SYSTEMATICS AND ZOOGEOGRAPHY OF THE SQUID GENUS ILLEX (OEGOPSIDA; CEPHALOPODA)

CHUNG-CHENG LU

SYSTEMATICS AND ZOOGEOGRAPHY OF THE SQUID GENUS ILLEX (OEGOPSIDA; CEPHALOPODA)

by

Chung-cheng Lu, B.Sc., M.Sc.

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ABSTRACT

A study of the systematics and the distribution of the squid genus *Illex* Steenstrup, 1880 was made, utilizing specimens and data from the collections of various institutions throughout the world. The thesis begins with an extensive survey of the literature on the four species of this ommastrephid genus.

Three species, *Illex illecebrosus* (Lesueur, 1821), *I. coindetii* (Verany, 1837) and *I. argentinus* (Castellanos, 1960) are here described and illustrated in detail, together with a modified description of *I. oxygonius* Roper, Lu and Mangold, 1969. Neotypes of *I. illecebrosus* and *I. coindetii* are established.

A selection of morphometric characters are studied to determine the growth pattern of each species. The growth patterns are expressed as linear regressions between the mantle length and various measurements and indices standard in teuthoid systematics.

The taxonomic and morphometric characters of all four species are compared. Strong sexual dimorphism in the head dimensions, arm lengths and sucker sizes exist in *I. coindetii*, *I. oxygonius* *I. argentinus*. Sexual dimorphism involving these characters in *I. illecebrosus* is not apparent.

The bathymetric range of *I. illecebrosus* is 0-500 m. During its inshore migration in Newfoundland waters it is in relatively shallow water of 15-30 m, in the Chesapeake Bay region it is concentrated in the upper 150 m. The bathymetric range of *I. coindetii* is 0-1080 m, but concentrated at 200-500 m in the Gulf of Mexico and at 400-600 m in the Caribbean Sea. In the eastern Atlantic, *I. coindetii* is found at 160-320 m in the Blanes region of Spain, 200-250 m along the Algerian coast, 40-500 m in the Port-Vendres and Las Rosas region, and at 37-485 m in the Gulf of Guinea. The bathymetric range for *I. argentinus* is 0-800 m and that of *I. oxygonius* is 50-555 m with greatest concentration at 50-300 m in the Chesapeake Bay region.

All four species appear to exhibit diel vertical migration in that they are closely associated with the bottom during the daylight hours and disperse at night.

The relationship between the occurrence of *Illex* and basic hydrographic conditions, e.g., temperature, salinity, and density are analyzed insofar as the available data permits. *I. coindetii* and *I. oxygonius* inhabit warmer, more saline water, while *I. illecebrosus* and *I. argentinus* are distinctly boreal and antiboreal species, inhabiting less saline cold water.

Noting the amphi-Atlantic distribution of *I. coindetii*, yet the lack of collections from the mid- Atlantic region, it is postulated that the distribution is associated with the gyre of water circulation in the northern Atlantic. The most important limiting factor appears to be temperature.

All four species are valid, although some characteristics commonly associated with cephalopod taxonomy are felt to be of little importance in delineating the species of this genera. It is further suggested that greater importance be given to some characters not commonly employed.

For my parents, and for Mairi,
Norman, and Jason Frederick.

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Portions of this thesis, particularly certain information pertaining to the species *Illex oxygonius*, have earlier been published under the title, "A new species of *Illex* from the western Atlantic and distributional aspects of other *Illex* species (Cephalopoda: Oegopsida)" by Roper, Lu and Mangold (Proceedings of the Zoological Society of Washington, 1969).

The author sincerely acknowledges with gratitude permission to incorporate Plates 1-5 as they appeared in that publication (as Figures 26-30). They are the work of Mr. J. Schroeder of Washington, D.C. In all other instances and in accord with the regulations of the Department of Biology of Memorial University, the illustrations are the original work of the author.

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INTRODUCTION

The squid *Illex illecebrosus* (Lesueur, 1821) has been a subject of active research in the Department of Biology of the Memorial University of Newfoundland since the early 1960's. To date, a number of theses and research papers have been completed on this decapodous cephalopod covering the fields of anatomy and morphology, general biology with particular reference to aspects of its functional morphology, parasitic burden, physiology, behavior, and biochemistry.

The author first became a student in the Department late in 1965 and conducted a morphometric study on this ommastrephid, submitting an M.Sc. thesis entitled, "Determination of Growth and Related Phenomena in *Illex illecebrosus illecebrosus* (Lesueur) (Decapoda: Cephalopoda) from Newfoundland". During this study, and while working as a research assistant to Professor F. A. Aldrich, the instability of the systematics of the genus *Illex* was realized. Discussions with him, and with others, including Dr. G. L. Voss, indicated the desirability of undertaking a total review of the systematics and distribution of the genus as a dissertation topic for doctoral research. Such a systematic revision of a group of animals requires the largest possible collection covering the widest possible range of distribution. No single collection meets these criteria, therefore the material used in this study is from the collections of several institutions.

It is in order to discuss the origins of some of these collections. The famous Michael Sars Expedition to the North Atlantic Ocean (1910) yielded several specimens belonging to the genus *Illex*, and they are now at the Zoological Museum of the University of Bergen. Although these collections are small, they are of value in that they cover a wide geographical range and were studied and reported upon by a teuthologist of repute, namely, Carl Chun.

The collections made on cruises of the research vessels Oregon and Oregon II in the Gulf of Mexico and the Caribbean Sea, now housed at the Institute of Marine Science of the University of Miami and in the United States National Museum, constitute the bulk of the material from those regions.

In 1962, the International Cooperative Investigations of the Tropical Atlantic (ICITA) was adopted as an official program by the Intergovernmental Oceanographic Commission (IOC). This program, being a multi-national, multiple-vessel oceanographic survey, included among the participating ships the Geronimo of the Bureau of Commercial Fisheries (BCF) of the United States of America. The 1963 and 1964 cruises of this vessel yielded a large number of cephalopods from the Gulf of Guinea region. Although this collection is currently being studied by Dr. C. F. E. Roper of the United States National Museum, the *Illex* samples form an important part of the material used in this study, and Dr. Roper's kindness in making them available is warmly acknowledged.

In 1964-1965, the Pillsbury of the Institute of Marine Science of the University of Miami participated in a deep-sea biological expedition to the Gulf of Guinea as part of the ICITA program. A large number of cephalopods were collected during the cruises and are being studied at IMSUM by G. L. Voss. The *Illex* collection is valuable in this study.

In addition, collections made by the Virginia Institute of Marine Science in the Chesapeake Bay region during 1967-1968 are especially valuable in that they are accompanied by detailed environmental data.

The study that is presented here is divided into three major parts. The first presents a review of the literature on *Illex*, in which various synonyms are verified. The second is a systematic treatment of the four species of *Illex*. The species *I. illecebrosus*, *I. coindetii* (Verany, 1837) and *I. argentinus* (de Castellanos, 1960) are re-described in detail and neotypes for the first two species are erected. The description of the recently established species, *Illex oxygonius* Roper, Lu and Mangold, 1969 is included for the sake of completeness. The geographical range for each species is established and also included are comparisons of the four species with an analysis of the relationship of *Illex* to other ommastrephid genera.

The third part is a study of the distribution of *Illex*.
A brief outline of the physical oceanography of the Atlantic Ocean is presented to serve as the basis for the discussion of the distribution of these ommastrephids. Special attention is given to *I. illecebrosus* and *I. coindetii* as more complete series of specimens are available for

these two species than for the others. Selected environmental factors known to govern the distribution of marine organisms, i.e., temperature, salinity and dissolved oxygen, are discussed and analyzed with respect to the observed distribution of the four species.

MATERIALS AND METHODS

The materials used in this study are the collections kept in various institutions. All specimens examined are listed according to the species. The following abbreviations are those of the institutions where the specimens are housed:

ANSP:	Academy of Natural Sciences of Philadelphia
BeM:	Zoologisk Museum, Universitetet I Bergen, Bergen, Norway.
CM:	Universitetets Zoologiske Museum, Copenhagen, Denmark.
FRB:	Fisheries Research Board of Canada, Biological Station, St. John's, Newfoundland, Canada.
IBMMP:	Instituto de Biologia Marina, Mar del Plata, Argentina.
IMSUM:	Institute of Marine Science (Rosenstiel School of Marine and Atmospheric Sciences), University of Miami, Miami, Florida, U.S.A.
LPM:	Museo de La Plata, La Plata, Argentina.
MUN:	Marine Sciences Research Laboratory and Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada.
NMC:	National Museum of Canada, Ottawa, Ontario, Canada.
OM:	Zoologisk Museum, Universitetet I Oslo, Oslo, Norway.
PM:	Museum National d'Histoire Naturelle, Paris, France.
USNM:	United States National Museum, Washington, D.C.

The abbreviations of ships and institutions in reference to the specimens are:

A:	*Atlantis*
AS:	*Albatross*
ATC:	*A. T. Cameron*

CB: *Combat*
CY: *Cryos*
DW: *Delaware*
FH: *Fish Hawk*
G: *Grampus*
GD: *Gerda*
GE: *Geronimo*
MS: *Michael Sars*
O: *Oregon*
O II: *Oregon II*
P: *John Elliott Pillsbury*
Pel: *Pelican*
USFC: U. S. Fish Commission
VIMS: Virginia Institute of Marine Science
WH: *Walther Herwig*

The measurements, indices, and counts are all standard in the teuthological literature. Sucker diameters were measured by means of a caliper, the remaining measurements were made by using an ordinary centimeter ruler. All measurements are presented in millimeters (mm). The definitions and abbreviations of the standard measurements and counts are as follows:

ML, dorsal mantle length: measured from the anterior-most point of the dorsal mantle to the tip of the united fins

VML, ventral mantle length: measured from the anteroventral border of the mantle in the midline to the tip of the united fins.

HL, head length: measured from posterior ridge to V-shaped juncture between arms I.

HW, head width: greatest width of head across eyes.

MW_1: width of mantle at the mantle opening.

MW_2: width of mantle at the midpoint between the mantle opening and the anterior insertion of fin.

MW_3: width of mantle at point in line with anterior insertion of fins.

FL, fin length: measured from the anterior border of the fin to the tip of the united fins.

FW, fin width: greatest width across both fins.

FBL, fin base length: measured from the midpoint between the two fin insertions to the tip of the united fin.

FA, fin angle: angle that the straight posterior border of one fin, exclusive of the lateral lobe, makes with the longitudinal axis of the body.

A_1L, A_2L, A_3L, A_4L, length of the dorsal (I), dorso-lateral (II), ventro-lateral (III), ventral arm (IV), respectively: measured from the first basal sucker to the arm tip.

HcAL, length of the hectocotylized arm: measured from the first basal sucker to the arm tip.

HcL, length of the modified portion of the HcA, i.e., the hectocotylus: measured from the first modified sucker to the tip.

CL: length of the tentacular club.

S_1, S_2, S_3, S_4, S_T: diameter of the largest sucker on the dorsal (I), dorso-lateral (II), ventro-lateral (III), ventral arm (IV) and tentacular club (T), respectively.

#S_1, #S_2, #S_3, #S_4: number of suckers on the dorsal (I), dorso-lateral (II), ventro-lateral (III), and ventral arms(IV), respectively.

GL: length of the gill, or ctenidium

#G: number of gill lamellae on one gill.

SpL: average length of selected spermatophores.

SpRL: average length of the sperm reservoir (sperm mass) portion of the spermatophores.

SpRW: average width of the sperm reservoir portion of the spermatophores.

CBL: average length of cement body of the spermatophores.

With few exceptions, all indices are the length (or width) of a given part expressed as a percentage of ML, e.g., VMLI is the ventral mantle length expressed as a percentage of ML, S_2I is the diameter of the largest sucker on arm II expressed as a percentage of ML. There are exceptions, however, as noted above, and these are:

HcLI: Hectocotylus length index: length of the modified portion expressed as a percentage of the total length of the hectocotylized arm.

SpRLI: Sperm reservoir length index: average length of sperm reservoir expressed as a percentage of the average length of the spermatophore.

SpRWI: Sperm reservoir width index: average width of spermatophores expressed as a percentage of the average length of the spermatophores.

CBLI: Cement body length index: average length of the cement body expressed as a percentage of the average length of the spermatophores.

All other abbreviations used are standard, e.g., m for meters, mm for millimeters, °C for degree centigrade, $^{o}/oo$ for parts per thousand parts, etc.

Statistical analyses were carried out by the Newfoundland and Labrador Computer Services, Ltd., on their computer IBM 370/155, using in part funds made available for the purpose from the Office of the Dean of Science of Memorial University of Newfoundland.

PART I. HISTORICAL REVIEW[1]

The literature on the squid genus *Illex* is extensive and is found scattered in many, sometimes obscure, journals. This survey of the literature is by no means exhaustive, although effort has been made to make it as complete as is possible. However, only articles of taxonomic and/or distributional interest are included. The page reference of each reference is that of the original publication, with few exceptions. The reference paginations for Steenstrup are those of Volsøe, et al. (1962); the paginations for Zuev (1966) and Nesis (1967) are from the translations produced for the Fisheries Research Board of Canada Translation Series. Full reference citations are presented in the "References Cited" section.

A member of the squid genus *Illex* was first mentioned and described by C. A. Lesueur in 1821 under the name *Loligo illecebrosa*. The events associated with the discovery and description of this species were rather dramatic. As Lesueur himself wrote, "When Mr. Maclure and myself were at Sandy Bay in 1816, we saw a great number of Loligos collected by the fishermen, and held in reserve as bait for cod-fish, which they catch in great numbers on the banks of Newfoundland. The beautiful color with which they were ornamented, induced me to take a drawing of one immediately, but not then having leisure to complete it, I took a specimen with me to finish the drawing at my leisure. But

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[1] Insofar as is possible or practical, the literature is here presented in chronological order, with little distinction between the systematic and zoogeographic elements.

recently upon comparing this specimen with my drawing, I was much surprised to perceive that I had brought with me a very distinct species from that which I had observed" (Lesueur, 1821, p. 94). Thus, we have a detailed description of the holotype of *Loligo pavo*, now known as *Taonius pavo;* and yet unfortunately, Lesueur's description of *Loligo illecebrosa* is brief and incomplete, based on his drawing in 1816. The original description is: "The body of this species is rather short, narrow, subequal anteriorly, terminated acutely posteriorly; fins approximated at their origin, terminated in a point, and taken together rhombiform; the two longer arms are narrow, delated at their extremity, and furnished with two series of suckers, the eight arms are almost equal and provided throughout their whole length with two ranges of suckers; the arms are long, and with the head they measure two-thirds of the length of the sac; the bone is very narrow in the middle, delated at each extremity, and terminated at the inferiority by a hollow inverted cone. Colors vivid and beautiful, passing from a brilliant red to a deep and clear blue, upon the back, the head, arms, tail and fin, which are covered with deeper points of the same color, the under part of the body is paler, region of the eyes finely tinted with yellow. This species is known by the name of squid at Sandy Bay, and is made use of by the fishermen as bait in the cod-fishery" (Lesueur, 1821, p. 95). The species name *illecebrosa* is a Latin adjective, meaning alluring or seductive.

In 1825, LaPylaie gave a detailed account of the morphology and habit of an apparent new species, *Loligo piscatorum,* from St. Pierre and Miquelon which apparently is a synonym of Lesueur's *Loligo illecebrosa.* Although LaPylaie was aware of the close similarity of his species to that of Lesueur's, he claimed priority for his name over Lesueur's: "Il reste maintenant à constater, sur nombre d'individus, si ce sont deux espèces distinctes, ou plutêt, comme je le présume, deux modifications du type que constitue l'espèce proprement dite. Ayant décrit et figuré ce *Loligo* en 1816, je suis le premier naturaliste qui s'en soit occupé; le Sueur ne l'a publié qu'en 1821" (LaPylaie, 1825, pp.334-335). Based on the dates of their respective publications, there can be no doubt that *L. illecebrosa* should take priority and *L. piscatorum* properly regarded as its synonym (Code[1], Chap. IV, Art. 11).

Verany (1837) reported six new species of cephalopods from Nice, France. One of the species described was *Loligo coindetii.* The English translation of the description is as follows: "Its body is oblong, cylindrical, pointed at the end which is furnished with two fins forming a slightly cupped heart; the cephalic region is furnished with two fairly large silvery eyes, and with ten arms, of which two are tentacles; the first and the fourth pairs are of equal length,

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[1] Throughout this work, "International code of zoological nomenclature adopted by the XV International Congress of Zoology" is referred to as "Code".

the second a little longer, and the third the longest; they are provided with a double row of very small stalked suckers which become imperceptible toward the tip. The tentacles are almost double the length of the others, they are provided with a dozen fairly large suckers, arranged in two rows, and about 20 small ones which precede and border the others; a bare space nearly one-fifth the total length terminates the tentacles. The body is whitish, transparent, with bluish and shiny patches; dotted with large irregular reddish-brown spots, some of which are most darkly ringed with the same color. The horny pen is almost straight, slightly dilated at the top part; it is much like that of *Loligo todarus*. - The total length of the mollusk is, including the tentacle, about five inches . . ." (p. 94). Verany also presented drawings of the dorsal view of the animal, a lateral view of the tentacle, and the gladius (Verany, 1837, fig. 4) of a very young individual; its rounded, heart-shaped fins were faithfully illustrated.

Ferussac and d'Orbigny in their monumental work on cephalopod systematics "Histoire naturelle generale et fossiles" (1835-1848) described *Ommastrephes sagittatus* in detail (pp.345-346). This species is described as having an elongated, cylindrical body with wide, rhomboidal fins; the tentacles are elongate with numerous suckers on the tip; the gladius is elongated with a lanceolate posterior end. The total length of the animal is 440 mm with a body length of 165 mm;

the length of the fins is 41% of the body length with the width of the fins 61% of the body length; the length of the gladius is 165 mm, the length of the terminal expansion (cone) is 21% of the gladius length, the width of the cone is 11% of the gladius length, the apical angle of the cone being four degrees. The animal has a long body slightly swollen in the middle of its length. The head is bulky, with large, long sessile arms equipped with suckers, the horny rings of the suckers being variable according to their position on the arm. The tentacular arms are compressed all over, the end broader and covered with suckers beginning in two rows, then increasing to four rows; two of these rows are slanted slightly, the lateral two more slanted with very small suckers. At the tip, these suckers are replaced by a multitude of very small suckers at least of eight rows abreast. The horny ring of the large suckers, either internally smooth or slightly cleaved. The color is a rosy shade, made by very little purple spots. The gladius is long and thin with"three longitudinal sides",of which the largest are the two lateral ones; the expansions at the lower end are large.

According to Ferussac and d'Orbigny, the species (their *Ommastrephes sagittatus*) is distinguished from *O. todarus* (= *Todarodes sagittatus* (Lamarck)) by its fins which occupy only a third of the body length, by the suckers of the tentacular arms being situated only at the end, and not on the whole of its length, and by the details of the horny rings of the suckers, and the beaks. The most prominent character of all is that it is characterized by a very large number of suckers (more than eight abreast) at the end of the tentacles, a character unknown in any other species.

This species is reported to be distributed in the boreal region of the Atlantic Ocean, in North America on the Newfoundland banks where it served as bait in the cod fishery, and in the Mediterranean Sea. Ferussac and d'Orbigny further stated that this species was confused with *Ommastrephes todarus* by Lamarck and that the names *sagittata, illecebrosa, harpago, brongniartii, piscatorum* and *coindetii* are all in synonymy.

This important work was published over a period of 14 years (1835-1848), with none of the sections bearing the actual date of its publication. According to Winckworth (1942), who did the research on the works of Ferussac and d'Orbigny, the systematic section of this monograph is entirely the effort of d'Orbigny, and that the section dealing with the Ommastrephidae was published in 1848 (p. 36). It is worth noting that d'Orbigny recognized the close similarity between *Loligo illecebrosa* and *L. coindetii,* and indeed he was the first author to synonymize these species. However, it is curious that he would assign the designation *sagittatus* for both Lesueur's *illecebrosa* and Verany's *coindetii,* consigning Raffinesque's (1814) *todarus* to Lamarck's *Loligo sagittata* var. A (Ferussac & d'Orbigny, 1835-1848), p. 349). It was Hoyle (1902) who first pointed out this confusion. According to Hoyle (1902, pp. 199-200), the "var. A" of Lamarck is given first and must therefore be regarded as the typical form of the species. Therefore, Lamarck's *Loligo sagittata* var. A is the type of the species which is now known as *Todarodes sagittatus* (Lamarck).

Gray (1849) listed *Ommastrephes sagittatus* in his "Catalogue of the Mollusca in the Collection of the British Museum" under the family Onychoteuthidae (p. 58), offering no further information other than that presented by Ferussac and d'Orbigny. Gray's *O. sagittatus* is an *Illex*, since he mentioned that it was characterized by having "eight rows of numerous small cups at the end near the tip" of the tentacular clubs (p. 58).

The first regional monograph on cephalopods, dealing with those of the Mediterranean Sea was published by Verany (1851). *Loligo coindetii* was redescribed, although the tip (dactylus) of the tentacular club was still described as "a space of one-sixth of the length of the tentacle" without mentioning its sucker arrangement (p. 110). It must be assumed that either Verany had overlooked the minute suckers on the dactylus or that this specimen was devoid of such suckers due to handling or damage. He recognized the difference between his *Loligo coindetii* and Lamarck's *Loligo sagittata* (= *Todarodes sagittatus*), yet in Pl. 2 a drawing of *Loligo coindetii* was used to illustrate the female of *Loligo sagittata*. Equally puzzling is the fact that his drawing of *Loligo pillae* in Pl. 36 actually illustrates *L. coindetii*.

Forbes and Hanley (1852) discussed the repeated confusion between *Ommastrephes sagittatus* (= *I. coindetii*) and *O. todarus* (= *T. sagittatus*) in the British waters, recording with certainty the former species from Brighton (p. 232).

Steenstrup (1857) discussed the characteristics of *Dosidicus eschrichtii*, a newly erected genus and species which he described earlier (Steenstrup, 1856-57). He erected the family Ommatostrephidae to cover both *Ommatostrephes* d'Orbigny and *Dosidicus* Steenstrup.

The nomenclature of both family and genus has long been in a confusing state. D'Orbigny (1835) first erected the genus *Ommastrephes*, but did not specify the type species (p. 47, *fide* Hoyle, 1902, p. 198). Confusion was first introduced by Loven (1846) and by Agassiz (1846), both of whom recommended the correcting of the "erroneous" writing ("*Ommastrephes*", scribatus: "*Ommatostrephes*") (Steenstrup, 1885, p. 163; Hoyle, 1902, p. 199). Steenstrup adopted this change throughout his numerous publications by using *Ommatostrephes* instead of *Ommastrephes*, and Ommatostrephidae instead of Ommastrephidae. In 1885 he accused Verrill of "proposed reformation of the original spelling", saying ". . . my esteemed colleague objects to my use of the linguistically correct form of the name *Ommatostrephes* as being untimely . . . I must call the attention of Prof. Verrill and those who follow him to some fallacies in this respect. . . . the name has been used in this correct form in all my papers on cephalopods, and the oldest of these was written more than 30 years ago; this correct form was also used before that time. . . . Thus on this side of the Atlantic Ocean the erroneous form had early given rise to objection, and 'for over forty years' independent scientists have replaced it by the correct form." (Steenstrup, 1885, after Volsøe, et al., 1962, p. 163).

Steenstrup's practice has been followed by most of the European teuthologists, especially the old German school including Chun, Pfeffer, Naef, Grimpe, and recently Jaeckel, in spite of Hoyle's discussion in 1902 (pp.197-199). According to the Code: "A family-group name is formed by the addition to the stem of the name of the type-genus, of -IDAE in the case of a family and -INAE in the case of a subfamily." (Art. 29). "The original spelling of a name is to be retained as the correct original spelling, unless i) it contravenes a mandatory provision of Articles 26 to 30; or ii) there is in the original publication clear evidence of an inadvertent error, such as a lapsus calami, or a copyist's or printer's error (incorrect transliteration, improper latinization, and use of an inappropriate connecting vowel are not to be considered inadvertent errors);

or iii) in the case of a family-group name, there has been a necessary correction of termination (other than necessitated by a change in the rank of the taxon), or a justified emendation in the stem of the name of the type-genus". (Art. 32a). Since *Ommastrephes bartramii* is regarded as the type species of the genus, and d'Orbigny's original spelling is *Ommastrephes*, and since *Ommastrephes* is the type genus of the family, the correct spellings for both the family and genus should be Ommastrephidae and *Ommastrephes*.

Fischer (1867) reported *O. sagittatus* as being rare on the west coast of France (p. 14). In the same list he included *Ommastrephes todarus* (p. 15). It is clear that Fischer was following d'Orbigny's understanding and that his *O. sagittatus* listed by him is *I. coindetii*.

Jeffreys (1869) recorded *O. sagittatus* (= *I. coindetii*) from Brighton (Dowager Marchioness of Hastings, *fide* Forbes and Hanley); Folkestone (Mackie, on same authority); Guernsey (Gallienne and Cooper); Falmouth (Cocks); Polperro (Laughrin); l'Orient (Gand, *fide* Tasle); Arcachon (Lafont); the Mediterranean, from Nice to Sicily (Risso, Philippi, and others); Venice (Nardo) (p. 129).

Jeffreys further discussed the validity of the *Loligo eblanae* of Ball (1841) and considered it to be a female of what he (Jeffreys) called *O. sagittatus* (p. 130). This statement is erroneous as Ball's *L. eblanae* represented a distinct, although closely related species now known as *Todaropsis eblanae* (Ball, 1841), a member of the subfamily Illicinae of the family Ommastrephidae.

Targioni-Tozzetti (1869) listed *O. sagittatus* as from the Atlantic off Newfoundland to the Mediterranean Sea (p. 597). Therefore, it appears that he recognized the North American and the Mediterranean forms to be conspecific.

Tryon's major work (1879, pp. 175-181) added great confusion to the systematics of the genus *Ommastrephes*. As a general introduction to the genus, he employed Verrill's (1873) description of the behavior of *O. illecebrosa*. He then divided the genus into four groups based on the features of the second and third sessile arms. The first group, which Tryon characterized as "second and third pairs of sessile arms without any membranaceous fringe on the inner edge of the ventral side, but replaced by a row of small, conical tubercles", was then subdivided into three subgroups. The characteristics of each subgroup, the species included therein and their distribution, are as follows:

Group 1. Tentacles with eight rows of numerous small cups near the end of the club;

O. sagittatus Lam. - Europe, Great Britain to Mediterranean; Newfoundland, New England coast.

O. crassus Lafont - Bay of Biscay.

Group 2. Tentacles with four rows of suckers, those of middle rows largest;

O. coindetii - Verany; Mediterranean.

O. aequipoda - Ruppell; Cape Verde Isles, Mediterranean.

Group 3. Tentacles with two series of small suckers at the end;

O. todarus - delle Chiaje; Southern Europe.

Tryon considered *O. sagittatus* and *O. illecebrosa* to be conspecific, stating, "I figure *O. illecebrosa*, Lesueur (fig. 342), the American representative of this species: it is considered distinct by some naturalists." (p. 177). *Ommastrephes crassus* (p. 178) from Bay of Biscay was considered to be closely allied to *O. sagittatus*. The characteristics he gave for this species leaves little doubt that it was actually an *Illex* he was describing, despite its enormous size (20 to 24 inches) and the poor figure presented by Tryon. Verany's (1851) figure of *O. coindetii* was reproduced by Tryon, yet he described it as being "deprived of suckers" at the tentacular tips (p. 178). Undoubtedly Tryon had copied Verany's description of his *L. coindetii* (Verany, 1837, p. 94) without actually examining a specimen of the species. Another consequence of his confusion can also be found in the case of *O. todarus*, which Tryon characterized as having "two series", rather than four series of small suckers at the ends of the tentacles (p. 179).

In 1880 Steenstrup attempted to clarify the complexity of the Ommastrephidae (Volsøe, et al., 1962, pp. 52-82). In contrast to the conventional method using relative dimensions of length and size of arms, tentacles, fins, body, etc., he suggested the taxonomic importance of such structures as the funnel groove, the fixing apparatus of the tentacular club, and the swimming keel on the lateral arms (pp. 54-58). Based on these criteria, along with the arrangement of the suckers on the sessile arms and the clubs, which Steenstrup believed to be the features independent of sexual differences, he divided the Ommastrephidae into four genera. These were:

a) *Ommastrephes* - with both central foveola and side pockets;

b) *Dosidicus* - with central foveola and side pockets and with exceedingly small, numerous, densely set suckers on the tips of all eight sessile arms;

c) *Todarodes* - with central foveola but no side pockets; and

d) *Illex* - without foveola and size pockets.

The genus *Illex* erected by Steenstrup was considered to be the least related to the typical genus *Ommastrephes* of d'Orbigny. It is characterized by its lack of membranes on the lateral arms, by its lack of a fixing apparatus on the tentacles, by the fact that the funnel is not in a deep folded groove, found merely in a simple depression, and, finally, by its eight series of small suckers on the dactylus. "Such forms are the species occurring along the coasts of Europe, which hitherto, owing to misinterpretation both of Lamarck's words and of the figures cited by him, generally went under the name '*Omm. sagittatus* (Lmk.)' or later (Lmk.) D'Orb., but whose proper specific name should be *Omm. coindetti* (Veran.); and more particularly the *Omm. illecebrosus* (Les.) specially known from the Newfoundland bank; the latter species greatly resembles the above mentioned species from the Mediterranean and the coasts of the European Atlantic, but still seems to be definitely specifically different." (Steenstrup, 1880, Volsøe, et al., 1962, p. 58).

The word *Illex* is the etymon of *illecebrosus*, meaning allurement or bait, for the type species *I. illecebrosus* is often used as the bait in the cod fishery.

This excellent work of Steenstrup's has indeed clarified some of the confusion in ommastrephid systematics. Of d'Orbigny's two "especes incertaines" (1835-1848), the four additional "doubtful species" listed by Gray (1849), and several others as listed by Verany (1851) and Tryon (1879) were discussed in detail by Steenstrup. Among these, Verany's *O. pillae* proved to be a young specimen of *I. coindetii* from the Mediterranean.

The confusion regarding the concept of *Loligo sagittatus* was also discussed. According to Steenstrup, the "variety a" of Lamarck's *L. sagittatus* was, without doubt, *O. todarus* (now *Todarodes sagittatus* (Lamarck)). It was Blainville who examined the same big specimen in the Museum of Seba and confirmed Lamarck's description, but, instead of using Lamarck's designation, he gave it a new name, *Loligo maxima* Bl. On the other hand, Blainville gave the name *L. sagittatus* to Lamarck's "variety b", which is the *O. bartramii* of the Atlantic (Blainville, 1829, *fide* Steenstrup, 1880). Steenstrup concluded that "*Illex coindetii* is not in Seba's Museum, neither is it included in Lamarck's dual species *L. sagittatus*, nor is it mentioned in Blainville in Diction, l.c., nor included by him in *L. illecebrosus* Les. (*Illex illecebrosus* (Les.)), which name the animal necessarily must bear if both the forms were found to be one species." (Steenstrup, 1880, Volsøe, et al., 1962, p. 77).

Later, in an article discussing the validity of *Xiphoteuthis ensifer* Owen, 1881, Steenstrup (1885, Volsøe, et al., 1962, pp. 163-176) listed *Loligo brongniartii* Blainville, 1823 and *Loligo todaropterus* delle Chiaje, 1822 as synonyms. He then proceeded to place the three in synonymy with *Ommastrephes pteropus* Steenstrup, 1857. It seems that Steenstrup had misinterpreted the figure illustrating *L. brongniartii* in d'Orbigny's work, for he relied upon the figure as the basis of his arguments. About this he wrote, "I was originally induced to refer this form to my *Omm. pteropus* because the older figure of *Lol. brongniartii* on pl. 4 made by Ferussac in the great work on Cephalopods differs, on the one hand, so essentially in its whole appearance from the species, to which d'Orbigny (for reasons which I do not understand at all) would refer to the *Omm. sagittata* (= *Illex coindetii* (Verany) Stp.) erroneously designated by him and many others, while on the other hand, it recalls, in all essential features, my *Omm. pteropus*". He also stated that his view was supported in 1859 when he studied the cephalopods in the National Museum of Natural History in Paris, finding a bottle of Ommastrephid labelled "*Lol. brongniarti* Blv." "Jacq. & Hombron 1841" (Volsøe, et al., 1962, p. 171). According to Steenstrup, the specimen "resembles my *Omm. pteropus*; ventral arms largest; also bears adhesive tubercles on tentacles" (Volsøe, et al., 1962, p. 171).

It is difficult to understand the above-mentioned statements of Steenstrup's, as the figure in d'Orbigny's work clearly shows the funnel groove being smooth, lateral arms being the longest, the fin being heart-shaped, and the suckers being confined to the club, with no tubercles. The specimen labelled "*Lol. brongniarti* Blv." "Jacq. & Hombron 1841" is still in the collections of the National Museum of Natural History in Paris. I have examined this specimen and found that it is not an *Illex*. Rather, it belongs to a new form of the genus *Symplectoteuthis*, first mentioned by Clarke (1965, p. 321; 1966, p. 115) but never fully described. The type specimen of *Loligo brongniartii* of Blainville (1823) is apparently no longer extant, however, the figure in d'Orbigny's work indeed represented an

Illex coindetii[1].

Verrill (1880) listed *Ommastrephes illecebrosa* as from Long Island Sound to Cumberland Gulf, from Cape Cod to Newfoundland and from Saybrook, Connecticut and Vineyard, Massachusetts (p. 289). He was of the opinion that the Mediterranean form differed from the North American form and that Lamarck's description of *Loligo sagittata* var. b. applied, in part, to *Ommastrephes bartramii* of the Gulf Stream region (p. 289).

Verrill (1880-1881)[2] later gave an intensive description of the species, based on specimens obtained by the research vessels of the then U.S. Fish Commission from the New England region. He retained the name *Ommastrephes illecebrosa*, with no reference to the name *Illex* erected by Steenstrup[3].

In the report prepared for 1879 (published in 1882), Verrill insisted on the name *O. illecebrosa*, placing *Illex illecebrosus* Steenstrup in synonymy. He argued, " . . . the distinction between *Illex* and *Todarodes*, it seems to me very slight and scarcely of

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[1] For further discussion, see "Remarks" under *Illex coindetii*.

[2] This article appeared in a period of about one and a half years, from June, 1880 to December, 1881. The section on *Ommastrephes* appeared from June, 1880 to January, 1881.

[3] Due to the above reason, the manuscript must have been prepared either prior to the publication of Steenstrup's paper on the Ommastrephidae (1880) or before Verrill had seen the article.

generic importance . . . but I have a species (which I refer to *O. sloanei* Gray) from Tasmania which agrees with *Illex* in having a smooth siphonal groove, but with *Todarodes* in having only four rows of distal tentacular suckers, and in the sharp denticulation of its large suckers. According to Steenstrup's system this would have to be made another genus, or else his generic characters would have to be entirely changed in order to admit it into either of his groups. . . . therefore, my own opinion is that *Illex* and *Todarodes* should be reunited and should retain the name *Ommastrephes* in a restricted sense. The absence of connective suckers and tubercles on the tentacular arms will be the most important diagnostic character to distinguish it from *Sthenoteuthis* and *Architeuthis*. *Dosidicus* is, perhaps, only an abnormal *Sthenoteuthis* with partially reproduced arms." (pp. 82-83).

As knowledge of cephalopods advanced, Verrill's argument can no longer be justified. His emphasis on the importance of the fixing apparatus (connective suckers and tubercles) of the tentacular arms can be explained due to his error in placing *Architeuthis* in the Ommastrephidae and in recognizing it to be a form closely allied to his *Sthenoteuthis* (=*Ommastrephes* d'Orb.). Furthermore, the ommastrephid foveolae are difficult to preserve and easily damaged in handling. His specimen of *O. sloanei* could have had a damaged funnel groove with the foveolae hardly distinguishable. From the characters and the locality data given by Verrill, it was probably a specimen of *Nototodarus sloani sloani* (Gray, 1849).

Carus (1889-1893) reported *Illex coindeti* to be distributed in the Atlantic Ocean, quoting various authors for its distribution: Alger (Aucapitaine); Marseille (Marion); Nizza, Genova (Verany); Napoli (Delle Chiaje); and Sicilia (Philippi) (p. 447). Girard in 1889 recorded it from the coast of Portugal (p. 204).

Norman (1890) in his "Revision of British Mollusca" discussed the spelling "*Ommastrephes*" versus "*Ommatostrephes*" and concluded that *Ommastrephes* should be retained (p. 475). For the classification of Ommastrephidae, he established a new system under which the family was divided into two genera, namely, *Ommastrephes* d'Orbigny and *Architeuthis* Steenstrup (pp. 475-480). The former was then subdivided into three subgenera. Both Steenstrup's *Ommatostrephes* and Verrill's *Sthenoteuthis* were synonymized in the subgenus *Ommastrephes* (s. str.) in which he listed *Loligo eblanae* Ball (=*Todaropsis eblanae* (Ball)) as the British representative. The subgenus *Illex* was composed of *O. illecebrosus* of the American waters and *O. coindeti* of the European waters. *Ommastrephes sagittatus* (=*Todarodes sagittatus* Steenstrup) was listed as the sole British representative of the third subgenus *Todarodes*. Apparently, Norman had accepted Verrill's erroneous view on the affinity of *Architeuthis* to the Ommastrephidae and recognized it as the second genus of the family.

Girard (1890a), without knowing Norman's system, adopted Verrill's position and proposed yet another system dividing the family into the genera *Stenoteuthis* Verrill and *Ommastrephes* d'Orbigny. The latter was then divided into four subgenera: *Ommastrephes* (s. str.); *Illex; Todaropsis*, and *Todarodes* (p. 259). He also discussed the validity of Verany's (1851) plates, concluding that the animal of plate 31 represented a *Todaropsis* while that of plate 32 was *O. coindetii* (pp.260-261). The geographical distribution of *O. coindetii* he reported as being along the Atlantic coastline of Europe and the Mediterranean (p. 260).

In a supplementary article, Girard (1890b) re-examined the classification of the Ommastrephidae with reference to the systems developed by Steenstrup (1880) and Norman (1890). He persisted in his earlier view, citing that the differences among those which he proposed as subgenera were not sufficiently significant enough to justify generic status. Therefore, the family Ommastrephidae consisted of two genera, *Stenoteuthis* and *Ommastrephes*, with the latter subdivided into four subgenera: *Ommastrephes*, *Illex*, *Todarodes*, and *Todaropsis*. *Ommastrephes* (*Todarodes*) *sagittatus* was considered to be the type species of the genus (p. 38). With additional specimens of *O. coindetii* that he obtained during the year, Girard concluded with certainty that the animal of Verany's plate 31 (Verany, 1851) was *Todaropsis*. For the first time both male and female *O. coindetii* were intensively described providing a comparison between the sexes and with *O. illecebrosus* (pp. 38-43).

Posselt's (1890) system of classification of the Ommastrephidae was basically that of Steenstrup's. However, it was he who, for the first time, subdivided the family into two subfamilies; the Ommastrephinae (*Dosidicus*, *Ommastrephes*, and *Todarodes*) and the Illicinae (*Illex*) (p. 304).

Joubin (1894; 1895) reported the cephalopods obtained by the yacht Hirondelle over the period 1886 through 1888. They included the ommastrephid *I. illecebrosus*, taken at 42°9'30"N, 44°7'45"W on the surface (Sta. 147), while on the cruise of Caudan, *I. coindeti* was captured off the west coast of France at a depth of 180 meters (Caudan Sta. 17) (Joubin, 1896, p. 249).

An intensive review of the synonyms of both the genus *Illex* and the species *I. coindetii* is to be found in Jatta's monograph on cephalopods (1896). He also gave a detailed description and excellent illustration of the species (pp. 69-75), reporting the depth of capture as being from 50 to 250 meters. Unfortunately, he erroneously described and illustrated its radula as having five rows of teeth (p. 73, pl. 12, fig. 1). He also erroneously used an *I. coindetii* to illustrate *Todaropsis veranyi* (pl. 2, fig. 6).

In his synopsis of the oegopsid cephalopods, Pfeffer (1900) recognized seven genera within the Ommastrephidae, namely, *Illex* Steenstrup, *Todaropsis* Girard, *Ommatostrephes* D'Orb. (=*Todarodes* Steenstrup), *Symplectoteuthis* Pfeffer, *Hyaloteuthis* Gray, *Dosidicus* Steenstrup, and *Stenoteuthis* Verrill (=*Ommastrephes* D'Orb.) (p. 178).

Within the genus *Illex* he recognized only one species, *Illex illecebrosus* (Lesueur, 1821), with two subspecies: *I. i. illecebrosus* (Lesueur) from the east coast of North America, and *I. i. coindeti* (Verany) of the Mediterranean Sea (p. 179).

In 1886 Hoyle published the first extensive catalogue of living cephalopods since the publication of Tryon's 'Manual of Conchology", which appeared in 1879. Hoyle divided the family Ommastrephini Steenstrup, 1861, into three subfamilies: Thysanoteuthidae Keferstein, 1866, Ommastrephidae Gill, 1871, and Mastigoteuthidae Verrill, 1881 (Hoyle, 1886a, pp. 242-247).[1] It seems that Hoyle treated the Ommastrephidae (actually, his Ommastrephini) as a melting pot of a large number of diverse forms. Indeed, it contained no less than six families now recognized: Thysanoteuthidae, Ommastrephidae, Architeuthidae, Brachioteuthidae, Bathyteuthidae, and Mastigoteuthidae. In the supplement to this catalogue, which appeared in 1897, he did not change his view of the family, adding in fact three new genera and nine new species to his lengthy list. These additions were *Ommastrephes caroli*, *O. gouldi*, *Todaropsis veranyi*, *T. eblanae*, *Martialia hyadesi*, *Chtenopteryx fimbriatus*, *C. cyprinoides*, *Architeuthis kirkii*, and *Tracheloteuthis guernei*. The only revisions in the new list of ommastrephids was the revision of *O. eblanae* to *Todaropsis* (pp. 370-372).

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[1] This same system of classification had also appeared in Hoyle's great work on the Challenger cephalopods (Hoyle, 1886b, pp. 32-36).

Hoyle (1902) listed the British cephalopods, stating that the nomenclature used differed from that adopted by Jeffreys (1869), yet was practically the same as that of Norman (1890) (Hoyle, 1902, p. 197). The British form of *Illex* was given by Jeffreys as *O. sagittatus* and that, in turn, was broken down to *O. (Illex) coindeti* and *O. eblanae* by Norman. Hoyle accepted Steenstrup's views and treated *Illex* as a full genus, as he had already shown in his 1886 catalogue. In 1902 he listed *I. coindeti* as the British representative of *Illex* (p. 199).

After the publication of "Synopsis der Oegopsiden Cephalopoden" (Pfeffer, 1900), Hoyle apparently changed his opinion on the systematics of the family Ommastrephidae. In his later publications (1904; 1909) *Thysanoteuthis*, *Architeuthis*, *Tracheloteuthis*, and *Bathyteuthis* were removed from the Ommastrephidae and placed in families of their own: *Ctenopteryx* (=*Chtenopteryx*, err. typ., *fide* Hoyle, 1910) was placed in the Bathyteuthidae; *Mouchezia* and *Steenstrupiola* were dropped; and *Mastigoteuthis* was placed in the Chiroteuthidae. The genera contained in the family Ommastrephidae are identical to those proposed by Pfeffer (1900) with the addition of *Rhynchoteuthis* Chun, 1903.

J. M. Clarke (1902) reported that two squid were caught in Lake Onondaga, a saline water lake in New York State. In judging the genuineness of the report, he suggested, "These squids are not to be at once cast out as a 'fake' simply because they are marine animals alleged to have been caught in a fresh-water lake . . . There was a time in post-glacial history when there was communication from this body of water to the sea by the way of the St. Lawrence Valley. It is within the limits of possibility that at such a time marine animals entered the present basin of Onondaga Lake as they did that of Lake Champlain." (p. 947). One of these two specimens was identified by Ortmann (1903) as *Illex illecebrosus*. As to the capture of this species in Lake Onondaga, Ortmann was doubtful and suggested that the specimen was merely bait abandoned by local fishermen (p. 31).

In 1908, Pfeffer persisted in his previous (1900) opinion on the systematics of *Illex* . Under the name *Illex illecebrosus* he included both European and North American forms. As for the distribution of the European form, he listed Brighton and the English Channel, the Firth of Forth and Eastbourne, the west and southwest coasts of France and Portugal, and the Mediterranean Sea. He further stated that the morphological distinction between the European and the North American forms were not confirmed (p. 90).

Although Williams'(1909) classic work on the anatomy of the common squid dealt mainly with *Loligo pealei*, a general account of *I. illecebrosus* was included. He noted that north of Cape Cod the "short-finned" squid were more common with *L. pealei* abundant between Cape Cod and Cape Hatteras, and south of Cape Hatteras other species of *Loligo* becoming more numerous. The fact that large quantities of

Illex ran ashore (November and December, 1902) on Cape Cod, and that 60 barrels were taken in a single trap haul (October), and also that small quantities of *Illex* were brought into the New York markets during winter months, led Williams to conclude that *Illex* does not over-winter scattered at the bottom in moderately deep water. The latter he believed to be the case for *Loligo* (p. 1).

In 1912, Pfeffer published his monumental work on cephalopods based primarily on materials obtained by the "Plankton-Expedition". Three subfamilies and eight genera were recognized among the family Ommastrephidae, which he spelled "Ommatostrephidae" as the majority of European authors. The subfamily Illicinae consisted of *Illex* and *Todaropsis*, the subfamily Ommatostrephinae consisted of *Nototodarus* and *Ommatostrephes*, and the subfamily Stenoteuthinae of *Hyaloteuthis*, *Symplectoteuthis*, *Stenoteuthis*, and *Dosidicus* (pp. 387-388). As in his previous publications (1900; 1908), Pfeffer considered the genus *Illex* to be monotypic, with two geographic forms distributed in completely separate geographic areas. According to Pfeffer, the distinction between *I. i. coindetii* and *I. i. illecebrosus* was based on secondary sexual characters.

As was mentioned earlier, Girard (1890b) presented a list of characters of the North American *Illex illecebrosus* which he considered to be distinct from the European form *I. coindeti*. These characters were the narrower body (in relation to the body length), the much shorter arms, the almost smooth horny ring of the large suckers on the tentacles, the somewhat different horny ring dentition of the large suckers of the lateral arms, the less pronounced sexual dimorphism of the large suckers of the tentacles and the lateral arms, and the differences in the hectocotyli. Pfeffer, in his Plankton-Expedition monograph, was of the opinion that these characters were not reliable. From comparative study, he concluded that the American form appeared to have shorter, but wider fins, and particularly so in the females; to have shorter arms, which are thinner in the males; the maximal sucker size on the arms and tentacles smaller, particularly in the males; and the more oblique indentation of the horny rings of the large suckers of the tentacles and arms (Pfeffer, 1912, p. 422).

Chun (1913) reported the cephalopods from the Michael Sars North Atlantic Deep Sea Expedition of 1910. A total of seven specimens of *Illex illecebrosus* was reported. Among them, two were from the Newfoundland banks, five from Stations 33 and 39B (31°17'N, 10°06'W and 26°03'N, 15°00'W, respectively (p. 5). I have examined these specimens now in the collections of the Bergen Museum, and conclude that the specimens from Stations 33 and 39B actually properly belong to *I. coindetii*.

The cephalopods obtained by the Princesse-Alice during the period 1898 through 1910 were reported by Joubin in 1920. Two specimens of *Illex* were recorded during the 1903 cruise from 45°21'N, 2°39'W (depth 130 m) and 45°13'N, 3°06'W (depth 358 m) respectively. Both of these were identified as *I. illecebrosus* (p. 59). In 1924, Joubin reported the cephalopods collected by the Prince of Monaco from the North Atlantic Ocean. Four specimens were recorded from 43°26'N, 59°03'W (depth 0-2500 m) (p. 76). The synonyms listed there for *I. illecebrosus* are Lesueur's *Loligo illecebrosa*, Verany's (1837) *L. coindetii*, Ferussac and d'Orbigny's (1839) *Ommastrephes sagittatus*, Verany's (1851) *L. sagittatus* (Verany, 1851, p. 110), Steenstrup's *I. illecebrosus* and *I. coindetii* and Pfeffer's *I. i. illecebrosus* and *I. i. coindetii*. Joubin stated that Pfeffer's subdivision of *I. illecebrosus* into two subspecies, based on geographic distribution, was not justifiable. He recognized only one species with two varieties within the genus *Illex*: *I. illecebrosus* (Lesueur) var. *illecebrosus* G. Pfeffer and *I. illecebrosus* (Lesueur) var. *coindetii* G. Pfeffer. The geographic distribution of this species was reported by Joubin to be the European coast of the temperate Atlantic, the Mediterranean, and the Atlantic coast between the United States and Brazil (p. 77).

Naef (1916, p. 12) postulated that Jatta (1896) had misspelled the trivial name for the "European" species (*Illex coindetii*) changing it to *I. coindeti*. He (p. 18) also pointed out that *Todaropsis veranyi* (Jatta, 1896, pl. 2, fig. 6) was actually a mature male of *I. coindeti*. Further, he explicitly held that *I. illecebrosus* and *I. coindeti* were different (p. 18). In 1921 (p. 538) he again listed *I. coindeti* amongst Mediterranean cephalopods.

Chadwick (1921, p. 17) reported a large specimen of *I. coindeti* as being stranded on the beach of Port Erin Bay, Isle of Man. The specimen was reported to have a length (from base of sessile arms to posterior extremity) of 95 cm, with a pen length of 71 cm. Chadwick stated, "The presence of six conical teeth on the distal circumference of the suckers borne by the sessile arms enabled the observer to identify the specimen as *Illex coindeti*." Through the kindness of Dr. John S. Colman of the Marine Biological Station, Port Erin, I have examined the remains (two arms, III and IV) of this specimen. They belong to an *Ommastrephes*, rather than an *Illex*. Therefore, this specimen, unique in its enormous size for an *Illex*, must be deleted from the *Illex* record.

Grimpe reported *Illex coindeti* from the neighborhood of Helgoland (Grimpe, 1921, p. 297). He considered it to be a variety of *I. illecebrosus* and presented it as *Illex* (*illecebrosus* Lesueur 1821 var.) *coindeti* Verany 1851. Apparently by 1922 he had changed his opinion regarding the systematics of *Illex*, for he listed *I. coindeti* and *I. illecebrosus* as separate species (Grimpe, 1922, p. 48). For distribution he listed the Mediterranean Sea, the West European Sea (30°-50°N, east of 30°W) and the North Sea for the former, and the Western North Atlantic (50° -80°N, west of 30°W) for the latter, respectively.

Naef (1923, p. 428) recognized two families within the family Ommatostrephidae, i.e., Illicinae Posselt, 1890 and Ommatostrephinae

Posselt, 1890. The former consisted of the genera *Illex* Steenstrup and *Todaropsis* Girard, and the latter *Ommatostrephes* d'Orbigny, *Nototodarus* Pfeffer, *Hyaloteuthis* Gray, *Eucleoteuthis* Berry (=*Symplectoteuthis luminosa* Sasaki, 1915), *Dosidicus* Steenstrup, and *Sthenoteuthis* Verrill. He clearly stated that he considered *I. illecebrosus* and *I. coindeti* as two separate species (p. 429), yet Steenstrup's *Illex illecebrosus*, Verrill's *Ommastrephes illecebrosus*, Girard's *Ommatostrephes illecebrosa* and Pfeffer's *Illex illecebrosus* were all curiously included as the synonyms of *Illex coindeti* (p. 430).

Grimpe (1924, p. 321) reported the first incident of a double hectocotylus. The specimen had both ventral arms hectocotylized, rather than only one of the ventral pair being hectocotylized as is the normal condition in the genus *Illex*. As in his previous work (Grimpe, 1922, p. 48), *I. illecebrosus* and *I. coindeti* were referred to separately, but here he referred to them as "Formen" rather than "Arten".

The cephalopods obtained by the Danish Oceanographical Expedition to the Mediterranean and adjacent seas (1908-1910) were reported by Degner in 1925. Two *I. coindeti* were reported from 40°54'N, 28°53'W (9 mm ML) and from 40°48'N, 27°59'W (15 mm ML) (Degner, 1925, p. 40). The significance of these specimens is that they represent the smallest *Illex* recorded, apart from one individual with 11.1 mm ML reported by Naef (1921, p. 437, Textfig. 222). The two specimens reported by Degner are deposited in the Zoological Museum of the University of Copenhagen and are in fair condition.

Grimpe (1925) gave a detailed description of *Illex illecebrosus coindeti* (pp. 76-80). He reported *Illex illecebrosus illecebrosus* to be distributed from Cape Hatteras to Cape Cod, the Newfoundland Banks northwards to Greenland and Iceland (from 35°N to 65°N), with *Illex illecebrosus coindeti* occurring from 26°N to 58°N (p. 76).

Later, Grimpe (1933) in reporting the Arctic cephalopods, indicated that there was little difference between the West and the East-Atlantic forms of *Illex* (p. 508). The eastern form, *Illex illecebrosus coindeti* he listed from the Mediterranean Sea, the southwest coast of Portugal, the French coast, and the English Channel, and was not to be considered as an Arctic form (p. 508). The typical form, *Illex illecebrosus illecebrosus* was listed as from Cape Hatteras northwards to Newfoundland and further north to the Gulf of Cumberland (p. 509).

In reporting the cephalopod fauna of the northwestern African waters, Robson (1926), indicated two specimens of *Illex* from western Morocco, under the subtitle "*Illex coindeti*, Verany? var." (p. 179). According to Robson, these two specimens possess characteristics of both *I. illecebrosus* and *I. coindetii*. Although Robson hesitated to assign them to either *illecebrosus* or *coindetii* (p. 185), they can be identified as *Illex coindetii* on the bases of the hectocotylized arm.

A report on the Newfoundland squid fisheries was published by Frost and Thompson in 1932, based on the Annual Reports of the Department of Mines and Fisheries and their own observations. *Illex illecebrosus*, called the "short-finned" squid, was said to be "of unique importance, in that it is the recognized bait for the fall cod-fishery" (p. 25). The contents of this paper on the Newfoundland squid fisheries are summerized as follows: 1) the leanest years of squid landing in Newfoundland between 1914 and the date of the publications (1932) occurred "at intervals of from approximately four to eight years", with the exception of 1926 (p. 26); 2) the animal occurs "from Cape Cod to Newfoundland" (p. 26); 3) the animal advances "northwards, along with a similar advance of the 4°C isotherm, at an average daily rate of 3-4 miles, reaching the latitude of the St. Pierre Bank by mid-June and Labrador by September" (p.26); 4) "for its abundance the temperature of the surface layer, down to at least 10 fathoms, must be not less than 5°, and preferably from 7° to 10°C" (p. 27).

In a continuing effort, Frost and Thompson later pointed out (1933, p. 85) that "the best temperature conditions for squid runs" were "when the surface temperature down to 5 fathoms (10 metres) is between 7° and 15°C (optium 11°C)" and "when the corresponding temperature at from 8 to 14 fathoms (15 to 25 metres) and probably much deeper is between 2° and 9°C (optium probably 5° or 6°C)". They concluded that "it is therefore highly probable that squid approach the Banks and the Newfoundland coast in the deeper water layers along with the influx of comparatively warm, saline Atlantic water . . ." (p. 85), and that the inshore migration is not impaired by comparatively low salinity near the coast (p. 86).

In 1933, the squid fishery in Newfoundland was a complete failure. Frost and Thompson (1934), in attempting to explain its failure, pointed out that "the survival values of annual broods from the spawning seasons" and "the suitability or otherwise of the physical conditions - temperature and salinity - of the sea in the various fall seasons" are the usual factors to receive investigation (p. 60). Due to the lack of information on the spawning and the early or juvenile stages of this species, Frost and Thompson had to concentrate on an investigation of physical factors in relation to the squid run. They suggested that "when a strong influx of Arctic water had just occurred, and the warmer and more saline 'slope' water is not found off Grand Bank at moderate depths, a poor squid run will follow" (p. 62). This generalization does not hold true at all times - as indicated by several exceptions in their report (pp. 62-63).

Boone (1933), with a description of two specimens of *Illex illecebrosus illecebrosus*, reported it from 200 fathoms (by dredge), 9 miles S.W. by W. of Port aux Basques, Newfoundland on September 1, 1926; and from off Halifax, Nova Scotia on August 3, 1923 (p. 168).

Bouxin and Legendre (1936) reported the cephalopods obtained from the stomach contents of the tuna (*Thynnus alalonga* Risso, *fide* Adam) of the Bay of Biscay area, including some 20 specimens of *Illex* with mantle lengths ranging from 60 to 110 mm. Bouxin and Legendre, following Grimpe's (1925) opinion, considered *I. illecebrosus* and *I. coindeti* as being two separate species and identified their specimens as *I. coindeti*, based on the locale of origin (p. 62).

Illex coindeti from various stations along the coasts of Senegal and Guinea were reported by Desbrosses (1938). It is interesting to note that he used the designation "variété" for his *I. coindeti*, and he used it in contrast with *Illex illecebrosus illecebrosus* (pp. 342-343).

Adam (1939) reported a specimen of *Illex illecebrosus* found in the stomach contents of *Orthagoriscus mola* L.* from St. George's Channel off Bristol, England. Adam stated, "Selon son lieu d'origine, l'animal appartient probalement à la race *Illex illecebrosus coindeti* (Verany) mais l'état de conservation de l'animal incomplet ne permet pas une décision à ce point de vue" (p. 2).

Illex coindetii was included in the 1942 report by Adam on cephalopods of the Red Sea. He observed that of the eight species which the Red Sea has in common with the Atlantic Ocean and the Mediterranean Sea, five occur also in the Indian Ocean. Of the remaining three species, the presence of two is doubtful. In fact, Adam stated that the presence of *Loligo forbesi* and *I. coindetii* in the Red Sea needed further confirmation based on additional collections. Hence, only one of the eight species mentioned is known with certainity to occur in the Red Sea, the Atlantic Ocean and the Mediterranean Sea alone. Adam thus concluded that the migration of cephalopods through

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*(=*Mola mola* (L.))

the Suez Canal is doubtful and the cephalopod faunae of the Red Sea and the Indian Ocean indicate the close zoogeogrpahical similarity of these two regions (p. 18).

Stephen (1944) reported the cephalopods of Scottish and adjacent waters, citing Norman's (1890, p. 476) record from the Firth of Forth as the sole Scottish record of *Illex illecebrosus coindeti* (Stephen, 1944, p. 264).

The cephalopod fauna of Iceland was reported by Bruun in 1945. He cited the following as *Illex illecebrosus* (p. 5): *Ommatostrephes illecebrosus* (Grøndal, 1891, p. 24), *I. illecebrosus* (Murray & Hjort, 1912, p. 592), *Ommatostrephes* (*Illex*) *illecebrosus* (Bardarson, 1919, p. 30). Further, he considered *I. illecebrosus* to be a rare guest in Iceland (Table I, p. 10) and "of no special zoogeographical significance in the present considerations" (p. 13). Clarke (1966) questioned Bruun's conclusions, stating "there is some reason to doubt Bruun's record for Iceland which was based on a note by Grøndal which could have referred to *I. coindeti* and a short passage in Murray & Hjort (1912) '*Illex illecebrosus* and *Ommatostrephes todarus* are northern forms, of great importance on the banks of Newfoundland, and along the coasts of Iceland and Norway'. Bruun understood this to mean that both species are important on both sides of the North Atlantic, but it seems much more likely that the authors meant that *I. illecebrosus* was important on the western and *O. sagittatus* (=*O. todarus*) on the eastern side of the northern Atlantic; particularly as the latter species is not found on the western side." (p. 119), The validity of the Icelandic records will be discussed later.

Study of western North Atlantic cephalopods was greatly ignored after the publication of Verrill's major work in 1882. It was for G. L. Voss, first in the early 1950's, to be instrumental in a reawakening of interest in the study of these forms. In 1954 he published the first systematic list of the cephalopods of the Gulf of Mexico, including 17 families, 27 genera, and 33 species. Among them was listed *Illex illecebrosus*. Voss observed that "there is a strong connection between the cephalopodan fauna of the Mediterranean Sea and the Gulf of Mexico" and stated that "Considering the sometimes rather long planktonic life of many of the larval forms and the sweep of the North Equatorial Current into the Caribbean and thence into the Gulf of Mexico, such distribution is not surprising" (Voss, 1954, pp. 475-476).

The collection of cephalopods obtained by the Atlantis off the coasts of Cuba in 1938 and 1939 containing 11 families, 21 genera and 25 species were reported by Voss in 1955. *Illex illecebrosus* was represented by 14 specimens (p. 103), with a distribution "across the upper North Atlantic to the European coast, New England to Cape Hatteras, the Gulf of Mexico and Cuba" (Voss, 1955, pp. 103-104).

Voss' (1956) monograph of the cephalopods of the Gulf of Mexico included 21 families, 35 genera and 42 species. Again, he reported the distribution of *Illex illecebrosus* as being "Northern

Europe as far south as the English Channel; east coast of the United States; Gulf of Mexico; Cuba" (Voss, 1956a, p. 146). In the same year, Voss (1956b) reported it from off Jacksonville Beach in 105 fathoms and from Dry Tortugas (p. 279).

A great loss to teuthology was the long neglect of the cephalopod collections in the Academy of Natural Sciences of Philadelphia. In fact, "from 1879 to date (1962) no staff member of the museum has devoted attention to this group and the collections have languished, unworked and unreported, except for occasional visits by interested students" (Voss, 1962, p. 1). These collections contained the type specimens of the several new species reported by Lesueur in 1821, including *Illex illecebrosus* and *Loligo pealei*, the two common western Atlantic squids. Voss, after searching through the collections, reported that "none of Lesueur's six or more types can now be found in the collections and they must be presumed lost or destroyed" (Voss, 1962, p. 1). For the specimens belonging to genus *Illex* in the collections, Voss listed five lots for *I. illecebrosus illecebrosus* and one lot for *I. i. coindetii* (p. 5). In January, 1969, I had an opportunity to make a short visit to the ANSP in order to verify the exact type locality of Lesueur's *I. illecebrosus*. Neither the original drawings of the said species nor any record which would enable me to verify the exact position of Sandy Bay was found in either the Library of the Academy or that of the American Philosophical Society, also in Philadelphia.

During 1964 and 1965, the Institute of Marine Science of the University of Miami carried out deep-sea biological investigations aboard R/V John Elliott Pillsbury in the Gulf of Guinea. Numerous cephalopods were captured and are currently studied by Voss and his group, and through his courtesy, part of the collections of *Illex coindetii* were provided for study. From the materials on hand, the narrative of the cruises published by Voss (1966a), and the dredging and trawling records as edited by Bayer (1966), it may be reported that *I. coindetii* was captured from depths ranging from 37 to 485 meters.

In 1952, Adam published on the cephalopods collected by the 1948-1949 Belgian Oceanographic Expedition to the African coast of the South Atlantic Ocean. The report includes one of the major contributions to the biology of *I. coindetii* (pp. 80-94). Numerous specimens of this species were taken in the area between 0°-14°05'S and 8°47'E-13°28'E, and at a station at 9°31'30"N, 16°23'W. The depths of capture range from 48 meters to 500 meters, with the temperature ranging from 7.8 to 22.7°C. Salinities ranged from 33.06 to 38.33^{o}/oo (pp. 82-83). Adam followed Pfeffer's views in that he considered the genus *Illex* to consist of one species and two geographic races. These he called *I. illecebrosus illecebrosus* (American Atlantic coast) and *I. i. coindetii* (eastern Atlantic, North Sea, and Mediterranean Sea). He identified the specimens from the African coast as *I. i. coindetii*, with those from the Bristol Channel assigned to *I. i. illecebrosus* (p. 92).

Squires (1957), based on data obtained from incidental trawl catches of *I. illecebrosus* by the Investigator II, reported on the distribution, relative annual abundance, growth, sexual maturity, food, parasites and the annual migratory movements of this species in the Newfoundland fishing area. A seasonal migration was reported to begin on the Grand Banks in early May, then northward and westward as far as Hamilton Inlet, Labrador, and to inshore Newfoundland bays by August (p. 693). The actual northern range of its distribution was extended as far north as Hebron Harbour, Labrador (approximately 58°11.8'N, 62°37.7'W) (p. 694).

In some years (e.g., 1958), the squid failed to appear in large numbers inshore. It was suggested that the "availability of food" and a "tendency to remain oceanic" are two of the most important contributing factors to explain this phenomenon (Squires, 1959, p. 25).

The monograph on North Sea and Baltic Sea cephalopods prepared by Jaeckel (1958) recognized *Illex* as being a monotypic genus, although the name *Illex coindeti* was used (p. 598). Morales (1958), reporting on the cephalopod fauna of Catalonia, noted that *Illex coindeti* is fished at depths between 112 and 400 meters (p. 22).

A third species now appears in the literature. In 1960, Castellanos described a new species of squid from Argentine waters and gave it the name *Ommastrephes argentinus*. Its distributional range was said to be along the coast at Buenos Aires, northward to

41°S, with the fishing zone in the deep littoral zone of Mar del Plata between 38° and 41°S, 55° and 60°W (p. 57). Subsequently, in an article describing the reproductive system of her new species, Castellanos indicated that its proper name should be *Illex illecebrosus argentinus* (Castellanos, 1962, p. 117). Despite this, the original name (*Ommastrephes argentinus*) was retained in both the title and text (Castellanos, 1962).

Muus (1962) reported on the cephalopods collected by the Godthaab Expedition in 1928, including *Illex illecebrosus* from the west coast of Greenland (about 62°N, p. 20). He commented that this species was an occasional guest from more southerly latitudes (p. 22).

Mangold-Wirz (1963a), in a study of the relative growth of three species of Mediterranean ommastrephids, noted sexual dimorphism in *I. i. coindetii*. This was soon followed by an article on the biology of the benthic and nectonic cephalopods of the Catalonian Sea, in which she (1963b) reported on the geographical distribution, habitat, annual distribution, growth, age and longevity, and reproduction of this form (pp. 157-166).

Crosnier (1964) reported *I. i. coindetti* is found only below the thermocline in waters off the Cameroun Republic (p. 36).

Aldrich (1964), showing that ommastrephids can be taken by midwater trawl, used the name *I. illecebrosus* throughout the text. In one place, however, he wrote "The form that exists here in Newfoundland is *I. illecebrosus illecebrosus* on the basis of current knowledge" (p. 6).

In 1964, Castellanos published a further article on the general biology of *I. i. argentinus*, extending its range to from 36° to 42°S, 55° to 62°W. The temperature of these sites of capture ranged from 5 to 12°C, with salinity ranging from 33 to 34^{o}/oo. Vertical distribution was reported from 7 to 250 meters (pp. 21-26).

During the period 1966 to 1968, the West German ship Walther Herwig carried out exploratory expeditions along the coasts of Argentina, Uruguay and Brazil. The cephalopods thus obtained (June to August, 1966) were reported on by Castellanos and Menni (1968). Again the distribution of *I. i. argentinus* was extended to between 35° and 47°S, 52° and 61°W with a vertical range to 800 meters (pp. 5-6). Eggs and the juveniles were reported from stations 234 and 419 at depths of 200 meters and 160-300 meters, respectively (p. 6).

Mercer (1965) reported on the growth, maturation, sex ratio, stomach contents, and parasites of *I. i. illecebrosus* from the Grand Banks and inshore Newfoundland from June to September, 1964. The results of his studies are not different from those presented by Squires (1957).

Zuev (1966), in a study based on 15 specimens of *Illex* - five from the west coast of Africa, six from the Adriatic Sea and four from the Newfoundland area - stated that the Adriatic squids are morphologically closer to the American specimens than to the European ones, but are different from both forms (p. 1). Based on this, Zuev concluded that the genus *Illex* included one species, *Illex illecebrosus*, which is "represented by several geographical forms, the total number of which may turn out to exceed three" (p. 5).

Clarke (1966) considered *I. illecebrosus* and *I. coindeti* to be distinct species and treated them as such (p. 119, p. 123). He has gathered together most extensively the published information regarding the distribution and the biology of these two species (pp. 118-125). Yet he obviously overlooked Castellanos' subsequent publications after her original description of *Ommastrephes argentinus*, for he treated this species under *Ommastrephes* (p. 113).

Squires (1967) suggested that *I. i. illecebrosus* spawned about one year of age, with a life span of not more than two years, but most probably one (p. 1209).

In a report on the biology and catching of Atlantic squid, *Illex illecebrosus*, Nesis (1967) considered *Illex* to be a monotypic genus with three subspecies (Translation, p. 3).

Adam (1967) listed *I. i. coindetii* from the Eastern Mediterranean as far east as between Cyprus and Turkey (p. 73).

Mercer (1968) in his synopsis of the recent Canadian cephalopods commented that records of *I. illecebrosus* from Greenland and Iceland cannot be confirmed and that "Since the species does not occur beyond the continental slope there is apparently no genetic interchange between populations on both sides of the Atlantic" (p. 268).

Lu (1968) reported on morphometric changes associated with growth of *I. i. illecebrosus* from Newfoundland waters.

Aldrich and Lu (1968) commented on the earlier work by Zuev (1966), concluding that Zuev's conclusions were misleading, and that the Newfoundland *Illex* do not agree with his "form C" and that his "forms" are not the "subspecies" accepted by many authors (p. 818).

Mangold, Lu, and Aldrich (1969) reported that *I. i. coindetii* from the Mediterranean Sea exhibits strong sexual dimorphism, while *I. i. illecebrosus* from Newfoundland lacks sexual dimorphism (p. 1153).

Mercer (1969a) reported on heterogeneity in Newfoundland inshore squid populations and suggested that "mixed age groups within a single year-class are present, this being related to a protracted spawning season and area".

In 1969 a new species of *Illex* was discovered and described under the name *Illex oxygonius* Roper, Lu, and Mangold, 1969 . Based on morphological characters, the three formerly accepted subspecies, *Illex illecebrosus*, *I. I. coindetii*, and *I. i. argentinus* were elevated to the status of full species (p. 317).

It is here that we find our story of the development of knowledge of the genus *Illex*.

PART II. SYSTEMATICS

Family OMMASTREPHIDAE Steenstrup, 1857

Ommatostrephidae Steenstrup, 1857, pp. 11-14 (Volsøe, et al., 1962, pp. 10-22). -Pfeffer, 1900, p. 176; 1908, p. 87; 1912, p. 368. -Chun, 1910, p. 201.

Ommastrephini Steenstrup, 1880, p. 89 (Volsøe, et al., 1962, p. 52). -Hoyle, 1886b, p. 32. -Joubin, 1895, p. 31; 1900, p. 44.

Ommastrephidae Gill, 1871, p. 1. -Tryon, 1879, p. 102, p. 175. -Verrill, 1882, p. 290. -Carus, 1890, p. 455. -Jatta, 1896, p. 55. -Hoyle, 1904, p. 3, p. 15. -Berry, 1912a, p. 338. -Sasaki, 1929, p. 276.

Todarodidae Okutani, 1967, p. 12. -Taki & Igaradhi, 1967, p. 16.

Diagnosis: Animal medium to large size; body hemifusiform, 4 to 6 times as long as broad; fins terminal, shorter than half the length of body, sagittate; eye openings distinctly sinuated in anterior margin; nuchal cartilage spatulate, with expanded part in front; funnel groove well-defined, often forming foveola or other folds in anterior part; funnel adductors bipaired; one pair of submedian, and the other, of lateral position; funnel cartilage inverted-T-shaped (⊥); buccal connectives attached dorsally to arm IV; armature of arms composed of biserial suckers; tentacular armature composed of suckers only, 2 to 4 series on carpal region without forming well-defined fixing apparatus, 4 series on manal region of which the central two series distinctly larger than the marginal two series, 4 to 8 series on dactylus region, small to minute; gladius thin, consisting chiefly of the rhachis, except for a short posterior part where the vanes are little developed, forming a slender lanceola with a short endcone; hectocotylization in one or both ventral arms. (In part,after Sasaki, 1929)

Type genus: *Ommastrephes* d'Orbigny, 1835

Genus *Illex* Steenstrup, 1880

Loligo, Lesueur, 1821, p. 25. -Blainville, 1823, p. 142. -Verany, 1837, p. 94; 1851, p. 106.

Ommastrephes Ferussac & d'Orbigny, 1835-1848, p. 345. -Forbes & Hanley, 1853, p. 231. -Jeffreys, 1869, V. p. 129. -Fischer, 1867, p. 14. -Verrill, 1881, p. 268. -Norman, 1890, p. 476. -Girard, 1890a, p. 259.

Illex Steenstrup, 1880, p. 82 (Volsøe, et al., 1962, p. 58). -Hoyle, 1886b, p. 34; 1902, p. 199; 1904, p. 3. -Carus, 1890, p. 447. -Jatta, 1896, p. 69. -Pfeffer, 1900, p. 179; 1908, p. 89; 1912, p. 390. -Naef, 1923, p. 429.

Diagnosis: Funnel groove smooth without foveola and side pockets; no fixing apparatus on tentacular stalks; tentacular club expanded; suckers in carpal region small, biserial; manal suckers tetraserial, suckers on lateral rows small, medial suckers large with smooth horny rings or bluntly crenullated; suckers on dactylus small to minute, arranged rather irregularly in about 8 rows; swimming membranes on all arms poorly developed; either right or left arm IV hectocotylized.

Type species: *Loligo illecebrosa* Lesueur, 1821
Illex illecebrosus (Lesueur, 1821)

Loligo illecebrosa Lesueur, 1821, p. 95.

Loligo piscatorum LaPylaie, 1825, p. 319.

Ommastrephes illecebrosa Tryon, 1879, p. 176, pl. 78, fig. 342. -Verrill, 1880, p. 289; 1880-1881, p. 268.

Illex illecebrosus Steenstrup, 1880, p. 90 (Volsøe, et al., 1962, p. 65). -Hoyle, 1886a, p. 245; 1886b, p. 34; 1909, p. 273; 1910, p. 410. -Posselt, 1890, p. 335. -Lönnberg, 1891, p. 34. -Joubin, 1894, p. 213; 1895, p. 32; 1924, p. 76. -Chun, 1913, p. 5. -Naef, 1916, p. 18; 1923, p. 429. -Grimpe, 1922, p. 48; 1924, p. 321. -Frost & Thompson, 1934, p. 59. -Bruun, 1945, p. 5. -Squires, 1957, p. 693; 1959, p. 23. -Muus, 1962, p. 20. -Clarke, 1966, p. 119. -Mercer, 1968, p. 267; 1969a, p. 618. -Roper, Lu & Mangold, 1969, p. 317.

Ommastrephes illecebrosus, Verrill, 1882, p. 83.

Ommastrephes (Illex) illecebrosus, Girard, 1890a, p. 261; 1890b, p. 42. -Norman, 1890, p. 477.

Illex illecebrosus illecebrosus, Pfeffer, 1900, p. 179; 1912, p. 405. -Boone, 1933, p. 168. -Grimpe, 1933, p. 509. -Mangold-Wirz, 1963a, p. 401. -Aldrich, 1964, p. 6. -Mercer, 1965, p. 4. -Zuev, 1966, p. 1. -Nesis, 1967, p. 3. -Squires, 1967, p. 1209. -Aldrich & Lu, 1968, p. 815. -Lu, 1968, p. 5. -Mangold, Lu & Aldrich, 1969, p. 1153.

Illex illecebrosa, Frost & Thompson, 1932, p. 25; 1933, p. 80.

Diagnosis: Mantle broadest at middle; fin angle mostly 45°, never exceeding 50°; hectocotylized portion of arm IV short, poorly developed, about 22% (13-30%) of the arm length. Cone at oral end of cement body of spermatophore a low right-isosceles triangle in shape with rounded corners.

List of Materials: (See overleaf)

List of Materials (*Illex illecebrosus*)

Sta. No.	Date	Time	Position	Temperature (°C) Surf.	Temperature (°C) Bottom	Salinity (°/oo) Surf.	Salinity (°/oo) Bottom	Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
	1879		Cape Cod Bay, Mass.						BeM 2452	1	144			
MS 72/73	1 VII 1910		44°35'N 51°15'W/ 45°58'N 51°25'W						BeM 26017	1	159	1	163	
USFC	1879		Cape Cod Bay, Mass.						CM			1	210	
	1868		St. Pierre and Miquelon						CM			2	173-213	
ATC 385	22 VIII 1968	1557	40°04'N 71°15'45'W	21.3	11.25			137.3	FRB			1	64	41.5'OT
ATC 388	22 VIII 1968	2145	40°12'N 71°16'45'W	21.7	11.73			Surface	FRB	1	58			Light
ATC 409	25 VIII 1968	0930	38°33'N 73°17'15'W	25.0	11.66			93.3	FRB			1	216	41.5'OT
ATC 429	27 VIII 1968	0923	37°28'30'N 74°32'45'W	25.2	11.10			91.5	FRB			1	168	41.5'OT
ATC 447	28 VIII 1968	1140	36°30'30'N 74°43'30'W	25.7	12.29			190.3	FRB			1	246	41.5'OT
ATC 459	30 VIII 1968	1430	34°36'N 75°43'W	27.1	12.29			225.1	FRB			3	157-175	41.5'OT
ATC 461	30 VIII 1968	1727	34°25'N 75°42'15'W	27.1	11.30			265.4	FRB	8	157-185	11	154-235	41.5'OT
ATC 463	30 VIII 1968	1925	34°25'N 75°39'45'W	26.9	09.81			464.8	FRB	4	163-200	2	189-205	41.5'OT
ATC 467	31 VIII 1968	1315	36°04'45'N 74°46'30'W	24.8	09.48			261.7	FRB	2	177-180			41.5'OT
ATC 473	1 IX 1968	1537	39°00'N 72°48'30'W	22.1	10.66			250.7	FRB			1	224	41.5'OT
	X 1967		La Scie, Nfld.						MUN	7	226-255	8	243-280	Squid jigger
	2 X 1967		Freshwater Bay, St. John's, Nfld.						MUN			1	118	Squid jigger
	17 X 1967		Summerville, B.B., Nfld.						MUN	4	247-260	11	265-317	Squid jigger
	26 X 1967		Cuckold's Cove, St. John's, Nfld.						MUN	19	181-247			Squid jigger
	1 IX 1968		Portugal Cove, C.B., Nfld.						MUN	2	192-242			Squid jigger
	22 VIII 1969		Portugal Cove, C.B., Nfld.						MUN	2	168-212	5	202-233	Squid jigger
	26 VIII 1969		Portugal Cove, C.B., Nfld.						MUN	25	187-246	14	190-258	Squid jigger
	31 VIII 1969		Portugal Cove, C.B., Nfld.						MUN	50	182-237	49	184-255	Squid jigger
	2 IX 1969		Cuckold's Cove, St. John's, Nfld.						MUN	8	170-221	10	170-233	Squid jigger

(continued)

Sta. No.	Date	Time	Position	Temperature (°C) Surf.	Bottom	Salinity (°/oo) Surf.	Bottom	Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
	4 IX 1969		Cuckold's Cove, St. John's, Nfld.						MUN	20	181-230	23	182-238	Squid jigger
	5 IX 1969		Cuckold's Cove, St. John's, Nfld.						MUN	18	200-237	18	200-260	Squid jigger
	5 IX 1969		Portugal Cove, C.B., Nfld.						MUN	31	183-245	32	180-253	Squid jigger
	1 X 1969		Cuckold's Cove, St. John's, Nfld.						MUN	2	240-265	4	250-290	Squid jigger
	5 V 1961		43°N 60°W						NMC 46719	1?	113			
	7 V 1961		43°00'30"N 61°59'30"W					133	NMC 55096	1	97	1	102	
AS									USNM 576987			1	260	
AS 2430	1885		42°58'N 50°51'W					322.2	USNM 50569			1	127	
AS 2505	1885		45°10'N 59°24'W		17.80			79.2	USNM 50571	3	149-192	1	158	
AS 2505	1885		45°10'N 59°24'W					79.2	USNM 576985			4	180-213	
AS 2528	13 VII 1885		41°47'N 65°37'W	20.5	3.8			1238.9	USNM 50572	3	54- 84	4	56- 80	Beam T
AS 2727	1886		36°35'N 74°03'W		3			2267.4	USNM 78821			1	27	
CB 433	18 VI 1957	0355	29°56'N 80°12'W					324	USNM 577012			1	175	40' Flat T
DW 68-10 Sta. 1	10 X 1968	0955	41°41'N 68°29'W	15	5.6	32.44		93.3	USNM	5	189-235	7	198-240	OT
DW 68-10 Sta. 2	10 X 1968	1330	41°52'N 68°02'30"W	14.1	6.3	32.63		91.5	USNM	4	203-225	7	205-277	OT
DW 68-10 Sta. 11	11 X 1968	1635	42°07'N 67°12'W	14.4	13.3	32.54		73.2	USNM	3	187-213	5	167-230	OT
DW 68-10 Sta. 34	14 X 1968	1525	40°30'N 67°48'W	14.4	14.0	32.64		109.8	USNM	3	200-238	3	122-252	OT
FH 923	16 VII 1881		40°01'24"N 70°46'W					179.2	USNM 576991	2 specimens (32, 37mm) sex undetermined				
FH 924	16 VII 1881		39°57'30"N 70°46'W					300.1	USNM 576991					
FH 925	16 VII 1881		39°55'00"N 70°47'W					419.1	USNM 576991					
FH 940	4 VIII 1881		39°54'00"N 69°51'30"W					245.2	USNM 576991					
FH 1152	4 X 1882		39°58'N 70°35'W	16.7	8.9			207	USNM 256	1	213			Hake stomach
FH 1174	6 IX 1883	1343	Off Martha's Vineyard, Mass.	20	17.2			9	USNM 484			2	169-189	
GE-1-13	16 V 1963	1230	36°26'N 70°22'W					Shallow	USNM	1	65			90'MT
GE-1-24	22 V 1963	0705	37°05'N 74°31'W					2420	USNM	2	49- 88			90'MT

(continued)

Sta. No.	Date	Time	Position	Temperature (°C) Surf.	Temperature (°C) Bottom	Salinity (‰) Surf.	Salinity (‰) Bottom	Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
Joast 1	26 VII 1970		41°21'N 66°10'W						USNM	1	107			
O 6800	20 VII 1967		29°48'N 80°09'30"W	27.7	10			333	USNM	7	153-172	8	155-195	65' ST
O 6801	20 VII 1967		29°39'30"N 80°08'30"W					383	USNM	6	145-162	2	144-200	
USFC 1145	21 IX 1882		40°03'N 70°28'W					243-288	USNM 577013	1	162	1	178	Cod T line
USFC 1158	23 VIII 1883	0800	40°16'N 70°29'15"W	19.4	7.2			113.5	USNM 576998			1	178	Goosefish stom
USFC 1162?	1879		Cape Cod Bay, Mass.						USNM 577014	1	173	1	116	
USFC 1169	4 VIII 1879		42°13'N 70°13'30"W	16.1	6.1			24.7	USNM 577016	4	100-160	1	155	
U.S.F.W.S.	6 XI 1968		42°06'N 66°33'W						USNM	1	67			
VIMS T159	24 VIII 1967	0642	37°55'N 74°28'W		6		32	52	USNM	4	93-200	5	104-202	27'OT
VIMS T160	24 VIII 1967	0942	38°09'N 74°22'W		6		32	45	USNM	1	191			27'OT
VIMS T162	24 VIII 1967	1600	38°34'N 74°07'W		6		32	54	USNM	11	156-190	15	157-215	27'OT
VIMS T164	25 VIII 1967	0706	38°22'N 74°05'W		5		32	61.2	USNM	3	153-174	5	165-186	27'OT
VIMS T165	25 VIII 1967	0948	38°30'N 74°53'W		6		33	56	USNM	1	174	1	190	27'OT
VIMS T166	25 VIII 1967	1300	38°34'N 73°33'W		9		33	72	USNM	5	151-192	7	158-200	27'OT
VIMS T167	25 VIII 1967	1530	38°27'N 73°23'W		13		34	187	USNM			1	215	27'OT
VIMS T168	25 VIII 1967	1906	38°21'N 73°40'W		12		35	124	USNM	1	176	4	160-217	27'OT
VIMS T169	26 VIII 1967	0706	38°03'N 73°55'W		12		35	113	USNM			3	176-200	27'OT
VIMS T170	26 VIII 1967	0954	38°02'N 74°08'W		8		32	74	USNM			2	133-162	27'OT
VIMS T171	26 VIII 1967	1230	37°51'N 74°08'W		12		35	131	USNM			2	206-213	27'OT
VIMS T174	26 VIII 1967	2112	37°43'N 74°38'W		7		32	52	USNM	1	188	2	132-186	27'OT
VIMS T177	27 VIII 1967	1236	37°22'N 74°47'W		7		32	49	USNM	1	175	2	186-187	27'OT
VIMS T178	27 VIII 1967	1536	37°22'N 74°30'W		12		33	92	USNM	2	175-212	1	152	27'OT
VIMS T179	27 VIII 1967	1812	37°13'N 74°34'W		11		34	95	USNM	1	155	3	165-187	27'OT
VIMS T180	30 VIII 1967	0536	37°07'N 74°45'W		8		32	70	USNM	9	125-174	11	121-181	27'OT
VIMS T181	30 VIII 1967	0854	36°51'N 74°41'W		11		33	86	USNM	3	128-178	5	143-213	27'OT
VIMS T182	30 VIII 1967	1200	36°36'N 74°44'W		12		31	112	USNM	6	133-171	12	134-195	27'OT
VIMS T183	30 VIII 1967	1442	36°42'N 74°45'W		11		34	70	USNM	2	138-140	5	136-151	27'OT
VIMS T184	30 VIII 1967	1718	36°53'N 74°47'W		6		33	56	USNM	4	125-165	4	167-198	27'OT
VIMS T188	31 VIII 1967	1206	36°18'N 74°52'W		7		33	67	USNM	6	127-169	6	120-190	27'OT
VIMS T189	31 VIII 1967	1442	36°05'N 74°52'W		13		33	79	USNM	11	139-191	4	166-213	27'OT
VIMS T231	2 XII 1967	1136	37°00'N 75°02'W		12		34	54	USNM	3	130-176	5	157-194	27'OT
VIMS T265	14 XII 1967	0830	37°06'N 74°35'W		12		36	191	USNM	5	184-220	2	180-275	27'OT

(continued)

Sta. No.	Date	Time	Position	Temperature (°C)		Salinity (°/oo)		Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
				Surf.	Bottom	Surf.	Bottom							
VIMS T003	18 I 1968	1254	38°17'N 73°38'W		10		35	176	USNM	3	177-181	5	178-203	27'OT
VIMS T014	20 I 1968	0836	37°57'N 74°06'W		11		35	119	USNM	2	161-171			27'OT
VIMS T035	28 I 1968	0842	37°08'N 74°31'W		11		34	270	USNM	7	163-226	4	167-213	27'OT
			Wood's Hole, Mass.						USNM 444			1	190	
			Eastport, Maine						USNM 577009			1	98	
									USNM 577010	1	156			
	1872		Eastport, Maine						USNM 365	1	186	2	100-176	
	1873		Casco Bay, Maine						USNM 576984			2	205-211	
	1875		Wood's Hole, Mass.	20	7.2			58.6	USNM	1	213			
	6 IX 1878		43°54'N 58°46'W						USNM 577011			1	190	
	VII 1879		Provincetown, Mass.						USNM 577017	1	189			
	13 VIII 1882		Fox Harbour, Lab.					27	USNM 34296			2	183-189	
	19 VIII 1883		39°41'15"N 71°41'15"W/ 39°30'30"N 71°44'30"W					Surface	USNM 39946			1	215	
	23 VIII 1883	1015	40°20'N 70°35'W	19.7	6.7			99	USNM 577008	1	178			
	25 VII 1884		Cox Lodge						USNM 39954	1	186	2	198-202	
	VIII 1884		Provincetown, Mass.						USNM 39958	14	179-225	15	160-270	
	26 IX 1886								USNM 577019			1	260	Squid jigger
	2 VIII 1893		Fry's Island (45°18'N 67°W).						USNM 577007	1	117			
	17 VI 1939		Petty's Bight, Long Is. Sound						USNM 575921			1	166	
	24 VI 1941		Petty's Bight Long Is. Sound						USNM 575921			1	162	
	17 VIII 1971		Old Scantum, N.H.					117	USNM	9	180-207	7	173-212	

All ATC sets are from Cruise 150
MT = Midwater Trawl
OT = Otter Trawl
ST = Shrimp Trawl
All times are local times

Description: Mantle long, slender, broadest at the middle, drawn out gradually to a long tip posteriorly (Fig. 2). Ventrolateral lobes on mantle opening inconspicuous, rounded (Fig. 2); dorsal lobe inconspicuous, slightly pointed (Fig. 1.). Thin, membranous flange encircles mantle opening. Mantle wall moderately thick. Fins sagittate, drawn out to acute point posteriorly; width (55.4% of ML) larger than length (43.8% of ML); posterior borders slightly concave forming about a right angle (FA = 45°); lateral borders rounded; anterior borders slightly convex; edge thin, thickened toward middle and posterior portions of fins (Fig. 1).

Funnel (Fig. 2) well developed, set in deep, smooth funnel groove; lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, broad, sheetlike. Dorsal funnel organ large; posterior limbs fleshy, thickened, broad anteriorly, tapered, pointed posteriorly; lateral shoulders conspicuous; antero-lateral borders concave; apical papilla spear-head shaped. Sharp, thin ridges extend from anterior mid-portion of limbs nearly to apex. Ventral pads oblong; lateral borders curved; medial borders nearly straight (Fig. 5A). Funnel valve broad.

Funnel locking cartilage (Fig. 3D) large, strong, inverted T-shaped. Medial, longitudinal groove narrow, relatively shallow, groove deepens and widens posteriorly to form deep, broad pit. Strongly developed cartilaginous knobs converge, nearly meet posterior to deep pit; lateral knob rounded, medial knob more pointed with narrow ridge extending dorsally into pit; pit undercuts anterior walls of knobs. Groove between knobs narrow, relatively deep, opens into lateral groove. Lateral groove very broadly inverted V-shaped, deepest anteriorly against posterior walls of knobs, shallows along posterior margin of locking-cartilage. Mantle locking-cartilage (Fig. 3C) strong, compliment of funnel lock. Longitudinal ridge low, narrow anteriorly, expands to large, sharply defined, swollen bulb posteriorly; posterior wall very deeply undercut toward base of mantle. Thin ridge extends from bulb to lateral ridge. Lateral ridge narrow, open V-shaped; anterior walls drop sharply into open grooves, posterior walls taper to mantle wall.

Head moderate large, broad, width about 17% of ML in males, 16.6% of ML in females; length about 16.4% of ML in males, 15.9% of ML in females. Three flaplike nuchal folds present; nuchal cartilage (Fig. 3E) long, spade-shaped, broad and rounded anteriorly, narrow, tapered posteriorly, terminally embedded in muscle; central groove deep, lateral ridges distinct. Eye openings subcircular, dorsoventrally elongate; anterior sinus deep, conspicuous. Posterior border of the head straight, occasionally wide open V-shaped.

Arms long, attenuate; order II $\geq$ III $\geq$ IV > I; occasionally III > II > IV > I; arms II and III robust; IV less robust; I least robust, very slender (Figs. 1 and 2). Swimming keels very low, weak on distal two-thirds of I; higher, better developed, full length of II; best developed on III, broadest in proximal quarter; low, second best developed, full length of IV. Protective membranes well-developed, particularly ventral membranes; trabeculae long, very strong, arise from base of sucker stalk, form high points along membranes (Fig. 4 A.B), most conspicuous on arm IV. Suckers equal in size in both sexes of comparable ML. Largest suckers on arms located at I: 5th-6th, II: 6th-7th (Fig. 4A), III: 6th-7th (Fig. 4B), IV: 4th-5th, pairs.

Arm sucker dentition: Largest sucker rings of arm I (Fig. 6A) with low, broad plate on proximal one-third, 3-5 low, truncate or slightly rounded teeth laterally, becoming narrower, longer distally; distal median tooth enlarged, elongate, pointed; teeth, particularly median tooth, more truncate, blunt on basal sucker pairs, more pointed on distal pairs. Largest rings of II (Fig. 6B) with low, broad plate on proximal one-fifth, 5-7 teeth laterally, broader, lower, more truncate proximally, narrower, higher more rounded distally; distal median tooth enlarged, triangular, pointed. Smaller rings smooth proximally and with fewer teeth, 5-7 long narrow teeth distally, grade in size to median tooth. Largest sucker ring of arm III (Fig. 6C) about as II; broad, low single or bifurcate plate on proximal one-third to one-fifth, 5-7 lateral teeth graded distally, median tooth enlarged, triangular, pointed. Smaller rings with broad, low plates proximally, graded to longest median tooth. Largest rings of IV (Fig. 6D) with broad, low plate at proximal one-third to one-half, 3-5 rounded to truncate lateral teeth, elongate, bluntly pointed or rounded distal median tooth.

Right or left ventral arm hectocotylized (Fig. 3B), equal to or occasionally longer, slightly shorter than, and equally robust to non-hectocotylized arm IV; modified tip about 22% of arm length; distal suckers reduced in size, rows separated, suckers of dorsal row transform to transversely broad, thin flaps; flaps gradually reduced in size distally, finally transform into series of minute papillae at arm tip, occasionally with suckers attached. Suckers of ventral row transform into conical, nipple-like papillae extending to arm tip. Papillae reduced in size distally. Low, weak zigzag ridge between papillae and flaps. Aboral keel broadly expanded along modified portion of hectocotylus tip. Trabeculae not modified to fringed lobes.

Tentacles robust, relatively short (about 67% of ML); stalk naked. Clubs (Fig. 3A) expanded, long, about 30% of ML. Distinct carpal cluster absent; suckers in carpal area small, biserial, 5 to 7 in number; carpal knobs lacking. Manal suckers tetraserial; suckers on lateral rows small; medial sucker rows arise distal to the proximal

5 carpal suckers; proximal 3-6 medial suckers small, gradually increasing in diameter distally; about 14 medial suckers on manus greatly enlarged, suckers on dorsal medial row slightly larger than corresponding suckers on ventral medial row; maximum size slightly greater in females than in males; manus terminates abruptly. Dactylus distinct, slender; suckers in 7-9 rows, extremely numerous, minute; tip with narrow, suckerless flange. Swimming keel along entire tentacular stalk aborally, broadest proximal to club, diminishes along carpal and manal region, expands to broad keel along dactylus. Lateral angles distinct on oral surface of stalk and continue as broad, heavily supported protective membranes along club, diminish significantly along dactylus especially on dorsal side. Dual V-shaped trabeculae arise from enlarged common base with lateral suckers along manus.

Club sucker dentition: Sucker rings of carpal region with low, broad plate on proximal half, 3-6 small teeth on distal half; lateral teeth broad, rounded; distal teeth narrow, bluntly pointed. Proximal-most lateral manal suckers with proximal plate, 1-2 low, rounded lateral teeth, 3-7 long, narrow, pointed distal teeth; distal lateral suckers toothed around entire margin with 6-12 low, rounded proximal teeth, 10-15 longer, sharply pointed lateral and distal teeth, occasionally small pointed secondary tooth between primary teeth. Proximal medial manal suckers (first 4-5) with low proximal plate, 1-2 low, rounded, lateral teeth, 2-3 narrower, bluntly pointed disto-lateral teeth, 1 bluntly pointed median tooth. Next distal 4-5 enlarged sucker rings with 8-14 teeth around margin, low, flat proximally, narrow, rounded or slightly pointed distally, no enlarged or pointed median tooth. Dentition lacking, rings entire, or occasionally with shallow notches on 7-8 distal enlarged manal suckers (Fig. 6E). Proximal dactyl sucker rings with 5-8 long, pointed distal teeth, 5-7 shorter, truncate or conical proximal teeth; teeth become more blunt, rounded on rings of middle dactylus suckers; teeth on suckers at distal tip few, minute. All dactyl suckers equipped with scaly fixing rims around apertures.

Gladius (Fig. 7A) long, slender, bluntly pointed anteriorly; median ridge and heavy lateral rods extend entire length of rhachis, converge posteriorly, fuse near vane, continue to tip. Vane short, about 23% of the gladius length; narrow (maximum width 3.8% of PL); forms short, hollow conus; only extreme tip solid.

Connectives of buccal membrane attach to dorsal, dorsal, ventral, dorsal borders of arms I-IV respectively. First suckers of arms I-IV locate opposite to buccal connectives: VVDV.

Mandibles: Upper mandible: rostrum strong, sharply pointed, long, curved, heavily pigmented; hood strong, long, curved, moderate pigmented; shallow notch and slight ridge separate rostrum and wing; wing with a large tooth near notch, cutting edge of wing slightly curved, serrated; lateral wall large, long, deep, pigmented anteriorly;

crest curved (Fig. 6F). Lower mandible: rostrum moderate long, sharply pointed, heavily pigmented; cutting edge slightly curved; rostral lamellae moderate long, relatively wide, thin; gular lamellae large; crest strong, posterior corner moderate long, bluntly pointed, curved; rostral width narrow (Fig. 6G).

Radula (Fig. 5B) with 7 transverse rows of teeth; rhachidian with long central tooth, blunt lateral cusps; first lateral tooth with blunt lateral cusp on outer side, inner side occasionally with short, blunt, bud-like cusp; second lateral tooth curved outward, no lateral cusp; third lateral tooth long, curved outward; marginal plates lacking.

Spermatophore (Fig. 7B, C) with sperm mass of about 57% of total spermatophore length, cone at oral end of cement body low right-isosceles triangle shape with rounded corners, connected aborally by long, narrow, neck; oral tube narrow.

Color (in isopropyl alcohol): Reddish-brown chromatophores cover entire body, more widely spaced ventrally, thickly packed dorsally; deep purple-red stripe along mid-dorsal line of mantle. (In nature): color vivid, chromatophores changing from reddish-brown to deep purple, deeper on arms, head, dorsal side of mantle and fins, paler ventrally. Body tinted with brilliant yellowish green.

Morphometry: Measurements of 19 chosen body parts from 271 specimens (122 males and 149 females) were plotted against mantle length to determine their allometric growth patterns. The range of the mantle length of the specimens measured is 67-260 mm for males and 87-317 mm for females.

A selected sample of scatter diagrams is presented in the Appendix. The relationships between the mantle length and measurements of various body parts are simple linear relations and can be expressed by the simple linear formula, Y=a+bX.

Table 1 shows this relation: Y=a+bX, where X is the ML in mm, Y is the measurement of the body part in mm, N is the sample size and r is the correlation coefficient. The correlation coefficient r in all cases is greater than the critical value, indicating the existence of true positive correlation between mantle length and measurements of various body parts in the sample studied.

The regression line for each Y for both sexes was analyzed for sexual difference by testing the regression coefficient, b. With the exception of HW, S_4, and S_T, all t values are smaller than the critical t value at the 95% confidence interval, indicating that the regression coefficient for each Y-pair for both sexes is similar.

Holotype: See Remarks (p. 73)

Holotype Locality: Sandy Bay, Massachusetts, U.S.A.

Neotype: Mature male, 199 mm ML, USNM 727456

Table 1

Regression, Y=a+bX, of the measurements of selected body parts against the mantle length in *Illex illecebrosus*.

All measurements in mm

N: Number of specimens in sample

X: ML

Y: Measurements of the chosen body part

r: Correlation coefficient of the regression

+: t-value greater than critical value at the 95% confidence interval

*: t-value greater than critical value at the 90% confidence interval, but less than critical value at the 95% confidence interval

-: t-value less than critical at the 90% confidence interval

		MALE				FEMALE				
Y	N	a	b	r	N	a	b	r	t	
VML	121	-1.356	0.965	0.994	149	2.707	0.943	0.994	1.671	*
HL	122	0.078	0.164	0.855	149	1.974	0.146	0.843	1.505	-
HW	122	-1.247	0.177	0.906	148	2.335	0.151	0.899	2.795	+
MW_1	122	-1.032	0.186	0.926	149	-1.514	0.184	0.914	0.203	-
MW_2	121	-5.196	0.230	0.869	149	-9.014	0.245	0.882	0.918	-
MW_3	122	-6.331	0.160	0.854	148	-5.442	0.150	0.876	0.899	-
FL	121	-7.457	0.487	0.975	149	-10.011	0.499	0.954	0.865	-
FW	121	-10.671	0.621	0.968	147	-7.625	0.588	0.960	1.578	-
FBL	121	-9.601	0.451	0.987	149	-9.691	0.447	0.925	0.212	-
A_1L	122	-21.795	0.527	0.854	149	-19.492	0.475	0.931	1.674	*
A_2L	122	-22.084	0.619	0.847	149	-19.940	0.554	0.901	1.616	-
A_3L	122	-21.163	0.614	0.854	149	-23.117	0.576	0.940	1.063	-
A_4L	122	-22.217	0.568	0.865	148	-18.661	0.509	0.938	1.857	*
S_1	122	-0.520	0.015	0.894	149	-0.831	0.015	0.931	0	-
S_2	122	-0.957	0.024	0.860	149	-1.211	0.023	0.933	0.742	-
S_3	122	-0.818	0.022	0.858	149	-1.285	0.023	0.923	0.662	-
S_4	122	-0.410	0.013	0.881	149	-0.765	0.015	0.913	2.673	+
S_T	118	-0.506	0.018	0.902	146	-1.654	0.024	0.927	4.795	+
GL	120	6.856	0.300	0.948	148	9.163	0.290	0.927	0.392	-

Neotype Locality: Old Scantum, 8-10 miles SE of Isles of Shoals, New Hampshire, SW edge of Jeffrey's Basin, 17-VIII-1971. 117 m. Fishing vessel Osprey, R. A. Stetson. Collected by C. F.E. Roper.

Distribution: East coast of North America from Cumberland Sound southwards to 29°39'30'N; Newfoundland (Fig. 10); Greenland (?); Iceland (?); Bristol Channel (?). However, these latter three sites are to be questioned, as is discussed later.

Remarks: As was mentioned in the "Historical Review", this species was first named *Loligo illecebrosa* by Lesueur in 1821. "Code" states that "A species-group name, if an adjective in the nominative singular, must agree in gender with the generic name with which it is at any time combined, and its termination must be changed, if necessary, when the species is transferred to another genus" (Art. 30, p. 29), and that "A noun of variable gender, masculine or feminine, is to be treated as masculine, unless its author states, when he first publishes the name, that it is feminine, or so treats it in combination with an adjectival specific name" (Art. 30, (a) (i) (2), p. 31). Although the word *Illex* is of variable gender, when Steenstrup changed *L. illecebrosa* from genus *Loligo* to genus *Illex*, he also changed the ending of the specific name in question. Thus, the name *Illex illecebrosus* conforms with the requirements of the "Code".

Since Lesueur did not keep any specimen of this species, the drawings (Fig. 9) made by him in 1816 may therefore serve as the lectotype ("Code" Art. 74 (b), p. 79). However, through thorough search in the Academy of Natural Sciences and the American Philosophical Society, both in Philadelphia, I have not been able to locate the drawings. They therefore must be considered no longer extant. The drawings, as can be seen in Fig. 9, do not show detailed features of the species. The erection of a neotype is considered necessary, due to the systematic confusion within the genus, in an effort to stabilize the systematics.

The neotype is a mature male specimen of 199 mm ML from Old Scantum, New Hampshire, U.S.A. Various measurements, indices, and counts are shown in Table 2.

The holotype locality was stated by Lesueur as Sandy Bay without mentioning the name of the province or state. According to E. T. Hamy (1968), the Sandy Bay mentioned by Lesueur is located in Massachusetts, north of Cape Ann at 42°40'N 70°37'W. This is also the type locality of *Taonius pavo* (Lesueur, 1821). The neotype locality, Old Scantum, is about 34 Km northwest of Sandy Bay.

With a few exceptions, allometric growth is the general growth pattern in cephalopods. *Illex illecebrosus*, within the extent of this study, offers a well-fitted example. It must be pointed out that the formula for simple allometry (Huxley & Teissier, 1937) is $Y=aX^b$ or

Table 2

Measurements (in mm), indices, and counts of the neotype of *Illex illecebrosus*.

	Measurement (mm)	Index (%)		Measurement (mm)	Index (%)
ML	199				
VML	188	94.5	HL	34.4	17.3
HW	27.5	13.8	MW_1	30.8	15.5
MW_2	35	17.6	MW_3	18.6	9.4
FL	85	42.7	FW	111	55.8
FBL	76	38.2	A_1L	74	37.2
A_2L	95	47.7	A_3L	94	47.2
A_4L	85	42.7	HcAL	81	40.7
HcL	14	17.3	CL	49	24.6
S_1	2.6	1.31	S_2	4.0	2.01
S_3	3.9	1.96	S_4	2.1	1.06
S_T	2.8	1.41	GL	65	32.7
S_pL	21	10.6	S_pRL	14.5	69.1
S_pRW	0.3	1.43	CBL	2.8	13.3
FA	41°		$\#S_1$	102	
$\#S_2$	100		$\#S_3$	98	
$\#S_4$	119		#G	69	

Right ventral arm hectocotylized

$\log Y = \log a + b \log X$. This formula of simple allometry is widely accepted and of great importance in the study of systematics and the problem of growth. It is, however, cumbersome in calculation in the transformation of raw data into logarithms, without the aid of a computer. D'Arcy Thompson in his classic work "On Growth and Form" pointed out that in some cases the simple linear relation, or in his words "simple-interest", $Y=a+bX$ seems to be adequate (Thompson, 1942, pp. 207-209). In the present study, the r value in each case is far greater than the critical value of r at the corresponding degree of freedom, and is close to 1, indicating the existence of a true, positive correlation between each pair of Y and X. The utilization of the simple linear formula $Y = a + bX$ instead of the simple allometric formula $Y = aX^b$ in this study is therefore both practical and justified. The simple allometry relation is, nevertheless, very useful and has solved some interesting taxonomic problems such as those of Clarke (1950) and Needham (1964, p. 35).

In Table 1, the Y intercept of each regression line a, is either a positive or a negative number. As Y is the measurement of a body part and X is the ML, according to the formula, when X = 0, Y is either positive or negative. For example, when ML = 0 mm, a male animal should have a VML of -1.356 mm, or a HL of 0.078 mm - clearly absurd results. It is evident, therefore, that the regression lines only hold true for animals within the size range studied.

The geographical distribution of *I. illecebrosus* has long been in confusion. In the western Atlantic Ocean the recorded northern-most limit is Cumberland Gulf (Verrill, 1880, p. 289; 1880-1881, p. 280). This record was based on one mutilated specimen collected by L. Kumlein and reported to be deposited in the USNM. It could not be found during my study of the USNM collections, and presumably it no longer exists. The name Cumberland Gulf does not appear in the National Geographic Atlas of the World or the Britannica Atlas. According to Squires (1957, p. 694), it is Cumberland Sound, which is located near the Arctic Circle. Verrill's account reads, "Its range extends quite to the Arctic Ocean" (1880-1881, p. 281), and this supports the identification of Cumberland Gulf as Cumberland Sound, as stated above. This record cannot be verified and it is may be that the specimen was part of the stomach contents of a predator. Until further evidence proves otherwise, this record is accepted as the northern-most limit of the species. Posselt (1898, p. 278) recorded this species from Frederikshaab, Greenland, but according to Mercer (1968, p. 268) the record cannot be confirmed.

