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Research paper

The fossil record of cnidarian medusae

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Abstract

Fossils of cnidarian medusae are extremely rare, although reports of fossil “medusoids,” most of which do not represent medusae, are rather common. Our previous inability to distinguish these fossils has hampered attempts to investigate patterns and processes within the medusozoan fossil record. Here we describe criteria for the recognition of *bona fide* fossil medusae and use them to assess the evolutionary, paleoenvironmental, and taphonomic history of the Medusozoa. Criteria include distinctive sedimentologic and taphonomic features that result from transport, stranding, and burial of hydrous clasts, as well as unequivocal body structures comparable to those of extant animals. Because the latter are uncommon, most fossil medusae remain in open nomenclature; many are assigned to stem-group scyphozoans.

The majority of described medusae are associated with coastal depositional environments (such as tidal flats or lagoons). They rarely occur in oxygen-poor deeper-water facies. All medusan groups have long geologic histories. Scyphozoa are known from the Cambrian, but more derived scyphomedusae were not demonstrably present until the Carboniferous; Mesozoic scyphozoans are rather diverse. Hydromedusae are known from the Ordovician but may extend back to the Cambrian. The record of cubozoans is shorter and sparser; the oldest definite cubozoan is Carboniferous in age.

Keywords: Medusae; Jellyfish; Scyphozoa; Hydrozoa; Cubozoa; *konservat-lagerstätten*

1. Introduction

In comparison with the modern world, the cnidarian fossil record is hugely biased toward biomineralized forms. Cnidarian medusae are abundant and widespread today, but only represented by rare and sporadic occurrences through the fossil record, mostly in *konservat-lagerstätten*. This study assesses the fossil records of the three major medusan groups: scyphozoan medusae, hydrozoan medusae, and cubozoans. Porpitid (chondrophorine) hydromedusae and conularids are not included because they possess tough or hard parts and have been the subject of recent reviews (e.g., Fryer and Stanley, 2004; Van Iten et al., 2006). Similarly, we do not present a comprehensive review of the many reported “medusoids” (i.e., medusa-like structures or fossils) that do not meet our criteria for recognition (Outlined in Section 2, below).

Fossil medusae usually tell us more about their preservational history than their palaeobiology (Schäfer, 1941, 1972). Nevertheless, in rare instances it is possible to identify unequivocal body structures comparable to those of extant organisms. More commonly, sedimentologic and taphonomic criteria are required to distinguish medusae from non-cnidarian medusoid structures. There is a long history of study of fossil medusoids (e.g., Haeckel, 1869; Walcott, 1898) and possible occurrences are spread through a great variety of literature. Most represent non-medusan fossils and trace fossils, or inorganic features such as fluid escape structures, microbial decomposition structures, and scratch circles. Only a few published medusoids represent unequivocal *medusae*, and we have been able to satisfactorily recognize only nine major medusa-bearing deposits (Table 1). Since these are in units spread across international and other mapping boundaries, there might appear to be more deposits than really exist: many occur in genetically related lithostratigraphic units. This is a shockingly small fossil record for groups with such importance in modern seas, but by considering them

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Table 1
Recognized occurrences of bona fide fossil cnidarian medusae. Occurrences are clustered into nine genetically related depositional groups (A–I).

