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34

Cephalopoda (Mollusca) of the Gulf of Mexico

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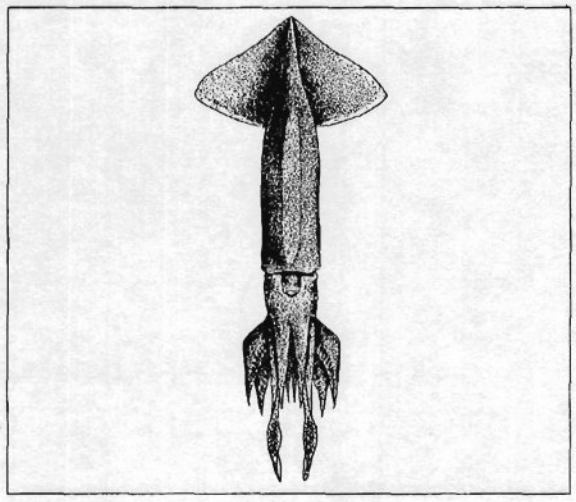
The cephalopods of the Gulf of Mexico (GMx) have not been studied comprehensively since Voss' (1956) monograph. Several cephalopod reports have included this region in broader studies (e.g., Vecchione 2002) or have examined distribution based on limited geographic area (e.g., Nesis 1975, Passarella and Hopkins 1991). Collectively, approximately 109 species of cephalopods in 31 families occur in the Western Central Atlantic and adjacent areas, including the Caribbean Sea and the Gulf of Mexico. Both squids and octopods are common in these waters (Vecchione 2002). The present chapter updates Voss' works and summarizes the species found in the Gulf of Mexico to date.

Two major groups of cephalopods exist today: the Nautiloidea, with a few species of the pearly nautilus confined to the Indo-West Pacific, and the Neocoleoidea, consisting of squids, cuttlefishes, octopods, and their relatives. Neocoleoidea comprise more than 700 species worldwide (see http://tolweb.org/tree?group=Cephalopoda&contgroup= Mollusca). The neocoleoids that exist today evolved from forms that first appeared in the upper Triassic and Lower Jurassic (between 200 and 150 million years ago). Although there are relatively few species of living cephalopods, they occupy a great variety of habitats in all of the world's oceans. Individual species may be very abundant and are important in marine food webs. Some species are major targets for commercial fisheries.

The Neocoleoidea contains 2 extant superorders: the Octopodiformes (octopods and vampire squid) and the Decapodiformes (squid and cuttlefishes). These groups occupy all major habitats in the oceans, from intertidal to great depths (deepest record is 7279 m, Aldred, Nixon, and Young 1983, Voss 1988) and from southern to northern polar seas. No cephalopods are found in salinities less than about 17.5 practical salinity units (psu).



Cephalopoda. After Vecchione 2002.

Many species of oceanic cephalopods undergo diel vertical migrations, wherein they occur at depths of about 400 m to 1000 m during the day, then ascend to the uppermost 200 m or so during the night (e.g., Enoploteuthidae, Ommastrephidae). Abundance patterns vary (depending on group, habitat, and season) from isolated territorial

individuals (primarily octopods and sepioids), through small schools with a few dozen individuals, to massive schools with millions of oceanic squids.

Although many cephalopods reach large sizes, generally they have a very short life span. The life expectancy appears to be about 1–2 years in most cephalopods, but large species of squids and octopods and those in coldwater habitats may live longer. Conversely, some small oceanic squids, such as pyroteuthids, may complete their life cycles in less than 6 months. This is part of a life-history strategy that seems designed for rapid increase in population size. It has been suggested that this life-strategy may guarantee survival against environmentally stressful conditions, including those by heavy predation or overfishing. However, as cephalopod fisheries experienced further extensive development, parallel concern developed regarding potential overexploitation (Jereb and Roper 2005).

Cephalopods are important in terms of food web relationships, commercial fisheries, and biomedical research. Cephalopods are born into the third trophic level and progress one or two stages through their life. Research has not shown them as achieving top-predator status, because there always seems to be some vertebrate that preys upon them (Summers 1983). Cephalopods are active predators that feed on shrimps, crabs, fishes, and other cephalopods, and, in the case of octopods, on other molluscs. In turn, cephalopods are major food items in the diets of toothed whales, seals, pelagic birds, and both benthic and pelagic fishes, as well as other cephalopods.