The Icelandic records of this species also lack confirmation: Grøndal's specimen no longer exists in the Museum of Natural History of Reykjavik and no other specimen is known from Icelandic waters (F. Gudmundsson, personal communication; Mercer, 1968, p. 268). Murray and Hjort (1912) did not specify any specimen. If the Icelandic specimen belongs to this species, we must agree with Bruun's opinion (1945, p. 10) that it is only a rare guest to Icelandic waters.

Adam in his monograph reported that the specimens from the Bristol Channel are *I. illecebrosus* (1952, p. 92). I have examined two specimens (a male of 192 mm ML, and a female of 210 mm ML) from Adam's collection, now housed in the IMSUM. Despite Adam's identification, they clearly belong to *I. coindetii*, this based on measurements, especially fin angle, and the structure of the hectocotylus. Collections from the Bristol Channel need to be re-examined in order to possibly confirm the occurrence of *I. illecebrosus* from this region.

The southern-most limit of *I. illecebrosus* on the east coast of North America is also in confusion. It has been pointed out previously (Roper, et al., 1969, p. 318) that past records from the Gulf of Mexico and the Caribbean Sea are possibly a mixture of *I. coindetii* and *I. oxygonius*, so these records can no longer be used as valid indications of the true distribution of the species. The southern-most samples in the present study come from 29°39'30"N 80°08'30"W (Oregon, Sta. 6801).

FIGURE 1. Photographs of *Illex illecebrosus* (Lesueur, 1821). Dorsal view. A. Male. B. Female. Scale: 2 cm. Specimens from MUN collections from Portugal Cove, Conception Bay, Newfoundland.


A
B.

FIGURE 2. Photographs of *Illex illecebrosus* (Lesueur, 1821). Ventral view. A. Male. B. Female. Scale: 2 cm. Specimens from MUN collections from Portugal Cove, Conception Bay, Newfoundland.

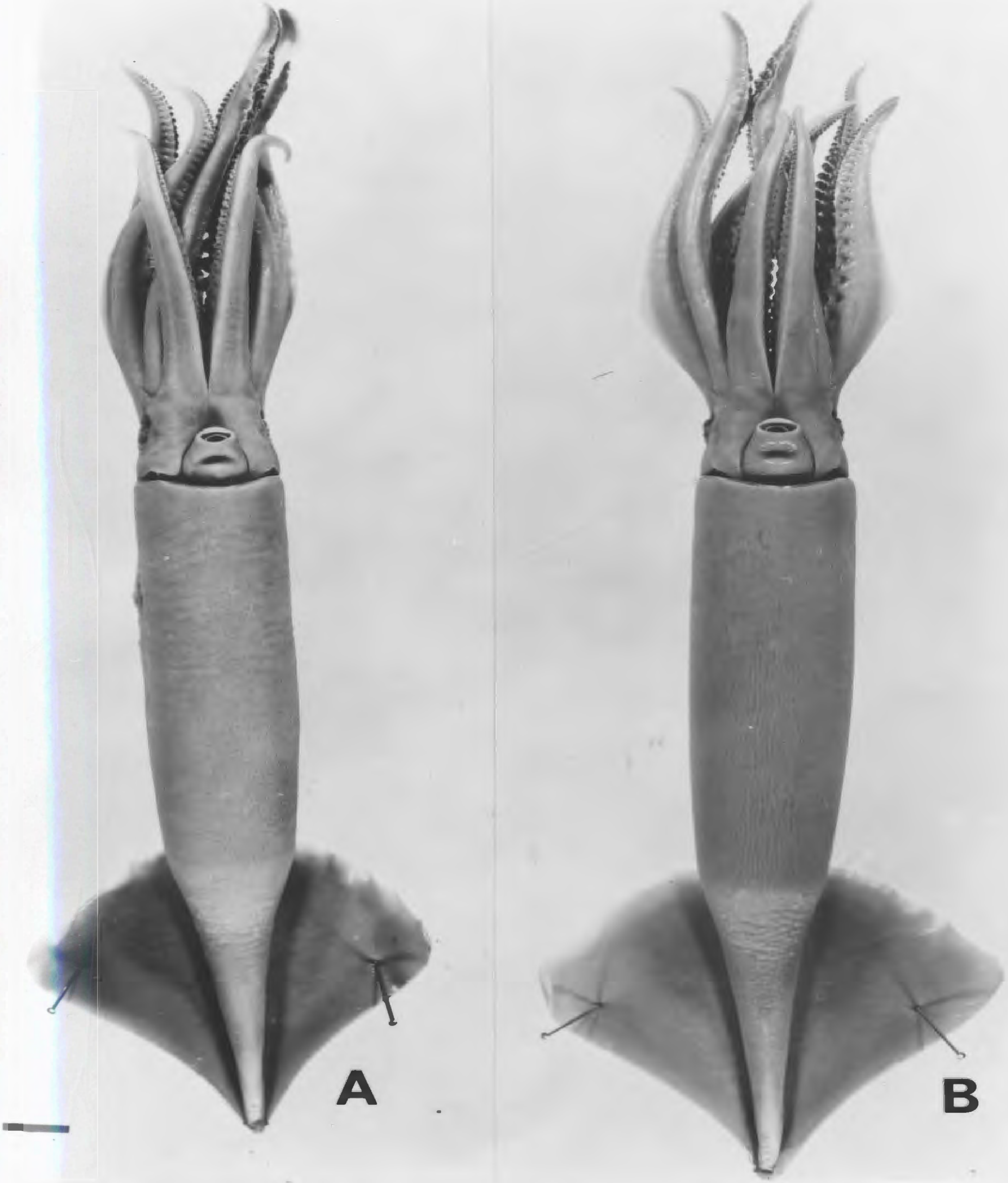

A
B

FIGURE 3. Photographs of tentacular, brachial and cartilageno[illegible] portions of *Illex illecebrosus* (Lesueur, 1821).

A. Tentacular club
B. Hectocotylized arm (L IV)
C. Mantle component of mantle-locking apparatus
D. Funnel component of mantle-locking apparatus
E. Nuchal cartilage

Scale: 1 cm

In C through E, anterior end uppermost.

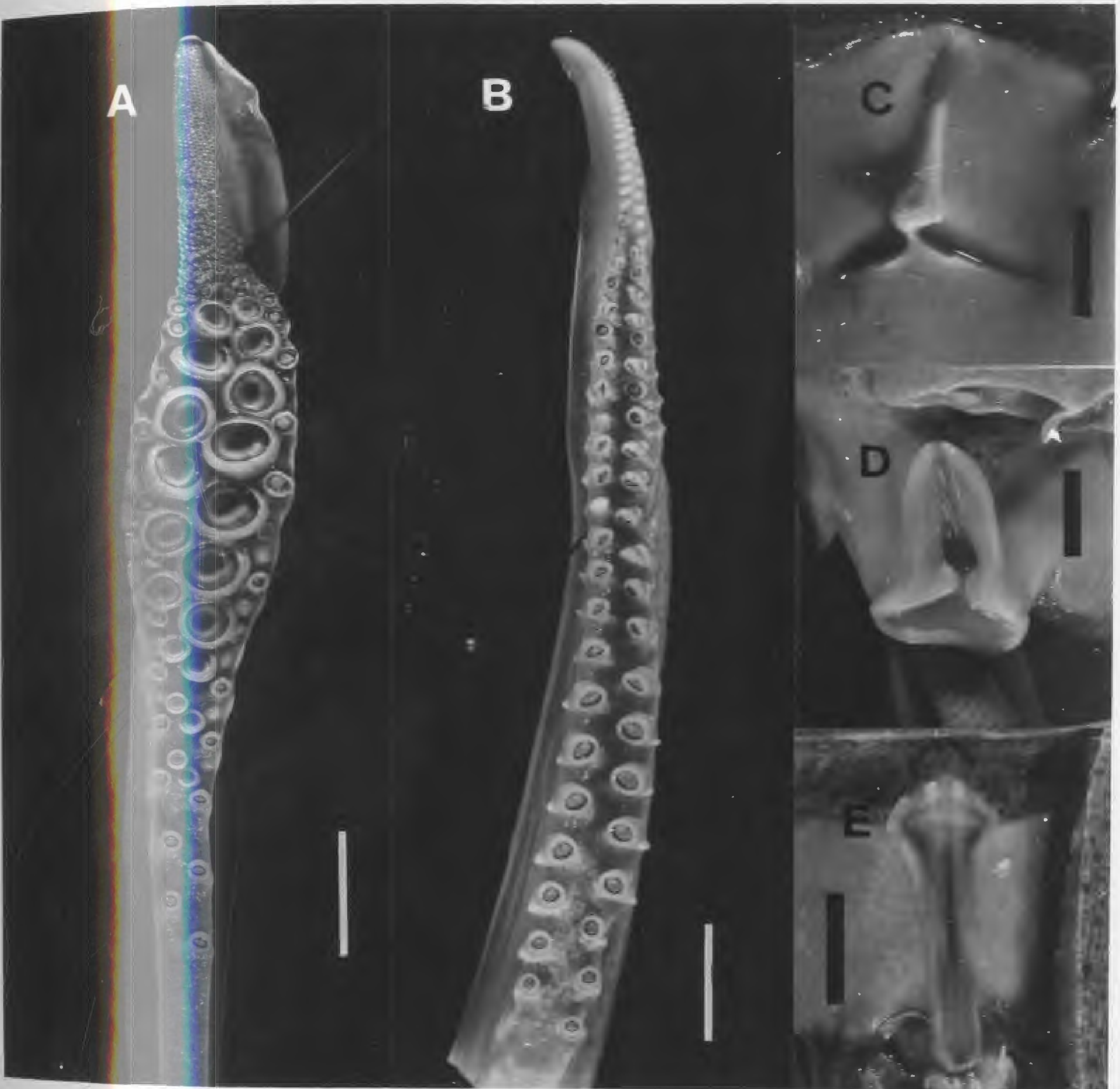

A
B
C
D
E

FIGURE 4. Photographs of dorso-lateral (L II) and ventro-lateral (L III) arms of a male specimen of *Illex illecebrosus* (Lesueur, 1821). A. Arm II. B. Arm III.

Scale: 1 cm.

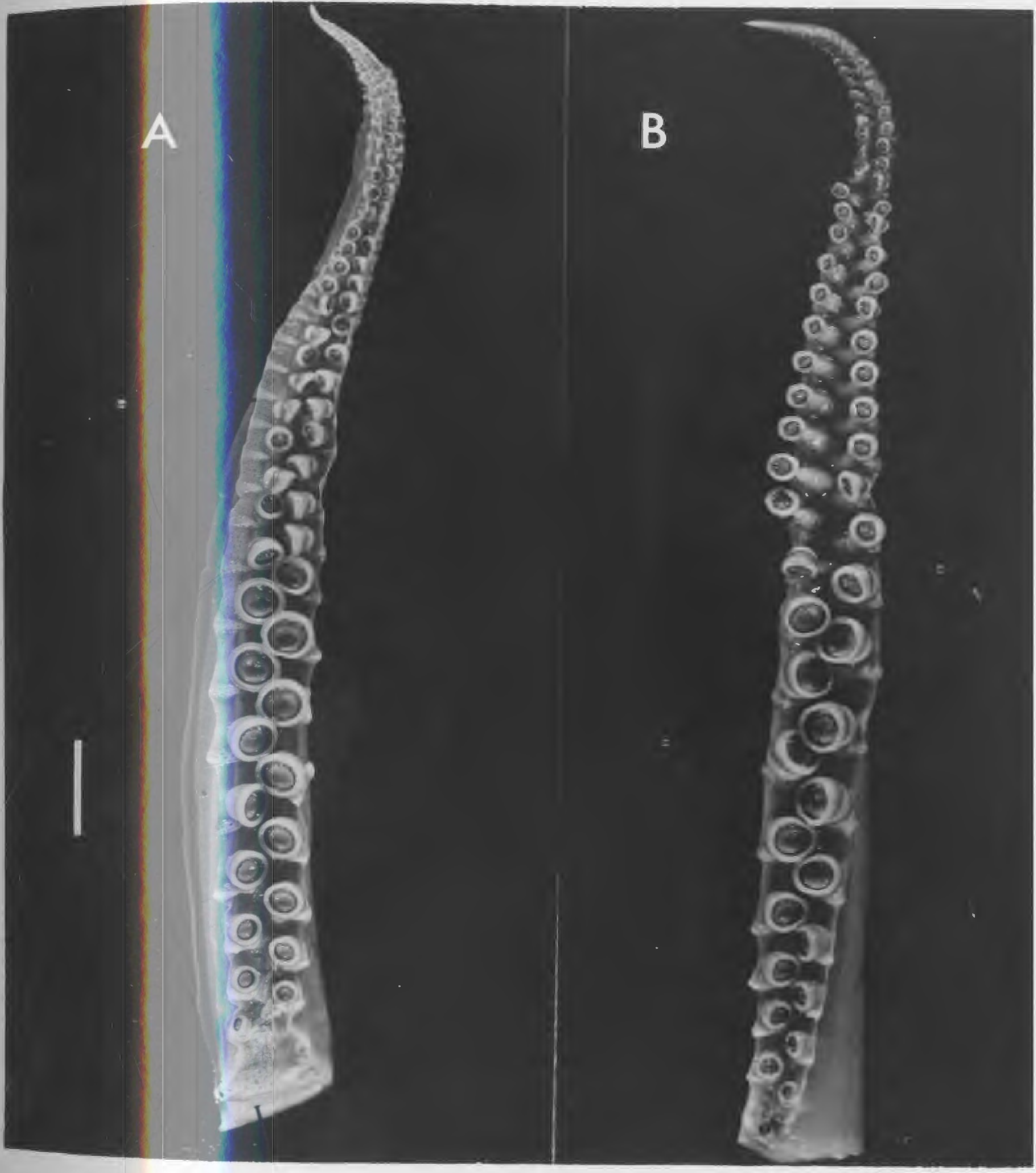
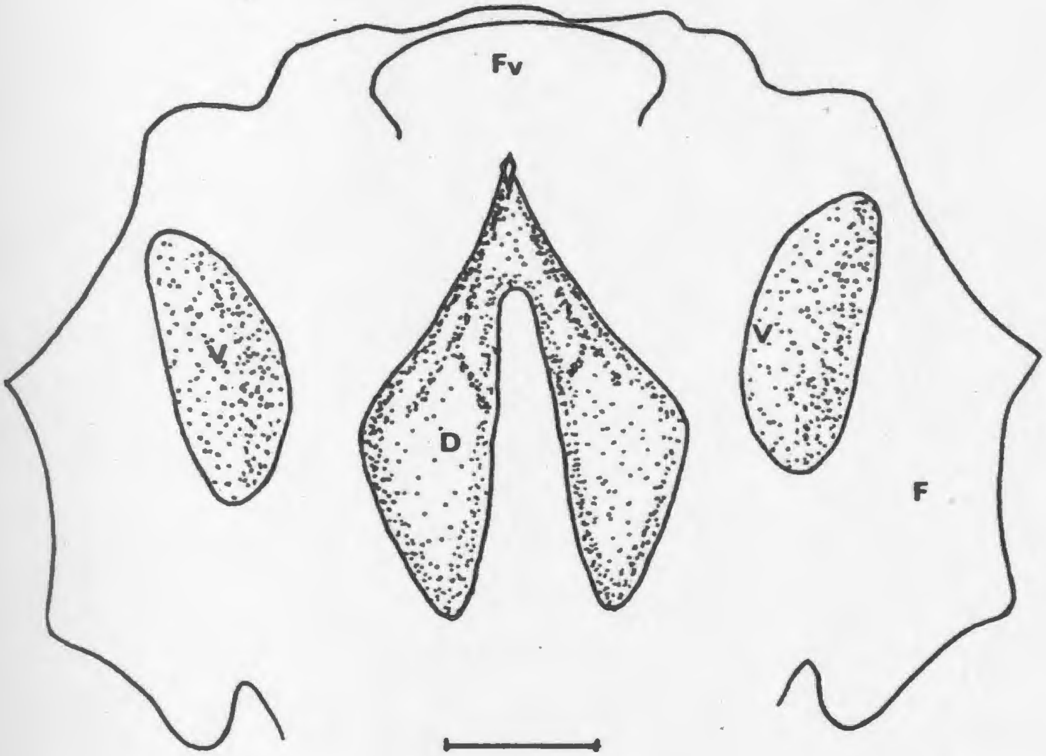

A
B

FIGURE 5. A. Drawing of funnel organs of *Illex illecebrosus.* Scale: 1 cm.

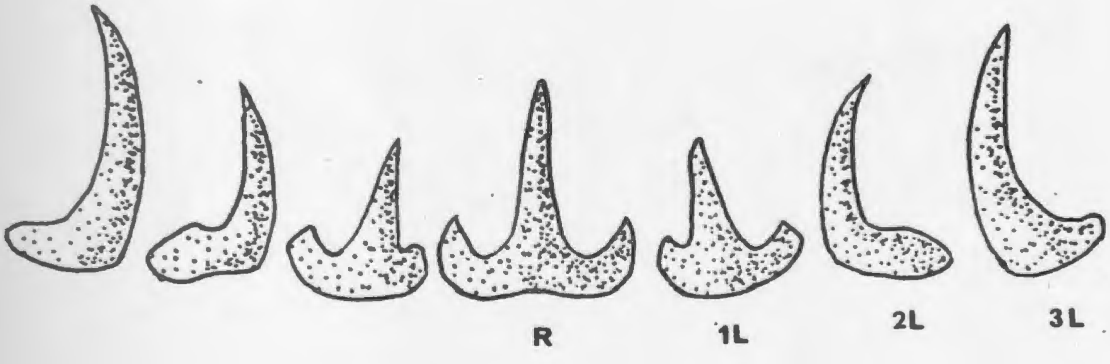
D = dorsal funnel organ
V = ventral funnel organ
F = wall of funnel
F_V= funnel valve

B. Drawings of a single row of teeth from the mid-portion of the radular ribbon of *Illex illecebrosus*.

R = rhachidian tooth
1L = first lateral tooth
2L = second lateral tooth
3L = third lateral tooth



A



B

FIGURE 6. A through E. Drawings of chitinous rings from specific suckers from sessile arms and tentacular manus of *Illex illecebrosus*.

A. Ring from largest sucker from dorsal arm (I)

B. Ring from largest sucker from dorso-lateral arm (II)

C. Ring from largest sucker from ventro-lateral arm (III)

D. Ring from largest sucker from ventral arm (IV)

E. Ring from largest sucker from manal portio[illegible] of tentacular club

F - G. Drawings of mandibles of *Illex illecebr*[illegible]

F. Upper mandible

G. Lower mandible

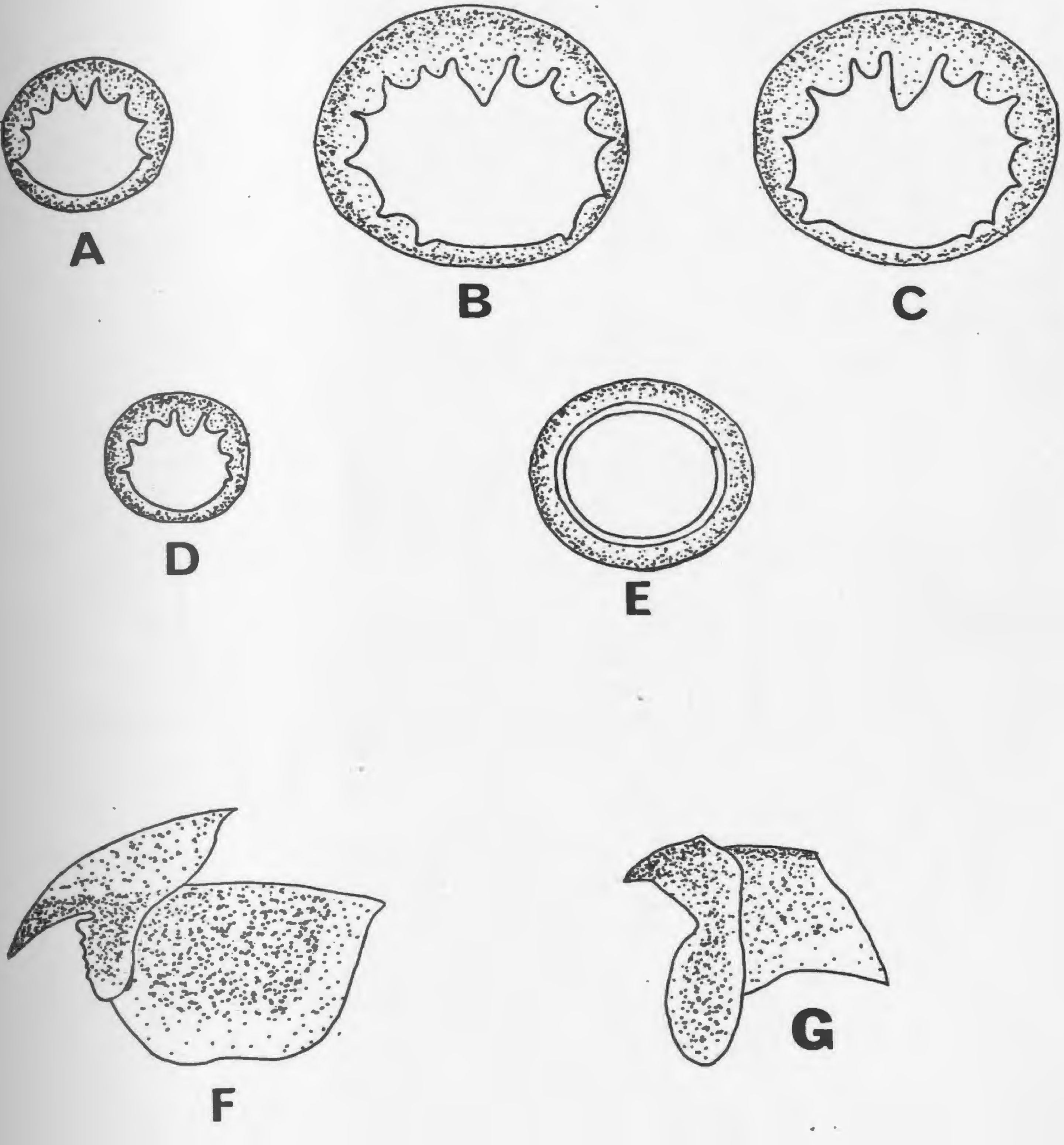

A
B
C
D
E
F
G

FIGURE 7. A. Drawing of entire gladius of *Illex illecebrosus.* Scale: 1 cm.

B. Drawing of entire spermatophore of *Illex illecebrosus.* Scale: 1 cm.

C. Drawing of portion of spermatophore of *Illex illecebrosus*, showing the cement body and adjacent structures.

C = cement body

Co = cone

S = sperm mass

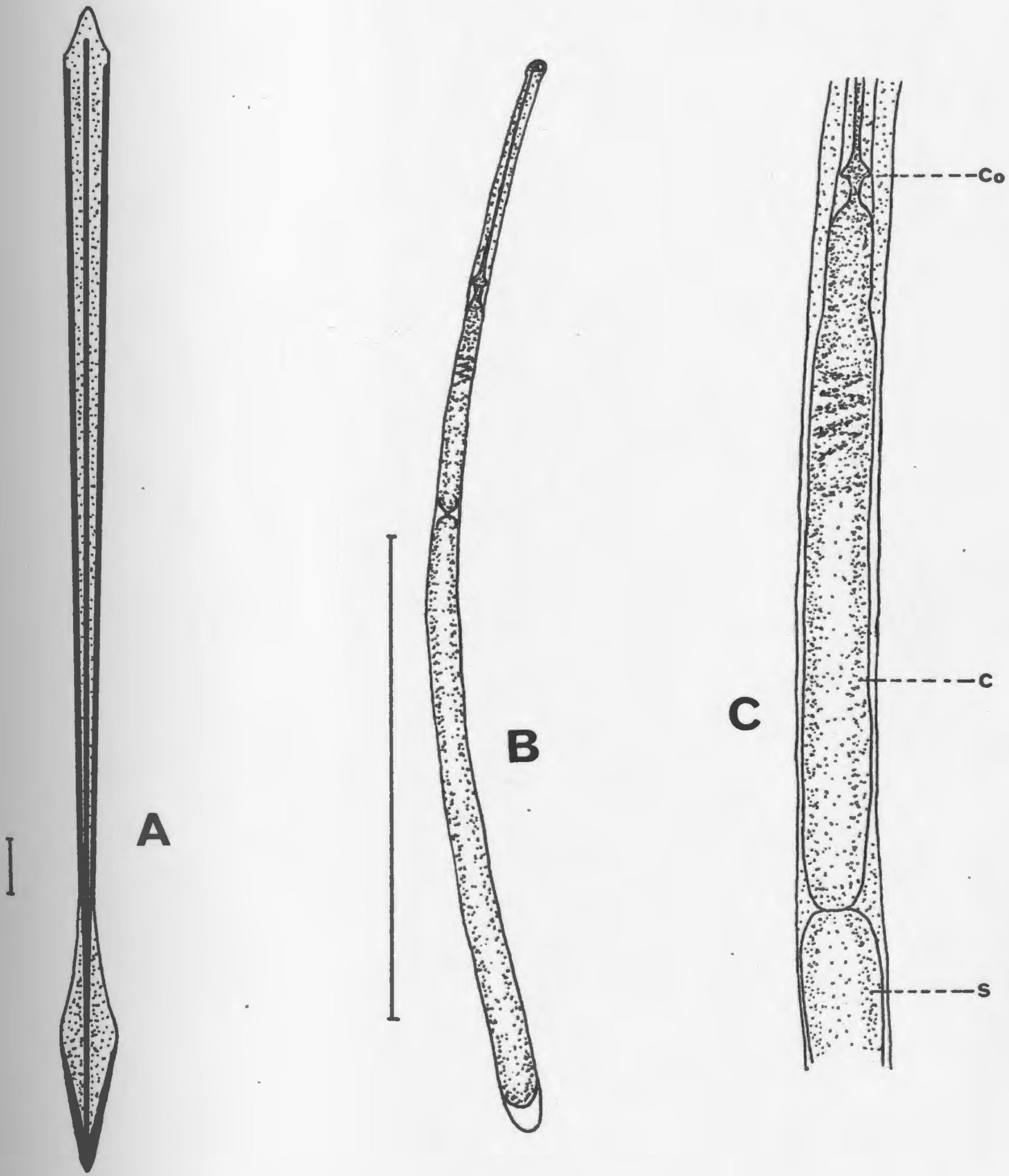

A
B
C
Co
c
s

FIGURE 8. Photograph of dorsum of the newly established neotype of *Illex illecebrosus*. Specimen from Old Scantum, New Hampshire.

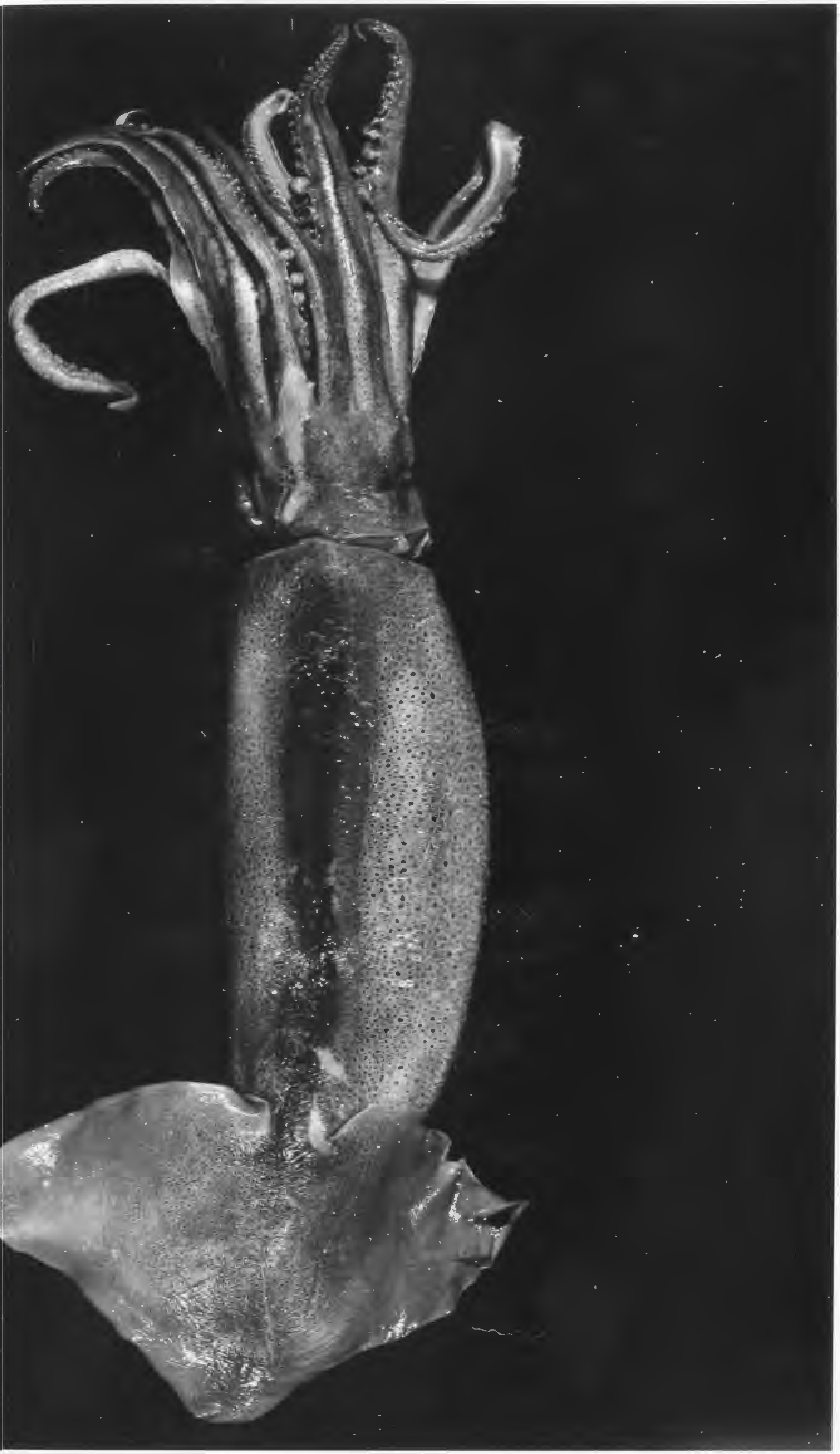


FIGURE 9. Reproduction of original plate by C. Lesueur in 1816, the lectotype of *Illex illecebrosus*. This plate first appeared in the Proceedings of the Academy of Natural Sciences, Philadelphia, of 1821.

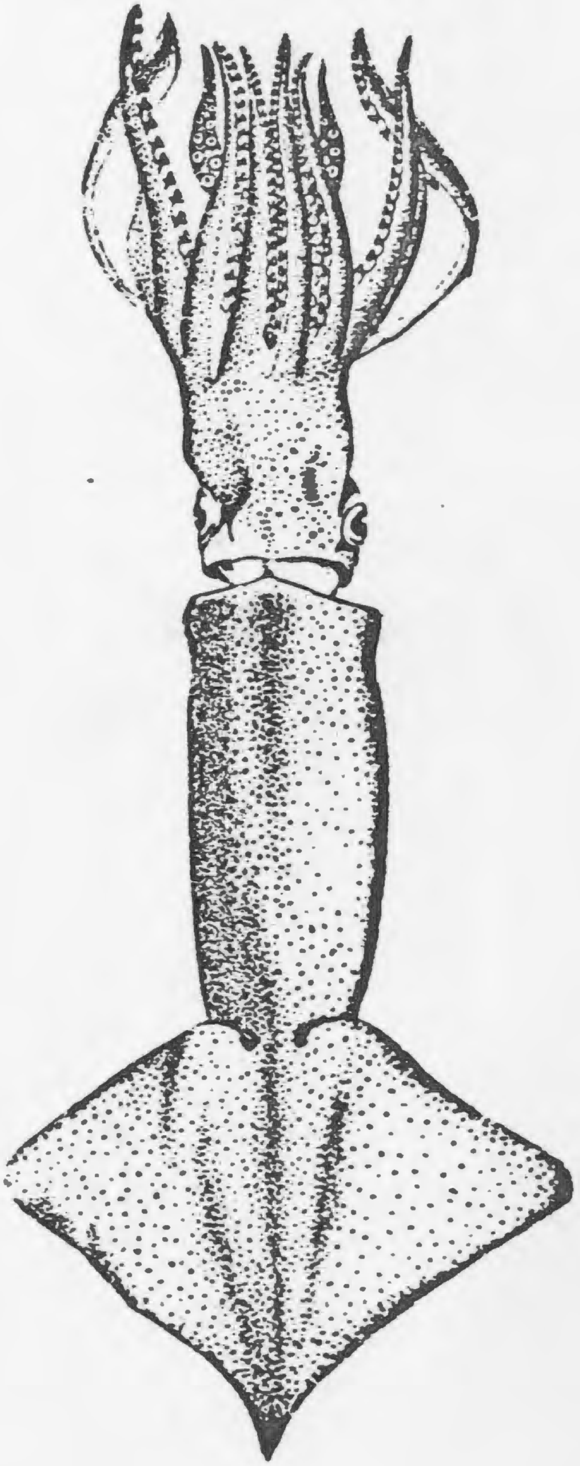


FIGURE 10. Map of the Atlantic Ocean and adjacent continents showing the world distribution of the four species of the genus *Illex*.

A = *Illex argentinus*

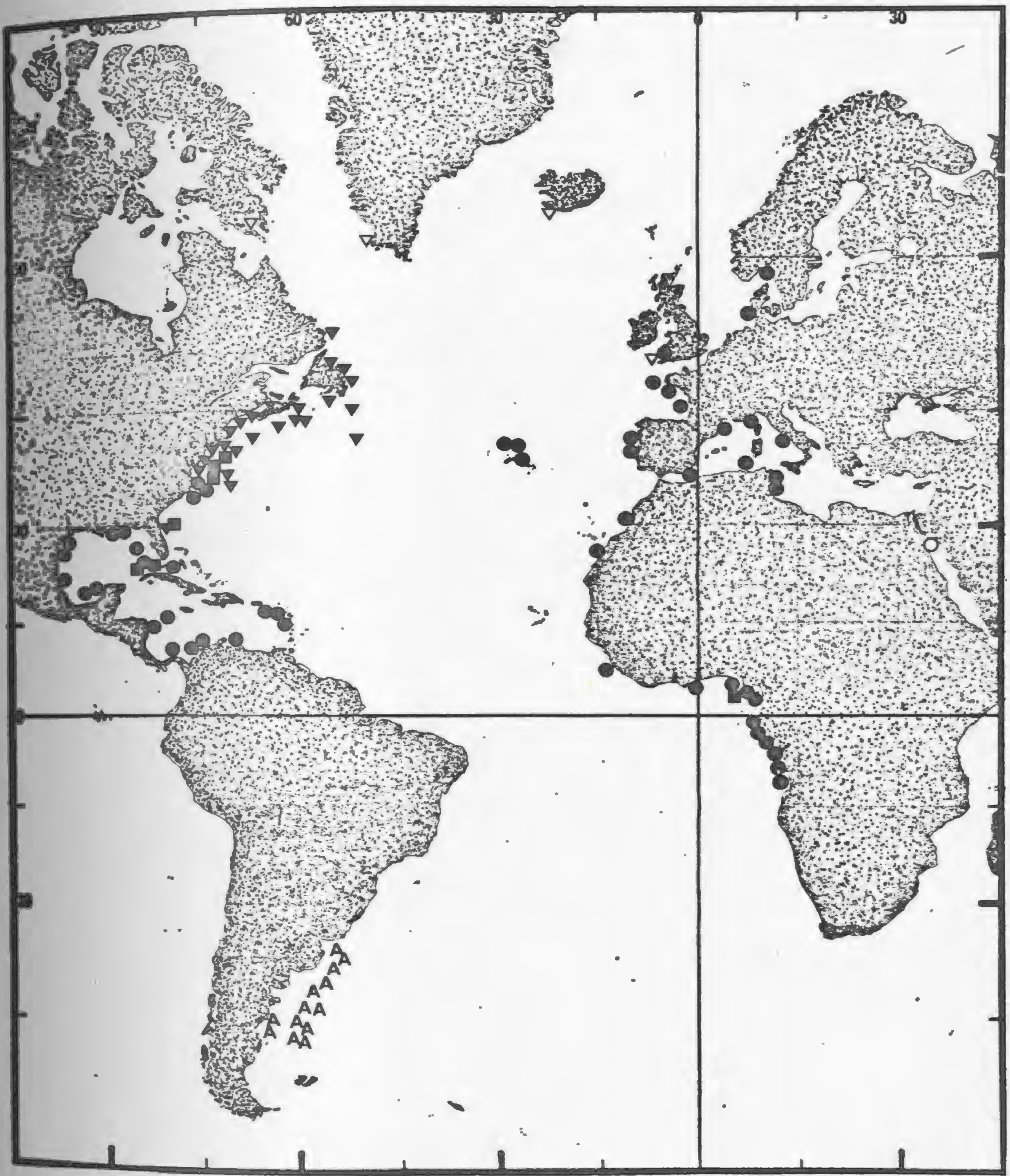
▼ = *I. illecebrosus*

■ = *I. oxygonius*

● = *I. coindetii*

○ = non-verified report of *I. coindetii*

▽ = non-verified report of *I. illecebrosus*


90
60
30
0
30
60
30
0
30

Illex coindetii (Verany, 1837)

Loligo brongniartii Blainville, 1823, p. 130. -Ferussac & d'Orbigny, 1835-1848, p. 345, Pl. 4. -Cuvier, 1837, pl. 1, fig. 5.

Loligo coindetii Verany, 1837, p. 94, fig. 4; 1851, p. 110, pl. 36.

Loligo coindeti, Philippi, 1844, p. 203.

Loligo sagittata, Verany, 1851, pl. 2.

Ommastrephes sagittatus, Ferussac & d'Orbigny, 1835-1848, p. 345. -Gray, 1849, p. 58. -Forbes & Hanley, 1852, p. 231. -Fischer, 1867, p. 14; 1875, p. 214. -Targioni-Tozzetti, 1869, p. 597. -Tryon, 1879, p. 177, pl. 78, figs. 341, 345. -Stossich, 1880, p. 159.

Ommatostrephes sagittatus, Jeffreys, 1869, p. 129, pl. 5, fig. 1.

Ommastrephes crassus, Tryon, 1879, p. 178, pl. 79, fig. 347.

Ommastrephes coindetii, Tryon, 1879, p. 178, pl. 78, fig. 348, pl. 79, fig. 349, pl. 80, figs. 366, 367.

Loligo pillae Verany, 1851, p. 112, pl. 36.

Ommatostrephes pillae, Steenstrup, 1880, pl. 71 (Volsøe, et al., 1962).

Ommatostrephes coindetii, Steenstrup, 1880, p. 71 (Volsøe, et al., 1962). -Nobre, 1931, p. 16.

Ommastrephes (Illex) coindeti, Norman, 1890, p. 476.

Ommastrephes (Illex) coindetii, Girard, 1890a, p. 260; 1890b, p. 38.

Illex coindetii, Steenstrup, 1880, p. 66 (Volsøe, et al., 1962). -Hoyle, 1886a, p. 245; 1886b, p. 34. -Posselt, 1890, p. 303, pl. 4, fig. 9, 13a, 16. -Jatta, 1896, p. 70, pl. 2, fig. 1, pl. 11, figs. 8-19, pl. 12, figs. 1-3. -Lozano y Rey, 1905, p. 175. -Lo Bianco, 1908, p. 647. -Adam, 1942, p. 13. -Roper, Lu & Mangold, 1969, p. 317.

Illex coindeti, Carus, 1889-1893, p. 447. -Lönnberg, 1891, p. 34. -Joubin, 1896, p. 249. -Hoyle, 1902, p. 197. -Tesch, 1908, p. 14. -Naef, 1916, p. 12; 1921, p. 538; 1923, p. 429. -Grimpe, 1922, p. 48; 1924, p. 321. -Robson, 1926, p. 179. -Bouxin & Legendre, 1936, p. 61. -Desbrosses, 1938, p. 342. -Dieuzeide, 1950, p. 34. -Adam, 1951, p. 780. -Jaeckel, 1958, p. 598. -Morales, 1958, p. 5. -Clarke, 1966, p. 123.

Todaropsis veranyi, Jatta, 1896, pl. 2, fig. 6 (male).

Illex illecebrosus coindeti, Pfeffer, 1900, p. 179. -Naef, 1916, p. 12; 1921, p. 538. -Grimpe, 1921, p. 297; 1925, p. 76. -Degner, 1925, p. 40. -Stephen, 1944, p. 264. -Nesis, 1967, p. 3. -Lu, 1968, p. 5. -Aldrich & Lu, 1968, p. 815.

Illex illecebrosus coindetii, Pfeffer, 1912, p. 393. -Adam, 1952, p. 80; 1967, p. 72. -Mangold-Wirz, 1963a, p. 401; 1963b, p. 157. -Zuev, 1966, p. 1. -Mangold, Lu & Aldrich, 1969, p. 1153.

Illex illecebrosus, Joubin, 1920, p. 59. -Adam, 1939, p. 1. -Pfeffer, 1908, p. 89, figs. 96-99. -Chun, 1913, p. 5. -Voss, 1954, p. 477; 1955, p. 103; 1956a, p. 143; 1956b, p. 279.

Illex illecebrosus coindetii, Crosnier, 1964, p. 36.

Illex coindetti, Steenstrup, 1880, p. 65 (Volsøe, et al., 1962).

Diagnosis: Fin angle broad, exceeding 50°; fin wide; males with robust head and brachials; trabeculae of hectocotylized arm modified into fringed lobes; cone at oral end of cement body of spermatophore rounded-triangle in shape, lens-shaped or diamond-shaped; neck of cement body short and indistinct.

List of Materials: (See overleaf)

Description: Mantle long, slender, cone-shaped, broadest at mantle opening and drawn out gradually to a long tip posteriorly (Fig. 12). Mantle width decreases posteriorly in males, less pronounced in females and especially at maturity. Ventro-lateral lobes on mantle opening inconspicuous, rounded; dorsal lobe inconspicuous, slightly rounded (Fig. 11). Mantle opening encircled by membranous flange. Mantle wall moderately thick. Fins wide, drawn out to blunt point posteriorly, fin width (56% of ML in males, 54% in females) greater than fin length (39% of ML); posterio-lateral borders of fins straight-cut, or varying to slightly convex, united posteriorly; fin angle 50°-60°; lateral borders rounded; anterior lobes well developed (Fig. 11).

List of Materials (*Illex coindetii*)

Sta. No.	Date	Time	Position	Temperature (°C)		Salinity (°/oo)		Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
				Surf.	Bottom	Surf.	Bottom							
			Naples, Italy						ANSP 94410			1	169.1	
Triton 1167	26 V 1953		South of Palm Beach						ANSP 190254	1	115	1	150	
			Azores (?)						BeM 2358	2	109.5-110			
			Naples, Italy						BeM 2451	1	133.5			
			Naples, Italy						BeM 5108			1	137	
MS 39B	21 V 1910		26°3'N 15°0'W					267-280	BeM 25942			1	153	
MS 33	11 V 1910		31°17'N 10°6'W					100	BeM 26018	2	113-117			
MS 39B	21 V 1910		26°3'N 15°0'W					267-280	BeM 26019	1	145			
			West coast of France						CM	2	206-213	2	234-264	
			Naples, Italy						CM	1	66			
			Mediterranean Sea						CM			1	49	
			Middelhavet						CM	1	122			
	12 IX 1876		Nice, France						CM	1	83			
	1 II 1891		Cote de Cezimbra						CM	1	157	1	230	
	1859		Adriater Flavet						CM	1	127			
									CM	1	77			
Thor 174	11 VIII 1910		40°54'N 28°53'W						CM	1 specimen (9 mm) sex undetermined				
Thor 175	11 VIII 1910		40°48'N 27°59'W						CM	1 specimen (15 mm) sex undetermined				
	9-22 XI 1946		51°30'N 4°W					100	IMSUM	1	192	1	210	
	22 VIII 1948		5°30'S 11°32'E					210	IMSUM	1	137	1	160	
P 245	13 V 1965	1510	4°32'N 5°7'E					64-119	IMSUM	8	52-92	5	53-70	40'OT
P 254	14 V 1965	1330	3°50'N 7°8'E					148-174	IMSUM	30	70-112.5	27	72-110	40'OT
P 255	14 V 1965	1802	3°49'N 7°38'E					264-269	IMSUM	41	83-121	57	54-140	40'OT
P 445	21 VII 1966	0959	9°2'18"N 81°23'48"W					340	IMSUM	2	110-116	4	114-146	40'OT
GD 1012	14 VI 1968	2000	23°35'N 79°33'W					522	IMSUM			1	137	10'OT
Atlantis	2 V 1939		23°5'30"N 79°40'W					539.9	IMSUM 31.333	1	171			
O 3623	6 VI 1962		16°8'N 81°13'W					192.2	IMSUM 31.516			1	213	40'ST
	22 IV 1969		Las Rosas*						MUN	8	141-166	11	135-232	
	13 V 1969		Las Rosas						MUN	2	158-177	3	191-205	

(Illex coindetii) continued

Sta. No.	Date	Time	Position	Temperature (°C) Surf.	Temperature (°C) Bottom	Salinity (°/oo) Surf.	Salinity (°/oo) Bottom	Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
	3 XI 1971		42°32'N - 42°35'N 3°36'E - 3°42'E	15.6				200-500	MUN	2	108-132			
	16 VI 1970		42°35'N - 42°40'N 3°14'E	19.5				80-90	MUN			1	187	
CY W11	28 IV 1970		47°53'N 7°11'W					180	MUN	2	175-213	4	195-255	BT
CY W17	29 IV 1970		46°38'N 4°42'W					164-170	MUN	2	172-188	5	182-268	BT
CY W69	4 V 1970		46°6'N 2°31'W					94-97	MUN	3	164-187	5	223-259	BT
			Oslo Fjord (?)						OM D28452	1	220			
	V 1887		Oslo Fjord						OM D28453			1	170	
GE-2-177	31 VIII 1963	0601	0°1'S 8°55'E	24.85	15.33	33.40	35.72	99	USNM	1	77.5	2	51-69	BT
GE-2-179	31 VIII 1963	1026	0°2'S 8°50'E	25.10	10.56	33.52	35.14	289	USNM			1	80	BT
GE-2-194	2 IX 1963	1543	1°18'S 8°23'E	24.65	16.98	33.91	35.82	126	USNM	2	86-130			BT
GE-2-196	3 IX 1963	0515	1°30'S 8°37'E	24.65	16.98	33.91	35.82	102	USNM	5	43-53	4	50-56	BT
GE-2-220	6 IX 1963	0840	3°2'S 9°21'E	21.52	16.46	35.81	35.60	120	USNM			1	135	BT
GE-2-227	7 IX 1963	0727	3°30'S 8°53'E	21.72	15.94	35.75	35.61	101	USNM	8	89-122	6	118-157	BT
GE-2-228	7 IX 1963	0945	3°31'S 9°53'E	22.16	11.50	35.74	35.09	395	USNM	2	105-108	2	130-168	BT
GE-2-229	7 IX 1963	1018	3°31'30"S 9°52'E	22.16	11.50	35.74	35.09	396	USNM			2	100-142	40'ST
GE-2-236	8 IX 1963	0900	4°3'S 10°22'E	22.53	09.18	35.60	34.91	406	USNM	1	118			BT
GE-2-237	8 IX 1963	1022	4°3'S 10°22'E	22.53	09.18	35.60	34.91	406	USNM			3	111-150	BT
GE-2-238	8 IX 1963	1055	4°6'S 10°23'E	22.53	09.18	35.60	34.91	402	USNM	1	108	1	150	BT
GE-2-245	9 IX 1963	0940	4°30'S 10°54'E	22.03	16.24	35.32	35.75	101	USNM			2	103-143	BT
GE-2-247	9 IX 1963	1240	4°38'24"S 11°1'12"E	22.39	09.98	35.49	35.06	368	USNM			3	109-146	BT
GE-3-130	26 II 1964	1830	4°58'N 0°30'W					Shallow	USNM	13	32-49	14	28-48	MT
GE-5-172	2 III 1965	0030	7°21'24"N 13°31'18"W					10-165	USNM			1	86	Night light
O 445	26 VIII 1951	0138	19°48'N 91°20'W	27.7	27.2			25.2	USNM 575131	5	145-176	2	208-216	100'ST
O 545	17 IV 1952	1200	27°36'30"N 95°43'6"W	20.5				366-549	USNM 575132	1	42			40'ST
O 548	18 IV 1952	0852	27°1'24"N 96°16'48"W	21.7				366-512	USNM 575134	1 specimen, sex undetermined				40'ST
O 550	18 IV 1952	1535	26°55'N 96°25'W	21	19			225	USNM 575135	1	85	2	76-158	40'ST
O 1343	16 VII 1955	1615	22°59'N 79°17'W	27.2				457.5	USNM 575257	1	50			40'ST

Sta. No.	Date	Time	Position	Temperature (°C) Surf.	Temperature (°C) Bottom	Salinity (°/oo) Surf.	Salinity (°/oo) Bottom	Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
O 1567	26 VI 1956	0335	29°11'N 88°5'W	22				450	USNM 575263			1	89	72'Balloon T
O 4411	10 III 1963		11°55'N 69°24'W	38.8	7.7			468	USNM	1	164			40'Flat T
O 5722	16 X 1965		9°36'N 76°22'W	29.4	10			504	USNM	1	120			65'ST
O 5925	4 III 1966		15°38'N 61°15'W	26.6	11			441	USNM	2	75-78	1	122	65'ST
O 6695	18 V 1967		17°41'N 62°50'30"W	31.1	8.8			540-576	USNM	6	167-185	1	73	40'Flat T
O II 195	19 XI 1968		14°17'N 81°55'W	27.7				324	USNM			1	217	71'ST
O II 289	5 XII 1968		11°24'N 73°47'W	26.6				270	USNM	1	138			ST
O II 10632	18 VI 1969		27°1'N 84°55'W	30				495	USNM 283990	1	152			124'ST
O II 10646	23 VI 1969		29°1'N 87°28'W	31.1				329	USNM 283990	1	134			26'BT
O II 10829	2 XII 1969		15°34'N 61°10'W	27.7				623	USNM 283990			1	285	71'ST
O II 10831	3 XII 1969		17°38'N 63°48'W	28.8				641	USNM 283990			1	254	70'ST
O II 10835	6 XII 1969		18°28'N 63°23'W	29.4				671	USNM 283990			1	126	70'ST
O II 10837	7 XII 1969		18°7'N 63°20'W	28.3				648	USNM 283990	1	102			70'ST
O II 10842	8 XII 1969		17°15'N 62°22'W	28.3				571	USNM 283990			2	111-270	40'ST
O II 10847	10 XII 1969		18°18'N 63°24'W	28.3				648	USNM 283990			1	160	40'ST
O II 10859	15 XII 1969		23°4'N 78°46'W	28.8				356.4	USNM 283990	1	75	1	128	40'ST
O II 10862	16 XII 1969		23°25'N 79°40'W	26.6				450	USNM 283990			1	370	40'ST
O II 10863	16 XII 1969		23°9'N 80°8'W	27.2				459	USNM 283990	3	156-275			40'ST
O II 10956	3 VI 1970		21°33'N 96°48'W	26.6				1080	USNM 283990			1	100	150'ST
O II 10996	15 VI 1970		19°16'N 92°50'W	27.7				270	USNM 283990	2	122-127			150'ST
O II 11134	9 VIII 1970		24°22'N 87°47'W	28.8				540	USNM 283990	1	166			71'ST
O II 11138	10 VIII 1970		24°19'N 87°45'W	28.8				544	USNM 283990	1	58	4	58-86	71'ST
O II 11141	12 VIII 1970		24°5'N 87°34'W	28.8				324	USNM 283990			2	105-111	40'ST
O II 11204	1 IX 1970		29°12'N 87°55'W	28.8				540	USNM 283990	1	113			71'ST
Pel 127	13-19 X 1962		8°52'N 79°33'W	27.7				5-9	USNM 574691			1	212	Lobster pot
VIMS T183	30 VIII 1967	1442	36°42'N 74°45'W		11		34	70.2	USNM			1	135	27'OT
VIMS T189	31 VIII 1967	1442	36°5'N 74°52'W		13		33	79	USNM	1	115	1	123	27'OT
VIMS T231	2 XII 1967	1136	37°0'N 75°2'W		12		34	54	USNM			1	187	27'OT

[*Illex coindetii*] continued

Sta. No.	Date	Time	Position	Temperature (°C)		Salinity (°/oo)		Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
				Surf.	Bottom	Surf.	Bottom							
VIMS T265	14 XI 1967	0830	37°6'N 74°35'W		12		36	190.8	USNM	2	170-190			27'OT
	2 VII 1932		24°20'N 83°W					243-281	USNM 119885			1	161	
	23 VII 1932		South of Tortugas, Florida					168.4-172	USNM 7069			1	54	
	16 VIII 1967		36°57'N 10°37'E					68	USNM	1	112	1	132	

BT = Bottom Trawl
OT = Otter Trawl
MT = Midwater Trawl
ST = Shrimp Trawl
All times are local times

*All specimens of *I. coindetii* supplied through the courtesy of the Laboratoire Arago, Banyuls-sur-Mer, are, as Professor F. A. Aldrich attests, secured at a fish market in the village of Las Rosas, Spain. Since these are bought in units along with other material in baskets of catch, it is virtually impossible to ascertain the location within the Mediterranean Sea at which these specimens were taken.

Funnel well developed; funnel groove deep; lateral adductor muscles conspicuous, strong, rod-like (Fig. 12); anterior adductors thin, broad, sheetlike. Dorsal funnel organ (Fig. 16A) large; posterior limbs fleshy, thickened, broad anteriorly, tapered, bluntly pointed posteriorly; lateral shoulders conspicuous, anterio-lateral borders slightly convex; apical papilla spearhead-shaped. Conspicuous thin ridges extend from anterior mid-portion of limbs nearly to apex. Ventral pads oblong; lateral borders curved; medial borders nearly straight; anterior end slightly pointed. Funnel valve broad.

Funnel locking cartilage large, strong, inverted-T-shaped (Fig. 13B). Medial, longitudinal groove narrow, relatively shallow; groove deepens and widens posteriorly to form deep, broad pit. Strong cartilaginous knobs converge, nearly meet posterior to deep pit; lateral knob rounded, medial knob slightly pointed, narrow ridge extending dorsally into pit; pit undercuts anterior walls of knobs. Groove between knobs narrow, deep, opens into lateral groove. Lateral groove very broadly open inverted-V-shaped, deepest anteriorly against posterior walls of knobs, shallowing along posterior margin of locking cartilage. Cartilage bordered by thin muscular flange. Mantle locking cartilage (Fig. 13C) strong. Longitudinal ridge low, narrow anteriorly, expands to large, sharply defined, swollen bulb posteriorly; posterior wall deeply undercut toward base on mantle. Thin ridge extends from bulb to lateral ridge. Lateral ridge narrow, widely open V-shaped.

Head large, broad, width about 21% of ML in males, 18% in females; length about 22% of ML in males, 19% in females. Three flaplike nuchal folds present; nuchal cartilage long, broad and rounded anteriorly, narrow, tapered posteriorly, terminally embedded in muscle; central groove deep, lateral ridges distinct; entire cartilage bordered by thin, muscular flange (Fig. 13D). Eye openings subcircular, dorso-ventrally elongate; anterior sinus deep, conspicuous.

Arms long, order II > III > IV > I; much longer in males than in females, especially II and III; arms II, III robust, especially in males; arm IV less robust; arm I least robust, slender (Figs. 11, 12, 14). Swimming keels very low, weak on distal half of arm I; higher, better developed, full length of II; best developed on III, broadest in proximal one-third; low, second best developed, full length of IV. Protective membranes well developed, especially ventral membranes; trabeculae long, very strong, arise from base of sucker stalks, form high points along membranes. Suckers of arms much larger in males than in females, especially on II and III. Suckers small on I and IV; about 6 pairs on II and III of males greatly enlarged (Fig. 14).

Arm sucker dentition. Largest rings of arm I (Fig. 17A) with low, broad plate on proximal one-third, 3-6 low, truncate, or slightly rounded teeth laterally, becoming longer, narrower distally; distal median tooth elongate, more rounded; teeth, especially median tooth, more truncate, blunt on basal suckers, more pointed, longer on distal suckers. Largest rings on arm II (Fig. 17B) of males with 17-19 low, truncate or rounded teeth around, teeth lower, broader proximally, higher, narrower, more rounded distally; distal median tooth greatly enlarged, triangular, curved outward, sharply pointed. Small rings with broad, low plate on proximal one-third, 1-2 rounded teeth laterally, 2-5 narrow, long, pointed teeth disto-laterally, graded to longest median tooth. Largest rings on arm II of females (Fig. 17D) with 2-3 low, broad, flat teeth on proximal one-third, 5-7 teeth laterally, broader, more truncate proximally, narrower, more rounded distally; distal median tooth slightly longer, triangular, pointed. Small rings as in males. Ring dentition of III about as II; males (Fig. 17C) with 17-19 teeth around, lower, broader, more truncate proximally, higher, narrower, more rounded distally; distal median tooth enlarged, triangular, sharply pointed. Small rings with low, broad plate on proximal one-third, 1-2 lateral teeth, rounded; 2-5 long pointed teeth disto-laterally, graded to longest median tooth. Largest rings on arm III of females (Fig. 17E) with broad, low, single or bifurcate plate proximally, 5-7 lateral teeth, more truncate, broader proximally graded distally, median tooth long, pointed, less conspicuous than in males. Small rings as in males. Largest ring of arm IV (Fig. 17F) with broad, low proximal plate, 3-5 lateral teeth, rounded to truncate, longer, narrower distally, distal median tooth bluntly pointed, or rounded, narrow.

Right or left arm IV hectocotylized (Fig. 15A), longer (about 4-5%), more robust than non-hectocotylized IV; modified portion about

25% of arm length. From proximal 7th sucker-pair sucker reduced in size, trabeculae modified into lobate flaps, fringed, papillose, about 10-14 pairs in number (12 pairs on neotype). Second or third pair of modified trabeculae largest, reduced in size distally. Sucker and protective membranes on modified tip disappeared. Dorsal row with 1-2 conical papillae, followed by series of transversely broad, thin, nearly truncate flaps (28 recognizable on neotype); flaps gradually reduced in size distally; distal tip with minute papillae (11 on neotype). Ventral row with series of conical papillae, gradually reduced in size to tip (36 recognizable on neotype). Low, weak zigzag ridge between papillae and flaps. Aboral keel broadly expanded along modified portion.

Tentacles robust, long; stalks naked. Clubs expanded, long (Fig. 13A). Distinct carpal cluster absent; carpal suckers small, biserial; carpal knobs lacking. Manal suckers tetraserial; suckers on marginal rows small; medial sucker rows arise distal to the proximal 5 carpal suckers; proximal 3-6 medial suckers small, gradually increasing in diameter; 13-16 medial suckers on manus greatly enlarged; maximum size greater in males than in females; manus terminates abruptly. Dactylus distinct, slender; with extremely numerous, minute suckers in 7-11 transverse rows, sucker at tip slightly enlarged; tip with narrow, suckerless flange. Swimming keel along entire tentacular stalk aborally, broadest proximal to club, slightly diminishes distally along carpal and manal region, expanded to broad keel along dactylus. Lateral angles distinct on oral surface of stalk, continue as broad, protective membrane along club, broadest along region with enlarged medial suckers, diminish significantly along dactylus. Dual V-shaped trabeculae arise from enlarged common base with lateral suckers along manus.

Club sucker dentition. Sucker rings of carpal area with low, broad plate on proximal half, 4-7 small teeth, narrow, bluntly pointed or truncate on distal half; 2-3 lateral teeth, broad, rounded. Proximal-most lateral manal suckers with proximal plate, 1-2 low lateral teeth, rounded, 4-7 long, narrow distal teeth, truncate or bluntly pointed; distal lateral suckers toothed around entire margin, with 4-8 low, rounded or conical teeth proximally, 14-18 longer, sharply pointed lateral and distal teeth, occasional small pointed secondary tooth between primary teeth. Proximal 4-6 medial manal suckers with low, proximal plate, 1-2 low, rounded, lateral teeth, 2-4 narrower, bluntly pointed, disto-lateral teeth, median tooth slightly longer, bluntly pointed; next distal 4-5 enlarged sucker rings with 7-16 teeth around margin, low, flat proximally, narrow, rounded distally, no conspicuous median tooth (Fig. 17G). Dentition lacking, rings entire or divided into broad, uneven plates on 7-8 distal medial manal suckers. Proximal dactyl sucker rings with 4-6 widely spaced, long, pointed distal teeth; teeth become more blunt or conical, few on rings of middle dactyl suckers; teeth on suckers at distal tip few, minute. All carpal, lateral manal, and dactyl suckers equipped with scaly grasping rim.

Gladius (Fig. 18A) long, slender, bluntly pointed anteriorly; median ridge and heavy lateral rods extend whole length of rhachis, converge posteriorly, fuse to form solid rod anterior to vane, continue to tip. Vane short (20% of PL), narrow (maximum width about 4.2% or PL); forms short, hollow conus; extreme tip solid.

Connectives of buccal membrane attach to dorsal, dorsal, ventral, and dorsal sides of arms I-IV in that order. The most proximal sucker on arms I-IV on ventral, ventral, dorsal, ventral rows, respectively.

Mandibles. Upper mandible (Fig. 16B): rostrum strong, sharply pointed, long, curved, heavily pigmented; hood strong, long, curved, moderate pigmented; shallow notch and slight ridge separate rostrum and wing; cutting edge of wing slightly curved, smooth or slightly waved; lateral wall large, long, deep, darker anteriorly, crest curved. Lower beak (Fig. 16C): rostrum moderate long, sharply pointed, darkly pigmented; cutting edge straight; rostral lamellae moderate long, wide, thin; gular lamellae large, crest strong, posterior corner moderate long, bluntly pointed, curved; rostral width narrow.

Radula (Fig. 17H) with 7 transverse rows of teeth; rhachidian with long pointed central tooth, blunt lateral cusps; first lateral tooth, long, sharply pointed, lateral cusp blunt; second lateral tooth curved outward, no lateral cusp; third lateral tooth long, curved, pointed; marginal plates occasionally present.

Spermatophores (Fig. 18B, C) about 18% of ML with sperm mass of about 53% of total length, cement body about 25% of total length. Cone at oral end of cement body rounded triangle shape, lens shape, or diamond shape, connected aborally by very short neck, broad, indistinct; oral tube broad.

Color (in isopropyl alcohol): reddish-brown chromatophores cover entire body, more sparse ventrally, thickly packed dorsally, deep purple stripe along dorsal mid-line of mantle and above eyes.

Morphometry. Measurements of 19 body parts from 263 specimens (123 males, 140 females) were plotted against the ML to show the allometric growth pattern. The range of the mantle length of the specimens measured was 43-275 mm for males and 44-370 mm for females.

As in the case of *Illex illecebrosus*, the allometric relation between the ML and the measurements of various body parts can also be expressed by simple linear formula, $Y=a+bX$. The values of a and b for each pair of Y and X, as well as N and r, are shown in Table 3. The definition of these variables is also shown in the table. A selected sample of scatter diagrams is also presented in the Appendix.

The regression line for each Y for both sexes is also analyzed for the sexual dimorphism by testing the regression coefficient b.

Table 3

Regression, Y=a+bX, of the measurements of selected body parts against the mantle length in *Illex coindetii*.

All measurements in mm

N: Number of specimens in sample

X: ML

Y: Measurements of the chosen body part

r: Correlation coefficient of the regression

+: t-value greater than critical value at the 95% confidence interval

-: t-value less than critical value at the 90% confidence interval

	MALE				FEMALE					
Y	N	a	b	r	N	a	b	r	t	
VML	121	7.272	0.874	0.991	139	7.521	0.879	0.994	0.078	-
HL	122	-4.704	0.263	0.937	138	-0.730	0.196	0.969	7.858	+
HW	122	-2.222	0.234	0.948	139	1.717	0.170	0.965	8.220	+
MW_1	122	-1.801	0.236	0.952	139	0.437	0.197	0.978	1.968	+
MW_2	121	-2.508	0.239	0.938	139	1.600	0.196	0.924	3.786	+
MW_3	121	-2.695	0.162	0.909	138	0.354	0.132	0.901	3.329	+
FL	123	-5.482	0.443	0.987	139	-2.987	0.421	0.987	2.837	+
FW	123	-8.259	0.643	0.976	137	-2.548	0.560	0.988	5.661	+
FBL	123	-6.945	0.404	0.989	139	-4.596	0.387	0.992	2.491	+
A_1L	123	-23.723	0.699	0.939	139	-9.251	0.461	0.957	12.528	+
A_2L	122	-31.116	0.918	0.937	138	-10.471	0.581	0.969	11.049	+
A_3L	123	-30.327	0.906	0.944	138	-12.183	0.594	0.966	10.559	+
A_4L	123	-28.025	0.813	0.941	140	-11.260	0.528	0.965	10.733	+
S_1	121	-0.709	0.023	0.935	139	-0.271	0.016	0.971	9.613	+
S_2	122	-1.329	0.042	0.897	138	-0.371	0.023	0.935	11.321	+
S_3	122	-1.359	0.042	0.892	139	-0.350	0.023	0.972	11.841	+
S_4	121	-0.759	0.022	0.939	139	-0.214	0.014	0.973	12.676	+
S_T	102	-0.663	0.027	0.913	113	-0.305	0.021	0.971	4.845	+
GL	121	5.528	0.278	0.966	137	7.190	0.256	0.969	2.373	+

With the exception of VML, all t values are greater than the critical t value at 95% confidence interval, indicating the existence of sexual dimorphism in the regression coefficient for each Y-pair.

Holotype: See "Remarks"

Holotype Locality: Nice, France

Neotype: Mature male (Figs. 11A, 12A), 132 mm ML, to be deposited in USNM.

Neotype Locality: 42°32'N-42°35'N, 3°36'E-3°42'E, off Port Vendres, France. Surface temperature 15.6 C. The specimen was collected from a depth of 200-500 m on 3-XI-1971. Gear used unknown.

Distribution: Western Atlantic: U.S. coast from 37°N southwards, off Florida Peninsula, Gulf of Mexico, Caribbean Sea. Eastern Atlantic: North Sea, European coast of Atlantic Ocean, Bristol Channel, Mediterranean Sea, African coast of Atlantic southward to 14°S. On continental shelf (Fig. 10).

Remarks: Due to the numerous faunal surveys in Europe in the 19th century, a serious nomenclature problem exists in the species in question.

The description of *Loligo sagittata* var. b by Lamarck (1799, pp. 13-15) is too brief and obscure for verifying its identity. Steenstrup (1880, p. 77) rejected it as an *Illex*, and Verrill considered that the description applied partly to *Ommastrephes bartrami* (Verrill, 1880, p. 289). None of the major workers such as Pfeffer, Naef, Grimpe, or Adam has considered it to be *Illex coindetii*. I follow this opinion and thereby reject *Loligo sagittata* var. b as a synonym of *I. coindetii*. No attempt has been made to verify its actual identity as it is beyond the scope of this study.

The earliest available name for the taxon in question is Blainville's *Loligo brongniartii* (Blainville, 1823, p. 130). Steenstrup rejected the thesis that *Loligo brongniartii* and *Illex coindetii* are conspecific, and considered the former to be *Ommasttrephes pteropus* (Steenstrup, 1885, p. 171). As was mentioned in the "Historical Review", the specimen mentioned by Steenstrup in 1885 is in fact *Symplectoteuthis*. The description of *Loligo brongniartii* given by Blainville is brief and no illustration of it could be located. However, the illustrations in the English translation of Cuvier's "Le Règne animal distribué d'après son organisation" (1837, vol. 3, pl. 1, fig. 5) and in Ferussac and d'Orbigny (1835-1848, G. Calmar pl. 4) clearly show *Illex* characteristics: funnel groove smooth, tentacular stalk naked, the horny ring of the large club sucker smooth. According to Blainville, the species probably came from the Mediterranean Sea (1823, p. 130). The fin angle is in the illustrations just mentioned indicate that it is *Illex coindetii*. The trivial name *brongniartii* is, therefore, the oldest available for the taxon and has priority of 16 years over *coindetii*!

Since the name *coindetii* has been widely accepted without challenge as the correct name, further confusion would undoubtedly arise if the senior synonym *brongniartii* were to be accepted to replace the junior synonym *coindetii*. Therefore, it is proposed that for the stability of the taxon, the senior synonym *L. brongniartii* should be treated as *nomen oblitum*.

The wording in the "Code" governing *nomen oblitum* (Art. 23b) is ambiguous. In November, 1969, a Declaration of improved wording was passed by the Commission. The new wording that concerns the case in question is as follows:

> (b) Limitation. A name that is in general current use and has been available for at least 50 years shall not be displaced after 1960 by an unused senior synonym.
>
> (i) A name is to be considered as in general current use when, in the immediately preceding 50 years, it has been applied to a particular taxon, as its presumably valid name, by at least five different authors and in at least ten publications.
>
> (ii) A senior synonym is to be considered unused when, during the immediately preceding 50 years, it has not once been applied to a particular taxon as its presumably valid name. An unused senior synonym employed after 1960 in violation of the provisions of Article 23b, whether explicitly

to replace the junior synonym or not, does not thereby lose its status as an unused name.

(iii) The mentioning of a name in a synonymy or its mere listing in an abstracting publication, or in a nomenclator or other index or list of names does not constitute usage in the sense of Article 23b.

It is understood that this improved wording of the "Code" is provisionally in force until it is ratified or rejected by the next International Congress of Zoology and only the Congress can repeal any provision of the rules. At any rate the new wording is, as stated by Mayr, et al., (1971, p. 1042), "a major step in the direction of greater stability of zoological nomenclature". Based on this declaration the name *coindetii* is to be retained for the taxon in question.

As Verany stated in his original publication, the name of this species, *Loligo coindetii* was given in honor of Dr. Coindet of Geneva (Verany, 1837, p. 94). "Code" states that "A species-group name, if a noun formed from a modern personal name, must end in *-i* if the personal name is that of a man, *-orum* if of men or of man (men) and woman (women) together, *-ae* if of a woman, and *-arum* if of women" (Art. 31). The name of the animal in question, after changing the generic name, should then be *Illex coindeti*. However, a vote in the International Congress of Zoology in Washington in 1963 deleted Art. 31 (of 1961) and replaced it with the above wording (of the 1961 Art. 31) as the Recommendation 31A. The name in question is then governed by Art. 32(a), that the original spelling of a name is to be retained as the "correct original spelling" (Mayr, 1969, pp. 361-362). Thus, the name of this species should be *Illex coindetii*.

Despite considerable and thorough searching, I have not been able to locate the holotype erected by Verany in 1837, and presumably it is missing. Therefore, a mature male is here erected as neotype. Table 4 shows the measurements, indices, and counts of the specimen.

The specimen is provided by Dr. Katharina Mangold. It was captured from 42°32'N - 42°35'N, 3°36'E - 3°42'E at a depth of 200-500 meters. The neotype locality is about 310 Km (straight line distance) SW of the holotype locality, Nice, France.

The geographical distribution of this species is widely spread. In the eastern Atlantic it has been reported from as far north as Oslo Fjord (OM D28453). It was reported from Helgoland (Grimpe, 1925), from the west coast of France and Portugal, the Mediterranean Sea, and the west coast of Africa southward to 14°S (Adam, 1952). The record of *I. i. illecebrosus* from the Bristol Channel is doubtful. I have verified two of these specimens (now in the IMSUM) as *I. coindetii*.

The two specimens reported to be from the Red Sea (Adam, 1942) are kept in the Museum National d'Histoire Naturelle de Paris. These two specimens are *I. coindetii*, but their original locality is doubtful. The specimens were said to be collected from the Red Sea by Clot in 1850 (the label accompanying the specimens; also Adam, 1942, p. 14). The modern Suez Canal was built between 1859 and 1869, although

Table 4

Measurements (in mm), indices, and counts of the neotype of *Illex coindetii*.

	Measurements (mm)	Index (%)		Measurement (mm)	Index (%)
ML	132				
VML	122	92.4	HL	29	22.0
HW	28.2	21.4	MW_1	30	22.7
MW_2	28.4	21.5	MW_3	14.7	11.1
FL	52	39.4	FW	75	56.8
FBL	45	34.1	A_1L	66	50.0
A_2L	86	65.2	A_3L	86	65.2
A_4L	74	56.1	HcAL	76	57.6
HcL	21	27.6	CL	66	50.0
S_1	2.9	2.20	S_2	4.9	3.71
S_3	4.9	3.71	S_4	2.5	1.89
S_T	3.4	2.58	GL	38.9	29.5
S_pL	24	18.2	S_pRL	12.5	52.1
S_pRW	0.3	1.25	CBL	5	20.8
FA	57°		#S_1	107	
#S_2	97		#S_3	99	
#S_4	119		#G	57	

Left ventral arm hectocotylized

connection between the Mediterranean Sea and the Red Sea existed before that date. Por (1971, p. 154) points out, "Although repeated pre-lessepsian faunal interchange was physically possible, only a restricted number of euryhaline species could have made good use of it. Considerable barriers of varied and rapidly changing salinities, always existed along the old waterways". If these two specimens are genuinely from the Red Sea, it is unlikely that a stenohaline form such as *Illex* could successively overcome these barriers. By ruling out the possibility of a pre-lessepsian migration, no other reasonable explanation can be had to account for the occurrence of *I. coindetii* in the Red Sea: *Illex* is an Atlantic endemic genus, never having been found in the Indian Ocean. It is likely, although speculative, that these two specimens have been mislabelled. At the present time the occurrence of *I. coindetii* from the Red Sea should be treated as a doubtful record and can only be confirmed by additional materials through further collection.

In the western Atlantic Ocean, the northern-most record of *I. coindetii* is 37°06'N 74°35'W (VIMS T265). It is distributed southward on the continental shelf along the Florida Peninsula, the Gulf of Mexico, and the Caribbean Sea. The southern-most record is from 9°02'18"N 81°23'48"W (P 445), its exact extent is not known due to the lack of collections along the Central and South American coast. The eastern-most record is 15°38'N 61°15'W (O 5925). No record is known from east of the Antilles Chain.

FIGURE 11. Photographs of *Illex coindetii* (Verany, 1837). Dorsal view. Scale: 2 cm.

A. Male; the neotype of the species

B. Female

Both specimens from the Mediterranean Sea.

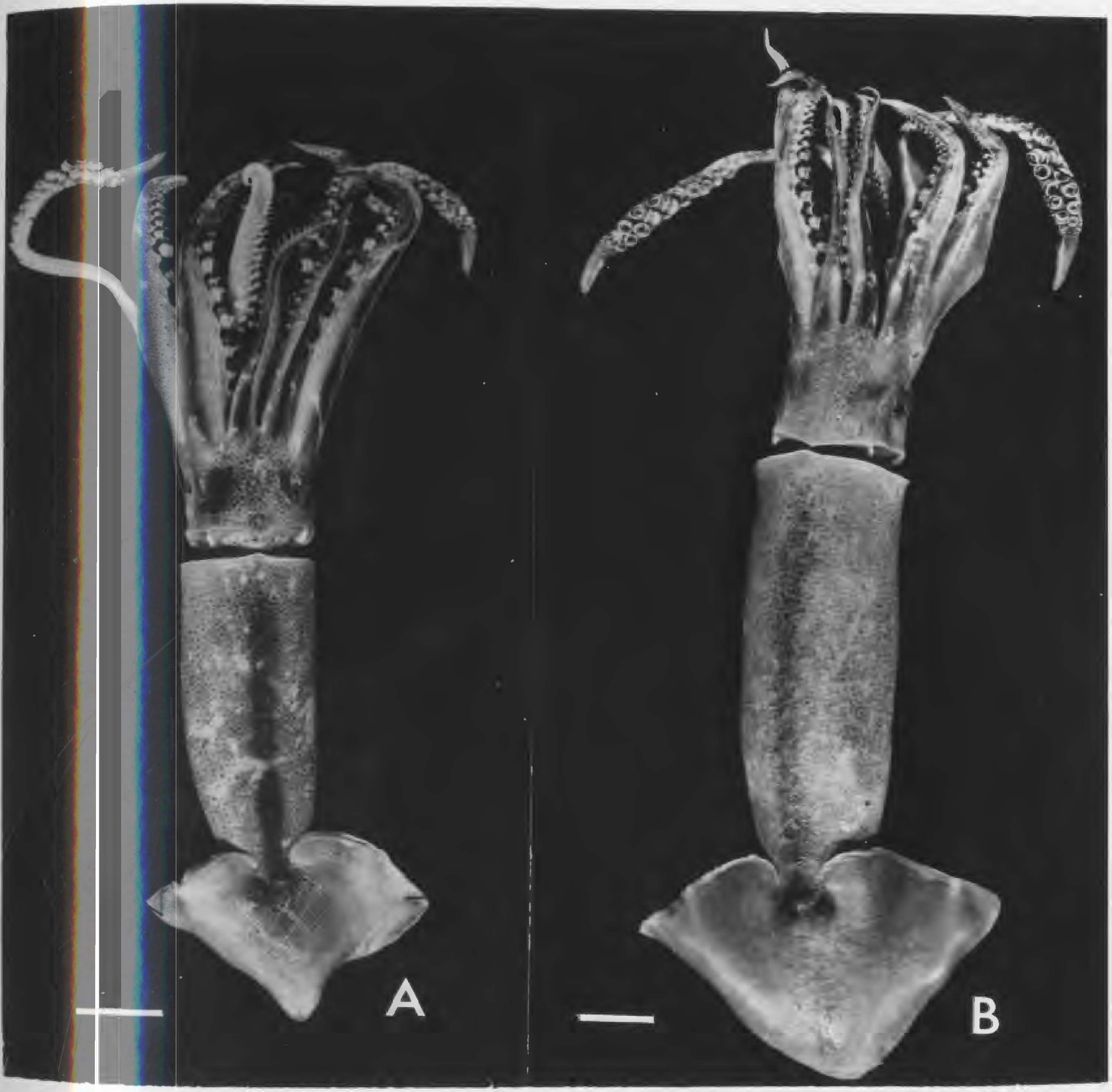

A
B

FIGURE 12. Photographs of *Illex coindetii* (Verany, 1837). Ventral view. Scale: 2 cm.

A. Male; the neotype of the species

B. Female

Both specimens from the Mediterranean Sea.

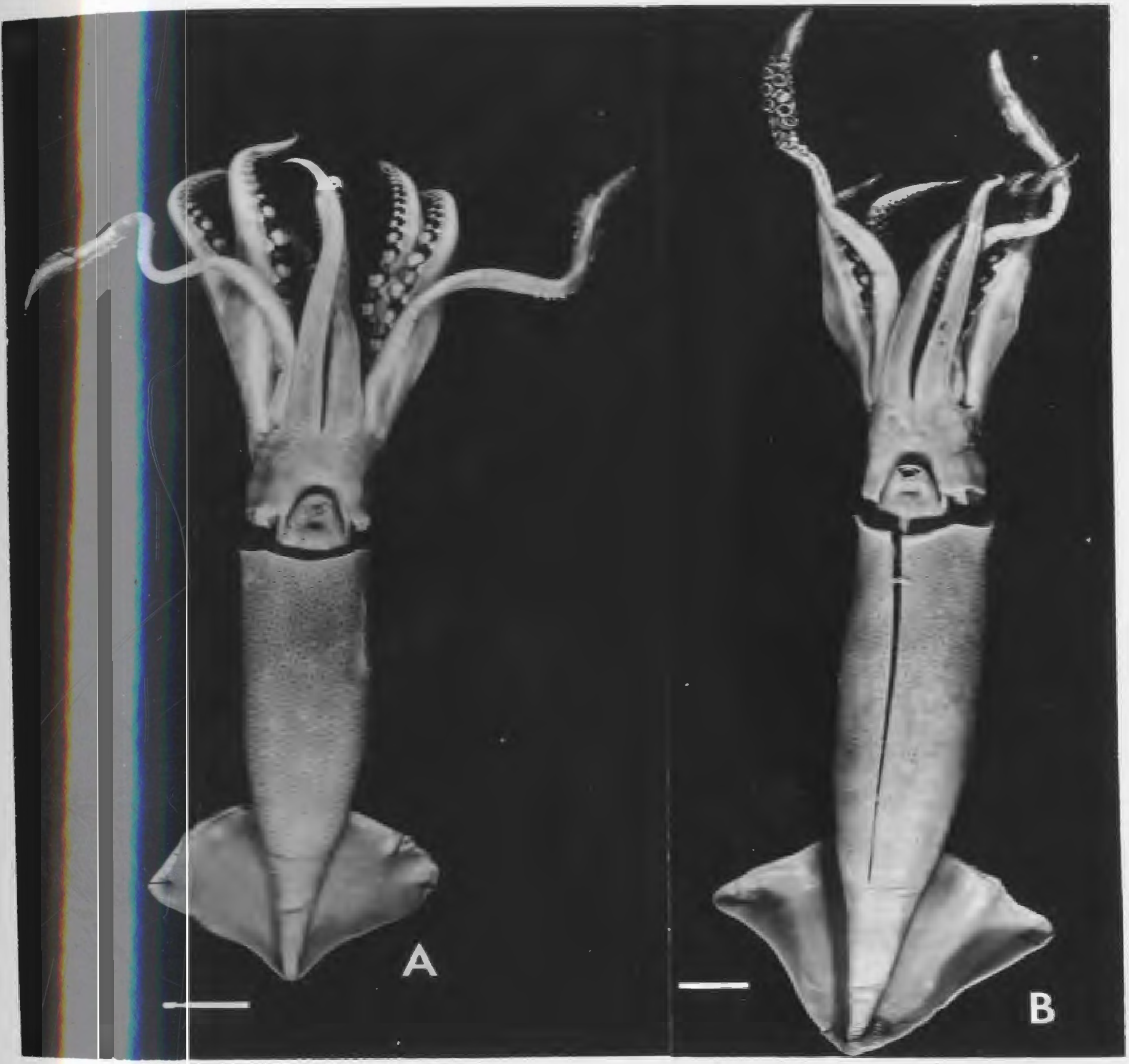

A
B

FIGURE 13. Photographs of tentacular and cartilagenous portions of *Illex coindetii*. Scale: 1 cm.

A. Tentacular club

B. Funnel component of mantle-locking apparatus

C. Mantle component of mantle-locking apparatus

D. Nuchal cartilage

In B through D, anterior end uppermost.

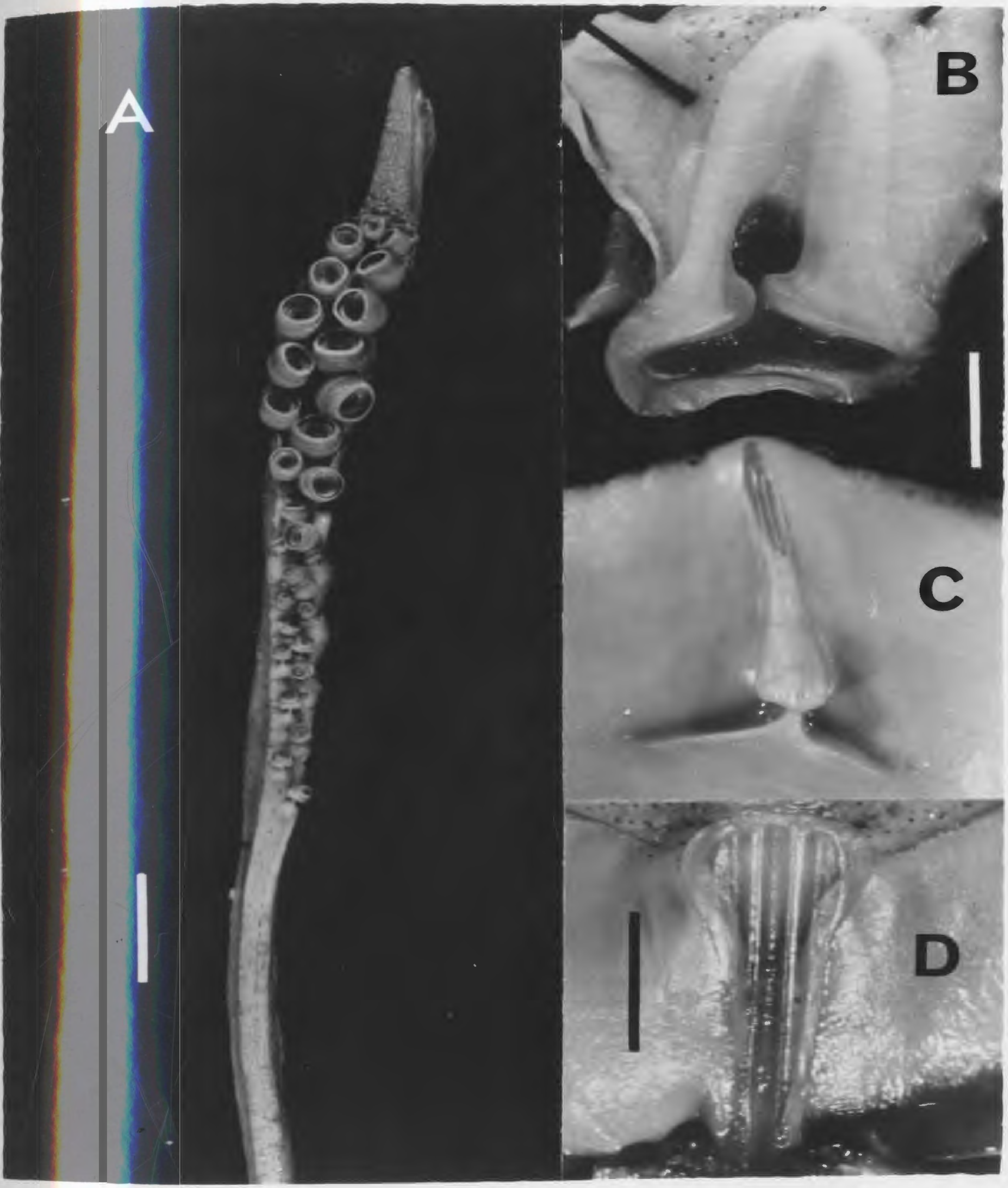

A
B
C
D

FIGURE 14. A. Photograph of dorso-lateral (II) arm of male specimen of *Illex coindetii*.

B. Photograph of lateral (III) arm of male specimen of *Illex coindetii*.

Scale: 1 cm.


A
B

FIGURE 15. A. Photograph of hectocotylized arm (IV) of *Illex coindetii*. Scale: 1 cm.

B. Photograph of female specimen of *Illex coindetii*, dissected to show spermatophores fixed to the mantle wall. Scale: 2 cm.

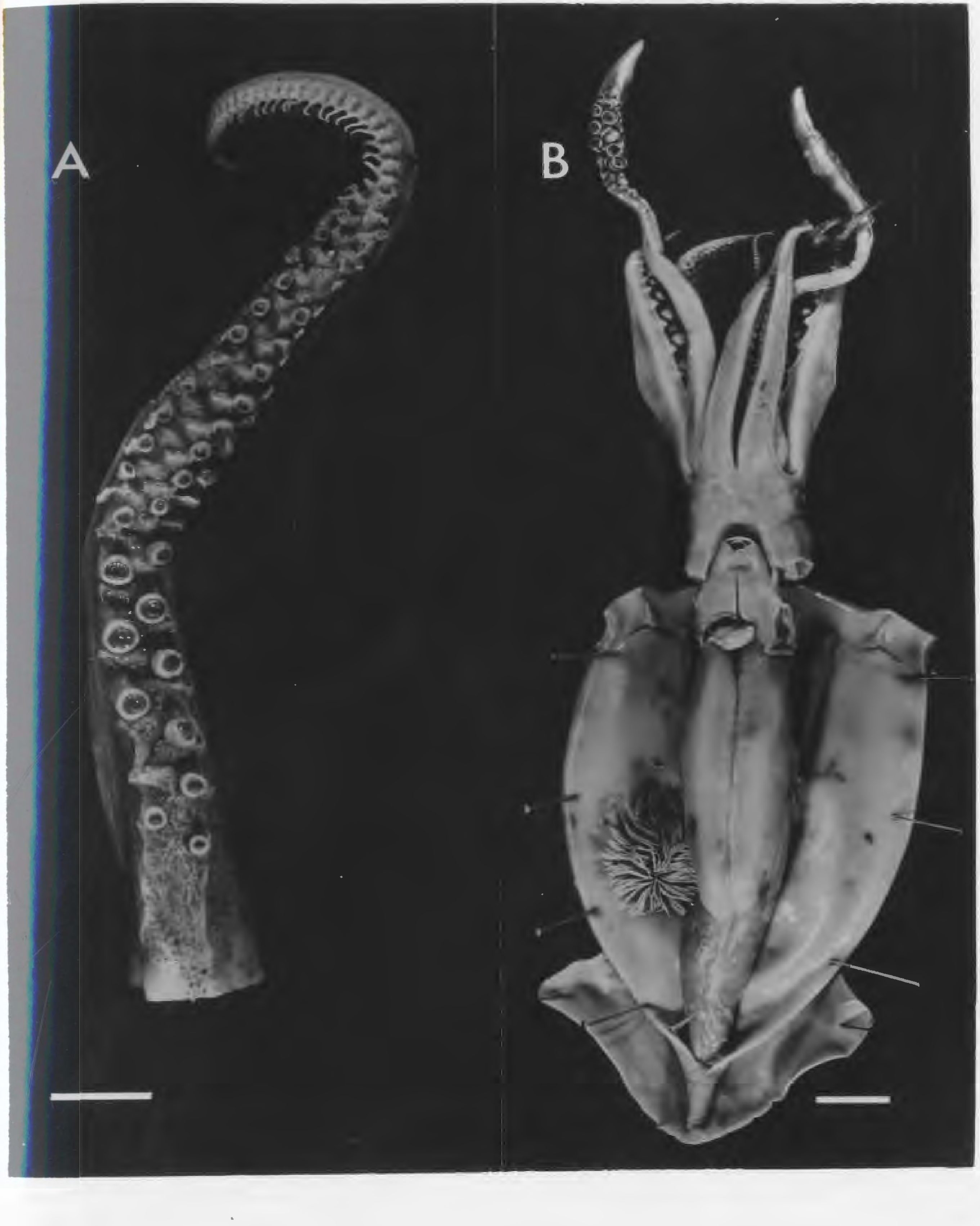
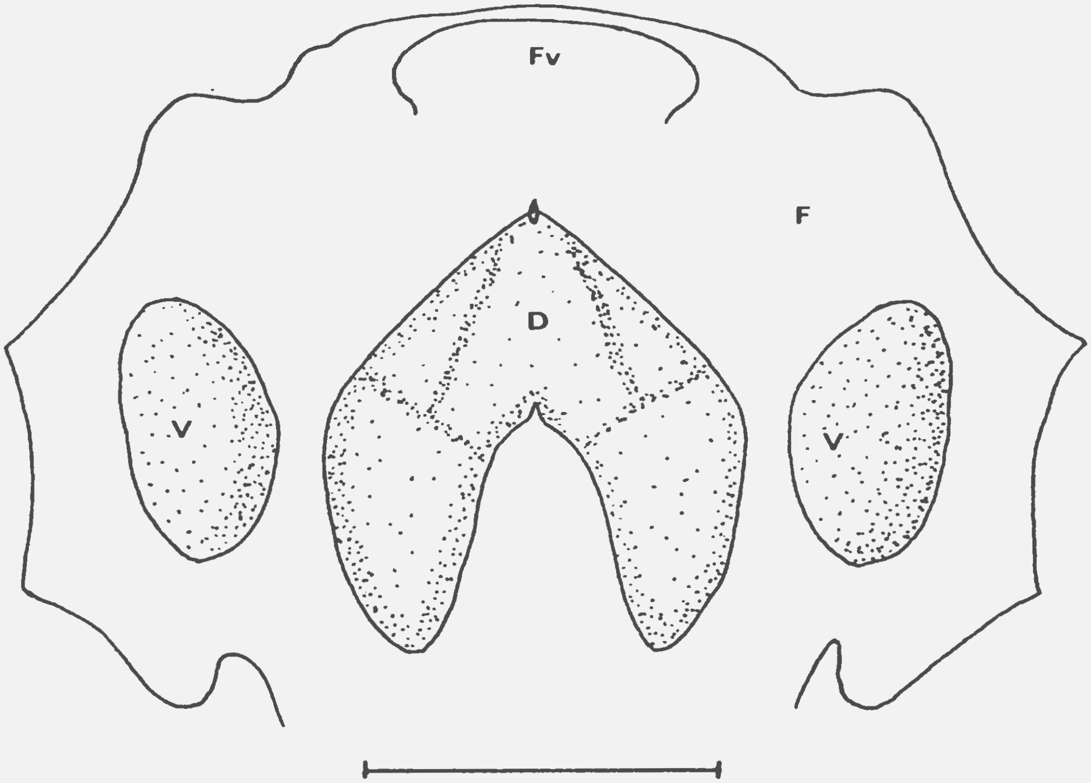

A
B

FIGURE 16. A. Drawing of funnel organs of *Illex coindetii*. Scale: 1 cm.

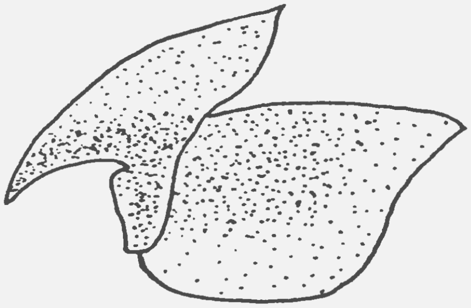
D = dorsal funnel organ
V = ventral funnel organ
F = wall of funnel
F_V = funnel valve

B. Drawing of upper mandible of *Illex coindetii*.

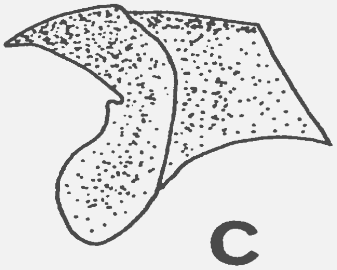
C. Drawing of lower mandible of *Illex coindetii*



A



B



C

FIGURE 17. A through G. Drawings of chitinous rings from specific suckers from sessile arms and tentacular manus of *Illex coindetii*.

A. Ring from largest sucker from dorsal arm (I)

B. Ring from largest sucker from dorso-lateral arm (II) of male specimen.

C. Ring from largest sucker from ventro-lateral arm (III) of male specimen.

D. Ring from largest sucker from dorso-lateral arm (II) of female specimen.

E. Ring from largest sucker of ventro-lateral arm (III) of female specimen.

F. Ring from largest sucker from ventral arm (IV).

G. Ring from largest sucker from manal portion of tentacular club.

H. Drawings of a single row of teeth from the mid-portion of the radular ribbon of *Illex coindetii*.

R = rhachidian tooth
1L = first lateral tooth
2L = second lateral tooth
3L = third lateral tooth
mp = marginal plate

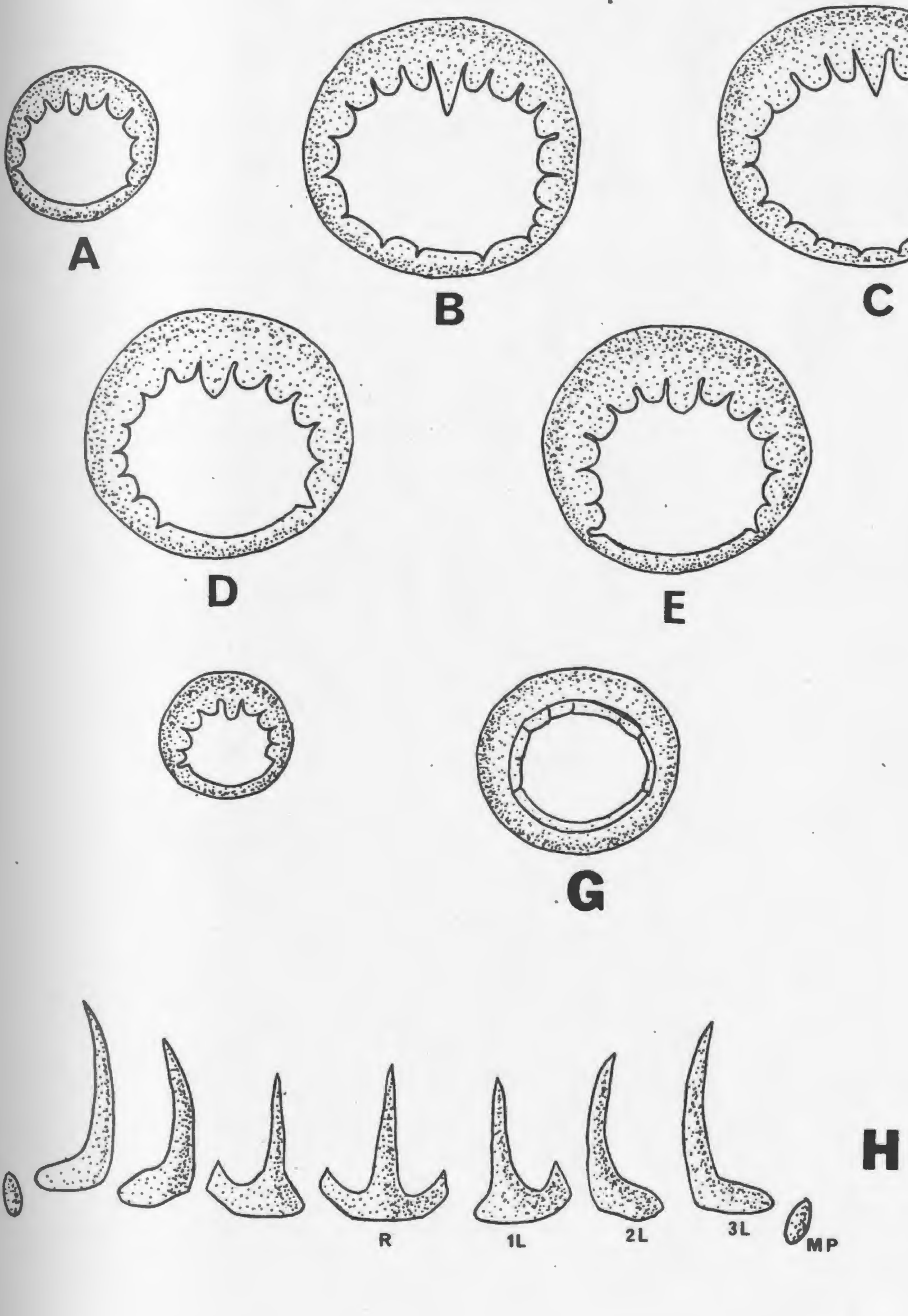
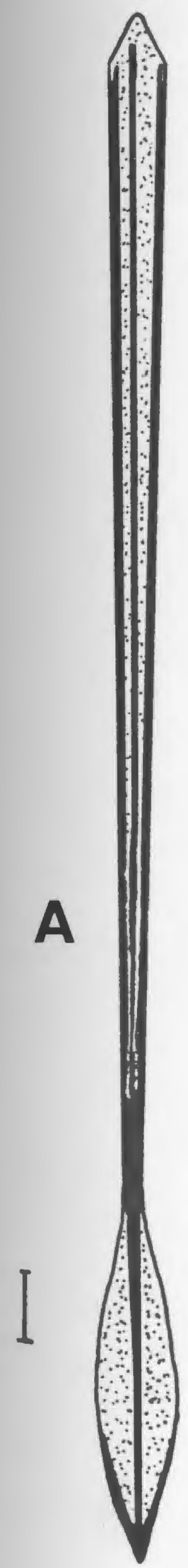

A
B
C
D
E
G
H
R
1L
2L
3L
MP

FIGURE 18. A. Drawing of entire gladius of *Illex coindetii*. Scale: 1 cm.

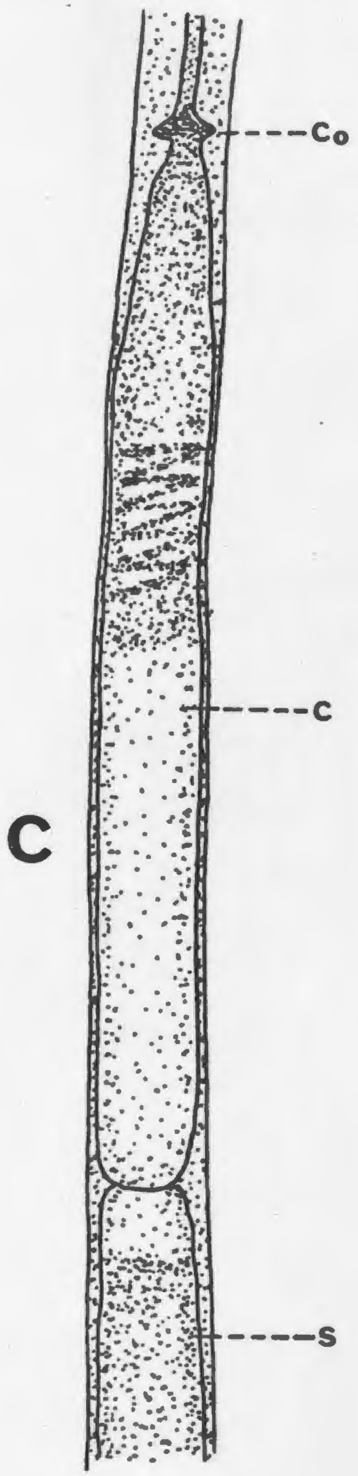
B. Drawing of entire spermatophore of *Illex coindetii*. Scale: 1 cm.

C. Drawing of portion of spermatophore of *Illex coindetii*, showing the cement body and adjacent structures.

C = cement body
Co = cone
S = sperm mass


A


B


Co
c
C
s

Illex argentinus (Castellanos, 1960)

[illegible]astrephes argentinus Castellanos, 1960, p. 55; 1962, p. 117. -Clarke, 1966, p. 113.

Illex illecebrosus argentinus, Castellanos, 1964, p. 3. -Nesis, 1967, p. 3. -Castellanos & Menni, 1968, p. 4. -Lu, 1968, p. 5. -Aldrich & Lu, 1968, p. 815. -Mangold, Lu & Aldrich, 1969, p. 1153.

Illex argentinus, Roper, Lu & Mangold, 1969, p. 317. -Castellanos & Menni, 1969, p. 67.

Diagnosis: Hectocotylus about 50% of total arm length, dorsal row with 10-16 enlarged, rounded suckerless knobs, 18-22 large truncate or rounded lamellae, ventral row with 7-10 low knobs, 7-12 nipple-like papillae; cone at oral end of cement body of spermatophore, flat lens-shaped. In both sexes marginal borders of posterior limbs of dorsal funnel organ parallel.

List of Materials: (See overleaf)

Description: Mantle moderately long, broadest at middle, drawn out posteriorly into attenuated tip (Fig. 20A, B). Ventro-lateral lobes on mantle opening inconspicuous, rounded; dorsal lobe more conspicuous, slightly pointed (Fig. 19A, B). Thin, membranous flange

List of Materials (*Illex argentinus*)

Sta. No.	Date	Position	Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)
		39°S 55°W		LPM 45.001			1	272
		39°S 55°W		LPM 45.002	1	203	1	287
WH 366	14 VII 1966	47°50'S 64°46'W	100	IBMMP	1	129	4	112-128
WH 372	15 VII 1966	45°15'S 65°22'W	90	IBMMP	1	184		
WH 373	15 VII 1966	44°48'S 64°07'W	90	IBMMP	1	198		
	I 1969	45°03'S 65°W		IBMMP			1	228
	VII 1960	37°S 55°W		IMSUM	4	165-178	4	168-218
	IV 1969	Mar del Plata, Argentina		MUN	64	170-256	40	201-285

encircles mantle opening. Mantle wall thick. Fins broad, drawn out posteriorly to blunt point; width (58% of ML) greater than length (42% of ML); posterior borders slightly convex; fin angle 49-50°; lateral borders rounded; anterior lobes well developed (Fig. 19A, B).

Funnel well developed, in deep funnel groove; lateral adductor muscle strong, rod-like (Fig. 20A, B); anterior adductor muscles thin, sheetlike. Dorsal funnel organ large (Fig. 23A); posterior limbs fleshy, thickened, broad anteriorly, tapered, elongated, acutely pointed posteriorly; lateral shoulders conspicuous; anterolateral borders concave, long; apical papilla spearhead in shape. Ventral pads oblong and kidney-shaped; lateral borders slightly convex; medial borders slightly concave. Funnel valve broad.

Funnel locking-cartilage large, strong, inverted T-shaped (Fig. 21B). Medial, longitudinal groove narrow, shallow; groove deepens and widens posteriorly to form deep, broad pit. Strongly developed cartilaginous knobs converge, nearly meet posterior to pit; lateral knob rounded, medial knob more pointed with narrow ridge extending dorsally into pit; pit undercuts anterior walls of knobs. Groove between knobs narrow, deep, opens into lateral groove. Lateral groove very broadly inverted V-shaped, deepest anteriorly against posterior walls of knobs, becoming shallow along posterior margin of the locking-cartilages. Cartilage bordered by thin, muscular flange. Mantle locking-cartilage (Fig. 21C) strong, complement of the funnel component of the mantle locking apparatus; longitudinal ridge low, narrow anteriorly, expands to large, well defined, swollen bulb posteriorly; posterior wall very deeply undercut toward base on mantle. Thin, short ridge extends from bulb to lateral ridge. Lateral ridge narrow, open V-shape; anterior walls drop sharply into open grooves, posterior walls taper to mantle wall.

Head large, longer than broad, width about 18% of ML in males, 16% in females; length about 20% of ML in males, 17% in females. Three flap-like nuchal folds present; nuchal cartilage long, broad and rounded anteriorly, narrowed and tapered posteriorly, terminally embedded in muscle; central groove deep, lateral ridges distinct (Fig. 21D). Eye orbits subcircular, dorso-ventrally elongated; anterior sinus deep, conspicuous.

Arms long, attenuate; order III ≥II > IV > I; longer in males than in females, especially II and III; arms II and III robust; IV less robust; I least robust, very slender (Figs. 19A, B, 20A, B). Swimming keels very low, weak on distal three-quarters of I; higher, better developed, full length of II; best developed on III, broadest in proximal quarter; low, and next best developed, full length of IV. Protective membranes well developed, particularly ventral membranes; trabeculae long, very strong, arise from base of sucker stalks, form high points along membranes. Suckers of arms larger in males than in females, especially on II and III. Suckers small on I and IV; about 5-6 pairs enlarged on II and III of male (Fig. 22A, B).

