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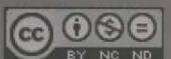
The Marine Fauna of New Zealand:

Cephalopoda: Oegopsida: Architeuthidae (Giant Squid)

Ellen Celia Förch

COVER PHOTO: Anterior end of Architeuthis dux Steenstrup, 1857, with tentacles directed toward observer. [Computer-modified image of a model in The Natural History Museum, London. Reproduced by permission.]

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by

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NEW ZEALAND

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Frontispiece: Artificially coloured photo of *Architeuthis* stranded on Princess Bay beach, Wellington, 12 May 1984. (= Specimen 4 in this monograph). Photo courtesy of *The Evening Post*, Wellington.

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ABSTRACT

A detailed study of 16 *Architeuthis* specimens obtained from New Zealand over a period of 15 years has revealed very high inter-individual variability. Each previously used taxonomic character has been measured and compared with the historical literature. Characters commonly used in other families, as well as several new characters, have also been noted and measured. New information is presented on external morphology, internal organs, diet, and distribution. Skin colours and textures have been recorded, arms and suckers have been examined in detail, and several tentacle clubs were available for study. Some food remains were identified which suggest that *Architeuthis* feeds mainly on mid-size deepwater fishes and a variety of smaller squid. Some crustacean fragments were also present. Trawl-caught specimens showed a preference for depths between 300 and 600 m deep, corresponding to the edge of the continental slope around New Zealand.

In the process of examining which of the four *Architeuthis* species previously described from New Zealand best fitted the present specimens, it became necessary to examine the rationale for the erection of *Architeuthis* species throughout the world. Progressive scrutiny of each taxonomic character used by previous authors, in the light of variation exhibited by the present set of specimens, has resulted in the proposal that the family Architeuthidae should reduce to a single genus and species. The only defensible species is that of the earliest adequate description, *Architeuthis dux* Steenstrup. A revised summary description is presented, diagnosing the characters of the family and genus.

This study concerns a creature that is still largely mythical. It has never been observed in its natural habitat. Accounts of live animals are scarce and prone to embellishment. The early life-history stages are almost unknown, and there is little information on distribution, mating, growth, longevity, or diet. For a long time the giant squid was thought to frequent only the North Atlantic (Newfoundland, Norway), the Southern Oceans, (especially New Zealand), and the North Pacific. More recently, specimens have been described from equatorial and South Atlantic Oceans and have been captured more widely in the Pacific. In keeping with their near-mythological status, giant squid generate enormous popular interest whenever they are encountered. Unfortunately, scientific knowledge has not advanced significantly for a number of reasons.

The squid usually occurs rarely, as single specimens and often in poor and incomplete condition. Because capture of a giant squid is an unusual event, the unsuspecting biologist is caught unprepared, and is unlikely to be familiar with the animal. A succession of different observers making non-standard measurements, coupled with the difficulty, expense, and unsatisfactory results of preservation explain the fragmentary and unreliable state of basic morphological data on this animal. The size and fragility of preserved specimens makes sending material between researchers impractical. Storage of more than a few specimens is prohibitively expensive, even if exceptional material were available. The samples are biased in numerous ways including a shortage of male specimens and underrepresentation of juvenile forms. Biologists are still very dependent on serendipitous captures, for not enough is known for fishermen to set out to catch a giant squid.

There is a great deal of confusion in the taxonomy of *Architeuthis,* largely as a result of the sporadic geographically and temporally isolated occurrences. Normally the taxonomist expects to compare a specimen directly or indirectly with other specimens. A specimen is also compared with documented variation for the species. This variation occurs as a result of a host of other factors (e.g., sexual, developmental, environmental). Without a knowledge of natural variation and the expression of characters, any attempts to define species will revert to the "one specimen = one species" situation which prevailed earlier this century. This problem has been recognised, and in recent decades authors have refrained from burdening the literature with additional names (Rae 1950; Kjennerud 1958; Clarke 1980). The biggest problems facing *Architeuthis* taxonomists are the scarcity of specimens and the poor state of species descriptions.

Previous Accounts of *Architeuthis*

Early *Architeuthis* records and writings have been well summarised in a number of reviews. The most useful of these are Tryon (1879), the monographical treatment by Pfeffer (1912), and the more popular publications of Lane (1960) and Ellis (1994). When combined with Muntz (1995) these form a summary of the early records of *Architeuthis* from the time of Pliny to the present.

The first systematic investigations were by the Danish naturalist Japetus Steenstrup who investigated early folk and court accounts of gigantic squids and gave public lectures on the subject. He initially received fragmentary material for which he erected the name *Architeuthis monachus.* He later received more substantial material which he described as *Architeuthis dux* and had circulated the plates to colleagues by 1857. The formal publication of the accompanying text entitled *Spolia Atlantica* was not published until 1898, a year after his death. Harting (1861) described unprovenanced material in a museum in Utrecht and referred to Steenstrup's plates. Owen (1881) provided a detailed description of an entire fourth arm of an *Architeuthis* in the British Museum; unfortunately the material is unprovenanced. By this stage more popular accounts had been published for Newfoundland (Harvey 1874a), Ireland (More 1875b), Teneriffe (Gervais 1875), and the Indian Ocean (Vélain 1877).

A.E. Verrill published extensively on the giant squids which arrived in Newfoundland in the last two decades of the 19th century, producing more than fifteen papers between 1874 and 1882. He described some 24 records, but most were fragmentary and the descriptions are heavily dependent on second-hand accounts and estimates. Verrill described one new species, *Architeuthis harveyi* and redescribed *Architeuthis princeps* (Kent, 1874). Both of these species descriptions have been the subject of considerable debate over the years and will be considered again in this study. Although, technically, Verrill could have claimed priority for the genus name *Megaloteuthis*

Kent, 1874, he chose to honour the name proposed by Steenstrup (1857) and used by Harting (1861) although neither work had been published nor had generic characters been adequately proposed. Verrill's reasons for doing so are elaborated by him in the footnotes of his summary publication "Report On The Cephalopods of the North-Eastern Coast of America" (1882b: 234–235). A summary of Verrill's specimens is contained in Frost (1934).

At about the same time that Verrill was writing about the Newfoundland specimens, the New Zealand naturalist T.W. Kirk and the New Zealand lighthouse keeper C.W. Robson were erecting four new *Architeuthis* species for the New Zealand region based on single specimens; *A. verrilli* Kirk, 1882, *A. stockii* (Kirk, 1882) (as *Steenstrupia* n. gen.), *A. kirkii* Robson, 1887 and *A. longimanus* Kirk, 1888. These species descriptions have been the subject of comment, generally of a critical or disbelieving nature (e.g., Pfeffer 1912; Clarke 1966; Dell 1970). Only one of the species descriptions (*Architeuthis kirkii* Robson 1887), has been applied to subsequent specimens, notably by Allan (1948), Dell (1970), and Gauldie *et al.* (1994). Kirk (1880) also published a record of the strandings of *Architeuthis* around New Zealand until that time, which was updated by Dell (1970). The record has been further extended in the present study.

Another species in the group of giant squids that has come to be referred to as "southern forms", was *Architeuthis sanctipauli* Vélain, 1875 from the Island of St Paul in the Southern Indian Ocean. Some material was retained, and a wood-cut illustration was published based on a photograph. The form of the posterior of the body and the elongate narrow fins have assumed considerable importance in the taxonomic decisions and identification of subsequent *Architeuthis* specimens.

The first Pacific *Architeuthis* specimens had been described in the North Pacific from Japan by Hilgendorf (1880) but his name (*Megateuthis martensii*)was discarded by later authors as a *nomen spurium* (Pfeffer 1912). The next *Architeuthis* record from Japan was a description by Mitsukuri and Ikeda (1895) of an unnamed species, later assigned the name *A. japonica* by Pfeffer (1912) in his monographic review of the family. This name was adopted by Sasaki for his 1916 specimen, described in detail in 1929. This species name has subsequently been applied to all *Architeuthis* captured in the northern Pacific with little further critical attempt at identification beyond capture location. The validity of the species *A. japonica* and assumptions involved in discarding *Megateuthis martensii* Hilgendorf, 1880 will be reexamined in the light of information from the present study.

The North Atlantic species have been the subject of debate since their inception, with Steenstrup (1898) doubting that the fin configurations described by Verrill (1879, 1882b) were correct. Most later authors have either contributed to further "speciation" (e.g., Robson 1933; Cadenat 1936; Rae 1950), or have been puzzled by the seemingly unique features of their particular specimens (Ritchie 1918; Pérez-Gándaras & Guerra 1978; Clarke 1980; Roeleveld & Lipinski 1991). A few authors have attempted to rationalise the proliferation of Atlantic species, amongst them Stephen (1962), Kjennerud (1958), Roper and Boss (1982), Nesis (1974), and Nesis *et al.* (1985).

Early records are listed in Tryon (1879), Steenstrup (1857), Verrill (1882b), and monographic works by Pfeffer (1912) and Frost (1934); Icelandic records are summarised by Bruun (1945) and world occurrences by Clarke (1966) and Nesis (1974). Reports and popular accounts are contained in the scholarly accounts of Ellis (1994) and Muntz (1995).

The distribution of *Architeuthis* is a popular source of speculation. Few of the authors describing a specimen of *Architeuthis* have been able to resist the temptation to propose distributions, particularly in North Atlantic (see Aldrich 1968, 1991). Many secondary sources of evidence for distribution exist based on beaks in predator stomachs. These have not been considered in this study, but published examples of this information include: Belyayev (1964), Clarke (1962a), Fiscus and Rice (1974), Clarke and MacLeod (1974, 1976), Dong (1984), Martin and Clarke (1986).

The publication of substantial data-sets are restricted to Verrill in the 19th century (24 specimens), Aldrich from 1960 onwards (15 specimens), and Nesis in the 1980s (more than 18 specimens). The present study deals with 16 specimens in detail, and presents measurements of eight additional records.

Studies on other aspects of the squid's morphology or physiology are limited. Studies on the biology of *Architeuthis* are not numerous and some key papers are listed below.

Physiology has been considered by Brix (1983); the heart by Martin and Aldrich (1970); ecological aspects of distribution and temperature by Brix *et al.* (1989); shape, locomotion, and energetics by Bidder (1968) and O'Dor (1988a,b); buoyancy by Boyle (1986), and Clarke *et al.* (1979); other aspects of the flesh and diet by Robison (1989), Pérez-Gándaras and Guerra (1978, 1989), and Fenaughty *et al.* (1988); parasites by Pippy and Aldrich (1968); spermatophore by Knudsen (1957), and Kjennerud (1958); brain by Maddock and Young (1987); statoliths by Young (1977), Roeleveld and Lipinski (1991), Jackson *et al.* (1991), and Gauldie *et al.* (1994); beaks by Clarke (1962b, 1980, 1986); and gladius by Toll (1982).

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History of Giant Squid in New Zealand

Architeuthis species from New Zealand were described from a number of strandings around Cook Strait in the late 19th Century. They comprise *Architeuthis verrilli* Kirk, 1880, *A. stockii* (Kirk, 1882), *A. kirkii* Robson, 1887, *and A. longimanus* Kirk, 1888.

Since last century only one New Zealand specimen (Dell 1970) has been identified as belonging to one of these species (*A. kirkii*). A specimen believed to be *A. kirki* was reported from the Tasman Sea near Australia (Allan 1948), but no detailed measurements were taken and the material cannot be located. Dell (1952) summarised previous New Zealand giant squid strandings and in 1970 redescribed *A. kirkii* based on a specimen stranded at Makara (Cook Strait) in 1956 and briefly reviewed the taxonomic state of the family. According to Dell the four New Zealand species names have been properly proposed but with insufficient detail. Dell's (1970) specimen is still in the Museum of New Zealand and has been remeasured and examined as part of this study. Other fragmentary, unprovenanced and illegibly labelled material exists in the Museum of New Zealand and the records have recently been reassessed by the Collection Manager for Mollusca, Mr Bruce Marshall (1996).

Other authors to mention *Architeuthis* from the New Zealand region are Gaskin and Cawthorn (1967a, b), Imber and Russ (1975), Powell (1979), Clarke and MacLeod (1981), Imber (1992), and Gauldie *et al.* (1994).

Additional publications on *Architeuthis* from the Southwest Pacific region include: a very small specimen recorded by Lu (1986); also Jackson *et al.* (1991), Förch (1983), Judd and Förch (1996), Zeidler and Gowlett-Holmes (1996).

Both Pfeffer (1912) and Dell (1970) have expressed reservations about the original descriptions. There seem to be inconsistencies between the material, the illustrations, and the descriptions on which the taxonomy was based. In New Zealand, as elsewhere, the literature is characterised by a lack of cross referencing to other descriptions and is almost exclusively dominated by reliance on single specimens. There has been no systematic attempt to examine the characters which the early taxonomists used to define the species.

Reductions in the number of species, including those from New Zealand, have been proposed by a number of authors e.g., Dell (1970), Aldrich (1968, 1991), Nesis (1974), and Nesis *et al.* (1985) but these have not been based on a rigorous examination of the literature, or on formal documentation of the extent of natural variation.

The Present Study

The extent of natural variation within the species of this genus is poorly known and this has been a major impediment in the taxonomic revision of the family. The arrival of the first "recent" New Zealand specimen in 1983 was an event provoking popular and scientific curiosity, but the rapid succession of additional specimens thereafter demanded a more rigorous approach. As the arrivals were examined it became clear that all the specimens differed from each other, and from previously described species in at least some respects. It was necessary to consider the morphology and intraspecific variation in some detail and, as a consequence, standard approaches and datasheets were developed and applied. The present New Zealand specimens afforded the rare opportunity for one cephalopod biologist to see a comparatively large number of samples in quick succession and in fresh condition. This presented a situation where it was possible to apply the same data sheet, have a single person making the measurements, and obtain specimens in similar condition, within a short space of time and restricted geographic area. This is as close as any *Architeuthis* taxonomist could approach to the recommended practice of placing squids side by side for direct comparison. This also presented an opportunity to note previously unrecorded features that might vary, including mantle texture, colour, head shape, internal organs, and many other features which are not available with preserved, stranded, or partially digested material.

The initial intention of this study was to document the range of variation within *Architeuthis* in the Australasian region, and to that extent it was fortunate that many of the recent specimens were similar in size, thus presumably eliminating major ontogenetic effects. However, links to past New Zealand "species" were too tenuous to enable identification. Rather than erect new species, this paper attempts to provide a sound descriptive base for specimens from the New Zealand region and discusses the implications for existing *Architeuthis* species. The implications have been more far-reaching than had been expected.

Table 1. *Architeuthis* material in the Museum of New Zealand.

NMNZ no.	Location	Parts known to be preserved	Present study specimen no.
10000[1]	Makara 1956	beaks, whole body	Dell (1970)2
77446[2]	Canterbury Bight	partial skinned club	
79971	New Plymouth	beaks	1
79972	Auckland Is.	-	2
79973	Castlepoint	beaks	3
79974	Princess Bay	partial body	4
79975	Sealords	sucker rings, partial body	5
79976	Puysegur Point	beaks, L & R tentacles with clubs, arm and tentacle sucker rings, partial body	7
86826	West coast South Island	beaks	6
102285	West coast South Island	L & R tentacles with clubs, R arm tip 2, 3, 4, Left arm 1 tip	6
—	?	tentacle club, radula, spermatophores, pen, male reproductive organs	8
—	?		9
102282	unknown	L & R tentacles with clubs	11
102269		beaks, arm sucker rings, tentacular suckers, radula, stomach contents, beak, radula, tentacle portion, sucker rings	12
			13
102278		arm sucker rings	14
102285		all arm tips, L & R tentacle clubs	
118003	*Kaiyo Maru 15* Stn 552/33	L & R tentacles with clubs	Collector Mr Munro
118019	43°55' S, 176°50' E, 515 m May 1994	buccal mass, beak, L & R tentacle clubs	FV *Dalmor*, G. Williams, ML 1850 mm, FL 760 mm, specimen in pieces
118020	43°48' S, 177° 35' E, 514 m	buccal mass, beak	ML 1110 mm, FL 490 mm specimen incomplete, abraded
118003	unknown	L&R tentacles with clubs	
118020		very small buccal mass	
125405		beaks	?*A. stockii* (Kirk, 1882)
125406	Cape Campbell	beaks	?Holotype *A. kirkii* Robson, 1887
?[3]	"Red Rocks" 13 June 1976	beaks	
131973	Makara, Otoranga Bay 1982	buccal mass, 1 club, arm tip, eyeball	Collector C.D. Paulin

Notes to above table:

1 M10000: The Makara specimen was reexamined at NMNZ in 1983 after long-term storage in formaldehyde. It is now stored in alcohol.

2 M77446: The club is very damaged. It has been cut off part way through the manus and only a portion of carpus remains.

3 The Red Rocks specimen reputedly had a "total length" of 169 cm.

4 In 1983 the Museum of New Zealand had an old frame with two pens mounted on it. My notes indicate that one was reputedly *A. kirkii* and the other reputedly *A. stockii*. This mount no longer exists in its previous form and only one pen remains (M125403). There is uncertainty as to the provenance of the remaining material. The remaining pen cannot be confidently linked to beaks believed to represent the holotypes of either *A. stockii* (Kirk, 1882) or *A. kirkii* Robson, 1887.

METHODS

The detailed morphological and anatomical study described below is based on sixteen specimens acquired by Fisheries Research Division of the Ministry of Agriculture and Fisheries and the National Institute of Water and Atmospheric Research between 1983 and 1996. All specimens were personally examined. No reliance was placed on eye-witness accounts or reported measurements. The capture details and dates of the sixteen specimens are contained within the tabulated and updated capture record for New Zealand specimens (see Appendix 2). Detailed measurements are to be found in the tabulations of specific body parts in the Results.

Additional measurements were collected by scientific observers from squid captures at sea but these have been recorded separately (Appendix 2, Table 1) to avoid compromising the veracity and internal consistency of the present dataset. They do not form a central part of the current detailed study, but have been dealt with, in part, by Gauldie *et al.* (1994).

All New Zealand material existing in the Museum of New Zealand prior to this study was examined, as well as some foreign material.

MEASUREMENTS

Procedures and Data Sheets

Measurements, abbreviations, indices, and terminology were based on Roper and Voss (1983). Beaks were measured according to Clarke (1966, 1980, 1986). Additional non-standard measures were made to enable comparison with measures in the existing *Architeuthis* literature. Other measures were devised to allow for missing parts. Later, additional measures were included as the number of specimens accumulated and familiarity with variation exhibited by them increased. These included:
• dimensions of the ventral neck folds
• dimensions and other features of the funnel groove
• sucker density on arms
• sculpture of the protective membranes and oral faces of the arms
• the anterior divergence of the fin insertions
• colour of the remaining parts of the epidermis
• colour of the internal organs
• thickness of the mantle wall and fins
• details of sculpture of connectives and other soft parts

The disparity in appearance between Specimens 1 and 2 from widely separated New Zealand zoo-geographic regions was fortunate in that it led to a more detailed collection of information than might otherwise have been attempted or appeared necessary. As a consequence, there has been a systematic collection of data limited largely by the condition of the material, and the time-and-space constraints when dealing with large, rapidly deteriorating animals.

During the examinations, variations in some features became evident that had not occurred to earlier workers to record. Hence the data forms used evolved in response to the material at hand and to measure similar features recorded by others in the literature. In order to assist future workers faced with the sudden arrival of a "huge problem", the final versions of the data sheets are included in Appendix 4. These include data sheets for general body parts, arms, arm suckers, sucker dentition, and tentacular clubs. Written qualitative descriptions have also been included as they may prove useful to other researchers.

It was not possible to obtain an accurate weight for any of the specimens. We did not have easy access to suitable facilities, nor would it have generated useful information since most specimens lacked one or more arms or were otherwise incomplete.

For a number of reasons (e.g., badly damaged sucker-bearing face) it was necessary to describe some arm measurements in terms of "mm ex base". These measurements are of necessity approximate. Where measures have been taken from the base of the arm, rather than from the basal sucker, the measure was taken from the junction of the sucker-bearing face with the buccal membrane. The difference amounted to c. 150 mm.

In some cases measurements are missing. This is largely because of damage, missing portions, or distortion of the specimens. Many measurements were difficult to make with precision and throughout the descriptions there is generous use of the word approximate.

Although this paper does not seek to establish neotypes, it was considered necessary to publish a complete description of each specimen in the expectation that each could, with the benefit of hindsight, turn out to be a new species, or otherwise unique record. The increasing impossibility of preserving the bulk of the specimens combined with the obvious individual variation placed a higher-than-usual importance on each specimen's written description,

which has been retained at NIWA. The relative isolation of New Zealand and the size of the specimens means that other workers' access to the fragmentary preserved material is limited.

Full records were written for the qualitative features, and separate spreadsheets were set up for the quantitative aspects. Standard measures were recorded in spreadsheets to facilitate comparisons and graphical representation of relationships. Wherever possible, descriptions have been backed up with a photographic record. The spreadsheet data and individual specimen descriptions are available on request from NIWA.

Effects of Condition

All measurements were made on either thawed material (Specimens 1, 2, 4, 5, 7–16), fresh material (Specimen 3), or iced material (Specimen 6). All the specimens were in fresh condition and there was no degree of spoilage of the flesh. The frozen specimens were stored continuously at, or colder than, -20°C and then defrosted for 12–24 hours. All measurements were made during the course of one working day. After thawing, the squids continued to lose large amounts of body fluid, visibly deflating arms and mantle appearance.

No attempts have been made to remeasure the present specimens after preservation. No body measurements have been based on preserved material since shrinkage is expected to be considerable (see below for records of shrinkage of Dell's (1970) specimen).

On receipt of the first specimen, as many relevant measurements as possible were made, but inevitably as more specimens arrived and experience was gained, additions and changes were made to what was recorded. Consequently, later specimens were much more extensively defined and described. Because entire specimens were not preserved, no retrospective measurements could be made.

Measurements were made to the nearest 5 mm where appropriate and larger body dimensions to the nearest 10 mm, while recognising that these measurements were approximate. Flexible tape was generally used, and emphasis was placed on obtaining circumference measures where possible to avoid the problems of body distortions and collapse. Externally entire suckers were measured with calipers. Sucker rings were then placed directly into 70% ethyl alcohol. Sections of the radula were taken from a region immediately proximal to the exposed face. All beak, sucker-ring and gladius measurements were made after preservation in 70% ethanol. Stomach contents were filtered through a sieve with approximately 1 mm square mesh and faunal specialists were approached to assist with identification of fish scales and otoliths.

The size and rarity of *Architeuthis* mean that handling of specimens is often less than optimal. Some parts of the body are more prone to damage and loss than others, and this accounts for most of the gaps in the datasheets. Some forms of loss and damage were commonly encountered. These were:

- missing buccal masses (extricated as souvenirs)
- very delicate and often badly fractured gladii
- missing tentacles, although some were recovered from the wings of the trawl nets
- missing arm-tips, creating difficulties in determining the arm formula
- distorted and torn mantle and head parts
- damaged posterior mantle tips
- deflated eyes and missing eye lenses
- rubbed-off sucker rings
- separation or breaking of squid at the neck region
- epidermis rubbed off
- rapid deterioration of gills, ovary, and funnel gland.

Preservation

Parts of Specimen 1 and the majority of Specimens 2, 3, 4, and 5 were sent to the Museum of New Zealand. Specimen 6 was examined on the Nelson Wharf (South Island) and rendered to fishmeal. Due to a shortage of space in the Museum of New Zealand parts only of Specimen 7 were preserved. Collections for preservation of later specimens were limited to portions of arms, tentacle clubs, fins, funnel and mantle connectives, male reproductive system, beaks, sucker rings, and radulae. Some opportunistic heavy-metal levels and DDT samples were collected (see Fenaughty *et al.* 1988) and occasionally parasites were obtained. Specimen 16 has been preserved largely intact at NIWA. Fleshy parts that were kept were fixed in 10% formaldehyde, followed by transfer to 70% isopropyl alcohol. Parasites have been dispatched to specialists. Statoliths, where recoverable (up to Specimen 7), were given to Dr M.R. Clarke (c/- Plymouth Marine Laboratory, U.K.) for inclusion in a statolith atlas.

Recommendations for Field Procedures

It is necessary to respond very rapidly to news of a squid stranding. Bystanders are very likely to indulge in wanton destruction, vandalism, and theft of body parts. If at all possible, leave dealing with the news media until after the scientific work has been done, or arrange for someone else to deal with the media.

Where possible, arrange storage facilities in advance. This may involve cold storage, or the facil-

Table 2: Foreign material examined by author.

Specimen	Locality	Remarks
University of Hawaii Specimen no. 4	Stranded on Oahu 26/2/1983	Arms 2, 3, 4 suckers, portion of arm 4. Measurement data from fresh material provided.
University of Hawaii Specimen no. 5	Nearshore capture 22/3/1983	Body frozen, Univ. Hawaii NSB 4th floor. Not examined, but copies of unpublished data obtained.
Museum of Zoology, Bergen, Cat. no. 63336 *Architeuthis monachus*	Valdersnes, Radoy, male, 22/8/1982	Sucker rings, tentacle clubs, gladius. Beak examined but not measured.
Trondheim Museum (on loan at Bergen) *Architeuthis* sp.	Ranheim 4/3/1928	Tentacle club
Trondheim Museum (on loan at Bergen) *Architeuthis* sp.	Ranheim 2/10/1954	Tentacle club
Trondheim Museum (on loan at Bergen) labelled *Architeuthis* sp.	Locality unknown 8/9/1896	Tentacle club

Note to table:

Press photographs were also obtained from the *Bergens Tidende* of *Architeuthis monachus* studied by Ole Brix, University of Bergen (*see* Brix 1983).

ities to fix and preserve the specimens. A full photographic record is very important, as their appearance changes rapidly, the animals are difficult to preserve well, and storage space is always limited. Use a detailed data format, e.g., that used by Roeleveld and Lipinski (1991) or that used in this study. It is easier to collect all possible data on each presenting face of the animal before changing its position. With repeated handling, the thawed specimen becomes increasingly heavy, slippery, and damaged as well as increasingly malodorous. Note all differences and details likely to be lost upon preservation, e.g., colouration and details of sculpture of soft parts. If at all possible, collect all the data required from fresh material. The difficulty of manipulating relatively delicate preserved material of this size and weight makes reexamination of specimens an unpleasant and hazardous task.

MULTI-DIMENSIONAL SCALING

Rationale

A desire to compare the specimens as entities, rather than a collection of highly variable parts, led to a search for a technique to permit simultaneous consideration of a number of characters. The various measurements collected do not lend themselves to visual discrimination, and the separation of the dataset into one or more "body forms" was not obvious or intuitive, despite the relatively small number of specimens (13) with sufficient characters available. Application of criteria for selecting characters for use in estimating a similarity measure raised several difficulties.

Sneath and Sokal (1973) list inadmissible characters as those which are meaningless through being environmentally determined, as well as those which are inadmissible through being logically correlated, i.e., a tautological consequence. The former may well be involved in the current analysis, but since in this study the basic taxonomic units (OTUs) are individuals from geographically separate areas, the characters may still yield useful information. Unfortunately, with the small data-set and wide scatter of points (see scattergrams for individual body parts in Results) it is not clear to what extent characters are linked or independent.

The relationship of any particular character to the body form exhibited by the specimen is unclear. This is a special problem with large-bodied, fast-growing squids. The extent to which body shape is determined by past feeding history is unknown. Change in growth

patterns as the maturation of gonads commences is likewise unknown.

The analysis is conducted in the knowledge that variations may be primarily in response to the environment, rather than the expression of an innate genetic code. Even so, if groupings appear to have a regional basis, some knowledge will have been gained. It is acknowledged that the information upon which this analysis is based represents gross phenotypic evidence and at this stage little more can be done. The historic proliferation of specific names based on single specimens, in itself, suggests a highly variable species.

The author is mindful of Sokal and Sneath's (1973) warning that "identical classifications are not produced from different sets of characters for the same OTUs" (operational taxonomic units); however, with the available data, little more can be done.

The sample used is unlikely to be representative. It is clearly size-weighted — with the majority of individuals lying between 1650 mm and 2100 mm dorsal mantle length (ML). The presence of only one male is also limiting for the analysis. Actual measurements (non-scaled) are used for characters which, taken together form only a small sub-set of classical taxonomic considerations. All the characters used are quantitative multistate characters.

In order to deal with problems of allometry, Sneath and Sokal (1973) suggest that the data express "the character values of each OTU as a ratio of a standard measure of size of the OTU". The ideal is said to be the cube root of weight or volume, which in the case of the present material is clearly impossible. Within the present comparatively small data-set, there are no obvious ontogenetic effects (with the possible exception of the more conical mantle shape of the smaller Specimen 5). Standard body indices have been calculated based on the linear dimension of the least plastic portion of the mantle (i.e., mantle length — ML) according to the protocol in Roper and Voss (1983).

The sub-set of characters used in the Multi-Dimensional Scaling Analysis are listed below (see generalised Fig. 1):

- dorsal mantle length (ML)
- ventral mantle length (VML)
- circumference at mantle aperture
- circumference at greatest mantle width
- distance of greatest width from mantle aperture
- width of mantle at fin insertion
- separation between anterior fin insertions
- fin length (FL)
- single fin width
- dorsal head length (HL) to nuchal crest
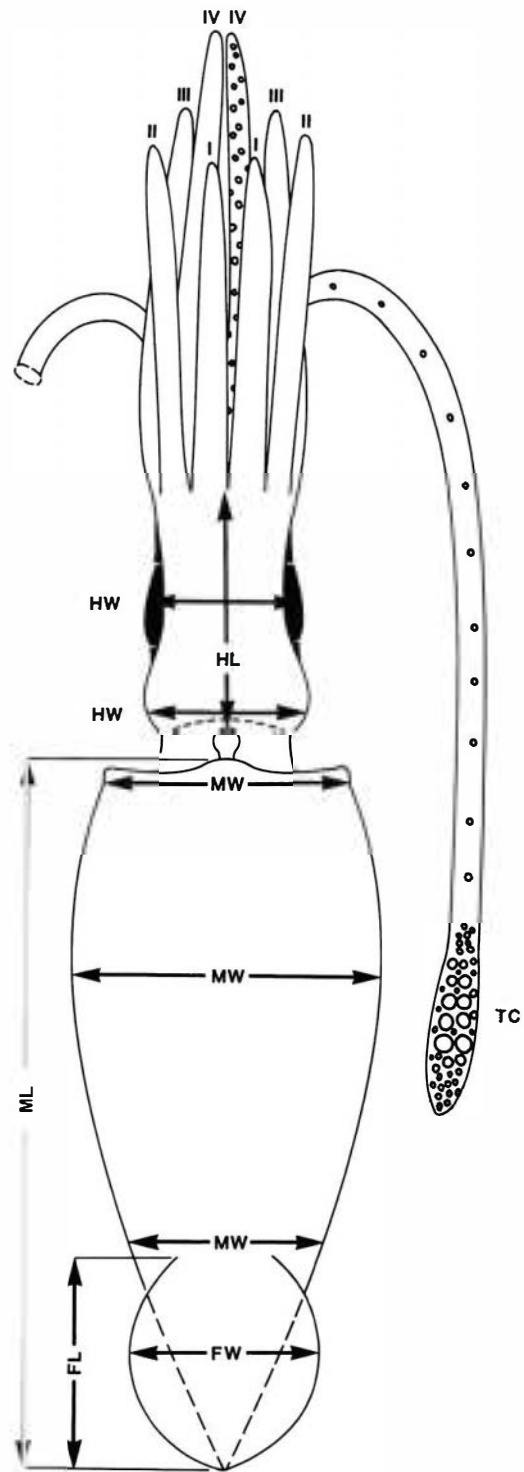- dorsal head width (HW) at nuchal crest

Fig. 1. Diagrammatic representation of *Architeuthis* indicating the position of some major measures. FL fin length; FW double fin width; HW head width; HL is indicated from the nuchal cartilage. The dotted line indicates the position of the nuchal crest. MW mantle width; ML dorsal mantle length; TC tentacle club. I–IV arms numbered from dorsal to ventral.

- head depth at nuchal crest (dorsoventral)
- horizontal eye opening
- funnel length, median ventral
- diameter of funnel distal aperture (flattened)
- ventral distance between funnel-locking cartilages
- length of funnel-locking cartilages (incl. overhang)
- length of nuchal cartilage
- width of expanded anterior section, nuchal cartilage
- length of gill base
- circumference at base of arm 1
- circumference at base of arm 2
- circumference at base of arm 3
- circumference at base of arm 4.

The assumptions are that:
- Mantle width/length are sufficiently independent.
- Head length and width and depth at the nuchal crest have a sufficient degree of independence. It is recognised that there may be an element of partial logical correlations between these head dimensions. Other head measurements have not been used because of difficulties in obtaining sufficient precision in the measurements.
- Funnel length and width operate independently.
- Fin length and width operate independently.
- Variations in relative ventral mantle length are real differences rather than a result of distortion.
- Circumference and position of greatest mantle width characterise mantle shape.

Characters of unknown significance have not been used. These include:
- funnel gland
- size of funnel valve
- number of gill lamellae
- colour of ink
- internal body-organ measurements.

Other characters which proved too difficult to incorporate within this form:
- the origin, number, and extent of keels on arms
- the sculpture and ornamentation of the oral surface of the arms
- robustness and colour of body parts
- beak measurements (M.R. Clarke's analytical techniques have been applied in a separate analysis).

Attempts to increase the number of characters (e.g., largest sucker-ring diameter, dentition) led to an increase in the "missing data" thus introducing further elements of uncertainty in the clustering or ordination. Given the very preliminary nature of this analysis, a minimalist approach has been adopted.

Methodology

The procedure for Multi-Dimensional Scaling (MDS) described by Clarke and Warwick (1994) was followed using the Plymouth Marine Laboratory programme PRIMER v4.0 beta. Clarke and Warwick (1994) describe the purpose of MDS as "constructing a 'map' or *configuration* of the samples, in a specified number of dimensions, which attempts to satisfy all the conditions imposed by the rank similarity matrix ...".

Non-metric multi-dimensional scaling was chosen for this data-set because little is known about the significance of actual size differences of body parts and shape in *Architeuthis*, and there was no expectation that there would be clearly defined groups. It was an attempt to obtain a visual map of the effects of variation of some of the characters, and to identify gradations, or drifts, in similarity.

To facilitate comparison between individuals, the standard conversion to body indices (Roper & Voss 1983). This effectively standardised the data as percentages of mantle length.

MORPHOLOGY AND ANATOMY OF NEW ZEALAND
ARCHITEUTHIS

GENERAL BODY AND MANTLE

The specimens were all in fresh condition. Most had been frozen at -20°C and thawed gradually as the examination proceeded. Despite their freshness, the squids all had a characteristic odour quite unlike that of common arrow squid (*Nototodarus* spp.). The odour is very persistent and has the ability to taint skin, clothing and laboratory notes, in the latter case for

many years, with the musky smell. Allan (1948) has also commented on the smell, describing it as "a peculiar, almost overpowering muskiness, not allied to decomposition or its salted state".

Body measurements are plotted diagramatically in Figure 2. Major body indices and detailed descriptions of the present specimens are given in the individual specimen descriptions available from NIWA.

Table 3. Mantle edge shape

Speci-men	ML (mm)	Mid-dorsal extension	Pallial projection	Ventral Emargination	Texture
1	2035	small	none	no	firm, not muscular
2	1930	low, broad	blunt point	yes	firm
3	1770	low, broad	yes	yes	firm, almost muscular
4	1825	yes	yes	-	firm, muscular
5	930	low, broad	flabby points 15mm	thin	posterior firm, anterior flabby
6	1560	small, triangular	blunt, soft point	yes	thin, flabby
7	2020	low, broad	soft, blunt point	yes	thick, firm, not muscular
8	1900	yes, standard			firm
9	1260	typical	triangular in X section	slight	firm
10	1830	large, broad	small, thick, indistinct	-	thin, flabby
11	1720	very low	weak, blunt point	straight	firm
12	1690	moderate	well-defined projection	straight	firm
13	1830	-	-	-	-
14	2140	small	slight		firm
15	2135	present			firm, thick
16	2000	pronounced	yes, blunt point	yes	firm, moderately thick

There are 10 specimens between 1825 and 2170 mm ML, a further 3 specimens between 1670 and 1770 mm ML, two smaller females (930, 1560 mm), and one smaller male (1260 mm ML). The placing of Specimen 5 in the genus *Architeuthis* is justified because, apart from its lack of fins, it fits the characteristics of the family (Pfeffer 1912; Sasaki 1929). It is presumed that the fins were lost as the result of an earlier accident.

Sex Ratio

The study is based on sixteen specimens, fourteen female. The sex of Specimens 1 and 13 was not definitely established, but presumed to be female through circumstantial evidence (photographs and descriptions by the finders). Specimens 8 and 9 were males. While the entire body was obtained of Specimen 9, only portions of Specimen 8 were received and the determination of sex was based on photos.

Mantle

The epidermis of the mantle is very delicate and is usually lost in the process of stranding or capture (Fig. 3A, B). The fragments that remain are a dark red-brown colour, paler brownish-pink (Specimens 11, 13) and occasionally red-purple (Specimens 8,10). The usual colour for the internal mantle is the same red-brown (Fig. 3D) as on the outside, evenly and densely coloured, including the membranes around the visceral sac, the funnel retractor muscles, and the sup-

porting structures for the gills. However, the inner mantle colour is less dense and unevenly distributed in Specimen 2, and pink, rather than dark red, in Specimen 8.

The ventral mantle length is shorter than the dorsal mantle length, except for Specimen 1. The ventral mantle length ranges from 82–95% of dorsal mantle length.

Mantle thickness was measured because of the great disparity in mantle wall thickness between the first two or three specimens. The dorsal mantle was particularly thick in Specimen 1 (72 mm), Specimen 14 (65 mm) and Specimen 16 (59 mm). In a squid of comparable size (Specimen 7) the dorsal mantle thickness was only 35 mm, thinning to 25 mm for Specimen 10 (1830 mm ML) and reaching a minimum of 8 mm for the smallest squid (Specimen 5, 930 mm ML). Similar variability is shown by the ventral mantle thickness, with a maximum of 60 mm for Specimen 12 and 55 mm for Specimen 10. The remainder of the measurements range from 35 mm (Specimen 4) through to 48 mm (Specimen 14), excluding the smallest squid (Specimen 5) with its ventral mantle thickness of only 21 mm.

There was no pattern as to whether the dorsal or ventral mantle was thicker. For those specimens for which we have both measurements, the dorsal mantle was thicker in Specimens 11 and 14 and the ventral thicker in Specimens 3, 5, 7, 9, 10 and 12. The disparity between the dorsal and ventral thickness was greatest in Specimens 5 (1: 2.6) and 10 (1: 2.2). These relative differences cannot be readily dismissed as a result of fluid loss or other post-mortem effects.
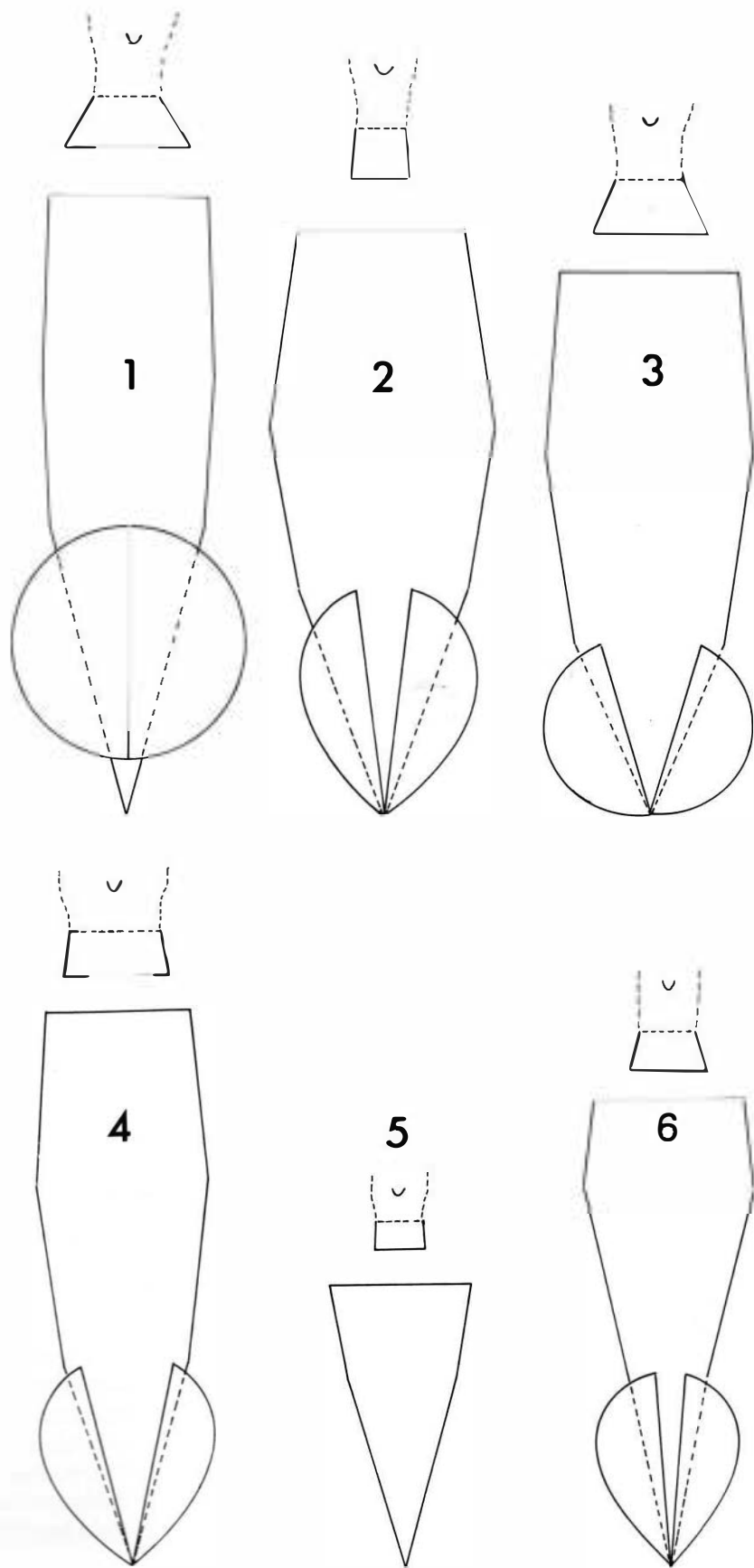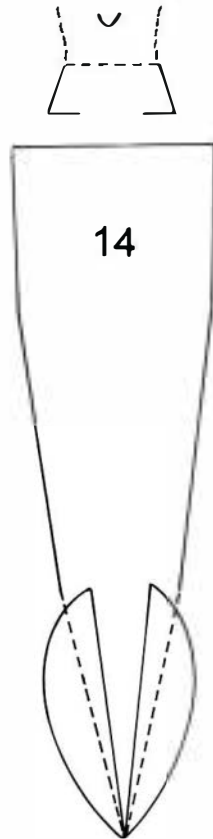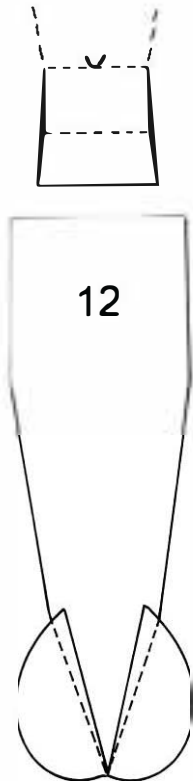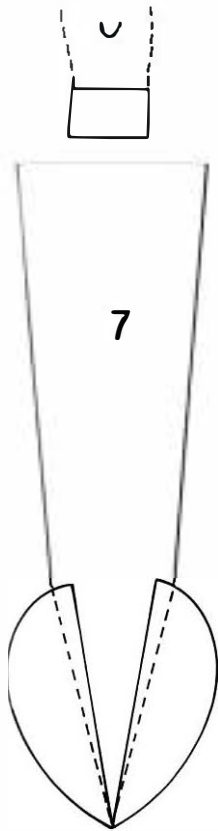
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Fig. 2. Diagrammatic plot of body measurements to demonstrate the range of body shapes encountered. Specimen number is shown on the mantle. Fin insertion, fin width, and head characteristics are also plotted.

7

9

10

11

12

14

16

17

The texture of the mantle is generally firm, but not particularly muscular. Specimens 3 and 4 were the most muscular of all the specimens, while the texture of Specimens 6 and 10 was flabby and thin. Specimen 5 was unusual in that the posterior mantle was quite firm, while the anterior was very flabby, and particularly thin in the region of the pallial connectives. The mantle tears readily when poorly handled and is easily sliced by ropes.

Mantle Elements

The forward projection of the mid-dorsal region of the mantle aperture ranged from 80 mm in Specimen 10 (ML 1830 mm) and 75 mm in Specimen 16 (2000 mm ML) to a minimal 10–20 mm in Specimen 1 (ML 2035 mm). The projection was most pronounced in Specimen 5 (projection 40 mm, ML 930 mm). The mid-dorsal extension was broad with the angle approximately 135°, a little broader for Specimens 10 and 11. At least part of the difference in "extension" is explained by the relative thickness of the dorsal mantle wall. Specimen 10 dorsal mantle was very thin, while that of Specimen 1 was very thick, thus possibly disguising the details of apertural projection.

The ridge of the pallial connectives (by which is meant the mantle component of the funnel mantle-locking cartilage) (Fig. 3D, E) projected anteriorly beyond the ventral mantle edge as a blunt point or finger-like process in most specimens other than Specimen 1. The ridge extended 50 mm beyond the mantle edge in Specimens 4 and 16, and less so in the other specimens. The visual impression was affected by how much the ventral margin was "scooped out" between the pallial connectives. This emargination was minimal in Specimens 1, 9, 11, and 12 but noticeable in Specimens 2, 3, 6, 7, and 16.

The appearance of the pallial connective was similar in all specimens. It consists of a simple ridge with some lateral curvature, particularly towards the anterior; the ridge is highest anteriorly, diminishing posteriorly. The ridge is associated with a tear-drop shaped (or elongate pear-shaped) unpigmented region in the internal mantle. This ridge is offset to the ventral medial edge of this unpigmented region (see Fig. 3D). There are no other thickenings, membranes, or other features associated with the connective.

The nuchal cartilage is spatulate with the anterior and posterior portions expanded into a rounded quadrangular shape. It is broadest anteriorly, narrowest two-thirds along the cartilage, and has a smaller expanded posterior section. A straight groove of constant depth, with a ridge immediately either side, runs the entire length of the cartilage. The outer edges of the cartilage are slightly thickened, particularly at the anterolateral corners. The cartilage is white, but is surrounded by a free membrane which extends outwards on all sides, being deep red on the underside. The membrane is widest at the anterior edge (15–20 mm), narrows laterally (3–8 mm) and expands again slightly on the posterior portion (Fig. 3E).

Differences between specimens were small. Some examples were the less quadrangular or expanded anterior portion (Specimens 3, 7, 9), the negligible posterior marginal membrane (Specimen 4), the formation of depressions just within the thickened anterolateral corners (Specimens 3 and 7), and a longitudinal depression or trough either side of the central ridge (Specimen 9).

Mantle component of the nuchal cartilage is a straight simple ridge with a groove either side, extending from the anterior of the mid-dorsal extension posteriad. Ridge and grooves fade posteriorly. Cross-sectional shape is a low broad W. The anterior end is triangular with thickened, raised fleshy anterolateral corners. The cartilage is slightly wider a short distance from the anterior, but sometimes continues to widen posteriorly, the lateral edges being delineated by slight thickenings. The width of the surrounding unpigmented region of the inner mantle is larger than that of the cartilage. The mantle component of the nuchal cartilage tends to be very easily damaged, particularly at the posterior extent where the neck joins the mantle and the gladius is prone to tear out (Fig. 3E).

Mantle Width

Mantle width was measured at several points — at the aperture, the widest point, and sometimes at fin insertion (see Fig. 2). Wherever possible, mantle circumference was used in preference to width because of the distortion and damage sustained by many of the specimens. The full range of body measurements and body indices are available from NIWA.

Some specimens are relatively narrower than others. The circumference of the mantle aperture varies from 57–77% of mantle length (except for Specimen 5 at 97%). When the greatest circumference (regardless of where that occurs) is compared, the range is 62–80% of mantle length (excluding Specimen 5). The regression of mantle circumference on mantle length shows a reasonable linear relationship ($r^2 = 0.6994$, y = 0.38 x + 459.16; Fig. 4).

The widest part of the mantle was well back from the aperture in Specimens 1, 2, 3, 4, 6, 9, 10, 14, 15, and 16, but at, or near, the aperture in Specimens 5, 7, 11, and 12. The position of greatest width was uncertain

Fig. 3. A. Specimen 4, demonstrating the frozen and still-turgid body shape. B. Specimen 16, after thawing and loss of body fluid. C. Specimen 6, mantle connective. D. Specimen 16, with a less-marked and more sinuous ridge on the pallial connective. Note the typical colour of the mantle interior. E. Specimen 6, with a well-developed pallial connective ridge projecting beyond the mantle edge.

for Specimen 8, and unknown for Specimen 13. The width and/or circumference measures indicate that the mantle varies from spindle-shaped with a narrowing at the aperture for the majority of the specimens, to a conical or cylindrical form (Specimens 7, 11, 12) and very conical (Specimen 5). The initial visual interpretation of the body shape of Specimens 11 and 12 was that they too, were spindle-shaped, however, when the circumference measure was taken it appeared that they tapered very gradually for the anterior part of the mantle.

