Chapter 2

Systematic and distributional relationships of *Illex coindetii* to the genus *Illex* (Cephalopoda: Ommastrephidae)

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Abstract: The systematic status of *Illex coindetii* is analysed based on a study of specimens from across the known geographic range of the species. On the basis of several morphological characters, some newly recognized, particularly on the hectocotylized arm, *I. coindetii* is shown to be a single, variable, widely distributed species, morphotypes of which occur throughout the Mediterranean Sea, the eastern Atlantic from Great Britain to Namibia and the western Atlantic from the southeastern Caribbean Sea, the Gulf of Mexico and the Straits of Florida. *I. coindetii* is distinct from the other species of *Illex* that occur in the western Atlantic. Species characters are compared and a diagnostic key to the four species of *Illex* is presented.

1   Introduction

Illex coindetii (Vérany, 1839) was described originally from the Mediterranean waters off Nice, France. It has been recorded subsequently from the entire Mediterranean Sea, the eastern Atlantic from the Bristol Channel, British Isles, southward to Namibia, and the western Atlantic from the Caribbean Sea, Gulf of Mexico and Straits of Florida (Lu 1973, Roper *et al.* 1984, Nesis 1987). The exceptionally widespread distribution throughout the eastern Atlantic and the Mediterranean, as well as its disjunct occurrence on opposite sides of the Atlantic, is an unusual distribution for a neritic cephalopod. This factor, coupled with the remarkable morphological variation observed throughout its range, has created considerable doubt as to the conspecific taxonomic status of the far-flung morphotypes. Does this pattern represent one widely distributed, highly variable species, or is it in fact a complex of closely related, yet distinct, species? The answers to these questions have broad significance biologically, e.g. recruitment, and, particularly, in relation to management and exploitation of the populations as a fishery resource.

The systematics of the genus *Illex* is currently being examined, primarily because of the confusing situation of the occurrence of three of the four described species in the waters of the western Atlantic, particularly in the Gulf of Mexico and from the Straits of Florida to the mid-Atlantic Bight (Zecchini *et al.* 1996, Roper *et al.* 1998). These species are *Illex illecebrosus* (Lesueur, 1821), *I. coindetii* (Vérany, 1839) and *Illex oxygonius* Roper, Lu and Mangold, 1969. Because all three species appear to co-occur in the common extremes of their ranges and because they also are morphologically similar, they are difficult to distinguish and identify (Roper *et al.* 1969). Furthermore, their biology is so poorly known in this geographical region that currently no biological clues exist to aid in discriminating these species. The fourth species, *Illex argentinus* (Castellanos, 1960), from the southwestern Atlantic, is sufficiently isolated geographically and morphologically to be quite distinct and easily identified.

The objective of this study is to determine the systematic status of *I. coindetii*. We attempt to define the range of variation in some distinct characters, a few newly discovered, that are especially useful for identifying adults of the species. This has been accomplished by examining specimens from a wide, although not completely comprehensive, sample of populations throughout the geographical range of the species. We

discovered these distinctive characters when we simultaneously compared specimens of *I. coindetii* with the other three species of *Illex*. Comparative information on the other three species is presented in tabular form and a key to the identification of all four species is also given.

2   Material examined

The specimens used in this analysis (listed below) were selected from as broad a coverage of the geographical range as possible, and they represent, as nearly as possible, fully mature animals. A number of specimens from the Mediterranean and off Vigo, Spain, were collected specifically for this study. All material was available for examination at the workshop conducted on *I. coindetii* systematics and fishery biology in Mazara del Vallo, Sicily, in October 1992. The remaining specimens are from the collections of the National Museum of Natural History, Washington, D.C. (USNM) or borrowed from the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami (UMML), Florida.

Mediterranean Sea
Greece - Sep 1992

1 male 159 mm ML   1 female 201 mm ML
Southern Adriatic - off Mola di Bari, Italy, 210 m, sand-mud bottom, 8 Oct 1992

3 males 119-120 mm ML   6 females 103–135 mm ML
Sicily - Strait of Sicily

5 males 131–141 mm ML   1 female 186 mm ML
Tunisia - Gulf of Tunis

2 males 151–154 mm ML   8 females 150–185 mm ML

- Gulf of Tunis, Mediterranean Marine Sorting Center, 64–75 m, 30 Mar 1967, USNM 884245

1 male 130 mm ML   3 females 151–164 mm ML

- Gulf of Tunis, Mediterranean Marine Sorting Center

2 males 130–141 mm ML
Catalonia - Port-Vendres, France, 42°33'30"N 003°39'E, 200–500 m, 03 Nov 1971, USNM 727457

