Ctenophores are gelatinous predators found throughout the world’s oceans, where they inhabit the shallowest coastal zone to the abyss, from the tropics to the poles. Ctenophores are diploblasts located near the triploblast boundary (Harbison 1985, Martindale and Henry 1998) that display considerable morphological diversity, ranging from freely swimming to creeping forms. All ~150 species of ctenophores may be divided into 2 distinct groups: Class Tentaculata, which bear tentacles during at least the larval stage, and Class Nuda, which lack tentacles at all stages. Most ctenophores are bioluminescent (Haddock and Case 1995, 1999). All ctenophores share a unique set of derived characteristics as follows. (1) A single, unique, cilia-based statocyst or aboral organ that regulates comb plate beating. (2) A unique early embryo that undergoes determinate biradial division. (3) Four distinct radially positioned quadrants demarcated by a tentacular plane (that passes through a pair of tentacular bulbs in the Tentaculata and is imaginary in the Nuda) and a stomodeal plane that passes through the stomodeum, both of which are radially organized around the oral-aboral axis. (4) Eight meridional (i.e., parallel to the oral/aboral axis) rows of unique ciliary comb plate paddles or “ctenes” composed of up to hundreds of thousands of conventional cilia (Afzelius 1961) that first develop in prehatchling larvae. (5) Rotational symmetry based on the unique placement of dual anuses (Martindale, Finnerty, and Henry 2002). (6) Nonstinging colloblasts used for prey capture (Bargmann, Jacob, and Rast 1972, Franc 1978); nematocysts found in Haekelia are obtained from cnidarian prey (Mills and Miller 1984). (7) True, multinucleate, smooth muscle cells that extend through the mesoglea as in a mesoderm; striated muscle is seen only in tentillae of Euplokamis (Mackie, Mills, and Singla 1987). (8) Planktonic larvae; in Class Tentaculata all have cydippid larvae (globose body with 2 long tentacles). (9) Flat or ruffled strips of ciliated epithelium flanking the statocyst in the stomodeal plane. The purpose of these so-called polar fields is unclear; however, they continually transport water over the statocyst.

Forward (mouthfirst) swimming in ctenophores is mechanically controlled by the statocyst. Inside the statocyst, a single statolith is borne by 4 compound balancer cilia. Each balancer connects to the aboralmost comb
plates of 2 comb rows by ciliated grooves (cg). As each balancer beats, the cg beats and stimulates a wave of comb row beating. Except in Cydippida and Nuda, intraplate ciliary grooves (icg) extend between plates to cause beating of the orally adjacent plate (Tamm 1973, 1982, 1984).

All ctenophores are simultaneous hermaphrodites, except for Bathycyroe (see Miller, Harbison, and Hilfer 2000) and Ocyropsis (see Harbison and Miller 1986). Male and female gonads typically line opposing sides of subrow canals, with the female gametes adjacent to the tentacular and substomodeal planes in Tentaculata (Moss, unpubl. obs.). Martindale (1987) reported larval reproduction in Mnemiopsis. Internal fertilization has been reported by Moss and Kideys (abstract, International Conference on Coelenterate Biology, 2003). Harbison and Madin (1982) and Harbison (1991) described ctenophore characteristics and presented a traditional morphological classification. Mianzan (1996) described Southern Hemisphere forms; all replace the previous standard, Hyman (1940).

### Previous Reports of Ctenophores from the Gulf of Mexico

Sears (1954) cited only 6 publications that described 12 Gulf of Mexico species; most were from very early in the 20th century or late 19th century. Despite considerably improved technology, the situation is little changed today. Few marine labs focus on ctenophore biology, and open-water ctenophores are poorly known. Mnemiopsis mccradyi and Beroe ovata are the common coastal species found around the perimeter of the Gulf of Mexico. Open-water Gulf ctenophores are almost certainly all in the Atlantic, if not all oceans (see the following checklist).