Relative Position of Fins

Since few authors have had the opportunity to view more than one specimen, the relative position of the fin insertion is not a feature which has received much attention. Specimen 5 is unique in having no fins, but irregular folds. These may indicate scarring on the mantle surface, suggesting the fins may have been lost prior to capture. Data on fin insertion relative to ML is available for 13 specimens. The anterior insertion point ranges from 54% (Specimen 1) to 72% (Specimen 12), with the average = 63% of the distance from the mantle aperture to posterior mantle tip. The position of insertion of fins in relation to the dorsal, lateral, and posterior aspects of the mantle is dealt with in the section on fins.

Posterior Termination of the Mantle

The posterior end of the mantle is often damaged, and the extreme tip is frequently missing. The degree of taper of the mantle varies between a regular conical taper commencing anterior to, or around, the fin insertion, through to a quite rapid taper commencing
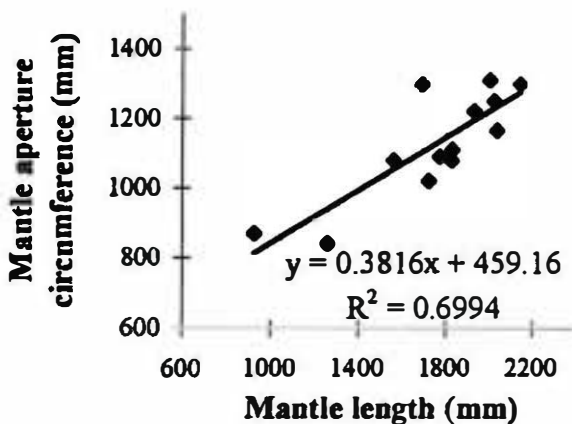

Fig. 4. Mantle circumference versus mantle length in New Zealand *Architeuthis* specimens.

approximately midway along the fins (see individual specimen descriptions, end-pocket fiche). The appearance of the extreme posterior of the mantle is generally that of a blunt rounded spike (Specimens 1, 7, 14, 15) but the spike may have a more triangular cross-section, with a flat dorsal side (Specimens 2, 3, 6, 8, 12, 14). A more abrupt taper of the posterior mantle was exhibited by Specimens 5, 8, and 9, possibly indicating an ontogenetic or sexual difference.

Variation in Mantle Shape

Although mantle shape can be distorted and interpretation complicated by damage, the similarity in treatment, standard measures, and freshness of the material suggest that substantial differences in mantle shape between specimens cannot be dismissed.

Some of the most outstanding differences are :
- the constricted and narrow aperture in Specimen 1
- the wide mantle aperture in Specimen 12
- the conical mantle and abrupt posterior taper in Specimen 5
- the cylindrical anterior mantle in Specimens 4 and 7
- the very posterior fin insertion in Specimen 12
- the short ventral mantle length in Specimen 7
- the emarginated ventral mantle aperture in Specimen 3.

Figure 2 was drawn up to demonstrate the gross differences in mantle, posterior head, and fin size. The illustrations are very diagrammatic, and the lines between points of measurement should not be taken as truly representative of actual body contours.

FINS

Fin Shape

As can be seen from Figures 2, 5–7 and from Table 4, the combined fin shapes exhibited range from almost transversely oval to round, regularly oval, elongate oval, through to ellipsoid with the narrower end posterior. Right and left fins are not always mirror images of each other. Analysis of shape is complicated by the fact that there may have been damage which subsequently healed. The form and function of the fins does not seem to be critical to *Architeuthis* survival, as is evidenced by the absence of fins in Specimen 5.

The degree of robustness also varies, as does the shape at the extreme posterior of the mantle.

Although the information is recorded individually in the specimen descriptions (held at NIWA), some

Table 4. Fin shape and texture.

Specimen no.	Combined fin shape	Fin texture	Divergence of anterior fin insertions	Posterior edge of fins
1	almost round	solid, thick	minimal	very short, shallow lateral keel
2	flattened oval	thin, weak, thins rapidly	small	fins to posterior
3	regular oval	small, thin, weak	large	possibly thin keel present
4	elongate oval		large	keel on right side only
5	none	no fins		
6	oval, narrower posteriorly	thin	small	narrows to only 65 mm wide at 200 mm from posterior
7	oval	very thin, insubstantial	moderate	lateral keel to extreme posterior
8			moderate	
9	rounded oval	firm insertion, membranous edges	small	convex posterior edge
10	oval, narrower posteriorly	firm, but thins abruptly	moderate	convex, short narrow keel
11	oval, narrower posteriorly	very thin, weak membranous	large	no information
12	oval	weak, membranous	moderate	convex posterior edge
13	almost round	thin, delicate		very thin and tapered
14	flattened oval	thin, weak	small	narrow keel to posterior
15	almost round	very thick, robust, tapers abruptly to membranous edges	moderate	convex, very thin keel along the lateral borders of the posterior mantle
16	rounded oval	thin, membranous at edges	large	damaged

small = ≤9% ML   moderate = 12–14% ML   large = >16% ML

elements have been extracted and tabulated for comparison (Table 4).

The fin length index ranges from 28–41%, with an average of 36% of ML, where n = 15. The scattergram (Fig. 8A) indicates that there a linear relationship with ML, although the relationship is less apparent in smaller animals.

For those specimens where the double fin width measure is available, the fin width index range is 27–40%, average = 31%, where n = 11. The double fin width increases more consistently with ML than does the single fin width, but the wide scatter of points at similar mantle lengths does not indicate a constant relationship (Fig. 8B).

The single fin width index range is 8–19% with an average of 12.6%, where n = 15. This represents a more than two-fold difference. Figure 8 indicates that the relationship to ML or FL is not clear, and is not well described by a linear relationship. The scatter of points does not suggest alternative relationships.

The ratio of fin length to fin width is indicated in Table 5. The range is from 1.95 for Specimen 1 to 4.53 for Specimen 14 — again, more than a two-fold difference. The fin length and corresponding fin widths do not suggest a regular relationship between the two parameters.

Fin Thickness

Fin thickness is a difficult and normally subjective measure. However, the difference between the first and second specimens was so pronounced that a method to measure fin thickness was devised. A slit was made in the fin midway along its dorsal attachment, large enough to insert a pair of calipers, and the thickness was measured at this point (see Table 5). The fin thickness of Specimen 1 was not measured as the significance was not recognised until the arrival of Specimen 2, with its much less substantial fin. Subsequently, the only other specimen comparable in bulk with Specimen 1 was Specimen 15 at 65 mm thickness. Relying on memory, Specimen 1 would have been as bulky, if not bulkier than this latter measure.

That would make the fins of Specimen 1 the largest of the current specimens and larger than all other *Architeuthis* specimens recorded (see Roeleveld & Lipinski's 1991 table). The contrast is evident when comparing Figures 6A,B with Figure 7D. Specimen 4 also had very thick fins.

Fig. 5. Specimen 1 photographed immediately after retrieval shows how the damaged fin assumes the controversial "arrow" shape described by Verrill (e.g., 1882b) for *A. princeps* and *A. harveyi*. (Photo courtesy of Taranaki Newspapers Ltd).

In Specimens 2–7, fin thickness midway along the insertion line varied considerably, with Specimen 2 = 27 mm, Specimen 3 = 28 mm, Specimen 4 = 37 mm, Specimen 6 = 30 mm, and Specimen 7 = 8 mm. In Specimen 7 in particular, the fins were very thin at the anterior insertions and rapidly thinned to only 1 mm thick near the lateral edges. The fins of Specimen 16 were also very insubstantial towards the outer edges. The outer edges of the fins of Specimen 1 were robust until the extreme outer edge; unlike the other specimens (e.g., 7, 16) where the fins thinned rapidly to become almost membranous and partially transparent at the outer edge.

Other specimens (7, 10, 14) had fins of only 8–11 mm thickness midway along the dorsal attachment of the fin. This is noteworthy, since Specimens 7 and 14 were amongst the largest specimens — at around 2000 mm ML. Thus the range in fin thickness represents a 6–8-fold difference, which in this limited dataset seems unrelated to mantle length, sex, or gonad maturity. The largely standard treatment of the specimens means that differences in the thickness of the fins are also not attributable to the state of freshness, loss of body fluid, or shrinkage in fixative.

Fin Insertion

Another feature to vary amongst the fins is the degree of separation between the anterior insertions of the fins (contrast Fig. 6B with Figs 7C and 7E). The range is from minimal separation in Specimen 1, to 340 mm in Specimen 16. Both squids were of comparable size. The arrangement of the anterior of the fins is almost continuous across the middorsal mantle surface in Specimen 1, slightly divergent in Specimens 2, 6, and 9 and almost dorsolateral in Specimens 3, 4, 7, and 16. No clear groupings emerge, except that obviously Specimen 1 insertions do not diverge significantly, while those of all the other specimens do to varying extents.

This variable degree of divergence between the anterior fin insertions leads to some difficulties in generating a standard fin measure or related indices, since twice the single fin width does not have a constant relationship to the double fin width. In this study, both measures have been presented wherever possible. The literature is often ambiguous as to whether the "fin width" refers to a single fin width or the combined structure.

It must be stressed that the distance between the anterior fin insertions should not be confused with the so-called "free anterior lobe". The latter feature is a separate character entirely. I am able to be very emphatic about this since the squids were all in fresh condition and this portion of the body was in most cases undamaged save for the loss of the thin, pigmented epidermis. As the squids deteriorated and lost increasing amounts of fluid, the fin attachments lost their turgid texture. It then became increasingly difficult to determine fin shape, particularly attachments and possible "free anterior lobes". By the end of a day, the fins on the majority of specimens could be so arranged as to extend forwards from the anterior insertion point. However, the feature was subtle, and the fins' forward extension takes the form of a blunt rounded lobe, rarely exceeding 50 mm in total anterior extent.

The loss of the pigmented outer skin makes any tearing or broken and missing flesh from fins and attachment regions less obvious. The potential for misinterpretation is clear from the loss of skin and associated information on the right fin of Specimen 1 (Figs 5, 6A–B). The effect of preservative on Dell's (1956) specimen (initially recorded and photographed without obvious lobes) also resulted in apparent 'free anterior lobes' when remeasured by me in 1983.

The posterior edges of the fins are convex until the point at which they approach the mantle posterior and become narrow lateral keels. On many of the specimens, the fin gradually became a very narrow keel or just a ridge along the lateral aspect of the "tail". This means that the measurement of fin length is not precise, and the cut-off point is not always easy to decide.

The fins appear to extend to the extremity of the body until they are damaged. There is also a tendency for the extreme posterior of mantle to be damaged, particularly after capture, freezing, and subsequent handling. The posterior edge of the fin in Specimen 1 finishes a clear 180 mm before the mantle tip. This was initially thought to be quite significant, but in the light of variation between right and left fin ends and the ease of damage to that area, it suggests this is probably a highly variable and unreliable character.
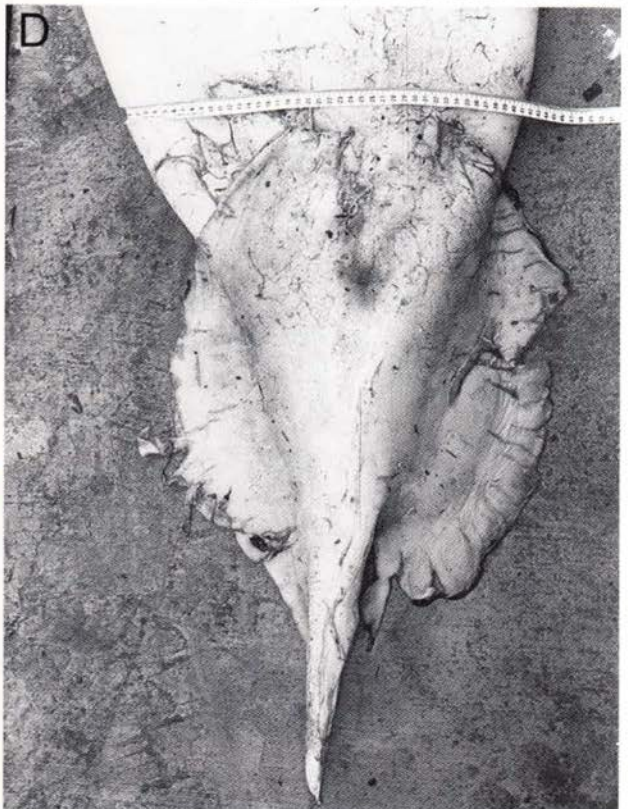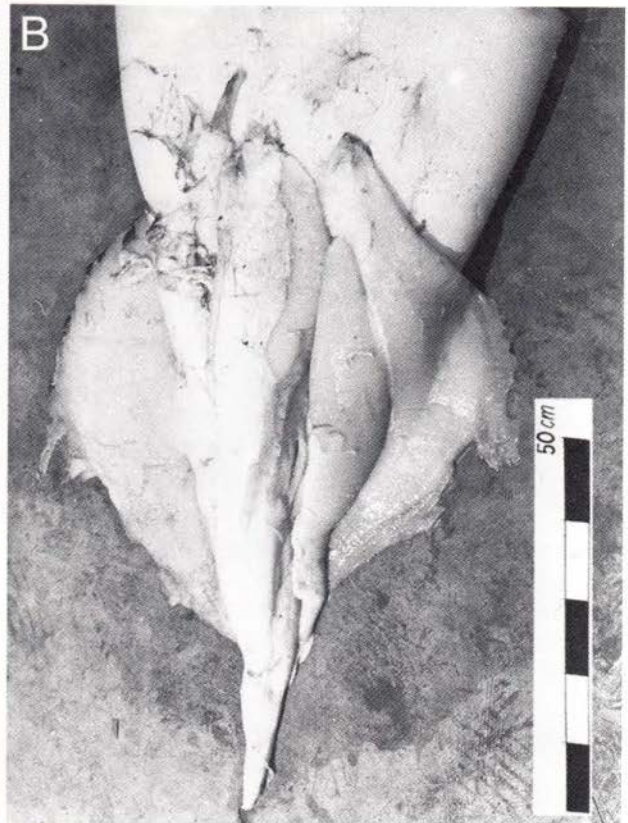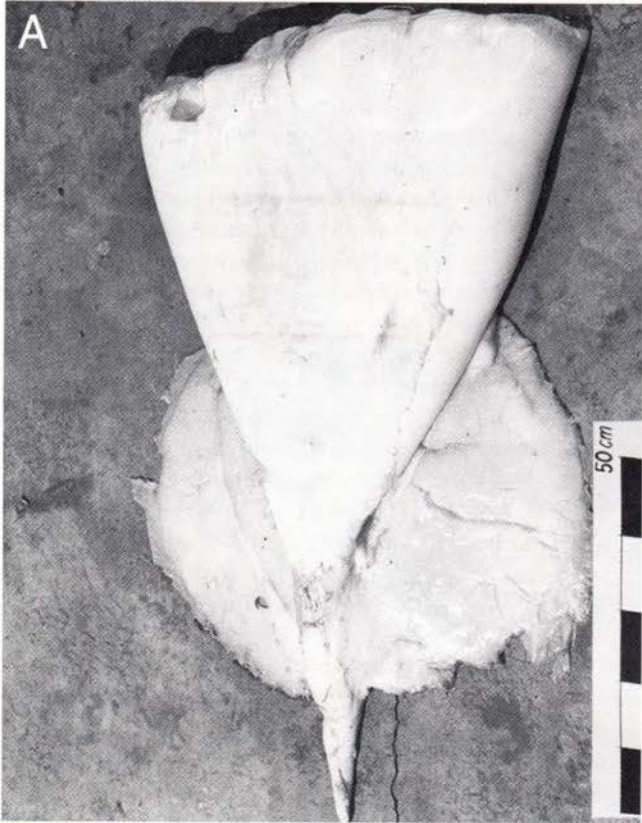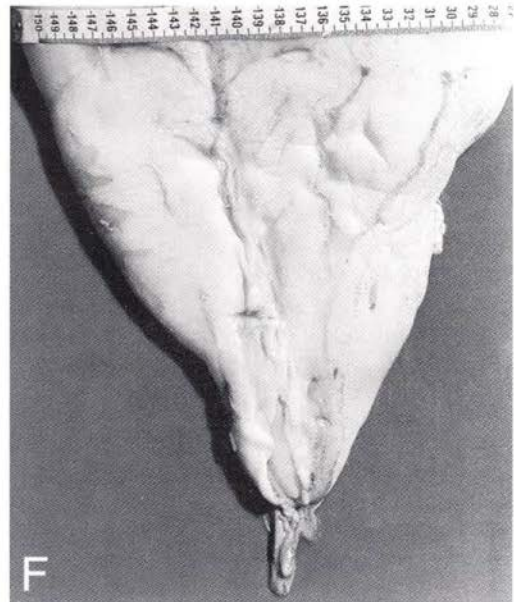
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Table 5. Fin measures and indices.

Fin Measures (mm) specimen number	1	2	3	4	6	7	8	9	10	11	12	13	14	15	16
sex		F	F	F	F	F	M	M	F	F	F	?F	F	F	F
dorsal mantle length	2035	1930	1770	1825	1560	2020	1900	1260	1830	1720	1690	1830	2140	2135	2000
width of mantle at fin insertion	500	560	480	405	250	-	330	200	340	330	350	-	370	480	420
separation between anterior fin insertions	0	180	320	300	100	250	280	110	250	320	230	-	180	250	340
fin length	760	750	550	660	645	730	720	400	730	690	480	620	770	820	700
single fin width	390	240	300	225	200	250	210	170	170	200	225	230	170	280	240
position of greatest width from fin anterior	-	-	-	330	170	270	270	100	300	300	300	320	300	300	
greatest double fin width	-	-	700	520	440	560	560	380	500	510	600	-	-	650	640
position of double fin width from fin anterior	-	-	330	330	170	290	270	150	300	300	320	-	-	300	310
thickness of fin midway along insertion line	-	27	28	37	30	8	35	27	10	20	35	25	11	65	-

Fin Indices (Fin Measure/ML) specimen number	1	2	3	4	6	7	8	9	10	11	12	13	14	15	16
dorsal mantle length (mm)	2035	1930	1770	1825	1560	2020	1900	1260	1830	1720	1690	1830	2140	2135	2000
width of mantle at fin insertion (%)	25	29	27	22	16	-	17	16	19	19	21	-	17	22	21
separation between anterior fin insertions (%)	-	9	18	16	6	12	15	9	14	19	14	-	8	12	17
fin length (%)	37	39	31	36	41	36	38	32	40	40	28	34	36	38	35
single fin width (%)	19	12	17	12	13	12	11	13	9	12	13	13	8	13	12
position of greatest width from fin anterior (%)	-	-	-	18	11	13	14	8	16	17	19	16	15	14	15
greatest double fin width (%)	-	-	40	28	28	28	29	30	27	30	36	-	-	30	32
position of double fin width from fin anterior (%)	-	-	19	18	11	14	14	12	16	17	19	-	-	14	16
fin length/fin width ratio	1.95	3.12	1.83	2.93	3.22	2.92	2.35	3.43	4.29	3.45	2.13	2.69	4.53	2.93	2.97

Fig. 6. (opposite) **A.** Specimen 1, posterior ventral mantle view; combined fin shape appears circular. The fins stop short of the extreme posterior of the mantle and do not appear to continue as lateral keels. This results in the appearance of a spike or free tail at the posterior of the mantle. The fins are very robust. **B.** Specimen 1, posterior dorsal view. Musculature is clearly visible and suggests how damage to this area could be mistaken for the form described by Verrill (1882b), or heal in such a way as to result in the fin shape resembling an "arrow". **C.** Specimen 2 posterior ventral view. Fin shape is more oval and the fins narrower than in Specimen 1. Fins extend almost to the extreme posterior of the mantle. The posterior mantle is more slender, and the fins thinner, particularly at the outer edges. **D.** Specimen 6, posterior dorsal view. Fins are narrow and elongate, with a combined oval outline. They taper to a narrow keel somewhat sooner than in the other specimens (65 mm wide at 200 mm from posterior tip of mantle), but damage obscured the fin termination. The extent of damage on this fin is typical of the present specimens.
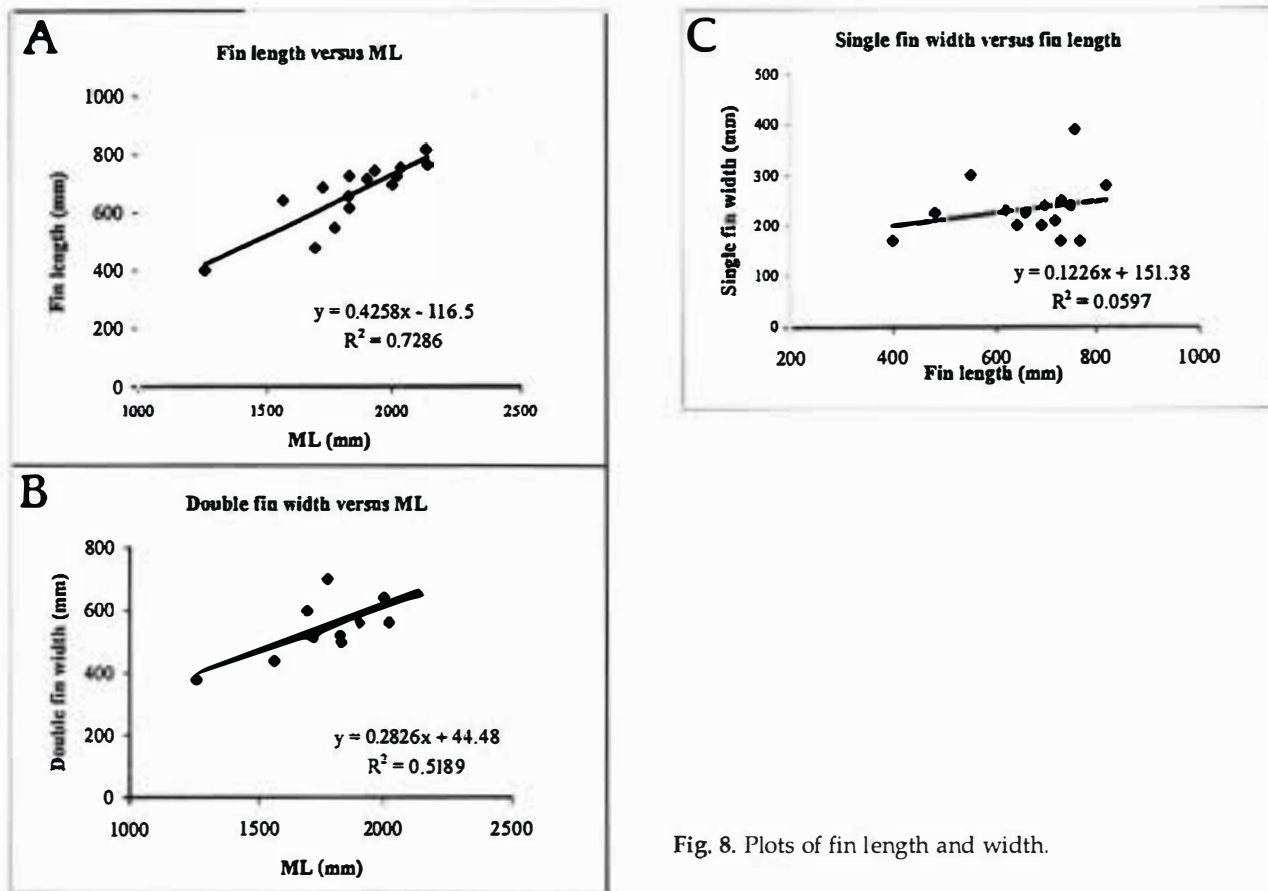
A Fin length versus ML

$y = 0.4258x - 116.5$
$R^2 = 0.7286$

B Double fin width versus ML

$y = 0.2826x + 44.48$
$R^2 = 0.5189$

C Single fin width versus fin length

$y = 0.1226x + 151.38$
$R^2 = 0.0597$
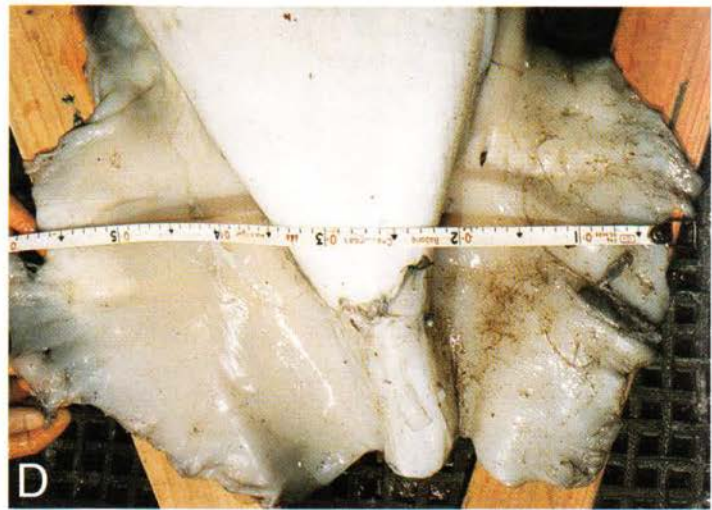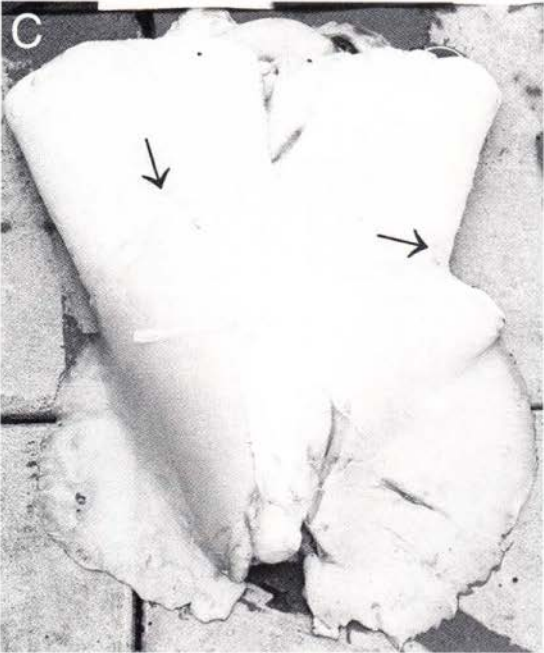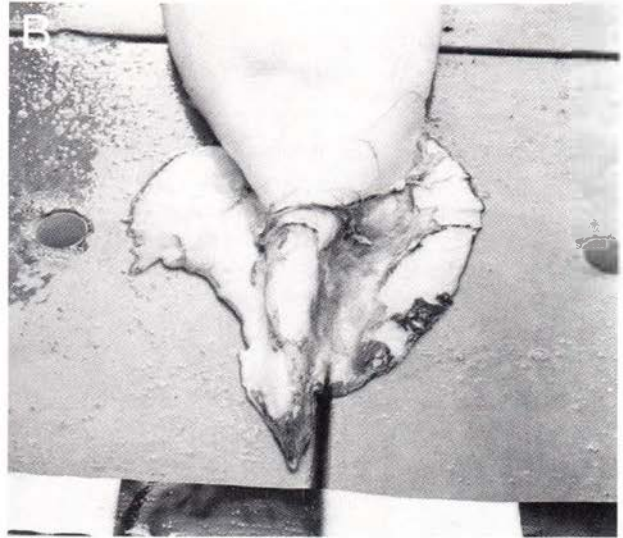
Fig. 8. Plots of fin length and width.

Fig. 7. (opposite) **A, B**. Specimen 4, fin damaged. The left fin is entire, but shorter than the right fin. The left fin ends abruptly, and subterminally, without a lateral keel extending to the posterior end of the mantle. The right fin is inserted more anteriorly than the left. It shows evidence of fresh damage, probably by predators, but continues to the extreme posterior tip of the mantle as a lateral keel. The posterior portion of the mantle was distorted and constricted in two places in a way that suggested old injuries rather than the result of capture and handling. **C**. Specimen 3, posterior dorsal mantle. This specimen had moderately robust fins and the broadest double fin width. The fin outline, even allowing for the damaged posterior portion, is almost oval in a transverse direction. This is one of the more pronounced examples of the divergence of the anterior insertion points of the fins (see arrows). The divergence measures 320 mm (exceeded only in Specimen 16 with 340 mm divergence). **D**. Specimen 16, posterior ventral mantle. Note the large but fragile fins, with almost membranous outer edges. Although the posterior tip of the mantle is missing, it suggests that the fins continue as broad keels, unlike the narrow keels in, for example, Specimen 6. **E**. Specimen 16, dorsal posterior mantle. The fin insertions are made more visible by the black plastic which has been tucked under the edges of the fins. The wide separation contrasts strongly with Specimen 1 (Fig. 6B). **F**. Specimen 5, posterior dorsal mantle. This specimen lacked all trace of fins, but irregular ridges and grooves and distortion of the mantle tip suggested healed injuries. This trawl-caught specimen represents the smallest of the current animals.

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HEAD

Head shape (Figs 10–12) can be variously described as square-, dumbbell-, or cylinder-shaped. For example, Specimen 7 has a very "square" head — short and uniformly broad, while Specimens 1 and 3 have longer dumbbell-shaped heads. The degree of constriction at the eyes on the dorsal head surface is marked in some specimens (1, 3, 6, 11, 14, 16) but scarcely evident in others (2, 4, 5, 7). This may be related to the degree of collapse of the eye region and should not be used as a differentiating characteristic. Most specimens show some degree of dorsoventral flattening of the head, which may be the result of distortion under its own weight.

Differences in appearance are further emphasised by varying head widths in relation to mantle aperture. Impressions of overall head shape have been recorded in column 9 of Table 6. They should be compared with the indices and relative width measures given in columns 2 and 3 of the same table, and have been investigated in various ways (Fig. 9A–D). The arm pillar too, appears to vary in relative "mass" but no satisfactory method was found to quantify this. Future *Architeuthis* researchers could possibly consider adding head-circumference measures to the range of measures taken in this study.

Damage in the neck region is frequent and consequently the head measure can be problematical. The literature seems to contain two types of head-length measurements, one to the nuchal crest, and another to the anterior of the nuchal cartilage. It is often not clear which has been used, and the literature needs to be used with caution. In addition, the measure of head length to nuchal crest can be a problem where the animal has a pronounced anterior flexure of the crest in the middorsal region.

Head depth is another way of describing head shape, but no rigorous way was found to assess this aspect. In some specimens the arm pillar (region of fusion of arm bases) appears bulkier than the nuchal crest (2, 7, 11, 14). In some specimens the eye region is bulkier than the arm pillar (4, 7) and, in another (14), it is very much less. Again, as for the fins, as the study day progresses, the specimen loses more body fluid and the head visibly sags and the eye region collapses.

Indices

Head length has been plotted against mantle length (Fig. 9A). The scatter of points does not suggest a linear relationship, nor any other relationship. There is also no obvious separation of head lengths into types, e.g., "short-headed" or "long-headed". Even gross onto-

genetic effects are not obvious from this scattergram, although Specimen 14, with a mantle length of 2140 mm, has the shortest head relative to mantle length. Head-length indices (Table 6) for the present data-set (based on length to the nuchal crest) range from 13 to 21% of mantle length.

Head width at the nuchal crest has been plotted against mantle length (Fig. 9B) and the indices have been listed in column 3 of Table 6. The scatter is just as wide and similarly uninterpretable as for the head length to nuchal crest. The head width ranges from 10–22% of mantle length.

The ratio of head width to head length (Fig. 9C) attempts to consider head shape in isolation from the remainder of the body. Again, a wide range of values is exhibited. Measured HW ranges from 0.55 to 1.48 of HL. This represents a three-fold difference in relative width. Again, the small size of the data-set and the wide scatter over such a short range precludes attaching significance to the ratio.

The perceived head shape of *Architeuthis* is influenced by the width of the adjacent mantle aperture. To investigate whether there was any relationship between the width of the mantle aperture and head width, the head width was divided by the mantle aperture circumference. Circumference was chosen, firstly because the data-set is slightly more complete, and secondly because the measure is less influenced by body "sag". The resultant measures are listed in Table 6. Head width ranged from 35% of mantle circumference (Specimen 1) to a mere 16% of mantle circumference (Specimen 2). To investigate whether the head width/mantle aperture relationship was influenced by the size of the animal the relevant measures were plotted in Figure 9D. The effect is a broad, even, scatter in which removal of one or two datapoints could entirely reverse the direction of any trends that might be suggested. There are no obvious ontogenetic effects on head length, head width, or head width relative to head length or mantle aperture over the range of 1500–2200 mm ML.

The animals presented a range of skin colours on the head, which often differed from that of the mantle. Colours of the dorsal and ventral head surfaces are listed in Table 6. In general, although the skin was more likely to have been rubbed off the dorsal and lateral surfaces of the head, the scraps that did remain indicated that the chromatophores were denser dorsally than on the ventral surface. The funnel groove itself was almost always colorless. The orange, pink, and purple shades were quite distinct from the more brownish-red (dried ox-blood colour) that was always evident on the mantle and in the mantle cavity. The colour differences appeared unrelated to treatment history, since the variations were evident on the same animal.
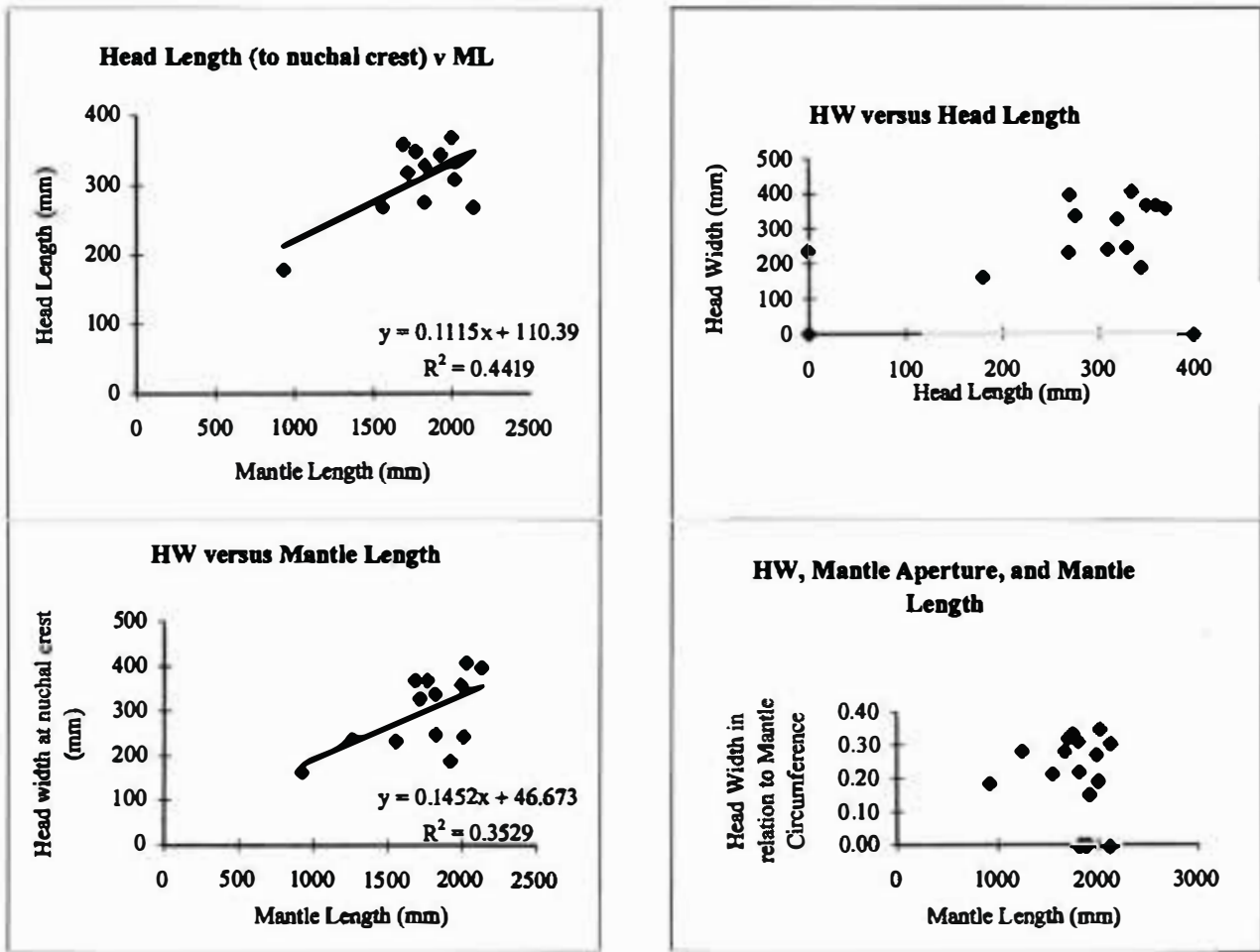
Head Length (to nuchal crest) v ML

Head Length (mm) vs Mantle Length (mm)

$y = 0.1115x + 110.39$
$R^2 = 0.4419$

HW versus Head Length

Head Width (mm) vs Head Length (mm)

HW versus Mantle Length

Head width at nuchal crest (mm) vs Mantle Length (mm)

$y = 0.1452x + 46.673$
$R^2 = 0.3529$

HW, Mantle Aperture, and Mantle Length

Head Width in relation to Mantle Circumference vs Mantle Length (mm)

Fig. 9. Plots of head length, width, and mantle parameters.

Eyelid

The eyelids were possibly round in normal condition, but damage during capture and handling generally resulted in collapsed eyes, with lenses missing and distorted eye lids. The skin around the eye aperture was elastic and the eyelid edge was frequently slightly irregular. The measures of eye aperture diameters are available from NIWA. There was no eye sinus present. Particular attention was paid to this feature. Although the eyelid margin was not always perfectly regular, none of the distortions resembled the shallow sinus sometimes mentioned in the literature. The eye aperture, measured horizontally from anterior to posterior edge, varied from 4 or 5% up to 11% of ML. The condition of the skin around the eye aperture varied from :

- quite smooth, without thickenings or lobes (Specimens 1, 3, 4, 5, 7, 10, 14, 16)
- to those with various irregular lobes on the posterior aperture edge (Specimens 6, 7, 11)
- to those with thickenings in skin surrounding the posterior and/or anteroventral corner of the eye (Specimens 2, 9, 12).

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Table 6. Indices, colouration, and appearance of head shape and skin.
"Missing" (msg) indicates that either the part was not present, or the measurement was not possible. The funnel groove often featured a depression in the cartilage with a skin-covering often presented as an evaginated sac.

Spec. no.	HL/ ML	HW/ ML	HW/ HL	HW/M circum	dorsal colour	ventral colour	funnel grove feature	general head shape	nuchal fold olfactory papillae
1	16	20	1.22	35	red/ brown	pink/ brown	sac + hole	large, D–V flattened	several small irregular lumps midlaterally
2	18	10	0.55	16	brown/ mauve	pale	none	narrow, laterally compressed	2 papillae ventrolaterally
3	20	21	1.06	34	red/ brown	not recorded	none	large, D–V flattened	3-4 very irregular thickenings, ventrolateral differs L &R
4	15	19	1.23	31	white	dark red/ brown	none	short, broad D–V flattened	2 irregular thickenings ventrolaterally
5	19	18	0.92	19	pale	pale	sac + hole	small, narrow dorsally	slight irregular thickenings near ventrolateral border
6	17	15	0.87	22	white	orange/ mauve	sac + hole	small, dumb-bell shaped	2 thickenings ventro-laterally
7	15	12	0.79	20	red/ brown	pink & mottled orange/brown	none	small, distorted, ?cyclindrical	1 hard lobe and soft lobe at anteroventral extent
8	21	msg	msg	msg	dkred/ brown	partmsg	partmsg	long.only slightly nar-rowed at eyes	nuchal fold indistinct
9	msg	19	msg	29	red/ brown sparse	orange	sac + ?	small, narrowed at eyes	no evidence of papillae
10	18	14	0.76	23	red/ brown	orange/red	hole	short, stout	2 irregular flaps ventrolaterally
11	19	19	1.03	32	red/ brown	palemauve	sac+hole	large, broad, solid, slightly narrowed at eyes	indistinguishable
12	21	22	1.03	28	white	white	sac + ? no hole	short, square	no papillae present
13	msg	msg	msg	msg	*	*	partmsg	msg	msg
14	13	19	1.48	31	dk red/ brown	white	flap + hole	short, broad	3 indistinct thickenings midlaterally
15	*	msg	msg	*	*	*	part msg	msg	no head
16	19	18	0.97	27	white	orange sparse	sac +? no hole	short, broad	1 papilla left lateral, irregular ridge
Dell 1970	16	20	1.26	31	red	unknown	sac + hole brown	large, broad dumb-bell shape	1 papilla at ventral extent

Fig. 10.A. Specimen 1, dorsolateral head. Note colour change at the nuchal crest, middorsal anterior flexure, and extension of fibrous skin onto aboral surface of arms. **B.** Specimen 1, left lateral view of head. Note substantial arm pillar, irregular posterior border of eye aperture, and collapsed eye.
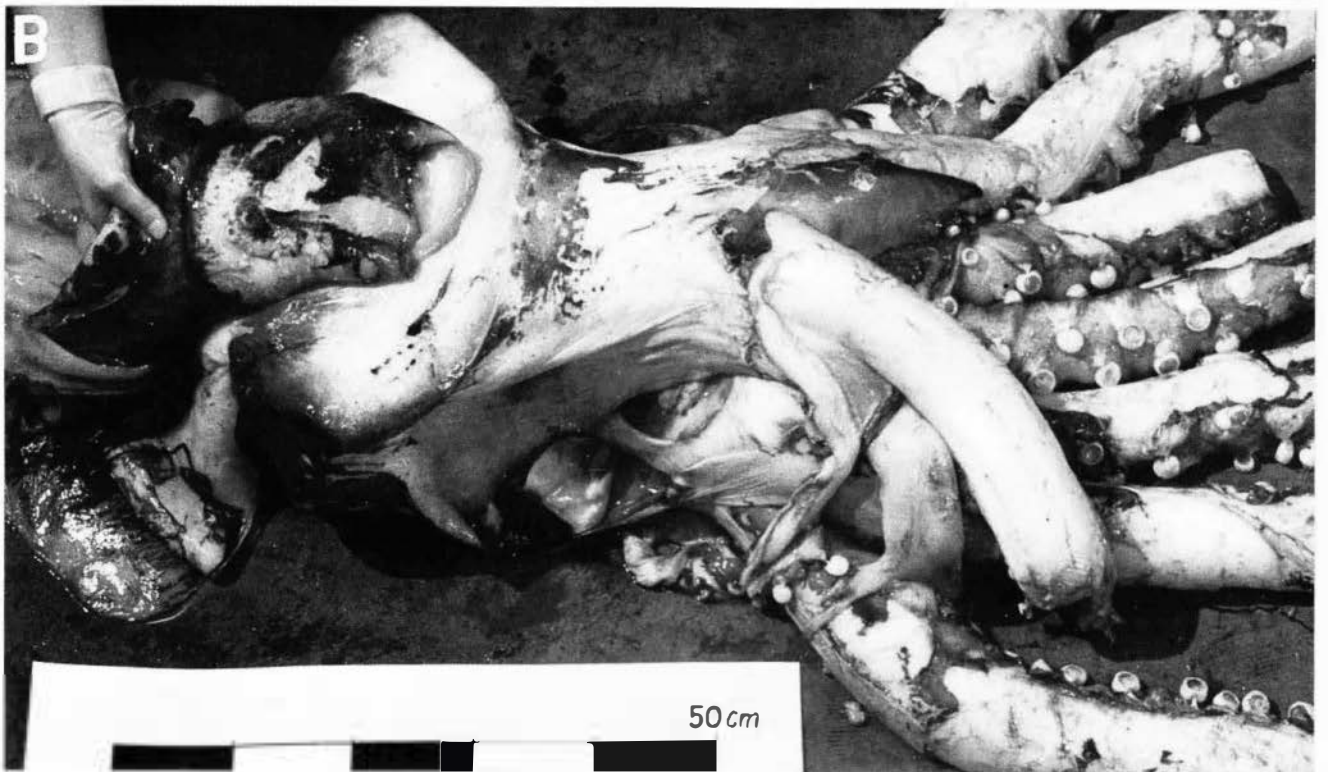
31

Fig. 11.A. Specimen 1, posterior view of nuchal fold and nuchal crest. Note irregular nuchal fold with thickenings. The fold and crest diverge midlaterally. **B.** Specimen 1, ventral head. Note wide ventrolateral extensions on either side of funnel groove.
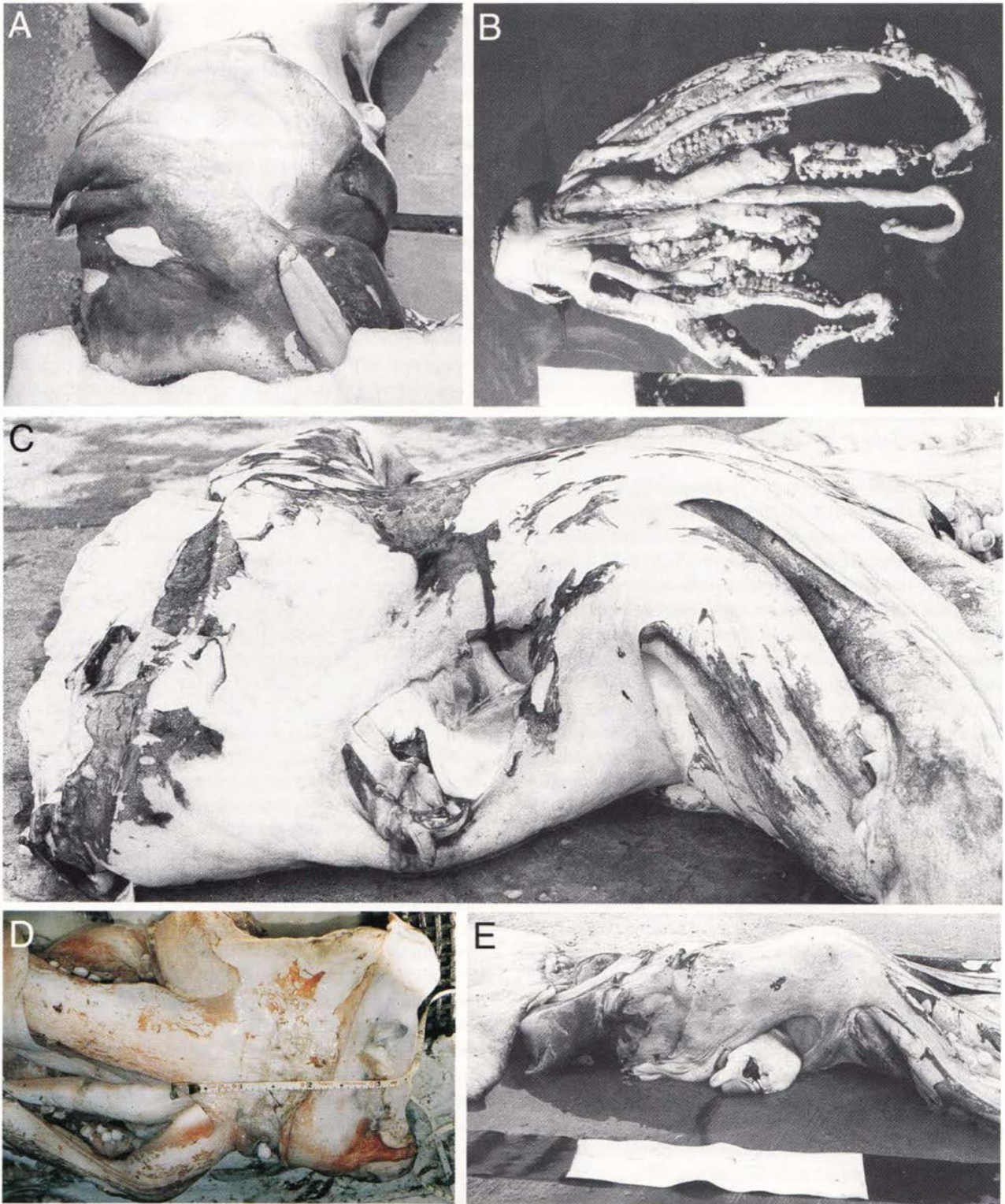
Fig. 12.A. Specimen 4, ventral head. Note less substantial ventrolateral flaps, broader funnel groove and merging of posterior border of the flaps with nuchal fold. B. Specimen 5, dorsal head. Note small head in relation to arms. C. Specimen 3, lateral view. One of the largest heads in this study. D. Specimen 16, ventral view of head. Note evaginated "finger" or sac on upper side of tape, and distorted appearance of funnel groove. E. Specimen 6. Note substantial arm pillar compared with flaccid posterior head region after a full day in the sun.