1 male 125 mm ML

- Barcelona, Spain

1 male 130 mm ML   2 females 115–132 mm ML
Eastern Atlantic Ocean
Spain -Vigo

4 males 105–130 mm ML   4 females 160–176 mm ML
Africa - Gulf of Guinea, R/V *Pillsbury* sta. 45, 05°05'N, 04°04.5'W, 73–98 m, 30 May 1964, UMML 31.1611

1 male 121 mm ML   1 female 160 mm ML; off Liberia

- Gulf of Guinea, R/V *Pillsbury* sta. 82, 04°57'N, 09°30'W, 144 m, 5 June 1964, UMML 31.1335

1 male 129 mm ML   1 female 188 mm ML

- off Namibia, R/V *Ocher* sta. 127, 18°56'S, 12°05'E, 130 m, 9 May 1988, USNM 884246

2 males 126–131 mm ML   3 females 97–141 mm ML
Western Atlantic Ocean
Caribbean - off Nicaragua, R/V *Oregon* sta. 3615, 14° 16'N, 81 °55'W, 400 m, 5 June 1962, UMML 31.648

1 male 170 mm ML

- off Nicaragua, R/V *Pillsbury* sta. 1356, 14°54'N, 81°23'W, 296–375 m, 31 Jan 1971, UMML 31.1899

2 males 152–163 mm ML
Gulf of Mexico -off Louisiana, R/V *Oregon* sta. 4607, 27°39'N, 93°46'W, 366 m, 18 Jan 1964, UMML 31.1889

1 male 185 mm ML

-off Mississippi, R/V *Oregon* sta. 481, 28°57'N, 88°41'W, 420 m, 7 Sep. 1951, UMML 31.353
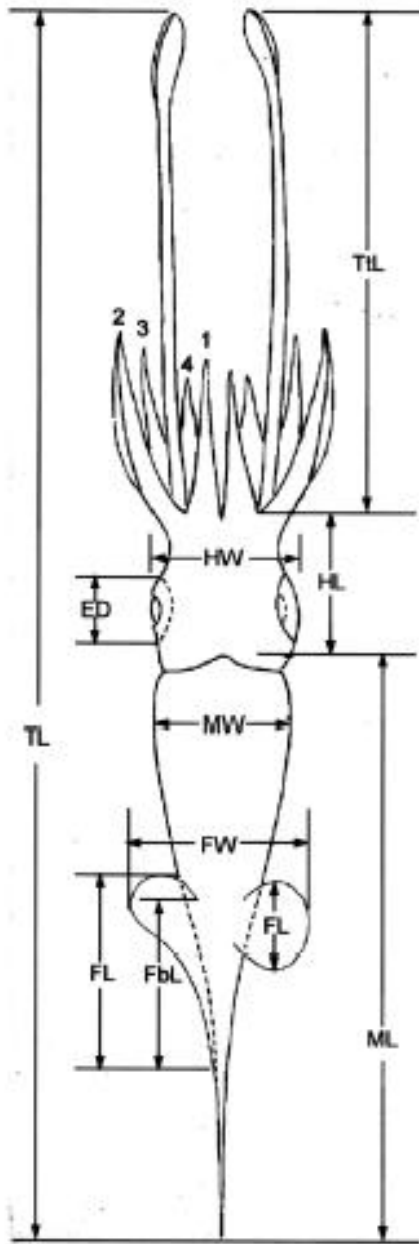
1 male 153 mm ML   1 female 185 mm ML
Straits of Florida, USA -R/V *Oregon* sta. 10862, 23°25'N, 79°40'W, 450 m, 16 Dec. 1969, USNM 729016
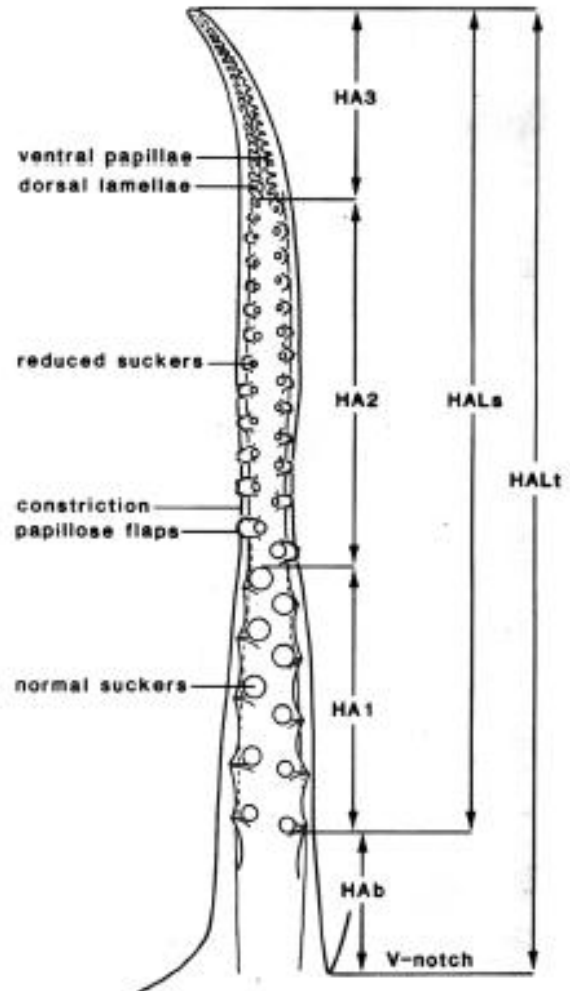
1 female 319 mm ML