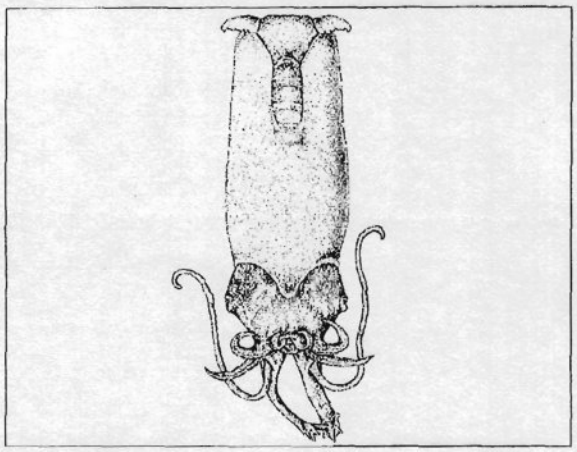
Cephalopod fisheries provide an important food source for humans around the globe. Over 3 million metric tons are caught each year worldwide (Jereb and Roper 2005). Squid fisheries have also existed in North America, historically, principally to provide bait for other fisheries, but recent decades have seen the development of substantial fisheries for food production, as well. The total commercial catch of cephalopods in the Western Central Atlantic varied during 1993 to 1998 between 19,000 tons and 31,000 tons, mostly landed in Mexico (Vecchione 2002). However, of the numerous species known on the coasts of Florida, the Gulf of Mexico, and the Caribbean Sea, "only about 12 species seem to have actual or potential (fisheries) importance" (Voss, Opresko, and Thomas 1973:1). Of those, species that are commercially important to the Gulf of Mexico include: *Octopus maya, Illex coindetii, Doryteuthis (Loligo) pealei,* and *Doryteuthis (Loligo) plei* (see Voss and Brakoniecki 1985).

Squids also are important to biomedical research; for instance, much of what is known about human neurophysiology results from experiments with the giant axon of squids. Scientists culture squid in laboratories in order to study the giant axon. Lee et al. (1994) cultured the Indo-West Pacific species *Sepioteuthis lessoniana* (Ferussac, 1830) for this purpose because of its large hatchlings and the quality of its large-diameter axons for study (Lee 1994). LaRoe (1971) previously had worked with a Caribbean species, *S. sepioidea,* for this purpose. Because of the highly developed brain and sensory organs, cephalopods are valuable in behavioral and comparative neuroanatomical studies as well.

The fauna of the Gulf of Mexico lacks the nautiloids and true cuttlefishes but includes sepiolids, myopsid and oegopsid squids, octopods, and the vampyromorph, *Vampyroteuthis infernalis.* Published records of cephalopod species in the Gulf of Mexico date back to LeSueur (1821), but the modern, comprehensive systematic studies begin with G. L. Voss, who reported 42 neritic and oceanic species in 1956 (Voss 1956). Since then, many oceanic species have been added to the list (Voss and Voss 1962, Roper 1964, Voss 1964, Roper, Lu, and Mangold 1969, Lipka 1975, Passarella 1990). Although the composition of the cephalopod fauna off southern Florida is known almost exhaustively, the fauna of the rest of the Gulf of Mexico is less well studied. The cephalopods of the Mexican waters of the Gulf were reviewed by Salcedo-Vargas (1991); using specimens and past literature, he reported some questionable identifications. The most recent compilation of the cephalopods in the Gulf of Mexico is that of Vecchione (2002).

Major Systematic Revisions Since 1954

The status of the systematics of cephalopods has rapidly changed, as research has increased substantially worldwide during the past 30 years. The families of living cephalopods are, for the most part, well resolved and relatively well accepted. Species-level taxa can usually be placed in well-defined families (Jereb and Roper 2005). However, phylogenetic relationships among families within the major groups remain uncertain (Vecchione 2002). Sweeney and Roper (1998: 561) addressed the confusion, stating, "We realize that numerous systematic problems exist at all taxonomic levels of the Cephalopoda. For example, several higher taxa have been proposed (i.e., superorder Pseudoctobrachia Guerra, 1992, and order Cirroctopodida Young, 1989)." The resolution of these



Cephalopoda. After Vecchione 2002, modified by F. Moretzsohn

problems requires considerable research and review, as new cephalopod research initiatives are being pursued globally.