Neck Region (see Figs 10–12)

This region is not suspected of having any taxonomic significance but since the data have been collected it is as well to characterise this region and establish the variations evident in these specimens.

The head surface has a fibrous, silvery appearance. There is a marked discontinuity at the nuchal crest with a transition from the slightly rough, fibrous and firm texture of the dorsal surface of the head to the skin in the neck region with its soft, smooth, almost liver-like quality. This region also tends to retain the epidermis, whereas this skin is frequently missing from the dorsal and lateral head surfaces.

The nuchal crest is always obvious as a marked colour change (except in Specimen 3). The sculpture of the nuchal crest shows the following variations :
- a well-developed firm and slightly elevated ridge (Specimens 3, 8, 9,12),
- a marked, firm but flat border (Specimens 1, 7, 11, 14, 16)
- a weak flabby structure (Specimens 2, 4, 5, 6, 10).

The nuchal crest generally has a pronounced mid-dorsal anterior flexure (Specimens 1, 3, 4, 6, 7, 8, 10, 12), however the feature is less well-defined in Specimens 2, 9, and 11, and does not occur in Specimens 5 and 14. The crest tends to be more pronounced mid-laterally (especially in Specimens 6, 9, 11, 12, 16) and continues ventrally until it fuses with the sides of the funnel groove. In Specimens 7 and 8 there is an additional anterior flexure in the crest midlaterally.

The neck region has one transverse fold (sometimes called the olfactory crest) which is arranged generally parallel to the nuchal crest. This fold is less well-marked middorsally, in some instances appearing to fuse with the nuchal crest middorsally. The distance between the crest and the fold varies from only 10 mm in Specimen 6, to around 70 and 75 mm in Specimens 4 and 16 respectively. The prominence of the fold varies from a well-formed ridge equivalent to the nuchal crest, to the condition in Specimen 9, where the fold is distinguishable only by a darker-coloured line in otherwise smooth flesh. The fold is not distinguishable in Specimen 8.

The appearance of the nuchal fold is generally somewhat irregular in outline and bore several thickenings and swellings. There is no set pattern to the number of "lumps", their shape, or positioning, other than that structures which could be interpreted as the "olfactory" papillae tended to occur in pairs and more often in the ventrolateral region of the fold. However, irregular thickenings and lumps were also found laterally. Specimen 7 was atypical in that it had one hard lobe of a size and appearance of a dog claw and an accompanying soft flap of skin (possibly a parasite). The range of papilla shape encountered is listed in Table 6.

In all specimens the lateroventral extent of the nuchal fold turned anteriorly and formed wide triangular flap either side of the funnel groove, tapering and meeting at the anterior wall of the funnel groove. Some of the specimens had very large, prominent and muscular lateroventral flaps measuring up to 100 mm in free width. Size estimates were made and are listed in the individual descriptions held at NIWA, however they should be taken as indicative only. The length of the flaps ranged from c. 110 mm in the small Specimen 5, to 220 mm in Specimen 16. The range in width of the flaps measured from the edge of the funnel groove was 60 mm (Specimen 5) to 150 mm (Specimen 14). It was noted that the corners of these flaps if turned midventrally would be sufficiently large to completely enclose the funnel.

Funnel Groove

The funnel groove in the ventral head surface varied in size, depth, edge delineation, position of insertion of the funnel adductors, and size of the posterolateral flaps. However, these differences were difficult to quantify and the general structure of the excavation was similar. Measurements were attempted for the length, width, and depth of the groove and are listed in the individual descriptions held at NIWA, however they should be taken as estimates. Distortion of the head during handling and freezing appears to impact on this region rather frequently. The insertion of the funnel adductor muscles was not always in the same portion of the funnel groove.

An unexpected feature noted on Specimen 1 was a deep hole, shaped like an oversized thimble, at the anterior end of the funnel groove. This discovery led to careful examination of this region in all subsequent specimens. Specimen 1 ultimately appeared to have the best-developed "hole", but then it also had the largest head in relation to mantle opening. The feature was absent in Specimen 2. Still other specimens had similar, if smaller, structures to Specimen 1, but frequently accompanied by an evaginated "finger" of skin, rather like a glove finger, which could be pushed back into the hole. Still others appeared to have the evaginated "finger" but the "hole" was indistinct, although possibly crushed or otherwise damaged. A summary of the findings is listed in column 8 of Table 6. Reexamination of Dell's specimen (from Makara in 1956) revealed a similar structure.

Buccal Membrane

The buccal membrane is briefly described for each specimen in the individual descriptions held at NIWA. The skin is web-like, elastic, sparsely dotted with chromatophores on the external surface in pink or mauve, and generally colourless on the internal face. There are seven lappets, which connect to the arms on the dorsal, dorsal, ventral, and dorsal sides of arms 1–4 respectively. No obvious differences were noted between the buccal membranes of the various specimens.

FUNNEL

Details of funnel and valve shape, orientation, colour, texture, and minor differences in the funnel cartilages and pallial connectives are recorded in the individual specimen descriptions held at NIWA.

Midventral funnel length relative to the mantle is greatest in Specimens 3, 5, 12, and 16 and least in Specimens 11, 13, and 14. The range is from 10 to 18% of mantle length (Table 7). Funnel length is not strongly or obviously linked to mantle length (Fig. 13). The range in funnel width measured ventrally between the anterior ends of the funnel-locking cartilages was also large (13–24% of mantle length), with Specimen 6 having the broadest funnel. The length of the funnel cartilages varied from 10 to 16% of ML.

Table 7. Funnel indices (% of mantle length).

Specimen no.	FL median ventral	FW between cartilages	Diameter aperture	Funnel cartilage length
1	16	14	8	11
2	16	14	7	.
3	18	17	9	13
4	16	13	8	11
5	18	17	9	16
6	16	24	7	11
7	13	12	5	10
9	15	16	3	12
10	15	15	8	10
11	12	13	10	12
12	18	17	8	13
13	10	-	7	.
14	12	14	7	11
16	18	15	7	11

Variations existed in the degree of ventral orientation of the anterior part of the funnel and the funnel aperture but these were difficult to quantify. The ventral direction was very marked in Specimens 3 and 7 and moderate in Specimen 6. Specimen 9 was the only male for which there are data and this specimen had an abnormally small funnel opening and a small valve, although the funnel length and distance between the funnel cartilages were comparable to those of the other specimens.

The funnel of the greatest width relative to ML (Specimen 6) did not belong to either the largest or smallest squid. The funnel was very strongly tapered and did not have a particularly large funnel valve. The funnel of Specimen 7 was smaller than the others in almost all dimensions.

The funnel textures were flabby and thin in Specimens 4, 5, 6, 9, 10, 11, 14, and 16. There was a distinct soft thin bulge in the dorsal wall of the funnel of Specimen 3 and a healed "bite" appeared to have been taken out of the funnel valve. In contrast, the funnel texture of Specimens 1, 2, and 7 was firm, indicating that post-capture handling was probably not the cause of the difference in texture. The funnels differed in their extent of extension onto the head — not reaching the posterior border of the eye aperture in Specimens 1, 7, 12, and 14, just reaching the posterior border in Specimens 4 and 9, and extending to level with the middle of the eye in Specimen 6. The funnel extended beyond the mantle aperture for 140 mm in Specimen 12, 180 mm in Specimen 5, and 300 mm in Specimen 2.

Considerable variation in the colour of the funnel was observed. The funnel was similar in colour to
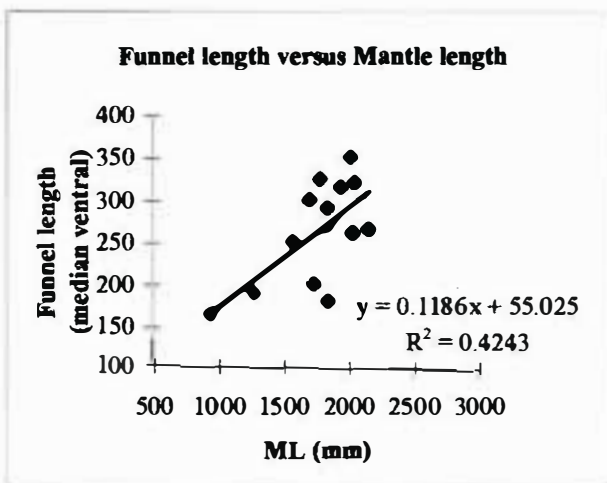

Funnel length versus Mantle length

$y = 0.1186x + 55.025$

$R^2 = 0.4243$

Fig. 13. Scattergram and regression of funnel length (ventral medial) against mantle length.
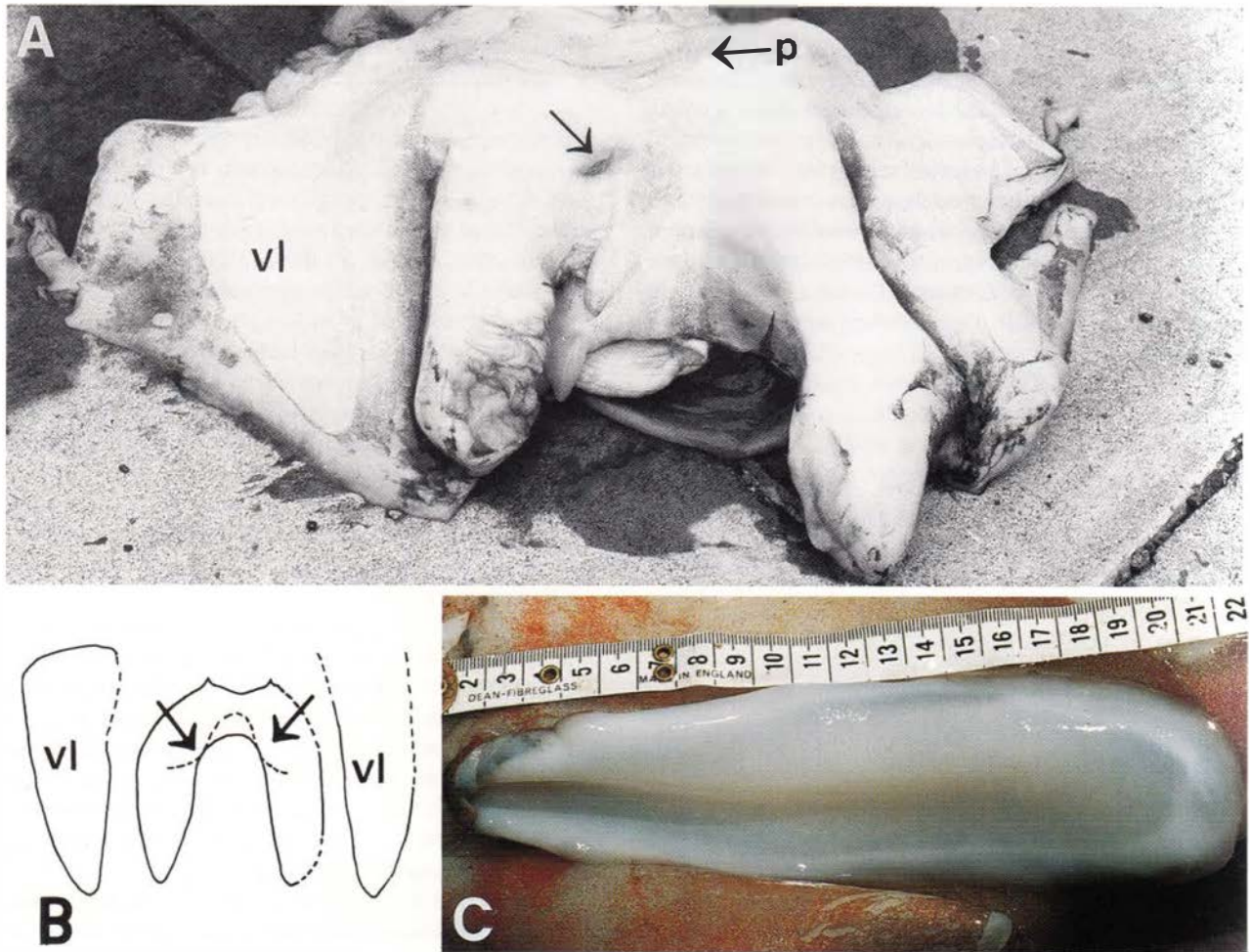
35

Fig. 14A. Interior of funnel from Specimen 3 cut along medial ventral line, exposing funnel organ. Note large ventral limbs and long dorsal limbs. The left papilla (P, arrow) is just visible, as is the dorsal overlay (arrow) and two free "flaps" in the funnel interior. B. Sketch of visible portions of funnel organ in Specimen 3. Note large ventral limbs (vl), two dorsal papillae, and the dorsal medial glandular overlay. C. Funnel-locking cartilage from Specimen 16. Note the unusually deep anterior region of the cartilage groove and the pigmented underside of the marginal membrane.

the mantle in Specimens 1, 2, 3, 4, and 9, and the internal funnel and funnel valve were white. In Specimens 5 and 16 the funnel had more orange colouration and in Specimen 5 the funnel valve, too, was red-brown. The exterior funnel of Specimen 7 was predominantly orange, while in Specimen 6 the funnel was purple laterally, pale dorsally, beetroot-red anteriorly and orange-brown ventrally in the region of the funnel cartilages. Purple-brown colouration was also evident on Specimen 12, and purple-red on Specimen 11. Specimen 10 was paler than the mantle, with a pinkish-brown colour.

The funnel valve appeared to vary somewhat from a D-shape through oval to circular. Subsequent to the field observations, examination of a photograph (Fig. 14A) indicates that there are one and possibly two additional structures on the dorsal wall of the funnel. They are medium-sized flaps, which in a relaxed state would partially occlude the funnel passage. Whether these are associated with the funnel organ is unknown.

Funnel Organ (Verrill's Organ)

The funnel or the relevant portion of the funnel was not available for Specimens 8, 9, 13, and 15. In the remaining material, funnel organs were not detectable in Specimens 1, 2, 11, and 12. Traces of the funnel

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organ were present in Specimens 14 and 16, but the shape could not be determined. The shape was at least partially discernible for Specimens 3, 4, 5, 6, 7, and 10. The brief description is extracted from the individual specimen descriptions (held at NIWA).

Specimen 3

Funnel organ conspicuous, appearance like a clear jelly overlaying the inner funnel surface (Fig. 14A). Dorsal limbs broad, crescent-shaped posteriorly, extending well beyond anus. At the anterior junction the dorsal limbs thicken and almost overlay the posterior branches with a secondary lobe or fold. Anterior edge of the dorsal junction drawn out into two small papillae (Fig. 14B). The ventral pads narrower, longer, but the shape at anterior extent was unclear.

Specimen 4

Funnel organ very thin, indistinct. Dorsal limb inversely V-shaped, bluntly rounded anteriorly, very narrow posteriorly, length 220 mm, maximum anterior width 80 mm, at 25 mm from anterior; posterior width 35 mm. Ventral pad length 230 mm, expanded anteriorly (80 mm wide, 30 mm from anterior), middle portion with straight sides, posterior section sickle-shaped.

Specimen 5

Funnel organ present but indistinct, dorsal limb present; ventral pads expand towards posterior, but asymmetrical.

Specimen 6

Funnel organ present, posterior portion of dorsal limbs and ventral pads damaged. Anterior extent of ventral pads quadrangular, width approximately 60 mm, total length estimated at 185 mm. Dorsal limb a thickened inverted V-shape, but the two pads did not fuse anteriorly and remained separated by approximately 30 mm. Entire dorsal limb irregularly glandular. Separation of anterior extent of dorsal limbs and ventral pads 70 mm.

Specimen 7

Funnel organ present. Ventral pads squared off at anterior extent, length 220 mm, tapered posteriorly, outer edges damaged; width could not be determined. Dorsal limbs form a thickened inverted V-shape, each limb approximately 280 mm long. Narrower than ventral pads. The area of junction of the dorsal limbs is rather irregularly glandular. There was one small anteriorly directed filament which may have been a papilla. The dorsal limbs do not join each other directly but are joined by what appears to be another, overlying, dorsal pad.

Specimen 10

Ventral pads banana- or sickle-shaped, dorsal limbs and pad indistinct.

For those funnel organs for which the shape could be distinguished, each was a little different from the others. The dorsal limbs met in a regular V-shape in Specimen 4, did not join in Specimen 6, and were joined by an irregular glandular pad in Specimens 3 and 7. A structure was detected in Specimen 7 which could be interpreted as a single dorsal papilla, but two more-distinct papillae were detected in Specimen 3. In Specimen 6 the anterior portions of the ventral pads had quadrangular sections, while they were crescent-shaped in the other specimens (5, 10). In Specimen 7, whereas the ventral pads were quadrangular at the anterior extent, they tapered posteriorly, becoming very thin and indistinct.

Funnel-Locking Cartilage

The funnel-locking cartilage is a simple, elongate, straight groove slightly offset laterally, which becomes more pronounced anteriorly. The cartilage is thicker and narrower anteriorly, more rounded, and shallower posteriorly (Fig. 14C). The cartilage is raised above the ventral surface of the funnel and surrounded by a narrow membrane which overhangs the cartilage on all sides. The cartilage is white, but the underside of the membrane is usually the colour of the funnel or mantle epidermis. In Specimen 4 the cartilage was pinkish-brown and rather flat. Minor differences were noted in the relative width of the surrounding membrane. No substantial differences were noted in the structure or proportions of the funnel-locking cartilage between specimens.

BEAKS

Upper and lower beaks are similar to those described for the genus (Clarke 1980). The lower beak has a short jaw edge in relation to wing length, a broad rostrum with a small hook, broad wings and hood, very low wing fold, jaw angle not obscured when viewed from side, and a prominent shoulder tooth (sometimes worn or chipped away).

The hood stands high above the crest with a deep notch in the hood midline, a thickened crest, and a large lateral wall often without ridges. The chitin is generally thin on the hood, wings, and lateral walls. Some specimens showed a transparent strip below the jaw angle similar to that in ommastrephids. Pigmentation is complete except in the outer margin of lateral

Table 8. Beak measurements (mm).

Specimen	1	2	3	6	7	12	13	14	16	Dell 1970	Red Rocks	Holotype *kirkii*	?Holotype *stockii*
Lower Beak													
Dorsal ML	2035	1930	1770	1560	2020	1690	1830	2140	2000	1829	-	-	-
rostral length	19.2	17.9	18.5	16.8	18	18	18	18.5	18.2	18	18	18.3	19
hood length	32.5	27.9	29	29	26.5	28	32	22.2	33	20.7	* 31	31.5	29.5
crest length	58	57	55	51.5	53	51	55	56	60	56.5	61	* 63	*52
wing length	57.5	63	56	50.5	57	51	57	61.5	58	60	*	52	54
rostral gap	15	15.2	16	14.8	14	16.3	16	16	13.7	16.5	*	*	15.9
Upper Beak													
rostral length	16.2	18.6	17.5	11.6	19.3	20	17.2	19	12.6	14	14.5	19.4	20
hood length	78.4	80.3	77.3	71	79	83	75.5	78.5	81	73	*45	* 98	77
crest length	114	116.9	116	101	105	110	110.5	110	112.5	108	118	*	* 102
wing length	35.8	34	33	32	32.5	31.4	36	29	31.5	38	35	*	27
rostral width	15.2	16.4	16.5	14	11.5	17	16	15	16.3	16	*	16.1	17

* = unmeasurable

walls, the wings, and the hood of upper and lower beaks. Tips of upper and lower rostra are often worn, and the shoulder tooth is variable in prominence.

Standard beak measurements after Clarke (1962, 1980, 1986) are given in Table 8. The lower rostral length has been plotted against dorsal mantle length (Fig. 15). The regression is not significant. The beak from Specimen 2 is illustrated in Figure 16.
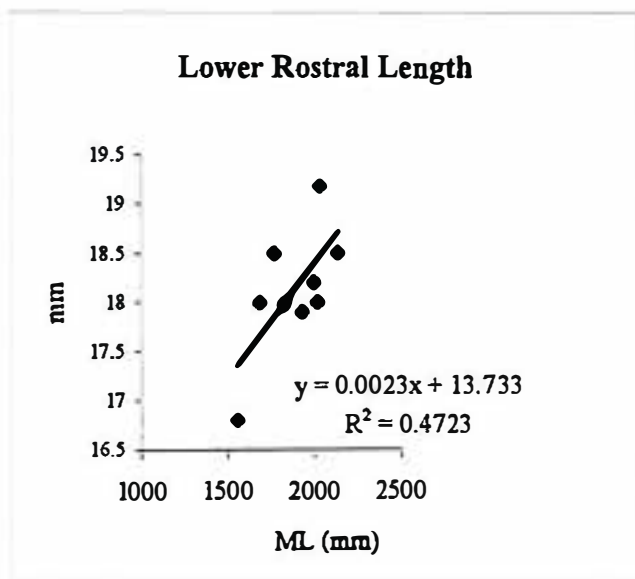

Lower Rostral Length

$y = 0.0023x + 13.733$
$R^2 = 0.4723$

Fig. 15. Regression of beak lower rostral length against mantle length.

Variation Among Specimens

Buccal masses from Specimens 4, 5, 9, 11 and 15 were never received. The beak from Specimen 8 has been misplaced. The beak from Specimen 2 was measured on receipt of the animal, but cannot now be located in the Museum of New Zealand. Specimens 3, 6, 7, 12, 13 and 14 beaks were remeasured as a group in early 1996. All additional beaks available in the Museum of New Zealand have been measured, including the suspected holotypes of *A. kirkii* and *A. stockii*.

Specimen 1
Upper beak with a light line running from the outer jaw angle, the rostral tip missing. Lateral wall of crest with a very short narrow midlateral ridge on one side only. Darkening on the wings is even. Lower beak with a very worn rostral point, shoulder, and a notch in the jaw angle; the rostral hook almost absent. Although very even darkening on the wing, the extreme outer edges are very transparent. No ridges or other features on the lateral walls of the crest.

Specimen 2
Not locatable in the Museum of New Zealand at the time of reexamination. Original notes indicate that the beaks of this specimen were similar to those of Specimen 1 but that the beak of Specimen 2 has very little wear on either upper or lower rostrum and has considerably more soft tissue on margins of upper and lower beaks than Specimen 1. Rostrum of lower beak
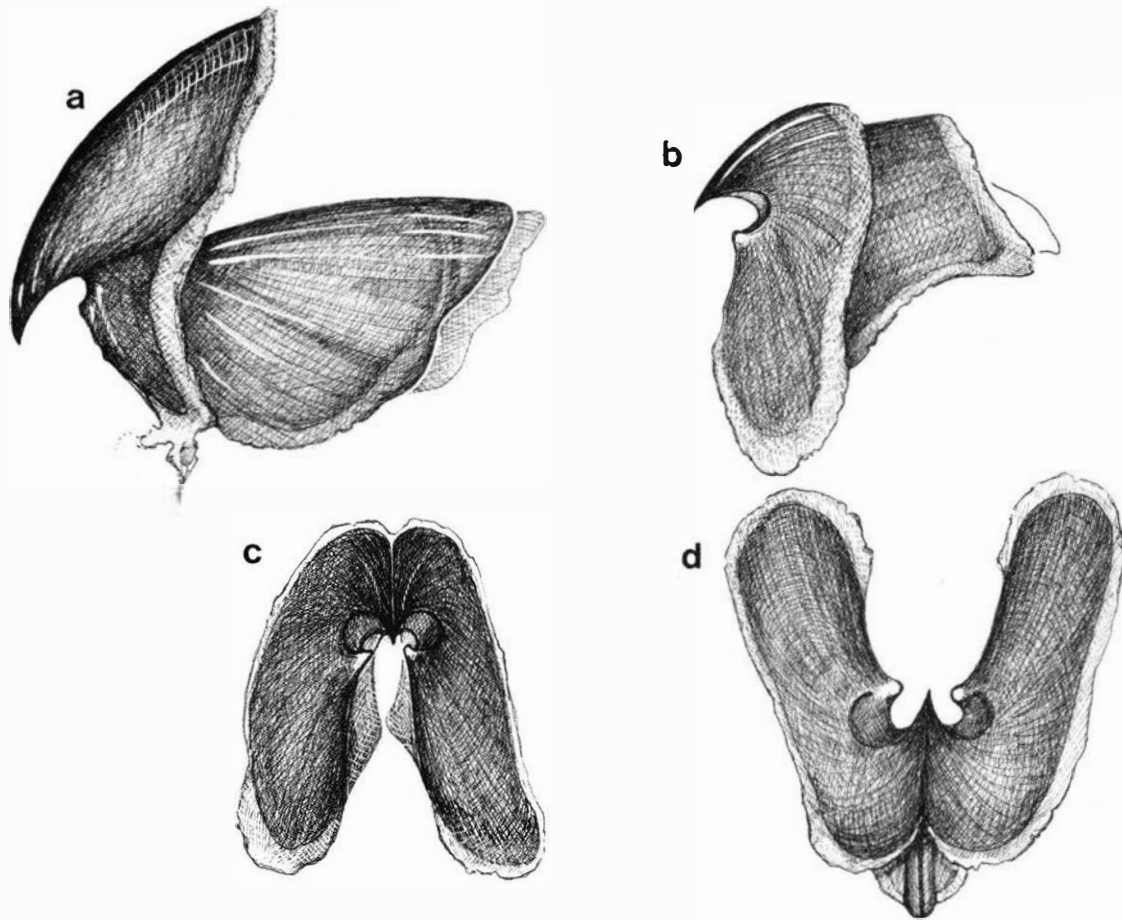
Fig. 16. Illustration of beaks from Specimen 2: **a,** profile of upper beak; **b,** profile of lower beak; **c,** front view lower beak; **d,** outer view lower beak.

split. Wear and colouration of beak suggests Specimen 2 younger than Specimen 1. Measurements recorded in Table 8 are those made on the fresh specimen, rather than on alcohol-preserved specimens as for the other measurements.

Specimen 3

Upper beak had no lines or pale regions running from the jaw angle. Lateral walls of the crest bore one ridge on each side, limited to the outer two-thirds of the crest wall. Lower beak wings exhibited even darkening and were without ridges or lines. Rostral tip missing, and the measure is an approximation. The crest bore about 5 mm of thin tissue on the outermost extremity.

Specimen 6

Upper beak had evenly darkened wings but very transparent edges. A dark line and ridge running from the jaw angle. Crest lateral walls without thickenings. Lower beak with a very slight rostral hook; a par-

ticularly weak and small shoulder notch, which appeared to be chipped. Darkening was even on the wings and lateral faces of the crest.

Specimen 7

Upper beak had a pale line from the jaw angle outwards on the wing. The crest had a thickened narrow region on the lateral wall, but limited to the outer half on one side of the beak only. The thickening consisted of a series of short parallel ridges. The lower beak was cracked and damaged particularly at the rostrum. The rostral gap measure is an estimate. The wings were evenly darkened, and there were no lateral thickenings or ridges on the crest or wings.

Specimen 12

Upper beak with a pale stripe running from the jaw angle to outer wing. A ridge starting to form on the extreme outer edges of the crest. Lower beak with very transparent edges, particularly towards the outer corners of the wing. Hood slightly ripped and the

measure is a best estimate. Although the crest has a broader thickened central ridge than other specimens, there is no other sculpture. Rostrum with a very slight, low hook. A very thin faint line runs from the region of the inner jaw angle along the lateral wall of the crest. Crest length was difficult to measure, being 51 mm to the end of the chitinised material, but having a further 20–25 mm of thin menbranous material to the extreme end of the crest.

Specimen 13

Upper beak still with extensive soft tissue. Specimen 13 appears to have a darker line running from the jaw angle to the outer wing (in contrast to other specimens). Crest with a ridge on either side on the outer half to one-third of the lateral wall. Lower beak with a distinct rostral hook. Tissue at the end of the hood still intact, Lower beak crest intact, with a thickened apex and a groove on either side. The darkening on the wing is even. The outer face of the jaw angle, i.e., the "wing fold" region, is rough and knobbly and hints at delamination. The colour an even dense brown on the inner face of the crest from the region of the jaw angle.

Specimen 14

Upper beak with an even degree of darkening. The beak from this largest squid a markedly deeper brown on the wing, although the outer edges of the beak are soft and transparent. A lighter streak runs outwards from the inner jaw angle on the lateral wall of the crest as well as several thin but distinct ridges midlaterally. Lower beak with a thickened crest fold and a lateral ridge either side. Hood notch very marked. Rostrum of lower beak with a slight hook, but cracked.

Specimen 16

Upper beak (true) left wing outer edge irregular. Crest with several pale streaks midlaterally, and wide transparent edges. Lower beak rostrum with a distinct hook. The jaw angle very worn, thickened, very black, and the tooth virtually absent. A crease or furrow exists in the (true) left wing. Crest ridge thickened and narrow and posteriorly almost keel-like. Crest lateral walls bear a brown streak. The edges of the hood and wings are transparent. Faint annular and radiating pigment lines are visible.

M10000 Makara Specimen (Dell 1970)

Upper beak measurements are best estimates as the extreme tip of the rostrum is missing. The crest bears a slight ridge on the lateral face, but this is restricted to the outer quarter on one side only.

Lower beak has no pale lines or ridges. Again, the tip of the rostrum is missing.

Red Rocks Specimen

Upper beak damaged, making it impossible to measure the rostral gap or wing length. It is very evenly chitinised with a single thickened ridge on each side of the lateral crest. Lower beak evenly darkened over the entire surface but, at a smaller scale, exhibits some clearer inner regions giving it an "annular" look. The hood is damaged and an estimate has been made.

M125406 — possibly from holotype of A. kirkii Robson

The bottle contains two unnamed mandibles recorded as having been sent to the Colonial Museum. The Collection Manager of Mollusca believes that these may be the holotype of A. kirkii Robson. Upper beak has dried and curled at outer edges of the hood and crest, rendering it unmeasureable. There is a very slight ridge on the (true) right midlateral wall of the crest. Lower beak with a slight rostral hook, a well-defined and formed shoulder notch. The hood is not measurable, but an estimate has been attempted for the crest. However, it should be regarded as a minimum measure.

The general form of the beak is similar to that of the beaks from the present study (Specimens 1, 2, 3, 6, 7, 12, 13, 14).

M125405 — possibly from holotype of A. stockii (Kirk)

Upper beak has no ridges or lines. Rostral length is the largest of the measures recorded for New Zealand specimens. Lower beak rostrum with a slight hook, but also without thickened ridges or lines. The hood is an approximate measure and the crest length a minimum measure, but the rostral length and wing length could be made with confidence. The general form corresponds to M125406 and those of the present study.

Summary

All the beaks available from the present specimens were from immature females. However, the lower rostral lengths (LRL) all exceeded 17.9 mm, and the degree of darkening in the chitin corresponds to that illustrated by Clarke (1986, fig. 8). This establishes that for a LRL of 17.9 mm all but the outer edges of the wing, hood, and crest are darkened.

Upper beak

Specimens 1, 7, and 14 showed a distinct pale line and Specimen 12 a wider pale streak from the jaw angle across the wing, whereas Specimens 6 and 13 showed a dark line in the same position. Another feature of the upper beak in some specimens was the horizontal narrow thickened ridge or ridges on the

outer portion of the lateral walls. This feature uni-lateral in Specimens 1, 7, and Dell's (1970) specimen, and bilateral in Specimens 3, 13. The form variable :

- Specimen 3 — ridge limited to outer two-thirds of lateral wall
- Dell's (1970) Makara specimen — slight unilateral ridge on outer quarter of lateral wall
- Specimen 13 — bilateral ridge on outer half to one-third of lateral wall
- Specimen 7 — unilateral feature of a parallel series of narrow thickened ridges on the outer half of lateral wall
- Specimen 1 — a unilateral short narrow ridge.

The most notable features amongst the present beaks relate to the pale streak in the wing of the *upper* beak, and also the variable ridges or thickenings on the midlateral walls of the *upper* beak.

Lower beak

The variation in appearance between specimens of the lower beak was less than that of the upper beak. Specimen 14 showed a light narrow streak from the jaw angle on the wing of the lower beak while Speci-men 16 had a darker brown streak along the mid-lateral walls of the lower beak. The degree of darkening of the beak was not in direct relation to size. The rostra were frequently split. The shoulder tooth and notch varied in profile.

GLADIUS

Most of the information in the present study is based on fragments reconstructed to elucidate overall shape. Length and width of the gladius, where available, are held at NIWA. Details of measurements, the points of origin of the lateral wings, and length of the end cone are contained in the individual specimen descriptions held at NIWA.

The gladius is extremely fragile, sometimes mem-branous anteriorly, and even in apparently intact specimens, the gladii have been shattered while still embedded in the flesh. Extraction is difficult and destructive to the remaining strength and integrity of the specimen. Once extracted the gladius dries out rapidly, distorts, and any handling has a tendency to further fragment the material. The only way to exam-ine the gladius is to create a "wet bed" and lay the pieces like a jig-saw puzzle.

The gladius does not extend to the posterior end of the mantle, but ends 100–300 mm short of it in a point which is sometimes obvious externally on the dorsal mantle. The gladius termination sits within a surrounding conical muscular envelope which is obvious only after opening the mantle cavity.

The gladius shape is broad and lanceolate. The texture is flexible but fragile, the colour is white or semi-opaque, sometimes almost transparent anteri-orly, and slightly yellowish-brown in association with the thicker ridges and end cone posteriorly.

The width of the gladius varies from 11% of mantle length (Specimens 2, 6, 7, 14); 12% (Specimens 1, 9, 11); 13% (Specimen 4); and 14% (Specimen 3). The position of the widest portion is difficult to judge in all specimens, but for the present material the widest point lies between the middle and the anterior third of the gladius. The extremes of the range are repre-sented by Specimen 11, where the widest portion is well forward of the midpoint, and Specimens 6 and 7, where the widest portion is situated on or about the midpoint of the gladius length.

Where the length of the gladius is available, it varies from 72% (Specimen 14) to 94% (Specimen 2) of dorsal mantle length.

The anterior termination of the gladius varies from an abrupt termination with a blunt point through to a narrow and attenuated termination. In Specimen 11 the extreme anterior of the gladius is slightly wrinkled, folded up, very soft. In Specimen 2 the anterior was drawn out into a sharp point (Fig. 17B). The anterior was very tapered in Specimen 6, measuring only 85 mm wide, 200 mm from the anterior. Specimen 6 was one of the smaller specimens, with a mantle length of 1560 mm. The free rachis length could not be determined; the vane tapered gradually and the rachis was not visually or structurally distinct from the vane, other than by a less opaque longitudinal strip in the gladius, and a slight dorsal concave depression when viewed in cross section.

The anterior third of the gladius was generally lacking in distinctive features. A weak lateral fold begins to develop parallel to the rachis and this continues posteriorly, sometimes with the addition of a second weaker fold lateral to the latter. Towards the midpoint of the gladius its outer edge thickens and becomes ridge-like. Other striae may also develop on the vane. Towards the posterior third, lateral wings start to develop to the outside of the earlier-thickened gladius edge. The wings gradually widen, while the thickened edge continues posteriorly, now within the body of the gladius. The specimens vary a little in the rigidity of the posterior portion and the number of additional longitudinal ridges that form, particularly on the wings. In some specimens they rival the thickened, formerly marginal, ridge in prominence. A short distance from the posterior the lateral wings taper abruptly and curl inwards to meet along the medial line. A thickened irregular ridge or keel develops for the last 10–20 mm on the dorsal side of
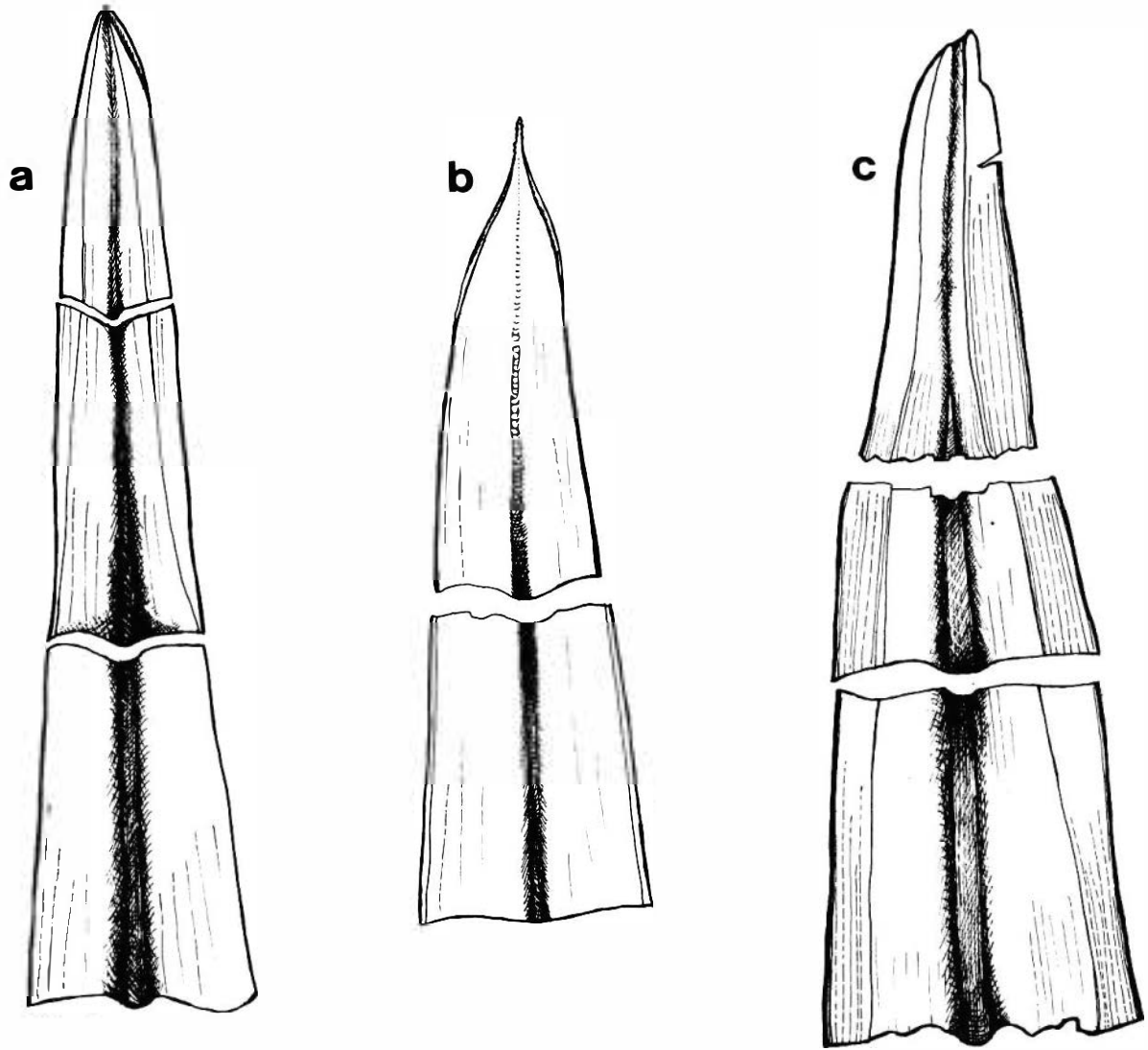
Fig. 17. *Architeuthis* gladius: **a,** posterior portion of gladius from Specimen 2; **b,** anterior portion of gladius from Specimen 2; **c,** posterior portion of gladius from Specimen 1.

the rachis in some specimens.

The end cone is hollow and varies in the extent of fusion. In some specimens there is a distinct seam, in other the edges fail to fuse completely. Cone length also varies to a small extent, but is generally a short cone (< 20 mm long).

RADULA

The radulae available from the present dataset conformed to the standard tricuspid central tooth, flanked by a bicuspid lateral, two unicuspid marginals, and a marginal boss. A photo and illustrations of Specimen 1 (Figs 18A–C) demonstrate the typical form. Not all radulae were received. The entire buccal mass was missing from a large number of specimens. It is suspected that this was because of "souvenir hunters"

Fig. 18. (opposite)   A. Specimen 1 radula.   B. Illustration of Specimen 1 radula to indicate size and orientation of cusps. C. Illustration of single row of radula teeth from mid-point of radula (Specimen 1).

5 mm

43
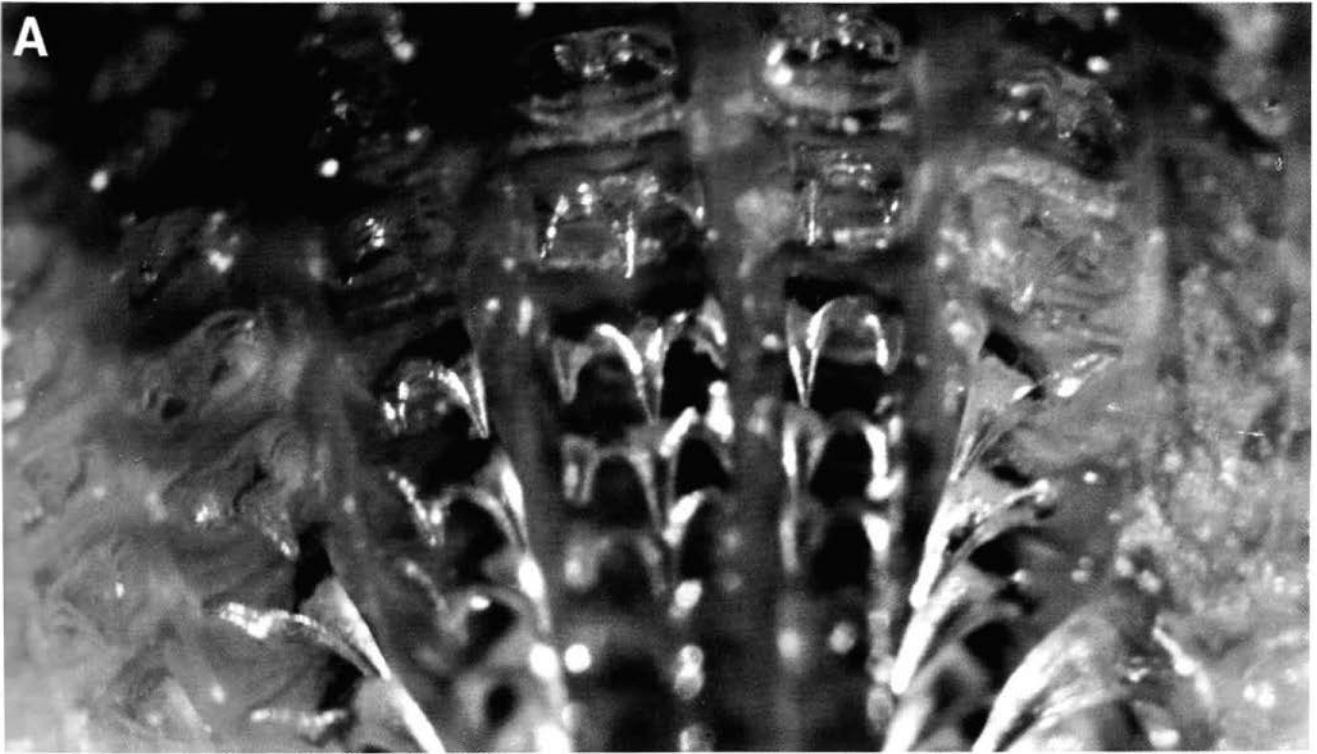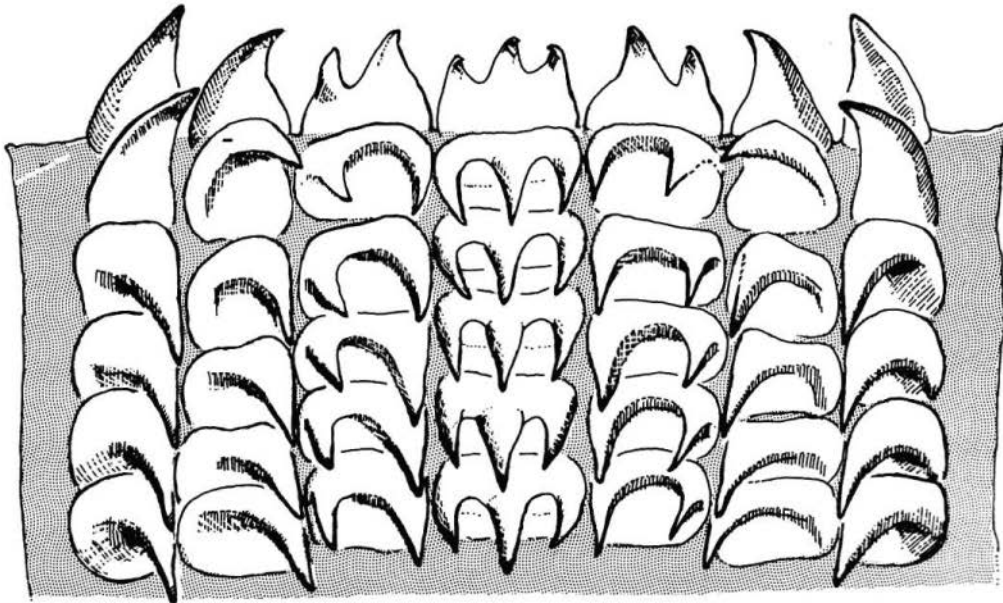
rather than a tendency for the buccal mass to be torn from the animal during its death struggles.

Table 9. Record of radulae of received material.

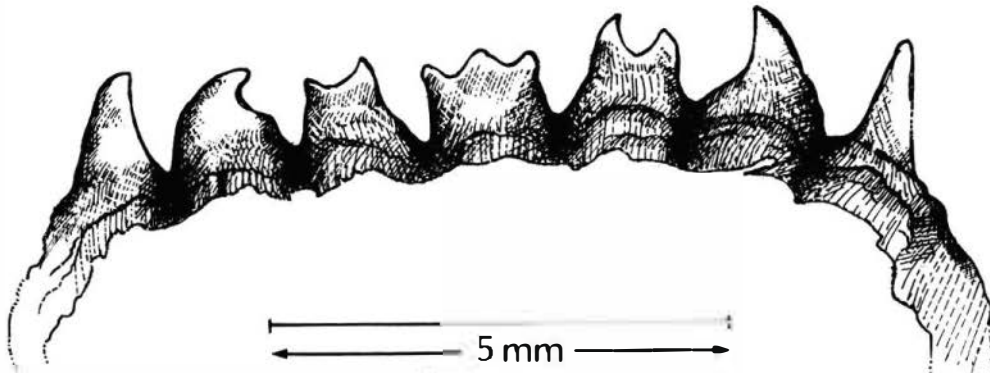| Specimen		Specimen	
1	radula	9	head anterior missing
2	radula	10	record misplaced
3	not available	11	missing from specimen
4	buccal mass missing	12	not available
5	buccal mass missing	13	radula
6	radula	14	radula
7	radula	15	not received
8	radula		

Radula length and widths are listed in the individual specimen descriptions held at NIWA for Specimens 2, 8, 13 and 14. Lengths averaged 61 mm, and widths decreased from 11–13 mm at the formation end of the radula to 9.5–10.4 mm at the "fold" and only 7.0–7.6 mm wide at the "old" end.

No differences have been identified between *Architeuthis* radulae which could suggest specific or regional differences (see Robson 1933; Verrill 1882b; Frost 1934; Cadenat 1936; Dell 1970; Roper & Boss 1982; Roeleveld & Lipinski 1991). Perez-Gandarez and Guerra (1978) also reported a standard arrangement. They were able to make a direct comparison with *A. physeteris*, described by Voss (1956), and report a generic similarity.

ARMS

Architeuthis arms (Figs 19, 20) are pigmented on all faces and the predominant colour is pink. The oral and aboral faces tend to be a pale pink; often the aboral surface is paler than the oral face. The lateral faces are a darker pink, often with additional hues of red, brown, mauve, or purple. The keels and protective membranes adopt the colour of the contiguous arm surface.

Specimens vary a little in colour detail. Oral faces of Specimen 7 arms were a pale orange-brown (see also head colour), the lateral faces of Specimen 8 arms

were a very dark red-brown (as for the mantle interior), while Specimen 10 exhibited an even pink colouration on all arm faces and Specimen 13 aboral surfaces were a red-brown with darker-red keels. Where available, the colours of the fresh material have been recorded in detail in the individual specimen descriptions (held at NIWA).

None of the specimens presented a complete set of intact arms. However, some information can be gleaned from comparing the minimum arm lengths and noting indices for those arms which were intact. Relevant information has been extracted from the individual descriptions for Specimens 3, 5, 6, 8, 11, 14, and 16 and presented in Table 10. The diameters of broken ends were measured at the same time but no useful way has been found to utilise this measure quantitatively.

From the very limited data it is possible to say that arm I is shorter than, or about equal to, mantle length. Arm IV is a little longer than the other arms with a validated maximum length up to at least 136% ML. In some cases (Specimens 8, 11, 14), arm IV only attains a length less than, or about, mantle length. The greater relative length of arm IV is indicated by photographs of Specimens 1, 4, 6, and 16 and the *Zuiyo Maru 3* Specimen, 26 July 1987 (see capture records in Appendix 2). A reasonable estimate from the photographs of Specimen 3 would describe all arms as subequal, or I, II, III subequal and IV slightly longer. The maximum relative length for any complete arm in this study was arm II on Specimen 16, at 140% ML.