-R/V *Oregon* sta. 10863, 23°09'N, 80008'W, 459 m, 16 Dec. 1969, USNM 729015

1 male 252 mm ML

Figure 2.1. Diagrammatic illustration of measurements of squid (adapted from Roper and Voss 1983), definitions given in text

Figure 2.2. Diagrammatic illustration of hectocotylized arm of *I. coindetii*, left arm IV, 125 mm ML; USNM 727457, definitions given in text

3   Expanded diagnosis

This diagnosis is detailed enough to permit the identification of *I. coindetii* using selected key characters, especially those associated with mature males. Figures 2.1–2.3 diagram the standard measurements used in this study and as defined in Roper and Voss (1983). A fuller description of the species, including the designation of a neotype, is presented in Roper *et al.* (1998).
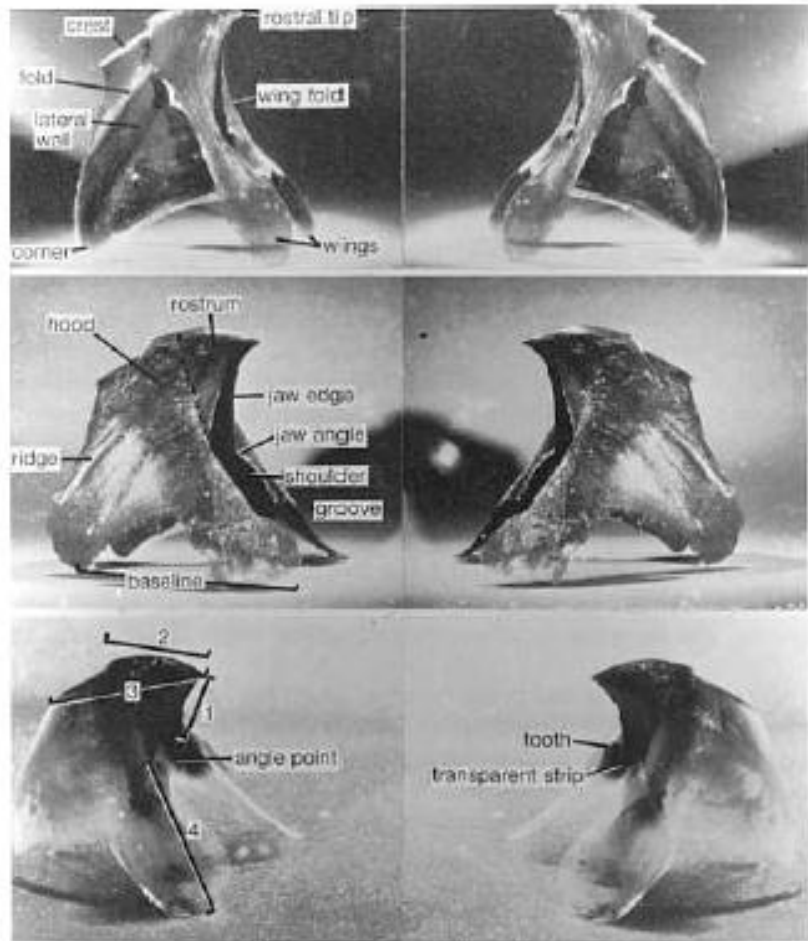
Figure 2.3. Illustration of the measurements and characters of the beaks of squid (from Clarke 1986 by permission Oxford University Press); these images can be viewed stereoscopically by placing a surface mirror vertically between the images, reflecting to the left. View the reflection of the left image with the left eye and the right image directly with the right eye.

3.1 Club suckers

The largest sucker rings on the manus of the club are notched, forming low, truncate to bluntly rounded crenulations, either in the distal half or all around; not smooth.