Comparative Assessment of Group in GMx

One of the elements absent in current cephalopod research is comprehensive studies of large oceanic or faunal regions. Numerous isolated island studies, studies from a fisheries perspective, or those for biomedical advances do exist, but the need for comprehensive studies of systematics, abundance, distribution, and ecology requires significant attention. The Broad Caribbean Realm, which includes the Caribbean Sea proper, the Gulf of Mexico, and waters that extend through the Bahamas, is an area that is in need of such comprehensive study. The first author of this chapter (HJ) currently is researching this area. Species that have been collected in the area allow the opportunity to further define phylogenetic relationships within the cephalopods as a whole as well as to address the trophic importance of cephalopods within the region, for example.

Because of the great diversity in the form, habitat, and behavior of cephalopods, no single method is adequate to capture and/or sample the complex cephalopod fauna (Rathjen 1991). The excellent vision and high mobility of most cephalopods traditionally means that they have been undersampled with standard trawling and collecting protocols. Despite their limitations, midwater trawls offer a starting point for population assessment of pelagic species and provide minimum estimates of oceanic cephalopod abundance (Passarella 1990). Numerous facilities around the Broad Caribbean Realm house unidentified cephalopods, which when identified, will add further insight to the diversity of the cephalopod families and ecology and will provide a better fisheries' perspective about potentially viable future catches in the region.

Explanation of Checklist

The classification and nomenclature used here follow that of Vecchione (2002), as it is the most recent compilation for the Western Atlantic region. Orders and families are arranged phylogenetically, and genera and species are arranged alphabetically. Cephalopods are not exclusively benthic, as are most other mollusca, and many are highly mobile, pelagic/oceanic species. This habitat niche requires the use of the term "central" in the Gulf of Mexico range column. Depth data and overall range for organisms are in italic where they could not be determined exclusively for the Gulf of Mexico. Depth ranges include paralarval through adult stages, so they represent the total known vertical range for the species. However, most pelagic species exhibit several more specific ranges during different phases of their life cycles: for example, paralarvae are epipelagic, restricted to the upper 100–200 m; many then undergo ontogenetic descent, moving into deeper waters with growth. Adults of many species then exhibit diel vertical migration from around 400 m to 1000 m during the day, into the upper 200–400 m at night to feed. Very little information is available on biology and lifestyle for many of the deep-sea cephalopods in the Gulf of Mexico; this explains the "unknown" notation in some columns.

Abbreviations

The abbreviations used in the Habitat-Biology category are as follows: bat = bathypelagic (> 1000 m); ben = benthic; cep = coastal surface and epipelagic; crr = coral reef; cts = continental shelf; dps = deep sea; end = endemic; epi = epipelagic (0–200 m); ins = insular; mes = mesopelagic (200–1000 m); ner = neritic; oce = oceanic; sft = mud, sands, clays; sgr = seagrass; shw = shallow water; slp = continental slope. The abbreviations used in the Overall Geographic Range category are as follows: AT = Atlantic Ocean; BE = Bermuda; BH = Bahamas; BR = Brazil; CH = Cape Hatteras, North Carolina; CT = Connecticut; CR = Caribbean; FL = Florida; IO = Indian Ocean; ME = Mediterranean; N = North; NE = New England; NS = Nova Scotia; PO = Pacific Ocean; S = South; SA = South America; ST = subtropical; T = tropical; TWA = Tropical Western

Atlantic; UR = Uruguay; USA = United States of America; VE = Venezuela; W = West; WA = Western Atlantic.

The abbreviations used in the Gulf of Mexico Range category vary because of the high mobility of the species. In some cases, a specific region cannot be defined at this time. Therefore, the term "central" (cen) is indicative of the mid-Gulf of Mexico species. The term "entire" (ent) is used where the species is found throughout all regions of the Gulf of Mexico. For those species that are found in more than one region, an overall region is used. For example, instead of "se" and "ne" being used, the term "e" (east) is used where appropriate.

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Taxonomic summary for cephalopods of the Gulf of Mexico.

Component subgroups	Total species	Endemic species*	Nonindigenous species
Spirulida	1	?	0
Sepioidea	5	?	1
Myopsida	6	?	0
Oegopsida	58	?	1
Octopoda	22	?	0
Vampyromorpha	1	?	0
Total	93	?	2

* Not enough study yet to give a good account of the endemics.

Checklist of cephalopods (Mollusca: Cephalopoda) from the Gulf of Mexico.