Arm Shape

Circumference measures taken at the base of the arms established the predominant pattern of relative thickness as arm I< II < III ≤ IV. Specimens 1, 2, 3, 4, 6, 7 and 14 conformed to, or closely approached, this pattern. Those which varied significantly from this pattern were Specimen 5 (where arm II was thickest), Specimen 12 (where arm I= II < III= IV), and Specimen 10. In this latter specimen arm IV was equal to the slenderest (arm I) at the base, but by 300 mm further outwards arm IV had expanded to become the thickest arm. Insufficient arm structure remained on Speci-

Fig. 19. (opposite) A. Anterior view of Specimen 1 with author (1983). Note the lack of keels on arms III and IV and the similar appearance of arm IV sucker face and sucker size to the other three arms. **B.** Anterior view of Specimen 1, showing relative thickness and length of arms. Left arm I is second from the right and has probably been shortened prior to capture. Arms I–III are seemingly subequal with arms IV (3rd and 4th from left) indicating a greater length. C. Anterior view of Specimen 3 (with author). In contrast with A, note bulky arms IV with a trapezoid shape and double keels. Aboral "ridges" can be seen on arms I, II, and III. D. Anterior view of a specimen from f.v. *Zuiyo Maru 3*, 26 July 1987. The length of arm IV on this specimen is comparable to the other three arms. E. Anterior view of Specimen 6 demonstrates arm formula I< II< III< IV. Both arms I and left arm II have been damaged. The relative length of right arm IV clearly exceeds that of the other arms.
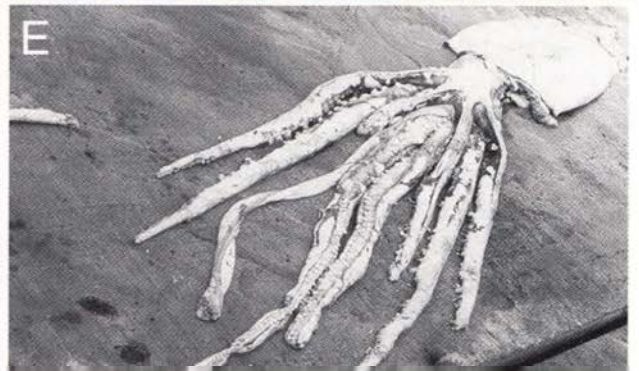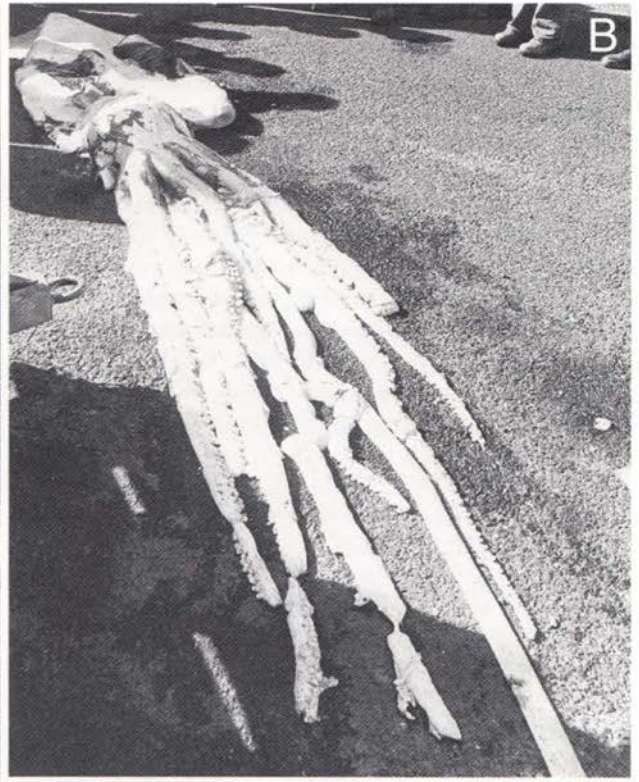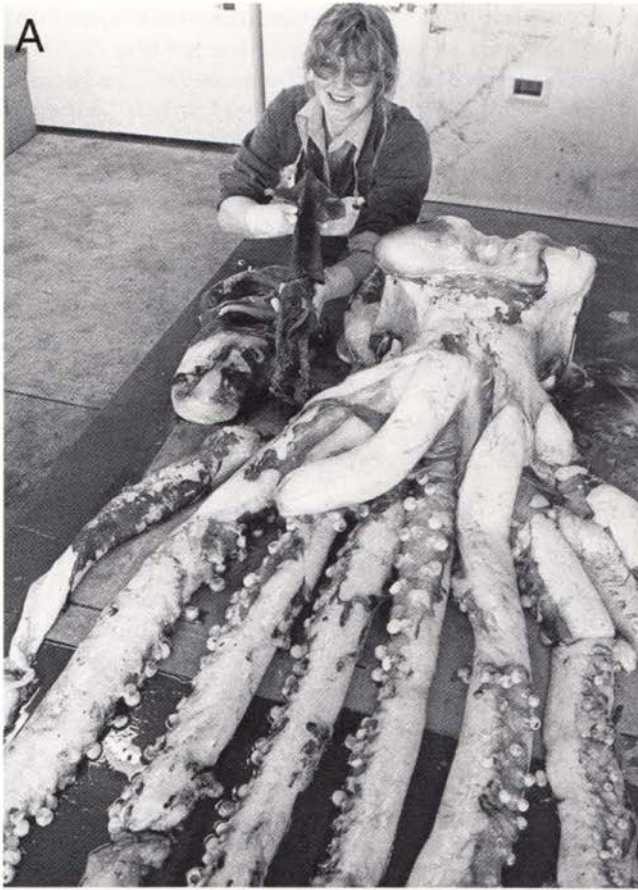
Table 10. Arm lengths. Bold font indicates entire or almost complete arms. Normal font indicates broken arms and hence minimum measures.

Specimen no	3	5	6	8	11	14	16
ML	1770	930	1560	1900	1720	2140	2000
arm I(mm)	**1710**	**935**	1010	920	**1240**	1410	**1590**
arm II (mm)	1420	460	**1304**		1200		**2800**
arm III(mm)	1485	685	1430		1380	**1400**	1660
arm IV(mm)	1500	1040	2120	**1960**	**1800**	1700	2700
arm I index	**97**	**101**	65	48	**72**	66	**80**
arm II index	80	49	**84**		70		**140**
arm III index	84	74	92		80	**65**	83
arm IV index	85	112	136	**103**	**105**	**79**	135

mens 9, 13 and 15 and only limited data were available for Specimen 8. The differences between the thickest and thinnest arms on a single specimen were not large. Differences between the arm-base circumferences exceeded 60 mm only in Specimen 7 (where the difference was 95 mm between arm I and arm IV).

A small expansion, particularly of arm IV from the base of the arm, appeared as a consistent feature. However, when an attempt was made to quantify the feature, it appeared that it was often illusory. The expansion was related to a small increase in the width of the sucker-bearing (or oral) face of the arm, without necessarily any attendant increase in bulk. This illusion was sometimes exaggerated by the increasing width of the swimming keels and/or protective membranes on the outer edges of the sucker face.

In order to track the shape of the arms, circumference measures were taken at points 300, 500, and 800 mm out from the base of the arm. Details are recorded in spreadsheets held at NIWA. The major features are extracted and summarised below:

- arm I tapers the most rapidly and, with one or two exceptions, is always the slenderest of the arms at 300, 500, and 800 mm from the base
- arm II is always slenderer than arm 3 at 300 mm from the base
- arm IV circumference measurements show an expansion from the arm base in Specimens 3, 5, 8 and 11
- arm IV maintains base circumference for at least 500 mm in Specimen 5, and Specimens 4 and 11 maintain initial circumference to 800 mm from the base
- arm IV tapers from the base in Specimens 6, 7, 10, 12, 14, and 16.

The absolute size of the arms is remarkably similar between specimens. Ignoring for the moment the smallest (Specimen 5), then the two extremes are represented by Specimen 6 with its 1560 mm ML and slender arms (circumference arm IV = 245 mm) and Specimen 7 at 2020 mm ML with the bulkiest arms (circumference arm IV = 350 mm).

All four arms differ in appearance from each other, despite the often similar circumference measures. There is considerable variation, but some common patterns emerge from the data recorded and held at NIWA. These are summarised below:

- Arm IV is best described as trapezoid in cross-section at the base as well as further along the arm, the shortest face being the sucker-bearing face. Sometimes the base is more quadrangular, but develops fairly quickly into the trapezoid shape a short distance along the arm
- Arm III varies in shape, sometimes adopting a trapezoid shape, albeit less marked than that of Arm IV (see Specimens 14, 10) but always tends to be more quadrangular than arms I and II.
- Arms I, II are generally best described as almost triangular or flattened oval in cross-section, always with the narrowest end as the sucker-bearing face. They may on occasions also appear as rounded-rectangular in cross-sectional shape.
- The distal tips of arms I, II, III were laterally flattened, but the tips of arms IV were orally-aborally flattened.

Arm Tip Regeneration

Arm damage appears to be a frequent event for *Architeuthis*. The arms were missing many suckers,

portions of flesh were missing, or arms were uneven in length and carried atypical examples and groups of smaller (?) regenerated suckers. Even sucker rings appeared to fracture *in situ* and heal again (see Suckers). Specimen 6 had lost the extreme tip of most of its arms in what is surmised was a single unhappy event. Figure 20B illustrates the smaller regenerating portion of two of the arms with their atypical smaller suckers. Figure 20C illustrates the healed and possibly regenerating portion of a dorsal arm which had lost a much larger portion of its length (Specimen 11).

Again, as for arm thickness, the interpretation of arm shape may be influenced by associated features, the most prominent of which are the swimming keels.

Keels

The number, size, point of origin, and persistence of structures along the aboral faces of the arms showed considerable variation in the specimens studied here. It should be noted that aboral faces of many arms were very damaged, and faint or delicate structures would not have been detected. The maximum width of a swimming keel was only 75 mm (Specimen 2). Often, where a keel might be expected, there was only a slight ridge marking the "corner" of the arm. The most remarkable aspect of the keels/ridges on the arms was the lack of a general pattern, as is evidenced by Table 11.

The majority of the ridges and keels originated at the base of the arm, with a smaller number originating at or about 200 mm out from the base of the arm. Where significantly different origins for the structures occurred these are listed in the notes column of Table 11. The ridge on arm III had a tendency to originate further along the arm. The maximum depths of arm IV dorsal keels tended to be slightly deeper than those of the corresponding ventral keel (Specimens 3, 4, 5, 6, 13, 14, 16), but the dorsal keel was approximately equal in Specimen 7 and narrower than the ventral keel in Specimen 11. As mentioned in the Fin section, the large contrast between Specimens 1 and 2 led to careful examination of the oral and aboral arm faces, resulting in a record for arm structures which encompasses a large number of variations of 0, 1, or 2 ridges and keels per arm. Keels are most frequently present on the ventral arms (arms IV) followed by arm III, where the structure is more likely to be single keel or ridge. Arms I and II are less likely to have aboral keels. The comparatively small data-set and the variability observed preclude any observations on "morphs" or sexual differences.

Protective Membranes

The protective membranes are supported by paired thick muscular ridges (trabeculae) originating each side of the sucker base. The trabeculae do not project beyond the edge of the protective membrane. The membranes themselves vary in width, robustness and appearance. Details of the measurements and the more qualitative descriptions are recorded the individual specimen descriptions (held at NIWA).

Limited measurements were taken for Specimens 1 and 2. Many more features were noted in later specimens. The dorsal and ventral protective membranes on each arm were generally very similar in width (Specimens 1, 3, 4, 5, 6, 8, 10, 16, 12), although the widths were less regular in Specimens 7, 11 and 14 and the ventral membrane was slightly wider in Specimen 7. In some cases the protective membranes of arm IV were narrower as well as being thinner and weaker than those of the first three arms (Specimens 2, 3, 4, 7, 8, 11, 14, 16). Arm IV protective membranes were about same the same width as those for the first three arms in Specimens 5, 6, 10 and 12, but were still generally less robust. In Specimens 2 and 3 the protective membranes of arm IV are thicker than those on the other three arms.

An additional feature is the tendency for the protective membrane to exist as separate lobes near the base of the arms. This was especially evident in Specimen 3 (arms II, III), Specimen 4 (arm I), Specimen 6 (arm IV), Specimen 11 (arm IV), Specimen 13 (arm IV), Specimen 14 (arms II, IV), and Specimen 16 (arms III, IV). It was also common for perforations to form in the base of the protective membrane between the trabeculae. This occurred near the base of the arms in Specimen 2 (arms II, III), Specimen 7 (arm IV), Specimen 6 (all arms), Specimen 12 (arms I, II, III), or towards the distal half of the arm (Specimen 3, arm II; Specimen 5, arm I; Specimen 7, arm IV; Specimen 11, arm IV; Specimen 16, arm I). Thus the lobate or perforated form of the protective membrane has no discernible pattern of occurrence, either within the arms of a single specimen or between specimens.

Arm Oral Face

Arm spreadsheets held at NIWA contain detailed measurements of the width of the sucker-bearing face for all arms at the position of the 5th sucker and the 10th sucker. The information has not been further considered, as the widths appeared to vary within and between specimens without apparent pattern. The

Table 11. Keels/ridges on *Architeuthis* arms.

Spec.	arm I	arm II	arm III	arm IV	notes
1	0	0	0	0	severed tip carried a single keel
2	1 weak keel	1 keel	1 keel	1 keel	
3	1 lateral ridge	1 lateral ridge	1 aboral ridge	2 keels	
4	2 ridges	2 ridges	2 ridges	2 keels	arm I ridges persist for 500 mm only
5	2 ridges	2 ridges	1 ridge	2 keels	arm III ridge originates at 420 mm
6	2 ridges	0	1 ridge	2 ridges	
7	2 ridges	2 ridges	1 ridge	2 keels	arm III ridge originates at 440 mm
10	1 ridge	0	0	?1 keel	arm I ridge originates at 500 mm
11	0	0	1 distal ridge	2 keels	arm III ridge originates at 750 mm
12	0	0	1 keel	1 keel	keels originate at 300, 350 mm
13			2 keels		
14	0	1 keel on tip	1 keel	2 keels	arm II originates at 800 mm, arm IV right keel disappears at 800 mm
16	2 ridges	2 ridges	1 ridge	2 ridges	arm III ridge originates at 350 mm

spreadsheets also describe the height of the sucker bases.

The height and degree of muscularity of the sucker bases vary. In many instances, as the size of the sucker decreases along the arm, the height of the sucker base increases until it forms a conical structure equivalent in size to the sucker. The oral face of arm IV is usually wider and flatter than the other three arms, and where the central "zigzag groove" is present, it tends to be more strongly developed on arm III.

Papillation of the sucker-bearing face is of general occurrence. On first examination, and in most specimens, the pattern of papillation appeared to be random within a narrow band each side of the central arm groove. However, the distribution noted in three particular specimens suggested that there may be an underlying pattern. The papillae in Specimen 5 were located in a regular fashion between the sucker bases on both sides of the central "zigzag groove". Specimen 7 had very pronounced papillae on arms I and II which appeared to elongate and run into each other to take the form of a rough zigzag ridge running parallel on either side of the central groove on the sucker bearing face. This pattern was also evident on arm III of Specimen 16.

Hectocotylus

Specimen 9 was a male. Only the right arm tip was available and resembled a hectocotylus as described by Kjennerud (1958). However, the degree of modification of the arm tip was minimal. The main feature appeared to be the loss of suckers from the extreme distal portion of the arm. The portion of arm available could not reliably be distinguished from arm tips from females where the suckers had been lost, presumably through accident. The "sucker bases" and protective membranes of Specimen 9 did not alter in form. The sucker stalk was still present and in some cases remnants of the sucker itself. The loss of suckers appeared to be accidental rather than an original condition. The arm tip has been deposited in the Museum of New Zealand.

TENTACLES

Specimens 6, 7, 8, 12, 13 and 16 were captured with tentacles (Fig. 21) and at least one club each. Where possible, details of measures and sucker numbers and arrangements are listed in Table 12. A large number of additional measures were collected on some of these clubs in anticipation of defining specific differences. Material available from the present dataset is listed below.

Fig. 20. (opposite) **A.** View of Specimen 6 arm bases to show protective membranes, sucker bases, and trabeculae. **B.** Specimen 6, regenerated tips of arms II and III with small crowded suckers. Note loss of suckers from the region immediately proximal to regeneration. **C.** Specimen 11, entire left arm I. Note the smaller regenerated section (left) with atypical, small crowded suckers.
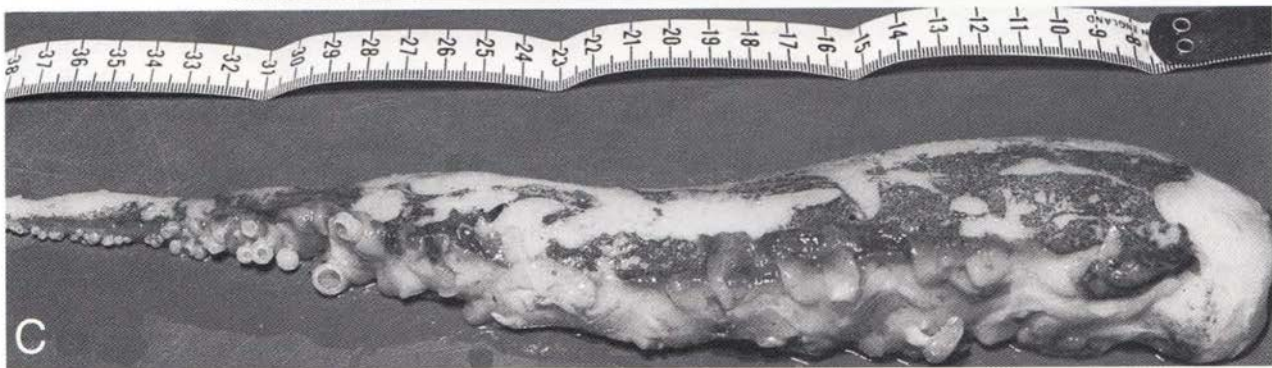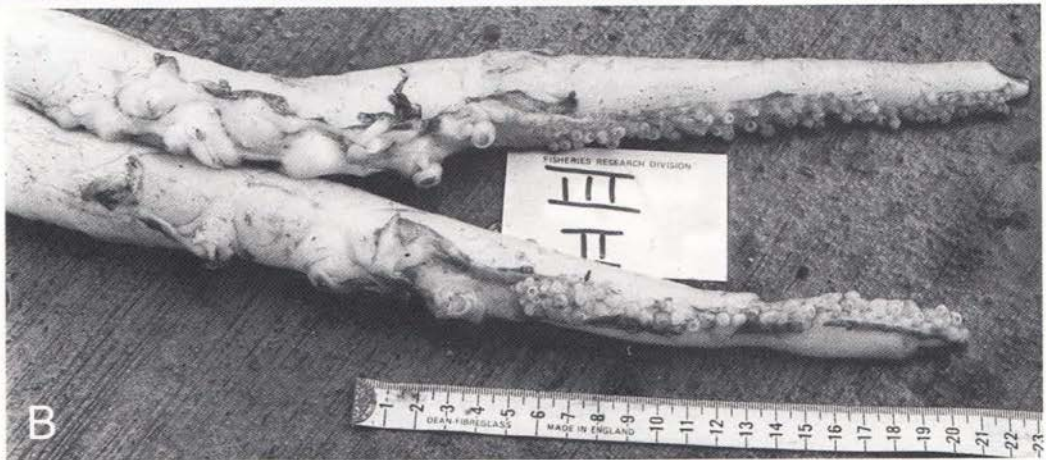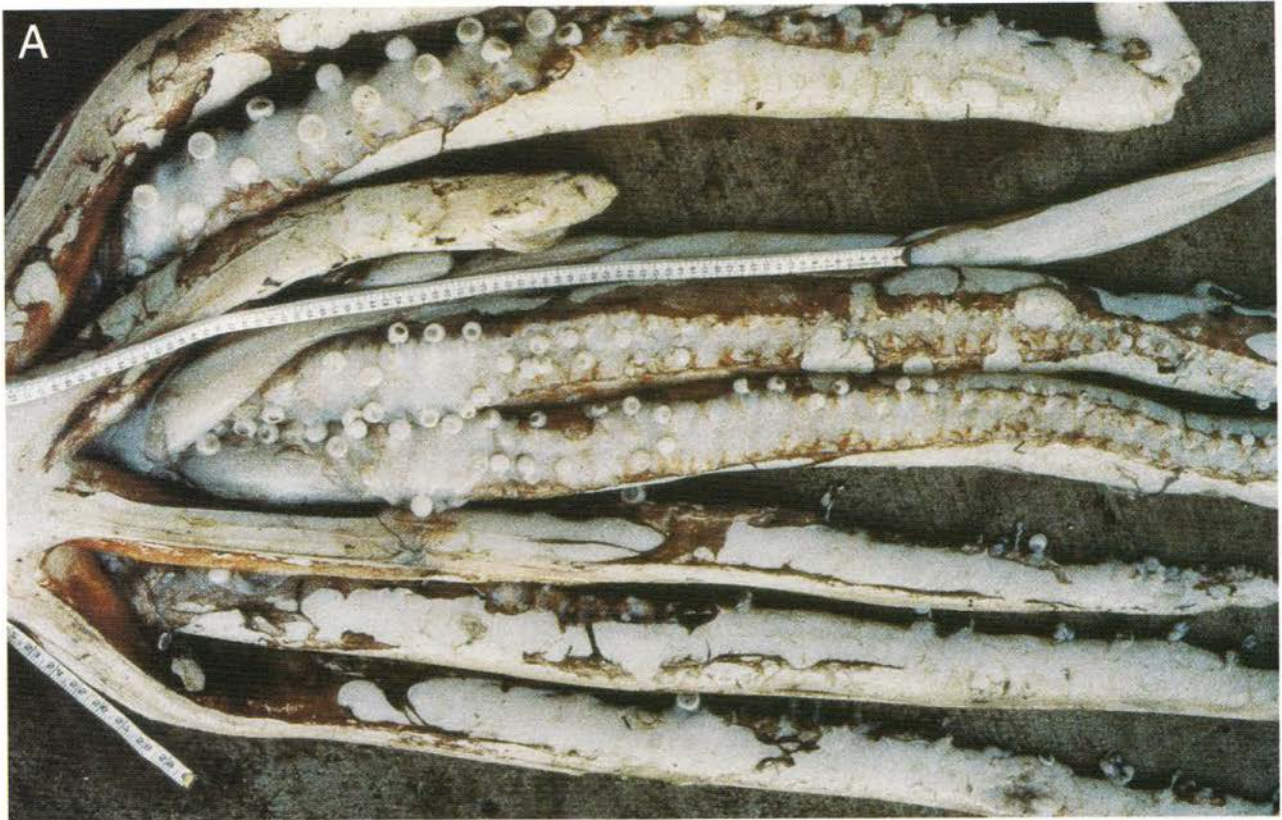
49

Table 12. Tentacle measurements of *Architeuthis* specimens (dimension in mm).

| Specimen	6, M102285 right	left	7	8	12 right	left	13	16 Z8436	M118003 right	left	M118019 club
Length of club			925	755			840	850			
Length of tentacle stalk	7500		6325		3110	3150		7300			
Approx. no. of stalk suckers			23		31			31	23	26	
No. of stalk knobs			29		30			28			
Colour of sucker face					pale			pink			
Colour of sides					pink			dkred			
Colour of aboral face					pink						
Colour of protective membranes	pink/ red										
Circumference stalk base			160		n/a			170			
Diameter of face stalk/carpal boundary					~ 40						
Circumference at base of carpus	97			145	110	120		120 fresh 110			
No. smooth-edged suckers on carpus	53	49	45-48	34	45	53		41-42			54
Approx. no. of knobs on carpus	49	39	45	25	48	44		39-42			
Sucker diameter at base of carpus	4.9		4.6	5.7	5	5		4-6			
Sucker diameter halfway along carpus	5.4- 5.6			5.5	5	5		4-6			
Diameter of face at stalk/carpal boundary	45			50	40	37		50			
Diameter of face at carpus/manus boundary	55		70	50	42	42		55			
Circumference at manus/carpus overlap	132			165	140	145		145			
Approx. length of carpus	150		160	100	150	145		180			
Approx. no. of suckers in carpal cluster	21	24	32	24	27	24		{14 + 4 v. small	31		38/39
Range of diameters of serrated carpal suckers	6.0- 9.0		6.0- 9.8	5.0- 8.5	4.5- 9.0	4.5- 8.5		5.0- 7.2			
Length of manus	470		480	405	355	390	420	450			
Quadriserial rows with enlarged central suckers	14	15	13	13	13	12	12	12 or 13	12+ 3	12+ 2	11+ 3
Diameter of largest central sucker	28.9		29.8	28	29	29	32	29			
Quadriserial row no. of largest sucker	5th		5th	6th	8th	6th	6, 7	6th			
Diameter of largest marginal sucker	12.1		12		14						
Diameter sucker-bearing face mid-manus	44		80	45	41	37	47	55			
Circumference midway along manus			120		110	115		130			
Maximum width of protective membrane	ventral 25		10- 12	20	20	20	26	13- 14			
Diameter of face at manus/dactylus	20		30	22	25	20		30			
Length of dactylus	280		240	250	250	235	225	230			
Arrangement of dactylus suckers (qs = quadriserial)	tri/ qs		ir- reg- ular		qs 30 rows	qs 31 rows					
Approx. no. dactylus suckers	118		157	110	125	130			42		
Smallest toothed sucker			2.4	7.5				3			
No. of "sessile" suckers in dactylus	14	10	>5		>6	>6		15			
Size of "sessile" suckers	1.2- 2.5		1.5	1.8	1.4- 1.5	1.4- 1.5		smaller			
Width of dactylus tip	8			10	9	10					
Maximum width of keel	15			21	15	18	22	~ 19			
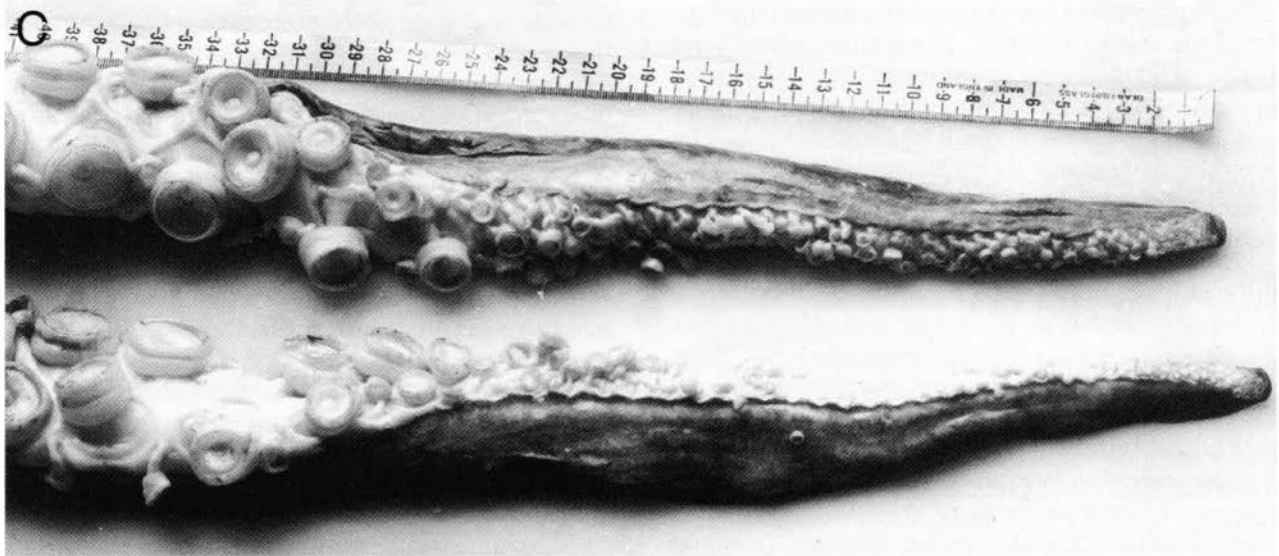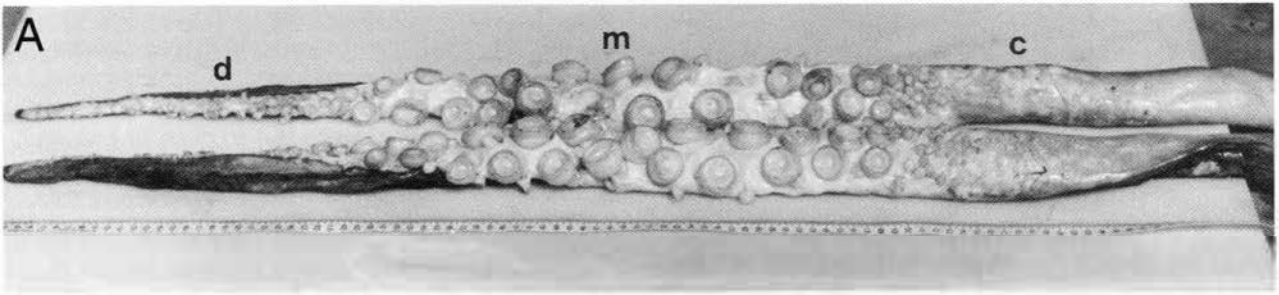
Fig. 21. Right and left tentacle clubs from Specimen 7 (d, dactylus, m, manus, c, carpus). B. Carpal and proximal manal region of tentacle club from Specimen 6. C. Dactylus and keel from Specimen 7.

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Specimen 6: total tentacle length 7500 mm (both tentacles and clubs recovered)

Specimen 7: total tentacle length 6325 mm, club length 925 mm (two tentacles and clubs)

Specimen 8: tentacle length unknown, club approximately 755 mm (one tentacle only)

Specimen 12: total tentacle length 3110 mm (both tentacles and clubs present)

Specimen 13: tentacle length unknown, club length 840 mm (one club only)

Specimen 16: tentacle length 7300 mm, right club 850mm (both tentacles and clubs attached)

Definitions

The proximal end of the carpus is defined as the point at which the tentacular stalk suckers first formed a line of three suckers diagonally across the stalk. Two distinct types of suckers occur in the carpal cluster. The proximal suckers are small and smooth-ringed, similar to those on the stalk, and loosely associated with a "knob". A short distance along the carpus, the knobs become larger and less distinct and appear to coalesce and disappear. The suckers continue to increase in size, their rings gradually becoming clearly and regularly toothed. The largest of these suckers is similar in form to those of the manus. There is a gradation in form of these toothed suckers from those with very short pedicels to those closer to the manus with longer pedicels. The first row of the manus is defined as the first quadriserial row in which the central two suckers are enlarged. This is generally a clear transition.

Arrangement of the suckers in the manus is quadriserial for at least 12 rows. The manal suckers have longer stalks than those found on the arms. The manal pedicel is also inserted more centrally into the sucker cup. Dentition is regular around the entire rim. The central manal suckers are the largest of all the suckers found on the squid, both on the arms and on the tentacles.

Defining the distal end of the manus is more difficult. Sometimes there is an abrupt finish to the enlarged central rows of suckers, but at other times the transition is less clear. The final few rows of the manus are occasionally triserial, with the suckers in the central positions still clearly enlarged.

The dactylus suckers undergo a similar, but reverse, transition in form to that of the carpus. The majority of suckers are regular, moderately sized, toothed suckers on stalks, similar to those of the lateral rows of the manus. The proximal suckers start out the same way, then gradually shorten, reduce in size, and lose dentition to become almost sessile, smooth-ringed suckers similar in form to those of the tentacle stalk. The arrangement varies between specimens. Some show a regular quadriserial arrangement for the proximal portion, others an irregular triserial arrangement, but always the pattern is less well-defined towards the distal tip. In all the specimens the extreme distal tip of the tentacle club is folded back over the last rows of suckers (containing 1–8 suckers).

Tentacular Stalk and Club

The tentacular stalk is smooth and lacks a keel or protective membranes. The cross-sectional shape of the stalk and base of the club is best described as oval or triangular. There are often colour differences between the various faces of the stalk. The oral sucker-bearing face is paler in colour and the skin semi-transparent, revealing a striated internal appearance. In some specimens a darker stripe (?blood vessel or nerve) runs up the centre of the stalk. The lateral and aboral faces are darker in colour, but generally still lighter than the mantle or outer surfaces of the arms. Protective membranes and keels are negligible or absent on the stalk. Towards the carpus there is a hint of protective membranes developing, but they are too insubstantial to measure. Similarly, a ridge develops on the aboral face of the tentacle but this cannot be described as a keel until part-way along the manus. The keel becomes fleshy and muscular in texture towards the distal end of the manus and continues to the end of the dactylus, although it rotates to become almost lateral in position. The colour of the keel is much darker than the main portion of the tentacle and club. The protective membranes are fleshy and widest along the edges of the manus, tapering towards the distal tip of the club. They are pale on the sucker-bearing face and darker on the aboral side. On Specimen 6 it was noted that the trabeculae do not extend to the outer edge of the membrane on the manus, but do so on the dactylus, giving a fluted appearance to the membrane edge.

The stalk carries very small suckers which appear to be almost sessile. The pedicels are very short and inserted centrally on the suckers. The numbers and spacing between the stalk suckers and knobs vary only slightly between specimens, as does the position of the first sucker. For example, Specimen 7 (ML 2020 mm) has 29 suckers and knobs on the tentacle stalk, with the first three suckers spaced over 3000 mm of tentacle stalk. Specimen 12 (ML 1690 mm) has 31 stalk suckers, while Specimen 16 (ML 2000 mm) has 26 suckers, with the first three suckers spaced over 2810 mm of stalk. The spacing between the suckers becomes progressively closer towards the club.

The number of smooth-ringed carpal suckers varies slightly between left and right club (e.g., Specimen 12 has 53 and 45 suckers respectively) and also between specimens. The number of toothed, stalked carpal suckers also varies slightly between specimens (e.g., Specimen 12 has 24–27 toothed carpal suckers, while Specimen 8 has 23–24, but Specimen 16 has a maximum of only 18 such suckers).

The number of quadriserial rows of manal suckers with two enlarged central rows of suckers varies little, beyond difficulties with counts caused by the transition mentioned earlier. The pedicels for the two central rows of enlarged suckers were thick and relatively short, inserted just off-centre in the back of the sucker cup. The marginal manal suckers had much longer pedicels than either the other tentacular or arm suckers.

The cross-sectional shape of the manus is oval, with a protective membrane on each side. Where the orientation of the club is known (Specimens 6, 7, 16), the "ventral" protective membrane along the manus is thicker and slightly wider than the "dorsal" protective membrane. The position of the widest portion of the protective membrane is between the proximal quarter and the midpoint of the manus. A keel begins to develop midway along the manus and becomes most pronounced by the proximal end of the dactylus. It then merges with the flesh of the dactylus and rotates laterally on the distal half of the dactylus. The keel/lateral ridge of flesh continues almost until the tip of the dactylus. The cross-sectional shape of the dactylus is very flattened orally, and triangular in cross-section.

The number of manal rows of enlarged suckers for the present dataset are listed below:

Specimen 6:   14 rows
Specimen 7:   13 rows
Specimen 8:   13 rows
Specimen 12:   right 13 rows, left 12 rows
Specimen 13:   12 rows
Specimen 16:   12–13 rows

The maximum size of the largest central suckers ranged from 28–32 mm in diameter, whereas the largest lateral manal suckers ranged from 12–14 mm in diameter. The marginal suckers were thus slightly less than half the size of the central suckers.

ARM SUCKERS

Suckers are biserial on all arms, with members of pairs arranged obliquely. The first sucker on all arms is smaller than those immediately following (Table 13). The distance from the junction of the oral surface of the arm with the buccal membrane to the first sucker is noted in the data spreadsheets held at NIWA. The arrangement of suckers on arm IV differed from that of the other three arms. In general, the arm IV sucker-bearing (oral) face was wider and flatter (or less creased), had fewer papillae, and less muscular sucker bases. The suckers are arranged in two longitudinal rows, but the separation between the rows was wider and sucker pairs appear to be inserted almost opposite each other rather than the more oblique arrangement prevailing on the other three arms. This pattern for arm IV is evident in Figures 19A–C. The general shape of the suckers remains the same although the form of the sucker ring changes progressively along the arm.

The shape of the suckers is illustrated (Fig. 20) and has been frequently and carefully described in the literature (e.g., Steenstrup 1857; Verrill 1882b; Pfeffer 1912; Sasaki 1929; Roeleveld & Lipinski 1991). An example of every version of the sucker shape described in the literature may be found in at least some of the present specimens.

The sucker consists of a globose muscular cup with a stalk inserted laterally and narrowed at the point of insertion. The length of the peduncle is approximately equal to or less than the diameter of the sucker. The lumen of the sucker is oblique, and the sucker teeth are relatively small and initially numerous. Dentition progressively changes from an outward orientation to a more oblique and inward orientation. The fresh colour of the teeth is either clear or white. The sucker ends in a narrow lip around the base of the teeth.

Sucker Density

Sucker density (Table 14) on the arms varies, particularly on arm IV where the suckers are always more densely arranged than on the other three arms (an exception is Specimen 1). Beyond that, there is more variability in the arrangement. A generalised pattern is not easy to discern, but it is obvious that with a small sample size it would be easy to identify different patterns, e.g.,

- the suckers on arm II are most widely spaced (Specimens 5, 7, 16)
- or, alternatively, the sucker density is the same on arms I–III (Specimens 6, 12, 14).

The greatest disparity in sucker patterns noted occurs between Specimen 1 and Specimen 2, although unfortunately the measurements were not collected in such a way as to enable easy comparison with the squids that followed. The most obvious feature was the less dense and comparable sucker spacing on all four arms of Specimen 1. This contrasted with the

Table 13. External diameter (mm) and description of dentition of first sucker on each arm.

Specimen	arm I	dentition	arm II	dentition	arm III	dentition	arm IV	dentition
1	7.7	missing	6.7	missing	13.9		14.2	
2	5.4	no teeth	5.6	4 lobes	13.4	-	-	-
3	4.6	?51 teeth	-		13.9	45 uneven	13.0	42 uneven
4	3.3	no teeth, lobed	14.5	50 teeth	12.0	41 regular	6.8	0, irreg. ring
5	3.7	7 lobes	4.1	no teeth	9.2	43 irregular	10.3	40 teeth
6	5.7	10 lobes	6.3	13 teeth	13.4	-	7.4	19 teeth
7	-		8.7	no teeth	14.0	-	14.0	43 irreg. ring
8	15.0	42 teeth	-		-		11.0	34 reg. teeth
10	6.0		small, lost		-		12.0	
11	6.0	4—6 lobes	7.0	6-8 lobes	12.5	38 reg. teeth	15.0	?42 teeth
12	4.5	4 lobes	6.5	4 teeth + lobes	17.5	45 teeth	14.0	38 teeth
14	9.0	17 reg. teeth	6.0	12-13 teeth	15.0	46 reg. teeth	14.0	-
16	7.0	7 teeth/blocks	8.0	-	15.0	-	14.0	35 teeth

Table 14. Density of suckers per first 500 mm and 1000 mm of arm (measured from first sucker).

Specimen	arm I	arm II	arm III	arm IV
1	34*/860	34*/930	27*/280	30*/860
2	21*/275	23*/298	22*/310	30*/310
3	16/500, 45/1000	21/500, 51/1000	20/500, 46/1000	34/500, 71/1000
4	18/500	25/500	22/500	41/500
5	31/500	28/460	32/500	46/500, 99/1000
6	19/500, 44/1000	19/500	20/500	36/500, 77/1000
7	21/500, 50/1340	18/500, 30/870	19/500, 42/1000	30/500, 74/1000
8	26/500			35/500, 84/1000
9	no arms			
10	arms severed			
11	20/500, 55/1000	24/500, 61/1000	23/500, 55/1000	34/500, 69/1000
12	24/500	23/500	36/500	
13			18/330	
14	18/500, 36/1000	18/500, 38/1000	18/500, 38/1000	30/500, 64/1000
15	not received			
16	17/500, 51/1000	16/500, 40/1000	26/500, 55/1000	29/500, 63/1000

* = number of suckers per arm distance covered in mm (standard 500/1000 mm not available).

more densely arranged suckers on Specimen 2, especially on arm IV. The arrival of the subsequent specimens in quick succession with a range of other density patterns forestalled the temptation to suggest that Specimens 1 and 2 represented separate species (see also the variation in keel arrangement).

For those arms which appeared to be complete, the total number of suckers per arm was as follows :

Specimen 3, arm I	110–120	ML 1770 mm
Specimen 5, arm I	?80–90	ML 930 mm
Specimen 8, arm IV	170–180	ML 1900 mm
		?male
Specimen 14, arm III	?60–70	ML 2140 mm
Specimen 16, arm I	60–70,	
arm IV	160–170	ML 2000 mm

These figures must be considered minimum counts since the suckers become very small and crowded near the tips and any loss from the arm tips will disproportionately reduce the counts. Total arm sucker counts are, however, a feature worth noting for future *Architeuthis* researchers. Figures quoted in the literature range to over 300 suckers per arm (Verrill 1882b; Robson 1933). It is unclear whether that number could occur here, even if the arms were unmutilated.

Sucker Size and Tooth Number

The intention was to measure every 5th sucker up to the 30th sucker and then every 10th sucker in order to follow changes in size and dentition. The data are recorded in the individual specimen descriptions (end-pocket fiche). The data-sets are incomplete for a number of reasons:

- truncated arms or fresh damage to the sucker-bearing face
- portions of suckers missing from the arm with apparently healed bases and peduncles
- either at capture or after freezing and thawing large numbers of sucker rings are lost or drop off.

Suckers on the first three arms increase in size from those listed in Table 13, to reach a maximum between the 10th and 15th sucker and then steadily decrease in external diameter with distal progression along the arm. The smallest suckers on the arm tips are barely visible to the naked eye (1–2 mm).

The largest suckers (Fig. 22) on the sessile arms are a very constant 21–24 mm in external diameter (Specimens 1, 2, 3, 6, 7, 8, 11, 12, 14, 16). A maximum sucker size of 24 mm is found on Specimen 11, arm II (ML 1720 mm), and Specimen 16, arm I (ML 2000 mm). Specimen 4 (ML 1825 mm) has slightly smaller suckers, with the largest on arms I–III attaining only 18–20 mm diameter. The suckers of the smallest squid, Specimen 5 (ML 930 mm), are considerably smaller, at just under 17 mm maximum diameter.

In most of the present specimens the sucker diameters on arm IV rarely exceed 17 mm. Suckers reach a maximum size by the 5th sucker, and diminish in size far more slowly than on arms I–III. Sucker sizes on arm IV reduce in size by only a few millimetres in diameter by the 30th sucker in Specimens 3, 4, 5, and 7. The exceptions are Specimens 12 and 16 where the difference in sucker size between arm IV and the other three arms is not particularly marked, and Specimen 1 where the maximum sucker size on arm IV is larger and very similar to that of the other three arms (21.9 mm).

On all arms, the first sucker is smaller than the next 10–15 suckers. The size of the first sucker is sometimes very small and easily missed, particularly when the arm is damaged. Occasionally it is impossible to reliably determine the size or position of the first sucker. Sometimes the sucker appears otherwise intact but the ring is missing.

"Small" first suckers (Fig. 23) appear to be of three types:

When 5 mm in diameter or smaller, the suckers do not have "teeth", but have either a smooth or slightly lobed or indented ridge around the lumen. This type of sucker generally only occurrs on arms I and II (exception arm IV, Specimen 4) and the smallest of these are reminiscent of the tentacle stalk sucker rings, but with a proportionally longer, eccentrically inserted stalk.

The next group of "small" suckers vary somewhat in size, but are generally < 8 mm in external diameter. The dentition grades from a larger number of irregular "blocks" or "lobes" (>6) up to 20 teeth. These types of first suckers are also generally found only on arms I and II (exception arm IV, Specimen 6).

The third type of first sucker is only slightly smaller than the following suckers and resembles them in form. This is the more usual form for the first sucker on arms III and IV. The number of teeth exceeds 35 (exception arm I, Specimen 8).

The absolute size of the first arm sucker does not relate to the mantle length of the squid (compare Specimens 4 and 5). Details of sucker shape and dentition are listed in the individual specimen descriptions (end-pocket fiche).

The maximum number of teeth on any particular sucker ring on an arm is often used as a taxonomic character. Relevant information has been extracted and tabulated below.

Table 15. Number of teeth in largest sucker rings of each arm.