3.2 Hectocotylized arm

Either left or right ventral arm is hectocotylized by modification into four sections, including the proximal-most non-suckered base of the arm (Fig. 2.2). The standard measure of arm length, including the hectocotylized arm, in squids is from the proximal-most sucker to the arm tip (Roper and Voss 1983). But because there is an area devoid of suckers along the base of the hectocotylized arm of *Illex* species, use of the standard method of arm length measurement would give a disproportionately short and misleading measurement. Therefore, the total length of the hectocotylized arm is measured from the very distinctive V-notch, formed where the bases of the two ventral arms are joined distally, to the distal tip of the arm. In Table 2.1 the value of the hectocotylized arm length index (HALtI) is given as total length of the hecto-cotylized arm as a percentage of mantle length. For purposes of comparison with material from previous studies, the value for the commonly used standard measure from proximal-most sucker to arm tip is given as HALsI, a value 7-10 percent smaller than the HALtI. The total length of the hectocotylized arm

(HALt) of mature males, measured from the V-notch, is about 67 percent (52–86 percent) of the mantle length (the small sample size from each area plus the possibility that some specimens might not be 100 percent mature, may account for the broad range). The fully formed hectocotylized arm is longer and more robust than its opposite arm IV, a feature that seems to occur on most specimens only in the last stage, as full maturity is attained.

The base of the hectocotylized arm (HAb) is characterized by an area devoid of suckers from the V-notch between arms IVL and IVR to the first proximal sucker. The hectocotylized arm base (HAb) measures about 13 percent (10–14 percent) of the HALt (index = HAbI).

The proximal sucker-bearing section (HAl) on mature males consists of 10–14 (mostly 10–12) suckers of normal configuration that like those on the opposite IV arm gradually increase in size distally, and it ends abruptly where the suckers distal to the last large, normal suckers are reduced in diameter by about one half; sucker rows are widely separated. This section (HAl) occupies about 27 percent (24–30 percent) of the HALt (index = Hat1I) and about 31 percent (26–35 percent) of HALs (index = HAslI) measured from the proximalmost sucker.

At the junction of suckered sections one (HAl) and two (HA2), the musculature of the arm is noticeably constricted for a distance of about two sucker pairs. This feature can be seen easily from the aboral as well as the oral surface of the arm, and it can be felt between the observer's fingers as an indentation, giving a reduced diameter to the arm.

About 25 (22–29) small suckers occur along suckered section two (HA2); they terminate at the major modification of the arm tip, section three (HA3). The trabeculae on section two, beginning with the first reduced proximal sucker, are modified as round, fringed, papillose flaps that diminish in size distally and terminate with the last suckers on the dorsal and ventral rows (the end of section two). The dorsal and ventral protective membranes terminate two sucker bases distal to the last suckers. Section two (HA2) occupies about 36 percent (34–38 percent) of the HALt (index = HAt2I) and 42 percent (38–43 percent) of the HALs (index = HAs2I) measured from the proximal-most sucker. The junction between suckered section two and the distal tip of the hectocotylus generally is not as abrupt as between suckered sections one and two. Instead, it consists of a transitional zone that covers the distance of about two sucker pairs.

The highly modified tip of the hectocotylus (HA3) is characterized by the loss of suckers and the development of lamella-like flaps and conical papillae. On the dorsal row are 1–2 conical sucker stalk bases without suckers, followed by about 23 (20–29) bases that are modified into flat, truncate lamellae. This row extends, with the lamellae decreasing in size, nearly to the arm tip, where the row terminates with up to 10–12 minute papillae (possibly precursors of additional lamellae, if any more develop just prior to mating). The suckerless stalk bases on the ventral row, the papillae, maintain a conical, papillose shape and decrease in size to the tip, about 35 in number. These are about 50 percent as tall as the corresponding lamellae on the dorsal row. During growth, suckers occur on these bases, then are lost as the animal reaches sexual maturity. The sucker loss seems to occur towards the tips, i.e. proximal-most suckers are lost first as maturity progresses. The hectocotylized tip (HA3) occupies 26 percent (25–29 percent) of the HALt (index = HAt3I) and 30 percent (28–31 percent) of the length of the HALs from the proximal-most sucker (index = HAs3I). The length of part three is directly dependent on the degree of maturity of the male, rapidly increasing as maturity increases.

3.3 Mantle width

The mantle width index (MWI) of mature males is 22 percent (19–27 percent) and of mature females is 21 percent (14–26 percent).