Taxon	Habitat-Biology	Depth (m)	Overall geographic range	GMx range	References/ Endnotes
Class: Cephalopoda					
Order: Spirulida					
Family: Spirulidae					
Spirula spirula (Linneaus, 1758)	oce	550–1000	T, ST worldwide	ent	*14, 29*
Order: Sepioidea					
Family: Sepiolidae					
Austrorossia antillensis (Voss, 1955)	oce	305–775	CR, N SA, GMx	se	*6, 12, 23, 34*
Heteroteuthis dispar Ruppell, 1845	mes, oce	200–1000	T, ST worldwide	e	*14, 16*
Rossia bullisi Voss, 1956	end, oce	?	T AT	ent	*12, 34*
Semirossia equalis (Voss, 1956)	sft	130–260	GMx, N SA	ne	*6, 12, 23, 34*
Semirossia tenera (Verrill, 1880)	sft	85–135	NE to GMx & CR	ent	*6, 12, 31*
Order: Myopsida					
Family: Loliginidae					
Doryteuthis pealeii (LeSueur, 1821)	cep, cts	1–366	WA, NS to VE, GMx and CR	ent	*12, 14, 29*
Doryteuthis plei (Blainville, 1823)	cep, cts, slp	1–366	WA, GMx, CR	ent	*12, 14, 29, 34*
Doryteuthis roperi (Cohen, 1976)	cep, cts	1–50	WA, GMx, CR	ent	*4, 34*
Lolliguncula brevis (Blainville, 1823)	cts, shw	1–18	WA, GMx, CR	ent	*12, 29*
Pickfordiateuthis pulchella Voss, 1956	sgr	1–30	FL–BR	se	*14, 34*
Sepioteuthis sepioidea (Blainville, 1823)	crr, shw	1–20	BE, FL, BH, CR	se	*12, 29, 34*
Order: Oegopsida					
Family: Architeuthidae					
Architeuthis dux Steenstrup, 1860	oce, cts	400–1000	AT	ent	*23*[1]
Family: Brachioteuthidae					
Brachioteuthis sp.	epi–mes	*1–300*	NA, PO, ME	e	*14, 16, 29*
Family: Cranchiidae					
Bathothauma lyromma Chun, 1906	mes	*1–1400*	T, ST	e	*16, 43*
Cranchia scabra Leach, 1817	oce	*2–1000*	T, ST worldwide	ent	*12, 14, 16*
Egea inermis Joubin, 1895	oce	*1–800*	T AT, W PO, IO	e	*14, 16, 43*
Helicocranchia pfefferi Massy, 1907	oce	*1–500*	T, ST worldwide	e	*14, 16*
Leachia atlantica (Degner, 1925)	oce	*1–2000*	T, ST	ent	*16, 43, 47*
Leachia cyclura LeSueur, 1821	oce	*1–2000*	T, ST worldwide	ent	*43*
Leachia lemur (Berry, 1920)	oce	*1–2000*	T, ST worldwide	ent	*43*
Liocranchia reinhardti (Steenstrup, 1856)	oce	*1–1200*	circumglobal	e	*12, 14, 16*
Megalocranchia spp.	oce	*1–2000*	T, ST worldwide	e	*16, 22*

(*continued*)

Checklist of cephalopods (Mollusca: Cephalopoda) from the Gulf of Mexico. (*continued*)