Specimen	arm I	arm II	arm III	arm IV
1	34-46*	34-46*	34-46*	34-46*
2	42-50*	42-50*	42-50*	33-41
3	49-51	53-55	49-53	42-45
4	46	46-50	47	41
5	50-53	47-51	46-56	43-48
6	43-45	38*-43-*71	37-45	37-38
7	-	46*-49	51	34-43
8	41	*	*	32-37*
11	52-59	49-54	43-47	37-39
12	52	42-48	38-43	42
14	49	46-53	43-51	35-44
16	44-47	41-47	42-49	30-41

* average, or best estimate

For many of the specimens listed in the table above, it is appropriate to combine arms I, II and III and contrast them with the maximum teeth found on arm IV suckers. Specimen 1 may well have fewer teeth than the other specimens, but unfortunately the data were combined at an early stage. The disparity in numbers of sucker teeth between the arms is most clearly expressed in terms of an individual specimen. When attempts are made to generate an overall formula for the range of teeth, the discontinuity
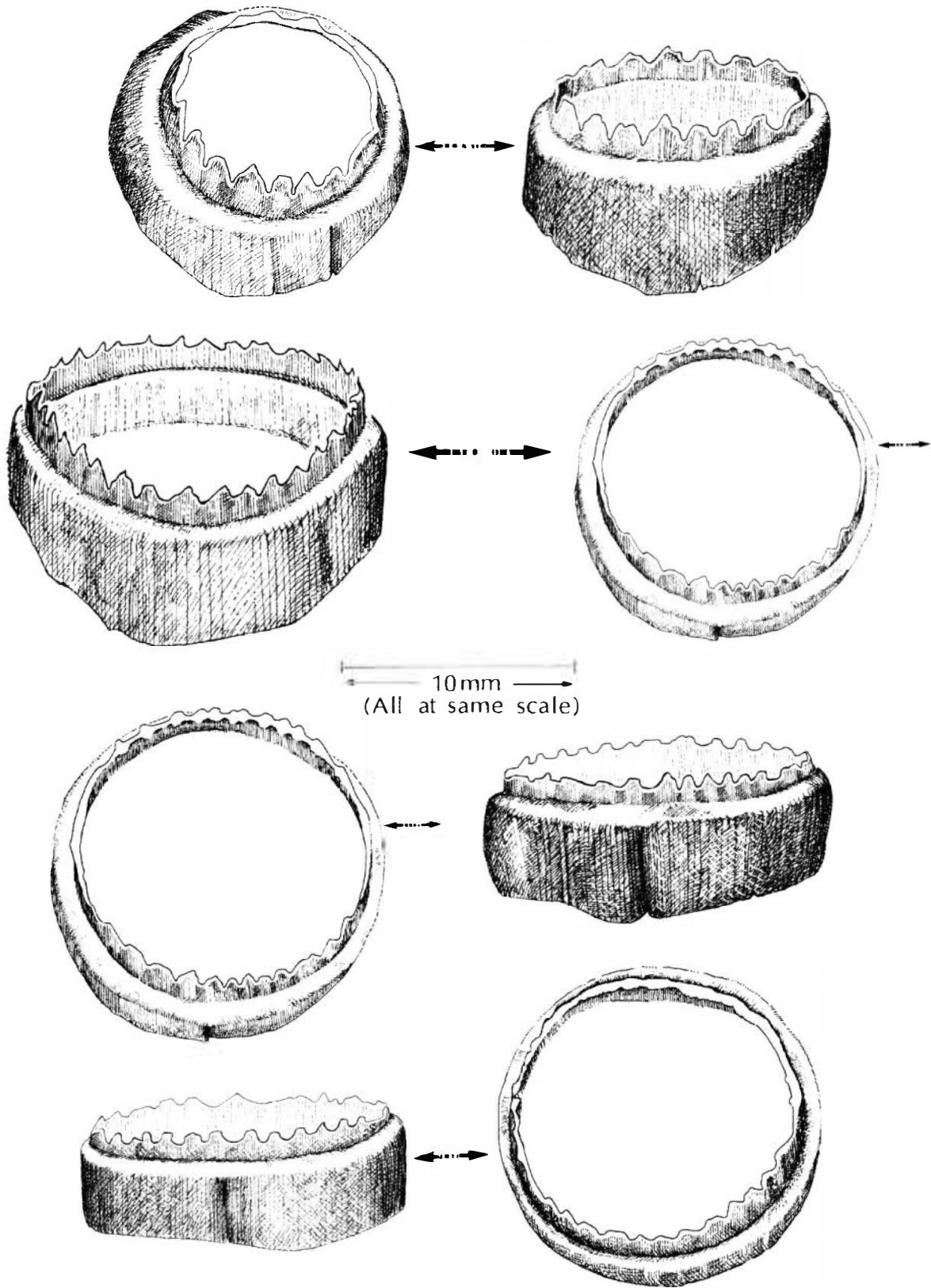
Fig. 22. A selection of the largest remaining suckers from Specimen 1. Note the uneven and worn dentition and a well-formed "shoulder" at the base of the teeth. The "collar", or proximal flange, is vertical and narrow with irregular vertical folds and striations.
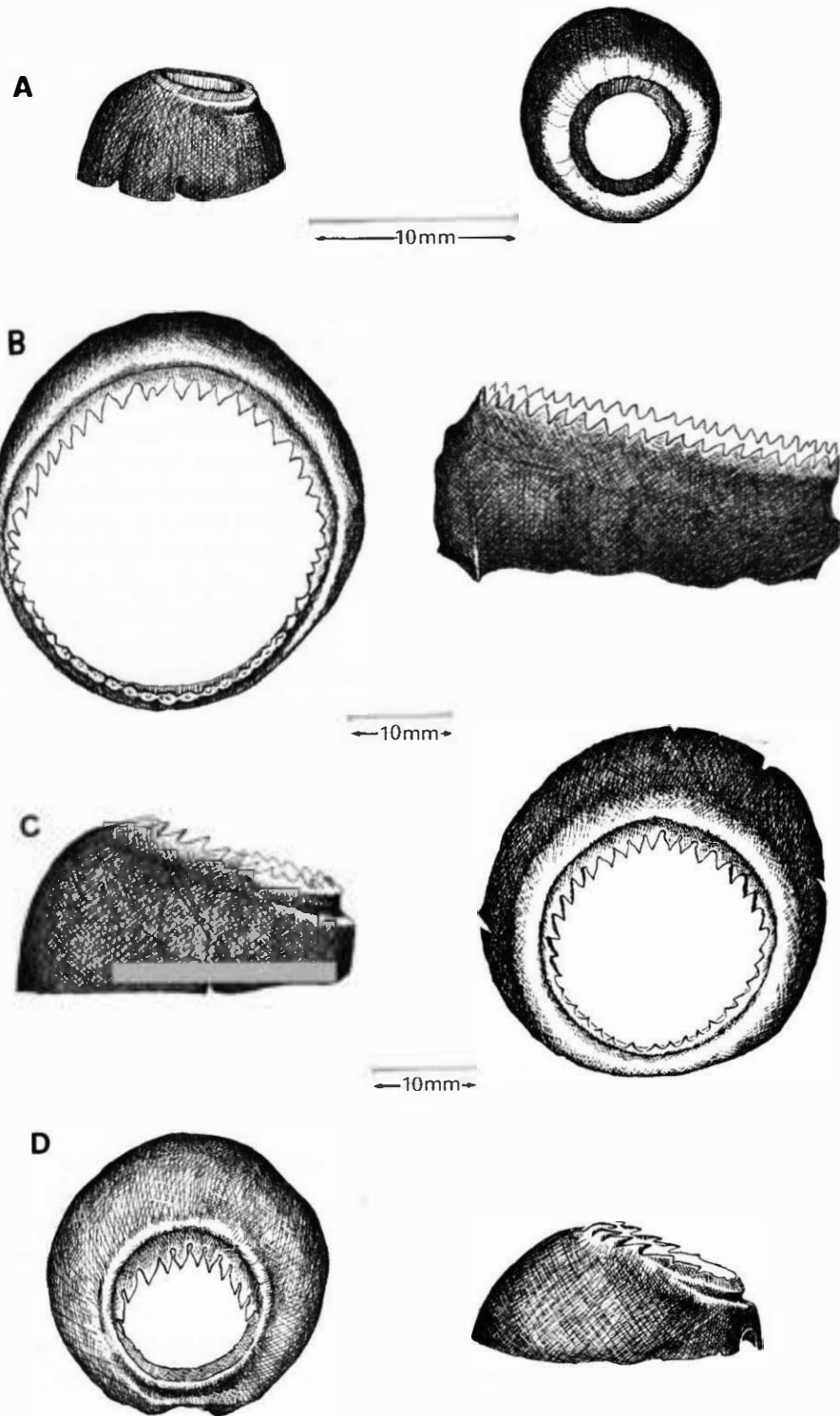
Fig. 23. A selection of suckers from Specimen 2, arm I. **A.** Small "sessile" first sucker. Note the lack of dentition, the lack of a "shoulder", and a wider curved "collar". **B.** The largest sucker, with sharp, regularly spaced teeth, a prominent "shoulder", and a narrow vertical irregular "collar". **C.** Sucker from mid-region of arm. Note the change in the orientation of teeth and lumen. The "shoulder" is prominent only proximally, and the "collar" is wider, smoother, and more curved distally. **D.** Sucker from distal portion of arm. Note the reduction in the number of teeth and an increase in their relative size on the distal part of the ring. Note the notch in the "collar" edge.

between arm IV and the other three arms is obscured (i.e., 37–59 teeth for arms I–III then substantially overlapping the 32–48 teeth range for arm IV).

Sucker Ring and Tooth Shape and Size

In general, the first few sucker rings on arms I–III are regularly round, with sides of almost even height all round. The teeth are triangular or peg-shaped, and are regular, occurring around the entire rim. The teeth are slightly smaller and more crowded on the adoral (proximal) edge. There is a marked constriction like a cinch creating a "shoulder" around the rim just below the base of the teeth and this "shoulder" is more pronounced and thickened proximally. The entire outer edge of the sucker ring bears fine vertical folds and a slightly irregular, or frilly internal edge. However, at this stage the teeth can also be very variable in shape, irregular, and range from separate peg-like structures, through spade-shaped structures to triangular shapes (Fig. 22).

With progression along the arm the form of the sucker ring changes. The teeth on the distal edge become larger and more triangular, those on the proximal edge become smaller and their bases begin to fuse, and orientation of the teeth is more oblique, towards the lumen of the ring. The "shoulder" becomes smoother distally and the distal sides of the sucker ring increase in height while becoming smoother and more rounded in shape. The proximal region becomes relatively narrower and the "shoulder" retains the ledge-like effect, but a broad notch develops in the proximal edge of the ring. At this stage the distal teeth are usually a flattened triangular shape, often with bevelled edges like a dagger. The proximal teeth may be limited to small irregular points projecting from a rim appearing to consist of semifused bases of teeth.

Still further along the arm, the sucker ring becomes increasingly globose, the distal side of the ring almost turns inwards again at the bottom, and the proximal edge remains narrow but also becomes smoother and more rounded. All that remains of the "shoulder" is a more opaque thickened region immediately below the teeth. The teeth become larger and fewer in number and are restricted to the distalmost edge and corners of the lumen, which has become quadrangular or horseshoe-shaped. The proximal edge has fused into a smooth ridge, or a series of rectangular plates or lobes.

This process of reorientation of teeth and lumen, curvature of the distal sucker rim, and fusion of the teeth on the proximal and lateral edges continues until there are only 2–3 teeth remaining in an otherwise smooth rim.

This general pattern above is considerably modified when there are regenerated suckers present. These suckers are often atypical, resembling those of the first suckers on arms III and IV, in their dentition and can usually be detected by their smaller size. Another source of difference arises when the sucker rings appear to have broken in life and undergone a repair process. These rings appear more "calcified" and are thickened around the region of the breaks. Sections of teeth are missing from around the rim. This was particularly evident in Specimen 2. Broken or misaligned teeth are also common. One atypical example had two suckers attached to one pedicel (Specimen 4, arm IV sucker 18). The degree of "wear and tear" on the suckers varied enormously between individuals. It was also curious how often fine grit was found deep inside the suckers of trawl-caught benthic specimens.

Individual patterns of sucker-ring transformation may be traced in the Sucker Ring Tables appended to the individual specimen descriptions held at NIWA.

In general, arm IV sucker rings are more globular, have a reduced number of teeth, have a more oblique lumen, increased height of the distal rim, and show earlier fusion of teeth on the proximal rim than occurs on sucker rings from the first three arms. The number of teeth on arm IV suckers reduces rapidly after sucker 15. On the first three arms the same range of tooth shapes occurs and the same fusion patterns and progression occur, though at a slower rate. Generalisation from individual specimens is still somewhat problematical (Table 16). An arbitrary number of teeth (10) was chosen and the sucker number at which this number is attained has been assessed. As can be seen, the result is highly variable. The full extent of the variation is tabulated in spreadsheets held at NIWA.

INTERNAL ORGANS

For many of the trawl-caught specimens, considerable damage was caused to the internal organs by spiny fish forced down into the mantle cavities. The stranded or floating and moribund specimens, although all recovered promptly, experienced several additional hours at ambient temperature, resulting in a visible difference to the colour and condition of delicate organs such as the heart, ovary, and gills. Where available, the size of organs in individual specimens is listed in the individual specimen descriptions held at NIWA. The internal organs were covered with a thick, almost muscular membrane with the same dark brown/red colouration as the inner mantle wall (Fig. 24).

Table 16. Sucker range at which the dentition on the sucker ring has reduced to 10 teeth distally and exhibits a fused proximal rim.

Specimen	arm I	arm II	arm III	arm IV
3	40-50	50-60	60	30
4	41	50	>40	30-40
5	40-50	>>26	>>39	40-50
6	?	?	>>25	30-40
7	43-47	>>29	?	41
8	>>29	-	-	>48
11	?40-50	?25 -60	>25	30-50
12	?	?	?	30
14	40	50-60	50-60	20-25
16	42-57	59	61	40-50

Table 17. Combined length of the ink sac and duct (mm).

Specimen	ML	sac + duct
2	1930	+725
3	1770	470
4	1825	500
5	930	465
6	1560	450
7	2020	600
9	1260	375
10	1830	530
11	1720	450
12	1690	550
14	2140	510

Ink Sac and Duct

The ink sac is very elongate, with the separation into ink sac and duct not easily determined externally. The posterior end of the ink sac is usually "free" of other membranes and organs, but the majority of the anterior length is associated with the rectum. Where the ink duct is visible it is either lateral or ventral to the rectum, not dorsal as is usual for squids (Nesis 1982). At the posterior end of the ink sac is an oval or hemispherical white gland of unknown function. This gland is present in all specimens and varies in length from 11 mm (Specimen 5), through 20 mm (Specimen 9) to 47 mm (Specimen 3).

The anterior of the ink duct opens within the rectum just posterior to the anus, i.e., at the base of the anal flaps. In Specimen 3 the ink duct opening was flanked by two distinct (?nephridial) pores. The ink sac varies in colour from white and blue-white through blue-black to black. The colour may depend upon the amount of ink remaining in the sac or the thickness of the ink sac wall. The ink itself also varies in colour from black (Specimens 7, 10, 11, 12) to blue-black (Specimens 9, 6), through green-brown or green-black (Specimens 2, 3, 4, 5) to yellowish-green (Specimen 14).

Data on the length of the free portion, sac, and duct are listed in the individual specimen descriptions held at NIWA. The length of the sac and duct combined was the more reliable measure and is given in Table 17. The ink sac and duct together range from one-quarter to half of the mantle length. The length of the ink sac was disproportionately longer in the smallest Specimen 5.

Digestive System

The rectum terminates in two semilunar flaps, one dorsal and one ventral. These are separated laterally by bilobed papillae (Fig. 25B). This was an invariable feature in the present specimens. The anal area was swollen with respect to the diameter of the rectum. The stomach is a grey structure (sometimes brown) occupying at least half the length of the mantle cavity, elongate, and pointed posteriorly. It often appears quite smooth and full, but when defrosted the contents are largely clear fluid, possibly seawater. The stomach is divided into two sections internally. The interior is very rugose, narrowing in the central region, with the anterior part thicker-walled. The stomach is lined with a delicate, transparent and extensively folded chitinous inner skin. In some specimens the rugae were tinged bright red. In all cases the stomach contents were minimal. Very little flesh remained, and the identifiable fragments were restricted to a few scales, fin rays, hooks, and broken beak and gladii pieces.

The caecum was a small organ in relation to the stomach. The shape was ovoid with 4-5 spiral striated bands visible on the exterior. The colour ranged from orange through to pink.

The digestive gland is large and oval, anterior to the stomach, and extends well up into the neck region. The anterior extent is not readily visible. The colour of the digestive gland is variable, generally orange-brown with an iridescent sheen, but sometimes light brown, beige, or pale apricot. The gland measured up to 780 mm long (Specimen 7). The digestive gland appeared to be largely absent in Specimen 11 where only 2 yellow-brown lobes about 100 mm in width were present at the anterior extent of the mantle cavity.
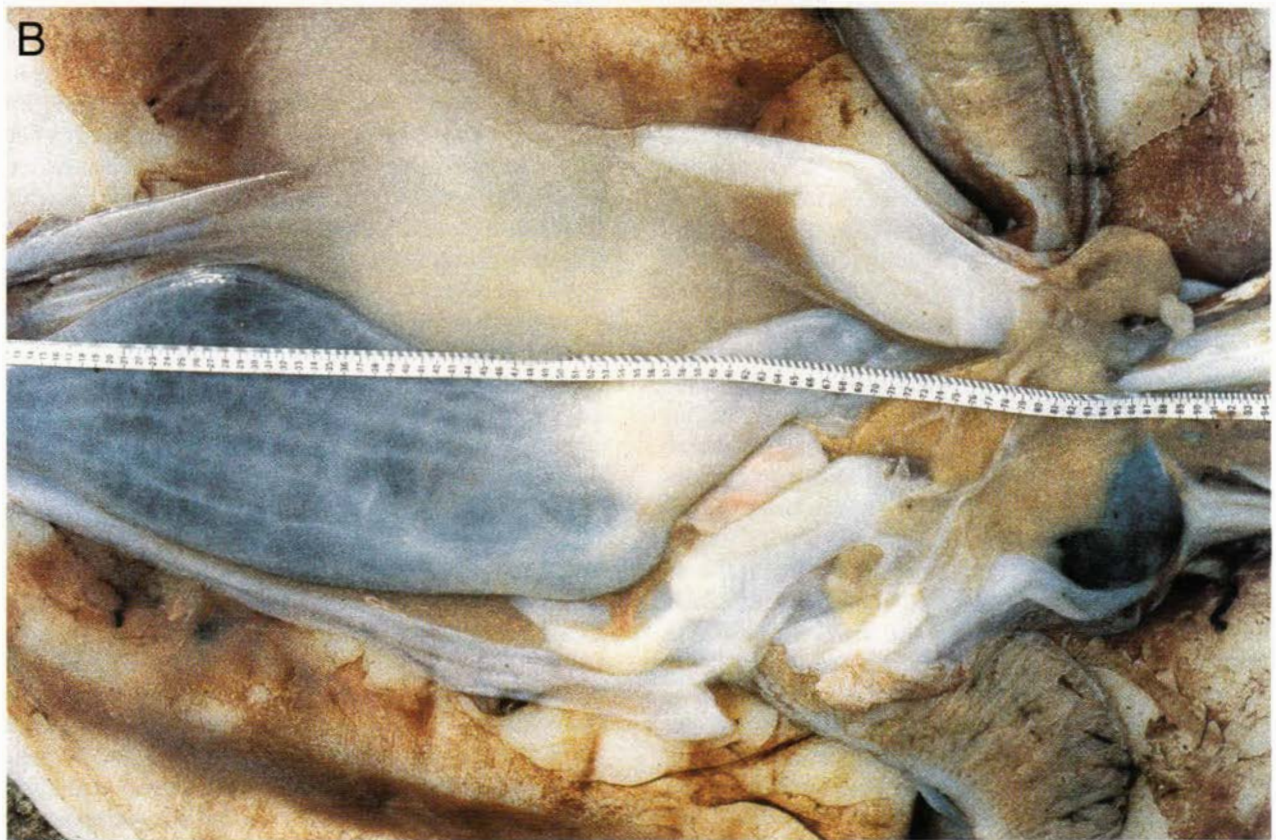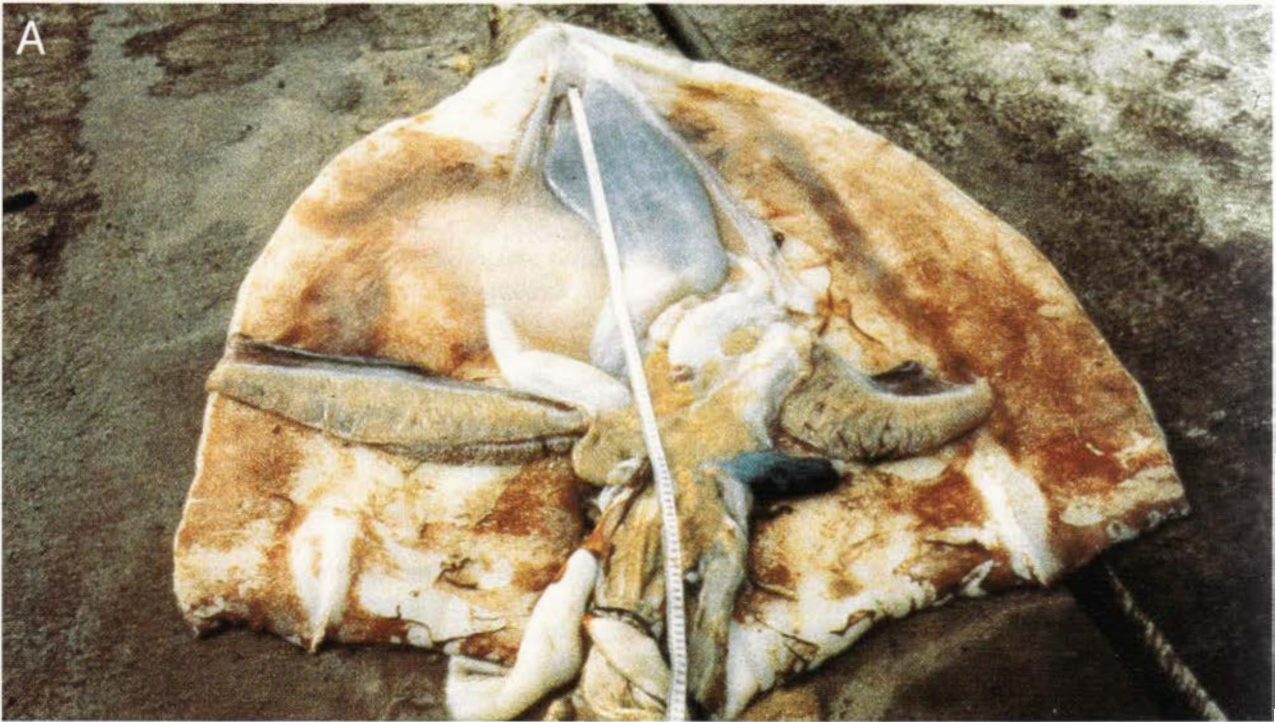
Fig. 24. **A.** Internal organs of Specimen 6 (immature female). **B.** Reproductive organs of Specimen 6.

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There was a grape-like, diffuse organ in association with the anterior extent of the stomach and extending anteriorly alongside the digestive gland. It was not possible to establish the presence or direction of ducts but it is thought that this organ was the "pancreas" or digestive gland appendages. The structure is present in all specimens, and ranges in colour from beige (Specimens 7, 9, 11, 12,) to pink (Specimens 3, 4, 10, 14), yellow (Specimen 6), and orange (Specimen 1).

Gills

The gill lamellae (Figs 24A, 25C, D) were in sufficiently good condition to make accurate counts. In general, the right gill lamellae were counted. The number of lamellae on a demibranch varies from 66 to 71, with the majority of specimens possessing either 69 or 70 lamellae. In very fresh specimens the lamellae were pink or blue-grey. In some specimens the brown-red colour of the mantle lining extended onto the supporting structures of the gill. Oval accessory branchial hearts were noted at the base of the gill, particularly in Specimens 3, 4, and 5, and the presence of a white branchial appendage was also noted.

The gills maintain a constant width for most of their length and taper abruptly at the outer tip, with the free edge turning toward the inner mantle wall. However, in Specimen 9 (one of the males) the gills taper very gradually. Some variability occurs in the proximity of the gill tip to the mantle aperture.

Heart and Reproductive Organs

The heart is located midventrally, is triangular, narrower posteriorly, and has a delicate semi-transparent appearance. The colour of the heart is very variable, predominantly beige, but with tinges of either pink, orange, green, or yellow. The length ranged from 100 to 200 mm.

The ovary (Fig. 24B) is a soft organ occupying the posterior of the mantle cavity. The shape ranges from triangular to oval and takes up 20–30% of mantle length. The colour is white or yellowish-beige and the texture is occasionally somewhat filamentous. Where the organ was sufficiently well developed, the eggs were examined. They are oval, approximately 1–1.5 mm long and range in colour from white-transparent to slightly yellowish.

The nidamental glands (Fig. 25C) are white, paired, elongate organs, pointed at both ends, and situated close to each other. They are sometimes partially or completely fused along the longitudinal axis. Each individual gland is also bilobed, as if sliced in the transverse plane, lying like two leaves on top of each other. Internal surfaces are covered with very fine lamellae (Specimen 6). The nidamental glands are not large, with a maximum length of 405 mm in Specimen 4 (24.6% of ML). The nidamental glands in Specimen 11 are small, pink, unusually firm, and deformed (?possibly diseased) (Fig. 25A).

The oviducts and accessory glands were variable in size, appearance, and presence. The most usual arrangement consisted of a pair of double oval or pear-shaped structures situated posterior to the nidamental glands. The anterior lobe was presumed to be the accessory nidamental (or oviducal) gland, and the posterior to be the oviduct (since this structure was coiled and sausage-like in Specimen 3).

Specimens 8 and 9 were male, but only the internal organs from Specimen 9 were received (Fig. 25D). The photograph of Specimen 8 indicates that a slender penis extends beyond the mantle by at least 300–400 mm. The male reproductive apparatus of Specimen 9 appears smaller by comparison. The testis is a very indistinct organ and a presumed vas deferens is thickened and irregular in shape. In Specimen 9, Needham's sac has burst and the spermatophoric gland is coiled and lobate with associated anterior and posterior diverticula. There is a well-developed elongate penis, which is, however, still contained within the mantle cavity. A large number of spermatophores and spermatophore packets are loose in the mantle cavity. A detailed description of the structure of the spermatophore has not been attempted here (see Knudsen 1957).

STOMACH CONTENTS

The stomachs of many of the specimens are either missing, damaged, or completely empty. Identifications of fragments found in the stomachs are listed below.

The Specimen 2 stomach contained lumps of flesh which could not be distinguished in any way, as well as some scales of *Caelorinchus fasciatus* and *Caelorinchus oliverianus* (rattail fishes, family Macrouridae) (Dr P. McMillan, NIWA, pers. comm.). Scales from one other unidentified fish species were also present. The fluid from the stomach also contained an unidentifiable crustacean fragment and a collection of copepods: *Centropages aucklandicus*, *Calanus australis*, *Euchaeta* sp., *Calanoides* "*carinatus*", and *Neocalanus tonsus*.

The stomach of Specimen 3 contained:
- the posterior portion of a tail of *Caelorinchus oliverianus*
- scales of *C. oliverianus* and *C. fasciatus*
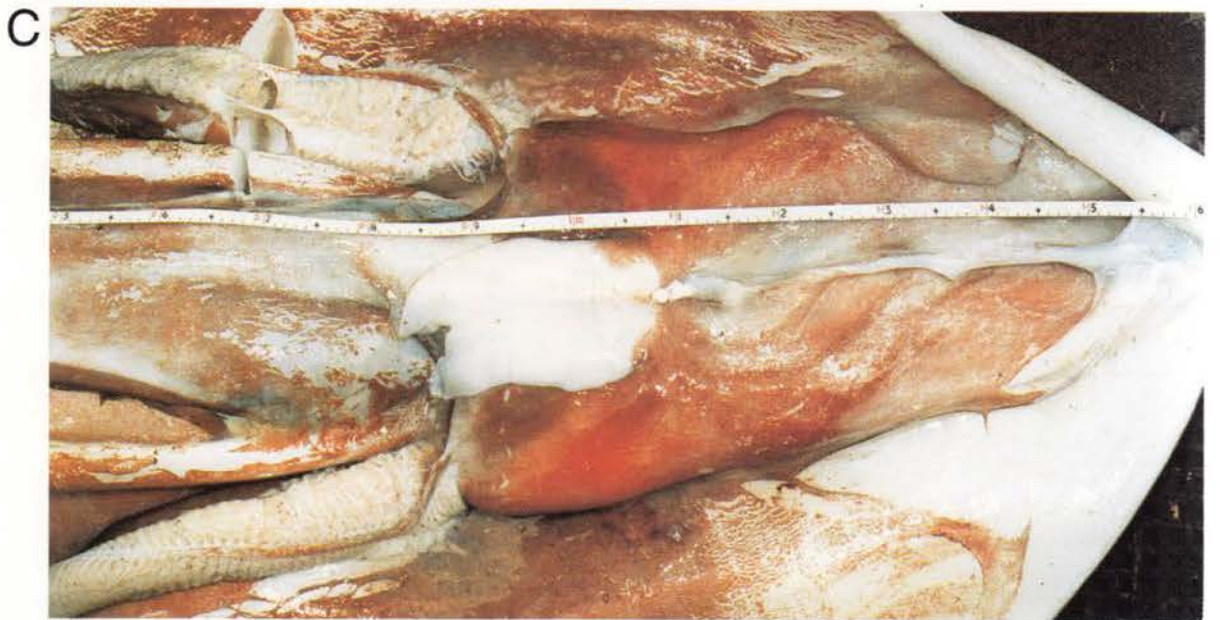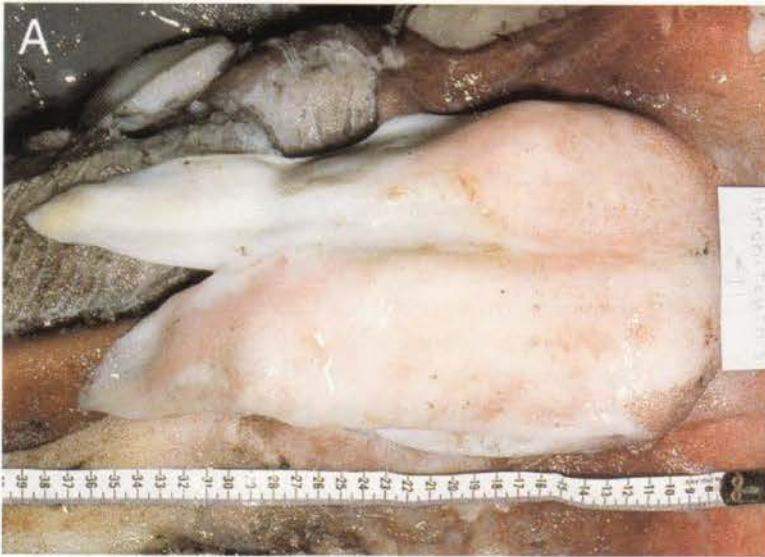
- an unidentified eyelens
- assorted small crustaceans, mainly copepods (Dr Janet Grieve, NIWA, pers. comm.).

The stomach of Specimen 4 was empty apart from a few copepods and a euphausiid.

The stomach of Specimen 5 contained:
- fish scales: possibly an orange roughy (*Hoplostethus atlanticus*)
- pieces of the skull of a macrourid fish
- 3 unidentified eyelenses
- radula, hooks, and sucker rings consistent with *Moroteuthis ingens*
- numerous gladii fragments and some presumed squid flesh.

The stomach of Specimen 6 contained a small amount of material. An approximate breakdown indicated:
- 90% consisted of broken squid gladii fragments
- the remaining material consisted of 20% slightly digested, 50% digested, 30% well-digested squid flesh
- one unidentified squid arm hook, possibly from *Moroteuthis ingens*.

Stomach contents of Specimen 7 consisted of 6–8 litres of fluid. The remains were well digested, with very few or almost no chunks of flesh. Flesh consistency resembled squid flesh and had the characteristic squid flesh shape, i.e., ovoid pieces, without noticeable fibres, in colours ranging through pink-grey-white-black. There were 3 upper and 3 lower beaks in good condition. Mike Imber (Department of Conservation) and Rob Mattlin (pers. comm.) independently identified the beaks as belonging to *Nototodarus sloanii*. Additional squid gladii fragments and portions of radulae were present as well as an assortment of fish scales, bones, and fin rays. The fish remains were tentatively identified as :
Lepidorhynchus ?denticulatus, Caelorinchus sp. scales, an otolith from *Caelorinchus* sp., 10 unidentified eye lenses.
A parasite found in the gut wall was presumed to be an early cestode stage.

The stomach of Specimen 9 appeared full but contained only a few unidentifiable fragments.

Specimen 12 stomach contents contained:
- 1 small squid beak - unidentified

- assorted pieces of gladii representing two different types of squid
- 2 spermatophores
- unidentifiable fish bones
- 1 fish otolith (not *Caelorinchus* sp.)
- scales from small (probably 10–15 cm TL) specimens of *Caelorinchus oliverianus* and *Caelorinchus sp.* (Type C).

Identifiable fragments from Specimen 16 stomach consisted of only two fish scales. Dr P. MacMillan (NIWA, pers. comm.) believed the scales belonged to rattail fishes (Macrouridae), probably *Kuronezumia leonis*. They were certainly not of the genus *Caelorinchus*.

The combined information on dietary items found in the present specimens is as follows:

Crustacea	chelae of unidentified crustaceans
	Copepoda (five species)
Squids	*Moroteuthis ingens*
	Nototodarus sloanii
Fish	*Caelorinchus oliverianus*
	C. fasciatus
	C. sp. (Type C)
	C. sp.
	?Kuronezumia ?leonis
	Lepidorhynchus ?denticulatus
	unidentified Macrouridae
	?Hoplostethus atlanticus

FLESH CHARACTERISTICS

Some opportunistic heavy-metal analyses were carried out on flesh from Specimens 4 and 5 by Wallaceville Animal Research Centre (Fenaughty *et al.* 1988). The results are extracted and reproduced in Table 18.

Comparison with New Zealand *Nototodarus* spp. (Ommastrephidae)

Mercury levels recorded for the *Architeuthis* mantle are of the same order of magnitude as for the ommastrephid squids *Nototodarus gouldi* and *N. sloanii* (0.08 and 0.025 mg/kg respectively (Fenaughty *et al.* 1988). Corroborating mercury analyses for *Nototodarus* spp. are published in van den Broek *et al.* (1981).

Fig. 25. (opposite) **A.** Reproductive organs of Specimen 11 (diseased?). **B.** Anal flaps and papillae of Specimen 16. **C.** Mantle interior of Specimen 16 showing the immature nidamental glands (white). **D.** Mantle interior of Specimen 9 showing male reproductive organs.

Table 18. Heavy-metal analysis of *Architeuthis* tissues from Specimens 4 and 5. All lead was below detectable levels. All figures are in ppm on a wet-weight basis.

Specimen	tissue	mercury	copper	zinc	lead	cadmium	selenium
4	mantle	0.07	0.08	11.7	*	0.05	0.22
	tentacle	0.08	2.8	9.7	*	0 .004	0.14
	gonad	0.06	2.0	12.8	*	0.04	1.14
5	mantle	0.07	0.8	12.9	*	0.09	0.12
	tentacle	0.09	0.8	13.9	*	0.06	0.18
	gonad	0.06	2.2	11.2	*	0.06	0.62
	digestive gland	0.07	61.9	23.1	*	8.6	2.52

On very limited data, cadmium levels in the digestive gland of Specimen 5 are an order of magnitude lower than in *Nototodarus* spp. (8.6 vs 78.10 mg/kg). Cadmium levels in *Nototodarus* gonad and mantle are also higher than those of *Architeuthis sp.* by a factor of about 10. Copper levels in the mantle of both *Architeuthis* sp. and *Nototodarus* spp. are comparable, but gonad and digestive gland levels in *Nototodarus* spp. are higher by a factor of 10. Zinc levels in the *Architeuthis* mantle are comparable to those of *Nototodarus* spp., but *Architeuthis* gonad levels are slightly lower. The sole digestive gland measure for *Architeuthis* indicates a zinc level of an order of magnitude less than for *Nototodarus* spp. *Architeuthis* lead levels were below detectable levels for mantle, tentacle, gonad, and digestive gland. Comparable figures for *Nototodarus* spp. were in the range of 0.02–0.15 mg/kg. Comparative selenium values were not available for *Nototodarus* spp.

MULTI-DIMENSIONAL SCALING

Results and Interpretation

A triangular Bray-Curtis similarity matrix (Bray & Curtis 1957) was constructed by PRIMER using both untransformed (Table 19) and 4th root transformed body-index data. A hierarchical agglomeration clustering was then performed using similarity matrices based on both untransformed (Fig. 26A) and 4th root transformed data. Clustering was carried out using single-linkage, complete-linkage, and group-average methods.

4th root transformed data led to extreme compression of the level of similarity and minimal differentiation between clusters. MDS ordination plots based on these matrices also lacked any defined groups and were accompanied by relatively high stress factor (0.12). The correspondence between the MDS

and cluster dendrogram was not good.

Untransformed data produced more clearly defined clusters which related more closely to the 2-dimensional arrangement and the corresponding MDS plots (compare relative proximity of specimens in Figs 26A, B). The stress value of the MDS plots was also lower (0.08).

As predicted in Clarke and Warwick (1994), applying the single linkage methodology led to ill-defined clustering with many single stepwise additions to the clusters. Complete-linkage and group-average methodologies resulted in better-defined clusters with identical membership. The correspondence between these latter two processes and the MDS plot was high, with only Specimen 2 varying in relative position.

The MDS ordination was run with a series of random numbers of starts from 6 to 30, to determine variation in the stress factor. The stress factor did not vary from 0.08. The programme steps were run again for another data series excluding several specimens (Figs 26C, D). The rationale for eliminating three specimens was degree of completeness, i.e., Specimen 5 was too small and lacked fins; Specimen 9 was the sole male and lacked arms; Specimen 7 had missing data.

When Specimens 5, 7, and 9 were removed from the clustering and MDS, some changes occurred. Again, Specimen 2 changed its relative position in the cluster dendrogram, but did not move substantially in the MDS plot. Although the cluster process grouped different specimens at the first four steps, the higher-order cluster corresponded exactly with the earlier analysis, particularly also in leaving specimens 1, 14, 6, and 12 less strongly linked to the other specimens (Fig. 26C). This distribution is confirmed by the MSD plot (Fig. 26D).

The MDS plot of the reduced dataset leaves all the specimens with the same immediate "neighbours" as for the earlier analysis, but alters the degree of proximity.

Table 19. Bray-Curtis Similarity Matrix. Untransformed body index data on specimens listed in column 1.

S1	S1	S2	S3	S4	S5	S6	S7	S9	S10	S11	S12	S14
S2	94.74											
S3	94.77	95.54										
S4	96.58	95.57	95.93									
S5	89.03	89.97	92.75	90.37								
S6	93.17	94.62	93.29	93.24	90.62							
S7	91.15	94.56	92.05	92.34	86.16	90.34						
S9	93.50	95.01	94.68	95.05	90.18	94.47	92.13					
S10	95.06	96.26	94.43	95.91	89.23	94.59	94.16	94.97				
S11	96.61	94.53	95.62	96.38	90.13	92.96	92.80	93.29	94.85			
S12	91.61	92.28	95.71	92.68	95.18	92.54	88.46	92.83	91.19	91.73		
S14	94.07	94.50	93.82	94.92	87.56	91.77	95.46	95.09	96.37	94.97	90.21	
S16	95.44	96.23	96.90	95.90	92.71	95.32	92.734	96.07	95.48	95.59	95.02	94.14

for the earlier analysis, but alters the degree of proximity.

In combining the results of the two runs certain consistencies emerge. Specimens 5, 7, and 9 were on the fringes of the group in the first analysis, as were Specimens 6 and 12.

In the second analysis, Specimens 5, 7, and 9 were removed from the analysis for reasons outlined above. The resulting analysis still continued to group the main bulk of the specimens, and continued to place Specimens 6 and 12 on the outer edges. However, the second analysis resulted in Specimens 1 and 14 becoming more distant from the main group (Specimens 2, 3, 4, 10, 11, 16).

The MDS plot stress value is also 0.08 in the second analysis. This places it in the < 0.1 level, which Clarke and Warwick (1994) consider "corresponds to a good ordination with no real prospect of a misleading interpretation; higher dimensional solutions will not add any additional information about the *overall* structure (though the fine structure of any compact groups may bear closer examination)".

Given that the OTUs in the present study are individuals, there is little to be gained from further analysis. There are no clear geographic, ontological, or morphological factors linking these specimens.

RE-EXAMINATION OF EARLIER NEW ZEALAND *ARCHITEUTHIS* MATERIAL

Makara Specimen

The Dell (1970) Makara specimen (Museum of New Zealand M10,000) was reexamined in 1983 by the present author. At that time it had been stored continuously since 1956 in formaldehyde. Where possible, original parameters of the Dell specimen were re-measured to check for standardisation of measures and effects of preservation. The specimen has since been transferred to 70% isopropyl alcohol and will be expected to show further changes in dimensions as a consequence of that transferral. The specimen was described by Dell (1970) and only a selection of additional features are reported on here.

Table 20. Changes in dimension with storage and preservation in Dell's 1956 Makara specimen.

Dell 1956 Specimen (Dell 1970)	Original measurements (mm)	Remeasure (1983) (mm)	Change in measure
ML	1829	1705	- 6.8 %
VML	1727	1435	- 16.9 %
width of mantle	457 (when collected)	570	+ 24.7 %
length fins	686	630	- 8.2 %
width across fins	572	500	- 12.6 %
width single fin	241	255	+ 5.8 %
length of head	292	280	- 4.1 %
funnel length	356	283	- 20.5 %

It is not clear whether all the measures published by Dell (1970) were based on the fresh specimen (obtained in 1956) or made after a period of preservation. The reference in Dell (1970) to a change in mantle width, and the lack of any trace of sucker rings suggests examination was after preservation. The differences in body measures over 27 years are large and emphasise the inadvisability of comparing specimens which have different handling or fixation histories (see also Andriguetto & Haimovichi 1988).

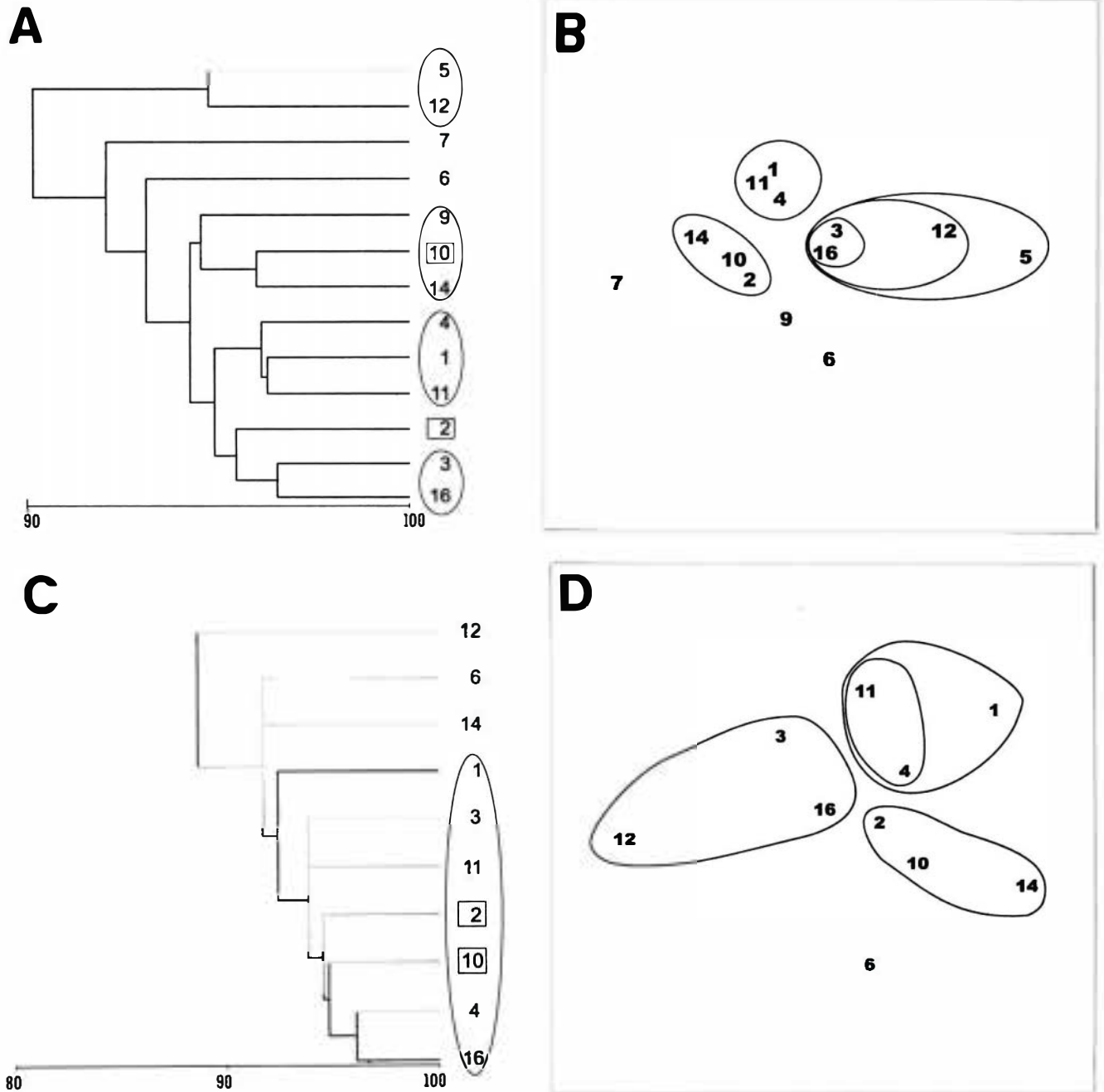The Dell specimen ventral mantle length (VML) was originally only 100 mm shorter than the dorsal

Fig. 26. A. Hierarchical Agglomerative Clustering carried out with group-average method on standardised but untransformed data (selected body indices). Specimen numbers are indicated at right. Bray-Curtis Similarity index % on X axis. **B.** Multi-dimensional scaling plot (Clarke & Warwick 1994), based on a Bray-Curtis Similarity matrix (Table 19). **C.** Hierarchical Agglomerative Clustering carried out with group average method on standardised but untransformed data (selected body indices). Specimen numbers are indicated at right. Bray-Curtis Similarity index % on X axis. Specimens 5, 7, and 9 have been omitted, altering the relative affinities of Specimens 2 and 10 when compared with A (Specimens indicated by square box). **D.** Multi-dimensional scaling plot (Clarke & Warwick 1994), based on a Bray-Curtis Similarity matrix. Specimens 5, 7, and 9 have been omitted. Circles on the plot correspond to the spatial patterns identified in **B**.

measurement. The later (1983) measure indicates that the VML has become disproportionately shorter. There was a marked middorsal extension at the mantle-locking cartilage and the ventral margin was sculptured by the forward extension of the pallial connectives. The mantle aperture diameter was 510 mm. The greatest diameter of the mantle (570 mm) occurred at a point 600 mm from the anterior mantle edge, whereas Dell recorded the widest measure only a few inches posterior to the mantle aperture. The mantle diameter at the anterior fin insertion was 360 mm. Posterior to the fin insertion, the mantle was conical with a markedly thinner mantle wall.

The divergence between the anterior fin insertions was 80 mm. There was a small "free anterior lobe" of approximately 60 mm. This feature was bilaterally symmetrical and not associated with any damage to the fin attachment. The extreme posterior of the mantle had been lost but it is presumed that the fins extended as narrow keels to the extreme posterior of the mantle. The preserved fins are thin, but firm — almost muscular in texture.

There was an indication that there had been a thimble-shaped depression on the floor at the anterior of the funnel groove. Unfortunately, the funnel-groove region had been distorted during storage and the structure could not be more precisely determined, nor could a depth be assigned to it. There was, however, a loose finger-like flap of skin (like a glove finger) which could have been the evaginated skin lining of the "hole". The triangular ventral extensions of the nuchal fold were very reduced in comparison with the recent fresh specimens. There was some thickening in skin around the eyes. The anterior border had very granular skin and there were irregular thickenings at the posterior edge and lesser amounts of thickening above the eye. No eye sinus was evident. An "olfactory" papilla was present at the ventrolateral extent of the nuchal fold.

Measures of the funnel dimensions were made (in 1983) for future reference: length of the funnel-locking cartilage 195 mm; width of funnel valve 90 mm; distance of the funnel valve from funnel aperture 90 mm; distance of anterior cartilage to funnel aperture 250 mm; length of funnel medioventral 283 mm.

The presence or shape of swimming keels could not be determined with confidence because of considerable distortion of the arms during preservation. There was a short web between the first pair of arms, but arms I and II did not appear to have any keels on the remaining proximal portions. Arm III had one aboral keel, which developed at about 300 mm from the base of the arm. The sucker-bearing face of arm III was deeply grooved in association with prominent sucker bases. Arm IV was extremely quadrangular

in cross-section and had carried two structures which could be interpreted as aboral keels. The dorsal keel was deeper than the ventral keel. All oral faces of the arms carried papillae, although they were scattered and infrequent on arm I. Arm II carried more papillae than arm I, but fewer than either arms III or IV.

Dell noted the sizes of the suckers on the arms, particularly the small first suckers on arms I and II (3.5 mm, 4.5 mm respectively). Although the sucker rings had all dissolved or been lost, it was possible to carry out a sucker count on a standard distance of the proximal 500 mm of arm, measured from the first sucker. Arm I: 26 suckers; arm II: 29 suckers; arm III: 28 suckers; arm IV: 40 suckers.

Characteristics of the protective membranes are listed below.

- Arm I protective membrane height at 5th sucker, 18.8 mm.
- Arm II protective membrane height at 5th sucker, 18 mm.
- Arm III protective membrane better-developed than those of arm IV. Height at 5th sucker 19 mm. Arm III has the largest suckers of all the arms, few or no perforations in the protective membrane. Membranes not only higher but also thicker than for the other arms.
- Arm IV protective membranes short, weak, perforated. Perforations occur in the protective membranes directly alongside the sucker. Height of the protective membrane at 5th sucker is 13 mm. Dorsal and ventral membranes are similar. Strongly bilobed trabeculae originate from both sides of the sucker base.

Other Museum of New Zealand Material

In 1983, the Museum of New Zealand had an old, undated and unprovenanced display board with two gladii mounted on it. This board has subsequently disappeared although M125403 was on public display for a period before closure of the old museum. One gladius is labelled *Architeuthis kirkii* and is presumably from the holotype of *A. kirkii* C.W. Robson. The other is reputedly *Steenstrupia stockii* and presumably from the holotype of *A. stockii* (Kirk) (M125403). Both gladii share characteristics of the recent specimens and are described and compared below.

The "*S. stockii*" gladius is very dry and somewhat distorted. It appears to have a similar end cone and exhibits the slight flaring of the wings before the commencement of the cone as for specimens in the recent dataset. The "*A. kirkii*" end cone appears broken, smaller, or possibly not as well formed.

The "*S. stockii*" gladius is from a reputedly

3378 mm body (including the head and possibly the arms) but the gladius measures only approximately 1920 mm. The "*A. kirkii*" gladius is from a 1981 mm body but measures approximately 1810 mm. If the reported body size of "*S. stockii*" is correct, then the gladius is proportionately shorter than has been reported for any other giant squid.

The "*S. stockii*" gladius had a maximum width of 185 mm at a point 630 mm from the anterior while the "*A. kirkii*" maximum width was 160 mm at a point 700 mm from the anterior. The position and relative width of the gladii are within the range exhibited by the present data-set (held at NIWA)

"*A. kirkii*" (although smaller) has a proportionately very much wider clear portion, or rachis, visible in the gladius vane. The width of the clear zone increases towards the anterior of the gladius. Close to the anterior tip of the gladius in "*A. kirkii*", the central clear portion is 25 mm wide. In the equivalent location on the "*S. stockii*" gladius, the clear portion is approximately 18 mm wide.

The origin of the "*A. kirkii*" lateral wings is 525 mm from the posterior end of the gladius, while the "*S. stockii*" lateral wings start 540 mm from the posterior end (possibly a little further, since there is some damage to the extreme posterior). The width of the "*S. stockii*" gladius at the anterior origin of the lateral wing is approximately 85 mm, but it is difficult to be more accurate because of the wrinkly nature of the gladius at that point. The width of the "*A. kirkii*" gladius at the anterior origin of the lateral wing is 80 mm. The maximum width of the lateral wing is near the posterior end of the gladius and is similar on both gladii. The width is approximately 15 mm.

In both gladii the central ridge narrows and develops a slight dorsal keel posteriorly.

M125406: possibly from Holotype of *A. kirkii* Robson
See beaks (p. 40) and gladius described above.

M125405: possibly from Holotype of *Architeuthis stockii* (Kirk) 1882
See beaks (p. 40) and gladius described above.