Arm sucker dentition. Largest rings of arm I (Fig. 24A) with low, broad plate on proximal one-third, 3-5 low, truncate or slightly rounded teeth laterally, becoming narrower, longer distally; distal median tooth enlarged, elongate, more pointed; teeth, especially median tooth, more truncate, blunt on basal sucker pairs, more pointed on distal pairs. Largest rings of II (Fig. 24B) with proximally 1-2 low, broad, flat plate(s), 5-7 teeth laterally, broader, more truncate proximally, narrower, more rounded distally; distal median tooth enlarged, triangular, pointed. Smaller rings smooth proximally, 4-7 long, narrow teeth distally, graded in size to median tooth. Largest ring on III with 1-2 broad plate(s) on proximal one-third to one-fourth, 4-7 lateral teeth, lower, more truncate proximally, higher, more rounded distally, median tooth larger, triangular, pointed (Fig. 24C). Small rings with broad, low proximal plate, 1-2 lateral teeth, rounded, 3-5 long, pointed distal teeth, graded to longest median tooth. Largest rings of IV with low, broad plate proximally, 3-5 rounded to truncate, or bluntly pointed, lateral teeth; triangular, bluntly pointed or elongate rounded distal median tooth (Fig. 24D).

Left or right ventral arm hectocotylized (Fig. 21E), longer (average about 6%), and more robust, than non-hectocotylized arm IV; modified tip about 50% of arm length, suckers absent, stalks in rows separated but indistinct. Dorsal and ventral rows with 8-13 (number varies greatly, occasionally may reach 19) normal suckers proximally; dorsal row continues with 10-16 enlarged, rounded, suckerless knobs, 18-22 large, distinct, truncate or rounded lamellae and 6-9 or more small, indistinct lamellae to tip; ventral row continues with 7-10 low, suckerless knobs, 7-12 nipple-like papillae, and 20 or more small, indistinct, narrow lamellae to tip. Aboral keel broadly expanded along modified portion of hectocotylized tip.

Tentacles long, slender; stalks naked. Clubs expanded, long, about 38-45% of ML (Fig. 21A). Distinct carpal cluster lacking; carpal suckers small, biserial; carpal knobs lacking. Manal suckers tetraserial; suckers on lateral rows extremely small; medial sucker rows arise distal of 5-6 proximal carpal suckers; proximal 3-5 suckers small, gradually increasing in diameter; 12-13 medial manal suckers greatly enlarged; maximum size greater in males than in females; manus terminates abruptly. Dactylus distinct, long, slender; suckers in 7-8 transverse rows, extremely numerous, minute; tip with narrow suckerless flange. Swimming keel along entire tentacular stalk aborally, broad proximal of club, diminishing distally along dactylus, broadest in middle of dactylus. Lateral angles distinct on oral surface of stalk and continue as broad, heavily supported protective membranes along club, broadest in middle of manus, diminishing significantly along dactylus. Dual V-shaped trabeculae arise from common base with lateral suckers along manus.

Club sucker dentition. Sucker rings of carpal region with low, broad plate on proximal half, 1-2 lateral teeth, broad, rounded, 4-5 distal teeth, small, rounded or bluntly pointed. Proximal-most lateral manal suckers with proximal plate, 1-2 low, rounded lateral teeth, 4-6 long, narrow, sharply pointed distal teeth; disto-lateral suckers toothed around entire margin with 6-8 low, conical teeth proximally, 12-13 longer, narrower, sharply pointed lateral and distal teeth. Proximal median manal suckers (first 3-5) with low proximal plate, 1-3 low, rounded lateral teeth, 2-3 narrower, longer, bluntly pointed disto-lateral teeth, the bluntly pointed distal median tooth the longest; next distal 1-3 enlarged suckers with 16-18 broad, truncate to rounded teeth around entire margin or with 1-2 broad proximal plate(s), 6-8 broad rounded teeth on distal half, no elongate distal median tooth; distal 8-10 enlarged suckers with anodont sucker rings; or with sucker rings unevenly divided into broad plates (Fig. 24E). Proximal dactyl suckers with rings bearing 6-8 long, sharply pointed distal teeth, 8-12 short, conical proximal teeth; the teeth become more blunt and fewer in number on the mid-dactyl suckers; teeth on suckers at dactyl tip few and minute. All dactyl and lateral manal suckers equipped with scaly grasping rims.

Gladius (Fig. 25A) long, slender, bluntly pointed anteriorly; median ridge and heavy lateral rods extend length of rhachis (77% of PL), converge posteriorly, fuse near vane, continue to tip. Vane short

(23% of PL), narrow; forms short hollow conus; only extreme tip solid.

Connectives of buccal membrane attach to dorsal, dorsal, ventral, dorsal borders of arm I-IV respectively.

Mandibles. Upper mandible (Fig. 24F): rostrum strong, sharp , moderately long and curved, heavily pigmented; hood strong, long, curved, moderately pigmented; shallow notch and slight ridge separate rostrum and wing; wing with a large round tooth near notch, cutting edge of wing curved and serrated; lateral wall large, long, deep, pigmented anteriorly; crest curved. Lower mandible (Fig. 24G): rostrum moderately long, sharply pointed, heavily pigmented; cutting edge curved; rostral lamellae moderately long, wide, thin; gular lamellae large; crest strong, posterior corner long, bluntly pointed, curved; rostral width narrow.

Radula (Fig. 23B) with 7 transverse rows of teeth; rhachidian tooth with long, pointed central cusp, sharply pointed lateral cusps; first lateral tooth with blunt lateral cusp; second lateral tooth curved outward, bluntly pointed, no lateral cusp; third lateral tooth long, curved, scythe-shaped; marginal plates lacking.

Spermatophore (Fig. 25B, C) with sperm mass of about 65% of total length, cement body about 10% of total length. Cone at oral end of cement body flat, lens-shaped, connected aborally with short, broad neck; oral tube relatively wide.

Color (in isopropyl alcohol). Reddish-brown chromatophores cover entire body, less dense ventrally, thickly packed dorsally; deep purple-brown tint with blue stripe along dorsal mid-line of mantle and dorsad of eye orbits.

Morphometry: A total of 115 specimens (69 males, 46 females) was measured and the measurements of 17 body parts were plotted against the ML to determine its growth pattern. The range of the ML of the specimens measured was 170-256 mm for males and 201-285 mm for females.

The relation between the ML and the measurements of various parts is expressed by the simple linear formula, $Y=a+bX$. The values of the intercepts (a) of the regression line, the regression coefficients (b), the correlation coefficients (r), and the sample size (N) for each pair of Y and X are shown in Table 5. In the formula Y is the measurements of the body parts, X is the ML.

The regression coefficients (b) for each Y-X pair were analyzed for sexual dimorphism. With the exception of FW, all t values are smaller than the critical t value at the 95% confidence interval,

Table 5

Regression, Y=a+bX, of the measurements of selected body parts against the mantle length in *Illex argentinus*.

All measurements in mm
N: Number of specimens in sample
X: ML
Y: Measurements of the chosen body parts
r: Correlation coefficient of the regression
+: t-value greater than critical value at the 95% confidence interval
-: t-value less than critical value at the 90% confidence interval

Y	MALE				FEMALE					
	N	a	b	r	N	a	b	r	t	
VML	69	-12.893	1.005	0.947	46	-2.746	0.945	0.984	1.211	-
HL	69	9.450	0.147	0.639	46	5.954	0.143	0.752	0.137	-
HW	69	6.347	0.146	0.604	46	5.648	0.136	0.698	0.317	-
MW_1	69	13.069	0.133	0.577	45	0.696	0.182	0.779	1.540	-
MW_2	69	12.976	0.142	0.605	45	6.077	0.197	0.814	1.041	-
MW_3	69	7.678	0.099	0.484	45	6.970	0.112	0.548	0.386	-
FL	69	-4.029	0.440	0.891	46	-22.260	0.510	0.739	0.941	-
FW	69	15.275	0.503	0.842	46	-12.100	0.616	0.927	2.148	+
FBL	69	-5.413	0.403	0.935	46	4.860	0.357	0.951	1.848	-
A_1L	69	40.241	0.353	0.604	46	16.014	0.394	0.833	0.590	-
A_2L	69	56.200	0.419	0.529	46	21.828	0.481	0.810	0.635	-
A_3L	69	71.787	0.350	0.431	46	18.194	0.508	0.756	1.053	-
A_4L	69	59.418	0.317	0.442	46	17.453	0.445	0.813	1.388	-
S_1	69	0.414	0.011	0.564	46	-0.164	0.013	0.775	0.773	-
S_2	69	2.329	0.015	0.437	46	-0.347	0.020	0.832	1.124	-
S_3	69	1.213	0.019	0.571	46	-0.340	0.020	0.827	0.257	-
S_4	69	0.596	0.010	0.553	46	-0.640	0.014	0.849	1.732	-

indicating that sexual dimorphism does not exist in the regression coefficients for most of the Y-X pairs.

Holotype: Museo de La Plate, Argentina (45.001).

Type Locality: 39°S 55°W.

Distribution: Continental shelf of the South Atlantic Ocean along the coast of the Republic of Argentina between 35° and 47°50'S 52° and 65°22'W.

Remarks: The description of this species by Castellanos (1960) is brief and incomplete, and it is for this reason that the species is redescribed here.

Castellanos presented several measurements of both the holotype and the allotype (1960, p. 57), however, it is evident that her definitions of several measurements are different from those used as standards by most teuthologists. Therefore, as I learned upon examination of the specimens in Museo de La Plata in 1969, her morphometric data on the holotype is not adequate in terms of currently accepted cephalopod systematics. Therefore I made measurements and computed indices for the holotype and these are presented in Table 6. The definitions as used by Castellanos are to be found in her 1964 paper (p. 11). The allotype (male) Museo de La Plata, No. 45.002 is

Table 6

[illegible]asurements (in mm), indices and count of the holotype of *Illex argentinus*.

	Measurement (mm)	Index (%)		Measurement (mm)	Index (%)
ML	272				
VML	260	95.6	HL	46.6	17.1
HW	48.8	17.9	MW_1	55	20.2
MW_2	62	22.8	MW_3	29	10.7
FL	123	45.2	FW	168	61.8
FBL	100	36.8	A_1L	108	39.7
A_2L	135	48.5	A_3L	136	47.1
A_4L	120	44.1	CL	98.7	36.3
S_1	3.8	1.4	S_2	5.5	2.0
S_3	5.5	2.0	S_4	3.4	1.2
S_T	5.7	2.1	GL	86.5	31.8
FA	48°		#G	62	

so badly distorted that it proved to be impossible to obtain the necessary measurements, especially ML, to a reasonably accurate degree. Both of the clubs are also dried out and unmanageable.

The growth pattern, as seen from an analysis of various body parts and the mantle length, is shown to exhibit a simple linear relationship. Although the correlation coefficients r are greater than the critical r values at the 95% confidence interval, the values in many cases are relatively low. This low correlation may be attributed to the state of preservation of the specimens or to the possibility that the size range studied is relatively too narrow.

Although the results of t-tests on the sexual differences on the regression coefficients in most cases are statistically insignificant, the intercepts, in most cases and especially in the arm lengths and sucker diameters, are different. Hence, sexual dimorphism does exist in this species. Most of the materials used in this study were purchased in a fish market in La Plata and Mar del Plata, both in Argentina, in April, 1969. I was unable to obtain any information about the catch locality other than the general area, Mar del Plata. Due to the lack of specific information, the exact distributional range and their relation to environmental parameters could not be determined. The range of distribution will undoubtedly be expanded when more

FIGURE 19. Photographs of *Illex argentinus* (Castellanos, 1960). Dorsal view. A. Male. B. Female. Scale: 2 cm.

Specimens from Mar del Plata, Argentina.


A
B

FIGURE 20. Photographs of *Illex argentinus* (Castellanos, 1960). Ventral view. A. Male. B. Female. Scale: 2 cm.

Specimens from Mar del Plata, Argentina.

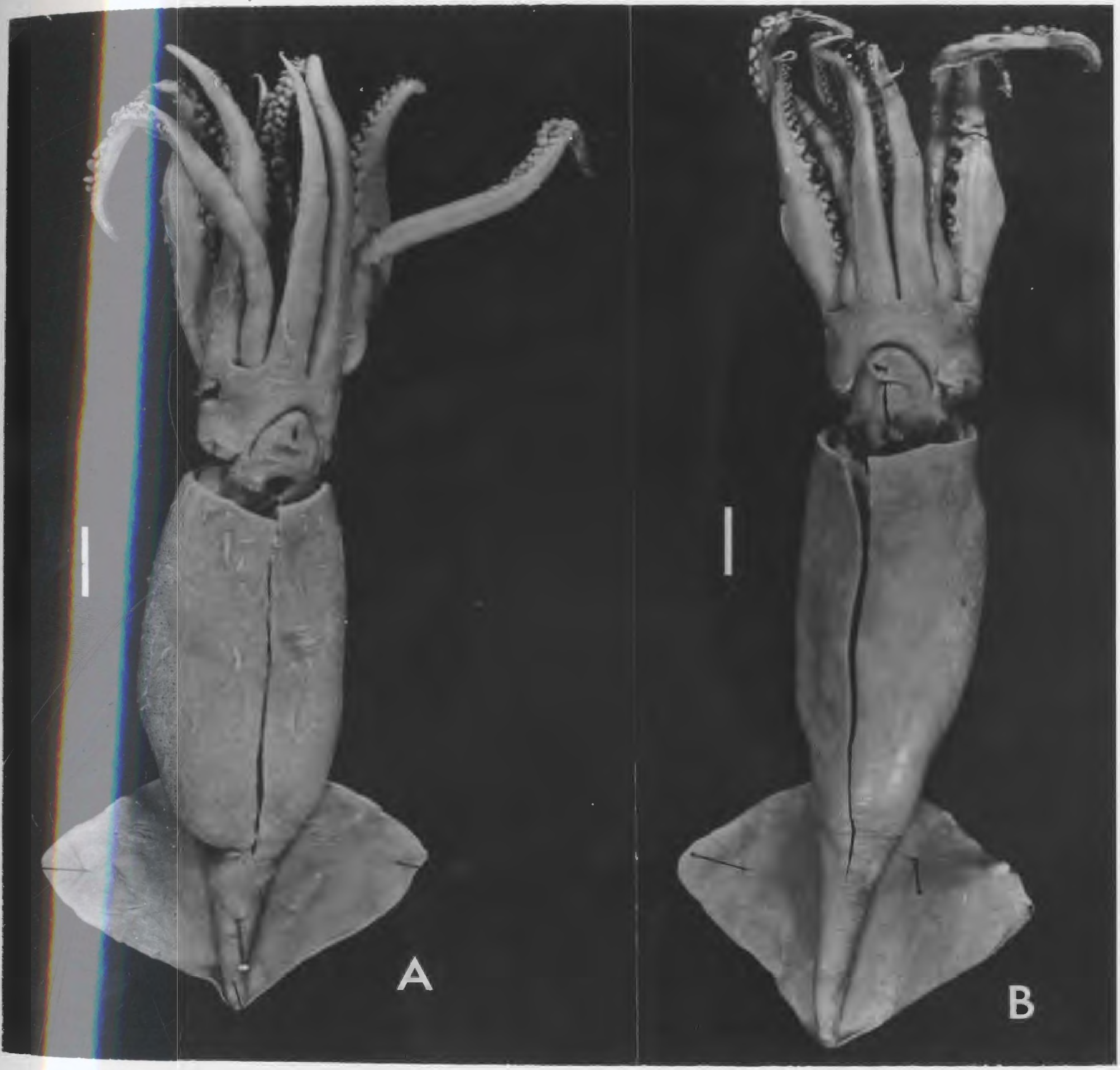

A
B

FIGURE. 21. Photographs of tentacular, brachial and cartilagenous portions of *Illex argentinus*.

A. Tentacular club.
B. Funnel component of mantle-locking apparatus
C. Mantle component of mantle-locking apparatus
D. Nuchal cartilage
E. Hectocotylized arm (R IV)

In B through D, anterior end is uppermost.

Scale: 1 cm.

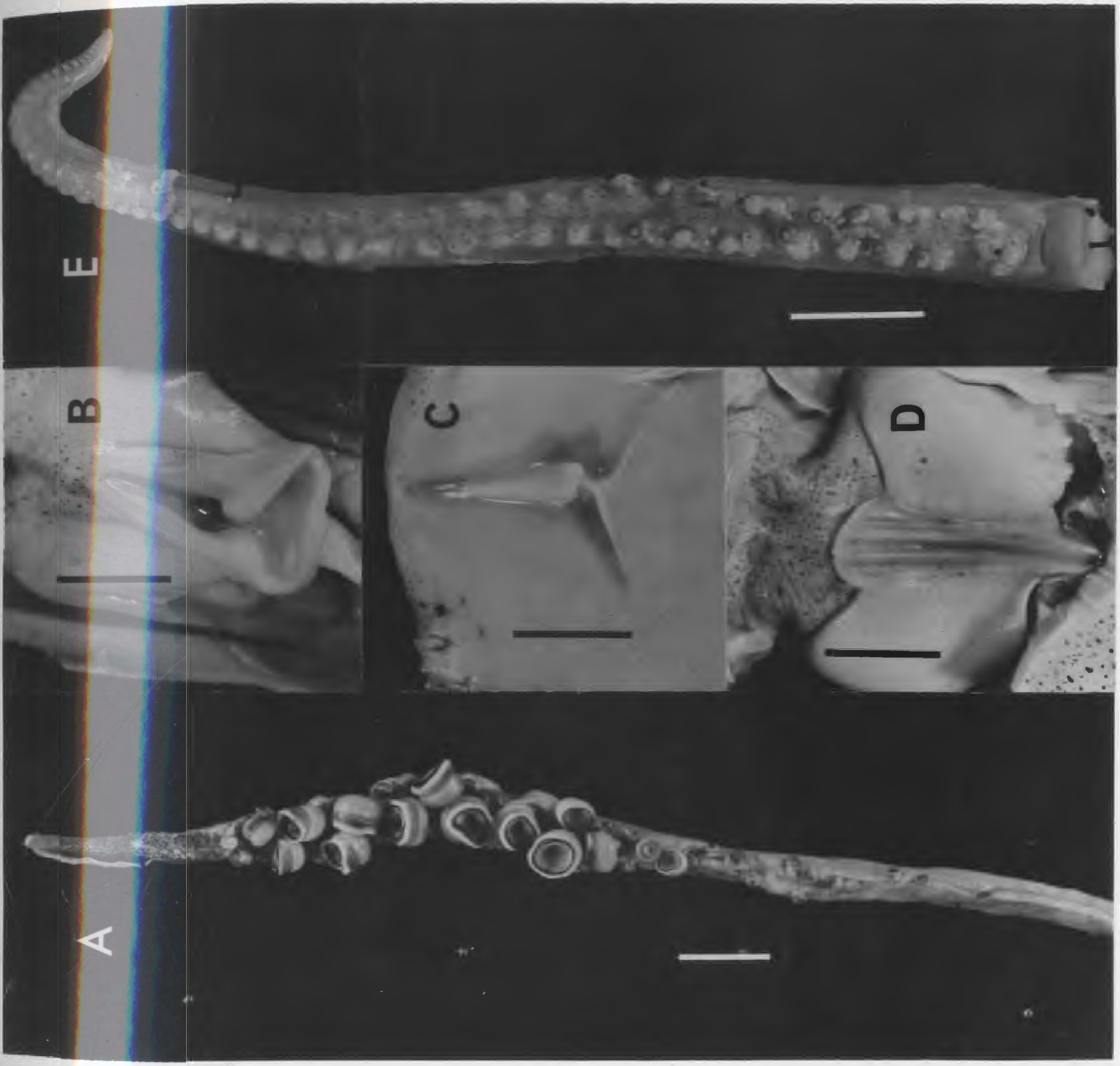

A
B
C
D
E

FIGURE 22. A. Photograph of dorso-lateral (II) arm of male specimen of *Illex argentinus*. Scale: 1 cm.

B. Photograph of ventro-lateral (III) arm of male specimen of *Illex argentinus*. Scale: 1 cm.

C. Photograph of mature female specimen of *Illex argentinus*, showing vastly enlarged nidamental glands. Scale: 2 cm.


A
B
C

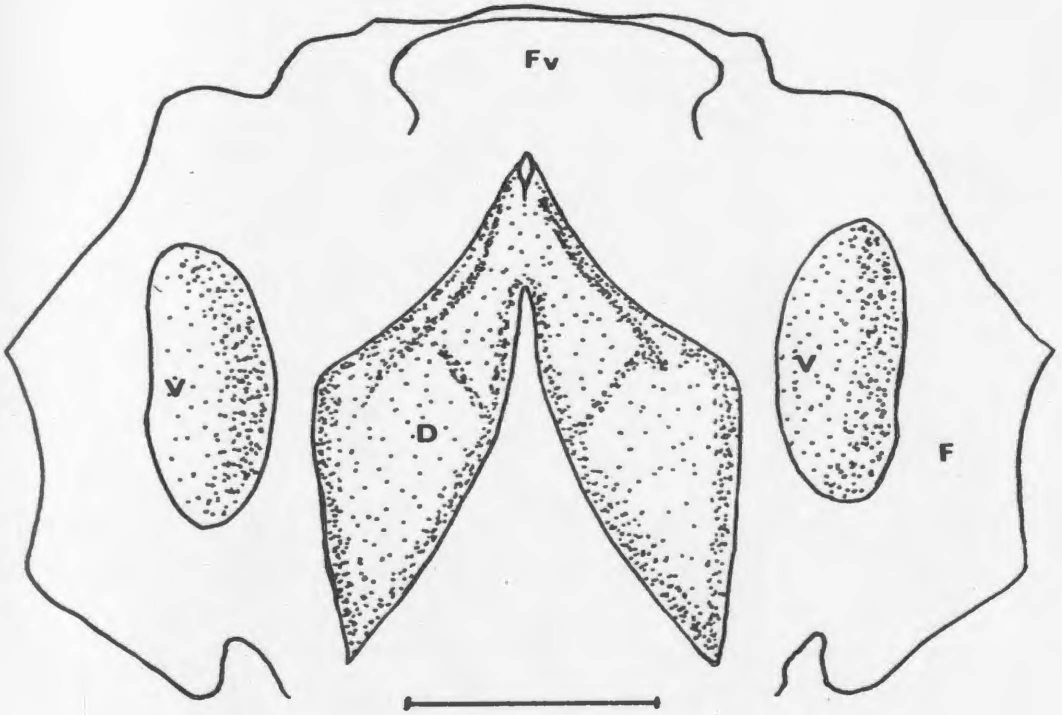
FIGURE 23. A. Drawing of funnel organs of *Illex argentinus*.

D = dorsal funnel organ
V = ventral funnel organ
F = wall of funnel
F_V = funnel valve

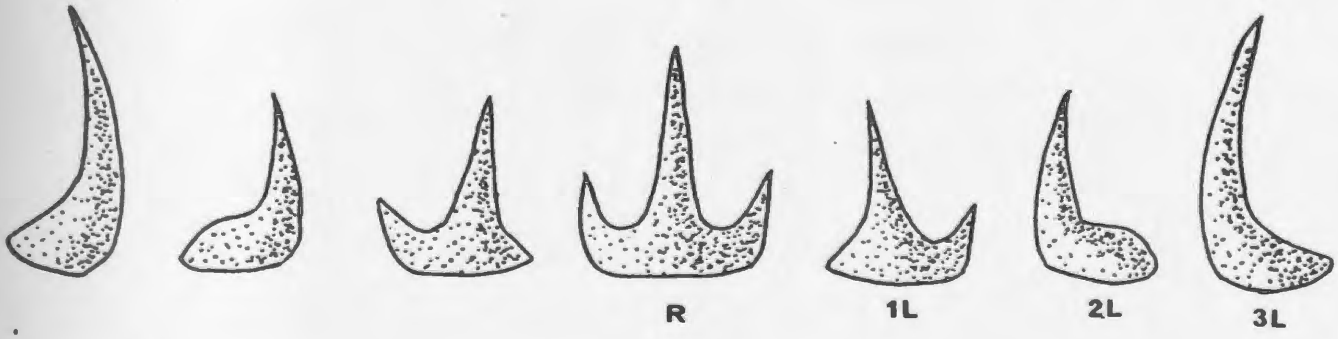
Scale: 1 cm.

B. Drawing of a single row of teeth from the mid-portion of the radular ribbon of *Illex argentinus*.

R = rhachidian tooth
1L = first lateral tooth
2L = second lateral tooth
3L = third lateral tooth



A



B

FIGURE 24. A through E Drawings of chitinous rings from specific suckers from sessile arms and tentacular manus of *Illex argentinus*.

A. Ring from largest sucker from dorsal arm (I).

B. Ring from largest sucker from dorsolateral arm (II).

C. Ring from largest sucker from ventrolateral arm (III).

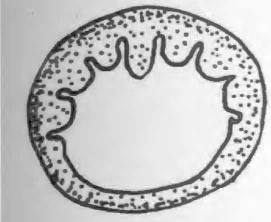
D. Ring from largest sucker from ventral arm (IV).

E. Ring from largest sucker from manal portion of tentacular club.

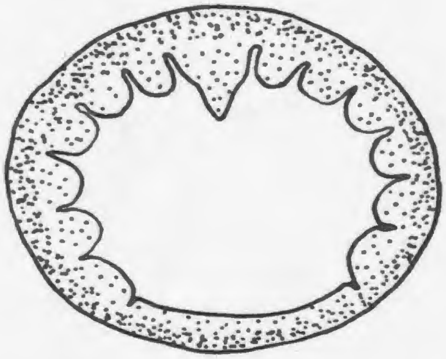
F-G. Drawings of mandible of *Illex argentinus*.

F. Upper mandible

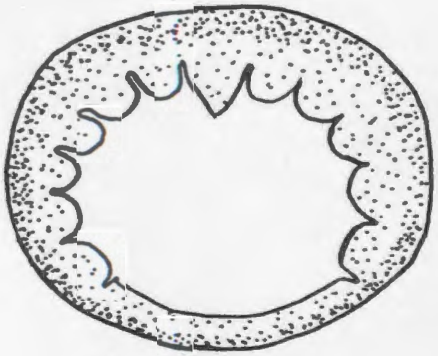
G. Lower mandible



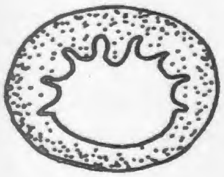
A



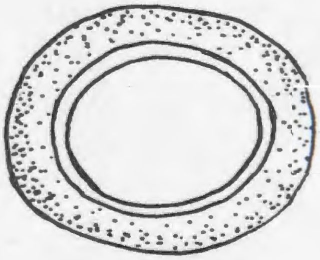
B



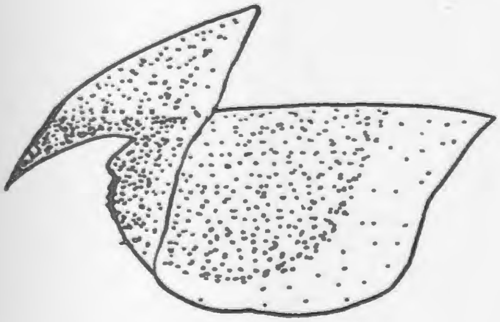
C



D



E



F

G

FIGURE 25. A. Drawing of entire gladius of *Illex argentinus*. Scale: 1 cm.

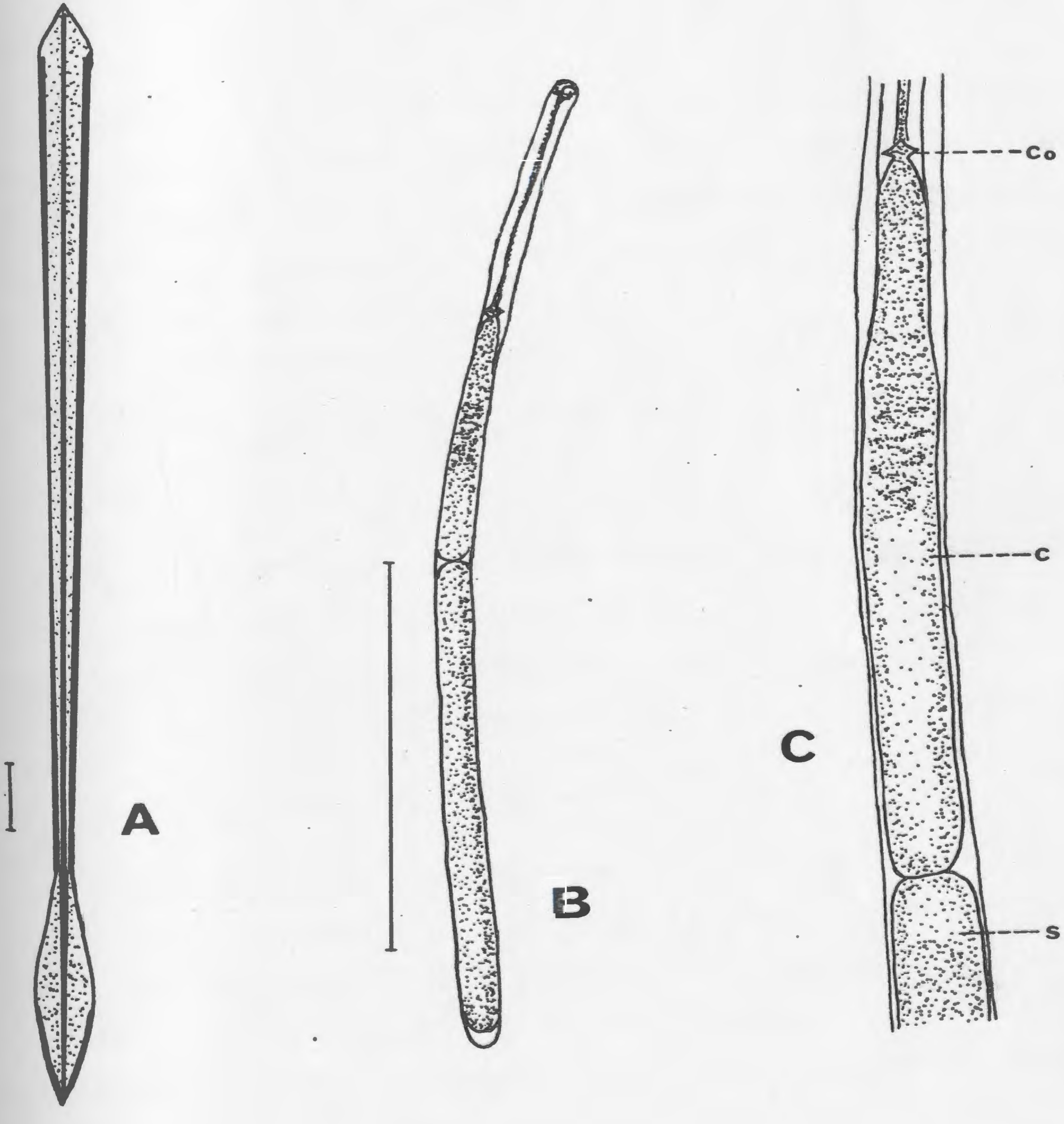
B. Drawing of entire spermatophore of *Illex argentinus*. Scale: 1 cm.

C. Drawing of portion of spermatophore of *Illex argentinus*, showing the cement body and adjacent structures.

C = cement body

Co = cone

S = sperm mass


A
B
C
Co
C
S

adequate collections with the necessary associated data, such as those from the Walther Herwig collections from the South Atlantic Ocean, are studied.

Castellanos & Menni (1969, p. 80) reported the distribution of this species to be from 35° to 47°S and 52° to 61°W and from depths of from 200 to 800 meters. The small number of specimens from the WH collections that I have examined extend its range to about 48°S and 65°W and from depths as shallow as 90 meters.

Illex oxygonius Roper, Lu and Mangold, 1969

Illex oxygonius Roper, Lu & Mangold, 1969, p. 299.

Diagnosis: Fin angle acute (25°-35°); fin width equal to fin length; mantle narrow, drawn out posteriorly; dorsal mantle lobe conspicuous, pointed in males; hectocotylized portion of arm IV long, 3 papillae on dorsal row; cone at oral end of cement body of spermatophore funnel-shaped.

List of Materials: (See overleaf)

Description: Mantle long, slender, broadest anteriorly, drawn out posteriorly into long attenuated tip (Fig. 26A). Mantle width decreases markedly posteriorly in males, less so in females especially at maturity. Ventro-lateral lobes on mantle opening inconspicuous, rounded; dorsal lobe inconspicuous, pointed (Fig. 26B). Thin, membranous flange encircles mantle opening. Mantle wall thin. Fins narrow, drawn

List of Materials *(Illex oxygonius)*

Sta. No.	Date	Time	Position	Temperature (°C) Surf.	Temperature (°C) Bottom	Salinity (⁰/oo) Surf.	Salinity (⁰/oo) Bottom	Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
ATC 414	25 VIII 1968	1458	38°30'N 73°12'W	25.7	9.54			236.1	FRB			1	176	41.5'OT
ATC 416	25 VIII 1968	1650	38°28'45"N 73°10'15"W	25.6	9.24			272.7	FRB			2	190	41.5'OT
ATC 418	25 VIII 1968	1855	38°29'45"N 73°09'15"W	25.6	6.27			382.5	FRB	1	165	2	176-194	41.5'OT
ATC 433	27 VIII 1968	1240	37°25'N 74°30'30"W	25.5	12.39			175.7	FRB	1	159			41.5'OT
ATC 438	27 VIII 1968	1925	37°23'45"N 74°28'15"W					289.1	FRB	2	168-180			41.5'OT
ATC 447	28 VIII 1968	1140	36°30'30"N 74°43'30"W	25.7	12.29			190.3	FRB			3	185-198	41.5'OT
ATC 449	28 VIII 1968	1340	36°29'N 74°42'30"W	25.7	10.10			239.7	FRB	3	154-160	1	202	41.5'OT
ATC 459	30 VIII 1968	1430	34°26'N 75°43'W	27.1	12.29			225.1	FRB	1	124			41.5'OT
ATC 463	30 VIII 1968	1925	34°25'N 75°39'45"W	26.9	9.81			464.8	FRB	1	160			41.5'OT
ATC 466	31 VIII 1968	1125	36°05'N 74°47'W	24.8	11.43			237.9	FRB	6	148-168	1	169	41.5'OT
ATC 467	31 VIII 1968	1315	36°04'45"N 74°46'30"W	24.8	9.48			261.7	FRB	2	152-163	1	168	41.5'OT
ATC 471	1 IX 1968	1315	38°58'N 72°48'30"W	22.8	9.16			316.6	FRB	1	180			41.5'OT
ATC 473	1 IX 1968	1537	39°00'N 72°48'30"W	22.1	10.66			250.7	FRB	2	180-182			41.5'OT
FH 7281	14 II 1902		24°13'N 81°58'W					555	USNM 577000	1	207			
FH 7296	26 II 1902		24°22'N 81°48'W					222	USNM 577002	1	205			
G-Line 2	8 X 1892		38°52'N 72°58'W					155	USNM 39409	1	228			
VIMS T165	25 VIII 1967	0948	38°30'N 74°53'W		6		33	56	USNM			2	185-196	27'OT
VIMS T166	25 VIII 1967	1300	38°34'N 73°33'W		9		33	72	USNM 577604	1	164			27'OT
VIMS T167	25 VIII 1967	1530	38°27'N 73°23'W		13		34	187	USNM 57760	1	178	3	174-196	27'OT
VIMS T167	25 VIII 1967	1530	38°27'N 73°23'W		13		34	187	USNM 577001	1	160			27'OT
VIMS T167	25 VIII 1967	1530	38°27'N 73°23'W		13		34	187	USNM 577003	1	176			27'OT
VIMS T167	25 VIII 1967	1530	38°27'N 73°23'W		13		34	187	USNM 577004			1	210	27'OT
VIMS T177	27 VIII 1967	1236	37°22'N 74°47'W		7		32	49	USNM 577603			1	177	27'OT
VIMS T180	30 VIII 1967	0536	37°07'N 74°45'W		8		32	70	USNM	1	159			27'OT
VIMS T183	30 VIII 1967	1442	36°42'N 74°45'W		11		34	70	USNM			1	138	27'OT
VIMS T188	31 VIII 1967	1206	36°18'N 74°52'W		7		33	67	USNM 577602	1	172			27'OT
VIMS T014	20 I 1968	0836	37°57'N 74°06'W		11		35	119	USNM			1	163	27'OT
O 1011	14 IV 1954		24°28'N 83°25'W					364	USNM 575146			1	136	27'OT
O 6801	20 VII 1967		29°39'30"N 80°08'30"W					383	USNM	1	135	1	181	

(*Illex oxygonius*) continued

Sta. No.	Date	Time	Position	Temperature (°C)		Salinity ($^0/oo$)		Depth (m)	Institute Number	No. M.	ML (mm)	No. F.	ML (mm)	Gear
				Surf.	Bottom	Surf.	Bottom							
O II 11186	27 VIII 1970		27 49'N 85 12'W	28.8				450	USNM	1	165			150'Balloon T
P 245	13 V 1965	1510	4 32'N 5 07'E					64-119	IMSUM			1	122	40'OT

All ATC sets are from Cruise 150
OT = Otter Trawl
All times are local times

out to acute point posteriorly; width (48-50% of ML) about equal to length (44% of ML); ratio of length to width 1:1.01 to 1:1.25; slightly concave posterior borders form acute angle of 25-35° (average about 30° in males, 32° in females); lateral borders rounded; anterior lobes well developed (Fig. 26B).

Funnel well developed, set in deep funnel groove; lateral adductor muscles conspicuous, strong, rod-like (Fig. 26A); anterior adductor muscles thin, broad, sheetlike. Dorsal funnel organ (Fig. 28A) large; posterior limbs fleshy, thickened, broad anteriorly, tapered, bluntly pointed posteriorly; lateral shoulders conspicuous; antero-lateral borders concave; apical papilla spearhead-shaped. Sharp, thin ridges extend from anterior mid-portion of limbs nearly to apex. Ventral pads oblong; lateral borders strongly curved; medial borders nearly straight. Funnel valve broad.

Funnel locking-cartilage large, strong, inverted T-shaped (Fig. 27B). Medial, longitudinal groove narrow, relatively shallow; groove deepens and widens posteriorly to form deep, broad pit. Strongly developed cartilaginous knobs converge, nearly meet posterior to deep pit; lateral knob rounded, medial knob more pointed with narrow ridge extending dorsally into pit; pit undercuts anterior walls of knobs. Groove between knobs narrow, relatively deep, opens into lateral groove; lateral groove very broadly inverted V-shape, deepest anteriorly against posterior walls of knobs, shallows along posterior margin of locking-cartilage. Entire cartilage bordered by thin, muscular flange. Mantle locking-cartilage (Fig. 27C) strong, complement of funnel lock. Longitudinal ridge low, narrow anteriorly, expands to large, sharply defined, swollen bulb posteriorly; posterior wall very deeply undercut toward base on mantle. Thin ridge extends from bulb to lateral ridge. Lateral ridge narrow, open V-shaped; anterior walls drop sharply into open grooves, posterior walls taper to mantle wall.

Head large, broad, width about 20% of ML in males, 17% in females; length about 17% in males, 15% in females. Three flap-like nuchal folds present; nuchal cartilage long, broad and rounded anteriorly, narrow, tapered posteriorly; central groove deep, lateral ridges distinct (Fig. 27D). Eye openings subcircular, dorso-ventrally elongate; anterior sinus deep, conspicuous.

Arms long, attenuate; order II $\geq$ III > IV > I; longer in males than in females, especially II and III; arms II, III robust; IV less robust; I least robust, very slender (Fig. 26A, B). Swimming keels very low, weak on distal half of I; higher, better developed, full length of II; best developed on III, broadest in proximal quarter; low, second best developed, full length of IV. Protective membranes well developed, particularly ventral membranes; trabeculae long, very strong, arise from base of sucker stalks, form high points along membranes. Suckers of arms larger in males than in females, especially on II and III. Suckers small on I and IV; about 6 pairs enlarged on II and III of males (Fig. 27E).

Arm sucker dentition: Rings on arm I (Fig. 29A) with low, broad plate on proximal one-third, 3-5 low, truncate or slightly rounded teeth laterally, becoming narrower, longer distally; distal median tooth enlarged; elongate, more pointed; teeth, especially median tooth, more truncate, blunt on basal sucker pairs, more pointed on distal pairs. Largest rings of II (Fig. 29B) with 2 low, broad, flat teeth proximally, 5-7 teeth laterally, broader, more truncate proximally, narrower, more rounded distally; distal median tooth greatly enlarged, triangular, pointed. Smaller rings with fewer teeth, smooth proximally, 5-6 long, narrow teeth distally, graded to median tooth. Ring dentition of III about as II; broad, low single or bifurcate plate proximally, 5-7 lateral teeth graded distally, median tooth very enlarged, elongate, pointed (Fig. 29C). Smaller rings with broad, low plates proximally, 1-2 rounded teeth laterally, 2-3 long pointed teeth laterally, graded to longest median tooth. Largest rings of IV (Fig. 29D) with broad, low proximal plate, 3-5 rounded to truncate lateral teeth (may be longer, narrower distally), elongate bluntly pointed or rounded distal median tooth.

Left or right ventral arm hectocotylized (Fig. 28B), longer (average about 6%), more robust than non-hectocotylized arm IV; modified tip 29-33% (average 31%) of arm length; distal suckers reduced in size, rows separated. Suckers of dorsal row give way to 3 conical papillae; remnant of protective membrane disappears distal to third papilla; next distal 1-2 protuberances become flattened, followed by series of transversely broad, thin, truncate flaps; flaps gradually reduced in size distally, finally giving way at arm tip to series of minute papillae that apparently are precursors to flaps (28 recognizable flaps on holotype - exclusive of proximal 3 papillae and 9 distal precursors). Suckers of ventral row give way to conical, nipple-like papillae that extend, gradually reduced in size, to tip of arm (42 papillae in holotype). Low, weak, zigzag ridge between papillae and flaps. Aboral keel broadly expanded along modified portion of hectocotylus tip. Trabeculae not modified as fringed lobes.

Tentacles robust, relatively short; stalks naked. Clubs expanded, long, about 28-30% of ML (Fig. 27A). Distinct carpal cluster absent; carpal suckers small, biserial; carpal knobs lacking. Manal suckers tetraserial; suckers on lateral rows small; medial sucker rows arise distal to the proximal 5 carpal suckers; proximal 3-5 medial suckers small, gradually increasing in diameter; about 15 medial suckers on manus greatly enlarged; maximum size greater in males than in females; manus terminates abruptly. Dactylus distinct, slender; suckers in 8 or 9 rows, extremely numerous, minute; suckers near tip slightly enlarged; tip with narrow, suckerless flange. Swimming keel along entire tentacular stalk aborally, broadest proximal to club, diminishes along carpal and manal region, expands to broad keel along dactylus. Distinct lateral angles orally on stalk continue as broad heavily supported protective membranes along club, diminish significantly along dactylus. Dual V-shaped trabeculae arise from enlarged common base with lateral suckers along manus.

Club sucker dentition: Carpal sucker rings with low, broad plate on proximal half, 4-6 small teeth on distal half; lateral teeth broad, rounded; distal teeth narrow, bluntly pointed. Proximal-most lateral manal suckers with proximal plate, 1-2 low, rounded lateral teeth, 4-7 long, narrow pointed distal teeth; distal lateral suckers toothed around entire margin with 5-8 low, rounded proximal teeth, 12-14 longer, sharply pointed lateral and distal teeth, occasional small pointed secondary tooth between primary teeth. Proximal medial manal suckers (first 5-7) with low proximal plate, 1-2 low, rounded, lateral teeth, 1-2 slightly narrower disto-lateral teeth, 1 bluntly pointed median tooth; next distal 4-5 enlarged sucker rings with 7-13 teeth around margin, low, flat proximally, narrow, rounded distally, no enlarged or pointed medial tooth (Fig. 29E). Dentition lacking, but rings entire on 7-8 distal enlarged manal suckers. Proximal dactyl sucker rings with 4-6 long pointed distal teeth; teeth become more blunt, rounded on rings of middle dactylus suckers, teeth on suckers at distal tip few, minute.

Gladius (Fig. 30A) long, slender, bluntly pointed anteriorly; median ridge and heavy lateral rods extend length of rhachis, converge posteriorly, fuse near vane, continue to tip. Vane short, narrow;

edges fold ventrally, fuse to form short, hollow conus; only extreme tip solid.

Connectives of buccal membrane attach to dorsal, dorsal, ventral, dorsal borders of arms I-IV respectively.

Mandibles (Fig. 29G, H). Upper Mandible: rostrum strong, sharp, long, heavily pigmented; dorsal hood very weak, thin, short, lightly pigmented; notch and slight ridge separate rostrum and rostral lamella; cutting edge of rostral lamella straight or slightly curved, smooth; palatine lamella large, long, deep, pigmented anteriorly, dorsal crest only slightly curved. Lower mandible: rostrum relatively long, pointed, heavily pigmented, inner edge curved; rostral lamellae narrow, short, wing lobate, thin; gular lamellae large, crest strong, posterior corner long, pointed, curved; rostral width broad.

Radula (Fig. 29F) with 7 transverse rows of teeth; rhachidian with long central tooth, blunt lateral cusps; first lateral tooth with blunt lateral cusp; second lateral tooth curved, no lateral cusp; third lateral tooth long, curved, scythe-shaped; marginal plates lacking.

Spermatophore (Fig. 30B) with sperm mass of about 60% of total length, cement body about 15% of total length. Cone at oral end of cement body funnel-shaped, connected aborally by short neck.

Color (in isopropyl alcohol): reddish-brown chromatophores over entire body, more widely spaced ventrally, thickly packed dorsally;

deep purple-red stripe along dorsal mid-line of mantle.

Morphometry: A total of 21 specimens (10 males and 11 females) were measured in a study to ascertain their growth pattern. The relation between the size of 19 body parts and the ML is expressed by the simple linear formula Y=a+bX, where Y is the measurement of the body parts in mm and X is the ML in mm. Table 7 shows the value of a and b as well as the sample size (N) and the correlation coefficient (r) for both sexes. With the exception of HL, MW_2, MW_3 and A_4 in males, all r values are greater than the critical r value at the 95% confidence interval. The r value for males in the case of A_4 is less than the critical value (95% level), but greater than the value at the 90% level.

Regression lines were analyzed for sexual dimorphism by testing the difference between each pair of regression coefficients. All t values are smaller than the critical t value at the corresponding degree of freedom, indicating that statistically no difference exists between the males and the females on the slope of the regression lines.

Holotype: United States National Museum (577000).

Holotype Locality: 24°13'N 81°58'W in Florida Current, about 22 nautical miles SSW of Key West, Florida; Fish Hawk station 7281, 14 February 1902, 555 m.

Distribution: Western Atlantic: off mid-Atlantic States, Florida Current, Gulf of Mexico. Eastern Atlantic: Gulf of Guinea (Fig. 10).

Table 7

Regression, Y=a+bX, of the measurements of selected body parts against the mantle length in *Illex oxygonius*.

All measurements in mm

N: Number of specimens in sample

X: ML

Y: Measurements of the chosen body parts

r: Correlation coefficient of the regression

-: t-value less than critical value at the 90% confidence interval

			MALE				FEMALE			
Y	N	a	b	r	N	a	b	r	t	
VML	7	-26.871	1.088	0.991	11	-15.113	1.050	0.984	0.399	-
HL	10	17.543	0.078	0.480*	11	1.446	0.154	0.723		
HW	10	-14.370	0.284	0.932	11	-0.680	0.179	0.865	1.967	-
MW_1	9	-0.962	0.193	0.949	11	10.170	0.117	0.879	0.685	-
MW_2	9	7.982	0.117	0.575*	11	8.777	0.127	0.762		
MW_3	9	9.844	0.052	0.286*	11	-2.995	0.126	0.740		
FL	10	0.609	0.446	0.959	11	-3.034	0.467	0.963	0.318	-
FW	10	28.256	0.349	0.672	11	0.676	0.481	0.665	0.546	-
FBL	10	-2.965	0.419	0.927	11	-1.750	0.410	0.966	0.132	-
A_1L	10	11.668	0.370	0.632	11	2.630	0.328	0.760	0.236	-
A_2L	10	11.403	0.481	0.715	11	10.929	0.366	0.735	0.586	-
A_3L	10	17.016	0.447	0.676	11	6.439	0.400	0.743	0.230	-
A_4L	10	28.387	0.312	0.550*	11	7.669	0.336	0.708	0.122	-
S_1	10	-0.136	0.016	0.801	11	-0.001	0.012	0.886	0.907	-
S_2	10	0.091	0.024	0.918	11	0.012	0.018	0.890	1.139	-
S_3	10	0.337	0.022	0.916	11	0.692	0.014	0.821	1.586	-
S_4	10	0.117	0.013	0.816	11	0.274	0.010	0.831	0.827	-
S_T	10	-1.666	0.027	0.744	10	1.086	0.010	0.657	1.905	-
GL	9	-3.295	0.314	0.830	9	-7.737	0.356	0.899	0.404	-

*r insignificant, except in A_4L which is significant at the 90% level.

Remarks: Although this species has only recently been described, it is included here, with minor changes, for the sake of completeness.

The number of specimens available for study was small. The ATC collections did not become available until most of the work reported herein was completed and morphometric data from these collections were not used in the computations.

As can be expected, due to the small number and the narrow size range (135-228 mm ML for males, 122-210 mm ML for females) of available specimens, correlation coefficients are generally low. In several cases (HL, MW_2, MW_3 and A_4 in males) it is smaller than the critical value at the 95% confidence interval. The r value in the case of A_4 in males is greater than the critical value at the 90% confidence interval, and is here considered to be significant. The r values for HL, MW_2 and MW_3 in males are also less than the critical value at the 90% confidence interval. Therefore, the linear relation between these measurements and the ML does not exist. These specific characters are omitted from computations to determine sexual dimorphism in the species and, subsequently, the statistical comparison of the four species of the genus.

This species is by no means rare. Past records of *I. illecebrosus* from Floridan waters and from Chesapeake Bay possibly are a mixture of

I. coindetii and *I. oxygonius*. At the present time, it is reported from the coast of the Mid-Atlantic States, Florida Current, the Gulf of Mexico, and the Gulf of Guinea. The single specimen from the Gulf of Guinea (P 245) constitutes the first record of this species from the eastern Atlantic. Although no specimen is yet known from the Caribbean Sea, it is likely that this species also occurs there.

FIGURE 26. Reproduction of original plate of the holotype (male) of *Illex oxygonius* Roper, Lu and Mangold, 1969.

A. Ventral view. B. Dorsal view.

(After Roper, Lu & Mangold, 1969; plate by J. Schroeder.)

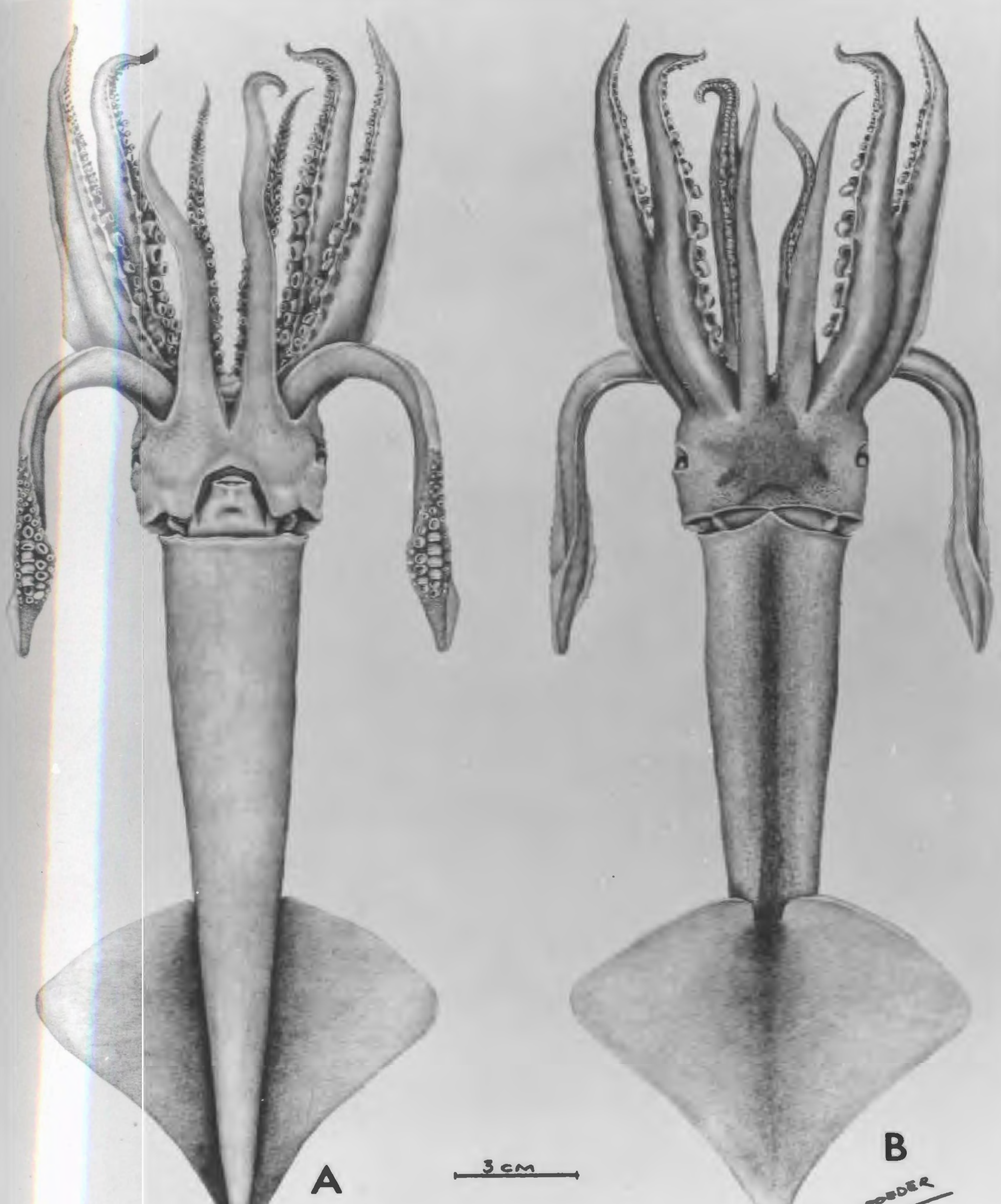

A
3 cm
B
J. SCHROEDER

FIGURE 27. Reproduction of plate showing drawings of tentacular, brachial and cartilagenous structures of *Illex oxygonius* (after Roper, Lu & Mangold, 1969; plate by J. Schroeder).

A. Tentacular club
B. Funnel component of mantle-locking apparatus
C. Mantle component of mantle-locking apparatus
D. Nuchal cartilage
E. Ventro-lateral (III) arm

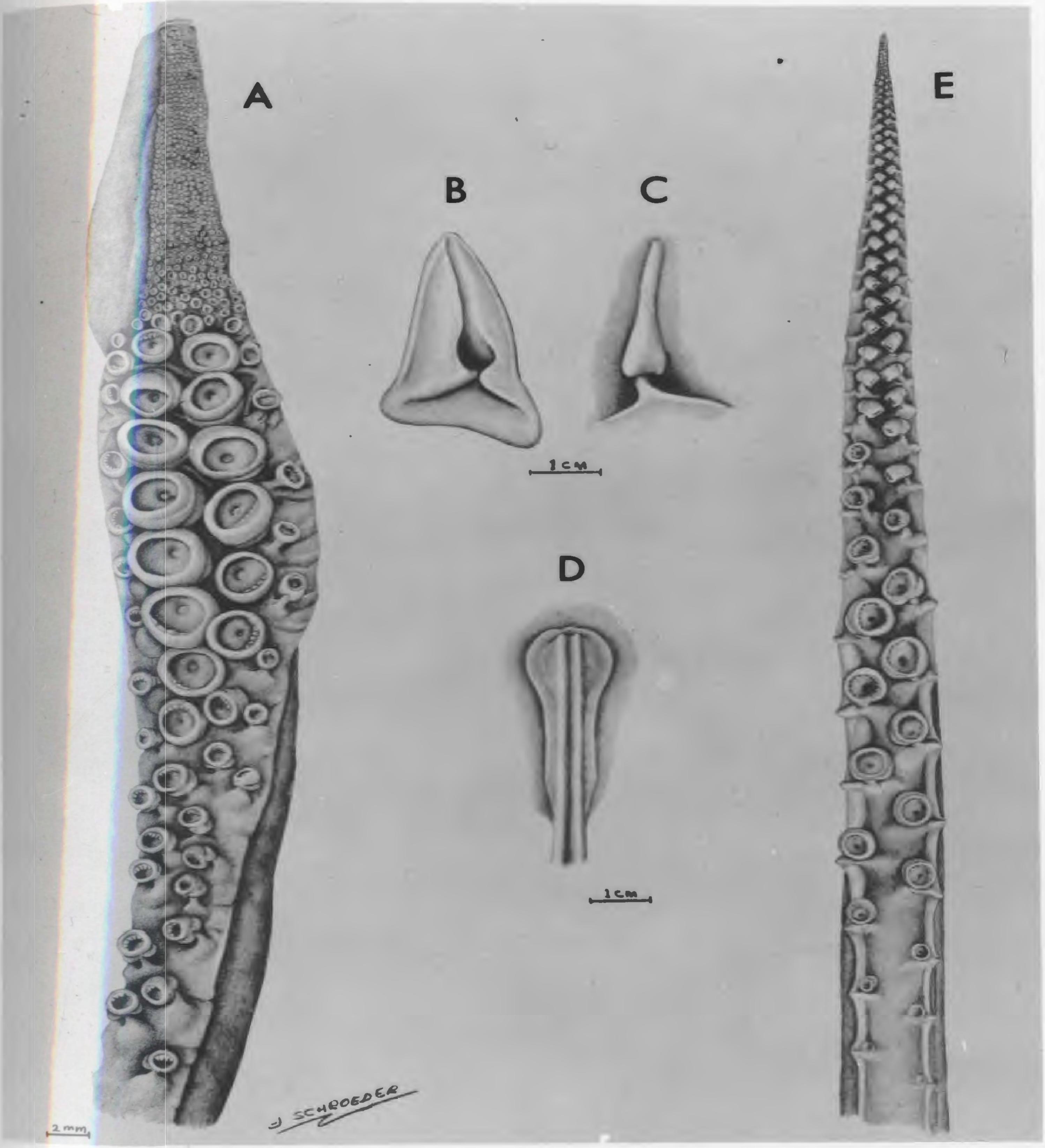
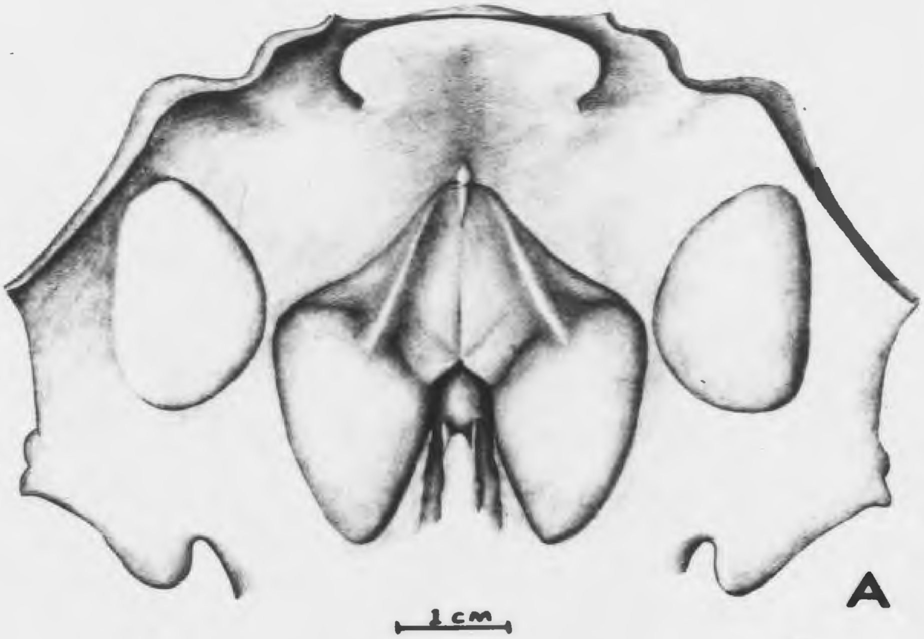
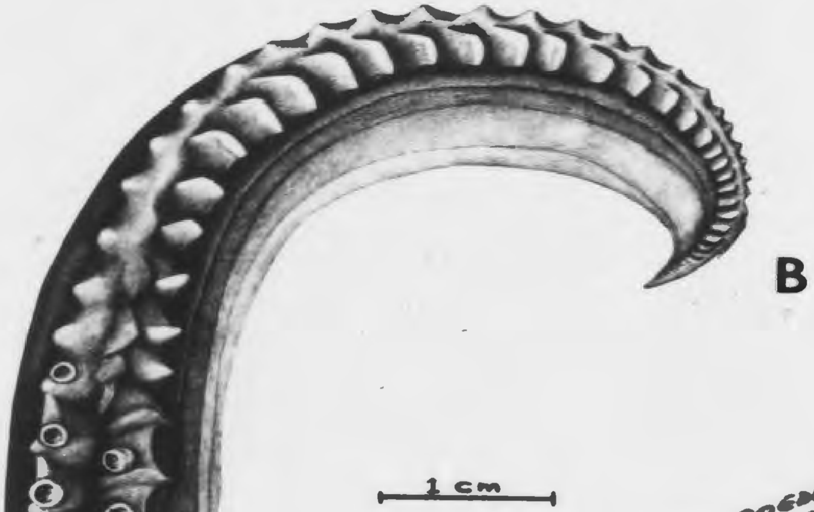

A
B
C
E
D
1 cm
1 cm
2 mm
J SCHROEDER

FIGURE 28. Reproduction of plate showing drawings of funnel organs and hectocotylus of neotype of *Illex oxygonius*. (After Roper, Lu & Mangold, 1969; plate by J. Schroeder)

A. Dissected funnel, showing dorsal and ventral funnel organs. (See key to Figures 5, 16 and 23)

B. Hectocotylus





J. SCHROEDER

FIGURE 29. Reproduction of original plate showing, in A through E, chitinous rings from specific suckers from sessile arms and tentacular manus; in F, a single row of teeth from the mid-portion of the radular ribbon; and in G and H, the mandibles, of the holotype *Illex oxygonius*. (After Roper, Lu & Mangold, 1969; plate by J. Schroeder)

A. Ring from largest sucker from dorsal arm (I)

B. Ring from largest sucker from dorso-lateral arm (II)

C. Ring from largest sucker from ventro-lateral arm (III)

D. Ring from largest sucker from ventral arm (IV)

E. Ring from largest sucker from manal portion of tentacular club.

F. Radular dentition (See key to Figures 5, 17 and 23).

G. Upper mandible

H. Lower mandible

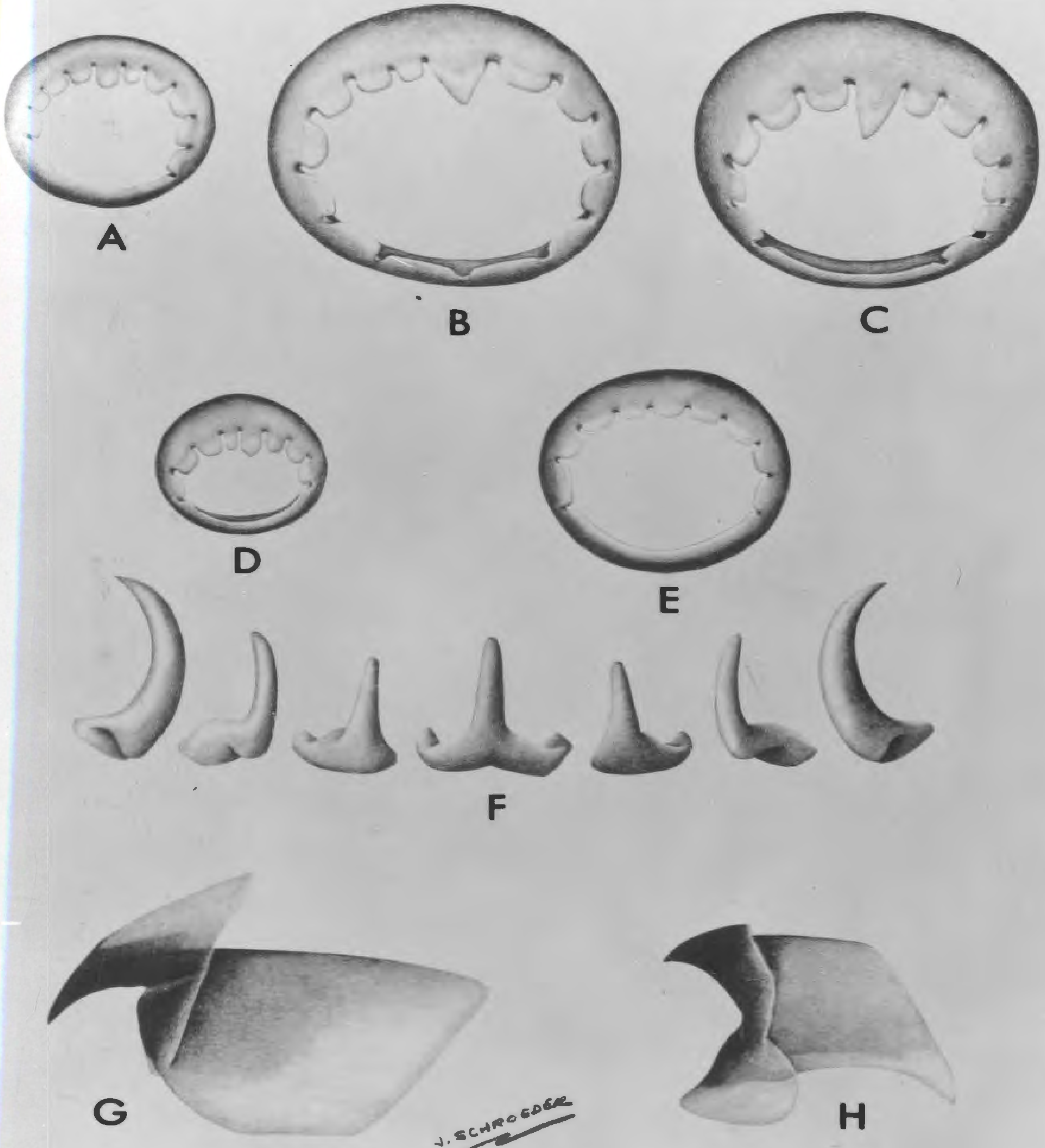

A
B
C
D
E
F
G
J. SCHROEDER
H

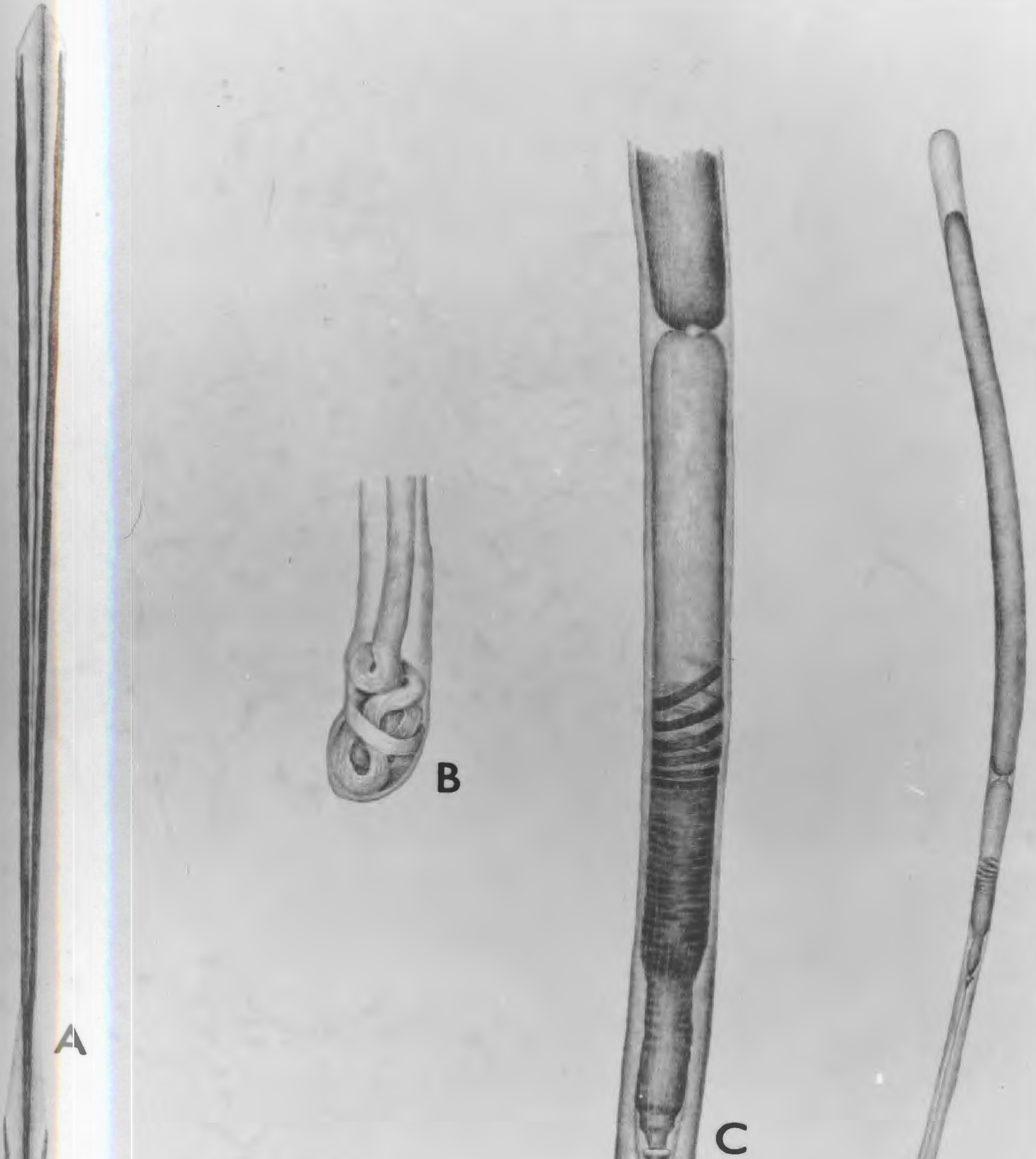
FIGURE 30. Reproduction of original plate showing drawings of the gladius and a spermatophore from a paratype of *Illex oxygonius*. (After Roper, Lu and Mangold, 1969; plate by J. Schroeder)

A. The gladius

B. Oral end or terminus of ejaculatory tube of spermatophore.

C. Portion of spermatophore showing the cement body and adjacent structures, namely, the cone and portions of the ejaculatory apparatus and the sperm mass.

D. Entire spermatophore


A
B
C
D
SCHROEDER

Comparison of Species

The four species of *Illex* differ in several characters. Information presented earlier in Tables 1, 3, 5, and 7, based on the data found in the Appendix, are presented for both sexes of all four species in the following series of tables. The morphometric indices given in these tables represent mean values of the sample, followed by the range observed in parentheses.

Head

Head length in *I. coindetii* is the greatest of the four species studied. In both sexes, head length indices (HLI) in decreasing order are *I. coindetii*, *I. argentinus*, *I. oxygonius* and *I. illecebrosus*.

Illex coindetii also has the greatest value for head width indices in both sexes, followed by *I. oxygonius*, *I. argentinus*, and *I. illecebrosus* in decreasing order for males, and *I. oxygonius*, *I. illecebrosus* and *I. argentinus* for females.

The HLI and HWI values for the four species of both sexes are given in Table 8.

Funnel Organ

The dorsal funnel organs of the four species of *Illex* differ considerably. In *I. illecebrosus* (Fig. 5) the antero-lateral border is concave and long, the posterior limbs being narrow anteriorly, the inner margins remaining parallel, the organ being narrowest at the juncture of the two limbs.

Table 8

Head length index (HLI) and head width index (HWI) as computed for both sexes, of the four species of *Illex*.

		Male		Female	
		Mean	Range	Mean	Range
HLI	*I. illecebrosus*	16.4	(10.6 - 24.7)	15.7	(11.4 - 22.6)
	I. coindetii	21.8	(13.7 - 29.6)	19.0	(10.1 - 23.6)
	I. argentinus	19.5	(16.0 - 23.9)	16.8	(14.3 - 19.7)
	I. oxygonius	18.2	(15.0 - 21.3)	16.3	(12.9 - 18.6)
HWI	*I. illecebrosus*	17.0	(10.0 - 21.8)	16.3	(12.9 - 20.4)
	I. coindetii	21.1	(13.2 - 29.1)	18.4	(12.9 - 25.1)
	I. argentinus	17.8	(11.8 - 21.1)	16.0	(11.7 - 18.8)
	I. oxygonius	20.0	(18.2 - 22.9)	17.5	(14.7 - 19.7)

In *I. coindetii* (Fig. 16), the antero-lateral border is slightly convex, the posterior limbs are short and, in contrast to the situation in *I. illecebrosus*, the organ is widest at the juncture of the limbs. Neither the inner nor outer margins are parallel.

In *I. argentinus* (Fig. 23), the antero-lateral borders are concave, the marginal borders of the posterior limbs are parallel,and the posterior end of the posterior limbs are acutely pointed.

In *I. oxygonius* (Fig. 28), the antero-lateral borders are concave, the posterior limbs being short with bluntly pointed ends.

Features of the Mantle

Mantle width is subject to great change during growth, particularly in maturing and mature females due to the great enlargement of the nidamental glands and ovaries. In general, in *I. coindetii* and *I. oxygonius* the mantle is widest at the mantle opening, while in *I. illecebrosus* and *I. argentinus* the widest part lies at a point half-way between the insertion of the caudal fins and the mantle opening. *Illex argentinus* and *I. coindetii* have greater MWI value than the other two species. In Table 9 is presented the values of MWI for the four species.

The mantle of *I. oxygonius* is long and narrow, and tapers evenly to a point posteriorly, while that of *I. coindetii* is shorter, less narrow, and less drawn out posteriorly. The mantle of both *I. argentinus* and *I. illecebrosus* is more full and robust. Males of *I. oxygonius* have

Table 9

Mantle width index (MWI) values of the four species of *Illex*, computed for both sexes.

		Male		Female	
		Mean	Range	Mean	Range
MW_1I	*I. illecebrosus*	18.0	(15.2 - 23.1)	17.5	(13.9 - 26.0)
	I. coindetii	21.9	(13.7 - 27.6)	20.3	(16.9 - 28.0)
	I. argentinus	19.8	(14.3 - 24.2)	18.5	(15.4 - 21.7)
	I. oxygonius	18.7	(16.9 - 19.9)	17.7	(16.0 - 20.8)
MW_2I	*I. illecebrosus*	19.7	(15.7 - 29.1)	19.5	(15.2 - 28.3)
	I. coindetii	21.5	(15.5 - 30.1)	20.4	(14.7 - 28.8)
	I. argentinus	22.7	(18.7 - 27.1)	22.3	(18.5 - 26.5)
	I. oxygonius	16.4	(13.1 - 19.8)	17.8	(15.3 - 20.5)
MW_3I	*I. illecebrosus*	12.0	(8.2 - 19.8)	12.0	(9.2 - 19.3)
	I. coindetii	13.6	(8.7 - 22.8)	13.0	(7.6 - 19.9)
	I. argentinus	13.3	(9.8 - 17.1)	14.2	(9.6 - 20.1)
	I. oxygonius	10.9	(8.1 - 16.4)	10.8	(9.0 - 14.3)

a sharp triangular dorsal lobe at the mantle opening. While small lobes may be present in some specimens of other species, they are not as distinct.

Caudal Fins

The greatest FLI and FBLI values were recorded for *I. oxygonius*, followed in decreasing order for *I. illecebrosus*, *I. argentinus*, and *I. coindetii*. When the FWI for the four species are ranked in order of decreasing values, the species then may be listed as follows: *I. argentinus*, *I. coindetii*, *I. illecebrosus*, *I. oxygonius*, in the case of males, and in the case of females *I. argentinus*, *I. illecebrosus*, *I. coindetii* and *I. oxygonius*. The values of FLI, FWI and FBLI in both sexes of the four species are presented in Table 10.

The angle of the caudal fins varies greatly with species. In *I. oxygonius*, it is acute, each fin forming an angle of 25° - 35°, occasionally 40°, with the longitudinal axis of the mantle. The fin angle in *I. illecebrosus* is between 40° - 50°, while in *I. coindetii* it exceeds 50° . The fin angle in *I. argentinus* is also large, being between 45° - 55° .

Arms

In both sexes, *I. argentinus* has the longest arms among the four species studied, followed in decreasing order by *I. coindetii*, *I. illecebrosus*, and *I. oxygonius*. The arm length indices of the four species of *Illex* are presented in Table 11.

Table 10

Fin length index (FLI), fin width index (FWI) and fin base length index (FBLI) of the four species of *Illex*, computed for both sexes.

		Male		Female	
		Mean	Range	Mean	Range
FLI	*I. illecebrosus*	43.8	(31.3 - 49.3)	44.1	(38.1 - 53.5)
	I. coindetii	39.2	(31.3 - 46.4)	39.4	(29.4 - 46.2)
	I. argentinus	41.9	(36.3 - 47.2)	42.3	(37.3 - 45.2)
	I. oxygonius	45.0	(42.0 - 47.9)	45.0	(42.5 - 48.1)
FWI	*I. illecebrosus*	55.4	(43.0 - 64.2)	54.6	(40.9 - 65.8)
	I. coindetii	56.4	(45.7 - 76.5)	53.7	(37.0 - 65.9)
	I. argentinus	58.0	(51.9 - 66.3)	56.4	(52.2 - 64.2)
	I. oxygonius	51.5	(43.8 - 62.4)	50.5	(43.1 - 56.9)
FBLI	*I. illecebrosus*	39.5	(28.4 - 44.3)	39.5	(33.8 - 50.3)
	I. coindetii	33.9	(19.3 - 40.7)	34.5	(25.0 - 41.6)
	I. argentinus	37.5	(35.2 - 43.0)	37.8	(34.4 - 40.3)
	I. oxygonius	40.2	(35.8 - 42.4)	40.0	(37.9 - 43.2)

Table 11

Arm length index (ALI) of the four species of *Illex*

	Arm	*I. illecebrosus*		*I. coindetii*		*I. argentinus*		*I. oxygonius*	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Male	I	39.1	(25.5-56.0)	47.4	(27.1-77.4)	55.6	(45.8-65.0)	43.9	(35.2-53.3)
	II	48.2	(32.4-70.0)	62.5	(37.4-96.6)	70.2	(57.9-84.2)	54.8	(45.0-64.2)
	III	48.2	(32.4-70.3)	61.0	(37.6-95.9)	71.2	(52.5-86.4)	54.7	(43.8-63.0)
	IV	43.0	(27.5-62.9)	54.1	(29.3-87.8)	61.6	(42.6-74.4)	47.9	(39.4-60.6)
Female	I	36.5	(29.2-49.3)	37.6	(25.0-56.1)	46.2	(39.3-53.7)	34.3	(27.9-39.3)
	II	44.5	(35.3-56.8)	48.7	(36.4-67.1)	57.4	(48.5-66.5)	42.9	(34.7-50.9)
	III	44.5	(34.7-57.6)	48.3	(36.4-67.7)	58.5	(47.1-70.0)	43.4	(36.5-54.0)
	IV	40.4	(29.4-52.6)	42.4	(25.0-63.5)	52.0	(43.4-59.7)	38.1	(31.9-46.0)

From these data, it is evident that males of the genus *Illex* have longer arms than do the females, particularly in *I. argentinus*, *I. coindetii*, and *I. oxygonius*. Such sexual dimorphism in arm length in *I. illecebrosus* is less pronounced. In *I. coindetii*, *I. argentinus*, and *I. oxygonius*, especially *I. coindetii*, arms II and III are much more robust in males than in females, and no such enlargement occurs in males of *I. illecebrosus*. Sexual dimorphism in sucker size also exists. The largest sucker on sessile arms is larger in males than in females. This sexual dimorphism in sucker size is especially evident in *I. coindetii*, *I. argentinus* and *I. oxygonius* (Table 12). The largest suckers on arms II and III of the males of those three species are greatly enlarged and no such enlargement occurs in *I. illecebrosus*.

In Table 12 is presented the sucker diameter indices of the four species of *Illex*, based on measurements of the largest sucker of each sessile arm and manus.

Roper (1969, pp. 75-79) reported that specific differences existed in the number of suckers on different arms of squid of the genus *Bathyteuthis*. In the genus *Illex*, such differences also exist, although not as clear-cut as in *Bathyteuthis*. For each of the four species studied, the range and mean number of suckers on arms I-IV of each size group, the number of samples in each group (N) and the coefficient of variability (CV) are presented in Tables 13 through 16.

Table 12

Sucker diameter indices (SI) of both sexes of the four species of *Illex*

		I. illecebrosus		*I. coindetii*		*I. argentinus*		*I. oxygonius*	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Male	S_1*	1.17	(0.80-1.76)	1.61	(0.82-3.12)	1.33	(1.05-1.65)	1.51	(1.31-1.74)
	S_2	1.75	(1.20-2.81)	2.94	(1.18-4.67)	2.71	(1.93-3.27)	2.47	(2.25-2.67)
	S_3	1.73	(1.19-2.74)	2.87	(1.36-5.68)	2.49	(1.92-2.96)	2.44	(2.18-2.59)
	S_4	1.02	(0.68-1.53)	1.47	(0.69-4.62)	1.43	(1.02-1.74)	1.39	(1.18-1.62)
	S_T	1.45	(1.00-2.02)	2.14	(1.27-2.30)	2.19	(1.88-2.84)	1.69	(0.93-1.95)
Female	S_1	1.13	(0.86-1.58)	1.35	(0.95-2.00)	1.23	(1.01-1.46)	1.20	(1.07-1.33)
	S_2	1.61	(1.21-2.41)	1.93	(1.42-2.67)	1.88	(1.56-2.28)	1.83	(1.58-2.04)
	S_3	1.61	(1.15-2.41)	1.94	(1.46-2.90)	1.86	(1.43-2.14)	1.80	(1.58-2.21)
	S_4	1.03	(0.76-1.50)	1.19	(0.79-1.60)	1.10	(0.84-1.28)	1.12	(1.01-1.31)
	S_T	1.51	(1.10-2.28)	1.81	(1.36-2.45)	1.95	(1.62-2.18)	1.65	(1.45-2.29)

*1-4 = sessile arm I-IV

T = tentacle

Table 13

Sucker complements (#S) of the first sessile arm (LI or RI) of males and females of the four species of the genus *Illex* in different size groups

		I. illecebrosus				*I. coindetii*				*I. argentinus*				*I. oxygonius*			
	ML (mm)	#S Mean	#S Range	N	CV	#S Mean	#S Range	N	CV	#S Mean	#S Range	N	CV	#S Mean	#S Range	N	CV
Male	30-60		(65)	1		77	(70- 84)	6	6.53								
	60-90	77	(75- 79)	2		83	(73-102)	16	9.53								
	90-120	85	(82- 91)	4	4.62	87	(57-108)	43	10.60								
	120-150	99	(81-111)	29	6.98	99	(78-127)	20	12.70						(94)	1	
	150-180	104	(84-115)	52	6.16	103	(91-120)	12	10.51	86	(59- 98)	8	13.66	101	(84-108)	6	8.53
	180-210	108	(102-118)	15	4.30	120	(114-124)	5	3.16	94	(74-111)	33	9.77		(101-102)	2	
	210-240	113	(105-117)	6	4.46	114	(87-134)	3	21.36	98	(81-109)	14	7.98				
	240-270	115	(108-126)	7	5.49						(98)	1					
	270-300						(98)	1									
Female	30-60					67	(50- 78)	8	16.73								
	60-90					81	(71-100)	18	10.71								
	90-120	93	(88- 99)	3	6.13	87	(71-108)	39	10.24								
	120-150	101	(91-110)	22	4.92	97	(80-118)	23	9.53					91	(81-101)	2	
	150-180	105	(84-117)	58	5.84	99	(70-128)	10	18.80		(94)	1		107	(104-108)	3	2.17
	180-210	108	(93-118)	42	5.13	110	(95-134)	7	12.89	90	(85- 97)	5	5.09	106	(94-114)	5	7.79
	210-240	104	(90-117)	12	8.27	115	(106-125)	6	7.65	98	(81-109)	16	7.55		(109)	1	
	240-270	115	(110-122)	4	4.37	124	(118-135)	4	6.07	96	(90-111)	11	14.33				
	270-300	118	(108-126)	10	4.92	115	(113-117)	2		78	(67- 89)	2					
	300-330		(112)	1													
	360-390						(105)	1									

Table 14

Sucker complements (#S) of the second sessile arm (LII or RII) of males and females of the four species of the genus *Illex* in different size groups

		I. illecebrosus				*I. coindetii*				*I. argentinus*				*I. oxygonius*			
	ML (mm)	#S Mean	Range	N	CV	#S Mean	Range	N	CV	#S Mean	Range	N	CV	#S Mean	Range	N	CV
Male	30-60		(63)	1		77	(66- 94)	6	12.09								
	60-90	87	(86- 88)	2		83	(76- 91)	15	6.39								
	90-120	87	(80- 94)	4	7.63	87	(64-108)	44	8.79								
	120-150	95	(87-104)	29	5.67	99	(80-118)	22	11.83						(98)	1	
	150-180	100	(92-108)	53	3.54	103	(98-110)	12	5.09	81	(70-96)	8	12.38	98	(94-105)	7	3.63
	180-210	104	(98-110)	15	4.08	115	(108-120)	5	3.88	92	(63-104)	33	10.93	96	(94- 98)	2	
	210-240	106	(100-111)	6	4.62	112	(90-132)	3	18.81	95	(83-103)	14	5.39				
	240-270	106	(98-114)	7	5.25						(66)	1					
	270-300						(80)	1									
Female	30-60					77	(63-100)	8	15.88								
	60-90					79	(69-101)	20	10.16								
	90-120	86	(84- 87)	3	1.77	87	(68-105)	39	10.08								
	120-150	97	(93-108)	22	4.64	96	(78-124)	23	11.19					82	(66- 98)	2	
	150-180	101	(90-110)	59	4.65	94	(82-101)	9	5.93		(88)	1		99	(96-100)	3	2.33
	180-210	102	(91-116)	42	5.82	104	(87-127)	7	14.99	85	(74- 99)	5	11.48	98	(90-106)	5	7.24
	210-240	102	(94-109)	12	5.02	108	(94-121)	7	8.39	94	(79-108)	16	7.12		(95)	1	
	240-270	107	(102-112)	4	4.45	113	(104-122)	4	6.54	98	(88-105)	11	5.19				
	270-300	108	(100-116)	10	4.33	105	(103-107)	2		91	(87- 95)	2					
	300-330		(106)	1													
	360-390						(123)	1									

Table 15

Sucker complements (#S) of the third sessile arm (LIII or RIII) of males and females of the four species of the genus *Illex* in different size groups

		I. illecebrosus				*I. coindetii*				*I. argentinus*				*I. oxygonius*			
	ML (mm)	#S Mean	#S Range	N	CV	#S Mean	#S Range	N	CV	#S Mean	#S Range	N	CV	#S Mean	#S Range	N	CV
Male	30-60		(60)	1		76	(70- 86)	6	7.36								
	60-90	85	(80- 90)	2		82	(75- 88)	15	5.77								
	90-120	85	(81- 90)	4	4.99	82	(59-103)	43	11.46								
	120-150	95	(88-104)	26	4.64	97	(76-115)	21	10.34						(106)	1	
	150-180	100	(80-108)	53	5.24	104	(76-118)	11	10.71	81	(67-104)	8	14.76	99	(92-103)	7	3.99
	180-210	104	(95-116)	15	5.95	111	(107-112)	5	1.87	91	(67-120)	33	12.26	101	(100-102)	2	
	210-240	105	(98-112)	6	4.43	117	(94-141)	3	20.10	93	(73-105)	14	9.01				
	240-270	110	(96-120)	7	8.51						(62)	1					
	270-300						(68)	1									
Female	30-60					70	(62- 78)	8	8.47								
	60-90					79	(60-100)	20	10.86								
	90-120	83	(81- 87)	3	3.85	84	(64-102)	40	9.21								
	120-150	97	(88-107)	22	5.01	92	(79-105)	22	7.31					83	(72- 94)	2	
	150-180	101	(88-112)	59	5.16	93	(84-106)	9	9.27		(88)	1		103	(99-108)	3	4.60
	180-210	103	(88-112)	42	5.41	102	(85-116)	7	11.50	82	(74- 97)	5	11.19	98	(84-106)	5	9.04
	210-240	102	(92-109)	12	6.96	106	(90-115)	7	8.70	92	(67-102)	16	9.12		(101)	1	
	240-270	108	(106-110)	4	1.51	110	(98-121)	4	8.75	94	(83-108)	11	8.22				
	270-300	111	(103-118)	10	4.74	112	(88-136)	2			(88)	2					
	300-330		(112)	1													
	360-390						(132)	1									

Table 16

Sucker complements (#S) of the fourth sessile arm (LIV or RIV) of males and females of the four species of the genus *Illex* in different size groups

		I. illecebrosus				*I. coindetii*				*I. argentinus*				*I. oxygonius*			
	ML (mm)	#S		N	CV	#S		N	CV	#S		N	CV	#S		N	CV
		Mean	Range			Mean	Range			Mean	Range			Mean	Range		
Male	30-60		(81)	1		87	(77-100)	6	9.92								
	60-90	95	(94- 96)	2		90	(80-100)	16	6.38								
	90-120	103	(96-112)	4	6.63	97	(68-118)	40	10.20								
	120-150	110	(98-122)	29	5.48	108	(90-142)	22	11.30						(116)	1	
	150-180	117	(92-127)	53	5.75	109	(92-130)	11	11.74	91	(60-108)	8	14.24	113	(101-121)	7	6.73
	180-210	119	(103-132)	15	6.51	122	(116-128)	5	3.75	104	(85-122)	33	10.02	100	(96-105)	2	
	210-240	122	(111-132)	6	6.16	118	(103-133)	3	12.71	107	(85-120)	14	8.13				
	240-270	126	(114-134)	7	6.60						(98)	1					
	270-300						(148)	1									
Female	30-60					75	(63- 98)	8	14.11								
	60-90					88	(76- 98)	20	6.75								
	90-120	100	(94-104)	3	5.15	94	(82-116)	39	8.59								
	120-150	113	(102-123)	22	4.92	103	(79-119)	23	10.18					98	(87-109)	2	
	150-180	117	(98-128)	59	4.55	104	(93-116)	10	6.31		(86)	1		116	(115-118)	3	1.49
	180-210	119	(71-130)	42	7.37	107	(92-130)	7	12.19	97	(90-104)	5	5.51	115	(99-123)	5	8.51
	210-240	119	(108-131)	12	5.70	120	(102-130)	7	8.04	108	(90-120)	16	8.41		(120)	1	
	240-270	127	(122-130)	4	2.70	119	(108-134)	4	9.95	108	(85-119)	11	8.35				
	270-300	126	(120-136)	10	3.94	125	(120-130)	2			(102)	2					
	300-330		(118)	1													
	360-390						(130)	1									

Within size ranges where sufficient numbers of specimens were available, the results indicate that the number of suckers on the sessile arms increase as the animal grows.

In size groups where sufficient materials of all four species were available, *I. coindetii* has the greatest number of suckers, followed by *I. illecebrosus*, *I. oxygonius* and *I. argentinus*. The paucity of suckers in *I. argentinus* is unmistakable, for the range of numbers only slightly overlapped, if at all, with the range for the other species. No sexual dimorphism in the number of arm suckers could be found. The greater values of CV for *I. coindetii* and some size groups of *I. argentinus* suggest the heterogeneity of the samples. The collections of *I. coindetii* consisted of material from both sides of the Atlantic Ocean and throughout its distributional range. However, no study was made of possible population differences at this time.

The number of suckers on arms I-IV agrees with the order of the diameter of the largest sucker on the respective arm. That is, the largest sucker on arms II and III are larger than their counterparts on arms I and IV, while the largest sucker on IV is smaller than the largest on the other arms. The ordering of the sessile arms, with respect to complement of suckers, is IV, I, II and III.

Mandibles

The mandibles of the four species of *Illex* differ in a number of features, and these are presented in Table 17.

Table 17

Comparison of the mandibles of the four species of *Illex**

	Feature	*I. illecebrosus*	*I. coindetii*	*I. argentinus*	*I. oxygonius*
Upper Mandible	Rostral hood	Long, strong	Long, strong	Long, strong	Short, very thin and weak
	Outline of rostral lamella	Serrated	Smooth	Serrated	Smooth, straight or slightly curved
	Jaw angle	Large, with tooth	Small	Large, with tooth	Small
	[illegible]strum	Long	Long	Long	Short
	Palatine lamella	Short, shallow; crest curved	Short, shallow; crest curved	Short, shallow; crest curved	Long, deep; crest straigh
	Rostral lamella	Short	Short	Short	Long
Lower Mandible	Cutting edge of rostrum	Straight, short	Straight. long	Curved, long	Curved, long
	Rostral lamella	Long, wide, no lobe; regular outline	Long, wide, no lobe; slightly irregular outline	Long, wide, no lobe; regular outline	Short, narrow, lobate; irregular outline
	Gular lamella	Short, blunt	Short, blunt	Short, blunt	Long, pointed
	Rostral width	Narrow	Narrow	Narrow	Wide

*Based, in part, on Roper, Lu & Mangold, 1969.

[illegible]ctocotylized Arm

Hectocotyli of the four species of *Illex* show the same basic structure, in that the tip of either the right or left ventral arm (IV) is modified by a series of lamellae, knobs and papillae. In *I. coindetii*, *I. argentinus* and *I. oxygonius* the hectocotylized arm is longer than its non-hectocotylized opposite member of the pair, while in *I. illecebrosus* it is shorter. The range, mean, standard deviation and the number (N) sampled for HcALI and HcLI are presented in Table 18. The calculations are based only on fully mature specimens demonstrating spermatophores upon dissection.

Table 18

Hectocotylized arm length index (HcALI) and hectocotylus length index (HcLI) for the four species of *Illex*

		Mean	Range	Standard Deviation	N
HcALI	*I. illecebrosus*	53.0	(39.7-66.0)	7.9	27
	I. coindetii	63.7	(42.3-87.1)	9.9	65
	I. argentinus	67.6	(49.5-82.0)	7.4	68
	I. oxygonius	51.5	(40.6-59.9)	5.7	10
HcLI	*I. illecebrosus*	22.1	(13.0-30.3)	4.6	27
	I. coindetii	25.1	(17.1-30.0)	2.7	65
	I. argentinus	50.3	(19.8-70.3)	11.0	68
	I. oxygonius	28.8	(23.8-32.0)	2.7	10

As can be seen from Table 18, *I. argentinus* has the longest hectocotylized arm, followed by *I. coindetii*, *I. illecebrosus* and *I. oxygonius* in decreasing order. The proportional length of the modified portion of the arm varies among the four species. In *I. argentinus* it is greater than 50%, in *I. oxygonius* about 29%, *I. coindetii* 25%, and *I. illecebrosus* 22%.

The hectocotylus of *I. coindetii* is unique in that the trabeculae distal to the 7th pair of suckers are transformed into papillose fringed flaps, a feature lacking in the other species. These modified trabeculae are larger and more papillose in *I. coindetii* from African waters than in specimens from the Gulf of Mexico, the Caribbean Sea or the Mediterranean Sea.

The length of the hectocotylized arms and their modified portion also vary with the site of collection. *Illex illecebrosus* from Newfoundland waters have shorter hectocotylized arms (HcALI average: 48.5%) and modified portions (HcLI average: 20.1%) than do those of the same species from the area of the middle-Atlantic States (55.3%, 23.1% respectively). *Illex coindetii* from the Mediterranean Sea have the longest hectocotylized arms (HcALI 71.1%), followed by those from the Caribbean Sea (68.5%), Gulf of Mexico (59.7%), and coastal seas of West Africa (58.6%). *Illex coindetii* from the Mediterranean Sea also have the longest modified tips (HcLI 27.3%) followed by those from the Caribbean Sea and the West African collections (both 25.0%) and the Gulf of Mexico (23.4%). The size of the lamellae in the dorsal row of the modified tip also varies; *I. oxygonius* has the largest, those of *I. coindetii* and *I. argentinus* being slightly smaller, and *I. illecebrosus*, the smallest.

A few knobs and papillae occur proximally in the dorsal row of fully developed lamellae. Specifically, *I. oxygonius* has three such knobs and two slightly flattened papillae, while *I. illecebrosus* and *I. coindetii* have one or two knobs. *Illex argentinus* has the most distinctive hectocotylus (Fig. 21E). The dorsal and ventral rows have 8-13 normal suckers proximally, the dorsal row continuing as 10-16 enlarged and rounded suckerless knobs, 18-22 large and distinct truncate or rounded lamellae and 6-9 (or more) small indistinct lamellae to the tip. The ventral row continues having 7-10 low, suckerless knobs, 7-12 nipple-like papillae, and 20 or more small and indistinct narrow lamellae extending the row to the tip.

Spermatophores

The major difference in the spermatophore of the four species occurs at the oral end of the cement body and the aboral end of the ejaculatory apparatus. In *I. oxygonius* the cone found there is funnel-shaped, of about equal sides in profile and with rounded corners. The oral tube is relatively broad, the aboral neck intermediate in width and length when compared with those of *I. illecebrosus* and *I. coindetii*. In *I. illecebrosus* the cone, in profile, is a low right-isosceles triangle with rounded corners, the oral tube is narrow and the neck is long and narrow. In *I. coindetii* there is a lens-shaped cone, giving a rounded triangle or diamond-shape in profile. The oral tube is broad, while the neck is very short, broad and indistinct. In *I. argentinus* the cone is flat and lens-shaped, the oral tube being broad and the neck broad and distinct.

Size and Maturity

In the species with sufficient material being available for study, females demonstrated a greater maximum size than did the males. In general, it was found that the males reached maturity at a smaller size than did the females. Males of *I. illecebrosus* in Newfoundland waters attain a maximum size of 270 mm ML, with an average ML of 245.3 mm in fully mature specimens. In comparison, females reach the maximum size of 310 mm ML, with no fully mature specimens having been observed. In waters to the south, along the middle-Atlantic States of the U.S.A., this species does not grow as large as in the Newfoundland waters and furthermore it reaches maturity at a smaller size. The average ML of fully mature males from the middle-Atlantic States was found to be 176.0 mm, while in the females it was 194.1 mm.

Similarly, *I. coindetii* from different geographical regions exhibits different sizes at maturity. The average ML for fully mature males and females of *I. coindetii* was 182.3 mm and 231.5 mm, respectively, for those specimens from the west coast of France; 148.2 mm and 192.3 mm for those from the Mediterranean Sea; and 113.2 mm and 136.2 mm for those from off west Africa. For Caribbean Sea specimens, the average mantle lengths were 169.0 mm (mature males) and 241.8 mm (mature females). These figures may be compared with those from the Gulf of Mexico, namely, 147.1 mm and 160 mm, for males and females, respectively, in both cases mature. Therefore, males of *I. coindetii* from the eastern Atlantic off the coast of West Africa reach maturity at a size smaller than that obtained elsewhere prior to sexual maturity. In increasing order of size, these are followed by those from the Gulf of Mexico, the Mediterranean Sea, the Caribbean Sea and, finally, from the west coast of France. For the females, specimens from the west coast of Africa also mature at the smallest size, followed by those from the Gulf of Mexico, the Mediterranean Sea, the west coast of France and the Caribbean Sea, in that order. For the fully mature males and females of *I. argentinus*, the average ML of the samples examined were 199.3 mm and 236.2 mm, respectively. In the species *I. oxygonius* from the middle-Atlantic States the average ML at maturity was 170.8 mm (males) and 180.1 mm (females).

Growth Patterns

The regression lines of the measurements of body parts on the ML of the four species, sex separated, were tested for interspecific differences using regression coefficients. The results of these tests are summarized in Table 19. The 95% confidence interval was used to determine the level of significance. In Table 19 "+" denotes significance, while "-" denotes a lack of significance.

It should be noted that "non-significance" merely indicates the similarity of the slope of the two regression lines involved, and does not suggest that the two lines are the same.

Number of Gill Lamellae

Although the number of gill lamellae has been considered to be useful in the study of octopods, in teuthoids it is regarded as being of dubious value because of its variance and the high number of lamellae (Voss, 1963, p. 10).

Within the extent of this study,in the genus *Illex* the number of gill lamellae increases as the animal grows. In Table 20 is presented the average number of gill lamellae and their range, with the coefficient of variability, for specimens grouped by size intervals for each of the four species. However, the small number of specimens of *I. argentinus* and *I. oxygonius* that were available permit less valid analyses. The results as presented show distinct differences between *I. illecebrosus* and *I. coindetii*.

From Table 20, it is evident, however, that *I. illecebrosus* has more gill lamellae than does *I. coindetii* of the same size, and

Table 19

Interspecific comparison of the four species of the genus *Illex* based on the regression coefficient of selected critical morphometric parameters grouped by sex. (Cf. "Morphometry" of each species).

	Male					Female				
	Sp.	I	C	A	O	Sp.	I	C	A	O
VML	I		-	-	+	I		+	-	+
	C			-	-	C			+	+
	A				-	A				-
HL	I		+	-		I		+	-	-
	C			+		C			+	+
	A					A				-
HW	I		+	-	+	I		+	-	-
	C			+	+	C			+	-
	A				+	A				-
MW_1	I		+	+	-	I		-	-	-
	C			+	-	C			-	+
	A				-	A				-
MW_2	I		-	+		I		+	-	-
	C			+		C			-	-
	A					A				-
MW_3	I		-	+		I		+	-	-
	C			+		C			-	-
	A					A				-
FL	I		+	-	-	I		+	-	-
	C			-	-	C			+	-
	A				-	A				-
FW	I		-	+	+	I		-	-	-
	C			+	+	C			-	-
	A				-	A				-
FBL	I		+	+	-	I		+	+	-
	C			-	-	C			-	-
	A				-	A				-
A_1L	I		+	+	+	I		-	-	-
	C			+	+	C			-	-
	A				-	A				-

	Male					Female				
	Sp.	I	C	A	O	Sp.	I	C	A	O
A_2L	I		+	+	-	I		-	-	-
	C			+	+	C			-	-
	A				-	A				+
A_3L	I		+	+	-	I		-	-	-
	C			+	+	C			-	-
	A				-	A				-
A_4L	I		+	+	-	I		-	-	-
	C			+	+	C			-	-
	A				-	A				-
S_1	I		+	-	-	I		-	-	-
	C			+	-	C			+	-
	A				-	A				-
S_2	I		+	+	-	I		-	-	-
	C			+	-	C			+	-
	A				-	A				-
S_3	I		+	-	-	I		-	-	-
	C			+	-	C			-	+
	A				-	A				-
S_4	I		+	-	-	I		+	-	-
	C			+	-	C			-	+
	A				-	A				-
S_T	I				-	I		+		+
	C				-	C				+
GL	I		+		-	I		-		-
	C				-	C				-

Sp. I = *Illex illecebrosus*
Sp. C = *Illex coindetii*
Sp. A = *Illex argentinus*
Sp. O = *Illex oxygonius*

+ = Significant, t-value greater than the critical t-value of the corresponding sample size at the 95% confidence interval.

- = Insignificant different, t-value smaller than the critical value of the corresponding sample size at the 95% confidence interval.

Table 20

Complement of ctenidial lamellae of the four species of the genus *Illex* grouped by sex and in different size groups

	ML (mm)	*I. illecebrosus*		N	CV	*I. coindetii*		N	CV	*I. argentinus*		N	CV	*I. oxygonius*		N	CV
		Mean	Range			Mean	Range			Mean	Range			Mean	Range		
Male	30-60		(49)	1		46.00	(38-53)	9	10.86								
	60-90	55.50	(49-62)	2		51.63	(48-57)	19	5.25								
	90-120	66.40	(64-69)	5	2.74	53.00	(45-67)	45	6.92								
	120-150	65.69	(59-70)	29	3.78	55.52	(50-62)	23	5.71						(61)	1	
	150-180	66.32	(52-73)	56	4.98	55.47	(50-62)	15	5.93	59.00	(54-65)	4	8.42	68.17	(61-73)	6	5.82
	180-210	66.79	(62-72)	15	4.03	58.58	(55-62)	7	5.38	58.13	(52-65)	8	6.78	67.50	(66-69)	2	
	210-240	67.33	(62-72)	6	4.95	58.00	(54-62)	2		53.33	(52-55)	3	2.87				
	240-270	65.00	(61-68)	7	4.52						(55)	1					
	270-300						(50)	1									
Female	30-60					46.23	(38-56)	13	10.60								
	60-90					51.57	(45-58)	21	6.83								
	90-120	59.50	(57-62)	2		52.05	(45-58)	41	5.74								
	120-150	65.45	(56-70)	22	4.98	53.69	(42-64)	29	9.61					55.00	(48-62)	2	
	150-180	67.42	(55-71)	52	4.66	54.08	(42-71)	13	12.57		(58)	1		63.33	(56-67)	3	10.03
	180-210	68.07	(53-72)	43	4.61	55.50	(53-57)	6	2.74		(62)	2		67.80	(64-71)	5	4.09
	210-240	68.73	(64-73)	11	3.80	55.25	(49-60)	12	7.80	58.00	(54-63)	6	6.64		(71)	1	
	240-270	70.50	(68-72)	4	2.45	53.75	(43-64)	4	20.06	61.25	(56-64)	4	5.86				
	270-300	69.50	(67-73)	10	3.12	55.00	(53-57)	2		58.00	(54-62)	2					
	300-330		(71)	1													
	360-390						(54)	1									

it should be noted that the CV values for the data on *I. illecebrosus* are smaller. As was the case in the analyses of the number of suckers on the sessile arms, the larger CV in *I. coindetii* may be due to the heterogeneity of the available sample. The significance of this difference in the number of gill lamellae will be discussed later under "Zoogeography".

Distribution

Since it has never been found elsewhere, *Illex* may be considered to be an Atlantic endemic genus. *Illex illecebrosus* is the northern form, as it is distributed along the east coast of North America from Cumberland Sound to about 29°N (the vicinity of Cape Kennedy, Florida). *Illex coindetii* occurs from 37°06'N southwards along the Florida Peninsula, into the Gulf of Mexico and the Caribbean Sea. In the eastern Atlantic it occurs in the North Sea, off the west coast of the European continent, the Bristol Channel, the Mediterranean Sea, and along the west coast of Africa to about 14°S. *Illex oxygonius* is reported from along the middle-Atlantic States from 38°34'N southwards, in the Gulf of Mexico, and from the Gulf of Guinea.

From the analysis herein presented, it is evident that the three species are sympatric in the western Atlantic between 38°N and 29°N. Further south, *I. coindetii* and *I. oxygonius* are also sympatric (Fig. 10). No actual overlap between *I. illecebrosus* and *I. coindetii* is known in the eastern Atlantic Ocean, unless the report of *I. illecebrosus* in the Bristol Channel can be confirmed. *Illex coindetii* and *I. oxygonius* are only sympatric in the Gulf of Guinea.

The distribution of *I. argentinus* is known to be between approximately 35° - 47°S and 52° - 65°W, but its actual range of distribution is possibly wider. Due to the lack of collections from the Central and South American coasts, the exact northern limit of this species and the southern limit of both *I. coindetii* and *I. oxygonius* are not known. The range of distribution of *I. argentinus* does not overlap with any other species of the genus, at least insofar as our current knowledge indicates.