Taxon	Habitat-Biology	Depth (m)	Overall geographic range	GMx range	References/ Endnotes
Family: Cycloteuthidae					
Cycloteuthis sirventi Joubin, 1919	oce	*200–1000*	T, ST AT	?	*15, 29*
Discoteuthis discus Young and Roper, 1969	oce	*1–700*	AT, S PO	e	*14, 16, 25*
Discoteuthis laciniosa Young and Roper, 1969	epi–mes	*400–1000*	T, ST, AT, IO, PO	?	*44, 46*
Family: Enoploteuthidae					
Abralia redfieldi Voss, 1955	epi, ins	1–200	T, ST WA	e	*12, 14, 34*
Abralia veranyi (Ruppell, 1844)	oce, slp	*20–800*	T, ST AT, E AT	ent	*12, 14, 34*
Abraliopsis atlantica Nesis, 1982	mes	1–1000	T, ST AT	e	*16, 46*
Abraliopsis pfefferi Joubin, 1896	mes–bat	*1–200*	T, ST AT, IO, W PO	e	*2, 12, 14, 16*
Enoploteuthis leptura (Leach, 1817)	oce	200–800	T, ST AT, IO, W PO	e	*12, 16*
Family: Magnapinnidae					
Magnapinna sp.	bat, oce	*1000–4000*	GMx, N AT	cen	*32*[2]
Family: Pyroteuthidae					
Pterygioteuthis gemmata Chun, 1908	oce	*1–600*	T worldwide	e	*16, 23*
Pterygioteuthis giardi Fischer, 1896	oce	*1–600*	T, ST worldwide	e	*12, 16, 23*
Pyroteuthis margaritifera (Ruppell, 1884)	oce	*75–500*	T, ST AT, IO, W PO	e	*12, 16, 25*
Family: Ancistrocheiridae					
Ancistrocheirus lesueuri Orbigny, 1839	mes	*1–700*	T, ST worldwide	e	*12, 14, 16, 25, 45*
Family: Histioteuthidae					
Histioteuthis bonnellii (Ferussac, 1834)	oce	1–2000	T, ST worldwide	cen	*14, 40*
Histioteuthis corona (Voss & Voss, 1962)	oce	200–1000	T, ST worldwide	e	*12, 16*
Histioteuthis reversa (Verrill, 1880)	oce	1–1000	?	cen	*12, 29, 34, 41*
Family: Bathyteuthidae					
Bathyteuthis abyssicola Hoyle, 1885	oce	200–4000	T, ST worldwide	e	*12, 16, 34*
Family: Chtenopterygidae					
Chtenopteryx sicula (Verany, 1851)	mes, oce	*200–1000*	AT, PO, ME	e	*14, 16*
Family: Lepidoteuthidae					
Lepidoteuthis grimaldii Joubin, 1895	oce	?	T worldwide	ent	*12, 14, 16*
Family: Lycoteuthidae					
Lampadioteuthis megleia Berry, 1916	mes, oce	*200–1000*	AT, S PO	e	*14, 16, 29*
Lycoteuthis lorigera (Steenstrup, 1875)	mes, oce	*200–1000*	WA, GMx	cen	*14, 21, 29, 34*
Lycoteuthis springeri (Voss, 1956)	end, oce	*200–1000*	T WA	cen	*12, 34*
Selenoteuthis scintillans Chun, 1900	oce	*200–800*	WA, GMx	e	*14, 16*
Family: Ommastrephidae					
Hyaloteuthis pelagica (Bosc, 1802)	oce	*1–200; 1700*	T, ST worldwide	ent	*12, 13, 23, 34*
Illex coindetii (Verany, 1839)	cts, ner, oce	1–1000	AT	ent	*14, 22, 25, 29*
Illex oxygonius Roper, Lu, & Mangold, 1969	ner, oce	50–500	WA	se	*12, 14, 29, 31*
Ommastrephes bartramii (LeSueur, 1821)	oce	1–1500	worldwide	ent	*12, 29, 31*
Ornithoteuthis antillarum Adam, 1957	ner, oce	*1–1000*	PO, AT	ent	*14, 16, 29, 31*
Sthenoteuthis pteropus (Steenstrup, 1855)	oce	1–1500	T, ST Pan-Atlantic	ent	*16, 29, 34*
Family: Chiroteuthidae					
Chiroteuthis joubini Voss, 1967	mes, oce	*200–1000*	ST AT, IO	e	*16, 46*
Chiroteuthis mega (Joubin, 1932)	mes, oce	*200–1000*	?	e	*16, 46*
Chiroteuthis veranyi (Fersussac, 1834)	mes, oce	*200–1000*	T, ST WA, E PO	ent	*12, 34*
Grimalditeuthis bonplandi (Verany, 1839)	oce	*200–1500*	AT, GMx	cen	*12, 29, 34*
Planctoteuthis danae (Joubin, 1931)	mes, oce	*200–1000*	T, ST worldwide	cen	*29*
Family: Pholidoteuthidae					
Pholidoteuthis adami Voss, 1956	oce	*20–230*	PO, GMx, AT	cen	*14, 34*
Pholidoteuthis boschmai Adam, 1950	mes, oce	*200–1000*	ST worldwide	cen	*29, 46*
Family: Octopoteuthidae					
Octopoteuthis megaptera (Verrill, 1885)	mes, oce	*200–1000*	T, ST AT	se	*12, 34*
Octopoteuthis sicula Ruppell, 1844	mes, oce	*200–1000*	T, ST AT, IO, W PO	?	*15, 46*
Tanangia danae Joubin, 1931	oce	*25–300*	T, ST worldwide	e	*12, 16, 24*

Checklist of cephalopods (Mollusca: Cephalopoda) from the Gulf of Mexico. (*continued*)