Table 2.1. Measurements (mm) and indices of specimens of *I. coindetti* used in this study

Specimens	Sex	No.	L-ML	H-ML	M-ML	MWI	HWI	HALtI	HALsI	HAbI	HAt1I	HAs1I	HAt2I	HAs2I	HAt3I	Has3I
Greece	M	1			159	23.9	23.9	79.2	69.8	11.9	29.4	33.3	36.5	41.4	26.2	29.7
Greece	F	1			201	20.9	21.4	–	–	–	–	–	–	–	–	–
So.Adriatic	M	2	119	120		21.4	21.6	63.2	55.6	12	27.2	30.9	33.8	38.4	27.2	30.9
So.Adriatic	F	2	134	135		23.7	22	–	–	–	–	–	–	–	–	–
Sicily	M	5	131	141	–	23.8	22.7	69.8	61.8	11.5	27.8	31.2	35.5	40	26.9	30.4
Sicily	F	1	–	–	186	23.1	18.8	–	–	–	–	–	–	–	–	–
Tunisia	M	3	141	154		22.9	24.1	69.2	60.4	12.7	28.6	32.8	33.5	40.2	27.3	31.4
Tunisia	F	8	150	185		23.2	19.3	–	–	–	–	–	–	–	–	–
Catalonia	M	2	125	130		22.4	23.8	68.2	60	12.2	27.7	30.9	33.8	38.4	27.2	30.9
Catalonia	F	2	115	132		22.6	19.5	–	–	–	–	–	–	–	–	–
N. Vigo, Spain	M		240					76.7	68.3	10.1	27.5	30.9	40.5	45.5	24.6	27.6
N. Vigo, Spain	M	–	220	–		–	–	74.1	65.9	9.57	29.8	33.5	40.0	45.0	20.9	23.5
S. Vigo, Spain	M	3	125	130		26.6	24.2	85.9	75.5	14	26.5	30.1	36.1	41.1	26	29.6
S. Vigo, Spain	F	4	160	176		25.9	20.7	–	–	–	–	–	–	–	–	–
Gulf Guinea	M	2	121	129		18.6	22.7	56.1	48.9	12.9	25	28.9	35.7	41	28.7	29.5
Gulf Guinea	F	2	150	188		17.1	16.8	–	–	–	–	–	–	–	–	–
Namibia	M*	1			131	20.6	19.1	51.9	46.6	10.3	23.5	26.2	36.8	41	25	27.9
So. Carib.	M	3	160	170		21.1	22.3	63.9	54.5	12.1	28	31.9	37.7	42.9	25.2	30
GulfMexico	M	2	153	185	–	21.7	22.4	59.7	52.9	14	27.9	31.7	35.4	41.6	26.3	29.1
GulfMexico	F	1	–	–	185	22.7	18.4	–	–	–	–	–	–	–	–	–
FlorStraits	M	1			252	23	25.8	64.3	55.6	13.6	30.2	35	35.8	41.4	25.9	30
FlorStraits	F	1			319	14.7	14.7	–	–	–	–	–	–	–	–	–
MALES	M					22.4	23.2	67	58.3	12.8	27.4	31.2	35.7	40.9	26.4	29.8
FEMALES	F					21.5	19.1	–	–	–	–	–	–	–	–	–

Mantle Length, ML; given as low measure, L; high measure, H; single specimen, M; other indices defined in Section 3.

3.4 Head width

The head width index (HWI) of mature males is 23 percent (19–26 percent) and of mature females is 19 percent (15–22 percent). .

3.5 Other characters

Tables 2.2–2.7 present measurements and indices of several characters that can be used to compare the four species of *Illex* (from Roper *et al.* 1998).

4 Discussion

The broad, disjunct distribution of *I. coindetii* in the Mediterranean and amphi-Atlantic seas (Fig. 2.4) is characterized by a number of more or less distinct morphotypes. These sometimes highly variant forms (Fig. 2.5) seem related not only to geographical distribution but to local or regional environmental factors as well (e.g. season, water mass, prey, etc.). The morphotypes are not well defined nor understood at this point. Because some of the morphotypes look so different from the "typical" *I. coindetii* from the Catalonian region, both in size and gross morphology, several workers have questioned the validity of using the specific name to apply to all forms. They suggesthat several distinct species or subspecies exist in an *I. coindetii* species complex.