### Diversity


Blue-water sampling (Hamner et al. 1975, Harbison and Madin 1979, Costello and Mianzan 2003), remotely operated and manned submersibles (Matsumoto and Harbison 1993, Johnson and Widder 1998, Hunt and Lindsay 1999, Lindsay and Hunt 2005), specialized imagers (Davis et al. 1992, Samson et al. 2001, Luo et al. 2004), and acoustic sensors (Monger et al. 1998) provide improved techniques for study of open-water ctenophores. The open-ocean Thalassocalyce and Bathocyroe (Madin and Harbison 1978a, b), were discovered by blue-water diving. Population estimates are more accurate today when determined with fast-imaging tows (Sutton et al. 2001, Remsen, Samson, and Hopkins 2004).

An up-to-date, continually updated list of species is maintained by Mills (1998). Nearly 170 species currently appear there, although this number may drop because of synonymy of names, and because reclassification based on new data will clarify phylogenetic relations among the Ctenophora. For instance, Mills (1987) revised the genus Euplokamis, based on tentacular morphology and ultrastructure (Mackie, Mills, and Singla 1987). Research in new locations is steadily adding to the number of valid new species.

### Evolution and Relationships with Other Groups

Fossil ctenophores are very rare. Discovery of a Devonian cydippid (Stanley and Stürmer 1983), a putative Cambrian beroid (Conway-Morris and Collins 1996), and a potential lobate and beroid from the lower Cambrian (Chen and Zhou 1997) indicate the Ctenophora to be ancient.
Podar et al. (2001) revealed considerable evolutionary distance between Ctenophora and other Metazoa, yet ctenophores have exceptionally low 18S rDNA diversity. This suggests that all extant ctenophore species arose relatively recently after a severe genetic bottleneck. Accordingly, Bayha, McDonald, and Gaffney (2003) found almost no ITS1/ITS2 variation between Mnemiopsis populations, and concluded that there may be only one Mnemiopsis species.

The paucity of fossil data leads to uncertainty as to whether the cydippids or beroids are basal among the Ctenophora. Ospovat (1985) concluded that, based on analyzed canal morphology, separation of Class Tentaculata and Class Nuda was artificial. His groups—subclass Cyclocoela (containing Beroida, Cestida, Ganeshida, Lobiferida, and Thalassocalyceda, Cambojida and Cryptolobiferida) and subclass Typhlocloca (Cydippida and Platycetenida)—are reflected in Mills (1998). Harbison (1985) similarly concluded that Ctenophora have few affinities with other Metazoa, but that Cydippida is polyphyletic. Podar et al. (2001) also support a polyphyletic Cydippida, based on 18 rDNA of 26 cydippids, lobates, platycetenids, and beroida. Cydippid polyphyly was supported by the observation that cydippid Haekelidae had strong affinity with Beroida and that cydippid Pleurobrachiidae grouped with Thalassocalyceda, Lobata, and Cestida. Platycetenida and Mertensiidae have several strong similarities, thus supporting cydippid polyphyly. Podar et al. (2001), like Harbison (1985), positioned Mertensiidae basal to the Ctenophora, and Platycetenids between Mertensiidae and the remaining orders.

The phylogenetic relationship between Ctenophora and other basal Metazoa (Placozoa, Porifera, and Cnidaria), and the Bilateria is still uncertain (Collins et al. 2005). Embryonic fate mapping suggests that ctenophores lie at the boundary of diploblastic Radiata and triploblastic Bilateria (Martindale and Henry 1998). Hox analysis suggests they may lie between Porifera and Cnidaria (Halanych and Passamaneck, 2001). The 18S and 28S rDNA studies reveal Ctenophora to be more distant to Bilateria than the Cnidaria (Kim, Kim, and Cunningham 1999, Medina et al. 2001), in contrast to results from morphological studies. Today, diploblast/triploblast boundaries are not as clear as once thought, because recent molecular analyses reveal higher animal axial patterning elements in Cnidaria and Ctenophora (Halanych, 2004). The hox and growth factor analyses reveal the cnidarian Nemastostella to have close affinity with Bilateria (Finnerty et al. 2004). The BAC library construction for Mnemiopsis should help clarify Ctenophora phylogenetics (Steele 2005).