M77446: Canterbury Bight Specimen

The material consists of one skinned club in very damaged condition. Only part of the carpus remains and the club has been severed part-way through the manus. The carpus has been cut off at a point where there are 4 smooth suckers across the stalk. There are 41 smooth-edged suckers present but the skin is too shrivelled to detect any "warts". The smooth carpal suckers range in size from 3.3 to 4.7 mm. There are approximately 22 small toothed suckers on the carpus immediately before the commencement of the manus. The small toothed suckers at the base of the manus increase in size from 4.4 to 9.4 mm.

The lateral manal suckers are small, and the suckers on the medial rows are larger. There are too many suckers missing to determine whether one medial manal row is larger than the other. The diameter of the largest remaining sucker ring is 28.8 mm; however, the sucker is so shrunken and thin that the sucker and the sucker-ring measurements are virtually the same. The largest sucker on the marginal rows of the manus is 13.0 mm

The Museum has a poor-quality photo of the entire specimen but it is difficult to identify the relative positions of the arms. Those arms presumed to be arms IV do not appear to have smaller suckers than the other arms. The mantle shape at the anterior end is also unclear.

Red Rocks Specimen

The record for this specimen consists of photographs and a beak (see p. 40). The dried gladius could not be located. The specimen reputedly had a "total length" of 1690 mm, but it is unclear how this measure was taken.

DISCUSSION OF MORPHOLOGY AND ANATOMY

BODY SHAPE

Pfeffer (1912) in his monographical treatment recognised two body shapes: those widest at the anterior end of the mantle, and those widest roughly in the middle of the mantle. He also recognised that the stoutness of the bodies varied: narrower in the North American species (*A. dux, A. harveyi, A. princeps*), and wider for *Architeuthis verrilli* (Kirk, 1882).

It is clear from Figure 2 that both forms described by Pfeffer (1912) are found in the New Zealand region. Indeed, almost the entire range of relative body widths and degree of taper of the posterior mantle are represented. This indicates that body shape over a very wide range cannot be reliably used to indicate geographic or presumed specific differences. The present data-set indicates that the mantle shape may be:

- conical
- anteriorly cylindrical and then conical
- expanded slightly from the mantle aperture and then taper.

There is a suggestion that the younger or smaller specimens are more likely to have a conical mantle form (Pfeffer 1912; Sasaki 1929; Roper & Young 1972; Clarke 1980; Toll & Hess 1981; Specimen 5, this study). Other authors have suggested that the mantle is widest half-way along its length (e.g., Roeleveld & Lipinski 1991) but these affirmations need to be based on circumference measures to have validity. The present author was several times mistaken when judging the point of greatest mantle width by eye.

Body-wall thickness and sculpture of the mantle aperture have been recorded by several authors (e.g., Clarke 1980; Aldrich 1991). Again, the present data-set suggests that body-wall thickness is either a feature of individual variability or a secondary effect of handling and fluid loss. The sculpture of the mantle aperture is a remarkably constant feature (Pfeffer 1912; Sasaki 1929; Clarke 1980; Roeleveld & Lipinski 1991) and is unlikely to assume taxonomic significance. The potential for distortion is high and, as has been observed in the present study, the degree of fluid loss and thickness of the mantle wall may contribute to the degree of definition of the sculptural features. The pallial and nuchal cartilages and the associated mantle connectives are entirely unremarkable, differing between specimens in only minor ways.

Robson (1933) proposed body shape as a specific character when erecting *A. clarkei*. He identified the mantle aperture as being only a little narrower than the maximum width of the mantle and thus believed that it differed from the descriptions of *A. princeps* and possibly *A. harveyi*. He also considered that the posterior mantle narrowed much more abruptly than in *A. princeps* and that the mantle was broader than that of *A. harveyi*. In light of the variation in the current data-set (Fig. 2) such differences can no longer be considered significant.

FINS

There is a long-standing argument concerning *Architeuthis* fins and whether the form of the fin described by Verrill (1882b) for *A. princeps* and *A. harveyi* is legitimate, or whether it represents an artefact or damage. Since overall variability in the genus is important in this paper, I will deal with the question in some detail. Although most authors include an opinion about this feature, most have not justified their views and most, other than Frost (1934), have not referred back to Verrill's description of the original material.

Verrill (e.g., 1879, 1882b) published excellent, detailed descriptions and illustrations of the arm and tentacular armature, the pharyngeal teeth, the radula, the beak etc. It is easy to form the impression that he had access to entire specimens and had presumably applied the same degree of care and detailed observation to other portions of the animal. He did illustrate the entire animals including the fin shapes. However, despite publishing records of over 25 specimens, most reports of the measures and shapes were second-hand and of questionable accuracy. Verrill's description of *A. harveyi* was based on only one specimen with fins, and, by his own admission, it was badly mutilated (Squid no. 5 from Logie Bay). From Verrill's table (1882b: p. 232) it appears that there was only ever one set of fin measures for any specimen of *A. harveyi* (the original description by Kent was based on a tentacle club). Verrill mentions the fins among the remaining preserved parts to which he eventually gained access, but the reconstruction of the body shape for the published figures was based heavily on the photographs (p. 219) and other species.

Architeuthis princeps was based on beaks (Verrill 1875). Subsequently Verrill (1877) assigned Squid Record no. 14, the Catalina, Trinity Bay Specimen, to *A. princeps*, but again the material was "somewhat mutilated, and not in a very good state of preservation when received ...". Verrill's justification for differentiating *A. princeps* was based on aspects of the arms and suckers (see relevant section) and on the fin being "broader and somewhat less acutely pointed ...". However, it is ambiguous in Verrill's text how much of the fin shape was based on the material before him, or interpreted in the light of the eyewitness reports.

Verrill's footnote (p. 235) indicates that he corresponded with Steenstrup, "from whom I learn that the caudal fin in his species does not agree with that of the species here described" ... but it is apparent from the text that he believed that the sucker arrangement and arm characteristics were more likely to be of specific importance. It appears not to have occurred to Verrill that the fin attachments might have been damaged. Resolution of this matter is now impossible, since the parts that were preserved had deteriorated badly both before and after preservation, even during the period of Verrill's examination of the material.

The only other author to lend support to the fin shape described by Verrill is Frost (1934, 1936). Frost (1934) described her Dildo specimen as having a sagittate fin. She reported that "through much handling, however, the external part had suffered considerable injury. The head and tail were detached from the body, and all the arms ... were hopelessly mutilated". She goes on to say, "the caudal fin was rather damaged and detached from the body ..., but the sketch is prob-

ably a fairly accurate presentation of its original form".

This is where I would differ, since the photo of the fins indicates that if the sagittate portion were aligned with the dorsal mantle surface, the shape would be comparable to those in the present study. This is also the case in the less well-known photo of the squid body taken (presumably by the Reverend Harvey) and brought to our attention by F.A. Aldrich (see Aldrich 1991).

The next year, Frost (1936) published the description of a Harbour Main specimen which she said "in many respects resembles *Architeuthis clarkei*, Robson." Its fins are "ovate with no anteriorly projecting lateral lobes". On the basis of the fin shape she says "The fins immediately differentiate this specimen from the species *Architeuthis harveyi* and *Architeuthis princeps*". Although this contrasts with her earlier description of a smaller male from Dildo, it did not cause her to reconsider apparent differences in the fin structure. The material was not preserved, and this matter cannot now be resolved.

By 1936, Cadenat had already described and figured an "intermediate" form of the fin, as *A. harveyi*, from the Bay of Biscay. The fin was almost cordiform, sharply pointed at the extremity, with two lobes that extended forwards for 12 cm from their anterior point of insertion. Thus Cadenat's information destroyed the geographic basis for species separation and called into question the morphological basis for separation of *A. princeps* and *A. harveyi* from the eastern Atlantic forms (*A. dux, A. clarkei*, and *A.* sp. (Rae)). Despite no further captures of specimens with sagittate fins, Stephen (1962) formed a key to separate the Atlantic species of *Architeuthis* without questioning the fin shapes. While incorporating Verrill's fin form as characteristic of the North American region, he was unsure how to treat Frost's (1936) Harbour Main specimen with its "*clarkei*-like" oval fins, otherwise characteristic of the eastern Atlantic.

If it can be postulated that Verrill's description influenced the interpretation by Frost and Stephen, then it can equally be postulated that Verrill's description influenced Kirk. Kirk held Verrill in sufficient regard to name a species after him, and as Dell (1970) has already commented, there is much in common between Kirk's (1888) illustration of *A. longimanus* and that of *A. harveyi* (Verrill 1880b, plate 2). The literature indicates that Verrill (1882b) was aware of Kirk's preliminary report (1879) of a specimen which was later (1882) to be named *A. stockii*. Kirk described the fins as "mere lateral expansions of the mantle. They did not extend over the back as in the case of *Onycho-teuthis* etc." Verrill (1882b) commented on this, "Altogether, the descriptions indicate that this New Zealand species is related to, and perhaps identical

with, the one discovered at the Island of Saint Paul, and first named by M. Vélain *Architeuthis mouchezi*: — Verrill may have been more correct than he knew".

In 1882 Kirk had accepted Verrill's generic definition of *Architeuthis* as having a "caudal fin very small sagittate." However, his specific description of the fin for *A. verrilli* was "obcordate, small dorsal" with the figure showing a middorsal insertion, only moderate free anterior lobes, and a convex posterior border. In the same publication he described *A. (Steenstrupia) stockii* as having a broad, rhomboidal fin with lateral insertions. Kirk's (1888) figure of *A. longimanus* indicates a fin with a small free anterior lobe and both a convex anterior and posterior border to the fins. In all of Kirk's figures the left and right fins are identical. None of the four species described from New Zealand approaches the fin form described for *A. harveyi* and *princeps*.

Since the fin shapes that form the basis of this study are incompatible with all of Kirk's early descriptions, the fin information cannot be used to assist in resolving the problems surrounding Kirk's New Zealand species descriptions.

It was C. W. Robson (1887), a lighthouse keeper in a remote location, who first described a New Zealand *Architeuthis* with an oval fin outline (*A. kirkii*). This description was based on fresh material and possibly without prior expectations of fin shape. This is the species to which Dell (1970) very reasonably ascribed his Makara specimen from 1956. No other conclusion was possible since there is no early New Zealand *Architeuthis* fin material remaining in the Museum of New Zealand.

The breadth of the fin "lobes", and the angle between them, is a feature which is subject to "push and pull". This present study establishes the variation in width of the fins. This study and many others point out that the tearing of the anterior attachments of a narrow pair of fins would result in the configuration described for *A. harveyi*. Stephen (1962) places importance on the relative lengths of fins and distinguishes them on the basis of less than one-third, about one-third, and as exceeding one-third of mantle length. But as can be seen from Table 4 in this study and Roeleveld and Lipinski (1991, Table 7, p. 472), such differences are within the normal variability exhibited by species in this genus. Stephen's work (1962) is incomplete because of his lack of reference to the work of Cadenat (1936), his failing to deal with the anomaly of Frost's (1936) Harbour Main specimen, and failure to note the Knudsen (1957) and Kjennerud (1958) papers which mention asymmetrical fins, one of which carried a projecting lobe.

Verrill's descriptions are now generally believed to be incorrect. Among authors to hold this opinion

are Bruun (1945), Aldrich (1968, 1991) and Roeleveld and Lipinski (1991). Aldrich believes that the *harveyi-princeps* fin configuration is caused by damage, citing some specimens with clearly cordate fins and "unilateral damage, giving the anomalous situation of a torn free hemisphere (i.e., *harveyi*) on one side of the fin, the roundly cordate *dux* fin on the other." Dr C.C. Lu (pers. comm.) has personally examined about 10 specimens with Aldrich in Canada and agrees with Aldrich's conclusion.

Figures 5 and 6B show that it is easy to misinterpret fin shape from photographs. As mentioned earlier, when a specimen loses freshness and turgidity, the point of anterior fin insertion appears to shrink and retract. The squids are difficult to handle and the fin attachments are weak and prone to damage. The loss of the pigmented outer skin is often complete, leaving featureless white flesh of a consistency which makes it difficult to detect rips or tears.

Roeleveld and Lipinski (1991) found that two out of their three specimens had a fin with a free anterior lobe measuring around 120 mm. The anterior lobes figured by Cadenat (1936) and Kjennerud (1958) are mentioned above. These are contrasted by records indicating fins with no anteriorly projecting parts — Ritchie (1918), Robson (1933), Rae (1950), Voss (1956), Kjennerud (1958), Clarke (1980), Boyle (1986) Villanueva and Sanchez (1993). Where the relevant details have been recorded, it appears that Pacific specimens of *Architeuthis* do not have "free anterior lobes" (Hilgendorf 1880; Mitsukuri & Ikeda 1895; Vélain 1887; Pfeffer 1912; Sasaki 1929; Roper & Young 1972, Nesis *et al.* 1985).

Thus there is preliminary and scant evidence that only some *Architeuthis* in the Atlantic exhibit free lobes, whereas (ignoring the early Kirk records), specimens from the North and South Pacific do not appear to do so.

Posterior Fin Border

The posterior border of the fins and termination of mantle vary within the present data set. Some specimens possess a robust "spike" or "tail" at the termination of the mantle, with or without the attenuation of the posterior border of the fins as a narrow keel to the posterior extremity of the mantle. Others have weak, flaccid, and insubstantial terminations of the mantle. In this data set, it is possible to suggest that all specimens had fins which extended as lateral keels to the posterior extremity of the mantle. With the initial contrast between Specimens 1 and 2, the possession of a terminal "spike" appeared to have

potential as specific character, but subsequent specimens had a wide range of intermediate forms suggesting that this feature was subject to wide variation. Similar variation appears in the forms from the Atlantic when contrasting the photos of Sivertson (1955) and R. Clarke (1955) in the Azores, with descriptions by Aldrich (1968) and Clarke (1980). This variation is particularly evident in Roeleveld and Lipinski's (1991) Plate 1 figures c and e where the Green Point and Orange River specimens appear to exhibit both extremes. The photo published by Arfelli *et al.* (1991) shows very broad, but relatively short, fins which converge on the posterior tip of the tail rather than forming a thin posterior keel. The body also appears to taper rather sharply.

There appears to be an ontogenetic change in the fin termination in *Architeuthis*, since Roper and Young (1972) record that in very small examples of *Architeuthis* in predator stomachs in both the Atlantic and Pacific (57 mm and 45 mm ML respectively) "no tail exists; the muscular portion of the mantle terminates anterior to the posterior borders of the fins; the bases of the fins are joined posteriorly along the midline and are supported by a turgid conical extension from the mantle which probably develops into the tail of the adult".

Dr C.C. Lu (pers. comm.), however, has never known an architeuthid with a "free tail" and believes that careful examination will usually reveal the fin borders do extend to the end, however small this may be.

I believe that there are specimens in which the fins do not extend to the posterior point of the mantle, but that this condition is secondary and occurs as a result of damage either before or after capture. The incongruously delicate and insubstantial nature of the fins and fin borders in many specimens makes this character an unprofitable subject for speculation.

Fins of widely varying thickness and muscularity occur on specimens in a way that appears unrelated to sex, size, and maturity. Few authors comment on this feature in any way that can be used as a comparative measure. It is hoped that the data recorded here will serve to indicate the range of variation and that fin thickness or robustness cannot be considered a specific, nor geographic or temporal feature within the Architeuthidae.

Fin Size

The juvenile specimens of Roper and Young (1972) had a fin-length index of 35% of ML (Atlantic) and 31% of ML (Pacific). These fall within the range that

occurs in the present data-set (28–41, average 36% ML, n = 15) but not within the range recorded by Nesis *et al.* (1985) for larger juveniles (FLI 38.4–41.6%, for ML 500–770 mm, n = 18).

In the North Atlantic, recorded indices range from 26% for a 1828 mm ML (Hamilton 1915), to 29% for 1790 mm ML (Sivertson 1955), to 40% for 1750 mm ML (Boyle 1986). A similar range is evident in the South Atlantic, with Villanueva and Sanchez (1993) recording a FLI of 44.6 for a 1220 mm ML individual and Roeleveld and Lipinski (1991) a FLI of 35.2%. Records for the South Atlantic and North Pacific do not (as yet) include fin-length indices under 30%, but I suspect that this reflects sampling inadequacy rather than a specific difference. As mentioned earlier, the posterior border of the fins is not always easy to determine and could easily account for variations in the order of 150 mm in the fin-length measure, particularly on large specimens.

This study records a *double* fin-width index range of 27–40% of mantle length and a single fin width index range of 8–19% of mantle length. The FWI indicated in the literature is largely within a range of 20–34% of mantle length. Clarke (1980), Perez-Gandarez and Guerra (1989), and Arfelli *et al.* (1991) record values at the low end of the range, while Kjennerud (1958), Ritchie (1918, no. 3 specimen), and Roeleveld and Lipinski (1991) record indices at the upper end of the range. The only record in the literature well outside this range is that of Nesis *et al.* (1985), but given that they also record among the highest fin-length indices, it is strongly suspected that the measures given (14.8–23.4% average 17.4%) relate to a *single* fin width, otherwise the authors would surely have commented on fins substantially narrower than those recorded by Voss (1956) for *A. physeteris* or an unnamed *Architeuthis* by Clarke (1980).

The fin-width: fin-length ratio in this study ranges from 1: 1.83–1: 4.53. Given the apparently random scatter of points for the fin ratios (Fig. 8), the ambiguities mentioned above over measuring fin length, and the uncertainty over single or double fin measures, it is not considered useful to analyse the published record any further.

Summary

This study has not identified features of the fins which indicate consistent differences with either size, sex, or geography.

A reexamination of the literature, coupled with the photographs and observations from this study has confirmed that the "free anterior lobes" which distinguish *A. harveyi* and *A. princeps* are artefacts.

It is accepted on the basis of observations by Cadenat (1936) and Roeleveld and Lipinski (1991) that there are some *Architeuthis* specimens which exhibit free anterior lobes of the order of 100–150 mm, with the proviso that these claims should always be validated by fresh material.

The free posterior tail is believed to be a secondary condition resulting from either old injuries, or damage during capture or handling.

The only New Zealand species description which corresponds to all specimens in the present study is *A. kirkii* Robson, 1887.

Fin texture varies from thick and robust to delicate and membranous. Total loss of fins does not appear to adversely affect the survival of the animal.

The present data-set encompasses all but a handful of the upper extremes of fin-length indices deducible from the literature.

The fin-width index may have potential as an indicator of local populations, but probably not species. Much greater care is needed with definition of the fin-width measure, and a standard approach adopted for dealing with the widely differing degree of dorsal separation of the anterior points of the fin insertion.

Based on the variation evident in the present study, the fin-length : fin-width ratio is not considered a useful measure.

HEAD

This study provides new information on head form in the Architeuthidae. The wide range in indices exhibited in the specimens obtained from a restricted geographic region and time period suggest that similar variability can be expected in other geographic zones. This leads to a reexamination of the literature and some of the previous "species" diagnoses.

Verrill's original separation of *A. princeps* and *A. harveyi* was based on a number of features, amongst which he did not list head length. Considering that he had only one relatively complete specimen of each species at his disposal (No. 5 Logie Bay for *A. harveyi*, and No. 14 Catalina for *A. princeps*) he did not include differences in head length amongst his diagnoses. The significance of head length was assigned by subsequent workers (Robson 1933, *A. clarkei*; Rae 1950, *Architeuthis* sp.) and adopted by Stephen (1962) in his key to the North Atlantic species. The head-length index of Verrill's *A. harveyi* is 12% and that of *A. princeps* 14%. To assign specific status to this difference is indefensible. Stephen (1962) acknowledged the contradiction of the occurrence of Frost's (1935) Harbour Main specimen (western Atlantic) with a

head-length index of 22%.

Examination of head-length measures from the literature and converted to head indices is a useful exercise. North Atlantic records range from 23 to 30% (Robson 1933; Rae 1950; Kjennerud 1958; Stephen 1962). These and many other measures have been tabulated by Roeleveld and Lipinski (1991).

In Aldrich's (1991) data-set there are 10 specimens for which the head index can be calculated. The range is from 9 to 26%. This establishes a lower limit for head length of 9% of ML and, combined with Verrill's limited data, would appear to restrict "short heads" to the western Atlantic. Aldrich (1991) considers that there may be small- or large- headed morphs. That suggestion would require more vigorous analysis, for, as has been established in this study, head length does not necessarily equate to head bulk (Fig. 9C).

The present range of 13–21% of ML (based on distance to the nuchal crest), or 15–26% (based on 5 specimens for which the length to the nuchal cartilage is available), indicates that head lengths are similar to those recorded in Newfoundland. Roeleveld and Lipinski's (1991) specimens from South Africa include a head-length index at the top end of the published records (30.1, 25.6, 19.3). When combined with the present data, the conclusion is that head-length variability is evident in all world oceans and the high level of this variability precludes the use of this characteristic to define species.

No eye sinus was detected in the present study, consistent with observations of Dell (1970), Roeleveld and Lipinski (1991), Aldrich (1991) and other North Atlantic authors.

Reference to an eye sinus, however, has occurred regularly in the literature. In Verrill's description of *A. harveyi* he mentioned that "the eyes were both burst" and that "The eyelids are badly mutilated, but the anterior sinus can be imperfectly made out." The evidence is not strong, particularly since Verrill made reference to the close relationship to the Ommatrephidae and probably expected to see a sinus. He used features of that family to complete the missing portions of the neck region in Plates 2 and 8 (1882b), thus probably also generating confusion over lateral neck folds in subsequent publications (e.g., Sasaki 1929). This misrepresentation continues to be reproduced (e.g., Roper *et al.* 1984; Nesis 1987) in the absence of more accurate line illustrations.

The next reference to the sinus is in Mitsukuri and Ikeda (1895), who received their specimen on the *fourth day* after capture. Considerable deflation and distortion would have taken place in this time. My translation (Translation Service for the Department of Internal Affairs, New Zealand) says "The eyes also appear to be large, with fairly distinct eyelids. It is not clear whether or not the lachrymal sinus is present; if it is present, its concavity must be extremely insignificant." It appears that Mitsukuri and Ikeda (1895) expected to find a sinus but were unconvinced as to its presence. Pfeffer (1912), reporting on the same specimen, translates their comment much more positively as "The eye aperture has a very small indistinct sinus." The evidence does not justify the continued reference to an eye sinus.

Since that time, reference to the sinus has been made by Sasaki (1929) and Nesis *et al.* (1985). The latter authors described the structure in their North Pacific specimens as "small" and "shallow". However, they did not figure or provide photographs of the sinus.

The present data indicate that in some specimens the eye aperture may have an irregular and at times almost lobate edge, thus making the interpretation, validity, and even existence of the eye-sinus doubtful.

The presence or absence of the "hole" in the funnel floor has all the requisites of an ideal character, i.e., robust, and either present or absent. Unfortunately the presence and function of the thimble-like depression in the head cartilage in the floor of the funnel groove is not mentioned in the literature. Only Robson (1933) mentions that *A. clarkei* has a "deep foveola", but this term is applied to a pocket formed by a membranous skin at the anterior end of the funnel groove. Sasaki (1929) specifically mentions that the funnel groove is quite smooth.

Of the thirteen specimens in the present study for which this character was observable, nine definitely possessed a form of this structure (Table 6). The most curious feature was the evaginated flap of skin which was found over the top of the hole and which could be pushed back into the hole and made to fit like a finger into a glove. This flap was frequently filled with long, blue ice crystals (presumed to be blood) in the frozen specimens.

Ms Martina Roeleveld (pers. comm.) said that she had observed this feature in one of the South African *Architeuthis*, but was not sure what to make of it. Dr Clyde Roper (pers. comm.) has also mentioned that while he was investigating the Neoteuthidae and Bathyteuthidae a feature was discovered that might be homologous to that described here. The Neoteuthidae has been proposed by several authors as a likely near-relative of the Architeuthidae, as it shares many other primitive states for other characters. Roper and Young (1972) have shown that similarities between Architeuthidae and Neoteuthidae (Alluroteuthidae), though weak, are the strongest amongst those families with the, presumably more primitive, straight locking mechanisms. At this stage no further explanations can be offered for this structure or its variable appearance.

Nuchal Fold

A significant contribution that this study makes is to indicate that the nuchal fold can vary from quite well-developed through to an apparent absence of a transverse folded structure posterior to the head cartilage. The triangular ventral extensions of the fold which border the funnel groove are quite muscular and large. It seems logical to suggest that they are involved with funnel functioning. The literature is contains much speculation that the weak funnel-mantle connectives would hamper the squid's manoeuvrability. I would like to suggest that the nuchal-fold extensions offer a means for greater control over the funnel and its placement. When this is coupled with a suggestion that the nuchal cartilage may be able to employ suction to ensure adhesion, the architeuthid begins to seem less handicapped. The true purpose of the nuchal-fold extensions will probably not be determined until the live animal's locomotion is observed.

FUNNEL

Most features of the funnel are unremarkable, although the wide range in coloration encountered in the present study is unexpected, particularly where it differs from the colour of the mantle exterior. Funnel colours have not previously been recorded in the literature. Where the funnel-locking cartilages have been figured, the shape appears very similar across all the nominal species.

The funnel organ (or Hoyle's organ) is a valuable taxonomic character in many squid families, e.g., Cranchiidae and Histioteuthidae, but its significance for the Architeuthidae is unknown. Only a few authors have detected and described the funnel organ; amongst these are Sasaki (1929), Roper and Young (1972), Clarke (1980), and Roeleveld and Lipinski (1991). However, each of these authors was dealing with information pertaining to a single specimen. Many other authors searched for, but did not find any trace of the organ, e.g., Aldrich (1991) for specimens #1, #2 and Voss (1956) for *A. physeteris*. Other authors do not mention the funnel or its features, notably Robson (1933, *A clarkei*), Frost (1934, 1936), Rae (1950, *Architeuchis* sp.), and Kjennerud (1958), despite having entire specimens in relatively good condition However, the funnel organ is frequently invisible in defrosted Cephalopoda and we can assume *Architeuthis* is no exception..

Clarke (1980) noted "paired oval ventral pads measuring 4.9 x 2.0 cm and an L-shaped dorsal pad with a right limb measuring 6.8 cm in length; the left limb is "indistinct" on specimen no. 3 from South Africa. The latter squid is only 665 mm ML, but a proportionate three-fold increase in the funnel organ measurements would make them comparable to the present Specimens 4, 6, and 7, (185–230 mm for around 2000 mm ML). The ventral pads in both Sasaki's (1929) and Clarke's (1980) descriptions appear to be shorter and rounder in relation to the dorsal limbs than in the present examples. Roper and Young's (1972) description of the Atlantic specimen is too sketchy to permit comparison, but their Pacific specimen's funnel-organ ventral limbs have some common elements with present Specimens 4 and 5. Roper and Young's Pacific specimen also shares with present Specimen 7 the feature of an irregular and ridged anterior extent or the dorsal pads together with a possible anterior papilla. However, Specimen 7 also shares the feature of the narrower and more tapered posterior extent of the ventral limbs in common with the Roeleveld and Lipinski (1991) description from South Africa.

In the present study no two funnel organs were identical, nor did any of them exactly match the existing descriptions in the literature. This suggests that the funnel organ in *Architeuthis* is not a good character for establishing the specific or generic status of specimens. The present study suggests, on very scant evidence, that the sole male may have a more conical funnel with a smaller aperture.

BEAKS

There is as yet no suggestion that beaks will serve as a useful taxonomic tool for separating species of Architeuthidae. Sadly, little has happened to change the opinion held by Pfeffer (1912) in his monographical treatment of Architeuthidae when he said (in translation) "If one were to take the stand that all the differences hitherto cited for the jaws were consistent, then one would have to erect a species of *Architeuthis* for each individual jaw". In the beak identification handbook edited by M.R. Clarke (1986) it is stated that, "... it is pointless to give *Architeuthis* beaks specific names but details of beak occurrence and size distributions may eventually prove extremely interesting when a world revision of the genus is possible."

Despite the additions from the present study, the sample base will need to be a great deal larger than at present in order to provide sufficient material to account for captures at different times of the year (and hence growth). However, there is the distinct advantage that beaks are more durable and easier to store and transport than other body parts of *Architeuthis*.

Akimushkin (1963) provides a beak key and all of

the present specimens conform to his genus description. However, he gives the colour as dark brown or even black, whereas the colour in the present specimens is better described as a deep walnut or chestnut brown. Only the older beaks from the Museum of New Zealand collection could be described as "black" around the rostra and jaw angles.

The only published regressions of the lower rostral length (LRL) in mm (r), against mantle length in mm (l), are by Clarke (1980), republished in Clarke (1986). For North Atlantic specimens the relationship is:

$$l = -180.4 + 109.38 \, r \quad (n = 4)$$

and for the smaller South African specimens (ex Sperm whales).

$$l = -55.6 + 59.31 \, r \quad (n = 11).$$

These figures do not correspond at all well to the equivalent calculation for the present study where :

$$l = +13.73 + .0023r \quad (n = 10).$$

Although in the present study, the lower rostral length is again based on a small sample, the mode is higher than for all length-frequency groups mentioned in Clarke's (1986) summary, and the LRL range is very compressed (16.0–19.2) despite a ML that ranges from 1560–2140 mm. When compared with the few estimates of ML that Clarke's material allows, then it is clear that the average ML of the New Zealand sample is also larger. Roeleveld and Lipinski (1991) also found that Clarke's (1986) formulas did not fit their data and attributed the closer agreement with the North Atlantic formula to the inclusion of larger specimens in that data-set.

Clarke and MacLeod's (1982) study of the diet of sperm whales in the north Tasman Sea produced a LRL range of 0.7–1.90 cm. This too, is on average higher than the length frequencies found in beaks from whales caught off South Africa. Clarke and McLeod (1982) proposed a seasonal difference since the capture time was offset by five months, but the size at darkening differs too. This they attributed to either a regional difference in one species or merely a sample variation.

Fiscus and Rice (1974) found *Architeuthis* beaks in 12 of 552 Sperm whales off California. Although most beaks were smaller than in the present data-set, remains were found of lower rostra of over 30 mm. This far exceeds any beak sizes in the present study. It seems to have become customary to name all *Architeuthis* found in the north-eastern Pacific *A. japonica* without any further justification of the identification (e.g., Kodolov 1970; Nesis *et al* 1985; Fiscus *et al.* 1989) but there has been no record of an identified specimen of *A. japonica* large enough to sport such a beak.

One feature of the present material of upper beaks is also reported by Perez-Gandarez and Guerra (1978). They likewise record a pale streak on the upper beak. Their specimen was a 200 kg *Architeuthis* from 27°42' S, 14°13' E.

One feature of the present material that should be commented on is the excessive fragility of some of the beaks, particularly the lower beak. The beaks in the present study differed in their degree of robustness, with the Specimen 16 lower beak being particularly fragile. No other reference can be located that mentions the variable ridge(s) on the lateral walls of the upper beak, other than Verrill (1882b, p. 252) for *A. princeps*. Verrill (1882b, p. 253) also comments on the firmer texture and more pronounced notch and shoulder tooth of *A. princeps* as compared with *A. harveyi*. This present study, however, suggests that variation in these features is unlikely to be of taxonomic significance.

ARMS

In *Architeuthis* taxonomy some species have been differentiated on the basis of the length of their arms. Arm lengths have been considered relative to each other, or to the length of the mantle, or to a combination of mantle and head length. The belief in the value of this character is reiterated by Roeleveld and Lipinski (1991) who state that "the relative lengths of the arms (arm-length formula) could well be of value but is frequently unavailable as the arm tips are missing to a variable extent in most *Architeuthis* specimens." Therefore an attempt has been made in this study to address the issue of the validity of the character.

In the literature, records of complete arm lengths were reported by Verrill (1882b, *A. princeps*), Mitsukuri and Ikeda (1895), Robson (1933), Cadenat (1936), Frost (1936), Rae (1950), Sivertsen (1955, photo), Voss (1956), Knudsen (1957), Kjennerud (1958), Stephen (1962), Roper and Young (1972), Boyle (1986), and Aldrich (1991).

In general, arm IV can reach a maximum of 160–170% of ML, whereas arms I–III are more often 100–130% of ML. The extremes are :

- Kjennerud (1958), *A. dux*, arm IV 164% ML
- Verrill (1882b), *A. princeps*, arm IV 170% ML
- Voss (1956), *A. physeteris,* arm I 144.8% ML
- Mitsukuri and Ikeda (1895), *A. japonica*, arm IV 169% ML
- Roper and Young (1972), the smaller specimen (45 mm ML) arms were 44–62% ML
- Verrill (1882b) for *A. harveyi* recorded all arms at 87.8% ML but, as Pfeffer (1912) pointed out, Verrill

could not verify that Harvey had measured intact arms only).

In contrast to most of the literature citations, some authors record arm IV as shorter than the other three arms (Cadenat 1936, *A. harveyi*; Rae 1950, *Architeuthis* n.sp.; Stephen 1962, *A. dux*). It is difficult to know whether this is another example of variability or whether these short arms IV are the result of accidental shortening. As has already been established in this study, as well as frequently in the literature, accidental arm shortening appears to be a common occurrence for *Architeuthis*.

However, the present study and Aldrich's (1991) data indicate a slightly lower average arm-length index for *Architeuthis*. An important aspect to remember is these two data-sets contain internal comparisons since they represent specimens from a restricted geographic area over a relatively short period of time and measurements made with consistency by the same researcher, rather than single specimens dislocated in time and space.

The present author has recalculated comparable data from Aldrich (1991) (Appendix 3). Arm lengths have been recalculated and where both left and right arm measures were available, the longest measure was adopted. Aldrich was able to obtain only one specimen for which he records all the arms as complete (Sunnyside specimen). An overview of the indices generated from Aldrich's data suggests that the arms were more "subequal" than any other records available (see Clarke 1980). While recognising that there are only two complete measures for arm IV, those arms are not significantly different from the first three arms. There is also no consistency between the specimens as to the shortest arm.

Aldrich's data vary within an extremely small range, whereas the present study indicates a much wider range at the lower end. The measures for shortest arms identified in the present study are supported by at least one other short arm within the same specimen's arm complement. Since there was no evidence of regeneration in those instances, this leads to the conclusion of genuinely shorter arms for some of the New Zealand specimens (especially Specimens 11 and 14). The maximum arm length in the present study, was an isolated 140% of ML (Specimen 16, arm II), and can be compared with Aldrich's isolated record of 155% ML (Wild Cove, arm II). Aldrich (1991) has assigned all of his (North Atlantic) specimens to *A. dux* and clearly did not consider arm length to be a significant taxonomic feature.

There appears to be an ontogenetic effect as evidenced by Roper and Young (1972) and an otherwise very wide range of values for both male and female specimens in both the Atlantic and the Pacific (this study; Aldrich 1991; and the literature cited above). Since very few specimens have come from the geographic region of Voss's (1956) *A. physteris*, it may be necessary to suspend conclusions in the case of that species. Pfeffer (1912) rejected *A. martensii* Hilgendorf, 1880 from Japan as a *nomen spurium* partly on differences in arm lengths with Misukuri and Ikeda's (1895) *A. japonica*. These differences now seem inconsequential in light of the variability established for specimens in the southern Pacific.

The distinction between *Architeuthis* species based on the length of the sessile arms in relation to body length must be refuted as a character of taxonomic value.

Keels

In other groups of squids the number of aboral keels and the cross-sectional shape of the arms is normally constant within a given species. *Architeuthis* arm keels are only infrequently mentioned in the literature :

- Mitsukuri and Ikeda (1895) state that there are no keels on the outer faces of arms II and III.
- Ritchie (1918) states that the arms lacked fin-like extensions on any of the sessile arms.
- Sasaki's (1929) description of *A. japonica* mentions a weak keel on arms I–III and two narrow keels on arm IV.
- Robson (1933) reports a keel on arm III and (?) two aboral keels on arm IV for *A. clarkei* (similar to some specimens in the present study).
- Voss (1956) says that all the arms of *A. physeteris* are slightly keeled.
- Kjennerud (1958) mentions indistinct keels on arms I and II, more distinct keels on arms III (although it is not clear how many), and two well-formed keels on arms IV.
- Clarke (1980) records a swimming membrane on the outer third of each arm of the *Architeuthis* specimens from Sperm whales off South Africa (corresponding to the pattern in Specimen 2 from this study).
- Roeleveld and Lipinski (1991) report a distal keel on arm III, and 2 keels on arms IV (the most commonly encountered pattern in the present study).
- Aldrich (1991) notes variability in the keel pattern within his data-set.

The significance of the aboral keels and ridges has not been established for the Architeuthidae. The present study has been rigorous in recording these

features and has provided an indication of the variation present within this sample. It is clear that the number and distribution of aboral keels in this present sample do not fall into any consistent patterns and consequently this feature is unlikely to be of taxonomic significance in wider considerations.

Arm Sculpture

Steenstrup (1898) illustrated part of an arm of *Architeuthis dux* and figured papillae on the oral surface but made no comment on the feature in the text. Owen (1881) also figured the papillae of what is clearly the fourth or ventral arm of an *Architeuthis* (*A. grandis*). Since last century, our knowledge has not substantially advanced. Roeleveld and Lipinski (1991) also reported the presence of papillae on their South African specimens.

The present study notes the formation of papillae into a near-continuous irregular ridge which parallels the central "zigzag" groove. This is a new observation. The prominence of trabeculae does not vary, nor does the width of the protective membrane vary consistently. The lobular nature of the protective membrane or perforations in the basal part of the membrane have also not been figured elsewhere. Unfortunately however, the wide variability of these two features precludes their usefulness as taxonomic characters.

Robson (1933), when establishing *A. clarkei*, described the arm surfaces as differing through having feeble sucker pads and a lack of elaborate folds. The differences between arms within one specimen, the differences evidenced along the length of a single arm, and particularly differences in the appearance of the oral surface of arm IV between specimens in the present dataset (see individual species descriptions held at NIWA) indicate that those aspects of arm sculpture are not a valid reason to segregate *A. clarkei* as a separate species.

Regeneration

This study indicates that regenerated arm tips are smaller in diameter and carry smaller and more-crowded suckers. These records add to the accounts of Verrill (1882b) and Aldrich and Aldrich (1968) of this phenomenon in Architeuthidae. Verrill (1882b) recorded regeneration of mutilated lateral and dorsal arms of *A. harveyi* and said "where the old part joins the new there is often an abrupt change in size ...". Aldrich and Aldrich (1968) provided an example of the left tentacular club arm where the new "large" suckers were smaller and the new "small" suckers

differed by a factor of 2.6 and lacked the normal pattern of arrangement.

TENTACLES

There are few detailed descriptions of tentacle clubs in the literature. The illustrations of Verrill (1882) for *A. harveyii* are among the most complete, detailed, and easy to compare with the present material. Features noted in his illustrations are entirely within the range of equivalent features in the present data-set.

The illustration of Voss (1956) of *A. physeteris* is too crude to enable good comparisons to be made. Voss indicated 15–16 rows of manal suckers but the accuracy of the illustration is unclear. There appear to be more carpal suckers and fewer dactylus suckers than in the present data-set. The comparison is not considered useful for the present purposes. Robison (1989) has a photo of a tentacle club (*A. (?) japonica*). In comparison with the present specimens, manal suckers on the medial rows appear relatively larger than the marginal suckers. However, the total length of his tentacle stalk is only 4270 mm, with the club accounting for 415 mm. The largest sucker on the manus is 18.5 mm, which is smaller than those of the present study. Perhaps there is an ontogenetic effect, where smaller animals or shorter tentacles have proportionately larger suckers. Akimushkin (1963, 1965) based a key in part upon the relative size of the marginal manal suckers: i.e., either half as wide as those in the median row or slightly wider, as compared to those much less than half as wide as those in the median rows. Without actual measures and a range of specimens to establish the natural variability in these proportions, there is no value in this arbitrary distinction. However, persistent differences between regions, sexes, or sizes of squid in the ratio of marginal to medial sucker widths may be useful.

Tentacle stalk length varies around the world, but not with any apparent pattern. Clarke (1980) recorded a Donkergat (South African) specimen with a total tentacle length of 1760 mm and a club length of 320 mm. He commented on the unusual shortness of the tentacles in this specimen. However, in the present study there is variation of almost 100% in tentacle lengths between Specimens 12 and 6, although their mantle lengths are very similar.

Aldrich (1991) has made few comments on the form of the tentacle and club of his Newfoundland specimens. Examination of his Table 3 (p. 463) reveals six specimens for which he has tentacle length and tentacle-length index. These range from 227–397% ML. Actual maximum measurement was 6600 mm. The relative length of tentacles did not appear to relate

in any obvious way to mantle length. Differences in length between left and right tentacles may indicate either uneven length or problems with obtaining accurate measures of such elastic structures. Description of the tentacle club of the Conche Specimen (#1) corresponds very closely to the present specimens, although Aldrich described the dactylus suckers as tetraserial. His specimens presented a club-length range of c. 10–18% of tentacle length, which is again within the range exhibited by the present dataset.

The recent Australian specimen described by Zeidler and Gowlett-Holmes (1996) measured 7390 mm for the right tentacle stalk and club. The ML was only 1530 mm, thus providing one of the longer relative tentacle lengths on record (483% ML). The measure is, however, close to the present Specimen 6 (7500 mm) and Specimen 16 (7300 mm). Zeidler and Gowlett-Holmes' largest diameter for a club sucker was 25 mm. Counts from their photograph suggest that the manus has 13 quadriserial rows of enlarged suckers. The relative sizes of the dactylus and carpus are also comparable to the present specimens. In fact, the similarity is remarkable.

Although Pfeffer (1912) believed that the individual species could be distinguished by the number of quadriserial rows on the club and the dentition, size, and arrangement of suckers, this is not borne out by the present study. No regular arrangements or invariable patterns of these characters have been discovered in the present specimens. No differences were noticed during my examination of tentacle clubs from Norway and Hawaii. Neither these actual club examinations nor the illustrations of the early North Atlantic specimens suggest that there is a consistent geographic or age-related difference in the structure or arrangement of suckers on the tentacle club.

ARM SUCKERS

Steenstrup (1898) illustrated a small proximal portion of an arm from an 1855 specimen. This illustration is still one of the most useful records of arm sculpture and the text confirms that the sucker ring of *A. dux* is evenly toothed all round. However, Steenstrup also had in his possession a single small sucker which had only 26–28 teeth, in which the teeth (in translation) "were not separated, but *coalesced, as it were on larger stretches*". Stephen (1962), in his key for the North Atlantic species, and others have overlooked the significance of this information. Verrill (1882) too, put a rider on his description of *A. harveyi*, which had numerous acute teeth all around the circumference "*for those so far seen*". Verrill also recognised the similarity between the proximal suckers of *A. princeps*

and those of *A. harveyi* and went on to describe a second type of sucker from *A. harveyi* as oblique with large teeth and imperfectly denticulated. Unfortunately, Verrill and Steenstrup were not able to compare their material directly and thus did not arrive at an understanding of the sequential changes in sucker dentition along the length of the arms.

Frost (1934) summarised *A. harveyi* and *A. princeps* sucker dentition in such a way that they do not appear to differ from each other. However, her Dildo specimen appears to be atypical, with the suckers being smallest on arms III and IV, followed by arms I and II. She described even the most proximal suckers as unevenly denticulated. By 1958, Kjennerud had concluded that there was no taxonomic value in dentition (in relation to specimens she assigned to *A. dux*). Robson (1933, *A. clarkei*) and Rae (1950, *A.* sp.) raised a number of differences in their specimens from those of Verrill (1882b) but, given the variation which occurs in the present data-set combined with that described by Roeleveld and Lipinski (1991), the differences Robson and Rae raised occur well within the normal range of variation. Aldrich (1968) too, believed that "on the basis of other characters, the Newfoundland specimens are best assigned to *A. dux*. The arrangement and form of the suckers and their dentition are those described for *A. dux*." Unfortunately Aldrich did not present the data for examination. Clarke (1980) compared his South African specimens with the "southern forms", stating that sucker dentition did not correspond to that recorded for *A. longimanus* from New Zealand.

Despite the similarities in general sucker form and overall pattern of transformation along the length of the arm, there are other aspects that deserve a closer examination. One such aspect is the total numbers of suckers per arm. Examples in the literature are as follows:

- Owen (1881) described a complete arm IV with 292 suckers.
- Verrill (1882b) (Specimen no. 24, *A. harveyi*) counted more than 300 suckers on arm II. These consisted of 100 oblique suckers with serrated margins and a further 200 at the tip.
- Ritchie (1918) recorded approximately 110 suckers on a perfect sessile arm.
- Sasaki (1929) recorded approximately 220 suckers on arms I–III, and 250 suckers on arms IV.
- Robson (1933, *A. clarkei*) recorded over 300 suckers on arm III and approximately 290 on arm IV.
- Kjennerud (1958) recorded arm I with 195–210 suckers, arm II with 149+ suckers, arm III with 185 suckers, and arm IV with 251 suckers.
- Aldrich (1991) (Specimen 1, Conche), reported arm II with 84 suckers but missing tip suckers.

When these sources are compared with the present dataset it appears that there is a wide range in the numbers of suckers per "intact" arm. The records of Owen (1881) are confirmed by an earlier paper by Kent (1874) on the same detached arm in the Natural History Museum (BM). Unfortunately, the origin of the arm remains unknown. The records of Robson (1933) and Kjennerud (1958) refer to results for more than one arm on each specimen and thus form an internal check on the degree of "completeness" of the arm. The record of Verrill (1882b) is of the same order of magnitude with over 300 suckers. The records of Aldrich (1991), with incomplete arm tips, present the same difficulties as the records for the present data-set for Specimens 5 and 14. At the other end of the range are the low numbers recorded by Ritchie (1918) and the present Specimens 3, 8, and 16, which barely attain 200 suckers for arm IV and considerably fewer for arms I–Ill (ML 1770–2000 mm).

However, as has been pointed out, the arm lengths in the present data-set and those of Aldrich (1991) are at the shorter end of the range identified in the present discussion on sessile arms, and the arms of Ritchie's (1918) specimen were also quite short and would probably have not even equalled the mantle length. This is an area which requires further data and careful study before it is finally resolved. I believe that the sucker numbers are related to arm length, and, as has been pointed out in the arm section, the arm lengths vary continuously and apparently in a way unrelated to geography or mantle length (ontogeny).

Another feature which needs to be considered is the range of sucker sizes. Maximum sizes recorded for arm suckers vary, (e.g., Owen (1881) arm IV, 20 mm; Steenstrup (1898) 24–25 mm; Sasaki (1929) 19 mm; Robson (1933) 18 mm; Clarke (1980) 17 mm; Aldrich (1991) Specimen 1 (Conche) 15.4 mm; Specimen 6 (Bonavista) 15 mm.

Frost (1934) compared the diameters of the 10th sucker on all four arms in a table in comparison with Robson's (1933) *A. clarkei*. The suckers of Frost's material were larger by 20–50%. However, Robson's *A. clarkei* was only 1651 mm ML while Frost's Harbour Main specimen was 2185 mm ML. There appears to be a similar ontogenetic effect in the present study, with comparable suckers being smaller on the specimen with the shortest mantle length (930 mm). However, despite this effect, the maximum sucker sizes in the present study (21–24 mm) are at the upper end of the size range recorded for *Architeuthis*.

The presence of a particularly small first sucker on arms I and II is reported for specimens from most of the major regions of *Architeuthis* occurrence, e.g., Rae (1950, North Atlantic) recorded a 3 mm sucker on arm I. Small basal suckers on arms I and II were also reported by Kjennerud (1958, North Atlantic), Dell (1970, South Pacific), and Roeleveld and Lipinski (1991, South Africa). A small first sucker is a frequent (but not invariable) feature of arms I and II of the present data-set. The detail on size range and variation in dentition of the first sucker of all arms in the present study form a baseline against which "atypical" patterns can be compared. The careful examination of this data should prevent undue emphasis being placed on this character for the purposes of taxonomic separation.

The present data indicate that both the size of the largest sucker and the number of teeth are smaller on arm IV than those of the other three arms. A selection of comparative data from the literature is listed below.

	No. of teeth on suckers of arms I–III	Max. size of suckers (mm) on arms I–III	No. of teeth on suckers of arm IV	Max. size of suckers (mm) on arm IV
Steenstrup 1898	46–54	21		
Sasaki 1929	45–55		?	
Frost 1934 (Dildo)		20–22		15
Clarke 1980	47–51	15–17	42	14
Pérez-Gándaras & Guerra 1989				
Spec. A	41–54	15–16	28–35	13
Spec. B	54–60	20.8	43	16.7
Aldrich 1991		15		

Sasaki (1929) listed the largest suckers as occurring on arm II, the next largest on arm III, and the smallest on the ventral arms. This is a pattern which is also found in the present Specimens 1, 4 and 11, and possibly 10. In contrast, however, the largest suckers are found on arm I in Specimens 2, 3, 6, 12, 14 and 16 and on arm III in Specimen 5. This demonstrates that minor variations in the distribution of the largest suckers over arms I–III are unlikely to be of taxonomic significance. Sasaki's record of the suckers on arm IV being half the size of the largest suckers on the other three arms seems to constitute a difference from the present data-set. However, given that the size range of arm IV suckers encountered in the present data is 66–94% based on only 13 examples, the smaller relative size of the arm IV suckers in Sasaki's single specimen of *A. japonica* probably does not constitute an unequivocal character.