Lagerstätte group	Age/unit(s)	Location	Lithology; Dep. Environment	Mode of preservation	Taxa	# of Specimens; # of Horizons	Diameter (mm)	Previous interpretation	Revised interpretation	Key reference(s)
A	Middle Cambrian (Series 3); Burgess Shale	Mount Field, British Columbia, Canada	Shale; subtidal	Organic carbon, aluminosilicate film	–	>30; Unknown	40–120	Unknown	Scyphozoa?	Devereux (2001)
B	Middle Cambrian (Series 3); Marjum Formation	House Range, UT, USA	Mudstone; subtidal	Organic film – composition unknown	–	10; >3?	7–15	Scyphozoa? (Semaeostomeae?, Coronatae?), Hydrozoa? (Narcomedusae?), Cubozoa?	Scyphozoa? (Semaeostomeae?, Coronatae?), Hydrozoa? (Narcomedusae?), Cubozoa?	Cartwright et al. (2007)
C	Middle Cambrian (Series 3); Elk Mound Group	Mosinee, WI, USA	F- to m-grained quartz arenites; intertidal	3D, mouldic	–	>10,000; >19	50–950	Cnidarian medusae	Scyphozoa	Hagadorn et al. (2002), Tarhan (2008)
C	Middle Cambrian (Series 3); Potsdam Group	Ausable Chasm, New York, USA; Havelock, Quebec, Canada	F- to m-grained quartz arenites; intertidal	Mouldic	–	>1000; >6	70–660	Scyphozoa (Semaeostomeae?, Rhizostomeae?)	Scyphozoa (Semaeostomeae?, Rhizostomeae?)	Hagadorn and Belt (2008), Lacelle et al. (2008), Tarhan (2008)
D	Upper Ordovician; Stony Mountain Formation	William Lake, Manitoba, Canada	F-grained argillaceous dolomudstone; intertidal – lagoonal	3D, mouldic and replacement	–	>100; >4	20–65	Hydrozoa, Scyphozoa?	Hydrozoa (Anthomedusae?, Leptomedusae?), Scyphozoa?	Young et al. (2007)
E	Upper Carboniferous; Carbondale Formation	Essex and Astoria, IL, USA	Siderite concretions in siltstone; restricted marine – lagoonal	Impressions	*Anthracomedusa turnbulli*	>20	28–100	Cubozoa (Carybdeidae)	Cubozoa (Chirodropidae)	Johnson and Richardson (1968), Foster (1979), Sroka (1997), Gershwin (2003), Selden and Nudds (2004)
					Octomedusa pieckorum	∼15	3–21	Scyphozoa (Coronatae?)	Hydrozoa or Scyphozoa (Narcomedusae or Coronatae)	
					Essexella asherae	>35,000	6–90	Scyphozoa (Rhizostomeae?)	Scyphozoa or Hydrozoa (Trachymedusae)	
					Reticulomedusa greenei	∼3	45	Scyphozoa (Rhizostomeae?)	Scyphozoa	
					Lascoa mesostaurata	1; 1	40	Scyphozoa (Semaeostomeae)	Scyphozoa (Semaeostomeae)	
F	Upper Carboniferous; Cherryville Formation	Limekiln Hollow, IA, USA	Shale; subtidal	Carbon films; mouldic?	*Prothysanostoma eleanorae*	7	∼30–50	Scyphozoa (Rhizostomeae)	Scyphozoa (Rhizostomeae)	Ossian (1973)

Table 1 (*Continued*)

Lagerstätte group	Age/unit(s)	Location	Lithology; Dep. Environment	Mode of preservation	Taxa	# of Specimens; # of Horizons	Diameter (mm)	Previous interpretation	Revised interpretation	Key reference(s)
G	Lower Triassic; Grès à Voltzia Formation	Vilsberg and Arzviller, Vosges Septentrionales, France	Silt and clay laminites; delta plain ponds	$CaPO_4$ replacement	*Progonionemus vogesiacus*	10; Unknown	8–40	Hydrozoa (Limnomedusae)	Hydrozoa (Limnomedusae)	Grauvogel and Gall (1962), Gall (1990), Selden and Nudds (2004)
H	Upper Jurassic; Cerin Lithographic Limestone Formation	Cerin, Jura Mtns, France	Lithographic limestones; lagoon	Mouldic	*Bipedalia cerinensis*	14; 1	45–70	Cubozoa (Carybdeidae)	Cubozoa (Carybdeidae)	Gaillard et al. (2006)
					Paracarybdea lithographica	5; 1	50	Cubozoa, (Carybdeidae)	Cubozoa? (Carybdeidae?)	
					Paraurelia cerinensis	>1000; >6	15–105	Scyphozoa (Semaeostomeae)	Scyphozoa (Semaeostomeae)	
					Paraurelia sp. A	~3; 2	120	Scyphozoa (Semaeostomeae)	Scyphozoa (Semaeostomeae?)	
I	Upper Jurassic; Solnhofen Formation	S. Franconian Alb, Bavaria, Germany	Laminated micritic limestones; lagoon	Mouldic	*Quadrimedusina quadrata*	1; 1	76	Cubozoa (Order Carybdeidae)	Cnidarian medusa, unknown affinities	Haeckel (1866, 1869, 1874), Walcott (1898), Maas (1906), Kuhn (1938), Kieslinger (1939), Kolb (1951), Harrington and Moore (1955, 1956a,b,c), Barthel et al. (1990), Selden and Nudds (2004)
					Epiphyllina distincta	Unknown	~13	Scyphozoa (Coronatae)	Scyphozoa (Coronatae)	
					Cannostomites multicirratus	1; 1	~200	Scyphozoa (Coronatae?)	Scyphozoa	
					Leptobrachites trigonobrachius	Rare; unknown	~170	Scyphozoa (Rhizostomeae?)	Scyphozoa	
					Semaeostomites zitteli	1; 1	~80	Scyphozoa (Semaeostomeae)	Scyphozoa (Semaeostomeae)	
					Eulithota fasciculata	1; 1	~70	Scyphozoa (Semaeostomeae)	Scyphozoa	
					Rhizostomites sp.	Many; unknown	>500	Scyphozoa (Lithorhizostomatida)	Scyphozoa (Lithorhizostomatida)	
					Acalepha deperdita	>1; Unknown	~70	Hydrozoa (Trachylinida?)	Cnidarian medusae, poss. Hydrozoa	
					Acraspedites antiquus	Unknown	~140	Hydrozoa (Trachylinida?)	Cnidarian medusae, poss. Hydrozoa	
					Hydrocraspedota mayri	>1; Unknown	~200	Hydrozoa (Trachylinida?)	Hydrozoa	