Artificial Key to the Species of Adult *Illex*

1. Posterior limbs of dorsal funnel organ with parallel marginal borders, hectocotylus greater than 50% of total length of the arm . . . . *I. argentinus* (Castellanos, 1960)

   Marginal border of posterior limbs of dorsal funnel organ not parallel, hectocotylus less than 50% of total length of the arm 2

2. Fin angle exceeds 50°, trabeculae of the hectocotylized arm modified into fringed and papillose lobes . . . . *I. coindetii* (Verany, 1837)

Fin angle less than 50°, trabeculae of hectocotylized arm not modified into fringed and papillose lobes 3

3. Fin angle not exceeding 40°, cone at oral end of cement body of spermatophore funnel-shaped, length of conal neck about equal to width . . . . *I. oxygonius* Roper, Lu & Mangold, 1969.

Fin angle exceeding 40°, cone at oral end of cement body of spermatophore in shape of a low right-isosceles triangle, length of conal neck greater than width . .*I. illecebrosus* (Lesueur, 1821).

Generic Relationships

The ommastrephids are widely distributed in the three major oceans, chiefly in the temperate and tropical regions. The members of the family support two of the largest squid fisheries in the world, namely, *Todarodes pacificus* in Japanese waters and *Illex illecebrosus* in Newfoundland waters. It is for this reason that the biology and ecology of these two genera and species are better known than for other oegopsids. The systematics of the family is greatly in need of revision, however. The following discussion on the familial characters and the generic groupings is based on Roper, Young, and Voss (1969).

The family Ommastrephidae is characterized by the unique inverted T-shaped mantle-locking apparatus, the dorsally attached buccal connective to sessile arm IV, and the biserial suckers on the arms. Currently three subfamilies are recognized within the family: Ommastrephinae, Todarodinae, and Illicinae. The Ommastrephinae is characterized by the presence of a central foveola and several lateral pockets in the funnel groove and by the presence of photophores. The Todarodinae is distinguished by the presence of a central foveola with no lateral pockets in the funnel groove and by the absence of photophores. The Illicinae has smooth funnel grooves without foveola or lateral pockets, and no photophores. The following scheme presents the presently recognized genera and species within each subfamily.

Ommastrephinae:

Ommastrephes: *O. bartrami* (Lesueur, 1821); *O. pteropus* (Steenstrup, 1855); *O. caroli* (Furtado, 1887).

Symplectoteuthis: *S. luminosa* Sasaki, 1915; *S. oualaniensis* (Lesson, 1830).

Dosidicus: *D. gigas* (d'Orbigny, 1835).

Hyaloteuthis: *H. pelagica* (Bosc, 1802).

Ornithoteuthis: *O. volatilis* (Sasaki, 1915); *O. antillarum* (Adam, 1957).

Todarodinae:

Todarodes: *T. pacificus* Steenstrup, 1880; *T. sagittatus* (Lamarck, 1799).

Nototodarus: *N. sloani sloani* (Gray, 1849); *N. sloani gouldi* (McCoy, 1888); *N. sloani philippinensis* Voss, 1962; *N. sloani hawaiiensis* Berry, 1912.

Illicinae:

Illex: *I. illecebrosus* (Lesueur, 1821); *I. coindetii* (Verany, 1837); *I. argentinus* (Castellanos, 1960); *I. oxygonius* Roper, Lu & Mangold, 1969.

Todaropsis: *T. eblanae* (Ball, 1841).

An additional ommastrephid is the species *Martialia hyadesi* Rochebrune & Mabille, 1898. The validity of this species is uncertain and it is so little understood that there has been no attempt to assign it to one of the ommastrephid subfamilies. Accordingly, it has been omitted from this and subsequent discussions herein.

Lateral pockets are not easily discernible in the genus *Ornithoteuthis*, and this fact has caused some dispute in the past concerning the proper subfamilial position of the genus. The presence of the foveolae and the lateral pockets in the funnel groove of

Ommastrephes, *Dosidicus*, *Hyaloteuthis*, and *Symplectoteuthis* is clear. Sasaki, when he first described the species, placed *Ornithoteuthis volatilis* in the genus *Ommastrephes* (=*Todarodes* Steenstrup, 1880) (Sasaki, 1915, p. 138). Okada (1927), in erecting the genus *Ornithoteuthis* for *O. volatilis* Sasaki, did not indicate its relationship with other ommastrephid genera (Okada, 1927, pp. 13-15). Okutani (1967) placed it under the subfamily Todarodinae (p. 12). It was Voss who pointed out the obscured nature of the side pockets in *Ornithoteuthis antillarum* and confirmed their presence (p. 371 and p. 377). In the genera *Todarodes* and *Nototodarus* the presence of foveolae and the absence of the lateral pockets are clear, as are also the total absence of foveolae and the lateral pockets in the genera *Illex* and *Todaropsis*.

The armature of the tentacles is generally of taxonomic importance. In *Ommastrephes* there are two to three carpal knobs in the carpal cluster (Voss, 1956a, p. 146; Sasaki, 1929, p. 291), the numbers of the carpal knobs in *Symplectoteuthis* are from two to four (Sasaki, 1929, p. 295 and p. 299). *Dosidicus* has four carpal knobs (Berry, 1912, p. 302) and *Hyaloteuthis* has one (Sasaki, 1929, p. 287). Carpal knobs have never been described for *Ornithoteuthis*, and examination of the one specimen of *O. antillarum* on hand (USNM 576999, 116 mm ML) did not reveal this structure. Therefore, at the present time it must be concluded that *Ornithoteuthis* lacks this feature. They are also lacking in the genera *Todarodes*, *Nototodarus*, *Illex* and *Todaropsis*.

The manus of the tentacular clubs of all ommastrephids demonstrate a tetraserial arrangement of suckers, with those of the two median rows being larger than those of the marginal rows. All ommastrephid genera possess four rows of small suckers on the dactylus of the tentacle, with the exception of *Illex* which, as we have seen, possesses eight rows of minute suckers.

The arrangement of the suckers on the sessile arms of all ommastrephids is biserial. *Dosidicus gigas* is unique amongst ommastrephids, in that the distal half of the arms is greatly attenuated, with the suckers there greatly reduced in size. The second arm of an individual of 1245 mm ML proved to have some 150 pairs of suckers crowded over this attenuated portion (Berry, 1912, p. 302).

The taxonomic value of the hectocotylus of cephalopods has been the subject of speculation and discussion by several authors. Steenstrup (1881) proposed a classification of several genera of sepiolids based largely on the location of the hectocotylus, (i.e., the identity of the "sex arm"). Later (1887) he reported the identity of the modified arm to be of considerable taxonomic importance. Of lesser importance was the exact nature of the modification in the hectocotylization, relegating to insignificance the laterality of the hectocotylus (*fide* Volsøe, et al., 1962, pp. 200-201).

Hoyle (1908) reviewed the problem extensively and most recently Adam (1960) discussed the taxonomic value of the hectocotylus in the Ommastrephidae. He pointed out that the hectocotylus in ommastrephids, although characteristic for each species, offers little of taxonomic value at the generic and subfamilial levels. He concluded that the present classification of subfamilies and genera of the Ommastrephidae cannot be sustained in light of information gathered from a review of hectocotylization.

The hectocotylus of most ommastrephids exhibits the same basic pattern, i.e., part of one or both of the ventral arms becomes modified by loss of suckers while the sucker stalks are transformed into series of papillae. Of the three recognized species of *Ommastrephes*, the hectocotylus is known only for two. In *O. bartrami*, according to Sasaki (1929, p. 290), only the extremity of the right ventral arm is modified. However, Young reported that it is usually LIV that is affected, although it is occasionally arm RIV that is modified (Young, 1972, p. 29).

In *O. pteropus* it is either the right or the left ventral arm that is hectocotylized (Adam, 1960, p. 6). Both *Symplectoteuthis luminosa* and *S. oualaniensis* have the left ventral arm hectocotylized (Sasaki, 1929, p. 294 and p. 299). The hectocotylus of *Ornithoteuthis* exhibits the most peculiar structure in that while the modified tip is of the basic pattern, part of the ventral protective membrane is transformed into a peculiar honeycombed structure (Voss, 1957, p. 374). In *O. volatilis* the right ventral arm is hectocotylized (Sasaki, 1929, p. 283), while in *O. antillarum* it is either the right or the left ventral arm (Adam, 1960, p. 4; and an original observation based on a mature male, USNM 576999, O 445, 116 mm ML). The hectocotyli of *Dosidicus* and *Hyaloteuthis* are unknown.

The hectocotylus of *Todarodes sagittatus* is poorly known. Hoyle reported that the left ventral arm was hectocotylized (Hoyle, 1908, p. 524), while Pfeffer (1912, p. 444) reported it to be the right ventral arm. Kaas and Broek (1939, p. 52, *fide* Adam, 1960, p. 3) reported that hectocotylization in this species affected the right ventro-lateral arm (RIII). Clarke (1966, p. 130) stated that a specimen in the British Museum has arm RIV hectocotylized. Mangold (personal communication) also held that the hectocotylization affects RIV of *T. sagittatus* from the Mediterranean Sea. The hectocotylus of *T. pacificus* was well described and illustrated by Sasaki (1929, pp. 278-279, textfig. 134), and it is RIV that is hectocotylized.

The status of the four "forms" in the genus *Nototodarus* is uncertain. Voss (1963) and Clarke (1966) regarded them as subspecies, and *N. sloani sloani*, *N. s. gouldi*, and *N. s. hawaiiensis* all have both ventral arms hectocotylized (Voss, MS; Adam, 1960, p. 4; Berry, 1918, p. 232; Dell, 1952, p. 109). No male specimen of *N. s. philippiensis* is known in museum collections, and therefore there is no information ncerning hectocotylization.

As for the members of the genus *Illex*, as already described separately and previously, either the right or the left ventral arm is ctocotylized. In *Todaropsis eblanae* both ventral arms are hectocotylized with the right arm being the better developed (Adam, 1952, p. 100).

All of the foregoing concerning the nature of hectocotylization in the different species is to be found summarized in Table 21.

From this analysis, among the seven genera that are known for their hectocotyli, two genera have hectocotyli on a fixed arm (RIV for *Todarodes* and LIV for *Symplectoteuthis*) two genera, *Nototodarus* and *Todaropsis*, have both IV hectocotylized, the remaining three genera, *mastrephes*, *Ornithoteuthis* and *Illex*, have either RIV or LIV ctocotylized.

The mode of spermatophoric transferral to females varies with the genus. In *Ommastrephes pteropus* and *O. bartrami* the spermatophores are fixed to the buccal membranes of the female (Sasaki, 1929, p. 292; Clarke, 1966, p. 108). This pattern is also found in several female specimens of *Ornithoteuthis antillarum* in the USNM. In *Symplectoteuthis* *alaniensis* the transferred spermatophores are also fixed to the

Table 21

Occurrence of the hectocotylus in the Ommastrephidae

Species	RIII	RIV	LIV	LIV and RIV	Author
[illegible]astrephes bartrami	-	+	-	-	Sasaki, 1929, p. 290
O. bartrami	-	+	+	-	Young, 1972, p. 29
O. pteropus	-	+	+	-	Adam, 1960, p. 6
[illegible]plectoteuthis luminosa	-	-	+	-	Sasaki, 1929, p. 294
S. oualaniensis	-	-	+	-	Sasaki, 1929, p. 299
[illegible]nithoteuthis volatilis	-	+	-	-	Sasaki, 1929, p. 283
O. antillarum	-	+	+	-	Adam, 1960, p. 4
Todarodes sagittatus	-	-	+	-	Hoyle, 1908, p. 524
T. sagittatus	-	+	-	-	Pfeffer, 1912, p. 444
T. sagittatus	+	-	-	-	Kaas & Broek, 1939, p. 52
T. sagittatus	-	+	-	-	Clarke, 1966, p. 130
T. sagittatus	-	+	-	-	Mangold (personal comm.)
T. pacificus	-	+	-	-	Sasaki, 1929, p. 278
Nototodarus sloani sloani	-	-	-	+	Dell, 1952, p. 109
N. s. gouldi	-	-	-	+	Berry, 1918, p. 232
N. s. hawaiiensis	-	-	-	+	Voss (MS)
Illex illecebrosus	-	+	+	-	p. 65
I. coindetii	-	+	+	-	p. 107
I. argentinus	-	+	+	-	p. 141
I. oxygonius	-	+	+	-	p. 170
Todaropsis eblanae	-	-	-	+	Adam, 1952, p. 100

buccal membrane of the females, and accordingly, about 60-70 small ovoid "seminal receptacles" are present on the membrane (Sasaki, 1929, p. 299). No record of the site of spermatophore transfer can be found for the genera *Hyaloteuthis* and *Dosidicus*.

For *Todarodes sagittatus*, Clarke (1966, p. 131) stated that the buccal membrane of the female bears "spermathecae" for the reception of sperm. Soeda (1956, pp. 9-10) reported "about 30 seminal receptables" on the buccal membrane of female *T. pacificus*, and that spermatophores are planted on the outer lip of the buccal mass. The method of spermatophore transplantation is unknown in *Nototodarus*. Adam (1952, p. 100) reported that in *Todaropsis eblanae* they are deposited in "seminal receptacles" at the base of the third arm.

In *I. coindetii* spermatophores are planted in large stellate or radiating bunches at the proximal termini of the gills, close to the mid-dorsal line, or directly in the opening of either, or both, of the oviducts (Steenstrup, 1880-81, p. 80, pl. III; this study, Fig. 15B). This same pattern is found in all the species of *Illex*.

The deposition of spermatophores on the buccal membrane would not seem to be as effective as in the mantle cavity, where a well secured attachment would tend to ensure successful fertilization. In this respect, *Illex* seems to possess a most effective mechanism favoring fertilization.

The luminescent phenomena in cephalopods have been an interesting field of study for many biologists. Harvey (1952) stated that cephalopods "include species with the most complicated lantern-like luminous organs with lenses, reflectors, and pigment screens", concluding that "it is not surprising that students of the cephalopods should be intrigued with the variety of light organs" (p. 269). Among the ommastrephid genera, only the Ommastrephinae possess photophores (Roper, 1963, p. 351) e.g., *Ommastrephes bartrami, O. pteropus, O. caroli, Symplectoteuthis oualaniensis, S. luminosa,* and *Dosidicus gigas.* These possess subcutaneous photophores randomly distributed over the entire animal (Roper, 1963, p. 344, and personal communication; Young, 1972, p. 30, 33 and 34). *Ommastrephes pteropus* and some specimens of *S. oualaniensis* possess in addition a large light organ on the dorsum (Clarke, 1965). Two additional visceral photophores embedded in the tissue of the dorsal wall of the intestine are present in *O. pteropus.* One lies just posterior to the anus, the other in the posterior end of the intestine. *Hyaloteuthis pelagicus* possesses 19 rounded or oval knob-like photophores on the ventral surface of the mantle. *Symplectoteuthis oualaniensis* and *S. luminosa* bear photophores in the form of patches on the head and longitudinal bands and zones on the ventral surface of the mantle (Roper, 1963, p. 344; Young, 1972, pp. 33-34). *Ornithoteuthis volatilis* possesses a longitudinal, elliptical photophore ventral to the tentacular nerve, as can be seen in a cross section of the stalk of the tentacle (Okada, 1927, pp. 13-14; Sasaki, 1929, p. 285). *Ornithoteuthis antillarum* bears an additional photophore on the rectum and photogenic tissue on the ventral surface of the eyeball (Voss, 1957, p. 377). No luminescent organs of any description have been reported for the remaining ommastrephid genera, i.e., *Todarodes*, *Nototodarus*, *Illex*, and *Todaropsis*.

In cephalopods, the presence or absence of such photogenic organs, their distribution on or within the body, their number, size and the details of their anatomy are of taxonomic importance, as was pointed out by Berry in his classic work on light production in cephalopods (Berry, 1920a, b). The phylogenetic significance of these organs is uncertain, however. Berry (1920b, p. 190) pointed out that one should not conclude that photogenesis is a primitive phenomenon in cephalopods because of the widespread distribution of photogenic organs in "comparatively, primitive" oegopsids and their relatively restricted distribution in more advanced myopsids and octopods. The varied pelagic environment of the oegopsids would tend to favor development of light organs. Berry further suggested that photogenic organs are probably of polyphyletic origin (Berry, 1920b, p. 190). Over three decades later, Harvey (1952, p. 279) classified luminous cephalopods into three categories, namely, (1) those associated with luminous bacteria, (2) those producing an abundant luminous secretion, and (3) those with well developed photophores and intracellular [illegible]inescence. The first two groups contain mainly the sepiolids, with the exception of *Loligo edulis* which belongs to the suborder Myopsida of the Order Teuthoidea. The third group contains exclusively the oegopsids. From this analysis, it seems that at least in some groups of cephalopods, the photogenic organs are of phylogenetic significance.

In the suborder Oegopsida, there are 23 recognized families at present, 14 of which contain one or more luminous species. Among these 14 families, 11,comprising 49 genera, including the 23 doubtful genera in the family Cranchiidae possess photophores. The remaining three families contain 17 genera of which only seven have examples of photogenic properties. Therefore, of the total of 79 oegopsid genera, 56 are luminous, including the genus *Gonatus* in which only one species, *G. pyros* Young, 1972, is known to possess photophores. From this survey, it is evident that the ability to generate light is characteristic of the majority of oegopsid genera.

Although many details of the familial relationships within the Oegopsida have yet to be established, the families Lycoteuthidae, [illegible]ploteuthidae and Octopoteuthidae have been and are considered to be the most primitive of the oegopsids (Naef, 1916, pp. 14-15; 1921 , p. 535; Young & Roper, 1968, pp. 201-202). These three families are usually listed first in systematics listings, indicating their primitive nature. It is interesting to observe that all members of these three families possess photophores suggesting that luminous organs are a primitive character in oegopsids. They may be retained or lost along different evolutionary lines that have led to modern oegopsids. Indeed, this is an area of contemplation which must, for the time being, be left to speculation in absence of definite information. Some such information may perhaps be learned from a study of embryonic or early juvenile forms where, it may be, now overlooked or misinterpreted *anlagen* may be present as incipient photogenic tissue or organs which fail to proceed to full development.

Admitting this absence of a complete story, it may be assumed that within a given family those genera possessing light organs are possibly the older or earliest established.

With specific reference to the ommastrephids, if we may follow this admittedly problematic scheme based on far from proven assumptions, the subfamily Ommastrephinae would appear to be the oldest. This complete absence of such organs in all genera of the subfamilies Todarodinae and Illicinae tend to indicate their being more recently evolved.

As was mentioned previously, the ommastrephids are widely distributed. While members of the Ommastrephinae and Todarodinae occur in all three major oceans (Clarke, 1966; Filippova, 1968), the Illicinae are restricted to the Atlantic Ocean. Considering the generic level, *Ommastrephes* and *Todarodes* occur in all the three oceans, *Symplectoteuthis* and *Nototodarus* occur in both the Pacific and Indian Oceans, *Ornithoteuthi* and *Hyaloteuthis* are found in both the Atlantic and Pacific Oceans, *Dosidicus* is found only in the Pacific Ocean, and *Illex* and *Todaropsis* are restricted to the Atlantic Ocean.

It is evident from this analysis that *Illex* and *Todaropsis* are among the most restricted genera of the Ommastrephidae, with *Illex* being distributed along both sides of the Atlantic Ocean and *Todaropsis* limited to the eastern Atlantic.

According to Allee & Schmidt (1951), the geologic age of a group has an important bearing on the extent of its distribution, and the greater geologic age seems to be an important factor in the wide distribution of categories such as genera and families (p. 149). One of the important assumptions of their "area and age" theory is that the organisms "just spread steadily in all possible directions from their places of origin" (Darlington, 1957, p. 548). Evidently this "spreading equally in all directions" (Darlington, 1957, p. 549) cannot be universally true, as it may be complicated by the presence of physical and ecological barriers and other factors. An understanding of the real causes of the restricted distribution of *Illex* and *Todaropsis* cannot be elucidated by a systematic study alone, but rather, must await information from extensive studies of permissive environmental and ecological factors as they affect all the genera.

The above factors used in a study of the generic relations of the ommastrephids are summarized in Table 22. From the table it is clear that *Illex* differs from other ommastrephid genera in many respects. It is likely that *Illex* is among the most recently evolved genera in the family Ommastrephidae.

Interspecific relationships will be discussed later.

Table 22

Analysis of subfamilies and genera of squid of the family Ommastrephidae with respect to selected features and oceanic distribution

	Foveolae (+ or -)	Lateral pockets (+ or -)	Carpal knobs (+ or -)	No. of rows of suckers on dactylus	Photophores	Hectocotylus		Site of spermatophore deposition upon transplantation	Distribution		
						One arm	Both arms		Atlantic Ocean	Pacific Ocean	Indian Ocean
Subfamily Ommastrephinae											
Ommastrephes	+	+	+	4	+	+	-	buc. m.	+	+	+
Dosidicus	+	+	+	4	+				-	+	-
Ornithoteuthis	+	+	+	4	+	+	-	buc. m.	+	+	-
Hyaloteuthis	+	+	+	4	+				+	+	-
Symplectoteuthis	+	+	+	4	+	+	-	buc. m.	-	+	+
Subfamily Todarodinae											
Todarodes	+	-	-	4	-	+	-	buc. m.	+	+	+
Nototodarus	+	-	-	4	-	-	+	buc. m.	-	+	+
Subfamily Illicinae											
Illex	-	-	-	8	-	+	-	m. c.	+	-	-
Todaropsis	-	-	-	4	-	-	+	buc. m.	+	-	-

+ = present
- = absent
buc. m. = buccal membrane
m.c. = mantle cavity

PART III. ZOOGEOGRAPHY

An Outline of the Atlantic Ocean Oceanography

Since the squids of the genus *Illex* are only confined to the Atlantic Ocean, it is essential to briefly outline the oceanography of this ocean in order to discuss the zoogeography of the genus.

The Atlantic Ocean was the first of the world's oceans to be explored and for long has been the best known. According to Sverdrup, et al., (1942) "The Atlantic Ocean extends from Antarctica northward and includes the North Polar Sea. It is separated from the Pacific Ocean by the line forming the shortest distance from Cape Horn (70°W) to the South Shetland Islands, and the boundary between the Atlantic and the Indian Oceans is placed at the meridian of the Cape of Good Hope (20°E)". Sverdrup's definition of an ocean includes the "semi-enclosed adjacent seas that connect with them" (p. 11). Thus, the Atlantic Ocean is that water body bounded by the Americas on the west, Eurafrica on the east, the shores of Antarctica on the south, and in the north includes the Arctic Ocean separated from the Pacific Ocean by the Bering Strait. Since *Illex* has never been recorded from the Arctic Ocean and the Southern Ocean, a review of the oceanography of these is omitted. The latter has recently been reviewed by Roper (1969).

For the convenience of discussion, the Atlantic Ocean proper and its marginal seas where *Illex* has been recorded will be treated separately. The data on which this outline is based are from Dietrich (1957), Ewing & Edgar (1966), Fairbridge, et al., (1966), Harding & Nowlin (1966), Ichiye (1962), King (1963), Montgomery (1958), Nowlin (1971), Parr (1937), Packard (1963) and Sverdrup, et al., (1942).

Water Masses

The water masses are stratified in the oceans according to their density, the most dense sinking to the greatest depth. Each individual water mass is identified by its characteristic temperature-salinity (T-S) relationship.

North Atlantic Ocean

On the surface of the North Atlantic Ocean, the North Atlantic Central Water covers a wide area but is restricted to shallow depths. This water mass is characterized by a nearly straight T-S curve between the points T = 8°, S = 35.10^{o}/oo and T = 19°, S = 36.70^{o}/oo. This water was found at all stations sampled by the Atlantis (A), the Armauer Hansen (AH), the General Greene (GG), and the Meteor (M), except at station GG 1990 to the south of Cape Farewell on Greenland, at station A 1175 at 6°15'N, and at AH 14a, south of Iceland. Water at A 1175 originates in the South Atlantic Ocean and is carried across the Equator. The water to the south of Cape Farewell corresponds to subantarctic water.

Below the North Atlantic Central Water, three types of intermediate strata are found. At station A 1175, the Antarctic Intermediate Water is present and is characterized by a salinity of 33.8^{o}/oo and a temperature of 2.2°. Originating in the South Atlantic Ocean and due to a lack of a well-defined equatorial water mass in the Atlantic, it extends across the Equator and can be traced as far north as 20°N. Arctic Intermediate Water is found at GG 1990 and AH 14a and it is characterized by a temperature of 3.5° and a salinity of about 34.88^{o}/oo. It is formed to the east of the Grand Banks of Newfoundland but only in small quantities. In the eastern Atlantic, a third type of water of high salinities is found at stations AH 43, AH 58, and M 272. The Mediterranean water that flows out along the bottom of the Strait of Gibraltar has a salinity of 38.1^{o}/oo and a temperature of 13.0°. This water is rapidly mixed with surrounding Atlantic water and spreads between the sigma-t surfaces sigma-t = 27.6 and sigma-t = 27.8. This water mass is also referred to as the North Atlantic Deep Water, occupying depths of from 1500-4000 m.

The upper layers of the North Atlantic are rich in oxygen. At depths between 500-900 m an oxygen minimum is found, except in the northern part of the ocean. In this layer, the oxygen content at the eastern side is considerably lower (1 ml/1) than at the western (3 ml/1).

Below the minimal oxygen layer the oxygen content increases with depth. The oxygen content of this deep water decreases from north to south. In the Irminger Sea, where the North Atlantic Deep Water is formed, the oxygen content is higher than 6.5 ml/1 at all depths. The oxygen content decreases to about 5.5 ml/1 at the Equator, and to less than 5 ml/1 at 45°S.

South Atlantic Ocean

A well-defined water mass is to be found in the upper layers between 41°S and the Equator. This mass is characterized by a nearly linear T-S relationship between the points T = 6°, S = 34.5°/oo and T = 18°, S = 36.0°/oo. It is called the South Atlantic Central Water and extends across the South Atlantic, extending north of the Equator (the thermal Equator being situated at 5°N). Like its northern counterpart,this water mass is shallow, rarely exceeding 600 m in depth.

The Antarctic Intermediate Water is formed at the surface near the Antarctic Convergence (between about 45° and 55°S). It is characterized by a salinity minimum, since at the latitudes of its formation precipitation exceeds evaporation. From its place of origin, with a salinity of about 33.8°/oo and a temperature of 2.2°C, this water sinks to depths of about 900 m while spreading northward mainly in the western part of the oceans. In the equatorial region the Antarctic Intermediate Water rises to about 800 m and can be traced to about 20°N.

Due to freezing in waters close to the Antarctic Continent, dense water with a temperature of -1.9° and a salinity of 34.63°/oo is formed. This mixes with some of the warmer North Atlantic Deep Water in the circumpolar current system, sinking to the bottom. Consequently, there is a potential temperature of -1.0°, with a salinity of 34.65°/oo. This water, the Antarctic Bottom Water, is channeled along the South Sandwich Trench into the western Atlantic Ocean where it can be traced to 40°N. Northward penetration into the eastern Atlantic Ocean is blocked by the

Walfish Ridge, while Antarctic Bottom Water enters the eastern Atlantic through a break in the Mid-Atlantic Ridge in the vicinity of the Equator.

Near the Equator, the oxygen content of the South Atlantic Central Water is low, with minimum values less than 0.5 ml/1 to be found at a depth of 350 m off west Africa. Such minimum values are less pronounced off the coast of South America, where minimal values of about 3 ml/1 have been recorded. The Antarctic Intermediate Water is characterized by a high oxygen content. Below the Intermediate Water an oxygen minimum is found (less than 4.5 ml/1), while in deep water the oxygen content is about 5 ml/1.

The Caribbean Sea and the Gulf of Mexico

The Caribbean Sea has as a section of its boundary, an arc of islands, called the Antillean chain, which is divided into two parts, the Greater and Lesser Antilles. The Greater Antilles are made up of the islands of Cuba, Hispaniola, Puerto Rico and Jamaica, forming the northern boundary of the Caribbean Sea. The Lesser Antilles are composed of many small islands which follow an arc running southeast from the Anegada Passage turning south to join the continential shelf of South America, and forming the east boundary of the Caribbean Sea. The southern boundary is the northern coasts of Venezuela and Colombia. The Isthmus of Panama and the east coast of Central America form the rest of the southern and southwestern boundaries. The 220 km wide Yucatan Strait separates the Caribbean Sea from the Gulf of Mexico.

The Gulf of Mexico opens into the Atlantic Ocean through the Straits of Florida in the east. The sill depths in the Yucatan Channel and the Straits of Florida are approximately 1600 m and 800 m, respectively. Therefore, the waters of the North Atlantic can pass freely through the Caribbean Sea and the Gulf of Mexico at depths less than 800 m. At greater depths, communication with the water bodies of the Atlantic Ocean is more or less restricted.

The water masses of the upper layers of the Caribbean Sea are similar in characteristics to those of adjacent North Atlantic waters. These upper waters are chiefly North Atlantic in origin, but they also contain considerable quantities of South Atlantic water. These waters are the surface waters and the Subtropical Underwater (50-200 m). They are separated from the cold water layers, namely, the Subantarctic Intermediate Water (700-850 m) and the North Atlantic Deep Water (1800-2500 m) by a layer of low oxygen (below 3.0 ml/l) water at 400-600 m. The waters between these layers are made up of a mixture of cold water due to normal vertical mixing processes.

Winter surface salinity values are highest along the South American coast ($>36^{o}/oo$). They decrease to the north, becoming less than $35.5^{o}/oo$ in the northern half of the Caribbean Sea. In the Cayman-Yucatan Basins, the salinity is highest south of Cuba ($>36^{o}/oo$) and decreases toward the southwest to the coast of Honduras ($<35.5^{o}/oo$).

In summer, the higher precipitation and greater land runoff make the surface salinities about 0.5°/oo lower in the south and up to 1.0°/oo lower in the north.

The Subtropical Underwater is a layer of maximum salinity and slopes down from depths of 50-100 m in the south to 200 m in the north. The salinity is greater than 37°/oo in the eastern Venezuela Basin, decreasing to 36.7°/oo at the Yucatan Channel.

The Subantarctic Water is characterized by absolute salinity minimum, sloping from depths of 600-700 m in the south to 800-850 m in the north. This layer is thicker in the south. West of 65°W the northern part of the Subantarctic Water thins, disappearing before reaching the northern land boundaries. The salinity is slightly less than 34.7°/oo in the east, and increases to the westward.

Below the Subantarctic Water is the North Atlantic Deep Water. Its salinity is slightly under 35°/oo and is fairly homogeneous.

The temperature of the Caribbean Sea is of tropical characteristics and a well-developed thermocline exists at 100-200 m. Below 1500 m, the temperature is about 4°C. At great depth (below 3000 m) the temperature is a few tenths of a degree warmer. Surface temperatures in late summer are 28.3°C in the south and 28.9°C in the north, winter temperatures being about 3° lower. The surface temperatures in the

Caribbean demonstrate small gradients with little seasonal variation. There is no seasonal variation at depths greater than 150 m.

The oxygen content in the Caribbean Sea is about 4.2 ml/1 at the surface with a minimum below 3.0 ml/1 existing at 500 m depth. Below this depth, values increase to a maximum of over 5.5 ml/1.

The surface temperature of the waters of the Gulf of Mexico in February (the coolest month) is about 18°C in the north and 24°C off the coast of Yucatan. Over the central Gulf the surface water salinity is greater than 36.0^{o}/oo, generally within the range 36.0 - 36.3^{o}/oo. The salinity of the nearshore surface water is influenced by local runoff and river discharge, evaporation, the intrusion of water from the Caribbean, and upwelling. The waters of the Mississippi River have been reported to a depth of 50 m and 150 km from the coast, with a consequent reduction of the salinity of the sea water to less than 35.5^{o}/oo. The surface salinity is reduced greatly near the river mouth and salinities less than 25^{o}/oo have been reported several miles offshore.

The waters of minimum salinity occur near the bottom of the major thermocline in the Gulf of Mexico. These are the last remnants of the Antarctic Intermediate Water, with a salinity of 34.86^{o}/oo and a temperature of 6.2°C at the Yucatan Channel. The depth of this layer is about 850-1000 m at the Yucatan Channel, becoming shallower in the Gulf proper, where it has been recorded as shallow as 550 m. At 1500 m the temperature and salinity are about 4.22°C and 34.97°/oo, respectively. Below 2000 m very small increases in mean temperature and salinity continue to the bottom. These increases are less than or equal to 0.1°C and about 0.002°/oo per thousand meters.

The data on the oxygen content in the Gulf of Mexico are fragmental. According to Dietrich (1939, *fide* Williams, 1954, p. 145), the oxygen content at a station in the western Gulf (25°47'N 94°23'W) was reported to be about 4.8 ml/l at the surface, increasing to about 4.9 ml/l at 25 m, then decreasing to a minimum of 2.35 ml/l at 300 m. Thereupon, it gradually increased to about 5.0 ml/l at 2400 m and remaining constant to depths of 3400 m.

The Mediterranean Sea

The water masses of the Mediterranean Sea are different in character from those of the adjacent North Atlantic. The surface salinity is higher than 37.00°/oo, exceeding 39°/oo to the south of Asia Minor. It is considerably lower in the inner portion of the Adriatic Sea and the Agean Sea, where considerable amounts of river water or surface water from the Black Sea are added. This is also true along the north coast of Africa as far east as Tunisia, where the surface current flows east from the Strait of Gibraltar.

Surface temperatures increase from the Strait of Gibraltar to the inner portions of the Mediterranean, except in winter, when the lowest surface temperatures are found in the most northern portions.

Seasonal variations in temperature are great, about 9° in most places and reaching 13° to 14° off the Riviera and in the northern part of the Adriatic Sea.

Below the surface water, there are four different water masses, namely, intermediate, transition, deep, and bottom water.

The surface layer extends to a depth of 100 to 200 m. Below this is a layer of intermediate water which is characterized by a salinity maximum at 300 to 400 m. In the western Mediterranean a temperature maximum is also present at the same depth, however in the eastern portion only a second layer of small temperature decrease is found. The intermediate water extends to about 600 m depth, where both temperature and salinity decrease rapidly. This decrease continues within the transition layer which extends to about 1500 m. Below the intermediate water are the deep and bottom waters. At about 1500 m a temperature minimum is found, while at greater depth temperatures increase slightly towards the bottom.

The surface water of the Mediterranean Sea, extending to a depth of 100 to 200 m has a high oxygen content. In the intermediate water the oxygen content is higher in the east. Conversely, in the transition layer, an oxygen minimum is found which is more pronounced in the eastern part. The deep water has a somewhat higher oxygen content. To demonstrate the oxygen distribution in the Mediterranean Sea, Table 79 of Sverdrup, et al., (1942, p. 650) is reproduced here and presented as Table 23.

Table 23

Characteristics of the oxygen distribution in the Mediterranean

Location		Depth (m)	Temp. (°C)	S ($^o/oo$)	O_2 (ml/l)
At salinity maximum	Ionian Sea	250	14.59	38.83	4.84
	Tyrrhenian Sea	420	13.91	38.65	4.30
	Balearic Sea	390	13.18	38.47	4.16
At oxygen minimum	Ionian Sea	1180	13.59	38.68	4.01
	Tyrrhenian Sea	960	13.30	38.51	4.12
	Balearic Sea	580	13.07	38.44	4.10
Below 2000 m	Ionian Sea		13.67	38.64	4.14
	Tyrrhenian Sea		13.23	38.41	4.25
	Balearic Sea		13.06	38.39	4.55

Fig. 209B of Sverdrup, et al., (1942, p. 741) is redrawn (after Pickford, 1946, p. 28) and presented as Fig. 31 to show the temperature-salinity relations of the principal water masses of the Atlantic Ocean.

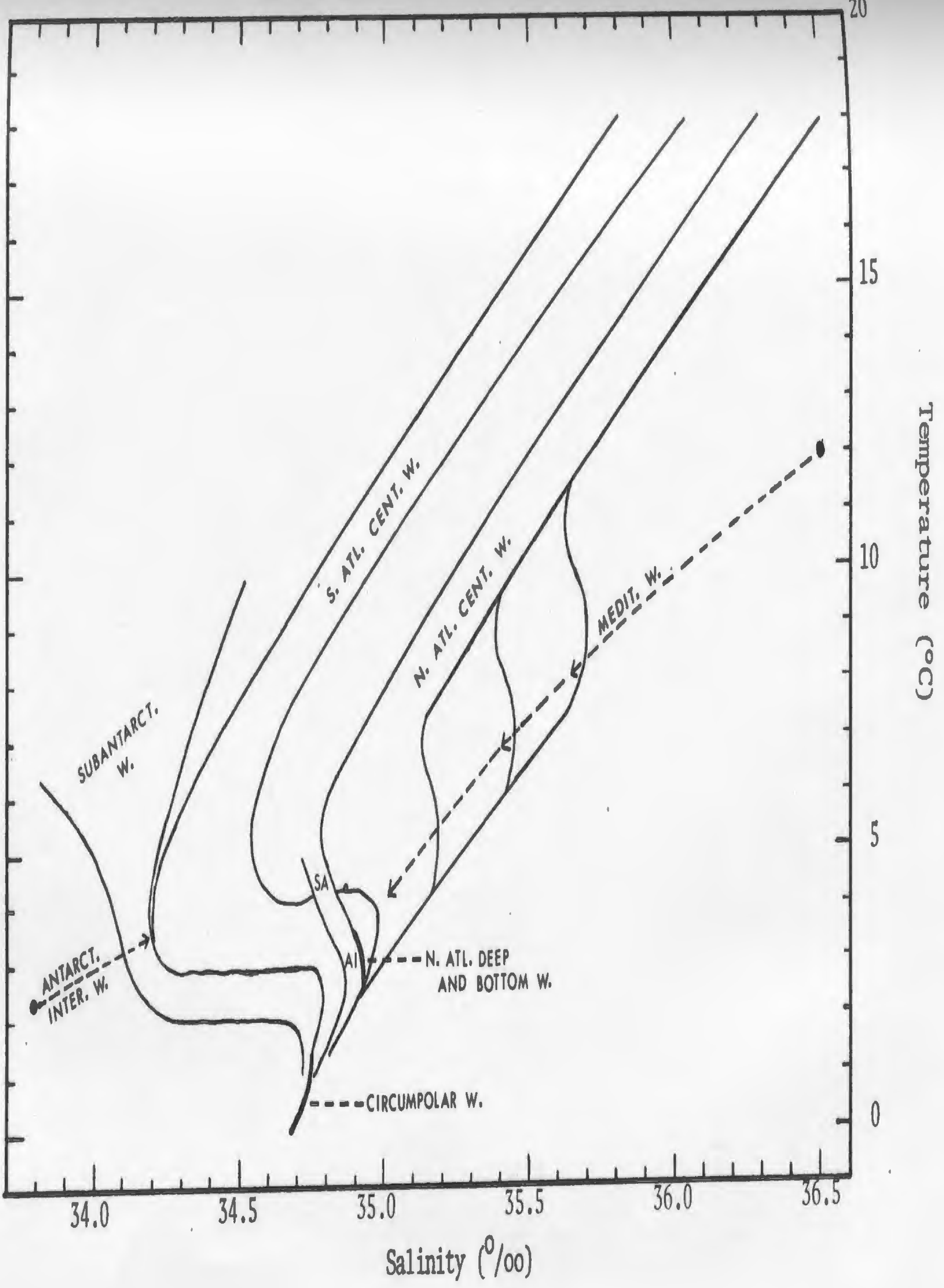
Upper Water Circulation in the Atlantic Ocean

The currents in the North Atlantic Ocean are dominated by the North Equatorial Current and the Gulf Stream system. The Equatorial Current flows east to west in the trade-wind region. It bends to the north when approaching the Mid-Atlantic Ridge and to the south after

FIGURE 31. Temperature-salinity relationships of the principal water masses of the Atlantic Ocean (after Pickford, 1946).

SA = Subarctic Water

AI = Arctic Intermediate Water



SUBANTARCT. W.
S. ATL. CENT. W.
N. ATL. CENT. W.
MEDIT. W.
ANTARCT. INTER. W.
SA
AI
N. ATL. DEEP AND BOTTOM W.
CIRCUMPOLAR W.
20
15
10
5
0
Temperature (°C)
34.0
34.5
35.0
35.5
36.0
36.5
Salinity (⁰/oo)

having passed the Ridge. In the western Atlantic the North Equatorial Current joins the branch of the South Equatorial Current. As mixing takes place between them, the waters in the Caribbean Sea become intermediate in character. The North Equatorial Current terminates in the current through the Yucatan Channel and the Antilles Current. The continuation of these currents marks the beginning of the Gulf Stream system. Iselin (1936, *fide* Sverdrup, et al., 1942, p. 672) defined the "Gulf Stream System" to include the whole northward and eastward flow, beginning at the Straits of Florida and including the various branches and whirls found in the eastern North Atlantic that can be traced back to the region south of the Newfoundland Banks. This system can be subdivided into three parts:

1. The Florida Current: The Florida Current starts from the Straits of Florida, moving northward along the continental slope to a point off Cape Hatteras where it ceases to follow the slope. This current can be traced back to the Yucatan Channel and it is joined by the Antilles Current after passing the Straits of Florida.

2. The Gulf Stream: The point off Cape Hatteras where the Florida Current turns eastwards marks the beginning of the Gulf Stream. The latter flows northeastward to the east of the Grand Banks at about 40°N 50°W where it begins to bifurcate.

3. The North Atlantic Current: As noted, at about 40°N 50°W, the Gulf Stream branches. The branch which flows east and north is called the North Atlantic Current. This branches at about 30°W. The northern branch, carrying a mixture of waters of Gulf Stream and Labrador Current, flows east-northeastwards and again divides. Part of the water flows across the Wyville Thompson Ridge into the Norwegian Sea, forming the Norwegian Current, while part turns north and northwestwards to form the Irminger Current along the southern coast of Iceland. A small portion of the Irminger Current flows around the west coast of Iceland, the greater portion of the water turning south to mix with the East Greenland Current. The southern branch of the North Atlantic Current flows about 45°N, carrying undiluted Gulf Stream water. It crosses the Mid-Atlantic Ridge and turns to the south between the Azores and Spain. Some of this water enters the Mediterranean Sea as a surface current through the Strait of Gibraltar and flows out again through the sill as water of very high salinity at intermediate depths. The Azores and Hispanic portion of the flow forms the Canary Current along the northwest coast of Africa. It continues to flow south, finally joining the North Equatorial Current.

The continuation of the Norwegian Current flows to the north to the Arctic Sea. The returning flow is the East Greenland Current, which is enhanced by the Irminger Current and additional water from the North Atlantic Current. This water flows along the east coast of Greenland and turns north along the west coast of Greenland, now to become the West Greenland Current. This current flows into Baffin Bay and the Labrador Sea. The Labrador Current flows south, in the western portion of the Labrador Sea, meeting the North Atlantic Current southeast of the Grand Banks.

Between the North and South Equatorial Currents is the Equatorial Counter Current, which flows to the east. This merges into the easterly flowing Guinea Current on the eastern side of the ocean, meeting the Benguela Current in the Gulf of Guinea.

In the South Atlantic Ocean, the Benguela Current flows northwards along the west coast of South Africa. It flows away from the coast to join the SouthEquatorial Current. The South Equatorial Current, generated by the trade-winds, flows westward. It extends north of the geographical Equator into the Northern Hemisphere, dividing at Cape Sao Roque off the east coast of Brazil. Part flows northwestwards, joining the North Equatorial Current to enter the Caribbean Sea, while part flows south as the Brazil Current along the east coast of South America. The Brazil Current flows southwards to about 30°S where it meets the cold, northerly-flowing Falkland Current from the Southern Ocean. These waters then turn east as the West Wind Drift, flowing across the South Atlantic Ocean, hence completing the surface circulation of the South Atlantic Ocean.

Vertical Distribution and Relation to Hydrographic Conditions

Despite the numerous publications concerning cephalopods, information regarding their vertical distribution is relatively sparse and incomplete. Among those that treat of the vertical distribution of one or more species in detail, there are several that are especially valuable. These are those of Bruun (1943), Clarke (1966, 1969), Gibbs & Roper (1970), Pickford (1946), Roper (1969, 1972), Roper & Young (MS), and Voss (1967).

This treatment represents an accumulation and correlation of the little information that exists concerning the vertical distribution of species of *Illex*. The data available for each species are first presented, then followed by a general discussion of vertical distribution throughout the genus.

The environmental data on *I. illecebrosus* in Newfoundland waters are taken from the manuscript report prepared by Snelgrove (1966) for the then existent Department of Fisheries of Canada. For *I. coindetii* Adam's (1952) data are incorporated with data from the GE, O and O II cruises or expeditions.

Illex illecebrosus

Joubin (1894, p. 216) reported the capture of *I. illecebrosus* at 42°9'3"N 44°7'45"W on the surface in July, 1887. Chun (1913, p. 5) reported its capture by the Michael Sars on the Newfoundland Banks at

70-75 m depth in July, 1910. In 1924, Joubin reported it at 43°26'N 59°3'W at depths ranging from 0-2500 m (August 26, 1913, Sta. 3452).

During this species' in-shore migration in Newfoundland waters, it is captured in shallow water about 15-30 m deep. Occasionally, they are seen at the surface. They have been reported in the coastal waters from mid-July to early November.

Boone (1933, p. 168) recorded *I. illecebrosus* at a point 9 miles SW by W of Port-aux-Basques, Newfoundland, from a depth of 366 m on September 1, 1926. On the Grand Banks, it has been taken from 55-366 m during the months of May and June (Squires, 1957, pp. 702-703).

Leaving the Newfoundland area, further south in the Chesapeake Bay area, it is taken at the surface and to depths of 500 m. The greater majority of these are from the upper 150 meters (Fig. 32). Off the Floridan coast (O 6800, O 6801) they have been taken from 333-383 meters (month of July, 1967).

By plotting the time of capture against the depth of capture, it appears that *I. illecebrosus* is closely associated with the bottom. Only the data accompanying the materials from the Chesapeake Bight area (VIMS and ATC materials) contain the information necessary for this analysis. Of the total 54 otter trawl hauls made by VIMS in August, 1967, 46 were made during the daylight hours while eight were night hauls. Of the 22 successful catches represented by the collections studied, only

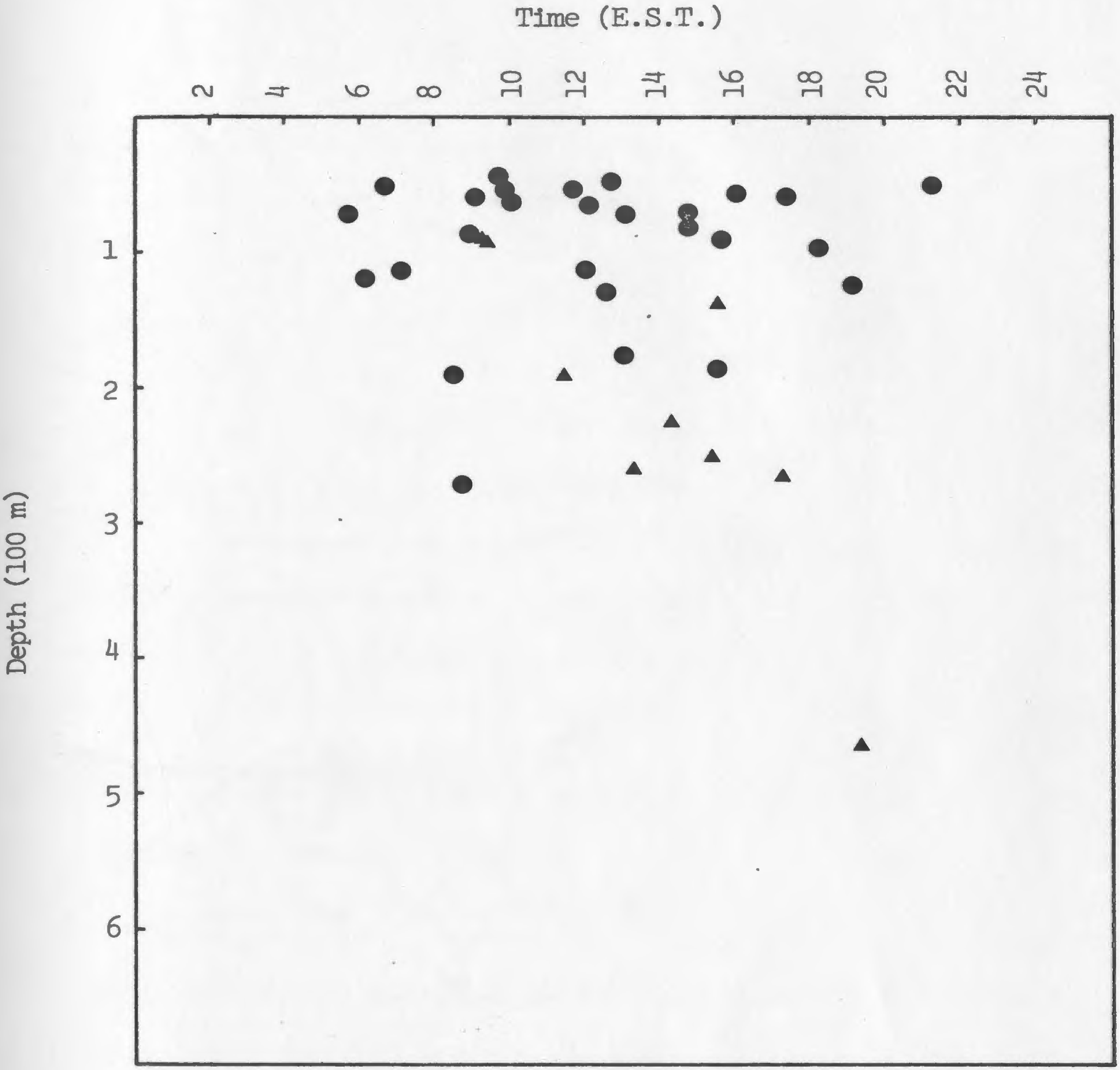


FIGURE 32. Graphic plotting of the depth and time of capture of *Illex illecebrosus* in the Chesapeake Bay region.

● = VIMS data

▲ = ATC data

two catches were made at night. In August, 1968, a total of 64 otter trawl hauls was made by the ATC, of which nine were made at night. According to Mercer (1969b, p. 6) all otter trawl sets except four (day hauls) in Raleigh Bay, North Carolina, successfully captured *Illex*. As only part of the capture was retained for study, only those catches represented in the collection can be identified to the species level. It must be pointed out that all VIMS catches are not necessarily represented in the collection, therefore the information regarding the negative hauls may not be conclusive. In Fig. 32 is shown the depth and time (EST) of the successful catches in the VIMS and the ATC collections.

From the available data, there appears to be little, if any, correlation between the temperature of the sea surface and the depth of capture of *I. illecebrosus* (Figs. 33 and 34).

The relationship between the depth of capture and the bottom temperature (the temperature of capture) is shown in Fig. 35 and Fig. 36. No clear interpretation can be found between the depth of capture and bottom temperature.

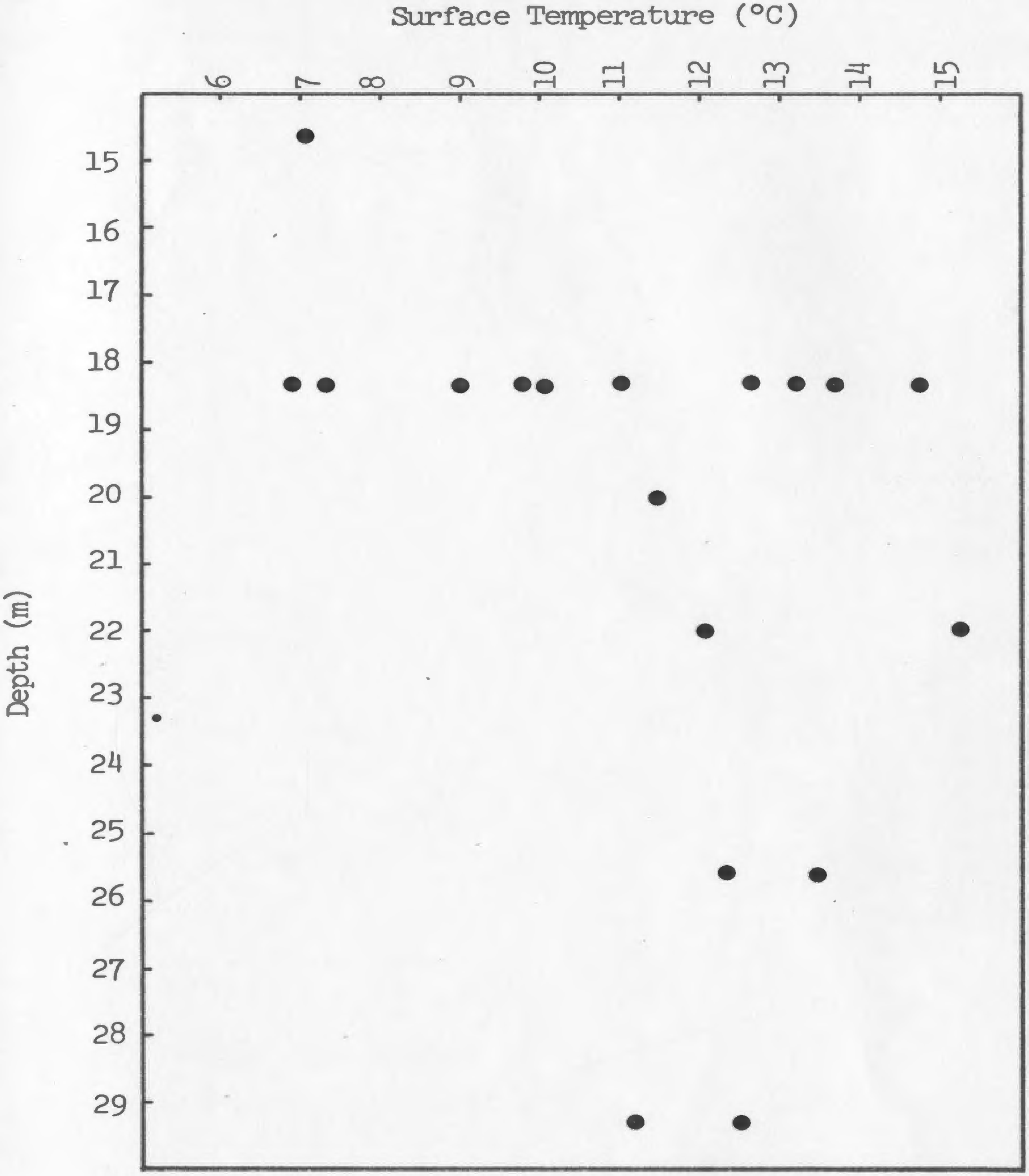


FIGURE 33. Graphic plotting of the depth of capture of *Illex illecebrosus* in the Newfoundland area and the coincident surface water temperature.

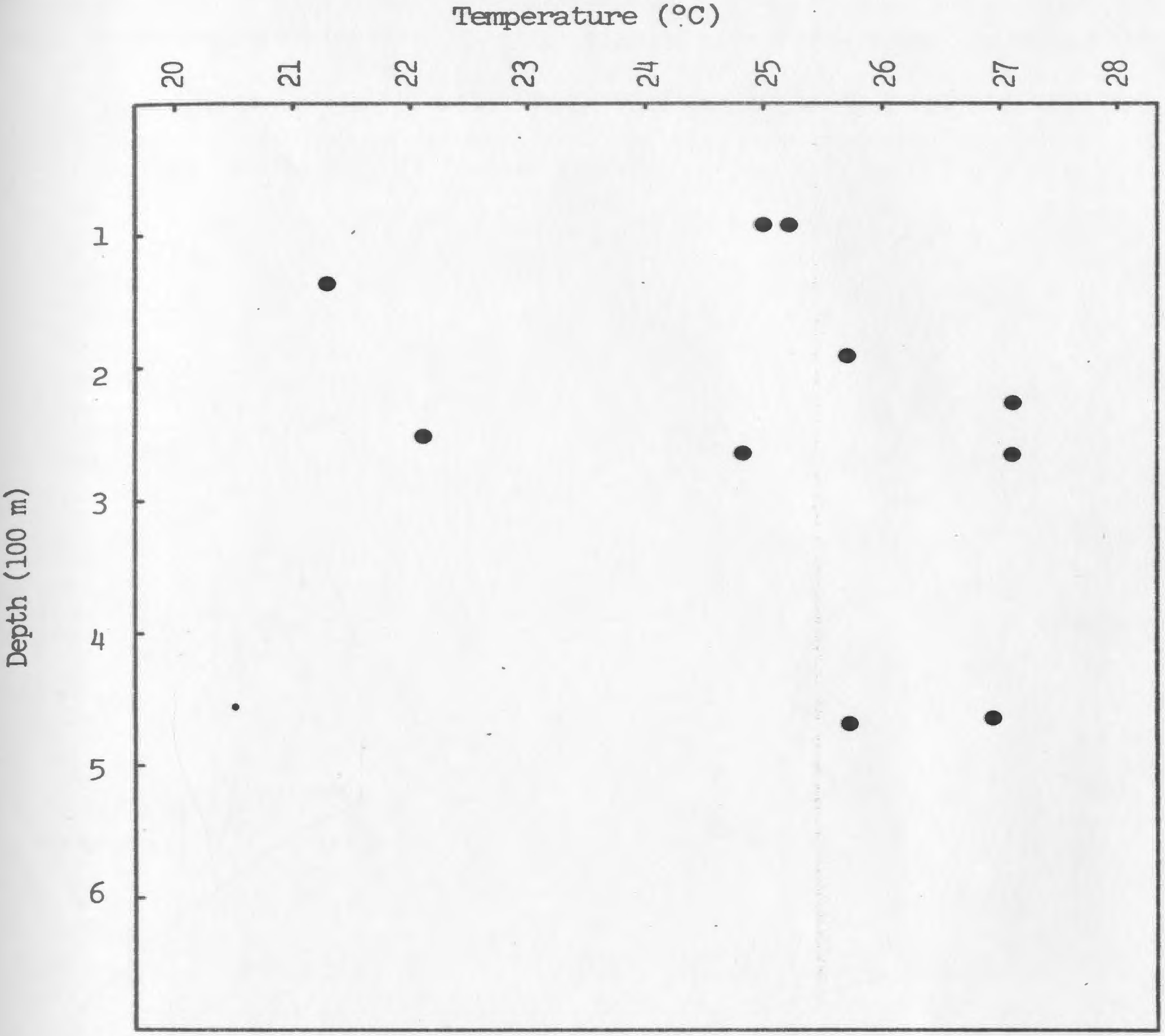


FIGURE 34. Graphic plotting of the depth of capture of *Illex illecebrosus* in the Chesapeake Bay area and the coincident surface water temperature.

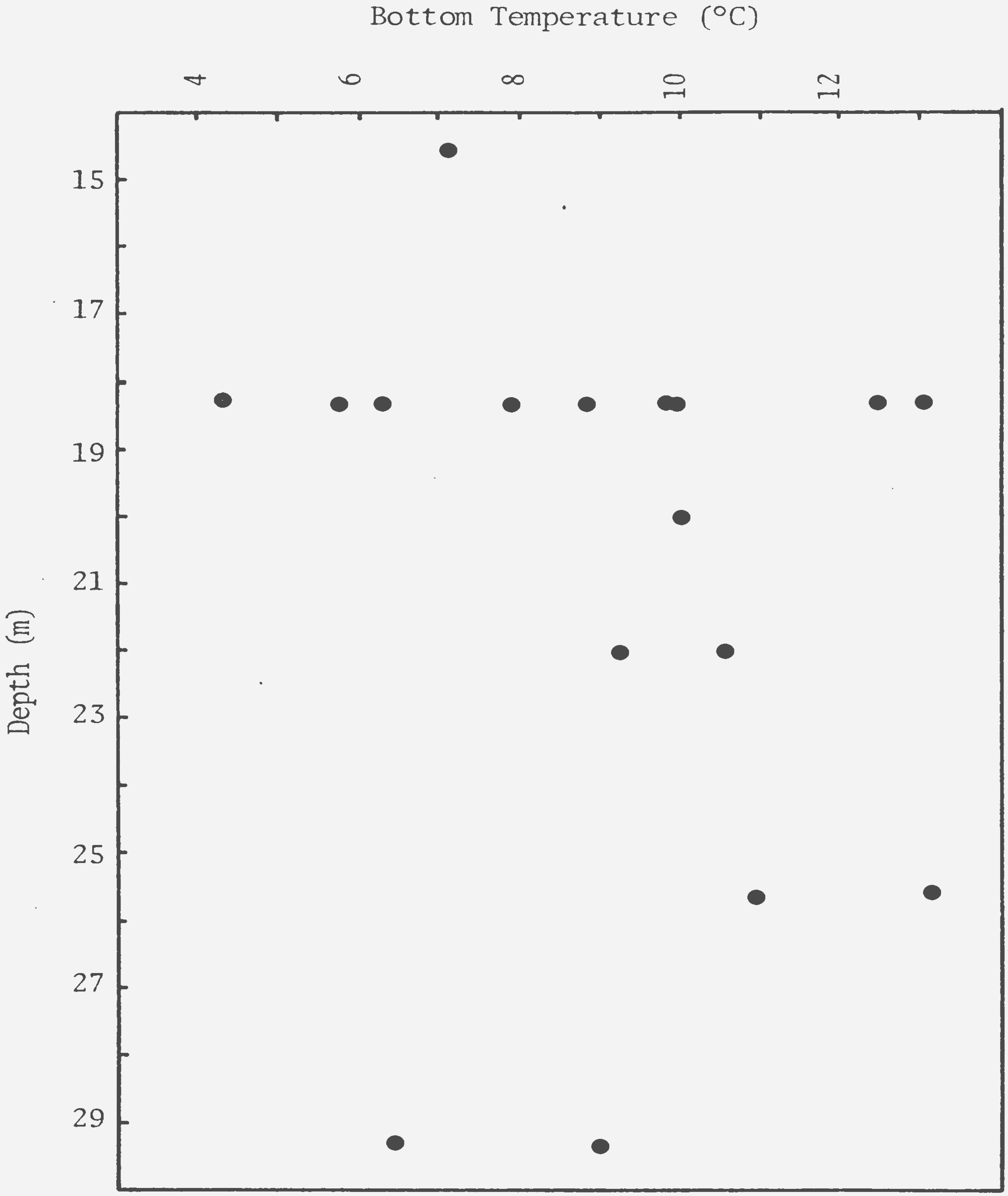


FIGURE 35. Graphic plotting of bottom water temperature and the depth of capture of *Illex illecebrosus* in the Newfoundland area.

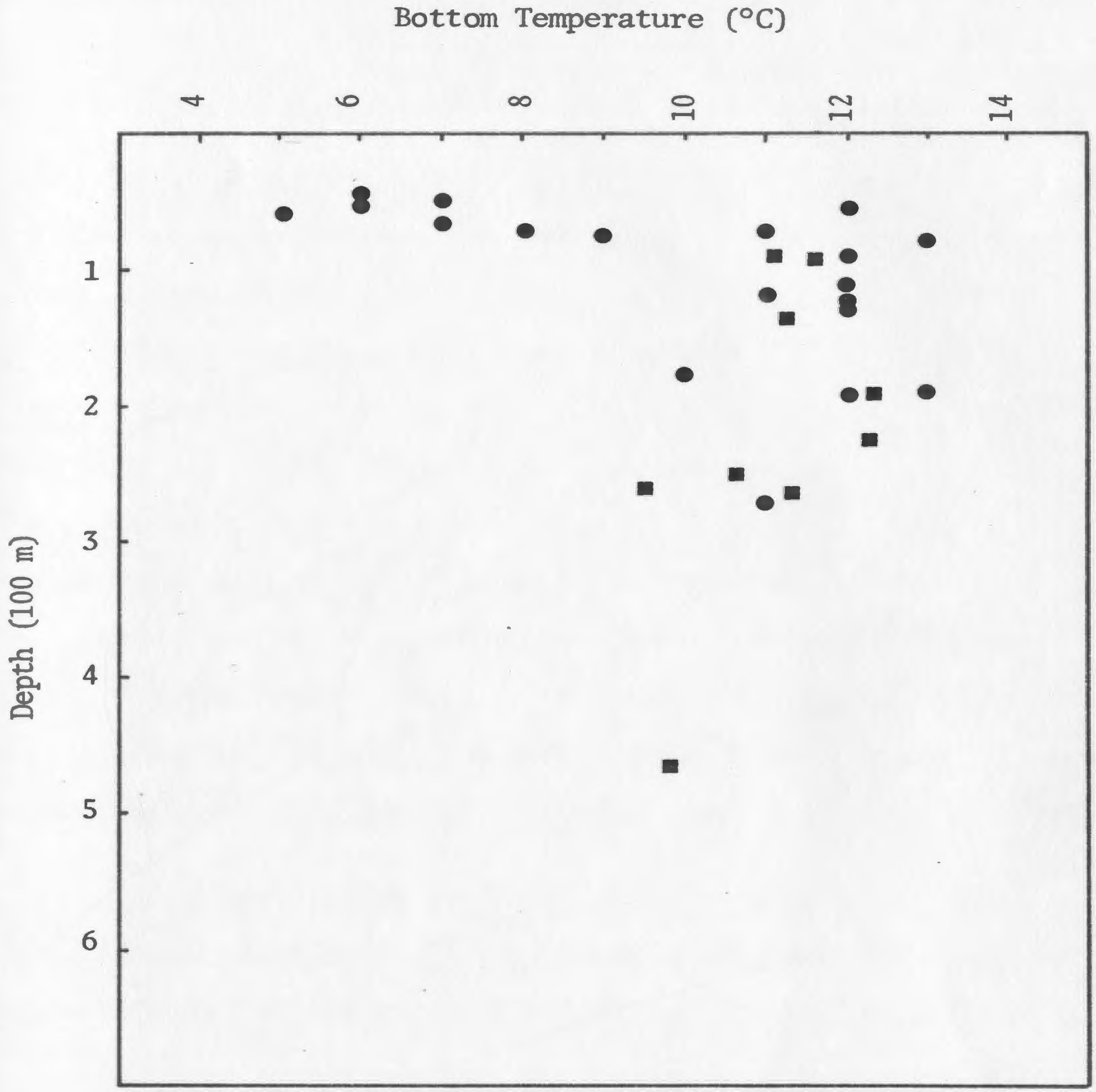


FIGURE 36. Graphic plotting of bottom water temperature and the depth of capture of *Illex illecebrosus* in the Chesapeake Bay area.

● = VIMS data

■ = ATC data

Illex coindetii

In the eastern Atlantic Ocean, Jatta (1896, p. 75) reported *I. coindetii* from 50-250 m depth over sandy bottom in the Gulf of Naples. During the Michael Sars expedition, Chun (1913, p. 5) reported it from 100-280 m, in May, 1910, around the coast of Morocco. Joubin (1920, pp. 82-83) reported the species taken by the Princesse Alice in July of 1903 off the west coast of France from depths of 130-358 m over fine sand or silt bottom. The three lots of specimens taken by the Cryos from the same area around the end of April and early May of 1970 were taken from 94-180 m. The Danish ship Thor obtained two larval *I. coindetii* by young fish net (Jungfisch-Netz) around the Azores in August of 1910 (Degner, 1925, p. 40).

In the Blanes region of Spain, Morales reported (1958, p. 22) that *I. coindetii* is fished all year round at depths between 112-400 m, particularly from 160-320 m, on silt beds.

Along the Algerian coast, Dieuzeide (1955, *fide* Mangold-Wirz, 1963b, p. 157) reported that it is fished from 50-550 m, particularly between 200-250 m. In the Port-Vendres and Las Rosas region they are found at 40-500 m during the daytime and ascend in the night in "the superficial layer" (Mangold-Wirz, 1963b, p. 158).

Off the west coast of Africa, Adam (1952, pp. 82-83) reported *I. coindetii* from 48-500 m, with the average depth being 191.2 m. Only one of the 57 stations listed by Adam is of rocky bottom, four are of a mixture of rock and sand, or silt, and the remaining 52 stations are of sand, silt or a mixture of both.

During the Geronimo cruise in September 1963 in the Gulf of Guinea, it was taken from 99-406 m depths. The Pillsbury cruises of May, 1964 and 1965, collected *I. coindetii* from 37-485 m in the same area(Voss, 1966a; Bayer, 1966; and the present study).

Off the Cameroun Republic, Crosnier (1964, p. 36) reported that *I. coindetii* is to be found only below the thermocline. The station data of the catches show the depth range to be 45-90 m over sand or silt bottom.

In the northern limit of their range, off Cape Hatteras, in the western Atlantic Ocean, *I. coindetii* is represented by only four records, in depths ranging from 54-191 m. Further south, in the Straits of Florida region, the depth range of the four stations represented in this study (GD 1012, O II 10859, 10862, 10863) is 356-522 meters. In the Gulf of Mexico proper from where a large number of specimens were available for study, it is reported from 25-1080 m, the greater majority being from 200-550 m.

In the Caribbean Sea the species has been taken from relatively shallow water (Pelican 127, 5-9 m) down to 671 m (O II 10835), with the majority of collections at 400-600 m.

Illex coindetii, at least in the Gulf of Guinea, appears to be associated with the bottom, especially during the day. Of the 49 bottom trawls made by the Geronimo during its 1963 cruise, only eight were made at night. Of the 13 successful captures represented in the collection, only one was made at night. This fact suggests that the squid are more closely associated with the bottom of the Gulf during the day and disperse during the night. In Fig. 37 is shown the depths and time (GMT) of the successful catches in the Gulf of Guinea, based on the Pillsbury and Geronimo data.

The water temperatures of the sea surface appear to be inversely correlated with the depth of capture of *I. coindetii*. In Fig. 38 is shown the depth and sea surface temperatures of successful captures of *I. coindetii* in the Gulf of Guinea, Gulf of Mexico and the Caribbean Sea. It is, however, not clear whether the resultant graph (Fig. 38) is merely a reflection of the different trawling depths in combination with the different temperatures in the different regions, or if it is a reflection of the true phenomenon.

The relationship between the depth of capture of *I. coindetii* and the bottom temperature (temperature at the depth of capture) is clear, as can be seen in Fig. 39.

Illex argentinus

Almost nothing is known about the vertical distribution of *I. argentinus*. The material used in this study is not suitable for

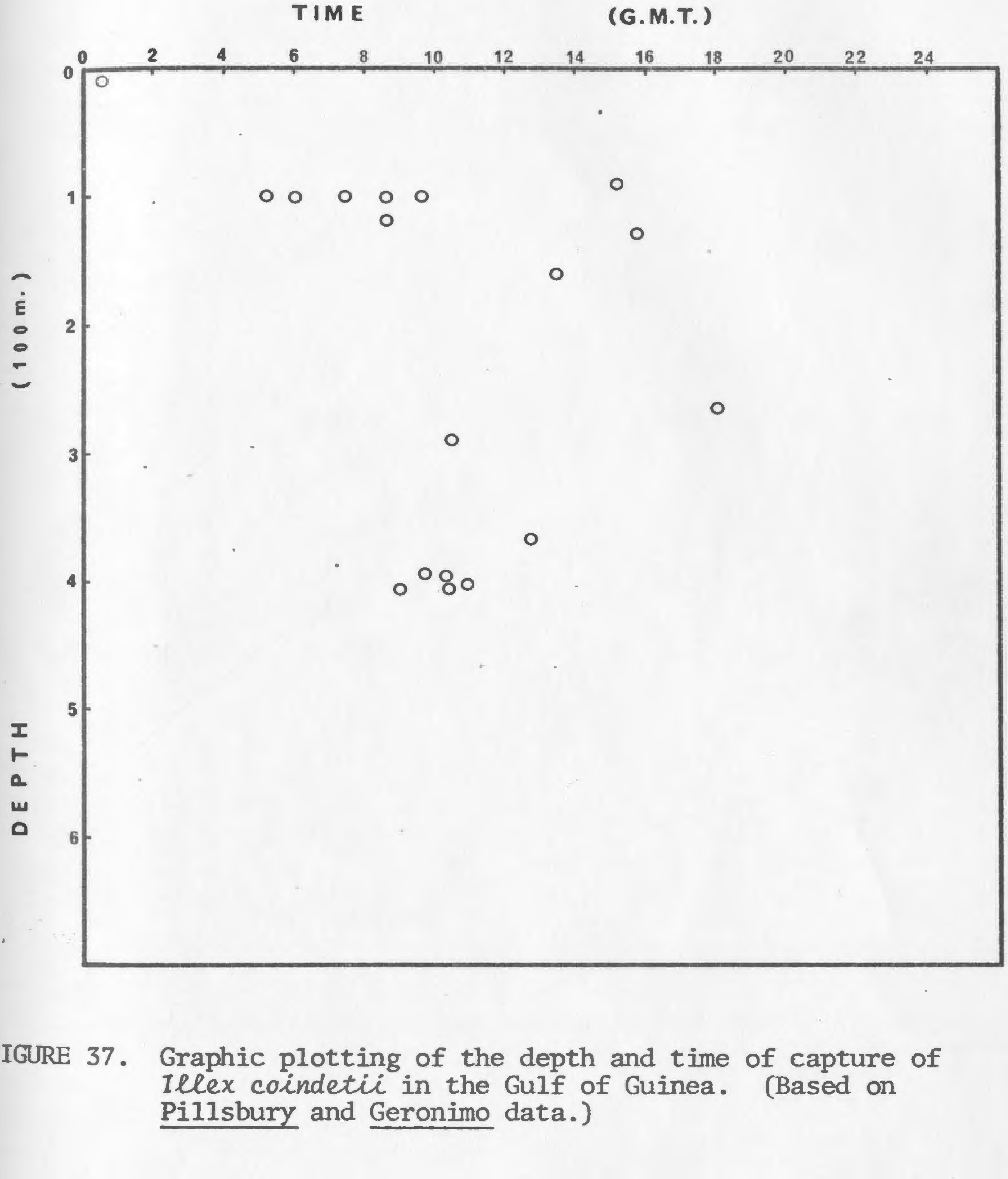


FIGURE 37. Graphic plotting of the depth and time of capture of *Illex coindetii* in the Gulf of Guinea. (Based on Pillsbury and Geronimo data.)

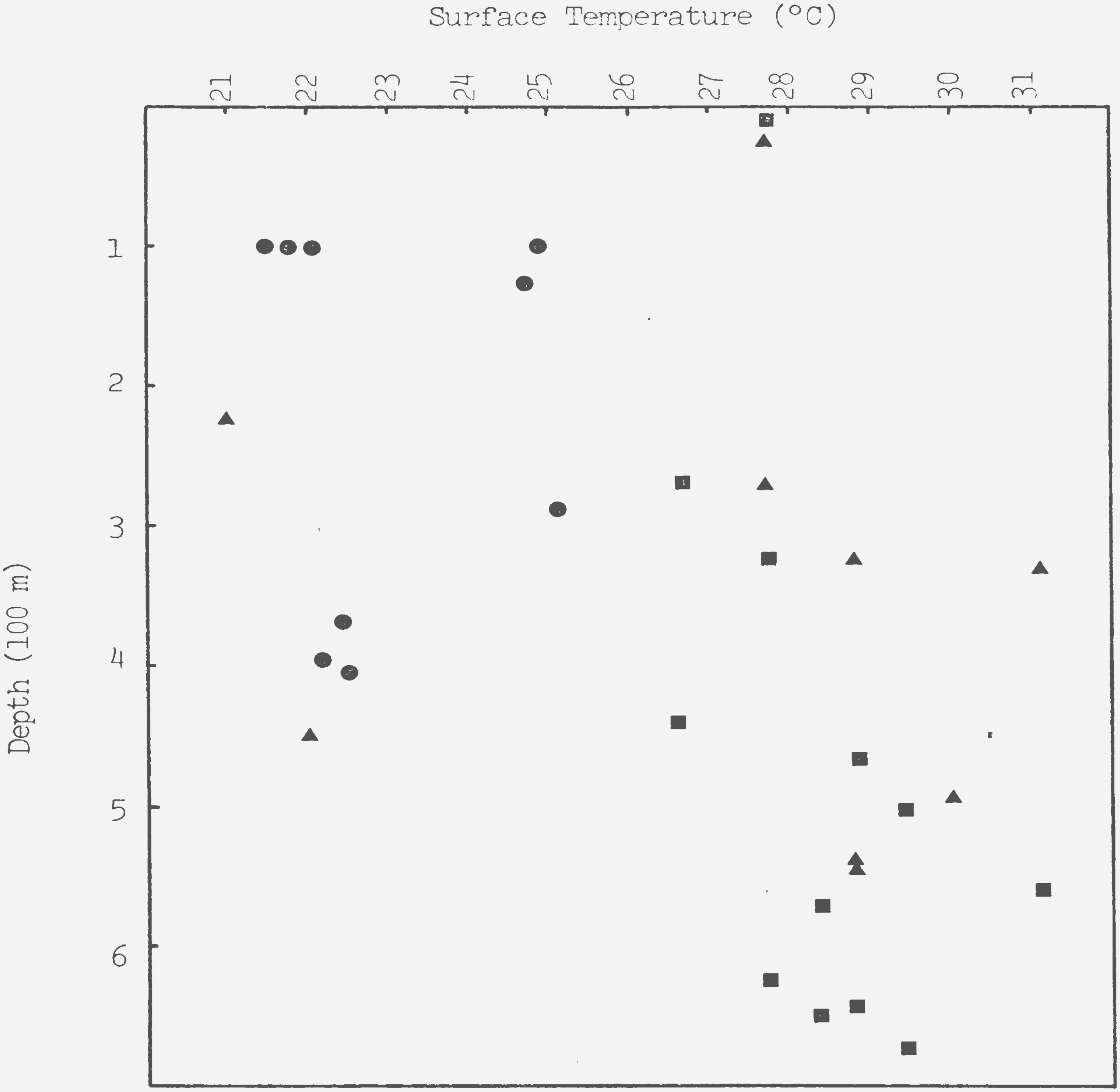


FIGURE 38. Graphic plotting of the depth of capture of *Illex coindetii* in the Gulf of Guinea, Gulf of Mexico, and the Caribbean Sea, and the coincident surface water temperature.

● = Gulf of Guinea

▲ = Gulf of Mexico

■ = Caribbean Sea

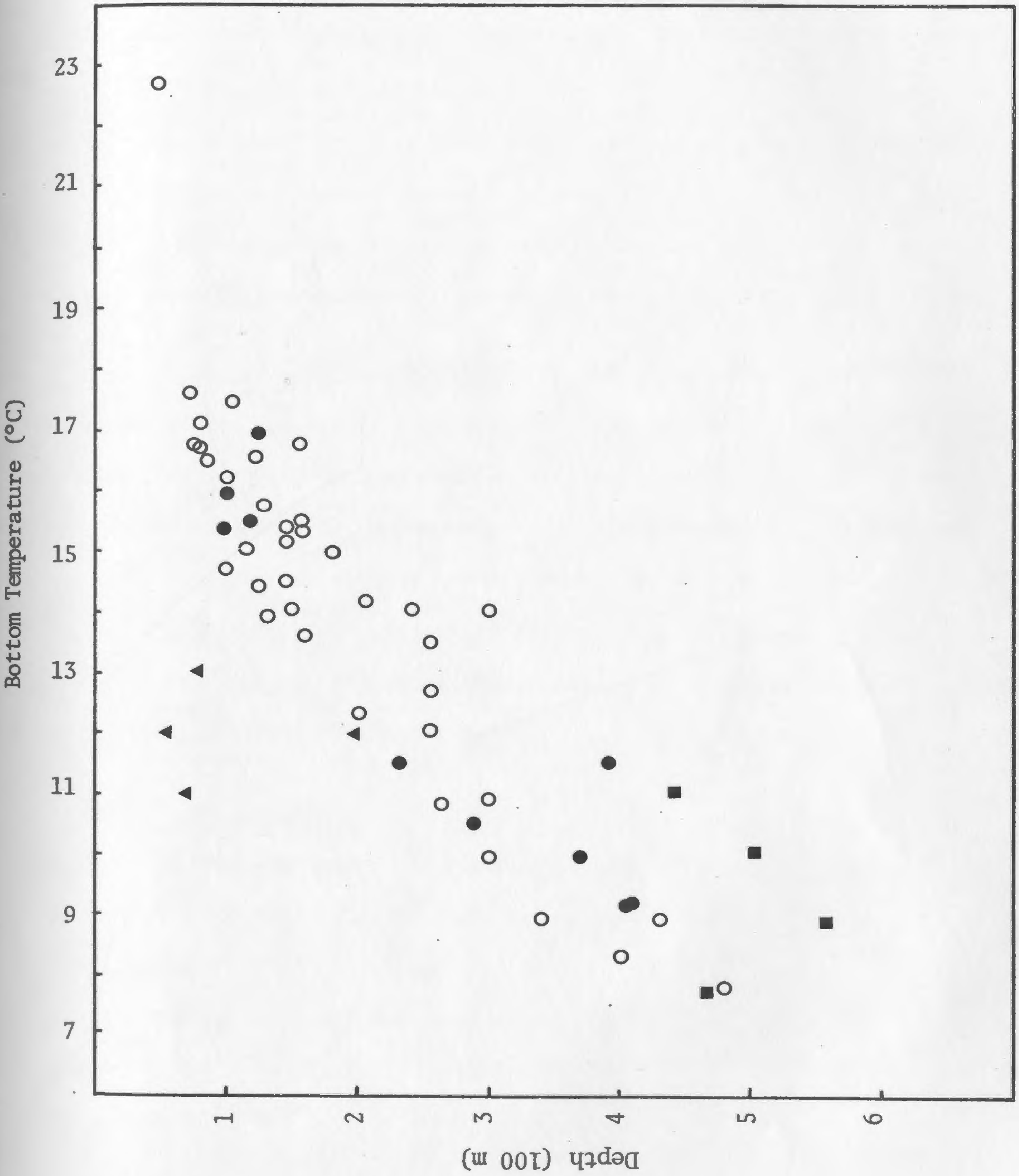
FIGURE 39. Graphic plotting of the depth of capture of *Illex coindetii* from the Gulf of Guinea and adjacent areas, the Caribbean Sea, and the Chesapeake Bay area, with bottom water temperatures. Data from several sources.

○ = Adam, 1952

● = Geronimo data

■ = Oregon data

▲ = VIMS data


Bottom Temperature (°C)
23
21
19
17
15
13
11
9
7
1
2
3
4
5
6
Depth (100 m)

zoogeographical study because station data accompanying the collections is incomplete. The series of articles published by Castellanos and her co-worker (Castellanos, 1964; Castellanos & Menni, 1968, 1969) reveal that it is captured with the hake-fish (*Merluccius merluccius hubbsi* (Marini, 1932)) in Argentine waters, and that the largest individuals are generally captured in the Buenos Aires area between 7-250 m during the winter months, with smaller individuals fished from 2-15 m during the summer months in the Patagonian region.

Angeluscu & Cousseau (1969) reported that *I. argentinus*, along with *Martialia hyadesi* and *Loligo gahi*, predominate in the hake diet in the area that is influenced by the subantarctic waters of temperatures of from 4-7°C (p. 71). According to Nikol'skii (1954), eastern Atlantic hake usually live at depths ranging from 200 to over 300 m. During the day it stays at the bottom and ascends to the surface at night (p. 339-340). Therefore, it may be assumed that *I. argentinus* and *M. m. hubbsi* occupy comparable bathymetric ranges.

Illex oxygonius

In the Chesapeake Bay area *I. oxygonius* was captured at depths of 50-464 m by otter trawl (VIMS and ATC-150 data), with the greatest concentrations at 50-300 m (Fig. 40). In the Straits of Florida, two captures (FH 7281, FH 7296) were made at depths of 555 m and 222 m, respectively. Nearly all ATC and VIMS trawls that captured this species

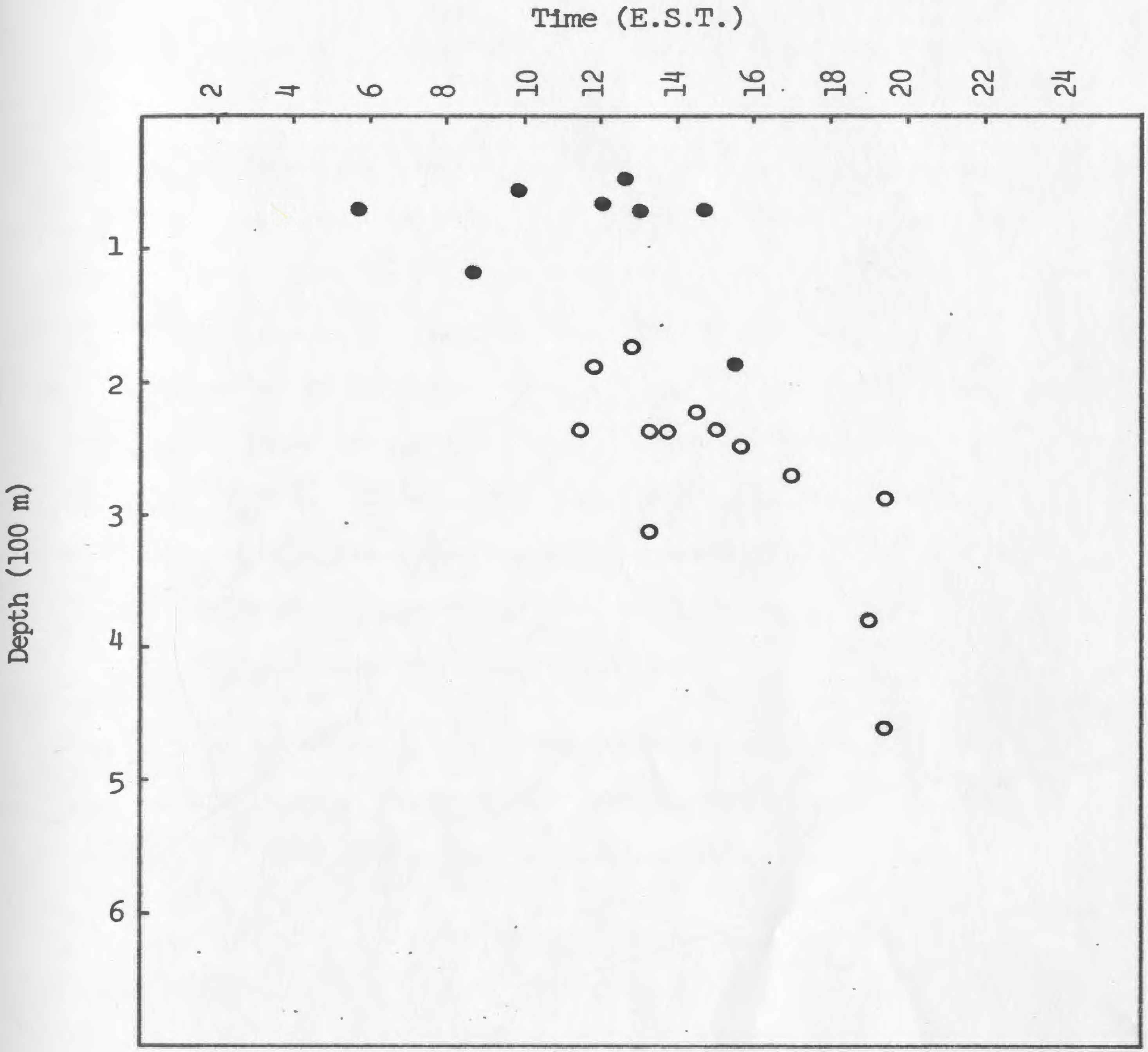


FIGURE 40. Graphic plotting of the depth and time of capture of *Illex oxygonius* in the Chesapeake Bay area.

● = VIMS data

○ = ATC data

were made during the daylight hours (Fig. 40). In August, 1967, a total of 46 otter trawl hauls was made by VIMS, among them eight were night hauls. None of these eight hauls successfully captured *I. oxygonius*. From August 16, 1968, through August 31, 1968, ATC carried out 64 otter trawl hauls in the Chesapeake Bight region. Of the nine night hauls made by the ATC, only three are known with certainty to have taken this species (cf. p. 251), and these specimens are represented in the collection studied. It appears that *I. oxygonius*, like *I. illecebrosus* and *I. coindetii*, is closely associated with the bottom, especially during the daylight hours.

Only ATC data contains surface temperature information. There appears to be no correlation between the surface temperature and the depth of capture of *I. oxygonius*, as is shown in Fig. 41.

The relationship between the bottom temperature and the depth of capture is not obvious (Fig. 42). The VIMS data clearly indicate that the animals live in deeper water where the bottom temperature is higher, while the ATC data show the exact opposite, that is, that the animals live in deeper water with lower bottom temperatures.

Roper, Lu & Mangold (1969, p. 318) have pointed out that records of *I. illecebrosus* from the Gulf of Mexico and the Caribbean Sea very possibly are misidentified, and in reality represent specimens of both *I. coindetii* and *I. oxygonius*. Therefore, the depth record of any specific species from the Cuban coast (Voss, 1955, p. 103), 265-476 m,

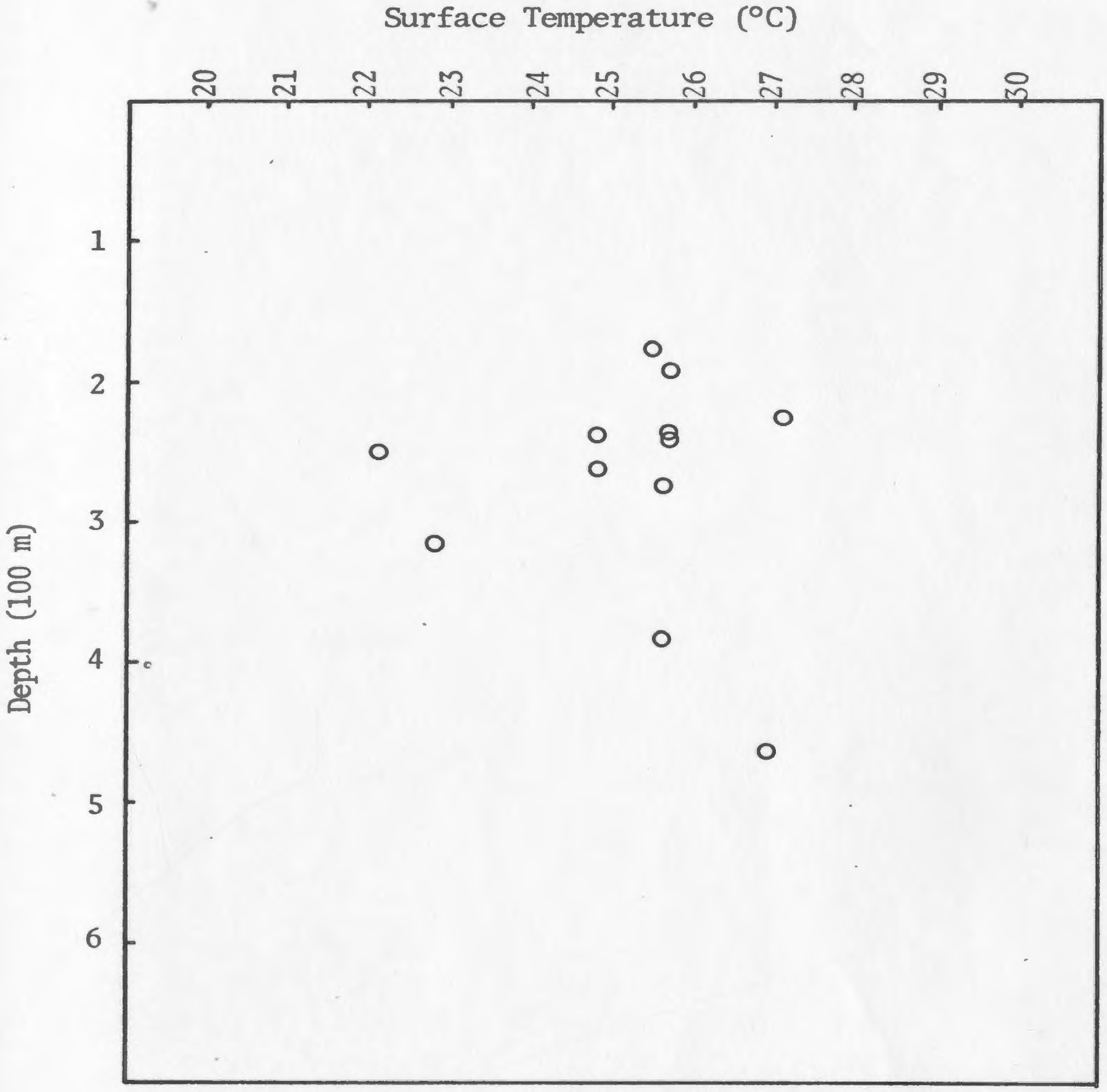


FIGURE 41. Graphic plotting of the depth of capture of *Illex oxygonius* from the Chesapeake Bay area, and the coincident surface water temperature.

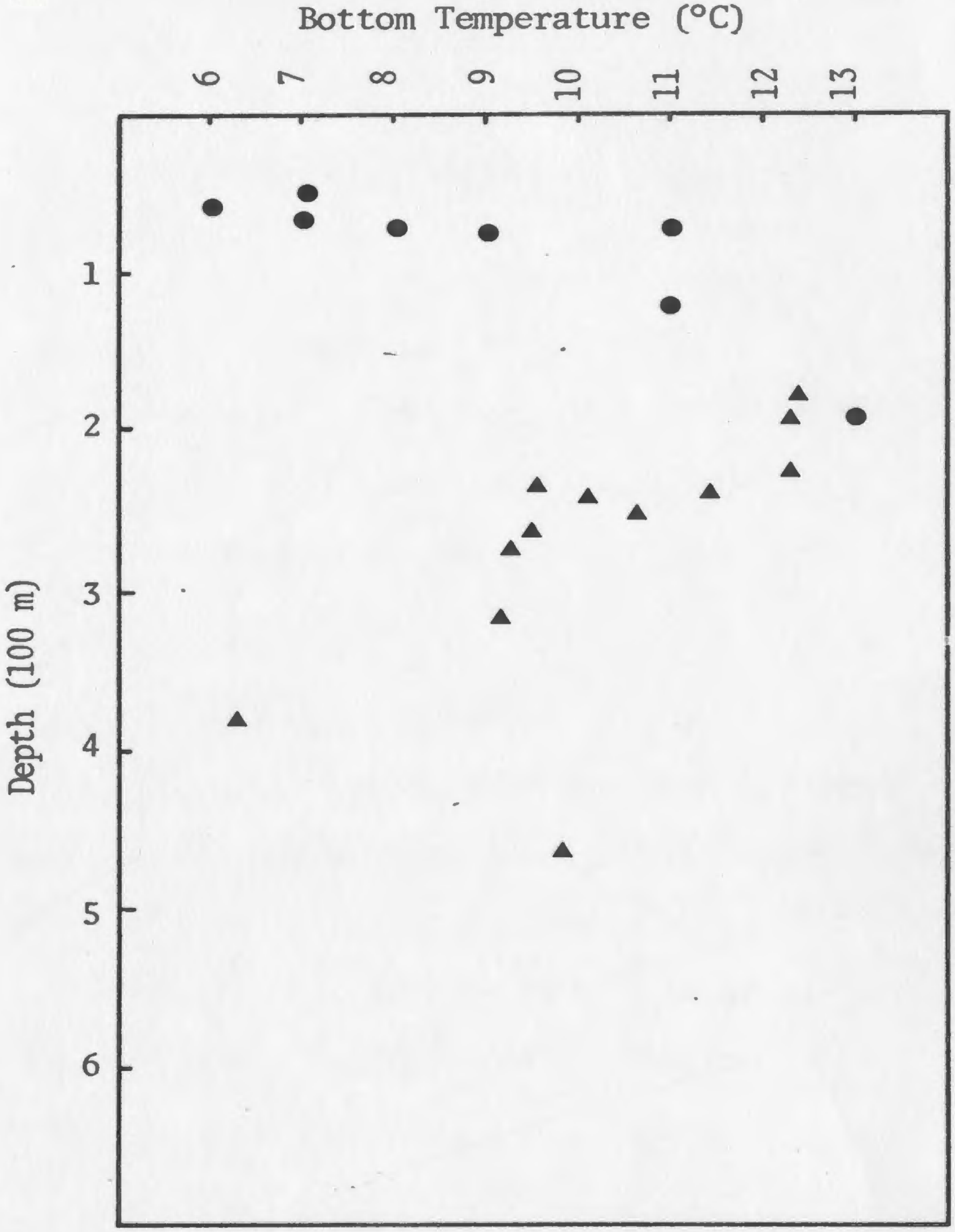


FIGURE 42. Graphic plotting of the bottom temperature and the depth of capture of *Illex oxygonius* in the Chesapeake Bay area.

● = VIMS data

▲ = ATC data

cannot be assigned for any particular species. Nevertheless, these depths still lie within the determined bathymetric range of both *I. coindetii* and *I. oxygonius*.

The sole record of *I. oxygonius* from the Gulf of Guinea (P 245) does not permit analysis. However, it is not unreasonable to speculate that in the eastern South Atlantic, and at least in the Gulf of Guinea, the depth range of *I. coindetii* and *I. oxygonius* overlap.

Discussion of Vertical Distribution

Roper & Young (MS) point out that an adequate knowledge of the vertical distribution of cephalopods must comprise more than merely the knowledge of the bathymetric range of a species, as often the extension of the bathymetric range extends over a broad vertical distance while the majority of the population occupies only a restricted depth zone.

The bathymetric range of *Illex* presented here undoubtedly may represent collections taken at the extremes of their range. On the other hand, however, it may reflect the true situation with respect to the vertical distribution of the members of the genus. At any rate, it is certain that their bathymetric ranges are wide, especially when one takes into account the real possibility of daily migrations from depth to superficial water layers.

The depth records of the stations AS 2528 (1239 m), AS 2727 (2267 m) and GE 1-24 (2420 m) are doubtful. It is possible that the specimens caught at these stations are contaminants captured during the descent or ascent of the gear. If, on the other hand, these represent actual depths of capture, they certainly are the deepest records for any species of *Illex*. It is worthy of note that the individuals captured at these stations were all juveniles, with mantle length ranging from 27 to 88 mm. No larval *I. illecebrosus* are known from surface waters. Indeed, very few mature females have been collected. It is possible that *Illex*, especially *I. illecebrosus*, spawns at depths well in excess of its "normal" range. Spawning at great depths by relatively shallow-living cephalopods may be a common phenomenon. At least one species, *Taningia danae* Joubin, 1931 was suggested to exhibit this behavior (Clarke, 1967, p. 140).

The biological significance of this phenomenon is easily understood in light of the well-known finding of M. J. Wells (1964) who discovered that the degree of the development of the gonad in *Octopus vulgaris* is controlled by a secretion produced by the optic glands which are, in turn, regulated from a center found dorsally in the basal lobe of the supraoesophagael brain. The activity of this center is affected extrinsically through the eyes. Blinding leads to precocious sexual maturity (Wells, 1964, p. 74). In the open ocean, through absorption and scattering, the quality and quantity of light from the sun is changed at successive depths. It is reported that no traces of light can be perceived by the adapted human eye at 700 m depth, even in the clearest waters (Jerlov, 1966, p. 622). At great depths, the light intensity and the quality of the light are greatly reduced or altered, if not totally absent. This condition would favor or induce the maturation of cephalopods, assuming all reacted to light intensity as *Octopus* does. Indeed, Wells (1968, p. 185) describes the optic gland and light control of spawning in "other cephalopods" in addition to the well-established phenomenon in *O. vulgaris*.

Although the diel vertical migration of some groups of marine animals is well documented, until recently references to that of cephalopods were scarce. Alcide d'Orbigny (1841, *fide* Voss, 1967) was probably the first to note that cephalopods occurred at the sea surface primarily at night and disappeared during the day. Recently, the program being carried out by the Smithsonian Institution, namely, the Ocean Acre Program in the Bermuda area, the Smithsonian's Mediterranean Biological Studies, and the Hawaii Study carried out by the University of Hawaii, together with many other such survey programs, have increased our knowledge of the vertical migrations of cephalopods considerably (Roper, 1972; Gibbs & Roper, 1970; Roper & Young, MS).

Clarke (1969) described the diurnal migration of several oceanic cephalopods, based on materials obtained from the SOND cruise near the southern end of Fuerteventura, Canary Islands. The gear used on the cruise were 1 m ring nets (N113H) and Isaacs-Kidd-midwater trawls (IKMT). Clarke concluded that the cephalopods are most numerous between the surface and 300 m and at 600-700 m during both daylight and darkness. They are sparse between 300-500 m in the daylight and 300-600 m in darkness. The main concentrations of cephalopods, excluding *Spirula*, lie at 0-300 m in daylight and 0-200 m in darkness. Among the species collected, a single specimen of *Todarodes sagittatus* was caught in IKMT at 110-(501) m in darkness.

Hartmann (1970) reported that no ommastrephid larvae were taken by means of a David-neuston net during daylight hours in samples from the upper 60 cm of the sea southwest of Madeira. He reported that larvae are most numerous at dusk.

Milliman & Manheim (1968) observed dense squid concentrations, estimated to be in the order of 500 per 1000 m^3 at depths between 220-250 m, during a dive in the submersible Alvin on the continental shelf northeast of Cape Hatteras during daylight hours (1050-1401 EST). A second squid-rich layer was observed at 490-510 m. The bottom was reported to be at 707 m. The observed squid were thought to be *I. illecebrosus*.

As was mentioned previously, of the materials used in this study, nearly all successful otter trawl or bottom trawl tows were made during the daylight hours. Voss (1966b, p. 95) reported that "no specimens of *Illex i. coindetii* were taken in the mid-water tows. However, they are common item in the diet of the tunas in the Gulf of Guinea. They occur in considerable numbers in bottom trawls and at the surface at night with light and dipnet in many areas over the shelf and slope". Evidently, that they are found on the bottom in the daytime is true not only for *I. coindetii* but also for the other three species as well. One can conclude that members of the genus *Illex* are closely associated with the bottom during the day and scattered at night.

Several theories have been proposed to explain the diurnal vertical migration of zooplankton. Cloudsley-Thompson (1961, p. 47) stated, "most planktonic animals avoid strong light, each species showing a preference for a certain strength of light to which it is adapted. For this reason, few animals are to be found on the surface layers of the sea during the hours of daylight but are distributed at various depths according to their specific light responses. On the approach of dusk, however,they all begin to swim upwards to the surface layers. That is why fish like herrings, which prey on plankton, also come to the surface of the sea at nightfall. Consequently this is the time when fishermen shoot their drift nets. Later, when all is dark and there is no light stimulus, planktonic animals tend to scatter. They migrate to the surface again at daybreak and later move downwards as the light strengthens".

Russell (1927, p. 242) states that "It would seem that in fairly homogeneous waters light intensity may be the factor of prime importance governing the distribution of the different species, though other factors such as temperature and salinity may play their part, perhaps in altering the sensitivity of the animal to light. Rate of movement must be an important factor in the various sudden changes in vertical distribution exhibited, and the distribution of food is not to be ignored".

It is not clear what factor is governing the diel vertical migration in *Illex*. Light is generally regarded as the initiating and controlling factor in the diurnal vertical migration of many marine invertebrates, although most evidences are indirect and circumstantial (Segal, 1970, p. 198, p. 211). No work has been done on *Illex* or any other cephalopod to determine whether light is the controlling factor in vertical migration. Hartmann's (1970) findings suggest that the larval ommastrephids exhibit negative phototaxis.

Cloudsley-Thompson (1961, p. 73) stated, "In general, on account of their larger size, primary factors of the physical environment such as light, temperature and humidity tend to be less directly important to vertebrates and secondary considerations, especially of predation and the availability of food, are governing factors in the time at which activity takes place". Although cephalopods are not vertebrates, they "functionally" may be likened to "fish" as Packard (1966, p. 524) suggested. Packard (1966), in discussing the similarities of the functional anatomy between cephalopods and fish, noted that cephalopod behavior is "vertebrate-like rather than typically invertebrate" (p. 529). It is likely that the diel vertical migration observed in *Illex* is due largely to the fact that in nature the feeding activity of *Illex* is more active at night than in the day, although feeding during the day was also observed (Verrill, 1880-81, p. 283).

In summing up the response to light or phototaxis in relation to fishing lamps, Uda (1959, *fide* Laevastu & Hela, 1970, p. 140) stated "Phototaxis of ecological groups, as revealed by observations and sampling, shows the zooplankton responding first, followed by small fish, and finally by large fish, i.e., in the order corresponding to the food-chain (prey-predator) relationship". In the undisturbed environment, when no stimulus of fishing lamps is present, the vertical migration of zooplankton is controlled by the natural light. At night, as we have seen, zooplankton ascend to the upper layers. These are followed by the fishes which feed on zooplankton, and these, in turn, are followed by their predators, such as *Illex*.

Thermocline is an important ecological boundary. It is often the border between two different communities (Angel, 1968; Allee & Schmidt, 1951, p. 196). Laevastu & Hela (1970, p. 35) classified marine animals into six groups on the nature of their diurnal vertical migrations:

"(A) Pelagic species with daytime occurrence slightly above the thermocline; migration to surface layer at sunset; dispersion between surface and thermocline during the night; descent to above the thermocline by sunrise.

"(B) Pelagic species with daytime occurrence in layers below the thermocline; migration through thermocline into surface layers during sunset; dispersion between surface and bottom during the night with bulk occurring above the thermocline; descent through thermocline into deeper layers during sunrise.

"(C) Pelagic species with daytime occurrence in layers below thermocline; migration to thermocline during sunset; dispersion between thermocline and bottom during the night; descent into deeper layers during sunrise.

"(D) Demersal species with daytime occurrence on or close to the bottom; migration and disperal into the water mass below (and occasionally also above) the thermocline during sunset; descent to the bottom during sunrise.

"(E) Species which are dispersed throughout the water column during the day but which descend to the bottom during the night.

"(F) Pelagic and demersal species without any distinct diurnal migrations."

The available information on *Illex* does not allow a detailed analysis in this respect. Of the 11 successful trawls listed by Crosnier (1964), only one station (Sta. 9) was sampled after sunset*, two other stations at around dawn, the remaining eight stations during the daylight hours. The depths of all these stations are below the thermocline. Bottom trawls were used in sampling all these stations. From Crosnier's data, *Illex*, at least *I. coindetii* from the Cameroun coast appears to belong to group (D), with respect to its daily vertical migration.

The actual relationship between the depth of capture of *Illex* and the temperature of the sea surface is difficult to determine. It is not clear whether the greater depth observed in the higher surface temperature stations is due to light or temperature. It is likely that it is best explained on the basis of a combination of the two factors, since normally no single environmental factor affects the distribution of animals exclusively.