Analysis of our data, as well as data available to us from other colleagues (e.g. C. Nigmatullin, AtlantiNIRO, Kaliningrad, Russia; A. Gonzales and A. Guerra, Instituto de Investigaciones Marinas, Vigo, Spain; F. Zecchini, Universita di Pisa, Italy), leads us to conclude that *I. coindetii* is a single, widely distributed, highly plastic and variable species. However, underpinning the local variability appear to be two basic, consistent morphological forms. Based on indices of mantle width, head width, and hectocotylized arm length (see Table 2.1 and Fig. 2.5) and other aspects of the habitus of the animals, these two identifiable types conform to distributions in the Mediterranean Sea and in the Atlantic Ocean. Additional specimens are required from the Atlantic adjacent to the Mediterranean to define more precisely the forms, but our data suggest that these differences are consistent. Further comparative morphological analysis of additional material from the eastern and western Atlantic is required to clarify populational differences that exist across the range. We believe that molecular genetic analyses will also be required to help define populations.

Although *I. coindetii* has been recorded from the Red Sea (Adam 1942), it seems unlikely that the species actually occurs there. The only two specimens recorded were captured in 1850 prior to the opening of the Suez Canal, so we concur with Lu (1973) that these specimens must have been mislabelled and that the species does not occur in the Red Sea.

Adam (1952) reported *I. illecebrosus* specimens from the Bristol Channel off southwestern England. Re-examination of some of Adam's specimens, especially of the hectocotylus and body and fin measurements, confirms that these specimens are *I. coindetii*, not *I. illecebrosus* (see Roper *et al.* 1998).

In spite of the apparently high degree of variation in general habitus across the geographical range of *I. coindetii*, the characters associated with the hectocotylus in particular are surprisingly constant, as are, ultimately, the indices of head and mantle widths. For example, the males from Greece look very different from males from Namibia in general habitus. The Greek male looks more robust with broad mantle and head and very robust arms II and III, while the Namibian form appears thin with narrow mantle and head and non-robust arms II and III. Yet, when the details of the four-part hectocotylus are examined, they are strikingly similar, certainly well within the range of variability accepted for conspecific squid. Further, mature, mated females from Vigo, Spain, look much more robust in head and mantle width than their counter-

Table 2.2. Head length indices (HLI) and head width indices (HWI) for males and females 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)	9.0	(10.0–23.6)
I. argentinus	19.5	(16.0–23.9)	16.8	(14.3–19.7)
I. oxygonius	18.2	(15.0–21.3)	6.3	(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)

Table 2.3. Mantle width indices (MWI) for males and females of the four species of *Illex*

	Male		Female	
	Mean	Range	Mean	Range
MWII:				
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)
MW2I:				
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)
MW3I:				
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	(9.6–22.1)
I. oxygonius	10.9	(8.1–16.4)	10.8	(9.0–14.3)

MW1 measured at mantle opening
MW2 measured at mid-point between mantle opening and fin insertion
MW3 measured at anterior point of fin insertion

Table 2.4. Fin length indices (FLI), fin width indices (FWI) and fin base length indices (FbLI) for males and females of the four species of *Illex*

	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	(45.7–66.5)	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	(35.8–42.2)	40.0	(37.9–43.2)

Table 2.5. Arm length indices (ALl) (hectocotylus not included) for males and females of the four species of *Illex*

	I. illecebrosus		*I. coindetii*		*I. argentinus*		*I. oxygonius*	
Arm	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Males:								
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)
Females:								
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)

Table 2.6. Hectoco!ylized arm length[a] indices (HALsI) and hecto-cotylized tip length[b] indices (HAs3I) for mature specimens of the four *Illex* species

	Mean	Range	Standard deviation	N
HALI:				
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
HA3LI:				
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

[a] Length of hectocotylized arm measured from most proximal sucker to arm tip.

[b] Length of hectocotylized tip measured from most distal sucker to arm tip.

[c] Includes HA2, which loses suckers at full maturity making it difficult to determine the junction point of HA2 and HA3.

Table 2.7. Comparison of the beaks of the four *Illex* species[a]

Feature	*illecebrosus*	*coindetti*	*argentinus*	*oxygonius*
Upper Beak:				
Hood	long, strong	long, strong	long, strong	short, weak very thin
Shoulder	serrated	smooth	serrated	smooth, straight or slightly curved
Jaw angle	large notch, with tooth	small notch	large, notch with tooth	small notch
Rostrum	long	long	long	short
Lateral wall	short, shallow; crest curved	short, shallow; crest curved	short, shallow; crest curved	long, deep; crest straight
Wing	short	short	short	short
Lower Beak:				
Jaw edge	straight, short	straight, long	curved, long	curved, long
Wing	long, wide, no lobe: regular outline	long, wide, no lobe: slightly irregular outline	long, wide, no lobe: regular outline	short, narrow lobate: irregular outline
Lateral wall	short, blunt	short, blunt	short, blunt	long, pointed
Rostral width	narrow	narrow	narrow	wide

