′N, 75°23′W, February 28, 1973, 420–590 m, ♀ ML: 26.—RV "Knorr": Stn. 300, 39°40′N 72°27′W, November 13, 1973, 110–182 m, ♂ ML: 26.—Stn. 301, 39°32′N, 72°24′W, November 13, 1973, 475–520 m, 4 ♂♂ ML: 20–33, ♀ ML: 28.—GI-75-08: Stn. 10, 37°53′N, 74°40′08W, September 9, 1975, 290–340 m, 2 ♂♂ ♀♀ (distorted).—Stn. 18, 37°04′07N, 74°34′03W, September 10, 1975, 200–215 m, 3 ♂♂, 1♀.—St. 19, 36°58′04N 74°37′05W, September 11, 1975, 190–250 m, 2 ♂♂, 3 ♀♀.—St. 22, 36°58′06N, 74°33′08W, September 11, 1975, 880–920 m, 3 ♂♂ ML: 24–42.—Stn. 99, 36°36′05N 74°39′W, September 20, 1975, 850–1000 m, ♀ ML: 50.

ZMUC:

"Albatros IV", cruise 76-02: Stn. 221, 40°07′N, 69°04′W, March 28, 1976, 465 m, ♀ ML: 30.—Stn. 237, 41°44′N, 69°46′W, March 30, 1976, 78 m, ♂ ML: 27.—Stn. 288, 41°53′N, 67°52′W, April 6, 1976, 52 m, ♂ ML: 19.—Stn. 300, 42°05′N, 68°15′W, April 7, 1976, 189 m, ♀ ML: 25.—Stn. 305, 42°18′N, 69°12′W, April 8, 1976, 230 m, ♀ ML: 38.—Stn. 309, 42°26′N, 70°06′W, April 8, 1976, 84 m, ♂ ML: 42.—Stn. 321, 42°45′N, 70°00′W, April 14, 1976, 163 m, ♀ ML: 41.—Stn. 322, 42°46′N, 69°35′W, April 14, 1976, 163 m, ♂ ML: 25, ♀ ML: 43.—Stn. 330, 42°59′N, 68°39′W, April 17, 1976, 187 m, 2 ♀♀ ML: 20, 22.—Stn. 332, 42°45′N, 67°47′W, April 17, 1976, 200 m, 2 ♂♂ ML: 38, 42.—Stn. 333, 42°34′N, 67°58′W, April 17, 1976, 206 m, ♀ ML: 20.—Stn. 339, 42°17′N, 66°49′W, April 18, 1976, 270 m, ♂ ML: 26.—Stn. 341, 42°19′N, 66°12′W, April 18, 1976, 262 m, 1 spm.—Stn. 405, 43°26′N, 67°34′W, April 29, 1976, 218 m, ♂ ML: 37, ♀ ML: 37.—Stn. 406, 43°06′N, 67°48′W, April 29, 1976, 200 m, ♀ ML: 29.—Stn. 409, 43°39′N, 68°17′W, April 29, 1976, 190 m, 3 ♂♂ ML: 18–29.—Stn. 426, 43°29′N, 69°01′W, May 6, 1976, 139 m, ♀ ML: 50.—Notre Dame Bay, Newfoundland: October 1975, 3 ♂♂ ML: 67–74.—USSR "Belogorsk", cruise 74–11: Stn. 142, 41°16′N, 68°41′W, October 12, 1974, 80 m, ♀ ML: 32.

Bathypolypus arcticus (Prosch) East Atlantic

BMNH:

60°03′N, 05°51′W, August 17, 1880, 540 fms. (labelled *B. faeroensis*) ♂ ML: 35, ♀ ML: 30.—HMS "Triton", Stn. 9, 60°05′N, 06°21′W, August 23, 1882, 608 fms. (syntypes of *Benthoctopus sasakii* Robson), ♂ ML: approx. 32, ♀ ML: 27.—Stn. 40, 57°34′N, 00°01′W, November 27, 1904, Tow net 100 m, ♀ ML: 30.—61°27′N, 01°47′W, July 25, 1909, 1240 m, ♀ ML: 43 (labelled *Benthoctopus piscatorum*) + ♀ ML: 20.—61°42′N, 02°00′W, July 25, 1909, 1236 m, ♀ ML: 31 (labelled *B. faeroensis*).—Stn. 77, 75°16′N, 24°46′E, June 1956, 85 m, E. Holt, 2 ♀♀ ML: 28, 29.—Cruise IV, Stn. 37, 60°25′N, 04°31′W-60°29′N, 04°22′W, W of Foula, 1973, 940–910 m, 2 ♀♀ ML: 20, 28.