The relationship between the depth of capture and the capture temperature is a reflection of local oceanographic conditions. One may

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*The "Duration of Daylight" table (Table 171, List, 1963, p. 507) was used to obtain the time of sunrise and sunset. Approximate time of sunrise or sunset was obtained by dividing the duration of daylight by 2 and substracting it from or adding it to the time of local noon (Berry, et al., 1945, p. 930).

expect a lower bottom temperature at a greater depth under normal sea conditions. The data for *I. coindetii* collected by Adam (1952) in the western African area, those obtained by the Geronimo in the Gulf of Guinea, and those collected by the Oregon and the Oregon II in the Caribbean Sea clearly demonstrate that the deeper the animals live, the colder the water (Fig. 39). This relationship can not be clearly established for *I. illecebrosus* and *I. oxygonius* (Figs. 35, 36 and 42). This is probably due to the shallow capture depth of *I. illecebrosus* from Newfoundland waters and the captures made by the VIMS of *I. illecebrosus* and *I. oxygonius* in the Chesapeake Bay region.

With respect to *I. coindetii*, what may be so clearly found in Figure 39 may be merely a statement of the obvious, namely, that the deeper the Atlantic waters, the lower the bottom temperature.

It is a well known fact that the nature of the substrate is of paramount importance for the distribution of benthos. Different bottom substrata, even within short distances, harbor strikingly different animal types,as was reported by Wilson (1951, *fide* G. L. Clarke, 1964, p. 68). Generally, fish are less dependent upon the substrate, but a significant number of them have some sort of connection with the bottom. Generally speaking, the relationship between the bottom and fish involves the preference of prey species for a particular substrate (Nikolsky, 1963, p. 62). The affect of the substrate on the distribution of teuthoids is almost totally unknown.

From the data contained in several works, namely, those of Jatta (1896), Joubin (1920), Adam (1952), Morales (1958) and Crosnier (1964), *I. coindetii* apparently demonstrates preference for a sandy or silt bottom, or a mixture of the two.

It is not known whether the preference for a certain type of bottom by cephalopods is due to feeding behavior or the physical nature of the substrate. It is known, however, that sandy bottom mixed with shells and gravel, or flat rocky reefs at about 30-100 m in depth are considered to be one of the criteria for good fishing grounds for the ommastrephid *Todarodes pacificus* (Uda, 1963, p. 273) in Japan. LaRoe, in his experiment on the rearing of *Sepioteuthis sepioidea* and *Doryteuthis plei,* discovered that adding sand to the tank bottom calmed captive squid (LaRoe, 1971, pp. 19-20). The beneficial addition of this substrate was observed to be immediately calming to the squid. They began to swim in a gentle rocking manner, preferentially hovering over certain areas where the sand was added, to such an extent that their position in the tank could be manipulated by replacement of the substrates.

It seems, then, the preference for the sandy or silt bottom in *I. coindetii,* possibly in all the members of the genus, is due largely to the physical nature of the substrate, although feeding behavior of the squid, that is, to feed on the organisms living on sandy or silt bottoms, cannot be ignored.

Further evidence supporting this speculation can be derived from the data of the stomach contents of *I. illecebrosus*. In the squid taken in the Grand Banks region, pelagic euphausids (*Thysanoessa* sp. and *Meganyctiphanes* sp.) are the most important items in the stomach contents, although fish, such as caplin (*Mallotus villosus*) are also present (Squires, 1957, p. 720). In larger squid taken inshore, fish, especially caplin, is the most important item (Squires, 1957, p. 720; Aldrich, 1964, p. 16; Mercer, 1965, p. 10; Lu, 1968, p. 40). The caplin is a pelagic fish of the high seas, coming inshore to spawn, chiefly at night. At this time, the caplin swim near the surface and come inshore to spawn on coarse sand or fine gravel beaches (Leim & Scott, 1966, p. 118). This evidence shows that feeding in *I. illecebrosus* chiefly takes place in the upper or mid-water regions, since *M. villosus* is not a demersal species.

Observations on captive squid in round tanks (275 gal. capacity) confirm this statement. When presented with dead caplin, the squid only accepted the food while the fish was freely floating or on descent in the tank. Very seldom would they pick up the fish from the bottom of the tank immediately after the fish reached the bottom.

These observations all indicate that *Illex* seldom feed on the bottom, therefore, the preference for the sandy or silt bottom in *I. coindetii*, and possibly in all members of the genus, must be due to the physical nature of the substrata.

Geographical Distribution and Relation to Hydrographic Conditions

Illex illecebrosus

Within the extent of this study, in Newfoundland waters *I. illecebrosus* has been taken from water of 4-13°C, with greatest concentrations at temperatures of 9-13°C. Further south in the range specimens have been taken from 3-17°C, with greatest concentrations at 10-12°C.

The salinity of the water in which this species occurs from July to November is reported to range from 32.00-34.36^{o}/oo, while in the Chesapeake Bay area it is recorded from 31-36^{o}/oo, with the majority of captures at 32-35^{o}/oo.

The temperature and salinity *in situ* are the factors determining the density of sea water. When the pressure is reduced to atmospheric, waters of different combination of temperature and salinity may have the same density. In Fig. 43, pertinent salinity values are plotted against temperatures,and the corresponding densities are calculated as sigma-t values (Anonymous, 1963). From this graph may be read the sigma-t value for waters of salinities ranging from 28 to 37^{o}/oo, and of temperatures from -2 to 30°C.

The density of Newfoundland waters in which *I. illecebrosus* is taken is approximately sigma-t = 24-27; in the Chesapeake Bay area the sigma-t range is from 23.5 to 27.5 with the majority of captures in sigma-t = 25.0-27.0 (Fig. 43). The sites of collection of this species from the Newfoundland and the Chesapeake Bay areas, as well as a combination of both areas, are shown in Table 24, with respect to the density (sigma-t) of the water.

Table 24

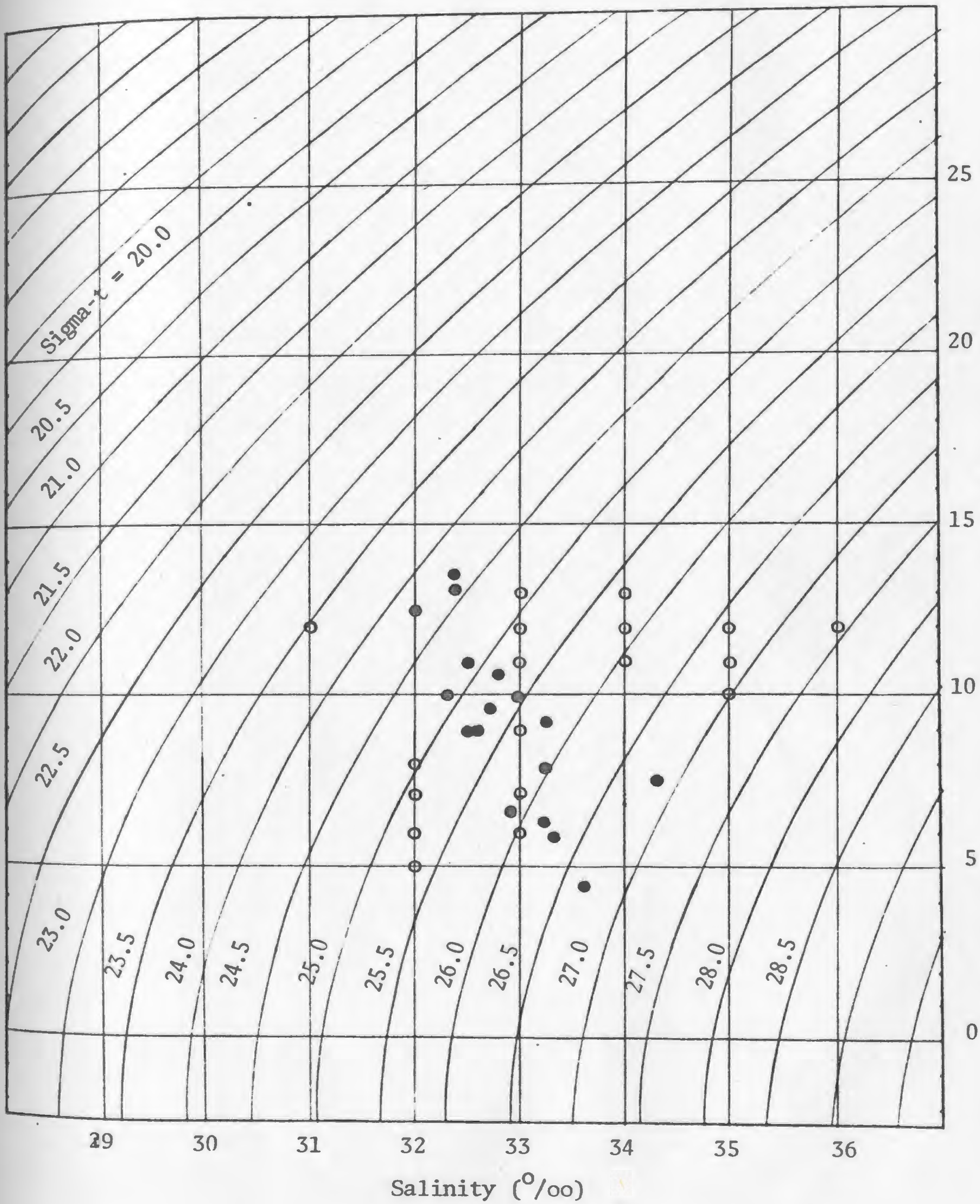
The distribution of sites of capture of *Illex illecebrosus* in sea water of different density in the Newfoundland and Chesapeake Bay areas

	NEWFOUNDLAND		CHESAPEAKE BAY		COMBINED	
Sigma-t (Density)	No. of Stations	% of Total No. of Stations	No. of Stations	% of Total No. of Stations	No. of Stations	% of Total No. of Stations
23.5-24.0	0	0	1	3.7	1	2.3
24.0-24.5	3	17.6	0	0	3	6.8
24.5-25.0	2	11.8	3	11.1	5	11.4
25.0-25.5	5	29.4	8	29.6	13	29.5
25.5-26.0	3	17.6	4	14.8	7	15.9
26.0-26.5	2	11.8	5	18.5	7	15.9
26.5-27.0	2	11.8	5	18.5	7	15.9
27.0-27.5	0	0	1	3.7	1	2.3
Total	17	100.0	27	99.9	44	100.0

FIGURE 43. The collections of *Illex illecebrosus* plotted against the temperature and salinity of the water at site of capture, with calculated densities of the water expressed as sigma-t values.

○ = VIMS data from the Chesapeake Bay area

● = Newfoundland data (based on Snelgrove, 1966)


Sigma-t = 20.0
20.5
21.0
21.5
22.0
22.5
23.0
23.5
24.0
24.5
25.0
25.5
26.0
26.5
27.0
27.5
28.0
28.5
25
20
15
10
5
0
Temperature (°C)
29
30
31
32
33
34
35
36
Salinity (°/oo)

Illex coindetii

In the Cape Hatteras region, *I. coindetii* was represented at four stations, the temperature and salinity of the water of which were 11-13°C and 33-36°/oo, respectively.

In the Gulf of Mexico and the Caribbean Sea the temperature and salinity data from the depth of capture are not available for most stations. From the available data (three stations for the Gulf of Mexico and five stations for the Caribbean Sea), *I. coindetii* was taken from water of 7.7-27.7°C; no salinity data are available. The depths of capture of *I. coindetii* in this area are shown in Table 25.

Table 25

Distribution of depth of capture of *Illex coindetii* in the Gulf of Mexico and the Caribbean Sea

	GULF OF MEXICO		CARIBBEAN SEA	
Depth (m)	No. of Stations	% of Total No. of Stations	No. of Stations	% of Total No. of Stations
0-100	1	7.14	1	4.55
100-200	1	7.14	1	4.55
200-300	3	21.43	1	4.55
300-400	2	14.29	3	13.64
400-500	4	28.57	5	22.73
500-600	3	21.43	6	27.27
600-700			5	22.73
Total	14		22	

In the Gulf of Mexico the majority of the captures were made below 200 m, while in the Caribbean Sea most captures were below 300 m. In general, *I. coindetii* appears to live in deeper water in the Caribbean Sea.

The material from the Gulf of Guinea, especially the Geronimo collection, provides the most complete station data. In this region, *I. coindetii* were taken from waters with temperatures of from 9-17°C, and salinities ranging from 34.91-35.83^{o}/oo, and densities of sigma-t 26.25-27.04 (Fig. 44). When the temperature and salinity data for the captures are plotted on the water mass chart (Fig. 31), it is found that many of the GE captures occurred in the South Atlantic Central Water envelope (Fig. 45).

The distribution of the captures along the density range for *I. coindetii* from the VIMS and GE collections, and from Adam (1952, pp. 82-83), as well as the combined values for all three collections, are shown in Table 26.

Illex argentinus

According to Castellanos (1964, p. 22), the range of temperature and salinity of waters in which *I. argentinus* is fished are 4.6-16°C and 33.31-35.28^{o}/oo, respectively, in the Patagonia region, and especially in the Golfo San Jorge and surrounding area.

Table 26

Seawater Density distribution of the captures of *Illex coindetii*

	VIMS		GERONIMO		ADAM (1952)		COMBINED	
Sigma-t (Density)	No. of Stations	% of Total No. of Stations	No. of Stations	% of Total No. of Stations	No. of Stations	% of Total No. of Stations	No. of Stations	% of Total No. of Stations
23.5-24.0	0	0	0	0	1	3.2	1	2.3
24.0-24.5	0	0	0	0	0	0	0	0
24.5-25.0	1	25	0	0	2	6.5	3	6.8
25.0-25.5	0	0	0	0	1	3.2	1	2.3
25.5-26.0	1	25	0	0	0	0	1	2.3
26.0-26.5	1	25	4	30.8	3	9.7	8	18.2
26.5-27.0	0	0	5	38.5	12	38.7	17	38.6
27.0-27.5	1	25	4	30.8	7	22.6	12	27.3
27.5-28.0	0	0	0	0	1	3.2	1	2.3
Total	4		13		27		44	

FIGURE 44. The collections of *Illex coindetii* plotted against the temperature and salinity of the water at the site of capture, with calculated densities of the water expressed as sigma-t values.

○ = Adam, 1952

● = Geronimo data

■ = VIMS data

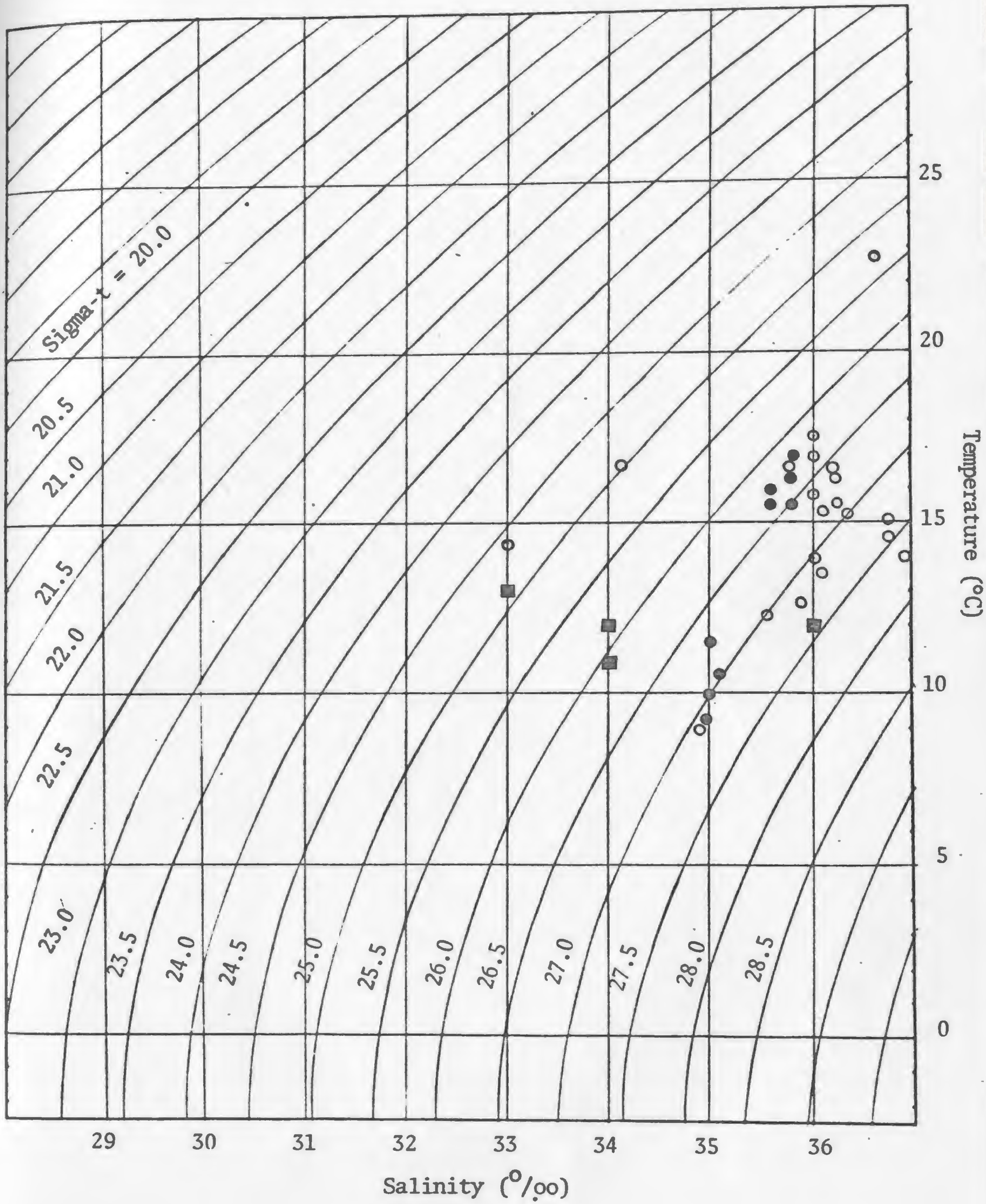
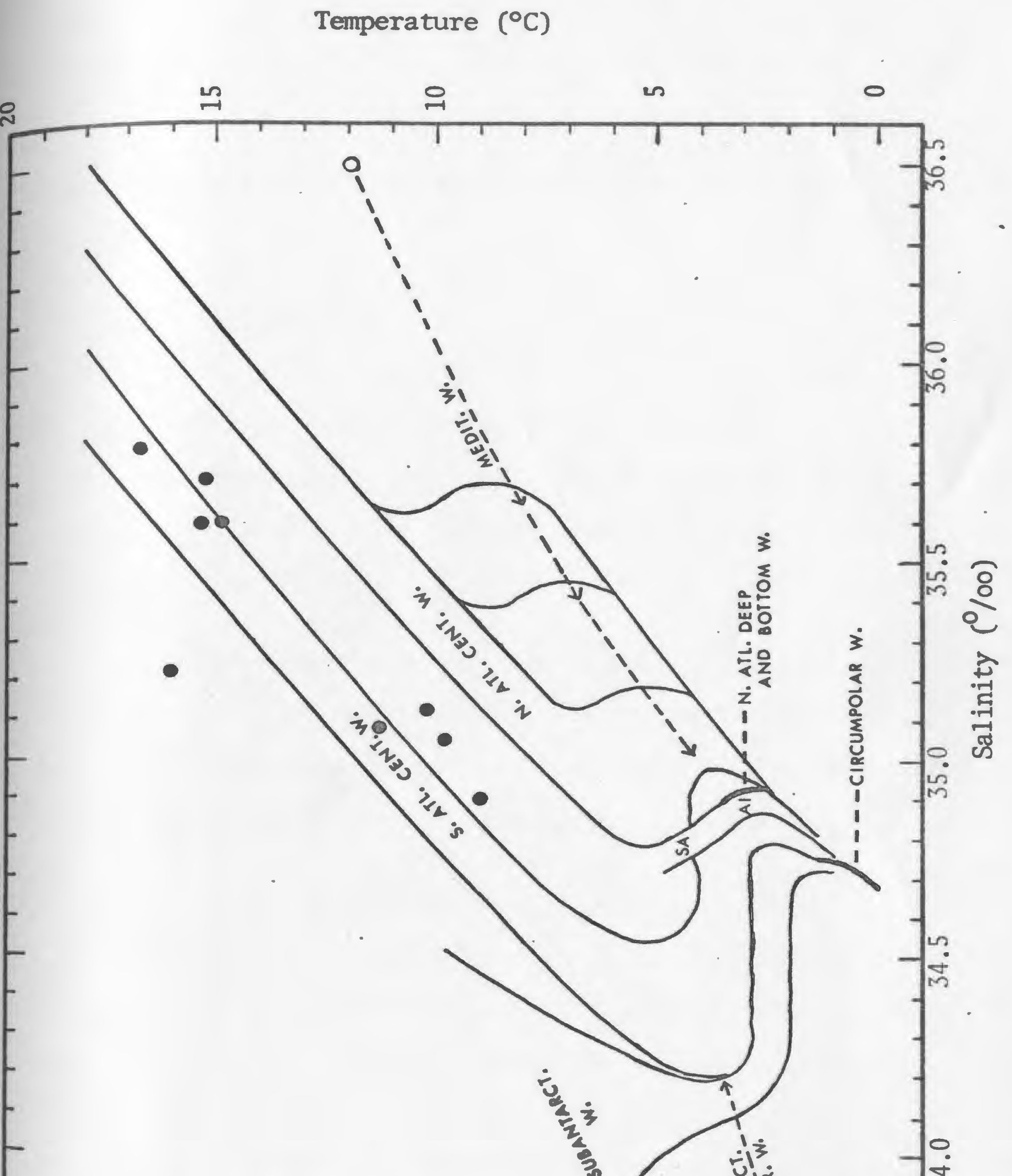

Sigma-t = 20.0
20.5
21.0
21.5
22.0
22.5
23.0
23.5
24.0
24.5
25.0
25.5
26.0
26.5
27.0
27.5
28.0
28.5
25
20
15
10
5
0
Temperature (°C)
29
30
31
32
33
34
35
36
Salinity (°/oo)

FIGURE 45. The collections of *Illex coindetii* from the Gulf of Guinea plotted on chart showing recognized oceanic water masses identified by salinity and temperature profiles. (Based on Geronimo data)


Temperature (°C)
20
15
10
5
0
36.5
36.0
35.5
35.0
34.5
34.0
Salinity (°/oo)
MEDIT. W.
N. ATL. CENT. W.
S. ATL. CENT. W.
N. ATL. DEEP AND BOTTOM W.
CIRCUMPOLAR W.
SA
AI
SUBANTARCT. W.
ANTARCT. INTER. W.

From the T-S plot of the captures, it appears that *I. argentinus* occurs in the Subantarctic Water and the South Atlantic Central Water masses (Fig. 46).

Illex oxygonius

To date, a total of only 59 specimens of *I. oxygonius* have been found properly identified and available for study. All of these were taken from water within the temperature range of 6-13°C, with 75% of them from waters of above 9°C. They all came from water of a restricted salinity range, namely, 32-35^{o}/oo.

In Fig. 47 the sites of capture are plotted against sigma-t density. As can be seen from this figure, the majority of captures were from waters characterized by sigma-t = 25.5-26.5. The range over which these 59 specimens were taken was sigma-t = 24.5-27.0.

Discussion of Geographical Distribution

Temperature is generally regarded as the most important single factor governing the occurrence and the behavior of marine life (Gunter, 1957, p. 159). Very little information is available on either lethal or optimal temperatures for cephalopods. Accordingly, the effect of temperature on cephalopod distribution is also poorly known.

Of the best studied ommastrephid, *Todarodes pacificus*, Sasaki (1921, p. 4) reported that the optimal temperature for occurrence is

FIGURE 46. The collections of *Illex argentinus* plotted on chart showing recognized oceanic water masses identified by salinity and temperature profiles. (Based on data from Castellanos, 1964).

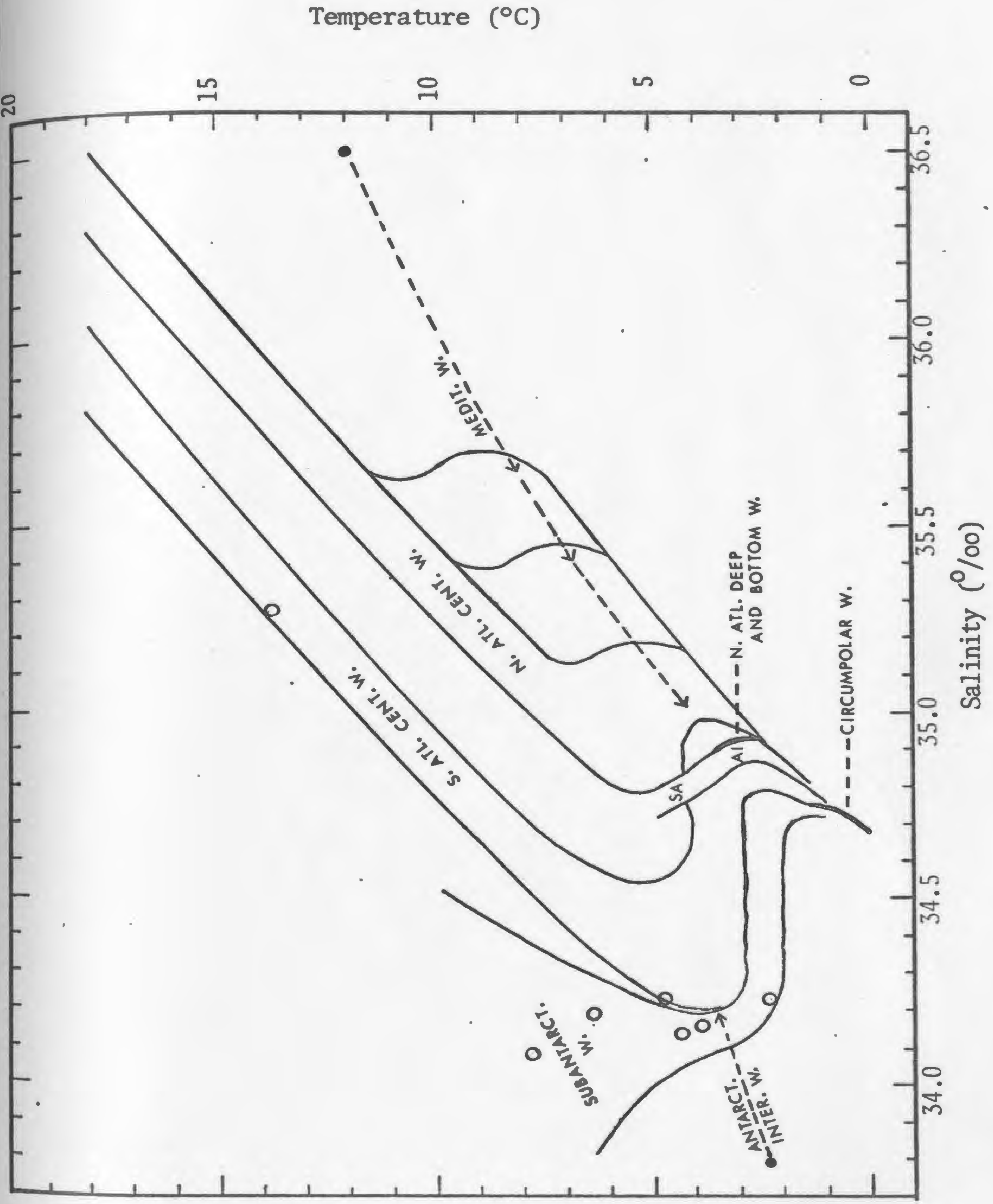
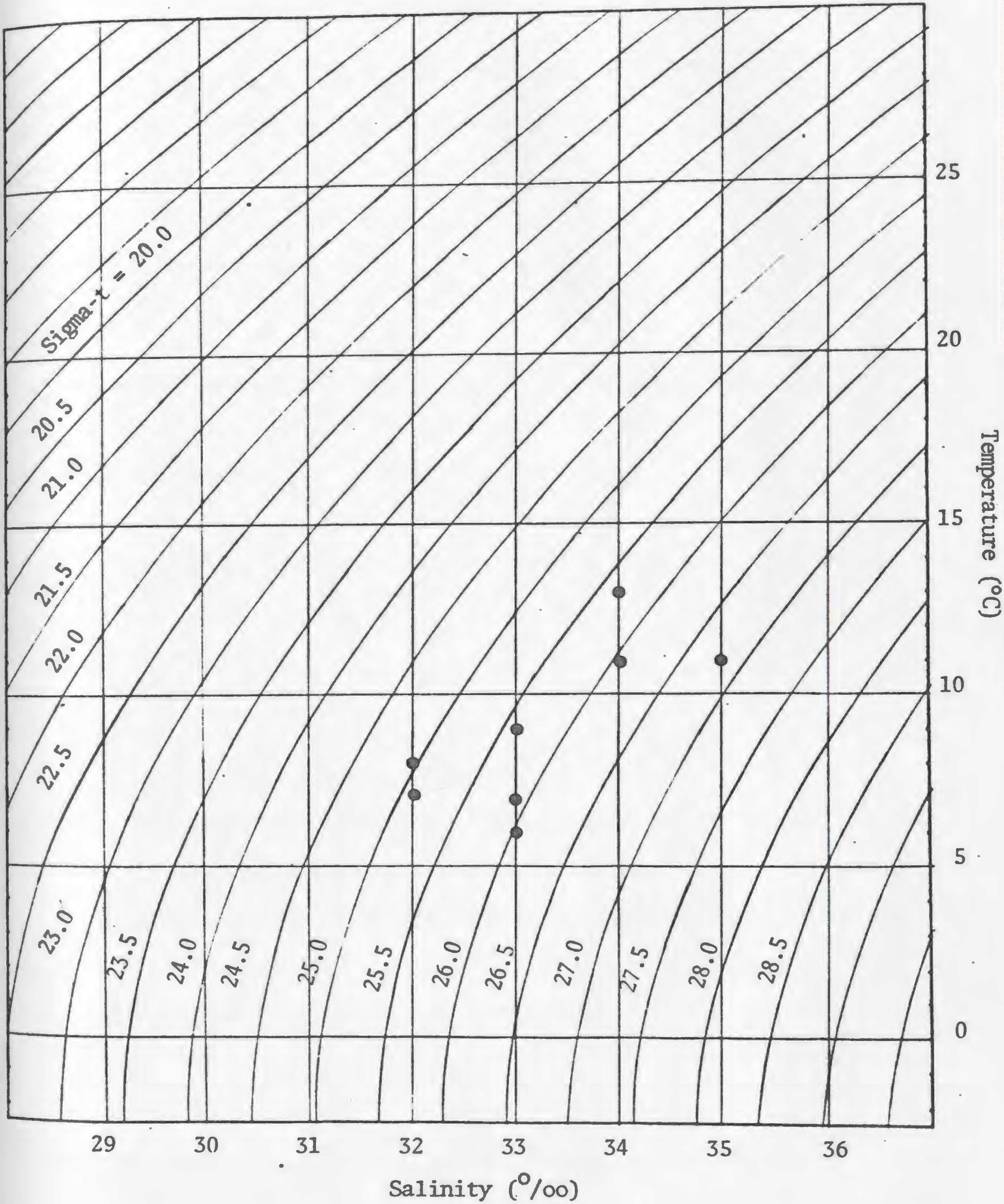

Temperature (°C)
20
15
10
5
0
Salinity (⁰/oo)
34.0
34.5
35.0
35.5
36.0
36.5
MEDIT. W.
N. ATL. CENT. W.
S. ATL. CENT. W.
N. ATL. DEEP AND BOTTOM W.
CIRCUMPOLAR W.
SUBANTARCT. W.
ANTARCT. INTER. W.
SA
AI

FIGURE 47. The collections of *Illex oxygonius* from the Chesapeake Bay area plotted against temperature and salinity of the water at the site of capture, with calculated densities of the water expressed as sigma-t values. (Based on VIMS data)


Sigma-t = 20.0
20.5
21.0
21.5
22.0
22.5
23.0
23.5
24.0
24.5
25.0
25.5
26.0
26.5
27.0
27.5
28.0
28.5
25
20
15
10
5
0
Temperature (°C)
29
30
31
32
33
34
35
36
Salinity (°/oo)

10-17°C, stating, however, that the species in the northern seas of Japan is adapted to colder water. Suzuki (1963, p. 148) reported the optimum temperature for the same species in the seas southeast of Hokkaido to be 4-10°C. Recently, LaRoe (1971, p. 22) reported that the minimum and maximum lethal temperature for young *Sepioteuthis sepioidea* are 17.5-18.0°C and 32.5-33.0°C, respectively.

The temperature preferences of *I. illecebrosus* and *I. coindetii* are distinctly different, although they overlap somewhat (Figs. 43 and 44). It is clear that *I. illecebrosus* is a cold water species, occurring in a temperature range of 3-17°C. No specimen is known from water above 17°C. On the other hand, *I. coindetii*, with a temperature range of 7-28°C, is a warm water species.

Vernberg & Vernberg (1970) studied the temperature tolerance of selected animals from the region near Cape Hatteras, North Carolina and concluded that animals with northern affinities do not survive high temperature as well as do those with more southerly geographical limits (p. 27). This phenomenon is easily understood since most animals live much closer to the upper limits of their thermal tolerance than to the lower limit. An organism is more quickly incapacitated by moving from its normal environment into warmer surroundings than by moving into cooler ones (McConnaughey, 1970, p. 299). Cape Hatteras, North Carolina, is a point of pronounced faunistic change for many groups of animals. It is at this point that the northerly flowing Gulf Stream with its warm water comes into contact with the cold, southerly flowing Virginia Current. The southern boundary of the Atlantic North American boreal fauna is therefore located at Cape Hatteras; south of this point, the fauna is tropical-subtropical water fauna (Ekman, 1953, p. 135).

The species of *Illex* offer no exception to this principle. *Illex illecebrosus* is a boreal species - for all but three captures were located north of Cape Hatteras. The three captures south of Cape Hatteras (O 6800, O 6801, and CB 433) could be expected, due to the influence of the Labrador Current which occasionally reaches as far south as Cape Canaveral (Cape Kennedy) at greater depths (Allee & Schmidt, 1951, p. 197). For this reason, certain workers consider Cape Canaveral as a zoogeographical boundary (Ekman, 1953, p. 135). Ekman (1953, p. 140) considered the fauna between Cape Hatteras and Cape Canaveral to be a mixed fauna. Along the mid-Atlantic coast of North America, the distribution of *I. illecebrosus* and *I. coindetii* support this concept.

Unfortunately, bottom temperature data was not available for the stations at which *I. coindetii* was collected in the Gulf of Mexico, and it was available for only four stations in the Caribbean Sea (Fig. 39). In an effort to gain missing information, in Table 27 are reproduced in part temperature and salinity data from these two areas, specifically areas termed by Parr (1935, *fide* Leipper, 1954, Table 4, p. 135) as "typical Gulf complex" and "typical Caribbean complex", respectively.

Table 27

Typical temperature and salinity data in the Gulf of Mexico and the Caribbean Sea (from Leipper, 1954)

	Gulf Complex Sta. 705 (27°42'N 86°00'W)		Caribbean Complex Sta. 701 (23°28'N 85°37'W)	
Depth (m)	Temp. (°C)	Sal. (°/oo)	Temp. (°C)	Sal. (°/oo)
0	23.75	35.52	25.34	36.18
100	18.59	36.32	25.28	36.32
200	14.94	35.96	21.88	36.73
300	12.30	35.52	18.21	36.44
400	-	-	14.96	35.94
500	7.88	35.08	-	-
600	-	-	9.12	35.08
700	5.91	34.87	-	-
800	-	-	6.86	34.86
900	4.94	34.92	-	-
1000	-	-	5.15	-
1200	4.21	34.95	-	-

Earlier it was noted that *I. coindetii* is found in water of temperatures ranging from 7-28°C. From Table 27 it is clear that temperatures in both bodies of water above 300 m are well within that range. It was evident from Fig. 38 that 300 m represents a point below which the majority of samples were taken. Indeed, "favorable" temperatures extend to at least 600 m in the Gulf of Mexico and 800 m in the Caribbean (Table 27). Therefore, the greater concentration of *I. coindetii* at depths greater than 500 m in the Caribbean Sea (Fig. 38) cannot be explained on the basis of vertical temperature distribution. It seems more likely that it is rather correlated with depth.

As stated previously, in the eastern Atlantic Ocean, *I. coindetii* is distributed as far north as Helgoland and the Oslo Fjord, as well as along the west coasts of France, Portugal and Spain. Despite the relatively high latitude of the North Sea, water temperatures there are high, since its waters are mainly from the North Atlantic Current. In the month of February when the surface temperature is at its minimum, it increases from 2° off the Danish coast to 7.5°C further north. The maximum surface temperature occurs in August, and it decreases northward from 18°C off the Danish coast to 13°C in the north. Minimum bottom temperatures occur in March ranging from 3-7°C. These increase northwestward, the maximum bottom temperature being 16-17°C off continental Europe in August (Fairbridge, Ichiye & Berry, 1966, p. 544).

In the Norwegian fjords, the arctic water does not reach the coastal areas unmixed, and at the great depths it is barred by sills at the entrance of the fjords. Consequently, the water temperature of the fjords at 600-700 m depth is higher than that of the Norwegian Sea at a similar depth. In these fjords and the Skagerrak, neither the water nor the fauna is classified as arctic (Ekman, 1953, pp. 104-105). For the eastern North Sea region, Grimpe (1925, p. 108) gave Helgoland Bay (Deutsche Bucht) in the southern North Sea as the only area where *I. coindetii* was captured. The range is now extended northward at least to the Oslo Fjord (OM D 28453).

The temperatures of the Skagerrak and the Norwegian fjords are clearly within the tolerable range for *I. coindetii*, explaining its more northerly distribution on the eastern side of the Atlantic. Although no records exist of it from areas such as the Skagerrak, its absence cannot be explained in terms of temperature, and further sampling should locate it.

In the western North Sea, *I. coindetii* was reported by Norman (1890, p. 476) from Firth of Forth, Scotland. The waters there are under the influence of the warm, saline North Atlantic Current.

According to Ekman (1953, p. 80), the Strait of Gibraltar is not an important zoogeographical boundary and the Mediterranean fauna is therefore not a distinct unit. It is associated with that of neighboring parts of the Atlantic and is termed the Mediterranean-Atlantic fauna. The neighboring areas are divided into the Lusitanian region in the north, whose northern limit is the entrance of the English Channel, and the Mauritanian region extending south from the Strait of Gibraltar to Capo Blanco, Mauritania. South of Capo Blanco a tropical-subtropical region extends as far south as Mossamedes, Angola (15°S).

In the eastern Atlantic Ocean, *I. coindetii* is distributed in all these regions. In the Mediterranean Sea the temperature range for *I. coindetii* is 12.5-18°C (Mangold-Wirz, 1963b, p. 236). In the western Mediterranean Sea annual changes of water temperature are slight, for instance the temperature off Monaco is 12.5-16°C at 70 m depth all year round, and *I. coindetii* is taken throughout the year in that area.

The coastal areas of continental Europe from the Straits of Gibraltar to the English Channel are influenced by the North Atlantic Current and its several branches. Water temperatures are higher in this region than they are at the same latitude in the western Atlantic. At 50°N where differences in annual surface temperature between the eastern and western Atlantic reach maximum it is 2°C on the American side and 12°C on the European coast (Neumann & Pierson, 1966, p. 432). This warm water allows *I. coindetii* to extend well northward along the coast of the eastern Atlantic Ocean.

South of the Strait of Gibraltar, *I. coindetii* is fished along the coast as far south as 14°S(Adam, 1952, p. 75). This area comprises what Ekman called the Mauritanian faunal zone and the Guinea faunal zone (p. 55). These zones are influenced by the warm Canary and Guinea Currents. The northward flowing Benguela Current with its cold water flows along the South African coast and turns westward at about 15°S. This cold current forms the barrier for the southward distribution of *I. coindetii*. Indeed, Adam (1952) reported the southernmost incidence of this species off

Angola, at 14°S, just in the area near the influence of the Benguela Current.

In the western South Atlantic Ocean, the cold Falkland Current flows northward along the South American coast to about 30-35°S where it meets the warm, southerly flowing Brazil Current. The Subtropical Convergence and Antarctic Convergence are located at about 35°S and 50°S, respectively. The region between these two convergences is called the Subantarctic region (Sverdrup, et al., 1942, p. 606) or, as Ekman (1953, p. 213) called it, the antiboreal region. The known distributional range of *I. argentinus* corresponds to the limits of the antiboreal region. The water masses of this region in the upper 1500 m are Subantarctic Upper Water (0-500 m) with temperatures of 4-10°C in the winter and up to 14°C in the summer, and the Antarctic Intermediate Water (500-1000m) with a year-round temperature of 2°C. The temperature range for *I. argentinus* as reported by Castellanos (1964) lies within the characteristics of these waters. The distribution is therefore limited by the warm Brazil Current in the north and the cold antarctic water in the south.

In the western Atlantic Ocean *I. oxygonius* is found from the Chesapeake Bay area southward. Its distribution generally overlaps that of *I. coindetii*. It has already been shown that the hydrographic characteristics of this area are strongly influenced by the Florida Current and the Gulf Stream.

It seems safe to assume that *I. oxygonius* is not only subject to, but limited by, temperature barriers similar to those effective for *I. coindetii*, although not necessarily identical.

The effect of salinity on the distribution in the open ocean is less pronounced since oceanic salinities are generally constant and rarely vary beyond the tolerance range of the animals.

Unfortunately, very little is known about the salinity tolerance of cephalopods. Yamamoto reported on it for the larvae of several species in Japanese waters (1940; 1942). According to him, at temperatures of 19.4-25.5°C, larval *Octopus ocellatus*, *Sepia esculenta*, *Sepiella japonica* and *Loligo japonica* demonstrated the ability to tolerate salinity ranges of 29-35°/oo, 24-35°/oo, 23-38°/oo, and 31-41°/oo, respectively (Yamamoto, 1940). For *Octopus vulgaris* and *Loligo bleekeri*, at temperatures of 18.4-23.5°C, salinity tolerance ranges were reported as 30-38°/oo and 30-41°/oo, respectively (Yamamoto, 1942). Along the Texas coast, Gunter (1950, *fide* Altman & Dittmer, 1966) reported ranges for *Octopus vulgaris* to be 30-35°/oo, 30.7-35.8°/oo for *Loligo pealei*, and 17.7-37.2°/oo for *Lolliguncula brevis*. Rees (1955) noting the poor cephalopod fauna of the eastern Mediterranean Sea, attributed it to low nitrate and phosphate content and higher salinity (over 39°/oo). LaRoe, in his breeding and culturing experiments, noted mortality of *Doryteuthis plei* at salinities below 27°/oo and at 23.7-27°/oo for *Sepioteuthis sepioidea* (LaRoe, 1971).

In the open ocean, salinities of about 34-36°/oo are relatively constant, however, in more onshore waters freshwater run-off from rivers in the estuarine regions affect the local salinity, and consequently, the occurrence of biota. Frost & Thompson (1933, pp. 85-86) suggested that *I. illecebrosus* approaches the Grand Banks and the Newfoundland coast in the deeper water along with the influx of saline Atlantic water, contending that their inshore migration is not impaired by the lower salinities of the bays. Aldrich (1964) noted that in Holyrood Bay, a branch of Conception Bay, Newfoundland, *I. illecebrosus* is caught only in the more saline north arm, no captures being made in the south arm receiving fresh water inflow from the Holyrood River (p. 10).

As was reported previously, *I. illecebrosus* is taken in Newfoundland waters with a salinity range of 32-34.36°/oo. This range is lower than that of the open ocean, but this is to be expected since in the Newfoundland water the squid fishery is in various embayments, which receive fresh water run-off from the land, either as river discharge or as ice and melting snow. In the Chesapeake Bay region, the salinity of the successful catches ranges from 31°/oo to 36°/oo. Although this range is greater than that in Newfoundland waters, the great majority of the stations (92.6% of the 27 stations) lies between 32 and 35°/oo, comparable, indeed, if not nearly identical, to that in the Newfoundland region.

Ketchum & Keen (1955) reported on the accumulation of river water over the continental shelf between Cape Cod, Massachusetts, and Chesapeake Bay. The general salinity feature of this region is that the isohalines parallel the coast line with values increasing from the shore seawards (Biglow & Sears, 1935, *fide* Ketchum & Keen, 1955) and that the salinity is at a maximum in the winter months, about 25% more river water being present in the summer. With respect to the relation of this to the distribution of squid, lack of sufficient winter catch data makes such an analysis impossible since only five VIMS stations (T 231, T 265, T 003, T 014, and T 035) were sampled during the months of December and January. At any rate, if the available data truly reflect the natural phenomenon, the higher salinity of the winter months in this region does not seem to favor *I. illecebrosus*, while the lower salinity of the summer months does not impair its distribution. The latter phenomenon was also observed by Frost & Thompson (1933, p. 85) for the summer of 1932. Due to a greater influx of Arctic water down the east coast of Newfoundland, the coastal waters were fresher than as reported in 1931, yet the squid were much more plentiful in 1932. From these observations, one may conclude that within a reasonable range (31-36^{o}/oo), changes of salinity do not influence the occurrence of *I. illecebrosus*.

As in the case of temperature, the salinity of water from which *I. coindetii* was taken is higher than that of *I. illecebrosus*.

In the Cape Hatteras, North Carolina, region the salinity range for the squid-yielding waters was 33-36^{o}/oo. Although no salinity data are available for the stations from the Gulf of Mexico and the Caribbean Sea, one can utilize Parr's data (Table 27) to analyze the distribution of *I. coindetii* in this region. The salinity ranges at the depths of capture are 34.87-36.32^{o}/oo in the Gulf complex and 34.86-36.73^{o}/oo in the Caribbean Complex.

The salinity in the Mediterranean Sea is higher than the adjacent Atlantic water, especially in the eastern Mediterranean where it exceeds 39^{o}/oo. The unusually high salinity in this region may form a barrier preventing the penetration of this region, with the resultant absence of this species in the eastern Mediterranean Sea.

In the Gulf of Guinea, the salinity range for the *Geronimo* stations is 34.91-35.82^{o}/oo. This is somewhat narrower than the range contained within Adam's (1952, pp. 82-83) results from waters further to the south (33.06-37.12^{o}/oo).

To sum up, the salinities, both minimum and maximum, for *I. coindetii* appear to be higher (33 and 38^{o}/oo respectively), than those for *I. illecebrosus* (31 and 36^{o}/oo). This may be expected since we have seen that *I. coindetii* is a warmer water species than is *I. illecebrosus*, and the former inhabits areas where evaporation generally is greater, thus with resulting higher salinities. However, both species have been reported from equally narrow ranges, both encompassing a 5^{o}/oo range in salinity. Apparently, one is no more euryhaline than the other.

Illex argentinus from the South American coast again presents problems in this discussion, due to the lack of available data. The salinity values reported by Castellanos (1964, p. 22), $33.31-35.38^{o}$/oo indicate a very narrow salinity range for this species. However, since there is no squid fishery *per se* in Argentine waters, the squid caught have been generally incidental to the hake fishery. What little environmental data are available are those of the hake fishing ground. An effort to learn the environmental parameters for squid distribution would doubtlessly yield a somewhat different picture, although the differences may not be great.

With respect to *Illex oxygonius*, salinity data accompanies only the specimens from the VIMS collections. Like *I. argentinus*, only some two or three parts per thousand of salinity are covered by the ranges represented in their collection sites. One hesitates to assign such a restricted stenohalinity to *I. oxygonius*, based on such limited data on such a small total number of samples. However, again by resources provided by Parr's data (Table 27), since this species was taken at depths ranging from 222 to 555 m in the Gulf of Mexico (see List of Materials, *I. oxygonius*), we may tentatively assign salinity values ranging 35 to 36°/oo for these depths. These are higher only 1°/oo than the maximal VIMS value (range 32-35°/oo) for the Chesapeake Bay collection sites, so it may be that the species does, in fact, exist in waters of a restricted salinity range, from 32-36°/oo. However, more data are certainly necessary.

Based on the admittedly limited data, all four species show a markedly stenohaline behavior. As noted, both *I. illecebrosus* and *I. coindetii* have been found over a 5°/oo range, while *I. oxygonius* has been taken only from waters embracing a 4°/oo range. Less than 2°/oo is covered by the salinity range represented in the data for *I. argentinus*. Probably the only valid analyses are those for *I. illecebrosus* and *I. coindetii*, however.

The most important effect of salinity to the aquatic organism is the osmotic relationship between the protoplasm of the organism and the surrounding environmental medium (Sverdrup, et al., 1942, p. 770). In general, cephalopods are strictly stenohaline. Robertson suggested that the absence of cephalopods in fresh and brackish waters is due to their naked skin which is probably freely permeable to water to a considerable degree (Robertson, 1964, p. 307). In the open ocean where salinities are relatively constant, temperature usually is the master factor controlling distribution (Kinne, 1964, p. 329). As they are active swimmers, the response of teuthoids to an unfavorable environment would be "escape by migration into more suitable conditions" (Kinne, 1964, p. 293). The phenomenon of spawning in deep water by *Illex*, as suggested earlier, would be beneficial in that there environmental conditions are more constant, therefore the eggs, embryos and larvae would be exposed to less varied environmental conditions with a consequent increase in their chances of survival.

In general, organisms tend to experience an increase in oxygen consumption when subjected to lower salinities (Pearse & Gunter, 1957, p. 135). However, Kao (1970) found the reverse to be true for *Illex illecebrosus* under laboratory conditions. He (1970, p. 43) suggested that decreasing salinities subjected the squid to an osmotic stress which had a narcotizing effect on the animals, thereby reducing oxygen consumption as the salinities decreased.

Raffy & Ricart (1939, *fide* Kao, 1970, p. 41) found that *Sepia officinalis* and *Octopus vulgaris* had no osmoregulatory mechanism and that oxygen consumption remained constant under sub- and supranormal salinities.

It is interesting to note that the salinities in the areas where *I. coindetii* occur are generally higher than those with *I. illecebrosus*. The oxygen content of the water is,on the other hand, lower in the habitat of *I. coindetii*. To compensate for this lower level of available oxygen in their environment and to more efficiently utilize the oxygen available, organisms generally tend to demonstrate a greater gill surface area. For instance, specimens of *Bathyteuthis abyssicola* from the oxygen-poor eastern Pacific have larger gills than do those from the oxygen-rich Antarctic waters (Roper, 1969, p. 84). Roper spoke of gill size, using measurements of length and width.

Perhaps of greater significance is the number of gill lamellae in each of the ctenidia of a given species. Roper ascertained such data for three populations of *Bathyteuthis abyssicola* and for B. *bacidifera*. He could not distinguish between populations of B. *abyssicola* on the gill lamellae count, but it was possible to separate B. *abyssicola* from B. *bacidifera* on this criterion.

In Table 20 was presented data on the number of gill lamellae for each of the four species. Although Roper (1969, p. 84) found "larger" gills in specimens of a species from oxygen-poor areas, while those of the same species from oxygen-rich areas had smaller gills, the data here indicate that I. *coindetii* (characteristically from waters of low oxygen content) has fewer lamellae than does I. *illecebrosus* (from waters of no deficiency of oxygen) of comparable size. Although Roper spoke here only of gill size and the data presented on *Illex* deals with gill lamellae number, an apparent contradiction exists.

Voss (1967, p. 528) suggested that the reduced gill area in deep sea octopods is due to lowered metabolic requirements. We cannot know whether or not this reduction in the number of gill lamellae in *I. coindetii* is due to lower metabolic requirements, as no work has been done on their metabolic requirements. To compare the metabolic rates of *I. coindetii* and *I. illecebrosus* by such measurements as oxygen consumption rate, would have to be undertaken under similar experimental conditions for both species. One thing is apparently clear, and that is that its existence in the colder waters of the boreal environment probably places a greater basal metabolic demand on *I. illecebrosus*. This species, with its normally oxygen-rich environment, has more available gill surface structures (lamellae) than does its southern counterpart.

On the other hand, *I. coindetii* exists not only in water of characteristically lessened oxygen titers, but also in water of greater density (compare Tables 24 and 26). To migrate through waters of higher density may place greater demands on the metabolism, yet this form has the more reduced lamellar structure of the two species. Either the number of gill lamellae is not of functional or physiological significance, or the genetically determined nature of the haemocyanin of the two species is markedly different in capacity and efficiency. Since little is known of teuthoid haemocyanin and nothing is known of that of the genus *Illex*, these are forced to be left as areas of speculation.

The first attempt to relate the distribution of a cephalopod to identifiable water masses was that of Pickford (1946) on *Vampyroteuthis infernalis* Chun. She was able to delimit the distribution of that species to certain water masses and the range of density. Roper (1969) did the same for species of the genus *Bathyteuthis*.

Plotting the temperature-salinity data for the distribution of *I. illecebrosus* on the water mass chart reveals that the waters inhabited by this species are not characteristic of a well-defined water mass. This is not surprising, since this species is captured only in the inshore waters of the Newfoundland coast. The freshwater run-off from the land as well as the melting of ice and snow in the spring and early summer certainly would result in a dilution of the sea water and cause a decrease of onshore salinity. The same characteristics mark the locations from which *I. illecebrosus* has been taken in the VIMS collections from the Chesapeake Bay region.

Therefore, this species could, perhaps erroneously, be designated merely as a coastal species, never coming in contact with distinctive oceanic water masses. However, in Newfoundland, all onshore or embayment collections are from the period mid-July to early November.

The group at Memorial University has long speculated where the species may be found after it leaves the Newfoundland coastal area in the month of November. That they are not found in the same areas they inhabit from mid-July to November is clear. All collections, regardless of time, are from coastal waters under the influence of freshwater dilution, yet the mystery of their whereabouts off Newfoundland from November through June remains basically unsolved.

For *I. coindetii*, most of the Geronimo stations in the Gulf of Guinea come from the South Atlantic Central Water mass. The density values for the water in which *I. illecebrosus* and *I. coindetii* were captured almost overlap over the entire density range, and, as was already shown, the ranges are great (Figs. 43 and 44). However, the concentration of the successful catches along the density ranges of these two species differ considerably. Of the 44 successful stations for *I. coindetii*, 84.1% lie within sigma-t = 26.0-27.5, while only 34.1% of the 44 successful stations for *I. illecebrosus* fall therein.

The effect of density of sea water on distribution is pronounced in organisms with more or less passive modes of locomotion, such as plankton and weak nekton. Pickford (1952, p. 208) found that *V. infernalis* is found only in water with densities of sigma-t = 27.0-27.9. She suggested (1946, p. 27) that temperature, salinity, and density are perceived independently by the organism and each affects biological processes independently. However, she concluded that density may be an important factor in restricting this species to a particular water body but that it cannot be considered to be the only delimiting factor, since water of optimal density is not inhabited by this species when the temperature or salinity is too low or too high (p. 28).

It is not clear how important a role density plays in the case of *Illex* species. Since the density of water depends primarily upon its salinity and temperature, the density increases as the salinity increases. On the other hand, density increases as the water temperature decreases to 4°C. Density is the result of these two variables, namely, salinity and temperature, assuming the pressure is constant. Therefore, if temperatures or salinities prove to be inimical to the presence of squid, this parameter, or parameters, in itself or themselves, will have a primary biological affect irrespective of the density.

The differences noted in the distribution of *I. illecebrosus* and *I, coindetii* along the range of densities where they were found, may be due not to the density but to either temperature or salinity factors or a combination of both.

The amphi-Atlantic distribution of *I. coindetii* is difficult to explain, since no *Illex* has been captured from the mid-Atlantic Ocean. However, as Voss (1954, p. 476) suggested, "the sometimes rather long planktonic life of many of the larval forms" and the flow of the North Equatorial Current into the Caribbean and the Gulf of Mexico would possibly transport larval forms of this species across the Atlantic Ocean. This trans-Atlantic transport of molluscan larval forms is not uncommon, as was reported by Scheltema (1966). Although no direct evidence is available on *Illex coindetii*, the possibility cannot be ruled out.

GENERAL DISCUSSION AND CONCLUSIONS

One has to agree with M. R. Clarke's statement that "Compared with most animal classes, very little is known of the Cephalopoda and within the Cephalopoda we are more ignorant of the oceanic squids than of the neritic squids and the octopods". (Clarke, 1966, p. 93). Indeed, our knowledge of oceanic squids is poor. Among the oceanic squids, the Ommastrephidae are the best known, however, our knowledge of these animals is far from satisfactory and, at best, fragmentary, despite the fact that they have been studied more than has any other oceanic group.

The purpose of this study has been two-fold. Not only was it conceived as an effort to uncover as much as possible of the systematics of the genus, but also, hopefully, to synthesize much of the existing fragmentary knowledge.

Earlier, in previous sections of this work, I have discussed points raised therein, and here it is the intention to discuss the overall comparative nature of this study of these four species.

The funnel organ is always described in great detail and is duly figured in all modern cephalopod literature in the description or revision of a species. Yet, this information has never really been adequately used in teuthoid systematics, and no workers have seemed willing to use the funnel organ as a character in the separation of species. This is in spite of the almost universal modern use of these organs in octopod taxonomy following Robson (1929, 1932). In the genus *Illex* the funnel organ is very distinctive, and the four species can be separated on this character. Reference to the four illustrations presenting these organs in the four species, and the appropriate descriptions in the text, indicate that they naturally fall into two groups of two species each. Specifically, *I. illecebrosus* (Fig. 5A) and *I. argentinus* (Fig. 23A) comprise one of these groups in that in both species the posterior limbs of the dorsal funnel organ arise from a shallow common base posterior to the apical papilla. In the species in the other group, *I. coindetii* (Fig. 16A) and *I. oxygonius* (Fig. 28A), the posterior limbs arise from a broad base. Within the two groups, the funnel organs are distinctive in each species, and proper identification of the species can be made on these criteria. It would be most interesting to investigate other families and genera to learn if these organs prove to be of the same systematic significance. They apparently are in the genus *Illex*.

Throughout this study, the repeated affinity or similarity of *I. illecebrosus* and *I. argentinus*, and that of *I. coindetii* and *I. oxygonius* became increasingly repetitious and apparent. In the following table, Table 28, data presented earlier is regrouped and summarized on each of the species in an effort to learn how extensive this apparent similarity proved to be.

When this data, both measurements and indices, are compared in this way, several phenomena become evident. There appears to be a grouping based on some criteria (HLI, HWI, MWI - all meristic characteristics - plus the configuration of the funnel organ) that substantiates pointing out similarities between *I. illecebrosus* *I. argentinus* and likewise, *I. oxygonius* and *I. coindetii*. The former pairing may be referred to as the boreal-antiboreal group, in Ekman's terminology, while the second, though clear in its existence, is less easily designated. In the western Atlantic they belong to tropical-subtropical fauna, while in the eastern Atlantic they are best described as temperate-tropical-subtropical. These differences may be imposed by environmental factors within tolerable limits.

The comparison in Table 28 also demonstrates sexual dimorphism to some degree in all the four species. It is most developed in the *coindetii-oxygonius* group, based primarily on maximal sucker size, the head width and head length, and the length of the sessile arms when considered as per cent differences in length. Of the other two species, *I. argentinus* shows the stronger

Table 28

Comparison of morphometric indices of selected variables of the four species of the genus *Illex*, separated by sex.

		I. coindetii	*I. oxygonius*	*I. illecebrosus*	*I. argentinus*
MALE	HLI	21.8	18.2	16.4	19.5
	HWI	21.8	20.0	17.0	17.8
	MW$_1$I	21.9	18.7	18.0	19.8
	MW$_2$I	21.5	16.4	19.7	22.7
	MW$_3$I	13.6	10.9	12.0	13.3
	A$_1$LI	47.4	43.9	39.1	55.6
	A$_2$LI	62.4	54.8	48.2	70.2
	A$_3$LI	61.0	54.7	48.2	71.2
	A$_4$LI	54.1	47.9	43.0	61.6
	S$_1$I	1.61	1.51	1.17	1.33
	S$_2$I	2.94	2.47	1.75	2.71
	S$_3$I	2.87	2.44	1.73	2.49
	S$_4$I	1.47	1.39	1.02	1.43
	S$_T$I	2.14	1.69	1.45	2.19
	FLI	39.2	45.0	43.8	41.9
	FWI	56.4	51.5	55.4	58.0
	FBLI	33.9	40.2	39.5	37.5
	HcLI	25.1	28.8	22.1	50.3
FEMALE	HLI	19.0	16.3	15.7	16.8
	HWI	18.4	17.5	16.3	16.0
	MW$_1$I	20.3	17.7	17.5	18.5
	MW$_2$I	20.4	17.8	19.5	22.3
	MW$_3$I	13.0	10.8	12.0	14.2

continued

	I. coindetii	*I. oxygonius*	*I. illecebrosus*	*I. argentinus*
A_1LI	37.6	34.3	36.5	46.2
A_2LI	48.7	42.9	44.5	57.4
A_3LI	48.3	43.4	44.5	58.5
A_4LI	42.4	38.1	40.4	52.0
S_1I	1.35	1.20	1.13	1.23
S_2I	1.93	1.83	1.61	1.88
S_3I	1.94	1.80	1.61	1.86
S_4I	1.19	1.12	1.03	1.10
S_TI	1.81	1.65	1.51	1.95
FLI	39.4	45.0	44.1	42.3
FWI	53.7	50.5	54.6	56.4
FBLI	34.5	40.0	39.5	37.8

sexual dimorphism in differences in arm length. This species is also distinctive in the fact that it has the greatest degree of modification in hectocotylization, in that the modified portion occupies over 50% of the total arm length.

The indices on fin dimensions (FLI, FWI and FBLI) summarized in Table 28 establish the fin as clearly one feature that is species diagnostic. The longest and narrowest caudal fins are characteristic of *I. oxygonius*, with *I. argentinus* being characterized by the widest caudal fins. The fins of *I. coindetii* are the shortest among the four species.

When squid of the four species of comparable size are compared it is evident that *I. argentinus* possesses the least number of suckers on the sessile arms, and the range of numbers only slightly overlaps those for the other species (Tables 13 through 16). In the future, the possible significance of this variable should not be overlooked in squid taxonomy.

The number of suckers increases as the animal grows, but at least in the genus *Illex*, a correlation exists in the number of suckers and the size of the largest sucker on a specific arm. In all four species, the greatest number of suckers is present on the ventral pair of arms (IV), but the largest sucker thereon is the smallest of those of maximal size on all four arms (Tables 12 through 16). It was Roper (1969) who first realized the potential importance of the count of suckers, and the results of the inclusion of such data in this study has confirmed his contention.

Clarke (1962) reported that the mandibles of teuthoids are diagnostic to the family level. It is clear that they afford little of value in attempting to distinguish the four species of *Illex* and one may conclude that generally they are of little, if any, value at the species level. Indeed in a study of the mandibles of five specimens of *Architeuthis* from Newfoundland waters, the anomalous situation was encountered where the two sides of a given mandible were found to present different configurations, indicating the possible unilateral variation caused by useage. Hence, the structure is of doubtful significance (Aldrich and Lu, unpublished data).

No differences could be detected in the configuration of the gladius or any of the cartilagenous structures such as the nuchal cartilage or the mantle-locking apparatus in the four species. They are classically characteristic of the family Ommastrephidae, if Clarke (1962) is right with respect to the mandibles, it is interesting to speculate upon the familial importance of "hard" parts of a cephalopod. Mayr (1969, p. 94) defines a family as a taxonomic group of genera of a common phyletic origin. The entire evolution of Cephalopoda has been historically explained in terms of the shell, specifically, its location, its form and its function. Evolution of hard parts must be a slow process resulting in the stability of familial characteristics upon which the variations taxonomists recognize as genera and species are superimposed.

The systematic significance of some of these chitinous or cartilagenous structures has been little studied and, therefore, little understood. The mandibles have been investigated (Clarke, 1962) it is true, as have the various configurations of the mantle-locking apparatus (Young & Roper, 1968). The cuttle bone of the *Sepia* and the shell of the nautiloids have been extensively studied from both morphological and physiological aspects. But little if any, significant work has been done on the gladius of a teuthoid. Bradbury & Aldrich (MS) have likened it to an invertebrate "backbone" in the squid endoskeleton, but what is needed is an investigation of the systematic significance of the gladius, throughout the entire Teuthoidea. Such a study would involve recording variations in configuration, chemical composition and attempts to interpret the structure in functional-morphological terms as it occurs in different groups. As noted earlier with respect to the funnel organ, the gladius is always, both classically and modern, included in a species description. Despite this, no serious attempt has ever been made to systematize this information. Much of the data already exists, but what now needs to be done is a synthesis of this data, in much the same manner as M. Aldrich (1969) did in gathering together species data on radulae.

For too long the classification of *Illex* as a monospecific genus of several subspecies was in vogue. It is clear from this systematic study that four valid species exist, despite the noted affinities distinguishing *illecebrosus-argentinus* and *oxygonius-coindetii* groups on the basis of certain characteristics.

The distribution of these species has been interpreted on the basis of available environmental data, noting that little adequate data exists with respect to *I. argentinus* and *I. oxygonius*. Despite the large and important fishery for *I. illecebrosus* in Newfoundland waters, a lamentable lack of hydrographic data exists. Therefore, only *I. illecebrosus* from the Chesapeake Bay area and *I. coindetii* collections are accompanied by sufficient data to permit extensive interpretations of limiting or permissive factors governing their distribution.

It is indeed fortunate that this information exists for *I. coindetii*, for this species, as noted, is amphi-Atlantic in distribution. That there are no mid-Atlantic collections of this species (or of any species, for that matter) has been pointed out earlier. The cause for this amphi-Atlantic distribution must therefore remain as a matter of speculation, but I contend that *I. coindetii*, probably first as larvae, experience an eastward, clockwise migration, and, as part of the water movement of the North Atlantic gyre, eventually reach the coastal waters of the eastern Atlantic. From there the distribution is to the south, as far as the area immediately north of the Benguela Current, then westward, which completes the clockwise North Atlantic gyre. It is clear that the northern extent of distribution along the Atlantic coast of North America is limited by temperature, through the southern movement of the Labrador waters in the Virginia Current - an area not far from the easterly course of the gyre. On both coasts the extent of distribution is associated with temperature barriers. The illustration by Ommanney (1963, p. 194), showing the clockwise migration of the elvers and adults of eels (although it is not here suggested that the squid are in any way characterized as being similar in the biological phenomena involved) is striking in that it is strongly similar to what I postulate to be the route followed by *I. coindetii* in its amphi-Atlantic distribution. There is even included the northernmost branch bringing water (and planktonic biota) to the non-boreal waters of the North Sea.

Much more work needs to be done, especially mid-Atlantic sampling, before this cycle can be confirmed.

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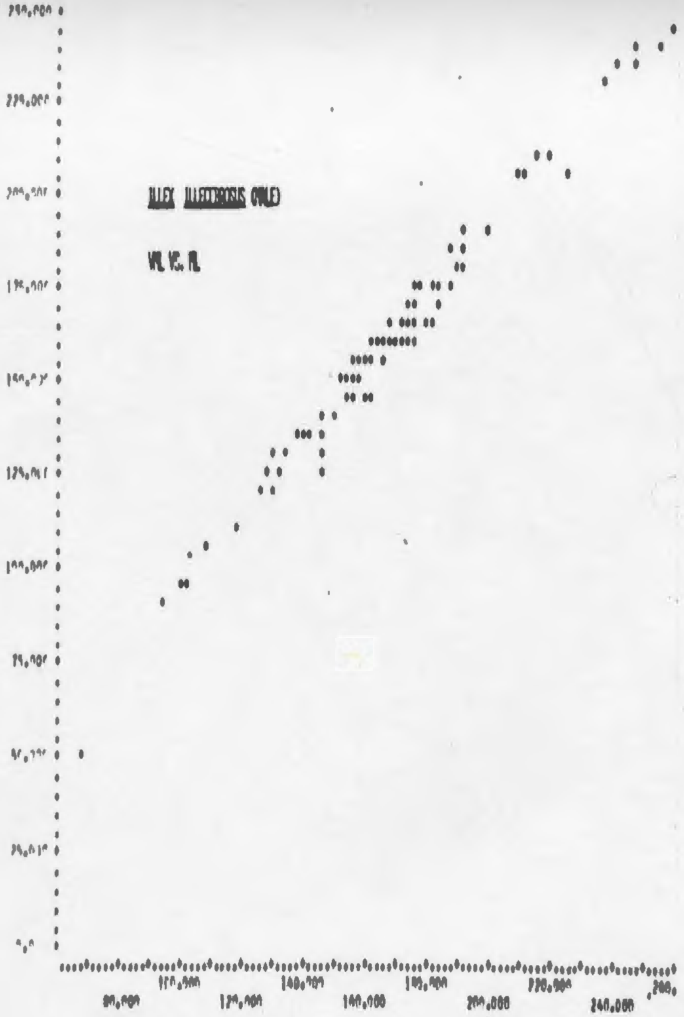
APPENDIX

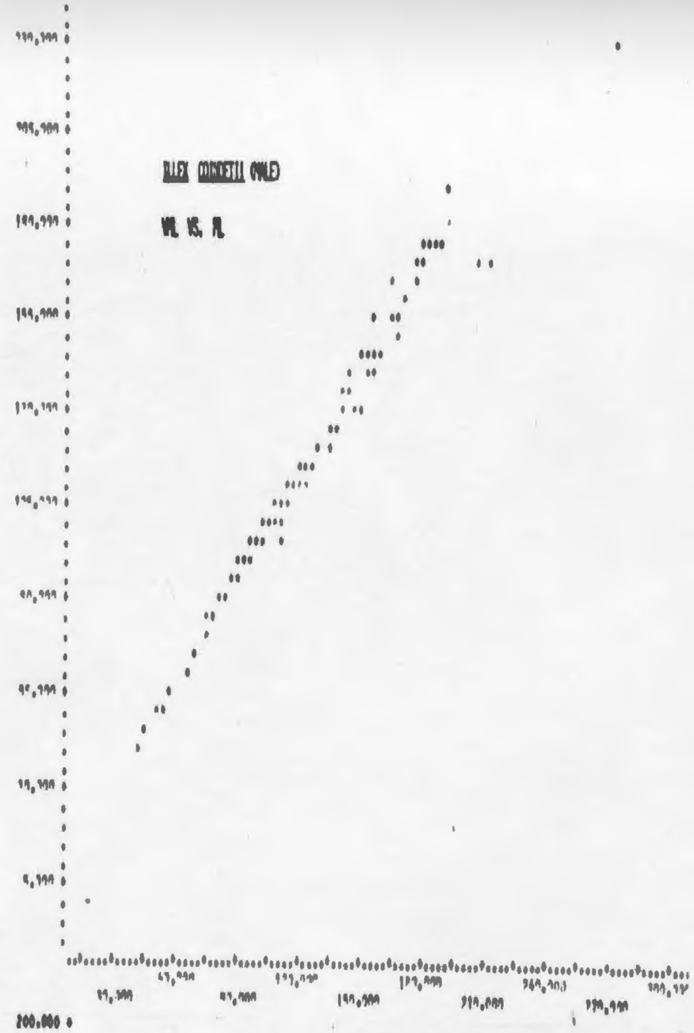
Computer print-outs plotting various measurements against mantle length for each of the four species of the genus *Illex*. The X-axis in all plottings are mantle length (ML) in mm.

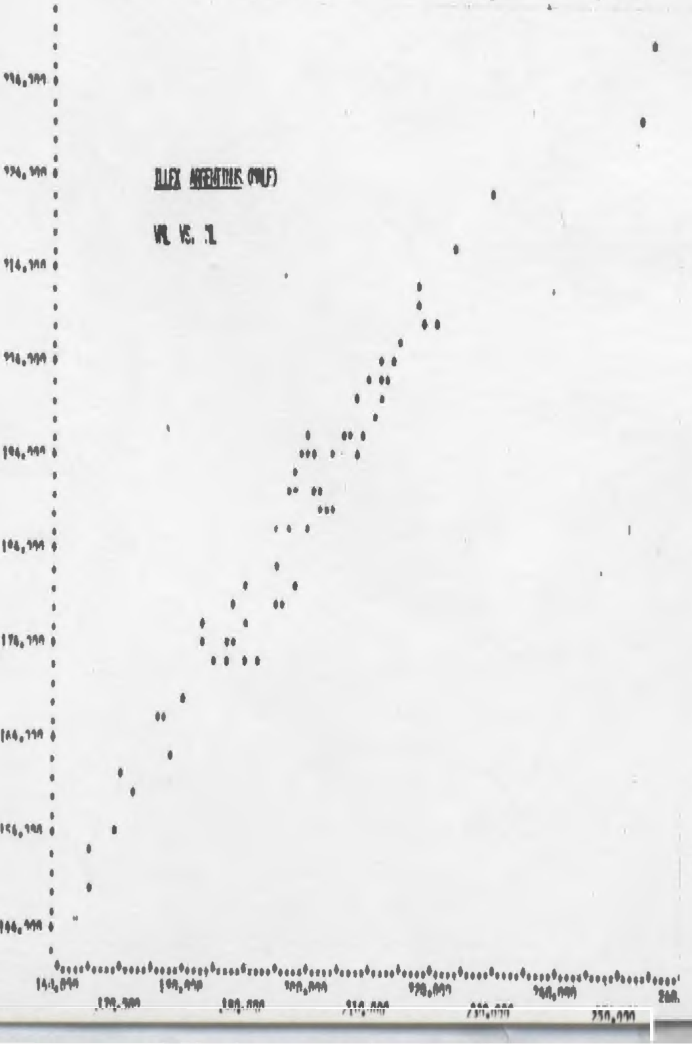
Key to the Appendix

Character* (Y-axis)	Pagination		Character* (Y-axis)	Pagination	
	Male	Female		Male	Female
VML	348	349	S_1L	368	369
HW	350	351	S_2L	370	371
FL	352	353	S_3L	372	373
FW	354	355	S_4L	374	375
FBL	356	357	S_TL	376	377
A_1L	358	359	$\#S_1$	378	379
A_2L	360	361	$\#S_2$	380	381
A_3L	362	363	$\#S_3$	382	383
A_4L	364	365	$\#S_4$	384	385
HcAL	366		GL	386	387
HcL	367		#G	388	389

*For definition of abbreviations, see "Materials and Methods" section.


ILLEX ILLECEBROSUS (MALE)
WL VS. ML
140,000
200,000
240,000


ILLEX COINDETII (MALE)
WL VS. ML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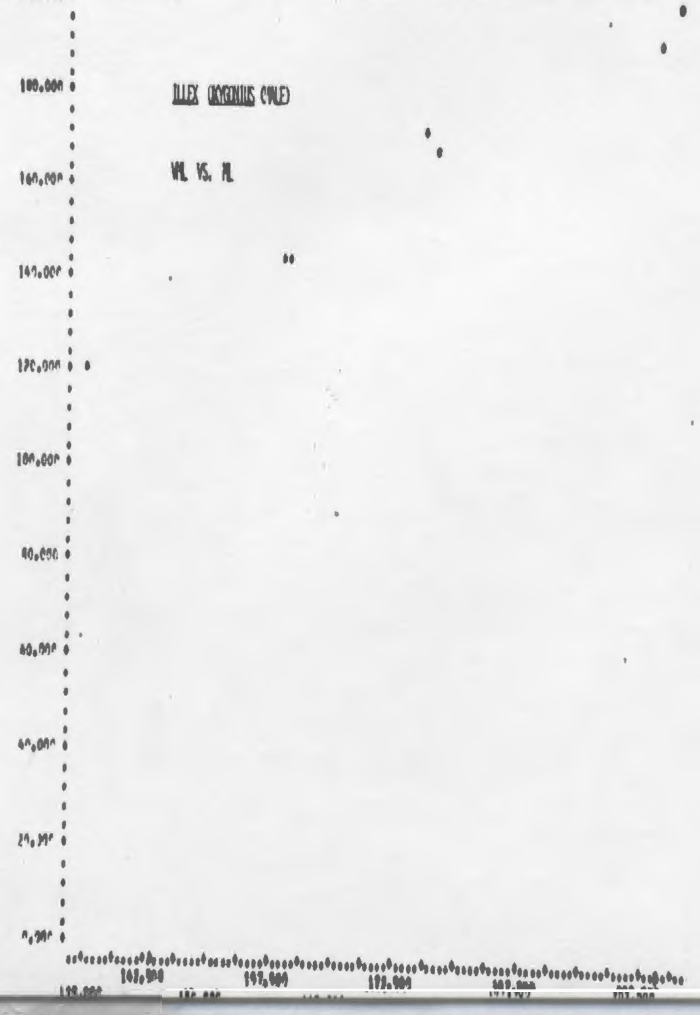
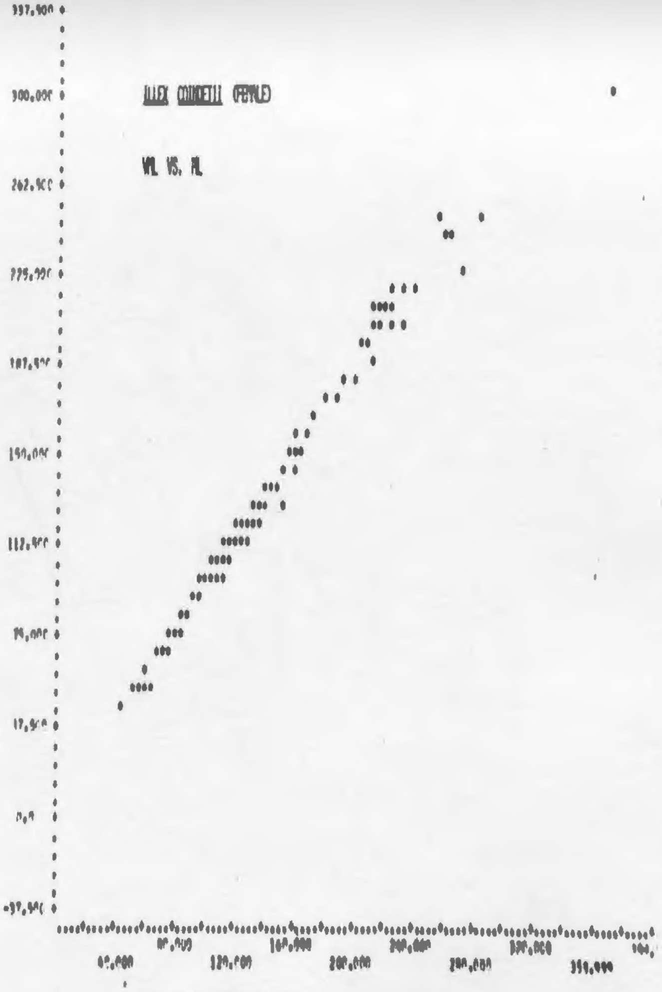
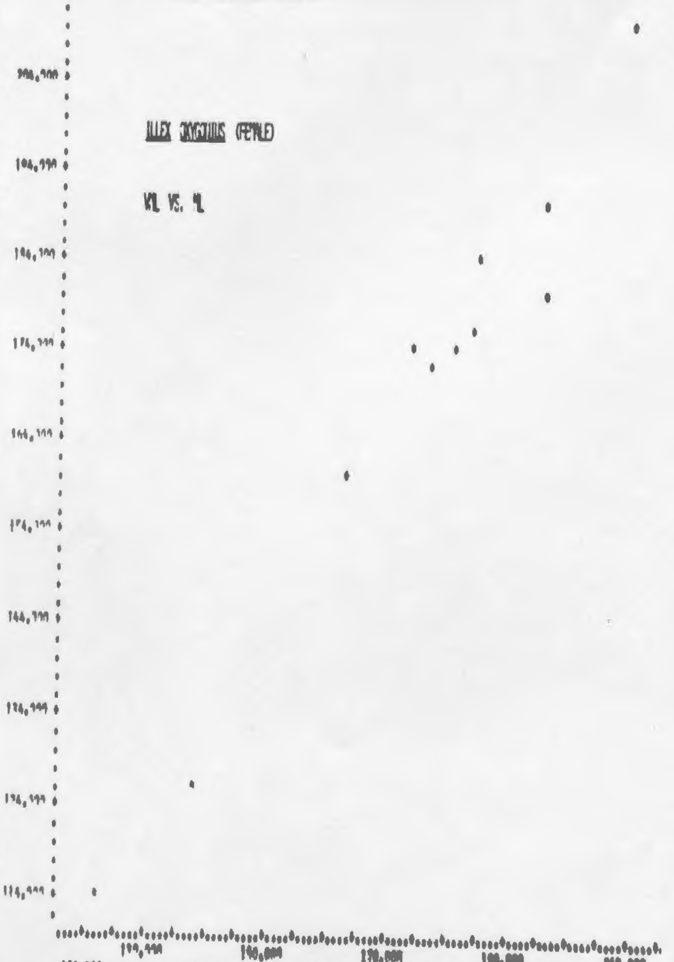
WL VS. ML


ILLEX OXYGONIUS (MALE)
WL VS. ML
200.000
180.000
160.000
140.000
120.000
100.000


ILLEX ILLECEBROSUS (FEMALE)
VML VS. ML


ILLEX COINDETII (FEMALE)
VML VS. ML
337.500
300.000
262.500
150.000
112.500
120.000
160.000
200.000


ILLEX ARGENTINUS (FEMALE)
VML VS. ML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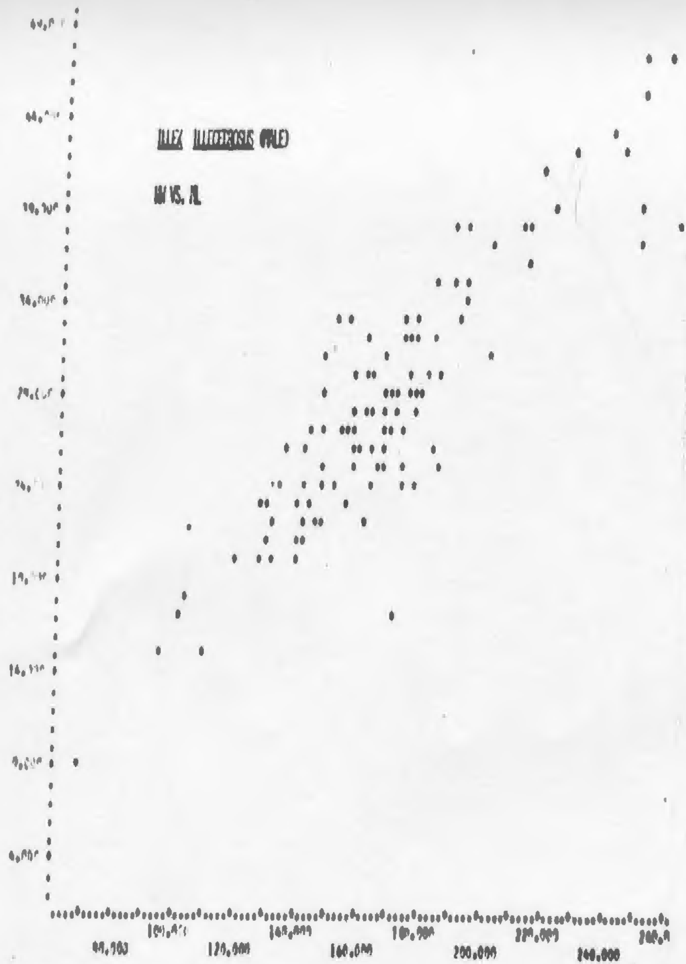
VML VS. ML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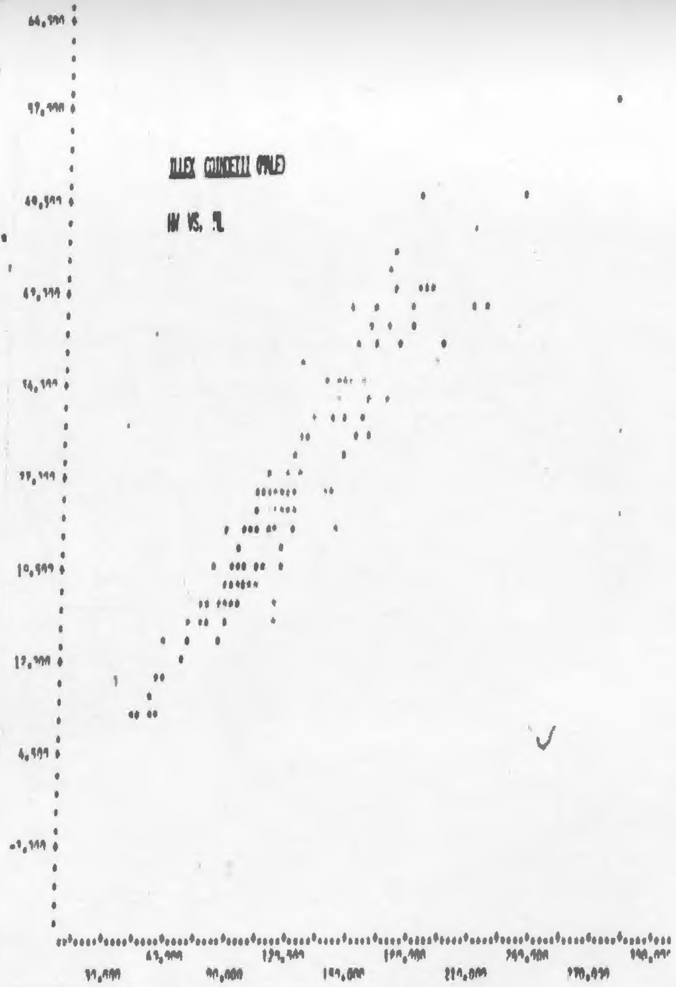
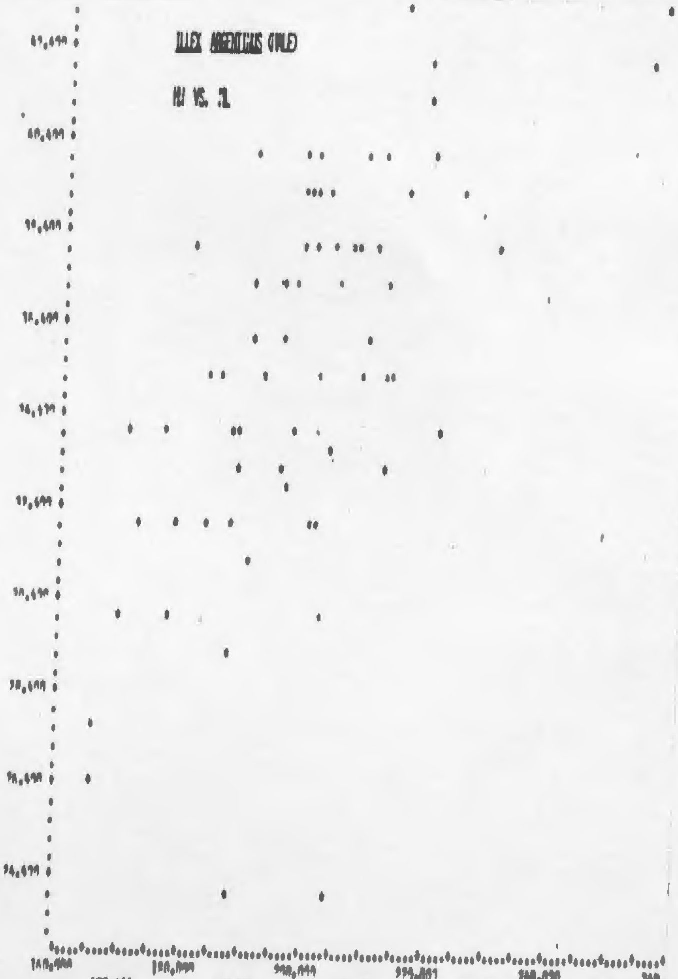
MW VS. ML


ILLEX COINDETII (MALE)
MW VS. ML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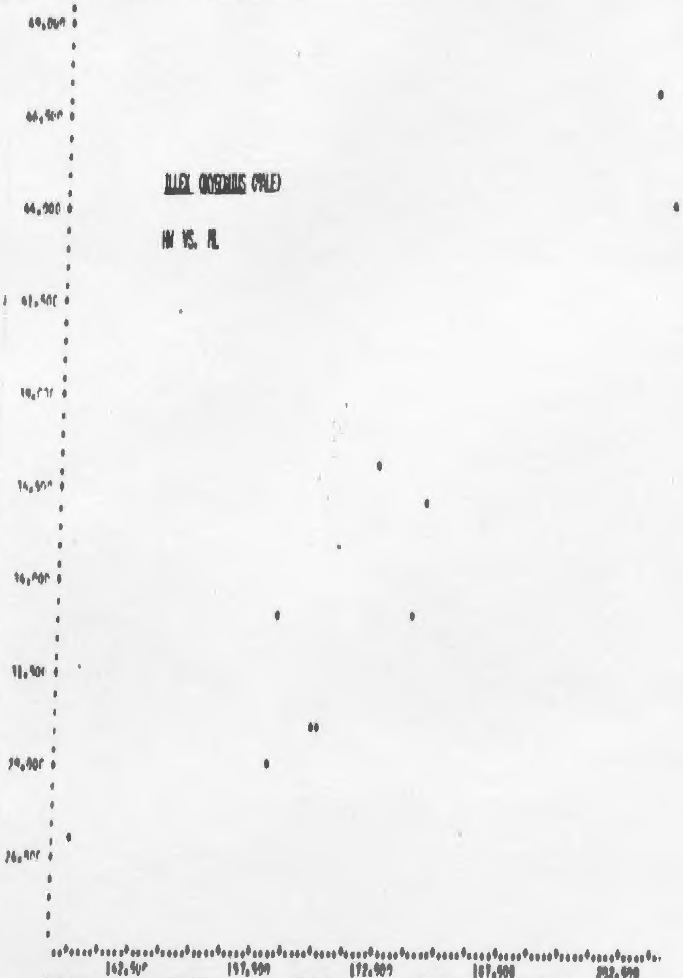
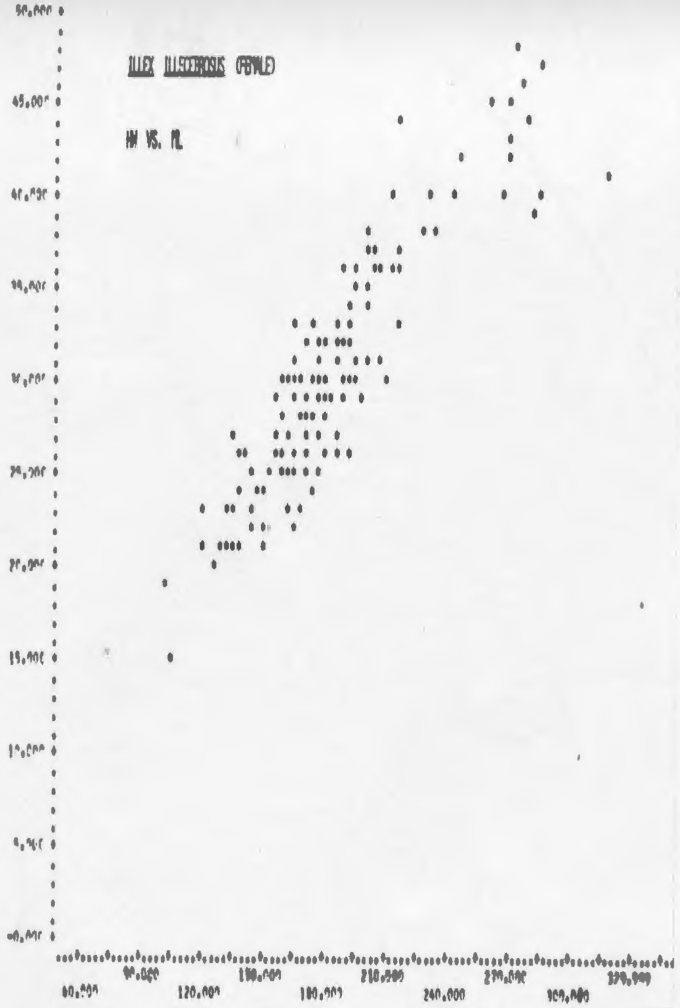
MW VS. ML


ILLEX OXYGONIUS (MALE)
MW VS. ML


ILLEX ILLECEBROSUS (FEMALE)
HW VS. ML
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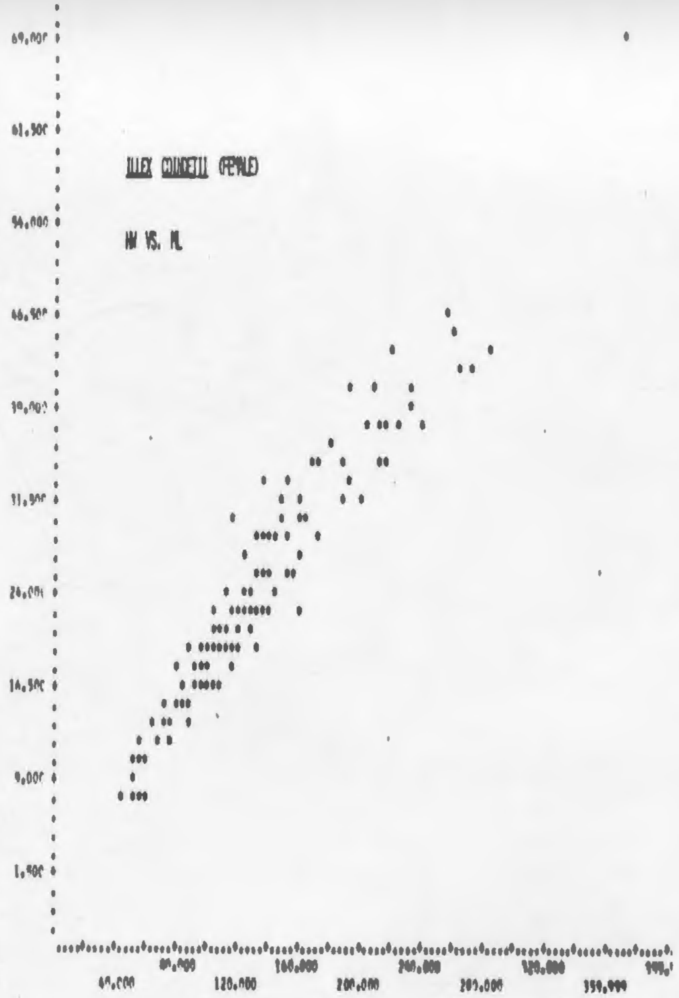
90.000
120.000
150.000
180.000
210.000
240.000
270.000
300.000
330.000


ILLEX COINDETII (FEMALE)
HW VS. ML
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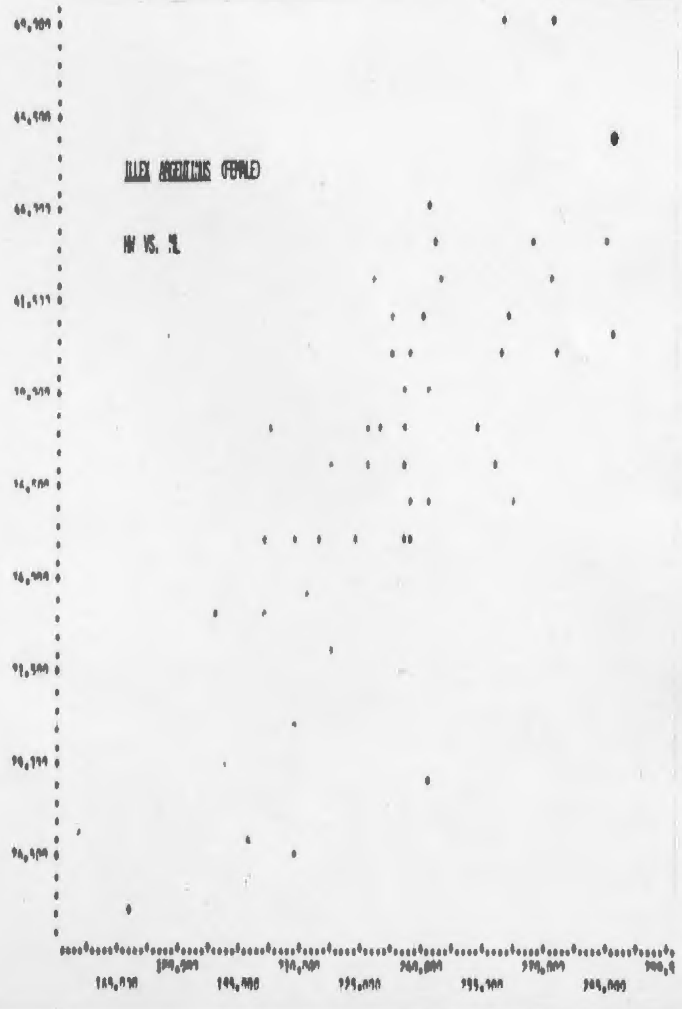
90.000
120.000
160.000
200.000
240.000
280.000
320.000
350.000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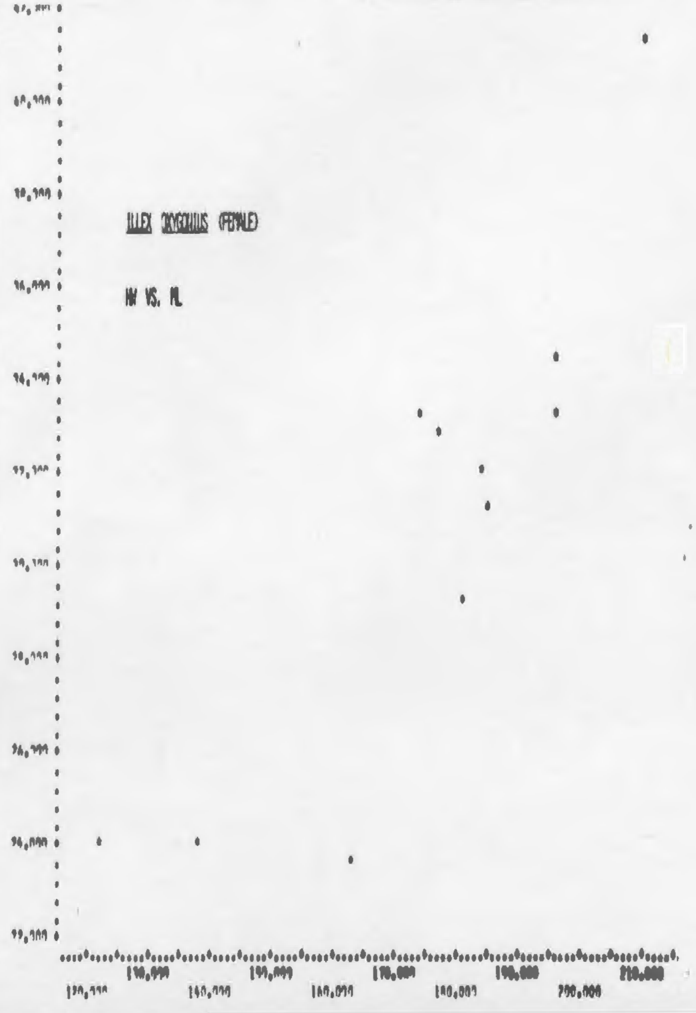
HW VS. ML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HW VS. ML
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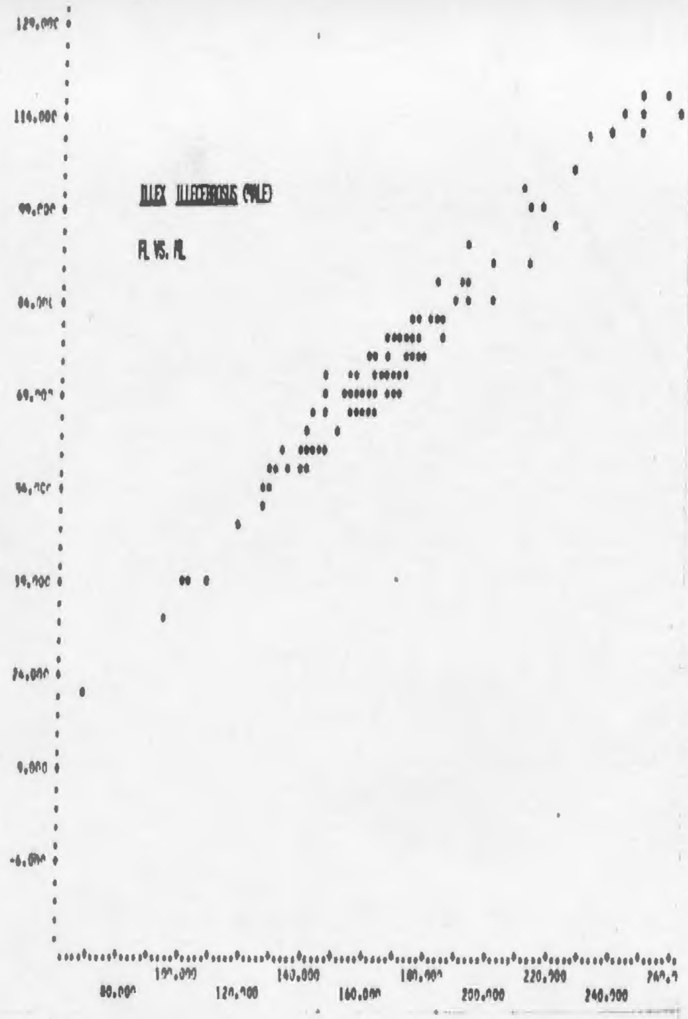
140.000
150.000
160.000
170.000
180.000
190.000
200.000
210.000


ILLEX ILLECEBROSUS (MALE)
FL VS. ML
129.000
114.000
99.000
84.000
69.000
54.000
39.000
24.000
9.000
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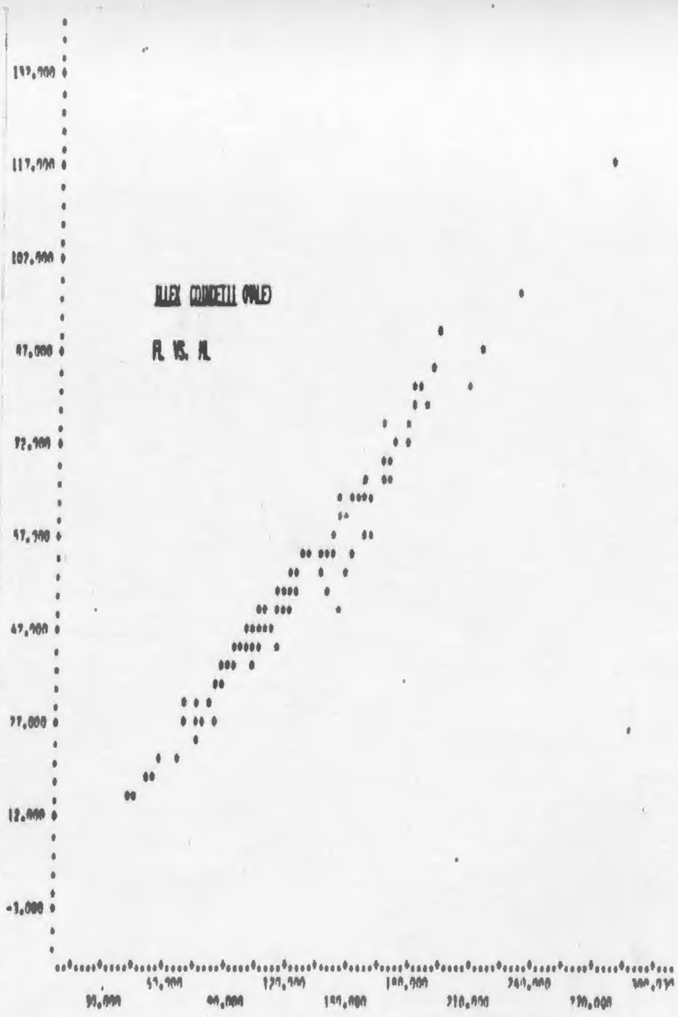
200.000
220.000
240.000
260.0


ILLEX COINDETII (MALE)
FL VS. ML
132.000
117.000
102.000
87.000
72.000
57.000
42.000
27.000
12.000
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60.000
90.000
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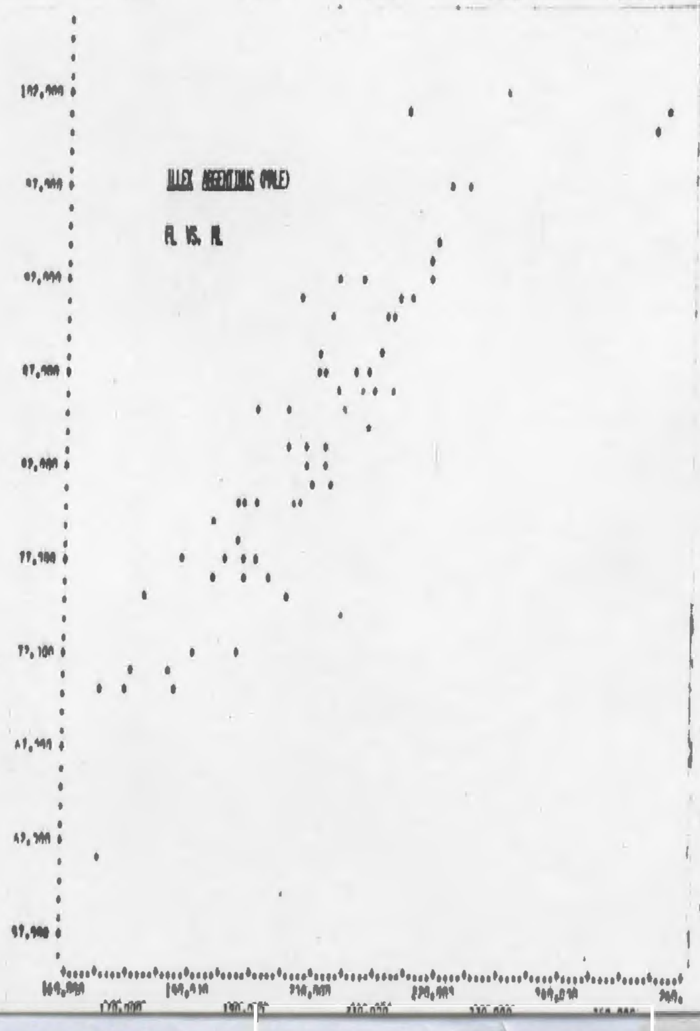
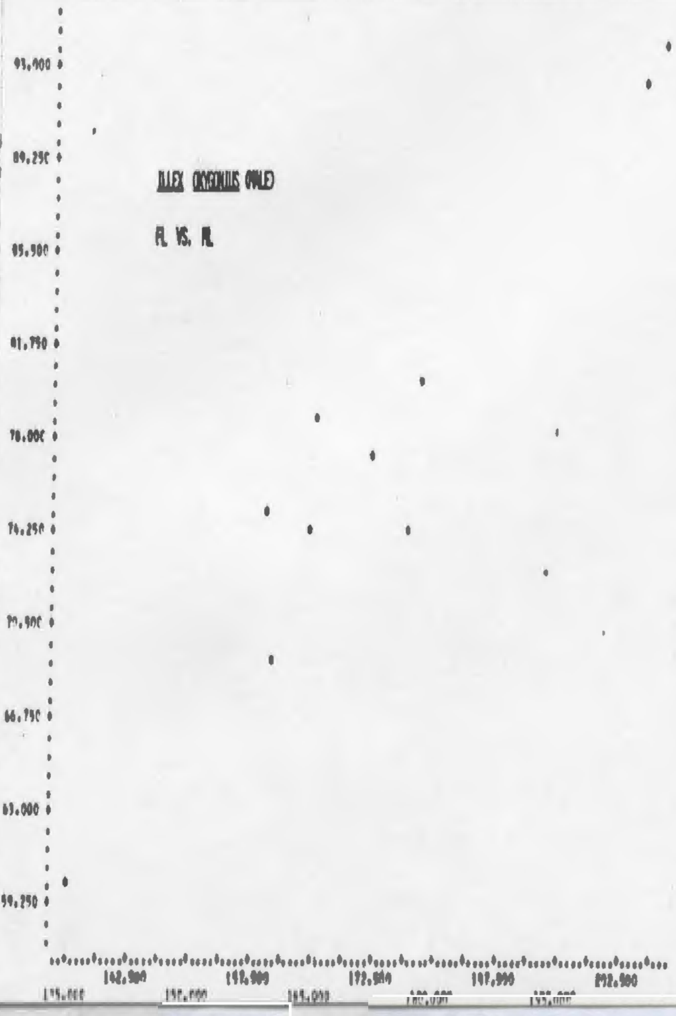
210.000
240.000
270.000
300.000