The conclusion must be that, given the patterns shown by the present data-set and the variations reported for the North Atlantic specimens, there is insufficient evidence to propose sucker size, shape, or counts as a basis for separating species.

À puzzling aspect has been the variable figuring or lack of mention of the ventral (or proximal/adoral) notch in the base of the sucker ring. In the present specimens, this notch was present in all but the first few suckers and the most distal suckers of an arm. Sasaki (1929) did not figure the ventral notch, but otherwise his sucker-ring illustrations are a good match with the present specimens. Verrill (1882, pl. 9, figs 3, 4) figured this feature for the more distal rings of A. princeps but not for the proximal rings. Verrill's suckers are indistinguishable in general form from the present ones. Robson (1933) did not figure or mention a ventral notch in the sucker rings. I do not have the illustrations of Mitsukuri and Ikeda (1895), but the description in the translated text matches the present data exactly.

Sucker-ring dentition does not seem useful in separating Architeuthis specimens. I am inclined to dismiss small differences in numbers of teeth in the largest suckers on each arm. This study found frequent damage to the suckers, e.g., rings broken, partially mended, missing, double suckers on one pedicel, or atypical small suckers occurring amongst the large ones, as well as the effects of wear on the appearance of the teeth. In many specimens, partial fusion and double bases for some teeth mean that counting sucker teeth becomes a very subjective exercise. Obviously, atypical single or even groups of atypical sucker rings should not be given diagnostic weight.

Without a detailed description of sucker dentition for an entire arm complement, authors cannot draw valid conclusions about apparent differences in arm-sucker dentition. The present study has moved a long way to providing this information (contained in the sucker dentition tables in the individual species descriptions held at NIWA). The variations are numerous and every individual has unique aspects (e.g., atypical suckers occurring in a series of regularly decreasing sucker-teeth numbers, variation in form of teeth — peg-like, hooked, blunt, dagger-like etc., differences in the shape or sculpture of the base of the sucker ring). These variations are considered to be due to individual variability and indicate that a large data-set showing one or more persistent differences is required before any taxonomic importance can be assigned to the form of the sucker ring.

GLADIUS

The gladius in New Zealand Architeuthis has the same general posterior end-cone structure as illustrated by Steenstrup (1898), Sasaki (1929), Frost (1936), Roper and Young (1972), and Toll (1982). However, unlike the example used by Toll (1982, Species A), the gladius is not sturdily constructed. The specimens in the present study are most similar to Toll's Species B described from Florida and the juvenile from the Atlantic in Roper and Young (1972). There is essentially no difference in general form between the present data set and the illustration by Verrill (1882b) for A. harveyi, and there is no difference with the illustration of Steenstrup (1898) for A. dux. Rae (1950) likens the gladius of Architeuthis sp. to that of A. dux.

A more detailed consideration reveals that although the posterior portion of the gladius in the present specimens is similar to that illustrated by Sasaki (1929) for A. japonica, the anterior shape does not correspond entirely to Sasaki's illustration. According to Mitsukuri and Ikeda (1895), however, the anterior end gradually narrows to a point in A. japonica, and the posterior end approaches a cone in form (but not a complete cone for it has ventral ridges/ grooves). Their description further corresponds to the present study in that the central rib is a convex curve, narrow posteriorly, and wider anteriorly. They also mention lateral ridges, although there are minor differences in positioning of these when compared with the present specimens.

Aldrich's (1991) description and photographs also agree in general form with the present data-set. He too, mentions the thickened edges (calling them rod-like lateral ridges) in his description of Specimen #2. Steenstrup's (1898) illustration of A. dux indicates that the widest part of the gladius is posterior to the midpoint. In contrast, Aldrich's (1991, p. 470) photograph shows the specimen from Springdale as having the widest portion of the gladius well to the anterior of the mid point, while in the photo of his Specimen #15 from Sandy Cove (fig. 10, p. 475) this feature is not as marked. The more gradual anterior taper in this latter specimen is very similar to the present data-set. The size and extent of the lateral wings in Aldrich's specimens also vary considerably (compare his fig. 7D, 10).

Cadenat (1936) provided a good description of the gladius in the text, particularly of the anterior region, which appears to match the present specimens in texture, taper, and wrinkling. He also described the posterior portion as having wings and two lateral folds — of which only the more important fold is carried forward anteriorly. This is entirely consistent with the present data-set. Clarke's (1980) illustration is sketchy but the taper in the anterior portion of his Architeuthis sp. appears to be intermediate in form between the present specimens and that of Sasaki (1929) and Toll (1982, Species A).

The anterior portion of Toll's Species A gladius does not correspond to that of the present specimens,

nor is the posterior narrowing of the gladius before the lateral wing formation observed in the present data-set. However, it should be noted that Toll's Species A comes from a mature male specimen of only 167 mm ML (see Toll & Hess 1981). Toll likens the gladius of this latter specimen to Sasaki's (1929) illustration, but I believe that this is only valid for the anterior aspect of the vanes. The posterior narrowing effect, as drawn by Sasaki, is very slight and could indeed be considered intermediate in form between the small Toll specimen and the current study specimens.

The conclusion is again that, in comparing the present data-set with the existing literature, there is a continuous gradation in form exhibited by *Architeuthis*. None of the variations in form seem restricted to particular geographic regions. The anterior portion and the posterior portion together do not form a constant "unit of form", and the recorded posterior end-cone variations are all represented within the current data-set; i.e., they range from edges curled inwards but not fully fused, through to a small well-fused end cone. There is a possibility that the gladius form with the more substantial anterior "shoulders" (or more definitive free anterior rachis) may be restricted to smaller specimens, but larger sample sizes are needed before ontogenetic difference can be demonstrated. The variation in the shape of the anterior termination of the gladii in the present specimens invalidates any descriptions that attempt to erect a species on the basis of the form observed in a single specimen.

INTERNAL ORGANS

The deep red-brown colouration of the inner surface of the mantle, the thick skin covering the visceral sac, and the supporting membranes of the gills appears to be a general condition for *Architeuthis* (see Aldrich 1991; Roeleveld & Lipinski 1991). Only Sasaki (1929) differs, and reports that the small posterior, thick- walled visceral sac and the region of the ventral pallial artery is evenly covered with "small yellowish-brown chromatophores".

Details of the anal papillae vary. Frost (1936) indicated that the papilla has a smaller lobe on the medial side, whereas in the present study (Specimen 16) the smaller lobe is on the outer side. Roeleveld and Lipinski (1991) indicated a narrow base for the anal papillae whereas the basal part of the papillae is very broad in Specimen 16.

The white knob described in the present study as the posterior of the ink sac was also noted independently by Roeleveld and Lipinski (1991). They too (pers.

comm.) were puzzled as to its function or relation to the more usual placement of the ink gland within and along the dorsal face of the ink sac (Nesis 1987). The structure of the sac and duct have not been previously recorded. Particularly, the variation in free length, apparent outward continuity of sac and duct, and variable degree of ventral and lateral association with the rectum are new observations. Voss (1956) recorded a large, free ink sac for *A. physeteris* and Frost (1934) illustrated a bilobed posterior portion of the ink sac for the Dildo specimen. This latter record is probably atypical as no other authors have encountered such a feature.

The form of the stomach and caecum appear to be relatively constant between *Architeuthis* from differing regions (see Frost 1934; Kjennerud 1958; Roeleveld & Lipinski 1991). Frost (1934), too, noted the red colour-ation inside the stomach. However, Arfelli *et al.* (1991) recorded that the colour of the caecum and stomach were pale yellow and Roeleveld and Lipinski (1991) noted that the stomach was white. The latter authors commented on the extreme length of the stomach (530 mm), but this length and relative occupancy of the mantle cavity is normal in the present data-set. However, they also report that the caecum was white and relatively small (40 mm) in the Orange River specimen. Both the lack of pink-orange colouration and the small size differ from the present specimens. In contrast, Roper and Young (1972) were surprised by the size of the stomach in their juvenile specimens, so much so, that they suggested that the stomach was atypically distended.

The relative size of the stomach and caecum was uncharacteristically constant for the present speci-mens. Given the difficulties inherent in accurate measurement of these organs and the presumably distensible nature of the stomach, the caecum size ranged over only 18–25% of the length of the stomach. Five of the seven calculations of relative caecum size available lay between 23 and 25% of stomach length. This does seem to place the Roeleveld and Lipinski (1991) Orange River specimen (at 7.5 %) at one extreme of the range.

There are few detailed observations on the repro-ductive system, and I have not made a particular study of them. The eggs are small and slightly coloured as has already been noted by Roper and Boss (1982), Boyle (1986), Perez-Gandarez and Guerra (1989), Aldrich (1991), and Roeleveld and Lipinski (1991). Estimates of egg numbers have been made by Boyle (1986) (10×10^6) and Roper and Boss (1982) (1×10^6). The ovary is variously described as large, loose, and spongy (Aldrich 1991), or yellowish-white and filamentous (Roeleveld & Lipinski 1991). Both of these descriptions can be applied to the present specimens.

The partial or complete fusion of the nidamental glands noted in this study has also been noted by Roeleveld and Lipinski (1991). However, the variable shape and positioning of the oviducts and oviducal glands demonstrated by the present specimens has been somewhat perplexing to the present author. It is clear from examination of Frost's (1934) photograph of the internal organs that this was in fact an immature female, not a male as she surmised. The penis of the only male organs received in the present study (Specimen 8) was shorter than reported elsewhere; however, the onboard photo of Specimen 9 shows a long thin penis extending well beyond the mantle aperture on the left side of the body. The spermatophores correspond in general structure to that described by Knudsen (1957), although the present end filament is shorter and broader.

The number of gill lamellae does not seem to be constant in *Architeuthis*, with Aldrich (1991) reporting differences between the left and right gill in the same specimen. Sasaki (1929) counted about 60 lamellae, Perez-Gandaras and Guerra (1989) 65 lamellae, and Roeleveld and Lipinski (1991) 55–60 pairs of lamellae, whereas the present specimens range from 66–71.

Other than the relative sizes of the stomach and caecum, few differences have been detected in the descriptions of the internal organs which could indicate specific differences. The Toll and Hess (1981) specimen was clearly unique, being characterised by maturity at a very small size. That leaves the Roeleveld and Lipinski (1991) Orange River specimen with its atypically small white caecum. However, atypical examples occur for digestive-gland structure and nidamental-gland colouration in the present data-set and I am reluctant to place too much weight on isolated, possibly aberrant, examples.

DISTRIBUTION AND ECOLOGY OF NEW ZEALAND *ARCHITEUTHIS*

Distribution of Giant Squid in New Zealand

The geography, density, and frequency of stranding, the location of capture, and occurrence in Sperm whale stomach contents have traditionally formed the basis for speculation about the lifestyle of *Architeuthis*. The present study adds little new data other than to reinforce or cast doubt on the speculations of earlier authors.

Both Kirk (1880) and Dell (1952) recognised Cook Strait as a "hot spot" for the strandings of giant squid. However, most of the present specimens have come from more recently developed major New Zealand fishing grounds. These grounds include the deep-water fishing activity for Orange Roughy (*Hoplostethus atlanticus*) along the Chatham Rise and off the Wairarapa coast, the more intensive fishing for Hoki (*Macruronus novaezelandiae*) off the west coast of South Island, and the trawl fishery for squid (*Nototodarus sloanii*) on the Auckland Islands Shelf and southern Snares Shelf. A complete record of verified New Zealand captures and occurrences of *Architeuthis* together with associated data is found in Appendix 2.

The capture locations of the present specimens range from 35° S to 51° S. Specimens 1 and 2 are from the two geographic extremes of the collection and might reasonably have been expected to differ. They are from subtropical waters and subantarctic waters respectively. Specimens 3, 4, and 5, however, came from the Cook Strait and Wairarapa coast — separated geographically by only a few miles and over a period of less than a month. Fishermen indicated that bottom temperatures were around a degree centigrade warmer than is normal for the month (April–May 1984) during which Specimens 3 (floating), 4 (stranded), and 5 (trawled) were found. Specimen 6 was also relatively close by. As a group, Specimens 3–6 could reasonably be expected to form part of the same population, or at least part of a continuous distribution for a species, i.e., there is no major biogeographic boundary between their locations.

Specimens 2, 5–8, and 10–15 were captured as a result of trawling activity. An article in a local fishing magazine was almost certainly responsible for the acquisition of at least three of the early specimens. New Zealand fishing techniques have evolved and the speed and power of trawlers has increased since the late 1970s. The deeper waters are being trawled more intensively than ever before by New Zealanders and this, combined with the presence of scientific observers on boats, would explain more frequent records and appear to make the squids seem more abundant.

The deepest capture record was that of Specimen 5. This was taken, along with its prey, Orange Roughy, at a depth of between 1100 and 870 m. Despite its lack of fins, this smallest specimen had been actively feeding. The shallowest capture was Specimen 11 at 295 m. The majority of captures have been between 400 and 600 m, and in most cases this corresponds to the depth of the outer shelf or continental slope. Until the records from trawling activity in the 1980s, there had been no indication that *Architeuthis* was so wide-

spread around New Zealand.

The captures seem to occur in clusters. This had already been noted in Verrill's numerous publications from 1874 to 1882, by Aldrich (1968), and was evident in the captures recorded by Ritchie (1918). Aldrich (1968) speculated on their occurrence in every third decade but does not believe it is due to reproductive migration since all nine of his specimens were immature. He believed hydrographic variations in the western North Atlantic are responsible for the cyclic occurrences. The New Zealand records form clusters around 1879–88, 1924–37, early 1950s, mid- 1970s, 1983–1988, and again in 1996 (3 specimens and reports of others). It has not been possible to link these occurrences to particular hydrological conditions.

The present study provides the southernmost confirmed records for live Architeuthis in the South-west Pacific. These records consist of Specimen 2 (51°16' S), Specimen 11 (50°50' S), and scientific observer reports of a specimen at 50°18' S from the F.V. Mys Kronotsky, and at 51°00' S from the F.V. Nikolaevskiy.

Clarke (1986) believed that Architeuthis are not found south of the Subtropical Convergence. In relation to this it is worth noting that, although the present study has several specimens from 50° S and beyond, these captures occur at a point where the Subtropical Convergence is deflected southwards to a varying extent, occasionally as far south as 50° S.

A lack of specific detail, figures, or capture positions makes interpretation or validation of material alluded to by Korabel'nikov (1959) and Klumov (1971) difficult. Vovk et al. (1978) mention smaller Architeuthis (1000–1600 mm ML) occurring in Sperm whale stomachs down to 66° S in the South Atlantic, and their Sperm whale feeding studies in the SE and SW Atlantic record Architeuthis from 30–43° S and 30–50° S respectively. In the Atlantic sector of the Antarctic, Architeuthis was also consumed by (male) Sperm whales between 53° and 60° S. In the Pacific sector of the Antarctic, remnants of Architeuthis were recorded in whales captured up to 66° S. Vovk et al. (1978) believed that "these inhabitants of subtropical waters reach high latitudes, probably because deep warm water masses intrude into these areas."

Food Web

The present study provides the most comprehensive data on the feeding of Architeuthis. The known range of prey items has been increased and indicates that relatively small fish and squid form the bulk of the diet. Previously only Perez-Gandarez and Guerra (1978) had identified stomach contents. In their case, these consisted of damaged eye-lenses and radulae suggesting ingestion of Histioteuthidae (possibly including H. reversa), Onychoteuthidae, and possibly Ommastrephes caroli (= O. bartramii).

Architeuthis appear to be palatable to a range of fish, mammals, and seabirds in the New Zealand and South Pacific region. Dunning et al. (1993) record Architeuthis as a minor item, occurring singly in the diet of oceanic sharks caught near Sydney (34° S), and Port Stephens (32° S) by recreational game fishers. Imber and Russ (1975) recorded one lower beak of juvenile Architeuthis in a fledgling Wandering Albatross — (Diomedea exulans) regurgitation at the Auckland Islands (50° S). Imber (1992) also found juvenile Architeuthis beaks in Wandering Albatross regurgitations at six circumpolar localities — Prince Edward, Macquarie, Auckland, Antipodes, South Georgia, and Gough Islands. Architeuthis is most important numerically and by biomass at Gough and Macquarie Islands. The modal lengths of 8.0–9.0 mm for the lower rostra indicate very young Architeuthis sp. are being eaten. Although the numbers are very low, Imber's records suggest that young Architeuthis are diel vertical migrators with some reaching the surface at night. This in turn suggests that the birds are feeding at night or alternatively that they are eating moribund squid or discards from fishing activity. The information cannot be used to infer Architeuthis distributions since the feeding range of the albatross may exceed 1000 km in a single trip.

Clarke and MacLeod (1982) found that the size distribution of Architeuthis beaks in Sperm whale stomachs in the Tasman Sea are different to those collected further west (i.e., Western Australia and South Africa). Although their sampling route followed a line from off Tasmania to the Three Kings Islands, the west and northwest of the Challenger Plateau (Stations 6, 7, 8) were the sites with the most numerous Architeuthis beaks in Sperm whale stomachs.
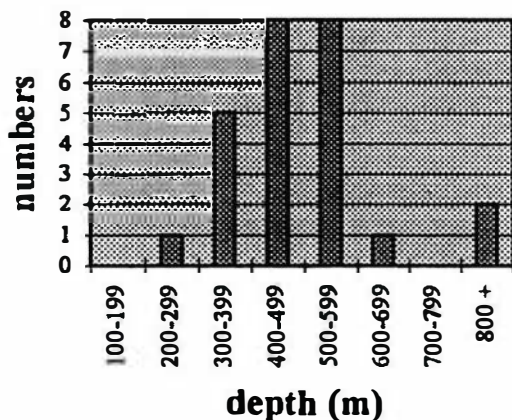

Fig. 27. Depth distribution of trawled New Zealand Architeuthis.

Gaskin and Cawthorn (1967a, b) record *Architeuthis* beaks from the stomachs of Sperm whales caught in the vicinity of Cook Strait. When the rostral lengths of their "Type E" are applied to the regression established by the present study, they indicate *Architeuthis* of 980 mm and 2300 mm ML as well as a less-likely specimen calculated to be in excess of 8000 mm ML. Either the current regression requires more refinement, or their beak was misidentified.

In a review article, Okutani *et al.* (1976) indicated that *Architeuthis* in the diet of Sperm whales off Japan represents only 0.2% by numbers (i.e., one body 585 mm ML and two detached tentacles found in a total of 4 out of 80 whales). In records from around Madeira (Clarke 1962) *Architeuthis* represents 1.7% by numbers, and in Sperm whales from Vigo (Clarke & MacLeod 1974) *Architeuthis* forms 1.4% of the diet by number. Okutani *et al.* (1976) noted that, "The giant squid *Architeuthis* has been usually regarded as the "main" food of Sperm whales, particularly in semi-scientific readings. However, the present findings as well as reports by Clarke and others, indicate that this squid never predominates over the whale's diet (by number)." Clarke (1980) noted a lack of seasonality in *Architeuthis* consumption by Sperm whales off South Africa and recorded more *Architeuthis* in medium- and large-sized whales.

Whales from the eastern Pacific provide less information. Clarke *et al.* (1976) examined Sperm whales off Peru and Chile during November, December, and February and noted that there were no *Architeuthis* beaks in the stomachs despite random samples from 4 whales, and non-random samples from an additional 10 whales.

There was a less consumption in the North Pacific, where Fiscus and Rice (1974) identified the beaks of *Architeuthis* from stomachs of only 12 of 552 Sperm whales. Fiscus and Rice (1974) quoted Berzin (1971) who claimed that *Architeuthis* accounts for 1.7% of numbers of rostra, but about one half of the total weight of food. Similar observations have been made in the North Atlantic, e.g., Clarke (1962) found that in Sperm whales off Madeira *Architeuthis* comprised only 1.73% of beaks, but about 51% of weight of food. However, Martin and Clarke (1986) in a study of Sperm whales captured between Iceland and Greenland found that *Architeuthis* were not a consistent part of the diet.

It would appear that *Architeuthis* occurs both rarely and singly in the diet of sperm whales. Clarke's (1980) data suggest that migration is not a reason for the infrequent consumption. R. Clarke (1955) noted that the average size of squids eaten by Sperm whales appears to be 1020 mm and 1295 mm respectively for whales from the North Atlantic and from the Antarctic, although he also noted that a Sperm whale swallowed whole a squid of 1980 mm ML. Clarke (1980) and Vovk *et al.* (1978) suggested that the consumption of *Architeuthis* may be limited by the large size of the squids.

Form and Function

Bidder (1968) made some useful observations on the form and inferred function in *Architeuthis*.

"In contrast to *Taningia*, the giant *Architeuthis* has flange-fins, but these are relatively small and restricted to the posterior tip of the mantle. At first sight they would seem to be only significant as stabilisers, but with the knowledge that *Architeuthis* has buoyancy comes the realisation that these small fins could be effective during gentle cruising. *Architeuthis* offers many problems not all related to its great size; one is the immense length of the tentacles, which are known to measure over 30 feet in an animal with a mantle only a little over 7 feet long. Another is the great length and mass of the arms, which, together with the small fins, would seem to make the animal top heavy. The mantle of *Architeuthis* is muscular, although not very thick, and active jet propulsion can be postulated. When this is not taking place, it seems likely that the animal cruises, poised at an oblique angle, head down. In this way it might be well placed to snatch prey from shoals of fish or squid cruising below it."

An oblique, head-down position was also postulated by Gauldie *et al.* (1994) on the basis of the internal shape and orientation of the statocyst. Coupled with the information from Boyle (1986) on the relative buoyancy of the body parts, these papers support Bidder's speculation.

Zuev (1966) considered that the caudal fin plays little if any role in creation of the propulsive forces in rapid squid locomotion. Thus the small and weak caudal fin need not be an obstacle to fast movement in *Architeuthis*. As has already been noted, the apparently healthy Specimen 5, without caudal fins, indicates that the fins do not play a critical role in survival.

The level of activity is still unresolved. Robison's (1989) analysis of *Architeuthis* tentacle established a low water content and high levels of protein. These are correlated with higher locomotory capabilities and metabolic activity levels in midwater fishes and crustaceans. He postulated that if the same is true of midwater squids, then *Architeuthis* could be considered an active animal. The present study and that of Perez-Gandarez and Guerra (1978) concerning stomach contents, suggest that *Architeuthis* are good swimmers and successful at capturing active prey, contrary to the opinions of Robson (1933) and Voss (1956).

Wellington:
Lyall Bay
Island Bay
Petone
Makara
Karori lighthouse
Princess Bay, 41°17' S, 174°47' E

Clifford Bay, Cape Campbell

Kaikoura:
Goose Bay
KieKie Bay
at sea near Rakautura

Wairarapa:
Pahau River mouth
1 km from Castlepoint lighthouse
    40°54' S, 176°14' E

Bluff

New Plymouth power station
    39°03' S, 174°04' E

Auckland Island
    51°16' S, 166°52' E

Others:
35°43' S, 174°20' E
41°05' S, 170°52' E
41°21' S, 170°30' E
41°31' S, 170°34' E
41°31' S, 176°43' E
42°03' S, 170°27' E
42°35' S, 170°23' E
42°50.9–49.8' S, 177°16.6–55.3' E
43°12' S, 178°20' W
43°12.3' S, 178°19.9' W
43°24–31' S, 169°20–10' E
43°26' S, 176°23' E
43°26.47' S, 176°23.17' E
43°38' S, 174°14' E
43°38' S, 174°43' E
43°43' S, 174°56' E
43°56.8–44 03.8' S, 175°51.6–30.1' E
44°00' S, 177°35' W
44°09' S, 173°35' E
44°20.4' S, 173°54.3' E
46°18' S, 166°30' E
46°24' S, 166°23' E
46°31' S, 166°30' E
46°32' S, 166°11' E
47°04' S, 169°32' E
47°28' S, 169°35' E
47°29' S, 169°35' E
47°30' S, 169°19' E
47°32' S, 169°10' E
50°50' S, 166°51' E
50°54' S, 166°55' E
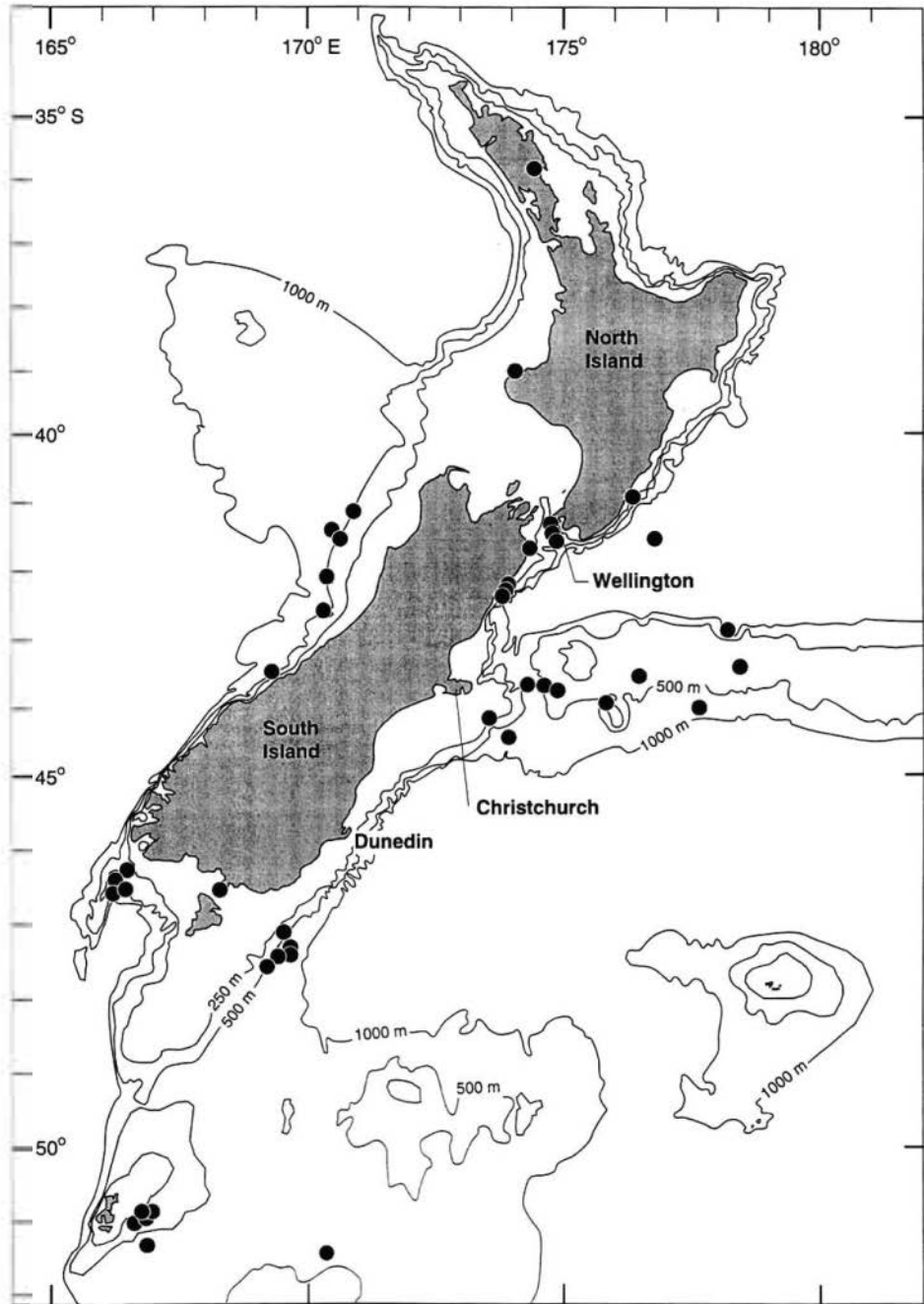51°00' S, 166°42' E
51°18' S, 170°23' E

Fig. 28. Positions of *Architeuthis* capture and stranding around New Zealand.

The effect of temperature and oxygen levels on *Architeuthis* activity is still in the realm of speculation. Clarke (1966) postulated that sudden rises in water temperature would cause osmotic shock and lower blood-oxygen levels. Brix (1983) demonstrated (with a large number of assumptions) that the oxygen-carrying capacity of *Architeuthis* blood dropped off dramatically with increasing temperature. He went on to make comparisons with active oceanic cephalopods and suggested that *Architeuthis* is consequently a "relatively poor swimmer and a passive and sluggish predator". It is not clear from his paper whether he considered the effect of buoyancy. Boyle (1986) discounts suffocation by rising temperatures as a likely cause of strandings around Scotland.

O'Dor (1988) presented calculations that suggest that there is no energetic barrier preventing *Architeuthis* travelling from the Arctic to the Antarctic on a seasonal basis. He further suggested that there are no energetic barriers to prevent global distributions of the larger squids. Maddock and Young (1987), in a study of the lobes of the brain, indicated that *Architeuthis* is unlike any other squid. There are particularly large brachial lobes (involved in arm control) but relatively smaller optic lobes than in any other decapod (in spite of the great size of its eyes). However, its photosensitive vesicles (for extraocular photoreception) are of a size comparable to those of mesopelagic squids.

Taken together, these observations by the above authors suggest that the traditional view of *Architeuthis* as a sluggish and weak creature may be incorrect.

SYSTEMATICS

SYSTEMATIC VALUE OF TRADITIONAL TAXONOMIC CHARACTERS IN *ARCHITEUTHIS*

The systematic value of traditional taxonomic characters has not been established in *Architeuthis* spp. Few authors have had a sufficiently large collection of specimens for direct comparison. Difficulties with preservation and transport have made it virtually impossible to create reference collections which can be used for traditional taxonomic studies.

Verrill's specimens were in poor condition. His observations were frequently based on eye-witness recollections and his own detailed observations were on limited numbers of incomplete specimens. Aldrich's collection was in much better condition and the photographic record has been invaluable. Unfortunately, measurements were not collected in a consistent manner and few details are directly comparable between specimens. Roeleveld and Lipinski (1991) attempted the first consistent collection of data but were limited by having only three specimens with differing storage histories.

It has now become possible to summarise the findings of the present study and draw conclusions as to the taxonomic value of the various characters traditionally used in cephalopod taxonomy.

Body Measures

The data spreadsheets document the range in body indices documented in the present study for ventral mantle length, gladius length, circumference of the mantle aperture, head length (to nuchal crest), head width at nuchal crest, length of combined ink sac and duct, and distance of fin insertion from the mantle aperture. The range in indices for each of these characters is unusually large. Given that the sample size in the present study is still very small for a morphometric analysis, these ranges must be taken as a minimum. The variability within a such a restricted sample in time and space is remarkable. Only the head length measure seems less variable.

The relative size, shape, and sculpture of the mantle aperture is here discarded as a feature of possible taxonomic significance. It is considered that the potential for distortion is too great. Changes occur according to specimen freshness and have been demonstrated to alter further with preservation (Dell, Makara specimen). Thus a "typical" mantle shape can be described only in the broadest terms, although the possibility for changes in shape with growth and sex have been hinted at in this study.

Gladius width is generally considered to be a feature which does not vary greatly within a species. However, the present dataset does not provide evidence that either the width, relative length, or shape of the gladius show variation that can be separated into distinct "forms". The additional data assist with definition of gladius shape but, as has been pointed out in the present study, the various forms of the anterior and posterior of the gladius do not seem to be linked together as a "unit".

The mantle and funnel connectives are, by contrast, very constant in form for all current specimens and appear to conform with the shape exhibited by the family over the entire geographic range. The sim-

plicity of the structures does not lend itself to identification of specific differences and none has been detected.

Figure 8 gives the range of fin indices encountered in the present study. These may be compared with figures available from other parts of the world. The world range includes figures relating to several nominal species. Published measurements have been obtained from Roeleveld and Lipinski (1991, Table 2 p. 438–440) as well as additional measures in the present study (see Appendix 2, for additional records). Fin shape was expected to be a feature of taxonomic significance. However, the high level of variability described in this paper and the continuous nature of that variation over what is still a comparatively small data-set suggest that the natural range is very wide. Features which would be noteworthy, should they occur on other specimens, would be the type of lobular anterior extensions described by Verrill (1879) and the fin shapes attributed to the various Kirk specimens (1882, 1887). However, the present study shows that these shapes are probably the result of damage or misinterpretation.

The divergence between the anterior points of the fin insertion is a feature which has not received attention from other authors. This feature deserves more scrutiny since it serves to describe the way in which the fin is attached to the mantle. Similarly, better measures need to be developed to describe the posterior termination of the fins and the posterior portion of the mantle. A possible sexual difference has been alluded to in this present study.

The present study has established a wide range of variation in head shape within a small geographic and temporal range (Fig. 9). The extent of this variation is unexpectedly high and precludes use of head measures as a specific character.

The presence of an eye sinus has, in the present author's opinion, not been authoritatively established for *Architeuthis*. The skin around the eye aperture is often irregularly thickened and the edge of the aperture sometimes almost lobular.

The thimble-shaped depression at the anterior end of the funnel groove appeared to have potential as a character, but unfortunately the "presence" of the feature is not always clear-cut, and the form, function, and significance of the feature are totally unknown. It has not been previously recorded in the literature and the only equivalent structure I am aware of is from a personal comment of Dr Clyde Roper who discovered a similar structure in the Neoteuthidae. The Neoteuthidae have been proposed as one of the nearest relatives of the Architeuthidae — sharing many other primitive states for characters (Roper & Young 1972; Roeleveld & Lipinski 1991). The feature deserves more

detailed investigation, but the present study suggests that it may be difficult to characterise.

The single transverse neck fold does not provide useful characters. The structure appears to be very "plastic". The ventrolateral expansions of this fold where they border the funnel groove were noticeably variable and were measured in the hope of quantifying this character. The irregular "lumps" on the lateral or ventrolateral aspects of the transverse fold have been variously interpreted as rudimentary lateral neck folds or "olfactory" tubercles. The shape or number of lumps shows no consistency between specimens.

Arms and Suckers

The length of the arms and the total number of suckers have potential as taxonomic characters. However, truncation and regeneration of arms is common and damaged or incomplete specimens will continue to frustrate efforts to use this character. An attempt has been made to illustrate the overlapping ranges of maximum arm length in relation to mantle length in Table 10. The two extremes of the global range are exhibited by juvenile specimens of Roper and Young (1972) and a recent Japanese record (Kubodera & Okutani, pers. comm. 1996).

The relative sizes and cross-sectional shapes of the arms are fairly constant. Prominence and form of the trabeculae varies from arm to arm, but shows reasonable consistency between specimens. This is not considered a useful character. The development of protective membrane varies within narrow limits and is also not a useful character.

Differences in sucker-ring shape and dentition can be defined only with a complete knowledge of the pattern evidenced by the entire sucker complement of a specimen (Tables 11, 12). This information needs to be tempered by a thorough knowledge of the extent of variation throughout the family. A consistent or obvious difference between the arms is that arm IV appears to have slightly smaller suckers with either immediate, or rapid, progression into the angled form of the sucker rings with associated differentiated dentition (the exception in the present data-set is Specimen 1). Consistent differences between groups of specimens have not yet emerged.

The variation in the origin and number of keels on the aboral face of the arms is remarkable. The range of patterns evident in the present data suggests that this feature is highly variable and not useful as a specific character.

Tentacle and tentacular club vary within very small ranges and have not provided characters which could be used to separate species, either between specimens

of the current data-set, or between world geographic zones. Material is still very limited and to date suggests only one species.

Small individual differences in beak thickening colouration, and striation have been identified in the present study. Differences claimed for specimens from other studies have not been supported by rigorous comparisons and are currently not considered useful. The radulae of all published or illustrated records are remarkably similar.

The size of the stomach and spiral caecum varies between specimens (Roeleveld & Lipinski 1991) but much larger datasets will be required to establish this as a valid taxonomic character. Variation in the length and degree of incorporation of the ink sac was evident in the present data-set, but again the significance of this cannot be determined. Gill lamellae numbers appear to vary randomly within a relatively narrow range for the family (or genus).

TAXONOMY OF THE NEW ZEALAND SPECIES

Architeuthis verrilli Kirk, 1882

As has been determined by the Museum of New Zealand Mollusca Collection Manager, Bruce Marshall (1996), there are no remains of *A. verrilli* extant in the Museum of New Zealand. All that remains is the short description and crude illustration by Kirk (1882). The description has several features that suggest that the specimen did not belong to the same genus as all other descriptions subsequently published in the literature or examined by the present author. It does not fit the generic description for *Architeuthis* in the following respects:

First, the extremely stout mantle circumference (122% ML) contrasts with the range of 62–80% of ML established in the present study (p. 18).

Second, the number of suckers is low in relation to arm length (i.e., only 65–71 suckers on arms of almost 3000 mm length — refer to p. 79 for a comparison with the literature).

In Kirk's (1882) description, the tentacles seem excessively long in relation to mantle length ("nearly three times the length of head and body"), and the clubs are armed with *three* rows of suckers. The tentacle length is well outside the range established here (see p. 50). All *Architeuthis* species possess four rows of suckers on the tentacle manus. However, these last two characters were not established by Kirk, for they were described on the basis of a report from a bystander. The fin shape ("obcordate"), with a strongly concave posterior border, is unlike all other *Architeuthis* descriptions. The neck folds, as illustrated, are not characteristic of *Architeuthis* and suggest that Kirk

was influenced by the work of Verrill (1880). Arm III is described as being the longest and stoutest with the greatest sucker density. Although this is not necessarily a contraindication for *Architeuthis*, it is very unusual, and it is more likely that arms III and IV have been confused. Apart from the great size of the squid and the pattern of smooth-rimmed suckers and corresponding tubercles on the tentacle stalks, there are no characters presented in this description to establish this animal as belonging to the Architeuthidae. Too many allowances need to be made for misreporting and illustration of errors to enable this specimen to be considered an architeuthid.

Steenstrupia stockii Kirk, 1882

The illustration of *S. stockii* Kirk, 1882 indicates a much more typical body shape for *Architeuthis* than *A. verrilli*. The gladius is also a typical *Architeuthis* shape, although the illustration shows the gladius upside-down with respect to the adjacent figure of the whole animal. Kirk (1882) referred to a rhomboidal fin otherwise completely unknown in *Architeuthis*. The arms were unusually short, with very few suckers. Although the illustration shows the arms rather abruptly truncated, it is possible that the arms had all been sheared off and healed. The lack of suckers or tubercles on the remaining portions of the tentacle stalk is not considered significant when compared with the present dataset. The gladius (M125403) and a beak possibly belonging to this specimen (M125405) are held in the Museum of New Zealand. I have re-examined these specimens, described earlier in this document. The form of the beak and gladius is consistent with the structures and range of measures identified for beaks and gladii in the present data-set. However, the *A. stockii* gladius may be very short, and may extend the lower limit of the recorded gladius index downwards from 72% (Specimen 14) to only 68% of dorsal mantle length. Kirk did not state by which diagnostic features he considered *Steenstrupia* n. gen. to differ from *Architeuthis*. By inference from his text, it may have been the lateral insertion of the fins, the equal sized arms, the slender body shape, and the long narrow head. These three features all show considerable variation within the present data-set and the measures presented by Kirk (1882) are not sufficiently different to support the erection of a separate genus. *Steenstrupia stockii* Kirk, 1882 is considered to belong to the same genus and species as the present data-set.

Architeuthis longimanus Kirk, 1888

The description of *A. longimanus* is much more sophisticated than that of *A. verrilli*. The description and illustration of the arm cross-sectional shape, the

keels, and protective membranes are not significantly different from the specimens in the present data-set. The sucker density and sizes are also within the range established in the present study. The descriptions of the tentacles and club sucker arrangement, the beak and radula, and the arm suckers and sucker-ring dentition are similar to the present data-set. There is a suggestion in the text that the beak may have been deposited in the Museum of New Zealand, and the detailed and careful illustration suggests that Kirk was able to carry out a leisurely examination. It is possible that the beaks in a bottle with an indecipherable label belong to *A. longimanus*. This represents an alternative opinion to that offered by Marshall (1996). However, regardless of whether the old beak specimens belong to *A. kirkii*, *A. stockii,* or *A. longimanus*, they are comparable in form to those of the present data-set and there are no features which suggest generic or specific differences. As has been pointed out by other authors (e.g., Pfeffer 1912; Dell 1970) the rhomboidal fin shape is unlike that of any described architeuthid. The length of the tentacles (six times the length of head and body combined) is more than three times longer than any other *Architeuthis* tentacle record. As with *A. verrilli*, no remains of *A. longimanus* have been unequivocally identified in the Museum of New Zealand, and the species rests upon a description alone.

A. kirkii C.W. Robson, 1887

The Museum of New Zealand Mollusca Collection Manager, Bruce Marshall, believes that it is probable that M125404 is the tentacle club from *A. kirkii*, and that it is possible that M125406 are the beaks from C.W. Robson's original specimen. The description of this specimen clearly identifies it as an architeuthid; specifically, the body colour, texture, and shape, the description of the arms, the pattern of suckers on the tentacles, and above all the oval shape of the fins. Robson also mentioned that the two sessile arms next to the tentacular clubs were thicker than the rest — the usual condition for *Architeuthis* species. The original description stated that the gladius was extracted from the specimen and this gladius is believed to be the same as the lot labelled *A. kirkii* and examined by the present author at Museum of New Zealand in 1983.

R.K. Dell's (1970) redescription of *A. kirkii*

In 1956, Dell received the first fresh specimen available to New Zealand science since the work of Kirk (1879, 1882, 1887) and Robson (1887). Dell (1952) had already noted that the remains of the earlier specimens consisted of a tentacle club and two pairs of beaks in bottles with illegible labels. The two mounted gladii appear to have escaped his attention.

The arrival of new material required Dell to review the New Zealand records and, as a result of his examination, he cautioned against placing too much reliance on the details of the figures prepared by Kirk. Dell's specimen agreed most closely with the description of *A. kirkii* C.W. Robson, 1887, and Dell (1970) re-described the species "so that the name is placed upon a firmer basis". He did not, however, erect a neotype. Dell's description of the 1956 specimen and the present author's reexamination of that specimen (see p. 65) indicate that it fits within the parameters established for all major characters in the present data-set.

Status of *Architeuthis kirkii* C.W. Robson, 1887

On the basis of the above evidence, all the present specimens could be assigned to *A. kirkii* Robson, as redescribed by Dell (1970). This interim assignment was adopted by Allan (1948) and Gauldie *et al.* (1994) in the absence of a more extensive comparison of *A. kirkii* with *Architeuthis* species from other parts of the world.

Dell (1970) had already noted that *A. kirkii* agreed very well with the description of *Architeuthis* sp. (Rae 1950) from near Aberdeen, Scotland. Dell (1970) considered that both his own specimen and *Architeuthis* sp. (Rae 1950) agreed in general with the description of *A. clarkei* G.C. Robson, 1933, "except as regards fin length and a number of less marked characters which are possibly of minor importance." He warned that little was known of the extent of variation. Dell (1970) did not compare his specimen directly with the descriptions of *A. dux* Steenstrup, 1857, *A. sanctipauli* Velain, 1875, *A. physeteris* (Joubin, 1900), *A. japonica* Pfeffer, 1912, or with Sasaki's (1929) specimen of *A. japonica*. Neither did Dell refer to the monographical work by Pfeffer (1912).

My conclusions are summarised as follows :
Architeuthis verrilli Kirk, 1882, *species dubium*
Architeuthis stockii (Kirk, 1882)
   = *A. kirkii* C.W. Robson, 1887
   = *A. longimanus* Kirk, 1888
   = *A. kirkii*, Allan (1948) specimen
   = *A. kirkii*, Dell (1970) specimen

OTHER SPECIES IN THE LITERATURE AND THEIR VALIDITY

Characters that are frequently used in the literature for other squid families have not been used, or have not been available for use, to justify the specific descriptions in the family Architeuthidae. Varying numbers of nominal species exist, depending on the criteria applied. An early monograph on the family

was produced by Pfeffer (1912). With very limited material on hand he could do little more than reiterate the published descriptions and point out some of the inconsistencies — particularly in the work by Kirk (1882, 1888) and Robson (1887). To quote Pfeffer (1912, p. 10) "Our morphological knowledge of the group was not broadened substantially by them." In discussing fin shape he wrote (1912, p. 3), "the differences are so great in the descriptions of fin shape given by Verrill, Kirk and Robson that we could not find a similar situation in any other family of Oegopsida". Pfeffer (1912, p. 7) also mentioned that if one were to take all the differing descriptions of the mandibles at face value, then a new species would need to be erected for each description.

Clarke (1966), in his review of oceanic squids, tabulated the nominal species and type material of family Architeuthidae, but offered no opinion on the validity of the names.

Stephen (1962) and Dell (1970) considered *A. bouyeri* Crosse & Fisher, 1862 to be a *nomen nudum* as it was "based on sketches of a live animal under water and of the posterior extremity and fin, and could hardly be reidentified" (Dell 1970). The descriptions of *A. hartingii* Verrill are based solely on a buccal mass in the Utrecht Museum illustrated by Harting (1861), and that of *A. grandis* (Owen, 1881), on a severed fourth arm alone. Dell (1970) believes that these, too, should be considered *nomina nuda*.

G. Voss (unpublished manuscript, pers. comm. 1988, reproduced in Appendix 1) reexamined the status of *Architeuthis* nomenclature and proposed elimination of 11 nominal species as *species dubia* : *A. bouyerii, A. hartingii, A. kirkii, A. martensii, A. mouchezii, A. nawaji, A. physeteris, A. proboscideus, A. stockii, A. titan,* and *A. verrilli.* G. Voss was not aware of the existence of the gladii of *A. stockii* and *A. kirkii* in the Museum of New Zealand, thus these species may be saved from relegation to *species dubia.* The description of *proboscideus* is more detailed than many others (see More 1875).

Architeuthis physeteris (Joubin, 1900) was based on a headless body and wrongly identified as a histioteuthid until corrected by Appellöf (1902) (see N. Voss 1969). Since G. Voss (1956) redescribed *A. physeteris* from Florida, we can assume that he was fully aware of the status of that original description and type material. It is not clear why he subsequently considered it to be a *species dubium.*

The epithet *titan* was the proof name for *A. dux,* and the type of *A. mouchezii* was the same specimen as the type of *A. sanctipauli* so these two names can readily be eliminated.

North Pacific

Pfeffer (1912) referred to one North Pacific speci-

men (Mitsukuri & Ikeda 1895) which he redescribed and named **A**. *japonica,* differentiating it from an earlier *Architeuthis* description from the same North Pacific region (*A. martensii* (Hilgendorf, 1880)). Based on the published description he surmised that the large Hilgendorf specimen (*Megateuthis martensii* Hilgendorf, 1880) had a smaller and broader fin and relatively shorter arm than the specimen of Mitsukuri and Ikeda (1895). As a result of the variation evident in the present study, it now seems that the characters he used to differentiate the two species were not valid, all being within the normal range of variation for specimens from the South Pacific (present study). Subsequent specimens of "*A. japonica*" (Nesis *et. al.* 1985; Fiscus and Rice 1974; Okutani *et al.* 1976; and the Hawaiian material examined by the present author) do not provide any additional characters that distinguish it from *A. martensii.* Therefore, and in the absence of any specific characters outside the presently established range of variation, *Architeuthis martensii* takes precedence over *A. japonica* :

Architeuthis martensii (Hilgendorf, 1880)
= *Architeuthis* sp. (Mitsukuri & Ikeda 1895)
= *A. japonica* Pfeffer, 1912 (same specimen)
= *A. japonica* — as described by Sasaki 1929

This opinion is supported by Nesis *et al.* (1985), Nesis (1987), and also Okutani (pers. comm. 1996). Sasaki (1916, 1929) likewise acknowledged that his specimen agreed "very well" with that of Mitsukuri and Ikeda (1895) and "in every particular" with that of Hilgendorf (1880).

Note: Dong (1984) published a photo of his specimen of *A. japonica* which appears to differ in several respects from other North Pacific *Architeuthis.* The arms do not appear as long, nor sufficiently robust, the suckers on the tips of the arms appear large in relation to the diameter of the arm, and the mantle shows a very large expansion posterior to the mantle aperture — whereas a more conical shape might be expected for this size range. However, the photo is the only substantial evidence for the shape of the animal, and is possibly misleading. This record indicates that there may be an additional species in the North Pacific.

North Atlantic

Pfeffer (1912) listed the descriptions and records of species from the North Atlantic and provided a useful account of Steenstrup's work in relation to the family. Pfeffer made no attempt to compare or question the validity of the species in existence at that time. Ritchie (1918) compared his Scottish specimen

with the literature, expecting to attribute it to *A. monachus* or *A. dux* on the basis of geography, but claimed he could not get good agreement with either *A. dux* or *A. harveyi* from the opposite side of the Atlantic. Unfortunately he gave no details or justification for this conclusion.

Stephen (1962) combined the feature of a "large head" in relation to mantle length with rounded or elongate cordate fins without large anterior lobes as characterising the European species *A. dux*, and alluded to similarities with the recently described *A. clarkei*. Stephen was already aware that Frost's (1936) Eastern Atlantic specimen did not fit neatly into his proposed key, in that the body resembled *A. clarkei*. Stephen admitted difficulties were compounded by lack of both sex information and a range of development stages.