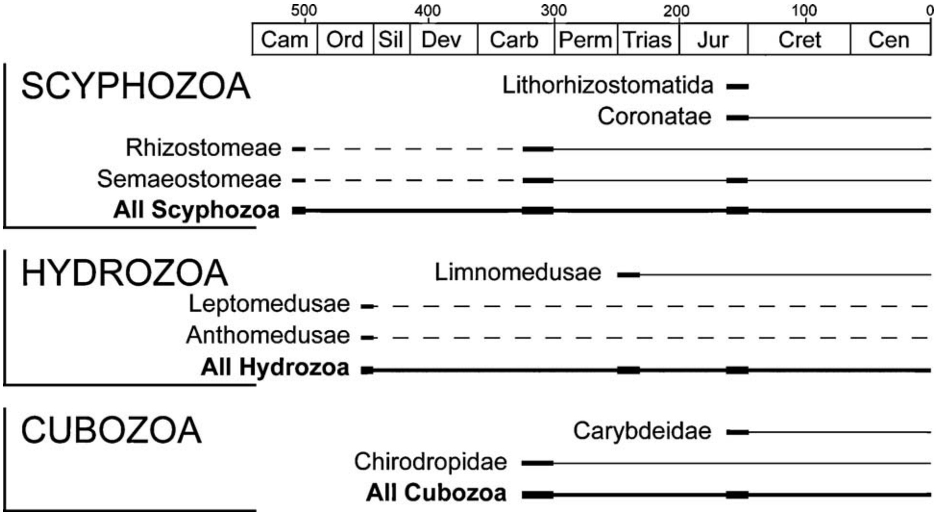

Fig. 1. Stratigraphic distribution of fossil medusae. Thick lines show intervals of known occurrence and thin lines show inferred occurrence. Dashed lines denote range extensions based on occurrences that have not yet been formally published.

together, we gain insights into the patterns of evolution and extinction among mobile cnidarians.

2. Fossilization of medusae and criteria for recognition

Medusae are relatively easy to study in modern intertidal to mid-water subtidal settings, and are commonly deposited *en masse* along coastlines. Studies of these stranded medusae, in combination with laboratory burial experiments and observations of premortem behaviour, have provided insights into medusan fossilization processes (Schäfer, 1941, 1972; Kornicker and Conover, 1960; Müller, 1984, 1985; Norris, 1989; Bruton, 1991). Together with our own studies of modern medusan taphonomy, these ecologic and taphonomic studies permit establishment of criteria for recognition of fossil medusae, which are summarized below.

Because they have nearly the same density as seawater and are difficult to bury, medusae are rare in sediments deposited below storm wave base, except where the latter are depleted of oxygen (Table 1A and B). Similarly, although mass strandings are common on sandy shorefaces, such settings often have too much scavenging, bioturbation, and hydraulic energy to preserve delicate carcasses. Preservation of medusae is best facilitated in low-energy tidal flats or lagoons (Schäfer, 1941, 1972). In such settings, most live stranded jellyfish will orient dorsal side up; these are commonly covered with sediment as wave energy wanes or tides ebb (Fig. 2A, B, and E). Medusae deposited after death are generally in hydrodynamically stable orientations, typically with dorsal side up or down (Fig. 2D). Most do not orient preferentially on their sides, with the exception of rhizostome scyphozoans (Schäfer, 1972).

Live medusae pump their bells in attempting to escape stranding; this can result in the ingestion of considerable amounts of sediment. As a result, fossil medusae commonly exhibit raised sediment mounds in the mouth area, moat-like depressions near the bell margins (Fig. 2H), and/or globular internal moulds (Schäfer, 1941, 1972; Müller, 1985; Bruton, 1991). Fossilization potential is enhanced by the cementation of sediment by decomposing fluids and bacteria, and by partial dehydration due to subaerial exposure. These processes favour the preservation of specimens deposited dorsal side up. Dehydration and shrinking of a medusa can result in the development of wrinkles or fissures and progressive loss of structure (Fig. 2I). Medusae buried by sediment may show a history of crumpling and slumping, and can collapse during decomposition to produce concave hemispheric structures (Fig. 2C).

Tentacles, an important feature of living jellyfish, are among the first features to disappear during decomposition. Fossil medusae rarely have recognizable tentacles (but see Fig. 2I), except members of groups that have particularly thick and tough tentacles in life (e.g., Cubozoa). Oral arms are often thicker, and may be preserved. Although impressions of radial canals may also be visible, tentacles and oral arms are never oriented in a perfectly radial pattern when medusae come to rest on or are entrained in sediment. Instead, they are usually dispersed or tangled like strands at the head of a mop.