IRSNB:

(*vide* Adam, 1939) 66°20′N, 12°28′W, June 21, 1938, 180–220 m, 2 ♂♂ juv. ML: 16, 10, ♀ ML: 13.—66°20′N, 12°28′W, June 22, 1938, 180–220 m, ♀ ML: ca. 18.

MNHT:

Haul 96, 62°59′N, 09°54′W, July 23, 1979, 481 m, ♀ ML: 46.—BIOFAR project: Stn. 15, 62°37′68N, 04°40′37W, July 17, 1987, 683 m, juv. ML: 12.—Stn. 95, 60°41′51N, 05°18′63W, July 23, 1987, 803 m, ♀ ML: 21.—Stn. 274, 63°00′79N, 07°49′22W, May 16, 1988, 698 m, ♀ ML: 42.—Stn. 294, 60°26′N, 07°28′W, July 17, 1988, 1096 m, ♂ ML: 30.—Stn. 502, 60°30′26″N, 08°04′W, July 25, 1989, 890 m, ♂ ML: 30.—Stn. 589, 60°40′N, 10°00′W, April 9, 1990, 250 m, ♀ ML: 15.—Stn. 726, 60°39′N, 06°54′W, September 29, 1990, 400 m, ♀ ML: 27.

IMNH:

D6-80-50, 67°11′N, 18°30′W, April 20, 1980, 430 m, ♂ ML: approx. 41.—B16-80, 66°50′N, 20°26′W, October 29, 1980, 415 m, ♀ ML: approx. 37.—B3-81-34,

62°59′N, 20°23′W, March 7, 1981, 910 m, ♀ ML: 95.—B4-81-137, 66°37′N, 12°58′W, April 1, 1981, 320 m, ♀ ML: 31.—BIOICE project: Stn. 2080, 67°22′79N, 17°20′77W, July 4, 1992, 897 m, ♀ ML: 46.—Stn. 2085, 67°15′67N, 17°26′41W, July 4, 1992, 754 m, ♀ ML: 61.—Stn. 2088, 67°02′35N, 13°25′05W, July 4, 1992, 903 m, ♂ ML: 40.—Stn. 2134, 66°44′46N, 18°54′93W, July 8, 1992, 504 m, ♂ ML: 17.—Stn. 2135, 66°44′37N, 18°57′32W, July 8, 1992, 418 m, ♂ juv. ML: 26.—Stn. 2320, 64°02′N, 09°44′W, May 2, 1993, 758 m, ♂ ML: 49.—Stn. 2322, 63°55′N, 10°04′W, May 3, 1993, 627 m, ♀ ML: 45.—Stn. 2326, 63°44′N, 10°09′W, May 3, 1993, 563 m, ♀ ML: 33.—Stn. 2328, 63°20′N, 10°57′W, May 3, 1993, 430 m, ♀ ML: 54.

TMDZ:

M/K "Asterias": Isfjord, Svalbard, July 18, 1955, 242–228 m, ♀ ML: 26.—Isfjord, Svalbard, August 14, 1958, 230–215 m, ♂ juv. ML: 23, ♀ ML: 23.

ZIASP:

92, Barents Sea, 140–150 m, Kondakov det., ♂ juv. ML: approx. 12.—119, between Spitsbergen and Frantz Josef Land, 210 m, Kondakov det., ♂ ML: 31.—120, Barents Sea, 201 m, ♂ ML: 19.—Nr. 607, Novaya Zemlya, 37 m, ♀ ML: 39.