ILLEX ARGENTINUS (MALE)
FL VS. ML


ILLEX OXYGONIUS (MALE)
FL VS. ML
93.000
89.250
85.500
81.750
78.000
74.250
70.500
66.750
63.000
59.250
135.000
142.500
150.000
157.500
165.000
172.500
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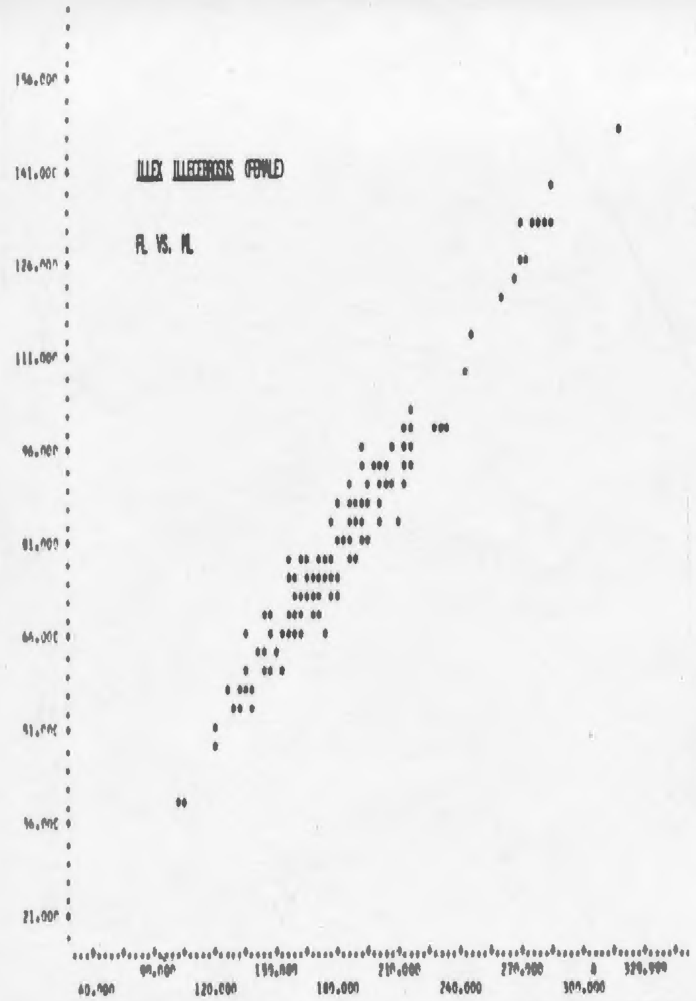
187.500
195.000
202.500


ILLEX ILLECEBROSUS (FEMALE)
FL VS. ML
156.000
141.000
126.000
111.000
96.000
81.000
66.000
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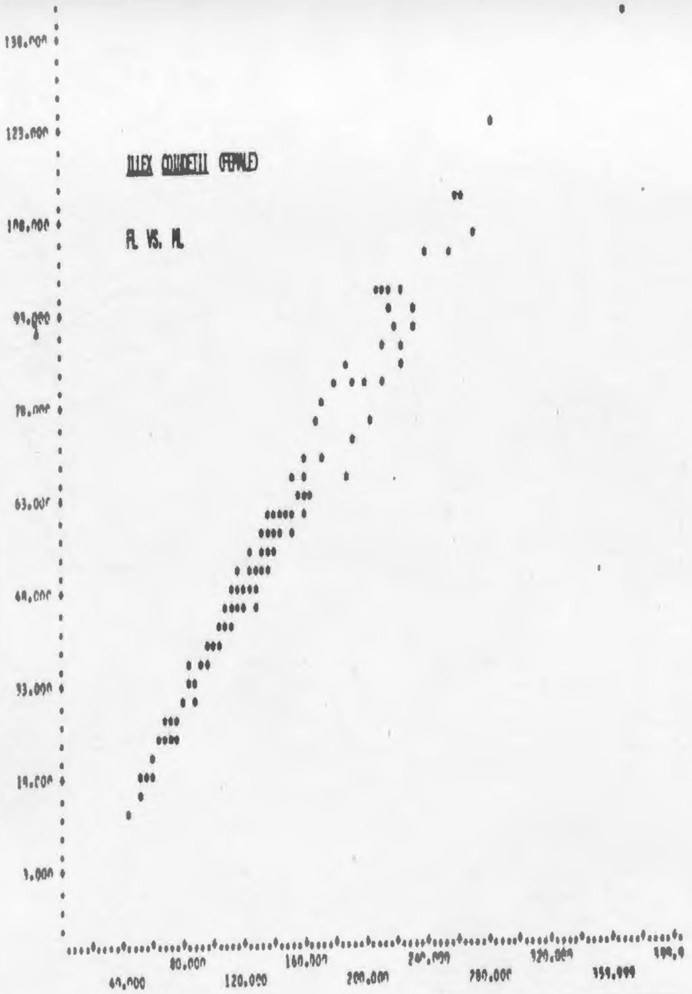
240.000
270.000
300.000
330.000


ILLEX COINDETII (FEMALE)
FL VS. ML
138.000
123.000
108.000
93.000
78.000
63.000
48.000
33.000
18.000
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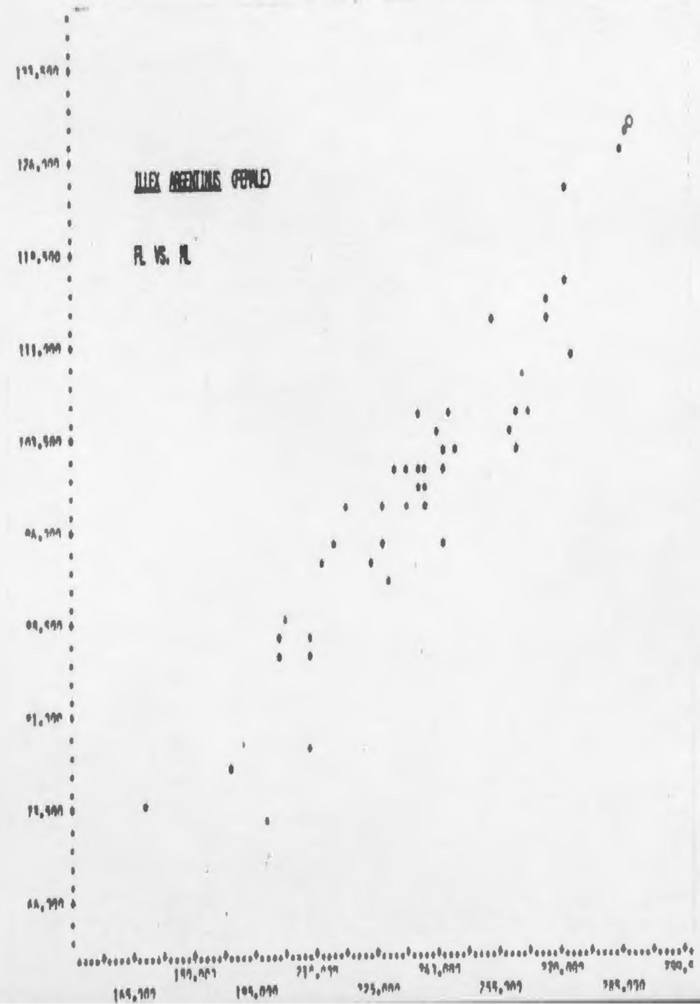
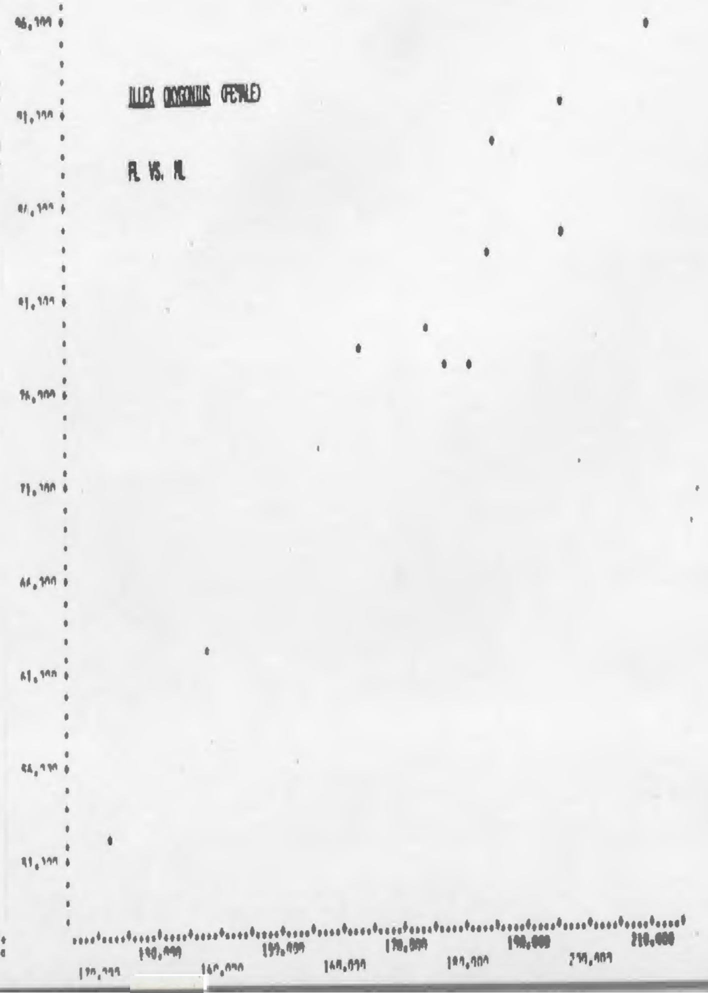
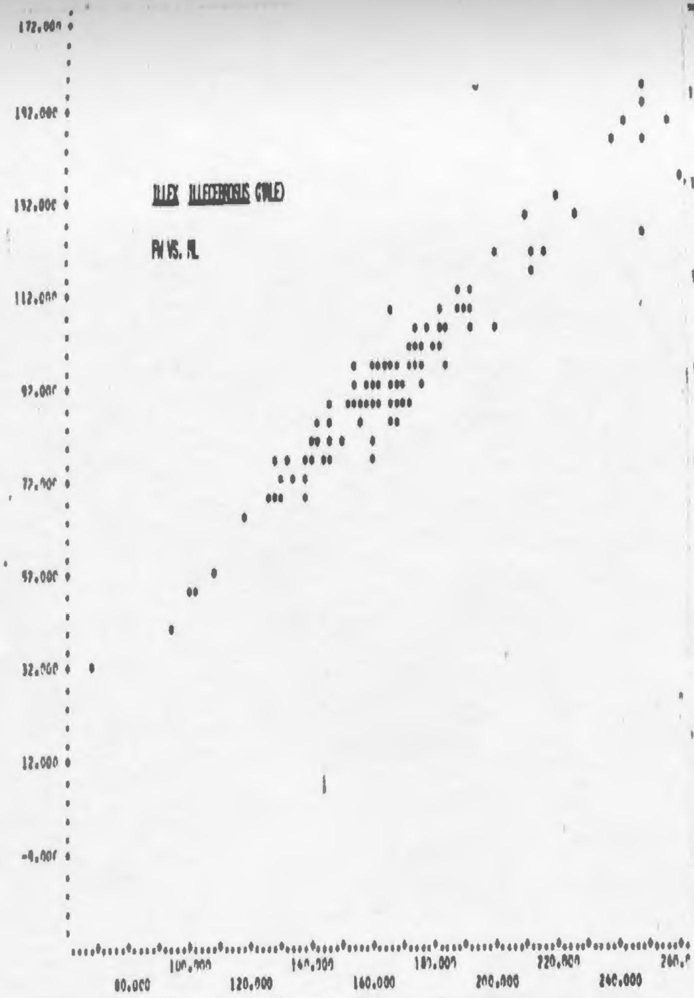
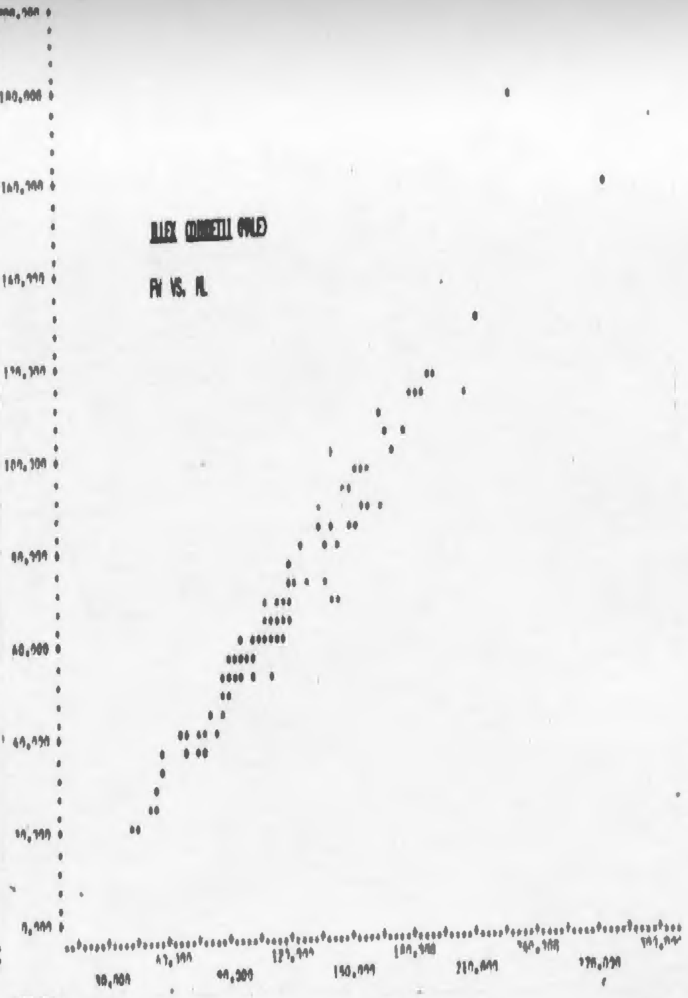
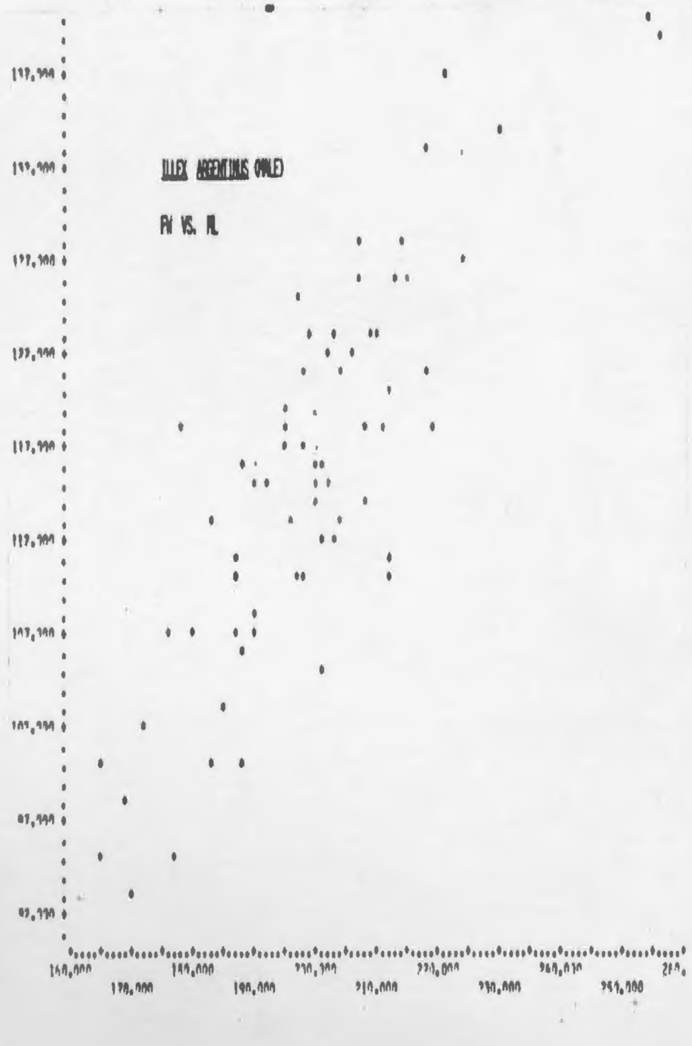
280.000
320.000
360.000
400.0


ILLEX ARGENTINUS (FEMALE)
FL VS. ML


ILLEX OXYGONIUS (FEMALE)
FL VS. ML


ILLEX ILLECEBROSUS (MALE)
FW VS. ML
172.000
152.000
132.000
112.000
92.000
72.000
52.000
32.000
12.000
-8.000
80.000
100.000
120.000
140.000
160.000
180.000
200.000
220.000
240.000
260.000


ILLEX COINDETII (MALE)
FW VS. ML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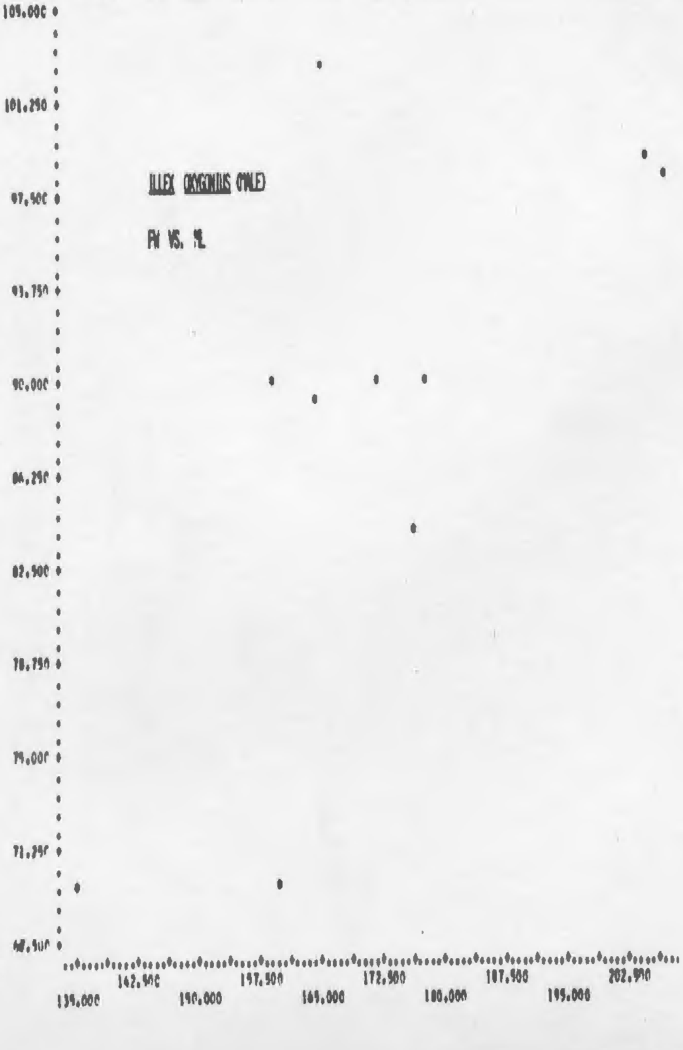
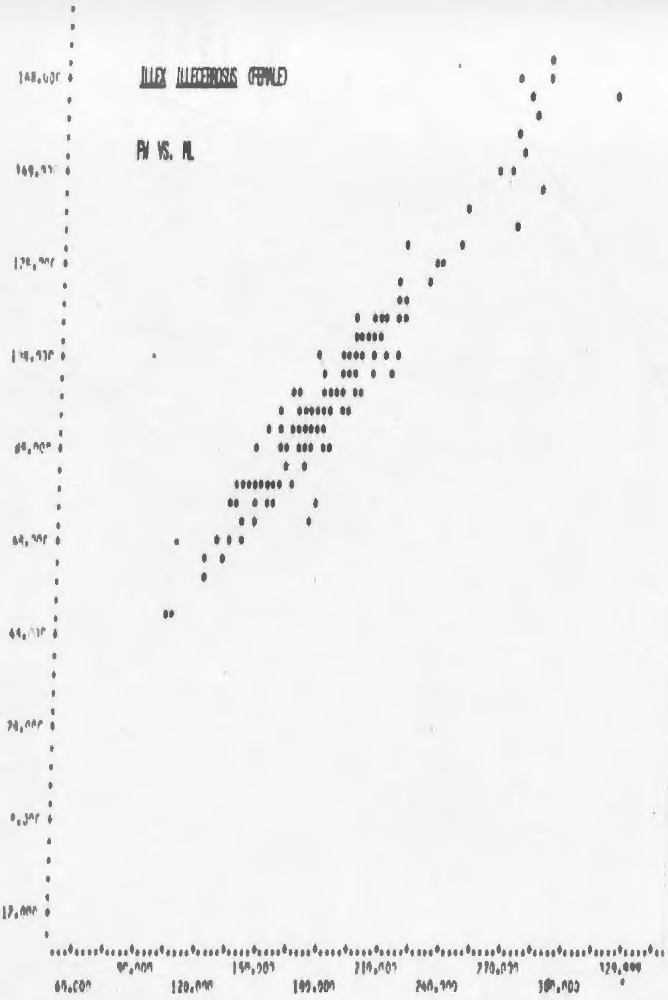
FW VS. ML
160.000


ILLEX OXYGONIUS (MALE)
FW VS. ML
105.000
101.250
97.500
93.750
90.000
86.250
82.500
78.750
75.000
71.250
67.500
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500


ILLEX ILLECEBROSUS (FEMALE)
FW VS. ML
168.000
148.000
128.000
108.000
88.000
68.000
48.000
28.000
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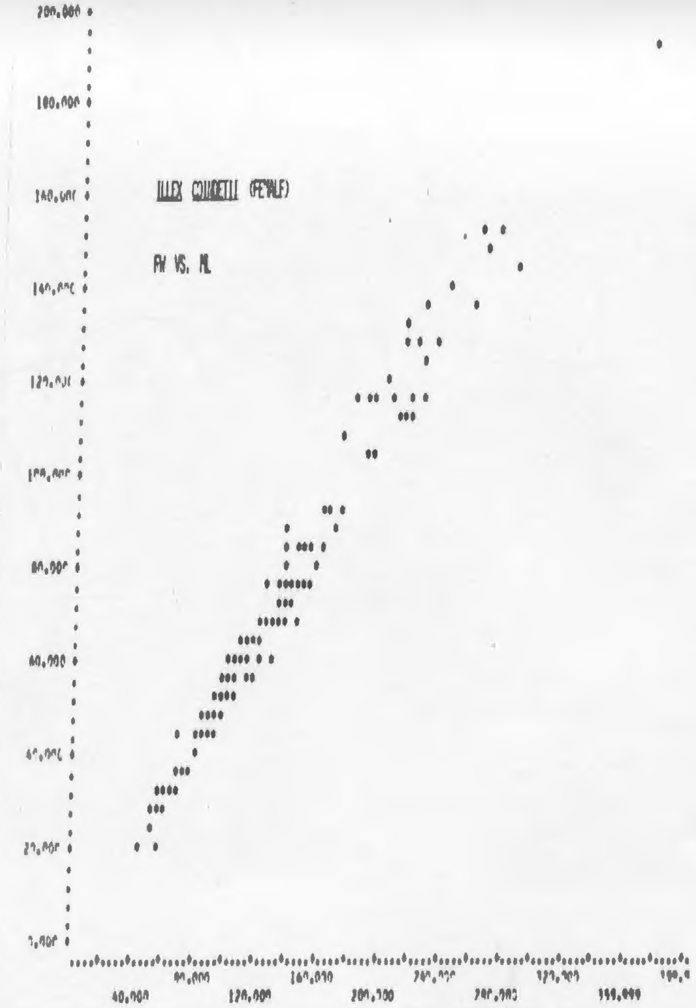
240.000
270.000
300.000
330.000


ILLEX COINDETII (FEMALE)
FW VS. ML
200.000
180.000
160.000
140.000
120.000
100.000
80.000
60.000
40.000
20.000
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40.000
80.000
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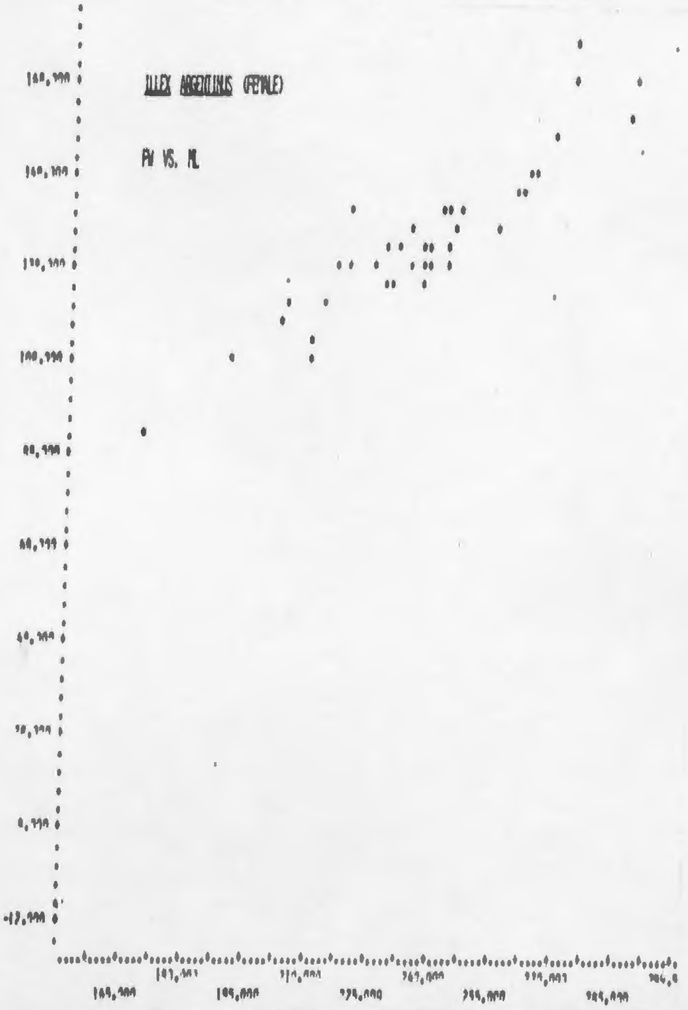
160.000
200.000
240.000
280.000
320.000
360.000
400.0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FW VS. ML
168.000
148.000
128.000
108.000
88.000
68.000
48.000
28.000
8.000
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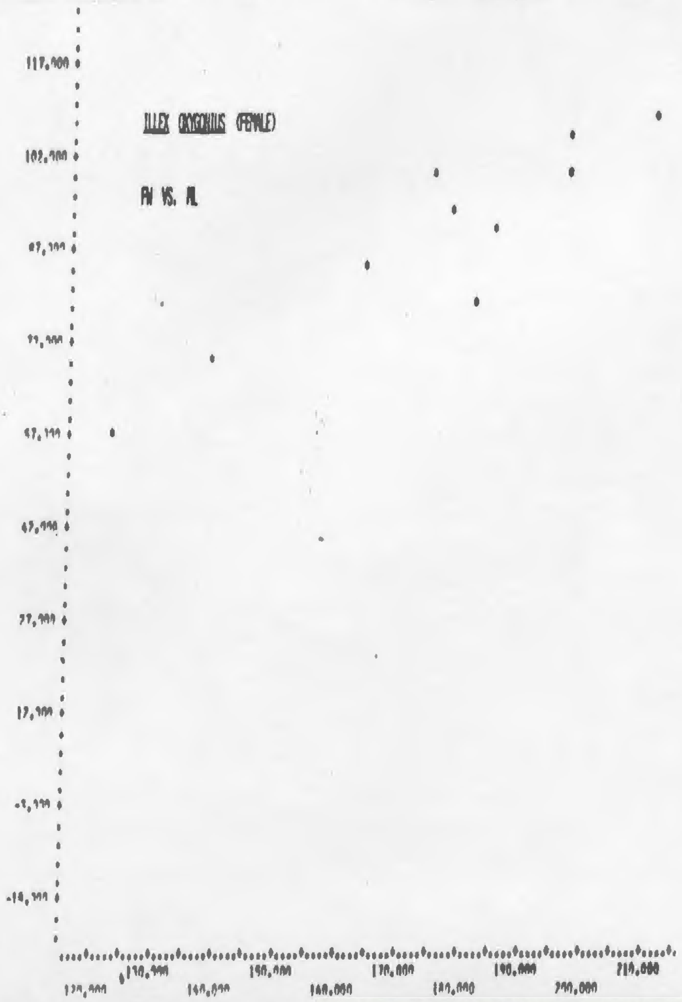
260.000
273.000
286.000
299.0


ILLEX OXYGONIUS (FEMALE)
FW VS. ML
117.000
102.000
87.000
72.000
57.000
42.000
27.000
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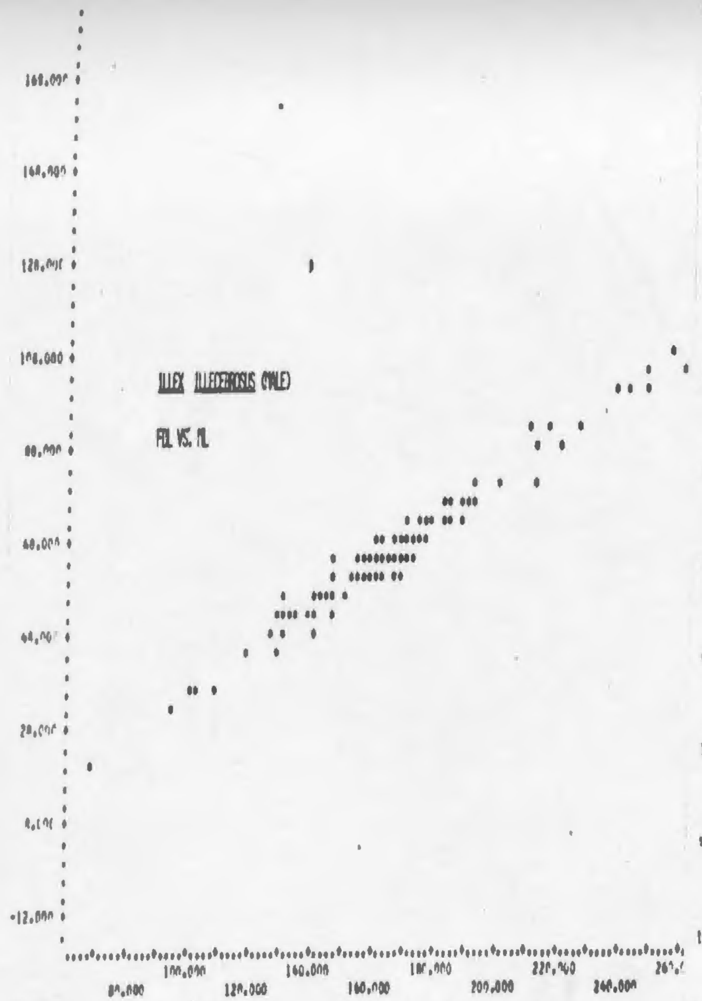
ILLEX ILLECEBROSUS (MALE)
FBL VS. ML
160.000
140.000
120.000
100.000
80.000
60.000
40.000
20.000
0.000
-12.000
80.000
100.000
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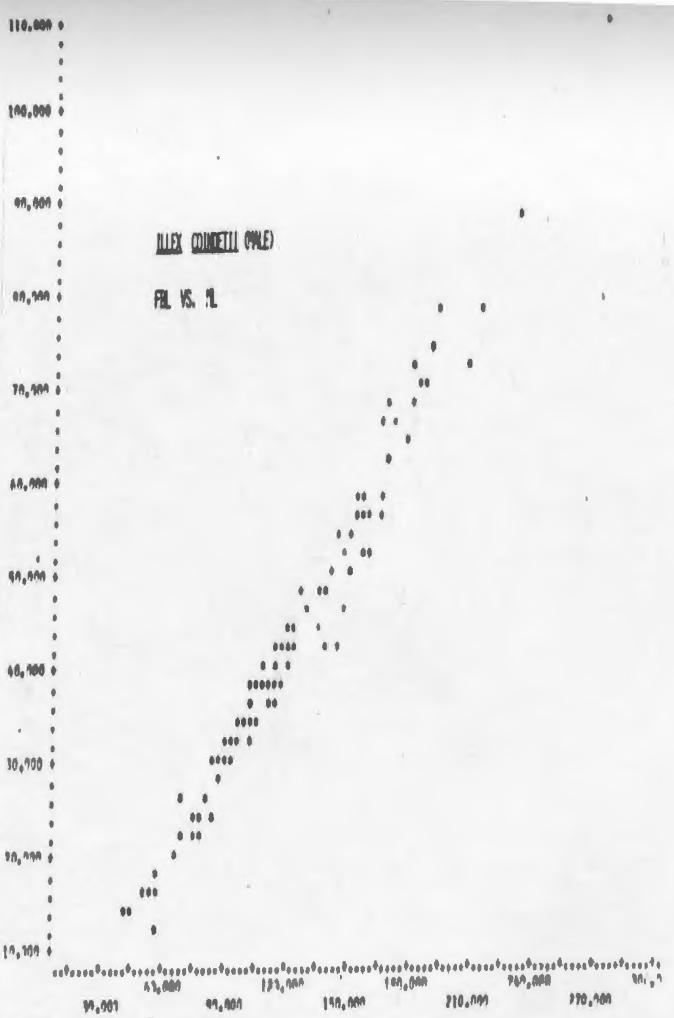
140.000
160.000
180.000
200.000
220.000
240.000
260.0


ILLEX COINDETII (MALE)
FBL VS. ML
110.000
100.000
90.000
80.000
70.000
60.000
50.000
40.000
30.000
20.000
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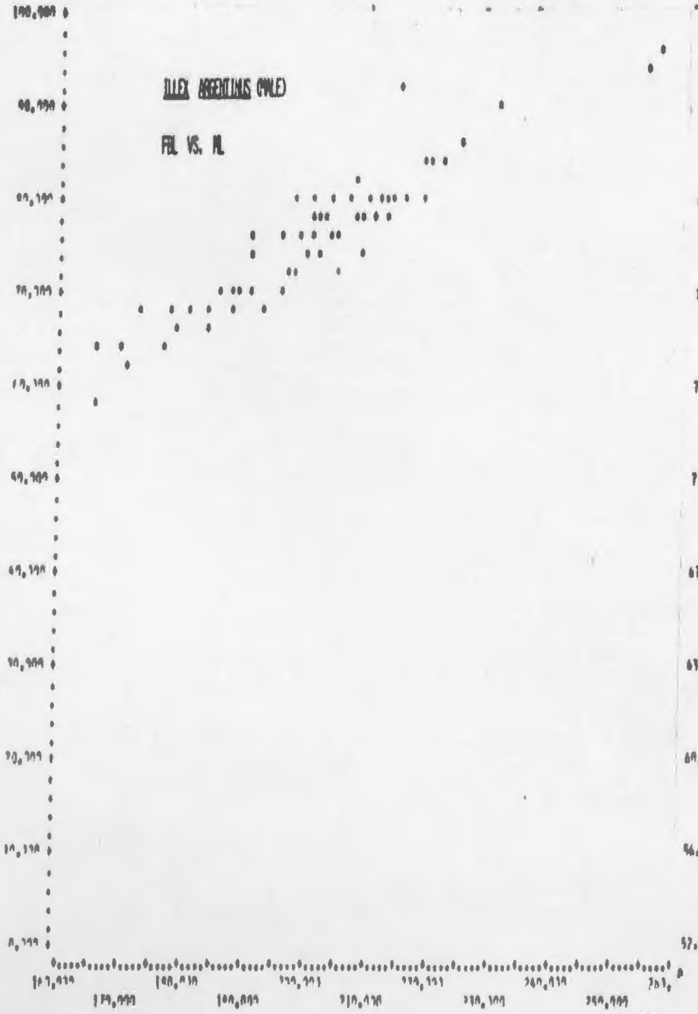
210.000
240.000
270.000
300.0


ILLEX ARGENTINUS (MALE)
FBL VS. ML
100.000
90.000
80.000
70.000
60.000
50.000
40.000
30.000
20.000
10.000
0.000


ILLEX OXYGONIUS (MALE)
FBL VS. ML
90.000
86.250
82.500
78.750
75.000
71.250
67.500
63.750
60.000
56.250
52.500
135.000
142.500
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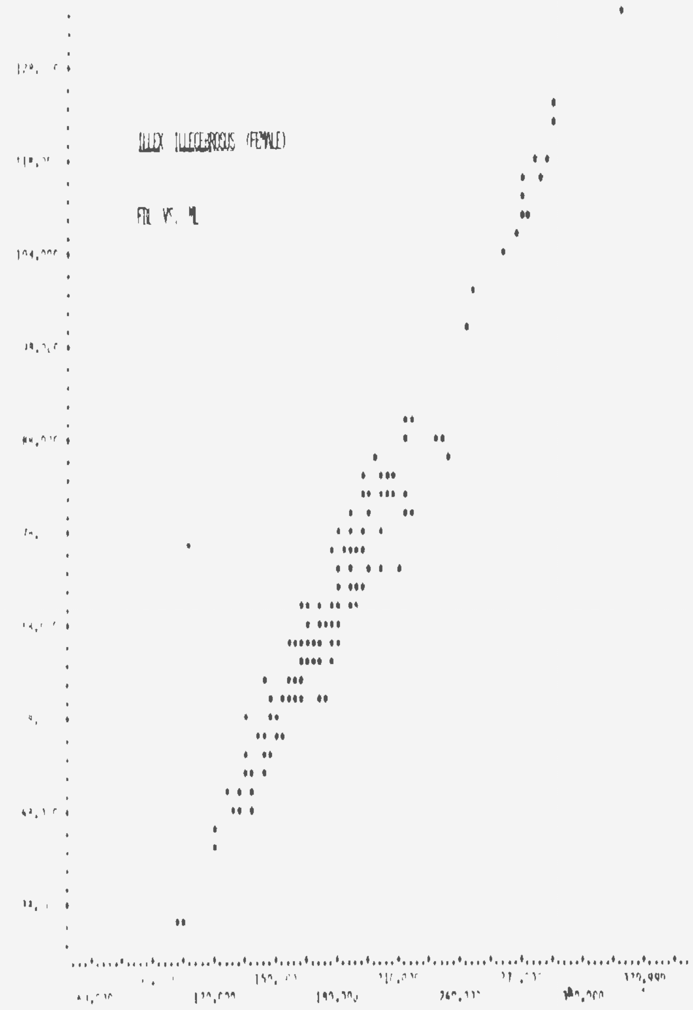
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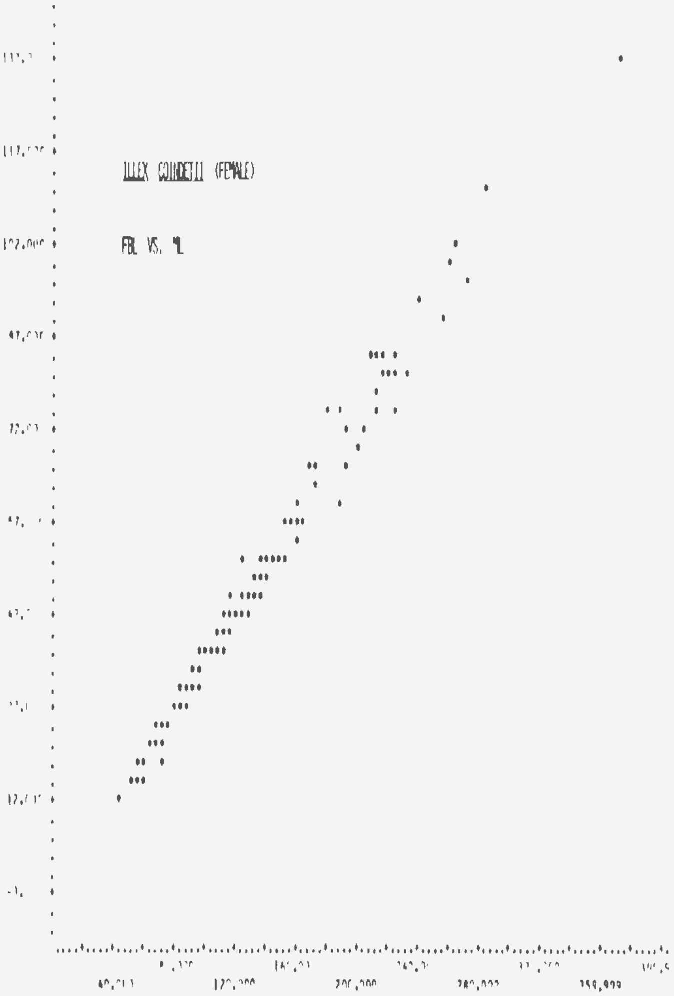
FBL VS. ML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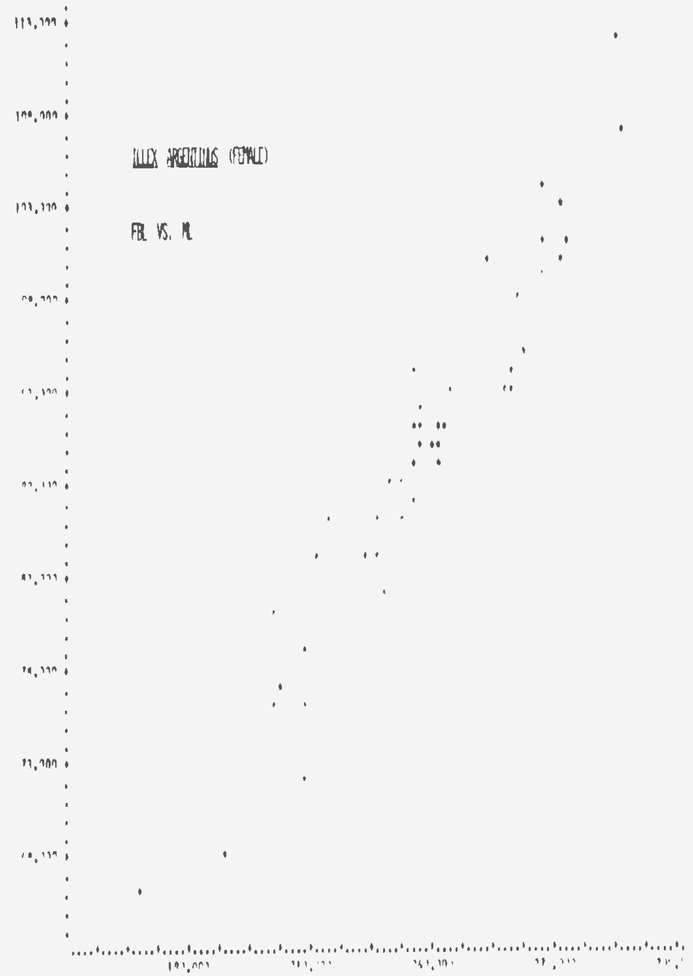
FBL VS. ML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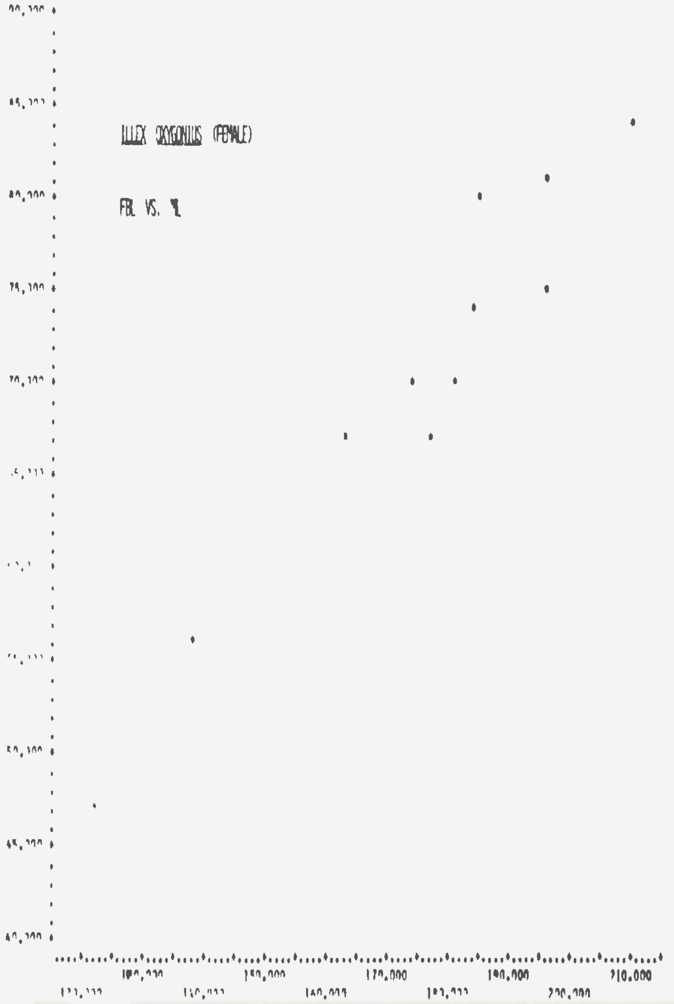
FBL VS. ML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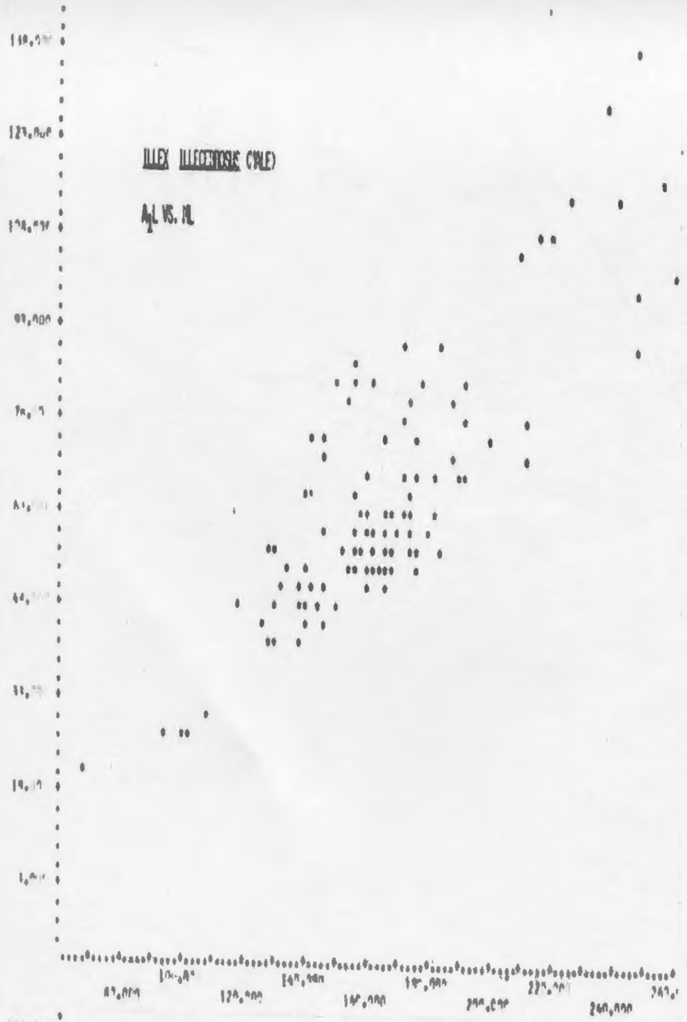
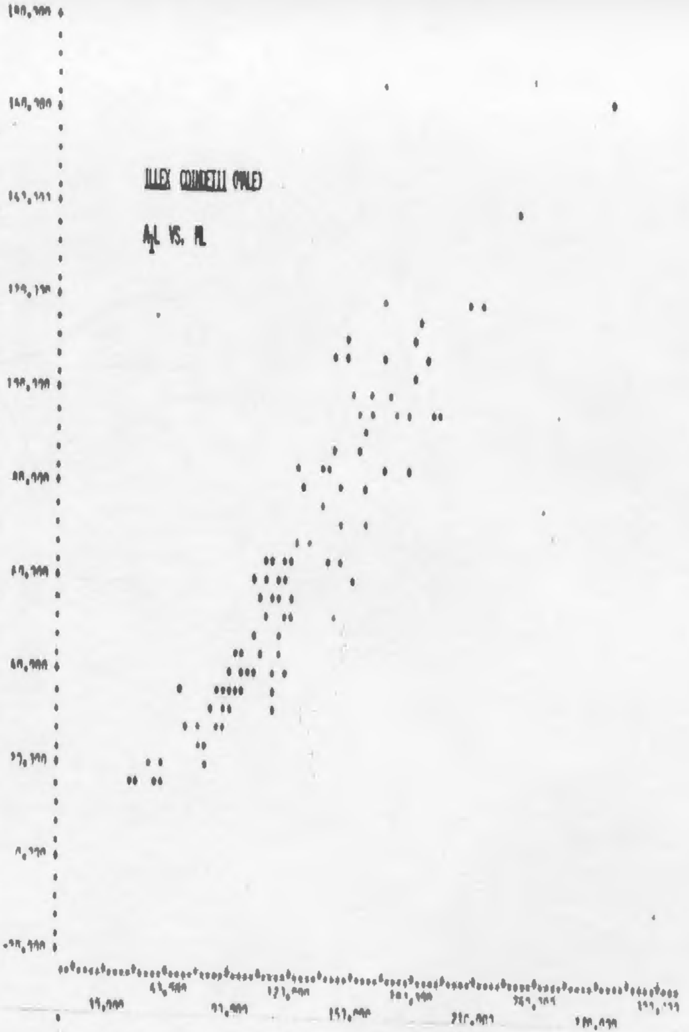
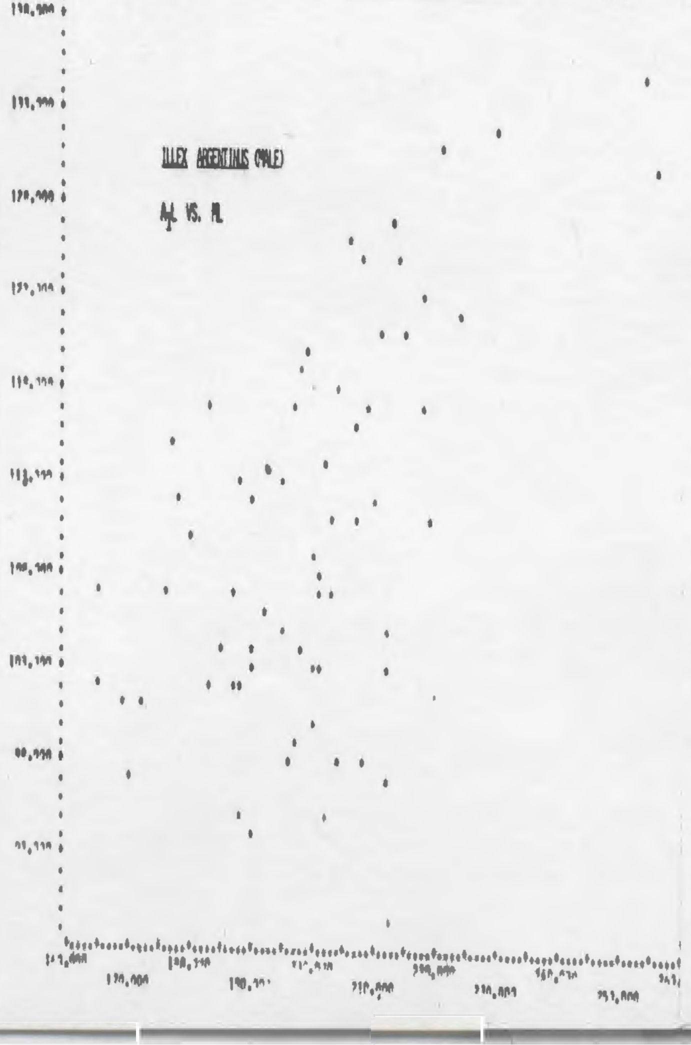
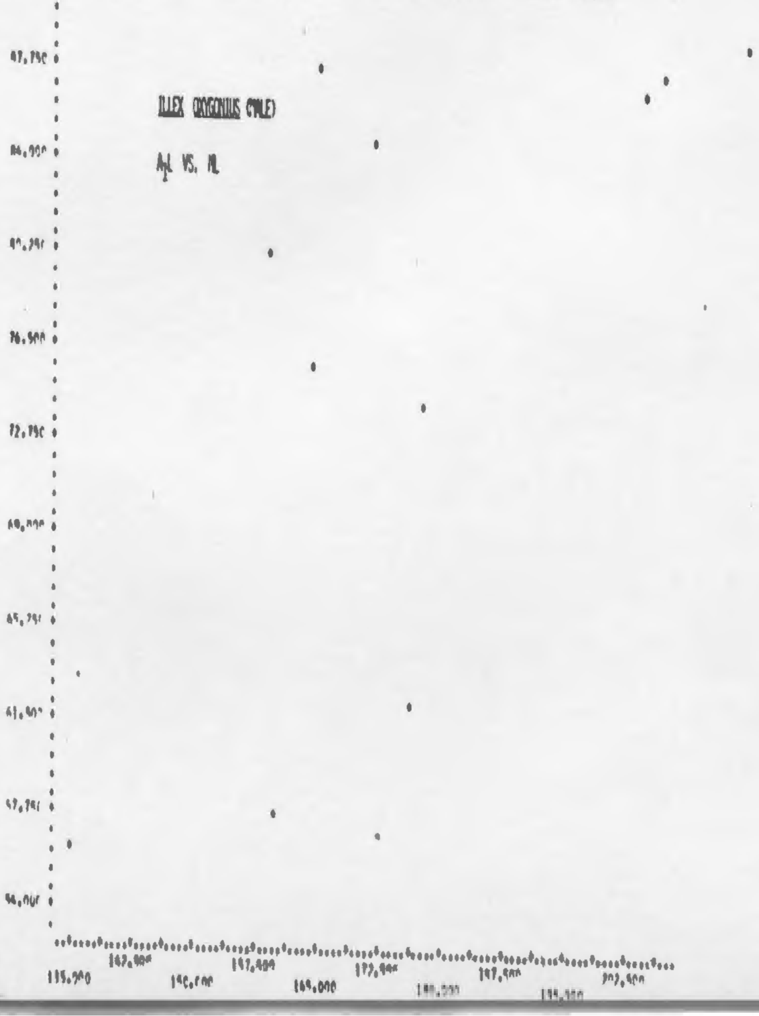
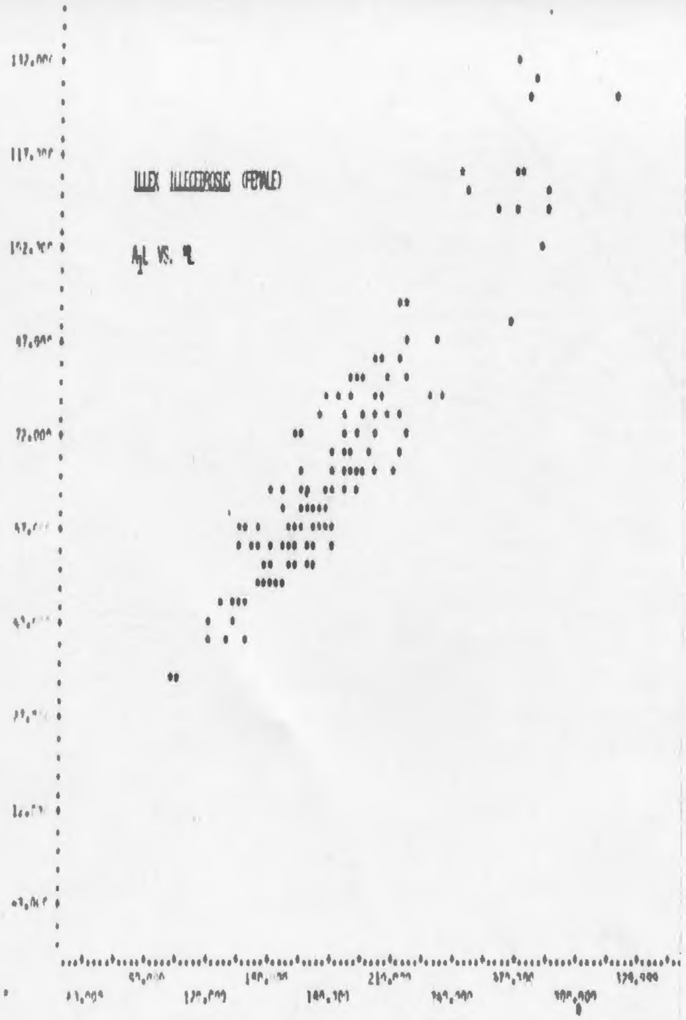
FBL VS. ML
210,000

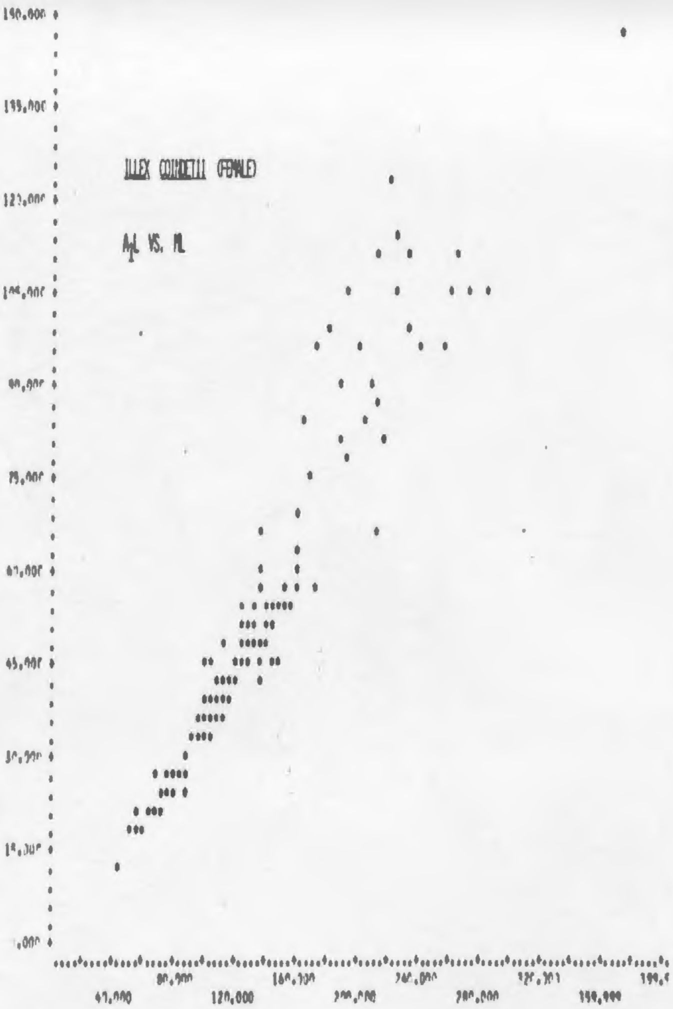

ILLEX ILLECEBROSUS (MALE)
A_1L VS. ML

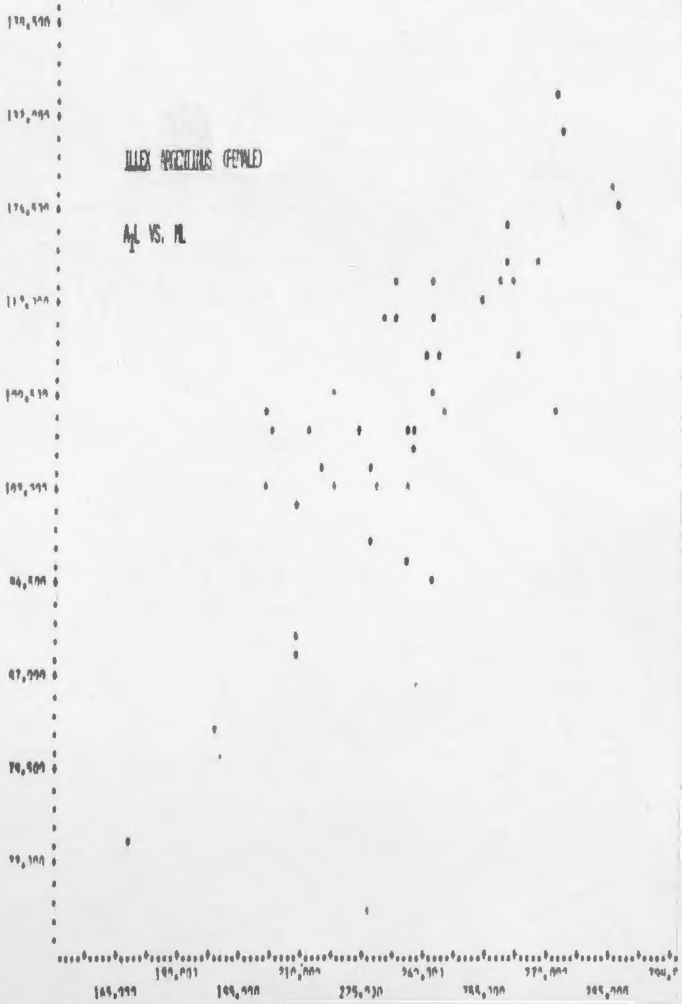

ILLEX COINDETII (MALE)
A_1L VS. ML

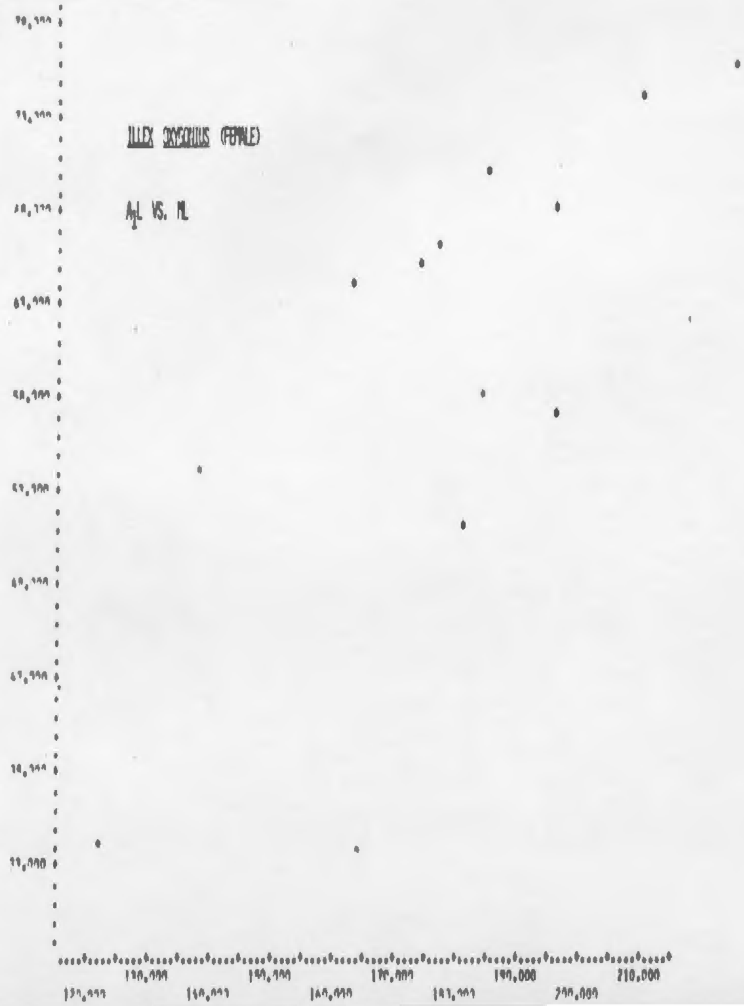

ILLEX ARGENTINUS (MALE)
A_1L VS. ML

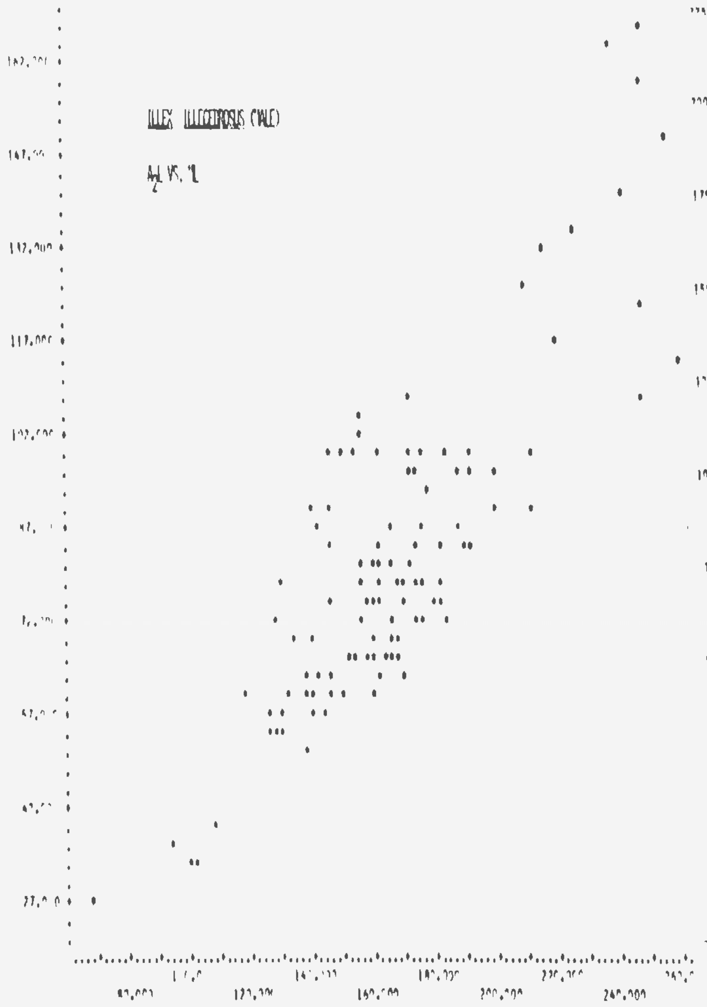

ILLEX OXYGONIUS (MALE)
A_1L VS. ML

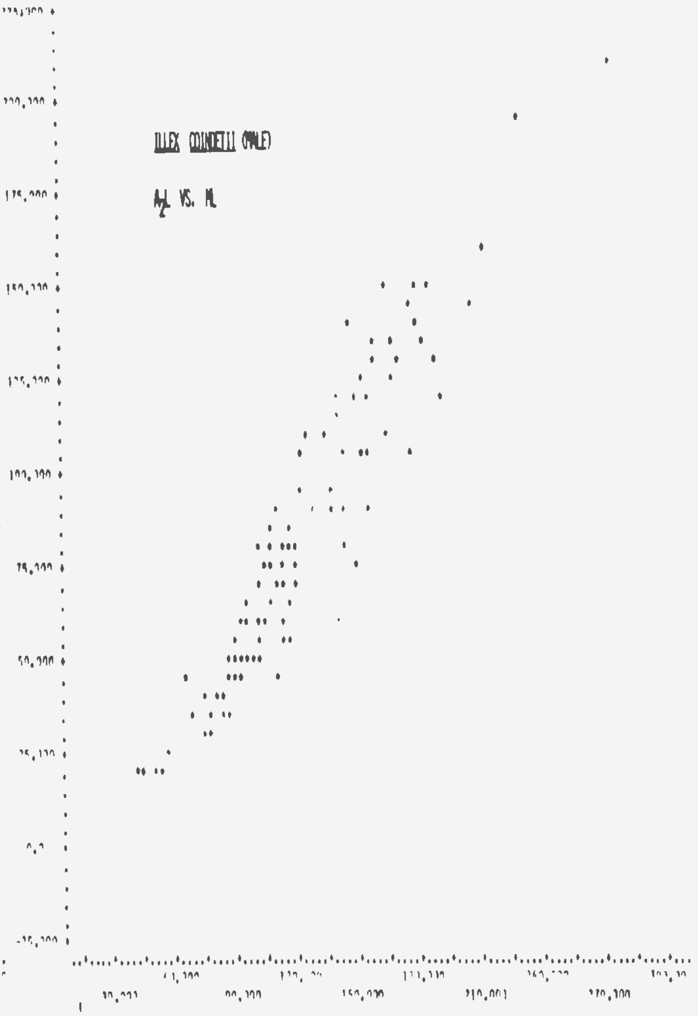

ILLEX ILLECEBROSUS (FEMALE)
A1L VS. ML

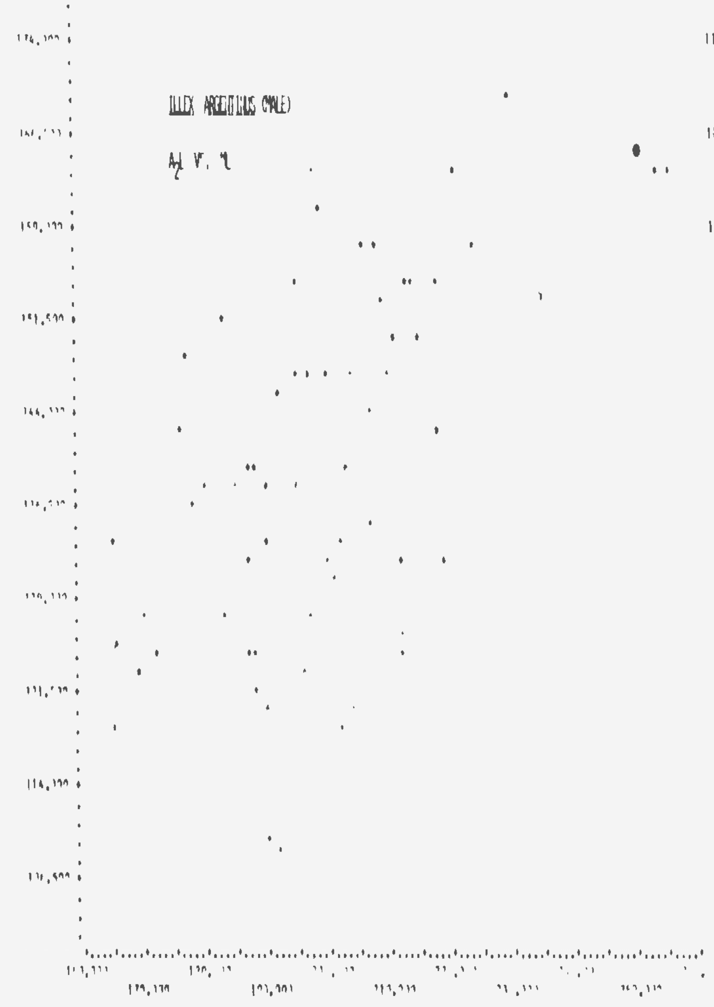

ILLEX COINDETII (FEMALE)
A1L VS. ML
150,000
135,000
120,000
105,000
90,000
75,000
60,000
45,000
30,000
15,000
.000
40,000
80,000
120,000
160,000
200,000
240,000
280,000
320,000
360,000

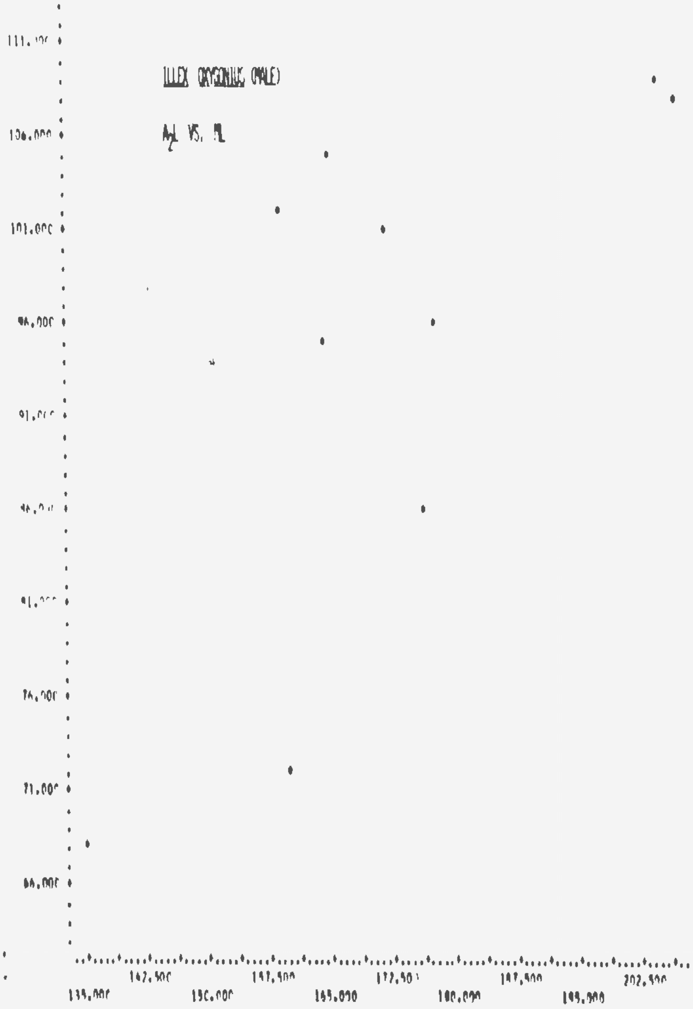

ILLEX ARGENTINUS (FEMALE)
A1L VS. ML

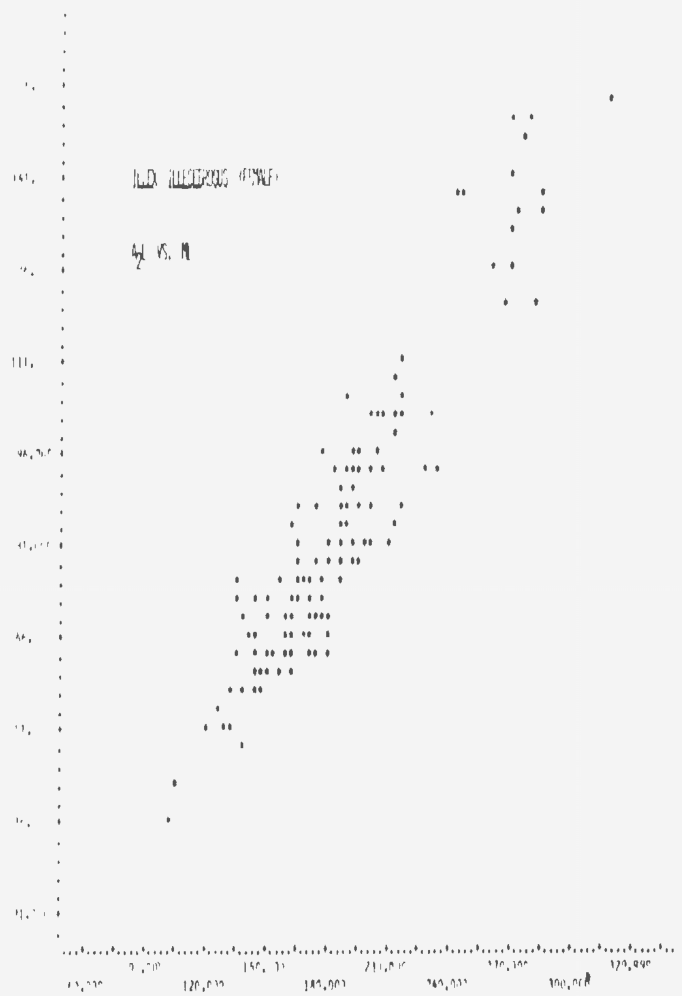

ILLEX OXYGONIUS (FEMALE)
A1L VS. ML
190,000
210,000

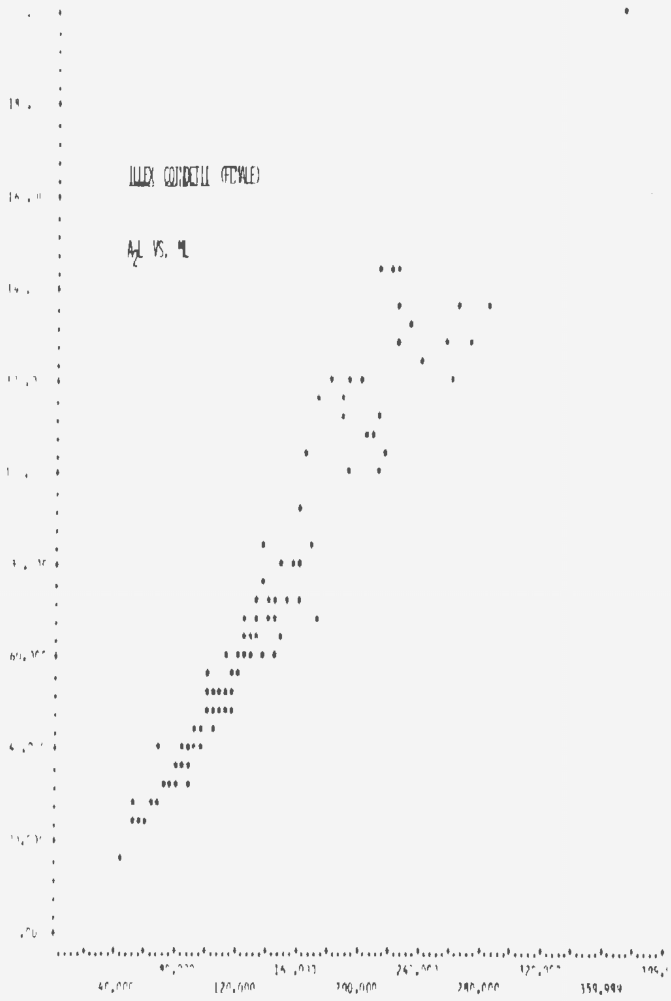

ILLEX ILLECEBROSUS (MALE)
A_2L VS. ML

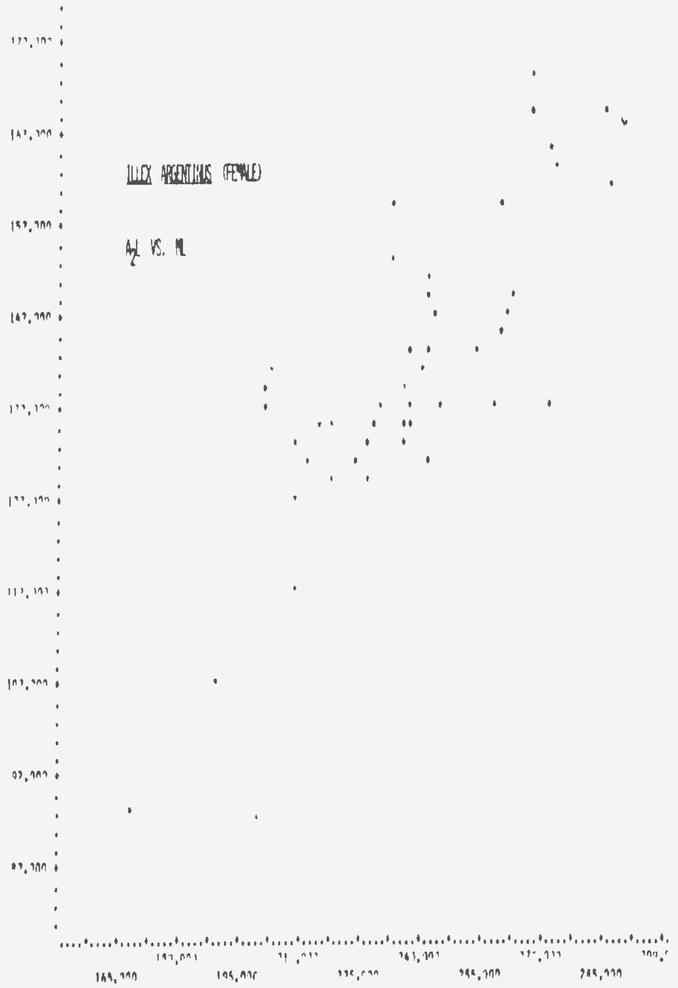

ILLEX COINDETII (MALE)
A_2L VS. ML
175.000
150.000
125.000
100.000
75.000
50.000
25.000

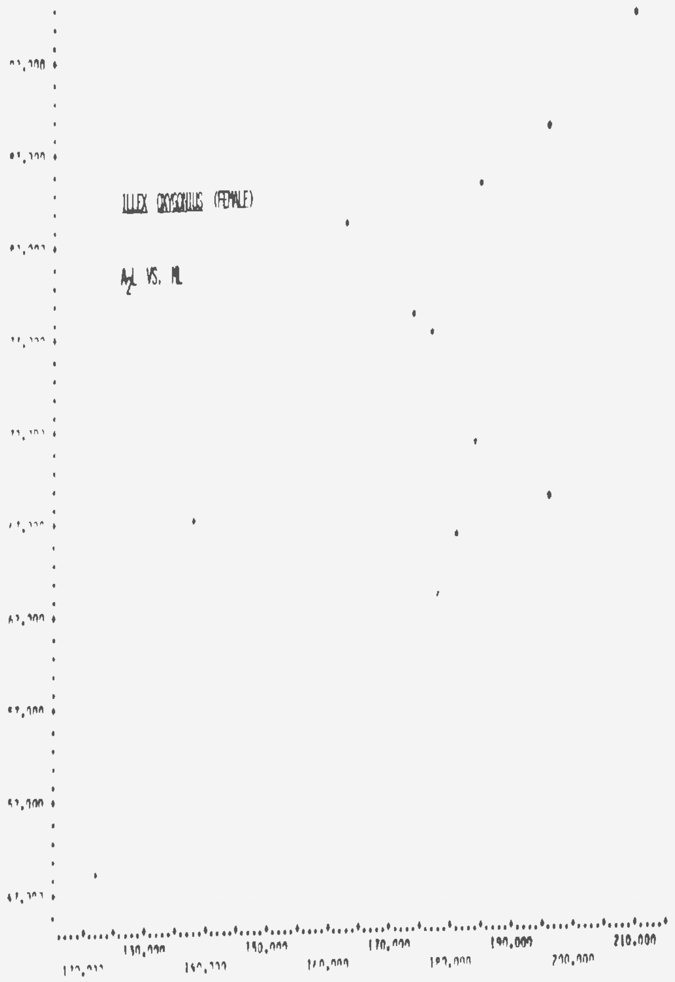

ILLEX ARGENTINUS (MALE)
A_2L VS. ML

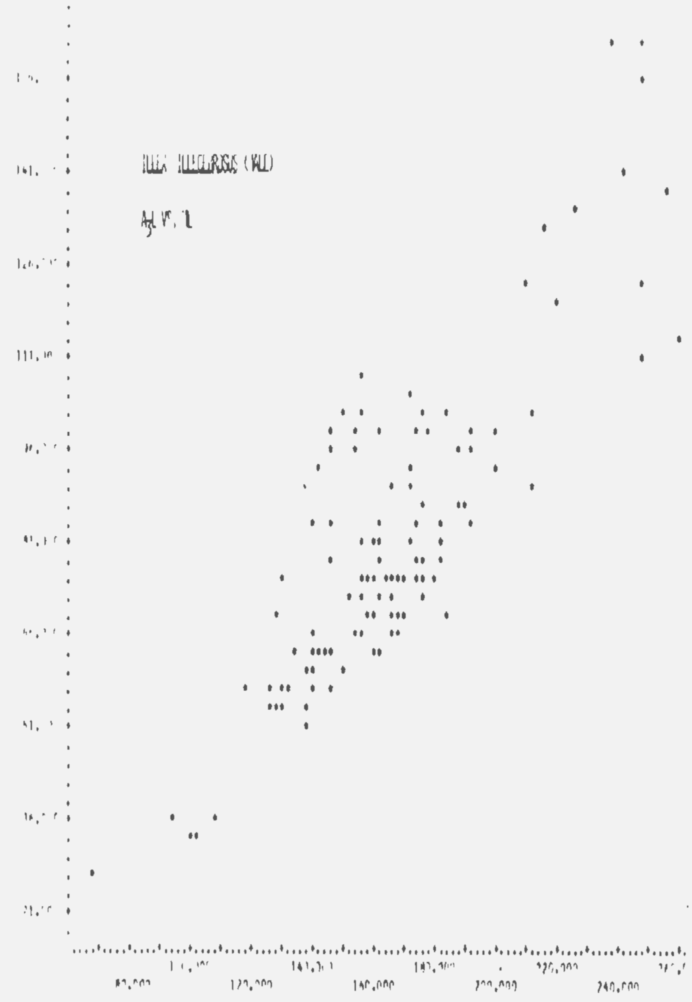

ILLEX OXYGONIUS (MALE)
A_2L VS. ML
106.000
101.000
96.000
91.000
86.000
81.000
76.000
71.000
66.000
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500

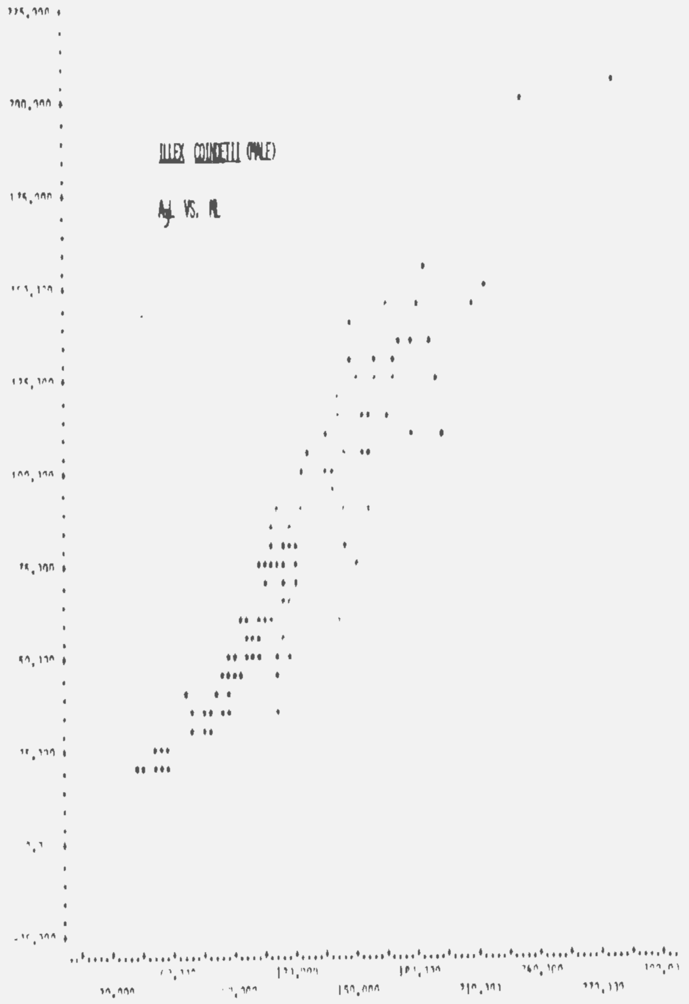

ILLEX ILLECEBROSUS (FEMALE)
A2L VS. ML

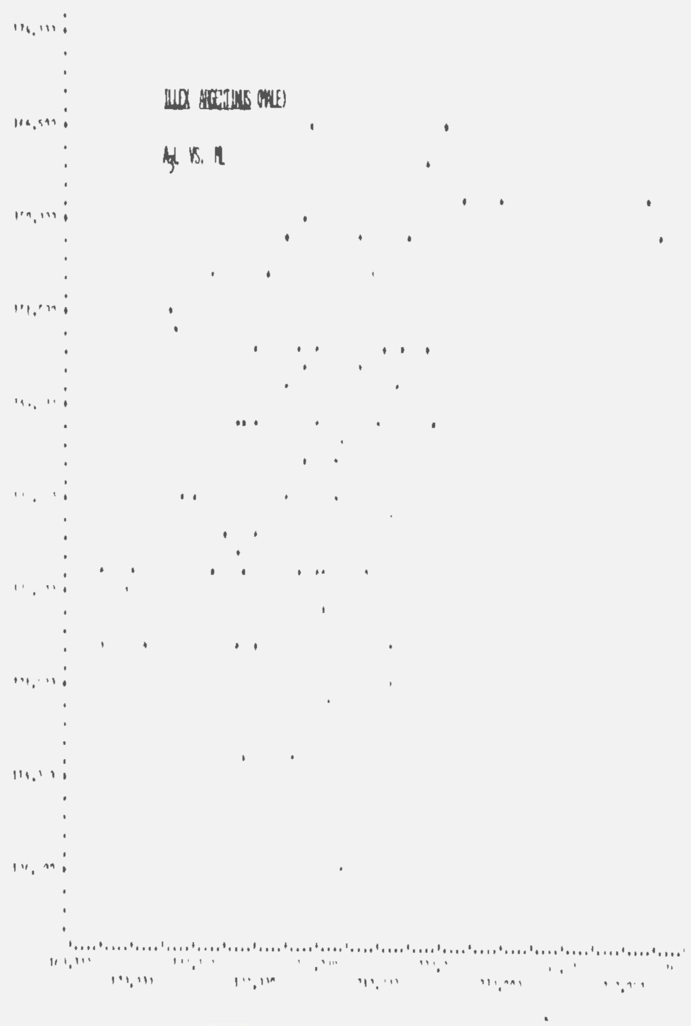

ILLEX COINDETII (FEMALE)
A2L VS. ML
40,000
120,000
200,000
280,000
359,999

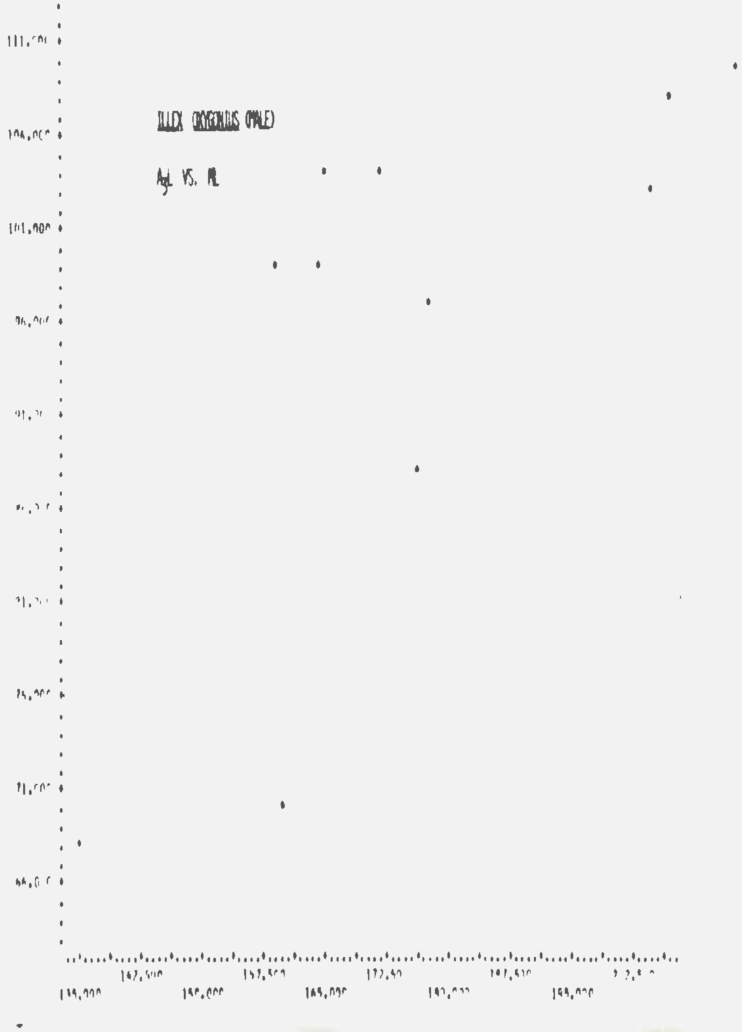

ILLEX ARGENTINUS (FEMALE)
A2L VS. ML

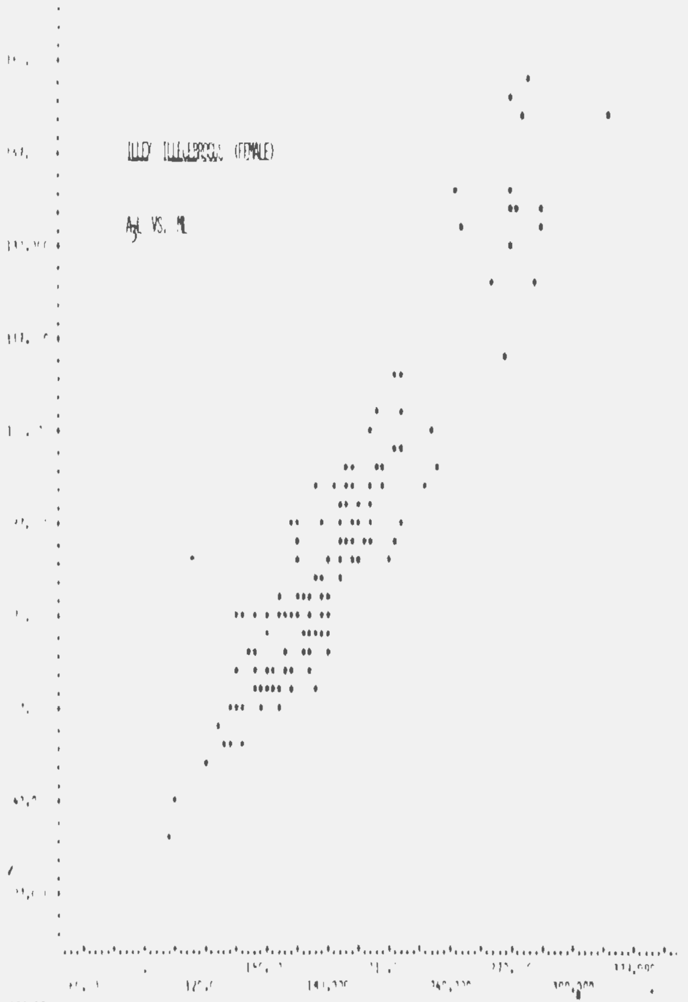

ILLEX OXYGONIUS (FEMALE)
A2L VS. ML
130,000
150,000
170,000
190,000
210,000
200,000

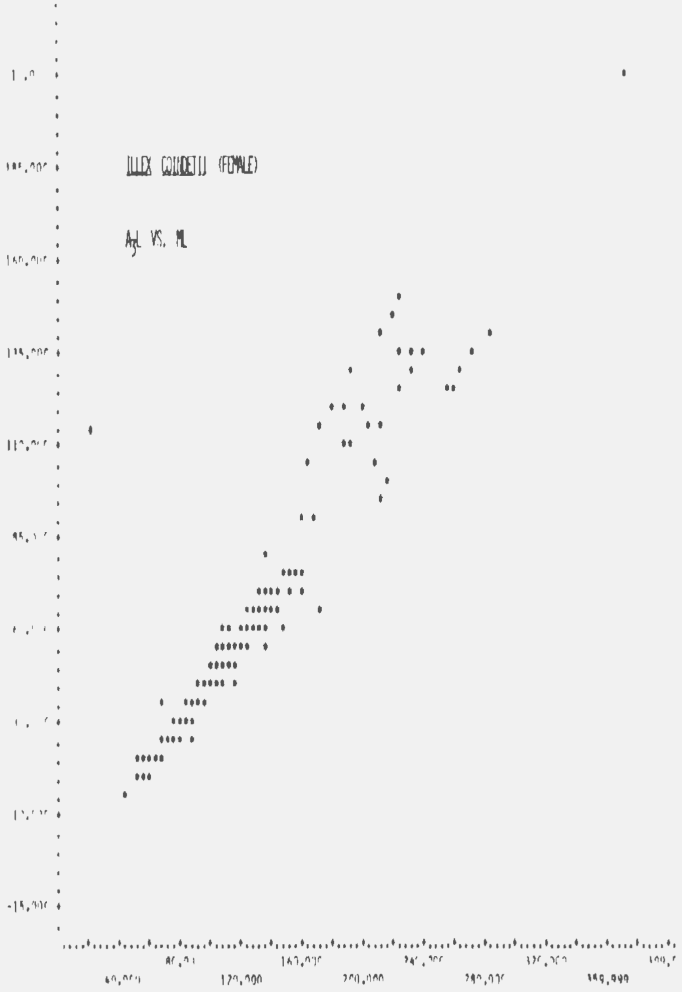

ILLEX ILLECEBROSUS (MALE)
AgL VS. ML
80,000
120,000
160,000
180,000
200,000
220,000
240,000

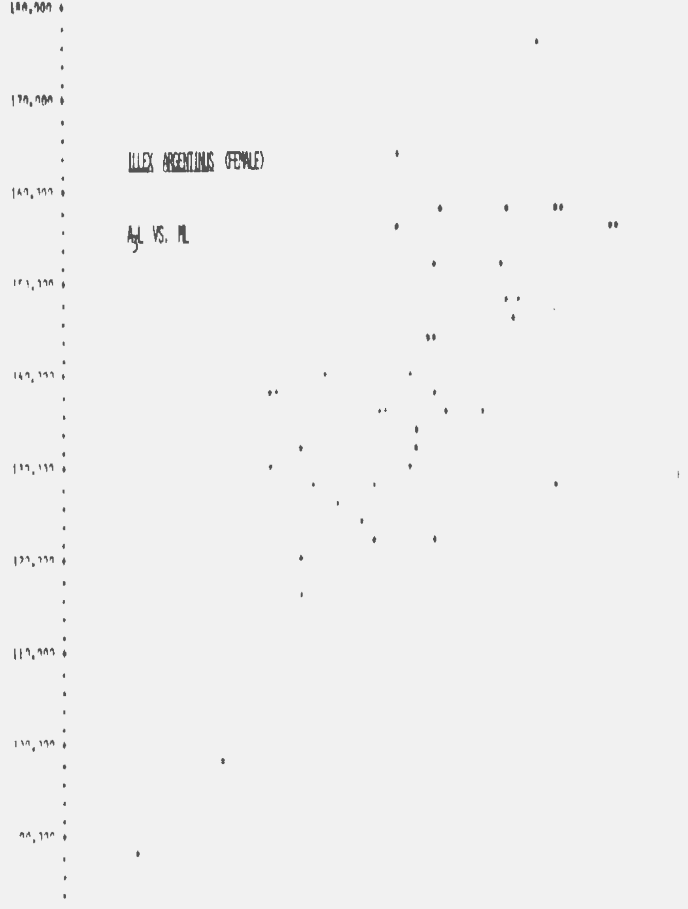

ILLEX COINDETII (MALE)
AgL VS. ML
225,000
200,000
175,000
100,000
75,000
50,000
150,000

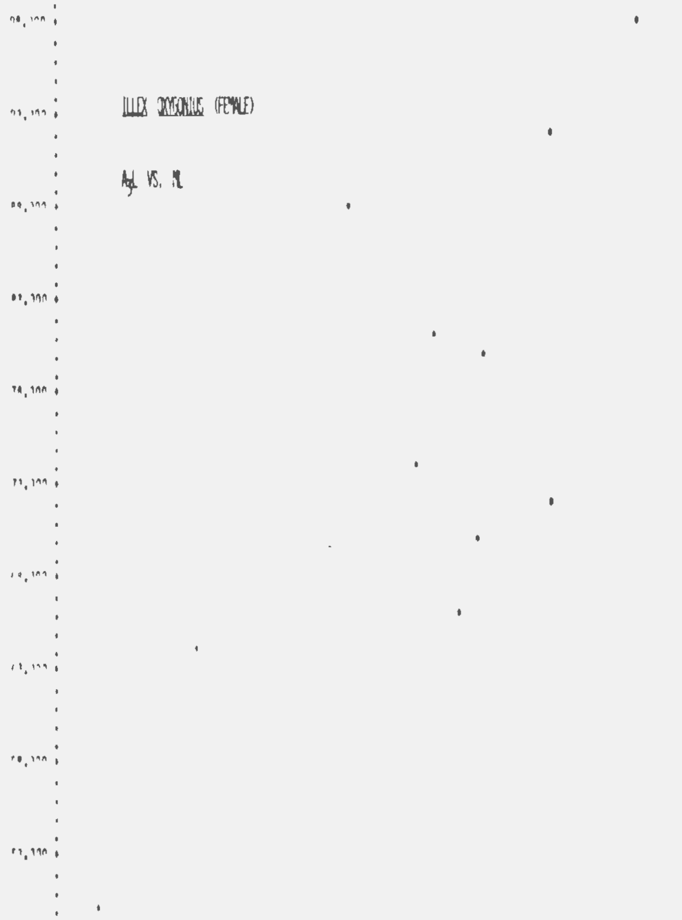

ILLEX ARGENTINUS (MALE)
AgL VS. ML

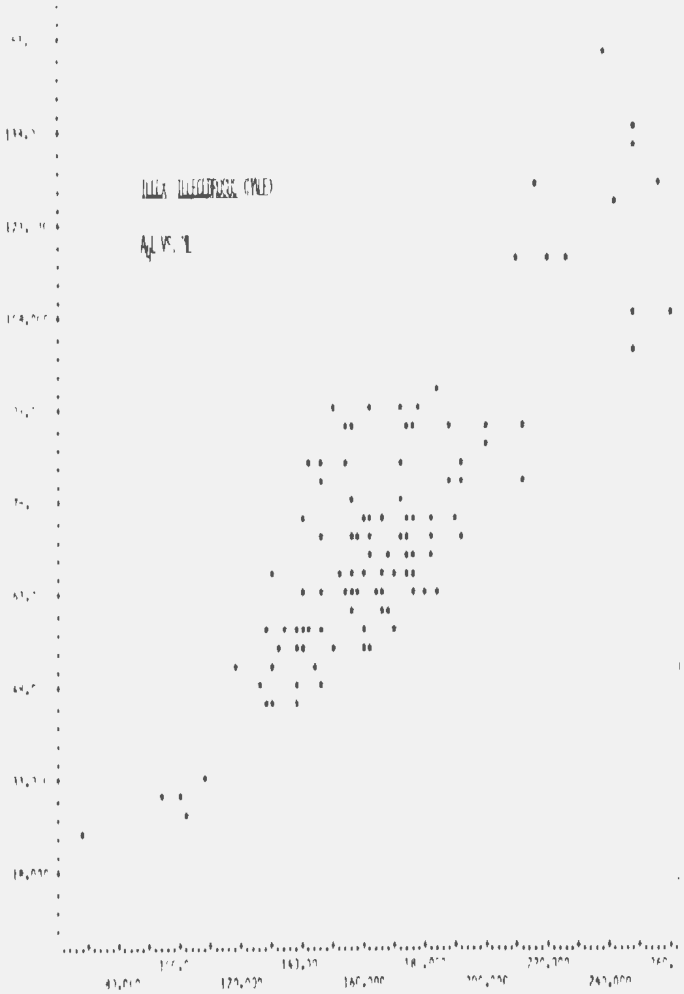

ILLEX OXYGONIUS (MALE)
AgL VS. ML
111,000
106,000
101,000
96,000
76,000
71,000
66,000
139,000
147,500
150,000
157,500
165,000
172,50
180,000
187,500
195,000