Several authors have stated that medusae can only fossilize as moulds (Schäfer, 1972; Bruton, 1991; Fürsich and Kennedy, 1975) but outer or inner soft tissues can be preserved by authigenic mineralization (cf. Briggs, 2003; Fig. 2F; Table 1A, B, D, F, and G). With mouldic preservation, any one specimen will show some structures but not others, depending whether it represents a dorsal or ventral surface, or internal structure. This necessitates study of multiple specimens. The complexity of studying mouldic material is further increased by the varied processes of decay and transport. Effects of waves or currents include twisting, folding, tearing, and preservation in varied orientations (Fig. 2G).

It is thus possible to establish taphonomic criteria for the identification of fossil medusae. They are almost never perfectly radially symmetrical, nor are they always oriented parallel to, or on top of, a single bed surface. Sites at which medusae occur demonstrate paleoenvironmental and sedimentologic features consistent with the deposition and preservation of jellyfish; often they occur in conjunction with sedimentary structures or fossils characteristic of hypersaline, brackish, or emergent conditions.

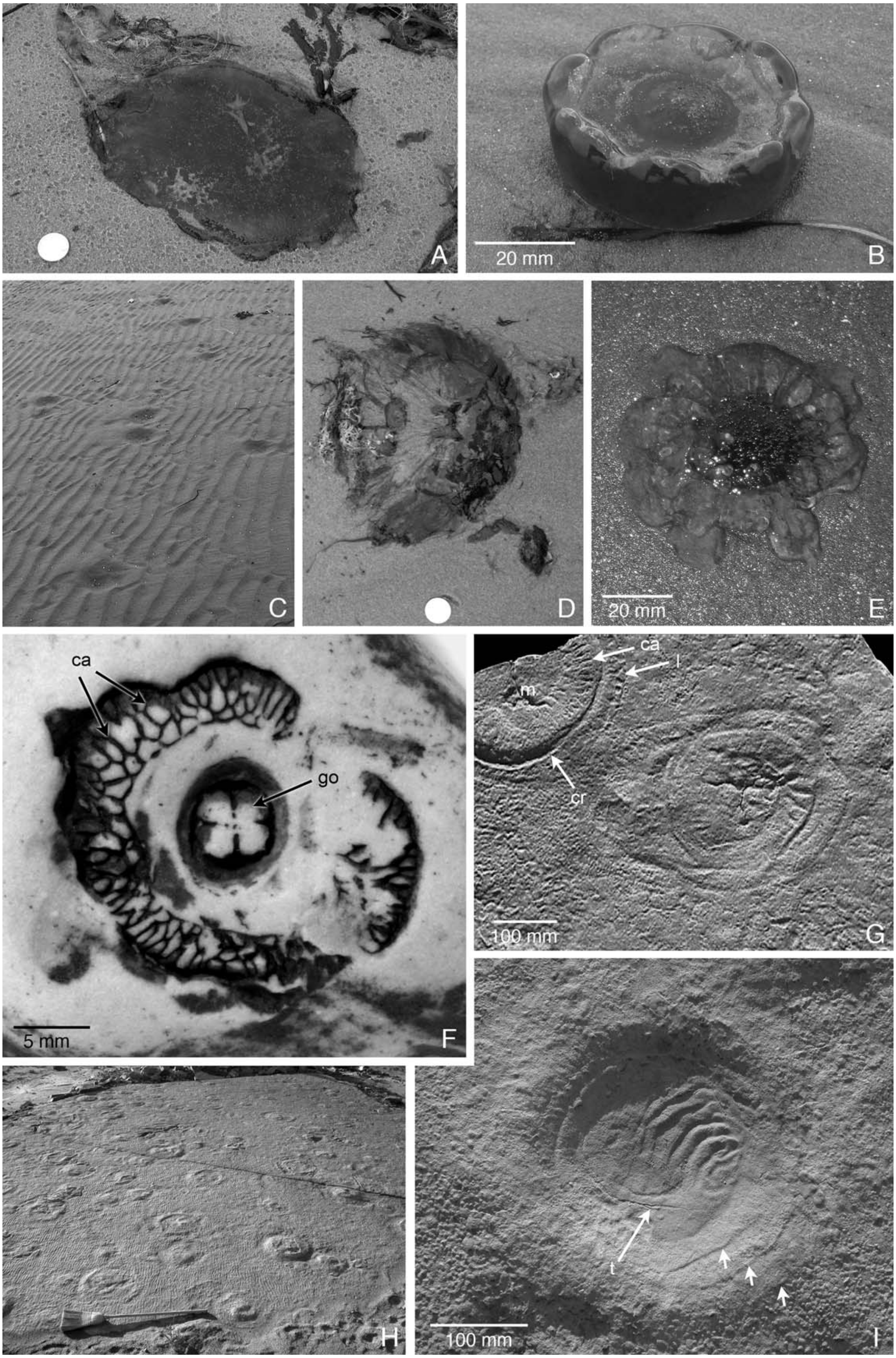

Fig. 2. Taphonomy of modern Scyphozoa, preservation of fossil medusae, and examples of Cambrian medusae. (A–E) Taphonomy of modern *Cyanea capillata* (Linnaeus) in shoreline environments, Prince Edward Island, Canada: (A) medusa with subumbrella down, note irregular outline and attached debris (coin diameter 24 mm); (B) medusa subumbrella down with muscles contracted; (C) pits resulting from decay of shallow-buried *Cyanea* (pits are about 50–200 mm wide); (D) medusa subumbrella up with attached debris and sediment (coin diameter 24 mm); (E) medusa with subumbrella down, bell margin damaged by birds and waves.

Bona fide medusae typically occur on many different horizons within a deposit, often with dozens to thousands of specimens on individual surfaces (Fig. 2H). Medusae occur in both clastic and carbonate rocks, representing a wide range of grain sizes; many of these rocks exhibit evidence of microbial binding and/or stagnation.

On the basis of this understanding of the fossilization of medusae, we have considered all documented occurrences of medusoids or medusae using several criteria: (1) evidence of original morphology consistent with cnidarian medusae; (2) evidence of preburial transport, deformation, tearing, and/or desiccation; (3) an appropriate paleoenvironment based on associated lithology, biota, and sedimentary structures; (4) number of individuals and horizons of occurrence; and (5) evidence that the medusoid(s) cannot be readily assigned to other phenomena, such as scratch circles, gas release structures, non-medusan body fossils, trace fossils, evaporite pseudomorphs, archaeological etchings, or inorganic concretions. Using these criteria, we divided all published medusoid and medusae occurrences into three categories: well documented fossil medusae (Table 1), possible medusae or those of uncertain affinities (many of which are based on single specimens), and non-medusae. With the exception of the Proterozoic medusoid record, only the *bona fide* medusae are treated here.