ZMUB:

ESE of Vardø (about 70°N, 32°E), August 10, 1902, ♀ ML: approx. 49.—"Solveig I", Stn. 52, Kongsfjord, Svalbard, June 22, 1938, 290–333 m, ♀ ML: 42.—42838, Stn. 64, Svalbard, 78°25′N, 12°06′E, July 7, 1939, ♀ ML: 44.—36145, "Sotra", Stn. 250, 78°04′N, 14°10′E, September 9, 1930, ♂ ML: 38.—"Tovik", Stn. 10, 77°44′N, 11°45′E, June 30, 1925, 185–228 m, ♂ juv. ML: 13.—78°03′N, 14°10′E, August 30, 1931, 147 m, ♀ ML: 31.—75°00′N 37°20′E, September 1, 1968, 100–150 m, ♀ ML: 57.—18678, "Michael Sars", Stn. 37, 62°43′N, 01°26′E, June 29, 1902, 775 m, ♂ ML: 36.

ZMUC:

61°27′N, 01°27′W, July 25, 1909, 1240 m, labelled *Polypus faeroensis* Russell Type. (leg. A. C. Stephen).

Greenland

ZMUC:

Lectotype of *Octopus arcticus* Prosch, 1849: ♂ ML: 42, SW Greenland, August 26, 1841, K. M. Jørgensen leg.—Paralectotype ♀, partly dissected, SW Greenland, July 27, 1840, K. M. Jørgensen leg.—Dissected male organs pictured by Prosch (1849: figs. 1–3).—3 ♀♀ in bad shape and partly dissected labelled Greenland and evidently from the 1840s.—Holsteinsborg, SW Greenland, 1892, Traustedt leg., ♀ ML: 64.—"Ingolf": Stn. 124, 67°40′N, 15°40′W, July 28, 1896, 932 m, 2 ♂♂ ML: 44, 44.—Near Nanortalik, SW Greenland, April 15, 1906, ♀ ML: 31.—Lichtenau fjord, SW Greenland, October 14, 1910, from stomach of Greenland halibut, ♀ ML: 45.—Lichtenau fjord, June 6, 1914, 220 fms., ♀ ML: 41.—Lichtenau fjord, July 3, 1947, Poul Hansen leg., ♀ ML: 51.—"Godthåb": Stn. 81, 75°35′N, 65°41′W, August 1, 1928, 490 m, ♂ ML: 54, ♀ ML: 23.—Stn. 87, 77°05′N, 71°13′W, August 4, 1928, 790 m, 14 ♂♂ ML: 32–58, 2 ♀♀ ML: 32–46, 1 juv. ML; : 22.—Stn. 90, 77°17′N, 69°59′W, August 5, 1928, 930 m, ♂ ML: 46, ♀ ML: 38.—Stn. 116, 76°08′N, 80°53′W, August 17, 1928, 80 m, ♂ juv. ML: 13.—"Godthåb"s summer cruise, Stn. 341, off Kap Hacker, Jameson Land, E Greenland, August 27, 1933, juv. ML: 15.—Ella Island, Kong Oscar Fjord, approx. 73°N, 25°W, October 10, 1931, 67–68 m, ♀ ML: 35.—Ymer Island, Frantz Joseph Fjord, E Greenland (approx. 73°20′N), August 8, 1932, ♂ ML: 43.—Frantz Joseph Fjord, off Engdalen, August 7, 1931, 45–36 m, ♂ ML: 52.—Lindenow Fjord, 60°30′N, 43°25′W, July 17, 1935, 100–150 m, Bertelsen leg., ♂ ML: 36.—Amerdlok Fjord, near Holsteinsborg (Sisimiut), July 26, 1938, approx. 500 m, ♀ ML: 54.—Skovfjord, SW Greenland, June 16, 1948, P. Hansen leg., ♂ ML: 58.—Young Sound, off Daneborg, approx. 74°15′N, 20°W, July 1947, ♀ ML: approx. 58.—Bylot

Sound, 76°31′N, 69°09′W, August 20, 1968, 240 m, Just & Vibe Stn. 45, ♂ ML: 54.—Kap Farvel Exp.: Stn. 56, 60°13′N, 44°13′W, July 31, 1970, 400–420 m, ♂ ML: 35.—Stn. 128, 60°01′N, 43°59′W, August 21, 1970, 530 m, ♀ ML: 51.—W Greenland, 66°21′N, 54°56′W, August 2, 1975, 280–290 m, Max Andersen leg., ♀ ML: 12.—Greenland Fish. Invest.: Stn. 3978, 63°53′N, 51°27′W, May 9, 1968, 230–250 m, ♀ ML: 35.—Stn. 4360, May 21, 1970, 240–250 m, ♂ ML: 43, ♀ ML: 34.—Stn. 5101, 66°34′N, 54°15′W, August 10, 1975, 300 m, 2 ♂♂ ML: 33 + juv.