**Ecological and Economic Importance**

Ctenophores have great impact on marine food webs. Hardy (1965) described predation on larval fish and eggs, copepods, and other gelatinous zooplankton. Beroe (Swanberg 1974, Tamm 1982), Mnemiopsis (e.g., Reeve and Walter 1978, Larson 1987), and Pleurobrachia (Hirota 1974, Reeve and Walter 1976) all strongly crop marine secondary production. Open-water species also have high predation potential (Harbison, Madin, and Swanberg 1978, Kremer, Reeve, and Symes 1986, Matsumoto and Harbison 1993). Mnemiopsis indirectly influences algal stocks (Deason and Smyda 1982) and may affect flagellate populations (Sullivan and Gifford 2004). Mnemiopsis adjusts to prey density and pumps more water (up to 2 L hr⁻¹) in the presence of more food (Larson 1988). The insensitivity of Mnemiopsis to low dissolved oxygen should aid foraging in oxygen-depleted waters (Decker, Breitburg, and Purcell 2004). Ctenophores are prey for many fish (Purcell and Arai 2001) and so have great economic impact. Mnemiopsis populations derived from ballast-water animals disrupted the Black Sea (Vinogradov 1989, Oguz et al. 2001) and Caspian ecosystems (Kideys and Moghim 2003), and those ctenophores that bear parasites may be especially problematic in exotic, new locations (Crowell 1976, Martorelli 2001, Moss et al. 2001, Torchin, Lafferty, and Kuris 2002).

**Checklist of Ctenophores of the Gulf of Mexico**

Taxonomic orders and families in the checklist are arranged according to Mills (1998), checked against Bisby et al. (2005), Cairns et al. (2002), and van der Land (2001). Wrobel and Mills (2003) and Cairns et al. (2002) provided general distributions. Bolinopsis vitrea is likely in the Gulf because it was mentioned by Sears (1954) and is seen in Cuba and Jamaica (Lalana, Ortiz, and Varela 2001, Persad et al. 2003). Suárez and Gasca (1994) report Mnemiopsis spp. from the northern Yucatán, and so it most likely occurs in the southwestern Gulf. Leucothea, Callianira, Hormiphora, Euplokamis, and Pleurobrachia spp. occurred in the west-southwest quadrant (Biggs et al. 1984). Agmayeria tortugensis, nomen nudum, previously reported by Bailey et al. (1994) and Bailey, Youngbluth,
and Owen (1995) from the North Atlantic and by Lindsay and Hunt (2005) from the Pacific, was reported also in a personal communication from Widder and Frank for the Gulf of Mexico (checklist, endnote 1) and may be the “red cydippid” of Haddock (1995; checklist, endnote 5). Llyria is undescribed, yet reported for the Gulf of Mexico via personnel communication from Haddock (see checklist, endnote 5). Lindsay and Hunt (2005) previously reported Llyria from the coast of Japan.

Abbreviations

The following abbreviations are employed in the checklist. Depth indicators: itd = intertidal (0–2 m); bns = bay/inshore (0–50 m); crr = reef (0–50 m); ocs = outer continental shelf (50–200 m); slp = slope (200–3000 m), and plk = planktonic.

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References


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...y bibliographia de los cteneleros (Cnidaria) y los ctenophoros (Ctenophora), de aguas Cubanas. Revista Biología 15: 158–169.
### Taxonomic summary for Ctenophora of the Gulf of Mexico.