3. The Proterozoic record

Since their initial discovery (Sprigg, 1947), many Ediacaran fossils have been considered to be allied with cnidarian medusae. Their hypothesized medusozoan affinity stems from their discoidal shape, pliability, antiquity (and thus proximity to basal nodes on the metazoan tree), and unusual preservation in sandstones. No Ediacaran medusoids exhibit evidence of transport (e.g., Peterson et al., 2003) and most possess radial structures and rooting features indicating that they grew below the sediment-water interface as attachments for frond-like Ediacarans (e.g., Jenkins and Gehling, 1978; Seilacher, 1992; Steiner and Reitner, 2001). Moreover, tentacle-like structures on Ediacarans are always radial or quasi-radial; they are never tangled, twisted, draped across/under/around the "bell," or enmeshed with adjacent specimens as one would expect from deposition of a mop-like jellyfish. Radial structures reported from Ediacarans often extend beyond the central disc and thus cannot be impressions of radial canals. Simple discoidal Ediacarans are still less plausible as cnidarians: they lack structures diagnostic of cnidarian morphology, including even the most basic radial patterns seen in anthozoan trace fossils such as *Bergaueria*, and do not show evidence of shearing or transport. Many Ediacaran medusoids exhibit margin-deformation features that suggest they grew in place next to one another, glued to or resting on the sediment surface. All Precambrian medusoids are Neoproterozoic in age, and most are Ediacaran. Cryogenian medusoids (e.g., *Bunyerichnus*) have been reinterpreted as inorganic scratch circles. Thus, there are no *bona fide* published Proterozoic medusae.

4. The Palaeozoic record

Nearly all Palaeozoic medusae belong to stem groups of the modern medusan classes (Table 1; Fig. 1), although medusae with derived features may have occurred as early as the Middle Cambrian. More complex forms appeared by the Late Carboniferous.

The oldest known medusae come from the Series 3 (i.e., middle) Cambrian. In the Burgess Shale, dozens of specimens are known, yet detailed taxonomic analysis of these medusae is lacking and at present they have only been broadly categorized as Scyphozoa (Devereux, 2001). Slightly younger occurrences from a Burgess-type deposit in Utah, USA (Cartwright et al., 2007) provide tantalizing hints that the major medusozoan clades diversified early. The Utah medusae are very small and few specimens are known, but they show remarkable preservation of features such as tentacles and muscles. Four informally recognized types show strong similarities to narcomedusan hydrozoans, semaeostome and coronate scyphozoans, and possibly cubozoans. The extreme rarity of medusae in these deeper-water *konservat-lagerstätten*, from which thousands of specimens of other groups are known, is consistent with the suggestion that the low density of medusae makes them unlikely to be deposited in such settings.