ZMUO:

Hoel's Greenland Exp.: Stn. 1101, Kong Oscar Fjord, E Greenland (approx. 72°20′N), August 12, 1930, 55–100 m, ♂ juv. ML: 17.—Stn. 1116, Kong Oscar Fjord, August 15, 1930, 250 m, ♂ ML: 30.—Stn. 1118, Kong Oscar Fjord, August 16, 1930, 120 m, 1 juv. ML: 26.—Stn. 1119, Kong Oscar Fjord, Vegasund, August 17, 1930, 190–250 m, 4 ♂♂ ML: 37–44.

American East Coast

No material.

Bathypolypus pugniger n. sp.

IRSNB:

66°23′N 12°53′W, June 14–15, 1938, 200–250 m, ♂ ML: 22, ♀ ML: 18 (*vide* Adam 1939).

MNHT:

Haul 25, 63°16′N, 09°30′W, July 6, 1979, 500 m, 2 ♂♂ ML: 27, 28.—BIOFAR project: Stn. 47, 61°02′31″N, 05°54′W, July 19, 1987, 280 m, ♀ ML: 19.—Stn. 80, 60°38′89N, 08°27′93W, July 22, 1987, 678 m, ♀ ML: 18.—Stn. 269, 62°49′84N, 08°15′55W, May 15, 1988, 510 m, ♂ ML: 33.—Stn. 503, 60°38′02N, 08°33′54W, July 25, 1989, 513 m, ♂ ML: 18.—Stn. 734, 60°10′06N, 07°57′03W, May 8, 1990, 634 m, ♂ ML: 31.—Stn. 738, 62°19′N, 10°13′W, October 1, 1990, 749 m, ♂ ML: 25.—Stn. 740, 62°29′N, 10°02′W, October 1, 1990, 597 m, ♂ ML: 18.

IMNH:

B5-77-36, 65°40′N, 28°20′W, March 21, 1977, 1000–970 m, ♀ ML: 36.—B5-77-40, 65°36′N 29°17′W, March 22, 1977, 870–910 m, ♀ ML: 33.—B5-77-42, 65°34′N, 29°29′W, March 22, 1977, 750–760 m, ♀ ML: approx. 44.—B5-77-46, 65°29′N, 29°33′W, March 23, 1977, 960 m, 2 ♂♂ ML: 36, 30, 3 ♀♀ ML: 27–40.—B5-77-50, 65°38′N, 29°27′W, March 23, 1977, 450–460 m, ♀ ML: approx. 32, ♂ ML: 30.—B5-78-44, 64°58′N, 27°44′W, March 14, 1978, 860–870 m, holotype 19990971. ♂ ML: 32.

ZMUC:

"Dana" Stn. 5840, 62°44′N, 06°06′W, May 14, 1938, 330 m, ♂ ML: 19.—Stn. 6001, 63°33′N, 11°25′W, July 24, 1938, 322 m, 5 ♂♂ (3 juv.) ML: 6–13, 2 ♀♀ (1 juv.) ML: 15, 23.—Stn. 16437, 64°14′N, 57°26′W, July 24, 1974, 760 m, ♂ ML: 54.—Stn. B5-77-36, 65°40′N, 28°20′W, March 21, 1977, 1000–970 m, ♀ ML: 36.—Haul 25, 63°16′N, 09°30′W, July 6, 1979, 500 m, 2 ♂♂ ML: 27, 38. BIOFAR project: Stn. 503, 60°38′N, 08°33′54W, July 25, 1989, 513 m, ♂ ML: 18.—Stn. 738, 62°19′N, 10°13′W, October 1, 1990, 749 m, ♂ ML: 25.—Stn. 734, 60°10′06N 07°57′03W, May 8, 1990, 634 m, ♂ ML: 31,