Taxon	Habitat-Biology	Depth (m)	Overall geographic range	GMx range	References/ Endnotes
Family: Onychoteuthidae					
Moroteuthis aequatorialis Theile, 1920	oce	*100–1000*	T, ST AT, IO, W PO	e	*12, 46*
Onychoteuthis banskii (Leach, 1817)	oce	*100–1000*	worldwide	se	*7, 12, 14, 34, 38*
Onykia carriboea LeSueur, 1821	epi, oce	*1–200*	T, ST worldwide	e	*12, 34*
Family: Thysanoteuthidae					
Thysanoteuthis rhombus Troschel, 1857	oce	*25–85 day nets*	AT, PO, IO, ME	e	*12, 14, 16, 25*
Family: Mastigoteuthidae					
Mastigoteuthis agassizi Verrill, 1881	oce	200–1000	T, ST AT	e	*16, 29*
Mastigoteuthis hjorti Chun, 1913	oce	200–1000	T AT	cen	*29*
Mastigoteuthis magna Joubin, 1913	oce	200–1000	N AT, GMx	cen	*29*
Family: Joubiniteuthidae					
Joubiniteuthis portieri (Joubin, 1912)	oce	*1–1500*	AT, PO	ent	*2, 3, 12, 14, 16*
Order: Octopoda					
Family: Opisthoteuthidae					
Opisthoteuthis agassizi Verrill, 1883	ben, cts	*100–1000*	AT, PO	ent	*12, 29, 33, 34, 36*
Family: Octopodidae					
Amphioctopus burryi (Voss, 1950)	cts	10–200	GMx, CH to BR	e	*12, 29*[3]
Benthoctopus januarii (Hoyle, 1885)	dps	400–750	GMx, CR, T AT	cen	*12, 29*
Callistopus macropus group	shw	?	T WA	se	*12, 29*
Macrotritopus defilippi group	shw	6– > 60	WA, FL to BR	e	*12, 16, 29*
Octopus briareus Robson, 1929	shw	?	W N AT, SE USA, BH, CR	s	*12, 29*
Octopus hummelincki Adam, 1936	shw	1–200	T WA, FL to BR	se	*29*
Octopus joubini Robson, 1929	cts, shw	1–80	T WA	ent	*12, 29*
Octopus maya Voss & Solis Ramirez, 1966	sgr, shw	1–50	S GMx	s	*12, 29*
Octopus mercatoris Adam, 1937	?	?	GMx	?	*29*
Octopus cf. *vulgaris* group	cts	1–200	WA, CT to BR	ent	*12, 29*
Pteroctopus schmidti (Joubin, 1933)	dps	300–1200	scattered	se	*29*
Pteroctopus tetracirrhus (Chiaie, 1830)	cts, sft	100–750	WA, CH to UR	ent	*12, 29*
Scaeurgus unicirrhus (Chiaie, 1839–1841)	sft	100–400	WA, CH to S BR	e	*15, 29*
Tetracheledone spinicirrus Voss, 1955	sft	200–400	GMx	s	*12, 29*
Family: Alloposidae					
Haliphron atlanticus Steenstrup, 1861	oce	*1–700*	T, ST worldwide	ent	*12, 14, 16, 34*
Family: Ocythoidae					
Ocythoe tuberculata Rafinesque, 1814	mes, oce	1–200	T, ST worldwide	cen	*46*
Family: Bolitaenidae					
Bolitaena pygmaea (Verrill, 1884)	oce	>1000	T, ST WA	?	
Japetella diaphana Hoyle, 1885	dps	*600–4000*	T, ST worldwide	e	*5, 12, 16, 45*
Family: Tremoctopodidae					
Tremoctopus violaceus Chiaie, 1830	oce	*1–250*	T, ST worldwide	se	*12, 14, 25, 34*
Family: Argonautidae					
Argonauta argo Linnaeus, 1758	oce	*1–155*	T, AT, PO, ME	e	*12, 16, 34*
Argonauta hians Lightfoot, 1786	oce		AT		*29*
Order: Vampyromorpha					
Family: Vampyroteuthidae					
Vampyroteuthis infernalis Chun, 1903	bat	*100–3000*	T, ST worldwide	ent	*12, 14, 16, 30, 34*

[1] N. A. Voss, personal communication, 2005.

[2] New record for Gulf of Mexico, Vecchione, In press.

[3] *Octopus burryi* Voss, 1950, was transferred to the genus *Amphioctopus* in the publication: Norman, M. D., and F. G. Hochberg. 2005. The current state of *Octopus* taxonomy. Phuket Marine Biological Center Bulletin 66: 127–154.