Abundant medusae also occur in Series 3 (middle) Cambrian coarser-grained clastic rocks deposited in intertidal settings at three sites in North America (Hagadorn et al., 2002; Hagadorn and Belt, 2008; Lacelle et al., 2008) (Fig. 2G–I). Their mouldic preservation is more similar to that of Ediacaran fossils than to preservation in younger Palaeozoic rocks; the Cambrian taphonomic regime permitted the preservation of carcasses that would presumably have been lost to bioturbation or decomposition later in the Palaeozoic. Despite their occurrence in fine- and medium-grained sands, part-counterpart molds and steinkerns of these fossils reveal radial canals, manubria, oral arms, coronal rings, and lappets. Most are likely semaeostome or rhizostome scyphozoans (Tarhan, 2008).

Numerous medusae occur in Upper Ordovician marginal marine dolostones at William Lake, central Canada (Young et al., 2007). The best-preserved specimens are three-dimensional. Tissues that are thick and tough in living medusae, such as

(F) Semaeostome scyphozoan medusa similar to modern *Aurelia*, with canals (ca) and gonads (go) preserved as pyrite in chert nodule (pyrite has been weathered), probably of Ordovician age, Manitoba, Canada (Manitoba Museum specimen, MM I-2555). (G–I) Cambrian scyphozoan medusae from Wisconsin, USA: (G), two medusae on bed sole which have "double impressions", having been shifted after first coming to rest subumbrella down on the sediment; note radial canals (ca), lappets (l), manubrium (m), and coronal ring (cr); (H) composite stranding surface bearing hundreds of large medusae that were buried in at least four successive depositional events (broom in foreground is 1.37 m long); (I) medusa on bed sole that exhibits post-depositional shrinkage of the bell (three successively smaller bell margin impressions are arrowed), and rippling of sand which was formerly encased in the stomach. Both events postdate initial excavation of a moat by the living jelly; also note pustular, possibly microbial, textures adjacent to carcass, radial lappet-like impressions at upper left, and diagonal strand across carcass that may be a sand-coated tentacle (t).

manubria, stomachs, and canals, have been replaced by calcareous and pyritic material (Fig. 3A–C). Bells and tentacle bases appear as colour variations in dolostone. The majority are hydromedusae, some showing affinities to the extant orders Anthomedusae and Leptomedusae. A few specimens are likely scyphozoans (Fig. 3D).

Unequivocal fossil medusae have not yet been discovered in Silurian or Devonian rocks, but the Carboniferous provides a rich assemblage of Palaeozoic medusae. Thousands of specimens occur in siderite concretions of the Mazon Creek *konservat-lagerstätte* of Illinois, USA (Fig. 3E–H). Some of these preserve external features such as bell margins and tentacles, but internal details are obscure. Mazon Creek medusae include the oldest definite cubozoan, a member of the still-extant family Chirodropidae (Johnson and Richardson, 1968; Gershwin, 2003; see Fig. 3E and F), and the oldest definite semaeostome scyphozoan (Foster, 1979). Other Mazon Creek medusae are more problematic; *Octomedusa pieckorum* Johnson and Richardson (1968; see Fig. 3H) may be a coronate scyphozoan (Foster, 1979) or a narcomedusan hydrozoan. *Essexella asherae* Foster (1979), by far the most abundant Mazon Creek medusan, is a blob-like form that could be either a scyphozoan or a hydromedusan.

The finest described Palaeozoic fossil medusae are the seven specimens of the Late Carboniferous *Prothysanostoma eleanorae* Ossian (1973) from Iowa, USA. These are preserved as carbon films in indurated black shale, showing remarkable details of the bell and oral arms; they are the oldest rhizostome scyphozoans.

5. The Mesozoic and Cenozoic record

The Mesozoic medusan record comprises some spectacularly preserved fossils, including forms that are distinctly more derived than their Palaeozoic precursors. Since all recognized medusae occur in just a few *konservat-lagerstätten*, all of them in Europe, it is possible that the Mesozoic record is even less complete than that for the Palaeozoic.

Progonionemus vogesiacus Grauvogel et Gall (1962) is the oldest known limnomedusan hydrozoan. In these specimens from the Lower Triassic Grès à Voltzia of France, soft tissues including gonads and tentacles occur, allowing direct comparison with the extant genus *Gonionemus.*

Upper Jurassic lithographic limestones in France contain mouldic medusae that bear tentacles and gonads. These medusae include the oldest definite carybdeid cubozoan and a semaeostome scyphozoan very similar to the widespread extant *Aurelia* (Gaillard et al., 2006).