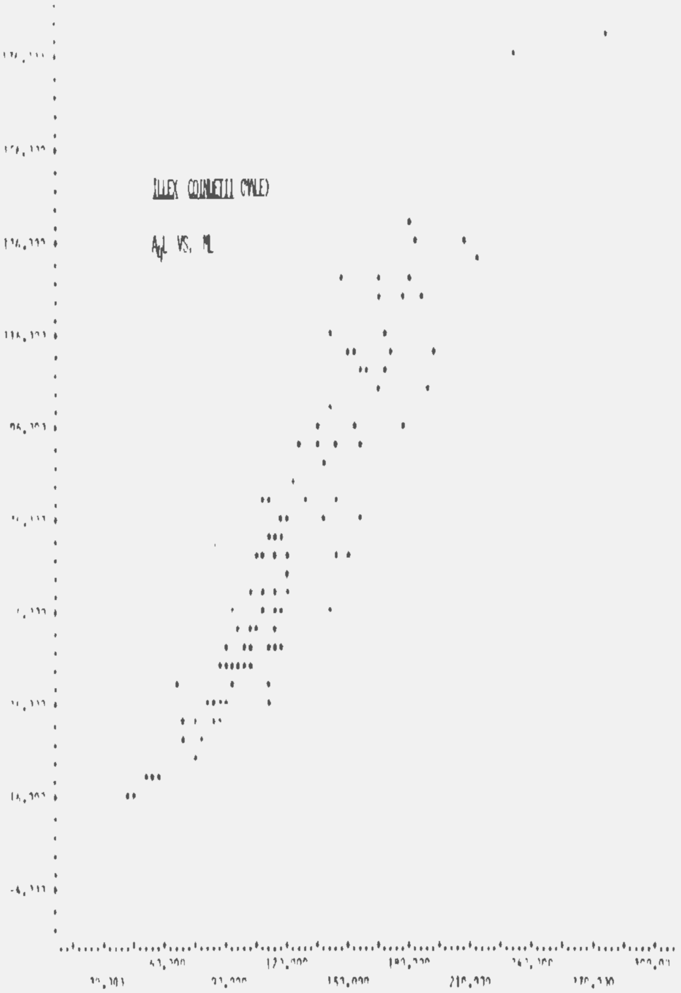

ILLEX ILLECEBROSUS (FEMALE)
AgL VS. ML
300,000

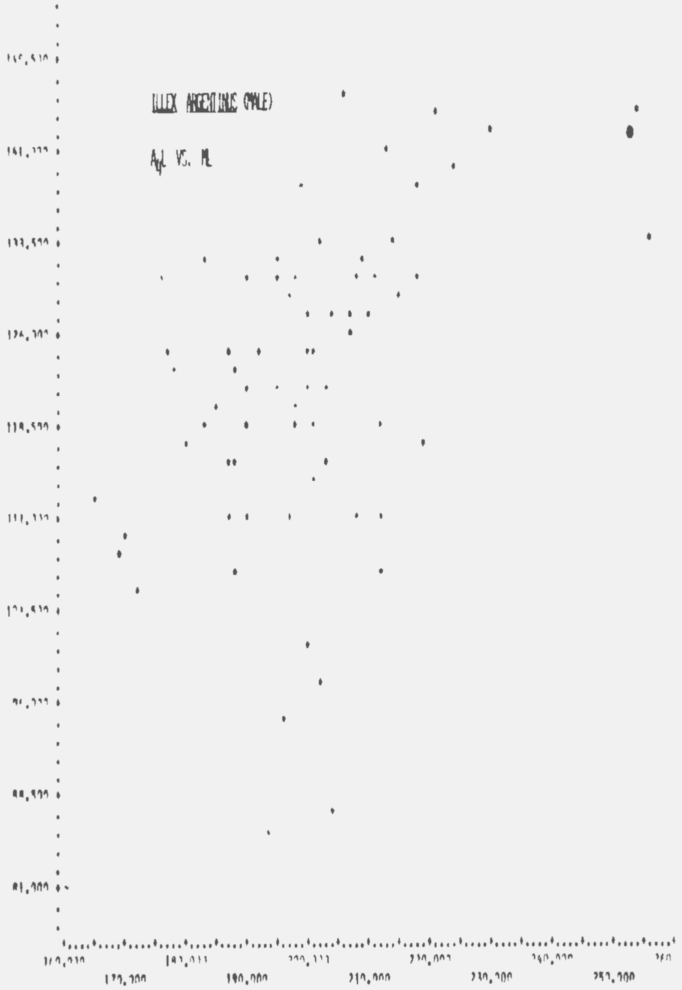

ILLEX COINDETII (FEMALE)
AgL VS. ML
-15,000
60,000
120,000
200,000
280,000


ILLEX ARGENTINUS (FEMALE)
AgL VS. ML
180,000
170,000
160,000
110,000
185,000
205,000
235,000


ILLEX OXYGONIUS (FEMALE)
AgL VS. ML
120,000
130,000
140,000
150,000
160,000
170,000
180,000
190,000
200,000
210,000

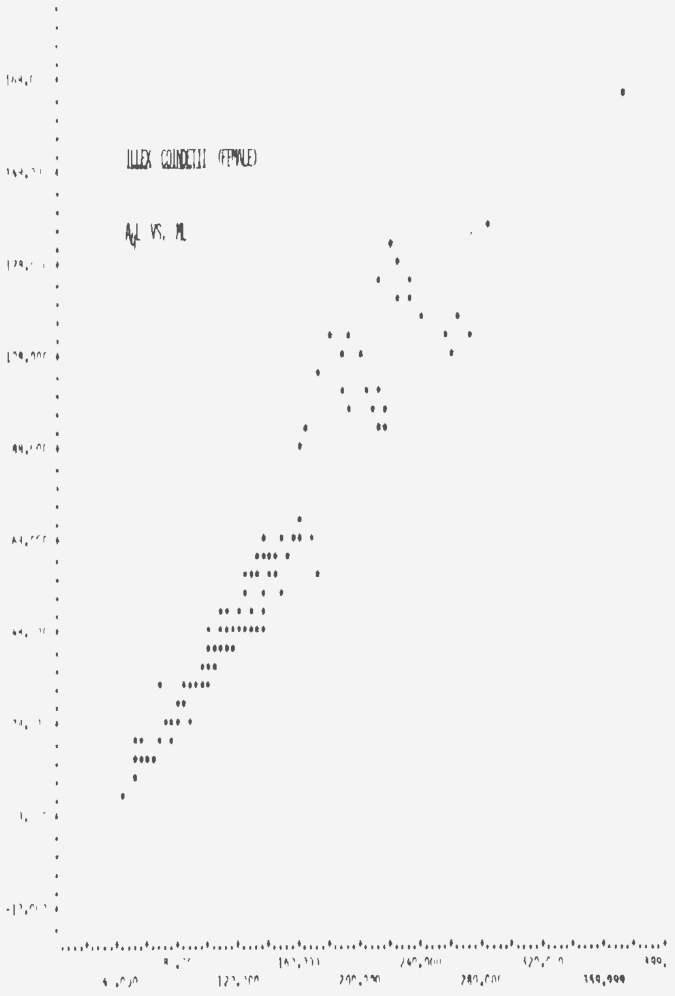

ILLEX ILLECEBROSUS (MALE)
A/L VS. ML

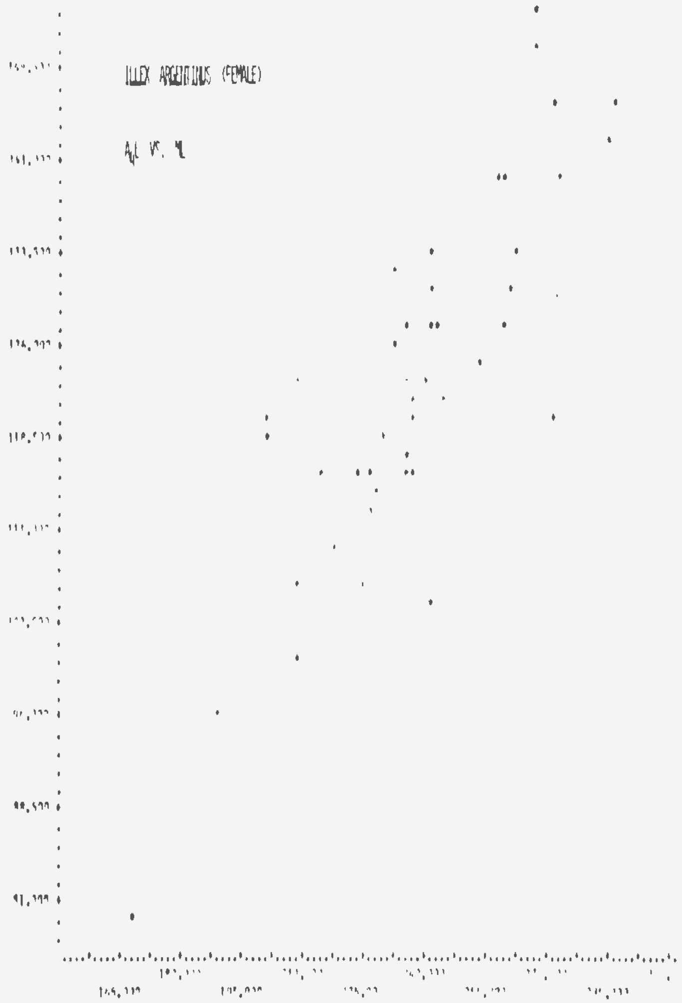

ILLEX COINDETII (MALE)
A/L VS. ML


ILLEX ARGENTINUS (MALE)
A/L VS. ML

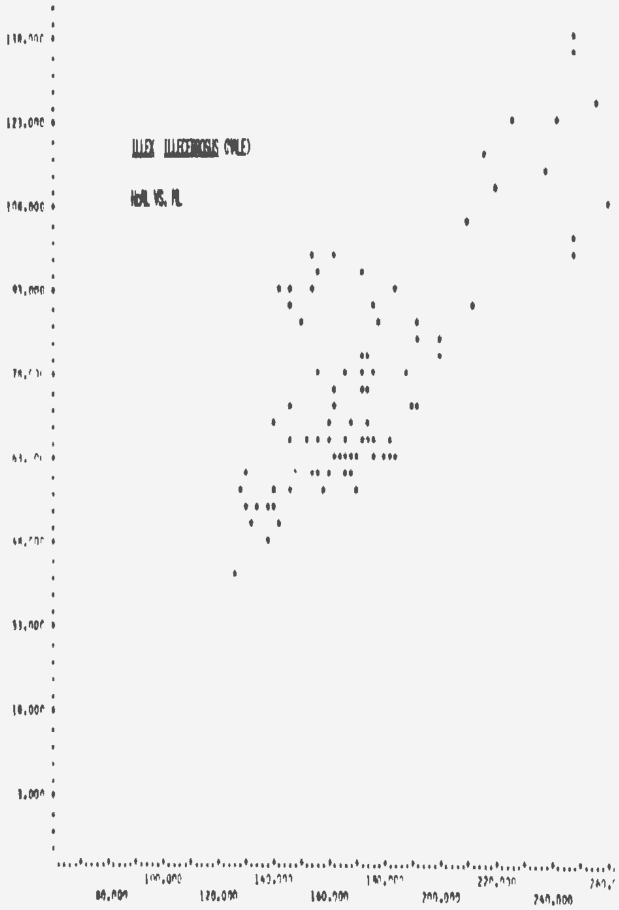

ILLEX OXYGONIUS (MALE)
A/L VS. ML

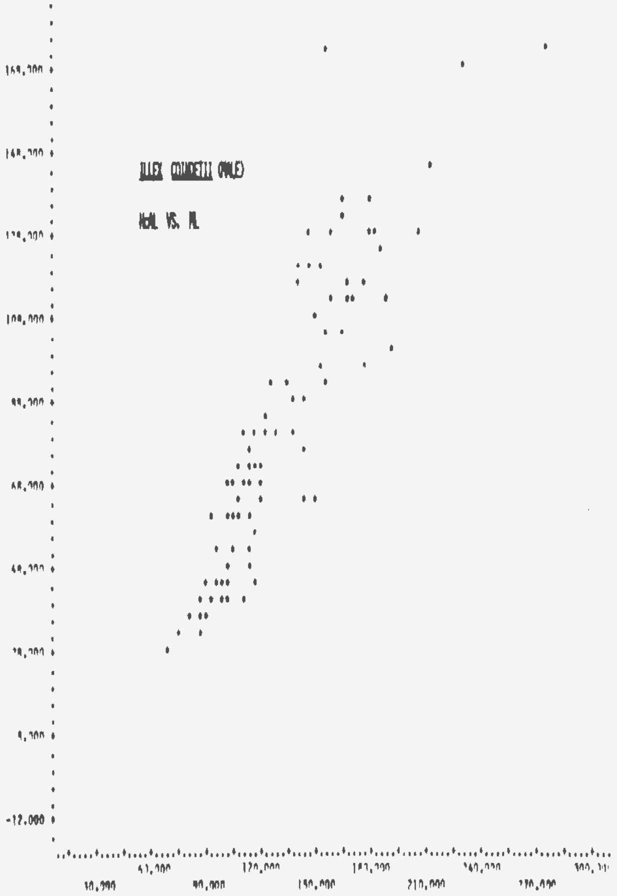

ILLEX ILLECEBROSUS (FEMALE)
A4L VS. ML

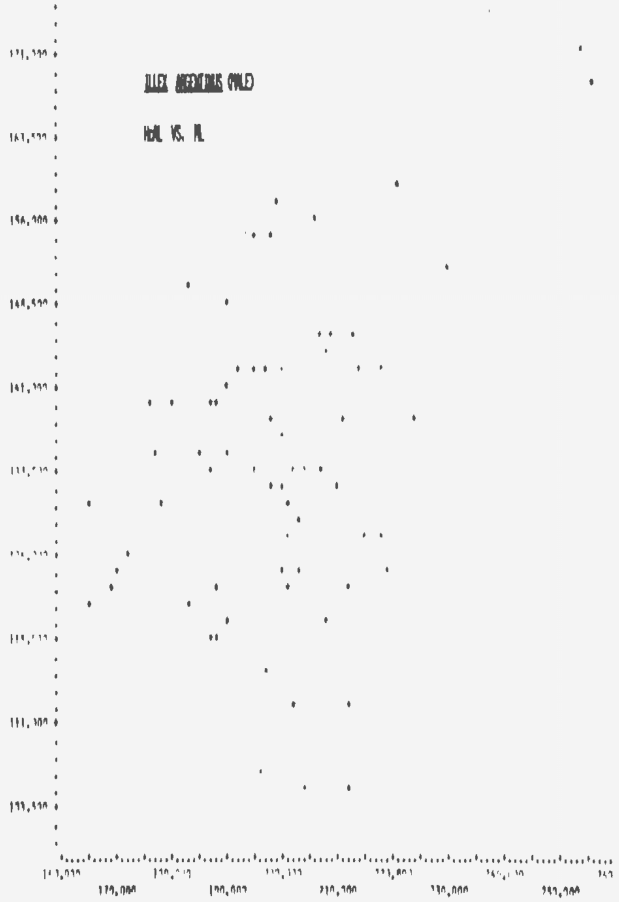

ILLEX COINDETII (FEMALE)
A4L VS. ML

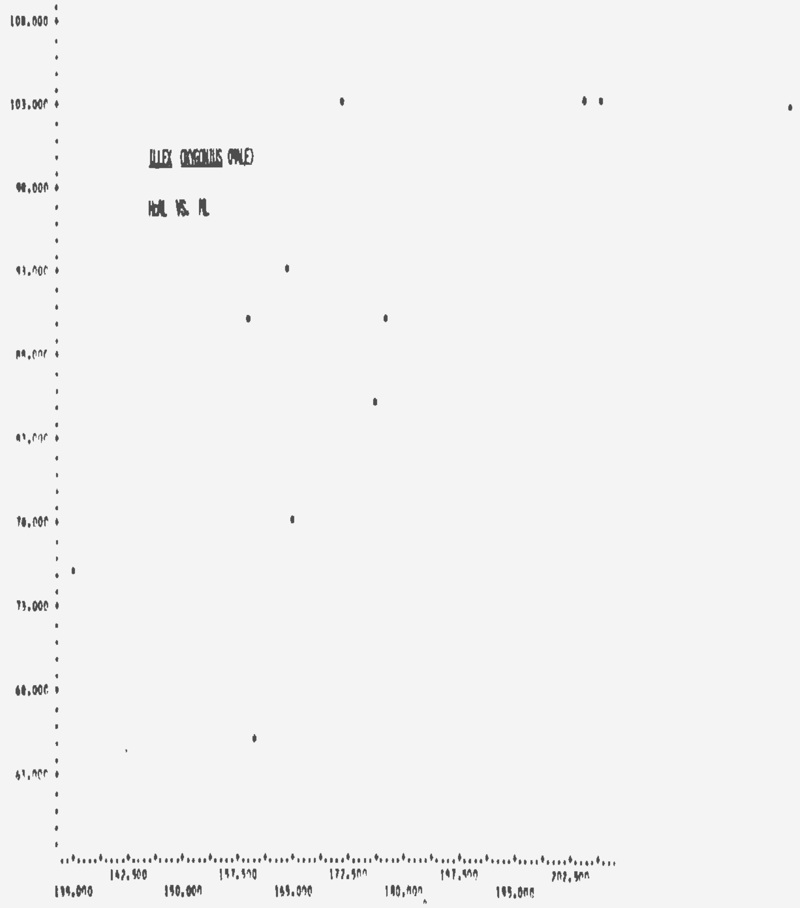

ILLEX ARGENTINUS (FEMALE)
A4L VS. ML

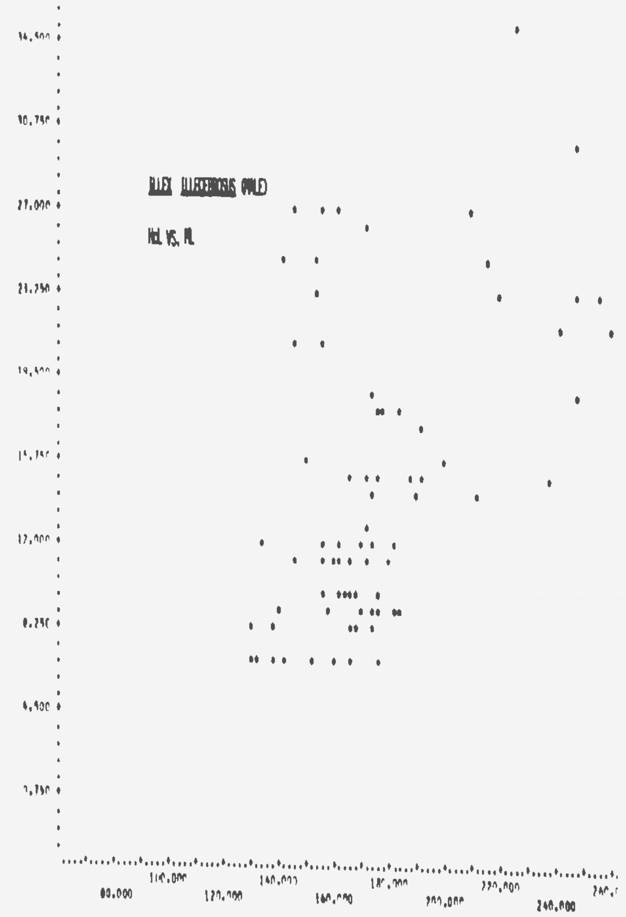

ILLEX OXYGONIUS (FEMALE)
A4L VS. ML
150,000
170,000
190,000
210,000

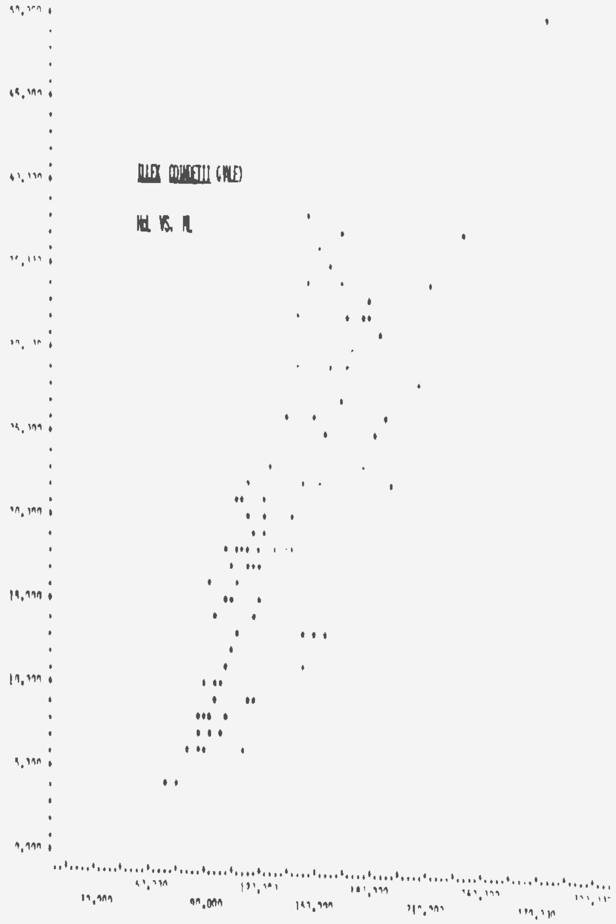

ILLEX ILLECEBROSUS (MALE)
HdL VS. ML
123.000
108.000
93.000
33.000
18.000
3.000
80.000
100.000
120.000
140.000
160.000
180.000
200.000
220.000
240.000

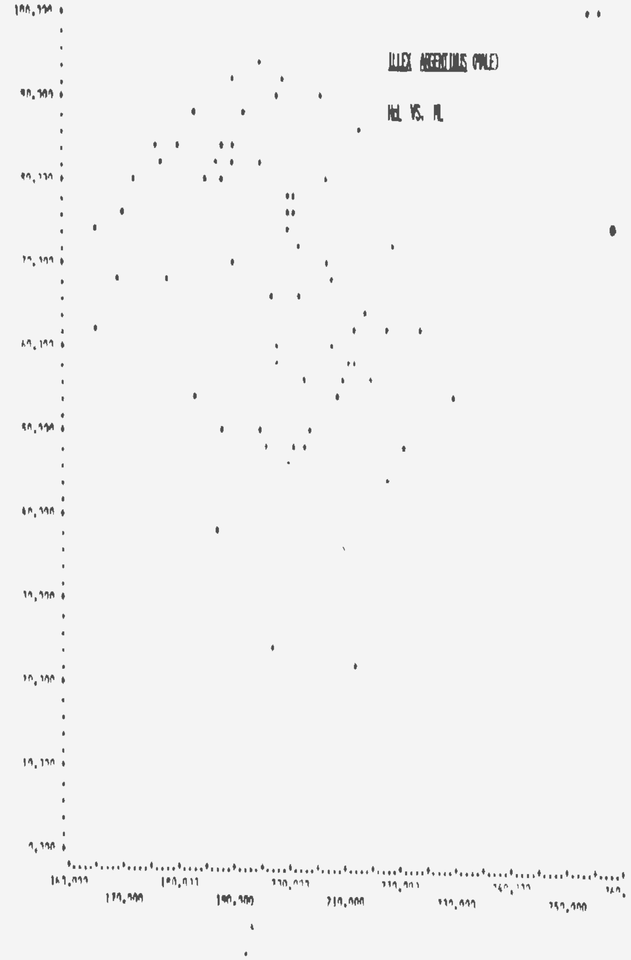

ILLEX COINDETII (MALE)
HdL VS. ML
100.000
68.000
-12.000
30.000
61.000
90.000
120.000
150.000
210.000
240.000
270.000
300.000

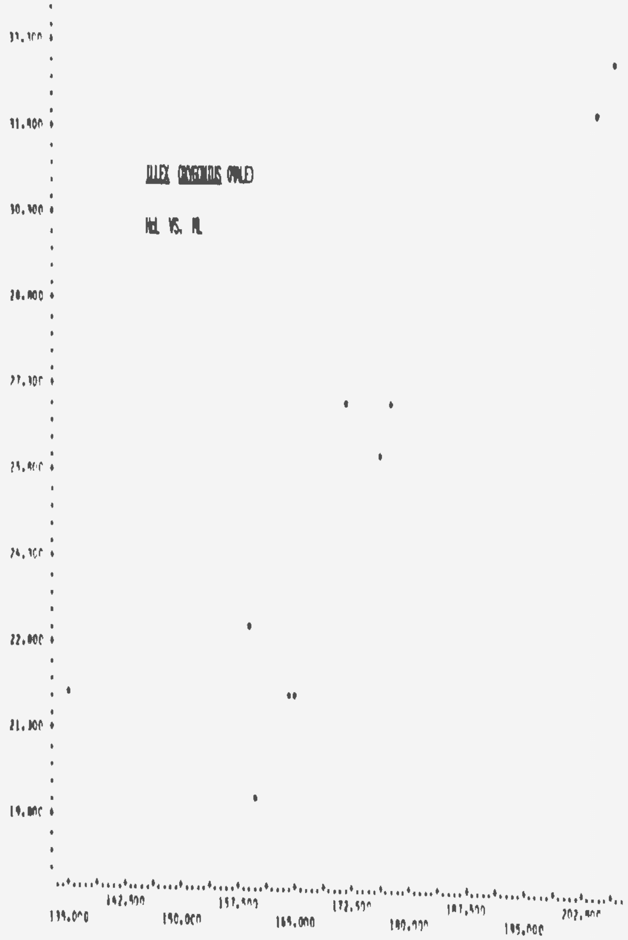

ILLEX ARGENTINUS (MALE)
HdL VS. ML
156.000
148.500
141.000
111.000
103.500
170.000
190.000
210.000
230.000
250.000

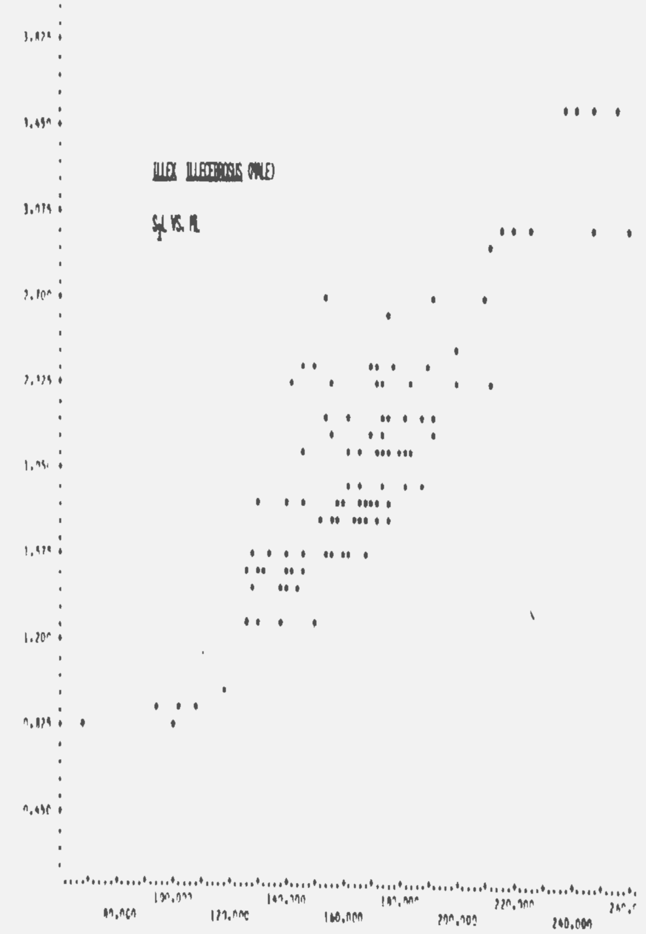

ILLEX OXYGONIUS (MALE)
HdL VS. ML
108.000
103.000
98.000
93.000
88.000
83.000
78.000
73.000
68.000
63.000
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500

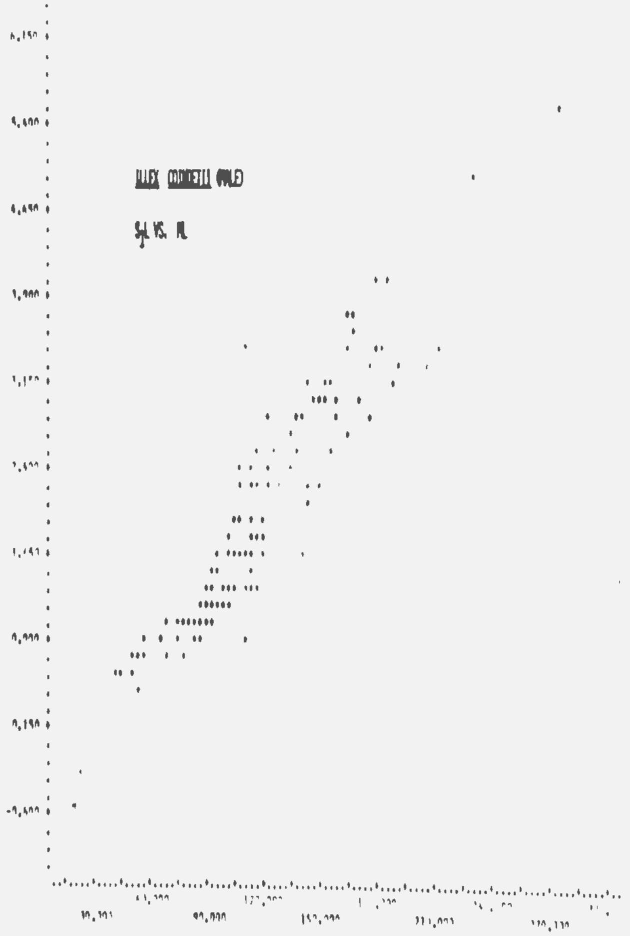

ILLEX ILLECEBROSUS (MALE)
HdL VS. ML
34.500
30.750
27.000
23.250
19.500
15.750
12.000
8.250
4.500
0.750
80.000
100.000
120.000
140.000
160.000
180.000
200.000
220.000
240.000

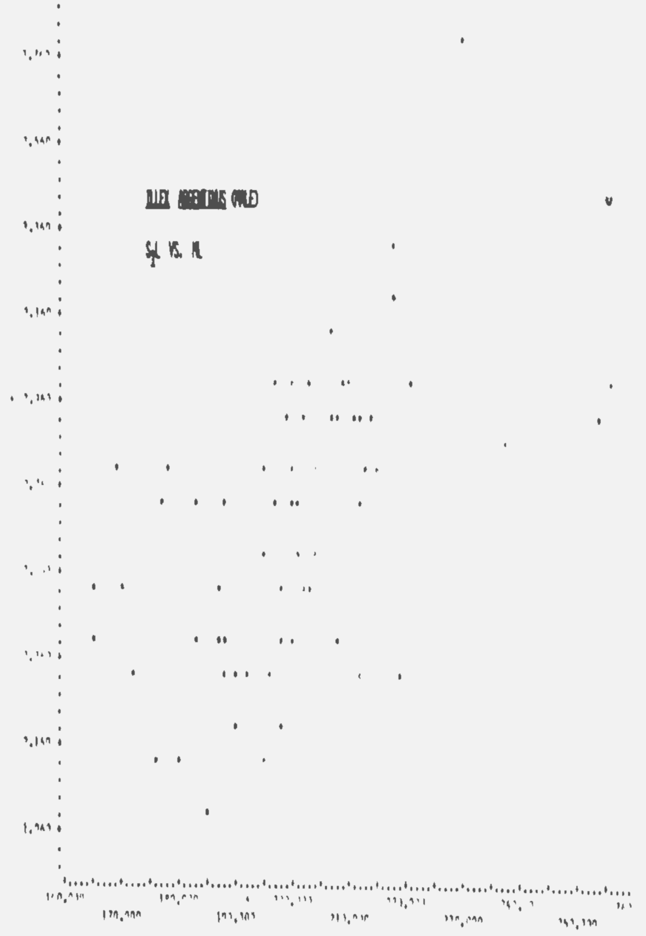

ILLEX COINDETII (MALE)
HdL VS. ML
90.000

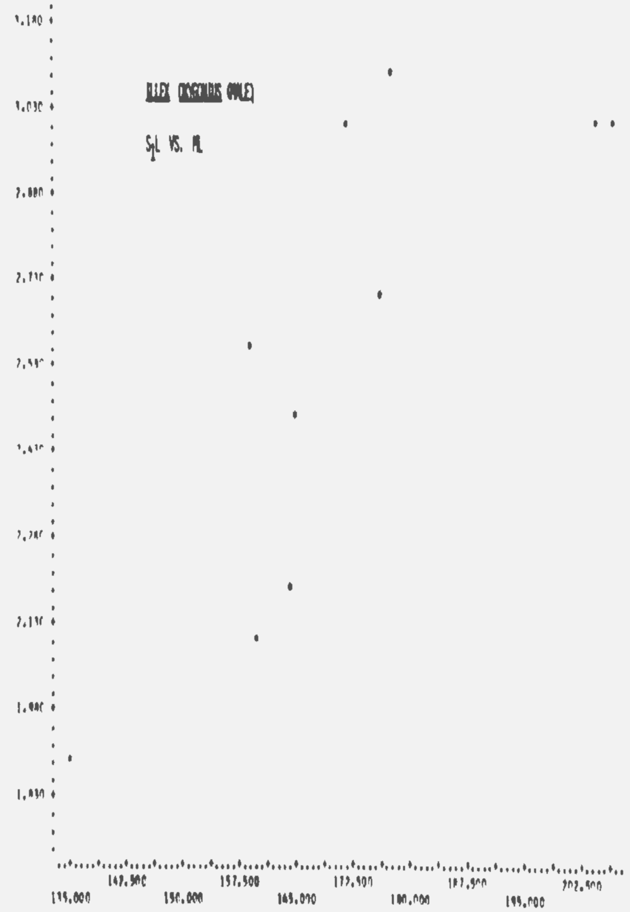

ILLEX ARGENTINUS (MALE)
HdL VS. ML

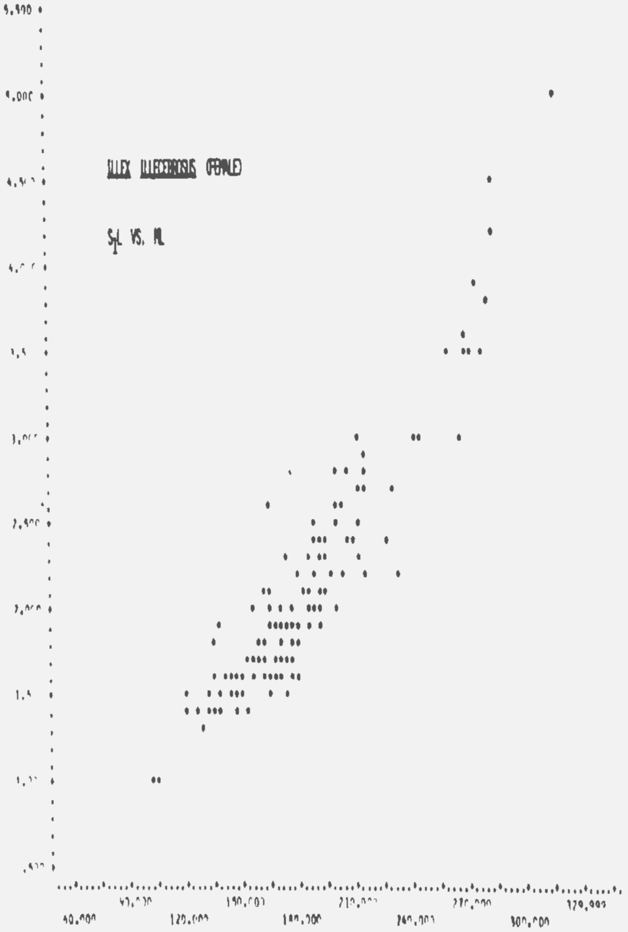

ILLEX OXYGONIUS (MALE)
HdL VS. ML
31.900
30.900
28.800
27.300
25.800
24.300
22.000
21.300
19.000
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500

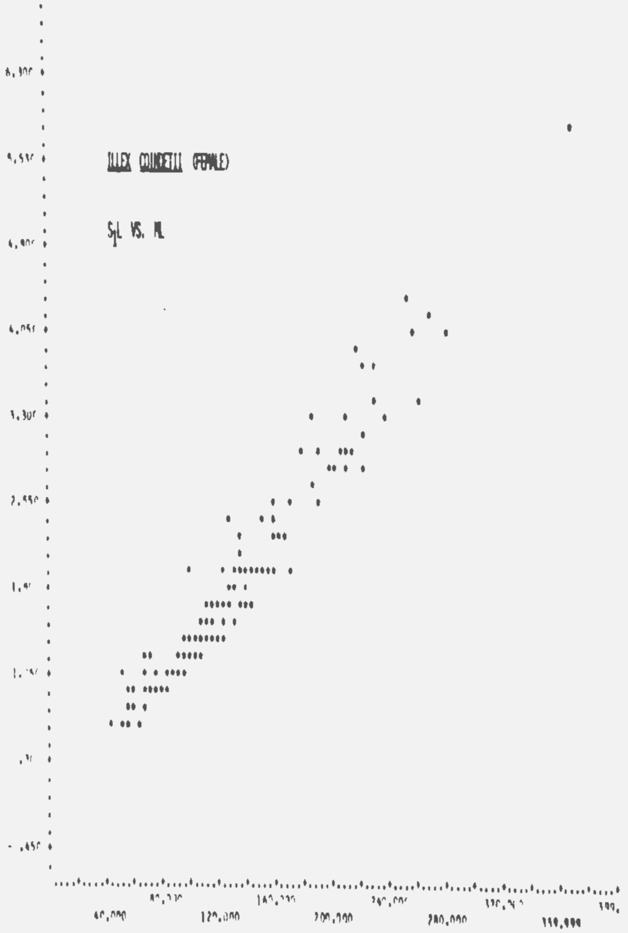

ILLEX ILLECEBROSUS (MALE)
SqL VS. ML
3.825
3.450
3.075
2.700
2.325
1.950
1.575
1.200
0.825
0.450
80.000
100.000
120.000
140.000
160.000
180.000
200.000
220.000
240.000

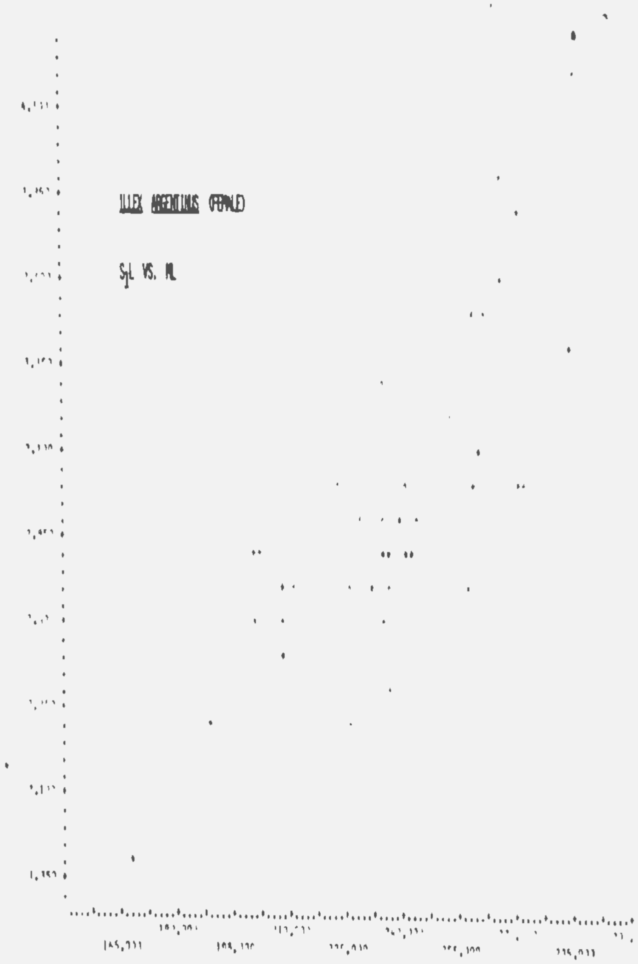

ILLEX COINDETII (MALE)
SqL VS. ML
6.150
5.400
4.650
3.900
3.150
2.400
1.650
0.900
0.150
-0.600
90.000

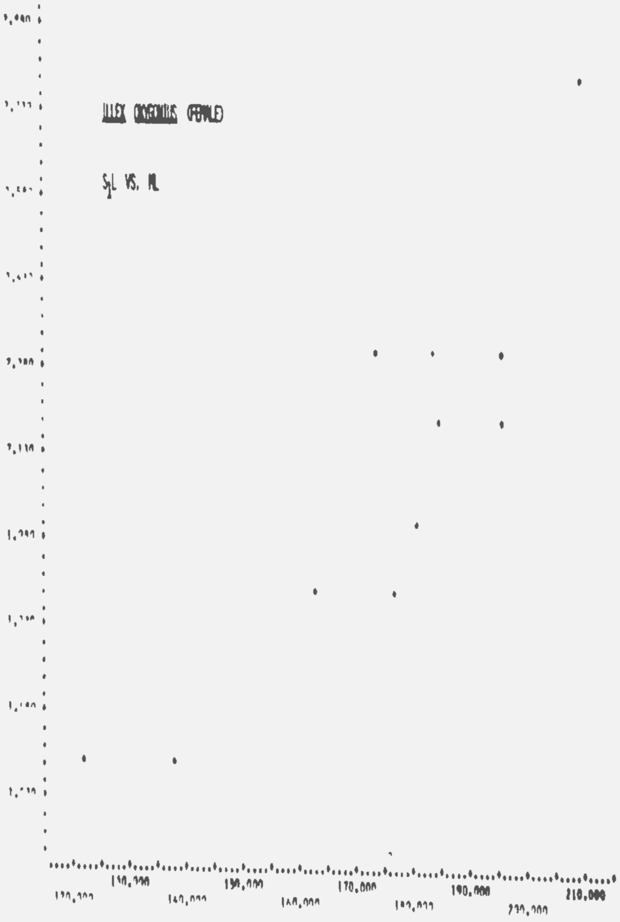

ILLEX ARGENTINUS (MALE)
SqL VS. ML
170.000

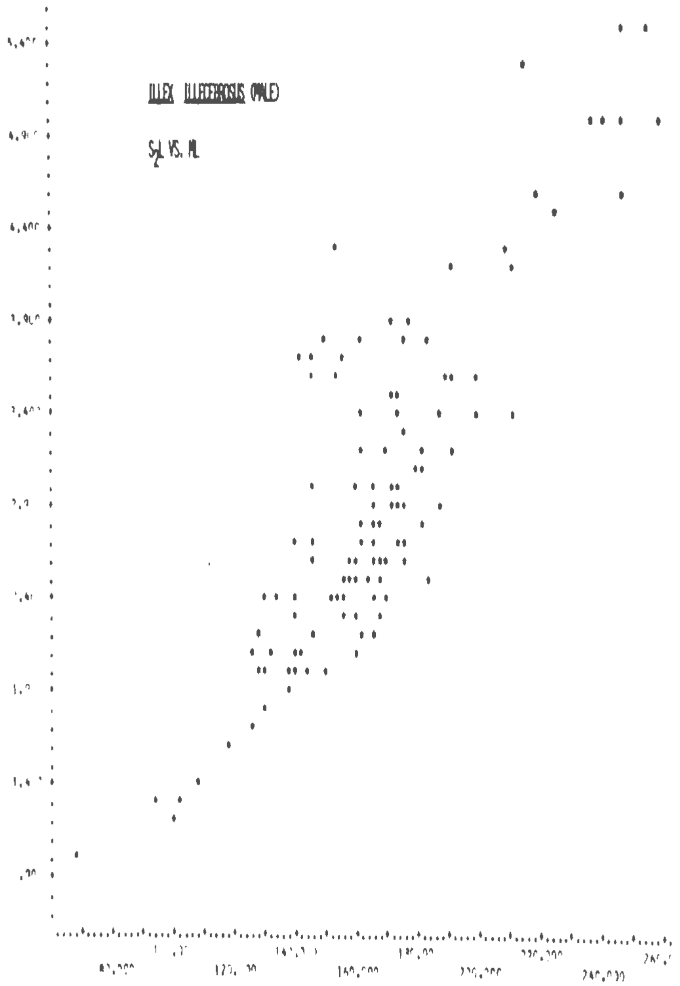

ILLEX OXYGONIUS (MALE)
SqL VS. ML
3.180
3.030
2.880
2.730
2.580
2.430
2.280
2.130
1.980
1.830
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500

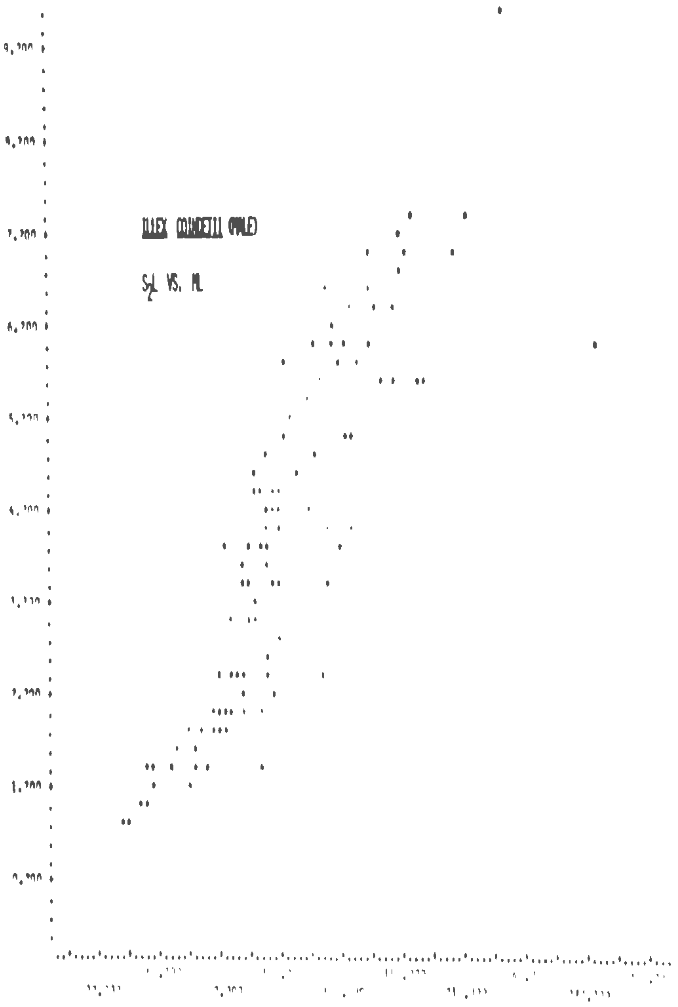

ILLEX ILLECEBROSUS (FEMALE)
S_1L VS. ML
60.000
120.000
300.000

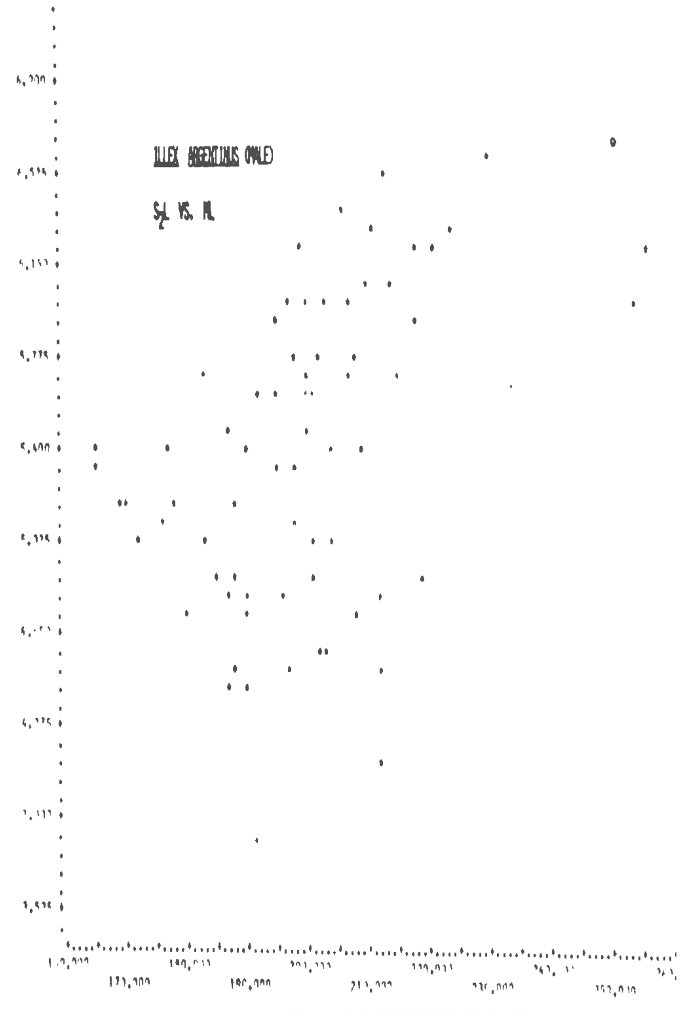

ILLEX COINDETII (FEMALE)
S_1L VS. ML
60.000
120.000
200.000
280.000

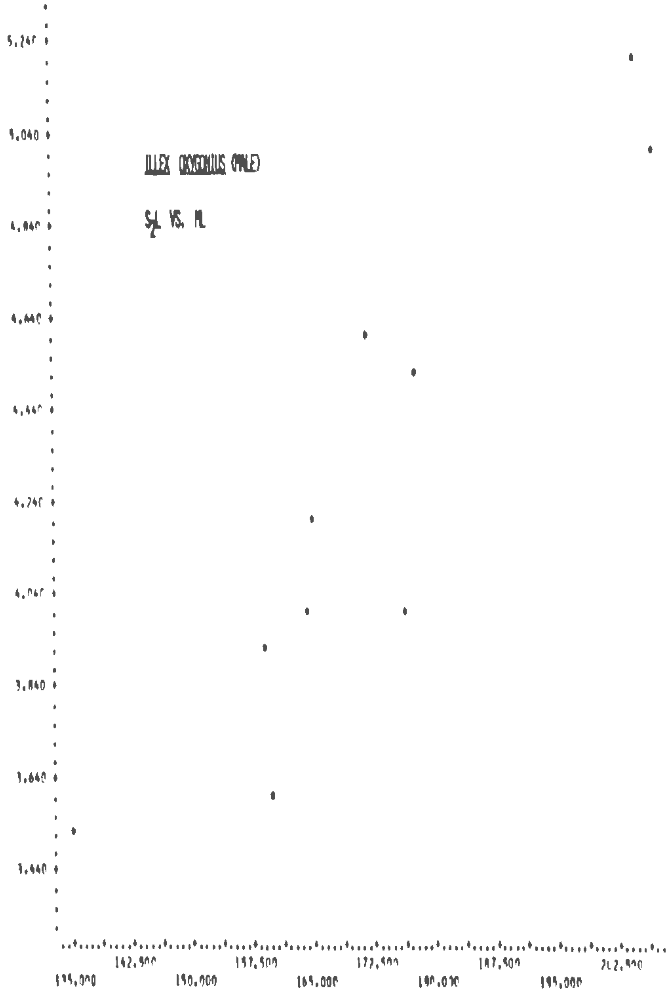

ILLEX ARGENTINUS (FEMALE)
S_1L VS. ML

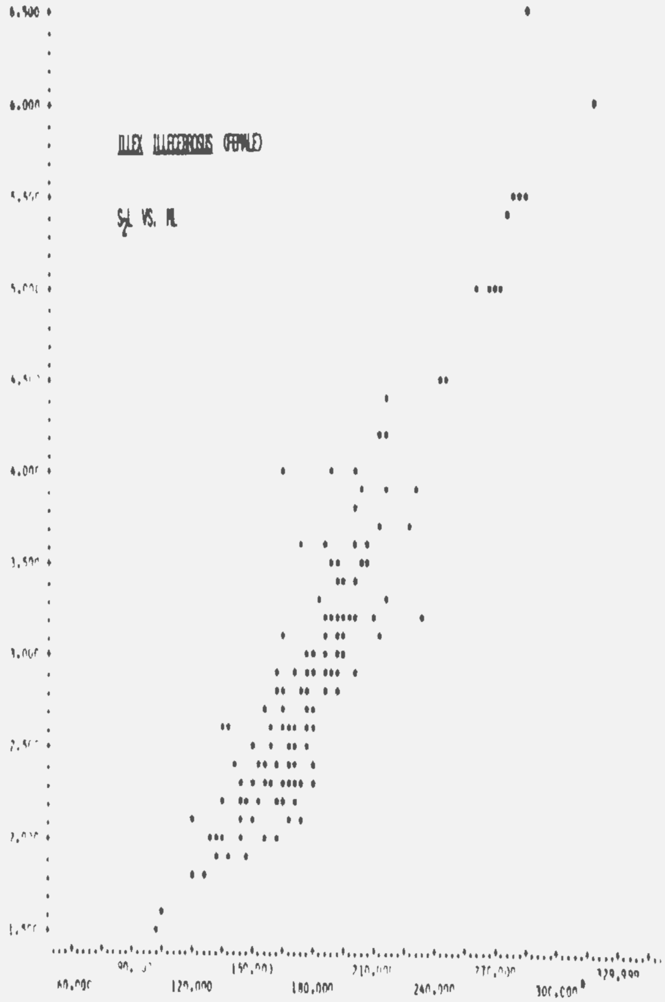

ILLEX OXYGONIUS (FEMALE)
S_1L VS. ML
130.000
150.000
170.000
190.000
210.000

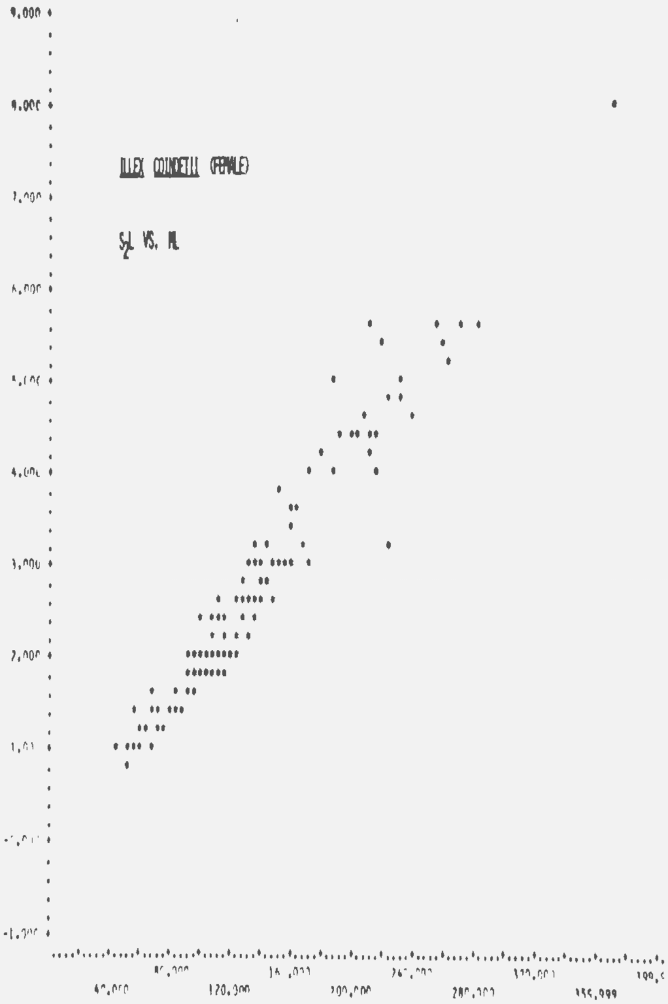

ILLEX ILLECEBROSUS (MALE)
S2L VS. ML
160.000
240.000

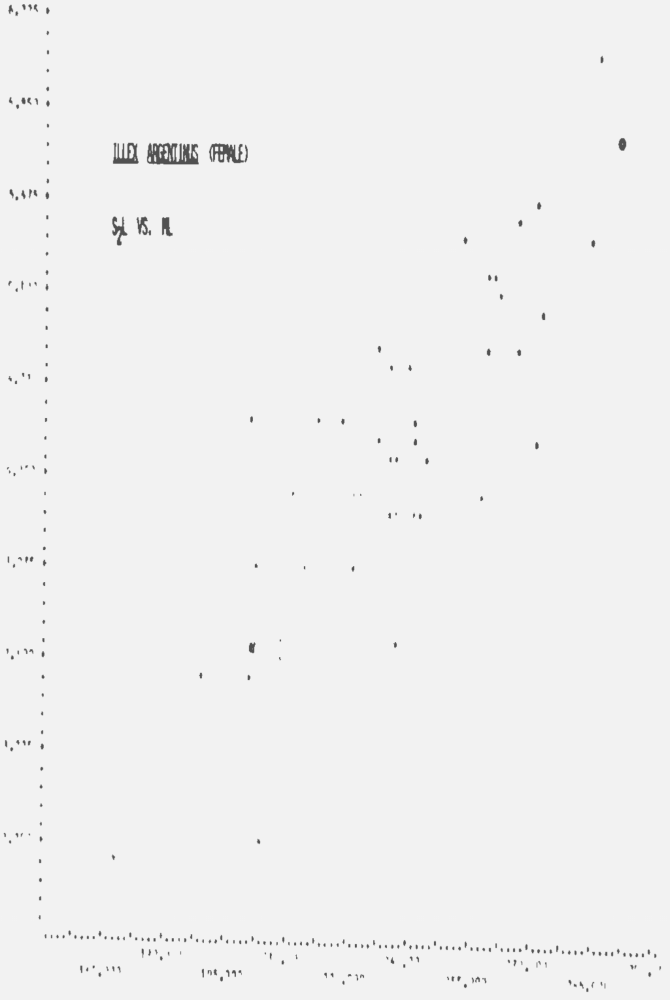

ILLEX COINDETII (MALE)
S2L VS. ML

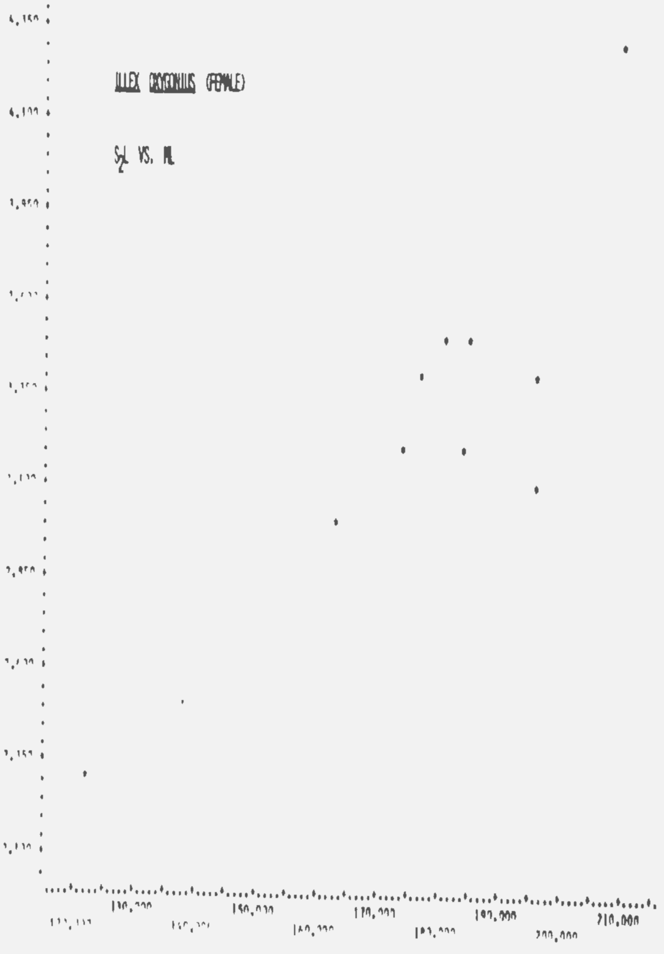

ILLEX ARGENTINUS (MALE)
S2L VS. ML
190.000

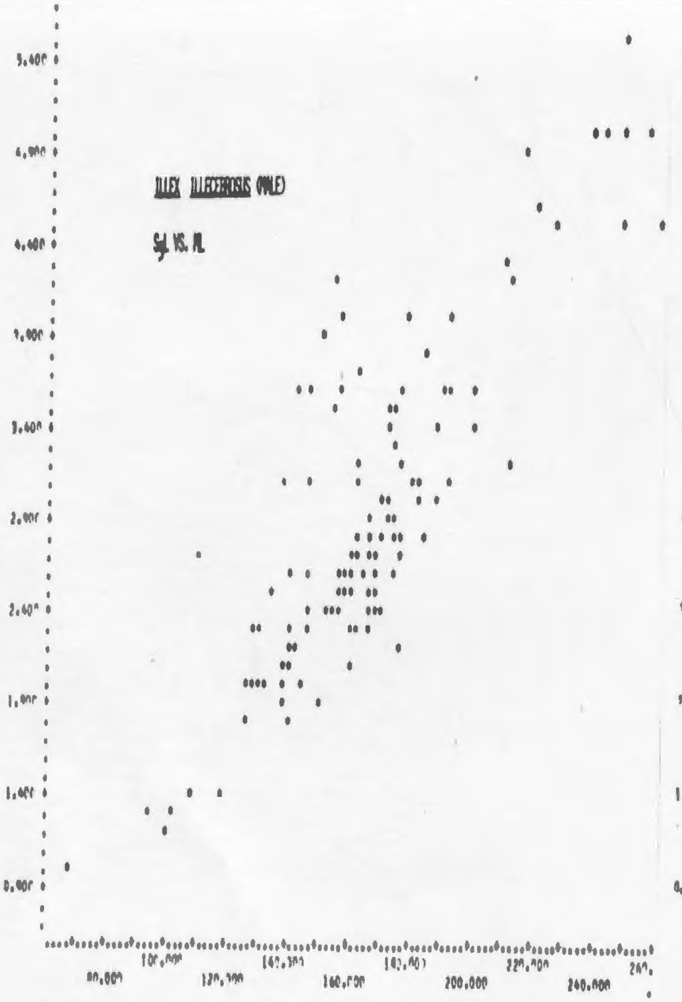

ILLEX OXYGONIUS (MALE)
S2L VS. ML
5.240
5.040
4.840
4.640
4.440
4.240
4.040
3.840
3.640
3.440
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500

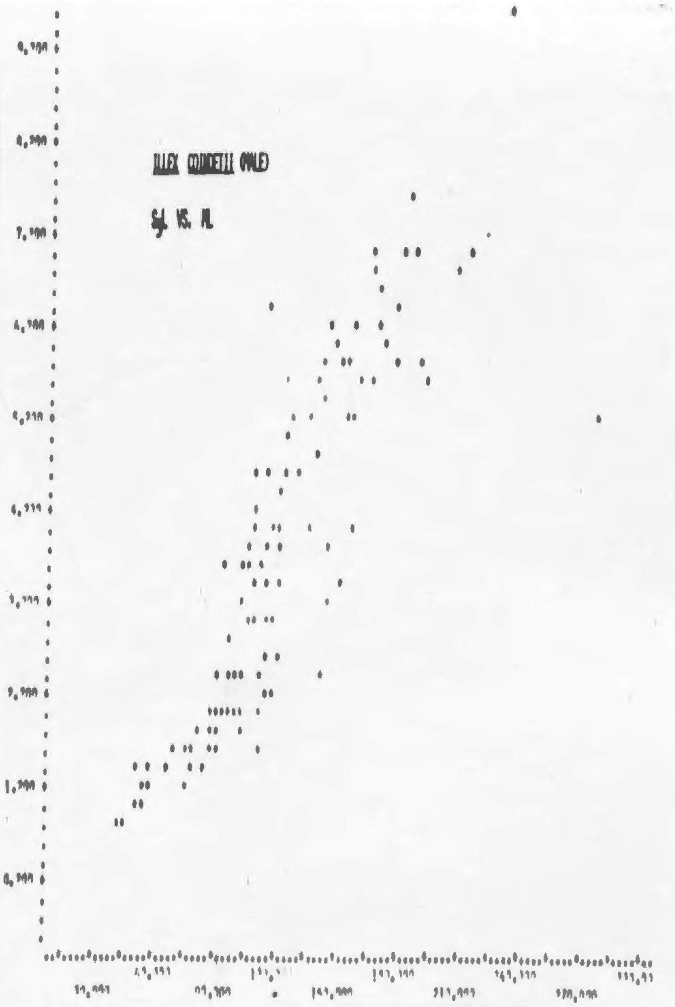

ILLEX ILLECEBROSUS (FEMALE)
SL VS. ML
6.500
6.000
5.000
4.000
3.000
60.000
120.000
150.000
180.000
240.000
300.000
329.999

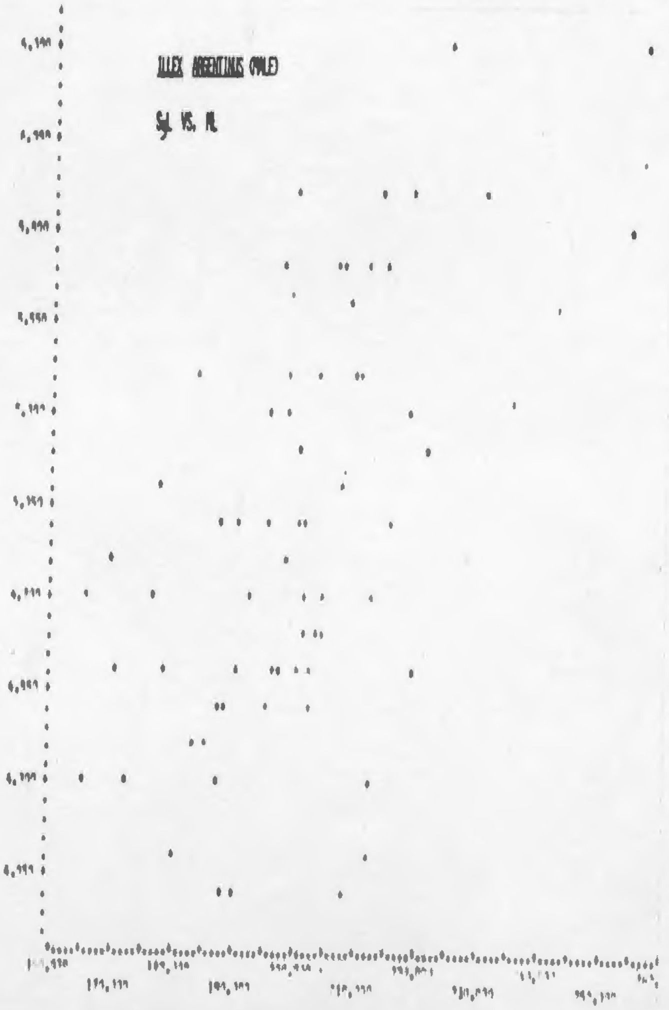

ILLEX COINDETII (FEMALE)
SL VS. ML
9.000
6.000
4.000
3.000
2.000
120.300
200.000


ILLEX ARGENTINUS (FEMALE)
SL VS. ML


ILLEX OXYGONIUS (FEMALE)
SL VS. ML
4.150
130.000
150.000
170.000
190.000
210.000

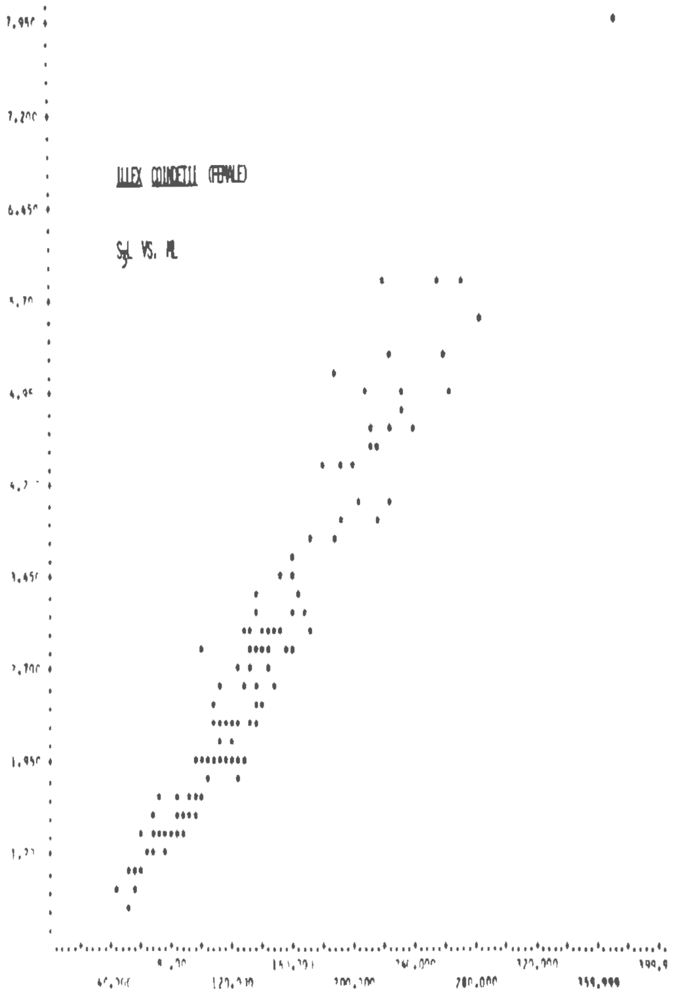

ILLEX ILLECEBROSUS (MALE)
SgL VS. ML
5.400
4.400
80.000
100.000
120.000
160.000
200.000
220.000
240.000
260.

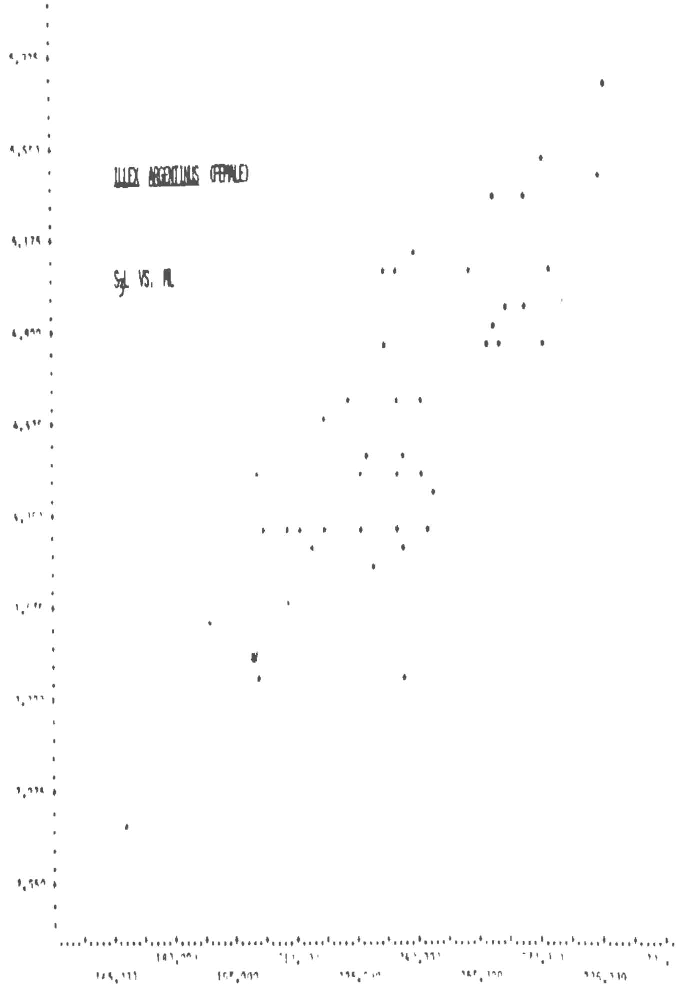

ILLEX COINDETII (MALE)
SgL VS. ML

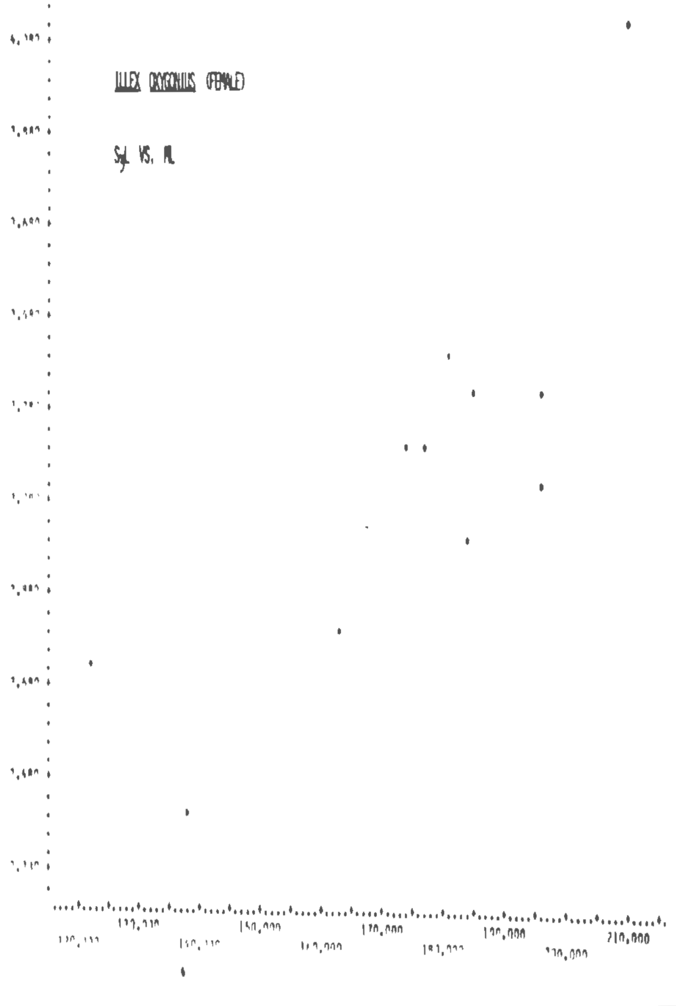

ILLEX ARGENTINUS (MALE)
SgL VS. ML

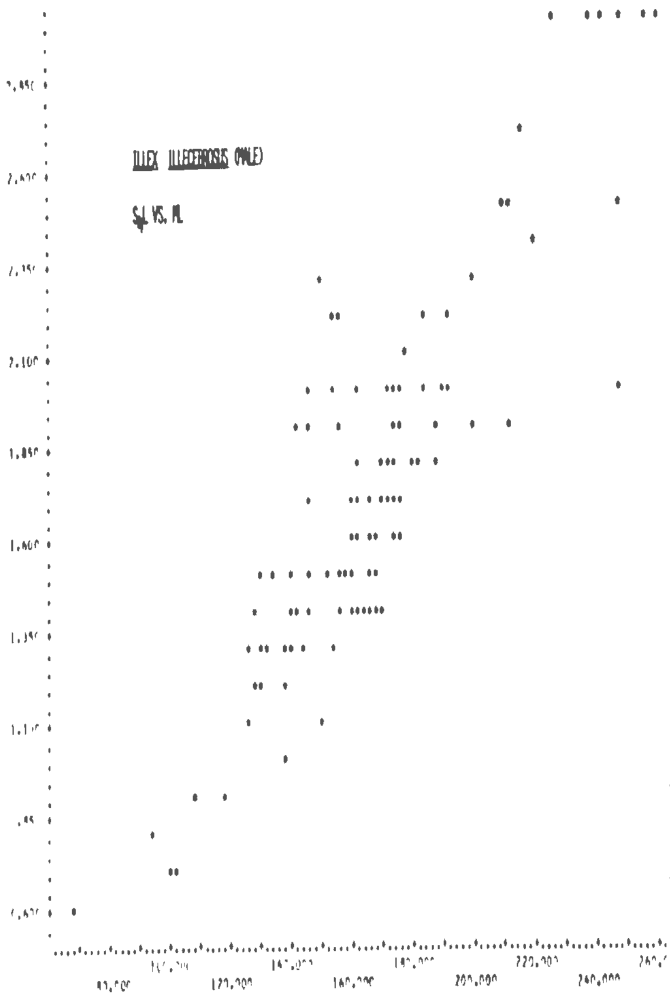

ILLEX OXYGONIUS (MALE)
SgL VS. ML
5.000
4.800
4.400
4.000
3.600
165.000
180.000
195.000

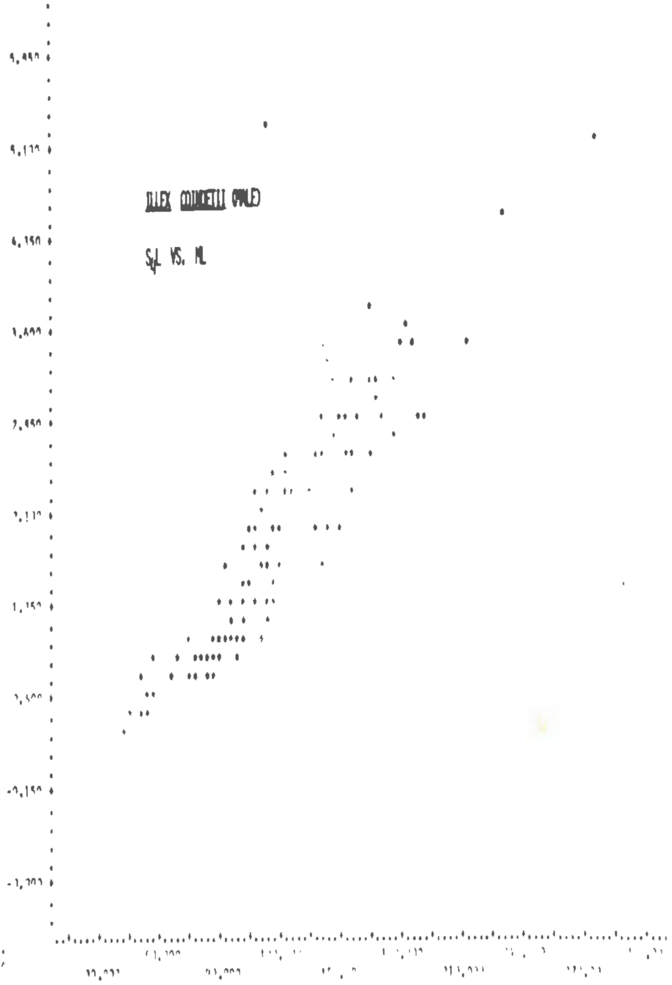

ILLEX ILLECEBROSUS (FEMALE)
SgL VS. ML
7,650
6,900
6,150
5,400
3,150
1,650
0,900
60,000
90,000
120,000
180,000
240,000
300,000

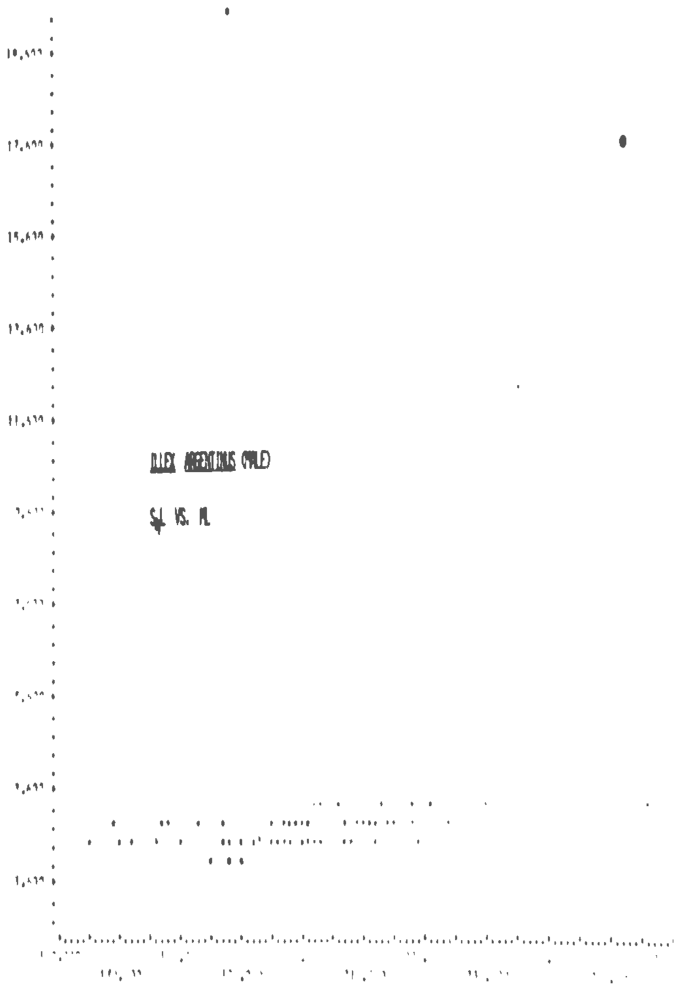

ILLEX COINDETII (FEMALE)
SgL VS. ML
7,950
7,200
6,450
3,450
1,950
120,000
200,000
280,000
360,000

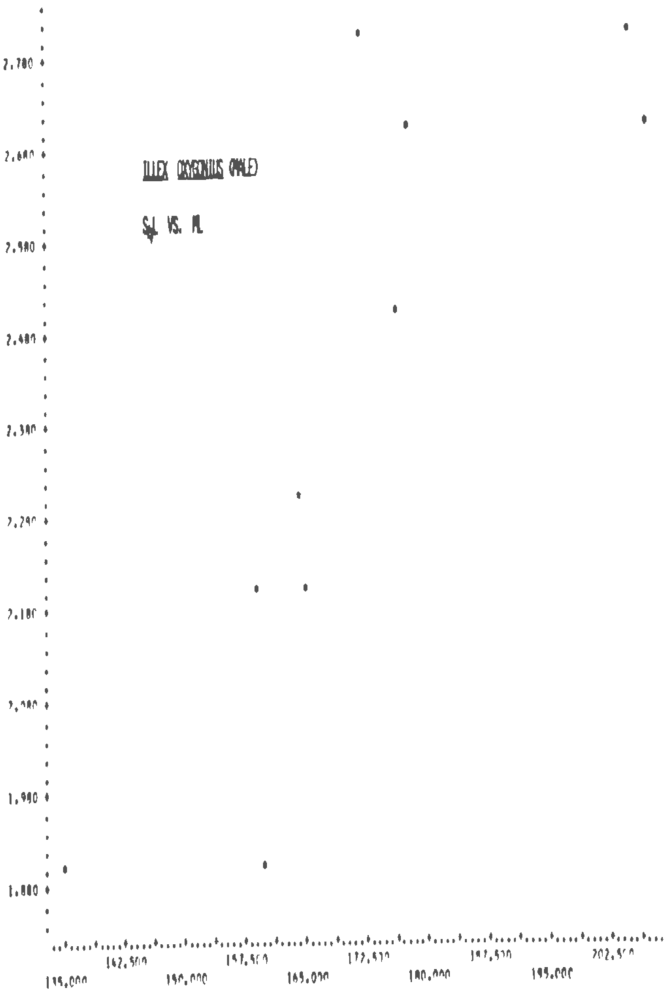

ILLEX ARGENTINUS (FEMALE)
SgL VS. ML


ILLEX OXYGONIUS (FEMALE)
SgL VS. ML
150,000
170,000
190,000
210,000

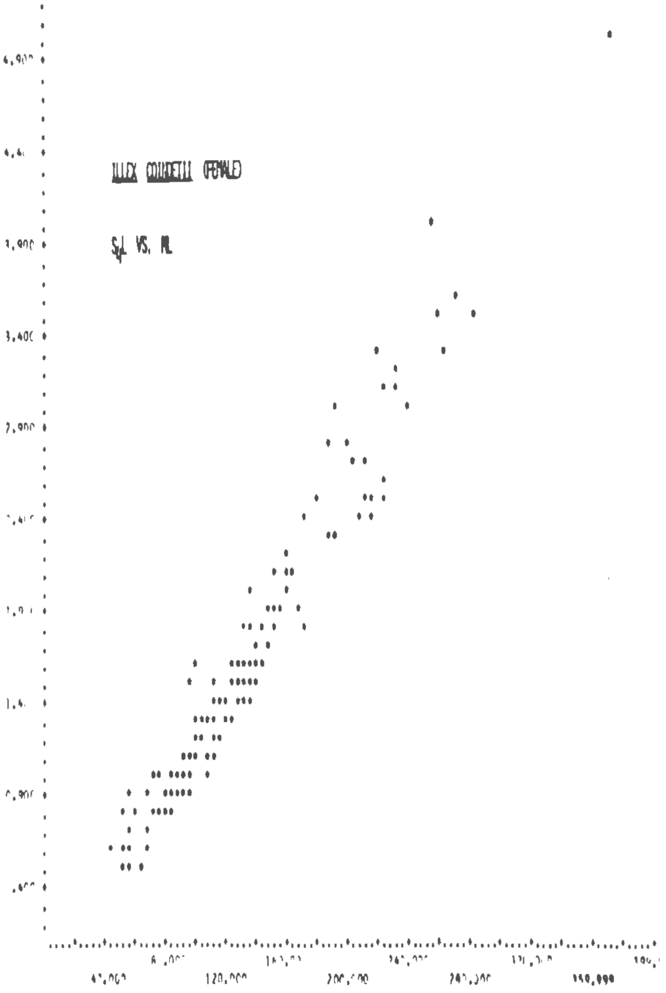

ILLEX ILLECEBROSUS (MALE)
SL VS. ML
2.100
1.850
1.600
.85
120.000
160.000
200.000
220.000
240.000

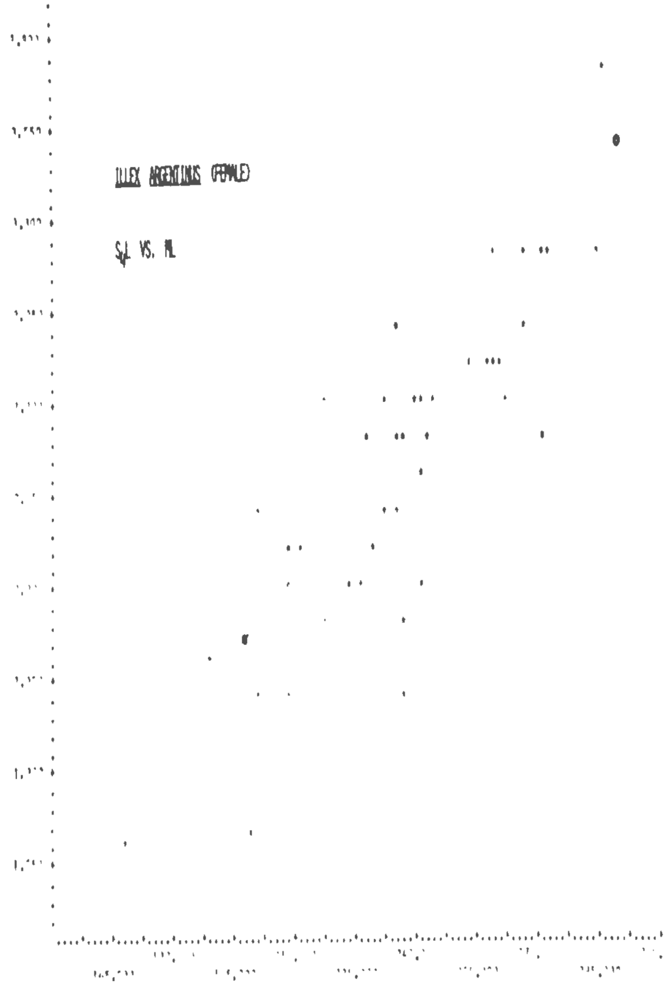

ILLEX COINDETII (MALE)
SL VS. ML

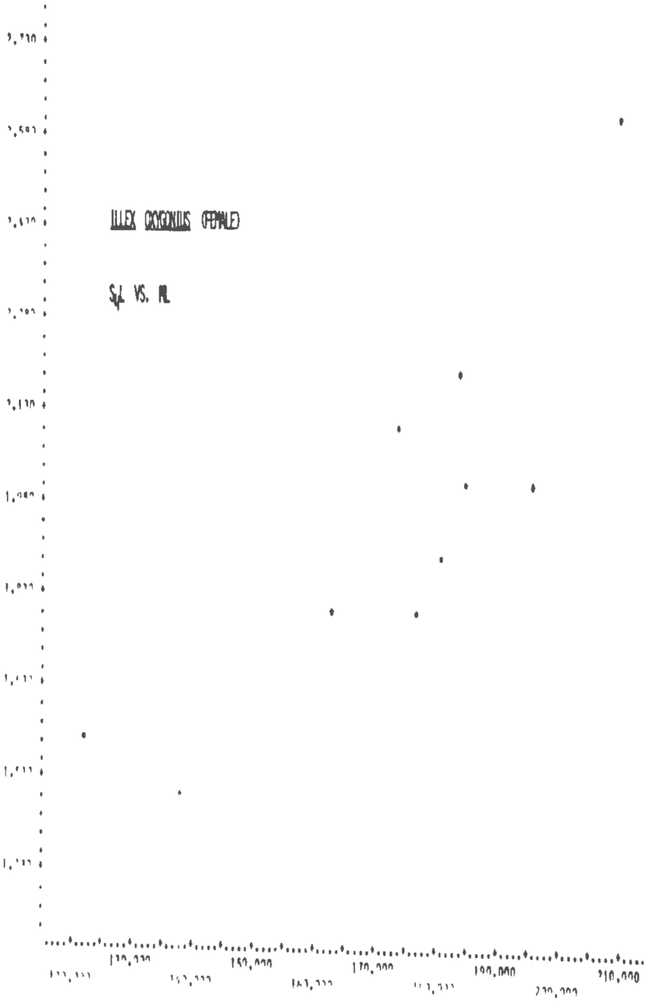

ILLEX ARGENTINUS (MALE)
SL VS. ML

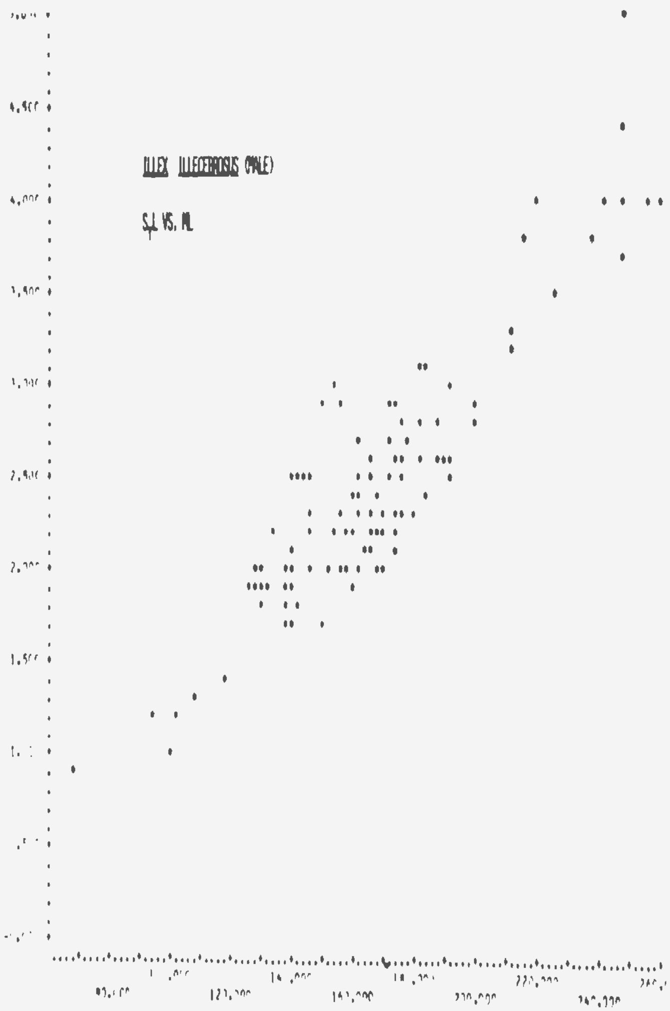

ILLEX OXYGONIUS (MALE)
SL VS. ML
2.780
2.680
2.580
2.480
2.380
2.280
2.180
2.080
1.980
1.880
142.500
157.500
172.500
187.500
202.500
135.000
150.000
165.000
180.000
195.000

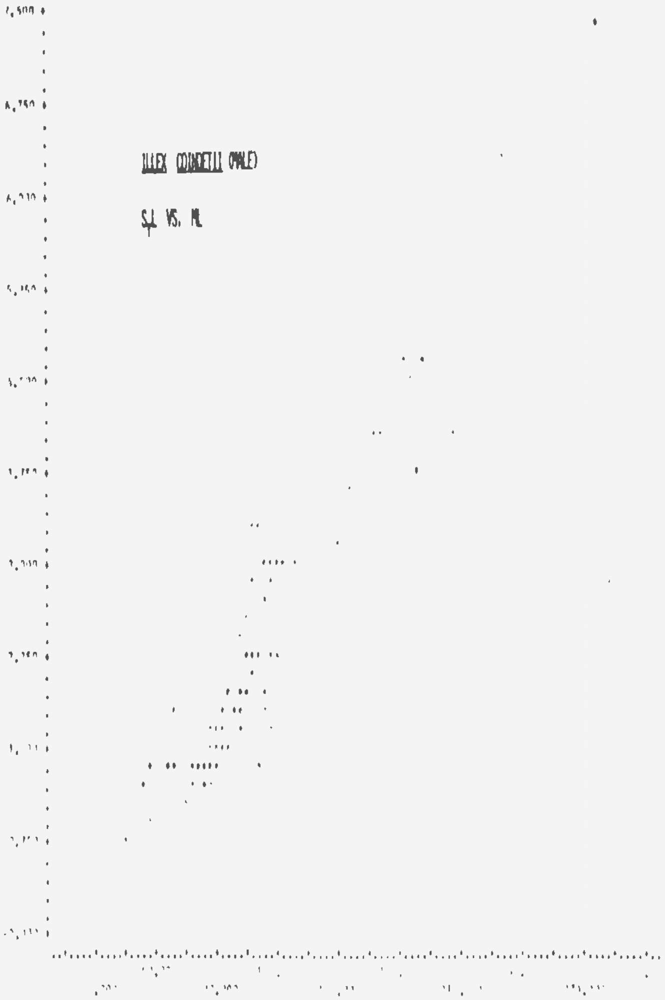

ILLEX ILLECEBROSUS (FEMALE)
SL VS. ML
4.050
3.675
3.300
2.925
2.550
2.175
1.425
1.050
120.000
300.000

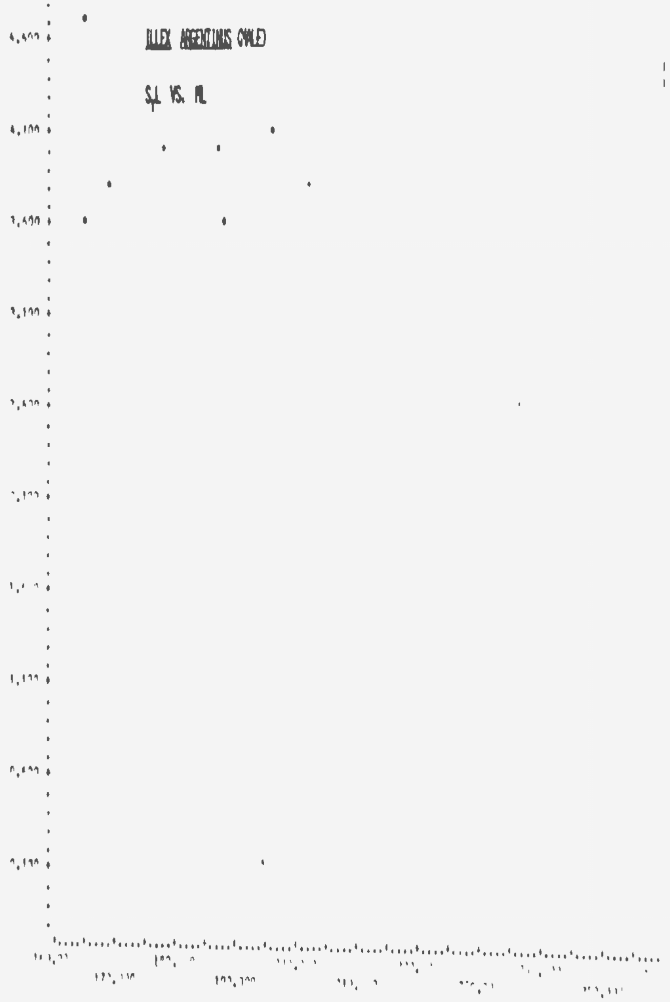

ILLEX COINDETII (FEMALE)
SL VS. ML
4.900
3.900
3.400
2.900
1.6
0.900
120.000
200.000
360.000

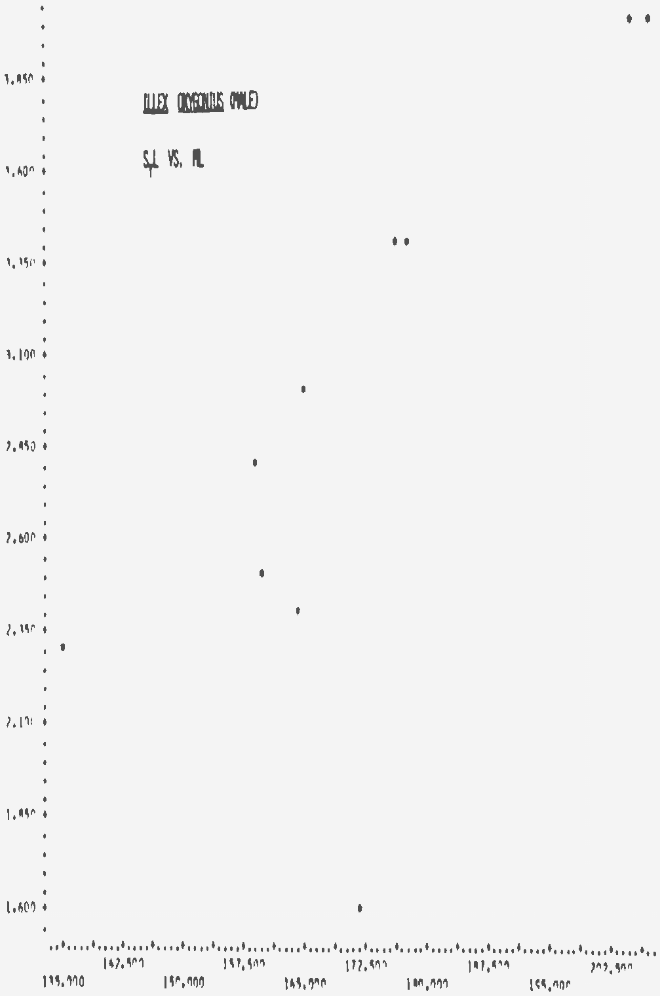

ILLEX ARGENTINUS (FEMALE)
SL VS. ML

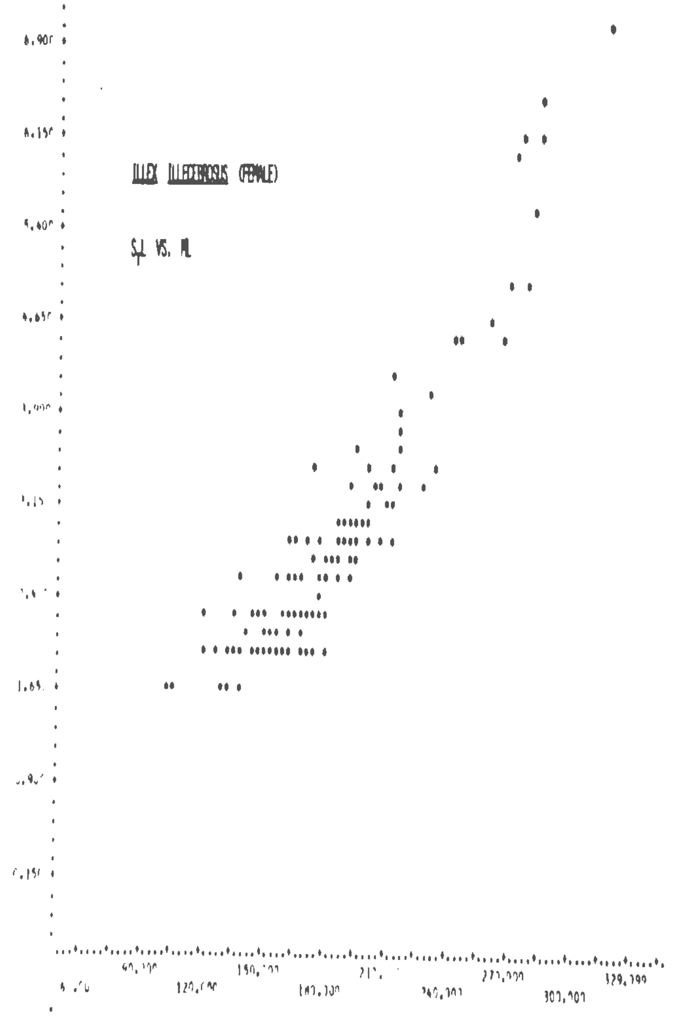

ILLEX OXYGONIUS (FEMALE)
SL VS. ML
2.730
150.000
170.000
190.000
210.000
200.000

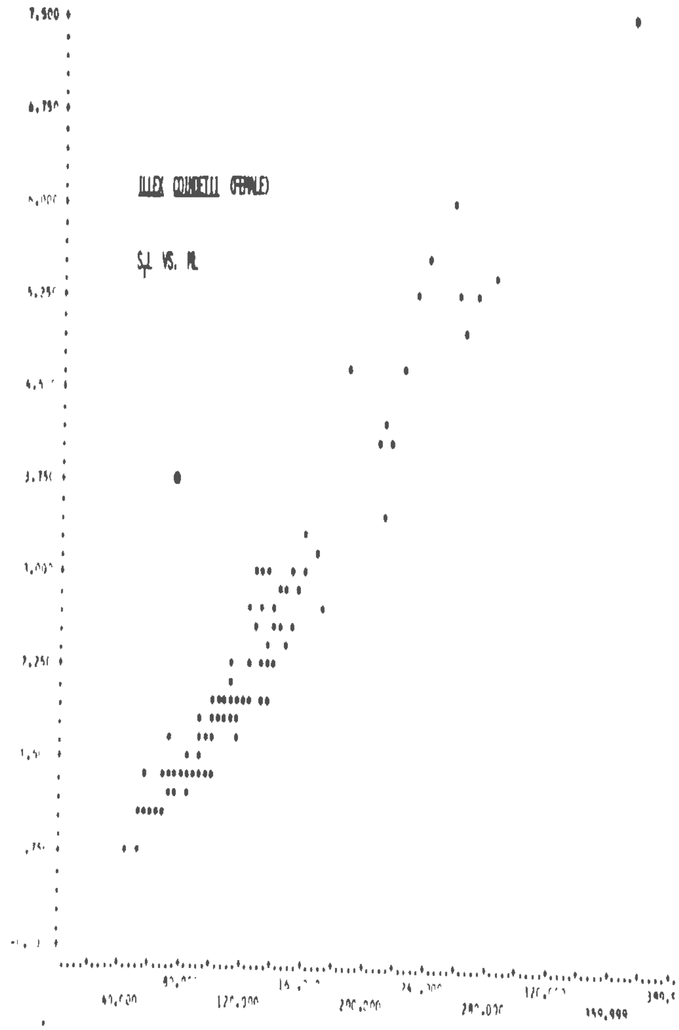

ILLEX ILLECEBROSUS (MALE)
SL VS. ML
4,500
4,000
3,500
3,000
2,500
2,000
1,500

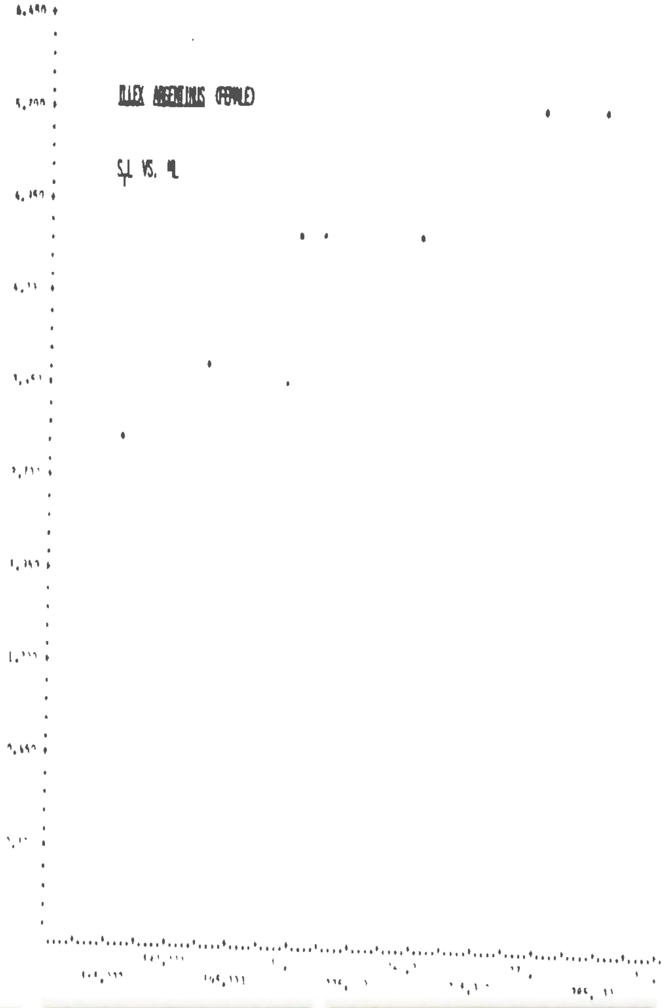

ILLEX COINDETII (MALE)
SL VS. ML

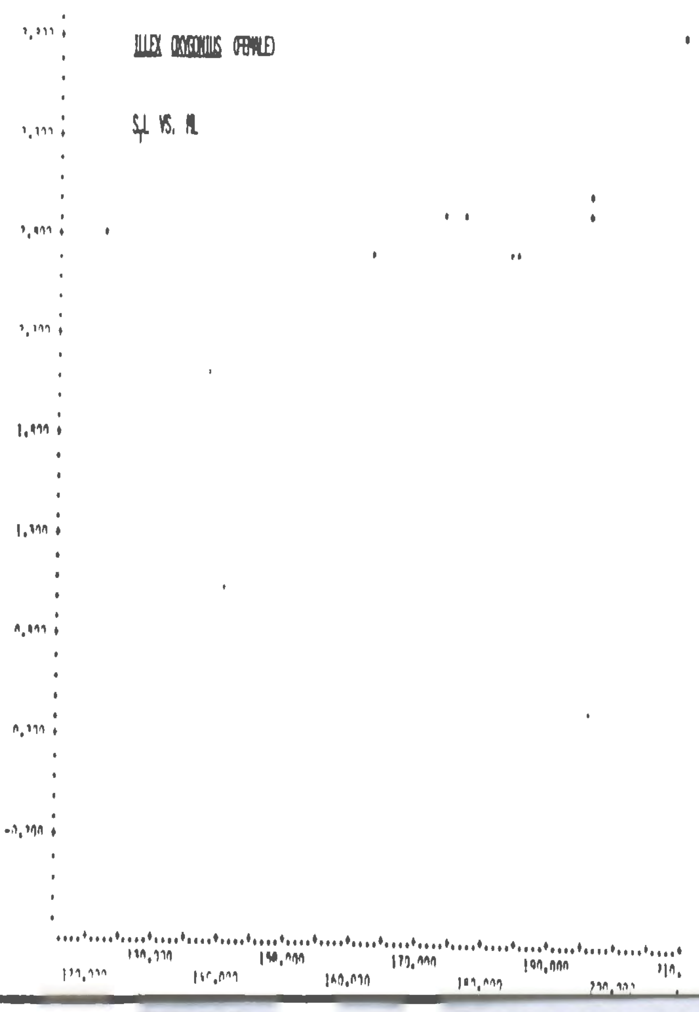

ILLEX ARGENTINUS (MALE)
SL VS. ML

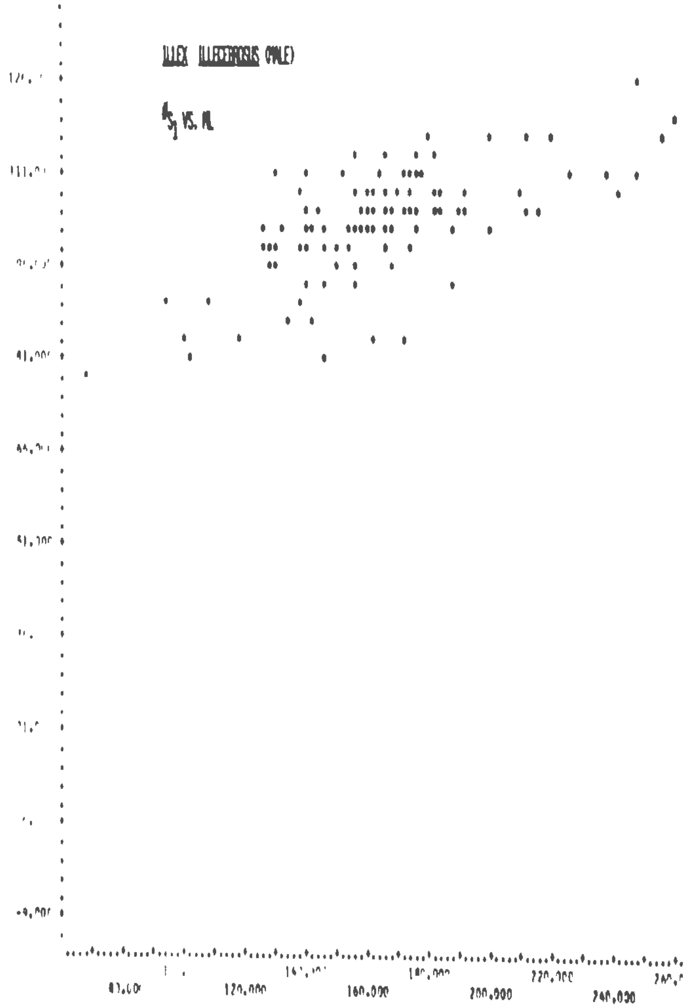

ILLEX OXYGONIUS (MALE)
SL VS. ML
3,850
3,600
3,350
3,100
2,850
2,600
2,350
2,100
1,850
1,600
135,000
142,500
150,000
157,500
165,000
172,500
180,000
187,500
195,000
202,500