<table>
<thead>
<tr>
<th>Component subgroups</th>
<th>Total species</th>
<th>Number endemic species</th>
<th>Number nonindigenous species</th>
</tr>
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<tr>
<td>Class Tentaculata</td>
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<td>0</td>
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<tr>
<td>Class Nuda</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>18</strong></td>
<td><strong>0</strong></td>
<td><strong>0</strong></td>
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### Checklist of phylum Ctenophora from the Gulf of Mexico.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Habitat-Biology</th>
<th>Depth (m)</th>
<th>Overall geographic range</th>
<th>GMx range</th>
<th>References/Endnotes</th>
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<tr>
<td>Class: Tentaculata</td>
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<td>Class/Subclass: Typhlocoela</td>
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<td></td>
</tr>
<tr>
<td>Family: Cestida</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cestum veneris</em> Lesueur, 1813</td>
<td>ocs, slp, plk</td>
<td>0–midwater</td>
<td>Circumsubtropical</td>
<td>wnw, wsw, ene</td>
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</tr>
<tr>
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<td>ene</td>
<td></td>
</tr>
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<tr>
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<td>0</td>
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<td>ene</td>
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<td>Family: Bathocyroidae</td>
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<td><em>Bathocyroe fosteri</em> Madin &amp; Harbison, 1978</td>
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<td>0</td>
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<td>ene</td>
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</tr>
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<td></td>
<td></td>
<td></td>
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<td><em>Mnemiopsis leidyi</em> A. Agassiz, 1865</td>
<td>itd, bns, ocs, slp, plk</td>
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<td>Atlantic</td>
<td>nne, ene, ese</td>
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<td><em>Mnemiopsis mccradyi</em> Mayer, 1900</td>
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<td>Atlantic</td>
<td>nne, ene, ese</td>
<td>40, 65, 66^4</td>
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<tr>
<td><em>Eurhaphaca vexilligera</em> Gegenbaur, 1856</td>
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<td>0</td>
<td>Atlantic, Pacific</td>
<td>wnw, ene</td>
<td>7^1</td>
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<tr>
<td><em>Kiyohimea aurita</em> Komai &amp; Tokioka, 1940</td>
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<td>0</td>
<td>Atlantic, Pacific</td>
<td>ene</td>
<td>1</td>
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<td>0</td>
<td>Atlantic</td>
<td>ene</td>
<td>1</td>
</tr>
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<td><strong>Family: Ocyropsida</strong></td>
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<td></td>
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<td></td>
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</tr>
<tr>
<td><em>Ocyropsis crystallina crystallina</em> Rang, 1828</td>
<td>ocs, slp, plk</td>
<td>0–15</td>
<td>Atlantic</td>
<td>nne, ene, ese</td>
<td>73, 1, 4</td>
</tr>
<tr>
<td><em>Ocyropsis crystallina guttata</em> Harbison &amp; Miller, 1986</td>
<td>ocs, slp, plk</td>
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<td>Atlantic Slope water</td>
<td>ese</td>
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<td><em>Ocyropsis maculata immaculata</em> Rang, 1828</td>
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<td>ocs, slp, plk</td>
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<td>Atlantic, Pacific</td>
<td>wnw, wsw, ene</td>
<td>7, 73^1</td>
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<tr>
<td><em>Thalassocalycine inconstans</em> Madin &amp; Harbison, 1978</td>
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<td>0–785</td>
<td>Atlantic, Pacific</td>
<td>wnw, wsw, ene</td>
<td>7^3</td>
</tr>
</tbody>
</table>
## Checklist of phylum Ctenophora from the Gulf of Mexico. (continued)

<table>
<thead>
<tr>
<th>Taxon</th>
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<th>Depth (m)</th>
<th>Overall geographic range</th>
<th>GMx range</th>
<th>References/Endnotes</th>
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<td>73², 7³</td>
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<td><em>Beroe ovata</em> Bruguère, 1789</td>
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<td>0–50</td>
<td>Atlantic</td>
<td>ene, ese</td>
<td>7³, 7⁶</td>
</tr>
</tbody>
</table>

---

1. Widder, E., and T. Frank, 1995, personal communication. Blue-water dives in the *Johnson Sea-Link* II, 27°05.269′N, 085°03.890′W to 26°31.613′N, 084°50.620′W.
3. Moss, A. G. unpubl. obs. We observe *M. leidyi* and *M. mccradyi* in shallow waters from the Gulf Coast Research Lab south and east to Rookery Bay, Florida, often very closely associated with the sediment.
5. Haddock, S., 1995, personal communication. *Johnson Sea-Link* II blue-water dives: 27°03.138′N, 085°01.669′W to 26°46.757′N, 084°52.720′W.