The diverse medusae found in the Upper Jurassic lithographic limestones of the Solnhofen lagerstätte of Germany are probably the most famous fossil jellies (Haeckel, 1866, 1869, 1874). The most striking specimens are very large (≥50 cm diameter) scyphozoans assigned to *Rhizostomites* (Fig. 3I), which have been placed in their own order, the Lithorhizostomatida (Harrington and Moore, 1956a). Other notable Solnhofen medusae include the oldest coronate scyphozoan and several hydrozoans (Maas, 1906). Unambiguous fossil medusae have not been described from post-Jurassic deposits. Most of the medusoids known from Cretaceous and Tertiary deposits have been demonstrated to represent other structures such as flysch trace fossils (e.g., Häntzschel, 1975).

6. Discussion

This preliminary analysis of the complete, screened fossil record of medusozoans affects our understanding of the evolutionary and phylogenetic history of the Cnidaria. For example, the general pattern of medusozoan diversification (Fig. 1) establishes an earliest known date for each group and provides a logical starting place for calibrating the timing of divergences predicted by molecular phylogenies (e.g., Collins, 2002). The major medusan groups were apparently established concomitant with or shortly after the Ediacaran-Cambrian metazoan diversification; more derived forms, including Cubozoa, appeared in the Late Palaeozoic and Mesozoic. The earliest published Scyphozoa are Middle Cambrian; at least two of the three major orders (Semaeostomeae and Rhizostomeae) may have been present at this time. Two orders of Hydromedusae (Anthomedusae and Leptomedusae) were probably present by the Late Ordovician; this group apparently diversified by the Mesozoic. Cubozoa resembling modern forms are known from the Late Carboniferous and Late Jurassic.

One striking feature for all three classes, even when considering Palaeozoic forms, is the general morphological similarity between fossil and living medusae; almost all well-preserved fossil medusae possess characters consistent with membership in extant groups. Although there has apparently been diversification through time, and convergence is difficult to assess without cnidarian biomarker or molecular data, it may be that medusozoan clades, once established, were unlikely to become extinct. Many jellyfish might thus be considered “living fossils”. This fits with the pattern recognized for other groups of plankton, which are notoriously conservative and long-lived (e.g., Rigby and Milsom, 2000). Huge numbers, wide geographic distribution, and limited interspecies competition may make extinction less likely.

Modern mass strandings of medusae are commonplace (e.g., Bruton, 1991). The huge numbers of fossil medusae in certain marginal marine deposits (e.g., Hagadorn et al., 2002; Table 1C) suggests similar mass strandings as early as the Cambrian. Modern mass strandings reflect the immense abundance of jellyfish and the ancient examples suggest that similar abundances existed but had low preservation potential. Thus, studies of large-scale patterns in marine trophic webs and guilds should presume the presence of medusae.

Evolutionary paleoecological changes may have influenced large-scale shifts in the taphonomic “windows” that foster medusan preservation. For example, there was relatively little pre-Silurian bioturbation in marginal marine environments (Buatois et al., 2005). Fossil medusae are only abundant in such facies prior to this increase in bioturbation. Further increases in bioturbation through the Mesozoic and early Cenozoic are paralleled by rarity and then disappearance of medusan fossils from such settings.