In his erection of *A. clarkei*, Robson (1933) proposed that the mantle aperture is only a little narrower than maximum width and therefore unlike *A. princeps* and possibly *A. harveyi*. He also claimed that the posterior mantle narrows much more abruptly than in *A. princeps* and is broader than in *A. harveyi*. Robson (1933) proposed that the *A. clarkei* head is longer (20–25% of ML) than in *A. harveyi* (13%) and *A. princeps* (19%). It is clear from the present data-set that such differences are not significant. Body shape varies considerably and head length varies from 13 to 21% of ML over only 14 specimens.

Aldrich (1968, 1991) synonymised all North Atlantic species with *Architeuthis dux* Steenstrup. He presented no detailed rationale except to say that the differences in the shapes of the fins could have been the result of damage. His conclusion on the effect of fin damage is supported by the present study. Aldrich also considered that there was great similarity in the sucker arrangements of the four North Atlantic "species", and in the vane and cap-like configuration of the conus.

Aldrich (1991) postulated that there may be a range of forms within a given genotype but did not see that as a reason to discontinue assigning all North Atlantic specimens to *A. dux* Steenstrup.

Bruun (1945) and Kjennerud (1958) indirectly supported the view that there is no evidence to maintain any *Architeuthis* species other than *A. dux* Steenstrup in the North Atlantic. Voss (unpublished manuscript, pers. comm. 1988, see Appendix 1) and Nesis *et al.* (1985) provide additional support for this present proposal .

There is a complex history surrounding the assignment of priority of *A. dux* over *A. monachus*. This has been fully expounded by Verrill (1882) and Pfeffer (1912), and *A. monachus* is placed in synonymy with *A. dux*. Robson (1933) believed *A. monachus* should be considered a *nomen nudum*. Thus, in the absence of examination of types and relying on the literature :

Architeuthis dux Steenstrup, 1857
  = *A. monachus* Steenstrup, 1857
  = *A. harveyi* Kent, 1874
  = *A. harveyi* Verrill, 1882
  = *A. princeps* Verrill, 1882
  = *A. clarkei* Robson, 1933
  = *A.* sp. (Rae 1950)

South Atlantic

Perez-Gandaras and Guerra (1978) compared their South Atlantic specimen with existing descriptions and concluded that their *Architeuthis* sp. was very similar to *A. kirkii* (see Dell 1970) and to *A. japonica* as described by Akimushkin (1963). Unfortunately, they did not detail their reasoning, but it was one of the first attempts (other than Dell 1970) to compare species from different oceans. They also stated that their specimen differed from *A. physeteris* Voss 1956; again no reasons were given. They claimed the beak was unlike that in Roper and Young (1972), Clarke and MacLeod (1974) and Fiscus and Rice (1974) but did not say in what way it differed.

Clarke (1980) was prevented from making adequate comparisons of his specimens with others by the poor existing descriptions of the southern forms (*A. kirkii, A. longimanus, A. sanctipauli, A. stockii, A. verrilli*). A feature of significance mentioned in the "Diet of Sperm Whales" was the lack of "anterior lobes", differentiating them from *A. harveyi* Verrill, 1882 and *A. princeps* Verrill, 1882. This had already been discounted as a character (e.g., Bruun 1945; Aldrich 1968). (See earlier discussion on the small free anterior lobes.) Sucker dentition, relative arm length, and the length of the tentacle stalk have been shown to exhibit wide variation. Comparisons with the four nominal New Zealand species are not possible because of the poor quality of the evidence available from the New Zealand literature. Clarke (1980) noted similarities between his *Architeuthis* sp. and *A. sanctipauli* (Vélain 1877). Vélain's woodcut of *A. sanctipauli* certainly resembles Clarke's (1980, fig. 37b b) posterior mantle and fin shape, but Vélain's illustration provides insufficient evidence to compare the tentacle length and club breadth. Features of note appear to be : the truncated shape of the arms, the very narrow lateral fins, the very long tentacles, and the posterior termination of the gladius. As Pfeffer (1912) has already noted, the arms are often damaged in *Architeuthis*. Single fin width can be very narrow in other geographic regions (e.g., Specimens 10 and 14 of the current study; "*A. physeteris*" G. Voss 1956) and does not form sufficient justification for *A. sanctipauli*

as a separate species. The relative length of the gladius varies over a wide range in the present study (72–94% ML) and "posterior" termination of the gladius is not unique. The "long" tentacles are not considered a useful character. Accordingly, it is proposed to consider *A. sanctipauli* Vélain, 1875 a synonym of *A. dux* Steenstrup, 1857. Again, Clarke (1980) used features from a limited number of incomplete specimens.

Roeleveld and Lipinski (1991) cautioned against classifying on the basis of nonoverlapping distributions or assuming that the oldest name in each region is the valid one. They established that their three specimens showed greater affinity with the beak-ML regression of the North Atlantic rather than that from the Southern Hemisphere, but that is hardly surprising given the inadequacy of the southern descriptions. The data on beaks and ML are still accumulating (see p. 38) and are dubious for establishing similarities. They correctly recognised that the anterior fin lobes must be treated with caution, and information from the present study suggests that the presence of "small anterior lobes" does not reliably identify or link specimens with particular regions or species. The sculpture of the oral arm surfaces has been established in the present study as yet another highly variable character, and suggests that the similarity noted between *A. dux* and Roeleveld and Lipinski's (1991) Green Point specimen is probably just fortuitous. M. Roeleveld (comment on this paper when in ms form) has observed these sculptures of the oral arm surface in all North and South Atlantic specimens she has examined and suggests that the present New Zealand data confirm that it occurs in all *Architeuthis* specimens to a greater or lesser extent. The conclusion must be that their specimens correspond quite well to the features of *A. dux*, rather than that they differ in specific features from the "southern forms".

The record for *A. physeteris* (Joubin, 1900) is based on only two specimens, both in poor condition, the latter described by G. Voss (1956). No subsequent specimens have been attributed to this species. Given the extreme variability that has been demonstrated in the present data-set for supposed diagnostic features — mantle shape, and fin size and shape — it is difficult to justify the species. The sucker dentition differences are not described in sufficient detail to permit valid comparisons. This may explain why G. Voss himself later regarded this as a *species dubium* (unpublished manuscript, Appendix 1). Consequently it is suggested that :

Architeuthis dux Steenstrup, 1857
  = *A. sanctipauli* Vélain, 1875 and Vélain (1877)
  = *A. physeteris* (Joubin, 1900)

  = *A. harveyi* Verrill *sensu* Cadenat (1936)
  = *A.* sp. A. (Perez-Gandaras & Guerra 1978)
  = *A.* sp. (Clarke 1980)
  = *A.* sp. (Roeleveld & Lipinski 1991).

All *Architeuthis* Species

Nesis *et al.* (1985) and Nesis (1987) have already proposed that there may be only three species of *Architeuthis* — *A. dux*, *A. japonica*, and *A. sanctipauli* or alternatively three subspecies *A. dux dux*, *A. dux sanctipauli*, and *A. dux japonica* dwelling in the North Atlantic, South Atlantic–Indian Oceans, and North Pacific respectively. However, Nesis does not present the evidence for this proposal, and speciation based solely on geographic distribution is not supportable.

As a result of the rationale presented above, I suggest reducing the number of species to the following : *A. dux*, *A. martensii,* and *A. kirkii*. Further reductions in the number of species are proposed below.

The descriptions of *A. japonica* by Pfeffer (1912) and Sasaki (1929) do not clearly contrast or differentiate the species from *A. dux*. Pfeffer (1912) drew attention to the relative sizes of the medial and marginal manal suckers, suggesting that the marginal suckers are smaller in *A. japonica* than in Verrill's illustration of *A. harveyi*. On examination of Plate 6 in Verrill (1882) I disagree with this conclusion. The claim of differential sizes in the ventral or dorsal medial rows of manal suckers is also not supported with actual measurements. As has been established in the present study, body and fin proportions, gladius structure, and arm length are highly variable in the group. These have not been formally presented as the reasons for separating *A. martensii* (Hilgendorf, 1880), *A. japonica* Pfeffer, 1912, and *A. japonica* (Sasaki 1929) from *A. dux* or other Atlantic or South Pacific species. Examination of the original descriptions of these Japanese specimens does not identify differences from descriptions of North Atlantic *A. dux* (Steenstrup 1898; Sivertson 1955; Knudsen 1957; Kjennerud 1958). Consequently it is suggested that *A. martensii* (Hilgendorf, 1880) is conspecific with *A. dux* Steenstrup, 1857 until such time as additional material or alternative characters serve to unequivocally separate this species.

The published description of *Architeuthis sanctipauli* Vélain 1875 has not proved useful or sufficiently distinctive for other researchers to utilise in identification or differentiation of their specimens (Dell 1970; Clarke 1980; Nesis *et al.* 1985; Roeleveld & Lipinski 1991).

Arguments have already been presented by Dell (1970) pointing out the similarity between *A. kirkii* and *Architeuthis* sp. (Rae 1950) and the agreement of both these specimens with *A. clarkei* Robson, 1933. The

present study confirms this conclusion and, for reasons already presented earlier, suggests that *A. kirkii* be synonymised with *A. dux* Steenstrup, 1857.

CONCLUSIONS ON THE TAXONOMY OF GIANT SQUID

The present study reduces all nominal species to the one earliest adequate species record (*Architeuthis dux* Steenstrup, 1857). Documentation of the high level of variation in characters normally used to differentiate squid species is the major contribution of this New Zealand study. The extensive and consistent documentation arising out of the current study serves as a baseline for determining the extent of variation present in characters of proposed taxonomic significance. The consideration of both standard morphological descriptions and multi-dimensional scaling techniques indicated that each specimen varied substantially from others in the data-set. The standard historical response to this situation was to erect a new species for each single occurrence. It became obvious from about the 1950s onwards that this could not continue (see Rae 1950; Clarke 1980). The data-set from New Zealand has been treated on the premise that there were likely to be fewer species than specimens. The extensive data from the present study are interpreted to indicate an extremely high level of natural variability in the species. This is not at odds with the habit proposed for the squid — fast growth rate, possibly solitary existence, low population density, and wide, possibly cosmopolitan, distribution. The level of variation has been documented for a relatively restricted size range and predominantly on females, but even so, in the majority of published records for *Architeuthis* the supposed taxonomic characters fit within the range of variation established for this present dataset from the Southwest Pacific. I suggest that the nominal species erected over the last 140 years can no longer be supported in the face of this evidence. Other, new characters and additional techniques will need to be employed to reliably establish any specific differentiation in the family Architeuthidae. With the possible exception of the Toll and Hess (1981) specimen, the conclusion of this study is that, on the present evidence, the family Architeuthidae supports a single genus and species — *Architeuthis dux* Steenstrup, 1857.

FAMILY DESCRIPTION

Family **ARCHITEUTHIDAE** Steenstrup, 1857

Large squid, mantle length can exceed 2000 mm for immature females. Smallest record 10.3 mm ML. Mantle thick, firm, but not muscular. Mantle extends middorsal anteriorly in low broad extension, ventral mantle opening slightly emarginated in association with the pallial connectives. Mantle shape varies from spindle-shaped through anteriorly cylindrical to narrowly conical. Posterior third of mantle tapers to a narrow conical spike. Mantle colour brownish-red, but may exhibit purple and orange shades. External skin usually abraded. Fins relatively small, weak and varying in thickness, and the combined outline may vary from round to narrow oval. In their natural condition the fins extend to the posterior end of the mantle as a narrow lateral keel. Free lobes of fins absent or restricted to an anterior extension of < 50 mm. Position of anterior fin insertion varies from almost dorsal to almost lateral.

Nuchal cartilage mantle component simple, straight groove with thickened anterior edges. Cross-sectional shape a broad "W". Funnel-mantle locking cartilage a simple ridge with slight lateral curvature, associated with tear-shaped unpigmented region in inner mantle. Inner mantle colour deep red-brown, thick skin covering internal organs also red-brown.

Head shape varies from narrow cylindrical, dumbbell-shaped, to short and broad. Dorsal surface often abraded, frequently with firm silvery tissue below the epidermis, ventral surface less intensely coloured. Nuchal cartilage white, spatulate, anterior and posterior portions rounded rectangular, greatest width on anterior portion, narrowest point two-thirds along length. Raised central portion of cartilage bears narrow longitudinal groove with a ridge either side.

Buccal connectives attach to dorsal, dorsal, ventral, dorsal sides of arms I–IV respectively. Buccal lappets thin, elastic, aboral faces mauve. Funnel groove shallow and broad with ill-defined edges. Thimble-shaped depression often present in anterior portion of funnel groove. Eye aperture may have irregular and thickened edges and lobes, but no sinus present. Nuchal crest weak and barely elevated, often with slight middorsal anterior flexure, generally exhibiting a strong colour change. Skin posterior to the nuchal crest deep red-brown. Two to three irregular thickenings on lateral or ventrolateral portion of nuchal fold. Fold extends ventrally into two large triangular flaps bordering the funnel groove. Insertion point of funnel adductors varies from posterior to extreme anterior end of funnel groove.

Funnel large, broad, sometimes ventrally directed, generally reaching posterior border of eye. Texture varies from thick and muscular to thin and weak. Funnel colour may vary somewhat from that of mantle and head. Funnel valve large, D-shaped. Funnel organ present but shape extremely variable. Some

specimens may possess one or more papillae at the anterior extent of the funnel organ. Funnel-locking cartilage white, elongate oval, pointed anteriorly, slightly raised above funnel surface. Cartilage is slightly overhung on all sides, skin red-brown on underside, groove simple, broad and frequently fading posteriorly.

Arms thick, length frequently $\oplus$ ML. Arm formula varies, but arms I and II generally shorter than III and IV. No webs between bases of arms, cross-sectional shape at base variable, but often oval (arms I, II, III) to trapezoid (arm IV). Sucker-bearing (oral) faces of arms pink, lateral and aboral faces darker. Short protective membranes on all oral faces of arms, ventral and dorsal membranes similar, supported by thick broad, bi-lobed trabeculae originating on either side of the sucker base. Thickness of the protective membranes variable, sometimes occurring as lobes, or as a continuous membrane with perforations near the region of the sucker pedicel. Swimming keels variable; may be present as single or double keels, originating at base of arms, be restricted to outer half of arms, or may be absent.

Suckers biserial on all arms. Arm IV sucker density generally higher, suckers smaller. The arrangement appears to result in opposite rather than alternating suckers. Suckers globular with eccentric pedicels and inserted into raised, almost conical muscular base of pedicel. First sucker on arms may be abnormally small, first 6–12 suckers rapidly increase to a maximum size and then decrease gradually to tip of arms. Sucker dentition proximally on arms generally commences as regular triangular teeth around entire rim of sucker (often 40–50) gradually reducing in number and increasing in size on outer edge, becoming irregular and fused on the proximal edge. Distal edge of sucker ring becoming more globular and extensive as the lumen tilts to face more proximally. A deep notch present in the proximal edge of the sucker ring and a thickened ridge-like ring around the outside of the teeth. Reduction in teeth and transition in sucker-ring shape occurs more rapidly on arm IV than the other three arms. All sucker-bearing faces of the arms with papillae at irregular intervals along the zigzag shaped groove which runs up the centre of the oral face of the arm. Hectocotylisation may be indistinct.

Tentacles very long, the club only slightly expanded with a keel on the aboral face. Minimal protective membranes. An alternating set of knobs and corresponding suckers present for most of length of the tentacle stalk, the spacing becoming closer towards the carpus. Carpus bears a cluster of smooth-ringed suckers, followed by small regularly toothed suckers. Manus has 11–14 rows of quadriserially arranged large suckers, the outer two rows smaller than the two inner rows. Dactylus suckers also smaller, regularly toothed, with very oblique quadriserial arrangement. Tentacle tip with smooth-ringed, almost sessile suckers, extreme tip of the tentacle with a flap that is folded back over the last row of suckers.

Gills with 68–71 lamellae, pink, base deep red-brown. Salivary glands apricot-coloured; ovoid caecum with 4–5 orange spiral bands; stomach white, large, elongate, separated into two compartments internally; digestive gland orange-brown. Rectum swollen, anal flaps D-shaped with bifurcated anal papillae. Ink gland elongate, posterior end partially free of intestine; a hemispherical white gland at posterior tip. Ovary white, filamentous, soft, positioned in apex of mantle cavity. Paired nidamental glands white, close to ventral midline, each tear-shaped, longitudinally bilobed. Oviduct variable in shape, accessory glands not always evident. Penis very long, spermatophores also very long. Needham's sac and vas deferens white and coiled.

Lower beak with short rostral edge in relation to wing length, a broad rostrum with a small hook, broad wings and hood, very low wing fold, jaw angle not obscured when viewed from the side, a prominent shoulder tooth present. Hood stands high above the crest, a deep notch present in hood midline, a thickened crest and a large lateral wall, often without ridges. Chitin thin on hood, wings, and lateral walls. Tips of upper and lower rostra may show considerable wear.

Gladius weak, brittle, partially transparent, rachis ill-defined with variable degree of narrowing anteriorly. Posterior end develops lateral wings with thickened outer edge and internal ridges. Wings taper, extreme posterior end of gladius has short, conical, ill-defined end-cone, partially fused and occasionally with a very small keel. Gladius does not extend to posterior end of mantle but terminates in a well-formed fleshy sac. Radula with tricuspid median row, two lateral rows of bicuspid teeth, further row of uni-cuspid teeth and marginal plates.

This description varies from the diagnosis offered by Pfeffer (1912) in that it suggests :

* the body is not flaccid
* account is taken of the variability in mantle and fin shape
* there is no eye sinus
* the "longitudinal neck folds" are believed to be too insubstantial to warrant this description
* variability in presence of keels is documented
* the dactylus suckers approach triserial rather than quadriserial arrangement
* hectocotylisation has not been observed on the male specimen to hand.

This description varies from the diagnosis offered by Sasaki (1929) in that it suggests :
- the funnel groove is not always well defined
- the inner surface of the funnel groove frequently has an unusual depression
- the mantle and fins are not sharply pointed behind
- there is a difference in terminology of the transverse nuchal fold and olfactory crest
- not all suckers are arranged quadriserially on clubs
- the conus of the gladius sometimes bears a ridge or spine

- the fins may sometimes have a small indentation in the anterior attachment.

This description varies from the diagnosis offered by Nesis (1987) in that it suggests :
- the "short tail" is believed to be the result of damage and definition problems
- there is no evidence that both ventral arms are hectocotylised
- the evidence for a 5 m mantle length is very scarce.

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APPENDIX 1

Notes on the genus *Architeuthis*
by G. Voss

Genus *Architeuthis* Steenstrup, 1857

The genus *Architeuthis* has been reviewed or discussed in detail by a number of writers (Gervais 1875; Verrill 1880; Steenstrup 1898; Pfeffer 1912; Robson 1933; Stephen 1962; Clarke 1966; Aldrich 1968; Dell 1970), yet it remains in a far from satisfactory state. Since 1857 when Steenstrup presented his first account of these animals, numerous remains — beaks, radula, arms, suckers, intestines, etc., — have been described, forming the basis for new names. Later, with increased interest, facilities, and students, whole animals in good states of preservation have been measured, studied, photographed, and preserved. Most of these specimens have been described in the literature or have been listed under specific names. In fact, there is now a considerable body of knowledge on the species inhabiting the North Atlantic, divided between five nominal species: *A. dux*, *A. harveyi*, *A. princeps*, *A. physeteris*, and *A. clarkei*. To the casual observer these names appear to have stability and the species are fairly well differentiated. The sad fact, however, is that these names have been applied without reference back to identifiable type material. Furthermore, except possibly for *A. japonicus*, none of the type material [is] now extant, nor the original descriptions upon which the names are based, is sufficiently detailed and accurate to permit specific identification, regardless of amplifications and detailed descriptions of subsequent specimens thought to belong to the nominal species.

Dell (1970: 27) has reviewed the status of the New Zealand species; no one has attempted a review on a similar basis of the Atlantic forms. As a contribution toward a clarification of the problem, Clarke (1966, p. 102) tabulated information on the 20 names applicable to the genus. A careful review of the original descriptions and type material has revealed a number of errors in Clarke's table. I therefore present a new tabulation (Table 1). All dates, authors, and type material available at the time the descriptions were written have been personally verified. In the last column I have given my own opinion as to the status of the nominal species based upon my evaluation of the systematic value of the parts for specific identification.

An examination of the tabulated information clearly shows that, with only three exceptions, the 12 nominal species from the North Atlantic are based upon only the beaks, a few suckers, twice including a tentacle, and twice upon laymen's cursory descriptions and sketches with no type material. *Architeuthis physeteris* and *A. clarkei* were both based upon mutilated material, the latter with great discrepancies in the description. Even the type of *A. nawaji* was in a very poor state of preservation when finally examined by Cadenat (1936: 277) and only selected pieces are preserved in the National History Museum at La Rochelle.

Setting aside the problem of specific identification based on type material, the basis for specific identification of subsequent material has been primarily the shape of the fins, whether marginal throughout (*physeteris, clarkei*) or with free anterior margins (*harveyi, princeps*); the relative length of the arms (almost all specimens have lost part or all of the arms); and minor differences in sucker dentition. It is my opinion, and here I join Steenstrup (1882a: 156) and Aldrich (1968: 394), that in fresh undamaged specimens there is no free accentuated anterior lobe as figured for *princeps* and *harveyi* (auct.) and that these are caused by separation of the anterior portion of the fins by decomposition and stranding. The relative lengths of arms of squids are variable in many species and we have insufficient data at present to indicate the validity of this character, even where it can be ascertained with some degree of satisfaction. The dentition of most oceanic squids is variable both along the length of a single arm, from arm to arm, and in some cases between the two sexes. Likewise, tentacular club sucker dentition is so variable that in some species of squids it is practically valueless.

What might be termed "good" specific characters have not so far been usable or available: details of the male and female genitals, method of hectocotylisation, structure of the spermatophores, form of the funnel organ, tentacular club sucker arrangement, and the

arrangement of the carpal suckers. The radulae so far illustrated show an amazing similarity between all the species illustrated.

At present, I am of the personal opinion that we may indeed be dealing with a single widely distributed oceanic species that exhibits at best subspecific characters in various parts of the world ocean. If such is proved true, *A. dux* Steenstrup, 1857 has distinct priority. If, however, it is shown to be a complex of species, it is my considered opinion that all of the present names with the possible exception of *A. japonicus* be considered *species dubia* and that proven species be renamed, the species based upon adequate material for positive specific identification, and the names protected by proper type material and detailed original descriptions. As an alternative, an appeal might be made to the ICNZ for the retention of certain names if considered necessary for stability. I do not agree with this, however.

Since this is a drastic move that may not be acceptable to present workers I here am presenting a modified list of what I consider may be acceptable species. They should be used, however, only in light of the above discussion.

Type species: *Architeuthis dux* Steenstrup, 1857; species first mentioned.

Architeuthis dux Steenstrup, 1857

None of the 12 names in the literature that have been applied to North Atlantic species of *Architeuthis* are based upon type material and original descriptions permitting positive specific identification of subsequent specimens. Based on the premise that there is probably only one species of *Architeuthis* in the North Atlantic, *A. dux* has priority by first mention and the remaining names must be considered synonyms. In actuality, in my opinion, they are all *species dubia* including *A. dux*. Their status is shown in the following table.

Clarke (1966: 98) has summarized the Atlantic records of *Architeuthis* which were all considered to refer to *A. dux*. The records extend from the Gulf of Mexico, and the Straits of Florida and Bahamas (Voss) along the eastern coast of North America to New-foundland, West Greenland, Iceland, Scandinavia to the British Isles, France, the Azores, and Madeira. While most of the reports are from cold waters, the animals are common in warm waters and valid reports of dozens of specimens on the surface of the Straits of Florida off Miami (Voss unpublished) tend to confirm the opinion that these are essentially warm-water forms. Clarke (1966: 98) has questioned the reason for lack of stranding records in warm waters such as the southeastern United States. The cause almost certainly lies in the large number of sharks in these waters and the near impossibility of such a large carcass reaching shore without attracting the attention of these predators. All of the specimens from southern waters examined by me have been partially mutilated by these animals. The species probably lives in moderate depths along the upper portion of the continental slope, where they must occur in large numbers to have been able to largely support the former great numbers of sperm whales, their major predator. With the decrease in these whales because of over-fishing, the number of *Architeuthis* may noticeably increase with time.

Arthiteuthis japonicus Pfeffer, 1912

This is almost certainly the same as *A. martensii* Hilgendorf, 1880 which, however, was inadequately described from poor material obtained in a fish market. Mitsukuri and Ikeda (1895) described a fresh specimen caught in a fish net near the bay of Tokyo but did not give it a name. Pfeffer (1912: 27) gave a new description based upon Mitsukuri and Ikeda's English version and gave the specimen the name *japonicus*. Sasaki (1929) fully described another specimen clearly referable to the same species. Its further distribution is unknown. The specimens closely resemble described North Atlantic forms.

Architeuthis kirki [sic] Robson, 1887

This species was described by C.W. Robson, a New Zealand lighthouse keeper. Another specimen was described by Dell (1970: 28) and ascribed to Robson's species. The description differs in only minor ways from the Atlantic species.

Table 1. List of type specimens of the genus *Architeuthis* (from Gil Voss).

Name	Locality	How caught	Type material	Comments
A. dux Steenstrup, 1857	W. Atlantic, N. of the Bahamas, 31° N, 76° W	Dead at surface injured by shark.	Arm, suckers, buccal mass, gladius, spiral stomach, etc.	
A. monachus Steenstrup, 1857	Denmark	Washed ashore	Beaks	
A. bouyerii Crosse & Fischer, 1862	Between Madeira and Teneriffe	Alive at surface	Description & sketches	Species dubium
A. harveyii Kent, 1874	Conception Bay, Newfoundland	Alive at surface	Tentacle complete with club	
A. princeps Verrill, 1875	1. Grand Banks 2. ? = syntypes	1. Dead at surface 2. Sperm whale stomach	1. Jaws 2. Jaws	
A. proboscideus More, 1875	Dingle, Kerry, Ireland	Washed ashore	Descriptions in letters dated 1673 and original sketch	Species dubium
A. sanctipaulii Vélain, 1875 *A. mouchezii* Vélain = same animal	St Paul Island, Indian Ocean	Dead at surface, washed ashore	Tentacle, beak, and pharynx	Species dubium
A. titan Steenstrup, 1875				Proof name published by Verrill, 1875, not valid.
A. hartingii Verrill, 1875	Unknown locality		Jaws, buccal mass, detached suckers	Species dubium
A. martensii Hilgendorf, 1880	Fish market, Yeddo, Japan (= Tokyo)		Various parts	Species dubium
A. verrilli Kirk, 1882	Island Bay, Cook Strait, New Zealand	Stranded	Complete animal, most since lost	Species dubium
A. stockii (Kirk, 1882)	Cook Strait, New Zealand	Stranded	Complete animal, part since lost	Species dubium
A. kirkii C.W. Robson, 1887	Cape Campbell, New Zealand	Stranded	Complete animal	
A. longimanus Kirk, 1888	Cook Strait, New Zealand	Stranded	Complete animal	
A. physeteris Joubin, 1900	Azores	Stomach of Sperm whale	Mantle with head and arms	Species dubium
A. japonica Pfeffer, 1912	Tokyo Bay, Japan	Caught in fish net	Complete animal	
A. clarkei G. C. Robson, 1933	Scarborough, Yorkshire, England	Stranded	Nearly complete animal	
A. nawaji Cadenat, 1935	Gulf of Gascony	Caught in net	Complete animal, partially decomposed	Species dubium

APPENDIX 2

Register of scientifically verified New Zealand records of *Architeuthis*.

Quote from Owen (1881: 8): "Any notice of Cuttlefish seen from the deck by seamen of any grade, the admiral inclusive, is unavailable for the prosaic naturalist, when no part of the alleged monster has been obtained, preserved, or described by a competent zoologist."

Date	Position	Capture Method	Collector	Identification	Reference	Other Data
1870	Wairnarama, east coast, Hawke Bay	stranded	F.H. Meinertz-hagen	T.W. Kirk	Dell (1970)	
1871	East coast, Wellington	stranded	W. Campbell	W. Campbell	Dell (1970)	
1876	Clifford Bay, Cape Campbell	stranded	?	C.W. Robson & T.W. Kirk	Dell (1970)	
23 May 1879	Lyall Bay, Cook Strait	stranded	E.R. Stock, F. & W. Morrah	T.W. Kirk	Kirk (1880) *Steenstrupia stockii* n. sp.	
6 June 1880	Island Bay, Cook Strait	stranded	James McColl	T.W. Kirk	Kirk (1882) *Architeuthis verrilli* n. sp.	
Oct 1880	Lyall Bay, Cook Strait	stranded	Mr Smith	T.W. Kirk	Kirk (1888) *Architeuthis longi-manus* n. sp.	
30 Jun 1886	Cape Campbell	stranded	C.W. Robson	C.W. Robson	C.W. Robson (1887) *Architeuthis kirkii* n. sp.	
9 Oct 1924	Bluff	? stranded	unknown	N.Z. Herald (9.10.1924)	Dell (1952)	
1930	Goose Bay, Kaikoura	stranded	unknown	W.R.B. Oliver	Dell (1952)	
22 July 1937	Petone Beach, Wellington Harbour	stranded	unknown	NZPA message	Dell (1952)	
1945	Pahau River mouth east coast, South Island	stranded	unknown	R.K. Dell	Dell (1952)	
Jan 1954	Kie Kie Bay, Kaikoura	trawl, shot close to shore	Messrs Samuel & Martyn Irvine and others	photos	Letter and photos to NIWA	
12 May 1956	near Makara, west coast, Wellington	stranded		R.K. Dell	Dell (1956)	measurements – see p. 110
1963–64	central east coast New Zealand	Sperm whale No. 63 stomach	Tory Channel Whaling Stn	D.E. Gaskin, M.W. Cawthorn & R.K. Dell	Gaskin & Cawthorn (1967)	measurements of beak larger than those of Dell (1956); 3 "type E" lower beaks attributed to *Architeuthis* sp.
Nov 1970	northern NZ, off north Challenger Plateau, Tasman Sea	Sperm whales	M.R. Clarke	Malcolm R. Clarke	Clarke & McLeod (1975)	one female, 415 mm, beaks from Sperm whales
1971–72	Auckland Islands	*Diomedea exulans* fledgling		M.J. Imber & R. Russ	Imber & Russ (1975)	juvenile *Architeuthis* beak

Date	Position	Capture Method	Collector	Identification	Reference	Other Data
July 1972	near Rakautura, Kaikoura	floating	L.B. & K.M. Garbes. Mr L. Mannering, lecturer, Edward Percival Marine Lab., Kaikoura	recounted to Dr C.F.E. Roper (1996) and newspaper clipping		Total length approx. 8 m, club suckers were retained but since lost
March 1976	Karori Lighthouse Wellington south coast	stranded	Chris Paulin (Museum of NZ)	ECF, based on photos	photos Museum of NZ	(beaks?)
July 1978	Gisborne	trawled	N/A	ECF, based on photos	Gisborne Herald photos	
July 1982	North Canterbury	trawled	N/A	ECF, based on photos	M77446, photo and partial club in Museum of NZ	partial club
19 Aug. 1983	New Plymouth power station, west coast North Island 39°03.' S, 174°04' E	cooling water intake screens	N/A	ECF	Specimen 1 (M79971)	2035 mm ML, sex unknown
8 Mar 1984	Auckland Islands 51°16' S, 166°52' E	trawled 533 m	f.v. *Shinkai Maru* Dr A. Yatsu (JAMARC)	ECF	Specimen 2 (M79972)	1930 mm ML, female
12 Apr 1984	Wairarapa 41°11' S, 176°44' E	trawled 1100–870 m	f.v. *Seafire*	ECF	Specimen 5 (M79975)	930 mm ML, female, 2200 h, Orange roughy catch
3 May 1984	1 km from Castlepoint	floating	Mr Kerry Pike	ECF	Specimen 3 (M79973)	1770 mm ML, female, c. 150 kg
12 May 1984	Princess Bay, Cook Strait, Wellington 41°17' S, 174°47' E	stranded	Ms Kylie Solomon & Mr Rangi Solomon	ECF	Specimen 4 (M79974)	1825 mm ML, female
June 1984	West coast hoki grounds, South Island	trawled	f.v. *Arrow*	Skipper Mike Connolly (pers. comm.)		
25 July 1984	West coast, South Island 41°05'S, 170°52'E	trawled 475 m	N/A	ECF	Specimen 6 (M86826)	1560 mm ML, female
24 sept 1984	Puysegur Bank 46°18' S, 166°30' E	trawled 365 m	f.v. *Tengawai* Mr Jeff Bowden	ECF	Specimen 7 (M79976)	2020 mm ML, female, alive when caught. Mixed catch, mainly Ling
6 June 1985	47°04' S, 169°32' E	trawled 310 m	f.v. *Daishin Maru 23*, scientific observer	ECF, photos		approx. 2000 ML, 0500 h, surface temp. 10.5° C; bottom temp. 6.5° C
31 Mar 1986	50°50' S, 166°51' E	trawled 296 m	f.v. *Akebono Maru 73*	ECF	Specimen 11 (M102282)	1720 mm ML, female, surface temp. 10.8° C; bottom temp. 7.5° C

Date	Position	Capture Method	Collector	Identification	Reference	Other Data
just prior to 11 Apr 1986	Off Houhora, NE North Island 35°43' S, 174°20' E	floating	Game boat, landed at Hiku- rangi Fisheries. Neil Martin, Fisheries Officer, Whangarei	ECF	Specimen 9	1260 mm ML, male, c. 40 kg reported as alive and being attacked by whales
17 Apr 1986	43°38'S, 174°43' E	trawled max. depth 470 m	f.v. *Banshu Maru 8*	ECF	Specimen 12	1815 mm ML, female, 1000 h
27 May 1986	46°32' S, 166°11' E	trawled 604 m	f.v. *Daishin Maru 28*. Scientific observers Chris Lalas & Rodger Good	ECF	Specimen 13	1830 mm ML, female. Estimated weight c. 180-190 kg
18 July 1986	42°03' S, 170°27' E	trawled 450 m tow 22	f.v. *Dolomit* Scientific observers Ms Ramari Stewart & Mr A.J. (Joe) Bell	ECF		1380 mm ML, sex unknown, 43.5 kg, 1235 h, catch mainly Hoki, measurements*
8 Sept 1986	43°43' S, 174°56' E	trawled 480 m	f.v. *Banshu Maru 8*. Scientific observer Mr Brent Wood	ECF	Specimen 14	2140 mm ML, female, bottom temp. 6.0° C
26 Feb 1987	Banks Peninsula 44°09' S, 173°35' E	trawled 312–356 m	f.v. *Daishin Maru 22*. Mr Alex Woods	ECF	Specimen 8	1900 mm ML, c. 250 kg, 0135–0400 h, catch mostly Hoki
3 May 1987	41°31' S, 176°43' E	trawled 360–485 m		ECF	Gauldie *et al.* (1994)	reported as 1610 mm ML, female ? body not received, head, without arms, tentacles
9 May 1987	43°38' S, 174°14' E	trawled 506 m	f.v. *Daishin Maru 28*. Scientific observers Mr Romero & Ms A. Conway	ECF	Specimen 15	2035 mm ML, female
late 1987	West coast, South Island hoki grounds	trawled	Mr Ken Atkinson No further information available	ECF	Specimen 10	1830 mm ML, female
1986–87 date un- known	Lord Howe Rise	trawled 950 m, tow 33	f.v. *Tampen* Scientific observer W.A. Stewart	ECF, photos		photos, measure- ments*
26 July	42°35' S, 170°23' E	trawled 503 m	f.v. *Zuiyo 3* Scientific observer	ECF		1300 mm ML, sex unknown, catch Hoki, weight c. 67 kg, 1000 h, surface temp. 11.9° C, bottom temp. 10.4° C measurements*

* measurements — see p. 110.

Date	Position	Capture Method	Collector	Identification	Reference	Other Data
16 Aug 1987	41°21' S, 170°30' E	trawled 464 m (headline over 521 m)	f.v. *Zuiyo 3* Scientific observer	ECF, photos		1370 mm ML, sex unknown, surface temp. 12.0° C; bottom temp. 10.8° C; c. 70 kg, 1330h, catch Hoki
25 Aug 1987	41°31' S, 170°34' E	trawled 410–608 m tow 165	f.v. *Ryuyo Maru* Scientific observers Henry Kavale & Steve Punnett	ECF		1230 mm ML, female, catch Hoki measurements*
2 Sept 1987	51°18' S, 170°23' E	trawled tow 10	f.v. *Mys Kro notsky* Scientific observer	ECF, photos		1780 mm ML, sex unknown, measurements*
13 Oct 1987	46°24' S, 166°23' E	trawled 487 m tow 48	f.v. *Chiyo Maru 2.* Scientific observers Bruce Manning & Rosalind Squire	Bruce Manning		1770 mm ML, prob. female, 1100 h, catch mixed, mostly Hoki, Ling
4 Nov 1987	47°32' S, 169°10' E	trawled tow 126	f.v. *Chiyo Maru 2.* Scientific observers Bruce Manning & Rosalind Squire	Bruce Manning		2010 mm ML, sex unknown, catch mixed, mostly Hoki, Ling, Hake, rattails, measurements*
5 Nov 1987	46°31' S, 166°30' E	trawled 550 m tow 6	f.v. *Chiyo Maru 2.* Scientific observers Bruce Manning & Rosalind Squire	Bruce Manning		1770 mm ML, sex prob. female, c. 60 kg, 0450 h, catch mostly Ling
26 Nov 1987	47°29' S, 169°35' E	trawled 540 m tow 103	f.v. *Chiyo Maru 2.* Scientific observers Bruce Manning & Rosalind Squire	Bruce Manning		length and sex unknown, c. 200 kg, 1110 h, catch Hoki
5 Dec 1987	47°28' S, 169°35' E	trawled 540 m tow 147	f.v. *Chiyo Maru 2.* Scientific observers Bruce Manning & Rosalind Squire	Bruce Manning		length and sex unknown, c. 80 kg, 1110 h, catch Hoki
6 Dec 1987	47°30' S, 169°19' E	trawled 550 m tow 152	f.v. *Chiyo Maru 2.* Scientific observers Bruce Manning & Rosalind Squire	Bruce Manning		length and sex unknown, c. 20 kg, 1130 h, catch Hoki
25 Jan 1988	51°00' S, 166°42' E	trawled 495 m tow 8	f.v. *Nikolaevskiy Korabel.* Scientific observers Christieson & Tate	ECF, photos		1880 mm ML, sex unknown, c. 150 kg, 1400 h, catch Arrow squid, measurements*

* measurements — see p. 110.

Date	Position	Capture Method	Collector	Identification	Reference	Other Data
May 1994	43°55' S, 176°50' E	trawled 515 m	f.v. *Dalmor* G. Williams	ECF	M118019 NMNZ	1850mm ML, 760 mm FL. In pieces
May 1994	43°48' S, 177°35' E	trawled 514 m	f.v. *Dalmor* G. Williams	ECF	M118020 NMNZ	1110mm ML, 490 mm FL. Incomplete and abraded.
31 Dec 1995	43°12' S, 178°20' W	trawled 425 m	r.v. *Tangaroa* Neil Bagley ? or Ms Di Tracey	ECF	Specimen 16 NMNZ	2000 mm ML, female, surface temp. 15.9° C, bottom temp. 9.1° C
? Feb 1996	43°26' S, 176°23' E	trawled 310 m	Darryn Mills skipper	Steve O'Shea	Not yet examined	surface temp. 16.0° C, bottom temp. 9.3° C

Additional Records (unconfirmed, no specimens received, no photos available)

Date	Position	Capture Method	Collector	Other Data
27 April 1979	Chatham Rise	trawled	f.v. *Toyo Maru* Sealord's J.-V. Dave Lucas	5-ft section of "tail". Catch mainly Barracouta and Mackerel
early 1980	North of Banks Peninsula	trawled	f.v. *Kiso Maru*	Reported by Ian Burgess to ECF by phone 16 January 1984. 3 squids caught, 2 in one net and still alive.
early March 1985	Auckland Islands squid grounds	trawled	f.v. *Banshu Maru*	Information received from crew during Open Day, March 1985.
March 1985	Red Rocks, south Wellington coast	floating portion	Observation in previous fortnight by Rock Lobster fisherman	Information received at an Open Day at Fisheries Research Centre, March 1985.
12 March 1987	Auckland Islands 50°09' S, 166°20' E	trawled 170 m tow 72	f.v. *Mramornyi* Scientific observers B. Manning & A. Bracey	arms and tentacles only
January 1988	Wairarapa coast	trawled	*Rijnmond V*	Rotted and was thrown out by Amaltal factory staff.
19 Feb 1988		trawled		unprovenanced photos
12 April 1988	mid Tasman Sea	trawled	f.v. *Matawhaerarua*	Reported to Dr John Booth. Reputedly frozen but never received.
July 1994	Cape Campbell	stranded	Farm station owner	Photo seen by Dr Dave Schiel, Canterbury University.
Within years 1990–95	landed at Kaikoura Fisheries	unknown	Jack v. Berkel	

Scientific Observer Data

Refer to Appendix 2 Date	1986–87 *Tampen*	18-7-86	26-7-87	25-8-87	2-9-87	13-10-87	4-11-87	25-1-88
sex	U	U	U	?F	U	?F	U	U
dorsal mantle length	1800	1380	1300	1230	1780	1770	2010	1880
width at mantle aperture	320	380	330	325	?320	470	510	420
greatest mantle width	400	430		325	480	520	560	540
width of mantle at fin insertion	280	310		230	230	300	390	500
fin length	660	530	360	400	?505		800	760
single fin width								
greatest double fin width	370	380	320	290	?150	480	500	540
dorsal head length to nuchal crest	210	300	350	230	390	300	370	300
dorsal head width at nuchal crest	310	?90	260	260	230		430	250
dorsal head width across eyes	3000	?160		160	270	190	240	3440
eye diameter	?40							
length arm 1 (complete)							est 1450	
length arm 2 (complete)						1400	1560	
length arm 3 (complete)							est 1700	
length arm 5 (complete)							est 2400	1800
tentacle (complete)							severed	*7650

* = minimum measurement
? = dubious measurement
U = sex unknown
F = sex female

APPENDIX 3

Table 1. Aldrich's (1991) complete arm lengths and arm-length indices calculated from these data.

	Conche	Lance Cove	Wild Cove	Sunnyside	Bonavista	Hare Bay
DML (mm)	**1850**	**1265**	**1067**	**1765**	**1320**	**1585**
Arm I	1778			1940	1280	1910
Arm 2	1791		1651	1900	1670	1735
Arm 3		1710		1870	1630	1870
Arm 4		1560		1980	610 (hecto)	
Arm 1 index	96			110	97	121
Arm 2 index	97		155	108	127	109
Arm 3 index		135		106	123	118
Arm 4 index		123		112		

APPENDIX 4

Standard datasheet and characters measured.

Standard Datasheet	Definition and Notes
specimen number	
sex	
dorsal mantle length	posterior to middorsal extension
ventral mantle length	midventral line
width at mantle aperture	measured horizontally
circumference at mantle aperture	use flexible tape
greatest mantle width	measured horizontally
circumference at greatest mantle width	measured with flexible tape – not estimated
distance of greatest width from mantle aperture	distance posteriad of middorsal extension
length middorsal projection	anterior extension from a line between lateral anterior edges of mantle
angle of middorsal projection	to provide a measure of acute/shallowness of extension
forward projection of pallial connectives	marked in some specimens
ventral distance between pallial connectives	following line of mantle edge
mantle thickness at dorsal midline	make a slit in the dorsal midline and insert calipers
distance of measurement from anterior	for comparability
mantle thickness at ventral midline	as above
distance of measurement from anterior	as above
width of mantle at fin insertion	horizontal dorsal width to edges of mantle
circumference of mantle at fin insertion	flexible tape – helps to define mantle shape and taper
distance of ant. fin insertion from mantle aperture	might provide an alternative measure in case of damage
separation between anterior fin insertions	dorsal distance between most anterior extent of fin insertions
free anterior lobe	measured as distance forward of line through insertions
fin length	maximum length including lobes and keels
single fin width	from insertion to outer edge
position of maximum width from fin anterior	a measure taken from the most anterior extent of fin along dorsal midline
greatest double fin width	broadest point (including dorsal surface where fins are very lateral)
position of double fin width from fin anterior	as above
thickness of fin midway along insertion line	make a slit in the fin insertions line and fit calipers into the gap
dorsal head length to nuchal crest	from junction between arms I to edge/colour difference at neck crest
dorsal head length to anterior of nuchal cartilage	only valid where the head and neck are still attached – from junction arms I
dorsal head width at nuchal crest	horizontal width measured between vertical rods placed against sides of head
dorsal head width across eyes	as above
dorsal head width at arm base	as above
ventral head width across eyes	as above, but ventrally
head depth at nuchal crest	measured to plane level with the dorsal surface of the head
head depth at eyes	as above
head depth at arms	as above
horizontal eye opening	based on best reconstruction
vertical eye opening	as above
eye diameter	very approximate
funnel length median ventral	measured from midway between funnel cartilages to funnel opening
diameter of funnel aperture (flattened)	opening is reduced to 2-dimensional shape
distance of funnel aperture to base of funnel valve	slide end of flexible tape into junction of valve and funnel wall, to opening
base to free edge of funnel valve	approximate, same base point as above
ventral distance between funnel-locking cartilages	measured in a straight line between anterior extent of cartilages
length of funnel-locking cartilages (incl. overhang)	total length was used since the cartilage grades into fleshy edges
greatest width of funnel-locking cartilages	includes thin lateral edges
length of nuchal cartilage	includes anterior edge of cartilage
width of expanded anterior section	includes thickened portions at anterolateral corners of cartilage
width of narrowest portion	straight edge to edge measure
width of expanded posterior portion	as above
length of gladius	rarely possible, may be best done in situ
greatest width of gladius	impossible to examine in situ, lay out on a large wet table like a jigsaw puzzle
distance of greatest gladius width from anterior	difficult to estimate if large pieces missing or fractured

Standard Datasheet	Definition and Notes
length of gill base	length of gill attached to inner mantle wall only
length of free edge of gill	entire outer edge, including free curved portion at extreme anterior end
number of primary gill lamellae	ideally count both left and right gill, easiest to count at arterial branch
* = minimum estimated measurement	indicate where parts are missing, or suspect the measure is short
arms, suckers, and dentition	see relevant spreadsheets held at NIWA
internal organs	see relevant individual specimen descriptions held at NIWA

ARCHITEUTHIS TENTACLE

Length of stalk
Number of stalk suckers
Number of stalk knobs
Colour of sucker face
Colour of sides
Colour of aboral face
Protective membranes
Keels
Cross-sectional shape of stalk
Circumference at base of stalk
Diameter of sucker-bearing face

Start of carpus taken as point where there is a diagonal row of three suckers. This is usually also the point at which protective membranes develop.

CARPUS

Number of smooth-edged suckers
Pedicels very short, inserted centrally (Y/N)
Numbers of warts
Sucker diameters at base of carpus
Sucker diameter halfway along carpus
Sucker sizes along outer edges and middle of carpus similar

Total carpal length approximate (including toothed suckers)
Total carpal length approximate (excluding toothed suckers)
NB. Above two measurements through longitudinal mid-
    line of sucker-bearing face.
Base of club is not narrower than the stalk (Y/N)
Diameter of sucker-bearing face at base of carpus
Diameter of face at carpus/manus boundary
Circumference at base of carpus
Circumference at manus/carpus overlap

MANUS

Number of toothed suckers in cluster at base of manus
Pedicels longer, thinner and more laterally inserted (Y/N)
Range of diameters of toothed basal suckers
Arrangement random, largest suckers nearest manus end
    (Y/N)

Number of quadriserial rows with enlarged central suckers
Diameter of largest sucker
Position in quadriserial rows of largest sucker
Pedicel thickness, relative shortness, off-centre insertion?
Diameter of sucker-bearing face midway along manus
Diameter of sucker-bearing face at row 13
Circumference midway along manus

DACTYLUS

Total length dactylus
Circumference at dactylus base

Arrangement is irregular base of dactylus
Approximate number of rows of quadriserially arranged
    suckers
Maximum sucker diameter
Minimum diameter of suckers at tip
Folded black flap at extreme tip (Y/N)
Number of irregularly arranged suckers at tip
Total counts of dactylus suckers
Diameter of sucker-bearing face at dactylus tip

CROSS-SECTIONAL SHAPE

Stalk and carpus cross-section triangular (Y/N)
Protective membranes visible (Y/N)
Maximum width of protective membrane
Cross-section of manus
Shape of keel along manus
Shape of keel on dactylus
Cross-sectional shape of dactylus

SUCKER RINGS TO BE COLLECTED FROM

Tentacle stalk
Base of carpus
Middle of carpus
Small serrated suckers at base of manus
Largest manus suckers
Selection of dactylus suckers

TAXONOMIC INDEX

GENERAL INDEX