Based on Roper *et al.* (1969) and Lu (1973).
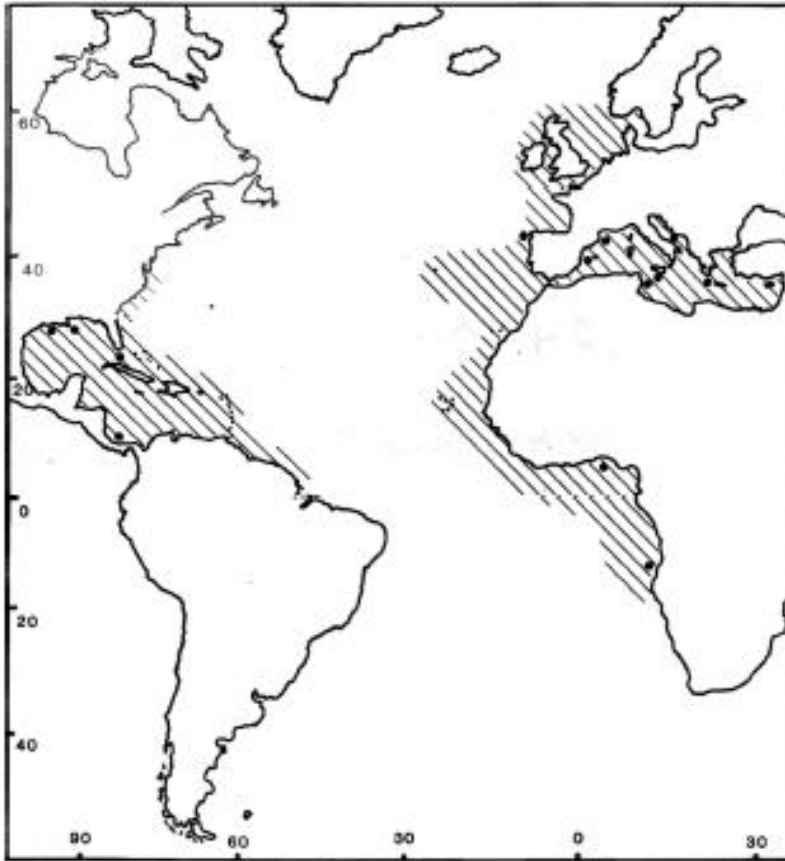
Figure 2.4. Geographical distribution of *I. coindetii* shown by hatched area; location of specimens used in this study shown in solid dots

parts from the Gulf of Guinea. Certainly some of the variability can be attributed to small sample size and the possibility that some specimens are not 100 percent mature.

Very large specimens, in excess of 250 mm ML, are occasionally captured. For example, large specimens are known from the Straits of Florida (male of 252 mm ML, female of 319 mm ML) and off Vigo, Spain (males to 270 mm ML, females to 370 mm ML; A. Gonzales, Instituto de Investigaciones Marinas, Vigo, Spain, *unpubl. data*). These unusually large specimens of the species seem to represent a small proportion of the population and co-occur with more numerous, smaller, fully mature specimens. Perhaps they are late-hatching members of the previous year class that do not reach full maturity, and consequently do not spawn during their first year. They may survive through the winter until the following year, continuing to add to somatic growth, then the next season they mature at an unusually large size and spawn. This phenomenon was suggested for exceptionally large *Loligo pealei* in the western Atlantic as early as the last century by Verrill (1881). The key question is whether size at maturity is genetically or ecologically based. Would a little mature male be rejected, even eaten, by a very large female if he tried to mate with her? Genetic difference would be very rapidly reinforced if this were the case.

The morphological changes observed in the growth of specimens during maturation are not isometric but allometric; the last-minute changes associated with maturation and spawning can be very dramatic. These changes probably occur in all areas and populations to one degree or another, but the changes that occur are not equally dramatic throughout the geographical range of the species. This phenomenon can account for a degree of the variation among the broadly dispersed populations.

Figure 2.5. Size morphotypes of fully mature males of *I. coindetii*, arranged geographically from east to west; left to right in photo: Greece, Sicily, Barcelona, Namibia, Straits of Florida.

The conditions discussed above now help us to understand why some workers questioned the single-species status of *I. coindetii*. That is, the different general habitus of animals from different geographical areas is not significant in terms of specific differentiation. It was the detailed analysis of a few distinctive morphological characters from representatives of populations across the whole range of the species that revealed that all these morphotypes, in fact, belong to one species. The question we cannot answer at this moment is: Why do these morphotypes exist and what sustains them?