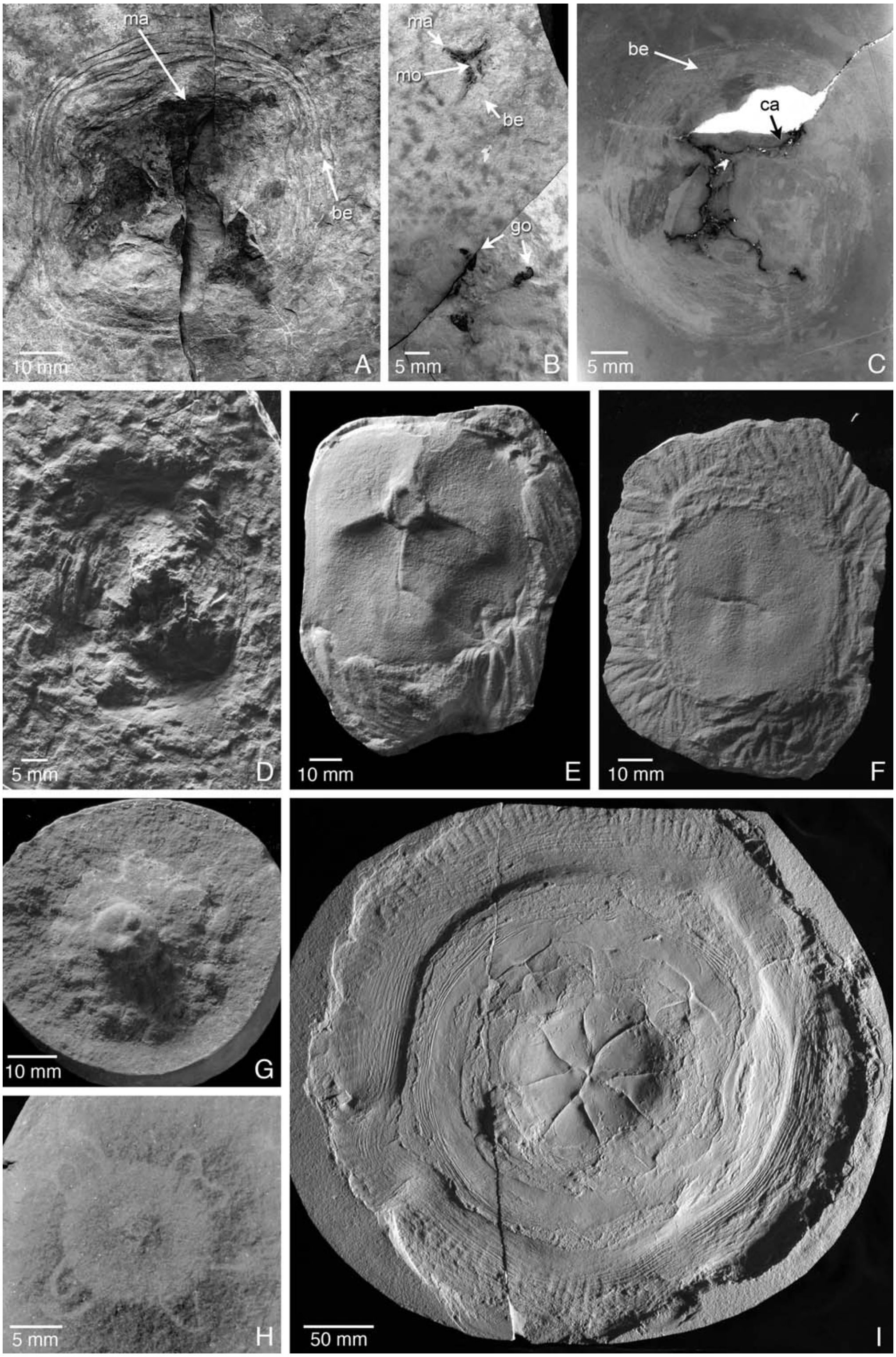

Fig. 3. Ordovician, Carboniferous, and Jurassic fossil medusae. A-D, Late Ordovician (Richmondian) medusae from the Williams Member, Stony Mountain Formation, at William Lake, Manitoba, Canada: (A) large medusa (Hydrozoa) on weathered surface, note quadrate manubrium (ma) and wrinkled bell (be) (MM I-4261); (B) Small anthomedusan (upper) and?leptomedusan hydrozoans on fresh bedding surface, with features including partly pyritized manubrium (ma), mouth (mo) bell (be), and probable gonads (go) (MM I-4058); (C) transverse thin section of a hydromedusan showing dark, partly pyritized canals (ca), and wrinkled bell (be) (MM I-4262B); (D), weathered medusa (?Scyphozoa) with dense axial structure and wrinkled bell (MM I-4055A). (E–H) Late Carboniferous (Westphalian) medusae from the “Mazon Creek” (Francis Creek Shale Member, Carbondale Formation), Illinois, USA: (E and F) two specimens of the cubozoan *Anthracomedusa turnbulli*, showing distinct axial structure and abundant tentacles (Royal Ontario Museum Invertebrate Palaeontology specimens, ROM 47980 and 53730); (G) the scyphozoan *Reticulomedusa greenei* (ROM 47991); (H) the problematic medusan *Octomedusa pieckorum*, showing distinct bell margin and tentacles (ROM 47540). (I) Late Jurassic (Tithonian) scyphozoan *Rhizostomites* sp. from the Solnhofen Formation, Franconian Alb, Bavaria, Germany, showing well-preserved bell and axis (ROM 18325).

Similarly, in the early Palaeozoic there are virtually no scavengers known to have operated at or above the strandline. By the late Palaeozoic there were many more potential shoreline scavengers of medusan carcasses (e.g., eurypterids, tetrapods), and this intensified in the late Mesozoic as birds and crabs colonized coastal settings. Moreover, early Palaeozoic coastal systems probably included immense tidal flats unlike anything in the modern world, because salt marsh, delta swamp, and mangrove communities were absent. The subsequent colonization of tidal flats by plants would have left far less area available for the deposition and preservation of medusae.

Given that the shifting of these medusae-rich taphonomic windows may be linked to large-scale evolutionary paleoecological changes in bioturbation, scavenging, microbial binding, and vegetation dispersal, there is a bright future for those of us with jellyfish on our minds. We can use this knowledge to search for new *konservat-lagerstätten* and enrich our understanding of the early evolutionary history of the Cnidaria.

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