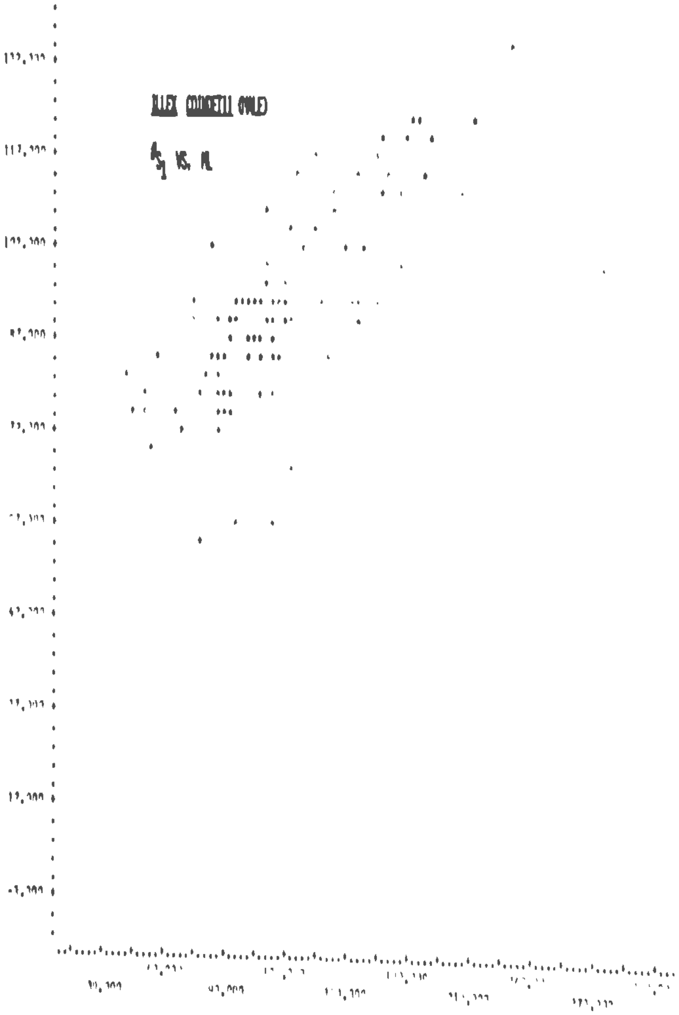

ILLEX ILLECEBROSUS (FEMALE)
SL VS. ML
6.900
1.65
270.000
300.000
329.999

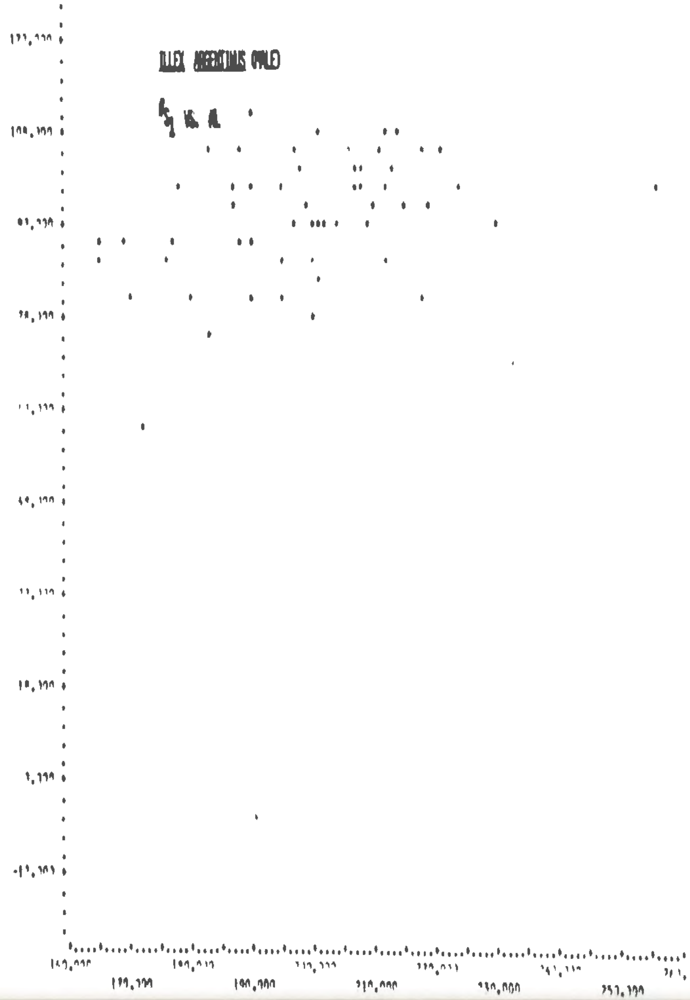

ILLEX COINDETII (FEMALE)
SL VS. ML
7.500
6.750
5.250
3.750
2.250
40.000
120.000
200.000
280.000
360.0

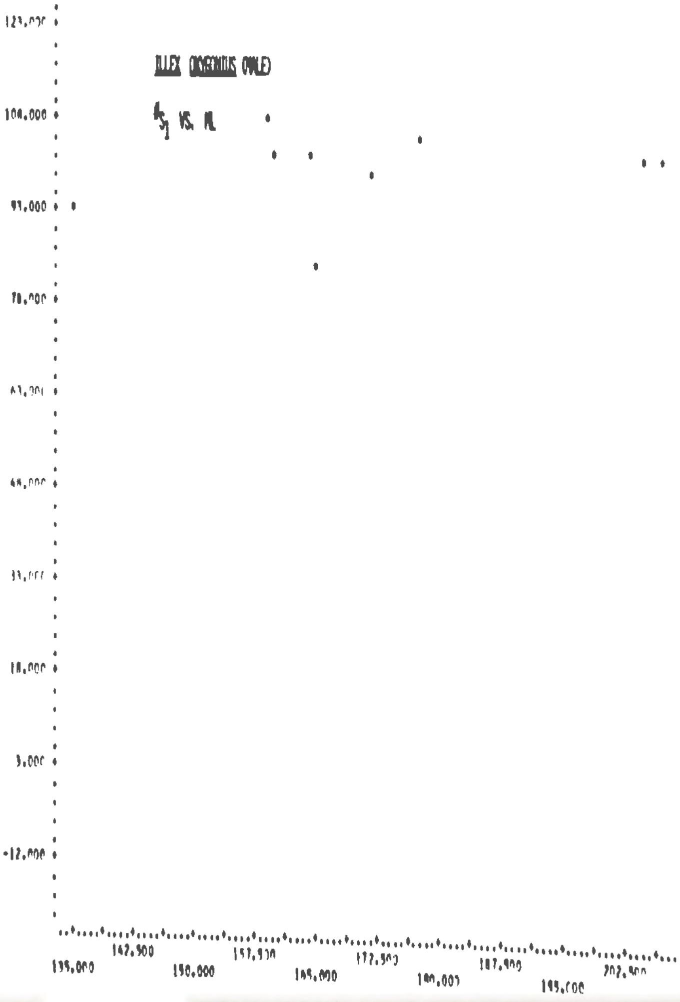

ILLEX ARGENTINUS (FEMALE)
SL VS. ML

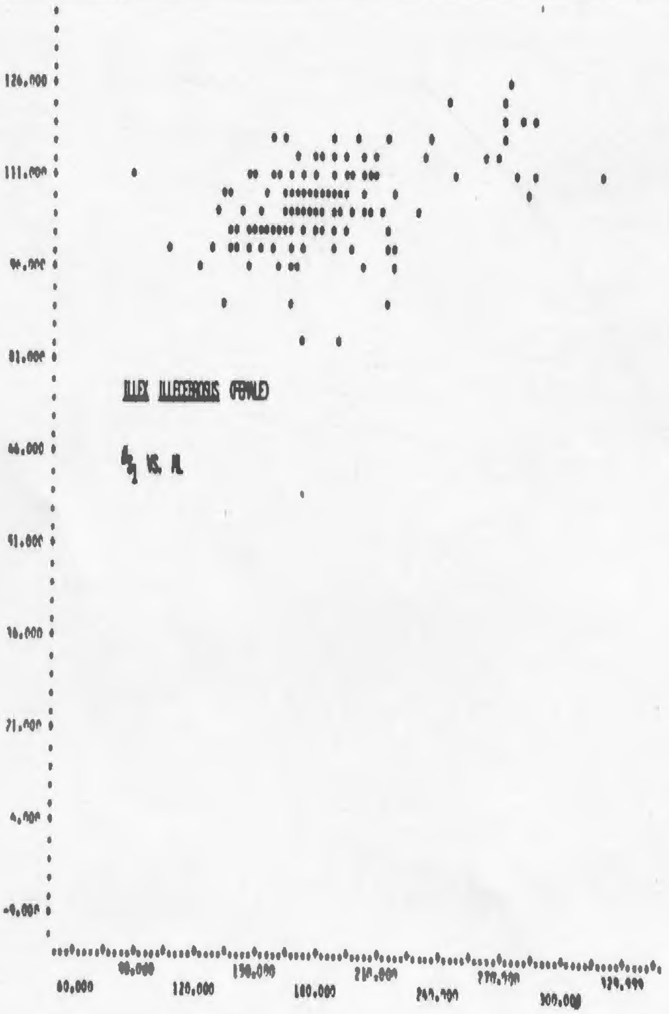

ILLEX OXYGONIUS (FEMALE)
SL VS. ML
1.800
1.300
0.800
0.300
-0.200
120.000
130.000
140.000
150.000
160.000
170.000
180.000
190.000
200.000

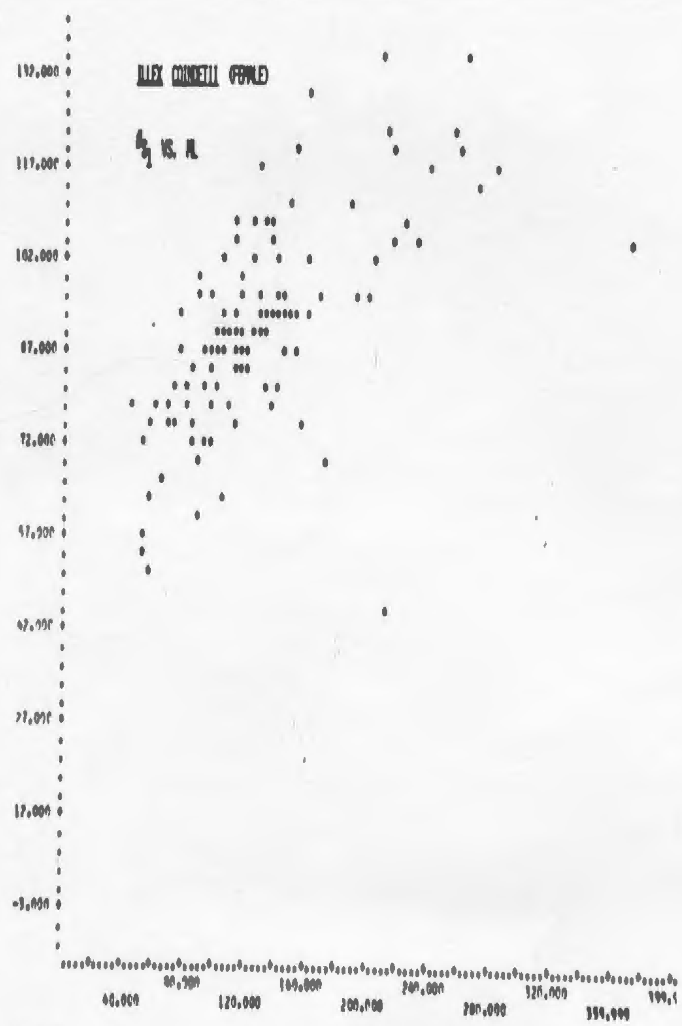

ILLEX ILLECEBROSUS (MALE)
R_{S1} VS. ML
80,000
120,000
160,000
200,000
240,000
-9,000

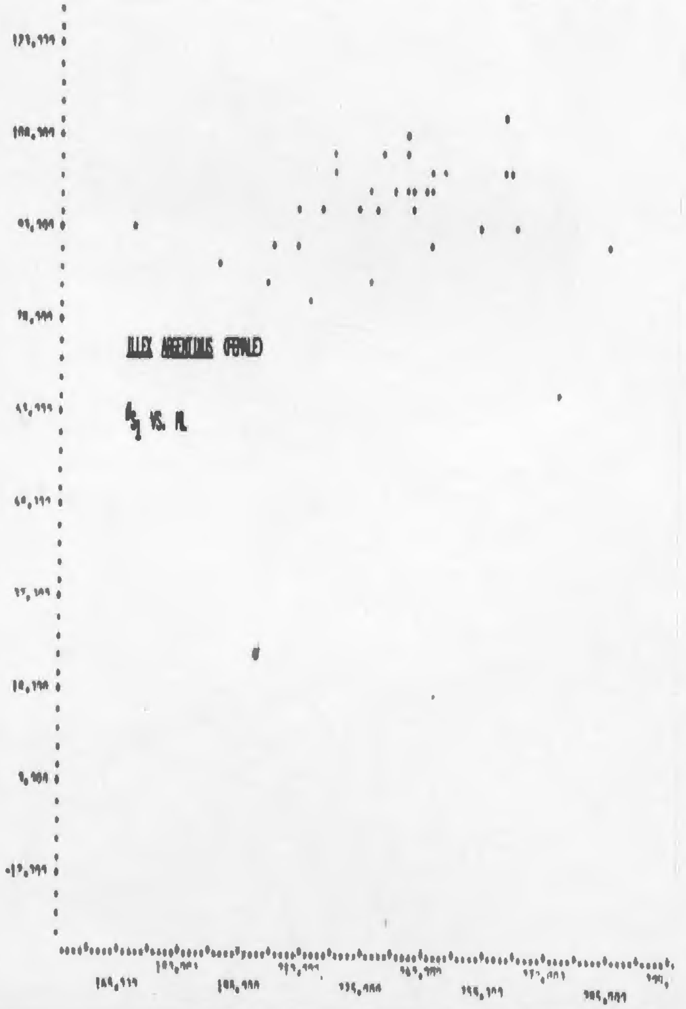

ILLEX COINDETII (MALE)
R_{S1} VS. ML

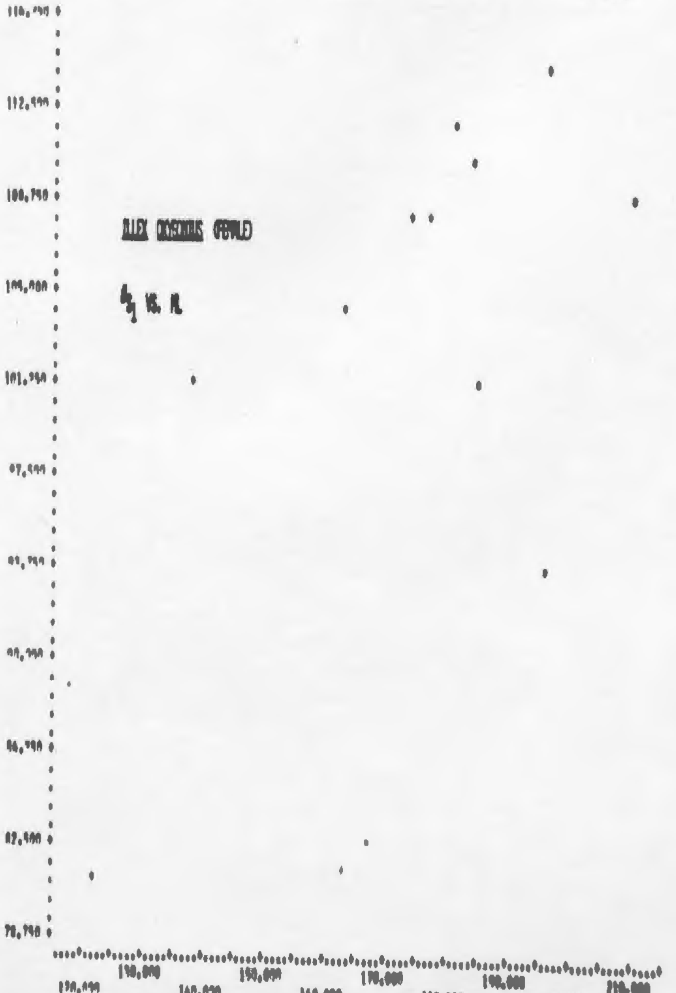

ILLEX ARGENTINUS (MALE)
R_{S1} VS. ML
180,000

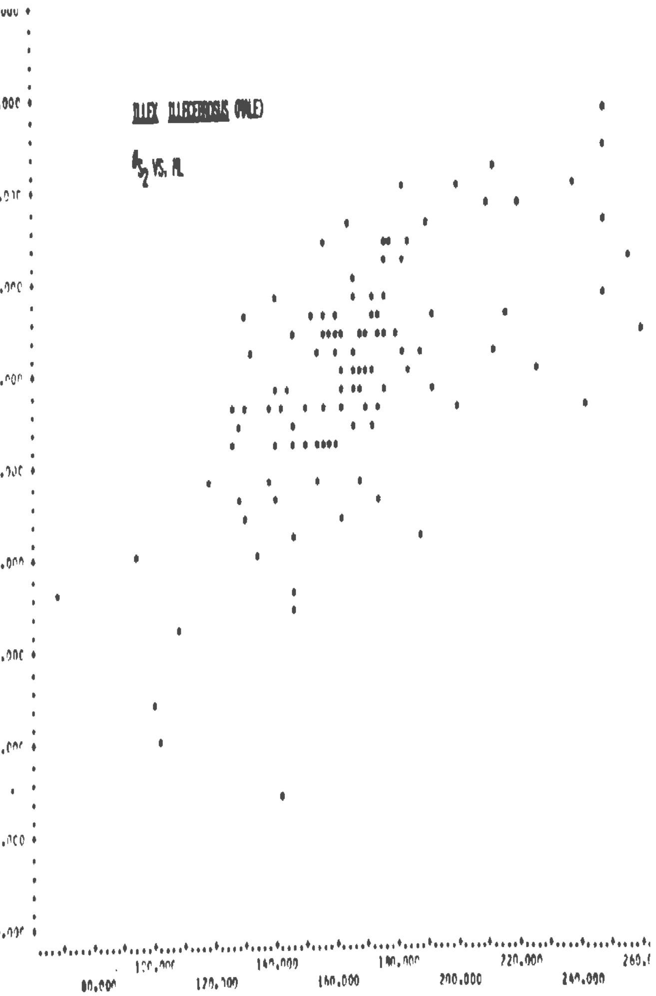

ILLEX OXYGONIUS (MALE)
R_{S1} VS. ML
108,000
93,000
78,000
63,000
48,000
33,000
18,000
3,000
-12,000
135,000
142,500
150,000
157,500
165,000
172,500
180,000
187,500
195,000
202,500

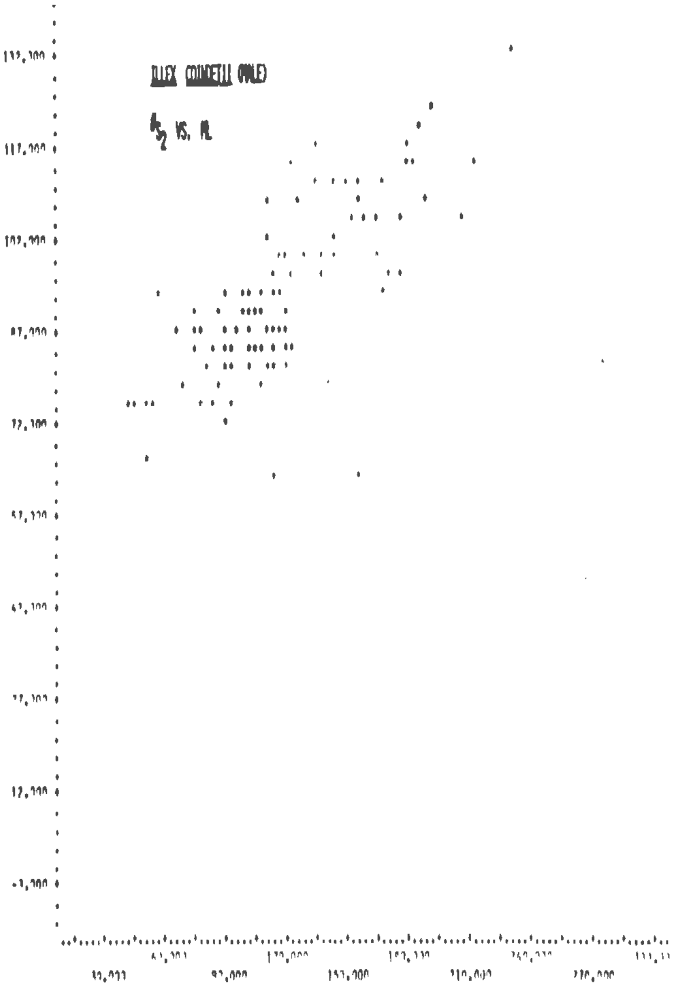

ILLEX ILLECEBROSUS (FEMALE)
VS. ML
126.000
111.000
96.000
81.000
66.000
51.000
36.000
21.000
6.000
-9.000
60.000
90.000
120.000
150.000
180.000
210.000
240.000
270.000
300.000
330.000

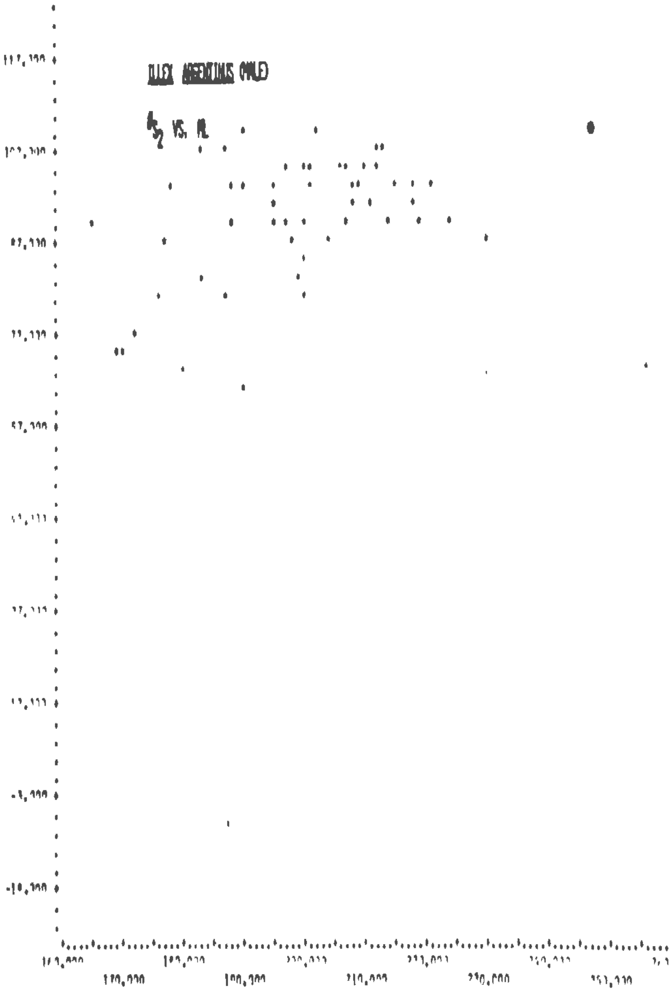

ILLEX COINDETII (FEMALE)
VS. ML
132.000
117.000
102.000
87.000
72.000
57.000
42.000
27.000
12.000
-3.000
40.000
80.000
120.000
160.000
200.000
240.000
280.000
320.000
360.000

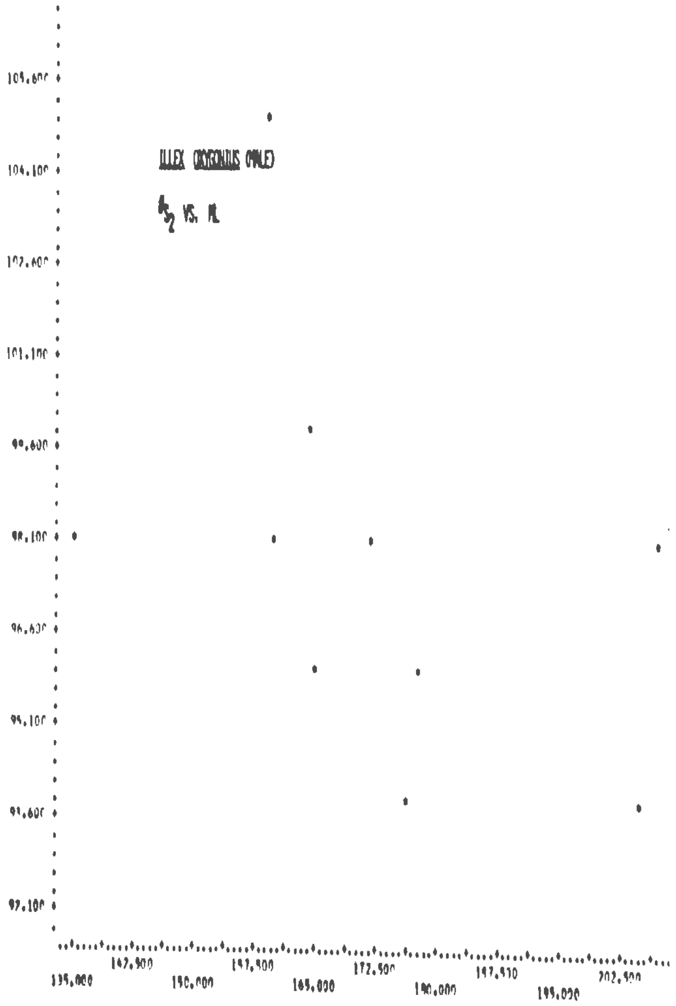

ILLEX ARGENTINUS (FEMALE)
VS. ML

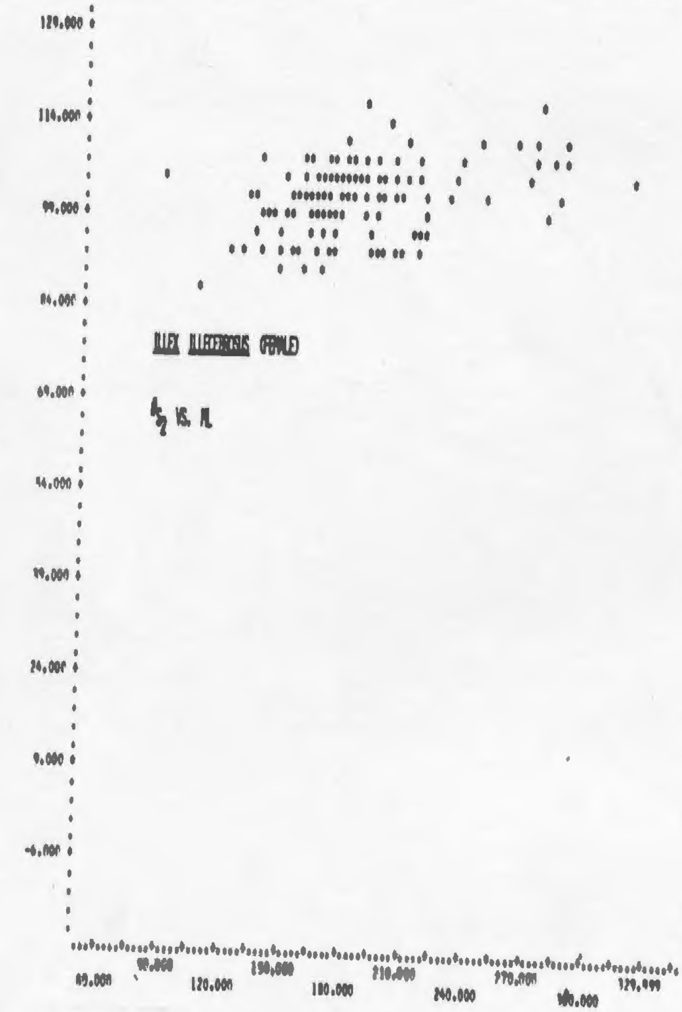

ILLEX OXYGONIUS (FEMALE)
VS. ML
112.500
108.750
105.000
101.250
97.500
93.750
90.000
86.250
82.500
78.750
120.000
130.000
140.000
150.000
160.000
170.000
180.000
190.000
200.000
210.000

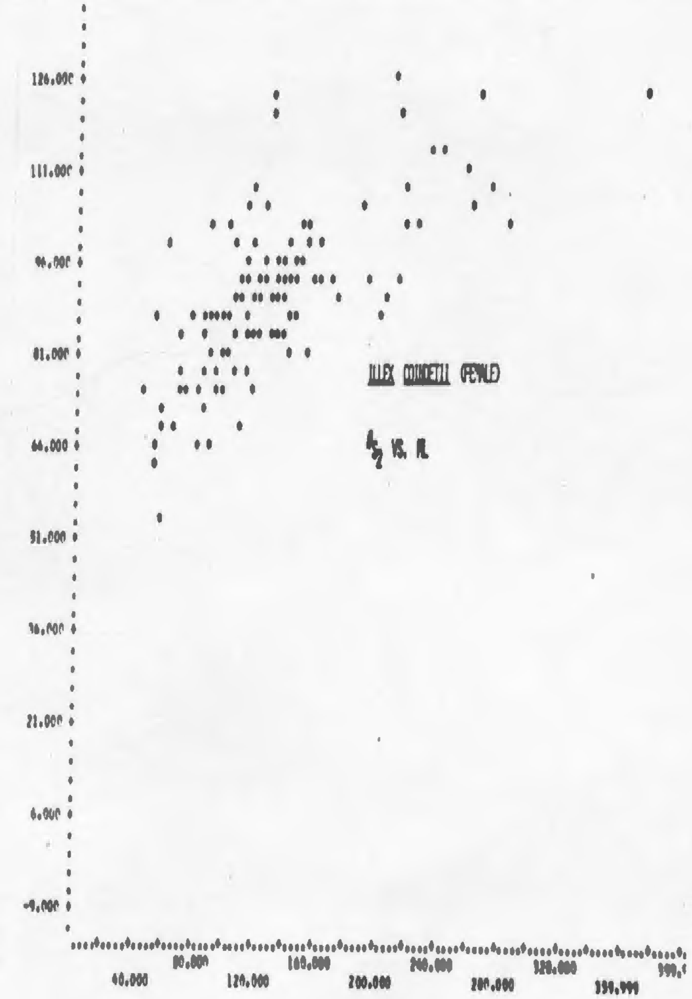

ILLEX ILLECEBROSUS (MALE)
B_2 VS. ML
120.000
115.000
110.000
105.000
100.000
95.000
90.000
85.000
80.000
75.000
70.000
80.000
100.000
120.000
140.000
160.000
180.000
200.000
220.000
240.000
260.0

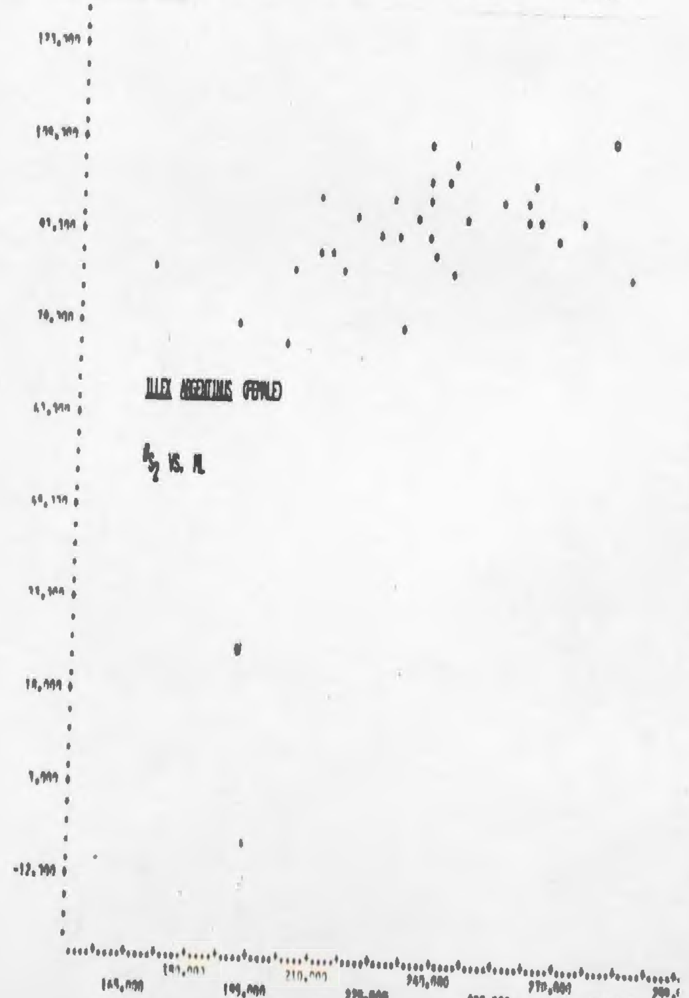

ILLEX COINDETII (MALE)
B_2 VS. ML

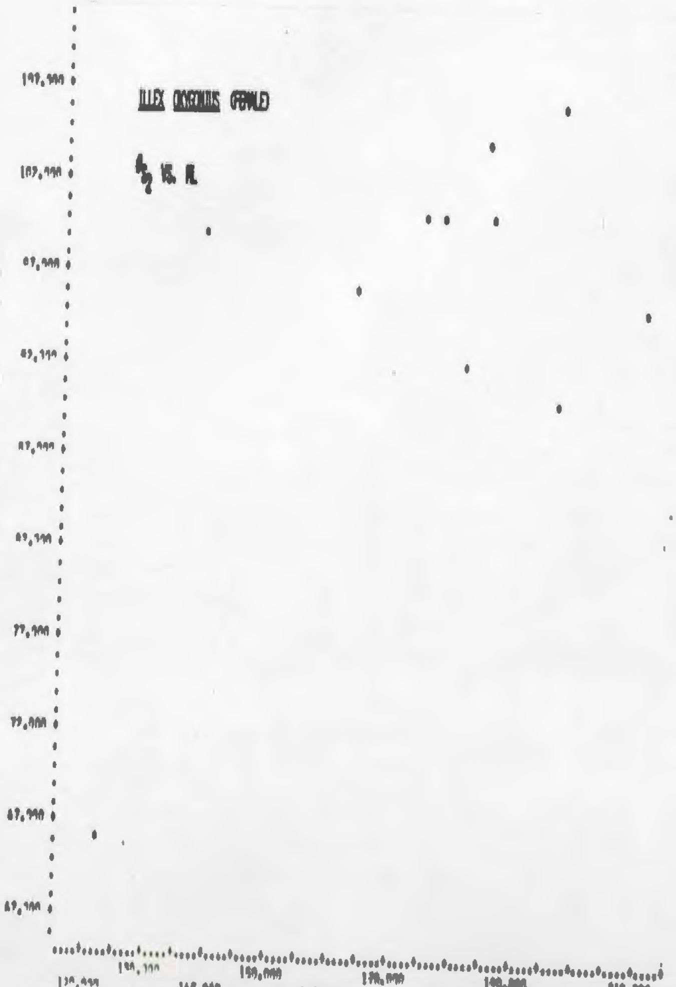

ILLEX ARGENTINUS (MALE)
B_2 VS. ML

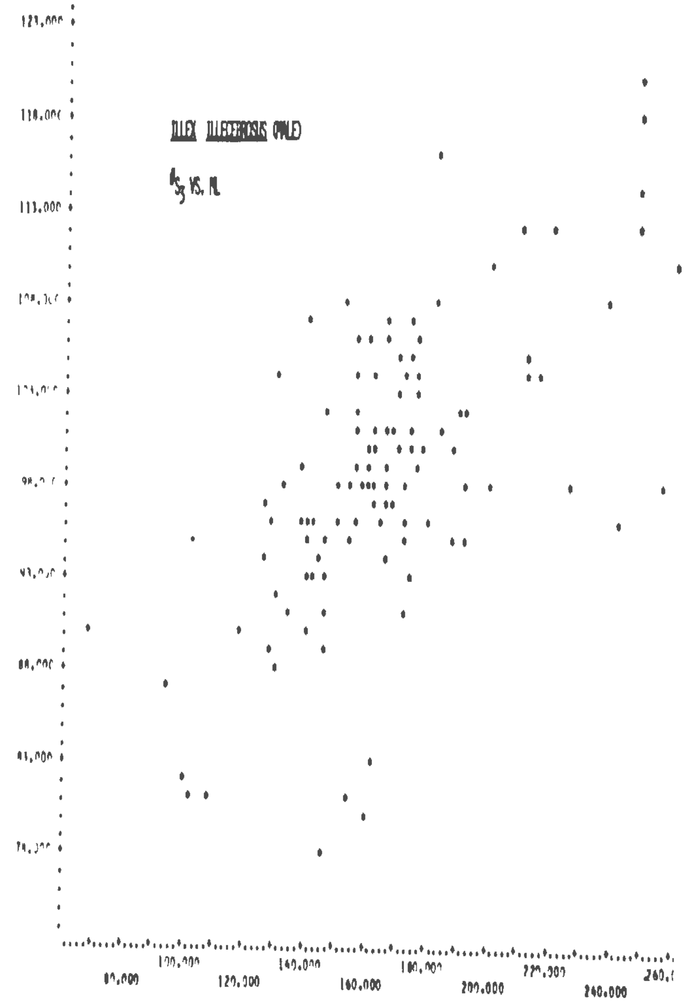

ILLEX OXYGONIUS (MALE)
B_2 VS. ML
105.600
104.100
102.600
101.100
99.600
98.100
96.600
95.100
93.600
92.100
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500

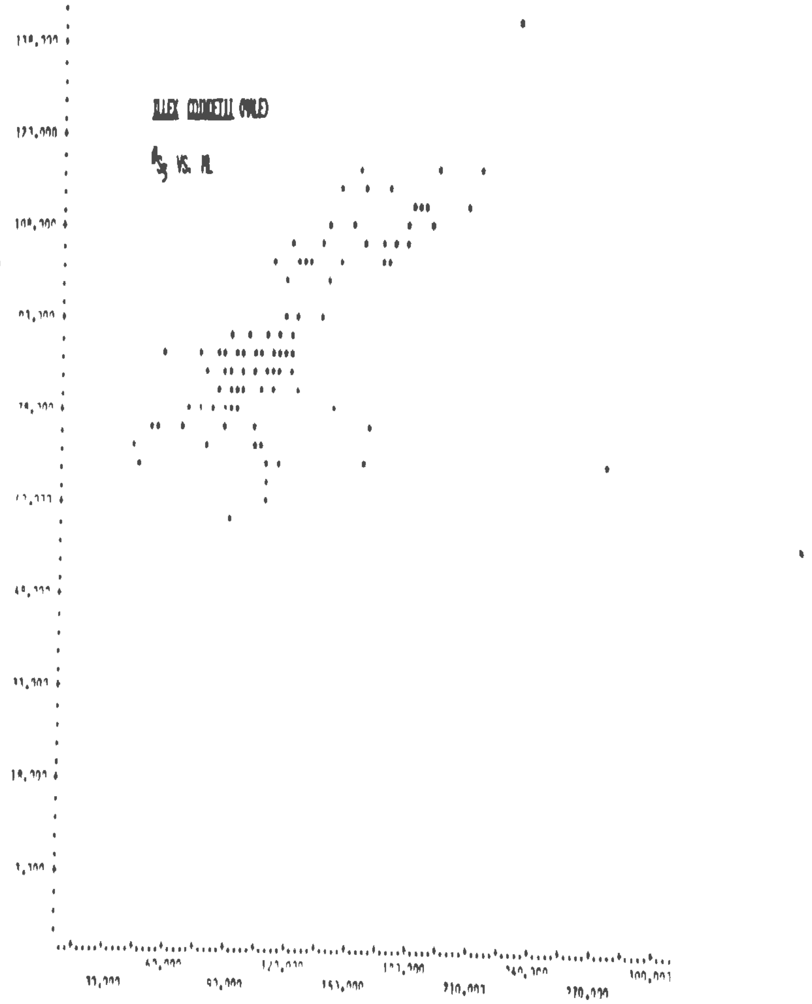

ILLEX ILLECEBROSUS (FEMALE)
A_2 VS. ML
129.000
114.000
99.000
84.000
69.000
54.000
39.000
24.000
9.000
-6.000
60.000
90.000
120.000
150.000
180.000
210.000
240.000
270.000
300.000
329.999

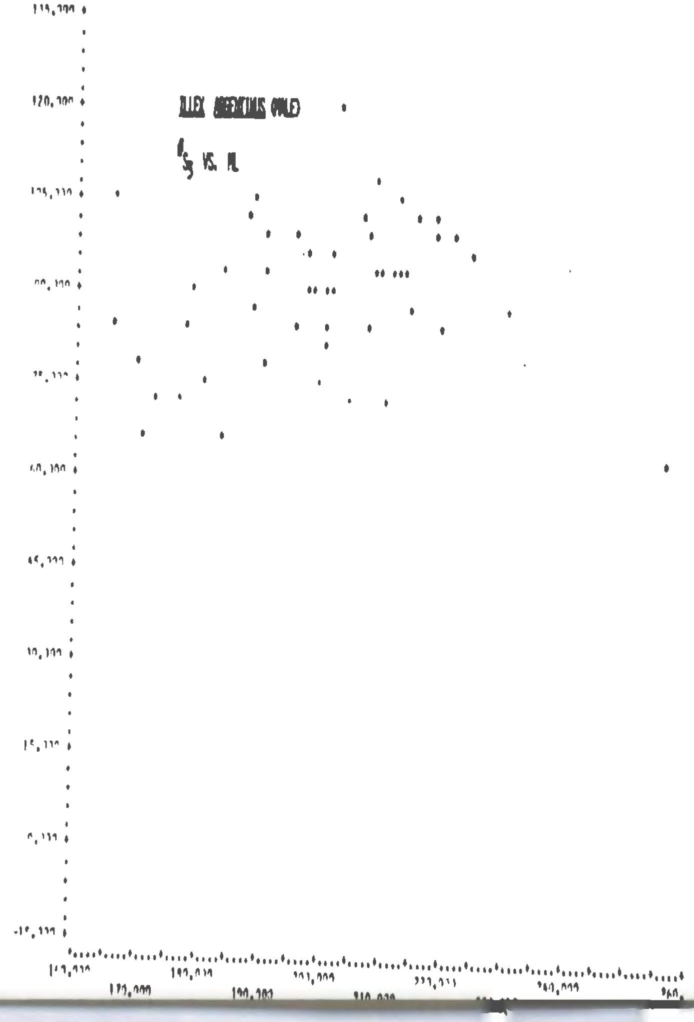

ILLEX COINDETII (FEMALE)
A_2 VS. ML
126.000
111.000
96.000
81.000
66.000
51.000
36.000
21.000
6.000
-9.000
40.000
80.000
120.000
160.000
200.000
240.000
280.000
320.000
359.999

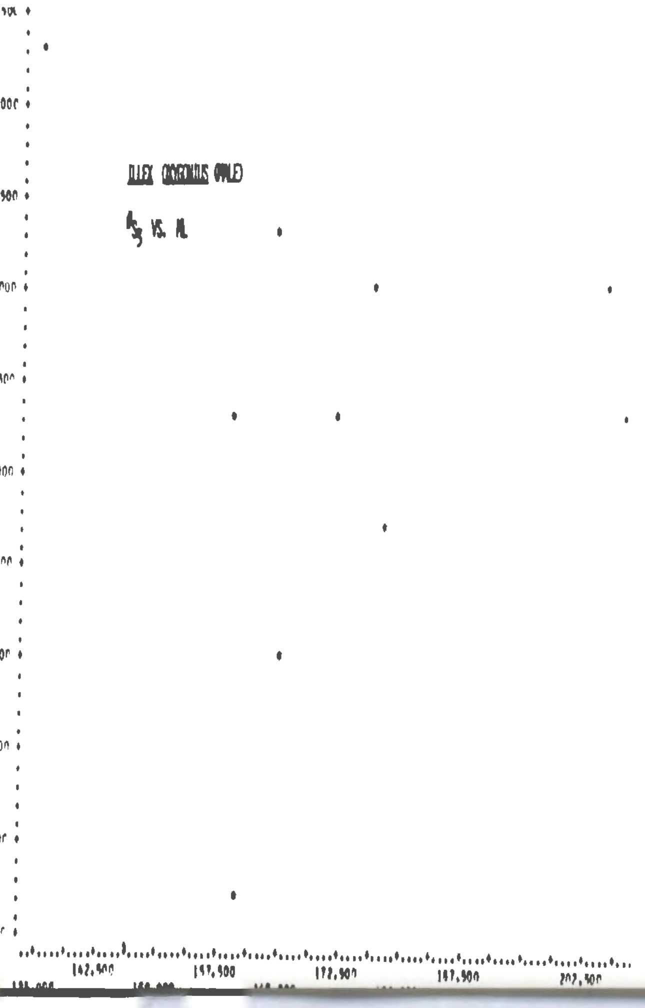

ILLEX ARGENTINUS (FEMALE)
A_2 VS. ML
165.000
225.000
240.000
255.000
270.000
285.000

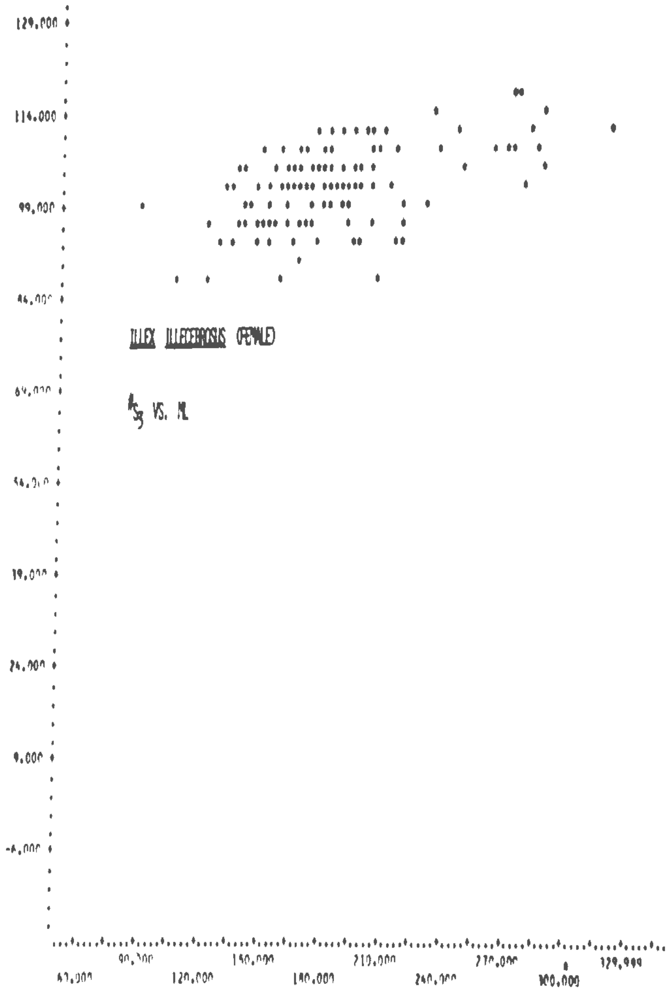

ILLEX OXYGONIUS (FEMALE)
A_2 VS. ML
150.000
160.000
170.000
190.000
210.000

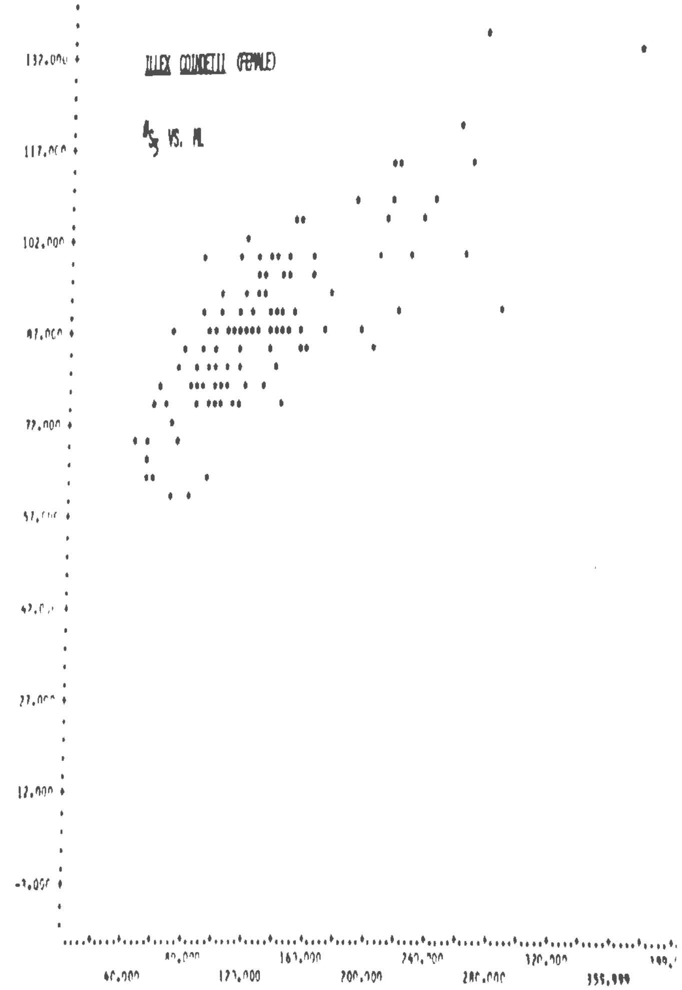

ILLEX ILLECEBROSUS (MALE)
A_{S3} VS. ML
118,000
113,000
88,000
83,000
80,000
100,000
120,000
140,000
160,000
180,000
200,000
220,000
240,000

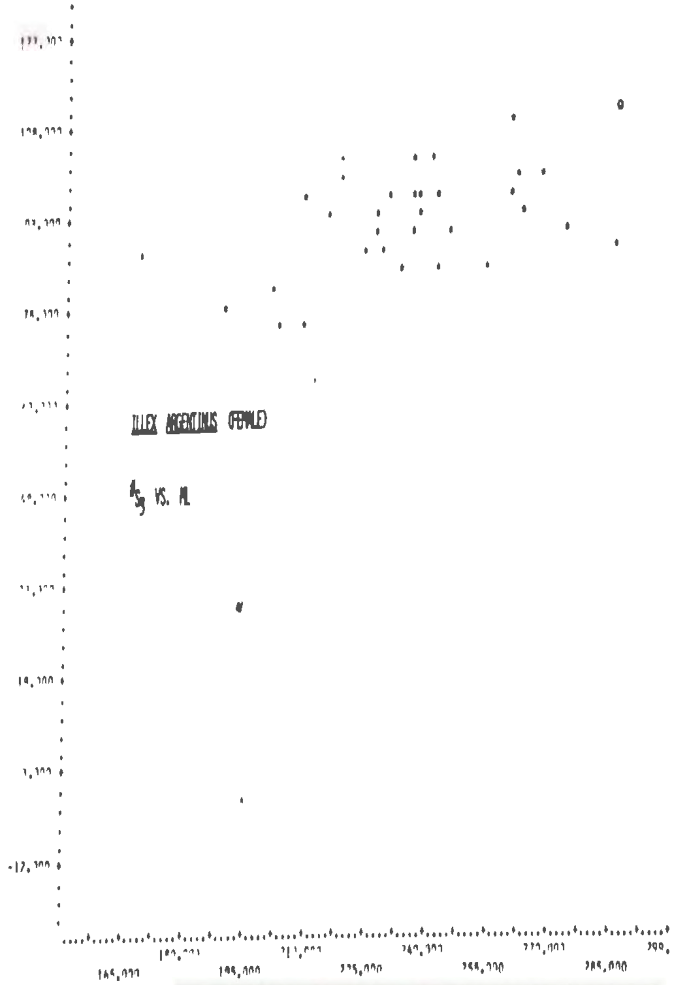

ILLEX COINDETII (MALE)
A_{S3} VS. ML
123,000
108,000
93,000
78,000
48,000
33,000
18,000
3,000

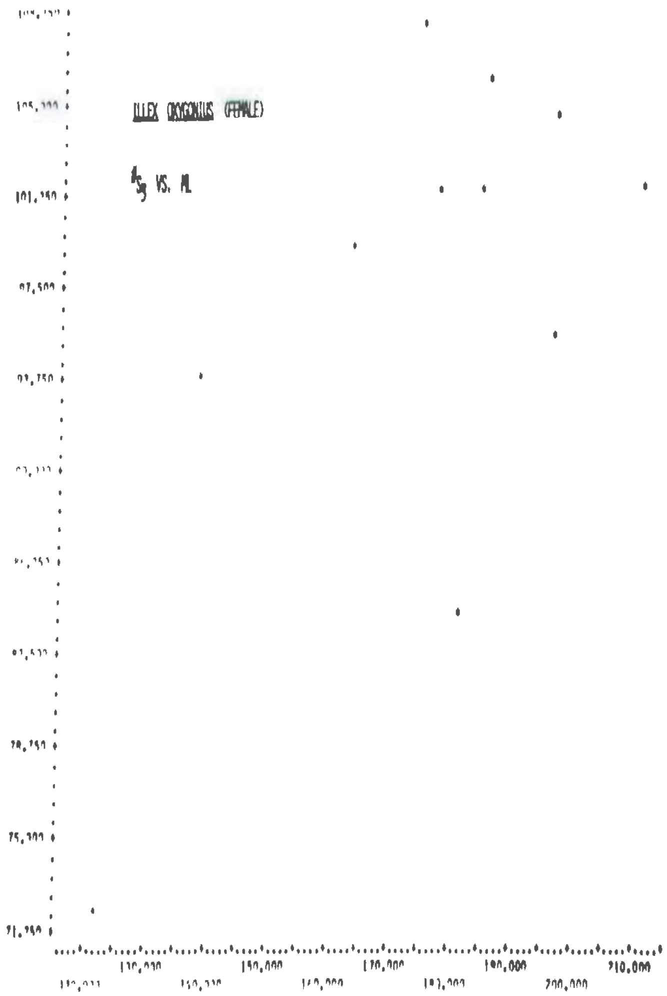

ILLEX ARGENTINUS (MALE)
A_{S3} VS. ML
120,000

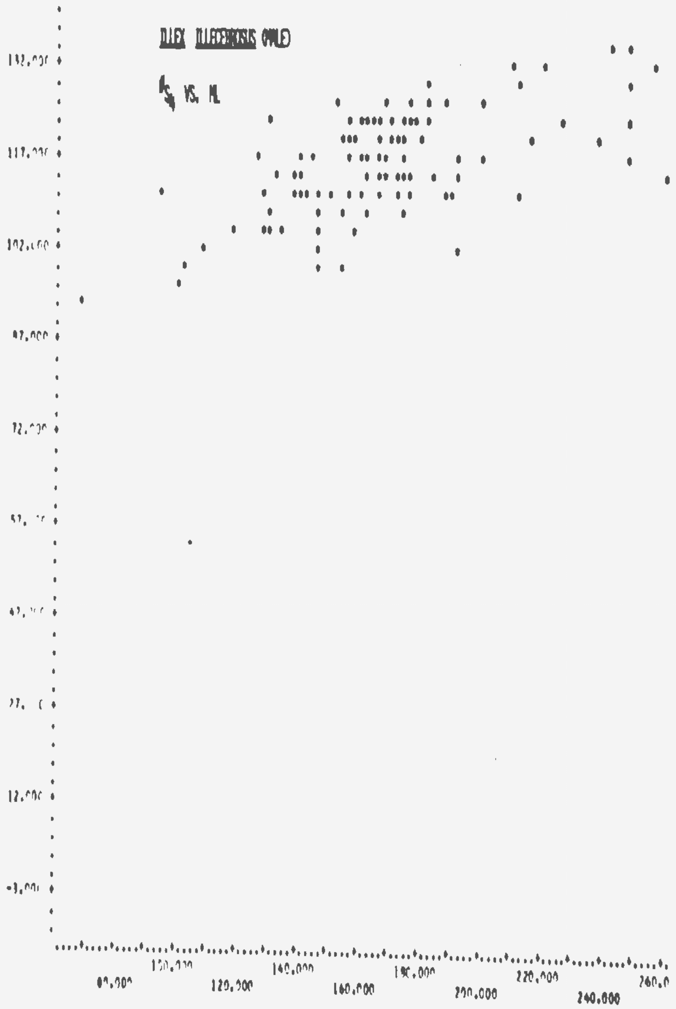

ILLEX OXYGONIUS (MALE)
A_{S3} VS. ML
105,000
103,500
102,000
100,500
99,000
97,500
96,000
94,500
93,000
91,500
142,500
157,500
172,500
187,500
202,500

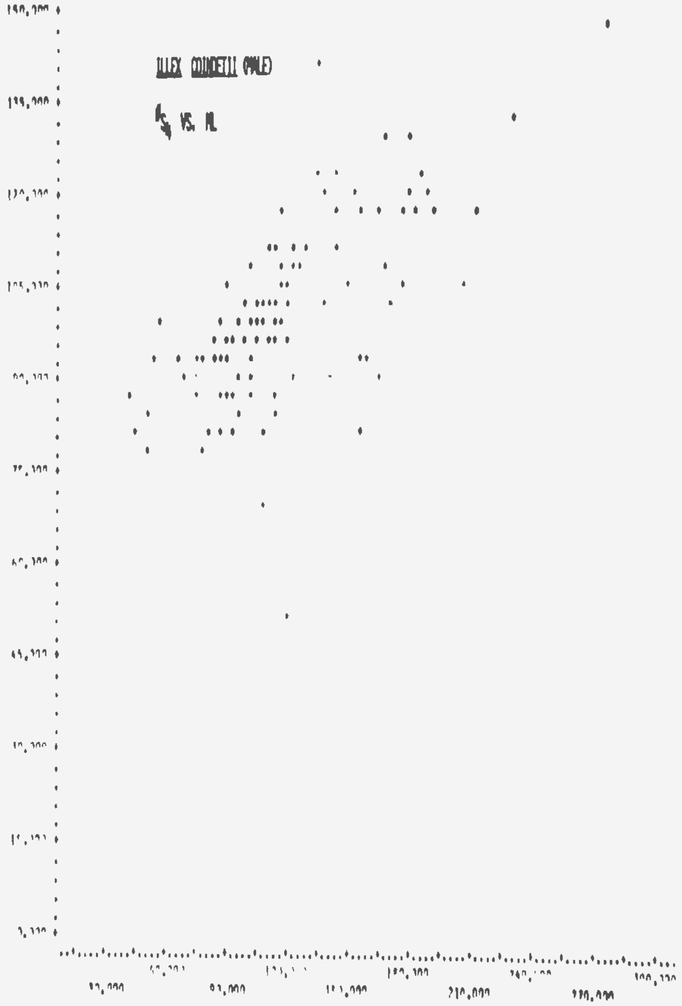

ILLEX ILLECEBROSUS (FEMALE)
AS3 VS. ML
129.000
114.000
99.000
84.000
69.000
54.000
39.000
24.000
9.000
-6.000
60.000
90.000
120.000
150.000
180.000
210.000
240.000
270.000
300.000
329.999

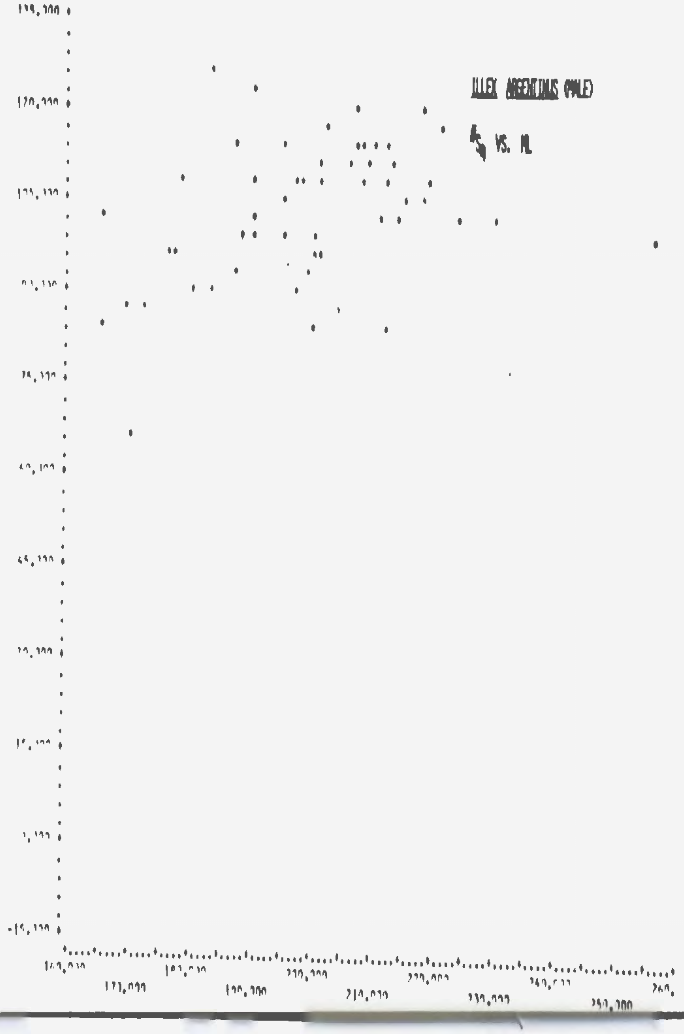

ILLEX COINDETII (FEMALE)
AS3 VS. ML
132.000
117.000
102.000
87.000
72.000
57.000
42.000
27.000
12.000
-3.000
40.000
80.000
120.000
160.000
200.000
240.000
280.000
320.000
355.999

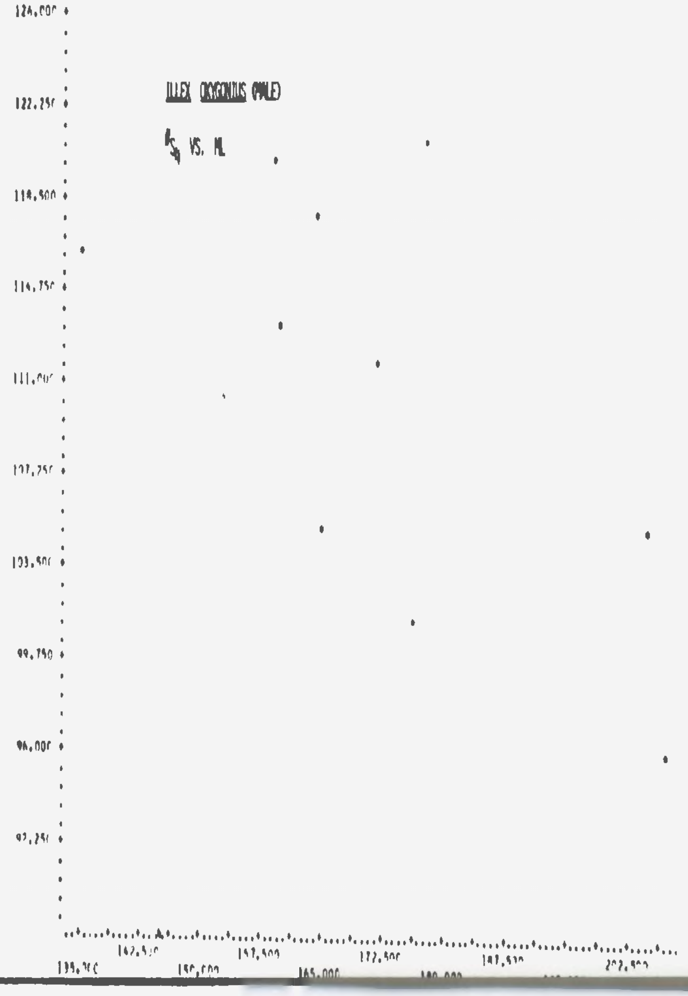

ILLEX ARGENTINUS (FEMALE)
AS3 VS. ML
18.300
3.300
-12.300
165.000
195.000
225.000
240.000
255.000
270.000
285.000
300.

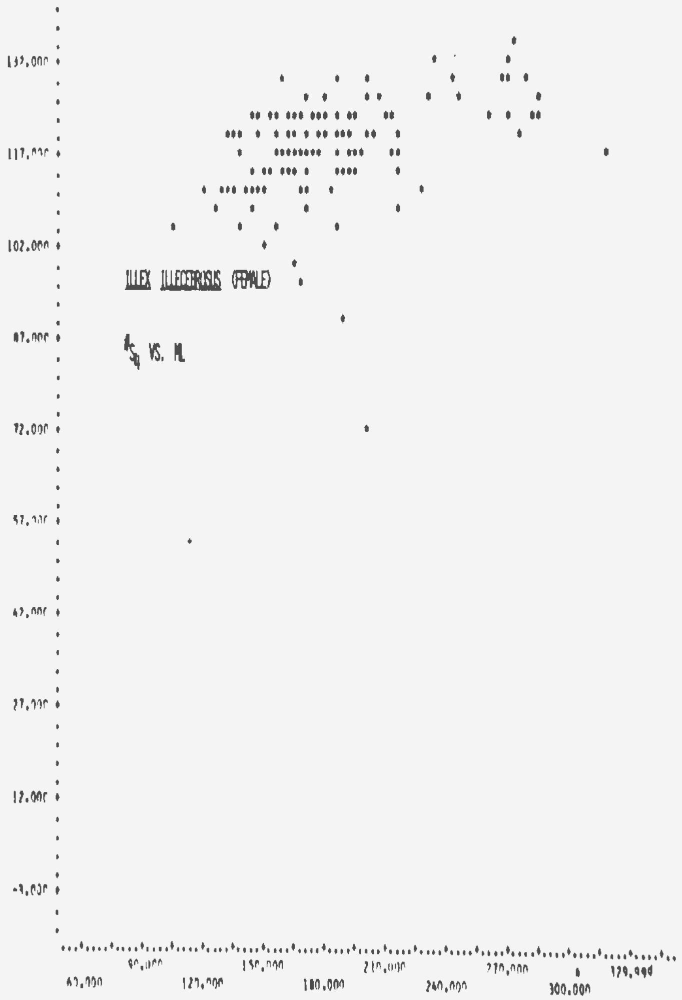

ILLEX OXYGONIUS (FEMALE)
AS3 VS. ML
105.000
101.250
97.500
93.750
78.750
75.000
71.250
130.000
150.000
170.000
180.000
190.000
200.000
210.000

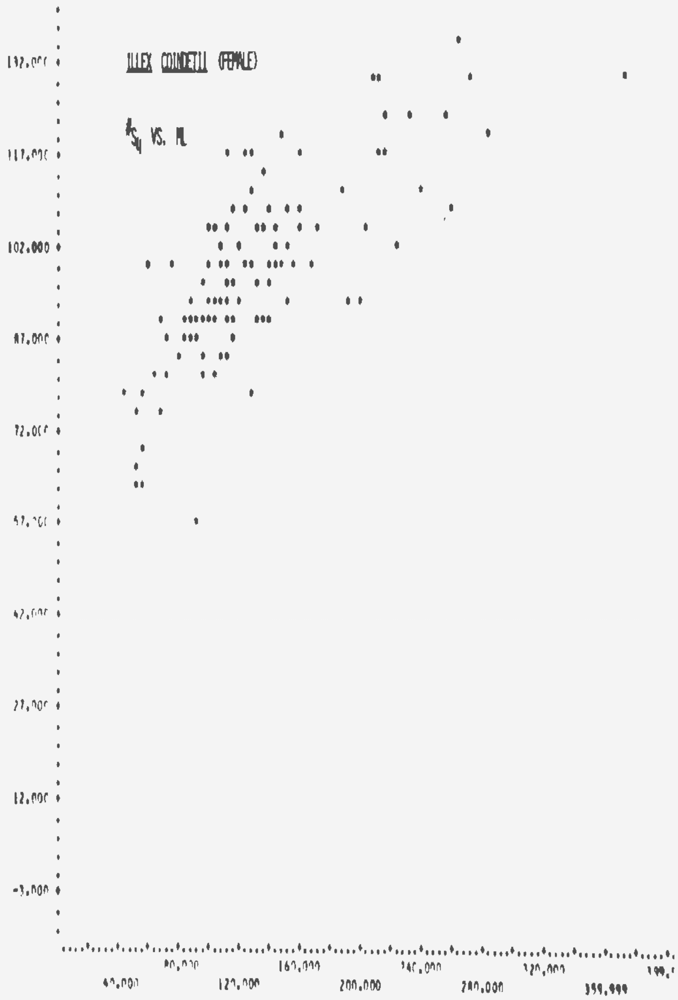

ILLEX ILLECEBROSUS (MALE)
HS VS. ML
132.000
117.000
102.000
87.000
72.000
57.000
42.000
27.000
12.000
-3.000
80.000
100.000
120.000
140.000
160.000
180.000
200.000
220.000
240.000
260.0

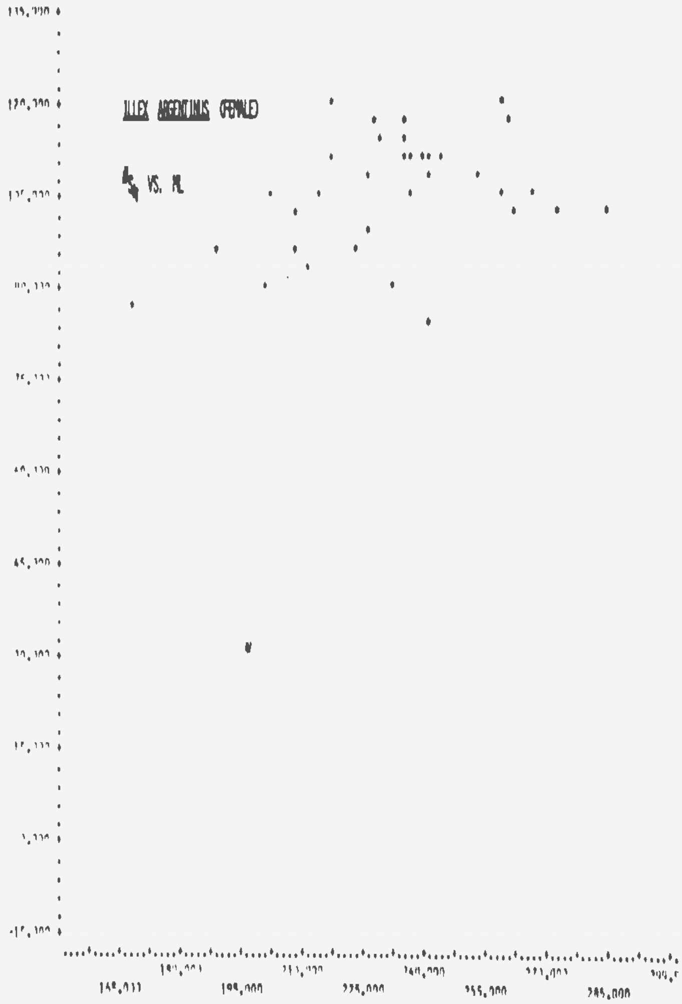

ILLEX COINDETII (MALE)
HS VS. ML
150.000
135.000
120.000
105.000
90.000
75.000
60.000
45.000
30.000
15.000
0.000
30.000
90.000
150.000
210.000
270.000
300.000

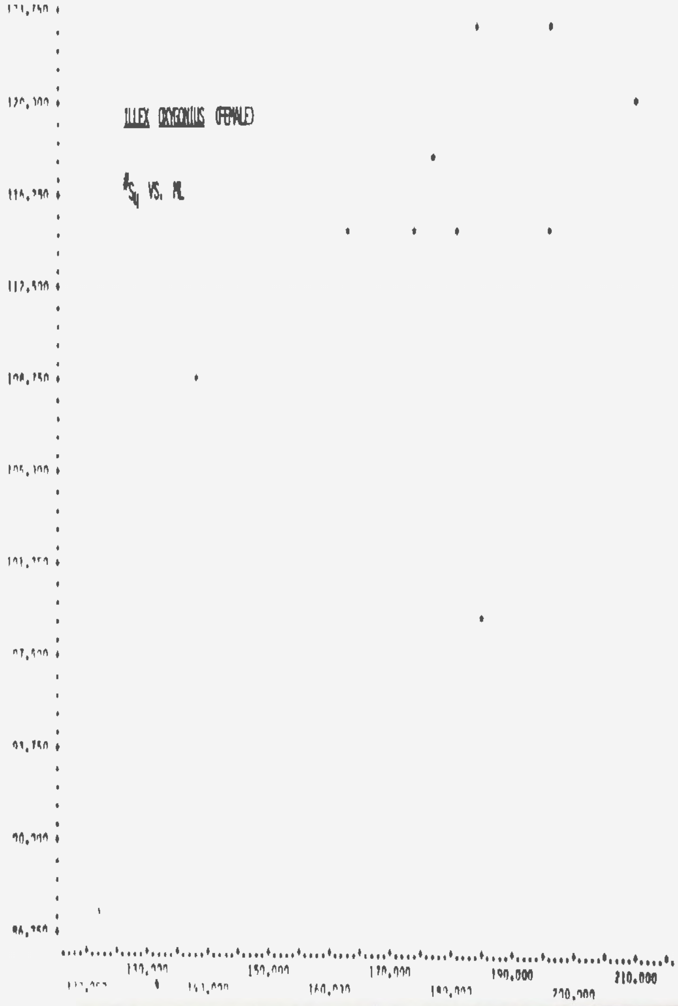

ILLEX ARGENTINUS (MALE)
HS VS. ML
135.000
120.000
105.000
90.000
75.000
60.000
45.000
30.000
15.000
0.000
-15.000
160.000
170.000
180.000
190.000
200.000
210.000
220.000
230.000
240.000
250.000
260.

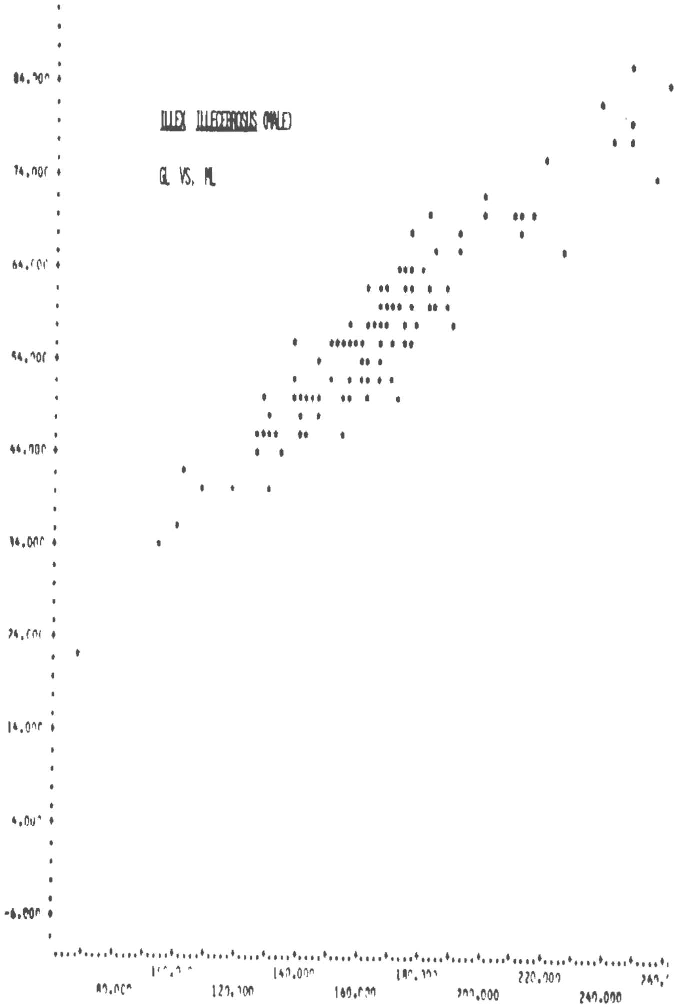

ILLEX OXYGONIUS (MALE)
HS VS. ML
126.000
122.250
118.500
114.750
111.000
107.250
103.500
99.750
96.000
92.250
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
202.500

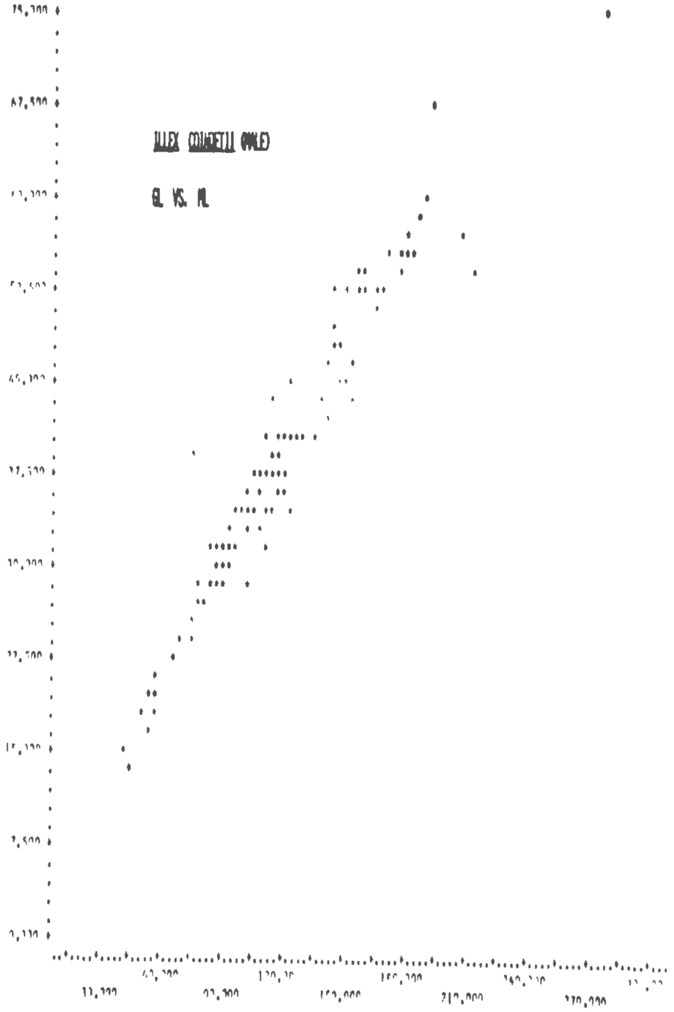

ILLEX ILLECEBROSUS (FEMALE)
#S4 VS. ML
132.000
117.000
102.000
87.000
72.000
57.000
42.000
27.000
12.000
-3.000
60.000
90.000
120.000
150.000
180.000
210.000
240.000
270.000
300.000
329.999

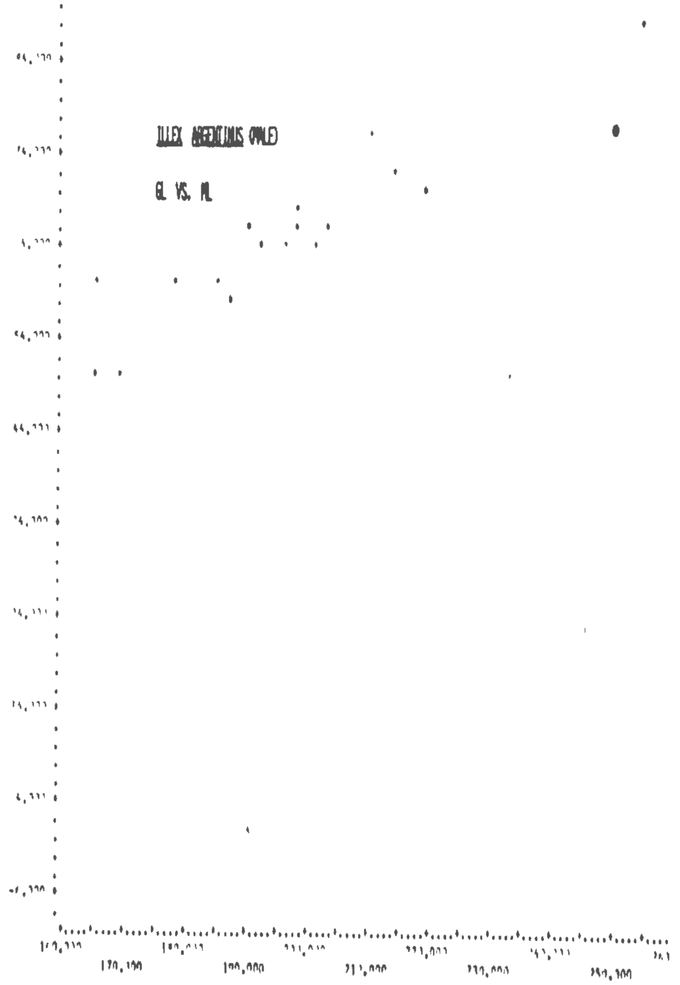

ILLEX COINDETII (FEMALE)
#S4 VS. ML
132.000
117.000
102.000
87.000
72.000
57.000
42.000
27.000
12.000
-3.000
40.000
80.000
120.000
160.000
200.000
240.000
280.000
320.000
359.999
400.000

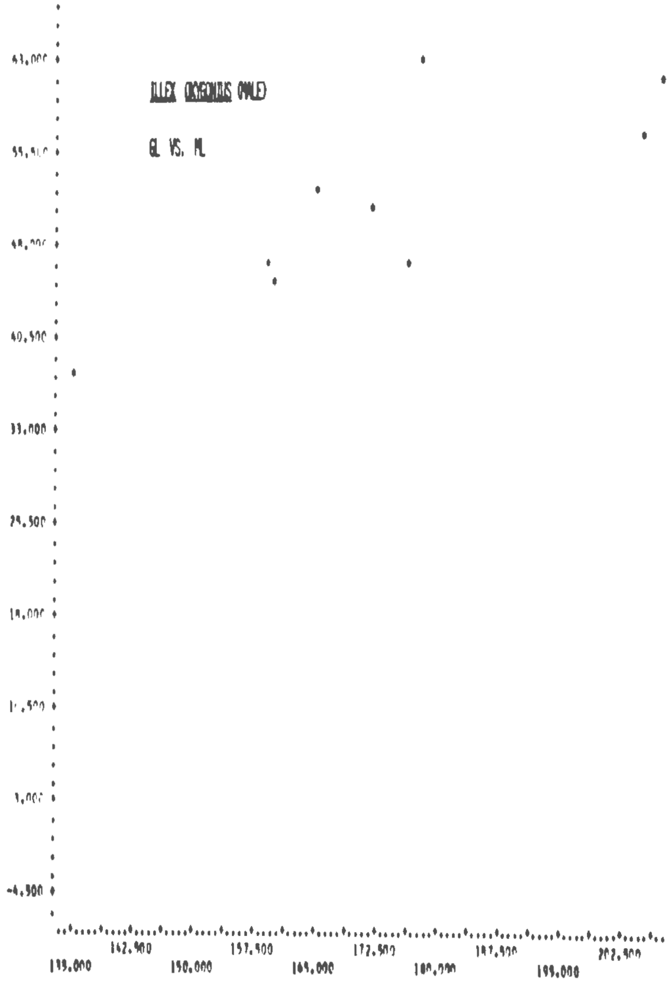

ILLEX ARGENTINUS (FEMALE)
#S4 VS. ML
120.000
105.000
90.000
75.000
60.000
45.000
30.000
15.000
0.000
-15.000
168.000
184.000
199.000
213.000
228.000
240.000
255.000
270.000
285.000
300.000

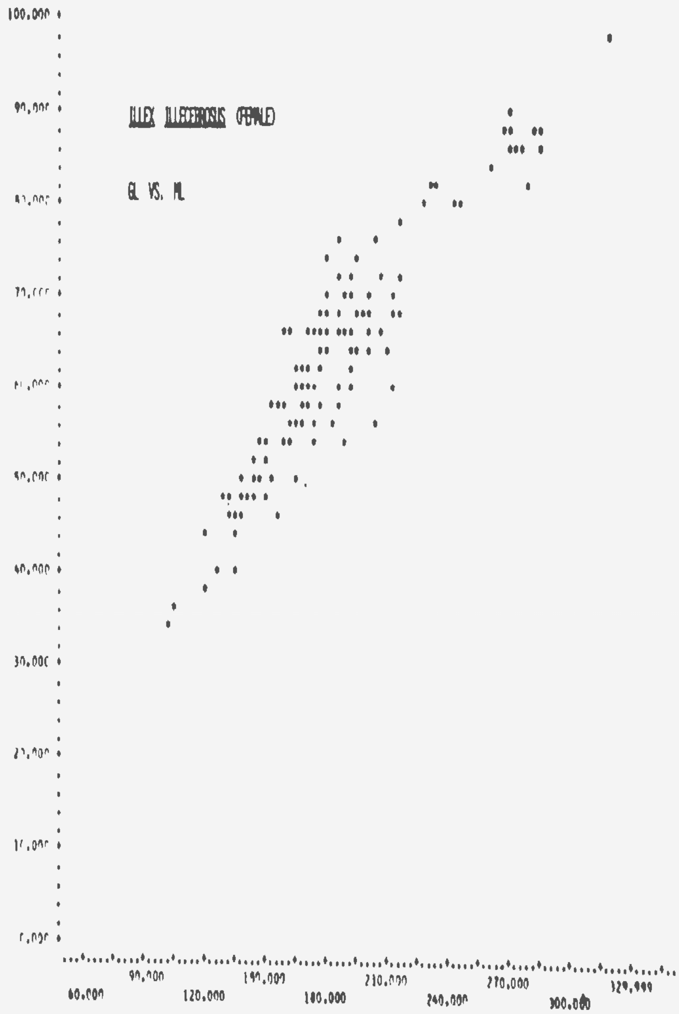

ILLEX OXYGONIUS (FEMALE)
#S4 VS. ML
121.250
120.000
116.250
112.500
108.750
105.000
101.250
97.500
93.750
90.000
86.250
130.000
140.000
150.000
160.000
170.000
180.000
190.000
200.000
210.000

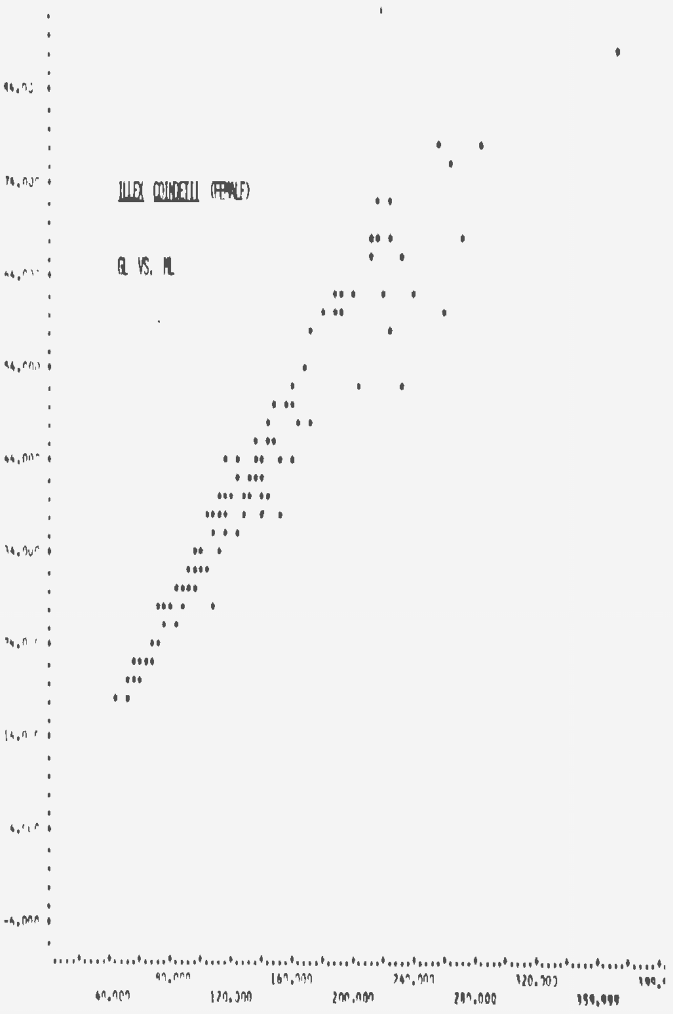

ILLEX ILLECEBROSUS (MALE)
GL VS. ML
84.000
74.000
64.000
54.000
44.000
34.000
24.000
14.000
4.000
-6.000
80.000
120.000
140.000
160.000
180.000
200.000
220.000
240.000

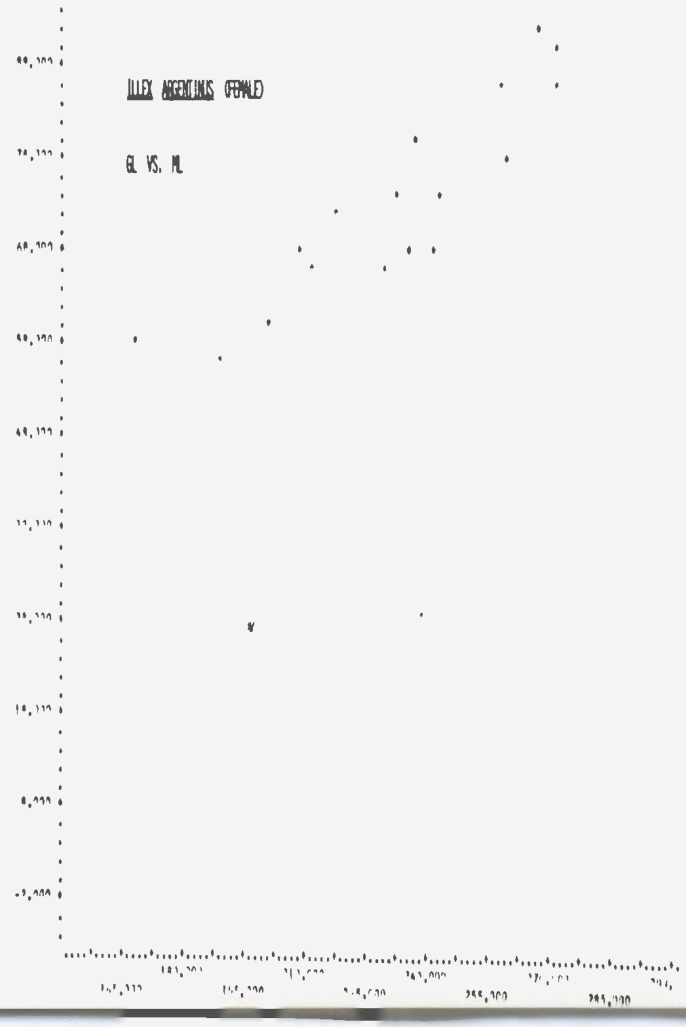

ILLEX COINDETII (MALE)
GL VS. ML
75.000
67.500
52.500
45.000
37.500
30.000
22.500
15.000
7.500
0.000
210.000

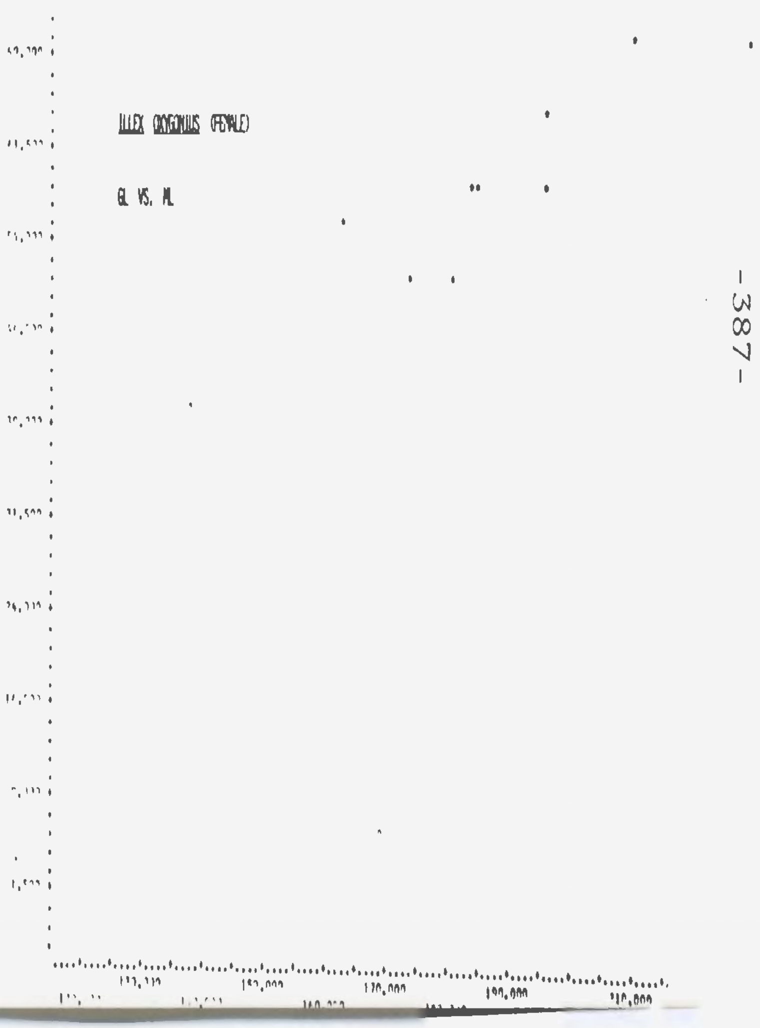

ILLEX ARGENTINUS (MALE)
GL VS. ML
190.000

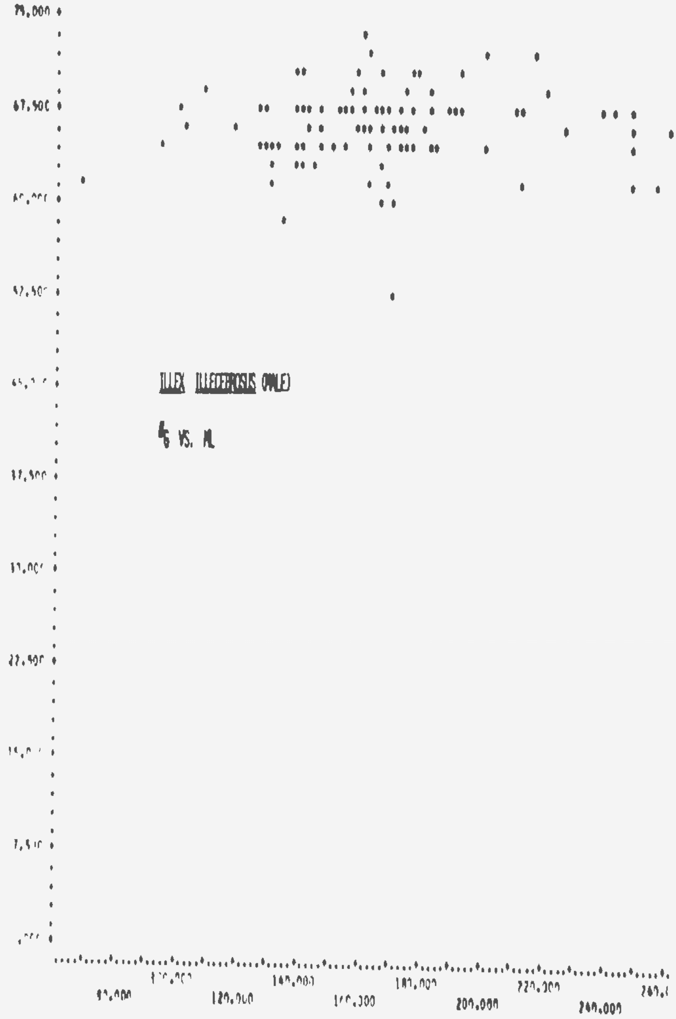

ILLEX OXYGONIUS (MALE)
GL VS. ML
63.000
55.500
48.000
40.500
33.000
25.500
18.000
10.500
3.000
-4.500
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500

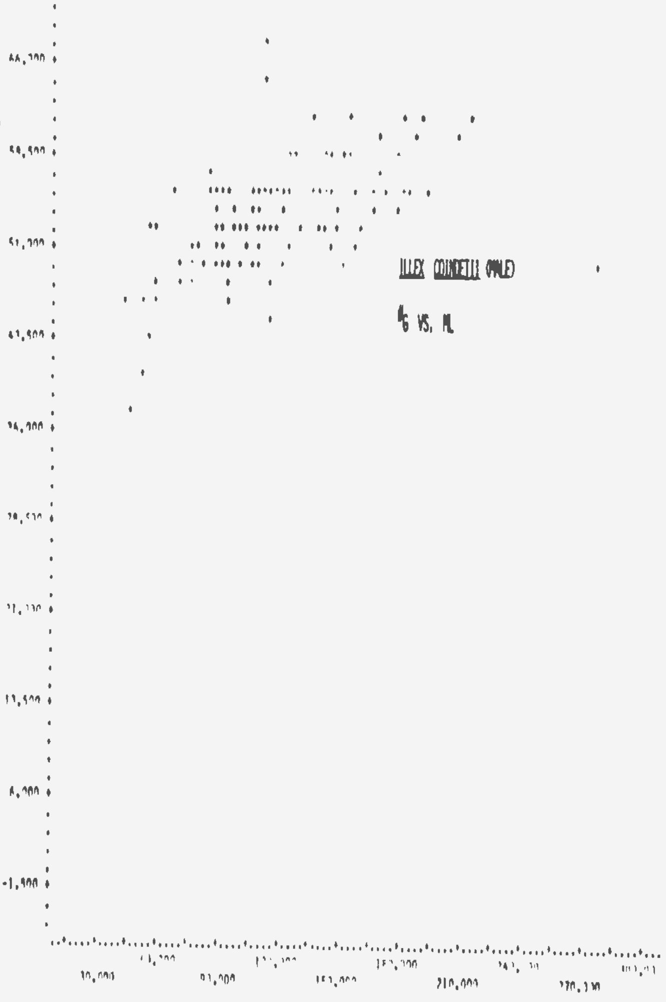

ILLEX ILLECEBROSUS (FEMALE)
GL VS. ML
100.000
90.000
70.000
50.000
40.000
30.000
90.000
60.000
120.000
180.000
210.000
240.000
270.000
300.000

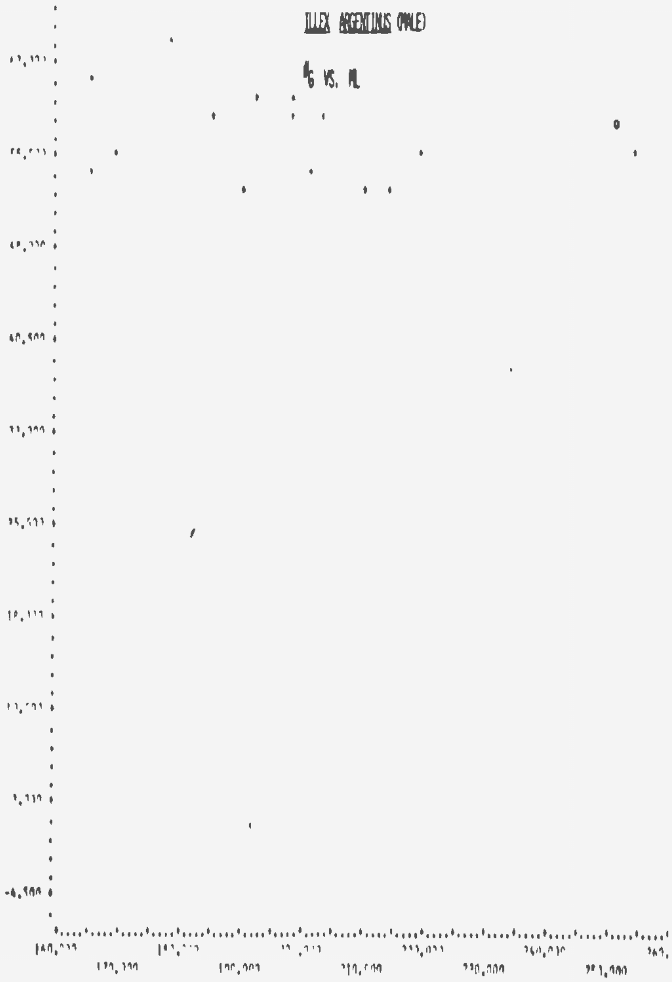

ILLEX COINDETII (FEMALE)
GL VS. ML
44.000
-6.000
60.000
120.000
160.000
200.000
240.000
280.000
320.000


ILLEX ARGENTINUS (FEMALE)
GL VS. ML
255.000

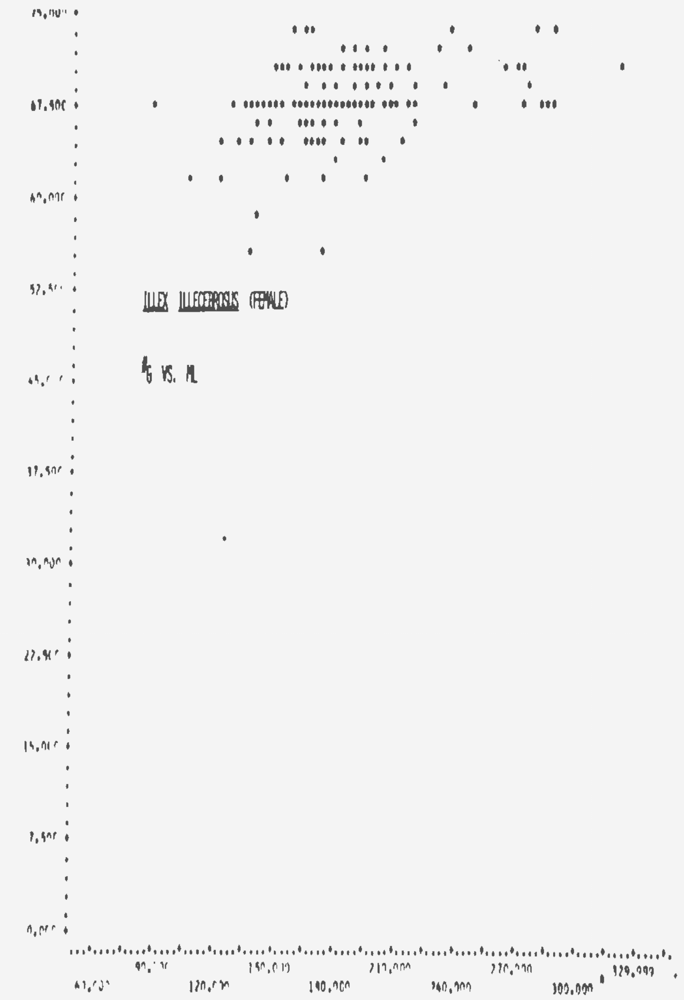

ILLEX OXYGONIUS (FEMALE)
GL VS. ML
170.000
190.000
210.000


ILLEX ILLECEBROSUS (MALE)
%G VS. ML
75.000
67.500
52.500
7.500
.000
80.000
120.000
140.000
160.000
180.000
200.000
220.000
240.000

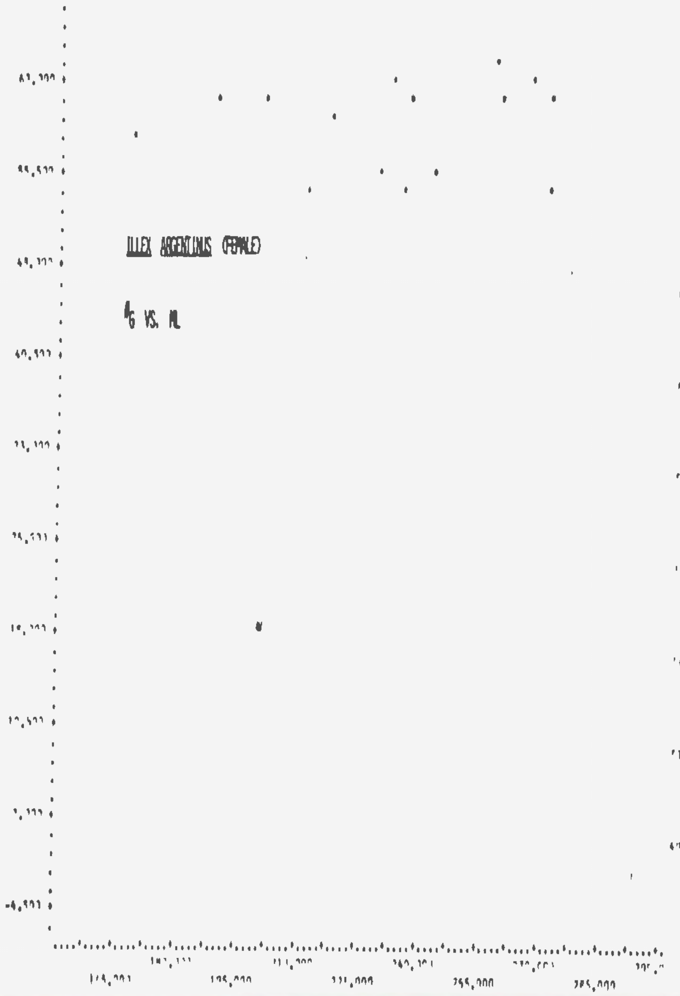

ILLEX COINDETII (MALE)
%G VS. ML
66.000
58.500
51.000
43.500
36.000
13.500
6.000
-1.500
30.000
90.000
210.000

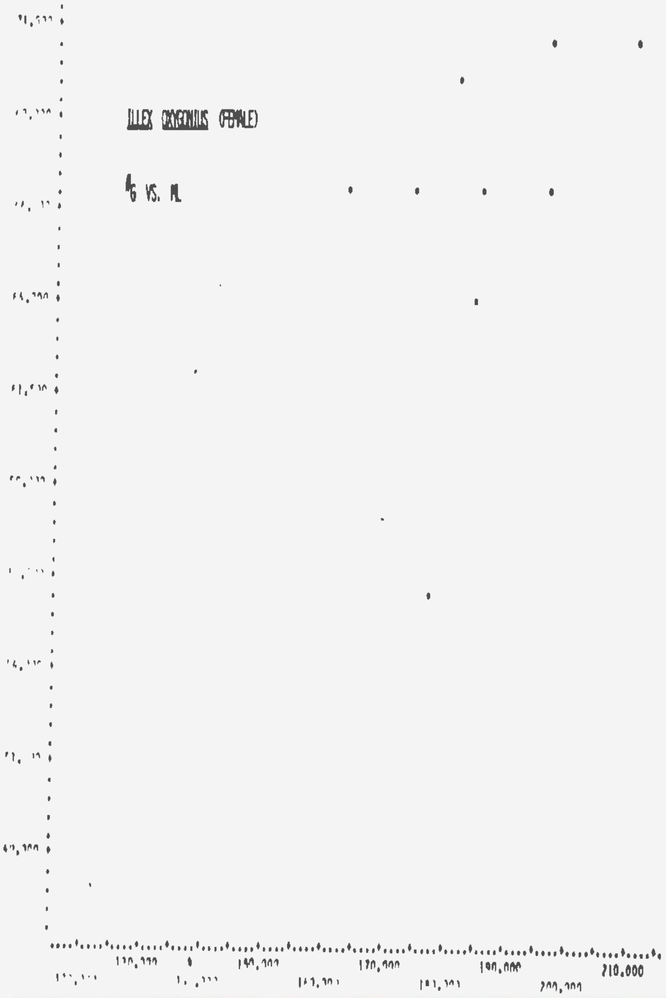

ILLEX ARGENTINUS (MALE)
%G VS. ML
-6.500
230.000
281.000


ILLEX OXYGONIUS (MALE)
%G VS. ML
75.000
67.500
60.000
52.500
45.000
37.500
30.000
22.500
15.000
7.500
0.000
135.000
142.500
150.000
157.500
165.000
172.500
180.000
187.500
195.000
202.500


ILLEX ILLECEBROSUS (FEMALE)
%G VS. ML
67,500
60,000
52,500
37,500
30,000
22,500
15,000
7,500
0,000
120,000
180,000
210,000
240,000
270,000
300,000
329,999


ILLEX COINDETII (FEMALE)
%G VS. ML
61,500
54,000
46,500
31,500
16,500
9,000
1,500
120,000
200,000
280,000
320,000
359,999


ILLEX ARGENTINUS (FEMALE)
%G VS. ML
195,000
225,000
285,000


ILLEX OXYGONIUS (FEMALE)
%G VS. ML
190,000
210,000
200,000