Particularly for identifications in the field, the easiest character to use to distinguish *I. coindetii* from the sympatric species of *Illex* in the western Atlantic, *I. illecebrosus* and *I. oxygonius*, is the length of the suckerless base of the hectocotylized arm (HAb). In *I. coindetii* this sucker-free area occupies approximately 13 percent of the total length of the arm, while in the other two species it amounts to only 6 percent and 4 percent, respectively. In addition, the reduced diameter of the hectocotylized arm at the junction of the two suckered sections (HAl and HA2) is clearly visible and can be felt with the fingers. No such reduction occurs in the other two species. The dentate and notched rings on the largest manal suckers of *I. coindetii* contrast with the smooth rings of the other two species, but a microscope, certainly a good hand lens, generally would be required to check this character in the field.

5   Comparison of species

While the purpose of this work is to define more precisely the systematics and distribution of *I. coindetii*, it is necessary to include basic information and data on the other three species of *Illex*, as well. Consequently, we include here Tables 2.2–2.7, which give measurements and indices of all four species, so their meristic characters can be compared. Figures 2.1–2.3 depict the measurements used. Further, a key

Table 2.8. Key to the species of *Illex* for mature adults

1. Relative length of all arms long; tentacular club not broadly expanded, medial suckers very enlarged, lateral suckers extremely small; distal modified portion of hectocotylized arm greater than 50 percent of total arm length (= HA2 plus HA3); distribution restricted to western South Atlantic Ocean, 23°–55°S…………………………………………………………………………………………***I. argentinus***

    Relative length of all arms moderate to short; tentacular club expanded, medial suckers enlarged, lateral suckers small (not radically disproportionate, as above); distal modified portion of hectocotylized arm (HA3) less than 33 percent of total arm length; North Atlantic, Caribbean, Gulf of Mexico, or Mediterranean………………………………………………………………………………….. **2**

2. Distal enlarged manal sucker rings notched, 7–8 low, broad, flat plate-like teeth; relative lengths' of fins and fin bases short; relative length of head long; relative length of arms long; base of hectocotylized arm (HAb) devoid of suckers for 13 percent of total arm length; trabeculae on hectocotylus midsection (HA2) modified to papillose, fringed flaps; distribution pan-Atlantic, the only *Illex* species in the eastern Atlantic and Mediterranean…………………………………………………………***I. coindetii***

    Distal enlarged manal sucker rings smooth, toothless, rarely with 1–2 notches; relative lengths of fins and fin bases long; relative lengths of head and arms short; base of hectocotylized arm (HAb) devoid of suckers for 4–6 percent of total arm length; trabeculae on hectocotylus midsection (HA2) not modified; distribution restricted to western North Atlantic…………………………………………………. **3**

3. Relative width of fins broad, 55 percent of mantle length; head length and width indices relatively low, 16–17 percerit; arm lengths relatively short in males, 39–48 percent of ML; arm sucker diameter indices relatively small, 1.02–1.75; hectocotylized arm equal to, or slightly shorter than, and the same thickness as, opposite arm IV; lower beak jaw edge straight, short; wing long, wide; lateral wall short, blunt; rostral width narrow …………………………………………………………………***I. illecebrosus***

    Relative width of fins narrow, 51 percent of ML; head length and width indices relatively high, 16–20 percent; arm lengths relatively long in males, 44–55 percent of ML; arm sucker diameter indices relatively large, 1.12–2.47, especially in males; hectocotylized arm relatively long, more robust than opposite arm IV; lower beak jaw edge curved, long; wing short, narrow; lateral wall long, pointed; rostral width wide………………………………………………………………………***I. oxygonius***

(Table 2.8) to the mature adults of all four species is included. Tables 2.2–2.8 are adapted from Roper *et al.* (1998), in which a detailed discussion of the systematics and distribution of all four species is presented.

6   Conclusions

Based on an analysis of some individual systematic characters in mature specimens of all four species of *Illex*, namely those associated with the hectocotylus and with head and mantle robustness, we conclude that *I. coindetii* is a single, variable, widely distributed species. We are unable to find sufficient morphological evidence in these character states to sustain the existence of a *coindetii* complex of closely related, distinct species. It is possible that future genetic analyses, in concert with morphological studies, might indicate specific status for some morphotypes, but that remains to be done.

The morphotypes of the species that occur throughout the Mediterranean Sea and along the eastern Atlantic neritic zone from Great Britain to Namibia and in the western Atlantic from the southeastern Caribbean Sea the Gulf of Mexico and the Straits of Florida. all should be referred to *I. coindetii*.

In the western North Atlantic it is morphologically distinct from both *I. illecebrosus* and *I. oxygonius* in their region of sympatry. Further, it is quite distinct from the species in the western South Atlantic, *I. argentinus*.

Acknowledgements

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